# Polarity patterns of stress fibers

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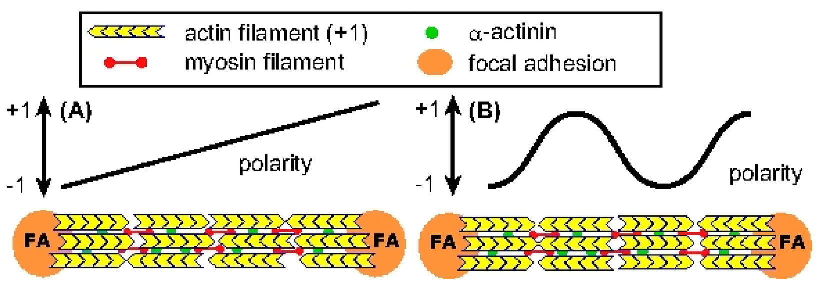
## Abstract

Stress fibers are bundles of actin filaments made contractile by interaction with myosin minifilaments, and elastic by crosslinking with alpha-actinin and other proteins. The spatial profile of the polarity of the actin filaments inside contractile actomyosin bundles is known to be either monotonic (graded) or periodic (alternating) [1]. In the framework of linear irreversible thermodynamics [2], we write the constitutive equations for a one-dimensional, polar, active elastomer and show that the transition from graded to alternating polarity patterns is a nonequilibrium Lifshitz point, where a diffusion constant changes sign. Active contractility is a necessary condition for the emergence of sarcomeric, alternating polarity patterns.

## Model




### A 1D active polar elastomer

- mesoscopic scales
- one-component system
- active $\Delta\mu > 0$
- polar
- elastic $t \gg \tau_{\rm viscoelastic}$
- without turn-over $t \gg \tau_{\rm turn-over}$

### Polar order parameter

$$\mathbf{p} = p(x,t)\,\mathbf{e_x}$$

- Mesoscopic average of the polarity of actin filaments
- Barbed ends face focal adhesions
- Boundary conditions:

$$p(0,t) = -1 \qquad p(L,t) = +1$$

Invariance under $p \to -p$, $x \to -x$

**Free energy density** obtained by expanding close to polarity $p = 0$, strain $e = 0$

$$f = \frac{1}{2} a\, p^2 + \frac{1}{2} K \left(\frac{\partial p}{\partial x}\right)^2 + \frac{1}{2} G\, e^2 + w\, e \left(\frac{\partial p}{\partial x}\right)$$

with $w^2 \le K\,G$ (thermodynamic stability)

- Molecular field: $h = -\frac{\delta f}{\delta p}$
- Elastic stress: $\sigma^{\rm el} = \frac{\delta f}{\delta e}$

**Entropy production rate** from thermodynamics and conservation equations:

$$\frac{R}{T} = \left(\sigma + P - \sigma^{\rm el}\right)\,\partial_x v + h\,\dot{p} + \Delta\mu\, r$$

**Constitutive equations:**

$$\sigma + P - \sigma^{\rm el} = \eta\,\partial_x v + \left(-\zeta + \beta\,\partial_x p\right)\Delta\mu$$

$$\frac{\mathrm{d}p}{\mathrm{d}t} = \frac{h}{\gamma} - \alpha\, p \partial_x p\, \Delta\mu$$

- We use force balance $\partial_x \sigma = 0$ to eliminate the strain $e$,
- We obtain diffusive dynamics for the polarity field, with a diffusion constant that may change sign depending on the value of $\Delta\mu$.

$$D = \frac{K}{\gamma}\left[1 - \frac{w^2}{KG}\left(1 + \frac{\beta\Delta\mu}{w}\right)\right]$$

## Conclusions and Outlook

- A phase transition explains the existence of graded and alternating polarity patterns.
- We also treat the case where polarity is a *conserved* field [3], possibly relevant in the absence of nucleation/annihilation and insertion/removal of actin filaments.
- Polarity profiles emerge in an active medium with a *uniform* activity.
- We need to bridge the gap with molecular descriptions, and to relate hydrodynamic coupling terms between strain and polarity with the interaction of F-actin with passive and active crosslinkers.

## References

[1] Cramer, L. P., M. Siebert and T.J. Mitchison. 1997. *J. Cell Biol.* **136**:1287-1305.

[2] Jülicher, F., K. Kruse, J. Prost, and J.-F. Joanny. 2007. *Phys. Rep.* 49:3–28.

[3] Yoshinaga, N., J.-F. Joanny, J. Prost, and P. Marcq. 2010. *Phys. Rev. Lett.* 105:238103.

## Graded polarity pattern

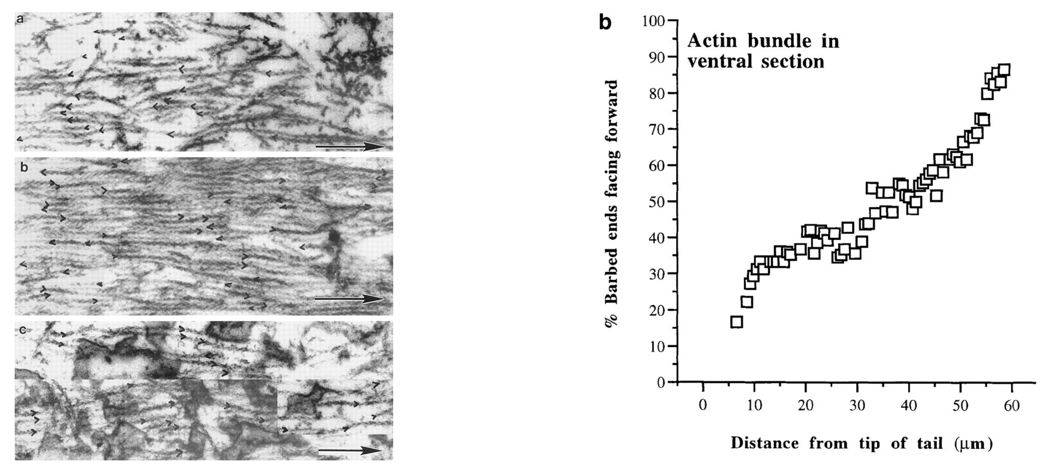
### Experiment [1]

Actomyosin bundles of polarizing fibroblasts at the onset of motility (bar: $0.2\mu$m)

Tip of the lamellum →

Cell center →

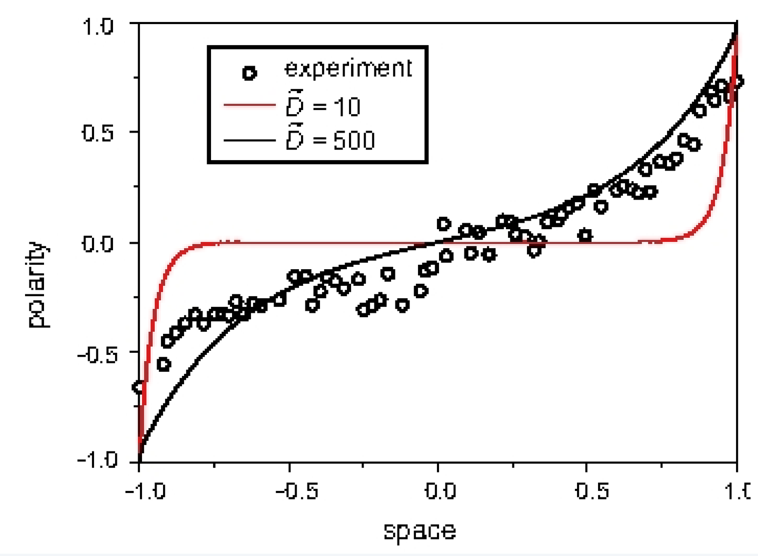
Cell rear →




### Positive diffusion $D > 0$ when $\frac{\beta\Delta\mu}{w} < \frac{KG}{w^2} - 1$

Stable monotonic stationary solutions of the (non-dimensional) damped Burgers equation

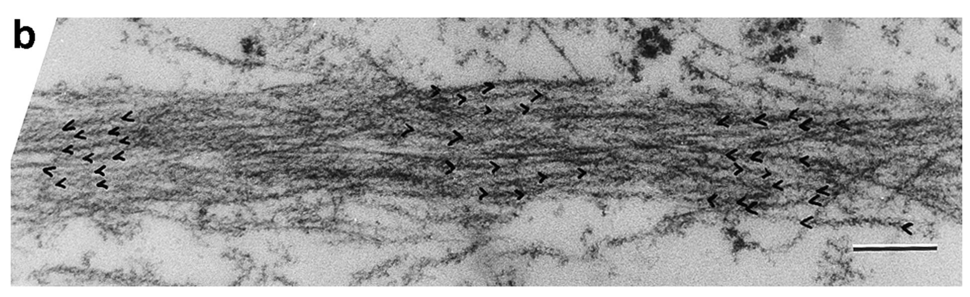
$$\frac{\partial p}{\partial \tilde{t}} + p\,\frac{\partial p}{\partial \tilde{x}} = -p + \tilde{D}\,\frac{\partial^2 p}{\partial \tilde{x}^2}$$

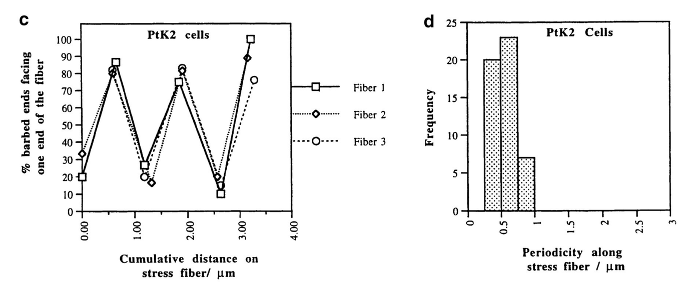



## Alternating polarity pattern

### Experiment [1]

Stress fibers of epithelial cells (bar: $0.2\mu$m)



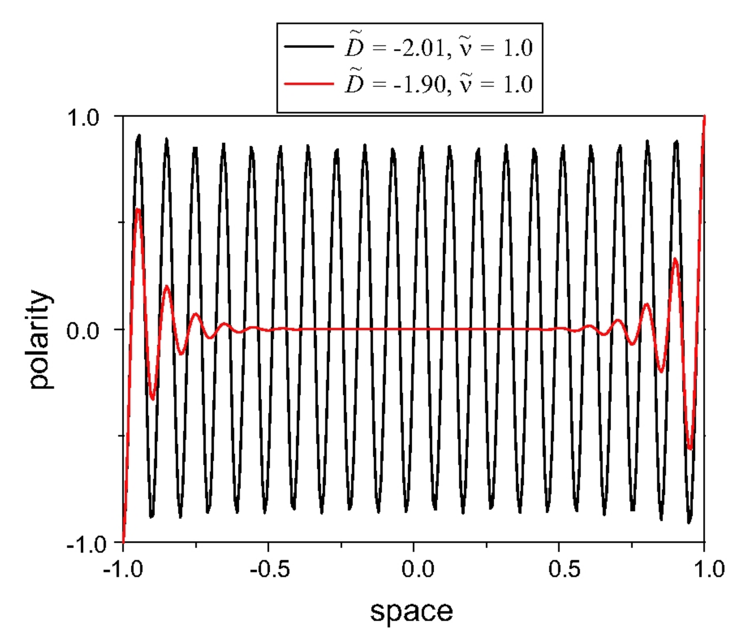




### Negative diffusion $D < 0$ when $\frac{\beta\Delta\mu}{w} > \frac{KG}{w^2} - 1$

A stabilizing ($\nu > 0$) higher-order term $\frac{1}{2}\,\nu\,\left(\frac{\partial^2 p}{\partial x^2}\right)^2$ must be added to the free energy.

Stable stationary solutions of the (non-dimensional) damped Kuramoto-Sivashinsky equation

$$\frac{\partial p}{\partial \tilde{t}} + p\,\frac{\partial p}{\partial \tilde{x}} = -\,p + \tilde{D}\,\frac{\partial^2 p}{\partial \tilde{x}^2} - \tilde{\nu}\,\frac{\partial^4 p}{\partial \tilde{x}^4}$$




- Alternating polarity patterns of wavelength $\lambda$ are found when $\tilde{D} < -2\sqrt{\tilde{\nu}}$

$$\lambda^2 = \frac{8\pi^2\nu}{K}\left[\frac{w^2}{KG}\left(1 + \frac{\beta\Delta\mu}{w}\right) - 1\right]^{-1}$$

- Without activity: $\Delta\mu = 0 \Rightarrow D > 0,\ \lambda^2 < 0$, periodicity is lost!
- Mixed polarity patterns ($p(x) = 0$) are found far from the tips when $-2\sqrt{\tilde{\nu}} < \tilde{D} < 0$.