

A Neuroethology of Electrocommunication: Senders, Receivers, and Everything In Between

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ABSTRACT

The neuroethological approach to studying the nervous system emphasizes the natural behavior of organisms and the environments in which they live. By focusing on model organisms that are exceptionally skilled at certain behavioral tasks or those that lend themselves to asking specific questions, neuroethologists have paved the way for the development of a number of basic principles in the operation of nervous systems. The neural basis of animal communication behavior is one area that has received a great deal of attention from neuroethologists, who have studied in detail both how communication signals are generated by motor systems and how they are analyzed by sensory systems. Weakly electric fish have served as a particularly rich source of insight into this subject. In this chapter, I will review our current knowledge of the neural basis of electrocommunication behavior in weakly electric fish, paying particular attention to the generalities of the concepts discussed and their applicability to a basic understanding of nervous system function.

Key Words: Central pattern generator; Combination—sensitive neuron, command neuron; Corollary discharge; Electric organ discharge; Electromotor; Electoreceptor; Electrosensory; Neuroethology; Pacemaker; Recurrent inhibition; Temporal coding.

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1. INTRODUCTION—THE NEUROETHOLOGICAL APPROACH

Neuroethology emphasizes the importance of understanding the natural behavior of an organism and its evolutionary history in addressing fundamental questions about nervous system function (Hoyle, 1984). Nervous systems have evolved to produce behavior, to process biologically relevant stimuli and respond in ways that enhance survival and reproduction. For the neuroethologist, a full understanding of nervous system function requires an appreciation of what the nervous system has been designed to do. Thus, in addition to asking general questions about neural structure and function, the neuroethologist also questions how an animal's nervous system produces a specific behavior that is part of its natural repertoire. This approach has yielded major insights into basic principles of nervous system organization and function through studies in a diverse, eclectic array of species chosen for their unique behavioral specializations (Marder, 2002).

Animal communication has always been an area of special interest to neuroethologists (Marler, 1992). Communication clearly serves an integral role in animal behavior. It is the means by which individuals share information (Otte, 1974), and therefore lays the foundation for every facet of social behavior. At the same time, a given signal is by necessity limited in its variability so that it may accurately transmit the information it represents (Barlow, 1977). This high degree of stereotypy is of great advantage to the neuroethologist. Firstly, the neural circuits involved are highly specialized, making it relatively straightforward to address basic mechanistic questions. Secondly, the signals can be easily quantified, categorized, reproduced, and manipulated, a crucial factor in dissecting the neural basis of a behavior.

Weakly electric fish are exemplary in this respect. Although their social behavior incorporates elaborate electrical displays, the structure of electric signals is relatively simple compared to other modalities. With reduced signal complexity comes reduced complexity in the neural circuits involved, making the study of their inner workings a much more tractable endeavor. The basic building blocks of these circuits are, however, shared across all animals. Increasing degrees of complexity are associated with greater and more intricate interactions among these building blocks, but not with any change in their fundamental properties (Heiligenberg, 1991). Research on electric fish has therefore facilitated the development of many general principles in neurobiology (Bullock, 1986; Zakon, 2003).

On the other hand, the very uniqueness of electric signaling has made its study instructive towards general issues in neurobiology. Electric fish epitomize the concept of 'champion' species whose nervous systems are highly specialized for specific tasks such as time coding, expectation generation, sensorimotor integration, and motor coordination, making them excellent

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signaling has made it easy. Electric fish epitomize these systems are highly expectation generation, making them excellent

model systems for understanding how nervous systems accomplish those tasks (Heiligenberg, 1991). Furthermore, electric communication appears to have evolved independently in different groups of fish (Bullock et al., 1983). Their electrosensory and electromotor systems have therefore developed under separate, parallel evolutionary trajectories. The existence of numerous similarities between these different systems underscores the many links between neural structure and function that have been described for these fish, and provides fertile ground for understanding the adaptive evolution of vertebrate nervous systems (Hopkins, 1995).

2. ELECTRICITY AS A CARRIER OF INFORMATION

Central to any neuroethological dissection of communication behavior is a description of the signals themselves. In this section, I will briefly describe the types of electric signals used and their general functions. For more detailed discussions of electric communication behavior, the reader is referred to Chapters 24 and 25 of this volume.

It is important to make a distinction between the two types of electric organ discharges, or EODs. While 'pulse' species produce discrete EODs separated by silent intervals, in 'wave' species the interval between each EOD is approximately equal to the duration of a single EOD, resulting in a continuous quasi-sinusoidal signal. Representatives of both types are found in the two main groups of electric fish. Among mormyriids, all species of the family Mormyridae produce pulse-type EODs, while the monotypic *Gymnarchus niloticus* produces a wave-type EOD. Among gymnotiforms there are several representatives of both groups: the Sternopygidae, Eigenmanniidae, and Aptereronotidae produce wave-type EODs, while the Gymnotidae, Electrophoridae, Hypopomidae, and Rhamphichthyidae produce pulse-type EODs (see Chapters 22 and 25 of this volume).

2.1 Sender Recognition: EOD Waveform and Frequency

In pulse-type fish, species recognition appears to be mediated by the EOD waveform (Hopkins and Bass, 1981; Hopkins and Westby, 1986), which demonstrates incredible species-specific diversity (Hopkins, 1981; Hopkins and Westby, 1986). In mormyriids, EOD duration may vary from less than 100 μ s in *Petrocephalus* to greater than 10 ms in *Paramormyroops gabonensis* (Fig. 27.1). EODs may also vary in polarity, the number of head-positive and head-negative peaks (phases), and in the overall shape. In gymnotiform wave-type fish, species recognition appears to be mediated by EOD frequency (Hopkins, 1976), which varies from as low as 50 Hz in *Sternopygus* to over 1000 Hz in *Aptereronotus* (Hopkins, 1974a).

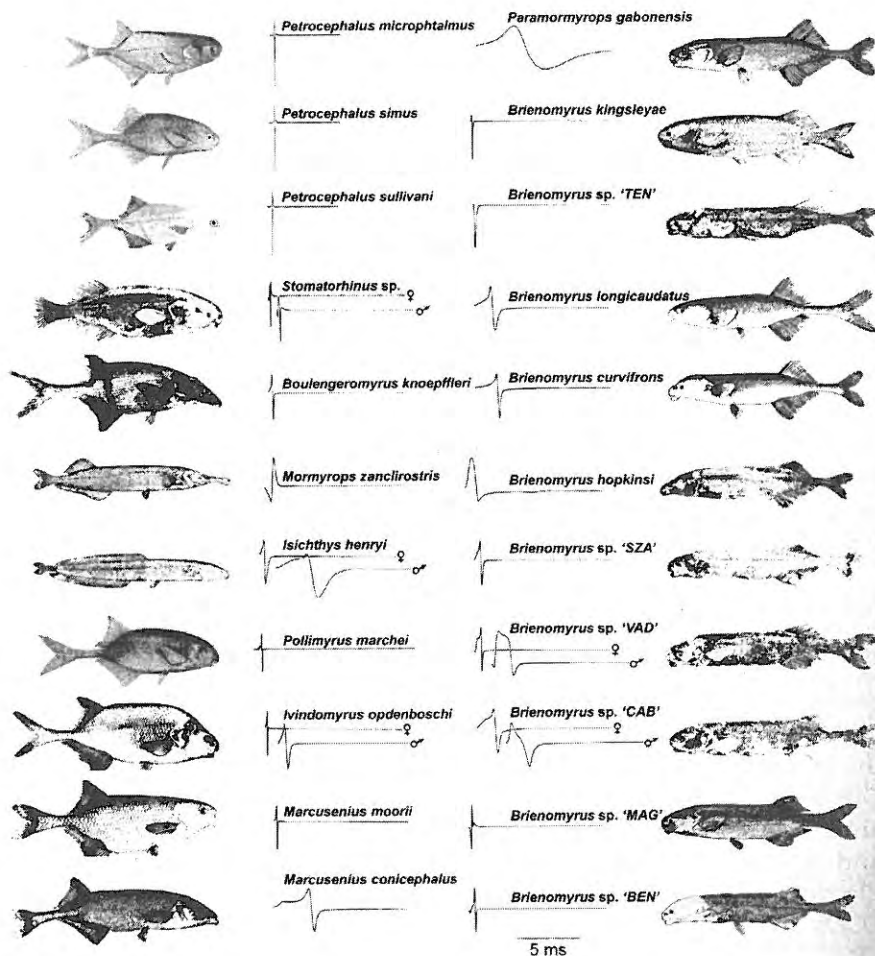
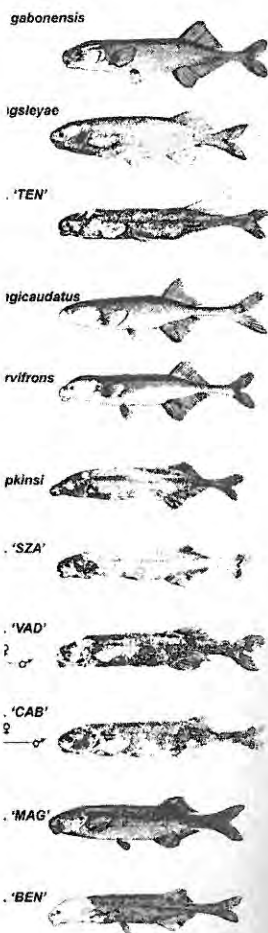


Fig. 27.1: The mormyrids of the Ivindo River, Gabon, along with their EODs. Several species in the genus *Brienomyrus* are not yet formally described, and are identified by three-letter codes after Sullivan et al. (2002). Modified after Hopkins (1986a, 1999). Line drawings and EODs from the three species of *Petrocephalus* kindly provided by S. Lavoué.

In addition to species-specific differences, EODs may vary according to the sex, dominance status, and even individual identity of the sender. Among pulse-type species, reproductively active males typically have elongated EODs, and among mormyrids, some species also exhibit sex-specific EOD waveforms (Hopkins, 1981; Westby, 1988). In the mormyrid *Brienomyrus brachyistius* and the gymnotiform *Brachyhypopomus occidentalis*, dominant males have longer, more 'male-like' EODs compared to subordinates (Hagedorn and Zelick, 1989;



their EODs. Several species identified by three-letter codes in the drawings and EODs from

may vary according to the sex of the sender. Among wave-type species, some have elongated EODs, and specific EOD waveforms. In *Mormyrus brachyistius* and *M. punctatus*, dominant males have longer EODs (Hagedorn and Zelick, 1989;

Carlson et al., 2000). In several species of wave-type gymnotiform, EOD frequency similarly exhibits sex- and dominance-related differences. In most species, reproductively active males have lower EOD frequencies than females; dominant males have the lowest frequencies, and dominant females have the highest (Hopkins, 1972; Hagedorn and Heiligenberg, 1985; Zakon and Dunlap, 1999).

2.2 Social Displays: Frequency Modulations and Temporal Patterning of the EOD

Mormyrid and gymnotiform fish employ the electric modality to produce a rich repertoire of signals in various social contexts. In wave-type species, such displays comprise modulations in the baseline frequency. Some gymnotiform species use sudden, dramatic frequency increases termed 'chirps' during aggression and courtship (Hopkins, 1974b; Hagedorn and Heiligenberg, 1985). Additional frequency modulations include gradual frequency rises, frequency falls, frequency warbles with complex increases and decreases in frequency, and discharge cessations, all of which play an important role in social behavior (Hopkins, 1974a, b; Hagedorn and Heiligenberg, 1985; Engler et al., 2000; Tallarovic and Zakon, 2002; Zakon et al., 2002). Similar displays have been described for the mormyrid *Gymnarchus niloticus* (Hopkins, 1977).

In pulse-type fish, the temporal patterning of EOD production, or the sequence of pulse intervals (SPI), plays an important role in social behavior. In pulse-type gymnotiforms, average intervals are typically around 10 to 100 ms, depending on the species (Hopkins and Westby, 1986). The resting SPI is highly regular, with coefficients of variation (CV) generally less than 0.05. Similar to wave-type gymnotiforms, pulse-type species produce a variety of displays involving modulations in the baseline firing rate including chirps, accelerations and decelerations, and discharge interruptions (Black-Cleworth, 1970; Westby, 1975).

In mormyrids, the SPI is much more irregular, with intervals typically ranging over hundreds of milliseconds at rest (Moller, 1970; Hopkins, 1986a; Carlson, 2002a). A variety of displays involving different patterns of EOD production have been described, including regularizations, accelerations, pulse pairs, interruptions, and bursts (Hopkins, 1986a; Carlson, 2002a). Certain types of bursts are characterized by highly stereotyped temporal patterns of EOD production, including 'rasps', which function in courtship and mating, and 'scallop', which appear to serve as advertisement signals in dominant fish (Hopkins and Bass, 1981; Serrier and Moller, 1989; Carlson and Hopkins, 2004a).

3. ELECTROMOTOR SYSTEMS—ORGANIZATION AND GENERATION OF ELECTRIC SIGNALS

3.1 General Organization of Electromotor Networks

The electromotor networks of gymnotiforms and mormyriforms share a number of basic organizational features (Fig. 27.2). Each EOD results from the activation of a specialized electric organ, the morphophysiological properties of which determine the EOD waveform (Bass, 1986). The frequency or rhythm of EOD production is established by the patterning of electric organ activation which is governed by a group of neurons in the medulla (Dye and Meyer, 1986).

These neurons receive inputs from several groups of neurons that influence EOD production. In gymnotiforms and mormyriids, three anatomically distinct inputs have been described (Heiligenberg et al., 1981; Metzner, 1993; Carlson, 2002b). The electromotor system of *Gymnarchus* has not been as thoroughly studied, but a single input has been identified (M. Kawasaki, pers. comm.). Apart from this basic theme, the mormyrid electromotor network is unique in having a feedback pathway by which the command to produce an EOD is relayed back to certain precommand centers that themselves regulate the generation of this command signal (Carlson, 2002b). As we shall see, this recurrent projection plays an important role in the temporal patterning of EOD production.

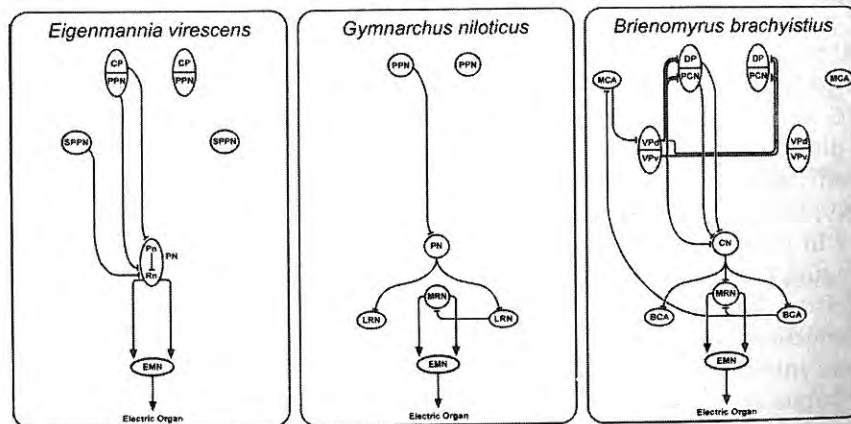


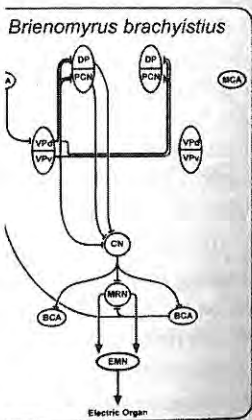
Fig. 27.2: Neuroanatomy of the electromotor control networks in the gymnotiform *Eigenmannia virescens* and the mormyriforms *Gymnarchus niloticus* and *Brienomyrus brachyistius*. BCA, bulbar command-associated nucleus; CN, command nucleus; CP, centroposterior nucleus; DP, dorsal posterior nucleus; EMN, electromotor neurons; LRN, lateral relay nucleus; MCA, mesencephalic command-associated nucleus; MRN, medial relay nucleus; PCN, precommand nucleus; PN, pacemaker nucleus; Pn, pacemaker neurons; PPN, prepacemaker nucleus; Rn, relay neurons; SPPN, sublemniscal prepacemaker nucleus; VPd, dorsal subdivision of the ventroposterior nucleus; VPv, ventral subdivision of the ventroposterior nucleus.

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mormyrids share a common EOD results from the physiological properties of the frequency or rhythm of electric organ activation (Dye and Meyer,

neurons that influence the anatomically distinct (Metzner, 1993; Carlson, 1994; not been as thoroughly investigated (Sawasaki, pers. comm.). The neural network is unique in that it produces an EOD is self-regulating. As we shall see, this neural patterning of EOD



the gymnotiform *Eigenmannia* *brachyistius*. BCA, bulbar posterior nucleus; DP, dorsal posterior nucleus; MCA, mesencephalic command nucleus; PN, precommand nucleus; Rn, relay nucleus; EMN, electromotor nucleus; EOD, electric organ discharge.

3.2 Electric Organs

With the exception of the apteronotids, electric organs are composed of a large number of highly modified muscle cells termed electrocytes that are arranged both in series and parallel, enclosed within a sheath of connective tissue. Each electrocyte generates an electrical potential of about 80 to 150 mV. When activated in synchrony by simultaneous input from spinal electromotor neurons (EMN), their resulting potentials summate to produce an EOD, which in weakly electric fish is typically on the order of a few volts. For detailed discussions of electric organs, the reader is referred to Bennett (1971), Bass (1986) and Caputi et al. (2005).

3.2.1 Structural Basis for EOD Waveform Diversity

In mormyrids, the electric organ is relatively short and restricted to the caudal peduncle, consisting of two columns of serially stacked electrocytes on either side of the spinal cord (Fig. 27.3a). The electrocytes are a homogenous population of thin, multinucleated discs oriented perpendicular to the longitudinal body axis. A series of stalks arise from the posterior or anterior face of each electrocyte and fuse to form a single large stalk that receives innervation from spinal electromotor neurons (Fig. 27.3b). Because of their homogeneity, the electrical potential recorded from a single activated

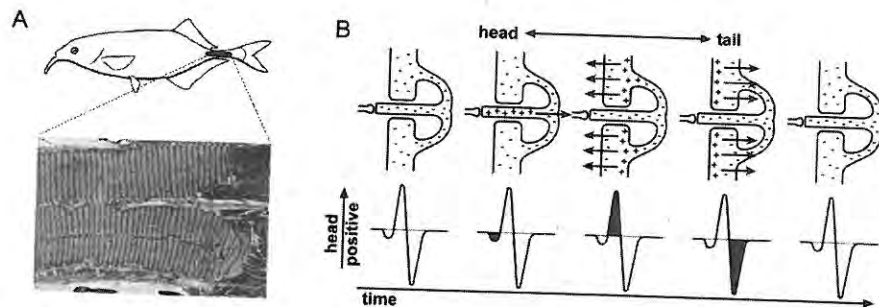


Fig. 27.3: The electric organ and EOD generation in mormyrids. (A) The electric organ is located in the caudal peduncle and consists of two columns of serially stacked electrocytes on either side of the spinal cord. Photomicrograph kindly provided by C.D. Hopkins. (B) The top row shows a schematic diagram of an electrocyte and the distribution of electrical potential over the duration of a single EOD. The bottom row shows the EOD resulting from the summated activity of all electrocytes, with the phase resulting from the corresponding electrocyte activity shown in black. At rest, each electrocyte has a negative resting potential. With the arrival of an action potential at the synapse between an electromotor neuron and stalk, the stalk becomes depolarized, leading to current flow in a head-to-tail direction and an initial head-negative EOD phase. This current then activates the posterior face of the electrocyte, leading to current flow in a tail-to-head direction, and a second, head-positive phase. This current then activates the anterior face of the electrocyte, leading to current flow in a head-to-tail direction and a final head-negative phase.

electrocyte exactly matches the EOD waveform on a miniature scale (Bennett and Grundfest, 1961).

Figure 27.3b provides an illustrative example of how the EOD waveform relates to electrocyte morphology for *Gnathonemus petersii*, which produces a triphasic EOD. In this species, the stalks arise from the posterior face, then reverse course and penetrate the electrocyte to receive anterior innervation. At rest, the electrocyte has a negative resting potential. Upon the arrival of a descending electromotor command, the stalk depolarizes, resulting in current flow in a head-to-tail direction, and a head-negative potential. As this depolarization traverses the length of the stalk, an action potential is generated by the posterior face of the electrocyte. This reverses the flow of current, leading to a head-positive potential. This current flow depolarizes the anterior face, which itself generates another action potential. This again reverses the flow of current, leading to a head-negative potential that completes the triphasic EOD waveform.

Across species, there is wide diversity in the morphology of the stalk system (Hopkins, 1999). Innervation may be on the posterior or anterior side, the stalks may or may not penetrate the electrocyte, and if they do, they may penetrate it once or twice. Based on these differences, five distinct forms have been recognized (Fig. 27.4): (1) non-penetrating, posterior innervation (NPp); (2) penetrating, anterior innervation (Pa); (3) penetrating, posterior innervation (Pp); (4) doubly penetrating and non-penetrating (DPNP); and (5) doubly penetrating, posterior innervation (DPp). By extension of the EOD waveform generation model shown in Fig. 27.3b, the morphological type is perfectly predictive of the polarity and number of phases in the EOD waveform (Fig. 27.4). Species differences in the duration of the EOD are also related to

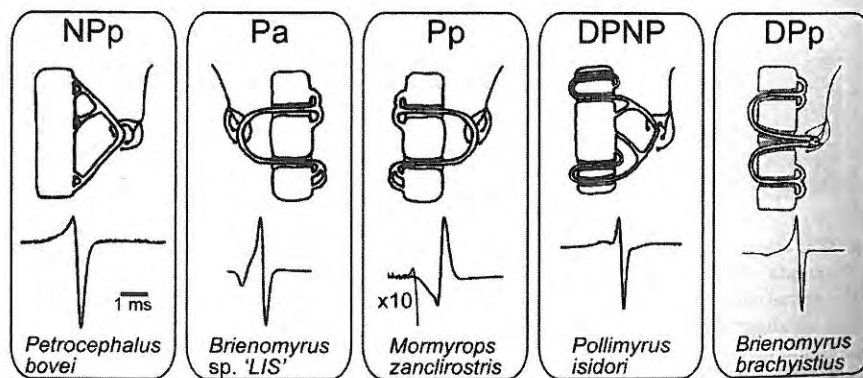
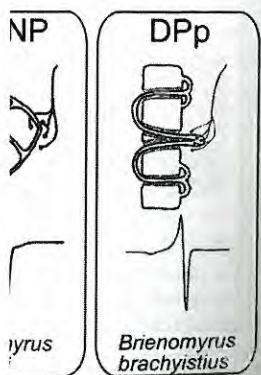


Fig. 27.4: Anatomical basis of EOD diversity among mormyrids. Schematic representations of the five known morphological types of electrocyte are shown, along with EODs from five different species that exemplify the different patterns. NPp, non-penetrating, posterior innervation; Pa, penetrating, anterior innervation; Pp, penetrating, posterior innervation; DPNP, doubly penetrating and non-penetrating; DPp, doubly penetrating, posterior innervation. Modified after Hopkins (1999).

miniature scale (Bennett

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Schematic representations of EODs from five different species: (1) posterior innervation; (2) anterior innervation; (3) doubly posterior innervation; (4) doubly anterior innervation. Modified after

electrocyte morphology. Species with longer EODs have thicker electrocytes and greater invaginations of the anterior face (Bass et al., 1986). Presumably, these features increase electrocyte membrane capacitance, which increases the time constant and prolongs the EOD.

The electric organ of *Gymnarchus* also consists of four serially stacked columns of electrocytes, although it extends further into the body cavity from the tail, to about midway along the body axis. The electrocytes are similar to those of mormyrids, although they are somewhat more cylindrical and lack a stalk system. They are innervated on the posterior face, which generates action potentials. The anterior face does not generate action potentials; the biphasic EOD results from the action potential of the posterior face followed by an electrical resonance response of the anterior face (Bennett, 1971). This resonance appears to result from the highly convoluted structure of the anterior face, which gives rise to a large capacitance.

The morphology of gymnotiform electrocytes is quite different from that of mormyrids. Rather than a flattened disc, the electrocytes are long, tubular cells oriented in a longitudinal direction (Bass, 1986). Accordingly, the biphasic EOD of the wave-type species *Sternopygus* and *Eigenmannia* are generated in a different fashion from *Gymnarchus*. Again, only the posterior face generates action potentials, but in this case there is no resonance response of the anterior face. Instead, the action potentials are superimposed on a head-negative baseline, which results in a biphasic EOD with no DC component. The electric organ consists of several columns of these cells, and traverses the entire length of the body trunk. In the apteronotids, the other family of wave-type gymnotiforms, the electric organ exhibits a remarkable distinction: specialized electrocytes are completely lacking. Instead, the electric organ is composed of the axons of spinal electromotor neurons (Waxman et al., 1972). This eliminates a synaptic transmission step, which is likely an adaptation for generating the highest EOD frequencies known (over 1000 Hz). The axons first head in the anterior direction, and then reverse course and head in the posterior direction. Thus, action potentials traveling down the axon give rise to a biphasic EOD.

In general, the electric organs of pulse-type gymnotiforms show the greatest degree of complexity (Caputi, 1999). Similar to wave-type gymnotiforms, the electric organ extends the entire length of the trunk. The electrocytes vary from cylindrical to drum shaped. Both the anterior and posterior faces may be electrically active, and each face may receive separate innervation. In addition, the electrocytes are often not homogenous: they may differ in these characteristics with respect to their position within the electric organ. These features create not only a high degree of temporal complexity in the EOD of many pulse-type gymnotiforms, but also a great degree of spatial variation (Assad et al., 1999). Figure 27.5 illustrates how this variability may contribute to spatiotemporal complexity and species-specificity in the EOD waveform for three species of pulse-type gymnotiform. Some pulse-type gymnotiform species also have accessory electric organs located either in the

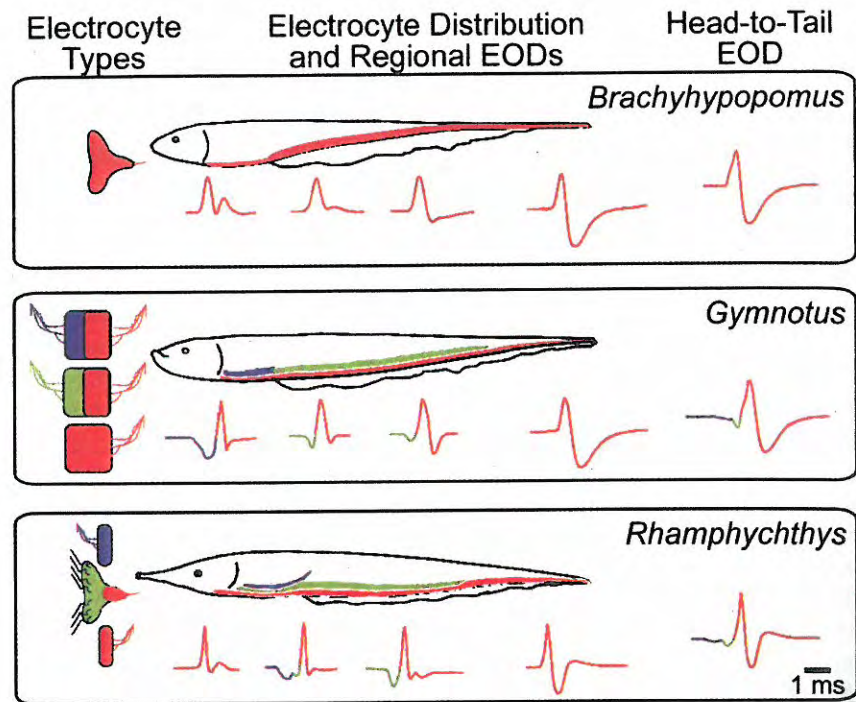


Fig. 27.5: EOD generation in three different pulse-type gymnotiform species, illustrating the diversity of electrocyte morphology and innervation both within the electric organs of a single individual and between species, and how it relates to spatial variation in EOD waveform along the length of the electric organ and species-specificity in the overall head-to-tail EOD. The different electrocyte types and their innervation are shown in the left column. In the middle column, a schematic diagram of each fish illustrates the distribution of the different electrocyte types, along with a recording of the regional EOD recorded at different points along the body surface. The right column shows the overall head-to-tail EOD recorded at a distance from the fish. Modified after Caputi et al. (2005).

chin region or just behind the operculum (Bennett, 1971). These typically fire just before the main electric organ, which results in further spatiotemporal complexity in the EOD waveform.

3.2.2 Hormonal Control of EOD Waveform Variation

In addition to species-specificity, the EOD frequently shows a high degree of intraspecific variation, in the form of both sex and individual differences. In mormyrids, the EOD of males typically elongates at the onset of the breeding season, a phenomenon that can be induced in females, juveniles, and non-reproductive males by administering androgen hormones such as testosterone (Bass and Hopkins, 1983). Many pulse-type gymnotiform species have a sex

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EOD*Brachyhypopomus**Gymnotus**Rhamphichthys*

iform species, illustrating the the electric organs of a single ation in EOD waveform along head-to-tail EOD. The different umn. In the middle column, a fferent electrocyte types, along s along the body surface. The stance from the fish. Modified

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difference in the same direction, and androgens are likewise responsible for this difference (Hagedorn and Carr, 1985).

In most wave-type gymnotiforms, the males have a longer EOD duration and a lower EOD frequency than females. In these species, androgen treatment induces an increase in EOD duration and a decrease in EOD frequency, dual effects that are necessary for maintaining a quasi-sinusoidal waveform (Zakon et al., 1991). Although coordinated, these two effects appear to be mediated independently by hormonal actions on both the electric organ and central electromotor control neurons (Few and Zakon, 2001). Interestingly, in one wave-type gymnotiform species, *Apteronotus leptorhynchus*, the sexual difference is reversed: males have a shorter EOD duration and a higher EOD frequency than females. Consequently, androgen treatment has the opposite effect in this species (Zakon and Dunlap, 1999).

For most species, the female-typical EOD appears to be the default, and androgens serve an activational role in establishing a male-specific EOD. In the wave-type gymnotiform *Sternopygus*, however, both male and female EODs differ from those of juveniles, which tend to have intermediate EOD frequencies. Accordingly, both androgens and estrogens have activational effects on the EOD: androgens induce a longer waveform and lower frequency, while estrogens induce a shorter waveform and higher frequency (Meyer, 1983).

In pulse-type fish from both groups, androgen treatment leads to an increase in electrocyte size and membrane surface area (Bass et al., 1986). By way of their effects on membrane capacitance, these changes appear to play an important role in elongating the EOD by increasing the action potential duration of single electrocytes (Hagedorn and Carr, 1985; Bass and Volman, 1987). In wave-type gymnotiforms, hormone-induced changes in EOD duration are mediated by modifications in the kinetics of voltage-dependent ion channels in the electrocyte membrane, a topic that has been extensively studied at the cellular level in *Sternopygus* (Ferrari et al., 1995; McAnelly and Zakon, 2000).

Several species have been known to exhibit dominance-related differences in the EOD. In males of the mormyrid *Brienomyrus brachyistius*, this variation is associated with differences in circulating androgen levels: dominant males have longer EODs and higher androgen levels than subordinates (Carlson et al., 2000). Similarly, EOD frequency in males of the wave-type gymnotiform *Apteronotus leptorhynchus* is correlated with relative status and circulating androgen levels (Dunlap, 2002). Thus, steroid hormones may also play a role in individual EOD variation.

3.3 Central Control of EOD Generation

In all mormyriiform and gymnotiform fish, EOD production is controlled by a group of neurons located on the ventral midline of the medulla, which all fire in synchrony, in a 1:1 fashion with each EOD (Fig. 27.6) (Dye and Meyer, 1986).

In gymnotiforms and *Gymnarchus*, they are referred to as pacemaker neurons, as they possess endogenous oscillatory mechanisms that cause them to continuously fire at the fish's EOD frequency (Fig. 27.6c) (Smith and Zakon, 2000). These pacemakers achieve a level of precision unmatched by any known biological oscillators (Moortgat et al., 1998). In mormyrids, which produce EODs with much less regularity, the neurons that control EOD production do not possess any endogenous oscillatory properties (Grant et al., 1986; Carlson, 2002a). Instead, they serve to integrate multiple descending inputs that influence the timing of each EOD pulse, and they are therefore referred to as command neurons (Fig. 27.6d).

The existence of a group of neurons that together function as a behavioral decision center illustrates the 'command neuron concept' (Kupfermann and Weiss, 1978), which defines a command neuron as one which is both necessary and sufficient for driving a behavior. In the case of electric fish, this concept has been expanded to include a group of neurons working in synchrony to drive a behavior. Corollaries of this concept include 'command elements' that may elicit a distinct component of a more complex behavior, or 'modulatory elements' that may alter the behavior produced, such as precommand/prepacemaker nuclei in electric fish (see Sect. 3.4).

The pacemaker and command neurons do not project directly down the spinal cord. Instead, their output is relayed through adjacent midline neurons that project down the spinal cord and drive the electromotor neurons (Figs. 27.2, 27.6e, f) (Dye and Meyer, 1986). In gymnotiforms, these relay neurons receive direct input from the pacemaker neurons. In mormyrids, an additional group of bilateral relay neurons receive input from the command/pacemaker neurons and project to the medial relay neurons. In *Gymnarchus*, this indirect pathway provides the only input to the medial relay neurons (Kawasaki, 1994), while mormyrids have both a direct and indirect projection from the command neurons to medial relay neurons (Bell et al., 1983).

3.3.1 Structure and Function in the Central Control of EOD Production

The medullary-spinal electromotor pathways of gymnotiforms and mormyrids possess a number of convergent anatomical specializations for signaling in the electric modality (Dye and Meyer, 1986). These adaptations relate to the need for maintaining a high degree of synchrony in the firing of neurons within the pathway. In pulse-type fish, synchronous activation of the electrocytes is critical for maintaining a constant EOD waveform, while in wave-type fish, synchrony between neurons serves to maximize the regularity of EOD frequency by coupling multiple individual oscillator neurons. This need for synchrony is reflected in the fact that pacemaker/command and relay neurons are located in unpaired midline structures, which is in stark contrast to the majority of nuclei in the brain that form distinct, bilateral populations of neurons. Presumably, the greater proximity between neurons reduces axonal

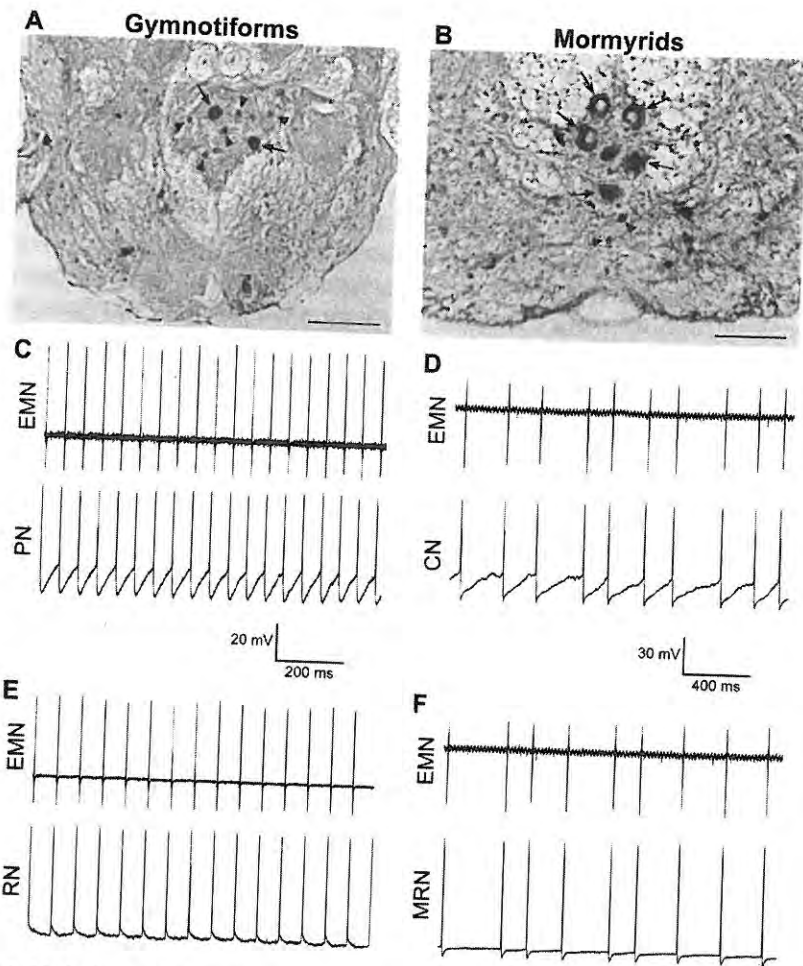


Fig. 27.6: Medullary electromotor neurons in gymnotiforms and mormyrids. (A) Transverse section through the hindbrain of the gymnotiform *Eigenmannia virescens*, visualized with Bodian staining. The pacemaker nucleus contains both pacemaker (arrowheads) and relay neurons (arrows). (B) Transverse section through the hindbrain of the mormyrid *Brienomyrus niger*, visualized with Bodian staining. Command neurons (arrowheads) are in a separate nucleus located ventral to the medial relay neurons (arrows). (C) Intracellular recording from a pacemaker neuron (PN) in relation to electromotor neuron (EMN) activity in the pulse-type gymnotiform *Brachyhyopomus occidentalis*. Note the regular sub-threshold oscillations that give rise to a highly regular EOD frequency. (D) Intracellular recording from a command neuron (CN) in relation to EMN activity in the mormyrid *Brienomyrus brachyistius*. Note the sub-threshold postsynaptic activity and irregular pattern of activation. (E) Intracellular recording from a relay neuron (RN) in relation to EMN activity in the pulse-type gymnotiform *Brachyhyopomus occidentalis*. Note the sudden onset of action potentials from a flat baseline. (F) Intracellular recording from a medial relay neuron (MRN) in relation to EMN activity in the mormyrid *Brienomyrus brachyistius*. Note the sudden onset of action potentials from a flat baseline. Scale bars in (A) and (B) are 100 μm . Data for (C) and (E) kindly provided by M. Kawasaki.

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conduction delays that may add variability to action potential arrival times (Bennett, 1968).

Electromotor pathways are also characterized by extensive electrical coupling, both between neurons within each level of the EOD command chain (horizontal coupling), as well as between neurons at different levels of the pathway (Bennett et al., 1967a, b). Because of the different functions served by synchrony, horizontal coupling is greatest among pacemaker neurons in wave-type fish, while it is greatest among those elements downstream from the command/pacemaker neurons in pulse-type fish. As another adaptation to generating high frequency EODs, the apteronotid pathway is characterized by the greatest degree of electrical coupling known. While synapses in the EOD command chain of other electric fish are generally mixed chemical and electrical, those of the apteronotids are purely electrical, which entirely avoids the problem of delays caused by chemical transmission.

One interesting parallel between mormyriforms and gymnotiforms is the existence of multiple electromotor levels in the medulla, rather than a direct projection from command/pacemaker neurons to spinal electromotor neurons (Caputi et al., 2005). Compared to the command/pacemaker neurons, the relay neurons are about twice as large, with correspondingly thick axons (Fig. 27.6a, b). This large size of the axons minimizes conduction times down the spinal cord and maximizes the effectiveness of electromotor neuron activation. As soma size increases, however, input resistance decreases, and it takes large amounts of current to alter the membrane potential and modulate EOD output. As a solution, the command center has been placed one level upstream in smaller neurons, where descending inputs do not need to overcome such high input resistance. Synchronous input from these command/pacemaker neurons easily provides sufficient current to drive the large relay neurons.

Even with these adaptations in place, there remains a crucial problem in achieving synchronous excitation of the electrocytes. The rostral end of the electric organ is closer to the brain than the caudal end, and action potential propagation occurs at a finite conduction velocity. Thus, if all were equal, descending EOD commands would arrive earlier at the rostral end and the electrocytes would not be activated in synchrony. In order to maintain synchrony, compensatory mechanisms have evolved to delay the activation of rostral segments. Such adaptations include smaller diameter axons and stalks to reduce conduction velocity and recurrent axonal loops (delay lines) so as to increase the path length (Bennett, 1968).

Differences in electromotor structure can also be informative of a functional link with signaling behavior. For example, there is considerable variation in the proximity between pacemaker and relay neurons in gymnotiforms (Dye and Meyer, 1986). In pulse-type species, they form relatively distinct subnuclei within the pacemaker nucleus (PN). In wave-type species, however, the two are intermingled. *Sternopygus*, a wave-type species with a relatively low EOD frequency, shows an intermediate form with partial segregation. Thus, the

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proximity of the two cell types increases with increasing EOD rate, presumably an adaptation to enhance the speed and strength of transmission between them. In all mormyriiforms that have been studied, the two cell types are located in distinct nuclei, the command/pacemaker nucleus (CN/PN) and medial relay nucleus (MRN).

A similar distinction is seen in the relative numbers of pacemaker/command and relay neurons (Dye and Meyer, 1986). In the wave-type apteronotids, which produce the highest EOD rates known, the ratio of pacemaker to relay neurons is about 4:1. In the wave-type species *Eigenmannia* and *Gymnarchus*, which have lower EOD rates, this ratio is about 2:1. In pulse-type gymnotiforms and mormyrids, this ratio is at or below 1:1. Thus, the relative number of command/pacemaker neurons increases with increasing EOD rates, which may represent an adaptation for greater pacemaker precision with increasing EOD frequency.

3.3.2 The Corollary Discharge

The mormyrid electromotor system is characterized by a unique feature: the EOD command issued by the CN not only descends the spinal cord to drive electromotor neurons, but also ascends the brain to project to additional regions (Bell et al., 1983). This ascending projection originates in the bilateral relay neurons, referred to as the bulbar command-associated nucleus (BCA), and ultimately gives rise to pathways that project to electrosensory regions as well as electromotor regions that influence the command nucleus (Bell and von der Emde, 1995; Bell et al., 1995; Carlson, 2002b). Because it provides the electrosensory and electromotor systems with a precise reference of the timing of EOD production, it is referred to as the electric organ corollary discharge pathway, and it plays an important role in electric communication. We will return to this issue in more detail in later sections on the electromotor (3.4.1) and electrosensory systems (5.3).

3.4 Precommand Regulation of EOD Output

The patterning of EOD production is not rigidly fixed by the activity of the command/pacemaker neurons, but can be modulated extensively by descending inputs to these neurons (Fig. 27.2). In both gymnotiforms and mormyrids, specific regions of the dorsal thalamus have been co-opted to serve the electromotor system. Specifically, the central posterior nucleus (CP) in gymnotiforms and the dorsal posterior nucleus (DP) in mormyrids provide a strong projection to the PN/CN (Zupanc and Maler, 1997; Carlson, 2002b). In both fish groups, a second group of neurons exists as a ventrolateral extension of the dorsal thalamic neurons, referred to as prepacemaker neurons (PPN) in gymnotiforms and precommand neurons (PCN) in mormyrids. The CP/PPN and DP/PCN complexes exhibit remarkable parallels in their anatomy and morphology, suggesting further convergence in the substrates for electromotor

control (Carlson, 2002b). Prepacemaker inputs in *Gymnarchus* have not been thoroughly explored, but a group of prepacemaker neurons (PPN) in a position similar to the DP/PCN and CP/PPN have been found (M. Kawasaki, pers. comm.).

In both gymnotiforms and mormyrids, an additional input to the pacemaker/command nucleus has been described. In mormyrids, a small group of large neurons at the ventral edge of the ventroposterior nucleus (VPv) in the torus semicircularis projects to CN, as well as to DP/PCN. In gymnotiforms, a small group of neurons located just below the lateral lemniscus (sublemniscal prepacemaker nucleus, or SPPN) projects to PN.

3.4.1 *A Recurrent Inhibitory Network for Temporal Pattern Generation*

Although the patterning of EOD production in mormyrids is irregular compared to other electric fish, the majority of EOD intervals fall within a limited range (about 100 to 300 ms, depending on the species). Thus, rhythmicity is an intrinsic property of electromotor output in mormyrids (Teyss  dre and Boudinot, 1987); the precision is simply not as great. Unlike the central pattern generators (CPGs) of other electric fish that generate rhythm through endogenous cellular properties (pacemakers), the mormyrid electromotor CPG generates rhythm through network interactions.

Figure 27.7 illustrates the operation of the mormyrid electromotor CPG. The DP/PCN provide tonic excitatory input to the command neurons (von der Emde et al., 2000; Carlson, 2003), which results in their gradual depolarization until they fire an action potential and initiate an EOD (Fig. 27.6d) (Grant et al., 1986). This also activates the corollary discharge pathway, which feeds into DP/PCN via an inhibitory projection from neurons in the dorsal region of the ventroposterior nucleus (VPd) of the torus semicircularis (Carlson, 2002b). These neurons respond to the corollary discharge input with a burst of action potentials that silence the ongoing activity of DP/PCN neurons (von der Emde et al., 2000; Carlson, 2003). This recurrent inhibition effectively puts the brakes on the excitatory input to command neurons, preventing them from discharging uncontrollably (Carlson and Hopkins, 2004b). Once the DP/PCN recover from this inhibition, they resume firing to initiate the next EOD cycle.

Thus, while other groups of electric fish generate rhythmic electromotor output through endogenous pacemaker activity, mormyrids do so through network connectivity. This distinction underscores the two general strategies used by motor networks to generate rhythmic behavior (Gettings, 1989; Marder and Bucher, 2001). In many cases, however, rhythmic motor output is generated by a combination of cellular and network features.

3.4.2 *Separate Motor Control Centers for Different Electrical Displays*

The generation of different electrical displays requires mechanisms for inducing discrete types of modulation in the output patterns of medullary electromotor

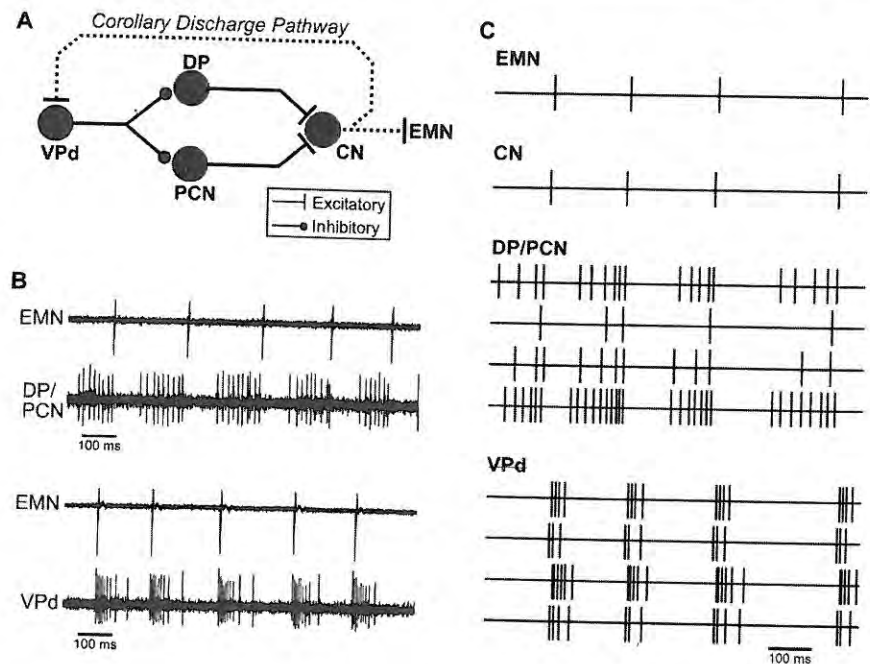


Fig. 27.7: Mormyrid electromotor CPG. (A) Simplified schematic representation of electromotor connectivity. CN, command nucleus; DP, dorsal posterior nucleus; EMN, electromotor neurons; PCN, precommand nucleus; VPd, dorsal subdivision of the ventroposterior nucleus. (B) Extracellular activity of a single neuron in the DP/PCN in relation to EMN activity, and extracellular activity of a single neuron in the VPd in relation to EMN activity in *Brienomyrus brachyistius*. (C) Simulated simultaneous activity patterns in the EMN, CN, DP/PCN, and VPd.

neurons. In both mormyrids and gymnotiforms, stimulation of the different precommand/prepacemaker inputs results in very different EOD output patterns (Fig. 27.8). In the mormyrid *Brienomyrus brachyistius*, stimulating DP leads to a smooth acceleration and regularization, while stimulating PCN induces the production of rapid, transient bursts (Carlson and Hopkins, 2004b). These two output patterns are similar to the naturally occurring behaviors termed accelerations and scallops, respectively (Carlson and Hopkins, 2004a). Similarly, in the gymnotiforms *Eigenmannia*, *Apteronotus*, and *Brachyhypopomus*, stimulating CP leads to smooth, gradual rises in EOD frequency, while stimulating PPN leads to rapid, transient bursts termed chirps (Kawasaki and Heiligenberg, 1988, 1989; Kawasaki et al., 1988). These two regions have therefore also been referred to as PPN-G (gradual) and PPN-C (chirp). Thus, anatomical convergence in these structures is linked to functional convergence in the behaviors they control. In *Brachyhypopomus*, an additional region near the CP/PPN (PPN-I) has been shown to induce EOD decelerations through inhibition (Kawasaki and Heiligenberg, 1989).

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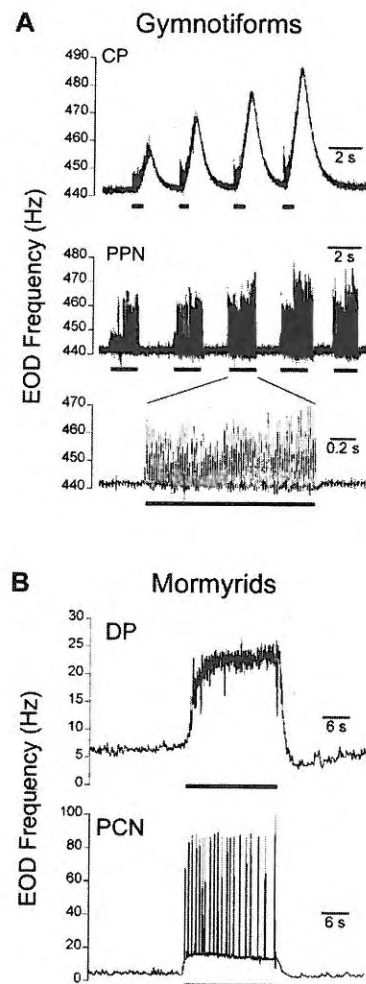


Fig. 27.8: Separate motor control centers for different communication displays revealed by focal brain stimulation. The horizontal bars beneath each plot correspond to the period of stimulation. (A) In the gymnotiform *Eigenmannia virescens*, electrical stimulation of the PPN-G leads to smooth accelerations in EOD frequency, while electrical stimulation of the PPN-C leads to chirp-like bursts. Modified after Kawasaki and Heiligenberg (1988). (B) In the mormyrid *Brienomyrus brachyistius*, stimulation using the excitatory neurotransmitter L-glutamate leads to smooth accelerations in EOD frequency in DP, and scallop-like bursts in PCN.

The role of the VPv neurons that project to the CN in mormyrids has not been explored. However, the SPPN in gymnotiforms is involved in behaviors distinct from those controlled by the CP/PPN. In *Eigenmannia*, this region provides tonic excitatory input to the PN. When inhibited, this results in a gradual deceleration in EOD frequency (Metzner, 1993). In *Sternopygus* and

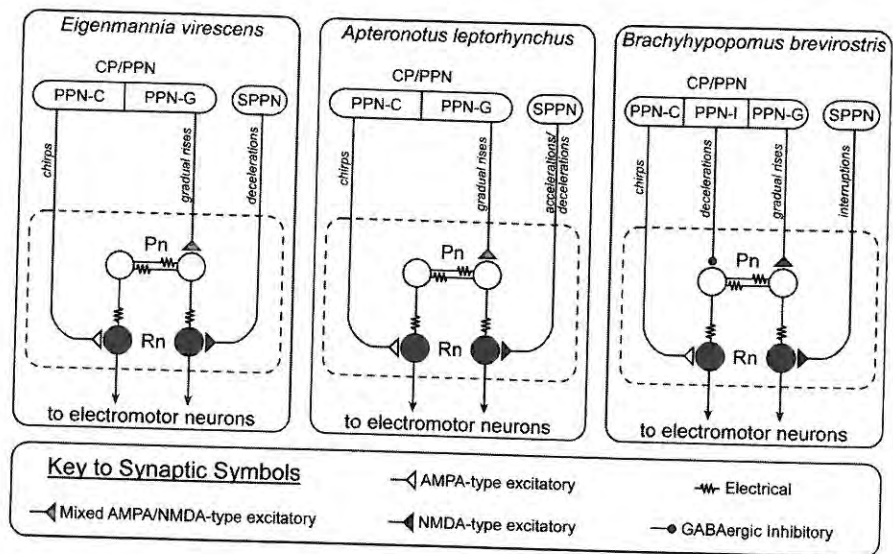


Fig. 27.9: Synaptic basis of signal production in the gymnotiforms *Eigenmannia virescens*, *Aptereronotus leptorhynchus*, and *Brachyhypopomus occidientalis*. CP/PPN, centroposterior/prepacemaker nucleus; Pn, pacemaker neurons; PPN-C, chirp region of CP/PPN; PPN-G, gradual rise region of CP/PPN; PPN-I, inhibitory region of CP/PPN; Rn, relay neurons; SPPN, sublemniscal prepacemaker nucleus. In each case, the pacemaker nucleus is delimited by a box with dashed lines.

Brachyhypopomus, the SPPN is responsible for generating EOD interruptions (Kawasaki and Heiligenberg, 1989; Keller et al., 1991). In *Aptereronotus*, the SPPN appears to play a dual role in both gradual frequency rises and falls, as well as interruptions (Heiligenberg et al., 1996). Along with this increased diversity in function comes increased anatomical diversity: the SPPN of *Aptereronotus* contains two cell types, while in the other gymnotiforms studied it contains only one (Heiligenberg et al., 1996). For both mormyriiforms and gymnotiforms, then, different electrical displays are driven by separate groups of neurons. The anatomical separation of these pathways provides a relatively simple mechanism for generating different displays.

3.4.3 Synaptic Mechanisms for Generating Different Electrical Displays

An important issue in understanding the motor control of signaling behavior is how these various inputs effect different modulations in electromotor output. This issue has been thoroughly explored in gymnotiforms, and the answer is that each prepacemaker region induces a different behavior because of differences in their postsynaptic targets and differences in the pharmacology of those synapses (Fig. 27.9).

In all gymnotiform species studied, the CP synapses onto the pacemaker cells in PN, while the PPN and SPPN synapse onto the relay cells. While all of

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the excitatory synapses are glutamatergic, the post-synaptic receptors may differ. For example, the PPN to relay neuron input responsible for driving chirps is mediated by AMPA-type glutamate receptors (Kawasaki and Heiligenberg, 1990; Heiligenberg et al., 1996; Juranek and Metzner, 1997, 1998). In contrast, the CP to pacemaker cell input responsible for driving gradual accelerations appears to be mediated by either NMDA-type glutamate receptors or a mix of both NMDA- and AMPA-type receptors (Kawasaki and Heiligenberg, 1990; Keller et al., 1991; Heiligenberg et al., 1996; Juranek and Metzner, 1997, 1998). The difference in electromotor output that results from stimulating these two regions is compatible with known differences in the kinetics of these two glutamate receptor subtypes (Gasic and Hollman, 1992). Gradual decelerations in *Brachyhyopomus* are mediated by an additional inhibitory input to pacemaker neurons from γ -aminobutyric acidergic (GABAergic) neurons (Kawasaki and Heiligenberg, 1990).

The SPPN input to the relay cells appears to be mediated exclusively by NMDA-type glutamate receptors (Kawasaki and Heiligenberg, 1990; Keller et al., 1991; Heiligenberg et al., 1996; Juranek and Metzner, 1997, 1998). However, this projection may be used to induce very different effects on electromotor output depending on the species. For example, in *Eigenmannia*, the SPPN is tonically active at rest, and when it is inhibited, there is an EOD frequency decrease (Metzner, 1993). In *Apteronotus*, this input is normally silent, but when stimulated, it leads to an EOD frequency increase (Heiligenberg et al., 1996). In *Sternopygus* and *Brachyhyopomus*, stimulating this input leads to an EOD interruption (Kawasaki and Heiligenberg, 1989; Keller et al., 1991). It may seem counterintuitive that an excitatory synapse could mediate a silencing of electromotor output, but this probably results from the inactivation of ion channels during a maintained depolarization. A similar effect is seen during chirps in some species, in which the sudden frequency rise is often accompanied by a reduction in EOD amplitude or a complete cessation before the frequency falls back to baseline (Hagedorn and Heiligenberg, 1985).

4. ELECTRIC SIGNAL TRANSMISSION

A detailed description of the physics of electric signals is beyond the scope of this chapter. However, a thorough understanding of the neuroethology of electric communication warrants a brief discussion of the unique physical properties of electric signals and how this affects their transmission between sender and receiver and thereby shapes their evolution. For a more detailed analysis of the spatiotemporal physical properties of the EOD, the reader is referred to Chapter 21 of this volume.

A critical feature that distinguishes electric communication from other modes of communication is that the signals do not propagate as an

synaptic receptors may be responsible for driving electroreceptors (Kawasaki and Kornhuber, 1997, 1998). The ability for driving gradual depolarization-type glutamate receptors (Kawasaki and Kornhuber, 1996; Juranek and Kornhuber, 1997) results from known differences in the properties of these receptors (Heiligenberg and Kornhuber, 1992). The input is mediated by an additional electroreceptor (Heiligenberg, 1990).

The input is mediated exclusively by electroreceptors (Heiligenberg, 1990; Kornhuber and Metzner, 1997, 1998). Every different effect on the output, for example, in *Eigenmannia*, is inhibited, there is an EOD. The input is normally silent, but an increase (Heiligenberg et al., 1989; Kornhuber et al., 1991). It could mediate a silencing in the inactivation of ion channels. A similar effect is seen during the rise in frequency is often accompanied by a decrease in frequency before the frequency (Heiligenberg, 1985).

is beyond the scope of the neuroethology of the unique physical transmission between electroreceptors. For a more detailed of the EOD, the reader is

communication from other electroreceptors not propagate as an

electromagnetic wave, but instead exist as an electrostatic field (Hopkins, 1986b). This is significant to electric communication in several respects (Hopkins, 1999). Firstly, the electric field magnitude decreases as the inverse cube of distance from the fish (Knudsen, 1975). Doubling the active space therefore, requires an eightfold increase in signal amplitude at the source. This severe constraint places energetic efficiency in signal production at a premium, and electric fish may meet this demand by impedance-matching their electric organs to the conductivity of the water (Hopkins, 1999). Despite such adaptations, however, the active space of electric communication is limited to at most a few meters (Squire and Møller, 1982).

A second important consequence is that electric signals are not corrupted by factors that affect signals in other modalities. Propagating waves such as those used for sound communication are affected by reflection, refraction, absorption, dispersion, and reverberation, which can distort the temporal features of a signal during propagation. Because electric signals are nonpropagating, these factors are of no consequence to electrical communication, and the fine temporal structure of the signals is preserved (Hopkins, 1986b). It is precisely because of this fact that electric fish are exquisitely sensitive to minute temporal features in electric signals, and this has had a profound effect on electric signal evolution (Hopkins, 1999).

5. ELECTROSENSORY SYSTEMS—RECEPTION AND ANALYSIS OF ELECTRIC SIGNALS

5.1 General Organization of Electrosensory Pathways

Similar to the electromotor networks of gymnotiforms and mormyriiforms, the electrosensory systems of these fish are very similar in their overall organization (Finger et al., 1986). Electric fields are received and transduced by specialized electroreceptors on the surface of the skin (Zakon, 1986). The afferent fibers that innervate these electroreceptors reach the brain via the lateral line nerves, where they terminate in a specialized region of the hindbrain called the electrosensory lateral line lobe (ELL). This structure is present in all electroreceptive teleosts, but is especially large in the electrogenic mormyriiforms and gymnotiforms where it consists of multiple, separate maps of the electroreceptive body surface (Bell and Szabo, 1986; Carr and Maler, 1986). The ELL performs a number of important computations in electrosensory processing, receiving not just afferent input, but also descending input from electrosensory feedback loops, other modalities, and in the case of mormyrids, corollary discharge input.

The ELL projects to two large structures, nucleus praeminentialis and the torus semicircularis (Bell and Szabo, 1986; Carr and Maler, 1986). Nucleus praeminentialis is involved in electrosensory feedback loops that project back

to the ELL (Bastian, 1986). In the torus semicircularis, or torus for short, a number of computations relevant to electric communication are performed. In both groups, the torus projects to the tectum mesencephali, a sensorimotor structure where electrosensory information is integrated with sensory input from other modalities (Bastian, 1982). In gymnotiforms, the torus also projects to the nucleus electrosensorius in the thalamus, a critical link in connecting electrosensory input to electromotor output, as it projects to prepacemaker regions involved in regulating EOD frequency (Keller et al., 1990).

5.2 Electroreceptors

Electroreceptors come in two main flavors: ampullary and tuberous. All electroreceptive fish possess ampullary receptors. They are tuned to 1–10 Hz, the range of most non-electrogenic, biological sources of electricity, and are used for passive electrolocation (Kalmijn, 1974). Weakly electric fish also possess tuberous receptors, which are sensitive to the much higher frequency components of their EODs (Bennett, 1967). In general, then, only tuberous electroreceptors are relevant to the topic of electric communication, and they will therefore be the focus here. It is important to note, however, that electrical displays in wave-type gymnotiforms such as chirps and frequency modulations contain low frequency components that are detected by ampullary receptors (Metzner and Heiligenberg, 1991; Naruse and Kawasaki, 1998). In addition, monophasic EODs or EODs with asymmetric head-positive and head-negative areas contain significant levels of DC, which may be detected by ampullary receptors and play a role in electrical communication (Stoddard, 2002). Unfortunately, the role of ampullary receptors in electrical communication has not been studied thoroughly.

There are two physiological classes of tuberous electroreceptors in mormyriiforms and gymnotiforms, which may be broadly categorized as time coders and amplitude coders (Zakon, 1986). The central pathways of these receptors remain segregated through several synaptic steps. Such parallel processing of different stimulus components is a common feature of sensory systems (Young, 1998). Time coders fire a single, phase-locked action potential at a fixed latency to outside-positive-going transients. Thus, for wave-type fish they fire 1:1 with each EOD cycle (Scheich et al., 1973; Bullock et al., 1975), while in pulse-type fish they fire 1:1 with each EOD pulse (Bastian, 1976; Hopkins and Bass, 1981). Amplitude coders, however, are not strongly phase-locked to the EOD. Instead, their activity is a function of EOD amplitude. In wave-type fish, these units fire continuously at a rate that is directly correlated with EOD amplitude (Scheich et al., 1973; Bullock et al., 1975). In pulse-type fish, these units produce a burst of spikes in response to each EOD pulse; the number of spikes per burst increases with increasing EOD amplitude (Bastian, 1976). In mormyrids, interspike intervals and latencies to the first spike in the burst also decrease with increasing EOD amplitude (Szabo and Hagiwara,

1967). For a detailed discussion of electroreceptor morphology and physiology the reader is referred to Zakon (1986).

5.3 Temporal Coding of EOD Waveform in Mormyrids

Mormyrids are unique in having clearly separable functions for the two types of tuberous electroreceptors (Bell, 1986). The time-coding receptors (called knollenorgans) function exclusively in communication, while the amplitude-coding receptors (called mormyromasts) are involved in active electrolocation. Knollenorgan receptors are about 10 to 20 times more sensitive than mormyromast receptors (Bennett, 1965). Thus, knollenorgans are well suited to detecting the EODs of distant conspecifics, while mormyromasts are better suited to detecting the fish's own EOD. Furthermore, the corollary discharge exerts very different effects on the central sensory pathways of these two receptor types (Bell, 1989). Responses in the mormyromast pathway are facilitated by the corollary discharge, such that sensitivity to the fish's own EOD is enhanced. In contrast, responses in the knollenorgan pathway are inhibited by the corollary discharge, eliminating sensitivity to the fish's own EOD. This functional separation has facilitated studies on the electrosensory basis of electric communication in mormyrids, the group that has received the most attention in this area (Hopkins, 1988).

5.3.1 Behavioral Significance of EOD Waveform

Early research on electric communication in mormyrids focused on the SPI (Møller, 1970; Møller and Bauer, 1973; Bell et al., 1974; Kramer, 1979), because it was assumed that the EOD acted simply as a carrier signal for information encoded in a temporal pattern, much like action potentials in the nervous system. The reasoning behind this was that EODs must be too brief for fish to extract any useful information from within. However, the first field recordings from a diverse group of mormyrids in the Ivindo River system of Gabon revealed incredible species-specific diversity, and often sex-differences in EOD waveform (Fig. 27.1), which raised the question of what this variation was for if not transmitting information (Hopkins, 1980, 1981).

Early field experiments demonstrated that males of an undescribed *Brienomyrus* species produce significantly more courtship rasps (Fig. 27.10a) to electrical recordings of conspecific females than to those of conspecific males or heterospecific females (Hopkins, 1981). Although these experiments did not distinguish between the relative importance of the EOD and SPI, playback of a single-cycle sine wave presented using a female conspecific SPI failed to elicit an increase in rasp production, strongly suggesting that the EOD waveform is critical.

Definitive evidence for the importance of EOD waveform in species and sex recognition came from additional playback experiments in the same species (Hopkins and Bass, 1981; Hopkins, 1983). In one experiment, three males were

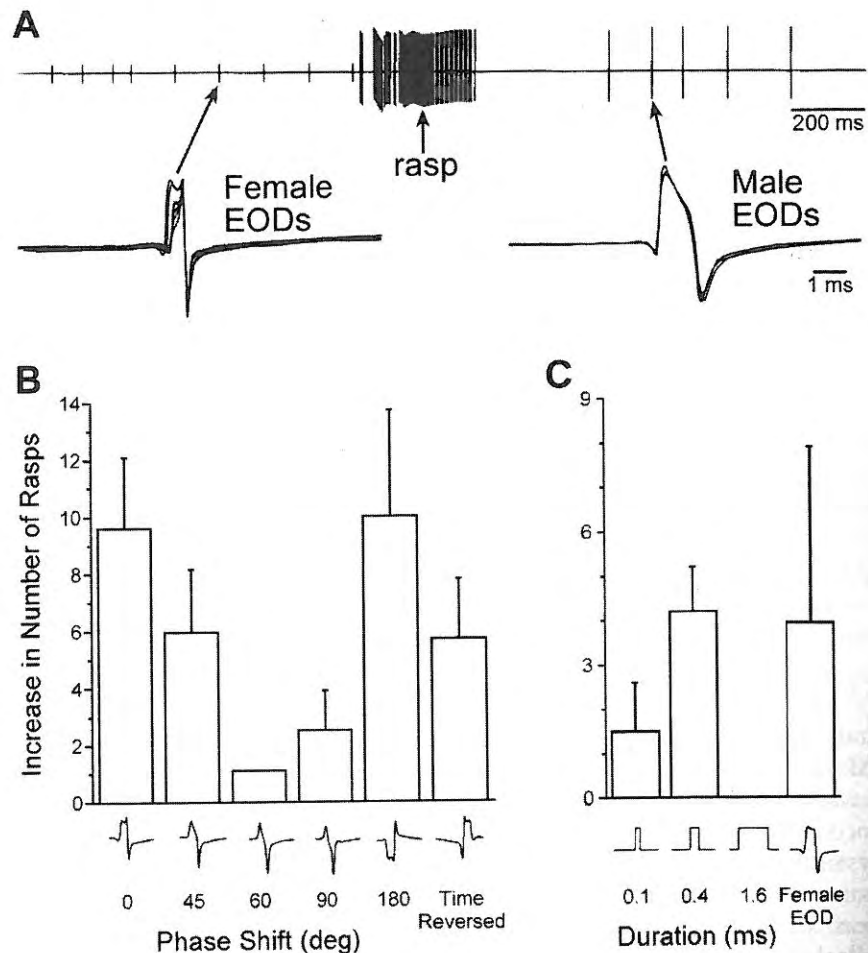
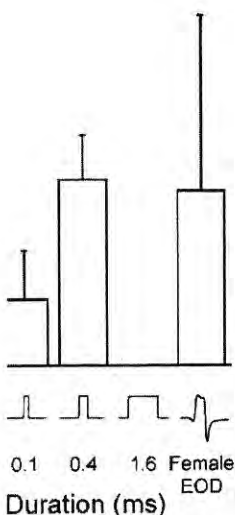
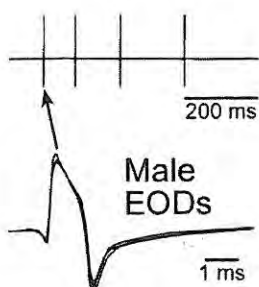


Fig. 27.10: Temporal coding of species and sex recognition in the mormyrid *Brienomyrus* sp. 'VAD'. (A) Examples of male and female EODs, and a long record showing rasping by a male in response to the approach of a female. (B) Increase in the number of rasps produced by three males (mean + sem) in response to phase-shifted and time-reversed female EODs differing in waveform, but not power spectra, played back using a scrambled female SPI. (C) Increase in the number of rasps produced by a single male (mean + sem) in response to playback of a female EOD and monophasic square pulses of different durations. Modified after Hopkins and Bass (1981).

presented with a conspecific female EOD, the same EOD phase-shifted to various degrees, and a time-reversed version of the same EOD (Hopkins and Bass, 1981). This resulted in EOD stimuli with different waveforms, but identical frequency spectra, all of which were played back using a randomly



e mormyrid *Brienomyrus* sp. showing rasping by a male in response to three different female EODs differing in duration. (C) Increase in the number of rasps produced by a male in response to playback of a female EOD identified after Hopkins and Bass

the EOD phase-shifted to the natural EOD (Hopkins and Bass, 1981). This male produced significantly more rasps to the natural female EOD and a square pulse of equal duration than to shorter or longer square pulses of different durations, using a scrambled female SPI (Hopkins and Bass, 1981). This male produced significantly more rasps to the natural female EOD and a square pulse of equal duration than to shorter or longer square pulses of different durations, using a scrambled female SPI (Hopkins and Bass, 1981). Furthermore, there was no significant difference in the number of rasps elicited by the female EOD or the equal duration square pulse. This demonstrates that EOD recognition is mediated by a temporal code; namely, that the relative timing of positive and negative voltage transients is the salient stimulus for species and sex recognition.

scrambled SPI from a female conspecific. Males produced significantly more rasps to a natural EOD and to an EOD phase-shifted by 180° (reverse polarity) than to the other stimuli (Fig. 27.10b). In another experiment, the EODs and SPIs recorded from a conspecific female, a conspecific male, and a heterospecific female were mixed and matched and played back in different EOD/SPI combinations (Hopkins, 1983). A significant increase in rasp production only occurred during presentation of a conspecific female EOD, whether it was driven with a conspecific SPI or heterospecific SPI.

So what features of the EOD waveform are involved in sender recognition? The answer to this question comes from a third playback experiment, in which one male was presented with a conspecific female EOD and monophasic square pulses of different durations, using a scrambled female SPI (Hopkins and Bass, 1981). This male produced significantly more rasps to the natural female EOD and a square pulse of equal duration than to shorter or longer square pulses of different durations, using a scrambled female SPI (Hopkins and Bass, 1981). Furthermore, there was no significant difference in the number of rasps elicited by the female EOD or the equal duration square pulse. This demonstrates that EOD recognition is mediated by a temporal code; namely, that the relative timing of positive and negative voltage transients is the salient stimulus for species and sex recognition.

5.3.2 Temporal Coding by Knollenorgan Receptors

Knollenorgan electroreceptors are broadly tuned to spectral frequencies that are well matched to the frequency spectra of the species-specific EOD (Hopkins, 1983; Bass and Hopkins, 1984). As with time-coding electroreceptors in all weakly electric fish, they fire a phase-locked spike in response to outside positive-going voltage changes. The EOD of a neighboring fish will cause current to flow into one half of the body surface and out the other half, meaning that knollenorgans on these two body surfaces will be exposed to opposite stimulus polarities (Fig. 27.11a).

Recording the response of a single knollenorgan to both normal and reverse polarity stimuli reveals how knollenorgans on opposite sides of the body would normally respond to a natural stimulus. Knollenorgans respond with a phase-locked spike to the onset of a normal polarity current, while they respond with a phase-locked spike to the offset of an opposite polarity current (Fig. 27.11b). In a natural situation, this would correspond to knollenorgans on one body surface responding to the start of an EOD, and knollenorgans on the opposite body surface responding to the end of an EOD (Fig. 27.11b, c). Thus, a fish could determine EOD duration and recognize its species-specific EOD waveform simply by comparing the interval between spikes coming from opposite sides of the body (Hopkins and Bass, 1981). This spike time comparison occurs within the central nervous system, in circuits specialized for detecting differences in spike arrival times.

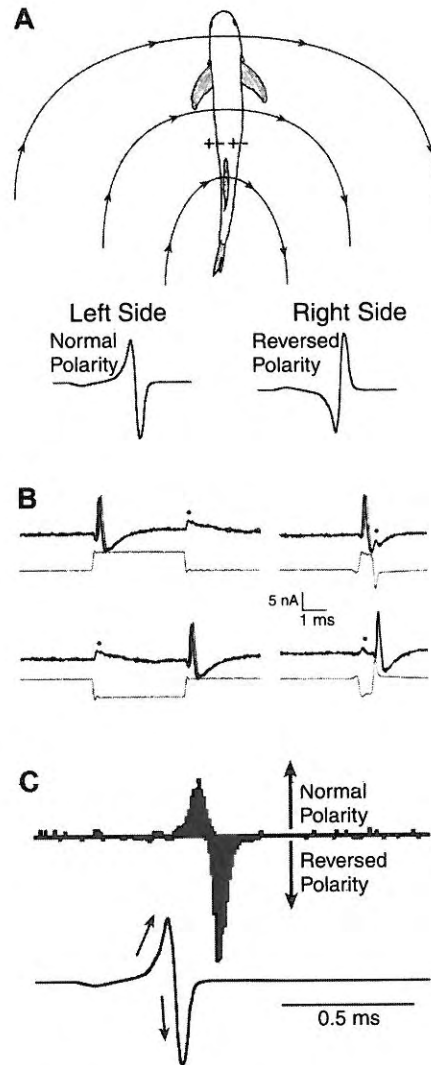


Fig. 27.11: Temporal coding by knollenorgan electroreceptors. (A) Current flow through a receiver's body resulting from EOD production by another fish. One side of the body is outside positive/inside negative, while the other half is outside negative/inside positive, meaning that the EODs detected across the two skin surfaces are of opposite polarities. (B) Knollenorgans fire to outside positive going voltage steps. Spikes occur on stimulus onset under normal polarity, while they occur on stimulus offset under reversed polarity. Dots mark the occurrence of the stimulus artifact. Modified after Hopkins and Bass (1981). (C) Response of a knollenorgan to an EOD stimulus presented multiple times in both normal and reversed polarity. Response is displayed as a post-stimulus time histogram, with responses to normal polarity on the upward histogram and responses to the reversed polarity on the downward histogram. Modified after Xu-Friedman and Hopkins (1999).

5.3.3 Time-coding Circuitry: A Novel Mechanism for Species Recognition

The primary afferents from knollenorgan receptors project to the ipsilateral nucleus of the electrosensory lateral line lobe, or NELL (Fig. 27.12a) (Bell and Russell, 1978), where they terminate with large, electrotonic synapses (Mugnaini and Maler, 1987a). The neurons in NELL are large and adendritic (Szabo and Ravaille, 1976), and send thick, heavily myelinated axons bilaterally up the lateral lemniscus to the torus semicircularis, where they terminate in the anterior exterolateral nucleus (ELa) (Fig. 27.12a) (Szabo et al., 1983). The NELL cells also receive a strong inhibitory projection onto the initial segment of their axons that originates from the electric organ corollary discharge pathway and prevents activity resulting from the fish's own EOD from ever reaching the torus (Fig. 27.12a) (Mugnaini and Maler, 1987a; Bell and Grant, 1989).

Within the ELa, there are two distinct cell types, large cells and small cells (Mugnaini and Maler, 1987b; Friedman and Hopkins, 1998). The axons from the NELL terminate on both cell types with large mixed chemical and electrical synapses (Mugnaini and Maler, 1987b). Upon entering the ELa, the axons of NELL cells terminate onto 1 or 2 large cells, and then proceed to wind their way extensively throughout the nucleus over distances of 3 to 4 mm before branching and terminating on a large number of small cells (Friedman and Hopkins, 1998). The large cells project entirely within the ELa, terminating with large GABAergic inhibitory terminals onto the small cells (Mugnaini and Maler, 1987b).

Both the NELL axons and large cells in the ELa fire spikes phase-locked to electrosensory stimuli (Amagai et al., 1998; Friedman and Hopkins, 1998). Thus, the small cells receive phase-locked input from two different sources: inhibitory input from ELa large cells and excitatory input from NELL axons. This excitatory input is, however, delayed by the time it takes an action potential to propagate down the long, winding path of the NELL axon. This suggests a novel 'anti-coincidence detection' model for EOD time-coding within the ELa (Friedman and Hopkins, 1998), which differs from the 'coincidence detection' models described for time difference detection in the auditory system of barn owls and the electrosensory system of gymnotiforms, as described in Section 5.4.3. Under this model, a given small cell receives inhibitory input from an ELa large cell with a receptive field on one side of the body, and a delayed excitatory input from an NELL axon with a receptive field on the opposite side of the body (Fig. 27.12b). If the duration of an EOD is sufficiently long such that the delayed excitatory input from the NELL arrives before the inhibitory input from the ELa, then the small cell will fire. If, however, the EOD is short enough that the delayed excitatory input from the NELL arrives coincident with or shortly after the inhibitory input from the ELa, then the small cell will not fire. Thus, a given small cell will only respond if an EOD is longer than some threshold duration, the value of which is set by the length of

s. (A) Current flow through a . One side of the body is outside re/inside positive, meaning that polarities. (B) Knollenorgans fire us onset under normal polarity. Dots mark the occurrence of the response of a knollenorgan to an reversed polarity. Response is normal polarity on the upward ward histogram. Modified after

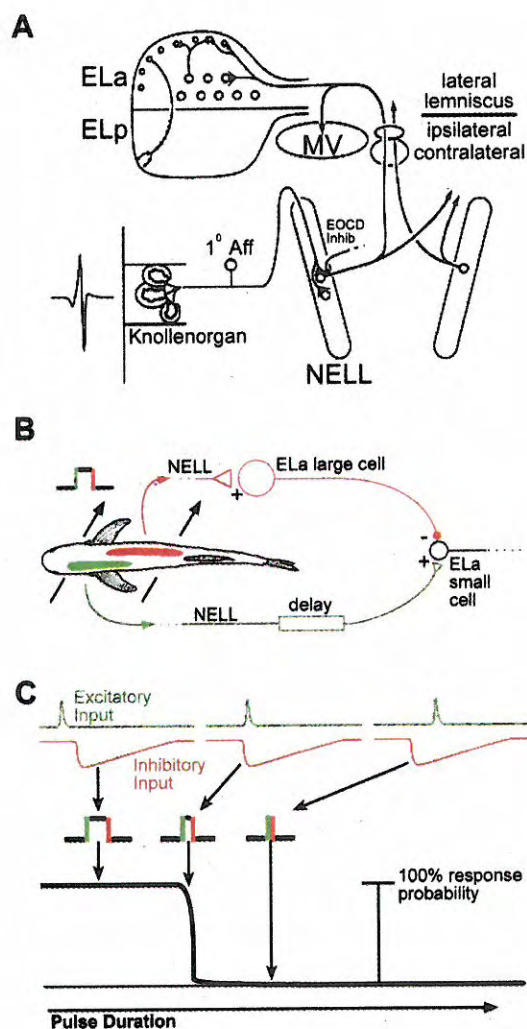


Fig. 27.12: EOD time-coding circuitry in mormyrids. (A) Schematic representation of the knollenorgan time-coding pathway. 1° Aff, primary afferent; ELA, anterior exterolateral nucleus; ELP, posterior exterolateral nucleus; EOC Inhib, electric organ corollary discharge inhibitory input; MV, medioventral nucleus; NELL, nucleus of the electrosensory lateral line lobe. (B) Model for the mechanism of EOD duration coding by small cells in ELA. Presentation of a transverse square-wave stimulus causes knollenorgans on one side of the body (green) to fire on stimulus onset, and knollenorgans on the other side of the body (red) to fire on stimulus offset. The former provides delayed, excitatory input to a small cell, while the latter provides inhibitory input to the same cell. (C) Response probability of the small cell in (B) as a function of stimulus duration. If the stimulus is enough such that the excitatory input arrives before the inhibitory input, then the small cell will fire. Otherwise, the inhibition will block the excitatory response. Modified after Xu-Friedman and Hopkins (1999).

the NELL axonal delay line (Fig. 27.12c). Assuming that different small cells receive input from NELL axons with varying delays, each small cell will have a different threshold value, and EOD duration will be reflected in the total number of active small cells.

The small cells in ELA project to the adjacent posterior extero-lateral nucleus (ELp) (Haugedé-Carré, 1979), where two physiological types of neurons have been described (Amagai, 1998). Type I neurons respond in a 'long-pass' fashion to all stimuli with durations above a certain cutoff, suggesting that they receive excitatory input from several ELA small cells. Type II neurons respond in a 'band-pass' fashion to stimuli that fall within a certain limited range of durations. These neurons may be second-order neurons that receive excitatory and inhibitory input from type I neurons with different cutoff durations. The band-pass responses of these type II neurons can fully account for the behavioral selectivity of responses to EODs and square-wave pulses within a limited range of durations, and could, therefore, function as 'EOD recognition units'.

5.4 Frequency Channels in Wave-type Electric Fish

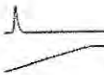
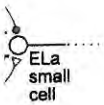
Wave-type electric fish employ a completely different method for EOD recognition. Because they 'hum' at a constant frequency that is species and sex specific, they can identify conspecific EODs by tuning into a narrow range of stimulus frequencies, much in the same way that one isolates a radio signal by dialing into a specific frequency. Thus, they can be said to communicate within their own species-specific frequency channel (Hopkins, 1974a, b, 1976).

None of the wave-type electric fish have an electric organ corollary discharge pathway (Heiligenberg et al., 1978; Kawasaki, 1994). Unlike mormyrids they are therefore unable to allocate different functions to their time-coding and amplitude-coding receptors, both of which are involved in active electrolocation as well as communication. In fact, because they generate EODs continuously, the EOD of an individual fish is always contaminated by the EODs of any neighbors, making it impossible to isolate self-generated from external EODs. The combination of two quasi-sinusoidal EODs results in an electric field that 'beats' in amplitude and phase at a frequency equal to the frequency difference between the two EODs, in a temporal pattern that depends on the direction of this frequency difference (Fig. 27.13). Thus, a fish can extract information about its neighbor's EOD frequency in relation to its own by analyzing this beat pattern, as described below in Sections 5.4.2 and 5.4.3 (Heiligenberg, 1991).

5.4.1 Behavioral Significance of EOD Frequency

The importance of EOD frequency for communication in wave-type gymnotiforms was first explored in *Eigenmannia* and *Sternopygus* (Hopkins, 1974a, b). In response to playbacks of EODs recorded from five different

lateral
lemniscus
ipsilateral
contralateral



% response
stability



Schematic representation of the (A) anterior extero-lateral nucleus; (B) corollary discharge inhibitory sensory lateral line lobe. (B) Model ELA. Presentation of a transverse body (green) to fire on stimulus re on stimulus offset. The former latter provides inhibitory input to a function of stimulus duration. before the inhibitory input, then excitatory response. Modified

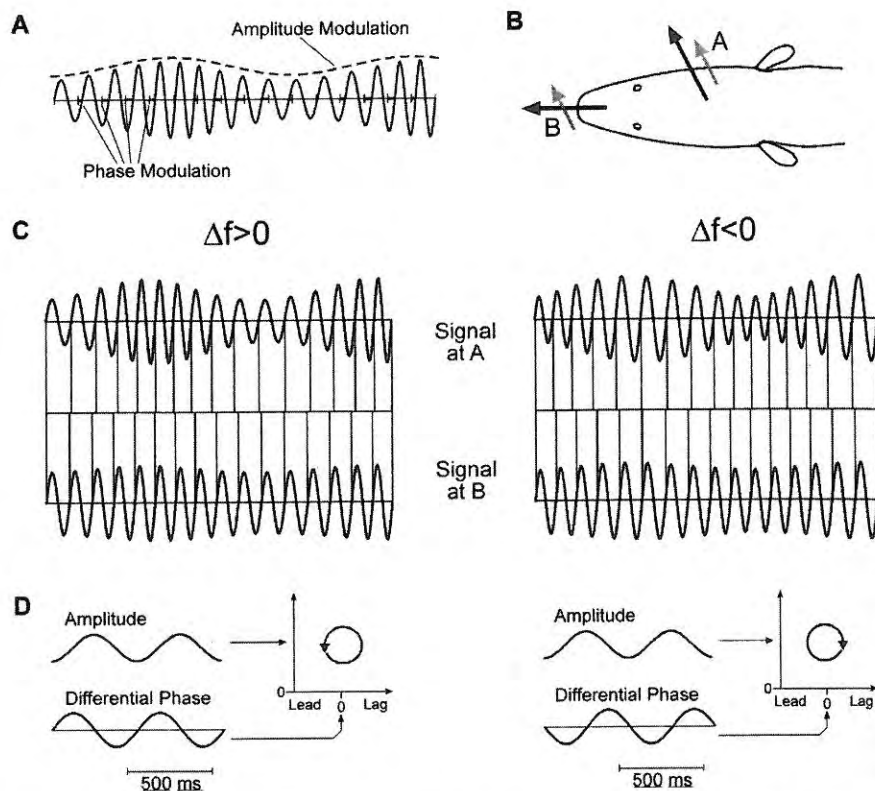


Fig. 27.13: Electric field modulation resulting from combining two quasi-sinusoidal EODs. (A) Combining two sinusoidal signals results in amplitude and phase modulation (AM and PM, respectively) at a frequency equal to the frequency difference between the two sinusoids. The vertical lines mark the timing of zero crossings in an uncontaminated signal. (B) The fish's individual EOD is generated internally, leading to current flow perpendicular to the skin surface at every point (black arrows), while the neighbor's EOD is generated externally, leading to current flow through the fish in a single direction (gray arrows). Because electroreceptors are maximally sensitive to current flow that is oriented perpendicular to the body surface, the fish's EOD will be more strongly contaminated at body surface A compared to B. (C) AM and PM at body surfaces A and B for opposite signs of Δf . The vertical lines mark zero crossings. (D) AM and differential PM of body surface A relative to B for opposite signs of Δf . The timing of differential PM relative to AM is reversed when switching the sign of Δf , which results in a different direction of rotation in a Lissajous graph. Modified after Kawasaki (1997).

wave-type gymnotiform species, *Eigenmannia* produced far more chirp displays and attacks on the playback electrodes in response to conspecific EODs than in response to the four heterospecific EODs (Fig. 27.14a) (Hopkins, 1974b). Furthermore, males responded to conspecific EODs with a greater number of chirps and attacks during the breeding season than in the non-breeding season (Fig. 27.14a). Similar responses could be elicited by the presentation of simple

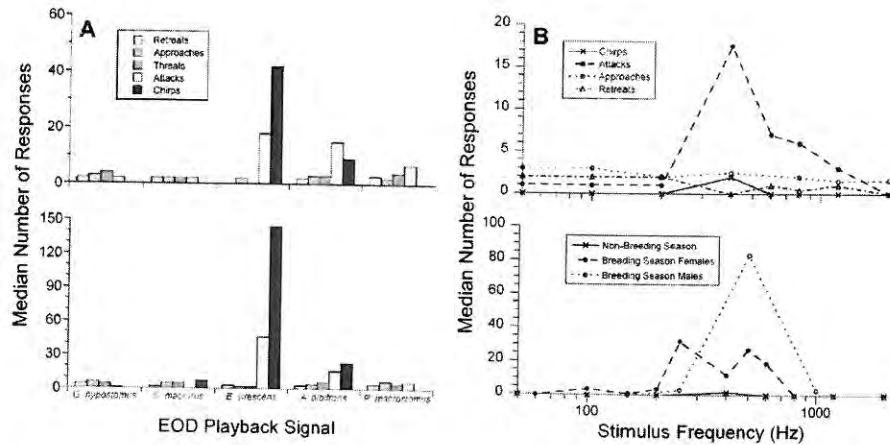
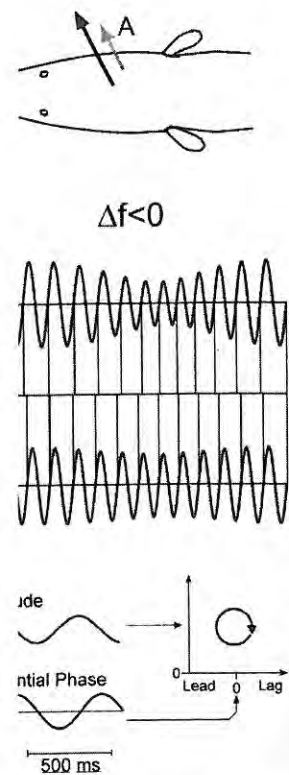


Fig. 27.14: Frequency coding in wave-type gymnotiforms. (A) Behavioral responses of *Eigenmannia* to tape-recorded signals of EODs from five different species of wave-type gymnotiform. The top graph shows responses of two males and four females during the non-breeding season. The bottom graph shows responses of six males during the breeding season. (B) Behavioral responses of *Eigenmannia* to sine-wave stimuli of varying frequencies. The top graph shows responses of three males and two females during the non-breeding season. The bottom graph compares chirping in two males and three females during the non-breeding season, seven females during the breeding season, and six males during the breeding season. Modified after Hopkins (1974b).

sine-wave stimuli (Fig. 27.14b). Stimuli at frequencies within the species' natural range of EOD frequencies elicited a greater number of attacks and chirps than stimuli at frequencies outside this range (Hopkins, 1974b). Again, the number of chirps elicited was greatest during the breeding season for both males and females.

Similarly, in *Sternopygus* males, presentation of sine-wave stimuli at frequencies within the females' natural range of EOD frequencies elicits strong increases in the production of EOD interruptions and frequency rises (Hopkins, 1974a). More recently, several studies in *Apteronotus leptorhynchus* have revealed an impressive diversity of frequency modulations that may be elicited by sine-wave stimuli (Zupanc and Maler, 1993; Engler and Zupanc, 2001; Zakon et al., 2002). The rate of production of different display types varies, depending on the sex and status of the receiver, and whether the sine-wave stimulus mimics the EOD of a male or female, a dominant or subordinate (Triefenbach and Zakon, 2003).

Various displays also have significant effects on the behavior of receivers. The addition of chirp-like modulations to a sine-wave stimulus reduces the number of chirps and attacks by male *Eigenmannia* during the breeding season (Hopkins, 1974b). Playback of male chirps to gravid females can elicit spawning behavior, even in the absence of any males (Hagedorn and Heiligenber, 1985).

vo quasi-sinusoidal EODs. (A) ase modulation (AM and PM, between the two sinusoids. The minated signal. (B) The fish's rpendicular to the skin surface ed externally, leading to current electroreceptors are maximally dy surface, the fish's EOD will o B. (C) AM and PM at body rk zero crossings. (D) AM and of Δf . The timing of differential h results in a different direction

ed far more chirp displays to conspecific EODs than 7.14a) (Hopkins, 1974b). with a greater number of the non-breeding season he presentation of simple

One important consequence of generating a wave-type EOD is that active electrolocation abilities may be impaired by interference from a conspecific EOD of similar frequency, as the two are operating within the same frequency channel (Heiligenberg, 1973). In response to such a 'jamming' stimulus, an individual will produce the 'jamming avoidance response' (JAR), in which it shifts its EOD frequency away from that of the jamming stimulus so as to increase the frequency difference and reduce interference (Bullock et al., 1975). Studies on the computational rules and neuronal implementation of the JAR in *Eigenmannia* have made it the best-understood neuroethological system, from sensory input and processing to motor coordination and execution (Heiligenberg, 1991). Although the JAR is not a communication behavior, much of what we know about the electrosensory and electromotor system of gymnotiforms comes from these studies.

5.4.2 Peripheral Stimulus Filtering

Tuberosus electroreceptors in gymnotiform fish are strongly tuned to the individual's own EOD frequency (Hopkins, 1976). As a result, they are most sensitive to their own EOD, and more sensitive to conspecific EODs than those of heterospecifics that operate in different frequency ranges (Fig. 27.15). Thus, the peripheral electrosensory system operates like a filter rendering the fish relatively insensitive to EODs outside the species' natural range. Peripheral stimulus filtering is a feature found in many sensory systems (Loewenstein, 1971).

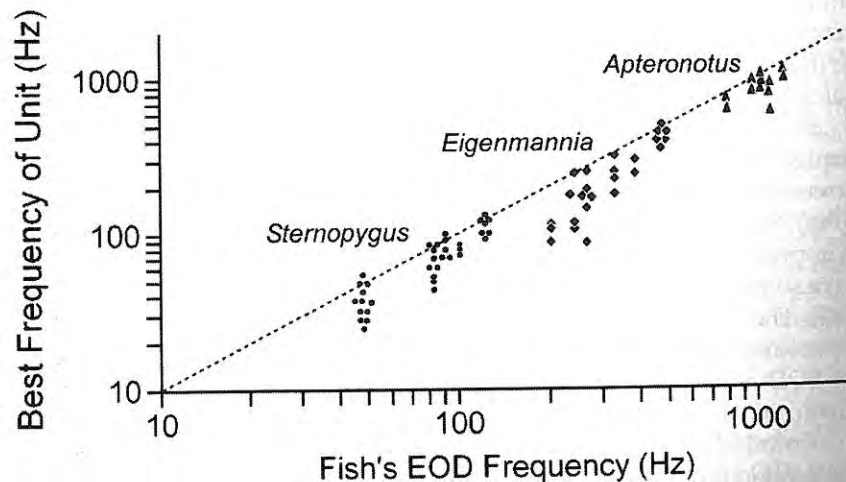
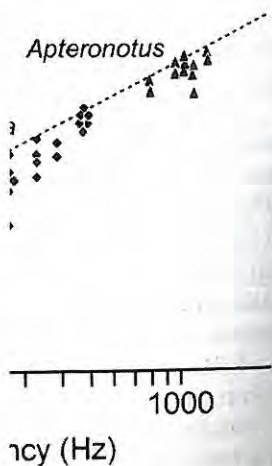


Fig. 27.15: Frequency filtering in wave-type gymnotiform electroreceptors, shown as a plot of tuberosus electroreceptor best frequency (stimulus frequency at lowest threshold) as a function of the EOD frequencies of the fish from which units were recorded. *Sternopygus* is shown as circles, *Eigenmannia* as diamonds, and *Aptereronotus* as triangles. Modified after Hopkins (1976).

Wave-type EOD is that active response from a conspecific within the same frequency range (JAR), in which it is a jamming stimulus so as to prevent the response (Bullock et al., 1975). The jamming response is a component of the JAR neuroethological system, which includes the modulation and execution of electrocommunication behavior, much like the electro-motor system of

are strongly tuned to the stimulus. As a result, they are most specific to EODs than those of other species (Fig. 27.15). Thus, the filter rendering the fish's response is within its natural range. Peripheral sensory systems (Loewenstein,



Receptors, shown as a plot of response threshold (lowest threshold) as a function of frequency. *Sternopygus* is shown as a dashed line. Modified after Hopkins (1976).

The time-coding and amplitude-coding receptors of wave-type gymnotiforms (T- and P-units, respectively) and the wave-type mormyrid *Gymnarchus* (S- and O-units, respectively), exhibit response properties that provide sufficient information for determining the frequency difference ($\Delta f = f_2 - f_1$) between a fish's own EOD frequency (f_1) and that of a neighbor (f_2) (Heiligenberg and Partridge, 1981). The firing rate of amplitude-coding units is in direct proportion to the amplitude of the electrosensory field (Scheich et al., 1973). Thus, their firing rate is modulated in synchrony with the amplitude modulation (AM) that results from combining two EODs (Fig. 27.13). This modulation rate, therefore, provides sufficient information to determine the magnitude of Δf . Determining the sign of Δf , however, requires a comparison with the activity of time-coding units.

Because the time-coding units phase-lock to positive zero-crossings in the electrosensory field, they fire 1:1 with each EOD cycle (Scheich et al., 1973). In relation to the firing times that would occur in response to an uncontaminated and thus unmodulated signal, the phase modulation (PM) that results from combining two EODs causes the firing times of these units to alternately lag and lead at the modulation rate. As with the modulations in firing rate for amplitude-coding units, this phase shifting is identical for opposite signs of Δf . However, the temporal relationship between the modulations of these amplitude-coding and time-coding units differs for opposite signs (Fig. 27.13): when $\Delta f > 0$, the phase lags while amplitude increases and leads while amplitude decreases; when $\Delta f < 0$, the phase leads while amplitude increases and lags while amplitude decreases.

In theory, then, it is possible to determine the magnitude and sign of Δf by simply comparing the activity of these two unit types. In practice, however, timing is all relative: the fish needs a reference signal to calibrate the spike times of time-coding units and determine whether they are leading or lagging. It does so by comparing the firing times of time-coding units on different portions of the body surface that are differentially affected by the neighbor's EOD. In other words, the fish analyzes differential PM (Fig. 27.13). In this way, the fish is able to determine a neighbor's EOD frequency in relation to its own, and respond appropriately. Thus, it may be said that the relevant stimulus for wave-type fish is not a given absolute EOD frequency, but a given relative EOD frequency. That is, small differences in EOD frequency indicate a conspecific of the same sex, greater differences indicate a conspecific of the opposite sex (the direction depending on the species), and still greater differences indicate a heterospecific.

5.4.3 Encoding Amplitude and Phase Modulation

Upon entering the electrosensory lateral line lobe (ELL), the primary afferents of time-coding and phase-coding units project to different cell types and, therefore, maintain separate, parallel time- and amplitude-coding pathways

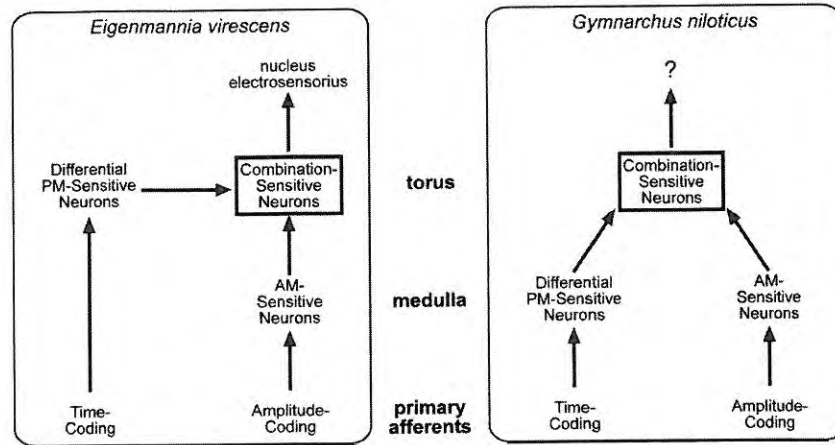
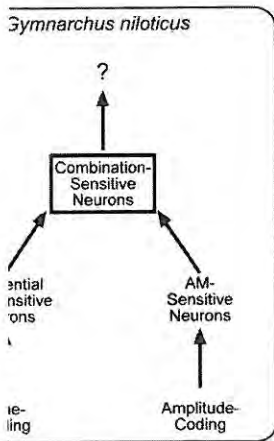


Fig. 27.16: Circuitry for determining sign and magnitude of Δf in the gymnotiform *Eigenmannia* and the mormyrid *Gymnarchus*. AM and PM are processed in separate, parallel pathways that converge within the torus semicircularis. In gymnotiforms, nucleus electrosensorius integrates information from the torus and relays it to pacemaker regions.

(Fig. 27.16) (Maler et al., 1981). In both gymnotiforms and *Gymnarchus*, two physiological types of AM-sensitive pyramidal cells have been described: E-units that respond to amplitude increases and I-units that respond to amplitude decreases (Bastian, 1981; Saunders and Bastian, 1984; Kawasaki and Guo, 1998). The former receive direct input from amplitude-coding afferents, while the latter receive indirect input via inhibitory interneurons. These neurons respond well to changes in electric field amplitude but not to steady state levels due to descending gain control from the nucleus praeminentialis feedback loop (Bastian, 1986). Both E- and I-units project to the torus.

In gymnotiforms, time-coding afferents project onto large spherical cells in the ELL via electrotonic synapses (Mathieson et al., 1987). The spherical cells relay timing information from the afferents to the torus, where they project somatotopically onto the dendrites of small cells and the soma of giant cells (Carr et al., 1986). The giant cells, in turn, project diffusely onto the somas of small cells throughout the torus. Unlike the mormyrid time-coding circuit, these projections appear to be excitatory. Thus, the small cells receive timing information from two different points on the body surface. A delay between the arrival times of those inputs appears to be established by differences in their synaptic delays. As a result, the small cells respond most strongly when stimuli at the two body surfaces occur at different times, so that the different synaptic delays are compensated for and the two synaptic inputs arrive at the small cell coincidentally, making the small cell sensitive to lags or leads of signals at one body surface relative to another (Heiligenberg and Rose, 1985). These small cells therefore code for differential PM (Fig. 27.16). A similar kind of



the gymnotiform *Eigenmannia* in separate, parallel pathways. The electrosensorius integrates these signals.

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coincidence detection model has also been described for sound localization in barn owls based on interaural time differences (Carr, 1986).

A similar situation is found in the time-coding system of *Gymnarchus*, but the differential phase comparison occurs one step earlier, within the ELL (Fig. 27.16). The time-coding afferents project to giant cells as well as to ovoidal cells, to which the giant cells also project (Matsushita and Kawasaki, 2004). The synapses from giant cells to ovoidal cells are mixed chemical and electrical, and are extremely large, embracing up to 84% of the ovoidal cell surface. The ovoidal cells make dendro-dendritic connections with pyramidal neurons that are sensitive to differential PM, although the mechanism for establishing this sensitivity is unknown (Kawasaki and Guo, 1996, 1998).

A number of features, such as large neurons and axons, thick myelination, and large, electrotonic synapses, are shared across the time coding pathways of the different groups of electric fish. These features are also characteristic of other sensory pathways involved in temporal coding, as they serve to enhance the rapidity and reliability of action potential propagation and synaptic transmission (Carr and Soares, 2002). Interestingly, similarities across time-coding pathways are much less obvious when it comes to comparing differences in timing between different inputs. While gymnotiforms use an excitatory delay-line mechanism, mormyrids use an inhibitory one, and additional variants are seen in other systems (Carr and Friedman, 1999). Nevertheless, the specialized adaptations for time coding, such as large neurons and large, electrotonic synapses, are lost at the site of comparison in all of these circuits, as the coding scheme shifts from phase-locked time coding to an alternative representation that no longer relies on precise spike times.

5.4.4 The Mystery of Multiple Maps: A Sensory Brain Map for Each Behavior?

In gymnotiforms, the ELL forms four separate somatotopically ordered maps of the body surface, termed medial, centromedial, centrolateral, and lateral segments (Heiligenberg and Dye, 1982). The medial segment is devoted to ampullary electroreceptor input. The remaining three segments all receive identical tuberous electroreceptor input; each individual afferent trifurcates and then projects to all three maps. This raises an interesting question: what is the function of having multiple maps of the electroreceptive body surface?

Detailed physiological studies have shown differences in the response properties of amplitude-sensitive pyramidal neurons within the three maps (Shumway, 1989). Compared to neurons in the lateral map, neurons within the centromedial map have smaller receptive fields and higher thresholds. In addition, neurons within the centromedial map show low-pass tuning to AM rates of 1–3 Hz, while neurons within the lateral map exhibit high-pass tuning to AM rates above 8 Hz. Neurons within the centrolateral map exhibit intermediate characteristics in these respects.

More recently, lesioning experiments in *Eigenmannia* and *Apteronotus* have indicated that the centromedial map encodes stimuli involved in the JAR, while

the lateral map encodes stimuli involved in chirping and other communication behavior (Metzner and Juranek, 1997). This finding makes sense in the light of physiological differences between the maps, given that the JAR is elicited most strongly in response to stimulus frequencies relatively close to the fish's own EOD frequency (modulation rates of 1–6 Hz), while chirps are elicited most strongly in response to greater frequency differences (modulation rates of 8–16 Hz) (Bullock et al., 1975; Dye, 1987). Thus, each map may have evolved to serve a different behavior.

5.4.5 Combination—Sensitivity and Feature Extraction

Determining the sign of the frequency difference between a fish's own EOD frequency and that of a neighbor requires a comparison of AM and PM. This comparison occurs within neurons in the torus, where amplitude and phase-coding pathways converge at the single neuron level onto combination-sensitive neurons (Fig. 27.16). Such neurons play an important role in many sensory systems, because information about a specific stimulus parameter often holds biological relevance only when combined with information about other parameters (Suga et al., 1978). Many of the combination-sensitive toral neurons are selective to the sign of Δf (Rose and Heiligenberg, 1986; Kawasaki and Guo, 2002). These so-called sign-selective neurons obtain their sensitivity through nonlinear interactions between their AM and PM inputs: when responses in the AM and PM inputs to a toral neuron coincide, a greater response occurs than when they are misaligned (Heiligenberg and Rose, 1986). Thus, sign-selective neurons function as neuronal AND gates. Those that are selective for $\Delta f > 0$ receive either E/lag inputs or I/lead inputs, while those that are selective for $\Delta f < 0$ receive either E/lead inputs or I/lag inputs (Fig. 27.13). Such non-linear encoding is employed by combination-sensitive neurons in many different sensory systems, as it represents an ideal solution for extracting specific stimulus features (Schnupp and King, 2001), although the mechanisms involved are only just beginning to be explored.

Neurons within the torus are also highly selective to the magnitude of Δf (Rose and Fortune, 1999). Various combinations of passive electrical filtering, voltage-dependent conductances, and frequency-dependent gain control give rise to neurons that show low-pass, band-pass, and high-pass responses to variation in AM rates. Thus, through both combination-sensitivity and temporal filtering, it is possible to determine the sign and magnitude of Δf , the relevant stimulus for electric communication in wave-type species.

Within the torus, there are also neurons that exhibit vigorous responses to chirps (Metzner and Heiligenberg, 1991). Many of these neurons receive input from both tuberous and ampullary electroreceptor pathways and are, therefore, also combination-sensitive. Because chirps contain both low and high frequency components, this convergence makes these neurons selectively responsive to chirp-like stimuli, and not to other stimuli that may activate

other communication makes sense in the light that the JAR is elicited very close to the fish's file chirps are elicited rates (modulation rates) may have evolved

when a fish's own EOD of AM and PM. This amplitude and phase-lock onto combination-sensitive toral neurons play an important role in many nucleus parameter often information about other sensitive toral neurons (1986; Kawasaki and retain their sensitivity and PM inputs: when coincide, a greater (Heiligenberg and Rose, 1986). gates. Those that are d inputs, while those s or I/lag inputs (Fig. combination-sensitive presents an ideal solution (King, 2001), although explored.

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vigorous responses to neurons receive input ways and are, therefore, both low and high e neurons selectively uli that may activate

either of the pathways alone. Thus, combination-sensitivity within the torus gives rise to neurons that extract specific features from external stimuli and thereby respond selectively to certain EOD frequency differences or social displays. In gymnotiforms, one of the primary projections of these toral neurons is to the nucleus electrosensorius in the thalamus (Fig. 27.16). This nucleus contains several subdivisions, including one sensitive to $\Delta f < 0$, one sensitive to $\Delta f > 0$, and one sensitive to chirps (Heiligenberg et al., 1991). These subdivisions project to pre-pacemaker regions that exert different effects on EOD frequency and thereby elicit the appropriate behavior for a given stimulus (see Sect. 3.4.2).

6. WEAKLY ELECTRIC FISH AS MODEL SYSTEMS FOR NEUROBIOLOGY

This chapter has focused on the many ways in which the nervous systems of electric fish are adapted for communicating by a relatively unconventional mode of signaling. Despite their uniqueness, however, many of the findings discussed exemplify basic principles in the organization and operation of nervous systems (Bullock, 1986; Zakon, 2003), as I have tried to emphasize throughout. There is clearly an abundance of information on the neuronal basis of electrocommunication, perhaps more so than for any other animal communication system. This is largely due to the relative simplicity of electric signals and the tractability of the neural networks involved. However, there are still many areas of electric fish neurobiology that have yet to be fully explored and many basic questions about the inner workings of nervous systems remain unanswered. Given their proven track record, electric fish should continue to provide ample opportunity for answering old questions and fostering new ideas.

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