Active gels and cell motility

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

Active polar gels: actin-myosin complexes

Hydrodynamic theory

Lamellipodia

Keratocyte motion

Keratocyte cells Verkhovsky

Lamellipodium spreading propagating waves: period 27s

Giannone et al.
C. Revenu, D. Louvard et al.

- **Treadmilling**: actin flow
- **Polar filaments**: local orientation, polarization vector \( \mathbf{p} \)
- **Gel-like structure**: physical gel
**Actin polarization**

**Polarization vector**

Local unitary vector $n$: polarization $p = \langle n \rangle$

Nematic order
Ferromagnetic order

**Conjugate field**

Conjugate field $dF = -h_{\parallel} d\ p$

Torque $\Gamma = K \nabla^2 \phi$

$K$ = Frank constant

Parallel field $h_{\parallel}$ fixes the degree of orientation $p$
Myosin motors

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 $\tau$
viscosity $\eta = E \tau$

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

velocity gradient

Reactive and Dissipative stress

Elastic stress reactive, viscous stress dissipative

\[
\sigma_{ij}^r = -\tau \frac{\partial \sigma_{ij}^d}{\partial t}
\]

\[
(1 - \tau^2 \frac{\partial^2}{\partial t^2}) \sigma_{ij}^d = 2\eta u_{ij}
\]
Onsager hydrodynamic theory of actin-myosin gels

Fluxes and forces

\[ \sigma_{ij} \quad P = \frac{dp}{dt} \quad r \quad \text{molecular fluxes} \]

\[ u_{ij} \quad h \quad \Delta \mu \quad \text{chem. pot gradients} \]

Onsager relations

\[ (1 - \tau^2 \frac{D^2}{Dt^2}) \sigma_{ij}^d = 2 \eta u_{ij} \]

\[ P_i^d = \frac{h_i}{\gamma_1} + \lambda_1 p_i \Delta \mu \]

\[ r^d = \Lambda \Delta \mu + \lambda_1 p_i h_i + U p_i \partial_i \mu_m \]
Reactive and dissipative fluxes

Reactive stress

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

Active stress

\[ \sigma_{ij}^a = \frac{1}{2} (p_i h_j - p_j h_i) \]

Convected derivative

\[ \nu \]

Reactive polarization rate

\[ P_i^r = -\omega_{ij} p_j - \nu_1 u_{ij} p_j - \nu_1' u_{kk} p_i \]

Antisymmetric stress

\[ \zeta \]

Vorticity

\[ \zeta' \]

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

\[ \frac{\partial \sigma}{\partial x} = \tau (v - v_c) \frac{\partial \sigma}{\partial x} + \zeta \Delta \mu \]

Gel constitutive equation

Maxwell model
Active stress

Gel reference frame
Contraction due to active stress

Viscous friction on substrate

\[ \frac{\partial \sigma}{\partial x} = \xi \frac{v}{\eta} \]

Boundary conditions

\[ \frac{dL_f}{dt} = v(L_f) + v_p \]
\[ \frac{dL_r}{dt} = v(L_r) + v_d \]
Liquid-like motion

Retrograde flow \( \alpha = -\zeta \Delta \mu / 2 \eta \ll 1 \)

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 \( \rho_{wa}(x) = \rho_0 \exp(-x/\lambda') \),  \( \lambda' = D_{wa}/v \)

Forces local polarization orientation

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

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 $\nabla^2 \phi = 0$

\[ \phi = \theta + \psi \]

a) vortex
b) aster
c) spiral
Active orientational defects

Rotating spiral

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

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

Two coupled vortices

advancing velocity 1μm/s

adhesion not treated
Other active gel problems

Propagating waves

1d travelling waves

\[ \omega = \tilde{c} q, \quad \tilde{c} = \frac{v_0}{1 + T_c k_{off}} \quad \frac{\zeta_c \Delta \mu c_0}{\tilde{\chi} + \zeta_c \Delta \mu c_0} \]

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