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A benchmark test for a quantitative assessment of simple neuron models

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Abstract

Several methods and algorithms have recently been proposed that allow for the systematic evaluation of simple neuron models from intracellular or extracellular recordings. Models built in this way generate good quantitative predictions of the future activity of neurons under temporally structured current injection. It is, however, difficult to compare the advantages of various models and algorithms since each model is designed for a different set of data. Here, we report about one of the first attempts to establish a benchmark test that permits a systematic comparison of methods and performances in predicting the activity of rat cortical pyramidal neurons. We present early submissions to the benchmark test and discuss implications for the design of future tests and simple neurons models.

Keywords: Spike timing prediction; Integrate-and-Fire model; Spike Response Model; Benchmark test

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1. Introduction

Neurons communicate by generating action potentials that are transmitted to other neurons in the network. Action potentials are generated in response to transmembrane currents elicited by presynaptic activation of various receptor types. Despite years of research, the exact nature of the neural code, that is how presynaptic activity is processed and encoded in outgoing action potentials, is still unknown. Is the neuronal firing rate sufficient to describe neural activity or does the timing of spikes on a millisecond timescale matter as well? Following the seminal work of Hodgkin and Huxley (1952), a lot of effort has been spent to build and study biophysically detailed models of single neuron electrical activity. These models can reproduce a large variety of neuronal behaviors as observed in experiments by a suitable combination of different ion currents (Bower and Beeman, 1995). However, only few studies have focused on the methodology of designing algorithms for automatic fitting of such models to data, so as to arrive at models with a quantitative predictive power (Druckmann et al., 2007; Huys et al., 2006; Markram, 2006; Prinz et al., 2003, 2004).

In contrast to detailed Hodgkin–Huxley models, very simple models only have a small number of parameters which can be automatically and easily extracted from electrophysiological recordings. As early as the 1970s and 1980s, neuroscientists have tried to develop methods for the evaluation of simple neuron models from neural data. Brillinger and Segundo, in particular, have used maximum-likelihood and optimal filtering techniques to evaluate the linear response curve and firing probability of neuronal membranes thus laying down the foundations for more modern approaches (Brillinger, 1988a,b; Brillinger and Segundo, 1979). More recently, different groups tried to extract not only parameters of interest from data but also to build neuron models with a true quantitative predictive power. More specifically, Rauch, La Camera and colleagues have demonstrated that the output frequency of cortical pyramidal neurons and interneurons recorded in vitro can be fitted by integrate-and-fire neurons (La Camera et al., 2004; Rauch et al., 2003). Beyond the output

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firing rate, Keat et al. have shown that the precise spike time of neurons recorded extracellularly in the visual pathway can be predicted almost exactly with a very simple model neuron (Keat et al., 2001). Similar results have been obtained on retinal ganglion cells by Pillow et al. (2005). Several techniques have been successfully applied to predict the membrane voltage and spike timing of cortical pyramidal neurons recorded intracellularly in vitro (Clopath et al., 2007; Jolivet et al., 2006; Paninski et al., 2005) and in vivo (Lansky et al., 2006). Finally, alternative methods have been proposed that still wait to be tested on experimental recordings (Jolivet and Gerstner, 2004; Kobayashi and Shinomoto, 2007).

While simple models can, at least qualitatively, reproduce a broad range of observed neuronal behaviors (Izhikevich, 2004), their simplicity also permits to mathematically analyze questions of neural coding (Arcas et al., 2003; Brunel et al., 2003; Keat et al., 2001; Pillow et al., 2005). Developing efficient simple models with quantitative predictive power is also of importance for implementation in neural prostheses where such models could be simulated at low cost or built in silico [see e.g. (Marmarelis and Berger, 2005; Song et al., 2007)].

Despite this intense activity, the community still lacks a benchmark test that could be used as a reference to compare cost and performances of different methods. Here, we describe such a benchmark test and report the first results from an international competition[1]. In short, the goal is to predict the spike times of a layer-5 pyramidal neuron recorded from the rat somatosensory cortex under current injection in various discharge regimes. A first set of spike trains was made publicly available together with the corresponding stimuli for model evaluation. Participants had to predict the spike times with a precision of ±2 ms for a different dataset for which only the stimuli were provided. Note that this initiative differs from the recent *Neural Prediction Challenge*[2] in the sense that the goal is to design a model that predicts spike times in response to a fluctuating current while the goal in the *Neural Prediction Challenge* is to design a model that predicts the responses of neurons to "natural" sensory stimuli in vivo. The benchmark test is described in the next section. A summary of results and submissions is then presented in section 3 and discussed in the last section.

2. Methods

2.1. Electrophysiological recordings

Data used for the challenge have been extensively described in Refs. (Jolivet et al., 2006; La Camera et al., 2006; Rauch et al., 2003) and we refer interested readers to these publications for details of the experimental protocol. In short, parasagittal slices of rat somatosensory cortex (300 μm thick) were prepared from 15- to 40-day-old female and male Wistar rats according to the institutional guidelines. We recorded in current-clamp whole cell configuration from the soma of layer 5 regular spiking pyramidal cells (McCormick et al., 1985). Four cells were recorded and trial repetitions of the input were performed ($N = 4$ repetitions). The input was generated with an Ornstein–Uhlenbeck process (Tuckwell, 1988). The total injected current $I(t)$ is given by

$$I(t+\mathrm{d}t) = I(t) - \frac{I(t)}{\tau_I}\mathrm{d}t + m_I\,\mathrm{d}t + s_I\xi(t)\sqrt{\mathrm{d}t} \qquad (1)$$

where m_I and s_I are parameters and $\xi(t)$ is a zero-mean, unit-variance Gaussian random variable, updated at every time step. The process was generated and injected at a rate of 5 kHz ($\mathrm{d}t = 0.2$ ms) and the correlation length τ_I was 1 ms. The resulting current $I(t)$ has a stationary Gaussian distribution with mean $\mu_I = m_I\tau_I$ and variance $\sigma_I^2 = s_I^2\tau_I/2$ (Cox and Miller, 1965). μ_I and σ_I were varied as follows: the total range $0 < \mu_I < 650$ pA and $0 < \sigma_I < 350$ pA was discretized and then explored in random order to prevent correlations over time. The duration of the stimulation was 6.8 s long for each pair of parameters μ_I, σ_I. The intervals between successive stimulations were 50–60 s long.

2.2. Measuring the similarity between two spike trains

In order to measure the similarity or dissimilarity between two spike trains and assess the quality of the predictions of simple models, we need a measure to compare spike trains as predicted by the model to spike trains as generated by the original cell. One possibility consists of comparing output firing rates (Hansel and Mato, 2003; Rauch et al., 2003). This is a very effective method but it misses all temporal structure in spike trains. Several measures exist that go beyond firing rates and consider precise firing times. Some measures are based on binning of the spike trains (Geisler et al., 1991; Kistler et al., 1997; MacLeod et al., 1998) or on cost functions (Aronov and Victor, 2004; van Rossum, 2001; Victor and Purpura, 1997, 1996). In precedent reports, some of us have consistently used the *coincidence factor* Γ as defined in Refs. (Clopath et al., 2007; Jolivet and Gerstner, 2004; Jolivet et al., 2004, 2006; Kistler et al., 1997). The coincidence factor can be computed quickly and easily. It is written

$$\Gamma_k = \frac{N_{\mathrm{coinc}} - \langle N_{\mathrm{coinc}}\rangle}{1/2(N_{\mathrm{data}}^k + N_{\mathrm{model}})}\frac{1}{N} \qquad (2)$$

where N_{data}^k is the number of spikes in the kth reference spike train S_{data}, N_{model} is the number of spikes in the predicted spike train S_{model} that is compared with the reference spike train, N_{coinc} is the number of coincidences with precision Δ between the two spike trains, and $\langle N_{\mathrm{coinc}}\rangle = 2f\Delta N_{\mathrm{data}}^k$ is the expected number of coincidences generated by a homogeneous Poisson process with the same rate f as the spike train S_{model}. The factor $N = [1 - 2f\Delta]$ normalizes Γ to a maximum value of one which is reached if and only if the spike train of the model reproduces exactly that of the cell. A homogeneous Poisson process with the same number of spikes as the minimal model would yield $\Gamma = 0$, which is, therefore, the chance level.

The sole free parameter in the estimation of Γ is the coincidence window $\pm\Delta$. Γ is relatively independent of the exact

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[1] http://icwww.epfl.ch/QuantNeuronMod2007/.

[2] http://neuralprediction.berkeley.edu/.