Critical Properties of Ring-shaped Autowaves on Curved Surfaces

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SUMMARY: Propagation of ring-shaped activation fronts on surfaces of revolution in the presence of an external electric field is studied for arbitrary two-variable excitable media described by nonlinear reaction-diffusion equations. A general local propagation condition is derived. It is shown that a curved surface can serve as a diode for activation fronts, which is controlled by the applied electric field.

Introduction

Autowave patterns occur in many physical, chemical, and biological systems [1)] and usually the system must be considered as an excitable medium with a curved surface. An important example is a heart, where the excitation waves have ring-like shape. Although during last decade some properties of excitation fronts on curved surfaces were studied theoretically [2-4)] and experimentally [5)], there are many gaps in our understanding of these processes. One of the most points, especially for biological systems, is the study of possible mechanisms for controlling autowaves. Recently some new qualitative properties of activation fronts on curved surfaces have been predicted and confirmed by computer simulations [6)]. In particular, it has been shown that under certain conditions a curved surface can serve as a diode for autowaves, i.e. the surface is "transparent" for autowave propagation only in one direction. The aim of this paper is to investigate the influence of an applied electric field on the diode properties of excitable media with curved surfaces.

Basic equations

In this work we consider a commonly used two-variable model of excitable 2-D media described by nonlinear reaction-diffusion equations [4)]. For autowaves propagating on a curved

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surface in the presence of an electric field, the basic equations can be written in the form

$$\begin{aligned}\frac{\partial u}{\partial t} &= F_1(u,v) + D_u \frac{1}{\sqrt{g}}\frac{\partial}{\partial \alpha^i}\left(g^{ik}\sqrt{g}\frac{\partial u}{\partial \alpha^k}\right) + \mu_u \frac{1}{\sqrt{g}}\frac{\partial}{\partial \alpha^i}\left(\sqrt{g}uE^i\right)\\ \frac{\partial v}{\partial t} &= \varepsilon F_2(u,v) + D_v \frac{1}{\sqrt{g}}\frac{\partial}{\partial \alpha^i}\left(g^{ik}\sqrt{g}\frac{\partial v}{\partial \alpha^k}\right) + \mu_v \frac{1}{\sqrt{g}}\frac{\partial}{\partial \alpha^i}\left(\sqrt{g}vE^i\right)\end{aligned} \quad (1)$$

where $u(\alpha^1,\alpha^2,t)$ and $v(\alpha^1,\alpha^2,t)$ are the activator and inhibitor variables respectively, α^i are coordinates on the surface, and $g = \det[g_{ik}]$ is the determinant of the metric tensor g_{ik}. For definiteness, we assume that $g > 0$. From here on summation over repeated indices is implied. Functions F_1 and F_2 specify reactions in the system and the formal rate coefficient ε determines the time scale for the recovery process (in many cases of interest ε may be regarded as a small parameter). The second terms in the right-hand sides of equations (1) represent the diffusion contributions, where D_u and D_v being the diffusion coefficients for both species. The last terms in equations (1) describe the field effects. In these terms E^i are the contravariant components of the electric field.. The quantities μ_u and μ_v may be interpreted as the effective activator and inhibitor mobilities. Equations (1) are very complicated and, in general, they can be solved only numerically with concrete model expressions for the generic reactivity functions F_1 and F_2. In order to study qualitative features of nonlinear dynamics in curved excitable media, we will concentrate on the propagation of ring-shaped autowaves on the surfaces of revolution. As we shall see below, in this case some interesting effects can be predicted for the arbitrary generic reactivity functions.

Let a surface of revolution be specified in Cartesian coordinates by the equation $r = f(z)$, where $r = \sqrt{x^2 + y^2}$. Ring-shaped autowaves lying in the xy plane and propagating along the z axis can be described by $u = u(z,t)$ and $v = v(z,t)$. It is more convenient, however, to introduce new coordinates $\alpha^1 = l$ and $\alpha^2 = \varphi$, where l is measured along the meridian of the surface and φ is the polar angle in the xy plane. The coordinate l can be expressed in terms of z from the relation $dl = \sqrt{1 + f'^2}\, dz$, where $f' = df / dz$ .Then it can easily be verified that, for coordinates l and φ, the metric tensor is

$$g_{11} = 1, \quad g_{12} = g_{21} = 0, \quad g_{22} = f^2 \quad (2)$$

Now, assuming that the electric field is applied along the z axis, equations (1) for ring-shaped autowaves become

$$\begin{aligned}\frac{\partial u}{\partial t} &= F_1(u,v) + D_u \frac{\partial^2 u}{\partial l^2} + D_u k_g \frac{\partial u}{\partial l} - \mu_u \frac{1}{f}\frac{\partial}{\partial l}(fuE)\\ \frac{\partial v}{\partial t} &= \varepsilon F_2(u,v) + D_v \frac{\partial^2 v}{\partial l^2} + D_v k_g \frac{\partial v}{\partial l} - \mu_v \frac{1}{f}\frac{\partial}{\partial l}(fvE)\end{aligned} \tag{3}$$

where E is the tangent projection of the field and

$$k_g = k_g(z) = \frac{f'}{f\sqrt{1+f'^2}}$$

is the local geodesic curvature of the surface. In what follows we assume that the surface is sufficiently smooth, i.e. the width δ_0 of the activation front everywhere satisfies the condition $\delta_0 \,|dk_g / dl| << |k_g|$. Then, in calculating the local velocity of the ring-shaped activation front, $c(z)$, the geodesic curvature $k_g(z)$ and the electric field $E(z)$ can be regarded as fixed parameters. Introducing in (3) the variable $\xi = l - ct$, we arrive at the stationary equations

$$\begin{aligned}D_u \frac{d^2 u}{d\xi^2} + F_1(u,v) + (c + k_g D_u)\frac{du}{d\xi} - \mu_u \frac{1}{f}\frac{d}{d\xi}(fuE) = 0\\ D_v \frac{d^2 v}{d\xi^2} + \varepsilon F_2(u,v) + (c + k_g D_v)\frac{dv}{d\xi} - \mu_v \frac{1}{f}\frac{d}{d\xi}(fvE) = 0\end{aligned} \tag{4}$$

The velocity of the front, $c(z)$, is determined from the condition that equations (4) have a non-trivial solution. Before proceeding to some interesting consequences which we can draw from equations (4), it is worthwhile to dwell on the calculation of the electric field E. Generally speaking, we have to derive an equation for the electric field with allowance made for perturbations caused by the autowave. This approach is self-consistent, but it leads to a rather complicated system of basic equations. Note, however, that good approximation for the electric field can be found by recognizing that the corrections to the electric field from the activation region may be neglected if the width of the front is small compared to the electrode distance. Assuming that this condition is fulfilled, we calculate E in the absence of autowaves. In the stationary (Ohmic) regime, $j(z) \propto E(z)$, where j is the current due to a voltage U applied to the system. Another obvious stationary condition for the current on a surface of revolution reads $2\pi f(z) j(z) = const$. Thus we find that

$$E(z) = \frac{A}{f(z)} \tag{5}$$

The value of A depends on the surface and is given by

$$A = U\left[\int_{z_1}^{z_2} \frac{\sqrt{1+f'^2(z)}}{f(z)}\,dz\right]^{-1} \tag{6}$$

where z_1 and z_2 are the electrode positions. Substitution of (5) into (4) gives

$$\begin{aligned} D_u \frac{d^2u}{d\xi^2} + F_1(u,v) + \left(c + k_g D_u - \mu_u \frac{A}{f}\right)\frac{du}{d\xi} = 0 \\ D_v \frac{d^2v}{d\xi^2} + \varepsilon F_2(u,v) + \left(c + k_g D_v - \mu_v \frac{A}{f}\right)\frac{dv}{d\xi} = 0 \end{aligned} \tag{7}$$

Recently [6] these equations were analyzed in the special case $E = 0$. The most intriguing result confirmed by computer simulations is that, depending on the behavior of the geodesic curvature $k_g(z)$, the surface can be transparent for autowave fronts propagating only in one direction. Note in this connection that equations (7) contain new terms due to the presence of the electric field. Of special interest is the influence of these terms on critical properties of the activation front since it provides a way for controlling autowave propagation.

Velocity of the activation front

Our further analysis is based on the fact that equations (7) are formally identical with the stationary equations describing ring-shaped autowaves on a *plane* if $k_g(z)$ is replaced by the usual curvature K, the function $A/f(z)$ is replaced by the normal projection of the electric field E_n, and the variable ξ is interpreted as $\xi = r - V(K, E_n)t$, where r is the radial coordinate on the plane and $V(K, E_n)$ is the corresponding velocity of the front [7]. This analogy allows us to write the relation

$$c(z) = V\left(k_g(z), Af^{-1}(z)\right) \tag{8}$$

which allows to evaluate the velocity of a ring-shaped activation front on the curved surface if the dependence of V on the curvature K and the field E_n is known. In the case of small curvature and a weak field, this dependence is given by the modified "eikonal equation"[7] $V = V_0 - D_u K + \mu_u E_n$, where V_0 is the velocity of a flat activation front on a plane in the absence of the field. Recalling (8), we conclude that the eikonal equation for ring-shaped autowaves on curved surfaces in the presence of an electric field reads

$$c(z) = V_0 - D_u k_g(z) + \mu_n A f^{-1}(z) \tag{9}$$

This is a generalization of the eikonal equation derived previously for activation fronts in the absence of the field [6]. It should be emphasized that in (9) V_0 is the only quantity which depends on the form of the generic reactivity functions F_1 and F_2.

The diode effect for ring-shaped autowaves

We now want to discuss the critical properties of ring-shaped activation fronts described by equations (7). It is well known that, for ring-shaped autowaves on a plane, there exists a critical curvature K^*, above which stable propagation becomes impossible [8]. An analogous situation occurs with ring-shaped autowaves on curves surfaces [6] and the local condition for stable propagation is $k_g(z) < K^*$. In this section we study the influence of the field on the critical properties of activation fronts. Let V^* be the critical velocity of a ring-shaped activation front on a plane in the absence of the external field. Let also z^* be the point where equations (7) describe the critical regime on the curved surface. Then, due to the above-mentioned analogy between stationary equations for activation fronts on a plane and on curved surfaces, we may write

$$
\begin{aligned}
c^* + k_g(z^*)D_u - \frac{\mu_u A}{f(z^*)} &= V^* + K^* D_u \\
c^* + k_g(z^*)D_v - \frac{\mu_v A}{f(z^*)} &= V^* + K^* D_v
\end{aligned}
\tag{10}
$$

where c^* is the critical velocity on the curved surface. Subtracting these equations leads to the equation for z^*:

$$
k_g(z^*) - \frac{A}{f(z^*)}\frac{\Delta\mu}{\Delta D} = K^* \tag{11}
$$

where we have introduced the designations $\Delta\mu = \mu_u - \mu_v$ and $\Delta D = D_u - D_v$. Thus the condition for stable propagation of activation fronts has the form

$$
k_g(z) - \frac{A}{f(z)}\frac{\Delta\mu}{\Delta D} < K^* \tag{12}
$$

This inequality determines all possible regions for stable propagation. It is valid for all excitable media described by equations (1) and K^* is the only parameter that depends on the form of functions F_1 and F_2.

As an illustration of the condition (12) we shall discuss the diode effect for ring-shaped autowaves [6] in the presence of an external electric field. For definiteness, we consider a "bottle-like" surface composed of two coaxial cylinders with radii R_1 and R_2 $(R_2 > R_1)$ connected by a transition layer. The corresponding function $f(z)$ will be taken in the form

$$f(z) = \begin{cases} R_1 & z \le 0, \\ R_1 + z\Delta R/\delta & 0 < z < \delta \\ R_2 & z \ge \delta \end{cases} \tag{13}$$

where $\Delta R = R_2 - R_1$ and δ is the width of the transition layer. In the case under consideration the geodesic curvature is equal to zero for $z < 0$ and $z > \delta$. For $0 < z < \delta$, formula (3) gives

$$k_g(z) = \frac{1}{(R_1 + z\,\Delta R/\delta)\sqrt{1 + (\delta/\Delta R)^2}} \tag{14}$$

Finally, calculating the integral in (6) with the function (13) and assuming that U is the voltage applied to the transition region ($z_1 = 0$ and $z_2 = \delta$), we find that

$$A = \frac{U}{\ln(1 + \Delta R/R_1)\sqrt{1 + (\delta/\Delta R)^2}} \tag{15}$$

Now we obtain from (12) the condition that ring-shaped autowaves can propagate through the transition region:

$$k_g(z) - \frac{\alpha U}{f(z)} < K^*, \quad 0 < z < \delta \tag{16}$$

where the parameter α is defined as

$$\alpha = \left(\frac{\Delta\mu}{\Delta D}\right)\frac{1}{\ln(1 + \Delta R/R_1)\sqrt{1 + (\delta/\Delta R)^2}} \tag{17}$$

Two comments are relevant concerning the propagation condition (16). First, the parameter α, as well as the voltage U, may be positive or negative. Second, the condition (16) applies to activation fronts propagating from the region $z < 0$. It can be shown that the analogous condition for autowaves propagating in the opposite direction follows from (16) by replacing $U \to -U$ and $k_g \to -k_g$.

Before we go into a discussion of (16), we briefly summarize qualitative conclusions concerning the case $U = 0$. Since the geodesic curvature (14) is positive and has a maximum at $z = 0$, the propagation condition in the absence of the field reads

$$K^* R_1 \sqrt{1 + (\delta/\Delta R)^2} > 1 \tag{18}$$

Ring-shaped autowaves propagating from the region $z > \delta$ are always stable. Thus, the surface (13) can serve as a diode for autowaves. Let us now suppose that the condition is satisfied and, consequently, the transition region is transparent for autowaves propagating along the z axis. Then, as seen from (16), the transition region can be "closed" by applying a voltage $|U| > U_{cr}$, where the critical value U_{cr} is given by

$$U_{cr} = \left|\frac{\Delta D}{\Delta\mu}\right| \ln(1 + \Delta R / R_1)\left(K^* R_1 \sqrt{1 + (\delta / \Delta R)^2} - 1\right) \tag{19}$$

The sign of U is determined by the condition $\alpha U < 0$. On the other hand, if the transition region is "closed" for $U = 0$, it becomes transparent for activation fronts propagating along the z axis by applying a voltage $|U| > U'_{cr}$ ($\alpha U > 0$), where

$$U'_{cr} = \left|\frac{\Delta D}{\Delta\mu}\right| \ln(1 + \Delta R / R_1)\left(1 - K^* R_1 \sqrt{1 + (\delta / \Delta R)^2}\right) \tag{20}$$

The above qualitative properties of the transition region can be observed for arbitrary curved surfaces with space-varying curvature. The quantity R_1 has the meaning of an effective radius of the local cross-section of the surface and δ is an effective width of the local barrier ΔR. Note that the diode effect with different mechanism was observed in a flat excitable system of special geometry [9].

Conclusion

It has been shown that the geometry of a curved surface and an external electric field have a pronounced effect on the propagation of autowaves and are responsible for the diode property of the surface. This property provides a way to exert control over the propagation of activation fronts by changing the form of the surface and electric field applied to the system.

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