MEMBRANES AND LYOTROPIC PHASESON SOME PROBLEMS IN THE THEORY OF ELASTIC AND FLEXOELECTRIC EFFECTS IN BILAYER LIPID MEMBRANES AND BIOMEMBRANES

A. Petrov, A. Derzhanski

ON SOME PROBLEMS IN THE THEORY
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IN BILAYER LIPID MEMBRANES AND BIOMEMBRANES

A. G. PETROV and A. DERZHANSKI

Liquid Crystal Group, Institute of Solid State Physics
Bulgarian Academy of Sciences, 72 bd Lenin, 1113 Sofia, Bulgaria

Résumé. — Les auteurs ont étudié l'influence de l'asymétrie moléculaire sur les propriétés élastiques et flexoélectriques des membranes bi-couches. D'abord on introduit la définition de l'asymétrie lipide. Ensuite on propose une expression pour l'énergie élastique d'une monocouche de molécules asymétriques lipides. D'après cette expression on étudie l'élasticité d'une membrane bi-couche lipide. On obtient des formules pour la courbe équilibrée de la membrane pour des asymétries identiques et différentes des deux monocouches. On étudie aussi la distribution des lipides entre les deux monocouches d'une membrane déformée et des expressions pour la polarisation indue par déformation. A la fin on détermine le coefficient flexoélectrique de la membrane lécithine-cholestérol.

Abstract. — The influence of the molecular asymmetry on the elastic and flexoelectric properties of bilayer lipid membranes is studied. At first a definition of the lipid asymmetry is introduced. Then an expression for the elastic energy of a monolayer of asymmetrical molecules is proposed and the curvature elasticity of bilayer lipid membrane is studied on such a basis. Formulas for the equilibrium curvature of a membrane are obtained at equal and different asymmetries of the two monolayers. After that the lipid distribution between two monolayers of a deformed membrane is studied and expressions for curvature-induced polarization are obtained. Finally the flexoelectric coefficient of a lecithin-cholesterol membrane is determined.

1. Introduction. — The questions under consideration in this work are related to the influence of the molecular asymmetry on the elastic and flexoelectric properties of bilayer lipid membranes (BLM). In the case of thermotropic nematics the connection between the molecular asymmetry and the flexoeffect [1] was studied theoretically in some papers, e. g. [2], [3], [4] and the influence of this asymmetry on elastic properties in papers [5], [6]. In a previous work [7] we introduced in analogy with [1] the notion of conical asymmetry of membrane — forming lipid molecules (Fig. 1) and using the simple one dimensional formula for splay flexoelectric coefficient we calculated the polarization of a BLM arrising upon curving it. But later we made some considerations (A. G. Petrov, unpublished) demonstrated that such a formula would be valid if the lipid molecule's reorientation took place from a position with polar head facing the water phase to a position with polar head facing the hydrophobic core, the molecule being in the same monolayer. It would be so if the energy differences between these two orientations were small comparing with $k_B T$. But estimated according to Frenkel [8] the polar head energy in a hydrophobic environment turn out to be $\sim 5 \times 10^{-13}$ erg, i. e. $\sim 12\, k_B T$. This means that a reorientation of lipid molecules can take place only by means of entire transition from one monolayer to the another — the so-called flip-flop, the polar head facing always water phase.
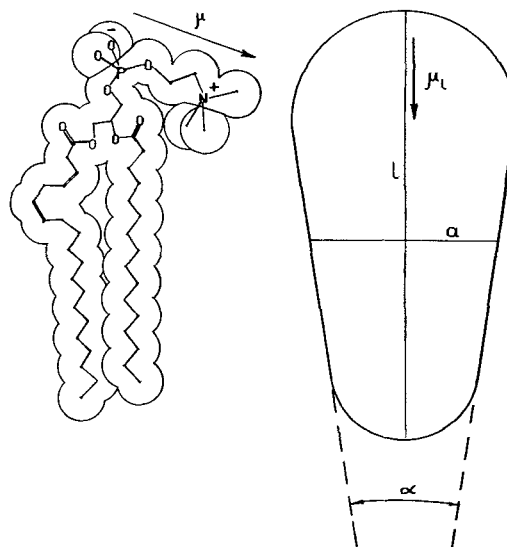
FIG. 1. — Lecithin molecule and its conical representation. In such conformation of the polar head the axial component of the dipole moment is small. On the other hand the polar head area is maximal.

Taking into account only the relative area change of the external (e) and the internal (i) layers of a deformed membrane and making the assumption that the flip-flop continues until the molecular densities as referred to the monolayers centre planes become equal, Helfrich

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has obtained [9] for the relative density change as refered to the bilayer's centre surface, the following formula :

$$x = \frac{v^e - v^i}{2\,v_0} = \frac{d}{4}(c_1 + c_2) \tag{1}$$

d : the membrane thickness, c_1 and c_2 : the two principal values of the curvature, v_0 : the mean density for a monolayer $v_0 = (\frac{1}{2})\,(v^e + v^i)$. Denoting the axial component of the dipole moment by μ_1 (Fig. 1) and making a calculation of the surface polarization (the dipole moment per unit area) for the Helfrich's case we will obtain :

$$P = 2\,v_0\,\mu_1\,x = e(c_1 + c_2) \tag{2}$$

where for the flexoelectric coefficient we will have :

$$e = \tfrac{1}{2}\,v_0\,\mu_1\,d\,. \tag{3}$$

Putting $v_0 = 2 \times 10^{14}$ cm^{-2}, $\mu_1 = 4 \times 10^{-18}$ cgs units and $d = 5 \times 10^{-7}$ cm we obtained

$$e = 2 \times 10^{-10} \text{ statcoulomb}\,.$$

So, unlike a nematic, a membrane will manifest curvature-induced polarization even when it is build up from symmetric molecules because of its layered structure.

The estimation in [4] was made according to the formula (4) which took into account the Boltzmann distribution and dealt only with the molecular asymmetry

$$e = K\,\frac{\mu_1\,c_1}{k_B\,T} \tag{4}$$

Here $K = 5 \times 10^{-13}$ erg is the curvature elastic modulus of the membrane [9] and c_1 : the factor of lipid asymmetry :

$$c_1 = \frac{2\,\alpha}{a} \tag{5}$$

α is the conical angle (Fig. 1) and a is the distance between two neighbour molecules. Putting $c_1 = 10^6$ cm^{-1}, $\mu_1 = 4 \times 10^{-18}$ cgs units and $k_B\,T = 4 \times 10^{-14}$ erg we obtained

$$e = 5 \times 10^{-11} \text{ statcoulomb}\,.$$

No matter that these two formulas are obtained by completely different assymtions the results are quite similar.

The aim of this work is to present a systematic study of the influence of the molecular asymmetry upon the elastic and flexoelectric properties of the membranes. As a result new expressions for the elastic and flexoelectric coefficients of a membrane build up from asymmetrical molecules will be derived.

2. Curvature elasticity of a monolayer of asymmetrical lipids. — First we will derive an expression for

the elastic energy of a monolayer of asymmetrical molecules. For this purpose another definition of the parameter of asymmetry has to be introduced. Namely we shall assume a lipid molecule asymmetrical if the following condition is fulfiled :

The polar head's area (A_{h0}) $\neq$ the hydrophobic (6) part's area (A_{c0}).

If $A_{h0} > A_{c0}$ we shall name it the case of positive asymmetry, in the opposite case $A_{h0} < A_{c0}$: negative asymmetry (Fig. 2a, 2b).
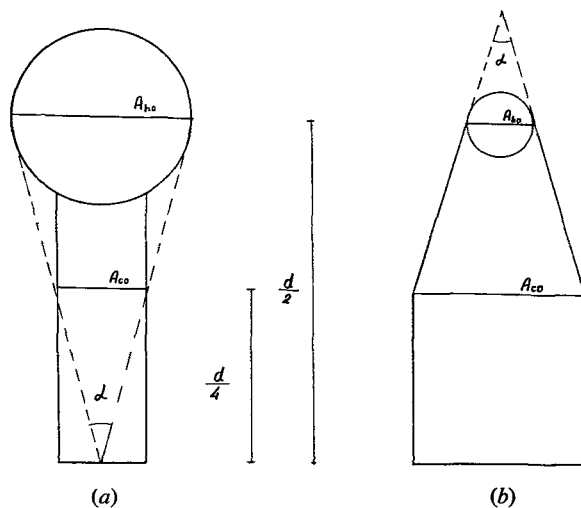

FIG. 2. — Schematical representation of the two lipid molecules with different asymmetries : a) Positive asymmetry (e. g. lysolecithin) ; b) Negative asymmetry (e. g. phosphatidylethanolamine).

Let us consider now a monolayer of such molecules. Following Marčelja [11] its elastic energy can be written as :

$$F = \frac{1}{2}\,k_h\left(\frac{A_h}{A_{h0}} - 1\right)^2 + \frac{1}{2}\,k_c\left(\frac{A_c}{A_{c0}} - 1\right)^2 \tag{7}$$

where k_h and k_c are the elastic constants for heads and chains respectively, A_h and A_c are the areas per polar head resp. chain in the monolayer.

The difference between (7) and the original Marčelja's expression is that in our case the condition (6) is valid i. e.

$$A_{h0} \neq A_{c0}\,.$$

Let v is the number of molecules per unit area of the hydrophobic end of the monolayer. Having in mind that the monolayer is part of a BLM we shall assume that upon curving the bilayer the area of the center plane between two hydrophobic ends remains constant, so v is a parameter independent of the curvature. Then if we have a curved monolayer and its principal curvatures [10] are c_1 and c_2 (we shall name them positive if the outer monolayer is curved fowards its hydro-

phobic part) for A_h and A_c we will have the following expressions

$$A_h = \left[1 + \frac{d}{2}(c_1 + c_2)\right] v^{-1}$$

$$A_c = \left[1 + \frac{d}{4}(c_1 + c_2)\right] v^{-1} . \tag{8}$$

From the generalized expression (7) it is evident that in the case $A_{h0} \neq A_{c0}$ a planar monolayer state is no longer the state of minimum elastic energy. For the equilibrium values of the density v_0^{eq} and the curvature c_0^{eq} we obtain

$$v_0^{eq} = (2 A_{c0} - A_{h0})^{-1} \tag{9}$$

$$c_0^{eq} = (4/d) (A_{h0} - A_{c0}) \cdot (2 A_{c0} - A_{h0})^{-1} . \tag{10}$$

Usually $2 A_{c0} > A_{h0}$. When $2 A_{c0} \rightarrow A_{h0}$, $c_0^{eq} \rightarrow \infty$.

It means that a collaps of the monolayer in micelles take place. That is just the case of lysolecithin molecules, one of which two chains is removed. If the concentration of lysolecithin exceedes 50 % lysis of the membrane occurs — it breaks up into micelles [12].

If we make a restriction for weak asymmetry i. e. $(|\alpha| \, d/2 \, a) \ll 1$ we will have

$$c_0 = \frac{4}{d} \frac{(\alpha d/2 \, a)}{1 - (\alpha d/2 \, a)} \approx \frac{2\alpha}{a} . \tag{11}$$

So in this case the old definition (5) coincides with the new one.

Let us consider now a planar monolayer

$$c_1 = c_2 = 0 \quad \text{i. e.} \quad A_h = A_c = A .$$

The condition $\partial F / \partial A = 0$ gives the equilibrium density of the planar state :

$$A = \frac{1}{v_0^{plan}} = \left(\frac{k_h}{A_{h0}} + \frac{k_c}{A_{c0}}\right) \cdot \left(\frac{k_h}{A_{h0}^2} + \frac{k_c}{A_{c0}^2}\right)^{-1} . \tag{12}$$

But in the planar state $F > 0$, so the monolayer is internally stressed. After some algebra from (7) and (8) we obtain a new form for the elastic energy expression (consisting of two terms, the first one depending only on the curvature and the second — on the density) :

$$F^{ML} = \frac{1}{2} (K_h + K_c) (c_1 + c_2 - c_0)^2 +$$

$$+ \frac{1}{2} \frac{K_h K_c}{K_h + K_c} \left(\frac{1}{d}\right)^2 \left[\left(4 + \frac{3 K_h}{K_c}\right) (vA_{h0} - 1)^2\right.$$

$$- 4(vA_{h0} - 1) (vA_{c0} - 1)$$

$$\left. - 4\left(4 + \frac{3 K_c}{K_h}\right) (vA_{c0} - 1)^2\right] \tag{13}$$

where K_h and K_c are curvature elastic moduli expressed by Marčelja's moduli k_h and k_c in the following way :

$$K_h = k_h \left(\frac{d}{2 \, vA_{h0}}\right)^2 , \qquad K_c = k_c \left(\frac{d}{4 \, vA_{c0}}\right)^2 .$$

The monolayer's asymmetry c_0 is given by

$$c_0 = \frac{2}{d} \frac{K_h(vA_{h0} - 1)^2 + 2 K_c(vA_{c0} - 1)}{K_h + K_c} . \tag{14}$$

If the monolayer is planar and possesses equilibrium density (12), then

$$c_0 = \frac{1}{d} \frac{k_h k_c}{A_{h0}^2} (A_{h0} - A_{c0}) \cdot \left(\frac{k_h}{A_{h0}^2} + \frac{k_c}{4 A_{c0}^2}\right)^{-1} \times$$

$$\times \left(\frac{k_h}{A_{h0}} + \frac{k_c}{A_{c0}}\right)^{-1} . \tag{15}$$

Expressions (10) and (15) give the two limitting cases of (14) and demonstrate that the monolayer's asymmetry depends on its curvature but it keeps the same sign if the density is equal to the equilibrium density for the state under consideration. Namely :

$$c_0 > 0 \quad \text{if} \quad A_{h0} > A_{c0}$$
$$c_0 < 0 \quad \text{if} \quad A_{h0} < A_{c0}$$

which gives explanation of the definition introduced at the beginning of this section.

3. Elasticity of a BLM composed of two asymmetrical monolayers.

— In his paper [9] Helfrich has written : *It should be noted that the new model is again a gross simplification. For instance, the inevitable asymmetry of the monolayers (which separately may have very strong spontaneous curvatures offsetting each other in the bilayer) is disregarded.* Now we will study just the influence of the spontaneous curvature of the monolayers upon the elasticity of the whole bilayer. In planar state each monolayer tends to deform in opposite sense to the another depending on the sign of c_0. These deformations being uncompatible with bilayer structure can not be realized but internal stresses can change very strongly the elastic properties of the bilayer.

Let us start our consideration with the problem of stability of such internally stressed membrane assuming that the flip-flop is blocked. Because of the constant molecular density the second term will not depend on the curvature and we will not consider it. Taking into account that the curvatures of the two monolayers have opposite signs, for the curvature energy per unit area we will have :

$$F^{BLM} = \frac{1}{2} K^e (c_1^e + c_2^e - c_0^e)^2 + \frac{1}{2} K^i (c_1^i + c_2^i - c_0^i)^2 , \tag{16}$$

where

$$K^e = K_h^e + K_c^e , \qquad K^i = K_h^i + K_c^i .$$

Let the two monolayers be absolutely equal, i. e.

$$K^e = K^i = K , \qquad c_0^e = c_0^i = c_0 .$$

If we consider spherical deformation with a radius of

the curvature of the centre plane R and $R \gtrsim d$ the curvatures of the two monolayers will differ :

$$c_1^e + c_2^e = \frac{2}{\left(R + \dfrac{d}{4}\right)}, \quad c_1^i + c_2^i = \frac{2}{\left(R - \dfrac{d}{4}\right)}.$$

After some algebra we obtain for F^{BLM}

$$F^{BLM} = Kc_0^2 + \frac{K}{\left[1 - \left(\dfrac{d}{4R}\right)^2\right]^2} \times$$

$$\times \left[\left(1 + \frac{c_0\,d}{2}\right)\left(\frac{2}{R}\right)^2 + \left(1 - \frac{c_0\,d}{2}\right)\frac{d^2}{4\,R^4}\right]. \quad (17)$$

With second order accuracy we will have

$$F^{BLM} = Kc_0^2 + K\left(1 + \frac{c_0\,d}{2}\right)(c_1 + c_2)^2 \quad (18)$$

which means that the asymmetry changes the elastic constant of the bilayer. Namely

$$K^{BLM} = K^{ML}\left(1 + \frac{c_0\,d}{2}\right). \quad (19)$$

When $c_0 > 0$, $K^{BLM} > K^{ML}$. But when $c_0 < 0$ $K^{BLM} < K^{ML}$ and if $c_0 = -2/d$, $K^{BLM} = 0$, which means that the bilayer possesses no curvature elasticity in second order. The reason for this is easy to be understood. In the case of bilayers with negative asymmetry the curvature deformation leads to an decrease of the torques in the internal monolayer and an increase in the external. But because of the greater curvature of the internal monolayer the decrease of its elastic energy can be greater than respective increase in the external monolayer and the elastic energy of the membrane as a whole can decrease (Fig. 3).
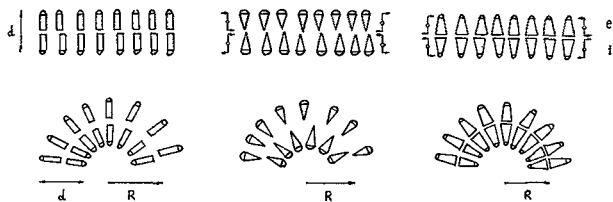

Fig. 3. — Bilayer membranes composed by lipid molecules with zero, positive and negative asymmetry. Internal torques due to the asymmetry are also shown.

If this is the case it leads to an interesting conclusion. When $c_0 \to -2/d$ the planar state of the membrane becomes unstable because of the internal torques. The expression (17) is typical for a second order phase transition. Regarding the curvature as an order parameter the field which drives the transition will be the field of internal torques $c_0\,d/2$. Increasing the absolute value of the asymmetry c_0 we can reach the threshold for deformation

$$c_0^{tr} = -\frac{2}{d}. \quad (20)$$

From the condition $(\partial F^{BLM}/\partial(1/R)) = 0$ one obtains for the curvature

$$\frac{1}{R} = 0 \quad \text{if} \quad |\,c_0\,| < |\,c_0^{tr}\,|,$$

$$\frac{1}{R} = \pm\frac{4}{d}\sqrt{\frac{|\,c_0\,d\,| - 2}{|\,c_0\,d\,| + 6}} \quad \text{if} \quad |\,c_0\,| > |\,c_0^{tr}\,|. \quad (21)$$

The threshold value of the spontaneous curvature is

$$c_0^{tr} = -4 \times 10^7 \text{ cm}^{-1}$$

which means a conical angle of 0.1 rad at a molecular width 5 Å. If $|\,c_0\,d\,|$ exceeds the threshold value only by 0.01, i. e. $|\,c_0\,d\,| = 2.01$ then from (21) we obtains

$$R \approx 7\,d = 350 \text{ Å}.$$

The case considered up to now corresponds to monolayers with completely equal asymmetries $c_0^e = c_0^i$. If $c_0^e \neq c_0^i$ the difference in asymmetries always leads to deformation without any threshold. In this case from (16) and the condition $(\partial F/\partial(c_1 + c_2)) = 0$ the equilibrium curvature is

$$c_1 + c_2 = \frac{K^e\,c_0^e - K^i\,c_0^i}{K^e + K^i}. \quad (22)$$

Let $K^e = K^i$ then

$$c_1 + c_2 = (c_0^e - c_0^i)/2.$$

Let at the beginning $c_0^e - c_0^i = 0$ and the membrane is planar. If upon the action of a definite chemical agent at the one side of the membrane a conformational change in the lecithin head groups is caused [13], it will diminish the head group's area and in such a way this monolayer will get local negative asymmetry which will lead to a deformation of this membrane sector (Fig. 4).
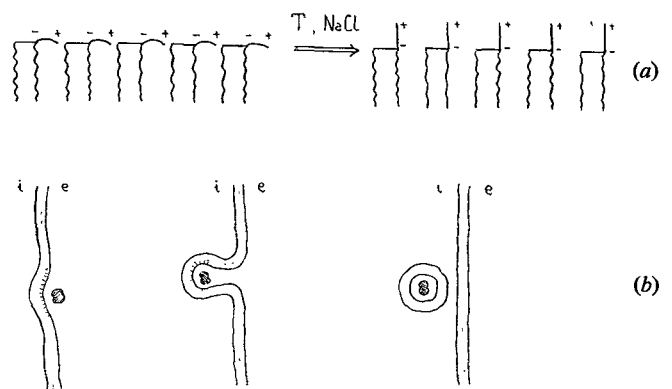

Fig. 4. — a) Conformational change in the lecithin polar head which results in negative lipid asymmetry ; b) The proposed model of pinocytosis based on locally induced negative asymmetry (see the text).

Let us make an estimation. If at first $c_0^e = c_0^i = 0$ and then c_0^e takes on a value an order smaller than the threshold one — $c_0^e = -5 \times 10^6$ cm^{-1} the resulted

curvature is significant : $R = 200$ Å. So we obtain a simple model explaining on the basis of the elastic membrane properties the ability of living cell to absorb or to excrete small amounts of matter covering them in vesicles which tear away of the cell membrane. This fenomenon is called pinocytosis. It gives an example for passing of macroscopical particles through cell walls.

4. Curvature induced polarization of a BLM with asymmetric molecules. — Here we will continue the consideration of the questions stated in the Introduction. We will assume that flip-flop is free and will calculate the change in lipid distribution between internal and external monolayer caused by deformation. In view of (7) and (8) making the assumption that $k_h^e = k_h^i$ and $k_c^e = k_c^i$ we have :

$$F^{BLM} = \frac{1}{2} k_h \left[\left(\frac{1 + \frac{d}{2}(c_1 + c_2)}{v^e A_{h0}} - 1 \right)^2 + \left(\frac{1 - \frac{d}{2}(c_1 + c_2)}{v^i A_{h0}} - 1 \right)^2 \right] +$$
$$+ \frac{1}{2} k_c \left[\left(\frac{1 + \frac{d}{4}(c_1 + c_2)}{v^e A_{c0}} - 1 \right)^2 + \left(\frac{1 - \frac{d}{4}(c_1 + c_2)}{v^i A_{c0}} - 1 \right)^2 \right] \quad (23)$$

with the relative density change x defined as in (1)

$$x = \frac{v^e - v^i}{2 v_0}$$

we have

$$v^e = v_0(1 + x) \qquad v^i = v_0(1 - x) .$$

(Positive sign of x means a transition of lipid molecules from the internal monolayer of the positively curved membrane to the external).

Now we can calculate the change of the membrane elastic energy for the case when only one molecule changes its position from the internal monolayer to the external. This quantity with negative sign will give us, like in [3] the energy difference between the two position of the choosen molecule :

$$\Delta F = - \frac{\partial F}{\partial x} \Delta x = - \frac{\partial F}{\partial x} \frac{1}{v_0} .$$

Making the approximation (for small x) that

$$(1 + x)^{-1} = 1 - x \qquad (1 - x)^{-1} = 1 + x$$

we obtain (for weak deformations $(dc)^2 \ll 1$), denoting $1/v_0$ by A_0 :

$$\Delta F = - \frac{2}{v_0} \left[k_h \left(\frac{A_0}{A_{h0}} \right)^2 + k_c \left(\frac{A_0}{A_{c0}} \right)^2 \right] x + \frac{A_0 d}{2 v_0} \left[\frac{2 k_h}{A_{h0}} \left(\frac{2 A_0}{A_{h0}} - 1 \right) + \frac{k_c}{A_{c0}} \left(\frac{2 A_0}{A_{c0}} - 1 \right) \right] (c_1 + c_2) . \quad (24)$$

The equilibrium value of x is given by Boltzman distribution. But because of the dependence of the energy difference on x itself we shall make a mean field approximation. Applying for small x Langevin's formula we will have :

$$x = \frac{\Delta F(x, c)}{2 k_B T} . \quad (25)$$

First we will give the result for symmetrical molecules when $A_{h0} = A_{c0} = A_0$. Then

$$x = \frac{d}{4}(c_1 + c_2) \left[\frac{k_h + k_c}{2 k_h + k_c} + \frac{v_0 k_B T}{2 k_h + k_c} \right]^{-1} . \quad (26)$$

Because at room temperature $v_0 k_B T \sim 10$ erg/cm^2 and $k_c \sim 200$ erg/cm^2 [11] (k_h is unknown), the temperature dependence of x is very weak and the second term in the denominator can be neglected. Putting down $k_h = 0$ one obtains Helfrich's result (1).

For the asymmetric case $A_{h0} \neq A_{c0}$ the result is :

$$x = \frac{2 A_0 \left(\frac{2 k_h}{A_{h0}^2} + \frac{k_c}{A_{c0}^2} \right) - \left(\frac{2 k_h}{A_{h0}} + \frac{k_c}{A_{c0}} \right)}{k_h \left(\frac{A_0}{A_{h0}} \right)^2 + k_c \left(\frac{A_0}{A_{c0}} \right)^2} A_0 \frac{d}{4}(c_1 + c_2) . \quad (27)$$

If the area per molecule A_0 corresponds to the equilibrium density v_0^{plan} (12) the numerator will have the form

$$2\, k_h^2 \frac{A_{co}^2}{A_{ho}} + 3\, k_h\, k_c\, A_{co} + k_c^2 \frac{A_{ho}^2}{A_{co}} > 0$$

i. e. the flip-flop is positive regardless of asymmetry. But if the area per molecule is smaller than a limmiting one

$$A^{Lim} = \frac{1}{2} \left(\frac{2\, k_h}{A_{ho}} + \frac{k_c}{A_{co}} \right) \left(\frac{2\, k_h}{A_{ho}^2} + \frac{k_c}{A_{co}^2} \right)^{-1} \quad (28)$$

the sign of the flip-flop can change to negative.

5. **Conclusion.** — At the end some comments will be made about the experimental evidences for existence of curvature — induced polarization in BLM. There are two experiments [14, 15] in which the influence of periodical deformation on the conductivity of artificial lipid membranes — modified [14] and unmodified [15] is studied. In both cases has been noticed that at the absence of any external potential difference between two sides of the membrane it is able to generate itself being periodically deformed, a. c. current with the same frequency. In [14] this effect was called definitily a peculiar kind of piezoeffect and in [15] — subharmonic noise (meaning that the frequency of the capacitive current in the presence of external voltage was twice as the frequency of the vibration). The data for the amplitude of this noise obtained in [15] on lecithin-cholesterol membrane allow determination of the value of the flexocoefficient e.

If the speed of the flip-flop is greater than the frequency of the periodical deformation

$$(\omega/2\,\pi = 50 \text{ Hz } [15])$$

the time dependence of the membrane polarization will have the form

$$P = P_{max} \cos \omega t . \quad (29)$$

As a result one obtains displacement current with density

$$i = \frac{dP}{dt} = -\omega P_{max} \sin \omega t = -\frac{I_{max}}{\pi r^2} \sin \omega t \quad (30)$$

where r is the membrane radius.

Here P_{max} is the volume polarization which is proportional in accordance to (2), to the maximal curvature of the membrane

$$P_{max} = \frac{e}{d} \cdot \frac{2}{R_{min}} . \quad (31)$$

From (30) and (31) we have

$$e = \frac{I_{max}\, R_{min}\, d}{4\,\pi r^2\, v} . \quad (32)$$

The amplitude was $I_{max} = 10^{-10}$ A (0.3 stat-coulomb.s^{-1}) at a frequency $v = 50$ Hz. The hole diameter was 2.5 mm but excluding the annulus according to [16] for the radius we get $r = 0.1$ cm. The minimal radius of the curvature can be determined from the relative change of the membrane area $\Delta A/A$ at maximal deformation

$$\frac{R_{min}}{r} = \frac{1}{2} \left(\frac{\Delta A}{A} + 1 \right) \left(\frac{\Delta A}{A} \right)^{-1/2} . \quad (33)$$

Taking the value given in [15] $\Delta A/A = 12$ % we determine

$$R_{min} = 1.9\, r .$$

Finally (32) gives

$$e = 1.5 \times 10^{-9} \text{ statcoulomb} .$$

This value is rather strong. According to the formula (3) it corresponds to a dipole moment $\mu_1 = 30$ Debye ($v = 2 \times 10^{14}$ cm^{-2}). It means that the polar head group must be in full trans conformation, because the total dipole moment of the lecithin is approximately 25 Debye [17].

But in exact determination of curvature — induced polarization a second feature should be taken into account as well : in mixed bilayers the cholesterol content of more than 30 mole % will increase the asymmetry in distribution of lecithin between the external and the internal parts of a curved bilayer (in our terms will increase x) in comparison with a pure lecithin bilayer [18]. The theory given in this report concerns only with pure bilayers. The properties of mixed bilayers, composed of lipid molecules with different asymmetry will be the object of a future work.

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