Equivalent networks of conductance- and current-driven neurons[⋆]

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Abstract. The concept of an equivalence between conductance-driven and current-driven neurons depends on the problem at hand. Here we show how it is possible to study a network of conductance-driven neurons by means of a mean field analysis of an equivalent network of current-driven neurons. The current drive is Gauss distributed and not voltage dependent. The equivalent network is composed by the same neurons and exhibits the same stable firing rates at the only price of having different connectivity.

1 Introduction

The problem of how conductance-driven neurons differ from current-driven neurons has become increasingly popular recently, to the point to question well established results obtained studying networks of current-driven spiking neurons [4]. To give a meaningful answer to this question, it is necessary to specify the observables with respect to which differently-driven neurons ought to behave equivalently. Here we study the problem of mean rates of asynchronous activity in large networks of spiking neurons. Population density approach provides a synthetic and reliable description of cortical phenomena like spontaneous or delay activity observed for example in many areas of behaving monkeys (see e.g. [1] and refs. therein). Briefly, neurons of the same kind are grouped in homogeneous populations which can be fully described by the population spike rate and whose neurons all share the same input *statistics*. The *stationary* patterns of activity in the network are given by the self-consistent solutions of *mean field equations* like $f^i_{out} = \Phi^i(\underline{f}_{in})$, where i labels the population and the frequencies f^i describe the state of the network. In such a framework, conductance- and current-driven neurons are to be considered equivalent if they are described by the same self-consistent equations. Given a network of conductance-driven neurons, we pose and answer positively the following question: is it possible to study an equivalent network of current-driven neurons and if yes, how does the latter relate to the first?

2 The network of conductance-driven neurons

For the sake of simplicity, we consider only two homogeneous populations, excitatory (e) and inhibitory (i). In the cortex, thousands of synaptic inputs delivered to the target cells by means of local conductance changes (independent or only

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[⋆] Published in: *O. Kaynak (Ed.): Supplementary Proceedings of ICANN/ICONIP 2003, LNCS 2714, pp. 449-452, Springer-Verlag (2003)* weakly correlated), can be described in terms of Gauss distributed conductances (see e.g. [2]), whose average μ and variance σ^2 are given by

$$\mu_{e,i} = \bar{g}_{e,i}\lambda_{e,i}\tau_{e,i}, \qquad \sigma^2_{e,i} = \frac{1}{2}\bar{g}^2_{e,i}\lambda_{e,i}\tau_{e,i} \tag{1}$$

Here: 1) $\lambda_{e,i} = N_{e,i}c_{e,i}\nu_{e,i}$ (N is the total number of neurons of a population, c is the fraction of neurons of this population which are directly connected and ν is the mean frequency of synaptic releases); 2) $\bar{g}_{e,i}$ is the mean conductance change induced by a single event; 3) τ is the time constant of the exponential decay of a single post-synaptic change in conductance, which allows ionic current to flow into the cell. Here we use $\tau_e = \tau_i = 1$ ms; for larger time constants we got similar results (not shown). Note how the statistics of the input is completely specified by the *quadruplet* $\Omega = \{\nu_e, \bar{g}_e, \nu_i, \bar{g}_i\}$. The input current is obtained by multiplying the total synaptic conductance by the corresponding voltage dependent driving force $I_{e,i}(\Omega, t) = g_{e,i}(\Omega, t)(V_{e,i} - V(t))$, where $V_i = V_{rest} - 10$ mV and $V_e = V_{rest} + 70$ mV are the reversal potentials, and V_{rest} is the membrane potential of the post-synaptic cell. Its total input current is $I_{cond} \equiv I_e + I_i$.

3 The equivalent Gaussian current to get the same mean firing rates

We next look for conditions under which it is possible to obtain the same mean firing rates of a network of conductance-driven neurons in an *equivalent* network of current-driven neurons, whose inputs (by definition) are Gauss distributed and *not* voltage dependent.

This problem is not trivial and may be very tricky. For example, if one injects a Gaussian current characterized by the same average and variance of the total current I_{cond} arising in conductance drive, in general one would *not* get the same spike rate as one would in the full simulation with the conductance drive. This is because the driving force can skew the Gaussian distribution of the conductances and can introduce complex correlations in the resulting current I_{cond}, not taken into account by a Gaussian current with the same average and variance as I_{cond}.

We propose here to seek the solution in terms of properly rescaled connectivities and synaptic efficacies. In formal terms, for each quadruplet $\Omega = \{\nu_e, \bar{g}_e, \nu_i, \bar{g}_i\}$ characterizing the statistics of the input, we build a Gaussian current $I_{cur}(\Omega)$ with mean $m_I(\Omega)$ and variance $s^2_I(\Omega)$ according to:

$$m_I = J_e N_e \tilde{c}_e \nu_e \tau_e - J_i N_i \tilde{c}_i \nu_i \tau_i$$

$$s^2_I = \frac{1}{2}J^2_e N_e \tilde{c}_e \nu_e \tau_e + \frac{1}{2}J^2_i N_i \tilde{c}_i \nu_i \tau_i$$

where $J_{e,i} = \bar{g}_{e,i}V^{e,i}_J$ are the peak currents per single pre-synaptic spike (units of current), and $\tilde{c}_{e,i} = \beta_{e,i}c_{e,i}$ are the rescaled connectivities in the network of current driven neurons. Two networks (of conductance- and current-driven neurons) will then be equivalent if values for $V^{e,i}_J$, $\beta_{e,i}$, *independent of* $\nu_{e,i}$, can be found such that the neuron's mean rate f_{cond} under conductance injection I_{cond} is the same as the mean rate f_{cur} under current injection I_{cur}. In such a case, in fact, the mean field activities for the two networks are the same. Note, however, that the scaling parameters $\{V_J^{e,i}, \beta_{e,i}\}$ may still depend on the other parameters defining Ω. It is important to stress that this procedure is *not* equivalent to finding effective potentials $V_J^{e,i}$ *only*, playing the role of average effective driving forces $V_{e,i} - \langle V \rangle$. In fact that would require $\beta_{e,i} = \beta_{e,i}^2$, i.e. $\beta_{e,i} \equiv 1$, and we show next that such a procedure fails in matching f_{cur} to f_{cond}.

4 Example: network of integrate and fire (IF) neurons

The above framework is general and in fact no model neuron had to be specified so far. In this section we show that for IF neurons not only a solution can be found, but the scaling parameters do not depend on the input Ω, i.e. $f_{cond}(\Omega) = f_{cur}(\Omega)$ *for all* Ω and not only for all the frequencies $\nu_{e,i}$. In other words, they depend only on the inherent properties of the cell, i.e. the capacitance of the membrane C, the membrane time constant τ_m, the resting potential, etc. For a given Ω, we simulated the dynamics of the membrane potential V according to the Eq:

$$\frac{dV}{dt} = -\frac{V}{\tau_m} + \frac{I}{C}$$

with $I = I_{cond}(\Omega)$. A spike is emitted whenever V reaches a fixed threshold θ, after which it is clamped to a reset potential V_r for a refractory period τ_r. Once the collection of input-output pairs $(\Omega, f_{cond}(\Omega))$ were obtained, we fitted with a Montecarlo least squares procedure the response of current driven neurons to the same inputs, i.e. we looked for four *fixed* parameters $\{V_J^{e,i}, \beta_{e,i}\}$ in order to get the best match between $f_{cur}(\Omega)$ and $f_{cond}(\Omega)$ for all Ω.

Fig. 1 shows the remarkable match obtained between f_{cond} (symbols) f_{cur} (full lines); they are both plotted as a function of the average input in current drive, $m_I(\Omega)$. No reasonable match was obtainable if the condition $\tilde{c}_{e,i} = c_{e,i}$ was imposed.

5 Discussion

In this work current- versus conductance-driven neurons were studied in the framework of the mean field theory of large recurrent networks of spiking neurons. For such networks, equivalence means having the same patterns of stable firing rates in homogeneous populations, regardless of the modality in which the input is delivered to the target cells, i.e. either in conductance or in current drive. Our main result is that it is possible to obtain the same mean firing rates of a network of conductance-driven neurons by studying an *equivalent* network of current-driven neurons, whose inputs are Gauss distributed and *not* voltage dependent. Compared to the original network, the companion one has the same number of neurons and the same stable firing rates at the only price of different connectivities and suitable synaptic efficacies. Our results also provide a bridge between *in vitro* experiments in which conductance injection is emulated *via* the *dynamic clamp* technique (see e.g. [3]), and *in vitro* experiments with current injection. To this purpose, the problem of an equivalent formulation in terms of current-driven neurons must be appropriately approached, and relies upon a correct choice of the relevant variables which are to be investigated. This work also represents an example of how such a procedure may be carried out.

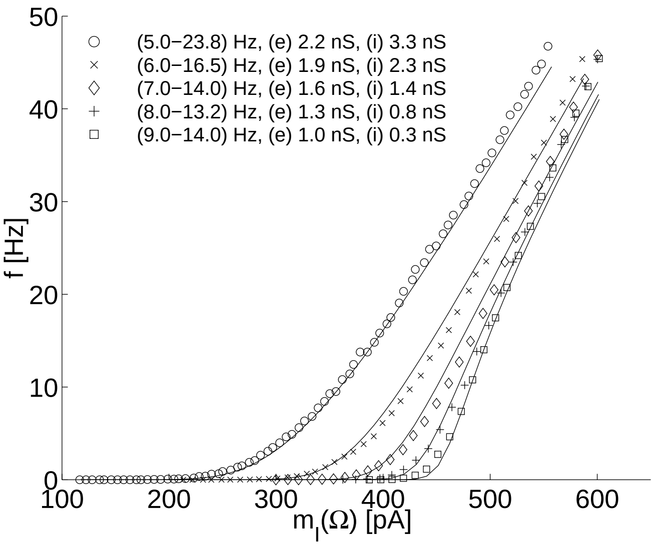

Fig. 1. Comparison between a conductance-driven (symbols) and a current-driven (full curves) IF neuron after rescaling (simulations). The frequency match was obtained with parameters $V_J^e \approx 11.93$ mV, $V_J^i \approx 33.65$ mV, $\beta_e = \tilde{c}_e/c_e \approx 4.28$ and $\beta_i = \tilde{c}_i/c_i \approx 0.81$. Each curve was generated by setting $\bar{g}_{e,i}$ to the values reported in the top left part of the figure (nS), and then by sweeping along the diagonal of the $\{\nu_e, \nu_i\}$ plane (i.e. $\nu_e = \nu_i$ for each point; ranges along each curve reported in the picture (in Hz); $N_{e,i}c_{e,i} = 10^3$ throughout). This procedure was chosen to explore different quadruplets Ω arising form realistic parameters and giving reasonable input currents and output frequencies. The results do not depend upon this choice, nor they depend upon the choice $\nu_e = \nu_i$, which was only convenient to restrict the parameters space. The meaning of the values found for $V_J^{e,i}$ and $\beta_{e,i}$ is not yet understood, but they are different for different networks (e.g. excitatory connectivity could decrease instead of increase in order to get the match). The other parameters were $\tau_r = 0$, $C = 500$ pF, $\theta = 20$ mV, $V_r = 10$ mV, $\tau_m = 20$ ms, $V_{rest} = 0$, $\tau_e = \tau_i = 1$ ms. Simulation lifetime for each point was 200 s; a transient of $4\tau_m = 80$ ms was discarded to allow the current to reach its stationary behavior.

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