ANALYSIS OF PULSED-SIGNAL TRANSMISSION IN A SYSTEM OF INTERACTING NEURAL OSCILLATORS WITH FREQUENCY-DEPENDENT CONNECTIONS

I. S. Prokin [1,2] * **and V. B. Kazantsev** [1,2]   UDC 534.1

In this paper, we study the influence of the frequency-dependent connection on the signal transmission in a system of two interacting pulsed neural oscillators. The system is a model of two neurons with synaptic connection having the synaptic-plasticity feature, i.e., synaptic-parameter variation as a function of the frequency characteristics of the signal. It is shown that plastic connection can control the signal-transmission efficiency depending on the pulse-repetition rate and ensures stable synchronization modes of the pulse trains with different ratios between the frequencies of the output and input pulses. Analytical estimates for the parameter ranges corresponding to generation of the pulse response at the detector neuron depending on the pulse-repetition rate at the oscillator neuron were obtained.

1. INTRODUCTION

The problem of the principles of coding, transmission, and conversion of information in the brain is among the key problems of modern science and attracts attention of researchers from various fields. It is assumed that signals in brain are transmitted by neural pulses with a duration of 1–2 ms and an amplitude of the order of 100 mV. Nerve cells (neurons) are united in the network by synaptic connections ensuring transmission of pulses and the pulse trains among the cells. Since synaptic connections are usually unidirectional, from the radiophysical viewpoint, the problem of synaptic transmission of signals is in fact the problem on the forced oscillations in the system of unidirectionally coupled pulse oscillators with complex connection type.

In the first approximation, neuron is a special generator of the nerve pulses in standard form (action potentials). In the absence of external actions, the cell is in the rest state. If the input signal exceeds a certain threshold (excitation threshold), then the response pulse or the pulse train are generated. It is assumed that information is coded in the pulse repetition frequency (frequency coding) and in the pulse-appearance phase with respect to a certain reference periodic signal (phase coding). In this aspect, the signal transformation during its passing through the synaptic connection shall be characterized by the frequency ratio between the input and output signals, as well as the phase shifts of the output signals with respect to the input signals. This, in principle, is the classical problem of the theory of nonlinear oscillations [1–4]. In particular, it is known that in such a system, various forced-oscillation regimes with the possibility of synchronization with different frequency ratios, the pulse-phase locking regimes, and quasiperiodic and chaotic oscillations are possible depending on the connection force [5]. For the neuron models with different degrees of biophysical particularization, such regimes are widely studied in [6–12].

* isprokin@gmail.com

763

The effects of the so-called synaptic plasticity have attracted much attention in recent decades during the study of the cell signaling in the brain [13–17]. In the simplest case, synaptic plasticity means that the connection force among neurons is not constant and can either increase (synaptic potentiation) or decrease (synaptic depression) depending on various conditions. In other words, the problem of signal transmission becomes more complicated because of the dynamic nature of interaction among the oscillators [18–20]. Short-term frequency-dependent plasticity for which the pulse transmission efficiency is a function of frequency of the pulse train transmitted through the synapse is one of the synaptic-plasticity types. The model of such plasticity is proposed in [21]. It describes the kinetics of the neurotransmitter (synaptic resource) with the help of the fourth-order dynamic system. The short-term plasticity depends only on the input pulses in time scales of the order of tens of milliseconds. Using this model, in particular, we managed to describe the formation mechanism of the population discharges in the form of the pulse packets in neural networks [21, 22]. Other models of short-term plasticity with different degrees of biophysical particularization were proposed in various neurodynamical aspects [23]. Usually based on the description of experimental phenomena, the plasticity models actually remain unstudied from the viewpoint of nonlinear dynamics and transformation of the pulse excitations among the neurons via the plastic synaptic connections.

In this work, we analyze the effect of the transmission of pulsed signals in a model of two unidirectionally connected neural oscillators with a frequency-dependent connection. Analytical estimates of the conditions of the signal transmission through such a connection, forced-oscillation appearance, and their synchronization are obtained. It is shown that the introduction of plasticity allows one to significantly change the dynamic range of the pulsed signals and ensure stable regimes of the pulsed transmission with different ratios among the input and output signals.

2. MODEL

Let us consider the simplest model of signal transmission through a frequency-dependent connection, which consists of transmitter neuron (presynaptic neuron), communication channel (synaptic connection), and receiver neuron (postsynaptic neuron) (see Fig. 1). The own dynamics of the neurons is described by the "threshold integrator" [24–27]:

$$\tau \frac{dV}{dt} = -V + V_{\text{syn}} + V_{\text{b}}, \qquad V_{\text{reset}} \leq V(t) \leq V_{\text{thr}}, \qquad t \neq t_i + \xi;$$

$$V(t_i) = V_{\text{thr}}, \qquad V(t_i + \xi) = V_{\text{reset}}, \qquad 0 < \xi < \tau_{\text{ref}}, \tag{1}$$
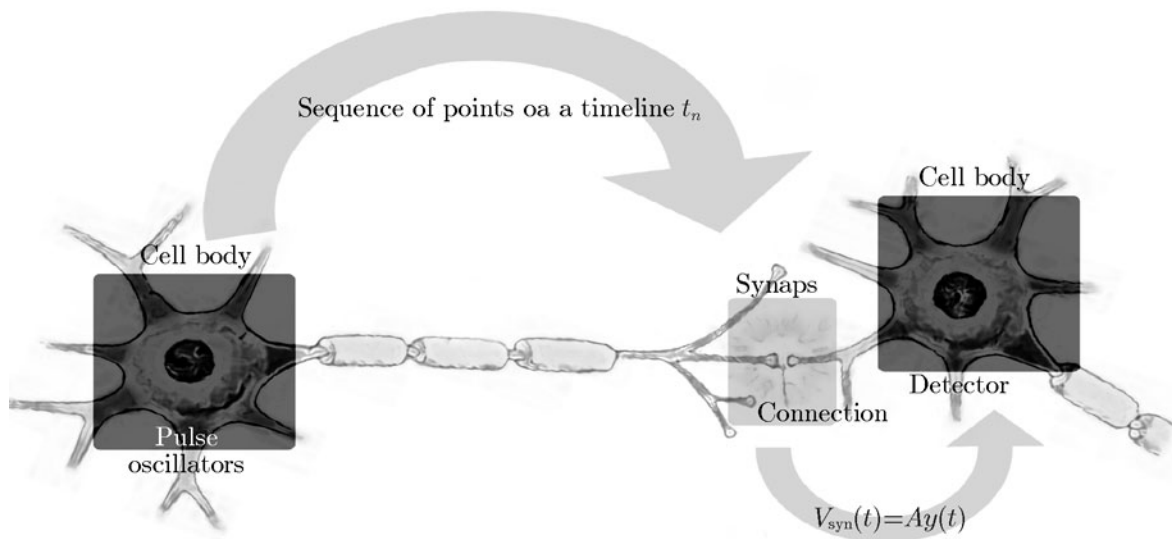

Fig. 1.Diagram of the pulsed transmission of signals through plastic synaptic connection.

Fig. 2. Dynamics of a neuron for $V_{\mathrm{syn}} = 0$. The dashed curve shows the depolarization-parameter variation $V_{\mathrm{b}}(t)$. The solid curve indicates the corresponding variation in $V(t)$. The arrows show the spike moments. For $V_{\mathrm{b}} \leq V_{\mathrm{thr}} = 15$ mV, we observe the membrane-potential relaxation to the equilibrium state $V = V_{\mathrm{b}}$ and the neuron is in the excitory regime. For $V_{\mathrm{b}} \geq V_{\mathrm{thr}}$, the neuron is in the self-oscillatory regime with frequency determined by the value of V_{b}.
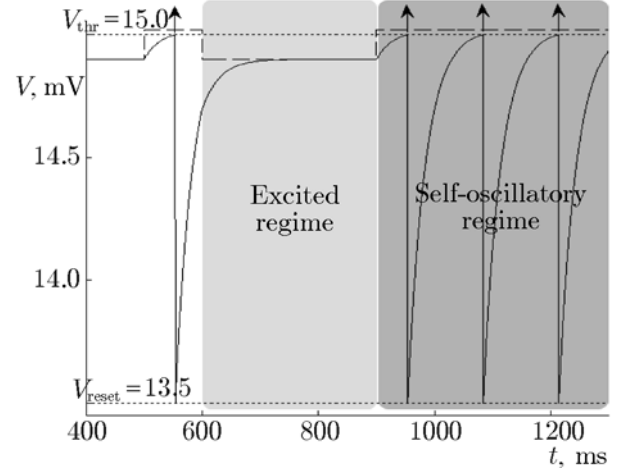
where V is the current value of the neuron membrane potential, V_{syn} is the product of synaptic current and the input resistance of the neuron, V_{b} is the depolarization parameter or the product of the input resistance of the neuron and the background (applied) current ensured by external actions, τ is the characteristic relaxation time of the membrane potential, τ_{ref} is the refractory time during which neuron does not respond to external actions, V_{thr} is the threshold level, V_{reset} is the reset level, t is the time, and t_i are the times corresponding to the threshold reaching by the membrane potential.

The system dynamics given in Eq. (1) is relatively simple. Each time when V reaches the threshold level V_{thr}, reset to the level V_{reset} occurs. After that, during the refractory period, the potential V is maintained equal to V_{reset}, and then exponentially evolves to the equilibrium state of the first-order linear differential equation from Eq. (1). The threshold reaching by the membrane potential is identified with the pulse generation (see Fig. 2). In the absence of the synaptic signals at the input ($V_{\mathrm{syn}} = 0$), own dynamics of the neural oscillator given in Eq. (1) is characterized by two main regimes, i.e., the excitatory regime (stable equilibrium state in the straight line described by the first Eq. (1)) for $V_{\mathrm{b}} \leq V_{\mathrm{thr}}$ and the self-oscillatory regime (stable periodic motion which emerges due to "matching" of the solutions of Eqs. (1)) for $V_{\mathrm{b}} > V_{\mathrm{thr}}$.

We assume that the refractoriness time τ_{ref} is small compared with the characteristic period of the input-pulse repetition, i.e., $\tau_{\mathrm{ref}} \ll \Delta t$. In this case, we easily write the analytic solution for $V_{\mathrm{reset}} \leq V(t) \leq V_{\mathrm{thr}}$:

$$V(t) = G[V(0), t] = [V(0) - V_{\mathrm{b}}] \exp(-t/\tau) + V_{\mathrm{b}}. \tag{2}$$

In numerical calculations, we fix for definiteness the following values of the parameters: $\tau = 30$ ms, $V_{\mathrm{reset}} = 13.3$ mV, $V_{\mathrm{thr}} = 15$ mV, and $\tau = 30$ ms. We also assume that the presynaptic oscillator is in the self-oscillatory regime, while the postsynaptic oscillator is in the excitory state.

Let us consider the model of synaptic connection [19]

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \frac{z}{\tau_{\mathrm{rec}}} - \sum_{i=1}^{N} ux\delta(t - t_i); \qquad \frac{\mathrm{d}y}{\mathrm{d}t} = -\frac{y}{\tau_1} + \sum_{i=1}^{N} ux\delta(t - t_i);$$

$$\frac{\mathrm{d}z}{\mathrm{d}t} = \frac{y}{\tau_1} - \frac{z}{\tau_{\mathrm{rec}}}; \qquad \frac{\mathrm{d}u}{\mathrm{d}t} = -\frac{u}{\tau_{\mathrm{fac}}} + \sum_{i=1}^{N} U(1 - u)\delta(t - t_i). \tag{3}$$

Here, t_i is the time of appearance of the ith presynaptic pulse, N is the total number of pulses, x, y, and z are the variables describing the fractions of the synaptic resources in the restored, active, and inactive states, respectively, u is the variable responsible for the synaptic depression or increase, U is the dynamics constant, τ_1, τ_{rec}, and τ_{fac} are some characteristic times of the synapse dynamics, and $\delta(x)$ is the Dirac delta function. In this work, the connection is assumed to be exciting and the synapse parameters have the following values: $U = 0.5$, $\tau_{\mathrm{rec}} = 800$ ms, $\tau_{\mathrm{fac}} = 0$ ms, and $\tau_1 = 3$ ms [21].

765

Interaction between the oscillators takes place via the variable y

$$V_{\text{syn}} = Ay(t), \tag{4}$$

where A is the weight coefficient of synapse with the voltage dimension. The weighted variable y defines the synaptic-current contribution to the dynamics of the membrane potential of the postsynaptic neuron. Therefore, each presynaptic pulse results in a sharp variation in the variable y after which y drops to zero for a relatively short time. The synaptic depression effect (decreasing effective force of the connection) manifests itself in that the value of variation in the variable y decreases with each subsequent input pulse, if the interval between the presynaptic pulses is not large enough for the synapse to recover to the initial state. Therefore, connection force decreases stronger and faster with increasing presynaptic-pulse frequency. In this case, the stationary amplitude of the jumps for periodic input action is determined by the nonlinear function of the input-action frequency.

3. SIGNAL TRANSMISSION

Let us study the main signal-transmission mechanisms in the system of equations (1)–(4). In the self-oscillatory mode, the presynaptic oscillator generates an infinite train of the input pulses transmitted to the postsynaptic neuron through the communication channel. We obtain the conditions for appearance of the regime of regular responses in the case of setting of integer relationships between the frequencies of the input and output pulse trains.

3.1. The case of fixed connection

Let us first consider the case of fixed connection without plasticity. To this end, we make the following substitution in the equation of postsynaptic neuron:

$$V_{\text{syn}} = Ay(t) = M[\text{mV} \cdot \text{ms}] \sum_{i=1}^{N} \delta(t - t_i),$$

where M is a certain constant. This substitution divides the solution for $V(t)$ into the interpulse intervals in which a continuous and smooth solution exists. Discontinuities arise only at the pulse-appearance times. Note that in this case, the jump value of the membrane potential of a postsynaptic neuron is constant and equal to M/τ with each presynaptic pulse. This constant difference is the matching condition for the solutions before and after the presynaptic pulse.

We choose the constant M so that an increase in the variable V under the action of a single input pulse in the system with plastic synapse and the initial conditions $V(0) = V_{\text{b}}$, $x(0) = 1$, $y(0) = 0$, $z(0) = 0$, and $u(0) = 0$ and in the system with non-plastic synapse and the initial conditions $V(0) = V_{\text{b}}$ are identical:

$$AU\frac{\tau_1}{\tau_1 - \tau}\left[\left(\frac{\tau}{\tau_1}\right)^{-\tau/(\tau-\tau_1)} - \left(\frac{\tau}{\tau_1}\right)^{-\tau_1/(\tau-\tau_1)}\right] = \frac{M}{\tau}.$$

Hence, we obtain

$$A = M\left/\left\{U\frac{\tau\tau_1}{\tau_1 - \tau}\left[\left(\frac{\tau}{\tau_1}\right)^{-\tau/(\tau-\tau_1)} - \left(\frac{\tau}{\tau_1}\right)^{-\tau_1/(\tau-\tau_1)}\right]\right\}\right. . \tag{5}$$

The periodic input action results in the point map for the membrane potential of the postsynaptic neuron (see Fig. 3):
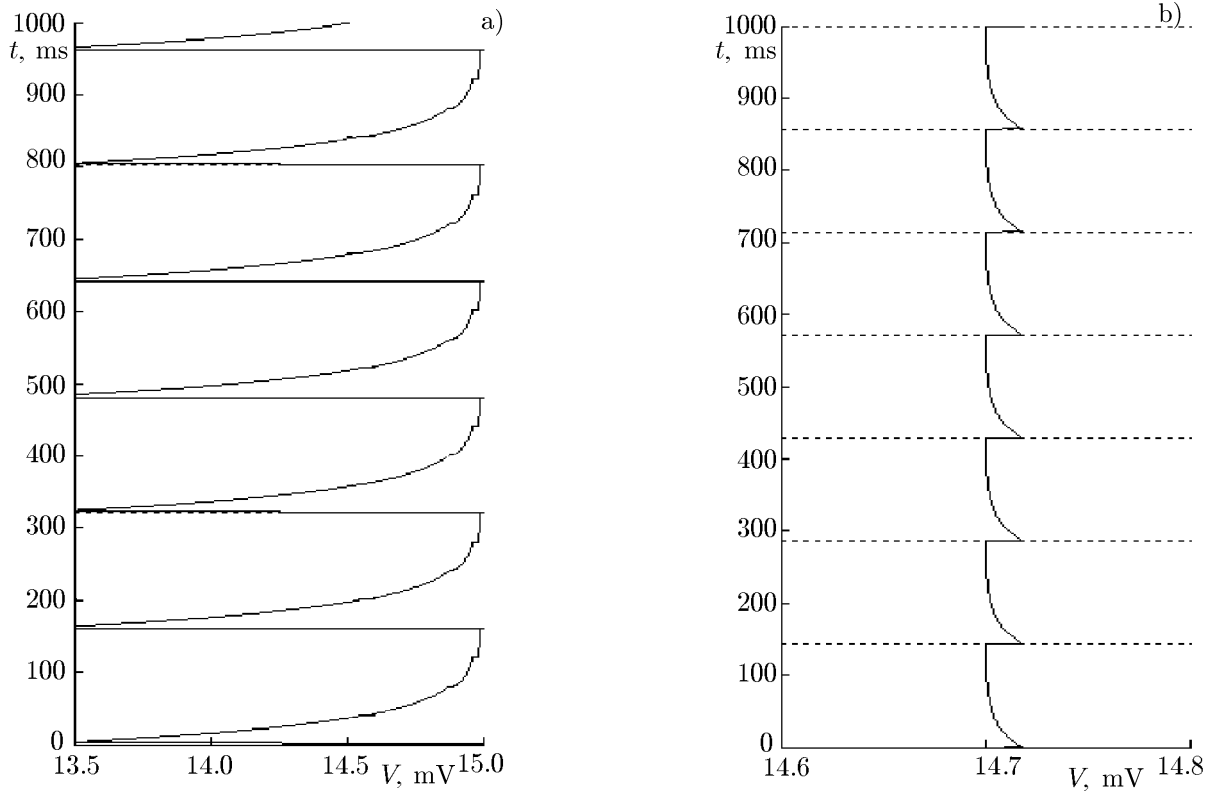
$$V_{n+1}(t') = G[V_{n+1}(0), t'],$$

Fig. 3. Expanded phase space of a neuron: the regime of the regular responses (*a*) and the regime of the pre-threshold oscillations (*b*). The solid curve shows the phase trajectory of the membrane potential. The dashed curve shows the Poincaré-secant location (for the secant shift $t' = 0$).

$$V_{n+1}(0) = \begin{cases} f[V_n(0)], & V_{\text{reset}} \leq f[V_n(0)] < V_{\text{thr}}; \\ V_{\text{reset}}, & f[V_n(0)] \geq V_{\text{thr}}. \end{cases} \tag{6}$$

Here,

$$f(x) = M/\tau + G(x, \Delta t), \tag{7}$$

the function G is the solution of the system of equations (1) in the interpulse interval if $V_{\text{reset}} \leq V \leq V_{\text{thr}}$, Δt is the interpulse interval, and $V_i(t')$ is the solution for the membrane potential in the interval between the ith and the $(i+1)$th pulses of the presynaptic oscillator, where the time t' is assumed to be reckoned from the ith pulse (i.e., determines the Poincaré-secant shift).

Let us consider the dynamics of this map in the case where the input-action frequency exceeds the output-action frequency by a factor of m (see Fig. 4*a*). The immobile points of the map in Eqs. (6) and (7) of the order m are determined by the condition $V_{n+m}(t') = V_n(t')$. They correspond to the regular periodic solutions with the m-tuple ratio of the frequencies of the input and output signals (one period of typical realization is shown in Fig. 4*a*). Such regimes are divided into two classes, i.e., the regime of regular responses (periodic motion has the fixed limits with respect to V ($V_{\text{reset}} \leq V \leq V_{\text{thr}}$) and the amplitude $V_{\text{thr}} - V_{\text{reset}}$, see Fig. 3*a*) and the regime of the subthreshold oscillations (in this case, m is always equal to ∞, which corresponds to the absence of response, while periodic motion has an amplitude of order M/τ, see Fig. 3*b*).

Let us discuss the regime of regular responses. Its realization condition can be written in the form

$$V_{\text{b}} + \frac{M}{\tau \left[1 - \exp(-\Delta t/\tau)\right]} = \bar{V} > V_{\text{thr}}, \tag{8}$$

where $\bar{V}$ is the immobile point of the map $x_{n+1} = f(x_n)$ determined by the function in Eq. (7). It exists for
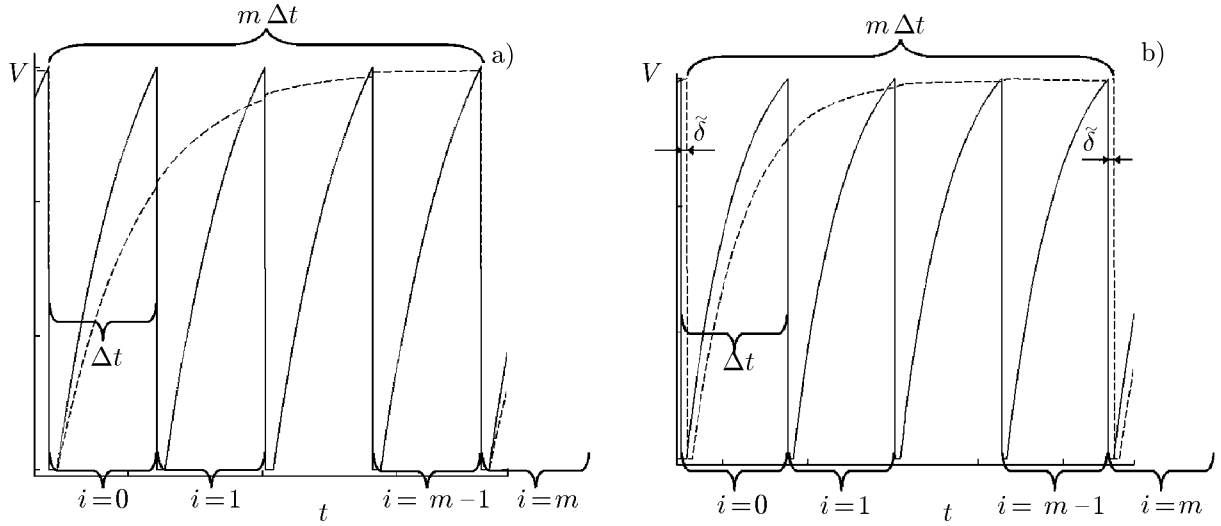
Fig. 4. Comments to derivation of the condition of regular responses for non-plastic (*a*) and plastic (*b*) cases. The solid curve shows the membrane potential of the presynaptic neuron which is used as an oscillator and the dashed curve shows the membrane potential of the postsynaptic neuron.

all finite Δt and τ and is always stable since its multiplicator is equal to $\exp(-\Delta t/\tau) < 1$ and in the case $\bar{V} \leq V_{\mathrm{thr}}$ it corresponds to the immobile map point in Eqs. (6) and (7).

In this case, the frequency ratio m is determined by the minimum number of iterations $x_{n+1} = f(x_n)$, which is required to map the point V_{reset} to the point above the oscillation threshold. In other words, it is the minimum number of iterations required to enable the map in Eqs. (6) and (7) for $t' = 0$

$$V_{n+1}(0) = \begin{cases} f[V_n(0)], & V_{\mathrm{reset}} \leq f[V_n(0)] < V_{\mathrm{thr}}; \\ V_{\mathrm{reset}}, & f[V_n(0)] \geq V_{\mathrm{thr}}, \end{cases}$$

to transfer the point V_{reset} into itself.

Using the point map in Eqs. (6) and (7) jointly with the condition of the regular responses in Eq. (8) and the condition in Eq. (5) of the connection between the constants M and A, we obtain the following relationship:

$$A = \left\{ U \frac{\tau \tau_1}{\tau_1 - \tau} \left[\left(\frac{\tau}{\tau_1}\right)^{-\tau/(\tau-\tau_1)} - \left(\frac{\tau}{\tau_1}\right)^{-\tau_1/(\tau-\tau_1)} \right] \right\}^{-1}$$
$$\times \tau \left[1 - \exp(-\Delta t/\tau)\right] \left[\frac{V_{\mathrm{thr}} - \exp(-m\,\Delta t/\tau)V_{\mathrm{reset}}}{1 - \exp(-m\,\Delta t/\tau)} - V_{\mathrm{b}} \right], \quad (9)$$

where Δt is the period of the input-pulse repetition $\Delta t = t_{i+1} - t_i$.

The condition given in Eq. (9) for different m allows one to obtain the regions corresponding to different dynamic regimes of the response (see Fig. 5*a*) on the plane of parameters (A, f). In Fig. 5*a*, the region bounded by the curves obtained for m and $m - 1$ corresponds to the regime with an m-tuple response. The curve constructed for a fixed m corresponds to the maximum repetition frequency of input pulses $f = 1/\Delta t$ for the given two other parameters for which realization of a regime with response to the mth pulse is possible. The membrane potential of the postsynaptic neuron has no time to approach the oscillation threshold by a significant value due only to its own dynamics and exposure to the action of the previous $m - 1$ presynaptic pulses with increasing stimulation frequency and crossing this boundary by the arrival time of the mth pulse. The potential approaches the threshold rather closely owing to the mth presynaptic pulse and subsequent autonomous dynamics so that it is beyond the threshold with the $(m + 1)$th presynaptic pulse, and the postsynaptic neuron generates the output pulse.
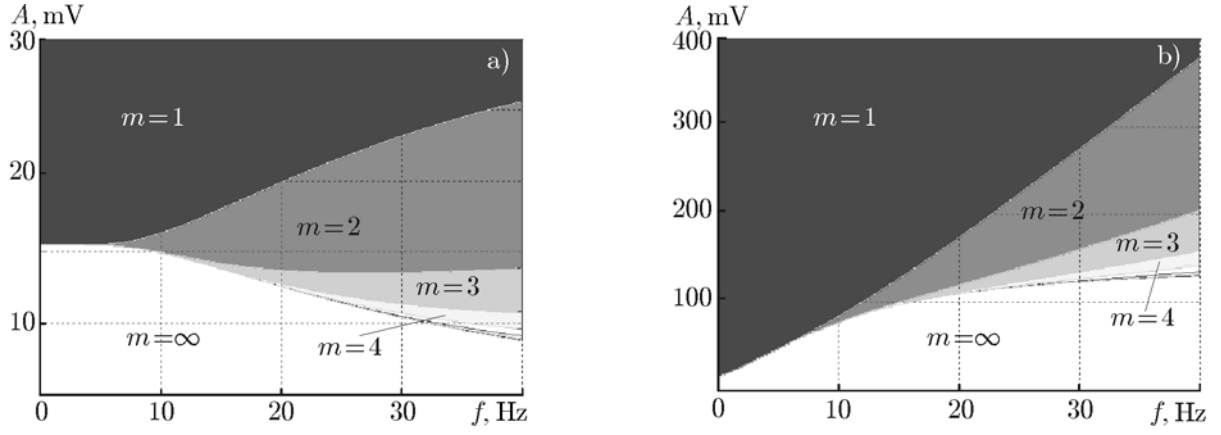
Fig. 5. The regions of the regular responses on the plane (A, f) for the value $V_{\mathrm{b}} = 14.4$ mV for the nonplastic (*a*) and plastic (*b*) synapses.

All other regions correspond to the no-response regime. Numerical experiment shows the validity of the obtained analytical estimate (9). When crossing the boundary between the regions m and $m-1$ on the plane of parameters (A, f), the dynamic-mode variation occurs in a jump.

3.2. The case of plastic connection

Let us consider the plastic synaptic connection given in Eq. (3). In this case, discontinuities during the presynaptic-pulse arrival times occur in the synaptic variable y. In this case, the time dependence of the membrane potential has jumps in the first derivative due to integration of the equation with $V_{\mathrm{syn}} = Ay$ on the right-hand side.

By analogy with the case of the fixed connection, it is easily shown that the input periodic pulsed signal generates the four-dimensional point map for the synaptic resources immediately after the nth and $(n+1)$th input pulses, which has the form

$$u_{n+1} = U + u_n(1-U)\exp(-\Delta t/\tau_{\mathrm{fac}}),$$

$$y_{n+1} = y_n\exp(-\Delta t/\tau_1) + [U + u_n(1-U)\exp(-\Delta t/\tau_{\mathrm{fac}})]$$
$$\times \left[C_1 - z_n\exp(-\Delta t/\tau_{\mathrm{rec}}) - \frac{y_n\tau_{\mathrm{rec}}}{\tau_{\mathrm{rec}} - \tau_1}\exp(-\Delta t/\tau_{\mathrm{rec}}) + \frac{y_n\tau_1}{\tau_{\mathrm{rec}} - \tau_1}\exp(-\Delta t/\tau_1)\right],$$

$$z_{n+1} = z_n\exp(-\Delta t/\tau_{\mathrm{rec}}) + \frac{y_n\tau_{\mathrm{rec}}}{\tau_{\mathrm{rec}} - \tau_1}\left[\exp(-\Delta t/\tau_{\mathrm{rec}}) - \exp(-\Delta t/\tau_1)\right],$$

$$x_{n+1} = C_1 - y_{n+1} - z_{n+1}, \tag{10}$$

where $C_1 = x(t) + y(t) + z(t) = x(0) + y(0) + z(0)$ determines the normalization condition.

The solution-matching condition for the membrane potential of the postsynaptic neuron before and after the $(n+1)$th presynaptic pulse is specified by the continuity condition

$$V_{n+1}(0) = V_n(\Delta t), \tag{11}$$

where $V_i(t')$ is the solution for the membrane potential in the interval between the ith and $(i+1)$th input pulses, Δt is the input-pulse repetition period, and t' is the time reckoned from the ith input pulse.

Let us consider the condition of appearance of regular responses when the ratio between the input and output frequencies is equal to m. Let us use $\tilde{\delta}$ to denote the response-pulse delay time with respect to the pulse of the presynaptic oscillator. This is the time during which the membrane potential of the postsynaptic neuron reaches the threshold level after the arrival of the mth presynaptic pulse (see Fig. 4*b*).
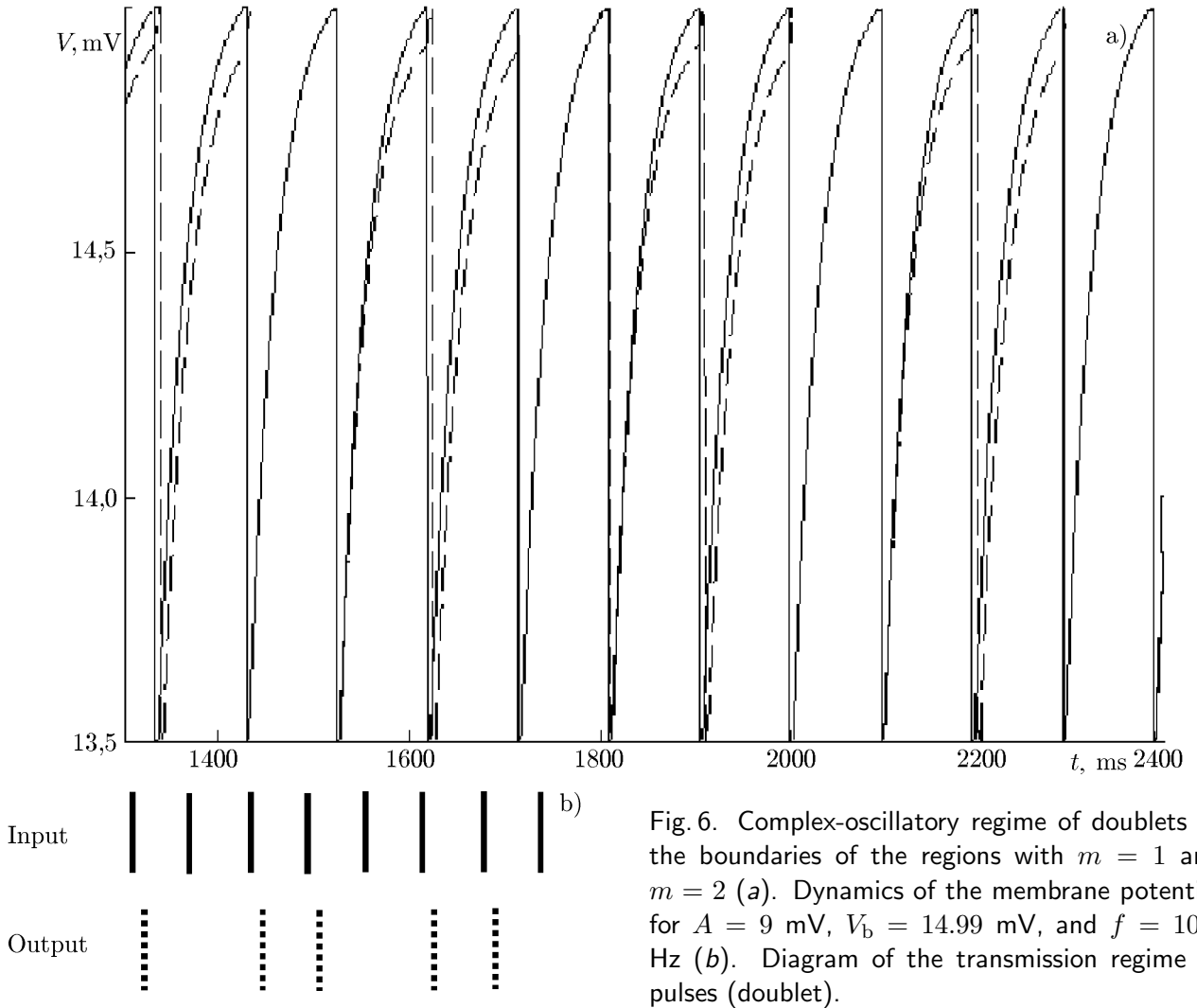
Fig. 6. Complex-oscillatory regime of doublets at the boundaries of the regions with $m = 1$ and $m = 2$ (*a*). Dynamics of the membrane potential for $A = 9$ mV, $V_{\mathrm{b}} = 14.99$ mV, and $f = 10.5$ Hz (*b*). Diagram of the transmission regime of pulses (doublet).

The existence condition of such a response can be written as

$$V_0(t' = \tilde{\delta} + 0) = V_{\mathrm{reset}}, \qquad V_m(t' = \tilde{\delta}) = V_{\mathrm{thr}}. \tag{12}$$

Using Eqs. (10) and (11) and assuming $\tilde{\delta} \ll \tau$, $\tilde{\delta} \ll \Delta t$, Eq. (12) can be rewritten in the form (for $m \geq 1$)

$$A = \left[\frac{V_{\mathrm{thr}} - \exp(-m\,\Delta t/\tau)V_{\mathrm{reset}}}{1 - \exp(-m\,\Delta t/\tau)} - V_{\mathrm{b}} \right] \bigg/ \left\{ \left[\frac{\exp(-\Delta t/\tau_1) - 1}{1 - \exp(-\Delta t/\tau)} + \exp(-\tilde{\delta}/\tau_1) \right] \bar{y}(\Delta t) \frac{\tau_1}{\tau_1 - \tau} \right\}, \tag{13}$$

where $\bar{y}(\Delta t)$ is the y coordinate of the immobile map point (10) for the given Δt. Note that the delay value $\tilde{\delta}$ in the numerical experiment was at most 3 ms. Ignoring the frequency dependence of this parameter and assuming it to be equal to 3 ms, we obtain from Eq. (13) the approximate division of the plane of parameters (A, f) into the regions of regular responses and the no-response region (see Fig. 5*b*). In this case, for the parameter values in the neighborhood of the regions of regular responses, the number of the response pulses alternates between m and $m - 1$. The oscillation period for such responses becomes equal to $[(m - 1)\,p + mq]\,\Delta t$, where p and q are the natural numbers. Figure 6 shows an example of transformation of the input periodic pulsed signal to the periodic train of the doublets of the response pulses with the period $3\,\Delta t$ near the boundary $m = 2$ and $m = 1$. Let us note that other values of p and q, are possible

in the vicinity of this boundary, which can correspond to the regime of the triplets and packets of pulses of a higher order. It is also noteworthy that the response mode in the form of the pulse packets is realized only in the case of plastic connection due to the appearance of an additional time scale in the synaptic-resource dynamics. In the analytical estimates given in Eqs. (10)–(13), this scale is determined by the delay time $\tilde{\delta}$, which actually corresponds to the delay of the signal transmission through the synapse. At the transition boundaries between the neighboring regions of the regular responses, the time difference of the threshold reaching for the neighboring pulses of the input train becomes comparable with $\tilde{\delta}$, which leads to the appearance of complex oscillatory dynamics.

4. CONCLUSIONS

In this work, we have studied the mechanisms of the pulsed-signal transmission in the simplest model of a neural system, consisting of a presynaptic oscillator, a frequency-dependent communication channel (synapse), and a postsynaptic oscillator, i.e., a pulsed-signal detector. The process of transmission of periodic pulsed trains can be described by nonlinear point maps whose immobile points determine periodic sequences of the response with different ratio of the numbers of the output and input pulses (frequency locking). It is found that different variants of such response are realized in the system depending on the coupling-coefficient value.

Unlike the case of fixed connection, in the case of allowance for the plasticity effect, an increase in the input-signal frequency leads to an increase in the threshold coupling coefficient which is required for the response generation (see Fig. 5). This in fact means that the plastic synapse can adjust the cell sensitivity to high-frequency impacts suppressing the response efficiency upon the frequency increase (synaptic depression).

Introducing the plastic communication channel, we add an additional time scale to the system, which leads to the possibility of realization of the complex pulsed responses at the transition boundaries among various response regimes.

REFERENCES

1. A. A. Andronov, A. A. Vitt, and S. E. Khaikin, *Theory of Oscillations* [in Russian] (1959).

2. M. I. Rabinovich and D. I. Trubetskov, *Introduction into the Theory of Oscillations and Waves* [in Russian], Nauka, Moscow (1984).

3. N. V. Butenin, Yu. I. Neymark, and N. A. Fufayev, *Introduction into the Theory of Nonlinear Oscillations* [in Russian], Nauka, Moscow (1987).

4. A. P. Kuznetsov, S. P. Kuznetsov, and N. M. Ryskin, *Nonlinear Oscillations (Ser. Modern Theor. Oscil. Waves)* [in Russian], Fizmatlit, Moscow (2006).

5. A. Pikovsky, M. Rosenblum, and J. Kurths, *Synchronization. A Universal Concept in Nonlinear Sciences*, Cambridge Univ. Press, New York (2001).

6. L. Glass and M. C. Mackey, *From Clocks to Chaos. The Rythms of Life*, Princeton Univ. Press, Princeton (1988).

7. N. Kopell and G. B. Ermentrout, *Handbook of Dynamical Systems II: Toward Applications*, Elsevier, Amsterdam (2002).

8. J. K. Lin, K. Pawelzik, U. Ernst, and T. J. Sejnowski, *Network: Comput. Neural Syst.*, **9**, 333 (1998).

9. L. Glass and M. C. Mackey, *J. Math. Biol.*, **7**, 339 (1979).

10. M. C. Mackey and L. Glass, *Science*, **197**, 287 (1977).

11. F. Zou and J. A. Nossek, *IEEE Trans. Circuits Syst. I. Fundam. Theory Appl.*, **40**, 166 (1993).

12. M. Kawato and R. Suzuki, *J. Theor. Biol.*, **86**, No. 3, 547 (1980).

13. A. Morrison, M. Diesmann, and W. Gerstner, *Biol. Cybern.*, **98**, 459 (2008).

14. D. O. Hebb, *The Organization of Behavior: a Neuropsychological Theory*, Wiley, New York (1949).

15. M. V. Tsodyks and H. Markram, *Proc. Nat. Acad. Sci. USA*, *bf 94*, 719 (1997).

16. H. Markram, Y. Wang, and M. Tsodyks, *Proc. Nat. Acad. Sci. USA*, **95**, 5323 (1998).

17. P. Dayan and L. F. Abbott, em Theoretical Neuroscience, MIT Press, Cambridge (2001).

18. A. P. Kuznetsov and V. I. Paksyutov, *Izv. Vyssh. Uchebn. Zaved. Prikl. Nelin. Din.,* **11**, No. 6, 48 (2003).

19. A. P. Kuznetsov and V. I. Paksyutov, *Izv. Vyssh. Uchebn. Zaved. Prikl. Nelin. Din.,* **13**, No. 4, 3 (2005).

20. A. P. Kuznetsov, V. I. Paksyutov, and Yu. P. Roman, *Izv. Vyssh. Uchebn. Zaved. Prikl. Nelin. Din.,* **15**, No. 4, 3 (2007).

21. M. Tsodyks, A. Uziel, and H. Markram, *J. Neuroscience*, **20**, RC1 (2000).

22. M. Chiappalone, M. Bove, A. Vato, et al., *Brain Res.*, **1093**, 41 (2006).

23. L. F. Abbott, J. A. Varela, K. Sen, and S. B. Nelson, *Science*, **275**, 220 (1997).

24. L. Lapicque, *J. Physiol. Pathol. Gen.*, **9**, 620 (1907).

25. H. C. Tuckwell, *Introduction to Theoretical Neurobiology*, Cambridge University Press, UK (1988).

26. W. Gerstner and W. Kistler, *Spiking Neuron Models: Single Neurons, Populations, Plasticity*, Cambridge University Press (2002).

27. E. M. Izhikevich, *Dynamical Systems in Neuroscience: the Geometry of Excitability and Bursting*, MIT Press (2007).