Chapter 1
A Brief History of Electrogenesis and Electroreception in Fishes

Bruce A. Carlson and Joseph A. Sisneros

Abstract The primary goal of this volume is to provide an updated perspective on the topics of electrogenesis and electroreception in fishes. Throughout, there is an emphasis on how comparative perspectives can inform general issues regarding the neural mechanisms of behavior, from detailed comparisons among related species having divergent phenotypes to broad comparisons across distantly related clades having similar phenotypes. The underlying theme throughout is that evolution provides a natural experiment that can be exploited to relate variation in behavior to variation in its neural substrates. This allows for the development and testing of hypotheses regarding the neural control of behavior and for distinguishing generally applicable principles from clade-specific differences. The chapters cover a range of topics including the evolution and development of electric organs and electroreceptors, electrosensory transduction, evolutionary drivers and biophysical bases of electric signal diversity, influences of hormones and motor systems on electrosensory processing, envelope and temporal coding, use of control theory to characterize active sensing, and the role of active electrolocation and spatial learning in behavior. In this introductory chapter, a brief history of research on electrogenesis and electroreception in fishes is presented, with a summary of some of the most important neuroethological studies in electric fish that have contributed greatly to our understanding of brain function and the neural basis of behavior. The field of electroreception research continues to provide fertile ground for using comparative frameworks to understand the neurobiology of animal communication, social behavior, orientation and navigation, and the evolution of information processing.

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B. A. Carlson et al. (eds.), *Electroreception: Fundamental Insights from Comparative Approaches*, Springer Handbook of Auditory Research 70,
https://doi.org/10.1007/978-3-030-29105-1_1

Keywords Active electrolocation · Corollary discharge · Electric organ · Electric organ discharge · Electrocommunication · Electromotor · Electroreceptor · Electrosensory · Jamming avoidance response · Neuroethology · Passive electrolocation · Reafference

1.1 Introduction

It has now been over 14 years since the publication of *Electroreception* by Bullock et al. (2005). That volume provided a wide-ranging review of general topics in the field, such as electrosensory anatomy and physiology, plasticity in electrosensory systems, electrosensory-mediated behavior, electromotor control, evolution and diversity of electric fishes, and broad comparisons between the electrosensory system and other octavolateralis systems. Rather than updating the previous volume by providing a comprehensive general review, this new volume, *Electroreception: Fundamental Insights from Comparative Approaches*, narrows in on specific research questions that span more than one of these various subfields. Thus, this volume should be viewed as complementary to *Electroreception* (Bullock et al. 2005). Indeed, readers are encouraged to use the earlier volume as a general reference when diving into topics explored in the current volume, although all the chapters in the current volume have been written to stand on their own so that readers can choose how much they want to explore.

The research topics chosen have a long and distinguished history in the field, but they are also areas of active research in which new discoveries continue to accrue. The editors invited reviews from leading authorities to review some of the fundamental insights gained from studies of electrosensory and electromotor systems while paying particular attention to broadly relevant insights that have come about through a detailed focus on particular neural circuits, broad comparative approaches across species, or some combination of the two. A major goal of this approach is to provide a comparative and integrative perspective that illustrates how intensive research into specific topics in the field has informed important general questions in neuroscience. This chapter starts with a brief historical overview of the discovery of electrogenesis and electroreception in fishes (see Sects. 1.2 to 1.4). This is followed by highlighting major areas in which research on electric fishes has contributed to understanding the neural basis of animal behavior (see Sect. 1.5), culminating in an overview of the various chapters within this volume (see Sect. 1.6). This chapter closes by highlighting future directions and how comparative approaches to the investigation of sensory and motor systems may continue to reveal evolutionarily conserved solutions to fundamental problems in neuroscience (see Sect. 1.7).

1.2 Early Fascination with Electric Fishes

The earliest evidence of a human fascination with electric fishes dates back more than 5000 years ago to ancient Egypt (Moller 1995b; Finger and Piccolino 2011). Some of the earliest recorded paintings of electric fish can be found on Egyptian tombstones. On the tomb of Ti in Saqqara, Egypt, there is a limestone bas-relief painting known as *Ti Watching a Hippopotamus Hunt* that depicts the "electric catfish of the Nile" or *Malapterurus electricus* in a hunting scene with a number of other local fish species (Fig. 1.1). The electric catfish was often associated with the Egyptian gods Aker and Ra because these fish were common in dark, muddy waters, and it was believed they could navigate in the dark and thus assist the earth god Aker, protector and border guardian of earth's horizon, by helping guide the sun god Ra on his nightly journey into the dark netherworld. Of course, the painful, numbing sensations that resulted from handling these fish most likely contributed to their mythical status.

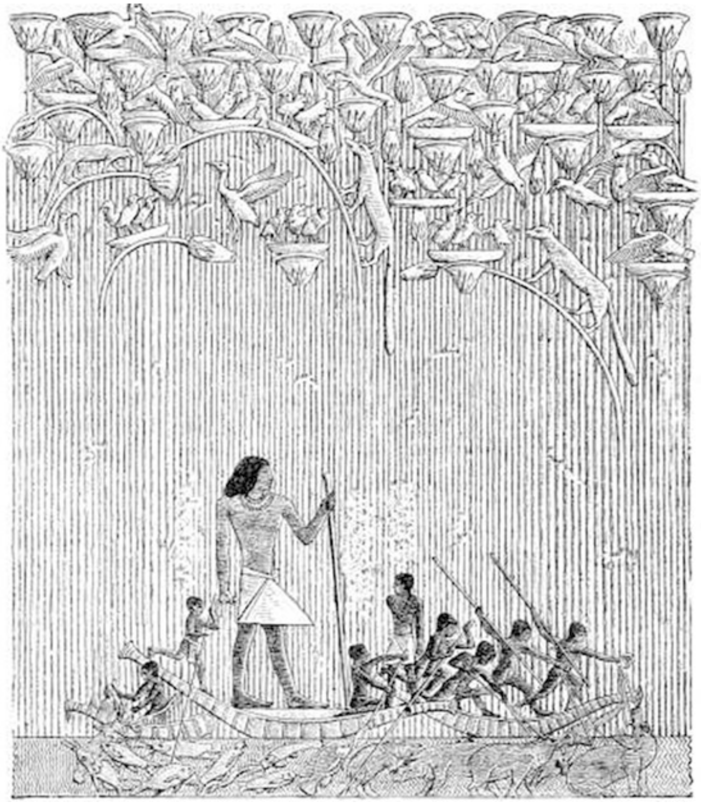

Fig. 1.1 A limestone bas-relief painting known as *Ti Watching a Hippopotamus Hunt* on the tomb of Ti in Saqqara, Egypt (c. 2400 BC). In this hippopotamus hunting scene in the marshes, the "electric catfish of the Nile" or *Malapterurus electricus* can be seen underneath the boat (*left*) with other local fish species

The Greeks and Romans were also familiar with electric fishes and the power of their strong electrical shocks, especially those of the electric torpedo ray (*Torpedo torpedo*). In the zoological treatise *Historia animalium*, Aristotle (374–322 BC; 1965) described how the electric torpedo ray captures prey by "…causing numbness in whatever small fishes it intends to overcome, catching them by the means which it possesses in its body, feeds on them; it hides itself in the sand and mud, and catches all the fish that swim towards it and become numbed as they are carried near." In another passage in *Historia animalium*, Aristotle mentions that torpedo rays can also cause numbness in humans. The Greek term for electric torpedo ray can be transliterated into "nárkē," whereas the Roman equivalent is "torporific." Both terms are based on the torpedo ray's ability to cause numbness. Several modern words have been derived from nárkē, including "narcotic," "narcotize," and "narcosis." The benumbing powers of the torpedo ray's electrical shocks were used in medicine during Greco-Roman times as a form of "electrotherapy" to treat pain and a variety of ailments, including gout and headaches (Finger and Piccolino 2011). During this time period, people could only speculate about the underlying source for the unusual power by which these fish produced such numbing shocks. The true physical basis of the fish's discharge would not be known until 2000 years later with the discovery of the force we now call electricity.

1.3 Discovery of Electrogenesis

By the early eighteenth century, the leading hypotheses as to the cause of the torpedo ray's powerful shocks were based on mechanical forces. The Italian scientist Stefano Lorenzini (1645–1725) first proposed that torpedo rays were capable of producing sudden contractions of specialized muscles known as *musculi falcati*. Lorenzini (1678) maintained that these violent contracting falciform muscles could produce a quick and explosive release of minute corpuscles that would then penetrate the receiver's nerves and block their function causing numbness. A similar hypothesis was put forth by the French scientist René-Antoine Ferchault de Réaumur (1683–1757), but he contended that the violent contractions of the *musculi falcati* alone could affect the nerves and muscles directly, causing numbness without the involvement of corpuscular emissions.

The case for animal electricity as the mechanism for the numbing effects produced by strongly electric fish was first put forth by the New Englander Edward Bancroft (1744–1820; Fig. 1.2), a physician, natural philosopher, and later fellow of the Royal Society of London. During the 1760s, Bancroft practiced medicine in Guiana where he had the opportunity to study *Electrophorus electricus* (known at that time as *Gymnotus electricus*), a fish feared by local natives. Bancroft referred to these fish as "torporific eels." Bancroft (1769) became convinced that "the shock of the Torporific Eel is not the immediate effect of muscular motion" but instead "is produced by an emission of torporific, or electric particles." Bancroft maintained that when a torporific eel is touched by a handheld rod while the other hand is joined

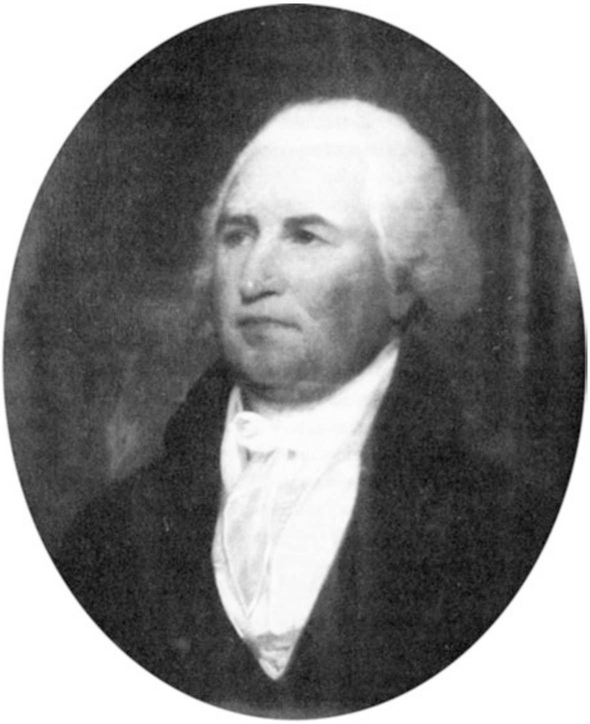

Fig. 1.2 Edward Nathaniel Bancroft (1744–1821) was an English physician, zoologist, botanist, and later a secret double agent during the American War of Independence. In 1763, Bancroft traveled to Dutch Guiana to practice medicine and would later write *An Essay on the Natural History of Guiana in South America* that includes details of his encounters with "torporific eels" (Bancroft 1769). After his return to London in 1771, Bancroft became a well-known authority on electric fishes

to another person, the eel can "communicate a shock perfectly resembling that of electricity, which is commonly so violent, that but a few are willing to suffer it a second time." In addition, Bancroft also observed when a person holds his finger in the water at a distance of two to three meters away from the eel and a discharge is elicited, the person at a distance can still receive a violent shock (Finger and Piccolino 2011). Thus, Bancroft's observations and experimental findings provided strong evidence as to the electrical nature of the torporific eel's shocks, and it is now typically referred to as the electric eel.

The first detailed analysis of the discharges from an electric fish was perhaps performed by John Walsh (1726–1795), a fellow of the Royal Society of London and member of the English Parliament. After his election into the Royal Society, Walsh was encouraged by Benjamin Franklin (1706–1790) to devote his scientific energies into studying torpedo rays and to specifically test the hypothesis that the torpedo ray's discharges were electrical in nature. Walsh traveled to La Rochelle and the Isle de Ré in France where he performed a number of experiments on torpedo rays. He focused on whether the shocks of torpedo rays could be transmitted from person to person in a long human chain similar to what could be elicited by a Leyden jar, an early form of electrical capacitor that consisted of a glass jar with metal foil layers on the inside and outside. Walsh discovered that the discharges of torpedo rays could be conveyed over distances up to 12 meters with metal wires (Finger and Piccolino 2011). He also noted that the shocks could not be conveyed by nonconductors such as glass or sealing wax. In addition, Walsh and his research team failed to detect any muscle movements from the torpedo rays before or during shocks that Réaumur claimed were fundamental for the shocks to be felt.

Following his experiments, Walsh concluded that the torpedo ray's discharges had to be electrical by a natural force he called "torpedinal electricity." Based on his own dissections and those later described by the English surgeon and anatomist John Hunter (1728–1793) that detailed the electric organ anatomy of Walsh's French torpedo rays (Hunter 1773), Walsh became more convinced that the torpedo ray's "animal electricity" was associated with the "honeycomb"-like structures found under the skin on the torpedo ray's disk, which he began to refer to as "electric organs," a term still used today.

Perhaps the most convincing demonstration of the electrical nature of the shocks produced by strongly electric fish was Walsh's demonstration in 1773 that the electric eel could produce visible sparks under the right conditions (Finger and Piccolino 2011). During the nineteenth century, no other electric fish captured the public's imagination more than the electric eel. The allure of this fish was, in part, made famous by the German explorer and naturalist Alexander von Humboldt (1769–1859; Fig. 1.3), who detailed his encounters with electric eels in South America in

Fig. 1.3 Alexander von Humboldt (1769–1859) was a German geographer, explorer, and naturalist. As a celebrated explorer, he detailed his dangerous travels and scientific explorations in the New World from 1799 to 1804 in many illustrated volumes of his writings

one of the many illustrated volumes of his writings that vividly highlighted his dangerous travels and scientific explorations in the New World (see Finger and Piccolino 2011). One of von Humboldt's more famous and fantastic accounts describes how South American Chayma natives used horses to collect electric eels (Fig. 1.4). This unusual collection method resulted in an epic battle between eels and horses that left the electric eels exhausted and "electrically spent," which then allowed the Chayma natives to safely collect live specimens for von Humboldt to study. In his accounts, von Humboldt (1807) described a self-defensive behavior in which electric eels leaped out of the water and pressed their chins against the horses to directly electrify them.

A study performed over 200 years later provided support for this legendary account, revealing that eels naturally leap out of the water to attack perceived threats and that this acts to increase the electrical current delivered to the target and effectively activate the target's nociceptors (Catania 2016). Indeed, studies have revealed that the electromotor behavior of electric eels is far more sophisticated than previously appreciated, involving remote control and immobilization of potential prey (Catania 2014), concentrating electric fields on challenging prey items (Catania

Fig. 1.4 The epic battle between eels and horses was vividly described by Alexander von Humboldt (1807) . It shows the use of horses by local Chayma natives to collect electric eels. This unusual collection technique involved horsemen driving a herd of about 30 wild horses into a stagnant pool of electric eels that resulted in the terrifying deaths of two horses in the first few minutes as the electric eels vigorously defended themselves by repeatedly discharging their electric organs. The Chayma natives kept the horses from exiting the pool by waving branches and reeds to force them back into the water. Eventually, the remaining horses stumbled out of the pool with their manes erect and panting in anguish while the electric eels were equally exhausted and "electrically spent." After the battle, the Chayma natives safely collected five live specimens for von Humboldt to study

2015a), and using their strong electric fields to actively track the location of their target prey (Catania 2015b).

By the latter half of the nineteenth century, other researchers, including the Scottish surgeon James Stark (1811–1890), began to discover the presence of apparent electric organs in other fishes besides the strongly electric catfish, torpedo ray, and electric eel. Stark (1844) discovered that the flapper skate (*Raja batis*) possessed bilateral organs in the tail that were similar in structure to those of torpedo rays and electric eels. The presence of similar organs was soon found in a number of other fishes, including the unusual-looking African elephant fishes in the family Mormyridae and the South American knifefishes in the order Gymnotiformes. However, at the time, no researcher was able to successfully detect electric discharges produced by these organs. Thus, the mormyrids and gymnotiforms were thought to be "pseudoelectric" or "imperfectly electric," as referred to by the German physiologist Emil du Bois-Reymond (1818–1896). Hence, the term "pseudoelectric organ" became used to reference electric organs in fish that were incapable of producing perceptible discharges.

The presence of such pseudoelectric organs in mormyrids and gymnotiforms were thought to represent an incomplete stage of electric organ evolution. This posed a serious problem for Charles Darwin's theory of natural selection, one of several that he addressed in a chapter of his landmark *On the Origin of Species* entitled "Difficulties of the Theory" (1859, p. 150):

> "The electric organs of fishes offer another case of special difficulty; for it is impossible to conceive by what steps these wondrous organs have been produced. But this is not surprising, for we do not even know of what use they are. In the gymnotus and torpedo they no doubt serve as powerful means of defence, and perhaps for securing prey; yet in the ray… an analogous organ in the tail manifests but little electricity, even when the animal is greatly irritated; so little that it can hardly be of any use for the above purposes."

The problem for Darwin's theory was that strongly electric organs must have evolved from muscle by first passing through an intermediate stage of weakly electric organs, and these weakly electric organs must have performed some adaptive function to have evolved in the first place. The true nature of these so-called pseudoelectric organs and the solution to Darwin's conundrum would not be understood until the next century when electrical recording equipment became available and the first electric organ discharges (EODs) of electric fish were recorded and characterized.

1.4 Discovery of Electroreception

Research on weakly electric fishes can be traced to the mid-twentieth century due to both technological advancements in the amplification and visualization of electrical signals (reviewed in Moller 1995b) and a series of elegant studies by the British zoologist Hans Lissmann (1909–1995) at the University of Cambridge, UK. Lissmann (1951) first showed that the African knifefish *Gymnarchus niloticus* (monotypic sister taxon to the Mormyridae, which together make up the

Mormyroidea or mormyroids) produced continuous weak, wave-like EODs at frequencies of about 250–300 Hz that originated from the tail, where anatomists had previously described an electric organ structure. Lissmann also noted that when the animal's own recorded discharges were fed back into the water using electrodes, the fish was able to locate and attack the stimulating electrodes.

Lissmann (1958) would later go on to record pulse-type EODs from several mormyrid species. Based on "bursts of discharges" when pairs of mormyrids were in proximity, he suggested that "the electrical discharges may play a social role in the life of the Mormyridae," in-line with earlier observations by Möhres (1957) at the University of Tübingen, Germany. Both Lissman and Harry Grundfest (1903–1984) at Columbia University, New York, NY, also described weak EODs in several South American gymnotiform species other than the electric eel (Grundfest 1957; Lissman 1958). Finally, Lissmann and his research assistant Kenneth Machin (1924–1988) developed a model based on their detailed measurements and analysis of the bioelectric fields produced by *Gymnarchus niloticus* that could explain a function for the EODs. Based on this model and operant conditioning experiments, Lissmann and Machin (1958) concluded that the weakly electric knifefish could detect changes in the conductance of its own self-generated bioelectric field to locate objects in its environment and distinguish objects of varying conductivity and chemical composition through a mechanism now referred to as "active electrolocation." The results of their behavioral experiments also suggested that these fish must possess some specialized sensory receptor system capable of detecting weak, biologically relevant electric stimuli (see Baker, Chap. 2; Leitch and Julius, Chap. 3).

1.4.1 Detection of Electric Fields

The discovery of an electric sense in weakly electric fishes (Lissman 1958; Lissman and Machin 1958) prompted an immediate search for the electric sense organs that Lissmann would later initially identify as "electric pores" (reviewed by Fritzsch and Moller 1995). These electric pores were first described in detail by Lorenzini (1678) in torpedo rays (*Torpedo* sp.) where he observed pits in the ray's skin that corresponded to the "mouths" of the long canals or "canaliculi" that are characteristic of this class of electroreceptors known as ampullary electroreceptors. In elasmobranch fishes (sharks and rays), these ampullary electroreceptors bear the name of the discoverer and are known as the "ampullae of Lorenzini." In terms of their functional significance, the ampullae of Lorenzini were first thought to be pressure receptors based on behavioral responses of the dogfish (*Mustelus canis*) when pressure was applied to the receptor area (Parker 1909). The ampullae of Lorenzini were later found to be very sensitive to gross step changes in water temperature (Sand 1938) and even sensitive to mechanical stimulation (Murray 1957; Loewenstein 1960), but the applied stimuli used in these studies were not biologically relevant in the animal's natural environment (Bullock and Szabo 1986).

Fig. 1.5 Sven Dijkgraaf (1908–1995) was a Dutch comparative physiologist who was well-known for his work and insights on lateral line function and hearing in fishes, echolocation in bats, and animal sound production. Along with his student Adrianus Kalmijn, Dijkgraf also performed early recordings from primary afferents of ampullary electroreceptors in elasmobranchs. Dijkgraaf was professor and director of comparative physiology at the University of Utrecht, the Netherlands, where he worked for over 26 years

Later, it would be Richard Murray (1960) at the University of Birmingham, UK, who would provide the first experimental evidence that the afferents of the ampullae of Lorenzini were responsive and highly sensitive to weak electric stimuli. Soon after, Sven Dijkgraaf (1908–1995; Fig. 1.5) and his student Adrianus Kalmijn, both at Utrecht University, the Netherlands, characterized the response properties of ampullary afferents in more detail and showed that the afferents of ampullary electroreceptors responded to natural, electrical stimuli at frequencies of 0.1 to 30 Hz, with a sensitivity as low as a few microvolts per centimeter (Dijkgraaf and Kalmijn 1962, 1963).

Later, Kalmijn would be the first to demonstrate a functional role for the ampullae of Lorenzini in sharks and rays and their use in the detection of weak electric fields. In a series of landmark behavioral experiments, he showed that elasmobranch fishes use their ampullae of Lorenzini in passive electroreception to detect and locate buried prey (Kalmijn 1971) and use electric fields for orientation and navigation in their environment (Kalmijn 1978, 1982). Kalmijn (1982) was able to train round stingrays (*Urolophus halleri*) to orient in an electric field as weak as 5 nV/cm and then locate and bite a pair of stimulating dipole electrodes for a food reward. Based on the high electrosensitivity of the ampullae of Lorenzini, Kalmijn (1978) also suggested that elasmobranchs should be able to perceive the weak electric currents induced by the animal swimming through the magnetic field of the earth by a process known as geomagnetic induction, which could be used theoretically by elasmobranchs for compass orientation during migration and navigation. Consistent

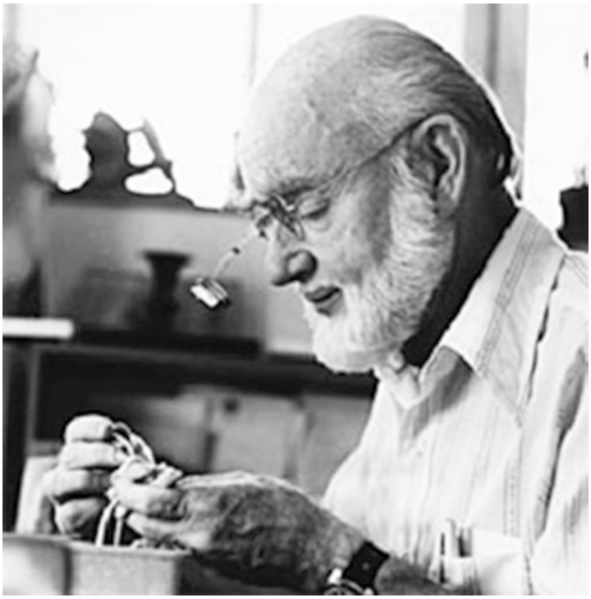

Fig. 1.6 Theodore "Ted" Holmes Bullock (1915–2005) was an American comparative neuroscientist who examined the physiology and evolution of the nervous system across many organizational levels and studied nearly all major groups including coelenterates, annelids, arthropods, echinoderms, mollusks, and chordates. Bullock was a pioneering and influential neuroscientist who championed the comparative approach and is considered to be one of the founding fathers of neuroethology. He spent most of his career at the Scripps Institution of Oceanography in La Jolla, CA, and was elected into the National Academy of Sciences in 1963. Photo from the Scripps Institution of Oceanography, with permission

with his hypothesis, Kalmijn (1982) demonstrated that round stingrays could be conditioned to orient within a magnetic field and thereby locate a specific place based on the magnetic field polarity for a food reward.

Around the same time that the ampullae of Lorenzini were discovered to be electrosensitive, two research groups, one led by Theodore Holmes Bullock (1915–2005; to whom this volume is dedicated; Fig. 1.6) at the University of California, Los Angeles, and the other group led by Alfred Fessard (1900–1982) and Thomas Szabo (1924–1993) at the National Center for Scientific Research, Paris, separately published their physiology studies that detailed the existence of a new class of electroreceptors known as tuberous receptors (Bullock et al. 1961; Fessard and Szabo 1961). The tuberous electroreceptors were identified in gymnotiforms and mormyroids, two groups of fish both capable of generating their own electric fields (Bullock 1982). These tuberous electroreceptors were named for their tuber-like anatomical arrangement in the skin and were found to respond to weak, high-frequency electrical stimuli greater than 50 Hz (Bullock et al. 1961; Fessard and Szabo 1961). The tuberous electroreceptors were later determined to be tuned at or near the frequency of the animal's own EODs and therefore play a critical role in active electroreception and electrocommunication. Future studies would go on to describe in detail the morphology and physiological response properties of tuberous electrosensory systems in weakly electric fishes (see Metzen and Chacron, Chap. 9; Carlson, Chap. 10; Perks and Sawtell, Chap. 11). Much of our current understanding of information processing in the central electrosensory systems of weakly electric fishes owes its origins to two giants in the field, Curtis Bell at the Oregon Health and Sciences University, Portland, and Leonard Maler at the University of Ottawa, Canada (Bell and Maler 2005).

1.4.2 Generation of Weak Electric Organ Discharges

During this exciting time of research, the electric organs of mormyroids and gymnotiforms were becoming described in better detail. Grundfest and his Columbia University colleague Michael Bennett began to investigate in more detail the structure and function of electric organs in fishes (Bennett and Grundfest 1959, 1961). Bennett (1971) would later go on to propose a comprehensive and detailed model of the physiological and anatomical bases for EOD production by electric organs (see Gallant, Chap. 4; Markham, Chap. 5).

1.5 Electric Fishes and the Neuroethological Approach to Animal Behavior

Neuroethological studies of electric fish have contributed greatly to a basic understanding of brain function by integrating studies of cellular and systems neuroscience, behavior, and evolution (Zakon 2003; Rose 2004; Carlson 2006). This is due, in large part, to several unique experimental advantages. There is a direct 1:1 correspondence between EOD output and the central pattern-generating circuits that generate each EOD (Caputi et al. 2005). In an intact animal, this means that EOD timing provides a direct, noninvasive monitor of the output of the central electromotor system. In an in vivo electrophysiological preparation, paralysis is typically induced by pharmacologically blocking the neuromuscular junction, which also silences the electric organ. Nevertheless, a fictive EOD can easily be recorded from spinal electromotor neurons by placing an electrode near the tail, and this likewise provides a direct 1:1 readout of electromotor output. Many natural behaviors are generated in such a preparation, allowing researchers to monitor, stimulate, or interfere with the activity of individual neurons or specific brain regions during both stimulus presentation and the production of behavior (Hitschfeld et al. 2009).

Although EOD timing is controlled by central circuits, the EOD waveform is determined by the morphological and physiological properties of electrocytes in the electric organ. Here, too, this allows researchers to directly relate EOD waveform to its underlying neural basis, and this has facilitated studies of species-, sex-, individual-, and dominance-related differences in EOD waveform as well as hormonal modulation of the EOD waveform (see Markham, Chap. 5; Silva, Chap. 6). With the advent of genomic and transcriptomic approaches, such studies have recently extended to the molecular level, linking the EOD waveform to ion channels and other proteins (see Gallant, Chap. 4). Comparative approaches ranging from the molecular to behavioral levels have addressed the roles of natural and sexual selection as well as drift in driving these evolutionary differences (see Krahe, Chap. 7).

On the sensory side, there is likewise a direct correspondence between individual EODs and receptor/primary afferent activation. This allows researchers to precisely manipulate the timing of presynaptic input to central sensory neurons in vivo by simply varying the timing of electrosensory stimuli. The same presynaptic inputs can be stimulated with the same timing using focal electrical stimulation in vitro. In both cases, the stimulation patterns have clear behavioral relevance because they represent patterns of electric signaling by the fish itself (in the case of active electrolocation) or by neighboring fish (in the case of electrocommunication). Thus, numerous studies have bridged in vivo studies of information processing with in vitro studies of synaptic and cellular physiology to gain insight into the processing of behaviorally relevant sensory input (see Metzen and Chacron, Chap. 9; Carlson, Chap. 10; Perks and Sawtell, Chap. 11). Recently, evolutionary developmental and electrophysiological studies have helped to elucidate the cellular and molecular basis of electrosensory transduction (see Baker, Chap. 2; Leitch and Julius, Chap. 3).

1.5.1 Active Electrolocation

The discovery of electroreception and its use in active electrolocation as first described by Lissmann and Machin (1958) provided an opportunity for a new generation of neuroethologists to examine this form of autocommunication in weakly electric fish. Autocommunication, in which the same individual is both sender and receiver, is also found in echolocating animals such as bats and dolphins (Griffin 1958). In this case, information about the surrounding environment is obtained by monitoring modulations (or in the case of echolocation, acoustic reflections) of their self-generated signals. During active electrolocation, the fish responds to changes in the local electrical impedance of its self-generated bioelectric field that enables it to "see" objects in the near field as changes in the intensity and waveform of electric signals across electroreceptors distributed throughout the body surface (von der Emde 1999). Objects with impedances that differ from the impedance of the surrounding water will cast electric "shadows" or "bright spots" on the electroreceptive surface, and the two-dimensional electric image of that object across the receptor array will depend on the object's electrical properties, shape, size, and distance from the fish. Although active electrolocation is effective for object detection and discrimination, the effective range of this active sensing system is limited to about one to two body lengths from the fish (von der Emde 1999; Nelson 2005). Active electrolocation is also important to help fish maintain their body posture relative to the substrate and to control their distance to objects in the environment. In Chap. 8, Stamper, Madhav, Cowan, and Fortune use control theory to characterize active electrosensing behavior. In Chap. 12, Jung and Engelmann review the current research that focuses on the role of active electrolocation during spatial learning and how weakly electric fish may form spatial memories using their electric sense to aid in navigation in the natural environment.

1.5.2 Jamming Avoidance Response

In wave-type weakly electric fishes, the presence of a nearby fish with a similar EOD frequency can result in interference with their active electrolocation system. Both African and South American wave-type fishes have evolved a jamming avoidance response (JAR) to mitigate this interference (Bullock et al. 1975). The JAR was first discovered in the gymnotiform glass knifefish, *Eigenmannia* sp., by Akira Watanabe and Kimihisa Takeda (1963), both at the Tokyo Medical and Dental University, Japan. Later, Bullock and his colleagues (1972) at the Scripps Institution of Oceanography, La Jolla, CA, would describe the behavioral response in more detail and name the behavior the “jamming avoidance response.”

The JAR and its underlying neural basis soon became the major research focus of Bullock’s postdoc Walter Heiligenberg (1938–1994; Fig. 1.7). Over the course of his career at the Scripps Research Institute, La Jolla, CA, Heiligenberg and his colleagues helped establish the JAR as one of the most iconic neuroethological case studies (as described in Heiligenberg 1991). The neural circuity underlying the JAR has been studied in exquisite detail in the gymnotiform *Eigenmannia virescens*, and to date, it remains the only nonreflex vertebrate behavior for which the neural basis has been described in detail, all the way from sensory receptors that encode the relevant sensory information to motor effectors that drive the change in behavior. In Chap. 9, Metzen and Chacron review the JAR and expand on the more general roles of EOD modulations (i.e., envelopes) in electrosensory-mediated behavior. In Chap. 10, Carlson describes in detail how both African and South American wave-type fish detect the small phase modulations that are crucial for accurate performance of the JAR. Work led by Masashi Kawasaki at the University of Virginia, Charlottesville, has shown, remarkably, that the independently evolved JARs of African and South American electric fishes rely on the exact same computational algorithm but quite different neural circuitry to perform these computations (Kawasaki 1993, 2009).

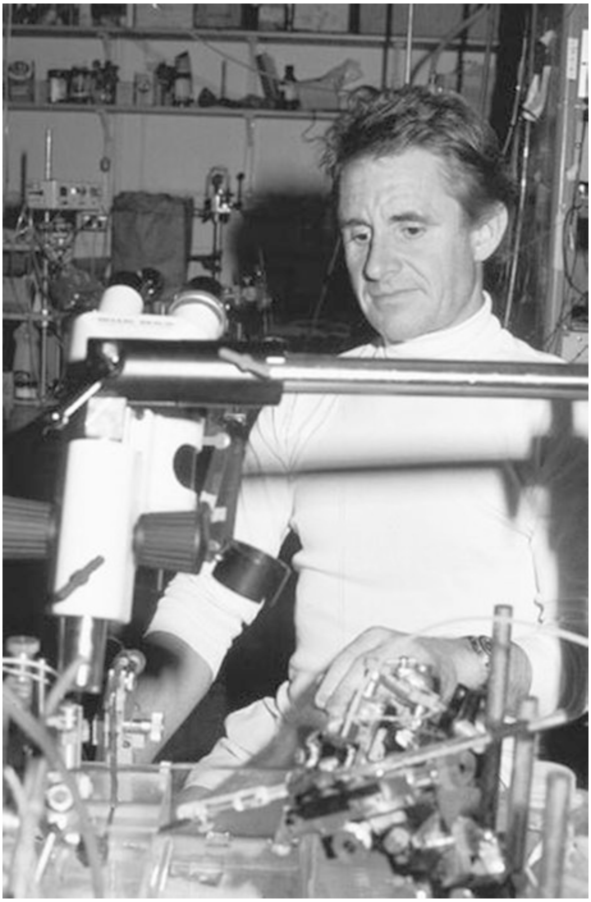

Fig. 1.7 Walter Heiligenberg (1938–1994) was a German comparative neuroscientist best known for his contributions to neuroethology based on detailed study of the jamming avoidance response (JAR) in the weakly electric glass knifefish *Eigenmannia virescens*. As a student of Konrad Lorenz, Heiligenberg studied the motivational behaviors of cichlid fish and crickets and conducted a successful quantitative demonstration of the law of heterogeneous summation. As a postdoc in Theodore Bullock's lab and later on the faculty at the Scripps Institution of Oceanography, Heiligenberg (1991) helped establish the JAR as the only nonreflex vertebrate behavior for which the neural basis has been described in detail, from sensory receptors that encode behaviorally relevant sensory information to motor effectors that drive the change in behavior

1.5.3 Electrocommunication

The study of the neural basis of electrocommunication in weakly electric fishes has been another rich area of investigation for neuroethologists. Möhres (1957) was the first to suggest that modulations of EOD rate in mormyrids had a communication function based on his observation that members of *Gnathonemus* sp. would often interrupt or vary the frequency of their EODs during bouts of aggression and physical fighting. Lissmann (1958) also suggested that EODs may play a role in the social behavior of mormyrids. A subsequent study by Moller (1970) demonstrated clear changes in EOD frequency in *Gnathonemus* sp. in response to playback of electric stimuli, and this was followed by a detailed observational study that described electrical interactions between pairs of *Gnathonemus* sp. that varied with the distance between the fish (Moller and Bauer 1973). Since that time, numerous playback and observational studies in several species of weakly electric fish have removed any doubt that EODs play a central role in communication and social behavior in both mormyroid and gymnotiform fishes (reviewed in Moller 1995a; Kramer 1996).

In the 1970s and 1980s, species diversity of EOD waveforms in pulse-type fishes and EOD frequency in wave-type fishes were established from field and laboratory recordings, and this diversity was shown to be species-specific (reviewed in Kramer 1990; Moller 1995a). In 1972, Carl Hopkins (to whom this volume is dedicated), then at the University of Minnesota, Minneapolis, was the first to show sexually dimorphic differences in EOD frequency among individuals from a breeding population of wave-type *Sternopygus macrurus*. After moving to Cornell University, Ithaca, NY, Hopkins, along with his colleague Andrew Bass, discovered that sex differences in the EOD waveforms of pulse-type mormyrids were influenced by steroid hormones (Bass and Hopkins 1983; also see Silva, Chap. 6). In addition to species and sex differences in EODs, individual and dominance-related differences as well as developmental changes in EODs were later observed (reviewed in Moller 1995a). In Chap. 5, Markham describes in detail the current understanding of how EOD diversity relates to the biophysics of electrocytes, the electrically excitable cells that constitute the “battery” that makes up the electric organ. In Chap. 6, Silva addresses the hormonal regulation of social behavior in the South American gymnotiforms, from hormonal actions on electrocytes and the central nervous system that drive changes in EOD waveform and frequency, respectively, to the role of hormones in seasonality, circadian rhythmicity, and territorial aggression. As in the early studies of the communicative significance of EODs, playback experiments were essential in demonstrating the behavioral significance of species, sex, and individual differences.

1.5.4 Reafference and Exafference

Given the experimental accessibility of both electromotor and electrosensory systems, a fundamental question in neuroscience that has been studied extensively in electric fishes is how the central nervous system distinguishes between self-generated sensory input (reafference) and externally generated sensory input (exafference). Distinguishing among these sources of input and processing them separately are crucial to all three forms of electrosensing: passive electrolocation, active electrolocation, and electrocommunication. In the 1980s, Curtis Bell at the Oregon Health and Sciences University, Portland, was one of the first researchers to investigate the role of sensory reafference in weakly electric fish and determine how animals perceive self-generated versus externally generated electric fields. Bell investigated the adaptive processing of electrosensory information that occurs in the cerebellum-like structures of the electrosensory lobes in weakly electric fish. In the context of electrolocation, Bell (1989) showed that associations between sensory inputs and corollary discharges within these cerebellum-like structures result in the generation of negative images of predictable features of sensory inflow that when added to the actual inflow of information removes the predictable features, thus allowing the unpredictable, externally generated sensory signals to be salient.

Similar noise suppression mechanisms were also observed in the elasmobranch electrosensory system by John Montgomery at the University of Auckland, New Zealand, and David Bodznick at Wesleyan University, Middletown, CT. In elasmobranch and teleost fishes, the animal's own ventilatory movements can create unwanted stimulation of the lateral line and electrosensory system that can potentially interfere with the detection of biologically relevant signals. Montgomery and Bodznick (1994, 1999) showed that there is an adaptive filter in the cerebellar-like circuits of medullary nuclei in the hindbrain for both senses (i.e., electrosensory dorsal nucleus and mechanosensory medial nucleus) that act to suppress self-stimulation through a common mode rejection mechanism. Montgomery and Bodznick (1994) also showed that fish can learn to cancel the effects of electrosensory and mechanosensory stimuli that are coupled to the fish's own movements. In Chap. 11, Perks and Sawtell describe in detail the underlying cells, circuits, and computations that underlie sensorimotor integration for processing exafferent and reafferent sensory input.

1.6 Fundamental Insights from Comparative Approaches

Comparative approaches to studying electrosensory systems have led to the identification of fundamental mechanisms for neuronal information processing and its relationship to natural behavior. A major goal of this volume is to provide a comparative perspective on the topics of electrogenesis and electroreception and to review some of the important insights gained from studies of electrosensory and electromotor systems.

In Chap. 2, Baker reviews the evolutionary and developmental origins of nonteleost lateral line electroreceptors with insights from comparative molecular approaches. Baker details how current gene expression results using “known candidate” gene and more recent unbiased transcriptomic (differential RNA sequencing) approaches suggest that the molecular mechanisms underlying electroreceptor development are highly conserved, with similar mechanisms underlying hair cell development. In addition, there exist a number of similar aspects in hair cell physiology of electroreceptor and lateral line systems, including transmission mechanisms at the level of the ribbon synapse. The high degree of similarity in the molecular development of the lateral line and electroreceptor systems suggests that electroreceptors most likely evolved in the vertebrate ancestor via the diversification of lateral line hair cells rather than an independent evolution of electroreceptors and hair cells from a secondary ciliated cell.

In Chap. 3, Leitch and Julius provide an overview of the physiological mechanisms underlying electrosensory transduction. This exciting review of electrosensory transduction includes recent advances in genetic and patch-clamp electrophysiological techniques that have made possible comparisons of the molecular mechanisms underlying transduction in electrosensory systems and other hair cell-based sensory systems. Such comparisons have the potential to shed light on the mechanisms of stimulus transduction and filtering across diverse species and potentially reveal shared fundamental mechanisms for extracting biologically relevant information across octavolateralis systems.

Chapters 4 and 5 focus on electric organ development and the biophysical basis of electric signal diversity, respectively. In Chap. 4, Gallant provides a comprehensive review of electric organ development and discusses recent advances in the understanding of molecular mechanisms involved in electric organ development in light of a new comparative study of gene expression across multiple lineages of electric fishes. In addition, Gallant identifies areas of need for additional data on electric organ development along with the application of new molecular techniques that could lead to new insights into the evolution and development of electric organs.

In Chap. 5, Markham addresses the morphological and physiological basis for the generation of EODs and focuses on specializations in electrocyte morphology and physiology, including the diversity of ion-channel expression patterns in electrocytes that can have a strong influence on waveform diversity. As described by Markham, electrocyte morphology and innervation patterns are a major source of signal diversity in the African mormyrid fishes, whereas diversity of ion-channel expression patterns is known to be a major influence on waveform diversity in the South American gymnotiform fishes. Although convergent evolution of ion channels in these clades contributes to signal diversity, little is known about the ionic mechanisms of signal diversity in mormyroids, which highlights the need for broader comparative studies.

Chapters 6 and 7 focus on the influence of hormones on social behavior and on the ultimate evolutionary causes of EOD diversification in weakly electric fishes, respectively. In Chap. 6, Silva addresses how the social behavior of South American weakly electric fishes is influenced by neuroendocrine actions on electrosensory and electromotor systems. Silva highlights the contributions of four iconic gymnotiform species that help explain how hormones regulate social behavior. The chapter details how steroid hormones have long-term effects on the kinetic properties of ion channels in electrocytes that can produce sexually dimorphic differences in EOD frequencies, whereas neuropeptides can have short-term effects on amplitude modulations of the EOD waveform. These changes in EOD properties are shown to be adaptive to environmental and social demands.

In Chap. 7, Krahe focuses on the ultimate evolutionary causes of EOD diversification in gymnotiforms and mormyroids, including ecological adaption, sexual selection, predation, and drift. Krahe provides an extensive review of the role of electric signaling in species diversification and how environmental and energetic constraints, ecological adaptations, predation, and sexual selection can be drivers of electric signal diversity.

Chapter 8 turns to active-sensing behavior. Stamper, Madhav, Cowan, and Fortune focus on the use of control theory to reveal functional relationships among active sensing, task-related behaviors, sensing, and motor control. Active sensing can be defined as the use of an animal's motor output to modulate the sensory information it receives. Stamper, Madhav, Cowan, and Fortune discuss a recently developed experimental system that uses artificially controlled feedback loops to perturb the natural reafferent feedback received by freely behaving animals to explore control strategies for active sensing in weakly electric fishes.

Then, in Chap. 9, Metzen and Chacron provide a comprehensive review on neural mechanisms utilized at different stages of sensory processing to extract behaviorally relevant information from stimulus envelopes and how stimulus envelope features can mediate behavior. The comparative focus of this chapter is on important parallels between the envelope-coding properties of the electrosensory system and other sensory systems, including how research on weakly electric fishes relates to fundamental insights into how envelopes are coded and processed by the mammalian auditory system. Metzen and Chacron also provide intriguing avenues for future research on envelope coding and processing.

In Chap.10, Carlson focuses on common themes and key differences in submillisecond temporal coding across electrosensory and auditory systems. The chapter highlights how comparative approaches can uncover shared fundamental mechanisms that have evolved convergently through natural selection to solve specific behavioral problems while at the same time revealing the ultimate causes for differences between systems. Carlson elaborates on how similar cellular and synaptic building blocks can be used to construct different circuit solutions to solve similar behavioral problems in different clades and how these differences may have arisen through some combination of chance, evolutionary history, and adaptation. As Carlson comments in Chap. 10, "these differences also make it clear that discoveries in one organism cannot be extrapolated to other organisms, highlighting the importance of comparative approaches in addressing general problems in neuroscience."

In Chap. 11, Perks and Sawtell provide a review of the substantial body of research that has elucidated the synaptic, cellular, and circuit mechanisms by which the electrosensory system of mormyrid fishes predicts and cancels self-generated and predictable sensory inputs. Additional functions of motor corollary discharge signals in weakly electric mormyrids fishes are explored and discussed. In the chapter, Perks and Sawtell address how motor systems and behavior can influence the electrosensory processing of reafferent sensory input, with implications for this research providing insight into other sensory systems and brain structures, including the mammalian auditory system and the cerebellum.

The final chapter provides an overview of the emerging research on spatial learning in weakly electric fish. In Chap. 12, Jung and Engelmann provide a summary of the mechanisms that can provide spatial information during active electrolocation and discuss how the complex dynamics of sensorimotor behaviors can enable weakly electric fishes to actively generate sensory flow. Jung and Engelmann also provide a summary of spatial learning mechanisms in nonelectric and weakly electric teleost fishes. They also discuss the neural mechanisms by which active electrolocation can provide spatial information and its neural basis in the dorsal telencephalon. The authors conclude that comparative approaches using the sensory specialties of the active electrosensory system in weakly electric fishes may ultimately provide novel insights into the relationship between spatial cognition and forebrain networks in other animals, including mammals.

1.7 Future Directions and Concluding Comments

Historically, neuroscientists have used a variety of approaches and a large diversity of animal taxa to gain insight into brain function and the neural basis of behavior (Carlson 2012). Neuroethologists often selected eclectic research organisms because they were uniquely suited to studying the neural basis of specific behaviors, which often led to fundamental insights into general neural mechanisms for behavior across species. Following the molecular revolution, neuroscience research became increasingly focused on a handful of inbred, genetically tractable laboratory species. This work has undoubtedly led to numerous important insights, but the generalizability of many of the resulting discoveries remains unknown. This is a problem for both better understanding human brains and seeking general, fundamental theories of brain function. There is, however, reason to think that neuroscience may soon experience a renewed appreciation of the importance of species diversity (Brenowitz and Zakon 2015; Yartsev 2017). Experimental tools that can be applied across species are rapidly expanding, from transgenic manipulations to large-scale neural ensemble recordings in freely behaving animals. Applying these techniques in a diversity of species carefully chosen with regard to phylogenetic position, behavior, genomics resources, practicality, and accessibility offer the best chance of elucidating fundamental theories of brain function (Striedter et al. 2014). This volume was assembled in this spirit.

Acknowledgments This work was supported by Grants IOS-1050701, IOS-1255396, and IOS-1755071 to Bruce A. Carlson and Grant IOS-1456700 to Joseph A. Sisneros from the National Science Foundation.

Compliance with Ethics Requirements Bruce A. Carlson declares that he has no conflict of interest.

Joseph A. Sisneros declares that he has no conflict of interest.

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