Network Dynamics and Information Transfer of Natural Stimuli in Electric Fish.

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Abstract

The neural architecture and spatiotemporal tuning of sensory systems are optimized to code naturalistic environments. Weakly electric fish use an electric sense to navigate their surroundings, hunt prey, and communicate with other fish. We show that electrosensory feedback dynamics support distinct network behavior in response to distinct natural stimuli. In addition, the receptive field structure optimizes information transfer when the spatiotemporal signatures of inputs match naturalistic stimuli. Thus, we give a concrete example of a neural system that uses coding strategies, which are appropriate for stimuli ensembles that they routinely code.

Summary

All sensory systems code a wide collection of signals. These systems often code inputs that are distinct in both their spatiotemporal characterization and behavioral relevance. How sensory system neural architecture and cellular dynamics interact with natural environments and allow for such diversity in coding is now a key question in

sensory neuroscience. Specific advances have been made in insect olfaction (Laurent 1996), mammalian vision (Sillito et al., 1994), and auditory systems (Carr and Konishi, 1990). Nevertheless, connections between natural inputs and the sensory brain are in general poorly understood. Weakly electric fish offer an ideal model system in which to study the relations between neural network dynamics, coding, and naturalistic sensory inputs (Heiligenberg, 1990).

Electric fish emit a low intensity and high frequency electric field from an organ in their hindquarters. Nearby objects and other fish modulate the amplitude of this field and cast an effective electric "image" on the skin of the animal. Electroreceptors that are sensitive to field modulations accurately code these images and transfer sensory information to higher processing centers. Two inputs are especially relevant for these animals. Weakly electric fish prey on small water insects that cast a low frequency and spatially compact electric image (Nelson and MacIver, 1999). This is to be contrasted with communication signals from conspecifics that can be quite high frequency and spatially extent inputs (Zupanc and Maler, 1993). Thus, prey and communication signals offer two relevant inputs that are dichotomous in their spatiotemporal distribution and quite easy to reproduce in laboratory conditions – ideal for comparative studies in natural stimuli.

Electroreceptor afferents project to a layer of pyramidal cells in the electrolateral line lobe (ELL). These pyramidal cells project to higher brain centers which process and subsequently project their inputs back to the ELL along several well-defined feedback loops (Berman and Maler, 1999). Thus ELL pyramidal cells interact via closed loop feedback connectivity often with appreciable axonal transmission delays. This layered

processing structure with easily manipulated feedback projections makes the ELL ideal for the study of feedback in sensory processing.

We experimentally mimic prey signals, background scenes, and communication stimuli and present them to awake fish. *In vivo* recordings of ELL pyramidal cell spike trains have near Poissonian statistics in response to prey and background stimuli. This is in marked contrast to non-Poissionian oscillatory spike-train discharge from the same cells in response to communication stimuli. Thus a single pyramidal neuron can give distinct stereotyped responses to distinct, yet naturalistic stimuli. The biophysical mechanisms that underlie this basic distinction process and their relations to the spatiotemporal signature of naturalistic stimuli are prime motivations for our research.

To explore these results we use a simple neural network model of electrosensory processing. The model neurons have only minimal neuron dynamics (leaky integrate-and-fire), yet the connectivity is all to all delayed inhibition. The model adequately reproduces the experimental observations with oscillatory discharge being reserved for communication-like inputs. Analysis of this model shows that the oscillatory dynamics emerge from the delayed nature of the feedback connectivity. This prediction is confirmed via a temporary blockade of descending feedback to the ELL that results in the loss of pyramidal cell oscillatory activity in the presence of communication stimuli.

Delayed interactions have long been known to give rise to oscillatory behavior in biological, physical, and chemical systems (Glass and Mackey, 1988). However, the selectivity of delay-induced oscillations to a specific input is a novel result. One key difference between these two stimuli categories is that prey and background stimuli are spatially uncorrelated inputs whereas communication stimuli are spatially correlated over

the entire sensory field. Using a linear response approximation we derive an analytic expression for the power spectra of a single spike train as a function of the spatial correlation of an applied input. The spatial correlation is shown to simply set the strength of oscillatory behavior that is determined by the single cell properties and the delayed coupling. Furthermore, the oscillation is a resonant phenomena dependent on a high frequency component of the signal. The combination of all of these results explain how the spatially correlated and high frequency communication stimuli elicit a stereotyped response in electrosensory networks.

Finally, we study the information transferred by ELL pyramidal cells about prey and communication type inputs. The receptive field structure, specifically the non-classical surround, is such that for inputs with prey-like spatial dimensions the frequency content must be low in order to maximize information transfer. This is in direct contrast to when stimuli have communication-like spatial dimensions the information transfer is maximized when the frequency content is high. This spatially dependent pyramidal cell tuning is ideal for environments with low frequency prey inputs and high frequency communication calls, as is the case for weakly electric fish.

In conclusion, we have begun to establish how delayed feedback and receptive field organization in electrosensory processing are such that the electric sense can distinguish and efficiently transmit information about a variety of distinct natural inputs. Since feedback pathways and receptive fields are core components of many sensory systems it is then likely that our results extend to other forms of sensory coding. The work summarized here has appeared in several publications and unpublished works (Doiron et al., 2003, 2004; Chacron et al., 2003).

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