Event-Driven Simulation of Spiking Neurons embedded in Very Large Networks

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Abstract

We present a new technique, based on a proposed event-based strategy (Mattia & Del Giudice, 2000), for efficiently simulating large networks of simple model neurons. The strategy was based on the fact that interactions between cortical neurons occur by means of events which are well-localized in time (the action potentials) and relatively rare. In the interval between two of these events, the state variables associated with a model neuron or a synapse evolved deterministically and in a predictable way. Here we extend the event-driven simulation strategy to the case in which the dynamics of the state variables in the inter-event intervals are stochastic. This extension captures the situation in which the simulated neurons are embedded in a very large network and receive a huge number of random synaptic inputs. We show how to effectively include the impact of large background populations into neuronal dynamics by means of the numerical evaluation of the statistical properties of single model neurons under random current injection. The new simulation strategy allows to study networks of interacting neurons with an arbitrary number of external afferents.
1 Introduction

Most of the observed in vivo cortical phenomena are believed to be the expression of the collective dynamics of large populations of interacting neurons. The richness and the complexity of these phenomena call for new powerful techniques for investigating in a systematic way the emergent behavior of large networks of neurons. In this respect, computer simulations are becoming an increasingly important tool to model realistic cortical modules ($10^4 - 10^5$ neurons and $10^7 - 10^9$ synapses), to relate single neuron/synapse properties to the collective dynamics of large networks and to check the validity of the numerous assumptions underlying the theories of neural networks as dynamical systems.

Traditional fixed time-step (synchronous) computer simulations are based on numerical methods for solving a set of coupled differential equations that describe the dynamics of the basic elements of the networks (the neurons and the synapses). The time axis is uniformly discretized and each state variable is updated at every time step. Under such conditions, the algorithmic complexity usually scales with the number of elements contained in the network multiplied by the number of time steps into which the simulated interval is divided. Such an approach also sets a cutoff on the temporal resolution of the simulation (the minimal time step) which is imposed on all the state variables, no matter whether they are characterized by completely different time scales. This represents an obvious drawback when slow and fast dynamic variables coexist, as all of them are updated at the very same pace, i.e. the one determined by the fastest variable. When the number of neurons and synapses approach realistic numbers for a cortical column ($\sim 10^5$), the traditional techniques become impracticable and new alternative simulation strategies should be devised.

One possible solution takes natural inspiration from the way the neurons exchange information and interact: most of the dynamical variables are coupled for relatively short time intervals only, during the emission and the transmission of action potentials. The emission of a spike is a relatively rare event (the typical cortical frequencies being of the order of several Hz) and well localized in time (i.e. the width of a spike is of the order of 1ms) with respect to the overall simulation times. Interestingly, it can be observed that within the interval between two consecutive relevant events (e.g. spikes as in our case, though the present approach can be generalized to other classes of events) the neurons and the synapses are essentially isolated, and each state variable is usually described by a deterministic, uncoupled differential equation. Therefore, given the initial state at the beginning of the interval and the length of the interval, the final state can be determined without iteratively updating the state variable at every time step. This approach is usually known as event-driven, it constitutes the fundamental principle of modern operating systems and it has already been applied successfully to large-scale simulations of networks of spiking neurons (Watts, 1994; Mattia & Del Giudice, 2000; Giugliano, 2000). The CPU time of these simulations depends mostly on the frequency of occurrence of relevant events, and not on the time simulated. If the relevant events are rare, as would be the spike frequency in the cortex, then the event-driven approach reduces dramatically the computational loads.

However, one drawback of this strategy manifests itself when the network to be studied is embedded in a very large population of neurons that provide an external background activity. This is usually meant to emulate the sensory inputs or, more in general, the inputs coming from other areas of the brain (see e.g. Amit & Brunel, 1997a; Wang, 1999). This interaction, at least on a first approximation, is modelled as a one-way connection (i.e. feed-forward input) in the sense that the local simulated activity of the network of neurons does not affect the background activity that
represents the external input. Each simulated (internal) neuron receives synaptic inputs from a group of $M_{\text{ext}}$ external neurons. The external population is assumed to be large and the overlap between the external groups corresponding to different internal neurons is usually small. Hence the total synaptic currents generated by the external neurons and injected into different internal neurons can be considered statistically independent. These inputs provide the external stimulation and allow the network to sustain the spontaneous activity observed in cortical recordings (Amit & Brunel, 1997a). In the case of the event-based simulation approach of (Mattia & Del Giudice, 2000), such an external activity was implemented by generating, for each of the $N$ neurons in the simulated networks, a large number of additional random presynaptic spike events, fired on the average at a frequency $\nu_{\text{ext}}$ by each of the $M_{\text{ext}}$ neurons of the external background populations. Such hypotheses give rise to an additional algorithmic complexity that can be quantified as $O(N \cdot \nu_{\text{ext}} \cdot M_{\text{ext}})$. As a consequence, the increased realism introduced in the simulated neuronal dynamics, by appropriately increasing the size of the individual background populations for each unit of the network, has to be paid in terms of a considerable portion of CPU loads, substantially slowing the event-driven approach. Moreover, as the size of the external population increases, the external spikes can saturate very quickly the list of events that have to be handled by the simulator, and the inter-event interval can be as short as a few nano-seconds (it scales as $O(1/(N \cdot \nu_{\text{ext}} \cdot M_{\text{ext}}))$). In particular, such short time intervals can easily produce roundoff errors (see e.g. Press et al, 1986) and require double precision floating point variables to encode the time of occurrence of the events.

In the present work we propose a possible solution to these problems. If the synaptic background activity is irregular, as in the in vivo phenomena to be modelled, the impact of the external neurons on each simulated neuron of the network can be approximated by a continuous random current injection with appropriate statistical properties, directly related to $\nu_{\text{ext}}$ and $M_{\text{ext}}$ (Gerstein & Mandelbrot, 1964; Tuckwell, 1988). Furthermore, by numerically solving the master equation that governs the density distribution of the state variables, it is possible to predict the behavior of each neuron under such a noisy stimulating current, during those time intervals where no synaptic input (relevant event) from the internal simulated neurons occurs. Actually it can be proved that if the (excitatory and/or inhibitory) postsynaptic potentials evoked by a single presynaptic spike are small compared to the threshold for triggering postsynaptic action potentials (i.e. diffusion approximation), the density equation can be reduced to a simpler Fokker-Planck equation which in many cases can be solved analytically (Ricciardi, 1977). These theoretical approaches have already proved to constitute a powerful tool for studying network properties in stationary conditions, such as in the studies on spontaneous activity, on the persistent, stimulus-selective delay activity observed in the cortex (see e.g. Amit & Brunel, 1997b; Yakovlev et al, 1998; Wang, 1999; Fusi & Mattia, 1999; Brunel 2000) or to study the network response properties to transient or oscillatory inputs (see Knight, 1972; or Gerstner & Kistler, 2002, for a review). By combining these strategies with an event-driven simulation approach, we show in the present paper how to effectively implement the global background activity, reducing its computational complexity to $O(N \cdot \nu_{\text{ext}})$.

2 The simulation algorithm

2.1 The general idea

In the event-driven approach described in (Mattia & Del Giudice, 2000) the dynamics of the neurons and the synapses were updated only upon the arrival of a spike.
Therefore, the action potential was the relevant event to trigger an update of the state variables. The new state was then computed on the basis of two elements: (i) the initial state, following the previous update, and (ii) the time that passed since the previous update. Because the dynamics of both synapses and neurons was deterministic in this interval, the final state could be determined for an arbitrary time interval by the solution of the differential equations governing the dynamics of the neurons.

In our case the external spikes are not explicitly treated as synaptic events. Instead, we assume that the external activity is highly irregular and that the total synaptic current coming from outside can be described as a stochastic process with some distribution. In a traditional fixed time-step simulation, at each step the external current should be randomly generated, independently for each neuron, and the state variables affected by it should be updated. Therefore the dynamics of the state variables would be non-deterministic, and the final state could not be determined by the initial condition and the time that has passed since the previous update. However, given the distribution of the external current, it is possible to determine the distribution of the state variables as a function of time. It is as if each state variable starts from some determined initial value at the preceding update time (when the distribution is a delta function), and then it evolves along all the possible trajectories determined by the different realizations of the input currents. This packet of trajectories would evolve until another relevant event occurs. At this time, the packet should be reduced to a single trajectory which is the one that has actually been followed by the neuron. The advantage is that it is not necessary to integrate iteratively, and presumably many times, the state variables during the interval between two relevant events. Deciding at the end what was the actual trajectory is completely equivalent to what would be obtained in a fixed time-step approach, provided that the trajectory is chosen according to the correct distribution of the state variables.

2.2 An example: networks of integrate-and-fire neurons

The approach for the proposed new event-driven algorithm is quite general and can be applied to a large class of neuronal models and synaptic interactions (see also Mattia & Del Giudice, 2000; Giugliano, 2000). In order to illustrate the algorithm we will focus on a network of randomly connected integrate-and-fire (IF) model neurons, whose state is fully determined by a single internal variable, the membrane potential $V$. In the Discussion we will then show how to generalize this approach to more complex models.

Formally, the differential equation that governs the dynamics of the membrane voltage below threshold for a generic neuron can be written as follows:

$$\frac{dV}{dt} = \frac{(V_{\text{rest}} - V)}{\tau_m} + I_{\text{int}}(t) + I_{\text{ext}}(t) \quad V_{\text{min}} \leq V < V_{\vartheta}$$

(1)

where $V_{\text{rest}}$ is the resting potential and $\tau_m$ is the passive membrane time constant. $I_{\text{int}}(t)$ represents the net charging current generated by synaptic inputs from other neurons within the simulated network, and $I_{\text{ext}}(t)$ is the current due to afferent spikes resulting from the external background activity only, coming from the feedforward neurons. We assume that each internal neuron receives the external input from a different group of $M_{\text{ext}}$ external neurons. If $V$ reaches a threshold $V_{\theta}$, the neuron emits a spike, and $V$ is reset to a value $V_{\text{reset}} < V_{\vartheta}$, where it remains during an absolute refractory period $\tau_{\text{arp}}$. A rigid (reflecting) barrier $V_{\text{min}}$ was included to restrict the membrane potential to the interval $V_{\text{min}} \leq V(t) < V_{\vartheta}$. Although unusual compared to the IF dynamics described in the literature, such a choice is...
reasonable, as the physiological range for \( V \) in a real neuron is anyway bounded by the ionic concentration ratios across the membrane.

If the spikes are point-processes (i.e. their time width is zero), \( I_{int}(t) \) can be written as a sum of Dirac deltas:

\[
I_{int}(t) = \sum_k J_k \delta(t - t_k)
\]

where the sum extends over all the afferent spikes. The efficacy of each spike is given by \( J_k \). In the interval between two successive synaptic inputs \( I_{int}(t) = 0 \), and the cell follows a random walk induced by the external input \( I_{ext}(t) \). If the external spikes are statistically independent, the total external synaptic current impinging on a generic neuron of the network can be well approximated by a Gauss-distributed, delta-correlated stochastic process characterized by a mean \( \mu \) and a variance \( \sigma^2 \) per unit time (Amit & Tsodyks, 1991; Gerstein & Mandelbrot, 1964; Tuckwell, 1988). \( \mu \) and \( \sigma^2 \) are explicitly related to the mean firing rate \( \nu_{ext} \) of the external population, its probability of feed-forward connectivity \( c_{ext} \), its size \( M_{ext} \) and the average synaptic strength \( J_{ext} \), according to the following equations:

\[
\begin{align*}
\mu &= \nu_{ext} \cdot c_{ext} \cdot M_{ext} \cdot J_{ext} \\
\sigma^2 &= \nu_{ext} \cdot c_{ext} \cdot M_{ext} \cdot J_{ext}^2
\end{align*}
\]  

(2)

As a consequence, the temporal evolution of the membrane potential \( V \) in the intervals between two consecutive internal spikes can be regarded as a stochastic diffusion process whose statistical properties are completely described by \( P_V(V, t) \), representing the probability density of having \( V(t) = V \) (Ricciardi, 1977; Tuckwell, 1988). Given that the neuron starts from \( V(t_0) = V_0 \) at time \( t_0 \) (the time of the last relevant event), \( P_V(V, t) \) describes the packet of depolarization trajectories generated by the external input when the neuron had a particular initial value \( V_0 \). Before the arrival of the next spike emitted by one of the network neurons, it might happen that the external synaptic current drives the voltage across the threshold \( V_\vartheta \). These crossings occur at any time \( t \) at a rate \( P_{fpt}(t_0, V_0; t) \) which expresses the probability density of reaching the threshold at time \( t \), given the initial state \( V = V_0 \) at time \( t_0 \). These probabilities can be computed numerically by solving the diffusion equations that govern \( P_V(V, t) \) (see Appendix). A solution is shown in Figure 1, where the temporal evolution of the probability density for the \( V \) and the corresponding inter-spike interval distribution are plotted. Note that there is an overall decrease of the distribution in time, because the fraction of neurons that cross the firing threshold are eliminated (we are interested in the first passage time only). As apparent from the inspection of the inter-spike interval distribution, there is at any time a non-zero probability of crossing the firing threshold at \( V_\vartheta = -50 \text{mV} \).

### 2.3 The extended event-driven algorithm

Unlike in the fully deterministic case, where the state of a neuron is only influenced by events having taken place before the current time, we now have to consider also the possibility of having uncertain events, i.e. predictions about the neuron’s future which may or may not come to happen: by drawing a random number according to the probability distribution given by \( P_{fpt} \), we obtain the predicted time \( (T_1) \) of a first threshold crossing. However, if the state of the neuron is influenced in any way before \( T_1 \), a new prediction has to be made based on the current state, and the old prediction becomes irrelevant.

To describe in some detail our algorithm, we consider a generic neuron, whose initial condition is \( V(t_0) = V_0 \) (cf Figure 2), embedded in a network:

1. First, we draw a pseudo-random number according to the distribution given
by \( P_{\text{fpt}}(t_0, V_0; T_1) \), which yields time \( T_1 \) as the predicted time of the next threshold crossing according to our neuron model (Figure 2, A1).

2. Two possible situations might now occur, and they can be outlined as follows:

a. No presynaptic (internal) spike arrives in the time interval \([t_0, T_1]\) from other neurons within the network. At time \( t = T_1 \), the neuron emits a spike (as determined in the first step) and enters the absolute refractory period, after which the neuron continues at step 1 using \( V_0^{\text{new}} = V_{\text{reset}} \) and \( t_0^{\text{new}} = T_1 + \tau_{\text{arp}} \) (Figure 2, A2). The spike emission leads to the creation of further events which represent the synaptic interactions that will take place in response to this spike after some axonal delay period.

b. A single internal spike arrives at time \( t_1^{sp} \) \((t_0 < t_1^{sp} < T_1)\). At this point, the membrane voltage \( V_1 \) is drawn from \( P_V(t_0, V_0; V_1, t_1^{sp}) \) and subsequently updated according to the synaptic strength \( \Delta V_1 = J \) associated with the incoming spike. Now again two scenarios are possible, depending on whether the new membrane potential \( (V_1 + \Delta V_1) \) is

i. below threshold, in which case the neuron continues at step 1 using \( V_0^{\text{new}} = V_1 + \Delta V_1 \) and \( t_0^{\text{new}} = t_1^{sp} \) (Figure 2B).

ii. equal or above threshold \( V_0 \), in which case the neuron emits a spike and the membrane voltage is reset to \( V_{\text{reset}} \) during the absolute refractory period, after which the neuron continues at step 1 using \( V_0^{\text{new}} = V_{\text{reset}} \) and \( t_0^{\text{new}} = t_1^{sp} + \tau_{\text{arp}} \) (Figure 2C). As before, the spike emission results in the generation of new events to be processed later in the simulation.

This is repeated during all the simulation time, or until no more events are to be processed.

A critical situation occurs when the statistics of the background activity change, because this affects also the probability distributions. In order to propagate the change to the whole network, all neurons must immediately be visited and the current state variables must be updated according to \( P_V \), using the old statistics. Then, using \( P_{\text{fpt}} \) with the new statistics, spontaneous spike times are determined as usual and the simulation continues as described above.

It is clear from this procedure that the statistics of the background activity can only change in time by discrete s.pdf, rather than in a continuous way. This is an inherent limitation of the event-driven approach. However, most physiological situations can be adequately described by piecewise constant (discontinuous) changes in the statistical properties of the external background populations. An example of such a change is given in Figure 3.

2.4 Implementation of the event list

As a consequence of the event-based simulation approach, a large number of events have to be processed in chronological order. The strategies involved in handling the events have to be chosen with care, given that a lack of efficiency could lower the performance of the algorithm considerably.

The problem reduces to having a single ordered list with random insertions (when creating new events), repetitive deletion of the lowest element (when the next event is processed), and occasional random deletions (when an uncertain event becomes irrelevant). An appropriate data structure for the storage of the events is given by the class of balanced trees, which ensure good performance: searching for one
element out of $E$ costs $O(\log(E))$ operations. However, maintaining the balance of the tree causes considerable overhead, especially in our situation where repetitive deletions occur at one place (Wirth, 1975).

In our implementation, we used the ‘skip list’ data structure, which is a probabilistic alternative to balanced trees (Pugh, 1990), based on linked lists. In this structure, maintenance of the balance comes as a consequence of the probabilistic nature of the structure, and the insertion and deletion algorithms are as simple as those for linked lists. Therefore skip lists strongly reduce the overhead of the event handling, while offering the performance benefits of balanced trees.

### 2.5 Look-up tables

In the general case, the processing of an event requires a partial differential equation (e.g. eq 3 in Appendix) to be solved numerically, which is time consuming. Although this computational load doesn’t directly depend on the assumed size of the external populations ($M_{ext}$), and therefore doesn’t affect the runtime performance scaling of our algorithm with respect to $M_{ext}$, it nevertheless reduces the overall performance of the simulation in a dramatic way. However, we can make use of the fact that the parameters governing the evolution of the probability distributions can only change in a discontinuous manner, and prepare tables of all needed distributions offline. These tables can be stored and used during the simulation, therefore reducing the computationally delicate task to simple table look-ups.

For a specific example see again Figure 1, where such an offline evaluated solution has been graphically represented. The time-varying probability density distribution $P_V$ and the corresponding inter-spike interval distribution density $P_{fpt}$ are plotted for a particular $V_0 = -70mV$. The density distribution represented by the surface starts as a Dirac-delta located at $V = V_0$ and, as the time goes by with no internal event occurring, it drifts towards the asymptotic value ($\mu \tau_m = 14.5mV$) and diffuses at a rate $\sigma$ (with $\sigma^2 \tau_m = 10.2mV^2$). Accordingly, the first-passage time probability density distribution $P_{fpt}$ first increases and then slowly decreases to zero for large time intervals. Of course, different initial conditions $V_0$ yield different profiles of $P_V$ and $P_{fpt}$.

### 3 Performance evaluation

#### 3.1 Numerical accuracy

The introduction of tabular discretizations will introduce numerical approximations which influence the accuracy of the simulations. The fact that a higher table resolution produces more accurate results leads to a trade-off between accuracy and table resolution (which directly affects memory consumption). This is illustrated also in Figure 3: the different lines in B correspond to different table resolutions. The deviations from the predicted frequency in B (23.6 Hz in the high noise regime) are plotted in panel C as a function of table resolution. Of the resolutions tested in C, best results were obtained with 0.1$mV$ and 0.5$ms$ in the voltage and time domains, respectively, and the number of elements contained in the corresponding table was of the order of $10^6$. Panel D demonstrates that the accuracy is very sensitive to the discretization of the voltage, and less sensitive to the time resolution.

In order to maximize accuracy and minimize memory usage, non-uniform discretizations and efficient interpolation methods can be used. In particular, voltages near the threshold and short time intervals should be represented with a refined discretization.
3.2 Runtime performance

The proposed algorithm provides fast simulations of large networks. In order to check the simulation results for correctness, the emergent behaviors were compared to the mean-field theory predictions (cf Figure 3). Minor discrepancies in the global firing rate were expected, since an additional reflecting lower barrier for the depolarization of the single neuron was set at \( V = V_{\text{min}} \), slightly altering the IF dynamics compared to those employed in the theory (Appendix, eq. 3). The achieved accuracy was anyway satisfying, and the typical transient overshots in the collective mean firing rate, expected after a sudden increase in the statistics of the background activity, was captured (see Figure 3B).

All the simulations were performed on a Pentium III 850MHz system running Linux, and they confirmed that excellent runtime performance can be achieved if the computation of the probabilistic dynamics (i.e. the online probability tables search and look-up, and the consequent random number extractions) is fast enough. Figure 4A reports a benchmark comparing our algorithm with the event-driven approach of (Mattia & Del Giudice, 2000). Both simulations were performed over a simulated time of 1 second with a network of 1000 IF neurons, characterized by a weak average internal synaptic coupling (i.e. \( J = 0.1 \text{mV} \)) and by a low connectivity probability (i.e. \( c = 0.1 \)). With the aim of accounting for differences in the output frequency, the execution times of both simulation approaches were normalized, and plotted as a function of the mean number of spikes received by each neuron from the external neurons (i.e. background activity, \( F_{\text{ext}} \)) divided by the number of spikes received by the other simulated neurons (i.e. internal activity, \( F \)):

\[
\frac{F_{\text{ext}}}{F} = \frac{M_{\text{ext}} \cdot c_{\text{ext}} \cdot \nu_{\text{ext}}}{N \cdot c \cdot \nu},
\]

where \( c \) and \( c_{\text{ext}} \) are set to 0.1 and 1, respectively, \( \nu_{\text{ext}} \) is calculated from the statistics of the background populations, and \( \nu \) is the fraction of simulated neurons which emit a spike per unit time. The ratio \( M_{\text{ext}}/N \) was varied systematically (0.1, 1, 10, 100, 1000). The figure demonstrates that the execution time of the extended event-driven approach scales very well (does not increase) with respect to the increase in the size of the background populations. Only in the case of very few external spikes per unit time, the approach of Mattia and Del Giudice performs better than ours, which can be explained by the lower time required to process a single event: only one random number has to be generated, compared to at least two in the extended algorithm (one for \( P_V \) and \( P_{\text{fpt}} \) each, and for each newly inserted event in the event list).

The execution time is also affected by the size \( N \) of the network to be simulated, scaling with the square of \( N \) (see Figure 4B), and for a given network size it increases almost linearly with the output frequency, as expected from the analysis of the traditional event-driven simulation paradigm.

As demonstrated by the simulation results, the main strength of the proposed approach is therefore related to the fact that the external populations were not modelled explicitly, resulting in an execution time independent of the number of external neurons (\( M_{\text{ext}} \)) and of the ratio of the external to internal spikes: \( O(N \cdot \nu_{\text{ext}}) \). As a consequence, \( M_{\text{ext}} \) enters the simulation only as a parameter in the expressions of the mean \( \mu \) and the variance \( \sigma^2 \) of the external current (see eq. 2).
4 Discussion

The considerable speed-up of simulation times makes our approach suitable for the investigation of the emergent collective behaviors in large-scale networks of neurons and extends the perspectives of the event-driven simulation approach. In our tests, a simulation of 1000 neurons with a connectivity probability of 0.1 was running in real time \(^1\) (i.e. 1 s of the simulated network was executed in 1 s, while the mean frequency was 4Hz), no matter how large the external population was. It is important to stress that our approach does not imply any approximation provided that the number of independent external afferents to be mimicked is large enough and that the solution of the density equation is accurate. Our simulations produce the same results as any traditional fixed-time-step approach, in which the external afferents are statistically independent. In this our strategy differs from the one of (Knight, 1972) who suggested to study the whole network dynamics by solving the density equations that govern the assembly of neurons. His strategy strongly relies on the assumption that the large number of neurons in the simulated network lose their identity, and hence, that the network state can be fully described by the probability density function of the state variables. In many cases this represents a good approximation, although finite size effects should be added artificially to the dynamic equations of the probability density function, to account for the finite size of the network under consideration (e.g. see Brunel & Hakim, 1999). Moreover, the weak statistical correlations introduced by the synaptic couplings, which cannot be modelled in a density approach, must be neglected. In our case all these elements emerge naturally from the simulation that still constitutes a useful tool to check the hypotheses of the density approach.

Our simulation strategy can be easily extended to events that are not well localized in time. For instance when the synaptic currents generated by the arrival of presynaptic spikes are not delta-correlated, the depolarization \(V\) cannot be updated instantaneously. A persistent current would affect the state variable of the neuron throughout the duration of the synaptic input. If the synaptic current goes instantaneously up upon the arrival of a spike and then decays exponentially with a time constant \(\tau\), we have that (see also Srinivasan and Chiel, 1993; Destexhe et al, 1994; Lytton, 1996; Giugliano, 2000):

\[
I_{int}(t) = \sum_k J_k e^{-(t-t_k)/\tau} = e^{-t/\tau} \sum_k J_k e^{t_k/\tau} = e^{-t/\tau} I_{sp}
\]

where \(I_{int}\), the total synaptic current, is updated when a spike arrives (a term is added to the sum \(I_{sp}\)) and decays exponentially during the inter-spike intervals. Such a dynamic behavior can be introduced in our approach by defining an effective external mean current \(\mu_{eff}(t)\):

\[
\mu_{eff}(t) = \mu(t) + e^{-t/\tau} I_{sp}
\]

The density equations should then be solved for every \(I_{sp}\). This makes the look-up tables for the probability density functions more complicated (it adds a dimension corresponding to \(I_{sp}\)), but it provides a possibility to have more realistic currents. In general, simulations with more complex model neurons or synapses require the addition of other dimensions in the probability density function. Moreover, solving high dimensional partial differential equations is difficult and the look-up tables

\(^1\)The software implementing the described algorithm can be obtained from the authors upon request.
would require a huge amount of memory. This is a major limitation of our approach because the problem becomes intractable already with few state variables. On the other hand, our strategy (as most of the event-driven approaches) is efficient when the problem and the model are already well defined, the relevant internal variables are known, and extensive simulations are needed to explore the parameter space.

Appendix

The probability density function $P_V(V,t)$ that describes the statistics of the dynamics during the intervals between two successive spikes evolves in the voltage-time domain according to the Fokker-Planck equation:

$$\frac{\partial}{\partial t} P_V(V,t) = -\frac{\partial}{\partial V} \phi(V,t)$$

(3)

where $\phi(V,t) = -\frac{\sigma^2}{2} \cdot \frac{\partial}{\partial V} p(V,t) + \left[ \left( \mu + \frac{V_{\text{rest}} - V}{\tau_m} \right) \cdot p(V,t) \right]$.

In the most general case, eq. 3 must be further complemented by the initial condition $P_V(V,t_0) = \delta(V - V_0)$ and by appropriate boundary conditions restricting, in the case of the leaky IF neuron, the potential

- at $V = V_{\text{min}}$, in terms of a reflecting barrier, since no neuron can have a depolarization which passes below $V_{\text{min}}$
  $$\forall t, \phi(V_{\text{min}},t) = 0$$
  (4)

- at $V = V_\vartheta$, in terms of an absorbing barrier, since neurons that are crossing such a threshold are absorbed and leave the interval $[V_{\text{min}};V_\vartheta]$
  $$\forall t, P_V(V_\vartheta,t) = 0$$
  (5)

Finally, at any time $t$, the probability density $P_V(V,t)$ must satisfy a normalization condition:

$$\int_{V_{\text{min}}}^{V_\vartheta} p(V,t) dV + \int_{t_0}^{t} \nu(t') dt' = 1$$

(6)

where $\nu(t) = \phi(V_\vartheta,t) = P_{fpt}(t) = -\frac{\sigma^2}{2} \cdot \frac{\partial}{\partial V} P_V(V,t)|_{V_\vartheta}$, represents the rate at which neurons are crossing the threshold $V_\vartheta$. We note that equation 6 accounts for the deflating time course of the surface $P_V(V,t)$, sketched in Figure 1: with time, the realizations of the process $V(t)$ leave the integration interval $[V_{\text{min}},V_\vartheta]$ after absorption at the threshold, and they irreversibly accumulate in the term $\int_{t_0}^{t} \nu(t') dt'$.

By preliminarily choosing a fixed set of values for $(\mu, \sigma)$ and by discretizing the interval $[V_{\text{min}};V_\vartheta]$ into a finite number of bins, the numerical integration of eq. 3 determines the desired time-dependent probability density distributions $P_V(\mu,\sigma^2,t_0,V_0,t_1;V_1)$ and $P_{fpt}(\mu,\sigma^2,t_0,V_0;t)$, as a function of $(\mu, \sigma)$ and given that $V(t_0) = V_0$.

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References


Figure 1: Numerical solution of the Fokker-Planck equation (see Appendix): the temporal evolution of the probability density for the $V$ (surface plot) and the the inter-spike interval distribution (thick line) are shown. Neuron parameters: $\tau_m = 20\text{ms}$, $V_{\text{rest}} = -70\text{mV}$, $V_0 = -50\text{mV}$, $V_{\text{min}} = -80\text{mV}$, $\tau_{\text{arp}} = 2\text{ms}$, $V_0 = -70\text{mV}$, $\mu\tau_m = 14.5\text{mV}$ and $\sigma^2\tau_m = 10.2\text{mV}^2$.

Figure 2: An illustration of the extended algorithm (see section 2.3). A1, A2: no internal event occurs before the estimated first passage time. B1, B2: The neuron receives a synaptic contribution $\Delta V_1$ at time $t_1^{\text{sp}}$. C1, C2: Same as B1/B2 with larger $\Delta V_1$, which leads to a threshold crossing.

Figure 3: Simulation of a population of IF neurons for two different regimes of the external input ($\mu_1\tau_m = 14.5\text{mV}$, $\sigma_1^2\tau_m = 10.2\text{mV}^2$, $\mu_2\tau_m = 16.5\text{mV}$, $\sigma_2^2\tau_m = 27\text{mV}^2$). A: raster plot of 30 out of 500 neurons and the corresponding instantaneous network firing rate (B, average over 100 runs), compared to the analytical prediction (dotted line) by the mean-field theory (see text; Amit & Tsodyks, 1991; Brunel, 2000; Fusi & Mattia, 1999). The three lines correspond to three different look-up table resolutions that were used. C: estimate of the inaccuracies induced by the discretizations of the look-up tables, measured in the last 200ms of B. D: sensitivity of the inaccuracies to changes in table resolution ($v$: change in voltage axis [0.4mV x 0.5ms, 0.2mV x 0.5ms, 0.1mV x 0.5ms; from right to left], t: change in time axis [0.1mV x 2ms, 0.1mV x 1ms, 0.1mV x 0.5ms]).

Figure 4: Execution performance of the proposed algorithm. A: comparison of the execution times of the state-of-the-art event-driven approach (as described in Mattia & Del Giudice, 2000, circles) and of the extended event-driven approach (crosses), as a function of the ratio between the number of the external and internal spikes (see section 3). The execution time is given per simulated second, and averaged over 5 runs of 4s simulation time each. B: The execution time scales with the square of the number of simulated neurons ($c = 0.05$, mean output frequency 4Hz). C: Execution time scales almost linearly with output frequency ($c = 0.05$, $J = 0.1\text{mV}$).
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