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Short Communication

Studies of Nonlinear Electrical Effects of Model Membranes*

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Abstract. The structure of lipid bilayer membranes is investigated by analysis of the harmonics generated by electrical *ac* excitation with *dc* bias. For the detection of nonlinear effects this method is complementary to current relaxation experiments and may be suitable for gating current measurements at nerve membranes.

Key words: Lipid bilayer membrane – Voltage dependence of electrical impedance – Harmonic analysis.

Introduction

The static capacitance of lipid bilayer membranes depends on voltage U. The first approximation is

$$C = C_0 + \sum \alpha_i U^2 . \tag{1}$$

The different contributing effects are distinguished by the index i. Using an excitation voltage

$$u(t) = U_0 + U_1 \sin 2\pi\nu t \tag{2}$$

the capacitive current contains the fundamental component at the frequency ν and harmonics at the frequencies 2ν and 3ν (Carius, 1976). Those effects which relax more slowly than $(2\pi\nu)^{-1}$ do not contribute to the generation of harmonics. Therefor the technique is complementary to relaxation measurements of voltage dependent capacitance (Benz and Janko, 1976; Sargent, 1975) where only those effects are detectable which relax more slowly than the time constant of the electrical circuit used. The method of harmonic analysis using an ac bridge circuit has the further advantage of high precision ($\Delta\alpha/C_0 \leqslant 0.005\ \mathrm{V}^{-2}$ with $|u(t)| \leqslant 0.1$ V). May be this technique will prove advantageous for the determination of gating currents at nerve membranes, which up to now is usually done by measurement of asymmetric cur-

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rent relaxations (Keynes and Rojas, 1976). There are two recent reports on capacitance changes of the squid axon membrane during depolarization (Takashima, 1976; Fishman et al., 1977). They are contrary as to the sign of these changes, presumably due to different experimental conditions.

Results

In addition to the bilayer system oxidized cholesterol/decane (Carius, 1976), bilayers made from egg lecithin/decane, and egg lecithin + cholesterol/decane in 0.1 nKCl solution were investigated. The results show that there is a large increase of α/C with decreasing frequency below ca. 20 Hz. This is attributed to electromechanical interaction at the membrane. At 350 Hz freshly formed cholesterol membranes show values of α/C up to 1.5 V^{-2}. In aging membranes α/C decreases drastically and reaches a final value in the range of 0.015–0.1 V^{-2}. The decrease of α/C at 350 Hz is a measure much more sensitive for membrane aging than the increase in the specifiic capcitance, a measure suggested by S. H. White (1970).

For egg lecithin membranes the values of α/C are in the range of 0.3–2.0 V^{-2}. When the applied voltage exceeds 60 mV, the voltage dependence of membrane capacitance distinctly deviates from Equation (1). Moreover, the voltage dependence of the loss factor of these membranes was measured. It can be fitted best by

$$a_0 + a_1 U^2 + a_2 |U|^n, \quad \text{with } 3 \leqslant n \leqslant 5, \quad \text{for } |U| \leqslant 70 \text{ mV}.$$

Conclusion

Harmonic measurements on bilayer membranes show the tendency that some structural characteristics of a membrane give rise to special types of voltage dependence of the harmonics. Variation of membrane composition in further experiments should help to clarify these relations and to identify the underlying physical effects, e.g. electrocompression, rotation of polar head groups, hyperpolarization.

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