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# Physiology of Tuberous Electrosensory Systems<sup>☆</sup>

**MG Metzen**, McGill University, Montreal, QC, Canada

**ES Fortune**, New Jersey Institute of Technology, Newark, NJ, United States

**MJ Chacron**, McGill University, Montreal, QC, Canada

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## 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** Refers to the ability of certain fishes, amphibians and mammals to sense electric fields. Many aquatic species have a passive electric sense whereas only two clades of fishes possess an active electric sense in which the animal detects autogenous (self-generated) electric signals.

**Envelope** Refers to a signal in which slow variations of the amplitude modulation carry sensory information.

**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 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 (ie, 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

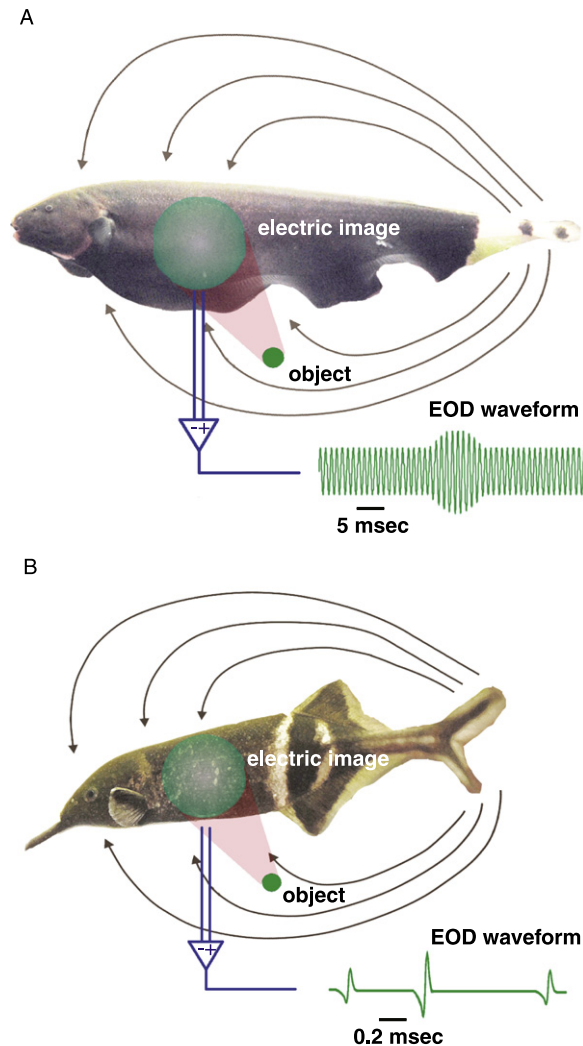
Weakly electric fish produce low voltage electric fields ( $< 2 \text{ V cm}^{-1}$ ) using specialized electrogenic organs. The electrical output of the organ is known as the electric organ discharge, or EOD. There are two phylogenetically independent orders of weakly electric fishes: the Gymnotiformes of South America and the Mormyriiformes of Africa. These clades evolved independently within two distantly related groups, the ostariophysans and osteoglossomorphs, respectively.

Gymnotiform and mormyriiform fishes can both be classified as either wave- or pulse-type depending on the temporal structure of their EOD. Wave-type weakly electric fish generate continuous, highly periodic EOD waveforms (**Fig. 1A**), 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 (**Fig. 1B**). 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 detect perturbations of the autogenous EOD using tuberous electroreceptors that are embedded in the skin and distributed over the body surface. This sensory system is referred to as active electrolocation since the animal actively generates the sensory signal. There are several classes of tuberous electroreceptors that encode different features of the animal's electric field. All species have two classes of tuberous electroreceptors, one type (amplitude coding) that encodes EOD amplitude modulations (AM), and another type (time coding) that primarily encodes EOD timing and frequency modulations (FM). Tuberous electroreceptors also detect the EODs of conspecifics in the context of communication. 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 next describe the encoding of second-order stimuli (ie, envelopes) by amplitude sensitive tuberous electroreceptors in wave-type gymnotiforms. We then review the characteristics of ELL neurons with a particular emphasis on the role of feedback pathways in wave-type gymnotiforms. We then finish by highlighting some of the characteristics of higher order neurons and their roles in behaviorally relevant computations.

<sup>☆</sup>*Change History:* December 2015. M.G. Metzen, E.S. Fortune, and M.J. Cacion updated the following sections: Glossary; Introduction; Amplitude coding in pulse-type fish; Comparison between wave-type gymnotiform and mormyriiform weakly electric fish; Further reading. The following sections have been added: Envelopes in wave-type gymnotiform fish; Envelope coding in wave-type gymnotiform fish. The following figures have been updated: Figs. 1 and 8. For the following figures and figure captions have been added: Figs. 3 and 4.



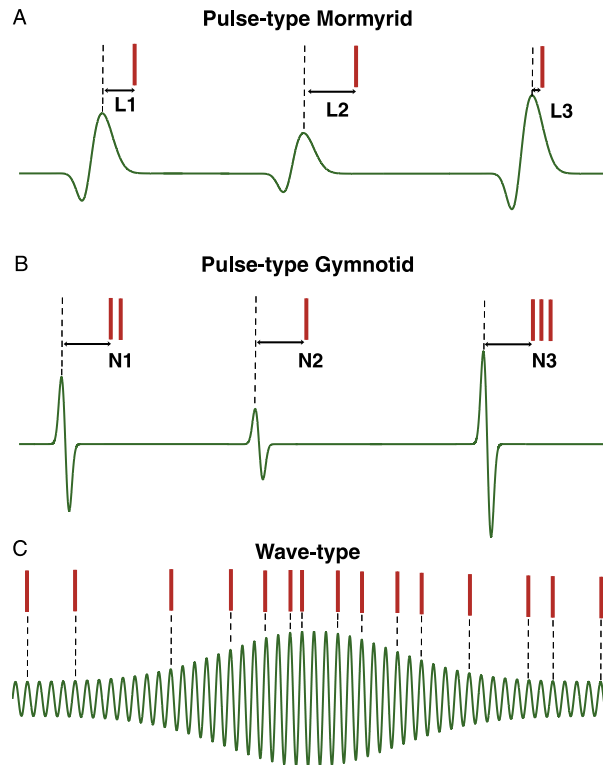
**Fig. 1** The principle of active electrolocation in weakly electric fishes. (A) The wave-type gymnotiform species *Aptereronotus albifrons* emits a highly periodic quasi-sinusoidal EOD. (B) The pulse-type mormyriiform species *Gnathonemus petersii* emits pulses of electricity with strong variability 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 (eg, rocks, plants, other fish, 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.

## Amplitude Coding

Both gymnotiform and mormyriiform weakly electric fish have tuberous electroreceptors embedded in the skin that can encode amplitude modulations of the EOD. In gymnotiform fish, these receptors are known as P-units as it was originally found that the probability of firing increased linearly with EOD amplitude. In mormyriiform pulse-type fish, these receptors are located in structures known as mormyromasts. [Fig. 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 can be regarded as electrosensory organs since they constitute of two distinct groups of sensory cells (type A and type B cells). Both of them are sensitive to amplitude modulations and send separate afferent fibers to pyramidal cells within the ELL. However, type B sensory cells are mainly sensitive to changes in the EOD waveform and less to changes in amplitude. Since research has focused primarily on amplitude coding, we will henceforth refer to the A cell type only. This cell type usually responds with one or more action potentials to each EOD pulse ([Fig. 2A](#)). The latency between the EOD



**Fig. 2** Amplitude coding in wave-type, pulse-type mormyrid, and pulse-type gymnotid weakly electric fishes. (A) Mormyromasts in mormyrid 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) In contrast, burst duration coders in gymnotid 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 gymnotid wave-type fish and O-units in mormyrid 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.

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.

Amplitude encoding in pulse-type gymnotid fishes involves a different strategy. Tuberous neurons in gymnotid 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 (Fig. 2B). These receptors are known as burst duration coders.

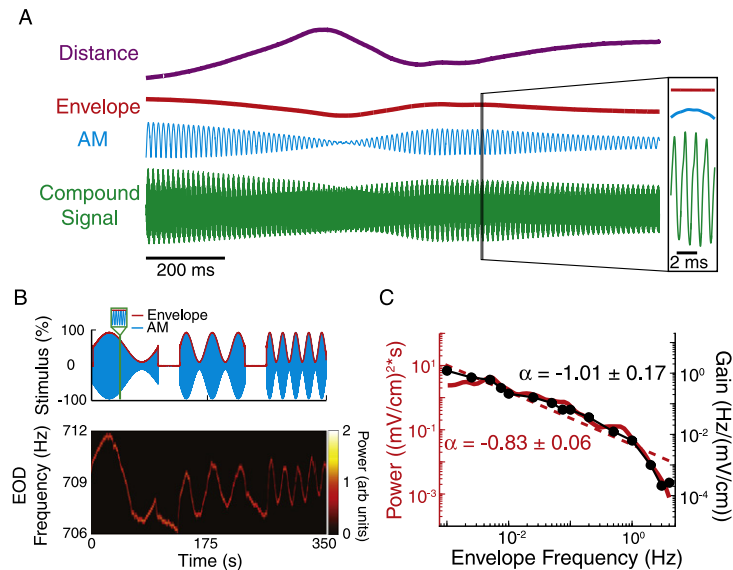
### Amplitude Coding in Wave-Type Fish

In wave-type gymnotid 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 (Fig. 2C). 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 (ie, the firing rate is equal to the inverse absolute refractory period) for very high EOD amplitudes. Studies have shown that these afferents have broad, flat tuning curves over the range of salient frequencies, from near DC to around 100 Hz.

In wave-type mormyrid fish, O-units have properties similar to those of P-units in wave-type gymnotid weakly electric fish. The similarities in coding strategies between O-units and P-units are particularly interesting as they evolved independently in these two clades, mormyrids and gymnotids, respectively, of weakly electric fishes.

### Envelopes in Wave-Type Gymnotid Fish

Natural electrosensory stimuli include sinusoidal modulations in the amplitude of each EOD (ie, the AM) (Fig. 3A, blue) that occur when two fish are in close proximity to each other. These modulations, which typically occur at rates of 10 to 100 s of Hz,



**Fig. 3** Envelope tracking in wave-type gymnotiform fish. (A) Electric organ discharge (EOD) waveform from *Apteronotus leptorhynchus* (green) with AM (cyan) and envelope (red) waveforms. We note that the envelope corresponds to the depth of modulation of the EOD AM that is due to relative movement (purple) between individuals. The inset (right) shows a snippet of all waveforms. (B) *Top*: Example stimuli that consist of a high frequency sinusoidal carrier (cyan) whose envelope (red) is also modulated sinusoidally. *Bottom*: EOD spectrogram in response to the stimuli shown. The EOD frequency tracks the detailed time course of the contrast. (C) Power spectrum of the envelope signal (red) recorded in freely moving fish and best power law fit (red dashed line) with the gain (black) measured for *A. leptorhynchus* superimposed.

can be further modulated at longer timescales, typically at rates less than a few Hz but often less than 0.1 Hz, thereby creating an envelope (Fig. 3A, red).

Recent studies have shown that envelopes can occur during two different behavioral contexts. First, when two or more fish interact, their relative movement generates envelopes. The envelope carries important information as to the distance between two animals (Fig. 3A, green). These envelopes include low frequency information, typically below a few Hz, that matches the locomotion rates of the fish (Fig. 3C, red). Second, envelopes can occur via complex interference patterns that emerge during interactions between the electric fields of three or more fish. This interference creates an envelope that varies sinusoidally at a frequency given by the difference between the two beat rates, that often is composed of higher, more than a few Hz, temporal frequencies.

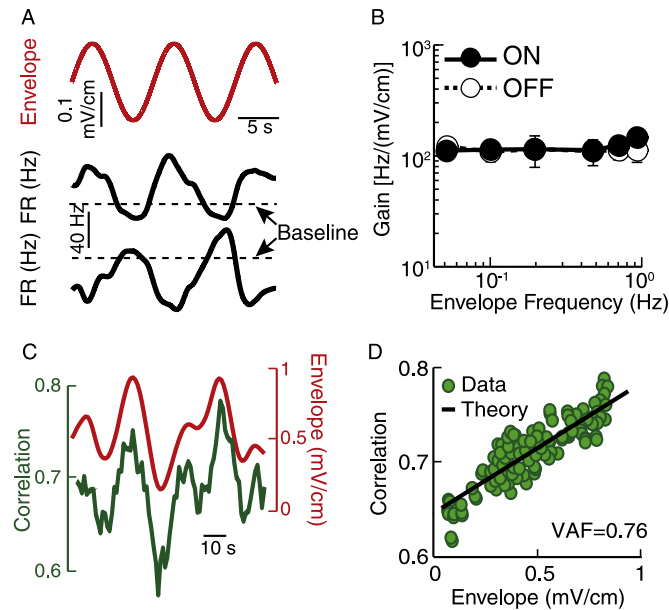
These “social” envelopes can hinder the animal’s ability to detect other signals (eg, those caused by prey). On the other hand, these fish use movement envelopes as they track the low frequency motions of nearby conspecifics (Fig. 3B, top) by changing their EOD frequency (Fig. 3B, bottom). They change their EOD frequency in relation to the envelope, which is affected by the distance and orientation of the nearby fish. Further, these behavioral responses are adapted to the statistics of movement envelopes as both the behavioral gain and the power spectrum decay as a power law as a function of temporal frequency (Fig. 3C). This tracking behavior demonstrates that detailed information about low frequency movement envelopes is retained in the brain.

### Envelope Coding in Wave-Type Gymnotiform Fish

Two different coding strategies can be identified in the responses of P-units to envelopes. First, P-units with a lower baseline firing rate (eg, less than half of the inverse of their refractory period) increase their firing rate with increasing envelope (Fig. 4A, middle). Second, P-units that have a higher baseline activity (eg, more than half of the inverse of their refractory period) decrease their firing rate in response to increasing envelopes (Fig. 4A, bottom). However, the response gains in both cases are similar and constant over the range of the frequencies found in movement envelopes (Fig. 4B). Hence, correlated activity of pairs of afferents transmits more information about time varying envelopes than a single neuron (Fig. 4C). This is due to the fact that P-units fire more coincident spikes when the envelope has higher amplitudes than when the envelope is at lower amplitude levels.

### Time Coding

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



**Fig. 4** Envelope coding in P-units. (A) Examples of an ON-type P-unit (middle) responding with an increase in firing rate and an OFF-type P-unit (bottom) responding with a decrease in firing rate to an increase in envelope (top, red). (B) Population-averaged gain as a function of envelope frequency (filled circles: ON-type, open circles: OFF-type). (C) Time varying envelope (red), and correlation coefficient (green) from a pair of P-units recorded from simultaneously. (D) Correlation coefficient as a function of envelope intensity obtained from data (green) and numerical simulations (solid line).

### Time Coding in Pulse-Type Fish

T-units in gymnotiform and Knollenorgans in mormyriiform pulse-type weakly electric fish fire one phase-locked action potential per EOD pulse. These units therefore track changes in the EOD frequency (Fig. 5A). In mormyrids, individual Knollenorgans respond at various phases of an EOD pulse, so that relative differences in the timing of action potentials amongst Knollenorgans additionally encode the EOD waveform.

### Time Coding in Wave-Type Fish

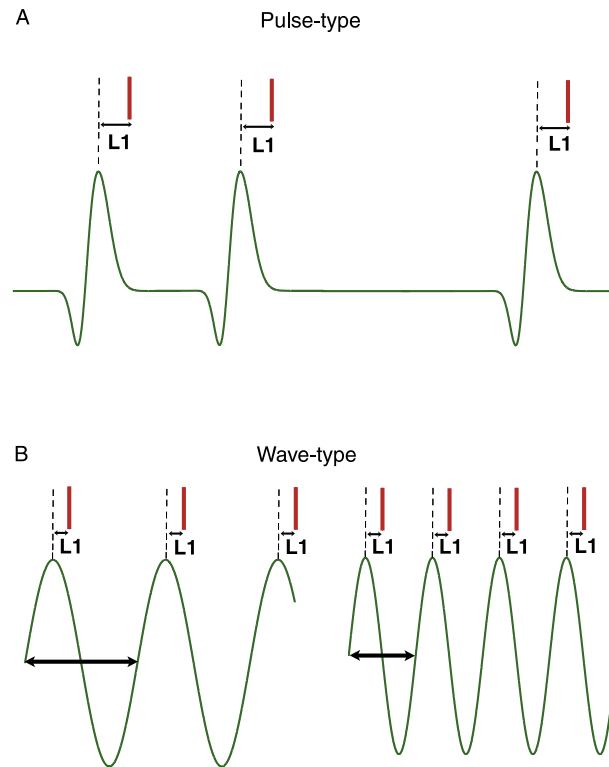
T-units in gymnotiform wave-type weakly electric fish and S-units in wave-type mormyriiform fish display phase-locked firing to the EOD cycle. These units encode a correlate of the instantaneous EOD frequency as they typically fire a single action potential per EOD cycle at a precise phase (Fig. 5B).

### Projections to Higher Order Neurons

All electroreceptor units send information into a hindbrain structure known as the ELL via the 8th nerve. Anatomical and physiological studies have shown that the time coding pathways in the ELL preserve fine temporal information carried by time coding afferents. In all classes of weakly electric fishes, neurons receiving input from time coding afferents have a similar physiology: they fire one action potential per EOD cycle or EOD pulse. These neurons receive no descending feedback from CNS circuits and thus appear to be a feedforward-only system.

In contrast, information from amplitude coding afferents is subject to complex processing that includes descending feedback in ELL circuits. Tuberous electroreceptors fire not only in response to the animal's own EOD pulse, but also to EOD pulses emitted by conspecifics.

Pulse-type mormyrid fish have a different approach for processing electrosensory information. These fish generate a corollary discharge of each EOD pulse in brain circuits, allowing them to distinguish between self-generated and externally generated EODs within the ELL. Mormyromasts give rise to a sensory pathway specialized for encoding self-generated EODs that is compared to the corollary discharge, whereas Knollenorgans give rise to a sensory pathway specialized for encoding externally generated EODs. The basic properties of all types of electroreceptors are summarized in Table 1.



**Fig. 5** Time coding in pulse-type and wave-type weakly electric fishes. (A) Pulse-marker units in pulse-type gymnotiforms and knollenorgans in mormyriiforms 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 mormyriiforms fire one action potential per EOD cycle (ie, 1:1 phase locking). Their instantaneous firing rates thus provide a measure of the instantaneous EOD frequency.

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

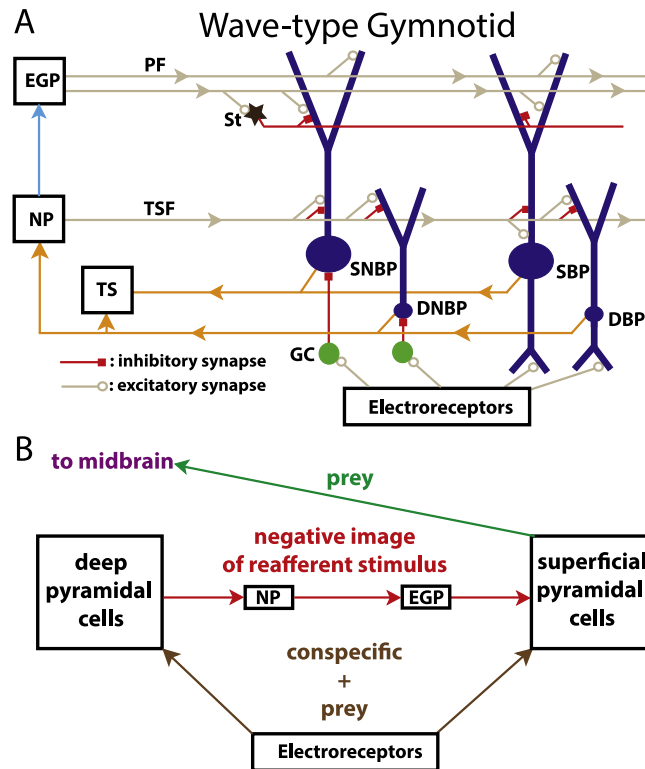
	<i>Amplitude coding</i>	<i>Frequency coding</i>
Wave type	<i>P-unit or O-unit.</i> Skips a random number of EOD cycles between firings. Probability of firing on any given EOD cycle increases with EOD amplitude.	<i>T-unit or S-unit.</i> Fires one action potential per EOD cycle. The phase of firing advances 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 mormyriiform	<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.

## 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 [Fig. 6A](#). P-type electroreceptor afferents project to pyramidal cells within the ELL. There are two types of pyramidal cells: basilar pyramidal cells (ON-type cells) receive direct electroreceptor input on their basilar dendrites whereas non-basilar pyramidal cells (OFF-type 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 non-basilar 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



**Fig. 6** (A) Simplified anatomy of the ELL in *Apteronotus leptorhynchus*. Electoreceptors project to pyramidal cells: basilar pyramidal cells receive direct excitatory input while superficial non-basilar pyramidal cells receive indirect inhibitory input via an interneuron (GC). There are large heterogeneities in the pyramidal cell population. Superficial basilar and non-basilar pyramidal cells (SBP, SNBP) have large apical dendrites while deep basilar and non-basilar 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 torus semicircularis (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 (PF). 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 electoreceptors 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. Information from these neurons is then sent to the midbrain for further processing.

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.

The physiological properties of the classes of pyramidal cells are well characterized. 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). Intermediate pyramidal cells have characteristics that are between the extremes seen in superficial and deep cells. 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 electoreceptor afferent input and include cancellation of reafferent input, regulation of burst firing, and gain control.

### 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.



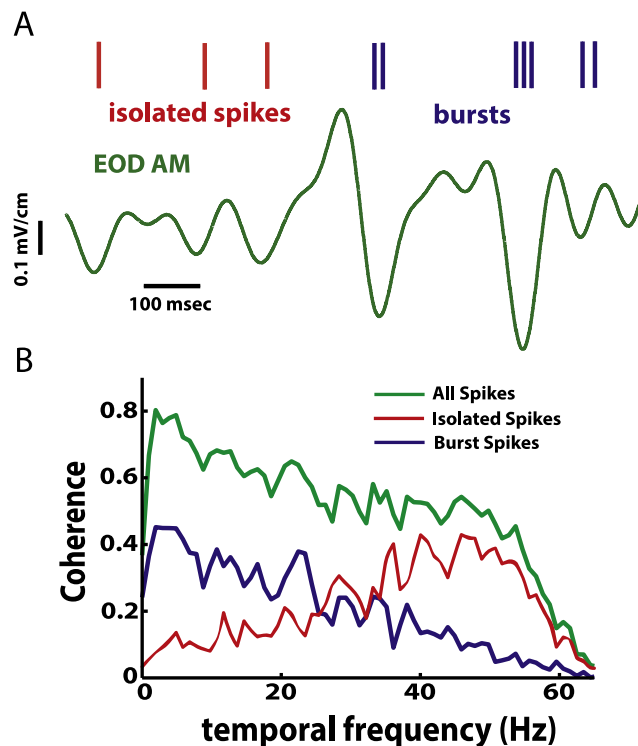
Such signals can interfere with the detection of signals caused by external sources. In many species, the movement-related information is canceled in the ELL. Different species use different neural architectures to achieve this cancellation. Pulse-type mormyrid fish use a corollary discharge of the EOD command and an efference copy in order to achieve this function. 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 has shown 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 have shown that tail bending is not required for cancellation; it can occur with tuberous electrosensory input only.

The necessary circuitry to achieve this has been uncovered: deep pyramidal cells are strongly modulated by self-generated stimuli. In fact, it is these cells that 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 appears to segregate spatially localized prey stimuli from spatially diffuse stimuli (Fig. 6B).

### 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 *Apteronotus leptorhynchus* have a well-characterized burst mechanism that is regulated by feedback pathways. Pyramidal cells have lower firing rates than receptor afferents (5–50 Hz) and they instead respond to changes in EOD amplitude with bursts of spikes (Fig. 7A). Interestingly, while receptor afferents use rate codes to transmit information about sensory stimuli, pyramidal cells use a timing code: bursts of spikes carry different information from isolated spikes. Bursts tend to code for low temporal



**Fig. 7** Physiology of ELL pyramidal cells in *Apteronotus 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.

frequencies of AM while isolated spikes code for higher frequencies (Fig. 7B). 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, have revealed remarkable parallels with gymnotiform weakly electric fish. In *Gymnarchus*, ELL neurons respond either to amplitude or frequency modulation, as is seen in Gymnotiform fishes. Surprisingly, *Gymnarchus* lacks a corollary discharge, which stands in stark contrast with their pulse-type relatives. In other words, *Gymnarchus* lost the corollary discharge as it evolved from its pulse-type ancestors into a wave-type species. Although correlation is not causation, it suggests that *Gymnarchus* has independently evolved similar coding strategies for behaviorally relevant stimuli – a nice example of convergent evolution. Further studies are however needed to understand the cancellation of self-generated stimuli in *Gymnarchus*.

### Physiology of Midbrain Neurons: Integration of Sensory Information

The torus semicircularis (TS) is a midbrain structure that is used to process information from the 8th nerve, including electro-sensory, auditory and mechanosensory information. In gymnotiform weakly electric fish, the TS is somatotopically organized and receives information from all of the electrosensory 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. These neurons send information to the ventral layers of TS. It is in the ventral layers of the TS where information from P-type and T-type tuberous electrosensory systems first converge. 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.

In 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 exterolateralis (EL) and nucleus medialis ventralis (NMV) receive input from knollenorgans.

### Emergence of Selectivity for Salient Stimuli

TS neurons exhibit more selective responses to electrosensory stimuli than do receptor afferents or ELL neurons. In other words, 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.

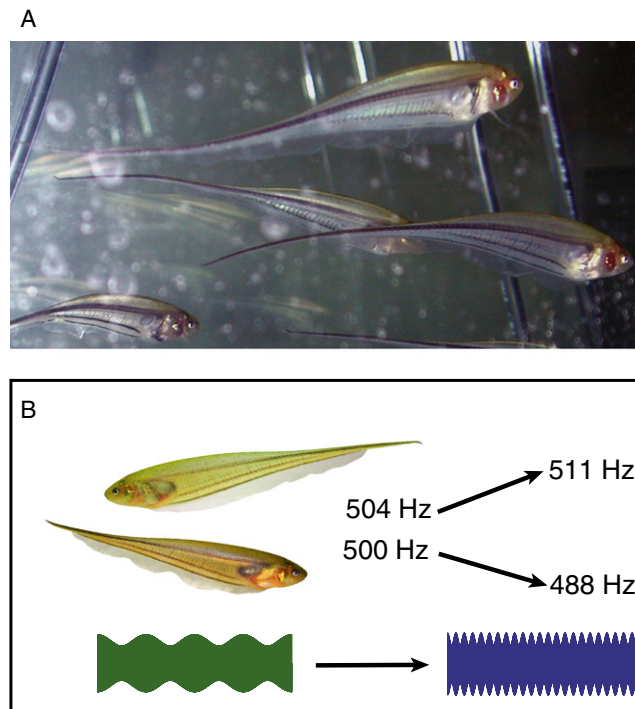
### Tuberous Mechanisms Underlying the JAR

The JAR behavior occurs in some wave-type species when two or more conspecifics with similar EOD frequencies (within about 10 Hz of each other) are within about a meter of each other (Fig. 8A). When fish are close to each other, the electric fields mix and produce interference patterns. Interference patterns of 3 to 8 Hz are detrimental and impair each fish's ability to electrolocate nearby objects. To avoid these detrimental interference patterns, each fish may change its EOD frequency.

There are differences in the JAR behavior between species: the JAR has been most studied in the gymnotiform wave-type weakly electric fish *Eigenmannia virescens* (Fig. 8B). 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 appear to have detrimental effects on electrosensory perception. The JAR behavior is most strongly elicited by interference patterns at rates of 3 to 8 Hz, but only weakly by electrosensory stimuli at rates above 20 Hz.

The JAR behavior is similar in both wave-type gymnotiforms and in the independently evolved *Gymnarchus niloticus*. Both compute the sign of the frequency difference using similar computational strategies, although the computations occur in different brain areas. These computations require simultaneous knowledge of the amplitude modulations as well as the phase modulations occurring on different parts of the body.

In wave-type gymnotiform fishes, amplitude modulations are encoded by P-units and subsequently encoded by ELL pyramidal cells. Studies have found that 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 *Gymnarchus niloticus*.



**Fig. 8** (A) *Eigenmannia viriscens* are gregarious (ie, 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.

Phase differences across the body give rise to timing differences between inputs from T-type (in wave-type gymnotiform fishes) or S-type (in *Gymnarchus 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 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. It is thought that these small cells 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 match the behavior.

Neurons in the deep layers of the TS receive input from both the amplitude coding and time coding pathways. These neurons are thought to 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 *Gymnarchus niloticus* where non-linear 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. It has been hypothesized that this circuit functions in an analogous manner to the circuit found within lamina 6 in gymnotiform wave-type fish. Specifically, small cells within the nucleus extero-lateralis pars anterior receive delayed excitatory input from nELL neurons and inhibitory input from giant cells within the same nucleus. It is thought that 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 electroreceptive perception of moving objects is an important for prey capture and locomotor control in weakly electric fishes. Weakly electric fishes can capture prey in complete darkness: the tuberous electroreceptive system has been shown to be the primary source of salient sensory information. A critical feature in prey capture 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 electroreceptive systems use a variety of coding strategies for natural sensory input. On one hand, the combination of neural mechanisms and strategies used to achieve the same computation in some distantly-related species show a remarkable level of convergence, but on the other hand, there is a remarkable level of diversity in brain mechanisms and computations among more closely-related species. Indeed, biological systems often can 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.

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