On the performance of voltage-stepping for the simulation of adaptive, nonlinear, integrate-and-fire neuronal networks.

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Abstract

In traditional event-driven strategies, spike timings are analytically given or calculated with arbitrary precision (up to machine precision). Exact computation is possible only for simplified neuron models, mainly the leaky integrate-and-fire model. In a recent paper, (Zheng et al., 2009) introduced an approximate event-driven strategy, named voltage-stepping, that allows for the generic simulation of nonlinear spiking neurons. Promising results were achieved in the simulation of single quadratic integrate-and-

1

fire neurons. Here, we assess the performance of voltage-stepping in network simulations by considering more complex neurons (quadratic integrate-and-fire neurons with adaptation) coupled with multiple synapses. To handle the discrete nature of synaptic interactions, we recast voltage-stepping in a general framework, the discrete event system specification (DEVS). The efficiency of the method is assessed through simulations and comparisons with a modified time-stepping scheme of Runge-Kutta type. We demonstrated numerically that the original order of voltage-stepping is preserved when simulating connected spiking neurons, independently of the network activity and connectivity.

Keywords: simulation, spiking neural networks, adaptive integrate-and-fire, voltage-stepping, local event-driven, time-driven.

1 Introduction

Computer simulations have become essential to understand the complex dynamics of the brain. Recently, large-scale simulations of realistic cortical networks have been undertaken (Izhikevich et al., 2008; Migliore et al., 2006). However, biophysically detailed neuron models have a high computational cost and the difficulty to tune their numerous parameters makes them inefficient for spike timing prediction (Gerstner et al., 2009). Simpler spiking neuron models of integrate-and-fire type are more suitable for efficient large-scale neural network simulations. The leaky integrate-and-fire (LIF) is computationally attractive and amenable to mathematical analysis. Yet, it is too simple and two key elements have to be incorporated into the model to reproduce the large range of spiking dynamics exhibited by cortical neurons: nonlinear spike generating currents that allow for an accurate description of the membrane potential near the threshold (Fourcaud et al., 2003), and adaptive currents that keep track of the past activity of the neuron yielding a considerable increase in neuro-computational properties (Izhikevich, 2003; Brette et al., 2005). Recently, a class of adaptive nonlinear spiking neuron models that captures both characteristics has been proposed (Izhikevich, 2003; Brette et al., 2005; Toubloul, 2008). If v is the membrane potential and w an adaptation variable, then the time-evolution of the neuron is given by

$$C\frac{dv}{dt} = f(v) - w + I + I_{syn}(t), \tag{1}$$

$$\frac{dw}{dt} = a\left(b(v - v_{rest}) - w\right) \tag{2}$$

with the reset condition $v \leftarrow v_{reset}$ and the update rule $w \leftarrow w + d$ at firing times obtained when v reaches a threshold value v_{th}. The parameter $d > 0$ represents the spike-triggered adaptation. In (1), C is the membrane capacitance, f is a nonlinear current-voltage function, I is an external constant input current, and I_{syn} is the synaptic current. In (2), parameter a describes the time scale of the adaptation current, b describes the sensitivity of w to the subthreshold membrane potential fluctuations and v_{rest} is the resting potential. The LIF model is obtained using a relaxation function $f(v) = -v$. More realistic models include nonlinear spike-generating currents like the adaptive quadratic model (Ermentrout, 1996; Izhikevich, 2003) obtained for $f(v) = v^2$, the adaptive exponential model (Fourcaud et al., 2003; Brette et al., 2005) for which $f(v) = -v + e^v$ or the quartic model (Toubloul, 2008) obtained for $f(v) = v^4 + 2\alpha v$. The class of models described by (1)-(2) has recently attracted a lot of attention mainly because of its relative simplicity (Izhikevich, 2004), its ability to reproduce a large variety of firing patterns (Izhikevich, 2003; Toubloul, 2008) and its predictive abilities (Brette et al., 2005). However the relative computational efficiency of the model is affected by the highly nonlinear dynamics. The numerical errors associated to the discontinuities of the membrane potential v at firing times can have severe consequences on the numerical integration and spurious dynamics can be generated (Hansel et al., 1998). At the the same time, the addition of an adaptation current can lead to a high sensitivity to the cutoff value v_{th} (Toubloul, 2009). An accurate numerical scheme requires a precise estimation of the membrane potential and the adaptation current at firing times. It is therefore necessary to develop specific integration schemes that treat correctly the numerical errors at the discontinuities without compromising the computational efficiency of the model.

Traditional time-stepping methods have to be modified to prevent the loss of accuracy at the firing times (Hansel et al., 1998; Shelley et al., 2001; Rangan et al., 2007). However an efficient treatment at the firing times cannot avoid a fundamental limitation of generic time-stepping methods that is imposed by the smoothness of synaptic in-

teractions (Shelley et al., 2001) and relatively small time steps, usually smaller than $0.01ms$, have to be used in numerical methods limiting the size of the network that can be simulated accurately. To illustrate our purpose, let us consider the commonly used exponential synaptic current $I_s^i = we^{-t/\tau_i}H(t)$, where w is the synaptic weight, τ_i the synaptic time constant and H the Heaviside step function. Exponential synaptic currents can be reformulated to give an efficient implementation as

$$\tau_i \frac{dI_s^i}{dt} = -I_s^i \tag{3}$$

with the jump condition $I_s^i \leftarrow I_s^i + w$ whenever the neuron receives a spike. Due to the discontinuous nature of the exponential currents, a time-stepping method falls into an accuracy of $O(\Delta t)$ and, therefore, a sufficiently small time step has to be used to correctly simulate the network. This drawback is illustrated in Figure 1.A where a time step of $\Delta t = 0.1$ ms leads to a spurious synchronous propagation along a synfire chain of adaptive quadratic integrate-and-fire neurons. The linear interpolation combined with the recalibration of the membrane potential cannot restore the accuracy of the second order Runge-Kutta methods (RK2) scheme. Artificial synchronizations are created, leading to an incorrect propagating activity. The correct behavior is however retrieved for $\Delta t = 0.05$ ms. The choice of a fixed time step for network simulations causes an antinomic problem. On the one hand, the time step is probably too small for slowly varying neurons. On the other hand, it may be too large for neurons sharply increasing their membrane potential near the threshold.

To overcome the crucial problem of determining the correct time step, event-driven strategies have been proposed (Brette, 2006, 2007; Tonnelier et al., 2007). Event-driven algorithms naturally deal with the discontinuities in the dynamics and do not require smooth postsynaptic changes. However they are limited to a small class of spiking neuron models, mainly the LIF and some variants for which exact computation of spike timings is possible. In a recent paper (Zheng et al., 2009), a new integration method, the 'voltage-stepping' scheme, has been proposed for the generic simulation of spiking neurons. The technique originates from the local approximation of the nonlinear neuron model with a LIF model that allows for event-driven computation where the events adapt to the voltage variation of the membrane potential. In (Zheng et al., 2009) the authors have evaluated the efficiency of voltage-stepping for the simulations of single

4

neurons. In this note we extend this previous work by considering network simulations and more complex neurons (nonlinear integrate-and-neurons with adaptation). We propose a network implementation of voltage-stepping using the Discrete Event System Specification (DEVS) (Zeigler et al., 2000) and assess its performance through simulations and comparisons with a modified time-stepping scheme of Runge-Kutta type.

2 Voltage-stepping for network simulation

The basic idea of the voltage-stepping approach is to approximate locally the nonlinear part of the neuronal dynamics by a linear variation so that a local event-driven algorithm can be used. The approximation is achieved using a discretization of the voltage state space with a fixed voltage step Δv. The numerical integration is performed through successive computations of timings at which a voltage step is achieved. As seen in Fig. 1.B, this approach induces local events that could be seen as implicit and adaptive time steps leading to a precise approximation of the firing time. The voltage-stepping scheme iterates between the following two steps: i) approximate the original nonlinear neuron model near the current voltage v_0 with a leaky integrate-and-fire (LIF) neuron and integrate formally the equations, and ii) search the exit time at which the membrane potential reaches $v_0 \pm \Delta v$ and advance the simulation at that time. These steps are detailed below.

2.1 Voltage-dependent LIF approximation and integration

We recall here the basic steps of the voltage-stepping method presented in (Zheng et al., 2009) and extend the formalism for networks with multiple synapses. Let us consider that a given neuron in the network has a membrane potential, v, in the voltage interval $v \in]v_0 - \Delta v, v_0 + \Delta v[$ (for convenience we use a voltage step of $2\Delta v$). The original nonlinear function $f(v)$ is replaced by $\tilde{f}(v) = -g(v - E)$, a linear approximation of f on the interval $v_0 \pm \Delta v$ where g is a voltage-dependent conductance and E a local resting potential obtained from the linear interpolation (see Appendix A.2). Replacing f by $\tilde{f}$ in (1) and using (3) lead to the linear differential system

$$\frac{dX}{dt} = AX + B \tag{4}$$

where $X = (X_{new} \ X_{syn})^t$ is the local state vector composed of two blocks

$$X_{new} = \begin{pmatrix} v \\ w \end{pmatrix} \text{ and } X_{syn} = \begin{pmatrix} I_s^1 \\ I_s^2 \\ \vdots \\ I_s^n \end{pmatrix}$$

describing, respectively, the state of the neuron and the exponential currents with the different synaptic time constants, τ_i (note that a change of variable $I_s \leftarrow I_s/C$ has been made), n is the number of synaptic inputs. The matrix A is a block matrix and B a vector given by

$$A = \begin{pmatrix} A_{new} & A_{syn} \\ 0 & A_{exp} \end{pmatrix}, B = \begin{pmatrix} B_{new} \\ 0 \end{pmatrix}$$

where the index neu is related to the neuron, syn to the inputs and exp to the exponential synaptic currents. Here, A_{new} is a matrix of order 2, A_{syn} is a $2 \times n$ matrix and A_{exp} a diagonal matrix of order n, given by

$$A_{new} = \begin{pmatrix} -g & -1/C \\ ab & -a \end{pmatrix}, A_{syn} = \begin{pmatrix} 1 & \dots & 1 \\ 0 & \dots & 0 \end{pmatrix}$$

$$A_{exp} = diag(-1/\tau_1, -1/\tau_2, \dots, -1/\tau_n)$$

and B_{new} is a vector with 2 entries

$$B_{new} = \begin{pmatrix} gE + I/C \\ -abv_r \end{pmatrix}$$

The formal resolution of the differential system (4) is detailed in appendix A.2 where the approximation of $v(t)$ and $w(t)$ are analytically given.

2.2 Computation of the events

The second stage of voltage-stepping is to compute the exit time t^*, i.e. the time at which the membrane potential trajectory reaches the threshold value $v_0 \pm \Delta v$ and enters a new voltage interval. The voltage-dependent approximation of the dynamics previously derived can be formally integrated using standard techniques of linear differential equations and the threshold crossing is rewritten as a root finding problem. The numerical integration is reduced to the computation of roots that define the local adaptive

time steps of the neuron. However, a standard root-finding algorithm, of Newton-Raphson type for example, may not converge or converge to a wrong value because of the non monotonicity of the membrane potential v on the considered interval. We use here a technique coming from the event detection in hybrid systems (Girard, 2002). The method is based on the computation of two sequences of lower-approximation and upper-approximation, $\underline{t}_i$ and $\bar{t}_i$, of t^*. The method is described in the appendix A.3 and gives two sequences such that:

$$
\begin{cases}
\underline{t}_i \leq t^* \leq \bar{t}_i \\
\bar{t}_i \rightarrow t^* \\
\underline{t}_i \rightarrow t^*
\end{cases}
\tag{5}
$$

It has been shown that the rate of convergence of the sequences is quadratic (Girard, 2002) and therefore the computation is very efficient. If the neuron stays in the current voltage interval, the sequences diverge and there is no exit time, indicating that a steady state is reached.

2.3 Network discrete-event specification

Several frameworks have been applied to the design of event-driven algorithms for spiking neurons, among them, MVASpike (Rochel et al., 2003) which is based on the DEVS formalism (Zeigler et al., 2000). The DEVS formalism describes the evolution of system components (here, neurons or populations) through 3 main functions :

- δ_{int} : update function that returns a boolean indicating if the state of the component has changed. For a neuron, it returns **true** when the membrane potential reaches the threshold value. δ_{int} takes the update time as parameter and performs the vLIF integration. This function is used to update the state of the neuron after the reception of a spike or after a local event.

- $\delta_{ext}()$: external function that manages the incoming external outputs (incoming spikes). δ_{ext} takes the incoming spike time and synaptic port as parameters. It updates the state of the neuron (by calling $\delta_{int}()$) before updating the synaptic currents.

- $ta()$: advance function gives the time to the next internal transition. In the case of the local event driven scheme, it performs the new vLIF approximation (see A.1) and returns the next local event time (by taking voltage stepping into account).

An additional function : 'reset' is used to reset the state of the neuron after the emission of a spike ($v \leftarrow v_{reset}$, $u \leftarrow u + d$ for adaptive models).

MVASpike handles the events with an event-driven simulation algorithm which sorts the events, updates the neurons and propagates the spikes. The general event-driven simulation is sketched in algorithm 1 below where we also incorporate possible connection delays between neurons:

enumeration EventType {δ_{int}_event; δ_{ext}_event;};

structure Event {Neuron neuron; double time; EventType type;};

PriorityQueue pq ;

for *each neuron n in the network* **do**
> Event e(n, n.ta(), δ_{int}_event);
>
> pq.insert(e);

end

while *(!pq.isEmpty())* **do**
> Event e1 = pq.dequeue() ;
>
> **if** *(e1.type == δ_{int}_event)/*in the case of a local event*/* **then**
>> **if** *(e1.neuron.δ_{int}(e1.time))/*check if $e1.neuron$ triggered a spike*/* **then**
>>> **for** *each post-synaptic neuron n connected to e1.neuron* **do**
>>>> Event e2(n , e1.time + connection delay, δ_{ext}_event);
>>>>
>>>> pq.insert(e2);
>>>
>>> **end**
>>>
>>> reset (e1.neuron);
>>
>> **end**
>
> **else**
>> $e1.neuron.\delta_{ext}$(e1.time, event port);
>>
>> /*reception of a spike*/
>
> **end**
>
> Event e3(e1.neuron.ta(), e1.neuron, δ_{int}_event);
>
> pq.insert(e3);

end

Algorithm 1: General event driven algorithm for the simulation of networks of spiking neurons.

In traditional event-driven simulations of spiking neural networks, the events correspond to the reception or the emission of a spike (Mattia et al., 2000; Brette, 2006, 2007; Tonnelier et al., 2007). In our scheme, the events are not only firing times or spike receptions but also the times t^* at which the voltage v reaches a new voltage interval $v_0 \pm \Delta v$. Therefore the DEVS approach can be used to design spiking neural network simulators and one has to distinguish between two types of events: global events associated to spike emission or reception and local events corresponding to a significant variation of the membrane potential of the neuron. Note that this event-based

formalism easily handles the discrete nature of synaptic interactions and allows an efficient treatment of the discontinuities. The membrane fluctuations due to presynaptic spikes are directly treated within the current voltage interval unlike modified Runge-Kutta methods where spike-spike interactions are not considered[1]. As noted in (Rangan et al., 2007), the first spikes computed within a large time step may jeopardize the simulation via spike-spike interactions in a way that the remaining spikes within the time step are spurious.

3   Numerical results

The local event-driven method resulting from a linear interpolation of the nonlinear spike-generating current at the boundaries of a voltage interval (section 2.1) induces a second order numerical scheme VS2 (Zheng et al., 2009). We compare the performance of VS2 to a standard fixed time step integration scheme of order 2. The modified Runge-Kutta method with linear interpolation of the spike time and a recalibration of the membrane potential after the reset (mRK2 hereafter) is a second order scheme for the simulation of neural networks with smooth synaptic interactions (Shelley et al., 2001; Hansel et al., 1998). The simulations are done with an extended version of the MVASpike software that incorporates the local-event driven method using DEVS. The MVASpike implementation of VS2 and mRK2 can be downloaded at

   http://webloria.loria.fr/∼kaabimmo/index.php?n=Main.Software.

We simulate two networks of $N = 101$ all-to-all coupled neurons. The inhibitory (resp. excitatory) network has inhibitory (resp. excitatory) connections randomly distributed in $[-2, 0[$ (resp. $]0, 2]$). The neurons are adaptive quadratic integrate-and-fire neurons given by (1)-(2) with $f(v) = k(v - v_r)(v - v_t)$ and the following parameter values : $k = 0.7$, $v_r = -60$, $v_t = -40$, $v_{reset} = -50$, $v_{th} = 35$, $C = 100$, $I = 70$, $a = 0.03$, $b = -2$, $d = 100$. The neurons are coupled with exponential synapses given by (3); each neuron receiving 50% of fast synapses, $\tau_1 = 5ms$, and 50% of slow synapses, $\tau_2 = 30ms$.

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[1]In Runge-Kutta methods, the spikes produced within the current time step are taken into account at the beginning of the next step, thereby neglecting possible interactions.

We evaluate the efficiency, i.e. accuracy versus time cost, of the algorithms as follows. The two networks are simulated for 2 seconds of biological time. The exact spike times are approximated using a time-stepping simulation with a very small time step of $10^{-6}ms$. We compute the error associated to the jth neuron as:

$$E_j = \frac{1}{M_j} \sum_f |t_f - t_{ap}|$$

where M_j is the number of spikes, t_f are the exact spike times and t_{ap} are the approximate spike times obtained by the VS2 or the mRK2 schemes. In all the simulations the time step or the voltage step are sufficiently small so that no spike is missed. We measure the network error of a simulation as the average error over the neurons:

$$E = \frac{1}{N} \sum_i E_i$$

The network error for the two test networks as a function of the time cost of the algorithms (duration of the simulation) is shown in Fig. 1. C-D. It is clear that, for a given simulation duration, the VS2 scheme gives a more accurate description of the spiking activity. Moreover, when a high accuracy is required, VS2 significantly outperforms the mRK2 method. This is explained by the inherent properties of the event-driven scheme obtained from the voltage-stepping technique where the time step is implicitly adapted to the membrane potential fluctuations. The variable time step allows us to speed up simulation when the neurons are at rest or weakly active, and to increase precision when the neuron presents strong variations. Moreover, the time steps are defined individually and independently for each neuron in the network and therefore the quickest varying neurons do not slow down the simulation of the network.

In Figs. 1. E-F, the error is plotted as a function of the voltage step and the time step in a logarithmic scale. The orders of the methods are estimated as the slopes of the linear regressions in the log-log plots. We observe that VS2 maintains a second order accuracy for the numerical simulation of connected networks. Numerically, the order is 2.06 for the inhibitory network and 2.44 for the excitatory network. In contrast, the error of the mRK2 scheme decreases linearly with the step-size and therefore mRK2 behaves like an Euler scheme (order of 1.003 for the inhibitory network and 1.166 for the excitatory network). The accuracy of the mRK2 scheme is degraded by the nonsmooth nature of

11

the synaptic interactions. A classical second order Runge-Kutta scheme produces an error having the following form :

$$e = \underbrace{0(\Delta t^2)}_{\text{integration error}} + \text{synaptic interaction error}$$

The synaptic interaction error (denoted sie hereafter) is a first order error composed of a spike detection error and a spike reception error. The latter is an error generated by the artificial delay due to the spike propagation introduced by the time-stepping scheme. Therefore,

$$sie = \underbrace{0(\Delta t)}_{\text{spike detection error}} + \underbrace{0(\Delta t)}_{\text{spike reception error}}$$

The spike detection error can be decreased by one order by using a linear interpolation to estimate the correct spike time (Shelley et al., 2001; Hansel et al., 1998). In contrast, the spike reception error can be avoided by using synaptic delays (Morrison et al., 2007) or can be decreased by several orders using sufficiently smooth synaptic interactions (Shelley et al., 2001). Therefore, unlike voltage-stepping, the error after one spike is of order Δt and a smooth synaptic interaction or synaptic delay is required to restore the accuracy of the scheme (here, the existence of the derivative at $t = 0$ is necessary to obtain second order accuracy). For these reasons, the mRK2, and higher order schemes of Runge-Kutta type, perform like a first-order method for the simulation of networks with exponential synaptic currents (Eq. 3).

We then study whether the order of the methods is affected by the network activity (average firing rate) and connectivity (probability of connection). As shown in Figs. 1. G-H, the second order of the VS2 method does not depend on the network firing rate and the level of connectivity. The mRK2 method behaves as a first order method independently of the network activity (Fig. 1 H). We note however that the order of mRK2 increases for low probabilities p of connection (Fig. 1 H), as mRK2 is a second order method for uncoupled neurons. For low level of connectivity, the number of synaptic events decreases and the contribution of the first order synaptic interaction error becomes less important. Nevertheless, mRK2 is not a second order method for the simulation of connected networks.

4 Conclusion

Recent efforts have been made to develop efficient schemes for the numerical simulation of spiking neural networks. Exact methods (Brette, 2006, 2007; Tonnelier et al., 2007) where the spike timings are found exactly (up to machine precision) and fast methods (Rangan et al., 2007) have been proposed. On the one hand, these methods are based on some analytic expressions for the state variables and are therefore limited to simple models (leaky or quadratic integrate-and-fire). On the other hand, the accuracy of generic time-stepping methods (Hansel et al., 1998; Shelley et al., 2001) are severely limited by the smoothness of synaptic interactions and are not computationally efficient in network simulations due to unnecessary updates of inactive neurons.

An alternative technique, the voltage-stepping method, has been recently proposed for combining the genericity of time-stepping schemes and the efficiency of event-driven approaches (Zheng et al., 2009). Promising results were achieved for the simulation of single neurons. Nevertheless, performance comparison on network simulations was still lacking. Here, we assessed the performance of voltage-stepping by considering network simulations and more complex neurons (quadratic integrate-and-fire neurons with adaptation, coupled with multiple synapses). For network simulations, the discrete event system specification formalism was applied to voltage-stepping. We demonstrated numerically that the method outperforms time-stepping schemes of Runge-Kutta type in terms of speed and accuracy. The original order of voltage-stepping is preserved in network simulations, independently of the network activity and connectivity. This outcome results from the efficiency of the activity-dependent time discretization implicitly generated by the voltage-stepping scheme for each neuron in the network.

The numerical integration is reduced to root-finding methods for which efficient techniques exist. Although the complexity increases with the number of synaptic currents, it is still manageable in practice as most neural network models do not use as many as four types of synaptic currents. Finally, our work can be extended to conductance-based synaptic currents that are more biologically plausible. This extension could be done through a complete linearization of the differential system and will require a conductance step in addition to the voltage step.

A Appendices

A.1 The vLIF model

The linear interpolation of $f(v)/C$ at the boundaries of the voltage interval $v_0 - \Delta v$ and $v_0 + \Delta v$ is $\tilde{f}(v) = -g(v - E)$ where

$$g = -\frac{f(v_0 + \Delta v) - f(v_0 - \Delta v)}{2C\Delta v}$$

and

$$E = v_0 - \Delta v + \frac{f(v_0 - \Delta v)}{gC}.$$

A.2 Formal integration of the vLIF network

The solution of system (4) is of the following form

$$X(t) = C_1^*(t)X_1^*(t) + C_2^*(t)X_2^*(t) + \sum_{i=1}^{n} C_i(t)X_i(t)$$

$X^*{}_1(t)$, $X^*{}_2(t)$ and the $X_i(t)$ are determined from the eigenvalues and eigenvectors of A.

The solution is obtained by solving $\frac{dX}{dt} = AX$ and applying variation of constants method to solve $\frac{dX}{dt} = AX + B$ (if A is invertible).

Let $\Delta = (a - g)^2 - 4\frac{ab}{C}$, the eigenvalues of A , for $\Delta > 0$, are

$$\lambda_{1,2}^* = -\frac{a+g}{2} \pm \frac{\sqrt{\Delta}}{2}$$
$$\lambda_i = -\bar{\tau}_i \quad 1 \leq i \leq n$$

for $\Delta > 0$, where $\bar{\tau}_i = 1/\tau_i$. If $\Delta < 0$, λ_1^* and λ_2^* are complex conjugate that we write $\lambda_{1,2}^* = \alpha \pm i\beta$. The eigenvectors of A are

$$e_1^* = \begin{pmatrix} \gamma_1 \\ 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix} \; ; \; e_2^* = \begin{pmatrix} \gamma_2 \\ 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix} \; ; \; e_i = \begin{pmatrix} \gamma_v^i \\ \gamma_w^i \\ 0 \\ \vdots \\ 1 \quad \text{(on the } (i+2)^{\text{th}} \; element) \\ \vdots \\ 0 \end{pmatrix}$$

where

$$\gamma_i = \frac{a + \lambda_i^*}{ab}$$

$$\gamma_v^i = \frac{a - \bar{\tau}_i}{(a - \bar{\tau}_i)(g - \bar{\tau}_i) + \frac{ab}{C}}$$

$$\gamma_w^i = \frac{ab}{(a - \bar{\tau}_i)(g - \bar{\tau}_i) + \frac{ab}{C}}$$

We define $I_0 = gE + \frac{I}{C}$ and $R = -abv_r$. The membrane potential $v(t)$ and the adaptation variable $w(t)$ are given by

- if $\Delta > 0$

$$v(t) = cst_v + \gamma_1 C_{10}^* e^{\lambda_1^*(t-t_0)} + \gamma_2 C_{20}^* e^{\lambda_2^*(t-t_0)} + \sum_{i=1}^n C_i \gamma_v^i e^{-\bar{\tau}_i(t-t_0)}$$

$$w(t) = cst_w + C_{10}^* e^{\lambda_1^*(t-t_0)} + C_{20}^* e^{\lambda_2^*(t-t_0)} + \sum_{i=1}^n C_i \gamma_w^i e^{-\bar{\tau}_i(t-t_0)}$$

  where

$$\begin{cases} cst_v &= \frac{\gamma_1(R\gamma_2 - I_0)}{\lambda_1(\gamma_1 - \gamma_2)} + \frac{\gamma_2(I_0 - R\gamma_1)}{\lambda_2(\gamma_1 - \gamma_2)} \\ cst_w &= \frac{R\gamma_2 - I_0}{\lambda_1(\gamma_1 - \gamma_2)} + \frac{I_0 - R\gamma_1}{\lambda_2(\gamma_1 - \gamma_2)} \\ C_{10}^* &= \frac{v(t_0) - cst_v - \sum_{i=1}^n C_i\gamma_v^i - \gamma_2(u(t_0) - cst_2 - \sum_{i=1}^n C_i\gamma_w^i)}{\gamma_1 - \gamma_2} \\ C_{20}^* &= \frac{\gamma_1(w(t_0) - cst_w - \sum_{i=1}^n C_i\gamma_w^i) - v(t_0) + cst_1 + \sum_{i=1}^n C_i\gamma_v^i}{\gamma_1 - \gamma_2} \\ C_i &= \frac{I_s^i(t_0)}{C} \end{cases}$$

- if $\Delta < 0$

$$v(t) = cst_v + e^{\alpha(t-t_0)}\left[\left(C_{10}^* \frac{a+\alpha}{ab} + C_{20}^* \frac{\beta}{ab} \right) cos(\beta(t - t_0)) + \right.$$

$$\left. + \left(C_{20}^* \frac{a+\alpha}{ab} - C_{10}^* \frac{\beta}{ab} \right) sin(\beta(t - t_0)) \right] + \sum_{i=1}^n C_i \gamma_v^i e^{-\bar{\tau}_i(t-t_0)}$$

$$w(t) = cst_w + e^{\alpha(t-t_0)}[C_{10}^* cos(\beta t) + C_{20}^* sin(\beta(t - t_0))] + \sum_{i=1}^n C_i \gamma_v^i e^{-\bar{\tau}_i(t-t_0)}$$

  where

$$\begin{cases} cst_v &= v_r - \frac{\gamma\beta + R\alpha}{b(\alpha^2 + \beta^2)} \\ cst_w &= -\frac{\gamma\beta + R\alpha}{\alpha^2 + \beta^2} \\ C_{10}^* &= w(t_0) - cst_w - \sum_{i=1}^n C_i\gamma_w^i \\ C_{20}^* &= \frac{ab}{\beta}(v(t_0) - cst_w - \sum_{i=1}^n C_i\gamma_v^i) - \frac{a+\alpha}{\beta}(w(t_0) - cst_w - \sum_{i=1}^n C_i\gamma_w^i) \\ C_i &= \frac{I_s^i(t_0)}{C} \end{cases}$$

A.3 Computation of local events

Let $d(t)$ be the distance from the membrane potential $v(t)$ to the boundary of the voltage interval $[v_0 - \Delta v, v_0 + \Delta v]$. We have $d(t) = min(d_l(t), d_u(t))$ where

$$d_l(t) = v(t) - v_0 + \Delta v, \text{ and } d_u(t) = v_0 + \Delta v - v(t)$$

A local event in our scheme corresponds to an exit time t^*, i.e. the smallest $t > 0$ so that $v(t^*) = v_0 \pm \Delta v$. The problem is equivalent to

$$\begin{cases} d(t) > 0 \ \ \forall t \in]t_0, t^*[\\ d(t^*) = 0 \end{cases} \tag{6}$$

To solve this problem, successive upper-approximations and lower-approximations, $\underline{t}_i$ and $\overline{t}_i$, of t^* are constructed. We start with $\underline{t}_0 = t_0$ and $\overline{t}_0 = +\infty$. Sequences are derived from an upper and a lower approximation of $d_e(t)$ ($e = l, u$) on $[\underline{t}_i, t^*]$ defined by two quadratic polynomials:

$$d_e(t) \ \leq \ P_e(t - \underline{t}_i) = d_e(\underline{t}_i) + v'(\underline{t}_i)(t - \underline{t}_i) + \frac{(t - \underline{t}_i)^2}{2} M \tag{7}$$

$$d_e(t) \ \geq \ p_e(t - \underline{t}_i) = d_e(\underline{t}_i) + v'(\underline{t}_i)(t - \underline{t}_i) + \frac{(t - \underline{t}_i)^2}{2} m \tag{8}$$

where

$$m \leq v''(t) \leq M \ \ \forall t \in [t_0, t^*].$$

We define the new values at the next iteration as

$$\begin{cases} \underline{t}_{i+1} \leftarrow \underline{t}_i + r_e^i \\ \overline{t}_{i+1} \leftarrow \overline{t}_i + R_e^i \end{cases}$$

where r_e^i and R_e^i are the smallest positive roots of the polynomials p_e and P_e, respectively. If P_e has no positive roots, we set $\overline{t}_{i+1} = +\infty$. Note that two lower and two upper approximations of the exit time are constructed (corresponding to a possible exit at $v_0 - \Delta$ and at $v_0 - \Delta$) and a one sequence ($e = l$ or $e = u$) can be removed if its lower approximation is greater than the upper approximation of the other one. Moreover, after an iteration, one may keep only one value for the lower (upper) approximation of the exit time taking the minimum of the two values.

To compute the bounds, m and M, of $v''(t)$ one may observe that

$$v''(t) = cX''(t) = c(A^2 X(t) + AB)$$

where $c = (1, 0, \ldots, 0)$. Let $\{x_1, x_2, .., x_p\}$ the 2^{n+2} vertices of the hyper-rectangle containing the state-vector $X(t)$, we can write

$$X(t) = \sum_{i=1}^{i=p} \lambda_i(t) x_i, \ \sum_{i=1}^{i=p} \lambda_i(t) = 1, \ \forall i \lambda_i \geq 0.$$

Consequently, we have

$$\begin{cases} m = min_{i=1}^{p}[c(A^2 x_i + AB)], \\ M = max_{i=1}^{p}[c(A^2 x_i + AB)]. \end{cases}$$

The $\{x_i\}_{1 \leq i \leq 2^{n+2}}$ are obtained using

$$\begin{cases} v_0 - \Delta v \leq v(t) \leq v_0 + \Delta v \\ w_{inf} \leq w(t) \leq w_{sup} \\ min(0, I_s^i(t_0)) \leq I_s^i(t) \leq max(0, I_s^i(t_0)) \ \forall 1 \leq i \leq n \end{cases}$$

We introduce an additional parameter Δw so that $w_{inf} \leq w(t) \leq w_{sup} \ \forall \ t \in [t_0, t^*]$ with

$$\begin{cases} w_{inf} = w_0 - \Delta w \\ w_{sup} = w_0 + \Delta w \end{cases}$$

Even if the variation on w is not important, w_{inf} and w_{sup} are required to run the algorithm. In practice, one chooses a large Δw, e.g. $= 10$.

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Figure caption.

Figure 1:

(A) Spike raster plot of synfire chain activity. The network consists of 10 layers, each one having 50 adaptive quadratic integrate-and-fire neurons (1)-(2) where $f(v) = k(v - v_r)(v - v_t)$ and $k = 0.7$, $v_r = -60$, $v_t = -40$, $v_{reset} = -50$, $v_{th} = 35$, $C = 100$, $I = 0$, $a = 0.03$, $b = -2$, $\tau = 5$, $d = 100$. Successive layers are fully connected with 80% excitatory (random weights in [13,15]) and 20% inhibitory (weights = -5) synaptic connections using exponential synaptic currents. Spike times are computed with a modified second-order Runge-Kutta (mRK2) method with $\Delta t = 0.05ms$ (plot at the top) and $\Delta t = 0.1ms$ (plot at the bottom). For $\Delta t = 0.1$ ms, the activity propagates along the chain. The correct behavior is found with $\Delta t = 0.05ms$ when the activity vanishes after the 5th layer.

(B) Schematic view, at the neuron level, of the voltage-stepping technique. The voltage state-space is discretized with a voltage step Δv. The state of the neuron is updated each time that a voltage step is completed, hence producing adaptive time steps that follow efficiently the trajectory of the neuron: time steps decrease near the firing times and increase during slowly varying periods.

(C) Network error (ms) versus time cost (s) for the numerical simulation of the inhibitory network with the VS2 ($\Delta v \in [0.05, 0.1]mV$) scheme (plain curve) and mRK2 ($\Delta t \in [0.002, 0.05]ms$) scheme (dashed curve).

(D) Same legend as in panel C but for the excitatory network.

(E) Log-log plot of the inhibitory network error as a function of the voltage step Δv and the time step Δt. The slopes of the regression lines indicate the orders of the methods. The slope for VS2 (plain line) is approximately 2 indicating that VS2 is a second order method for network simulations. In contrast, the slope for mRK2 (dashed line) is approximately 1 revealing the loss of the original second order mRK2 scheme when simulating a network with non-smooth synaptic interactions.

(F) Same legend as in panel E but for the excitatory network.

(G) Orders of the VS2 and mRK2 methods as a function of the network activity (average firing rate). The network consists of $N = 100$ adaptive quadratic integrate-and-fire neurons with parameters given in the section 'Numerical results'. The neurons are connected all-to-all and the weights are randomly drawn from the interval $[1, 2]$. Simulations were performed for different input currents $I \in [60, 150]$ mA so as that the network average firing rate is within the range $[50, 90]$ Hz. For each network activity, the network error is plotted as a function of the voltage step for VS2 and the time step for mRK2. The order of the method is then estimated as the slope of the linear regression in the log-log error plot. The plain and dashed curve represents the order of VS2 and mRK2, respectively.

(H) Orders of the VS2 and mRK2 methods as a function of the network connectivity (probability of connection). Same legend as in panel G except that the input current $I = 60$ and the synaptic weights $w = 2$. The connectivity is randomly generated with probability p. The plain and dashed curve represents the order of VS2 and mRK2, respectively.