Fast and exact simulation methods applied on a broad range of neuron models

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Abstract

Recently, van Elburg and van Ooyen (2009) published a generalization of the Event-Based Integration Scheme for an Integrate-and-Fire neuron model with exponentially decaying excitatory currents and double exponential inhibitory synaptic currents, introduced by Carnevale and Hines. In the paper, it was shown that the constraints on the synaptic time constants imposed by the Newton-Raphson iteration scheme, can be relaxed. In this note, we show that according to the results published in D'Haene et al. (2009), a further generalization is possible eliminating any constraint on the time constants. We also demonstrate that in fact a wide range of linear neuron models can be efficiently simulated with this computation scheme, including neuron models mimicking complex neuronal behavior. These results can change the way complex neuronal spiking behavior is modeled: instead of highly non linear neuron models with few state variables, it is possible to efficiently simulate linear models with a large number of state variables.

In Carnevale and Hines (2002) and Hines and Carnevale (2004), an event driven approach was described for three types of Integrate-and-Fire Models. The most general model in these contributions, `IntFire4`, uses four time constants, τ_e for fast excitatory currents, τ_j and τ_i for a slower inhibitory current with rise time, and τ_m for the membrane. The model was described by the following set of differential equations:

$$\begin{cases} \dfrac{dV}{dt} & = -\dfrac{1}{\tau_m} V\left(t\right) + a_e e + a_i i \\ \dfrac{de}{dt} & = -\dfrac{1}{\tau_e} e \\ \dfrac{dj}{dt} & = -\dfrac{1}{\tau_j} j \\ \dfrac{di}{dt} & = -\dfrac{1}{\tau_i} i + a_j j. \end{cases}$$

In order to assure correct convergence of a Newton-Raphson iteration scheme, the following restrictions were imposed: $\tau_e < \tau_j < \tau_i < \tau_m$. These constraints imply a significant limitation on the biological realism of the simulations, e.g. the decay times of excitatory AMPA synapses are typically larger than the rise times of inhibitory GABA currents (Bier et al., 1996; Häusser and Roth, 1997), or the simulation of high conductance states involves the use of small membrane time constants (Destexhe et al., 2003).

Recently, van Elburg and van Ooyen (2009) showed that these non-physiological constraints on the time constants can be relaxed. It was shown that multiple time constants can be used with the only restriction that the slowest decaying excitatory synaptic current should decay faster than the fastest decaying inhibitory current, i.e. $\tau_{e_\nu} < \tau_{i_\mu}$ for any combination of ν and μ. The authors proved that when these constraints are applied, a normal Newton-Raphson iteration scheme can be used in order to find the firing time. Moreover, since there are no overestimations of the exact firing time, the overhead of firing time predictions can be reduced for each incoming spike by performing only a single Newton-Raphson iteration at a time. After each iteration, an internal *self*-event with the current estimated time is rescheduled in the event-driven environment.

The generalizations discussed in van Elburg and van Ooyen (2009) already allow to simulate more general neuron models in an event driven way. The remaining constraint that all excitatory currents should decay faster than any inhibitory current is also assumed in many related publications on integrate-and-fire models with multiple synaptic time constants, since this significantly simplifies the threshold finding mechanism, e.g. Brette (2007), Rudolph and Destexhe (2006). However, in some circumstances, this is still a (physiologically) unacceptable restriction. For example, the simulation of NMDA-like currents, which can be modeled by an excitatory double exponential current (when ignoring non-linear effects such as the magnesium block), requires slower excitatory time constants (van Elburg and van Ooyen, 2009).

A similar approach for finding the firing time was proposed in D'Haene et al. (2009). This paper presents an efficient integration scheme which can be used for arbitrary integrate-and-fire neuron models with multiple exponentially decaying synaptic time constants, with *no* limitations on the time constants or the number of different time constants. The analytical solution of the membrane function is a sum of exponential functions. It is shown that the convergence problems with Newton-Raphson based iterative methods can only occur when there are negative contributions in the membrane function (which is a sum of exponential functions) with a time constant larger than any of the positive terms. In this case, the first derivative of the membrane function, used to perform a Newton-Raphson iteration, can underestimate the membrane function and converge to the wrong firing time or even not converge at all. To prevent this, all contributions to the first derivative which can cause convergence problems are replaced by a virtual contribution in which the time constant of the exponential function is set to the smallest time-constant that occur in all positive terms.

The applicability of the algorithm of D'Haene et al. (2009) is not limited to integrate-and-fire neuron models with multiple exponentially decaying synapses. Since the solution of the double exponential inhibitory currents used in the `IntFire4`-model also takes the form of the sum of two exponential functions, the algorithm in D'Haene et al. (2009) can be applied without modifications. In general, arbitrary synaptic functions can be efficiently simulated when they can be approximated as a sum of exponential functions. From the simulators point of view, these synapse functions are represented by multiple interconnections between two neurons, each implementing a simple exponential decaying synapse. Using also the propagation delay of the interconnections, synaptic responses with multiple peaks can be easily approximated.

It can be shown that if the constraints from van Elburg and van Ooyen (2009) are applied to the `IntFire4`-model, the membrane function will never contain negative exponential terms with larger time constants. In this case, the algorithm of D'Haene et al. (2009) will not need to replace any negative contributions during the computation of the first derivative of the membrane function. On this level, both methods would perform the same computations. However, it was also shown in D'Haene et al. (2009) that the computationally costly Newton-Raphson iterations can be completely eliminated most of the time, as are the update of all state variables after each incoming spike. This accounts for the largest part of the high speedups that were reported.

One of the main ideas behind many of the recently presented neuron models is limiting the number of state variables in order to decrease the simulation time, while maximizing the number of biologically observed neuron properties such as frequency adaptation and bursting (e.g. Izhikevich (2004), Brette and Gerstner (2005)). These models are generally characterized by strongly non-linear differential equations and thereby a lack of an analytical solution for the firing times. Although the limitation of the number of state variables simplifies the model and allows a faster time-step based simulation compared to biologically realistic neuron models (e.g. compartmental Hodgkin-Huxley neurons), the lack of an analytical solution as well as the complex non-linearities makes the simulation of these models hard to optimize computationally using event-based methods. This stands in contrast to the high speedup-ratios that can be reached by the event-based simulation of linear models (D'Haene et al., 2009). An important side-effect of the optimizations presented in that work is that the simulation time is almost not affected by the number of state variables that are used to describe the neuron model. Therefore, there is an increasing interest in powerful linear models which try to mimic more complex behavior by adding *more* state variables. An excellent example of this is the model recently presented by Mihalaş and Niebur (2009). This model starts with a simple Integrate-and-Fire neuron model with exponential synapses. But the paper shows that the addition of membrane voltage dependent threshold dynamics can mimic much of the rich behaviors that are normally only possible in non-linear models. The model is described by the following system:

$$\begin{cases} \dfrac{dI_j}{dt} & = -\dfrac{1}{\tau_j} I_j\left(t\right); \qquad j = 1, \ldots, N \\ \dfrac{dV}{dt} & = \dfrac{1}{C}\left(I_e + \sum_j I_j\left(t\right) - G\left(V\left(t\right) - E_L\right)\right) \\ \dfrac{d\theta}{dt} & = a\left(V\left(t\right) - E_L\right) - b\left(\theta\left(t\right) - \theta_\infty\right). \end{cases}$$

This system of differential equations is analytically solvable, and moreover, the solution for both the membrane $V(t)$ and the threshold $\theta(t)$ takes the form of a sum of exponential functions. The firing time can be easily found for $V(t) - \theta(t) = 0$, which is also a sum of exponential functions. Therefore, the optimization methods presented in D'Haene et al. (2009) can be directly applied to this model, giving it an important computational benefit over non-linear neuron models.

We conclude that there exists an interesting alternative to the recent trend of using highly non-linear neuron models with the least possible number of state variables (and which cannot well be accelerated using event-based techniques): neuron models where the membrane potential can be written as a sum of (possible many) exponentials can be very efficiently simulated using the techniques discussed in this note, and this both in simple single cell simulations and in large scale biologically plausible networks (D'Haene et al., 2009). Moreover, these algorithms do not require any additional constraint on the time constants of the different state variables. The introduction of these novel event-based simulation techniques could lead to a paradigm shift in the way complex neuronal spiking behavior is modeled, moving from low-order non-linear to high-order linear differential equations. This was already demonstrated in Mihalaş and Niebur (2009) where a complex neuron model was introduced which can exhibit rich neuronal behavior, usually only observed in non-linear models.

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