Fast neural network simulations with population density methods

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Abstract

The complexity of neural networks of the brain makes studying these networks through computer simulation challenging. Conventional methods, where one models thousands of individual neurons, can take enormous amounts of computer time even for models of small cortical areas. An alternative is the population density method in which neurons are grouped into large populations and one tracks the distribution of neurons over state space for each population. We discuss the method in general and illustrate the technique for integrate-and-fire neurons.

Key words: Probability Density Function; Network Modeling; Computer Simulation; Populations

1 Introduction

One challenge in the modeling of neural networks in the brain is to reduce the enormous computational time required for realistic simulations. Conventional methods, where one tracks each neuron and synapse in the network, can require tremendous computer time even for small parts of the brain (e.g. [10]).

In the simplifying approach of Wilson and Cowan [11], neurons are grouped into populations of similar neurons, and the state of each population is summarized by a single quantity, the mean firing rate [11] or mean synaptic drive

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[8]. Crude approximations of this sort cannot produce fast temporal dynamics observed in transient activity [2,5] and break down when the network is synchronized [1].

In the population density approach, one tracks the distribution of neurons over state space for each population [4,7,9,3]. The state space is determined by the dynamic variables in the explicit model for the underlying individual neuron. Because individual neurons and synapses are not tracked, these simulations can be hundreds of times faster than direct simulations. We have previously presented a detailed analysis of this method specialized to fast synapses [5] and slow inhibitory synapses [6].

2 The general population density formulation

We divide the state variables into two categories: the voltage of the neuron's cell body, denoted by $V(t)$, and all other variables, denoted by $\vec{X}(t)$ which could represent the states of channels, synapses, and dendrites, and any other quantities needed to specify the state of a neuron.

For each population k, we define $\rho^k(v,\vec{x},t)$ to be the probability density function of a neuron: $\int_\Omega \rho^k(v,\vec{x},t)dv\,d\vec{x} = \Pr\left(\text{the state of a neuron} \in \Omega\right)$. For a population of many similar neurons, we can interpret ρ as a *population density*:

$$\int_\Omega \rho^k(v,\vec{x},t)dv\,d\vec{x} = \text{Fraction of neurons whose state} \in \Omega. \tag{1}$$

From each ρ^k, we also calculate a population firing rate, $r^k(t)$ the probability per unit time of firing a spike for a randomly selected neuron.

To implement the network connectivity, we let $\nu^k_{e/i}(t)$ be the rate of excitatory/inhibitory input to population k, and W_{jk} be the average number of neurons from population j that project to each neuron in population k. Then, the input rate for each population is the weighted sum of the firing rates of the presynaptic populations:

$$\nu^k_{e/i}(t) = \nu^k_{e/i,o}(t) + \sum_{j\in\Lambda_{E/I}} W_{jk} \int_0^\infty \alpha_{jk}(t')r^j(t-t')dt', \tag{2}$$

where $\alpha_{jk}(t)$ is the distribution of synaptic latencies from population j to population k, $\Lambda_{E/I}$ indexes the excitatory/inhibitory populations, and $\nu^k_{e/i,o}(t)$ is any imposed external excitatory/inhibitory input rate to population k.

3 The population density for integrate-and-fire neurons

The voltage of a single-compartment integrate-and-fire neuron evolves via the equation $c\frac{dV}{dt} + g_r(V - \mathcal{E}_r) + G_e(t)(V - \mathcal{E}_e) + G_i(t)(V - \mathcal{E}_i) = 0$, where c is the membrane capacitance, g_r is the fixed resting conductance, $G_{e/i}(t)$ is the time varying excitatory/inhibitory synaptic conductance, and $\mathcal{E}_{r/e/i}$ is the resting/excitatory/inhibitory reversal potential. A spike time T_{sp} is defined by $V(T_{sp}) = v_{th}$, where v_{th} is a fixed threshold voltage. After each spike, the voltage V is reset to the fixed voltage v_{reset}. The fixed voltages are defined so that $\mathcal{E}_i < \mathcal{E}_r$, $v_{reset} < v_{th} < \mathcal{E}_e$. The synaptic conductances $G_{e/i}(t)$ are functions of the random arrival times of synaptic inputs, $T^j_{e/i}$. We denote the state of the synaptic conductances by $\vec{X}$ whose dimension depends on the number of conductance gating variables.

4 Population Density Evolution Equation

The evolution equation for each population density is a conservation equation:

$$\frac{\partial \rho}{\partial t}(v, \vec{x}, t) = -\nabla \cdot \vec{J}\left(v, \vec{x}, \nu_{e/i}(t)\right) + \delta(v - v_{reset}) J_V\left(v_{th}, \vec{x}, \nu_{e/i}(t)\right) \quad (3)$$

where $\vec{J} = (J_V, \vec{J}_X)$ is the flux of probability. Note that the total flux across voltage, $\int J_V\left(v, \vec{x}, \nu_{e/i}(t)\right) d\vec{x}$, is the probability per unit time of crossing v from below minus the probability per unit time of crossing v from above. Thus, the population firing rate is the total flux across threshold: $r(t) = \int J_V\left(v_{th}, \vec{x}, \nu_{e/i}(t)\right) d\vec{x}$. The second term on the right hand side of (3) is due to the reset of voltage to v_{reset} after a neuron fires a spike by crossing v_{th}.

The speed at which one can solve (3) diminishes rapidly as the dimension of the population density, $1 + \dim \vec{x}$, increases. When $\dim \vec{x} > 0$, dimension reduction techniques are necessary for computational efficiency.

4.1 Fast Synapses

When all synaptic events are instantaneous, $\dim \vec{x} = 0$. In this case, $G_{e/i}(t) = \sum_j A^j_{e/i}\, \delta(t - T^j_{e/i})$, where the synaptic input sizes $A^j_{e/i}$ are random numbers with some given distribution, and the synaptic input rates $T^j_{e/i}$ are given by a modulated Poisson process with mean rate $\nu_{e/i}(t)$. In this case, no state variables are needed to describe the synapses, and $\rho = \rho(v, t)$ is one-dimensional.

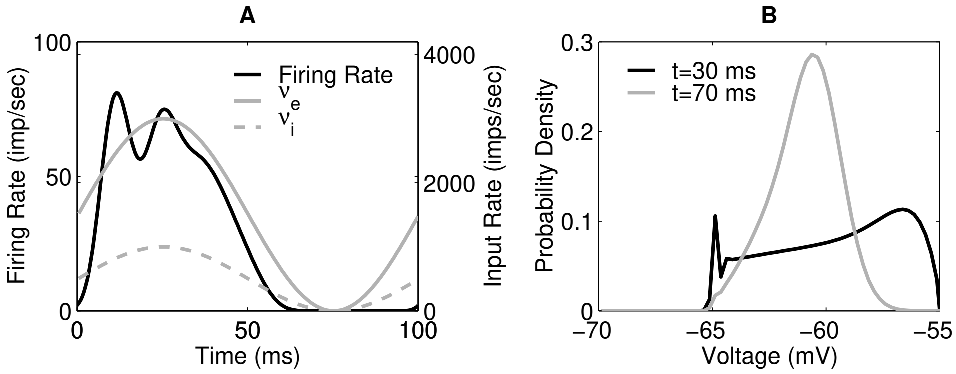

Fig. 1. Results of a simulation of an uncoupled population with fast synapses. **A**: Population firing rate in response to sinusoidally modulated input rates. **B**: Snapshots of the distribution of neurons across voltage for simulation shown in A.

The resulting specific form of (3) (described in detail in [5]), can be solved much more quickly than direct simulations.

Figure 1 shows the results of a single uncoupled population with fast synapses in response to sinusoidally modulated input rates. The snapshots in panel B show that many neurons are near $v_{th} = -55$ mV when the firing rate is high at $t = 30$ ms.

4.2 Slow Inhibitory Synapses

The assumption of instantaneous inhibitory synapses is often not justified by physiological measurement. Furthermore, the fact that inhibitory synapses are slower than excitatory synapses can have a dramatic effect on the network dynamics [6]. Thus, for the inhibitory conductance $G_i(t)$, we may need to use a set of equations like:

$$\tau_i \frac{dG_i}{dt} = -G_i(t) + S(t) \tag{4}$$

$$\tau_s \frac{dS}{dt} = -S(t) + \sum_j A_i^j \ \delta(t - T_i^j), \tag{5}$$

where $\tau_{s/i}$ is the time constant for the rise/decay of the inhibitory conductance ($\tau_s \leq \tau_i$). The response of $G_i(t)$ to a single inhibitory synaptic input at $T = 0$ is $G_i(t) = \frac{A_i}{\tau_i - \tau_s}\left(e^{-t/\tau_i} - e^{-t/\tau_s}\right)$, unless $\tau_i = \tau_s$, in which case $G_i(t) = \frac{A_i}{\tau_i}\frac{t}{\tau_i}e^{-t/\tau_i}$.

In this model, two variables describe the inhibitory conductance state, $\vec{X}(t) = (G_i(t), S(t))$, and each population density is three-dimensional: $\rho = \rho(v, g, s, t)$. Thus, direct solution of equation (3) for $\rho(t)$ would take much longer than it would for the fast synapse case.

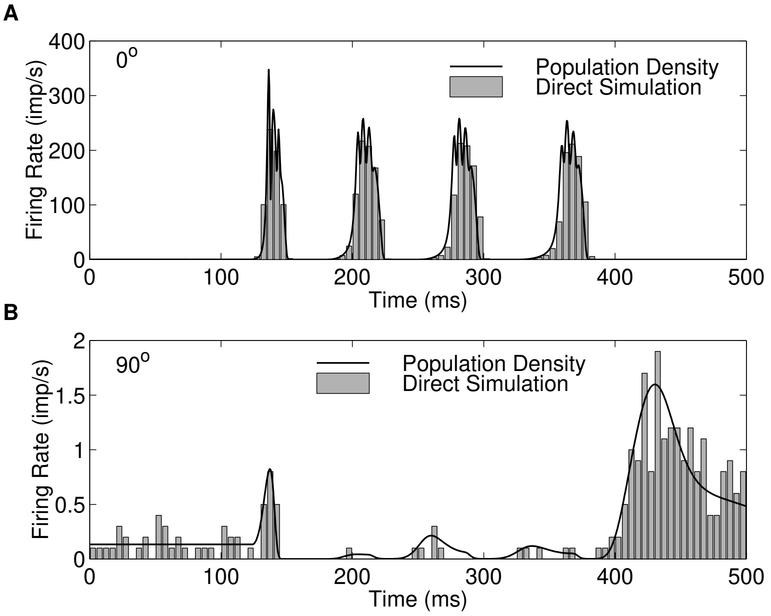

Fig. 2. Comparison of population density and direct simulation firing rate for a model of a hypercolumn in visual cortex. Response is to a bar flashed at 0 deg. **A**: Response of the population with a preferred orientation of 0 deg. **B**: Response of the population with a preferred orientation of 90 deg. Note change of scale. $\tau_s = 2$ ms, $\tau_i = 8$ ms. All other parameters are as in [5].

In the case of fast excitatory synapses, $r(t)$ can be calculated from the marginal distribution in v: $f_V(v,t) = \int \rho(v,g,s,t)dg\,ds$. Thus, we can reduce the dimension back to one by computing just $f_V(v,t)$. The evolution equation for f_V, obtained by integrating (3) with respect to $\vec{x} = (g,s)$, depends on the unknown quantity $\mu_{G|V}(v,t)$, which is the expected value of G_i given V [6]. Nonetheless, this equation can be solved by assuming that the expected value of G_i is independent of V, i.e., $\mu_{G|V}(v,t) = \mu_G(t)$, where $\mu_G(t)$ is the expected value of G_i averaged over all neurons in the population. Since the equations for the inhibitory synapses (4–5) do not depend on voltage, the equation for $\mu_G(t)$ can be derived directly.

Although the independence assumption is not strictly justified, in practice, it gives good results. We illustrate the performance of the population density method with a comparison of the population density firing rates with those of a direct simulation implementation of the same network. We use a network model for orientation tuning in one hypercolumn of primary visual cortex in the cat based on the model by Somers et al. [10]. The network consists of 18 excitatory and 18 inhibitory populations with preferred orientations between 0 and 180 deg [5]. The responses of two populations to a flashed bar oriented at zero deg are shown in figure 2. The population density simulation was over 100 times faster than the direct simulation (22 seconds versus 50 minutes on a Silcon Graphics Octane computer) without sacrificing accuracy in the firing rate.

5 Conclusion

Population density methods can greatly reduce the computation time required for network simulations without sacrificing accuracy. These methods can, in principle, be used with more elaborate models for the underlying single neuron, but dimension reduction techniques, like those considered here, must be found to make the method practical.

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