Control of sampling rate in map-based models of spiking neurons

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Abstract

The discrete-time (map-based) approach to modeling nonlinear dynamics of spiking activity in neurons enables highly efficient numerical simulations for capturing realistic neurobiological behavior by utilizing a large time interval between computed states (samples) of neuron activity. The design and parameter tuning of these models assumes a fixed and preset sampling rate. When change of the time step is needed, it requires revisiting stages of the model design and parameter tuning. This paper presents an approach to the design of map-models in a new form where time step is added as a control parameter and can be easily changed to vary the time scale of the model behavior, i.e. sampling rate, essentially preserving the model behavior. It also discusses modification of the noise generator models needed to support simulation of map-based neurons with the modified sampling rate. The effects caused by direct control of time scale on model dynamics and limitations of this approach are discussed.

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1. Introduction

Numerical simulations of network models for neuronal activity is an important component of many neurobiological studies [1]. Such simulations usually deal with large scale networks capturing both dynamic and stochastic properties of neurons, representing the nodes of the network, and synapses, forming the network connectivity structure [2]. Due to strong nonlinearity and diversity of time scales involved in the generation of neuronal activity, a realistic conductance-based neuronal model contains a rather complex set of differential equations. Computational complexity of such models is the main obstacle in studies of the dynamics and functionality of large networks. A frequently used approach is to implement a reduced model for each neuron that captures its important dynamical features with a small set of simple equations [3,4]. In particular, neuronal models in the form of a nonlinear maps, known as map-based models or discrete-time models, have demonstrated high computational efficiency, due to their simplicity and large time step associated with each iteration, while capable of capturing important dynamical and physiological features of neuronal spiking activity [5–7]. Applications range from single neuron dynamics and computation [8–11] to the studies of functioning of large networks [12–14], including brain networks [6,15–18].

The map-based models are built and tuned to reproduce important features of intrinsic and responsive spiking activity of a neuron with a sequence of samples at fixed moments of time. To design a computationally efficient map-based model
the iteration time step or the sampling period is usually set as large as possible, i.e. up to levels comparable with the duration of action potential (a spike). Physiologically plausible value for sampling period is often set around 0.5 ms and then the map is designed to mimic dynamics of a modeled neuron with this time step. In contrast to continuous time models, where the integration step can be easily changed, any need for a change of time step in map-based models requires revising the model, such as alternation of model equations and/or tuning parameters which are not directly related to time. Tuning the time step is necessary when the map-based network is used as a part of large hybrid network models. In such networks the map-based nodes are linked to conductance-based, continuous-time nodes, which require a much smaller time step for proper simulations [19–21]. The ability to control sampling rate in map dynamics is also a useful feature in embedded implementations of neuronal networks in Digital Signal Processors (DSP), Field-Programmable Gate Array (FPGA) or microprocessor for real-time operation [22–24].

In this paper we show how a map-based model can be modified to enable selection of time step of iteration and therefore the sampling rate. We discuss the modifications to the map equations for synaptic inputs and methods for simulations of noise with the selected time step. To make this paper self-consistent we first briefly describe a 2-D map model (Section 2) used in previous studies as a model of a regular spiking neuron representing a pyramidal cell, see for example [6]. Section 3 focuses on the introduction of the time step parameter and its influence on the deterministic dynamics of the 2-D map. Section 4 is devoted to stochastic dynamics of the map and shows how to model noise and to characterize response to time-varying stimuli in terms of mutual information.

2. Map-based neuron and synaptic models

Consider a map [5] used as a model of pyramidal cells [6,16]:

\[
\begin{align*}
x_{n+1} &= f_u(x_n, y_n + \beta_n), \\
y_{n+1} &= y_n - \mu (x_n + 1) + \mu \sigma + \mu \sigma_n, 
\end{align*}
\]

where parameters \(\alpha = 3.65\) and \(\mu = 5 \times 10^{-4}\) define the type of neuronal behavior as a non-bursting neuron, parameter \(\sigma\) sets the baseline level of neuronal activity, \(\beta_n\) and \(\sigma_n\) are external variables describing synaptic and other inputs to the neuron, and the nonlinear function \(f_u(x_n, u)\) in (1) is [18],

\[
f_u(x_n, u) = \begin{cases} 
\alpha/(1 - x_n) + u & \text{if } x_n < -0.5 \\
1 & \text{if } -0.5 \leq x_n < 1 \\
-1 & \text{if } x_n \geq 1, 
\end{cases}
\]

where \(u = y_n + \beta_n, [15]\). Note, that a time step which would specify the sampling rate in generation of neuronal waveforms, is not an explicit parameter of models (1) and (2). Rather the time step is implicitly assumed to be fixed at 0.5ms. 

A map-based model for synaptic current was introduced in [15] as

\[
P_{syn}^n = -g_n (x_{post}^n - x_{pre}),
\]

where the parameter \(x_{pre}\) defines the type of synapse. For an inhibitory synapse its value is usually set as \(x_{pre} = -1.1\), while \(x_{post} = 0\) for an excitatory synapse (see for details see [15]). The response of synaptic conductance \(g_n\) to presynaptic spikes can be modeled with two exponents, reflecting the rise (R) and decay (D) of synaptic current [25], which in the discrete time case results in a linear map,

\[
\begin{align*}
g_n &= e^D - e^R, \\
e^R_{n+1} &= \gamma_R e^R_n + S_{syn}^n, \\
e^D_{n+1} &= \gamma_D e^D_n + S_{syn}^n,
\end{align*}
\]

where parameters \(\gamma_{R,D} \in (0, 1)\) define the time constants of rise, \(\tau_R\), and decay, \(\tau_D\). Due to linearity of the synaptic model (4,5), \(\gamma_{R,D} = \exp(-h/\tau_{R,D})\), where the time step, \(h\), is included explicitly as a parameter. In (4,5), \(S_{syn}^n\) is the sum of weighted presynaptic inputs, \(S_{pre}^n\).

\[
S_{syn}^n = \sum_{pre} W_{pre \rightarrow post} S_{pre}^n,
\]

where summation is taken over all presynaptic inputs, \(S_{pre}^n\), weighted by a matrix \(W_{pre \rightarrow post}\). Synaptic inputs are,

\[
S_{pre}^n = \begin{cases} 
1 & \text{if there is a presynaptic spike} \\
0 & \text{otherwise.}
\end{cases}
\]

Note that, the adoption of linear equations for synaptic conductance (4,5) allows us to set strengths of individual synaptic inputs using dimensionless weights \(W_{pre \rightarrow post}\) in summation (6). This approach enables a very efficient computation for large numbers of synaptic inputs thanks to Multiply and Accumulate operations (MAC) [26,27].

The synaptic and other currents are added together with proper weights and introduced to the map model using input variables,

\[
\beta_n = \beta^{ext} + \beta^{syn} S_{syn}, \quad \sigma_n = \sigma^{ext} + \sigma^{syn} S_{syn},
\]
where the weights $\beta^\text{syn}$, $\sigma^\text{syn}$ and $\beta^e$, $\sigma^e$ are used to control the response dynamics of neurons to synaptic $I^\text{syn}$ and other external $I^\text{ext}_n$ currents applied to the neuron.

3. Sampling control in deterministic map-based model

To describe our approach to sampling control, let us consider a 1-D map for variable $v_n \in \mathbb{R}$,

$$v_{n+1} = P(v_n),$$  \hspace{1cm} (8)

where $P(v_n)$ is a continuous nonlinear function. We assume that the map (8) is designed to generate a sequence, $v_n$, which fits a real-time sequence of a modeled process sampled at times $t_n = h_0 n$ with the time interval $h_0$. Our goal is to modify the map with a new sampling interval $h$, while keeping the real-time dynamics of the modeled process unchanged or sufficiently close to the original system, i.e. when modeled with the sampling interval $h_0$. The simplest way to achieve this goal is to treat the map (8) as an iterative scheme for numerical integration of an ODE with dimensionless continuous time, measured in units of the original time interval, $h_0$. For example, for the explicit Euler scheme we obtain,

$$v_{n+1} = v_n + \frac{h}{h_0} (P(v_n) - v_n) \equiv P_h(v_n).$$  \hspace{1cm} (9)

The limit $h \to h_0$, recovers the original map (8), while the limit $h \to 0$ leads to the ODE for the continuous-time variable, $v(t)$,

$$\frac{dv}{dt} = (P(v) - v).$$ \hspace{1cm} (10)

Comparing ODE (10) and the corresponding map (9), one can see that the ODE model and the map can demonstrate qualitatively similar dynamics only if all trajectories generated by the map change in time monotonically towards a fixed point or infinity. These are the only types of trajectories supported by a continuous one-dimensional ODE model. Therefore, continuous-time interpretation and approximation of the 1-D map with the 1-D ODE is valid only when

$$\frac{dP_h(v)}{dv} \geq 0$$

for the values of $v_n$ within the expected range of model operation. If this condition is satisfied, then the parameter $h$ can be used to set the sampling rate of the map, while keeping the timing of dynamical processes close to that of the original map (8) in real time. Of course, such a simple change of the time scale is not precise and can affect the dynamics of the map similar to the change of the integration step in simulations of the ODE model, but it gives a very simple and computationally efficient model of the modified map.

Next we show how to apply such an approach to modify the model Eqs. (1) and (2) and study how the change of the sampling period of the map works to keep the dynamics of the modified map consistent within a range of sampling periods $h$. First we focus on the analysis of the 1-D portion of the map (1) that is frequently used as a stand alone model for simple tonic spiking neurons. Through the rest of the paper we will assume that the time step of the original map model is $h_0=0.5$ ms and we introduce a new time step $h$ given in ms.

3.1. 1-D map of spiking activity

In 1-D map model, Eq. (1) is used independently of the slow subsystem by fixing value $y_n = \beta$, where the parameter $\beta$ controls the baseline state of a spiking neuron. To introduce the time step of the map, we modify its nonlinear function as described above to obtain

$$x_{n+1} = F_n(x_n, \beta + \beta_n).$$ \hspace{1cm} (11)

where nonlinearity $F_n(\cdot)$ includes parameter $h$ and can be written in the following form

$$F_n(x_n, u) = \begin{cases} x_n + 2h \left( \frac{\sigma}{1 - x_n} - x_n + u \right), & \text{if } x_n < V_{\text{th}} \\ -1, & \text{if } V_{\text{th}} \leq x_n < 1 \\ -1, & \text{if } x_n \geq 1. \end{cases}$$ \hspace{1cm} (12)

where $u = \beta + \beta_n$ and $V_{\text{th}} = -0.5$. Note that for $h=0.5$ ms, nonlinear functions (3) and (12) match, $F_n(x_n, u) = f_n(x_n, u)$.

The value of parameter $h$ controls the shape of the nonlinear function as illustrated in Fig. 1. The decrease of time step $h$ flattens the nonlinear interval of the function and moves it close to the diagonal $x_{n+1} = x_n$. This slows down the trajectory as it iterates in a smaller gap between the function and diagonal. Consequently, the number of iterations between the spike events increases as $h$ decreases. Each spike in the waveform is given by a single iteration and, therefore, has duration $h$ in the waveform of the $x_n$ variable. As in the case of integrate-and-fire models the spike in this type of map-based model defines only the time moments of spiking events ignoring the shape of individual spikes. Waveform $(x_n \text{ vs } n)$ evoked by a rectangular depolarizing pulse computed for the cases of Fig. 1(a) and (b) are shown in Fig. 1(c) and (d), respectively. Note that simulation of 1000 ms in these two cases requires 2000 and 20,000 iterations, respectively, while the shape of
the response activity in real time remains very similar. The discrepancy occurs in the number of evoked spikes, indicating a shift in spiking rate with the change of time step. Similar effects occur in nonlinear integrate-and-fire models simulated with the fixed step Euler scheme.

3.2. 2-D map and transient dynamics

To introduce time step $h$ in the two-dimensional map (1.2) we rewrite it in the following form

$$x_{n+1} = F(x_n, y_n + \beta_n),$$

$$y_{n+1} = y_n - \mu Q(x_n) [1 + x_n - \sigma - \sigma_n],$$

where the form of $F(x_n, y_n + \beta_n)$ (12) was described above for the case of 1-D map, and $Q(x_n)$ is:

$$Q(x_n) = \begin{cases} 2h, & \text{if } x_n < V_{th} \\ 1, & \text{otherwise}, \end{cases}$$

where $V_{th} = -0.5$. Note that for $h = 0.5$ ms Eqs. (13) and (14) are equivalent to Eqs. (1) and (2). One can see that parameter $h$ in models (13,14) affects only iterations between the spikes. During the spike formation both fast and slow variables do not depend on $h$ because spike formation always requires 2 iterations.

3.2.1. Autonomous dynamics

Analysis of autonomous dynamics of the 2-D map (13,14) carried out with $\sigma_n = 0$ and $\beta_n = 0$, shows that as in the case of (1,2) it has a single fixed point $O$ located at $x_0 = \sigma - 1$ and $y_0 = x_0 - \alpha/(1 - x_0)$. Following the analysis of local bifurcation of the fixed point in map (1,2) described in [28] one can show that 2-D map (13,14) demonstrates the same type of bifurcation (subcritical Neimark-Sacker) as the original map (1,2), but the threshold value of $\sigma$ at which fixed point $O$ changes stability depends on the value of $h$ as follows,

$$\sigma_{th} = 2 - \sqrt{\alpha/(1 - 2h\mu)},$$

which for small $0 < \mu \ll 1$ gives the linear dependence on the sampling time step,

$$\sigma_{th} \approx (2 - \sqrt{\alpha}) - (\sqrt{\alpha} \mu) h, \quad 0 < \mu \ll 1,$$

indicating that sensitivity of $\sigma_{th}$ to variation of $h$ (i.e. the slope) is proportional to small parameter $\mu$ and thus is small. For example, in the considered case of the pyramidal cell model, where $\alpha = 3.65, \mu = 0.0005$ and baseline state is set with...
σ = 0.06, the bifurcation of a fixed point O occurs at σ_{th} = 0.089025 for h = 0.5 ms and at σ_{th} = 0.089498 for h = 0.005 ms. Therefore, the transition from silence to sustained tonics spiking requires l_0 > (σ_{th} − σ), i.e. l_0 > 0.029025, for h = 0.5 ms, and l_0 > 0.029498, for h = 0.005 ms. This makes about 1.6% difference between these threshold current values, while h changes 100 times.

The characteristic multipliers of the fixed point O at the bifurcation threshold are

\[ \rho_{1,2} = 1 - 2h^2\mu \pm i2h\sqrt{\mu(1 - h^2\mu)} = \cos\psi \pm i\sin\psi, \]

which remain a complex-conjugate pair in a wide range of sampling period 0 < h < 1/\sqrt{\pi}. The phase shift per iteration, \( \psi = \arccos(1 - 2h^2\mu) \), determines the period of subthreshold oscillations in vicinity of the fixed point O. In units of iteration, the period is \( T_F = 2\pi/\psi \), and in real time units, \( T_F = hN_F = 2\pi h/\arccos(1 - 2h^2\mu) \). For 0 < \mu ≪ 1 we obtain,

\[ T_F \approx \frac{\pi}{\sqrt{\mu}} - \frac{\pi\sqrt{\pi}}{6} h^2, \quad 0 < \mu \ll 1, \]

and so the period of subthreshold oscillations is essentially invariant with respect to variations of the sampling period, h.

### 3.2.2. Response dynamics

As it has been suggested in [15] the response behavior of the 2-D map evoked by external stimulus is convenient to examine following the trajectories plotted in the phase plane \((u_n, x_n)\), where \(u_n = y_n + \beta_n\). In projection to this plane of variables the manifolds of slow motions formed due to 0 < \mu ≪ 1 are not affected by the external stimulus \(l_n\) and the fixed point of the map moves along the manifold as the model is depolarized or hyperpolarized by the input. Fig. 2 shows the trajectories of the 2-D map computed with two different values of \(h\) in response to a stimulus in the form of a rectangular pulse. Despite significant difference in the step size the shape of trajectories in the phase portraits Fig. 2(a) and (b) and the corresponding waveforms of spiking Fig. 2(c) and (d) evoked by the pulse are qualitatively very similar.

Some quantitative differences caused by the significant change of iteration step include reduction of spiking rate with the increased value of \(h\). Compare the number of spike after tonic spiking settles down in Fig. 2(c) and (d). The exact timing of the spikes in the pattern fired by the map in response to the stimulus is also changed with the step size, compare spike timing rastograms in Fig. 3(a) and (b) computed for two different step sizes and gradually changing values of pulse amplitude. The rastograms show that while the exact spike timing is changed the main properties of spike timing behavior remains qualitatively similar. For example, the deceleration rate indicated by the dense area of spiking at the beginning of stimulus is very similar in both cases. These changes can be seen more clearly in the rastogram for a spike pattern generated at a fixed value of \(A\) versus \(h\), as presented in Fig. 4(a). Here one can see that spiking rate shifts with the change of \(h\) value.
Fig. 3. Rastrogram of spike timing patterns generated for increasing values of pulse amplitude $A$ of the injected current $I_e$. The parameter values of the map and the stimulus $I_e$ timing are the same as in Fig. 2.

Fig. 4. (a) Rastrogram of spike timing patterns generated for increasing values of time step $h$ and fixed value of pulse amplitude $A = 0.1$, where mean frequency of spiking is about 45Hz. (b) Similar rastrogram computed with correction of $V_{th}$ value, $c_{th} = 0.22$, as discussed in Section 3.3. The other parameter values of the map and the stimulus $I_e$ timing are the same as in Fig. 2.

Fig. 5. (a) Dependence of time averaged firing rate, $f$, on the time step of the map, $h$, for the indicated values of stimulus amplitude, $A$. (b) The same dependencies computed with correction of $V_{th}$ on $h$ with $c_{th} = 0.22$. Note that firing rates in (a) and (b) are the same at $h = 0.5$ ms.

To capture the elements of transient dynamics for comparative analysis of models at various $h$ we compute average firing rate in response to the rectangular stimulus as the number of generated spikes divided by the duration of the stimulus (500 ms). Due to deceleration effect this spiking rate differs from the rate of settled tonic spiking for the corresponding depolarization level. The dependence of such a firing rate on the time step for various excitation levels (determined by the stimulus amplitude, $A$) is summarized in Fig. 5(a). At low and moderate levels of excitation (spiking rate is below 100 Hz), the firing rate is weakly sensitive to variations of $h$. On the contrary, at high levels of excitation (e.g. $A = 0.3$ and $A = 0.4$), the monotonic increase of firing rate with the decrease of $h$ becomes substantial, e.g. cases $A = 0.3$ and $A = 0.4$.

3.3. A method for improvement of firing rate consistency

Variation of firing rate with the time step stems from the corresponding changes in the shape of the map shown in Fig 1(a) and (b). Therefore the effect of nonlinearity on the firing rate with changing value of $h$ can be mitigated by appro-
priate corrections of the map function, $F\nu(x_n, u)$, which would control the number of iterations needed to reach the firing threshold, $V_{th}$.

For example, introduction of linear dependence of $V_{th}$ on $h$ can improve the consistency of spiking rate for the 2-D model. Using the 2-D map model, with parameters tuned to mimic dynamics of pyramidal cell at $h = 0.5$ ms we set the threshold as

$$V_{th} = -0.5 + C_{th}(0.5 - h).$$

where $C_{th}$ is the slope of the dependence of threshold value $V_{th}$ on $h$. The effect of such correction with $C_{th} = 0.22$ is shown in Fig. 4(b). Comparing it with Fig. 4(a) one can see that spike pattern and timing of the individual spikes become more consistent for the considered range of $h$. Spike time jitter for $h > 0.1$ is due to unavoidable discrete time effects, whereby the exact number of iterations of the map leading to a spike depends on the time step. It slightly affects the timing of spikes in the generation of the rest of the pattern. This effect becomes noticeable for larger values of $h$ and for higher firing rates. Analysis of the corrections by adjusting $V_{th}$ in a wide range of excitation levels shows that at high spiking rates this type of correction becomes less efficient. For example, Fig. 5(b) shows significant dependence of firing rate on $h$ at high excitation levels ($A > 0.3$).

In the remaining part of the paper we will consider a fixed value of threshold $V_{th} = -0.5$ and focus on the analysis of step size effects on the dynamics of the 2-D map in the response to noise.

4. Sampling control in stochastic map-based model

Effects of white Gaussian noise on the dynamics of the neuronal map model were studied in a number of publications, e.g. using Fokker–Planck equation formalism [29] and stochastic sensitivity function [9,30]. Instead, here we study the effect of colored synaptic noise, which can be modeled as Ornstein–Uhlebeck (OU) process [31], mimicking low-pass filtering of discrete random synaptic events. The OU noise is governed by the stochastic differential equation [32],

$$\frac{d\xi}{dt} = -\frac{1}{\tau_c} \xi + \sqrt{\frac{d^2}{\tau_c}} w(t),$$

where $\tau_c$ is the OU correlation time, $d$ is its standard deviation (SD), and $w(t)$ is white Gaussian noise. The autocorrelation function and the power spectral density (PSD) of the OU process (18) are

$$C(\tau) = d^2 \exp\left(-\frac{|\tau|}{\tau_c}\right), \quad G_{\xi\xi}(\omega) = \frac{2d^2 \tau_c}{1 + \omega^2 \tau_c^2}.$$  

Note specific parametrization of the OU noise used here: its variance is $d^2$ and so is invariant with respect to variation of the correlation time, $\tau_c$.

An accurate algorithm for numerical solution of (18) with the fixed integration time step, $h$, can be written as [33],

$$\xi(t + h) = e^{-h/\tau_c} \xi(t) + d[1-e^{-2h/\tau_c}]^{1/2} g(1),$$

where $g(1)$ is a random number drawn from a Gaussian distribution with variance 1. Thus, the OU process can be modeled by the linear stochastic map,

$$\xi_{n+1} = q \xi_n + p w_n,$$

(19)

gaussian white noise of unit SD, $w_n$, and parameters $q = e^{-h/\tau_c}$ and $p = d\sqrt{1-q^2}$. The noise term, $\xi_n$, is added to synaptic current, $I_n^{syn}$. Eq. (7). Thus, the stochastic map (19) extends the neuron model (14), forming a closed 3-D map system, with iteration interval $h$ as a parameter. We note, that similar mapping can be derived for other types of noise. For example, narrow-band noise can be modeled by a two-dimensional map [34].

To study the effect of iteration interval on response dynamics, we used band-limited Gaussian noise with the cutoff frequency, $f_c$, as a stimulus which modulates synaptic input. The PSD of the stimulus is,

$$G_{ss}(f) = \begin{cases} 2\sigma_s^2 / f_c, & f \leq f_c \\ 0, & f > f_c \end{cases}$$

(20)

where $\sigma_s$ is the stimulus SD. Note, that the stimulus SD is invariant with respect to variations of cutoff frequency, $f_c$. Gaussian process with the PSD (20) can be created as follows. First, white Gaussian noise is generated and Fourier transformed. Second, a low-pass filter in the frequency domain is applied to Fourier transformed white noise. Finally, the inverse Fourier transform of the result gives Gaussian process, $s(t)$, with desired PSD. Its discrete version, $s_n$ can be added to synaptic current of Eq. (7). This procedure can be repeated for different sampling intervals, $h$. To study the effect of iteration interval, the stimulus was generated for the smallest sampling interval, e.g. $h = 10^{-4}$ ms, and then decimated for the desired interval, $h$.

We simulated the 2-D version of the neuron models (13,14), extended with synaptic noise map (19). The input current to the model contains a constant component, $I_0$, broad-band OU synaptic fluctuations, $\xi_n$, and stimulus, $s_n$: $I_n = I_0 + \xi_n + s_n$. 


The input current enters via input parameters $\beta_n$ and $\sigma_n$ (7): $\beta_n = \beta_i I_n$, and $\sigma_n = \sigma_i I_n$. Thus, the resulting 3D map-based model is,

$$
x_{n+1} = F_0\{x_n, y_n + \beta I_n + \xi_n + s_n\},$$

$$y_{n+1} = y_n - \mu Q(x_n)\{1 + x_n - \sigma - \sigma^k (I_n + \xi_n + s_n)\}.$$

$$\xi_{n+1} = e^{-h/\tau} \xi_n + dv \Delta t = e^{-2h/\tau} w_n,$$

(21)

where the map functions $F_0(\cdot, \cdot)$ and $Q(\cdot)$ are given by (12) and (15), respectively. In the following the correlation time of synaptic noise was taken as $t_c = 1$ ms, which corresponds to a 1 ms synaptic constant [31] and stimuli parameters were set as, $\beta^0 = 0.133$ and $\sigma^k = 1$.

The 3D map, (21) was used to generate sequences of spike times, $\{t_k\}_k = 1, \ldots, K$. Spike train, $z(t)$, is then represented as sequence of delta-peaks centered at spike times,

$$z(t) = \sum_{k=1}^K \delta(t - t_k).$$

(22)

Variability of spiking was studied using statistics of inter-spike intervals (ISI), $I_k = t_{k+1} - t_k$, such as the mean firing rate, coefficient of variation of ISIs and ISI probability density. In addition we also estimated the PSD of spike trains.

To study the response dynamics, $T = 60$ s long sample of band-limited stimulus, $s(t)$, was applied repeatedly to the model. We then estimated the post stimulus time histograms (PSTH), $r(t) = \langle z(t) \rangle$, where the averaging was taken over $N = 10^5$ stimulus trials. A bin size $\Delta t = 1$ ms was used to calculate the PSTH. Stimulus coding was assessed with the information carried by a single spike about the stimulus as [35],

$$I = \frac{1}{T} \int_0^T \log_2 \left( \frac{r(t)}{\bar{r}} \right) \, dt,$$

(23)

where $\bar{r}$ is the mean, i.e. time averaged, firing rate, $\bar{r} = (1/T) \int_0^T r(t) \, dt$. The dependence of the stimulus coding on the map's time step, $h$, can be characterized by the relative change of information as,

$$\delta I(h) = \frac{I(h) - I(h_0)}{I(h_0)}.$$

(24)

where $I(h_0)$ is the average information for the map with the original time step, $h_0$; $h_0 = 0.5$ ms throughout this paper.

4.1. Spontaneous stochastic dynamics

Fig. 6 illustrates the effect of step size on spike train statistics generated by stochastic map. The mean firing rate increases with the increase of constant current, Fig. 6(a), leading to less variable spiking as shown in Fig. 6(b). In the deterministic model tonic spiking starts when the constant current exceeds its bifurcation value, $I_{th} = \sigma_{th} - \sigma$, where $\sigma_{th}$ is given by Eq. (16) and $\sigma$ defined the baseline state. For values of constant current smaller than the spike onset threshold $I_0 < I_{th}$, the model possesses a stable fixed point and spikes are generated due to random synaptic excitation only. Noise-induced spiking results in large ISI variability, quantified by large values of the coefficient of variation (CV), approaching 1 for rare Poissonian spiking for the values of $I_0$ approaching 0. Fig. 6(b). This tendency is consistent for various step sizes. With the decrease of $h$, the mean firing rate and CV approach their limiting values.

For relatively low firing rates even large time step ($h = 0.5$ ms) provides consistent ISI distributions [Fig. 6(c)]. The effect of discreteness becomes apparent for higher firing rate (larger value of $I_0$), whereby low numbers of iterations, weakly affected by noise are needed to reach $x = -0.5$ boundary leading to a spike. Consequently, the ISI distributions in Fig. 6(d) show distinct peaks. In the case, e.g. of $h = 1$ ms, the next spike occurs mostly after 13 iterations of the map. However, due to noise the map neuron can fire after 14, or less probable, after 15 or 12 iterations. Similar interpretation is indeed valid of $h = 0.5$ ms. Decrease of time step to 0.1 ms and below narrows iteration time window for the map (see Fig. 1), allowing spike times to diffuse due to noise, and thus leading to essentially unimodal ISI distributions. However, even for high firing rates of 200 Hz, the dependence of ISI statistics on the map step size becomes insignificant for $h < 0.1$ ms.

4.2. Response dynamics and information coding

In this section we study how the map’s time step affects encoding of time-varying Gaussian band-limited stimulus. Indeed, the stimulus bandwidth imposes the fundamental limitation on $h$ due to the sampling theorem, $h < 1/(2f_c)$, where $f_c$ is the stimulus’s cutoff frequency. For the parameter set chosen, PSTHs on Fig. 7 indicate weak dependence of the stimulus coding on the time step, $h$. Even for high frequency stimulus, the responses of the map are similar for various sampling steps. This is assessed quantitatively in Fig. 8(a) which shows the average information carried by a single spike, $I$, as a function of stimulus frequency band, $f_c$. This dependence shows a characteristic shape with a maximum corresponding to the mean firing rate of the map. Importantly, these dependencies $I(f_c)$ are very similar for $h \leq 0.1$ ms, but deviate slightly for $h = 0.5$ ms.
The activity level, expressed by the mean spontaneous firing rate, is a crucial factor affecting the dependence of the model response on the time step. This is illustrated in Fig. 8, which shows the average information vs stimulus frequency bands for two distinct values of constant current, corresponding to slow (low activity) and fast (high activity) firing of Fig. 6(c) and (d). While variation of time step for the slow neuron, Fig. 8(a), shows relatively weak dependence of the average information with percentage change $\delta I \leq 15\%$, (see Fig. 8(c)), variation of the time step of fast neuron (Fig. 8(b)) affects the response of the neuron dramatically, as the average information changes by 50% for 100 Hz bandwidth stimulus and by 90% for higher frequency, 200 Hz, stimulus.
5. Conclusion

We have presented an approach to modify equations for the map-based model of a tonic spiking neuron that enable us to directly control the sampling rate of the model, while preserving shapes of the spiking patterns of neuronal activity in real time. In the modified map-based model, the time step, \( h \), enters as a parameter in a similar way as in an ODE system solved numerically with a fixed time step scheme. The change of \( h \) in both cases, the map-based discrete time system and discrete approximation of continuous system, affects the accuracy of computations. The key difference is in the definition of \( h \) for the ODE system which is tuned to fit the behavior of a modeled neuron. In the ODE model the time step is determined by the underlying dynamics of a continuous system and is usually small. Alternatively, for the sake of computational efficiency the nonlinear neuronal map-based model is designed with a large fixed time step size, which does not appear as a direct parameter of the map.

However, adjustments of the time step are often needed, such as when map-based models are used along with continuous time models, operating at higher sampling rates, or when external stimuli possess high-frequency components beyond corresponding map-based sampling. Here we have presented an approach that allows one to introduce and change \( h \) for both deterministic and stochastic map-based models. This allowed us to estimate response and coding properties of the model for continuous time-varying stimuli. The method of sampling rate control used here is rather simple and retains the computational efficiency of the model.

We have studied the consistency of response dynamics in the map-based model for various sampling rates and stimuli and have showed that the approach has limitations in the range of the activity level. For low and intermediate levels of activity, i.e. when the neuron model fires on average at levels \( < 100 \text{ Hz} \), the iteration step \( h \) can be changed over a wide range. However at higher activity levels of 100 Hz and higher the proposed modification starts to fail for relatively large time steps, \( h > 0.1 \text{ ms} \), and additional adjustments of the map are needed, such as the exemplified dependence of the threshold on \( h \) (17).

Special care must be taken when a modeled neuron exhibits transitions from tonic spiking to bursting regimes accompanied by a complex sequence of bifurcations and chaotic bursting regimes (36–38). Such regimes are indeed observed in the map model for the parameter values \( \alpha > 4 \) (28). In the map model transitions from tonic spiking to bursting regimes form a fine and rather dense structure of various transitions in the parameter space (8) and corresponding attractors (regular or chaotic) are not robust with respect to small variations of parameters. Consequently, we expect that such regimes are highly susceptible to variation of the time step and the characteristics of limiting sets, such as Lyapunov exponents, could vary...
significantly as the value of $h$ changes. Nevertheless, the explicit introduction of the time step should allow for appropriate tuning of other parameters to bring the map to a desired regime.

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