

Event-based simulation strategy for conductance-based synaptic interactions and plasticity

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Abstract

The immense computational and adaptive power of the cerebral cortex emerges from the collective dynamics of large populations of interacting neurons. Thus, for theoretical investigations, optimal strategies for modeling biophysically faithful neuronal dynamics are required. Here, we propose an extension of the classical leaky integrate-and-fire neuronal model, the gIF model. It incorporates various aspects of high-conductance state dynamics typically seen in cortical neurons *in vivo*, as well as activity-dependent modulation of synaptic weights. The analytic description of the resulting neuronal models allows their use together with the *event-driven* simulation strategy. The latter provides an efficient tool for exact simulations of large-scale neuronal networks.

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1. Introduction

Although electrophysiological and neuroimaging techniques allowed huge advances in characterizing neural activity *in vivo* at the network level [11], these methods are subject to stringent constraints concerning their spatio-temporal resolution. Modeling approaches remain one of the main paths to assess the collective dynamics of large populations of neurons on arbitrary spatio-temporal scales [5]. However, computer simulations of very large neuronal populations still go beyond the limits set by available conventional computational hardware. The reason for this limit is that biophysical models of neurons are usually described by systems of coupled differential equations which can be solved numerically only by discretization of space and time (*clock-driven* methods). In this case, the algorithmic complexity and computational load scale linearly with the spatio-temporal resolution. Moreover, the restriction to a fixed time-grid has an impact on the precision of the simulation [3], which might turn out to be

crucial for models with spike-timing depending plasticity (STDP).

Recently, a new and more efficient approach was proposed [9], in which the computational complexity scales linearly with the number of neuronal units, independent on the temporal resolution. This *event-driven* simulation strategy makes use of the fact that synaptic events occur rather isolated, causing neurons to spend most of the time dynamically decoupled from the network. The most efficient implementation of this strategy is achieved if membrane equations are analytically solvable. Simulations of realistic network states must take into account the high-conductance state of cellular membranes typically seen *in vivo* [1], but such neuronal models are usually not analytically solvable. We present here analytic extensions of the classical leaky integrate-and-fire (LIF) model, the gIF models, which incorporate various aspects of the high-conductance state dynamics seen in cortical neurons *in vivo*. The analytic form of these extensions allows the application of event-driven simulation strategies, therefore providing the basis for efficient and exact simulations of large-scale networks with realistic synaptic interactions.

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2. Integrate-and-fire neuron models with high-conductance state dynamics

In what follows, we restrict to the simplest LIF neuron model [7], for which the evolution of the state variable $m(t)$ is described by the explicitly solvable first-order differential equation (τ_m denotes the membrane time constant)

$$\tau_m \frac{dm(t)}{dt} + m(t) = 0. \quad (1)$$

Upon arrival of a synaptic input at time t_0 , $m(t)$ is instantaneously updated by Δm , after which it decays exponentially with τ_m until the arrival of a new synaptic input. If $m(t)$ crosses a threshold value m_{thres} , the cell fires and is reset to its resting value m_{reset} , at which it stays for a refractory period.

In real neurons, the effect of synaptic inputs can be described by transient changes in the conductance of the postsynaptic membrane (Fig. 1A, top). Here, the synaptic conductance component $G_s(t)$ adds to a constant leak conductance G_L (for simplicity, the contribution of active membrane conductances will not be considered here), yielding a time-dependent total membrane conductance $G_m(t)$ which shapes the post-synaptic potentials (PSPs) and, hence, the response of the cellular membrane to subsequent synaptic inputs.

In the case of an exponential synapse, $G_s(t)$ increases by a fixed amount ΔG_s upon arrival of a synaptic event, after which it decays with time constant τ_s . The most straightforward consequence of this transient change in G_m is a change in the effective membrane time constant $\tau_m(t)$ (Fig. 1A, middle). At time t after arrival of a synaptic event, the actual value of $\tau_m(t)$ is given by

$$\frac{1}{\tau_m(t)} = \frac{1}{\tau_m^0} + \frac{1}{\tau_m^s(t_0)} e^{-(t-t_0)/\tau_s}, \quad (2)$$

where $\tau_m^s(t)$ and τ_m^0 denote the synaptic and leak component of the membrane time constant, respectively. This time-dependent membrane time constant generalizes earlier notions which specifically focused on capturing the effect of active membrane conductances after generation of spikes [6].

Replacing τ_m in Eq. (1) by the time-dependent $\tau_m(t)$ given in Eq. (2), we obtain the defining state equation for the gIF neuron model, which incorporates the effect of synaptic conductances and can be solved analytically, yielding

$$m(t) = m(t_0) \exp \left[-\frac{t-t_0}{\tau_m^0} - \frac{\tau_e(1 - e^{-(t-t_0)/\tau_e})}{\tau_m^e(t_0)} - \frac{\tau_i(1 - e^{-(t-t_0)/\tau_i})}{\tau_m^i(t_0)} \right]. \quad (3)$$

Here, $\tau_m^e(t_0)$ and $\tau_m^i(t_0)$ denote the excitatory and inhibitory synaptic contributions to the membrane time constant at time t_0 , as well as τ_e and τ_i the decay time constants for excitatory and inhibitory conductances, respectively. In contrast to the classical LIF neuron model, in the gIF

model the state variable $m(t)$ (Fig. 1A, bottom) decays with an effective time constant which depends on the synaptic activity.

The response behavior of the gIF model was compared with that of the LIF model as well as of a biophysically detailed model of a cortical neuron in a broad range of driving synaptic inputs. First, the statistical investigation of the spontaneous discharge activity with respect to output rate ν_{out} and irregularity (quantified by the coefficient of variation C_V) for corresponding synaptic input parameters showed that the gIF models were much closer to the biophysical model than the LIF neuron models (Fig. 1B). Second, due to the explicit incorporation of high-conductance state dynamics, the gIF neuron model showed a temporal resolution of synaptic inputs which was comparable to that seen in the more realistic biophysical model. Finally, due to the state-dependent dynamics of the gIF models, aspects of gain modulation seen in the biophysical model were much better captured by the gIF models than the LIF neuron model. This gain in biophysical realism was paralleled by only a marginal increase in computational load (Fig. 2A).

The gIF neuron model defined by Eq. (3) was extended to incorporate both the effect of the actual membrane time constant on the PSP amplitude, as well as the effect of the distance of the actual membrane state to the corresponding synaptic reversal states. In all cases, the defining state equations provide either exact solutions or simple approximations which yield excellent descriptions of neuronal behavior in states of intense synaptic background activity (details can be found in Rudolph & Destexhe, submitted for publication).

3. Models of STDP for use in event-driven simulations

To endow networks of spiking neurons with self-organizing capabilities, we incorporated various models of STDP and short-term synaptic dynamics into the gIF neuronal models. In the simplest version, long-term modification of the efficacy of excitatory synaptic terminals was modeled based on the temporal difference between pre- and post-synaptic event pairs [10]. Here, upon arrival of a synaptic input at time t_{pre} and the nearest postsynaptic spike at time t_{post} , synaptic weights are changed according to $g \rightarrow g + F(\Delta t) g_{\text{max}}$, where $F(\Delta t) = \pm A_{\pm} \exp\{\pm \Delta t / \tau_{\pm}\}$ for $\Delta t = t_{\text{pre}} - t_{\text{post}} < 0$ and $\Delta t \geq 0$, respectively (Fig. 2B, inset). A_{\pm} quantify the maximal change of synaptic efficacy, whereas τ_{\pm} determine the range of pre- to postsynaptic spike intervals in which synaptic weight changes occur.

The implemented models were tested with respect to long-term synaptic weight changes (simulated neural activity was 10,000 s) for a broad range of synaptic input drive, and reproduced the results reported in the literature, such as the convergence to a bimodal weight distribution for the STDP model of Song and Abbott [10] (Fig. 2B). We also considered other models of synaptic dynamics, such as

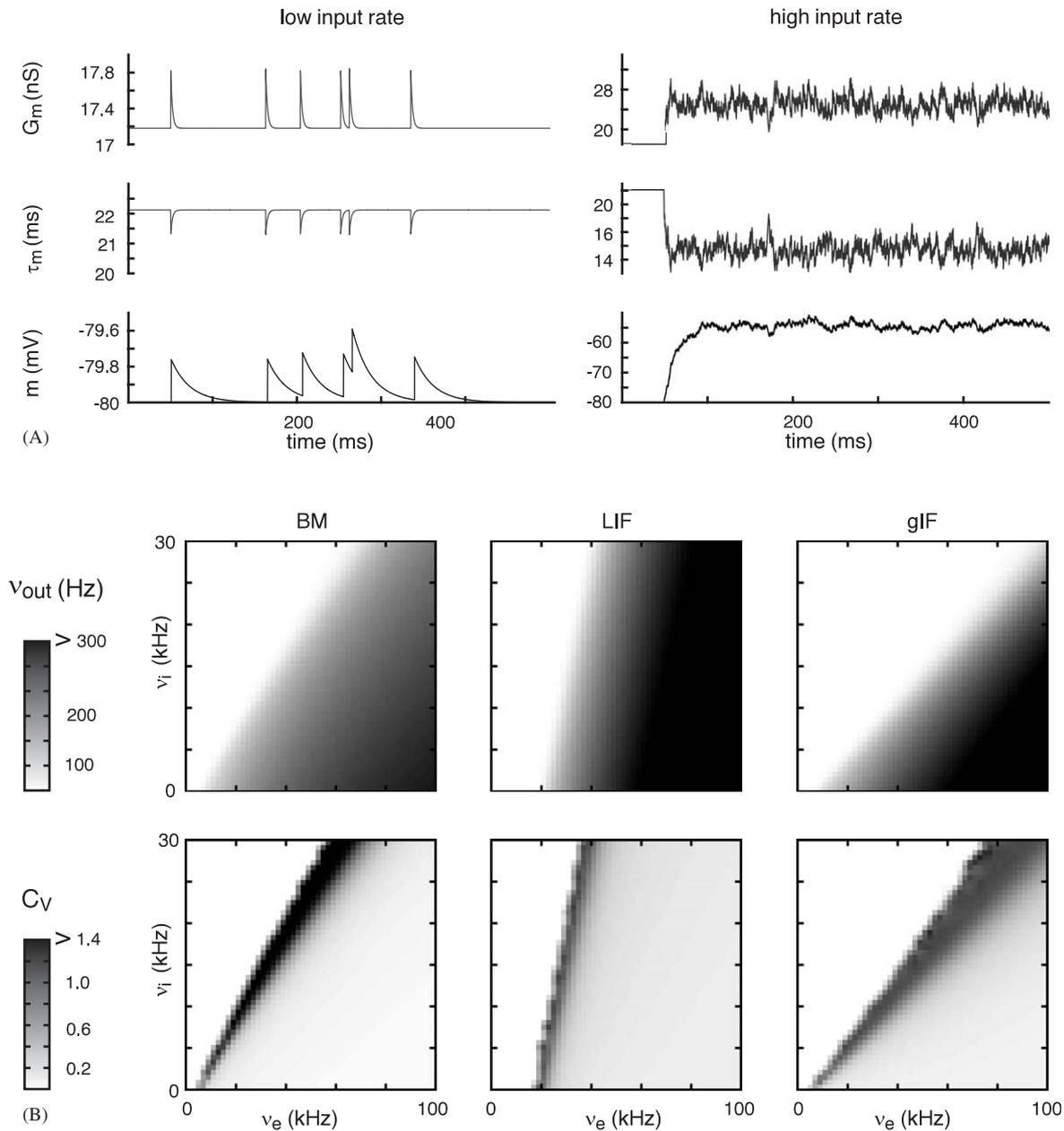


Fig. 1. Membrane dynamics in the presence of synaptic inputs. (A) Synaptic inputs cause transient changes in the total membrane conductance G_m , which translate into changes of the actual membrane time constant τ_m and determine the time-course of the membrane state m . (B) Comparison of the discharge rate v_{out} and coefficient of variation C_V as function of excitatory and inhibitory input rates v_e and v_i , respectively, for a detailed biophysical model (BM) with Hodgkin–Huxley spike generation and 2-state kinetic models for synapses, the LIF and gIF neural models.

the model of frequency-dependent dynamic synapses by Markram et al. [8], or the STDP model of Froemke and Dan [2] incorporating spike triplet interactions. In all cases, we observed no significant increase in the computational load for comparable network size and connectivity. In the computationally most expensive model, about 10^6 events can be modeled in real-time without specific optimization of the simulation code using NEURON [4] on a 3 GHz Pentium 4 processor running under the Linux operating system. Scripts for the gIF neuron models are available at <http://cns.iaf.cnrs-gif.fr/>.

4. Discussion

Here we presented an extension of the classical LIF neuron model by incorporating conductance-based synaptic interactions and synaptic plasticity. This gIF model is explicitly solvable or allows analytic approximations, which open the possibility for using it in event-driven simulation strategies. This provides a novel framework for simulating large-scale neural networks with realistic synaptic interactions, and therefore realistic emergent network states, such as high-conductance states.

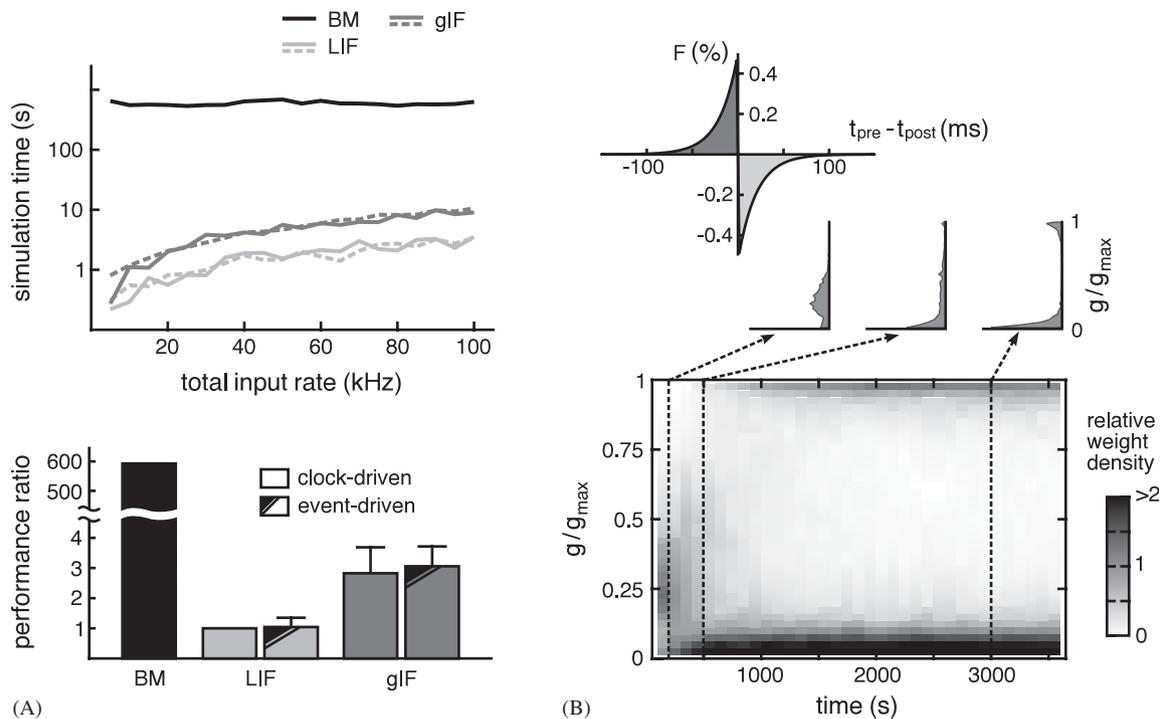


Fig. 2. Simulations with biophysically detailed and simple integrate-and-fire neurons. (A) Performance evaluation of the biophysical model (BM), the LIF and gIF neuron models. The time for simulating 100 s neural activity is shown as a function of the total synaptic input rate for clock-driven (time resolution: 0.1 ms for BM, 0.01 ms for LIF) and event-driven simulations. Whereas in the investigated input parameter regime the gIF neuron models were only about 3 times slower than the LIF neuron models, the BM showed an about 600 times performance deficit. (B) Time evolution of the synaptic weight distribution in a single postsynaptic cell together with example weight histograms for a model of STDP [10]. In accordance with [10], weights stabilize already after a few thousand seconds in a bimodal distribution.

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