Active gels and cell motility

F.Jülicher, K.Kruse, J.Prost, K.Sekimoto

Active polar gels: actin-myosin complexes

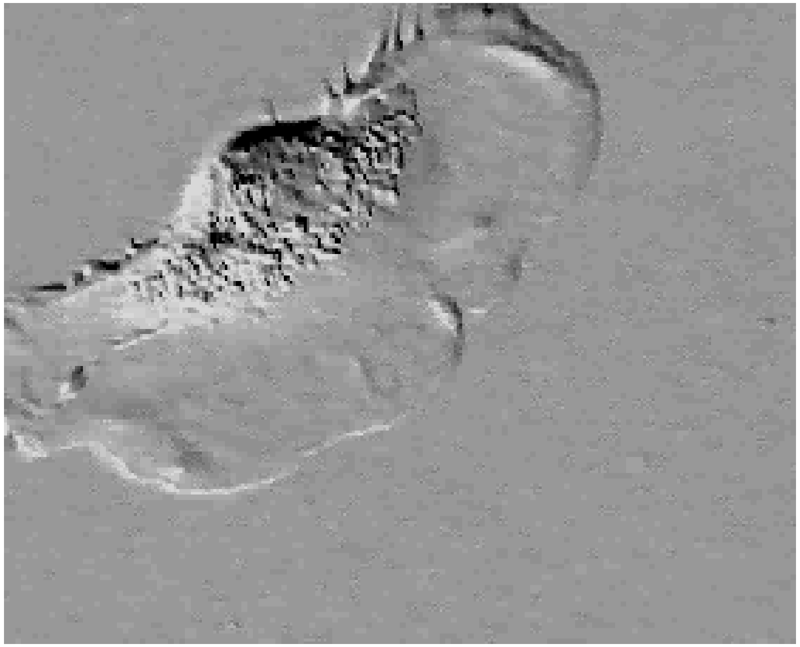
Hydrodynamic theory

Lamellipodia

Keratocyte motion

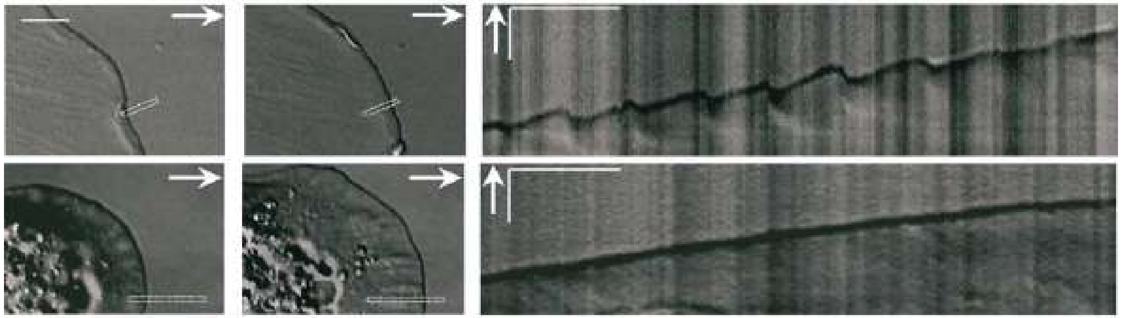
Physical Review Letters **92**, 078101 (2004), European Physical Journal E in press

Keratocyte cells Verkhovsky



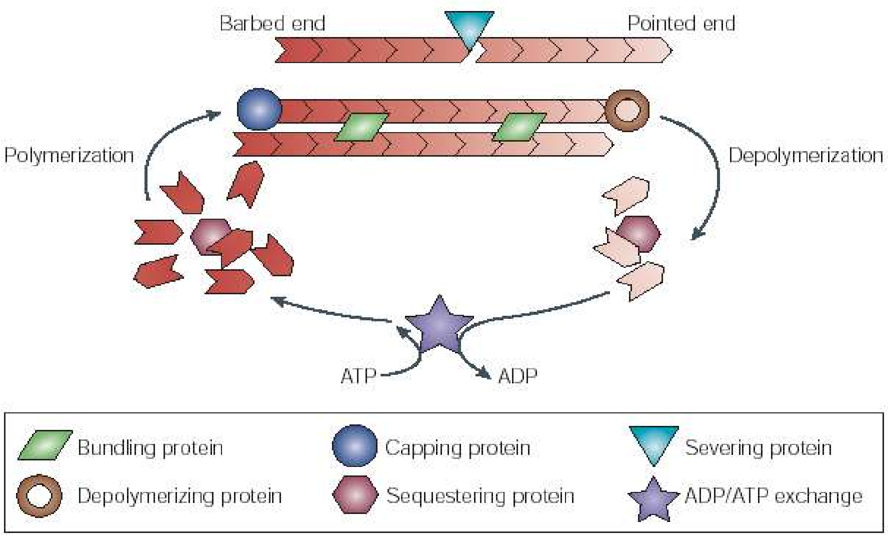
Lamellipodium spreading

propagating waves: period 27s

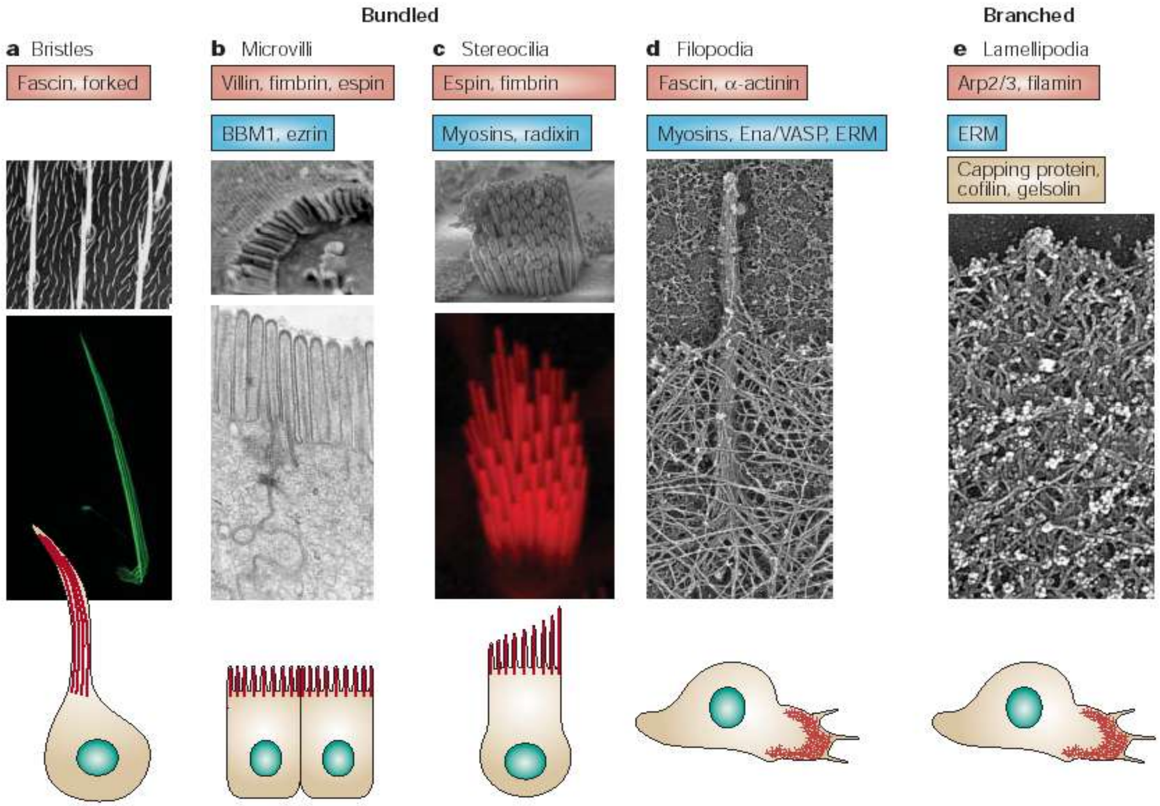


Giannone et al.

Actin filaments



C.Revenu, D.Louvard et al.



- Treadmilling: actin flow
- Polar filaments: local orientation, polarization vector **p**
- Gel-like structure: physical gel

Actin polarization

Polarization vector

Local unitary vector **n**: polarization **p**=<**n**>

Nematic order

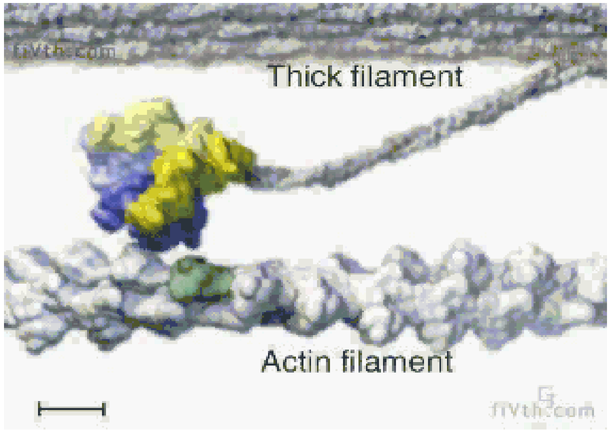
Ferromagnetic order

Conjugate field $\mathrm{dF} = -\mathbf{h}\,\mathrm{d}\,\mathbf{p}$

Torque $\Gamma = \mathrm{K}\,\nabla^2 \phi$ K =Frank constant

parallel field h_{ll} fixes the degree of orientation p

Myosin motors



R.Vale

Myosin motor proteins

- Form small aggregates
- Move along actin polar filaments towards + end
- Consume energy (ATP)
- Provoke contractions (muscles) and actin flow

Maxwell viscoelasticity

Maxwell model

Elastic at short time, viscous at long time
single relaxation time τ
viscosity η=Eτ

$$\frac{\partial \sigma_{ij}}{\partial t} + \frac{\sigma_{ij}}{\tau} = 2 E u_{ij}$$

velocity gradient

Reactive and Dissipative stress

Elastic stress reactive, viscous stress dissipative

$$\sigma^{r}_{ij} = -\tau \frac{\partial \sigma^{d}_{ij}}{\partial t}$$

$$\left(1 - \tau^2 \frac{\partial^2}{\partial t^2}\right) \sigma^{d}_{ij} = 2 \eta u_{ij}$$

Onsager hydrodynamic theory of actin-myosin gels

Fluxes and forces

fluxes	σ_{ij}	$\mathbf{P}=d\mathbf{p}/dt$	r	molecular fluxes
forces	u_{ij}	$\mathbf{h}$	$\Delta\mu$	chem.pot gradients

Onsager relations

time inversion
translational and
rotational invariance

$$\left(1-\tau^2\frac{D^2}{Dt^2}\right)\sigma_{ij}^d=2\,\eta\,u_{ij}$$

$$P_i^d=\frac{h_i}{\gamma_1}+\lambda_1\,p_i\,\Delta\mu$$

$$\mathbf{r}^d=\Lambda\,\Delta\mu+\lambda_1\,p_i\,h_i+U\,p_i\,\partial_i\,\mu_m$$

Reactive and dissipative fluxes

reactive stress

active stress

$$\sigma^r_{ij} = -\tau\left[\frac{D\sigma^d_{ij}}{Dt}\right] + \nu_i \sigma^d u - \zeta\Delta\mu p_i p_j - \zeta'\Delta\mu\delta_{ij} + \frac{\nu_1}{2}(p_i h_j + p_j h_i) + \nu_1' p_k h_k \delta_{ij}$$

$$+\frac{1}{2}(p_i h_j - p_j h_i)$$

convected derivative

coupling to polarization

antisymmetric stress

reactive polarization rate

$$P^r_i = -\omega_{ij} p_j - \nu_1 u_{ij} p_j - \nu_1' u_{kk} p_i$$

vorticity

reactive ATP consumption rate

$$r^r = \zeta p_i p_j u_{ij} + \zeta' u_{kk}$$

Energy dissipation

$$T\dot{S} = \int d\mathbf{x}\, r\Delta\mu$$

Motion of a thin gel layer

Gel constitutive equation $$2\eta \frac{dv}{dx} = \sigma + \tau (v - v_c) \frac{d\sigma}{dx} + \zeta \Delta \mu$$

Maxwell model   active stress

gel reference frame
contraction due to active stress

Viscous friction on substrate $$\frac{\partial \sigma}{\partial x} = \frac{\xi v}{h}$$

Boundary conditions

$$\frac{dL_f}{dt} = v(L_f) + v_p \qquad \frac{dL_r}{dt} = v(L_r) + v_d$$

Liquid-like motion

Retrograde flow $\alpha = -\zeta \Delta\mu / 2E \ll 1$

Friction length $\lambda^2 = \frac{2\eta h}{\xi}$

velocity profile $v = \frac{\zeta \Delta\mu h}{\lambda \xi} \frac{\sinh(x/\lambda)}{\cosh(L/2\lambda)}$

Stability of movement even if the friction force is a non-monotonous function of velocity

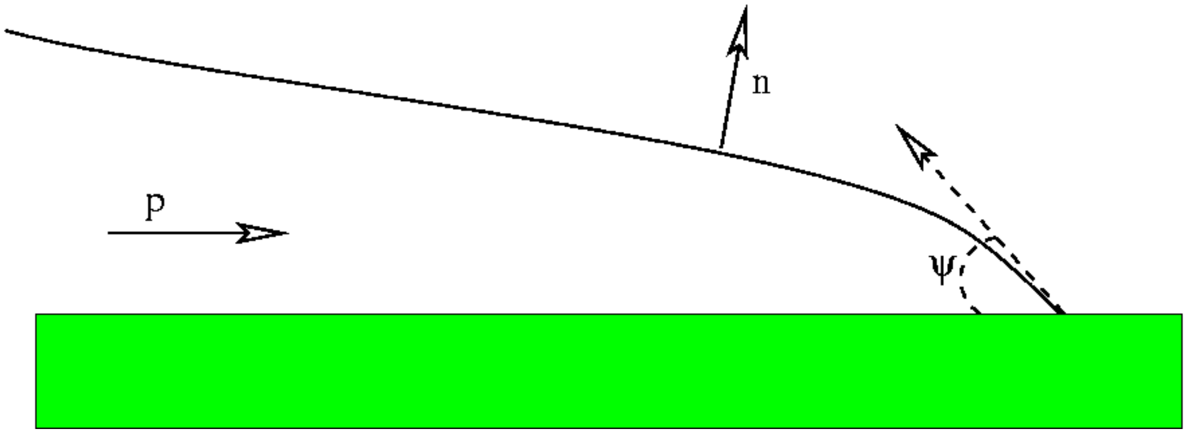
Gel velocity

$v_c = (v_p + v_d)/2$

Critical polymerization velocity $v_p^c = v_d - \frac{2\ \zeta \Delta\mu h}{\lambda \xi}$

Density profile Contraction at the back

Polymerization kinetics



Actin polymerization promoter

Concentrated at the contact line $\rho_{wa}(\mathbf{x}) = \rho_0 \exp(-\mathbf{x}/\lambda'), \qquad \lambda' = D_{wa}/v$

Forces local polarization orientation

Polymerization velocity $\mathbf{v}_p = k_p \rho_{wa}(\mathbf{x})$

Lamellipodium thickness $h = \rho_0 k_p \lambda'/v_d$

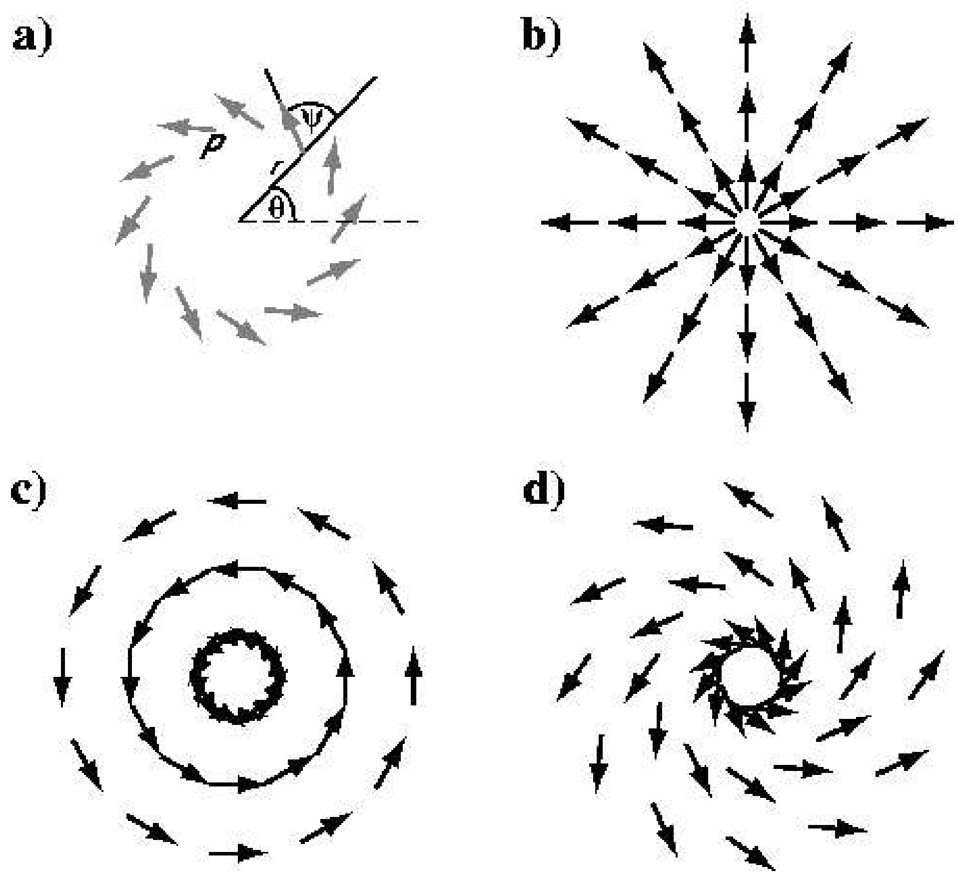
Polarization defects

Nematic point defects in two dimensions

topological charge 1

singular solutions of the director equilibrium equations $\nabla^2 \phi = 0$

$\phi = \theta + \psi$



aster

vortex

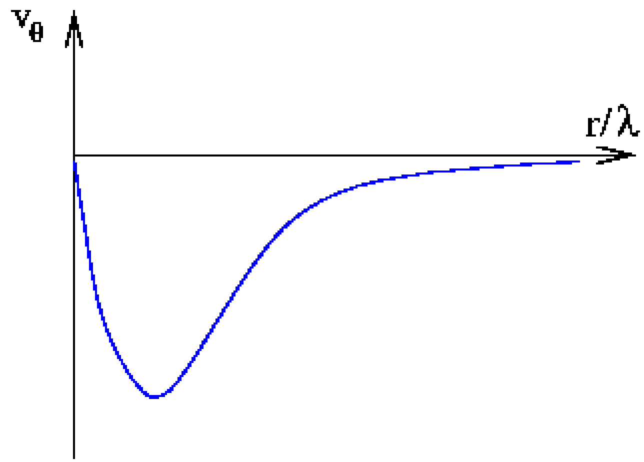
spiral

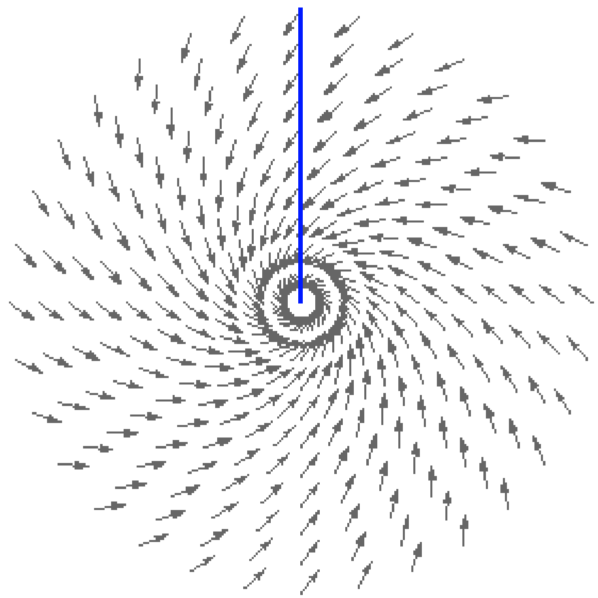
Active orientational defects

Rotating spiral

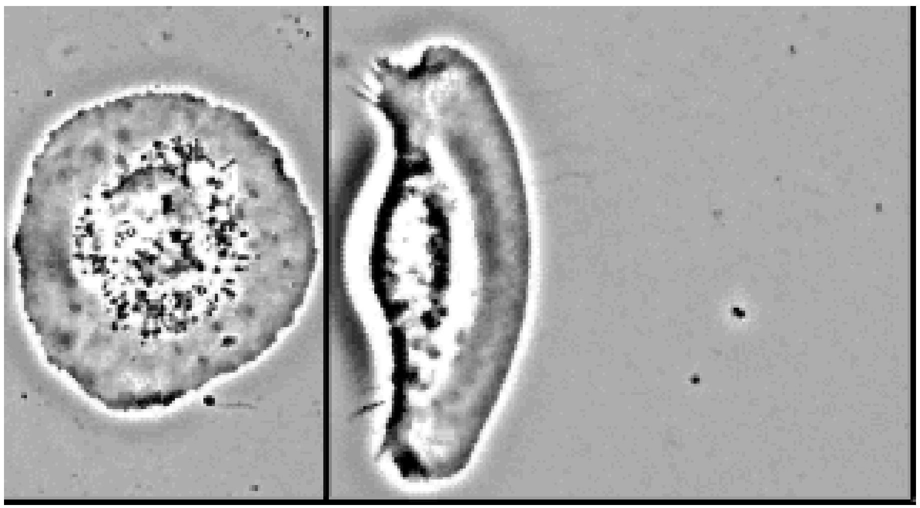
nematodynamics $\cos 2\psi = \frac{1}{\nu_1}$ stable if $\nu_1 > 1$

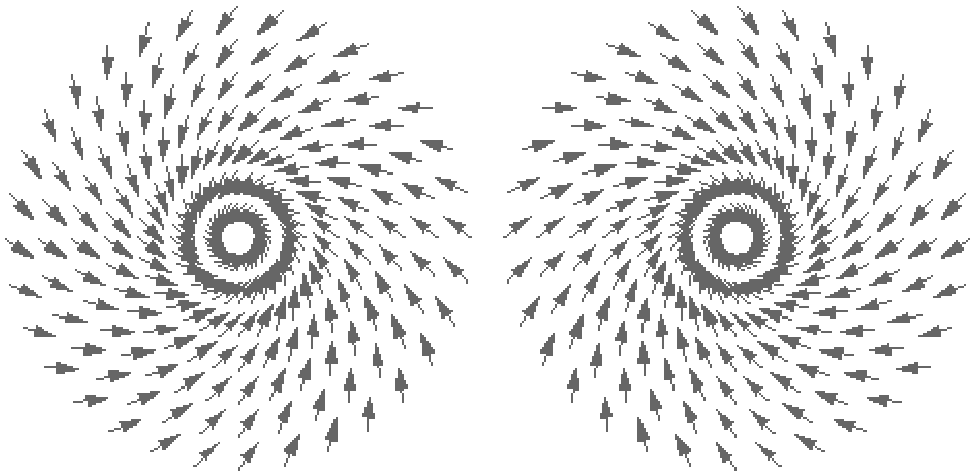
short distances $v_\theta = \omega_0 \, r \log(r/r_0), \quad \omega_0 = \frac{2\zeta_1 \Delta\mu \sin 2\psi}{4\eta + \gamma_1 \nu_1^2 \sin^2 2\psi}$





Keratocyte motion





Two coupled vortices

advancing velocity 1μm/s

adhesion not treated

Other active gel problems

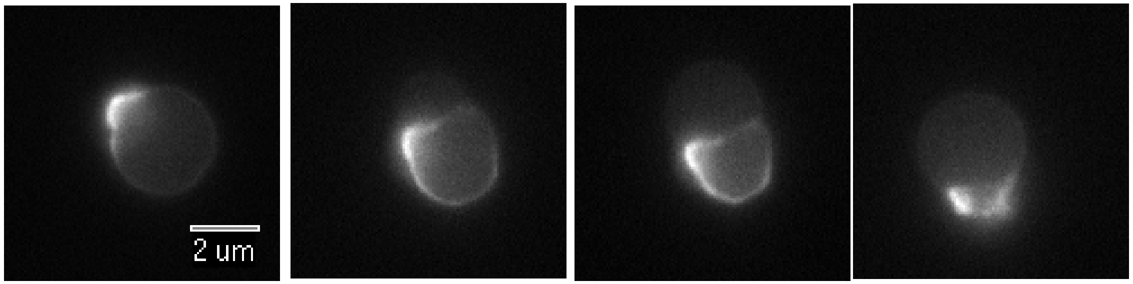
Propagating waves

1d travelling waves $\omega = \tilde{c}\, q\,, \quad \tilde{c} = \dfrac{v_0}{1 + T_c k_{off}} \; \dfrac{\zeta_c \Delta\mu\, c_0}{\tilde{\chi} + \zeta_c \Delta\mu\, c_0}$

Cortical actin K.Storm

Finite thickness if $-\zeta\Delta\mu$ large enough
Unstable

C.Sykes, E.Paluch



Bacterial « Turbulence » R.Voituriez

Compressible gel unstable towards lattice of rotating vortices