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**[REVIEW]**

# Evolution of Time-Coding Systems in Weakly Electric Fishes

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**Weakly electric fishes emit electric organ discharges (EODs) from their tail electric organs and sense feedback signals from their EODs by electroreceptors in the skin. The electric sense is utilized for various behaviors, including electrolocation, electrocommunication, and the jamming avoidance response (JAR). For each behavior, various types of sensory information are embedded in the transient electrical signals produced by the fish. These temporal signals are sampled, encoded, and further processed by peripheral and central neurons specialized for time coding. There are time codes for the sex or species identities of other fish or the resistance and capacitance of objects. In the central nervous system, specialized neural elements exist for decoding time codes for different behavioral functions. Comparative studies allow phylogenetic comparison of time-coding neural systems among weakly electric fishes.**

**Key words:** temporal coding, electric fish, electroreception

## INTRODUCTION

Sensory systems capture various types of stimuli at sensory organs and send encoded signals to the central nervous system where behaviorally relevant information is extracted. Neural coding is an essential step in the information processing by which neurons represent certain information as patterns of synaptic events and action potentials. Fundamentally different modes of neural coding are known (Somjen, 1972). The most ubiquitous type of coding is rate coding, in which magnitude of a sensory or neural event is represented as the number of action potentials per unit time. Another type of neural coding uses labeled lines or ensemble codes, in which the stimulus or neuronal information is represented as a pattern of neuronal activity across a population of individual neurons. A third type is time coding, in which information about a stimulus is represented as the temporal pattern of spikes in individual or multiple neural pathways (Theunissen and Miller, 1995). In time coding, the timing or temporal pattern of neural activities signals various information about the stimulus. For example, information on the horizontal position of a sound source is encoded as the inter-aural time difference of the sound arrival. This time difference is represented by spike timing from the right and left ears of birds and mammals. Other examples of time coding are found in a wide range of sensory systems including the electrosensory system (Carr, 1993; Jones et al., 2004; Katz, 2003; Panzeri et al., 2001).

The electrosensory system of weakly electric fishes uses time coding for a variety of behavioral functions for which physiological mechanisms are well understood (Carr and Friedman, 1999; Moller, 1995). The widespread occurrence of time coding in the electrosensory system stems from the precisely timed electric organ discharges (EODs) that these fish emit from the electric organ in the tail. The time precision of EODs is on the order of microseconds. The feedback signals of EODs are sensed by a fish's own electrosensory system for electrolocation or that of other individuals for electrocommunication. The time precision of the electrosensory system is equivalent to that of EODs. The electric resistivity and capacity of electrolocation objects are sampled by a type of electroreceptor organ at the periphery in a form of time coding and are decoded by central neurons. The duration of EOD pulses, which carries species and sexual information in some species, is also time coded at the periphery and decoded by central neurons. In still another electrical behavior, the jamming avoidance response, information on the frequency of EOD from other individuals is coded by a complex time pattern of stimulus parameters which are again decoded by central neurons. These electrical behaviors are distributed over different positions in the phylogenetic tree of weakly electric fishes, allowing fruitful comparative studies. In this review, I survey electrical behaviors that require time processing and the neural mechanisms underlying them, and attempt to place these behaviors into an evolutionary perspective.

## PHYLOGENY OF ELECTRIC FISHES WITH THE TUBEROUS ELECTROSENSORY SYSTEM AND THE ELECTRIC ORGAN

Fig. 1 shows a phylogenetic tree of fishes and early vertebrates illustrating the very early occurrence, later loss, and more recent recurrence of electric capabilities (Bullock, 1982). The ancestral electroreceptors may have been similar to the end bud and ampullary type electroreceptors

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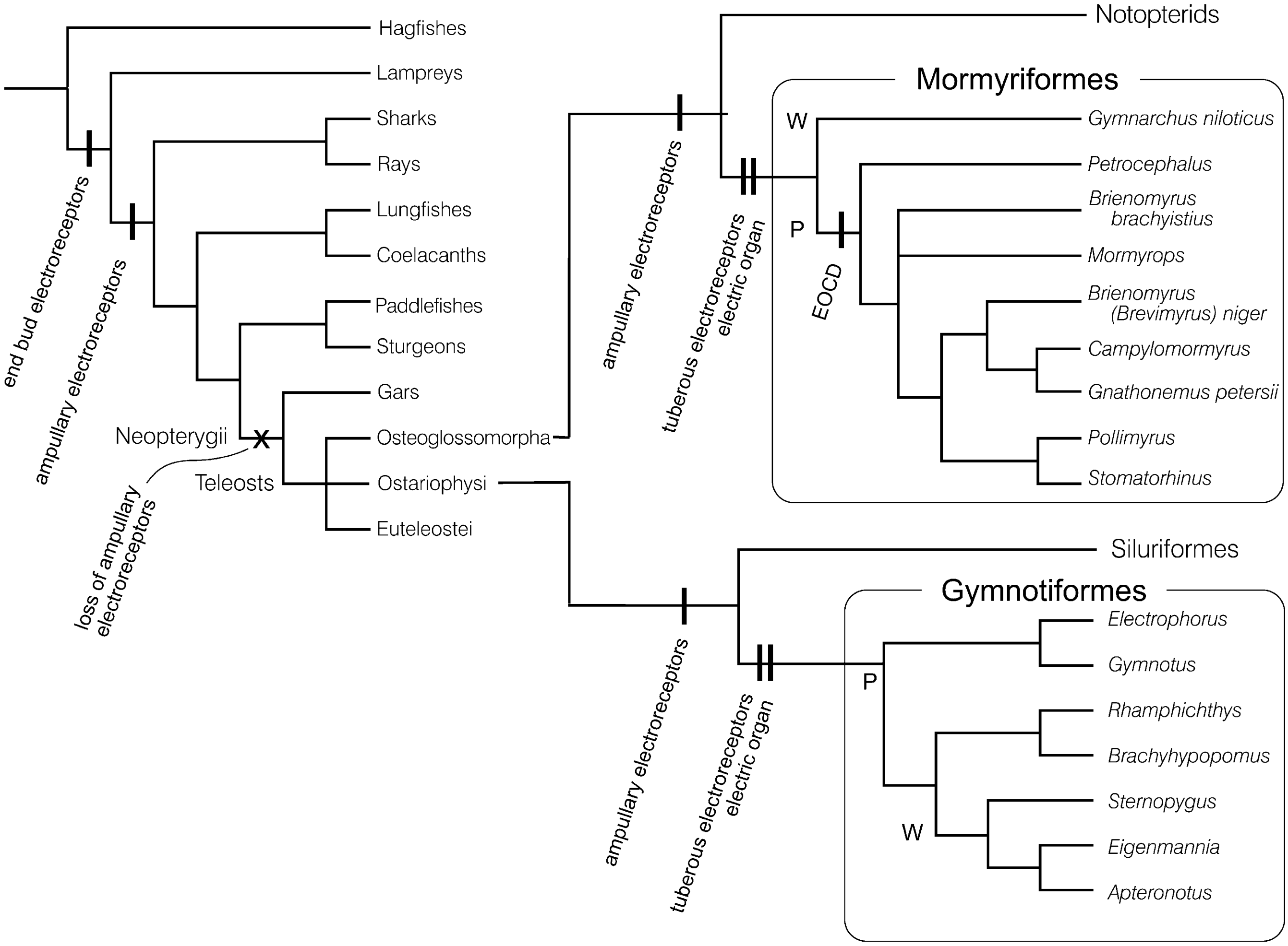

**Fig. 1.** Occurrence, loss, and recurrence of electric capabilities in early vertebrates and fishes (left) and teleost fishes (right). P, W, descendants are pulse- and wave-type electric fishes, respectively. The left cladegram is based on Lauder and Liem (1983), Northcutt (1986), and Bullock et al. (1983). The right cladegram is synthesized from Alves-Gomes et al. (1995), Lavoue and Sullivan (2004), Sullivan et al. (2000), and Albert and Crampton (2005), studies that involved analyses of multiple molecular markers. In Mormyriformes and Gymnotiformes, representative genus names, which are often found in the behavioral and physiological literature, are given for family-level taxonomy.

that detect weak, low-frequency (<50 Hz) signals from living organisms such as their prey (Bodznick and Montgomery, 2005). Ampullary electroreceptors occur in lampreys and early fishes (sharks, rays, sturgeons, paddlefishes, lungfishes and coelacanths) (Bodznick and Boord, 1986; Northcutt, 1986; Roman, 1986). The ampullary electrosensory system was lost in the common ancestor of more modern fishes, at the level of the Neopterygii, making all descendants non-electric. The ampullary electrosensory system, however, reappeared independently in two groups of teleosts, Osteoglossomorpha and Siluriformes/Gymnotiformes. Within these groups, Gymnotiformes (South American electric fishes) and Mormyriformes (African electric fishes) evolved the electric organ, making them capable of generating EODs. Concurrently with the rise of the electrogenesis, they evolved a new, tuberous electrosensory system with electroreceptors specialized for detecting an animal's own EODs and those of other individuals, while maintaining the ampullary electroreceptor system. The ampullary electrosensory system of all fishes possesses electroreceptors that encode stimulus strength by the rate of firing.

In both Gymnotiformes and Mormyriformes, the waveform of EOD may take the form of a wave or a pulse. Gymnotiformes comprises two wave-type families and four pulse-type families, each containing one to several genera. Mormyriformes include a sole species of wave-type fish, *Gymnarchus niloticus*, and numerous pulse-type fishes belonging to the family Mormyridae. Wave species in both orders continuously emit quasi-sinusoidal EODs at a constant frequency. In these EODs, the duration of a single EOD is comparable to the inter-EOD interval, making a continuous EOD wave. Pulse species emit short pulses with durations much shorter than the inter-pulse intervals. EOD frequencies range from ~50 Hz to 1.5 kHz in wave species, and from ~10 to ~100 Hz in pulse species. This wide range of frequencies suggests considerable diversity in the behavioral functions of EOD and the underlying neuronal mechanisms. The frequency of the EOD in wave species is constant over time (hours), except during agonistic and sexual displays (but see Oestreich and Zakon [2002] and

Oestreich et al. [2006] for long-term changes). The frequency of discharges in pulse-type gymnotiform fish is also relatively constant but is modified with time constants of seconds according to behavioral situations. Mormyrid pulse-type fishes modulate the EOD rate with more rapidly changing inter-pulse intervals.

The coevolution of electroreception and electrogenesis thus occurred independently in two electric fish groups, each of which evolved both wave- and pulse-type species. Tuberous electroreceptors respond to a fish's own pulse- or wave-type EODs or those of neighboring fish, and the EODs often carry behaviorally important information through temporal coding. This review focuses on behaviors, and the neural mechanisms involving electrogenesis and the tuberous electrosensory system, that utilize temporal coding (see Kawasaki [2005] for the anatomy and physiology of the tuberous electrosensory system). Crampton et al. (2006) discussed the evolution of electric signal diversity in gymnotiform fishes.

## BASIC MECHANISMS OF ELECTROGENESIS AND ELECTRORECEPTION

### The electric organ and the pacemaker/command nucleus

The electric organ is located in the tail and contains electrically excitable cells called electrocytes that generate current flow across themselves due to asymmetric firing of their excitable membrane (Bennett, 1971). The electrocytes are arranged serially and excited simultaneously, giving rise to EODs with amplitudes up to a few volts.

While the waveform (whether wave or pulse type) of a cycle of EOD is determined by properties of electrocytes and fixed in a given species, sex, and breeding condition, the timing of each EOD is determined by the activity of a pacemaker or command nucleus in the medulla. In either case, the brain nucleus has the intrinsic capability of generating a regular or irregular train of command signals that projects to a relay nucleus, which in turn sends spikes to the spinal cord that activate electromotor neurons, which fire the EODs. There is considerable variation between the groups of electric fishes in the connectivity between pacemaker/command nucleus and the relay nucleus (Fig. 2). EODs continuously and regularly stimulate a fish's own electroreceptors except during aggression and courtship displays (Dye and Meyer, 1986; Grant et al., 1986; Kawasaki, 1994).

EODs from some of the wave species are the most precise biological oscillation known. Variation in the inter-EOD intervals in *Gymnarchus* and *Apteronotus* is on the order of $10^{-7}$ to $10^{-6}$ seconds (Bullock, 1970; Guo and Kawasaki, 1997; Moortgat et al., 2000). As will be mentioned below, this precision is reflected in neural time coding and behavioral sensitivity.

### Electric organ corollary discharges (EOCDs)

In mormyrid pulse species, EOD command signals are sent not just to the electric organ but also to the electrosensory system as corollary discharges for the modification of sensory information. The command nucleus projects bilaterally to the bulbar command-associated nucleus (BCA). Each projection axon from the BCA bifurcates to project to the medullary relay nucleus and to midbrain nuclei (Fig. 2). These electric organ corollary discharges (EOCDs) play a major roll in distinguishing afferent signals induced by an animal's own discharges (reafference) from stimulation by EODs from neighboring fish (exafference). EOCDs are precisely timed so that they arrive at sensory areas at times when a gating of sensory information is necessary (Bell and von der Emde, 1995; Bell et al., 1983). No EOCD system is found in gymnotiform fishes, nor in *Gymnarchus*, itself a mormyriform and a close relative of the Mormyridae (Kawasaki, 1994).

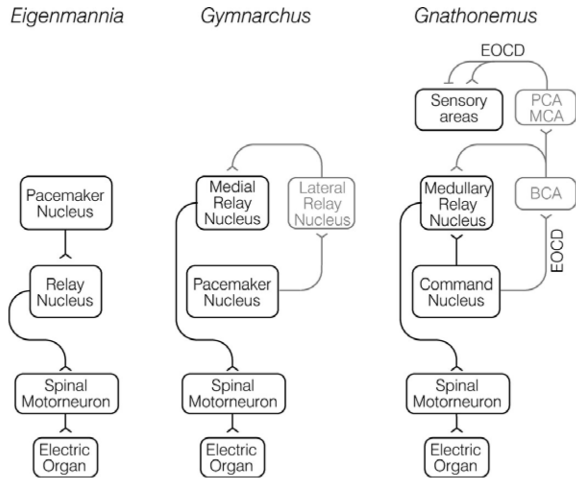

**Fig. 2.** Comparison of central electromotor pathways. *Eigenmannia* (left) represents the pattern in pulse- and wave-type gymnotiform fishes. A mormyriform pulse-type fish, *Gnathonemus* (right), involves a complex EOCD system that projects to sensory areas including the nucleus of electrosensory lateral line lobe (nELL). A mormyriform wave-species, *Gymnarchus niloticus* (center), has intermediate complexity. The pacemaker and command nuclei are the site of generation of the time of each EOD. Neurons in all following structures fire one action potential for one EOD. The structures and connections with black lines are unpaired structures. Those shaded with grey are actually bilateral but only one side is shown for brevity. Note the lack of a projection from the pacemaker nucleus to the medial relay nucleus in *Gymnarchus*, and the duplicated projections to the medullary relay nucleus in *Gnathonemus*. The left, center, and right diagrams are from Bennett (1968), Kawasaki (1994), and Bell et al*.* (1983), respectively.

### Tuberous electroreceptors and their afferent activities

Time-coding electroreceptors were first found by Hagirawa and Morita (1963) and Bullock and Chichibu (1965) in gymnotiform wave-type electric fishes. The primary afferent fibers from these electroreceptors fire at exactly the same frequency as the fish's EODs, with a precise one-to-one phase locking between EODs and action potentials (Fig. 3). Since the firing rate does not vary, information in the stimulus is encoded only as firing time. Time-coding afferents of this type exist in all wave-type electric fishes in Gymnotiformes and Mormyriformes (Guo and Kawasaki, 1997; Szabo and Fessard, 1974). Time-coding afferents in wave species show very precise firing, with the standard deviation of the periods on the order of $10^{-6}$ to $10^{-5}$ seconds, reflecting the firing precision of the EOD (Carr et al., 1986a; Guo and Kawasaki, 1997). A similar type of time-coding electroreceptor afferents, called 'pulse markers' and 'Knollenorgan

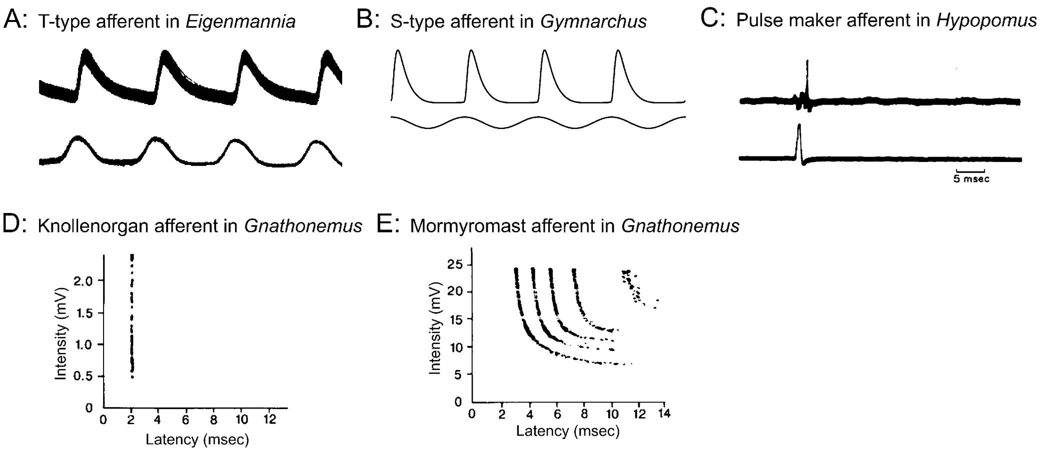

**Fig. 3.** Examples of time-coding primary afferents. **(A)** A wave-type gymnotiform fish, *Eigenmannia*. **(B)** A wave-type mormyriform fish, *Gymnarchus*. **(C)** A pulse-type gymnotiform fish, *Hypopomus*. **(D, E)** A pulse-type mormyriform fish, *Gnathonemus*. In (A–D), one cycle or pulse of EOD produces one action potential. (A–C) Recording from an afferent (top) in response to an electrosensory stimulus (bottom). (D, E) are intensity-latency plots. While the Knollenorgan afferent fires at a constant latency with various intensities (D), mormyromast afferents fire various numbers of action potentials with various latencies (E). (A) from Hagiwara and Morita (1963); (B) from Kawasaki (1994); (C) from Bastian (1976); (D, E) from Bell (1990). Reprinted with permission.

afferents,' were respectively found in pulse-type gymnotiform and mormyrid fishes (Bastian, 1976; Bell, 1990). These afferents fire a single action potential in response to each EOD. As will be shown in later sections, these time-coding afferents carry various kinds of information for different behavioral functions. The temporal precision of Knollenorgan afferents is sufficient to encode waveform information for the rather short EODs of mormyrid species (Friedman and Hopkins, 1995). The time-coding electroreceptor afferents in weakly electric fishes are unique among all sensory systems in animals in that they carry information for known behavioral functions entirely by spike timing.

The remaining types of electroreceptor afferents are specialized for rate coding. The firing times are not precisely locked to each EOD stimulus, but the rate, frequency, or probability of firing does relate to the intensity of the EOD stimulus. These 'probability coders' are found in all wave- and pulse-type species in which the firing rate increases with larger stimulus intensities.

## BEHAVIORAL FUNCTIONS OF TIME-CODED ELECTRICAL SIGNALS

### Species and sex recognition

A remarkable example of temporal coding of communication signals has been found in mormyrid pulse-type electric fishes where the duration of each EOD pulse carries information on the species and sex of the signaler. The duration of pulses is sampled by populations of electroreceptors on opposite sides of a fish's body (Hopkins, 1986b). Since the current from an external source (a neighbor's electric organ) enters into one part of fish's body and exits from another, and since all Knollenorgan electroreceptors fire only in response to inward current, Knollenorgans from opposite sides of the body fire at different phases of the EOD waveform. Thus the duration of a neighbor's EOD is encoded in the time difference between the firing of Knollenorgan electroreceptors on opposite sides of the fish.

Hopkins and Bass (1981) discovered that the mormyrid fish *Brienomyrus* discriminates pulse durations in courtship encounters. In a field study, female pulses of various durations were played back from a pair of electrodes presented in a male's territory to evoke the male's reproductive electrical 'rasp' display. By counting male rasps, these researchers were able to show the male's preference for a particular duration of square pulse that corresponded to the duration of the female's natural EOD pulses. As in *Brienomyrus,* pulse duration is often sexually dimorphic in other mormyrid fishes in which males produce longer pulses during sexual maturation. In all electric fishes, longer pulses are energetically costly to produce and thus may be an honest indicator of male quality (Stoddard, 1999). Shorter pulses are, however, advantageous for electrolocation of capacitative objects, as will be mentioned later. In addition to being sexually dimorphic, pulse durations in mormyrid fishes are often species specific. An extremely wide range of pulse durations is found among species or even within a genus. The genus *Campylomormyrus* consists of species with pulse durations ranging from 200 μsec to over 30 msec. *Petrocephalus simus* exhibits the shortest EOD pulses among all electric fishes, approximately 100 μsec (Hopkins, 1999). This is probably the shortest action potential in all excitable cells in neurophysiological literature.

Differences in the pulse duration are considered to be a major factor driving speciation among mormyrid pulse-type electric fishes by ethological isolation (Arnegard et al., 2005, 2006; Sullivan et al., 2002).

### Electrolocation

A second key function of the electrosensory system is the electrolocation of objects in which fish determine the location, distance, size, shape, and material of objects based on their electrical properties such as resistance and capacitance. Electrolocation behavior also involves time coding. The capacitive component of objects induces slight delays, on the order of microseconds, in EOD feedback signals, while resistive components change only the amplitude of the feedback signals. Electric fishes are shown to discriminate between capacitive and resistive objects even when the absolute values of complex impedances of the objects are identical (Meyer, 1982; von der Emde, 1992, 1993). These studies have suggested that the fish detect time differences between time-coded sensory signals from different parts of the body.

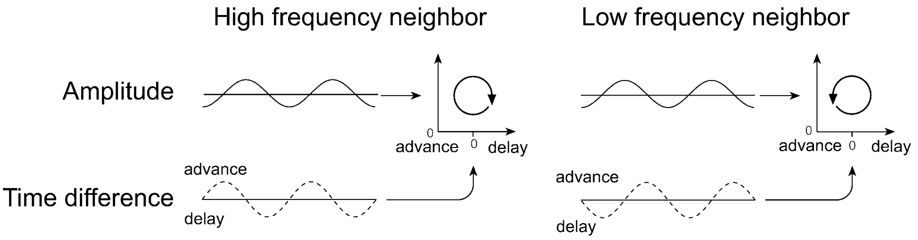

**Fig. 4.** Stimuli causing the JAR in *Gymnarchus* and *Eigenmannia*. The left and right panels, respectively, depict situations where the fish decrease and increase the EOD frequency in their JARs. Due to contamination of a fish's own EOD by a neighbor's EOD, modulations occur in both the amplitude and time difference between afferent signals from different body areas. The Lissajous graphs complete their cycle in 0.5 sec when the frequency difference between two fish is 2 Hz, which induces the strongest JAR in most individuals of *Gymnarchus*. See Kawasaki (1993) for further explanation of stimuli that cause the JAR.

Objects with a resistive component alone do not induce time shifts in the EOD feedback signal. Hall et al. (1995) demonstrated detection of a resistive component by an amplitude-dependent latency shift in afferent signals in behavioral responses in a mormyrid fish.

## Jamming avoidance response

Gymnotiform and mormyriform wave species exhibit a jamming avoidance response (JAR) (Heiligenberg, 1991; Kawasaki, 1993; Watanabe and Takeda, 1963) when presented with wave discharges with frequencies similar to their own EODs. The JAR is an electrical behavior in which fish shift their EOD frequency away from another one of similar frequency, as would happen when two fish with similar frequencies come together. If a fish with a 400 Hz EOD encounters with a fish with 398 Hz, for example, the 400 Hz fish increases its EOD to about 405 Hz, and the fish with 398 Hz lowers the EOD to about 393 Hz. For this behavior, the brain makes the decision whether to raise or lower its frequency based on the frequency difference between its own and the neighbor's EODs. Despite the independent evolution of their electrosensory systems (Fig. 1), gymnotiform and mormyriform wave species perform almost identical JARs using identical computational rules for this behavior (Kawasaki, 1993, 1996). During the JAR, electroreceptors are exposed to a mixture of a fish's own EODs and those of its neighbor. The signal mixture exhibits periodical modulations in amplitude and time[1] at a frequency equal to the frequency difference between the two fish (initially 2 Hz in the example above). As shown in Fig. 4, amplitude and time modulations are sinusoidal and their time relationship depends on whether a neighbor's frequency is higher or lower than a fish's own EODs. Thus, a fish decides whether to raise or lower its EOD frequency based on the time course of the amplitude and time modulation. These modulations occur on a time scale of milliseconds.

Time modulation is the shift in EOD cycles in time and needs to be measured against a time reference. The brain, however, lacks a constant time reference signal for comparison. Although pacemaking signals or EOCD signals from the pacemaker nucleus would serve as a time reference, the pacemaking neurons in the nucleus never project to other areas than the electromotor system and cannot provide a reference signal against which the times of sensory signals could be measured (Fig. 2) (Heiligenberg et al., 1978b; Kawasaki, 1994). Time modulation is instead detected as differences in the timing of electrosensory signals from different areas of the body. Due to differential contamination of a fish's own EODs by those from a neighbor across areas of the body, different areas of the body experience time modulations of different depth (Kawasaki, 1993, 2007). The time-difference modulation occurs on the time scale of microseconds.

JARs occur with extremely small amounts of amplitude and phase modulations, still using the time code between them (Guo and Kawasaki, 1997; Kawasaki, 1997; Kawasaki et al., 1988; Rose and Heiligenberg, 1985a). The thresholds for the depths of amplitude and phase modulations are ~0.02% and 100–300 nsec, respectively, both for *Eigenmannia* (Gymnotiformes) and *Gymnarchus* (Mormyriformes).

Pulse-type electric fishes also exhibit EOD behaviors that serve to avoid the jamming of their electrolocation system. Mormyrid fish exhibit 'echo' responses in which an individual fires its own EOD immediately after receiving an EOD from another fish, thus minimizing the chance its own EOD pulses coinciding with those from the other (Russell et al., 1974). Gymnotiform pulse-type fishes transiently delay or advance the timing of EODs to avoid the EODs coinciding with those from other fish (Baker, 1980; Heiligenberg et al., 1978a; Kawasaki et al., 1996; Lorenzo et al., 2006). Although these behaviors in pulse-type gymnotiform fishes seem to heavily involve time coding, the underlying neuronal mechanisms are not fully understood.

## Sequence of pulse intervals (SPIs)

While wave species change their EOD frequency only on special occasions, such as in the JAR, pulse species change the pulse rate more often. One function implied in the frequency change is to increase the sampling rate of the electrolocation signal. The second major function is communication. Many types of sequences of pulse intervals (SPIs) have been described as communication signals in mormyrid pulse fishes. The list of SPIs includes various types of acceleration, cessation, regularization, pulse pairing, and rasps (Hopkins, 1986a, 1988). Most SPI types are associated with special behavioral contexts such as aggression and courtship, suggesting that they have communicative value. The range of intervals within SPIs in mormyrids is from ~20 to ~200 msec. This contrasts with the time scale of another communication signal in mormyrids, the duration of EOD pulses, which are 100 μsec to 30 msec.

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[1] The term 'phase' is often used in the literature to indicate a 'time' in the cyclic firing of neurons or EODs of wave-type electric fishes. 'Time' and 'phase' are used interchangeably throughout this review. 'Time comparison' or 'time-locked' in this review is synonymous to 'phase comparison' or 'phase-locked' that may be found in the literature.

## BRAIN MECHANISMS FOR PROCESSING TIME-CODED SIGNALS

### Neural mechanisms for the detection of pulse duration in Mormyrids

As mentioned earlier, sex and species identities are expressed in the duration of EOD pulses and encoded in the time differences in firing between Knollenorgan afferents from opposite sides of the body, which are stimulated with the up and down strokes of EOD pulses from neighboring fish. Knollenorgans are, however, also strongly stimulated by a fish's own EODs. Due to the geometry of a fish's electric organ and the skin surrounding the fish, Knollenorgans in all body locations are stimulated simultaneously, with the same edge of the fish's own pulses sending to the brain simultaneous action potentials that are meaningless as signals for communication. The action potentials that are generated in Knollenorgan afferents by a fish's own EODs are inhibited by EOCD signals in the first brain station, the nucleus of the electrosensory lateral line lobe (nELL). EOCD signals from the command nucleus, the source of EOD motor commands, are relayed via a few midbrain nuclei to the nELL, where the EOCDs create massive, precisely timed inhibition blocking excitatory input from the Knollenorgan afferents (Bell and Grant, 1989; Bell and von der Emde, 1995; Mugnaini and Maler, 1987b). Neurons in the nELL thus relay the firing at the edges of EOD pulses to the next station in the midbrain, the anterior exterolateral nucleus (ELa), only when the afferent firing originates from the EODs of a neighbor and does not coincide with self-stimulation (Zipser and Bennett, 1976). The firing of the output neurons of the nELL is precisely time locked to the stimulus.

The ELa receives input solely from the nELL, making it a unique brain nucleus dedicated to processing sensory signals for communication. The ELa consists of only two types of neurons, large cells and small cells, both of which are adendritic and receive input from the nELL. The large cells again show time-locked responses and project to the small cells (Friedman and Hopkins, 1998; Mugnaini and Maler, 1987a). Fig. 5A shows the projection pattern of the nELL axons and the small and large cells. This pattern suggests that the small cells compare firing times between inputs and detect pulse duration or waveform information. The axons of the large cells in the ELa exhibit extensive arborization, which may act as a delay line to adjust the arrival times of action potentials to the time-comparing small cells (Friedman and Hopkins, 1998; Xu-Friedman and Hopkins, 1999). The small cells project to an adjacent nucleus, the posterior exterolateral nucleus (ELp), where neurons are sensitive to the duration of EOD pulses (Amagai, 1998). The pulse durations that evoke the strongest responses in type-II neurons of the ELp range from ~100 μsec to ~10 msec, which corresponds to the naturally occurring EOD pulse durations of sympatric species. Some neurons in the ELp show selectivity for the SPI patterns of EODs of certain duration (Carlson, 2008).

### Neural mechanisms for the detection of time differences in wave species

Action potentials from time-coding afferent fibers from the electroreceptors of wave-type electric fishes transmit to the brain local phase information by their firing times. The time differences between these action potentials reflect the electrical properties of electrolocation objects and the presence of a neighbor's EODs in the JAR. Time-comparing neural mechanisms have been found in the hindbrain of a mormyriform fish, *Gymnarchus* (Kawasaki and Guo, 1996) (Fig. 5B), and in the midbrain of gymnotiform fish,

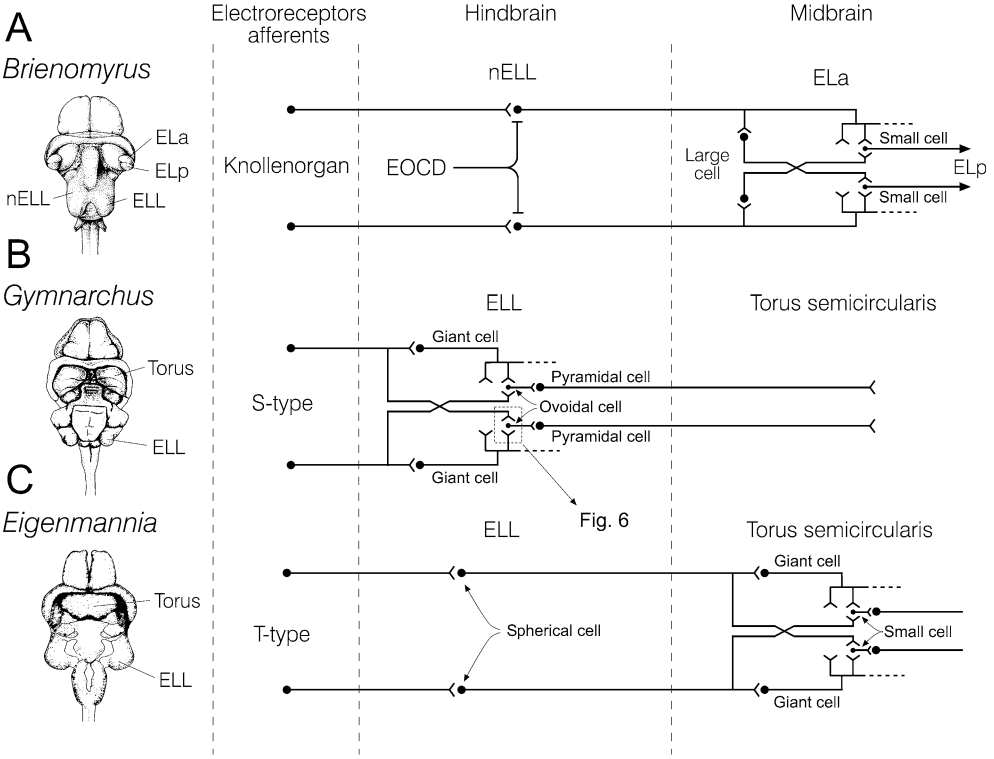

**Fig. 5.** Time-comparison circuits in **(A)** a mormyriform pulse-type fish, *Brienomyrus*; **(B)** a mormyriform wave-type fish, *Gymnarchus*; and **(C)** a gymnotiform wave-type fish, *Eigenmannia*. The left column shows dorsal views of the brain. The covering brain structures were removed for a clear view of the underlying structures involved in time processing. The two parallel channels in each row represent signal paths from different areas of the body between which a time difference is detected. The small cells in *Brienomyrus* and *Eigenmannia*, and the ovoidal cells in *Gymnarchus*, are thought to compare the times of firing of input neurons. Note the similar topographical organization of the time-comparison circuits in all species. An expanded view of the square area in *Gymnarchus* is shown in Fig. 6.

*Eigenmannia* (Carr et al., 1986a, b) (Fig. 5C).

In *Gymnarchus*, the time-coding afferents (S-type afferents) bifurcate on entering the hindbrain. One branch terminates on a type of neuron, the ovoidal cell, in the inner cell layer (ICL) of the ELL, and the other on the soma of an adentritic giant cell. The giant cells fire one action potential in response to an input synaptic potential from S-type afferents, preserving phase information with a small delay (Kawasaki and Guo, 1996). The giant cells send axons to the ICL, where these synapse on ovoidal cells. The ovoidal cells are unique in that each of them receives only two giant synapses, one from an S-type afferent, one from a giant cell (Fig. 6). The giant synapse from the axon terminal of a giant cell covers ~85% of an ovoidal cell's soma, and the giant synapse from an S-type afferent covers almost entire surface of the only dendrite of an ovoidal cell (Matsushita and Kawasaki, 2004). The ovoidal cells presumably detect time differences between signals from different electroreceptors represented by the two inputs. The output neurons of the ovoidal cells are the pyramidal cells of the ICL, which change their firing rate according to the time difference between signals at different body locations (Kawasaki and Guo, 1996). Here, the neural code for phase differences transforms from a time code to a rate code: while phase information is expressed as the timing of action potentials in the time-lock input neurons, the output pyramidal cells express phase-difference information by means of firing rate. The pyramidal cells are highly sensitive to small time differences: they respond to time differences on the order of a few microseconds or phase differences of ~0.2° (Matsushita and Kawasaki, 2005). The entire time-comparison mechanism is confined to the hindbrain in *Gymnarchus*.

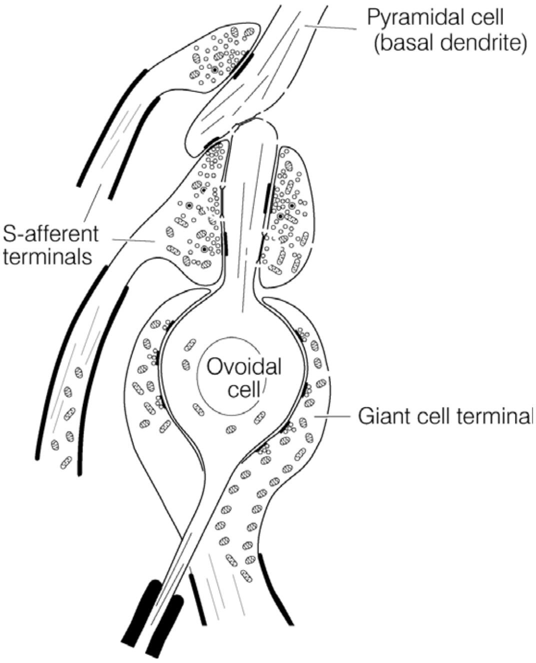

**Fig. 6.** The ovoidal cell and its two input synapses in the ELL of *Gymnarchus.* The projection sites of ovoidal cell axons are unknown. The dendro-dendritic connection to the pyramidal cell is thought to be the output path. From Matsushita and Kawasaki (2004). Reprinted with permission of Wiley-Liss, Inc. a subsidiary of John Wiley & Sons, Inc.

A gymnotiform wave type electric fish, *Eigenmannia,* possesses a similar time-comparison circuit that extends to the midbrain (Fig. 5C). The difference from *Gymnarchus* is that the time-locking afferents (T-type afferents) terminate only on relay neurons in the hindbrain (ELL), the spherical cells, which send time-coding action potentials via their axons to the torus semicircularis of the midbrain. The axons of spherical cells branch and terminate on giant cells and small cell in Lamina VI of the torus semicircularis (Carr et al., 1986b). The giant cells are also time locked and spread their axons within Lamina VI. Each small cell receives input from a giant cell and from several spherical cells. Heiligenberg and Rose (1985) made intracellular recordings from and labeled small cells, and showed that these respond to phase differences by varying their firing rate much as do the pyramidal cells in the ELL of *Gymnarchus*. Other types of neurons in different layers of the torus also respond specifically to time disparities between electrosensory signals applied in different body locations (Bastian and Heiligenberg, 1980; Rose and Heiligenberg, 1985b).

The organization of the time-comparison circuit is remarkably similar among *Brienomyrus, Gymnarchus,* and *Eigenmannia* (Fig. 5). The input time-locked axons divide into direct and indirect paths to provide inputs to time comparators; the time-comparator neurons (the small cells in *Eigenmannia* and *Brienomyrus* and the ovoidal cells in *Gymnarchus*) receive inputs from the indirect and direct paths for time comparison. Other similar properties include (1) large-diameter and fast-conducting axons in the time pathways, (2) adendritic somata in time-locked neurons, and (3) the existence of mixed synapses (electrical and chemical), both time-conserving synapses that conserve spike time sequence and time-comparing synapses that drive time-comparator postsynaptic neurons (Carr et al., 1986b; Matsushita and Kawasaki, 2004). Fast conduction is believed to contribute to the accurate conduction of time-locked firing with minimal jitter. Fast-conducting axons with large diameters are also found in time-locked auditory systems in birds and mammals. Adentritic postsynaptic cells are probably advantageous for the fast electrotonic propagation and integration of synaptic potentials (Carr, 1993; Carr and Friedman, 1999).

These similarities are remarkable because the circuit occurs both in different brain areas in relatively closely related species (*Brienomyrus* and *Gymnarchus*) and in the same (homologous) brain area in distantly related species (*Brienomyrus* and *Eigenmannia*).

## Neural mechanisms for time-sequence detection in the JAR

The JAR in wave-type electric fishes is an electrical behavior whereby a fish raises or lowers its discharge frequency when a neighbor's discharge frequency is lower or higher than its own, respectively. These two situations correspond, respectively, to counterclockwise and clockwise rotation of the Lissajous graphs in Fig. 4. A fish detects the sense of rotation by examining the temporal sequence of four sensory events occurring on the amplitude- and time-difference axes: amplitude increase and decrease, and time advance and delay. In *Gymnarchus*, amplitude increases and decreases are represented by excitatory and inhibitory types of amplitude-sensitive neurons in the ELL that fire a burst of action potentials in rising and falling phases of amplitude modulation, respectively. Likewise, two types of neurons that are sensitive to time differences in the ELL fire a burst of action potentials for time difference advances and delays, respectively. These ELL neurons respond identically to either sense of rotation, because they respond only to a parameter belonging to one axis of the graph, the amplitude or time difference, each of which follows an identical time course for either sense of rotation. These neurons do not interact with each other in the ELL, but project to common areas in the midbrain (Kawasaki and Guo, 1998). There, 'sign selective' neurons selectively respond to the sense of rotation of these two stimulus parameters (Carlson and Kawasaki, 2004; Kawasaki and Guo, 2002).

While some neurons prefer the clockwise rotation, other neurons prefer the counterclockwise rotation. For example, a neuron may show stronger firing in response to the time sequence of amplitude up – time delay – amplitude down – time advance, than to the sequence of amplitude up – time advance – amplitude down – time delay; another neuron may show the opposite preference. How do these neurons differentiate the time sequence of otherwise identical inputs? Carlson and Kawasaki (2006) made intracellular recordings from these 'sign-selective' neurons with the *in-vivo* whole-cell technique to reveal synaptic potentials interacting within these neurons (Fig. 7). Shown in Fig. 7A and B are synaptic potentials recorded in response to a singular presentation of amplitude or time modulation. Positive and negative peaks in synaptic potentials in response to a singular presentation of amplitude or time modulation occur in any time position, depending on neurons indicating various latencies or delays from the stimulus peaks to peaks in the synaptic potentials in midbrain neurons. These delays arise from various physiological mechanisms existing between the electroreceptor and these neurons. They presumably include adaptation of transduction mechanisms, firing mechanisms of membranes, and excitatory and inhibitory synapses. Whatever the cause or magnitude of the delay, the synaptic potential peaks in these midbrain neurons are aligned in time, resulting in a maximum response to either a clockwise or a counterclockwise combination of input signals (Fig. 7C). Thus the time relations particular to a sense of rotation in the Lissajous graphs in Fig. 4 are detected by the coincidence of postsynaptic potentials in the midbrain neurons. Coincident postsynaptic potentials are enhanced by a voltage-sensitive membrane process to give a stronger preference to the sense of rotation (Carlson and Kawasaki, 2006).

Similar neuronal mechanisms for detecting the sense of rotation have been found in *Eigenmannia* (Heiligenberg and Rose, 1985, 1986; Rose and Heiligenberg, 1986). The only differences are that neurons responding to the time difference appear only in the midbrain, and that midbrain 'sign selective' neurons are abundant in *Gymnarchus* but relatively scarce in *Eigenmannia*.

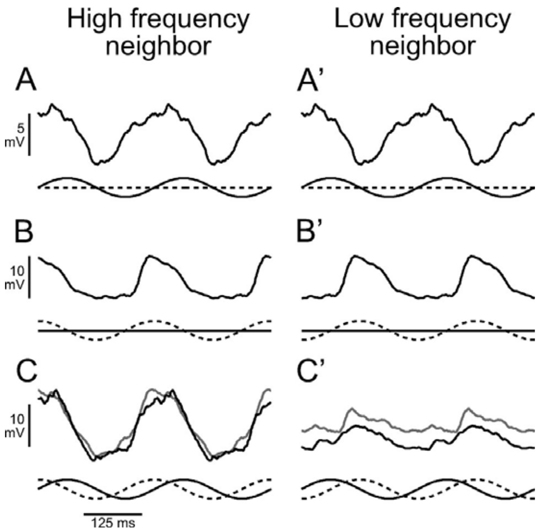

**Fig. 7.** Interaction of postsynaptic potentials in 'sign-selective' neurons in the midbrain torus semicircularis of *Gymnarchus*. **(A, A', B, B')** Spike-removed, intracellularly-recorded membrane potentials in response to a singular presentation of amplitude modulation (solid line) or modulation in time difference (broken line). **(C, C')** Membrane potentials in response to the simultaneous presentation of the two stimulus modulations in (A), (A'), (B), and (B'). The amplitude and time modulations are aligned in time in all panels and represent situations with a high-frequency neighbor (left column) and a low-frequency neighbor (right column). Black lines in (C) and (C') indicate actual membrane potentials, grey lines indicate the numerical sums of actual responses to component stimuli in (A), (A'), (B), and (B'). This neuron strongly preferred the situation in the left column, giving deep excitatory synaptic potentials and spikes that were removed for analyses and for presentation in this figure. From Carlson and Kawasaki (2006). Reprinted with permission.

## EOCD-related time processing

In addition to gating Knollenorgan inputs for discriminating a neighbor's from a fish's own signal, the EOCD in mormyrids has two major functions in the temporal processing of sensory signals: decoding the temporal code for amplitude information, and adaptive filtering.

In pulse-type mormyrid fishes, amplitude information for electrolocation is encoded in the response latency of the mormyromast, which is measured against the timing of an EOCD arrival at the ELL. Fig. 3E shows that mormyromast afferent fibers generate more spikes of shorter latency with increasing stimulus strengths (Bell, 1990). The use of time codes for amplitude information was suggested by a behavioral study in which a fish accelerated its EOD rate in response to a novel stimulus. This novelty response was compared for amplitude and latency changes in the EOD feedback (Hall et al., 1995). Novelty responses are an increased frequency of EODs when a fish encounters a novel stimulus, such as a looming object. Increasing the stimulus amplitude and deceasing the stimulus latency had equivalent effects in a manner predicted by the amplitude-latency relationships in the mormyromast electroreceptors in Fig. 3E. Moreover, no novelty responses were observed either to an amplitude or a latency shift if an EOD feedback pulse was delivered at a moment when no EOCD was expected in the ELL. These experiments suggest that the spike times of mormyromast afferents are compared with EOCDs, probably in the ELL, and are used to decode amplitude information.

The adaptive filter is a self-adjusting filter by which neurons in the ELL become adapted to ongoing sensory signals from EOD self-stimulation. Electrolocation relies on deviation in the EOD feedback signal from relatively large, constant baseline feedback signals that exist when no electrolocation object is present. The strength of the baseline feedback signals, however, changes for various reasons, such as a change in water conductivity. What is remarkable in the adaptive filter is that EOCD forms a negative image of the most recent sensory feedback and continuously updates the signal necessary to cancel it out. Electrosensory neurons in the ELL receive EOCD inputs as well as sensory inputs. The excitatory subtype of these neurons responds to a sensory stimulus with augmented baseline activity when the stimulus is time locked with spontaneously active EOCDs (Bell, 1982). This mimics a situation where a fish's baseline environmental condition changes. After continuing the pairing of EOCDs and the electrosensory stimulus for a few minutes, the neural responses diminish. If the stimulus is turned off at this time, inhibitory responses to EOCDs alone, which did not exist before, appear. This means that the neurons did not merely reduce their sensitivity to sensory stimuli, but subtracted constant responses, maintaining responsiveness to a new stimulus change. The inhibitory response is a mirror image of the excitatory response at the beginning of the pairing, and the time courses match perfectly. If a stimulus is presented at different time delays from the EOCD, the timing of the inhibitory response to EOCDs alone after the pairing also shifts according to the delay in the paired stimulus. Adaptation did not occur when the stimulus was presented at delays longer than 120 msec. The generation of a temporally matched negative image requires that ELL neurons receive EOCD signals with different delays and that the adaptation of the synapses at the ELL neurons is sharply tuned to temporal matching between EOCDs and sensory inputs. Bell et al. (1992) demonstrated that parallel fibers descending from a midbrain nucleus, the eminentia granularis, to ELL neurons show various delays from the times of EOCDs measured at the command nucleus. Adaptive synapses that are sharply tuned to the timing between the activities of the ELL neurons and their parallel fiber inputs have been demonstrated in *in-vitro* preparations of the ELL (Bell, 2001; Bell et al., 1993, 1997) .

## EVOLUTIONARY PERSPECTIVE

### Emergence of time-coding tuberous electroreceptors

The independent origins of tuberous electroreceptors and weak electric organs in both gymnotiform and mormyriform fishes suggest that these structures have coevolved in each group independently (Fig. 1). The close correspondence between the frequency tuning of tuberous receptors and the major frequency component of EODs in each species or individual also supports this notion. Tuberous electroreceptor organs are believed to have evolved independently in the Gymnotiformes and Mormyriformes after the independent origin of ampullary receptors in these two lineages. This is supported by the discovery of shared derived ampullary organs in the Siluriformes, the sister group to the Gymnotiformes, and in the Notopterids, the sister group to the Mormyriformes (see Siluriformes and Notopterids in Fig. 1). All ampullary electroreceptors known in fishes are typical rate coders that modulate the frequency of action potentials according to the voltage difference across the skin and are sensitive to relatively low frequencies (<50 Hz). Ancestral fishes with EODs probably began as pulse species that fired low-frequency EODs that stimulated ampullary-like electroreceptors that encoded stimulus amplitude by the firing rate.

### Time coding in gymnotiform electric fishes

The rate-coding tuberous electroreceptors of pulse gymnotiforms, the so-called "burst duration coders," generate several action potentials in response to each stimulus EOD, en-coding the amplitude of a stimulus by the number of action potentials in a burst (Bastian, 1976). This receptor type is a rate coder and is reminiscent of the ampullary electroreceptors. Adaptation to the detection of fast moving objects may have increased the demand for temporal resolution for amplitude information and is a possible factor in the evolution of fishes with higher-frequency EODs. As EOD frequency increases, the available number of action potentials between pulses decreases. This may have led to the emergence of the pulse-marker tuberous electroreceptors of pulse-type gymnotiform fish that generate only one action potential per EOD (Bastian, 1976; Kawasaki, 2005). These time-coding electroreceptors can carry information only by the times of action potentials, because the number of action potentials is always one, regardless of the amplitude of the stimulus. The amplitude-coding tuberous electroreceptors in wave-type gymnotiform fishes also resemble ampullary electroreceptors in being rate coders. Selection pressure for temporal resolution similar to that in pulse-type fishes may have resulted in the emergence of time-coding tuberous receptors that fire one action potential per cycle of a wave-type EOD. The major physiological difference between rate and time coders is sensitivity. Increased sensitivity results in firing a single action potential regardless of input amplitude and makes the receptor a time coder. The distinction between rate- and time-coding tuberous electroreceptor types has been found in all gymnotiform species so far examined.

The timing of the action potentials generated by time-coding electroreceptors carries various types of information, as mentioned above. This may be information on the resistivity or capacity of electrolocation objects, or phase shifts due to the interference of a fish's own EODs by another fish's EODs. Whatever is encoded, the times of action potentials from the electroreceptors must be compared with a time reference. A potential source of a time reference is the pacemaker nucleus in the medulla that determine the firing time of each EOD. As mentioned earlier, no gymnotiform fish is known to have any neural connections between the pacemaker nucleus and sensory systems. Instead of referring to the pacemaker nucleus, gymnotiform fishes have a time-comparison mechanism in the midbrain, where time-coded signals from different parts of the body surface are compared. The magnocellular layer of pulse-type species and Lamina VI of wave-type species in the midbrain contain large time-coding neurons that spread thick, fast axons within the layer (Carr and Maler, 1986; Réthelyi and Szabo, 1973). In the wave-type fish *Eigenmannia,* neurons occur in this and near layers that 'read out' the time differences between input action potentials.

## Sensory hyperacuity and preadaptation to electrolocation

Time-decoding mechanisms in the midbrain were discovered first in a gymnotiform electric fish, *Eigenmannia,* and have been studied extensively as a part of the neural substrate of the JARs (Heiligenberg, 1991). These and amplitude-sensitive mechanisms are, however, also well suited to electrolocation behavior. The amplitude-sensitive electroreceptors and central neurons are suited to detecting the resistive components of electrolocation objects — the time difference-sensitive system is suited for detecting the capacitive components of electrolocation objects because local capacitance delays sensory feedback signals from the EOD. These two systems are remarkably acute. As mentioned earlier, both *Eigenmannia* and *Gymnarchus* can determine the sense of rotation of Lissajous graphs in Fig. 4 by performing correct JARs (frequency shifts in the correct directions) even when the magnitude of amplitude and time modulation are ~0.02% and 100 to 300 nsec, respectively (Guo and Kawasaki, 1997; Kawasaki et al., 1988; Matsushita and Kawasaki, 2005; Rose and Heiligenberg, 1985a). The acuity exhibited by the JAR is better than that seen at the level of individual sensory receptors or afferent nerve fibers. These hyperacute JARs, however, are small in the magnitude of frequency shift and slow in time course. The function of the JAR is to increase the frequency of amplitude and time modulation by increasing the frequency difference between a fish's own and a neighbor's EODs, and such slow, small changes in an EOD would hardly function in jamming avoidance. The selection pressure for hyperacute JARs is uncertain. The electrolocation of objects, however, demands high sensitivity. That is, because the magnitude of the electric dipole field that a fish sets around itself attenuates with the inverse cube of distance, detection of resistive and capacitive objects at some distance requires high sensitivity. Thus, extreme sensitivities to amplitude and time may have evolved in both Gymnotiformes and Mormyriformes under selection pressure for the detection of extremely small modulations of feedback signals for the electrolocation of objects distant from the fish.

Various forms of JARs are known in all gymnotiform electric fishes except the genus *Sternopygus*. Fishes in this basal genus of wave-type gymnotiform fish do not shift their EOD frequencies in response to the EODs of other fish (Fig. 1) (Bullock et al., 1975). They nevertheless possess amplitude- and time-coding electroreceptors and central neurons much like those of other gymnotiform fishes that perform JARs. Moreover, *Sternopygus* possesses central neurons that respond to the sense of rotation in the Lissajous graphs in Fig. 4 that would evoke JARs in other fishes (Rose et al., 1987). *Sternopygus* can even be trained to swim forward and backward in response to sensory signals that would evoke frequency increasing and decreasing JARs in other fishes, respectively (Rose and Canfield, 1991). These neurons in *Sternopygus* must serve as a neuronal substrate for electrolocation behavior, and are regarded as a preadaptation for the mechanisms of the JAR in successive species of Gymnotiformes.

## Time coding in Mormyriformes

The tuberous electroreceptors of mormyriform fishes are also thought to have evolved from the ampullary electroreceptors found in the closest outgroup fish, *Xenomystus* (Notopteridae), which is electroreceptive but lacks the electric organ. As in gymnotiform phylogeny, the divergence to pulse- and wave-type groups occurred at the most basal branching point. The most basal mormyriform, *Gymnarchus niloticus,* is the only mormyriform species with wave discharge — all other mormyriforms are pulse type. The many independent evolutionary innovations in time-coding pathways in pulse-discharging mormyrids and the wave-discharging *Gymnarchus* make evolutionary comparisons exceedingly difficult. Differences between them include (1) the behavioral function, (2) the brain location of time-difference detection, and (3) the involvement of EOCD gating. In the pulse-type mormyrids *Gnathonemus* and *Brienomyrus*, time-coded signals are processed to detect the duration of EODs or SPIs of other individuals for communication. Neural processing for this function occurs in the midbrain. EOCD signals completely block the afferent signals generated through EOD self-stimulation, allowing only afferent signals from other individuals' EODs to be passed to the midbrain. In contrast, *Gymnarchus* utilizes time-comparison mechanisms for electrolocation and JAR. The time-comparison circuit lies in the hindbrain, where no EOCD occurs. If any homology is sought between the time-comparison systems of pulse-type mormyrid fish and *Gymnarchus*, one may assume the existence of an intermediate trait that might have served for both electrolocation and electrocommunication. As mentioned earlier, while electrolocation may rely on small time differences (~$10^{-4}$ sec) between electrosensory signals from different parts of body surface in wave species, electrocommunication relies on time differences between the up- and down-edges of an EOD pulse ($10^{-4}$ to $10^{-2}$ sec) in pulse species. If EOD pulses in pulse species are sufficiently short, a time-comparison system may code both electrolocation and communication signals. If the ancestral pulse mormyrid fish lacked EOCD inhibition in the nucleus of the nELL, its midbrain mechanisms might have been used for both electrolocation and communication. Time-comparison and EOCD mechanisms have not been studied in basal groups of mormyrid fishes. It is noteworthy that the basal pulse-type group, *Petrocephalus*, contains species with extremely short pulses.

The origin of the EOCD system is also difficult to trace. The most basal fish in Mormyriformes, *Gymnarchus*, lacks the EOCD system (Fig. 2) (Kawasaki, 1994). The electromotor system of *Gymnarchus*, however, shows an intriguing functional and anatomical organization which may suggest that the lack of the EOCD system in *Gymnarchus* is a derived character, i.e., a lost function (Kawasaki, 1994). In *Gymnarchus*, an intrinsic pacemaking signal for EODs is generated in the pacemaker nucleus, an unpaired midline nucleus in the hindbrain. All projection neurons from the pacemaker nucleus project bilaterally and exclusively to the lateral relay nucleus, a paired nucleus in the hindbrain. The projection neurons in the lateral relay nucleus in turn project exclusively to an unpaired midline nucleus, the medial relay nucleus. The medial relay nucleus sends output axons to electromotor neurons in the spinal cord, which in turn fire electrocytes in the electric organ for EODs. The existence of the lateral nucleus is intriguing because if the pacemaker nucleus projected directly to the medial relay nucleus, as is the case in gymnotiform fishes (*Eigenmannia* in Fig. 2), the lateral relay nucleus would be unnecessary. The electromotor system of *Gnathonemus* is similar to that of *Gymnarchus* in that a paired lateral nucleus relays EOD command signals to a midline relay nucleus, the medullary relay nucleus (Bell et al., 1983). The bilateral nucleus, called the bulbar command associated nucleus (BCA), is a relay nucleus that provides EOCD signals to two nuclei in the midbrain (the mesencephalic command-associated nucleus and the paratrigeminal command-associated nucleus), which in turn distribute the EOCD signals over extensive areas in the midbrain and hindbrain. Each axon from the BCA to command-associated midbrain nuclei gives off an axon co-lateral that projects to the medullary relay nucleus. This projection does evoke an action potential in neurons in the medullary relay nucleus, but this action potential is preceded by an action potential generated by a direct projection from the command nucleus to the medullary relay nucleus, which is responsible for the generation of an EOD (Bell et al., 1983). Thus, the first action potential in the two-spike volley evokes an EOD, but the second action potential in the volley lacks an apparent function. Comparison of the electromotor systems of *Gymnarchus* and *Gnathonemus* reveals puzzling neural organizations that include neuronal activities and anatomical connections without apparent present functions. Future examination of the electromotor and EOCD systems in other groups of mormyrid fishes, particularly basal groups such as *Petrocephalus*, should provide insight into the missing links.

## CONCLUSIONS

Analyses of time coding and decoding neural systems have uncovered some design principles underlying the behavioral functions of phylogenetically close and distant species. Some of these neural properties and performances are, however, difficult to understand in terms of behavioral function. Only knowledge of phylogenetic development and the relationships between neural circuits and their behavioral functions may explain these intriguing properties. We know only a small number of behavioral functions and their neuronal implementation in limited number of species among the hundreds of diverse electric fish species. Time-coding systems have been relatively well analyzed in wave species of gymnotiform fishes, but little is known in pulse gymnotiform species. The EOCD system has been investigated only in several species of mormyrid fish. Much remains to be learned about behavioral functions and neuronal mechanisms in fishes in important phylogenetic positions.

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