



Computational Neuroscience

Spike, rate, field, and hybrid methods for treating neuronal dynamics and interactions

P.A. Robinson^{a,b,*}, J.W. Kim^a^a School of Physics, The University of Sydney, Sydney, New South Wales 2006, Australia^b Brain Dynamics Center, Sydney Medical School – Western, The University of Sydney, Westmead, New South Wales 2145, Australia

ARTICLE INFO

Article history:

Received 21 September 2011

Received in revised form

25 December 2011

Accepted 31 January 2012

Keywords:

Neural computations
Computational methods
Neural models
Neural networks
Neural field theory
Neural simulations
Analytic methods

ABSTRACT

Spike-, rate-, and field-based approaches to neural dynamics are adapted and hybridized to provide new methods of analyzing dynamics of single neurons and large neuronal systems, to elucidate the relationships and intermediate forms between these limiting cases, and to enable faster simulations with reduced memory requirements. At the single-neuron level, the new approaches involve reformulation of dynamics in synapses, dendrites, cell bodies, and axons to enable new types of analysis, longer numerical timesteps, and demonstration that rate-based methods can predict spike times. In multineuron systems, hybrids and intermediates between spike-based and field-based coupling between neurons are used to provide stepping stones between descriptions based on pairwise spike-based interactions between neurons and ones based on neural field-based interactions within and between populations, including arbitrary spatial structure and temporal delays in the connections in general. In particular, a new *neuron-in-cell* approach is introduced that is a hybrid between neural field theory and spiking-neuron models in analogy to particle-in-cell methods in plasma physics. This approach enables large speedups in computations while preserving spike shapes and times. Various approaches are illustrated numerically for specific cases.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

There are two well-known limiting perspectives on modeling large neural systems. One is to simulate large numbers of individual neurons that interact pairwise by means of spikes. In the opposite limit, neural firing rates are followed and neural properties and states are averaged over many neurons to study large-scale mean dynamics using field theories. These limits are analogous to molecular vs. continuum approaches to analysis of materials, or to microscopic vs. thermodynamic approaches to phase transitions. However, as the present paper elucidates, they are not the only possibilities and many intermediate forms can exist.

Spiking neural networks are most directly linked to the underlying neural biophysics, but are extremely computationally intensive to simulate. On the other hand, neural field theories omit more biophysical details, but are better suited to uncovering multiscale and emergent phenomena. Choosing the correct level of description is essential to obtain insights in a tractable form, and the most biophysically detailed approach is not always optimal. For example, this parallels the fact that it is much easier (and usually more

useful) to analyze pressure waves in a gas by treating it as a continuum than by computing the trajectories and collisions of all its constituent molecules, even though these ultimately determine its properties.

To understand the dynamics of any complex, multiscale system in detail, it is necessary to understand not only its limiting cases and the methods applying to them, but intermediate cases and the boundaries and overlaps between their regimes of validity. Thus, in more established areas of physics, one encounters disciplines such as nonequilibrium thermodynamics, and the theory of fluctuations in mesoscopic systems that bridge between the limiting cases of molecular dynamics and thermodynamics and allow an informed choice of the correct level of description to treat specific phenomena. To date, however, much less has been done to understand intermediate cases between spiking-neuron and neural-field approaches – the major emphasis of the present paper.

Two aspects determine the feasibility of large scale neural computations – the dynamics of individual neurons, and that of interactions between neurons. Thus, apart from the large numbers of neurons and synapses involved [e.g., up to 10^4 neurons to represent 1 mm² of cortex (Markram, 2006), or $\sim 10^7$ neurons to represent the thalamocortical system (Izhikevich and Edelman, 2008)], a limiting factor is the need to track neural dynamics on the timescale of individual spikes (typically requiring timesteps $\ll 1$ ms) even though spike rates may be only a few per second.

* Corresponding author at: School of Physics, The University of Sydney, Sydney, NSW 2006, Australia. Tel.: +61 2 9351 3779; fax: +61 2 9351 7726.

E-mail address: robinson@physics.usyd.edu.au (P.A. Robinson).

Adaptive stepsize control can be implemented to speed computations for a single neuron by increasing the stepsize between spikes, but when large numbers of neurons are simulated, the timestep is set by the finest required resolution because spikes are always present.

One way to speed simulations has been to use simplified neuronal dynamics that can be computed in fewer operations per timestep, an approach that has been extensively discussed elsewhere and shown to be able to yield large speedups (Gerstner and Kistler, 2002; Izhikevich, 2004), leading to rapidly increasing use. The reader is referred to the cited references for details on the dynamics of networks of spiking neurons, as the literature is too vast to review here and our present focus is on methods, rather than specific applications. One class of simplified neuronal dynamics results if one views each neuron as undergoing spike-generating nonlinear oscillations. It is then possible to define the oscillation phase, as in Kuramoto's influential work (Tass, 1999; Gerstner and Kistler, 2002; Kuramoto, 1984; Acebron et al., 2005). One aim of the present work is to show how phase can, perhaps paradoxically, be used to extract spike-timing information from rate-based analyses.

Another approach to dealing with large assemblies of interacting neurons has been to replace individual spikes by a mean spike rate for each individual neuron (Ermentrout, 1994; Robinson et al., 2008), or more commonly to average this spike rate over many neurons to yield a population rate (Wilson and Cowan, 1973; Bressloff and Coombes, 2000; Gerstner and Kistler, 2002; Deco et al., 2008; Freeman, 1975; Dayan and Abbott, 2001; Kempter et al., 1999; Nunez, 1995; Shriki et al., 2003; Ostojic and Brunel, 2011). These approaches avoid integration of spike profiles and enable faster and larger simulations of rates. Neural field theories (NFTs) take this to the next stage by examining the dynamics of means (and sometimes higher moments) of rates, soma potentials, and other neural properties, averaged over spatial scales large enough to include many neurons in the average to yield mean-field descriptions of neural activity (Beurle, 1956; Amari, 1974; Wilson and Cowan, 1973; Nunez, 1974, 1995; Ermentrout, 1994; Wright and Liley, 1996; Jirsa and Haken, 1996; Robinson et al., 1997; Steyn-Ross et al., 1999; Robinson, 2005; Deco et al., 2008; Gerstner and Kistler, 2002; Coombes, 2005; Marrieros et al., 2008; Touboul and Ermentrout, 2011). Neural mass theory (NMT) is valid when the spatial scale of each neural population is sufficiently small that spatial structure and time delays within it can be neglected compared to the scales of the phenomena of interest; in this limit each population acts as a single lumped entity, or mass (Freeman, 1975; Deco et al., 2008). The works cited, and numerous others, have explored the requirements to obtain rate-based descriptions from spike-based ones, and to derive neural field theory. However, the focus has chiefly been on the limiting cases, rather than what intermediates can exist, which is the present aim.

It appears to be widely assumed that if a rate-based approach is adopted, all information about spike timings is lost. Consequently, studies have not fully exploited the fact that, because the instantaneous spike rate of even a single neuron is related to its rate of phase change, rate-based formulations can be used to estimate spike timings, as the present paper demonstrates. Thus, the choice between spike- and rate-based approaches is not an all-or-nothing decision – intermediate approaches exist, and can yield significant computational advantages through simplicity and longer numerical timesteps.

Turning from internal neuronal dynamics to interactions between members of large neural ensembles, we show here that close examination of axonal, synaptic, and dendritic dynamics enables spike-based interneuronal communications to be treated without resolving the spike timescale. This can be achieved by applying synaptic and dendritic dynamics (which temporally broaden the influence of spikes on postsynaptic neurons) to

the spikes *before* axonal transmission, rather than after, thereby enabling longer simulation timesteps.

Spike-based communications between neurons are usually computed pairwise, leading to a runtime $T \sim N^2$ for N neurons, in general. However, if the interactions between neurons depend only on their relative locations, we show that large speedups can be achieved by communicating spikes as contributions to fields that mediate the interactions, just as electric fields mediate interactions between charged particles. This approach reduces the runtime to $T \sim N$, as in analogous particle-in-cell (PIC) simulations of plasmas (Dawson, 1983); we thus term it the *neuron-in-cell* (NIC) method. Notably, it retains local spiking dynamics while speeding computation of neuronal interactions.

Fields are commonly used to communicate rates in continuous systems. More generally, the present work shows that these rates can also apply to individual neurons in rate-based NIC methods, or to averages over populations in population network models, with pairwise interactions between neural populations that represent nodes in a coarse-grained representation of neural tissue (Kaiser, 2007; Kaiser et al., 2007; Bullmore and Sporns, 2009; Gray and Robinson, 2008). The latter approach enables computations in a time $T \sim P^2$ for P populations, independent of N . Alternatively, if each type of neuron is taken to constitute a population that is parametrized by the geometrical coordinates of its constituents, one arrives at neural field theory (NFT), which enables computations in a runtime $T \sim P$, independent of N . NFT then reduces to neural mass theory (NMT) when the tissue can be viewed as a lumped mass (Freeman, 1975; Deco et al., 2008), making T independent of N and P .

The present work thus re-examines a number of assumptions, methods, and insights in the literature to elucidate the relationship between spike-based and rate-based neural dynamics, and between pairwise and field-based interactions. Contrary to most analyses, the emphasis is on the intermediate cases, rather than the limiting forms, and each yields new methods and insights. The work ties together existing results and provides multiple new starting points for theoretical and computational analyses that will enable increased speed of computation and flexibility in choosing the best method to balance physiological realism and numerical tractability in applications. This array of intermediate possibilities will enable increased clarity with regard to the domains in which spike-based, rate-based, and hybrid approaches are most useful, and boundaries and overlaps of these domains.

The structure of the paper is as follows: because the statements and derivations of the various methods are themselves the main results of the paper, Section 2 is a combined Methods and Results section, with each subsection containing a specific set of outcomes. In Section 2.1 we briefly review a spike-based description of fast-spiking and bursting neurons to serve as a concrete benchmark system for testing and verifying a number of the ideas in the paper. We also briefly explain how these ideas can be generalized to other systems. In Section 2.2 it is demonstrated that a rate-based approach to this system yields excellent approximations of both spiking and bursting dynamics. Section 2.3 shows how spike timings can be extracted from single-neuron rate-based dynamics. Section 2.4 then expresses the external current that drives single-neuron dynamics in terms of spikes from afferent neurons, placing it in a form suitable for analysis in subsequent sections. In Section 2.5 it is shown that the effects of synaptic and postsynaptic dynamics (synaptic processes, dendritic propagation, and soma charging) can mathematically be replaced by a form of preaxonal spike smoothing, thereby increasing the allowable timestep in simulations of networks of interacting neurons. Runtimes and storage requirements for large-scale pairwise-coupled spiking neurons and neuronal population simulations are briefly reviewed in Section 2.6. We introduce our *neuron-in-cell* (NIC) approach in Section 2.7, in

Download English Version:

<https://daneshyari.com/en/article/6269315>

Download Persian Version:

<https://daneshyari.com/article/6269315>

[Daneshyari.com](https://daneshyari.com)