Mechanics of Electrocompression of Lipid Bilayer Membranes

Dear Sir:

Considerable discussion has appeared in the literature concerning the elastic response of bilayer membranes to the application of normal surface traction, created by electrical potential differences across the membrane (White, 1974; Crowley, 1973; and Requena et al., 1975). The letter by Requena et al. (1975) was properly addressed to the problem of the containment of the solvent in the bilayer during the electrocompression of the membrane. Their conclusion that the large change in membrane capacitance (for time constants of 100 ms or greater) reflects the flow of solvent into small lenses and the toroidal periphery of the bilayer appears reasonable. However, their deduction that the initial 1% change in capacitance represents dilation in the area per molecule in the bilayer surface must be carefully considered. Secondly, if it is accepted that the surface area per molecule was expanded by this amount (because the bilayer volume remained constant), elastic energy storage in the bilayer is not uniquely specified by a single elastic modulus.

Recently, the mechanics describing elastic behavior in lipid bilayers were developed (Evans and Simon, 1975). The formulism showed that in general three elastic constants are required to characterize the equilibrium response to external forces. The stress resultants on a surface element are illustrated in Fig. 1. The tension, T_o (force per unit length on the element sides), is isotropic in the plane of the membrane; the normal surface traction, $-\sigma_o$ (force per unit surface area), as shown here is compressive, analogous to electrocompression. The anisotropy of the bilayer is represented by the difference between the three general elastic constants ($\bar{\lambda}_z$, $4\bar{\lambda}_\alpha$, $2\bar{\lambda}_{\alpha z}$) and "bulk" modulus of the bilayer, K_B (Evans and Simon, 1975).

$$K_B \equiv -V(\partial P/\partial V)_{\text{const. temp.}},$$

$$2\lambda_{\alpha z} = K_B,$$

$$K_\alpha \equiv 4\lambda_\alpha - K_B,$$

$$K_z \equiv \lambda_z - K_B,$$

where P is the internal or hydrostatic pressure of the bilayer; V is the bilayer volume. The elastic constants K_α, K_z represent the response of the membrane to external forces when the membrane volume is constant; K_z is the energy density (per unit strain) for changes in membrane thickness; K_α is the energy density (per unit strain) for changes in area per surface molecule.[1] The stress resultants can be expressed in terms of the fractional change in thickness (strain in the z-direction) and the fractional change in area per molecule (sum of strains in the bilayer plane).[2]

$$(\text{dyn/cm})\, T_o = t_m K_B(\epsilon_{zz} + \alpha) + \gamma + t_m K_\alpha \alpha, \tag{1}$$

$$(\text{dyn/cm}^2) - \sigma_o = K_B(\epsilon_{zz} + \alpha) + K_z \epsilon_{zz}, \tag{2}$$

[1] Because of the liquid-like hydrocarbon interior above the transition temperature of bilayer membranes, the coupling coefficient, $2\bar{\lambda}_{\alpha z}$, is assumed to be equal to the "bulk" modulus K_B because the normal stresses are coupled to the in-plane stresses by the liquid interior.

[2] The mechanics of small deformations is used; therefore, only terms of first order in the strain components appear.

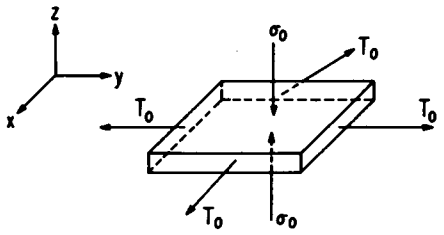

FIGURE 1 Stress resultants on a bilayer membrane material element.

where $\alpha = \epsilon_{xx} + \epsilon_{yy}$; t_m is the bilayer thickness; and γ is the energy density of hydrophobic interaction. For a nearly incompressible bilayer ($K_B \gg K_\alpha$ or K_z), Eq. 1 and 2 become,

$$T_o = -t_m P + \gamma + t_m K_\alpha \alpha, \tag{3}$$

$$-\sigma_o = -P + K_z \epsilon_{zz}. \tag{4}$$

Eliminating the pressure from Eq. 3 and 4 yields a relation between the normal compressive traction and the boundary tension in the bilayer.

$$-\sigma_o = (T_o/t_m) - (\gamma/t_m) + K_z \epsilon_{zz} - K_\alpha \alpha. \tag{5}$$

Examining Eq. 5 shows that in equilibrium changes in compression of the bilayer can result in changes in bilayer tension as discussed by Requena et al. (1975). The change in tension is given by the change in compression of the bilayer and changes in the anisotropic elastic energy components of the bilayer.

$$\Delta T_o = -t_m(\Delta\sigma_o + K_z \Delta\epsilon_{zz} - K_\alpha \Delta\alpha). \tag{6}$$

If solvent is free to escape from the bilayer and no change in anisotropic elastic energy occurs, then the tension change is equal to the compression change times the membrane thickness and results from the increase in bilayer internal pressure P. On the other hand, if the solvent cannot escape (or if no solvent is present), then the tension change would be,

$$\Delta T_o = -t_m[\Delta\sigma_o + (K_z + K_\alpha)\Delta\epsilon_{zz}], \tag{7}$$

because the bilayer volume would remain constant (i.e. $\Delta\epsilon_{zz} = -\Delta\alpha$). Therefore, in order to obtain an elastic constant, which is the sum of two characteristic material constants, it is necessary to simultaneously measure the changes in bilayer tension, compression, and thickness.

In conclusion, it is emphasized that both normal compression and tension must be determined for the bilayer in order to establish changes in the anisotropic elastic components of the bilayer *and* that these measurements are only sufficient when the system is in static equilibrium (otherwise viscous forces created by solvent flow must be included, assuming the bilayer intertia is negligible). Also, electro-compression experiments will not uniquely specify elastic interactions between the surface molecules of the bilayer (represented by K_α) unless the compression modulus in the thickness direction is negligible ($K_z \ll K_\alpha$).

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