Propagation of Curved Activation Fronts in Anisotropic Excitable Media

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Abstract. We study theoretical and numerical propagation of autowave fronts in excitable two-variable (activator-inhibitor) systems with anisotropic diffusion. A general curvature-velocity relation is derived for the case that the inhibitor diffusion is neglected. This relation predicts the break of an activation front when the front curvature exceeds a critical value, which is corroborated by computer simulations of a particular reaction-diffusion model. Some qualitative effects associated with the inhibitor diffusion are studied numerically. It is found that the critical value of curvature decreases with an increase in the inhibitor diffusion coefficient. The core of a spiral wave increases in size and turns through an angle which depends on the inhibitor diffusion coefficient.

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1. Introduction

Now it is common knowledge that many of the biological systems can be considered as reaction-diffusion excitable media. In general, such systems are characterized by anisotropic diffusion. An example is cardiac tissue where the electrical conductivity along fibers differs essentially from the conductivity across fibers [1, 2].

Anisotropic excitable media are as yet little studied in comparison with isotropic media. In particular, no one has yet derived the so-called 'curvature-velocity relation' which relates the front's curvature and the local speed of propagation in anisotropic media. Such a relation is required, for instance, to explain the critical behavior of autowaves, i.e., the observed break of an activation front when a certain critical curvature is reached [1]. On the other hand, the curvature-velocity relation as well as the critical properties of activation fronts in isotropic media have been widely treated in the literature (see, e.g., [3, 4]). Note also that, in the isotropic case, some important effects associated with the curvature of activation fronts do not depend of the nature of reactions in a system and follow directly from symmetry

properties of reaction-diffusion equations under coordinate transformations and scaling. This fact allows one to describe different excitable media within a unified approach [5–7]. It is interesting to inquire to what extent such a general approach can be applied to anisotropic media.

In this paper we study theoretically and numerically a typical class of two-dimensional reaction-diffusion systems described by equations

$$\begin{aligned}\frac{\partial u}{\partial t} &= F_1(u, v) + \sum_{i,j} \frac{\partial}{\partial x_i} D_{ij}^{(u)} \frac{\partial u}{\partial x_j}, \\ \frac{\partial v}{\partial t} &= \varepsilon F_2(u, v) + \sum_{i,j} \frac{\partial}{\partial x_i} D_{ij}^{(v)} \frac{\partial v}{\partial x_j},\end{aligned}\tag{1.1}$$

where $u(x_1, x_2, t)$ and $v(x_1, x_2, t)$ are the activator and inhibitor variables respectively, $D_{ij}^{(u)}$, $D_{ij}^{(v)}$ are the diffusion tensors of both species. Functions F_1 and F_2 specify the local reactions in the system, and the parameter ε is introduced to determine the time scale for the inhibitor relaxation. In many cases of interest ε can be regarded as a small parameter.

The paper is organized as follows. In Section 2, we derive a curvature-velocity relation which is valid for all the models with $D_{ij}^{(v)} = 0$. To first approximation in the curvature value, this relation leads to the ‘eikonal equation’ for activation fronts in anisotropic media. We also study the dependence of the front velocity on the parameter ε in Equations (1.1). In Section 3, the curvature-velocity relation is used to calculate the critical curvature value, above which propagation is impossible, and the corresponding critical velocity of a front. The predicted critical behavior of curved fronts in anisotropic media is corroborated by explicit numerical solution of the reaction-diffusion equations for a typical two-variable model. Finally, in Section 4 we present the results of numerical simulations showing the influence of the inhibitor diffusion on the behavior of curved activation fronts and spiral waves in anisotropic media.

2. Velocity of a Curved Activation Front

We first assume that the inhibitor diffusion can be neglected. As will be shown below, in this case we obtain the curvature-velocity relation in the explicit form.

Setting $D_{ij}^{(v)} = 0$ in Equations (1.1), it is convenient to introduce a coordinate system with the axes x and y directed along the principal axes of the tensor $D_{ij}^{(u)}$. Then we arrive at the set of equations

$$\begin{aligned}\frac{\partial u}{\partial t} &= F_1(u, v) + D_x^{(u)} \frac{\partial^2 u}{\partial x^2} + D_y^{(u)} \frac{\partial^2 u}{\partial y^2}, \\ \frac{\partial v}{\partial t} &= \varepsilon F_2(u, v),\end{aligned}\tag{2.1}$$

where $D_x^{(u)}$ and $D_y^{(u)}$ are the activator diffusion coefficients in the new coordinate system. The essential point is that Equations (2.1) can be transformed into equations for an isotropic medium. To do this, we define new coordinates x' and y' through relations

$$x = \lambda_x x', \quad y = \lambda_y y', \quad (2.2)$$

where λ_x and λ_y are some scaling parameters. If they are so chosen that

$$D = D_x^{(u)} / \lambda_x^2 = D_y^{(u)} / \lambda_y^2, \quad (2.3)$$

Equations (2.1) take the form of equations for an isotropic medium with the effective diffusion coefficient D . The above procedure determines only the ratio of the parameters

$$\lambda_x / \lambda_y = (D_x^{(u)} / D_y^{(u)})^{1/2}, \quad (2.4)$$

so that one of them can be prescribed arbitrarily. In what follows we will use this freedom in the choice of the scaling parameters.

Thus, in the case under consideration, the evolution of an activation front in the anisotropic medium (in the xy plane) corresponds to the evolution of the rescaled front in the isotropic medium (in the $x'y'$ plane). This fact makes it possible to derive the curvature-velocity relation for anisotropic media proceeding from simple considerations.

Let A be a point on a curved activation front in the xy plane and A' the corresponding point on the rescaled front in the $x'y'$ plane. We shall assume that the width of the front is small compared to its curvature radius K^{-1} , which is typical for real situations. Then the velocity of the front in the isotropic medium, V_{is} , is determined from the following equations [4, 5]:

$$\begin{aligned} D \frac{d^2 u}{d\xi^2} + F_1(u, v) + (V_{is} + K_{is} D) \frac{du}{d\xi} &= 0, \\ \varepsilon F_2(u, v) + V_{is} \frac{dv}{d\xi} &= 0, \end{aligned} \quad (2.5)$$

where $\xi = r' - V_{is}t$, and r' is the radial variable on the polar axis directed along the normal $\mathbf{n}'$ to the front in the $x'y'$ plane. The quantity K_{is} is the local curvature of the rescaled front at the point A' . From Equations (2.5) it is clear that V_{is} depends parametrically on D , $K_{is}D$, and ε , i.e., $V_{is} = V_{is}(D, K_{is}D, \varepsilon)$. For the time being, the dependence of the velocity on ε will not be indicated explicitly.

We now want to show that the local velocity of the front in the anisotropic medium, V , can be expressed in terms of the velocity V_{is} in the isotropic medium. As a first step, we shall derive a relation between the local curvatures of the fronts, K and K_{is} , in the anisotropic and isotropic (rescaled) plane, respectively. Let us introduce polar coordinates r' and φ' in the vicinity of the point A' by

$$x' = r' \cos(\vartheta' + \varphi'), \quad y' = r' \sin(\vartheta' + \varphi'), \quad (2.6)$$

where ϑ' is the angle between the normal $\mathbf{n}'$ to the rescaled front and the x' axis. Then a small part of the front in the isotropic $x'y'$ plane can be described by the equation $r' = K_{\text{is}}^{-1}$. Recalling Equations (2.2), we find that, in the xy plane, the points lying on the front in the vicinity of the point A have the coordinates

$$x_f(\varphi') = \lambda_x K_{\text{is}}^{-1} \cos(\vartheta' + \varphi'), \quad y_f(\varphi') = \lambda_y K_{\text{is}}^{-1} \sin(\vartheta' + \varphi'). \quad (2.7)$$

The standard procedure can now be used to calculate from Equations (2.7) the local curvature K of the front at the point A (i.e., for $\varphi' = 0$). The fixed angle ϑ' can then be eliminated in favor of the angle ϑ between the normal $\mathbf{n}$ to the front in the anisotropic medium and the x axis by means of the relation

$$\tan \vartheta' = (\lambda_y/\lambda_x) \tan \vartheta = [D_y^{(u)}/D_x^{(u)}]^{1/2} \tan \vartheta, \quad (2.8)$$

which follows from Equations (2.2). After simple algebra which is omitted, we obtain the desired relation in the form

$$K_{\text{is}} = \lambda_x K \frac{D_y^{(u)}}{D_x^{(u)}} [\cos^2 \vartheta + (D_y^{(u)}/D_x^{(u)}) \sin^2 \vartheta]^{-3/2}. \quad (2.9)$$

We next consider propagation of the front in an infinitesimal time interval dt . Calling the displacement of the front in the xy plane ds , we notice that the points A and B with the coordinates

$$\begin{aligned} x_A &= \lambda_x K_{\text{is}}^{-1} \cos \vartheta', & y_A &= \lambda_y K_{\text{is}}^{-1} \sin \vartheta', \\ x_B &= x_A + ds \cos \vartheta, & y_B &= y_A + ds \sin \vartheta \end{aligned}$$

lie on the activation fronts at times t and $t + dt$, respectively. Since the corresponding points A' and B' in the $x'y'$ plane lie on the circles with the radii K_{is}^{-1} and $K_{\text{is}}^{-1} + dR$, where dR is the displacement of the rescaled front, we may write

$$\frac{(x_A + ds \cos \vartheta)^2}{\lambda_x^2} + \frac{(y_A + ds \sin \vartheta)^2}{\lambda_y^2} = (K_{\text{is}}^{-1} + dR)^2, \quad (2.10)$$

where Equations (2.2) have been used. Equation (2.10) is to be linearized in ds and dR . Taking also into account that $V = ds/dt$ and $V_{\text{is}} = dR/dt$, a simple algebra gives

$$V = \lambda_x [\cos^2 \vartheta + (D_y^{(u)}/D_x^{(u)}) \sin^2 \vartheta]^{1/2} V_{\text{is}}(D, K_{\text{is}} D), \quad (2.11)$$

where the functions of the angle ϑ' have been eliminated by means of Equations (2.8).

Equation (2.11), along with Equations (2.3) and (2.9), determines the local front's velocity in the anisotropic medium, $V = V(K, \vartheta)$, for given K and ϑ , if the curvature-velocity relation for the isotropic medium is known. However, one comment is relevant concerning Equation (2.11). As already mentioned, the parameter λ_x in this equation may have an arbitrary value. This might appear at first

sight to be strange since there must exist a unique relation between the velocities V and V_{is} . To show that the validity of Equation (2.11) does not depend on the value of λ_x , we notice that the velocity V_{is} determined from Equations (2.5) possesses a scaling property under the transformation $D \rightarrow \lambda^2 D$ and $K_{\text{is}} D \rightarrow \lambda K_{\text{is}} D$, where λ is some parameter. Indeed, making this transformation in Equations (2.5) and then changing the variable $\xi \rightarrow \lambda \xi$, we find that

$$V_{\text{is}}(\lambda^2 D, \lambda K_{\text{is}} D) = \lambda V_{\text{is}}(D, K_{\text{is}} D). \quad (2.12)$$

On the other hand, Equations (2.3) and (2.9) show that under the transformation $\lambda_x \rightarrow \lambda_x/\lambda$ the effective diffusion coefficient D and the curvature K_{is} transform as $D \rightarrow \lambda^2 D$ and $K_{\text{is}} \rightarrow \lambda^{-1} K_{\text{is}}$. Thus, according to the scaling property (2.12), Equation (2.11) holds for an arbitrary value of λ_x . It is convenient to set the parameter λ_x equal to

$$\lambda_x = [\cos^2 \vartheta + (D_y^{(u)}/D_x^{(u)}) \sin^2 \vartheta]^{-1/2}. \quad (2.13)$$

Then, Equations (2.9) and (2.11) take the form

$$K_{\text{is}} = K \frac{D_x^{(u)} D_y^{(u)}}{D^2(\vartheta)}, \quad (2.14)$$

$$V(K, \vartheta) = V_{\text{is}}(D(\vartheta), K D_x^{(u)} D_y^{(u)}/D(\vartheta)) \quad (2.15)$$

with the effective diffusion coefficient given by

$$D(\vartheta) = D_x^{(u)} \cos^2 \vartheta + D_y^{(u)} \sin^2 \vartheta. \quad (2.16)$$

Equation (2.15) may be considered as the curvature-velocity relation for activation fronts in anisotropic excitable media described by reaction-diffusion equations (2.1). In the special case that $K = K_{\text{is}} = 0$, Equation (2.15) reduces to the relation between the velocity $V^0(\vartheta)$ of a planar front in the anisotropic medium and the velocity V_{is}^0 of a planar front in the isotropic medium:

$$V^0(\vartheta) = V_{\text{is}}^0(D(\vartheta)). \quad (2.17)$$

Setting $K_{\text{is}} = 0$ in Equation (2.12), we obtain $V_{\text{is}}^0 \propto \sqrt{D}$, so that Equation (2.17) can also be written as

$$V^0(\vartheta) = \frac{V_{\text{is}}^0(D_{\text{is}})}{D_{\text{is}}^{1/2}} (D_x^{(u)} \cos^2 \vartheta + D_y^{(u)} \sin^2 \vartheta)^{1/2}, \quad (2.18)$$

where D_{is} is an arbitrary diffusion coefficient in the isotropic medium. Our result (2.18) is equivalent to the relation derived in Reference [8] by other means.

A practical implementation of Equation (2.15) requires that the curvature-velocity relation for the isotropic medium be known. We shall now derive another equation for V , in which all one would need to know is the dependence of the velocity of a

planar activation front in the isotropic medium on the diffusion coefficient and the parameter ε .

Let us turn back to Equations (2.5) describing stationary propagation of a curved front in the isotropic medium. The corresponding velocity of the front will be denoted by $V_{\text{is}}(\varepsilon)$. We now introduce a new parameter [9]

$$\varepsilon' = \varepsilon \frac{V_{\text{is}}(\varepsilon) + K_{\text{is}}D}{V_{\text{is}}(\varepsilon)}. \quad (2.19)$$

Then Equations (2.5) can be transformed into

$$\begin{aligned} D \frac{d^2 u}{d\xi^2} + F_1(u, v) + V_{\text{is}}^0(\varepsilon') \frac{du}{d\xi} &= 0, \\ \varepsilon' F_2(u, v) + V_{\text{is}}^0(\varepsilon') \frac{dv}{d\xi} &= 0 \end{aligned} \quad (2.20)$$

with

$$V_{\text{is}}^0(\varepsilon') = V_{\text{is}}(\varepsilon) + K_{\text{is}}D. \quad (2.21)$$

Obviously Equations (2.20) describe propagation of a *planar* front with velocity $V_{\text{is}}^0(\varepsilon')$. Thus, it follows from Equations (2.19) and (2.21) that

$$V_{\text{is}}(D, K_{\text{is}}D, \varepsilon) = V_{\text{is}}^0 \left(D, \varepsilon \frac{V_{\text{is}}(D, K_{\text{is}}D, \varepsilon) + K_{\text{is}}D}{V_{\text{is}}(D, K_{\text{is}}D, \varepsilon)} \right) - K_{\text{is}}D. \quad (2.22)$$

Inserting this expression with $D = D(\vartheta)$ and $K_{\text{is}} = K D_x^{(u)} D_y^{(u)} / D^2(\vartheta)$ into Equation (2.15) gives

$$\begin{aligned} V(K, \vartheta, \varepsilon) &= \\ V_{\text{is}}^0 \left(D(\vartheta), \varepsilon \frac{V(K, \vartheta, \varepsilon) + K D_x^{(u)} D_y^{(u)} / D(\vartheta)}{V(K, \vartheta, \varepsilon)} \right) &- K \frac{D_x^{(u)} D_y^{(u)}}{D(\vartheta)}. \end{aligned} \quad (2.23)$$

In contrast to the curvature-velocity relation (2.15), formula (2.23) is an *equation* for $V(K, \vartheta, \varepsilon)$ since this quantity enters the argument of V_{is}^0 . Nevertheless, the virtue of Equation (2.23) is that, for concrete systems, the properties of V_{is}^0 are much simpler than the properties of V_{is} , especially in regard to the curvature dependence of the latter velocity. The other point is that usually ε plays the role of a small parameter in the problem and, therefore, one can apply perturbation theory to Equation (2.23).

To discuss some consequences of Equation (2.23), it is convenient to rearrange this equation into a more compact form. As already noted, for the models where the inhibitor diffusion is neglected, we have $V_{\text{is}}^0(D, \varepsilon) \sim \sqrt{D}$ and, therefore,

$$V_{\text{is}}^0(D, \varepsilon) = D^{1/2} C(\varepsilon), \quad (2.24)$$

where the form of the function $C(\varepsilon)$ depends on the type of reactions in the medium. Using the representation (2.24), we can rewrite Equation (2.23) as

$$V(K, \vartheta, \varepsilon) = D^{1/2}(\vartheta) w(\alpha, \varepsilon), \quad \alpha(\vartheta) = K \frac{D_x^{(u)} D_y^{(u)}}{D^{3/2}(\vartheta)}, \quad (2.25)$$

where w satisfies the equation

$$w = C \left(\varepsilon \frac{w + \alpha}{w} \right) - \alpha. \quad (2.26)$$

This equation is a convenient starting point for different approximations. Let us first assume that the curvature of the front is sufficiently small, more precisely that $\alpha \ll C(\varepsilon)$ or, what is the same, $K D_x^{(u)} D_y^{(u)} / D(\vartheta) \ll V^0(\vartheta)$. Then, to first order in α , Equation (2.26) gives

$$w = C(\varepsilon) - \left(1 - \frac{d \ln C(\varepsilon)}{d \ln \varepsilon} \right) \alpha. \quad (2.27)$$

Multiplying both sides by $D^{1/2}(\vartheta)$, we obtain the approximate expression for the front's velocity:

$$V(K, \vartheta) = V^0(\vartheta) - \left(1 - \frac{\partial \ln V_{\text{is}}^0}{\partial \ln \varepsilon} \right) K \frac{D_x^{(u)} D_y^{(u)}}{D(\vartheta)}, \quad (2.28)$$

where we have used the relation $d \ln C / d \ln \varepsilon = \partial \ln V_{\text{is}}^0 / \partial \ln \varepsilon$ which follows from Equation (2.24). Formula (2.28) is the 'eikonal equation' for curved activation fronts in anisotropic media. In principle, it is valid for arbitrary values of ε , but typically this parameter is small and one can take in the first approximation [4]

$$C(\varepsilon) = C_1 - \varepsilon C_2, \quad C_2 > 0. \quad (2.29)$$

In this case we have $|d \ln C(\varepsilon) / d \ln \varepsilon| \approx \varepsilon C_2 / C_1 \ll 1$, so that Equation (2.28) reduces to

$$V(K, \vartheta) = V^0(\vartheta) - K \frac{D_x^{(u)} D_y^{(u)}}{D(\vartheta)}. \quad (2.30)$$

If $D_x^{(u)} = D_y^{(u)} = D(\vartheta) \equiv D$, Equation (2.30) coincides with the well-known eikonal equation for an isotropic medium (see, e.g., [4, 9]).

Assuming $\varepsilon \ll 1$, Equation (2.26) can be solved for arbitrary values of the parameter α , i.e., for arbitrary curvature values. Using expression (2.29) for $C(\varepsilon)$, we find that

$$w = \frac{1}{2} (C(\varepsilon) - \alpha) + \frac{1}{2} \left[(C(\varepsilon) - \alpha)^2 - 4\varepsilon C_2 \alpha \right]^{1/2}. \quad (2.31)$$

The corresponding expression for $V(K, \vartheta)$ can easily be obtained by Equations (2.25).

3. The Critical Properties of a Curved Front

Recall that for an isotropic system described by Equations (2.5), there exists a critical curvature $K_{\text{is}}^*(D)$, above which stable propagation becomes impossible [3]. It can easily be seen from Equations (2.5) that K_{is}^* and the corresponding critical velocity $V_{\text{is}}^*(D) = V_{\text{is}}(D, K_{\text{is}}^*(D)D)$ possess the scaling properties

$$K_{\text{is}}^*(\lambda^2 D) = \lambda^{-1} K_{\text{is}}^*(D), \quad V_{\text{is}}^*(\lambda^2 D) = \lambda V_{\text{is}}^*(D). \quad (3.1)$$

Using them together with Equations (2.14) and (2.15), we obtain the critical curvature $K^*(\vartheta)$, and the critical velocity $V^*(\vartheta)$, in anisotropic media:

$$K^*(\vartheta) = K_{\text{is}}^*(D_{\text{is}}) \frac{D_{\text{is}}^{1/2}}{D_x^{(u)} D_y^{(u)}} (D_x^{(u)} \cos^2 \vartheta + D_y^{(u)} \sin^2 \vartheta)^{3/2}, \quad (3.2)$$

$$V^*(\vartheta) = \frac{V_{\text{is}}^*(D_{\text{is}})}{D_{\text{is}}^{1/2}} (D_x^{(u)} \cos^2 \vartheta + D_y^{(u)} \sin^2 \vartheta)^{1/2}. \quad (3.3)$$

Again, D_{is} is an arbitrary diffusion coefficient in the isotropic medium. Equations (3.2) and (3.3) give the universal ϑ -dependence of the critical properties of autowaves described by reaction-diffusion equations (2.1). Although the quantities K_{is}^* and V_{is}^* depend on the concrete form of functions F_1 and F_2 , the ratios $K^*(\vartheta_1)/K^*(\vartheta_2)$ and $V^*(\vartheta_1)/V^*(\vartheta_2)$ are completely determined by the parameter $D_x^{(u)}/D_y^{(u)}$. In particular, for the fronts propagating along the x - and y -axes, we obtain the relations

$$\frac{K^*(0)}{K^*(\pi/2)} = \left(\frac{D_x^{(u)}}{D_y^{(u)}} \right)^{3/2}, \quad \frac{V^*(0)}{V^*(\pi/2)} = \left(\frac{D_x^{(u)}}{D_y^{(u)}} \right)^{1/2}. \quad (3.4)$$

They show that more stable activation fronts are those propagating along the axis with a larger value of the diffusion coefficient.

For small ε , the existence of the critical curvature can be seen directly from Equation (2.31). We have a real solution for w only if $\alpha < \alpha^*$, where

$$\alpha^* = C_1 \left(1 - 2\varepsilon^{1/2} \left(\frac{C_2}{C_1} \right)^{1/2} + \varepsilon \frac{C_2}{C_1} \right). \quad (3.5)$$

Recalling the definition of α , Equation (2.25), we obtain the critical curvature. To the leading approximation in ε , it is given by

$$K^*(\vartheta) = C_1 \frac{D^{3/2}(\vartheta)}{D_x^{(u)} D_y^{(u)}} \left(1 - 2\varepsilon^{1/2} \left(\frac{C_2}{C_1} \right)^{1/2} \right). \quad (3.6)$$

The critical velocity, $V^*(\vartheta)$, can be calculated from Equations (2.25), (2.31), and (3.5). To the leading approximation in ε , the result is

$$V^*(\vartheta) = [\varepsilon C_1 C_2 D(\vartheta)]^{1/2} \left(1 - \varepsilon^{1/2} \left(\frac{C_2}{C_1} \right)^{1/2} \right). \quad (3.7)$$

The dependence of the critical curvature on the angle ϑ between the normal $\mathbf{n}$ to the front and the x axis, Equation (3.2), was confirmed in computer simulations of the reaction-diffusion system (2.1). The idea of the numerical experiments is as follows. Consider a small round front propagating in an isotropic medium described by Equations (2.1) with $D_x^{(u)} = D_y^{(u)} = D_{\text{is}}$. The curvature of this front must be sufficiently large but not exceed the critical value $K_{\text{is}}^*(D_{\text{is}})$. Assume now that at some instant of time the diffusion coefficient $D_y^{(u)}$ decreases drastically. As follows from Equation (3.2), the critical curvature for the front propagating along the y -axis will fall. Thus, if the initial radius of the circle is sufficiently small, the front will be broken in the vicinity of $\vartheta = \pi/2$ and $\vartheta = 3\pi/2$.

For simulations we used a model described by Equations (2.1) with the generic reactivity functions F_1 and F_2 given by (see, e.g., [3])

$$F_1(u, v) = f(u) + v, \quad (3.8)$$

$$F_2(u, v) = \begin{cases} k_v u - v, & k_v u - v \geq 0, \\ k_\varepsilon (k_v u - v), & k_v u - v < 0. \end{cases} \quad (3.9)$$

where

$$f(u) = \begin{cases} -k_1 u, & u < \sigma, \\ k_u (u - a), & \sigma \leq u \leq 1 - \sigma, \\ k_2 (1 - u), & 1 - \sigma < u, \end{cases} \quad (3.10)$$

$$k_1 = \frac{a - \sigma}{\sigma} k_u, \quad k_2 = \frac{1 - \sigma - a}{\sigma} k_u, \quad (3.11)$$

We used the following values of parameters:

$$a = 0.1, \sigma = 0.01, \varepsilon = 0.35, k_u = 1.7, k_v = 2.0, k_\varepsilon = 1.0. \quad (3.12)$$

Equations (2.1) were integrated in a 2D array of 128×128 elements using Euler's method of integration with Neumann's boundary conditions. The spatial and temporal steps were chosen small enough so that a further decrease of their values would improve the accuracy of calculations by a few percent only.

The results of the simulations are illustrated in Figure 1 where one can see the break of the front after the anisotropy jump. It is important to note that in our simulations we have not seen the breaks of circles with sufficiently large radii. This demonstrates the existence of the critical curvature of activation fronts in anisotropic media.

4. Effects of the Inhibitor Diffusion

So far we have been concerned with anisotropic systems in which the inhibitor diffusion is negligible. It would be tempting to generalize our discussion by introducing the inhibitor diffusion. Unfortunately, in this case we cannot follow the

Figure 1. The break of a curved activation front in the anisotropic medium with $D^{(v)} = 0$: a) The initial condition at $t = 0$ is an isotropic medium ($D_x^{(u)} = D_y^{(u)} = 5.0 \cdot 10^{-5}$); b), c), d) The evolution of the front at $t > 0$ ($D_x^{(u)} = 5.0 \cdot 10^{-5}$, $D_y^{(u)} = 1.385 \cdot 10^{-5}$).

analytic method of the previous sections since, for arbitrary diffusion tensors $D_{ij}^{(u)}$ and $D_{ij}^{(v)}$, we cannot transform our basic equations (1.1) into a set of equations for an isotropic medium. On the other hand, the inclusion of the inhibitor diffusion is of interest in applications to real biological systems as far as new qualitative effects may appear. So, at this point of our consideration, we shall turn to computer simulations of reaction-diffusion equations. This will allow us to see how the inhibitor diffusion modify the properties of autowave patterns in anisotropic media.

We will assume that the medium is described by a set of equations

$$\begin{aligned} \frac{\partial u}{\partial t} &= F_1(u, v) + D_x^{(u)} \frac{\partial^2 u}{\partial x^2} + D_y^{(v)} \frac{\partial^2 u}{\partial y^2}, \\ \frac{\partial v}{\partial t} &= \varepsilon F_2(u, v) + D^{(v)} \Delta v, \end{aligned} \quad (4.1)$$

which corresponds to the assumption that the inhibitor diffusion is isotropic. The advantages of this model are twofold. First, it is best suited to show qualitative effects of the inhibitor diffusion. Second, the model described by Equations (4.1) is in fact rather general. Indeed, our basic equations (1.1) can be recast into Equations (4.1) by the following transformations of coordinates: 1) Transformation to the principal axes system for the inhibitor diffusion tensor $D_{ij}^{(v)}$; 2) Scaling transformation (2.2) to make the inhibitor diffusion isotropic; 3) Transformation to the principal axes system for the activator diffusion tensor. Note that, with no harm, it is possible to obtain a set of equations where the activator diffusion is isotropic while the inhibitor diffusion tensor has only diagonal components.

Based on the properties of autowaves in isotropic media, one can suppose some characteristic properties of autowaves described by Equations (4.1). First, it is known that if the diffusion coefficient $D^{(v)}$ is sufficiently small, it has little effect on the curvature-velocity relation for *continuous* activation fronts in isotropic media [5]. It would appear reasonable that this property would also be valid for anisotropic media. On the other hand, the inhibitor diffusion has a pronounced effect on the kinematics of *broken fronts* [10], especially on the tangential velocity of the front edge (tip). Taking also into account that, in anisotropic media, the normal velocity depends on the orientation of the front with respect to coordinate axes, there is little doubt that the inhibitor diffusion must significantly affect the kinematics of spiral waves.

To check the above predictions, we have performed computer simulations of Equations (4.1) with the nonlinear functions F_1 and F_2 described in the previous section.

In the first set of our experiments we studied the influence of the inhibitor diffusion on the propagation of continuous activation fronts in anisotropic media. A small domain of the initial excitation gave rise to the propagating front which, with time, became elliptically shaped. The experiments were performed for different values of the diffusion coefficient $D^{(v)}$. The results are shown in Figure 2. As long as $D^{(v)}$ is small in comparison with $D_x^{(u)}$ and $D_y^{(u)}$, the ratio of elliptical semi-axes of the front remains practically constant, while the front's velocity decreases but little with the increase of $D^{(v)}$. Hence it follows that a small inhibitor diffusion indeed has a minor effect on the curvature-velocity relation in anisotropic media. The further increase of $D^{(v)}$ leads to a marked change of the front shape and even to the break of the wave in the direction of lesser diffusion coefficient of the activator. We would like to emphasize that the break of the wave in the medium with $D^{(v)} \neq 0$ was also observed in the cases where the propagation is stable for $D^{(v)} = 0$. To gain a qualitative understanding of this effect, we recall that, in the isotropic case, the inhibitor diffusion coefficient enters into the curvature-velocity relation through the difference $D^{(u)} - D^{(v)}$ [5]. Thus the break of activation fronts in anisotropic media with $D^{(v)} \neq 0$ can be interpreted as arising from the fact that the role of the effective diffusion coefficient in the y-direction is played by $D_y^{(u)} - D^{(v)}$, resulting in the break of the front for larger values of $D_y^{(u)}$ than is observed for $D^{(v)} = 0$.

Figure 2. The shapes of activation fronts at $t = 20$ in the anisotropic medium for different values of the inhibitor diffusion coefficient $D^{(v)}$: $D_x^{(u)} = 4 \cdot 10^{-4}$, $D_y^{(u)} = 2 \cdot 10^{-4}$, a) $D^{(v)} = 0$, b) $D^{(v)} = 0.3 \cdot 10^{-4}$, c) $D^{(v)} = 0.7 \cdot 10^{-4}$, d) $D^{(v)} = 0.9 \cdot 10^{-4}$, e) $D^{(v)} = 1.0 \cdot 10^{-4}$, f) $D^{(v)} = 1.1 \cdot 10^{-4}$. The ratio of the elliptical semi-axes remains constant and equal to $(D_x^{(u)} / D_y^{(u)})^{1/2}$.

In the next set of simulations, we studied the properties of spiral waves in the medium with $D^{(v)} \neq 0$. The evolution of the rectangular front of excitation led to the formation of a spiral wave rotating around the core. Figure 3 shows the core shapes for different values of $D^{(v)}$. As one would expect, the inhibitor diffusion strongly affects the properties of spiral waves, in particular, the size and shape of the core. A somewhat surprising feature is that the quasi-elliptical core of the wave turns through the angle dependent on $D^{(v)}$.

5. Concluding Remarks

From the foregoing discussion, we might conclude that the properties of autowave patterns in anisotropic media are much more complicated as compared with the isotropic case. Nevertheless, we have seen that the models where the inhibitor diffusion is neglected can be studied analytically. In this case, the scaling transformation of coordinates allows one to describe all the properties of autowave patterns in the anisotropic medium in terms of the isotropic picture.

Figure 3. The shapes of spiral wave cores in the anisotropic medium for different values of the inhibitor diffusion coefficient $D^{(v)}$: $D_x^{(u)} = 4.0 \cdot 10^{-4}$, $D_y^{(u)} = 2.0 \cdot 10^{-4}$, a) $D^{(v)} = 0$, b) $D^{(v)} = 0.15 \cdot 10^{-4}$, c) $D^{(v)} = 0.3 \cdot 10^{-4}$, d) $D^{(v)} = 0.45 \cdot 10^{-4}$.

The inhibitor diffusion leads to the appearance of new interesting effects, for instance, the turn of the spiral wave core mentioned in Section 4. In this connection the development of analytic methods with allowance made for the inhibitor diffusion is very important. We hope to discuss this issue in future publications.

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