Non-equilibrium Statistical Mechanics of Recurrent Networks with Realistic Neurons

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Abstract. Experimental evidence suggests that the precise timing of spikes might well be used by neurons for processing and storing information. Unfortunately, the mathematical analysis of recurrent networks with spiking neurons is highly non trivial. Most analytical studies have therefore focused on rate-based models, whereas recurrent networks with more realistic neurons tend to be studied numerically. We aim to bridge this gap, and construct realistic spiking neuron models which in recurrent networks still allow for the application of non-equilibrium statistical mechanical techniques.

1. Introduction

The nature of the neuronal code is one of the most intensively debated issues in modern neuro-sciences. In particular, the question of whether the exact timing of single spikes is important for transmitting information is still open (see [1] for an overview of neural coding). Synchronization and temporal correlation are observed experimentally in different brain areas and in different behavioral contexts [2, 3, 4, 5, 6], yet the role of such phenomena is still to be understood. Does a rate code capture the essential information to represent stimuli, or does the temporal sequence of spikes contain additional information ? In the latter case, what type of information is contained in the temporal code ? These questions have stimulated the development of new techniques for detecting temporal relationships in the firing of neurons, and to clarify their contribution to coding (see for example [7, 8, 9]). Spike timing has also become relevant in synaptic plasticity: adaptation of synaptic efficacy was shown to depend on the relative timing of the pre- and post synaptic spikes (see [10] for a review).

To the (mathematical) theorist spikes are unpleasant. Models based on firing rates are much easier to solve, and gave rise to a large body of theoretical research on many classes of recurrent neural networks with often sophisticated synapses, using tools from equilibrium and non-equilibrium statistical mechanics (see e.g. [11, 12] for overviews). When faced with the need to incorporate spikes, the difficulty of the theorist is to find a compromise between mathematical complexity and biological realism. The most accurate description of neural processes in recurrent networks is achieved upon

using Hodgkin-Huxley neurons, with spike-dependent synaptic plasticity. The Hodgkin-Huxley model describes the detailed dynamics of the ion channels generating the action potential, and there is no need to impose resets or time delays by hand [13]. However, solving analytically the equations of a recurrent network of such neurons is out of the question. Even at a the reduced level of two-dimensional spiking neuron models such as FitzHugh-Nagumo [14, 15], Morris-Lecar [16] or Abbott and Kepler [17] , we are not aware of attempts to apply the techniques of statistical mechanics to recurrent networks.

Most studies of recurrent networks with spiking neurons have been based on numerical simulations of integrate-and-fire type neurons (see e.g. [18]), including versions with additional conductances to reproduce different modes of firing [19]. Several such models have been proposed (see [20] for an excellent review). Attempts to carry out also a mathematical analysis are hampered by the presence in such models of a hard reset and refractory period, imposed by hand, which cause discontinuities in the dynamical laws (in contrast to the Hodgkin-Huxley equations, where such phenomena are generated autonomously by the non-linear equations). Those statistical mechanics analyses which have been published on networks of integrate-and-fire neurons (e.g. [21, 22, 23]) have been restricted to relatively simple synapses and uncorrelated synaptic currents.

Our research programme has two aims. Firstly, to construct a realistic (spiking) neuron model, which in a network model still allows for the application of non-equilibrium statistical mechanics. Secondly, to carry out statistical mechanical studies of recurrent neural networks, equipped with such neurons, to shed light on the various open questions relating to the information processing potential of spikes. Let us now be specific. We regard a neuron model as sufficiently realistic if it satisfies the following:

- It must describe spikes, with properties (height, frequency, inter-spike interval statistics, etc) which can be tested against experiments.
- It must involve transparent physical model parameters, such as characteristic time-scales and voltages, which can be assigned realistic values.
- It must describe a qualitatively correct dynamics of membrane and axon potentials.

The competing requirements of mathematical tractability are:

- A small number of dynamical variables per neuron, described by coupled and *continuous* first-order differential equations.
- For a *given input current*, the core differential equations must be linear in the dynamical variables (i.e. all non-linearities come in via the input currents).

The origin of the second mathematical requirement will be made clear in the section two. Although many spiking neuron models have been proposed over the years, none appears to meet the last two criteria (the models with continuous equations, e.g. [14, 15, 16, 17], are all fundamentally non-linear; integrate-and-fire type models require the membrane potential reset). There are two routes which one could try to find a canonical model: the first is to attempt transformations of existing continuous models, the second is to construct a phenomenological model in the spirit of [24]. In section three we present and analyze a phenomenological spiking model which appears to meet our criteria.

2. Non-equilibrium statistical mechanics of graded-response neurons

To illustrate the origin of our mathematical conditions, and thereby justify our introduction of a new neuron model, we first turn to a simpler situation, viz. recurrent networks of N so-called graded response neurons:

$$\frac{d}{dt}u_i(t) = f_i(\mathbf{u}) + \eta_i(t) \qquad f_i(\mathbf{u}) = \sum_j J_{ij}\ g[u_j(t)] - u_i(t) \qquad (1)$$

with u_i giving the membrane potential of neuron i (the microscopic state vector is $\mathbf{u} = (u_1, \ldots, u_N)$), J_{ij} defines the synapse connecting neuron j to neuron i, $g[z] = \frac{1}{2}[\tanh(\gamma z) + 1]$ (or a similar sigmoidal function), and with a Gaussian white noise $\eta_i(t)$. The objective in statistical mechanics is to derive from (1), in the limit $N \to \infty$, closed deterministic equations for suitable macroscopic quantities ('order parameters').

In the simplest case $J_{ij} = J/N$ the suitable macroscopic object is the membrane potential distribution $\rho(u) = \frac{1}{N}\sum_i \delta[u - u_i]$, which for $N \to \infty$ is found to obey

$$\frac{d}{dt}\rho(u) = -\frac{\partial}{\partial u}\left\{\rho(u)\left[J\int du'\ \rho(u')g[u'] - u\right]\right\} + T\frac{\partial^2}{\partial u^2}\rho(u) \qquad (2)$$

This equation is of the so-called Time-Dependent-Ornstein-Uhlenbeck form (TDOU), and therefore has the Gaussian solution

$$\rho_t(u) = [2\pi\Sigma^2(t)]^{-\frac{1}{2}}e^{-\frac{1}{2}[u-\overline{u}(t)]^2/\Sigma^2(t)} \qquad (3)$$

in which $\Sigma(t) = [T + (\Sigma^2(0) - T)e^{-2t}]^{\frac{1}{2}}$, and $\overline{u}$ evolves according to

$$\frac{d}{dt}\overline{u}(t) = J\int\frac{dz}{\sqrt{2\pi}}e^{-\frac{1}{2}z^2}\ g[\overline{u}(t) + \Sigma(t)z] - \overline{u}(t) \qquad (4)$$

We can now calculate virtually anything we like (see [12] for details). For many-particle systems with real-valued degrees of freedom the order parameters will normally be distributions. The crucial property which allowed us here to solve (2) (which one generally will not be able to do), is the TDOU form, which relies on the explicit u-dependent part in the first (force) term of (2) to be *linear*.

To confirm that it is not the simple choice $J_{ij} = J/N$ for the synapses in (1) which led to solvability, one can inspect attractor networks of the type (1), in which p binary patterns $\boldsymbol{\xi}^\mu = (\xi_1^\mu, \ldots, \xi_N^\mu) \in \{-1, 1\}^N$ are stored via separable Hebbian-type synapses: $J_{ij} = (2/N)\sum_{\mu=1}^p \xi_i^\mu\xi_j^\mu$. Adding suitable thresholds $\theta_i = -\frac{1}{2}\sum_j J_{ij}$ to the currents in (1), and choosing the same non-linearity $g[z] = \frac{1}{2}(1 + \tanh[\gamma z])$ would then give

$$\frac{d}{dt}u_i(t) = \sum_{\mu\nu}\xi_i^\mu A_{\mu\nu}\frac{1}{N}\sum_j \xi_j^\nu\tanh[\gamma u_j(t)] - u_i(t) + \eta_i(t)$$

It turns out [12] that the order parameters are now more complicated than the simple membrane potential distribution, but one one again finds a TDOU process, and after further (exact) mathematical manipulations one can derive the following equation for the recall quality $m(t)$ during retrieval of a pattern from memory:

$$m(t) = \int Dz\ \tanh\left[e^{-t}\log[\frac{1+m_0}{1-m_0}]^{\frac{1}{2}} + \gamma[\int_0^t ds\ e^{s-t}m(s) + z\sqrt{T(1-e^{-2t})}]\right] \qquad (5)$$
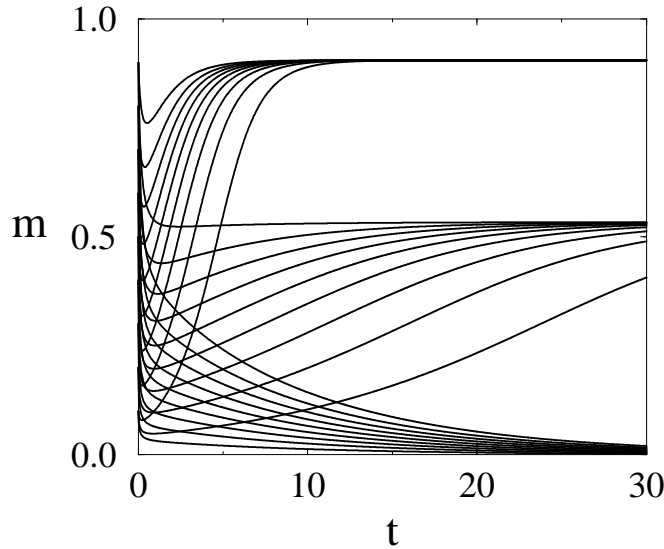
Figure 1. Recall in attractor networks with graded-response neurons and Hebbian synapses, away from saturation. Gain parameter: $\gamma = 4$. Lines: recall amplitudes $m = (2/N) \sum_i \xi_i^\nu s_i$ as functions of time, for $T = 0.25$ (upper set), $T = 0.5$ (middle set) and $T = 0.75$ (lower set), following different initial values $m_0 \in \{0.1, 0.2, \ldots, 0.8, 0.9\}$.

Solving (5) numerically leads to graphs as shown in figure 1 for $\gamma = 4$ and noise levels $T \in \{0.25, 0.5, 0.75\}$. Compared to recall in large networks of binary networks (away from saturation, where m would simply follow from the trivial equation $\frac{d}{dt} m = \tanh(m/T) - m$) one immediately observes richer behaviour, e.g. non-monotonicity.

3. The canonical neuron model and its properties

Full details of our model and the rationale behind its ingredients will be given elsewhere. It combines the spirit of [24] with the notion that we do not aim to *explain* spikes (unlike the Hodgkin-Huxley model), but may take them as given. We accept the existence of an oscillating system, described by a phase ϕ, and an instantaneous frequency (or inverse inter-spike interval) $f_i = \frac{d}{dt}\phi$. A silent neuron has $f = 0$; an input current (provided above a critical value) leads to an increase of f and initiates firing:

$$\frac{d}{dt}\phi = f \qquad \tau_c \frac{d}{dt} f = F(I) - f \tag{6}$$

Spikes are generated when $\phi = 0, 1, 2, 3, \ldots$. The membrane potential U_m is seen as the sum of a passive part U and a 'spike' part V. The latter is a periodic function of the phase ϕ (peaked at $\phi = 0, 1, 2, 3, \ldots$), the former evolves according to a leaky integrator equation, complemented by a term which generates a reset upon spike emission:

$$V \quad = \tau_s V_{\max} \; \delta_{\tau_s}\left[\frac{\sin(\pi\phi)}{\pi f}\right] \tag{7}$$

$$C \frac{d}{dt} U = I - \frac{U}{R} - 2CU \; \delta_{\tau_s}\left[\frac{\sin(\pi\phi)}{\pi f}\right] \tag{8}$$
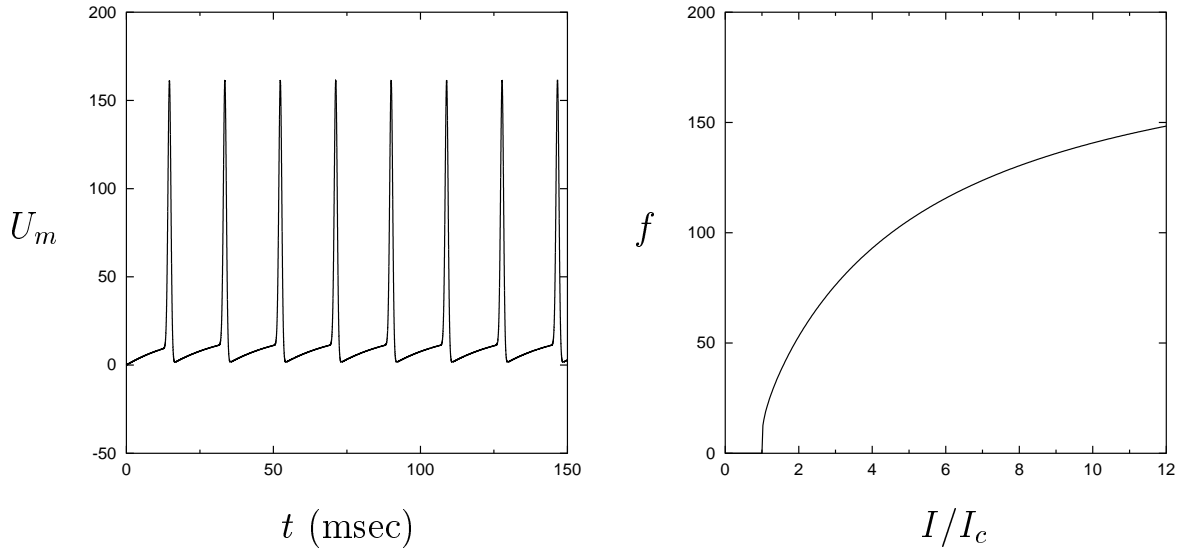
Figure 2. Properties of our neuron model. Left: combined membrane potential $U_m = U + V$, for constant input current of strength $I = 2I_c$ (see main text for model parameters). Right: stationary state current-to-frequency relation (with f in Hz).

Here τ_s is the spike duration, and $\delta_{\tau_s}[u]$ is a peaked function of width τ_s, normalized according to $\int du\ \delta_\tau[u] = 1$ and obeying $\lim_{\tau \to 0} \delta_\tau[u] = \delta[u]$. The rest membrane potential is defined as zero. The function $F(I)$ in (6) follows self-consistently from (8) using standard arguments (see e.g. [20]) and upon assuming the existence of a threshold membrane potential U_c and a refractory period τ_r:

$$I < I_c = U_c/R: \quad F(I) = 0 \tag{9}$$

$$I > I_c = U_c/R: \quad F(I) = \{\tau_r - RC \log[1 - U_c/RI]\}^{-1} \tag{10}$$

(shown in figure 2). The function V also serves as the axon potential. The model (6,7,8) has seven measurable parameters: four characteristic times, τ_s (spike duration), τ_c (ion channel response time), $\tau_m = RC$ (membrane leakage time), τ_r (refractory period), two voltages, U_c (threshold membrane potential), $V_{\max}$ (spike height), and R (membrane resistance). Given realistic values for these parameters, one observes realistic behaviour (see figure 2, which was generated with $I = 2I_c$, $\tau_s = 1$ ms, $\tau_c = 0.5$ ms, $\tau_m = 20$ ms, $\tau_r = 5$ ms, $U_c = 10$ mV, $V_{\max} = 100$ mV).

Mathematically, the key feature of our model is that equation (8) for the membrane potential is a *slave* equation: it was only relevant in finding $F(I)$, but we do not need $U(t)$ if we are interested only in spike dynamics ! Even in a network, any axonal signal $V_i(t)$ will be a function only of $\phi_i(t)$, so when dealing with N neurons, involving $\{\phi_i, f_i\}$ for $i = 1, \ldots, N$, the equations for the $\{\phi_i, f_i\}$ would close in themselves (with currents also expressed in terms of the $\{\phi_i\}$). Since (6) are *linear* in (ϕ, f), the non-linearities are concentrated in the input current, and one will find TDOU processes for distributions of the (ϕ_i, f_i); thus we can launch non-equilibrium statistical mechanical calculations.

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