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Review Article

The neuroethology of electrocommunication: How signal background influences sensory encoding and behaviour in Apteronotus leptorhynchus

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ABSTRACT

Weakly-electric fish are a well-established model system for neuroethological studies on communication and aggression. Sensory encoding of their electric communication signals, as well as behavioural responses to these signals, have been investigated in great detail under laboratory conditions. In the wave-type brown ghost knifefish, *Apteronotus leptorhynchus*, transient increases in the frequency of the generated electric field, called chirps, are particularly well-studied, since they can be readily evoked by stimulating a fish with artificial signals mimicking conspecifics. When two fish interact, both their quasi-sinusoidal electric fields (called electric organ discharge, EOD) superimpose, resulting in a beat, an amplitude modulation at the frequency difference between the two EODs. Although chirps themselves are highly stereotyped signals, the shape of the amplitude modulation resulting from a chirp superimposed on a beat background depends on a number of parameters, such as the beat frequency, modulation depth, and beat phase at which the chirp is emitted. Here we review the influence of these beat parameters on chirp encoding in the three primary stages of the electrosensory pathway: electroreceptor afferents, the hindbrain electrosensory lateral line lobe, and midbrain torus semicircularis. We then examine the role of these parameters, which represent specific features of various social contexts, on the behavioural responses of *A. leptorhynchus*. Some aspects of the behaviour may be explained by the coding properties of early sensory neurons to chirp stimuli. However, the complexity and diversity of behavioural responses to chirps in the context of different background parameters cannot be explained solely on the basis of the sensory responses and thus suggest that critical roles are played by higher processing stages.

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1. Introduction

During social encounters, many animals use communication signals to transmit a variety of information, such as individual identity and motivational state, that is used to dynamically modulate behavioural strategies. Across taxa, signals involving mechanical (including acoustic and vibrational stimuli; Hill, 2009; Kelley and Bass, 2010), visual (Osorio and Vorobyev, 2008), chemical (Stacey et al., 2003; Johansson and Jones, 2007) and electric modalities as well as a mixture of them (Bro-Joergensen, 2010) have been characterized. Responding to these signals appropriately can be crucial for reproductive success, as well as the survival of an individual (Kelley and Bass, 2010). Accordingly, understanding why and how signals are produced has been a central goal in animal ethology.

The accurate detection of communication signals depends crucially on signal encoding by the nervous system which can be limited by internal and external noise (Waser and Brown, 1986; Schmidt et al., 2011). In the auditory and electrosensory systems, communication signals can be produced in the presence of an ongoing background signal that is a consequence of the interaction itself (Zupanc and Maler, 1993; Kelley and Bass, 2010). Different aspects of this background signal, including its frequency and contrast also provide behaviourally relevant information about social context, i.e. the identity and proximity of interacting individuals (Engler and Zupanc, 2001; Bastian et al., 2001; Yu et al., 2012).

To explore both the meaning of communication signals, and the mechanisms by which they are encoded, it is necessary to consider an integrated description of how sensory stimuli, neural responses, and behaviour change during the social interactions. The study of communication also offers a framework for studying the encoding of sensory stimuli, in that encoding principles and stimulus sensitivities can be inferred directly from behavioural experiments. Behavioural adjustments produced in response to conspecific or simulated communication signals provide evidence that the receiving individual has detected the sensory stimuli. A combined analysis of neuronal encoding and behaviour is therefore profitable for both neurophysiology and ethology.

In this review, our goal is to exemplify this neuroethological approach in the context of electrocommunication among the Gymnotiform weakly electric fish *Apteronotus leptorhynchus*. Environmental conditions involving low-light and low electrosensory signal-to-noise ratio set a premium on efficient detection and processing of electrocommunication signals. For decades, studies examining the neurophysiological systems of weakly electric fish have provided insights into how natural behaviours are generated using relatively simple sensorimotor circuits (for recent reviews see: Chacron et al., 2011; Fortune and Chacron, 2011; Marsat et al., 2012). Further, electrocommunication signals are relatively easy to describe, classify and simulate, facilitating quantification and experimental manipulation. Weakly electric fish are therefore an ideal system for examining how communication signals influence sensory scenes, drive sensory system responses, and consequently exert effects on conspecific behaviour.

Electric communication signals can be analyzed by measuring properties of the complex electric field that results from the interaction of nearby fish. In *A. leptorhynchus*, the dipole-like electric field (electric organ discharge, EOD) oscillates in a quasi-sinusoidal fashion at frequencies from 700 to 1100 Hz (Zakon et al., 2002) with males emitting at higher frequencies than females (Meyer et al., 1987). When two fish with different EOD frequencies interact, the combination of their signals results in an amplitude modulation called a "beat"; the beat signal oscillates at the frequency difference between the fish. Beat signals are a direct consequence of social interactions and thus set the background of the electrosensory scene. In addition, through the individual EOD frequencies, information about sex, relative size and individual identities are represented in the beat signal. Physical movements result in slow amplitude modulations of the beat that can encode, among other things, aggressive approach and retreat behaviours (Yu et al., 2012). Electrocommunication signals are produced in these social contexts and thus must be detected amidst the resulting complex background.

One type of electrocommunication signal, the chirp, involves brief amplitude and frequency modulations of the EOD and thus induces transient perturbations of the ongoing beat signal (Zupanc and Maler, 1993). Chirp production in this species is sexually dimorphic: males emit chirps at high rates during agonistic encounters, while females do not. Chirp production is strongly influenced by steroid hormones (e.g. testosterone; Dulka and Maler, 1994; Dunlap, 2002) and neuromodulators (e.g. serotonin; Maler and Ellis, 1987; Smith and Combs, 2008). Recent physiological results suggest that encoding is influenced by serotonin as well (Deemyad et al., 2011).

Behavioural studies have focused on chirping behaviours under diverse conditions: from stimulating a restrained fish with signals mimicking a conspecific (Zupanc and Maler, 1993; Bastian et al., 2001; Engler and Zupanc, 2001) to observing freely-moving fish during social interactions (Dunlap and Larkins-Ford, 2003; Hupé and Lewis, 2008; Triefenbach and Zakon, 2008). The neural encoding of chirps has also been studied at successive stages from electroreceptor afferents (Benda et al., 2005, 2006), through the hindbrain (Marsat et al., 2009; Marsat and Maler, 2010, 2011), and up to the midbrain (Vonderschen and Chacron, 2011), albeit in limited and simplified background contexts. Furthermore, the neural circuitry that controls the production of these signals is well known (Zupanc, 2002).

We here focus on how context-dependent properties of the beat signal influence the neural encoding of chirps and correlate with chirp production and aggression responses to chirp stimuli. We begin with a description of the different beat perturbations that are generated by the interplay of chirps with the different background