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Modified Firing-Rate Model Reproduces Synchronization of a Neuronal Population Receiving Complex Input[1]

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Abstract—Synchronization plays important role in generation of brain activity patterns. Experimental data show that neurons demonstrate more reproducible activity for noise-like input than for constant current injection, and that effect can not be reproduced by standard oversimplified Firing-Rate (FR) models. The paper proposes a modification of FR model which reproduces these kinds of activity. The FR model approximates the firing rate of an infinite number of leaky integrate-and-fire neurons, considered as a population, and in contrary to conventional models it accounts for not only a steady-state firing regime but a fast rising excitation as well. Comparison of our simulations with the experimental data shows that the synchronous firing of the neuronal population strongly depends on the synchrony of neuronal states just before spiking. This effect is reproduced by the proposed FR model in contrary to the conventional FR models and is in agreement with the direct Monte-Carlo simulation of individual neurons.

Key words: integrate-and-fire neurons, firing-rate model, synchronization, noise.

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1. INTRODUCTION

Synchronization is an essential and important feature of the nervous system. When spiking patterns in the population of neurons correlate such state of firing activity is called synchronous and asynchronous in the opposite case. When the neurons in the population are strongly correlated, they can produce significant effect on the neurons receiving the synaptic input from this population. Therefore maintaining synchrony for a long time can play important role [1]. The brain shows different kinds of synchronous behavior and different mechanisms underlying such synchrony [2]. In this work we concentrate on one of the simplest mechanisms of synchronization when the group of cells receives the same stimuli. We construct a mathematical model of a neuronal population defined as a large set of neurons receiving the same input and differed by an individual noise. This noise reflects the difference of the cells by their intrinsic properties and inputs. Such statement of the problem is equivalent to the consideration of many stimulation trials for an one neuron. Hence the synchrony in such population relates to the reliability of a neuron's spiking activity as its ability to reproduce approximately the same spike train in response to the same stimulus when external or internal noise is present. Experimental and theoretical works show that the predictability of a neuronal behavior improves if the repeated stimulus resembles a noise [1, 3, 4]. On the other hand, the noise-like stimulus could be more realistic for a neuron, because the real cell in the nervous system receives a lot of uncorrelated impulses coming to dendritic tree and soma [1, 5].

The authors of the paper [3] experimentally studied the membrane potential of a neuron in reply to giving stimuli. When a current step was injected into the cell, the spike trains differ in different trials and the mismatches in spike timings grew in time. On the contrary, when the neuron receives a complex stimulus resembling a colored noise the mismatches are smaller and practically do not change. Thereby it has been shown that the complex profile of the stimulus can essentially increase the predictability or reliability of a neuron. It is supposed that such repeated stimulations of one cell can estimate a hypothetical plural registration in many neurons of one neuronal population, thus one can conclude that the complex stimuli can essentially synchronize the population of neurons.

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The models of individual neurons based on the Hodgkin-Huxley equations can reproduce the behavior of one cell in many details. However they are computationally expensive and do not suit to the purposes of large-scale simulations and mathematical analysis, for which neuronal population models are more preferable [5]. Among the population models, the probability density approach, or more specifically, the Refractory Density (RD) approach [5–8] provides the utmost precision whereas the Firing-Rate (FR) type models provide their simplicity. In the present paper we test the applicability of the modified FR model proposed as an implication of the RD approach in [6, 9] to describe the population of neurons. In the present paper we consider a population as a set of an infinite number of uncoupled similar Leaky Integrate-and-Fire (LIF) neurons, each receiving the complex noise-like stimuli and different input noise. Solution of the proposed model is compared with the direct Monte-Carlo simulation of a great number of individual neurons and with RD model.

2. FIRING-RATE MODEL

We consider the FR model of a population of LIF neurons and study its behavior under the influence of the step current and noise-like signal. The full description of the model construction and justification by the comparison with the much more detailed RD model can be found in the papers [6, 8].

The model of one LIF neuron consists of: (i) the equation for the membrane potential V, which includes the leak current $I_L = g_L(V - V_L)$ and external "synaptic" current I_a; and (ii) the threshold condition for the potential V. When the potential crosses the voltage threshold V^T, its value is updated to V_{reset} and each such event is called a spike:

$$C\frac{dV}{dt} = I_a - g_L(V - V_L), \tag{1}$$

$$\text{if } V > V^T, \text{ then } V = V_{reset}.$$

We consider the population under the following assumptions: (1) the spontaneous activity is taken into account in the form of a white noise; (2) the thresholds of all neurons have the same constant value; (3) all neurons receive common stimulus. We imply that in our case a set of trials of stimulation of one neuron is equivalent to the consideration of the neuron ensemble. The output signal of the population is the spike firing rate $\nu(t)$ which is the number of spikes from all neurons of the ensemble per number of neurons in a unit time interval, when the number of neurons tends to the infinity and the time interval tends to zero.

The equation for a single cell has the following form:

$$C\frac{dV}{dt} = I_a - g_L(V - V_L) + \sigma g_L \xi(t), \tag{2}$$

$$\text{if } V > V^T, \text{ then } V = V_{reset}.$$

Here $\xi(t)$ is the white Gaussian noise with unit amplitude and zero mean; σ is the noise amplitude.

The population is characterized by the mean sub-threshold voltage $U(t)$ governed by the equation:

$$C\frac{dU}{dt} = I_a - g_L(U - V_L). \tag{3}$$

The population firing rate $\nu(t)$ depends on the mean sub-threshold voltage $U(t)$ as follows:

$$\nu(t) = A(U) + B(U, dU/dt), \tag{4}$$

$$A(U) = \left[\tau_m\sqrt{\pi}\int\limits_{(v_{reset} - U)/\sigma}^{(V^T - U)/\sigma} e^{u^2}(1 + erf(u))du\right]^{-1}, \tag{5}$$

$$B(U, dU/dt) = \frac{1}{\sqrt{\pi}\sigma}\left[\frac{dU}{dt}\right]_+ \exp\left(-\frac{(V^T - U)^2}{\sigma^2}\right), \tag{6}$$

$$\tau_m = C/g_L, \tag{7}$$

$$[x]_+ = \{x \text{ } if \text{ } x > 0, \text{ } 0 \text{ } otherwise\}.$$

The component $A(U)$ estimates the firing rate in the stationary state when the potentials are widely distributed between V_{reset} and V^T (it was derived by Johannesma [10] and can be found in [5]); $B(U, dU/dt)$

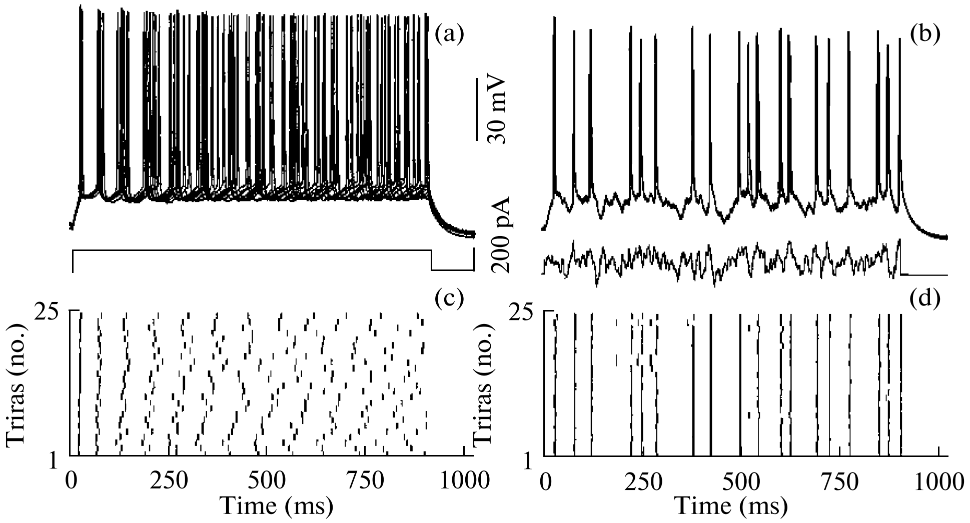

Fig. 1. (adapted from the work [3]). (a) 10 trials of the voltage recordings in one neuron, caused by the current step of 150 pA, (c) the spike rastrogram; (b) one potential recording from the same neuron receiving the "frozen" noise signal with the fixed parameters: $\mu_s = 150$ pA, $\sigma_s = 100$ pA, $\tau_s = 3$ ms, (d) the corresponding rastrogram.

estimates the rate in unsteady regime when the potentials correspond to the Gaussian distribution near V^T. Thus, Eqs. (3–7) describe the behavior of a population of neurons receiving the common "synaptic" stimulus.

Parameters: $C = 0.0007$ mF/cm^2, $V_{rest} = 0$ mV, $V_{reset} = 0$ mV, $V_L = 0$ mV, $S_{neuron} = 27.5 \times 10^{-5}$ cm^{-2}, $V^T = 11.6$ mV, $\sigma = 1$ mV, $g_L = 1$ mS/cm^2, $\tau_m = 15$ ms.

3. SIMULATIONS

3.1. Synchronization in the Model and Experiment

In this section we use the model of a population of uncoupled neurons to examine the effect of synchronization by complex external signal. Then we compare our numerical results with the experiment known from the literature [3]. We consider two stimulation protocols: first, when the neurons receive a constant current step and, second, when the stimulus represents a complex current profile constructed as a colored noise with fixed parameters.

Experiment. In the experiment [3] the membrane potential from one neuron was registered when the cell receives the input current. The spike trains vary from one trial to another (Fig. 1a, 1c). The mismatches of spike times grow in time after the beginning of stimulation. As mentioned above, in terms of neuronal population such multiple registrations in one cell are equivalent to the consideration of one hypothetical neuronal ensemble which consists of similar cells that differ by theirs input noise. The firing rate of this population as a response to current-step stimulation is gradually damping to the averaged level of steady-state activity, whereas the neurons demonstrate completely asynchronous behavior (Fig. 1c) because of the influence of the uncorrelated intrinsic noise.

On the contrary, when a neuron receives the complex signal like a colored noise (Fig. 1b, 1d) the spike time mismatches are much less and do not change in time. In this case we observe rather stable and predictable activity. The authors of the paper [1] explain this kind of synchronization by the effect of neuron phase shifting by every pulse of an input current. Because the neurons have similar susceptibility dependent on the phase between spikes, they reveal similar "preferences" of the input profile features. Hence when receiving similar complex input they come to the similarly evolving states and thus synchronize. It is to the contrary to the constant current stimulation case, when neurons obtain different states.

FR Model. The solutions of the Eq. (1) for different noise realizations are shown in the Fig. 2a, from which one can see qualitative agreement of spike times in the model and experiment (Fig. 1a). The population firing rate is shown on the Fig. 2c, where the first peak of activity corresponds to the first synchronous spikes and then the rate damps to the stationary level because of gradually growing desynchronization.

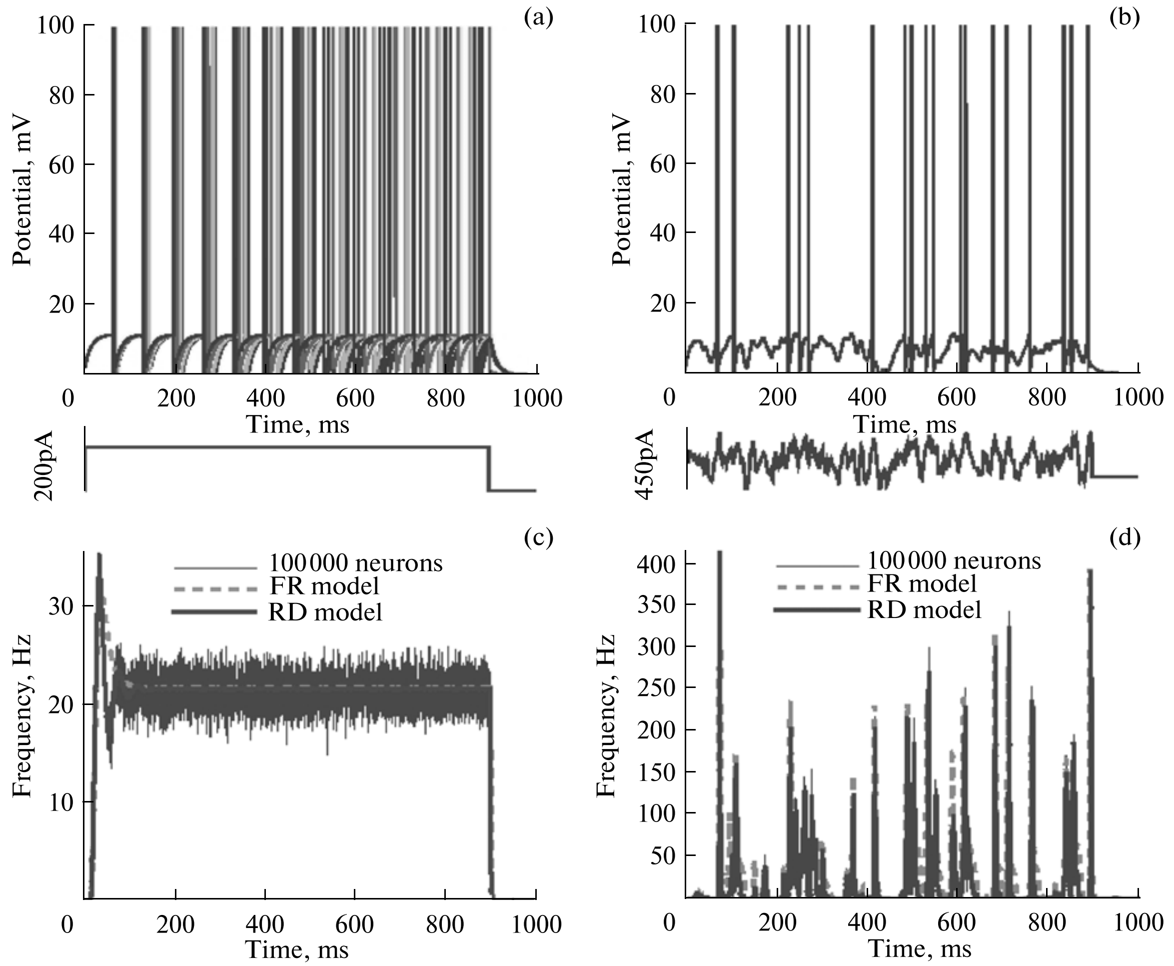

Fig. 2. (a) Seven voltage responses of LIF neurons receiving the step current stimulus and different noise realizations (compare to Fig. 1a); the amplitude of spikes is conventional. (b) one realization of the neuron's response to the noise-like current as in experiment (Fig. 1b). (c), (d) the firing rate of the population receiving the step- and noise-like stimuli correspondingly. The responses are obtained by the firing-rate (FR) model based on the Eq. (4), the direct simulation of 100000 individual leaky integrate-and-fire neurons (LIF), Eq. (2), and the refractory density (RD) model [7].

Figure 2b presents the solution for a LIF neuron receiving the noise-like stimulus as in the experiment. We can see that the spike trains in the model (Fig. 2b) and in the experiment (Fig. 1b) correlate. The solution for a population firing rate is shown in the Fig. 2d, where one can see the essential peaks during the whole period of stimulation which correspond to the moments of synchronization.

To check the accuracy of the FR model we compare it with the RD model [6–8] and direct simulation of 100000 LIF neurons, Eq. (2). The results are depicted in the Fig. 2. In the case of constant stimulus, the FR model well reproduces the first peak and the stationary state of activity, but gives low precision in the transient regime. For the complex stimuli, it reproduces the most part of the peaks of the firing rate. However, when the sharp peaks in the stimulus occur frequently, FR model fails to describe the second and following bursts of activity. It is limited to the consideration of excitation starting only in the quasi-steady state.

The synchronization is caused by the noise-like input which keeps the neurons in similar states of refractoriness, which actually could be characterized for each cell by the time elapsed since the previous spike [6–8]. As shown in [1], the group of neurons can be synchronized by the stimulus if, first, the cells receive a partially correlated input, second, the neurons have similar firing rates and, third, the cells possess the same susceptibility to the stimuli. In our case the population of LIF neurons satisfies these requirements. The peaks of synchronous activity seen in the Fig. 2d occur because of the complexity of the stimulus which only occasionally becomes supra-threshold. When the time between two supra-thresh-

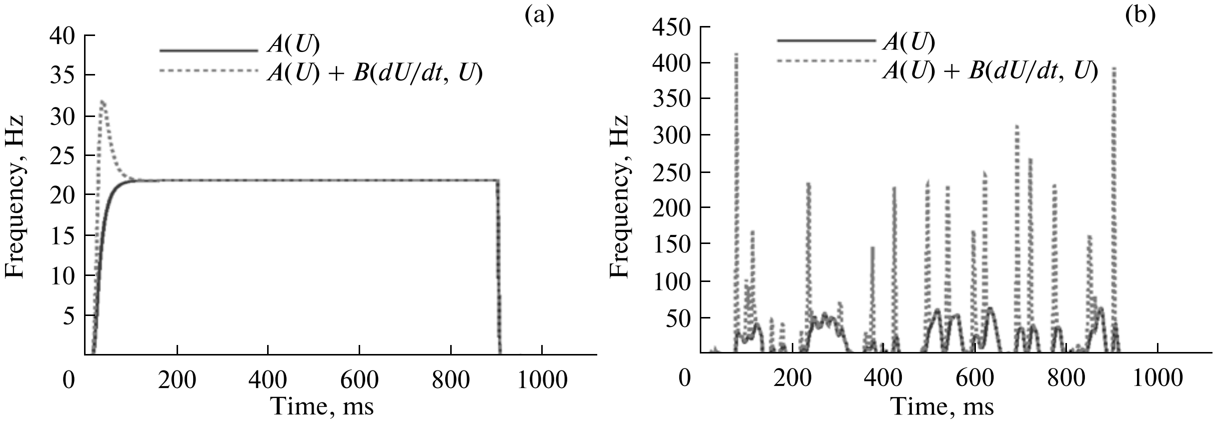

Fig. 3. (a) The full firing rate ν(t) (dotted line) for the case of current step of 150 pA and the rate when only the stationary term $A(U)$ is taken into account (solid line); (b) similar curves for ν(t) in the case of "frozen" colored noise-like stimulation as in Fig. 2d.

old peaks of the current is too short the neurons can't respond due to the fact that all together they are in the state of refractoriness.

Comparing model and experiment, we conclude that the quality of the tested model is rather good if taking into account that it neglects by the effects of many ionic currents that are present in real neurons.

3.2. Role of Non-stationary Term in the FR Model

The firing rate of the population calculated by: (i) the Eq. (4) $A(U)$ and $B(U, dU/dt)$ terms and (ii) Eq. (4) with $A(U)$ term only for the case of the constant and complex stimuli is shown in the Fig. 3. We see that if neglect by the non-stationary term $B(U, dU/dt)$ and account for only the stationary state term $A(U)$ as it is commonly done in the classical FR model, then in the case of constant stimulus the firing rate will be underestimated only for the initial part of the response. Whereas in the case of complex stimulus the result is inadequate during the whole period of stimulation. The reason is that when the neurons are synchronized by their refractory state their potentials are distributed according to the Gaussian distribution near V^T, whereas the formula for $A(U)$ implies the potentials to be widely distributed between V_{reset} and V^T. Most of widely used firing rate models use the same or similar assumptions. For example, the stationary dependence of the firing-rate on the input, Eq. (5), can be considered as one of the simplest FR models. Its application to quasi-stationary regimes is valid when neurons are dispersed by their voltage values, thus it is limited to weak changes of stimuli. Figure 3 demonstrates the limitation of these models. Thus we conclude that the full description of a population activity requires the usage of both stationary, Eq. (5), and non-stationary, Eq. (6), terms in the formula for the population firing rate.

4. CONCLUSIONS

—The populations of uncoupled neurons demonstrate the long-lasting synchronous behavior in the case of stimulation by the complex, colored noise-like stimuli, but the synchronization is impossible in the case of a constant stimulus.

—The proposed modified FR model can adequately simulate a population activity with the bursts of synchronization.

5. ACKNOWLEDGMENTS

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