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How much can we trust neural simulation strategies?

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Abstract

Despite a steady improvement of computational hardware, results of numerical simulation are still tightly bound to the simulation tool and strategy used, and may substantially vary across available simulation tools or for different settings within the same simulator. Clock-driven simulation strategies proved efficient for large and highly active networks but are outperformed with respect to precision by the recently introduced event-driven strategies. Focusing on most commonly used clock-driven and event-driven approaches, in this paper we evaluate to which extent the temporal precision of spiking events impacts on neuronal dynamics of single as well as small networks of IF neurons with plastic synapses. We find that the used strategy can severely alter simulated neural dynamics and, therefore, turns out to be crucial for the interpretation of the result of numerical simulations. Drastic differences were observed in models with spike timing dependent plasticity, arguing that the speed of neuronal simulations should not be the sole criteria for evaluation of the efficiency of simulation tools, but must complement an evaluation of their exactness, possibly in disfavour of their speed.

Keywords: Integrate-and-fire; Event-driven; Asynchronous; STDP

1. Introduction

Computational neuroscience provides a growing number of tools which, together with the steady improvement of computational hardware, allow for simulations of neural systems with increasing complexity ranging from detailed single cells to large-scale neural networks. However, despite these advances, the results and, hence, qualitative interpretation of numerical simulations are still tightly bound to the simulation strategy used, and may vary across available simulation tools or for different settings within the same simulator. Specifically for networks of integrate-and-fire (IF) neurons, crucial differences in the appearance of synchronous activity patterns were observed, depending on the temporal resolution of the neural simulator [2] or the integration method used [5] (for an evaluation of the dependence on initial conditions, see [1]).

Recently, a new event-driven simulation approach was proposed [11,7,8] which, at least in principle, can be applied to each type of neuron model [4] and, therefore, challenges traditional clock-driven strategies (reviewed in [6]). In contrast to the latter, where spiking and synaptic release events are bound to a temporal grid of finite resolution, event-based methods keep the precise timing of events. In this contribution, we evaluate to which extent the temporal precision of spiking events impacts on neuronal dynamics of single as well as small networks of IF neurons with plastic synapses. Drastic differences were observed in models with spike timing dependent plasticity, arguing that the speed of neuronal simulations should not be the sole criteria for evaluation of the efficiency of simulation tools, but must complement an evaluation of their exactness.

2. Neuronal models and simulation strategies

In what follows, we will restrict to one of the simplest analytically solvable neuronal models, namely the classic leaky integrate-and-fire (LIF) neuron. It is described by the state equation $\tau_m \, dm(t)/dt + m(t) = 0$, where τ_m denotes the membrane time constant and $0 \leqslant m(t) \leqslant 1$. Upon arrival of a synaptic event at time t_0, $m(t)$ is updated by a constant Δm after which it decays according to $m(t) = m(t_0) \exp[-(t-t_0)/\tau_m]$. If m exceeds a threshold $m_{\mathrm{thres}} = 1$, it is

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reset to a resting state $m_{rest} = 0$ in which it stays for a refractory period t_{ref}.

In simulations with plastic synapses, spike timing dependent synaptic plasticity (STDP) was incorporated according to a model by Song and Abbott [9]. Upon arrival of a synaptic input at time t_{pre}, synaptic weights are changed according to $g \to g + F(\Delta t)g_{max}$, where $F(\Delta t) = \pm A_{\pm} \exp\{\pm\Delta t/\tau_{\pm}\}$ for $\Delta t = t_{pre} - t_{post} < 0$ and $\Delta t \geqslant 0$, respectively. Here, t_{post} denotes the time of the nearest postsynaptic spike, $A_{\pm}$ quantify the maximal change of synaptic efficacy, and $\tau_{\pm}$ determine the range of pre- to postsynaptic spike intervals in which synaptic weight changes occur.

All simulations were performed using the NEURON simulation environment [3,4] running on PC-based workstations under the LINUX operating system. The same neuronal models were simulated using various implemented simulation strategies. In the classical *clock-driven* approach (Fig. 1A), the state variables of the neural system in question are evaluated for specific points on a discretised time-axis. For realistic large-scale networks, the algorithmic complexity and, hence, computational load scales linearly with the number of neurons, but also linearly with the temporal resolution (Fig. 1B). The latter determines the accuracy of the numerical simulation and introduces an artificial cutoff for time-scales captured by the simulation [2,10]. In contrast, the *event-driven* approach is free from the dependence on the temporal resolution by using the exact times of events (Fig. 1A,B). This gain in accuracy comes at the cost that, now, the computational load scales with the number of events, i.e. the average activity, in the network, which rises linearly with the number of neurons in realistic large-scale neuronal networks.

3. Neural systems with static synapses

In a first set of simulations, we investigated the activity of single LIF neurons subject to a frozen synaptic input pattern drawn from a Poisson distribution with rate ν_{inp}. The model parameters were $\tau_m = 20$ ms, $t_{ref} = 1$ ms, $\Delta m = 0.1$ and $\nu_{inp} = 250$ Hz. Already after short periods of simulated neural activity, spike times observed in simulations with $dt = 0.01$ ms deviated from those seen in clock-driven simulations with higher temporal precision and event-driven simulations. Such deviations were caused by subtle differences in the subthreshold integration of synaptic input events whose times were altered by the

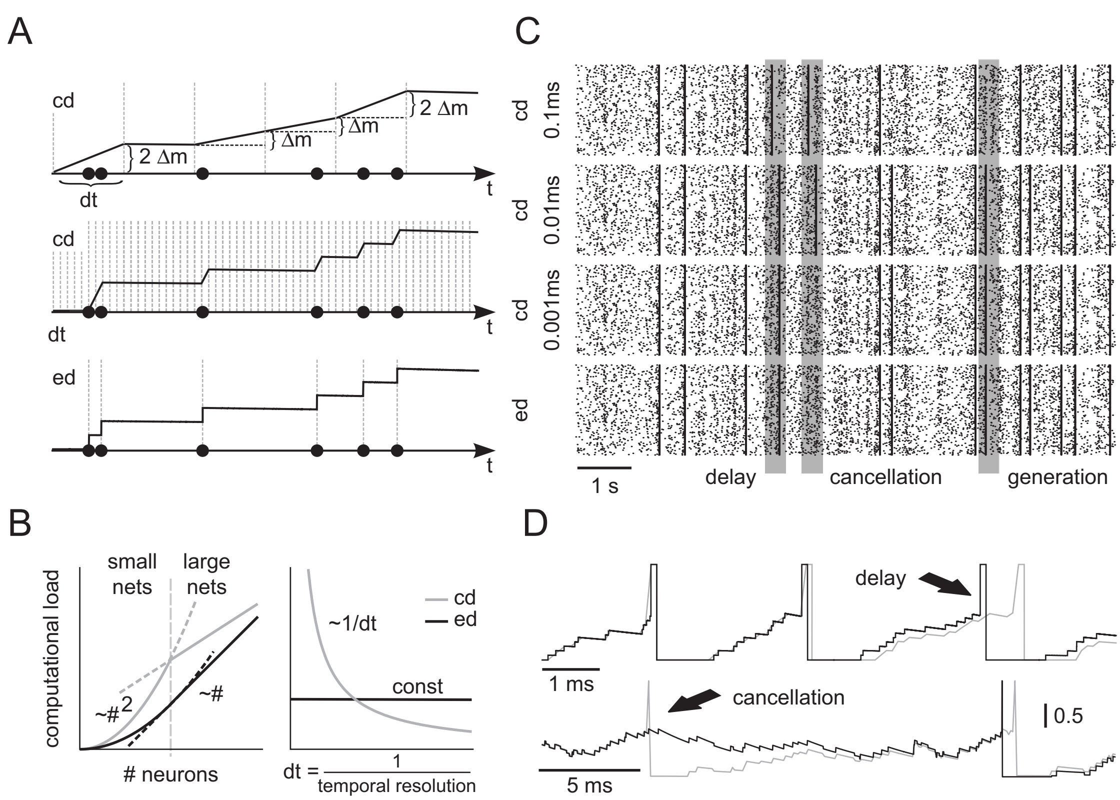

Fig. 1. Modelling strategies and dynamics in neuronal systems with static synapses. A. Comparison between clock-driven (cd; top: low temporal resolution, middle: higher resolution) and event-driven (ed; bottom) modelling strategy. B. Scaling behaviour of clock-driven and event-driven simulations. Whereas for small network size the computational load (left panel) is quadratic in the number of neurons, it scales linear for large networks due to the fact that in biological neural networks the number of synapses per neuron is fixed. However, marked differences between event- and clock-driven strategies are observed as function of the temporal resolution. Whereas the load is nearly unaffected in the event-driven case, it scales with the inverse of dt in the clock-driven case. C. Rasterplots of spike events in a neuronal network simulated in the clock-driven with different temporal resolution and event-driven approach show differences in the occurrence of synchronous events in the network. D. Small differences in spike times can accumulate and lead to severe delays (top, arrow) or even cancellation (bottom, arrow) of spikes, depending on the used simulation strategy.

temporal binning procedure in clock-driven approaches. Interestingly, these subtle differences, although decaying with the membrane time constant, could accumulate and lead to marked delays in spike times, cancellation of spikes (Fig. 1D) or occurrence of additional spikes compared to the more precise event-driven simulations.

At the network level, small differences in spike times of individual neurons can lead to crucial differences in the global activity pattern, such as synchronisation [2,5]. We considered a network of 15×15 LIF neurons (see above) with all-to-all excitatory connectivity with fixed weights ($\Delta m = 0.0085$) and not distance-dependent synaptic transmission delay (0.2 ms). The network was driven by a fixed pattern of superthreshold random synaptic inputs to each neuron (average rate 250 Hz; weight $\Delta m = 0.1$). Although in this case the activity in the network was mainly driven by the external inputs, small differences in spike times caused by temporal binning could have severe effects on the occurrence of synchronous network events where all (or most) cells discharge at the same time. Such events could be delayed, cancelled or generated if higher temporal precision in clock-driven simulations ($dt = 0.001$ ms) or event-driven simulations were considered (Fig. 1C).

4. Neuronal systems with STDP

The above described differences in the temporal aspects of neuronal dynamics observed between commonly used simulation strategies appear to have only minor impact when statistical measures, such as average firing rates, are considered. However, more severe effects are expected if mechanism depending on the exact times of spike events are incorporated, so we studied neuronal models with plastic synapses. If multiple synaptic input events arrive in between two state updates at t and $t + dt$ in a clock-driven simulation, the times of these events are assigned to the end of the interval (Fig. 2A). In the case these inputs drive the cell over firing threshold, the synaptic weights of all three synaptic input channels will be facilitated by the same amount according to the implemented STDP model (see above), as the exact time and temporal order of the inputs is not available. In contrast, as seen above, the same input pattern could cause in event-driven simulations a discharge already after only two synaptic inputs arrived. In this case the synaptic weights linked to these inputs will be facilitated, whereas the weight of the input arriving after the discharge will be depressed.

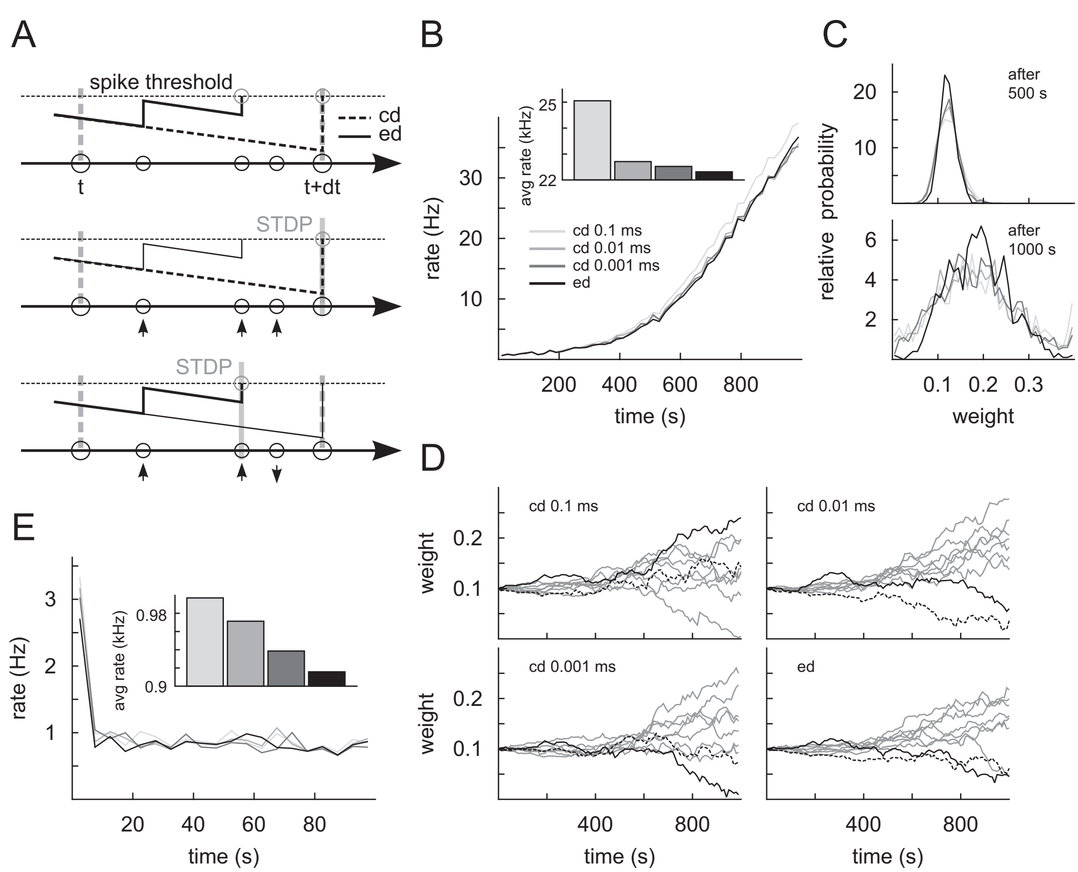

Fig. 2. Dynamics in neuronal systems with STDP. A. Impact of the simulation strategy (clock-driven: cd; event-driven: ed) on the facilitation and depression of synapses. B. Time course and average rate (inset) in a LIF model with multiple synaptic input channels for different simulation strategies and temporal resolution. C. Synaptic weight distribution after 500 and 1000 s. D. Weight development for specific synaptic channels (black solid and dashed) can lead to contrasting results depending on the simulation strategy used. E: Time course and average rate (inset) in a small network of LIF model with plastic synaptic connections for different simulation strategies and temporal resolution.

First, we investigated to which extent such scenarios impact on the temporal development of the average firing rate and weight development of a single LIF neuron. Chosen cellular parameters were $\tau_m = 4.424\,\text{ms}$, $t_{\text{ref}} = 1\,\text{ms}$, $A_+ = 0.005$, $A_-/A_+ = 1.05$, $\tau_+ = 20\,\text{ms}$, $\tau_- = 20\,\text{ms}$, $g_{\max} = 0.4$ with 1000 independent Poisson driven input channels (average rate 5 Hz, $\Delta m = 0.1$). Surprisingly, in simulations of 1000 s neural activity marked differences in the temporal development of the average rate were found between clock-driven simulations with a commonly used $\mathrm{d}t = 0.1\,\text{ms}$ and event-driven simulations (Fig. 2B). Considering the average firing rate over the whole simulated window, these clock-driven simulations led to an about 10% higher value compared to the event-driven approach. The latter value as well as temporal development was only approached when the temporal resolution was markedly increased ($\mathrm{d}t = 0.001\,\text{ms}$), thus leading to a marked increase in the simulation time which exceeded by several orders of magnitude that of the corresponding event-driven simulation.

The finding of a strong dependence of the average firing rate of plastic neural networks on the simulation strategy was paralleled by marked differences in the synaptic weight distribution (Fig. 2C). Within the investigated time interval, the distribution was always sharper in event-driven simulations, and the occurrence of a bimodal distribution was only observed, with less significance the smaller $\mathrm{d}t$, in the clock-driven approach. Both findings show that the small differences in the precision of synaptic events can have a severe impact even on statistically very robust measures. Considering the temporal development of individual synaptic weights, both depression and facilitation were observed depending on the simulation strategy and temporal resolution in clock-driven simulations (Fig. 2D). The latter could have severe impact on the qualitative interpretation of the temporal dynamics of structured networks, as the results show that synaptic connections in otherwise identical models can be strengthened or weakened based on the simulation strategy used.

Finally, we looked at a small network of LIF neurons (15×15 neurons with $\tau_m = 20\,\text{ms}$, $t_{\text{ref}} = 1\,\text{ms}$) with all-to-all excitatory connectivity with plastic weights ($A_+ = 0.005$, $A_-/A_+ = 1$, $\tau_+ = 20\,\text{ms}$, $\tau_- = 20\,\text{ms}$, $g_{\max} = 0.4$) with one independent Poisson driven input channel (average rate 4000 Hz, $\Delta m = 0.01$) to one LIF neuron. Although here differences in the average firing rate across the different simulation approaches were within the observed temporal variations, a nearly 10% difference was found between event-driven and clock-driven ($\mathrm{d}t = 0.1\,\text{ms}$) when the average firing rate was considered (Fig. 2E). Also here the value obtained in precise event-driven simulations was obtained in clock-driven simulations only by increasing the temporal resolution on the expense of a marked increase in the time needed to simulate neural activity in a corresponding time window.

5. Discussion

Here we addressed the question to which extent existing strategies for numerical simulations might impact on the modelled neuronal activity. Focusing on clock-driven and event-driven approaches and, thus, on the temporal precision of synaptic input events, we found that the used strategy can severely alter simulated neural dynamics and, therefore, turn out to be crucial for the interpretation of the result of numerical simulations. We observed serious mismatches for simulations involving STDP, and conclude that such simulations should be done using most precise integration techniques, possibly in disfavour of their speed. To which extent the observed deviations hold in simulations of neuronal models for which no exact analytic solution exists is subject of current investigations.

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