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Comparison between networks of conductance- and current-driven neurons: stationary spike rates and subthreshold depolarization

Giancarlo La Camera*, Walter Senn , Stefano Fusi

Institute of Physiology, University of Bern, Bühlplatz 5, Bern CH-3012, Switzerland

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Abstract

The problem of an equivalence between conductance- and current-driven neurons in terms of mean stationary output rates is investigated. We show that 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. In addition, the differences in the subthreshold depolarization and the interspike-interval distribution can be studied at parity of output rates, providing a method to study those effects of the conductance drive which do not arise in a network of current-driven neurons.

Keywords: Conductance drive; Current drive; Integrate-and-fire neurons; Mean field; Coefficient of variability

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1. Introduction

The problem of how conductance-driven neurons differ from current-driven neurons has become increasingly popular recently, to the point of questioning the results obtainable by studying networks of current-driven spiking neurons [7]. To give a meaningful answer to this question, it is necessary to specify the observables with respect to which

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* Corresponding author. Tel.: +41-3163-18722; fax: +41-31-63-14611.

E-mail addresses: lacamera@cns.unibe.ch (G. La Camera), wsenn@cns.unibe.ch (W. Senn), fusi@cns.unibe.ch (S. Fusi).

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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 in many areas of behaving animals (see e.g. [1] and references 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 $f^i_{\rm out} = \Phi^i(\underline{f}_{\rm in})$, 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 show how to build an equivalent network of current-driven neurons which exhibit the same stationary spike rates.

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, hundreds of synaptic inputs delivered to the target cells by means of local conductance changes (independent or only weakly correlated), can be described in terms of Gauss distributed conductances $g_{\rm e,i}(t)$ (see e.g. [3]), whose average $\mu_{\rm e,i}$ and variance $\sigma^2_{\rm e,i}$ are given by

$$\mu_{\rm e,i} = \bar{g}_{\rm e,i} N_{\rm e,i} c_{\rm e,i} v_{\rm e,i} \tau_{\rm e,i},$$

$$\sigma^2_{\rm e,i} = \tfrac{1}{2}\, \bar{g}^2_{\rm e,i} N_{\rm e,i} c_{\rm e,i} v_{\rm e,i} \tau_{\rm e,i},$$

where N is the total number of neurons of a population; c is the fraction of neurons of this population which are directly connected; v is the mean frequency of synaptic releases; $\bar{g}$ is the peak conductance change induced by a single event; 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. A good choice to match experimental data is $\tau \sim 5$ ms [3], and therefore we use $\tau_{\rm e} = \tau_{\rm i} = 5$ ms.

Note that the statistics of the input are completely specified by the *quadruplet* $\Omega = \{v_{\rm e}, \bar{g}_{\rm e}, v_{\rm i}, \bar{g}_{\rm i}\}$. The input current is obtained by multiplying the total synaptic conductances $g_{\rm e,i}(\Omega, t)$ by the corresponding voltage-dependent driving forces

$$I_{\rm e,i}(\Omega, t) = g_{\rm e,i}(\Omega, t)(V_{\rm e,i} - V(t)),$$

where $V_{\rm i} = V_{\rm rest} - 10$ and $V_{\rm e} = V_{\rm rest} + 70$ mV are the reversal potentials, and $V_{\rm rest}$ is the resting membrane potential of the post-synaptic cell. Its total input current is $I_{\rm cond} \equiv I_{\rm e} + I_{\rm i}$.

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

If one injects a Gaussian current characterized by the same average and variance of the total current $I_{\rm cond}$ 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}.

The problem, then, is to find the *effective* or *rescaled* Gauss distributed, voltage-independent current which, given a large pool of inputs $\{\Omega\}$, gives for each Ω the same output frequency f_Ω which would be obtained under conductance drive. This would *map* a network of conductance-driven neurons in a network of current-driven neurons *which exhibit the same stationary spike rates*. The two networks will then be equivalent in the sense that their stationary mean field activities are the same.

The most natural candidate for an equivalent Gaussian current is probably that coming from the attempt to linearize the dynamical equations for the couple (V, I) around an holding potential $V^* = V(\Omega^*)$, where Ω^* represents a typical input in cortical conditions, as done e.g. in [2]. Such procedure amounts to looking for effective 'average' potentials $V_J^{\mathrm{e,i}}$ (playing the role of 'average' driving forces $V_{\mathrm{e,i}} - \langle V \rangle$, see [2]) such that the Gaussian current with average and variance given by

$$\hat{m}_I = \bar{g}_{\mathrm{e}} V_J^{\mathrm{e}} N_{\mathrm{e}} c_{\mathrm{e}} v_{\mathrm{e}} \tau_{\mathrm{e}} - \bar{g}_{\mathrm{i}} V_J^{\mathrm{i}} N_{\mathrm{i}} c_{\mathrm{i}} v_{\mathrm{i}} \tau_{\mathrm{i}},$$

$$\hat{s}_I^2 = \tfrac{1}{2} (\bar{g}_{\mathrm{e}} V_J^{\mathrm{e}})^2 N_{\mathrm{e}} c_{\mathrm{e}} v_{\mathrm{e}} \tau_{\mathrm{e}} + \tfrac{1}{2} (\bar{g}_{\mathrm{i}} V_J^{\mathrm{i}})^2 N_{\mathrm{i}} c_{\mathrm{i}} v_{\mathrm{i}} \tau_{\mathrm{i}}$$

gives the same output frequency at parity of input Ω. Although this may work for a single Ω, it does not work *for all* Ω's in a large pool (results not shown).

Note that in the above procedure, the map is given in terms of effective synaptic efficacies $J_{\mathrm{e,i}} \equiv \bar{g}_{\mathrm{e,i}} V_J^{\mathrm{e,i}}$. It is natural then to increase the number of degrees of freedom and look for a solution in terms, for example, of properly rescaled connectivities in addition to synaptic efficacies. In formal terms, for each quadruplet $\Omega = \{v_{\mathrm{e}}, \bar{g}_{\mathrm{e}}, v_{\mathrm{i}}, \bar{g}_{\mathrm{i}}\}$ characterizing the statistics of the input, we build a Gaussian current $I_{\mathrm{cur}}(\Omega)$ with mean $m_I(\Omega)$ and variance $s_I^2(\Omega)$ according to

$$m_I = J_{\mathrm{e}} N_{\mathrm{e}} \tilde{c}_{\mathrm{e}} v_{\mathrm{e}} \tau_{\mathrm{e}} - J_{\mathrm{i}} N_{\mathrm{i}} \tilde{c}_{\mathrm{i}} v_{\mathrm{i}} \tau_{\mathrm{i}},$$

$$s_I^2 = \tfrac{1}{2} J_{\mathrm{e}}^2 N_{\mathrm{e}} \tilde{c}_{\mathrm{e}} v_{\mathrm{e}} \tau_{\mathrm{e}} + \tfrac{1}{2} J_{\mathrm{i}}^2 N_{\mathrm{i}} \tilde{c}_{\mathrm{i}} v_{\mathrm{i}} \tau_{\mathrm{i}},$$

where $J_{\mathrm{e,i}} = \bar{g}_{\mathrm{e,i}} V_J^{\mathrm{e,i}}$ are, as above, the peak currents per single pre-synaptic spike, and $\tilde{c}_{\mathrm{e,i}} = \beta_{\mathrm{e,i}} c_{\mathrm{e,i}}$ 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 $V_J^{\mathrm{e,i}}$, $\beta_{\mathrm{e,i}}$, *independent of* $v_{\mathrm{e,i}}$, 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 that the scaling parameters $\{V_J^{\mathrm{e,i}}, \beta_{\mathrm{e,i}}\}$ may still depend on the other parameters defining Ω, i.e. $\bar{g}_{\mathrm{e,i}}$, and yet the equivalence be achieved. We found that, for a network of integrate-and-fire neurons, a remarkable match can be found with unique (i.e. Ω-independent) scaling factors (Fig. 1, top left). These scaling factors depend only on the parameters of the neurons (capacitance, membrane time constant, reset potential, threshold for spike emission, etc.)

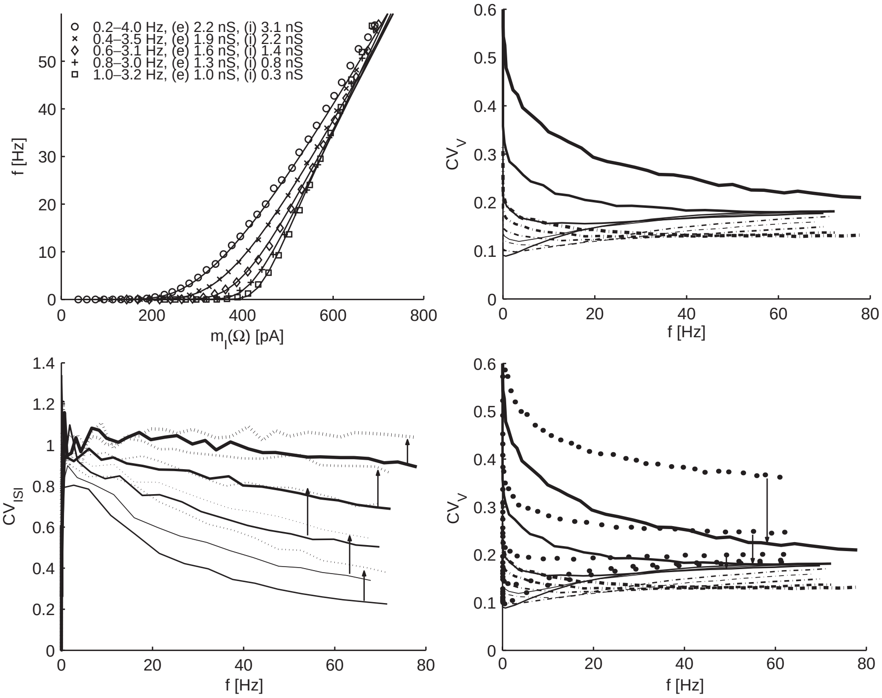

Fig. 1. *Top left*: Comparison between a conductance-driven (symbols) and a current-driven (full curves) IF neuron after rescaling (simulations). The dynamics of the subthreshold membrane potential V evolve according to the Eq. $\mathrm{d}V/\mathrm{d}t = -V/\tau_\mathrm{m} + I/C$, with $I = I_\mathrm{cond}(\Omega)$, and thresholded at $\theta = 20$ mV to emulate a spike emission, with reset at $V_\mathrm{r} = 10$ mV and no refractory period ($C = 500$ pF, $\tau_\mathrm{m} = 20$ ms, $V_\mathrm{rest} = 0$). The frequency match was obtained through a Montecarlo minimization of the squared difference between the observed frequencies and the output mean rates of a current-driven neuron driven by the same inputs (whose stationary spike rate is given in [4] as a function of m_I, s_I). The best-fit parameters values were $V_J^\mathrm{e} \approx 24.7$ mV, $V_J^\mathrm{i} \approx 59.1$ mV, $\beta_\mathrm{e} = \tilde{c}_\mathrm{e}/c_\mathrm{e} \approx 2.2$ and $\beta_\mathrm{i} = \tilde{c}_\mathrm{i}/c_\mathrm{i} \approx 0.5$. Each curve was generated by setting $\bar{g}_\mathrm{e,i}$ equal to constant values (reported in the top left corner of the figure), and then by sweeping along the diagonal of the $\{\nu_\mathrm{e}, \nu_\mathrm{i}\}$ plane (i.e. $\nu_\mathrm{e} = \nu_\mathrm{i}$ for each point; ν_e ranges reported in the plot. $N_\mathrm{e,i}c_\mathrm{e,i} = 1000$). This procedure was chosen to explore different quadruplets Ω arising form realistic parameters and giving reasonable input currents and output frequencies. *Top right*: Coefficient of variability of the depolarization in conductance (dot-dashed) and current (full) drive. A *thickness code* replaces the symbol code of the top left panel, with the thickest line corresponding to the circles. *Bottom left*: CV_ISI as a function of the output frequency for both drives (same convention as for top right panel). Arrows help link corresponding curves. *Bottom right*: Same as top right panel plus the CV_V for the case of an equivalent Gaussian, delta-correlated current (dots; see text). The arrows show the effect (in current drive) due to the time correlation length of the input (τ_s). A residual difference with the CV_V in conductance drive remains and cannot be accounted for by τ_s.

4. Beyond the spike rates

The scheme outlined above is not enough to get a complete match in the response as quantified by the entire spike train, but it allows to study conductance vs. current-driven neurons *at parity of output spike rates* for all inputs, in particular enables us to study the statistics of the depolarization and of the interspike intervals (ISIs). For a given quantity, higher moments like the variance, or equivalently the *coefficient of variability* (CV=standard deviation/mean), are usually different even if the mean spike rates are the same (and often they *have* to be different in order to achieve the same spike rates, as shown in the previous section). In general, the rescaled Gaussian current is in a complex relationship with the input current in conductance drive, but for the subthreshold depolarization a clear feature emerges: its standard deviation is always larger in current drive, while its average is smaller, causing its coefficient of variability (CV_V) to be smaller in conductance drive (Fig. 1, top right).

Surprisingly, such voltage variability is anticorrelated with the variability of the ISIs, as the $\mathrm{CV}_{\mathrm{ISI}}$ is always larger in conductance drive (Fig. 1, bottom left). The different statistics of the depolarization can be due to at least three different factors: (a) the correlations between current and depolarization; (b) the presence of an effective reflective barrier for the depolarization located at the inhibitory reversal potential V_{i} (below V_{i}, inhibitory inputs become excitatory and as a result excursions below V_{i} are forbidden in conductance drive); (c) the correlation length τ_{s} of the current which naturally arises in conductance drive, here equal to 5 ms (the $\mathrm{CV}_{\mathrm{ISI}}$ is always increased by a larger synaptic time [5], both in conductance and current drive). To investigate the effect of the correlation length, we found the unique scaling parameters which give the frequency match with a *δ-correlated* Gaussian current ($\tau_{\mathrm{s}} = 0$). The effect of τ_{s} on the CV_V is shown in Fig. 1 (bottom right), in which one can see that there is still a residual difference in the CV_V between conductance and current drive, which cannot be accounted for by the correlation length only. We also checked that the presence of a reflecting barrier at V_{i} for the depolarization in current drive has a negligible effect (not shown). As a result, the cross-correlations between depolarization and current in conductance drive is likely to be the factor responsible for the differences in the depolarization and in the ISI statistics, at parity of output rates. These correlations may in fact also change the effective correlation length of the current, so that a comparison at parity of τ_{s} would be unfair. This suggests that the dynamics of the two (equivalent) networks may be different although the steady states of asynchronous activity are the same (but see [4]).

5. Discussion

In this work current- vs. 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 network has the same number of neurons and the same stable firing rates at the only price of different connectivities and suitable synaptic efficacies. This result was obtained with a method that allows comparison, at parity of output rates, of the statistics of important quantities like the subthreshold depolarization and the ISI distribution. Finally, our results also provide a bridge between in vitro experiments in which conductance injection is emulated via the *dynamic clamp* technique (see e.g. [6]), and in vitro experiments with current injection. To this purpose, the problem of an equivalent formulation in terms of current-driven neurons must be approached carefully, and its solution relies upon a correct choice of the relevant variables which are to be investigated. This work presents an example of how such a procedure may be carried out.

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