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Neurocomputing 69 (2006) 1070–1075
NEUROCOMPUTING
www.elsevier.com/locate/neucom

Altered sensory filtering and coding properties by synaptic dynamics in the electric sense

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Available online 13 February 2006

Abstract

This modeling study examines the short-term synaptic plasticity properties of the electrosensory lateral lobe (ELL) afferent pathway in the weakly electric fish, *Apteronotus leptorhynchus*. We studied the possible functional consequences of a simple phenomenological model of synaptic depression by taking into consideration the available in vivo and in vitro results [N. Berman, L. Maler, Inhibition evoked from primary afferents in the electrosensory lateral line lobe of the weakly electric fish (*Apteronotus leptorhynchus*), J. Neurophysiol. 80(6) (1998) 3173–3196; M.J. Chacron, B. Doiron, L. Maler, A. Longtin, J. Bastian, Non-classical receptive field mediates switch in a sensory neuron's frequency tuning, Nature 26(424) (2003) 1018–1022]. Filtering and coding properties were examined. We find that simple short-term phenomenological synaptic depression can change steady-state filtering properties and explain how the known physiological constraints influence the coding capabilities of the ELL pyramidal cells via dynamic synaptic transmission.

Keywords: Short-term synaptic dynamics; Neural coding; Neural filtering; Synaptic depression; Electric fish; Electroreception; ELL

1. Introduction

The objective of this research is to understand the synaptic plasticity properties between the primary electrosensory afferents and sensory pyramidal cells in the afferent pathway of the weakly electric fish. Pyramidal cells in the electrosensory lateral lobe (ELL) receive multiple convergent mono-synaptic excitatory and di-synaptic inhibitory inputs from the primary electrosensory afferents (P units). These afferents carry information about the amplitude modulated quasi-sinusoidal electric organ discharge (EOD) and are able to transmit signals with high fidelity over frequencies ranging from low to very high values [1]. Here, we studied the effect of short-term synaptic plasticity on coding and filtering of time varying signals. In vitro studies from the ELL have demonstrated that these P-unit synapses show both short-term facilitation and depression; the biophysical substrates of this plasticity are unknown and it is possible that the depressive component involves postsynaptic inhibition as well as mechanisms intrinsic to the synapses [2]. We focus here on the depressive component since, over longer time scales, it predominates over facilitation. We employed computational models incorporating the key known physiological properties of the synapse and the postsynaptic pyramidal cells. Our strategy was to constrain the P-unit-to-pyramidal cell synaptic properties based on in vitro data from electric fish [2] as well as on the time constants of synaptic depression in similar auditory brainstem systems [6,13]. We then quantitatively varied the synaptic time constants to determine what dynamics could support the frequency filtering seen in vivo.

2. Methods: mathematical model

A modulated Poisson process is given as an input to a pyramidal cell model with synaptic depression. This input

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doi:10.1016/j.neucom.2005.12.048

is meant to mimic the signal received from the electroreceptor afferents, which encodes amplitude modulations of the EOD. Two sets of simulations were performed. In order to study filtering properties, sinusoidally modulated (SAM) Poisson inputs were generated. In these simulations, we changed the sinusoidal modulation frequency of the mean rate parameter of the Poisson input. Secondly, we designed simulations with the aim of determining coding properties. For these purposes low-pass filtered Gaussian noise was used as a time-dependent rate parameter for Poisson spike generation. In both cases, these input spike trains drove a leaky integrate-and-fire neuron (LIF) via a phenomenological synaptic depression model. Computer simulations were performed on a laptop (Clevo 5620D 2 GHz Pentium-IV), using Fortran-77 language on a Debian Linux (kernel version 2.0.34) platform. For the computation of filtering and coding properties, we used MatLab 6.5 software running under Windows-XP platform on the same machine. The Euler integration method was used with an integration time step of 0.025 ms.

2.1. Poisson input modulated by sinusoids and by low-pass filtered Gaussian noise

The mean rate parameter λ of the Poisson input was modulated according to:

$$\lambda(t) = A + M\sin(2\pi f t), \tag{1}$$

where M is the modulation depth, f is the modulation frequency, and A is an additive constant term (which determines the mean rate without SAM). We looked at the effect of varying f in order to approximate the frequency filtering properties of the synaptic dynamics. Bode plots (gain-vs-frequency) for SAM Poisson input were computed from the steady-state responses of the system.

To examine the coding properties of our model, low-pass filtered Gaussian noise was generated and then we considered a doubly stochastic Poisson process, where the rate of occurrence $\lambda(t)$ was the low-pass filtered Gaussian noise. We constructed this process in order to mimic the physiologically plausible environmental input of the ELL pyramidal cells. Gaussian white noise was generated by using the Box–Muller algorithm and we have used a fourth order filter to low-pass filter the noise. The cutoff angular frequency was chosen to be 120 Hz because this (0–120 Hz) regime corresponds well with the environmentally plausible AM modulation range of the EOD. The low-pass filtered noise was multiplied by a scalar ($q = 0.125$) in order to adjust the physiologically realistic presynaptic input rate.

2.2. Synaptic depression model

The model of synaptic depression used in our study has been described in [5]. The variable D denotes the recovery from synaptic depression. Between input spikes, it evolves according to the following equation:

$$\frac{dD}{dt} = \frac{1-D}{\tau_d}. \tag{2}$$

The G variable is the synaptic conductance, which is governed by

$$\frac{dG}{dt} = \frac{-G}{\tau_g}. \tag{3}$$

At every incoming spike in the modulated Poisson input, the depression variable is updated as $D \to Dd$ where d is a constant factor. Likewise, the synaptic conductance G gets updated according to $G \to G + Dg$ where g is a constant factor. In our simulations we used $d = 0.3$ and $g = 0.2$.

2.3. Leaky integrate and fire neuron

The leaky integrate and fire model is described by the following equation:

$$\frac{dV}{dt} = \frac{-V}{\tau_m} + \frac{I_{syn}}{C} + \frac{I_{inj}}{C}, \tag{4}$$

$$I_{syn} = g_{max} G(V - E_{syn}), \tag{5}$$

where V is the membrane potential, τ_m is the membrane time constant and C is the membrane capacitance. When V reaches threshold we reset the membrane to V_{reset}. The following parameters are used: $\tau_m = 10$ ms, $E_{syn} = 0$ mV, $C = 1$ nF, $V_{reset} = -80$ mV, $V_{thres} = -55$ mV, $g_{max} = 0.2$, $A = 0.2$, $M = 0.2$. For the firing rate drop compensation, the following DC currents were used: ($I_{inj} = 0.25, 0.57, 0.805, 1.14, 1.37$) for ($\tau_g = 20, 17.5, 15, 12.5, 10$ ms), and ($I_{inj} = 1.05, 0.95, 0.805, 0.65, 0.5$) for ($\tau_d = 20, 17.5, 15, 12.5, 10$ ms), respectively.

We performed two sets of simulations. (A): We let the firing rate change as we altered the synaptic dynamics parameters. In these simulations I_{inj} was zero; unless the synaptic (noisy) input is present, the LIF neuron does not fire. (B): The LIF firing rate was kept constant (72 Hz) by adjusting the values of bias current (I_{inj}) while changing the synaptic depression parameters. This allowed us to follow the changes in coding properties without the effect of the firing rate drop [11].

3. Model performance analysis

3.1. Quantification of filtering properties

In order to study filtering properties, SAM Poisson input drives the synapses and the postsynaptic LIF neuron according to the equations described in the previous section. In all of the simulations where we studied the filtering properties, we used the A-type simulations (see Methods) where the input injected current I_{inj} was set to zero. For each modulation frequency, we numerically constructed the rate histogram from the LIF spike train outputs, and compared its modulation to that of the input