

Oscillatory activity in the neural networks of spiking elements

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Abstract

We study the dynamics of activity in the neural networks of enhanced integrate-and-fire elements (with random noise, refractory periods, signal propagation delay, decay of postsynaptic potential, etc.). We consider the networks composed of two interactive populations of excitatory and inhibitory neurons with all-to-all or random sparse connections. It is shown by computer simulations that the regime of regular oscillations is very stable in a broad range of parameter values. In particular, oscillations are possible even in the case of very sparse and randomly distributed inhibitory connections and high background activity. We describe two scenarios of how oscillations may appear which are similar to Andronov–Hopf and saddle-node-on-limit-cycle bifurcations in dynamical systems. The role of oscillatory dynamics for information encoding and processing is discussed.

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1. Introduction

Despite the fact that many experimental recordings of neural activity clearly show that oscillations and other types of complex dynamics are typical and widespread modes of neural activity, the question of how neural dynamics are used to code information in the brain is still open. Three main encoding schemes have been suggested to describe the activity of an individual neuron or a neural population. (1) **Spatio-temporal coding**: the fine spatio-temporal structure of neuronal spiking

is used as a basis for coding and information processing (Mainen and Sejnowski, 1995). The code is determined by the characteristics of spatio-temporal patterns. Time and space variation of neural activity defines the functional correlates of information processing. For example, the synchrony between spike trains is related to feature binding, learning and memory (Von der Malsburg, 1995; Singer, 1999; Borisyuk et al., 2000b, 2001). (2) **Rate coding**: the spiking rate/activity of a single neuron or of a neural population, or the average membrane potential of neurons are used as the neural code (Shadlen and Newsome, 1998). There are many examples of oscillatory activity at the level of population rate coding recorded in the

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form of multi-unit activity and the local field potential (Singer, 1999). (3) **Phase-frequency coding**: there is experimental evidence that some neurons have frequency preference due to the resonance between the input signal and internal oscillations of the neuronal membrane potential (Hutcheon and Yarom, 2000). The phases and frequencies of oscillations/rhythms are used as characteristic variables to describe neural activity represented in most cases by EEG data (Vinogradova, 1995, 2001; Nikolaev et al., 2001).

It is important to emphasise that not only a final state of the neural system that appears as a result of stimulation by an input signal, but the whole spatio-temporal dynamics of the system should be taken into account to properly reflect what kind of coding is accomplished (Kryukov et al., 1990; Arbib et al., 1998). Many investigations confirm that oscillatory dynamics of neural activity and its synchronisation play a key role in the models of information processing in the brain (e.g. Singer, 1999; Castelo-Branko et al., 2000).

In this paper, we study a neural network composed of enhanced integrate-and-fire elements. We start from the model of two interactive neural populations (excitatory and inhibitory) with all-to-all connections and study the oscillatory dynamics and its dependence from parameter variation. We show that regular oscillations (single spikes or bursts) exist in a very wide region of parameter values. We investigate the mechanisms according to which oscillations can appear and disappear. Instead of a critical parameter value, which is typical for average activity models (dynamical systems) analysed by the bifurcation theory, here we can see a critical interval of parameter values where oscillations and non-oscillatory regimes co-exist. This critical interval is similar to metastable states in physical systems (Kryukov et al., 1990). Neural networks with a periodic external input have also been studied. Then, we present the results of the study of oscillatory dynamics in the network of excitatory and inhibitory neurons with sparse and randomly distributed connections. We have found that in this model, the number of connections can be drastically reduced without any damaging effect on oscillatory dynamics.

2. Model description

We consider a neural network of enhanced integrate and fire elements (Perkel, 1976). A discrete-time version of the model neuron is used with the time increment equal to 1 ms. The state of each neuron at the moment t is characterised by a threshold and total potential. If the value of the total potential has reached the threshold, the neuron generates a spike. The spike propagates to other neurons with a time delay τ . When a spike reaches another neuron, the postsynaptic potential jumps up or down depending on whether the spike is from an excitatory or inhibitory neuron, respectively. The value of the connection strength controls the jump height. The postsynaptic potential exponentially decays to the resting potential if there are no incoming spikes. After spike generation, the neuron is unable to generate a spike during an absolute refractory period. After this period expires, the threshold gets the highest value and then exponentially decays to the asymptotic threshold value. This decay is used to model a relative refractory period. A random noise is added to the membrane potential. The amplitude of the noise exponentially decays with time and a normally distributed random variable is added to it at each time step. The noise is independent random process for each element. The formal description of the enhanced integrate-and-fire element is given in [Appendix A](#).

3. Oscillations in networks with all-to-all connections

It is well known that interactive populations of excitatory and inhibitory neurons can demonstrate regular oscillations. For example, a two-dimensional non-linear dynamical system describing the average activities of excitatory and inhibitory elements can show limit cycle oscillations (Wilson and Cowan, 1972; Borisyuk and Kirillov, 1992). Unlike the Wilson–Cowan dynamical system, a neural network of excitatory and inhibitory neurons is described by multi-dimensional stochastic processes with interactive components. Despite this non-similarity, we find that oscillations appear

by the mechanisms that are similar to Andronov–Hopf and saddle-node-on-limit-cycle bifurcations in the dynamical systems.

Suppose that a network consists of two populations of neurons, excitatory and inhibitory. The parameters of all excitatory neurons are uniformly distributed with some S.D. around the mean values, which are chosen to correspond to available experimental/modelling evidence on cortical pyramidal cells (Shadlen and Newsome, 1998). The same approach is applied to the parameters of inhibitory neurons. Table 1 summarises one set of parameter values that has been used in simulations.

The architecture of connections is of the all-to-all type. We suppose that excitatory neurons send excitation to all other excitatory neurons (including self-excitation) and to all inhibitory neurons. Each inhibitory neuron sends inhibition to all the other inhibitory neurons (including self-inhibition) and to all excitatory neurons. Connection strengths are uniformly distributed near the characteristic values:

$$w \in (w_{pq}, w_{pq} + \text{S.D.}_{pq}), \quad p \in \{e, i\}, \quad (1)$$

$$q \in \{e, i\}.$$

Also, each synaptic connection is characterised by the decay rate of the synaptic potential α_{PSP} and the time delay of the signal propagation τ . The choice of these parameters is similar to rule (1), that is they are chosen according to a random

uniform distribution with proper parameters. The parameter values are summarised in Table 2.

Fig. 1 presents a typical oscillatory regime observed in the network. This example shows rather regular single spike oscillatory activity in the gamma range. The top frame of Fig. 1(A) shows internal details of spike generation by a typical excitatory neuron. The middle frame shows the firing rates of the inhibitory (top) and excitatory (bottom) populations. The bottom frame shows the scatter plot of spikes of all inhibitory neurons (top) and excitatory neurons (bottom). Each period of oscillations' is characterised by the increased spiking of excitatory neurons, which is immediately followed by almost simultaneous spiking of inhibitory neurons. The period of oscillations is 43 ms. This period of oscillations is rather typical for gamma oscillations in the cortex.

Fig. 1(B) shows an inter-spike interval (ISI) histogram of excitatory (left) and inhibitory (right) neurons. The inhibitory neurons mainly generate single spikes. The excitatory neurons' histogram has two peaks: the first peak corresponds to the 43 ms interval and the second peak corresponds to the 86 ms interval. It means that an excitatory neuron sometimes misses to produce a spike and waits until the next possibility is provided. Fig. 1(C) shows the autocorrelation function for typical excitatory neuron (left) and the crosscorrelation for excitatory and inhibitory neurons (right). The auto- and cross-correlations clearly show the

Table 1
The parameter values that have been used in simulations

Parameter	Excitatory		Inhibitory	
	Mean	S.D.	Mean	S.D.
r_{max} (mV)	−25	5.0	−25	5.0
r_{∞} (mV)	−55	3.0	−55	3.0
Resting potential (mV)	−70		−70	
α_{th}	3.0	1.0	10.0	2.0
α_{N}	10.0	0.1	1.0	0.1
σ_{N} (mV)	6.0	0.5	5.0	0.5
α_{V}	20.0	2.0	30.0	1.0
V_{AHP} (mV)	−100.0	2	−100.0	1.0
I_{ext} (mV)	0.0	1.0	0.0	1.0
Ref (ms)	3	2	2	2
Number of neurons	200		50	

Table 2

	Exc to Exc w_{ii}		Inh to Inh w_{ii}		Inh to Exc w_{ei}		Exc to Inh w_{ie}	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Connection strength	0.8	0.1	-1.1	0.1	-1.7	0.1	1.0	0.1
Decay rate	3.0	3.0	10.0	3.0	10.0	3.0	3.0	3.0
Time delay	4	2	4	2	4	2	4	2

presence of non-decaying oscillations with the period of ≈ 43 ms which indicates rather regular spiking of single neurons.

While studying the oscillatory activity under the variation of parameter value, we have found that oscillatory dynamics are very stable. Oscillations exist in a very wide range of parameter values. Of course, some features of oscillations may change, for example instead of single spikes, the doublets or bursts can appear. Also the duration of the oscillation period can vary drastically. Fig. 2(A–C) shows an example of bursting behaviour. All parameters for this simulation are the same as in Fig. 1 with the exception of the value of the connection strength between excitatory neurons, which is made 1.6 times greater. Now the oscillatory activity is of a bursting type with eight to nine spikes per burst, the period is ≈ 83 ms. Fig. 2(B,C) shows the typical histograms and auto-correlation functions of excitatory and inhibitory neurons, respectively.

Let us fix all parameter values as they are listed in Tables 1 and 2 and choose another value of the external input to excitatory neurons (note, that this value is constant and does not change with time). We have found that the oscillatory regime exists if the value of the external input belongs to the interval $(-11.0, +88.0)$. If the value of the input signal is less than -11 , the oscillatory activity is stopped and all neurons demonstrate their specific background activity. If we gradually increase the value of the input, the oscillations with small but distinguishable amplitude may appear (Fig. 3A). The scenario of how oscillations appear is similar to an **Andronov–Hopf bifurcation** in dynamical systems when oscillations with a small amplitude and a definite period appear near

the critical parameter value. The amplitude of oscillations increases with the increase of the input signal. It is worth noting that at the beginning of the oscillatory period, the amplitude of the firing rate of the excitatory population increases and causes the increase of the amplitude of the firing rate of the inhibitory population (Fig. 3(A), right panel). Unlike the situation with dynamical systems, the appearance of oscillations is a rather fuzzy phenomenon that exists if the external input has a value in the critical range $(-14, -10)$. For parameter values in this interval, the low background activity and oscillatory activity coexist. The probability to get oscillations increases with the increase of the input value. For parameter values taken from the critical range, the dynamics of neural activity can be characterised as a metastable state (Kryukov et al., 1990). For a large input value (> 88), oscillations disappear and the high level of background activity emerges.

There is another scenario of the appearance of oscillations which is similar to the **bifurcation of a limit cycle on a saddle-node**. Again, for a low input value the neurons have a very low level of background activity (note, that in this example we have reduced the amplitude of the noise in comparison to the previous simulations). If we increase the input to the excitatory neurones, oscillations appear. These oscillations have a rather large amplitude (firing rate) and a very irregular oscillatory dynamics with a long average period. If we continue to increase the input value, then the regularity of oscillations will increase. Fig. 3(B) shows an example of this scenario. The parameter values are the same as in Tables 1 and 2 with the exception of four parameters: $\alpha_N = 1$, $\sigma_N = 5$, $w_{ee} = 1.9$, $w_{ei} = -2.6$.

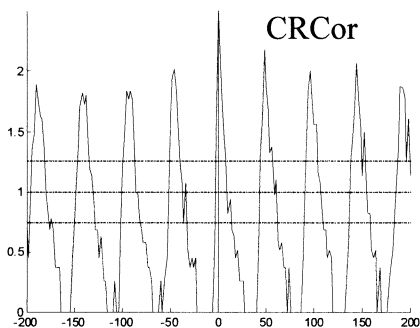
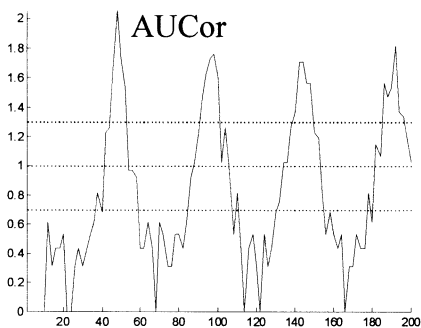
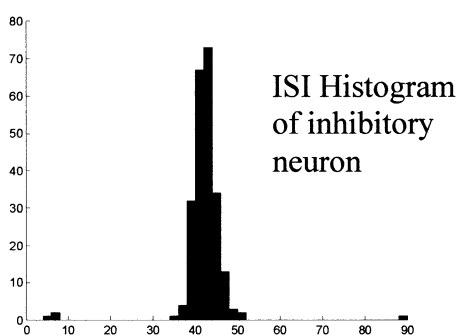
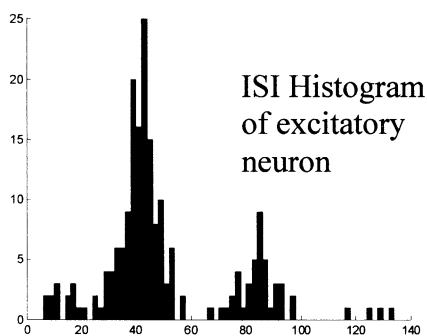
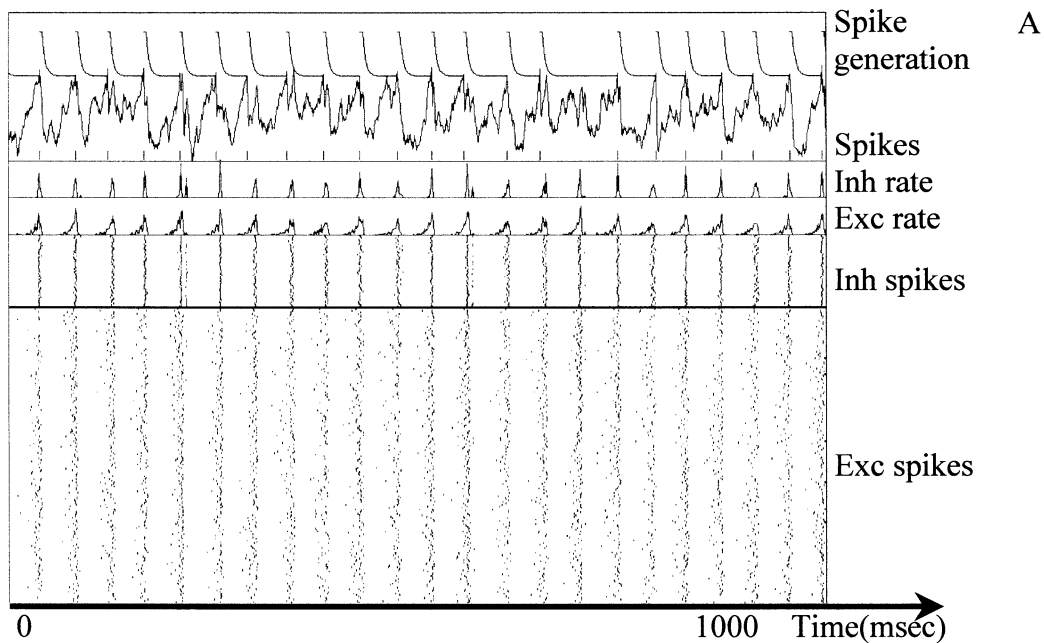


Fig. 1

4. Oscillations under periodical forcing

Consider the case when neural network elements are forced by a periodic input. It means that we add to the potential of each excitatory and inhibitory neuron an additional potential that changes periodically in time:

$$P(t) = a \sin(2\pi/T + \varphi),$$

here a is the forcing amplitude, T is the forcing period and φ is the forcing phase. If a is large enough, the neural network demonstrates oscillatory behaviour with the period of forcing T , that is the network is synchronised with the forcing input. Note that in the case of a ‘small’ forcing period (smaller than the natural period of oscillations without forcing) the synchronisation requires a greater amplitude of the forcing signal than in the case of synchronisation with a ‘large’ forcing period. Fig. 4(A) shows an example of oscillations induced by forcing with a ‘large’ period. In this example, the natural period of oscillation (due to the choice of parameters of elements and connections without periodical forcing) is 75 ms and the forcing period is about three times larger at 250 ms). The network parameter values are the same as in Table 2 except $w_{ee} = 1.5$ and $w_{ei} = -3.0$. The parameters of forcing are $a = 90$, $T = 250$, $\varphi = 1$. In this case oscillations of a complex shape arise with three synchronisation zones for each period of oscillations.

It is interesting to force the system by the signal with a ‘resonance’ period. Unlike a linear system, where the amplitude of oscillations during the resonance increases drastically, non-linear systems responds in a different manner due to the limits on the range of admissible values of system variables. For example, the firing rate can only change in the range between 0 and 1 even in the resonant state. Fig. 4(B) shows an example of the resonance state in the same neural network as in Fig. 4(A) with the

exception that $a = 10$, $T = 86$ (period of natural oscillations (for $a = 0$) is the 75 ms). The plot of autocorrelation functions clearly shows a combination of two oscillations. The first one is a fast oscillation with the period ≈ 75 ms and the second one is a slow oscillation with the period ≈ 400 ms. Note that quasiperiodic (two-periodic) oscillations may be very useful for modelling in the neuroscience. For example, in the paper of Borisyuk et al. (2000a) we have discussed an application of two-periodic oscillations for modelling the feature binding.

5. Oscillations in networks with sparse connections

In this section we consider sparse and random connections between oscillators. We study how the sparseness of connections influences the oscillatory dynamics. The answer is that oscillatory regimes are extremely robust: one can randomly delete many excitatory and inhibitory connections and still the oscillatory activity will persist.

We start from a neural network with all to all connections and the same parameter values as in Fig. 2. Then for each neuron we randomly chose k incoming connections (with possible repetition of the same connections) and make their values equal to zero. (Since it may happen that some connections are chosen several times, the number of non-zero incoming connections varies for different neurons). Fig. 5(A) shows oscillations in a neural network with sparse connections. In this example, the mean number of non-zero connections incoming to an excitatory neuron from the other 250 excitatory neurons is 110. The oscillations in this case are very regular and there are no significant difference between these oscillations and oscillations in case of all-to-all connections (compare with Fig. 2). Further reduction of the number of incoming connections will result in less regular

Fig. 1. A typical example of oscillatory activity. (A) The first frame shows the total membrane potential, the threshold and spikes of typical excitatory neuron. A spike appears when the membrane potential reaches the threshold. The other two frames showing the firing rates of excitatory (bottom) and inhibitory (top) neurons and the scatter plot of spikes of excitatory neurons (bottom) and inhibitory neurons (top). (B) Inter-spike interval histograms of excitatory (left) and inhibitory (right) neurons. (C) Autocorrelation functions of typical excitatory neuron (left) and crosscorrelation of excitatory and inhibitory neurons (right).

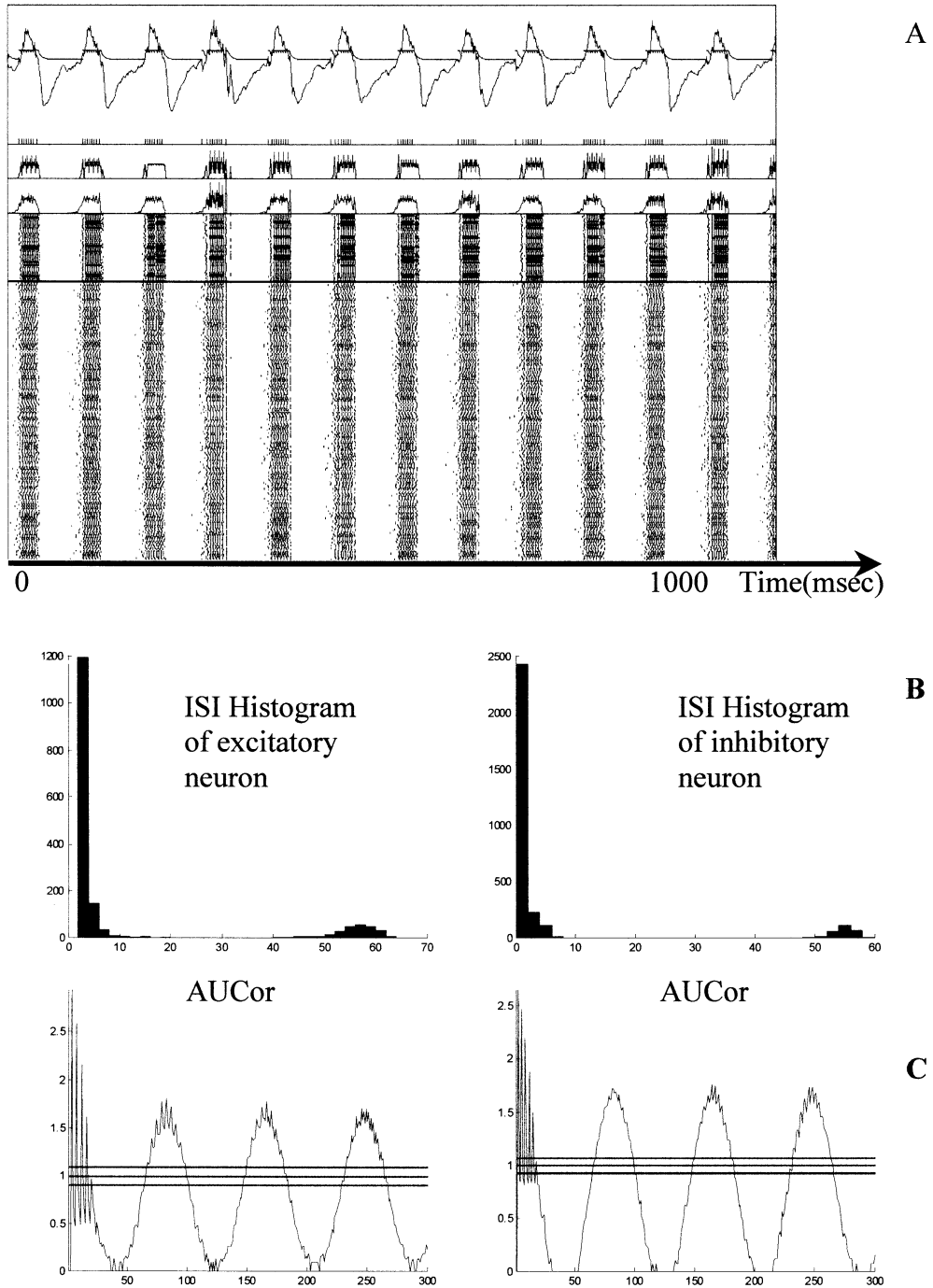


Fig. 2. An example of bursting oscillations. (A,B) The frames here are the same as in Fig. 1(C): Autocorrelation functions of typical excitatory (left) and inhibitory (right) neurons.

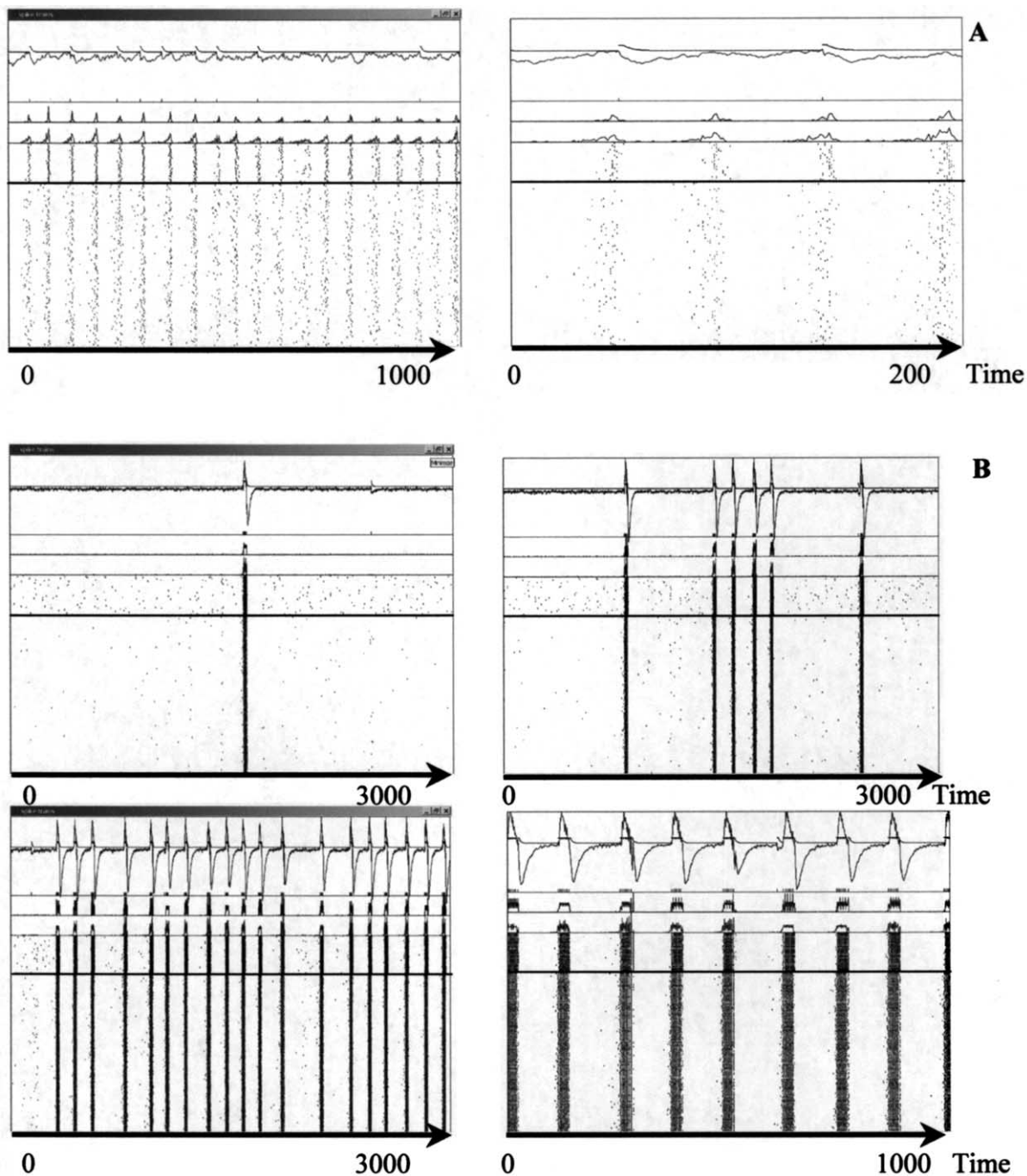


Fig. 3. Two scenarios of oscillation appearance. (A) Appearance of oscillations via scenario similar to Andronov–Hopf bifurcation. External input to excitatory neurons equals -10 . There is increased scale on spiking rate frames of each population: inhibitory firing rate is scaled in the interval $[0, 0.6]$ and excitatory firing rate is scaled in the interval $[0, 0.17]$. B: Appearance of oscillations via scenario similar to a ‘saddle-node on limit cycle’ bifurcation. The values of external input are: -3 (left top), -2 (right top), -1 (left bottom), 0 (right bottom). Scale of firing rate is $[0, 1]$ for each population.

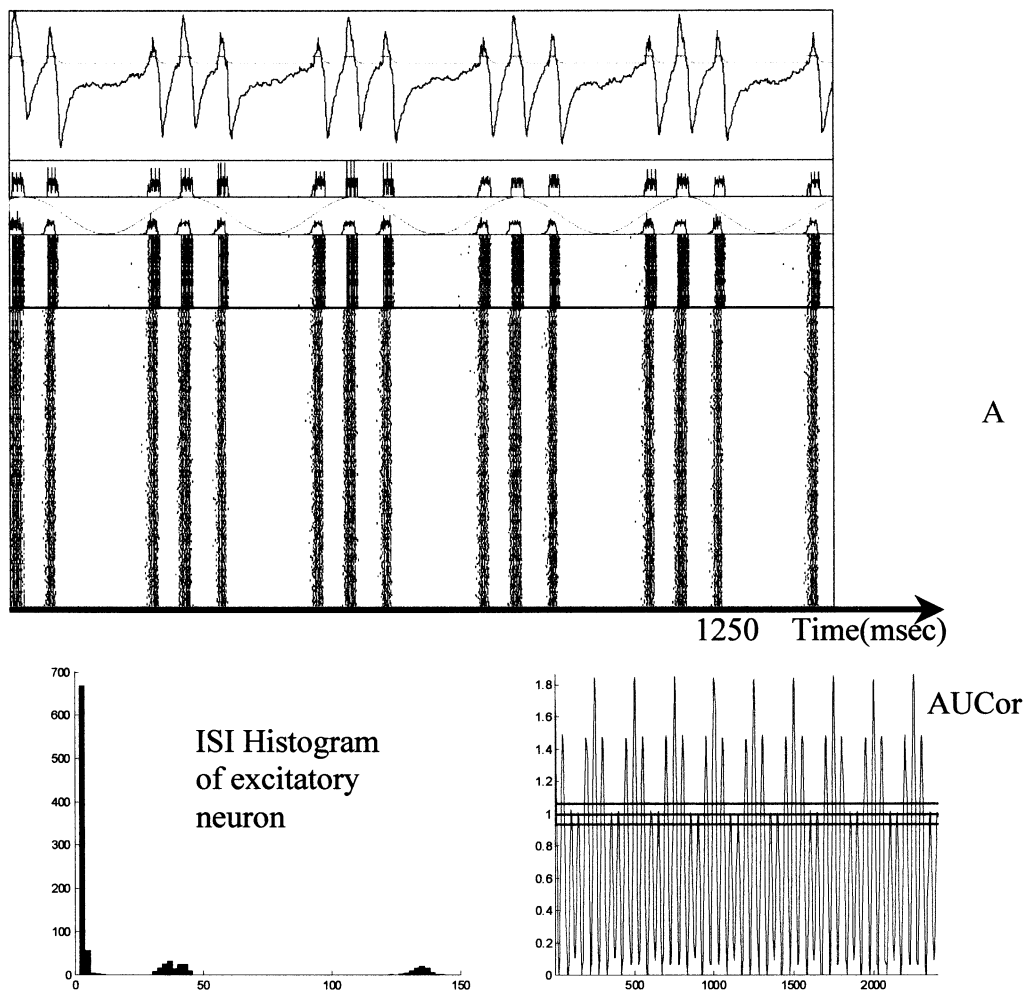


Fig. 4. Examples of oscillations with periodic forcing. The top panel shows (from top to bottom) internal potential and threshold of a typical excitatory neuron; firing rate of inhibitory population; firing rate of excitatory population the sinusoidal forcing input; the scatter plot of spikes of inhibitory and excitatory elements. The bottom panels show ISI histogram (left) and autocorrelation function of spike train of a typical excitatory neuron. (A) Forcing with a 'large' forcing period (about three times larger than a natural period). (B) Forcing with a 'resonant' forcing period.

oscillations. There is a lowest boundary for the mean value of incoming excitatory to excitatory connections when oscillations still survive. In our simulations this boundary is about 75. For a proper choice of parameters, it is possible to get oscillations in the neural network with only a few non-zero incoming excitatory to excitatory con-

nections per neuron. Fig. 5(B) shows oscillations in the same neural network when the mean number of incoming excitatory to excitatory connections is ≈ 8 and all values of the connection strength have been multiplied by the factor 5. Of course, in this case the oscillations are not very regular. Nevertheless, the spatio-temporal pattern

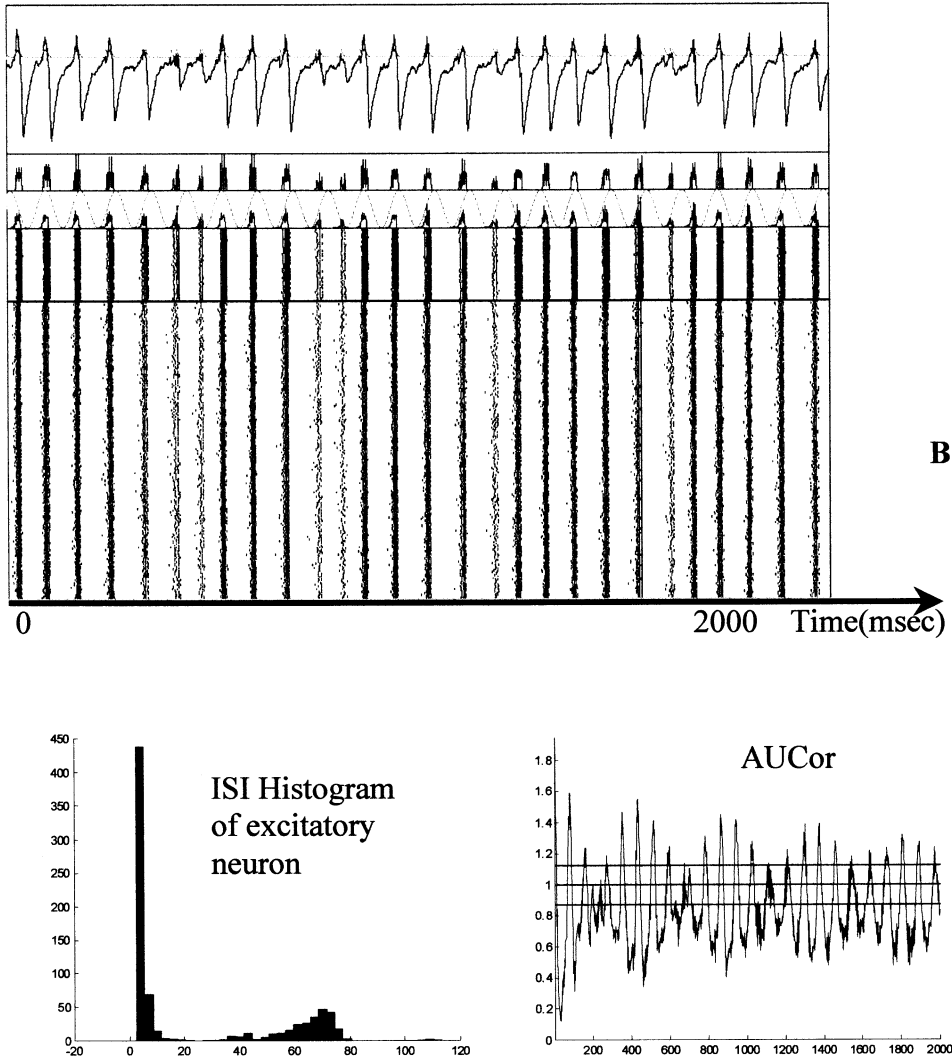


Fig. 4 (Continued)

of neural activity typical for oscillatory dynamics is easily visible.

6. Oscillations in networks with inhibitory connections

The level of the background activity of excitatory neurons is rather high in all our simulations. Due to this property of the model neural network, oscillations emerge according to a simple mechanism:

excitatory neurons spontaneously increase their activity, therefore the total excitatory input to inhibitory neurons increases, then (with a time delay) inhibitory neurons increase their activity and inhibit the activity in the whole network for some period of time. This process is repeated periodically. The majority of excitatory neurons generate spikes almost simultaneously as well as the majority of inhibitory neurons, but there is a time delay between spiking of excitatory and inhibitory neurons. Taking into account the high

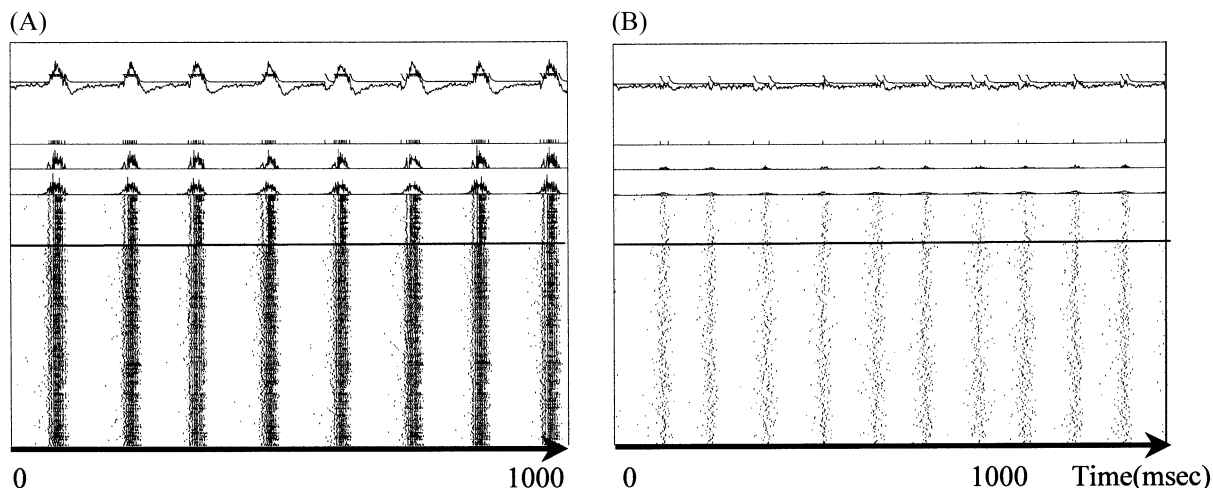


Fig. 5. Oscillations in a sparse neural network. (A) Mean of excitatory to excitatory connections is 110. (B) Mean of excitatory to excitatory connections is 8.

level of the background activity of excitatory neurons, let us consider a neural network that consists of inhibitory neurons with all-to-all connections. The parameter values are chosen the same as in Fig. 2 for excitatory neurons except the value of the input to the population, which equals 13 now. The values of connection strengths are uniformly distributed in the interval $[-5, 0]$, the decay rate is uniformly distributed in the interval $[10, 12]$ and the delay is uniformly distributed in the interval $[10, 20]$. The number of neurons is 500.

The results of simulations are shown in Fig. 6. The background activity of neurons with zero connection strength (Fig. 6(A), left) as well as an oscillatory regime (Fig. 6(A), right) are shown. The oscillation of a single typical neuron is rather irregular and of a very specific type: there are prescribed moments of spike generation allocated periodically in time with the period of ≈ 60 ms (the neuron sometimes generates a spike at these moments and sometimes spiking is missed). Oscillations are clearly visible on the scatter plot and on the graph of the firing rate (Fig. 6(A), right). The ISI histogram and the autocorrelation function show oscillatory activity with the minimal silence interval of ≈ 60 ms (Fig. 6C). A typical ISI histogram and an autocorrelation function are also shown for the background activity (Fig. 6B). In this case, the ISI histogram is different from the

exponential density function, the value of the coefficient of variation is ≈ 0.35 and the autocorrelation function is rather flat. It means that the background spike train is rather a renewal than Poisson process.

7. Discussion

This paper is the first in the series of publications about dynamical behaviour in neural networks of enhanced integrate-and-fire neurons. These neurons have many important features of real neurons and they are very convenient for modelling and comparing with experimental evidence because in this model we can ‘measure’ the internal dynamics of an element, the average activity of a neural population and frequencies and phases of oscillations.

Due to the noise term in the enhanced integrate-and-fire model, there is a background activity of a single neuron. This background activity persists without any external influence on the neuron. Thus, from a mathematical point of view the enhanced integrate-and-fire element is described by a stochastic process and the neural network dynamics are described by a multidimensional stochastic process with interacting components.

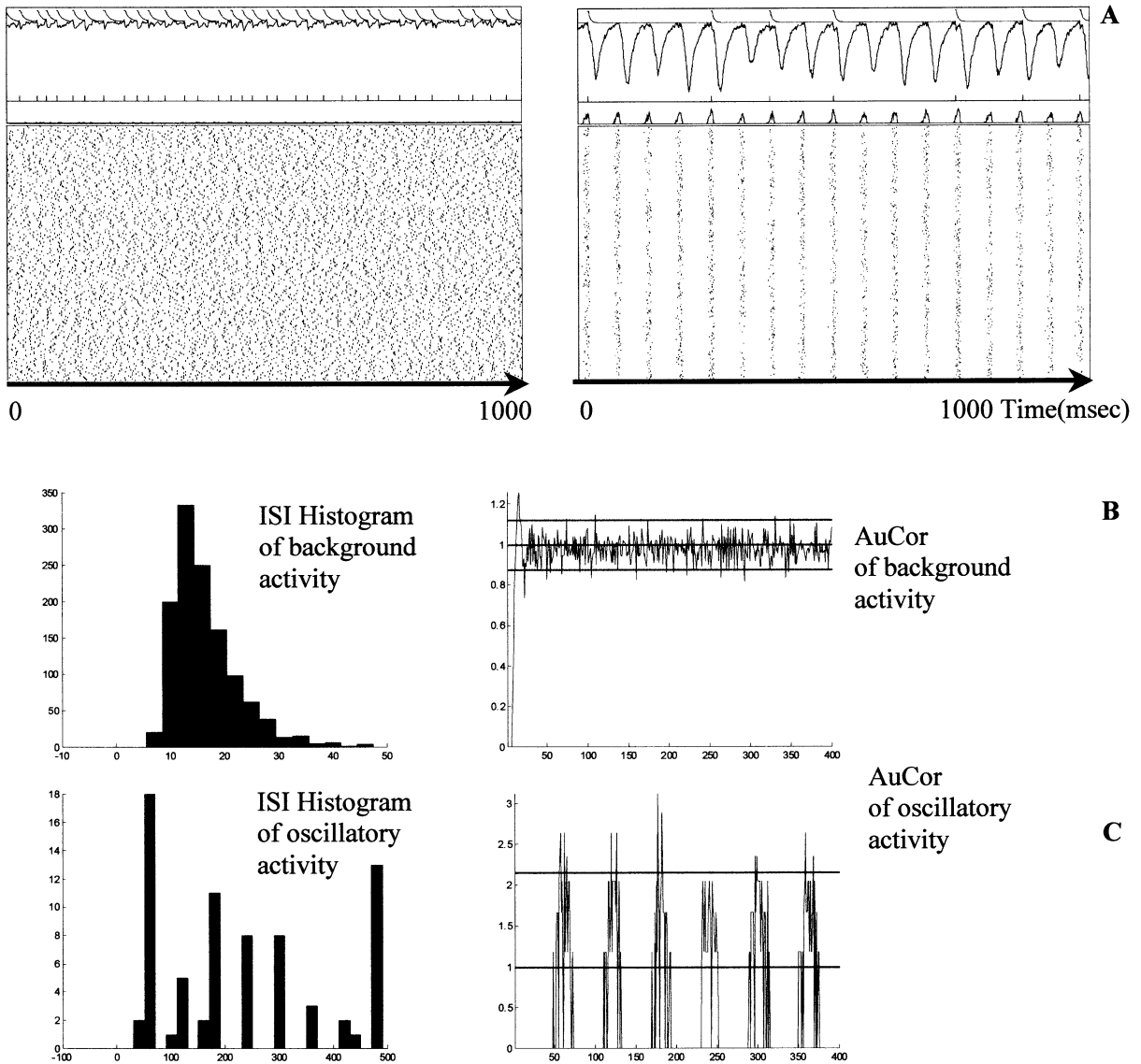


Fig. 6. Oscillations in the neural network of inhibitory neurons with high level of background activity. (A) Oscillation mode (right) and background activity with zero connection strengths (left). (B) Typical ISI histogram and autocorrelation function of background activity. (C) Typical ISI histogram and autocorrelation function of oscillating neuron.

We find that in a neural network with excitatory and inhibitory elements, the regime of oscillations exists in a very wide region of parameter values for different connection architectures. Even in a neural network with inhibitory connections only, the oscillation mode is possible if the background activity is high enough. It is possible to control the

dynamics of a neural network by varying the parameter values. For example, the period of oscillations drastically depends on several parameters. We discuss different scenarios of how oscillations can emerge in the neural network. Unlike the bifurcation theory, a critical region exists in the parametric space where the transition

from a ‘steady state’ regime to oscillations happens. In the case of periodic forcing, we have found interesting peculiarities of non-linear resonance dynamics.

The oscillatory mode is a very useful dynamical regime for modelling information processing in the brain. Models of such important functions as feature binding, attention, novelty detection, memorisation of sequences can be based on oscillatory dynamics (Borisyuk et al., 2001). We believe that using neural network with enhanced integrate-and-fire elements for modelling information processing in the brain is very promising.

Acknowledgements

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Appendix A

The dynamics of an integrate-and-fire neuron is governed by the following equations (Perkel, 1976):

- 1) The threshold:

$$r(t+1) = (r_{\max} - r_{\infty}) \exp(-(t - t_{\text{sp}})/\alpha_{\text{th}}) + r_{\infty}$$

where r_{\max} is the maximum value of the threshold; r_{∞} is the asymptotic threshold value when $t \rightarrow \infty$; α_{th} is the threshold decay rate; t_{sp} is the last spike moment before t .

- 2) The post-synaptic potential for the input of the neuron:

$$\text{PSP}^j(t+1) = \text{PSP}^j(t) \exp(-1/\alpha_{\text{PSP}}^j) + a,$$

$$a = \begin{cases} w^j, & \text{if } t_{\text{sp}}^j + \tau^j = t + 1 \\ 0, & \text{otherwise} \end{cases}$$

where w^j is the connection strength, positive for the excitatory connection and negative for the inhibitory one; τ^j is the time delay; α_{PSP}^j is the j th neuron PSP decay rate; t_{sp}^j is the last spike moment of the j th neuron before t .

- 3) The noise:

$$N(t+1) = N(t) \exp(-1/\alpha_N) + \xi, \quad \xi \in N(0, \sigma),$$

where α_N is the noise decay rate; ξ is a random variable with the normal distribution.

- 4) The soma’s membrane potential:

$$V(t+1) = V_{\text{AHP}} \exp(-(t - t_{\text{sp}})/\alpha_V)$$

where V_{AHP} is the value of after spike hyperpolarisation; α_V is the soma’s membrane potential decay rate; t_{sp} is the last spike moment before t .

- 5) The total potential:

$$P(t+1) = \sum_j \text{PSP}^j(t+1) + N(t+1) \\ + V(t+1) + I_{\text{ext}}(t+1),$$

where I_{ext} is the value of the external input.

- 6) Spike generation:

$$\text{if } P(t+1) > r(t+1), \quad \text{then } t_{\text{sp}} = t + 1.$$

- 7) The absolute refractory period: There is no spike generation for the time interval $t \in (t_{\text{sp}}, t_{\text{sp}} + \text{ref})$.

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