Spiral waves in anisotropic excitable media

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An approximate analytic theory of spiral waves in an anisotropic excitable medium is developed by considering the kinematics of their motion. The main parameters and shape of a spiral wave are calculated in the framework of this semi-phenomenological theory. A description is proposed of the unusual resonance effects accompanying the periodic change of the degree of anisotropy.

INTRODUCTION

Autowave phenomena in excitable media are attracting at present increased interest.[1–3] A distributed excitable medium consists of locally interconnected active elements capable of producing a pulse in response to an arriving external signal. This medium has a single quiescent state stable to perturbations that are small enough. Higher-intensity perturbations can give rise to solitary autowaves. A solitary self-wave in a one-dimensional medium constitutes an excitation pulse that propagates undamped with constant velocity and preserves its form. After passage of the pulse, the medium returns to the initial quiescent state. The pulse propagation velocity is determined uniquely by the properties of the active medium and is independent of the initial conditions. Examples of excitable media are solutions subject to a Belousov–Zhabotinskiĭ chemical reaction,[4] cardiac-muscle tissue,[5] semiconductors' distribution of the system[6,7] current-carrying magnetic superconductors,[8] and others.

A special type of elementary autowave regimes in two-dimensional excitable media are rotating spiral waves. The rotation frequency of single-arm spiral wave in an unbounded homogeneous excitable medium is constant and constitutes a fundamental property of the particular medium.

Excitable media are described as a rule by a system of nonlinear partial differential equations. In most cases of practical interest, two equations suffice:

$$\dot{u}=f(u, v)+D_u\Delta u, \quad \dot{v}=g(u, v)+D_v\Delta v, \tag{1}$$

in which one of the zero-isoclines $[f(u,v)=0]$ is N-shaped and the other $[g(u,v)=0]$ is a monotonic function. In frequently used models one neglects also the diffusion of the variable v (or the inhibitor), i.e., it is assumed that $D_v=0$.

Investigations of self-wave processes in excitable media are confined as a rule to isotropic (but possibly inhomogeneous and nonstationary) excitable media.[9] At the same time, excitable media (such as semiconductor systems or biological tissues) are essentially anisotropic, so that an investigation of the autowave structures produced in them is of considerable interest. Some aspects of this problem are dealt with in the present article.

The diffusion coefficients in anisotropic excitable media are tensors. Thus, the diffusion term in the first equation of the system (1) is of the form div $(\hat{D}_u \operatorname{grad} u)$. We shall neglect the diffusion of the inhibitor v $(\hat{D}_v=0)$, and drop therefore the diffusion-tensor subscript u. Note, however, that all our results remain in force also if the tensor $\hat{D}_v$ is not zero, provided that its components are proportional to the components of the tensor $\hat{D}_u$.

1. KINEMATICS OF SELF-WAVES IN ISOTROPIC MEDIA

We base ourselves below on the results of the kinematic approach developed in Refs. 9–15 for isotropic excitable media. In the kinematic description, the autowave is completely specified by indicating the lines of its front. Each section of the front moves in a normal direction with a velocity $V=V(K)$ determined by the front curvature K on this section (a front convex in the direction of its propagation moves slower the larger its curvature). Since the state of the excitable medium is the same before and after the passage of the pulse, the front in a two-dimensional medium can have a free end which not only moves in a normal direction with velocity $V(K_0)$, where K_0 is the curvature of the front on approaching the free end, but also expands or contracts at a rate $C=C(K_0)$. At sufficiently low curvatures K_0, the free end begins to grow, the rate C vanishes at a certain critical curvature $K_0=K_{cr}$, and at larger values the growth gives way to contraction. Near $K_0=K_{cr}$ one can put approximately $C=\gamma(K_{cr}-K_0)$, where $\gamma>0$ is a constant.

The shape of the front is specified by a natural equation $K=K(l)$ that relates the curvature of the front line with the path length l; it is expedient to measure the latter from the free end. In the course of wave propagation the curvature K depends also on the time t. This dependence is described by the equation[10,11]

$$\frac{\partial K}{\partial t}+\frac{\partial K}{\partial l}\left[C+\int_0^l KV\,dl'\right]+K^2V+\frac{\partial^2 V}{\partial l^2}=0. \tag{2}$$

Equation (2) is the fundamental equation of the kinematic model and makes it possible to track various regimes of autowave front motion.

The natural equation determines the form of the front accurate to its position on the plane. For a unique determination of the front evolution it suffices to indicate the law governing the motion of the free end of the autowave, i.e., of the point with $l=0$. If $x_0(t)$ and $y_0(t)$ are the coordinates of the free end, and $\alpha_0(t)$ is the angle between the tangent to the front at the point $l=0$ and the x axis, they obey the following equations:

$$\dot{x}_0(t)=-V(0)\sin\alpha_0(t)-C\cos\alpha_0(t), \tag{3}$$

$$\dot{y}_0(t)=V(0)\cos\alpha_0(t)-C\sin\alpha_0(t),$$

$$\dot{\alpha}_0(t)=\left.\frac{\partial V}{\partial l}\right|_{l=0}+CK_0, \tag{4}$$

where $V(0)=V(l=0,t)$ and the dot denotes a derivative with respect to time.

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Equation (2) together with (3) and (4) describes fully the evolution of the autowave front. The stationary solution of Eq (2) yields a steady-state regime in the form of a spiral wave. The curvature on the free end is $K_0 = K_{cr}$, so that this end moves along a normal to the front and traces in the course of time a circle. Inside this circle (referred to as the core of the spiral wave) the medium preserves a quiescent state. The rotation frequency ω_0 of a spiral wave was determined in Refs. 9 and 11. For a linear dependence of the velocity on the front curvature, $V = V_0 - DK$, and under the condition $DK_{cr} \ll V$, the frequency is described by the expression

$$\omega_0=\xi(DV_0)^{1/2}K_{cr}, \quad \xi=0.685. \tag{5}$$

Accurate to small terms of order DK_{cr}/V_0, the radius of a spiral-wave core is $R_0 = V_0/\omega_0$.

Equation (2) makes it also possible to determine the shape of the spiral-wave front[12,13]:

$$K(l)=\begin{cases} K_{cr}-(\omega_0/D)l, & l\leqslant l_0 \\ (\omega_0/2lV_0)^{1/2}, & l>l_0 \end{cases}, \tag{6}$$

where $l_0 \sim (D/K_{cr}V_0)^{1/2}$, and it follows from (5) that $l_0/R_0 \ll 1$. The relation is thus linear inside a narrow layer of width l_0 (the same relation describes the Cornu spiral), and outside this layer we have $K \propto l^{-1/2}$, i.e., the front takes the form of the evolvent of a circle of radius R_0.

Highly convenient and effective in the investigation of nonstationary propagation of autowave fronts is the so-called quasistationary approximation.[14,15] To describe the nonstationary evolution in this case in a wide range of excitable-medium parameters it suffices in this case to determine the character of the motion of only one end point ($l = 0$) of the front. The curvature K_0 on the free end obeys then the equation

$$\dot{K}_0=-\xi(V_0/D)^{1/2}\gamma K_0^{3/2}(K_0-K_{cr}). \tag{7}$$

In the quasistationary regime, Eq. (4) takes the form

$$\dot{\alpha}_0=\omega+CK_0, \tag{8}$$

where ω is given by Eq. (5) in which K_{cr} is replaced by K_0. The quasistationary-approximation equations (7), (8), and (3) can be used if $\gamma/D \ll (V_0/DK_{cr})^{1/2}$. This condition is rather weak, since $p = DK_{cr}/V_0$ is a small parameter of the problem.

The quasistationary approximation has made it possible to study the drift of spiral waves in an inhomogeneous medium[15] and predict the resonance of spiral waves in nonstationary excitable media, which was recently observed in experiments with the Belousov–Zhabotinskiĭ reaction.[16]

2. SPIRAL AUTOWAVE IN A STATIONARY ANISOTROPIC MEDIUM

We proceed now to anisotropic media. In the system of its principal axes, the diffusion tensor is diagonal and Eq. (1) takes the form ($\hat{D}_v = 0$):

$$\dot{u}=f(u,v)+D\frac{\partial^2 u}{\partial x^2}+D_1\frac{\partial^2 u}{\partial y^2}, \qquad \dot{v}=g(u,v). \tag{9}$$

We introduce new coordinates $x' = x$ and $y' = \lambda y$, where $\lambda = (D/D_1)^{1/2}$. In these coordinates Eqs. (9) coincide with Eqs. (1) ($D_v = 0$). In other words, in the new coordinates the medium becomes isotropic and the diffusion coefficient is equal to D. To investigate the motion of an autowave in an anisotropic medium it suffices therefore to carry out the calculations, as in Sec. 1, in the "primed" system, where the medium is isotropic, and then return to the earlier "laboratory" frame.

It is thus easy to obtain the dependence of a plane autowave front in an anisotropic medium on the direction of its propagation:

$$V_0(\theta)=V_0(\lambda^2\cos^2\theta+\sin^2\theta)^{1/2}/\lambda,$$

where V_0 is the plane-front velocity in an isotropic medium with a diffusion coefficient D, and θ is the angle between the propagation direction and the x axis.

We obtain now an expression for the shape of a spiral-wave front in an anisotropic medium. Let the wave front be described in the primed coordinate frame by a natural equation $K' = K'(l')$. From the definition of the curvature.

$$K'(l')=-d\alpha'/dl', \tag{10}$$

where α' is the angle between the tangent to the front and the x axis, it is easy to obtain the following equations for the laboratory coordinates of a section of the front:

$$x=x_0+\int_0^{l'}\cos\left[\alpha_0'-\int_0^{\xi_1'}K'(\xi_2')d\xi_2'\right]d\xi_1',$$
$$y=y_0+\frac{1}{\lambda}\int_0^{l'}\sin\left[\alpha_0'-\int_0^{\xi_1'}K'(\xi_2')d\xi_2'\right]d\xi_1'. \tag{11}$$

Equations (11) can be treated as a parametric specification of a curve, the parameter being the path length l' in the primed coordinates. Having a parametric description of the curve, we can calculate its curvature in standard fashion:

$$K(l')=\lambda^2K'(l')\left\{1+(\lambda^2-1)\cos^2\left[\alpha_0'-\int_0^{l'}K'(\xi')d\xi'\right]\right\}^{-3/2}. \tag{12}$$

To obtain the natural equation (i.e., the dependence of K on l) of the curve in the lab, we must express l' in terms of l with the aid of the equation

$$\frac{dl}{dl'}=\frac{1}{\lambda}\left\{1+(\lambda^2-1)\times\cos^2\left[\alpha_0'-\int_0^{l'}K'(\xi')d\xi'\right]\right\}^{1/2}. \tag{13}$$

Expressions (12) and (13) determine the natural equation of the curve in the lab if the natural equation of the same curve in the primed system is known. Thus, substitution of Eq. (6) (in which K and l are replaced by K' and l') in (12) and (13) leads to a natural equation of the line of a spiral wave front in an isotropic medium. An examination of this equation shows that the shape of the front in an anisotropic medium is not stationary, and the curve oscillates with a period π/ω_0 (recall that $\alpha_0' = \omega_0 t + \varphi$, where $\varphi = \alpha_0'|_{t=0}$). Thus, the curvature at the approach to the end point has the following time dependence:

$$K_0(t)=\lambda^2 K_{cr}\,[1+(\lambda^2-1)\cos^2(\omega_0 t+\varphi)]^{-3/2}. \qquad (14)$$

The time dependence of the front curvature notwithstanding, one can speak of stationary circulation of a spiral wave in an anisotropic medium, stressing the fact that the wave core, which is an ellipse with semiaxes R_0 and R_0/λ, remains immobile.

This premise is illustrated in Fig. 1, which shows the calculated motion of a spiral autowave of form (9) in an anisotropic medium for $D=1$ and $D_1=2$. The form of the functions $f(u,v)$ and $g(u,v)$ corresponds here to the two-component model proposed for an excitable medium in Ref. 17 and modified in Ref. 9:

$$f(u,v)=N(u)-g,$$

$$N(u)=\begin{cases}-uk_1, & u<\sigma\\ (u-a)k_f, & \sigma\leqslant u\leqslant 1-\sigma,\\ (1-u)k_2, & 1-\sigma<u\end{cases}$$

$$g(u,v)=\begin{cases}\varepsilon(k_g u-v), & k_g u>g\\ k_e\varepsilon(k_g u-v), & k_g u<g\end{cases},$$

where the coefficients are $k_f=1.7$, $k_g=2.0$, $a=0.1$, $\sigma=0.01$, $\varepsilon=0.3$, $k_e=6.0$. The coefficients k_1 and k_2 are chosen to obtain continuity of the piecewise-linear function $N(u)$.

Examination of the successive positions of the boundary of the excited region on Fig. 1 shows that the form of the boundary is not stationary and varies periodically. The free end of the spiral wave, however, describes in this case an ellipse whose shape and location remain unchanged.

3. JUMPLIKE CHANGES OF THE DEGREE OF ANISOTROPY OF THE MEDIUM

We proceed now to consider nonstationary problems. We investigate first the evolutions of a spiral wave following instantaneous changes of the anisotropy of the medium. Let a stationary spiral autowave rotate at $t<0$ in an isotropic excitable medium with a diffusion coefficient D, and let the anisotropy of the medium change instantaneously at $t=0$, so that the diffusion tensor acquires the form

$$\hat{D}=\begin{pmatrix}D & 0\\ 0 & D-\Delta D\end{pmatrix},\qquad \Delta D\ll D. \qquad (15)$$

We put $\mu=\Delta D/D$. At the instant $t=0$ the profile of the spiral-wave front is described by relation (6). The initial

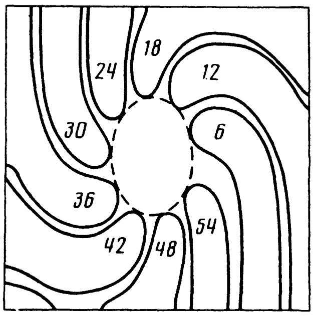

FIG. 1. Successive positions of a spiral autowave in an anisotropic medium at indicated instants of time. Calculation using a model of the reaction–diffusion type.

profile (6) relaxes next to the "stationary" profile (12), (13) of a spiral wave in an anisotropic medium. The center of the spiral-wave core is shifted thereby. Let us calculate this shift. We change to the primed frame. In this frame, as follows from (14), curvature on approaching the free end of the front is equal at $t=0$ to

$$K_0'=K_{cr}[1-\mu(1-\tfrac{3}{2}\cos^2\varphi)], \qquad (16)$$

where φ is the angle between the tangent to the front at its end point and the x axis at the instant $t=0$ (we confine ourselves to terms linear in μ).

Substituting (16) in the solution of Eq. (7), we obtain the time variation of the curvature of the end point of the front in the primed frame

$$K_0'(t)=K_{cr}[1-\mu(1-\tfrac{3}{2}\cos^2\varphi)\exp(-\gamma\omega_0 t/D)]. \qquad (17)$$

Substitution of (17) in (4) leads to the following time dependence of the angle between the tangent to the front at the end point and the x axis:

$$\alpha_0'=\omega_0 t+\varphi+\tfrac{1}{2}\mu\{\sin\varphi\cos\varphi-3(1-\tfrac{3}{2}\cos^2\varphi)\times(D/\gamma)[1-\exp(-\gamma\omega_0 t/D)]\}. \qquad (18)$$

We obtain the shift of the spiral-wave in the laboratory frame by substituting (17) and (18) in (3), averaging over the time, and returning to the variables $x=x'$ and $y=y'/\lambda$:

$$\overline{\Delta x_0}=\frac{\mu V_0}{2\omega_0}F_1\left(\frac{\gamma}{D},p,\varphi\right),\qquad \overline{\Delta y_0}=\frac{\mu V_0}{2\omega_0}F_2\left(\frac{\gamma}{D},p,\varphi\right),$$

$$F_1=\sin^2\varphi\cos\varphi-\left(3-2\frac{\gamma}{D}p^{1/2}\right)\left(1-\frac{3}{2}\cos^2\varphi\right)\times\frac{(\gamma/D)\sin\varphi+\cos\varphi}{(\gamma/D)^2+1}. \qquad (19)$$

$$F_2=\sin^3\varphi+\left(3-2\frac{\gamma}{D}p^{1/2}\right)\left(1-\frac{3}{2}\cos^2\varphi\right)\frac{(\gamma/D)\cos\varphi-\sin\varphi}{(\gamma/D)^2+1}.$$

We have left out of (19) terms of higher orders, which are small in view of the condition $p=DK_{cr}/V_0\ll 1$.

We can similarly calculate the displacement of the center of a spiral wave following a rapid transition from an anisotropic medium (15) to an isotropic with diffusion coefficient D:

$$\overline{\Delta x_0}=-\frac{\mu V_0}{2\omega_0}F_1\left(\frac{\gamma}{D},p,\varphi\right),\qquad \overline{\Delta y_0}=-\frac{\mu V_0}{2\omega_0}F_2\left(\frac{\gamma}{D},p,\varphi\right). \qquad (20)$$

It follows thus from (19) and (20) that a jump change of the anisotropy of the medium displaces the center of the spiral-wave core in a direction determined by the ratio F_1/F_2 which depends only on the initial phase φ of the spiral wave, on the parameter p, and on the "inertia" γ/D. Stationary rotation of the wave around the new center begins after a characteristic time $\tau=D/\gamma\omega_0$.

4. PERIODIC MODULATION OF THE DEGREE OF ANISOTROPY

With expressions (19) and (20) we can proceed to investigate resonance effects connected with the action, on a rotating spiral wave, of a periodic change of the anisotropy of the medium. Let the diffusion-coefficient tensor $\hat{D}$ of the excitable medium have the following time dependence:

$$\hat{D}=\begin{pmatrix} D & 0 \\ 0 & D-{}^1\!/_2\Delta D\,[1+\operatorname{sign}(\sin\omega_1 t)] \end{pmatrix}, \qquad (21)$$

where $\Delta D \ll D$, $|\omega_1-\omega_0| \ll \omega_0$.

Relation (21) describes a jumplike periodic, with frequency ω, onset and vanishing of anisotropy in a medium. Let a spiral wave be excited in this medium. The center of the spiral wave is shifted by each anisotropy jump and traces in the course of time a certain curve. Let us find the shape of this curve.

To avoid unwieldy expressions, we confine ourselves to excitable media with sufficiently low inertia, i.e., we assume that $\gamma/D \gtrsim 1$. In this case a time interval $t_1 = \pi/\omega_1$ between two succeeding jumps (note that t_1 is close to half the rotation period of the spiral wave) is sufficient for relaxation to a new stationary value of the rotation-center coordinates. This means that Eqs. (19) and (20) can be used to determine the trajectory of the center of the spiral wave when the anisotropy is varied periodically. Using the fact that $F_{1,2}(\gamma/D, p, \varphi+\pi) = -F_{1,2}(\gamma/D, p, \varphi)$, we obtain recurrence relations for the coordinates of the spiral-wave core center after the nth jump of the anisotropy of the medium:

$$x_n=x_{n-1}+\frac{\mu V_0}{2\omega_0}F_1\left(\frac{\gamma}{D}, p, \varphi+\beta n\right),$$
$$y_n=y_{n-1}+\frac{\mu V_0}{2\omega_0}F_2\left(\frac{\gamma}{D}, p, \varphi+\beta n\right), \qquad (22)$$

where $\beta = \pi(\omega_0-\omega_1)/\omega_1$. We assume in (22) that the jump with number $n=0$ occurred at $t=0$. Prior to this jump, the center of the spiral wave was at the origin.

Recognizing that $\mu \ll 1$, we transform from the discrete relations (22) to differential equations for the trajectory of the center of a spiral wave:

$$\frac{dx}{dt}=\frac{\mu V_0}{2\pi}F_1\left(\frac{\gamma}{D}, p, \varphi+(\omega_0-\omega_1)t\right),$$
$$\frac{dy}{dt}=\frac{\mu V_0}{2\pi}F_2\left(\frac{\gamma}{D}, p, \varphi+(\omega_0-\omega_1)t\right). \qquad (23)$$

Integrating (23) with respect to time, we easily obtain equations that specify in parametric form the sought spiral-wave-center trajectory. These equations, however, are quite unwieldy and will not be given here.

Relations (22) and (23) show that when the anisotropy of the excitable medium varies periodically the spiral-wave center moves along a closed curve. The characteristic dimensions of this curve are inversely proportional to the modulus of the difference between the modulation frequency ω_1 and the spiral-wave proper rotation frequency ω_0. A resonance effect is thus produced. It is most remarkable, however, that in contrast to the resonance of a spiral wave in an isotropic medium,[15] the trajectory of the core center is not a circle. Nor is it an ellipse with eccentricity governed by the degree of anisotropy.

Calculation of the spiral-wave kinematics for steplike variation of the anisotropy, using Eqs. (22) or (23), shows that the trajectory of the core center has a quite complicated shape and can be significantly altered by varying the parameters (see Fig. 2). It is important to note, however, that the form of the trajectory is determined by the properties of the medium itself (by the parameter p and by the inertia γ/D) and does not depend on the initial phase φ of the external action and on the modulus $|\omega_1-\omega_0|$ of the frequency difference. It is easily seen, in particular, that the initial phase φ depends only on the position of the trajectory relative to the origin, while the modulus $|\omega_1-\omega_0|$ determines only the dimensions of the trajectory. The shape of the trajectory and its orientation are determined by the parameters of the medium and are therefore important properties of the latter. By way of illustration, Fig. 2 shows spiral-wave core-center trajectories calculated on the basis of (22) for a number of different values of the inertia γ/D under the condition $(\gamma/D)(DK_{cr}/V_0)^{1/2} \ll 1$ (recall that this inequality is the condition for the quasistationary approximation to be valid).

In the case of full resonance ($\omega_0=\omega_1$) the spiral-wave center moves along a straight line at a velocity

$$U=\frac{\mu V_0}{2\pi}\left[F_1^2\left(\frac{\gamma}{D}, p, \varphi\right)+F_2^2\left(\frac{\gamma}{D}, p, \varphi\right)\right]^{1/2} \qquad (24)$$

in a direction determined by the phase φ and by the inertia γ/D. In contrast to the case of resonance in an isotropic medium (where the center of the core moves with constant velocity at any φ), the velocity U in an anisotropic medium depends substantially on φ [see (24)].

It is of interest to compare the results of a kinematic analysis of spiral-wave motion in an excitable medium having a periodically modulated anisotropy with calculations by the reaction–diffusion model[9] given above, in which the diffusion coefficient is described by expression (21). Figure 3a shows a spiral-wave-center trajectory calculated for $\Delta D = 0.2$ and $\omega_1 = 0.12$. Note for the simulated medium the propagation velocity V_0 and the circulation frequency ω_0, measured in the computer experiment, are $V_0 = 1.3$ and $\omega_0 = 0.11$. Since $D=1$, we can determine from these data the parameter $p = DK_{cr}/V_0 = 0.21$ by using (5). As shown by the analysis above, given the parameter p the shape of the resonance trajectory is determined only by the inertia γ/D, which we do not know. Figures 3b–3e show three trajectory shapes calculated from Eqs. (22) for different values of γ/D. It can be seen that for $\gamma/D = 3.3$ the trajectory has no concave sections, in contrast to Fig. 3a. Such sections appear

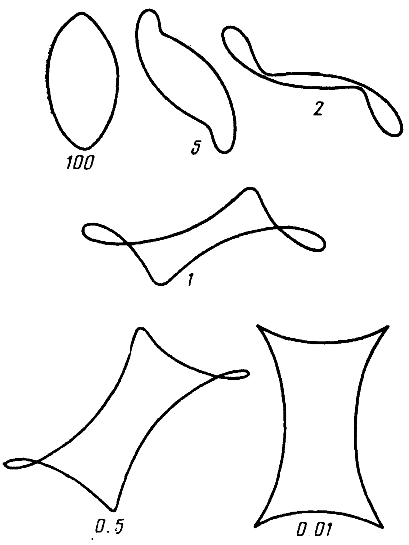

FIG. 2. Spiral-wave core-center trajectory, calculated for periodic variation of the degree of anisotropy using the kinematic relations (22) for $p \ll 1$ and for the marked values of γ/D.

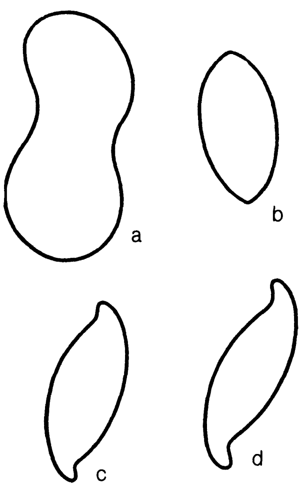

FIG. 3. Resonance trajectories of a spiral-wave core center, obtained in the reaction–diffusion model (a) and calculated using the kinematic relations (22) for $\gamma/D = 3.3$ (b), 6 (c), and 9 (d).

when γ/D is increased (Figs. 3c and 3d), but the trajectory of Fig. 3d has too large a slope relative to the y axis. Comparison of Figs. 3a and 3c shows that the kinematic approach gives a correct picture of the considered phenomenon. It can be assumed on this basis that $\gamma/D \approx 6$ for the simulated medium. More accurate quantitative results should be expected for media with smaller values of the parameter p.

CONCLUSION

The foregoing analysis has revealed a number of unexpected and unusual resonance phenomena in anisotropic excitable media. Furthermore, the results of the analysis of anisotropic media are also of more general significance. The kinematic description developed in Refs. 9–15 and in this paper is at present the only approach that yields analytic (i.e., not requiring a computer) results in the theory of propagation and interaction of autowaves in two- and three-dimensional media. Many effects known from computer experiments (such as the drift of spiral waves in inhomogeneous media,[18] collapse and expansion of spiral rings,[19] evolution of twisted vortices[20]) can be analytically described by the kinematic approach.

Just as macroscopic electrodynamics, the kinematic approach is a phenomenological theory in which the excitable medium is described by a small set of parameters, viz., D, V_0, K_{cr}, and γ. These phenomenological parameters must be determined either from experiments with actual excitable media, or from computer experiments with models of the reaction–diffusion type. The first three parameters D, V_0, and K_{cr} are relatively easy to determine. In fact, for any model such as in Ref. 9, D is the diffusion coefficient, the determination of V_0 (of the velocity of a plane front) calls for "merely" integrating a system of type (1) in the one-dimensional case, and the critical curvature K_{cr} can be measured for a stationary rotating spiral wave or calculated with the aid of (5) if the angular velocity ω_0 of the spiral wave is known. No simple method, however, of estimating the parameter γ has been proposed so far. Recall that the parameter γ determines the rate of expansion (or contraction) of the free end of an autowave, and assumes the leading role in the investigation of nonstationary effects. The spiral-wave-core drift investigated above for periodic variation of the anisotropy of the medium permits a simple estimate of the parameter γ by investigating the shape of the resonance trajectory.

It must be noted that the presented analysis touches upon only a small fraction of the problems connected with autowave propagation in anisotropic media. In particular, computer experiments performed by us recently on a two-component model of type (1) show that in all cases in which the diffusion of the activator is anisotropic while the diffusion of the inhibitor is isotropic (we emphasize that by an appropriate transformation of the parameters it is possible to reduce to this problem the most general case of diffusion that is anisotropic also with respect to the inhibitor) the motion of a spiral wave exhibits a large number of singularities. The shape of the trajectory of the free end of the spiral can in this case differ strongly from an ellipse even in a stationary medium. If the diffusion coefficient of the inhibitor is large enough, the boundary of the core is no longer a convex curve, and acquires subsequently self-intersection points. Moreover, open free-end trajectories may appear and lead to a drift of the spiral wave. However, the construction of theoretical models of these interesting phenomena observed in computer experiments are outside the scope of the present paper.

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