



The effects of SDS at subsolubilizing concentrations on the planar lipid bilayer permeability: Two kinds of current fluctuations

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ABSTRACT

Detergent effects on lipid bilayers of artificial and biological membranes at subsolubilizing concentrations are known to include the membrane permeabilization which manifests itself through both a flip-flop of detergent molecules from the outer monolayer to the inner monolayer and the membrane leakage of entrapped solutes. We have explored the current fluctuations occurring in planar BLM of asolectin in the presence of ionic detergent SDS at subsolubilizing concentration. Two groups of current fluctuations which the average duration differs by two orders of magnitude can be distinguished. We assume that these differences in the duration of current fluctuations are associated with a different number of SDS molecules in the walls of the putative toroidal hydrophilic pores. We associated short pulses with the formation of short-lived lipid hydrophilic pores. Impulses of greater duration (steps) were associated with the formation of hydrophilic pores, the walls of which contain detergent. Taking into account the characteristics of these pores, we estimated the pore energy, as well as the edge energy of these two kinds of pores. We believe that the flip-flop of SDS molecules in liposomes is provided by long-lived pores, and the contents of the liposome leakage occurs through all pores.

1. Introduction

Detergents are amphiphilic molecules which are highly soluble in water, interact with the cellular membranes and modify their properties. Detergent-induced solubilization of lipid membranes is often interpreted within the framework of a three-stage model (Heerklotz, 2008; Ahyauch et al., 2010; le Maire et al., 2000; Lichtenberg et al., 2013). The processes that occurs at subsolubilizing surfactant concentrations that correspond to the first stage give the greatest amount of information about the mechanisms of interaction between detergents and the cellular membranes, and in particular with their lipid part. Despite the large number of studies, these processes have been least studied.

It has been shown that the addition of detergents at subsolubilizing concentrations causes membrane permeabilization of liposomes (le Maire et al., 2000), which manifests itself through both a flip-flop of detergent molecules from the outer monolayer to the inner monolayer and the membrane leakage of entrapped solutes (Heerklotz, 2008; Ahyauch et al., 2010; Lichtenberg et al., 2013).

The increase in permeability of the bilayer caused by detergents is associated with the possible formation of toroidal lipid pores (Heerklotz, 2008). However, the mechanism of membrane permeabilization by detergents remains unclear.

Sodium dodecyl sulfate (SDS) is one of the commonly used anionic detergents, and its interaction with lipid membranes is intensively studied by equilibrium dialysis using radioactively labeled surfactant, or by isothermal titration calorimetry (Heerklotz, 2008; Alonso et al., 1982; Tan et al., 2002; Keller et al., 2006).

Studies of the influence of detergents on the properties of lipid bilayers were also carried out on planar bilayer membranes. The possibility of forming stable planar bilayer lipid membranes was shown in (Tien, 1967) when charged detergents were added to the solution; it was shown in (Bangham and Lea, 1978) that when the SDS is symmetrically added from two sides of the membrane in the concentration range from 0.01 mM to 0.1 mM, the specific conductivity of the membrane increases by approximately an order of magnitude. In (Ksenzhek et al., 1974) random current fluctuations in a membrane with SDS in the voltage clamp regime were investigated.

To study the interactions between the lipid and detergent, molecular dynamics methods are also used (Bandyopadhyay et al., 2001; Xu et al., 2017). It was shown in (Bandyopadhyay et al., 2001) that the addition of SDS to the membrane from DMPC leads to the increase in the order parameter of the hydrocarbon chains of both the lipid and the detergent and, correspondingly, to the denser packing of the molecules in the bilayer. It was shown in (Xu et al., 2017) that the addition of SDS to the membrane from DPPC in a certain concentration range enhances

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the interaction between lipid DPPC molecules, and SDS molecules act as an intermedia. In this case, straightening of the hydrocarbon tails and a closer packing of molecules in the plane of the bilayer are observed.

Most studies on the effect of ionic detergents on membranes were performed on bilayers of neutral lipids. The interaction of charged asolectin vesicles with an anionic SDS was investigated by titration calorimetry (Kresheck et al., 1980).

In this paper we show experimental data on SDS-induced current fluctuations in a planar lipid membrane of asolectin. In the presence of detergent at subsolubilizing concentrations, two groups of current fluctuations which the average duration differs by two orders of magnitude were observed. We associate these current fluctuations with the disturbances in the packing of the bilayer and the formation of pores of the two kinds. The amplitude and temporal characteristics of current fluctuations in the asolectin flat lipid membrane with symmetric SDS additions on both sides of the membrane at constant voltage are studied. We also study the dependence of the characteristics of current fluctuations and putative hydrophilic pores on the ionic strength of the bulk solution. Taking into account the characteristics of these pores, we estimated the pore energy, as well as the edge energy of these two kinds of pores.

2. Materials and methods

2.1. Lipid, detergent, and electrolytes

Asolectin (Avanti Polar Lipids, Alabaster) was used for the formation of planar BLM. Bulk solutions contained NaCl (all reagents were of analytical grade) and SDS (Sigma) were used.

2.2. Planar lipid bilayer membranes

The BLMs were formed according to (Mueller et al., 1962) over a 1 mm² circular hole in the wall of a Teflon chamber at room temperature of $21 \pm 1^\circ\text{C}$. The asolectin concentration in decane was 30 mg/ml. The measurements were carried out in the symmetrical conditions.

2.3. Electrical measurements

Ag-AgCl electrodes were placed into both compartments of the chamber. Transmembrane currents were detected on a low-current measuring apparatus (Pushchino, Russia) in voltage clamp mode. Current fluctuations were recorded with a sampling rate of 1 kHz in a 16-digit ADC (L-Card, Moscow, Russia). The measurements were carried out in the voltage-clamp conditions.

3. Results

In the following we investigate current fluctuations in asolectin membranes in 0.05 (7 membranes), 0.1 (11) and 0.5 (5) M NaCl for various transmembrane voltages between -100 mV and $+100$ mV. The SDS concentration in the bulk solution have been chosen in the range 0.02–0.1 mM. The presence of SDS at about the same concentrations is known to cause both the release of contents (leakage) from large unilamellar vesicles and SDS molecules flip-flop (Ahyayauch et al., 2010).

The mean lifetime of the membranes was 27 ± 20 min. Typical current traces through the membranes and the current histograms are shown in Fig. 1. We can see two or three maxima in the histograms, one of which corresponds to the membrane current in the absence of fluctuations. We can distinguish two different kinds of fluctuations.

In Fig. 1a one can see well-resolved isolated current pulses of duration less than 0.5 s with an amplitude several times greater than the noise level. Single short current pulses are shown for different

concentrations of NaCl in a bulk solution (50 mM, 100 mM, 500 mM) with a membrane voltage of 50 mV. The amplitudes of these current fluctuations are proportional to the specific conductivities of the bulk solution. The ratio of the maximum amplitudes of current pulses on the upper, middle and lower tracks is about 15 : 30 : 120. This is close to the specific conductivity ratio for solutions of corresponding concentrations of 0.56 : 1.07 : 4.68 S/m.

Fig. 1b presents the current trace showing the appearance of current pulses with an amplitude of about 25 pA over a long time interval. These pulses can be associated with the opening of pores with a conductivity of about 0.5 nS. Using the data presented, we can not say whether the same pore or different pores open and close.

The current traces shown in Fig. 1c are very different from the records in Fig. 1a and b. We can see steps of a current of much longer duration. Sometimes, well-resolved individual short-time pulses are superimposed on a current step. We can also see the similar step in Fig. 1a, in the bottom record. We believe that both the well-resolved individual short-time impulses and the current steps are results of hydrophilic pore formation. In Fig. 1c five current tracks obtained in four membranes are presented. The two upper records were recorded on the membrane at different applied voltages -50 and -100 mV. The ratio of the amplitudes of the current steps at two different voltages is about 15 : 40. This suggests that the amplitudes display a linear dependence on the transmembrane voltage and the putative pores are close to ohmic pores. The third undulating current track resembles bursts with one conduction step (flicker) (Laub et al., 2012). We can see two steps in fourth and fifth records and three maximums in the histograms. In the fourth record, the ratio of the amplitudes of the steps is 5 : 6, which suggests the presence of two pore-steps. In the fifth record, the amplitudes of steps differ significantly: the ratio of amplitudes is 40 : 120, which may be due to a change in the pore size. It should be noted a significant increase in the variance of the pore-steps conductance in the 0.5 M NaCl solution (see Fig. 1a and c, lower entries).

We investigated changes in the amplitudes of current pulses (pore conductivity), pulse durations (pore lifetimes), and interpulse intervals as the ionic strength of a solution changes. The distributions of these parameters are shown in Fig. 2. In Fig. 2a an increase in the conductivity of the pores with increasing NaCl concentration can be seen, as well as a significant increase in the variation in the pore conductivity with 0.5 M NaCl compared to the variation in the pore conductivity at lower concentrations.

The distributions of lifetimes and interpulse intervals vary slightly with changes in the concentration of the bulk solution. (see Fig. 2b and c).

The duration of the current pulses ranged from 0.004 to 50 s. Two kinds of fluctuations are observed at all concentrations of bulk solutions studied. We considered pores with lifetimes of less than 0.5 s as short-lived, and pores with lifetimes of more than 1 s as long-lived. The total number of short-lived pores was equal to 246, the total number of long-lived pores was equal to 20. The average lifetime of the short-lived pores was equal to $\tau_{\text{pore}} = 0.08 \pm 0.08$ s, the average lifetime of the long-lived pore-step was equal to $\tau_{\text{step}} = 13 \pm 15$ s. The average lifetime of the putative pores, which manifest themselves in the form of current steps, exceeds the average lifetime of the pores, which manifest themselves in the form of short pulses by more than two orders of magnitude.

The dependence of the average conductivity of pores and pore-steps on the specific conductivity of NaCl is shown in Fig. 3. It can be seen that the ratio of the average conductivities is close to the ratio of the specific conductivities of NaCl. This suggests that, at different ionic strengths, pores of approximately the same size appear.

4. Discussion

The addition of ionic detergent SDS in subsolubilizing

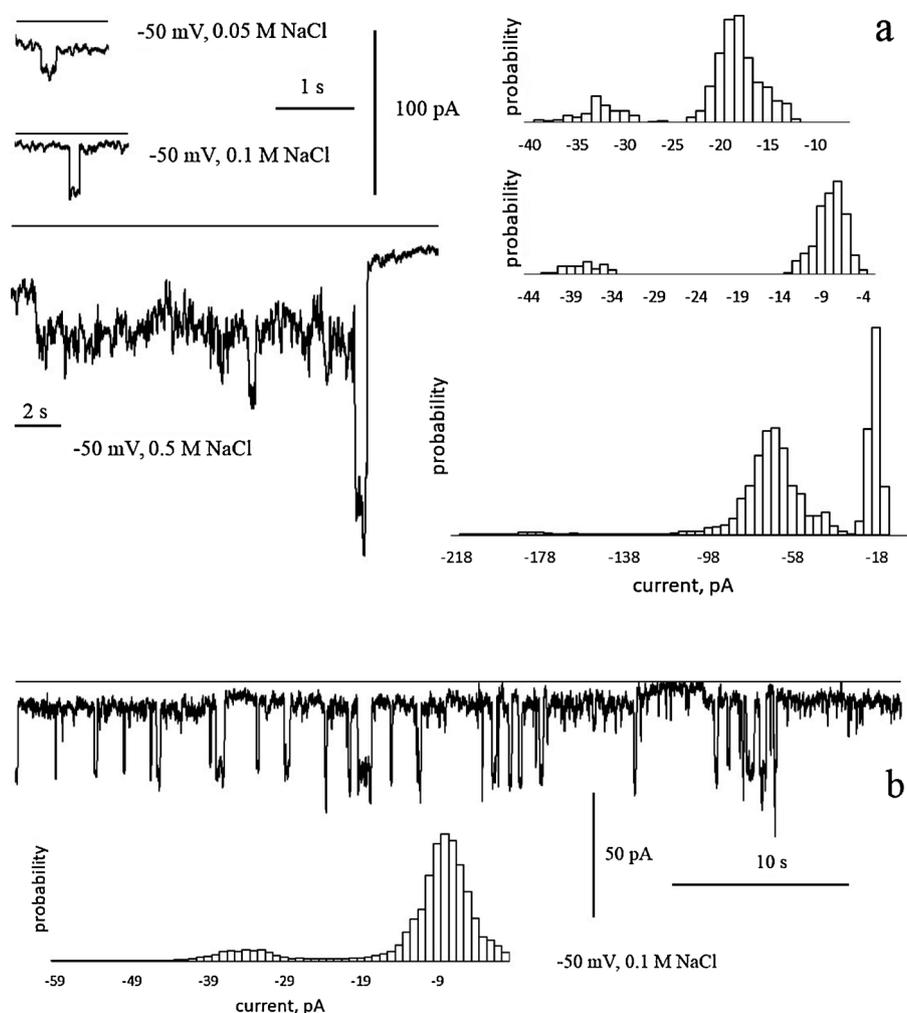


Fig. 1. Traces and histograms of current fluctuations: horizontal lines correspond to zero currents; the applied voltage and the concentration of the bulk solution are indicated. The SDS concentration is 0.07 mM. a – single pulses, b – recording of current fluctuations in a large time interval, c – current steps.

concentrations of 0.02–0.1 mM leads to various permeability events in bilayer lipid membranes of neutral lipids. Let us compare the obtained results with the data given in the literature. Concentrations of SDS in the bulk solution in the range 0.02–0.1 mM corresponded to concentrations at which the flip-flop and vesicle leakage in the liposomes from the mixture Egg-yolk phosphatidylcholine and C6-NBD-PS and 1-oleoyl-2-[6(7-nitrobenz-2-oxa-1,3-diazol-4-yl)amino]caproyl-sn-glycero-3-phosphoserine with SDS were observed (Ahyayauch et al., 2010). In addition, the conductivity of BLM of phosphatidylcholine and phosphatidylethanolamine (Bangham and Lea, 1978) increased by almost an order of magnitude in the same concentration of SDS. The current steps, similar to the ones obtained in our study, were recorded in the work (Ksenzhek et al., 1974). BLMs were made of phospholipids of the bull's brain; the range of used SDS concentrations 0.0004–0.016 mM was an order of magnitude lower than in our study. The durations of the current steps obtained in (Ksenzhek et al., 1974) were of the same order, and the amplitudes at the same voltage applied to the membrane of 50 mV are an order of magnitude smaller: in (Ksenzhek et al., 1974) – about 1.4 pA, in our work – 13–20 pA. Single short-lived pores were not observed in (Ksenzhek et al., 1974).

In this work, the current fluctuations in the BLM of the charged anionic asolectin were investigated when the SDS anionic detergent was incorporated into the bilayer. The surface charge of the lipid bilayer influences the adsorption and incorporation of SDS. The presence of a negative charge on the membrane leads to the appearance of a negative surface potential and to a decrease in the SDS concentration near the

membrane surface compared with the bulk concentration. However, we did not find a significant dependence of the studied characteristics (size, lifetime, interval interval) of current fluctuations on the ionic strength. Further research is required to clarify the causes of this phenomenon.

Two kinds of fluctuations were observed in all experiments with different NaCl concentrations. These are short pulses with an average duration of 0.08 s and pulses with an average duration of 13 s. We believe that short-time current pulses are coupled with the existence of hydrophilic pores in a bilayer, in the walls of which SDS molecules are absent or present in small quantities, and long-duration pulses are associated with hydrophilic pores whose walls are enriched or filled with SDS.

The similarity of the characteristics (amplitudes and durations) of the above-described SDS-induced current fluctuations in a membrane of asolectin with current fluctuation characteristics during phase transitions (Antonov et al., 2005; Heimburg, 2010) suggests similar mechanisms for their occurrence. In the paper (Anosov et al., 2018), we assumed the following mechanism for the hydrophilic pores formation during phase transition. Since the area of the lipid molecule in the bilayer plane decreases at the liquid-gel phase transition, additional hydrophobic defects appear in the bilayer. The solid domains of the gel phase in the heterogeneous bilayer structure restrict the free diffusion of molecules from the torus, i.e. they create mechanical barriers like those presented in (Tieleman and Bentz, 2002). This leads to the increase in size of hydrophobic defects and their transformation into hydrophilic pores. On the other hand, in the article (Xu et al., 2017) the

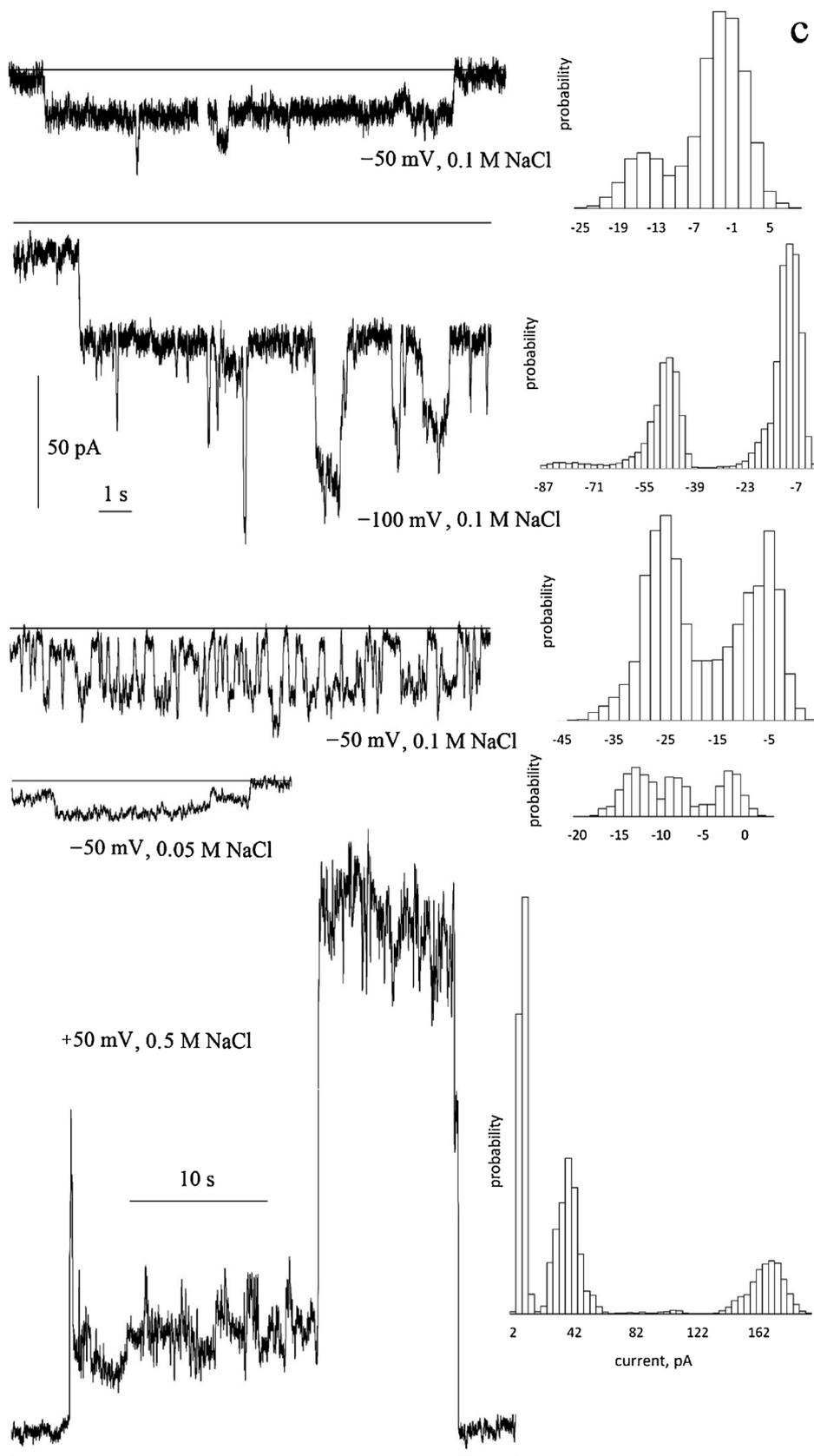


Fig. 1. (continued)

effect of SDS (when the fraction of SDS is less than 28%) on the bilayer structure was investigated by molecular dynamics methods. It was shown that the insertion of SDS causes a decrease in the bilayer area and increases in the bilayer thickness and lipid tail order, i.e. changes

similar to those that occur at the liquid-gel phase transition.

Let us estimate the average radius of the toroidal pores as the cylinder radius, having the same volume (Antonov et al., 2008):

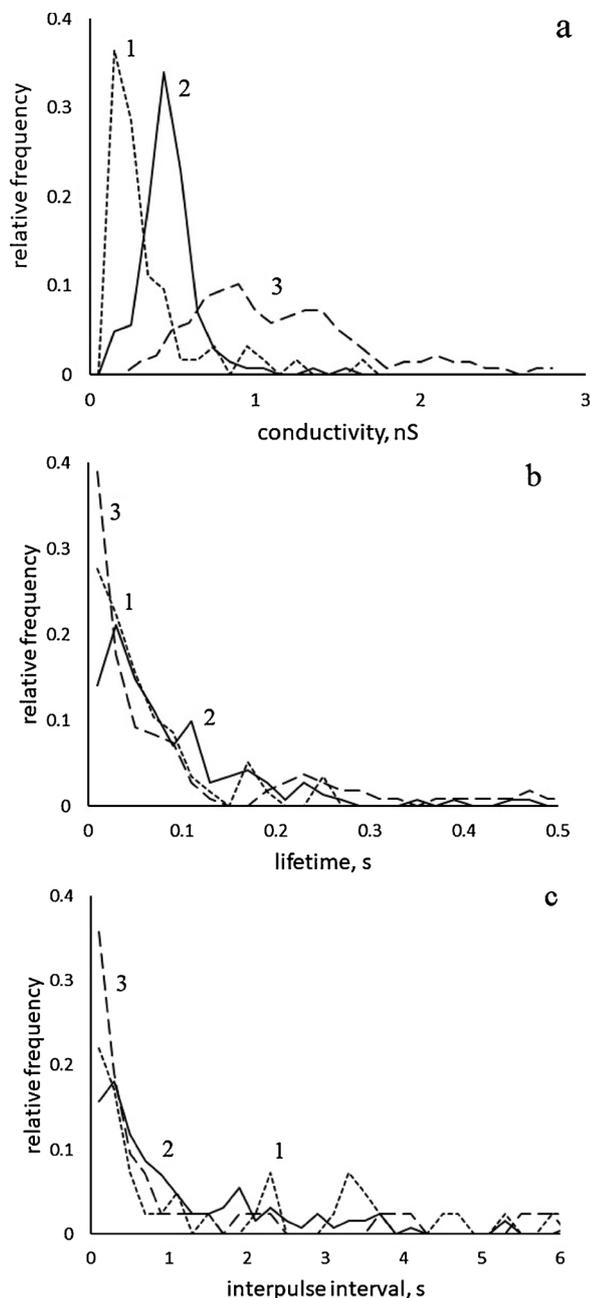


Fig. 2. Distributions of conductivity (a), the lifetimes of the pores (b), and the duration of the interpulse intervals (c) at the different ionic strength of the bulk solution: 0.05 M NaCl (1), 0.1 M NaCl (2), 0.5 M NaCl (3), SDS concentration is 0.07 mM.

$$R = \sqrt{Gh/\pi g}$$

where $h = 5$ nm is the membrane thickness, G is the pore conductivity, and $g = 1.07$ S/m is the specific conductivity of 0.1 M NaCl solution at room temperature. The average radius of the short-lived pores is equal to 0.84 ± 0.22 nm. The average radius of the long-lived pores is equal to 0.66 ± 0.19 nm.

The current steps observed in the experiments can be associated with the SDS flip-flop (Ahyayauch et al., 2010). In (le Maire et al., 2000; Heerklotz, 2008), there are suggestions that at sufficiently high concentrations (in the second phase of the three-stage model), detergent molecules interact in the membrane and can create large membrane fragments filled exclusively with detergent molecules. In these areas, long-lived toroidal pores, the walls of which are formed by detergent

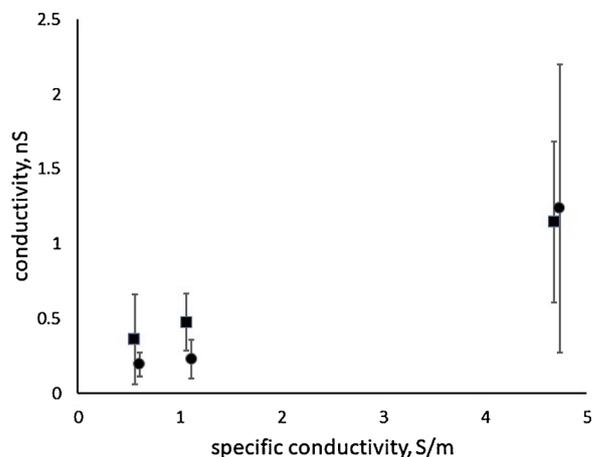


Fig. 3. Conductivities of the pores (■) and pore-steps (•) as a function of the specific conductivity of the bulk solution. The SDS concentration is 0.07 mM.

may occur. Based on our data, it can be assumed that such processes also occur at low concentrations of detergent. Corresponding enrichment of the edge of some pores with a detergent with positive spontaneous curvature (le Maire et al., 2000), which leads to a decrease in the linear tension of the edge of such pores (Petrov et al., 1981) and an increase in the lifetime.

The parameters obtained make it possible to estimate the energy characteristics of the pores observed in the experiment. The height of the pore destruction energy barrier δ_d which prevents the hydrophilic pore from turning into a hydrophobic pore, for short-lived pores can be estimated from the mean pore lifetime $\tau_{pore} = 0.08$ s by the formula (Freeman et al., 1994)

$$1/\tau_{pore} = \nu_0 V \exp(-\delta_{d,pore}/kT)$$

where $\nu_0 \approx 2 \times 10^{42}$ 1/(s \times m³) is the attempt rate density, $V = N V_1$ is the volume of N molecules forming a pore, the fluctuations of which can lead to a transition of the hydrophilic pore into a hydrophobic pore, $V_1 = 1.3 \times 10^{-27}$ m³ is the volume of one lipid molecule. We estimate the number N as follows. We consider a toroidal pore with two radii: $R = \frac{h}{2} + \Delta$ (Δ is the minimal radius of the toroidal pore), and $r = \frac{h}{2}$ (h is the membrane thickness). If the minimal radius is equal to 0.5 nm then the area of the pore wall (the area of the inner part of a toroid) is $2\pi^2 Rr - 4\pi r^2 = 69.5$ nm². If the molecule area is 0.6 nm² then the number of the molecules forming the pore is equal to 116. With these parameters, the pore trends energy barrier $\delta_{d,pore} = 37.7$ kT. If the barrier energy of the hydrophobic pore transition to hydrophilic pore is equal to 50 kT, as is customary in the literature (Glaser et al., 1988; Smith et al., 2004), the energy of the hydrophilic pore is $E_{min,pore} = 12.3$ kT. Corresponding value for the «step» $\delta_{d,step} = 42.8$ kT and energy minimum $E_{min,pore} = 7.2$ kT. Assuming that at small radii the energy of the pore is determined only by the edge energy of a hydrophilic pore $E_{min} = 2\pi r_{min} \gamma$, where $r_{min,pore} = 0.9$ nm for pores and $r_{min,step} = 0.6$ nm for steps, we can estimate the linear tension in these two kinds of pores: $\gamma_{pore} = 9.5$ pN, $\gamma_{step} = 7.1$ pN. These data can be compared with the values of the linear tension provided by the trilamellar structure arising in the process of fusion of membranes for membranes of different specimens were presented by Chernomordik et al., 1985. In that work, for the membranes from asolectin/decane $\gamma = 9.2$ pN, which is close to our value for a short-lived pore. Adding lysoPC molecules with positive curvature to the PC/decane membrane results in a decrease in the linear tension from 8.6 to 3.3 pN, that is in 2.6 times. In our case, the proposed integration of SDS molecules, resulting in the formation of a long-lived step, reduces the linear tension by 1.34 times.

The appearance of the current pulses obtained in the experiment is connected with the formation of the toroidal hydrophilic pores (follow

for Heerklotz, 2008). The lifetime of these pores is varied in more than two orders of magnitude. The difference in the linear tension of the short-lived and long-lived pores allows to suggest that these pores have a different number of SDS molecules in the walls. The long-lived pore-steps contain a fair amount of the SDS molecules. The short-lived pores contain no SDS molecules. We assume that the formation of pores-steps can be related to the flip-flop of the detergent molecules observed in experiments with liposomes (Ahyayauch et al., 2010). On the other hand, both the short-lived and long-lived pores are responsible for the vesicle leakage.

Conflict of interest

The authors declare that they have no conflict of interest.

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