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Electric Organs and Their Control

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1. Introduction: Why Aquatic Animals Evolve Electrogenic Systems

It has been known for more than 2000 years that some fish can induce painful, numbing sensations when handled. In the late 1600s, it was discovered that this sensation resulted from the production of strong electrical currents produced by the fish (Kellaway 1946). In *On the Origin of Species by Means of Natural Selection* (1859), Darwin paid special attention to difficulties with his theory, devoting an entire chapter to the subject. The evolution of electrogenesis was one such area of concern. He noted the difference in structure, innervation, and electrical power of different electric organs (EOs), and the absence of geological evidence for a possible common ancestor between the different taxa exhibiting EOs. He concluded that rather than being homologous structures, the EOs of different fishes should be considered analogous structures that evolved independently. He also raised questions about potential functions for weak EOs. Although electric emissions from weakly electric fish had not yet been discovered, Darwin believed that a functional, weak EO was a necessary step in the evolution of strong EOs. About a century later, the rigorous study of a fish that was found to produce weak electric fields provided answers to such questions (Lissman 1951). Behavioral experiments clearly demonstrated that weak EOs function in electrosensory imaging of the environment (active electrolocation) and communication (Lissman 1958; Lissman and Machin 1958). Since these initial discoveries, there has been a wealth of research into the biology of active electrosensory and electromotor systems.

1.1 Evolution of Electroreception and Electrogenesis

All aquatic animals generate weak electric fields as a result of the uneven distribution of ions between the interior of the animal and its environment (Kalmijn 1974). In teleost fish, DC potentials may reach amplitudes in the hundreds of

microvolts to millivolt range near the mouth, and ventilatory movements of the head lead to a characteristic AC modulation of this field that is detectable up to a distance of a few centimeters (Barham et al. 1969; Kalmijn 1974). Such biological sources of electrical potential serve as important cues for predatory fish with electroreceptors and were likely a powerful selective force in electro-receptor evolution (Kalmijn 1987).

More recently, AC potentials resulting from respiratory movements in the round stingray (*Urolophus halleri*) have been shown to serve as an important cue for males to locate females buried under the sand during the breeding season (Tricas et al. 1995). It is likely that similar kinds of electrical cues served as precursors to the evolution of genuine electric signals in the ancestors of extant electrogenic species. Once electrical information could be used for identifying and locating conspecifics, the stage was set for signal evolution and ritualization of electric cues into stereotyped weak electric organ discharges (EODs) for use in communication (Otte 1974). In the sea lamprey (*Petromyzon marinus*), res-piration results from highly synchronized muscle activity, which leads to a tri-phasic potential reaching amplitudes of 200 to 300 μV at a distance of 1.5 to 2 cm (Kleerokoper and Sibakin 1956). Such synchronized muscle activity is a plausible evolutionary precursor to specialized EOs, which are thought to have evolved independently at least six times (Bass 1986). They are composed of highly modified muscle or nerve cells termed electrocytes, whose summated activity results in an EOD.

1.2 Weakly Electric Fish: Electric Energy as a Carrier of Information

Measured close to the fish's body, field amplitudes of weakly electric fish are generally on the order of a few hundred millivolts per centimeter. Weak EOs are known to exist in four different groups of fish: the African mormyriforms (*Gymnarchus niloticus* and the Mormyridae, or "elephant nose fish"), the South American gymnotiforms (knifefish), several species of siluriforms (catfish), and the rajids (skates).

The EODs of mormyriforms and gymnotiforms are produced nearly contin-uously throughout the life of the animal and are highly constant within individ-uals, showing stereotypic variation that may be used to determine species (Hopkins and Bass 1981), sex (Bass and Hopkins 1983), relative dominance (Carlson et al. 2000), and possibly even individual identity (McGregor and Westby 1992). Variation in the patterning or frequency of the EOD plays an important role in electrical communication during behaviors such as aggression, courtship, and mating (Hagedorn 1986; Hopkins 1986; Carlson 2002a). In ad-dition, active electrolocation provides information on the size, shape, distance, and electrical properties of objects (Bastian 1986).

The EODs of skates and catfish are generally less stable within individuals and in some cases are produced only rarely throughout life (Bratton and Ayers 1987; Hagedorn et al. 1990). The available evidence suggests that they play a

role in communication (Bratton and Ayers 1987; Baron et al. 1994), although a role in active electrolocation cannot be ruled out. It is likely that these relatively variable EODs are similar to those of a primitive stage in the evolution of electric organs in mormyriforms and gymnotiforms.

1.3 Strongly Electric Fish: Electric Energy as a Weapon

The evolution of strong electric organs represented the addition of a new function to EODs: that of offensive and defensive weaponry. The electric fields produced by the electric eel (*Electrophorus electricus*), electric rays (torpedinids), and African electric catfish (*Malapterurus electricus*) can reach amplitudes of hundreds of volts per centimeter, and are extremely effective in stunning both predator and prey (Bauer 1979; Belbenoit et al. 1979; Belbenoit 1986; Lowe et al. 1994). Certain species of stargazers (genus *Astroscopus*) produce somewhat weaker fields (up to tens of volts per centimeter), and although evidence suggests they play a role in predation, their effectiveness is unclear (Pickens and McFarland 1964). In some species, strong EODs may also play a role in electrical communication (Rankin and Moller 1986).

2. What Is the Output of the Electromotor System?

One common method for measuring the output of the electrogenic system is to record in water the temporal course of the head-to-tail associated field of the EOD in the absence of surrounding objects (Coates et al. 1954). In most weakly electric fish these fields consist of species-specific waveforms emitted repetitively. These waveforms can be broken down into segments that are referred to as EOD wave components. The head-to-tail recording of the EOD is of great help in taxonomy and gender identification, but it oversimplifies the description of the electric field. Potentials recorded in the water along the fish body show site-specific, multiphasic waveforms that reveal the true spatiotemporal complexity of the EOD (Bennett 1971; Caputi 1999). The head-to-tail EOD is therefore insufficient to describe the stimulus for the electrosensory system when the interest is to find changes in reafferent waveform in the presence of objects or to analyze the communication signals of conspecifics.

This introduces the general problem of defining the output of an effector organ. The simplest and most general parameter for assessing this output is the external power, defined as the amount of energy transferred from the individual to the surrounding environment per unit time. However, external power is a synthetic magnitude in several senses.

First, it is the synthesis of three quantities: the mass or charge moved, the speed, and the acceleration at which the mass or charges are moved. In the case of an electromotor system, external power is the product of the drop in voltage across an external load (the work necessary to move a single charge) times the generated current (the number of charges moved per unit of time).

Second, the effector organs are connected to the external loads through passive tissues having their own filtering properties. Aponeurotic sheaths, tendons, skeleton, and tegument make it possible to transmit muscle action to the external loads. Owing to the impedance of these elements part of the generated mechanical work is dissipated internally. Similarly, part of the electrical work generated by the electrogenic tissue is dissipated internally because of current flow through internal tissues and skin.

Third, in real systems energy transfer does not occur at a single point. At the soles of the feet and at the pads of the fingers (and even the whole surface of the body in contact with the air or water when the speed causes enough resistance), mechanical energy is transferred according to a spatiotemporal pattern. Thus, the power transferred to the environment in every instant is the spatial synthesis (or integration) on all relevant surfaces. In the case of the electromotor system, the power results from the integration of current density and electric potential throughout the skin surface of the animal.

2.1 The Nervous System Controls Electromotive Force Generation

Electric fish inspired the famous Voltaic pile, which was described by its designer as an "artificial electric organ." At that time it was recognized that the complete description of such a system requires at least two parameters describing the "force" required to expel a certain "quantity" of electricity through the skin (for an historical review see Moller 1995). In fact, the fish body may be represented as a battery having an electromotive force (EMF) and an internal resistance (R_i) connected in series (Cox and Coates 1938; reviewed by Caputi 1999; Fig. 14.1) When a fish is isolated in air, and its rostral and caudal extremes are connected by a resistive load (R_{load}), the generated current is a linear and decreasing function of voltage across the load. When the connection is open, current is null and voltage is equivalent to the EMF. It is important to note that the EMF is not the battery output but its ability for generating a given output when connected to a load. When the external load resistor decreases in value the current increases up to a maximum at short circuit. The equivalent circuit for the fish consists of a time variant EMF with both poles connected to fixed internal and external resistors. The amount of energy transferred to the environment is at a maximum when both resistors are equal.

The larger the resistance of the internal tissues, the smaller the maximum current (and therefore the power) that the fish body is able to yield (Fig. 14.1B). To illustrate this feature Figure 1B compares the voltage versus current plots obtained from two fish of different size. Small fish (filled symbols) and large fish (open symbols) generate the same electromotive force but the larger fish can deliver a larger amount of current, because internal resistance decreases with body size (Caputi et al. 1989; Caputi and Budelli 1995).

It is clear that the electromotor system (i.e., the neural network and the electric organ under their control) is only a part of the electrogenic system, which also
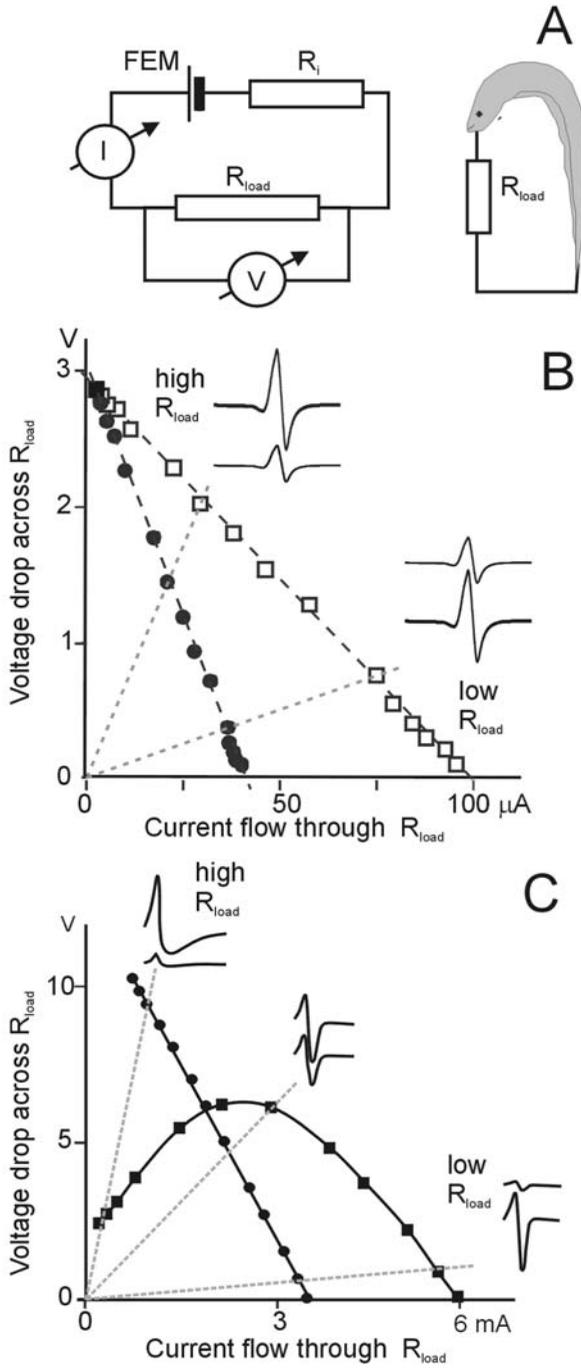
includes nonelectrogenic tissues that set the internal resistance. The nervous system directly controls the EO and determines its stereotyped time course of activation. When the load is exclusively internal (fish tissues), the electrical output resulting from the EOD is the equivalent EMF of the fish body. However, the electrical output is contingent on the external impedance and thus the nervous system does not control the actual output of the electrogenic system but only its EMF (Caputi 1999).

Furthermore, minor but behaviorally significant changes in EMF may depend on the external load. As shown in the example in Figure 14.1C, late waves of the EOD do not result from the neural activation of the EO but are a consequence of the initial, externally dependent EO output. In these cases the function relating current and voltage is not linear, indicating that either electromotive force, internal resistance, or both, are dependent on external load and the analogy with a simple electric battery is unsatisfactory (Bell et al. 1976; Caputi et al. 1998; see Section 4.2). On a different time scale the impedance of the fish's tissues is controlled by the complex homeostatic system under environmental and neuroendocrine control (see Section 4.2). Interestingly, fish growth is a harmonic process that keeps the generated EMF by adult animals as a constant species-specific feature independent of body length.

2.2 Geometry of the EO and Nonelectrogenic Tissue Determines the Field Shape

If the EO were relatively short and immersed in a medium of homogeneous impedance, the external field could be approximated by a dipole. However, the bodies of freshwater fish have an internal resistance much lower than the external resistance, while the reverse is true for marine fish (Kalmijn 1974). This discordance between the impedance of internal tissues and the external medium means that one of the main determinants of the external field is the species-specific body geometry.

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FIGURE 14.1. Equivalent electric source parameters. (**A**) The fish body can be considered as a simple battery in which V is the voltage drop across the load resistance R_L, and I is the current through the circuit (*left*). The air-gap recording system that allows one to evaluate the equivalent electromotive force (EMF) and internal resistance (R_I) in electric fish is shown in the schematic diagram at the right. (**B**) The plot shows the positive peak voltage across R_L as a function of the corresponding peak current, measured in two differently sized fish [*Gymnotus carapo* of 8 cm (*filled circles*); 20 cm (*open squares*)]. Note that, in spite of the difference in length, the ordinate intersection (the electromotive force, EMF) is approximately the same while the slope of the line (R_I) decreases with animal length. $V = EMF - R_{i\,I}$. (Modified from Caputi 1999.) (**C**) In *Gnathonemus petersii*, while the positive wave (*circles*) the negative phase exhibits a maximum (*squares*). This is because loading the EO causes a change in the emitted waveform: the negative phase is a function of the current generated during the positive phase. (Modified from Bell et al. 1976.)

Pulse mormyrids have a relatively short EO localized at the caudal peduncle, which makes it easier to understand this posteffector conditioning of EO output. The specific conductance of the fish's body is more than 20 times larger than that of the surrounding water, whereas the transverse surface area and the length of the main body are much larger than the EO (Budelli et al. 2002; Caputi et al. 2002). For these reasons the resistance that the body opposes to current flow in the rostral direction is less than the resistance that the water opposes; thus most of the current is funnelled through the fish's body (Castello et al. 2000). This means that the passive fish body acts equivalently to an additional electric source located rostrally.

The situation is more complex when the EO is not localized but is instead distributed along an extended portion of the body. This is the case in most gymnotiforms and the mormyriform *Gymnarchus niloticus*. In these cases each longitudinal portion of the EO can be considered an independent source, having its own internal resistance and being loaded by different portions of the fish either in the rostral or caudal directions.

Therefore, geometry plays an even more important role in fish having extended EOs than in pulse mormyrids. Gymnotiforms and *Gymnarchus* have a fusiform shape with an asymmetric tapering angle to both poles. In the caudal two thirds of the body, the cross-sectional area and the cross-sectional area/perimeter ratio decrease from head to tail. This causes a parallel increase of the generator series resistance and the body attenuation coefficient. As a consequence of the increase in the ratio between series and load resistance, for an identical distance, the body attenuation coefficient causes a larger voltage decay in the caudal than in the rostral direction. In this way, fish geometry orients currents longitudinally and polarizes current flow in a caudal to rostral direction (Caputi et al. 2002).

Because of the difference in internal resistance, caudal regions of the EO behave as "current" sources (high internal resistance), while rostral regions behave as "voltage" sources (low internal resistance). As a consequence, geometry and impedance are weighting factors for the contribution of every fish portion to the whole EOD-associated field (Caputi et al. 2002). Moreover, in these fishes the EO is not synchronously activated and in some species different EO portions do not generate identical waveforms. Therefore, the external field shows a complex, site dependent temporal waveform (see Section 4.2).

In conclusion, there is not a single measure of electromotor output and the most comprehensive way to assess the output of the electromotor system is to measure the EMF and internal resistance distribution along the fish to construct a model of the fish body as an electric source. This kind of model was recently implemented and applied for calculating the EOD-associated field in different circumstances and also to calculate electric images of nearby objects and neighboring conspecifics (Budelli et al. 2002; Caputi 2004).

3. Two-Step Strategy for Electrogeneration

The temporal course of the EMF is a stereotyped spatiotemporal function organized at the spinal and peripheral levels and repetitively triggered by the discharge of a command nucleus located in the brain stem. The discharge of the command nucleus activates a relay structure that projects to the spinal structures. Thus, the electromotor system is organized as two networks hierarchically linked at the command-relay level. The superior network receives multiple influences including those from sensory modalities and internal motor collaterals, and has a single output: the synchronized discharge of the command nucleus. This event decides the activation time of the lower network that in turn transforms the series of command impulses into a series of stereotyped EODs.

3.1 Classification of Electric Fish According to Their EODs

The relationship between the duration of the EOD and its timing have permitted the differentiation of two main groups of weakly electric fish. In *wave-type fish*, the discharge interval is regular and similar to the duration of the EOD. The electrogenic output therefore has a continuous sinewavelike shape. In these fish the discharge frequencies range from about 100 to 1000 Hz depending on the species. The inter-EOD interval shows a very small coefficient of variation (less than 0.0001 in the resting fish, Bullock 1986). Wave-type fish are represented in both main groups of weakly electric fish. In mormyriforms they are represented by a single species (*Gymnarchus niloticus*) and in gymnotiforms by two families (*Stermopygidae* and *Apteronotidae*). In these fish, the command neurons function as coupled oscillators (Moortgat et al. 2000). The relay neurons project on spinal neurons innervating the electrocytes (the electromotorneurons, EMNs), driving them at the command frequency.

The rest of the weakly electric fish are referred to as *pulse-type fish* because the interval between command discharges is much larger than the duration of the EOD and the electrogenic output consists of a series of discrete beats of similar waveform. Pulse-type fish are represented in the two main groups of weakly electric fish. Their electrogenic strategy is based on completely different mechanisms at the three levels of the system: (1) the command nucleus of pulse-type mormyrids show an irregular pattern of discharge, in contrast to the pacemaker of pulse-type gymnotids, which exhibits a very regular discharge rate (coefficient of variation less than 0.05); (2) pulse-type mormyrids have a short and localized EO that generates a synchronous and uniform discharge while gymnotiforms have extended organs producing different regional waveforms in a rostrocaudal sequence; and (3) their different body geometry causes a different distribution of internal resistance and posteffector spatial filtering of the generated EOD.

The less studied weakly electric fishes (skates and catfishes), and the strong discharging fishes, may also be considered pulse-type fish. In the case of skates the command drives an EO located at the tail. The location of the EO poses a

similar electrogenic problem as in pulse-type mormyrids. However, the peculiar shape of the fish body and the relatively low resistance of the habitat may cause important although still unexplored posteffector conditioning.

In conclusion, electric fish show a two-step strategy for electrogenesis based on two networks hierarchically linked at a command nucleus. According to their electrogenic strategy, they can be classified into three main types: wave-type fish (some gymnotiforms and *Gymnarchus niloticus*), pulse-type fish with localized organs and irregular discharge timing (pulse mormyrids, rajids, and some siluriforms), and pulse-type fish with extended organs and regular discharge timing (pulse gymnotiforms).

3.2 Variations in the EOD Waveform Within a Species

The EO and its innervation pattern and the neural command wiring seem to be organized to assure a constant species-specific waveform that does not vary across individuals of the same species and along the life span of each individual. In general it could be stated that every discharge of the command nucleus is followed after a fixed time by a stereotyped discharge of the EO. Within a large confidence interval around the average discharge rate of the command the spinal network is able to control the EO to generate the species-specific waveform.

Nevertheless, simpler waveforms have been described for larval electric fish. In addition, the electric power of the EOD increases with fish length and weight, both of which are dependent on age. In some aggressive species (i.e., *Gymnotus carapo*), it is common to find individuals with regenerated tails. Some small individual variation in waveform has been observed in relation to regeneration.

Sex differences in waveform have been reported in many different species (Hopkins 1972; Hagedorn and Carr 1985). These changes are generally associated with reproductive cycles, which are about annual in most cases, and are regulated by sex steroid hormones (Zakon 1993). Amplitude and duration changes in the EOD have been observed in *Brachypopomus,* where action potential propagation that provokes the late head-negative wave is under endocrine and thermal control (Silva et al. 2002). In the wave fish *Sternopygus*, the change in waveform (slower frequency in the maturing male) results from an EOD with a longer duration combined with a slower repetition rate. As described below, this implies a dual action of androgens both at central and peripheral structures (Zakon 1993).

Water temperature can also modulate the EOD waveform. During winter undifferentiated *Brachyhypopomus pinnicaudatus* ("pez ratón") show high waveform sensitivity to temperature but sensitivity decays in spring to a minimum in the reproductive summer months. In the temperate zone, water temperature exhibits circadian and annual cycles covering a large range (6 to 30°C). Silva et al. (2002) hypothesized that sustained warm temperature is an environmental cue for sexual maturation and that low waveform sensitivity to temperature

might be a requirement for sexual communication, recognition, and mating. Present evidence supports this hypothesis: lowering waveform sensitivity to temperature could be induced both by testosterone treatment and by acclimation to maintained high water temperature (28°C; see review by Silva et al. 2002).

Finally, a tradeoff between active electrolocation and communication occurs during social interaction. In these circumstances command rate may increase in the form of transient bursts (so-called "chirps") or decrease in the form of long pauses. These modulations of the EOD waveform constitute communication signals during sexual and aggressive interactions. Chirps are accompanied by changes in the waveform and amplitude of the EOD that probably jeopardize the ability to electrolocate. Pauses not only block active electrolocation but also are followed by changes in the peripherally organized late waves (Schuster 2000).

4. Organization of the EOD Waveform

The electromotor system is organized in parallel to the skeletomotor system. Most fish have an EO composed of series of electrocytes derived from muscle tissue that are controlled by electromotor neurons located in the spinal cord. The Apteronotidae evolved a different electrogeneration strategy. In adults the EO is completely of neural origin. It consists of an array of electromotor neuron axons running in parallel along the fish's body. Its electrogenic mechanism is discussed in previous reviews of this topic and is not treated in detail here (Bennett 1968, 1971; Bass 1986).

In fish having myogenic EOs the EMF is the sum of postsynaptic currents and action currents generated in hundreds of electrocytes. As in the skeletomotor system, each electromotor neuron innervates a set of synergistic effector units (a set of similarly oriented electrocytes in series). In most cases, however, each electrocyte receives innervation from several electromotor neurons. Because of this convergence on the same effector structures (a set of electrocyte faces), the sum of activities evoked by a set of individual electromotor neurons is smaller than the activity evoked by the synchronized activation of the same set. An additional difference from the skeletomotor system of vertebrates derives from the fact that the effector target of synergistic electromotor neurons is a subcellular structure; in some species a single electrocyte implements antagonistic actions depending on the activated region of its membrane. In pulse gymnotiforms, different electromotor neuron types innervating opposite faces of the same electrocyte elicit coordinated antagonist effects (see Section 4.3). Therefore, to organize the EOD waveform, the nervous system has to coordinate the activity of different electromotor neuron types to activate similarly oriented electrocyte faces synchronously and sequentially activate opposite oriented electrocyte faces.

4.1 Contribution of Single Electrocytes to Waveform Generation: Roles of Shape, Ion Channel Repertoire, and Innervation Pattern

Three elements are important to determine the contribution of a single electrocyte to the discharge of the whole EO: (1) electrocyte morphology, (2) repertoire and distribution of ion channels, and (3) innervation pattern.

As currently believed for most excitable cells the electrical activity of electrocytes depends on the change in conductance of different populations of "membrane channels" having differential conductance for specific ion types (Hille 2001). As observed in other cells, channel density is heterogeneously distributed over the surface of the electrocytes, and therefore different electrocyte regions may have different current components. These components summate in the extracellular space to generate the contribution of each individual electrocyte to the EOD.

The basic rule for understanding current flow resulting from electrocyte activation was stated long before currents were measured in individual electrocytes. Paccini observed that "the innervated faces of the electroplaques become negative during the discharge whatever the orientation of the organ" (cited by Keynes et al. 1961). In the resting situation there is no external current flow because of the prominence of potassium conductance. During and shortly after synaptic activation, localized changes in various conductances produce an uneven distribution of the membrane parameters that results in a "macroscopic" external current. Because of the decrease in net EMF (or even inversions) and conductance near the synaptic contact the negative interior of the electrocyte becomes "electrically closer" to the innervated region.

These changes in potential may cause regenerative action potentials that propagate to other regions of the electrocyte membrane. In different species, electrocytes adopt different shapes, and within species, electrocytes may have different shapes in different regions of the EO. As a consequence, local attenuation (generally constant in a fine cylinder such as an axon, and estimated by the length constant) governing action potential propagation depends on the shape and membrane region of the electrocyte. Combinations of all these elements, associated with the localization of the synaptic contacts and their activation timing determine the propagation of electrical activity on the cell surface and the waveform of the electrocyte output characteristic of the region of the EO in each species.

Electrocyte activity results in different types of locally generated waveforms. There is a broad repertoire of waveforms displayed by the various types of electrocytes. They are described extensively elsewhere (Bullock and Heiligenberg 1986; Kramer 1990; Moller 1995; Hopkins 1999). Figure 14.2 shows some examples illustrating the principal electrogenic mechanisms at the electrocyte level.

Monophasic waveforms depend on the activation of the innervated face. In some fish, such as strong marine electric fish, rajids and the electric eel *Elec-*
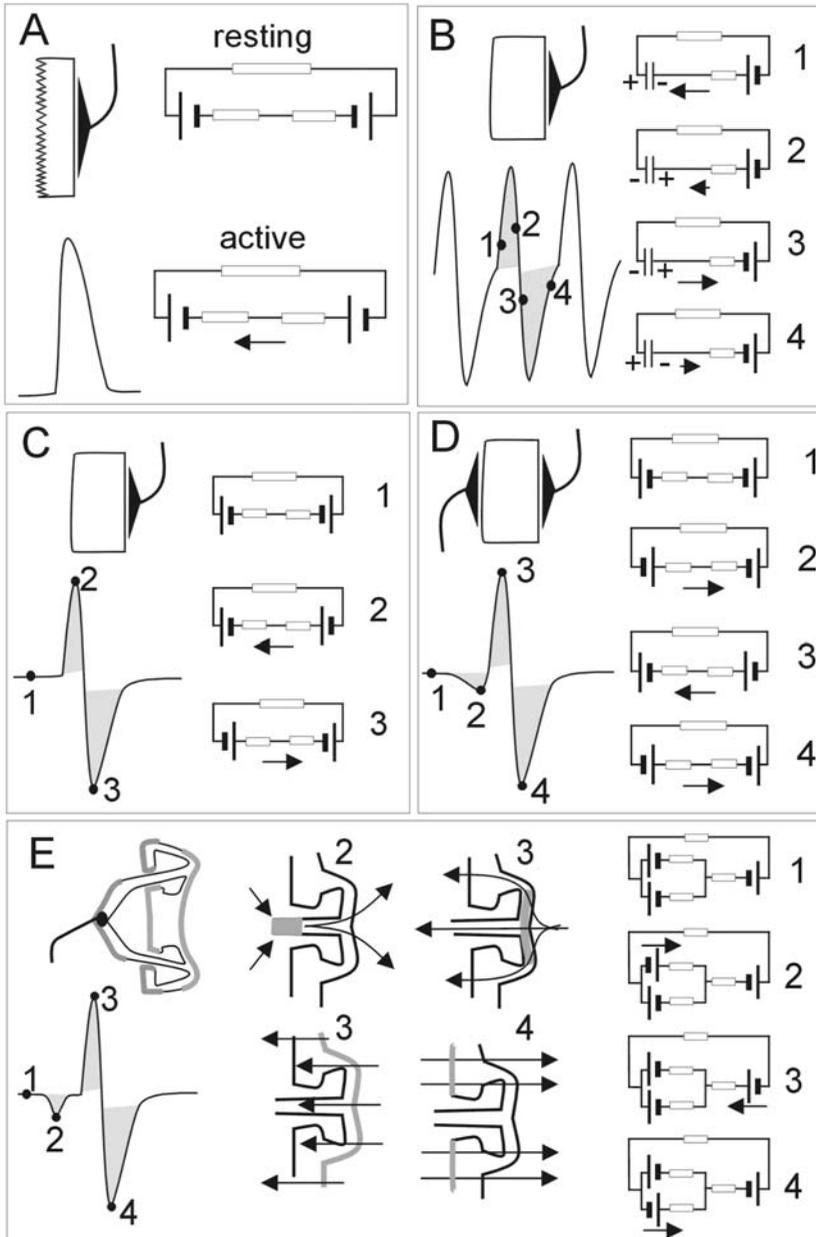
FIGURE 14.2. Different strategies for generating the elementary components of the EOD waveform at the electrocyte level (as suggested by Bennett 1961, 1971). (**A**) Monophasic waveforms. (**B**) Biphasic waveforms: electrocyte resonance. (**C**) Biphasic waveforms: the propagation of action potentials. (**D**) Bi- and triphasic wavefoms generated by double innervated electrocytes. (**E**) Triphasic waveforms generated by stalked electrocytes.

trophorus electricus (Fig. 14.2A), the electrocytes receive innervation on a single face and generate postsynaptic potentials or action potentials restricted to the innervated face. The opposite face has very low resistance. As explained above, the innervated face becomes transiently negative and the resulting EOD is monophasic.

A derived wave with reverse polarity can be generated in the face opposite to the innervated one. This could be implemented by different mechanisms. In *Gymnarchus niloticus* and other wave-type fish, electrocytes receiving innervation on a single face generate postsynaptic potentials or action potentials that do not propagate to the opposite face. However, because of its large resistance the admittance of the opposite membrane is mainly capacitive. As a consequence negativity occurs transiently at the innervated face and the current flow accumulating at the opposite face changes polarity. Subsequently, while the innervated face returns to the resting situation the noninnervated face discharges, resulting in a biphasic EOD. The charging-discharging period is similar to the pacemaker interval, resulting in a continuous sinewavelike discharge (Fig. 14.2B). Alternatively, in most fish exhibiting biphasic waveforms, electrocytes receiving innervation on a single face generate postsynaptic potentials or action potentials that propagate to the opposite face. As a consequence negativity occurs transiently at the innervated face and subsequently at the opposite face, again leading to a biphasic EOD. The asymmetry in area and channel repertoire between both faces generates asymmetry between both phases of the discharge (Fig. 14.2C).

Local multiphasic waveforms could be generated by two different mechanisms that evolved separately. The electrocytes of pulse mormyrids exhibit a singular topological organization. They are thin fenestrated discs that give rise to many stalks that fuse at the site of innervation (Bass 1986). In the example shown in Figure 14.2E, the stalks arise from the caudal face, then reverse course and penetrate the disc to receive innervation on the anterior side. Synaptic activity on the stalks generates a small head negative current. This is followed by a strong head-positive phase resulting from action potential propagation to the caudal face and subsequently by a head-negative phase due to action potential propagation to the rostral face of the main disc, leading to a triphasic EOD (Fig. 14.2E).

Pulse gymnotiforms (*Gymnotus* or "morenita" and *Rhamphychthys* or "pez bombilla") evolved doubly innervated electrocytes, which not only allows them to generate multiphasic waveforms, but also to coordinate a temporally complex discharge. Head-negative waves result from postsynaptic potentials or action potentials elicited in the rostral faces by terminal branches of electromotor nerves and head-positive waves result from action potentials evoked at the caudal faces by a delayed activation volley. A final head-negative wave resulting from the propagation of the action potential to the rostral face may also be present in some electrocytes (Fig. 14.2D).

4.2 Peripheral Mechanisms for Waveform Plasticity

Although neural activation of the EO seems to be a very robust mechanism for producing a constant EOD waveform, changes in the properties of the effector cells are the main mechanisms involved in waveform plasticity. Water conductivity and temperature naturally affect the EOD waveform. The former changes the electric load and thus the current flow associated with the EOD. In some species, such as the elephant nose fish, *Gnathonemus petersii,* the flow of current underlying the early phase of the EOD is involved in stimulating the noninnervated face of the electrocytes. As seen in Figure 14.1C, in the initial phase, the voltage and current are linearly related, indicating that the number of active electrocytes that are recruited by the neural volley is constant and independent of the external load. However, recruitment of the opposite electrocyte faces and the equivalent EMF for the late wave depend on the external current, which is highly affected by water conductivity. When the load increases the current generated by the innervated faces decreases dramatically. Below a certain water conductivity, the currents generating the first phase are subthreshold for stimulating the opposite face. This explains why at the late phase the voltage increases as a function of current as electrocytes are being recruited, reaches a maximum about complete EO activation and finally when conductivity is high it decays as a function of current approximating a straight line (Fig. 14.1C). Thus, any factor that regulates the excitability of the noninnervated faces and the shape of the action potential will modify the EOD waveform.

In pulse mormyrids and pulse gymnotids, action potential propagation from the caudal to the rostral face is under endocrine control (Bass 1986; Moller 1995).

Although the EOD waveforms of immature *Brachyhypopomus pinnicaudatus* are not sensitive to load, the late waves of both the male and female EODs are relatively enhanced when the EO is loaded by low resistances. This indicates that the electrogenic activity is enhanced during sexual differentiation (Caputi et al. 1998). Temperature appears to diminish the responsiveness of the noninnervated face, causing a reduction in the late wave in nondifferentiated animals. However, this reduction is compensated in differentiated fish by an opposing hormone-dependent effect as evidenced by the increase in the late wave in low conductivity. Androgen-induced changes in electrocyte membrane excitability and action potential shape have been related to sex-specific features of the EOD waveform (Hagedorn and Carr 1985; Bass and Volman 1987).

A more complex phenomenon occurs in wave gymnotiforms, in which androgens cause a coherent change in both EOD waveform and frequency (Zakon 1993). The best-studied example is *Sternopygus*, which emits a sexually dimorphic wave-type EOD. In these fish the frequency is lowered by systemically applied androgens, which also leads to a corresponding increase in the duration of single EODs, while estrogens have the exact opposite effect. A recent study suggests that steroid-mediated changes in EOD duration and frequency result

from independent peripheral and central actions, respectively (Few and Zakon 2001).

Androgen-induced changes in the EOD may also be paralleled by morphological changes in the electrocytes (Bass 1986). In pulse-type mormyrids, the degree of surface invaginations is generally greater in species with longer duration EODs. Among species with sexually dimorphic EODs, natural males and females treated with gonadal steroid hormones have longer-duration EODs and thicker electrocytes with more surface invaginations along the anterior face. Presumably, these morphological changes affect the capacitance of the electrocyte membrane, thereby increasing its time constant of activation.

4.3 The EO as a Population of Electrocytes

The electromotor output results from the sum of activities of subcellular units, electrocyte faces similarly oriented and orderly recruited by the electromotoneuron pools. Membrane properties and the innervation-activation pattern determine each electrocyte contribution to the regional waveform. Electrocyte size and density determine amplitude. Owing to the impedance of nonelectrogenic tissues, electrocyte location determines both the amplitude of the discharge and the ratio between internal and external work.

There are multiple types of EOs according to the structural organization of their electrocyte population types. In one extreme some fish exhibit a uniform population of electrocytes densely packed in a short localized EOs, in the other multiple populations differing in type, size, and density are distributed along an extended EO. The following examples describe the main types of EO following a criterion of increasing complexity in organizational features.

4.3.1 Case 1. The Uniform EO of Pulse-Type Mormyrids

In pulse-type mormyrids the EO is located within the caudal peduncle and consists of four columns of electrocytes. Almost the entire cross section of the caudal peduncle is made up of EO. Each column of electrocytes occupies one quadrant and the only other structures are the spinal column, the tendons to the fin, and the skin. The electrocytes are a homogeneous population of thin, multinucleated discs, each containing a series of stalks that arise from the posterior or anterior face and fuse to form a single large stalk that receives electromotor neurons innervation (Bass 1986). The stalks actively propagate action potentials to the electrocytes, where both the anterior and posterior faces are also active (Bennett 1971). There is wide diversity in the morphology of this stalk system across species, and electrocytes may be classified according to the site of innervation (anterior versus posterior) and as penetrating, doubly penetrating or nonpenetrating, based on whether the stalks reverse course and penetrate the electrocyte face once or twice before fusing (Hopkins 1999). These differences in morphology are directly linked to species differences in EOD polarity and number of phases. Because the EO is formed from a homogeneous population

of electrocytes, the EOD can be understood as a simple amplification of the electrical activity of a single electrocyte.

4.3.2 Case 2. The Extended EO of Wave-Type Gymnotiforms

Wave gymnotiforms such as *E. virescens* have a single type of electrocyte innervated only on their caudal face. However, their extended EO is not homogeneous: electrocyte size and separation diminish exponentially from head to tail. Although the EOD waveform is similar among different regions, the amplitude is not. Consistently, the amplitude of the local EOD shows an exponential increase along the EO, indicating that the amplitude of the local EOD is proportional to the number of generating units.

4.3.3 Case 3. The Complex EO of Pulse-Type Gymnotiforms

Pulse-type gymnotiforms show up to four different degrees of complexity: type, innervation, size, and density are not constant along the EO, causing different local features in the EOD (see reviews by Macadar 1993 and Caputi 1999).

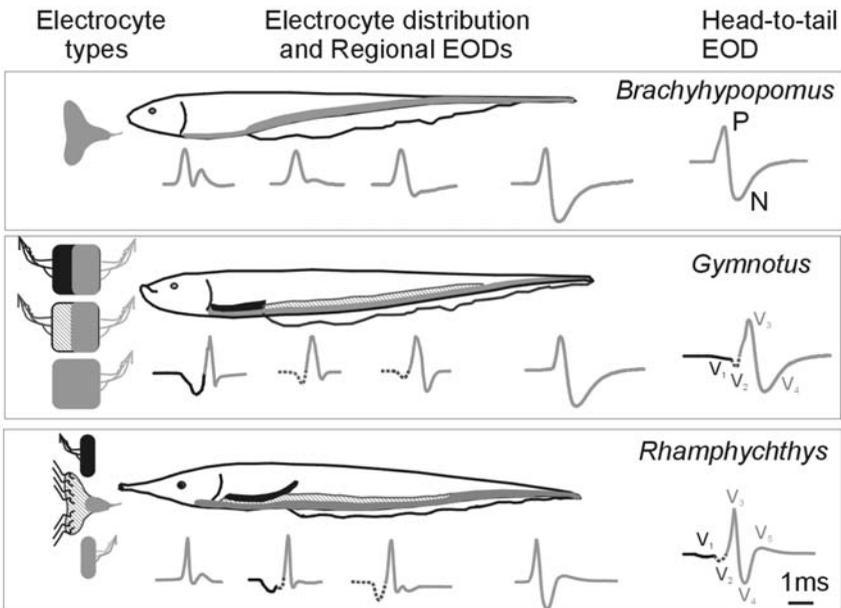Three paradigmatic examples are shown in Figure 14.3 to illustrate different

FIGURE 14.3. Comparing different anatomical and functional complexity of the EO in pulse gymnotids. This semischematic drawing (modified from Caputi 1999) correlates different electric organ (EO) portions with samples of the regional electric organ discharges (EODs) recorded in air-gap conditions in three species. It also illustrates the distribution of the different electrocyte types along the EO.

degrees of complexity. The simplest example is *Brachyhypoppomus pinnicaudatus*, which exhibits singly innervated electrocytes differing in size, density, and membrane responses along the EO. Two pairs of tubes extend from the tip of the tail to the anal papilla while the other rows do not extend beyond the rostral edge of the anal fin. All the electrocytes are caudally innervated (Trujillo-Cenoz et al. 1984). This simple innervation plan is consistent with the observed biphasic head-to-tail EOD waveform and with the spatiotemporal pattern of the EMF. Nevertheless, owing to size and density the amplitude of the local discharge increases exponentially from head to tail. In addition, the ratio between the amplitude of the late wave-components and the amplitude of their preceding waves is not constant along the fish body. This feature depends on the membrane properties of electrocytes. Whereas large electrocytes located at the rostral regions of the EO produce a monophasic local waveform, small and caudally located electrocytes generate a biphasic local waveform (Fig. 14.3). As explained in Section 3, late wave components are due to the propagation of the neurally elicited action potentials from the innervated to the noninnervated face. This indicates that the intinsic properties determining the efficiency of action potential propagation along the electrocyte membrane are correlated with electrocyte location along the EO.

A remarkable feature that appears in pulse-type gymnotiforms is the presence of doubly innervated electrocytes. This strategy allows the nervous system to control the timing of activation of different electrogenic structures and construct complex electromotor outputs. The best-studied example is the EO of *Gymnotus carapo*, which consists of eight longitudinal tubes running parallel, on parasagittal planes, four on each side of the body. The dorsal tube on each side (tube 1) has doubly innervated electrocytes in its abdominal and central portions but not in its caudal portion. The other tubes contain only caudally, singly innervated electrocytes. Tube 1 (containing the doubly innervated electrocytes) and tube 2 extend within the abdominal wall to the anal papilla while the others do not. On the other hand, all electrocytes in the caudal portion of the EO are innervated exclusively on the caudal face. Thus, the EO of *Gymnotus carapo* has three different zones according to their innervation pattern (Fig. 14.3). Four wave components (V_1 to V_4; Fig. 14.3) are present in *G. carapo*. V_1 results from the postsynaptic potentials at the rostral faces of abdominal doubly innervated electrocytes; V_2 results from the action potentials at the rostral faces of doubly innervated electrocytes at the central region; V_3 results from the action potential elicited at the caudal faces of most electrocytes; and V_4 results from propagation of this action potential to the rostral faces.

An even more complex example is the EO of *Rhamphychthys rostratus* ("pez bombilla"). This fish shows three types of electrocytes with dissimilar innervation pattern: caudally innervated, rostrally innervated, and marginally caudally innervated. These doubly innervated electrocytes show three distinctive features: (1) the nerve fibers arriving at the rostral side form a regular palisade all over the electrocyte margin; (2) synaptic junctions occur in the marginal membrane; and (3) the caudal faces bear large ridges receiving most of the caudal inner-

vation (Fig. 14.3C). In the subopercular region, the EO of *Rhamphychthys ros-tratus* consists of a pair of tubes containing only caudally innervated electrocytes. In the abdominal region the EO consists of three pairs of tubes. Each pair contains one of the described electrocyte types. In the central region, most tubes contain doubly innervated electrocytes and in the caudal 25% exclusively caudally innervated electrocytes occur. This electrocyte variety supports a more complex EOD pattern that exhibits five wave components. V_1 results from the activity of the rostral faces of rostrally innervated electrocytes; V_2 results from the activities of rostral faces of marginally caudally innervated electrocytes; and V_3 results from the activities of caudal faces of most electrocytes. V_4 and V_5 are not directly elicited by neural activity and probably result from repetitive activity of single innervated electrocytes resulting from action potential propagation from one face to the other.

4.4 Coordination of Electrocyte Activity: The Neural Network

To organize the stereotyped pattern of EO activation, the nervous system must determine the timing of activation of the electrocyte faces. As explained above, EOs show great variability in their organization. While some taxonomic groups (i.e., pulse mormyrids) use the simple strategy of summing the synchronized activities of a large population of electrocytes, each one generating a similar response to their synaptic drive, in other groups (i.e., pulse gymnotiforms) the EOD is the sum of subcellular responses to a highly organized neural activation pattern. In these last cases (1) the same subset of electrocytes faces must be activated in a very fast rostrocaudal sequence along the EO and (2) different subsets of electrocyte faces located at different sites along an extended organ have to be recruited in the temporally correct order. From the simplest to the most complex case, performance of these tasks depends on interactions among three types of excitable cells: the relay neurons (RN), the electromotor neurons (EMNs), and the electrocytes (Fig. 14.4A). RNs receive the EOD command and project onto electromotor neurons, which in turn project onto electrocytes. Each subset of excitable cells may be considered a layer in a network arranged with a lattice hierarchy. At both projection levels there is convergence and divergence, ensuring by a distributed control strategy, the timing of activation of electromotor neurons and electrocyte faces. In addition to the neural mechanisms of synchrony, the electric interaction between neighboring electrocytes facilitates synchrony (Albe-Fessard and Buser 1950).

   The synchronous activation of equally oriented faces of the same kinds of electrocytes requires equalization of the time taken by the neural volley from the pacemaker to the electrocyte face response. Several mechanisms act synergistically to equalize this time: whereas in pulse-type mormyrids the most important is the similarity in length of spinal and peripheral pathways resulting from the occurrence of a short EO localized at the tail, in gymnotiforms the presence of a long and in some cases heterogeneous EO requires time equali-
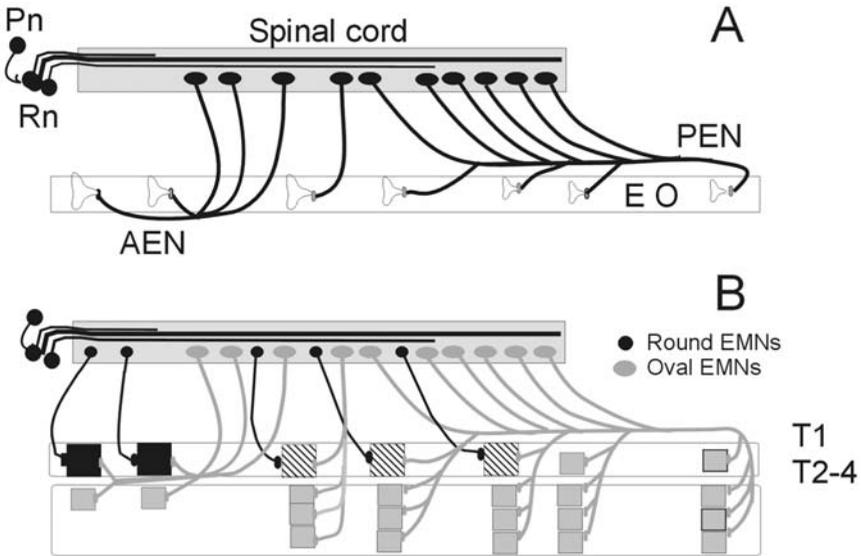
FIGURE 14.4. The neural network organizing the EOD waveform in pulse gymnotids. (**A**) *Brachyhypopomus* is the simplest example to show the main elements of the network. The descending tract contains fibers of different length, the longest fiber being the thickest. There is a single pool of electromotor neurons whose domain along the spinal cord is shorter in length than the EO. This difference in length is accounted rostrally by a recurrent nerve (anterior electromotor nerve, AEN) and caudally by an antecurrent nerve (posterior electromotor nerve, PEN). All electrocytes are innervated in their caudal faces. (**B**) While synchronism is similar to that in *Brachyhypopomus*, in *Gymnotus* wave sequencing depends on the orderly recruitment of two different electromotoneuron pools, one of small round neurons (*black*) and a second of large oval neurons (*grey*) innervating the rostral and caudal faces of the electrocytes, respectively. (Modified from Caputi 1999.) Note the different distributions of both electromotor neuron types and the distribution of different types of electrocytes along the different tubes composing the EO (T1 to T4; see also Fig. 14.3).

zation at the different stages of the neural network as those suggested by Bennett (1971) and experimentally described by Albe-Fessard (1954), Trujillo-Cenoz et al. (1986), Lorenzo et al. (1990), and Caputi and Trujillo-Cenóz (1994). The relative importance of these mechanisms depends on the species and can be characterized by field potential analysis in the intact fish (Caputi and Aguilera, 1996). It is important to note that rather than synchronizing the activity of similar electrocyte faces the nervous system provides the EO with an activation sweep running about 1 km/s along the EO and yielding a head to tail delay of 0.2 to 0.4 ms which is in the neighborhood of a cycle in a wave fish discharging at 300 Hz.

The organized recruitment of different sets of homologous faces generating

the different waves composing the EOD appears to be based on the presence of different electromotor neuron pools corresponding to each subset of electrocyte faces. In *Gymnotus carapo,* wave sequencing appears to be based on two mechanisms related to electromotor neuron size and location. First, Hennemann's size principle (Hennemann 1957) appears applicable to the electromotor system. As mentioned, some pulse gymnotiforms, such as *Gymnotus carapo,* have doubly innervated electrocytes and exhibit two morphological types of electromotor neurons (Fig. 14.4B): ones with small-round somata and others with large-oval somata (Caputi and Trujillo-Cenoz 1994). The rostral regions of the spinal cord contain exclusively small-round electromotor neurons; in the intermediate portions, large and small neurons coexist; and the caudal region contains only large neurons. Furthermore, electromotor neuron location along the spinal cord is correlated with their projection site along the EO (Caputi and Trujillo-Cenoz 1994). Thus, large electromotor neurons innervating a large population of caudally innervated electrocytes would be recruited later and with lower safety factor than small electromotor neurons projecting to the rostral face of rostrally innervated electrocytes. Therefore head negative waves will precede head-positive waves (Caputi and Trujillo-Cenóz 1994).

A second mechanism for sequencing the activation of opposite faces is that the rostral faces of the abdominal electrocytes are innervated by a pool of small electromotor neurons located rostral to the electromotor neurons innervating the caudal faces of the same electrocytes (Trujillo-Cenoz et al. 1984; Caputi and Trujillo-Cenoz 1994). As a consequence, the neural path from the pacemaker to the rostral faces of abdominal electrocytes is much shorter than the path serving all other electrocytes.

The process of EO activation in *Gymnotus carapo* is one of the best known examples of motor pattern organization (see review by Caputi 1999). This example illustrates how a simple network synchronizes and sequences about a thousand independent effector units transforming a single impulse into a complex stereotyped electromotor pattern.

5. Timing Control of the EOD: Roles in Communication and Active Electrolocation

Wave-type fish produce very regular firing patterns, with interval durations approximately equal to pulse duration, thus resulting in a continuous quasi-sinusoidal discharge of 150 to 1200 Hz, depending on species, sex, and behavioral state. Pulse gymnotiforms generate pulses of 1 to 5 ms, separated by intervals of ten (or more) times longer duration. EODs are repeated at quite regular frequencies (coefficient of variation less than 0.05). While gymnotiforms and *Gymnarchus* modulate a regular pulse train (frequency control), pulse mormyrids utilize pulse-by-pulse control (interval control). Correspondingly, the former have a pacemaker command with an endogenous rhythm that may be modulated by descending prepacemaker centers, while the latter have a com-
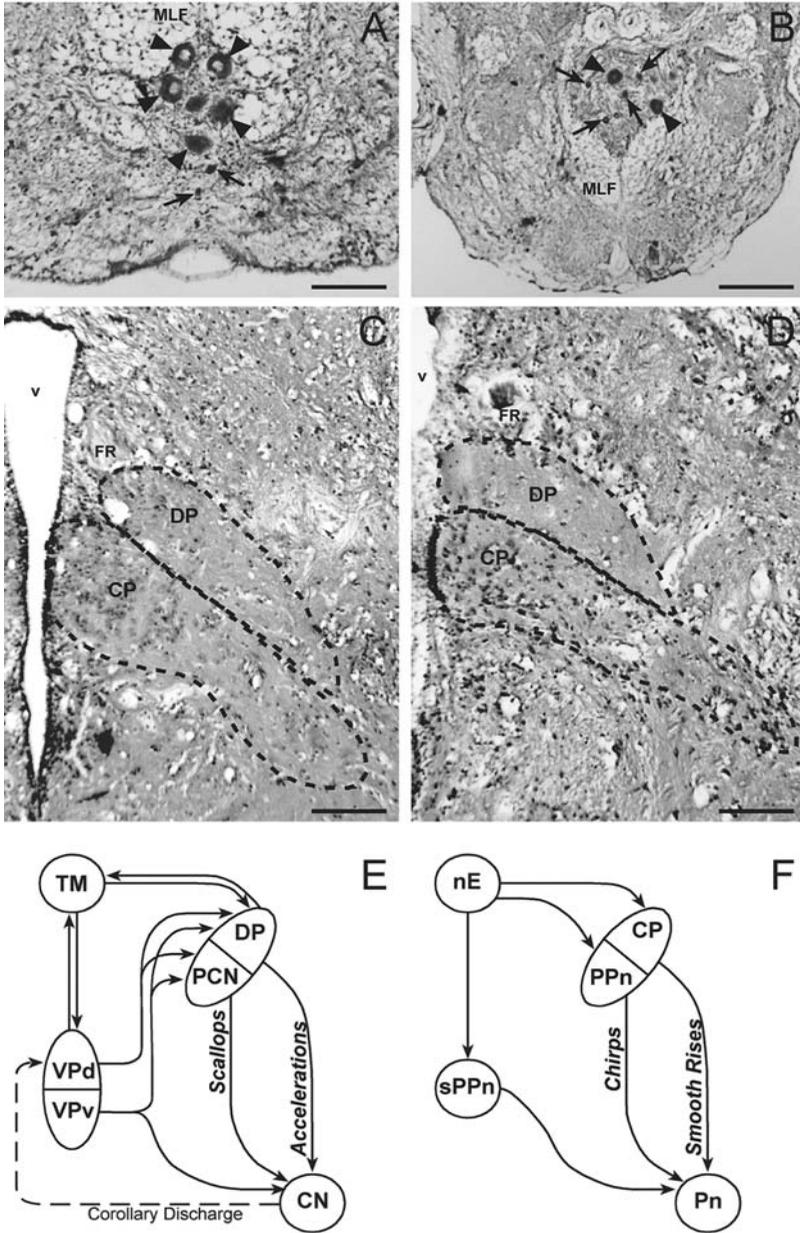
FIGURE 14.5. Comparison of gymnotiform and mormyrid electromotor networks. Transverse sections through the hindbrains of (**A**) the pulse-type mormyrid *Brienomyrus niger* and (**B**) the wave-type gymntiform *Eigenmannia* virescens. Cells and fibers are labeled

mand nucleus whose discharge results from the integration of incoming descending influences.

Long-lasting frequency variations have been described in relation to seasonal changes in water temperature, and they are probably also influenced by the reproductive cycle (Dunlap et al. 2000; Silva et al. 2002). A circadian cycle of EOD frequency has also been observed. EOD amplitude and frequency increase during the night, which has been attributed to the nocturnal increase in motor activity (Moller 1995). Similar changes in the EOD can be induced by the administration of serotonin (Stoddard et al. 2003).

Short-term frequency modulations occur in different behavioral contexts related to the preservation or improvement of electrolocation ability: environmental exploration (electrolocation), foraging, identification and entering of hiding places, identification of novel stimuli, and detection and escape from predators. In all of these behavioral contexts, an increase in the discharge rate increases the information per unit time gathered by the active electrolocating system.

The EOD of a nearby conspecific distorts the electric image produced by the self-generated discharge, resulting in a deleterious effect to electrolocation abilities. Avoidance of such jamming is solved with different strategies: frequency increases or decreases in wave-type fish, phase locking in pulse mormyrids, and persistent frequency change and transient frequency increases in pulse-type gymnotiforms.

Modulations of the temporal patterning of emitted discharges are also the main communication signals in electric fish. During agonistic displays or courtship, sudden transient increases and decreases in frequency, as well as discharge interruptions may occur. In some species, transient increases in frequency are associated with a decrease in EOD amplitude and distortion of its waveform.

5.1 Common Solutions for Timing Control in Gymnotiforms and Mormyriforms

In both gymnotiforms and mormyriforms, the medullary neurons that drive EOD production are located in unpaired midline nuclei (Fig. 14.5A, B; Bennett et al. 1967a,b; Bell et al. 1983). In addition, there is extensive electrotonic coupling among neurons within each level of the EOD command chain (horizontal

FIGURE 14.5. *Continued*
with Bodian staining. The location of command/pacemaker neurons and relay neurons are indicated by *arrows* and *arrowheads*, respectively. Scale bar = 100 μ MLF, Medial longitudinal fasciculus. Transverse sections through the dorsal thalamus of (**C**) *B. niger* and (**D**) *E. virescens*. Cells and fibers are labeled with Bodian staining. The dorsal posterior nucleus (DP) is located just dorsal to the central posterior nucleus (CP). Scale bar = 65 μm. (**E**) Summary diagram of the mormyrid electromotor system, indicating the pathways for scallop and acceleration production. (**F**) Summary diagram of the gymnotiform electromotor system, indicating the pathways for chirp and smooth rise production.

coupling), as well as between levels (Bennett et al. 1967a,b; Dye and Meyer 1986).

In both groups of fish, there are two different types of midline medullary neurons in the electromotor pathway: command/pacemaker neurons that control EOD production and relay neurons that receive input from the command/pacemaker neurons and project down the spinal cord to the electromotor neurons (Fig. 14.5A, B). Compared to the command/pacemaker neurons, the relay neurons are extremely large, with correspondingly thick axons (Szabo and Enger 1964; Ellis and Szabo 1980; Bell et al. 1983). This large size of the axons presumably maximizes the effectiveness of electromotor neuron driving. However, as soma size increases, input resistance decreases, and it therefore takes large amounts of current to exact the significant change in membrane potential required for precise control of EOD timing. Overcoming this problem, both fish groups have the decision center (command or pacemaker) one level upstream in smaller neurons, where descending inputs do not need to deal with low input resistance. Synchronous input from these command/pacemaker neurons easily provides sufficient current to drive the large relay neurons.

The primary input to the command/pacemaker nucleus is from a column of cells that starts rostrally within the dorsal thalamus, and then heads caudally and ventrolaterally toward the mesencephalon. In gymnotiforms, it is the centro-posterior nucleus of the thalamus that has been co-opted by the electromotor system (Fig. 14.5D; Zupanc and Maler 1997), while in pulse mormyrids, it is the dorsal posterior nucleus (Fig. 14.5C; Carlson 2002b). In both cases, the rostral cells within the dorsal thalamus are relatively small with thin intrinsic dendrites, while the caudal cells are relatively large with thick extrinsic dendrites. Furthermore, these morphological and anatomical differences are likely linked directly to their divergent roles in modifying behavioral output: in both cases, the rostral cells are responsible for driving smooth accelerations, while the caudal cells are responsible for driving transient, intense bursts (Fig. 14.5E, F).

In both groups of fish, the command/pacemaker nucleus receives an additional input from a relatively small group of cells within the mesencephalon, the sublemniscal prepacemaker nucleus (sPPn) in gymnotiforms and the ventral subdivision of the ventroposterior nucleus (VPv) in pulse mormyrids (Fig. 14.5E, F; Bell et al. 1983; Metzner 1999; Carlson 2002b). However, these two nuclei are quite distinct anatomically, as VPv is a small group of large cells located within the torus semicircularis, and sPPn is a group of small cells located just ventral to the lateral lemniscus. Whereas the sPPn is typically involved in driving frequency decreases or interruptions, the role of VPv in pulse mormyrids is unclear.

The descending inputs to the command/pacemaker nucleus appear to be largely regulated by a single sensorimotor interface in both groups. In pulse mormyrids, it is the tectum mesencephali, whereas in gymnotiforms, it is the nucleus electrosensorius (Fig. 14.5E, F; Metzner 1999; Carlson 2002b). These nuclei receive input from multiple sensory regions, and thereby may provide a

pathway for electrosensory, auditory, lateral line, and visual information to influence electromotor output.

5.2 Control of Timing in Gymnotiformes: Behavioral Patterns and Neural Circuit

The timing patterns most frequently displayed by Gymnotiforms may be grouped into four behavioral contexts (Fig. 14.6):
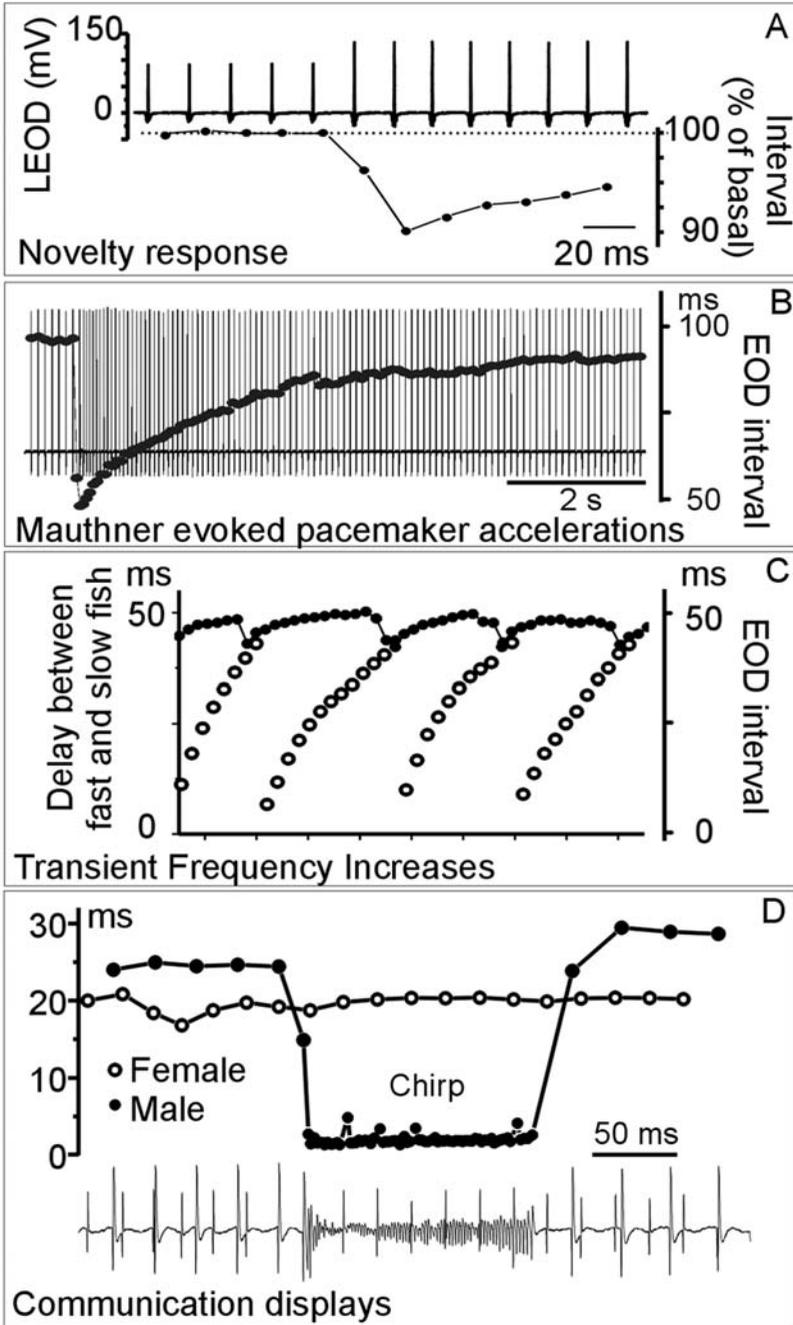
1. Novelty responses: Transient, smooth frequency increases (Fig. 14.6A) are observed as a response to novel stimuli in different species of pulse gymnotiforms, particularly in *Gymnotus carapo* (Bullock 1969). The response increases frequency by 5 to 10 Hz and decays smoothly in about 3, and is dependent on the magnitude of the stimulus and the previous history of stimulus presentation (Caputi et al. 2003).

2. Pacemaker acceleration associated with the escape response: Escape reactions (particularly valuable in avoiding predators) in teleost fish depend on a set of giant reticulospinal neurons among which the Mauthner cell is the most conspicuous. During escape reactions, large accelerations occur (Fig. 14.6B). This frequency increase can be interpreted as an enhanced sampling rate aimed at improving electrolocating ability when the animal is performing a fast movement that requires exploration of a novel environment (Falconi et al. 1995).

3. Jamming avoidance responses: The detrimental effect of EODs generated by a nearby conspecific is avoided in wave-type fish by shifting the EOD frequency away from an interfering signal of similar frequency (less than 4 Hz difference). Heiligenberg and co-workers have studied this behavior described as the *jamming avoidance response* (JAR) and identified the neural circuit subserving this function in wave-type fish (see Heiligenberg 1991).

In pulse-type fish, the interference is limited to the occurrence of coincident EODs. Coincidences will occur more frequently if both signals have similar frequencies. *Gymnotus carapo* increases its frequency to avoid jamming by a lower frequency conspecific (Capurro et al. 1998), but it is unable to lower its discharge rate if the interfering signal has a higher frequency. On the other hand, *Gymnotus carapo* also shows a novel strategy: the fish with a faster firing rate is able to transiently increase its frequency just before the occurrence of a coincident discharge (Fig. 14.6C). These transient frequency increases lower the probability of repeated coincidences that are most deleterious to electrolocation ability (Capurro et al. 1998), although single coincidences are not lowered significantly.

4. Communication displays: During agonistic displays or courtship, sudden transient increases in frequency, transient decreases and discharge interruptions occur. In some species, special transient increases in frequency are associated with a decrease in EOD amplitude and a distortion of its waveform. In *Brachyhypopomus pinnicaudatus*, these signals (called "chirps") are emitted mostly by courting males and have been shown to have communication value. A variation from "weak" to "strong" chirps has been described, implying different

A Novelty response   20 ms

B Mauthner evoked pacemaker accelerations   2 s

C Transient Frequency Increases

D Communication displays   Chirp   50 ms
   ○ Female
   ● Male

degrees of frequency increase associated with corresponding amplitude attenuations and waveform distortions (Kawasaki and Heiligenberg 1989). In similar behavioral and physiological conditions, females of this species are observed to interrupt their discharge from 0.5 to several seconds (Fig. 14.6D).

5.2.1 Structural and Functional Bases of EOD Frequency Modulation in Gymnotiforms

The command signal for EOD generation is initiated in an unpaired medullary nucleus with the functional properties of a cellular pacemaker (Bennett et al. 1968; Dye and Meyer 1986). This nucleus is composed of two cell types: pacemaker neurons (PMn), which are small cells with short axons and a slow depolarizing membrane potential that is initiated after each action potential and reaches threshold to generate the next spike; and relay neurons (Rn), which are larger neurons with large axons that descend the spinal cord and terminate on the spinal electromotor neurons; they have a flat interspike membrane potential and generate an action potential only when pacemaker neurons excite them (Bennett 1968; Smith 1999). Both cell types are clearly separated into two parts of the nucleus in pulse-type fish, with pacemaker neurons being dorsal, while they are intermingled in wave-type species. Another difference between wave and pulse Gymnotiforms in the cellular organization of the pacemaker nucleus is that the ratio in numbers of PMn to Rn is large (close to 2) in wave-type fish, while it is small (close to 0.5) in pulse fish. PMn axons make mixed (electric and chemical) excitatory synaptic connections with Rn. Electrical coupling among PMn is relatively large compared to that among Rn (Dye and Meyer 1986). A third type of cell, called parvocells, was described in wave fish (Smith et al. 2000). These parvocells have been labeled with an antibody against the neuronal calcium-binding protein, parvalbumin, and were dye coupled to the other two main cell types. They receive electrotonic inputs from and make chemical synapses back onto pacemaker and relay cells. The function of these neurons in regulating the EOD frequency is unknown.

Figure 14.6. Control of EOD timing in pulse gymnotids, behavioral patterns. (**A**) Novelty response. Left axis and continuous trace: local EOD; right axis and open circles: inter-EOD interval (species *G. carapo,* modified from Caputi et al., 2003). (**B**) Mauthner evoked transient acceleration. *Left axis* and *continuous trace*: local EOD; *right axis* and *open circles*: inter-EOD interval (species *G. carapo*, figure provided by M. Borde). (**C**) The jamming avoidance strategy in *Gymnotus carapo* consists of brief frequency increases that the faster fish of a pair generates when the slower fish's EOD is about to coincide with the former. The figure shows the inter-EOD intervals of the faster fish (*open circles*) and the phase of the slower relative to the faster (*filled circles*). These transient frequency increases (TFIs) lower the probability of repeated coincidence (figure provided by A. Capurro). Mating *Brachyhypopomes pinnicaudatus* generate sudden changes of discharge train; female (*open circles*), male (*filled circles*). (**D**) Males generate sharp increases in frequency that usually decrease EOD amplitude and distort waveform. These signals are produced in bursts of up to 50 per minute and can last 200 ms.

The pharmacological profiles of the ionic currents in the pacemaker nucleus of gymnotiforms are similar to those of ionic currents involved in other cellular pacemakers (Smith 1999). The oscillatory interaction of these ionic currents dramatically influences the pacemaker and the EO firing frequency is probably a target of steroid hormone action in producing sexual dimorphisms in EOD frequency.

The rate modulations described above depend on the descending influences of excitatory and inhibitory connections to the Pn. Tract tracing has demonstrated the existence of a bilateral prepacemaker nucleus (PPn) in the diencephalon, at each side of the midline, which extends ventrolaterally from the centroposterior nucleus of the thalamus (CP). CP/PPn can be divided into a dorsomedial subnucleus composed of small ovoidal cells and a ventrolateral part composed of large multipolar neurons. Another input to the Pn comes from the sublemniscal prepacemaker nucleus (sPPn), a small, bilateral group of cells located ventral to the lateral lemniscus. Most projections from the sPPn are glutamatergic and terminate on the relay cells of the Pn (Kawasaki et al. 1988; Kawasaki and Heiligenberg 1989).

Gradual accelerations in EOD rate can be induced in *Brachyhypopomus* by stimulation of a portion of the dorsomedial region of CP/PPn, while stimulation of a different (smaller) portion gives rise to decelerations and even interruptions. Both discharge modulations occur with maintenance of the normal activation sequence (pacemaker-relay), as demonstrated by intracellular recordings (Kawasaki and Heiligenberg 1989), and they depend on glutamatergic excitation and γ-aminobutyric acid-ergic (GABAergic) inhibition of PMns, respectively.

Stimulation of the ventrolateral region of CP/PPn induces the generation of chirps by acting directly on relay cells while PMns do not alter their discharge rhythm. Sudden interruptions of the EOD are provoked by activation of sPPn by acting directly on relay cells that become strongly depolarized, while PMns keep their normal rhythm. When the relay cell repolarizes the resting activity is resumed (Kawasaki and Heiligenberg 1989).

In the wave-type fish *Eigenmannia*, EOD accelerations associated with the JAR are induced by glutamatergic excitatory inputs to Pn from the dorsomedial region of CP/PPn (Metzner 1999). sPPn provides tonic glutamatergic excitatory input to Pn: EOD decelerations associated with the JAR are induced by GABAergic inhibition of sPPn and a consequent removal of tonic excitation.

The sudden increase in discharge rate induced by Mauthner cell activation depends on glutamatergic excitation of pacemaker cells involving both *N*-methyl-*D*-aspartate metabotropic receptors and non-NMDA metabotropic receptors (Curti et al. 1999).

In addition to sexual hormone effects to the pacemaker there are other hormone-dependent structural differences between male and female brains related to differences in behavior. Nonspawning males consistently chirp, whereas females do not. This behavioral dimorphism is paralleled by sex differences in CP/PPn that regulates chirping behavior. Neurogenesis and changes in the morphology of dendritic trees in PPn was proposed by Zupanc (1999) as the bases

of seasonal changes associated with courtship and the associated production of chirps.

5.3 Control of Timing in Pulse Mormyrids: Behavioral Patterns and Neural Circuit

Unlike gymnotiforms, which produce EODs at highly regular rates, mormyrid electrical behavior is characterized by variable timing (Fig. 14.7A. At rest, there is a general tendency toward EOD intervals of around 100 to 300 ms (Teyssedre and Boudinot 1987), and because they are nocturnal, EOD intervals are generally lower and less variable at night (Carlson 2002a). However, there can be extensive variation around this basic pattern, as the sequence of pulse intervals may fluctuate from less than 10 to several hundred milliseconds (Fig. 14.7A). As in gymnotiforms, pulse mormyrids increase their EOD rates while actively probing their environment (von der Emde 1992). They also produce transient rate increases as a novelty response (Post and von der Emde 1999) and use phase-locking (echo response) as a jamming avoidance strategy (Russell et al. 1974).

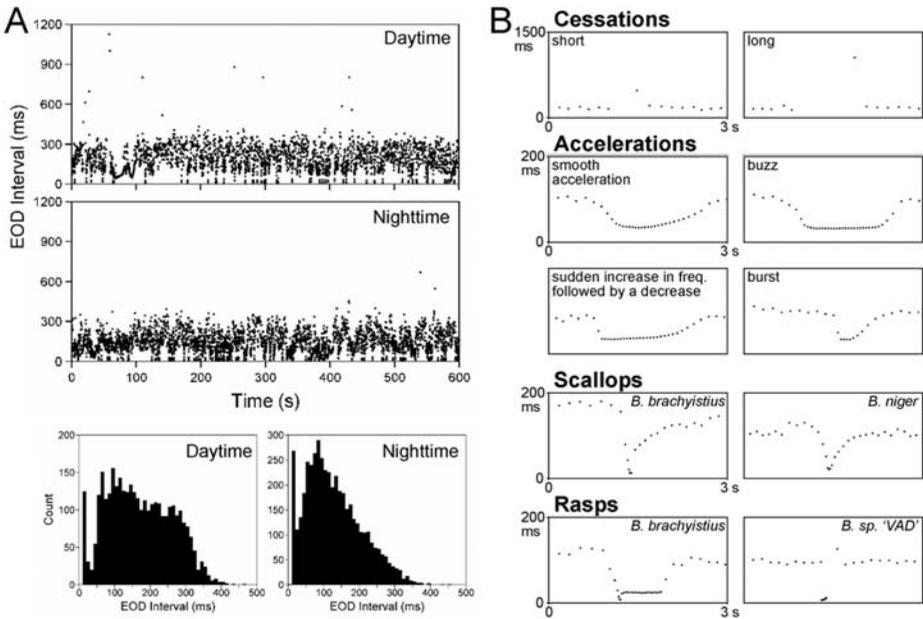The electrical behavior of mormyrids is analogous to action potential activity

FIGURE 14.7. The sequence of pulse intervals (*SPI*) in mormyrid electromotor output. (**A**) Long-term SPI plots from a single *Brienomyrus brachyistius* during the day and night. Below the SPI plots are histograms of EOD interval distributions. (**B**) Phasic modulations of the SPI that have been implicated in a variety of behavioral contexts (see Carlson 2002a for details).

in single neurons: there is a stereotyped pulse of electricity produced with variable timing. The temporal patterning of action potential activity can encode a wide range of complex information in the nervous system, and the sequence of pulse intervals similarly provides pulse mormyrids with a rich repertoire of social signals (Carlson 2002a). Several studies have described different phasic patterns that are correlated with a variety of social contexts such as aggression, submission, courtship, and spawning (Hopkins 1986; Carlson 2002a). These patterns include cessations in electromotor output, as well as a wide variety of bursts (Fig. 14.7B). In Brienomyrus brachyistius, three basic burst types have been described: accelerations, scallops, and rasps (Carlson and Hopkins 2004a). Accelerations are modest, sustained decreases in interval to values of around 25 to 40 ms that are quite variable in both duration and in the minimum EOD intervals reached during the burst. Scallops are highly stereotyped, phasic bursts that begin with a sudden drop in interval to values of 10 to 20 ms, followed by an immediate increase back to resting intervals. Rasps have an initial scalloplike phase followed by an accelerationlike tail, supporting the notion that novel signal types may arise in evolution by combining preexisting signal types, while also suggesting a combinatorial mechanism for their production.

These different displays are associated with different functions in social behavior: scallops may function as an advertisement signal, accelerations as an aggressive display, rasps as a male courtship display, and long cessations as a submissive display (Carlson 2002a; Carlson and Hopkins 2004a). Thus, much as the nervous system encodes information into temporal patterns of action potentials, pulse mormyrids appear to encode social information into temporal patterns of EOD production.

5.3.1 Structural and Functional Bases of Inter-EOD Interval Control in Pulse Mormyrids

Production of each EOD is initiated in a command nucleus (CN) located on the ventral midline of the medulla (Fig. 14.8A) (Bell et al. 1983; Grant et al. 1986, 1999). Immediately dorsal to CN is the medullary relay nucleus (MRN), which receives a direct projection from CN, as well as an indirect projection through the bilateral bulbar command-associated nucleus (BCA). The axons of MRN neurons project down the spinal cord to terminate on the electromotor neurons (EMNs) that drive the electric organ. Unlike gymnotiforms and *Gymnarchus*, the pulse-type mormyrids electromotor network also gives rise to a corollary discharge pathway that originates in BCA and relays the timing of EOD production to higher brain centers. Details on this pathway and its role in electrosensory processing are discussed elsewhere in this volume (Bell and Maler, Chapter 4 and Kawasaki, Chapter 7).

Although the electric organ is silenced by drugs that immobilize fish for physiological recording, electromotor output can be monitored by placing an electrode next to the tail and recording the field potential that results from the synchronous activation of electromotor neurons, which occurs about 5 ms before

the EOD in freely behaving fish. Neurons in both CN and MRN fire in a strict
1:1, phase-locked relationship with electromotor output (Fig. 14.8B) (Grant et
al. 1986). Unlike gymnotiforms, there is no evidence that CN functions as a
pacemaker. Instead, neurons within CN integrate descending inputs, and be-
cause they are tightly electrotonically coupled (Elekes and Szabo 1985), the
nucleus essentially functions as one large integrate-and-fire unit (Carlson 2002a).

The mesencephalic precommand nucleus (PCN) and the thalamic dorsal pos-
terior nucleus (DP) provide the primary excitatory input to CN (Carlson 2002b,
2003; Carlson and Hopkins 2004b). These two nuclei form a bilateral column
of cells that start rostrally in the dorsal thalamus and extend caudally and ven-
trolaterally into the rostral mesencephalon. CN also receives bilateral input from
10 to 15 large multipolar neurons along the ventral edge of the toral ventropos-
terior nucleus (VPv). The dorsal region of the same nucleus (VPd) contains
relatively small, ovoid neurons that provide strong inhibitory input to DP/PCN
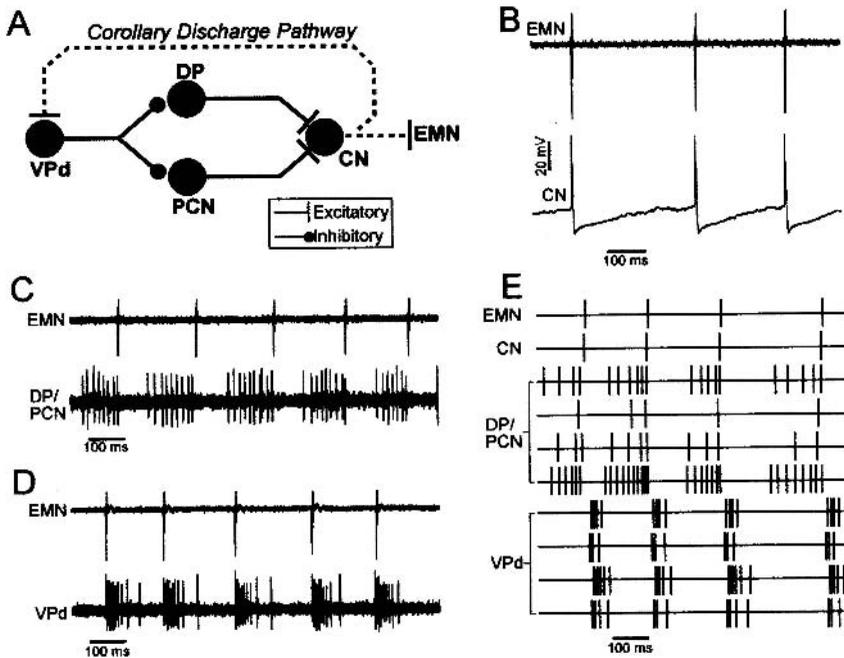(Carlson 2002b, 2003; Carlson and Hopkins 2004b). This region, in turn, re-

FIGURE 14.8. Mormyrid electromotor network. (**A**) Simplified schematic of electromotor
connectivity (for details on the anatomy see Bell et al. 1983 and Carlson 2002b). (**B**)
Intracellular recording from a CN neuron in relation to the electromotor neuron volley
in *B. brachyistius*. (**C**) Extracellular activity of a single DP/PCN neuron in relation to
the electromotor neuron volley in *B. brachyistius*. (**D**) Extracellular activity of a single
VPd neuron in relation to the electromotor neuron volley in *B. brachyistius*. (**E**) Simu-
lated simultaneous activity patterns in electromotor neurons, CN, DP/PCN, and VPd.

ceives a projection from the medullary command associated nucleus (MCA), an important relay of the corollary discharge pathway. The pulse mormyrids electromotor pathway can therefore be broken down into a relatively simple functional circuit: CN integrates descending excitatory input from DP/PCN, and an internal collateral associated with the corollary discharge pathway provides negative feedback to DP/PCN via VPd (Fig. 14.8A).

Neurons in DP/PCN and VPd exhibit characteristic patterns of activity in relation to the electromotor neuron cycle (von der Emde et al. 2000; Carlson 2003). DP/PCN neurons vary widely in their average firing rates, but each unit has an increased probability of firing about 4 to 10 ms before the electromotor neuron volley, and then goes silent for about 50 to 150 ms before resuming activity prior to the next volley (Fig. 14.8C). VPd neurons are silent throughout the entire cycle, except for firing a stereotyped burst of action potentials starting right around the time of electromotor neuron activation, which exactly coincides with the silent period in DP/PCN units (Fig. 14.8D). Thus, our working model of the underlying mechanism for regulating the sequence of pulse intervals is that this network functions as a relatively simple central pattern generator: DP/PCN fires tonically to depolarize CN and drive EOD production, which activates a recurrent inhibitory pathway that silences DP/PCNand imparts a baseline rhythm to electromotor output (Fig. 14.8E).

If DP and PCN both provide excitatory input to CN and contain neurons with similar basic properties, this raises the question of why there are two separate populations. In *B. brachyistius*, stimulating DP with the excitatory neurotransmitter L-glutamate results in smooth increases in EOD rate and regularity similar to accelerations, while stimulation of PCN induces transient, intense bursts similar to scallops (Carlson and Hopkins 2004b). This suggests that these two nuclei are involved in generating distinct communication displays (Fig. 14.9). Thus, much as many sensory systems use "labeled lines" to code for specific stimulus features, so too can motor systems employ "labeled lines" that are dedicated to generating specific motor acts. The anatomical separation of these pathways provides a relatively simple mechanism for generating different displays. Because rasps appear to result from a combination of scallop and acceleration production, their production likely relies on activation of both groups of neurons (Fig. 14.9).

The question that arises at this point is what differs between the neurons in DP and PCN and how does this translate into different effects on electromotor output for *B. brachyistius*? There is extensive variation in the activity patterns of individual DP/PCN neurons, ranging from units that are almost completely silent to those that fire tonically at high rates (Carlson 2003). Relatively silent neurons get recruited during accelerations, which increases the number of descending units driving CN, leading to increases in the rate and regularity of EOD output. During scallops, however, units that are already firing at high rates experience a further increase in activity, which may saturate the membrane potential of CN neurons, leading to an intense, stereotyped burst of activity (Carlson 2003). Thus, DP neurons appear to have a lower baseline activity level
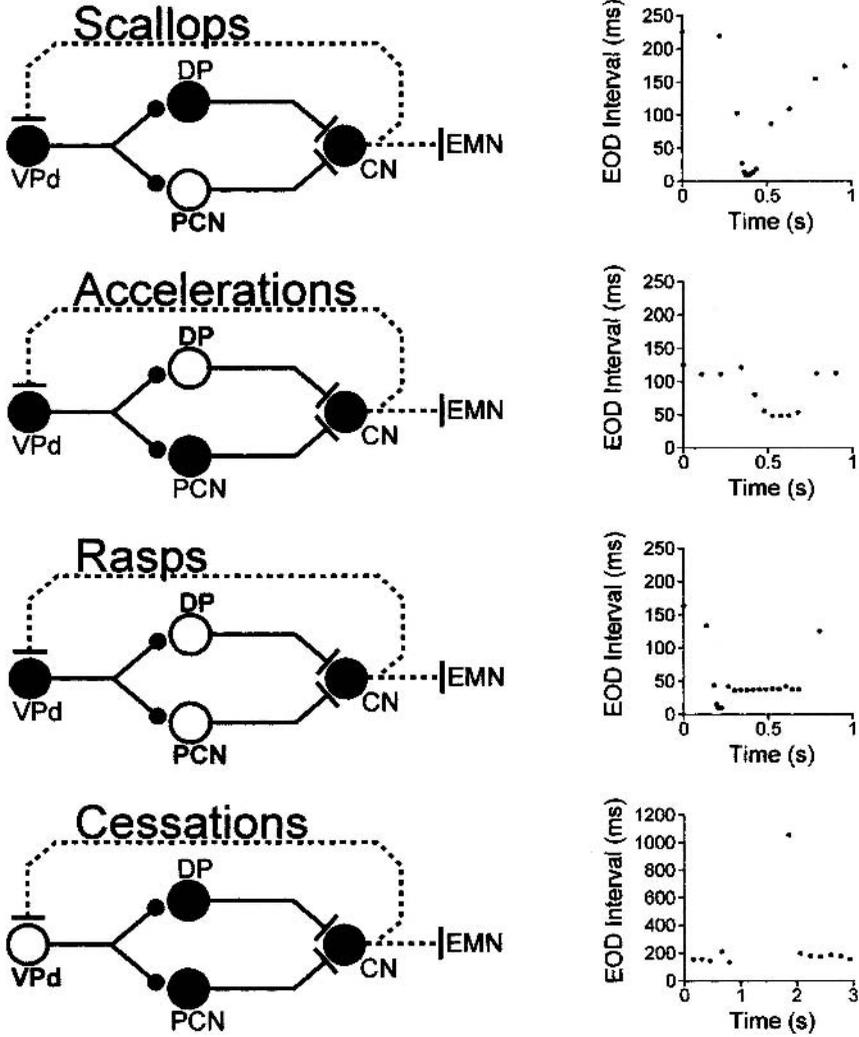
FIGURE 14.9. Central control of electric communication displays in mormyrids. In the left column, simplified schematics of the electromotor network, taken after Fig.14.8A are shown. For each row, the nucleus/nuclei thought to be responsible for generating a given electrical display are highlighted, with an example of the respective display shown as an SPI plot in the right column.

compared to PCN neurons, which leads to different patterns of output when activating each population.

Stimulation of VPd using L-glutamate typically results in an immediate cessation of electromotor output (Carlson and Hopkins 2004b), suggesting that cessations may be driven by increases in the inhibitory feedback provided by VPd (Fig. 14.9). This inhibition appears to be GABAergic, as preliminary evidence indicates that PCN neurons are surrounded by terminals containing GABA (Niso et al. 1989), and iontophoresis of GABA into DP or PCN causes a reduction in EOD rates (Carlson and Hopkins 2004b).

The bursts produced by VPd neurons show little variation from cycle to cycle, and there is no correlation between this variation and the resting sequence of pulse intervals (von der Emde et al. 2000; Carlson 2003). During both scallops and accelerations, however, the activity of these units decreases markedly (Carlson 2003), suggesting that their production results at least in part via disinhibition of DP/PCN. In support of this hypothesis, application of the GABA$_A$ receptor blocker bicuculline methiodide to either DP or PCN results in tonic bursting behavior (Carlson and Hopkins 2004b). Thus, it appears that recurrent inhibition regulates the resting cadence of the sequence of pulse intervals, while disinhibition frees DP and PCN from their normal rate-limiting factor, providing a permissive mechanism for driving bursts. Furthermore, after blocking inhibitory feedback, electromotor output patterns resulting from stimulating DP and PCN with L-glutamate are indistinguishable (Carlson and Hopkins 2004b). This suggests that differences in the strength of recurrent inhibition to DP and PCN are responsible for differences in their baseline activity levels and therefore different effects on electromotor output when stimulated.

6. Common Principles in the Organization of Skeletomotor and Electromotor Systems

The phylogenetic evidence strongly indicates that mormyriforms and gymnotiforms share no common electrogenic or electrosensory ancestors (Bullock et al. 1983). Thus, their electromotor systems are thought to have evolved independently (Darwin 1859, Bullock et al. 1983). It is therefore quite remarkable to find multiple, striking similarities in the electromotor systems of these two groups (Hopkins 1995). Such convergent evolution supports the argument that there are certain basic design features underlying the evolution of vertebrate neural circuits that may be typified by the electromotor systems of these fish.

Electric fish have proven to be an excellent model system for studying the central mechanisms for generating motor output. Many vertebrate behaviors involve several complex interacting elements, making it difficult to form a direct link between the production of a behavior and its neural control. Electric fish are unique in this respect, since their electrical behavior may be characterized by just two parameters: the waveform of each EOD and its frequency or temporal pattern of production. The relative simplicity of timing control in electric

fish makes them an excellent model system for understanding how vertebrate neural circuits generate different temporal patterns. Thus, research on the central control of electric signaling behavior has proven successful in addressing general issues in vertebrate motor control, and several basic principles have emerged that likely apply to more complex systems.

6.1 Central Pattern Generators: Neurons and Networks for Rhythmic Behaviors

The electromotor output of both mormyriforms and gymnotiforms is characterized by inherent rhythmicity. Despite the many similarities between the electromotor systems of these two groups of fish, rhythmic motor output is generated in distinctly different ways. In gymnotiforms and *Gymnarchus*, regular EOD rates are maintained by a set of pacemaker neurons (Kawasaki 1994; Metzner 1999). Thus, rhythmic motor output relies on endogenous neuronal characteristics. By contrast, the command neurons of pulse mormyrids do not have any pacemaker properties. Instead, they integrate tonically active descending inputs that drive EOD production (Grant et al. 1999, Carlson 2002a). These descending units receive input from a recurrent inhibitory pathway that silences them after each EOD, and this negative feedback imparts a baseline rhythm to EOD production. Thus, rhythmic motor output in this case appears to rely predominantly on network features. These two different mechanisms for generating rhythmic motor output exemplify common strategies that have been described for a number of invertebrate central pattern generators (Marder and Calabrese 1996; Marder and Bucher 2001).

6.2 Central Pattern Generators: Coordination of Agonist and Antagonist Effectors

The presence of spinally coordinated motor programs is a control strategy present in all vertebrates. The reflex control of posture and movement was known before Descartes (1637) formalized this idea in "Les passions de l'âme." The open loop control of motor patterns was first put in evidence by Lashley (1917), who described a spinal cord injured patient that was able to move his hindlimbs despite complete anesthesia below the injury level of the spinal cord. This observation led to the identification of spinally organized units in motor programs. The coordinated activation of these units by descending commands appears to be a general strategy for skeletomotor control. The control systems of the EOD waveform goes from the extreme simplicity of the effector response to a nerve volley in pulse mormyrids to a complex electromotor act that involves the central coordination of different electromotor pools by a fixed motor program that is genetically determined and stored in the circuitry of the spinal cord in pulse gymnotiforms (Caputi 1999).

   The electromotor system illustrates various general principles for the orga-

nization of the neural circuits. First, the system is redundant; several mechanisms converge synergistically for the implementation of the delay lines subserving the synchrony of homologous faces of the electrocytes generating each wave. Second, the orderly recruitment of electromotor neurons appears to be dependent on their size and represents another example of Hennemann's size principle (Hennemann 1957) occurring in the skeletomotor system of vertebrates and invertebrates. Smaller neurons having larger input resistance fire earlier than large neurons in the same stimulus conditions. Third, the different electromotor pools along the spinal cord of some pulse gymnotiforms are collectively controlled by a common descending drive also involved in skeletomotor control (De Luca and Erim 1994). The specific architecture of the system and the different excitability of electromotor neuron types allows that a single, relatively synchronous descending volley provokes a timed recruitment of different effector units. This type of organization relieves the nervous system from the necessity to monitor and control every unit in a separated way and therefore enhances efficacy (Lemon 1988). Finally, as observed in skeletomotor systems the electromotor output depends on the transduction properties of the effector cells and the filtering properties of the passive tissues linking the effector units with the exterior. Posteffector filtering of muscle fiber output is an important factor for controlling muscle performance and enhancing mechanical efficacy (Hoffer et al. 1992) These structures are also the target for sexual hormones, as found for muscles, tendons, and bones in the vertebrate skeletomotor system.

7. In Conclusion

Electric fish have evolved a peculiar effector system that serves as a weapon and as a carrier of information for the electrosensory system. These fish create an electric field that allows them to communicate with each other and to detect objects that have a different impedance than the surrounding water. Therefore, understanding electrogenesis is a necessary step for understanding the action-perception electrosensory cycle. The electromotor output of the two main groups of electric fish, mormyriforms and gymnotiforms, is characterized by species-specific EODs of stereotyped waveform, generated according to specific temporal patterns. Organizing the electromotor units and regulating their emission patterns are the two main functions of the electromotor system. The emission pattern results from the effect of a small number of brain stem and thalamic nuclei on a single electrotonically coupled bulbar nucleus where EOD timing is determined. This single command activates a robust, hard wired, spinal and peripheral system responsible for the constancy of EOD waveform. While EOD emission patterns may be highly variable, EOD waveform is mainly modulated by slow changes depending on hormonal or acclimation effects. The comparative study of the neural organization of these two signal features reveals a number of different strategies for motor organization. Most regular EOD emission patterns are maintained by a set of pacemaker neurons while the most flexible and centrally modulated patterns are organized by a command nucleus

that integrates tonically active descending inputs that drive EOD production. The coordinated activation of spinally organized units by descending commands appears to be a general strategy for skeletomotor control that illustrates three general principles for the organization of spinal motor units: (1) a common descending drive for the timed recruitment of spinal units, (2) the role of Hennemann's size principle in motorneuron recruitment, and (3) the presence of redundant, synergistic mechanisms for securing the final output.

Abbreviations

AC	Alternating currents
AEN	Anterior electromotor nerve
BCA	Bulbar command-associated nucleus
CN	Command nucleus
CP	Centroposterior nucleus of the thalamus
DC	Constant current
DP	Thalamic dorsal posterior nucleus
EMF	Electromotive force
EMN	Electromotor neurons
EO	Electric organ
EOD	Electric organ discharge
JAR	Jamming avoidance response
MCA	Medullary command associated nucleus
MLF	Medial longitudinal fasciculus
MRN	Medullary relay nucleus
PCN	Mesencephalic precommand nucleus
PEN	Posterior electromotor nerve
PMn	Pacemaker neurons
PPn	Pre-pacemaker nucleus
R_{load}	Load resistance
Ri	Internal resistance
Rn	Relay neurons
sPPn	Sublemniscal prepacemaker nucleus
VP	Ventroposterior nucleus
VPd	Dorsal region of the toral ventroposterior nucleus
VPv	Ventral region of the toral ventroposterior nucleus

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