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An explicit comparison of spike dynamics and firing rate dynamics in neural network modeling

François CHAPEAU-BLONDEAU, Nicolas CHAMBET
Institut de Biologie Théorique, Université d'Angers,
10 rue André Boquel, 49100 ANGERS, FRANCE.

Abstract. We develop a neural network model based on a description of spike dynamics modulated by synaptic conductances. The variables are endowed with realistic physical units and plausible numerical values. This allows to reach both qualitative and quantitative significance. At the same time, the model is kept simple enough to enable its application to the study of collective behaviors among large populations of neurons. The model is used to investigate the conditions for the derivation of a neuron transfer function for firing rates. Then, a reduction to a network model involving firing rates instead of spikes is performed. The spike and the rate models are compared to describe equilibrium as well as dynamic network properties, and differences in the results of the two descriptions are pointed out.

1. Introduction

Ten years after the two seminal papers by Hopfield [1] has come the age of what is sometimes called *second-generation neural networks.* The two Hopfield papers constituted a landmark in neural modeling. Based on a few simple but cardinal properties belonging to biological neurons (threshold nonlinearities, high connectivity, through plastic couplings), they demonstrated that, at the level of a population of neurons, collective behaviors emerged that could form the support of information processing abilities (attractor dynamics for memory processes). Models derived from Hopfield's work have received considerable attention leading to deep understanding of many of their properties [2]. To follow on the same path, more and more models are now considered that incorporate more realistic elements in the description of neurons, while keeping the emphasis on the investigation of collective behaviors among large networks, and interpreted in terms of information processing. In this trend, we discuss here a neural network model based on a description of spike dynamics modulated by synaptic conductances. We pay special attention to treat the parameters of the model, not as mere mathematical variables, but as genuine physical quantities endowed with realistic units together with plausible numerical values. This model is used here to investigate different issues of importance in neural network modeling, and especially the comparison between descriptions based on spike dynamics or on firing rate dynamics.

2. A neural network model with spike dynamics

For a neuron i, we introduce G_{ij} the membrane conductance in a postsynaptic region j. G_{ij} varies with the presynaptic activity $E_j(t)$ that represents the train of spikes impinging on the synapse j endowed with a synaptic efficacy w_{ij}. We model this variation as a discrete first-order low-pass linear system, that we write for the dimensionless parameter $g_{ij} = G_{ij}/G_m$, where the constant G_m is the total conductance of the neuron membrane at rest:

$$g_{ij}(t+\Delta t) = (1 - \frac{\Delta t}{\tau_s})g_{ij}(t) + \frac{\Delta t}{\tau_s} w_{ij} E_j(t) \; . \tag{1}$$

Changes in membrane conductance due to many synapses j produce a variation of the membrane potentiel $V_i(t)$ of neuron i, that we model as:

$$V_i(t+\Delta t) = (1 - \frac{\Delta t}{\tau_m})V_i(t) + \frac{\Delta t}{\tau_m} \sum_j g_{ij}(t)[V_{\text{rev},ij} - V_i(t)] \; . \tag{2}$$

The zero reference for the potentials is taken at the resting potential of the neuron. $V_{\text{rev},ij}$ is the reversal potential of synapse j to neuron i; it is positive (i.e. above the resting potential) for an excitatory synapse, and negative for an inhibitory synapse.

If the membrane potential V_i reaches the threshold V_{th}, a spike is fired by neuron i. The output activity of neuron i is described by a variable $S_i(t)$ that evolves according to:

$$\begin{aligned} &\text{If } V_i(t+\Delta t) > V_{\text{th}} \quad \text{then} \quad S_i(t+\Delta t) = 1, \quad V_i(t+\Delta t) = 0; \\ &\qquad\qquad\qquad\qquad\quad\;\; \text{else} \quad S_i(t+\Delta t) = 0. \end{aligned} \tag{3}$$

It is then possible to define the total synaptic current I_i to neuron i, as:

$$I_i(t) = G_m \sum_j g_{ij}(t)[V_{\text{rev},ij} - V_i(t)] \; . \tag{4}$$

We pay special attention to assigning realistic values, at least in order of magnitude, together with physical units, to the parameters of the model. For the membrane time constant we take $\tau_m = 10\,\text{ms}$. In biological neurons, the synapse time constant τ_s can vary from below $1\,\text{ms}$ to above $100\,\text{ms}$; for this study we chose $\tau_s = 10\,\text{ms}$. In these conditions, we take for the iteration step $\Delta t = 1\,\text{ms} \ll \tau_m$ and τ_s. This Δt is of the order of the absolute refractory period T_r of a neuron, and, through eq. (3), ensures that no more than one spike can be emitted by a neuron within a refractory period. The threshold V_{th} is $20\,\text{mV}$ above the resting potential. For an excitatory synapse $V_{\text{rev},ij}$ is $V_{\text{exc}} = 70\,\text{mV}$ above rest, and $V_{\text{inh}} = -10\,\text{mV}$ for an inhibitory synapse. $E_j(t)$ and $S_i(t)$ are dimensionless discrete signals that assume values 0 or 1 to represent the absence or presence of a spike at time t. According to eq. (1), the synaptic efficacy w_{ij} is also dimensionless. A critical issue is to propose a meaningful quantitative evaluation for this parameter. For this purpose, we rely on the typically plausible situation that follows. We assume that, on an excitatory monosynaptic pathway, when the presynaptic neuron j is firing at its maximum rate ($E_j(t) = 1$, $\forall t$), the postsynaptic neuron i will just reach the firing threshold (asymptotically), provided that the synapse w_{ij} is at its maximum of efficacy w_{max}. Then, eq. (1, 2) lead asymptotycally to the relationship $(V_{\text{rev},ij} - V_{\text{th}})w_{\text{max}} = V_{\text{th}}$, from which we estimate $w_{\text{max}} = 0.4$. Finally, for the membrane conductance at rest we take $G_m = 10\,\text{nS}$.

A first assessment of the model can be obtained by the computation of its impulse response, that is, the change in the postsynaptic membrane potential $V_i(t)$ produced by a single presynaptic spike. This quantity is experimentally measurable, and constitutes what is known as a unitary postsynaptic potential. Figure 1 represents a computed unitary postsynaptic potential together with a typical experimental one, and shows good agreement, both qualitative and quantitative, between the two.

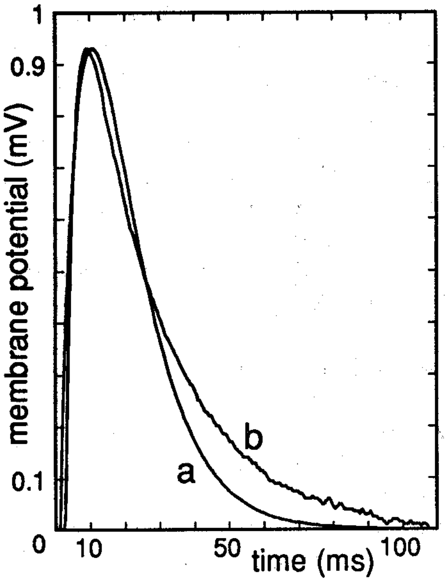

Fig. 1. Unitary excitatory postsynaptic potential: (a) computed with the model, (b) experimentally recorded.

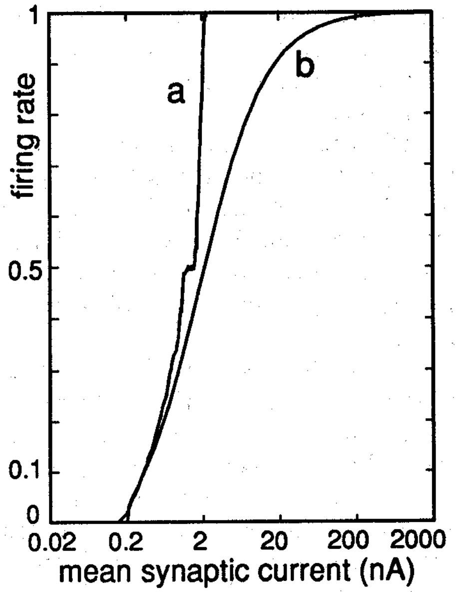

Fig. 2. Neuron transfer function: (a) measured with the model with $\tau_h = 100$ ms, (b) analytical approximation of eq. (7).

3. Derivation of a transfer function for the firing rate

A question that can be addressed with the model is the derivation of a transfer function for the neuron firing rates. This issue is of interest in neural modeling. First, because a sigmoid is often used in place of this transfer function, but this sigmoid is postulated rather than derived from underlying mechanisms; in particular, this raises difficulties to assign meaningful values to the parameters of the sigmoid (its slope and threshold). Second, because the conditions of existence of such a transfer function are themselves questionable. Its use implicitly assumes that the mean output activity can be deduced from the sole mean input activity, yet it is known that with an arbitrary nonlinear input–output relation-

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ship, the first statistical moment (the mean) of the output, generally depends not only upon the first moment of the input, but upon all its moments.

At time t, we define a mean value $\overline{x}(t)$ of a signal $x(t)$ over a time horizon τ_h, through:

$$\overline{x}(t) = (1 - \frac{\Delta t}{\tau_h})\overline{x}(t - \Delta t) + \frac{\Delta t}{\tau_h} x(t) . \qquad (5)$$

Equation (5) maintains an exponentially weigthed mean of the form:

$$\overline{x}(t) = \frac{\Delta t}{\tau_h} \sum_{t'=-\infty}^{t} x(t') \exp(-\frac{t - t'}{\tau_h}) . \qquad (6)$$

This type of mean exhibits several advantages. From a computational standpoint, it is accessible through a first order recursion. From a physical standpoint, it is the natural mean that is implemented by any (ubiquitous) first-order low-pass linear system with time constant $\tau_h \gg \Delta t$; as such it is thus "computable" by the neuron, when its membrane for instance is approximated by a leaky integrator.

The firing rate of neuron i at time t is then defined as $\overline{S}_i(t)$, and we examine its dependence upon the mean synaptic current $\overline{I}_i(t)$. Neuron i has been driven with input spike trains $E_j(t)$ with different independent stationary statistics (Poisson or Gaussian interspike times). The resulting means $\overline{S}_i(t)$ and $\overline{I}_i(t)$ were evaluated. We found a relationship between $\overline{S}_i(t)$ and $\overline{I}_i(t)$ that appears largely independent of the statistics of the inputs $E_j(t)$, and which is depicted in fig. 2a.

The result of fig. 2a tends to support the possibility of a transfer function that relates input and output first moments, independent of higher-order moments of the input. This outcome is not a specific property of the neuron nonlinearity, but rather it appears to be related to what we can call the central limit theorem of stochastic point processes. This theorem states [3] that, under not too restrictive conditions, a superposition of a large number of independent stochastic point processes (used as models for spike trains) tends to a Poisson process. The Poisson process has only one independent statistical moment. Consequently, in conditions where the input spike trains to a neuron are independent, and when they are in sufficient number (it is usually the case to reach the firing threshold of the postsynaptic neuron), then their superposition tends to approach a Poisson process, and as a result, independent influence of moments of order above one tends to disappear. We have verified that for the results of fig. 2a, the synaptic current $I_i(t)$ itself, generally displays negligible dependence upon the variance of the input trains $E_j(t)$ provided that they superpose in sufficient number to produce $I_i(t)$. Therefore, in conditions where the central limit theorem operates, the possibility of extracting an input–output transfer function $\overline{S}_i(t) = \text{fct}[\overline{I}_i(t)]$ relating first moments only, seems to be justified. In contrast, when these conditions break down, there is no *a priori* justification for a fixed input–output relationship between first moments only. With highly correlated input spike trains, we have observed that the output firing rate $\overline{S}_i(t)$ may indeed bear dependence upon higher-order moments of the input.

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Conditions where the central limit theorem applies may often be plausible in neural networks. However, they may not be of thorough validity. Futhermore, behaviors of individual spikes may sometimes be critical for the function of neural assemblies. These points have to be born in mind when developing neural network models where firing rate dynamics with input–output relationship on means, are used in place of individual-spike dynamics.

Under certain assumptions, it is possible to derive an analytical expression that approximates the input–output neuron transfer function [4], and that can be cast into the so-called Lapicque form [5]:

$$\begin{aligned} \overline{S}_i &= 0 && \text{if } \overline{I}_i \leq I_{\text{th}} , \\ \overline{S}_i &= \frac{1}{1-(\tau_m/T_r)\ln\left(1-I_{\text{th}}/\overline{I}_i\right)} && \text{if } \overline{I}_i > I_{\text{th}} , \end{aligned} \tag{7}$$

with $I_{\text{th}} = G_m V_{\text{th}}$. Equation (7) defines a neuron transfer function $\overline{S}_i = f(\overline{I}_i)$ that is depicted in fig. 2b for a refractory period $T_r = 1\,\text{ms}$. Other models use a sigmoid for this transfer function.

4. Reduction to a model for firing rates

In order to derive a model describing the operation of the network only in terms of neuron firing rates, we shall linearize the previous equations. We approximate, in eq. (2) and (4), $[V_{\text{rev},ij} - V_i(t)]$ simply by $V_{\text{rev},ij}$. This simplification suppresses the possibility of nonlinear interactions between incoming spikes. We then deduce an equation that governs the mean synaptic current to neuron i, that reads:

$$\overline{I}_i(t+\Delta t) = (1-\frac{\Delta t}{\tau_s})\overline{I}_i(t) + \frac{\Delta t}{\tau_s} I_{\text{th}} \sum_j W_{ij}\overline{E}_j(t) , \tag{8}$$

with, for an excitatory synapse $W_{ij} = w_{ij} \times V_{\text{exc}}/V_{\text{th}}$, and for an inhibitory synapse $W_{ij} = w_{ij} \times V_{\text{inh}}/V_{\text{th}}$.

The output firing rate follows through the use of an input–output transfer function for the neurons $\overline{S}_i(t) = f[\overline{I}_i(t)]$, as given by eq. (7). In a network, the neuron inputs $\overline{E}_j(t)$ are formed by the outputs $\overline{S}_j(t)$.

5. Dynamic versus equilibrium properties

We have used separateley the model with spikes of eq. (1)–(3) and the model with rates of eq. (8), (7) to describe a situation that can be viewed as a phase transition in a neural network. In the model with spikes the temporal means are explicitly computed on the variables $S_i(t)$, and they can then be compared to the variables $\overline{S}_i(t)$ as they are produced by the model with rates.

A fully connected network of $N = 100$ neurons, is constructed with N^2 excitatory synapses w_{ij} which are randomly drawn with uniform probability out of the interval $[0, w_0]$, with w_0 a control parameter. We define an average activity of the network at time t as $\langle\overline{S}_i(t)\rangle = N^{-1}\sum_{i=1}^{N}\overline{S}_i(t)$. This average activity $\langle\overline{S}_i\rangle$ is computable (altough differently) in the model with spikes as well

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as in the model with rates, and it can be interpreted as an order parameter. Both models are initialized in a state with $\langle \overline{S}_i(0) \rangle = 1/2$, and the network is let to evolve. We observed that, for w_0 small, the network evolves to a final state with $\langle \overline{S}_i(+\infty) \rangle = 0$ (disordered phase). For w_0 large, the network evolves to a final state with $\langle \overline{S}_i(+\infty) \rangle > 0$ (ordered phase). The transition between disordered and ordered phases occurs at $w_0 = w_c$.

We found that the critical value w_c turns out to be different in the models with spikes ($w_c = 0.33$) and with rates ($w_c = 0.14$). Different also are the relaxation times that are required, at a given $w_0 > w_c$, to reach the equilibrium state $\langle \overline{S}_i(+\infty) \rangle > 0$ (of the order of 20 ms in the model with spikes, and about 10 times larger in the model with rates, for w_0 just above w_c). It is in fact not too surprising that these parameters that characterize critical or dynamic phenomena are predicted differently by a model with spikes or by a model with (mean) rates. But in addition, equilibrium properties, namely the value of $\langle \overline{S}_i(+\infty) \rangle > 0$ recorded at a given $w_0 > w_c$, come out different. For w_0 just above w_c we have $\langle \overline{S}_i(+\infty) \rangle = 1$ in the model with spikes, and $\langle \overline{S}_i(+\infty) \rangle = 0.56$ in the model with rates.

6. Conclusion

The neural network model that we presented here, although neglecting many aspects of neuron functioning, is detailed enough to convey both qualitative and quantitative significance. At the same time, it remains simple enough to allow the study of collective behaviors among large populations of neurons. It is specially useful under the discrete form adopted here, that leads to direct computer implementation. We believe that such a model provides a good compromise for many investigations on neural networks, with both qualitative and quantitative prospects. As illustrated here, it can help to assess the derivation of rate models, and it points to discrepancies between network properties when described with spike or rate dynamics.

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