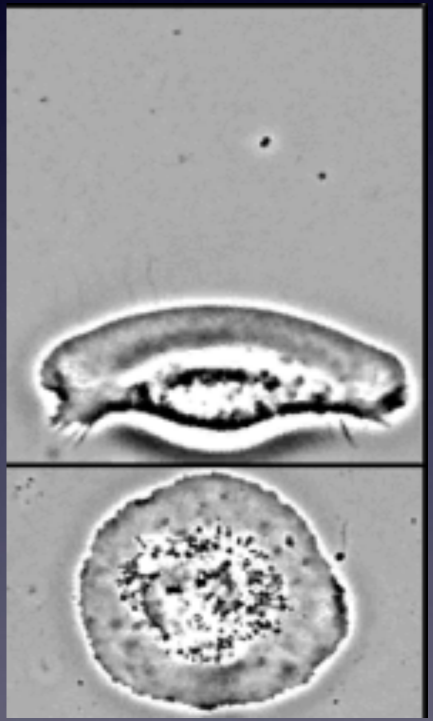
Out-of-equilibrium physics in biology

Karsten Kruse

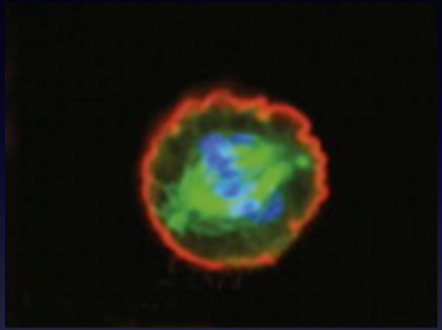
Universität des Saarlandes

Equilibrium physics out of biology

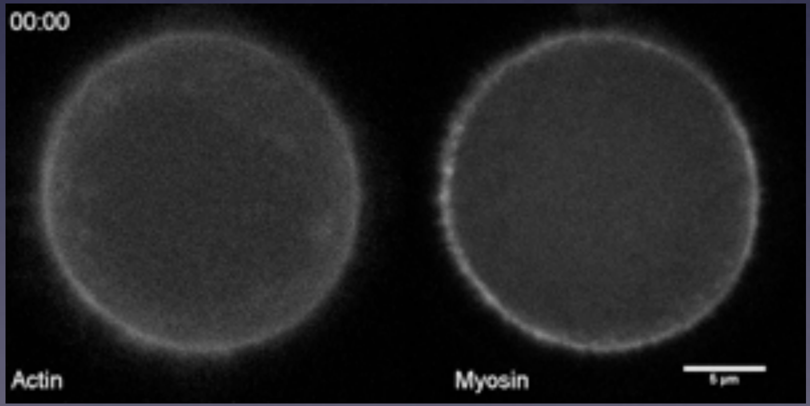
The cytoskeleton drives vital processes



A.B. Verkhovsky et al.



Kunda et al, Curr. Biol. (2008)



Wollrab et al, Nat. Commun (2016)

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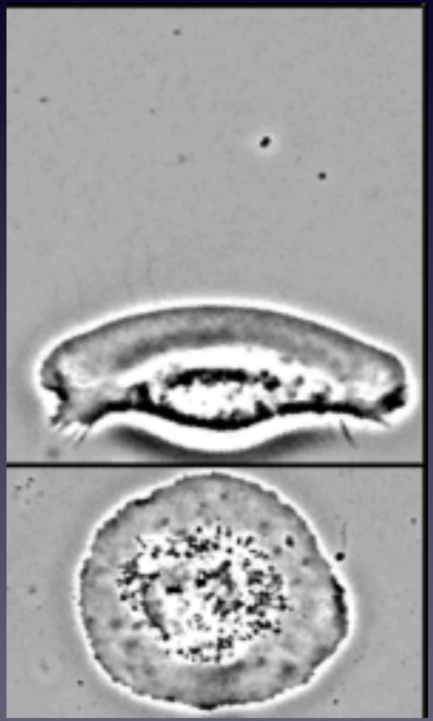

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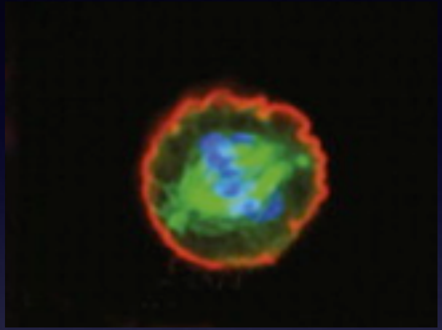
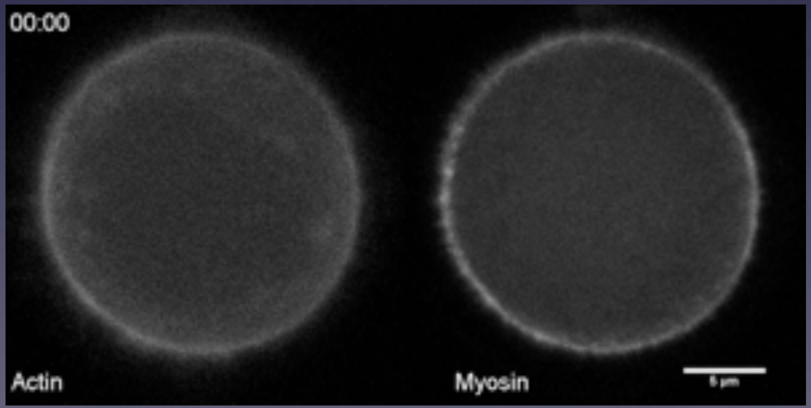
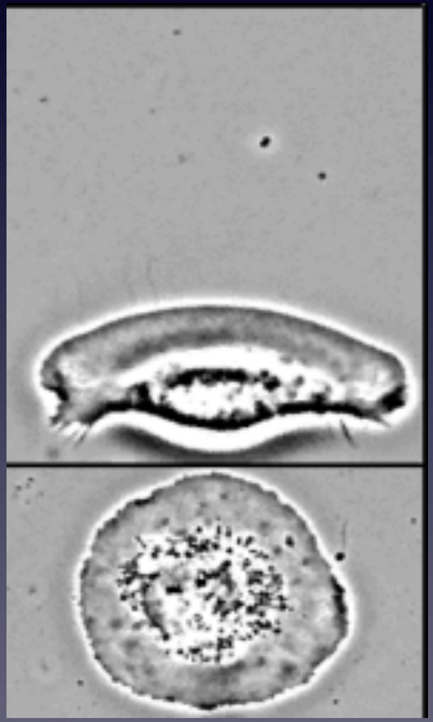


Kunda et al, Curr. Biol. (2008)



Wollrab et al, Nat. Commun (2016)

The cytoskeleton drives vital processes



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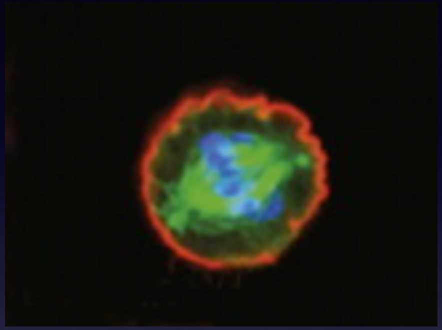
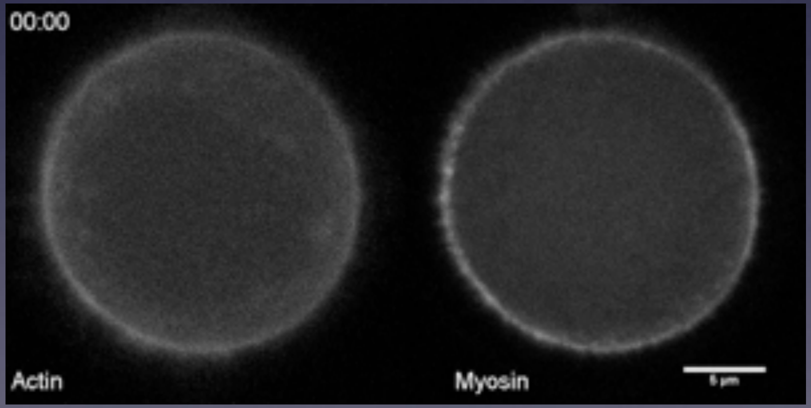
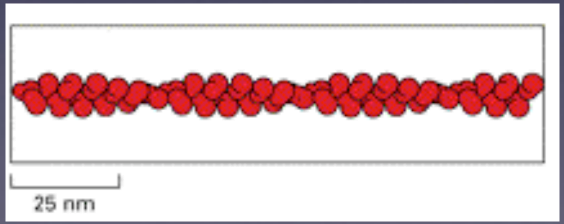


Kunda et al, Curr. Biol. (2008)

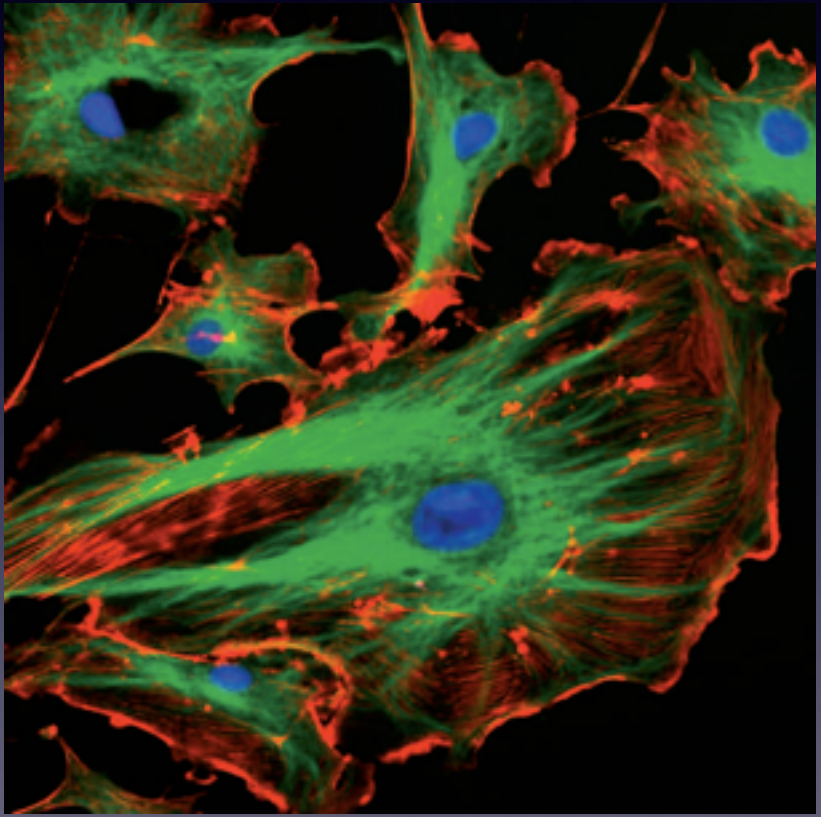


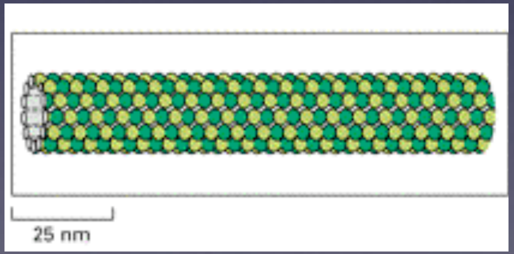
Wollrab et al, Nat. Commun (2016)

The cytoskeleton is a network of polar protein filaments



F-actin

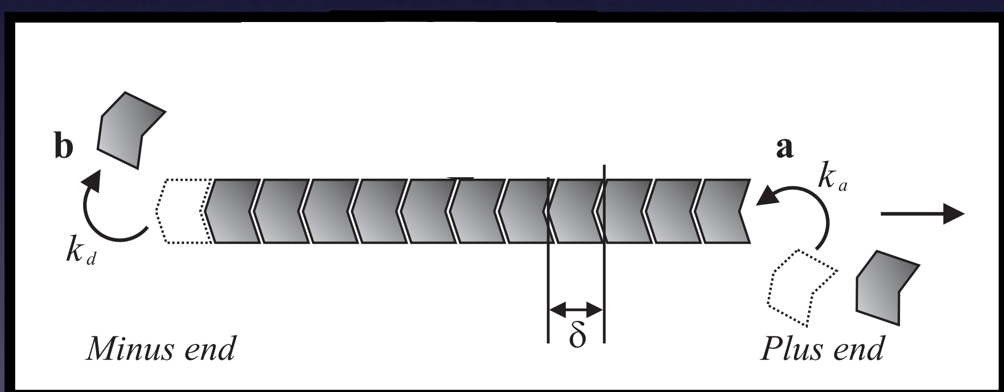


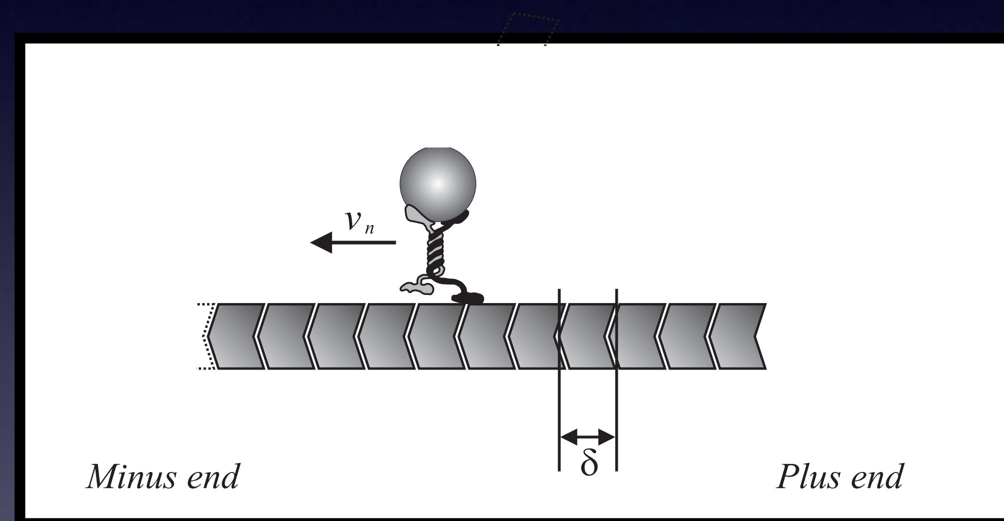


microtubules

MBoC5

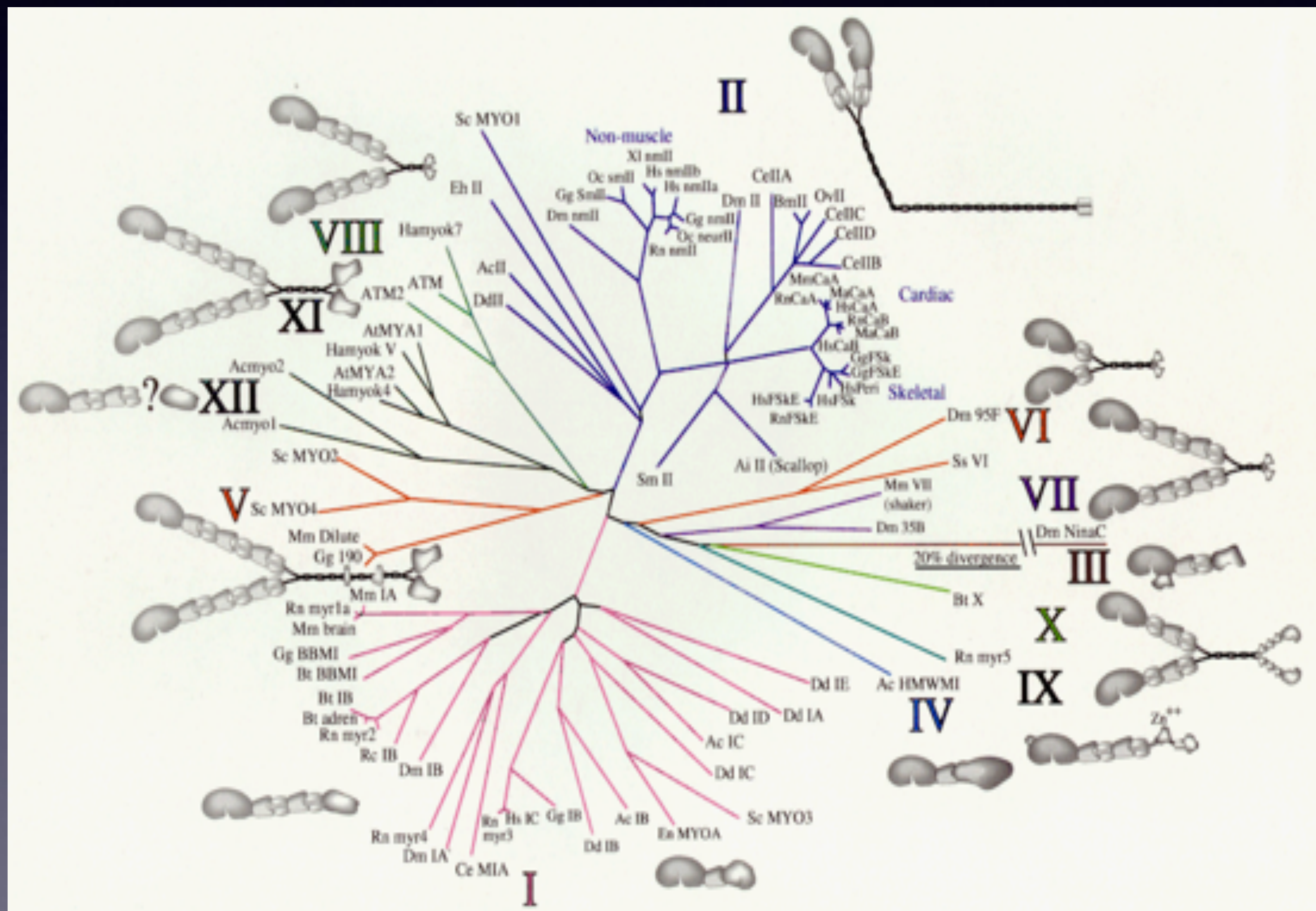
Active cytoskeletal processes are driven by ATP hydrolysis





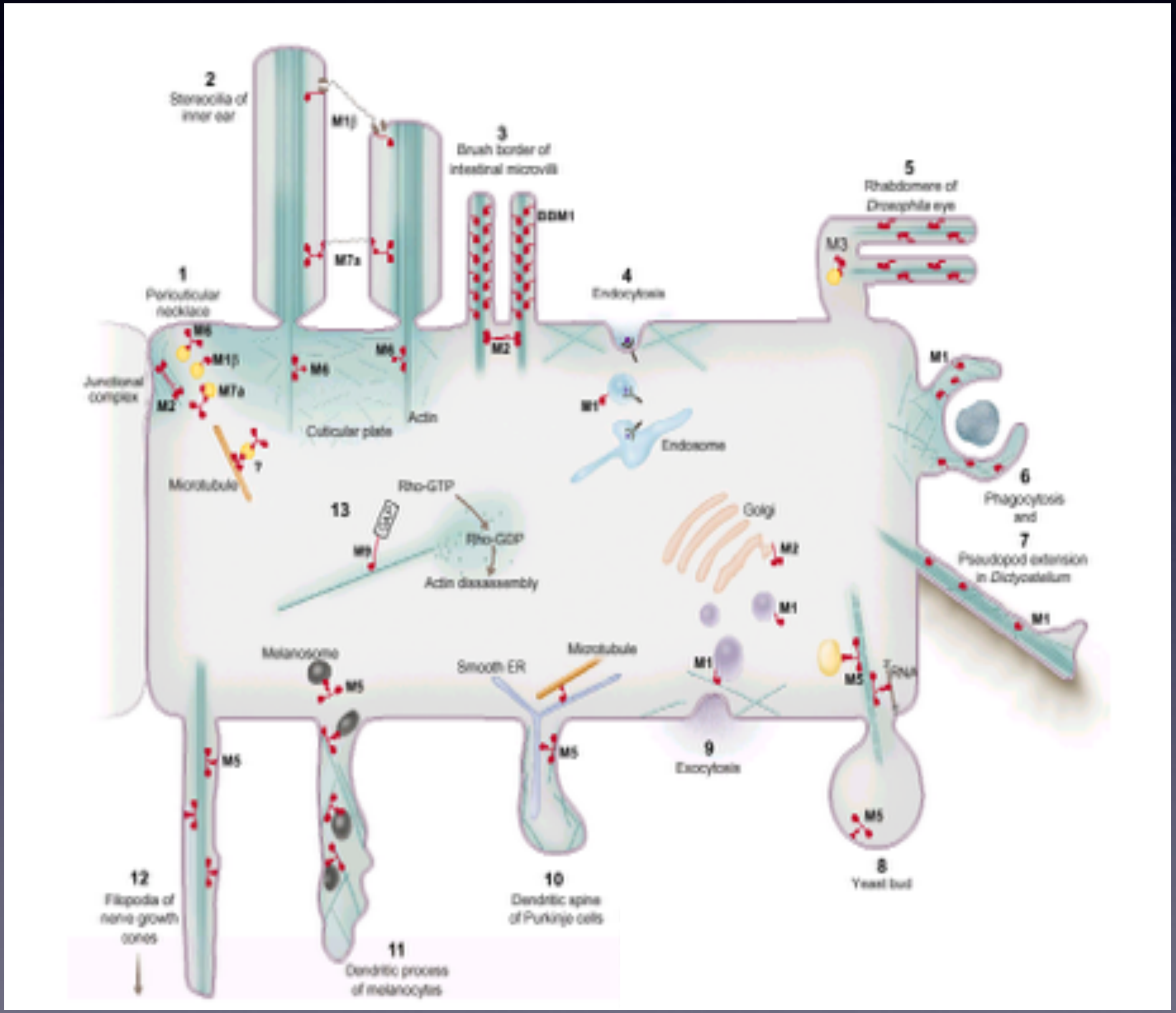
$$\mathrm{ATP} \rightleftharpoons \mathrm{ADP} + \mathrm{P_i}$$

There are many different kinds of myosin motors…



Tony Hodge, LMB Cambridge

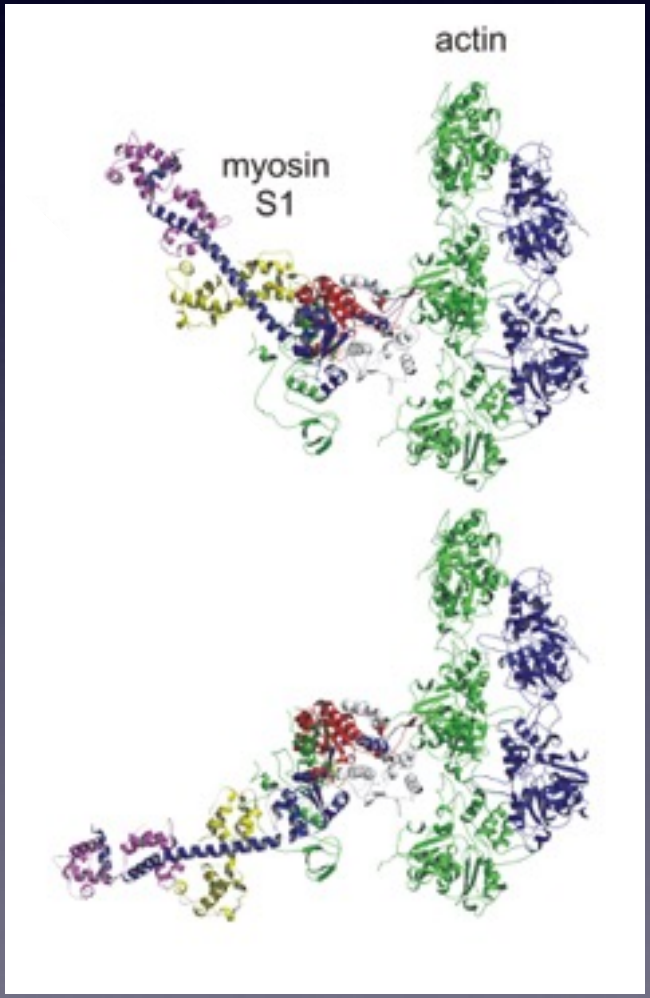
… that are involved in various cellular processes



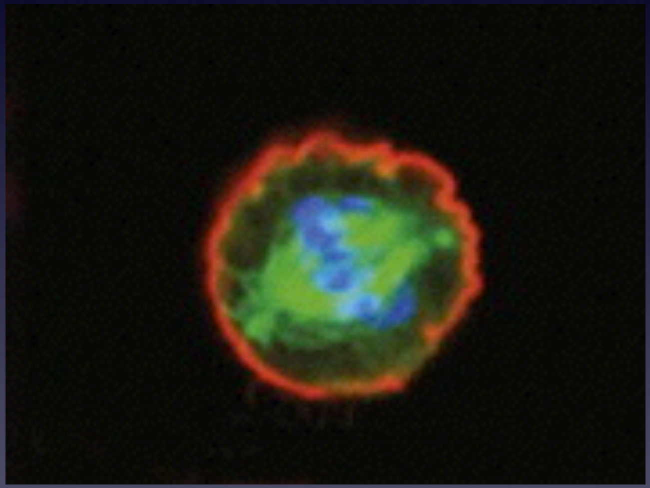
Mermall, Post, and Mooseker, Science (1998)

Claudia Veigel: Single motors

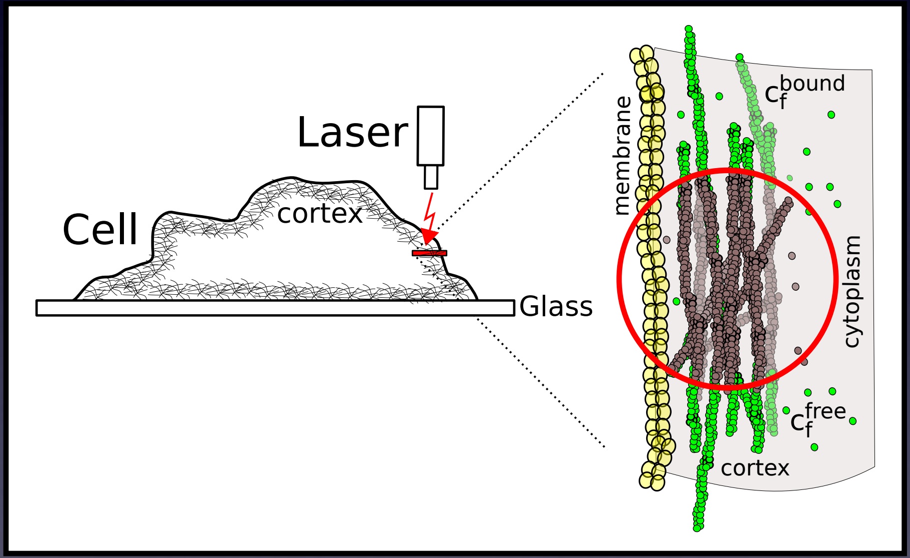
- Basic mechanisms of chemo-mechanical energy transduction
- Properties of ensembles of motors in the cellular context



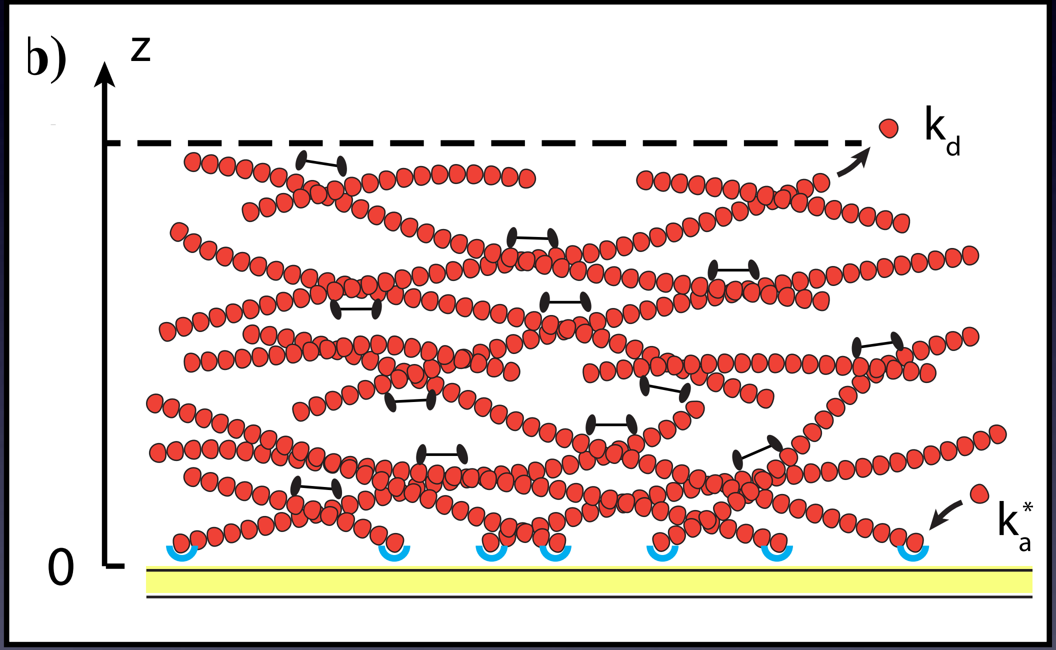
The actin network forms a well-defined cortical layer



Kunda et al, Curr. Biol. (2008)



The cortex dynamics is governed by three essential processes

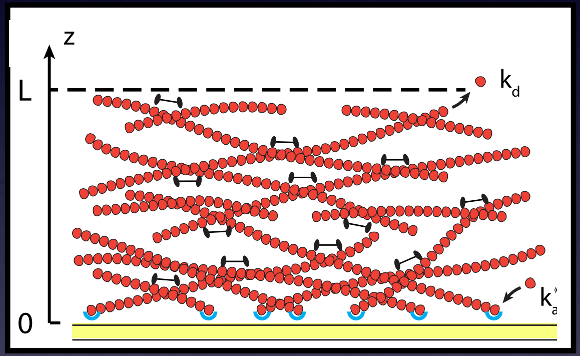


- polymerization at the surface
- disassembly in the bulk
- active contractile stresses

The actin network disassembles in the bulk

Mass conservation

$$\partial_t \rho + \nabla \cdot \rho \mathbf{v} = -k_d \rho$$

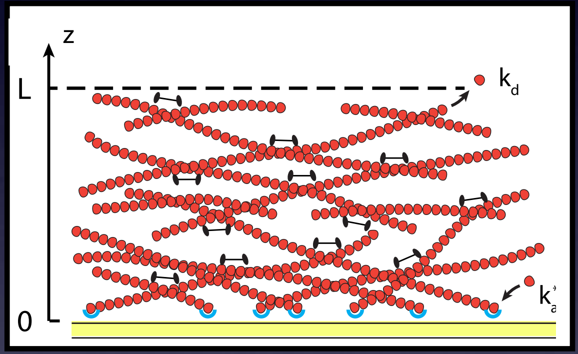


Joanny et al, EPJ E (2013).

The actin network disassembles in the bulk

Mass conservation (1d)

$$\partial_t \rho + \partial_z \rho v = -k_d \rho$$



Joanny et al, EPJ E (2013).

At the membrane, nucleators generate a flux into the system

Mass conservation (1d)

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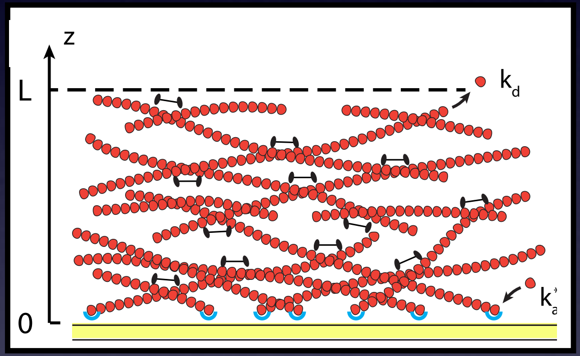


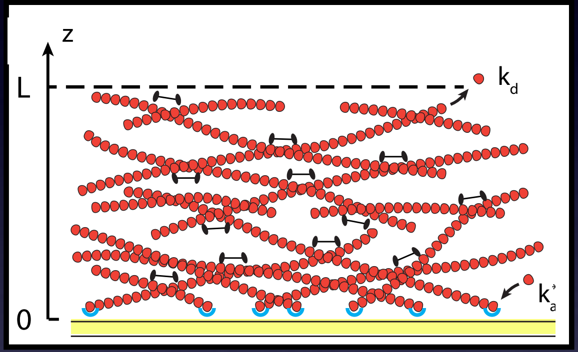
boundary condition: $j_z\big|_{z=0} = \rho v\big|_{z=0} = \rho_0 v_p$

Joanny et al, EPJ E (2013).

At the membrane, nucleators generate a flux into the system

$$\partial_t \rho + \partial_z \rho v = -k_d \rho$$

$$\rho v\big|_{z=0} = \rho_0 v_p$$



Momentum conservation (1d)

$$\partial_t \rho v - \partial_x \sigma^{\mathrm{tot}} = f_{\mathrm{ext}}$$

Joanny et al, EPJ E (2013).

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$$\partial_t \rho + \partial_z \rho v = -k_d \rho$$

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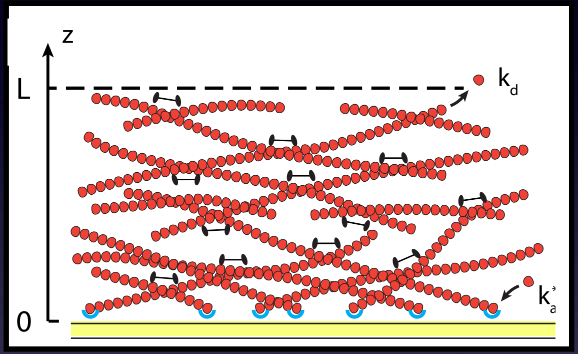

Momentum conservation (1d)

$$\partial_t \rho v - \partial_x \sigma^{\mathrm{tot}} = 0$$

Joanny et al, EPJ E (2013).

At the membrane, nucleators generate a flux into the system

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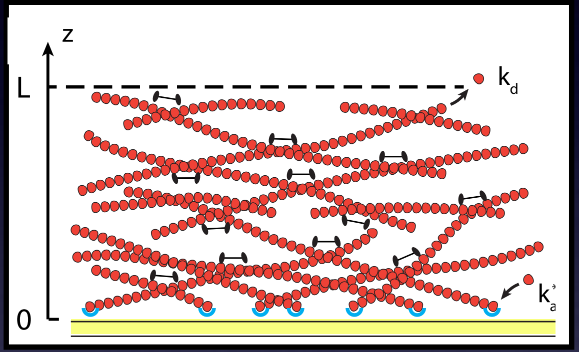

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$$\partial_x \sigma^{\mathrm{tot}} = 0$$

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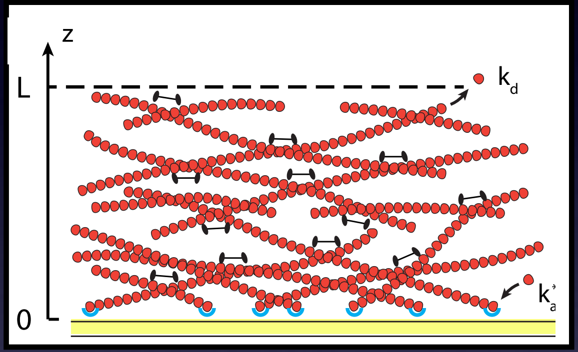


Momentum conservation (1d)

$$\partial_x \sigma^{\text{tot}} = 0$$

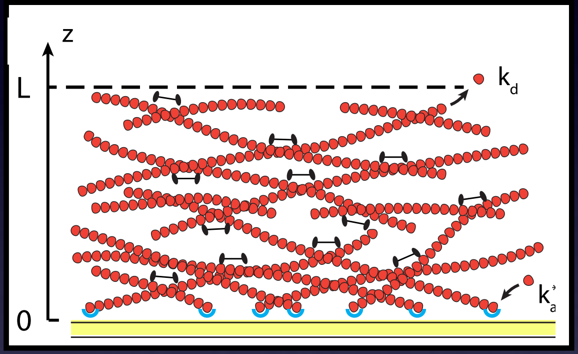
$$\sigma^{\text{tot}} = 2\eta\partial_z v - \tilde{\Pi}(\rho) - \zeta\Delta\mu$$

Joanny et al, EPJ E (2013).

At the membrane, nucleators generate a flux into the system

$$\partial_t \rho + \partial_z \rho v = -k_d \rho$$

$$\rho v|_{z=0} = \rho_0 v_p$$



$$2\eta \partial_z^2 v - \partial_z \Pi(\rho) = 0$$

Joanny et al, EPJ E (2013).

At the membrane, nucleators generate a flux into the system

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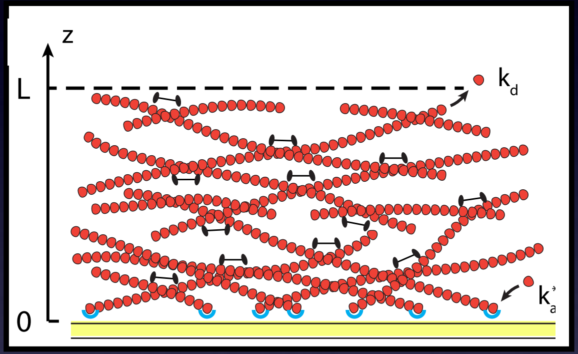


$$2\eta \partial_z^2 v - \partial_z \Pi(\rho) = 0$$

Effective (osmotic) pressure

$$\Pi = a\rho^3 + b\rho^4$$

accounts for activity: a<0 for contractile stress

Joanny et al, EPJ E (2013).

The density profile can be obtained explicitly

$$f(\rho) = -k_d\eta - a\rho^3 - b\rho^4$$

$$\frac{d\rho}{dz} = A(\rho)f(\rho) \quad \text{with} \quad A(\rho) \geq 0$$

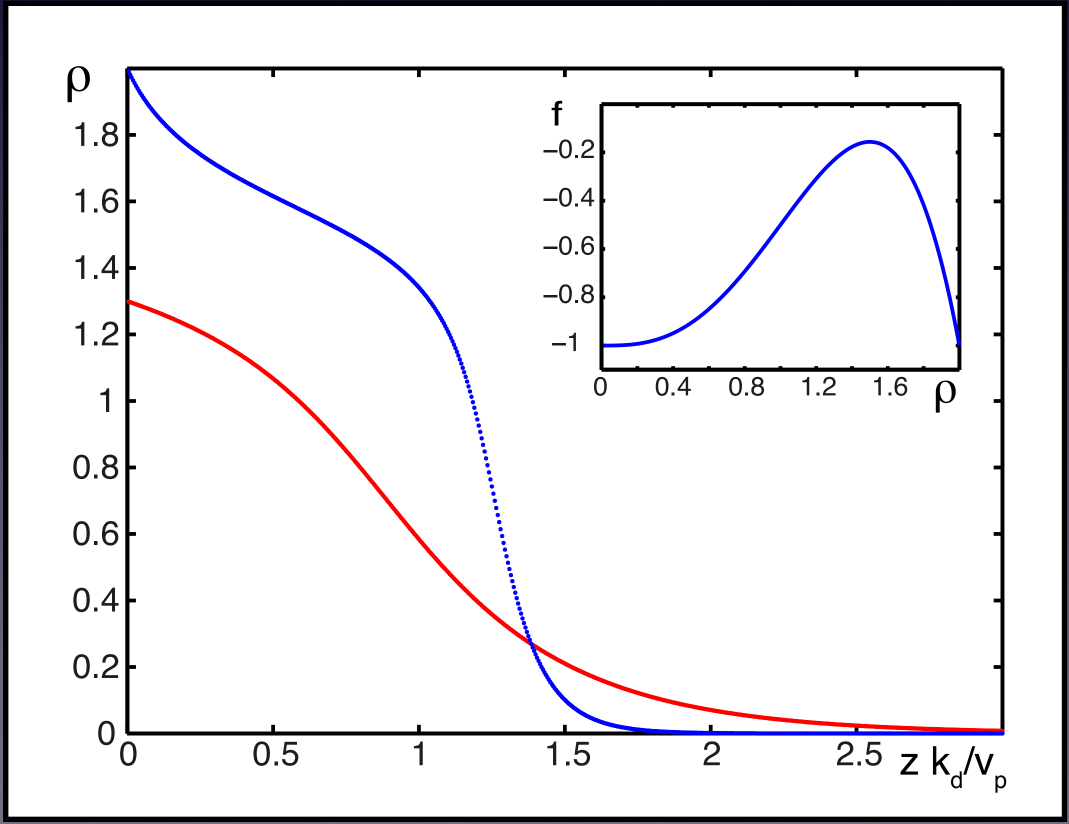
Joanny et al, EPJ E (2013).

The density profile can be obtained explicitly

$$f(\rho) = -k_d \eta - a\rho^3 - b\rho^4$$

$$a > a_c$$

$$\frac{d\rho}{dz} = A(\rho) f(\rho)$$



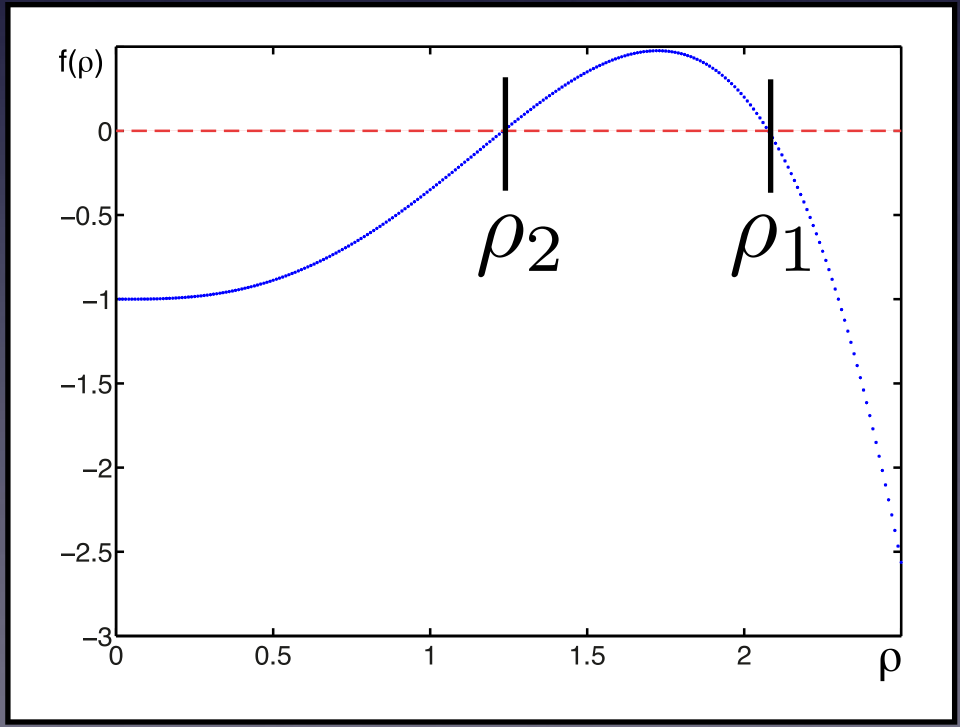
Joanny et al, EPJ E (2013).

The density profile can be obtained explicitly

$$f(\rho) = -k_d\eta - a\rho^3 - b\rho^4$$

$$a \leq a_c < 0$$

$$\frac{d\rho}{dz} = A(\rho)f(\rho)$$



Joanny et al, EPJ E (2013).

There is no actin flux beyond zeros of f

$$f(\rho) = -k_d\eta - a\rho^3 - b\rho^4$$

$$v = \frac{\rho_0}{\rho} v_p \exp\left\{-\int_{\rho_0}^{\rho} \frac{k_d\eta}{\rho' f(\rho')} d\rho'\right\}.$$

Joanny et al, EPJ E (2013).

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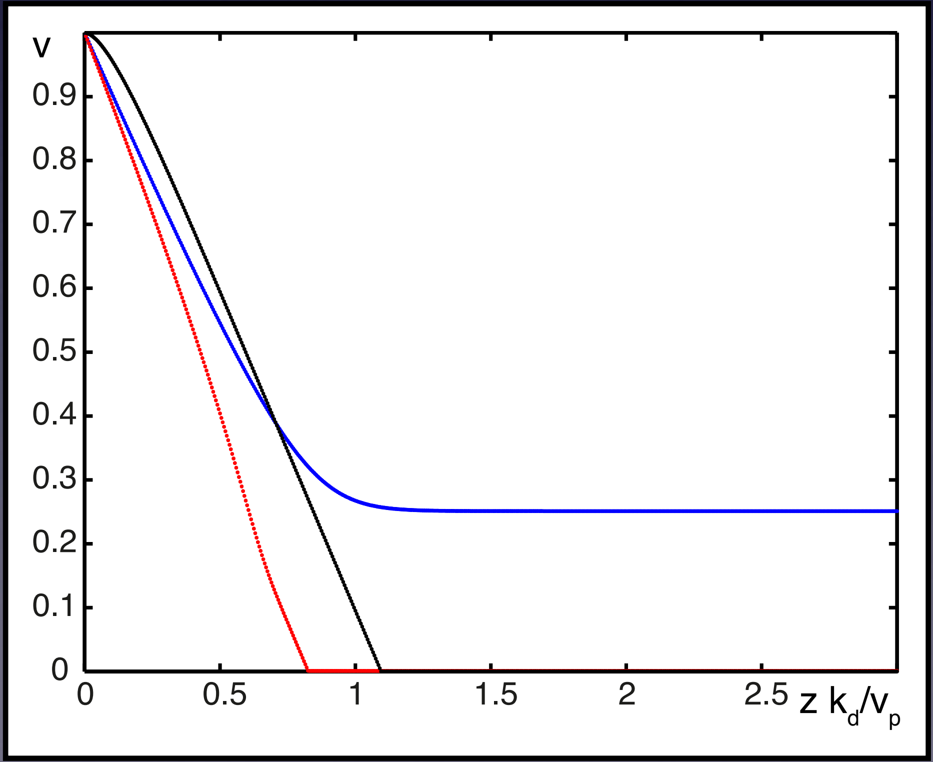
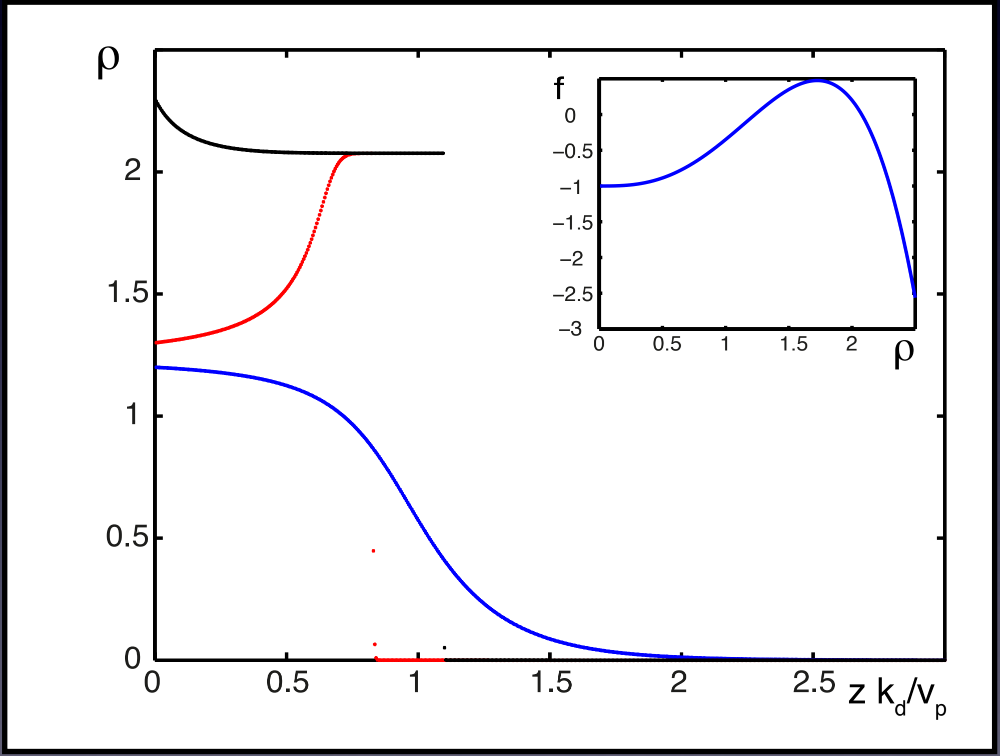


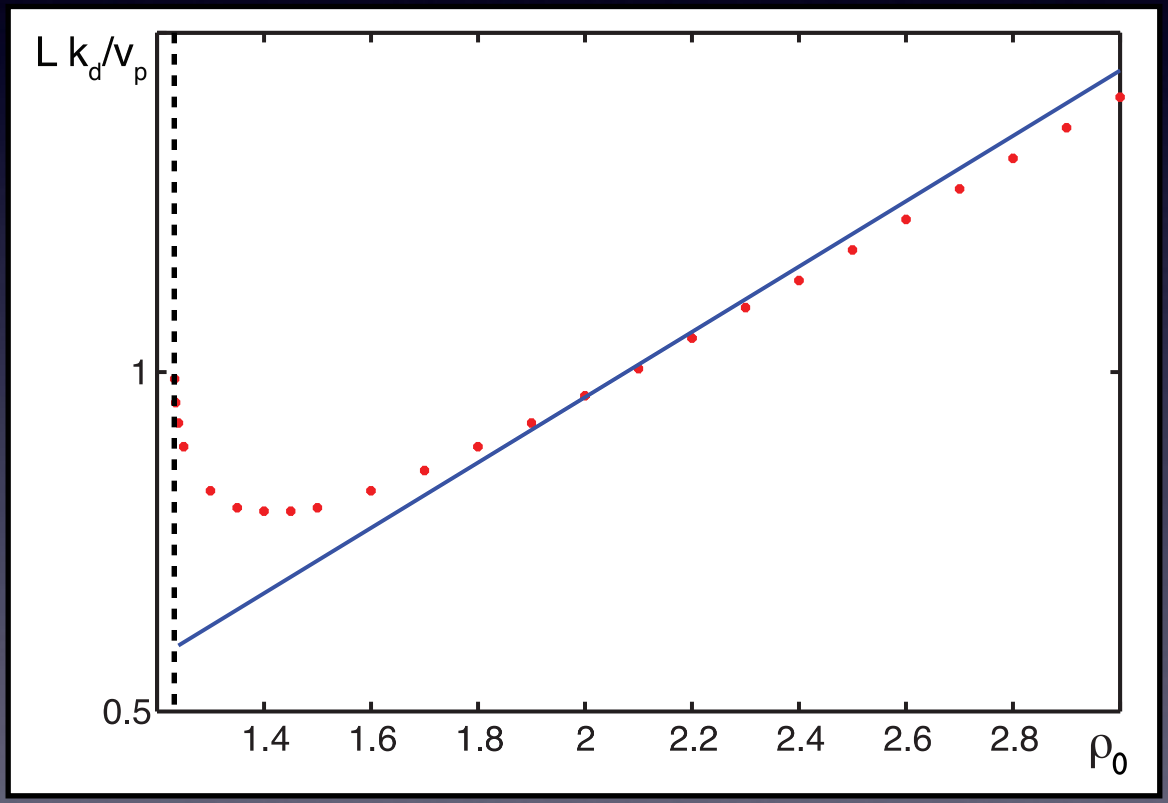
Joanny et al, EPJ E (2013).

A well-defined cortical layer forms beyond the bifurcation



Joanny et al, EPJ E (2013).

Cortex thickness depends non-monotonically on actin nucleation



$$L \sim \frac{\rho_0}{\rho_1}\frac{v_p}{k_d}$$

$$L = \frac{v_p}{k_d} \quad \text{for} \quad \rho_0 = \rho_1 \text{ and } \rho_0 = \rho_2$$

Joanny et al, EPJ E (2013).

Hydrodynamics of a simple fluid is based on conservation laws

Mass conservation:

$$\partial_t \rho + \nabla \cdot (\rho \mathbf{v}) = 0$$

Momentum conservation:

$$\partial_t \mathbf{g} - \nabla \cdot \sigma^{\rm tot} = \mathbf{f}_{\rm ext}$$

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Generalized fluxes and forces are identified by analysis of entropy production

$$f = \frac{g^2}{2\rho} + f_0$$

$$F = \int f d^3\mathbf{r}$$

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$$f = \frac{g^2}{2\rho} + f_0 \qquad F = \int f d^3\mathbf{r}$$

$$T\dot{\Theta} = -F = \int (\sigma_{\alpha\beta}^{\text{tot}} - P\delta_{\alpha\beta}) v_{\alpha\beta} d^3\mathbf{r}$$

P: hydrostatic pressure

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$$T\dot{\Theta} = -F = \int \underbrace{\left(\sigma^{\mathrm{tot}}_{\alpha\beta} - P\delta_{\alpha\beta}\right)}_{\equiv\, \sigma^{\mathrm{d}}_{\alpha\beta}} v_{\alpha\beta} d^3\mathbf{r}$$

$\equiv \sigma^{\mathrm{d}}_{\alpha\beta}$ deviatory stress

P: hydrostatic pressure

The constitutive relations for the currents are linear expressions in the forces

$$\sigma^{\mathrm{d}}_{\alpha\beta} = 2\eta(v_{\alpha\beta} - \frac{1}{3}v_{\gamma\gamma}\delta_{\alpha\beta}) + \bar{\eta}v_{\gamma\gamma}\delta_{\alpha\beta}$$

The extension to active fluids

$$T\dot{\Theta} = -F = \int \left\{ \sigma^{\mathrm{d}}_{\alpha\beta} v_{\alpha\beta} + r \Delta\mu \right\} d^3\mathbf{r}$$

$$\Delta\mu = \mu_{\mathrm{ATP}} - \mu_{\mathrm{ADP}} - \mu_{\mathrm{P}}$$

r: rate of ATP hydrolysis

Kruse et al, Phys. Rev. Lett. (2004).

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Kruse et al, Phys. Rev. Lett. (2004).

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$\zeta\Delta\mu < 0$ for contractile active stresses

Kruse et al, Phys. Rev. Lett. (2004).

The hydrodynamic equations of an active fluid

$$\nabla \cdot \sigma^{\mathrm{tot}} = 0 \qquad \sigma^{\mathrm{tot}} = \sigma^{\mathrm{d}} + P\mathbb{I}$$

$$\sigma^{\mathrm{d}}_{\alpha\beta} = 2\eta(v_{\alpha\beta} - \frac{1}{3}v_{\gamma\gamma}\delta_{\alpha\beta}) + \bar{\eta}v_{\gamma\gamma}\delta_{\alpha\beta} + \zeta\Delta\mu\delta_{\alpha\beta}$$

$$2\eta\partial_\beta v_{\alpha\beta} + (\bar{\eta} - \frac{2}{3}\eta)\partial_\alpha v_{\gamma\gamma} = -\partial_\alpha(P + \zeta\Delta\mu)$$

$$P + \zeta\Delta\mu \equiv \Pi$$

Kruse et al, Phys. Rev. Lett. (2004).

Hydrodynamics of an active *polar* fluid

Mass conservation:

$$\partial_t \rho + \partial_\alpha (\rho v_\alpha) = 0$$

Momentum conservation:

$$\partial_t g_\alpha - \partial_\beta \sigma^{\mathrm{tot}}_{\alpha\beta} = 0$$

Angular momentum conservation:

$$\partial_t \ell_{\alpha\beta} - \partial_\gamma M^{\mathrm{tot}}_{\alpha\beta\gamma} = 0$$

Free energy density:

$$f = \frac{g_\alpha g_\alpha}{2\rho} + f_0(n, p_\alpha, \partial_\alpha p_\beta)$$

Fürthauer et al, New J. Phys. (2012).

Constitutive relations for an active polar fluid

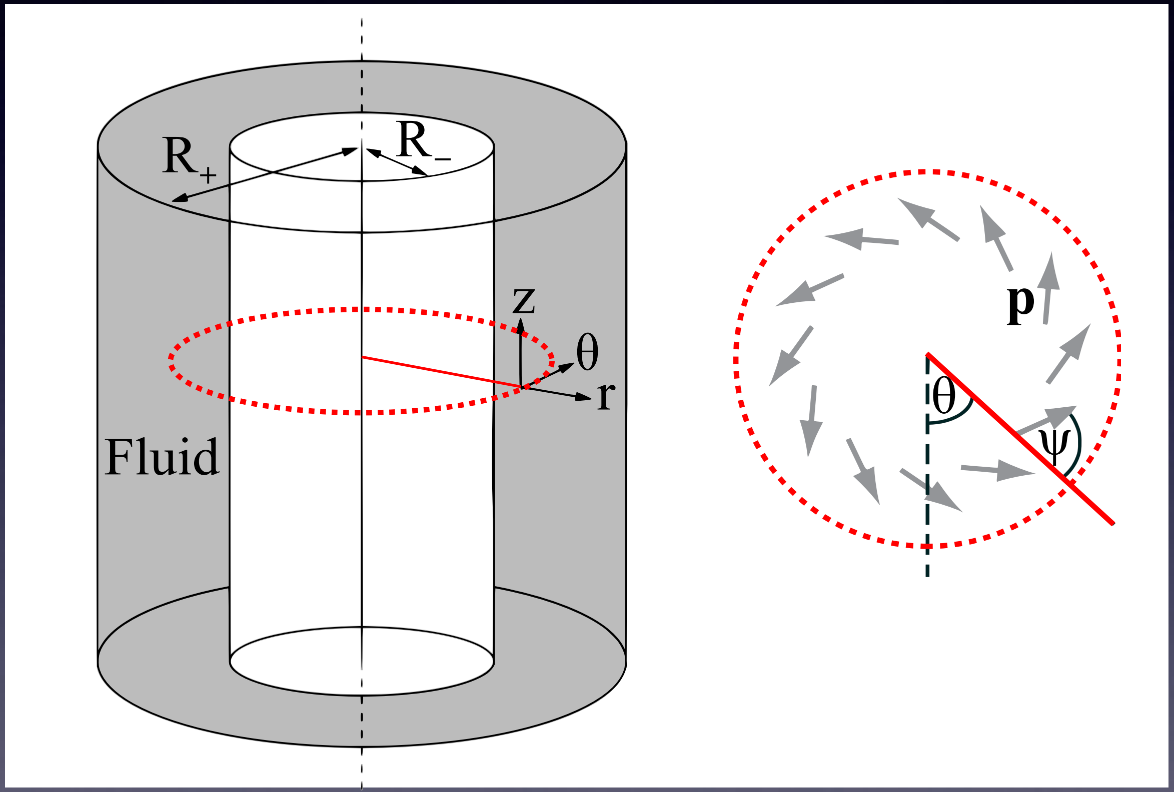
$$2\eta u_{\alpha\beta} = \sigma_{\alpha\beta} - \frac{\nu_1}{2}\left(p_\alpha h_\beta + p_\beta h_\alpha\right) - \bar{\nu}_1 p_\gamma h_\gamma \delta_{\alpha\beta}$$
$$+ \bar{\zeta}\delta_{\alpha\beta}\Delta\mu + \zeta p_\alpha p_\beta \Delta\mu + \zeta' p_\gamma p_\gamma \delta_{\alpha\beta}\Delta\mu$$

$$\frac{Dp_\alpha}{Dt} = \frac{1}{\gamma}h_\alpha - \nu_1 p_\beta u_{\alpha\beta} - \bar{\nu}_1 u_{\beta\beta} p_\alpha + \lambda_1 p_\alpha \Delta\mu$$

$$r = \Lambda\Delta\mu + \bar{\zeta} u_{\alpha\alpha} + \zeta p_\alpha p_\beta u_{\alpha\beta} + \zeta' p_\alpha p_\alpha u_{\beta\beta} + \lambda_1 p_\alpha h_\alpha$$

Kruse et al, Phys. Rev. Lett. (2004), Fürthauer et al, New J. Phys. (2012).

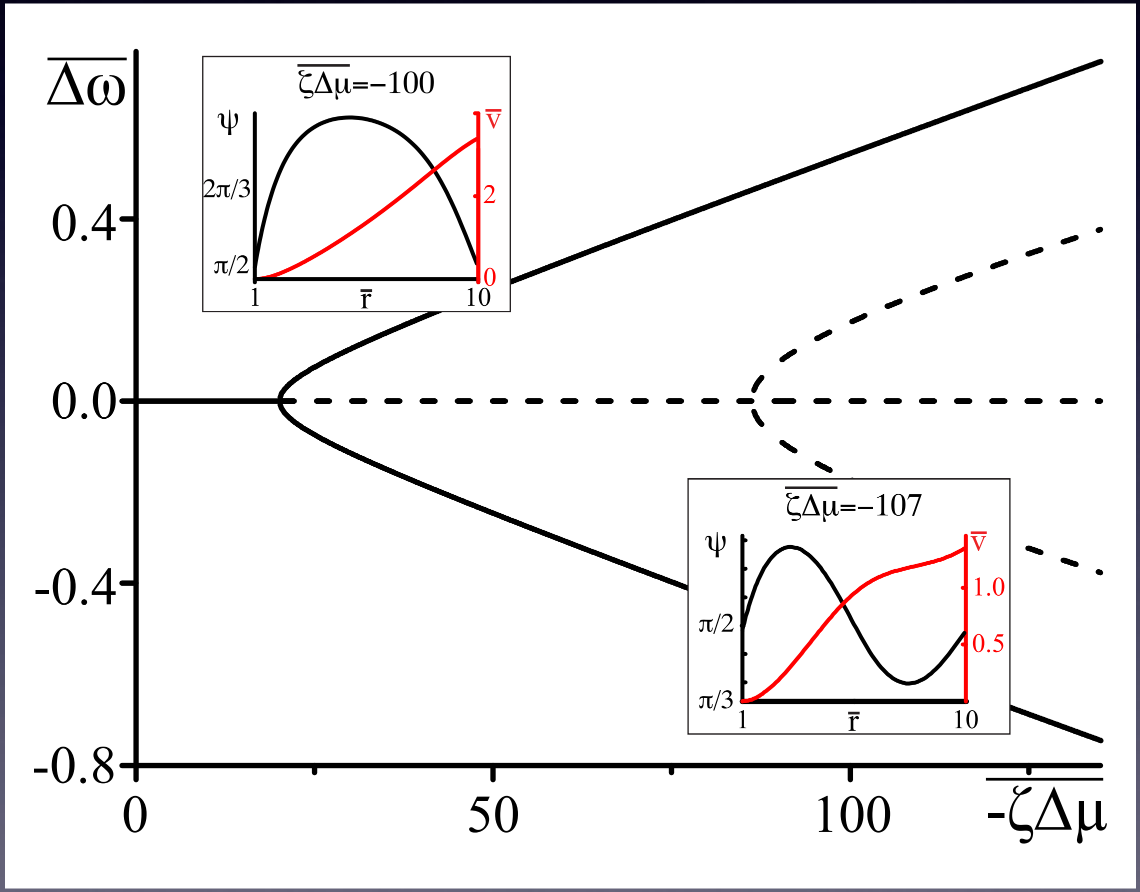
The Taylor-Couette motor illustrates the emergence of spontaneous flow



$$\mathbf{p}^2 = 1$$

Fürthauer et al, New J. Phys. (2012).

The system spontaneously generates flows in the absence of external torques



Fürthauer et al, New J. Phys. (2012).

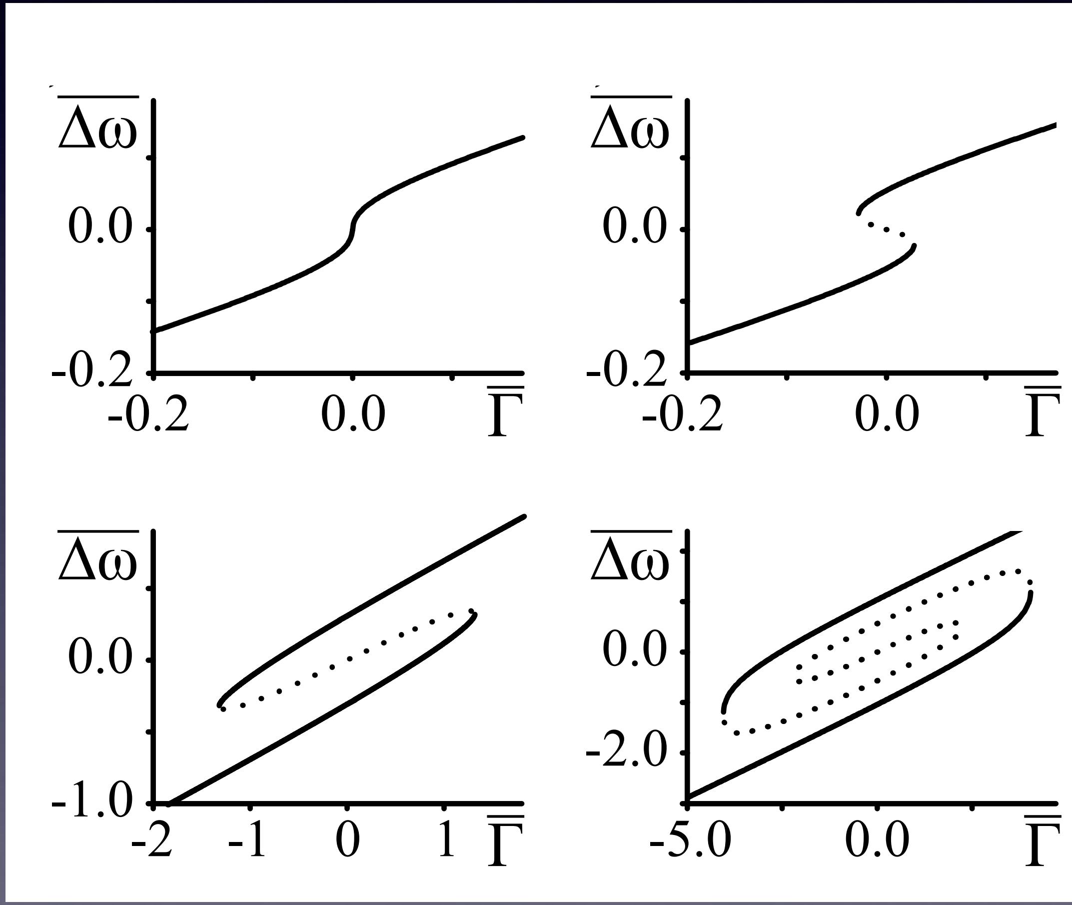
The torque-angular velocity relation shows multiple branches for high activity

$\overline{\zeta\Delta\mu} = -20$

$\overline{\zeta\Delta\mu} = -22$

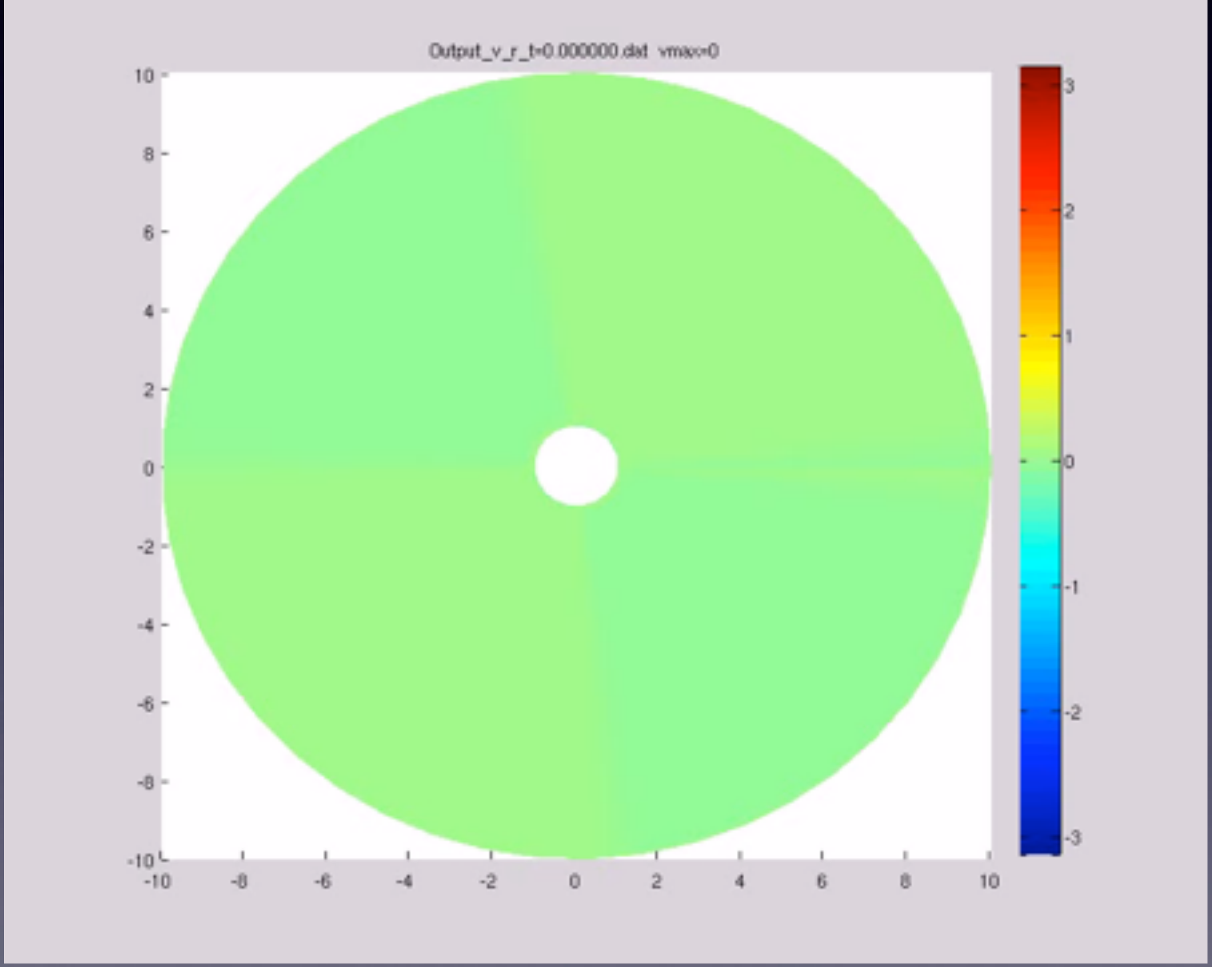
$\overline{\zeta\Delta\mu} = -100$

$\overline{\zeta\Delta\mu} = -150$



Fürthauer et al, New J. Phys. (2012).

Formation of spontaneous flow



M. Neef and K. Kruse, Phys. Rev. E (2014).

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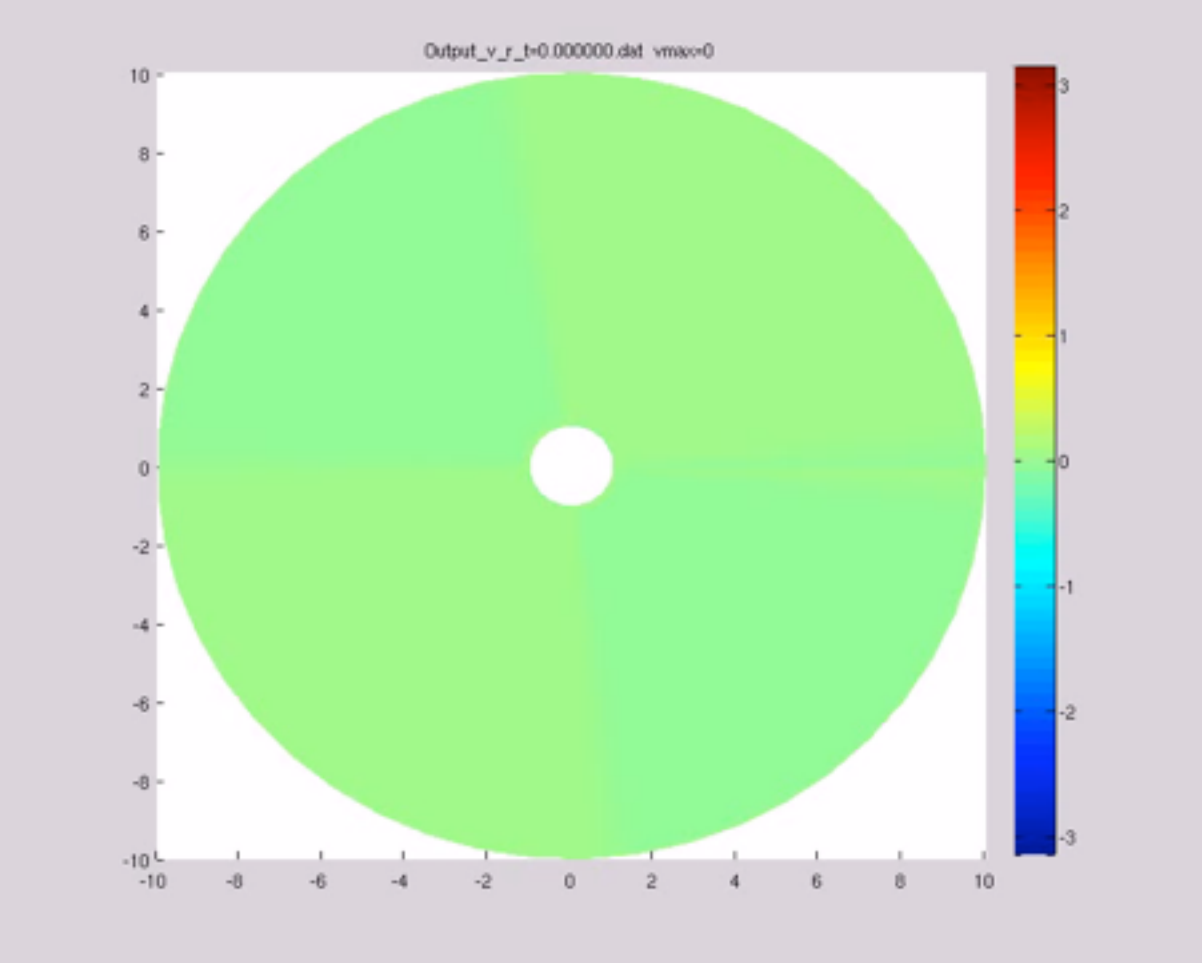
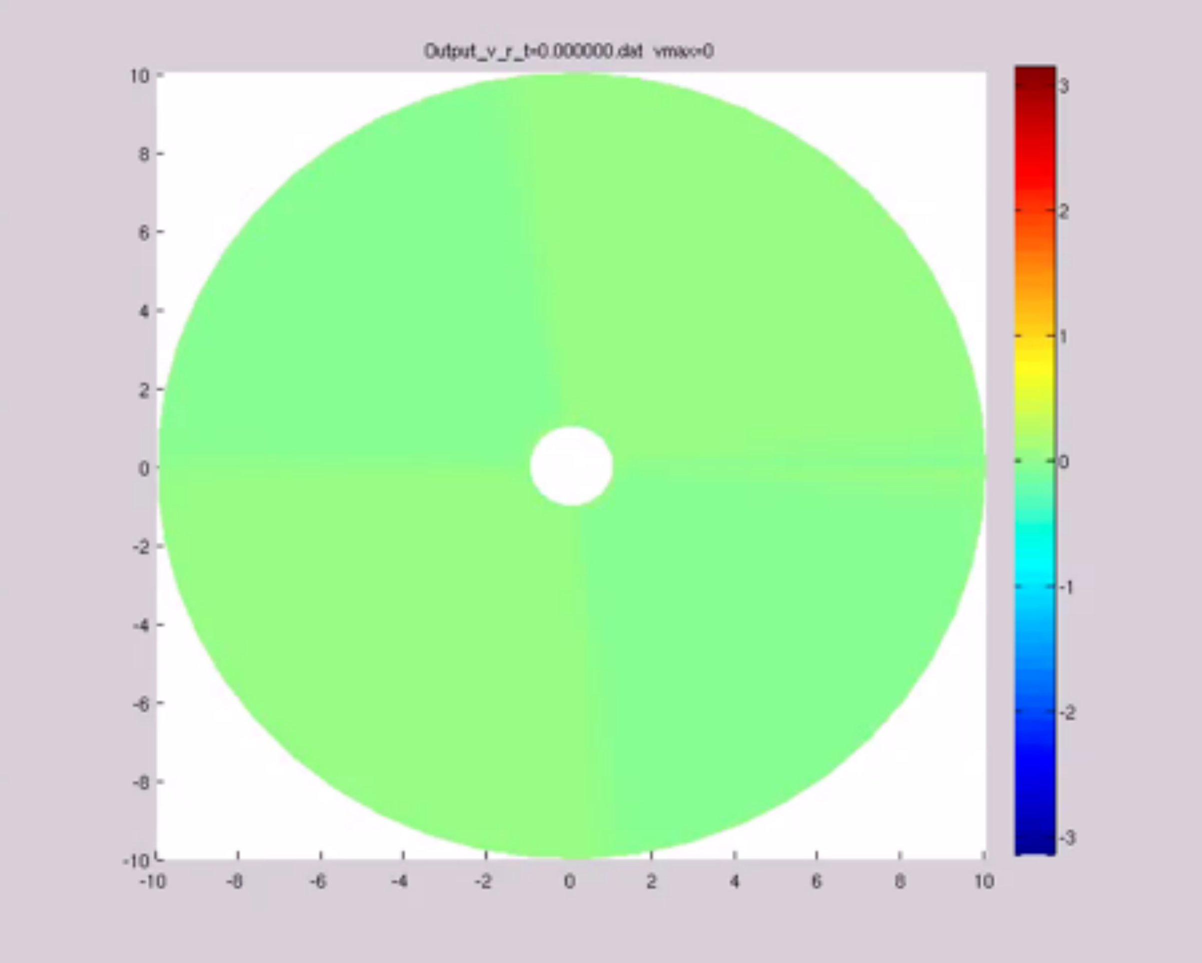


M. Neef and K. Kruse, Phys. Rev. E (2014).

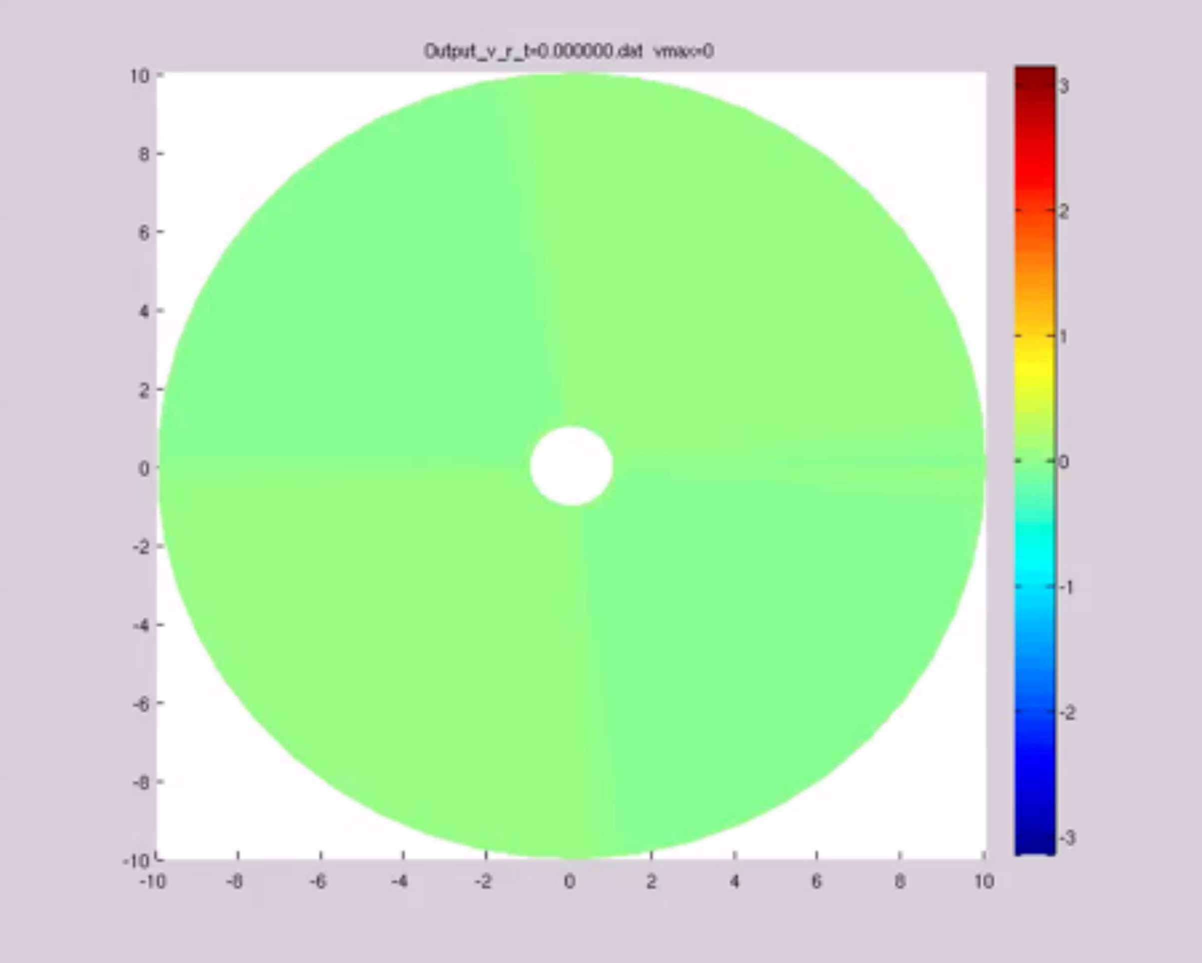
Jacques Prost:
Hydrodynamics of active gels

More complex flow fields exist: vortices



M. Neef and K. Kruse, Phys. Rev. E (2014).

More complex flow fields exist: vortices



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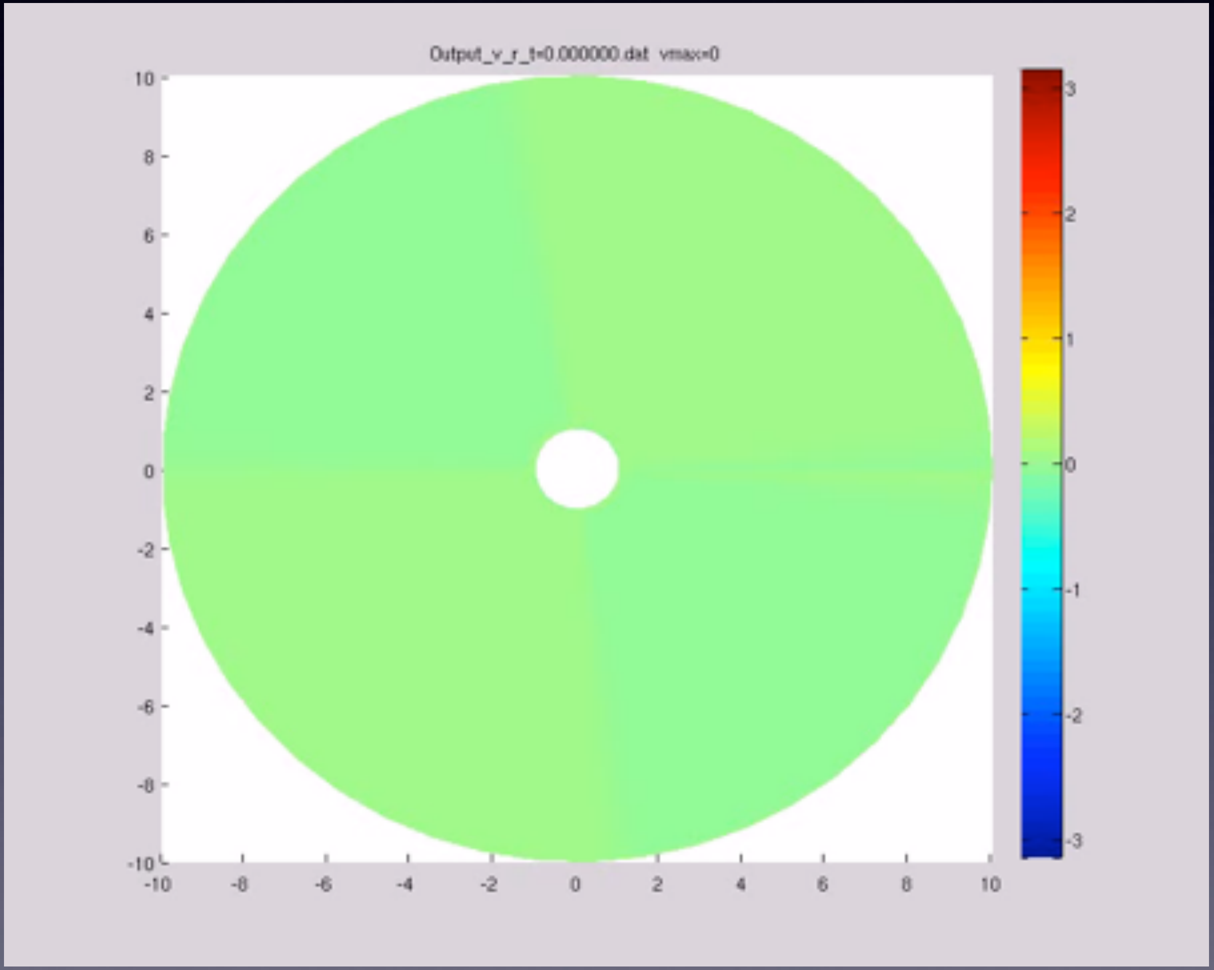
Non-stationary states exist



M. Neef and K. Kruse, Phys. Rev. E (2014).

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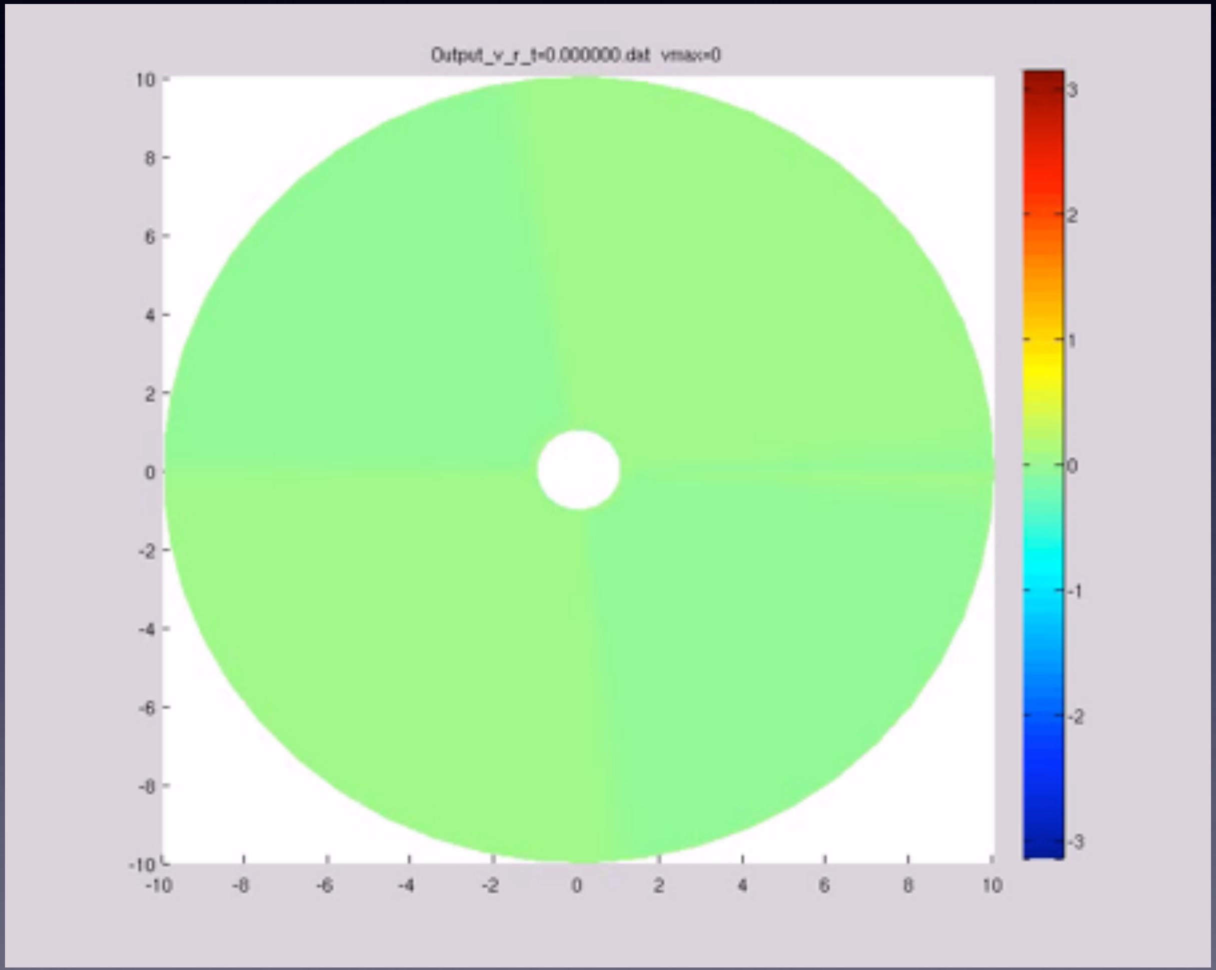
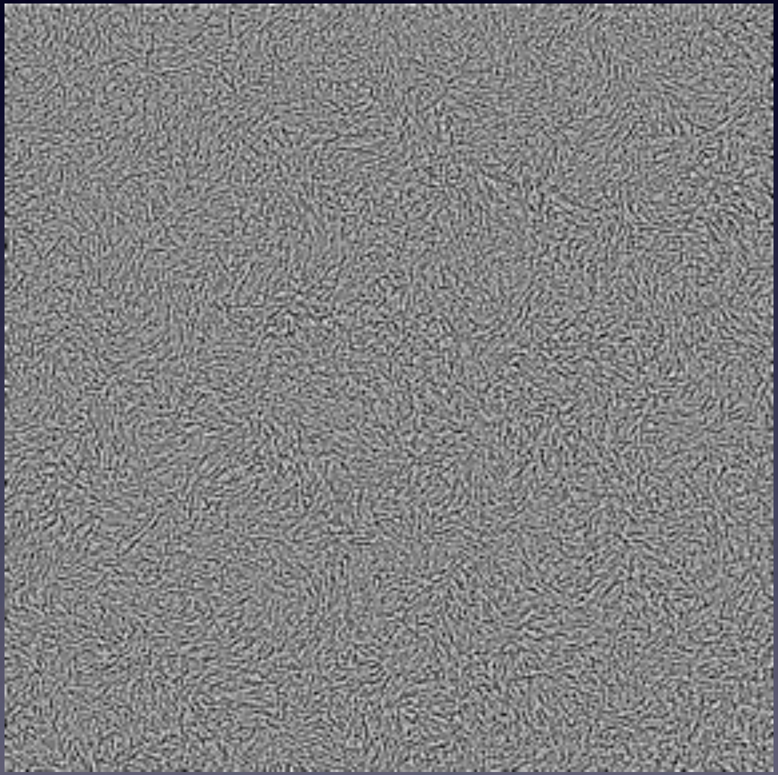


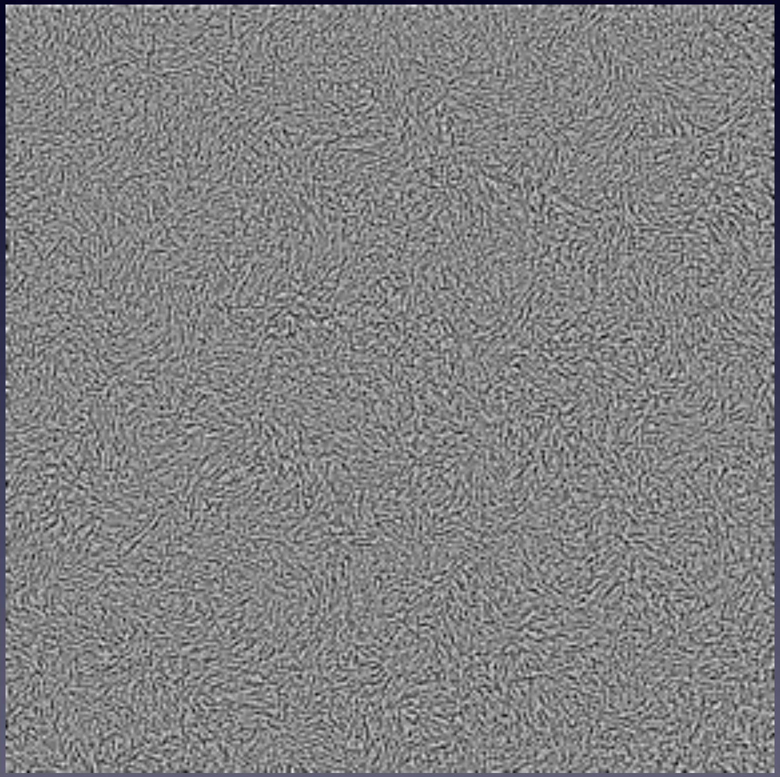
M. Neef and K. Kruse, Phys. Rev. E (2014).

Turbulent flows in a bacterial suspension



H H Wensink et al PNAS (2012)

Turbulent flows in a bacterial suspension



H H Wensink et al PNAS (2012)

Julia Yeomans:
Active matter

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