Absence of Buckling in Nerve Fiber

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In this study we give a geometrical model which employs the smoothness of nerve fibers as differentiable curves. We show that a nerve fiber may encounter large curvature due to the possible helical bending and hence it could cause the fiber to buckle. However, its membrane structure provides a mechanism, entirely geometrical to avoid it. To overcome the challenge of emerging helix we project it into a plane.

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I. INTRODUCTION

Biological applications of geometry, especially differential geometry, is an attractive and newly expanding branch of science that explains common grounds in both disciplines [1, 2]. Differential geometry is known to find vast application in geometrical formulation of Einstein’s general relativity. The metric structure, continuity, differentiability, connections, curvature, torsion, etc. are well-known concepts that are instrumental for the formulation of gravity as a geometrical theory. The elements of geometry are lines, surfaces, volumes of any sort and their product combinations to define the underlying topology. With the advent of exotic objects such as black holes, wormholes, singularities, cosmic strings and others which make subject matters for the present gravitational theory it becomes natural to innovate similar concepts as different applications of geometry elsewhere, such as biological systems. The geometry of cells which is in essence a cylinder with circular or elliptical radial cross section can be adapted to imitate axons (as fibers) and similar structures in a biological system [3]. It is these cylindrical structures through which electric conduction occurs and the rules of diffusion between different parts take place. The walls of these cells are membranes separating different regions which are seriously effected by swellings and non-isotropic deformations. Any such geometrical deformation manifests significant changes in electric flow signal’s voltages and in the underlying inter cellular current distributions. It is natural therefore to associate neurodegenerative diseases such as Alzheimer, Parkinson, HIV etc. to such deformations.

In a recent study [3] a general cell’s equation has been derived with physical consequences whenever swellings took place in the circular cross-sectional cylindrical models. The resulting diffusion equation contains beside the geometrical term an external source term which was phrased as the geometrical diffusion term. The cross section of cell, however, was restricted only to the circular ones which didn’t cover the non-circular/elliptical shapes. Our principal aim in this study is to remove this restriction and consider more general geometric cross-sections. In other words, our cylindrical membranes will be a function of both the length of the cell as well as the angular variable as a requirement to remove the planar isotropy. The mathematical tool which we shall employ will be analogous to Ref. [3] where an appropriate Frenet-Serret triplet frame will be constructed as our reference frame. The geometrical change of the vector triplet, i.e. $\vec{T}$ = tangent vector, $\vec{N}$ = normal vector and $\vec{B} = \vec{T} \times \vec{N}$, along the curve parametrized by arc length $s$ and axial angle $\phi$ will be satisfying the standard Frenet-Serret equations [5]. The axon’s body in the nerve cell, for instance will be expressed as a linear combination of the three vectors $\vec{T}$, $\vec{N}$ and $\vec{B}$. The surface of the membrane can be represented by

$$\vec{F} = \vec{a}(s) + \nu(s, \phi)\vec{N} + \beta(s, \phi)\vec{B},$$  \hspace{1cm} (1)

where $\vec{a}(s)$ (along $\vec{T}$), $\nu(s, \phi)$ and $\beta(s, \phi)$ are functions of their arguments, which are to be determined from the geometrical ansatz model. From the first fundamental form $g_{ij}$ of the surface we derive the second fundamental form $K_{ij}$. The latter describes how a given surface is embedded in the $3-$dimensional Euclidean space in which we can embed our surface. The determinant and trace of the tensor $K_{ij}$ are useful geometrical
quantities that guide us in analyzing the geometrical structure of membranes. Beside these, the cross-sectional area of a cylindrical structure is a useful parameter in studying buckle formation. From the principles of differential geometry it is known that at a corner point where two lines (or surfaces) intersect at an angle the vectors are not differentiable, which amounts to a singular point/line. Namely, approach of tangent vectors from different directions do not match in slopes. We shall borrow the same terminology in application to the fibers to eliminate such singularities which will amount ultimately to the absence of buckling in structures such as fibers. Let us recall that the concept of singularity in physics is an infamous one and in a biological system specifically is totally non-acceptable. Geometrically we employ the bending energy of the fluid membrane \[2\] which is expressed in Gaussian and extrinsic curvatures. That must be finely-tuned in order to have a tractable model. The extremals of such an energy yield the well-known helix, for instance, wherever planar isometry is imposed. For a more general treatment, however, we admit that isotropy in this cross-section of the fiber structure must be relaxed. To this end we appeal to the Hamiltonian formalism developed by Helfrich and search for the extremal (the minimum) energy conditions. Tubular fibers with circular cross-section is relative a simple problem, however, extending this to non-circular cross-sections seems to be challenging. Although it is known that at a corner point where two lines (or surfaces) intersect at an angle the vectors are not differentiable, which amounts ultimately to the absence of buckling in structures such as fibers. Let us recall that the concept of singularity in physics is an infamous one and in a biological system specifically is totally non-acceptable. Geometrically we employ the bending energy of the fluid membrane \[2\] which is expressed in Gaussian and extrinsic curvatures. That must be finely-tuned in order to have a tractable model. The extremals of such an energy yield the well-known helix, for instance, wherever planar isometry is imposed. For a more general treatment, however, we admit that isotropy in this cross-section of the fiber structure must be relaxed. To this end we appeal to the Hamiltonian formalism developed by Helfrich and search for the extremal (the minimum) energy conditions. Tubular fibers with circular cross-section is relatively a simple problem, however, extending this to non-circular cross-sections seems to be challenging. Although this makes the ultimate aim of the present article we admit that we were able to solve the problem under restricted conditions. Organization of the paper goes as follows. In section II we introduce our mathematical formalism and study the case of circular cross-sections. Non-circular projection of a helical bending is analyzed in Section III. The paper is completed with our Conclusion in Section IV.

II. THE FORMALISM

We start with the mathematical model of an axon embedded in a three dimensional Euclidean space given by the recent work of Lopez-Sanchez and Romero \[3\]. In this model an axon is built on a three dimensional continuous curve $\vec{\alpha}(s)$ in which \(s\) is the arc length parameter of the curve. Using the above parametrization, one uses the Frenet-Serret coordinate system with the following three unit vectors

$$T = \frac{d\alpha(s)}{ds},\quad N = \frac{dT/ds}{\|dT/ds\|},\quad B = T \times N,$$

where $\vec{\alpha}$ itself is an angle measured from a given reference point. Having the surface of the axon defined and parametrized as in Eq. (3) one adopts the first fundamental conditions. Organization of the paper goes as follows. In section II we introduce our mathematical formalism and study the case of circular cross-sections. Non-circular projection of a helical bending is analyzed in Section III. The paper is completed with our Conclusion in Section IV.

\[
\begin{align*}
\frac{d}{ds} \begin{pmatrix} T \\ N \\ B \end{pmatrix} = \begin{pmatrix} 0 & \kappa(s) & 0 \\ -\kappa(s) & 0 & \tau(s) \\ 0 & -\tau(s) & 0 \end{pmatrix} \begin{pmatrix} T \\ N \\ B \end{pmatrix},
\end{align*}
\]

in which $\kappa(s)$ and $\tau(s)$ are the curve’s curvature and torsion, respectively. Following Ref. \[3\] we construct the surface of the axon, using $\vec{\alpha}(s)$ as the skeleton of the model and two new functions $\nu(s, \phi)$ and $\beta(s, \phi)$, which give the normal extensions to the skeleton of the axon’s body expressed by

$$\vec{F} := \vec{\alpha}(s) + \nu(s, \phi) N + \beta(s, \phi) B.$$

Herein both $\nu(s, \phi)$ and $\beta(s, \phi)$ are analytic in terms of $s$ and $\phi$ whereas $\phi$ itself is an angle measured from a given reference point. Having the surface of the axon defined and parametrized as in Eq. (3) one adopts the first fundamental form given by

$$g_{ij} = \begin{pmatrix} E & F \\ F & G \end{pmatrix},$$

where $E = \frac{\partial \vec{F}}{\partial s} \cdot \frac{\partial \vec{F}}{\partial s}$, $G = \frac{\partial \vec{F}}{\partial \phi} \cdot \frac{\partial \vec{F}}{\partial \phi}$ and $F = \frac{\partial \vec{F}}{\partial s} \cdot \frac{\partial \vec{F}}{\partial \phi}$ are given by

$$E = (1 - \kappa(s) \nu)^2 + (\nu_s - \tau(s) \beta)^2 + (\beta_s + \tau(s) \nu)^2,$$

$$F = (\nu_s - \tau(s) \beta) \nu_{,\phi} + (\beta_s + \tau(s) \nu) \beta_{,\phi}$$

and

$$G = (\nu_{,\phi})^2 + (\beta_{,\phi})^2,$$

in which \((\cdot)_x = \frac{\partial (\cdot)}{\partial x}\). For the parametrized surface \(\mathbf{F}\) one defines

\[
\hat{n} = \frac{\partial \mathbf{F} / \partial s \times \partial \mathbf{F} / \partial \phi}{\| \partial \mathbf{F} / \partial s \times \partial \mathbf{F} / \partial \phi \|}
\]  

(9)

to be the unit normal vector at any point of the surface explicitly given by

\[
\hat{n} = \frac{1}{g} \left[ \left( \nu_s \beta_\phi - \beta_s \nu_\phi - \frac{1}{2} \tau (\nu^2 + \beta^2)_\phi \right) \mathbf{T} - (1 - \kappa \nu) \beta_\phi \mathbf{N} + (1 - \kappa \nu) \nu_\phi \mathbf{B} \right],
\]

(10)
in which \(g = \det (g_{ij}) = EG - F^2\). The element of area on the surface is given by

\[
dA = dsd\phi \sqrt{g} = dsd\phi \sqrt{ \left( \nu_s \beta_\phi - \beta_s \nu_\phi - \frac{1}{2} \tau (\nu^2 + \beta^2)_\phi \right)^2 + (1 - \kappa \nu)^2 \left( \beta_\phi^2 + \nu^2_\phi \right) }.
\]

The second fundamental form i.e., the extrinsic curvature tensor is defined by

\[
K_{ij} = \frac{\partial^2 \mathbf{F}}{\partial u^i \partial u^j} \cdot \hat{n},
\]

in which \(u^i \in \{ s, \phi \} \). The general expression of the curvature tensor’s components are too long to be given here. Our ultimate reason is to calculate the extrinsic curvature tensor and to investigate the behavior of the two scalar invariants of the surface, namely the Gaussian curvature and the total curvature which are given respectively by \(K = \det K_i^i\) and \(H = K^i_i = \text{Tr} K_i^j\). We define the smooth surface to have analytic / differentiable \(K\) and \(H\).

To make our analysis practical we consider some specific, yet important cases. The first case which has also been considered in Ref. [3] is the circular cross sectional axons defined by \(\nu (s, \phi) = R(s) \cos \phi\) and \(\beta (s, \phi) = R(s) \sin \phi\) in which \(R(s)\) refers to the radius of the circular cross section.

**A. Circular Cross Section**

The Gaussian and total curvature for this circular cross sectional axon are found to be

\[
K = \frac{2 \left( -\omega^2 R'' + ((3\omega + 1) \cos \phi - \kappa R) \kappa R'^2 + R \omega (\kappa' \cos \phi + \kappa \tau \sin \phi) R' + \kappa \omega^2 \cos \phi \right)}{R (R^2 + \omega^2)^2},
\]

(12)

and

\[
H = \frac{\omega R R'' - (2 + 3\omega) R'^2 - R^2 (\kappa' \cos \phi + \tau \kappa \sin \phi) R' - \omega^2 (2\omega + 1)}{R (R^2 + \omega^2)^{3/2}},
\]

(13)
in which \(\omega = R \kappa \cos \phi - 1\) and a prime stands for the derivative with respect to \(s\). Let’s add that Eq. (11) is the generalized expression of Eq. (15) of Ref. [3] where \(R(s) = R_0 = \text{const.}\).

As mentioned above the smooth surface implies that the Gaussian and total curvature are finite everywhere on the surface. Hence, Eq. (11) and Eq. (12) manifestly imply that to have the surface differentiable / analytic everywhere a nonzero \(R'(s)\) is a sufficient condition but not necessary indeed. In other words, if \(R'(s)\) is nonzero at a point then both \(H\) and \(K\) are finite but if \(R'(s)\) vanishes at a point then \(\omega\) must be nonzero at that point. This, however, imposes that \(R \kappa < 1\). We note that, imposing the strong constraint \(R \kappa < 1\) is also sufficient to have the manifold to be differentiable, but this is not necessary. Section B considers the particular case as follows.

**B. \(R(s) = R_0 = \text{const.}\)**

Now, let’s assume that \(R(s) = R_0\) and \(R_0 \kappa \geq 1\) where one finds

\[
K = -\frac{\kappa (s) \cos \phi}{R_0 \omega},
\]

(14)
and

\[ H = \frac{(2\omega + 1)}{R_0\omega}, \]  

which are not analytic at the critical $\phi$ where $\omega = R_0\kappa \cos\phi - 1 = 0$, and consequently the axon buckles at those points. Based on the fact that the Gaussian curvature of the surface of the axon is a continuous function of $\phi$ (provided $R_0\kappa(s) < 1$), it admits two local extrema at $\phi = 0$ and $\phi = \pi$ such that

\[ K|_{\phi=0} = -\frac{\kappa(s)}{R_0(1 - R_0\kappa(s))} \]  

and

\[ K|_{\phi=\pi} = \frac{\kappa(s)}{R_0(1 + R_0\kappa(s))}. \]

Furthermore, we expect the two extremals to occur at points $\phi = 0$ and $\phi = \pi$. Hence, one finds out that the reference of $\phi$ is the point $\phi = 0$ as the innermost point toward the center of curvature. When we relax the constraint on $R_0\kappa(s)$ we observe that for the case $R_0\kappa(s) = 1$ there would be only a single point i.e., $\phi = 0$ where the axon buckles but for $R_0\kappa(s) > 1$ there are two points where the Gaussian curvature diverges which are given by

\[ \phi = \cos^{-1}\left(\frac{1}{R_0\kappa(s)}\right) = \pm \phi_b, \]

in which $0 < \phi_b < \frac{\pi}{2}$ and in the limit where $R_0\kappa(s)$ gets very large the value of the angle $\phi_b$ approaches to $\frac{\pi}{2}$. We note that the physical interpretation of $\kappa(s) \geq \frac{1}{R_0}$ is that the center of curvature of the curve $\alpha(s)$ is inside the body of the axon.

If the surface of the axon were not made of the lipid membrane, the actual situation would be as we described above. But the fact is that the lipid membrane of the axon leaves its radius to be a function of $\phi$ in the vicinity of the large curvature of the curve $\alpha(s)$ (i.e., the place where $\kappa(s)$ is very large). Hence from Eq. (11) one finds that $K$ remains finite and this results in a smooth transition without a buckling. It is remarkable to observe that the term which rescues the surface from buckling is not $R$ itself but its first derivative i.e., $R'$. Therefore there would not be any restriction on the radius of the axon in general, no matter what would be their passage condition within the body. In the following section we consider the case of an axon with non-circular cross section which generalizes the analysis of Ref. [3].

### III. Curve of Bending

In this section we assume that the axon’s radius is constant i.e., $R(s) = R_0$ and the axon’s curvature satisfies the condition $\kappa(s) R_0 < 1$. Upon these assumptions we look for the equation of the curve which joins two straight line parts of the axon.

The total energy of a lipid bilayer is expressed by the Helfrich Hamiltonian (see Ref. [6])

\[ E = \int dA \left\{ \sigma + \frac{1}{2} k_1 (H - H_0)^2 + k_2 K \right\}, \]

where $\sigma$ is the surface tension, $H_0$, $H$ and $K$ are spontaneous, total and Gaussian curvatures, respectively, $k_1$ and $k_2$ are bending and the Gaussian curvature moduli. The integral is taken over the whole surface of bilayer membrane. Therefore, as can be observed from this Hamiltonian, the energy of a lipid membrane is a function of bilayer’s geometrical / topological properties, emerged in shape of its curvatures. Here $\sigma$ is assumed to be an independent thermodynamic surface tension, which reflects the chemical potential of lipids, and therefore is taken as a constant. Also, it is worth mentioning that except for some certain types of lipid membranes [7, 8] in case the two sides of a bilayer are not distinguishable, the spontaneous curvature $H_0$ vanishes [9]. In the following sections, when the variation of Helfrich Hamiltonian is evaluated, $\sigma$ is treated as a constant and the sides of the membrane are assumed indistinguishable. Upon these assumptions and our results in previous section i.e.,

\[ K = \frac{\kappa(s) \cos\phi}{R_0(R_0\kappa(s) \cos\phi - 1)} \]  

(20)
and
\[ H_T = \frac{1 - 2R_0 \kappa(s) \cos \phi}{R_0 (1 - R_0 \kappa(s) \cos \phi)} \]  

with the areal element
\[ dA = dsd\sqrt{g} = dsd\phi R_0 (1 - R_0 \kappa(s) \cos \phi) \]

one finds the bending energy of the axon given by
\[ E = \int_0^s ds' \int_0^{2\pi} \left( -\xi_1 R_0^2 \kappa(s')^2 \cos^2 \phi + \frac{2\xi_2 \kappa(s') \cos \phi + \xi_3}{2R_0 (R_0 \kappa(s') \cos \phi - 1)} \right) d\phi, \]

in which
\[ \xi_1 = R_0^2 (2\sigma + k_1 H_0^2) + 2R_0 (k_2 - 2k_1 H_0) + 4k_1, \]
\[ \xi_2 = R_0^2 (2\sigma + k_1 H_0^2) + R_0 (k_2 - 3k_1 H_0) + 2k_1 \]

and
\[ \xi_3 = -R_0^2 (2\sigma + k_1 H_0^2) + 2k_1 R_0 H_0 - 2k_1. \]

The integral on $\phi$ can be calculated by using the Residual theorem from complex analysis. Let’s introduce
\[ I = \int_0^{2\pi} \frac{-\xi_1 R_0^2 \kappa(s')^2 \cos^2 \phi + 2\xi_2 \kappa(s') \cos \phi + \xi_3}{2R_0 (R_0 \kappa(s') \cos \phi - 1)} d\phi \]

such that a change of variable of the form $z = e^{i\phi}$ yields
\[ I = \frac{i}{4} \int_C \frac{\xi_1 R_0^2 \kappa(s')^2 (1 + z^2) - 4\xi_2 R_0 \kappa(s') z (1 + z^2) - 4\xi_3 z^2}{R_0 z^2 (R_0 \kappa(s') (1 + z^2) - 2z)} d\phi, \]

in which the contour $C$ is the unit circle. This integral is equal to
\[ I = 2i \left( 2\pi i \sum a_{-1} \right), \]

where $a_{-1}$ are the residue of the poles inside contour $C$. There are three poles located at $z_{01} = 0$, $z_{02} = \frac{1 - \sqrt{1 - e^2}}{e}$ and $z_{03} = \frac{1 + \sqrt{1 - e^2}}{e}$ which upon the choice $e = R_0 \kappa(s') < 1$, only $z_{01}, z_{02}$ of order $m = 2$ and $m = 1$, respectively, are located inside the contour with residues
\[ a_{-1} (z_0 = 0) = \frac{i (\xi_1 - 2\xi_2)}{2R_0} \]

and
\[ a_{-1} \left( z_0 = \frac{1 - \sqrt{1 - e^2}}{e} \right) = -\frac{i (\xi_1 - 2\xi_2 - \xi_3)}{2R_0 \sqrt{1 - e^2}}, \]

respectively. Finally we find
\[ I = \frac{2\pi}{\sqrt{1 - e^2}} \]

and consequently the energy integral reduces to
\[ E = \pi \int_0^s ds' \left\{ \frac{k_1}{R_0 \sqrt{1 - R_0^2 \kappa(s')^2}} + \left( R_0 (2\sigma + k_1 H_0^2) - 2k_1 H_0 \right) \right\}. \]
\( E \) is a functional depending on the function \( \kappa(s') \) only such that we are looking for a specific \( \kappa(s') \) which makes the functional \( E \) stationary. Using the calculus of variation or the Euler equation we find

\[
\kappa(s') = \kappa_0, \tag{34}
\]

in which \( \kappa_0 \) is a constant. Hence, the curve of the bending is a constant-curvature curve. Here the boundary conditions are imposed by the two curves joined to this constant-curvature at the initial and final points of the curve.

Let’s assume that the curve is planar and joins two straight parts of the axon located on the same plane as projection of the curve itself. In this case one finds the total energy to be

\[
E_{\text{Planar}} = \pi s \left\{ \frac{k_1}{R_0 \sqrt{1 - \frac{R_0^2}{r^2}}} + \left( R_0 \left( 2\sigma + k_1 H_0^2 \right) - 2k_1 H_0 \right) \right\}, \tag{35}
\]

in which \( s \) is the arc length of the circle of radius \( r = \frac{1}{\kappa_0} \). Hence, \( s = \psi r \), where \( \psi \) is the angle of total bending and is a constant dictated by the initial conditions. As a result we find the total energy of the curve to be

\[
E_{\text{Planar}} = \pi \psi r \left\{ \frac{k_1}{R_0 \sqrt{1 - \frac{R_0^2}{r^2}}} + \left( R_0 \left( 2\sigma + k_1 H_0^2 \right) - 2k_1 H_0 \right) \right\}, \tag{36}
\]

where we have used \( \kappa_0 = \frac{1}{r} \). The final step is to find \( r \) such that \( E_{\text{Planar}} \) is stationary. Here \( E_{\text{Planar}} \) is a function of \( r \) only and upon \( \frac{dE_{\text{Planar}}}{dr} = 0 \) one finds the radius of the bending. Two particular cases are considered in the sequel.

**A. Case 1**

Let’s assume also that

\[
R_0 \left( 2\sigma + k_1 H_0^2 \right) - 2k_1 H_0 = 0 \tag{37}
\]

which yields

\[
E_{\text{Planar}} = \frac{k_1 \pi \psi r}{R_0 \sqrt{1 - \frac{R_0^2}{r^2}}} \tag{38}
\]

whose minimum occurs at

\[
r = \sqrt{2}R_0. \tag{39}
\]

Therefore, we have found the radius of the circle under which the axons bend such that the bending energy of the curling becomes an extremum which can easily be shown to be a minimum.

**B. Case 2**

For a more general case where

\[
R_0 \left( 2\sigma + k_1 H_0^2 \right) - 2k_1 H_0 = \lambda \neq 0 \tag{40}
\]

the stationary radius is found to be

\[
r = R_0 \sqrt{\frac{\sqrt{4k_1^2 \alpha}}{6 (R_0^2 \lambda^2 - k_1^2)} - \frac{(3R_0^2 \lambda^2 - 4k_1^2) k_1^2 \sqrt{16}}{6 (R_0^2 \lambda^2 - k_1^2) \sqrt{4k_1^2 \alpha}} + \frac{3R_0^2 \lambda^2 - 4k_1^2}{3 (R_0^2 \lambda^2 - k_1^2)}}, \tag{41}
\]

in which

\[
\alpha = (3\lambda^3 R_0^3 - 3\lambda R_0 k_1^2) \sqrt{3} \sqrt{27R_0^2 \lambda^2 - 32k_1^2 + 27R_0^4 \lambda^4 - 45R_0^2 \lambda^2 k_1^2 + 16k_1^4}. \tag{42}
\]

Since we assumed a priori that \( \lambda \neq 0 \), we don’t take the limit \( \lambda \to 0 \) in this particular solution.
IV. CONCLUSION

In a rough analogy nerve fibers are tubes with cylindrical topology. Since physics aims to describe every kind of systems, including biological ones, in mathematical terms, differential geometry becomes the right tool for this purpose. In order to have buckling in the fibers these must be singularities in the underlying geometrical structure. Divergence in the curvature scalars is not the only criterion that determines such singularities in the present problem. Instead, differentiability analysis for each curve on the tubular manifold determines the regularity and therefore absence of buckling. Recall that differentiability implies continuity but the converse statement need not be true. Derivative of radius function in terms of arclength / angle exists everywhere, which can be interpreted as an indication of regularity, or absence of buckling. We aim fibers with non-circular cross sections and we show, with reference to the minimal energy of the Helfrich Hamiltonian, that fibers don’t buckle. In doing this we project the helix structure into the plane and investigate the continuity of the tangent vectors everywhere. In particular examples we attain results, leaving more general cases to future studies in which possible double-helix structures may also be taken into account.

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