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A population density method for large-scale modeling of neuronal networks with realistic synaptic kinetics

E. Haskell[a,1], D.Q. Nykamp[a,2], D. Tranchina[a,b,c,*]

[a]Courant Institute of Mathematical Sciences, New York University, 251 Mercer Street, New York, NY 10012, USA
[b]Department of Biology, New York University, New York, NY 10003, USA
[c]Center for Neural Science, New York University, New York, NY 10003, USA

Abstract

Population density function (PDF) methods have been used as both a time-saving alternative to direct Monte-Carlo simulation of neuronal network activity and as a tool for the analytic study of neuronal networks. Computational efficiency of the PDF method is dependent on a low-dimensional state space for the underlying individual neuron. Many previous implementations have assumed that the time scale of the synaptic kinetics is very fast on the scale of the membrane time constant in order to obtain a one-dimensional state space. Here, we extend our previous PDF methods for synapses with realistic kinetics; synaptic current injection for inhibition is replaced with more realistic conductance modulation. © 2001 Published by Elsevier Science B.V.

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1. Introduction

Conventional methods of neuronal network modeling where one tracks each neuron and synapse in the network can require enormous amounts of computer time

* Corresponding author. Courant Institute of Mathematical Sciences, New York University, 251 Mercer Street, New York, NY 10012, USA. Tel.: + 1-212-998-3109; fax: + 1-212-995-4121.

E-mail address: tranchina@cims.nyu.edu (D. Tranchina).

[1] Current address: Cognitive Neuroscience Unit, SISSA International School for Advanced Study, 34013 Trieste, Italy.

[2] Current address: Department of Mathematics, UCLA, Los Angeles, CA 90095, USA.

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and memory, even for models of small sections of the brain. Much of the computational load stems from the fact that realistic models require the simulation of the stochastic behavior of neurons in the central nervous system. Population density function (PDF) methods [5,6,4,8,9,3,1] provide a statistical mechanical approach to the problem of large numbers of stochastic neurons and synapses. In the population density approach, similar neurons are grouped together into populations. Rather than tracking the state of each individual neuron and synapse, a probability density function is evolved over the state space of the population. The computation time now depends on the number of populations rather than the number of neurons. This can result in a dramatic reduction in computation time, but only if the state space of the underlying individual neuron is sufficiently low, i.e. one or two.

The dimension of the state space for integrate-and-fire (I&F) neurons is one (for voltage) plus the number of variables needed to describe the state of the excitatory and inhibitory conductances or currents. In a previous paper, we developed a one-dimensional (1-D) model for I&F neurons with realistic synaptic kinetics [2]. In the 1-D model, the firing rate of a population was determined by the marginal density function for voltage $\rho_V(v,t)$. The evolution equation for $\rho_V(v,t)$ was an advection–diffusion–dispersion conservation equation. The temporal coefficients of the three probability flux terms in that equation gave the correct evolution equation for the first three moments of the random voltage V, in the presence of synaptic input, if voltage threshold and the lower bound on membrane voltage were removed. These methods only work when both excitatory and inhibitory synaptic inputs are modeled as current injection. Current injection is a reasonable approximation for excitatory synapses, because the reversal potential for excitatory synaptic current is so much higher than typical threshold voltages, but the same argument does not apply to inhibition. A current injection model for inhibition can lead to unrealistic hyperpolarization levels of the cell. In addition, current injection misses the increased efficacy of inhibitory events for cells in a depolarized state, and the shunting effect of inhibition on excitation is ignored. Here we extend our previous work [7,2] and model I&F neurons with realistic kinetics for excitatory synaptic current and inhibitory synaptic conductance in the population density framework.

2. The population density method

The PDF methods here are based on an integrate-and-fire neuron with inhibitory conductance modulation and excitatory current injection. The voltage, V of such a neuron obeys the equation:

$$\tau_m \frac{dV}{dt} + (V - \mathscr{E}_r) + G_i(t)(V - E_i) - I_e(t) = 0, \qquad (1)$$

where τ_m is the (resting) membrane time constant, $\mathscr{E}_{r/i}$ is the resting/inhibitory reversal potential, $G_i(t)$ is the normalized stochastic inhibitory conductance, and $I_e(t)$ is the normalized stochastic excitatory current. Here, the inhibitory conductance and excitatory current will be described by single exponentials:

$$\tau_i \frac{dG_i}{dt} = -G_i + \sum A_i^k \delta(t - T_i^k), \tag{2}$$

$$\tau_e \frac{dI_e}{dt} = -I_e + \sum A_e^j \delta(t - T_e^j), \tag{3}$$

where $\tau_{e/i}$ is the time constant of decay for the excitatory/inhibitory event waveform, $T_{e/i}$ is the arrival time of an inhibitory or excitatory event, and $A_{e/i}$ is the jump in the excitatory/inhibitory state due to an event arrival.

As in our prior paper we will model the voltage marginal density function, $\rho_V(v,t)$. The excitatory flux expression will be approximated by an advection–diffusion–dispersion approximation [2]. The inhibitory flux will be approximated by an advection equation following Nykamp and Tranchina [7]. This is equivalent to making a mean-field approximation on the inhibitory conductance random variable $G_i(t)$. The resulting evolution equation for the PDF can be expressed as

$$\frac{\partial \rho_V}{\partial t} = -\frac{\partial}{\partial v}\left(-\frac{1}{\tau_m}(v - \mathscr{E}_r)\rho_V(v,t) + J_i(v,t) + J_e(v,t)\right), \tag{4}$$

$$J_i(v,t) = -\mu_{A_i} \int_{-\infty}^{t} h_i(t - t')\nu_i(t')\, dt'(v - \mathscr{E}_i)\rho_V(v,t), \tag{5}$$

$$J_e(v,t) = \sum_{k=0}^{2} \frac{(-1)^k}{k!} \frac{\partial^k}{\partial v^k} \mu_{A_e^{k+1}} \int_{-\infty}^{t} dt' h_e(t - t') q_e^k(t - t') \nu_e(t') \rho_V(v,t), \tag{6}$$

$$h_{e/i}(t) = H(t)\frac{1}{\tau_{e/i}} \exp\left(-\frac{t}{\tau_{e/i}}\right), \tag{7}$$

$$q(t) = [H(t)e^{-(t/\tau_m)}] * h(t), \tag{8}$$

where, $J_{e/i}(v,t)$ is the excitatory/inhibitory flux, and $\mu_{A_e^k}$ is the kth moment of the random total charge injected by a unitary excitatory postsynaptic current event. In the case of coupled populations, the rates of excitatory and inhibitory synaptic inputs depend on the firing rates of the presynaptic populations:

$$\nu_{e/i}^k(t) = \nu_{e/i,0}^k(t) + \sum_j W_{jk} \int_0^{\infty} \alpha_{jk}(t') r^j(t - t')\, dt', \tag{9}$$

where $\nu_{e/i,0}^k$ is a prescribed external input rate to population k, W_{jk} is the average number of neurons from population j that project onto a neuron in population k, and $\alpha_{jk}(t)$ is the distribution of synaptic latencies from population j to population k.

The performance of the 1-D PDF model is demonstrated in Figs. 1 and 2. In Fig. 1, a single uncoupled population of neurons receives Poisson excitatory and inhibitory input at rates specified by temporally rich sums of sinusoids (upper panel, black and grey lines, respectively). Note that the population firing rates given by the PDF method (solid line) match the temporal structure of the rates given by direct Monte-Carlo simulation (histogram) reasonably well. However, the PDF method

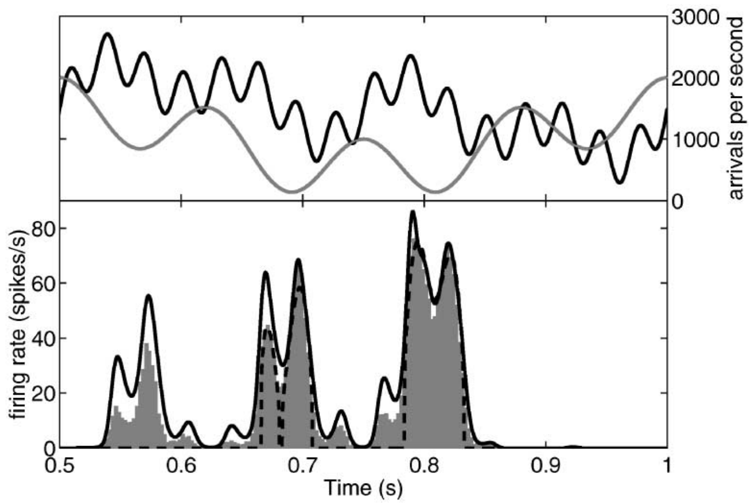

Fig. 1. Single uncoupled population of neurons. The upper panel shows the specified rates of Poisson excitatory (black) and inhibitory (grey) synaptic input to the population. Population firing rates determined by three methods are compared: PDF (solid line), Monte Carlo (histogram) and mean field (dashed line). Parameters: $\tau_m = 20\,\mathrm{ms}$, $\tau_e = 5\,\mathrm{ms}$, $\tau_i = 10\,\mathrm{ms}$, $\mu_{EPSP} = 0.5\,\mathrm{mV}$, $\mu_{IPSP} = 0.25\,\mathrm{mV}$, $\mathscr{E}_r = -65\,\mathrm{mV}$, $\mathscr{E}_i = -70\,\mathrm{mV}$.

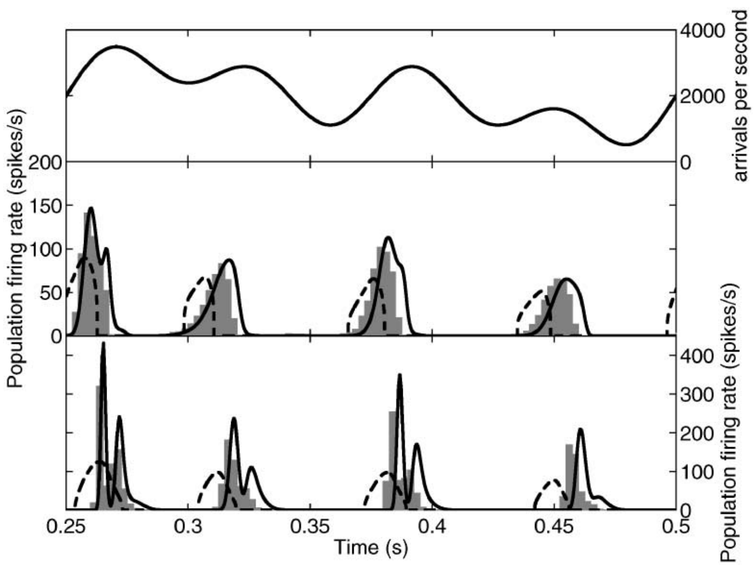

Fig. 2. Coupled excitatory and inhibitory populations. Each population supplies on average 40 synapses per neuron to the other population. The rate of external Poisson excitatory input to the excitatory population is shown in the upper panel. Middle and bottom panels show the firing rates of the excitatory and inhibitory populations, respectively. Results from the PDF method (solid line) are compared to those from Monte Carlo (histogram) and mean field (dashed line) methods. Parameters: $\tau_m = 20\,\mathrm{ms}$, $\tau_e = 5\,\mathrm{ms}$, $\tau_i = 22\,\mathrm{ms}$, $\mu_{EPSP,peak} = 0.5\,\mathrm{mV}$, $\mu_{IPSP,peak} = 0.25\,\mathrm{mV}$ (starting from $\mathscr{E}_r$), mean synaptic delay, 3 ms.

overestimate low firing rates. The mean field method (dashed line) completely misses some periods of activity. Fig. 2 shows results obtained for two coupled populations, one excitatory and the other inhibitory. The excitatory population receives external excitatory Poisson input at the rate shown in the upper panel. Each population supplies on average 40 synapses per neuron to the other population. Firing rates, computed by the PDF method, for the excitatory and inhibitory populations match those given by Monte-Carlos simulations (histograms) fairly well. The timing and magnitude of activity given by the mean field method (dashed line) are substantially off the mark.

3. Conclusion

Population density methods for computing activity in sparsely coupled populations of I&F neurons can be much faster than conventional, direct (Monte-Carlo) methods when the state space of the underlying single neuron is of low dimension. A typical unitary postsynaptic conductance waveform is well approximated by a difference of exponentials. Thus, two state variables are needed for each type of synaptic conductance. Consequently, the state space of an I&F neuron receiving just one type of excitatory and one type of inhibitory input is five dimensional. In this situation, exact PDF methods would be much slower than conventional methods for computing network activity.

We reported here on a model for a high-dimensional stochastic process that reduces the dimension of the problem down to one. The cost of this reduction is some loss in accuracy, but our PDF method is still a great deal more accurate than the mean field method appropriate for the underlying I&F neuron. The evolution equation for the marginal voltage density function in our model is of the advection–diffusion–dispersion type. It is possible that the coefficients of the various flux terms in this equation could be modified to produce more accurate results. In any case, the qualified success of our 1-D reduction suggests that other more sophisticated dimension reduction techniques might succeed in producing even more accurate results while retaining the computational efficiency of the population density method.

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