

activated glomeruli, (ii) the spatial combination of active neurons, (iii) the slow temporal sequence of activity patterns imposed by sampling-related process, (iv) the rapid synchronization of neuronal subpopulations relative to the network oscillatory regime. Therefore coding in the olfactory system is not a static phenomenon but a dynamical process with different temporal components, each of them probably readout by an adapted mechanism. This spatio-temporal representation is moreover dynamically reorganized by experience.

Sampling related process and odor characteristics impose the slow temporal dynamics, while intrinsic network dynamics established the fast LFP oscillatory regimes. Thus both dynamics are generated by system functioning. Dynamical representation of odors can nevertheless stand for a code provided that the neural network uses these temporal clues as a computational variable for coding. Firstly, the slow respiration-related rhythm could subserve a filtering function whereby neuronal responses could be selected on the basis of their respiratory phase. Such a functional phase-coding relative to theta cycle (i.e. related to respiratory frequency) has been evidenced in hippocampus place cells [10]. Secondly, the fast network oscillations probably intervene in a second step by refining the pattern of activated neurons through a synchronization binding process. This coding principle is better understood in other systems [10]. In such conditions, temporal dynamics, although epiphenomenal, are used by the system and thus may be considered as supporting temporal coding. The ultimate evidence would be provided in mammals if behavioral experiments could show changes in behavior in relation with a modification of the bulbocortical dynamics.

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## Temporal Coding in Electroreception

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### Synonyms

Time coding, electrosensory

### Definition

Confronted with a variable environment, organisms are faced with the task of extracting information to guide their behavior. A massive amount of raw information is encoded by the peripheral nervous system, which is then winnowed down, processed, and analyzed by the central nervous system in order to obtain behaviorally-relevant information. Time is an inherent element of neural coding. The timing of neural activity reflects the timing of stimuli responsible for that activity, and thereby informs the organism of the stimulus time of occurrence. An organism's accuracy in determining when something occurred is thereby limited by the degree of temporal precision achieved by its nervous system.

The nervous system can also use time to encode information beyond the stimulus time of occurrence. For instance, barn owls compare the arrival times of sounds at the two ears to determine the horizontal location of sound sources in space, bats use the delay between their echolocation calls and returning echoes to determine the distance to a target, and many organisms use precise temporal patterns to convey information in their communication signals. Neuroethological studies of the underlying neural mechanisms for such behaviors have revealed a great deal about the specializations that nervous systems have evolved for preserving and representing temporal information. Time plays an especially critical role in electroreception, perhaps more so than for any other sensory system. Weakly electric fish have therefore served as important model systems for studying the neural basis of accurate and precise

► temporal coding.

## Characteristics

### Quantitative Description

Weakly electric fish possess an electromotor system that generates weak **▶electric organ discharges**, or **▶EODs**, from a specialized electric organ, as well as an electrosensory system for receiving and analyzing these EODs. Unlike acoustic signals that propagate as traveling pressure waves, electric signals exist as non-propagating electrostatic fields [1]. This is a behaviorally significant, distinguishing feature of electric signals. The temporal structure of acoustic signals is distorted by factors such as reflection, refraction, absorption, dispersion, and reverberation. This has the effect of smearing the fine temporal structure of the signal, limiting the amount of information that may be transmitted using temporal features. By contrast, electric fields are not subject to these sources of distortion. As a result, the fine temporal structure of electric signals is preserved, and information may be encoded at very minute time scales [1]. For this reason, weakly electric fish are exquisitely sensitive to temporal features of electric signals, with sensitivity in some species extending to the submicrosecond range [2].

### Higher Level Structures

Although the available evidence indicates that electrosensory systems have independently evolved multiple times, the electrosensory pathways of weakly electric fish share a common overall design [3]. Electric signals are first received by specialized electroreceptors located in the skin and distributed throughout the body [4]. Primary afferent fibers, located in the lateral line nerves, transmit electroreceptor input to the hindbrain, where they terminate in a derived brain region termed the **▶electrosensory lateral line lobe (ELL)**. The first steps in electrosensory processing occur within the ELL, where primary afferent input, feedback loops from higher electrosensory regions, and descending input from other modalities and motor pathways converge [3]. ELL neurons project primarily to two distinct areas, the preeminent nucleus between the hindbrain and the midbrain, and the **▶torus semicircularis** in the midbrain [3]. The preeminent nucleus gives rise to a prominent ELL feedback pathway. In the torus semicircularis, additional electrosensory processing occurs. Studies on temporal coding and processing in electrosensory pathways have focused on the preservation of timing by primary afferents and ELL neurons, and on the extraction of information, by comparing differences in timing between different inputs within specialized circuits in the ELL and torus semicircularis.

### Lower Level Components

#### Electroreceptor Organs

In weakly electric fish, the encoding of sensory information within the EOD is achieved by tuberos

**▶electroreceptor organs**, which give rise to two distinct types of afferents: amplitude coders and time coders [4]. Amplitude-coding afferents encode the amplitude of EODs in their firing rate, relative latency to the first action potential, or number of action potentials. Time-coding afferents are much more sensitive than amplitude-coding afferents. In response to each outside positive-going voltage step, they fire a single action potential at a short fixed latency, thereby providing a precise marker of the EOD time of occurrence.

#### Specialized Features of Time-Coding Circuitry

The electrosensory pathways of weakly electric fish are characterized by several unique anatomical specializations, which have been associated with neural circuits in which action potential timing precision is of the utmost importance [5]. The neurons are relatively large, which increases input resistance, thereby rendering the neurons less sensitive to synaptic noise. These large neurons are typically spherical and adendritic, which minimizes differences in the arrival times of multiple synaptic inputs, and shortens the distance between synapses and the action potential initiation zone of the axon, thereby minimizing the attenuation of synaptic current. The axons are correspondingly large and heavily myelinated, which increases conduction velocity, thereby minimizing the effect of jitter on the timing of spike arrival at the synaptic terminal. These axons give rise to large club endings that engulf a large portion of the postsynaptic soma. This large size ensures sufficient synaptic current for overcoming the high input resistance of the postsynaptic cell. In addition, these synapses are often mixed chemical/electrical, which helps ensure rapid activation of the postsynaptic cell.

### Higher Level Processes

#### Species Recognition in Pulse-Type Mormyrids

In mormyrid electric fish from Africa, electric communication appears to be mediated exclusively by time-coding electroreceptors called **▶knollenorgans** [6]. Knollenorgans are much more sensitive than other tuberos electroreceptor organs, making them well-suited to detecting the EODs of distant conspecifics. Perhaps the strongest evidence for their privileged role in communication comes from the fact that every time a fish generates its own EOD, knollenorgan input is blocked by inhibition at the projection site of primary afferents in the nucleus of the electrosensory lateral line lobe (nELL). This inhibitory input comes from an electric organ corollary discharge pathway, which originates in the command center for EOD production, and provides a precise reference of EOD timing. As a result, activity caused by the fish's own EOD production never reaches higher processing centers in the midbrain.

Mormyrids generate a pulse-type EOD, in which the duration of a single EOD pulse is much shorter than

the interval between pulses [7]. The EOD waveform is highly stereotyped and conveys several aspects of the sender's identity, such as its species, sex, dominance, and possibly even its individual identity. The total duration of the EOD is a particularly salient variable across species, ranging from as little as 100  $\mu$ s to over 10 ms, and it may also exhibit sex- and status-related differences, with dominant males having a longer EOD than females [7]. Early playback studies in the field have demonstrated that this temporal variation plays an important role in electrocommunication [6]. Specifically, the relative timing of positive and negative voltage transients in the EOD plays a critical role in sender recognition.

Knollenorgans are able to faithfully encode the timing of these transients. The EOD of a neighboring fish will cause current to flow into one half of the body surface and out the other, meaning that knollenorgans on these two surfaces will be exposed to opposite stimulus polarities (Fig. 1a).

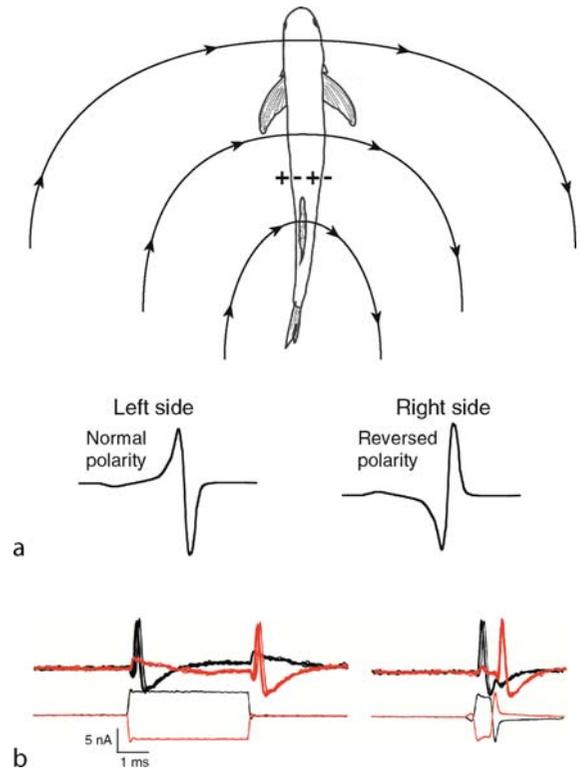
As knollenorgans only respond to positive-going voltage steps, those located where current is entering the skin respond to the EOD onset, while those located where current is exiting the skin respond to the EOD offset (Fig. 1b). Thus, by comparing spike times from opposite sides of the body, a mormyrid can determine the duration of the EOD waveform [6]. A similar mechanism for waveform discrimination in wave-type electric fish has also been proposed [8].

#### The Jamming Avoidance Response in Wave-Type Species

In contrast to pulse-type electric fish, wave-type species generate an EOD in which the duration of each pulse is approximately equal to the intervals between pulses, resulting in a continuous, quasi-sinusoidal waveform. When an object enters the electric field, it causes modulations in the EOD that are used by the fish to extract information about the object, a process called ►active electrolocation (Fig. 2a).

However, when fish encounter another individual with a similar EOD frequency, they experience mutual jamming of their electrolocation systems (Fig. 2b). To avoid this jamming, the fish shift their EOD frequencies away from each other, a behavior termed the ►jamming avoidance response (JAR) [2].

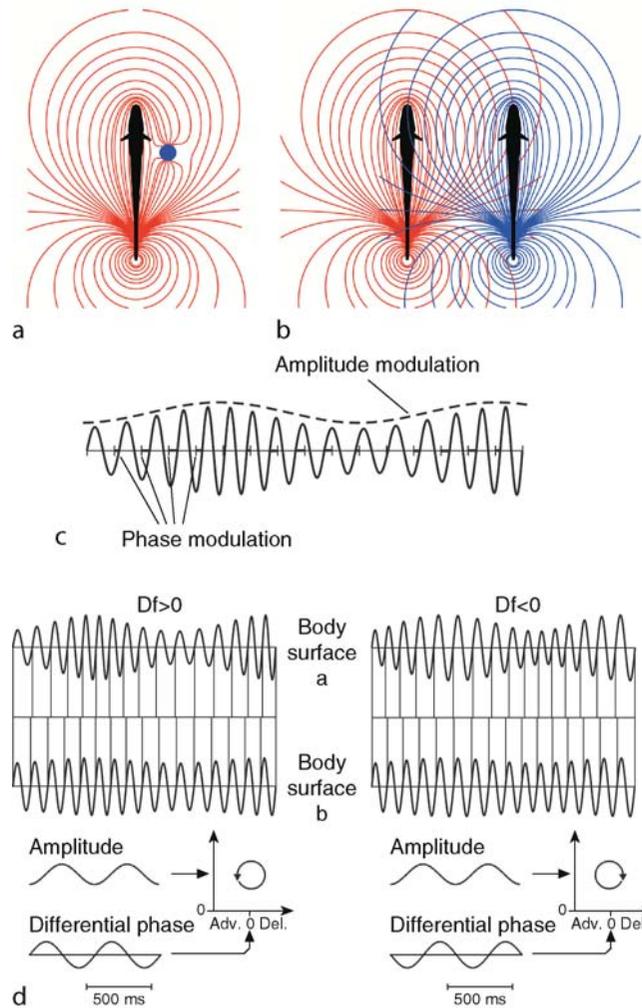
Properly executing the JAR requires that a fish determine whether it has a higher or lower EOD frequency than its neighbor. Extensive studies in a gymnotiform fish, *Eigenmannia*, and a mormyrid fish, *Gymnarchus*, have revealed a common algorithm for making this distinction [2]. The combination of two EODs leads to sinusoidal modulations in amplitude and phase (timing), at a frequency equal to the frequency difference between the two EODs (Fig. 2c). However, the temporal relation between amplitude and phase modulation is reversed, depending on whether the fish



#### Temporal Coding in Electroreception.

**Figure 1** Temporal coding by knollenorgan electroreceptors in mormyrids. (a) Current flow through a fish's body resulting from EOD production by another fish. One side of the body is outside positive/inside negative, while the other half is outside negative/inside positive, meaning that the EODs detected across the two skin surfaces are of opposite polarities. (b) By stimulating a single knollenorgan with both normal and reversed polarity currents, one can emulate the response of knollenorgans located on opposite sides of the body. Action potentials occur on stimulus onset under normal polarity (black), while they occur on stimulus offset under reversed polarity (red). In a natural situation, the difference in action potential times would occur between different knollenorgans, which could then be compared to determine the stimulus duration.

has a higher or lower EOD frequency than its neighbor (Fig. 2d). Thus, by comparing these two features, the fish can make the correct decision to either increase or decrease its EOD frequency [2]. However, detecting phase modulation requires that the fish have a timing reference. As the fish's own EOD and its neighbors EOD have different spatial distributions, different portions of the body surface are subject to different depths of modulation (Fig. 2d). Thus, the fish can extract phase information by comparing inputs from time-coding afferents on two different regions of the body surface, one that is strongly modulated with one that is weakly modulated (Fig. 3).



**Temporal Coding in Electroreception. Figure 2** (a) In active electrolocation, the electric field of a weakly electric fish (shown as isopotential lines in *red*) is distorted by the presence of an object (shown in *blue*). (b) The electric field (*red*) may also be distorted by the EOD of another individual (*blue*). (c) To avoid jamming of active electrolocation systems by another individual with a similar EOD frequency, the fish performs the JAR, which relies on comparing modulations in amplitude and phase that result from combining the two EODs. (d) Two different body surfaces are subjected to stronger (a) and weaker (b) interference from a neighbor's EOD, which results in different depths of modulation. The temporal relationship between amplitude and the phase of "body surface a" relative to "body surface b" is reversed when switching the sign of  $Df$ , which results in a different sense of rotation in a Lissajous graph.

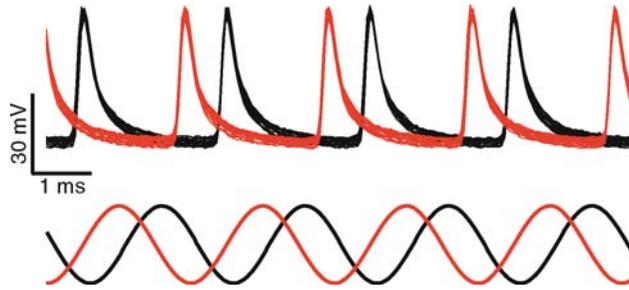
A different algorithm for the JAR, one which relies on temporal asymmetries in the natural EOD waveform that are encoded exclusively by time-coding afferents, has also been proposed [8].

#### Mechanisms of Temporal Feature Extraction

The previous sections dealt with the problem of neural encoding, or how precise temporal information can be represented by the timing of action potentials in sensory neurons. We now turn to the problem of how these action potential trains may be used to extract information about specific stimulus features; in this case, how precise spike times may be compared to extract

information about timing differences. Although similar adaptations are in place for preserving timing information in the early stages of sensory processing, these temporal comparisons are achieved by quite different mechanisms in different species.

In mormyrids, the nELL neurons relay phase-locked knollenorgan input to the torus semicircularis, where their axons terminate in a region called the anterior extero-lateral nucleus (ELa). Within ELa, there are two distinct types of neurons, large cells and small cells, both of which receive excitatory input from nELL axons (Fig. 4a). Upon entering ELa, the nELL axons immediately terminate onto one or two large cells, and



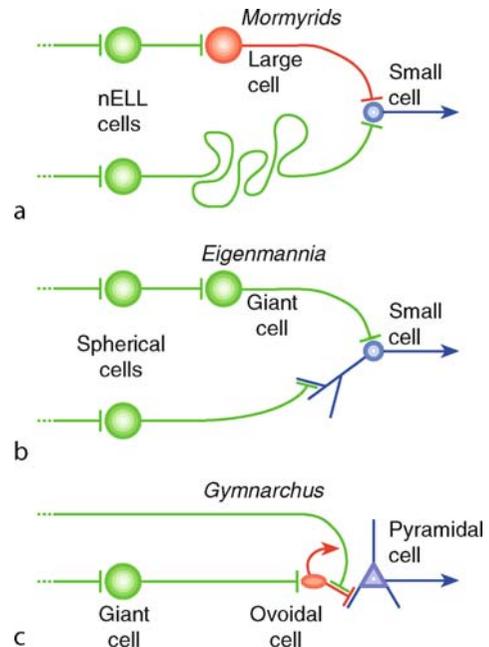
**Temporal Coding in Electroreception. Figure 3** Time-coding afferent activity in the wave-type fish *Gymnarchus*. The *top* traces show action potentials recorded from a single afferent (multiple sweeps are superimposed), while the *bottom* traces show the stimuli that elicited these responses. The *black* traces show the response to an unmodulated sine wave, while the *red* traces show the response to a sine wave advanced in time. The action potential times precisely follow the stimulus cycle. In a natural situation, the difference in action potential times would occur between afferents at different body surfaces that are exposed to different depths of phase modulation. The action potential times could then be compared to extract information about timing differences.

then wind their way throughout the nucleus, twisting and turning over distances of 3–4 mm before branching and terminating onto a large number of small cells [9]. The large cells project exclusively within ELA, terminating on small cells with large inhibitory synapses [9]. Thus, the small cells receive phase-locked input from two different sources: excitatory input from nELL axons responding to EOD onset from one part of the body, and inhibitory input from ELA large cells responding to EOD offset from another part of the body (Fig. 4a).

As the excitatory input is delayed by the time it takes an action potential to propagate down the long, winding path of the nELL axon, a given small cell will only respond to EODs longer than a certain duration, such that the delayed, excitatory response to EOD onset arrives before the inhibitory response to EOD offset [9].

In *Eigenmannia*, temporal comparisons are also made in the torus semicircularis. Large spherical cells within the ELL relay phase-locked afferent input to both giant cells and small cells within the torus in a somatotopic fashion (Fig. 4b). The giant cells then project widely across this somatotopic map onto several small cells, which therefore receive timing information from different portions of the body surface and are sensitive to temporal disparities between those surfaces [2,3]. The giant cells synapse directly onto the soma of the small cells, while the spherical cells synapse on the small cell dendrites, thereby delaying the arrival of the signal at the soma due to the passive propagation of synaptic current along the dendrite (Fig. 4b).

In *Gymnarchus*, temporal comparisons occur within the ELL rather than the torus. Nevertheless, the underlying circuitry for time disparity detection shares several similarities with the circuits in mormyrids and *Eigenmannia* [10]. Time-coding primary afferents synapse onto the dendrites of small ovoidal cells in the ELL and also project to giant cells within the ELL



**Temporal Coding in Electroreception. Figure 4** Circuits for making temporal comparisons in weakly electric fish. Neurons known or thought to be inhibitory are shown in red. Based on physiological recordings, neurons that are known to be sensitive to temporal disparities between different body surfaces are shown in blue. The *dashed lines* from the *left* represent incoming primary sensory afferents, while the *arrows* pointing to the *right* represent axonal projections to other regions. (a) Knollenorgan pathway in mormyrids. (b) Time-coding pathway in *Eigenmannia*. (c) Time-coding pathway in *Gymnarchus*.

(Fig. 4c). The giant cells, in turn, project to the soma of ovoidal cells. The ovoidal cells thereby receive convergent timing input from different body surfaces [10]. Although physiological recordings from ovoidal cells have not yet been made, their dendrites make

dendro-dendritic connections with nearby pyramidal cells [10], which are remarkably sensitive to temporal disparities between different body surfaces [2]. This sensitivity appears to be due, at least in part, to a complex adaptation mechanism, and preliminary evidence suggests that inhibition may play a role at the ovoidal cell-pyramidal cell synapse.

Despite the differences among these neural circuits, certain generalizations can be made (Fig. 4). In each pathway, there is an obvious shift in size from large, spherical neurons that are involved in preserving and relaying timing information, to small neurons that make the actual timing comparisons between different inputs. Once the temporal comparison is made, spike times do not need to be as precise, because the presence or absence of some stimulus feature (a particular timing difference) may now be represented by the overall level of neural activity (firing rate). Thus, there is no need for the neurons to be so large at the point of comparison. Furthermore, it may be that the small size of the comparator neurons reduces the attenuation of rapid synaptic currents by minimizing membrane capacitance. Although employing different mechanisms, delaying the arrival of spikes from one input to the comparator neuron seems to be another general feature. By adjusting this neural delay, the circuit can determine the stimulus delay that will result in a simultaneous arrival of inputs from different sources. If both inputs are excitatory, this particular delay will elicit the strongest response. If one input is inhibitory, then this particular delay will elicit the weakest response. Either way, the comparator neuron is tuned to differences in the arrival times of different inputs.

### Function

It is clear that knowledge of precise stimulus timing can be used to obtain a wealth of information from the environment. The three examples discussed come from organisms with disparate evolutionary histories that use timing information for different purposes. Nevertheless, there are strong similarities between their temporal coding pathways, suggesting that the unique features of these pathways represent specialized adaptations. Although the examples discussed in this chapter come from an eclectic group of organisms for which time holds special significance, the unique features of their time coding pathways are also found in other temporal coding systems [5]. This finding underscores the fact that basic principles in neuroscience may best be realized through a comparative, neuroethological approach to neural structure and function.

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## Temporal Coding in Sensation

### Definition

The process by which nervous systems encode the precise timing of stimulus events.

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## Temporal Integration in Photoreceptors

### Definition

A term referring to the photoreceptor's ability to sum individual photons over time. The period of integration often determines the temporal resolution a photoreceptor. Photoreceptors with short integration time, such as cones, are well adapted to detect rapid changes in the images, while those with longer integration time, such as rods, are well suited for low light vision.

### ► Photoreceptor