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A brief history of excitable map-based neurons and neural networks

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ABSTRACT

This review gives a short historical account of the excitable maps approach for modeling neurons and neuronal networks. Some early models, due to Pasemann (1993), Chialvo (1995) and Kinouchi and Tragtenberg (1996), are compared with more recent proposals by Rulkov (2002) and Izhikevich (2003). We also review map-based schemes for electrical and chemical synapses and some recent findings as critical avalanches in map-based neural networks. We conclude with suggestions for further work in this area like more efficient maps, compartmental modeling and close dynamical comparison with conductance-based models.

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1. Introduction

The number of neurons in the human brain (86 billions (Azevedo et al., 2009)) is nearly six times the number of trees in Amazonia. So, brain modelers must not forget that their job is comparable to modeling patches of Amazonia, a staggering task. Since well developed models for single neurons already exist (Bower and Beeman, 2003; Carnevale and Hines, 2006), with complex dendritic geometry and tens of equations and parameters (Dayan and Abbott, 2001), it is not obvious what modeling level we should use in general.

As the proverbial forest not seen because of the trees, the detailed study of singular neurons is an interesting subject *per se*, but it is perhaps not necessary to understand the macroscopic dynamics and function of neuronal networks. Indeed, neuronal networks present collective phenomena, like synchronization (Ibarz et al., 2011), waves (Cross and Hohenberg, 1993; Gua et al., 2013; Wua et al., 2013) and avalanches (Chialvo, 2010). The history of neuronal networks modeling is marked by this trade-off between analytical/computational tractability and biological realism.

Since the connection between neurons is only sensitive to the action potentials that arrive at (electrical or chemical) synapses, the important thing is to model the dynamics of these action potentials (their frequency or inter-spike intervals, if they come in bursts or single events, etc.). The emphasis in modeling the transmembrane voltage dynamical behavior is called a phenomenological approach (in contrast to a mechanistic or biophysical approach), leading to a class of neuron models where map-based neurons are a new and promising tool. This paper gives a brief account of the pioneering proposals of neuronal maps due to Chialvo (1995), Pasemann (1993, 1997), Kinouchi and Tragtenberg (1996) and Kuva et al. (2001) and compare them with more recent proposals due to Rulkov (2001, 2002) and Izhikevich (2003), Izhikevich and Hoppensteadt (2004).

There are two main routes to achieve map-based neuron models with realistic dynamical properties. The first one is to start from Hodgkin–Huxley (HH) type models, composed by coupled nonlinear ordinary differential equations (ODE) which are already a simplification (due to spatial discretization) of full partial differential equations that describe the neuron membrane. Computational neuroscience models based on the HH formalism, called conductance-based neurons, is a well developed subject (Dayan and Abbott, 2001), but suffers from some limitations (de Schutter, 2010):

- The HH-type models consist in several nonlinear coupled ODEs: the simulation of a single neuron is orders of magnitude more costly than simplified neuron models;
- The biophysical data for constraining the parameter values (like capacitances, axial resistances, density of ion channels, etc.) is scarce and often obtained from diverse preparations (different animals, in vitro experiments, etc.). Most of the parameter ranges used in simulations are simply informed guesses.
- The remaining parameter space of these models is huge and suffer from the so called curse of dimensionality (Bellman, 2003). It is very costly to trace full phase diagrams, since with P parameters, for example, we can have $P(P-1)/2$ parameter planes. The minimal model of Hodgkin–Huxley, with only two active ion channels, has at least $P=40$ parameters (Dayan and Abbott, 2001).
- The set of parameters to be used for reproducing a given firing pattern is subdetermined. This means that the same dynamical behavior can be achieved by different sets of parameters. Adjusting these parameters to the known neuron behavior is susceptible of overfitting: the model reproduces the given data but do not generalizes well, for example, for different input situations.

In order to deal with these drawbacks, we may opt to reproduce the dynamical behavior of neurons instead of reproducing the involved biophysical mechanisms (mechanistic modeling). Starting from a complicated HH-model, perhaps even a multicompartmental model, we can perform a sequence of simplifications more or less justified in order to obtain simpler models with fewer equations and lumped parameters (de Schutter, 2010). Examples of these reduced ODE based models are the FitzHugh–Nagumo excitable neuron (FitzHugh, 1955; Nagumo et al., 1962), the Hindmarsh–Rose bursting neuron (Hindmarsh and Rose, 1984) and the Izhikevitch model (Izhikevich, 2003). If we numerically integrate these ODEs with the Euler method with a large time step, we can arrive at maps with similar dynamical properties as the original systems (Rulkov, 2002; Izhikevich, 2004).

Phenomenological modeling can start the other way around. This occurs because the phenomena to be studied set the level of modeling. Continuing with our forest modeling analogy, if our interest is to study a single tree (or neuron), a biophysical HH-like modeling is desirable. But if we want to understand, say, the propagation of a forest fire, the modeling of the tree biophysics is mostly immaterial, and trees could be represented by sites with two states (0 = normal, 1 = burnt) (Christensen et al., 1993). In the same vein, McCulloch and Pitts (1943) proposed a binary threshold neuron, whose state is given by 0 = rest and 1 = firing. With this method, one starts with discrete time systems and searches for increasing complexity until a dynamical model that reproduces the full phenomenology of neuronal dynamics is achieved.

Both approaches tend to converge at a middle ground formalism: dynamical systems with discrete space and discrete time, but with continuous state variables, that is, dynamical maps (Ibarz et al., 2011). Neuronal networks composed by these maps will be an instance of coupled maps lattices (CMLs) (Kaneko, 1993, 1994). In this paper, we review the early proposals of map-based neuron models and the coupling schemes used to create such coupled maps networks. We also suggest some unexplored research topics that could be examined both with conductance-based neurons and map-based neurons, in order to stimulate computational neuroscientists to use both approaches in a synergetic way.

This review is intended to organize the map-based neuron models in sequential time (Section 2), highlighting two families of map-based modeling: (I) back from McCulloch and Pitts (1943) approach to the Kinouchi and Tragtenberg (1996) and its extension (Kuva et al., 2001) and (II) back from Chialvo (1995) to Rulkov (2002) and Izhikevich (2003). Then, we perform a short computational comparison of the main neuronal models (Section 3). The main purpose of Section 4 is to neatly list the most relevant couplings which may be used to link maps into networks, only pointing to the most prominent results obtained with them. We finally terminate the review with some important remarks in Section 5.

2. History of map-based neurons

This section is devoted to draw a line which connects the early modeling of neurons, as state machines, to the most recent and powerful models, which are dynamical systems on their own, presenting their most relevant features and reviewing some models that are still not well known, although they have been used recently to model neural networks.

The generalized mathematical form of any map is:

$$\vec{X}(t+1)=\vec{F}(\vec{X}(t)), \tag{1}$$

where $\vec{F}:\mathbb{R}^n\to\mathbb{R}^n$ is any vector function and we are assuming that the curve given by the set of values $\left\{\vec{X}(0),\vec{X}(1),\vec{X}(2),\ldots\right\}$ defines the temporal evolution the system. In the case of neurons,