

Relaxation Oscillations in a System of Two Pulsed Synaptically Coupled Neurons

S. D. Glyzin^{a, b, *}, A. Yu. Kolesov^{a, **}, and E. A. Marushkina^{a, ***}

^aDemidov Yaroslavl State University, Yaroslavl, 150003 Russia

^bScientific Center in Chernogolovka, Russian Academy of Sciences, Chernogolovka, Moscow oblast, 142432 Russia

*e-mail: glyzin@uniyar.ac.ru

**e-mail: kolesov@uniyar.ac.ru

***e-mail: marushkina-ea@yandex.ru

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Abstract—In this paper, we consider a mathematical model of synaptic interaction between two pulse neuron elements. Each of the neurons is modeled by a singularly perturbed difference-differential equation with delay. Coupling is assumed to be at the threshold with the time delay being taken into account. The problems of existence and stability of relaxation periodic movements for the systems derived are considered. It turns out that the critical parameter is the ratio between the delay caused by internal factors in the single-neuron model and the delay in the coupling link between the oscillators. The existence and stability of a uniform cycle for the problem are proved in the case where the delay in the link is less than the period of a single oscillator, which depends on the internal delay. As the delay grows, the in-phase regime becomes more complex; specifically, it is shown that, by choosing an adequate delay, we can obtain more complex relaxation oscillations and, during a period, the system can exhibit more than one high-amplitude splash. This means that the bursting effect can appear in a system of two synaptically coupled neuron-type oscillators due to the delay in the coupling link.

Keywords: neural models, differential-difference equations, relaxation oscillations, asymptotic behavior, stability, synaptic coupling

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1. FORMULATION OF THE PROBLEM

In this paper, we consider a new approach to chemical synapse modeling that was formulated in [1]. In terms of asymptotic analysis methods, this work continues the studies initiated in [2–6] and devoted to relaxation self-oscillations in neural systems with delay.

Our approach is based on a modification of the idea of fast threshold modulation (FTM). This phenomenon, which was described for the first time in [7, 8], is a specific way of coupling dynamic systems. It is characterized by abrupt changes in the right-hand sides of the corresponding differential equations when certain control variables exceed their thresholds. In neural systems, the FTM is generally implemented as follows.

Suppose that the voltage $u = u(t)$ and the current intensity $v = v(t)$ in a single neural cell satisfy the system of differential equations

$$\varepsilon \dot{u} = f(u, v), \quad \dot{v} = g(u, v). \quad (1)$$

Here, $\varepsilon > 0$ is a small parameter and the standard constraints [9] are imposed on the right-hand sides $f, g \in C^\infty$ to ensure the existence of a stable relaxation cycle. A typical example of model (1) is the well-known FitzHugh–Nagumo model [10].

Now, consider the simplest network consisting of two synaptically coupled neurons. In this case, according to the current views (see, for example, [11]), the electrical variables (u_j, v_j) , $j = 1, 2$, corresponding to these neurons satisfy the system of equations

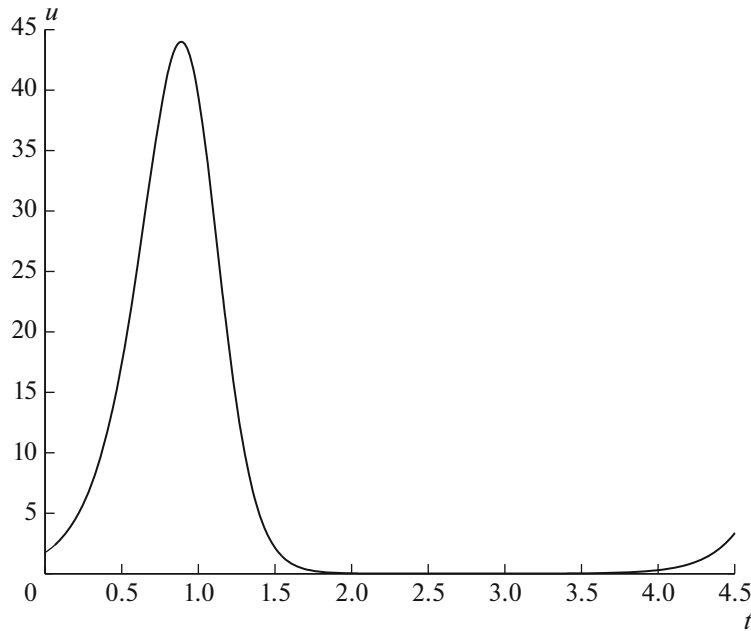


Fig. 1.

$$\begin{aligned}\varepsilon \dot{u}_1 &= f(u_1, v_1) + bs_2(u_2)(u_* - u_1), & \dot{v}_1 &= g(u_1, v_1), \\ \varepsilon \dot{u}_2 &= f(u_2, v_2) + bs_1(u_1)(u_* - u_2), & \dot{v}_2 &= g(u_2, v_2).\end{aligned}\quad (2)$$

Here, b is a positive parameter characterizing the maximum conductivity of a synapse, u_* is the resting potential (also known as the Nernst potential), and the functions $s_j(u_j)$, $j = 1, 2$, are the postsynaptic conductivities that depend on the presynaptic potentials u_j .

It should be noted that there are several different ways of selecting the functions $s_j(u_j)$, which are described in [11]. In this work, following the idea of FTM, we use the simplest of them. Thus, we assume that

$$s_j(u_j) = H(u_j - u_{**}), \quad H(x) = \begin{cases} 0 & \text{for } x < 0, \\ 1 & \text{for } x > 0, \end{cases}\quad (3)$$

where u_{**} is a threshold exceeding which one cell begins to influence another. For example, if $u_1 < u_{**}$, then the first neuron does not affect the second one, but if $u_1 > u_{**}$, then it does.

Here, our primary objective is to adapt the chemical synapse modeling technique described above to difference-differential equations of the Volterra type. For this purpose, it is assumed that a single neuron is modeled by the equation

$$\dot{u} = \lambda f(u(t-1))u \quad (4)$$

for the membrane potential $u = u(t) > 0$. The parameter $\lambda > 0$, which characterizes the rate of the electrical processes in the system, is assumed to be large, and the function $f(u) \in C^2(\mathbb{R}_+)$, $\mathbb{R}_+ = \{u \in \mathbb{R} : u \geq 0\}$, possesses the following properties:

$$f(0) = 1; \quad f(u) + a, \quad uf'(u), \quad u^2 f''(u) = O(1/u) \quad \text{as } u \rightarrow +\infty, \quad (5)$$

where $a = \text{const} > 0$. An example of this function is

$$f(u) = (1 - u)/(1 + u/a). \quad (6)$$

Equation (4), which is a certain modification of Hutchinson's equation [12], was proposed and investigated in [13]. In [13], it was shown that, for all $\lambda \gg 1$, this equation allows an exponentially orbitally stable relaxation cycle $u_*(t, \lambda) > 0$ of the period $T_*(\lambda)$ that satisfies the limit relations

$$\lim_{\lambda \rightarrow \infty} T_*(\lambda) = T_0, \quad \max_{0 \leq t \leq T_*(\lambda)} |x_*(t, \lambda) - x_0(t)| = O(1/\lambda), \quad \lambda \rightarrow \infty, \tag{7}$$

where $T_0 = (1 + a)t_0$, $t_0 = 1 + 1/a$, $x_*(t, \lambda) = (1/\lambda) \ln(u_*(t, \lambda))$, and the T_0 -periodic function $x_0(t)$ is defined as

$$x_0(t) = \begin{cases} t & \text{for } 0 \leq t \leq 1, \\ 1 - a(t - 1) & \text{for } 1 \leq t \leq t_0 + 1, \\ t - T_0 & \text{for } t_0 + 1 \leq t \leq T_0, \end{cases} \quad x_0(t + T_0) \equiv x_0(t). \tag{8}$$

Figure 1 shows the relaxation behavior of this cycle on the plane (t, u) for the case of (4) and (6) at $\lambda = 5$ and $a = 2$.

Now, suppose that two neurons synaptically interact with each other and this interaction is delayed in time (see also [14, 15]). In this case, according to the technique described above, we can shift from Eq. (4) to the following system similar to (2):

$$\begin{aligned} \dot{u}_1 &= \lambda f(u_1(t - 1))u_1 + bs_2(u_2(t - h))(u_* - u_1), \\ \dot{u}_2 &= \lambda f(u_2(t - 1))u_2 + bs_1(u_1(t - h))(u_* - u_2), \end{aligned} \tag{9}$$

where the functions s_1 and s_2 are given by equalities (3) and the positive parameter h is responsible for delay in the coupling link between oscillators.

Moreover, in this case, we can reject the generally accepted view (see [1]) and, as a mathematical model of the neural network under study, take a slightly different system

$$\begin{aligned} \dot{u}_1 &= [\lambda f(u_1(t - 1)) + bg(u_2(t - h)) \ln(u_*/u_1)]u_1, \\ \dot{u}_2 &= [\lambda f(u_2(t - 1)) + bg(u_1(t - h)) \ln(u_*/u_2)]u_2, \end{aligned} \tag{10}$$

in which $b = \text{const} > 0$, $u_* = \exp(c\lambda)$, $c = \text{const} \in \mathbb{R}$, and the function $g(u) \in C^2(\mathbb{R}_+)$ is such that

$$\begin{aligned} g(u) &> 0 \quad \forall u > 0, \quad g(0) = 0; \quad g(u) - 1, \quad ug'(u), \\ u^2 g''(u) &= O(1/u) \quad \text{as } u \rightarrow +\infty. \end{aligned} \tag{11}$$

The reasons for selecting system (10) in [1] were as follows. First, when transferring from (9) to (10), the general qualitative character of synaptic coupling is preserved because, in both cases, the corresponding coupling summands $bs_2(u_2(t - h))(u_* - u_1)$, $bs_1(u_1(t - h))(u_* - u_2)$ and $bg(u_2(t - h))u_1 \ln(u_*/u_1)$, $bg(u_1(t - h))u_2 \ln(u_*/u_2)$ change their sign from “+” to “-” as the potentials u_1 , u_2 grow and exceed the critical value u_* . Second, and most importantly, we have managed to correctly identify the limit object for system (10), which proves to be a certain relay system with delay.

Indeed, upon transferring to new variables $x_j = (1/\lambda) \ln u_j$ ($j = 1, \dots, m$), system (10) is rewritten as

$$\begin{aligned} \dot{x}_1 &= F(x_1(t - 1), \varepsilon) + b(c - x_1)G(x_2(t - h), \varepsilon), \\ \dot{x}_2 &= F(x_2(t - 1), \varepsilon) + b(c - x_2)G(x_1(t - h), \varepsilon), \end{aligned} \tag{12}$$

where $\varepsilon = 1/\lambda \ll 1$, $F(x, \varepsilon) = f(\exp(x/\varepsilon))$, and $G(x, \varepsilon) = g(\exp(x/\varepsilon))$. Note that, due to the properties of (5) and (11), the following limit equalities hold:

$$\lim_{\varepsilon \rightarrow 0} F(x, \varepsilon) = R(x) \stackrel{\text{def}}{=} \begin{cases} 1 & \text{for } x < 0, \\ -a & \text{for } x > 0, \end{cases} \quad \lim_{\varepsilon \rightarrow 0} G(x, \varepsilon) = H(x), \tag{13}$$

where $H(x)$ is the function that appears in (3). Hence, for $\varepsilon \rightarrow 0$, system (12) turns into a relay system

$$\begin{aligned} \dot{x}_1 &= R(x_1(t - 1)) + b(c - x_1)H(x_2(t - h)), \\ \dot{x}_2 &= R(x_2(t - 1)) + b(c - x_2)H(x_1(t - h)). \end{aligned} \tag{14}$$

The presence of limit object (14) significantly facilitates the search for attractors of system (12) and allows one to apply the general results [16] on the correspondence between stable cycles of relay and relaxation systems.

Let us now find the simplest relaxation regimes of system (12).

2. FINDING A UNIFORM SOLUTION WITH ONE SPLASH PER PERIOD

First of all, note that system (12) has a synchronous solution $x_1 \equiv x_2$. Therefore, we can transfer from (12) to the equation

$$\dot{x} = F(x(t-1), \varepsilon) + b(c-x)G(x(t-h), \varepsilon). \quad (15)$$

A solution of system (12) such that $x_1 \equiv x_2 \equiv x(t)$, where $x(t)$ is a solution of Eq. (15) is hereinafter referred to as uniform.

Let us find out whether relaxation periodic regime exists for auxiliary equation (15). For this purpose, based on the properties of (13), we first move from (15) to the corresponding relay equation

$$\dot{x} = R(x(t-1)) + b(c-x)H(x(t-h)). \quad (16)$$

This equation is analyzed under the additional conditions

$$t_0 + 1 < h < T_0, \quad (17)$$

where the parameters t_0 and T_0 are the same as in (7) and (8). These constraints are explained below.

As in [2–6, 17, 18], the concept of a solution to Eq. (16) is defined constructively. For this purpose, we fix a sufficiently small $\sigma_0 > 0$ (the upper estimate on σ_0 is refined below) and consider a set of functions

$$\varphi(t) \in C[-h - \sigma_0, -\sigma_0], \quad \varphi(t) < 0 \quad \forall t \in [-h - \sigma_0, -\sigma_0], \quad \varphi(-\sigma_0) = -\sigma_0. \quad (18)$$

In addition, we denote a solution of Eq. (16) with arbitrary initial condition from class (18) by $x_\varphi(t)$, $t \geq -\sigma_0$.

When integrating Eq. (16), it is important that the functions $R(x(t-1))$ and $H(x(t-h))$ on its right-hand side are piecewise-constant and vary only if $x(t-1)$ or $x(t-h)$ changes its sign. In particular, due to (17) and (18), for $-\sigma_0 \leq t \leq 1 - \sigma_0$, we have $\varphi(t-1) < 0$ and $\varphi(t-h) < 0$ simultaneously. That is why, on the given interval, the function $x_\varphi(t)$ is a solution of the Cauchy problem

$$\dot{x} = 1, \quad x|_{t=-\sigma_0} = -\sigma_0,$$

and, therefore, is given by the formula

$$x_\varphi(t) = t. \quad (19)$$

Moreover, equality (19) can be “stretched” over t as long as the conditions $x_\varphi(t-1) < 0$ and $x_\varphi(t-h) < 0$ hold. Therefore, it a priori holds on the time interval $-\sigma_0 \leq t \leq 0$.

For $0 \leq t \leq h$, the above considerations imply that $x_\varphi(t-h) < 0$ and, hence, $H(x_\varphi(t-h)) = 0$. Therefore, on this time interval, the solution $x_\varphi(t)$ satisfies the equation

$$\dot{x} = R(x(t-1)). \quad (20)$$

As for Eq. (20), its properties were analyzed in [13], where it was shown that any solution $x(t)$ of this equation such that $x(t) < 0$ for $-1 \leq t < 0$ and $x(0) = 0$ for all $t \geq 0$ coincides with the function $x_0(t)$ (see (8)).

Returning to the original equation (16) and taking into account all of the above considerations, we arrive at the equality

$$x_\varphi(t) = x_0(t), \quad 0 \leq t \leq h. \quad (21)$$

The further analysis concerns the time interval $h \leq t \leq h + t_0$, where t_0 is the instant that appears in (8). For $t \in (h, h + t_0)$, formula (21) and the properties of the function $x_0(t)$ imply an estimate $x_\varphi(t-h) > 0$ and, therefore, $H(x_\varphi(t-h)) = 1$. Moreover, we a priori assume that

$$x_\varphi(t) < 0 \quad \text{for} \quad h \leq t \leq h + t_0. \quad (22)$$

By uniting relations (8), (21), and (22) with conditions (17), we find that $x_\varphi(t-1) < 0$ for $h \leq t \leq h + t_0$ and, therefore, for the given values of t , the solution $x_\varphi(t)$ satisfies the Cauchy problem

$$\dot{x} = 1 + b(c-x), \quad x|_{t=h} = h - T_0.$$

A simple analysis of this problem leads us to the equality

$$x_\varphi(t) = (h - T_0 - c - 1/b) \exp(-b(t-h)) + c + 1/b, \quad h \leq t \leq h + t_0. \quad (23)$$

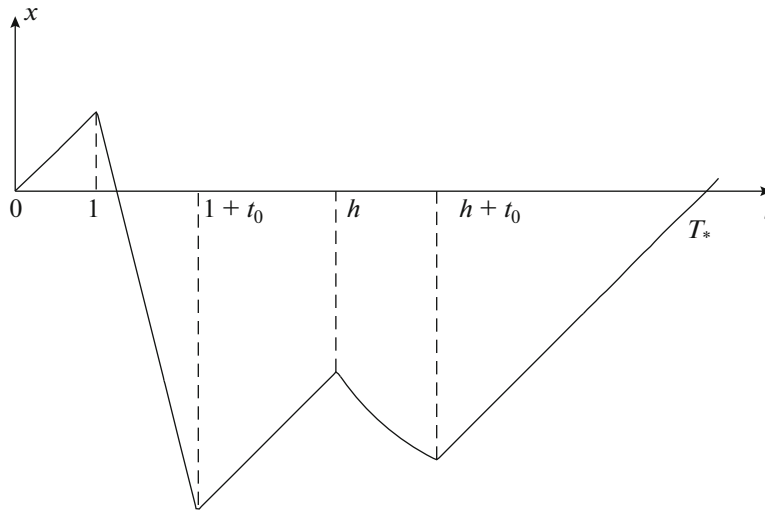


Fig. 2.

It should be recalled, however, that formula (23) is derived under a priori assumption (22) whose validity is equivalent to the condition

$$c + 1/b < \frac{T_0 - h}{\exp(bt_0) - 1}, \tag{24}$$

which hereinafter is assumed to be satisfied.

For $h + t_0 < t \leq h + t_0 + 1$, due to (8), (21), and (22), we have $x_\varphi(t - 1) < 0$, $x_\varphi(t - h) < 0$. Therefore, in this case, the solution $x_\varphi(t)$ is found from the Cauchy problem

$$\dot{x} = 1, \quad x|_{t=h+t_0} = x_\varphi(h + t_0)$$

and is given by the equality

$$x_\varphi(t) = t - T_*, \quad \text{where } T_* = h + t_0 - x_\varphi(h + t_0) > 0. \tag{25}$$

Note also that formula (25) is preserved for $t > h + t_0$ such that $x_\varphi(t - 1) < 0$ and $x_\varphi(t - h) < 0$ simultaneously. Hence, this formula is a priori applicable for $h + t_0 \leq t < T_* + 1$.

Let us now select the free parameter σ_0 (see (18)). Below, we assume that the following condition is satisfied:

$$\sigma_0 < \min(T_* - h - t_0, T_0 - h), \tag{26}$$

which ensures that the function $x_\varphi(t + T_*)$, $-h - \sigma_0 \leq t \leq -\sigma_0$ belongs to set (18). Moreover, (26) implies that, on the interval $(0, T_* + 1]$, the equation $x_\varphi(t - \sigma_0) = -\sigma_0$ has exactly two roots $t = t_0 + \sigma_0/a$, $t = T_*$ (which is required to substantiate a theorem below).

Thus, under condition (26) on the parameter σ_0 , the solution $x_\varphi(t)$ on the time intervals $rT_* - \sigma_0 \leq t \leq (r + 1)T_* - \sigma_0$ ($r = 1, 2, \dots$) is constructed cyclically. This means that, for $t \geq -\sigma_0$, any solution $x_\varphi(t)$ with initial condition (18) coincides with the T_* -periodic function

$$x_*(t) = \begin{cases} x_0(t) & \text{for } 0 \leq t \leq h, \\ (h - T_0 - c - 1/b)\exp(-b(t - h)) + c + 1/b & \text{for } h \leq t \leq h + t_0, \\ t - T_* & \text{for } h + t_0 \leq t \leq T_*. \end{cases} \tag{27}$$

Figure 2 shows function (27) for $a = 4$, $b = 0.9$, $c = -5$, and $h = 4$.

Let us turn our attention to the relationship between the periodic solutions of Eqs. (15) and (16). The following statement is valid.

Theorem 1. *Suppose that conditions (17), (24), and (26) on the parameters a, b, c, h , and σ_0 are satisfied. Then there is a sufficiently small $\varepsilon_0 > 0$ such that, for all $\varepsilon \in (0, \varepsilon_0]$, Eq. (15) allows a single exponentially orbitally stable cycle $x_*(t, \varepsilon)$, $x_*(-\sigma_0, \varepsilon) \equiv -\sigma_0$ of the period $T_*(\varepsilon)$ that satisfies the limit equalities*

$$\lim_{\varepsilon \rightarrow 0} \max_{0 \leq t \leq T_*(\varepsilon)} |x_*(t, \varepsilon) - x_*(t)| = 0, \quad \lim_{\varepsilon \rightarrow 0} T_*(\varepsilon) = T_*. \quad (28)$$

The proof of this theorem is omitted as it is similar to that of the corresponding statement in [1].

3. STABILITY OF A UNIFORM SOLUTION

Let us now address the problem of stability of the uniform solution to system (12). Suppose that the original functions of relay system (14) are selected in such a way that one of them is negative for $t < 0$ on a delay interval $[-h, 0)$ and is zero at the zero point, while another is zero at a point $\Delta > 0$ and is negative for $t < \Delta$ on this interval. The value of Δ is selected to be sufficiently small. In this case, relay system (14) is easily integrated step by step and the instants at which the functions $x_1(t)$ and $x_2(t)$ have a second consecutive zero for $t > \Delta$ can be calculated. By analyzing the distance between the roots, we can find out whether the solutions approach each other and, therefore, judge on the stability of the uniform solution. As in the previous section, system (14) is analyzed under conditions (17). When integrating system (14), we use the piecewise constancy of the functions $R(x(t-1))$ and $H(x(t-h))$, which vary only if $x_j(t-1)$ or $x_j(t-h)$ ($j = 1, 2$) change their sign. In particular, due to (17) and the negativeness of $x_j(t)$ ($j = 1, 2$) for $t < 0$, we have $H(x_j(t-h)) = 0$ for $\Delta < t < 1$. Hence, on the given interval, the functions $x_{j\varphi}(t)$ are a solution of the Cauchy problem

$$\dot{x}_1 = 1, \quad x_1|_{t=\Delta} = \Delta, \quad \dot{x}_2 = 1, \quad x_2|_{t=\Delta} = 0,$$

and are given by the formulas

$$x_{1\varphi}(t) = t, \quad x_{2\varphi}(t) = t - \Delta. \quad (29)$$

Taking into account that the summand containing $H(x_j(t-h))$ remains zero for $\Delta < t < h$, it is easy to see that, on the given interval, $x_{1\varphi}(t) = x_0(t)$ and $x_{2\varphi}(t) = x_0(t - \Delta)$.

On the interval $h < t < h + \Delta$, the equation for x_1 preserves its form; therefore, the equality $x_{1\varphi}(t) = x_0(t)$ holds and the second equation in system (14) takes the form

$$\dot{x}_2 = 1 + b(c - x_2), \quad x_2|_{t=h} = h - \Delta - T_0.$$

Hence, on this interval, we have

$$x_{1\varphi}(t) = x_0(t), \quad x_{2\varphi}(t) = 1/b + c + (h - \Delta - T_0 - 1/b - c) \exp(-b(t - h)). \quad (30)$$

On the next interval $h + \Delta < t < t_0 + h$, the Cauchy problem, which defines the solution of relay system (14), is written as

$$\begin{aligned} \dot{x}_1 &= 1 + b(c - x_1), \quad x_1|_{t=h+\Delta} = h + \Delta - T_0, \\ \dot{x}_2 &= 1 + b(c - x_2), \quad x_2|_{t=h+\Delta} = 1/b + c + (h - \Delta - T_0 - 1/b - c) \exp(-b\Delta), \end{aligned}$$

with the first component of its solution being

$$x_{1\varphi}(t) = 1/b + c + (h + \Delta - T_0 - 1/b - c) \exp(-b(t - h - \Delta)) \quad (31)$$

and the second one being calculated by formula (30).

On the next interval $t_0 + h < t < t_0 + h + \Delta$ of finding the solution to relay system (14), $x_1(t-h)$ is also negative and, therefore, $H(x_1(t-h))$ becomes zero. This leads us to the original Cauchy problem

$$\begin{aligned} \dot{x}_1 &= 1 + b(c - x_1), \quad x_1|_{t=t_0+h} = 1/b + c + (h + \Delta - T_0 - 1/b - c) \exp(-b(t_0 - \Delta)), \\ \dot{x}_2 &= 1, \quad x_2|_{t=t_0+h} = 1/b + c + (h - \Delta - T_0 - 1/b - c) \exp(-bt_0). \end{aligned}$$

The first component of the solution to this problem is calculated by formula (31), while the second one has the form

$$x_{2\varphi}(t) = t - t_0 - h + 1/b + c + (h - \Delta - T_0 - 1/b - c) \exp(-bt_0). \quad (32)$$

Consider the last interval $t > t_0 + h + \Delta$ for relay system (14). On this interval, we have the Cauchy problem

$$\begin{aligned} \dot{x}_1 &= 1, & x_1|_{t=t_0+h+\Delta} &= 1/b + c + (h + \Delta - T_0 - 1/b - c) \exp(-bt_0), \\ \dot{x}_2 &= 1, & x_2|_{t=t_0+h+\Delta} &= \Delta + 1/b + c + (h - \Delta - T_0 - 1/b - c) \exp(-bt_0), \end{aligned}$$

whose second component has the form of (32) and whose first component is

$$x_{1\varphi}(t) = t - t_0 - h - \Delta + 1/b + c + (h + \Delta - T_0 - 1/b - c) \exp(-bt_0). \quad (33)$$

Using formulas (32) and (33), it is easy to find points $T_{1\varphi}$ and $T_{2\varphi}$ such that $x_{1\varphi}(T_{1\varphi}) = 0$ and $x_{2\varphi}(T_{2\varphi}) = 0$. By the difference $\bar{\Delta} = T_{2\varphi} - T_{1\varphi}$, we can assess the stability of the uniform solution to relay system (14). Taking into account that

$$\bar{\Delta} = \Delta(2 \exp(-bt_0) - 1) \quad (34)$$

for all parameter values ensuring the existence of the uniform solution $x_*(t)$ (the value of $2 \exp(-bt_0) - 1$ is less than unity in the modulus), we can conclude that this solution is stable. This, together with the theorem proved, allows us to assert that if the conditions of this theorem hold, then the uniform cycle $x_1 \equiv x_2 \equiv x_*(t, \varepsilon)$ is an exponentially orbitally stable solution to system (12).

In summary, it should be noted that system (10), which models the synaptic interaction between pulse neurons provided an adequate selection of the delay h in the coupling link, contains a uniform cycle whose structure is more complex than that in the problem without interaction.

4. CONCLUSIONS

The results of this work have been obtained under severe constraints on the delay h , which must satisfy inequalities (17). Taking into account that parameter h models the delay in the coupling link and can have large values, it is interesting to analyze the relaxation oscillations in system (10) with increasing h when its value is close to several periods of the solution of a single oscillator (T_0). In this case, equation (15) with two delays can have a periodic solution with several positive intervals, which corresponds to the same number of high-amplitude splashes per period of a uniform cycle for system (10). It is well-known that self-oscillations in real neural systems are characterized by the alternation of pulse packets (sets of several consecutive high-amplitude splashes) and relatively smooth intervals of change in the membrane potential; this phenomenon is referred to as the bursting effect (bursting behavior). There are many works devoted to investigation of the bursting effect [19–23]. Generally, the mathematical model of this effect uses singularly perturbed systems of ordinary differential equations with two fast and one slow variables; under certain conditions, these systems can contain stable bursting cycles (periodic movements with the bursting effect). In [17], we proposed another approach to solve this problem that implies introducing several time delays into a pulse neuron model.

The structure of equation (15) with two delays is close to that of the model equation for a pulse neuron from [17]. Specifically, when solving relay equation (16) for all $0 \leq t \leq h$, the problem is reduced to the same equation

$$\dot{x} = R(x(t-1))$$

as in [17]. This means that the selection of the parameter h in accordance with the constraints

$$n(2 + a + 1/a) + 2 + 1/a < h < (n + 1)(2 + a + 1/a) \quad (35)$$

gives rise to a uniform cycle with n splashes per period in original system (10); all that is left to do is to select the other parameters of the problem in such a way that, after these splashes on an interval exceeding h , the solution is asymptotically small.

The solution of this problem and the determination of the parameter values that guarantee the existence and stability of a uniform cycle with a predefined number of splashes per period allow us to conclude that the bursting effect in a system of two synaptically coupled neuron-type oscillators can be caused by delay in the coupling link.

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REFERENCES

1. Glyzin, S.D., Kolesov, A.Yu., and Rozov, N.Kh., On a method for mathematical modeling of chemical synapses, *Differ. Equations*, 2013, vol. 49, no. 10, pp. 1193–1210.
2. Glyzin, S.D., Kolesov, A.Yu., and Rozov, N.Kh., Relaxation self-oscillations in neuron systems: I, *Differ. Equations*, 2011, vol. 47, no. 7, pp. 927–941.
3. Glyzin, S.D., Kolesov, A.Yu., and Rozov, N.Kh., Relaxation self-oscillations in neuron systems: II, *Differ. Equations*, 2011, vol. 47, no. 12, pp. 1697–1713.
4. Glyzin, S.D., Kolesov, A.Yu., and Rozov, N.Kh., Relaxation self-oscillations in neuron systems: III, *Differ. Equations*, 2012, vol. 48, no. 2, pp. 159–175.
5. Glyzin, S.D., Kolesov, A.Yu., and Rozov, N.Kh., Discrete autowaves in neural systems, *Comput. Math. Math. Phys.*, 2012, vol. 52, no. 5, pp. 702–719.
6. Glyzin, S.D., Kolesov, A.Yu., and Rozov, N.Kh., Self-excited relaxation oscillations in networks of impulse neurons, *Russ. Math. Surv.*, 2015, vol. 70, no. 3, pp. 383–452.
7. Somers, D. and Kopell, N., Rapid synchronization through fast threshold modulation *Biol. Cybern.*, 1993, vol. 68, pp. 393–407.
8. Somers, D. and Kopell, N., Anti-phase solutions in relaxation oscillators coupled through excitatory interactions *J. Math. Biol.*, 1995, vol. 33, pp. 261–280.
9. Mishchenko, E.F. and Rozov, N.Kh., *Differentsialnye uravneniya s malym parametrom i relaksatsionnye kolebaniya* (Differential Equations with a Small Parameter and Relaxation Oscillations), Moscow, 1975.
10. FitzHugh, R.A., Impulses and physiological states in theoretical models of nerve membrane, *Biophys. J.*, 1961, vol. 1, pp. 445–466.
11. Terman, D., An introduction to dynamical systems and neuronal dynamics, *Tutorials Math. Biosci. I, Lect. Notes Math.*, 2005, vol. 1860, pp. 21–68.
12. Hutchinson, G.E., Circular causal systems in ecology, *Ann. N. Y. Acad. Sci.*, 1948, vol. 50, pp. 221–246.
13. Kolesov, A.Yu., Mishchenko, E.F., and Rozov, N.Kh., A modification of Hutchinson's equation, *Comput. Math. Math. Phys.*, 2010, vol. 50, no. 12, pp. 1990–2002.
14. Glyzin, S.D. and Kiseleva, E.O., The account of delay in a connecting element between two oscillators, *Model. Anal. Inform. Syst.*, 2010, vol. 17, no. 2, pp. 133–143.
15. Glyzin, S.D. and Soldatova, E.A., The factor of delay in a system of coupled oscillators FitzHugh–Nagumo, *Model. Anal. Inform. Syst.*, 2010, vol. 17, no. 3, pp. 134–143.
16. Kolesov, A.Yu., Mishchenko, E.F., and Rozov, N.Kh., Relay with delay and its C^1 -approximation, *Proc. Steklov Inst. Math.*, 1997, vol. 216, pp. 119–146.
17. Glyzin, S.D., Kolesov, A.Yu., and Rozov, N.Kh., Modeling the bursting effect in neuron systems, *Math. Notes*, 2013, vol. 93, no. 5, pp. 676–690.
18. Glyzin, S.D. and Marushkina, E.A., Relaxation cycles in a generalized neuron model with two delays, *Model. Anal. Inf. Syst.*, 2013, vol. 20, no. 6, pp. 179–199.
19. Chay, T.R. and Rinzel, J., Bursting, beating, and chaos in an excitable membrane model, *Biophys. J.*, 1985, vol. 47, no. 3, pp. 357–366.
20. Ermentrout, G.B. and Kopell, N., Parabolic bursting in an excitable system coupled with a slow oscillation, *SIAM J. Appl. Math.*, 1986, vol. 46, no. 2, pp. 233–253.
21. Izhikevich, E., Neural excitability, spiking and bursting, *Int. J. Bifurcation Chaos*, 2000, vol. 10, no. 6, pp. 1171–1266.
22. Rabinovich, M.I., Varona, P., Selverston, A.I., and Abarbanel, H.D.I., Dynamical principles in neuroscience, *Rev. Mod. Phys.*, 2006, vol. 78, pp. 1213–1265.
23. Coombes, S. and Bressloff, P.C., *Bursting: The Genesis of Rhythm in the Nervous System*, World Scientific Publishing Company, 2005.

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