Covariant Stringlike Dynamics of Scroll Wave Filaments in Anisotropic Cardiac Tissue

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It has been hypothesized that stationary scroll wave filaments in cardiac tissue describe a geodesic in a curved space whose metric is the inverse diffusion tensor. Several numerical studies support this hypothesis, but no analytical proof has been provided yet for general anisotropy. In this Letter, we derive dynamic equations for the filament in the case of general anisotropy. These equations are covariant under general spatial coordinate transformations and describe the motion of a stringlike object in a curved space whose metric tensor is the inverse diffusion tensor. Therefore the behavior of scroll wave filaments in excitable media with anisotropy is similar to the one of cosmic strings in a curved universe. Our dynamic equations are valid for thin filaments and for general anisotropy. We show that stationary filaments obey the geodesic equation.

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Introduction.—Scroll waves in excitable media are an important example of three-dimensional self-organization. They have been observed in a wide range of systems, including the Belousov-Zhabotinsky reaction [1], the slime mould *Dictyostelium discoideum* [2], and cardiac tissue [3,4]. In the latter, scroll waves of electrical excitation have been associated with cardiac arrhythmias and ventricular fibrillation [5]. Understanding the dynamics of scroll waves is therefore likely to improve the current therapies for cardiac arrhythmias.

Cardiac tissue consists of interconnected cells that have more end-to-end than side-to-side connections, leading to a complicated fibrous structure. The electrical conductivity is much higher along than across muscle fibers, making cardiac tissue highly anisotropic for electrical propagation [6]. Several numerical studies have been dedicated to the role of tissue anisotropy on the dynamics of scroll waves [7–10]. Recently, Wellner *et al.* performed a study of stationary scroll wave filaments [11], the organizing centers around which the excitation waves rotate. They postulated a *minimal principle*, such that stationary filaments describe geodesics in a three-dimensional space whose metric is given by the inverse diffusion tensor of the medium. Ten Tusscher and Panfilov reformulated this principle using the Hamilton-Jacobi theory and showed that the geodesic is equivalent to the shortest path for wave propagation through the medium [12]. The minimal principle was verified numerically for specific examples of anisotropy in cardiac tissue [11,12]. However, it still lacks an analytical proof.

In this Letter, we provide an analytical derivation of the dynamic equations for thin filaments in anisotropic media. Our approach is inspired by a similar problem found in cosmology: the calculation of the motion of cosmic strings in curved space time (see [13] and references therein). In this case, the string equations can be deduced in leading order by expanding the action in a small dimensionless parameter λ, which is essentially the ratio of the string width and its radius of curvature. From a topological point of view, scroll waves in excitable media are similar to cosmic strings. However, one major difference prevents the direct application of the above-mentioned method to the current problem: excitable media are dissipative systems, for which no action principle has been formulated.

We work in the same regime as Wellner *et al.* [11], where two-dimensional spiral waves have a circular core. First, we construct a comoving curvilinear coordinate system, with one axis oriented along the filament, in which the metric is locally Euclidean in the plane orthogonal to the filament. Second, we expand the scroll wave solution in λ, the ratio of the width of its filament (a measure of the core's diameter), and its radius of curvature. We then calculate, in the comoving frame of reference, the scroll wave's motion in leading order by substitution of our expansion in the system equations. The obtained dynamic equations are fully covariant under general spatial coordinate transformations and provide a generalization of earlier work on isotropic cardiac tissue [14,15]. For stationary filaments, our dynamic equations reduce to the geodesic equation.

Comoving curvilinear coordinates.—Excitable media are commonly described by means of a reaction-diffusion equation:

$$\partial_t \mathbf{u} = \partial_i (D^{ij} \partial_j \hat{P} \mathbf{u}) + \mathbf{\Phi}(\mathbf{u}) \tag{1}$$

where $\mathbf{u}$ is a vector of state variables, $\mathbf{\Phi}$ are nonlinear functions that determine the dynamical properties of the system, and D represents the diffusion tensor of the medium. The projection operator $\hat{P}$ was inserted to ensure that only one component (the electrical potential) diffuses, as is the case in myocardial models. The 3D scroll wave solution $\mathbf{u}_s(\vec{x}, t)$ satisfies (1).

In an isotropic 2D medium ($D^{AB} = \delta^{AB}$ with $A, B = 1, 2$), Eq. (1) has an exact rotating spiral wave solution $\mathbf{u}_0(\rho, t) = \mathbf{u}_0(\rho, \theta - \omega_0 t)$ where $\mathbf{u}_0$ obeys the time-independent equation in the rotating frame

$$\Delta_2 \hat{P} \mathbf{u}_0 + \omega_0 \partial_\theta \mathbf{u}_0 + \Phi(\mathbf{u}_0) = 0 \tag{2}$$

and θ is the angular polar coordinate in 2D.

Isotropic scroll waves in 3D can be constructed as a stack of 2D spiral waves along a curve $\vec{X}(\sigma, \tau)$ connecting the spiral waves' centers of rotation, i.e., the filament, where σ parameterizes the filament and τ represents time in the comoving frame of reference. We introduce comoving coordinates $\vec{x} = \vec{x}(\rho^A, \sigma, \tau)$ $(A = 1, 2)$, where ρ^A indicate curvilinear coordinates locally transverse to the filament given by $\vec{X}(\sigma, \tau) = \vec{x}(0, 0, \sigma, \tau)$ [16].

In the isotropic case, this construction only yields an exact 3D solution if the filament is straight and stationary. For a general curved filament, there are corrections of order $\lambda = d/R$:

$$\mathbf{u}_s = \mathbf{u}_0(\rho^A) + \lambda \tilde{\mathbf{u}}(\rho^A, \sigma, \tau) + \mathcal{O}(\lambda^2) \tag{3}$$

where d is the width of the filament and R its radius of curvature. For isotropic media, this procedure was realized by Keener [14] and Biktashev *et al.* [15] using singular perturbation theory and Frenet-Serret coordinates. Dynamic equations were obtained to lowest order in λ.

For the anisotropic case, we need to work in general curvilinear coordinates and rewrite the reaction-diffusion Eq. (1) in an explicitly covariant way. To do this, we make the assumption that the determinant of the diffusion tensor is a constant in space. This condition is fulfilled in homogeneous anisotropic excitable media such as myocardium. Note that deviations from this assumption lead to drift terms in the equation of motion, which fall outside the scope of this Letter. Introducing the contravariant metric tensor $G^{ij} = D^{ij}$ or $G_{ij} = (D^{-1})_{ij}$, we can write the diffusion term as a covariant Laplacian in curved space, for constant $G = \det G$:

$$\partial_i(D^{ij}\partial_j) = \frac{1}{\sqrt{G}} \partial_i(\sqrt{G} G^{ij} \partial_j) = \mathcal{D}_i \mathcal{D}^i \tag{4}$$

where $\mathcal{D}_i V^j = \partial_i V^j + \Gamma^j_{ik} V^k$ stands for the covariant derivative, defined using the Christoffel symbols of the second kind $\Gamma^j_{ik} = \frac{1}{2} G^{jl}[\partial_i G_{kl} + \partial_k G_{il} - \partial_l G_{ik}]$.

To solve equations in curved space, one usually chooses local Euclidean coordinates (or in general relativity, local Minkowski) so that the metric is locally Euclidean up to second order. In our case, we want to solve the reaction-diffusion equations in curved space not locally at one point, but along the complete filament and this at least up to distances of the order of the width of the filament. For this purpose, we choose a comoving coordinate system which, at each point of the filament, is locally Euclidean in the plane orthogonal to the filament. It can be obtained by expanding $\vec{x}$ in the plane orthogonal to the filament (up to second order):

$$x^i = X^i(\sigma, \tau) + c^i_A(\sigma, \tau)\rho^A + \frac{1}{2} C^i_{AB}(\sigma, \tau)\rho^A \rho^B. \tag{5}$$

Defining $\vec{e}_\mu$ and $\vec{e}^\mu$ as the local frame and its dual (obeying the orthonormality condition $\vec{e}_\mu \cdot \vec{e}^\nu = \delta^\nu_\mu$)

$$\vec{e}_A = \frac{\partial \vec{x}}{\partial \rho^A}, \qquad \vec{e}_\sigma = \frac{\partial \vec{x}}{\partial \sigma} \tag{6}$$

$$\vec{e}^A = \vec{\nabla} \rho^A, \qquad \vec{e}^\sigma = \vec{\nabla} \sigma, \tag{7}$$

we have that $c^i_A = e^i_A(\rho = 0, \sigma, \tau)$.

We fix the comoving coordinate system by first imposing the condition that $\mathcal{D}_B \vec{e}_A = \mathcal{O}(\rho)$, i.e., $\mathcal{D}_B \vec{e}_A = \vec{0}$ on the filament $(A, B = 1, 2)$, which ensures that it is locally Euclidean orthogonal to the filament. One can easily check from the definition of the covariant derivative that this condition leads to $C^i_{AB} = -\Gamma^i_{jk} e^j_A e^k_B$. Since $\mathcal{D}_\mu \vec{e}_\nu = \Gamma^\lambda_{\mu\nu} \vec{e}_\lambda$, we have $\Gamma^\mu_{AB} = 0$ $(\mu = 1, 2, \sigma)$ on the filament.

Furthermore, the frame $\vec{e}_\mu$ (and thus the coefficients c^i_A) is chosen is such a way that on the filament, it is orthonormal in the curved metric:

$$G_{\mu\nu} = e^i_\mu G_{ij} e^j_\nu = \delta_{\mu\nu}. \tag{8}$$

This fixes our local frame up to an arbitrary rotation around the filament. Since we do not want to discuss the effects of twist in this Letter, as they decouple in lowest order from the translational degrees of freedom [15], we let the frame rotate with the constant frequency ω_0 and without twist:

$$\dot{\vec{e}}_A = -\omega_0 \epsilon^B{}_A \vec{e}_B, \qquad \mathcal{D}_\sigma \vec{e}_A \cdot \vec{e}^B = 0 \quad (A \neq B) \tag{9}$$

with

$$\epsilon^A{}_B = \begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix}$$

the antisymmetric rank 2 tensor with $\epsilon 12 = 1$.

On the filament, we have $G_{AB} = \delta_{AB}$ and $\Gamma^\mu_{AB} = 0$, which implies $G_{AB} = \delta_{AB} + \mathcal{O}(\rho^2)$. Together with the no twist condition (9), one easily finds that $\Gamma^B_{\sigma A} = 0$ on the filament, which along with $\Gamma^\sigma_{AB} = 0$ yields that $G_{A\sigma} = 0 + \mathcal{O}(\rho^2)$. Using Eq. (5), we finally obtain

$$G_{\mu\nu} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 - 2\vec{e}_A \cdot \mathcal{D}^2_\sigma \vec{X} \rho^A \end{pmatrix} + \mathcal{O}(\rho^2). \tag{10}$$

The component $G_{\sigma\sigma}$ can be obtained by expanding the metric G_{ij} around the filament, applying the coordinate transformation Eq. (5), and choosing the filament parameter σ so that it measures the distance along the filament in curved space. We observe that if the filament is a geodesic $(\mathcal{D}^2_\sigma \vec{X} = 0)$, the metric is Euclidean up to second order.

Equation of motion.—There are two types of curvature effects which will generate non trivial dynamics for the filament in anisotropic media. The first type, measured by $\lambda = d/R$, is due to extrinsic curvature of the filament and also occurs in the isotropic case. The second curvature effect is due to curvature of space (anisotropy) and describes how locally parallel geodesics deviate. In the plane orthogonal to the filament, this effect is proportional to $\kappa = d^2 R_{1212}$, where $R_{\lambda\mu\nu\delta}$ is the Riemann tensor. We will assume that the anisotropy is small enough so that deviation of geodesics is negligible over distances of order of the filament width d. The second order deviations from Euclidicity in (10) generate extrinsic curvature effects of order $\mathcal{O}(\lambda^2)$ and intrinsic curvature effects of $\mathcal{O}(\kappa)$ due to anisotropy and can be dropped in the sequel.

We expand the 3D solution as in Eq. (3):

$$\mathbf{u}_s = \mathbf{u}_0(\rho^A) + \lambda\tilde{\mathbf{u}}(\rho^A, \sigma, \tau) + \mathcal{O}(\lambda^2, \kappa) \tag{11}$$

with $\partial_\sigma \tilde{\mathbf{u}}$ an order λ higher than $\partial_\rho \tilde{\mathbf{u}}$, i.e., $\partial_\sigma \tilde{\mathbf{u}} = \partial_\rho \tilde{\mathbf{u}} \cdot \mathcal{O}(\lambda)$.

Using Eq. (5) and $\partial_t = \partial_\tau - (\vec{e}^\mu \cdot \partial_\tau \vec{x})\partial_\mu$, we obtain after some calculations and using $\epsilon^A{}_B \rho^A \partial_B = \partial_\theta$

$$\partial_t \mathbf{u}_s = \lambda\partial_\tau\tilde{\mathbf{u}} - (\vec{e}^A \cdot \dot{\vec{X}})\partial_A \mathbf{u}_0 - \omega_0 \partial_\theta(\mathbf{u}_0 + \lambda\tilde{\mathbf{u}}) + \mathcal{O}(\lambda^2, \kappa). \tag{12}$$

On the other hand, the diffusion term can be rewritten as

$$\partial_i(G^{ij}\partial_j \hat{P}\mathbf{u}_s) = \partial_i(G^{iA}\partial_A \hat{P}\mathbf{u}_s) + \mathcal{O}(\lambda^2) \tag{13}$$

$$= (\partial_i G^{iA})\partial_A \hat{P}\mathbf{u}_0 + G^{AB}\partial^2_{AB}\hat{P}\mathbf{u} + \mathcal{O}(\lambda^2) \tag{14}$$

$$= (\partial_i G^{iA})\partial_A \hat{P}\mathbf{u}_0 + \Delta_2 \hat{P}(\mathbf{u}_0 + \lambda\tilde{\mathbf{u}}) + \mathcal{O}(\lambda^2, \kappa). \tag{15}$$

Introducing the perturbation operator $\hat{L}$ as

$$\hat{L} = \Delta_2 \hat{P} + \omega_0 \partial_\theta + \Phi'(\mathbf{u}_0) \tag{16}$$

and the fact that $\mathbf{u}_0$ is an exact 2D solution of Eq. (2), the reaction-diffusion equation finally gives

$$\lambda(\partial_\tau \tilde{\mathbf{u}} - \hat{L}\tilde{\mathbf{u}}) = (\partial_i G^{iA})\partial_A \hat{P}\mathbf{u}_0 + (\vec{e}^A \cdot \dot{\vec{X}})\partial_A \mathbf{u}_0 + \mathcal{O}(\lambda^2, \kappa). \tag{17}$$

To proceed, we must remember that by introducing the filament coordinate $\vec{X}(\sigma, \tau)$, we have augmented the number of degrees of freedom and hence must impose a gauge condition on $\tilde{\mathbf{u}}$. We demand that $\tilde{\mathbf{u}}$ be orthogonal to the time-independent translational modes $|\psi_A\rangle \sim \partial_A \mathbf{u}_0$ ($A = 1, 2$):

$$\langle \bar{\psi}^B | \tilde{\mathbf{u}} \rangle = 0 \tag{18}$$

where the inner product $\langle \bar{v}, w \rangle = \int \bar{v} w d\rho^1 d\rho^2$ [14,15]. The eigenfunctions of $\hat{L}$ and $\hat{L}^+$ are normalized such that $\langle \bar{\psi}^B | \psi_A \rangle = \delta^B_A$. One can check from Eq. (16) that $\hat{L}|\psi_1\rangle = -\omega_0|\psi_2\rangle$ and $\hat{L}|\psi_2\rangle = \omega_0|\psi_1\rangle$. Since in 2D there are only two rotationally invariant tensors, $\delta^B{}_A$ and $\epsilon^B{}_A$, we generally have

$$\langle \bar{\psi}^B | \hat{P} | \psi_A \rangle = \gamma_1 \delta^B{}_A + \gamma_2 \epsilon^B{}_A. \tag{19}$$

γ_1 and γ_2 are real constants depending on the medium characteristics, and have been calculated in [17] for a given model. Projecting Eq. (17) on the translational mode, we obtain

$$\vec{e}^A \cdot \dot{\vec{X}} = -\gamma_1 \partial_i G^{iA} - \gamma_2 \epsilon^A{}_B \partial_i G^{iB} + \mathcal{O}(\lambda^2, \kappa). \tag{20}$$

We note that G^{iA} is a mixed tensor (i is Cartesian and A is curvilinear). Under transformation of the Cartesian coordinate, the tensor G^{iA} transforms as a three-vector, and since $\det G =$ constant in Cartesian coordinates, we have

$$\partial_i G^{iA} = \frac{1}{\sqrt{G}}\partial_\mu(\sqrt{G}G^{\mu A}) = \partial_\mu G^{\mu A} + \Gamma^\mu_{\mu\alpha} G^{\alpha A} \tag{21}$$

where we have used the well-known fact that $\Gamma^\mu_{\mu\alpha} = \frac{1}{\sqrt{G}}\partial_\alpha \sqrt{G}$. By virtue of the Ricci identity $\mathcal{D}_\mu G^{\mu A} = \partial_\mu G^{\mu A} + \Gamma^\mu_{\mu\alpha} G^{\alpha A} + \Gamma^A_{\mu\alpha} G^{\mu\alpha} = 0$, we thus find

$$\partial_i G^{iA} = -\Gamma^A_{\mu\alpha} G^{\mu\alpha} = -\Gamma^A_{\sigma\sigma} G^{\sigma\sigma} + \mathcal{O}(\lambda^2, \kappa) \tag{22}$$

because of Eq. (10). From the definition of the Christoffel symbol $\Gamma^A_{\sigma\sigma} = \vec{e}^A \cdot \mathcal{D}_\sigma \vec{e}_\sigma$, we readily find

$$\partial_i G^{iA} = -\vec{e}^A \cdot \mathcal{D}_\sigma \vec{e}_\sigma + \mathcal{O}(\lambda^2, \kappa). \tag{23}$$

Using the definitions of the cross product in Riemannian space $(\vec{v} \otimes \vec{w})_i = \frac{G_{ik}}{\sqrt{G}} \epsilon^{klm} v_l w_m$ and $(\vec{v} \otimes \vec{w})^i = G^{ik}\sqrt{G}\epsilon_{klm} v^l w^m$, we have

$$\epsilon^A{}_B e^B_i = \frac{G_{ik}}{\sqrt{G}} \epsilon^{klm} e^\sigma_l e^A_m = (\vec{e}^\sigma \otimes \vec{e}^A)_i, \tag{24}$$

and we finally obtain after substitution of Eqs. (23) and (24) in Eq. (20), and after dropping $\mathcal{O}(\lambda^2, \kappa)$ terms

$$\vec{e}^A \cdot \dot{\vec{X}} = \vec{e}^A \cdot [\gamma_1 \mathcal{D}_\sigma \vec{e}_\sigma - \gamma_2 \vec{e}_\sigma \otimes \mathcal{D}_\sigma \vec{e}_\sigma]. \tag{25}$$

This equation describes the motion of the filament in the (ρ^1, ρ^2)-space orthogonal to the filament. It is easily shown that a similar equation holds along the filament as well. Indeed, from $\vec{e}_\sigma \cdot \vec{e}^\sigma = 1$, we find that

$$\vec{e}^\sigma \cdot [\gamma_1 \mathcal{D}_\sigma \vec{e}_\sigma - \gamma_2 \vec{e}_\sigma \otimes \mathcal{D}_\sigma \vec{e}_\sigma] = 0. \tag{26}$$

On the other hand, reparametrization invariance of the filament allows us to impose a transversality condition on the filament velocity, i.e., $\vec{e}^\sigma \cdot \dot{\vec{X}} = 0$, and relying on the completeness of the set of base vectors $\{\vec{e}^A, \vec{e}^\sigma\}$, we finally obtain our main result

$$\dot{\vec{X}} = \gamma_1 \mathcal{D}_\sigma \vec{e}_\sigma - \gamma_2 \vec{e}_\sigma \otimes \mathcal{D}_\sigma \vec{e}_\sigma. \tag{27}$$

Since $\vec{e}_\sigma = \partial_\sigma \vec{X} = \mathcal{D}_\sigma \vec{X}$, we can write the equation of motion as

$$\dot{\vec{X}} = \gamma_1 \mathcal{D}^2_\sigma \vec{X} - \gamma_2 \mathcal{D}_\sigma \vec{X} \otimes \mathcal{D}^2_\sigma \vec{X}. \tag{28}$$

Discussion.—The dynamic Eqs. (28) we have obtained are fully covariant under general spatial coordinate transformations for the filament and describe Aristotelian string dynamics in curved space where curvature is due to anisotropy of the fiber orientation in cardiac tissue. In the stationary case, taking the scalar product of (28) with $\mathcal{D}_\sigma^2\vec{X}$ yields $\gamma_1|\mathcal{D}_\sigma^2\vec{X}|^2 = 0$, or if $\gamma_1 \neq 0$, we find that

$$0 = \mathcal{D}_\sigma^2 X^i = \partial_\sigma^2 X^i + \Gamma^i_{jk}\partial_\sigma X^j \partial_\sigma X^k \qquad (29)$$

where $\Gamma^i_{jk} = \frac{1}{2}D^{il}(\partial_k D_{jl} + \partial_j D_{kl} - \partial_l D_{jk})$ and $D_{ij} = (D^{-1})_{ij}$, i.e., the inverse diffusion tensor. Equation (29) is the geodesic equation, which validates the minimal principle postulated by Wellner *et al.* [11] for thin filaments. Since $\sqrt{G} = (\sqrt{\det D})^{-1}$, we can rewrite the dynamical Eqs. (28) in terms of the diffusion tensor, more commonly used in cardiac electrophysiology, as

$$\dot{X}^i = \gamma_1 \mathcal{D}_\sigma^2 X^i - \gamma_2 \frac{D^{ik}}{\sqrt{\det D}} \epsilon_{klm}\partial_\sigma X^l \mathcal{D}_\sigma^2 X^m \qquad (30)$$

with $\mathcal{D}_\sigma^2 X^i$ as in Eq. (29). Therefore, if we know the initial position of the filament $X^i(\sigma, t = 0)$ parameterized by its arclength σ, we can compute its dynamics from Eq. (30), which is just a system of one-dimensional partial differential equations. The γ_1-term in Eq. (30) plays the role of string tension and can be positive or negative depending on the properties of the cardiac tissue [15,18]. The γ_2-term is typical for string dynamics in cardiac tissue and does not occur for systems where diffusion is the same for all components, as is, for example, the case for cosmic strings in a gravitational field [13]. It plays the role of a "spin"-string tension which, for fixed endpoints of the filament, makes the string spin around the geodesic. For isotropic cardiac tissue, our equations reduce to the filament equations of Keener and Biktashev *et al.* [14,15].

Our derivation predicts $\mathcal{O}(\kappa)$ corrections due to intrinsic curvature of space, and it remains to be seen how they will affect the stationary case. These corrections will also play an important role in the dynamical case and might affect the stability of the filament, not investigated here, and potentially providing an explanation for the destabilizing effects of anisotropy that were observed computationally [8,9].

This work can be generalized in several ways. First, the constraint that $\det D$ is constant can be relaxed at the cost of an additional conservative drift term in the equation of motion. Second, higher order corrections can be calculated both in λ and κ. The first type describes rigidity of the filament under bending, while the second type describes tidal effects due to the deviation of geodesics in curved space. It would be interesting to investigate what kind of dynamical effects these tidal forces could have. Third, we have neglected the effects of twist, since in lowest order, they decouple from the filament dynamics [15]. Effects of twist have been described elsewhere and shown to potentially destabilize filaments [15,19–21]. Our approach can be applied to these studies to covariantize the equations to curved space and investigate the effects of twist in general anisotropy [22]. Finally, the approach developed in this Letter can be applied to the dynamics of wave fronts in two and three-dimensional anisotropic cardiac tissue. In three-dimensional tissue, for example, the movement of wave fronts can be described by covariant 2-branes equations in curved space [22].

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