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The neuronal response at extended timescales: a linearized spiking input-output relation

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Abstract

Many biological systems are modulated by unknown slow processes. This can severely hinder analysis - especially in excitable neurons, which are highly non-linear and stochastic systems. We show the analysis simplifies considerably if the input matches the sparse "spiky" nature of the output. In this case, a linearized spiking Input-Output (I/O) relation can be derived semi-analytically, relating input spike trains to output spikes based on known biophysical properties. Using this I/O relation we obtain closed-form expressions for all second order statistics (input - internal state - output correlations and spectra), construct optimal linear estimators for the neuronal response and internal state and perform parameter identification. These results are guaranteed to hold, for a general stochastic biophysical neuron model, with only a few assumptions (mainly, timescale separation). We numerically test the resulting expressions for various models, and show that they hold well, even in cases where our assumptions fail to hold. In a companion paper we demonstrate how this approach enables us to fit a biophysical neuron model so it reproduces experimentally observed temporal firing statistics on days-long experiments.

1 Introduction

Neurons are modeled biophysically using Conductance-Based Models (CBMs). In CBMs, the membrane time constant and the timescales of fast channel kinetics determine the timescale of Action Potential (AP) generation in the neuron. These are typically around $1-20\,$msec. However, there are various modulating processes that affect the response on slower timescales. Many types of ion channels exist, and some change with a timescale as slow as $10\,$sec [1]. Additional new sub-cellular kinetic processes are being discovered at an explosive rate [3, 43, 11]. This variety is particularly large for very slow processes [33].

Generally, current CBMs can be considered as strictly accurate only below a certain timescale, since they do not incorporate most of these slow processes. A main reason for this "neglect" is that such slow processes are not well characterized. This is especially problematic since neurons are excitable, so their dynamics is far from equilibrium,