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A new approach to mathematical modeling of chemical synapses

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Abstract. *The purpose* of this work is to study a new mathematical model of a ring neural network with unidirectional chemical connections, which is a singularly perturbed system of differential-difference equations with delay. *Methods.* A combination of analytical and numerical methods is used to study the existence and stability of special periodic solutions in this system, the so-called traveling waves. *Results.* The proposed methods make it possible to show that the ring system under study allows the number of stable traveling waves to increase with the number of oscillators in the network. *Conclusion.* In this article, we rethink and refine the previously proposed method of mathematical modeling of chemical synapses. On the one hand, it was possible to fully take into account the requirement of the Volterra structure of the corresponding equations and, on the other hand, the hypothesis of saturating conductivity. This makes it possible to observe the principle of uniformity: the new mathematical model is based on the same principles as the previously proposed model of electrical synapses.

Keywords: circular neural network, chemical synapses, relaxation cycles, asymptotics, stability.

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1. Description of the research object

One of the fundamental principles for constructing mathematical models of neural systems is the so-called equivalence hypothesis. The essence of this hypothesis is that we a priori assume the equivalence of a biological neuron to some physical generator with lumped parameters. In turn, the mentioned generator is modeled by a nonlinear system of ordinary differential equations or a similar system with a delay. And since the oscillations of the membrane potential are obviously relaxation in nature, the corresponding system, as a rule, turns out to be singularly perturbed.

The principle mentioned above underlies the well-known Hodgkin-Huxley model [1] and many other mathematical models of an isolated neuron (see the monograph [2] and the detailed bibliography contained therein). In this work, adhering to the equivalence hypothesis, as a model of an individual neuron we use a scalar nonlinear differential equation with delay of the form

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

for membrane potential $u = u(t) > 0$. Here the parameter $\lambda > 0$ characterizing the rate of electrical processes in the neuron is assumed to be large, the point is differentiation with respect to t, and the function $f(u) \in C^2(\mathbb{R}_+)$, $\mathbb{R}_+ = \{u \in \mathbb{R} : u \geqslant 0\}$, has the following properties:

$$f(0) = 1, \quad f(u) = -a + O\left(\frac{1}{u}\right), \quad uf'(u) = O\left(\frac{1}{u}\right), \quad u^2 f''(u) = O\left(\frac{1}{u}\right) \tag{2}$$

as $u \to +\infty$, where $a = \text{const} > 0$. An example of such a function is

$$f(u) = \frac{1-u}{1+u/a}. \tag{3}$$

Since in the method proposed below for modeling chemical synapses, the equation (1) is taken as a basis, it makes sense to dwell briefly on the history of its origin and properties. In this regard, let us draw attention to the fact that our approach to modeling neural activity is based on ideas belonging to Yu. S. Kolesov [3] and V.V. Mayorov [4], namely, in the monograph [3] describes the general principle of mathematical modeling of biological processes using special Volterra-type delay systems, similar to the well-known Hutchinson equation [5]. Further, in the work [4], based on this principle and the idea of delayed conduction with saturation, a certain equation with delay, similar to (1), was proposed as a model of an individual neuron. And finally, in the article [6], after proper modification, the mentioned equation acquired the required form(1), (2).

It should also be noted that previously, regardless of neurodynamic applications, the equation (1) was considered in the work [7] as one of the possible generalizations of the Hutchinson equation. In this work it was established that for all $\lambda \gg 1$ it admits an exponentially orbitally stable cycle $u(t, \lambda) > 0$, $u(0, \lambda) \equiv 1$ of period $T(\lambda)$, satisfying limit relations:

$$\lim_{\lambda \to +\infty} T(\lambda) = T_0, \quad \max_{0 \leqslant t \leqslant T(\lambda)} |x(t, \lambda) - x_0(t)| = O\left(\frac{1}{\lambda}\right), \quad \lambda \to +\infty, \tag{4}$$

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 given by

$$x_0(t) = \begin{cases} t & \text{for } 0 \leqslant t \leqslant 1, \\ 1 - a(t-1) & \text{for } 1 \leqslant t \leqslant t_0 + 1, \\ t - T_0 & \text{for } t_0 + 1 \leqslant t \leqslant T_0, \end{cases} \qquad x_0(t + T_0) \equiv x_0(t). \tag{5}$$

A visual representation of the relaxation properties (4) of this cycle is given by its graph on the (t, u) plane, constructed numerically for the case (1), (3) at $\lambda = 5$, $a = 2$ (Fig. 1), as well as the graph of the function (5) (Fig. 2).

Let us now turn to the question of modeling chemical synapses that interests us and recall that a corresponding attempt has already been made earlier in the article [8]. Precisely speaking,

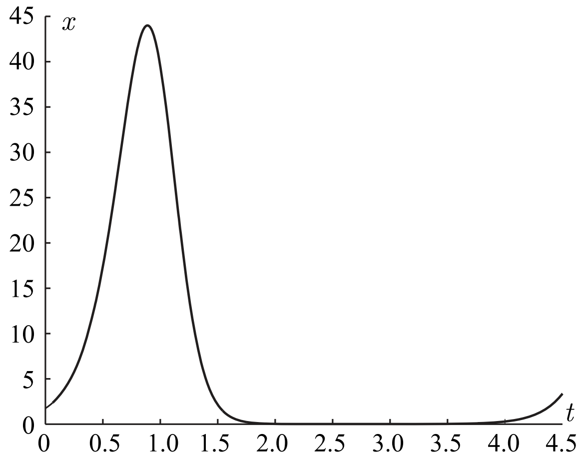

Fig 1. Graph of the solution $x(t)$ of the equation (1) with the function $f(u)$ satisfying the formula (3) for $\lambda = 5$, $a = 2$

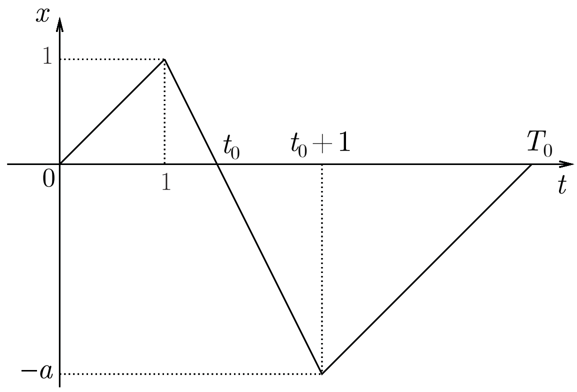

Fig 2. Graph of the function $x_0(t)$ for $a = 2$

in [8] some approach to this problem was proposed, which was based on a suitably modified idea of fast threshold modulation.

The phenomenon of fast threshold modulation (FTM), first described in the works [9, 10], is a special way of coupling dynamic systems. A characteristic feature of this method is that the right-hand sides of the corresponding differential equations change abruptly when some control variables pass through their critical values. In neural systems, the idea of FTM is implemented, as a rule, as follows.

Let us assume that the voltage $u = u(t)$ and current $v = v(t)$ in an individual neuron cell satisfy a system of differential equations

$$\varepsilon \dot{u} = f(u, v), \quad \dot{v} = g(u, v). \tag{6}$$

Here $\varepsilon > 0$ is a small parameter, and standard restrictions are imposed on the right-hand sides $f, g \in C^\infty$ [11, p. 45–55], ensuring the existence of a stable relaxation cycle. A typical example of the (6) model is the well-known FitzHugh–Nagumo system [12].

Let us next consider a simple network consisting of two synaptically connected neurons. In this case, according to the concepts developed to date (see, for example, [13]), the corresponding electrical variables (u_j, v_j), $j = 1, 2$ satisfy the system of equations

$$\begin{aligned} \varepsilon \dot{u}_1 &= f(u_1, v_1) + b\, s_2(u_2)(u_* - u_1), \quad \dot{v}_1 = g(u_1, v_1), \\ \varepsilon \dot{u}_2 &= f(u_2, v_2) + b\, s_1(u_1)(u_* - u_2), \quad \dot{v}_2 = g(u_2, v_2). \end{aligned} \tag{7}$$

Here b is a positive parameter characterizing the maximum conductance of the synapse, u_* is the resting potential (or Nernst potential), and the functions $s_j(u_j)$, $j = 1, 2$ are postsynaptic conductivity dependent on presynaptic potentials u_j.

It should be noted that there are several different ways to select functions $s_j(u_j)$, a description of which can be found in [13]. We, guided by the idea of FTM, will focus on the simplest of them, namely, we will assume that

$$s_j(u_j) = H(u_j - u_{**}), \quad H(x) = \begin{cases} 0 & \text{for } x < 0, \\ 1 & \text{for } x \geqslant 0, \end{cases} \tag{8}$$

where u_{**} is the threshold from which one cell influences another. For example, if $u_1 < u_{**}$, then the first neuron does not act on the second, but if $u_1 > u_{**}$, then it acts.

Let us now assume that there is unidirectional synaptic interaction in a network of m, $m \geqslant 2$ neurons united in a ring. If we assume that each individual neuron is modeled by the equation (1), then we can, guided by the methodology described above, move from (1) to a similar (7) system

$$\dot{u}_j = \lambda f(u_j(t-1))u_j + b\, s_{j-1}(u_{j-1})(u_* - u_j), \quad j = 1, 2, \ldots, m, \tag{9}$$

where $u_0 = u_m$, $s_0 = s_m$, functions s_j are set by (8).

The given model (9) has a right to exist. However, in our opinion, in this situation we should abandon generally accepted ideas. The first step in this direction was made in the article [8], where instead of (9) the system

$$\dot{u}_j = [\lambda f(u_j(t-1)) + b\, g(u_{j-1}) \ln(u_*/u_j)]u_j, \quad j = 1, 2, \ldots, m, \quad u_0 = u_m, \tag{10}$$

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

$$\begin{gathered} g(u) > 0 \quad \forall\, u > 0, \quad g(0) = 0; \quad g(u) = 1 + O\left(\frac{1}{u}\right), \ \ ug'(u) = O\left(\frac{1}{u}\right), \\ u^2 g''(u) = O\left(\frac{1}{u}\right) \quad u \to +\infty. \end{gathered} \tag{11}$$

The reasons why we chose the (10) system in [8] were as follows. Firstly, when we move from (9) to (10) the general qualitative nature of the synaptic coupling is preserved, since in both cases the corresponding connecting terms $b\, s_{j-1}(u_{j-1})(u_* - u_j)$ and $b\, g(u_{j-1})u_j \ln(u_*/u_j)$ change sign from "+" to "−" when the potentials u_j increase and when they pass through the critical value u_*. Secondly, in accordance with the methodology of works [3,4] the system (10) has the required Volterra structure.

However, over time, it became clear that the (10) system also needed some improvement. This is due to the fact that the function $\ln(u_*/u)$ appearing in (10) does not satisfy the hypothesis of saturating conductivity, according to which all nonlinearities included in the model should tend to the finite limits as $u \to +\infty$.

In order to correct the situation, let's move from (10) to the system

$$\dot{u}_j = \lambda[f(u_j(t-1)) + b\, g(u_{j-1})h(u_j/u_*)]u_j, \quad j = 1, 2, \ldots, m, \quad u_0 = u_m. \tag{12}$$

Here the function $h(u) \in C^2(\mathbb{R}_+)$ has similar (2), (11) properties:

$$\begin{aligned} &h(u) > 0 \ \text{ for } \ 0 \leqslant u < 1, \quad h(u) < 0 \ \text{ for } \ u > 1, \ \ h(1) = 0, \ \ h'(1) < 1, \\ &h(0) = 1, \ \ h(u) = -c + O\left(\frac{1}{u}\right), \ \ uh'(u) = O\left(\frac{1}{u}\right), \ \ u^2 h''(u) = O\left(\frac{1}{u}\right) \end{aligned} \tag{13}$$

$u \to +\infty$, where $c =$ const > 0.

Properties (13) guarantee that $\operatorname{sign} h(u) = \operatorname{sign}(\ln(1/u))$ for all $u > 0$, and this means that the qualitative nature of the coupling in the models (10) and (12) is identical. The required saturation property also holds for $h(u)$. However, it is appropriate to make one more non-trivial assumption, namely, we will assume that for each equation from (12) the corresponding rest potential u_*, assumed constant, now depends on time and coincides with $u_{j-1}(t)$. Thus we arrive at the system

$$\dot{u}_j = \lambda[f(u_j(t-1)) + b\, g(u_{j-1})h(u_j/u_{j-1})]u_j, \quad j = 1, 2, \ldots, m, \quad u_0 = u_m, \tag{14}$$

where, recall, the functions f, g, h have the properties (2), (11), (13) respectively, $b = \text{const} > 0$, $\lambda \gg 1$. This system is the new mathematical model of chemical synapses that interests us.

Concluding the description of the object of study, we note that the model (14) proposed in this article is quite similar to the mathematical model of electrical synapses considered in [14], that is, the so-called principle of uniformity is observed. It is for the sake of this principle that the replacement of u_* with u_{j-1} was carried out in (12).

2. Traveling waves of a relay system

A characteristic feature of the (14) system is the fact that after replacement $x_j = \varepsilon \ln u_j$, $j = 1, 2, \ldots, m$, $\varepsilon = 1/\lambda \ll 1$ and the subsequent tendency of the parameter ε to zero, it admits a certain limit object . Indeed, the indicated replacements transform it to the form

$$\dot{x}_j = \mathcal{F}(x_j(t-1), \varepsilon) + b\,\mathcal{G}(x_{j-1}, \varepsilon)\mathcal{H}(x_j - x_{j-1}, \varepsilon), \quad j = 1, 2, \ldots, m, \tag{15}$$

where $x_0 = x_m$,

$$\mathcal{F}(x, \varepsilon) = f\left(\exp\left(\frac{x}{\varepsilon}\right)\right), \;\; \mathcal{G}(x, \varepsilon) = g\left(\exp\left(\frac{x}{\varepsilon}\right)\right), \;\; \mathcal{H}(x, \varepsilon) = h\left(\exp\left(\frac{x}{\varepsilon}\right)\right). \tag{16}$$

Note further that, due to the properties (2), (11), (13) for the functions (16) for any fixed $x \in \mathbb{R}$, $x \neq 0$ the limit equalities are satisfied

$$\begin{gathered} \lim_{\varepsilon \to 0} \mathcal{F}(x, \varepsilon) = 1 - (a+1)H(x), \quad \lim_{\varepsilon \to 0} \mathcal{G}(x, \varepsilon) = H(x), \\ \lim_{\varepsilon \to 0} \mathcal{H}(x, \varepsilon) = 1 - (c+1)H(x), \end{gathered} \tag{17}$$

where $H(x)$ is a function from (8).

The relations (17) indicate that as $\varepsilon \to 0$ the initial system (15) moves into relay system

$$\dot{x}_j = 1 - (a+1)H(x_j(t-1)) + b\, H(x_{j-1})[1 - (c+1)H(x_j - x_{j-1})], \quad 1 \leqslant j \leqslant m, \tag{18}$$

where $x_0 = x_m$. In turn, the presence of a limit object (18) significantly simplifies the problem of finding attractors of the system (15) and allows, in particular, to apply to it the general results from [15] on the correspondence between rough relay cycles and relaxation systems. The results mentioned below are used to find special periodic motions, the so-called traveling waves.

According to generally accepted terminology, a traveling wave with number $k \in \mathbb{N}$, $1 \leqslant k \leqslant m-1$ is a special periodic solution of the system (15) that can be represented

$$x_j = x(t + (j-1)\Delta), \quad j = 1, 2, \ldots, m. \tag{19}$$

Here $\Delta =$ const > 0 is some phase shift, and the function $x(t)$ is a T-periodic solution of the auxiliary equation

$$\dot{x} = \mathcal{F}(x(t-1), \varepsilon) + b\,\mathcal{G}(x(t-\Delta), \varepsilon)\mathcal{H}(x - x(t-\Delta), \varepsilon), \tag{20}$$

where $T = m\Delta/k$. A similar definition of a traveling wave is preserved for a relay system (18), but in this case $x(t)$ is a periodic solution of the period $T = m\Delta/k$ of the auxiliary equation

$$\dot{x} = 1 - (a+1)H(x(t-1)) + b\,H(x(t-\Delta))[1 - (c+1)H(x - x(t-\Delta))]. \tag{21}$$

As it turns out, for a relay system (18) the traveling waves (19) with proper choice of parameters a, b, c, k, m can be found explicitly. In order to verify this, let us analyze the equation (21), namely, we will establish the fact that it has some periodic solution a, b, c, Δ in a suitable range of parameters $x = x_*(t, \Delta)$ of period $T_* = T_*(\Delta)$.

Assuming that the condition $\Delta > 1$ is satisfied, in the phase space $C[-\Delta, 0]$ of scalar functions $\varphi(t)$ continuous for $-\Delta \leqslant t \leqslant 0$ we introduce into consideration a special family $\varphi_{\tau_1,\tau_2}(t)$ of initial conditions for equation (21). This family depends on two auxiliary parameters τ_1, τ_2, satisfying the inequalities

$$0 < \tau_1 < \frac{a}{a+b+1}\tau_2, \quad \tau_2 < 1, \quad \frac{a}{b+1} + \tau_2 + 1 < \Delta < \tau_2 + 1 + a. \tag{22}$$

The functions themselves $\varphi_{\tau_1,\tau_2}(t)$ are given by the formula

$$\varphi_{\tau_1,\tau_2}(t) = \begin{cases} t + \Delta - \tau_1 + a(\tau_2 - \tau_1) & \text{at} \quad -\Delta \leqslant t \leqslant -\Delta + \tau_1, \\ -a(t + \Delta - \tau_2) & \text{at} \quad -\Delta + \tau_1 \leqslant t \leqslant -\Delta + \tau_2 + 1, \\ -a + t + \Delta - \tau_2 - 1 & \text{at} \quad -\Delta + \tau_2 + 1 \leqslant t \leqslant -\Delta + \tau_3, \\ (b+1)t & \text{at} \quad -\Delta + \tau_3 \leqslant t \leqslant 0, \end{cases} \tag{23}$$

where

$$\tau_3 = \Delta + \frac{1}{b}(\Delta - \tau_2 - 1 - a). \tag{24}$$

Let us note that, due to the relations (22)–(24), the following inequalities are true:

$$\begin{gathered} -\Delta < -\Delta + \tau_1 < -\Delta + \tau_2 < -\Delta + \tau_2 + 1 < -\Delta + \tau_3 < 0, \\ \varphi_{\tau_1,\tau_2}(t) > 0 \ \text{ for} -\Delta \leqslant t < -\Delta + \tau_2, \quad \varphi_{\tau_1,\tau_2}(t) < 0 \ \text{ for} -\Delta + \tau_2 < t < 0, \end{gathered} \tag{25}$$

which means that the graph of any function $\varphi_{\tau_1,\tau_2}(t)$ from our family has the form shown in Fig. 3.

Let us denote by $x = x_{\tau_1,\tau_2}(t)$, $t \geqslant 0$ the solution to the equation (21) with the initial condition $\varphi_{\tau_1,\tau_2}(t)$, $-\Delta \leqslant t \leqslant 0$. Let $t = T > 0$ is the second positive root of the equation $x_{\tau_1,\tau_2}(t) = 0$ (if it exists). As will be shown below, under some additional restrictions on a, b, c, Δ and on the parameters τ_1, τ_2, the function $x_{\tau_1,\tau_2}(t+T)$, $-\Delta \leqslant t \leqslant 0$ coincides with $\varphi_{\bar{\tau}_1,\bar{\tau}_2}(t)$, where the new parameters are $\bar{\tau}_1$, $\bar{\tau}_2$ depend linearly on τ_1, τ_2. Moreover, the corresponding mapping $(\tau_1, \tau_2) \mapsto (\bar{\tau}_1, \bar{\tau}_2)$ has a single fixed point $(\tau_1^*(\Delta), \tau_2^*(\Delta))$. As for the desired periodic solution $x_*(t, \Delta)$ of the equation (21), then it itself and its period $T_*(\Delta)$ are given by the relations

$$\begin{aligned} &x_*(t, \Delta) = x_{\tau_1,\tau_2}(t)|_{\tau_1=\tau_1^*(\Delta),\tau_2=\tau_2^*(\Delta)}, \\ &T_*(\Delta) = T|_{\tau_1=\tau_1^*(\Delta),\tau_2=\tau_2^*(\Delta)}. \end{aligned} \tag{26}$$

In order to implement the action program described above, we will integrate the equation (21) using the step method, namely, we will sequentially consider different time intervals and obtain for the solution we are interested in $x_{\tau_1,\tau_2}(t)$ on in these intervals there are some explicit formulas.

In the first step, let's look at the interval

$$0 \leqslant t < t_*, \quad t_* = \frac{a}{a+b+1}\,\tau_2. \tag{27}$$

In this case, due to inequalities (22), (25) we have

$$t-1 \in [-1, t_*-1) \subset (-\Delta+\tau_2, 0), \quad x(t-1) = \varphi_{\tau_1,\tau_2}(t-1) < 0,$$

which means $H(x(t-1)) \equiv 0$. Further, taking into account inequality $\tau_1 < t_*$, following from (22), (27) we arrive at the formula

$$x(t-\Delta) = \varphi_{\tau_1,\tau_2}(t-\Delta) = \begin{cases} t-\tau_1+a(\tau_2-\tau_1) & \text{for } 0 \leqslant t \leqslant \tau_1, \\ -a(t-\tau_2) & \text{for } \tau_1 \leqslant t \leqslant t_*. \end{cases} \tag{28}$$

From here and from (25) it automatically follows that $x(t-\Delta) > 0$, $H(x(t-\Delta)) \equiv 1$. And finally, in the case of the function $x(t)-x(t-\Delta)$ we a priori assume that the inequality

$$x(t)-x(t-\Delta) < 0 \quad \forall\, t \in [0, t_*). \tag{29}$$

Taking into account the listed facts, we come to the conclusion that at the first step the Cauchy problem must be considered

$$\dot{x} = b+1, \quad x|_{t=0} = \varphi_{\tau_1,\tau_2}(0) = 0.$$

Thus, on the interval (27) the solution $x = x_{\tau_1,\tau_2}(t)$ is given by the equality

$$x = (b+1)t. \tag{30}$$

It should be recalled, however, that this equality was derived under the assumption (29). But from the formulas (28), (30) it is easy to deduce that the mentioned a priori condition is indeed satisfied.

The second step involves considering the interval

$$t_* < t < t_{**}, \quad t_{**} = \tau_2. \tag{31}$$

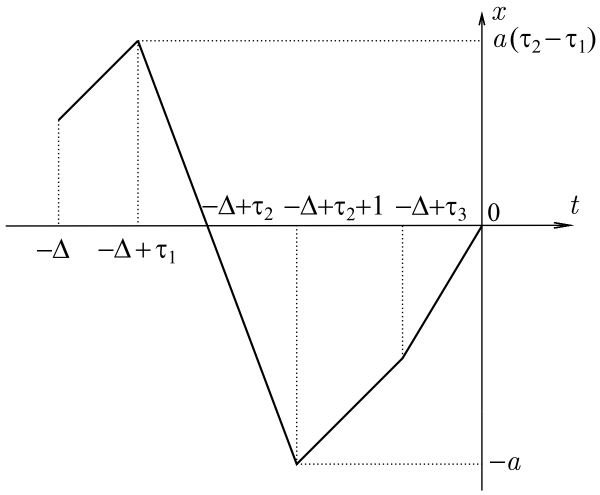

Fig 3. Graph of function $\varphi_{\tau_1,\tau_2}(t)$ from the family (23) under conditions (22), (24), (25)

Let us immediately note that at the point $t = t_*$ the solution $x_{\tau_1,\tau_2}(t)$ is further determined by continuity, that is, $x_{\tau_1,\tau_2}(t_*) = (b+1)t_*$. Taking this circumstance into account, we come to the conclusion that for $t = t_*$ the corresponding inequality from (29) turns into a strict equality. Therefore, it is appropriate to assume that at point $t = t_*$ switching occurs and

$$x(t) - x(t-\Delta) > 0 \quad \forall\, t \in (t_*, t_{**}). \tag{32}$$

Let us further analyze the signs of the functions $x(t-1)$, $x(t-\Delta)$. As in the previous case, for the first of them we have

$$t - 1 \in (t_* - 1, t_{**} - 1) \subset (-\Delta + \tau_2, 0), \quad x(t-1) = \varphi_{\tau_1,\tau_2}(t-1) < 0, \quad H(x(t-1)) \equiv 0.$$

The second one on the interval (31) is given by the formula

$$x(t-\Delta) = \varphi_{\tau_1,\tau_2}(t-\Delta) = -a(t - t_{**}), \tag{33}$$

from which, in turn, it follows that $x(t-\Delta) > 0$, $H(x(t-\Delta)) \equiv 1$.

The above facts indicate that on the interval (31) we are dealing with the Cauchy problem

$$\dot{x} = 1 - bc, \quad x|_{t=t_*} = (b+1)t_*,$$

which means that in this case the solution $x = x_{\tau_1,\tau_2}(t)$ has the equality

$$x = (b+1)t_* - (bc-1)(t - t_*). \tag{34}$$

Combining it with (33), we come to the conclusion that

$$x(t) - x(t-\Delta) = (a + 1 - bc)(t - t_*) \quad \forall\, t \in [t_*, t_{**}).$$

Thus, the a priori requirement (32), under which the formula (34) was obtained, is obviously valid under the condition (which we assume to be satisfied everywhere below)

$$bc < a + 1. \tag{35}$$

Let us also add that, as usual, at the point $t = t_{**}$ the solution $x_{\tau_1,\tau_2}(t)$ is further determined by continuity, and the condition (35) guarantees that

$$x_{\tau_1,\tau_2}(t_{**}) = \frac{(b+1)(a+1-bc)}{a+b+1}\, t_{**} > 0. \tag{36}$$

Before proceeding to the subsequent construction of the solution $x_{\tau_1,\tau_2}(t)$, let us make one useful observation. Since, by virtue of (25), the inequality $x(t-\Delta) < 0$ is valid for $t \in (t_{**}, \Delta)$, then automatically $H(x(t-\Delta)) \equiv 0$. Thus, on the interval (t_{**}, Δ) instead of (21) we must consider a simpler equation

$$\dot{x} = 1 - (a+1)H(x(t-1)). \tag{37}$$

In the third step, we turn to the interval

$$t_{**} < t < 1 \tag{38}$$

and note that according to (25) for the specified t the relations $x(t-1) < 0$ are valid, $H(x(t-1)) \equiv 0$. And from here and from (36), (37) we conclude that on the interval time (38) solution $x_{\tau_1,\tau_2}(t)$ is given by the formula

$$x = t - t_{**} + \frac{(b+1)(a+1-bc)}{a+b+1}\, t_{**}, \tag{39}$$

and at the point $t = 1$ it is further determined by continuity.

Before considering the next period of time, let us set

$$t_{***} = 1 + \frac{1}{a}\left(1 - t_{**} + \frac{(b+1)(a+1-bc)}{a+b+1}\,t_{**}\right) > 1 \tag{40}$$

and we will consider the following condition to be fulfilled

$$t_{***} + 1 < \Delta. \tag{41}$$

The fourth step is related to the interval

$$1 < t < t_{***} + 1, \tag{42}$$

on which, due to (41), we are still dealing with the equation (37). Moreover, we assume a priori that for the specified time values

$$x(t-1) > 0. \tag{43}$$

Taking into account the condition (43), from (37), (39), (40) we conclude that here for the solution $x_{\tau_1,\tau_2}(t)$ the equality

$$x = -a(t - t_{***}) \tag{44}$$

holds. Further, combining the formula (44) with the previously obtained formulas for $x_{\tau_1,\tau_2}(t)$ in the first three steps (see (30), (34),(39)), we come to the conclusion that the required condition (43) is valid on the time interval (42). Thus, the equality (44) takes on legal force, and at the point $t = t_{***} + 1$, by continuity we obtain

$$x_{\tau_1,\tau_2}(t_{***} + 1) = -a. \tag{45}$$

In the fifth step, we turn to the interval

$$t_{***} + 1 < t < \Delta, \tag{46}$$

assuming that for the specified t the following inequality is true:

$$x(t-1) < 0. \tag{47}$$

Further, taking into account in (37) the identity $H(x(t-1)) \equiv 0$ following from (47) and supplementing the resulting equation with the initial condition (45), for $x_{\tau_1,\tau_2}(t)$ we arrive at the next formula

$$x = t - t_{***} - a - 1. \tag{48}$$

Let us assume that the condition is met

$$\Delta < t_{***} + a + 1. \tag{49}$$

Then, by virtue of formulas (44), (48), the a priori requirement (47) is automatically satisfied. Thus, on the interval (46) the equality (48) actually holds by continuity

$$x_{\tau_1,\tau_2}(\Delta) = \Delta - t_{***} - a - 1 < 0. \tag{50}$$

Before moving on to the final stage of constructing the solution $x_{\tau_1,\tau_2}(t)$, we introduce into consideration the quantity

$$T = \Delta + \frac{1}{b+1}\,(t_{***} + a + 1 - \Delta), \tag{51}$$

additionally assuming that

$$\Delta + t_{**} < T < \Delta + 1. \tag{52}$$

We emphasize that according to (51) the condition (49) means that $T > \Delta$. Thus, the requirements of (52) are stronger than the constraint (49).

In the sixth step, consider the interval

$$\Delta < t \leqslant T \tag{53}$$

under the assumption that the inequalities are satisfied

$$x(t) \leqslant 0, \quad x(t-1) < 0, \quad x(t-\Delta) > 0. \tag{54}$$

Next, taking into account the information (54) on the right side of the equation (21) and relying on the formulas (50), (51), to find $x_{\tau_1,\tau_2}(t)$ we arrive at the Cauchy problem

$$\dot{x} = b + 1, \quad x|_{t=\Delta} = (b+1)(\Delta - T).$$

Thus, in the case (53) the solution $x_{\tau_1,\tau_2}(t)$ has the form

$$x = (b+1)(t - T). \tag{55}$$

As for the a priori conditions (54), their validity is guaranteed by the inequalities (52), the formula (55) and the previously obtained explicit expressions for $x_{\tau_1,\tau_2}(t)$ in the previous five steps (see. (30), (34), (39), (44), (48)).

A visual representation of the process of constructing a solution $x_{\tau_1,\tau_2}(t)$ of (21) gives Fig. 4, which shows the graph of $x_{\tau_1,\tau_2}(t)$ on the segment $0 \leqslant t \leqslant T$. From this graph and from the conditions (52), in particular, it follows that the function $x_{\tau_1,\tau_2}(t+T)$ has on the interval $-\Delta \leqslant t \leqslant 0$ exactly three breaks (as well as the original initial condition $\varphi_{\tau_1,\tau_2}(t)$). Moreover, based on the relations (39), (44), (48), (55), it is easy to see that $x_{\tau_1,\tau_2}(t+T) = \varphi_{\bar{\tau}_1,\bar{\tau}_2}(t)$, $-\Delta \leqslant t \leqslant 0$, where

$$\bar{\tau}_1 = 1 + \Delta - T, \quad \bar{\tau}_2 = \Delta + t_{***} - T. \tag{56}$$

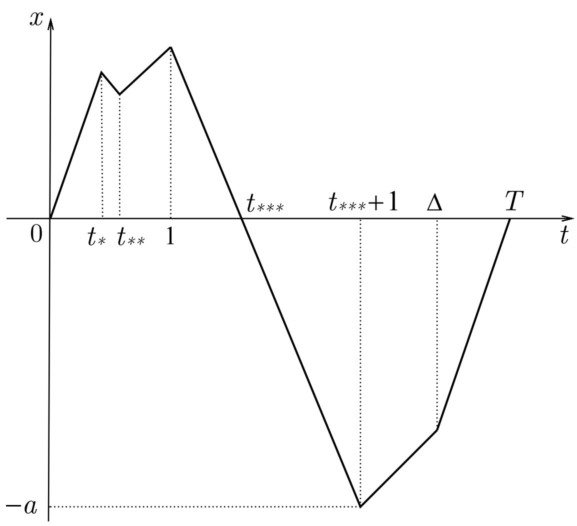

Fig 4. Graph of function $x_{\tau_1,\tau_2}(t)$ for $t \in [0, T]$

Let us now show that the mapping $(\tau_1, \tau_2) \mapsto (\bar{\tau}_1, \bar{\tau}_2)$, generated by the relations (56) has a unique fixed point $(\tau_1^*(\Delta), \tau_2^*(\Delta))$. For this purpose, let us substitute explicit formulas for t_{***} and T into (56) (see (40), (51)). As a result, after some transformations we come to the conclusion that the components of the fixed point of interest to us are given by the equalities

$$\tau_1^*(\Delta) = \frac{1}{b+1}\left(\Delta + b - a - \frac{1}{a} - 1\right) + \frac{b(a - c(b+1))}{a(b+1)(a+b+1)}\,\tau_2^*(\Delta), \tag{57}$$

$$\tau_2^*(\Delta) = \frac{a+b+1}{a(a+1)(b+1) + b(a+cb(b+1))}\,(a\Delta - (a+1)(a-b)). \tag{58}$$

Let us summarize. Let us denote by $\boldsymbol{\Omega}_1$ the set of all possible sets of parameters (a, b, c, Δ) satisfying the conditions (22), (35), (41), (52), in which τ_1, τ_2 are given by the equalities (57), (58). From the above constructions, the statement follows.

Theorem 1. *For any set $(a, b, c, \Delta) \in \boldsymbol{\Omega}_1$ the equation (21) has a periodic solution $x = x_*(t, \Delta)$ of period $T_*(\Delta)$, given by the formulas (26), (57), (58). Moreover, for $T_*(\Delta)$ the following relations hold true:*

$$T_*(\Delta) = \theta_1\Delta + \theta_2, \quad \theta_1 = \frac{b}{b+1}\left(1 + \frac{a - c(b+1)}{a(a+1)(b+1) + b(a+cb(b+1))}\right),$$
$$\theta_2 = \frac{a+1}{a(b+1)}\left(a + 1 - \frac{(a-b)b(a - c(b+1))}{a(a+1)(b+1) + b(a+cb(b+1))}\right). \tag{59}$$

The established theorem makes it possible to obtain in explicit form some traveling waves of the relay system (18). In order to do this, we fix an arbitrary natural number $k : 1 \leqslant k \leqslant m-1$ and, based on the formulas (59), from the equation $T_*(\Delta) = m\Delta/k$ let's find

$$\Delta_*^{(m,k)} = \frac{\theta_2}{m/k - \theta_1}. \tag{60}$$

Next, let $\boldsymbol{\Omega}_2$ denote the set of tuples (a, b, c, m, k) for which

$$m/k - \theta_1 \neq 0, \quad \Delta_*^{(m,k)} > 0, \quad (a, b, c, \Delta)\big|_{\Delta = \Delta_*^{(m,k)}} \in \boldsymbol{\Omega}_1, \tag{61}$$

where $\Delta_*^{(m,k)}$ is the value (60). It is easy to see that under conditions (61) the system (18) admits a traveling wave of the form (19) with number k. This wave is given by the equalities

$$x_j = x_*^{(m,k)}(t + (j-1)\Delta_*^{(m,k)}), \quad j = 1, 2, \ldots, m, \tag{62}$$

where $x_*^{(m,k)}(t) = x_*(t, \Delta)\big|_{\Delta = \Delta_*^{(m,k)}}$, and has a period $T_*^{(m,k)} = m\Delta_*^{(m,k)}/k$.

3. Traveling waves relaxation system

Let us now turn to the question of the existence of a similar (62) traveling wave in the original relaxation system (15). To do this, we first turn to the corresponding auxiliary equation (20). The analogue of theorem 1 here is the following statement.

Theorem 2. *Let us assume that the functions $f(u)$, $g(u)$, $h(u)$ appearing in (16) satisfy the monotonicity conditions*

$$f'(u) < 0, \quad g'(u) > 0, \quad h'(u) < 0 \quad \forall\, u \geqslant 0. \tag{63}$$

Then, for any set of parameters $(a, b, c, \Delta) \in \Omega_1$, one can specify a sufficiently small $\varepsilon_0 > 0$ such that for the specified a, b, c, Δ and for all $0 < \varepsilon \leqslant \varepsilon_0$ the equation (20) admits a periodic solution $x_*(t, \varepsilon, \Delta)$, $x_*(0, \varepsilon, \Delta) \equiv 0$ of period $T_*(\varepsilon, \Delta)$ with asymptotics

$$T_*(\varepsilon, \Delta) = T_*(\Delta) + O(\varepsilon), \qquad \max_{t \in [0, T_*(\varepsilon, \Delta)]} |x_*(t, \varepsilon, \Delta) - x_*(t, \Delta)| = O(\varepsilon), \ \varepsilon \to 0. \tag{64}$$

Here $x_*(t, \Delta)$ is a periodic solution to the equation (21) of period $T_*(\Delta)$, from the theorem 1.

Since the proof of the theorem formulated is based on general results from [15], we will limit ourselves to only describing its general scheme, consisting of three stages.

At the first stage, we fix sufficiently small $\sigma_0, \sigma_1 > 0$ and introduce into consideration the set S of initial functions $\varphi(t) \in C[-\Delta - \sigma_0, -\sigma_0]$ satisfying the conditions

$$|\varphi(t) - x_*(t, \Delta)| \leqslant \sigma_1 \ \text{for} \ -\Delta - \sigma_0 \leqslant t \leqslant -\sigma_0, \quad \varphi(-\sigma_0) = -(b+1)\sigma_0.$$

Next, let us denote by $x_\varphi(t, \varepsilon, \Delta)$, $t \geqslant -\sigma_0$ the solution to the equation (20) with an arbitrary initial function $\varphi \in S$. Based on the conditions of monotonicity (63) and the apparatus of differential inequalities, it is possible to show that the second positive root $t = T_\varphi(\varepsilon, \Delta)$ of the equation $x_\varphi(t - \sigma_0, \varepsilon, \Delta) = -(b+1)\sigma_0$ exists and is simple. Thus, the Poincaré succession operator is correctly defined on S

$$\Pi_\varepsilon(\varphi) = x_\varphi(t + T_\varphi(\varepsilon, \Delta), \varepsilon, \Delta), \quad -\Delta - \sigma_0 \leqslant t \leqslant -\sigma_0 \tag{65}$$

with values in $C[-\Delta - \sigma_0, -\sigma_0]$. A complete proof of the existence and simplicity of the second positive root of the equation for defining the Poincaré operator $\Pi_\varepsilon(\varphi)$ is given, for example, in articles [14] and [16]. This proof, with minor technical changes, is carried over to the case under consideration. Considering that the corresponding calculations are rather cumbersome, they are not given here.

At the second stage, we introduce into consideration the solution $\overline{x}(t, \varepsilon, \Delta)$ of the equation (20) with initial function $x_*(t, \Delta)$, $-\Delta - \sigma_0 \leqslant t \leqslant -\sigma_0$. Asymptotic integration of the corresponding Cauchy problem leads to the conclusion that as $\varepsilon \to 0$ the asymptotic equalities hold

$$T_\varphi(\varepsilon, \Delta)|_{\varphi = x_*(t, \Delta)} = T_*(\Delta) + O(\varepsilon), \ \max_{t \in [0, T_\varphi(\varepsilon, \Delta)]} |\overline{x}(t, \varepsilon, \Delta) - x_*(t, \Delta)| = O(\varepsilon). \tag{66}$$

The relations (66) mean that the function $x = \overline{x}(t, \varepsilon, \Delta)$ is an approximate (up to $O(\varepsilon)$) periodic solution of the equation (20).

At the third stage, consider the linear operator

$$A(\varepsilon, \Delta) = \partial_\varphi \Pi_\varepsilon(\varphi)|_{\varphi = x_*(t, \Delta)} : C_0[-\Delta - \sigma_0, -\sigma_0] \to C_0[-\Delta - \sigma_0, -\sigma_0], \tag{67}$$

where $\partial\varphi\Pi_\varepsilon(\varphi)$ is the derivative of the Fréchet operator (65),

$$C_0[-\Delta - \sigma_0, -\sigma_0] = \{\varphi(t) \in C[-\Delta - \sigma_0, -\sigma_0] : \ \varphi(-\sigma_0) = 0\}.$$

An asymptotic analysis of the linear equation corresponding to the equation (20) in variations on the solution $x = \overline{x}(t, \varepsilon, \Delta)$ allows us to conclude that the operator (67) admits a simple real eigenvalue $\lambda = \lambda_0(\varepsilon)$:

$$\lim_{\varepsilon \to 0} \lambda_0(\varepsilon) = \frac{b^2(a - c(b+1))}{a(b+1)(a+b+1)} < 1. \tag{68}$$

The rest of the spectrum of this operator lies in the ball $\{\lambda \in \mathbb{C} : |\lambda| \leqslant r(\varepsilon)\}$, where $r(\varepsilon) \to 0$ as $\varepsilon \to 0$.

To summarize, we note that the relations (66)–(68) guarantee applicability to the equation $\Pi_\varepsilon(\varphi) - \varphi = 0$ at the point $(\varepsilon, \varphi) = (0, x_*(t, \Delta))$ implicit mapping theorems. Thus, the operator (65) admits a fixed point $\varphi_*(t, \varepsilon, \Delta) \in S$, asymptotically close to $x_*(t, \Delta)$. It is also clear that in the original equation (20) this fixed point corresponds to a periodic solution, which, after an appropriate time shift, will transform into the desired periodic solution $x_*(t, \varepsilon, \Delta)$ with asymptotics (64).

From the first equality (64) it obviously follows that in the case

$$(a, b, c, m, k) \in \Omega_2 \tag{69}$$

for all sufficiently small $\varepsilon > 0$ the equation $T_*(\varepsilon, \Delta) = m\Delta/k$ allows for solution

$$\Delta_*^{(m,k)}(\varepsilon) = \Delta_*^{(m,k)} + O(\varepsilon), \quad \varepsilon \to 0. \tag{70}$$

In turn, substituting the relation (70) into $x_*(t, \varepsilon, \Delta)$, we obtain the function $x_*^{(m,k)}(t, \varepsilon)$, periodic with period $T_*^{(m,k)}(\varepsilon) = m\Delta_*^{(m,k)}(\varepsilon)/k$. This means that we have constructed a traveling wave of the system (15) of the form

$$x_j = x_*^{(m,k)}(t + (j-1)\Delta_*^{(m,k)}(\varepsilon), \varepsilon), \quad j = 1, 2, \ldots, m. \tag{71}$$

In principle, the question of the stability of the cycle (71) can be solved theoretically (see, for example, [8, 17]). However, the formulas obtained along this path cannot be analyzed by analytical methods. In this regard, we undertook a series of numerical experiments, consisting of two stages.

At the first stage, the parameters $a = 2, b = 1, c = 2$ and when the number of oscillators m changes from 10 to 50, it becomes clear at what values of k for the set of parameters (a, b, c, m, k) the inclusion (69) is valid. The choice of values a, b, c is largely random; the only requirement is that for different values of the number of oscillators m, the number of stable traveling waves should be as large as possible.

In Fig. 5 shows the dependence of the value $N(m)$, determined by the number of suitable values k, on the parameter $10 \leqslant m \leqslant 50$. It turned out that $N(m)$ grows with increasing m according to a nearly linear law.

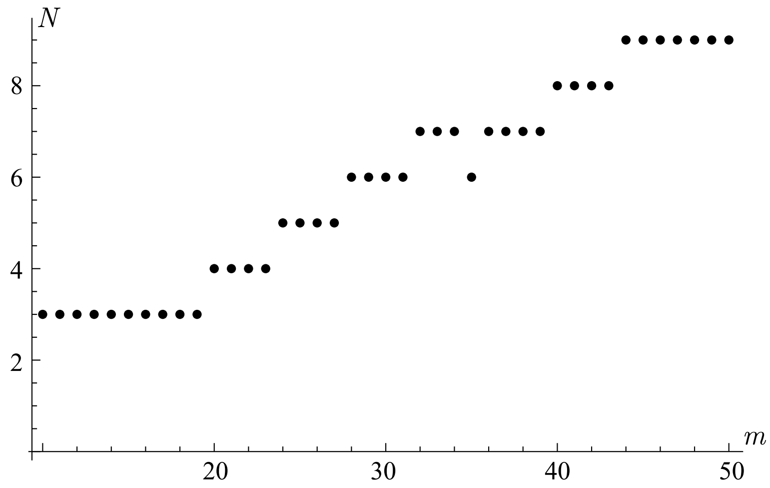

Fig 5. Number $N(m)$ of stable traveling waves (71) (suitable values of k) at $10 \leqslant m \leqslant 50$

At the second stage, for the sets of parameters to which traveling waves correspond, the relay system of equations with delay is numerically integrated (18). We use the VODE method, which checks the problem for rigidity and for non-rigid problems is the implicit Adams method, and for hard problems is the method from the BDF (backward differentiation formulas) class (see, [18]). The functions (62) for $-1 \leqslant t \leqslant 0$ with the addition of small random disturbance. Recall that these functions are known to us in explicit form. Based on the results of this integration, a conclusion is made about the stability or instability of the traveling wave with number k.

Calculations have shown that for the number of oscillators m from 5 to 20, only one of the available traveling waves turns out to be stable. At $m \geqslant 21$ it is possible to obtain two stable waves. It was not possible to obtain a larger number of coexisting stable waves within the framework of this experiment. At the same time, numerical calculations showed that the relay system (18), and therefore the relaxation system (15), also have other stable periodic regimes.

Fig. 6 shows the dependence on t of the first component $x_1(t)$ of a stable traveling wave of the system (18) for $m = 19$ and $k = 16$, all other components of the solution to this system represent the same function $x_1(t)$ with a shift corresponding to the wave number (см. формулу (71)).

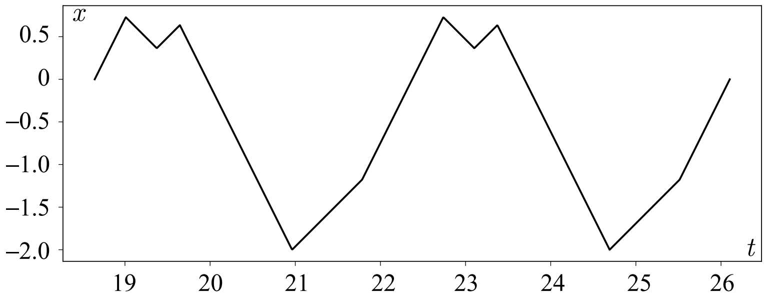

Fig 6. Dependence on t of the first component $x_1(t)$ of a stable traveling wave of the system (18) for $m = 19$ and $k = 16$

Conclusion

In this article, we rethought and refined the method of mathematical modeling of chemical synapses proposed in [8]. Unlike the model (10), its new version (14) fully takes into account the requirements of the Volterra structure of the corresponding equations and the hypothesis of saturating conductivity. In addition, as noted above, the so-called principle of uniformity is observed: the new mathematical model (14) is similar to the model of electrical synapses proposed in [14].

Concluding our consideration of the model (14), we note two unsolved problems. The first one is related to the threshold value $u = u_{**}$ from (8). In the case of the system (14), we initially assumed that the analogue of this value was equal to one. If this is not so, then instead of (14) we arrive at the system

$$\dot{u}_j = \lambda[f(u_j(t-1)) + b\,g(u_{j-1}/u_{**})h(u_j/u_{j-1})]u_j, \quad j = 1, 2, \ldots, m, \tag{72}$$

where $u_0 = u_m$, $u_{**} = \exp(\lambda\, d)$, $d = \text{const} \in \mathbb{R}$.

As in the case of (14), the (72) system corresponds to a similar (18) relay system

$$\dot{x}_j = 1 - (a+1)H(x_j(t-1)) + b\,H(x_{j-1} - d)[1 - (c+1)H(x_j - x_{j-1})],\ 1 \leqslant j \leqslant m, \tag{73}$$

where $x_0 = x_m$. Of interest is the problem of finding stable traveling waves, first for the limiting object (73), and then for the original system (72). It is clear that, by analogy with the analysis done in this work, the formulated problem can well be solved through an appropriate combination of analytical and numerical methods.

Another unsolved problem is to study the attractors of a similar (14) fully connected network of interacting neurons. The corresponding mathematical model has the form

$$\dot{u}_j = \lambda\Big[f(u_j(t-1)) + b\sum_{\substack{s=1\\ s\neq j}}^{m} g(u_s)h(u_j/u_s)\Big]u_j, \quad j = 1, 2, \dots, m, \tag{74}$$

where the functions f, g, h are the same as in (14), $b = \text{const} > 0$, $\lambda \gg 1$. According to the general results from [16, 19], both periodic modes of two-cluster synchronization and traveling waves can exist in the (74) system. The problems of finding these periodic solutions have not yet been solved.

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