

Forces in vertex models

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I. CELL POTENTIAL ENERGY

We introduce for each cell i a reference perimeter P_i^0 and a reference area A_i^0 , and for each of its cell corner $\mu \in \Omega_i$ a force whose effect is to bring the cell's perimeter P_i and area A_i to their reference quantities. A possible force derives from the following potential energy [1–4]

$$E_{\text{VM}} = \sum_{\text{cells } i} \left[\frac{1}{2} K_i (A_i - A_i^0)^2 + \frac{1}{2} \Gamma_i (P_i - P_i^0)^2 \right], \quad (1)$$

where K_i and Γ_i are respectively area and perimeter elastic constants. We denote \mathbf{r}_μ , \mathbf{r}_i the position of vertices μ, i (see Fig. 1). The cell's perimeter can be written

$$P_i = \sum_{\mu \in \Omega_i} |\mathbf{r}_\mu - \mathbf{r}_{\mu-1}|, \quad (2)$$

and the cell's area can be computed with the shoelace formula

$$A_i = \sum_{\mu \in \Omega_i} \frac{1}{2} [(\mathbf{r}_\mu - \mathbf{r}_i) \times (\mathbf{r}_{\mu-1} - \mathbf{r}_i)] \cdot \hat{\mathbf{e}}_z. \quad (3)$$

Note that, by convention of ordering of cell corners, each term in this sum *must be* positive. With these notations, we thus write the force acting on vertex μ

$$\mathbf{F}_{\text{VM},\mu} = -\nabla_\mu E_{\text{VM}}, \quad (4)$$

where $\nabla_\mu \equiv \partial/\partial \mathbf{r}_\mu$. We compute

$$\nabla_\mu (|\mathbf{r}_\mu - \mathbf{r}_{\mu-1}|) = \frac{\mathbf{r}_\mu - \mathbf{r}_{\mu-1}}{|\mathbf{r}_\mu - \mathbf{r}_{\mu-1}|}, \quad (5)$$

as well as

$$\nabla_\mu [(\mathbf{r}_\mu - \mathbf{r}_i) \times (\mathbf{r}_{\mu-1} - \mathbf{r}_i)] \cdot \hat{\mathbf{e}}_z = (\mathbf{r}_{\mu-1} - \mathbf{r}_i) \times \hat{\mathbf{e}}_z \quad (6)$$

to write (4) in its full form

$$\begin{aligned} \mathbf{F}_{\text{VM},\mu} &= - \sum_{\text{cells } i, \mu \in \Omega_i} \left[\frac{1}{2} K_i (A_i - A_i^0) [(\mathbf{r}_{\mu+1} - \mathbf{r}_i) \times \hat{\mathbf{e}}_z - (\mathbf{r}_{\mu-1} - \mathbf{r}_i) \times \hat{\mathbf{e}}_z] \right. \\ &\quad \left. + \Gamma_i (P_i - P_i^0) \left[\frac{\mathbf{r}_\mu - \mathbf{r}_{\mu-1}}{|\mathbf{r}_\mu - \mathbf{r}_{\mu-1}|} + \frac{\mathbf{r}_\mu - \mathbf{r}_{\mu+1}}{|\mathbf{r}_\mu - \mathbf{r}_{\mu+1}|} \right] \right] \\ &= \sum_{\text{cells } i, \mu \in \Omega_i} \left[\frac{1}{2} K_i (A_i - A_i^0) \underbrace{(\mathbf{r}_{\mu-1} - \mathbf{r}_{\mu+1})}_{\text{towards cell interior}} \times \hat{\mathbf{e}}_z + \Gamma_i (P_i - P_i^0) \left[\underbrace{\frac{\mathbf{r}_{\mu-1} - \mathbf{r}_\mu}{|\mathbf{r}_{\mu-1} - \mathbf{r}_\mu|}}_{\text{towards neighbour}} + \underbrace{\frac{\mathbf{r}_{\mu+1} - \mathbf{r}_\mu}{|\mathbf{r}_{\mu+1} - \mathbf{r}_\mu|}}_{\text{towards neighbour}} \right] \right], \end{aligned} \quad (7)$$

where underbraced vectors are represented in Fig. 1. It is noteworthy that, with potential (1), the force acting on each cell centre is zero

$$\mathbf{F}_{\text{VM},i} = -\nabla_i E_{\text{VM}} = -\frac{1}{2} K_i (A_i - A_i^0) \sum_{\mu \in \Omega_i} (\mathbf{r}_\mu - \mathbf{r}_{\mu-1}) \times \hat{\mathbf{e}}_z = 0. \quad (8)$$

[1] Reza Farhadifar, Jens-Christian Röper, Benoit Aigouy, Suzanne Eaton, and Frank Jülicher, “The Influence of Cell Mechanics, Cell-Cell Interactions, and Proliferation on Epithelial Packing,” *Current Biology* **17**, 2095–2104 (2007).

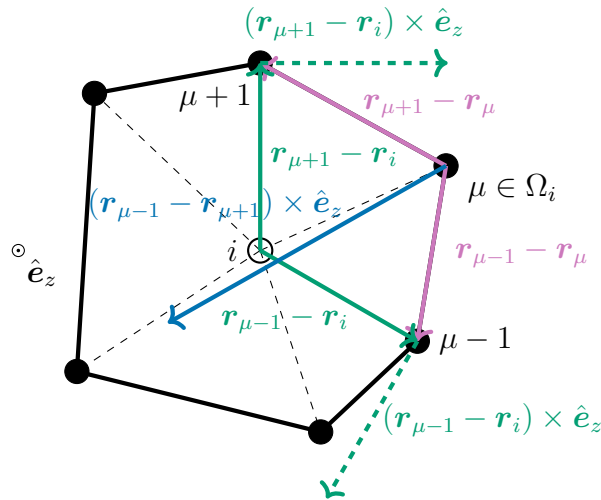


FIG. 1. Vertex representation of a single cell. By convention, cell centres are denoted by latin indices, and cell corners are denoted by greek indices. We denote Ω_i the ensemble of cell corners μ of the cell whose centre is i . By convention, $\mu + 1$ (respectively $\mu - 1$) denotes the next cell corner of i after μ in anticlockwise (respectively clockwise) order.

- [2] Alexander G. Fletcher, Miriam Osterfield, Ruth E. Baker, and Stanislav Y. Shvartsman, “Vertex Models of Epithelial Morphogenesis,” *Biophysical Journal* **106**, 2291–2304 (2014).
- [3] Dapeng Bi, Xingbo Yang, M. Cristina Marchetti, and M. Lisa Manning, “Motility-Driven Glass and Jamming Transitions in Biological Tissues,” *Physical Review X* **6**, 021011 (2016).
- [4] Rastko Sknepnek, Ilyas Djafer-Cherif, Manli Chuai, Cornelis Weijer, and Silke Henkes, “Generating active T1 transitions through mechanochemical feedback,” *eLife* **12**, e79862 (2023).