

A STUDY OF PHASE TRANSITIONS IN PHOSPHATIDYLCHOLINE AND PHOSPHATIDYLETHANOLAMINE MODEL MEMBRANES USING POLARIZING MICROSCOPY

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A modification of the polarizing microscope and its use for the measurement of phase transition temperature in model phosphatidylcholine and phosphatidylethanolamine membranes are described in the present paper. The accuracy of the method is comparable to the accuracy of differential scanning calorimetry. In the dipalmitoylphosphatidylcholine model membrane, the intensity of the light transmitted through a sample placed between crossed nicols shows a sharp maximum at the main gel — liquid crystal ($P_g \rightarrow L_\alpha$) phase transition temperature 314.9 ± 0.1 K and than abrupt decrease within 0.4 K. It is supposed that the cusp-like behaviour of the light intensity is connected with the critical phenomena at the phase transition.

I. INTRODUCTION

Phospholipids are thought to be basic constituents of biological membranes. The most important of these are phosphatidylecholines and phosphatidylethanolamines. The basic structure of the phospholipid moiety of biological membranes seems to be a bimolecular layer into which the other constituents are inserted [1]. Structural and dynamical properties of the bilayer affect the ordering, the rotational and translational diffusion of the membrane constituents as well as the transport of different substances through the membrane, i.e. they also control the biological processes in which the membranes participate [2]. Bilayers of phospholipids are also the basic structural unit of lamellar lyotropic liquid crystals, which form spontaneously because of interactions of amphiphilic lipids with water. This is why lyotropic liquid crystals are widely used as experimental models of the lipid part of biological membranes in studies of the physical

properties of bilayers [3]. One of the principal physical parameters characterizing the thermotropic properties of lyotropic systems are the temperatures of phase transitions between solid-like (gel) and fluid (liquid crystalline) states. In our paper we describe the use of polarizing microscopy for the automatic detection of phase transitions in model phospholipid membranes. A similar experimental technique has been described by several authors, for example Suter [4] and Onogi et al. [5] used it for the investigation of phase transitions in thermotropic liquid crystals, Sakakurai and Iwayanagi [6] applied it in the studies of structural changes in the dipalmitoylphosphatidylcholine single crystal, and, finally, Petrov et al. [7] and Gawrisch et al. [8] in lyotropics. Our work was inspired by the papers [7, 8], we use similarly as experimental model membranes the lyotropic systems phosphatidylcholine — water and phosphatidylethanolamine — water.

II. MATERIAL AND METHODS

The basic component in measurements of phase transition temperatures of model membranes was a polarizing microscope. The microscope was supplemented by a temperature stabilized cell with a sample holder, an unit for the temperature measurement and control and an unit for the measurement of polarized light intensity.

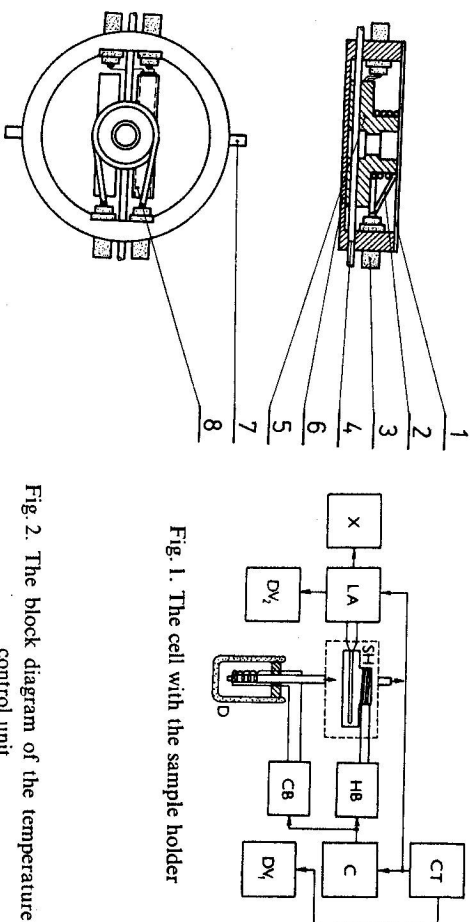


Fig. 1. The cell with the sample holder

Fig. 2. The block diagram of the temperature control unit

The cell with the sample holder is schematically depicted in Fig. 1. The sample in a glass capillary 4 is inserted into a brass sample holder 5. The sample holder can be heated electrically by a canthal wire 2; it can be also cooled by gas passing through the tubes 7. The temperature is measured using a platinum

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resistor 8 placed in the sample holder 5 close to the sample capillary 4. The whole sample holder is encased in a teflon mantle 6, and covered by a teflon cap 1. The connectors 3 are built into the teflon mantle 6.

The block diagram of the unit for the temperature measurement and control is shown in Fig. 2. The comparator C compares the temperature set by the control block CT (and read by a digital voltmeter DV₁) with the temperature measured by a platinum resistor, and regulates the heating block HB and the cooling block CB according to the heating and cooling rates (i.e. the heater output and rate of gas flow, respectively) set up independently. The temperature of the sample holder SH (measured by the platinum resistor) is converted into voltage directly proportional to the temperature by the linearizing amplifier LA. The reading of the measured temperature (voltage on the LA) is possible via a digital voltmeter DV₂ and/or via an X input of the XY recorder. The digital voltmeters DV₁ and DV₂ have a BCD output.

The optical layout is schematically shown in Fig. 3. The sample holder SH in the teflon mantle is clamped to the microscope object stage. The light source LS is fed from the stable power supply PS, which is used also for the feeding of the other electrical components of the whole apparatus. The light from the light source LS passes through the polarizer P, substage condenser SC, sample holder SH, objective OB, and analyser A. The sample is observable visually in the eyepiece EP. The intensity of the polarized light transmitted through the sample is measured by a phototransistor PT₁ placed on the mechanical holder which can easily slide in and out the microscope tube. The light intensity is measured as a difference of signals measured by the phototransistor PT₁ and by the phototransistor PT₂ placed in the neighbourhood of the light source LS. Both signals are conducted into differential amplifier DA. The last block is an integrator I with variable time constant, the output of which is connected to the Y input of the XY recorder.

Using our home-built apparatus, it is possible to measure the intensity of the light transmitted through a sample as function of temperature within an interval of 300—400 K. The accuracy of the temperature measurement is ± 0.1 K. The heating/cooling rate can be set from 0.5 K/min to 1 K/sec. After changing the set-temperature from 303 K to 323 K, the measured temperature stabilizes at 323.0 ± 0.1 K within 2 minutes. The long term stability of the pre-set temperature was measured to be ± 0.1 K/hour at 314 K. With the used phototransistors (Tesla KP 101) it is possible to measure the intensity of light with a wavelength from 400 nm to 1000 nm with a sensitivity of $1.8\text{--}3.0 \mu\text{A/lx}$ at the illumination of 2500—4000 lx [9]. Since the illumination can be changed by changing the feeding voltage of the light sources and/or by the change of diaphragm, the light intensity on phototransistors can be adjusted to cover their linear response range. The parameters of the apparatus built by us satisfy the

conditions necessary for measurements of phase transition temperatures in phospholipid model membranes, and are comparable to if not better than those described in [4, 7].

Samples for measurements were prepared from 1,2-dipalmitoyl-sn-glycero-3-phosphorylcholine (DPPC) or 1,2-dipalmitoyl-sn-glycero-3-phosphorylethanolamine (DPPE) which are analytically pure chemicals, commercially available from Fluka (Buchs, Switzerland). Microcrystals of lipid were filled into a glass capillary with a 0.7 mm internal diameter, redistilled water was added and the capillary was then sealed. The weight of the lipid as well as that of water were determined by gravimetry with an accuracy of $\pm 2 \cdot 10^{-6}$ g using Mettler (Zürich, Switzerland) microbalances. Samples in the sealed capillaries were mechanically homogenized by repeated forwards—backwards centrifugation for 1—3 hours.

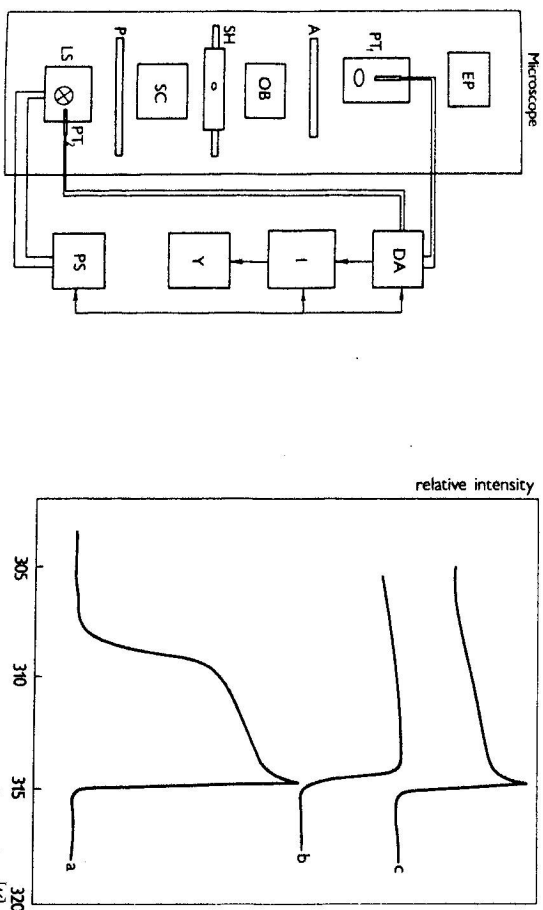


Fig. 3. The block diagram of the unit for the light intensity measurement

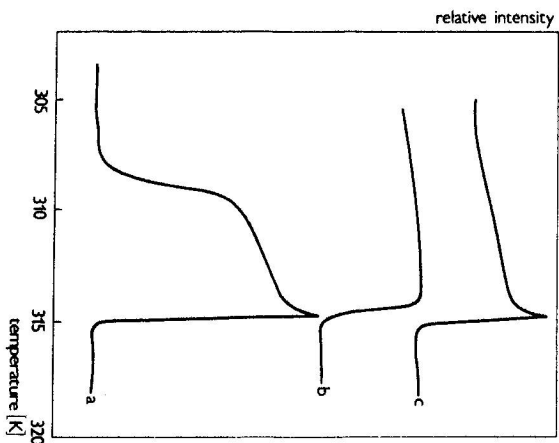


Fig. 4. The temperature dependence of the intensity of light (in relative units) transmitted through the DPPC : H₂O = 1:10 (w:w) sample placed between crossed nicols. a — first heating scan, b — cooling scan, c — second heating scan. Heating and cooling rates were 1 K/min.

The weight ratio DPPC : H₂O of the prepared samples was within an interval of 2:1 to 1:200. After mechanical homogenization, the samples with DPPC were heated at about 325 K for 1—2 hours and stored at about 275 K in a refrigerator for (at least) 24 hours. In the case of DPPE we prepared the samples with the

DPE: H₂O weight ratio from 1:1.2 to 1:140. However, only the samples with the weight ratio of DPPE:H₂O ≤ 1:15 were homogeneous. We found empirically that the sample had to be heated at 358 K for about 5 minutes and homogenized by a short-time centrifugation at 2000 rev/min immediately before the measurement to reach a spatial homogeneity of the sample.

III. RESULTS AND DISCUSSION

Typical changes in light intensity transmitted through the DPPC + H₂O samples placed between crossed nicols as observed during heating and cooling scans in our experiments are shown in Fig. 4. In the first heating scan after sample preparation, a sigmoidal increase in the light intensity occurs in the temperature interval from 307.5 K to 310.5 K, as clearly seen from the curve a. The point of inflexion obtained by a numerical differentiation of several similar curves occurs for the DPPC + H₂O systems at $T = 308.8 \pm 0.2$ K. With the further increase of temperature the light intensity increases from about 313 K reaching a sharp maximum at $T = 314.9 \pm 0.1$ K. Thereafter, the light intensity sharply decreases within the temperature interval of 0.4 ± 0.1 K and levels off at higher temperatures. In the cooling scan (curve b), the light intensity increases sigmoidally in the temperature region from 315.2 K to 313.1 K with the point of inflexion at $T = 314.3 \pm 0.2$ K. When the samples were heated immediately after the first cooling scan, substantial changes in the light intensity were observed only in the temperature region from 313 K to 316 K — a sharp maximum at $T = 314.9 \pm 0.1$ K and a sharp decrease within the interval of 0.4 ± 0.1 K (curve c). The same result as in the first heating scan (curve a) has been observed in the subsequent heating scans only if the samples were equilibrated at 298 K for a time interval longer than 30 minutes after each heating and/or cooling scan.

In the temperature intervals where we observed the changes in light intensity, phase transitions were detected by several experimental methods. X-ray diffraction methods have shown that the lyotropic system DPPC + H₂O is in a one-dimension lamellar solid-like (gel) phase L_{β} at molar ratios [H₂O]:[DPPC] > 15:1 and temperatures $T < 307$ K; in this phase the DPPC acyl chains are ordered and tilted with respect to the director [10—12]. At temperatures $T > 315$ K, the system has a structure of an one-dimensional lamellar fluid-like (liquid crystalline) phase L_a with mobile disordered acyl chains [9, 10]. In the temperature interval 309 K < T < 313 K, an intermediate two-dimensional solid-like (gel) monoclinic phase P_{β} was observed with rippled lamellae and ordered acyl chains oriented parallel with respect to the director [13—15]. The endothermic $L_{\beta} \rightarrow P_{\beta}$ phase transition (called also pre-transition) observed by differential scanning calorimetry occurs at temperatures

$T_c = 305.4$ K — 308.5 K [16—20], the width of this transition is $\Delta T_c = 2.0$ K — 2.6 K [20]. The phase transition $P_{\beta} \rightarrow L_a$ (called also the main transition or gel — liquid crystal transition) is endothermic too and occurs at $T_c = 314.90 \pm 0.06$ K according to calorimetric data [20, 21]. Comparing our experimental data with the data from literature discussed above, we can ascribe the point of inflexion at $T = 308.8 \pm 0.2$ K and the maximum at $T = 314.9 \pm 0.1$ K to the phase transition temperatures $T_c(L_{\beta} \rightarrow P_{\beta})$ and $T_c(P_{\beta} \rightarrow L_a)$, respectively. Noteworthy is the hysteresis in the $L_a \rightarrow P_{\beta}$ vs. the $P_{\beta} \rightarrow L_a$ transition, in our experiments there was a shift of 0.6 ± 0.3 K between T_c in the heating vs. the cooling scan. This also agrees with the published data (see [22]). The absence of the $L_{\beta} \rightarrow P_{\beta}$ transition in the reheating scans of non-equilibrated samples as well as its appearance after equilibration have been observed by calorimetry too [23, 24]. These effects are caused by a relatively long relaxation time of the $P_{\beta} \rightarrow L_{\beta}$ transition in the temperature region of 298 K < T < 308 K.

While the temperatures in cases when changes in light intensity were observed could easily be ascribed to the phase transition temperatures, the physical processes responsible for these changes are far from clear to us. We know from literature (see, for example, [49]) that the polarized light intensity after transmission through an uniaxial crystal between crossed nicols is given by

$$I \sim \sin^2(2\varphi) \sin^2(\delta/2) \quad (1)$$

where φ is an angle between the plane of light polarization and one of the crystal polarizing planes, δ is a phase shift between the ordinary ray and extraordinary ray, and n_o and n_e are the refractive indices of the ordinary and the extraordinary rays, respectively.

In the case of an oriented lamellar system, the phase shift is given by

$$\delta = \frac{2\pi d}{\lambda} (n_e - n_o) \frac{\sin^2 \vartheta_1}{\cos \vartheta_2} \quad (2)$$

where λ is the wavelength, d is the thickness of the sample, ϑ_1 is an angle between the optical axis and the light, and ϑ_2 is an angle between the light and the director. According to literature [50, 51], the polarized light intensity after transmission through a nematic liquid crystal and in the first approximation also through a lamellar lyotropic liquid crystal — see [7] is given by

$$I \sim \sin^2(2\varphi) \sin^2(\pi d \Delta n / \lambda) \quad (3)$$

where $\Delta n = (n_e - n_o)$, $\sin^2 \vartheta_1$ and ϑ_2 is an angle between the optical axis and the director. The values of the product $d \cdot (n_e - n_o)$ can be calculated from the data of the X-ray diffraction analysis [11, 12, 15], and from conoscopic measurements

[26]. For the phases L_β , P_β and L_α these values are equal to 0.11 nm, 0.12 nm, and 0.08 nm for one lamella, respectively, so that the increase of the light intensity at the $L_\beta \rightarrow P_\beta$ transition, and its decrease at the $P_\beta \rightarrow L_\alpha$ transition could be simply caused by the changes in the d ($n_e - n_o$) values. However, we observed in our experiments that the absolute change of the light intensity at the $P_\beta \rightarrow L_\alpha$ transition was becoming smaller after each of the first 3–5 heating-cooling cycles. Since the absolute change is dependent on the history of the sample, the changes in the light intensity are influenced also by secondary effects, such as the change in the sample texture, orientation effects on the glass walls, re-orientation of multilamellar domains within the sample, etc. It is clear that further work is needed (probably with oriented multilamellar systems) for the quantitative description of the observed effects.

The cause of the light intensity maximum at the T_c of the $P_\beta \rightarrow L_\alpha$ transition is not clear to us either. It is well known from experimental [27–29] as well as from theoretical [30–32] studies that the $P_\beta \rightarrow L_\alpha$ transition is a first order phase transition. Formally, if the maximum in the light intensity was caused by critical fluctuations in our system, the light intensity would be described by the equation (see [33])

$$I \sim \left| \frac{T - T_c}{T_c} \right|^{-\nu} \quad (4)$$

We calculated the values of the critical exponent ν from plots such as in Fig. 5 for temperatures $0.1 \text{ K} < T - T_c < 2.0 \text{ K}$. We have found in 4 experiments $\nu = 0.113 \pm 0.042$. We can state therefore that the effect is caused by critical fluctuations in the system. However, we do not know which fluctuating physical parameter is responsible for the observed effect. It could be the thickness d , the refractive indices n_e and n_o , the angle ϑ , or their mutual combinations. It is also important to note that in some samples we did not observe any maximum at T_c . Instead of it, we observed a sigmoidal decrease at the $P_\beta \rightarrow L_\alpha$ transition temperature $T_c = 314.9 \pm 0.1 \text{ K}$ corresponding to the point of inflexion. We observed that such results were obtained with samples containing a large amount of water, typically in the range of DPPC:H₂O = 1:100 – 1:200 (w:w). An ultrasonication of samples also caused the disappearance of the maximum at T_c . It is well known that at high water concentration and after ultrasonication, unilamellar spherical vesicles with a diameter of 20 nm form from the lamellar liquid crystalline phases [34]. Phase transition from the solid-like to the fluid-like phase seems to be of the second order type, probably because of the small diameter of the vesicles [29, 35]. Consequently, the physical dimension of the system seems to be less than the correlation length of the critical fluctuation. Using this approach, Mitaku et al. [29] have explained why the maximum

of the scattered light intensity (critical opalescence) is small in experiments with unilamellar vesicles of DPPC [36].

Hence, the presence or absence of the maximum of light intensity in our experiments could be caused by the relative amounts of lipids in the lamellar phase or in the unilamellar vesicles.

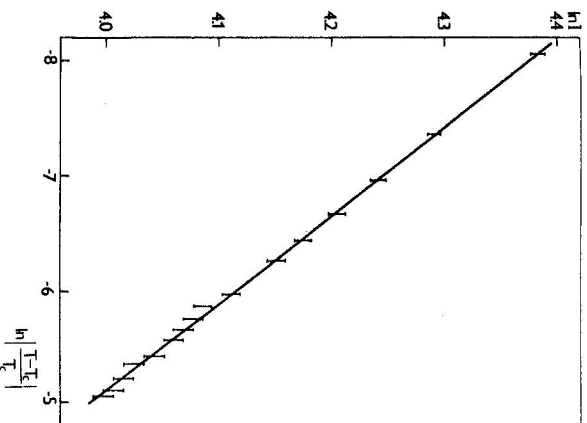


Fig. 5. The dependence of the light intensity I (in relative units) transmitted through the DPPC:H₂O system placed crossed nicols on the reduced temperature

$$\frac{T - T_c}{T_c}$$

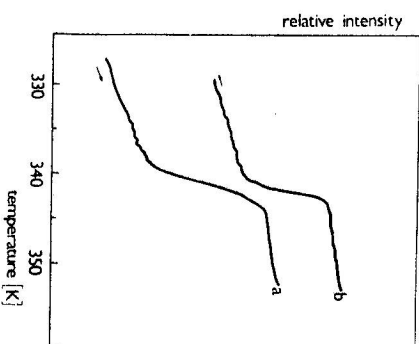


Fig. 6. The temperature dependence of the intensity of light (in relative units) transmitted through the DPPC:H₂O sample placed between crossed nicols.
a — heating scan, b — cooling scan. Heating and cooling rates were 1 K/min.

Sigmoidal dependence of the light intensity was observed also in heating and cooling scans of samples with DPPC + H₂O systems (Fig. 6). For the fully hydrated DPPC, two phases were observed by X-ray diffraction methods. At lower temperatures, a solid-like (gel) phase of the type L_β was observed, with the acyl chains of DPPC parallel with the director; a fluid-like (liquid crystal) phase L_α was observed above the phase transition temperature of $T_c = 336.4 \text{ K}$ [37]. However, if the DPPC molecules are not fully hydrated, at temperatures near the $L_\beta \rightarrow L_\alpha$ phase transition there occurs also hydration, so that the maximum at the endotherm determined calorimetrically is observed at higher temperatures

— for example in one particular case at $T = 338.1\text{ K}$ [42]. Several authors [38—42] discussed this interesting behaviour in detail. Because of problems with sample preparation described in *Material and Methods*, our samples were probably not fully hydrated. This is why we observed phase transition temperatures (inflections of the sigmoidal curves) in a rather broad range — from 336.65 K to 338.15 K. This is in agreement with the calorimetric data of several authors [39, 40, 42—47], who also observed the $L_{\beta} \rightarrow L_{\alpha}$ transition at temperatures in the interval 336.15 K—338.15 K. The dependence of the phase transition temperature on hydration, as well as the higher value of temperature at which the gel — liquid crystal transition occurs in comparison to DPPC, are caused by the formation of the hydrogen bonds network in the polar part of the DPPC model membranes in which the oxygens of phosphate groups and the nitrogens of amine groups of DPPC molecules participate [48].

Finally, we would like to mention that the microscopic technique we used to be as sensitive as standard calorimetric methods in the detection of phase transition temperatures of model phospholipid membranes. We are using it routinely in the studies of drug-membrane interactions [52].

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**ИССЛЕДОВАНИЕ ФАЗОВЫХ ПЕРЕХОДОВ В МОДЕЛЬНЫХ МЕМБРАНАХ
ИЗ ФОСФАТИДИЛЭТАНОЛАМИНА И ФОСФАТИДИЛЭТАНОЛАМИНА ПРИ ПОМОЩИ
МЕТОДА ПОЛЯРИЗАЦИОННОЙ МИКРОСКОПИИ**

В работе описана модификация поляризационной микроскопии и ее применение для измерения температур фазовых переходов в модельных мембранах из фосфатидилхолина и фосфатидилэтанолламина. Точность метода сравнивается с точностью дифференциальной сканирующей калориметрии. Интенсивность света, пропускаемого через образец модельной мембраны из дипальмитилфосфатидилхолина, который помещен между двумя скрещенными призмами Николя, имеет острый максимум при температуре главного фазового перехода ($314,9 \pm 0,1$ К) гель-жидкий кристалл ($P_{\beta} \rightarrow L_{\alpha}$), после чего скачкообразно падает в пределах $0,4$ К. Предполагается, что скачкообразное поведение интенсивности света обусловлено критическими явлениями при фазовом переходе.