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Review

# Electricity and mechanics of biomembrane systems: Flexoelectricity in living membranes

Alexander G. Petrov *

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

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**Abstract**

Flexoelectricity provides a reciprocal relationship between electricity and mechanics in membranes, i.e., between membrane curvature and polarization. Experimental evidence of biomembrane flexoelectricity (including direct and converse flexoelectric effect) is reviewed. Biological implications of flexoelectricity in membrane transport, membrane contact, mechanosensitivity, electromotility and hearing are underlined. Flexoelectricity enables membrane structures to function like soft micro- and nano-machines, sensors and actuators, thus providing important input to molecular electronics applications.


*Keywords:* Biomembrane; Curvature; Polarization; Flexoelectricity; Mechanosensitivity; Electromotility; Hearing; Soft membrane machines

**Contents**



## 1. Introduction

Biomembranes are built up according to the general principles of lyotropic liquid crystals [1]. The celebrated "fluid lipid–globular protein mosaic model" [2–4] implies that lipids

* Tel.: +359 2 875 80 61; fax: +359 2 975 36 32.
*E-mail address:* director@issp.bas.bg.

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are organized in a liquid crystal bilayer in which integral proteins are embedded. However, membranes with high protein concentration [5], where lipids do not form a continuous bilayer but rather patch the spaces between proteins, while proteins themselves are arranged in a double-tiered pattern, are also well known (cf. "structure–function unitization model of biomembranes" [6]). In both cases, though, the principles of liquid crystal physics [7] (viz., long range translational disordering versus long range orientational ordering of constituent chain or rod-like molecules) are valid.

Flexoelectricity is a liquid crystal analogue of piezoelectricity. Instead of a translational mechanical degree of freedom of a membrane in the case of piezoelectricity (i.e., area stretching, thickness compression, etc.), flexoelectricity involves an orientational degree of freedom, the membrane curvature. First striking impression when looking at an electron micrograph of a cell is that cell membranes very often tend to be strongly curved on a nanometer length scale. Unlike tensile or compressive strains, it is very easy to sustain curvature strains (i.e., torques) in a membrane because of the smallness of its curvature elastic modulus $K$ [7]. In many cases this curvature is dynamic [56].

The first consideration that membranes might have piezoelectric properties goes 64 years back in a discussion of the possible origin of inductance in the squid giant axon [8]. The first biological implication of flexoelectricity in membrane ion transport is half that age [9]. Recently, experimental evidence of native membrane flexoelectricity emerged that will be reviewed below. Most up-to-date methods of membranology (patch clamp, AFM, laser tweezers and confocal microscopy) are employed today for that purpose. Therefore, the effective use of flexoelectricity concept in most membrane processes, where curvature changes are taking place, is now broadly open. 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 tips of spiculae in echynocytes, the microvilae between contacting cells, the stereocilia in the hearing organ, etc.

Nowadays, it becomes increasingly clear that in nanoscience of condensed matter (living matter included) mechanics plays a very important role. It is often so tightly coupled to electricity that it could not be considered separately. Unlike microelectronics where as a rule only electrons are moving, while nuclei stay at rest, in molecular electronics both charges and nuclei are supposed to move. This makes nanosystems much more similar in their performance to machines, as compared to microsystems. The basic reason for this is the softness of molecular electronics media: liquid crystals, lyotropics, macromolecules, etc.

Flexoelectricity is the basic mechanoelectric effect which enables the nanometers thick membranes of living matter to function like soft machines, thus converting electric stimuli of the living world into mechanical ones, and vice versa. It also permits, by using model nanomembranes, to construct mechanosensors and electric actuators for molecular electronics applications.

Present review is concentrated upon the manifestation of flexoelectricity in living membranes and the lessons one can learn from the living matter about perspective flexoelectric applications in molecular electronics.

## 2. Flexoelectricity, membrane curvature and polarization

Flexoelectricity is a basic mechanoelectric phenomenon in liquid crystal physics [10]. The original phenomenological expression of Meyer [10] for the *bulk* polarization of a 3D liquid crystal subjected to a splay or bend deformation reads:

$$P_V = e_{1z}(s_1 + s_2) + e_{3x}b, \tag{1a}$$

where $P_V$ is the electric polarization per *unit volume* (in C/m$^2$), $s_1$ and $s_2$ the two components of splay, $b$ the component of bend (all these being expressed by the partial space derivatives of the liquid crystal director [10], in m$^{-1}$) and $e_{1z}$ and $e_{3x}$ are splay and bend flexoelectric coefficients in C/m, respectively.

In the case of a 2D liquid crystal membrane, flexoelectricity means curvature-induced *area* membrane polarization, or electric field-induced membrane curvature. For the curvature-induced membrane polarization the phenomenological expression of Petrov in 1975 reads [9,7]:

$$P_S = f(c_1 + c_2). \tag{1b}$$

Here $P_S$ is the electric polarization per *unit area* (in C/m), $c_1$ and $c_2$ the two principal radii of membrane curvature (in m$^{-1}$) and $f$ is the area flexoelectric coefficient (in coulombs (C)), typically a few units of electron charge. The flexocoefficient is regarded positive if polarization points outward the center of curvature. This effect is manifested in liquid crystalline membrane structures because a curvature of membrane surface leads to a liquid crystal deformation of splay type (cf. [10]) of lipids and proteins. These molecules are otherwise oriented parallel to each other along the local membrane normal in flat state. A correspondence between the two phenomenological formulae (1a) and (1b) can be established by considering that bend deformation of the director is not allowed in a 2D membrane, director itself is represented by membrane normal, and director splay is expressed by the principal membrane curvatures $c_1 = 1/R_1$ and $c_2 = 1/R_2$. Then, from dimensional arguments one can conclude that $f = e_{1z}d$, where $d$ is membrane thickness. Thus, phenomenologically there is a close analogy between liquid crystal and membrane flexoelectricity. However, molecular mechanisms of the two are very different, e.g., molecular shape asymmetry is not a precondition for membrane flexoelectricity (see [7] and below). According to the Helmholtz equation an electric potential difference appears across a polarized surface. In view of Eqs. (1a) and (1b) the curvature-dependent part of this potential difference is:

$$\Delta U = \frac{P_S}{\varepsilon_0} = \left(\frac{f}{\varepsilon_0}\right)(c_1 + c_2), \tag{2}$$

and it is a measure of the direct flexoelectric effect. By measuring the total curvature and the curvature-induced potential difference we can determine the flexoelectric coefficient of any given membrane.