PATTERN FORMATION AND NEURAL MODELS

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Keywords: Open distributed systems, self-organization, autowaves, mechanochemical autowaves, mathematical models of morphogenesis, neuron-like systems, autowaves in the cerebrum structures, neurocomputers

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Summary

The theory of autowave processes in open distributed systems was started by the works of Fisher, Kolmogorov, Petrovskii, and Piskunov (1937) and was sharply accelerated by the works of Winner and Rozenblute (1946) and Turing (1952). Nowadays, one cannot find a field in theoretical biology in which the models of active distributed systems were not examined. These are: propagation of electrical excitations in the nerve fibers and tissues of cortex; the autowaves in electrically excitable systems of heart and intestine; the mechanochemical waves in living cells; the morphogenesis processes; the propagation of the epidemic autowaves, etc. In what follows, mathematical models of the autowaves in the systems “reaction–diffusion” and in the neuron-like systems with nonlocal connections are classified and considered. Various examples of such systems are presented and corresponding experimental data are given. The connection of autowaves in biology with processes in chemical systems is emphasized and their place in medicine is indicated. The role of the investigation of the neuron-like systems in designing the new neurocomputers is shown.

1. Introduction to the Pattern Formation Theory

All living systems are not only open non-equilibrium systems; they are also distributed in space. This means that all variables, i.e., the quantities to be found, are functions not only of time, but also of spatial coordinates. In fact, all parts of living system are connected in space among themselves. Such a connection can be realized by the diffusion of substances, hydrodynamic flows, migration of living species, mechanical stress waves, and electric signals. If velocities of the processes in a system of finite size are small as compared to the velocities of transfer processes, then such a system can be regarded as a “point” system. This means that a complete mixing occurs in the system, all processes are synchronous at every point of space, and the sought values are the functions only of time.

The biosphere, any biogeosenosis, any complex organism from higher plants and mammals to the simplest single-celled organisms are open distributed non-equilibrium systems (ODNES). In a complex system, it is possible to separate the ODNES that are its subsystems, for example, the nerve system of animals or the electricity conducting system in herbs. All real ODNES are to some extent heterogeneous systems, whose parameters depend on the coordinates and often on time: for example, the illumination conditions, temperature, etc. vary. Even such a classic example of an active ODNES as a squid’s axon changes a little its radius and other parameters. The same can be said about the small intestine or the giant cell, Physarum policephalum, in which complex peristaltic wave motions occur ensuring the push-pull flows of the intestine’s content or plasma.

There is one more important feature of the ODNES: they all slowly evolve in time: not only the exterior conditions vary, but the number of variables participating in the evolution changes and new chemical substances and new kinds of living species appear.

The biosphere as a whole continuously evolves. But, even if one regards an ODNES as a completely homogenous and uniform system with parameters independent of time, it is impossible to suggest a unified and observable mathematical model. However, as for the point systems, one can propose a number of basic models with increasing complexity for the homogeneous ODNES. We start with the models with local (diffusive) connections in space and then consider neuron-like models with nonlocal connections.

2. Mathematical Models of Autowave Systems of the Type “Reaction–Diffusion” or the Models with Local Connections

2.1. Basic Model of an Autowave System. Classification of Autowave Processes in Living Systems

An autowave process (AWP) is understood as a self-maintained wave process (including stationary structures) that preserves its characteristics constant at the expense of the energy of a source of energy and matter distributed in the medium. Period, wave length (or pulse length), propagation velocity, etc. are such characteristics. The amplitude and form in a steady regime depend only on local properties of the medium and are independent of initial conditions. The AW are an analogue of self-oscillations in a concentrated of point system, (the term AW was suggested by R.V. Khokhlov) and a connection of diffusion type is assumed in space.

Let $x_i\ (t,\mathbf{r})$ be the components interacting between themselves, and let $\mathbf{r}$ be a vector defining a point in a 1D, 2D, or 3D space. The following physical quantities can serve as x : temperature, difference of electric potentials, concentration of chemical substances, the number of living species of given kind per a unit of volume or area, and so on. In this case, a model is presented by the equations of material balance:

$$\partial x_i / \partial t \ = \ F_i(x_1, x_2, \ldots, x_n) \ - \ \mathrm{div}\, \mathbf{I}_i \tag{1}$$

Here, $\mathbf{I}_i$ – is the flux of the *i*-th component:

$$\mathbf{I}_i = \ \mathbf{V} x_i - \sum_{k=1}^{n} D_{ik} \ \mathrm{grad}\, x_k \quad , \tag{2}$$

where $\mathbf{V}$ **–** is directed velocity of a component and D_{ik}– is the matrix of diffusion coefficients, *i*, *j* = 1,2,…..*n*. Its diagonal terms are the coefficients of self-diffusion x_i , and the off-diagonal terms are called the coefficients of interdiffusion; they account for the fluxes of an *i*-th component induced by the flows (gradients) of the *k*-the component. The equations of type (1) describe a wide class of processes: formation of turbulence, chemical kinetics under conditions of convection, formation of waves in excitable living tissues, etc. However, even a simplified model (at $\mathbf{V} = \mathbf{0}$) opens a possibility to describe and comprehend a host of complex phenomena. For the sake of simplicity, let us write this model for the case of the 1D space:

$$\frac{\partial x_i}{\partial t} = F_i\left(x_1, x_2, \ldots . x_n\right) + \frac{\partial}{\partial r}\left[\sum_{k=1}^{n} D_{ik}\left(x_1, x_2, \ldots .., x_n\right) \frac{\partial x_i}{\partial r}\right] \tag{3}$$

or, in a simpler case, when D_{ik} are independent of x_i :

$$\frac{\partial x_i}{\partial t} = F_i\left(x_1, x_2, \ldots\ldots\ldots, x_n\right) + \sum_{k=1}^{n} D_{ik} \frac{\partial^2 x_k}{\partial r^2} \qquad (3a)$$

Here, as in (1), F_i - are nonlinear functions describing the interaction of components. Boundary conditions for (1)–(3) are determined by specific problems; most often, the impenetrability conditions at the ends of a finite interval $[0,\ L]$ are imposed:

$$\left.\frac{\partial x_i}{\partial t}\right|_{\substack{r=0\\ r=L}} = 0 \qquad (4)$$

At final L and $D_{ik} \to 0$, the mixing in the "volume" $[0,\ L]$ occurs at a sufficiently fast rate, the processes in all its parts are synchronous, and the system is described by the point system:

$$dx_i / dt = F_i(x_1, x_2, \ldots, x_n) \qquad (5)$$

An analysis of system (5) always precedes the examination of the basic model.

2.2. Classification of the Autowave Processes

The following types of AW that can be described by the basic Eqs. (1)-(3) are well known.

- The propagation of a single excitation front: motion of the boundary of phase transition or of the trigger-front, i.e., the Traveling front (TF).
- Propagation of a pulse of stable form (TP).
- Autonomous localized sources of waves (ASW).
- Standing waves (SW).
- Reverberator (RB)
- Synchronous self-oscillations in space (SSO).
- Quasistochastic AW or patterns (QSAW).
- Stationary in time inhomogeneous distributions in space, the dissipative structures (DS).Note that some understand the DS as a broader concept. For example, the self-oscillations in various generators are included in [3].

This classification is based on demonstrative physical concepts, and it is mathematically justified by the existence of such self-similar variables that the transition to the latter can significantly decrease the dimensionality of the space of the original model. In a self-similar model, the structures are represented by special trajectories between the stationary points or the limit cycles in a phase or configuration space. The possibility to single out such trajectories is conditioned by the fact that they are either attracting or differentiating. The AWP have a certain similarity with the solitons that arise in a nonlinear conservative medium. However, the behavior of solitons is quite different from the behavior of the AWP. The solitons restore their form and velocity after a collision, while the TP and TF annihilate each other in collision.

2.3. Experimentally Observed Autowaves

In Tables 1, 2 the summarized data on processes observed in various biological systems are presented. For the sake of commonality, they also contain the data on the AWP in chemical, physical, and some technological systems. The AWP in population systems are also considered in other related chapters, for example, the propagation of waves in populations.

Object	**Specific velocity**	**AWP type**
Physical		
Polymeric film	10^{-2} - 10 cm/min	TF
Boiling film	0 - 1 cm/s	DS, TF
Semiconductor film on a substrate	1 cm/s	TF, TP
Magnetocrystal film	10^{4} m/s	TF
Electron-hole plasma (n-GaAs)	0	DS
Technical		
Networks of connected self-generators		SA
Active RC-line		TF
Distributed luminescent image transformers		DS
Distributed luminescent image transformers		TF, TP, DS,
Neuron-like two-dimensional optic active medium with positive nonlocal feedbacks and their television analogues		REV,SAW, QSAW
Laboratory plasma of a gaseous discharge		DS, TP
Superconducting wire		TF
Chemistry		
Combusting media		TF
Barretor (conducting wire in H_2 and/or He atmosphere)	0 - 2 cm/s	DS, TF
Belousov-Zhabotinsky reactions	10^{-2} - 10 cm/s	DS, SA, TP
Iron wire in nitric acid	2 m/s	TP
Oxidation reaction of ammonia on platinum	0.5 cm/s	TF
Oxidation reaction of carbon monoxide	5 m/s	TF
High-temperature synthesis (titanium-carbon and other similar chemical reactions)	1 - 15 cm/s	TF
Halogenation reaction and hydrohalogenation of solid hydrocarbons at low temperatures	0.1 - 2 cm/s	TF
Polymerization reactions of an epoxidal oligomere by the amines	10^{-2} cm/s	TF
Biological		
Squid axon		
Conducting system of the heart	21 m/s	TP
Myocardium muscle	25 - 300 cm/s	TP, AWS
Nonstriated muscles	30 cm/s	TP

Neuron networks: a) fast waves	5 - 10 cm/s	TP, AWS
Neuron networks: b) slow waves	10 - 50 cm/s	TP
Retina	2 - 5 mm/min	TP, AWS
Active filaments in algae	2 - 5 mm/min	TP, AWS
Corals	50 μm/s	TP
Plasmodium of myxomycetes	50 μm/s	TP
Populations of amoeboid cells	10 - 50 μm/s	SO, TP, AWS
Populations of speedy lizards	1 - 5 μm/s	TP, AWS
Formation of thrombus-patterns in blood vessels		

Notes:

(i) For an AW media in technology and for combusting substances, the order of magnitude of specific velocities depends on particular conditions and special features of devices, so we do not present these data here.

(ii) AWP in morphogenesis — see Table 3.

Table 1: Experimentally observed autowave processes

Beside the search for sufficient existence conditions for the AWP in the general form, the formulation of the basic 1D-, 2D- and 3D-models of the AWP is also a subject of mathematical modeling.

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Bibliography

1. Vasilev V.A, Romanovskii Yu.M.,Chernavskii D.S., and Yakhno V.G.(1987). *Autowave processes in Kinetic Systems*. VEB Deutscher Verlag der Wissenschaften, Berlin; D.Reidel Publishing Company, Dordrecht, Boston, Lancaster, Tokyo. [Various experimental results and mathematical models involving physical, chemical and biological objects and the fundamentals of the autowave theory are reviewed.]

2. Ebeling W. and Feister R.(1989). *Evolution of Complex Systems*. Kluwer, Dordrecht. [Brief scenario of physical evolution, oscillations and chaos in mechanical, electrical, chemical, and biological systems.]

3. Nicolis G, and Prigogine I., (1977). *Self-organization in nonequilibrium systems. From dissipative structures to order through fluctuations*. John Wiley & Sons, New York, London, Sidney, Toronto. [The appearance of order in the open distributed nonequilibrium systems is considered, in particular, the self-oscillations and autowaves in chemically active mediums, prebiotic evolution, various level of the regulation in biological systems.]

4. Belintsev B.N**. (**1991) *Physical Bases of Biological Pattern Formation*. Moscow, Nauka. (in Russian) [Mathematical models of the morphogenesis, based on the theory of distributed structures are designed and examined with regard to the mechanical stresses in developing embryo.]

5. Meinhardt H. (1999) *The Algorithmic Beauty of Sea Shells*, Berlin, Heidelberg, N.Y. Springer Verlag.

[Models of growth, making the form, and paining of a sea shell are considered in detail. It was shown, haw appear the variations of form. A diskette is attached containing the algorithms for obtaining the desired structures.]

6. Romanovskii Yu.M. and Teplov V.A. (1995) *The physical bases of cell movement. The mechanisms of self-organization of amoeboid motility*. Physics Uspekhi, vol. 38, 521—542. [The protoplasm of amoeboid cells is considered as an active medium, in which the gel-like structures continuously assemble and disassemble. A number of mathematical models of these movements in Physarum plasmodium and in Amoeba proteus are presented.]

7. Field R.J. and Burger M. (1984). *Oscillations and traveling waves*. N.Y. [The autowave processes are considered in chemical reactions and, in particular, in the Belousov–Zhabotinskii reactions.]

8. Murray J.D. (1977) *Lectures on Nonlinear Differential Equation. Models in Biology*. Clarendon Press. Oxford.[Special attention is paid to the dependence between the transfer mechanisms and chemical reactions, and also to the consistent application of asymptotic methods to nonlinear models.]

9. Yakhno V.G. (1955) *Basic models of hierarchy neuron-like systems and ways to analyze some of their complex reactions*. “Optimal Memory & Neural Network”, vol. 4, № 2, 141–155. [Space-time solutions are considered for the models of homogeneous neuron-like mediums. The applications are discussed to medicine and to systems of parallel processing of complex information flows.]

10. M.A.J. Chaplain, G.D. Singh, and J.C. McLachlan Eds.(1999). On Growth and Form: *Spatio-temporal Pattern Formation in Biology*. Wiley: Chichester. [The book contains an interplay of processes across scales of biological organization from cell and molecular biology up to functional morphology and an overview of the state-of-the art in the mathematical modeling of spatio-temporal systems.]

Biographical Sketch

Yuri Romanovsky worked from 1967 to 1981 at the Lomonosov Moscow State University, in the department of physics, first as an assistant professor and then as a full professor and head of the laboratory of laser and mathematical biophysics. He is a well-known specialist in the field of nonlinear dynamics, radio physics, and theoretical biophysics. In the recent years, he has been working in the biophysics of the motility of living cells, bioelectric processes in the higher plants, and molecular dynamics of the proteins–enzymes. He is the author of five monographs in radio physics, biophysics, and synergetics.