

Electric-field-dependent thermal fluctuations of giant vesicles

M. D. Mitov

Laboratory of Liquid Crystals, Institute of Solid State Physics, Sofia 1784, Bulgaria

P. Méléard and M. Winterhalter

Centre de Recherche Paul Pascal, CNRS, Avenue A. Schweitzer, F-33600 Pessac, France

M. I. Angelova

Central Laboratory of Biophysics, Bulgarian Academy of Sciences, Sofia 1113, Bulgaria

P. Bothorel

Centre de Recherche Paul Pascal, CNRS, Avenue A. Schweitzer, F-33600 Pessac, France

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The influence of an ac electric field on the shape and thermal fluctuations of giant vesicles is theoretically investigated. The experiments show that at high frequencies (dielectric regime) vesicles deform into oblate ellipsoids with the symmetry axis parallel to the applied electric field, while at low frequencies (conductive regime) they deform into prolate ones. Depending on the medium conductivity, the transition frequency between both regimes may be as low as a few kilohertz.

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Since the pioneering work of Helfrich [1] the deformation of giant vesicles under the action of an applied electric field has drawn the attention of many authors [2–5]. In these works, the vesicle is modeled as thin dielectric shell in a conducting medium and Maxwell's stress tensor is used to calculate the electric forces acting on the membrane. The common understanding is that the external field acts basically via a Maxwell stress at the equator. This causes the vesicle to deform into a prolate ellipsoid with its symmetry axis parallel to the applied electric field. Recently, Kummrow and Helfrich [5] used this induced stress to measure the bending elasticity of a lipid membrane. In this paper, we would like to point out the influence of a coupling between the external field and the thermal fluctuations of lipid bilayers, the underlying model being that of a thin dielectric shell (dielectric constant ϵ_m) embedded in another dielectric medium (dielectric constant ϵ_w). This approximation is valid if the frequency ω of the applied field is high enough for neglecting the conductivity of the aqueous phase.

According to Maxwell's equation

$$\nabla \times \mathbf{H} = (4\pi/c)\kappa\mathbf{E} + (\epsilon_w/c)(\partial\mathbf{E}/\partial t), \quad (1)$$

there are two contributions on the right-hand side, a conductivity and a displacement current, respectively. For an external electric field with a frequency $\omega \ll 4\pi\kappa/\epsilon_w$, the surrounding medium can be considered as a conductor of conductivity κ , while in the opposite case $\omega \gg 4\pi\kappa/\epsilon_w$, the medium behaves as an ordinary dielectric with dielectric constant ϵ_w . For poor conductors, the dispersion frequency $4\pi\kappa/\epsilon_w$ can be as low as few kilohertz. Applying a measured value of $\kappa \sim 5 \times 10^{-6}$ S/m shows that for frequencies in the range 0.01–1 MHz, the dielectric approximation is then very appropriate.

Let the shape of the membrane midsurface be given by the radius vector $\mathbf{r}(\theta, \varphi)$, or explicitly in polar coordinates, $r = R[1 + \varepsilon u(\theta, \varphi)]$. Only quasi-spherical vesicles

will be considered so $|\varepsilon u| \ll 1$. Let $\mathbf{n}(\theta, \varphi)$ be the normal to the midsurface pointing to the vesicle exterior. Then the parametric equations of the surfaces surrounding the membrane are

$$\mathbf{r}_{\pm}(\theta, \varphi) = \mathbf{r}(\theta, \varphi) \pm \mathbf{n}(\theta, \varphi)(d/2), \quad (2)$$

where d is the membrane thickness. The upper and lower signs are for the outer and inner membrane surfaces, respectively.

Let the applied electric field in the absence of the vesicle \mathbf{E} be homogeneous and point along the Oz axis of a polar coordinate system. The potential due to the vesicle polarization in the external field is the solution of the Laplace equation [6]

$$\nabla^2 \psi(r, \theta, \varphi) = 0 \quad (3)$$

in each of the three homogeneous regions: $\psi^-(r, \theta, \varphi)$ in the interior of the vesicle, $\psi^m(r, \theta, \varphi)$ in the membrane and $\psi^+(r, \theta, \varphi)$ in the exterior, with $\lim_{r \rightarrow \infty} \psi^+(r, \theta, \varphi) = \psi_0(r, \theta, \varphi) = -Er \cos \theta$. On the interfaces between these regions the potential satisfies the usual boundary conditions for continuity of the potential and discontinuity of its normal derivative [6]:

$$\psi^m(r_{\pm}, \theta_{\pm}, \varphi_{\pm}) = \psi^{\pm}(r_{\pm}, \theta_{\pm}, \varphi_{\pm}), \quad (4)$$

$$\epsilon_m [\partial \psi^m(r_{\pm}, \theta_{\pm}, \varphi_{\pm}) / \partial n] = \epsilon_w [\partial \psi^{\pm}(r_{\pm}, \theta_{\pm}, \varphi_{\pm}) / \partial n].$$

At both boundaries $(r_{\pm}, \theta_{\pm}, \varphi_{\pm})$, the parametric equations (2) of the corresponding surfaces are dependent on the deformation ε , so the solution $\psi^m(r, \theta, \varphi)$ is a function of ε as well. Because the membrane interfaces (2) do not coincide with coordinate surfaces (except when $\varepsilon = 0$), the mathematical problem as defined by (3) and (4) is not separable in spherical coordinates. For quasispherical vesicles however, the deviation from the spherical shape is small and we can use the perturbations method to find the solution in a power series of ε :

$$\psi(r, \theta, \varphi, \varepsilon) = \sum_{k=0}^{\infty} \varepsilon^k \psi_k(r, \theta, \varphi). \quad (5)$$

Substituting the series into (3) leads to trivial separation into Laplace equations for each of the terms:

$$\nabla^2 \psi_k(r, \theta, \varphi) = 0. \quad (6)$$

The same substitution into the boundary conditions (4) gives

$$\begin{aligned} \sum_{k=0}^{\infty} \varepsilon^k \psi_k^m(r_{\pm}, \theta_{\pm}, \varphi_{\pm}) &= \sum_{k=0}^{\infty} \varepsilon^k \psi_k^{\pm}(r_{\pm}, \theta_{\pm}, \varphi_{\pm}), \\ \varepsilon_m \sum_{k=0}^{\infty} \varepsilon^k \frac{\partial \psi_k^m(r_{\pm}, \theta_{\pm}, \varphi_{\pm})}{\partial n} &= \varepsilon_w \sum_{k=0}^{\infty} \varepsilon^k \frac{\partial \psi_k^{\pm}(r_{\pm}, \theta_{\pm}, \varphi_{\pm})}{\partial n}. \end{aligned} \quad (7)$$

In addition to the explicit ε dependence, now we have an implicit one via parametric equations (2), so it is not trivial to separate them into a series of boundary conditions as in the case of the Laplace equation. First, we expand the terms $\psi_k(r_{\pm}, \theta_{\pm}, \varphi_{\pm})$ and $\partial \psi_k(r_{\pm}, \theta_{\pm}, \varphi_{\pm})/\partial n$ into a power series of ε around the point $\varepsilon = 0$. Then, we combine the like powers of ε in (7) obtaining a series of boundary conditions which become progressively more complicated when k increases.

We have calculated the first three terms and we present the final results only for a homogeneous electric field. (The detailed perturbative procedure for finding the solution of the electric-field problem will be published in a separate paper.) In the approximation of a very thin membrane ($d \approx 4$ nm, $R \approx 10$ μ m, $d/R \approx 10^{-3}$), the

electric field out of the membrane coincides with the applied field and we have first- and second-order corrections for the electric field \mathbf{E}_m in the membrane only:

$$\mathbf{E}_m = \mathbf{E} - [(\varepsilon_m - \varepsilon_w)/\varepsilon_m](\mathbf{n} \cdot \mathbf{E})\mathbf{n}. \quad (8)$$

To find the vesicle energy in the electric field when the potential on the electrodes is kept constant [6], one has to integrate $(1/8\pi)(\varepsilon_m - \varepsilon_w)\nabla\psi^m \cdot \nabla\psi_0$ over the volume occupied by the vesicle membrane. So, for a quasispherical vesicle in a homogeneous electric field the electric energy per unit area is

$$F_e = d[(\varepsilon_m - \varepsilon_w)/8\pi]E^2 - d[(\varepsilon_m - \varepsilon_w)^2/8\pi\varepsilon_m]E^2 n_E^2. \quad (9)$$

The first term is independent of the shape of the vesicle and is equivalent to an electric surface tension proportional to E^2 . The second term is the nontrivial part dependent on the vesicle shape via n_E , the projection of vesicle normal onto the direction of the applied electric field E . The vesicle electric energy (9) adds to the Helfrich curvature elastic energy [7] and the area and volume conservation constraints [8, 9]. Thereafter, the vesicle total energy \mathcal{F}

$$\mathcal{F} = \oint F_c ds + \oint F_e ds + \sigma \oint ds - p \oint dv \quad (10)$$

is minimized using the standard variational procedure described in [8, 9].

The equation for the equilibrium shape of a quasispherical vesicle in a homogeneous electric field obtained by minimizing the vesicle total energy (10) is

$$\begin{aligned} \nabla^2 \nabla^2 u + (2 - \bar{\sigma}) \nabla^2 u + 2(\bar{\sigma} - \bar{p})u \\ = (\bar{p} - 2\bar{\sigma}) + e^2 [2Y_1^0 Y_1^0 + \nabla^2 Y_1^0 Y_1^0] + e^2 [\frac{1}{2} Y_1^0 \nabla^2 \nabla^2 (Y_1^0 u) - \frac{1}{4} \nabla^2 \nabla^2 (Y_1^0 Y_1^0 u) - \frac{1}{4} Y_1^0 Y_1^0 \nabla^2 \nabla^2 u - \frac{1}{2} (\nabla^2 Y_1^0 Y_1^0) u \\ + \frac{1}{2} (\nabla^2 Y_1^0 Y_1^0 + 6Y_1^0 Y_1^0) \nabla^2 u], \end{aligned} \quad (11)$$

where

$$\begin{aligned} \bar{\sigma} &= \{\sigma + d[(\varepsilon_m - \varepsilon_w)/8\pi]E^2\}(R^2/k_c), \quad \bar{p} = p(R^3/k_c), \\ e^2 &= (dR^2/8\pi k_c)[(\varepsilon_m - \varepsilon_w)^2/\varepsilon_m](4\pi/3)E^2 > 0, \end{aligned}$$

and $Y_n^m(\theta, \varphi)$ are the spherical harmonics as defined in [10]. We have two electrically dependent terms on the right-hand side of the equilibrium shape equation (11). The first acts as a driving force for the vesicle deformation and is independent of the deformation itself. This term is small when the applied electric field is weak. As far as the approximation used is valid for small deformations only we shall restrict ourselves to the case of weak electric fields, the second term being then a small correction.

The eigenfunction-eigenvalue equation of our problem obtained from the second variation of vesicle total energy (10) as described in [8, 9] is

$$\begin{aligned} \nabla^2 \nabla^2 Z_n^m + (2 - \bar{\sigma}) \nabla^2 Z_n^m + 2(\bar{\sigma} - \bar{p}) Z_n^m \\ = \Lambda_n^m Z_n^m + e^2 [\frac{1}{2} Y_1^0 \nabla^2 \nabla^2 (Y_1^0 Z_n^m) - \frac{1}{4} \nabla^2 \nabla^2 (Y_1^0 Y_1^0 Z_n^m) \\ - \frac{1}{4} Y_1^0 Y_1^0 \nabla^2 \nabla^2 Z_n^m - \frac{1}{2} (\nabla^2 Y_1^0 Y_1^0) Z_n^m \\ + \frac{1}{2} (\nabla^2 Y_1^0 Y_1^0 + 6Y_1^0 Y_1^0) \nabla^2 Z_n^m]. \end{aligned} \quad (12)$$

If the vesicle fluctuations $V(\theta, \varphi, t)$, i.e., the deviations from the equilibrium shape, are decomposed into a series of its eigenfunctions $Z_n^m(\theta, \varphi)$,

$$V(\theta, \varphi, t) = \sum_n \sum_m U_n^m(t) Z_n^m(\theta, \varphi), \quad (13)$$

the second variation of total energy $\delta^2 \mathcal{F}$ can be transformed [8, 9] into the very simple form of the sum of harmonic oscillators with amplitudes $U_n^m(t)$. Thereafter, the mean-squared amplitudes $\langle |U_n^m(t)|^2 \rangle$ are obtained by applying the equipartition theorem

$$\frac{1}{2} \delta^2 \mathcal{F} = \frac{k_c}{2} \sum_n \sum_m \Lambda_n^m |U_n^m(t)|^2 \longrightarrow \langle |U_n^m(t)|^2 \rangle = \frac{kT}{k_c} \frac{1}{\Lambda_n^m}. \quad (14)$$

Since (12) contains the electric field as a parameter, the eigenvalues and the eigenfunctions depend on the electric field as well, this influence being investigated now in more detail.

For weak electric fields, we apply the perturbations method to find the corrections to the spherical shape eigenfunctions $Y_n^m(\theta, \varphi)$ and the calculated eigenvalues

λ_n [8, 9]:

$$\lambda_n(\sigma_0, p_0) = (n-1)(n+2)[\sigma_0 + n(n+1)] - 2(p_0 - 2\sigma_0). \quad (15)$$

We suppose

$$\begin{aligned} \bar{\sigma} &= \sigma_0 + \sum_{k=1}^{\infty} e^{2k} \sigma_k, \quad \bar{p} = p_0 + \sum_{k=1}^{\infty} e^{2k} p_k, \\ Z_n^m(\theta, \varphi) &= Y_n^m(\theta, \varphi) + \sum_{k=1}^{\infty} e^{2k} {}_k V_n^m, \\ \Lambda_n^m &= \lambda_n + \sum_{k=1}^{\infty} e^{2k} {}_k \Lambda_n^m. \end{aligned} \quad (16)$$

The first-order corrections to the eigenfunctions have the form

$${}_1 V_n^m = A_{n-2}^m Y_{n-2}^m + A_{n+2}^m Y_{n+2}^m, \quad (17)$$

with

$$\begin{aligned} A_{n-2}^m &= \frac{3}{4\pi} \frac{3n^2 - 3n - 2}{\lambda_n - \lambda_{n-2}} \sqrt{\frac{[(n-1)^2 - m^2][n^2 - m^2]}{(2n-3)(2n-1)^2(2n+1)}}, \\ A_{n+2}^m &= \frac{3}{4\pi} \frac{3n^2 + 9n + 4}{\lambda_n - \lambda_{n+2}} \sqrt{\frac{[(n+1)^2 - m^2][(n+2)^2 - m^2]}{(2n+1)(2n+3)^2(2n+5)}}, \end{aligned}$$

and the first-order corrections to the eigenvalues read

$$\begin{aligned} {}_1 \Lambda_n^m &= (n^2 + n + 2)\sigma_1 - 2p_1 \\ &\quad - \frac{3}{4\pi} (n^2 + n + 2) \frac{2n^2 + 2n - 1 - 2m^2}{(2n-1)(2n+3)}. \end{aligned} \quad (18)$$

In principle, the calculations can be done up to any desired precision, the problems being of technical character only. The parameters σ_k and p_k are arbitrary for the moment and will be determined later on, when the equilibrium shape is found.

To find the equilibrium vesicle shape, we need two supplementary conditions to determine the membrane tension $\bar{\sigma}$ and the transmbrane hydrostatic pressure difference \bar{p} . These are [8, 9] the condition for constant vesicle volume

$$\oint [u + u^2] d\Omega + \oint \langle V^2 \rangle d\Omega = \frac{4\pi}{3} v \quad (19)$$

and constant membrane area

$$\oint [2u + u^2 - \frac{u \nabla^2 u}{2}] d\Omega + \oint \left\langle V^2 - \frac{V \nabla^2 V}{2} \right\rangle d\Omega = 4\pi s, \quad (20)$$

where v is the vesicle excess volume, s is the membrane excess area, and $d\Omega = \sin \theta d\theta d\varphi$. Substituting the fluctuations V with the series of eigenfunctions (13) for a given electric field we get the explicit form

$$\oint \langle V^2 \rangle d\Omega = \sum_n \sum_m \langle |U_n^m(t)|^2 \rangle = \frac{kT}{k_c} \sum_n \sum_m \frac{1}{\Lambda_n^m(e^2)}, \quad (21)$$

$$\oint \left\langle V^2 - \frac{V \nabla^2 V}{2} \right\rangle d\Omega = \frac{kT}{k_c} \sum_n \sum_m \frac{n^2 + n + 2}{2} \frac{1}{\Lambda_n^m(e^2)}. \quad (22)$$

Once again, we use the perturbations method to solve the set of the equilibrium shape equation (11) and both supplementary conditions (19) and (20) in a power series of e^2 , and we expand $1/\Lambda_n^m(e^2)$ in a series of e^2 as well:

$$u = \sum_{k=0}^{\infty} e^{2k} u_k, \quad \frac{1}{\Lambda_n^m(e^2)} = \frac{1}{\lambda_n} \left[1 - \frac{{}_1 \Lambda_n^m}{\lambda_n} e^2 + \dots \right]. \quad (23)$$

In the limit $e^2 \rightarrow 0$ one gets the set of equations for the sphere [8, 9]. Choosing R to be the radius of the equilibrium sphere ($e^2 = 0$) as in [11], we find $u_0 = 0$ and the well-known Laplace relation between the membrane tension and the transmbrane pressure difference $p_0 = 2\sigma_0$ [8, 9]. In that case, the last term in (15) vanishes and the expression becomes identical to that obtained by Milner and Safran [11]:

$$\lambda_n(\sigma_0) = (n-1)(n+2)[\sigma_0 + n(n+1)].$$

Equations (19) and (20) determine the excess volume and area as functions of membrane tension σ_0 .

Because $u_0 = 0$ the solution of equilibrium shape equation starts in the first order of e^2 :

$$u(\theta, \varphi) = -\sqrt{16/5\pi} [e^2/\lambda_2(\sigma_0)] Y_2^0(\theta, \varphi). \quad (24)$$

We see that the electric field deforms spherical vesicles into *oblate* ellipsoids with symmetry axis parallel to it and that the amplitude of the deformation at a given E depends on the membrane tension as well. The larger the tension, the smaller the deformation.

The first-order correction to the vesicle shape determines the parameters $p_1 = 0$ and $\sigma_1 = 1/4\pi$. So, the first-order corrections (18) to the eigenvalues finally read

$${}_1 \Lambda_n^m = -\frac{1}{2\pi} (n^2 + n + 2) \frac{[n(n+1) - 3m^2]}{(2n-1)(2n+3)}. \quad (25)$$

Due to the explicit m dependence in (25) there is no more degeneracy with respect to m as in (15). This is a straightforward consequence of the applied electric field that breaks the spherical symmetry. It is interesting to mention that $\sum_{m=-n}^n {}_1 \Lambda_n^m = 0$, indicating that the sum $\sum_{m=-n}^n \langle |U_n^m(t)|^2 \rangle$ does not change in the first order of e^2 . There is only a redistribution among the different m modes, keeping their sum constant. Because ${}_1 \Lambda_2^0 < 0$ and ${}_1 \Lambda_2^{\pm 1} < 0$ the electric field enhances the mean-squared amplitudes $\langle |U_2^0(t)|^2 \rangle$ and to a lesser extent $\langle |U_2^{\pm 1}(t)|^2 \rangle$, but suppresses $\langle |U_2^{\pm 2}(t)|^2 \rangle$ (${}_1 \Lambda_2^{\pm 2} > 0$). In order to give an idea of the magnitude of this effect for an electric field $e^2 = 1$ and zero membrane tension $\sigma_0 = 0$, we have calculated the deformation from the sphere $|u(\theta, \varphi)/Y_2^0(\theta, \varphi)| \approx 4\%$. At the same conditions the relative increase of the above-mentioned mean-squared amplitudes is 2%, 1%, and -2%, respectively.

The giant vesicles were prepared from egg lecithin according to the procedure described in [12, 13]. Two different experimental chambers were used. The first one is built from two microscope slides separated by two parallel platinum wires of diameter 0.2 mm at a distance of 2 mm, generating an electric field perpendicular to the optical axis. In the second one, the optical axis is parallel to the applied electric field. This cell consists of two microscope slides covered with a transparent conductive

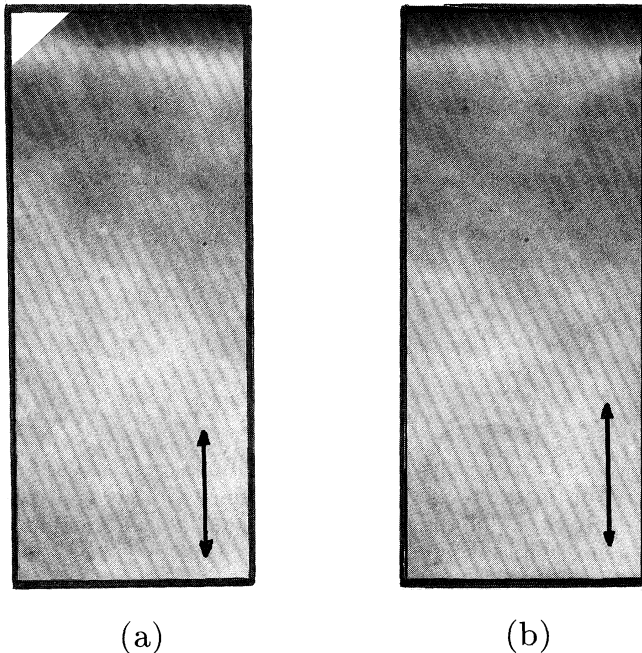


FIG. 1. Strongly fluctuating giant ($R \sim 8 \mu\text{m}$) vesicle under ac electric field perpendicular to the direction of observation. The arrows mark the direction of the electric field. The dark region on top is one of the electrodes. (a) At the low-frequency conductive regime, the vesicle is deformed into the prolate ellipsoid, $f = 1 \text{ kHz}$, 1 V (rms) on the electrodes; (b) at the high-frequency dielectric regime, the vesicle is deformed into the oblate ellipsoid, $f = 13 \text{ kHz}$, 20 V (rms) on the electrodes.

layer of indium tin oxide and separated by a silicon spacer of 0.3 mm . Pure (Milli-Q) water ($\kappa < 5 \times 10^{-6} \text{ S/m}$) was used in all the experiments.

A strongly fluctuating giant ($R \sim 8 \mu\text{m}$) vesicle was selected for the experiment. The ac electric field was applied using the first cell and the result is shown in Fig. 1. When the frequency is low ($f = 1 \text{ kHz}$), we are in a conductive regime and the vesicle deforms into prolate ellipsoid, Fig. 1(a), as already observed by many authors [5]. But at high frequency ($f = 13 \text{ kHz}$), it

deforms into *oblate* ellipsoid, Fig. 1(b).

Another experiment was performed on strongly fluctuating vesicles subjected to an electric field parallel to the optical axis (second cell, not shown). At low frequency ($f = 1 \text{ kHz}$), the vesicle radius decreases when the field is on and increases back when the field is off. At high frequency ($f = 13 \text{ kHz}$), on the contrary, the effect is now reversed.

The experimental findings are in *qualitative* agreement with the model predictions that a high-frequency electric field deforms quasispherical vesicles into an *oblate* ellipsoid. Quantitative measurements are currently in progress.

We have to point out that this effect can only be observed with a high-purity sample (lipid and water as well). Even small amounts of ions can dramatically increase the water conductivity and shift the dispersion frequency $\omega = 4\pi\kappa/\epsilon_w$ beyond the experimentally reachable frequencies.

We have also observed some facts that cannot fit in our (*small deformations only*) model, but are otherwise quite understandable. In both regimes, conductive as well as dielectric, the fluctuation amplitude visibly decreased when the field was very strong and resumed again when the field was reduced. At the same time the observed deformations were relatively large (see Fig. 1). We believe this effect is due to the significant ellipsoidal deformation induced by the strong electric field. When the vesicle volume is constant, some membrane area is needed for the vesicle deformation. The necessary membrane area is taken from the area available to the thermal fluctuations, so their amplitudes decrease. This is the same fake stretching elasticity theoretically proposed by Helfrich and Servuss [14] and used by Evans and Rawicz [15] to measure the *bending* elasticity k_c . The same effect of reducing the fluctuations by sucking part of the vesicle membrane into a pipet is already observed in [15]. A more elaborate model, suitable to account for larger shape deformations, is currently into development.

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- [1] W. Helfrich, Z. Naturforsch. C **29**, 182 (1974).
 [2] M. Winterhalter and W. Helfrich J. Colloid Interface Sci. **122**, 583 (1988).
 [3] G. Bryant and J. Wolfe, J. Membr. Biol. **96**, 129 (1987).
 [4] J. W. Ashe, *et al.* Ferroelectrics **86**, 311 (1988).
 [5] M. Kummrow and W. Helfrich, Phys. Rev. A **44**, 8356 (1991).
 [6] L. Landau and E. M. Lifshitz, *Electrodynamics of Continuous Media, Course of Theoretical Physics* (Pergamon, New York, 1960), Vol. 8.
 [7] W. Helfrich, Z. Naturforsch. C **28**, 693 (1973).
 [8] J. F. Faucon *et al.* J. Phys. (Paris) **50**, 2389 (1989).
 [9] M. D. Mitov *et al.*, in *Advances in Supramolecular Chemistry*, edited by G. W. Gokel (JAI, Greenwich, CT, 1992), Vol. 2, p. 93.
 [10] G. Arfken, *Mathematical Methods for Physicists* (Academic, New York, 1970).
 [11] S. T. Milner and S. A. Safran, Phys. Rev. A **36**, 4371 (1987).
 [12] M. I. Angelova *et al.*, Prog. Colloid Polym. Sci. **89**, 127 (1992).
 [13] M. I. Angelova *et al.*, Springer Proc. Phys. **66**, 178 (1992).
 [14] W. Helfrich and R. M. Servuss, Nuovo Cimento D **3**, 137 (1984).
 [15] E. Evans and W. Rawicz, Phys. Rev. Lett. **64**, 2094 (1990).

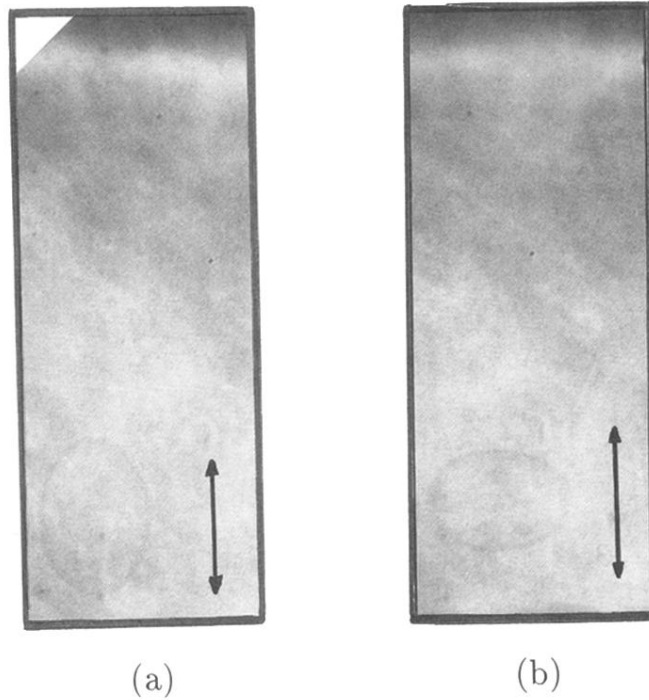


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