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Orientational Order within Biological Membranes

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Abstract – *Recently developed approaches analyzing the degree of in-plane orientational ordering are compared. The first one originates from an intrinsic anisotropic shape of membrane constituents, based on which the mismatch curvature tensor $\underline{M}$ is introduced. The second one originates from the nematic tensor order parameter $\underline{Q}$ reflecting average local degree of orientational ordering. Based on these tensors free energy of systems are derived taking into account symmetry allowed combinations of tensors. From both approaches the degree of local orientational ordering is determined as a function of membrane shape. In the paper we discuss relevance of these approaches.*

Keywords: *Vesicles, Orientational Order, Topological Defects*

Nomenclature

a_0	Surface area of a membrane
A_0, B, k	Material constants
$\underline{C}$	The effective curvature tensor
$\underline{C}_m$	The intrinsic curvature tensor
C_1, C_2	The principal curvatures
C_{1m}, C_{2m}	The intrinsic principal curvatures
D	The curvature deviator
D_m	The intrinsic curvature deviator
Det	Determinant
$\vec{e}$	A temporal local orientation of a nanodomain
$\{\vec{e}_1, \vec{e}_2\}$	The unit vectors of $\underline{C}$ eigenframe
$\{\vec{e}_{1m}, \vec{e}_{2m}\}$	The unit vectors of $\underline{C}_m$ eigenframe
f_c	The curvature free energy density
f_o	The orientational free energy density
F_o	The orientational free energy
g	The genus of the surface
H	The mean curvature
H_m	The mean intrinsic curvature
$\underline{I}$	The Identity tensor
I_n	The Bessel function of n-th order
k_B	The Boltzmann constant
k_1, k_2	The elastic constants
K	The total Gaussian curvature
m	The topological charge
m_{tot}	The total sum of topological charges
$\vec{n}$, $\vec{n}_\perp$	The orthogonal unit vectors and eigenvectors of $\underline{Q}$
$\underline{M}$	The mismatch curvature tensor
$\underline{R}$	The rotation matrix
s	A distance along meridians
$\underline{Q}$	The nematic tensor order parameter
Q	The partitition function of a single nanodomain
x	The measurement of differences between membrane principal curvatures
T	Temperature
T_c	The phase transition temperature between orientationally disordered and ordered phase
Tr	Trace
w	The elastic energy density
w_0	The minimal possible value of w
η	The average orientational degree of anisotropic nanodomains
$\vec{v}$	The outer unit normal
φ	The azimuthal angle
λ	The degree of ordering
χ	The Euler-Poincare characteristic
ξ	The order parameter correlation length
ω	The angle between the principal axes of tensors $\underline{C}_m$ and $\underline{C}$
θ	The angel between $\vec{e}$ and $\vec{n}$
ΔF_c	The free energy of the flexible membrane nanodomain
∇_s	The surface gradient operator

I. Introduction

Influence of various parameters on biological membrane structure is of interest for years. Membrane shape changes are linked with various cellular processes of vital biological importance.

Structural reshaping might be provoked by varying external conditions (temperature, pressure, concentration…), changes in effective elasticity by adhering nanoparticles or colloids, by onset of orientational order within a biological membrane, or by some other means.

A membrane might exhibit an in-plane membrane surface orientational ordering.

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Such ordering might arise due to tilting of lipid molecules relative to the normal of a membrane or in-plane averaged orientational ordering of lipid molecules due to their intrinsic anisotropic shape [1]-[3]. Besides the lipids and dimeric detergents the origin of anisotropic membrane components (nanodomains) might be also membrane embedded or membrane attached proteins [4]-[7].

Pioneering study of the impact of in-plane ordering on membrane shape was performed by MacKintosh and Lubensky [8]. Their mean-field theory suggested the coupling between in-plane ordering of membrane anisotropic components and membrane curvature could trigger membrane shape transitions. Further experimental and theoretical works demonstrated a rich variety of such changes.

For example, it was demonstrated in [6] and [9] that strongly anisotropic dimeric cationic amphiphiles induce tubular membrane budding while isotropic amphiplhiles promote spherical membrane budding. Further studies [10] showed that in-plane ordering might suppress vesicle structures exhibiting neck-type profiles. On the other hand saddle-like membrane components may stabilize highly curved membrane necks [2],[5].

If tangential orientational ordering exists within a closed two-dimensional system then topological defects (TDs) in orientational order could unavoidable appear due to topological reasons [11]. The main topological characteristic of a topological defect is its topological charge m. The total sum of topological charges m_{tot} of all defects residing on a closed surface is a conserved quantity and is determined by a theorem of Poincare [12]. It claims that m_{tot} must equal the Euler-Poincare characteristic $\chi=2(1-g)$ of the surface, which is determined by the total Gaussian curvature K of the surface.

The integer g is the genus of the surface, reflecting to the number of "handles" that the surface contains. For example, an object with the spherical topology corresponds to $g=0$, therefore $m_{tot}=2$.

Furthermore, spatial dependence of K could have strong impacts on position and even number of defects. It was demonstrated [13] that positive (negative) K attracts defects with positive (negative) topological charge m. It was also suggested that surfaces exhibiting both negative and positive Gaussian curvature might trigger unbinding of topological pairs defect - antidefects. The former and the latter correspond to $m>0$ and $m<0$, respectively.

In this paper we present and compare two recently developed mesoscopic approaches which consider impact of membrane curvature on degree of in-plane orientational ordering. The plan of the paper is as follows.

In Sec. II we present the approach based on the mismatch curvature tensor. In Sec. III the modeling based on tensor orientational order parameter is presented. In the last section applicability of both approaches are discussed.

II. Mismatch Curvature Tensor Approach

II.1. Free Energy Density

It is assumed that a thin membrane consists of equal nanodomains. They are treated as two-dimensional anisotropic flexible plates of area a_0 and their intrinsic shape is determined by the intrinsic curvature tensor commonly labeled by $\underline{C}_m$. The latter reflects average anisotropic character of membrane constituents [1],[2],[3],[9]. The interaction between nanodomains determines an actual membrane shape, which is locally given by the effective curvature tensor $\underline{C}$. These tensors are in their corresponding eigenframes determined by unit vectors $\{\vec{e}_1, \vec{e}_2\}$ and $\{\vec{e}_{1m}, \vec{e}_{2m}\}$ expressed as:

$$\underline{C}_m = C_{1m}\left(\vec{e}_{1m}\otimes\vec{e}_{1m}\right)+C_{2m}\left(\vec{e}_{2m}\otimes\vec{e}_{2m}\right) \tag{1}$$

$$\underline{C} = C_1\left(\vec{e}_1\otimes\vec{e}_1\right)+C_2\left(\vec{e}_2\otimes\vec{e}_2\right) \tag{2}$$

Here $\otimes$ marks the tensorial product and C_{1m}, C_{2m}, C_1, C_2 stand for principal curvatures. Both eigenframes are in general oriented along different directions. The miss-alignment of these tensors is quantified by the mismatch curvature tensor [2], [3], [9]:

$$\underline{M} = \underline{R}\underline{C}_m\underline{R}^{-1}-\underline{C} \tag{3}$$

The rotation matrix:

$$\begin{aligned}\underline{R} = &\left(\vec{e}_1\otimes\vec{e}_1+\vec{e}_2\otimes\vec{e}_2\right)cos\,\omega+\\ &+\left(\vec{e}_2\otimes\vec{e}_1-\vec{e}_1\otimes\vec{e}_2\right)sin\,\omega\end{aligned} \tag{4}$$

determines the mutual rotation of the principal axes of tensors $\underline{C}_m$ and $\underline{C}$ by an angle ω in the tangent plane of the membrane. It is assumed that the system aims to locally minimize value of $\underline{M}$ and $\underline{M}$ represents the key local quantity affecting the elastic energy density w per surface area a_0 of a membrane. In the lowest approximation the $w(\underline{M})$ dependence is expressed as a Taylor expansion up to the second order in powers of invariants of $\underline{M}$:

$$w = w_0+\frac{k_1}{2}\left(Tr\underline{M}\right)^2+k_2\ Det\underline{M} \tag{5}$$

here $Det\underline{M}$ and $Tr\underline{M}$ stand for determinant and trace of $\underline{M}$, respectively, while k_1 and k_2 are elastic constants.

The requirement $w\geq 0$ imposes inequalities [14]:

$$k_2<0,\quad k_1>-\frac{k_2}{2} \tag{6}$$

The quantity w_0 equals minimal possible value of w.

For simplicity we henceforth set $w_0=0$ and $k_m\equiv k_1=|k_2|$. It follows:

$$w = k_m \begin{pmatrix} (H - H_m)^2 + \\ + \left(D^2 - 2DD_m \cos(2\omega) + D_m^2 \right) \end{pmatrix} \quad (7)$$

where the mean curvature H, mean intrinsic curvature H_m, curvature deviator D and intrinsic curvature deviator D_m are defined as:

$$H = \frac{C_1 + C_2}{2}, H_m = \frac{C_{1m} + C_{2m}}{2}, \quad D = \frac{|C_1 - C_2|}{2}, D_m = \frac{|C_{1m} - C_{2m}|}{2} \quad (8)$$

For D_m=0 (i.e. C_{1m}=C_{2m}) the expression Eq. (7) transforms into the Helfrich isotropic energy [15].

The free energy of the flexible membrane nanodomain ΔF_c can be expressed as:

$$\Delta F_c = f_c a_0 = -k_B T \, lnQ \quad (9)$$

where the subcript c refers to the curvature contribution.

The quantities f_c, k_B and T stand for curvature free energy density, Boltzmann constant and temperature, respectively. The partitition function of a single nanodomain is given by:

$$Q = \int_0^{2\pi} e^{-\frac{wa_0}{k_B T}} d\omega \quad (10)$$

Taking into account Eq. (7) it follows:

$$f_c = k_m \left((H - H_m)^2 + \left(D^2 + D_m^2 \right) \right) + - k_B T \, ln(I_0 \left(\frac{2k_m a_0 DD_m}{k_B T} \right) \quad (11)$$

and I_n labels the Bessel function of n-th order. Average orientational degree of anisotropic nanodomains can be obtained via equation:

$$\eta = \langle \cos(2\omega) \rangle = \frac{1}{Q} \int_0^{2\pi} \cos(2\omega) e^{\frac{-wa_0}{k_B T}} d\omega \quad (12)$$

The brackets <...> mark ensemble averaging and η plays the role of order parameter.

It follows:

$$\eta = \frac{I_1(x)}{I_0(x)} \quad (13)$$

$$x = \frac{2k_m a_0 DD_m}{k_B T} \quad (14)$$

II.2. Degree of Ordering

In Fig. 1 we plot $\eta(x)$ dependence, where x measures differences between membrane principal curvatures. In the high temperature regime (x∼0, i.e. $2k_m a_0 DD_m >> k_B T$) one obtains $\eta = \langle \cos(2\omega) \rangle \sim 0$ reflecting absence of orientational ordering. On the other hand in the low temperature regime (x∼1, i.e. $2k_m a_0 DD_m << k_B T$) it follows $\langle \cos(2\omega) \rangle^{(low)} \sim 1$, revealing perfect alignment of nanodomain eigenframe along the curvature eigenframe.

Furthermore:

$$f_c^{(low)} = k_m \left((H - H_m)^2 + (D - D_m)^2 \right) \quad (15)$$

The superscript $^{(low)}$ marks the low temperature regime. By comparing Eq. (7) and Eq. (15) we see that the latter expression corresponds to the situation where w exhibits minimal value, corresponding to "perfectly" oriented nanodomains.

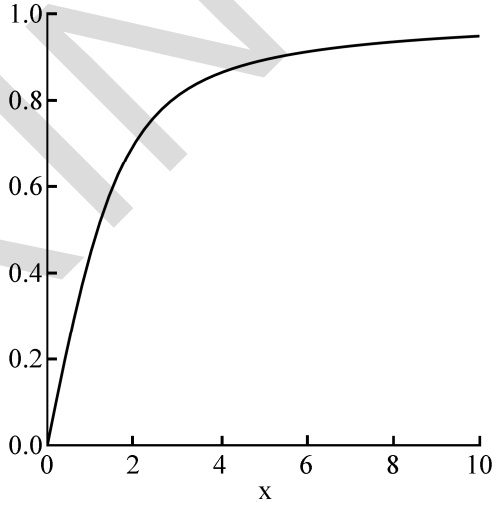


Fig. 1. Degree of local ordering η as a function of $x = 2k_m a_0 DD_m/(k_B T)$

III. Nematic Tensor Order Parameter Approach

III.1. Free Energy Density

In the following we describe minimal mesoscopic theory describing orientational in-plane ordering of a membrane in terms of nematic tensor order parameter for a given membrane shape. Details are given in [16].

We assume that nanodomains lie on the local membrane tangent plane the orientation of which is given by its the outer unit normal $\vec{\nu}$. A temporal local orientation of a nanodomain is given by the unit vector $\vec{e}$. The corresponding tensor order parameter is defined as [16]:

$$\underline{Q} = \left\langle \vec{e} \otimes \vec{e} - \frac{1}{2} \left(\underline{I} - \vec{\nu} \otimes \vec{\nu} \right) \right\rangle \quad (16)$$

where $\underline{I}$ stands for the Identity tensor and $Tr\underline{Q}=0$.

Alternatively, we can express the order parameter as

$$\underline{Q}=\lambda\left(\vec{n}\otimes\vec{n}-\vec{n}_{\perp}\otimes\vec{n}_{\perp}\right) \tag{17}$$

The orthogonal unit vectors $\vec{n}$ and $\vec{n}_{\perp}$ are eigenvectors of $\underline{Q}$, where $\vec{v}=\vec{n}\times\vec{n}_{\perp}$. The eigenvalue λ corresponding to the eigenvector $\vec{n}$, also referred to as nematic director field, can be expressed as:

$$\lambda=\vec{n}\cdot\underline{Q}\vec{n}=\left\langle\left(\vec{e}\cdot\vec{n}\right)^2-\frac{1}{2}\right\rangle=\frac{\left\langle cos\left(2\theta\right)\right\rangle}{2} \tag{18}$$

where $\vec{e}\cdot\vec{n}=cos\theta$. Furthermore, $\vec{n}_{\perp}\cdot\underline{Q}\vec{n}_{\perp}=-\lambda$. We relate $\vec{n}$ to positive value of λ, where $\lambda\in[0,1/2]$.

The corresponding orientational free energy density f_o can be expressesd as a Landau-type expansion in terms of $\underline{Q}$ taking into account symmetry allowed terms. In the lowest order approximation it is given by:

$$f_0=\frac{A_0 t}{2}Tr\underline{Q}^2+\frac{B}{2}\left(Tr\underline{Q}\right)^2+\frac{k}{2}\left|\nabla_s\underline{Q}\right|^2 \tag{19}$$

here $t=((T-T_c)/T_c$ stands for the reduced temperature, T_c describes the phase transition temperature between orientationally disordered and ordered phase, A_0, B, k are material constants and ∇_s marks the surface gradient operator.

In elastically undistorted bulk system the equilibrium degree of ordering in orientationally ordered phase is given by:

$$\lambda_b=\lambda_0\sqrt{-t} \tag{20}$$

where $\lambda_0=\sqrt{A_0/(2B)}$. The competition between the condensation (the first two terms in Eq. (19)) and elastic (the last term in Eq. (19)) free energy contributions defines order parameter correlation length of the system, which is roughly given by:

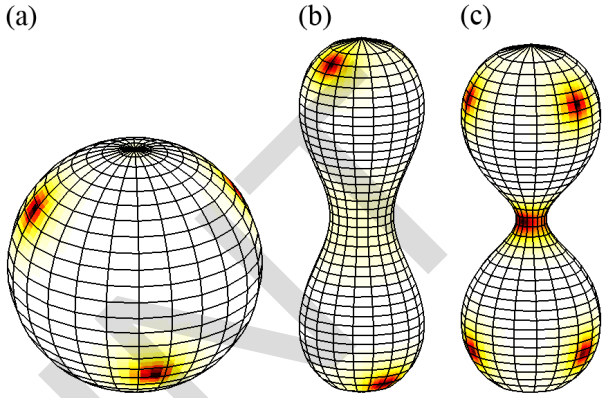
$$\xi\sim\frac{\xi_0}{\sqrt{|t|}} \tag{21}$$

and $\xi_0\sim\sqrt{k/A_0}$.

III.2. Degree of Ordering

In the following we show some qualitatively different orienational textures on membranes exhibiting spherical topology which are calculated by minimizing the orientational free energy $F_0=\oint f_0 da$ for a given membrane shape.

The integral is carried over the total surface of the membrane and da stands for an infinitesimal surface area. For simplicity we restrict to axially symmetric membrane. Technical details are given in [16]. In Fig. 2 we plot three different membrane shapes where degree of ordering λ is superimposed. Regions with white color exhibit degree of ordering comparable to λ_b. Within colored regions the degree of orientational ordering is essentially melted. These regions reveal existence of topological defects (TDs).



Figs. 2. Two-dimensional plot of λ superimposed on membrane shapes possessing spherical topology. Colored points reveal existence of topological defects

Relative position of defects, their number and core structure is better visualized by plotting degree of ordering in the (s, φ) plane, see Figs. 3. Here φ is the azimuthal angle and s measures a distance along meridians (the upper point in structures correspond to s=0 and the lower point to the length s_0). The corresponding director profiles are depicted in Figs.4.

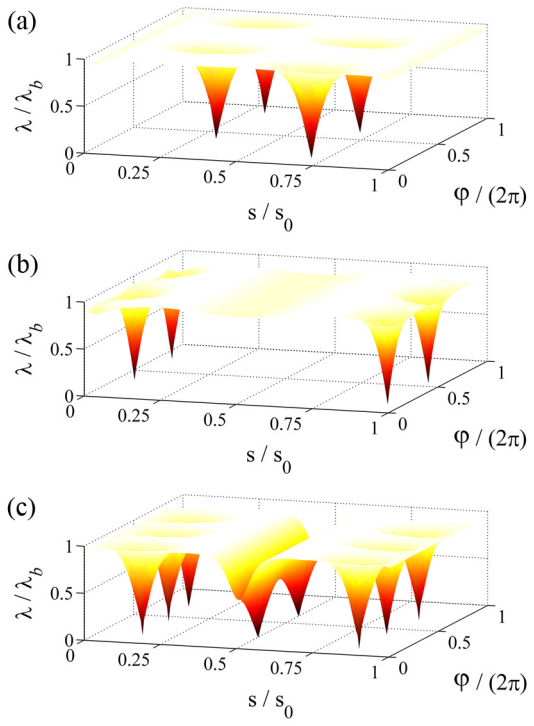
Within a spherical membrane (Figs. 2(a), 3(a), 4(a)) there are four TDs exhibiting topological charge m=1/2. These defects repeal each other and consequently they fall at the vertices of a tetrahedron in order to maximize their mutual separation [17].

Structures shown in Fig. 2(b) and Fig. 2(c) exhibit spatially dependent Gaussian curvature K. The latter is known to have similar impact on topological defects as electric field on electric charges. In Fig. 2(b) the central region exhibits K<0.

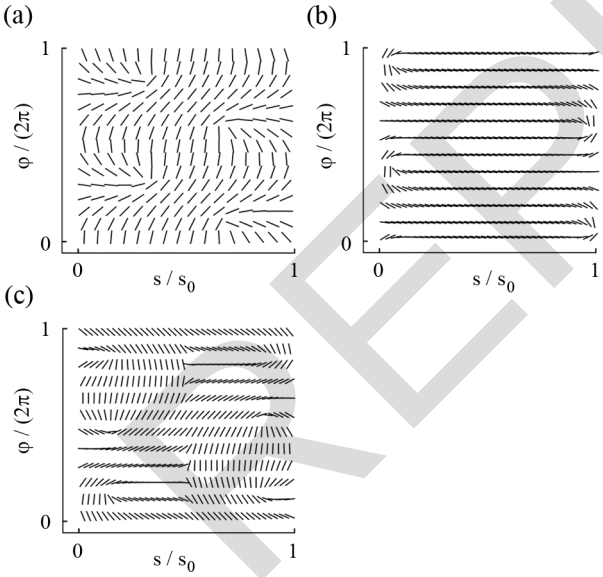
Consequently, TDs bearing m=1/2>0 are pushed towards the poles of membranes. In structure shown in Fig. 2(c) elastic distortions in region where K<0 is strong enough to trigger unbinding of TDs. Two additional pairs of defects appear, where each pair consist of TDs bearing m=1/2 and m=-1/2. Defects with m=1/2 tend to assemble in the region exhibiting maximal value of K.

Their relative position compromises this tendency and their mutual repulsion.

On the other hand defects with m=-1/2 assemble at the neck of the structure shown in Fig. 2(c), which exhibits most negative value of K.



Figs. 3. Two-dimensional plot of λ in the (φ,s) plane. There are four topological defects in (a) and (b) and eight in (c). The core size of defects is roughly given the by order parameter correlation length ξ



Figs. 4. Two-dimensional plots of director profiles. Configurations in (a) and (b) posses four topological defects exhibiting topological charges m=1/2. In (c) there are six defects with m=1/2 and two defects with m=-1/2. In all cases the total topological charge of structures equals two due to membrane's spherical topology

IV. Conclusion

In the paper we present two different approaches considering the impact of membrane's shape on its in-plane orienational ordering. Both assume that building blocks (nanodomains) exhibit the so called head-to-tail symmetry. The first approach [2] is derived at a semi-microscopic level, where essential elastic property of an average nanodomain is given by its intrinsic curvature tensor. The latter determines locally favored membrane shape. Deviations from this reference are measured by the mismatch tensor $\underline{M}$, the symmetry invariants of which determine the membrane interaction energy w. The latter depends on the relative angle ω between the intrinsic membrane curvature eigenframe and actual membrane curvature eigenframe.

Statistical averaging yields average degree of local ordering $\eta=\langle\cos(2\omega)\rangle$ which depends on dimensionless quantity $x=2k_m a_0 D D_m/(k_B T)$. In case of D=0 or D_m=0 or $k_B T\rightarrow\infty$ it follows m=0, suggesting absence of preferred local field and consequently absence of ordering. On the other hand in the low temperature limit and for cases where both D and D_m>0 a local filed is present, giving rise to finite degree of local ordering. Note that positive values of curvature deviators reflect difference of local principal curvatures. Using this approach we estimate only impact of local membrane conditions on average orientation of a nanodomain constituting a membrane. Furthermore, from the partition function curvature membrane free energy is derived. This approach does not take into account global topology of the problem. It only identifies semi-microscopic origin of local fields affecting in-plane ordering. In the second approach [16] one originates from local tensor order parameter $\underline{Q}$, revealing average degree of ordering at mesoscopic level. The corresponding elastic energy is constructed via Tylor expansion in $\underline{Q}$ taking into account symmetry allowed terms. This approach takes into account global topology of the system. Derivation presented in [16] assumes fixed membrane shape. Furthermore, because of its mesoscopic character it does not take into account microscopic details. To simulate mutual influence of membrane curvature and orientational ordering symmetry allowed coupling terms between curvature tensor and tensor order parameter should be taken into account, where both $\underline{C}$ and $\underline{Q}$ are treated as variational parameters. These coupling terms introduce local field-type terms, one of which naturally emerges from the approach based on $\underline{M}$. This is the main goal of our future study.

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International Review of Biophysical Chemistry (IREBIC)

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