Self-Sustained Relaxation Oscillations in Time-Delay Neural Systems

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Abstract. A new method to model the phenomena 'bursting' and 'buffering' in neural systems is represented. Namely, a singularly perturbed nonlinear scalar differential difference equation with two delays is introduced, which is a mathematical model of a single neuron. It is shown that for suitably chosen parameters this equation has a stable periodic solution with an arbitrary prescribed number of asymptotically high impulses (spikes) on a period interval. It is also shown that the buffering phenomenon occurs in a one-dimensional chain of diffusively coupled neurons of this type: as the number of components in the chain grows in a way compatible with a decrease of the diffusion coefficient, the number of co-existing stable periodic motions increases indefinitely.

1. Introduction

Self-sustained oscillations in neural systems have two characteristic features, the so-called bursting phenomenon and the buffering phenomenon. The first consists of the alternation of packets of pulses (strings of several spikes) and pieces of relatively moderate variation of the membrane potentials. The second term is commonly used in situations when an arbitrary prescribed number of co-existing attractors can be realized by an appropriate choice of parameters of the corresponding dynamical system.

The bursting phenomenon has been considered by many authors (see, for instance, [1, 2, 3, 4, 5] and the literature in these papers). To construct a mathematical model of this phenomenon, authors usually use singularly perturbed systems of ordinary differential equations with one slow and two fast variables, in which stable bursting-cycles (that is, periodic motions exhibiting the bursting phenomenon) can exist under certain assumptions. However, there is also another possible approach to this problem which is based on taking into account time delays.

The situation with the buffering phenomenon is somewhat different. Although it is quite common for nonlinear models in various fields of natural sciences [6, 7, 8, 9, 10], it has never got the appropriate attention in the neurodynamics literature. On the other hand this feature is important for neural sciences: it reflects a competitive interaction between different concepts and ideas in the neocortex part of human brain and can be used to explain the mechanisms behind associative memory. Thus we arrive at the problem of realizing both the phenomena described above in the framework of a single mathematical model. We put forward such a model in this paper.

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2. Description of the Mathematical Model

First models of the dynamics of the electric potential of neurons are due to A.L. Hodgkin and A.F. Huxley [11, 12], who presented a phenomenological model based on balance-type relations such that (if the parameters have been suitably chosen) its dynamics is consistent with experimental data about the oscillations of the membrane potentials of neurons.

Their model is quite complicated and many authors attempted to simplify it while preserving the main characteristic features of neural dynamics. The surveys [3, 4] present a list of requirements for a pulse neuron model and enumerated many model systems. The most important of these requirements is that a model has a stable periodic pulse-type regime. Another important condition is that the model must display the bursting phenomenon (for some values of parameters).

To describe the new mathematical model of an spiking neuron we use the fundamental idea in [11, 12] that a biological neuron can be replaced by an equivalent generator of electric oscillations. We shall only take into account the potassium and sodium currents, and take the maximum polarization level of the membrane for a reference point by assuming that $u(t) \geq 0$ is the deviation of the potential from this level. Then, discounting the leakage current, we can write the current balance equations:

$$c\dot{u} = -I_{\mathrm{Na}} - I_{\mathrm{K}}, \tag{1}$$

where $c > 0$ is usually called the membrane capacity.

To construct a reasonable model we make several additional assumptions.

Assumption 1. *We assume that the currents I_{Na} and I_K can be represented as follows:*

$$I_{Na} = -\chi_{Na}(u) \cdot u, \qquad I_K = -\chi_K(u) \cdot u, \tag{2}$$

where $\chi_{Na}(u)$ and $\chi_K(u)$ are functions characterizing the sodium and potassium conductance.

Assumption 2. *We assume that $\chi_{Na}(0) = -\alpha_0$ and $\chi_{Na}(u) \to -\beta_0$ as $u \to +\infty$, where α_0 and β_0 are positive constants. We also assume that $\beta_0 > \alpha_0$.*

Assumption 3. *We assume that $\chi_K(0) = \alpha_1$ and $\chi_K(u) \to -\beta_1$ as $u \to \infty$, where α_1 and β_1 are positive constants, as above.*

Assumption 4. *We assume that the values of the potassium and sodium conductance lag behind the current value of the membrane potential. We take the value of the first, potassium lag for a unit of time and assume that the second lag is $h \in (0, 1)$. Thus we have $\chi_K = \chi_K(u(t-1))$ and $\chi_{Na} = \chi_{Na}(u(t-h))$.*

Assumption 5. *We assume that*

$$\chi_{\mathrm{Na}}(0) + \chi_{\mathrm{K}}(0) > 0. \tag{3}$$

We can present many arguments, biophysical and mathematical alike, in favour of these assumptions. We start with biophysical considerations. Relations (2) ensure that $u(t)$ is positive (as it must be) and reflect the traditional approach to use Volterra-type equations for simulating biophysical and ecological processes. We make the assumption that $\chi_{\mathrm{Na}}(0)$ is negative because for strong polarization ($u \ll 1$) there is a surplus of sodium ions on the inner surface of the membrane. Pumping them out of the cell is what ion transporters are for (see [12]). Since sodium ions are positively charged, this process reduces the membrane potential, so $\chi_{\mathrm{Na}}(u) < 0$ for $u \ll 1$. Now we go over to the behaviour of $\chi_{\mathrm{K}}(u)$. When polarization is strong, the flow of potassium ions is directed inside the cell thus contributing to the growth of the membrane potential, so $\chi_{\mathrm{K}}(u) > 0$ for $u \ll 1$. However, after passing the peak of the potential, the flow of potassium ions changes direction. Hence there exists a level of the potential such that $\chi_{\mathrm{K}}(u) < 0$

for values of u higher than this level. Thus we arrive at Assumption 3. As regards Assumption 4, we can only say that a conductance time lag is an important feature of ion channels, which must therefore be taken into account. And as regards inequality (3), it reflects the fact that when polarization is strong, the membrane potential is increasing. On the mathematics level, Assumptions 1–5 ensure that all the requirements for neural models stated above are fulfilled. Namely, we show below that equation (1) has periodic pulse regimes with an arbitrary prescribed number of pulses on a period interval.

Under the Assumptions 1–5, from (1) we obtain

$$c\dot{u} = [\chi_{\mathrm{Na}}(u(t-h)) + \chi_{\mathrm{K}}(u(t-1))]u. \tag{4}$$

It is easy to see that for $h = 1$ the model (4) reduces to the generalized Hutchinson equation, which was thoroughly investigated in [13]. Note that a model with one delay was constructed in [14] in a similar way.

For further analysis we reduce (4) to a more convenient form. To do this we set

$$\begin{gathered}\chi_{\mathrm{Na}}(u) = (\chi_{\mathrm{K}}(0) + \chi_{\mathrm{Na}}(0))f(u) - \chi_{\mathrm{K}}(0),\ \chi_{\mathrm{K}}(u) = \chi_{\mathrm{K}}(0) - (\chi_{\mathrm{K}}(0) + \chi_{\mathrm{Na}}(0))g(u),\\ \lambda = (\chi_{\mathrm{K}}(0) + \chi_{\mathrm{Na}}(0))/c.\end{gathered} \tag{5}$$

Then we obtain the equation

$$\dot{u} = \lambda[f(u(t-h)) - g(u(t-1))]u. \tag{6}$$

As previously, here $u(t) > 0$ is the membrane potential of a neuron. The positive parameter λ characterizes the speed of electric processes in the system, so it must be large; and h is a fixed parameter in the interval $(0, 1)$. As concerns the functions $f(u)$, $g(u) \in C^1(\mathbb{R}_+)$, where $\mathbb{R}_+ = \{u \in \mathbb{R} : u \geq 0\}$, in accordance with Assumptions 1–5 and equalities (5) we assume that they have the following properties:

$$\begin{gathered}f(0) = 1,\ \ g(0) = 0;\ \ f(u) = -a_0 + O(1/u),\ \ uf'(u) = O(1/u),\ \ u^2 f''(u) = O(1/u),\\ g(u) = b_0 + O(1/u),\ \ ug'(u) = O(1/u),\ \ u^2 g''(u) = O(1/u)\ \text{ as }\ u \to +\infty,\end{gathered} \tag{7}$$

where $a_0 = -\dfrac{\alpha_1 - \beta_0}{\alpha_1 - \alpha_0}$ and $b_0 = \dfrac{\alpha_1 + \beta_1}{\alpha_1 - \alpha_0}$ are positive constants. Examples of such functions are given by

$$f(u) = (1-u)/(1+c_1 u) \text{ and } g(u) = c_2 u/(1+u),\ \ c_1, c_2 = \text{const} > 0. \tag{8}$$

The main results of this paper concern relaxation properties of equations (6) and systems of coupled equations of this type. It is important to note that the model we obtain is quite meaningful: for parameters chosen appropriately it has regimes with a single spike on a period interval (for example, for $h = 1$), as well as regimes with any prescribed number of such spikes. In particular, we shall see that for any fixed positive integer n we can pick parameters h, a_0, and b_0 in (6) and (7) such that for any sufficiently large λ equation (6) has an exponentially orbitally stable cycle $u = u_*(t, \lambda)$ with period $T_*(\lambda)$, where $T_*(\lambda)$ approaches a finite limit $T_* > 0$ as $\lambda \to \infty$. Furthermore, on an interval of length $T_*(\lambda)$ the function $u_*(t, \lambda)$ shows precisely n asymptotically high impulses (of order $\exp(\lambda h)$) with duration $\Delta t = (1 + 1/a_0)h$ following one another, and u_* is asymptotically small for the rest of time. In other words, $u_*(t, \lambda)$ is a bursting-cycle for this choice of parameters.

We get a graphic impression of the relaxation properties of the bursting-cycle $u_*(t, \lambda)$ from its graph in the plane (t, u) (see Figure 1), which is plotted to scale $1 : 25$ in the case of $h = 1/26$ and $\lambda = 130$ for the functions in (8) with $c_1 = 0.5$ and $c_2 = 4$.

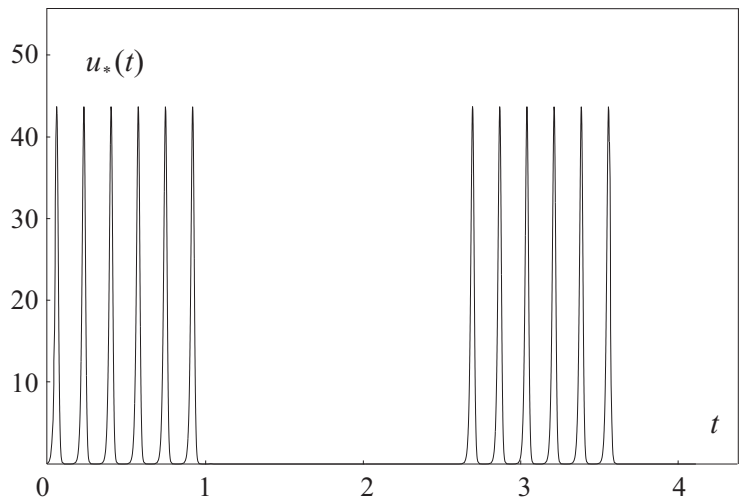

Figure 1. Stable periodic solution $u_*(t, \lambda)$ of equation (6) for $h = 1/26$ and $\lambda = 130$ for the functions in (8) with $c_1 = 0.5$ and $c_2 = 4$

As we have already said, (6) is a mathematical model of an isolated neuron. Now let us look at a one-dimensional chain of m such neurons, $m \geq 2$, each of which interacts with its two immediate neighbours. Then instead of (6) we obtain the system

$$\dot{u}_j = d\,(u_{j+1} - 2u_j + u_{j-1}) + \lambda[f(u_j(t-h)) - g(u_j(t-1))]u_j, \;\; j = 1, \ldots, m, \tag{9}$$

where $u_0 = u_1$, $u_{m+1} = u_m$, and the parameter $d > 0$, which has the order of 1, characterizes the strength of coupling between neurons. Clearly, system (9) possesses the so-called homogeneous (or synchronous) cycle

$$u_1 \equiv \ldots \equiv u_m = u_*(t, \lambda), \tag{10}$$

where $u_*(t, \lambda)$ is the stable periodic solution of (6). Our central result claims that for suitably decreased d and all $\lambda \gg 1$ this system has at least m exponentially orbitally stable inhomogeneous periodic motions (apart from the stable cycle (10); recall that m is the order of the system). We call each of these motions a discrete autowave process, or simply an autowave.

System (9) is the required mathematical model, in which buffering and the bursting phenomenon occur at the same time. In fact, we show below that all the m stable autowaves in this system are bursting-cycles. This means that each component u_j of an autowave, $j = 1, \ldots, m$, displays the same asymptotic behaviour as $u_*(t, \lambda)$ on a period interval. For each positive integer n we can pick parameters a_0, b_0, and h such that each of these components shows precisely n asymptotically high impulses on a period interval for these values of the parameters.

3. Relaxation Properties of a Single Neuron

In this section we investigate the question whether equation (6) has a stable relaxation bursting-cycle. In (6) we make the substitution $u = \exp(\lambda x)$, which takes this equation to the form

$$\dot{x} = F(x(t-h), \varepsilon) - G(x(t-1), \varepsilon), \tag{11}$$

where $F(x,\varepsilon) = f(\exp(x/\varepsilon))$ and $G(x,\varepsilon) = g(\exp(x/\varepsilon))$, $\varepsilon = 1/\lambda \ll 1$. It follows from the properties (7) of the functions $f(u)$ and $g(u)$ that

$$\lim_{\varepsilon\to 0} F(x,\varepsilon) = R(x),\ \lim_{\varepsilon\to 0} G(x,\varepsilon) = H(x),\ R(x) = \begin{cases} 1 & \text{for } x < 0, \\ -a_0 & \text{for } x > 0, \end{cases}$$
$$H(x) = \begin{cases} 0 & \text{for } x < 0, \\ b_0 & \text{for } x > 0. \end{cases} \tag{12}$$

Relations (12) allow us to proceed from (11) to the limiting relay equation with delays

$$\dot{x} = R(x(t-h)) - H(x(t-1)). \tag{13}$$

As in [13, 15, 16], we define the notion of a solution to (13) in a constructive way. To do this we fix an arbitrary positive integer n and assume that the parameters h, a_0, and b_0 in (6) and (7) satisfy

$$\frac{1}{(n+1)(2+a_0+1/a_0)} < h < \frac{1}{n(2+a_0+1/a_0)+2+1/a_0}, \tag{14}$$

$$b_0 > 1 + a_0. \tag{15}$$

Next we fix a sufficiently small $\sigma_0 > 0$ (we indicate an upper bound for σ_0 in what follows), consider the set of functions

$$\begin{aligned} &\varphi \in C[-1-\sigma_0, -\sigma_0],\ \ \varphi(t) < 0 \\ &\text{for } t \in [-1-\sigma_0, -\sigma_0],\ \ \varphi(-\sigma_0) = -\sigma_0 \end{aligned} \tag{16}$$

and let $x_\varphi(t)$, where $t \geq -\sigma_0$, denote the solution of (13) with an arbitrary initial function (16).

Concerning the integration of (13) we note that the right-hand side of this equation is a piecewise constant function, which changes value only when $x(t-h)$ or $x(t-1)$ changes sign. In particular, for $-\sigma_0 \leq t \leq -\sigma_0 + h$ we have simultaneously $\varphi(t-h) < 0$ and $\varphi(t-1) < 0$. Hence by (13) and (16) the function $x_\varphi(t)$ solves the Cauchy problem $\dot{x} = 1$, $x(-\sigma_0) = -\sigma_0$ on this interval of time, and therefore

$$x_\varphi(t) = t. \tag{17}$$

It is also clear that (17) holds as long as $x_\varphi(t-h) < 0$ and $x_\varphi(t-1) < 0$. Thus, it also holds for $-\sigma_0 \leq t \leq 0$.

In view of our constructions, for $0 \leq t < 1$ we have $x_\varphi(t-1) < 0$, so that $H(x_\varphi(t-1)) = 0$. Hence the solution $x_\varphi(t)$ satisfies the auxiliary equation

$$\dot{x} = R(x(t-h)) \tag{18}$$

on this interval. As regards equation (18), its properties were thoroughly analyzed in [13], where it was shown, in particular, that if a solution $x(t)$ of this equation satisfies $x(0) = 0$ and $x(t) < 0$ for $-h \leq t < 0$ then for $t \geq 0$ it must coincide with the periodic function

$$x_0(t) = \begin{cases} t & \text{for } 0 \leq t \leq h, \\ h - a_0(t-h) & \text{for } h \leq t \leq t_0 + h, \\ -a_0 h + t - t_0 - h & \text{for } t_0 + h \leq t \leq T_0, \end{cases} \qquad x_0(t+T_0) \equiv x_0(t), \tag{19}$$

where $t_0 = h(1+1/a_0)$ and $T_0 = h(2+a_0+1/a_0)$. Returning to (13) and taking into account all the above we arrive at the equality

$$x_\varphi(t) = x_0(t),\ \ 0 \leq t \leq 1. \tag{20}$$

For further analysis we require the special function $y_0(t)$ solving the Cauchy problem

$$\dot{x} = 1 - H(x_0(t)), \;\; x|_{t=0} = 0. \tag{21}$$

In view of (19), it is easy to see that for $t \geq 0$ this function is given by the relations

$$\begin{aligned} y_0(t) = \begin{cases} -(b_0 - 1)t & \text{for } 0 \leq t \leq t_0, \\ t - b_0 t_0 & \text{for } t_0 \leq t \leq T_0, \end{cases} \quad y_0(t) = (k-1)(T_0 - b_0 t_0) + \\ + y_0(t - (k-1)T_0) \;\text{ for }\; (k-1)T_0 \leq t \leq kT_0, \;\; k \in \mathbb{N}, \;\; k \geq 2. \end{aligned} \tag{22}$$

We note that condition (15) ensures the following properties of y_0:

$$y_0(t) < 0 \;\; \forall\, t \geq 0, \;\; \lim_{t \to +\infty} y_0(t) = -\infty. \tag{23}$$

Now we consider the next time interval $1 \leq t \leq 1 + h$. Note that because of (14), $t = 1$ lies in the interval $(nT_0 + t_0 + h, (n+1)T_0)$. Hence, from (19) and (20) we obtain $x_\varphi(t - h) < 0$ for $t \in [1, 1 + h]$, so that the function $x_\varphi(t)$ solves a Cauchy problem similar to (21) on this interval:

$$\dot{x} = 1 - H(x_0(t-1)), \;\; x|_{t=1} = x_0(1).$$

Hence, for $1 \leq t \leq 1 + h$ we conclude that

$$x_\varphi(t) = x_0(1) + y_0(t-1). \tag{24}$$

In the next step we observe that if we know a priori that

$$x_\varphi(t - h) < 0 \tag{25}$$

then (24) also holds for $1 \leq t \leq 2$. However, (25) holds indeed because, by (14) and (19)

$$x_0(1) = x_0(1 - nT_0) = 1 - (n+1)T_0 < 0 \tag{26}$$

and from (23) we obtain $y_0(t-1) < 0$ for $t \geq 1$. Thus (24) holds for $1 \leq t \leq 2$.

For $t \geq 2$ we shall assume by (25) that we have the a priori estimate

$$x_\varphi(t-1) < 0. \tag{27}$$

Then the solution $x_\varphi(t)$ in question solves the Cauchy problem

$$\dot{x} = 1, \;\; x|_{t=2} = x_0(1) + y_0(1),$$

so that it can be defined by the formula

$$x_\varphi(t) = t - T_*, \quad T_* = (n+1)(T_0 + b_0 t_0), \tag{28}$$

which follows from (22) and (26). It remains to add that by (24) and (28) the a priori assumptions (25) and (27) are certainly valid on the interval $2 \leq t \leq T_*$, and by the inequality $T_* - 2 > 0$ (following from (14) and (15)) this interval has positive length.

Now we will assume that the parameter σ_0 (see (16)) satisfies

$$\sigma_0 < (n+1)T_0 - 1. \tag{29}$$

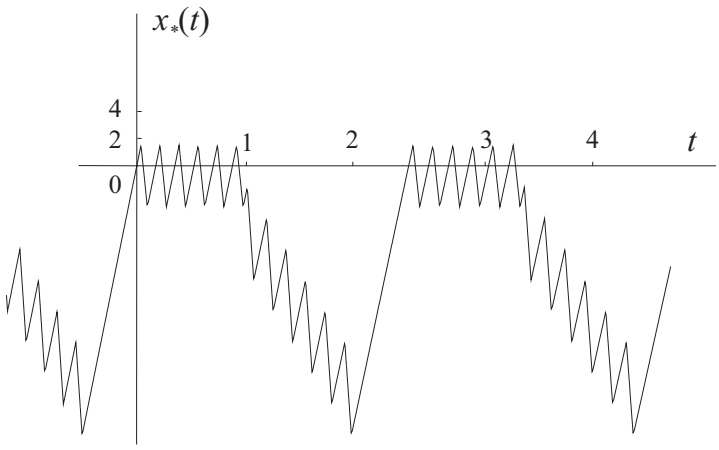

Figure 2. Function $x_*(t)$ for $a_0 = 2$, $b_0 = 4$, and $h = 1/26$ (inequalities (14) with $n = 5$ hold for these values of the parameters)

Then it follows from the above constructions that $x_\varphi(t + T_*)$, $-1 - \sigma_0 \le t \le -\sigma_0$, is a function of the set (16) and the equation $x_\varphi(t - \sigma_0) = -\sigma_0$ has precisely $2n + 2$ zeros on the interval $(0, T_*]$. Thus for $t \ge -\sigma_0$ each solution $x_\varphi(t)$ with initial condition (16) coincides with the same T_*-periodic function

$$x_*(t) = \begin{cases} x_0(t) & \text{for } 0 \le t \le 1, \\ x_0(1) + y_0(t-1) & \text{for } 1 \le t \le 2, \\ t - T_* & \text{for } 2 \le t \le T_*, \end{cases} \qquad x_*(t + T_*) \equiv x_*(t). \tag{30}$$

We show the graph of this function for $a_0 = 2$, $b_0 = 4$, and $h = 1/26$ in Figure 2 (inequalities (14) with $n = 5$ hold for these values of the parameters).

Now we consider the connections between periodic solutions of (11) and (13). We have the following result.

Theorem 3.1. *For all sufficiently small $\varepsilon > 0$ equation* (11) *has a unique orbitally exponentially stable cycle $x_*(t, \varepsilon)$, $x_*(-\sigma_0, \varepsilon) \equiv -\sigma_0$, whose period $T_*(\varepsilon)$ satisfies the limit relations*

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

We omit the full proof of this theorem and refer the reader to [13, 16] for technical details. We only present the scheme of the proof.

Apart from the constant σ_0 satisfying (29), we also fix $q_1 > \sigma_0$ and $q_2 \in (0, \sigma_0)$ and let $S(\sigma_0, q_1, q_2) \subset C[-1 - \sigma_0, -\sigma_0]$ denote the closed bounded set of functions φ satisfying the conditions $-q_1 \le \varphi(t) \le -q_2$ and $\varphi(-\sigma_0) = -\sigma_0$. Then for an arbitrary function $\varphi \in S(\sigma_0, q_1, q_2)$ we look at the solution $x = x_\varphi(t, \varepsilon)$, $t \ge -\sigma_0$, of equation (11) with the initial condition $x = \varphi(t)$ for $-1 - \sigma_0 \le t \le -\sigma_0$. We denote by $t = T_\varphi$ the $(2n + 2)$nd positive root of the equation $x_\varphi(t - \sigma_0, \varepsilon) = -\sigma_0$ (we assume that this equation has at least $2n + 2$ roots on the half-axis $t > 0$, which are numbered in ascending order). Finally, we define the Poincaré first return operator $\Pi_\varepsilon : S(\sigma_0, q_1, q_2) \to C[-1 - \sigma_0, -\sigma_0]$ by

$$\Pi_\varepsilon(\varphi) = x_\varphi(t + T_\varphi, \varepsilon), \quad -1 - \sigma_0 \le t \le -\sigma_0. \tag{31}$$

The rest of the scheme is standard (see [13] and [16]). First we prove that the solution $x_\varphi(t,\varepsilon)$, is asymptotically close to $x_*(t)$ as $\varepsilon \to 0$ uniformly with respect to $\varphi \in S(\sigma_0, q_1, q_2)$ and $t \in [-\sigma_0, T_* - \sigma_0/2]$. This implies that for appropriately chosen parameters σ_0, q_1, and q_2 the operator (31) is defined on the set $S(\sigma_0, q_1, q_2)$ and transforms it into itself. It remains to analyse the variational equation along the solution $x_\varphi(t,\varepsilon)$ and to verify that Π_ε is a contraction operator.

Additionally to Theorem 3.1, we point out that the relaxation cycle

$$u_*(t,\lambda) = \exp\big(x_*(t,\varepsilon)/\varepsilon\big)\big|_{\varepsilon=1/\lambda} \tag{32}$$

of equation (6) has the required asymptotic features of a bursting-cycle. In fact, its period $T_*(\lambda)$ satisfies $\lim\limits_{\lambda\to\infty} T_*(\lambda) = T_*$. Moreover, the cycle (32) shows $n+1$ successive asymptotically high impulses (of the order of $\exp(\lambda h)$) on the interval $0 \le t \le T_*(\lambda)$. These spikes correspond to the intervals $kT_0 < t \ < t_0 + kT_0$, $k = 0, 1, \ldots, n$, on which the function in (30) is positive. On the other hand, if t is a fixed moment of time in the set $[0, T_*) \setminus \bigcup_{k=0}^{n}[kT_0, t_0 + kT_0]$, then $u_*(t,\lambda)$ has order $\exp(-\lambda q)$, where $q = \text{const} > 0$.

4. Relaxation Properties of Neural Chains

Now we turn to system (9), where we assume, as before, that the parameters a_0, b_0, and h satisfy (14) and (15). For the analysis of this system we introduce new variables x, $y_1, \ldots, y_{m-1}$:

$$u_1 = \exp(x/\varepsilon), \ \ u_j = \exp\left(x/\varepsilon + \sum_{k=1}^{j-1} y_k\right), \ j = 2, \ldots, m, \ \ \varepsilon = 1/\lambda \ll 1. \tag{33}$$

Substituting (33) into (9) we obtain the relaxation system

$$\begin{gathered}\dot{x} = \varepsilon d\,(\exp y_1 - 1) + F(x(t-h),\varepsilon) - G(x(t-1),\varepsilon),\\ \dot{y}_j = d\,[\exp y_{j+1} + \exp(-y_j) - \exp y_j - \exp(-y_{j-1})] +\\ +F_j(x(t-h), y_1(t-h), \ldots, y_j(t-h), \varepsilon) - G_j(x(t-1), y_1(t-1), \ldots, y_j(t-1), \varepsilon),\\ j = 1, \ldots, m-1,\end{gathered} \tag{34}$$

where $y_0 = y_m = 0$, the functions F and G are as in (11), and the functions F_j and G_j have the following form:

$$F_j(x, y_1, \ldots, y_j) = \frac{1}{\varepsilon}\left[f\left(\exp\left(x/\varepsilon + \sum_{k=1}^{j} y_k\right)\right) - f\left(\exp\left(x/\varepsilon + \sum_{k=1}^{j-1} y_k\right)\right)\right],$$

$$G_j(x, y_1, \ldots, y_j) = \frac{1}{\varepsilon}\left[g\left(\exp\left(x/\varepsilon + \sum_{k=1}^{j} y_k\right)\right) - g\left(\exp\left(x/\varepsilon + \sum_{k=1}^{j-1} y_k\right)\right)\right].$$

Let us fix a positive constant σ_0 satisfying (29). Next we introduce at the interval $-\sigma_0 \le t \le T_* - \sigma_0$, where T_* is the quantity in (28). For $z = (z_1, \ldots, z_{m-1}) \in \mathbb{R}^{m-1}$ let $y_1^0(t,z)$, …, $y_{m-1}^0(t,z)$ denote the components of the solution of the impulse system

$$\begin{gathered}\dot{y}_j = d\,[\exp y_{j+1} + \exp(-y_j) - \exp y_j - \exp(-y_{j-1})],\\ j = 1, \ldots, m-1, \ \ y_0 = y_m = 0;\end{gathered} \tag{35}$$

$$\begin{gathered} y_j(h+kT_0+0) = y_j(h+kT_0-0) - (1+a_0)y_j(kT_0), \\ y_j(t_0+h+kT_0+0) = y_j(t_0+h+kT_0-0) - (1+1/a_0)y_j(t_0+kT_0), \\ y_j(1+kT_0+0) = y_j(1+kT_0-0) - b_0 y_j(kT_0), \\ y_j(1+t_0+kT_0+0) = y_j(1+t_0+kT_0-0) - (b_0/a_0)y_j(t_0+kT_0), \\ k=0,1,\dots,n, \quad j=1,\dots,m-1, \end{gathered} \tag{36}$$

which satisfies the initial condition

$$(y_1,\dots,y_{m-1})\big|_{t=-\sigma_0} = (z_1,\dots,z_{m-1}) \tag{37}$$

and is defined on this interval. Finally, we consider the map

$$z \to \Phi(z) \stackrel{\text{def}}{=} (y_1^0(t,z),\dots,y_{m-1}^0(t,z))\big|_{t=T_*-\sigma_0} \tag{38}$$

from $\mathbb{R}^{m-1}$ to $\mathbb{R}^{m-1}$.

Theorem 4.1. *To each fixed point $z = z_*$ of the map (38) which is exponentially stable or dichotomous there corresponds for sufficiently small $\varepsilon > 0$ a relaxation cycle $(x(t,\varepsilon), y_1(t,\varepsilon),\dots,y_{m-1}(t,\varepsilon))$ of system (34) with the same stability properties and which satisfies $x(-\sigma_0,\varepsilon) \equiv -\sigma_0$ and has period $T(\varepsilon)$. Furthermore,*

$$\begin{gathered} \lim_{\varepsilon\to 0} T(\varepsilon) = T_*, \quad \max_{-\sigma_0\le t\le T(\varepsilon)-\sigma_0} |x(t,\varepsilon) - x_*(t)| = O(\varepsilon), \\ \lim_{\varepsilon\to 0} \max_{t\in\Sigma(\varepsilon)} |y_j(t,\varepsilon) - y_j^0(t,z_*)| = 0, \quad \max_{-\sigma_0\le t\le T(\varepsilon)-\sigma_0} |y_j(t,\varepsilon)| \le M, \ \ j=1,\dots,m-1, \end{gathered} \tag{39}$$

where $x_*(t)$ is the function in (30), $M = \text{const} > 0$, and $\Sigma(\varepsilon)$ is the interval $[-\sigma_0, T(\varepsilon)-\sigma_0]$ from which the subintervals

$$\begin{gathered} (h+kT_0-\varepsilon^\delta, h+kT_0+\varepsilon^\delta), \ \ (t_0+h+kT_0-\varepsilon^\delta, t_0+h+kT_0+\varepsilon^\delta), \\ (1+kT_0-\varepsilon^\delta, 1+kT_0+\varepsilon^\delta), \ \ (1+t_0+kT_0-\varepsilon^\delta, 1+t_0+kT_0+\varepsilon^\delta), \ \ k=0,1,\dots,n, \\ \delta = const \in (0,1) \end{gathered}$$

have been removed.

We omit the proof of this theorem since for quite similar situations it was presented in [17] with details.

Theorem 4.1 is of fundamental nature as it reduces the problem of finding discrete autowave processes in system (9) to the problem of identifying stable fixed points of the map (38). We can represent this map in an invariant form, independent of the choice of σ_0. Let $P^t(z)$, $z \in \mathbb{R}^{m-1}$, $P^0(z) = z$, be the shift operator along the trajectories of system (35). It is easy to see that after the change of variables $P^{\sigma_0}(z) \to z$ the map (38) takes the invariant form

$$z \to \Phi_0(z) \stackrel{\text{def}}{=} (y_1^0(t,z),\dots,y_{m-1}^0(t,z))\big|_{t=T_*}, \tag{40}$$

where $(y_1^0(t,z),\dots,y_{m-1}^0(t,z))$ is the solution of the impulse system (35), (36) with the initial condition $(z_1,\dots,z_{m-1})$ for $t=0$ (analogous to (37)).

We start the investigation of attractors of the map (40) by analysing the stability properties of its fixed point $z=0$. We establish the following result by simple verification.

Theorem 4.2. *There exists a sufficiently small $d_0 > 0$ such that for all $d \in (0, d_0]$ the fixed point $z = 0$ of the map (40) is exponentially stable.*

Corresponding to the fixed point $z = 0$ there is a cycle of system (34) with components $x = x_*(t, \varepsilon)$, $y_j \equiv 0$, $j = 1, \ldots, m-1$, where $x_*(t, \varepsilon)$ is the periodic solution of (11) established by Theorem 2.1. In system (9) the same point corresponds to the homogeneous cycle (10), where $u_*(t, \lambda)$ is the function (32). Theorems 4.1 and 4.2 imply that this cycle is exponentially orbitally stable for each fixed $d \in (0, d_0]$ and all sufficiently large λ.

Now we look for stable fixed points of the map (40) which are distinct from $z = 0$ under the assumption $d \ll 1$. In this case we can asymptotically integrate (35), (36) for $0 \le t \le T_*$ and

$$(a_0, b_0) \in \mathcal{U}_1 \cup \mathcal{U}_2 \cup \mathcal{U}_3, \tag{41}$$

where

$$\mathcal{U}_1 = \{(a_0, b_0) : \ a_0 > 1, \ a_0 + 1 < b_0 < 2a_0\}, \ \mathcal{U}_2 = \{(a_0, b_0) : \ a_0 > 1, \ b_0 > 2a_0\},$$
$$\mathcal{U}_3 = \{(a_0, b_0) : \ 0 < a_0 < 1, \ b_0 > a_0 + 1\}.$$

Then we get the following result.

Theorem 4.3. *Let h, a_0, and b_0 be fixed parameters satisfying* (14) *and* (41)*. Then for all sufficiently small $d > 0$ the map* (40) *has m exponentially stable fixed points*

$$O_{r_0}(d) = (z_{1,r_0}(d), z_{2,r_0}(d), \ldots, z_{m-1,r_0}(d)), \ \ r_0 = 0, 1, \ldots, m-1, \tag{42}$$

such that for $(a_0, b_0) \in \mathcal{U}_1$ their location is determined by the asymptotic behaviour

$$\begin{aligned} z_{j,r_0} &= -\frac{b_0 - a_0}{a_0} \ln \frac{1}{d} + O(1), \ \ j = 1, \ldots, r_0; \\ z_{j,r_0} &= \frac{b_0 - a_0}{a_0} \ln \frac{1}{d} + O(1), \ \ j = r_0 + 1, \ldots, m-1 \end{aligned} \tag{43}$$

as $d \to 0$, while for $(a_0, b_0) \in \mathcal{U}_2 \cup \mathcal{U}_3$ their asymptotic behaviour is as follows:

$$z_{j,r_0} = -\ln \frac{1}{d} + O(1), \ \ j = 1, \ldots, r_0; \ \ z_{j,r_0} = \ln \frac{1}{d} + O(1), \ \ j = r_0 + 1, \ldots, m-1, \tag{44}$$

as $d \to 0$.

We do not justify this result here and refer the reader to [18], which contains the proof in a quite similar case.

Theorem 4.1 leads in combination with the asymptotic properties of the map (40) (see Theorems 4.2 and 4.3) to the main result of this paper.

Theorem 4.4. *Let h, a_0, and b_0 be fixed parameters satisfying* (14) *and* (41)*. Then for any sufficiently small d_1 and d_2, $d_2 > d_1 > 0$, there exists a sufficiently large $\lambda_0 = \lambda_0(d_1, d_2) > 0$ such that for $d_1 \le d \le d_2$ and $\lambda \ge \lambda_0$ the system of m equations* (9) *has at least m exponentially orbitally stable spatially inhomogeneous cycles co-existing with the stable homogeneous cycle* (10).

It follows from this theorem that when we decrease d and when we increase λ and the number m of neurons in an appropriate way then the buffer phenomenon occurs in (9): the number of co-existing stable cycles increases unbounded. Moreover, all these cycles display the bursting phenomenon. In fact, by (39) each of these cycle has components u_j, $j = 1, \ldots, m$, with the asymptotic representation $u_j = \exp(\lambda x_*(t) + O(1))$ as $\lambda \to \infty$, $j = 1, \ldots, m$, which holds uniformly with respect to $t \in [0, T(\varepsilon)]$, where $x_*(t)$ is the function in (30). Hence, the graphs of the u_j are similar in shape to the graph in Figure 1, that is, they contain a string of $n+1$ spikes. To any given natural number n the parameters h, a_0, and b_0, we can be chosen select appropriately.

For example, on Figure 3 for $m = 5$ we show a graphs of components of one of the five coexistent stable periodic solutions of system (9) (parameter values are the same as above, $h = 1/26$, $\lambda = 130$, $c_1 = 0.5$ and $c_2 = 4$).

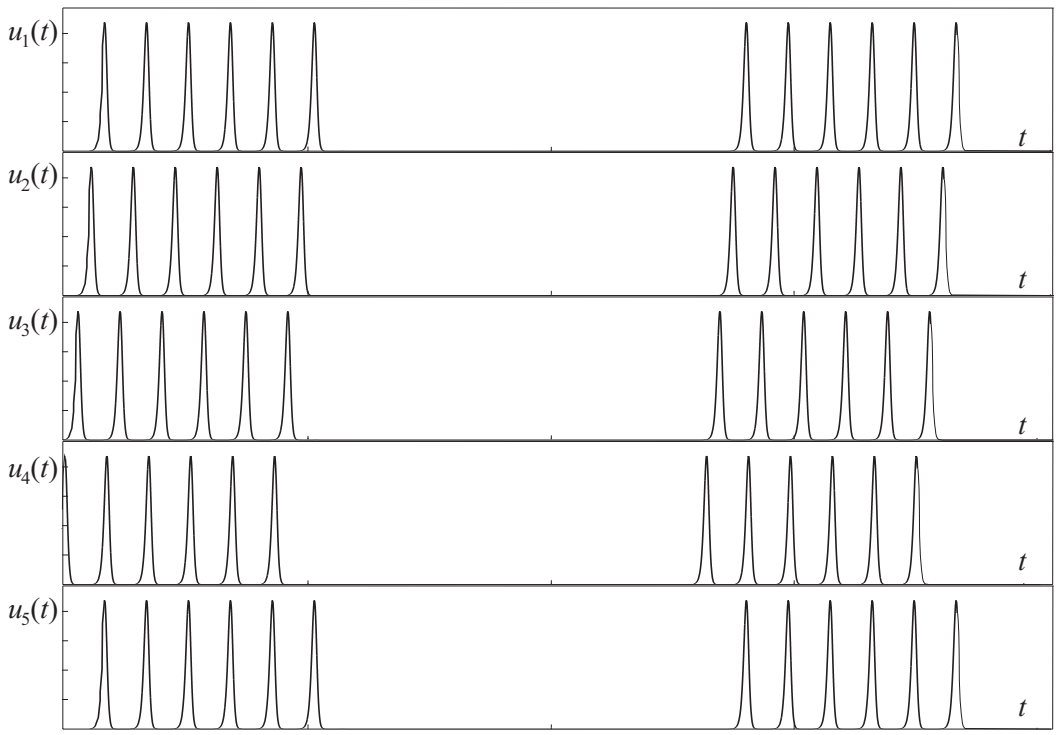

Figure 3. Components $u_1(t), \ldots, u_5(t)$ of the stable periodic solution of system (9) for $m = 5$, $h = 1/26$ and $\lambda = 130$ for the functions in (8) with $c_1 = 0.5$ and $c_2 = 4$

5. Conclusion

Mathematical results presented in the paper show that our new model (9) of single neuron operation combines simplicity of its form with rich dynamical properties. We show that this model can describe such fundamental neurodynamical phenomena as bursting-effect and buffer phenomenon.

Historically main attention of researchers was paid to "bursting behavior". This is not the case for buffer phenomenon. Although this phenomenon is one of the fundamental laws of operation of nonlinear systems from different fields [9, 10], it is still not properly described in neurodynamical literature. At the same time it is clear that buffer phenomenon is important for neuron subjects as it can be useful in describing the associative memory. We shall discuss this in detail.

According to [19, 20] in the simplest case associative memory operates like is shown on fig. 4. That is, there exist some storage medium implemented as a neuron system and storing blocks of data R_n, $n = 1, 2, \ldots, n_0$. Next, in order to obtain from system a certain result R_n it is necessary to feed to its input the corresponding symbolic key K_n and a certain additional data C_n referred to as context.

Now assume that storage medium mentioned above is described by equation (6) or by system of coupled equations of the form (9). Next, let parameters of this system be taken so that it permits n_0 coexistent stable cycles enumerated with $n = 1, 2, \ldots, n_0$. Finally, assume that with every such cycle connected is a corresponding data block R_n.

The operation of mathematical model described above is clear: in order to receive the necessary data R_n, we have to keep the system in a stable periodic regime with number n. This can be fulfilled by introducing the key $K_n = n$ and additional context C_n. We take as C_n the initial conditions of mentioned periodic regime.

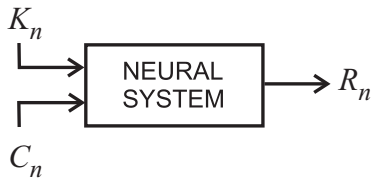

Figure 4. Model of memory with associative access

We should particularly mention the following feature. All the results presented in the paper hold for more general forms of $f(u)$, $g(u)$ from (9). That is, we can assume that as $u \to +\infty$, instead of (7) the following asymptotic equalities are valid

$$f(u) = -a_0 + O(1/u^{\gamma_1}), \quad uf'(u) = O(1/u^{\gamma_1}), \quad u^2 f''(u) = O(1/u^{\gamma_1}),$$
$$g(u) = b_0 + O(1/u^{\gamma_2}), \quad ug'(u) = O(1/u^{\gamma_2}), \quad u^2 g''(u) = O(1/u^{\gamma_2})$$

for arbitrarily fixed $\gamma_1, \gamma_2 > 0$.

Now we dwell on several unsolved problems. It might be interesting to look at the neural chain (9) for other boundary conditions. For example, we can set $u_0 = u_{m+1} = 0$ (Dirichlet-type conditions) or $u_0 = u_m$, $u_{m+1} = u_1$ (periodicity conditions). The question of autowave regimes in 2-dimensional lattices of diffusively coupled neurons of the form (6) is also of interest. Finally, it is still an open question whether the buffering phenomenon survives the transition from discrete chains (9) to the corresponding distributed model, when we set $d = m^2 D$ with $D = \text{const} > 0$ and let $m \to \infty$.

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