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REVIEW

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Encoding and processing biologically relevant temporal information in electrosensory systems

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Abstract Wave-type weakly electric fish are specialists in time-domain processing: behaviors in these animals are often tightly correlated with the temporal structure of electrosensory signals. Behavioral responses in these fish can be dependent on differences in the temporal structure of electrosensory signals alone. This feature has facilitated the study of temporal codes and processing in central nervous system circuits of these animals. The temporal encoding and mechanisms used to transform temporal codes in the brain have been identified and characterized in several species, including South American gymnotid species and in the African mormyrid genus *Gymnarchus*. These distantly related groups use similar strategies for neural computations of information on the order of microseconds, milliseconds, and seconds. Here, we describe a suite of mechanisms for behaviorally relevant computations of temporal information that have been elucidated in these systems. These results show the critical role that behavioral experiments continue to have in the study of the neural control of behavior and its evolution.

Keywords Information processing · Time domain · Comparative approaches · Jamming avoidance response · *Eigenmannia* · *Gymnarchus*

Abbreviations AM: Amplitude modulation · Df: Difference in frequency · DPM: Differential phase modulation · ELL: Electrosensory lateral line lobe · EOD: Electric organ discharge · EPSP: Excitatory post-synaptic potential · JAR: Jamming avoidance response · PM: Phase modulation · PSP: Post-synaptic potential

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The importance of temporal processing of sensory information in behavior

Animals receive and encode sensory information as spatiotemporal patterns of activity across sensory arrays. For many behaviors in a wide range of taxa, behaviorally relevant sensory information is present in the temporal structure of sensory signals. Indeed, the temporal structure of sensory signals is commonly the most salient feature for behavior (Rose 1986; Carr 1993; Pollack 2001). Understanding how such time-varying stimuli are represented in the nervous system and the transformations of these representations is a central problem in behavioral neuroscience. How is temporal information encoded and decoded in central nervous system (CNS) circuits?

Significant progress has been made in understanding how time-varying information is represented in the temporal patterns of spiking activity in the CNS, particularly in model systems in which there is a tight correlation between the temporal structure of specific sensory signals and behavior (Rose 1986). Because temporal processing plays a particularly important role in the biology of many species of weakly electric fish, electrosensory research has contributed significantly to this pursuit. Certain species exhibit a behavior that relies almost exclusively on temporal information for its control: the jamming avoidance response or "JAR." This behavior is remarkable because the stimuli that most strongly elicit the behavior differ in only the temporal structure with stimuli that do not elicit the JAR.

Over the past several decades, studies of temporal processing in electrosensory systems in weakly electric fish have largely been directed at understanding the neural control of the JAR. These studies, which have included behavioral, neurobiological, and comparative

approaches, have produced a complete sensory algorithm and neural circuit for the control of the JAR (Heiligenberg 1980, 1991; Kawasaki 1993) and have elucidated aspects of the evolution of the JAR (Green and Rose 2004). This work has been reviewed many times before (Heiligenberg 1986, 1991; Rose 2004) and will not be exhaustively reviewed here. Further, this review will not cover temporal coding in the Knollenorgan systems of mormyrid fish (Hopkins 1995; Xu-Friedman and Hopkins 1999). Here, we will focus on an exciting emergent theme in the field: studies that examine the properties and mechanisms for the transformation of temporal codes in CNS circuits.

What is a temporal code?

Initially, temporal information in stimuli must be coded by variations in the distribution of action potentials over time within and/or across neurons (Rose 1996; Eggermont 1998; Pollack 2001). In this "timing-dependent" temporal coding (Theunissen and Miller 1995), the time course of firing defines how information is represented. In some cases, temporal variations in responses of individual neurons reflect some time-varying feature of a sensory signal (e.g., amplitude modulations may be coded in the temporal fluctuations of firing rates of neurons). In an extreme case, variations in the precise timing of individual spikes or bursts of spikes may be used to represent variations in temporal features of sensory signals over time. At the other end of the temporal coding spectrum, temporal information may be represented, following central transformations, in the activity of neurons that respond selectively to particular temporal features of stimuli without necessarily showing temporally structured firing (Rose et al. 1988; Rose 1996). In this form of "temporal filter" representation, the biologically relevant temporal information in a stimulus can be represented in the relative response levels across a population of temporal filter neurons. These types of codes are, of course, not mutually exclusive. Both appear to be important for the normal processing of temporal information; the two coding strategies are differentially employed across the various levels of electrosensory processing. Finally, in some cases (Laurent 1999), nontemporal features of stimuli may be represented in the temporal pattern of firing ("temporal *en*coding"; Theunissen and Miller 1995).

The study of temporal processing in electrosensory systems is facilitated by the fact that the JAR behavior includes information in sensory signals that occur over three distinct time horizons, ranging from microseconds to seconds. This broad range has proven to be a powerful tool for understanding how temporal information is represented and processed in the CNS. The challenge of studying temporal codes in the brain is that the ultimate interpretation of any neural code is in the responses of downstream targets and eventually in the behavioral output of the animal. In this light, electric fish are an ideal model system for the study of temporal codes in the brain because the codes can be studied over this wide band of time horizons in direct relation to the JAR behavior.

Wave-type electric fish and the JAR

Wave-type weakly electric fish produce nearly sinusoidal electric signals using a series of modified muscle cells (electrocytes) collectively known as the electric organ. Electric organ discharges, or "EODs," are synchronous firing of electrocytes that are repeatedly triggered by a brain nucleus, the pacemaker. In *Eigenmannia* and *Gymnarchus*, EODs occur on the order of hundreds of Hertz. The frequency of EODs of each fish can be stable over periods of days to months. The electric fields generated by EODs are detected by tuberous electroreceptors embedded in the skin. The fish "electrolocate" by detecting distortions of the electric field produced by nearby objects.

Interference of the electrolocation system occurs when two fish with similar EOD frequencies meet and their electric fields mix (Fig. 1). Modulations (beat) occur at the difference in EOD frequencies of the two fish, and beat rates of between 3 and 8 Hz are most detrimental to electrolocation, whereas beat rates of 20 Hz do not impair electrolocation. To avoid such interference, both fish shift their EOD frequencies away from each other to increase the difference. This simple electric behavior is the JAR. If a fish encounters a neighbor with a lower frequency than its own, it will increase its EOD frequency; and if it encounters a neighbor with a higher frequency, it will decrease its own. Beat rates that are most detrimental (3–8 Hz) also elicit the strongest JARs, whereas beat rates of above 20 Hz elicit weak or no JAR behavior (Bullock et al. 1972a, b; Heiligenberg et al. 1978; Heiligenberg and Partridge 1981; Bastian and Yuthas 1984). The JAR behavior appears to be common in the wild, as *Eigenmannia* are typically found with 20 Hz or greater differences in EOD frequencies (Tan et al. 2005).

The behavioral evidence demonstrates that the fish detects two features for the control of the JAR. First, the fish identifies the slow modulation rates (3–8 Hz) that preferentially drive the JAR. Second, the fish determines the sign of the frequency difference, Df = (neighbor's discharge frequency) − (own discharge frequency), and accordingly changes its EOD frequency in the correct direction. For example, if the nearby fish has a higher EOD frequency, then the Df is positive and the fish lowers its own EOD frequency.

In an elegant series of behavioral experiments, Walter Heiligenberg and colleagues revealed an entire sensory algorithm for the control of the JAR (Heiligenberg 1991). The essential parameters for JAR are the temporal patterns of amplitude modulations (AMs) and phase modulations (PMs) in the signal mixture of EODs from two nearby fish. As shown in Fig. 1, both AMs and

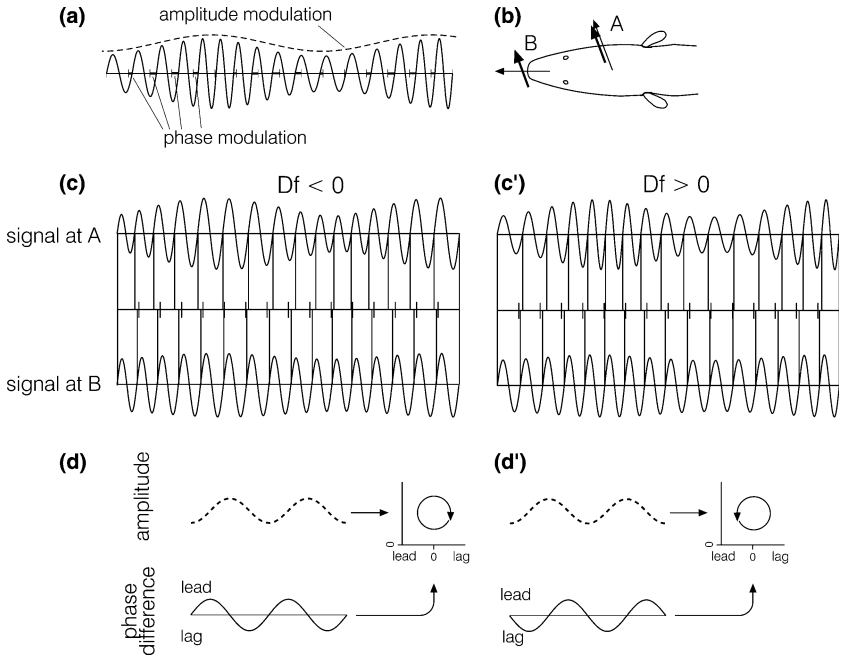

Fig. 1 Elements of the stimulus for the jamming avoidance response. **a** Mixture of fish's own and a neighbor's EODs creates a periodical modulation in two parameters, amplitude and phase. Amplitude modulation is indicated by a *broken line*. Phase modulation is the change of zerocrossing times in reference to the constant time marks indicated by the *tick marks*. **b** Different geometries of the fish's own EOD (*radial thin arrows*) and a neighbor's EOD (*thick parallel arrows*) cross at different angles at different body areas (*A* and *B*) resulting in different degrees of contamination. **c** Signal mixture experienced by the areas *A* and *B* shows different degrees of phase modulation creating the modulation in *phase differences* (time differences between long vertical lines). Time courses of amplitude and phase difference modulations are different for Df > 0 (**c**) and Df < 0 (**c′**). **d** The temporal relations between amplitude and phase difference modulations are plotted in Lissajous graphs at *upper right corner* for Df < 0 (**d**) and Df > 0 (**d′**)

PMs occur at a rate equal to the difference in EOD frequencies of the two fish, or |Df|. For the JAR, fish detect when these modulations occur within the range of 3–8 Hz.

The rate of modulations alone cannot, however, unambiguously encode the *sign* of the frequency difference between the EODs of the two fish. The information about the sign of the difference in EOD frequencies is necessary for the fish to determine whether it increases or decreases its own EOD frequency for the "correct" JAR. The sign of Df is encoded in the temporal combination of these two modulations (Fig. 1, panels d and d′). The PM information is computed from microsecond differences in the timing of firing between phase coding afferents from different body areas (see below). Although the small phase shifts introduced in the time coding afferent signal from a given body location could in theory be compared with the phase of the pacemaker nucleus in the brain that creates a constant firing of EOD rhythm and drives each cycle of EODs, this solution is not employed. The JAR behavior is driven via electrosensory feedback: it is a response to the frequency difference between two afferent sinusoidal signals (feedback signals from its own EODs and those from a neighboring fish) regardless of the frequency relation between the neighbor's EOD and the fish's own pacemaker (Heiligenberg et al. 1978; Kawasaki 1993) (Fig. 2).

The widely held understanding of the relation of amplitude and phase information in the control of the JAR was recently challenged, however, when it was observed that *Eigenmannia* lowers its EOD frequency in response to AMs alone in the absence of PMs (Takizawa et al. 1999). The EOD frequency decrease has a similar time course and amplitude as seen in the JAR. AM rates of around 5 Hz elicited strongest responses, whereas AM rates higher than approximately 20 Hz had little effect. Unlike the JAR, however, the direction of the frequency shift was always downward. This downward response to AMs alone has not yet been observed in other wave-type gymnotiform electric fish or in *Gymnarchus*. Some pulse-type gymnotiform electric fish, however, exhibit similar behaviors (Kawasaki et al. 1996). While the behavioral and functional significance of this response is not understood, it appears to shed light on seemingly paradoxical results from previous physiological studies of motor control mechanisms for the control of EOD frequency (Rose et al. 1987, 1988; Kawasaki et al. 1988a; Keller 1988; Keller et al. 1988, 1990, 1991; Dye et al. 1989; Heiligenberg et al. 1991, 1996; Green and Rose 2004).

Despite these new revelations concerning the control of the JAR, the behavior can nevertheless be divided into three distinct time scales or horizons. Each of these time horizons presents unique computational challenges for the nervous system. The JAR is triggered by

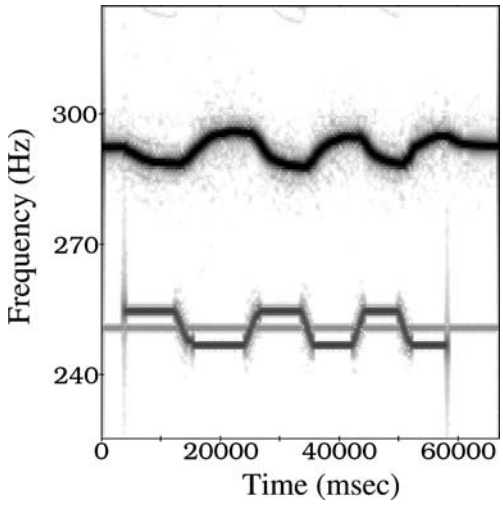

Fig. 2 The JAR is not controlled with reference to the frequency of the pacemaker which normally drives the EOD. The fish was immobilized using Flaxedil and respirated by a continuous flow of water through a tube placed in the mouth. A pair of wires was placed onto the tail at the location of the electric organ. Although the neuromuscular junction is blocked in these preparations to silence the EOD, the motor command can be recorded in the preparation. The *top trace* is a sonogram of this motor command signal from such a fish. *Below two traces* are the stimuli in the water that elicited the JAR behaviors in this fish. Note that the stimulus traces, which were artificially generated, are about 40 Hz different than the actual EOD frequency. Nevertheless, the JAR behavior was robust. This experiment demonstrates that an efference copy is not used in the control of the JAR and suggests that the behavior is controlled solely using sensory information

ongoing stimuli that occur at rates below 10 Hz. This information, therefore, occurs on the order of hundreds of milliseconds. This is the longest time horizon. The sensory information used in the control of the JAR is composed of the modulations of a fish's EOD; information encoded by EODs occurs at rates on the order of milliseconds. Ongoing EODs are, in a sense, the "carrier" of electrosensory information, and this carrier frequency determines the middle time horizon of sensory processing for the control of the JAR. Finally, behavioral experiments have demonstrated that very fast time comparisons from across the electroreceptor array are necessary to elicit aspects of the JAR behavior. These comparisons from across the receptor surface occur at rates on the order of microseconds and are the fastest time horizon used in the control of the JAR.

Encoding of electrosensory information by tuberous receptors

As stated above, behaviorally relevant temporal signals for the control of the JAR occur on three time scales in *Eigenmannia* and *Gymnarchus*. Information is encoded by specialized "tuberous" electroreceptors in each of these time horizons. There are two types of tuberous receptors, T-type and P-type. T-type receptors exhibit the greatest temporal acuity and can encode behaviorally relevant phase shifts from across the receptor sheet on the order of 10^{-7}–10^{-4} s (Rose and Heiligenberg 1985b; Zakon 1986; Kawasaki et al. 1988b; Guo and Kawasaki 1997). The middle time horizon is roughly equal to the EOD frequency of the fish, on the order of hundreds of Hertz or 10^{-4}–10^{-3} s. This time horizon is also encoded in the ongoing activity of T-type tuberous electroreceptors. P-type tuberous receptors also operate in this time domain, as these receptors are roughly tuned to the EOD frequency of the fish. The longest time horizon occurs in the sensory modulations, the beat rates that result from the interaction of the EODs of nearby conspecifics. These signals occur on the order of Hertz, or 10^{-2}–10^{-1} s. Amplitude modulations occurring on this time horizon are encoded by the P-type tuberous receptors (Zakon 1986; Kawasaki 2005), and information from T-type receptors can be "read" on this time horizon as well.

Encoding of phase differences on the order of microseconds to milliseconds

T-type receptors are largely responsible for encoding the two fastest time horizons that occur between 10^{-7} and 10^{-3} s. Each T-type receptor is phase locked and fires in every cycle of the EOD. The jitter at the level of the receptors occurs on the order of tens of microseconds, which is refined in CNS circuits to microseconds.

The sensory signals used in the control of the JAR include microsecond phase shifts across the electroreceptor sheet. The phase at each body area is sampled by phase coding electroreceptors (Scheich et al. 1973; Zakon 1986; Kawasaki 2005). The afferent fibers from these electroreceptors fire one action potential for each cycle of stimulus. Under natural conditions the stimulus would be the fish's EOD, but under experimental conditions it can be an EOD mimic (typically a sine wave near the fish's own EOD frequency), carrying precise phase information (jitter of tens of microseconds) at each area of the body to the brain (Carr et al. 1986a; Guo and Kawasaki 1997). With some convergence at each level, the phase information is relayed by the spherical cells in the electrosensory lateral line lobe (ELL) and passed to midbrain giant cells, which occur exclusively in a structure known as "lamina VI," in the torus semicircularis of *Eigenmannia*. In *Gymnarchus*, the phase coding afferents terminate on giant cells within the ELL. Spherical cells in *Eigenmannia* and giant cells both in *Eigenmannia* and *Gymnarchus* fire one action potential per stimulus cycle, as do phase coding afferents, but code phase with less jitter (< 10 μs). These phase-locking neurons are large, highly myelinated, and spread large axon terminals to diverse regions of the respective brain structures (the torus semicircularis in *Eigenmannia*, the ELL in *Gymnarchus*).

Small cells in lamina VI of the torus of *Eigenmannia* receive inputs from giant cells (also in lamina VI) on their soma and an input from spherical cells in the ELL on the dendrites. The terminal of the giant cell to the small cell indents into the soma (Carr et al. 1986b). The small cells are sensitive to differential phase modulation (DPM) over the body surface (Rose and Heiligenberg 1985a). Small cells extract DPM information from phase-locked inputs from different areas on the body surface. In *Gymnarchus*, a similar organization is found in the ELL (Kawasaki and Guo 1996). A terminal of a giant cell terminates on to the soma of the ovoidal cell. The terminal in *Gymnarchus* also shows a peculiar specialization in which a large area of somatic surface (~85%) is covered by a terminal synapse (Carr 2004; Matsushita and Kawasaki 2004) (Fig. 3). The phase coding afferent terminates onto a dendrite of the ovoidal cell. The small cells in *Eigenmannia* and the ovoidal cells in *Gymnarchus* distribute the DPM information to other neurons in the structure. These secondary DPM neurons show high sensitivity to DPM on the order of a few to tens of microseconds (Rose and Heiligenberg 1986; Kawasaki and Guo 1996). To date, physiological recordings from ovoidal cells have not been performed.

Physiological mechanisms by which the DPM-sensitive neurons achieve sensitivity to time differences on the order of microseconds are currently unknown. A study using a Hodgkin–Huxley single compartment model, however, demonstrated that interaction of synaptic currents whose time constants are on the order of a few hundreds of microseconds may result in differential phase sensitivity comparable to that observed in real neurons (Takagi and Kawasaki 2003).

Integration of phase information on the order of hundreds of milliseconds

The temporal relations between AM and DPM at lower beat frequencies carry critical information, the sign of Df, for the control of JARs both in *Eigenmannia* and *Gymnarchus*. Figure 1 shows how amplitude and phase modulate in time when $Df < 0$ (d) and $Df > 0$ (d′). For EOD combinations with a particular $|Df|$, amplitude and phase are *each* modulated at frequency $|Df|$ regardless of the sign of Df. However, the temporal relations between them are unique for negative and positive signs of Df. The phase modulation information is computed from the phase difference as mentioned above. Because the electric field geometry of the animal's own and a neighbor's EOD differs under natural conditions, the PMs vary over the body surface (Fig. 1). Artificial elimination of phase information abolishes normal JAR, demonstrating the essential role of DPM in the control of the JAR (Heiligenberg et al. 1978; Kawasaki 1993).

Encoding of AMs on the order of Hertz

P-type tuberous electroreceptors encode the amplitude of electric signals with frequencies near the fish's own EOD frequencies (Zakon 1986; Kawasaki 2005). The rate of firing of P-type afferents is roughly proportional to the amplitude of the electrosensory stimulus. At the level of the ELL, the dynamic range of firing rates in neurons that receive P-type information is from near zero to around 100 Hz (Shumway 1989). Descending

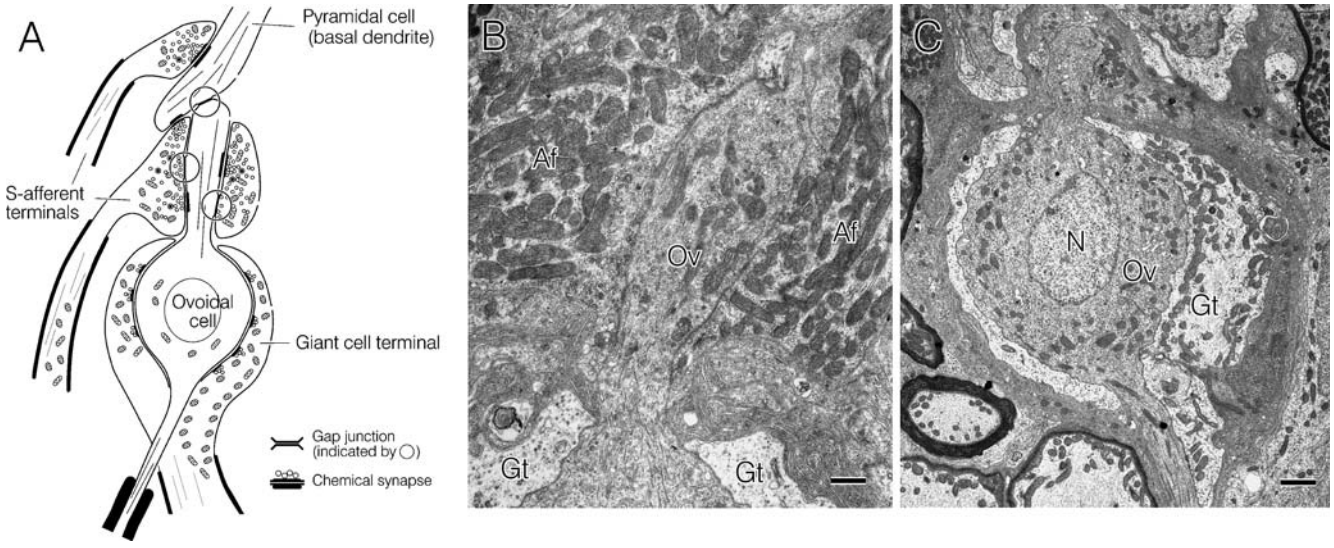

Fig. 3 The ovoidal cell and phase-locked afferents in *Gymnarchus*. **a** An ovoidal cell receives a terminal of a phase-lock primary afferent on its dendrite and a large synapse from a terminal of a giant cell on its soma. **b** Ovoidal cell dendrite is surrounded by an afferent terminal. **c** The soma of the ovoidal cell is surrounded by a terminal of a giant cell. The dendrite of the ovoidal cell contacts its output neuron, the pyramidal cell. *Af* afferent terminal, *Gt* giant cell terminal, *Ov* ovoidal cell, *N* nucleus. *Scale bar* 0.5 μm in **b**, 1 μm in **c**. (Modified after Matsushita and Kawasaki 2004)

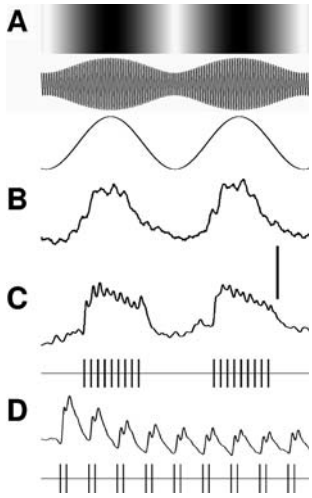

Fig. 4 Frequency relations between sensory stimuli and neural representations. **a** Representations of time-varying sensory stimuli from different modalities. Signals shown are 400 ms in duration. **b** Current-clamp recording of an electrosensory neuron in the midbrain of *Eigenmannia* to the 5 Hz sinusoidal stimulus above it. *Scale bar* 10 mV. **c**, **d** Responses of a midbrain neuron to direct stimulation of its afferents at temporal frequencies of 5 Hz (**c**) and 20 Hz (**d**). **c** Pulse trains are 100 ms in duration, pulses are presented at a rate of 100 Hz. This pattern of afferent stimulation elicits EPSPs similar to those elicited by 5 Hz sensory stimulation [compare with EPSPs in **b**; data from the same neuron]. **d** Pairs of pulses presented at a 20 Hz periodicity. The same total number of stimulus pulses as in **c**. There is a large response at the onset of the stimulus that is then depressed; depression continues as long as the stimulus pattern is maintained. This response profile is similar to the 20 Hz sensory stimulation (not shown). (Modified after Fortune and Rose 2001)

negative feedback from the midbrain (N. praeeminentialis) ensures that ELL output (pyramidal) cells respond in a "bursting" fashion primarily to the rate of change of stimulus amplitude (Bastian 1986a, b; Gabbiani et al. 1996). As a first approximation, the spiking activity generated by an ongoing, constant temporal frequency AM stimulus is, therefore, a series of "bursts" of spikes with silent intervals (Fig. 4). These bursts occur at the same rate as the amplitude modulations of the EOD. In other words, low temporal frequency information is represented using bursts of high firing rates. Quantitative differences in AM selectivity exist between neurons of the three tuberous somatotopic maps of the ELL (Shumway 1989).

An exciting new finding is that the temporal filtering properties of ELL neurons differ in relation to spatial aspects of the stimulus. These differences are mediated by feedback pathways and are strongest for "broad-field" or "global" modulations, such as those stemming from social interactions (Doiron et al. 2003). Spatially restricted modulations, such as those experienced during electrolocation of prey, are less effective stimuli for the feedback pathways. Consequently, the AM filtering properties of pyramidal cells are influenced by the spatial structure of electrosensory stimulation (Chacron et al. 2003, 2005).

Further, information theory has been used to characterize the information content of and feature extraction by these AM-sensitive neurons (Gabbiani et al. 1996; Wessel et al. 1996; Metzner et al. 1998; Gabbiani and Metzner 1999; Krahe et al. 2002). Potential problems with such analyses are that they may look upstream, back to the stimulus to assess the information content in the activity of a neuron, and/or may use generalized models for neurons that decode the information. The behaviorally relevant information content of any neural code is derived from its impact on downstream targets in the intact system. The relations between these approaches to the study of neural codes will be directly determined in the coming years as quantitative methodologies are applied to the targets of the ELL, especially neurons in the torus semicircularis. These experiments will offer a unique and important evaluation of the use of information theory in the analysis of neural codes in the CNS.

The responses of P-type ELL neurons span two of the time horizons, milliseconds to seconds. The millisecond horizon is the instantaneous firing rates of these neurons that represent EOD amplitude. The tens of milliseconds to seconds time horizon is the modulation of the instantaneous firing rate over time. Both time horizons are encoded within the same train of activity in this CNS circuit.

From the perspective of downstream targets, the representation of AM information by P-type receptor systems involves a sort of frequency inversion (Fig. 4). A burst of high-frequency firing indicates, from the standpoint of representation of sensory information, a low temporal frequency electrosensory stimulus. Thus, a low-pass filter in relation to the electrosensory stimulus would indeed have to pass high-frequency bursts of afferent activity. A high-pass filter in the sensory domain would potentially have to reject the high-frequency spiking activity.

This inversion of the representation of information is manifest in the post-synaptic potentials (PSPs) of toral neurons. Incoming bursts of activity elicited by low temporal frequency stimuli result in Gaussian or sinusoidally shaped PSPs (Fig. 4). Remarkably, the PSPs of such neurons can recover the analog waveform of the sensory stimulus (Rose and Call 1993). These analog representations of the sensory stimulus are the zenith of the inversion in the neural representation: the highest firing rates/frequencies are most associated with the slowest PSPs with the lowest frequencies. Similarly, the lowest firing rates are associated with PSPs that are best characterized as having the highest frequencies (Fig. 4). Note that the overall rate of firing of toral afferents from the ELL for low and high temporal frequency stimuli may nevertheless be similar (Fortune and Rose 2001). Importantly, the transformation of the incoming code by toral neurons must, therefore, be dependent on the temporal distribution of spikes (Fortune and Rose 2000).

The incoming code represents information in two distinct ways, depending on the context with which the

spike code is viewed. In the context of the amplitudes of electrosensory signals in water, the representation of information is a rate code. In the context of the representation of AM rates, the information is encoded in the timing/temporal distribution of spikes.

Mechanisms underlying the transformation of P-type tuberous information in the torus

The electrosensory codes of P-type tuberous electroreceptors are transformed in the ascending electrosensory system. The primary P-type afferents encode the beat rate in the periodicity of their discharges for rates up to at least 40 Hz. P-type receptors are represented in the ELL in three somatotopic maps. These maps exhibit average differences in their temporal filtering properties (Shumway 1989; Metzner and Juranek 1997; Young 1998). Most neurons in the midbrain, however, have strong low-pass or band-pass characteristics, responding best to beat rates below 8 Hz (Heiligenberg and Rose 1985; Fortune and Rose 1997). A minority of midbrain neurons shows all or high-pass filtering characteristics (Fortune and Rose 1997). These temporal response properties largely emerge in the responses of midbrain neurons (Fortune and Rose 2000).

Intracellular recordings have been used to identify and characterize all of the major mechanisms used in the transformation of the codes in midbrain electrosensory neurons used in the control of the JAR (Fortune and Rose 1997, 2000; Rose and Fortune 1999a, b). The data demonstrate that three cellular functions account for almost all of the temporal filtering that emerges at the level of the midbrain. These include (1) passive membrane properties, (2) "active" all-or-none voltage-gated conductances, and (3) short-term synaptic plasticity. Each of these mechanisms operates uniquely between the time horizons of milliseconds to seconds.

Passive electric filtering is the result of the resistive and capacitive properties of the cell membrane and is correlated with the spine density of toral electrosensory neurons (Rose and Call 1993; Fortune and Rose 1997). These properties were evaluated by injecting sinusoidal current (2–30 Hz) and current pulses into electrosensory toral neurons and recording the resulting depolarization (Fortune and Rose 1997). Spiny neurons were found to have long time constants that resulted in smooth, sinusoidal excitatory post-synaptic potentials (EPSPs). These time constants result in an interesting feature of these neurons: as the afferent spike rate increases, the frequency of the intracellular response (EPSPs) decreases. As the instantaneous afferent spike rate is lowered, conversely, the frequency of intracellular responses in post-synaptic neurons increases.

"Active" membrane conductances can enhance temporal filtering and dramatically increase the "inversion" of high firing rates to low temporal frequency PSPs. Voltage-dependent conductances amplify the responses of approximately one-third of toral neurons to particular stimulation rates. These conductances give rise to depolarizations of 10–20 mV that ride on top of EPSPs and are independent of those responsible for spike generation (Fortune and Rose 1997). For these neurons, increasing the level of negative current-clamp beyond a particular point results in an abrupt decrease in the amplitude of stimulus-related EPSPs, i.e., the voltage-dependent, "all-or-none" component drops out. In many cases, hyperpolarization of the neuron by only 5–10 mV is sufficient to eliminate these all-or-none components of EPSPs. For neurons that do not exhibit evidence of prominent voltage-dependent conductances, other than those responsible for action potentials, PSP amplitude increases when the holding potential of the neuron is made more negative (Fortune and Rose 1997).

All-or-none PSP components appear to fall into two classes: those with time courses that vary in concert with the temporal frequency of the stimulus and those with short time courses that are largely independent of the temporal frequency of the stimulus. Those with short time courses, approximately 50 ms (20 Hz), appear to be mediated by a Na^+ current (Fortune and Rose 2003). These conductances are most often found in high- or band-pass cells. The slow type, which is mediated by synaptic inputs and a voltage threshold, amplifies the low-pass filtering properties of neurons. These features suggest that this conductance may be mediated by *N*-methyl-D-aspartate (NMDA) receptors. The activation and inactivation kinetics of voltage-gated channels probably govern the time course of the conductance changes that differentially amplify responses to particular temporal frequencies (Haag and Borst 1996). The enhancement of the frequency inversion is mediated by the slow-type active conductances. This type of active conductance has a long temporal window and will therefore act as a low-pass filter.

Finally, activity-dependent declines in PSP amplitude can increase temporal filtering by an additional 400% (~12 dB) (Rose and Fortune 1999a, b). These declines in PSP amplitude are neither caused by inhibitory post-synaptic input, because they remain intact when neurons are hyperpolarized, nor are they the result of changes in the input resistance of these cells. Results from in vivo "paired-pulse" stimulation of the electrosensory afferents via direct stimulation of the lateral lemniscus demonstrated that these activity-dependent declines in PSP amplitude are most likely caused by homosynaptic short-term depression (Fortune and Rose 2001).

In these neurons, depression and facilitation are elicited by different patterns of afferent activity (Fortune and Rose 2000). Depression is activated by patterns similar to those elicited by 20 Hz or greater beat rates. These are the beat rates that occur after the JAR has been completed. Facilitation is best observed only after depression has been induced by an ongoing post-JAR stimulus. Short-term synaptic facilitation is elicited by slow beat rates—those that drive the JAR. The net result of the differential activation of short-term synaptic depression and facilitation is that neuronal responses to

Table 1 Nonlinear interaction of amplitude and phase modulations in the sign-selective neuron in the midbrain of *Gymnarchus*

Response to Df > 0	Response to Df < 0		
	Suppression	Linear	Facilitation
Nonselective responses			
Suppression	17	2	0
Linear	5	15	5
Facilitation	0	4	3
Df < 0-selective responses			
Suppression	8	7	2
Linear	0	1	3
Facilitation	0	0	1
Df > 0-selective responses			
Suppression	11	0	0
Linear	8	3	0
Facilitation	5	11	0

Suppression, linear, and facilitation, respectively, mean that the sum of responses to singular presentation of AM and PM is smaller, not significantly different, and larger than responses to joint presentation of AM and PM

low temporal frequency stimuli are enhanced in the presence of ongoing high temporal frequency interference. In short, the facilitation is a mechanism that overcomes the potentially deleterious effects of the depression.

Temporal combination-sensitive neurons in the midbrain

The time course of AMs and PMs are independently processed by neurons in the ELL and the torus semicircularis. The critical stimulus feature for the JAR, the sign of Df, is encoded in the temporal relation between the AM and DPM. Therefore the two independently processed signals must converge onto neurons that detect the temporal pattern between them. The convergence occurs in the torus semicircularis in the midbrain both in *Eigenmannia* (Heiligenberg and Rose 1985, 1986; Rose and Heiligenberg 1986) and *Gymnarchus* (Kawasaki and Guo 1998, 2002). In both species, neurons in the torus exhibit a wide range of response selectivity, from being sensitive exclusively to AM or PM to being sensitive to a particular temporal pattern between them (Heiligenberg and Rose 1986; Carlson and Kawasaki 2004). Table 1 shows the diversity of types of interactions between the two signals in the neurons found in the torus of *Gymnarchus* that responded to AM and PM. Neurons that are not selective to a particular sign of Df tend to show linear summation of responses to AM and PM, or sign-independent suppression of responses. Neurons that are selective to one sign of Df, however, tend to show various types of sign-dependent nonlinear interactions. Both excitation and inhibition appear to be important for the generation of sign selectivity. Figure 5 shows representative response histograms of these neurons.

Neural codes for motor control on the order of seconds

As mentioned above, the convergence of AM encoded by the P-type tuberous electroreceptors and timing difference information from the T-type system occurs in neurons of the torus semicircularis, homolog of the inferior colliculus. How is this sensory representation read by the nervous system to produce behavior? In *Eigenmannia*, the discrimination of relative frequency is largely completed and then interfaced with motor control circuits in the diencephalic target of the torus, the nucleus electrosensorius (NE).

Unlike the torus, there is no clear somatotopic organization in the NE. Instead, NE neurons seem to receive convergent information from across the body surface. Single neurons have been recorded in the NE of *Eigenmannia* that respond highly selectively to the sign of the Df (Bastian and Yuthas 1984), and this preference is rather independent of the orientation of the jamming field, i.e., they code the sign of Df without ambiguity (Keller 1988). The NE contains a simple "motor map"; stimulation of specific regions of the NE [NE↑ (increases EOD frequency) or NE↓ (decreases EOD frequency)] by glutamate iontophoresis can produce slow increases or decreases, respectively, in the frequency of the EOD (Keller and Heiligenberg 1989).

These changes in EOD frequency are mediated through one division of the prepacemaker (PPn-G) and sublemniscal prepacemaker (SPPn) motor control regions. Lesions of these areas eliminate rises or falls in frequency, respectively (Metzner 1993, 1999). The reduction in EOD frequency following activation of the NE↓ region implies that the SPPn is tonically active and inhibited by input from the NE↓. This notion is supported by the finding that blockade of GABA-A inhibition at the SPPn elicits frequency increases. These findings lead to a model of premotor control wherein negative Df stimuli selectively activate the NE↑ to PPn-G, and positive Df stimuli selectively activate the NE↓ to SPPn.

A puzzling subsequent finding, however, was that after lesion of the PPn-G, negative Df stimulation elicited *decreases* of the EOD frequency (Metzner 1993). Either no change or frequency increases were expected (the latter possibly stemming from inhibition of the NE↓ region by the NE↑, which releases the SPPn from inhibition). The frequency lowering responses mentioned above (Takizawa et al. 1999) may shed some light on this paradox. Recent behavioral work showed that pure AMs (no differential phase) elicit frequency decreases, in *Eigenmannia*. Sensory control of the SPPn, therefore, may not be highly selective for the sign of Df. These considerations lead to the hypothesis that some NE↓ neurons may respond somewhat to negative Df stimuli (because of their AM sensitivity). This hypothesis could be tested with intracellular recording and labeling of NE neurons in *Eigenmannia*.

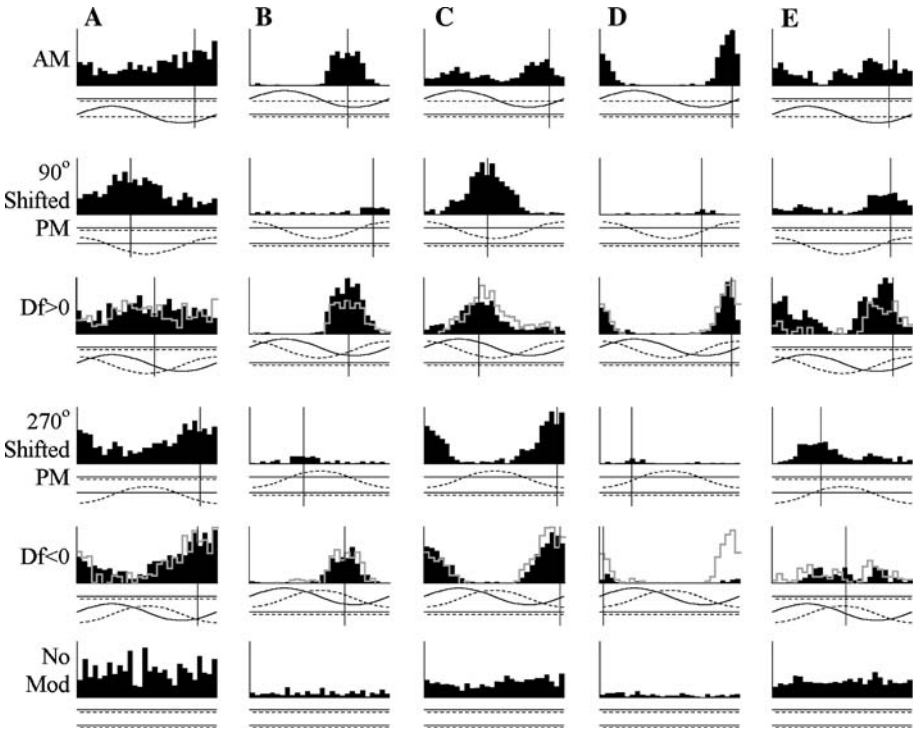

Fig. 5 Responses of toral neurons in *Gymnarchus* to AM and/or PM input. Response histograms are shown in *black*, and the expected linear summation of AM and PM responses for Df > 0 and Df < 0 are shown in *gray*. Two histograms are shown for the PM responses of each unit, one shifted by 90° to align the response with the Df > 0 stimulus and one shifted by 270° to align the response with the Df < 0 stimulus. Note that these two histograms are identical except for their time bases. **a** An E/advance-type unit that showed a linear summation for both signs of Df and is nonselective. **b** An I/delay-type unit that was Df > 0 selective, resulting from facilitation in response to Df > 0, and a linear combination in response to Df < 0. **c** An E/advance-type unit that was Df < 0 selective, resulting from suppression in response to Df > 0, and a linear combination in response to Df < 0. **d** An E/delay-type unit that was Df > 0 selective, resulting from suppression in response to Df > 0, and a linear combination in response to Df > 0. **e** An E/delay-type unit that was Df > 0 selective, resulting from facilitation in response to Df > 0, and suppression in response to Df < 0. *No Mod* No modulation. (From Carlson and Kawasaki 2004)

Summary and future directions

A great deal is now known concerning how temporal aspects of electrosensory signals are represented and processed. Led by elegant behavioral work, these advances have principally come from investigations of the neural control of JAR behaviors and electrolocation; these studies have increased our understanding of temporal processing across time scales ranging from microseconds to seconds. The JAR of *Eigenmannia* is probably the best understood vertebrate behavior at the neural level. Substantial advances have been made on a number of fronts including identifying the sites of fundamental computations, the transformations in representations, and the mechanisms that underlie selectivity to AM rate.

Classic behavioral experiments identified major JAR-related temporal processing tasks of the central electrosensory system (Heiligenberg 1991). The neural implementations of this "sensory algorithm" have largely been identified. These include DPM computations and the integration of AM and DPM information to generate sign selectivity. The "holy grail" of the system, the sign-selective neurons that are on top of the sensory hierarchy for the control of the JAR, remains poorly understood from a mechanistic point of view. Intracellular recordings are needed to elucidate the mechanisms that underlie sign selectivity in *Eigenmannia* and *Gymnarchus*. The selectivity of these neurons to temporal patterns of inputs may be explained by the interaction of PSPs (Carlson and Kawasaki in preparation).

Investigations of sign selectivity have uncovered a few surprises; the "tallying of votes" from the midbrain neuronal democracy results in highly selective units at the top of the hierarchy (Heiligenberg et al. 1978). With regard to reflecting the sign of Df, many neurons in the PPn are as reliable as the behavior itself (Rose et al. 1988). Because there appears to be no logical necessity for such "recognition" (of the sign of Df) units, their existence remains to be explained; perhaps the underlying assumption itself is incorrect. It will be informative to determine if comparable units are present in *Gymnarchus*. Also, mechanistically, we currently have little understanding of the neural basis of the "tallying" process that gives rise to this strong sign selectivity.

Recent behavioral studies have opened new questions regarding the neural control of the JAR. The finding

that AMs alone elicit prominent frequency decreases (in *Eigenmannia*) has shed light on apparently paradoxical results of lesion (PPn) experiments and enabled us to generate more specific hypotheses concerning the stimulus selectivity of neurons in the NE↓ and SPPn regions. Recordings from cells in these areas are needed to test these predictions, as well as fill in details concerning the neural circuit for the control of the JAR. These considerations serve as a reminder of the critical roles that behavioral experiments continue to play in elucidating the neural control of behavior and its evolution.

Finally, a great deal of progress has been made in understanding the mechanisms that underlie the transformations in the coding of temporal information that generate selectivity for particular AM rates. Processes that contribute to AM filtering include passive and active membrane properties, descending control (network) mechanisms, and synaptic plasticity. The net result of these processes is that the codes that represent AM information at the level of the receptors are in a sense inverted to represent the behaviorally relevant information. This inversion uses filtering processes that read bursts of high-frequency firing as low temporal frequency information. While voltage-gated Na^+ channels have been shown to enhance responses to mid-range AM rates, the identity of channels that are responsible for amplifying responses to slow AM rates is still unknown. The long-standing mystery of the function of the multiple maps in the ELL may be best investigated through their roles in AM filtering. It seems likely that processes such as synaptic plasticity have more generalized roles in spatiotemporal processing related to electrolocation (Ramcharitar et al. 2005). In particular, synaptic plasticity may be fundamentally important in generating the time shifts in response maxima required for directional selectivity (Fortune and Rose 2001).

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