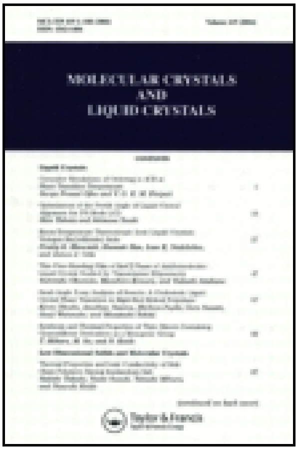

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Liquid Crystal Physics and the Physics of Living Matter

Alexander G. Petrov [a]

[a] Biomolecular Layers Department, Institute of Solid State Physics, Bulgarian Academy of Sciences, 72 Tzarigradsko chaussee, 1784, Sofia, Bulgaria

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Liquid Crystal Physics and the Physics of Living Matter

ALEXANDER G. PETROV

Biomolecular Layers Department, Institute of Solid State Physics, Bulgarian Academy of Sciences, 72 Tzarigradsko chaussee, 1784 Sofia, Bulgaria

Nowadays, a modern physical theory becomes of a principle importance in understanding the complexities of the living world: the physics of lyotropic states of matter. We demonstrate here what kind of specification is necessary in the molecular description of lyomesogens, in the theory of elastic and flexoelectric phenomena, in order to make this part of liquid crystal physics suitable for describing and understanding the complex behaviour and structure-function relationship of biomembranes. We underline the role of a mechanical degree of freedom, the curvature, of liquid crystal systems, both model and living ones. Moreover, we stress the interrelation of the mechanical degree of freedom to the electrical, optical and chemical degrees of freedom of membranes, resulting in the sophisticated living cellular mechanisms.

Keywords: lyotropics; biomembranes; elasticity; flexoelectricity

INTRODUCTION

Today it is broadly recognized that the mesomorphic, liquid crystal state is the most suitable state for living matter, as it combines molecular order and disorder in a very special manner that is between the fully disordered isotropic fluid state which is dead, and the complete order of solid state that is again dead.

Biophysical studies of the lyotropic state are already based on the established general principles and methods of liquid crystal physics. However, in view of the higher and increasing degree of complexity of the structural organization of the new mesomorphic objects the need for a considerable specification and justification of these general principles must be underlined.

We show below what kind of specification is necessary in the molecular and continual description of lyotropics in order to make this part of liquid crystal physics suitable for describing and understanding the complex behaviour and structure-function relationship of biomembranes.

Schrödinger (1943) has observed that unlike dead matter that in most cases follows statistical laws, living matter obeys dynamical laws producing order out of order, i.e., that existing order in the living matter tends to support itself and to replicate in ordered phenomena[1]. To follow dynamical laws, a cell should function like a mechanism (the famous "clock mechanism analogy" of Schrödinger). On the other hand, any mechanism requires the existence of a mechanical degree of freedom.

MEMBRANE CURVATURE AND CURVATURE ELASTICITY

Biomembranes constitute the basic building units of the majority of cells and cellular organelles. The plasma membrane is the envelope of the cell; it serves a barrier function and manages the recognition of the same and other cell types. Endoplasmic reticulum membranes form a complicated network within the cytoplasm. Mitochondrial and chloroplast membranes enable the processes of energy transformation in the cell. The nuclear membrane separates the genetic substance, DNA, from the cytoplasm in the cells of higher organisms (eukaryotes), etc.

It appears that most membranes are built up according to the general principles of lyotropic liquid crystal structures. The basic molecules of biomembranes are lipids and proteins. A common feature of these qualitatively different types of biomolecules is their biphilicity. According to the widely accepted "fluid lipid-globular protein mosaic model"[2-5] lipids and proteins are arranged in the membrane in such a way that their hydrophilic groups are in contact with the water environment while hydrophobic groups are isolated from it. Lipids are organized in a bilayer in which the proteins are immersed. Model membranes containing lipids only, or lipids with just one type of protein, etc., are also well known.

A membrane has a number of mechanical degrees of freedom: area stretching, thickness compression, shear deformation, chain tilting, and, notably, curvature deformation. The last one, curvature, is just a liquid crystal degree of freedom since membrane curvature is equivalent to a splay of lipid chains (under the condition that chains remain parallel to the local normal in each point of the curved bilayer). Curvature free energy per unit area up to the second order reads[6]:

$$w_c = \frac{1}{2}K\left(c_1 + c_2 - c_0\right)^2 + \overline{K}\, c_1 c_2 \,, \tag{1}$$

where $c_1 = 1/R_1$, $c_2 = 1/R_2$ are principal curvatures of the membrane, K and $\overline{K}$ are elastic moduli of curvature and saddle curvature (with a dimension of J) and c_0 (m^{-1}) is the so-called "spontaneous curvature". K and $\overline{K}$ are analogical to k_{11} and k_{24} in Oseen-Frank elastic theory of liquid crystals; however, these are measured in J, not in N, since Eq.(1) represents an area density, not a volume one. Roughly speaking then, it holds: $K = k{\cdot}d$, where d is membrane thickness.

A number of experimental techniques, micromechanical and fluctuation ones, were developed in the last 20 years in order to measure curvature elastic moduli of both model and living membranes (for recent data collection see [7]). Typical order of magnitude of K is 10^{-19} J. This means that it requires very little energy to induce membrane curvature; even thermal energy k_BT can do that. Therefore, in many cases extensive thermal fluctuations of membrane curvature can be observed. The condition for this is a vanishing lateral membrane tension (another mechanical degree of freedom). Configurations of liquid crystal membranes and giant vesicles, involving also remarkable topological changes, are well understood in terms of curvature elasticity theory[8,9].

Another important step is the development of theoretical models for curvature elastic moduli. A rather general model describes these in terms of integrals of the lateral stress distribution $s(z)$ across a flat membrane, involving also derivatives[10, 11]:

$$\begin{aligned} K &= \int (z - z_0)\left(\frac{\partial\, s(z)}{\partial\, c_+}\right)_{0,0} dz \,, \\ Kc_0 &= -\int (z - z_0)\, s(z)\, dz \,, \\ \overline{K} &= \int (z - z_0)^2\, s(z)\, dz \,, \end{aligned} \tag{2}$$

where z_0 is the neutral surface of the membrane and $c_+ = c_1 + c_2$. If we assume a model stress distribution in the form (δ is Dirac δ-function):

$$s(z) = P_H\,\delta\left(z - \delta_H\right) + P_C\,\delta\left(z - \delta_C\right), \tag{3}$$

where

$$P_H = \frac{k_H}{H}\left(\frac{A_H}{H} - 1\right), \qquad A_H = A_0[1 + \delta_H(c_1 + c_2) + \delta_H^2 c_1 c_2]$$

$$P_C = \frac{k_C}{C}\left(\frac{A_C}{C} - 1\right), \qquad A_C = A_0[1 + \delta_C(c_1 + c_2) + \delta_C^2 c_1 c_2]$$

we shall immediately obtain from Eqs. (2) the corresponding elastic moduli of the PDM-model[12, 7] in terms of 4 parameters: k_H, k_C, H and C. PDM-model provides a transparent presentation of the effect of steric asymmetry $(H - C)$ of membrane molecules upon its elastic properties.

Besides steric asymmetry, several other types of molecular asymmetry (electric, biphilic, flexible) have been introduced and their description in terms of generalized multipoles (monopole, dipole, quadrupole) forms the framework of the generalized molecular asymmetry (GMA) model[7]. In this way an important task of the liquid crystal physics: to trace the way of how to relate membrane chemistry to membrane mechanics, has been fulfilled.

MEMBRANE CURVATURE AND FLEXOELECTRICITY

In the case of membranes flexoelectricity stands for curvature-induced membrane polarization[13, 7]:

$$P_s = f(c_1 + c_2), \tag{4}$$

where P_S is the electric polarization per unit area in C/m and f is the *area* flexoelectric coefficient in C (coulombs) -- not in C/m like the bulk case. This effect is manifested in liquid crystalline membrane structures where an overall curvature is related to an orientational deformation of splay type of membrane molecules (lipids, proteins) (*cf.* [14]). Across a polarized membrane a potential difference will develop according to Helmholtz equation:

$$\Delta U = P_s/\varepsilon_0 = (f/\varepsilon_0)(c_1 + c_2) \,. \tag{5}$$

Like piezoelectric effect in solid crystals, the flexoelectric one can also be manifested as a direct effect (Eq. 5) and a converse effect, featuring electric field-induced curvature[15]:

$$c_1 + c_2 = (f/K)E, \tag{6}$$

where E is the transmembrane electric field and K is curvature elastic modulus, see Eq. (1). Eq. (6) is valid for a tension-free membrane (identically zero lateral tension), which is the case in an osmotically balanced cell.

Exploring molecular mechanisms of flexoelectricity is a central task of the liquid crystal approach in the membranology[16, 17, 7]. Analogically to elastic moduli, f can also be represented as an integral over the derivative of $P_z(z)$, the distribution of bulk polarization across the membrane:

$$f = \int \left[\partial P_z(z) / \partial c_+ \right] dz \qquad (7)$$

Model distributions including monopoles, dipoles and quadrupoles of lipids and proteins have been considered[7], revealing respective contributions to f.

Existence of flexoelectricity was proven both in model membranes[18-23] and in patches excised from native membranes of locust muscle[22, 23]. If we take $f = 1 \cdot 10^{-20}$ C and a relatively mild curvature for a biomembrane surface of a radius 100 nm (i.e. 20 times membrane thickness), we can calculate from Eq. (5) a transmembrane voltage amplitude of 23 mV, a very substantial value. It can be produced by spending curvature elastic energy as low as $4\pi K$ (for a hemispherical bleb), i.e. $8.8 \cdot 10^{-20}$ J = 22 k_BT. The curvature, induced by transmembrane potential due to converse effect (Eq. 6) is also very large.

First striking impression when looking at an electron micrograph of a cell is that cell membranes very often tend to be strongly curved. Unlike tensile or compressive strain, it is very easy to sustain curvature torques in a membrane because of the smallness of the curvature elastic modulus (see above). Examples include the highly convoluted cristae of inner mitochondrial membranes in energized mitochondria, the edges of retinal rod outer segments and discs, the tylakoid membranes of chloroplasts, the brush borders of intestinal epithelial cells, the spiculae tips in echynocytes, the microvilae between contacting cells, the stereocilia in the hearing organ, etc., etc. In many cases this curvature is dynamic. There is a good evidence that the peripheral protein network of a red blood cell membrane is capable of producing membrane curvature at its contraction.

Many important membrane functions are connected with the creation of membrane curvature at a certain stage (e.g., endocytosis, virus budding, cell and organelle morphogenesis, cell movement by pseudopodia, and cell contact). The out-of-plane fluctuations of membranes (e.g., the flicker phenomenon in erythrocytes) provide a typical example of fluctuating membrane curvature. In all these phenomena curvature-induced polarization is by no means present, and the acknowledgement of the consequences of its presence can be of crucial importance for deeper understanding of what happens[7]. Therefore, the prospect of flexoelectricity as a intricate relationship between membrane mechanics and membrane electrodynamics, is rather high.

To begin with, it is closely related to the mechanosensitivity and mechanotransduction, basic features of living systems[24].

PHOTOFLEXOELECTRICITY

A further, optical degree of freedom of membrane systems remained until recently relatively unexplored in a flexoelectric context. The prospective value of such a development seems obvious from the discussion above. An opto-mechano-electric membrane model system would greatly increase the number of possible combinations between its three degrees of freedom (serving either as inputs or outputs). Above all, due to the ultimate existence of these degrees of freedom in some native membranes, new hints about the structure-function relationship in photosynthetic membranes, retinal rods and discs, and other photoactive membranes could be obtained.

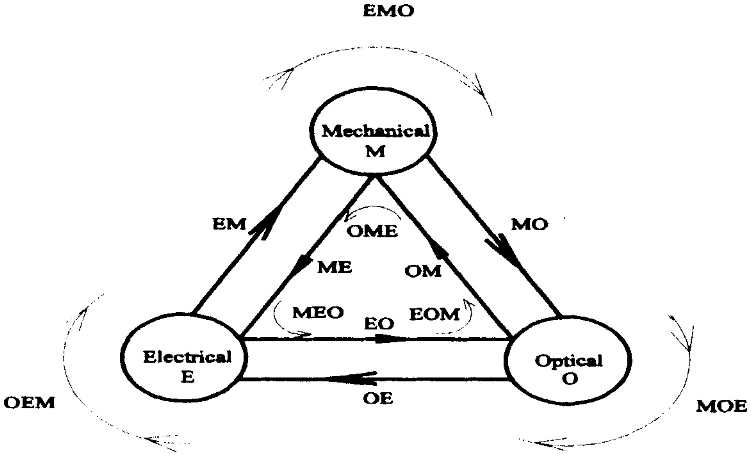

FIGURE 1 Possible mechanisms of energy interconversion in flexible photoactive membranes. Effects involving two degrees of freedom of the membrane system are marked by 2 letters (e.g., ME and EM, the direct and converse flexoeffect) and those involving 3 degrees of freedom by 3 letters (e.g., OME, opto-mechano-electric effect, *viz.* photoflexoelectric effect).

Black lipid membranes decorated with nanoparticles of photo-semiconductors, "nanomembranes"[25] represent a new model system having the three degrees of freedom into consideration. Like some biomembranes, they are then capable of the transformation of the three types of energy one into another. The new effect, called photoflexoelectricity, was recently observed in nanomembranes[26], and earlier in photoactive BLM containing bacteriorodopsin or retinal-acetate.

In a physical system with 3 degrees of freedom (mechanical, electrical and optical) the possible energy interconversion effects, involving 2 or 3 degrees of freedom simultaneously, can be classified in the way shown in Fig. 1.

Besides photoflexoelectricity, the rest of the combined 3-degrees' effects in Fig. 1 has not been demonstrated yet, and represents a promising field for future studies. Chemical degree of freedom was not specially discussed here, although it is inherent to all the others, for the values of elastic moduli, flexoelectric coefficient, etc., depend crucially on the membrane chemistry.

Finally, we should underline a very important feature of a membrane system having two or more degrees of freedom: the possibility of occurrence of deterministic chaos in it[27]. According to the Bendixon-Poincaré theorem, a dynamic system can be chaotic only in a three- or higher-dimensional phase space. On the other hand each degree of freedom provides one generalized coordinate and one generalized force. Therefore, a flexoelectric membrane does possess all the necessary features for the arising of dissipative, self-organizing structures. These should have played a very important role already at the level of prebiotic evolution of matter[27].

CONCLUSION

We underlined the role of a mechanical degree of freedom, the curvature, of liquid crystal systems, both model and living ones. Moreover, we stressed the interrelation of the mechanical degree of freedom to the electrical, optical and chemical degrees of freedom of membranes. This really makes the clock mechanism analogy of Schrödinger richer, as the "live" clock could now be not just mechanical, but, for example, electro-mechano-optical (note a perfect analogy with the electronic wristwatch, based on Schadt-Helfrich twist effect), chemi-mechanical, etc.[7]. Thus, a modern physical theory: the physics of lyotropic states of matter becomes of a principal importance in understanding the complexities of the living world.

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