

12 Electoreception and Electrogenesis

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I. INTRODUCTION TO ELECTRORECEPTION AND ELECTROGENESIS

The capacity to respond to electrical stimuli is a general property of all cells. Yet only vertebrates are known to possess a specialized sensory system that transduces ambient electric fields into action potentials with the use of dedicated sensory cells and organs and transmits this information with spatial integrity by means of dedicated nerve fibers to the central nervous system.^{49,52} The capacity to produce coordinated, stereotypical external electric fields by means of specialized electric organs is also known only in certain fishes, where it is used for predation, defense, orientation, or communication.^{30,155} Because the flow of electrical current requires a conductive medium, all species capable of electroreception or electrogenesis are aquatic, with the peculiar exception of the echidnas (monotreme mammals), which have electroreceptors on their snouts and probe moist soil for prey items.¹⁸⁶ Most amphibians are electroreceptive during their aquatic larval phase, and many species retain electroreception into the adult stage.^{93,229}

Electroreception is a sensory modality entirely unfamiliar to humans and other terrestrial vertebrates. Like the sense of hearing, electrosensory information is organized using timing and frequency cues. Like the sense of vision, electrosensory information is transmitted almost instantaneously. Like the senses of smell, taste, and hearing, the perceived intensity of electrical stimuli increases with proximity to the source. Like the sense of touch, electrosensory inputs convey information about the shape and electrical texture of objects in the local environment. Like the senses of hearing and vision, electroreception acts at a distance. However, the perceptual experience of electroreception is unlike that of the other vertebrate senses, and the natural stimuli (electrical conductances and impedances) to which this sense attends are otherwise entirely imperceptible.¹⁵⁵

For centuries, interest in electric fishes focused on animals such as the marine torpedos and the South American electric eel that produce strong discharges with high voltages and currents. Since the discovery of weak electric discharges in the middle of the 20th century,^{142,143} interest has expanded dramatically to include the role of electrogenesis in sensory reception, perception, navigation and social communication. Electroreception has attracted the attention of investigators in a wide range of sciences, including neurophysiology, behavior, and neural computation.^{52,101,126,134,155,225} Several species of weakly electric fishes have been developed into “model organisms” for neuroethological research into the physiological foundations of natural behaviors. This literature is large and expanding rapidly, including topics as varied as the molecular basis of neuronal and synaptic **plasticity**,⁸⁹⁻²⁵ neuronal regeneration and adult neurogenesis,^{250,252} changes in electric signals mediated by steroid and peptide **hormones**,⁸⁴⁻²⁴⁶ modeling electrosensory images,^{164,216} assembly rules for neural networks,^{58,227} hormonal effects on sex and animal communication,^{1,2,90,205} ecological physiology of metabolic rate and habitat,^{71,76,77,120} and the genetic and epigenetic mechanisms underlying the evolution of sensory and motor specializations.^{6,82,167,247}

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It is not possible to review all the active areas of research into electroreception in a single chapter. Rather, we focus on the diversity of vertebrate electrosensory and electrogenic systems, summarizing recent advances in three broad areas: (1) passive and active electroreception, (2) electric organs and electric organ discharges, and (3) the physiological ecology of the electric sense. A major goal of this chapter is to highlight some of the most exciting new developments now being explored in this fascinating area of the physiology of fishes.

II. PHYLOGENY OF ELECTRORECEPTION AND ELECTROGENESIS

Among animals, tissues specialized for electroreception are known to be present only among vertebrates, in which approximately 8,600 species are electroreceptive, or about one in six of the approximately 55,000 extant species (Table 12.1). About 41% of these electroreceptive species are amphibians, and another 41% are catfishes. In most species, the peripheral electroreceptor organs, as well as the mechanosensory neuromasts, are innervated by one of six lateral line nerves.¹⁶⁹ The only exceptions are monotreme mammals, in which an electroreceptive system has evolved within the somatosensory trigeminal nerve system.¹⁸³

The phylogenetic distribution of electroreception among living vertebrates indicates a complex evolutionary history with at least eight events (Figure 12.1)⁵³: (1) an origin in the common ancestor of extant vertebrates (lampreys + gnathostomes), (2) evolutionary losses in the ancestors of amniotes, (4) neopterygian fishes (including teleosts), and the subsequent acquisition in one group of amniotes, (5) monotreme mammals and at least three groups of fresh-water teleosts, (6) Xenomystinae, (7) Mormyriiformes, and (8) Siluriphysi (Siluriformes + Gymnotiformes). **Because** 42% of living vertebrate species are amniotes and 46% are teleosts, a large majority do not possess an electroreceptive system.

Electroreception is known in all three groups of living amphibians: frogs, cecilians, and salamanders.⁹³ Approximately 25 to 33% of the 5,000+ amphibian species undergo direct development from embryo to miniature adult, thereby bypassing the plesiomorphic aquatic larval stage with its associated laterosensory system. However, electroreceptor organs have been observed in at least some species of directly developing plethodontid salamanders,²²⁹ but the phylogenetic distribution of this condition is unknown (D.B. Wake, personal communication). Therefore, a conservative estimate for the number of amphibian species with electrosensory systems is approximately 3,500 to 4,000 species.

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TABLE 12.1
Diversity Estimates of 13 Electroreceptive Vertebrate Taxa and Salient Features of Electroreceptive Systems

Electroreceptive Taxon	Common Name(s)	Spp.	Electroreceptive Mode	Electroreceptor Organs	Habitat
Petromyzontiformes	Lampreys	38	Passive	End buds	Marine Fresh water
Elasmobranchii	Sharks, skates, rays	1,000	Passive	Ampullary	Marine
Chimaeriformes	Chimeras	43	Passive	Ampullary	Marine
Coelacanthiformes	Coelacanths	2	Passive	Ampullary	Marine
Dipnoi	Lungfishes	9	Passive	Ampullary	Fresh water
Lisamphibia	Amphibians	3,850 ¹	Passive	Ampullary	Fresh water
Monotremata	Platypus, echidnas	3	Passive	Mucous glands	Fresh water
Polypteriformes	Bichirs	15	Passive	Ampullary	Fresh water
Chondrosteans	Sturgeons, paddlefishes	28	Passive	Ampullary	Fresh water
Xenomystinae	African knifefishes	2	Passive	Ampullary	Fresh water
Mormyriiformes	African electric fishes	235	Passive, Active	Ampullary, tuberous	Fresh water
Siluriformes	Catfishes	3,571	Passive	Ampullary ²	Fresh water ³
Gymnotiformes	Neotropical electric fishes	173	Passive, Active	Ampullary, tuberous	Fresh water

Note: Forty-one percent of electroreceptive vertebrate species are amphibians and another 41% catfishes. (1) Excluding c.1,500 spp. with direct development (Lisamphibia with 5,350 spp.). (2) Tuberous organs known in at least one cetopsid catfish (*Pseudocetopsis*).⁹ (3) Ariidae and Plotosidae are marine.

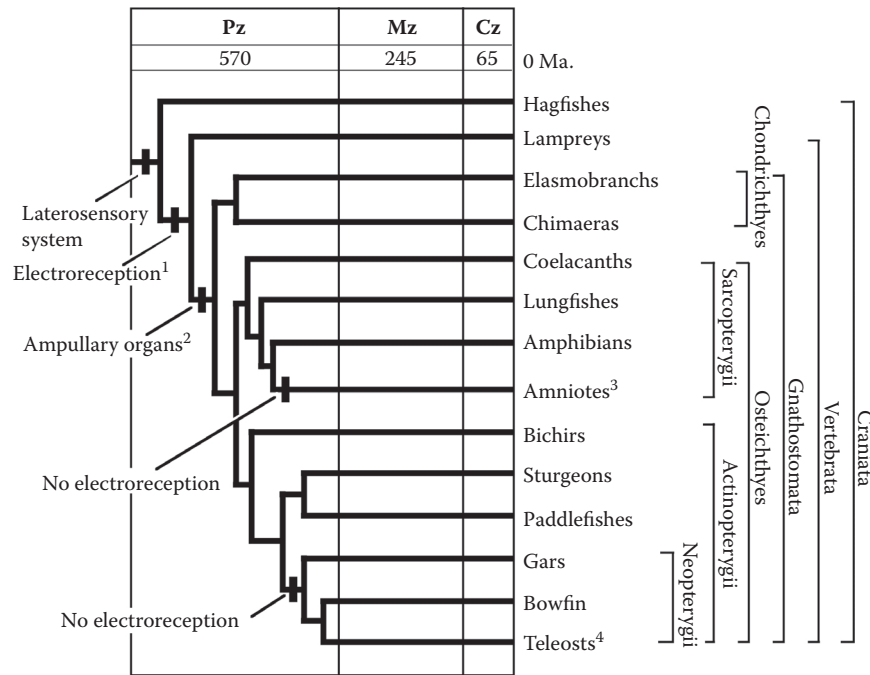


FIGURE 12.1 Phylogeny of vertebrate electroreception and gnathostome ampullary organs. (1) Vertebrate passive electroreception with hair cell receptors, cathodal (outside negative) stimulation (DC to 50 Hz), lateral line nerve innervation, and central processing via nuclei of the lateral lemniscus (see text). (2) Gnathostome ampullary organs with hair cells bearing an apical kinocilium. (3) Monotreme electrosensory systems (3 spp.) with mucous gland receptors, cathodal stimulation, and trigeminal nerve innervation. (4) Mormyriformes, Siluriformes, and Gymnotiformes electrosensory systems with hair cell receptors bearing apical microvilli, anodal stimulation, and lateral-line nerve innervation. Abbreviations: Cz, Cenozoic; Ma., millions of years ago; Mz, Mesozoic; Pz, Paleozoic. Stem-group clade age estimates from fossils³⁴. See Table 12.1 for diversity estimates and salient features of electroreceptive systems.

Among teleosts, electroreception is present in two groups of African osteoglossomorph fishes (Xenomystinae and Mormyriformes) and in a distantly related clade of ostariophysan fishes, the Siluriphysi, comprising the cosmopolitan Siluriformes (catfishes) and the neotropical Gymnotiformes (see Table 12.1; Figure 12.2). Recent work on the phylogeny of osteoglossomorphs suggests that the Xenomystinae and Mormyriformes are not sister taxa¹⁰⁶ and that their electrosensory systems may not be derived from a common ancestor⁵¹ (see section III-D).

Within vertebrates, the capacity to produce regular coordinated electric discharges has evolved independently in at least 11 lineages, all of them fishes (Table 12.2). The discharges of some electric fishes are strong (10 to 600 volts) and readily detectable by humans by touch. The discharges of most electric fishes, however, are weak (millivolts).⁵³ There are approximately 716 species of electric fishes currently known. The most diverse group is the Mormyriformes with about 235 species (33% of electric fishes). Mormyriformes are restricted to African fresh waters and includes the species-rich Mormyridae and also the monotypic *Gymnarchus niloticus* (Gymnarchidae) from the northern parts of tropical Africa (Senegal to Ethiopia). There are 228 named species of marine skates (Rajidae) representing some 32% of electric fishes, 176 species of Gymnotiformes from neotropical fresh waters representing 25% of electric fishes, and about 50 species of the cosmopolitan marine electric rays (Torpedinidae) representing 7% of electric fishes.

The remaining 27 or so known species of electric fishes are all teleosts. Several groups of fresh-water catfishes are known to be electrogenic, and although a systematic survey of electrogenesis

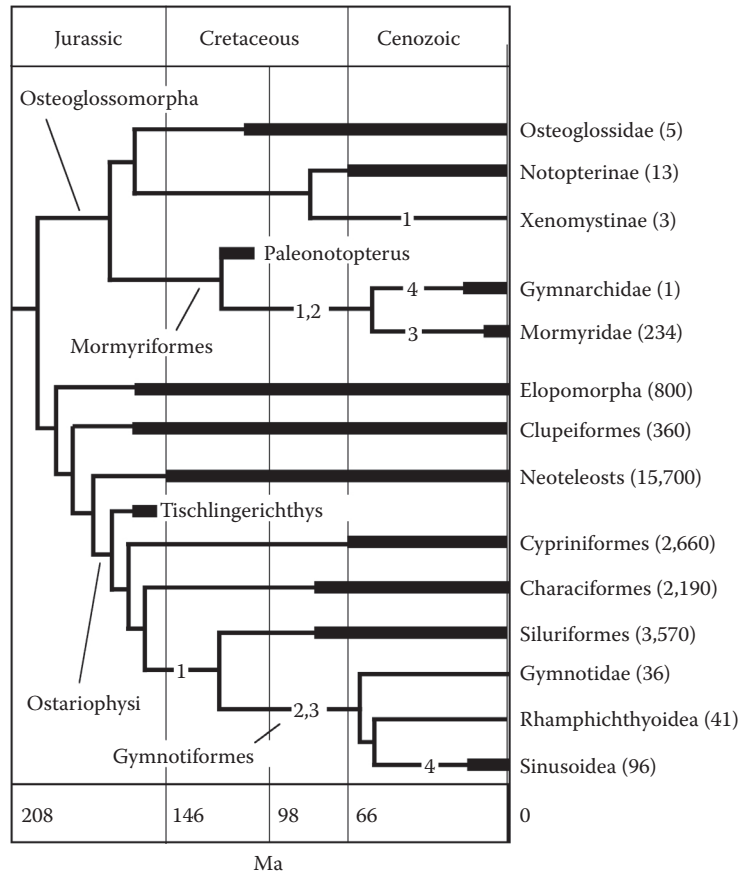


FIGURE 12.2 Phylogeny of teleost fishes showing repeated evolution of electroreceptive and electrogenic systems. (1) Passive electroreception with low-frequency (DC to 50 Hz) sensitive ampullary organs, bearing hair cells with apical microvilli and anodal stimulation. (2) Active electroreception with high-frequency (50 Hz –to 2 kHz) sensitive tuberous organs. (3) Pulse-type EOD. (4) Wave-type EOD. Tree topology and divergence times from multiple sources (see text); some low-diversity taxa omitted for clarity. Thick lines represent known minimum ages from fossils; thin lines are ghost lineages inferred from ages of sister taxa. See Table 12.2 for common names of electrogenic taxa; estimated numbers of extant species in parentheses. Age of Siluriformes estimated before final separation of Africa and South America (~100 Ma). Rhamphichthyoidea = Rhamphichthyidae + Hypopomidae; Sinusoidea = Sternopygidae + Aptereronotidae.

among catfish clades has not been conducted, many more taxa are likely to be discovered.⁵⁰ African electric catfishes (*Malapterurus*, 12 spp.) are the only catfishes that produce strong discharges, which are used in predation and communication. The strength of these discharges is correlated with body length, with voltages of up to 150 volts in large specimens of 20 cm.¹⁵⁵ Other catfishes generate only weak discharges, which have been implicated in social communication. This has only been confirmed in the two unrelated African groups: *Clarias* and *Synodontis*.^{15,97} In three species of the African upside-down catfish genus *Synodontis*, the electric discharge is produced in association with sound from a specialized swim-bladder muscle (see section III-D).^{18,175} Weak electrical discharges of undetermined origin have also been reported in the African bagrid catfish *Auchenoglanis occidentalis*,¹⁸ the Eurasian sheatfish *Ompok*,¹⁶² and at least three species of North American *Ictalurus*.^{179,182} Electrogenesis is only known in one group of marine teleosts, the uranoscopid stargazers, including *Astroscopus* (4 spp.) and *Uranoscopus scaber*.¹⁶

TABLE 12.2
Diversity of Electric Fish Taxa and Salient Features of Electrogenic Systems.

Electrogenic Taxon	Common Name(s)	Higher Taxon	Spp.	Electric Organ(s)	EOD	Use	Voltage	Habitat	Refs
Torpedinidae	Electric rays	Torpediniformes	50	Branchial/axial m.	Wave	Interm.	weak, strong	Mar.	—
Rajidae	Skates	Rajiformes	228	Axial m. (tail)	Wave	Interm.	weak	Mar.	119
Gymnarchidae	Gymnarchus	Mormyriformes	1	Axial m.	Wave	Contin.	weak	FW	155
Mormyridae	African electric fishes	Mormyriformes	234	Axial m.	Pulse	Contin.	weak	FW	209
Auchenoglanis	Giraffe catfishes	Situriiformes	≥1	NA	?	Interm.	weak	FW	18
Clarias	Walking catfishes	Situriiformes	≥1	NA	Pulse	Interm.	weak	FW	17
Ictalurus	Bullhead catfishes	Situriiformes	≥2	NA	DC	Interm.	weak	FW	182
Malapterurus	Electric catfishes	Situriiformes	12	Pectoral m.	Pulse	Interm.	strong	FW	155
Ompok	Sheatfish	Situriiformes	≥1	NA	?	Interm.	weak	FW	162
Synodontis	Upside-down catfishes	Situriiformes	≥3	Swim-bladder m.	Pulse	Interm.	weak	FW	101
Gymnotidae	Gymnotids/electric eels	Gymnotiformes	35	Hypaxial m.	Pulse	Contin.	weak, strong	FW	5
Hypopomidae	Bluntnose/pintail knifefishes	Gymnotiformes	29	Hypaxial m.	Pulse	Contin.	weak	FW	5
Rhamphichthyid	Sand knifefishes	Gymnotiformes	13	Hypaxial m.	Pulse	Contin.	weak	FW	5
Sternopygidae	Glass & rattail knifefishes	Gymnotiformes	39	Pterygiophore/epaxial m.	Wave	Contin.	weak	FW	5
Apterontidae	Ghost knifefishes	Gymnotiformes	60	Spinal motoneurons	Wave	Contin.	weak	FW	5
Astroscopus	Stargazers	Uranoscopidae	4	Extrinsic eyeball m.	Pulse	Interm.	strong	Mar.	16

Abbreviations: contin., continuous or with transient cessation; DC, direct current; interm., intermittent, used only during courtship and aggressive displays; Spp., species-richness estimates; EOD, electric organ discharge; Mar, Marine; FW, Fresh water; Refs, references. Electric organ(s) refers to adult condition; all derived from muscles except the neurogenic organ of Apterontidae. Voltage: weak <1V, strong >10V.

The known distribution of animal electroreception and electrogenesis is restricted to vertebrates and gnathostomes (jawed vertebrates), respectively, within which there have been multiple evolutionary origins and losses of these systems. Although systematic surveys for electroreception among nonvertebrate taxa are lacking, this sensory modality has not been found in targeted studies of several arthropod and cephalopod species.⁵⁰ Crayfish have been noted to orient and respond with feeding behaviors to low-strength (microvolt) electric fields.²³² However, the stimulus voltages required to elicit the responses are an order of magnitude larger than those generated by natural prey items, and the investigators have therefore concluded that this behavior results from nonspecific activation of sensory neurons from other modalities such as chemo- and mechanoreceptors (C.D. Derby, personal communication), much like we see light flashes when pressure is applied to the eyeball. It is perhaps significant that fully developed electroreceptive systems only emerge in animal taxa with large brains and with a preexisting and sensitive mechanosensory apparatus. Further, the only electrogenic animals are active predators with high-standard metabolic rates, myelination within the central nervous system (CNS), and rapid axonal conduction required to achieve coordinated whole-organism behavioral responses.

III. PASSIVE ELECTRORECEPTION

Animals with passive electroreception orient and locate prey by detecting external electric fields emanating from inanimate sources or from living tissues (including animals with or without specialized electrogenic organs). Passive electroreception differs from active electroreception in that an animal does not have to generate its own electric field in order to detect these objects.⁴⁹ Here, we restrict the term “passive electroreception” to (1) the detection of low frequency, generally weak electric signals emanating from inanimate sources or from living tissues using ampullary-shaped electroreceptor organs; and (2) the detection of low-frequency fields emanating from electrogenic fishes by nonelectrogenic fishes using ampullary electroreceptors. An example would be a catfish (nonelectrogenic) using ampullary receptors to locate a mormyrid or gymnotiform (electrogenic) prey (e.g., Hanika and Kramer⁹⁸). In one exceptional instance, a South American catfish (*Pseudocetopsis* sp.) possesses a specialized tuberous-shaped organ whose function is unknown.⁹ Active electroreception is the detection of distortions of a self-generated electric field in electrogenic animals by an array of specialized high-frequency-sensitive, tuberous-shaped electric organs. We also include within this definition instances of electrogenic fishes detecting other electrogenic fishes, either of the same species (conspecific) or other species, using tuberous electroreceptors — even though the detection may not involve the distortion of the self-field in the classic sense of active electrolocation. In gymnotiforms, the range of electrolocation is much shorter than the range of electrocommunication.¹³² Thus, two conspecifics which are generating signals within their respective ranges of communication will be able to detect each other, even if they are outside each other’s range for electrolocation. If one fish switches off its discharge, it will continue to be able to passively monitor the other fish’s discharges but not *vice versa*.

Electric fields of abiotic origin are present in many aquatic environments. Most abiotic fields are direct current (DC) or low-frequency fields of alternating current (AC), ranging from less than one to several cycles per second (Hz). These fields are caused by geochemical processes and the flow of water currents through the earth’s magnetic field. Electric fields of biotic origin range from DC to some of the most rapid and stable oscillators in the natural world (see section IV-A). All cells leak ions and are therefore sources of DC current. Some of the most ecologically important sources of oscillating dipole fields are produced by rhythmic muscle contractions during gill ventilation and undulatory locomotion.^{73,198} More than 60 species of animals representing nine phyla have been reported to generate low-frequency electric fields around their bodies.¹²⁶ Passive electroreception in vertebrates is associated with a common suite of peripheral and central neural structures, including integumental hair-cell receptors innervated by afferents of the lateral line nerves, with primary targets in particular hindbrain nuclei and central processing in the hindbrain,

midbrain, and thalamus.^{23,65,88} (A *nucleus* is a cluster of neuronal cell bodies within the CNS; a *ganglion* is a neuronal cluster in the peripheral nervous system [PNS]).

A. ELECTRORECEPTION AND MECHANORECEPTION: VERTEBRATE LATEROSENSORY SYSTEMS

In all vertebrates, the peripheral and central structures of the electrosensory and mechanosensory lateral lines develop from a series of epidermal placodes that give rise to mechanoreceptive neuromasts located in grooves or canals on the body surface and electroreceptive ampullary organs dispersed throughout the dorsal and ventral parts of the rostrum.^{53,169,172} These two systems collectively transduce near-field stimuli (voltage gradients and mechanical vibrations) from the surface of the skin into action potentials and transmit them somatotopically (point-to-point) to laminated sheets of neurons in the brain. The electrosensory and mechanosensory components of vertebrate laterosensory systems share many specialized features, including hair cell integumental receptors, receptor organs in which hair cells extend into a fluid-filled lumen, lateral line afferents which project to brainstem medullary nuclei, and central processing through the nuclei of the lateral lemniscus.¹⁴⁰ The neurotransmitter used by all vertebrate hair-cell systems (laterosensory, vestibular, cochlear) is L-glutamate or a similar substance.^{3,230,208} Whereas the mechanosensory lateral line is organized into six tracts of branching canals enclosing the neuromast organs in the head and body, electrosensory ampullary organs are dispersed into broad bands or patches along the paths of these six tracts.^{169,173}

Under low-light conditions, mechanoreception and electroreception play similar roles in many behavioral tasks such as prey capture, orientation and navigation, and social interactions.¹⁰⁷ Due to the similar spatial organization and dipole-like nature of many mechanosensory and electrosensory stimulus fields, the information processing demands of these two systems are also similar, including neural mechanisms for improving signal-to-noise ratios and the spatiotemporal integration adaptive noise suppression.^{37,74} In addition, information processing in low-frequency passive electrosensory and mechanosensory systems operates on similar time scales (1 to 10 Hz),⁶⁶ although these systems do have different propagation delays (mechanical stimuli at the speed of sound versus electrical stimuli at the speed of light).

B. ELECTRORECEPTION IN LAMPREYS

The electrosensory system of lampreys (Petromyzontiformes) retains many primitive features of the vertebrate electrosensory apparatus. Hagfishes (Myxinoidei) do not possess any of the structures associated with electroreception, in the peripheral or central nervous system. In addition to electrosensory end organs in the skin, lampreys share with jawed vertebrates (Gnathostomata) the presence of a central electrosensory processing pathway, including the dorsal octavolateralis nucleus (DON) of the brainstem medulla and the corpus of the cerebellum. As in gnathostomes, adult lamprey electrosensory terminals have both afferent (projections to) and efferent (projections from) connections with the DON and also have a convergence of electrosensory and visual pathways in the midbrain multimodal centers (see section IV-E). Unlike gnathostomes, the octavolateral area in the medulla of lampreys, which receives primary input from the octaval (eighth or vestibulocochlear) and lateral line nerves, is involved in the premotor organization of body movements through secondary projections to the reticular formation.^{72,94}

The peripheral electrosensory system of the adult lampreys consists of small swellings (25 to 65 microns diameter) called “end buds” distributed on the epidermal surface over the whole body, with highest densities on the head.¹⁸⁸ Each end bud organ consists of 3 to 25 slender multivillous hair cells (i.e., with numerous apical microvilli) surrounded by a cluster of support cells and is innervated by axons of the laterosensory system. In *Lampetra* and *Petromyzon*, these receptors are excited by very-low-frequency (1 Hz)⁴⁰ cathodal (outside negative) stimulation fields (-0.1 to $-30.0 \mu\text{V cm}^{-1}$), and inhibited by anodal (outside positive) fields,⁷² and these fields have a corresponding effect to increase (or decrease) behavioral activities. Larvae (ammocetes) of *Lampetra* and *Petromyzon* do

not possess well-organized end bud organs but do have multivillous receptor cells in the skin that respond to electrical stimuli.²³⁵ Lateral line efferents are known in adult lampreys but not in larvae.¹⁸⁹

C. ELECTRORECEPTION IN GNATHOSTOMES

In jawed fishes (gnathostomes) and their amphibian derivatives, the electroreceptor hair cells are included within subdermal ampullary-shaped organs (ampullae of Lorenzini). These ampullary organs are restricted to the head, except for batoids (skates and rays), in which they are also found on the pectoral fins, and lungfishes, in which they are present on the trunk as well (see below). Each ampullary organ consists of a small ovoid or pear-shaped chamber (the ampulla) and a subdermal jelly-filled canal that projects to a single pore visible on the surface of the skin.²⁴³ The inner wall of the ampullary lumen is composed of a single layer sensory epithelium containing hundreds of hair cell receptors and support cells. Tight junctions between the receptor and support cells form a highly resistive barrier to current flow so that the apical and basal surfaces of the sensory epithelium are electrically insulated. The basal surface of the receptor cell forms a chemical (L-glutamate or L-glutamate-like) synapse with one or more afferents of the lateral line and possesses no efferent innervation.²⁴³ The wall of the ampullary canal is composed of two layers of flattened epithelial cells and is also highly resistive. The canal lumen and ampullary chamber are filled with a conductive low-resistance mucopolysaccharide jelly that allows the ampullary chamber to be maintained in isopotential with a charge at the surface pore. Each hair cell has a kinocilium that projects into the ampullary lumen from the apical surface and synapses at its base with afferent nerve fibers that terminate in the dorsal nucleus of the rhombencephalic medulla. The functional differences of hair cells with cilia or microvilli on their apical membranes is not well understood.^{69,243} The kinocilium anchors the hair cell within the mucopolysaccharide gel of the ampullary lumen, and microvilli increase the surface area of the apical membrane.²⁴³ Microvilli in the electroreceptor organs of a catfish (*Ictalurus nebulosus*) play a part in signal filtering.¹⁰⁰

Gnathostome ampullary organs respond to low-frequency electrical stimuli, ranging from DC up to about 50 Hz.^{41,87} At least in some sharks, these ampullary organs may also function in thermoreception.⁴⁶ The ciliary-based ampullary electroreceptors of gnathostomes and the microvilli-based receptors of lampreys code both positive and negative voltage changes. In all vertebrates, the afferent nerve fibers of hair cells are tonically active in the absence of mechanical or electrical stimulation, and a decreased amount of synaptic transmitter leads to a decrease in nerve impulse frequency. An outside negative (cathodal) stimulus relative to the interior depolarizes the apical hair cell membrane, evoking an outward current flow across the basal membrane and increasing transmitter release.^{174,243} An outside positive (anodal) stimulus causes the opposite effect; for example, hyperpolarization of the apical membrane resulting in a decrease of synaptic transmitter release.

1. Electroreception in Chondrichthyans

In chondrichthyans (elasmobranchs and chimeras), ampullary organs are clustered into discrete fields on the head and also on the pectoral fins of batoids, and their canals radiate up to 20 cm through the skin to connect with pores distributed widely on the epidermal surface. The ampullary organ fields receive innervation from one of five cephalic lateral line nerves (e.g., anterodorsal, anteroventral, otic, middle, and supratemporal).¹⁶⁹ This morphological organization allows ampullary electroreceptors to detect potential differences between a common internal potential at the ampullary cluster and the somatotopic charges on the skin. Total stimulus voltage depends on the spatial separation between the ampulla and its canal pore. Within a uniform electric field, longer canals sample over a greater distance and provide a larger potential difference for receptor cells (and sensitivity) than do shorter canals. The morphological arrangement of the ampullary canals permits detection of local dipole-like stimuli produced by small prey organisms as well as large uniform electric fields produced by the general environment.³⁶

The ampullary organs of elasmobranchs (sharks, skates, and rays) are most sensitive to frequencies between 1 and 8 Hz.¹⁵⁷ Although the firing rate of individual hair cell receptors can be changed by a minimum stimulus of $2 \mu\text{V cm}^{-1}$, whole animals may respond to stimuli weaker by an order of magnitude by averaging over many receptor cells located in multiple ampullae.^{32,124} In the chimera *Hydrolagus colliei*, ampullary organs are tuned to low frequencies (~5 Hz) and are not sensitive to DC current. In behavioral experiments, *H. colliei* respond to fields as weak as $0.2 \mu\text{V cm}^{-1}$.⁸⁷ The high sensitivity of ampullary receptor cells results from the interaction of positive and negative conductances generated by ion channels in the apical and basal cell membranes.¹⁴⁷

The number of ampullary organs ranges over an order of magnitude between species, from as few as 148 in the horned shark *Heterodontus francisci* to more than 2,800 in the hammerhead shark *Sphyrna lewini*.²⁴³ In most species, the receptors are distributed on both the dorsal and ventral surfaces of the head, providing complete circumcephalic directional information. Interspecific differences in ampullary organ abundance and distribution are correlated with ecological and life history attributes in many species.^{41,121–123} For example, in the bull shark *Carcharhinus leucas*, the distribution of ampullary organs and their superficial pores is functionally related to foraging and prey capture rather than navigation.⁷³ The least developed electrosensory systems are observed in the filter-feeding manta rays (*Manta*), in which the ampullary organs are restricted to the hyoid region. The ampullary organ distributions of the largest filter feeding sharks (the whale shark *Rhincodon typus* and the basking shark *Cetorhinus maximus*) are not known.

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The electrosensory system of elasmobranchs functions in a wide number of behavioral contexts, including prey detection,^{38,124,125,211} predator detection,^{43,45,199} mate detection,²¹² and social communication.¹⁹⁹ Together with the olfactory organs, the ampullae of Lorenzini form the main sensory systems for foraging in many gnathostome fishes.^{103,108,123} Unfortunately, the literature on the natural social, predatory, and antipredatory behaviors of elasmobranchs is limited as these animals are large bodied, wide ranging, and difficult to maintain in the laboratory or observe in the wild. Most neuroethological research on electroreception in sharks and rays has focused on response dynamics and central neuroanatomy, with relatively few new studies on other possible biological functions.

The role of passive electroreception in elasmobranch navigation and migration is intriguing yet remains poorly understood.^{73,158} In principle, the ampullary organs of at least some elasmobranchs are sensitive enough to detect electric fields as weak as those induced through their bodies as they swim through the earth's geomagnetic field.^{124,178,211} A shark should be able to determine the direction of its motion relative to the earth's magnetic field during turns, from lateral asymmetries in the voltage change, by comparing vestibular and electrosensory signals.¹⁷⁸ Anecdotal observations of shark behavior do, in fact, report tidal, daily, and seasonal movement patterns.¹⁵⁸ However, true navigation using electroreception has not yet been demonstrated, and the sensory mechanisms underlying movement patterns in sharks remain speculative. Geomagnetic orientation could be mediated by the electrosensory system and a magnetite-based sensory system.

One of the most important sources of ecologically relevant electrical stimuli for ampullary electroreceptor organs is the organism itself.²²⁵ Recent work on nonelectrogenic stingrays demonstrates that males use their ampullary electroreceptors to locate mates¹⁹⁷ and that the electric sense is used during reproduction and courtship for conspecific detection and localization.¹⁹⁷ Androgen-induced changes in the frequency response properties of electrosensory afferents enhance mate detection by male stingrays and may ultimately increase the number of male reproductive encounters with females. Furthermore, differences in primary afferent sensitivity among short and long canals may facilitate detection, orientation, and localization of conspecifics during social interactions.

2. Passive Electroreception in Electric Skates and Rays

The ampullary electrosensory systems of marine electric skates (Rajidae) and torpedos (Torpedinidae) are similar to other (nonelectric) batoids in being able to detect and accurately locate prey items

within a narrow perimeter extending about 10 cm from the body margin or about half the diameter of the fish's body.¹⁵⁵ The ampullary organ system of skates can also encode weak electric discharges produced by conspecifics during social and reproductive interactions (section IV-B). Rajids generate occasional electric discharges for use in communicating during social and reproductive interactions. The temporal structure and power spectra of these discharges are effective stimuli for the skate's own ampullary organs, which are broadly tuned to low-frequency electric stimuli and are most sensitive to sinusoidal stimuli of 0.1 to 10 Hz.¹⁶⁵ The peak frequency responses in the primary electrosensory afferents of skates range from 0.1 to 0.5 Hz in the black sea skate (*Raja clavata*) to 1 to 5 Hz in the little skate (*R. erinacea*). These peak frequency response differences presumably represent species differences related to behavior and natural ecology, although many of the details remain unclear.¹⁹⁹ In the clearnose skate (*Raja eglanteria*), the peak frequency sensitivity of electrosensory primary afferents (2 to 3 Hz) is aligned with average electrical pulse rate (2.5 Hz) produced by conspecifics during social and mating behaviors. Such matches between the electrosensory encoding capabilities and electric discharge properties of skates may serve to facilitate communication during social interactions.

3. Nonteleost Bony Fishes

The electrosensory systems of basal sarcopterygian (nonamniote lobe-fin) fishes and basal actinopterygian (nonteleost ray-fin) fishes are very similar to those of chondrichthyans. Behavioral and physiological studies on several basal osteichthyans, including the Australian lungfish *Neoceratodus forsteri*,²³¹ and the fresh-water paddlefish *Polyodon spathula*²⁴⁰ have demonstrated the use of the electrosensory system in foraging. In *Polyodon*, the maximum firing rate of electrosensory brainstem neurons corresponds to the first derivative of the stimulus, that is, the rate of change in intensity of an electric field.¹⁰⁹ The number of ampullary organs on the head of nonteleost bony fishes varies from about 1,000 in the bichir *Polypterus* to as many as 75,000 in *Polyodon*,^{163,238} In coelacanth (*Latimeria*), the ampullary organs are clustered in the snout to form a large rostral organ, with nervous innervation from the anterodorsal lateral line.¹⁷¹ Behavioral observations indicate coelacanth use this rostral organ when foraging on the sea floor in a head-down posture.⁹²

Chondrichthyes and dissimilar to those of teleosts.¹⁶⁸ The taxonomic distribution of hair-cell morphologies on the phylogenetic tree of Figure 12.1 suggests the following evolutionary sequence: (1) microvilli evolved in the hair cells of Osteichthyes, in addition to the kinocilium of other gnathostomes; (2) microvilli were lost in the line leading to extant Chondrostei (the sturgeons *Acipenser*, *Huso*; *Pseudoscaphirhynchus*, *Scaphirhynchus*, and the paddlefishes *Polyodon*, *Psephurus*); and (3) the kinocilium was lost along with passive electroreception in the line leading to extant neopterygian fishes (gars + *Amia* + teleosts). The morphology and physiology of laterosensory hair cells in coelacanth have not been characterized. Lungfishes (*Neoceratodus*, *Protopterus*, *Lepidosiren*) share the derived presence of postcranial electroreceptors on the surface of the body and tail (but not the paired pectoral and pelvic fins), with innervation from a recurrent branch of a cephalic lateral line nerve.¹⁶⁸ Lungfishes and amphibians share the presence of hair cells with both a kinocilium and microvilli.¹⁶⁸ Among the three clades of extant amphibians, anurans and cecilians have hair cells with a kinocilium and microvilli, and salamander hair cells have microvilli only.⁹³ Electroreception may play a role in the courtship behaviors of some salamanders. Among basal actinopterygians, the hair cells of bichirs (*Polypterus*, *Calamoichthys*) have both microvilli and cilia. The behavioral significance of passive electroreception outside the context of foraging and predation in other nonteleost gnathostomes is less well documented.

D. ELECTRORECEPTION IN TELEOSTS

Ampullary organs have evolved in at least two or perhaps three independent lineages of fresh-water teleost fishes (see Figure 12.2)^{53,243}: Xenomystinae, Mormyriiformes, and Siluriformes +

au: please check and correct this sentence.

Gymnotiformes). The morphology and physiology of the ampullary receptor organs is similar in each of these groups and differ in several ways from those of marine elasmobranchs; the canals are shorter (100 μm), there are fewer hair cells per organ (1 in *Gymnarchus*, 20 to 30 in Gymnotiformes), and there is usually only a single afferent fiber to each organ or organ-cluster.²⁴³ The hair cells of most teleost ampullary organs possess microvilli (instead of cilia), are excited by outside positive (anodal) stimuli, and respond to voltage gradients of about 100 mV cm^{-1} .^{32,106} The ampullary organs of *Xenomystus* differ from other teleosts in that the hair cells have a cilium,^{51,243} supporting the hypothesis that the electrosensory systems of Xenomystinae and Mormyriiformes are not homologous. Like the ampullae of Lorenzini, teleost ampullary organs respond only to low frequencies, with effective frequency ranges of 3 –to 15 Hz in Siluriformes and up to 50 Hz in some Mormyriiformes and Gymnotiformes. Teleost ampullary organs are also spontaneously active, encoding both positive and negative outside stimuli.

Among catfishes, the electrosensory system is most well studied in North American Ictaluridae, in which electroreception has been suggested to play a role in prey detection, navigation and orientation, and social interactions.^{88,179,181,182,243} The heightened activity of the silurid catfish *Silurus asotus* in the hours before an earthquake has been part of Japanese folklore for centuries, although the exact mechanism remains unclear.⁹⁹ In most catfishes, ampullary organs are distributed over the entire body, including the fins, although excluding the barbels (“whiskers”). In the channel catfish *Ictalurus punctatus*, there are about 4,000 ampullary organs distributed over the entire body, with highest densities on the snout and the dorsal surface of the head, and innervation by one of five nerves: the anterodorsal, anteroventral, otic, middle, and posterior lateral line nerves¹⁷³ (there is no supratemporal lateral line nerve). This broad distribution allows discrimination of the longitudinal as well as the vertical components of the external electric field, which is projected as a point-to-point (electrotopic) map of the body surface onto laminated brain nuclei. Ampullary organs are generally absent from the body regions where the body’s own electric field is strongest, for example, around the mouth, gill openings, and anus.^{173,180,181}

Two clades of electrosensory catfishes, Ariidae and Plotosidae, are largely marine, although members of both these families also occur in fresh waters.³⁵ Ampullary organs in these taxa have long tubes, as in marine elasmobranchs. Ampullary organs of plotosid catfishes have up to several hundred hair cells, each with 200 to 300 orderly rows of microvilli.^{236,243} The structure of ampullary organ canals in catfishes varies from such species as the transparent catfish *Kryptopterus bicirrhus* (Siluridae), which have no canals and few receptor cells to species with long canals and hundreds of receptor cells, such as the marine *Plotosus anguillaris* (Plotosidae).²⁴³ Interestingly, as predicted by the functional analysis of Kalmijn,¹²⁴ the canals of a fresh-water plotosid species from Australia are short.²³⁷

The ampullary organs of Gymnotiformes differ from those of other teleosts in having innervation of all trunk electroreceptors from a cranial single nerve, the anteroventral laterosensory nerve,^{170,221–223} and by the clustering of the ampullary organs into rosettes of up to 20 individual ampullae all innervated by a single afferent fiber.²⁴³

1. Passive Electroreception in Weakly Electrogenic Siluriformes

Weak and occasional electric organ discharges in some catfishes function in communication for reproductive and other social roles.^{15,17,97} Fresh-water catfish are surrounded by stationary electrical DC fields, on which AC components related with respiration are superimposed. Such fields have been found in many aquatic species, and they reveal electrically the presence of an individual to other electrosensitive species. Such fields can be used for the detection and recognition of prey. In other words, these catfish can “feel” each other electrically. Many behaviors (e.g., foraging, excretion) have an electrical component, which contribute to the strength and shape of the extraorganismal electric field. There are also indications that part of the electric field is generated by the skin by means of homeostatic ion transport.¹⁸²

au: what does this refer to — the behaviors or the electric component?

2. Transition from Electric Communication to Active Electroreception

Electrical discharges are known in several groups of catfishes, in which they are often irregular in structure, display both positive and negative components, and have a longer duration than those of pulse-generating mormyrids or gymnotiforms. Most of the energy of these signals is in the low-frequency range to which ampullary electroreceptors are sensitive. In at least three species of the African mochokid catfish *Synodontis*, electric signals are generated by a simple electric organ modified from bilaterally paired muscles attached to the dorsal surface of the swim bladder.⁹⁷ Recordings made in the field (Gambia) showed that the electric signals of *Synodontis* are species specific; that is the electric discharges of each species are distinct and diagnostic. These discharges are produced in intermittent bursts of 90 to 300 ms duration during social interactions and can be generated independently from sound production. The pulses are biphasic and are much weaker and more variable than those of other weakly electric fishes, ranging in amplitude from 50 μV to 20 mV cm^{-1} , with repetition rates ranging from 2 to 240 Hz, and mean pulse durations of about 4 ms (corresponding to a peak power frequency in a Fourier transform of about 100 Hz). *Synodontis* species are not known to modulate the amplitude of their electric discharges, although at least one species is known to increase the repetition rate from 2 to 10 Hz during aggressive interactions.

In *Synodontis*, as well as many other catfish species, the extrinsic swim-bladder muscles are used to generate sounds for communication.¹³⁸ In this regard, it is interesting to note that the electrogenic myocytes of *Synodontis* resemble the sonic muscles of sound-producing teleosts in several regards¹³⁸; the electrogenic myocytes are hollow, smaller (20 versus 78 μm in diameter), and less well organized into regularly arranged rows of Z-bands than is the contractile assembly of unmodified striated muscle fibers.⁹⁷ The electrogenic myocytes of *Synodontis* are also innervated by electromotoneurons located in the dorsomedial portion of the caudal medulla, very much like the electrocytes of mormyrids and gymnotiforms, but unlike the ventrolateral position of sonic motor neurons in other teleosts.¹³⁸

In combination, these observations suggest that the phylogenetic origin of electrogenesis in *Synodontis* arose for use in social communication by enhancing and regulating the electrical potentials that naturally accompany the production of muscle-generated sound signals. Such an evolutionary transformation is an ecologically reasonable response to selective pressures from predators with sensitive hearing but poor electroreceptive abilities (e.g., characins, cichlids). Reasoning by analogy, the original function of weak electric discharges in mormyrids and gymnotiforms may have been as communication signals, only after which they came to be used in active electrolocation. However, this interpretation must be viewed with some caution as the electric organs of both mormyrids and gymnotiforms develop from the hypaxial swimming muscles, which are not known to be involved in sound production in any fish species.²¹ The transition from simple, relatively asynchronous electric signals with a purely communicative function in fishes with ampullary electroreceptor alone (e.g., the ancestor of catfishes and gymnotiforms) to the active electroreception signals of modern gymnotiforms would have involved several additional steps: (1) an increase in the amplitude and structural integrity of the electric discharges; (2) the evolution of two entirely new categories of electroreceptors (amplitude and time-coding tuberous electroreceptors) and; (3) a concomitant increase in the frequency composition of the electrical discharges. While the active electroreceptor signals of gymnotiforms may have evolved from simple communication signal precursors and while such apparent “intermediates” do exist in some catfish taxa, little is known of the genetic, developmental, or ecological details of how this transition occurred.

IV. ACTIVE ELECTRORECEPTION

Weakly electric fishes navigate, orient, and communicate using weak (less than 1 V) electric fields generated by the electric organ discharge (EOD) and the sensory processing of electrical images to extract information about the local environment.^{142,143} This combined electrogenic and electrosensory

system is used to detect nearby objects that distort the self-generated field and also for electrocommunication — the signaling of identity or behavioral states and intentions to other fishes. Active electroreception may also be used in predation.¹³⁹ Objects with an impedance different from that of water interfere with and distort the self-generated electric field, thereby modulating the basal pattern of transcutaneous currents.⁹⁶

Active electroreception, involving the continuous emission and sensory processing of stereotypical EODs, has evolved in parallel into two groups of strictly fresh-water teleosts: the African Mormyriiformes and the Neotropical Gymnotiformes.^{53,113} Although these taxa are only distantly related (see Figure 12.1), there are many interesting parallels in the functional,^{88,206} developmental,^{28,245} and ecological^{150,239} attributes of their electrosensory systems. The electric organs of both groups are derived from muscle cells,^{130,131} with neural coordination from a neuron cluster in the medullary central pattern generator.²² In both groups, high-frequency-sensitive tuberous electroreceptor organs are derived from low-frequency-sensitive ampullary organs,²⁴³ and both groups evolved active electroreception in the nocturnal fresh waters of Gondwanaland (the Mesozoic southern supercontinent) during the Late Cretaceous Period (see Figure 12.2)⁴ The anatomy and physiology used to produce and detect high-frequency electric currents in these groups is very similar.^{6,101,207,225} Derived features are known from all major divisions of the peripheral and central nervous systems (see sections IV-D and IV-E).

A. ELECTRIC ORGAN DISCHARGES

The external electric field is generated by the coordinated spatial and temporal activation of electrocytes (also known as electroplates), which act in concert to create a stereotypical EOD.^{1,2,58} The summed current flow of the activated electrocytes transforms the whole body of the fish into a distributed electrical source.⁵⁸ The EOD generates an electric field around the animal that approximates the shape of an oscillating dipole (i.e., dumbbell-shaped) enveloping the head and tail of the fish with alternating head-positive and head-negative phases that cycle with the EOD repetition rate (Figure 12.3).^{23,145,146,187} A transverse plane of zero voltage is located in the posterior region of the body, near the caudal peduncle in mormyrids, near the base of the caudal appendage (caudal end of the anal fin) in *Gymnarchus* and most gymnotiforms,¹² and at the level of the first lateral-line ramus in the gymnotiform genus *Gymnotus*.²⁰⁴ The EOD of *Gymnotus* generates currents in the order of 10^{-4} A near the surface of the body.¹⁴ The EOD field amplitude decays from the body surface with the inverse cube of distance so that the effective range of sensory perception is limited

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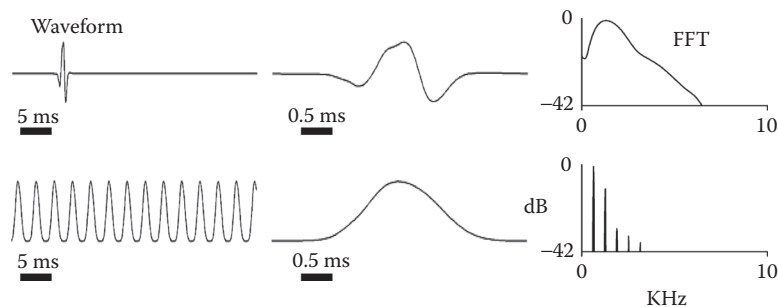


FIGURE 12.3 Pulse- (above) and wave-type (below) EOD waveforms from *Gymnotus varzea* and *Eigenmannia cf. virescens*, respectively. Left and center, EOD waveform with 5 ms and 0.5 ms scale bars. Right, power spectrum of Fast Fourier Transform (FFT) of the waveform with amplitude (dB) on y-axis, and frequency (kHz) on x-axis. Note harmonic content to the FFT of the wave-type EOD.

to within about 5 –to 10 body lengths from the animal.^{102,132} Active electroreception is therefore sensitive to objects in the near-field only. Because of the high sensitivity of one class of tuberous organs (see section IV-D), the range of electrocommunication is much larger than that of electrolocation. In many species with a wave-type EOD, electrocommunication is effective in a range up to several meters in contrast to the centimeter range of electrolocation.¹³²

1. Pulse versus Wave EODs

The EODs of weakly electric teleosts, both Mormyriiformes and Gymnotiformes, are readily partitioned into two functional types, representing different solutions for electroreception, with no known functional intermediates.^{49,78} Pulse-type EODs are trains of relatively short pulses separated by periods of electric silence, in which each pulse may exhibit one to six discrete phases of alternating polarity. Wave-type EODs are a continuous quasi-sinusoidal wave, without periods of electrical silence, and with –one to four phases. Pulse-type signals in Gymnotiformes are generated at rates of from 1 to 120 Hz,⁷⁸ whereas Gymnotiformes with wave-type signals are generated at rates of from 20 to 2,200 Hz.⁷⁸ Pulse-type signals of Mormyridae discharge at rates of 1 to 150 Hz, whereas *Gymnarchus niloticus* with a wave-type signal discharges at 250 to 300 Hz.¹⁵⁵ The energy of pulse-type discharges is distributed in broad power and phase spectra (see Figure 12.3). The energy of wave-type discharges is partitioned into several discrete harmonics, and the receptors of wave-type species are tuned to the predominant frequency component.²⁴³

Species with pulse- or wave-type EODs possess morphologically and physiologically distinct classes of electroreceptor organs as well as many adaptations of the CNS for sensor –processing.^{23,50,58,68,243} The distinct electroreceptor organ types observed in pulse- and wave-type species are described in section IV-D. Here, it is important to note that the receptor organs of species with pulse- or wave-type EOD have different preferred response curves tuned to the peak frequency of their own self-generated EOD. This tight functional connection between pulse- and wave-type discharges and their associated suites of electroreceptor organs underlies a major and unreversed evolutionary dichotomy in weakly electric fishes (Figure 12.4).⁷⁸ In Mormyriiformes, species with wave- and pulse-type EODs are monophyletic sister taxa, and the polarity of the EOD is unresolved. In Gymnotiformes, wave-type EODs evolved only once from a pulse-type ancestor.^{4,5}

2. Neuroanatomy of Electrosensory and Electromotor Systems

The entire brain of weakly electric fishes is specialized for active electroreception. There is a tremendous hypertrophy of structures dedicated to processing electrosensory and electromotor information and a reduction of many nonelectrosensory areas. Mormyriiform and gymnotiform brains are large and metabolically active, occupying up to 2% of total body weight, and in mormyrids, the brain uses perhaps 20 to 60% total body oxygen consumption.^{71,166} The hypertrophied electrosensory system of mormyriiforms and gymnotiforms is associated with a pronounced reduction of several other sensory systems. Mechanosensory receptors are entirely absent from the head of mormyrids.⁶⁹ The gustatory system of mormyrids is reduced compared with other osteoglossomorph fishes, with fewer taste buds and reduced central projections and nuclei of the facial, glossopharyngeal, and vagus nerves.¹⁴¹ The visual and olfactory systems of gymnotiform are greatly reduced.^{6,149} However, the peripheral motor and sensory components of sound production and detection are well developed in mormyrids as are the central auditory pathways.

The central electrosensory pathways involved in active electrolocation extend from the medullary electrosensory lateral line lobe (ELL) and the cerebellum to the midbrain and forebrain via several specialized electrosensory nuclei. The neural analysis taking place leads to the three-dimensional location of an object and to the recognition of object properties.²²⁸ Some of the important neural structures are (1) tuberous electroreceptor organs and lateral line afferents; (2) primary electrosensory structures of the hindbrain (rhombencephalon) such as the ELL and cerebellar eminentia granularis (EG), (3) nuclei of the lateral lemniscus (e.g., nucleus preemientialis;

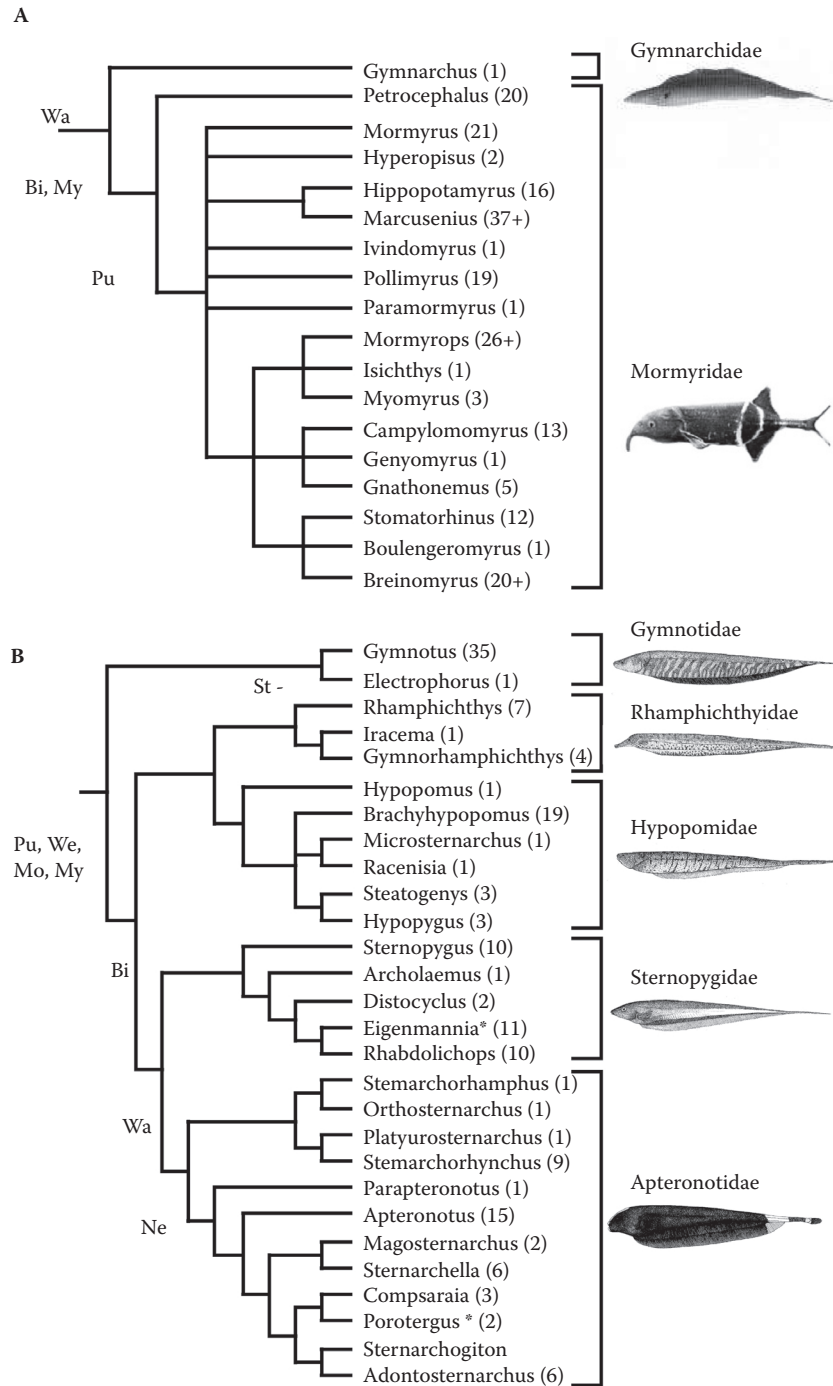


FIGURE 12.4 Phylogeny of mormyrid (A) and gymnotiform (B) genera and salient features of electric organ and EOD diversity. Numbers in parentheses are estimates of species richness. *, generic monophyly not documented. Abbreviations: Bi, biphasic EOD waveform; Mo, monophasic EOD; My, myogenic organ; Ne, neurogenic organ; Pu, pulse-type EOD; St, strong discharge (>10V); Wa, wave-type EOD; We, weak discharge (<1V).

PE), (4) dorsal midbrain (mesencephalic) structures such as the torus semicircularis (TS; = inferior colliculus of mammals) and mesencephalic tectum (also called the tectum opticum [TO] = superior colliculus of mammals); (5) forebrain (prosencephalic) structures including derived prepacemaker circuits of the diencephalon (including the thalamus) and telencephalon (including the pallium); (6) medullary pacemaker cells; and (7) spinal electromotor neurons that innervate the electric organ(s) (see section IV-C).

3. Control of the EOD

Mormyriiformes, Gymnotiforms (and presumably Rajiformes) communicate species and sexual identities using one or more properties of the continuously emitted train of EODs: (1) the pulse *repetition rate* (or cycle rate of a periodic “wave” discharge); (2) *modulations* of the pulse/cycle repetition rate during social behavior; and (3) *waveform*, the shape and duration of individual pulses in pulse-type species (or just shape in each cycle length of wave type species).

a. Repetition Rate

In all weakly electric fishes, the rate of electrocyte activation (the EOD repetition or cycle rate) is under the direct control of a cluster of neurons in the brainstem medulla, called the command nucleus (CN) in mormyriiforms and the pacemaker nucleus (PM) in gymnotiforms. Action potentials from the CN or PM are transmitted by spinal neurons (relay cells and electromotoneurons) to depolarize the electrocyte membranes on a 1:1 basis. The CN or PM activates a set of relay cells, whose axons descend along the spinal cord and project to electromotor neurons, which, in turn, project to electrocytes in the electric organ. These relay neurons, electromotor neurons, and electrocytes form a network able to coordinate the spatiotemporal pattern of postsynaptic and action potential currents generated by the electrocyte membranes. Electrocyte activation is synchronized by a synergistic combination of delay lines; electromotor neuron axons innervating posterior body segments have larger diameters and faster conduction velocities than those innervating anterior body segments. The activation of oppositely oriented faces is coordinated in a precise sequence resulting from the orderly recruitment of electromotor neurons according to a “size principle” and to their position along the spinal cord.⁵⁸

Mormyriiform CN and gymnotiform PM neurons are specialized cells of the medullary reticular formation, sequestered and dedicated to regulating the EOD repetition rate. Neurons of the medullary reticular formation are involved in the control of many autonomous rhythmic behaviors in vertebrates, including, for example, locomotion (e.g., lateral undulation of axial muscles or anal-fin rays), ventilation (e.g., gills arch muscles, diaphragm), and mastication (e.g., mandibular or pharyngeal muscles).²² In *Gymnotus* with a pulse-type EOD, an abrupt increase of about 25% in the EOD repetition rate occurs for periods of about 30 seconds after direct stimulation of the Mauthner cells.²¹⁴ Mauthner cells are a single pair of large reticulospinal neurons located on each side of the brainstem in most fishes and amphibians, which initiate a C-start escape response by a forceful bend of body and tail.⁵⁴ During this fright response in *Gymnotus*, the Mauthner cells act directly on the pacemaker neurons in the PM, and the pulse waveform is not affected.⁸⁵ In *Eigenmannia*, a gymnotiform with a wave-type EOD, the Mauthner-cell-mediated response is integrated with the electrosensory system allowing the brain to continuously monitor the environment in order to produce accurate escape behaviors.⁵⁴

Phylogenetic changes in the connections of the CN or PM may contribute to the diversity of electric signals in weakly electric fishes. In both mormyriiform and gymnotiform fishes, EOD repetition rate is under the control of a central electromotor network, including inputs from the TO and thalamus.⁶³ In mormyriiforms, the CN receives excitatory input from the midbrain precommand nucleus (PCN) and the thalamic dorsal posterior nucleus (DP), both of which are regulated by a recurrent inhibitory projection from a part of the TS. In gymnotiforms, the PM receives input from an analogous midbrain prepacemaker nucleus (PPM), as well as the thalamic nucleus DP. EOD

repetition rate may also be influenced by forebrain voluntary control centers. As in other ray-finned (actinopterygian) fishes, the dorsal (pallial) areas of the telencephalon in mormyriforms and gymnotiforms have discrete receptive areas for several sensory modalities, including electrosensory, water displacement, auditory, and visual stimuli.^{7 185} However, the sensory-evoked potentials in the dorsal telencephalon are more segregated in mormyriforms and gymnotiforms than they are in other fishes, in some ways resembling the cortical areas in mammals.

Studies on the ionic currents that influence the rhythm of the medullary pacemaker cells suggest that the physiological mechanisms underlying EOD repetition rate are similar among gymnotiform fishes.^{210,244} In *Sternopygus*, a gymnotiform with a wave-type EOD, at least three ionic currents contribute to the pacemaker rhythm.²⁰¹ The pharmacological profiles of these currents are similar to those of currents known to regulate firing rates in other spontaneously oscillating neural circuits.²⁰⁰ Stimulation of NMDA receptors in the PM causes a longlasting (tens of minutes to hours) change in the EOD repetition rate.²⁴⁴ This NMDA receptor-dependent change may occur in reflexive responses, like the jamming avoidance response (JAR), as well as after longlasting social signals. NMDA-receptor dependent increases in EOD repetition rate during the JAR adaptively shift the EOD repetition rate to avoid jamming by another fish.

The EODs of gymnotiforms in the family Apterontidae are among the most temporally precise of all known biological rhythms. Repetition rates of wave-type fishes are remarkably constant and, apart from temperature and conductivity, are unaffected by a wide variety of stimuli.^{196 10,148} In one well-studied species, the brown ghost knifefish *Apteronotus leptorhynchus*, the coefficient of variation (standard deviation/mean \times 100) is 2×10^{-4} (EOD repetition rate of 800 to 1,200 Hz).^{159,161} In *A. leptorhynchus*, the PM contains approximately 100 to 150 neurons, including pacemaker cells with intrinsic oscillations, and relay cells. The precision of the EOD arises from both network and cellular influences of cells in the medullary PM.¹⁶⁰ Species of the apteronotid clade *Sternarchella*, which inhabit deep Amazonian river channels, have the fastest known EODs⁷⁸ and the largest PMs,⁴ achieving a maximum repetition rate of 2,179 Hz in *S. schotti*. A correlation between EOD repetition stability and PM size is also observed in gymnotiforms with a pulse-type EOD, for example, in the genus *Steatogenys*.⁷⁹

b. Modulations

In mormyrids and gymnotiforms transient modulations of EOD pulse- or wave-cycle rate can occur spontaneously or during social interactions.^{83,86,115} These frequency modulations may last from a few milliseconds to tens of minutes and are used to communicate information about sexual identity, sexual arousal, and position in a dominance hierarchy.²⁴⁴ Frequency modulations are used for social purposes, and neural control of the frequency modulations involves pacemaker and prepacemaker mechanisms.¹²⁷ Many mormyrid and gymnotiform pulse type taxa are able to stop their EOD spontaneously or as a fright response. *Gymnarchus niloticus* is the only wave-generating electric fish that can cease generating EODs for prolonged periods of time in response to external electrical signals.¹²⁸ By contrast, gymnotiforms species with a wave-type discharge cannot switch off the EOD for more than a few hundred milliseconds.⁷⁷

Like many mormyrids, *Brienomyrus brachyistius* produces periodic frequency modulations called EOD bursts that fall into two display categories: “scallop” and “accelerations.” A third category termed “rasps” combines the other two. In *B. brachyistius*, these communication behaviors are regulated by different brain regions.⁶⁴ In mormyriforms, the PCN and DP generate different burst types (scallop and acceleration, respectively). Differences in the strength of recurrent inhibition are related to physiological differences between PCN and DP; recurrent inhibition regulates the resting electromotor rhythm, while disinhibition releases PCN and DP, allowing them to generate bursts. Recurrent inhibition and disinhibition between these midbrain and thalamic nuclei and the CN therefore influence the behavior of frequency modulations.

Two prominent forms of frequency modulations in apteronotids (gymnotiforms with wave-type EODs) are chirps and gradual frequency rises. Chirps are complex frequency and amplitude

modulations lasting from tens to hundreds of milliseconds. Gradual frequency rises consist of a rise in discharge frequency, followed by a slow return to baseline frequency, with a time course of a few 100 ms to 100 s.²⁵¹ The EOD frequency of *Apteronotus leptorhynchus* is sexually dimorphic: female EODs range from 600 to 800 Hz and male EODs range from 800 to 1,000 Hz. In *A. leptorhynchus*, chirps are readily evoked by the presence of the EOD of a conspecific or a sinusoidal signal designed to mimic another EOD, and the frequency difference between the discharge of a given animal and that of an EOD mimic is important in determining which of two categories of chirp an animal will produce.²⁴ Type-I chirps — EOD frequency increases averaging 650 Hz and lasting approximately 25 ms — are emitted most often during courtship and mating. Type-II chirps consist of shorter-duration frequency increases of approximately 100 Hz and are typically produced by females as agonistic displays. In female *A. leptorhynchus*, short rises may have an intrasexual aggressive function, while long rises may advertise status or reproductive condition in intersexual interactions.²¹⁰ As in many vertebrates,^{7,242} the repertoire of chirps and gradual frequency rises is regulated by visual information mediated through the dorsal thalamus (e.g., central posterior nucleus and PPM) and preoptic area.²⁴¹

In gymnotiforms, different classes of glutamate receptors mediate the generation of smooth rises versus chirps. In species representing both pulse-type (*Brachyhypopomus pinnicaudatus*) and wave-type (*Eigenmannia gr. virescens*) EODs, sustained modulations such as smooth rises are mediated by NMDA receptors, whereas brief and rapid accelerations (chirps) are mediated by kainate-/quisqualate-sensitive receptors.¹²⁹ However, these two species differ in the mechanism by which they slow the PM repetition rate. Whereas *Brachyhypopomus* uses GABAergic inhibition to slow and ultimately silence its pacemaker cells, *Eigenmannia* reduces tonic, NMDA sensitive excitation originating from its PPM, and lacks GABAergic inhibition in the PM.

The neural and hormonal mechanisms involved in the control and modulation of EOD waveform in pulse- and wave-type gymnotiform species are thought to be similar.^{86,91,205,244} In *Sternopygus macrurus*, plasma androgens modulate EOD repetition rate in males during the reproductive season; plasma levels of testosterone and 11-ketotestosterone, but not 17-estradiol, were inversely correlated with EOD repetition rate in males but not females.²⁴⁹

Many gymnotiform species also use EOD amplitude modulations in electrolocation and communication. Amplitude modulations are relative changes in local peak-to-peak amplitude. Waveform modulation depends on both the distance and the electrical characteristics of the object. Changes in waveform are indicated by the amplitude ratio of the larger positive and negative phases of the local EOD on the skin. Using the peak-to-peak amplitude and the positive-to-negative amplitude ratio of this discharge, a perceptual space which is strongly correlated with the capacitance and resistance of objects is defined.⁴⁷ When objects are moved away, the perceptual space is reduced but keeps the same proportions, that is, the positive-to-negative amplitude ratio is a linear function of the peak-to-peak amplitude. Amplitude modulations are used in sexual communication and enhance electrosensory resolution in the wave gymnotiform fish *Apteronotus*.^{70,202,215,225}

c. Waveform

The aggregate waveform as recorded at one body-length from the body surface is the summed waveforms of all the electrocytes and may result partly from local and global EO effects, the contribution of accessory electric organ (in some taxa) as well as properties of the central nervous system.⁵⁸ The waveform is a function of electrocyte geometry, insulation patterns, innervation patterns, and the activation, concentration of electrocyte membrane proteins (e.g., Na/K-ATPase, ACh receptors).²⁴⁶ In gymnotiforms with a myogenic electric organ, the great majority of electrocytes are innervated on the posterior membrane only.^{58,243} Depolarization of this membrane opens ACh receptors and results in a head-positive current. Subsequently, the wave of depolarization sweeps around to the anterior electrocyte face, where voltage gated channels are opened, allowing a head-negative current. These two currents constitute the dominant biphasic portion of the waveform observed in most electric fish species with a pulse-type EOD.

Gymnotiforms with a pulse-type EOD share a common pattern of organization of the electrogenic system, and the EOD waveform of these species has several homologous features: a central biphasic component with an early head-positive and late head-negative deflection, a double-positive peak generated at the abdominal level, a head-to-tail activation wave along the length of the body, an exponential increase in the electromotive force from head to tail (differentially attenuated by the passive tissues in male and females), a complex species-specific waveform in the abdominal region, and a highly stereotypical and similar biphasic discharge in the tail region across all species.^{58,59}

In fishes with a pulse-type EOD, the highest amplitude head-positive phase is referred to as P1, subsequent phases as P2, P3, and so on in sequential order, and phases preceding P1 as P0, P-1 and so on in reverse sequential order.⁷⁸ Comparative studies of electric organ physiology suggest that the two major elements of the EOD of all pulse-type gymnotiforms (P1 and P2) are based on common anatomical substrates and physiological processes. These include similar electromotor neuron innervation patterns of electrocytes and similar membrane receptor activation patterns.^{1,62} Phases P1 (P in *Brachyhypopomus*, V3 in *Gymnotus* and *Rhamphichthys*) and P2 (N in *Brachyhypopomus*; V4 in *Gymnotus* and *Rhamphichthys*) are functionally equivalent in all three pulse species so far examined in detail (*Gymnotus inaequilabiatus*, *Rhamphichthys rostratus*, and *Brachyhypopomus pinnicaudatus*).⁵⁸ From a phylogenetic perspective, only P1 may be conclusively regarded as homologous among all pulse species, in the sense of being derived from a common ancestor.^{4,5} All pulse species possess a head-positive monophasic EOD as juveniles, and some gymnotid species (e.g., *Electrophorus electricus*, *Gymnotus cylindricus*, *G. maculosus*) retain a monophasic EOD into maturity. The presence of a biphasic waveform with a P2 — a high-voltage hyperpolarizing phase immediately following P1 — has evolved independently in at least two separate clades of pulse-type gymnotiforms (i.e., within Gymnotidae, and in Rhamphichthyidae + Hypopomidae). Additional low-voltage, low-amplitude pre- and postpotentials (e.g., P-1, P0, P3, P4) are more homoplastic, having evolved independently multiple times within Mormyriiformes and Gymnotiformes.

B. ELECTROLOCATION AND ELECTROCOMMUNICATION

Electric fishes explore the near environment by detecting changes in their self-generated EOD caused by objects that differ in impedance from that of water.⁴⁹ In active electrolocation, an object's electric image consists of modulations in the transcutaneous voltage profile generated by the fish's own discharge.^{12,48,61} The electrosensory system achieves contrast discrimination by comparing the departure of an instantaneous input with a moving average of past images.⁶⁰ The electrosensory system compares the difference between successive reafferent electrosensory images and a neural representation of past electrosensory images.

The external electric field created by the EOD produces a spatiotemporally complex pattern of current densities that stimulate electroreceptors distributed in the skin over the surface of the body.^{12,204} This field constitutes the carrier for active electrolocation signals, resulting from its modulation by objects with impedances different from that of water. The difference between the basal pattern of transcutaneous current density and the pattern in the presence of an object constitutes the electrical image of the object on the skin. Behavioral experiments have shown that both mormyriiform and gymnotiform fishes can discriminate objects on the basis of their capacitances.^{224,226} Fishes with active electroreception evaluate successive electrosensory images generated by the self-emitted electric discharges, creating a neural representation of the physical world⁴⁹ (section IV-B).

Communication signals are represented as patterns of transcutaneous currents generated by the EOD of one fish on the skin of another and also in the cadence of successive discharges. In pulse-emitting gymnotiforms, electrolocation and electrocommunication signals are carried by different field components generated by different regions of the electric organ.² Differences in carrier waveform are used to distinguish between reafferent and communication signals.⁶² Electric currents

generated by the EOD are funneled by the high conductivity and geometry of the fish's body through the perioral region of maximum electroreceptor abundance called the electrosensory fovea. Within this region, electrical field vector directions are collimated, constituting the most efficient stimulus for electroreceptors. The electrosensory fovea is necessary for implementing complex impedance discrimination.¹ The skin impedance of weakly electric fishes is relatively low (400 to 11,000 Ohm cm²) and largely resistive. This low skin impedance enhances the local electric organ discharge modulation, the center-surround effect, the signal-to-noise ratio for electrolocation, and the active space for electrocommunication.⁶¹

1. Species-Specific Electric Signals

The use of electric signals for social communication (both sexual and nonsexual) is the topic of a large volume of literature, focusing almost completely on gymnotiforms and mormyriiforms. This literature has been extensively reviewed recently,^{23,135,155} and hence we will not attempt to review this field here. Communication signals have also been studied in the strongly electric catfish *Malapterurus* spp.¹⁵⁵ and the weakly electric catfishes *Synodontis*⁹⁷ and *Clarias*.¹⁵

Several studies have noted that the electric signals of the freshwater electric fishes are divergent at the species level within local communities. In gymnotiforms, unquantified observations of “species-characteristic” EODs in multispecies assemblages have been made by several authors. EODs in local communities of pulse-generating species differ on the basis of a combination of waveform shape and EOD repetition rate features.^{75,105,116,234} In multispecies assemblages of wave-type gymnotiform fishes from the central Amazon, the electric signals are species specific.^{76,78} A quantitative, landmark-based decomposition of the EOD waveforms of species of *Gymnotus* from a sympatric + syntopic community in the Central Amazon basin showed a complete absence of overlap of signal parameters.⁷⁸ Nonquantitative observations of species-typical EODs in local assemblages of mormyrids have been published by Hopkins,^{110,114,115} with species differences based primarily on the shape and duration of the EOD. Arnegard and Hopkins¹¹ used a landmark-based decomposition of EOD waveforms of seven species of *Brienomyrus*, part of a diverse monophyletic species “flock” in Gabon, Central Africa, and quantified differences between species based on EOD waveform shape.

Gymnotiforms and mormyriiforms possess electroreceptors tuned to the self-generated field. Moreover, species differences in the peak-power frequency of the discharge of syntopic species has been observed in several field studies.^{75,105,116} These observations have led to the hypothesis that the dominant spectral features of the EOD might encode species identity. It is also possible that the electric fishes discriminate species on the basis of waveform analysis. Heiligenberg and Altes¹⁰⁴ were the first to demonstrate that pulse-type gymnotiforms are sensitive to phase changes in the EOD (where the EOD shape is modified while maintaining spectral properties). Hopkins and Westby¹¹⁸ postulated and tested a “scan-sampling” hypothesis: pulse gymnotiforms generate regularly spaced EODs such that the pulses of two nearby fish will overlap frequently, producing characteristic successive amplitude modulations, or beats, perceived by each individual. By analyzing the modulation envelope of the combined signals, fishes are able to analyze or “scan” the EOD waveform of a neighbor. Hopkins and Bass¹¹⁷ demonstrated that the temporal characteristics of the EOD mediate conspecific recognition during courtship in a species of the mormyrid *Brienomyrus*. Modulations of the EOD rate of at least one mormyrid (but no gymnotiform) species are known to allow species recognition.¹³⁶

Understanding the evolutionary links between species diversity and communication signals in animals in which mate recognition signals play a role in species recognition has been the focus of studies involving animals that exploit various sensory modalities — including color, sound, vibration, and chemical cues.¹⁹³ Given the species-specific nature of gymnotiform and mormyriiform electric signals, there are strong reasons to presume that electric fishes also utilize signals for species

recognition. However, the mechanisms underlying assortative mating are still largely unknown. Playback experiments in which temporal versus spectral aspects of single EOD waveforms are manipulated may be revealing.⁸¹ Electric fishes may also serve to be a useful group for testing the hypotheses of signal divergence and reproductive character displacement.

C. ELECTROCYTES AND ELECTRIC ORGANS

1. Electrocytes

The electric organs of weakly electric fishes are composed of tens to hundreds of electrically charged compartments called electrocytes. Myogenic electrocytes (derived from myoblasts) range in shape from that of flattened coins (*Electrophorus*) to elongated cigars (sternopygids) and may have complex surfaces with interdigitating membranes (*Electrophorus*)⁹⁵ or penetrating stalks (mormyrids).^{114,115} Adult apteronotid gymnotiforms have neurogenic electrocytes. The number of electrocytes is highly diverse, ranging from several hundred in mormyrids to millions in the electric catfish *Malapterurus*.¹⁵⁵ Electrocytes may have nervous innervation on the anterior or posterior membranes, or both, and the nervous innervation is always highly restricted to small portions of the membrane, often on morphologically specialized stalks. Electrocytes are arranged within the electric organ in series and in parallel. Like batteries, a geometry in which electrocytes are arranged in series increases the discharge voltage, whereas an arrangement in parallel increases total current flow (amperage). Hopkins¹¹⁴ noted that ecological correlates between electrocyte organization and water conductivity impose a tradeoff in the design of the electric organ to maximize signal power. In species inhabiting low-conductivity water (e.g., 10 to 50 μS^{-1}) the caudal appendage and electric organ are long and thin (more electrocytes columns, fewer rows) which serves to increase voltage in order to maximize the power output of the EOD. By contrast, species inhabiting high-conductivity water (e.g., 50 –to 200 μS^{-1}) have a caudal appendage that is short and deep (more electrocytes rows, fewer columns), which serves to increase amperage.

In the strongly electric fish *Electrophorus*, Na^+/K^+ -ATPase pumps in the electrocyte membrane act continually to generate a weak-voltage gradient (285 mV) across the electrocyte membrane.⁹⁵ Current flow is generated by the opening of voltage-gated ion channels in the electrocyte membrane, which may be depolarized by action potentials from innervating electromotoneurons or the depolarization of nearby electrocytes.⁵⁸ When stimulated, activated ACh receptors generate end-plate potentials, triggering Na^+ -channel-mediated action potentials peaking at 165 mV on the innervated membrane. The noninnervated membrane contains no voltage-gated Na^+ channels and maintains the 285-mV resting potential. The result is a transcellular potential difference of approximately 150 mV. Since each cell is stimulated simultaneously, electrocyte transcellular potentials summate. The potentials of three electrocytes, for example, culminate to produce 450 mV. Currents generated by stimulated electrocytes flow down electrocyte columns in the posterior-to-anterior direction. The circuit is closed by current flowing out of the head, through the water, and back into the tail region.⁹⁵

2. Electric Organs in Rajidae

Marine skates produce weak (from 20 to 40 mV) monophasic, intermittent (not continuous), head-negative discharges from bilaterally paired spindle-shaped electric organs that develop within the axial muscles of the tail. These electrogenic organs consist of disc- or cup-shaped electrocytes that are arranged in series anterioposteriorly and are depolarized by spinal electromotoneurons.¹¹⁹ Skate electrocytes differ from those of the strongly electric torpedinids in being innervated on the anterior surface, resulting in the caudally oriented flow of current. Electric organs among skate species range in length from about 30% total length in *Gurgesiella plutona* (17 cm total length) to 90% total length in *Raja alba* (26 cm total length).¹¹⁹ The known range of maximum discharge voltages is relatively small, from 1.5 V in *R. erinacea* to 4 V in *R. clavata*.⁴³ The discharges are controlled by descending input from an electric organ command nucleus located in the medulla.¹⁶⁵ The weak electric discharges

of skates are used for communication during social and reproductive interactions, not for electrolocation, prey capture, or defense.¹⁹⁸ Electric signals in skates are species specific in duration, ranging from 31 to 216 ms. Skate electric organs differ in length among species and may be sexually dimorphic.^{45,119} Skates often produce electric discharges during interactions with conspecifics, and electrical interactions are often more frequent when skates are in pairs or groups than in isolation.⁴³

3. Electric Organs in Mormyriformes

Both the larval and adult electric organs of pulse-type mormyrids and wave-type *Gymnarchus* are derived from the axial mesoderm. The electric organ *Gymnarchus* is located in the caudal region, the EOD repetition rate is 250 to 300 Hz, and the EOD amplitude is 0.1 mV cm^{-1} .¹⁵⁵ Larval *Gymnarchus* are electrically silent while in the nest for up to about 20 days after hatching. The myogenic electric organ of *Gymnarchus* retains sparsely distributed contractile elements.²⁰ The larval organ of mormyrids is located in both the epaxial and hypaxial trunk muscles (above and below the horizontal myoseptum), extending along the majority of the length of the body but not onto the caudal peduncle.²⁰ The larval organ has a pulse type EOD. In the mormyrid *Pollimyrus isidori*, the larval organ degenerates by about 90 days after hatching and is replaced by an adult organ which dominates discharge function by day 60.¹¹¹

The adult electric organ of mormyrids is small, with about 800 electrocytes, and is restricted to the region of the caudal peduncle. This compact organ is a very short dipole source, which creates a spatially uniform external electric field and allows for more precisely coordinated electrocyte activation and shorter pulse durations (200 to 800 μs), with very high PPFs of up to 25 KHz.¹¹⁰ The geometrical design of mormyrid electrocytes is complicated and correlated with the EOD waveform.^{30,114,115} Mormyrid electrocytes have stalks on the posterior surface, which may be nonpenetrating or penetrating. In the primitive condition, nervous innervation on stalks of the posterior electrocyte membrane results in a biphasic discharge with a head-positive phase followed by a head-negative phase. In some mormyrids (*Gnathonemus petersii*), the stalks along with their nervous innervation perforate the electrocyte and emerge from the anterior side of each electrocyte. This anatomical organization results in an EOD of reversed polarity.

4. Electric Organs in Gymnotiformes

In all larval and most adult gymnotiform fishes, the electric organ is derived from hypaxial muscle and extends along the majority (80 to 90%) of the fish's body length. All gymnotiforms with a pulse-type EOD (Gymnotidae, Hypopomidae, Rhamphichthyidae) retain the larval hypaxial electric organ through development. The adult electric organ of many gymnotiforms with a pulse-type EOD is regionally differentiated and sometimes include anatomically discrete accessory electric organs.⁴ About 35% of gymnotiform species are apteronotids, in which the adult electric organ is formed from proliferation and elongation of the spinal motoneurons that innervate the larval myogenic organ.^{130,131} In gymnotiforms with a wave-type EOD (Sternopygidae, Apterontidae), the larval electric organ degenerates during early ontogeny to be replaced by a myogenic adult electric organ in Sternopygidae and by a neurogenic organ in Apterontidae. Accessory electric organs are known in only one gymnotiform genus with a wave-type EOD — *Adontosternarchus*, in which the organ has been reported to be derived from electrosensory fibers.³⁰ Most gymnotiform species generate weak EODs that never exceed more than a few hundred millivolts.

In addition to a weak discharge, the electric eel *Electrophorus electricus* generates a strong electric discharge (up to 600 V) which is used to stun prey and for defense. These are produced from the main electric organ and the anterior two thirds of the more ventral Hunter's electric organ. The strength of these discharges is correlated with body length, increasing by about 100 V for each 30 cm total length. The trains of strong discharges are under voluntary control and are used in aggressive and predatory behaviors. The posterior one third of Hunter's organ, together

with the organ of Sach's lying dorsal and posterior to the other two electric organs, generates a continuous, variable, low-frequency (1 to 5 Hz) weak (1 to 10 V) electric discharge. The continuous weak EOD of *E. electricus* is a head-positive monophasic pulse that generates the electric field used in navigation and sexual communication.²⁰ All the electric organs of *E. electricus* are derived developmentally from a germinal zone located on the ventral margin of the hypaxial musculature.³⁰

5. Electric Organ and EOD Diversity

EODs are known to vary with species, gender, and social status.^{58,86,151,152,213,246} These aspects of EOD variation are mediated by steroid and peptide hormones that influence the flow of ion currents through the electrocyte membranes, as well as changes in gene expression or phosphorylation states. Among electric fish species with a pulse-type discharge, important inter- and intraspecific differences are observed in the EOD repetition rate (interpulse or interdischarge interval), waveform, and pulse duration (see section IV-C). Among species with a wave-type discharge, the most important differences are EOD waveform, repetition rate, and harmonic content.⁷⁸ Many of the principles underlying intraspecific EOD variation also apply to interspecific differences.

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The unique EOD of each electric fish species is based on differences in the coordinated activation of electrocyte faces. Patterns of electrocyte activation depend on the anatomical and physiological organization of their nervous innervation (on the posterior, anterior, or both electrocyte faces), and on their size, shape (e.g., coin, barrel, or cigar shaped), and electrical insulation. Electrocytes may also differ regionally within an electric organ in the nature and abundance of membrane receptor proteins.¹⁵³ In mormyrids, EOD waveforms are species specific within an ecological community,^{115,136} and the interdischarge intervals (IDI, or "interpulse interval") is highly variable both within and between species.^{137,233} Intervals between discharges (system resolution) are controlled by the PM under the influence of reafferent signals. Novel sensory stimuli cause transient accelerations of the pacemaker rate (novelty responses).⁶⁰ An extensive body of work on mormyrids has demonstrated the functional role of both EOD waveform and IDI in communication.^{29,44,133,136,143} Mormyrids typically generate short (about 1 ms) EODs separated by much longer IDIs (c.10 to 1,000 ms). The EOD waveform of an individual fish is usually constant over longer periods of time. In several gymnotiforms, the elongate hypaxial electric organ is not physiologically homogeneous.⁵⁸ The size, shape, and configuration of electrocytes within the electric organ may vary dorsoventrally or anteroposteriorly and, in some cases, is differentiated into morphologically discrete accessory electric organs.⁴ In these species, the electrocytes are arranged in two to five tubes along the ventral portion of the body. The elongate electric organ of pulse-type gymnotiforms generates complex spatiotemporal fields and waveforms that are highly dependent on the position within the field.⁵⁸ The local EOD is most complex and species typical in the abdominal region.^{2,55-57,59,112,145}

6. Electrocyte Development and Regeneration

During normal development, electric organs are derived from myoblast precursors located in a zone of proliferation on the ventral margin of the hypaxial musculature. Electrocyte differentiation and proliferation continue throughout life. Like the myocytes from which they are derived phylogenetically, myogenic electrocytes are multinucleated compartments that differentiate during ontogeny from the fusion of multiple myoblasts.^{217,218,220} All muscle cells produce very-low-amplitude and irregular electrical discharge during contraction. Muscle action potentials are about 1 ms, and the EODs of weakly electric fishes show a 200-fold variation in action potential duration, from about 200 μ s in many mormyrids to 40 ms in the gymnotiform *Sternopygus*.^{80,246}

Electrocytes have very low abundance of proteins in the cytoplasm and a concentration of the few expressed proteins in or near the nuclear and cell membranes. This suggests that many of the changes required to convert developing myoblasts into mature electrocytes involve downregulation or switching off of protein expression associated with the contractile machinery and upregulation of the proteins associated with the production of excitable membranes and cytoskeletal filaments

that are required to establish and maintain the highly specialized changes in membrane potentials.¹⁵⁴ Several proteins known to differ greatly in abundance between myocytes and electrocytes include actin, myosin, desmin, and Na⁺ channels.¹⁹⁰ As in other teleosts, gymnotiforms have six Na⁺ channel genes, each of which is orthologous to an Na⁺ channel gene or gene cluster on a different mammalian chromosome.¹⁴⁴ Two of these genes are expressed in muscle (Na1, Na6), compared with one in mammals (Nav1.4), possibly as a result of a genome-wide duplication in the ancestor of teleosts.¹⁸⁴ Na6 has lost its expression in muscle and is expressed only in the electric organ.²⁴⁵

Gymnotiforms also possess a unique capacity to regenerate the entire caudal (postcoelomic) portion of the body, including muscles, electrocytes, spinal cord, and spinal nerves.⁴ During regeneration, fully differentiated adult myocytes transdifferentiate to mature electrocytes.^{176,177} In the early stages of regeneration, a blastema forms, the blastemal cells cluster and express desmin, fuse into myotubes, and then express alpha-actinin, tropomyosin, and myosin. Myotubes in the periphery of the blastema continue to differentiate as muscle; those in the center grow in size by fusing with one another and lose their sarcomeres as they become electrocytes. Tropomyosin is rapidly downregulated, while desmin, alpha-actinin, and myosin continue to be diffusely expressed in newly formed electrocytes. During this time, an isoform of keratin that is a marker for mature electrocytes is expressed.²⁴⁸ Nervous innervation is required for their fusion and subsequent transdifferentiation into electrocytes.²¹⁸ Electrocytes briefly coexpress sarcomeric proteins such as myosin and tropomyosin as well as keratin, a protein not found in mature muscle. The sarcomeric proteins are subsequently downregulated, but keratin expression persists. The maintenance of the electrocyte phenotype depends on nervous innervation. After spinal cord transection, which silences the electromotor neurons that innervate the electrocytes, or destruction of the spinal cord, which denervates the electrocytes, mature electrocytes reexpress sarcomeric myosin and tropomyosin.^{19,248}

D. ELECTRORECEPTIVE PERIPHERY: TUBEROUS ORGANS

Active electrolocation involves projecting physical electric images onto a mosaic of tuberous-shaped cutaneous electroreceptor organs. In mormyrid and gymnotid fishes, the entire body surface is covered with hundreds to thousands of these tuberous organs, which respond to the high-frequency stimuli (from 50 to as high as 2,200 Hz, depending on the species) generated by their own EODs, as well as those emitted by other electric fishes.^{30,191} Tuberous organs are most densely arrayed in an electrosensory fovea on the jaw and snout, with densities of 25 mm⁻² on the head and 1 mm⁻² on the caudal portion of the body.^{1,62} In adult specimens of *Apteronotus albifrons*, there are about 13,000 to 17,000 tuberous organs distributed on both sides of the head and body, compared with about 700 ampullary organs and 250 mechanosensory neuromast organs.⁷⁴ Two features of tuberous organs act as prereceptor mechanisms that shape the nature of the signals delivered to the brain to build up perceptual images: (1) the geometry of the sensory mosaic that funnels currents to the perioral region, and (2) a center-surround response profile that enhances edge detection.⁶⁸

Tuberous organs are phylogenetically derived from, and share many features with, teleost ampullary organs.²⁴³ Like ampullary organs, tuberous organs possess an epidermal chamber embedded about 100 microns within the skin, with a sensory epithelium at the base that contains the electrosensory hair cells and a canal extending to a superficial pore. The canal of tuberous organs is filled with a plug of loosely packed cells instead of jelly. The electrical impedance of the canal's interior is relatively low because of large extracellular spaces, and the canal and chamber walls are composed of many layers of flattened cells that provide efficient electric isolation. As a result, transdermal current potentials are channeled from the body surface to the embedded chamber of receptor cells. The hair cells of tuberous organs are also like those of ampullary organs in that the apical membrane is densely packed with microvilli and lacks cilia. Microvilli greatly increase the membrane surface area, increasing its capacitance and decreasing its resistance.²⁴³ These membranes

depolarize in response to anodal transmembrane voltage gradients and hyperpolarize in response to cathodal stimulation, thereby increasing (or decreasing, respectively) the tonic rate of spontaneous discharges of the lateral line nerve afferent that project from each organ to medullary targets in the brain. Unlike those of ampullary organs, tuberous organ hair cells lie mostly within the organ lumen.

1. Tuberous Organ Diversity

Eight morphologically and physiologically distinct tuberous organs are known in teleosts, each coding timing or amplitude information, in mormyriforms or gymnotiforms, and in pulse- or wave-type species.^{110,243} The wave-type *Gymnarchus* has “S” (timing) and “O” (amplitude) units; pulse-type mormyrids have knollenorgans and mormyromasts; pulse-type gymnotiforms (gymnotids, rhamphichthyids, hypopomids) have pulse marker coders (“M” units) and burst duration coders (“B” units); and wave-type gymnotiforms (sternopygids, apteronotids) have phase coders (“T” units) and probability coders (“P” units). Each of these organ types is characterized by a unique suite of morphological and physiological features.²⁴³ In *Gymnarchus* and Gymnotiformes, both the time coders and amplitude coders are used in electrolocation as well as electrocommunication. The time-coding knollenorgans of mormyrids are used for communication only.

Time-coding receptors usually fire 1:1 with each EOD pulse or wave cycle, except at very low (nonphysiological) stimulus intensities. Time-coding receptors are generally more sensitive than the amplitude coders of the same species and are generally not sensitive to amplitude changes. The afferents of time-coding receptors are characterized as “fast” because they possess large diameter axons and electrical synapses, ensuring rapid accurate transmission of timing information to the brain.⁶⁵ Amplitude-coding receptors encode changes in the self-generated EOD by matching the numbers of spikes with local voltage amplitude. The voltage thresholds of amplitude coders are usually just a little lower than the local EOD amplitude of the self-generated field. In pulse species, a burst of spikes is fired for each EOD, with the number of spikes per burst increasing and spike latencies decreasing when the EOD amplitude is increased.³² In Gymnotiformes, time-coding receptors are tuned to lower frequencies (50 to 100 Hz) and are more sharply tuned than are amplitude coders (1.2 to 2 kHz). Mormyrid timing-coding knollenorgans are also tuned to lower frequencies (100 Hz) than are the amplitude-coding mormyromasts (10 kHz), but all mormyrid tuberous organs are broadly tuned (except the amplitude-timing “O” units of *Gymnarchus*). Mormyrid knollenorgans are similar in overall morphology to gymnotiform tuberous organs, although they typically have fewer (1 to 10) hair cells, and each cell is enclosed within a cavity within the larger capsule. Knollenorgans in the mormyrid *Petrocephalus* have up to 60 such cells. Knollenorgans have very sensitive thresholds (about 200 mV cm⁻¹) which can code the exact timing of the EODs of other electric fish.

The amplitude-coding mormyromasts relay information used in both electrolocation and communication. Mormyromasts are complex organs composed of two distinct chambers, each with separate nervous innervation; a superficial ampullary-like chamber, and a deeper knollenorgan-like chamber. The mormyromasts of some mormyrids with very short pulses respond up to 18 kHz.^{111,118} Mormyromasts have no functional or morphological analog in gymnotiforms. Larval mormyrids possess three physiologically distinct populations of electroreceptor organs, two of which degenerate at metamorphosis and one of which (the promormyromasts) differentiate into the adult mormyromasts.³³

2. Culteriform Body Shape

A combination of derived features gives the mormyriform *Gymnarchus* and all Gymnotiformes a knifelike or “culteriform” body shape.⁴ In these two groups of fishes, propulsion is achieved by undulations of an elongated median fin; a dorsal fin in *Gymnarchus*, and an anal fin in Gymnotiformes. This contrasts with swimming by means of alternating constrictions of the axial muscles, as occurs in most other fishes. The culteriform body shape is extreme in gymnotiforms, which

possess a highly elongated body and an elongated anal fin (containing 100 to 350 rays) extending along the majority of the ventral portion of the body. Each anal-fin ray has a ball-and-socket articulation with the bony supports of the axial skeleton (pterygiophores) permitting 360° rotation. The culteriform body shape facilitates the use of the external body surface as a sensory sheet, and in at least one species with a wave-type EOD (e.g., *A. leptorhynchus*), individuals learn to associate proprioceptive feedback from tail bending with changes in electroreceptor activity.²⁶ A semirigid body posture also stabilizes the electric organ generation of the stereotypical three-dimensional electric field.^{13,187}

E. CENTRAL PROCESSING OF ELECTROSENSORY INFORMATION

The central nervous system of electric fishes with active electrolocation decodes perturbations of their self-generated electric fields that result from interactions with inanimate objects, prey items, and, importantly, the discharges of other electric fishes. These sensory circuits are specialized to process amplitude-modulated signals and to detect microsecond variations in spike timing.²⁴⁶ The brain circuitry and dynamics for analyzing electrosensory input and formulating electromotor output is better understood than perhaps any other vertebrate sensory motor system.¹⁰¹ The neuroethology of several natural behaviors has been the subject of intense study, including the role of EOD amplitude and frequency modulations in a variety of behavioral circumstances.²⁵¹ Understanding how the nervous system processes impulselike inputs to yield a stereotypical, species-specific electromotor output is contributing to a general understanding of the mechanisms underlying the coordination of complex effector patterns.^{8,60}

The valvula of the cerebellum, present in all actinopterygian fishes, is highly hypertrophied in mormyrids, extending over the dorsal surface of the rest of the brain. In most gymnotiforms (and siluriforms), the anterior lobe of the corpus of the cerebellum is enlarged and covers the rest of the brain.^{4,206} In gymnotiforms, the primary rhombencephalic electrosensory centers of the brain (i.e., the electrosensory lateral line lobe and corpus cerebellum) constitute approximately 50% of the total brain volume.⁶ This hypertrophy of electroreceptive brain structures is accompanied by a substantial reduction in other sensory systems. The eye is small and subdermal in all gymnotiform taxa, except two sternopygids genera (*Sternopygus* and *Archolaemus*), and the accessory optic system is absent in all gymnotiforms, except the Sternopygidae.¹⁴¹ Gymnotiformes do not possess extra-oral taste buds, integumental club cells, or Schreckstoff.⁴

In both mormyriforms and gymnotiforms, the ELL is divided into four segments, each containing a separate electrotopic map of the body surface. Each ELL segment receives information from dedicated receptor types. In mormyrids, low-frequency ampullary organ (passive electrolocation) information terminates in a single map in the ventrolateral zone of the ELL cortex; mormyromast (active electrolocation) information terminates in two maps in the medial and dorsolateral ELL zones; and knollenorgan (electrocommunication) information terminates in a map in the nucleus of the ELL. In gymnotiforms, the ampullary organs terminate in a map on the medial ELL segment and the tuberous receptors terminate on three separate maps on the central-medial, central-lateral, and lateral segments. In gymnotiforms, P- and T-type tuberous receptor afferents project onto three shared maps, each of which is devoted to certain aspects of electroreception, with the emphasis on either spatial or temporal processing.^{194,195} Information from the time-coding and amplitude-coding tuberous organs converge in the ELL, where they are used for the two main functions of the electrosensory motor system: electrolocation and electrocommunication. Time-coding and amplitude-coding tuberous organs are used to analyze the self-generated train of EODs as well as those emitted by other electric fishes. Electrosensory maps of the body surface from ampullary and tuberous receptor arrays are maintained in spatial register through several layers of sensory processing in hindbrain (e.g., DON, ELL,) and midbrain (e.g., TS and TO) structures. Information from these different laterosensory subsystems are sequentially integrated with one another and then

with other sensory modalities (e.g., acoustical-vestibular, visual) to build a multimodal percept of the external environment.¹⁵⁶

In both mormyriforms and gymnotiforms, the primary electroreceptive brain centers have a laminated, cerebellum-like cellular organization.^{27,28} In this regard, they also resemble the primary targets of octavolateralis afferents in the medulla of most vertebrates.²⁶ These structures include the DON-receiving primary electroreceptor input; the medial octavolateral nucleus (MON)-receiving primary mechanosensory lateral line input, and the dorsal cochlear nucleus (DCN)-receiving afferents from the cochlea of the inner ear.²⁰⁶ All these cerebellum-like structures are composed of a sheetlike array of principal cells (Purkinje-like or Eurydendroid cells), whose basilar regions are contacted by somatotopically organized primary (sensory) afferents and whose apical regions are contacted by descending (motor) neurites of the cerebellum. This anatomical organization facilitates the use of cerebellum-like structures in sensory-motor integration.

The cerebellum plays an important role in the control and coordination of movements in all vertebrates, and in electric fishes, parts of the cerebellar cortex are concerned with tracking movements of objects around the animal rather than with controlling the movements of the animal itself.²⁸ The cerebellum and the cerebellum-like structures like the ELL and DON serve as adaptive sensory processors, in which learned predictions about sensory inputs are generated and subtracted from actual sensory input, allowing unpredicted inputs to stand out.²⁶ The suppression of self-generated electrosensory noise (reafference) and other predictable signals is accomplished in the cerebellum and cerebellum-like structures by an adaptive filter mechanism.⁴² Such a filter has been demonstrated in the ELL of mormyriforms and gymnotiforms, the electrosensory DON of skates, and the mechanosensory MON of both teleosts and elasmobranchs. The form of the cancellation signal is stable and well preserved between bouts of a particular behavior and can also be modified within minutes to match changes in the form of the refference associated with that behavior.

V. STRONGLY ELECTRIC DISCHARGES

Torpedos (Torpedinidae) use intermittent strong discharges (30 to 60 V) of up to 5 ms duration in predation and defense.^{67,155} In *Torpedo marmorata*, electrocytes begin to differentiate while still in the embryo case and are fully functional although very weak immediately after hatching.¹⁵⁵ Maturation of the EOD involves an increase in amplitude of 10⁵-fold. In addition to emitting a strong electric discharge from the main organ, *Narcine brasiliensis* also produces intermittent weak (0.1 to 1 V) electric discharges from paired accessory electric organs located immediately caudal to the main organs. The main organ is innervated by portions of three cranial nerves (facial, glossopharyngeal, vagus), whereas the accessory organ is innervated by portions of the vagus nerve only. In *N. brasiliensis*, each accessory electric organ is composed of about 10 electrocyte columns, containing about 200 electrocytes each, for a total of about 4,000 electrocytes in the whole animal.³¹ These columns are twisted in their courses from proximal to distal such that the nervous innervation is dorsal, in contrast to the ventral innervation of the electrocytes in the main organ. The evolutionary origin of weak organs from strong electric organs in torpedos, or *vice versa*, is unknown.

The strong discharges of *N. brasiliensis* do not require a large energy output. Blum et al.³⁹ used depletion of phosphocreatinine (PCr) to determine the activity of the Na⁺/K⁺-ATPase after electric organ discharges and to measure the net flux from PCr to ATP through the creatine phosphokinase (CPK) reaction. The reaction was also assessed in skeletal muscle as a control. The rate constant for the CPK reaction at 24°C in resting electric organ was 0.000 ± 0.002 s⁻¹ (n = 10) and in skeletal muscle was 0.08 ± 0.03 s⁻¹ (n = 3). This demonstrates that in the resting electric organ, which is well supplied with CPK, there is no measurable flux.

The strong electric discharges of *Malapterurus* (to 150 V), and *Electrophorus* (to 600 V) are used in predation and communication.^{20,30} The strong discharges of *Astroscopus* are used in predation and in *Uranoscopus* may also be used in social communication.^{16,155} The electric organ and

electromotor control system of *Malapterurus* is very similar to that of ictalurid catfishes, and unlike mormyriiform and gymnotiform electric fishes, the electromotor control of *Malapterurus* is mainly accomplished at the level of the electromotoneurons.¹⁹²

VI. PHYSIOLOGICAL ECOLOGY OF THE ELECTRIC SENSE

A. ECOLOGICAL DISTRIBUTIONS

Both the mormyriiform and gymnotiform fishes are restricted to fresh waters. Their small, discrete electric organs would be short circuited by the extremely low resistance of sea water — rendering them useless for electrolocation or communication. In electric marine rays (Rajidae and Torpedinidae), the short circuiting problem has been overcome by developing twin-electric organs that are physically separated from each other.¹⁵⁵ In the case of the strongly electric Torpedinidae, the organs are especially large and separated on the far extremes of the “wings.” Nonetheless, the effective range of communication (weak discharges) and aggressive (strong) discharges is highly limited in sea water.

In both the mormyriiform fishes of Africa and the gymnotiform fishes of the New World, a phylogenetically and physiologically deep-set division separates wave-generating and pulse-generating species. In the New World, wave-type signals are thought to have evolved just once, forming the group Sinusoidea (Sternopygidae + Apterontidae).⁴ This group radiated considerably and is represented by 97 known species, representing 55% of the 176 known gymnotiform species.⁷⁸ Pulse- and wave-type species are about equally successful in terms of species diversity in the New World. In contrast, only one of around 235 known mormyriiform species, *Gymnarchus niloticus*, generates a wave-type EOD. This species is capable of air breathing, lives in swamps, and grows to a large size (around 1 m).¹⁵⁵ Since the habitats in which wave-type gymnotiforms live are common throughout Africa (including large rivers and small streams), the absence of large radiations of wave-type fishes may be nothing more than a consequence of evolutionary chance. On the other hand, the mormyriiform and gymnotiform radiations, as a whole, may be viewed as approximately matched for species richness at the continental scale (in the order of a couple hundred species), and mormyrids are present in all equivalent habitats dominated by the wave-type species in the Neotropics. Under this view, the paucity of wave-type mormyriiforms may result from the spectacular diversification of pulse-type mormyrids. The reasons for the strong disparity in the diversity of pulse- versus wave-type electric fishes in the New and Old Worlds remain obscure.

Crampton and Albert⁷⁸ describe the distribution of wave- and pulse-type species among the main aquatic habitats of the New World and divide aquatic systems into three main categories: (1) major rivers, (2) floodplains, and (3) streams and small rivers not exposed to seasonal flooding. Among these major habitats types, there are striking disparities in the distribution of pulse- versus wave-type species. The disparity is greatest in river channels and flood plains. In river channels, 13 of 90 (14%) species generate pulse-type EODs in contrast to 77 of 90 (86%) that generate wave-type EODs. In flood plain environments, 35 of 50 species (70%) generate pulse-type EODs, while the remaining 15 species (30%) generate wave-type EODs. Finally, in small streams, 49 of 71 species (69%) generate pulse-type EODs, while the remaining 22 species (31%) generate wave-type EODs. In short, river channels are dominated by species with wave-type EODs, while flood plains and streams are dominated by species with pulse-type species. River channels, flood plains and streams differ in three **principal** physicochemical properties that might limit or encourage the distribution of gymnotiform species: dissolved oxygen, temperature, water flow, and substrate geometry.^{76,78}

B. DISSOLVED OXYGEN AND SIGNAL ENERGETICS

Gymnotiforms with wave-type EODs are rare or absent in the seasonally hypoxic waters of the large “várzea” flood plains of whitewater rivers and are physiologically intolerant of hypoxia.⁷⁷

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These distributional patterns and experimental results were hypothesized to be a consequence of the higher energy requirements of wave-type EODs — which are usually generated at higher repetition rates (~25 to 2,200 Hz) than the EODs of pulse-type species (<1 to 120 Hz). Using oxygen consumption as a proxy for metabolic rate, oxygen consumption in pulse- and wave-type gymnotiforms has been shown to be similar.¹²⁰ Further, oxygen consumption in both types of fishes was about half that expected by extrapolation from temperate teleosts to a similar temperature (26°C). These observations concur with the expectation that the energy allocation for electrogenesis may be low.¹¹⁴ On the basis of voltage and current measurements of the EOD of a mormyrid and extrapolating from published basal metabolic rates of fishes, Hopkins¹¹⁴ estimated that the EOD may represent only about 1% of the basal metabolic rate; in other words, the energy cost for electrogenesis is surprisingly small.

Nonetheless, the maintenance of “scan swimming” (forward and backward probing movements associated with foraging in many wave type gymnotiforms) in one species, *Apteronotus albifrons*, resulted in a 2.83 ± 0.49 fold (mean ± SD) increase in oxygen consumption when compared with the oxygen consumption of a resting fish.¹²⁰ The observation is noteworthy because scan swimming is thought to improve the resolution of the active electric sense in a number of important ways.²²⁵ As such, the cost of scan swimming can be considered part of the energy bill for the electric sense of most wave-type gymnotiforms but not that of pulse-type gymnotiforms. These results suggest that if, indeed, oxygen is a limiting factor on the distribution of species with wave-type EODs, the metabolic costs of scan swimming rather than the generation of the electric signal are the decisive factor.¹²⁰ Nonetheless, it is not clear why wave-type gymnotiforms have not evolved air breathing adaptations to allow them to tolerate hypoxia as has the single African wave-type mormyrid *Gymnarchus niloticus*.⁷⁷

C. TEMPERATURE AND THERMAL TRAPS

Deep river channels and stream habitats are generally more thermally stable than are flood plain environments.⁷⁸ The hypotheses of “thermal traps” postulates that wave-type electric fishes may be restricted to habitats with relatively narrow temperature ranges due to the narrow tuning of their tuberous electroreceptors.²⁰³ While changes in ambient temperature provoke changes in the EOD frequency with Q10s of around 1.5, changes in the tuning of electroreceptors lag far behind. Therefore, temperature differentials of more than 3 to 4°C from the normal ambient temperature result in a spectral mismatch between the electroreceptors and the self-EOD, rendering the fish insensitive to its own EOD — in essence making it electrically blind.

D. WATER FLOW

Among gymnotiforms, species with higher EOD rates tend to have more active lifestyles, that is, inhabiting fast flowing rivers (versus flood plain lakes), and foraging in open water on fishes or plankton (versus benthic insect larvae or crustaceans)^{77,78} The repetition rate of the EOD of gymnotiforms represents the perceptual sampling rate of the environment in a manner analogous to the flicker-fusion rate of visual systems (the threshold at which observed movement becomes perceptually seamless). Hence, higher EOD rates might be expected to correlate with faster-flowing water or faster-moving prey. Nonetheless, there are many gymnotiform species in river channels with relatively low repetition rates, with both pulse- (e.g., *Rhamphichthys*) and wave- (e.g., *Sternopygus*) type EODs. These species may occupy microhabitats on the riverbed protected from fast currents such as intervarve troughs and eddies.

E. SUBSTRATE STRUCTURE AND THE DETECTION OF CAPACITANCES

Weakly electric fishes perceive the electrical texture of nearby objects by monitoring transcutaneous voltage changes. Objects close to an electrolocating fish cast an “electrical shadow” on the skin,

which is detected by the amplitude-coding receptors. This electrical shadow may be thought of as analogous to the “black and white” component of images in the visual system known as form vision. In addition, electric fishes use their time-coding electroreceptors to conduct time measurements during electrolocation.²²⁵ Time (phase) coding allows the detection of the capacitive features of objects that are absent in natural inanimate objects. Because EODs are AC signals, the capacitive features of living objects evoke frequency-dependent amplitude changes as well as phase shifts (temporal distortions) of the local EOD waveform. The time coding of capacitive features therefore brings a second dimension to electroreceptive perception, which may be thought of as analogous to “color” in the visual system.²²⁵

These two aspects of objects the local electrical environment — their impedance (resistance) and capacitance — form the basis of Crampton’s hypothesis⁷⁶ on the distribution of pulse- versus wave-type gymnotiforms. Since capacitors are frequency dependent, the harmonic content of wave-type EODs renders species with wave-type EODs relatively poor at detecting the wide range of natural capacitances that characterize a complex living substrate such as a root tangle. The Fourier transform of wave-type signals is characterized by narrow and concentrated peaks of spectral energy (see Figure 12.3). In contrast, pulse-type EODs contain a broad range of frequencies with attenuations that stimulate tuberous electroreceptors, that is, the Fourier transform is characterized by a broad shallow curve around the peak power frequency traversing a wide range of frequencies (see Figure 12.3). Moreover, gymnotiforms with pulse-type EODs also possess electroreceptor categories tuned to a broader range of frequencies than those of wave-type species. In principle, wave-type species should be better at resolving the electrical surface texture of complex structures like root mats. While the spatial resolution afforded by pulse-type signals is expected to be superior to that of wave-type EODs, Crampton⁷⁶ hypothesized a tradeoff between spatial resolution and temporal resolution — the ability to track moving objects. By merit of faster EOD rates, wave fishes should have better temporal but inferior spatial resolution. The ecological distribution of pulse-versus wave-type species matches these theoretical predictions.⁷⁶ Pulse-type species are dominant in habitats where food is found on and among dense and geometrically complex root tangles but where flow rates are low (flood plains and streams). In contrast, wave-type species are dominant in habitats with relatively simple and inanimate substrates such as the sand-and-silt bottoms of rivers but where flow rates are higher.

VII. SUMMARY

Passive electroreception is the detection of external electric fields emanating from inanimate sources or from living tissues for use in orientation and locating prey objects. Active electroreception is the detection of distortions of a self-generated electric field by an array of specialized high-frequency-sensitive, tuberous-shaped electroreceptor organs. Passive electroreception differs from active electroreception in that an animal does not have to generate its own electric field in order to detect objects. Fishes with active electroreception navigate, orient, and communicate using weak electric fields generated by the coordinated spatial and temporal activation of electrocytes, which act in concert to create a stereotypical electric organ discharge (EOD). The EOD generates an electric field around the animal that approximates the shape of an oscillating dipole (i.e., dumbbell shape) enveloping the head and tail of the fish with alternating head-positive and head-negative phases that cycle with the EOD repetition rate.

Passive and active electroreception are ecologically and phylogenetically important components of vertebrate sensory diversity. Passive electroreception is a primitive vertebrate feature, and about one in six living vertebrate species is electroreceptive. Lampreys retain superficial electrosensory hair cells that respond to low frequency (DC to 50 Hz) electrical stimuli. Most electrosensory hair cells of gnathostomes (jawed fishes and their amphibian derivatives) are contained in subdermal ampullary-shaped organs. Electroreception was lost in the evolutionary lines leading to modern amniotes (reptiles, birds, and mammals) and teleosts. Novel electrosensory systems subsequently

evolved in one group of amniotes (monotreme mammals, within the trigeminal nerve system) and in at least three independent lineages of fresh-water teleosts (in each case within the laterosensory system). The morphology and physiology of ampullary organs is similar in each of these teleost groups and differs in several ways from those of chondrichthyans and other nonteleost gnathostomes.

Electrogenesis is known in more than 700 species representing at least 11 independent lineages, all of them fishes. Electric fish discharges range from weak (millivolts) to strong (10 to 600 volts). Active electroreception has evolved in parallel in two groups of strictly fresh-water teleosts, the African Mormyriiformes and the Neotropical Gymnotiformes, which possess high-frequency (50 –to 2,200 Hz) sensitive tuberous organs. Tuberous organs share many features with and are phylogenetically derived from teleost ampullary organs. Mormyriiform and gymnotiform species produce either pulse- or wave-type EODs. Pulse-type EODs are trains of relatively short and stereotypical pulses separated by periods of electrical silence, whereas wave-type EODs are continuous periodic discharges, without intervals of electrical silence. Pulse- and wave- type mormyriiforms and gymnotiforms possess morphologically and physiologically distinct tuberous organs, each specialized to encode either EOD timing or amplitude information. EODs vary with species, gender, and social status. Intraspecific **waveform** differences are mediated by steroid and peptide hormones. Interspecific **EOD** differences are influenced by electrocyte shape, electrocyte configurations, nervous innervation patterns, and, in some taxa, accessory electric organs. Pulse-type EODs differ in repetition rate, waveform, and pulse duration; wave EODs differ in repetition rate, waveform, and harmonic content.

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