BIOPHYSICS OF COMPLEX SYSTEMS. MATHEMATICAL MODELS

FORMATION OF PULSES IN AN EXCITABLE MEDIUM*

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The paper considers the evolution of the initial perturbation in an excitable non-linear medium. The division of movements into "fast" and "slow" makes it possible to give a simple analytical description of all the stages of the process leading to the formation of divergent steady pulses with acute fronts.

1. The theoretical description of excitable structures now under intensive study in chemistry and biology (see for example [1, 2]) has so far run into considerable mathematical difficulties. Some results can be obtained by means of generalized models although many important properties of the process are fundamentally associated with the regulation of the system and their description requires solution of non-linear equations with partial derivatives. For a one-dimensional system of active elements with a diffusion link these equations in many cases may be written in the form

$$\mu\frac{\partial U}{\partial t}=D_U\frac{\partial^2 U}{\partial x^2}+\Psi(U,V),$$
$$\frac{\partial V}{\partial t}=D_V\frac{\partial^2 V}{\partial x^2}+\varphi(U,V), \tag{1}$$

where μ, D_U, D_V are constants and $\Psi(U, V)$, $\varphi(U, V)$ are given non-linear functions. Only some numerical solutions for non-steady processes in such systems are now known [2, 3]. The steady pulses of excitation have been considered in some detail but it is common to use for their analysis additional quite rigid simplifying assumptions [1, 4, 5].

Here we propose a simple analytical approach for obtaining a graphic picture of the processes of formation and spread of the pulses. The analysis is based on the fact that in actual conditions the processes, as a rule, have a relaxation character. Mathematically this means smallness of the parameter μ in the first equation (1). This point may as usual be used to separate the wave processes into "fast" and "slow".

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In the stage fast in time and occurring in a period of the order μ the function V does not have time to change and from (1) we get

$$\frac{\partial U}{\partial \xi} - D_U \frac{\partial^2 U}{\partial x^2} - \Psi(U, V) = 0, \qquad V = V(x), \tag{2}$$

where $\xi = t/\mu$ is the "fast" time. For slow processes it is possible to discard in (1) the term $\mu \frac{\partial U}{\partial t}$ obtaining first order equations in respect of t.

The possibility of isolating the fast and slow changes in the values in space is also important. If the characteristic scales of these changes are large as compared with the diffusion length $L = \sqrt{D_{U,V} \cdot T}$ (T is the characteristic time of the process), then the diffusion terms in (1) may be disregarded. As a result we get ordinary differential equations. In this approximation the changes in U and V occur independently at all points of space and again division into fast and slow movements in respect of t is possible. The fast changes in space have the form of quite sharp moving boundaries (falls) which generally speaking, are described by equation (2). Below, for specificity we set the form of the functions φ and Ψ as follows. $\varphi = -\gamma U - V$, $\Psi = V - f(U)$ where γ is a constant

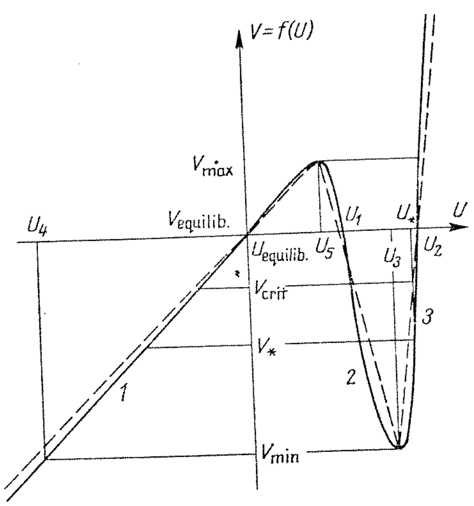

FIG. 1. Form of non-linear function of $f(U)$ (solid curve) and its bit-linear approximation (broken line).

and $f(U)$ has a N-shaped form (Fig. 1). Such an approximation is sufficient to describe the main features of the wave process and to obtain a solution in analytical form. We shall here consider that the equation of equilibrium $\gamma U = -V$ and $f(U) = V$ has only one solution U_{equilib}, V_{equilib}, corresponding to the stable state (see Fig. 1).

2. We shall first discuss the processes fast in time and described by the non-linear equation (2). Its solutions for V=const were already considered in [1, 6–8]. For the set $V=V_0$ in (2) it has either one or in the more interesting case, two and three states of equilibrium determined by the zeros of the function $\Psi(U, V_0)$. The points *1* (refractoriness) and *3* (excitation) in Fig. 1 correspond to the states stable in relation to

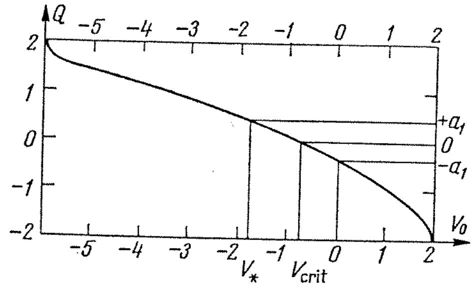

FIG. 2. Rate of steady fall as a function of the parameter V_0 for the broken line in Fig. 1 ($V_{max}=2$, $V_{min}=-6$; $U_5=2$; $U_3=4$; $U_2=4{\cdot}6$).

the fast movements. A special role among the solutions of (2) is played by the steady (running without deformation) wave in which U depends on one variable $\eta=x-a\xi$ (a—rate constant). The limited solutions of this type have the form of steady falls (separatrix) joining these points of equilibrium. It is necessary to distinguish waves taking the system from the unstable state (*2*) to the stable (*1* or *3*) from the transitions between two stable states. A particular case of waves of the first type (when $\dfrac{\partial f}{\partial U}$ is a monotonic function) was discussed for example, in [6]. There exists a set of such waves with arbitrary values of speed a, exceeding $a_{min}=2\sqrt{D_U f_U'(2)}$ where f' (2) is taken at the point *2*. In our case, of the greatest interest are the solutions of the second type joining the stable points *1* and *3* (see also [7]). To such solutions corresponds the single speed $a=a(V_0)$ the direction of which depends on V_0 and changes for a certain $V_0=V_{crit}$. The value V_{crit} is determined by the condition $\int_{(1)}^{(3)} \Psi(U, V_{crit})\,dU=0$. Since $a(V_{crit})=0$ and hence $\dfrac{\partial U}{\partial t}=0$ then for $|V-V_{crit}|\lesssim\mu$ the movement investigated cannot be considered fast in time and for the correct description of the process it is necessary to use the full system (1). As an example Fig. 2 gives the dependence $a(V_0)$ for a wave of the second type calculated analytically for the bit-linear function $f(U)$.

We would also note the intermediate case in which for $V_0=V_{max}$ or $V_0=V_{min}$ (see Fig. 1) the positions of equilibrium *2* and *3* or *1* and *2* merge. It is possible to show that, as with the waves of the first type, here there is a continuum of solutions joining the two special points.

These steady waves possess definite asymptotic properties. Thus, the wave of the first type with $a=a_{min}$ is asymptotic for the initial perturbations of a definite class occupying a restricted interval [6], the same applies to the single wave of the second type

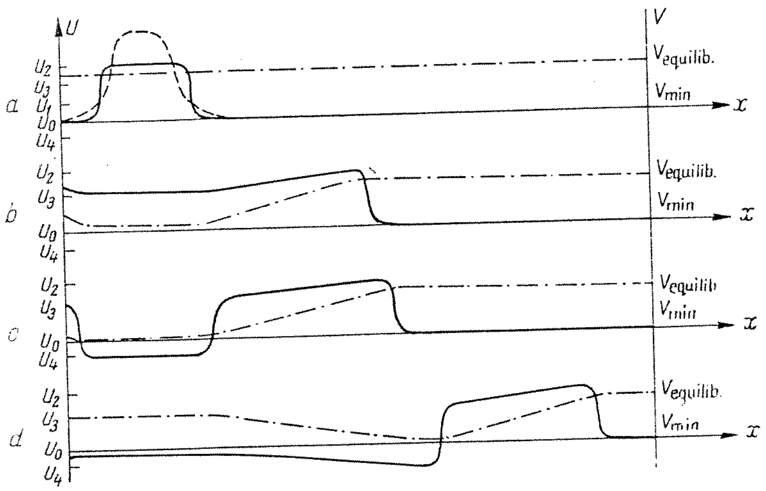

FIG. 3. Process of formation of pulses for $V > V_{crit}$ (solid line – U, dot-dash line – V).

[8]. It is also important to note that all the steady waves are exponentially stable in relation to minor (linear) perturbations. As a result it appears possible to state (although this statement cannot be considered to be strictly demonstrated in all cases) that any initial perturbation in the form of a sufficiently sharp drop in the function U with $V = V_0 = \text{const}$ in the "fast" period will lead to one of the steady running waves discussed above. Therefore, the whole region of excitation consists of portions of slow movements separated by rapid quasi-steady falls.

3. We shall now consider the process of evolution of the pulse in a relaxation medium using the division into "fast" and "slow" movements. We shall set a quite smooth initial perturbation of the function $U = U(x, 0)$, the characteristic dimension of which considerably exceeds the diffusion scale. The value V at the initial moment for simplicity will be taken as constant and equal to its equilibrium value $V_{equilib} > V_{crit}$.

In line with the above remarks the process of evolution of the pulse may be divided into the following stages (Fig. 3).

A. The initial profile of the perturbation (dot-dash line in Fig. 3*a*) rapidly (in the period $\Delta t \sim \mu$) changes and assumes an almost rectangular form (Fig. 3*a*). The margins of the pulse formed are shaped into steady drops of the second type and spread to different sides. The breakdown of the initial perturbation occurs symmetrically and, therefore, it suffices to follow the evolution of the pulse in one direction.

B. The margin of the pulse moves at a constant speed $a = a_1$ which is determined by the value $V_{equilib}$. The apex of the pulse is formed by slow movements independently at each point and its change may be found from an ordinary differential equation. The law of change in U in slow movement is given by the formula

$$\tau = \int_{U_2}^{U} \frac{df(U)}{-\gamma U - f(U)} = \tau(U_2, U). \tag{3}$$

C. When the values U and V reach the magnitudes U_3 and $V_{\min}$ there is a breakdown in the state of refractoriness with appearance of a new rapid steady fall–fall in the pulse (Fig. 3*c*). It begins to move at the speed $a_2 = a(V_{\min})$ to the same side as the first jump and together with it forms the pulse of excitation with a duration $\tau_H = \tau(U_2, U_3)$.

The further evolution of the pulse depends on the type of function $f(U)$. For a relatively symmetrical $f(U)$ always $a_2 > a_1$ and the fall in the pulse shifts to the region with $V > V_{\min}$ where its speed is clearcut. The length of the pulse monotonically falls. The rate of the jump diminishes and at the limit $t \to \infty$ it becomes equal to the speed of the front for $V = V_*$ (Fig. 1). As a result the whole pulse assumes a steady form, asymptotically compressed to the length $L_{st} = a_1 \tau (U_2, U_*)$ where U is found from the condition $f(U_*) = V_*$ (branch *3* in Fig. 1).

For a fundamentally non-symmetrical function $f(U)$ the case in which $a_2 \leqslant a_1$ is possible. The slow movements before the fall lead the points into the state with $U = U_3$, $V = V_{\min}$ from which there occurs the rapid breakdown into the state of refractoriness *I*, with a constant delay τ_H after excitation and, consequently, the speed of movement of the point of breakdown is always equal to a_1. The fall in the pulse corresponds to the steady wave of the "intermediate" type with $V = V_{\min}$; the speed of its spread $a(V_{\min})$ is equal to the speed of the front. The duration of the pulse does not change.

D. After passage of the pulse a zone of refractoriness forms where the points of the medium slowly return to the equilibrium state (Fig. 3*d*).

Thus, the non-steady process leads to the formation of a steady pulse. In one case this occurs asymptotically and, in the other, the pulse becomes steady immediately after the formation of a sharp fall. We would emphasize that the resultant pulse is a steady solution of the initial system (1). The acute front and fall are determined by the solutions of the "fast" equation (2) and are connected by slow movement which as such is not equilibrium at each point but thanks to the spatial correlation due to the movement of the front forms a steadily moving apex of the pulse.

The conclusions drawn above on the course of the process are confirmed by the calculations with the computer which were made by us for the initial system (1).

The pattern of the formation of the pulse described is realized for $V_{\text{equilib}} > V_{\text{crit}}$. If $V_{\text{equilib}} < V_{\text{crit}}$ and the initial perturbations corresponds to $V = V_{\text{equilib}}$, at the state *A* a square pulse again forms although its margins now move in the direction towards the middle. The perturbation "disperses" and disappears for a finite time.

The "fixed" falls with $V = V_{\text{crit}}$ not described by equation (2) alone, require special discussion. Here we would merely note that the possibility of the appearance of some auto-oscillatory regimes is associated with such falls.

As for the area of application of the phasic approach considered in actual situations it apparently is quite wide, in particular, for concentration waves in chemical systems. For example, in the case of the reaction of oxidation of bromomalonic acid by bromate catalysed by cerium ions [9] $\mu = 5 \times 10^{-3}$ and for the reactions considered in [2] $\mu = 1{\cdot}3 = 10^{-2}$. The equations describing the transmission of excitation over nerve fibre also contain a small parameter ($\mu \approx 5 \times 10^{-2}$) although for them the ation is somewhat more complicated.

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REFERENCES

Collection: Vibratory Processes in Biological and Chemical Systems (in Russian). **1**: 1967; 2: 1971
PRIGOGINE, I. and NIKOLIS, Zh., Uspekh. fiz. nauk, **109**: 517, 1973
SHCHERBUNOV, A. I., Biofizika **17**: 103, 1972
KRINSKII, V. I., Probl. kibern. **20**: 59, 1968
UNDROVINAS, A. I. *et al.*, Dokl. Akad. Nauk SSSR **204**: 229, 1972
BARENBLATT, G. I. and ZEL'DOVICH, Ya. B., Uspekh. mat. nauk **26**: 115, 1971
IL'INOVA, T. N. and KHOKHLOV, R. V., Radiotekh. i elektronika **8**: 2007, 1963
KANEL', Ya. I., Dokl. Akad. Nauk SSSR **132**: 268, 1960
ZHABOTINSKII, A. N. *et al.*, Kinetika i kataliz **12**: 584, 1971

THE WAVE REGIME OF THE ACTIVITY OF THE NEURONAL NETWORK*

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The paper considers the problem of the spread of the wave of activity in an homogeneous isotropic neuronal network. All the neurones are considered (in the subthreshold region) as possessing a finite memory as a summator of synaptic current. An expression is found for the synaptic current for the individual neurone in the regime of the steady spread of the wave activity. An equation is also obtained and analysed for the speed of the spread of the wave of activity; the possible limiting relations are considered. The results are compared with the Beurle analysis.

NUMEROUS investigations into possible modes of work of neuronal networks are known d in most cases nets not distributed in space and described by a matrix of interneu-nal links with an identical time of passage of the signal for each link are considered. ch an approximation, in fact, does not allow for the geometry of the link but only r its topological aspect. An exception (of course not the only one) is provided by the rk of Beurle [1] and Caianello [2] where an attempt is made to consider the wave activity in a distributed neuronal net [1] and equations are formulated describing

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