Autowave processes in distributed kinetic systems

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The basic experimental data and the theory for autowave processes in active kinetic systems are reviewed. Each volume element in such a system is in a state far from thermodynamic equilibrium, and the different volume elements are coupled by transport processes. Some examples of these systems are certain chemical and biological objects in which various types of waves and stable structures can be produced. Mathematically, autowave processes are described by quasilinear and nonlinear parabolic equations. These autowave processes are quite different from processes which occur in conservative systems, e.g., solitons. A classification of autowave processes is offered, and the experimental data are summarized. In accordance with this classification, the review itself is organized in sections on the physics of the basic models for autowave systems in a one-dimensional space and qualitative methods for studying them. The basic cases are wave propagation, autonomous wave sources, spontaneous oscillations and quasistochastic waves which are synchronized over the entire space, and the formation of dissipative structures. At present, the primary fields of application of the theory of autowave processes are neural conductivity, combustion, self-organization in living systems, etc. The necessary conditions for these autowave situations are listed.

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CONTENTS

"... In the complex field of nonlinear oscillations, some specific general concepts, positions, and methods will crystallize and be adopted for general use by the physicist to an even greater extent than is the case today. These concepts, positions, and methods will become obvious and natural, and they will enable the physicist to analyze complicated sets of phenomena. They will become a powerful heuristic tool for new research.

The physicist interested in the modern problems of oscillations must, in my opinion, be taking this approach right now. He must understand the existing mathematical methods and approaches which are at the basis of these problems, and he must learn how to use them."

L. I. Mandel'shtam

(Preface to the book Theory of Oscillations, by A. A. Andronov, A. A. Vitt, and S. É. Khaikin, published in 1935)

INTRODUCTION

Active distributed systems are a subject of considerable interest in several scientific disciplines. A variety of complex wave processes can form, propagate, and be

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transformed in distributed systems. Important examples of these active media are discussed in recent monographs and reviews in nonlinear optics, hydrodynamics, and plasma physics. The theory of wave processes has been described in the pages of this journal.[1-4,6]

Over the last decade, the methods of the theory of nonlinear oscillations have come into use for the study of entirely new phenomena in "active kinetic systems." In chemistry and biology these are media in which autocatalytic reactions occur, biologically active membranes and tissue, and communities of living organisms. Some characteristic features of active kinetic media are as follows: (a) There is a distributed source of energy or of energy-rich substances. (b) Each volume element of the medium is far from thermodynamic equilibrium; in other words, it is an open thermodynamic system in which some of the energy supplied by the distributed source is dissipated. (c) A volume element is coupled with neighboring volume elements by transport processes.

By analogy with self-excited oscillator systems, R. V. Khokhlov has suggested that kinetic systems in which waves or structures can arise as the result of an instability of a homogeneous state be called "autowave" systems.[1)]

Some scientists abroad single out the theory of spontaneous organization and, in particular, the theory of wave processes and structures in complex systems of various natures, as a separate science: "synergetics."[7] The theory of autowave processes, in contrast, is presently treated as a branch of general biophysics.[8]

The theory of autowave processes is of particular importance for a rapidly developing branch of theoretical biology: the mathematical simulation of biological kinetics at various levels of life. The primary goal of this approach is to develop simple "basic" mathematical models of extremely complex objects such as neurons, differentiating cells, the chemical-mechanical organs of motion, "life waves" in ecological systems, and several others. In addition, there are some manmade media, or physical analogs, in which autowave processes evolve in much the same way as they would in chemical and biological systems. The main requirement imposed on these "basic" models is that it be possible to qualitatively predict the bifurcations, discontinuities, and instabilities "over the course of the life" in time and space. As will be shown below, the qualitative theory of quasilinear parabolic systems turns out to be a suitable method for studying autowave processes in many cases.

This review consists primarily of a formulation of these basic models and a discussion of them in connection with the physical processes which occur in active kinetic systems. At present we are still far away from a unified and "elegant" theory of autowave processes, but the models which have been developed, and the analysis of their solutions, have already led to several important results in biological and chemical kinetics and for certain highly nonequilibrium physical objects.

(a) Classification of autowave processes; basic experimental data

We begin by listing the types of autowave processes which are presently known.

1. Propagating perturbations in the form of a traveling pulse. 2. Wave generation by autonomous pulsed sources—the case of "echos" and a stable guiding center. 3. Standing waves. 4. Synchronized self-excited oscillations over the entire space. 5. Quasistochastic waves. 6. Dissipative structures—a steady-state, inhomogeneous distribution of the variables in space.

The basic characteristics of the various types of autowave processes and the main requirements which follow from the sufficient conditions for the existence of these processes are listed in Table III at the end of this review.

Before we go into the mathematical description, we would like to discuss some typical autowave processes which are observed in active systems. The basic characteristics of these processes in various objects are listed in Table I. We cannot guarantee that all the phenomena described here can be described by quasilinear parabolic systems, but they all have certain features in common: All occur in active (nonconservative) sys-

TABLE I. Types of autowave processes which have been observed experimentally.

Object	Velocity of traveling-pulse front	Duration of isolated traveling pulse	Scale dimension, wavelength
a) Isolated cells			
1. Squid axon[9,10]	21 m/sec	1—3 msec	2—6 cm
2. Flattened embryonic cell[12,13]	0.2 μ/sec	60 sec	10 μ
3. Myxomycetes plasmodium[13]	30 μ/sec	130—170 sec	4—5 mm
b) Cell populations			
4. Conducting system of the heart[14,15]	25—300 cm/sec	50—500 μsec	1,5—150 cm
5. Dog myocardium muscle[15]	30 cm/sec	100 μsec	3 cm
6. Dog deltoid muscle[16]	5 m/sec	10 msec	5 cm
7. Myofibril tissue culture[17]	50—200 μ/sec	50—200 msec	10—20 μ
8. Population of amebiform cells[18,19]	40 μ/sec	5 min	1 cm
9. Coral polyps[20]	50 cm/sec	0.02 sec	1 cm
10. Neuron network:			
a) fast waves[21,22]	10—50 cm/sec	0.2 sec	2—12 cm
b) slow waves[23]	2—5 mm/min	3—5 min	6—25 mm
c) Chemical reactions			
11. Oxidation of an iron wire in nitric acid[24,25]	2 m/sec	0.075 sec	15 cm
12. Oxidation of tribromoacetic acid by bromate in the presence of cerium or iron catalyst ions; Belousov–Zhabotinskiĭ reactions[5,26,27]			
a) traveling pulses	10^{-2}—10 cm/sec	1—10 sec	1 mm
b) dissipative structures	0	—	1—10 mm
13. Oxidation of ammonia on platinum[28,29]	0.5 cm/sec		
14. Oxidation of carbon monoxide on platinum[28]	5 m/sec		
d) Physical media			
15. Standing striations[30]			
16. Lines of optoelectronic elements[31]			

[1)]Khokhlov used this definition in a comment on the doctoral dissertation of A. M. Zhabotinskiĭ.[5] [The Russian word for "self-excited oscillatory" and the Russian word for "autowave" both begin with the prefix "авто-" (auto-). (Translator's note)].

tems, and the spatial coupling is through transport processes in the broad sense of this term. In particular, the similarities can be seen in the fact that the waves in such systems cancel out when they collide. This is the primary distinction from solition waves.[3,9] Let us briefly describe some of these objects and processes (see Table I).

(1) A well-known example of an autowave process is the propagation of a traveling pulse along a nerve fiber. The active device is the membrane of the fiber, which uses chemical energy to create a nonequilibrium distribution of Na^+, K^+, Ca^{2+}, etc., ions (on both sides of itself). The physics of this process is described is some recent reviews[10,32] and books.[9,33] Strictly speaking, the propagation of a traveling pulse along a membrane is described by hyperbolic telegraphist's equations. These equations reduce to a parabolic system, which we will examine below, for the case in which the resistance per unit length is high (in the giant axon of the squid, for example, it is $\sim 10^{10} \Omega/\mathrm{cm}$).[32]

(4) The conducting system of the heart consists of a large number of cells of a variety of types. The activity of each cell is maintained by mechanisms analogous to those which operate in the axons of neurons. The coupling between cells in the intercellular medium is apparently governed by ion currents and special substances ("mediators"). We know that a traveling pulse can propagate "under normal conditions" along the fibers of cardiac muscle. The appearance of autonomous wave sources results in arrhythmia and fibrillations (unsynchronized activity of the heart), which are pathological for the organism.

(7) When myofibrils are treated with theophylline in a culture of skeletal-muscle tissue, a wave-propagation process is observed which does not involve a change in the electric potential of the cell membrane.[17]

(8) At a certain stage in the existence of a population of amebiform cells, an aggregation is observed which is associated with a wavelike motion of these cells. This aggregation process occurs in the following manner: One of the cells begins to periodically secrete a special substance, an "attractant" (cAMP). In response, the neighboring cells secrete their own pulse of cAMP about 15 sec after receiving the signal. Then the cells move toward the source of the original signal. There is a delay of about 100 sec in this motion. While each cell is moving, it is apparently not susceptible to further stimulation. This feature of the signaling mechanism and of the response to the signnal guarantees the propagation of a diverging signal wave and the convergence of cells toward the central source.[18]

(10) In networks of checking and exciting neurons, waves of a collective pulsed activity of the neurons may propagate. For example, in one of the structures of the brain—the hippocampus—a wave of discharges of pyramidal cells (exciting neurons) is observed.[22] The propagation velocity of the wave is 18–60 cm/sec. The length of the responses and the repetition periods of the regions of elevated pulsation are of the order of hundreds of milliseconds. Similar results have been obtained with an isolated stria of the cerebral cortex.[21]

When the cerebral cortex is stimulated locally by a chemical, mechanical, or electrical agent, a depression wave arises and propagates along the cortex away from the stimulus at 30–90 μ/sec. The propagating depression is always accompanied by a change in the constant cortex potential.[23]

(12) There are two reasons for the interest in Belousov–Zhabotinskiĭ reactions. First, experimentally, chemical oscillations are very reproducible and are comparatively easy to observe, on the basis of a change in color. Second, these reactions are analogous to the autowave processes which occur in real biological objects. In a distributed homogeneous system of this type, A. M. Zhabotinskiĭ and A. N. Zaikin observed sources of activity which appeared only as the result of an inhomogeneous initial perturbation, which they called "guiding centers" (Fig. 1). It was in the same system that dissipative structures (Fig. 2) and a two-dimensional autowave process ["reverberators" (spiral waves)] were first observed.[33] There is also a situation in which self-excited oscillations occur in an unsynchronized manner at different points in space. This case, sometimes called "chemical turbulence," is illustrated in Fig. 3 (see also the photographs in Refs. 5 and 33–35).

(13, 14) In oxidation on platinum, three mechanisms (gas-diffusion, migration, and thermal) can operate to cause the propagation of a catalytic-reaction wave. The joint effects of the various mechanisms lead to the appearance of several interesting new autowave pheno-

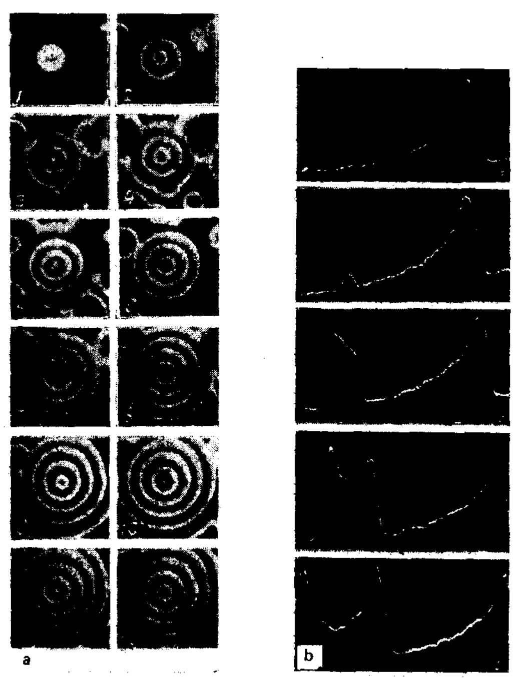

FIG. 1. Guiding centers in a self-excited oscillatory chemical reaction. a: The interval between successive frames is 30 sec. $T_{GC} = 56$ sec, $\lambda_{GC} = 0.55$ cm (Ref. 5). b: Oscilloscope traces of wave profiles at successive times t (sec). 1) 0; 2) 0.8; 3) 5.4; 4) 9.2; 5) 23.6 (Ref. 27).

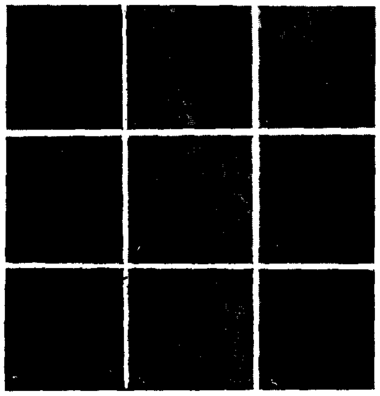

FIG. 2. Cellular dissipative structure in a self-excited oscillatory chemical reaction. The time interval between successive frames is 2 min (Ref. 5).

mena: (a) the propagation of a wave with a periodic change in velocity, (b) pulsations in the coordinate of the front near the equilibrium positions, (c) spontaneous halts of the wave, and (d) dissipative structures.[28,29]

(b) Mathematical model for an active kinetic system

To show what is meant by "active distributed kinetic system," we will describe an adequate for the purpose and quite general mathematical model. We denote by x_i the components which are interacting with each other. In chemistry these would be the temperature and the concentrations of the reactants, while in biology they would be the numbers of some living objects or other per unit volume (or per unit area or per unit length). When the interaction of the x_i and their diffusion are taken into account, the kinetic equations for a one-dimensional space become

$$\frac{\partial x_i}{\partial t}=F_i(x_1, x_2, \ldots, x_n)+\frac{\partial}{\partial r}\left(\sum_{j=1}^{n} D_{ij}\frac{\partial x_j}{\partial r}\right) \quad (i=1, 2, \ldots, n); \qquad (I.1)$$

where D_{ii} and D_{ij} $(i\neq j)$ are the diffusion coefficient and the coefficient of mutual diffusion or the thermal conductivity, and the F_i are nonlinear functions which describe the interaction of the components. In most of the models under consideration, the coefficients D_{ii} are constant, and the coefficients D_{ij} (with $i\neq j$) are zero. We will accordingly adopt these conditions for our analysis of the general model below, and we will make the

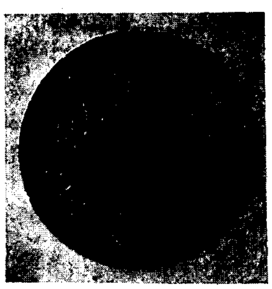

FIG. 3. Transition from regular wave propagation to complicated, nearly random, motion of wavefronts ("chemical turbulence").[35]

appropriate refinements where necessary. The construction of a model becomes substantially more difficult if there are directed fluxes of the components in the system or if there are variable external sources.

If mixing occurs rapidly in the volume occupied by the system, then the processes in any part of the volume are synchronized, and the system can be described by the "point" equations[34]

$$\frac{dx_i}{dt}=F_i(x_1, x_2, \ldots, x_n). \qquad (I.2)$$

One of the basic mathematical indications of activity in a kinetic system is the presence of unstable singularities. This result is closely associated with the autocatalytic properties of the objects under consideration.

In this review we will consider systems whose properties are governed by the nonlinear parabolic equations in (I.1). We will also assume that at the boundaries of the interval under consideration:

$$\left.\frac{\partial x_i}{\partial r}\right|_{r=0,\ r=L}=0. \qquad (I.3)$$

This condition is an extremely natural one for many biological and chemical systems (it corresponds to impermeable boundaries). Before we take up the analysis of system (I.1) we wish to point out that axiomatic models have played an important role in the study and identification of the characteristic modes of behavior of active biological objects.

(c) Axiomatic models for active media

Historically, the development of the theory for the propagation of nonlinear waves which is described by models like that in (I.1) was accompanied by the development of an "axiomatic" theory of excitable media. The goal of this work was to describe propagation processes in nervous systems and muscle systems and, especially, fibrillations of the heart. The axiomatic theory was founded in 1946 in a paper by Wiener and Rosenbluth.[36] In 1960, this approach was developed by Gel'fand and Tsetlin,[37] and at present the axiomatic theory is being successfully developed in the Soviet Union.[33,38]

In the axiomatic theory of active media, an object can be described on different levels. In the simplest version of the theory, the active medium consists of discrete elements— finite automatons, which can be in only one of two states: excited and refractory. Obviously, the axiomatic theory can be applied without a detailed knowledge of the kinetics of the real objects. Another important advantage of this approach is that it is possible to analyze a broad class of problems in general for form; furthermore, computer simultations are simple. Axiomatic models are presently being used to study not only nervous tissue but also chemical systems[39] and genetic networks.[40] For example, spiral waves or reverberators, which apparently are important in pathological functioning of the heart, were predicted and qualitatively explained before their experimental observation by Zhabotinskiĭ and Zaikin.[5,33,41]

We must always face the question, however, of whether axiomatic models are suitable for the phenomena under study. For example, the "echo" (a mutual retriggering of neighboring elements of a medium) was discovered in a study of such a model, but the question arose immediately of whether this effect actually occurred in kinetic systems.[135] The work was accordingly continued, and the net result was the construction of corresponding kinetic models of the type in (I.1), whose analysis proved the existence of this effect.[33,71,81] Mathematically, the question of the correspondence of the axiomatic and dynamic models is resolved by a series of theorems, which assert, in particular, that any discrete automaton is dynamically representable; the converse assertion is generally not correct.[42] In practice, the properties of discrete automatons must be postulated from the dynamic properties of the point system and a knowledge of the diffusion-coefficient matrix D_{ij}. Attempts in this direction have been made, for example, in Refs. 33, 34, 43, and 44. The Bulgarian scientists Sendov and Tsanev have proposed models which combine the discrete and kinetic descriptions of associations of differentiating cells.[45,46]

1. PROPAGATION OF PERTURBATIONS

(a) Propagation of a wavefront

The problem of wavefront propagation in active kinetic systems first arose in connection with work on combustion, the propagation of epidemics, and "genes."[47,48] In the simplest case, of a one-dimensional space and a single kinetic variable, the autowave processes are described by the equation

$$\frac{\partial x}{\partial t} = F(x) + D\frac{\partial^2 x}{\partial r^2}. \tag{1.1}$$

Here $x(t,r)$ can represent the concentration of "burnt" fuel, the temperature, the number of living individuals with certain properties per unit length, and so forth. The function $F(x)$ describes the rate of change of x in the corresponding point system [Eq. (I.2)]. Ordinarily, $F(x)$ can be described by curve 1 or curve 2 in Fig. 4.

If a growth law $F_I(x)$ holds in the system, any small initial conditions or fluctuations above the zero level can lead to the appearance of a "pulse" in a certain region of the space. In case 2, the system is protected by some threshold γ, and autocatalytic growth can occur where x exceeds the threshold γ. This is the situation in the case of appearance of nerve pulses, "spontaneous combustion," etc.

Introducing the self-preserving variable

$$\eta = r - vt \tag{1.2}$$

we can reduce the problem of the propagation velocity of the front in (1.1) to the problem

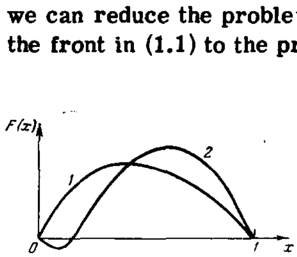

FIG. 4. Two types of variation of the reaction rates with the concentrations, corresponding to (1) no-threshold and (2) threshold propagation of the wavefront.

$$DW\frac{dW}{dx} + vW + F(x) = 0, \tag{1.3}$$

where $W = dx/d\eta$. The velocity v is found by solving this nonlinear equation with the boundary conditions $W(0) = W(1) = 0$.

The wave propagation velocity in system (1.1) was found for the case $F = F_I$ by Kolmogorov, Petrovskiĭ, and Piskunov[47] back in 1937. As it turns out, the propagation velocity for an autowave process in this case lies in the range $v_{min} \leq v < \infty$, where

$$v_{min} = 2\sqrt{DF_1'(0)}. \tag{1.4}$$

However, only a front moving at the minimum velocity is asymptotically stable. The velocities higher than v_{min} are a consequence of the instability of the original homogeneous state.

If $F(x) = F_{II}(x)$, then steady-state wavefront propagation can occur only at the velocity v_0. No general analytic methods have been developed for solving the boundary-value problem in (1.3). In some cases, a piecewise-linear approximation of $F_{I,II}(x)$ has been used. If $F_{II}(x)$ is an antisymmetric polynomial, then $W = x^k(1-x)^L$. Let us assume, as an example,

$$F_{II}(x) = 2\tau[x^2(1-x) - \gamma x(1-x)]; \tag{1.5}$$

then setting $W = x(1-x)$ in (1.3), we find[49]

$$v_0 = (1-2\gamma)\sqrt{\tau\frac{D}{2}}. \tag{1.6}$$

Representation (1.6) is used to study the propagation of cold flames in gas mixtures[49] or the propagation of the activity zone over the surface of a heterogeneous catalyst.[28,29] In the latter case, x is the surface density of active centers. We might also point out that if the function $F(x)$ has five or more zeros then several stable waves, with different amplitudes, can be excited in system (1.1) (Ref. 50).

(b) Basic model for a distributed relaxation system

Many of the phenomena associated with traveling pulses which were mentioned in the Introduction can be described by simple "basic" models for propagation of perturbations:

$$\frac{\partial x}{\partial t} = F_1(x, y) + D_x\frac{\partial^2 x}{\partial r^2}, \tag{1.7}$$

$$\frac{\partial y}{\partial t} = F_2(x, y) + D_y\frac{\partial^2 y}{\partial r^2}. \tag{1.8}$$

In the models for chemical reactions, x and y represent the reactant concentrations, while $F_1(x,y)$ and $F_2(x,y)$ are the rates of the corresponding reactions.

In the simplest model for neural conductivity,[9,10,33,69] x is the voltage on the cell membrane, and y is the slowly varying conductivity of the potassium channels of the membrane. The function $F_1(x,y) = [I_{Na}(x) + I_{Ca}(x,y) + I_K(x,y)]/I_{max}$ is the total current across the membrane (normalized to a certain maximum value I_{max}), the sum of the ion currents; $F_2(x,y)$ is a function which determines the change in the slow potassium current; $D_y = 0$; and $D_x = b/2RC$, where C is the capacitance per unit length of the membrane, b is the fiber radius, and R is the resistivity of the axoplasm. We note that the model in (1.7), (1.8) must be refined even further for certain specific systems, e.g., cardiac fibers. At present it is not clear how to take into account the circumstance that the fiber is not a hollow cable but instead has a system of internal membranes. Furthermore, higher-order systems are used in the Hodgkin–Huxley theory for neural conductivity. Results from these higher-order systems can be obtained primarily on computers, but as a rule they simply refine the solutions found with the basic models.[9,10,41]

The model of a neuron network consisting of exciting and checking neurons can also be reduced to system (1.7), (1.8) (Refs. 51 and 52). Here x and y represent the numbers of fibers in the active state per unit volume of the network, in the axon trees of the exciting and checking neurons, respectively.

In the modeling of objects of this type, the system (1.7), (1.8) has the following particular features: (a) The scale times for changes in the variables x and y are greatly different. (b) In the case y = const, the function $F_1(x)$ has an N-shaped curve. For chemical systems, this means that x is an autocatalytic variable. (c) For many processes, $D_x \gg D_y$. Equations (1.7) and (1.8) can thus be written in the following dimensionless, normalized form:

$$\varepsilon\frac{\partial x}{\partial t}=F(x,\ y)+\frac{\partial^2 x}{\partial r^2}\ , \qquad (1.9)$$

$$\frac{\partial y}{\partial t}=\varphi(x,\ y), \qquad (1.10)$$

where $\varepsilon \ll 1$. The maxima of F and φ over the range of the variables are of the same order of magnitude. Here x is the "fast" variable, while y is the "slow" one. The null isoclines of system (1.9), (1.10) are shown in Fig. 5. From the relative arrangement of the null isoclines we can see which cases occur in the corresponding point systems: the slave case (I), the trigger case (II), or the self-excited oscillatory case (III). System (1.9), (1.10) can be studied by either numerical or approximate analytic methods. Let us briefly describe these analytic methods.

(1) One method is similar to the iteration method. First, the system of point equations is solved. Then the resulting solutions are substituted into the right sides. The results are linear diffusion equations with a source which depends on the coordinates and the time. This method has been used to calculate the velocity of a traveling pulse in a nerve fiber,[9,10,53] to determine the effect of inhomogeneities of the fiber on the traveling pulse,[54] and to study the interaction of the traveling pulse.[55]

(2) Another method is the separation of the space-time motions into fast and slow motions. This method can be used to study time-dependent processes. The fast motion is the propagating excitation front. The front velocity is determined from Eq. (1.9), where y is treated as a fixed parameter. In this manner we determine the variation of the front velocity $v=v(y)$ with the slow variable y near the front. In turn, y is found from the equation for slow motions [Eqs. (1.9) and (1.10) with $\varepsilon=0$]. The desired solution turns out to be composed of regions of slow motions separated by fast-moving wave fronts. This method has been used to study the formation of a steady-state traveling pulse and the disappearance of an extended perturbation over a finite time,[56] the propagation of a traveling pulse through a medium with smooth inhomogeneities, the stopping of the decay of a pulse, and the breakup of a stopped front.[57,58] This method of course does not work for problems involving the formation of a fast front, and it cannot be applied to a medium with inhomogeneities having a scale dimension of the order of the length of the front.

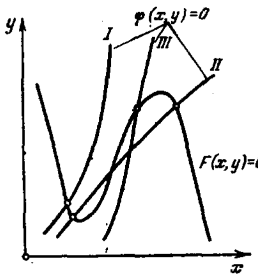

FIG. 5. Null isoclines of the basic model of a traveling pulse. I) Slave mode; II) trigger mode; III) self-excited oscillatory mode.

(c) Stationary traveling pulses

The stationary traveling pulse is one of the best-studied autowave processes.[9,10,32] To determine the shape of the stationary traveling pulse, we use the self-preserving variable of (1.2) to make the transition from (1.9) to (1.10) to a system of ordinary equations, and we find the homocline trajectories in the phase space of this system (these are the trajectories which go from saddle to saddle). Figure 6 shows an illustrative numerical calculation for the Nagumo system,[9]

$$\frac{d^2x}{d\eta}+\varepsilon v\frac{dx}{d\eta}+y-x+\frac{1}{3}x^3=0,\quad v\frac{dy}{d\eta}=0.8y-x-0.7, \qquad (1.11)$$

which is a good basic model for a nerve pulse.

Two pulsed solutions can occur in system (1.11). One corresponds to a stable traveling pulse of system (1.9), (1.10). The corresponding phase trajectory and the shape of the pulse are shown by curves 1 in Figs. 6b and 6c. For small values of ε, the phase trajectories corresponding to the rise and decay of the traveling pulse lie in the $(x, \dot{x})$ planes with $y\approx$const. This feature is shown by the hatching in Fig. 6b. The second solution (2 in Figs. 6b and 6c) corresponds to an unstable solution according to system (1.9), (1.10). Both solutions can exist only at small values of ε—below some critical value ε_0 (Fig. 6a). The unstable pulse is a sort of boundary which separates those perturbations which relax to a stable equilibrium state and those which lead to the formation of a stable traveling pulse. There are also integral inequalities for perturbations which will be damped.[9,59] However, the problem of analyzing the excitation conditions for traveling pulses is not fully resolved yet.

The eigenvalue problem in (1.11) has been solved analytically for the case $\varepsilon \ll 1$ through a separation of the motions into fast and slow motions in Ref. 60. Approximate equations were derived there for the velocities of

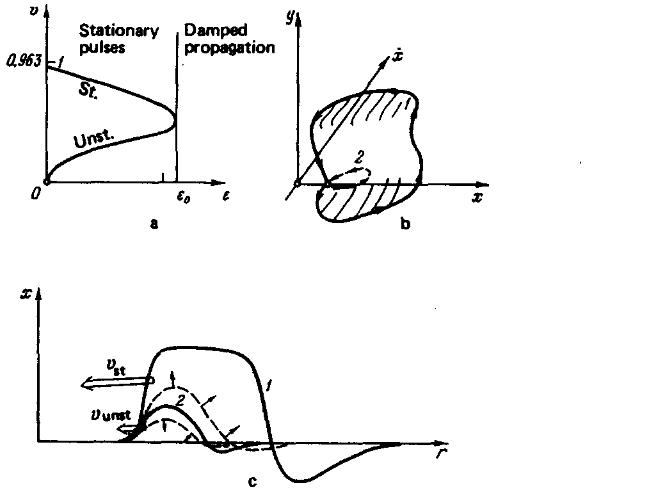

FIG. 6. A traveling pulse in the Nagumo system, (1.11) (Ref. 9). a: Variation of the propagation velocity of stationary traveling pulses with the extent to which the system is of a relaxation nature (ε). b: Trajectories of traveling pulses in the $(x, \dot{x}, y)$ phase space. c: Stable (1) and unstable (2) stationary traveling pulses. The dashed curves show examples of perturbations which relax to an equilibrium state or to a stable traveling pulse (1).

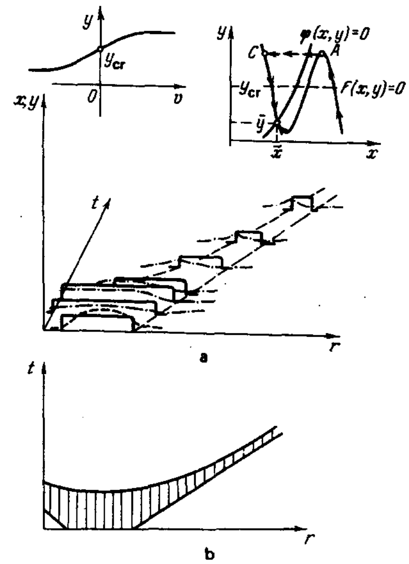

FIG. 7. Formation of a traveling pulse in the case $\bar{y}<y_{cr}$. Top: The function $v=v(y)$ and the null isocline of the system. a) Spatial distributions of x (solid curves) and y (dot-dashed curves); b) formation of the pulse on the (r, t) plane. The hatching corresponds to the region of the excited state.

both stationary traveling pulses.

Systems (1.7), (1.8) and, in particular, (1.11), also permit stationary periodic solutions in the form of a sequence of traveling pulses. This case corresponds to periodic external agents. Some calculations of the parameters of such sequences can be found in Ref. 9.

(d) Formation of pulses

The process by which a stable, stationary traveling pulse is formed can be traced easily for a system with pronounced relaxation properties.[56] For a qualitative analysis we need to know the null isoclines of the system $F(x, y)=0$ and $\varphi(x, y)=0$, and we need to know how the front propagation velocity varies with the slow variable near the front, $v=v(y)$. For any active medium, a plot of the function $v(y)$ intersects the Oy axis. We denote the corresponding value of y by y_{cr}.

Let us examine the simplest time-dependent process: the formation of a traveling pulse in a system with slave properties. Figure 7 shows the phase plane of the point system. There is a single stable equilibrium point, $(\bar{x}, \bar{y})$. If the initial conditions in the point system are specified in such a manner that $x_0>\bar{x}$ but $y_0=\bar{y}$, then the working point reaches the isocline $F(x, y)=0$ almost instantaneously. Then it moves slowly to the breakoff point A, along the fast trajectory AC, and slowly back to the intersection $(\bar{x}, \bar{y})$. Consequently, in response to an initial perturbation the point system generates a single pulse, which is nearly square.

In the distributed system in (1.9), (1.10), the events occur in the following manner: We assume that the initial condition $x(0, r)$ is specified in the form of a smooth perturbation over a region of size greater than the diffusion length L_D and that $y_0=\bar{y}$ and $\max x(0, r)=x_0$. Then the initial profile of the perturbation becomes nearly square over a time $\Delta t\sim\varepsilon$. The edges of the perturbed region are shaped into stationary fronts (see Section 1), which propagate in a symmetric manner in opposite directions at the velocity $v(\bar{y})$. It is thus sufficient to examine the evolution of the pulse in only one direction (Fig. 7a). The crest of the traveling pulse is shaped by the slow motion nearly independently at each point in space. When the center of the region of the initial perturbation reaches the fast trajectory AC, there is again a fast decay: the trailing edge of the traveling pulse, which is moving in the same direction as the leading edge, with the initial velocity $v(y_A)$. The process by which the traveling pulse is formed is such that the velocities of the leading and trailing edges become equal (Fig. 7).

The behavior is completely different if the intersection lies above the critical value $(\bar{y}>y\ )$. In this case a traveling pulse cannot propagate. The initial perturbation collapses over a finite time interval (Fig. 8). The cases in which a traveling pulse is formed in a medium with a trigger characteristic are studied in Refs. 61 and 62. The null isoclines of the corresponding point system are shown in Fig. 9, along with the variation of the velocity with the slow variable. Depending on the relation between the velocities of the leading edge (v_l) and

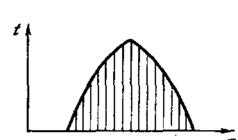

FIG. 8. Formation of a traveling pulse for the case $\bar{y}>y_{cr}$. Relaxation of a perturbation to a homogeneous state, represented on the (r, t) plane.

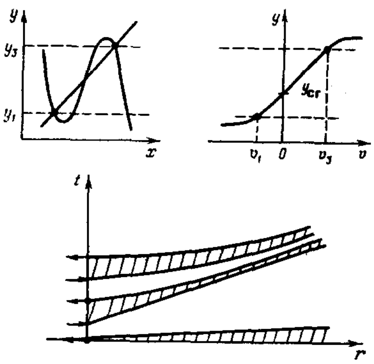

FIG. 9. Diagram illustrating the formation of a traveling pulse in a trigger system. The upper part shows the null isoclines of the system and the functions $v=v(y)$. The maximum propagation velocity of the trailing edge of the pulse is higher than the maximum velocity of the pulse front ($v_3>v_1$).

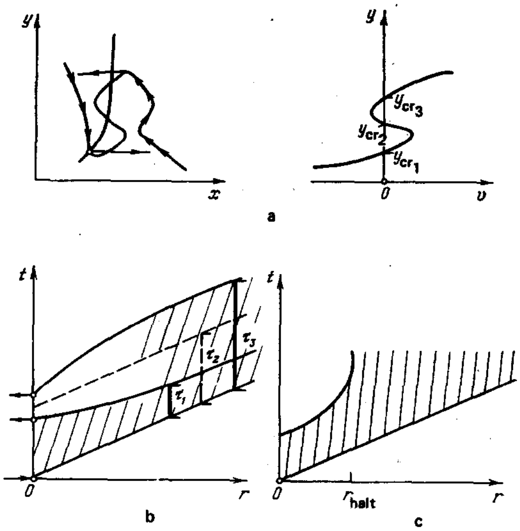

FIG. 10. Propagation of a traveling pulse in the case of a nonmonotonic function $v=v(y)$. a) The function $v=v(y)$ and the null isocline of the system; b) formation of three traveling pulses of different duration (τ) as a function of the initial perturbation; c) halt in the decay of a traveling pulse.

the trailing edge (v_t), there can be different wave-propagation regimes. If $v_t=v_3>v_1=v_l$ (Fig. 9), then a traveling pulse of an excited state against the background of an unexcited surrounding can propagate in this system, in addition to the ordinary propagation of an isolated wavefront. The arrows in Fig. 9 show the times at which the external agent shapes the leading edge (if the arrow points along the positive r axis) or the trailing edge (if the arrow is in the opposite direction) of the excitation pulse. In the opposite case ($v_3<v_1$), this traveling pulse of an excited state cannot be stationary. It increases in activity during the propagation. Then the traveling pulse of the unexcited state assumes a stationary shape against the background of the excited surroundings.

There are many pieces of experimental evidence in physiology that the function $v(y)$ may be nonmonotonic. We could cite, for example, papers which show a nonmonotonic variation of the velocity of a traveling pulse with the level of the slow current across the membrane of a cardiac fiber.[63-66] Several stationary traveling pulses can form in distributed media with such properties.[67] Figure 10 shows examples of the formation of traveling pulses of various durations: If the duration of the initial perturbation is below the critical value, $\tau_0<\tau_2$, a pulse of short duration τ_1 arises in the system, but if $\tau_0>\tau_2$ then a traveling pulse of duration τ_3 is produced. Furthermore, the trailing edge of the pulse may come to a halt under certain conditions.[57] A nonmonotonic variation $v(y)$ could explain, in particular, the experimental bifurcation and extreme acceleration of the cardiac action potential during high-frequency stimulation or when the fiber is subjected to certain drugs.[63]

In summary, the simple model in (1.9), (1.10) leads to a qualitative explanation of many characteristic features of the production and propagation of traveling pulses in active media. The same model yields good qualitative predictions in a number of cases. When applied to the neuron network with the parameters from Refs. 21–23, for example, the model in (1.9), (1.10) leads to the following characteristics for a traveling pulse which is a region of elevated neuron pulsation: a velocity ~10 cm/sec, a traveling-pulse length ~2 cm, and a rise time ~2 mm. These estimates agree well with the experimental data available (see the Introduction).

It is important to note the distinction between these traveling pulses and the nonlinear waves which are called "solitons." A soliton is formed as the result of a balancing of the effects of a nonlinearity and dispersion in a conservative system. A soliton is a solitary wave of the type which retains its shape and velocity in collisions with other such waves.[9] The stability of the traveling pulse under discussion here, which is also a solitary wave, is governed by the active properties of the system. In a traveling pulse there is also a balance, but in this case between the energy stored in the system and its dissipation in the traveling pulse. When two traveling pulses meet, they annihilate each other. Naturally, the methods used to study these solitary waves differing in mechanism are different in many respects. Caution should thus be exercised in taking a common approach to the analysis of similar phenomena in different objects on the sole basis that they are both solitary waves. On the other hand, these objects do have certain general features, so that there are also general features in the models used for studying them. For example, the method of separating wave motions into fast and slow which was used successfully to analyze the models in (I.1) was first proposed by Khokhlov[70] in a study of processes in nonlinear electronics systems which are described by hyperbolic systems of equations, rather than by (I.1).

The most important features of the propagation of fast pulses can be described perfectly well by the basic model in (1.7), (1.8), which contains only two variables: A fast variable and a slow one. This model can be used to study the propagation of action potentials in nerve and muscle fibers, regions of collective activity in neuron ensembles, activity waves in autocatalytic chemical reactions, and other phenomena.

At the present time the development of the theory of traveling pulses in active media involves the following topics: inhomogeneous media,[10,41,68] the interaction of several traveling pulses,[10] and the use of models with many variables.[28]

2. AUTONOMOUS WAVE SOURCES

In the preceding section we discussed the mechanism for the propagation of waves in active media. The next step is to study wave generation. If there is a region in space in which the characteristic oscillation frequency is higher than elsewhere, traveling waves will propagate away from this region. If there are several such sources, the medium is synchronized by the highest-frequency source. This conclusion had already been reached on the basis of the axiomatic theory.[4,33,36,37,41] Using this theory, Krinskiĭ and Kholopov[135] predicted, in 1967, the possible production of an autonomous wave source of the "echo" type. Pursuit of this theory showed that such sources are also predicted reliably in kinetic models of the type in (I.1).[33,71,81] Zhabotinskiĭ and Zaikin experimentally discovered a new type of wave source—a "guiding center" (see the Introduction)—in a homogeneous, chemically active medium. The first models for guiding centers were offered in Refs. 27, 84, and 85.

We will accordingly examine wave-generation problems on the basis of the model in (I.1). We will study separately those solutions of (I.1), (I.3) which are nearly harmonic and definitely of a relaxation nature.

(a) Stability of homogeneous state

If the distributed system is in a homogeneous stationary state, the values of its variables are equal to the coordinates of the singularity of the corresponding point system, (I.2), which we denote by

$$\{\bar{x}_{1m},\ \bar{x}_{2m},\ \ldots,\ \bar{x}_{nm}\}\quad (m=1,\ 2,\ \ldots,\ M), \tag{2.1}$$

where m is the index of the singularity. We call equations which are written in a coordinate system with origin at the m-th singularity the "reduced" equations. It is easy to see that the homogeneous state $x(t,r)=\bar{x}_{im}$ is actually a trivial solution of the boundary-value problem for system (I.1) with neutral boundary conditions of the second kind, (I.3), and also with boundary conditions of the first kind and periodic conditions (a ring reactor).

The analysis of autowave systems should begin with a study of the stability of a stationary homogeneous state. In many cases, we need to study only small perturbations of this state, i.e., the linearized reduced systems. Any perturbation can be written as a superposition of waves of the type

$$x'_{im}=x_i-\bar{x}_{im}=\alpha_{im}\exp\left(p_{mk}t+\frac{j\pi k}{L}\right); \tag{2.2}$$

here k is the wave number, which determines the wavelength, $\lambda_{mk}=2L/k$. Everywhere below, where we can do so without causing any confusion, we will omit the subscript "m," which labels the singularity. Substituting (2.2) into the linearized system of equations, and using the condition for the existence of nontrivial solutions of this system, we find a dispersion relation which relates the complex frequencies ($p_{mk}=\delta_{mk}\pm j\omega_{mk}$, the wavelength λ_{mk} (or the wave numbers k), and the coefficients in system (I.1)[34]:

$$p^n_{mk}+q_{n-1}(k^2)\,p^{n-1}_{mk}+\ldots+q_0(k^2)=0. \tag{2.3}$$

If this state is unstable, then there is at least one complex frequency p_{mk} with $\delta_{mk}>0$. There are two types of instabilities in active kinetic systems. In the case in which the dispersion relation (2.3) for a wave with a wavelength $2L/k$ has an even number of roots, $p_{mk}c\delta_{mk}>0$, the instability is "oscillatory." An odd number of roots corresponds to a "Turing instability," which leads to the formation of stationary dissipative structures (see Section 4 below).

Before analyzing the dispersion relation (2.3), we would like to point out yet another problem in whose solution this relation is used—namely, the study of discrete analogs of autowave systems, consisting of several diffusion-coupled reactors. Many of the general properties of autowave systems can be determined by studying the discrete analog, since they are governed by the structure of the phase space of the corresponding point system and the particular features of the diffusion coupling. Analysis of discrete systems consisting of few elements is also of independent interest.[71-74,94]

The simplest discrete system consists of two diffusion-coupled reactors:

$$\begin{aligned}\frac{d}{dt}x_{1i}&=F_i(x_{11},\ x_{12},\ \ldots,\ x_{1n})+d_i(x_{2i}-x_{1i}),\\ \frac{d}{dt}x_{2i}&=F_i(x_{21},\ x_{22},\ \ldots,\ x_{2n})+d_i(x_{1i}-x_{2i});\end{aligned} \tag{2.4}$$

where the first subscript on a variable specifies the reactor, while the second specifies the variable. The model in (2.4) can be used to help make the transition from a point system to a distributed system. For example, if the steady-state concentrations in the first and second cells are different, and if this situation is stable for certain values of the permeability coefficients d_i, then we should expect nontrivial stationary states in the corresponding distributed system. In (2.4) it is frequently convenient to use different variables:

$$\Delta_i=\frac{1}{2}(x_{2i}-x_{1i}),\quad S_i=\frac{1}{2}(x_{1i}-x_{2i}), \tag{2.5}$$

which pick out antisymmetric states. The coordinates in (2.5) are normal coordinates. Characteristic equations for (2.4) can be found from (2.3) by setting $k=0$ and $\pi^2k^2=2$. The existence of roots with $\delta_k>0$ for Eq. (2.3) in the case $k=0$ implies an instability with respect to in-phase perturbations, while the existence of such roots in the case $\pi^2k^2=2$ implies an instability with respect to out-of-phase perturbations.

An informative characteristic of system (I.1) is the variation of δ_k with the wave number k. Figures 11a and 11b show variations of δ_k with k typical of systems with two variables.[34] Other plots of this behavior can be found by making a parallel translation with respect to the coordinate axes of the curves in Figs. 11a and 11b. Analysis of these curves shows that in systems with two variables the oscillatory instability for waves of finite length can exist only when the corresponding point sys-

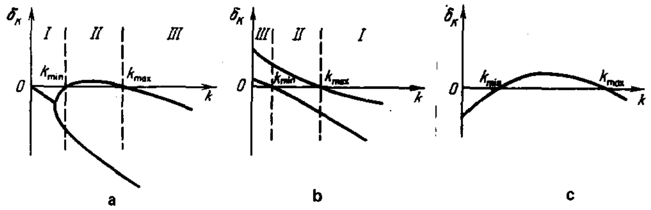

FIG. 11. Typical curves of the real parts of the roots of the dispersion relation (2.3) vs the wave number k. a, b) Systems with two variables[34]; c) system with three variables $[q_0(k)>0$ in the corresponding dispersion relation in (2.3)].[75]

tem ($k=0$) is a self-excited oscillatory system. The Turing instability, on the other hand, can occur even if the stationary state of the point system is stable (this situation could not occur for a system with a single variable). If the point system is a self-excited oscillatory system, then there are always possible values of the diffusion coefficients such that the Turning instability occurs.

Among self-excited oscillatory systems with three and more variables, there are some in which the Turning instability does not occur, regardless of the diffusion coefficients. On the other hand, in certain three-component systems the self-excited oscillatory instability can occur even if there are no self-excited oscillations in the point system. The corresponding variation of δ_k with k is shown in Fig. 11c (Ref. 75).

The mechanism for this effect can be illustrated for the following system[76]:

$$\left.\begin{aligned}\frac{\partial x}{\partial t}&=A+x^2y-(B+1)x+D_x\frac{\partial^2 x}{\partial r^2},\\ \frac{\partial y}{\partial t}&=Bx-x^2y+D_y\frac{\partial^2 y}{\partial r^2},\\ \frac{\partial A}{\partial t}&=W+Kx-RA+D_A\frac{\partial^2 A}{\partial r^2}.\end{aligned}\right\} \tag{2.6}$$

For a fixed value of A ($B>A^2+1$), the first two equations in (2.6) describe a self-oscillatory subsystem or a "brusselator."[64] The third equation in (2.6) describes a feedback which retards the growth of the oscillations and can in fact turn them into damped oscillations. The diffusion of component A smooths over those spatial inhomogeneities in this component which arise in the course of the oscillations; this diffusion thus reduces the effect of this feedback. Then for small wave numbers, at which diffusion is relatively unimportant, the feedback through the variable A can be strong enough to damp the perturbations. At higher wave numbers, the feedback is weakened, the oscillation growth rate may become positive, and the perturbation amplitude will increase (Fig. 11c). At large wave numbers, as in two-component systems, δ necessarily becomes negative because of the diffusion of the variables x and y.

We would especially like to emphasize the possible occurrence of instabilities of a homogeneous state in distributed systems with mutual diffusion of the components in the case in which the point systems have a stable singularity for arbitrary values of the parameters. Interestingly, these oscillatory instabilities can occur only in systems having three or more variables, while the Turing instabilities can also occur in systems with two variables. The coefficients of mutual diffusion can be small in comparison with those for self-diffusion. This result implies that it is important to study transport processes in nonequilibrium media being investigated.

(b) Standing waves

An analysis of the quasiharmonic self-excited oscillations in a distributed system, (I.1), and that of oscillations in the simple discrete model in (2.4) have much in common. Specifically, any solution of system (I.1) can be written as the series

$$x_i(t,\,r)=\bar{x}_i+\sum_{k=0} A_{ki}(t)\cos\frac{\pi kr}{L}. \tag{2.7}$$

In the description of a quasiharmonic standing wave, only a few terms of the series in (2.7) are important. Substituting the truncated version of series (2.7) into (I.1), and averaging over the spatial variable, we find ordinary differential equations for the mode amplitudes A_{ki}. Pursuing the analysis for two modes ($k=0$ and $k\neq 0$), we find that the resulting equations for A_{ki} are equivalent to the equations of the simple discrete system in (2.4), written in terms of the normal coordinates in (2.5). These equations are analyzed by the method of slowly varying amplitudes: $A_{ki}(t)=a_{ki}(\varepsilon t)\cos(\omega_k t)(\varepsilon \ll \min_k\{\omega_k\})$. As a result, we find truncated equations for the a_{ki}, and the analysis of these equations is a rather simple problem.[75,76]

In two-component systems which have only odd nonlinearities, there is an asynchronous damping of out-of-phase oscillations [the variables Δ in (2.4) or modes with $k\neq 0$] by in-phase oscillations (the variables S or the mode with $k=0$). In other words, only in-phase oscillations are stable. If the nonlinearities of the reduced system also contain even terms, as is characteristic of "chemical" systems, then out-of-phase oscillations are possible. The shape of these oscillations, however, is far from harmonic.[5,33,71,76-78] Quasiharmonic standing waves are unstable in two-component systems.[34,76,78]

In three-component systems, out-of-phase oscillations can suppress synchronous oscillations.[75,76] In these cases, a standing wave is obviously stable. A standing wave is observed in its "purest" form when self-excited oscillations do not arise in the point system. If, on the other hand, the conditions for self-excitation of in-phase oscillations are satisfied, these oscillations are also stable. Several standing waves with different wavelengths and oscillation frequencies can be stable. The switch from one mode to another is initiated by finite perturbations. Such systems can thus be thought of as frequency triggers. The frequencies of the out-of-phase stable oscillations are higher than the frequency for self-excited oscillations of the point system.

These standing waves exist, for example, in the system in (2.6) (Ref. 75). Another example[76] is one of the Belousov–Zhabotinskiĭ reaction models, the "oregonator,"[79,80]

$$\left.\begin{aligned}\frac{\partial x}{\partial t}&=y(1-x)-\gamma x+D_x\frac{\partial^2 x}{\partial r^2},\\ \frac{\partial y}{\partial t}&=\beta y(1-x)-\rho yz-cy^2+\varkappa z+D_y\frac{\partial^2 y}{\partial r^2},\\ \frac{\partial z}{\partial t}&=x-qyz-\tau z+D_z\frac{\partial^2 z}{\partial r^2};\end{aligned}\right\}\qquad(2.8)$$

where x, y, z are the concentrations of Ce^{4+} (Fe^{3+}), the autocatalyst, and the inhibitor (bromide), respectively. This system differs from (2.6) in that a self-excited oscillatory subsystem cannot be segregated within it, so that the mechanism for the building up of the out-of-phase oscillations is different from that described for (2.6). It is pertinent to note that such build-up occurs at large values of D_z, and stationary dissipative structures exist in this model at large values of D_x, as will be shown in Section 4 below.

(c) The guiding-center problem

We turn now to the problems of generation of traveling pulses in relaxation systems. In inhomogeneous systems, the source of traveling waves may be regions in which the characteristic frequency of the oscillations is higher than in the surrounding space, so that the situation is stable. A source of this type is called a "rhythm leader" or "pacemaker." The basic problem of the wave theory, however, is to study traveling-wave sources in homogeneous media.[5,33,34,95]

This problem was first studied on the basis of the axiomatic models.[33,38,41] Wave sources were found and labeled "echoes." These sources exist because of a sequential retriggering of neighboring elements of the medium. On the other hand, the wave sources which arise in the course of chemical reactions in a homogeneous medium have been labeled "guiding centers."[5] The medium can be either a self-excited oscillatory medium or a slave medium. In the latter case it is particularly clear that it is the guiding-center mechanism which is responsible for the periodic situation. Since the echo mechanism does not completely explain the experimental facts, other types of wave sources have been studied with the help of models with three variables. In certain cases below we will refer to the wave sources with a common term, "guiding centers," but it should be recalled that different mechanisms are responsible for their operation.

Let us examine the echo mechanism in more detail. A study of the axiomatic models shows that the echo can exist only if the pulse length τ is related to the refractory time R in accordance with $\tau/R > 0.5$; with the source having a zero dimension.[33,38] Analogous conditions have been found for two slave relaxation oscillators coupled by diffusion.[71] The further development of the echo theory is based on the use of model (I.1), which contains two variables.

For a system with pronounced relaxation properties, (1.9), (1.10), it has been shown by means of the characteristic $v = v(y)$ that the excitation front must come to a stop for a pulse source to form. The subsequent evolution of the stopped excitation front can take either of two paths. If the velocities of the slow motions on the opposite sides of the fixed front are chosen appropriately (when the nonlinear characteristics $f = 0, \varphi = 0$ are symmetric—the velocities of the slow motions are equal[57,58]), the front will split up (Fig. 12a). If the slow motions are not matched, the front moves off in the direction in which the changes in the slow variable are faster (Fig. 12b). These processes result from instabilities for certain perturbations, which carry the front off in one direction or the other or lead to a breakup. The condition $\tau > R/2$ when applied to Eqs. (1.9) and (1.10) means that the velocity of the slow motions in the rest region is higher than the velocity of the slow motions in the excitation region. Here the following processes occur (Fig. 13): After the stop, the excitation front propagates into a region in which the system is in a state of rest. As long as the front is immobile, however, an inhomogeneity forms in the distribution of the slow variable at the stopping point, r_s. The result is the formation of a new stopped front, which again moves away (after a certain time) into a region in which the system is in a state of rest. At a certain instant, however, the front—after stopping—nevertheless goes into the region of the excited state. This happens the sooner, the greater is the difference between the velocities of the slow motions in the states of rest and excitation. Then a source of the echo type ceases to exist.[58,81] An opposite case is that in which the length of the excitation pulse is shorter than the time required to restore the system to the rest state[70] ($\tau < R/2$). Then the pulse stops at $y = y_{cr}$, and after a certain time the front moves off in the direction in which the system is in the excited state. After this time, the system can no longer be excited by internal processes.

Periodic operation of an echo source is possible in self-excited, slave, and trigger systems. In this case, however, there must be a definite matching of the velocities of the slow motions on the different sides of the fixed excitation front, so that a special choice of parameters for the system is necessary. Figure 14 shows a periodic breakup of the front. Small deviations from the selected parameter values lead to destruction of the source after generation of a few pulses. The periodic

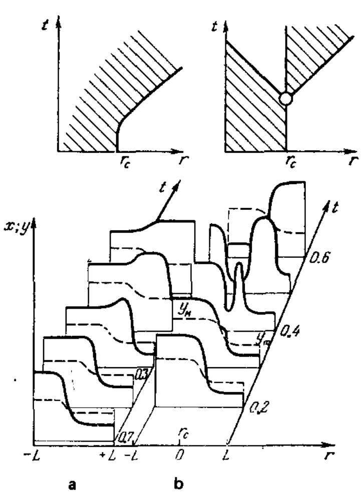

FIG. 12. Evolution of an excitation front at the point at which it stops. Shown at the top are diagrams of the processes in the (r, t) plane. a) Separation of the front from the stopping point; b) departure of the front from the stopping point.

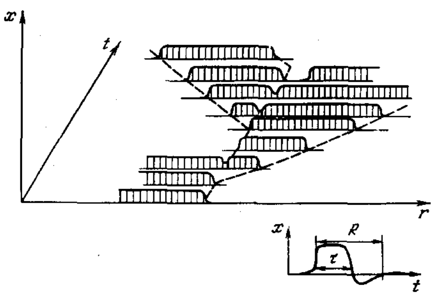

FIG. 13. Evolution of excitation regions as a function of the relationship between the pulse duration τ and the refractory period R. In the case $\tau > \frac{1}{2}R$ there is an "echo" wave source.

operation of a one-dimensional source is thus not a "coarse" situation with respect to variations in the parameters of the system.

The destruction of guiding centers also occurs when the dimensions of the system are reduced to the characteristic dimension of the guiding center. A guiding center of the echo type has a characteristic dimension of the order of the length of the excitation front.[58]

For systems with two variables there are also examples of numerical calculations of one-dimensional sources; the details of the operation of these sources are still difficult to explain by qualitative methods.[82] It should be noted that in the operation of such a source there are also situations which are similar to the breakup of a stopped excitation front. Another example is a source in a medium with a trigger inhomogeneity.[83] An excitation pulse is incident on an inhomogeneity with trigger properties; then the fixed front begins to generate pulses. The mechanism for the operation of such a source is not yet fully understood.

(d) Stable guiding centers

In the system discussed above, with two variables, stable periodic pulse generation can occur only if the parameters have certain special values. Guiding centers of the echo type which are stable with respect to variations in the parameters can apparently be obtained in a model with two variables if the function $v = v(y)$ is not monotonic.

Another approach to the study of stable self-excited wave generation is to use models with three variables. Stabilization of the echo through the use of a third variable is possible, but the corresponding models have not yet been studied. On the other hand, we do know of three-component systems in which the mechanism for the stabilization of non-echo guiding centers is based on differences in the nature of the processes which occur in the region in which the traveling pulse is formed and in the region of its steady-state propagation. It is because of the third variable that these differences can accelerate the slow-motion step in the region of wave initiation, leading to the formation of a stable guiding center.

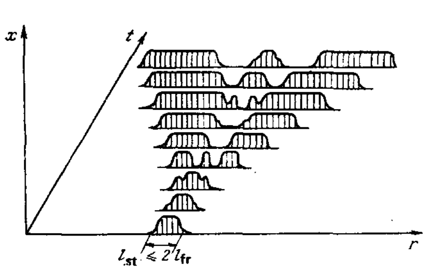

FIG. 14. Examples of the operation of traveling-wave sources—periodic division of fronts.[57,58]

Let us examine two types of models. Their point systems contain a self-excited oscillatory subsystem of two variables, and the third variable determines the additional, retarding feedback, which has an important effect on the parameters of the self-excited oscillation. In a distributed system, a traveling pulse is formed primarily by a self-excited oscillatory subsystem, while the nature of the propagation of the third variable is governed by changes in the shape of this pulse. For example, let us consider the following model[27] (a similar model has been studied in Ref. 84):

$$\frac{\partial x}{\partial t} = y(1-x) - (\gamma_0 + z)x + D_x \frac{\partial^2 x}{\partial r^2},$$
$$\varepsilon \frac{\partial y}{\partial t} = y(1-x) - \frac{(py-\varkappa)x}{qy+\tau} - cy^2 + D_y \frac{\partial^2 y}{\partial r^2}, \qquad (2.9)$$

$$\frac{\partial z}{\partial t} = W + Kx^2 - Rz + D_z \frac{\partial^2 z}{\partial r^2} \qquad (2.10)$$

or

$$\frac{\partial z}{\partial t} = K\theta(x_0 - x) - Rz + D_z \frac{\partial^2 z}{\partial r^2}, \qquad (2.11)$$

where $D_x \gg D_y, D_z$; $\theta(\xi) = 0$ for $\xi < 0$ or $\theta(\xi) = 1$ for $\xi > 0$.

The variables x and y in (2.9) for a fixed value of z and for $\varepsilon \ll 1$ form a relaxation self-excited oscillatory subsystem, for which the corresponding phase plane is shown in Fig. 15. This subsystem is a reduced model of the Belousov–Zhabotinskiĭ reaction in (2.8). For a given distribution of null isoclines, the motion of the representative point of the subsystem along the upper part of the y-null-isoclines is essentially independent of the values of z, while the motion along the lower part does depend on z: specifically, this motion is accelerated at large values of z.

In a distributed system, the projection onto the x-y phase plane of the representative point in the guiding-

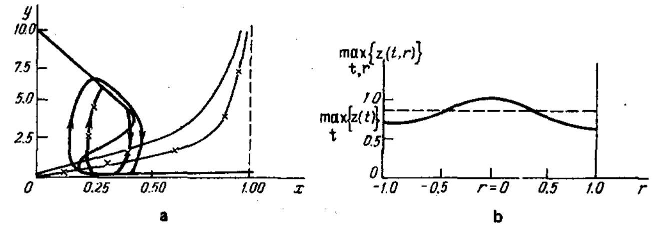

FIG. 15. Guiding center in system (2.9)–(2.10). a: Null isoclines of subsystem (2.9) and projections of the integral curves ("limiting" cycles) onto the phase plane of the subsystem from the spatial points $r_0 = 0$ and $r = 1$. b: Distribution of $\max\{z(r,t)\}$ (the results of a numerical integration on a computer; $K = 1$, $\varepsilon = 1/\beta = 10^{-2}$, $p = 5$, $\varkappa = 10^{-3}$, $q = 4$, $\tau = 1$, $c = 0$, $\gamma = 0.02$, $W = 0$, $R = 0.1$, $D_x = D_z = 0$, and $D_y = 0.2$).

center region is a cycle which envelops all the phase trajectories corresponding to traveling waves in the regions of space far from the guiding center. By this we mean that in the region of the guiding center diffusion retards the transition of the representative point from the lower to the upper branch of the y-null-isocline. In other regions of space, the waves which are traveling away from the guiding center simply accelerate this transition. It thus follows from the third equation of the system [(2.10) or (2.11)] that in the wave-trigger region there will be a $\max_{t,r}\{z(t,r)\}$, as shown in Fig. 15, which is plotted from the results of a numerical simulation. Such a distribution of $\max_{t,r}\{z(t,r)\}$ leads to a sharp decrease in the time of the slow motions in the trigger region and thus to a stable guiding center.

To illustrate another mechanism for stabilization of a guiding center, we use the method[27]

$$\frac{\partial x}{\partial t}=zy+x^2y-(B+1)x+D_x\frac{\partial^2 x}{\partial r^2},$$

$$\frac{\partial y}{\partial t}=Bx-x^2y+D_y\frac{\partial^2 y}{\partial r^2}, \qquad (2.12)$$

$$\frac{\partial z}{\partial t}=W+Kx-Rz+D_z\frac{\partial^2 z}{\partial r^2}, \qquad (2.13)$$

where now $D_z \gg D_x, D_y$.

Figure 16 shows the phase plane of the relaxation self-excited oscillatory subsystem in (2.12) (z is fixed). The velocity of the working point depends on z: in the vertical region I it increases with increasing z, while in the horizontal region III it decreases. In the sloping region II there are fast motions, which are only slightly dependent on z. In the complete system of equations, (2.12), (2.13), z increases when the projection of the representative point is in the horizontal region or decreases in the vertical region.

Figure 17 shows profiles of waves traveling away from the region of the guiding center. The diffusion of the z component leads to a flattening of its spatial profile. This effect has the following consequences: (a) When the projection of the representative point of the guiding-center region is in the horizontal region, the diffusion slightly reduces the value of the z component in this region. (b) When this projection is in the vertical region, the diffusion increases the value of the z component. The diffusion of the z componenet thus accelerates the motion in the region of the guiding center in comparison with the motions in other parts of the space. These processes make the guiding-center situation stable.

Stable guiding centers can exist in the systems dis-

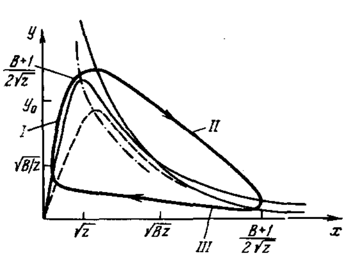

FIG. 16. Structure of the phase plane for self-excited oscillatory subsystem (2.12).

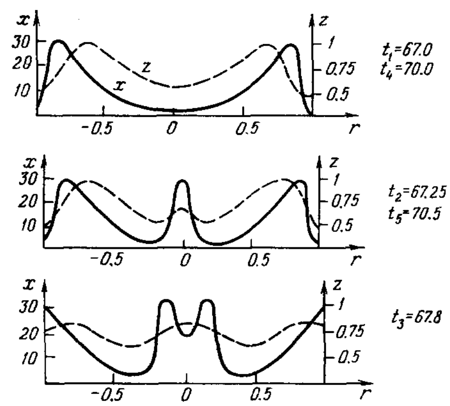

FIG. 17. Wave profiles at successive times in the guiding-center mode of system (2.12)–(2.13). These are the results of a numerical integration on a computer. $B=36$, $W=0.36$, $K=0.05$, $R=1$, $D_x=2.5\cdot10^{-4}$, $D_y=0$, $D_z=2.5\cdot10^{-3}$($T_{GC}=3.3$; $T_0=3.6$) (Ref. 27).

cussed above even when oscillations do not arise in the point system. For a guiding center to exist, as a rule, the point system must possess a high degree of relaxation. Otherwise there will be a situation with "moving" guiding centers; i.e., the region of the wave source will change its coordinate in space from period to period. With a subsequent lessening of the degree of relaxation of the system, a standing wave may be obtained.

Up to this point we have been talking about systems with a simple diffusion (i.e., with a diagonal diffusion matrix). However, mutual diffusion of components can be extremely important in autowave systems. In Ref. 85, for example, there is a study of a three-component model in which the self-excited oscillatory subsystem ("brusselator") acts on the third variable only through mutual diffusion; without this mutual diffusion, the events would be the same as in a two-component system. A numerical simulation has shown that this model has a stable guiding center. The mechanism for the formation of a stable guiding center is precisely the same as discussed in the example of system (2.12), (2.13).

A variety of sources of wave self-excitation in active media have now been identified. A common feature in the operation of these sources is that the oscillation frequency throughout space is higher than the frequency corresponding to the in-phase case. On the basis of this property we can suggest a simple and reliable method for determining whether autonomous wave sources can exist. A perturbation, localized in space and time, should be introduced into the medium, and the change in the oscillation frequency at a point in space accessible experimentally should be monitored.

Let us compare the experimental data with the models for autonomous wave sources. Figure 1 shows the distributions of Fe^{3+} at successive times for the guiding-center case of the Belousov–Zhabotinskiĭ reaction (here Fe^{3+} is a slow variable). The scale time for the increase in the Fe^{3+} concentration in the traveling pulse is about $\frac{1}{8}$ of the oscillation period. Since the condition

$\tau/R > 0.5$ must be satisfied for the echo case to occur, wave generation in these experiments cannot be explained by any mechanism of this type. At the same time, the basic guiding-center models with three variables give a correct description of the general features of the observed effects.

Guiding centers arise because of supertheshold perturbations of the homogeneous state. Experimentally, guiding centers may appear spontaneously in the course of in-phase oscillations. Macroscopic fluctuations can thus occur in the these reactions. The existence of such fluctuations has yet to be explained theoretically.

Finally, we wish to point out that mutual diffusion can have an important effect on the stability of a homogeneous state in nonequilibrium systems and can lead to the formation of guiding centers.

3. THE SYNCHRONIZATION PROBLEM

(a) Synchronous self-excited oscillations in inhomogeneous systems

Some of the basic autowave modes which are important in the activity of an individual cell or an entire organism are the synchronous self-excited oscillations of kinetic variables over the entire space under consideration. A theory for the synchronization of second-order two-component systems with diffusion coupling is derived in Ref. 34. Let us examine the basic results of this theory.

If the system is inhomogeneous because the functions F_i vary with the coordinate, e.g., because of a variation in the temperature, the illumination, etc., then synchronization is not mandatory.

A discrete analog in radio physics of a self-excited oscillatory system with diffusion coupling would be represented by chains of N self-excited, galvanically coupled oscillators. Such a chain is described by a system of equations of the type

$$\frac{dx_i}{dt} = F_i(x_i, y_i) + d_x(x_{i+1} - 2x_i + x_{i-1}), \quad \frac{dy_i}{dt} = \varphi_i(x_i, y_i) + d_y(y_{i+1} - 2y_i + y_{i-1}); \tag{3.1}$$

where x_i and y_i are the dynamic variables in generator i, $d_x = D_x(N/L)^2$, $d_y = D_y(N/L)^2$, and the structure of the equations for the first and N-th elements is governed by the boundary conditions (L is the length of the system).

In biology, the discrete analogs could be tissues consisting of individual cells, and the coupling coefficients d_x and d_y would be governed by the permeability of the membranes and the intercellular gaps. Self-excited oscillatory biochemical reactions such as dark photosynthesis[93] or glycolysis[33] can occur in the individual cells.

Equations (3.1) have been studied in detail for the case of nearly harmonic oscillations. Under these conditions, the effective step-by-step truncation method developed by Khokhlov[86] can be used for the equations describing the evolution of the amplitudes and phases of the chain of self-excited oscillators. The synchronization band Δ_s is given by

$$\Delta_s = (d_x + d_y) f(N). \tag{3.2}$$

The function $f(N)$ depends on N, the number of generators, and on the nature of the distribution of characteristic frequencies of the self-excited oscillations. This function reaches a maximum if the deviation from resonance is introduced in the generator which is at the center of the chain.[34,87]

As a rule, autowave processes are of a relaxation nature in nonequilibrium kinetic systems. Let us assume, as before, that x is the fast variable, while y is the slow variable, and let us assume that the growth rate in the self-excited oscillatory system increases by a factor of $\varkappa$. Then according to Ref. 88 we have, instead of (3.2),

$$\Delta_s \sim d_y\varkappa + \frac{d_x}{\varkappa}. \tag{3.3}$$

This means that the synchronization efficiency in the case of coupling through the slow variable is increased by a factor of $\varkappa$, while that in the case of coupling through the fast variable is, on the contrary, reduced. In the following subsection we will consider some cases in which desynchronization of self-excited oscillations in space occurs in a relaxation system with $d_y = 0$; i.e., we consider cases in which $\Delta_s \to 0$ in the limit $\varkappa \to \infty$.

Along a chain of generators which are detuned with respect to each other, or, correspondingly, along a distributed, inhomogeneous self-excited oscillatory system, a stationary distribution of the phase "gradient" is established. As a result, a phase wave will travel along the system once per period. Visually, this effect is observed as a traveling color wave in thin and long tubes in which a Belousov–Zhabotinskiĭ reaction is occurring, when some sort of inhomogeneity is introduced in the tube.[5] (Phase waves should not be confused with waves which diverge from a guiding center.)

We can demonstrate the usefulness of models in the form of a chain of diffusion-coupled oscillators for interpreting the guiding-center phenomenon. As mentioned in Section 2, stable guiding centers can apparently exist only in three-component self-excited oscillatory systems. In radio physics, such a distributed system would correspond to a chain of oscillators with "one and one-half" oscillatory degrees of freedom, e.g., oscillators with an inertial nonlinearity. The stable out-of-phase case of synchronized self-excited oscillations can occur along with the in-phase case in systems of two such diffusion-coupled oscillators with three dynamic variables.[76] The synchronization frequency here is higher than the frequency of the partial self-excited oscillations. Let us assume that at first all the oscillators in the chain are operating in the mode of in-phase synchronous self-excited oscillations. If the phase of the self-excited oscillations in one of these oscillators changes abruptly by an angle on the order of π, then a local "region" with self-excited oscillations at a higher frequency forms in the chain. Such a region can be interpreted as a guiding center.

If inhomogeneous initial conditions are specified in a distributed system, then the synchronous self-excited oscillations are established throughout the system in a finite time. The propagation velocity of the synchronous regime for a quasiharmonic autowave process can be estimated from ($\omega \gtrsim \delta$)

$$v = 2\sqrt{\delta D}. \tag{3.4}$$

For simplicity we are assuming $D_x = D_y = D$ here.

Using (3.4), we can estimate the maximum volume of total internal mixing, within which all the processes are synchronized. The characteristic dimension of this volume, L^*, is found from

$$\frac{L^*}{v} \leqslant \frac{2\pi}{\omega} = T \quad \text{or} \quad L^* \leqslant 4\pi \frac{\sqrt{\delta D}}{\omega}. \tag{3.5}$$

For estimates we can also use the propagation velocities of traveling pulses, from Table I.

Using L^*, we can determine the minimum number of partitions of the distributed system in the construction of its discrete analog:

$$L^* \leqslant \frac{L}{N}, \quad N \leqslant \frac{L}{L^*}. \tag{3.6}$$

Table II shows estimates of L^* for various self-excited oscillatory processes. It can be seen that biochemical self-excited oscillations are synchronous self-excited oscillations within individual living cells and even entire "organs," for example, for cardiac muscle and for the leaf of a green plant. On the other hand, molecular diffusion is not always sufficient to synchronize a Belousov–Zhabotinskiĭ reaction. Complex autowave processes which occur in a plane are observed in reactors with a thin layer of reactant solution (with a thickness less than 1 mm).

(b) Desynchronization of self-excited oscillations. Quasistochastic waves

When there is a random perturbation of the phase difference between the self-excited oscillations at two points in space, c and d, a complex transitional case can arise: quasistochastic waves.

Yakhno *et al.*[77] have derived specific conditions for the existence of complex relaxation-type self-excited oscillations in space [for systems of the type in (1.9), (1.10) with two N-shaped null isoclines], and they have reported a corresponding computer simulation. To find an analytic equation, they adopted the following assumptions: A perturbation was imposed on the homogeneous distribution of the variables x and y at the initial time. The change in the variable y at the two points c and d was studied. It was assumed that $\Delta y = y_c - y_d \ll y_{\max} - y_{\min}$ and $l_f < L_{cd} \ll vT_0$, where l_f is the length of the traveling-pulse front, L_{cd} is the distance between points c and d, and T_0 is the period of the characteristic self-excited oscillations. If the values of y at points c and d do not converge with the passage of time, a desynchronization occurs in the system. The desynchronization conditions can then be written

$$\delta^* = \frac{\Delta y\,(t+T)}{\Delta y\,(t)} > 1. \tag{3.7}$$

The growth rate δ^* can be expressed in terms of the characteristics of the slow motions at points c and d.

Figure 18 shows an example of the formation of a quasistochastic wave in a system of the Nagumo type, in (1.11) (Ref. 77), calculated through a computer simulation. The perturbations in case c are found by shifting the initial x and y distributions for case b over a distance $0.01L$. We see that, beginning at $t = 6.0$, the x and y distributions are very different. The smooth distribution of the slow variable converts into a random "cellular" structure (cf. the photograph in Fig. 3).

Complicated spatial regimes have also been found through numerical calculations for other self-excited oscillatory models of chemical systems.[7,27,82,89-91] It can be suggested that the process by which a quasiharmonic concentration wave forms is closely related to the processes by which the solutions of dynamic systems become stochastic, i.e., processes of the strange-attractor type.[4]

These complex regimes can be used as one explanation for the fibrillation regime in the self-excited oscillatory regions of cardiac muscle.[33,77] It is tempting to use this desynchronization process to explain the complex picture of the motion of excited regions which is observed in the cerebral cortex (see Fig. 18d, taken from Ref. 92).

It can be seen from Figs. 18a and 18d that the features of the process on the (r, t) plane are very similar. It should be noted, however, that it is not yet possible to use the existing models for neuron ensembles to explain the origin of the spatial desynchronization of oscillations.[52]

In summary, if a point system has self-excited oscillatory properties, then two opposing processes always occur. One maintains the synchronous self-excited oscillations through diffusion coupling in the slow variable, while the other can lead to a desynchronization and to the appearance of quasistochastic waves through coupling in the fast variable.

TABLE II. Estimates of the dimensions of the synchronous region.

			L^*, cm		
Self-excited oscillatory process	$T = \frac{2\pi}{\omega}$	δ/ω	Molecular diffusion, $D \sim 10^{-5}$ cm/sec	Forced mixing, $D_{eff} \sim 10^{-5}$ cm/sec	Excitable medium
Dark photosynthesis reactions	10 h	0.2 0.5	4.0 10.0		
Self-excited oscillations in glycolysis	10 min	0.2 0.5	0.45 1.13	45 11.3	
Belousov-Zhabotinskiĭ reactions	0.1—1 min	0.2 0.5	0.06—0.15 0.15—0.37	5—15 12.5—37.5	
Self-excited oscillations of cardiac muscle	1 sec				1 mm
Self-excited oscillations in a neuron network (fast waves)	0.5 sec				10 cm

T) period of self-excited oscillations; ω) angular frequency; δ) growth rate of system.

4. INHOMOGENEOUS STATIONARY STATES. DISSIPATIVE STRUCTURES

An organic part of the large and interesting range of problems of the theory of active kinetic systems consists of the problem of the spontaneous disruption of

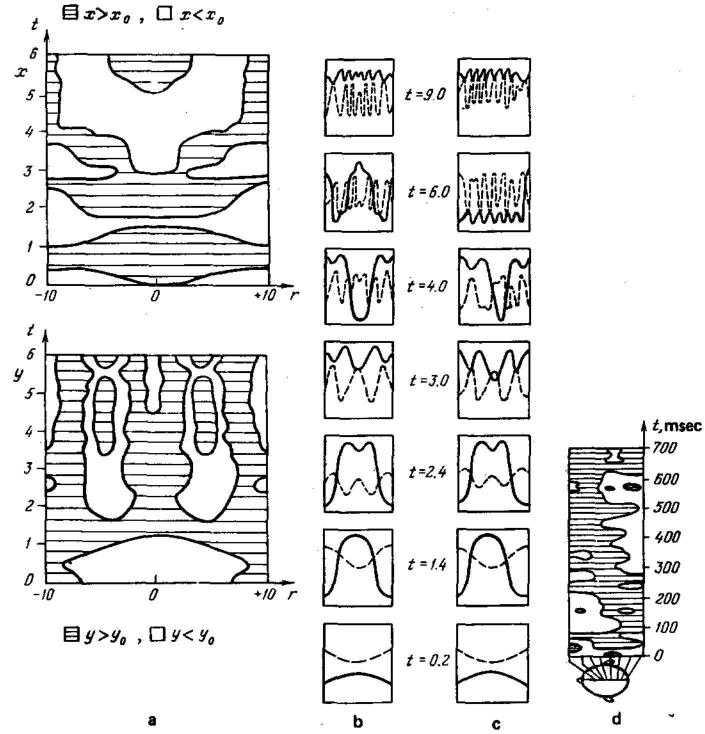

FIG. 18. Quasistochastic self-excited oscillations in distributed systems. a) A case of the quasistochastic process, shown on the (r, t) plane, in a system of the Nagumo type ($T_0=2.8$, $L=20$, $\varepsilon=10^{-2}$); b, c) distributions of the variables x (solid curves) and y (dashed curves) (there is a relative displacement of $0.01L$ in the corresponding initial conditions[77]); d) recordings of brain potentials, mapped onto the (r, t) plane.[92]

homogeneous states and disruptions of the symmetry of systems. In Section 3 it was shown that the general model in (I.1) describes two types of instabilities of a homogeneous state. The oscillatory instability leads to the formation of standing waves and also of other, more complicated dynamic modes. In the present section we are concerned with the stationary inhomogeneous states which result from the Turing instability. The study of these states was begun by Turing[96] in 1952 and has been continued by the Prigogine school at Brussels,[2,97,98,112,137] where these structures have been named "dissipative structures". This term emphasizes the thermodynamic aspect of the problem: The dissipative structures are created and exist in thermodynamically open systems because of dissipative processes involving the utilization of entropy, energy, etc. Prigogine and his colleagues were the first to point out the common nature of such phenomena as chemical dissipative structures and shaping in hydrodynamics, where Bénard cells, for example, are also dissipative structures.

Frequently, especially by authors working abroad, the term "dissipative structure" is understood as representing a variety of self-organization phenomena in nonequilibrium media, not only the chemical dissipative structures described by (I.1). In Ref. 99, dissipative structures are classified according to the types of gradients of the variables (chemical or electric potentials, the pressure, etc.) which maintain the existence of these structures. There are many papers reporting the observation of dissipative structures in whose formation several factors are simultaneously important: chemical reactions, hydrodynamic forces, electric fields, and biological phenomena (e.g., chemotaxis).[7,99-108]

Research on dissipative structures is important in biology, especially for the biology of growth, in the problem of the shaping of organisms. It was not without reason that the first and fundamental paper by Turing was entitled "Chemical foundations of morphogenesis."[96] The problem is as follows: In the development of an organism from a fertilized egg cell to an adult individual, we can distinguish several stages in which there is a spontaneous disruption of symmetry. The first is the formation of an axial axis, i.e., the disruption of the cylindrical symmetry of the embryo. In the later stages, an orginally homogeneous fragment breaks up (there is a disruption of the translational symmetry), and there are other effects of the same type. As a rule, external agents which are capable of disrupting the symsymmetry are so weak that they can be ignored as causal factors. The capability of disrupting symmetry is thus an internal property of the developing organism. The shape of the organism (either the final shape or the shape in one of the intermediate stages) is predetermined; i.e., information on this shape is already present in the fertilized egg. A dissipative structure which appears in the organism can accordingly be called an "intrinsic structure," and this term would serve to emphasize the fact that information on this structure is incorporated in the system itself, rather than introduced into the system from without. Several questions arise: Under what conditions can this occur? How does the process evolve? How is it regulated? These questions are obviously typical of the theory of autowave processes, so in answering them we can use the results from the study of the basic models of dissipative structures.

In this review we are dealing with only those systems which can be modeled by equations like (I.1). Among these systems are not only chemical (or biochemical) systems but also ecological systems[104,105,116] and systems of population genetics.[106] An interesting example of a dissipative structure was suggested by Blumental,[107] who studied lateral diffusion on the surface of a membrane for the case in which cooperative effects occurred as the components were transported across the membrane. The system describing standing striations[30] is similar to (I.1).

The basic goals of this section are thus to introduce the reader to the methods for solving the problems and to the results which have been found and to discuss briefly the applications and the directions for further development of the theory.

(a) Conditions for the existence of dissipative structures

Mathematical models of the type in (I.1) can describe spatially inhomogeneous states (dissipative structures) as well as stationary homogeneous states, as in (1.1). Let us examine the conditions for the existence of such stationary solutions. We will assume that the following natural restriction is met: The point kinetics of the models under study is physically realizable; i.e., the point system has no solutions which increase without bound.

Turing used the following conditions for the appearance of stable dissipative structures: (1) The stationary state of the point system is a stable focus (the basic model with two variables). (2) There is an interval of wave numbers $(k_{\min}, k_{\max})$ for which the dispersion relation in (2.3) has two real roots with different signs. If the conditions are satisfied, the variation of δ_k with k is as shown in Fig. 11a.

These conditions do not cover all the cases in which the models in (I.1) have stationary solutions of the dissipative-structure type. A more general condition, which is not restricted to two-component systems, is the following condition[75,76]: If the free term in the dispersion relation (2.3) is negative at a certain wave number $k[q_0(k) < 0]$, then the distributed system has at least one stationary solution of the dissipative-structure type. The use of these conditions for the existence of solutions, in contrast with the preceding conditions, presupposes that the next step in the study of the model is to analyze the stability of the dissipative structures.

For the simplest discrete models and for single-component systems, this assertion can be proved rigorously and in fact quite simply. For multicomponent systems, no proof which is completely rigorous mathematically has been found. For systems with a single variable (neutral boundary conditions), Chafee[109] showed that inhomogeneous stationary states of systems of this type are unstable. An analogous assertion was proved independently by Belentsev *et al.*,[110] who also showed that in a single-component system with permeable ends there is a stable inhomogeneous stationary state. Metastable dissipative structures are possible in single-component systems if the diffusion coefficients vary along x. This case is discussed in more detail in subsection d; for the time being we will consider systems with $n \geq 2$.

It is useful to keep in mind that the conditions listed for the existence of dissipative structures are analogous to the conditions for a "trigger" nature of lumped systems. Furthermore, in many regards dissipative structures can be thought of as states of a distributed trigger. The condition $q_0(k) < 0$ means that the dispersion relation has an odd number of roots with positive real parts, i.e., that the homogeneous state is unstable (the Turing instability). These conditions are only sufficient conditions. Below we will discuss some situations in which dissipative structures exist, in which the condition $q_0(k) < 0$ does not hold, and in which dissipative structures are produced under stringent conditions.

The inequality $q_0(k) < 0$ is the condition for the self-excitation of a mode with a period $2L/k$. If there are no zero terms among the diagonal elements of the diffusion-coefficient matrix, the spectrum of excited modes is finite. Then near bifurcation values of the parameters we can use the methods of perturbation theory to construct solutions. If the diffusion coefficient of an autocatalytic variable is zero, and if the conditions $q_0(k) < 0$ hold for some k, then the spectrum of excited modes is unbounded. In this case the solutions—the so-called contrasting dissipative structures—have discontinuities.[76]

The stationary states of the model in (I.1) satisfy the system of equations

$$D_{ii}\frac{d^2x_i}{d^2r^2}+F_i(x_1,\ x_2,\ \ldots,\ x_n)=0, \tag{4.1}$$

supplemented with boundary conditions, e.g., those in (I.3). Written in this form, these equations clearly show the similarities between this problem and the problems of the theory of nonlinear oscillations. The only distinctive feature is that the boundary conditions must be taken into account. In the subsections below we will discuss separately the cases of quasiharmonic and "contrasting" dissipative structures. First, however, we will consider the example of the simplest discrete model, since the results are quite graphic and at the same time give a qualitatively correct picture of the stationary inhomogeneous states in active systems.

The well-known "brusselator" model, proposed in Ref. 115, has played a role in the development of the theory of dissipative structures like that played by the van der Pol system for the theory of nonlinear oscillations. The corresponding point system,

$$\begin{aligned}\frac{dx}{dt}&=A+x^2y-(B+1)x,\\ \frac{dy}{dt}&=Bx-x^2y,\end{aligned} \tag{4.2}$$

has a single stationary state: $\bar{x}=A, \bar{y}=B/A$. At $B>B_{osc}=1+A^2$, there is a stable limiting cycle. In a system of two such reactors, coupled by diffusion, as in (2.4), other stationary states may exist. If we use the normal coordinates in (2.5) we can reduce the problem to the simple equation[75]

$$(\Delta_x^2)^2-(\Delta_x^2)\left[2A^2-2d_x-\frac{B-(1+d_x)}{2d_y}\right]+\frac{A}{2(1+d_x)}q_0(2)=0, \tag{4.3}$$

where $q_0(2)$ is the free term in the dispersion relation of the model, and d_x and d_y are the coefficients of the diffusion coupling. If $q_0(2) < 0$, the equation of the inhomogeneous states in (4.3) obviously has a real solution in all cases. This conclusion means that a system of two diffusion-coupled reactors is analogous to an electronic flip-flop with two stable stationary states [$\pm\Delta_x^*$, where Δ_x^* is the solution of (4.3)]. The state with $\Delta_x=0$ is unstable. There can also be so-called subcritical flip-flops [$q_0(2)>0$]. In this case the states $\Delta_x=0$ and $\pm\Delta_{x2}^*$ are stable, while the states $\pm\Delta_{x1}^*(|\Delta_{x1}^*|<|\Delta_{x2}^*|)$ are unstable. The state diagrams of the discrete model are similar to those shown for the distributed system in Fig. 19. We note that the subcritical flip-flops result from the quadratic terms in the reduced system. The boundedness of the solutions is a consequence of the cubic terms. This circumstance should be kept in mind in choosing approximate methods for analyzing distributed systems.

(b) Quasiharmonic distributions

The simplest approach to the solution of problem (4.1) is to use the harmonic-balance method.[111] It is useful to keep in mind that, if we restrict this analysis to the zeroth ($k=0$) and fundamental modes, then the equations for the corresponding amplitudes are equivalent to the equations for the stationary solutions of the discrete model in (2.4), written in terms of the variables S and Δ in (2.5) (Ref. 75). A more systematic approach to the solution of the problem is to use the various modifications of the small-parameter method which is traditional in the theory of non-linear oscillations.[75,98,112,113] We can outline the use of this method to solve the boundary-value problem.

Following the method of Bogolyubov, we find a bifurcation value of the new parameter $B=B_k$ for the equation $q_0(k,B)=0$ (Here B is the parameter of the point system). From system (4.1) we pick out the linear operator $\hat{\mathscr{L}}_k(B_k)$ (the generating system), which has a nontrivial eigenfunction of period $2L/k$ for the zeroth eigenvalue. The eigenfunction satisfies the boundary conditions. We write it as $P_k\mathbf{x}_k(r)$. We rewrite (4.1) as

$$\hat{\mathscr{L}}_k(B_k)\,\mathbf{x}=(B_k-B)\,\mathbf{x}+\Phi(\mathbf{x}), \tag{4.4}$$

where Φ contains only terms which are nonlinear in $\mathbf{x}$. We further assume

$$B-B_k=P_k\gamma_{\rm I}+P_k^2\gamma_{\rm II}+\ldots, \tag{4.5}$$

and we expand the solution in (4.1) in powers of P_k:

$$\mathbf{x}(r)=P_k\mathbf{x}_k(r)+P_k^2\mathbf{x}_{\rm I}(r)+P_k^3\mathbf{x}_{\rm II}(r)+\ldots\,. \tag{4.6}$$

Substituting (4.5) and (4.6) into (4.4), and collecting terms with identical powers of P_k, we find a sequence of linear systems for determining $\mathbf{x}_{\rm I}$, $\mathbf{x}_{\rm II}$, etc. The right side of the system for $\mathbf{x}_{\rm I}$ contains $P_k\mathbf{x}_k$, while that for $\mathbf{x}_{\rm II}$ contains only $P_k\mathbf{x}_k$ and $\mathbf{x}_{\rm I}$. As usual, the P_k are found from the condition for the absence of secular terms terms in (4.4). For this condition to hold, the right side of (4.4) must be orthogonal to the eigenfunction of period $2L/k$ of the adjoint operator $\hat{\mathscr{L}}_k(B_k)$:

$$\int_0^L[(B_k-B)(P_k\mathbf{x}_k+P_k^2\mathbf{x}_{\rm I}+P_k^3\mathbf{x}_{\rm II}+\ldots)+\Phi(\mathbf{x}_k+P_k^2\mathbf{x}_{\rm I}+\ldots)]\,\mathbf{x}_k^+\,dr=0. \tag{4.7}$$

From Eq. (4.7) we can find the amplitude of the stationary dissipative structure. It is easy to see that the left side is equal to the nonlinear correction for the oscillation period, and this correction must be zero by virtue of the boundary conditions. A particular feature of the boundary-value problem in (4.1) is that the generating system can be constructed for various values of B_k. Equation (4.7) has real solutions P_k for those wavelengths $2L/k$ for which $q_0(k,B)<0$. The systems can thus have dissipative structures with different periods.[75,111,114]

Let us examine the characteristics of the dissipative structures in (I.1) using the example of the brusselator distributed model. The corresponding point system was given earlier, in (4.2). The problem with periodic boundary conditions for the same model was solved in Ref. 113, and that with conditions of the first kind was solved in Refs. 75, 98, and 112. For boundary conditions of the second kind in (I.3), in the approximation which retains cubic terms in P_k^3, the steady-state distribution is[75]

$$x(r)=A+P_k\left[\cos\left(\frac{2\pi k}{L}r\right)+P_kC_0+P_kC_2\cos\left(\frac{2\pi k}{L}r\right)+P_k^2C_3\cos\left(\frac{3\pi k}{L}r\right)\right],$$

where C_0, C_2, and C_3 are constants which depend on A, B, D_x, and D_y. An equation for $y(r)$ can be written in a similar way. The amplitude P_k is determined from (4.7), which takes the following form after the integrals are evaluated:

$$P_k\left[\frac{q_0(k)}{2k^2D_y}L^2+a_1P_k^2+a_2P_k^4\right]=0. \tag{4.8}$$

The coefficients in (4.8) are expressed in terms of the parameters of the distributed model; a_2 is always positive, so that if $q_0(k)<0$ then Eq. (4.8) has a nontrivial solution. The expression for a_1 can be either positive or negative if $B<B_k$. In the latter case there are subcritical dissipative structures. Both types of bifurcations are shown in Fig. 19. These curves are drawn from the results of a numerical integration of the system. These results agree well with the results calculated from (4.8) in the case $a_1>0$ with $B=B_k$. For bifurcations of another type, this approximation is much less accurate, because the convergence of the method improves with increasing values of the ratios P_k/A and $q_0(k)/(2k^2D_y/L^2)$. Nevertheless, this method does lead to an accurate picture of the bifurcations at the point $B=B_k$.

An important problem in the theory of dissipative structures is to analyze the stability of inhomogeneous states. The simplest approach is to analyze the stability of dissipative structures with respect to perturbations with a fixed shape.[111] In this manner it is found that for the large values $B>B_{\rm osc}$ the dissipative structures are unstable with respect to in-phase perturbations[75] (Fig. 19).

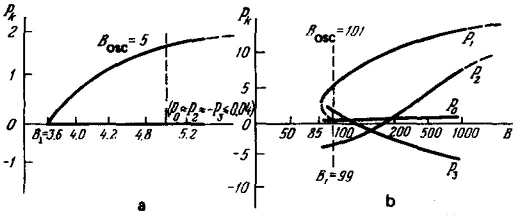

FIG. 19. Dissipative structures in a "brusselator" system, (4.6). a, b) Variation of the amplitudes of the harmonic components with the values of the parameter B (the dashed curves show unstable states). a) $A=2$, $D_x=0.08$, $D_y=0.4$, $L=1$; b) $A=10$, $D_x=0.75$, $D_y=1.0$, $L=1$.

We can describe one class of sufficient conditions for the instability of dissipative structures. We project the stationary solution $\{x(r), y(r)\}$ onto the (x, y) phase plane. For a boundary-value problem, this projection is an unclosed curve. If this projection lies entirely in the incremental region of the corresponding point system, then such a dissipative structure is unstable. These conditions lead to the following fact: If $B_k < B_{osc}$ for bifurcations of the first kind (Fig. 19a), then stable dissipative structures with a period $2L/k$ cannot occur in the system. The fact that any dissipative structure becomes unstable at large values of B is also a consequence of these conditions.

Systems can have stable solutions of the dissipative-structure type with different wavelengths. How is a transition between these solutions made in the case of slow changes in the parameters? Figure 20 shows how P_k varies with L, the length of the system.[114] Characteristic features of this variation are the presence of a hysteresis loop and an abrupt transition between dissipative structures with different shapes. In the language of the theory of oscillations, this hysteresis would be attributed to a nonequivalence of the nonlinear transformations of the first harmonic into the second and back; i.e., the hysteresis is not a consequence of the particular model but a common feature of dissipative structures.

(c) Contrasting dissipative structures

In the theory of dissipative structures, the case of small diffusion coefficients for the autocatalytic variable D_x in (4.6) deserves special consideration.[76] As an example we consider the system

$$\begin{aligned} \frac{\partial x}{\partial t} &= y(1-Vx) - \gamma x + D_x \frac{\partial^2 x}{\partial r^2}, \\ \frac{\partial y}{\partial t} &= \beta y(1-x) - \frac{(py-\varkappa)x}{qy+\tau} - Cy^2 + D_y \frac{\partial^2 y}{\partial r^2}; \end{aligned} \qquad (4.9)$$

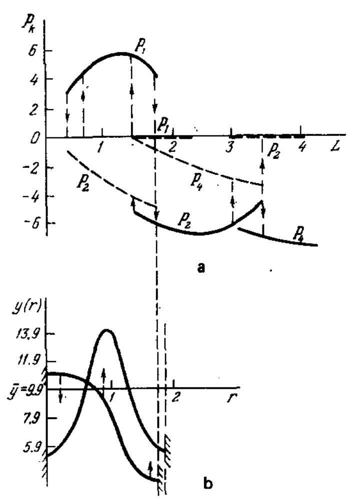

FIG. 20. Hysteresis transitions between dissipative structures with different shapes upon a change in the length of the system (4.6). a) Variation of the amplitudes of the harmonic components (P_k) with L ($A=10$, $B=99$, $D_x=0.75$, $D_y=1$); b) initial and final states in the transition from a dissipative structure with $k=1$ to a dissipative structure with $k=2$.

where y is the autocatalytic variable. Equations (4.9) are derived from the models for the Belousov–Zhabotinskiĭ self-excited oscillatory reaction proposed in Refs. 5 and 80 [see (2.8)]. The characteristics of the dissipative structure in this system, for diffusion coefficients which are comparable in magnitude, are the same as those discussed above. Since this system is a model of a medium in which dissipative structures have been studied experimentally, it is interesting to compare the experimental and calculated wavelengths: For reasonable parameters of the point system and for diffusion coefficients of 10^{-5} cm^2/sec, the model describes dissipative structures with a period of 0.2–2 cm, in agreement with experiment.

Let us construct some discontinuous stationary solutions of system (4.9). For this purpose we consider the null isoclines of the corresponding point system (Figs. 21 and 22). We assume $D_y = 0$; then the projection of any stationary solution must be situated on a y-null isocline which is N-shaped. This null isocline is described by a multivalued function $y(x)$ which can be approximated by three single-valued functions: $y_A(x)$, $y_{AB}(x)$, and $y_B(x)$—for each of the regions of the isocline. Substituting y_A and y_B in turn into the first equation of system (4.9), we find three parabolic equations for the single variable x.

The projection of the dissipative structure is in regions A and B (Figs. 21 and 22). In region A, the local terms of the diffusion equation for x, are positive, while the diffusion term in negative; in region B, we have the opposite situation. For the equations in these regions

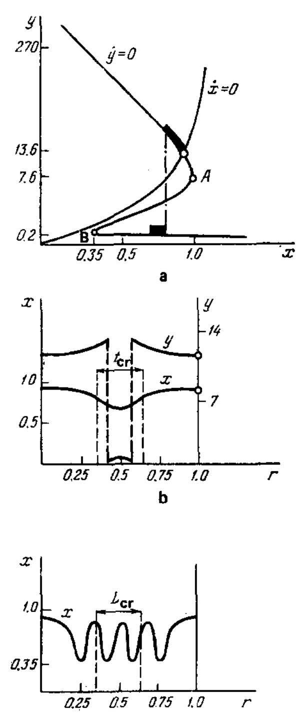

FIG. 21. Localized dissipative structures in system (4.6) (Ref. 76). a) Projection of the dissipative structure onto the phase plane of the point system ($V=1, \gamma=0.5, p=\beta=500, \varkappa=1, q=8, \tau=0.5, c=1, D_x=0.05, D_y=0$); b, c) shape of localized dissipative structures (in case c, the length of the region of the initial perturbation is greater than the critical length L_{cr}).

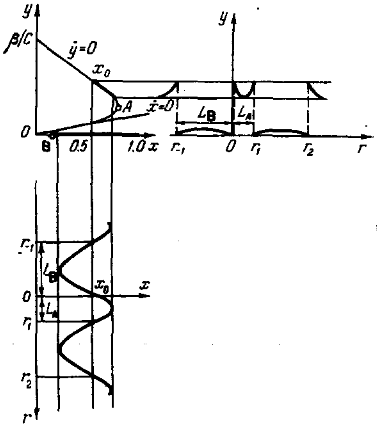

FIG. 22. Contrasting dissipative structure in system (4.9). $L_A = 0.1, L_B = 0.26$ ($V = 0, \gamma = c = 0.01, \beta = \tau = 1, q = 4, p = 5, \varkappa = 0.01, D_x = 0.5, D_y \to 0$).

we can solve the first boundary-value problem: $x_A|_{r=r_p} = 0$ etc., where r_p is the coordinate of the discontinuity. The resulting solutions should be joined at the discontinuities in the continuous variable x. Taking into account the difference in signs of the local terms at A and B, we easily see that the joining results is a closed system of equations. The coordinates x_0 of the "discontinuities" are governed by the initial conditions; in other words, they are quite arbitrary. Figure 21 shows localized dissipative structures. The parameters of such a dissipative structure do not depend on the length of the system, but they are governed by the initial conditions. Specifically, for perturbations in small regions, the dissipative structures have a single peak, while for broader perturbations the distribution has several peaks.

In the case $D_y = 0$ there can, in principle, be aperiodic dissipative structures with a varying period. This is a consequence of the arbitrariness in the choice of the y coordinate of the joining point x_0. If our problem is to find solutions which are also meaningful at small but nonvanishing values of the coefficients D_y, then x_0 is determined unambiguously. Specifically, with $D_y \neq 0$, the discontinuities should develop into a steep front. In a stationary state, this front should be fixed. This event is possible only if $x = x_{cr}[v(x_{cr}) = 0$; see Section 1]. Since the values of x_0 are the same for all the discontinuity fronts, there can be only periodic solutions in the limit $D_y \to 0$. The period of these solutions is always less than some λ_{max}. Short waves, however, are established only after specially chosen initial conditions. There is a wide range of perturbations which lead to the formation of long waves.

As a rule, "contrasting" dissipative structures are established by a self-adjustment process: A peak forms in the distribution near the local perturbation; then another peak forms beside it; and so forth. In the previous system, this case was typical of only subcritical structures which arise under stringent conditions. Self-adjustment has also been observed experimentally.[5]

In system (4.9), continuous solutions are possible in the case $D_y = 0$. Their amplitudes are smaller than the "contrasting" values, and these solutions are projected onto region AB of the null isocline (Fig. 22). Stationary states of this type, however, are unstable. Their projection lies in the incremental region of the phase plane of the point system. This fact can also be explained on the basis that these states are described completely by a single homogeneous equation, and such dissipative structures are unstable, as mentioned earlier.[109]

If the parameters of the system depend on a spatial variable, then structures analogous to localized dissipative structures (Fig. 21) can also be observed when all components of the system are diffusing.[2,136] The "absence of diffusion" of certain components is possible in compartmentalized (discrete) systems, e.g., in biological objects having a cellular structure. Furthermore, in media of this type the equation $v(x_{cr}) = 0$ has an interval of values of x_{cr} as a solution.[117]; in other words, at small values of D_y the aperiodic dissipative structures turn out to be stable. Stable, localized dissipative structures are apparently also possible in multicomponent systems in the case of very nonlinear transport processes, even for a nonvanishing mobility of the components. For many "nonbiological" objects, the equation $D_i = 0$ should be understood in a limiting sense, and only periodic "contrasting" dissipative structures should be considered.

(d) Metastable dissipative structures

Up to this point we have been discussing the simplest basic models of dissipative structures, which contain no fewer than two kinetic variables and which have constant diffusion coefficients. In the case in which the diffusion coefficient or thermal conductivity itself varies with the kinetic variables, even single-component systems acquire completely different properties.

The possibility of self-organization was predicted theoretically by Samarskiĭ, Kurdyumov, *et al.*[118,119] in dissipative media which are described by the nonlinear heat-conduction equations

$$\frac{\partial}{\partial t} T = \alpha T^l + \frac{\partial}{\partial r}\left(\beta T^m \frac{\partial}{\partial r} T\right), \tag{4.10}$$

where α, β, l, and m are constants, and T is the temperature.

Let us examine some of the predicted effects.[2)]

1. In the case $l > m+1$ (the L mode in the terminology of Refs. 118 and 119), the heat wavefront does not propagate into the cold medium but instead forms a region of a metastable heat-localization region, which contracts over a finite time. In this region, the temperature and the amount of heat can increase to infinity. Realistically, an upper bound would be imposed by either heat loss or by the exhaustion of fuel. The reason for the heat localization is the formation of a concave temperature profile at the heat wavefront.

2. If the initial conditions are such that several metastable-localization regions develop, these regions will interact with each other. Then either one of the regions

[2)]The case $\alpha = 0$ was discussed previously by Zel'dovich, Kompaneets, and Barenblatt.[120-122]

will survive, or a certain structure of these regions will be established.

3. The dimension or the fundamental length L^* of the metastable region is predicted by the theory:

$$L^* \approx \sqrt{\frac{\beta T^m}{\alpha T^l}} = \sqrt{\frac{\beta}{\alpha}}\, T^{(m-l)/2}. \tag{4.11}$$

4. Metastable regions are also formed in two-dimensional spatial regions; these regions are called "thermal crystals" in Ref. 123. The shape of these crystals has been determined by computer simulation.

Figure 23a shows the evolution of the metastable region and, for comparison, the behavior of the initial thermal fluctuation in the case in which the condition $l > m+1$ does not hold (Fig. 23b). It is important to note that during the period in which the metastable region is established (in the accentuation regime) gasdynamic effects are negligible. The equations thus ignore the diffusion of the fuel and of the reaction products.

It is most likely that a prediction of these effects is important for a study of the processes which occur in a laser plasma, in cosmogony, and in fusion reactors.[124]

Using Prigogine's terminology,[97,98] we can justifiably call these metastable combustion regions "metastable dissipative structures."

(e) Some comments and conclusions

The most important theoretical problem in the initial stages of studying a new effect is to predict the properties of the objects in which the effect can be observed and to predict the conditions for the occurrence of the effect. Analysis of dynamic models like that in (I.1) leads to the basic characteristics of the media in which dissipative structures can be produced, and it leads to an explanation of the experimental data. Let us briefly examine the results.

In distributed two-component systems without mutual diffusion, stationary dissipative structures can arise if the corresponding point systems are either self-oscillatory systems or trigger systems or potentially self-excited oscillatory systems (i.e., if there is a limiting cycle for certain values of the kinetic coefficients). If all the D_{ii} are equal, then dissipative structures are possible only in self-excited oscillatory trigger systems. In such media, dissipative structures compete with the regime of in-phase self-excited oscillations, and the range of parameters in which dissipative structures are stable is small in comparison with the range corresponding to self-excited oscillation. Potentially self-excited oscillatory systems are thus of particular interest. In such systems, dissipative structures are possible only if the diffusion coefficient of a nonautocatalytic variable (a variable for which $\partial F_i/\partial x_i < 0$) is large. The number of media in which dissipative structures can be observed expands considerably if mutual diffusion is taken into account. Let us consider an example. The lumped system

$$\frac{dx}{dt} = Ax - Bx - x^2, \quad \frac{dy}{dt} = Bx - py \tag{4.12}$$

has a single singularity, with positive coordinates. This singularity is a stable point for any positive values of the parameters. Nevertheless, in the distributed system in (I.1) for any $D_{xy} = D_{yx} < 0$ there is a value A_{cr} such that at $A > A_{cr}$ stationary dissipative structures are created. It is pertinent to recall here that the equalities $D_{xy} = D_{yx} = 0$ are possible only if $D_{xx} = D_{yy}$ (Ref. 125). In the same monograph there are data from measurements of the mutual diffusion coefficients in strong electrolytic solutions. It turns out that in certain cases these coefficients are comparable in magnitude to the coefficients of self-diffusion.

There is a single distinction between systems with two and with more variables with regard to dissipative structures. The presence of a limiting cycle in a two-component model indicates that at certain values of D_{ii} there will be stationary solutions of the dissipative-structure type. In the case of a "stringent" limiting cycle, dissipative structures can be produced only in a stringent case. Already among three-component models we can find examples of systems with limiting cycles in which no stationary dissipative-structure solutions exist for any values of D_{ii}. Apart from this an analysis of models more complicated than the basic models reveals no qualitatively new properties of dissipative structures.

A natural extension of the dynamic theory of dissipative structures would be to study the fluctuations of variables near critical points, e.g., at the critical length of a system (Fig. 20). This problem has not yet been completely solved, but experience has been acquired in the stochastic modeling of dissipative structures.[7,126] Work of this type reveals new properties of active systems and is of assistance in pursuing the analogy between transitions in nonequilibrium systems and phase transitions in equilibrium systems.[7,127] On the other hand, stochastic modeling should establish the range of applicability of the theory of dissipative structures for certain biological objects which are characterized by extremely low concentrations.[126]

The range of applications of the theory of dissipative structures is growing steadily. New approaches to the modeling of dissipative structures are also being developed. In Refs. 51 and 52, for example, the language of

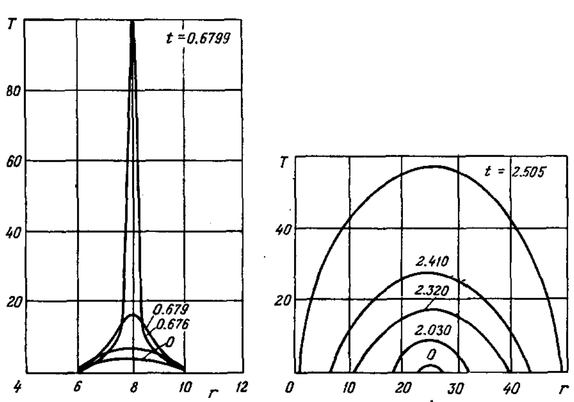

FIG. 23. Fronts of the combustion region in system (4.10) (Refs. 118 and 119). a) Metastable self-focusing region ($l > m + 1$); b) propagation of a temperature front ($l < m + 1$).

the theory of dynamic systems and of finite automatons is combined in a description of the structure of a colony of cells which are dividing and differentiating. If *a priori* conditions are incorporated in these models regarding the switching of modes in the cell, then in the representations proposed by Chernavskiĭ and Ruygrok[128] the switching events during the differentiation of the cells are consequences of the physical picture of the phase space of the corresponding point system. In this model, the point system can have both one and three stationary states. It can thus be used to follow bifurcations of the saddle-point type upon changes in the parameters. The appearance of several states is interpreted in biological terms as the appearance of an ability to differentiate. The model thus makes it possible to study the mutual effects of two important processes: morphogenesis and differentiation. The model dissipative structures and processes in specific biological objects (in particular, in hydra) have been compared by Belousov, Chernavskiĭ, and Dorfman.[129,130] It is important to note that these processes occur against the background of a lengthening of the object. In this connection, it becomes particularly important to study the bifurcations along the length of the system. In particular, hysteresis transitions (Fig. 20) correspond to the fact that bud formation in hydra begins when a certain length is reached.[131] The processes associated with dissipative structures are apparently also important at other levels of organization of living material. In Refs. 76 and 82, for example, the role played by dissipative structures and guiding centers in memory mechanisms is discussed.

Finally, we list some problems faced by the theory of dissipative structures: (1) a detailed study of fluctuations near critical points, (2) a study of dissipative structures in systems with active transport and also in systems in which the diffusion coefficients are strongly dependent on the concentrations, (3) a search for the stability conditions of dissipative structures with various shapes in a plane and in a volume (as of the present, only numerical results[132] are available), and (4) a study of the conditions for the existence of dissipative structures in active systems with convection.[30,133]

CONCLUSION

We will conclude with Table III, which lists the basic sufficient conditions for the existence of various types of autowave processes. In addition to the equations, this table gives references to the literature and to figures which illustrate the conditions for the existence of some basic model or other. The following notation is used here: (1) $\varkappa_1$, $\varkappa_2$, and $\varkappa_3$ are constant parameters of the point system, which are to be determined; (2) x_2 and D_{22} are the concentration and diffusion coefficient of the autocatalytic variable; (3) a point system of type T is a trigger system, one of type 0 is a self-excited oscillatory system, one of PO is a potentially self-excited oscillatory system, and one of type NO is a non-self-

TABLE III. Summary of the characteristics of the autowave processes which have been studied.

Type of autowave process	Number of variables in basic models	Dimensionality of the space	Diffusion coefficient	Characteristics (type) of point system	Velocity	Reference
1. Synchronized self-excited oscillations	2	1	$D_{11}, D_{22} > \varkappa_1$ $\lvert D_{11}-D_{22}\rvert > \varkappa_2$	O	—	34, 87
2. Desynchronization (quasistochastic waves)	2	1	$D_{11} \gg D_{22}$	O, PO, $\partial^2 F_i/\partial x_j^2 \rvert_{x_i=\bar{x}_i} \neq 0$	—	27, 77, 89–91
3. Wave propagation:				T, Fig. 4	$v=\varkappa_3\sqrt{D}$	9, 49
3.1 Isolated front	1	1–2	$D > \varkappa_4$	Fig. 4, $\partial F/\partial x\rvert_{x=0}=k>0$	$v \geqslant 2\sqrt{kD}$	47
3.2. Traveling pulses	2	1–2	$D_{22} \gg D_{11}$	x_2-null isocline of *N* sample, Figs. 7, 8, 9.	$v=\varkappa_3\sqrt{D_{22}}$	9, 53, 56
4. Stable guiding centers:						
4.1. Division of wave-fronts (echo)	2	1	$D_{11} \gg D_{22}$	T, O, PO; Fig. 10	$v \to \varkappa_3\sqrt{D_{22}}$	33, 58, 83
4.2. Stabilization of the starting region of the wave	3	1		O, PO; Figs. 15, 16	$v \to \varkappa_3\sqrt{D_{22}}$	27, 84, 85
5. Standing waves	3	1	$D_{ij}=0\ (i \neq j)$ $D_{ij} \neq 0\ (i \neq j)$	O, PO O, PO, NO	0	75, 76
6. Dissipative structures:						
6.1 Metastable	1	1–2	$D=\alpha x^l$	$F(x)=\beta x^m,\ l \geqslant m+1$	0	118, 119, 133
6.2. Quasiharmonic	2	1	$D_{11} \gg D_{22}$ $D_{ij} \neq 0\ (i \neq j)$	T, O, PO T, O, PO, NO	0	84, 75, 96–115, 128
6.3. Contrasting and localized	2	1	$D_{22} \sim 0$	x_2-null isocline of *N* sample, Figs. 21 and 22	0	76

excited oscillatory system (it has a single stable singularity, which is stable for any values of the parameters).

Finally, we would like to pose the following question: Are the basic models discussed here sufficiently general? In other words, is it possible to use a single model to describe and study the entire range of observed effects? This question should be answered in the affirmative. For example, the basic model in (2.8) for the Belousov–Zhabotinskii reactions describes all possible regimes. The model is switched from one regime to another (from a guiding center to a dissipative structure ture, from synchronous self-excited oscillations to a guiding center, and so forth) through a variation of the coefficients in the corresponding equations. This flexibility of the basic models can be adopted as a basic measure of their quality and suitability. Furthermore, there is hope that these models can be used to construct a general qualitative theory for the autowave phenomena discussed above.

As Khokhlov[134] has shown so well, the modern theory of nonlinear wave processes is intimately related to all the scientific work by Leonid Isaakovich Mandel'shtam, a pioneer in the physics of nonlinear oscillations. In particular, the emerging qualitative theory of autowave pehnomena is based entirely on the qualitative theory of nonlinear lumped systems which was developed by Mandel'shtam's pupil A. A. Andronov, and by other eminent Soviet scientists.

We wish to thank D. S. Chernavskii, at whose initiative this review was undertaken, for many useful discussions.

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