Spontaneous tubulation of membranes and vesicles reveals membrane tension generated by spontaneous curvature

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In Section 6 of Ref.[1], lipid vesicles enclosing two aqueous phases, α and β, have been considered. These phases typically form two droplets that partially wet the vesicle membrane and, thus, partition this membrane into two distinct membrane segments, $\alpha\gamma$ and $\beta\gamma$, with surface areas $A_{\alpha\gamma}$ and $A_{\beta\gamma}$. In Section 6.1, it was argued that the vesicle shapes involve only a single Lagrange multiplier tension, Σ, which is conjugate to the total membrane area $A = A_{\alpha\gamma} + A_{\beta\gamma}$, because we have only a single constraint acting on this total area. The latter argument is, however, deceptive: in general, we need two Lagrange multiplier tensions $\Sigma_{\alpha\gamma}$ and $\Sigma_{\beta\gamma}$ as one can see most clearly if one views these two quantities as the mechanical tensions that act to stretch (or compress) the two membrane segments.

Thus, consider the equilibrium shapes of vesicles with minimal energy $\mathcal{E}_{\rm ve}$ for fixed droplet volumes V_α and V_β as a function of total membrane area A. For each value of A, these equilibrium shapes are characterized by certain segmental areas $A_{\alpha\gamma}$ and $A_{\beta\gamma}$. Likewise, the bending energy of these shapes consists of two terms, $\mathcal{E}_{be,\alpha\gamma}(A_{\alpha\gamma})$ and $\mathcal{E}_{be,\beta\gamma}(A_{\beta\gamma})$, corresponding to the two segments. The mechanical tensions $\Sigma_{\alpha\gamma}$ and $\Sigma_{\beta\gamma}$ within these segments are then given by

$$\Sigma_{\alpha\gamma} = -\left(\frac{d}{dA_{\alpha\gamma}}\mathcal{E}_{ve}\right)_{V_\alpha,V_\beta} = -\left(\frac{d}{dA_{\alpha\gamma}}\mathcal{E}_{be,\alpha\gamma}\right)_{V_\alpha,V_\beta} + \ldots \qquad (1)$$

and

$$\Sigma_{\beta\gamma} = -\left(\frac{d}{dA_{\beta\gamma}}\mathcal{E}_{ve}\right)_{V_\alpha,V_\beta} = -\left(\frac{d}{dA_{\beta\gamma}}\mathcal{E}_{be,\beta\gamma}\right)_{V_\alpha,V_\beta} + \ldots \qquad (2)$$

where the derivatives are taken at constant volumes V_α and V_β. The dots indicate terms arising from additional energy contributions[2] of

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the $\alpha\beta$ interface and the contact line. The values for $\Sigma_{\alpha\gamma}$ and $\Sigma_{\alpha\gamma}$ as obtained from (1) and (2) will, in general, differ because the two membrane segments are exposed to different environments and are, thus, characterized by different elastic parameters. In addition, the segmental areas $A_{\alpha\gamma}$ and $A_{\beta\gamma}$ can depend on the total membrane area A in a nonlinear manner, reflecting the variable partitioning of this area between the two segments.

For $\Sigma_{\alpha\gamma} \neq \Sigma_{\beta\gamma}$, the equations (66) and (67) in Ref.[1], which describe the total membrane tensions $\hat{\Sigma}_{\alpha\gamma}$ and $\hat{\Sigma}_{\beta\gamma}$, assume the form[3]

$$\hat{\Sigma}_{\alpha\gamma} = \Sigma_{\alpha\gamma} + \sigma_{\alpha\gamma} = \Sigma_{\alpha\gamma} + 2\kappa_{\alpha\gamma}\, m_{\alpha\gamma}^2 \tag{66*}$$

and

$$\hat{\Sigma}_{\beta\gamma} = \Sigma_{\beta\gamma} + \sigma_{\beta\gamma} = \Sigma_{\beta\gamma} + 2\kappa_{\beta\gamma}\, m_{\beta\gamma}^2\,. \tag{67*}$$

Furthermore, the relation (73) in Ref.[1] is then replaced by

$$\frac{\Sigma_{\alpha\gamma} + \sigma_{\alpha\gamma}}{\Sigma_{\alpha\beta}} - \frac{\Sigma_{\beta\gamma} + \sigma_{\beta\gamma}}{\Sigma_{\alpha\beta}} = \frac{\sin(\theta_\beta)}{\sin(\theta_\gamma)} - \frac{\sin(\theta_\alpha)}{\sin(\theta_\gamma)} \tag{73*}$$

and the equations (77) - (79) are no longer valid. Finally, equation (80) in Ref.[1] now attains the more general form

$$\Sigma_{\alpha\beta}\, \cos(\theta_{\rm in}) = \hat{\Sigma}_{\beta\gamma} - \hat{\Sigma}_{\alpha\gamma} = \Sigma_{\beta\gamma} + \sigma_{\beta\gamma} - \Sigma_{\alpha\gamma} - \sigma_{\alpha\gamma}\,. \tag{80*}$$

If the $\alpha\gamma$ membrane segment forms nanotubes, the mechanical tension $\Sigma_{\alpha\gamma}$ of this segment can be neglected because it is much smaller than the spontaneous tension $\sigma_{\alpha\gamma}$,[1] and the total tension

$$\Sigma_{\beta\gamma} + \sigma_{\beta\gamma} \approx \sigma_{\alpha\gamma} + \Sigma_{\alpha\beta}\, \cos(\theta_{\rm in}) \tag{3}$$

within the $\beta\gamma$ segment must balance both the spontaneous tension $\sigma_{\alpha\gamma}$ of the $\alpha\gamma$ segment and the interfacial tension $\Sigma_{\alpha\beta}$ of the liquid-liquid interface between the two droplets.

References

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