Symposium 5

Animal communication: signalling, signal control and signal reception in electrosensory systems

Introduction to Symposium 5
What general lessons have we learned from the study of communication in electric fish?

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The study of electrosensation in fish has yielded a variety of powerful model systems for the exploration of phenomena at various levels, ranging from the behavioral to the cellular and synaptic. Particularly rewarding has been the close integration of behavioral, anatomical, and physiological approaches, and studies at a higher level of integration have generally identified the biological relevance of phenomena to be explored at the next lower level.

Although the number of laboratories involved in the study of electrosensation is comparatively small, their research has been well focused, and the integration of their efforts has driven the neuronal analysis of behavioral phenomena so far that some forms of behavior in electric fish can be considered the most thoroughly studied complex behaviors in vertebrates.

Electrosensory systems offer particular experimental advantages by appearing more transparent and less "cluttered" than more highly evolved systems, such as vision and audition in birds and mammals. Yet, the basic neuronal designs found in electrosensation, appearing old and conservative in the evolutionary sense, are largely the same as those in higher and more derived systems. Most significantly, some behavioral responses of electric fish are so robust that they remain intact in physiological preparations, thus allowing simultaneous studies at the behavioral and cellular level.

The reviews in this section focus on the perception and generation of particular forms and modulations of electric organ discharges that serve in the social communication of electric fish. In some instances, the generation of signals has been analyzed down to the synaptic level and to the identification of transmitters and their receptors, and this study has shown how a seemingly "fixed" network of neurons can be modulated by a variety of inputs to produce very different behavioral outputs. At the perceptual end, the analysis of the coding and processing of certain types of signals has unveiled an almost complete chain of neuronal events, from the receptor to the motor level, including inputs to hypothalamic structures that appear to modulate the fish's motivational and endocrine states in response to the perception of specific social signals.

The following set of brief reviews includes a description of electric signals used in social communication in the genus *Eigenmannia* (Metzner and Heiligenberg), a comparative study of gymnotiform pacemaker nuclei and their modulation by diencephalic and mesencephalic inputs (Kawasaki), a description of the innervation of the electric organ and the generation of the waveform of its discharge in the genus *Gymnotus* (Macadar), a comparative presentation of the motor control of signal generation in mormyrids and gynnotiform fish (Grant), and the plasticity of the electric organ discharge waveform in mormyrids (Landsman and Moller).

Electrocommunication in weakly electric fish: review of signals sent and received

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The alternative strategies of discharging one's weakly electric organ in an either pulsatile or wave-like fashion are reviewed in the Mormyriformes of Africa and the Gymnotiformes of South America. Which types of display of electric organ discharges (EODs) have recently been identified to convey socially relevant information, and what signal parameters are recognized? What do we know about the biological function of these fishes' remarkable sensory capacities (in the context of communication)?

Twenty years ago we used to put the word "electrocommunication" in quotation marks, reflecting a certain uneasiness about the fact that, strictly speaking, there was little formal proof at that time. Today we feel certain about electrocommunication as an especially rich and varied form of communication, with spectacular high-points concerning sensory capacities and information processing in these "lower" aquatic vertebrates (reviews: Hagedorn 1986; Hopkins 1986a, 1988; Kramer 1990a, b, 1993).

Being a pulse or a wave fish does neither appear to be linked to ecology nor to a certain adaptation, but rather depends on phylogeny: all mormyrids (altogether nearly 200 species) are pulse fishes, all sternopygids are wave fishes (and so on). However, it is possible to state several differences between the signal types which might result in advantages or disadvantages for certain types of signalling. For example, pulse EODs have a broad-band amplitude spectrum, with a continuous region of constituent frequencies, while wave EODs have a harmonic amplitude spectrum, composed of discrete spectral lines at octave intervals, and no energy in-between. In contrast to wave EODs, pulse EODs often have a D.C. component; their amplitude tends to be stronger and their discharge rate lower than observed in most wave EODs. The discharge rate of pulse fish is often lower than the discharge frequency of wave fish; in addition, the former tends to be variable while the latter is extremely stable. Pulse fishes seem to follow a time sharing strategy of communication while wave fishes rather use a frequency sharing strategy.

The sequence of inter-discharge time intervals, or discharge rhythm, is of prime importance in the mormyrid communication system. This has been demonstrated by ethological analysis and experiments for several functional contexts: (1) species recognition, (2) agonistic behaviour, (3) specific discharge latency responses, and (4) group cohesion or schooling (Bauer and Kramer 1974; Bell et al. 1974; Russell et al. 1974; Kramer 1974; Kramer and Bauer 1976; Moller 1976; Moller and Serrier 1986; Kramer and Lücker 1990; Kramer and Kuhn, submitted).

An only recent addition to this list is courtship and spawning behaviour (Crawford et al. 1986; Kirschbaum 1987). *Pollimyrus isidori* males and females engage in the same pattern of constant EOD intervals at a repetition rate of below 10 pulses per second (pps) during the most critical stages of courtship and spawning, while the male switches back to more variable patterns of higher mean discharge rate each time the female leaves the male territory. Female visits occur 2-3 times per min for about 15 s each over about 6 h during a spawning night (Bratton and Kramer 1989).

In *P. isidori* there is a high intraspecific variability of EOD waveforms, with statistically significant differences between male and female populations [in spite of considerable overlap (Bratton and Kramer 1988; Crawford 1992)]. In playback experiments this variation was found to be of no importance for a courting male (as measured by its sound production which is probably an advertisement call; Crawford et al. 1986); however, the correct inter-pulse time interval pattern of a female ready to spawn was very important (Crawford 1991). These conclusions are consistent with the observation that females of widely differing EOD waveforms spawned successfully and repeatedly, including females with rather male-like EODs (Bratton and Kramer 1989).

However, EOD waveforms *are* of importance in mormyrids: (1) trained *P. isidori* discriminated playback EOD waveforms as recorded from different individuals even when only slightly different (Graff and Kramer 1989, 1992). Thus a parental, brood-caring male would be able to discriminate between conspecifics individually, for example, the female he is courting and who is ready to spawn on one hand, and potential egg-eaters whom he must attack and drive away on the other. (There may be several batches of eggs in one nest; conspecific females are among the most dangerous egg-eaters.) At the present time there is no good candidate for a sensory mechanism capable of discriminating EOD waveforms of similar duration in mormyrids, except perhaps the one recently proposed in the context of active electrolocation (von der Emde and Bleckmann 1992b) which is based on the demonstration of two functionally different sensory cell types within mormyromast electroreceptor organs (Bell 1990b). (2) The species-characteristic differences in EOD waveform (Hopkins 1981) have been used in systematics and facilitated the discovery of a new species (Crawford and Hopkins 1989); however, the opposite case of two morphs within one species with totally different EOD waveforms has also been observed (Moller and Brown 1990; Kramer and Kuhn, submitted). (3) Intraspecific EOD waveforms markedly different in duration have been reported to underlie mate recognition in *Brienomyrus brachyistius* (Hopkins and Bass 1981). The Knollenorgan electroreceptor pathway is capable of preserving such signal variations as a left/right time difference of afferent impulses at least in the periphery (reviews Hopkins 1986a, 1988; Bell and Szabo 1986); it is, however, unknown whether the necessary central nervous comparison is performed (Bell 1989).

Variations in water conductivity tend to disrupt communication as based on EOD waveform. An abrupt decrease of water conductivity may evoke the failure of the second, head-negative main phase of an EOD (Harder et al. 1964; Bell et al. 1976; Bratton and Kramer 1988). However, at least in two *Campylomormyrus* species the electric organ is capable of impedance matching: after about 2 days in water of the new conductivity the EOD waveform has largely recovered, assuring a degree of independence from environmental constraints (Kramer and Kuhn 1993).

Individual recognition by EOD waveform has recently also been shown in a South American gymnotiform with a pulse discharge, *Gymnotus carapo*. In a resting *G. carapo* with two conspecific neighbours, one on each side of its territory, the playback of an EOD waveform (recorded from one of its two neighbours) from the "wrong" side evoked significantly more attacks compared to the playback of the same EOD waveform from the "correct", "expected" side (McGregor and Westby 1992).

In at least two *Hypopomus* species sexually dimorphic EOD waveforms of the pulse type correspond to differences in gross and fine anatomy of the tails and the electric organ. The second, head-negative phase of male EODs is of longer duration compared to female EODs (Hopkins et al. 1990a). The stimulation with single-cycle, bipolar sinusoids of male duration evoked more courtship signals (the "decrement burst"; Hagedorn 1988) from females than stimulus pulses of female duration (Shumway and Zelick 1988). Currently discussed sensory mechanisms of discrimination include spectral analysis (Shumway and Zelick 1988), but also temporal mechanisms such as EOD duration encoding, or even EOD waveform interference (Hopkins and Westby 1986).

Wave gymnotiforms, such as *Eigenmannia* sp., usually discharge at constant frequency but males display "chirps" (short interruptions preceded and ended by very brief frequency modulations) when courting (Hopkins 1974a; Hagedorn and Heiligenberg 1985). Chirps may be especially conspicuous because of the added feature of a D.C. component which is detectable only during the brief "off" time of the electric organ, stimulating the most sensitive, the ampullary, category of electroreceptors (Metzner and Heiligenberg 1991). Several kinds of frequency modulations without interruptions are known to accompany specific behaviours (review Hagedorn 1986).

One type of frequency modulation *not* accompanying any specific behaviour, and known only from the laboratory, is the Jamming Avoidance Response (JAR) given to a stimulus wave sufficiently close in frequency to a fish's own, by lowering its EOD frequency to a stimulus of slightly higher frequency, and increasing its frequency to a stimulus of lower frequency. The JAR has been known for 30 years now and has usually been seen as a behaviour protecting a fish's active electrolocation system (review Bastian 1986c), by minimising the effect of the "noise" from conspecifics (Heiligenberg 1973; Bastian 1987).

However, adult *Eigenmannia* showed JARs of only one sign, by lowering their EOD frequency to stimuli of slightly higher frequency, and would not raise their EOD frequency to stimuli of slightly lower frequency. The responses of adult males were extremely weak and sometimes could not be detected at all, even at the most effective stimulus frequency and an increased intensity. Adult males seemed more inclined to chirp and attack than to display a JAR. The disconcertingly high variability of the JAR observed in juveniles (which responded in both directions, although not always the "correct" one) is also difficult to reconcile with the electrolocation explanation (Kramer 1987).

A new hypothesis maintains that the JAR may also serve to maximize the effect of another fish's EOD in order to allow for better waveform and frequency estimation of the other fish's EOD by beat analysis of the superimposition signal (Kramer and Otto 1991; see below). Beat analysis by afferent input from P and T electroreceptors (reporting the amplitude of the beat envelope, and the phase modulation of the zero crossings during a beat cycle), allows the fish to determine the frequency difference between its own EOD and the stimulus. This has been worked out in detail over many years, especially by Scheich (1977a, b, c) and Heiligenberg et al. (1978); recent review, Heiligenberg (1991b). Unlike mormyrids (review, Bell 1989) gymnotiforms do not seem to have a (central nervous) efference copy of their EOD command; for an estimation of their own EOD frequency they entirely rely on electrosensory feedback and analysis of the beat pattern (reafference; Heiligenberg et al. 1978).

Eigenmannia is exceedingly sensitive to small frequency variations of a stimulus wave, especially at frequencies close to its own, and rivals the most sensitive mammals (for acoustic frequency discrimination) in this regard (Kawasaki et al. 1988b for the spontaneous JAR; Kramer and Kaunzinger 1991 for trained fish showing conditioned discrimination). However, at exactly its own discharge frequency (and also two times that frequency) *Sternopygus'* absolute sensitivity for a stimulus wave is significantly reduced (Fleishman et al. 1992); this has also been shown in *Eigenmannia* using frequency-clamped stimuli (Kaunzinger and Kramer, in press). This is further proof that beat analysis is involved.

Eigenmannia discriminates the sexually dimorphic EOD waveform of members of its own species by temporal, and not spectral, analysis, as shown by the use of stimulus signals identical in amplitude spectra but not in waveform (because of different phase relationships between harmonics; Kramer 1985; Kramer and Otto 1991; Teubl and Kramer, in press). The sensory basis for the waveform discrimination appears to be a left/right (or front/tail) comparison of the time differences between the zero-crossings of the fish's own EOD, as modulated by the superimposed signal from another fish (the additively and the subtractively generated superimposition signals are contrasted simultaneously, yielding the maximum phase differences possible). This phase modulation of zero-crossings follows a time course resembling the superimposed signal waveform on a greatly expanded time scale, a beat cycle (Kramer and Otto 1991).

The sensory "hardware" to perform this calculation is present in the form of Szabo's rapid electrosensory pathway (Szabo 1967; Szabo and Fessard 1974), leading from the peripheral T-receptors to layer 6 of the *torus semicircularis* in the midbrain where giant and small cells reside. The small cells receive both ipsi- and contralateral input and probably represent the stage of differential phase sensitivity required for the proposed model of temporal waveform discrimination (Carr et al. 1986a, b; review, Carr 1990).

This neural circuit would provide an elegant adaptation to the physics of electrocommunication which, in contrast to auditory communication, offers the advantage of signal wave form (or phase spectrum) not affected by transmission distance nor incident angle (except a simple polarity reversal of the perceived EOD when a fish turns around; Hopkins 1986b). Studies of active space (Squire and Moller 1982; Moller et al. 1989) and mechanisms of electrosensory localization of conspecifics have added important aspects to our knowledge of the electrocommunication system (Davis and Hopkins 1988; Schluger and Hopkins 1987).

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Neuronal coding of communicatory signals in *Eigenmannia*

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In the context of aggression and courtship, *Eigenmannia* repeatedly interrupts its otherwise continuous, nearly sinusoidal electric organ discharges (EODs) (Hopkins 1974b, 1988; Hagedorn and Heiligenberg 1985; Kawasaki et al. 1988a; Metzner and Heiligenberg 1991). At the beginning and at the end of such EOD interruptions, *Eigenmannia* usually also briefly modulates its EOD frequency, which gives these EOD interruptions the acoustic quality of "chirps". In the present paper, however, we will focus only on the neuronal processing of interruptions of the fish's EOD and the terms "chirp" and "EOD interruption" are used interchangeably.

Behavioral studies have demonstrated that females will only spawn after prolonged exposure to sequences of these EOD interruptions, which are usually performed by a courting male in their vicinity (Hagedorn and Heiligenberg 1985; J. Gomez, pers. comm.). This suggests that these signals influence the hormonal state of the sender. Some males also interrupt their own EOD in response to EOD interruptions produced by a neighboring fish.

During EOD interruptions, which may last as long as 2 s, the fish's head-tail voltage remains at the negative base level of the EOD waveform (Fig. 1). Therefore, EOD interruptions contain two components; first, a low-frequency (DC) component which is caused by the shift in the base level of the head-tail voltage and second a high-frequency transient at the beginning and at the end of each EOD interruption (see Fig. 1). These two components stimulate ampullary and tuberous electroreceptors, respectively (Metzner and Heiligenberg 1991).

The base level of the head-tail voltage maintained during the EOD interruption depends on the geometry of the electric field of a chirping fish (Fig. 2). The sender's head voltage remains negative during an EOD interruption (Fig. 2, left fish). For a neighboring fish, which is exposed to these chirps, the base level is negative for the side of the body wall opposite to the chirping fish whereas it is positive for the body side facing the chirping fish (Fig. 2, right fish; stippled).

We identified several elements of a neuronal pathway that are involved in the sensory processing of EOD interruptions and that could ultimately both control the production of EOD interruptions and regulate the hormonal state of the animal. The pathway starts from ampullary and tuberous electroreceptors, passes through the hind- and midbrain, and finally leads through the diencephalon to the vicinity of the pituitary (Metzner and Heiligenberg 1991, 1992; Heiligenberg et al. 1991). Two types of tuberous primary electroreceptive afferents have been identified, P- and T-units (Scheich et al. 1973); P-units code modulations in the amplitude of an EOD-like signal, while T-units encode the timing of the signal's zero-crossings. T-units and their associated central nervous pathways apparently do not participate in the processing of EOD interruptions. P-type tuberous afferents and ampullary afferents, on the other hand, do participate in such processing. Information from these

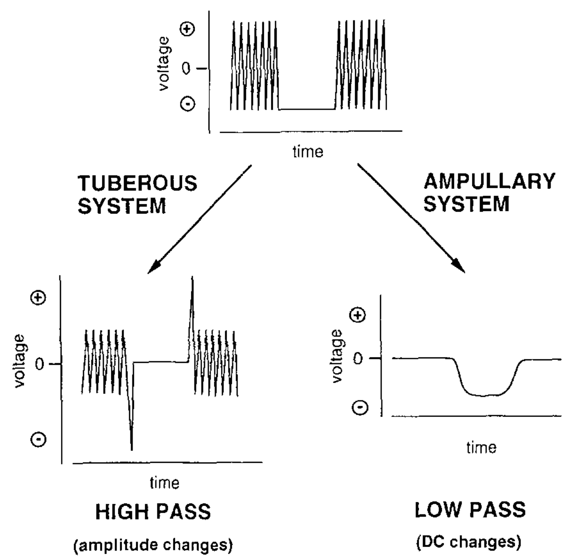

Fig. 1. Schematic drawing of an EOD interruption in *Eigenmannia*. The fish's head-tail voltage remains at the negative base level during the interruption. The tuberous system functions as a high pass filter and processes the high-frequency transients, whereas the ampullary system is driven by the DC component

List of abbreviations

AEN, ascending efferent neuron (anterior electromotor nerve); AIR, abrupt increase in rate; AMPA, α-amino-e-hydroxy-5-methyl-4-isoxalone-propionic acid; CF, cf, constant frequency; ChAT, cholinacetyltransferase; DCN, DCoN, dorsal cochlear nucleus; DGR, dorsal granular ridge; Dlp, posterior portion of dorsolateral region (telencephalon); Dm, dorsomedial region (telencephalon); DML, dorsal molecular layer; DN, dorsal octavolateral nucleus; EAA, excitatory amino acid; EGp, eminentia granularis posterior; ELa, nucleus exterolateralis pars anterior; ELL, ELLL, electrosensory lateral line lobe; ELp, nucleus exterolateralis pars posterior; EMF, electromotor fibre; EO, electric organ; EOD, electric organ discharge; EPSP, excitatory postsynaptic potential; F, frequency; FM, fm, frequency modulated; GABA, gamma-aminobutyric acid; GAD, GABA-amino-decarboxylase; HRP, horseradish peroxidase; IPI, interpulse interval; IPSP, inhibitory postsynaptic potential; ISI, inter-stimulus interval; JAR, Jamming avoidance Response; LED, light emitting diode; LN, linear-nonlinear; MC, Mauthner cell; MD, mediodorsal toral nucleus; MEN, medullary electromotor nucleus; MN, medial octavolateral nucleus; nEAR, nucleus electrosensorius – acousticolateral region; nELL, nucleus of electrosensory lateral line lobe; NMDA, N-methyl-D-aspartate; nMV, nucleus medialis ventralis; OSP, omitted stimulus potential; PD, nucleus praeeminentialis dorsalis; PEN, posterior electromotor nerve; PN, pacemaker neuron; PPn, prepacemaker nucleus; PPn-C, ventrolateral part of PPn; PPn-G, dorsomedial part of PPn; PSP, postsynaptic potential; RN, relay neuron; SPPn, sublemniscal prepacemaker nucleus; ST, stellate cell; T, testosterone; TSF, Tsf, tractus strati fibrosi; TSd, torus semicircularis dorsalis; TSv, torus semicircularis ventralis; VML, ventral molecular layer

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