

Apparent flexoelectricity in lipid bilayer membranes due to external charge and dipolar distributions

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In this Rapid Communication we show that the interplay between the deformation geometric-nonlinearity and distributions of external charges and dipoles lead to the renormalization of the membrane's native flexoelectric response. Our work provides a framework for a mesoscopic interpretation of flexoelectricity and if necessary, artificially “design” tailored flexoelectricity in membranes. Comparisons with experiments indicate reasonable quantitative agreement.

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I. INTRODUCTION

There is growing evidence that flexoelectricity provides one of the key mechanisms that permits biological membranes to couple mechanical deformation to electrical stimuli. Specifically, flexoelectricity refers to the development of polarization upon change in membrane curvature. Mathematically,

$$\mathbf{P}^S = \gamma \kappa \mathbf{n}, \quad (1)$$

where \mathbf{P}^S is the area density of the electric polarization, γ is the flexoelectric coefficient, κ is the mean curvature, and \mathbf{n} is the unit normal vector of the surface. While this effect was first appreciated in liquid crystals [1], parallel developments have also occurred in crystalline materials (cf. [2], and references therein). In the context of biological membranes, the pioneering work is that due to Petrov who has also authored two review articles on this topic [3,4] that summarize a fair amount of the literature on this topic.

Recent attention to this phenomenon has primarily been spurred via the postulated ramifications of flexoelectricity in various biological functions, e.g., outer hair cell electromotility and its role in cochlear amplification and sharp frequency discrimination [5–9], tether formation [10,11] and ion transport [12]. It is also worthwhile to point out a recent work by Brownell *et al.* [11] that provides the most compelling experimental evidence to date of the converse flexoelectric effect.

In this work we examine the effect of external charges or dipolar distributions on the apparent flexoelectricity of a lipid bilayer membrane (Fig. 1). In a naively linearized setting, external charges do not change the apparent flexoelectricity. We show, however, that carefully accounting for geometric nonlinearity and the associated change in the polarization permits the observation of some nontrivial coupling effects. Insightful works in this direction have appeared earlier. For example, Ref. [13] developed a simple model to understand the contribution of electric double layers on the flexoelectric coefficient. The focus of the present work is to (i) provide a rigorous framework to link external charges and dipoles to flexoelectricity which can then easily be generalized to complex situations, (ii) show that the external charges and dipoles renormalize the flexoelectric coefficient *because* of the interaction of geometric nonlinearity of deformation and

electrostatics, and (iii) make some simple predictions to interpret existing experiments showing low and high values of flexoelectricity for different types of membranes. We emphasize here that the limited experimental work on flexoelectricity so far does indicate that flexoelectricity in real living cells is *nonlinear*, e.g., [5].

II. THEORETICAL FRAMEWORK

We begin with the three-dimensional theory of flexoelectric materials and derive the theory for membrane by making some kinematic assumptions. Let $\mathbb{U} \subset \mathbb{R}^2$ be an open bounded domain in the XY plane. Consider a thin dielectric membrane occupying $\Omega_R = \mathbb{U}(-h/2, h/2) \subset \mathbb{R}^3$, where h is the thickness of the membrane and the subscript R indicates the *reference configuration*. Let $(\boldsymbol{\chi}, \mathbf{P}) : \Omega_R \rightarrow \mathbb{R}^3 \times \mathbb{R}^3$ be the deformation and polarization describing the thermodynamic state of the membrane, $\mathbf{X} = (X, Y, Z)$ [respectively, $\boldsymbol{\chi} = (x, y, z)$] be the Lagrangian (respectively, Euler) coordinates, $\mathbf{F} = \text{Grad } \boldsymbol{\chi}$ be the deformation gradient, $\mathbf{C} = \mathbf{F}^T \mathbf{F}$ is the Cauchy–Green strain tensor, and $J = \det \mathbf{F}$ be the Jacobian. Also, assume that there exist external or “extrinsic” polarization $\mathbf{P}_0^e : \Omega_R \rightarrow \mathbb{R}^3$ and charge density $\rho_0^e : \Omega_R \rightarrow \mathbb{R}$ attached to the material points of the membrane, and the two surfaces of the membrane are short-circuited—the reader is referred to [14] regarding this assumption. In the reference configuration the Maxwell equation can be written as

$$\text{Div } \mathbf{D} = \rho_0^e, \quad (2)$$

where $\mathbf{D} = -\epsilon_0 J \mathbf{C}^{-1} \text{Grad } \xi + \mathbf{F}^{-1}(\mathbf{P} + \mathbf{P}_0^e)$ is the electric displacement defined in Ω_R , and the potential $\xi = 0$ on both the surfaces. Since the membrane is thin, bending is presumably the dominating mode of deformation and hence the Kirchhoff hypothesis is enforced [$\boldsymbol{\chi} = (x, y, z)$]:

$$\begin{aligned} x &= X - Z \frac{\partial w(X, Y)}{\partial X}, & y &= Y - Z \frac{\partial w(X, Y)}{\partial Y}, \\ z &= Z + w(X, Y), \end{aligned} \quad (3)$$

where $w(X, Y)$ is the out-of-plane displacement of the mid-plane ($Z = 0$). Further, we introduce polarization per unit area

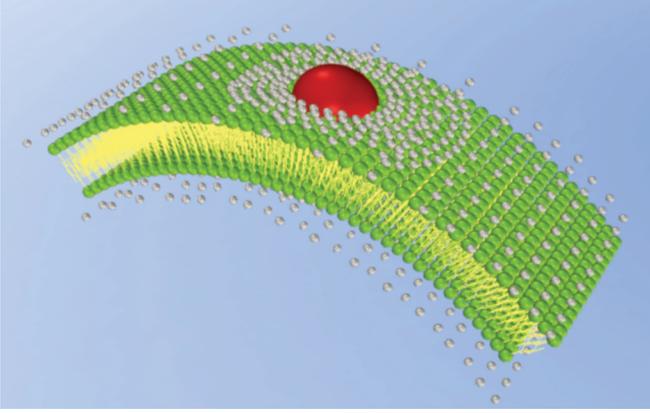


FIG. 1. (Color online) Lipid bilayer inside an electrolyte bath. The head molecules are charged and due to curvature there will ensue a net polarization inside the membrane, $P(r)$. Also the ionized water molecules are attracted by the negative head molecules of the membrane and make an external dipole layer, $P^e(r)$.

as

$$\mathbf{P}^S = (P_X^S, P_Y^S, P_Z^S) = \int_{-h/2}^{h/2} \mathbf{P}(X, Y, Z) dZ.$$

To model the flexoelectric effect, we postulate that the internal or stored energy of the membrane is given by

$$U[\chi, \mathbf{P}] = \int_{\mathcal{U}} \left[\frac{1}{2} k_b (\Delta w)^2 + f P_Z^S \Delta w + \frac{1}{2} a |\mathbf{P}^S|^2 \right], \quad (4)$$

where $\Delta(\cdot) = \frac{\partial^2(\cdot)}{\partial X^2} + \frac{\partial^2(\cdot)}{\partial Y^2}$ is the in-plane Laplace operator with respect to the Lagrangian coordinates, and k_b , f , and a are material constants. In particular, the first term is the classical Helfrich-Canham bending energy, the second gives rise to flexoelectric coupling, and the last term describes the dielectric property of the membrane. By the principle of minimum free energy we claim that the equilibrium state of the membrane is determined by the minimization problem

$$\min_{(\chi, \mathbf{P})} \{ F[\chi, \mathbf{P}] := U[\chi, \mathbf{P}] + \mathcal{E}^{\text{elect}}[\chi, \mathbf{P}] \}, \quad (5)$$

where $\mathcal{E}^{\text{elect}}$ is the electric energy associated with the electric field and boundary devices [16]

$$\mathcal{E}^{\text{elect}}[\chi, \mathbf{P}] = \frac{\epsilon_0}{2} \int_{\Omega_R} J |\mathbf{F}^{-T} \text{Grad } \xi|^2.$$

To find the Euler-Lagrange equations associated with (5), we now consider the variations of displacement and polarization:

$$w \rightarrow w_\delta = w + \delta \tilde{w}, \quad \mathbf{P} \rightarrow \mathbf{P}_\delta = \mathbf{P} + \delta \tilde{\mathbf{P}}.$$

Then the first variation of the total free energy shall vanish for any $(\tilde{w}, \tilde{\mathbf{P}})$:

$$\left. \frac{d}{d\delta} F[\chi_\delta, \mathbf{P}_\delta] \right|_{\delta=0} = 0.$$

By tedious yet standard calculation and keeping only the leading order terms [17], we obtain the following Euler-

Lagrange equations on the midplane \mathcal{U} :

$$\begin{aligned} a P_X^S + \xi_{,X} &= 0, & a P_Y^S + \xi_{,Y} &= 0, \\ f \Delta w + a P_Z^S + \xi_{,Z} &= 0, \\ \Delta(k_b \Delta w + f P_Z^S) - f_Z^{\text{elect}} &= 0, \end{aligned} \quad (6)$$

where

$$f_Z^{\text{elect}} = \int_{-h/2}^{h/2} [\Sigma_{31}^{\text{MW}} - \Sigma_{13}^{\text{MW}}]_{,X} + [\Sigma_{32}^{\text{MW}} - \Sigma_{23}^{\text{MW}}]_{,Y} dZ$$

is the Z component of the electrostatic force and

$$\Sigma_{\text{MW}} = -\frac{\epsilon_0}{2} J |\text{grad } \xi|^2 \mathbf{F}^{-T} - \text{grad } \xi \otimes \mathbf{D} \quad (7)$$

is the *Piola-Maxwell* stress. We remark that Eqs. (6) and (7), together with the Maxwell equation (2) for electrostatics form a closed system with five equations and five unknowns $\xi, w, P_X^S, P_Y^S, P_Z^S$. Analytical solutions to the above set of nonlinear differential equations promises to be an interesting albeit challenging endeavour and not addressed in this Rapid Communication.

In this Rapid Communication we will study a simple problem to assess the role of external charges and dipoles on the ‘‘apparent flexoelectricity’’ of a membrane. To this end, we conduct a thought experiment and redefine the flexoelectric coupling coefficient f in terms of change of electric displacement. Consider a flat membrane with zero curvature which is referred to as the initial state, whereas the final state of our experiment is a bent membrane having a net polarization. We denote by \mathbf{D}^i and \mathbf{D}^f the electric displacement of the initial and final states in the reference configuration, respectively. For simplicity, suppose that the in-plane components of the polarization are negligible and the membrane is under one-dimensional uniform bending—fairly reasonable assumptions for small curvatures. Since the potential difference across the thickness of the membrane is zero and the polarization density is constant along the thickness of the membrane, then from the third equation of (6) we obtain $P_Z^S = -\frac{f\kappa}{a}$, where $\kappa = \Delta w = \text{const}$. We further assume that the polarization density is constant along the thickness and obtain the polarization (per unit volume) $\mathbf{P} = \frac{\mathbf{P}^S}{h}$. The measurable quantity is the electric current in this process. Recall that the electric displacement in the reference configuration is given by $\mathbf{D} = -\epsilon_0 J \mathbf{C}^{-1} \text{Grad } \xi + \mathbf{F}^{-1}(\mathbf{P} + \mathbf{P}^e)$. We denote by D_Z^f and D_Z^i , the final and initial out-of-plane components of the electric displacement, respectively. By an ammeter we can measure the change in the electric displacement in two stages as below:

$$Q = \int_0^\infty I(t) dt = (D_Z^f - D_Z^i) \Big|_{Z=0} A,$$

where A is the area of the membrane. Now, in the absence of external charges and polarization, i.e., $\mathbf{P}_0^e = \rho_0^e = 0$, the solution to the electrostatic problem (2) is clearly given by $\xi = 0$ in Ω_R , and therefore, $D_Z^f - D_Z^i = \frac{P_Z^S}{h}$, and hence

$$f = -\frac{Q}{\kappa A} ah = -\frac{D_Z^f - D_Z^i}{\kappa} ah. \quad (8)$$

Since the current (or charge Q) is the quantity that is measured in experiments, we now *define* the ‘‘apparent’’ or effective

flexoelectric constant, pristine or with external charges and dipoles, by the above equation. Before proceeding further, it is instructive to examine the relation between the flexoelectric constant in our model f to the one often found in the literature and cited in the Introduction (1): γ . In our theoretical framework, for a homogenous membrane and in the absence of an external electric field, the third equation of (6) implies that $P = -\frac{f}{a}\kappa$. In view of (1), we obtain that $\gamma = -\frac{f}{a}$.

III. FLEXOELECTRIC COEFFICIENT IN THE PRESENCE OF EXTERNAL CHARGES AND DIPOLES

The primary constituent of most biomembranes is a molecule with two different subdomains. One is hydrophilic, usually negatively charged, and therefore tends to attract the positive charges inside the electrolyte, while the other part is hydrophobic. When these molecules are exposed to water, they arrange themselves into two sheets in a way that the hydrophobic tails group points towards the midplane of the bilayer, while the hydrophilic head molecules tend to be in contact with the ionized water molecules. During deformation, the density of charges and dipoles inside and on the surfaces of the membrane alters and results in a nonzero net polarization [18]. For simplicity, here we consider a small part of a cylindrically deformed lipid membrane inside an electrolyte bath (Fig. 2). Lipid molecules may carry dipoles or charges either along the thickness of the membrane or on the surfaces. These dipoles and charges might be “external” or the intrinsic properties of the lipid molecules. The former may be due to proteins and ion channels, for instance. In the following section, we consider the simplest possible case, in which the distributions of the charges and dipoles are radial neglecting any angular variation. The simplifying assumption is useful for illustration, however, the framework described earlier can be used for more general cases also. Consider a cylindrically deformed membrane of radius R , as shown in Fig. 2. Let ρ_0^e, P_0^e be the external charge density and the out-of-plane polarization in the reference configuration that are independent of in-plane positions. Assume that the induced out-of-plane polarization P is also independent of in-plane positions. Then in the current configuration, the external and induced polarization (p^e, p)

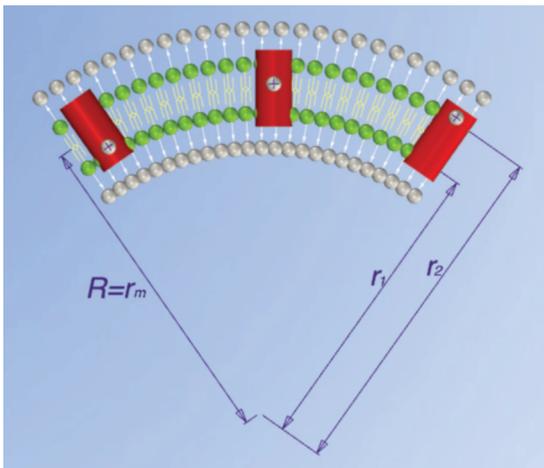


FIG. 2. (Color online) Lipid bilayer under external charges and dipoles.

together with the external charge density ρ^e , to the leading order, orient radially. They can only be a function of r , and for $r \in (r_1, r_2)$,

$$\begin{aligned} p(r) &= P(r - r_m)/J, & p^e(r) &= P_0^e(r - r_m)/J, \\ \rho^e(r) &= \rho_0^e(r - r_m)/J, \end{aligned} \quad (9)$$

where r_1, r_2 , and r_m are the radii of the inner, outer, and middle surfaces, respectively, and $r_2 - r_1 = h$ is the thickness of the membrane. Cylindrical symmetry dictates that the electric potential is also radial: $\xi = \xi(r)$. Then in the current configuration and polar coordinates, Eq. (2) can be written as

$$\frac{1}{r} \frac{d}{dr} \left\{ r \left[-\epsilon_0 \frac{d}{dr} \xi + p(r) + p^e(r) \right] \right\} = \rho^e(r). \quad (10)$$

Let $d(r) = -\epsilon_0 \frac{d}{dr} \xi + p(r) + p^e(r)$ be the radial electric displacement in the current configuration. Imposing the short-circuit condition, we obtain

$$d(r_1) = \frac{1}{h} \int_{r_1}^{r_2} \left[p + p^e - \frac{1}{r} \int_{r_1}^r r' \rho(r') dr' \right] dr. \quad (11)$$

To assess the change in dielectric displacement, we subtract the electric displacement at zero curvature. Based on the small curvature assumption, we have $J(r) = \frac{r}{r_m}$.

We denote by d^i and d^f the initial and final electric displacements in the current configuration, respectively. Let $\varepsilon = \kappa(r - r_m)$. Then the change in the out-of-plane electric displacement is

$$\begin{aligned} d^f(r_1) - d^i(r_1) &= \frac{1}{h} \int_{r_1}^{r_2} \left(\frac{P_0(r) - \varepsilon P_0^e(r)}{J} + \frac{1}{r} \int_{r_1}^r r' \frac{\varepsilon \rho_0^e(r')}{J} dr' \right) dr \\ &= -\kappa \left\{ \frac{r_m f}{r_1 a h} + \frac{1}{h} \int_{r_1}^{r_2} \left(\frac{r_m(r - r_m)}{r} P_0^e(r) \right. \right. \\ &\quad \left. \left. - \frac{1}{r} \int_{r_1}^r r_m(r' - r_m) \rho_0^e(r') dr' \right) dr \right\}. \end{aligned}$$

As before, we need to evaluate the change of electric displacement in the reference configuration. Noting that $\mathbf{D} = J\mathbf{F}^{-1}\mathbf{d}$ and neglecting the higher order terms, we obtain

$$D^f(r_1) - D^i(r_1) = \frac{r_1}{r_m} [d^f(r_1) - d^i(r_1)]. \quad (12)$$

Using Eq. (8), we obtain an expression for the apparent flexoelectric coefficient:

$$f_{\text{eff}} = -\frac{D^f(r_1) - D^i(r_1)}{\kappa} a h =: f + f_P^e + f_C^e,$$

where f_P^e and f_C^e , given by

$$f_P^e = a \int_{r_1}^{r_2} \frac{r_1(r - r_m)}{r} P_0^e(r) dr, \quad (13)$$

$$f_C^e = -a \int_{r_1}^{r_2} \frac{1}{r} \int_{r_1}^r r_1(r' - r_m) \rho_0^e(r') dr' dr, \quad (14)$$

are the flexoelectric coefficients due to external polarization and charge distributions, respectively. We now consider, in turn, as also discussed in Petrov [3], the dipolar and monopole charge contributions to the effective flexoelectricity.

IV. RESULTS AND DISCUSSION

A. Contribution of external charges to the effective flexoelectricity

In this part we estimate $-\frac{f_C^e}{a}$. The charges may be either due to the negative head of the lipid molecules or positive ions of electrolyte which are attracted by the fully hydrated head groups or the ion pump channels along the thickness of the membrane, as shown in Fig. 2. For simplicity, we only focus on the first case—the charges are distributed over the inner and outer surfaces of the membrane. After deformation, the charge densities on both sides differ in an opposite sense. The outer surface charge density will be smaller due to stretching of the surface, while the converse is true for the inner surface due to compression. Also we can estimate the ion per head lipid to be a few units of the electron charge, $-1.6 \times 10^{-19} C$. Assuming that the thickness of the membrane is about 5 nm, we evaluate Eq. (14) and obtain $-\frac{f_C^e}{a} = 2.85 \times 10^{-18} C$. This value is of the same order of magnitude as the experimental results.

B. Contribution of external dipoles and integral proteins to the effective flexoelectricity

In this case, we refer to Fig. 2, in which a membrane is endowed with uniform external dipole layers on the inner and outer surfaces. First we estimate the external polarization density (per area). According to [19] the thickness of the fully hydrated region is about 0.5 nm and the area per lipid head is about 70 \AA^2 . Based on these values, we obtain the polarization density (per area) as $P^S = 1.14 \times 10^{-10} \text{ C m}^{-1}$. Integrating Eq. (13) over the thickness of the membrane results in $-\frac{f_P^e}{a} = 5.7 \times 10^{-19} \text{ C}$. Here we note that experimentally the value of $-\frac{f_P^e}{a}$ has been measured to be a few times of 10^{-18} C [3]. The results obtained above depend on the magnitude of the dipoles on the surface. The thickness of the dipole layers is between 0.3 and 1 nm. Therefore, the resultant flexoelectric coefficient can be larger by a factor of 2. Our model allows us to approximately assess the effect of dipole carrying proteins on the effective flexoelectricity. Proteins often carry very large dipole moments, e.g., the following have been measured: 480D for chymotrypsin and 637D for carboxypeptidase A [20]. A detailed boundary value solution for an embedded protein is left for future work, however, a simple approximation that the protein dipole moment is uniformly smeared across the membrane can readily yield analytical results. While this approximation will ignore a geometrical effect, our model, however, can then be used trivially to obtain an estimate via the expression for f_P^e . To this end we need to estimate the dipole density due to the integral proteins along the thickness of the membrane. The diameter of the protein's structure is also a few nanometers. Using $P^P = 500D = 1667.8 \times 10^{-30} \text{ C m}$ for the dipole moment of the protein, $A^P = \pi \times 10^{-18} \text{ m}^2$ for the area of the protein and $h = 5 \times 10^{-9} \text{ m}$, we obtain $1.3 \times 10^{-18} \text{ C}$ for the flexoelectric coefficient.

As can be seen from the above calculation, the effect of the dipole carrying integral proteins is fairly substantial and explains the large values that are sometimes experimentally observed [3].

C. Curvature-dependent flexoelectric coefficient

While flexoelectricity relates changes to the development of membrane polarization, the flexoelectric coefficient itself, f or γ , is considered to be curvature independent. In this section we show that this is not necessarily correct. To simplify Eq. (11) for $d(r_1)$ we assumed that the ratio of $h/r_m \ll 1$. This condition is definitely violated in several biologically relevant cases. In the presence of some proteins, lipid membranes may undergo very large curvatures, even comparable to the thickness of the membrane, [21]. As Ref. [21] catalogs, several bionanostructures exist with large curvatures. In such cases the exact solution for $d(r_1)$ may have to be modified:

$$d(r_1) = \frac{f(r_1)}{h} \int_{r_1}^{r_2} \left(p + p^e - \frac{1}{r} \int_{r_1}^r r' \rho(r') dr' \right) dr, \quad (15)$$

in which $f(r_1) = \frac{h}{r_1 \ln(1 + \frac{h}{r_1})} \approx 1 + \frac{h}{2r_m} + \frac{h^2}{6r_m^2} + \dots$. Accordingly, the flexoelectric coefficient depends nonlinearly on the curvature:

$$\begin{aligned} f_P^e &= \left(1 + \frac{h}{2r_m} + \frac{h^2}{6r_m^2} + \dots \right) a \int_{r_1}^{r_2} \frac{r_1(r - r_m)}{r} P_0^e(r) dr, \\ f_C^e &= - \left(1 + \frac{h}{2r_m} + \frac{h^2}{6r_m^2} + \dots \right) \\ &\quad \times a \int_{r_1}^{r_2} \frac{1}{r} \int_{r_1}^r r_1(r' - r_m) \rho_0^e(r') dr' dr. \end{aligned} \quad (16)$$

If we assume that $h/r_m \approx 1/2$, the correction can be as large as 30%. More importantly, the nonlinear dependence of flexoelectricity on the curvature provides an interesting avenue for further research on electromechanical stability analysis of high-curvature bio-nano structures.

V. CONCLUSIONS

The key conclusion of the present work is that it is the interplay between the geometrically nonlinear deformation and electrostatics that lead to the renormalization of flexoelectricity in the presence of external charges and dipoles—this effect will not be seen in a purely linearized setting where careful distinction is not made between reference and deformed configurations. Our framework is general and can be used to examine the flexoelectric response for membranes with complex electrostatic environment (albeit the calculations may have to proceed numerically). Using simple approximations, we are, however, able to provide illustrative and transparent analytical solutions to several cases and make reasonable estimates of the flexoelectric response of different types of membranes. Interestingly, our results point also to the prospect of artificially designing high or low flexoelectricity in model membrane systems.

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