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CURVATURE ELASTICITY OF SMECTIC A LIPID BILAYERS AND CELL PLASMA MEMBRANES

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I. INTRODUCTION

The bending elasticity (in the language of liquid crystal physics called splay elasticity) is an important property of (tension free) monolayers of amphiphiles and lipid bilayers. It plays a role in the formation and stabilization of microemulsions[1], the swelling of lipid bilayers[2], and the shape transformations of cells and vesicles[3,4]. The bending stiffness also determines the amplitudes of thermally excited surface undulations and in this way contributes to the interplay of Van-der-Waals attraction dehydration forces, electrostatic and steric repulsion between flaccid interfaces and cells[5,6]. For the above mentioned reasons, precise measurements of the bending elastic moduli of lipid layers and natural membranes have become an important task of lyotropic liquid crystal research. Such measurements can be performed by classical perturbation methods such as the micropipette technique[3] or the recently developed electric field jump technique[4], 7. A completely different, non invasive method is based on the Fourier analysis of thermally excited surface undulations of vesicles or cells[7,8,9,10]. In the following, we present measurements of the bending elasticity of giant vesicles and erythrocyte membranes by the latter technique. It is shown that, by determining the mean square amplitudes of the undulations as a function of their wavevector, it is possible to improve the accuracy of the measurement remarkably. Secondly, we address the question of modification of the bending elasticity of lipid bilayers by solutes. Thirdly, we report experiments which provide evidence that the red blood cell controls the membrane elasticity in an active

way. This is suggested by quasiperiodic oscillations of the bending stiffness.

II. THERMALLY EXCITED SURFACE UNDULATIONS

Consider an infinitely large plasma membrane. The average mean square amplitudes, $\langle u_q^2 \rangle$ of the thermally excited undulations of wavevector q depend on the two-dimensional bending (or splay) elastic modulus K_c, the shear elastic modulus μ, and the lateral tension σ as follows:

$$\langle u_q^2 \rangle \propto \frac{k_B \cdot T}{K_c q^4 + \mu q^2 + \sigma q^2} \tag{1}$$

The long wavelength excitations are dominated by the bending elasticity provided μ and σ are small compared to $K_c \cdot q^2$. For the microscopic techniques described in the following text, the upper limit of observable wavevectors is about $q < 10^5 cm$. Since the bending elastic modulus is of the order of $K_c \approx 10^{-12} erg$, the other two elastic constants would have to be small compared to $10^{-2} mN \cdot m^{-1}$. The dynamic technique is thus restricted to lipid layers in the smectic A state for which $\mu = 0$. In order to eliminate the tension term it is sufficient to study non-spherical vesicles or cells. For these the lateral tension does not contribute since the elastic energy is a minimum with respect to the total membrane area.

III. BENDING STIFFNESS OF LIPID BILAYERS

Quasi-spherical vesicles exhibit pronounced shape fluctuations if the lipid bilayer is in a fluid (= smectic A) state. These can be described in terms of spherical harmonic excitations of the vesicle shell[8,10,12]. The excess elastic free energy is

$$\langle F_{el} \rangle = \frac{1}{2} \cdot K_c \cdot \frac{\sum_{l,m}^{\infty} (l+1)^2 \cdot (l-2)^2}{a^2} \cdot U_l^{m\,2} \tag{2}$$

In phase contrast microscopy, one only observes fluctuations of the contour $R(\varphi)$ of the vesicles. The shape fluctuations are analyzed in

terms of a Fourier expansion of $\Delta R(\varphi) = R(\varphi) - R_0(\varphi)$ where $R_0(\varphi)$ is the average contour. .

$$R(\varphi) \propto \sum_{q}^{\infty} u_q \cdot e^{iq\varphi} \tag{3}$$

Fortunately, a 1:1 correspondence exists between the mean square amplitudes $\langle u_q^2 \rangle$ and $\langle U_l^{m2} \rangle$ so that K_c can be determined. The advantage of the present method is that the mean square amplitude of each mode yields a value of the elastic constant which improves the accuracy of the measurement drastically. In addition, it is possible to detect wavevector dependencies of the elastic bending stiffness.

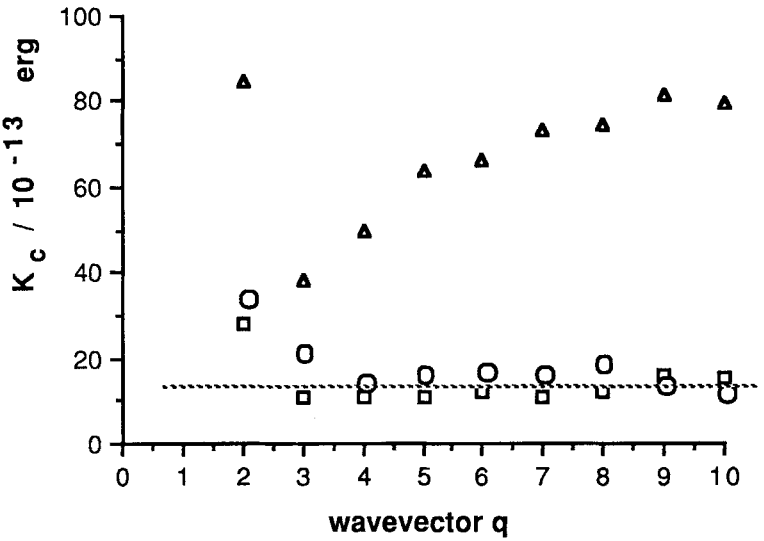

FIGURE 1. (□, ○) Plot of bending elastic constant K_c as function of the wavevector q for vesicles of DMPC.
(△) wavevector dependence of K_c for vesicles composed of 70% DMPC and 30% cholesterol.

FIG 1. (□, ○) shows measurements of K_c for different vesicles of DMPC. In all cases, the value found for the second mode ($l = 2$) is by a factor of two higher than those obtained for $l > 2$. The

values are reliable up to the 8^{th} mode. The values of K_c obtained for the different vesicles range from $K_c = 1.0 \cdot 10^{-12}$ *to* $2 \cdot 10^{-12} erg$. However, the vesicles with the highest values are certainly not single walled whereas those with the two lowest values appear very thin and are most probably single-walled. Thus we conclude that the smallest value of $K_c = 1,1 \cdot 10^{-12} erg$ corresponds to the bending elastic modulus of a single-walled bilayer.

FIG 1. ($\triangle$) shows a similar K_c - measurement for DMPC vesicles containing $30 mole$ % of cholesterol. Firstly, flexural rigidity for long wavelength modes increases K_c by a factor of four which agrees with micropipette measurements of Evans and Needham[14]. Secondly, the bending rigidity increases remarkably with decreasing undulation wavelengths. Possibly this effect is due to the hindrance of the mutual slip of the two opposing monolayers by cholesterol.

IV. BENDING ELASTICITY OF ERYTHROCYTE PLASMA MEMBRANE

When erythrocytes are viewed through a phase contrast microscope, one observes pronounced fluctuations of the light intesity passing the cells. The origin of this famous flickering phenomenon are cell thickness fluctuations caused by thermally excited membrane oscillations. According to Brochard and Lennon, the bending elastic modulus can be obtained by analysing the power spectrum of the intensity fluctuations of the light passing the cell [9]. Each overdamped undulation mode contributes a Lorentian line, and the total power spectrum is given by

$$P(\omega) = \frac{2 \cdot S \cdot k_B \cdot T}{\eta} \cdot \int_{q_{min}}^{q_{max}} \frac{dq}{\omega^2 + (K_c q^3 / 2\eta)^2} \qquad (4)$$

where η is the viscosity of the cytoplasm, S the area of the cell surface, and q the undulation wave vector. The above quotation holds if the undulations of the two membranes of the cell are uncorrelated. The elastic modulus K_c and the viscosity of the cytoplasm are obtained

by computer simulation of the flicker power spectrum $P(\omega)$. This technique is very sensitive and is best suited to detect and to analyze changes in the membrane bending elasticity caused by drugs or physiological changes of the cells but it is difficult to obtain absolute values for K_c. This goal is better achieved by a recently developed technique of analysis of membrane undulations, the reflection interference contrast (RIC) microscopy[13] (cf. Fig. 2).

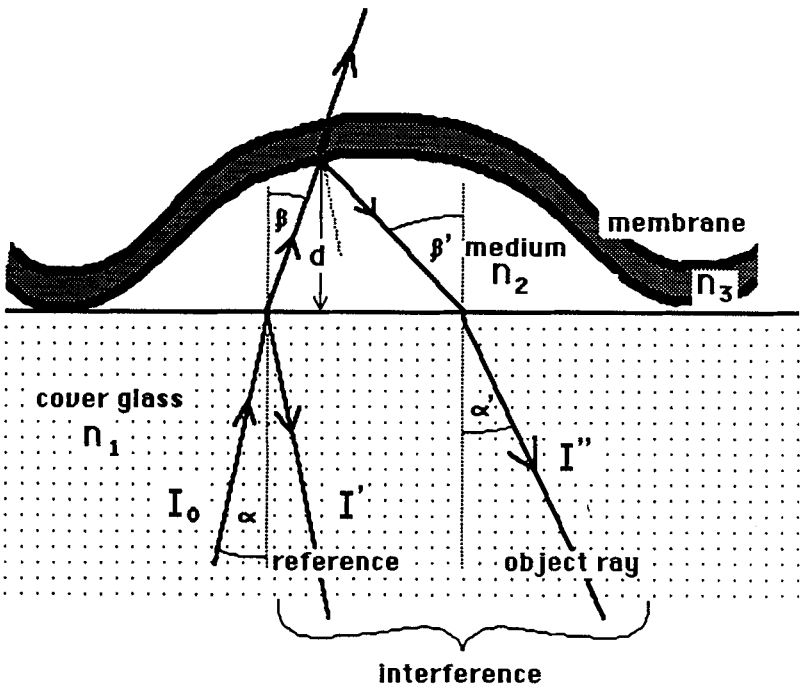

FIGURE 2. Principle of interference contrast microscopy. The light rays reflected from the glass plate and the cell surface interfere and form a Newtonian type of interference pattern. Flickering leads to dynamic lateral distortions of the Newtonian rings.

The mean square amplitude and thus K_c can be determined by Fourier analysis of the transient lateral deformations of a Newtonian ring in analogy to the analysis of the contour of the vesicles[11]. A much more precise method is based on the Fourier transformation of the RIC image. This goal has been achieved by numerical methods (A. Zilker, Diploma Thesis, Munich 1986). Figure 3 presents measurements of K_c for three different cells of different donors as well as for an aged cell. It is seen that K_c does not depend remarkably on the wavelength of the undulations between $0.5\mu m$ *and* $1.0\mu m$ as predicted by the theory. The K_c values measured in this region can thus be regarded as reliable. Their apparent increase at $l > 1\mu m$ is caused by interference of the Fourier transformations of the undulations and the resting form.

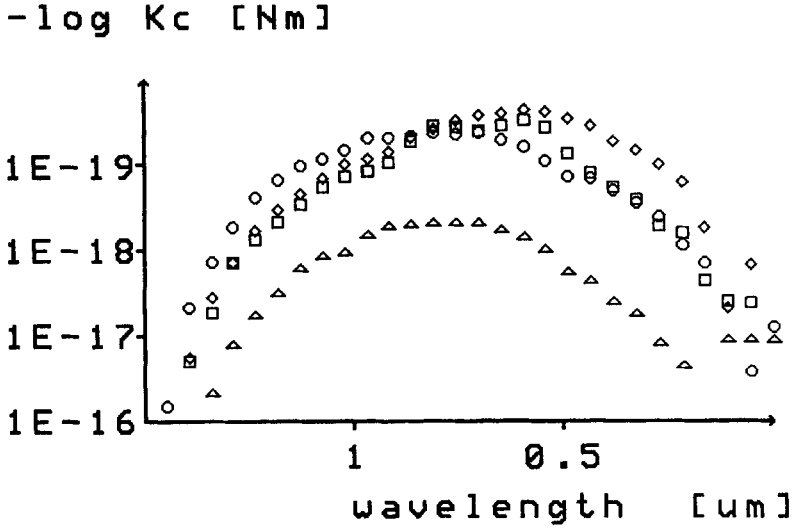

FIGURE 3: Plot of the negative logarithm of bending elastic modulus of erythrocytes as measured by reflection interference contrast technique. Measurements of three different freshly drown cells of three different donors ($\Box, \circ, \Diamond$) and of a cell which was aged photochemically ($\triangle$) are shown. Obviously, reliable values for K_c are obtained for wavelengths between 0.5 and $1\mu m$ (plateau region).

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