

## Physiology of Tuberous Electrosensory Systems

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[Introduction](#)

[Amplitude Coding](#)

[Time Coding](#)

[Physiology of ELL Neurons Receiving Input from Amplitude-Sensitive Electroreceptors](#)

[Physiology of Midbrain Neurons: Integration of Sensory Information](#)

[Conclusion](#)

[Further Reading](#)

### Glossary

**Amplitude modulation** Refers to a signal in which changes in amplitude carry sensory information.

**Corollary discharge** Refers to a copy of a motor command that is sent from motor areas to sensory areas in the brain. It is often used to predict and eliminate sensory responses to self-generated stimuli.

**Electrosense** Ability to detect electric fields. A passive electrosense is one in which external electric fields are detected, whereas an active electrosense is one in which self-generated electric fields are detected.

**Feedback** Refers to projections from central brain areas back to more peripheral sensory areas.

**Frequency modulation** Refers to a signal in which changes in instantaneous frequency carry sensory information.

**Information theory** Refers to the mathematical theory of communication developed by Claude Shannon that is used in a variety of applications today.

**Neural code** Refers to the patterns of neural activity and transformations by which sensory input to motor outputs to give rise to behavioral responses by the organism.

**Phase locking** Refers to the tendency of certain neurons to fire at a preferred phase of a periodic signal.

**Rate code** Refers to a neural code in which information is carried solely by the firing rate (i.e., the number of action potentials per unit time) of a neuron.

**Temporal code** Refers to a neural code in which information is carried by the specific timings of action potentials.

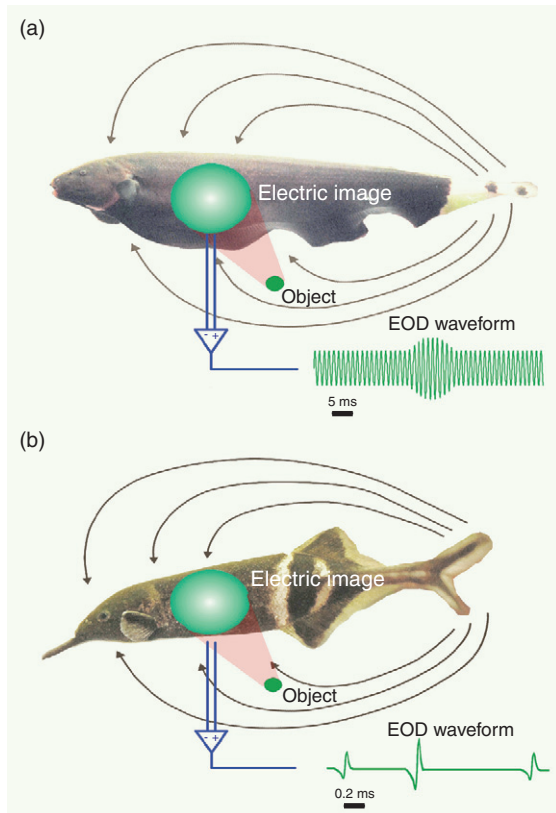
### Introduction

Weakly electric fish produce weak electric fields using specialized electrogenic organs. The electrical output of the organ is known as the electric organ discharge, or EOD (see also **Detection and Generation of Electric Signals: Electric Organs and Generation of Electric Signals**). There are two phylogenetically independent orders of weakly electric fishes: the Gymnotiformes of South America and the Mormyriiformes of Africa. These clades evolved within two distantly related groups, the ostariophysans and osteoglossomorphs, respectively.

Gymnotiform and mormyriiform fishes can both be classified as either pulse type or wave type, depending on the temporal structure of their EOD. Wave-type weakly electric fish generate continuous, highly periodic EOD waveforms (**Figure 1(a)**), whereas pulse-type weakly electric fish emit short, typically less than 2 ms, stereotyped pulses with longer periods of silence,

typically greater than 10 ms, between pulses (**Figure 1(b)**). In some species the inter-pulse intervals are nearly constant, whereas in other species the inter-pulse intervals can vary over orders of magnitude.

Both wave- and pulse-type weakly electric fish can detect perturbations of the autogenous EOD using tuberous electroreceptors that are distributed on their skin surface: this is referred to as active electrolocation since the animal actively generates the sensory signal (see also **Detection and Generation of Electric Signals: Active Electrolocation**). Tuberous electroreceptors also detect the EODs of other individuals in the context of communication (see also **Sensory Systems, Perception, and Learning: Shocking Comments: Electrocommunication in Teleost Fish**). There are several classes of tuberous electroreceptors that encode different features of the animal's electric field. All species have at least two classes of tuberous electroreceptors, one type (amplitude coding) that encodes EOD amplitude modulations (AMs), and another type (time



**Figure 1** The principle of active electrolocation in weakly electric fish. (a) The wave-type gymnotiform species *Aptereronotus albifrons* emits a highly periodic quasi-sinusoidal EOD. (b) The pulse-type mormyriiform species *Gnathonemus petersii* emits pulses of electricity with strong variability in the interpulse interval. In both cases, one can easily record the EOD by placing a pair of metal wires close to the animal and connecting them to an amplifier. Objects with a conductivity different than that of the surrounding water (e.g., rocks, plants, other fish, and plankton) will distort the EOD; for example, a conductive object will locally increase the EOD amplitude. The projection of this distortion on the animal's skin surface is referred to as the electric image.

coding) that encodes EOD timing and frequency modulations (FMs). Information from these electroreceptors is transmitted to the electrosensory lateral line lobe (ELL) in the hindbrain. ELL neurons in turn project to the electrosensory midbrain and higher-order areas.

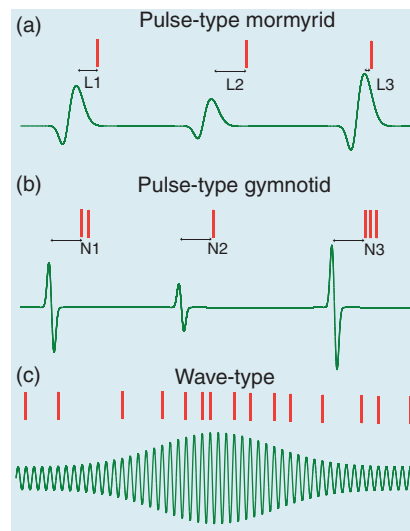
We first review the characteristics of amplitude- and timing-sensitive peripheral electroreceptive neurons in wave- and pulse-type gymnotiform and mormyriiform weakly electric fishes. We then review the characteristics of ELL neurons with a particular emphasis on the role of feedback pathways in wave-type gymnotiforms. We conclude by highlighting some of the characteristics of higher-order neurons and their roles in behaviorally relevant computations.

## Amplitude Coding

Both mormyriiform and gymnotiform weakly electric fish have tuberos electroreceptors embedded in the skin that can encode AMs of the EOD. In gymnotiform fish, these receptors are known as P-units since it was originally found that the probability of firing increased linearly with EOD amplitude. In mormyriiform pulse-type fish, these receptors are known as mormyromasts. **Figure 2** illustrates the coding strategy used by wave-type as well as pulse-type gymnotiform and mormyriiform weakly electric fishes.

## Amplitude Coding in Pulse-Type Fish

Mormyromasts in pulse-type mormyriiform fishes usually respond with one or more action potentials to each EOD pulse (**Figure 2(a)**). In mormyromasts, the latency between the EOD pulse in the water and the first action potential decreases for increasing EOD amplitudes. There is very low trial-to-trial variability in the relationship between latency and EOD amplitude – these afferents use a timing code to transmit information about EOD amplitude (see also **Detection and Generation of Electric Signals: Active Electrolocation**).



**Figure 2** Amplitude coding in wave-type, pulse-type mormyriiform, and pulse-type gymnotiform weakly electric fishes. (a) Mormyromasts in mormyriiform pulse-type fish typically fire a single action potential (red bars) in response to each EOD pulse. However, the latency  $L$  between the EOD pulse and the action potential decreases monotonically with increasing EOD amplitude. (b) By contrast, burst duration coders in gymnotiform pulse-type fish fire a burst of action potentials in response to each EOD pulse. While the latency to first spike does not vary much with increasing EOD amplitude, the number of spikes in the burst ( $N$ ) increases monotonically with increasing EOD amplitude. (c) P-units in gymnotiform wave-type fish and O-units in mormyriiform wave-type fish fire action potentials that are phase-locked to the EOD but skip a random number of EOD cycles between firings. Their probability of firing an action potential increases with EOD amplitude.

Tuberous encoding in pulse-type gymnotiform fishes involves a different strategy. Tuberous neurons in gymnotiform fish exhibit little variation in the latency to the first spike, but instead modulate the number of spikes per burst as a function of EOD amplitude (Figure 2(b)). These are known as burst duration coders.

### Amplitude Coding in Wave-Type Fish

In wave-type gymnotiform fishes, P-units exhibit some phase locking to the EOD with preferred phase near a local maximum. As the firing rates of P-units are usually lower than the EOD frequency, these neurons skip a more-or-less random number of EOD cycles between action potentials (Figure 2(c)). Increases and decreases in EOD amplitude will increase or decrease the firing rates of these units: the firing rate varies roughly linearly with EOD amplitude. These neurons encode AM information in a rate code. As one might expect, these units exhibit rectification for very low EOD amplitudes, because the firing rate cannot by definition be negative, and these units also saturate for very high EOD amplitudes. Recent studies have shown that these afferents have broad, flat tuning curves over the range of salient frequencies, from near 0 Hz to around 100 Hz.

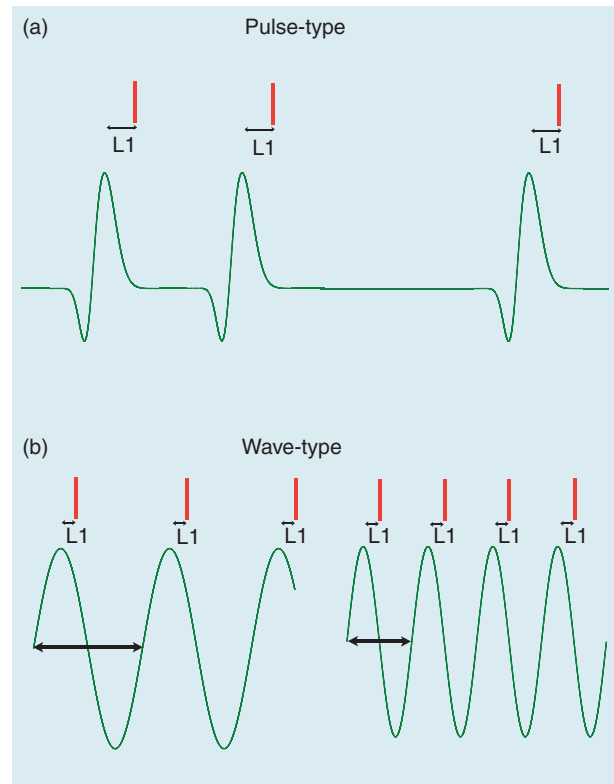
In wave-type mormyiform fish, O-units have properties similar to those of P-units in wave-type gymnotiform weakly electric fish. Because both gymnotiform and mormyiform clades evolved independently, it is interesting to note that they evolved similar coding strategies for AM information carried by wave-type EODs.

### Time Coding

As mentioned previously, weakly electric fish can also detect the timing of their EODs and therefore FMs (i.e., transient changes in the EOD frequency). Contrary to amplitude-coding strategies, time-coding strategies follow the same general principles in both pulse- and wave-type gymnotiform and mormyiform fishes.

#### Time Coding in Pulse-Type Fish

Pulse-marker units in gymnotiform and knollenorgans in mormyiform pulse-type weakly electric fish fire one phase-locked action potential per EOD pulse. These units therefore track changes in the EOD frequency (Figure 3(a)). In mormyrids, individual knollenorgans respond at various phases of an EOD pulse, so that relative differences in the timing of action potentials among knollenorgans additionally encode the EOD waveform (see also **Sensory Systems, Perception, and Learning: Shocking Comments: Electrocommunication in Teleost Fish**).



**Figure 3** Time coding in wave-type and pulse-type weakly electric fishes. (a) Pulse-marker units in pulse-type gymnotiforms and knollenorgans in mormyiforms fire one action potential per EOD pulse and this tracks changes in EOD timing and frequency. (b) T-units in wave-type gymnotiforms and S-units in wave-type mormyiforms fire one action potential per EOD cycle (i.e., 1:1 phase locking). Their instantaneous firing rates thus provide a measure of the instantaneous EOD frequency.

#### Time Coding in Wave-Type Fish

T-units in gymnotiform wave-type weakly electric fish and S-units in wave-type mormyiform fish encode the timing of each EOD cycle and therefore the instantaneous EOD frequency by firing one action potential per EOD cycle at a precise phase (Figure 3(b)).

#### Projections to Higher-Order Neurons

The various types of electroreceptor units all project into a hindbrain structure known as the ELL. Anatomical and physiological studies have shown that the time-coding pathways preserve fine temporal information carried by time-coding afferents. In all classes of weakly electric fish, neurons receiving input from time-coding afferents have similar physiology: they fire one action potential per EOD cycle or EOD pulse. These neurons receive no descending feedback from central nervous system (CNS) circuits and thus appear to be a feedforward-only system. By contrast, information from amplitude-coding afferents is subject to complex processing that includes

**Table 1** Summary of coding strategies used by tuberous electroreceptors

	<i>Amplitude coding</i>	<i>Frequency coding</i>
Wave type	<i>P-unit or O-unit.</i> Skips a random number of EOD cycles between firings. Probability of firing on any given EOD cycle increases with EOD amplitude.	<i>T-unit or S-unit.</i> Fires one action potential per EOD cycle. The phase of firing advances with increasing EOD frequency or amplitude.
Pulse-type gymnotiform	<i>Burst duration coder.</i> Fires a burst of spikes for each EOD pulse. The number of spikes in the burst increases with increasing EOD amplitude.	<i>Pulse marker unit.</i> Fires one action potential per EOD pulse at a precise phase.
Pulse-type mormyridform	<i>Mormyromast.</i> Fires one or more action potentials in response to each EOD pulse. The latency to the first action potential decreases with increasing EOD amplitude.	<i>Knollenorgan.</i> Fires a single phase-locked action potential in response to each EOD pulse.

descending feedback in ELL circuits. Tuberous electroreceptors fire not only in response to the animal's own EOD pulse, but also in response to EOD pulses emitted by conspecifics. As described below and reviewed in detail (see also **Detection and Generation of Electric Signals: Active Electrolocation**), pulse-type mormyrid fish generate a corollary discharge of each EOD pulse, allowing them to distinguish between self-generated and externally generated EODs within the ELL. Mormyromasts thereby give rise to a sensory pathway specialized for encoding self-generated EODs, whereas knollenorgans give rise to a sensory pathway specialized for encoding externally generated EODs. The basic properties of the electroreceptor types reviewed here are summarized in **Table 1**.

## Physiology of ELL Neurons Receiving Input from Amplitude-Sensitive Electroreceptors

### Amplitude Coding in Wave-Type Gymnotiform Fish

The ELL contains multiple segments devoted to processing tuberous input with the number of segments varying from species to species. The anatomy of an ELL segment in the gymnotiform weakly electric fish *Apteronotus leptorhynchus* is shown in **Figure 4(a)**. P-type electroreceptors project to pyramidal cells within the ELL. There are two types of pyramidal cells: basilar pyramidal cells receive direct electroreceptor input on their basilar dendrites, whereas nonbasilar pyramidal cells receive indirect electroreceptor input through local inhibitory interneurons. More recent studies have shown large morphological and molecular heterogeneities within the pyramidal cell population. Pyramidal cells are organized in both basilar and nonbasilar columns each consisting of superficial, intermediate, and deep cells. Pyramidal cells are the sole output neurons of the ELL. While all pyramidal cells project to the midbrain, only deep pyramidal cells give rise to the feedback input that is received mostly by

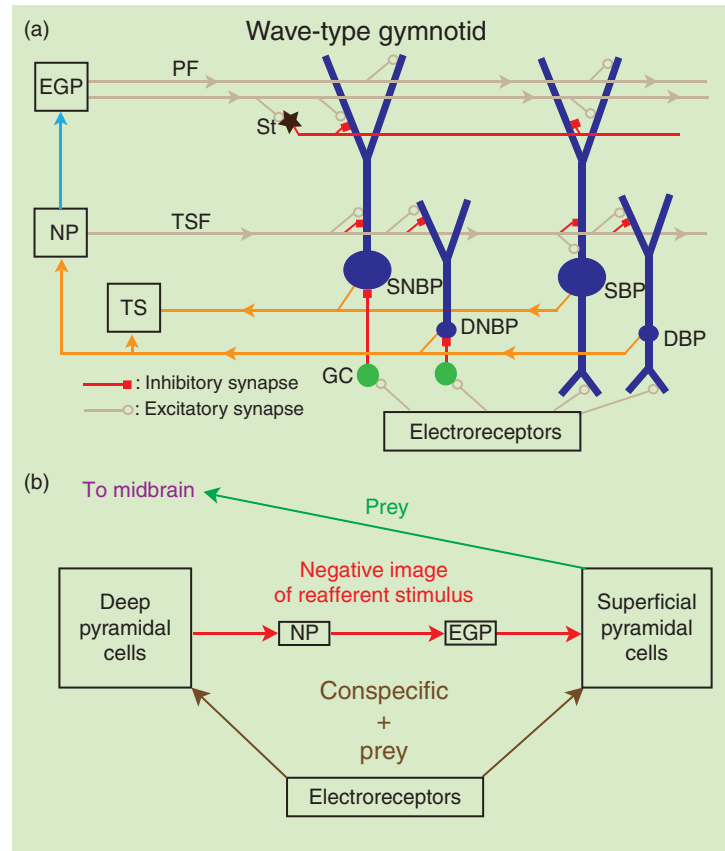
superficial and intermediate pyramidal cells. These feedback projections can account for up to 95% of synaptic input to ELL pyramidal cells.

Pyramidal cell physiology is well characterized in general *in vivo* and there are important differences between superficial, intermediate, and deep pyramidal cells. Deep pyramidal cells have broad tuning curves and the highest spontaneous firing rates (>35 Hz) while superficial pyramidal cells have narrower tuning curves and the lowest firing rates (<15 Hz) with intermediate pyramidal cells having characteristics between these limits. Studies have shown that pyramidal cell tuning is both segment and context specific: pyramidal cells can change their tuning to match the temporal frequency content of both prey-related and communication-related stimuli.

Feedback pathways play important roles in regulating pyramidal cell responses to electroreceptor afferent input and many studies have elucidated their functions, which include gain control, cancellation of reafferent input, and regulation of burst firing, as described below.

### Cancellation of Self-Generated stimuli

Sensory processing of electrosensory information is context dependent. For example, a given fish might be more interested in detecting a suitable mate or a prey item at different times of day and periods of its life. Indeed, tuberous electrosensory systems are modulated to vary the relative salience of information from conspecifics or prey items. Another example of context-dependent processing of electrosensory stimuli is the perception of movement. The fish's locomotion through the environment generates broad stimulation of the electrosensory system. This reafferent sensory stimulation must in turn be distinguished from external sensory stimuli such as a nearby predator or prey item. For weakly electric fish, tail movements that bring the tail closer/farther from a given point on the skin will increase/decrease the local EOD amplitude. Such signals can interfere with the detection of signals caused by external sources. In many species, the movement-related information is cancelled in the ELL. Different



**Figure 4** (a) Simplified anatomy of the ELL in *A. leptorhynchus*. Electroreceptors project to pyramidal cells: basilar pyramidal cells receive direct excitatory input while superficial nonbasilar pyramidal cells receive indirect inhibitory input via interneurons called granule cells (GC). There are large heterogeneities within the pyramidal cell population. Superficial basilar and nonbasilar pyramidal cells (SBP, SNBP) have large apical dendrites while deep basilar and nonbasilar pyramidal cells (DBP, DNBP) have small apical dendrites. Only deep pyramidal cells project to the nucleus praeminentialis (NP) while all pyramidal cell types project to the midbrain TS. Most interestingly, it is superficial pyramidal cells that receive the most feedback directly from NP via the tractus stratum fibrosum (TSF) and indirectly from granule cells in the eminentia granularis posterior (EGP) via parallel fibers (PFs). The direct projection from NP to ELL is called the direct feedback pathway while the indirect projection via EGP is called the indirect feedback pathway. (b) Functional circuit for cancellation of spatially diffuse electrosensory stimuli. Both superficial and deep pyramidal cells receive input from electroreceptors that respond to both conspecific and prey-related stimuli. Conspecific-related stimuli are spatially diffuse while stimuli caused by prey are spatially localized and only the former activate the negative image that is received mostly by superficial pyramidal cells, thereby allowing these cells to respond exclusively to prey stimuli.

species use different neural architectures to achieve this cancellation. Pulse-type mormyrid fish use a corollary discharge of the EOD command and an efference copy in order to achieve this function (see also **Detection and Generation of Electric Signals: Active Electrolocation**). Wave-type fish, however, have no such efference copy and must rely on other sensory signals and feedback pathways.

While electroreceptors in wave-type fish are sensitive to EOD AMs caused by tail movement, superficial ELL pyramidal cells are mostly insensitive to these same AMs. A series of elegant experiments performed by Bastian revealed that these neurons receive a negative image of the expected reafferent stimulus: the two inputs will cancel if the negative image has the right amplitude. Tail movements activate proprioceptors that project to the EGP and participate in generating the negative image.

However, later studies revealed that tail bending is not required for cancellation; it can occur with tuberous electrosensory input only.

The necessary circuitry to achieve this was recently uncovered: deep pyramidal cells are strongly modulated by self-generated stimuli. In fact, these cells provide the necessary cancellation input to superficial pyramidal cells through feedback pathways. This mechanism relies on the fact that the electric images caused by different behaviorally relevant signals have different spatial extents: electric images caused by a fish's own EOD will cover the entire body surface, electric images caused by conspecifics will tend to cover most, if not all, of the animal's skin surface (these are often referred to as global stimuli), and the electric images caused by prey will only cover a small fraction of the animal's skin (local stimuli). Studies

have shown that prey stimuli will not activate the negative image but that spatially diffuse stimuli will. As such, the cancellation circuit segregates spatially localized prey stimuli from spatially diffuse stimuli (**Figure 4(b)**).

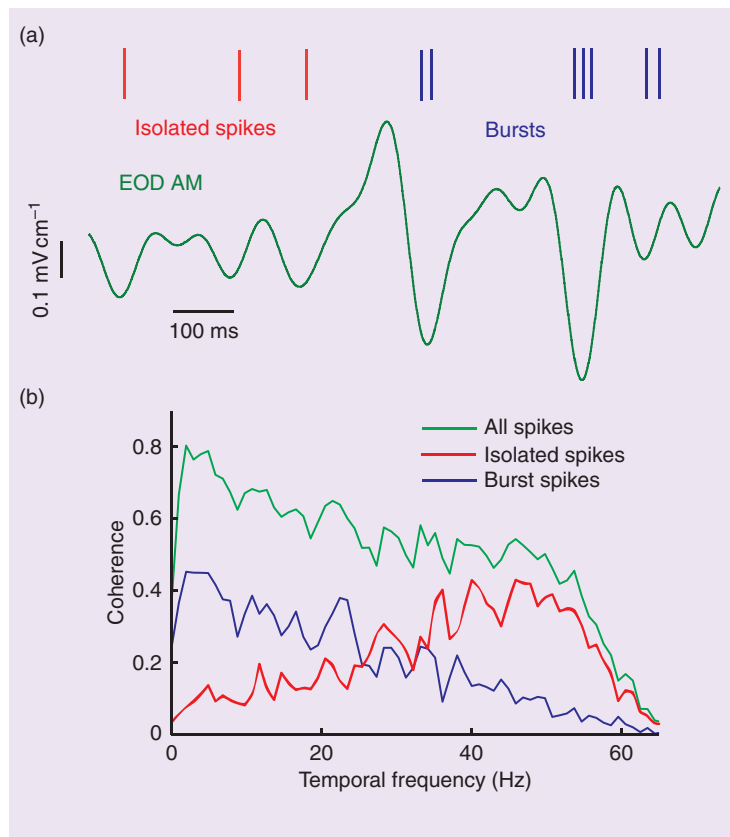
### Regulation of Burst Firing

Another major role for feedback pathways is to regulate the strength of pyramidal cell responses to sensory inputs. ELL pyramidal cells in *A. leptorhynchus* have a burst mechanism that is heavily regulated by feedback pathways. Pyramidal cells have much lower firing rates than receptor afferents (5–50 Hz) and they instead respond to changes in EOD amplitude with bursts of spikes (**Figure 5(a)**). Most interestingly, while receptor afferents use rate codes to transmit information about sensory stimuli, pyramidal cells use a timing code: spike bursts carry different information from isolated spikes. Bursts tend to code for low temporal frequencies of AM, while isolated spikes code for higher frequencies (**Figure 5(b)**).

Recent studies have focused on understanding the contributions of both ion channels and regulation of ion channel conductances by neuromodulators toward altering the responses of ELL pyramidal cells to sensory input.

### Comparison between Wave-Type Gymnotiform and Mormyriiform Weakly Electric Fish

Electrophysiological studies of ELL neurons in *Gymnarchus niloticus*, the only known species of mormyriiform wave-type fish, show remarkable parallels with gymnotiform weakly electric fish. Separate neuron classes in the ELL respond to either AM or FM. Most surprisingly, these fish also lack a corollary discharge in stark contrast with their pulse-type cousins. Thus, tuberous electrosensory systems that have evolved independently apparently use similar strategies to code for behaviorally relevant stimuli, providing a nice example of convergent evolution. Further studies are needed, however, to understand the cancellation of self-generated stimuli in *G. niloticus*.



**Figure 5** Physiology of ELL pyramidal cells in *A. leptorhynchus*. (a) Time-varying EOD amplitude (green) and spiking response of an example ELL pyramidal cell. This cell fired action potentials that were either isolated (red bars) or part of bursts (blue bars). (b) Coherence between the spike train of an example pyramidal cell and time-varying EOD amplitude. The coherence computed from the spike train (green) shows that this cell responds to all frequency components contained within the stimulus. However, the coherence computed from burst spikes alone (blue) was greater for low frequencies while the coherence computed from isolated spikes alone (red) was greater for higher frequencies. Hence, action potentials can code for different aspects of the stimulus (here temporal frequency), depending on whether they are isolated or belong to a burst.

## Physiology of Midbrain Neurons: Integration of Sensory Information

The torus semicircularis (TS) is a midbrain structure that is used to process electrosensory as well as auditory and mechanosensory information. In gymnotiform weakly electric fish, the TS is somatotopically organized and receives information from all of the maps in the ELL. It is hypertrophied and has distinct layers. Some of the layers in the dorsal torus receive direct tuberous inputs from ELL pyramidal cells, while others receive ampullary inputs (see also **Detection and Generation of Electric Signals: Physiology of Ampullary Electrosensory Systems**). These neurons send information to the ventral layers of TS. Information from P-type and T-type tuberous electrosensory systems is first sent to the ventral layers of the TS. Thus, the TS is a site of convergence, first from the various maps of the ELL in the dorsal TS, and second from P-type and T-type neurons in the deep layers of the TS. The TS is also where selectivity for specific behaviorally relevant stimulus features emerges in the ascending electrosensory pathway.

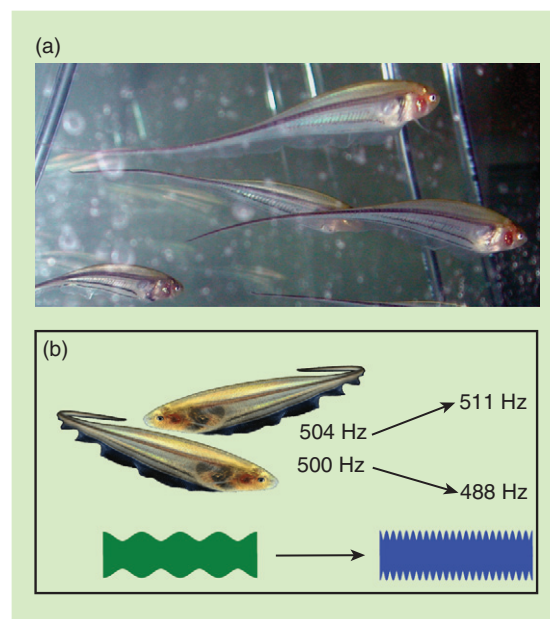
By contrast, the TS of mormyrid pulse-type fish is divided into separate nuclei that receive input from different groups of afferent neurons: neurons within the nucleus lateralis (NL) receive ampullary/mormyromast input while neurons in the nucleus extero-lateralis (EL) and nucleus medialis ventralis (NMV) receive input from knollenorgans. We review some of the properties of midbrain neurons in both gymnotiform and mormyrid fish below.

### Emergence of Selectivity for Salient Stimuli

TS neurons exhibit more selective responses to electrosensory stimuli than do receptor afferents or ELL neurons. Specifically, these neurons often respond to a much narrower range of temporal frequencies or spatiotemporal features than ELL pyramidal cells. The mechanisms underlying the increase in selectivity in the TS have been intensively studied in relation to two behaviorally relevant stimuli – social stimuli related to the ‘jamming avoidance response’ (JAR) and moving electrosensory images.

### Tuberous Mechanisms Underlying the JAR

The JAR behavior occurs in some wave-type species when two or more conspecifics are near each other, within  $\sim 1$  m, and the fish have similar EOD frequencies, within about 10 Hz of each other. This tends to occur more in gregarious species such as *Eigenmannia virescens* (Figure 6(a)). When fish are close to each other, the electric fields mix and produce interference patterns. Interference patterns of 3–8 Hz are detrimental and impair each fish’s ability to electrolocate nearby objects. To avoid these detrimental



**Figure 6** (a) *Eigenmannia virescens* are gregarious (i.e., they tend to stay in groups). (b) The JAR of *Eigenmannia*. When two conspecifics are in close proximity and the EOD frequencies are within about 10 Hz (504 and 500 Hz shown here), the electric fields combine to produce spatially widespread AMs at the difference in frequencies in the EOD, which here is 4 Hz. The trace below shows a 1-s sample with a 4-Hz AM. This combined electric signal elicits the JAR, in which the higher EOD frequency fish raises its frequency, and vice versa for the lower EOD frequency fish. The result is a higher AM rate; 23 Hz is shown here.

interference patterns, each fish may change its EOD frequency. The JAR behavior differs between species and is best studied in the gymnotiform wave-type weakly electric fish *E. virescens* (Figure 6(b)). In this species, the animal with the lower EOD frequency decreases its EOD frequency while the animal with the higher EOD frequency increases its EOD frequency. This behavior thereby increases the frequency of the interference patterns produced by the interactions of the EODs to 20 Hz or more. Interference patterns greater than 20 Hz do not have detrimental effects on electrosensory perception. The JAR behavior is most strongly elicited by interference patterns at rates of 3–8 Hz, but only weakly by electrosensory stimuli at rates above 20 Hz.

Most surprisingly, the JAR behavior is similar in both wave-type gymnotiforms and *G. niloticus*. Overall, both groups compute the sign of the frequency difference similarly although some computations occur in different brain areas. These computations require simultaneous knowledge of the AMs as well as the phase modulations occurring on different parts of the body.

In wave-type gymnotiform fish, these AMs are encoded by P-units and subsequently encoded by ELL pyramidal cells. Many neurons within the layers 1–5 of TS respond strongly to low-frequency stimuli below

10 Hz and weakly to higher-frequency stimuli above 20 Hz. These low-pass responses are generated by a suite of mechanisms in TS, including passive membrane properties, short-term synaptic depression, and subthreshold membrane conductances. Similar mechanisms are found in the TS of *G. niloticus*.

Phase differences across the body give rise to timing differences between inputs from T-type (in wave-type gymnotiform fishes) or S-type (in *G. niloticus*) afferents across the animal's body. In *Gymnarchus*, these timing differences are detected by ELL neurons, whose sensitivity matches that of the animal's behavior. In wave-type gymnotiform fish, these differences are detected by neurons in lamina 6 of the TS. Specifically, giant dendritic cells within this layer receive input from multiple ELL spherical cells and are thought to average this input. Giant cells then project broadly across lamina 6 onto the somata of small cells that also receive local input from spherical cells on their dendrites. These small cells possibly perform a comparison of the local EOD phase with respect to an EOD phase that is averaged across the animal's body by responding specifically when input from the dendrites is coincident with input from the soma. The sensitivities of small cells to timing differences are still significantly less than that of the animal's and, in contrast to *Gymnarchus*, further integration appears to take place: one must look in the diencephalon to find neurons whose sensitivity matches the behavior.

As mentioned above, some neurons in the deep layers of the TS receive input from both the amplitude-coding and time-coding pathways. These neurons likely play a critical role in the JAR as they compute the sign of the frequency difference between fish, which is required to determine the proper direction of the change in EOD frequency. Some neurons are active when the frequency difference is positive, while others respond when the frequency difference is negative. Similar neurons are found within the TS of *G. niloticus* where nonlinear voltage-dependent conductances enhance their selectivity to particular combinations of AM and PM information.

### Processing of EOD Waveform

Some neurons within the TS of pulse-type mormyrids are sensitive to small differences in EOD waveform. This circuit potentially functions in an analogous manner to the circuit found within lamina 6 in gymnotiform wave-type fish. Specifically, small cells within the EL pars anterior receive delayed excitatory input from nELL neurons and inhibitory input from giant cells within the same nucleus. This circuit would allow the small cells to respond selectively to EOD pulses of

certain duration in a 'delay line blanking' mechanism. A major difference between the duration coding circuit in pulse-type mormyrids and similar circuits found in wave-type gymnotiform fishes is that the former uses both excitation and inhibition while the latter uses only excitation.

### Tuberous Mechanisms for Processing Moving Objects

The electrosensory perception of moving objects is an important function in weakly electric fish. Prey capture can be achieved in complete darkness: under these conditions, it is likely that the tuberous electrosensory system is the primary source of salient sensory information for the control of the behavior. A critical feature for the behavior is the determination of the direction of movement of the prey stimulus. Selectivity for the direction of object motion first emerges at the level of the TS. P-type tuberous neurons in the dorsal layers can have strongly directionally selective responses to moving objects, whereas neurons in the ELL do not. Such neurons respond vigorously when an object moves in a particular direction (head-to-tail or tail-to-head) but weakly or not at all when the object moves in the opposite direction. Direction selectivity in these neurons is thought to derive from short-term synaptic plasticity and further studies are needed to understand the mechanisms giving rise to this computation.

### Conclusion

Tuberous electrosensory systems use a variety of strategies to code for natural sensory input. On the one hand, the combination of neural mechanisms and strategies used to achieve the same computation in some distantly related species shows a remarkable level of convergence; on the other, a remarkable level of diversity exists in brain mechanisms and computations among more closely related species. Indeed, biological systems can often implement multiple solutions for the same functions, and the comparative approach is required in order to identify and understand the fundamental principles underlying neuron computations and behavioral control.

**See also:** Detection and Generation of Electric Signals: Active Electrolocation; Electric Organs; Generation of Electric Signals; Physiology of Ampullary Electrosensory Systems. **Sensory Systems, Perception, and Learning:** Shocking Comments: Electrocommunication in Teleost Fish.



## Further Reading

- Bastian J (1999) Plasticity of feedback inputs in the apteronotid electrosensory system. *Journal of Experimental Biology* 202: 1327–1337.
- Bastian J, Chacron MJ, and Maler L (2004) Plastic and non-plastic cells perform unique roles in a network capable of adaptive redundancy reduction. *Neuron* 41: 767–779.
- Bell CC, Han V, and Sawtell NB (2008) Cerebellum-like structures and their implications for cerebellar function. *Annual Review of Neuroscience* 31: 1–24.
- Bullock TH (1982) Electroreception. *Annual Review of Neuroscience* 5: 121–170.
- Carlson BA and Kawasaki M (2008) From stimulus estimation to combination sensitivity: Encoding and processing of amplitude and timing information in parallel, convergent sensory pathways. *Journal of Computational Neuroscience* 25: 1–24.
- Chacron M (2007) Electrolocation. *Scholarpedia* 2(1): 1411, <http://www.scholarpedia.org/article/Electrolocation> (accessed January 2010).
- Chacron MJ, Doiron B, Maler L, Longtin A, and Bastian J (2003) Non-classical receptive field mediates switch in a sensory neuron's frequency tuning. *Nature* 423: 77–81.
- Fortune ES (2006) The decoding of electrosensory systems. *Current Opinion in Neurobiology* 16: 474–480.
- Hagiwara S, Kusano K, and Negishi K (1962) Physiological properties of electroreceptors of some gymnotids. *Journal of Neurophysiology* 25: 430–449.
- Heiligenberg W (1991) *Neural Nets in Electric Fish*. Cambridge, MA: MIT Press.
- Kawasaki M and Guo YX (1998) Parallel projection of amplitude and phase information from the hindbrain to the midbrain of the African electric fish *Gymnarchus niloticus*. *Journal of Neuroscience* 18: 7599–7611.
- Krahe R and Gabbiani F (2004) Burst firing in sensory systems. *Nature Reviews Neuroscience* 5: 13–23.
- Maler L (2009) Receptive field organization across multiple electrosensory maps- I. Columnar organization and estimation of receptive field size. *Journal of Comparative Neurology* 516: 376–393.
- Maler L (2009) Receptive field organization across multiple electrosensory maps- II. Computational analysis of the effects of receptive field size on prey localization. *Journal of Comparative Neurology* 516: 394–422.
- Mehaffey WH, Ellis LD, Krahe R, Dunn RJ, and Chacron MJ (2008) Ionic and neuromodulatory regulation of burst discharge controls frequency tuning. *Journal of Physiology (Paris)* 102: 195–208.
- Oswald AMM, Chacron MJ, Doiron B, Bastian J, and Maler L (2004) Parallel processing of sensory input by bursts and isolated spikes. *Journal of Neuroscience* 24: 4351–4362.
- Sawtell NB, Williams A, and Bell CC (2005) From sparks to spikes: Information processing in the electrosensory systems of fish. *Current Opinion in Neurobiology* 15: 437–443.
- Scheich H, Bullock, TH, and Hamstra RH (1973) Coding properties of two classes of afferent nerve fibers: High frequency electroreceptors in the electric fish, eigenmania. *Journal of Neurophysiology* 36: 39–60.
- Szabo T and Hagiwara M (1967) A latency-change mechanism involved in sensory coding of electric fish. *Physiology and Behavior* 2: 331–335.
- Xu-Friedman MA and Hopkins CD (1999) Central mechanisms of temporal analysis in the knollenorgan pathway of mormyrid electric fish. *Journal of Experimental Biology* 202: 1311–1318.

## Relevant Websites

- <http://alumnus.caltech.edu> – Caltech Alumni Web Server, Weakly Electric Fish.
- <http://www.fiu.edu> – FIU, Florida International University; Neuroethology and Behavioral Ecology of Communication in Electric Fish.
- <http://www.bio.indiana.edu> – Indiana University, Department of Biology, G. Troy Smith.
- <http://www.zoologie.uni-bonn.de> – Institut für Zoologie der Universität Bonn, Neuroethologie Bonn.
- <http://www.medicine.mcgill.ca> – McGill, Computational Systems, Neuroscience Laboratory.
- <http://www.neuromech.northwestern.edu> – Northwestern University, McCormick School, Biomedical & Mechanical Engineering.
- <http://people.virginia.edu> – University of Virginia, What Is an Electric Fish?