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To cite this version:

A. Petrov, Y. Pavloff. A NEW MODEL FOR FLEXOELECTRIC POLARIZATION OF BILAYER LIPID MEMBRANES AT BLOCKED "FLIP-FLOP". Journal de Physique Colloques, 1979, 40 (C3), pp.C3-455-C3-457. <10.1051/jphyscol:1979391>. <jpa-00218787>

HAL Id: jpa-00218787
https://hal.archives-ouvertes.fr/jpa-00218787
Submitted on 1 Jan 1979

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A NEW MODEL FOR FLEXOELECTRIC POLARIZATION OF BILAYER LIPID MEMBRANES AT BLOCKED «FLIP-FLOP»

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Résumé. — La polarisation flexoélectrique d’une membrane courbée avec libre flip-flop a été calculée par l’un des auteurs quelques années auparavant. Si le flip-flop est bloqué, le nombre de molécules lipidiques dans chaque monocouche de la membrane ne change pas. Dans ce cas le changement de leurs densités d’empaquetage a comme résultat le changement des composantes normales des dipôles lipidiques. On obtient une formule pour le calcul du coefficient flexoélectrique et on utilise les données expérimentales des monocouches pour calculer les coefficients flexoélectriques de différentes substances. Les résultats sont du même ordre qu’avec libre flip-flop mais ce mécanisme doit agir beaucoup plus vite.

Abstract. — The flexoelectric polarization of a curved membrane at free flip-flop was calculated by us earlier. At blocked flip-flop the number of lipid dipoles in each monolayer remains unchanged. In this case the change of their packing densities results in change of the normal component of the lipid dipole. A formula for the flexoelectric coefficient is derived and monolayer data are used in order to calculate the flexoelectric coefficient for different substances. The order of magnitude is the same as with free flip-flop. But this mechanism should be faster.

1. Introduction. — A phenomenological expression have to take place until the lipid densities become equal. In this case [2]:

\[ e = (1/2) \mu \bar{v} d (2 k_h + k_c)/(k_h + k_c) \]  

where : 
- \( \mu \) is the normal component of the lipid dipole,
- \( \bar{v} \) is the mean lipid density,
- \( d \) is the membrane thickness, 
- \( k_h, k_c \) is the elastic moduli per head, resp. chains.

2. The model. — In the case of blocked flip-flop lipid transitions are impossible. The change of lipid packing (more compact in the inner monolayer and more loose in the outer-one in comparison with the non-deformed state) results in some changes in the polar head’s conformation and in the water structured around each head. Consequently, the resultant normal component of the dipole moment per lipid molecule in the outer expanded monolayer and in the inner compressed monolayer will change in an opposite manner. So, a dipole debalance in respect to the mid-plane (non-stretched) will arise and the curved membrane will be polarized (see Fig. 2). For the calculation of the flexoelectric coefficient, expressing the proportionality between curvature and polariza-
3. Monolayer data. — Experimental data for surface potential measurements are used here in order to calculate flexoelectric coefficients for different substances. The surface potential \( \Delta V \) due to the presence of dipolar lipid molecules spread at an interface can be measured experimentally. It is determined by the following expression [5] (see Fig. 3):

\[
\Delta V = 4 \pi \mu / A
\]  

where:

\[
\mu = \mu_{\text{head}} + \mu_{\text{H}_2\text{O}} + \mu_{\text{end}}
\]  

The polarization \( P \) in this case is merely similar to the polarization under bending of a bimorph plate, composed by two halves with opposite directions of the polar axes. Considering dipolar densities as spread over the whole membrane thickness one can reach an equivalent description in terms of quadrupolar densities [3]. A quadrupolar model was recently applied to layered smectic systems [4].

4. Results. — A. Dipalmitoyl lecithin, air-water interface [6]:

- \( \mu (60 \, \text{Å}^2) = 0.72 \, \text{D cons.} \)
- \( \mu (44 \, \text{Å}^2) = 0.64 \, \text{D cons.} \)

\[
d\mu / dA \approx \Delta \mu / \Delta A = 5 \times 10^{-5} \, \text{statcoul., so:}
\]

\[
e = 5 \times 10^{-11} \, \text{statcoul. at 52 Å}^2
\]  

B. Dipalmitoyl lecithin, air-water interface [7] (see Fig. 4). From the slope of the curve \( \mu (A) \) at 25°C below 45 Å² (condensed state of the monolayer) we obtain:

\[
e = 8.3 \times 10^{-11} \, \text{statcoul. at 44 Å}^2 \text{ and 25°C.}
\]  

![Fig. 3](image-url)  

**Fig. 3.** Schema of the surface potential measurements: lipid dipoles and oriented water dipoles contribute to \( \Delta V \).

![Fig. 4](image-url)  

**Fig. 4.** Surface potential (\( \Delta V \)), area (\( A \)) and surface dipole moment per molecule (\( \mu \)) curves for L-α-dipalmitoyl lecithin at air/water interface (after Vilallonga, ref. [7], Fig. 1). The flexoelectric coefficient is determined from the slope of the curve \( \mu (A) \) for 25°C in the region below 45 Å².
In this case, the maximal value of the flexocoefficient corresponds to the area at which no dependence of $\Delta V$ on $A$ is observed, so that in expression (8) one can put $d\Delta V/dA = 0$ (see Fig. 5). The results are:

$$e = 8.7 \times 10^{-11} \text{statcoul.} \text{at } 59 \, \AA^2 \text{and } 20 \, ^\circ\text{C} \quad (11)$$
$$e = 7.4 \times 10^{-11} \text{statcoul.} \text{at } 73 \, \AA^2 \text{and } 6 \, ^\circ\text{C}. \quad (12)$$

5. **Conclusion.** — The arising of a polarization in our new model is, as we pointed out, merely similar to the polarization under bending of a bimorph plate, composed by two halves of piezoelectric material with opposite directions of the polar axes. The order of magnitude is the same as with free flip-flop [9]. But this mechanism should be faster, because no redistribution of the lipid material after bending is necessary. In fact, the two mechanisms appear as two limiting cases — when the first is operating, the second is not active (no change of the area per head) and vice versa.

It was found very recently that in a mixed system (dipalmitoyl lecithin + sphingomyelin) the variation $d\psi/dA$ is more pronounced [10]. These findings increase the importance of our new mechanism for native membranes, which are complicated mixtures of different lipids.

**References**


