

CONSTITUTIVE RELATION FOR RED CELL MEMBRANE

CORRECTION

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ABSTRACT The intention of this note is to correct a subtle and somewhat esoteric error that the author discovered in his previous publications on membrane elastic behavior. The constitutive relation between membrane force resultants and large, elastic deformations of a membrane surface involves a strain tensor, characterizing the finite deformations. The original strain tensor that appeared in the equations was the Lagrangian strain tensor; however, the proper strain representation (also Lagrangian in nature because it is "measured" relative to the undeformed material state) is transformed by rotations of coordinates in the deformed material state (whereas the Lagrangian strain tensor is transformed by rotations of coordinates in the undeformed state). The principal membrane tensions are unchanged by this correction; the material elastic constants remain the same; and therefore, the material behavior in shear and isotropic tension is the same. However, the tensor, constitutive relation can be properly applied to coordinate systems other than the principal axis system.

In the author's previous publications on membrane elastic behavior, which contain a subtle error, the first order constitutive relation between membrane force resultants and large, elastic deformations of a membrane surface, which has high resistance to area changes, was developed (Evans, 1973; Evans, 1975) using an elastic potential energy function (e.g., Helmholtz free energy at constant temperature). The force resultants were obtained by taking the variation of the elastic potential with respect to small membrane area changes and finite deformations of the membrane surface at essentially constant area. Internal, viscous energy dissipation was also included to represent viscoelastic membrane behavior. The intrinsic distribution of forces in the membrane surface is expressed in the form of a resultant tensor, whose principal components (when the principal axes system is chosen) are membrane tensions (force per unit length acting along the principal surface coordinates). The resultant tensor is related to the deformation and rate of deformation by the first order material properties: K_B , elastic area compressibility modulus (dyn/cm); μ , "shear" elastic modulus (dyn/cm); and η , coefficient of surface viscosity in shear (dyn-s/cm). The original con-

stitutive relation was (Evans, 1975):

$$T_{ij} = (K_B \alpha) \delta_{ij} + \mu \epsilon_{ij} + 2\eta V_{ij}, \quad (1)$$

where α is the fractional change in area per molecule (area "strain"); ϵ_{ij} is the Lagrangian strain tensor for finite deformations; the V_{ij} is the rate of deformation tensor. The indices ($i, j = 1, 2$) refer to the two surface coordinates tangent to the "plane" of the membrane. For finite deformations, the initial material state must be recognized as distinct from the instantaneous or deformed material state and vice versa. If we choose (a_1, a_2) and (x_1, x_2) as the initial and instantaneous (deformed) material element coordinates, respectively, the Lagrangian strain tensor and rate of deformation tensor can be written (Evans and Hochmuth, 1976);

$$\begin{aligned} 2\epsilon_{ij} &\equiv (\partial x_k / \partial a_i)(\partial x_k / \partial a_j) - \delta_{ij} \\ V_{ij} &= (\partial \epsilon_{pq} / \partial t)(\partial a_p / \partial x_i)(\partial a_q / \partial x_j). \end{aligned} \quad (2)$$

The *correct* form for Eq. 1 is obtained using a different "Lagrangian"-type strain tensor:

$$T_{ij} = (K_B \alpha) \delta_{ij} + \mu \bar{\epsilon}_{ij} + 2\eta V_{ij} \quad (3)$$

where the strain tensor, $\bar{\epsilon}_{ij}$, is a Lagrangian variable (i.e., measured relative to the initial material state) but has different transformation properties.

$$2\bar{\epsilon}_{ij} = (\partial x_i / \partial a_k)(\partial x_j / \partial a_k) - \delta_{ij}.$$

The rate of deformation tensor is correct. The two tensors ϵ_{ij} and $\bar{\epsilon}_{ij}$ have equal invariants:

$$\epsilon_{ii} \equiv \bar{\epsilon}_{ii}$$

and,

$$\epsilon_{ij}\epsilon_{ji} - \epsilon_{ii}\epsilon_{jj} \equiv \bar{\epsilon}_{ij}\bar{\epsilon}_{ji} - \bar{\epsilon}_{ii}\bar{\epsilon}_{jj};$$

therefore, the material relation derived for a membrane, which is assumed to be isotropic for its two surface directions, is unchanged. The Lagrangian strain tensor, ϵ_{ij} , is transformed by rotations about a material point of the coordinate axes in the initial state (a_i); on the other hand, $\bar{\epsilon}_{ij}$ is transformed by rotations of the coordinate axes in the instantaneous state (x_i).

When a material element is chosen to correspond to the principal axes, the principal strain and rate of deformation components are related to the principal extension ratios for each axis:

$$\begin{aligned} \lambda_1 &\equiv dx_1/da_1, \\ \lambda_2 &\equiv dx_2/da_2, \\ \epsilon_1 &= \bar{\epsilon}_1 = (\lambda_1^2 - 1)/2, \\ \epsilon_2 &= \bar{\epsilon}_2 = (\lambda_2^2 - 1)/2; \end{aligned} \quad (4)$$

$$\begin{aligned} V_1 &= (1/\lambda_1)(\partial\lambda_1/\partial t), \\ V_2 &= (1/\lambda_2)(\partial\lambda_2/\partial t), \end{aligned} \quad (5)$$

where $\partial\lambda/\partial t$ is the time rate of change of an extension ratio. The principal tensions are the same for either Eq. 1 or 3:

$$\begin{aligned} \alpha &\equiv \lambda_1\lambda_2 - 1, \\ T_1 &= K_B\alpha + (\mu/2)(\lambda_1^2 - 1) + (2\eta/\lambda_1)(\partial\lambda_1/\partial t), \\ T_2 &= K_B\alpha + (\mu/2)(\lambda_2^2 - 1) + (2\eta/\lambda_2)(\partial\lambda_2/\partial t). \end{aligned} \quad (6)$$

The relative values for these constants have been measured for red cell membrane to be:

$$\begin{aligned} K_B &\simeq 300 \text{ dyn/cm} \\ \mu &\simeq 7 \times 10^{-3} \text{ dyn/cm} \\ \eta &\simeq 10^{-3} \text{ dyn-s/cm} \end{aligned}$$

(Evans et al., 1976; Evans and LaCelle, 1975; Evans and Hochmuth, 1976). Because the area compressibility modulus is much larger than the "shear" modulus, the membrane area (per molecule) remains essentially constant and Eqs. 6 can be rewritten in terms of a membrane isotropic tension ($-p_M$) analogous to "hydrostatic pressure" in a bulk liquid,

$$\begin{aligned} -p_M &\equiv K_B\alpha \\ T_1 &= -p_M + (\mu/2)(\lambda_1^2 - 1) + (2\eta/\lambda_1)(\partial\lambda_1/\partial t) \\ T_2 &= -p_M + (\mu/2)(\lambda_1^{-2} - 1) - (2\eta/\lambda_1)(\partial\lambda_1/\partial t) \end{aligned} \quad (7)$$

where the constant area relation, $\lambda_1\lambda_2 \cong 1$, has been employed. Eqs. 7 can be decomposed into relations that characterize the "mean" membrane tension, \bar{T} (isotropic in the membrane plane) and the membrane "shear" resultant (deviator).

$$\bar{T} = \frac{1}{2}(T_1 + T_2) = -p_M + \mu[(\epsilon_1 + \epsilon_2)/2] \quad (8)$$

where,

$$\begin{aligned} (\epsilon_1 + \epsilon_2)/2 &= (\lambda_1^2 + \lambda_1^{-2} - 2)/4, \\ T_s &= |T_1 - \bar{T}| = |T_2 - \bar{T}|, \\ T_s &= \mu\epsilon_s + 2\eta V_s, \end{aligned}$$

where $\epsilon_s \equiv |(\epsilon_1 - \epsilon_2)/2|$ and $V_s = |V_1| = |V_2|$, or,

$$T_s = (\mu/4)(\lambda_1^2 - \lambda_1^{-2}) + (2\eta/\lambda_1)(\partial\lambda_1/\partial t). \quad (9)$$

Therefore, there are no changes in the material constitutive behavior resulting from the error in the strain tensor definition.

Superficially, it appears that this correction contributes little to membrane rheology; however, for the application of the constitutive relation to any choice of coordinates

in the deformed material, it is essential to utilize the correct strain tensor and to recognize its transformation properties. In the general formalism for the elastic contribution (Evans, 1975), the resultant tensor is properly expressed as:

$$T_{ij} = \left(\frac{\partial F}{\partial \alpha} + \frac{1}{(1 + \alpha)} \frac{\partial F}{\partial \beta} \right) \delta_{ij} + \left(\frac{2}{(1 + \alpha)} \frac{\partial F}{\partial \beta} \right) \bar{\epsilon}_{ij},$$

$$\beta \equiv (\lambda_1^2 + \lambda_2^2 - 2)/2,$$

$$\alpha \equiv \lambda_1 \lambda_2 - 1, \quad (10)$$

where the strain tensor $\bar{\epsilon}_{ij}$ replaces the Lagrangian strain tensor, ϵ_{ij} ; F is the elastic free energy density per unit of initial material area (or per mass if normalized by the initial density); β is the "stretch" of the material element diagonal, specifically, the fractional change in the radius of gyration of the material element. For a solid membrane, Eq. 10 is the general mechanochemical equation of state because α is the change in area per surface molecule and β is the change in molecular configuration (i.e. radius of gyration). This equation is not restricted to small area per molecule changes; it is completely general for reversible thermodynamic processes and within the continuum approximation of two-dimensional isotropy in the membrane surface.

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REFERENCES

- EVANS, E. A. 1973. A new material concept for the red cell membrane. *Biophys. J.* 13:926.
- EVANS, E. A. 1975. Two-dimensional, hyperelastic materials. In *Comparative Physiology: Functional Aspects of Structural Materials*. L. Bolis, S. Maddrell, and K. Schmidt-Nielsen, editors. North-Holland Publishing Co., Amsterdam. 9.
- EVANS, E. A., and P. L. LACELLE. 1975. Intrinsic material properties of the erythrocyte membrane indicated by mechanical analysis of the deformation. *Blood*. 45:29.
- EVANS, E. A., and R. M. HOCHMUTH. 1976. Membrane viscoelasticity. *Biophys. J.* 16:1.
- EVANS, E. A., R. WAUGH, and L. MELNIK. 1976. Elastic area compressibility modulus of red cell membrane. *Biophys. J.* 16:585.