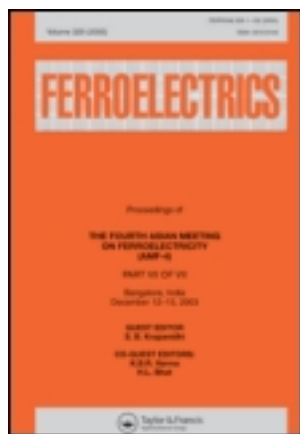


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## PHASE TRANSITIONS IN THE FERROELECTRIC-ACTIVE MODEL OF ION CHANNELS OF BIOMEMBRANES

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**Abstract** The ferroelectric-superionic transition model explains many of the properties of excitable ion channels. It describes the channel as a component of a ferroelectric liquid crystal that, on opening, undergoes a transition from a ferroelectric state to a paraelectric state, which is taken to be a superionic conductor. At the molecular level, the transition is postulated to involve melting of hydrogen bonds in the four S4 segments of the polypeptide.

### INTRODUCTION

Voltage-sensitive cation channels are the macromolecular components of the membranes of nerve and muscle cells responsible for the conduction of action potentials. Embedded in the phospholipid bilayer bounding the cell, these glycoprotein molecules act as voltage-dependent switches. In the resting state, the interior of the cell is negative (about -70mV). In response to a depolarization, sodium channels become highly permeable to Na<sup>+</sup> (and Li<sup>+</sup>), potassium channels to K<sup>+</sup>, etc., although other ions also pass through these channels at lower conductances [1]. These channels have been subjected to intense theoretical and experimental study [1-5]. Molecular biology has determined the primary protein structure of the sodium and potassium channels [6-8].

A common assumption is that ions pass through a water filled pore in the channel, but this model is unable to provide explicit physical mechanisms for the ionic selectivity and voltage-dependent gating of the channels [1]. Leuchtag [9-12] proposed that the ion channel undergoes a firstorder phase transition from a ferroelectric (closed) state to a paraelectric state (open), and that the open state acts as a superionic conductor [11,12].

### THE MODEL

A quantitative description of the phase transition model of ion channels in the framework of the thermodynamics approach may be obtained in reduced dimensionless

form, if we introduce following variables [13-18]:

$$\begin{aligned} P_r &= P[\gamma/(-\beta)]^{1/2} \\ E_r &= (E/2)[\gamma^{3/2}/(-\beta)^{5/2}] \\ T_r &= \alpha(T)\beta/\gamma^2 \end{aligned} \quad (1)$$

where  $P$  is polarization (an order parameter of the system),  $E$  is the external electric field,  $T$  is the temperature and  $\alpha$ ,  $\beta$ ,  $\gamma$  are the expansion coefficients of the Landau- Ginzburg-Devonshire theory [19]. In this case we obtain the same anomalous nonlinear behaviour of the main physical characteristics (dielectric permittivity  $\epsilon$ , relaxation time  $\tau$ , piezomodulus  $d$ , etc.). In the vicinity of the phase transition, the form of the generalized Curie-Weiss law is:

$$\epsilon_r/2\pi = \tau_r = d_r P_r = 1/[T_r \pm 3P_r^2 + 5P_r^4] \quad (2)$$

Qualitative arguments indicate that the optimum nonlinearity is one where the capacitance increases with decreasing voltage.

The form of Eq. (2) is general, not only for pure ferroelectrics but also for all ferroelectric-active systems [18], including ferroelectric liquid crystals and superionic systems. The physical, concrete system is described by Eq. (1).

As result of this approach we have following:

- 1) dielectric permittivity (Curie-Weiss constant) was fit ted by Leuchtag [20] from the data of Palti and Adelman [21],
- 2) time relaxation processes were fitted by Bystrov [17] from the data of Kazachenko et al. [22],
- 3) experimental data from Tasaki et al. [23] should make it possible to obtain an estimate of the piezomodulus.

Because ion channels are components of a liquid crystal membrane based on a phospholipid bilayer, the glycoprotein channels may be assumed to be components of a smectic liquid crystal. Structural studies [24] suggest that the S4 segments are both tilted and chiral, which places them in the Sm C\* class. Liquid crystals of this class are known to be ferroelectric, which supports the hypothesis [25].

## CONCLUSION

The ferroelectric-superionic transition model provides a means of describing the behavior of voltage-dependent ion channels qualitatively and quantitatively. Although its development is not complete, it provides a number of predictions for future experiments. A number of its predictions, including the magnitude of surface charge and the Curie-Weiss law, have already shown agreement with the model. It is also in good agreement with the molecular structure models so far obtained [26]. A number of features of the channel remain to be incorporated into the framework of the model, notably the phenomenon of inactivation found in sodium channels.

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