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Reducing the sequential dynamics of excitatory neural networks to cellular automata

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An approach is developed for the description and analysis of sequential dynamics of excitatory neural networks. It is based on the reduction of dynamics of networks to the dynamics of cellular automata on the graph of connections. We apply our approach to network of Hodgkin–Huxley neurons coupled by chemical synapses.

One of the significant problems of neurodynamics is development of analytical methods for studying of models of complex neural networks.

Recently in [1] an approach for the study of neural networks has been proposed. It consists in reducing a given network to a discrete model. In this model [2] each neuron is represented by a finite number of states and there are rules which determine how a neuron goes from one state to another. However, the approach has some limitations. It is based essentially on a specific character of the dynamics of neurons. Indeed, the neurons are assumed to be relaxational. In this case each neuron can be in one of three consecutive phases: active phase, when a neuron can excite other neurons, refractory phase, when a neuron is non-responsive to the action of other neurons, and rest phase, when a neuron can be excited (activated) by other neurons. The duration of the refractory phase is assumed to be a multiple of the duration of the active phase. Thus the duration of the active phase is considered as a discretization time step. The interaction between neurons is taken into account in the following way. If a neuron receives an excitatory input, the excitation occurs instantaneously. On the other hand, if a neuron receives an inhibitory input, then it becomes excited due to the post-inhibitory rebound only when the inhibition ends. Moreover, the approach can be rigorously applied only to excitatory-inhibitory networks. In [3] the examples of application of this approach to specific biophysical models are presented.

Unlike [1, 3], here we offer an approach for analyzing the dynamics of excitatory neural networks. It consists in reducing continuous dynamics of neural networks to a discrete dynamical systems in the form of a cellular automaton (CA) on the graph of connections. In the approach the main role is played by the dynamics of synapses but not by the specific features of neurons. In fact, the CA represents a network of synapses with a finite number of states which alternate each other according to some fixed rules. To determine the rules one needs to study only the responses of an individual synapse onto actions of neighboring (in graph of connections) synapses through corresponding neurons. As a result the numerical integration of the whole system of ordinary differential equations (ODEs) is not needed. Moreover, since the form of the neuron responses is not important, the approach is applicable to a broad set of networks including those consisting of neurons, which possess the neural excitability property (neurons of the class 2 excitability in the terminology of Izhikevich [4]).

Model. To manifest our approach we consider the network of coupled identical Hodgkin–Huxley neurons with architecture shown on Fig. 1. The interaction between neurons are realized by excitatory chemical synapses with short-term plasticity property [5]. We assume that due to short-term plasticity a synapse has two types of responses (waveforms of synaptic conductance $s(t)$, see Fig. 2) depending on the presynaptic neurons activity – fast (Fig. 2a) and slow (Fig. 2b) ones which are distinguished by the characteristic rise times (T_2 and T_1) of the synaptic conductance. Such behavior may be caused, for instance, by the competition of presynaptic facilitation and postsynaptic desensitization processes [6–8]. The dynamics of such network is given by following system of ODEs:

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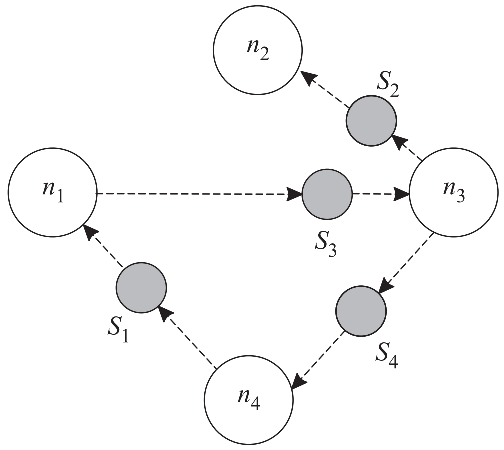

Fig. 1. The architecture of excitatory neural network. Here n_i and s_i signify the neurons and synapses, respectively

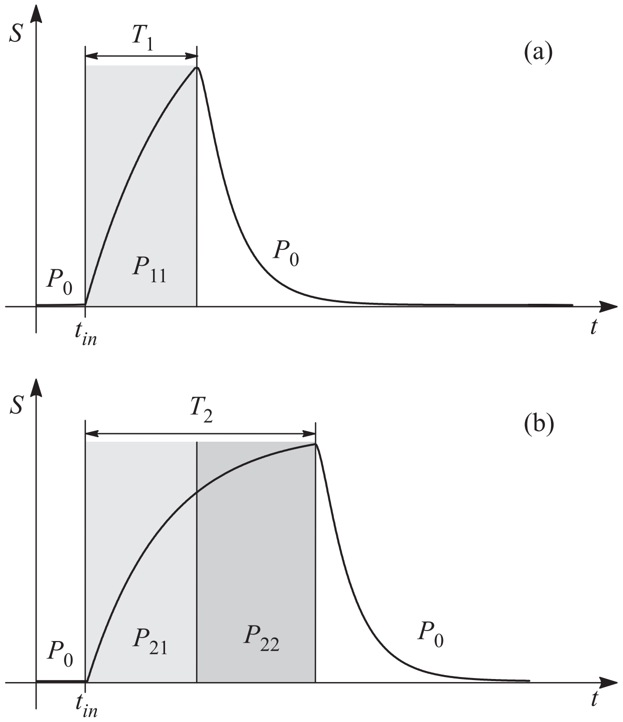

Fig. 2. Qualitative waveforms of synaptic conductance $s(t)$ corresponding to fast (a) and slow (b) synaptic responses ($T_2 \simeq 2T_1$). Symbols P_0, P_{11}, P_{21}, P_{22} signify the discrete states of a synapse (see below, for details)

$$\dot{v}_i = I_i - g_L(v_i - 10.613) - g_{Na} m_i^3 h_i (v_i - 115) - \tag{1}$$
$$- g_K n_i^4 (v_i + 12) - g_{\text{syn}} s_i (v_i - 150),$$
$$\dot{x}_i = [x_\infty(v_i) - x_i]/\tau_x(v_i), \tag{2}$$
$$\dot{r}_i = f_1(r_i) - s_i + 0.617, \tag{3}$$
$$\dot{s}_i = 0.005(f_{2i} - s_i + 0.218). \tag{4}$$

Equations (1) and (2) describe dynamics of membrane potential v_i and gating variable $x_i = m_i, h_i, n_i$ respectively ($i = 1, ..., 4$). The terms at the RHS of (1) describe the currents flowing through the cell membrane of the ith neuron: leak ($g_L = 0.3$), sodium ($g_{Na} = 120$), potassium ($g_K = 36$), external (I_i), and synaptic ($g_{\text{syn}} = 0.066$) currents. We borrow the equilibrium function $x_\infty(v_i)$ and the characteristic relaxation time $\tau_x(v_i)$ for each ionic current from [9]. To describe aforementioned plasticity property, we introduced a phenomenological model of synapse in the form of system (3), (4) with specially designed functions f_1 and f_2. The function f_1 is piecewise linear and resembles the shape of a polynomial of degree 5, and

$$f_{2i} = \begin{cases} (0.4 + 2.23\zeta_i \chi_i) r_i, \ r_i < 0, \\ 2r_i, \ r_i \geqslant 0. \end{cases} \tag{5}$$

Here, $\chi_i = \sum_{\substack{j=1, \\ j \neq i}}^{4} H(v_j - \theta_{ji})$ describes an action of presynaptic neurons onto the synapse of ith neuron, $\zeta_i = H(0.01 - s_i)$ accounts for refractory property of the synapse, $H(\dots)$ is the Heaviside function. The parameters $\theta_{13} = \theta_{34} = 20$, $\theta_{32} = 10$, $\theta_{41} = 50$ (other $\theta_{ij} = 150$) are synaptic thresholds. They characterize the initial instants of activation of synaptic processes caused by action of presynaptic neurons.

In [10] it was shown that networks of class 2 excitable neurons coupled by excitatory synapses described by system of equations similar to (3), (4) can demonstrate a variety of sequential activity regimes characterized by successive firing of neurons in the form of bursts (bunches of spikes). Also the mechanisms of activation of the synaptic coupling and features of the neuron response to an excitatory synaptic action were studied. It was established that the neurons and the synapses possess the following basic dynamical properties:

(*a1*) the time course of synaptic conductance completely determines the dynamics of postsynaptic neuron. In particular, when synaptic current is absent (the conductance $s = 0$) a neuron is at rest. On the other hand, when the synaptic conductance overcomes some threshold value which is close to its maximum a neuron generates spikes. Note that the temporal intervals of generation of spikes are relatively short with respect to the characteristic timescales of evolution of the synaptic conductance. Firing of the neuron then triggers the processes of activation of corresponding synaptic couplings;

(*a2*) when a synapse is active it is non-sensitive to the presynaptic stimulation, i.e. it is in refractory state.

For our purposes we also assume that:

(*a3*) there is a "resonance" relation between the value T_2 for the slow response and T_1 for the fast one such that $T_2 = 2T_1$.

Construction of a cellular automaton. Let us consider a neural network consisting of N neurons coupled by excitatory synapses and assume that neurons and synapses of the network possess the properties (*a1*)–(*a3*). Next we show that these properties allow one to reduce continuous dynamics of the network to a discrete one in the form of cellular automaton on the graph of synaptic connections.

Graph of connections. Let us first define directed graph $G = \langle Q_G, K_G \rangle$. It has N vertices $Q_G = \{Q_1, Q_2, ..., Q_N\}$ which signify the synapses of the network. The set $K_G = \{K_1, K_2, ..., K_N\}$ reflects the architecture of the connections in the network. Each K_i is a collection of indices such that $j \in K_i$ if and only if there is a connection from the j-th synapse of the network to the i-th synapse through the j-th neuron. In the graph collection K_i defines a set of arrows started at the vertices $j \in K_i$ and ended at i. This possibility follows from the property (*a1*).

Discrete states of a synapse. We will define discrete states of a synapse according to the behavior of the s-variable describing its dynamics. Here we use the assumption (*a3*). We say that the i-th synapse is in the state $\psi_i(s_i)$ that is equal to:

- P_{11} if $s_i(t)$ undergoes the fast response and $s_i'(t) > 0$ (see Fig. 2b);
- P_{21} if $s_i(t)$ undergoes the response of the slow type, $s_i'(t) > 0$ and $t_{in} \le t \le T_1 + t_{in}$, where $s_i(t_{in}) = 0$, $s_i'(t_{in}) > 0$, i.e. $s_i(t)$ starts growing at the instant of time t_{in} (see Fig. 2a);
- P_{22} if $s_i(t)$ again undergoes the response of the slow type and $s_i'(t) > 0$, but $T_1 + t_{in} \le t \le 2T_1 + t_{in}$;
- P_0 if it is not in one of the previous states, i.e. either it is in the equilibrium state $s_i(t) = 0$ or $s_i'(t) < 0$ in both the slow and fast cases (see Fig. 2).

Thus, we have replaced the continuous description of the behavior of the i-th synapse in terms of $s_i(t)$ by a discrete description in terms of $\psi_i = \psi_i(s_i)$. The set of values of ψ_i, $i = 1, ..., N$, is the collection of the symbols $\mathcal{P} = \{P_0, P_{11}, P_{21}, P_{22}\}$. For the sake of convenience we identify P_0 with 0, P_{11} with 1, P_{21} with 2, and P_{22} with 3, so $\mathcal{P} = \{0, 1, 2, 3\}$. We will use both notations below.

The rules of CA. Now we define the rules of evolution in time of ψ_i, i.e. the rules of a CA. They can be formulated on the basis of properties (*a1*) and (*a2*).

(*i*) If i-th synapse at the instant of time t is in the state P_0 ($\psi_i[s_i(t)] = P_0$), and there is $j \in K_i$ such that $\psi_j[s_j(t)] = P_{11}$ or $\psi_j[s_j(t)] = P_{22}$ then it will be excited at the instant $t + T_1$, i.e. $\psi_i[s_i(t + T_1)] = P_{11}$ or $\psi_i[s_i(t+T_1)] = P_{21}$ depending on the values of threshold constants θ_{ji}.

(*ii*) If i-th synapse at the instant of time t is in the state P_{21}, i.e. $\psi_i[s_i(t)] = P_{21}$, then $\psi_i[s_i(t + T_1)] = P_{22}$, independently of other synapses. Moreover, the P_{21}-synapse cannot excite another synapse.

(*iii*) If $\psi_i[s_i(t)] = P_{11}$ or $\psi_i[s_i(t)] = P_{22}$, then $\psi_i[s_i(t + T_1)] = P_0$, independently of the states of other synapses.

(*iv*) Because of the existence of the refractory period, the synapses in the states P_{11}, P_{21}, P_{22} do not feel the action of other synapses.

These statements imply that for the fixed i the state $\psi_i[s_i(t+T_1)]$ at the instant $t+T_1$ is uniquely determined by: the state $\psi_i[s_i(t)]$ at the previous instant of time t; the states of the j-th synapse, $j \in K_i$, at the instant of time t; the values of the threshold constants θ_{ji}, $j \in K_i$. Hence,

$$\psi_i[s_i(t + T_1)] = \\ = F_i(\psi_i[s_i(t)], \{\psi_j[s_j(t)]\}, \{\theta_{ji}\}, j \in K_i), \qquad (6)$$

where F_i is a function determined by the statements (*i*)–(*iv*). The relation (6) is a synaptic CA determined on the graph of connections G. In Table 1 we summarize the rules of the CA. In what follows we identify $\psi_i[s_i(t)]$ with the symbol ψ_i and $\psi_i[s_i(t + T_1)]$ with the symbol $\overline{\psi_i}$. Thus, given constants θ_{ji} the rules of the CA take the following form:

$$\overline{\psi_i} = F_i(\psi_i, \{\psi_j\}, j \in K_i), \qquad (7)$$

where $\overline{\psi_i}, \psi_i \in \mathcal{P}$.

Table 1

Synaptic dynamics rules (Rules F_i of CA)

ψ_i / $\psi_j,\ j \in K_i$	P_0	P_{11}	P_{21}	P_{22}
$\forall j \in K_i$, $\psi_j = P_0$ or $\psi_j = P_{21}$	P_0	P_0	P_{22}	P_0
$\exists j \in K_i$, such that $\psi_j = P_{11}$ or $\psi_j = P_{22}$	P_{11} or P_{21} depending on θ_{ji}	P_0	P_{22}	P_0

Specific example of CA. Here, we illustrate building of a cellular automaton for the neural network modeled by the system of Eqs.(1)–(5) with the architecture presented on Fig. 1. First of all the graph of connections must be constructed. For this purpose we single out the elementary clusters of the neural network. Each cluster C_i is defined as part of the network including the i-th synapse and j-th synapses coupled with the i-th one through j-th neurons. It is easy to see from the architecture of the network that it contains only four elementary clusters: C_1–C_4, which are shown on Fig. 3a. Based on

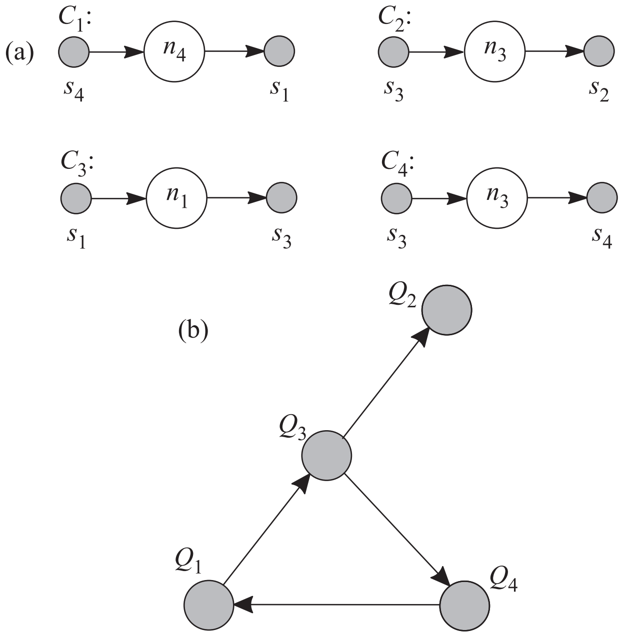

Fig. 3. Elementary clusters of the network (a) and corresponding graph of connection $G = \langle\{Q_i\}, \{K_i\}, i = \overline{1,4}\rangle$ (with $K_1 = \{4\}$, $K_2 = \{3\}$, $K_3 = \{1\}$, $K_4 = \{3\}$) (b)

the structure of each elementary cluster one can construct the graph of connections G shown on Fig. 3b. Next one needs to specify the rules F_i for the CA. For this purpose we determine the responses of the clusters, i.e. for each cluster C_i, we find the responses of the i-th synapse caused by the different (fast and slow) actions of the j-th synapse through the j-th neuron, $j \in K_i$. It is implied that a collective action of groups of several j-th synapses also has to be studied if K_i consists of more than one element. For example, let us consider the cluster C_1. The state of the synapse s_1 depends only on the state of the synapse s_4 ($K_1 = \{4\}$). Numerical study shows that the response of the synapse s_1 (while it is in the state P_0) to the action of the synapse s_4 is always of the double time scale T_2, independently of the state (P_{11} or P_{22}) of s_4, i.e. $F_1(P_0, P_{11}|P_{22}) = P_{11}$. In Table 2 full description of the rules F_1 defining transitions of synapse s_1 from one state to another are presented.

Analogously one can obtain the responses of other clusters and specify the corresponding rules of the CA. It turns out that $F_2(P_0, P_{11}|P_{22}) = P_{11}$, $F_3(P_0, P_{11}|P_{22}) =$

Table 2

The rules $\overline{\psi_1} = F_1(\psi_1, \psi_4)$

ψ_4 \ ψ_1	P_0	P_{11}	P_{21}	P_{22}
P_0	P_0	P_0	P_{22}	P_0
P_{11}	P_{21}	P_0	P_{22}	P_0
P_{21}	P_0	P_0	P_{22}	P_0
P_{22}	P_{21}	P_0	P_{22}	P_0

P_{21}, and $F_4(P_0, P_{11}|P_{22}) = P_{21}$. By using these rules one can see that the CA has the only nontrivial attractor A that is the periodic trajectory (2000) $\to$ (3000) $\to$ (0020) $\to$ (0030) $\to$ (0102) $\to$ (0003) $\to$ (2000). On the Fig. 4 a part of the basin of A is shown. The periodic points in the attractor are marked by the grey color.

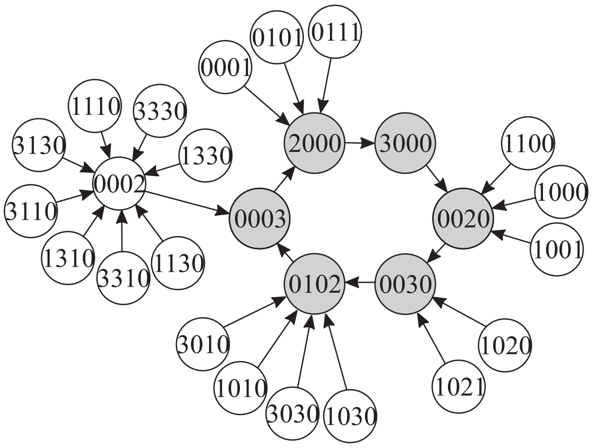

Fig. 4. A part of the basin of the periodic attractor in CA

Note that the attractor define the scenario of activation of synapses of the network and so firing pattern of neurons. From the symbolic sequence corresponding to A it is easy to obtain the following order of firings of neurons: $1 \to 3 \to 2 \to 4$ and so on. Indeed, a neuron fires the spikes when corresponding synaptic conductance overcomes some threshold value close to maximal conductance. In our case it corresponds to narrow time windows in the vicinity of transitions of synapses from the state P_{11} (or P_{22}) to P_0.

For the confirmation of the validity of these results we have performed the direct numerical study of the original system (1)–(5). It was obtained that the only sequential activity regime can be formed in the network. Results of numerics are presented on Fig. 5. Figures 5a, b illustrate the behavior of synaptic variables. One can see the process of the activation of synapses is not precisely periodic. It is related to the fact that the resonance con-

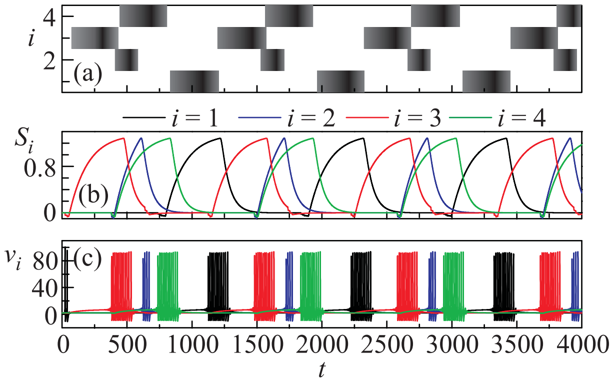

Fig. 5. Spatio-temporal diagram of synaptic variables s_i ($s_i > 0.01$ – black, $s_i < 0.01$ – white)(a), realizations for synapses (b) and neurons (c) for established regime in the network (1)–(5)

dition $T_2 = 2T_1$ is satisfied only with some (nonzero) accuracy. Nevertheless the spatial order of activation of synapses is exactly the same as for the CA, and also temporal intervals of activation are approximately the same as for the CA up to the scaling factor T_1. From Fig. 5c one can also obtain that order of firing of neurons coincides fully with that obtained by means of the synaptic CA approach.

We have shown that under some conditions the continuous sequential dynamics of excitatory neural network can be reduced to the dynamics of a CA. Note that it adequately describes "turn on/turn off" behavior of the synapses as well as neurones of the network. The reduction is based on the dynamics of synapses but not on the specific features of neurons. Indeed the internal dynamics of the neurons may be very complex and even chaotic. Thus the approach is applicable to a broad set of excitatory neural networks. Another advantage of our approach is that the numerical integration of the whole system of ODEs is not needed. In fact, the approach requires to study only the responses of an individual synapse onto actions of neighboring (in graph of connections) synapses through corresponding neurons.

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