

Simplicity and efficiency of integrate-and-fire neuron models

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Abstract

Lovelace and Cios recently proposed a “very simple spiking neuron (VSSN) model” for simulations of large neuronal networks as an efficient replacement for the integrate-and-fire neuron model [Neural Comput 20:65–90, 2008]. We argue that the VSSN model falls behind key advances in neuronal network modeling over the past 20 years, in particular techniques that permit simulators to compute the state of the neuron without repeated summation over the history of input spikes and to integrate the subthreshold dynamics exactly. State-of-the-art solvers for networks of integrate-and-fire model neurons are substantially more efficient than the VSSN simulator and allow for routine simulations of networks of some 10^5 neurons and 10^9 connections on moderate computer clusters.

1 Introduction

The simulation of large-scale neuronal networks requires efficient algorithms. To this end, Lovelace & Cios (2008) recently developed a “very simple spiking neuron (VSSN) model” as an alternative to the widely used integrate-and-fire neuron model. Lovelace & Cios claim that their model is mathematically sim-

pler than the integrate-and-fire neuron, more accessible to visual inspection and understanding, and significantly more efficient to simulate numerically. We beg to differ.

Considering the mathematical simplicity of the models, the subthreshold dynamics of the integrate-and-fire neuron with α -function current input is described completely by three linear first-order time-invariant ordinary differential equations (see below). The full power of mathematical analytical techniques can thus be applied to networks built of integrate-and-fire neurons. Burkitt (2006a; 2006b) recently summarized the state-of-the-art in integrate-and-fire neuron modelling, and Brunel (2000) is an example for a specific influential result. Without re-deriving such results or arriving at exciting new ones, the claim of simplicity of the VSSN is hardly substantiated. The VSSN is specified by a set of equations applying to different aspects of neuronal dynamics, and yielding a description of neuronal dynamics by piecewise linear functions. While these functions might look simple, they are difficult to handle analytically, requiring many case distinctions.

Neuronal network simulations require solutions for three tasks: subthreshold integration of neuronal dynamics, determination of threshold crossings, and spike exchange. In what follows, we first review the state-of-the-art in

subthreshold integration and demonstrate that well-established techniques are far simpler than the VSSN approach. We then compare the benefits of push and pull methods for spike exchange. Finally, we present benchmark results supporting our analysis. Methods for the determination of threshold crossings, receive much attention in the literature at present and we do not cover them here (Hansel et al., 1998; Shelley & Tao, 2001; Morrison et al., 2007; Brette, 2007).

2 Integrating subthreshold dynamics

At first sight, the most difficult part of integrating the subthreshold dynamics of point neurons is to handle all impinging synaptic currents. Lovelace & Cios (2008) dismiss the leaky integrate-and-fire model because they consider it necessary to sum explicitly over the entire input history of each neuron in every time step to calculate the neuron state and to integrate the subthreshold dynamics with a very small time-step to achieve the desired accuracy. Fortunately, this is not so: the α -function, commonly used to describe the time course of synaptic input currents, is the solution to the critically damped harmonic oscillator subject to a velocity kick. Since this is a second order

linear time-invariant (LTI) dynamic system, the total current resulting from the entire input history of a synapse is the solution of the differential equation for the superposition of all velocity kicks, that is, all input spikes. Thus, the state variables automatically conserve the history of events and no book-keeping of spike times, or repeated summation over past spikes, is required. Furthermore, the equations of all synapses with identical time constants can be lumped into a single set of equations. Individual synaptic events can still have arbitrary amplitudes or “weights” because, unlike the time constant, the weight only enters through the initial condition set by the kick. Wilson & Bower (1989) and Bernard et al. (1994) are early accounts of this approach, while Srinivasan & Chiel (1993) arrived at an exact solution with two state variables without reference to differential equations.

Rotter & Diesmann (1999) showed that the equation for the synaptic currents and the membrane potential of integrate-and-fire neurons can be integrated exactly based on general properties of LTI systems; note that Eq. (1.9) in Lovelace & Cios (2008) is identical to Eq. (3) in Rotter & Diesmann (1999). If synaptic events only occur on an equidistant time-grid, a constant propagator matrix evolves the state of the system from one position

on the grid to the next by multiplication with the state vector:

$$\begin{pmatrix} \alpha_1 \\ \alpha_2 \\ V \end{pmatrix} \leftarrow \begin{pmatrix} a & 0 & 0 \\ b & a & 0 \\ c & d & e \end{pmatrix} \times \begin{pmatrix} \alpha_1 \\ \alpha_2 \\ V \end{pmatrix} .$$

Here, V is the membrane potential and α_1 and α_2 the two variables describing the synaptic current. The coefficients a, \dots, e are given by analytical expressions, which only depend on the parameters of the system and the computation step size (see Morrison et al., 2007, for the particular example studied here). As the matrix is lower triangular, the state variables can be updated “in place” in the sequence $\alpha_1 \rightarrow \alpha_2 \rightarrow V$; no temporary variable is required. The propagator matrix takes a particularly simple form ($c = 0$, $b = d = 1$) in a suitable basis, allowing for very efficient hardware implementations of this updating scheme (Guerrero-Rivera et al., 2006). Rotter & Diesmann (1999) also showed that a wide range of neuroscientifically relevant input functions can be integrated exactly using this scheme, including constant, piecewise linear and sinusoidally oscillating functions.

3 Spike exchange

Besides the efficiency of the simulation of individual neurons, it is the representation of connections and the exchange of spike events that determines the efficiency of a network simulation. Lovelace & Cios (2008) correctly state that a simulation scheme in which the synaptic state is stored with the presynaptic neuron scales linearly with the number of synaptic connections and is independent of spike rate. This does not guarantee, though, that a scheme where the postsynaptic neuron requests the neuron state from the presynaptic one is faster than the reverse scenario, where the presynaptic neuron notifies all postsynaptic targets about spikes.

The postsynaptic neuron has to interrogate the presynaptic neuron in each computation time step, leading to NK operations in each time step, where N is the number of neurons and K the (average) number of connections per neuron. The presynaptic neuron, however, only needs to transmit information upon the emission of a spike, leading to $\lambda h NK$ operations, where λ is the average firing rate and h the computation time step. Thus, the presynaptically triggered update is faster as long as $\lambda h < 1$ corresponding to $\lambda = 1000 \text{ Hz}$ at a resolution of $h = 1 \text{ ms}$, well outside the physiological regime.

In very sparse networks, where the number of synapses is on the same order of magnitude as the number of neurons, summing over all inputs may be a plausible strategy. In most biologically realistic networks, though, the number of connections exceeds the number of neurons by several orders of magnitude, demanding activity-dependent algorithms to ensure efficiency. We conclude that it is more efficient to have neurons page their postsynaptic targets whenever the former fire a spike, than to have all neurons interrogate their presynaptic neurons upon every time step; this is also the basis of event-based simulation of neuronal networks (Delorme & Thorpe, 2003; Makino, 2003; Rochel & Martinez, 2003; Brette, 2006, 2007; Tonnelier et al., 2007).

4 Benchmarks

The notion of the efficiency of a simulation scheme is rather loosely defined in the computational neuroscience literature. Morrison et al. (2007) argue that efficiency should be defined as the simulation time required to achieve a prescribed accuracy goal. A scheme which constrains spike times to a time-grid is unsatisfactory in this respect if high accuracy is required, because the integration error drops only linearly with decreasing computation time step

(Hansel et al., 1998; Shelley & Tao, 2001).

Lovelace & Cios (2008) use their VSSN model to simulate a model of the echolocation circuitry in bats. Their network contains 13,000 neurons and 38,000 synapses, i.e., fewer than three synapses per neuron, corresponding to a connectivity of just 0.02%. This is an extremely low value: local connectivity in cortical tissue is typically estimated at about 10%, leaving each neuron with some 1300 synapses and the network with some 17 million synapses in total.

Lovelace & Cios report that simulating 4.2 *milliseconds* biological time requires 40 seconds wall-clock time on a 1.6 GHz Pentium with a simulation time step of $h = 1\mu s$. For comparison, we simulated a variant of the Brunel network with 13,000 neurons and 39,000 synapses (Brunel, 2000) using the NEST simulator (Gewaltig & Diesmann, 2007) on an IBM ThinkPad X60s computer using one core of an Intel Centrino Duo processor at 1.6 GHz clock speed. Using our implementation of the integrate-and-fire neuron providing precise spike times independent of the resolution of the time grid (Morrison et al., 2007, canonical model), we observed simulation times of 3.2 seconds and 0.34 seconds, respectively, for resolutions $h = 1\mu s$ and $h = 10\mu s$ when simulating 4.2 ms biological time. This is between one and two orders of

magnitude faster than the simulations reported by Lovelace & Cios on comparable hardware.

5 Discussion

We believe that the problem of integrating the subthreshold dynamics of the integrate-and-fire model has largely been solved. Currently, work in the field focuses on more accurate and efficient methods to predict the time of the next threshold crossing of model neurons (Brette, 2007; Morrison et al., 2007). Another frontier is the development of simulators optimally exploiting the power of modern multi-processor, multi-core hardware (Djurfeldt et al., 2005; Migliore et al., 2006; Plesser et al., 2007). State-of-the-art simulators have reached a performance where networks of 100,000 neurons with realistic connectivity of 10%, i.e., 10^9 connections, can routinely be studied on moderate computer clusters with no more than 100 CPU cores (Morrison et al., 2007; Izhikevich & Edelman, 2008). Reaching this scale constitutes a qualitative step, because it allows us to study neurons with all their synapses: no scaling is required.

Choosing the right simulation strategy and software for a given research

problem is a crucial, but difficult task. A recent, collaborative review of existing simulators provides at least an overview over the functionality provided by various existing packages (Brette et al., 2007). A fair comparison of the efficiency of simulators for a set of given tasks would require a similar collaborative effort, as all simulator developers should be given a fair chance to ensure that their simulators are used in the best manner.

It appears that the development of simulation technology for computational neuroscience is still at a level of organization where we keep reinventing the wheel. In our opinion, there are two main causes for this regrettable situation: the lack of large-scale coordination in the field, in contrast to elementary particle physics, for example, and the difficulty of publishing the complex concepts and algorithms underlying advanced neuronal network simulations in an accessible format. Four recent reviews have partially addressed these problems (Brette et al., 2007; Djurfeldt & Lansner, 2007; Cannon et al., 2007; Djurfeldt et al., 2008) and one of us experiences successful coordination on a large scale within the EU FACETS project, while the International Neuroinformatics Coordinating Facility (INCF) provides a world-wide forum for coordinating our efforts in simulator development. We are confident that these initiatives will help the computational neuroscience community to es-

tablish shared standards within the coming years.

Acknowledgments

We thank Abigail Morrison for inspiring discussions. HEP acknowledges financial support from the Research Council of Norway (Grant no. 178892/V30 *eNeuro*), the Norwegian node of the INCF, a travel grant from the Norwegian University of Life Sciences and the hospitality of the RIKEN Brain Science Institute. MD acknowledges partial funding by DIP F1.2 and EU Grant 15879 (FACETS).

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