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To cite this version:

Gang Zheng, Arnaud Tonnelier, Dominique Martinez. Voltage-stepping schemes for the simulation of spiking neural networks. Journal of Computational Neuroscience, 2009, 26 (3), pp.409-423. 10.1007/s10827-008-0119-1 . inria-00189386v3

HAL Id: inria-00189386

https://inria.hal.science/inria-00189386v3

Submitted on 21 Nov 2007 (v3), last revised 11 Jun 2009 (v4)

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Voltage-stepping schemes for the simulation of spiking neural networks

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Abstract

The numerical simulation of spiking neural networks requires particular attention. On the one hand, time-stepping methods are generic but they hardly reproduce accurately the short-time scale fluctuations of spiking neurons and need specific treatments to avoid the errors associated with the discontinuities of integrate-and-fire models. On the other hand, event-driven methods are exact but restricted to a limited class of models. We present here a voltage-stepping scheme that combines the advantages of these two approaches and consists of a discretization of the voltage state-space. The numerical simulation is reduced to a *local* event-driven method that induces an implicit activity-dependent time-stepping scheme: long time-steps are used when the neuron is slowly varying whereas small time-steps are used in periods of intense activity. Our method accurately approximates the neuronal dynamics and we show analytically that such a scheme leads to an high-order algorithm. We illustrate the voltage-stepping method on nonlinear integrate-and-fire models. In this situation, our method consists of an approximation of the original model by a voltage-dependent integrate-and-fire. We compare our method with time-stepping schemes of Runge-Kutta type.

1 Introduction

Neuronal information processing involves action potentials, or spikes. Recent findings in neuroscience emphasize the importance of the precise timing

of spikes. In biological systems where the processing-speed is required to be high, the timings of spikes are very precise and reliable [Mainen and Sejnowski, 1995, VanRullen et al., 2005]. In many specialized systems the precision of spikes has a fundamental role such as odor recognition [Latham et al., 2000] or source detection [Carr and Konishi, 1990, AgmonSnir et al., 1998]. Submillisecond precision of spike timing have been recorded [Bair and Koch, 1996, Ariav et al., 2003] and small differences in the precision of synaptic events have severe impact on the plasticity of synapses.

Numerical simulations of neural networks are commonly used to explore the spike coding paradigm. It is thus crucial to have accurate and efficient schemes to simulate spiking neural networks. Different strategies have been developed for the simulation of spiking neural networks: event-driven schemes where the timings of spikes are calculated exactly and time-stepping methods that approximate the membrane voltage of neurons on a discretized time (see [Brette et al., 2007] for a review of simulation environments). In pure event-driven strategies the spike timings are analytically given and are calculated with an arbitrary precision (up to the machine precision). This scheme allows an exact simulation where no spike is missed. This method has become increasingly popular [Mattia and Giudice, 2000, Makino, 2003, Rochel and Martinez, 2003, Brette, 2006, Brette, 2007, Rudolph and Destexhe, 2006, Tonnelier et al., 2007]. However only a limited class of simplified neuron models of integrate-and-fire type is amenable to exact stimulations.

Time-stepping schemes are generic since they can be applied to any models. Classical integration schemes of Runge-Kutta type have to be modified to properly handle the discontinuities of integrate-and-fire neuron dynamics generated by the resetting and the synaptic events [Hansel et al., 1998, Shelley and Tao, 2001]. However when the membrane potential crosses threshold twice during one time step, the spike event may be missed. Due to the discontinuous nature of integrate-and-fire network, a failure to detect a spike may cause dramatic changes on the behavior of the system and artificial dynamical states may be created if the time step is badly chosen [Hansel et al., 1998]. Moreover a fundamental limitation on the accuracy of these methods is imposed by the smoothness of the postsynaptic potentials [Shelley and Tao, 2001].

In this paper we define a generic scheme for the simulation of neural networks based on a voltage-space discretization that we call voltage-stepping scheme. This scheme retains the advantage of the activity-dependent computational cost of event-driven strategies while allowing generic simulation of any neural models. The greatest asset is to define an implicit and adaptive time-discretization for each neuron that depends on its own activity. A neu-

ron that evolves slowly allows long time step and has a low computational cost whereas small time steps are require for fast varying neuron. Here we show that this implicit and variable time-stepping scheme allows high-order integration methods. Since recent efforts have been made on the numerical simulations of integrate-and-fire networks [Brette, 2006, Brette, 2007, Brette et al., 2007, Ros et al., 2006, Morrison et al., 2007, Rangan and Cai, 2007, Rudolph and Destexhe, 2006] we illustrate in the next section our method using the nonlinear integrate-and-fire models. Generalization to different classes of spiking neuron models are proposed. In section 3 we present numerical results and compare the performance of the voltage-stepping scheme with standard time-stepping integration methods.

2 Method

2.1 Voltage-stepping scheme

Consider the kth integrate-and-fire neuron in a network described by its membrane potential, v^k, that evolves according to the equation

$$C\frac{dv^k}{dt} = f(v^k) + I_0 + I^k_{syn}(t), \tag{1}$$

where C is the membrane capacitance, $f(v)$ the nonlinear current-voltage characteristic of the membrane, I_0 an external constant input current and I^k_{syn} the total synaptic input received by neuron k. A spike is triggered when v^k reaches a threshold v_{th} upon when it is instantaneously reset to v_r. Specific instances of the the non-linear integrate-and-fire (NLIF) model (1) are the quadratic model [Ermentrout and Kopell, 1986], [Hansel and Mato, 2001] and the exponential model [Fourcaud-Trocmé et al., 2003].
Let us consider a discretization of the voltage state-space $V_i = [v_i, v_{i+1}[$ where $v_i = i\Delta v$ and Δv is a fixed voltage-step. The basic idea of our method is to approximate (1) by the voltage-dependent integrate-and-fire neuron

$$C\frac{dv}{dt} = -g_i(v - E_i) + I_0 + I_{syn}(t) \tag{2}$$

for $v \in V_i$. For clarity, the subscript k has been dropped. g_i is a voltage-dependent conductance and E_i is a voltage-dependent resting potential. Parameters g_i and E_i are such that the linear function $f_{\Delta v}(v) = -g_i(v - E_i)$ approximates the non-linear characteristic $f(v)$ on V_i. For instance, using

the approximation of f by the linear interpolation function at the boundaries of V_i gives

$$g_i = -\frac{f(v_{i+1}) - f(v_i)}{\Delta v}$$
$$E_i = v_i + \frac{f(v_i)}{g_i}$$

In this case the voltage-dependence of the approximated IF parameters is piecewise linear.
Note that we keep the same notation for the membrane potential and its approximation (if ambiguity we will note $v_{\Delta v}$ the approximation of v). We note $V_{reset} = [v_r, v_r+\Delta v[$ and $V_{th} = [v_{th}, v_{th}+\Delta v[$ the resetting and threshold intervals. Let t_0 the time at which the membrane potential of the neuron reaches V_i ($v(t_0) = i\Delta v$) and assume that the neuron stays in V_i during a non-empty time interval. Integrating (2) between t_0 and t yields

$$\begin{aligned} v(t) &= i\Delta v\ e^{-(t-t_0)/\tau_i} + (E_i + I_0/g_i)(1 - e^{-(t-t_0)/\tau_i}) \\ &\quad + \int_{t_0}^{t} e^{-(t-y)/\tau_i} \frac{I_{syn}(y)}{C} dy \end{aligned} \tag{3}$$

where $\tau_i = C/g_i$ is the voltage-dependent membrane time constant. The synaptic current I_{syn} is given by

$$I_{syn}(t) = w \sum_{t^f_{pre}} \alpha(t - t^f_{pre}) \tag{4}$$

where the t^f_{pre} are the firing times of the presynaptic neurons, w represents the weight of the synapse, $\alpha(t) = 1/\tau_s e^{-t/\tau_s} H(t)$ or $\alpha(t) = 1/(\tau_1 - \tau_2)(e^{-t/\tau_1} - e^{-t/\tau_2})H(t)$ where H is the Heaviside step function with $H(t) = 1$ if $t > 0$ and $H(t) = 0$ else. Since I_{syn} is a combination of exponential functions the integral in (3) can be computed analytically and an event-driven method can be used to calculate the next *exit* time, t_1. Three possibilities occur: (i) the membrane potential goes back to its value at time t_0, i.e. $v(t_1) = v_i$ (ii) the membrane potential reaches the interval V_{i+1}, i.e. $v(t_1) = v_{i+1}$ and (iii) the neuron is at rest, i.e. $t_1 = +\infty$. If the spiking interval V_{th} is reached, then a firing event occurs, $t^f = t_1$ and the neuron is reset. The event-driven method is applied on a voltage-step and therefore our method may be seen as a *local* event-driven method.
Let $(t_k)_{k\in N}$ be the sequence of times at which the successive intervals $(V_i)_{i\in I}$

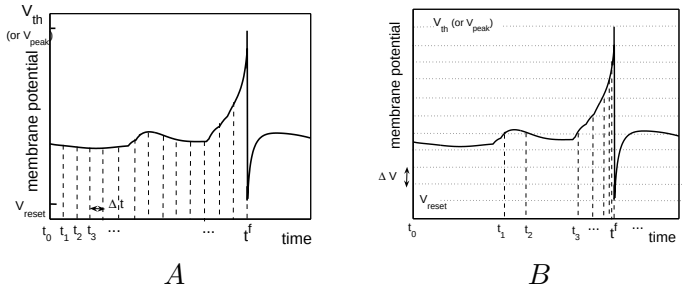

Figure 1: Schematic view of the numerical integration of an integrate-and-fire neuron using (A) a time-stepping scheme and (B) a voltage-stepping scheme. The time stepping method with a fixed time step Δt requires calculations at each step independently of the membrane potential fluctuations. The voltage-stepping approach induces an adaptive time-step leading to a precise approximation of the firing time.

are reached. This sequence defines the integration points of an implicit variable time-step method. The numerical integration is reduced to the detection of the occurrence of discrete events that is achieved using symbolic computation (when it is possible) or a Newton-Raphson algorithm (that is very efficient and only few iterations are needed). On a time-step, a symbolic expression of the membrane potential is given by (3). The result is schematically illustrated Fig. 1B and compared with a fixed-step method (Fig. 1A). Advantages are clearly seen. At the neuron level, when the membrane potential is slowly varying the corresponding time-steps are large whereas small time-steps are used when the membrane potential strongly fluctuates. Near the threshold, due to the nonlinear voltage-dependent current, the membrane voltage changes quickly leading to short time steps to accurately follow the trajectory. Note that the approximated solution has a symbolic expression given by (3). At the network level, voltage stepping method presents interesting properties. Firstly, the computational cost of the simulation is significantly reduced when the activity of the network is sparse. Serial activation of areas, like propagating wave or synfire activity, frequently occur in neuronal tissue, notably the cortex, the thalamus and hippocampus. Neurons that participate to the wave activity are excited while the others are at rest or poorly activated. Time steps are used to update excited neurons whereas no computation is done for the others.

Secondly, the spike-spike interactions [1] which is usually ignored in modified Runge-Kutta scheme [Rangan and Cai, 2007] is naturally handled in our local event-driven strategy. Moreover unlike standard time-stepping scheme, the implicit time-discretization defined by our technique is different for each neuron in the network and only depends on its activity.
The basic idea of the voltage-stepping approach is to define a local variable-step integrator using an approximation of the nonlinear characteristic f by a function that is amenable to an event-driven scheme. The piecewise linear interpolation of the nonlinear current $f(v)$ leads to an approximation of the original model by a voltage-dependent linear integrate-and-fire (LIF) neuron (2). As v evolves, parameters of the LIF change. This approach is reminiscent to the piecewise linear caricature of neuron models [McKean, 1970, Tonnelier and Gerstner, 2003]. In general, as we show in the Appendix, the voltage-dependent LIF, defined using an interpolation of the nonlinear currents at the boundaries of V_i, leads to a numerical integration with an accuracy of $O(\Delta v^2)$. A clever choice of the interpolation points within a voltage-step leads to an error of order $O(\Delta v^4)$. However it should be noted (see Appendix) that the fourth order accuracy is only reached for the simulation of one-dimensional neuron models. A lower order scheme ($O(\Delta v)$) is obtained using a voltage-dependent non-leaky IF model ($f_{\Delta v}$ is piecewise constant). Similarly, a more accurate scheme is obtained using a piecewise quadratic approximation and the corresponding approximated model is a voltage-dependent QIF model.

2.2 Generalization

The voltage-stepping strategy is not limited to the simulation of one dimensional integrate-and-fire neurons. Below we sketch how to apply this technique for different widely used neural models.
A. **Integrate-and-fire neurons with adaptation.**
An improvement of the NLIF model is achieved by adding a second variable [Izhikevich, 2003, Brette and Gerstner, 2005]

$$C\frac{dv}{dt} = f(v) - u + I_0 + I_{syn}(t) \quad (5)$$

$$\frac{du}{dt} = a(bv - u) \quad (6)$$

where u represents an adaptation current. At each firing time, the variable u is increased by an amount c ($u \leftarrow u + c$). As previously, we derive a

[1] interactions between spikes that are in the same time interval

voltage-dependent LIF using a linear interpolation of f on V_i. The system is now two-dimensional but since the equations are linear on a voltage-step the approximated model can be solved analytically in this interval, then the local event-driven scheme is similarly applied in this case. Note that (i) nonlinear currents can be added in the adaptation equation provided that a piecewise linear approximation is used. (ii) Without resetting on v and without spike-triggered-adaptation (5)-(6) has the FitzHugh-Nagumo model as a special instance.

B. **Conductance based synaptic currents.**

More realistic descriptions of synaptic current incorporate conductance changes

$$I_{syn}(t) = g_{syn}(v_e - v) \sum_{t^f_{pre}} \alpha(t - t^f_{pre}) \tag{7}$$

where v_e is a reversal potential. Recently the event-driven simulation of LIF models has been extended to synaptic conductances [Brette, 2006]. Thus we can adapt the voltage-stepping method to neural models with synaptic conductances. The computational cost of the simulation can be reduced using the following approximation $v_e - v = v_e - v_i$ on the voltage-step $V_i = [v_i, v_i + \Delta v[$ but we introduce an error of order ΔV. To restore the accuracy of the scheme, we rewrite equation as

$$\begin{aligned} C\frac{dv}{dt} &= f(v) + I_0 + g(v_e - v) \\ \frac{dg}{dt} &= -g/\tau_s \end{aligned}$$

where an incoming spike triggers an instantaneous additive change $g \to g + w$. Nonlinearities appear both in the characteristic, f, and in the conductance, gv. To achieve a local event-driven scheme, it is necessary to discretize the state-space (v, g). The method is similar to conductance-based models and is detailed below.

C. Hodgkin-Huxley type neurons.

Our approach is not limited to integrate-and-fire neuron models and can be used to simulate detailed neuron models including spike-description such as Hodgkin-Huxley type models. For clarity we consider the Morris-Lecar model

$$\begin{aligned} C\frac{dv}{dt} &= \bar{g}_{Ca} m_\infty(v)(v_{Ca} - v) + \bar{g}_K u(v_K - v) + \bar{g}_l(v_l - v) + I \\ \frac{du}{dt} &= \frac{u_\infty(v) - u}{\tau(v)} \end{aligned}$$

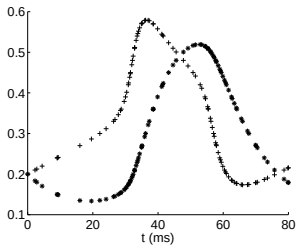

Figure 2: Numerical simulation of the Morris-Lecar model with a state-stepping algorithm. We simulate the model over one period of its oscillatory regime. Crosses are the membrane potential and stars are for the potassium channel. We use a voltage-step of $6mV$ and a step of 0.03 for the recovery variable. For convenience the membrane potential has been rescaled.

that describes an instantaneously responding voltage-sensitive Ca2+ conductance for excitation and a delayed voltage-dependent K+ conductance for recovery (see [Rinzel and Ermentrout, 1998] for a complete definition). Since the nonlinearity involves both v and u, it is necessary to discretize the entire state space (v, u) (the term state-stepping is more appropriate in this case). The state space is partitioned in subdomains where the function is approximated by a linear system $F_i(X) = A_i X + b_i$ where $X = (v, u)$. The shape of subdomains is triangular and a simplicial partition (i.e. triangulation based on a rectangular partition) can be used [Girard, 2002]. In each triangle the approximated neuron model has a symbolic expression from which we calculate the switching time, i.e. the time at which a new triangle is reached. In Fig. 2 we show the result of the numerical integration. The method performs like an adaptive time-stepping scheme. The neuron is updated frequently when one state variable has large variation, specially near the threshold and at the peak of the spike where the membrane voltage present abrupt polarization. Note that the integration points are not only determined by the membrane potential but also by the recovery variable. The fastest changing variable imposes the time-steps of the neuron.
The algorithm can be extended to general n-dimensional conductance-based neuron using a simplicial subdivision of the neuron state-space and interpolating the vector field at the vertices of the simplex.

2.3 Algorithm

Each neuron maintains a mode (i.e. its location in the discretized voltage space) and an exit time. The exit time is a spike timing if the neuron reaches the threshold interval.

- Initialization: We compute the events, i.e. the exit-times of each neuron (including spike timings) and insert the events in a priority queue.
- Process events. Extract the event with the lowest timing. Note that local events do not have repercussions on the overall dynamics of the network and only require a local updating of the corresponding neuron state and a computation of the new exit time. For a spike timing, the neuron is reset and the event is propagated, i.e. the exit-time of the target neurons are updated.

Optimization of the code can be obtained using precalculated tables of the exit-time in each voltage-step without input. If spikes are received, these timings can be used as an initial guess for the iterative search algorithm.

2.4 Link with previous works

Traditional event-driven methods are in fact spike-driven schemes; the neuron state variables are updated when a spike is received or emitted. The voltage-stepping technique produces new events: the events are not only firing times or spike reception but also the times of mode switching, i.e. when the neuron reaches a new voltage interval. The number of events is increased and thus the computational cost is increased. Local events do not have a repercussion on the overall activity of the network and are only used to update the corresponding neuron parameters. When the cost of managing events become prohibitive, it is possible to combine the event-driven simulation with a time window that processes several spikes over one step [Morrison et al., 2007]. However like every time-step methods some spikes may be missed and the order of the method is reduced.
The voltage-stepping scheme combines event-driven and discretization techniques. A method based on a combination of event-driven and time-driven schemes has been recently developed but is limited to the linear IF neuron and does not take the advantage of the sparseness of neural activity [Morrison et al., 2007]. To simulate more realistic neural models an alternative approach has been proposed by Ros et al. (2006) where an event-driven scheme that uses lookup tables is developed. The simulation is reduced to a

consultation of a precalculated table of function values. This scheme combines the advantages of the use of realistic neural models and high-speed simulations but becomes cumbersome to manage when a good accuracy is required for the numerical simulation.
Adaptive time-stepping schemes provide short time-step integration for active neurons and long-time step when the neuron is at rest or slightly activated. These methods have a clear advantage when the entire shape of the spike is calculated. When simulating neural networks, classical variable-step integrators fails to be efficient since the time-steps have to be independent from one neuron to another to avoid that the fastest changing neuron imposes the time-discretization for the entire network. In a recent study, Lytton and Hines (2005) used for each neuron an independent variable time-step integrator. A critical problem is to coordinate the local integrators and to properly handle the events. Indeed when an event arrives at a neuron at time t_e it is necessary to have all the states of the receiving neuron at time t_e. In our approach events are simply handled in an event-driven scheme. The variable time-steps induced by the voltage-stepping scheme present interesting properties: (i) by construction the threshold event lies on an integration time-step boundary. (ii) Integration points are independent, i.e. in network simulation, the time steps are different from one neuron to another. (iii) Time-steps are imposed by the voltage-trajectory and when the neuron is at rest, no step is computed. Note that the error is controlled through Δv.
Approximation by piecewise linear systems has became a classical tool for the global qualitative analysis of dynamical systems and has been proposed as a technique for numerical simulations [Girard, 2002]. The voltage-stepping method is a variant of the hybrid computation method where the simulation is done using an approximation of the vector field [Dora et al., 2001]. The hybrid computation requires a full discretization of the state space that appears to be prohibitive for large dynamical systems. Taking the advantage of point-like interactions between neurons this scheme could be efficiently implemented for the simulation of spiking networks. Following the hybrid-system framework (differential equations with discrete events), we interpret spiking neural networks as an hybrid system where global events are spikes and local events are mode switches. During simulation the neuron switches between modes of operation based on the value of the voltage, i.e. parameters of the model change when a mode transition is detected.

3 Numerical Results

To illustrate our numerical scheme we consider the quadratic integrate-and-fire (QIF) model. The QIF model includes nonlinear spike generating current and represents the normal form of any type I neuron model near the bifurcation [Ermentrout, 1996, Ermentrout and Kopell, 1986]. It is widely used as a realistic neural model [Brunel and Latham, 2003, Fourcaud-Trocmé et al., 2003, Hansel and Mato, 2001]. The dynamics of the QIF model is described by

$$\tau \frac{dv}{dt} = v^2 + I_0 + I_{syn}(t) \tag{8}$$

where v, I_0 and I_{syn} are dimensionless membrane potential, input current and synaptic current, respectively. Parameter τ is the membrane time constant. We treat synaptic current of the form

$$\begin{aligned} I_{syn}(t) &= w\ exp(-(t-t^f)/\tau_s), \quad t \geq t^f \\ &= 0, \quad t < t_f \end{aligned} \tag{9}$$

where τ_s is the synaptic time constant and w the synaptic weight. Numerical values of QIF neurons are taken from [Martinez, 2005], the membrane time constant is $\tau = 0.25ms$, $v_r = -0.0749$ and $v_{th} = 0.7288$. The synaptic time constant is $\tau_s = 6ms$ and the synaptic strength is $w = 5 \times 10^{-4}$. Note that the membrane potential, in voltage unit, is obtained using the variable change $V \leftarrow C/qv + V_0$ where $C = 0.2nF$, $q = 0.00643mS.V^{-1}$ and $V_0 = -60.68mV$. Therefore a factor of $C/q = 31.1mV$ has to be applied to the voltage step Δv to retrieve the physical unit.
One of the goals of our numerical scheme is to simulate accurately the dynamics of spiking neurons and to investigate temporal coding properties. Therefore we are interested in reproducing the exact timing of spikes and we use the following measure of error

$$Error = \frac{1}{N} \sum_f |t^f_{\text{exact}} - t^f_{\text{appro}}| \tag{10}$$

where N is the number of spikes, t^f_{exact} are the exact firing times (i.e. with an arbitrary precision) and t^f_{appro} are the corresponding approximated firing times that depends on ΔV for voltage-stepping methods or Δt for time-stepping methods. Using (10) we implicitly assume, as a minimal requirement, that the number of spikes between the exact and the approximated spike trains does not differ. This is achieved using a sufficiently accurate

numerical scheme, i.e. the steps are small enough to capture all the spikes. Therefore, the error only concerns the accuracy of individual spike timings. We have shown that the QIF model is amenable to an exact simulation [Tonnelier et al., 2007] that we will use for t^f_{exact} in the error analysis. We focus on the voltage-stepping scheme with a piecewise linear approximation. Parameters of the approximated voltage-dependent LIF, using an interpolation at the boundaries of V_i (we will call VS2 scheme), are $g_i = -\Delta v(2i+1)$ and $E_i = \Delta v\ i(i+1)/(2i+1)$ where Δv is a fixed voltage-step. We also consider the voltage-stepping scheme using a linear interpolation at gaussian abscissas (hereafter VS4 scheme). Since fixed time-step methods remain the simulation standard, we compare fixed time-step performance with our method. We examine the error of our second order scheme (VS2)and compare with the 'corresponding' second order time-stepping algorithm, the modified RK2 (the second order Runge-Kutta scheme with a linear interpolation) that is known as a second order scheme [Shelley and Tao, 2001]. Since the accuracy is activity-dependent we use different networks and different input scenarios. A single test neuron is used under a constant current in both excitable and oscillatory regimes. In addition, the quality of the numerical schemes is assessed using a more realistic paradigm: *random input current*. Finally, we demonstrate the accuracy of voltage-stepping schemes by applying it to a spiking neural network.

3.1 Constant current input

We ignore the synaptic current, $I_{syn} = 0$, and consider a QIF neuron with a constant external driving current I_0. For $I_0 < 0$ there is a pair of equilibrium points. One is stable and the other is an unstable fixed point above which a spike is emitted. The neuron is said to be excitable. For $I_0 > 0$ the neuron oscillates. We examine the error in both regime by calculating the error on the first spike time and the error on the frequency in the periodic firing regimes.

Let $I_0 < 0$ and consider an initial condition $v(0)$ slightly above the unstable fixed point $\sqrt{-I_0}$. Without further input, the membrane potential is given by

$$v(t) = -\sqrt{-I_0}\coth(\sqrt{-I_0}t/\tau - \operatorname{atanh}(\sqrt{-I_0}/v(0))).$$

and the spike timing is given by

$$t^f \quad = \quad \tau/\sqrt{-I_0}\left(\operatorname{atanh}(\sqrt{-I_0}/v(0)) - \operatorname{atanh}(\sqrt{-I_0}/v_{peak})\right) \qquad (11)$$

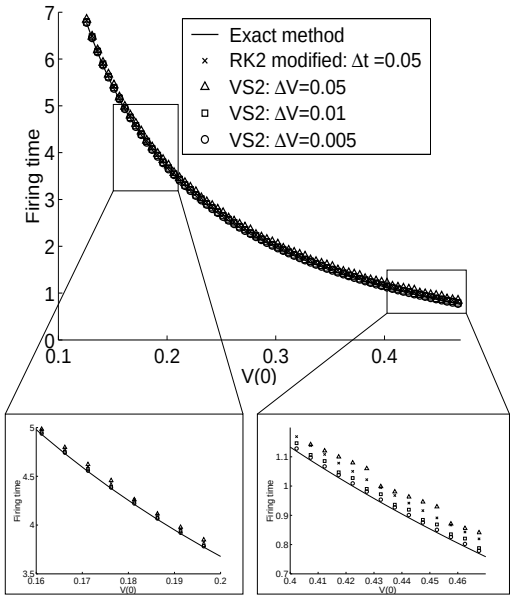

Figure 3: Firing time t^f of the QIF neuron as a function of $v(0)$ for different algorithms. Solid line is the exact value of the firing time, x's are the modified RK2 with $\Delta t = 0.05$, circles, squares and triangles are VS2 with $\Delta v = 0.05$, $\Delta v = 0.01$, $\Delta v = 0.005$, respectively. The enlarged figures show the firing time for small and large superthreshold initial conditions.

We compare the exact value of firing time to the value numerically obtained with the voltage stepping method VS2 and the modified RK2 scheme (Fig. 3). Both algorithms perform similarly for $\Delta v = 0.05, 0.01, 0.005 mV$ and $\Delta t = 0.05\ ms$ that is for a nearly equal number of integration points. A precise comparison is given further.

We also examine the errors of VS2 and VS4 schemes as a function of the voltage-step (Fig. 4). As expected, the errors of our VS2 scheme decreases quadratically with Δv while the error of the VS4 scheme diminishes as the fourth power of Δv.

To have an idea of how the time-step and the voltage-step are related, we determine the time-step versus the voltage-step required to reach a given pre-determined precision (Fig. 3.1A). Note that since this graph is activity-dependent it cannot be used as a generic $\Delta v/\Delta t$ relationship. In Fig. 3.1B we compare the computational cost of each method, i.e. the number of integration points that is used to calculate the firing time (with a given

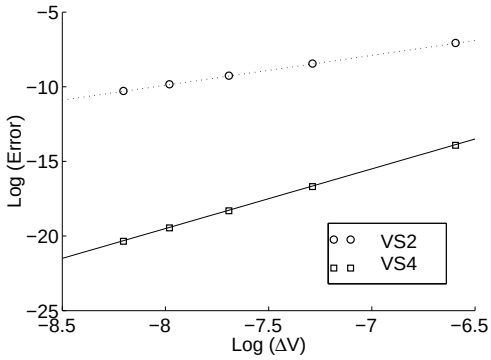

Figure 4: Log-log plot of the error on the first spike timing as a function of the voltage-step. Circles and squares are voltage-stepping methods with a piecewise linear interpolation at the boundaries of the voltage-interval (VS2) and at the gaussian abscissas (VS4), respectively. The lines (not fits) indicate the order of the methods. Dotted-line is second order and solid-line is fourth order.

precision). Note that the computational cost of the zero-search algorithm used in voltage-stepping method is not considered. We use Newton's method and practically only four or five iterations are sufficient to reach a very high precision. Note also that in general the modified Runge-Kutta methods need a zero-search algorithm to estimate the spike time (not for RK2 since the spike time is obtained by solving a linear equation). Results show that for moderate value of error (two-digits accuracy) both methods use similar discretized time steps. When higher accuracy is required, the number of time steps of the modified RK2 method dramatically increased. A major reason is that the uniform distribution of the discretized time in time-stepping methods implies the use of unnecessary time steps at the initiation of the spike in order to have short time steps at the peak of the spike.
For $I_0 > 0$ the neuron fires regularly and the firing rate is given by

$$\nu = \frac{\sqrt{I_0}}{\tau\left(\arctan\frac{\vartheta}{\sqrt{I_0}} - \arctan\frac{v_r}{\sqrt{I_0}}\right)} \tag{12}$$

In Fig. 3.1, we compare the exact value of the firing rate given by (12) with the approximated value given by our voltage-stepping method (VS2) and the modified RK2 method for different values of voltage-step and time-step. The order of the voltage-stepping methods VS2 and VS4 is numerically

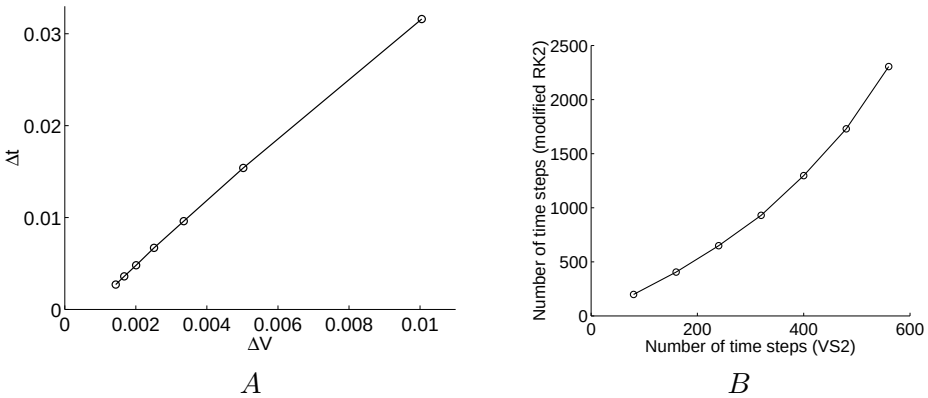

Figure 5: (A) Time-step of the modified RK2 required to reach a given precision on the calculation of the firing time as a function of the voltage-step of the VS2 method. Seven error tolerances are used that are approximately: $Error = 2 \times 10^{-2}, 3 \times 10^{-2}, 6 \times 10^{-3}, 5 \times 10^{-3}, 4 \times 10^{-3}, 3 \times 10^{-3}$ (from right to left). (B) Number of time steps of the modified RK2 scheme as a function of the respective number of time steps of the voltage-stepping method that are associated to the seven error values given in (A), from left to right.

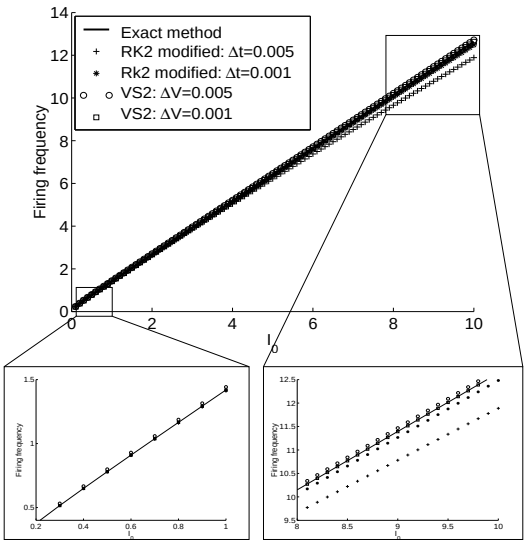

Figure 6: Firing rate of the QIF neuron as a function of the input current. The solid line is the exact value. The + and $*$ correspond to the firing rate given by the modified Runge-Kutta method of order 2 with a time-step $\Delta t = 0.005\ ms$ and $\Delta t = 0.001\ ms$, respectively. Circles and squares represent VS2 with $\Delta v = 0.005$ and $\Delta v = 0.001$. The enlarged figures show the frequency for different values of the input current.

evaluated in Fig. 3.1. Results support those obtained for the computation of the first spike time.

3.2 Random current injection

We consider a simple test neuron receiving a synaptic activity modeled by a fluctuating spike train. Note that we use a current injection and a more realistic input scenario would be stochastic conductance changes. However a random conductance scenario can be replaced, to a high degree of accuracy, by a random current injection [Ridchardson, 2004]. For clarity, we keep the current injection paradigm. We investigate two scenarios that reproduce two different regimes of neural activity.

In the first scenario, we use a fixed excitatory spike train generated by a Poisson process with rate $\nu_E = 10^4 spikes/s$ that models the interaction with 1000 excitatory presynaptic neurons firing at 10 Hz. In this scenario, the

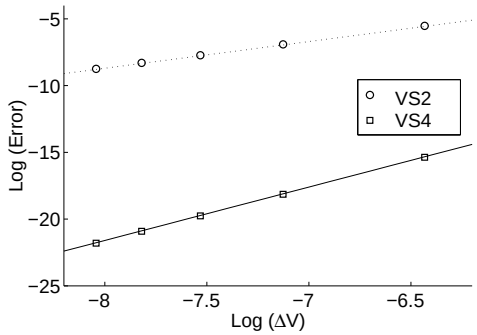

Figure 7: Errors on the firing rate as a function of the voltage-step for the voltage-stepping methods VS2 (circle) and VS4 (square). The lines (not fits) indicate the order of the methods. Dotted-line is second order and solid-line is fourth order.

neuron operates in a high activity regime with a firing rate $\sim 400 spikes/s$. The second scenario is described by two fluctuating synaptic currents, one excitatory Poisson process ($\nu_E = 10^4 spikes/s$) and one inhibitory Poisson process ($\nu_I = 10^4 spikes/s$). The neuron operates in a fluctuation-driven regime with a moderate firing rate ($\sim 30 spikes/s$). We compute the error on the spike timings of the QIF model using the voltage-stepping method (VS2) for different voltage-steps. To evaluate the performance we determine, in each scenario and for a given voltage-step, the corresponding number of time-steps of the modified RK2 method that is necessary to reach the same accuracy.

In the first scenario the neuron fires regularly with monotonic subthreshold membrane voltage trajectories. Results are given in Table 3.2. For different values of the voltage-steps we compute the error and the number of integration points use by the simulation. To preserve the accuracy of spike times up to $1s$ of simulation time, we had to use numerous integration points. In this scenario, we found that time-stepping schemes gave comparable results. For instance, using a fixed time steps $\Delta t = 0.02ms$, the modified RK2 scheme integrates 50000 times during $1s$, and it gives $log(Error) = -6.06$ (i.e. a six-digit accuracy). Such accuracy is reached using voltage-stepping scheme VS2 with a bit more integration points (see Table 3.2). The disadvantage is due to the fact that trajectory of the membrane potential are abrupt and the spike time is well approximated by the linear interpolation used by the

$N_{\Delta v}$	$Log(Error)$	N_{IPs}
50	-3.69	18950
100	-5.18	37900
150	-5.99	59550
200	-6.39	75800

Table 1: Error on spike timings in the regular firing regime for different voltage-steps. We simulate one test neuron over 1 *second* with different voltage-steps. $N_{\Delta v}$ gives the number of voltage steps used to discretize the voltage space between v_r (resetting potential) and v_{th} (peak of a spike). $Log(Error)$ is calculated according to (10) and N_{IPs} represents the corresponding number of integration points for different voltage-steps.

modified RK2 scheme whereas, in voltage-stepping scheme, several voltage-steps are used without enhancing the accuracy.
In the second scenario, the membrane potential is driven by the balanced of excitation and inhibition. In this regime, the spike-times are irregular. For a fixed voltage-step, the accuracy of the voltage-stepping is affected (see table 3.2) but on the other hand the number of integration point significantly decreases. The accuracy of Runge-Kutta type schemes dramatically

$N_{\Delta v}$	$Log(Error)$	N_{IPs}
50	-1.64	1718
100	-3.01	3417
150	-3.63	5151
200	-3.87	6843

Table 2: Error on spike timings in the irregular firing regime for different voltage-steps. The notations of $N_{\Delta v}$, $Log(Error)$ and N_{IPs} represent the same meaning as those in Table (3.2).

decrease and small time-steps are necessary to compute accurately the spike times. For instance, with $N_{\Delta v} = 150$ the VS2 method uses 5151 integration points. The modified RK2 method requires approximatively 25000 time steps ($\Delta t = 0.04ms$) to reach the same accuracy. In this regime, the advantage of the voltage-stepping scheme is clear.

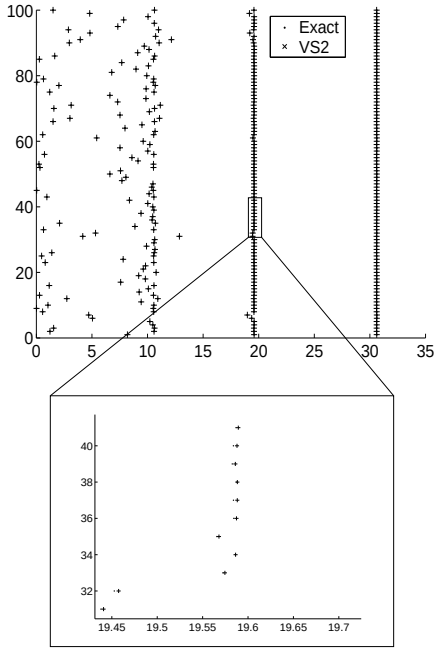

Figure 8: Simulation of a network of 100 inhibitory neurons. Spike times are computed exactly (dots) and with the VS2 method using $N_{\Delta v} = 250$ voltage-intervals ('+'). A high degree of accuracy is obtained and spikes are superimposed most of time.

3.3 Network activity

We demonstrate the accuracy of our integration scheme by applying it to a small network of $N = 100$ inhibitory neurons. Such network shows rapid synchronization through mutual inhibitions and variations of this model have been widely studied [Wang and Buzsaki, 1996, Martinez, 2005, Ambard and Martinez, 2006]. We consider all-to-all coupling between inhibitory neurons with a synaptic strength $g_i = 0.005$. Each inhibitory neuron is driven by a pre-synaptic excitatory spike train (Poisson process, $\nu_E = 10^4 spikes/s$) with a synaptic weight $g_e = 0.005$. We integrate until $t = 40ms$ and use the VS2 method with a subdivision of the voltage-space into $N_{\Delta v} = 250$ voltage-intervals. The exact and approximated spike times are shown in Figure 3.3.

4 Conclusions

Recent efforts have been made to simulate integrate-and-fire neuronal networks. Specific methods like event-driven schemes [Makino, 2003, Brette, 2006, Brette, 2007], fast methods [Rangan and Cai, 2007] or exact time-stepping schemes [Morrison et al., 2007] are limited to linear integrate-and-fire models. Voltage-stepping methods are generic numerical schemes that realize an efficient and accurate numerical integration of spiking neural networks. Important elements in our approach are (i) the variable time-steps that are different for each neuron in the network depending on their activity (ii) the treatment of the possible discontinuities of the dynamics (iii) the event-driven nature of the simulation. This event-driven treatment presents significant advantage when delays have to be considered.
Our voltage-stepping method is not necessarily restricted to uniform voltage step Δv. There exists efficient algorithms [Breiman, 1993] that can be used to optimize both the non-uniform intervals V_i and their associated linear approximations. A possible extension of our approach is to use a voltage-discretization adapted to the non-linear voltage-dependent current of the model.

Appendix:Order of voltage-stepping schemes

For simplicity, we consider a general neuron model described as follows

$$\frac{dv(t)}{dt} = f\left(v(t)\right) \tag{13}$$

For consistency, we keep the same notations used in Sections 2 and 3. Over V_i, one possible linear interpolation for function $f(v)$ can be achieved by interpolating it at the boundaries v_i and v_{i+1}. It should be noted that other possible linear interpolations for $f(v)$ are also existed, and we will discuss it in the second part of this appendix.

Linear interpolation at boundaries (VS2 method)

Let us consider $v_{\Delta v}$ the solution of the following dynamical system:

$$\frac{dv}{dt} = f_{\Delta v}(v) \tag{14}$$

where $f_{\Delta v}$ is the piecewise linear function as follows:

$$f_{\Delta v}(v) = \frac{v_{i+1} - v}{\Delta v} f\left(v_i\right) + \frac{v - v_i}{\Delta v} f\left(v_{i+1}\right)$$

Then it can be proved that the error of approximation is bounded by

$$|f(v) - f_{\Delta v}(v)| = O\left(\Delta v^2\right) \tag{15}$$

Considering the following theorem:

Theorem 1 *(Fundamental Inequality [Hubbard and West, 1991]) For a differential equation $\dot{X} = F(x)$ satisfying the Lipschitz condition with $K \neq 0$ and if $u_1(t)$ and $u_2(t)$ are two continuous, piecewise differentiable functions satisfying $|\dot{u}_i(t) - F(u_i(t))| \leq \varepsilon_i$ for all t at which $u_1(t)$ and $u_2(t)$ are differentiable and if $|u_1(0) - u_2(0)| \leq \delta$, then*

$$|u_1(t) - u_2(t)| \leq \delta e^{K|t|} + \frac{\varepsilon_1 + \varepsilon_2}{K}\left(e^{K|t|} - 1\right).$$

Applying Theorem 1 into (13) and (14), with (15), it has been proved that $v - v_{\Delta v} = O\left(\Delta v^2\right)$, which follows $\Delta t = \left|t^f_{exact} - t^f_{appro}\right| = O\left(\Delta v^2\right)$. It means that if using boundaries of each V_i to linearly interpolate $f(v)$ over V, the estimate error of exact spike time is with an accuracy of $O\left(\Delta v^2\right)$.

Moreover, the following two special remarks should be noted:

- At the neural network level, the incoming spikes generated by presynaptic neurons introduced a second order error (since $\left|t^f_{exact} - t^f_{appro}\right| = O(\Delta v^2)$). However, noting the fact that $f_{\Delta v}$ linearly approximates f, and do not change the order of the approximation given by (15). Consequently, the proposed voltage-stepping scheme (VS2) guarantees still the same accuracy of network level with as that of neuron level, even after considering the effect of propagation of estimate error of spike time.

- For the p-dimensional case, the only difference is to approximate $f(v)$ over $V_i \subseteq R^p$ by a linear system: $f_{\Delta v}(v) = A_i v + b_i$, which is uniquely determined as the linear interpolation vector field of $f(v)$. The same result can be achieved by using $\|\cdot\|$ to replace $|\cdot|$ (refer to [Girard, 2002] for more details).

Linear interpolation at gaussian abscissas (VS4 method)
Over V_i, let us reconsider (13) and (14), which follows

$$\Delta t_i = t^i_{exact} - t^i_{appro} = \int_{v_i}^{v_{i+1}} \left(\frac{1}{f(v)} - \frac{1}{f_{\Delta v}(v)}\right) dv \tag{16}$$

where t^i_{exact} represents the exact exit time of (13) over V_i, and t^i_{appro} represents its approximation. The objective is to minimize (16). Note that $\frac{1}{f_{\Delta v}(v)} \in C^\infty$, if $\frac{1}{f(v)}$ is C^k, $k \geq 4$, then according to Gaussian quadrature rule, if we use linear interpolation at gaussian abscissas: $f_{\Delta v}$ to approximate f, then we have

$$\int_{v_i}^{v_{i+1}} \left(\frac{1}{f(v)} - \frac{1}{f_{\Delta v}(v)} \right) dv = O\left(\Delta v^5\right) \tag{17}$$

The only point is to calculate the gaussian abscissas over V_i. According to Gaussian quadrature rule, for linear interpolation case (i.e., the number of evaluation points is 2), the Legendre polynomials to obtain these two evaluation points on the interval $[-1, 1]$ are $\pm\frac{1}{\sqrt{3}}$. Hence, over $V_i = [v_i, v_{i+1}[$, the gaussian abscissas are as follows:

$$\begin{aligned} v_{i,1} &= \frac{\sqrt{3}-1}{2\sqrt{3}} v_{i+1} + \frac{\sqrt{3}+1}{2\sqrt{3}} v_i \\ v_{i,2} &= \frac{\sqrt{3}+1}{2\sqrt{3}} v_{i+1} + \frac{\sqrt{3}-1}{2\sqrt{3}} v_i \end{aligned}$$

based on which, the linear interpolation of $f(v)$ can be described as follows:

$$f_{\Delta v}(v) = \frac{v_{i,2} - v}{v_{i,2} - v_{i,1}} f(v_{i,1}) + \frac{v - v_{i,1}}{v_{i,2} - v_{i,1}} f(v_{i,2})$$

Consequently, over each V_i, by using linear interpolation at gaussian abscissas, the accuracy of approximation of exact spike time is of an order $O\left(\Delta v^5\right)$, thus over all V, the estimate error of exact spike time is with an accuracy of $O\left(\Delta v^4\right)$.

It should be noted that this method cannot be generalized into high dimensional system. The major reason is that (17) cannot be always fulfilled in high dimensional case. Moreover, at neural network simulation, since the incoming spikes generated by presynaptic neurons introduced a fourth order error, which makes also equation (17) failed, thus the proposed voltage-stepping scheme (VS4) cannot be generalized into neural network simulation. For this moment, this method works only for single neuron simulation, and how to preserve hight approximation accuracy when applying it into neural network simulation is still an open problem.

Acknowledgments

Research supported by the INRIA cooperative research initiative RDNR.

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