ICMMA 2014, 'Crowd Dynamics', Meiji University, 2015/01/08

Collective Motion of Self-Propelled Objects: From Molecule to Colloid

Masaki Sano

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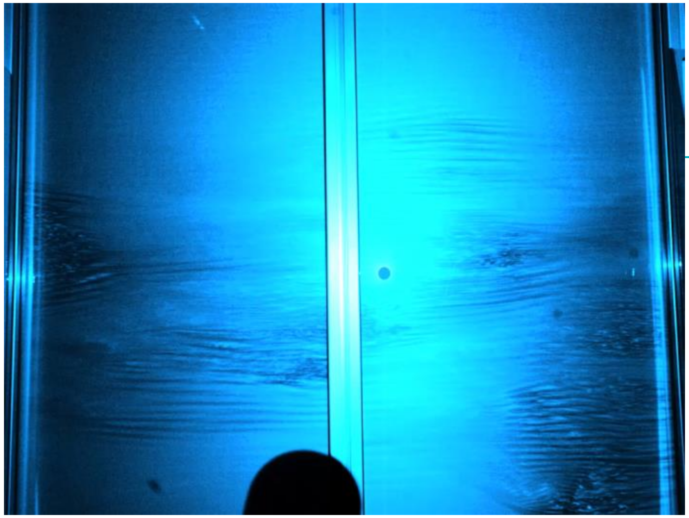
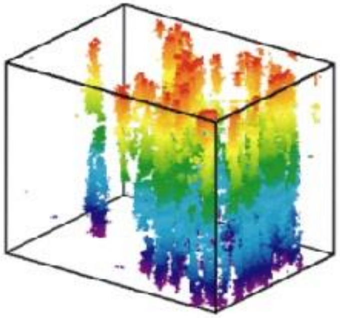
The University of Tokyo

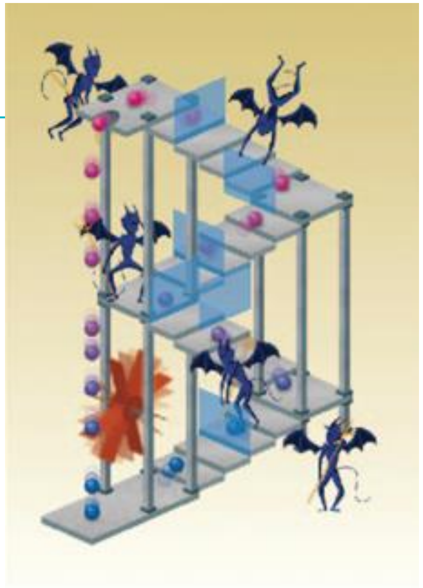
Non-equilibrium Phase Transition & Turbulence





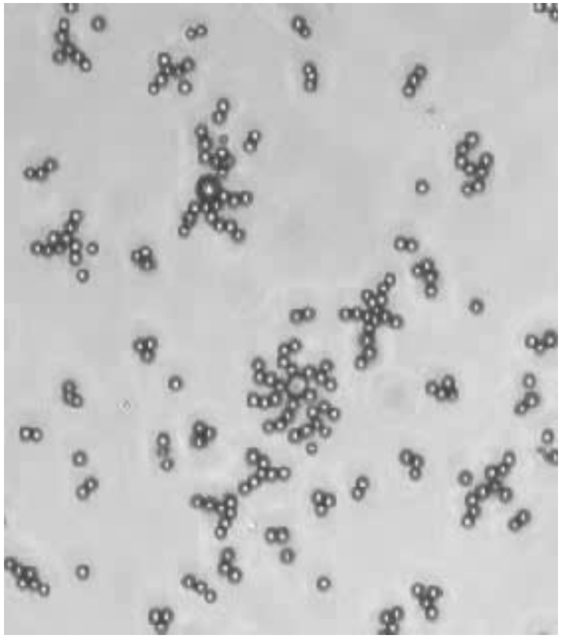
Information Thermodynamics

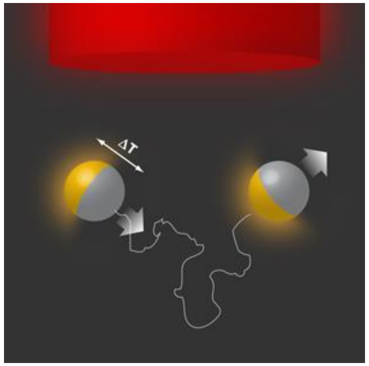
$$\langle e^{(\Delta F - W)/k_B T} \rangle = \gamma$$



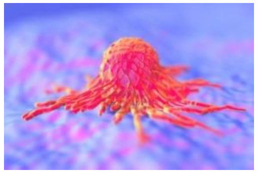
Non-equilibrium Statisical Mechanics

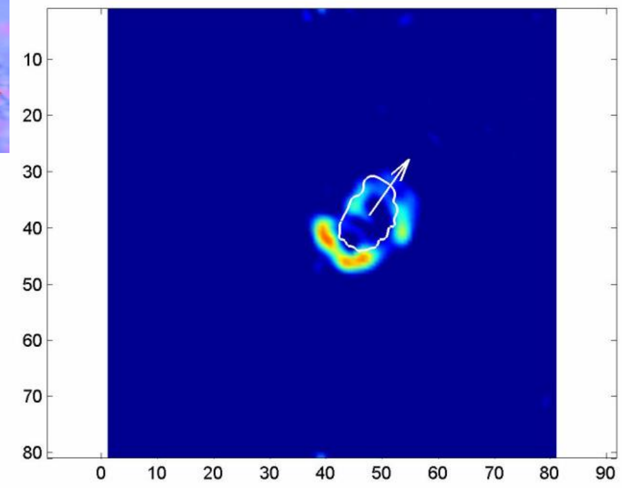
Active Colloids





Cell Motility



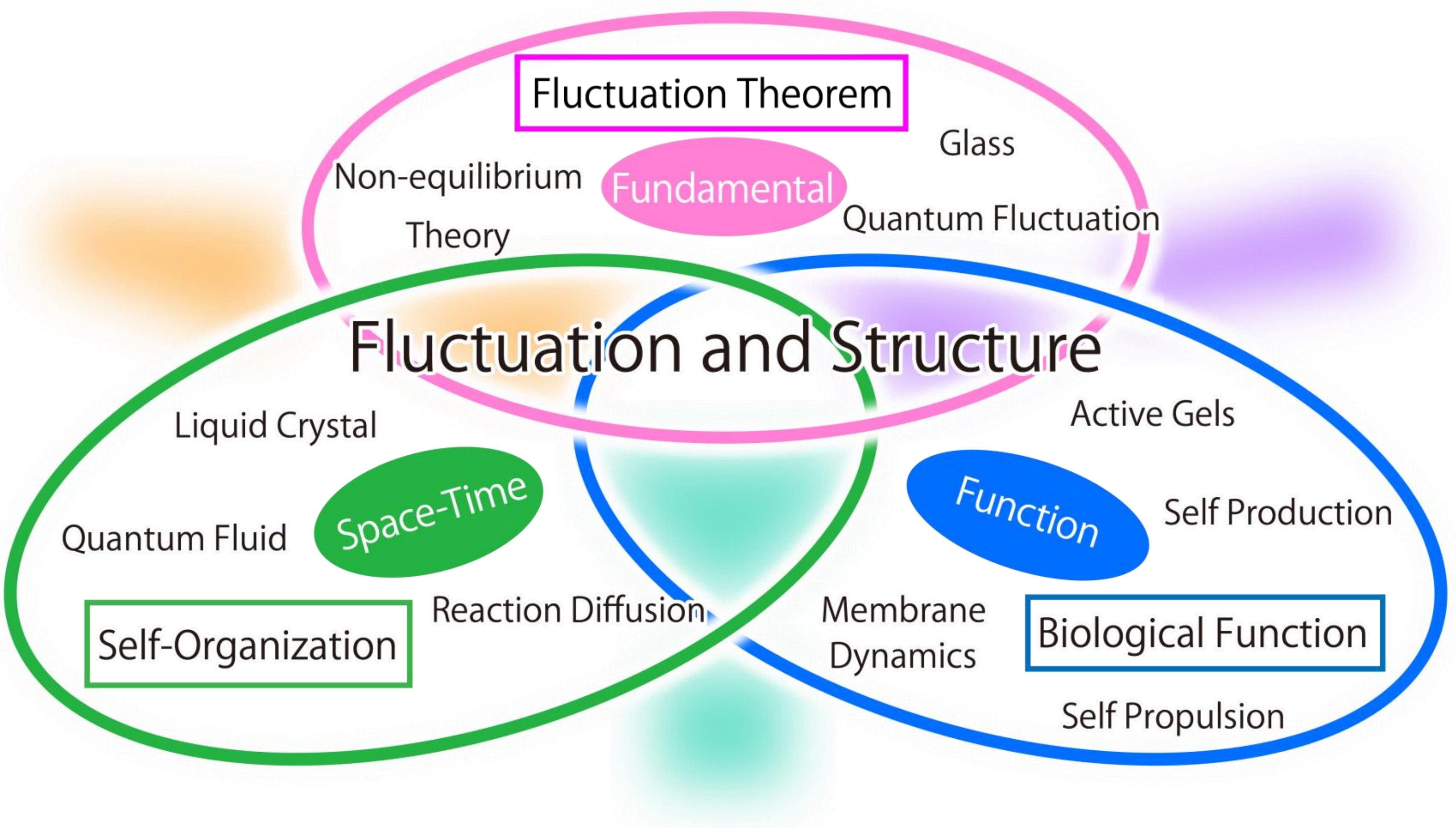


Traction Force Microscopy

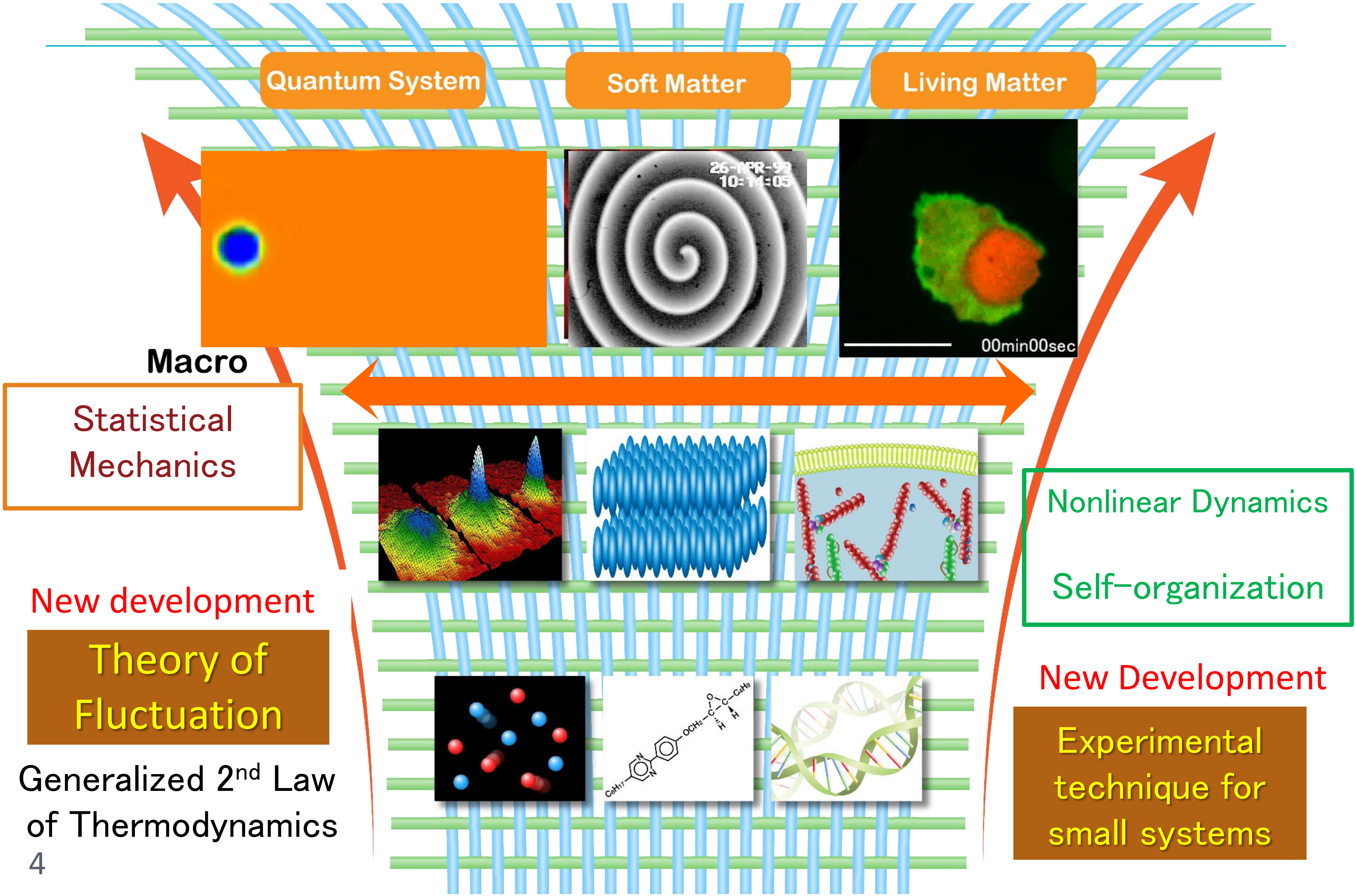
Active Soft Matter

Synergy of Fluctuation and Structure
— Quest for Universal Laws in Non-Equilibrium Systems —

Grant-in-Aid for Scientific Research on Innovative Areas of MEXT, JAPAN
(FY2013-2017)



Quest for Universal Laws in Non-Equilibrium Systems



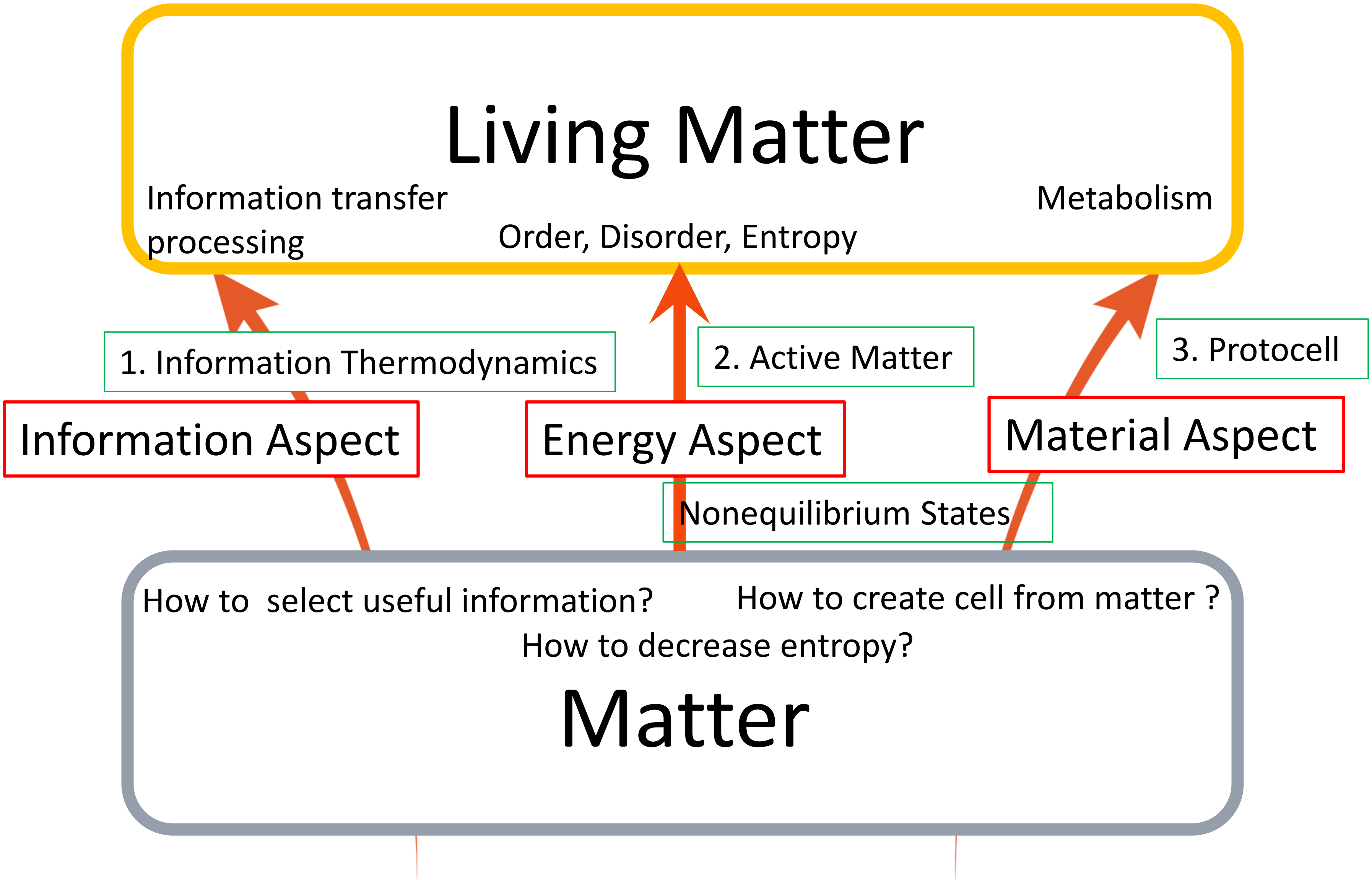
Objectives and Research Contents of Our Project

- How to extract useful information from fluctuations
- How do self-organized structures arise from fluctuations?
- Are there universal laws in nonequilibrium systems?

- How are nonequilibrium fluctuation and structure interacting in soft/solid condensed matter, active matter, and biomatter?

- How can a collection of mere matter exert basic functions of life, such as self-production, self-propulsion, information processing?

Bridging gaps between matter and life



Collective Motion of Active Matter

Artificial Systems

- Self-Propelled Colloid
- Single Particle Motion
- Dense Suspension

Biological Systems

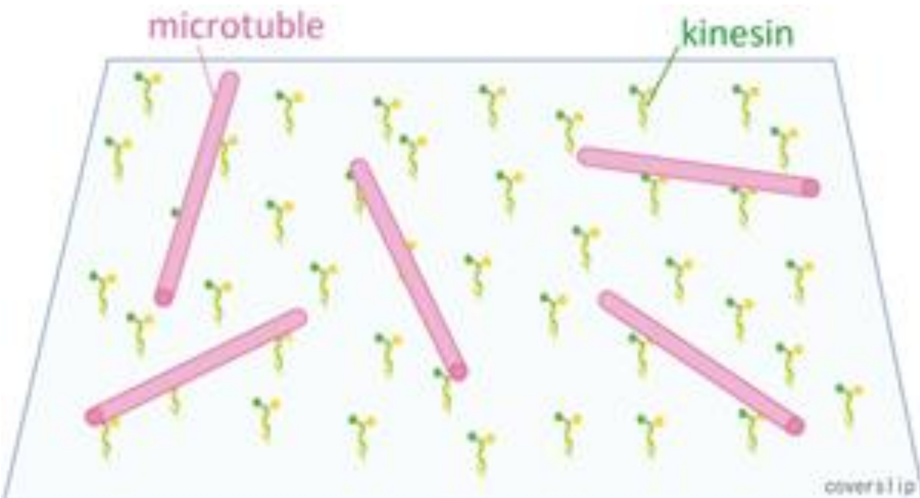
- Molecular Motor + Track
- Single Cell Migration
- Multicellular Migration

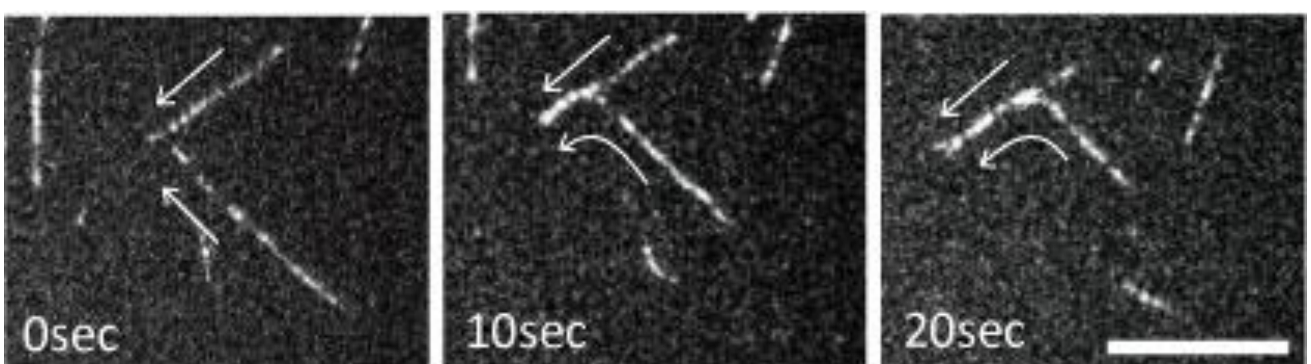
Directed Movement	Interaction	Noise (Fluctuation)
Polar	Polar	Thermal Fluctuation
Nematic	Nematic	Deterministic Chaos, etc.

Collective Motion of Microtubules on Kinesin Bed

Motility assay of kinesin motors and microtubules

Poster by Sakurako Tanida
“Pattern Frmation of Microtuble”



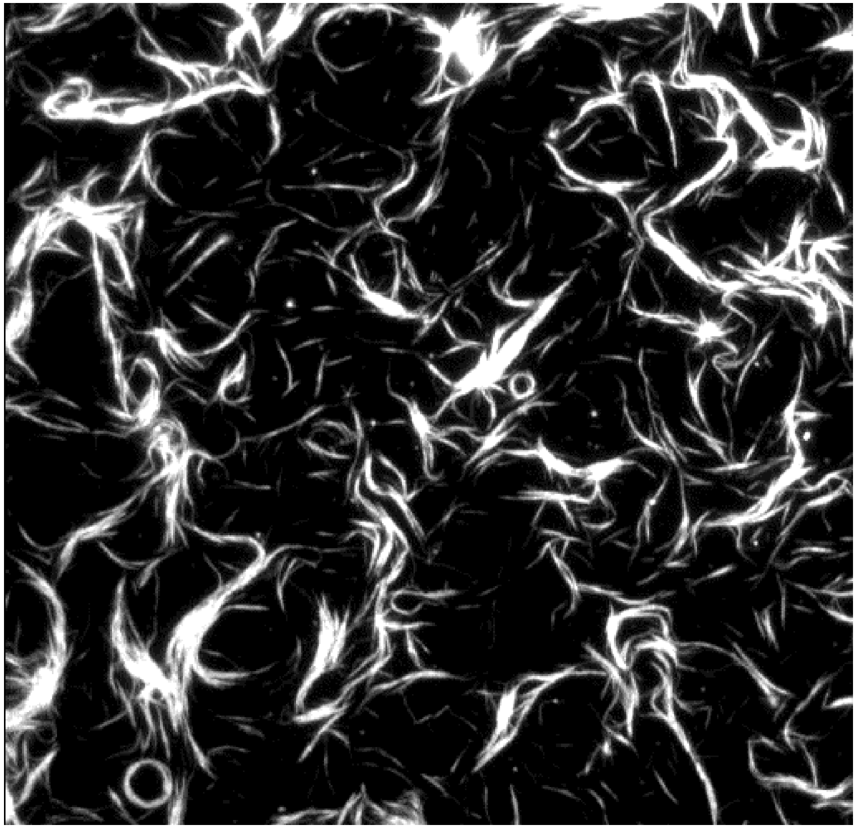


Collision Dynamics

Alignment Effect

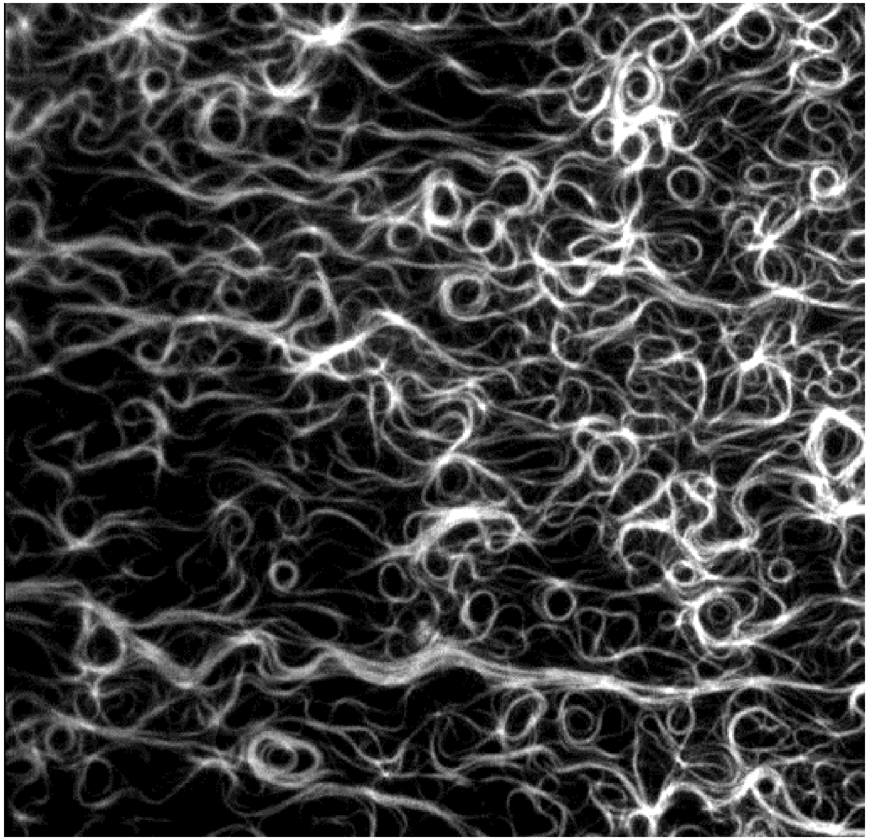
Collective Motion of Microtubules on Kinesin Bed

Short Microtubules (~ 1 um)



Bundle formation with nematic ordering

Long Microtubules (~ 5 -7um)



Loop formation, Oscillating Bundles

Cell Migration

Actin polymerization

force generation by molecular motor

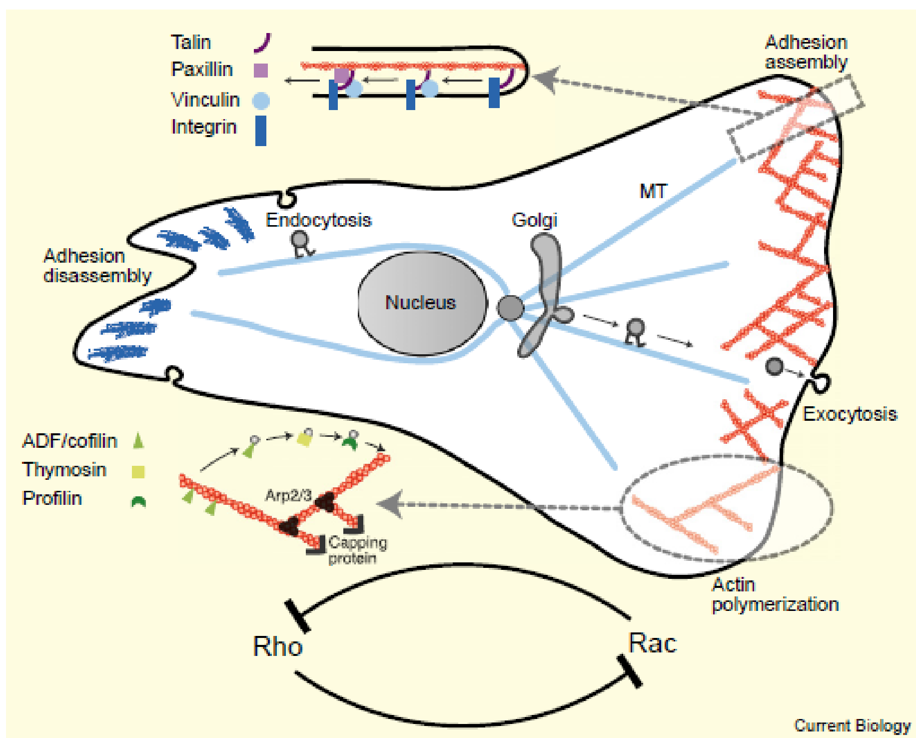
membrane deformation

polarity (symmetry breaking),

sensing direction

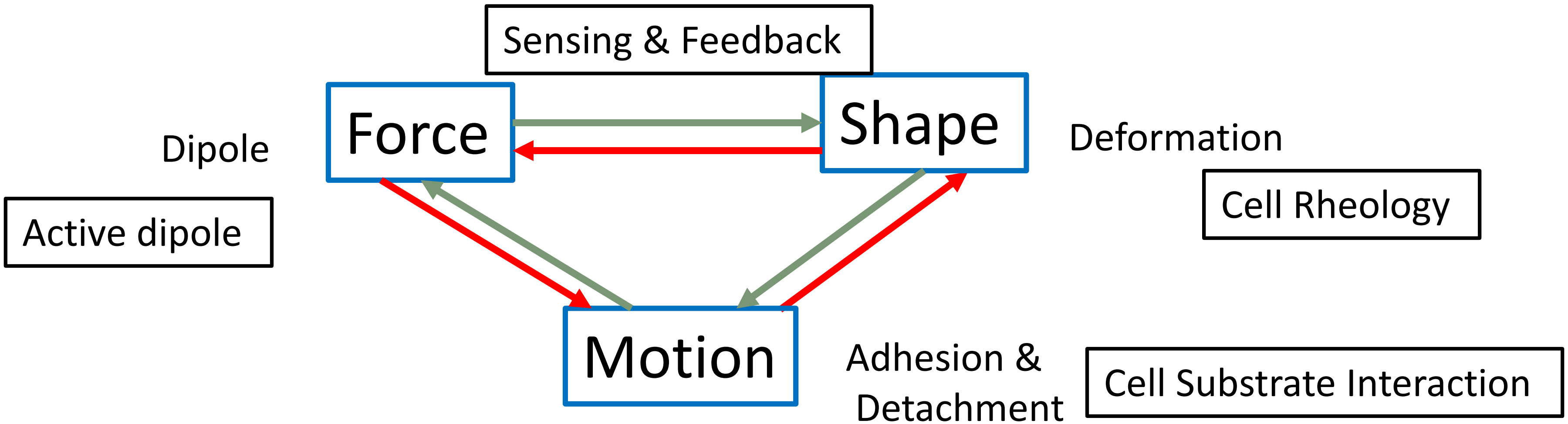
cell-cell/substrate contact
(focal adhesion),

Cell Motility



How cells coordinate deformation and movement?

What is the relationship between Force, Shape, and Motion?



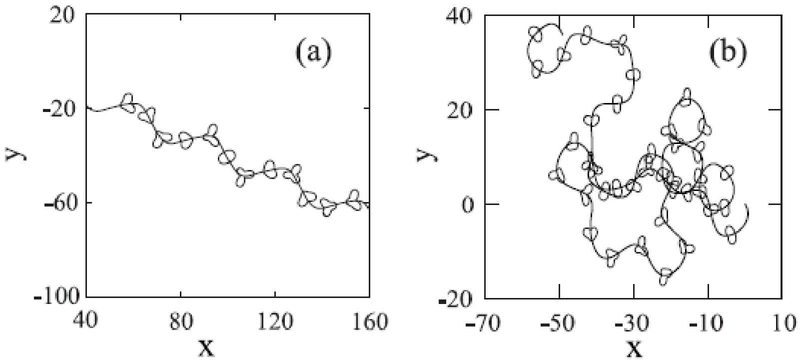
Cell migration might be understood as a collective non-equilibrium dynamics of matter.

→ Look at dynamics of slow variables: Shape, Force, Centroid Motion

Various Modes in Migration

1) Steady motion :ballistic
2) Turning(Oscillation, Rotation) :short term behavior
3) Random migration :long term behavior

Spontaneous Symmetry Breaking of Cell Shape



Hiraiwa, Matsuo, Ohkuma, Ohta, Sano, EPL (2010)

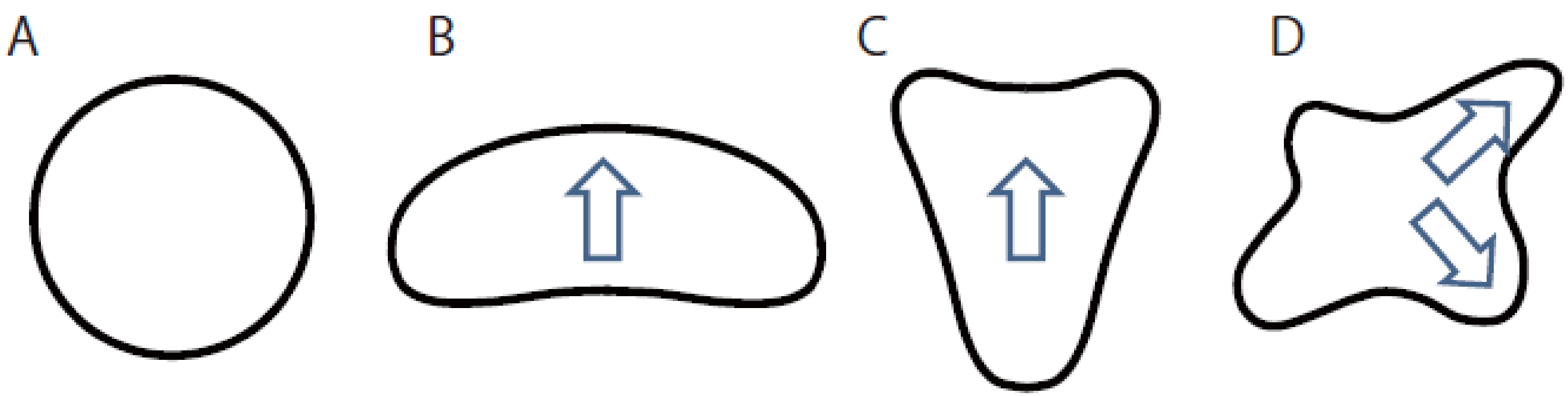
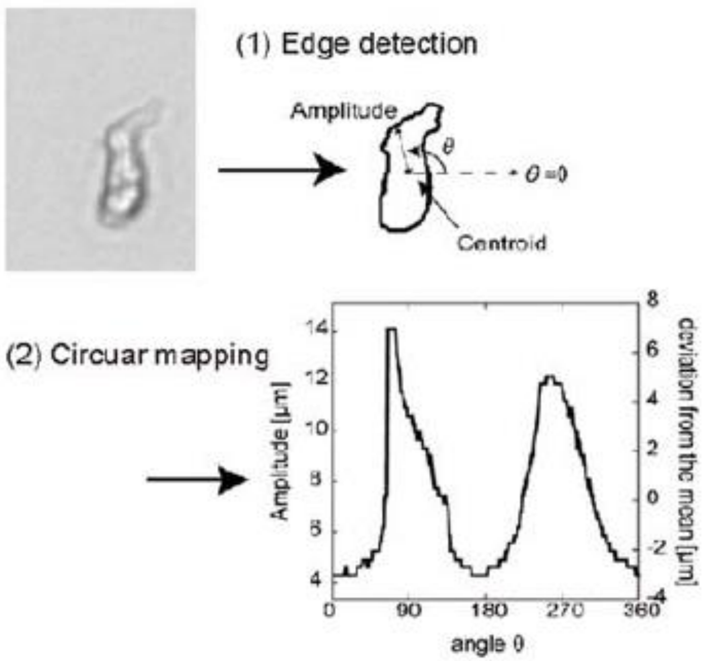


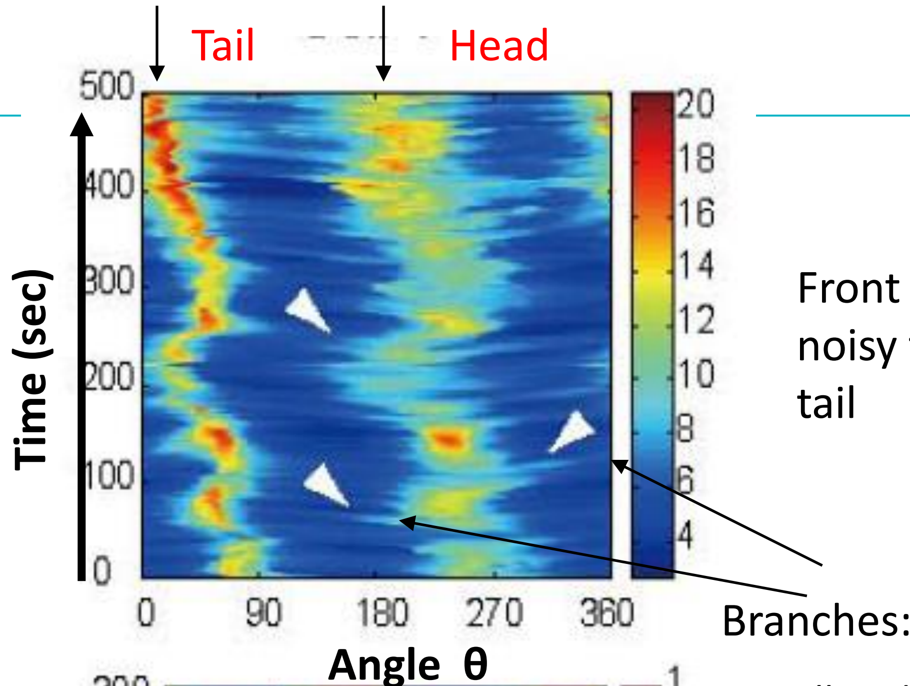
Fig. 1.12. Spontaneous symmetry breaking in cell shape. (A) Circular cell (Actin polymerization is prohibited by latrunculin A.) (B) Keratocyte cell. (C) Polarized cell in chemotaxis. (D) Amoeboid cell.

Sano, Ohta, Matsuo, (World Scientific, 2011)

Ordered Patterns of Cell Shape & Cell Migration

Maeda, Inose, Matsuo, Iwaya, MS , Plos One, 3, e3734 (2008)



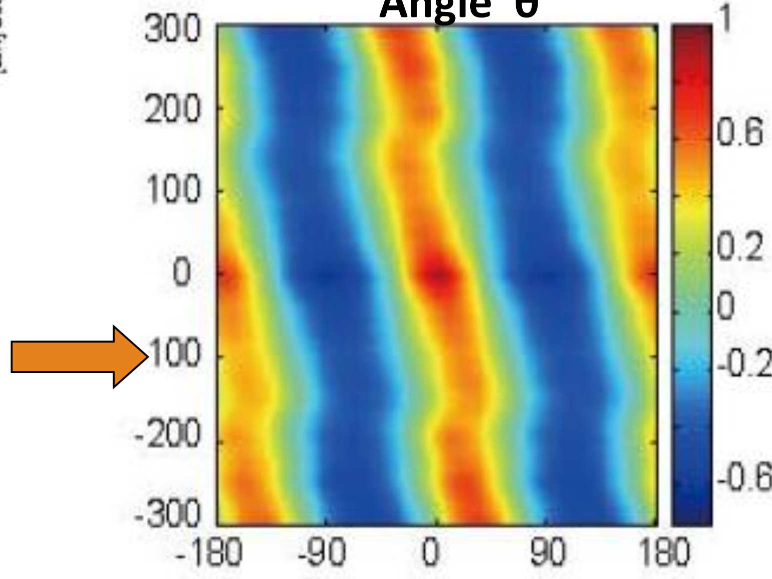


Front is more noisy than the tail

Lamellipodia adhere to the substrate and fixed while cell body moved forward.

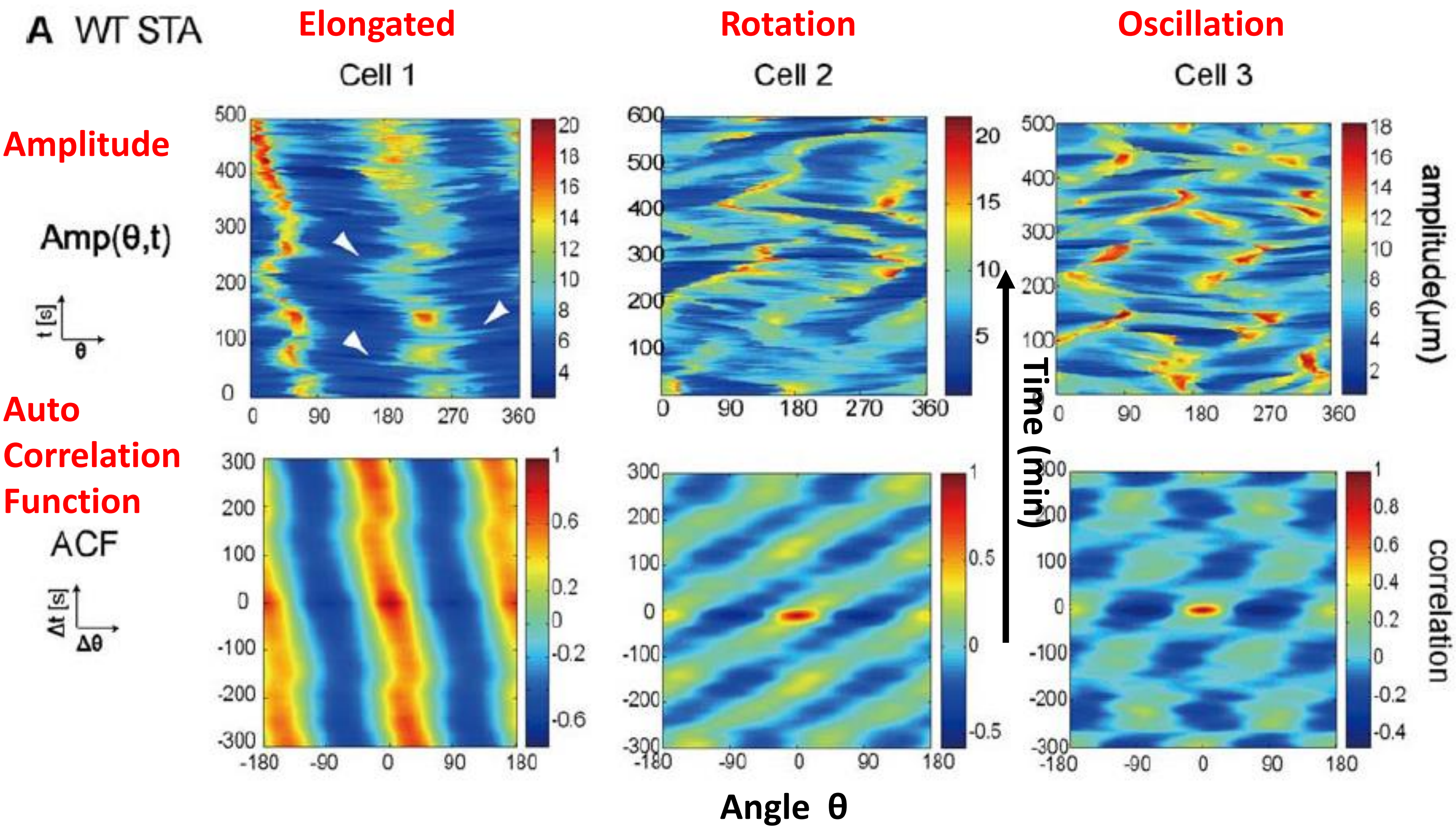
Auto Correlation Function:

$$C = \frac{\left\langle A(\theta,t)A(0,0)\right\rangle_{0,0}}{\left\langle A(\theta,t)^2\right\rangle_{\theta,t}}$$



Ordered Patterns in Cell Shape Dynamics: Starved Cells

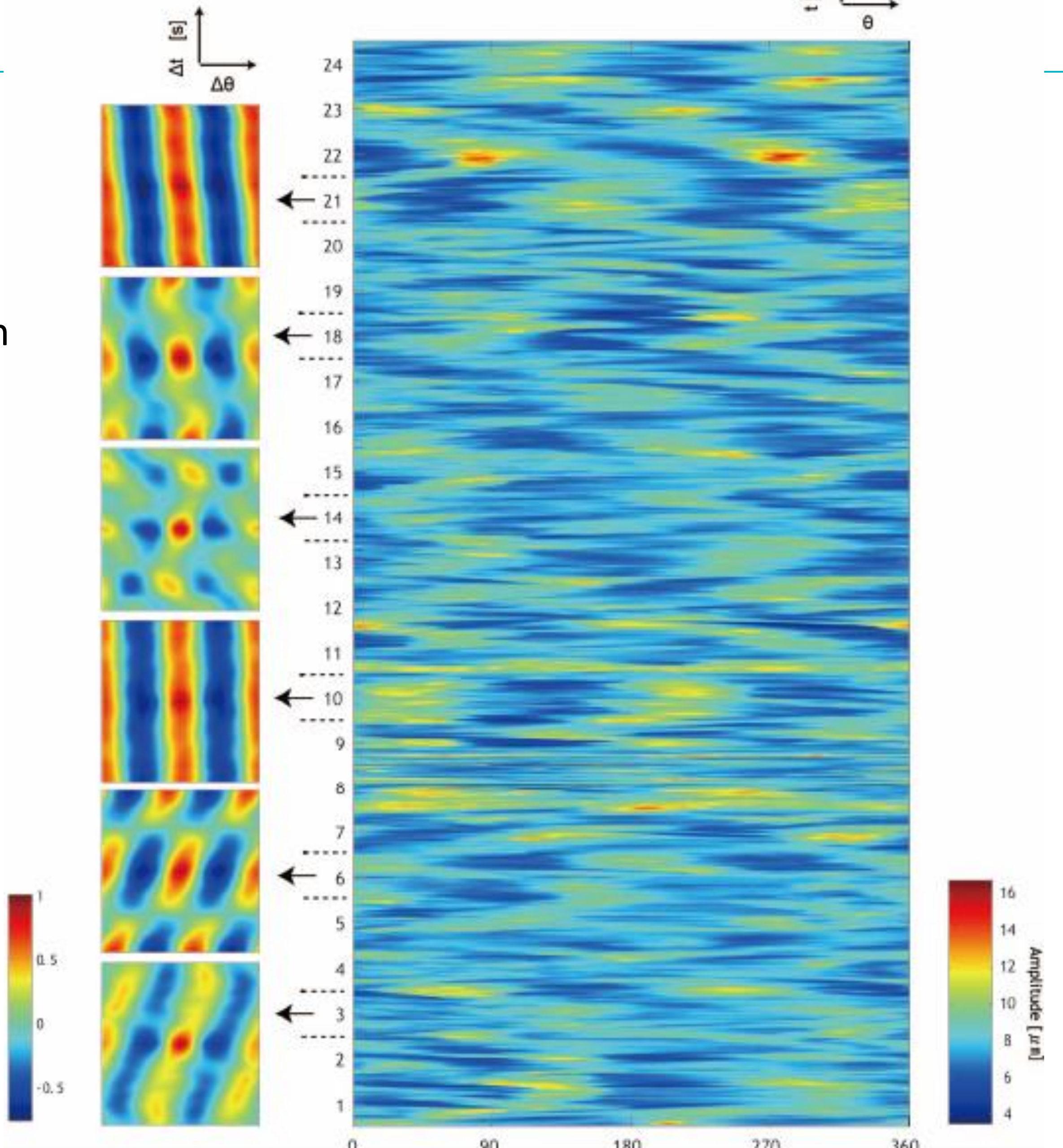
Maeda, Inose, Matsuo, Iwaya, MS , Plos One, 3, e3734 (2008)

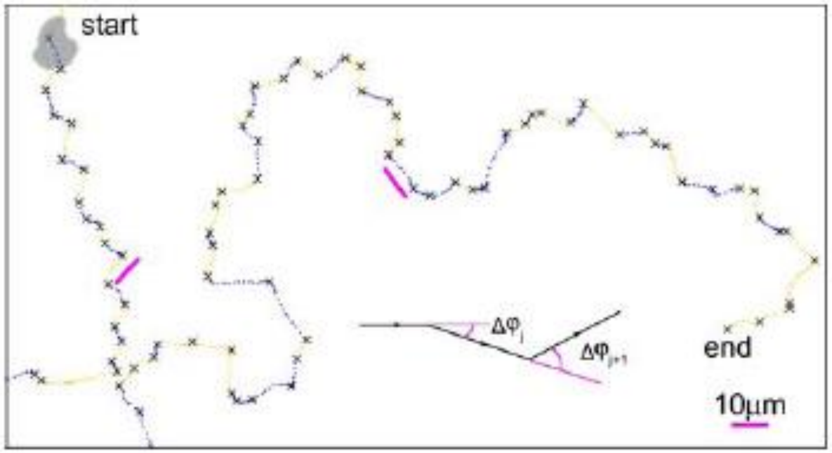


About 70% of time series are classified into 3 ordered patterns.

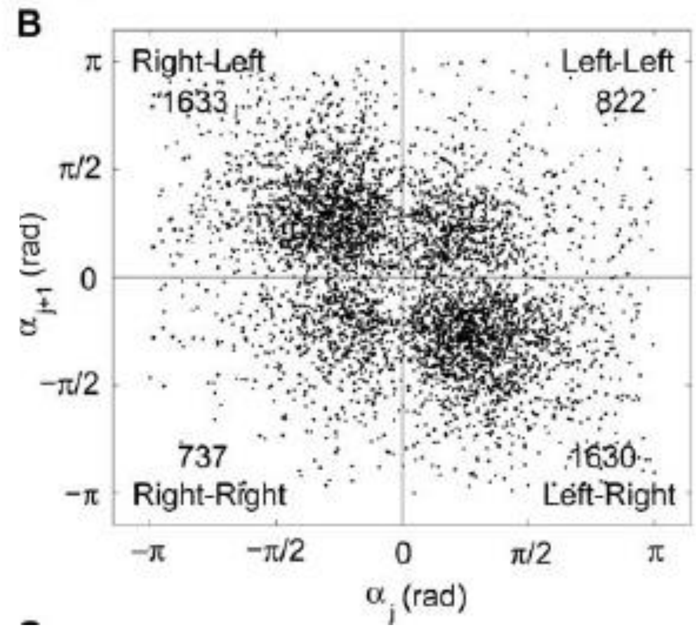
Transition of patterns occurs in a single cell along the time course.

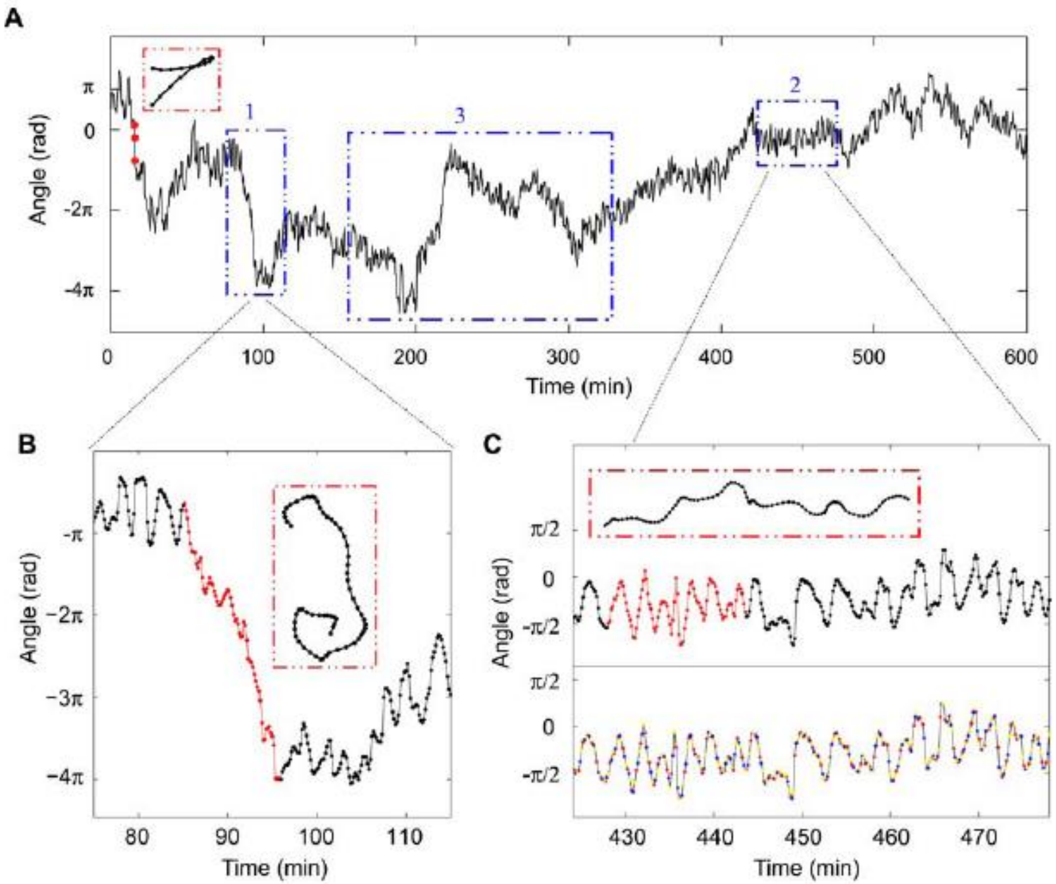
Time series and ACF of a single cell for time duration 30min.





Liang, Cox, PLoS one (2008)





Cells show zig-zag motion.

Goal and ideas for measuring traction force

- Goal
  - Find out a force-motion relationship of migrating cells
- Challenge
  - Characterize the spatial properties of the traction stress
- Ideas
  - **Force spot tracking**: Fine-grained approach
  - **Multi-pole analysis**: Coarse-grained approach

Net Traction Force Vanishes for Small Cells

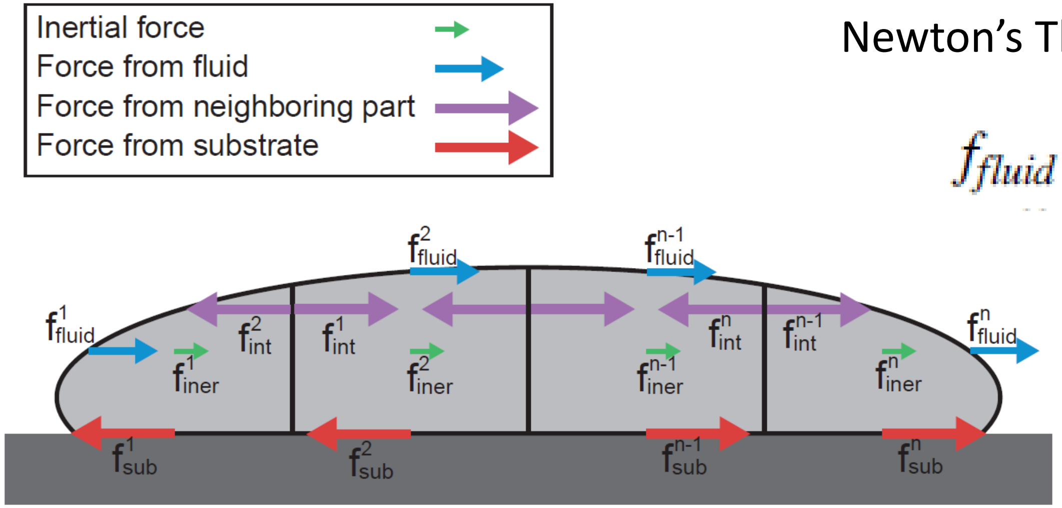
$$\underbrace{\sum_i m^i \frac{dv^i}{dt}}_{\propto L^3} - \Big(\underbrace{\sum_i f^i_{int}}_{=0} + \underbrace{\sum_i f^i_{fluid}}_{\sim 1\text{ Pa}} + \underbrace{\sum_i f^i_{sub}}_{\sim 100\text{ Pa}} \Big) = 0.$$

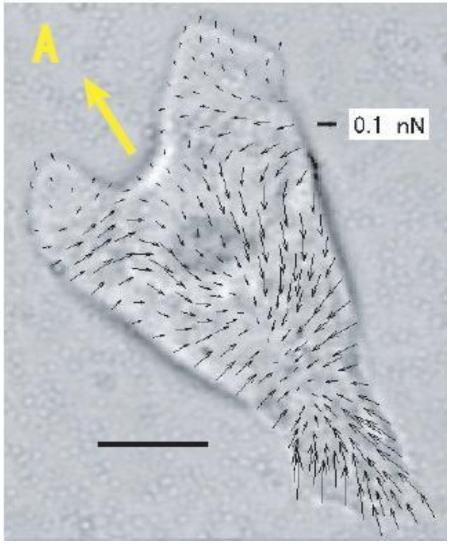
$\propto L^2$

Newton's Third Law: $\sum_i f^i_{int} = 0.$

$$f_{fluid} \sim \eta \Delta v / \Delta z\, S \ll \sum_i f^i_{sub}$$

$$\sum_i f^i_{sub} = 0$$





Sum of traction force (torque) is zero.

$$\sum f_i = 0, \quad \sum M_i = 0$$

Measurement of Traction Force in Single Cell

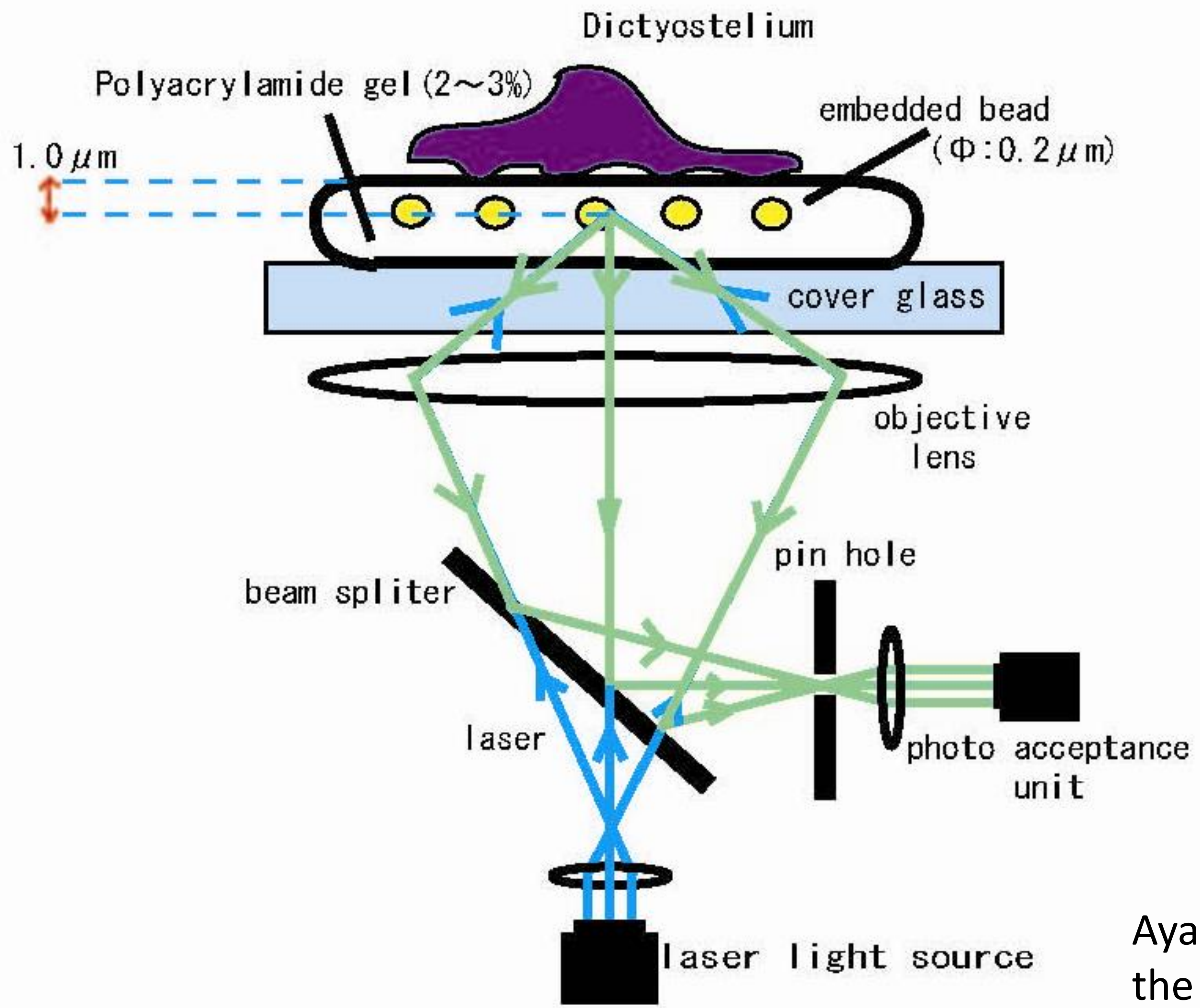
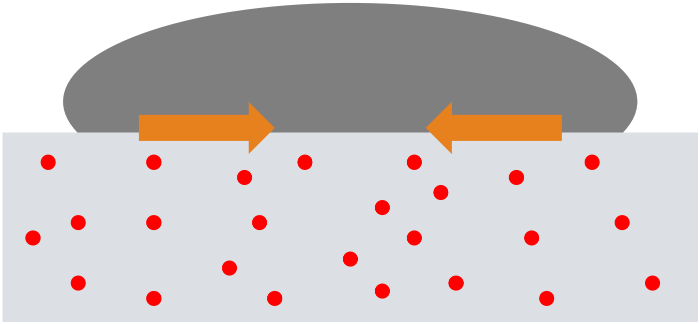
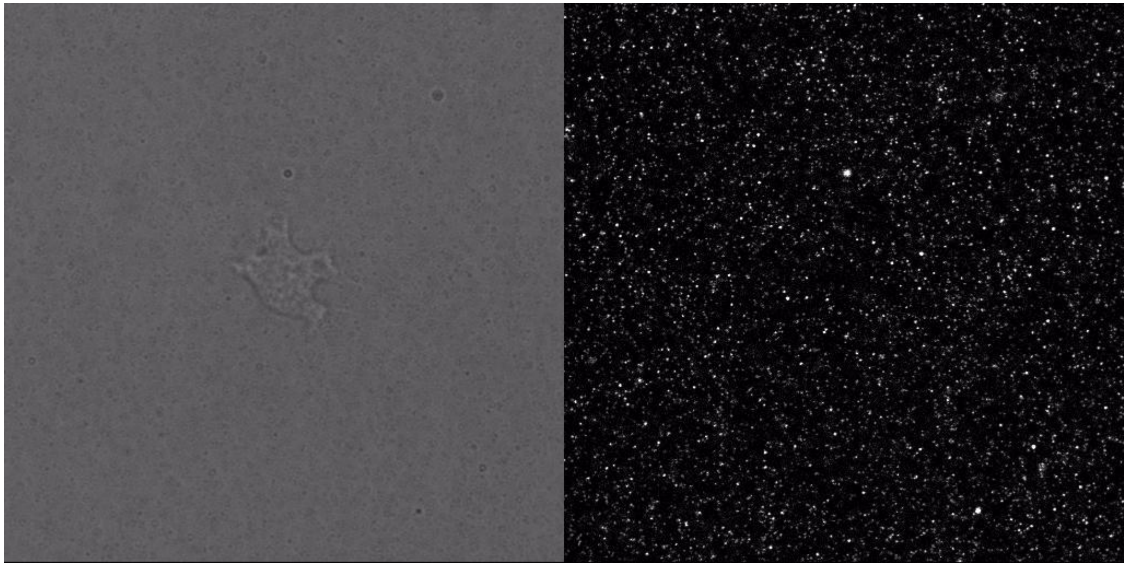


Fig.1 experimental setup

Ayari et al. Cell Motility and the Cytoskeleton (2008)

Traction Force Microscopy



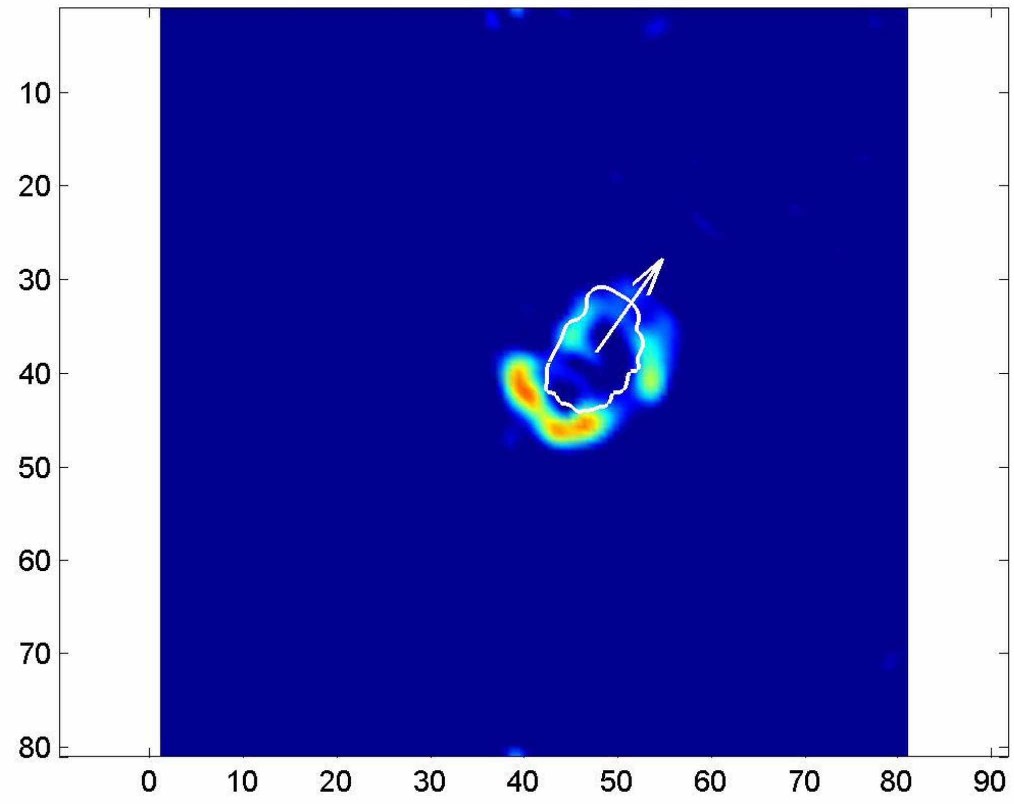


Transmission   Fluorescence (beads)

We quantified the traction stress of migrating *Dictyostelium* cell (simple uni-cellular amoeba) using flexible poly-acrylamide gel embedded with fluorescence beads.

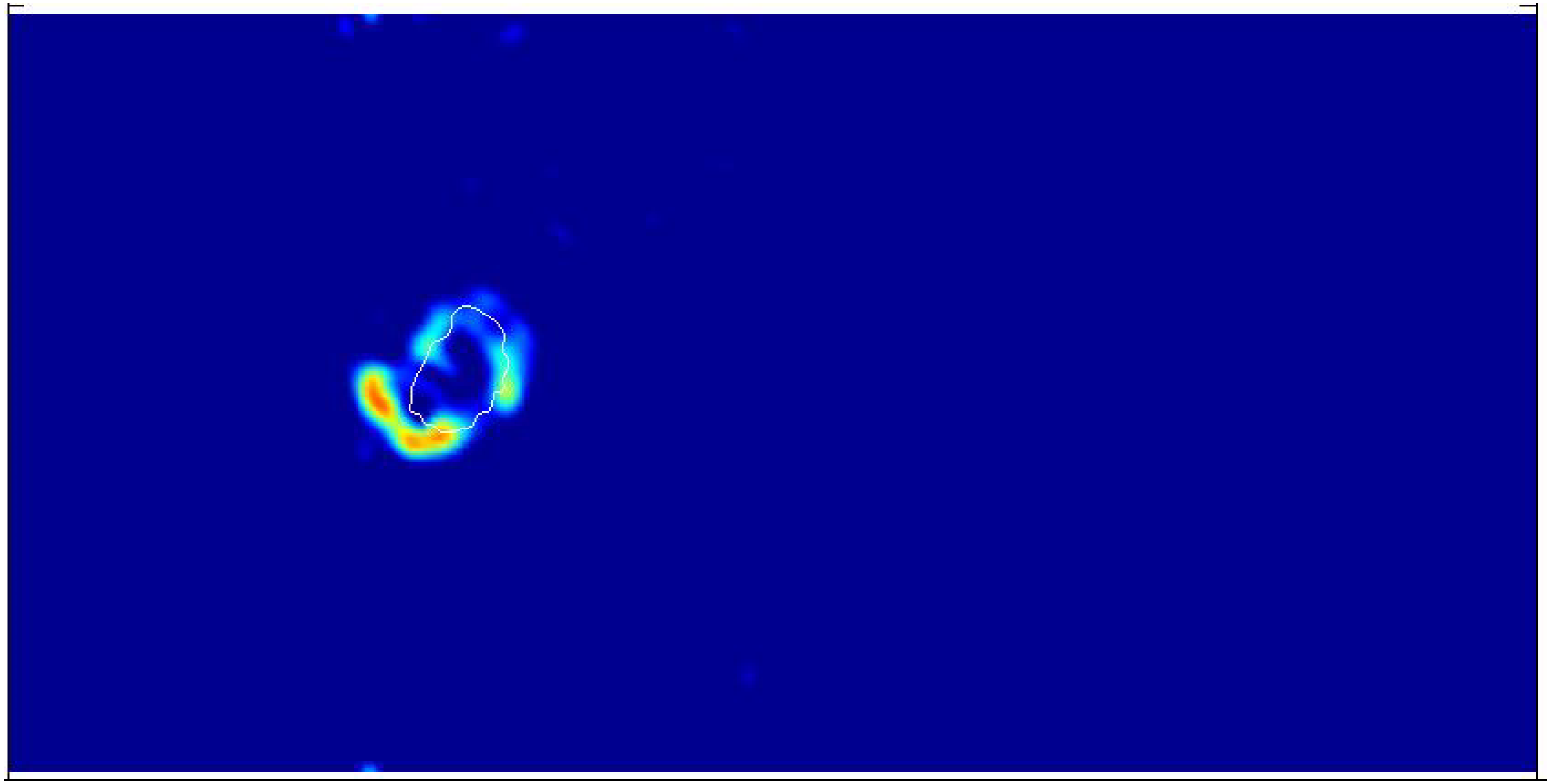
Substrate: poly-acrylamide gel (E=800Pa)
Bead: red (diameter 200nm, excitation 543nm)

Traction Force Microscopy 3



Improving measurement protocol, we measured the traction stress of migrating Dicty more than one hour with a better spatio-temporal resolution.

Highly localized traction stress 2



Traction stress amplitude | Lab-frame integration

The force spots are evident in the integrated plot.

- 'foot prints' of migrating cell.

Multi-pole expansion

$$M_i = \int T_i dS$$

0th moment: net force

Anti-mirror symmetric

$$M_{ij} = \int x_i T_j dS$$

1st moment: force dipole

Mirror symmetric

Multi-pole expansion

$$M_i = \int T_i dS$$

0th moment: net force

Anti-mirror symmetric

$$M_{ij} = \int x_i T_j dS$$

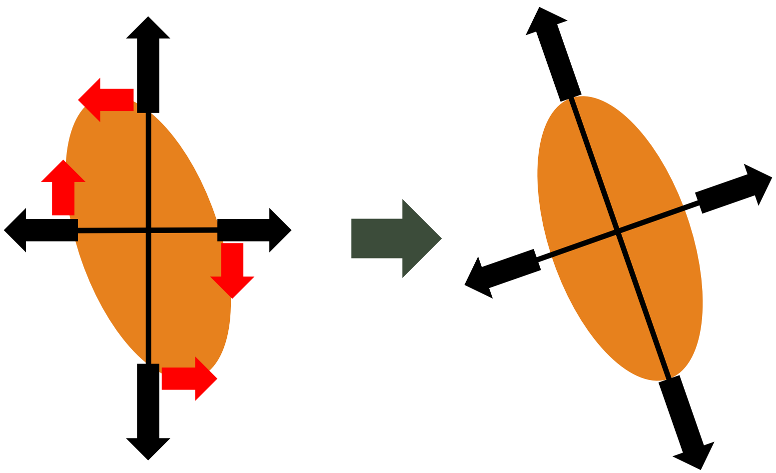
1st moment: force dipole

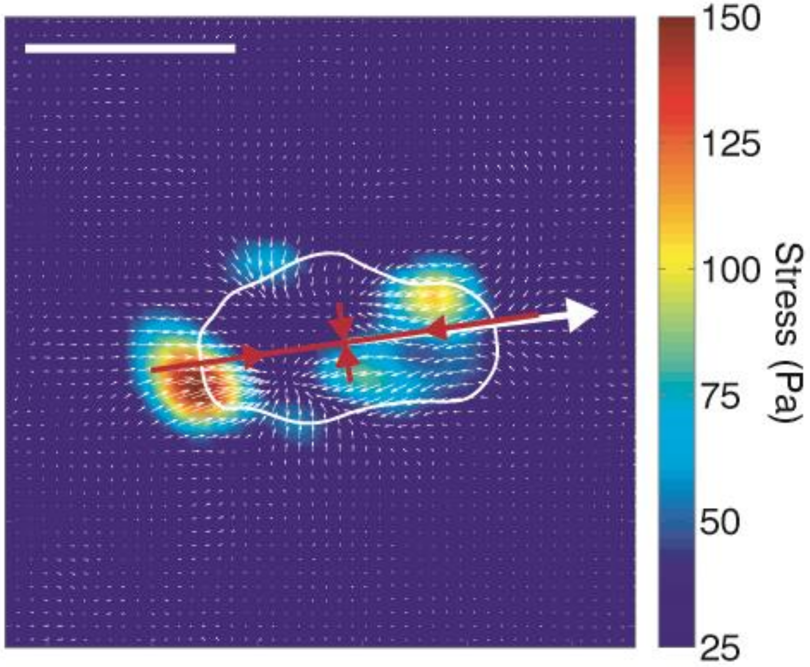
Mirror symmetric

Force Dipole → Deformation

Force dipole

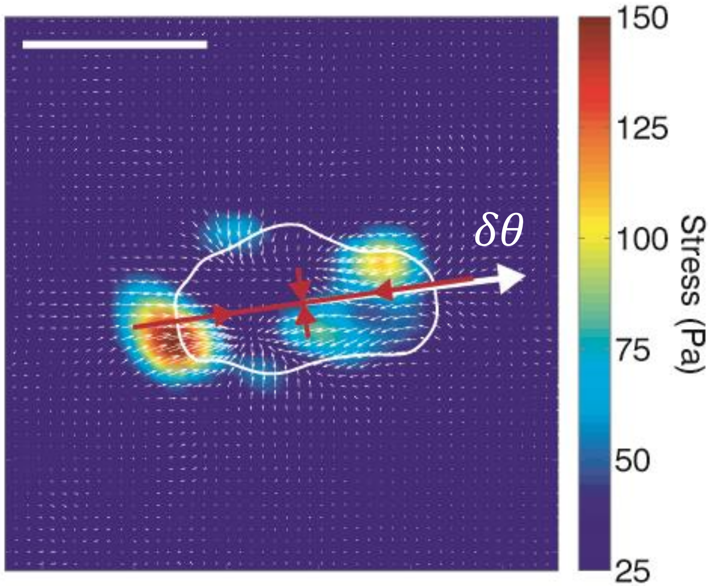
$$M = \begin{pmatrix} xT_x & xT_y \\ yT_x & yT_y \end{pmatrix}$$

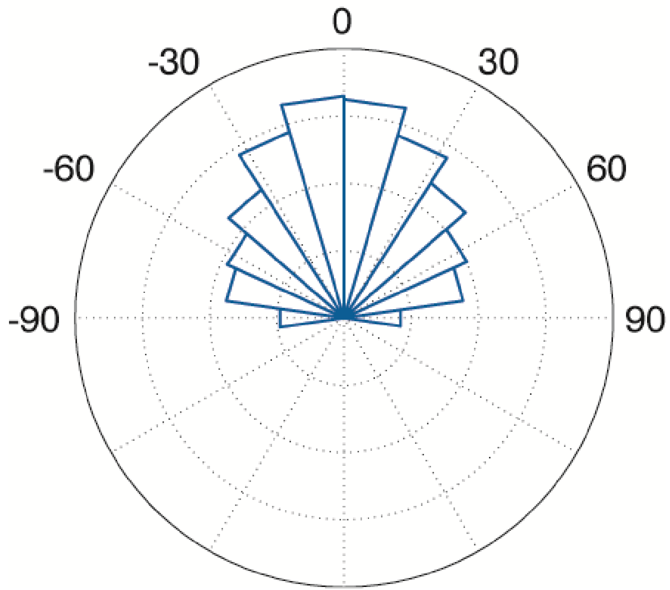




The force dipole is a 2*2 symmetric matrix with two orthogonal eigenvectors.

Force dipole
Relationship with motion





The dipole axis and cellular velocity orientation are agreed well.

- <u>Cell migrates along with its force dipole axis.</u>

Left: Snapshot (white arrow: velocity vector)
Right: PDF of angle formed by dipole and velocity axes (N=5; ~3000frames)

Multi-pole expansion

$$M_i = \int T_i dS$$

0th moment: net force

Anti-mirror symmetric

$$M_{ij} = \int x_i T_j dS$$

1st moment: force dipole

Mirror symmetric

Multi-pole expansion

$$M_i = \int T_i dS$$

0th moment: net force

Anti-mirror symmetric

$$M_{ij} = \int x_i T_j dS$$

1st moment: force dipole

Mirror symmetric

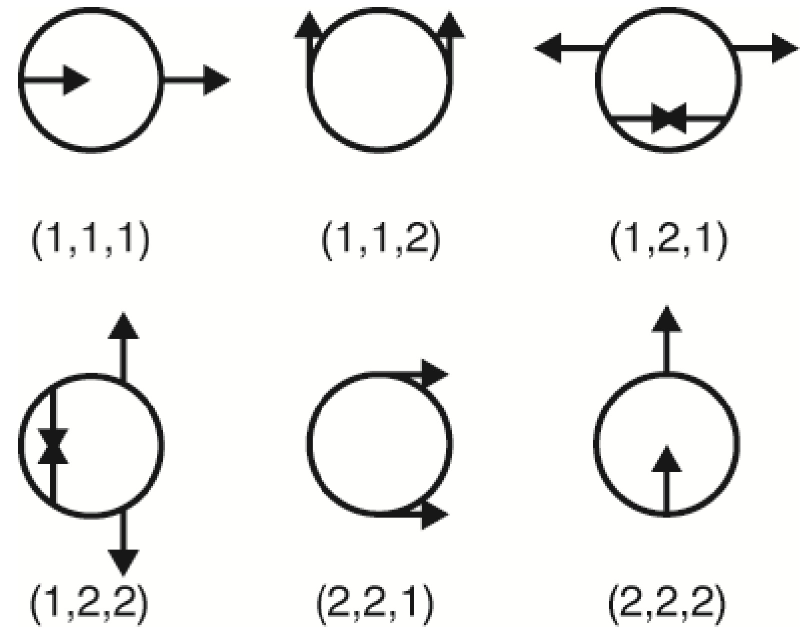
$$M_{ijk} = \int x_i x_j T_k dS$$

2nd moment: force quadrupole

Anti-mirror symmetric

Force quadrupole

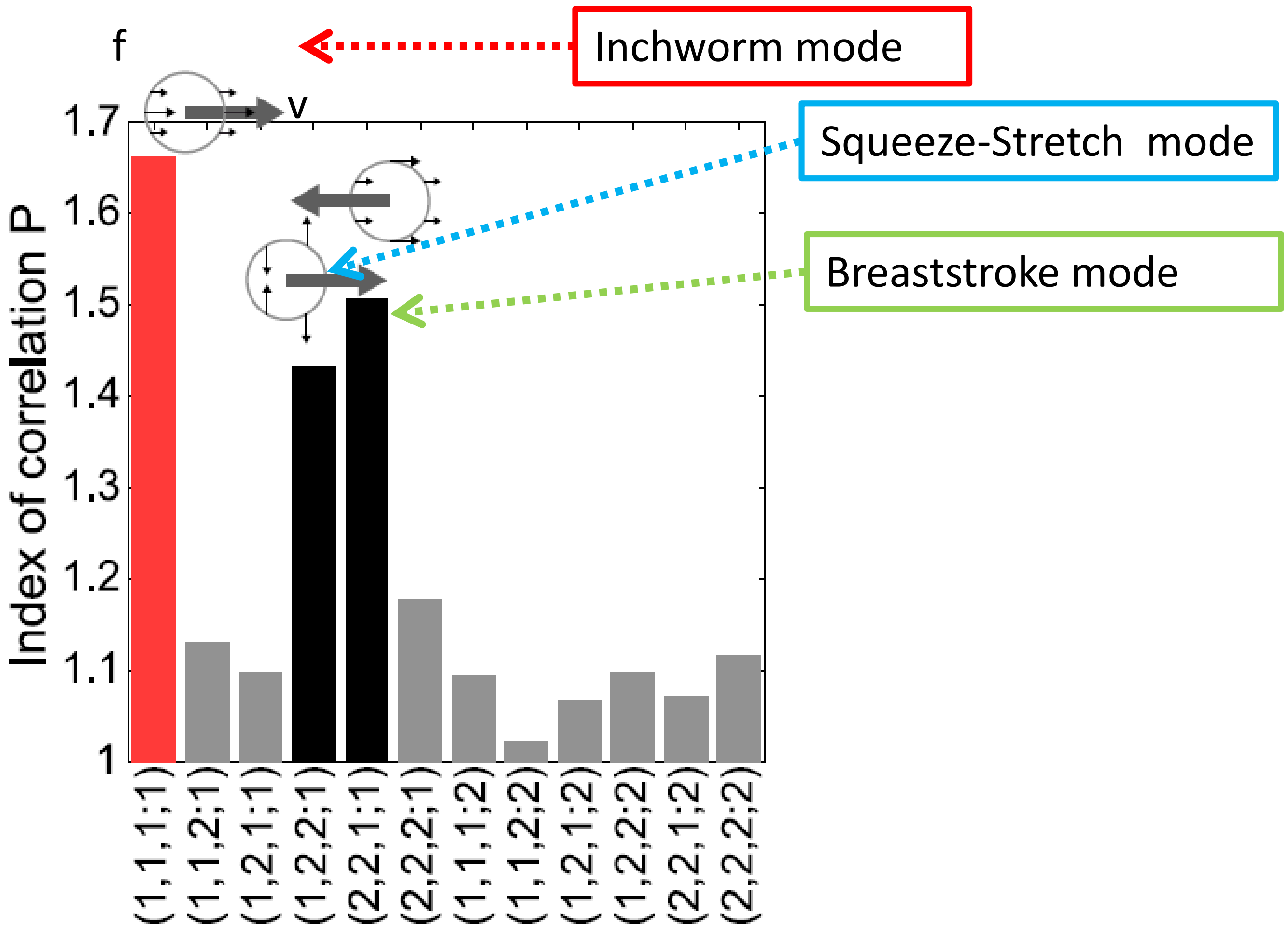
$$M_{ijk} = \int x_i x_j T_k dS$$



The force quadrupole is a 3rd order tensor with 6 independent components.

Force quadrupole
Relationship with motion

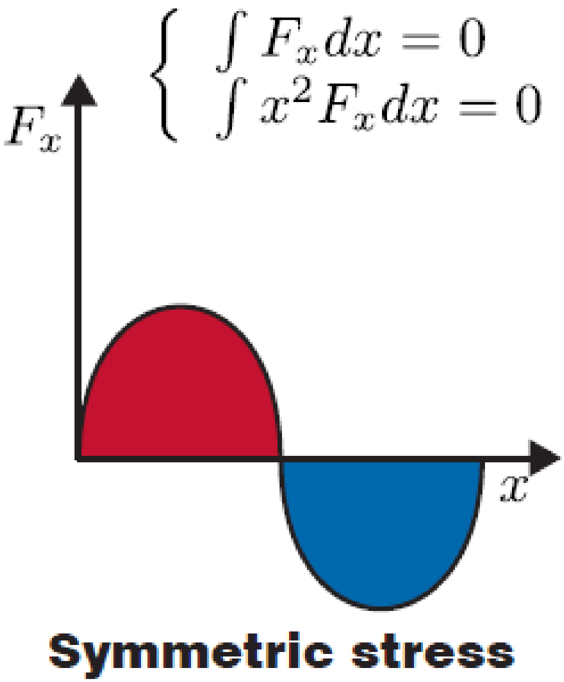
3 Different Modes
in Crawling Cells

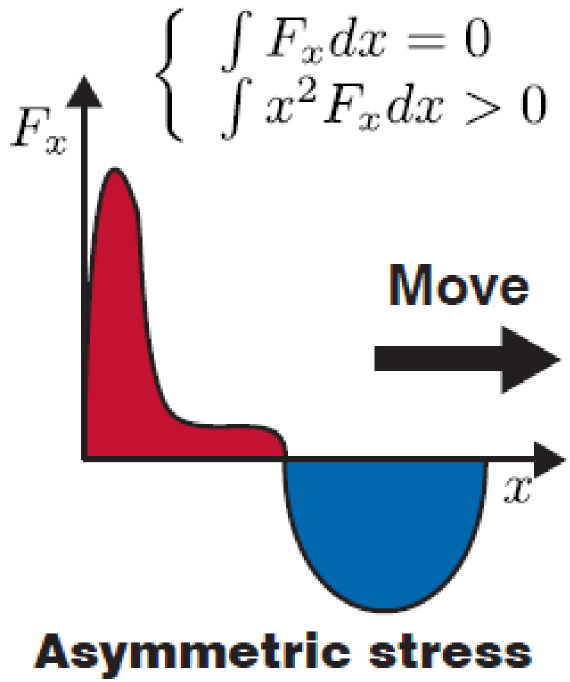


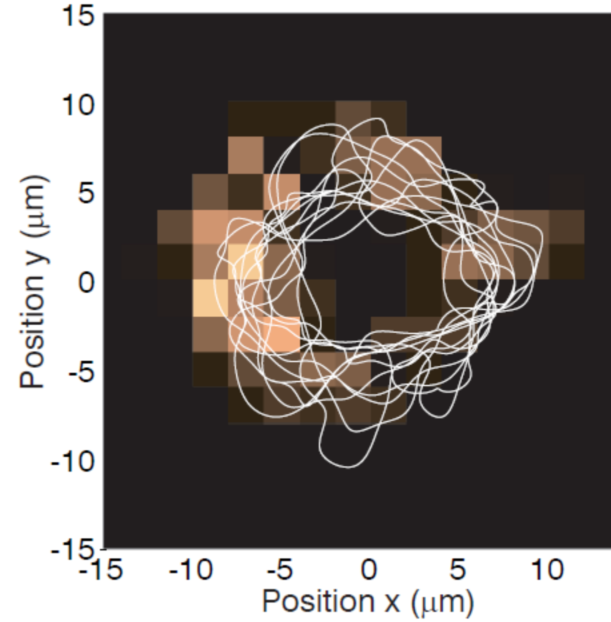
One strongly correlated pair: (1,1,1) and Vx

- <u>The sign of (1,1,1) determines the direction along the dipole axis.</u>

(1,1,1;1) correlation







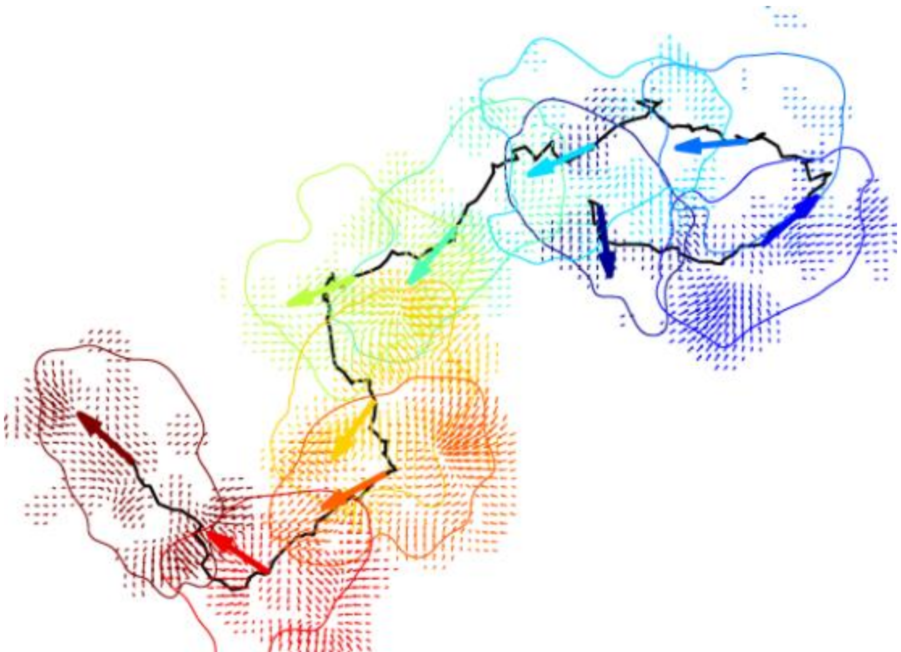
Symmetric stress pattern

Asymmetric stress pattern

Force quadrupole determines direction of migration

Predicting amoeboid motion of the cell

Multi-pole analysis reveals a simple force-motion relationship in cell migration

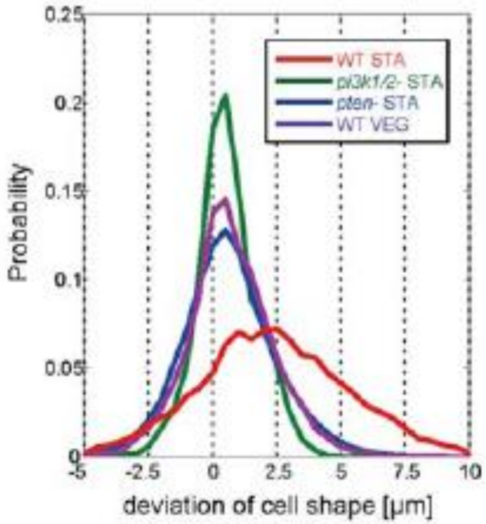


Normal equations for multi-pole traction force and shape is required.

$$\dot{u}_i = f(u_i, M_{ij}, M_{ij;k})$$
$$\dot{M}_{ij} = g(u_i, M_{ij}, M_{ij;k})$$
$$\dot{M}_{ij;k} = h(u_i, M_{ij}, M_{ij;k})$$

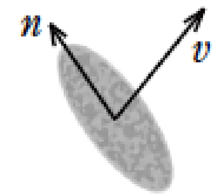
- The lowest two moments are coupled with
- Consistent with the force spot tracking

H. Tanimoto and MS, Biophys. J. 106, 16-25 (2014).
H. Tanimoto and MS, Phys. Rev. Lett. 109, 248110 (2012).

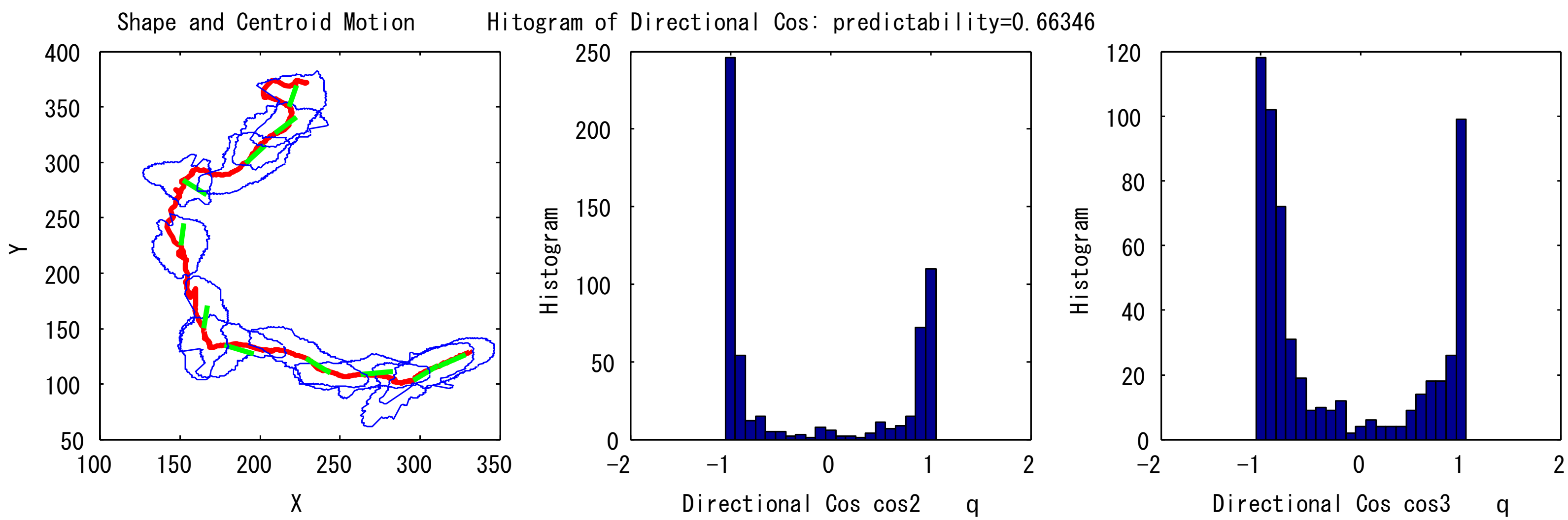


Correlation between Fourier modes and centroid velocity

M. Sano, unpublished



Fourier Expansion of Shape: $$r(\theta,t)=\sum_n a_n(t)e^{in\theta}$$

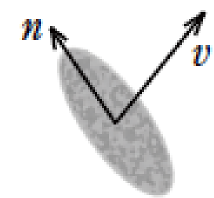


$\langle v\cdot a_1\rangle$ $\langle v\cdot a_3\rangle$

Deformable self-propelled particle

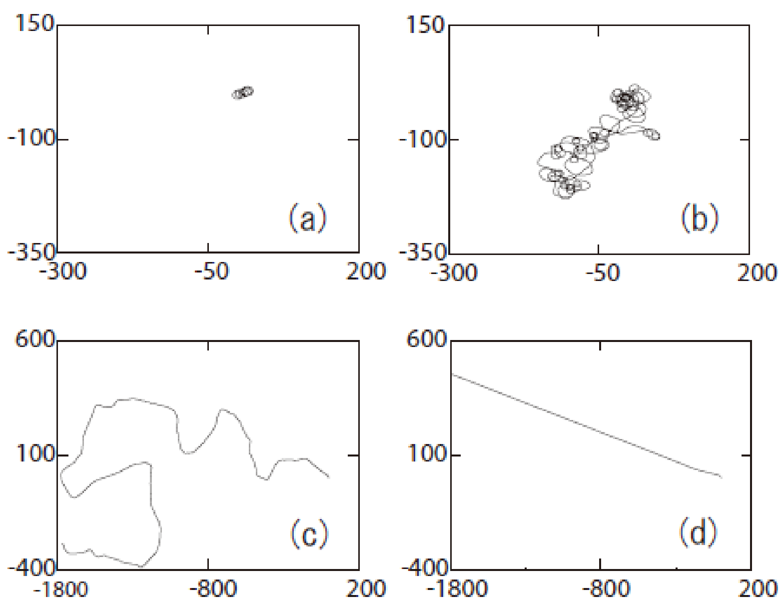
Ohta, Ohkuma PRL (2009)

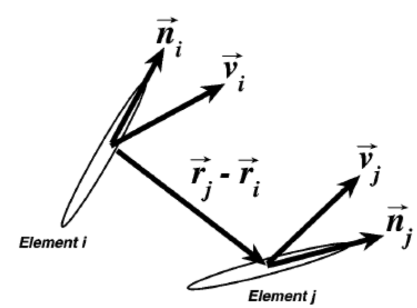
$$\frac{d}{dt}v_\alpha = \gamma v_\alpha - |v^2|v_\alpha - aS_{\alpha\beta}v_\beta$$



$$\frac{d}{dt}S_{\alpha\beta} = -\kappa S_{\alpha\beta} + b\left(v_\alpha v_\beta - \frac{1}{2}|v^2|\delta_{\alpha\beta}\right)$$

$$S_{\alpha\beta} = s\left(n_\alpha n_\beta - \frac{1}{2}\delta_{\alpha\beta}\right)$$





Introducing 3rd order rank tensors

$$
\begin{aligned}
\frac{d}{dt}U_{ijk} &= -\kappa_3 U_{ijk} - d_3(U_{\ell mn}U_{\ell mn})U_{ijk} \\
&+ d_1\left[v_i v_j v_k - \frac{v_\ell v_\ell}{4}(\delta_{ij}v_k + \delta_{ik}v_j + \delta_{jk}v_i)\right] \\
&+ \frac{d_2}{3}\left[S_{ij}v_k + S_{ik}v_j + S_{jk}v_i\right. \\
&- \left.\frac{v_\ell}{2}(\delta_{ij}S_{k\ell} + \delta_{jk}S_{i\ell} + \delta_{ki}S_{j\ell})\right] \\
&- d_4 v^2 U_{ijk} - d_5(S_{mn}S_{mn})U_{ijk} \\
&+ \frac{2d_6}{3}\left[S_{ij}S_{k\ell}v_\ell + S_{jk}S_{i\ell}v_\ell + S_{ki}S_{j\ell}v_\ell\right. \\
&- \frac{1}{2}(\delta_{ij}S_{nk}S_{n\ell}v_\ell + \delta_{jk}S_{ni}S_{n\ell}v_\ell \\
&+ \left.\delta_{ki}S_{nj}S_{n\ell}v_\ell)\right] .
\end{aligned}
$$

$$\boldsymbol{z}_1 = \boldsymbol{v}_1 - \boldsymbol{i}\boldsymbol{v}_2,$$

$$\boldsymbol{z}_2 = \frac{1}{2}(\boldsymbol{S}_{11} - \boldsymbol{i}\boldsymbol{S}_{12}),$$

$$\boldsymbol{z}_3 = \frac{1}{2}(\boldsymbol{U}_{111} + \boldsymbol{i}\boldsymbol{U}_{222})$$

Normal Form Equations

$$
\begin{aligned}
\dot{z}_1 &= f(z_1, z_2, z_3) \\
\dot{z}_2 &= g(z_1, z_2, z_3) \\
\dot{z}_3 &= h(z_1, z_2, z_3)
\end{aligned}
$$

Collective Behavior is much more rich !

Normal Form Equations

- Invariant under a transformation;

$$(z_1, z_2, z_3) \to (e^{i\theta} z_1, e^{2i\theta} z_2, e^{3i\theta} z_3) \ ,$$

$$\begin{aligned}
\dot{z_1} &= (\gamma + d_{11}|z_1|^2 + d_{12}|z_2|^2 + d_{13}|z_3|^2) z_1 \\
&+ e_{11}\bar{z_1} z_2 + e_{12}\bar{z_1}^2 z_3 + e_{13}\bar{z_2} z_3 + e_{14}\bar{z_3} z_2^2 \ ,
\end{aligned}$$

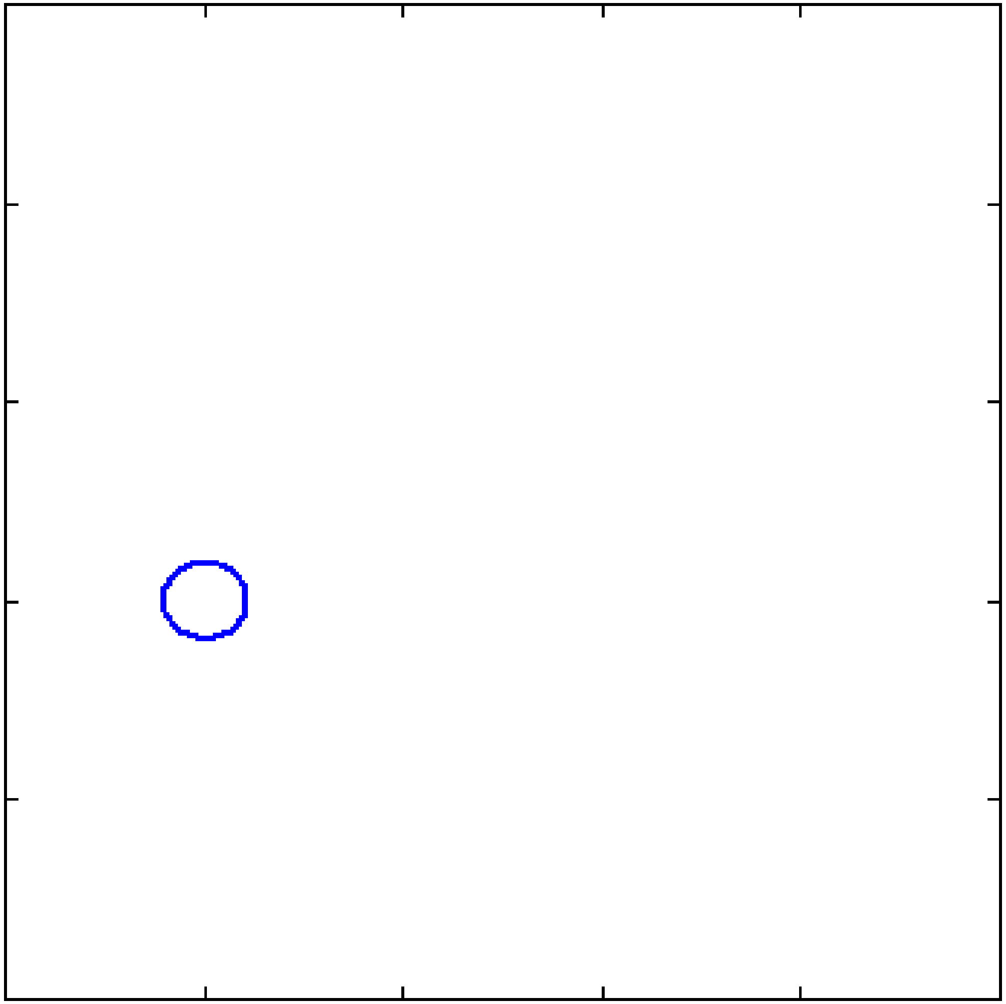
$$\begin{aligned}
\dot{z_2} &= (-\kappa_2 + d_{21}|z_1|^2 + d_{22}|z_2|^2 + d_{23}|z_3|^2) z_2 \\
&+ e_{21} z_1^2 + e_{22}\bar{z_1} z_3 + e_{23}\bar{z_2} z_3 z_1 \ ,
\end{aligned}$$

$$\begin{aligned}
\dot{z_3} &= (-\kappa_3 + d_{31}|z_1|^2 + d_{32}|z_2|^2 + d_{33}|z_3|^2) z_3 \\
&+ e_{31} z_1^3 + e_{32} z_1 z_2 + e_{33}\bar{z_1} z_2^2 \ ,
\end{aligned}$$

Hiraiwa, Matsuo, Ohkuma, Ohta, Sano, EPL (2010).

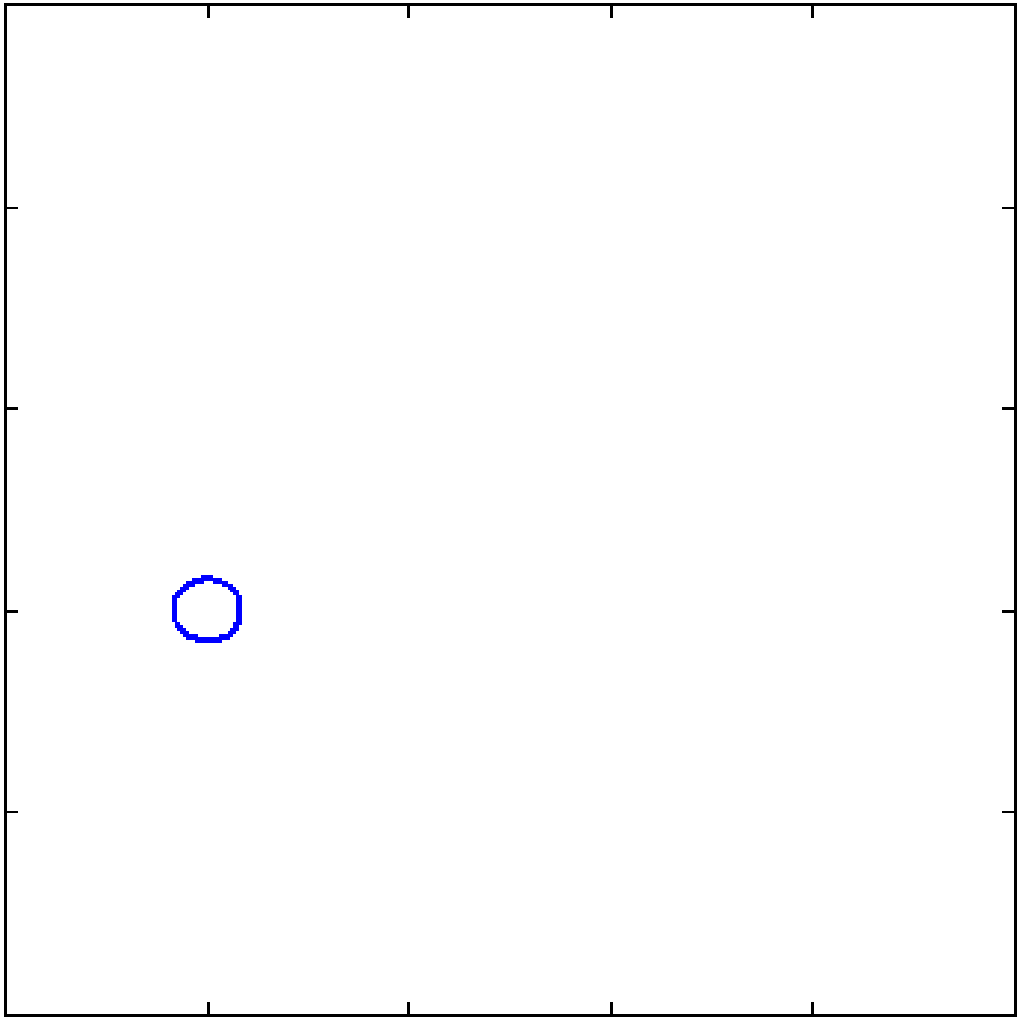
Straight motion

Ohta-Ohkuma model



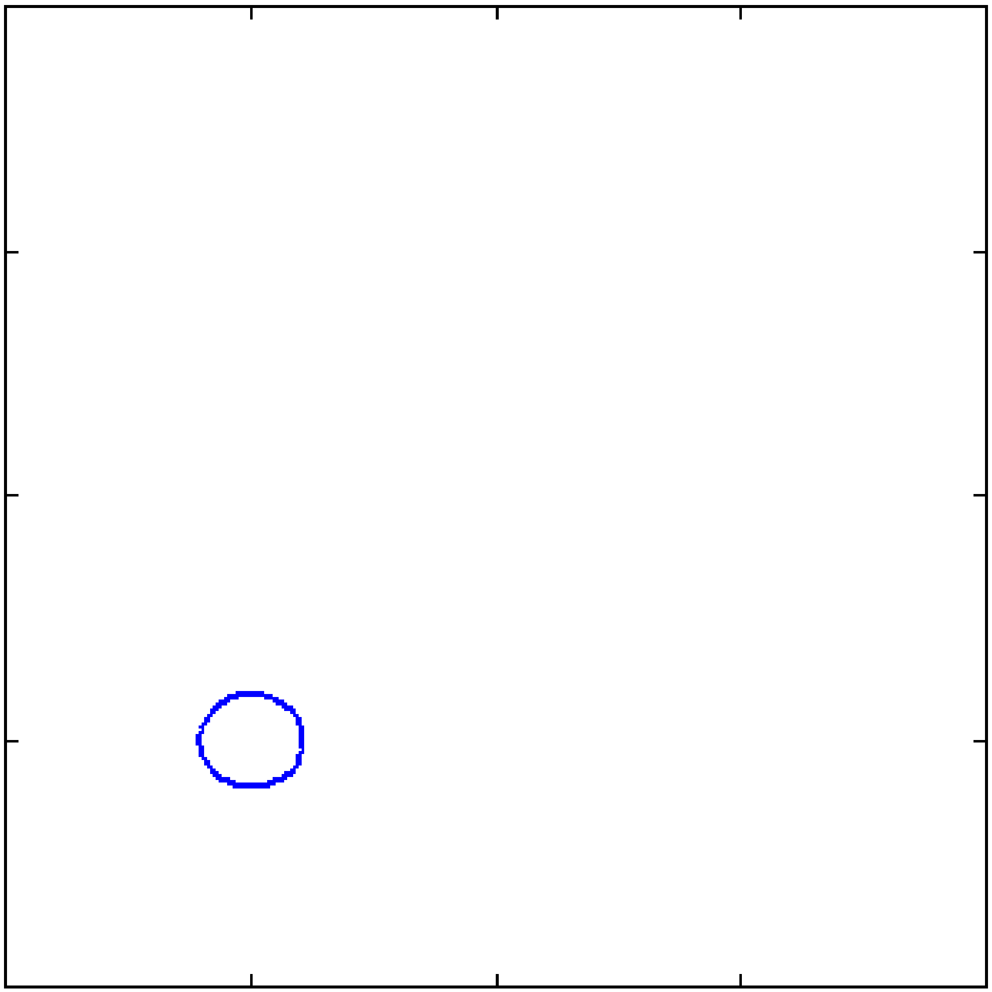
Zig-zag motion

Ohta-Ohkuma model



Chaotic motion

Ohta-Ohkuma model



Non-polarized cell (Vegetative Cell)

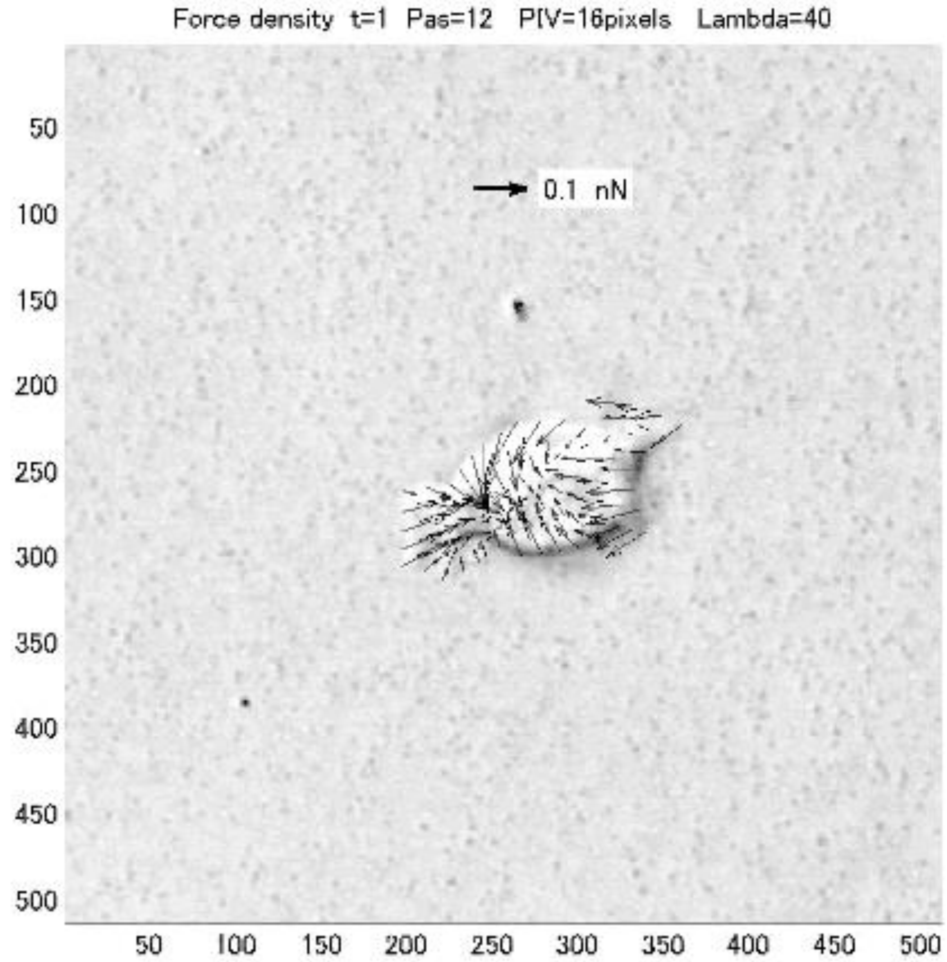
Traction force of migrating cell

Dicyostelium cell

In two states:

1. Starved state

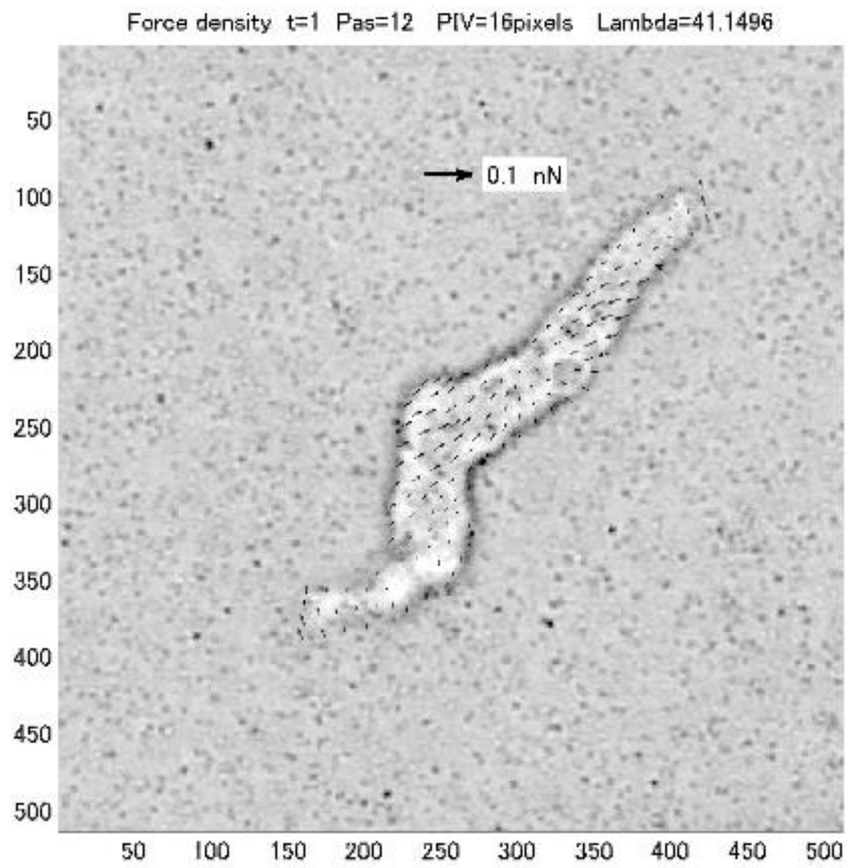
2. Vegetative stated



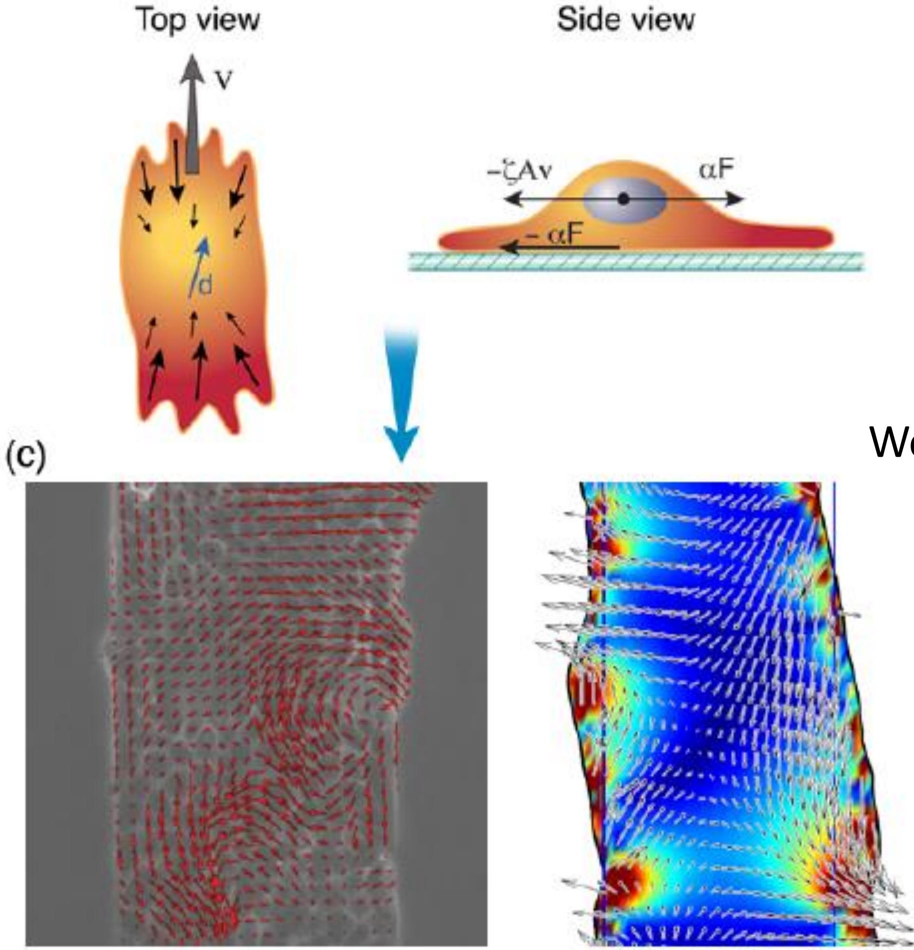
Force Distribution

Traction force of migrating cell

Polarized cell (Starved Cell)



Single Cell motility to Collective Motion



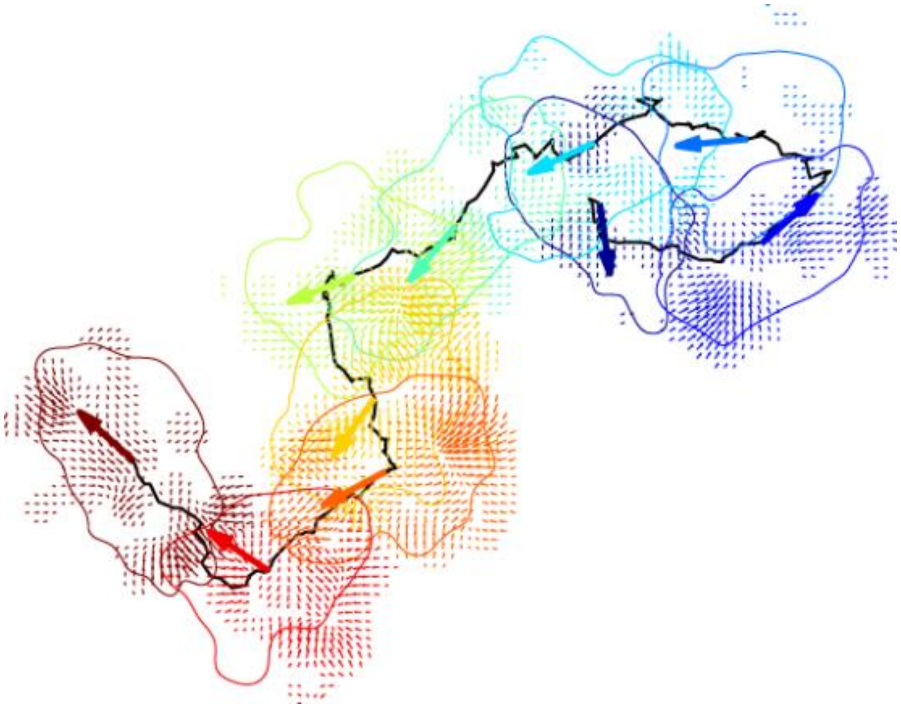
Wound healing

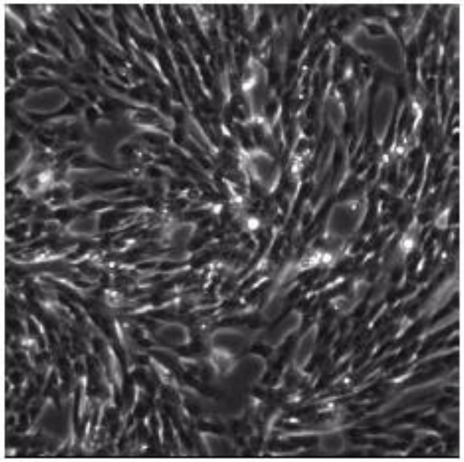
C.W. Wolgemuth, Physics 4, 4 (2011)

Short Summary

1. Multi-pole analysis reveals a simple force-motion relationship in cell migration

2. Collective motion of NS cells can be analyzed by nematicaly interacting moving (active nematic) material





- The lowest two moments are coupled with cell migration
- Consistent with the force spot tracking

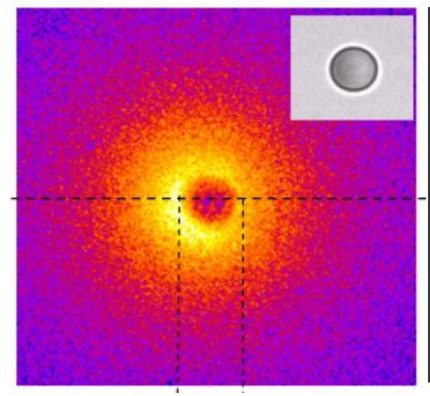
What are active colloids?

Self-propelled colloid:

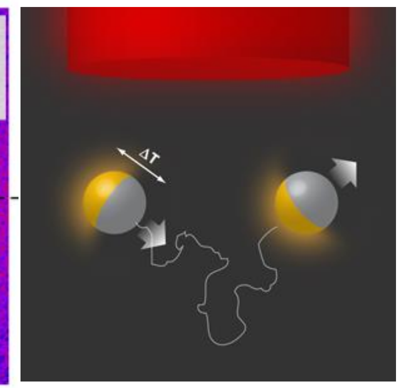
Self-propelled Janus particles moving their own directions

- By a local temperature gradient

  Self-Thermophoresis



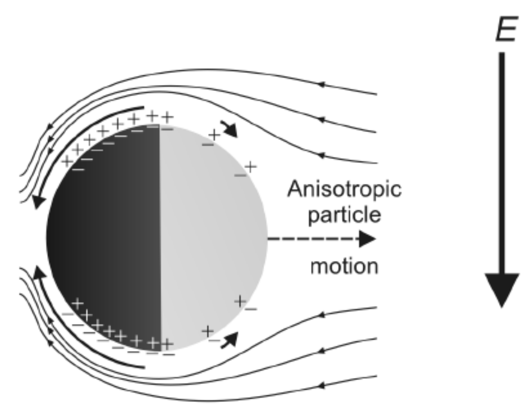
Jiang, Yoshinaga, Sano, PRL (2010)



APS Physics Viewpoint(2010)

- By electric field:

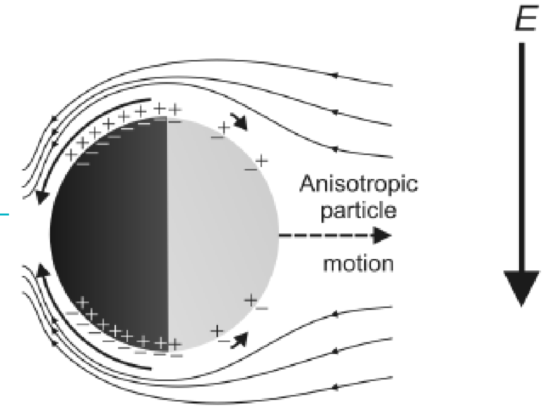
  Induced Charge Electro-Osmosis (ICEO)



Gangwal et al. PRL (2008)

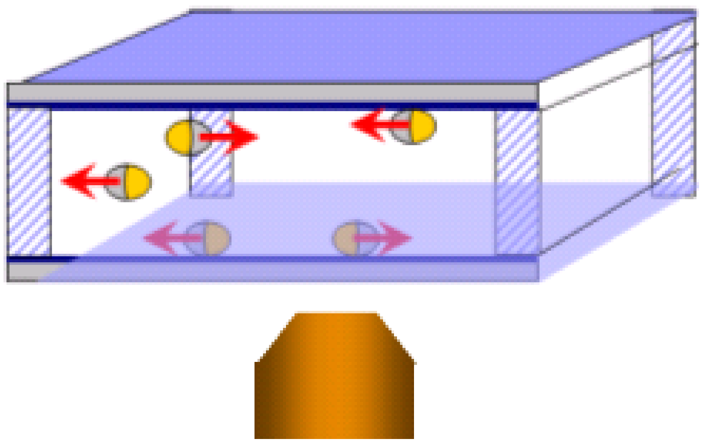
Self-propulsion of Janus particle II : by Electric field

ICEO (Induced Charge Electro Osmosis)

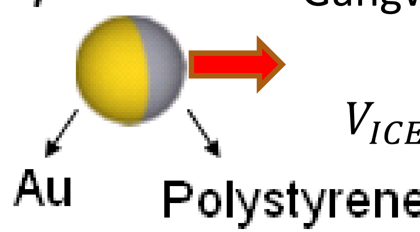


Gangwal et al. PRL (2008)

(a)



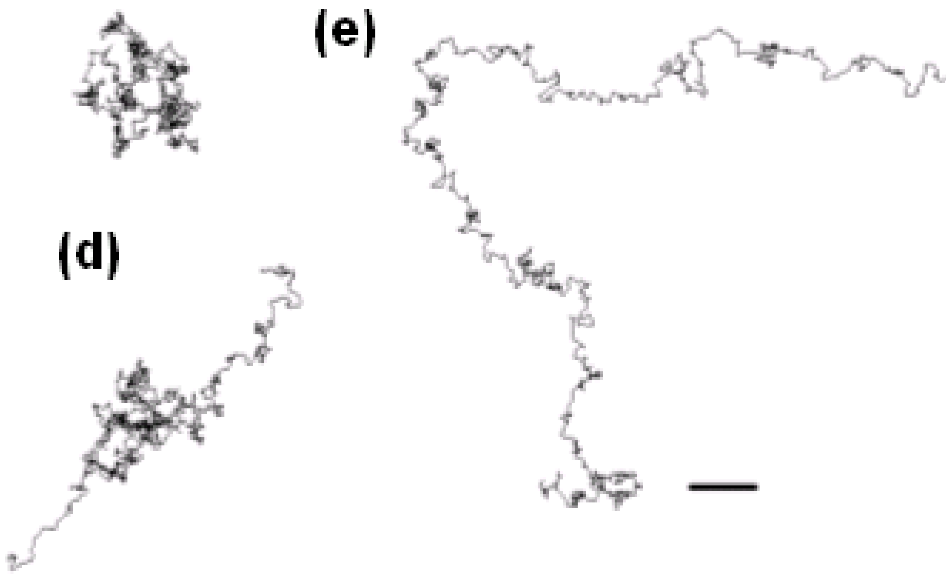
(b)



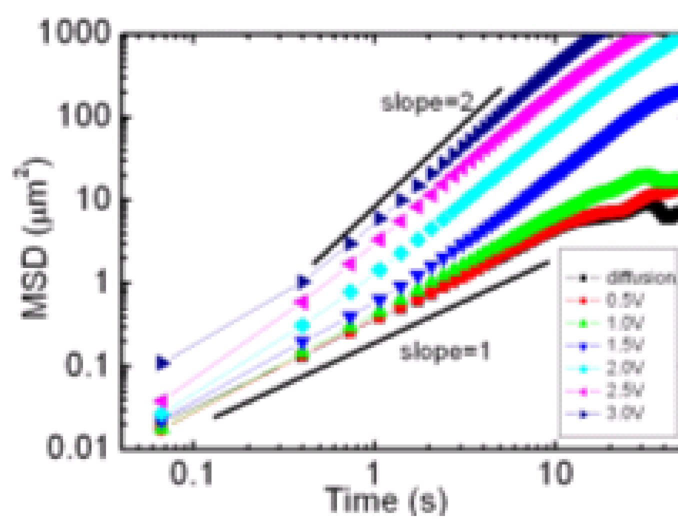
$$V_{ICEO} \sim \frac{\epsilon \varepsilon R E^2}{\gamma}$$

$$\langle \Delta r^2 \rangle \approx 4Dt + V^2 t^2$$

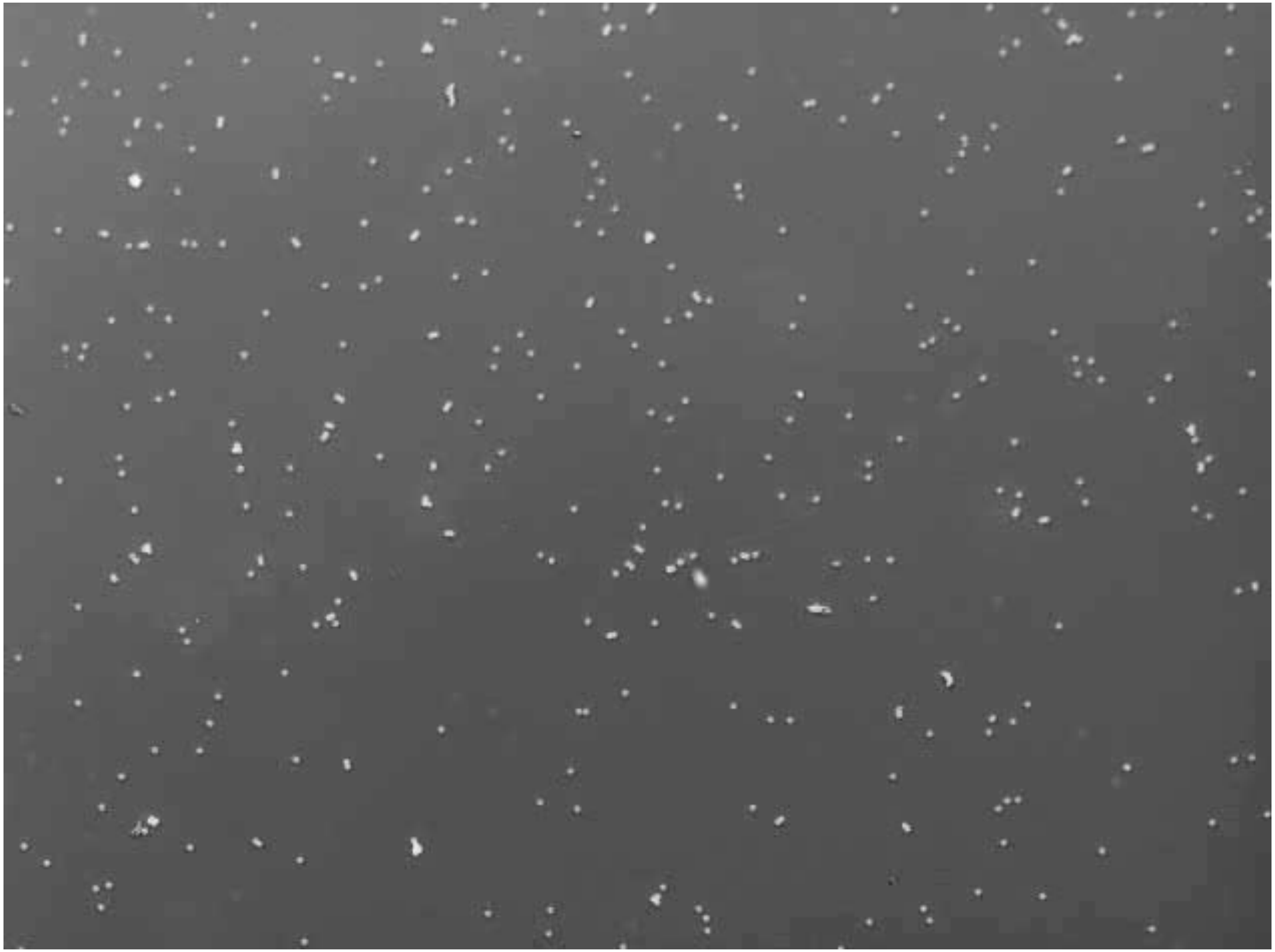
(c) (d) (e)



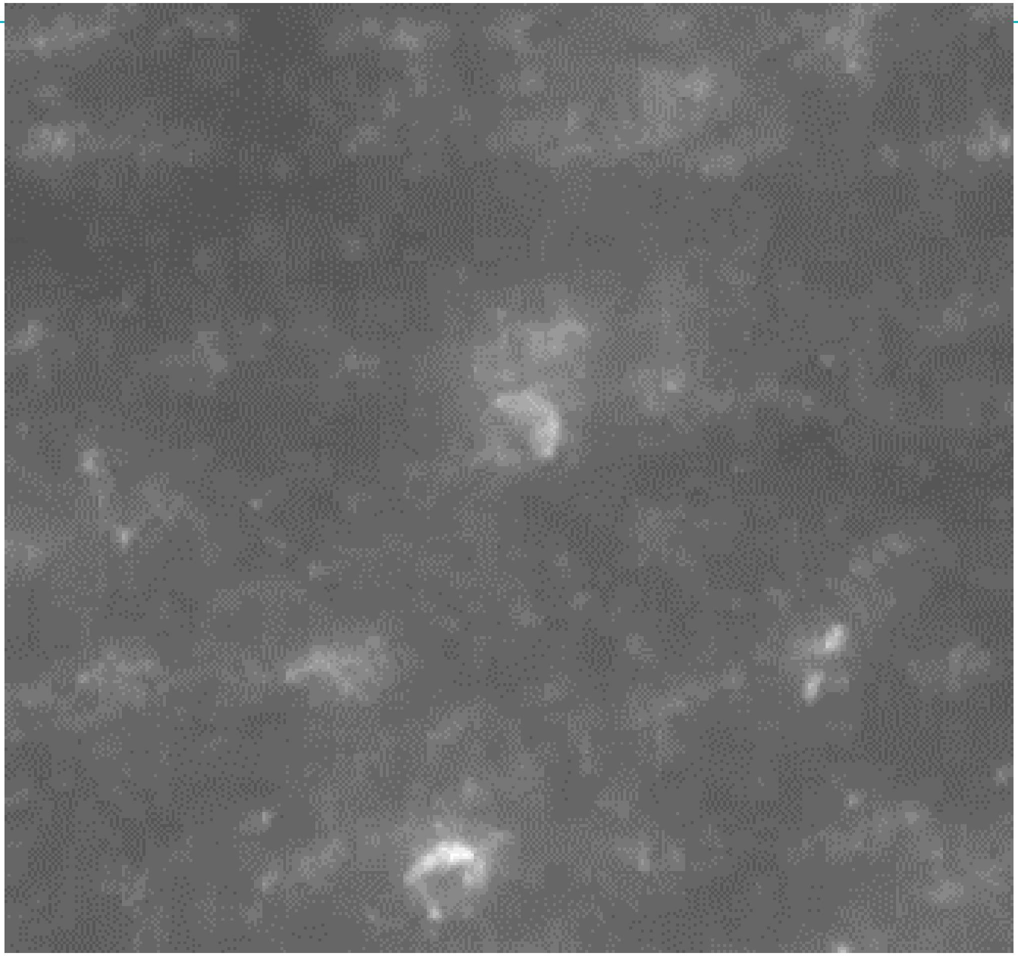
(f)

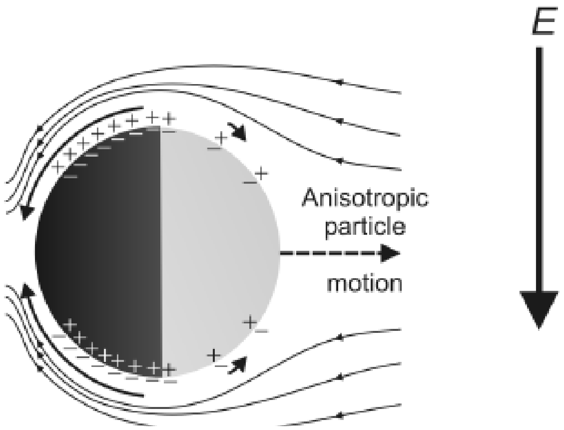


Motion of Janus Particle: Top View



Surface slip flow drives particle

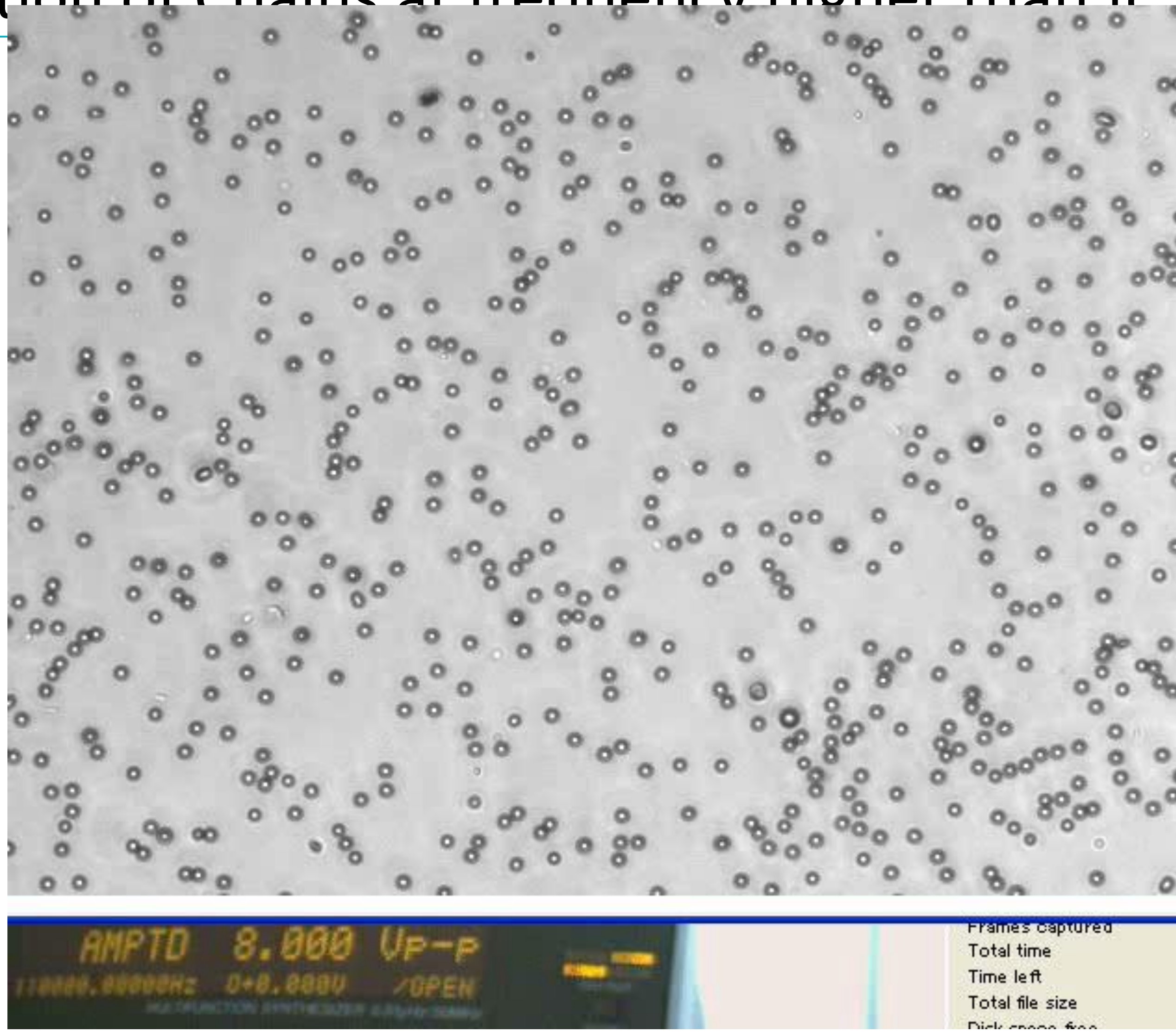


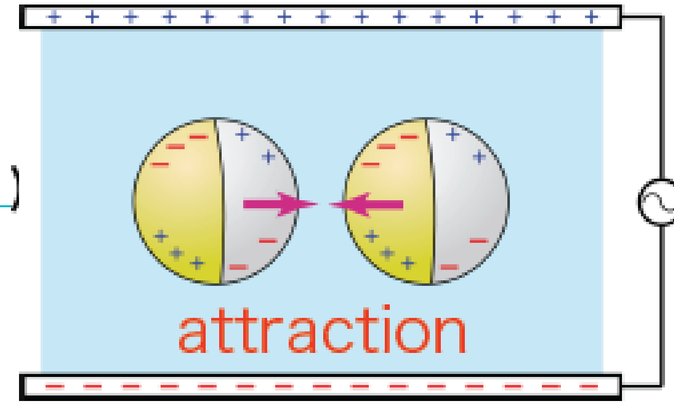


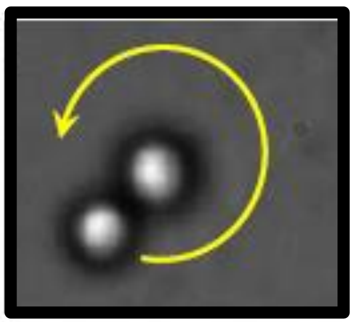
Visualization: Tracer particle 200nm fluorescent beads

Janus Particle: 6 μm

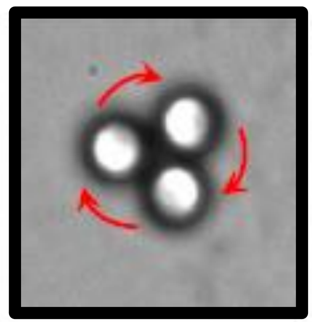
Formation of Chains at frequency higher than fc



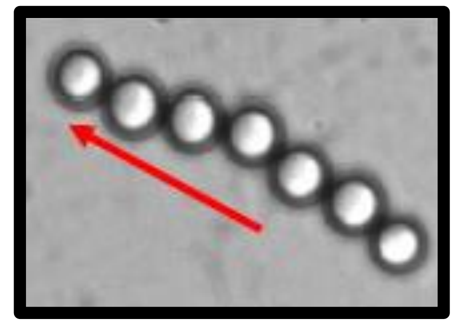




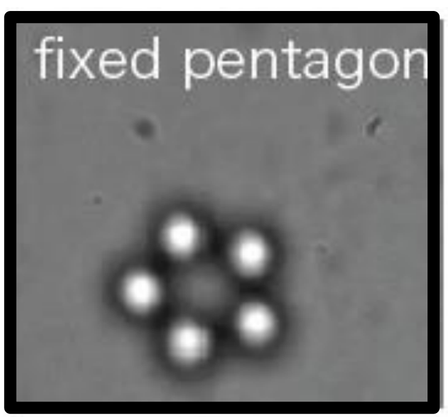
Doublet

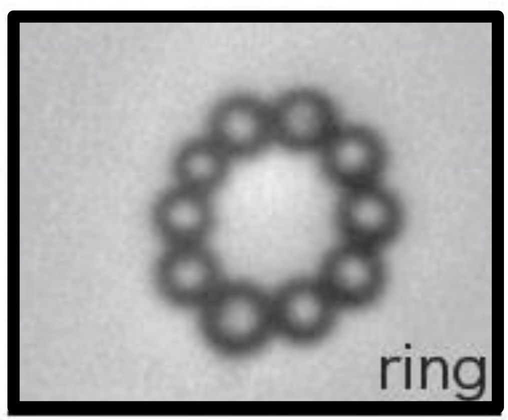


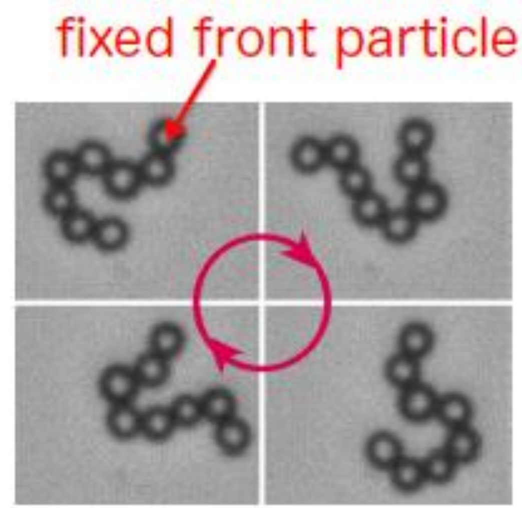
Triplet



Linear Chain

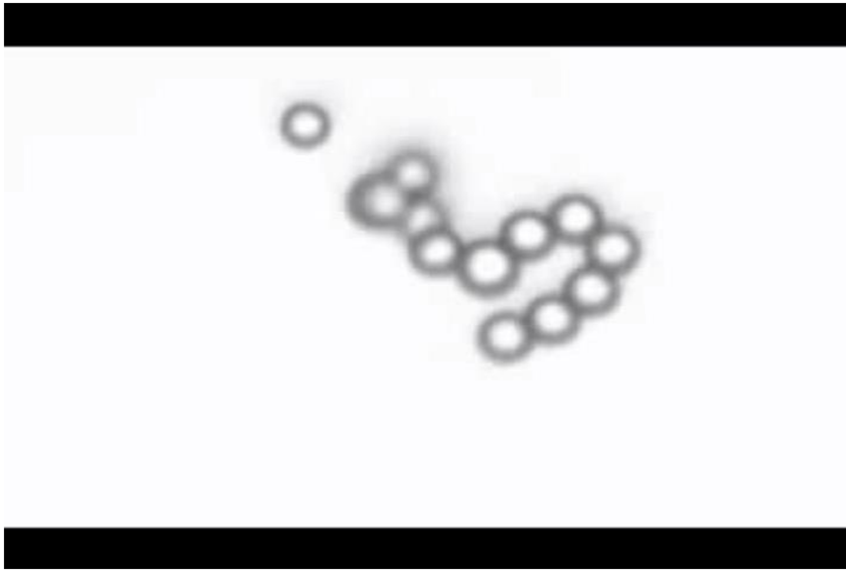






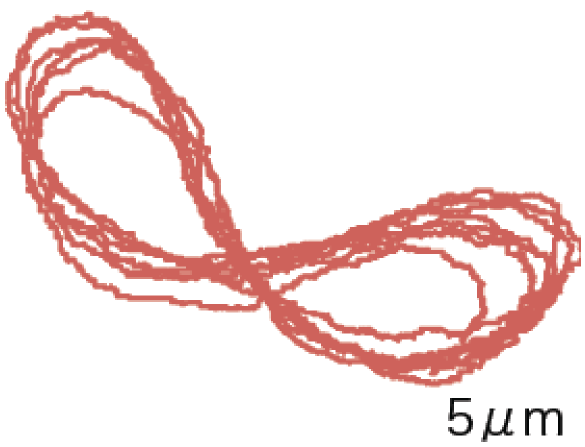
Oscillation, Wave

Deformable self-propelled chain

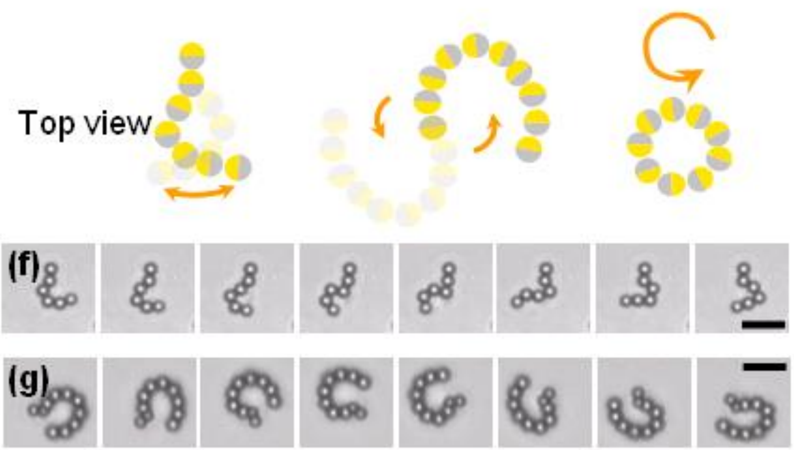


Waving motion

Spiraling motion



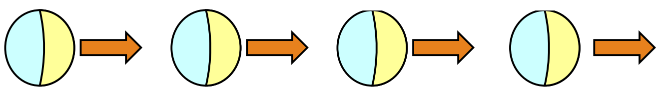
Trajectory of the tail particle



Problem of self-propelled flexible chain

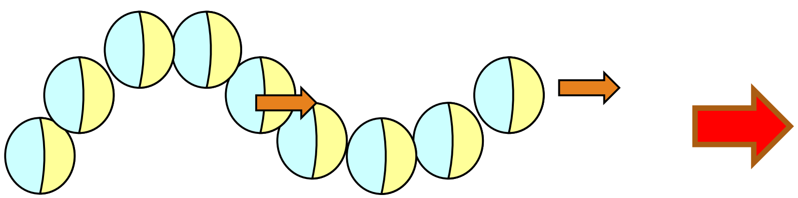
Self-propelling force

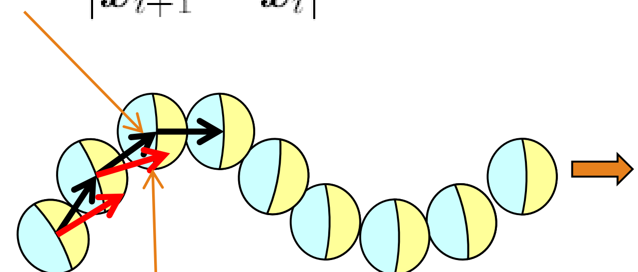
$\boldsymbol{P}_i$: Porality



$\boldsymbol{x}_i$: position of the particle

$$\boldsymbol{u}_i \equiv \frac{\boldsymbol{x}_{i+1} - \boldsymbol{x}_i}{|\boldsymbol{x}_{i+1} - \boldsymbol{x}_i|} \quad : \text{unit vector}$$



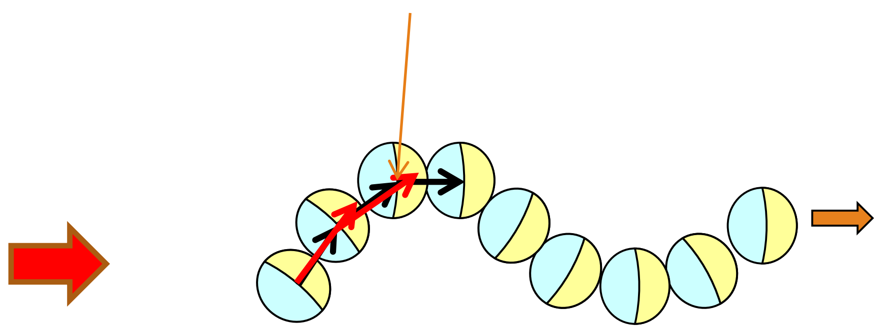


Self-propelled string

Continuum approximation

$\boldsymbol{P} \neq \boldsymbol{u}$

$\boldsymbol{P}_i$: Porality



$\boldsymbol{P} \,//\, \boldsymbol{u}$

Self-propelled (swimming) string

Motion of active filaments

$$\zeta \frac{d\boldsymbol{r}_i}{dt} = \boldsymbol{F}_i$$

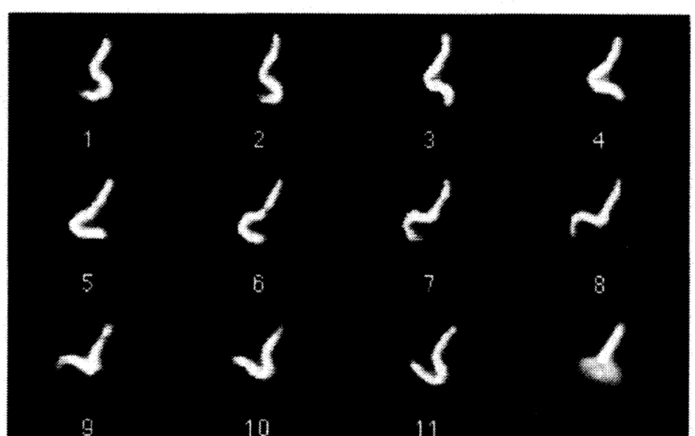
$$\boldsymbol{F}_i = (T_i \boldsymbol{u}_i - T_{i+1}\boldsymbol{u}_{i+1}) + f_0 \boldsymbol{u}_i + B(\boldsymbol{u}_{i-1} - 3\boldsymbol{u}_i + 3\boldsymbol{u}_{i+1} - \boldsymbol{u}_{i+1}) + \eta_i$$

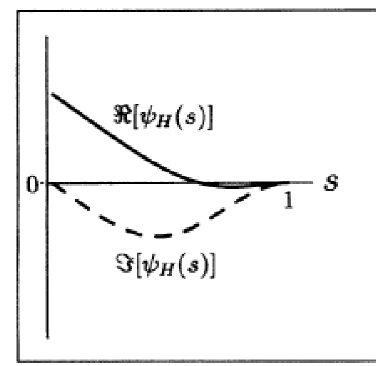
$$\zeta_\perp \frac{\partial u_\perp}{\partial t} = -B\frac{\partial^4 u_\perp}{\partial s^4} - f_0 s \frac{\partial^2 u_\perp}{\partial s^2}, \; 0 < s < \ell \,,$$

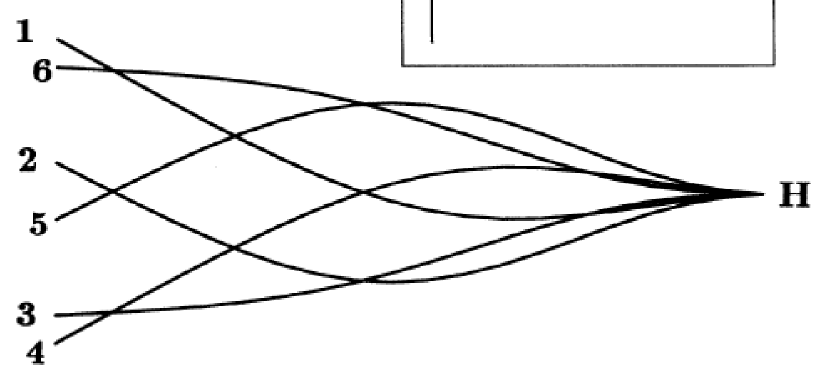
K. Sekimoto, PRL (1995)

Motion of actin filaments on myosin bed.

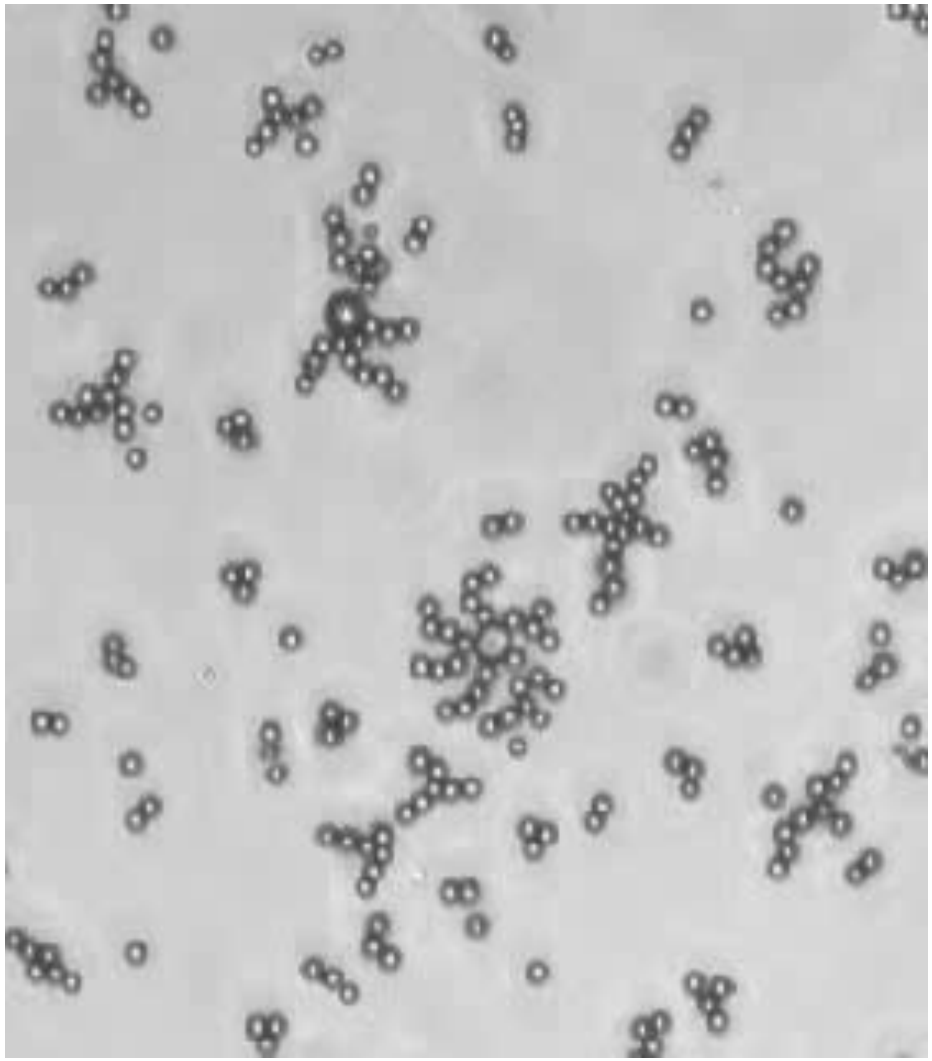
Bourdieu, Leibler, Libchaber, PRL (1995)







Emergent dynamics of self-propelled string with cargo



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