Order and flow in active filament solutions

Tanniemola B Liverpool
Department of Applied Mathematics
University of Leeds

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A Ahmadi, MC Marchetti
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1) Cell Movement and Mechanics
   a) The Cell Cytoskeleton
   b) Filaments and Molecular Motors
2) Dynamics of filament/motor mixtures
3) Self-organisation of homogeneous bulk phases
4) Inhomogeneities and hydrodynamic description
5) Rheology and flow
6) Conclusions and outlook
Acto-myosin molecular motor

- F-actin and Myosin use Adenosine TriPhosphate (ATP) to turn chemical energy into mechanical work.

Rigor

muscle contraction
Cell Movement

• A transition from stationary to translation associated with changes in distribution of actin and myosin

• Dynamics of myosin II concentrations in stationary cell

• Myosin

Borisy Lab [http://www.borisylab.nwu.edu/pages/movies.html](http://www.borisylab.nwu.edu/pages/movies.html)

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Cell Movement

- Actin (cyan)
- Myosin (red)

Verkhovsky, Svitkina, Borisy, Current Biology 9, 11-20 (1999)

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Kinesin-Tubulin molecular motor

- Another ATP-driven active filament/motor pair
- Microtubules and Kinesin turn chemical energy into mechanical work

http://www.dentistry.leeds.ac.uk/biochem/MBWeb/mb2/part1/kinesin.htm

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Model Systems

- Microtubules and Kinesin/Ncd show self-organisation on mesoscopic lengthscales.
  In-vitro experiments on simplified ‘cell’ extracts of filaments and motors
- Motor constructs & Taxol-stabilised microtubule mixture
- **ACTIVE** temporary cross-links


- Simulations got similar patterns

25 µg/ml Kinesin
37 µg/ml Kinesin
50 µg/ml Kinesin
<15 µg/ml Kinesin

http://www.embl-heidelberg.de/ExternalInfo/nedelec/

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Model Systems

- In-vitro experiments on simplified ‘cell’ extracts of filaments and motors
- Myosin II & length-stabilised F-Actin mixture (J. Käs group)
- Myosin tail is hydrophobic and forms proto-thick filaments or ‘micelles’ with heads on the surface ($N_c \sim 10$)
- ACTIVE temporary cross-links

Questions?

- How does the effects of the motor affect the states of a solution of filaments.
- What is the phase behaviour of a motor/filament mixture.
- What are the changes to the mechanical properties (viscoelasticity) of an isotropic solution of filaments (e.g. F-actin) due to the presence of motors (e.g. Myosin II) and ATP.
- Can we predict (from a microscopic model) what happens when we add the motors?
- What role does the flexibility of the filaments play?
Describing Active Filaments

“Microscopic” simulations
Explicit filaments - expensive computation
Very successful at models for particular structure e.g. mitotic spindle.

Mean-field (effective theory)

“Hydrodynamic” equations
Dynamics of order parameter fields.
Huge number of terms allowed on symmetry grounds.
Non-equilibrium so there is no ‘variational’ principle.

Polymer Physics - Doi model

Equations give pattern formation - asters, vortices…
How does one parametrise them? …
Lyotropic Liquid Crystals

Recall the isotropic (I) to nematic (N) transition of a solution of thin \((l >> b)\) hard rods.

Onsager - I-N transition upon increasing density.

\[ \rho_{IN} \approx \frac{4}{l^2 b} \]

Orientation Distribution function \( \Psi(\hat{n}) \)

\[ \ddot{Q} = \int d\hat{n} (\hat{n}\hat{n} - \frac{1}{d} \delta) \Psi(\hat{n}) \]

Competition between rotational and translational entropy.
Active Polar Rods

- Take into account rod excluded volume
- Approximately take into account confining effect of other chains, ‘entanglement’
- Ignore semi-flexibility (valid for $l << L_p$ and for timescales longer than those required to relax internal modes)
- Rigid rods of length $l$ and diameter $b << l$
- Position, $\vec{r}$, Orientation $\hat{n}$
- Filament Probability distribution $\Psi(\vec{r}, \hat{n}, t)$

1. Extension of the Doi model of rods in solution
2. Motor induced velocities like Kruse/Julicher sliding filaments

$\Rightarrow$ continuum model

- Doi and Edwards (1986)

$d=2,3$

TBL, MC Marchetti (2003)
Evolution of Rod distribution

Conservation of Probability

$$\partial_t \Psi + \nabla \cdot J + R \cdot J = 0$$

Distribution function

$$\Psi(r, \hat{n}, t)$$

Active Currents

$$R = \hat{n} \times \partial_n$$

Potential

“excluded volume”

$$V_{ex}(r, \hat{n}, t)$$

Diffusion of hard rods (excl. vol., entangle.) and local driving from motors

$$J_i = -D_{ij} \partial_j \Psi - \frac{D_{ij}}{T} \Psi \partial_j V_{ex} + J_{i}^{act}$$

$$J_i = -D_i R_i \Psi - \frac{D_r}{T} \Psi R_j V_{ex} + J_{i}^{act}$$

$$D_{ij} = D_\perp (\delta_{ij} - \hat{n}_i \hat{n}_j) + D_\parallel \hat{n}_i \hat{n}_j$$

TBL, MCMarchetti, PRL 90, 138102 (2003)

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Active Interactions

Active translation currents

\[
J^{\text{act}}(r, \hat{n}_1) = \Psi(r, \hat{n}_1) v^{\text{act}}(r, \hat{n}_1)
\]

\[
v^{\text{act}}(r, \hat{n}_1) = \int_{n_2} \int_{\Omega_{\text{int}}} d^d \xi \ v(\xi, \hat{n}_1, \hat{n}_2) \Psi(r + \xi, \hat{n}_2)
\]

Active rotation currents

\[
J^{r,\text{act}}(r, \hat{n}_1) = \Psi(r, \hat{n}_1) \omega^{\text{act}}(r, \hat{n}_1)
\]

\[
\omega^{\text{act}}(r, \hat{n}_1) = \int_{n_2} \int_{\Omega_{\text{int}}} d^d \xi \ \omega(\xi, \hat{n}_1, \hat{n}_2) \Psi(r + \xi, \hat{n}_2)
\]

Model for motor induced active ‘velocities’

\[
v(\xi, \hat{n}_1, \hat{n}_2), \omega(\xi, \hat{n}_1, \hat{n}_2)
\]
Microscopic Model for velocities

• How does the motor-induced velocity depend on the separation of centres and relative orientations?

• Motors walk with inhomogenous velocity profile as a function of $s_i$, the distance (along filament) active cross-link is from filament centre. Could be that motors stall at the end / Crowding?

• Motor velocity profile is a step function which goes to zero at some distance $l_m$ from the end.

TBL, MC Marchetti, Europhysics Letters (2005)

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Microscopic Model

- Start with rigid motor clusters. Dimer made up of two heads walking along each filament at speed $u(s)$ (separation of rod centres)
- Cross-link position $r_1^x = r_2^x$
  $$r_2 - r_1 = \xi = s_1 \hat{n}_1 - s_2 \hat{n}_2$$
  $$r_a^x = r_a + \hat{n}_a s_a ; \quad -l/2 < s_a < l/2 ; \quad a \in \{1, 2\}$$
- Over-damped dynamics. Motor friction is negligible.
- Cluster is a torsional spring
Microscopic Model

- Anisotropic friction tensor of rods.
  \[ \zeta(\hat{n}_a) = \zeta_\perp (\delta - \hat{n}_a \hat{n}_a) + \zeta_\parallel \hat{n}_a \hat{n}_a ; a \in \{1,2\} \]

- Velocity of filament \( a \), \( \mathbf{v}_a(s_1, \hat{n}_1, s_2, \hat{n}_2) \)
- Angular velocity of filament \( a \), \( \omega_a(s_1, \hat{n}_1, s_2, \hat{n}_2) \)
- No external forces - any force/torque applied on rod 1 by an active cross-link is balanced by equal and opposite force on rod 2.

\[ \zeta(\hat{n}_1) \cdot \mathbf{v}_1 + \zeta(\hat{n}_2) \cdot \mathbf{v}_2 = 0 \]
\[ \zeta_r \omega_1 + \zeta_r \omega_2 = 0 \]

- Torsional spring

\[ \dot{\theta} = \frac{\kappa}{\zeta_r} \theta \approx \frac{\kappa}{\zeta_r} \sin \theta = \gamma \sin \theta \]


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Microscopic Model

- Velocity of the motor head attached to filament
  \[ v^m_a = \frac{dr^x_a}{dt} = v_a + \mathbf{\hat{n}}_a u(s_a) + s_a \omega_a \times \mathbf{\hat{n}}_a; \quad a \in \{1, 2\} \]

- Angular velocity of motor cluster
  \[ \omega^m_a = \omega_a + (-1)^a \mathbf{\hat{n}}_1 \times \mathbf{\hat{n}}_2 \left( \frac{\mathbf{\hat{n}}_1 \cdot \mathbf{\hat{n}}_2}{|\mathbf{\hat{n}}_1 \times \mathbf{\hat{n}}_2|} \right); \quad a \in \{1, 2\} \]

- Motors in cluster rigidly attached to each other
  \[ v^m_1 = v^m_2 \quad \omega^m_1 = \omega^m_2 \]

- Solve for the ‘velocities’ of the filaments
  \[ \omega_1 = -\omega_2 = \gamma (\mathbf{\hat{n}}_1 \times \mathbf{\hat{n}}_2)(\mathbf{\hat{n}}_1 \cdot \mathbf{\hat{n}}_2); \quad v_1 = v/2 + V \quad ; \quad v_2 = -v/2 + V \]

\[ v = (\alpha_0 + \alpha_1 (\mathbf{\hat{n}}_1 \cdot \mathbf{\hat{n}}_2)) \frac{\xi}{\ell} + (\beta_0 + \beta_1 (\mathbf{\hat{n}}_1 \cdot \mathbf{\hat{n}}_2))(\mathbf{\hat{n}}_1 \cdot \mathbf{\hat{n}}_2) \]

\[ V = (\lambda_0 + \lambda_1 (\mathbf{\hat{n}}_1 \cdot \mathbf{\hat{n}}_2))(\mathbf{\hat{n}}_1 + \mathbf{\hat{n}}_2) \]

\[ \lambda_{0,1} \approx \beta_{0,1} \approx v_0 \quad ; \quad \alpha_{0,1} \approx \frac{\ell}{\ell} v_0 \]

TBL, MC Marchetti, Europhysics Letters (2005)

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Polar Clusters

Does the spring differentiate between parallel and antiparallel configurations

$$\omega_1 (\xi, \hat{n}_1, \hat{n}_2) = -\omega_2 = (\gamma_0 + \gamma_1 (\hat{n}_1 \cdot \hat{n}_2))(\hat{n}_1 \times \hat{n}_2)$$

$$g = \frac{\gamma_0}{\gamma_1} \text{ Cluster 'polarity'}$$

A Ahmadi, TBL, MC Marchetti, PRE 72 060901(R) (2005)

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Excluded Volume Interactions

Filaments separated by a distance $\xi$

Filaments interact only if $\xi$ is in interaction volume

$$\Omega_{\text{int}} = v_0 |\hat{n}_1 \times \hat{n}_2| = v_0 \sqrt{1 - (\hat{n}_1 \cdot \hat{n}_2)^2}; v_0 = l^2 b^{d-2}$$

Excluded volume interaction

$$V_{\text{ex}}(r_1, \hat{n}_1) = k_B T \int_{n_2} \int_{\Omega_{\text{int}} \text{ restrict}} d^d r_2 \Psi(r_2, \hat{n}_2)$$

$$= k_B T \int_{n_2} \int_{\Omega_{\text{int}}} d^d \xi \Psi(r_1 + \xi, \hat{n}_2)$$

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Hydrodynamic description

Active currents

\[ J^{\text{act}}(\mathbf{r}, \hat{n}_1) \propto \Psi(\mathbf{r}, \hat{n}_1) \int_{n_2} \int_{\Omega_{\text{int}}} d^d \xi \, v(\xi, \hat{n}_1, \hat{n}_2) \Psi(\mathbf{r} + \xi, \hat{n}_2) \]

Expansion of `local’ distribution, integration over \( \Omega_{\text{int}} \)

\[ \Psi(\mathbf{r} + \tilde{\xi}, \hat{n}_2) = \Psi(\mathbf{r}, \hat{n}_2) + \tilde{\xi} \cdot \nabla \Psi(\mathbf{r}, \hat{n}_2) + \frac{1}{2} (\tilde{\xi} \cdot \nabla)^2 \Psi(\mathbf{r}, \hat{n}_2) + \cdots \]

Coordinate system for integration over \( \Omega_{\text{int}} \)

\[ \tilde{\xi} = \xi_1 \left( \frac{\hat{n}_1 + \hat{n}_2}{|\hat{n}_1 + \hat{n}_2|} \right) + \xi_2 \left( \frac{\hat{n}_1 - \hat{n}_2}{|\hat{n}_1 - \hat{n}_2|} \right) \quad ; \quad \int_{\Omega_{\text{int}}} d^3 \xi = b \int_{\Omega_{\text{int}}} d\xi_1 d\xi_2 \]

Project on to local density, local orientation (polarisation) - to obtain hydrodynamic equations ↓

\[
\begin{pmatrix}
\rho(\mathbf{r}, t) \\
p(\mathbf{r}, t) \\
\ddot{Q}(\mathbf{r}, t)
\end{pmatrix} = \int d\hat{n}_1 \begin{pmatrix}
1 \\
\hat{n}_1 \\
\hat{n}_1 \hat{n}_1 - \frac{1}{d} \delta
\end{pmatrix} \Psi(\mathbf{r}, \hat{n}_1, t)
\]
Bulk Phases

Equations for homogeneous order parameters

\[ \rho_0 = \text{constant} \]
\[ \partial_t p_i = - \left( D_r - m_0 \rho_0 \gamma_0 \right) p_i + \left[ \frac{8 D_r}{3 \pi} - m_0 (2 \gamma_0 - \gamma_1) \right] \rho_0 S_{ij} p_j , \]
\[ \partial_t S_{ij} = - \left[ 4 D_r - \frac{8 D_r \rho_0}{3 \pi} - m_0 \rho_0 \gamma_1 \right] S_{ij} + 2 m_0 \rho_0 \gamma_0 \left( p_i p_j - \frac{1}{2} \delta_{ij} p^2 \right) . \]

Look for non-equilibrium steady states

Define (dimensionless) cluster activity

\[ \mu = \frac{\rho N m_0 \gamma_1}{D_r} \]

Cluster polarity (\(g=0 \Rightarrow \) non-polar)

\[ g = \frac{\gamma_0}{\gamma_1} \]
Bulk Phases

Phase diagram for $g<1/4$

$$g = \frac{\gamma_0}{\gamma_1}$$

$$\mu = \frac{\rho_N m_0 \gamma_1}{D_r}$$

Phase diagram for $g>1/4$

Critical activity, $\mu_x$
Hydrodynamic modes

Examine fluctuations about the homogenous states

\[ \rho(r,t) = \rho_0 + \delta \rho(r,t), \quad p(r,t) = p_0 + \delta p(r,t), \quad Q(r,t) = Q_0 + \delta Q(r,t) \]

Long lived, long wavelength hydrodynamic modes
(conserved quantities, broken symmetry)

Isotropic phase ↓ density \( \delta \rho \sim e^{z_{\rho}(k)t} \), \( z_{\rho} = -k^2 \left[ \frac{1}{6} - 2\mu \tilde{\alpha} \right] \).

Polarized phase ↓ density, polarization director \( p(r,t) = p(r,t)\hat{n}(r,t) \)

In broken symmetry phase we choose wlg polarization director along y axis

\[ \delta n = n - \hat{y} = \hat{x} \delta n_x \quad \delta \rho \sim e^{z_{\rho}(k)t}, \quad \delta n_x \sim e^{z_{n}(k)t} \]

\[ z_{\rho} = ikc_1 \mu \tilde{\beta} - \frac{k^2}{8} \left[ 1 - \frac{g \mu}{6} - 20\mu \tilde{\alpha} \right], \quad k = k\hat{y} \]

\[ z_{n} = -ikc_2 \mu \tilde{\beta} - \frac{5k^2}{48} \left[ 1 + \frac{2}{5} \mu (g - 6\tilde{\alpha}) \right], \]

In general coupled travelling density and polarization modes

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Hydrodynamic modes

Long lived, long wavelength hydrodynamic modes
(conserved quantities, broken symmetry)

Nematic phase \( \downarrow \) density, nematic director

\[
Q(r,t) = Q_0 + \delta Q(r,t) \quad Q(r,t) = S(r,t)(\hat{n}(r,t)\hat{n}(r,t) - \frac{1}{2}\delta)
\]

In broken symmetry phase we choose w.l.g, nematic director along y axis

\( \hat{n} = \hat{y} \)

\[
\delta n = n - \hat{y} = \hat{x}\delta n_x \quad \delta \rho \sim e^{z_\rho(k)t}, \quad \delta n_x \sim e^{z_n(k)t}
\]

\[
z_\rho = -k^2 \left[ \frac{1}{6} - 2\mu\tilde{\alpha} \right], \quad z_n = -\frac{k^2}{8} \left[ 1 + \frac{19}{36}\mu \right]. \quad k = ky
\]

In general coupled diffusive density and nematic director modes
Linear stability - modes

Orientation modes, density mode
\[ \delta \mathbf{n}(r, t) = \sum_{k} n_k e^{ik \cdot r} , \quad \delta \rho(r, t) = \sum_{k} \rho_k e^{ik \cdot r} \]

(d - 1) Degenerate Transverse modes
\[ n^T_k = \hat{k} \times n_k \]

Longitudinal modes
\[ n^L_k = \hat{k} \cdot n_k \]

Eigenvalues
\[ \lambda_{\pm}(k) \]

\[ \partial_t \begin{pmatrix} n^L_k \\ \rho_k \end{pmatrix} = M \cdot \begin{pmatrix} n^L_k \\ \rho_k \end{pmatrix} \]
\[ \partial_t n^T_k = \lambda^T(k) n^T_k \]

‘Entanglement’ (tube) estimated in diffusion constants
\[ D_\perp \approx \frac{D}{\left(1 + \tilde{\rho}_0 \left(\frac{l}{b}\right)^{d-2}\right)^2} , \quad D_r \approx \frac{6D}{l^2 \left(1 + \tilde{\rho}_0 \left(\frac{l}{b}\right)^{d-2}\right)^2} , \quad D_\parallel \approx D \]

Combined Phase diagram

Inhomogeneous states

A Ahmadi, TBL and MC Marchetti (2005)
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Flow

- Momentum - Stokes Equation at low Re

\[ \eta \nabla^2 \mathbf{v}(\mathbf{r}, t) - \nabla p = \left\langle \sum_i \int_{-\ell/2}^{\ell/2} ds \, f_i(s) \, \delta (\mathbf{r} - \mathbf{r}_i(s, t)) \right\rangle = -\nabla \cdot \sigma^{\text{ro}} ds \]

- Evolution of probability \( \Psi(\mathbf{r}, \hat{n}, t) \)

\[ \partial_t \Psi + \nabla \cdot (\Psi \mathbf{v} + \mathbf{J}) + R \cdot \left( \Psi \left[ \hat{n} \times (\hat{n} \cdot \nabla) \mathbf{v} \right] + \mathbf{J} \right) = 0 \]

- Force and torque dipoles due to motors
- Derive a microscopic expression for the average (filament) stress tensor
Stress Tensor

• Microscopic expression for the stress tensor

\[
\sigma_{ij}^p(r) = A Q_{ij}(r) + B \left( p_i(r) p_j(r) - \frac{1}{2} p^2 \delta_{ij} \right) + C \delta_{ij} + O(\nabla)
\]

\[
A = \left(2 - \frac{\rho}{\rho_N}\right) k_B T + \frac{1}{16} \zeta \rho \alpha_0 \mu \ell^3
\]

\[
B = \frac{1}{32} \zeta \rho \alpha_1 \ell^3
\]

\[
C = \left(2 + \frac{\rho}{\rho_N}\right) \rho k_B T + \frac{1}{32} \zeta \rho^2 \alpha_0 \mu \ell^3 + \frac{1}{16} \zeta \rho^2 \alpha_1 \mu \ell^3
\]
Mechanical properties - Rheology

- **Linear Rheology** - Apply small shear strain and measure shear stress

- **Shear Modulus**

\[
\sigma_{xy}(t) = \int_{-\infty}^{t} dt' G(t - t') \dot{\gamma}_{xy}(t')
\]

\[
\dot{\gamma}_{xy} = \frac{V}{D}
\]
Linear Rheology

- Active contributions to stress even without deformation.

- Stiffening seen in actin-myosin networks

Linear Rheology

- Shear flow \( \kappa_{ij} = \nabla_i v_j = \varepsilon \delta_{ix} \delta_{jy} \)
- Isotropic regime, linear order in \( \varepsilon \)

\[
\frac{\partial}{\partial t} + \frac{1}{\tau} Q_{xy} = \frac{\varepsilon}{4} \rho ; \quad \frac{1}{\tau} = 4 D_r \left( 1 - \rho / \rho_N \right) - m_0 \gamma_1 \ell^2 \rho
\]

- Step strain

\( \dot{\gamma}_{xy}(t) = \kappa_0 \delta(t) \) \( \sigma_{xy}(t) = G(t) \kappa_0 + G^a \mu \)

- Maxwell model

\[
G(t) = \frac{A}{4} \exp \left[ -t / \tau \right] ; \quad D_r = \frac{k_B T}{\ell^3 \eta}
\]
Semiflexible Polymers

- Wormlike Chain Model (WLC)
- Conformations have Bending Energy
\[ H_{\text{bend}}[\mathbf{R}(s)] = \frac{A}{2} \int ds \left( \frac{\partial^2 \mathbf{R}}{\partial s^2} \right)^2 \]
- Inextensible
\[ \left( \frac{\partial \mathbf{R}}{\partial s} \right)^2 = 1 \]
- Tangent correlation function
\[ \{t(s) \cdot t(0)\} = \exp\left(-\frac{s}{L_p}\right) \]
- Persistence length
\[ L_p = \frac{A}{k_B T} \]
Anisotropic Dynamics

\[ \partial_t r_\perp (s,t) - \gamma \mathbf{r}_\perp = \frac{1}{\zeta_\perp} \left[ -A \partial_s^4 r_\perp + \partial_s \left( \Lambda(s,t) \partial_s r_\perp \right) \right] + f_\perp (s,t) \]

\[ \partial_t r_\parallel (s,t) - \gamma \mathbf{r}_\parallel (\mathbf{r}_\parallel - \mathbf{s}) = \frac{1}{\zeta_\parallel} \left[ -A \partial_s^4 r_\parallel - \partial_s \Lambda \right] + f_\parallel (s,t) + \hat{n} \cdot f_{act} (s,t) \]

\[ \partial_s r_\parallel = \frac{1}{2} |\partial_s r_\perp|^2 + \ldots \]

- Self-consistent solution
- Average over transverse fluctuations and use inextensibility

Solve for fluctuating \( \nu(r) \) with \( \langle \nu(r) \rangle \) given by the prescribed flow \( \gamma \mathbf{r} \). Step strain \( \dot{\gamma} (t) = \epsilon \delta(t) \)

Microscopic calculation of stress - configurational average

\[ \eta \nabla^2 \nu + \nabla p = \sum_i \int \frac{ds}{a} F_i(s,t) \delta(\mathbf{r} - \mathbf{R}_i(s,t)) \quad ; \quad \nabla \cdot \nu = 0 \]

TBL, Maggs & Ajdari, PRL 86, 4171, 2001

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S1-Myosin/F-Actin Solution

Experiments on F-Actin and Myosin S1 fragments

\[
\langle |S| (s + x) \rangle
\]

Tangent correlation function

\[
G_{eq}(\omega) \propto \omega^{3/4} \quad \text{and} \quad G_{act}(\omega) \propto \omega^{7/8}
\]

\[
\langle x^2(\omega) \rangle = \frac{2k_B T G''(\omega)}{6\pi R\omega |G(\omega)|^2}
\]

Le Goff et al, PRL 88, 018101 (2001)

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Activity \downarrow \text{anomalous fluctuations}

- Active force correlations
\[ \langle f_{act}^i(s,t)f_{act}^j(s',t') \rangle = \Theta \zeta_perp^2 \delta^i \delta(s-s') \Phi(t-t') \]
\[ \Phi(t) = \exp(-|t|/\tau) \]

- Tangent correlation function
\[ \Theta \tau \zeta = k_BT_{act} \]
\[ L_p \approx L_p \left(1 + \frac{T_{act}}{T}\right)^{-1} \]

- High Frequency shear modulus

- WHY?

Numbers

- Assume motors arrive at random times with a constant rate
- Fraction of bound motors
- Distance between aggregates
- Activity Parameter

\[ \Theta \approx \left( f_0 a \right)^2 / \ell_m \]

\[ \phi = \rho_a / (k_a + \rho_a) \]

\[ \ell_m \approx \left( \phi \rho_m \xi^2 \right)^{-1} \]

\[ \rho_a a \approx \xi^{-2} \]

F-actin \( \rho_a = 14 \mu M \), S1 myosin \( \rho_m = 5 \mu M \)

Motor stall force \( \sim 5 \text{pN} \)

Actin diameter \( \sim 7 \text{nm} \)

Motor cycle time, \( \sim 5 \text{ms} \)

Actomyosin eq. binding const. \( \sim 500 \text{nM} \)

Actin concentration

Meshsize

Almost full coverage

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Tangent correlation

\[ \langle t(s) \cdot t(0) \rangle \approx \exp \left( -s \cdot \frac{2\Theta}{L_p} \cdot \frac{1 - \cos qs}{q^2 (q^4 + (A\tau/\zeta)\cdot\tau)^{-1}} \right) \]

**Length-scale dependent rigidity**

**Crossover length-scale**

\[ \ell_C \approx \left( \tau \cdot \frac{A}{\zeta} \right)^{1/4} \]

**TBL, PRE 67, 031909 (2003)**

**Active ‘temperature’ scale**

\[ \Theta \tau \zeta = k_B T_{\text{act}} \]

\[ L_p \approx L_p \left( 1 + \frac{T_{\text{act}}}{T} \right)^{-1} \]

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High frequency viscoelasticity

Tension in filament

\[ \Lambda(s, \omega) \approx \frac{\hat{X}(\omega) \cdot \hat{n}}{i \omega K(\omega)} \]

Stress

\[ \sigma_{ij} = \rho \langle \Lambda n_i n_j \rangle \Rightarrow G(\omega) = \frac{2\rho}{15K(\omega)} \]

\[ K_{eq}(\omega) = 2^{-3/4} (k_B T)^{1/4} L_p^{5/4} (i \omega \zeta_{\perp})^{-3/4} \]

Morse, Gittes/MacKintosh (1998)

\[ K_{act}(\omega) \sim 2^{-3/4} \Theta \tau \zeta_{\perp} (k_B T L_p)^{-5/4} \]
\[ \times \left[ (i \omega \zeta_{\perp})^{-3/4} - \frac{1}{4} \left( \zeta_{\perp} / 2\tau \right)^{-3/4} \right] \]

Active compliance crosses over from high effective persistence length at high frequencies to low effective persistence length at lower frequencies.
Conclusions

- Active filament solutions are significantly different from passive ones.
- Non-equilibrium analogues of bulk phase transitions.
- Development of inhomogeneous states can also be driven by motor activity. Type of defect structures depend on homogeneous states.
- From a simple microscopic model, bundling is due to mean motor velocity which decreases close to + end.
- Explicit expression for the stress tensor in terms of microscopic parameters.
Perspectives

ONGOING WORK

• Non-linear analysis of inhomogenous states
• Detailed study of dynamics of motor density
  \[ \Rightarrow \partial_t n_m = F(n_m, Q, u, \rho) \]
• Effect of (shear) flow on instabilities.
• Many body interactions, frustration

FUTURE WORK

• Polydispersity, treadmilling \[ \Rightarrow \]
• Hydrodynamic interactions
• Include passive cross-linkers
• Couple semiflexibility to self-organisation

\[ \Psi(r, \hat{n}, \ell, t) ; \quad \frac{d\langle \ell \rangle}{dt} \]