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Voltage–morphology coupling in biomimetic membranes: dynamics of giant vesicles in applied electric fields

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An electric potential difference across the plasma membrane is common to all living cells and is essential to physiological functions such as generation of action potentials for cell-to-cell communication. While the basics of cell electrical activity are well established (e.g. the Hodgkin-Huxley model of the action potential), the reciprocal coupling of voltage and membrane deformation has received limited attention. In recent years, studies of biomimetic membranes in externally applied electric fields have revealed plethora of intriguing dynamics (formation of edges, pearling, phase separation) that challenge current understanding of membrane electromechanics.

1 Introduction

Living cells maintain an electrical potential across the plasma membrane as a result of the activity of membrane-bound ion channels[1,2]. Modulation of the transmembrane electric field is often associated with membrane deformation, e.g., electromotility of outer hair cells[3–10], axon swelling (volume increase) during action potential propagation[11,12], and possibly phase transitions[13,14]. External electric fields can have more dramatic effects, e.g., directing cell growth[15], migration[16–19] or causing membrane poration[20]. Reversible electroporation, in which the pores reseal thereby restoring cell integrity after the field is turned off, is of great interest for biomedical technologies such as gene transfection[21], while irreversible electroporation leading to cell death is desirable in cancer treatment[22].

Basic understanding of membrane deformation and stability in electric fields remains elusive[23–25], and has spurred research with model biomimetic systems[20,26–28]. A cell-sized closed lipid bilayer (giant unilamellar vesicle) provides a natural model system to study the coupling between transmembrane potential and membrane shape[27,29,30]. First, the vesicles' "giant" size (10-100 μm) allows direct observation of dynamic features of the membrane, e.g., shapes and composition, in real time with optical microscopy. Second, experiments with vesicles in a spatially uniform electric field (the simplest possible geometry) reveal morphological changes that closely mimic cell behaviors, e.g., elongation into a spheroid[31–33], pearling of a tubular vesicle[34], and phase–separation ("raft" formation) in multicomponent membranes[35]. Other intriguing dynamics have also been observed: lipid flows and mixing[36], wrinkling[37], and burst[38]. While some of these behaviors , e.g., vesicle elongation, are reasonably well understood[24,27,39], *a long-standing puzzle remains:* a vesicle in a DC field can form edges and become a spherocylin-

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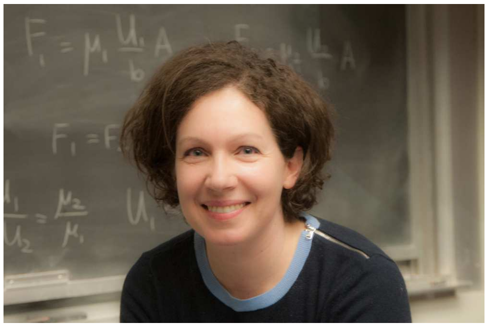

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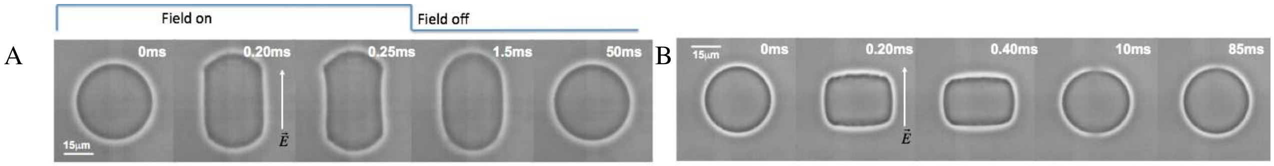

Fig. 1 **Vesicle "squaring":** A quasi–spherical vesicle exposed to a square DC pulse deforms into a spherocylinder with long axis parallel (A) or perpendicular (B) to the field depending on the conductivity ratio of the inner and outer solutions Λ, $\Lambda > 1$(A) and $\Lambda < 1$ (B). Image courtesy of R. Dimova and K. Riske[40]. Pulse duration $0.25ms$ (A) and $0.4ms$ (B).

der, a phenomenon dubbed "vesicle squaring"[40], see Figure 1; the extreme curvature of the edges may affect poration[41] and curvature-sensitive processes, e.g., protein or lipid sorting. Furthermore, while there is a consensus theoretically that the bending modulus should increase with the electric field[42–44], comprehensive experimental data is lacking. Given the wide use of the electrodeformation method[45–48] (which relies on vesicle elongation in a uniform AC electric field) to measure bending rigidity, it is important to have a clear estimate about the electric field effect in order to interpret the experimental data.

2 Basic membrane electromechanics

2.1 Membrane bending and shape fluctuations

The molecularly thin bilayer resists bending because a change in curvature involves compression and expansion of the two opposing monolayers. The energy cost is described by the classical Helfrich model[49–51]

$$E_b = \frac{\kappa}{2}(2H - C_0)^2 \tag{1}$$

where κ is the bending elastic modulus, H is the mean curvatures. C_0 is the bilayer spontaneous curvature, which is intrinsic curvature due to asymmetry in packing density of the lipid molecule's head and tail[52].

The self–assembled lipid bilayer is held together by non-covalent bonds, which allow for the lipid molecules to rearrange freely. As a result, the membrane behaves as a fluid, more precisely, a nearly incompressible two–dimensional fluid due to the high energy cost of increasing the area per lipid[29,53]. The area–incompressibility implies that the membrane tension is not a material property (as for fluid-fluid interfaces) but a Lagrange multiplier enforcing the area-constraint.

Vesicles display a rich spectrum of equilibrium shapes, which is in stark contrast with drops and bubbles whose equilibrium shape is a (plain) sphere. Equilibrium vesicle shapes correspond to minima of the membrane bending energy subject to the constraints of constant area (because the number of molecules in the bilayer is fixed) and volume (because the membrane is impermeable to ions and osmotic pressure resists changes in volume). Alternatively the shapes can be found as solutions of the generalized Laplace's equation[54–56]

$$\Delta p = 2H\sigma_0 + \tau^\kappa, \tag{2}$$

where the equilibrium tension $\sigma_0 = const$, τ^κ is the bending traction, derived from Eq.[1][54,55,57,58], and Δp is the hydrostatic pressure jump between the vesicle interior and exterior.

The bending rigidity of lipid bilayers is $\kappa \sim 20k_BT$[29,59,60] (here k_B is the Boltzmann constant and T is the absolute temperature). As a result, lipid membranes are easily bent by thermal noise. The thermal undulations store area which can be pulled out without stretching the true area (specified by the area per lipid) by application of pressure either by suction in a micropipette[61] or electric field[45,47]. A quasi-spherical vesicle deforms in response to externally applied stress and the vesicle apparent area A_0 (which is observable within the optical resolution of the microscope) increases due to flattening of the shape undulations; this effect is called entropic elasticity. Restricting the fluctuations raises the tension[61,62]

$$\sigma = \sigma_0 \exp\left[\frac{8\pi\kappa}{k_BT}\alpha\right], \quad \alpha = \frac{A - A_0}{A_0} \tag{3}$$

where σ_0 is the membrane tension in absence of applied forces. Eq.[3] can be used to obtain the membrane bending rigidity κ if the area increase and tension can be measured independently, see e.g. the electrodeformation method discussed in Section 2.4.

2.2 Fluctuation analysis to determine membrane bending rigidity and tension

Because the cost of membrane bending is comparable to the thermal energy, vesicle shapes are not static and “flicker”. The deviation of the membrane from its equilibrium shape can be decomposed into Fourier modes, $u(\mathbf{x},t) = \sum_k u_k \exp(ikx - t/t_k)$. The amplitudes have averaged spectrum[47,62–68]

$$\langle |u_k|^2 \rangle = \frac{k_B T}{\kappa k^4 + \sigma_0 k^2}\,, \tag{4}$$

where $u(\mathbf{x},t)$ is the deviation of the membrane from its equilibrium shape. $\langle |u_k|^2 \rangle$ can be determined from measured vesicle contours, and Eq.[4] is then used to obtain the membrane bending rigidity κ and tension σ_0. The correlation time at wave number k (which characterizes how fast a shape fluctuation with wavenumber k decays) is[63],

$$t_k = \frac{\kappa k^3 + \sigma_0 k}{4\mu}\,, \tag{5}$$

where μ is the medium viscosity (it is assumed that the membrane separates fluids with the same viscosity, which is the typical case for vesicles since the inner and outer fluids are aqueous solutions).

2.3 Membrane electrostatics

2.3.1 Renormalization of the bending rigidity and tension: The electrostatic effects on membrane elasticity have been studied in two contexts:

Charged lipids in the absence of external fields: Increasing surface charge stiffens the membrane because the repulsion between the charged lipids effectively suppresses the membrane undulations thereby increasing the membrane bending rigidity. Spontaneous curvature arises if there is charge asymmetry between the membrane physical surfaces, e.g., if the inner and outer Debye lengths (which characterize the thickness of the diffuse double layers adjacent to the membrane surfaces) are different. These effects have been described theoretically[69–74], however, experimental verification is lagging[60] even though techniques for preparing vesicles with asymmetric membranes have been developed[75,76].

Neutral lipids in external electric field: Application of electric field leads to the accumulation of ions (carried by conduction) at the membrane physical surfaces because the bilayer hydrophobic core is impermeable to ions. Unlike the fixed charges due to lipid ionization, these are mobile charges with surface density Q determined by the membrane capacitance

$$C_m = \varepsilon_{\mathrm{mm}}/h\,, \qquad Q = V_m C_m \tag{6}$$

where V_m is the transmembrane potential (difference between the electric potential at the inner and outer physical interfaces of the membrane), h is the membrane thickness and $\varepsilon_{\mathrm{mm}}$ is the membrane dielectric constant.

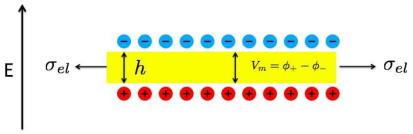

Fig. 2 The electrostatic attraction between the charges on the opposite physical surfaces of the membrane gives rise to compressive electric stresses which decrease the membrane tension

The electrostatic interaction between the charges on the physical surfaces of the membrane, see Figure 2, modifies the membrane tension, $\sigma = \sigma_0 - \sigma_{\mathrm{el}}$[25,77–79] (similarly to the Lippmann effect in electrocapillarity), and bending rigidity, $\kappa = \kappa_0 + \kappa_{\mathrm{el}}$[42–44,74]. The electrostatic corrections are predicted to be

$$\sigma_{\mathrm{el}} \sim C_m V_m^2\,, \quad \kappa_{\mathrm{el}} \sim C_m V_m^2 h^2 \tag{7}$$

The numerical prefactors in Eq.[7] found by different authors vary. Furthermore, in reality the induced charge Q is not located exactly at the membrane physical surfaces but spatially distributed in diffuse layers. Intriguingly, $\kappa^{\mathrm{el}} > 0$ and this membrane stiffening by the transmembrane potential is at odds with the slight softening measured by the electrodeformation method[47] (the method is described in the next section). A possible explanation for the apparent softening may be flexoelectricity[80],

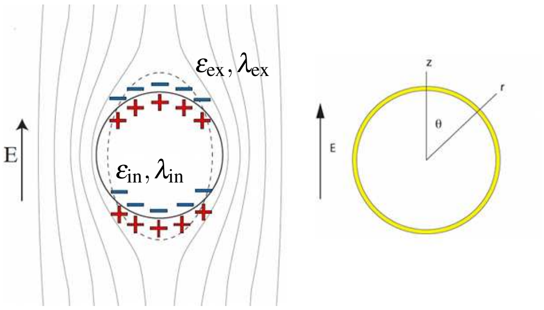

Fig. 3 Electric field lines around a fully charged spherical capacitor. The dashed line shows that the vesicle elongates along the field direction. θ is the angle with the applied field direction, $\theta = 0, \pi$ are the vesicle poles. Vesicle elongation depends of the conductivity ratio $\Lambda = \lambda_{\mathrm{in}}/\lambda_{\mathrm{ex}}$.

i.e., membrane polarization due to curvature changes[6,81] (bending a bilayer creates charge asymmetry and changes membrane polarization; conversely, changing the applied field changes the curvature.) The flexoelectric coefficient k_f is related to the spontaneous curvature[44] $k_f = \kappa C_0^{\mathrm{el}}/E_m$ ($E_m = V_m/h$ is the electric field in the membrane). Indeed, the tubular protrusions observed in giant vesicles exposed to strong electric pulses[82] might be a manifestation of high spontaneous curvature generated locally by the field.

2.4 Electrodeformation method for measuring the bending rigidity of lipid bilayers:

If the capacitor is fully charged, i.e., the charge density on the inner and outer interface is the same, the electric field inside the vesicle is zero, see Figure 3, and the only possible steady shape of a nearly–spherical vesicle in a uniform applied electric field is a prolate ellipsoid. The electrodeformation method for measuring the bending rigidity relies on this result[45]. The prolate vesicle deformation results from nonuniform radial electric pressure, $p^{\mathrm{el}} = p_e(\omega,\Lambda)\varepsilon_{\mathrm{ex}}E_0^2\,(1+3\cos(2\theta))$, which modifies the mechanical equilibrium condition for a quasi-spherical vesicle (for which $\boldsymbol{\tau}^{\kappa} = 0$ and deformation results solely from pulling area stored in the fluctuations) Eq.[2]

$$\Delta p + p^{\mathrm{el}} = 2\sigma H(\theta)\,, \tag{8}$$

Vesicle elongation is characterized by the major and minor axes, $a_{||} = 1+2s$ and $a_{\perp} = 1-s$, where $s^2 = 5\alpha/8$. Subtracting Eq.[8] at the pole ($\theta = 0$) and equator ($\theta = \pi/2$) eliminates the constant hydrostatic pressure Δp and yields

$$p_e\varepsilon_{\mathrm{ex}}E_0^2 = \frac{2s}{a}\sigma\,, \tag{9}$$

Hence, given the asphericity s (from experimental measurement), the above equation can be solved for the tension σ and then the bending rigidity κ is determined from Eq.[3], see Gracia et al.[47] for details. The method relies on the assumption of fully charged capacitor which implies low frequency AC field, where p_e is approximately $3/32$ (independent of the conductivity ratio Λ)[39].

3 Open problems:

- Membrane bending rigidity, tension, and spontaneous curvature are modulated by the transmembrane potential, but the theoretical predictions vary and experimental data is lacking. Extensive theoretical effort has focused on the electrostatics of a charged membrane in the absence of external electric field, in which case the transmembrane field arises from fixed surface charge[69–74]. The problem of a neutral membrane in applied electric field, i.e., the effect of induced surface charge on membrane elasticity, has received little attention and the theoretical predictions differ[25,43,44,83].

  While the tension decrease in electric field has been experimentally detected in a floating lipid bilayer[84,85], there is only one attempt to measure the bending rigidity of a lipid bilayer as a function of electric field strength (to the best of the authors's knowledge): using flickering spectroscopy[35], the time-correlations were utilized to extract the bending rigidity from relaxation rates Eq.[5][67]. The preliminary results suggest that the bending rigidity in an electric field increases. However, a direct comparison with the theoretical prediction Eq.[7] can not be made because the transmembrane potential along the vesicle surface is not constant, see Eq.[10]. Furthermore, membrane dynamics in electric field may be quite complex and Eq.[5] not applicable[86–89].

- The existing models are limited to a symmetric planar membrane (separating identical fluids) subjected to a perpendicular electric field; in this case, the transmembrane potential is uniform along the membrane. However, curved membranes (such as spherical vesicles) have transmembrane potentials that depend on the geometry of the system. For a sphere[90,91]

  $$V_m(t,\theta) = \tfrac{3}{2} a E_0 \left[1 - \exp\left(-\tfrac{t}{t_{\mathrm{mm}}}\right)\right] \cos\theta\,, \qquad (10)$$

  where t_{mm} is the characteristic time scale for the capacitor charging $t_{\mathrm{mm}} = a C_m \left(\frac{1}{\lambda_{\mathrm{in}}} + \frac{1}{2\lambda_{\mathrm{ex}}}\right)$, which is sensitive to the conductivities of the inner and suspending solutions.

  A position- and time-dependent transmembrane potential, as well as asymmetry in the diffuse charge on the two sides of the membrane (due to difference in the solutions conductivities) may result in (*i*) membrane shape fluctuations that do not obey the equilibrium spectrum Eq.[4], and (*ii*) instabilities leading to singular shapes such as edges.

  It has been suggested[35] that the edge in "squared" vesicles may separate a porated zone around the poles and intact (insulating) sides. The membrane conduction in the porated zone results in $V_m \sim 0$, while in the intact zone $V_m \sim aE\cos\theta$. The discontinuity in $V_m(\theta)$ gives rise to a sharp change in the membrane elastic properties (because of their dependence on V_m, see Eq.[7]) thereby causing extreme membrane curvature (edge) at the boundary between porated and intact regions.

- Dynamics of multicomponent or asymmetric membranes in electric fields is virtually unexplored. Lipid demixing has been investigated in supported bilayers[92,93], and only recently in vesicles[36,94]. Intriguingly, electric fields induce membrane flow which can change the morphology of the domains: domains may undergo break up or coalescence[36].

A systematic investigation of bilayer deformations in response to changes in the transmembrane potential, and, in particular, of the small thermally-driven bilayer undulations and the large buckling-like deformations in an applied electric field, requires approach blending mechanics, electrostatics, and biophysics. It is likely that the findings will uncover new physics relevant to a broad range of physiological processes involving excitable cells. The author hopes that the highlight will stimulate greater interest in this topic.

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