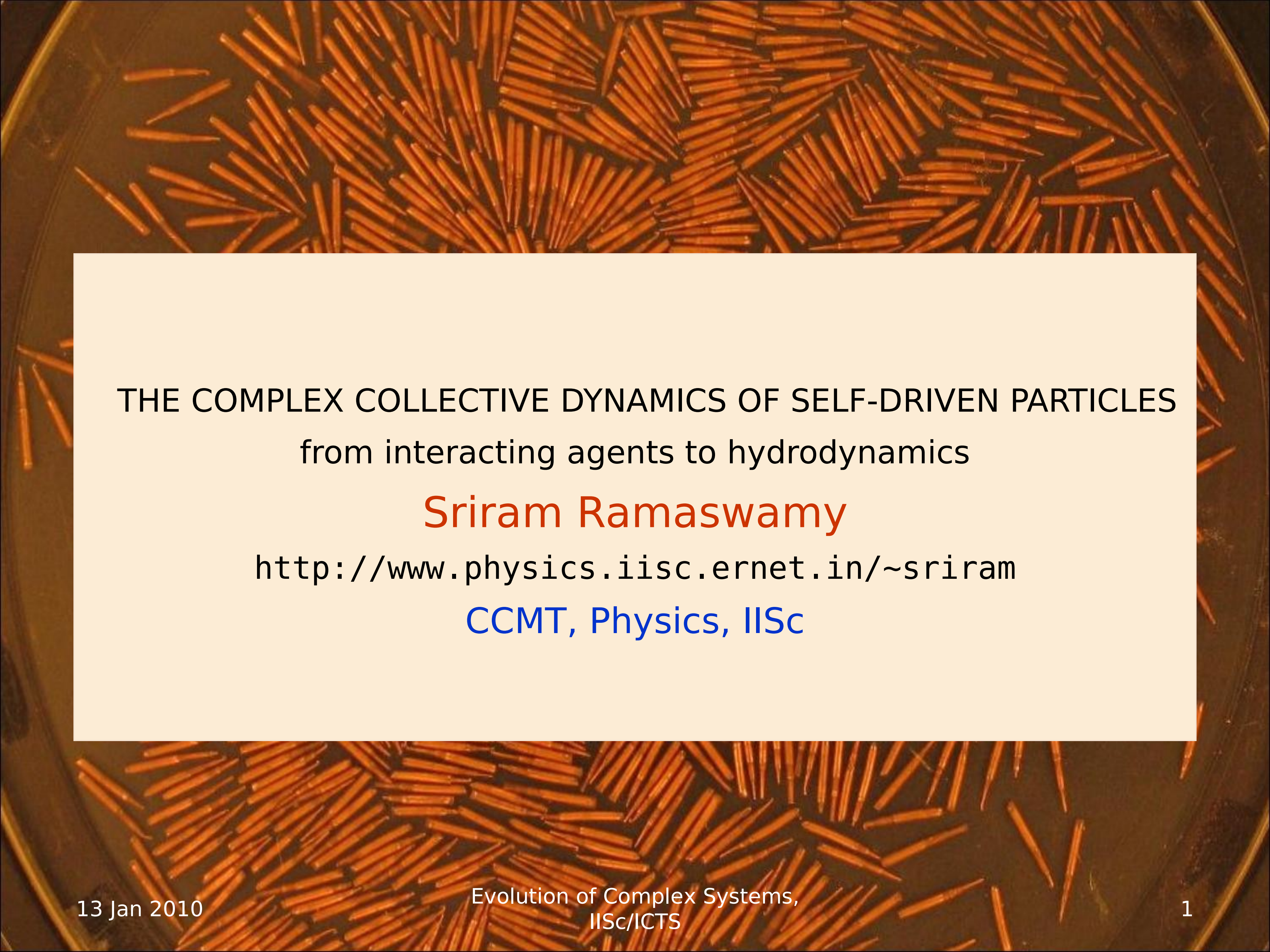


THE COMPLEX COLLECTIVE DYNAMICS OF SELF-DRIVEN PARTICLES

from interacting agents to hydrodynamics

Sriram Ramaswamy

`http://www.physics.iisc.ernet.in/~sriram`

CCMT, Physics, IISc

OUTLINE

- Background
  - self-driven particles
  - who should care and why

- Summary of results
  - theory, simulation
  - experiments: living & nonliving

- How we got these results
  - interacting agents and flocking models
  - self-driven hydrodynamics
  - tabletop experiments, simulations
  - self-propelled elastic dimer

- Prospect
  - where do we go from here? Evolution?

Students, collaborators and support

Sumithra Sankararaman
Norio Kikuchi

IISc Centenary
POST-DOCTORAL
FELLOWSHIP

DST Math-Bio Centre
SR/S4/MS:419/07

Tapan Adhyapak, K Vijay Kumar
Ananyo Maitra, Saroj Nandi
Suropriya Saha
Shradha Mishra (Syracuse)
Vijay Narayan (Cambridge)
Aditi Simha (IITM)
Y Hatwalne (RRI), G Menon (IMSc)
M Rao (RRI/NCBS), JF Joanny (Curie)
D Lacoste, J Prost (ESPCI)

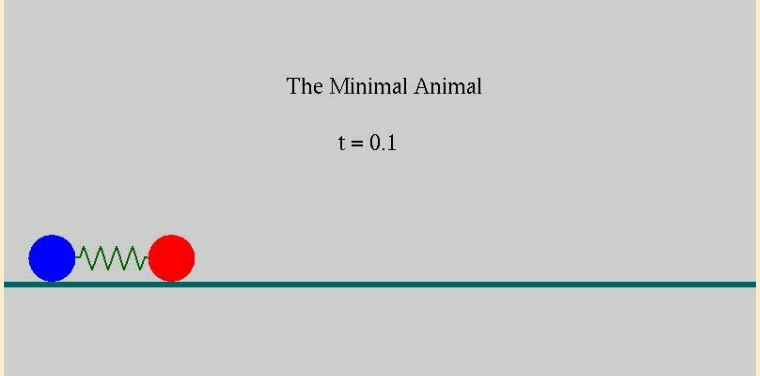
Council of Scientific and Industrial Research
Serve the Nation

Department of Science & Technology
Ministry of Science & Technology

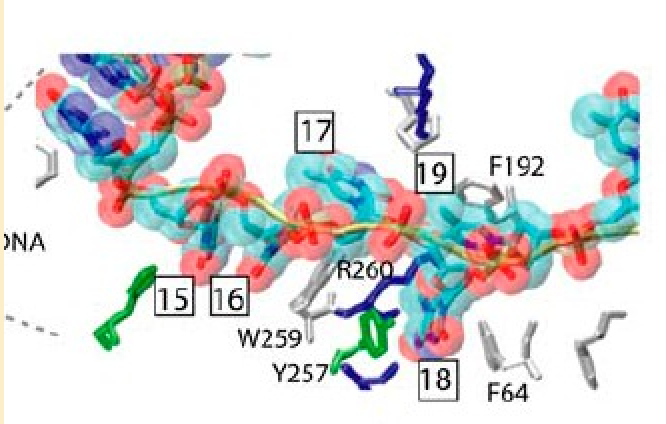
CEFIPRA | IFCPAR

N Menon (Amherst), H Chaté (Saclay), F Ginelli (Inst Sys Complexes)
D Marenduzzo (Edinburgh), S Puri (JNU), J Toner (Oregon),
M C Marchetti (Syracuse), T B Liverpool (Bristol)

BACKGROUND: SELF-DRIVEN PARTICLES



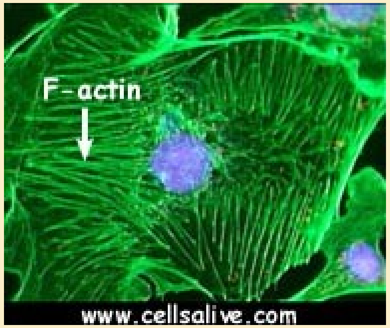
K Vijay Kumar *et al.* PRE **77** (2008) 020102 R



PcrA helicase: Yu *et al.*, Biophys J **91** (2006) 2097

Fuel in
Free energy dissipated
Internal coordinate cycles
Reaction products out
Result: translation, rotation, pulsation…

Organized states of self-driven particles



CYTOSKELETON `http://www.cellsalive.com/cells/cellpix/cytosk2.jpg`

MYXOBACTERIAL SWARM
`www.bio.indiana.edu/img/app-profiles/`
`gvelicer/velicer_swarming_EM.jpg`

What’s this?

BIRDS `http://www.bbc.co.uk/iplayer/`
`images/clip/p00381fg_126_71.jpg`

FISH: `http://i.dailymail.co.uk/i/pix/2009/08/07/`
`article-0-05FBBBB2000005DC-727_634x392.jpg`

Who should care and why

- Physicists, engineers, materials scientists
  - new kind of matter, new laws
  - order, fluctuations and response?
  - phases and phase transitions
  - uses: stirring, pumping, swarming
  - inanimate mimics of active matter?

Who should care and why

- Cell biologists, biochemists, ethologists
  - collective dynamics of motors
  - single and collective cell mechanics
  - Biofilms, quorum sensing
  - tissue mechanics and growth
  - animal flocks, swarms, migration

Who should care and why

- Complex systems scientists
  - Emergent complex behaviour
  - Patterns, instabilities, chaos
  - Unexpected links between disciplines

SUMMARY OF RESULTS

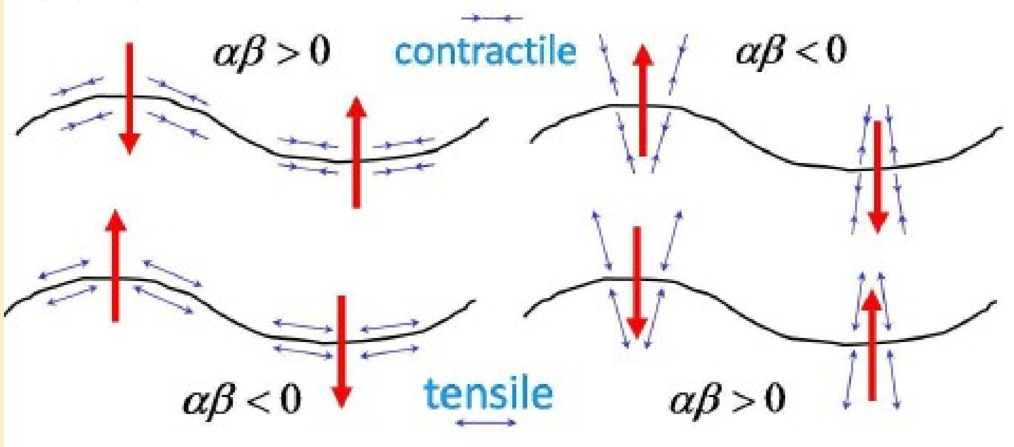
complex dynamics in or near ordered state

- Filament amidst self-driven particles: negative dissipation
- Strong tendency towards high inhomogeneity
- Rods on vibrated surface self-propel: test-bed for theories
- Self-propelled elastic dimer: model for helicase?
- Swimming affects viscosity: experiments!

SR – Annual Review of Condensed Matter Physics 2010 to appear

- Bacteria can't swim straight: turbulence at Re = 0

Tense filament as probe of active medium

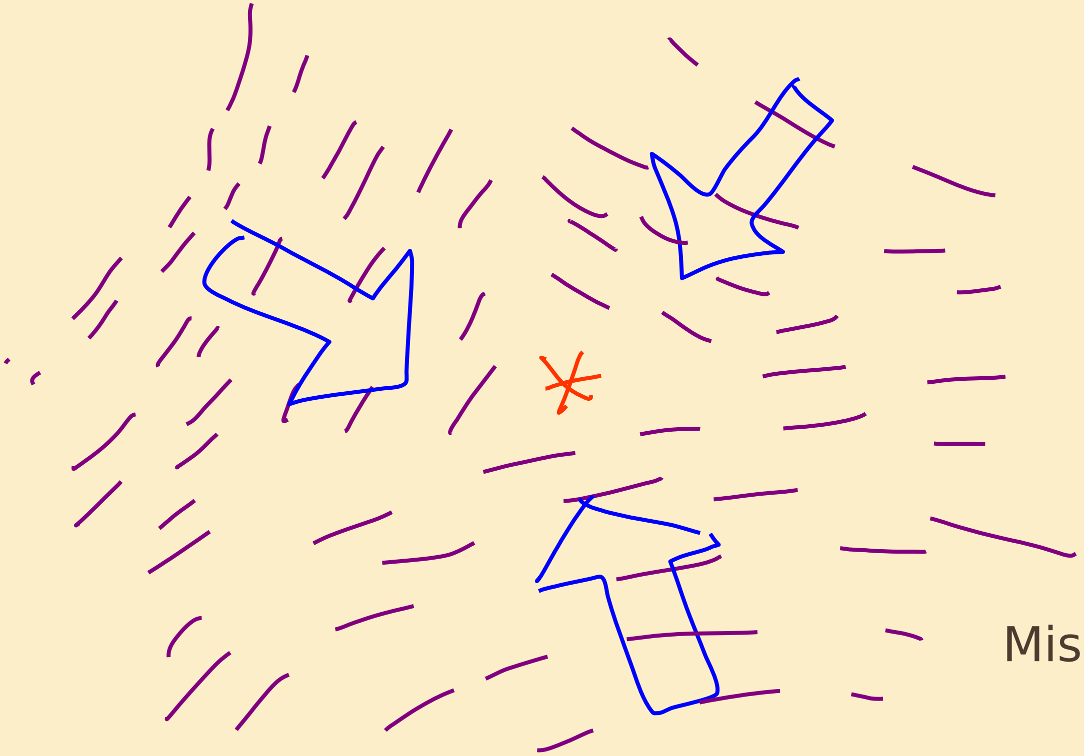


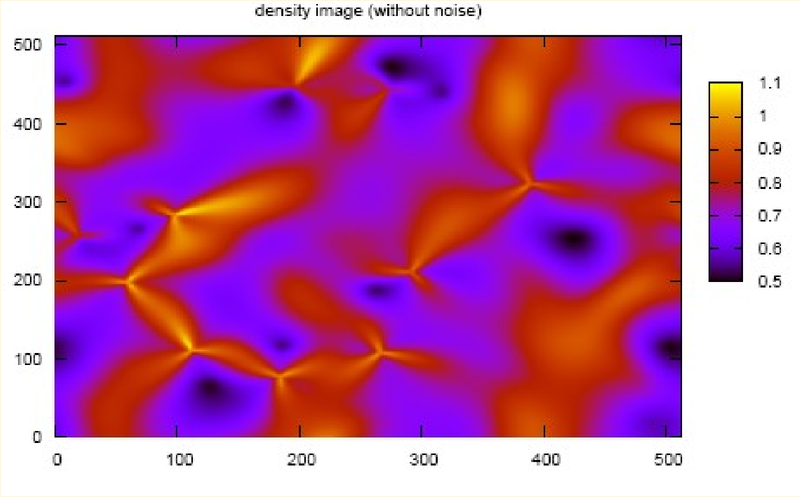
Kikuchi,,Ehrlicher, Koch,
Kaes, Ramaswamy, Rao
PNAS **106** (2009) 19776

- One long stiff filament (“microtubule”) in background of self-driven particles (“actomyosin”)
- Activity + anchoring enhances or reduces tension
- Can get: waves without inertia; negative dissipation

Spontaneous inhomogeneity as system orders

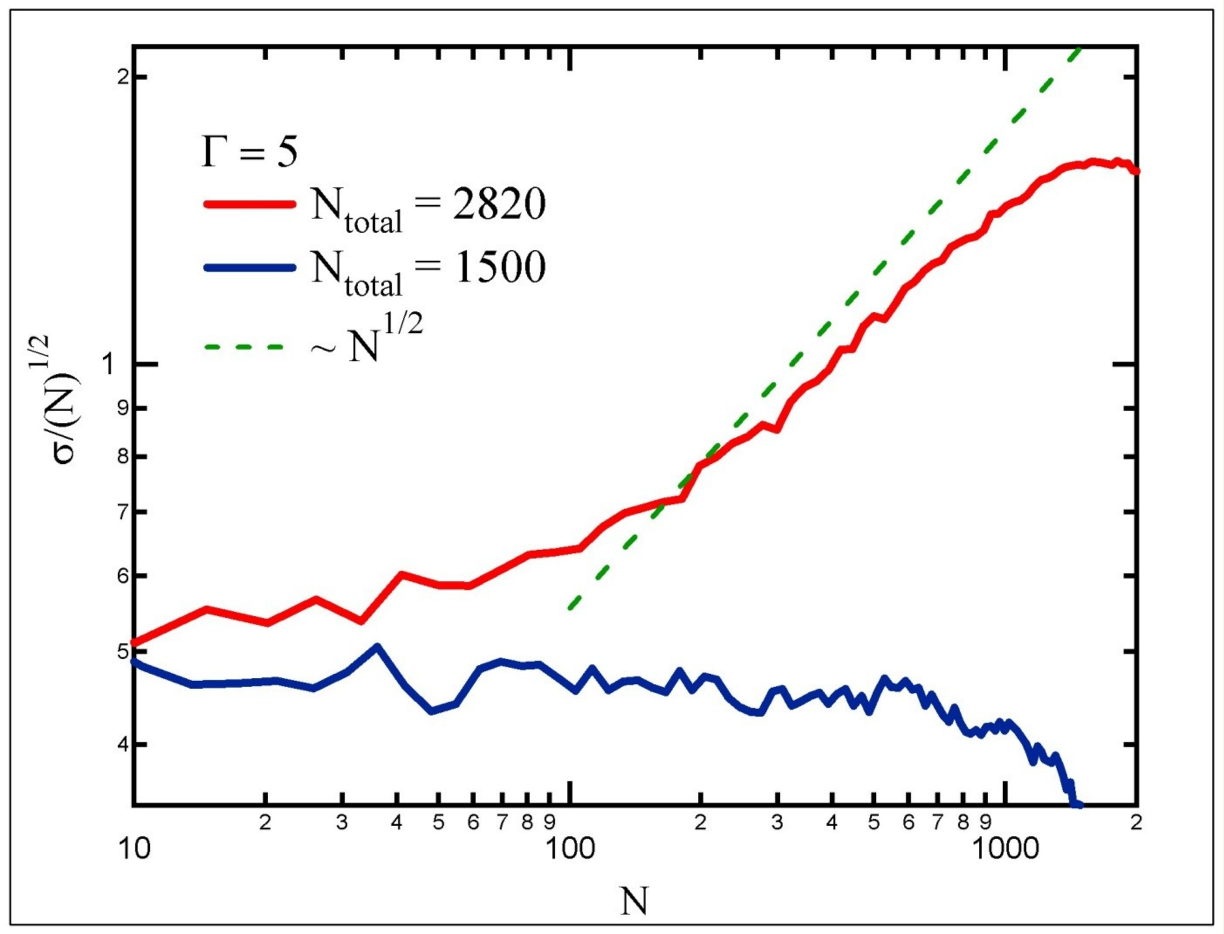
Initially: isotropic state, uniform density
Watch onset of oriented state
Defect motion causes strong clumping





Mishra, Ginelli, Chate, Puri, SR 2010

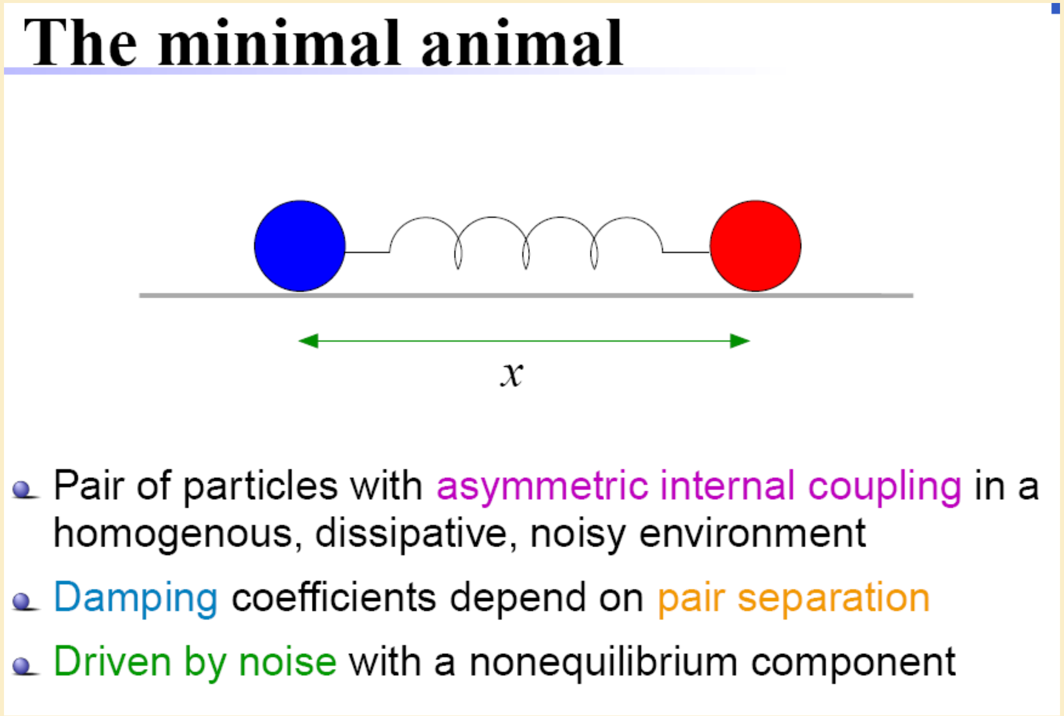
Giant density fluctuations in ordered phase



V Narayan, SR, N Menon
Science **317** (2007) 105:
experiments on a vibrated
layer of wire segments
confirm prediction of
SR, Simha, Toner 2003

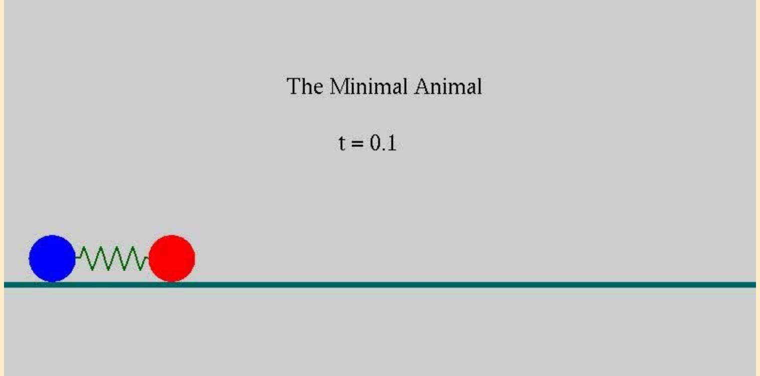
A self-propelled elastic dimer

directed motion from noise



The minimal animal

- Pair of particles with asymmetric internal coupling in a homogenous, dissipative, noisy environment
- Damping coefficients depend on pair separation
- Driven by noise with a nonequilibrium component

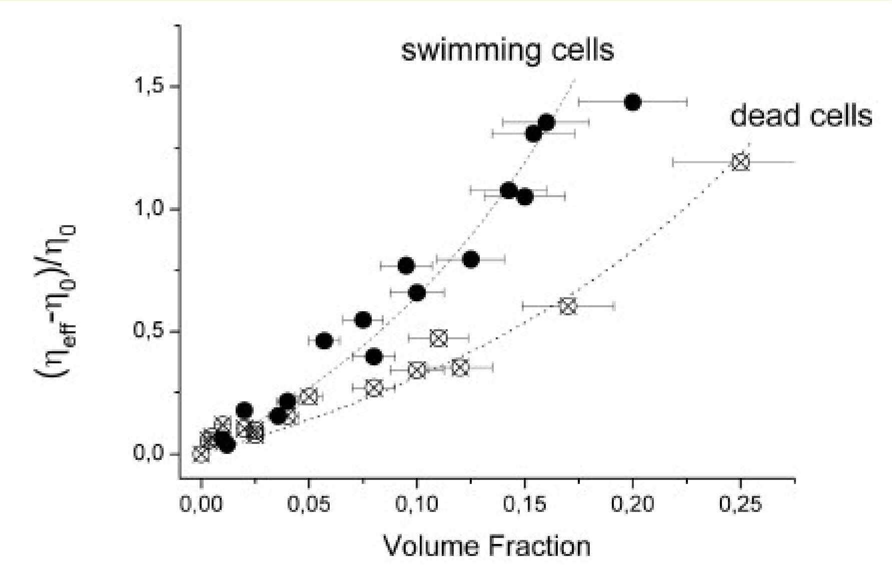


It moves!

K V Kumar, SR and M Rao Phys Rev E 2008
A Baule, K V Kumar and SR JSTAT 2008

Swimming affects viscosity

Prediction (Hatwalne *et al.*, PRL 2004): bacteria lower viscosity, algae raise it
Confirmed: Rafai *et al.*, arXiv:0909.4193v1, Sokolov + Aranson PRL 2009

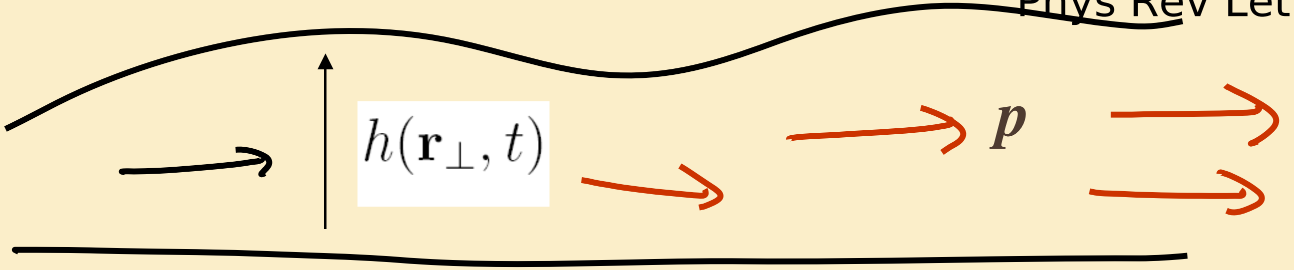


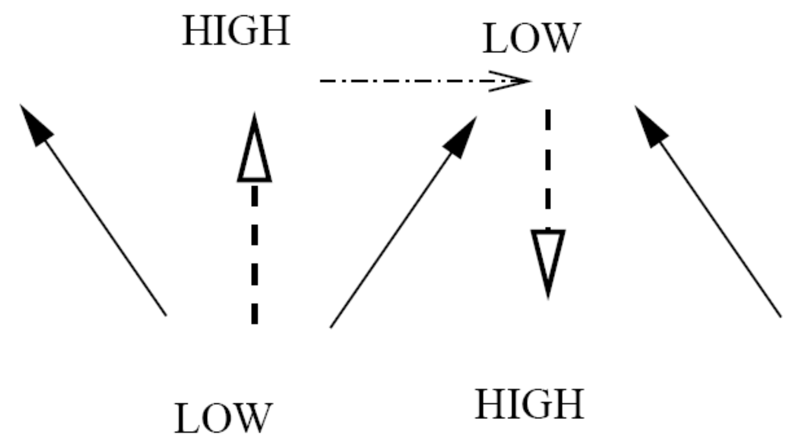
S Rafai *et al.* 2009
arXiv:0909.4193v1

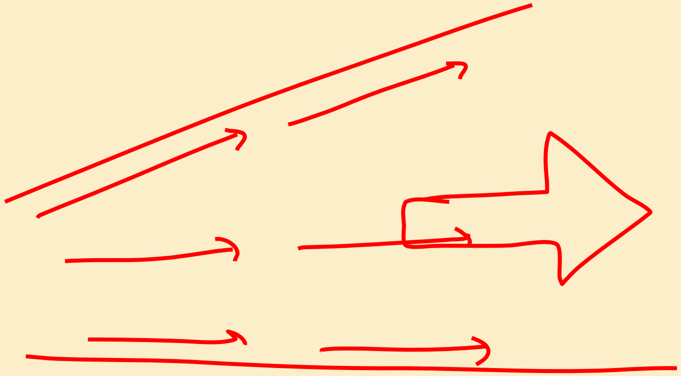
Bacteria can't swim straight

thin film instability of aligned swimmers

Sankararaman +
SR
Phys Rev Lett 2009







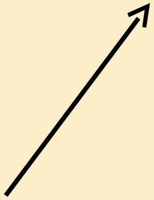
HOW WE GOT THOSE RESULTS

interacting agents and flocking models

Reynolds 1987
Vicsek *et al.* 1995

Each agent has position and direction
Updates it by interaction with neighbours
Simplest models: ignore fluid flow

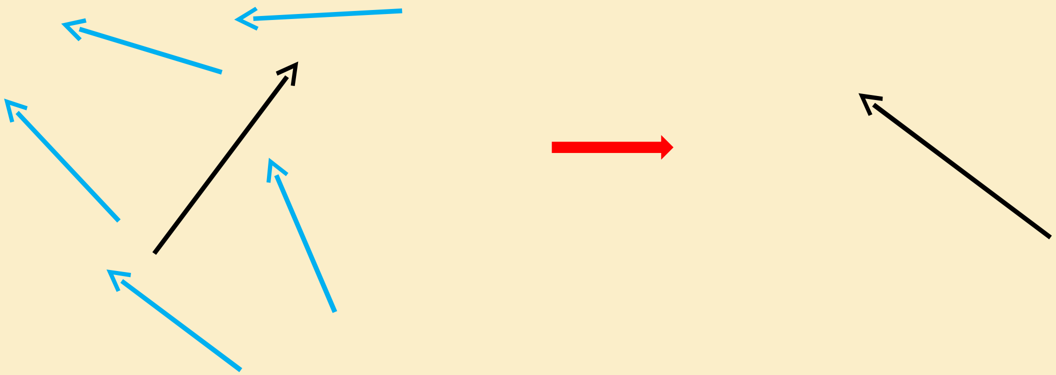
Agent: animal, bird ,fish, bacterium



Borkar, Jain, Rangarajan adap-org 9804004:
“direction” in strategy space
Neighbourhood: adjacency matrix, not metric distance
Specialisation: freezing of spin
Diversification: spin glass
Single strategy for all: ferromagnet = flock

How we got those results

interacting agents and flocking models

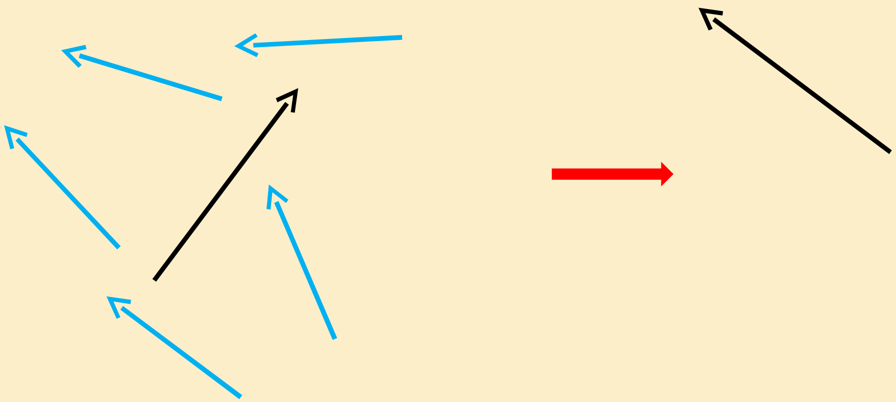


Each agent has position and direction
Aligns with mean of neighbours + noise

Reynolds 1987
Vicsek *et al.* 1995

How we got those results

interacting agents and flocking models

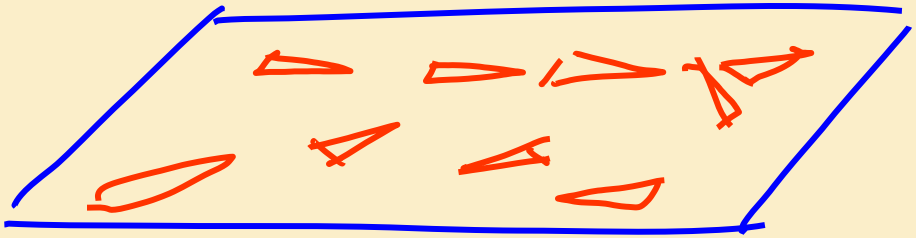


Each agent has position and direction
Aligns with mean of neighbours + noise
Follows her/his nose

Low noise, high density: ordered flock
High noise, low density: isotropic state
Reynolds 1987
Vicsek *et al.* 1995

Coarse-grain →

Continuum field theory



Toner-Tu 1995, 1998

Orientation = velocity

$$\partial_t c = -\boldsymbol{\nabla} \cdot c\,\mathbf{p}$$

Concentration field *c*

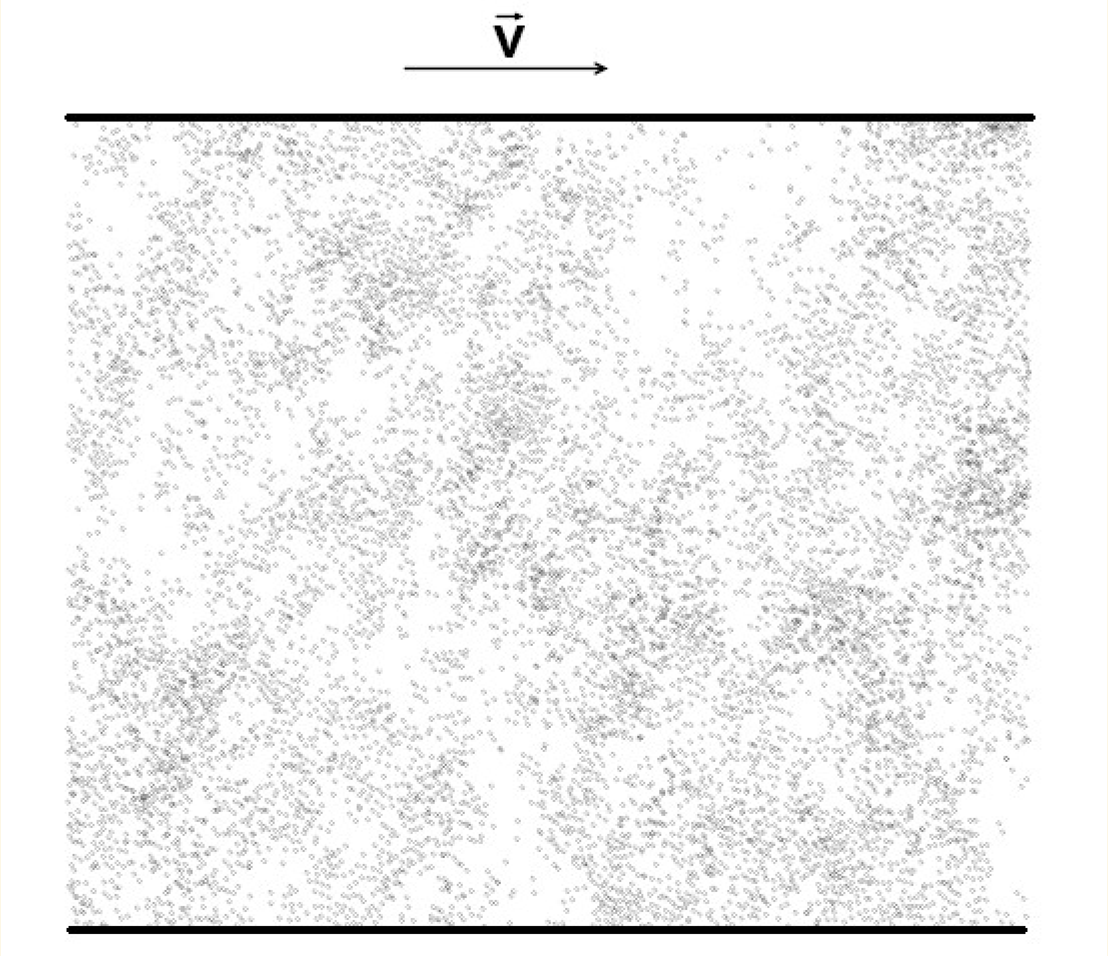
Particle velocity field ***p***

$$\partial_t \mathbf{p} + \lambda \mathbf{p} \cdot \nabla \mathbf{p} + \ldots = (\alpha - \beta \mathbf{p} \cdot \mathbf{p})\mathbf{p} + \Gamma \nabla \nabla \mathbf{p} - \nabla P(c) + \mathbf{f}$$

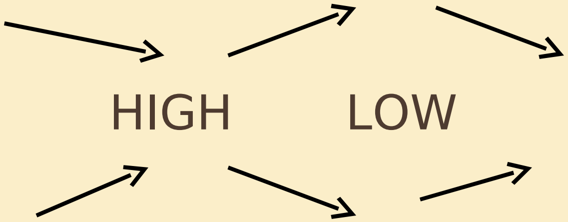
advection Preferred length alignment pressure noise

Bertin et al 2003
Mishra 2009

Flocks have big density fluctuations



Toner and Tu PRE 1998

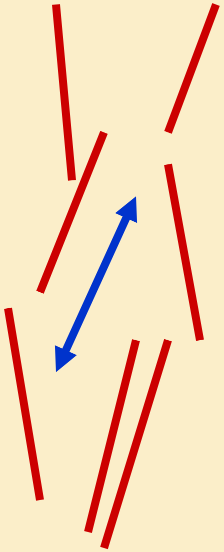


HIGH LOW

Easy orientational
fluctuations lead to
large fluctuating mass flux

Headless flockers: Chaté *et al.*'s model

PRL **96**, 180602 (2006)



No head-tail distinction

Align with mean of neighbours
+ small angular noise

Fixed small step forward or back along length

Parameters: angular noise, number density

Coarse-grain

find SR-Simha-Toner equations of motion for alignment tensor Q

Mishra, Ginelli, Chaté, Puri, SR 2010

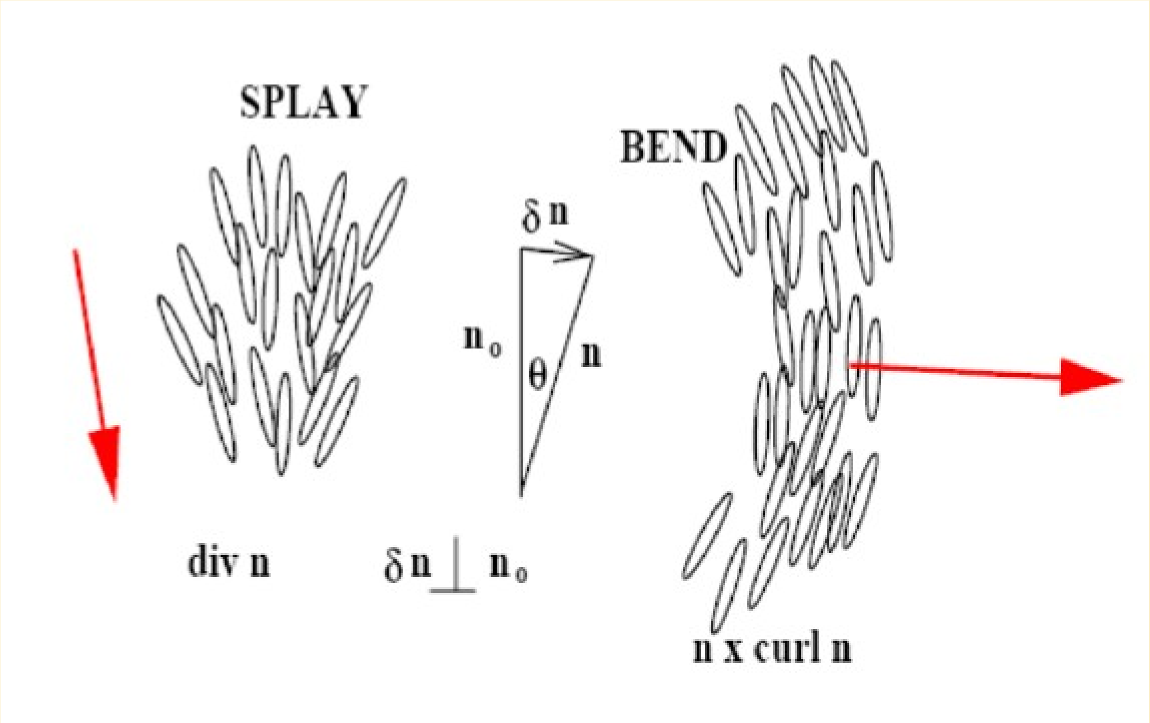
$$\frac{\partial \rho}{\partial t} = a_2\,\partial_\alpha \partial_\beta \left(\rho\,[\mathbf{Q}]_{\alpha\beta}\right) + \frac{a_2}{2}\nabla^2 \rho + a_1 \nabla \cdot \sqrt{\rho}\,\mathbf{n}\eta$$

anisotropic diffusion term $T_m \equiv a_2 \partial_\alpha \left([\mathbf{Q}]_{\alpha\beta} \partial_\beta \rho\right)$

non-equilibrium term $T_c \equiv a_2 \partial_\alpha \left(\rho \partial_\beta [\mathbf{Q}]_{\alpha\beta}\right)$

$\mathbf{n}$ = local principal axis of $\mathbf{Q}$

Headless flocks have big density fluctuations too



Easy orientational fluctuations lead to large fluctuating mass flux in steady state
Giant density fluctuations: a major prediction

SR, Simha, Toner 2003

Numerical studies: continuum and particle models

- Approach to ordered phase, with and without noise
- Ordered phase: giant fluctuations, time-correlations
- Subtleties associated with noise
- Random *vs* ordered initial conditions

Mishra, Ginelli, Chaté, Puri, SR
2010

Approach to ordered phase

Initial state: random orientation, uniform density
Final state: macroscopically oriented
How does your garden grow?

Start with Chaté *et al.* flocking rule

Build coarse-grained PDEs with noise

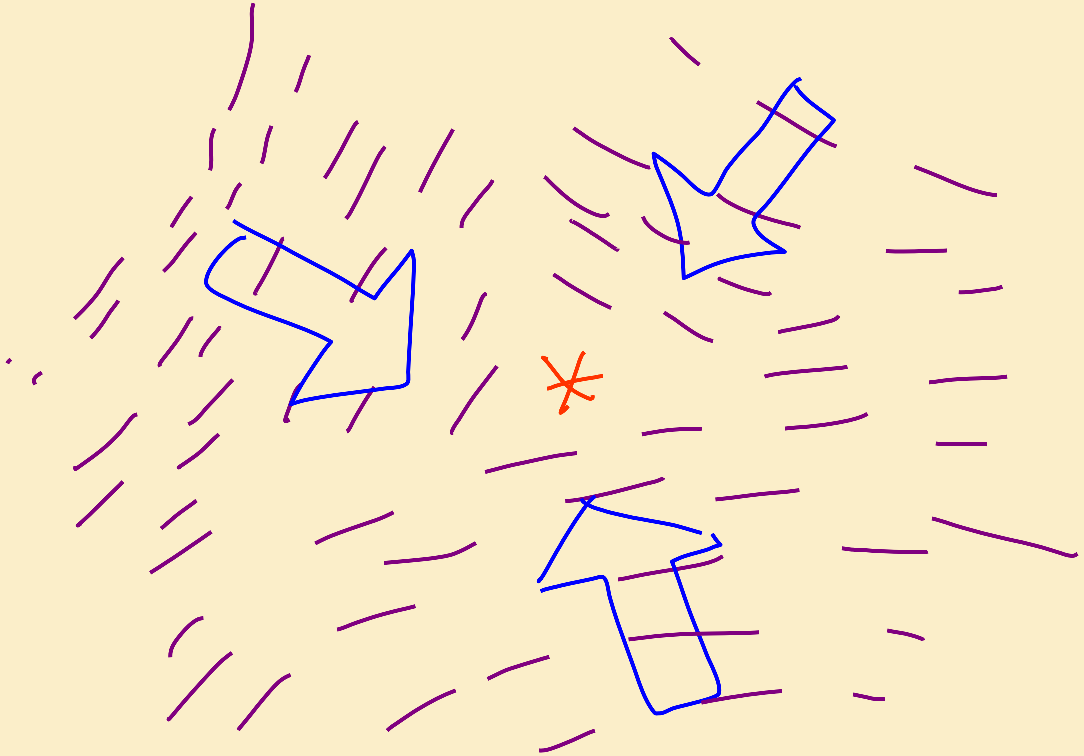
Compare behaviours

Compare PDEs with SR/Simha/Toner

Shradha Mishra (now at Syracuse) *et al.* 2010

Kinetics of domain growth

Start with isotropic state, uniform density:
Defect motion causes clumping as nematic orders

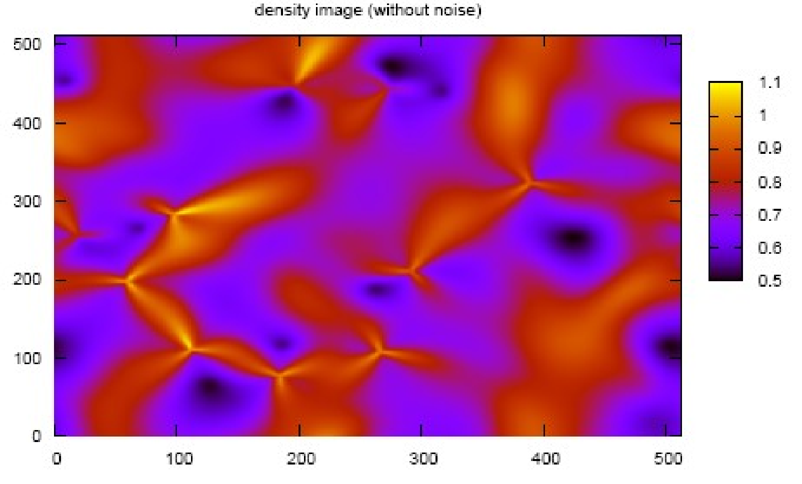


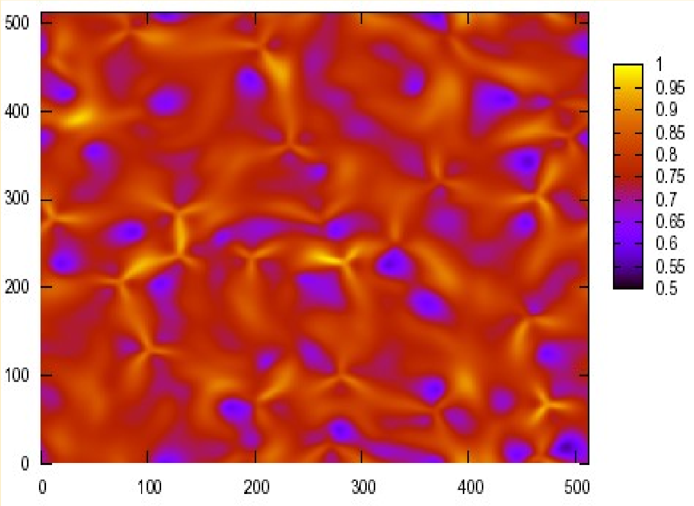
Curvature → mass flux

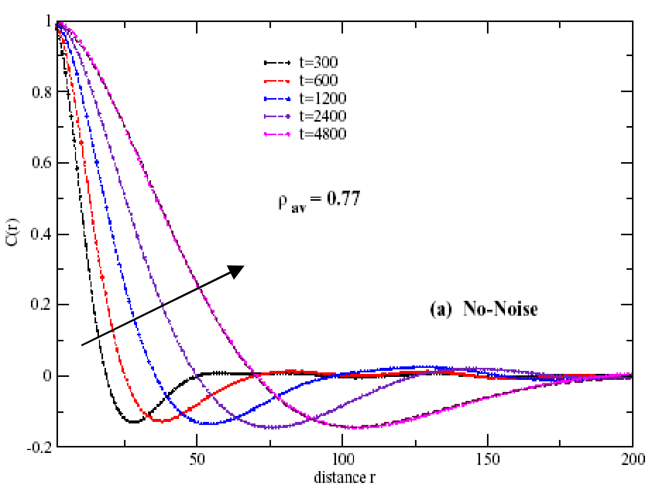
Shradha Mishra *et al* 2010

Strong inhomogeneity as domains grow

3-armed density bands around -1/2 defects





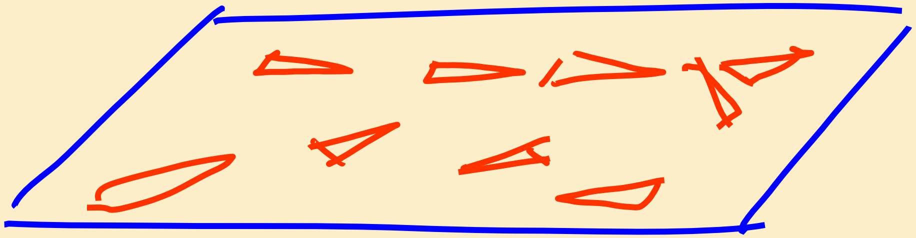


Initially uniform density, random orientation

Nematic order grows, density clumps strongly

Mishra et al. 2010

Towards self-driven hydrodynamics



Toner-Tu 1995, 1998

Orientation = velocity

$$\partial_t c = -\boldsymbol{\nabla} \cdot c\,\mathbf{p}$$

Concentration field *c*

Particle velocity field ***p***

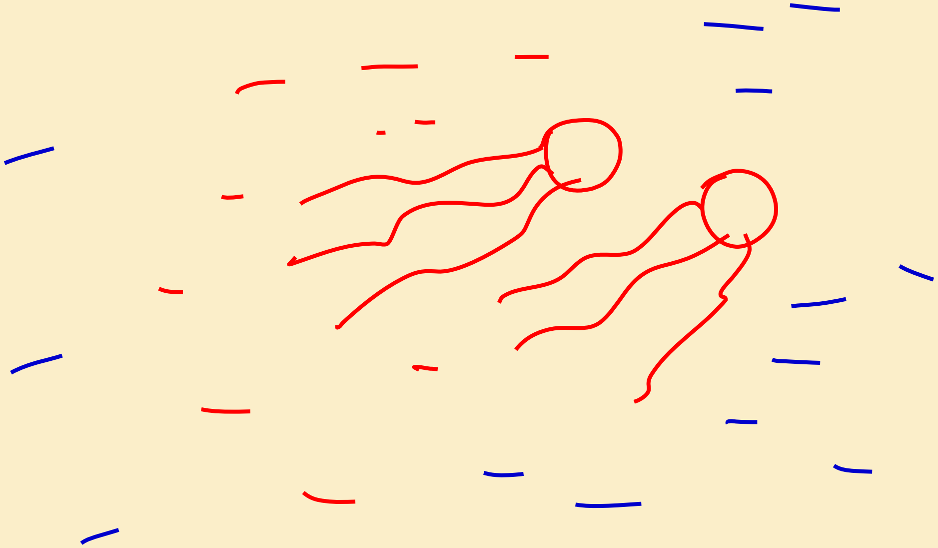
$$\partial_t \mathbf{p} + \lambda \mathbf{p} \cdot \nabla \mathbf{p} + \ldots = (\alpha - \beta \mathbf{p} \cdot \mathbf{p})\mathbf{p} + \Gamma \nabla\nabla \mathbf{p} - \nabla P(c) + \mathbf{f}$$

advection Preferred length alignment pressure noise

Bertin et al 2003
Mishra 2009

Including fluid flow

collective dynamics of self-driven particle with fluid



Density, orientation, fluid velocity fields

Self-propulsion produces flow

flow carries and aligns agents

LEADING TO →

Liquid-crystal hydrodynamics with a difference

F = free energy relative to isotropic fluid
A = deformation rate tensor, Dt = comoving, corotating derivative

$$D_t \mathbf{p} + \lambda \mathbf{p} \cdot \nabla \mathbf{p} + ... = \gamma \mathbf{A} \cdot \mathbf{p} - \frac{\delta F}{\delta \mathbf{p}} + \mathbf{f}$$

inertia

$$\rho(\partial_t + \mathbf{u} \cdot \nabla)\mathbf{u} = -\nabla \cdot (\sigma^a + \sigma^h) - \eta \nabla^2 \mathbf{u} - \nabla \Pi$$

$$\partial_t c = -\boldsymbol{\nabla} \cdot c\,\mathbf{p}$$

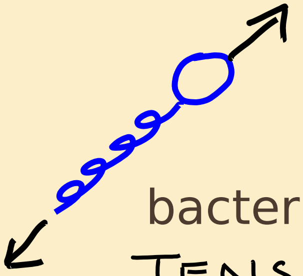
$$\sigma^a = W c(\mathbf{r}, t)\mathbf{p}\mathbf{p}$$

active stress

+ advection by flow

Simha and SR 2002; Hatwalne *et al.* 2004
Kruse, Juelicher, Joanny, Prost, Voituriez, Sekimoto
Curie/ESPCI/Dresden 2004-present

Minimal model for self-driven particle in fluid

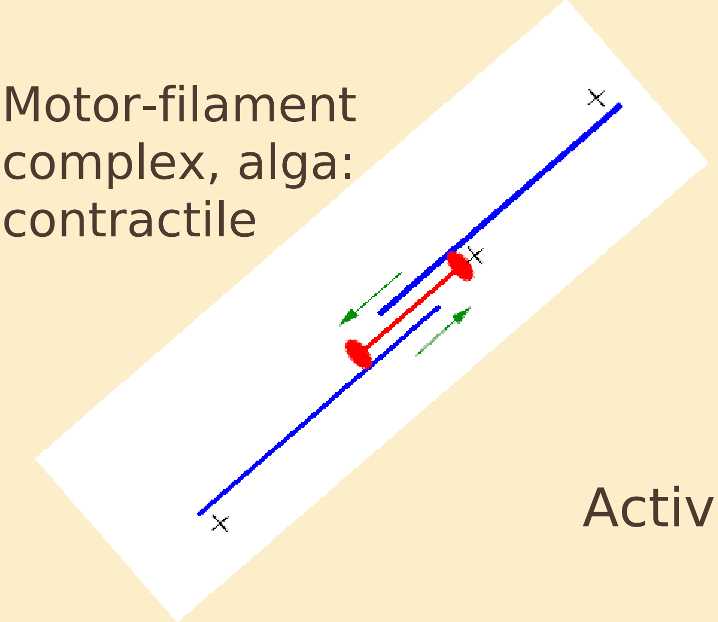


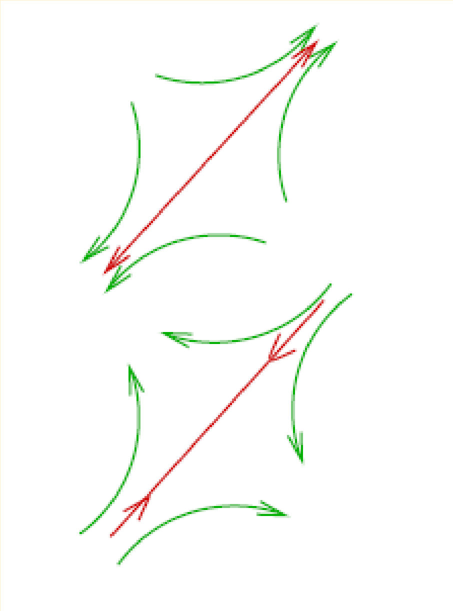
=

bacterium

TENSILE

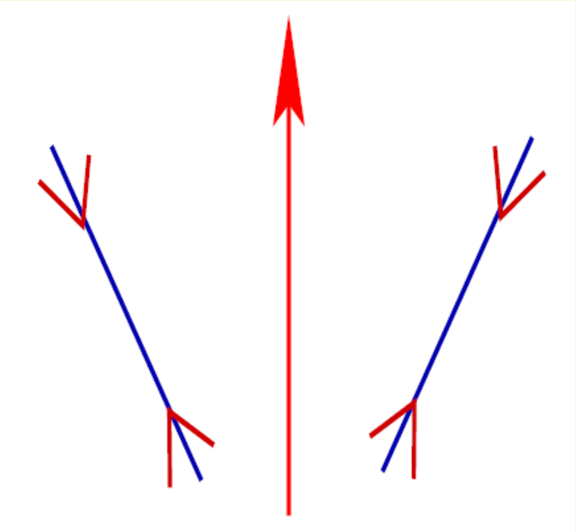
Motor-filament complex, alga: contractile

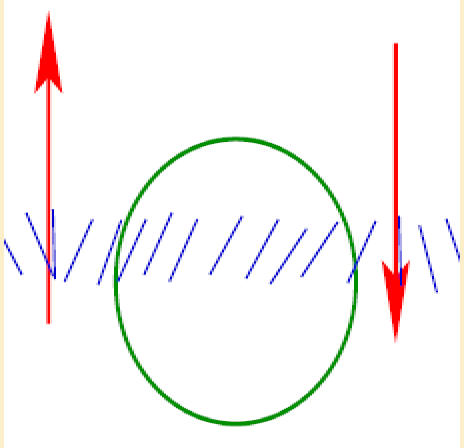




Active particles generate local straining flows

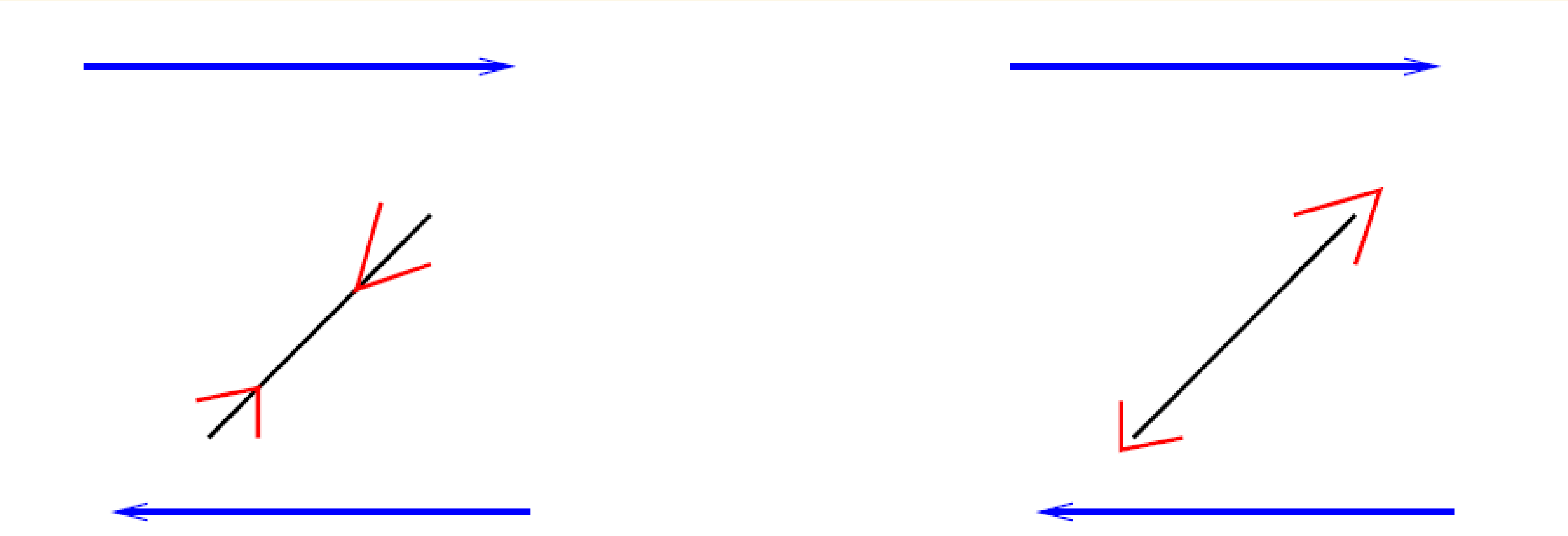
Curvature pumps fluid; flow reorients filaments





Apply these ideas to fluid film
and viscosity behaviour

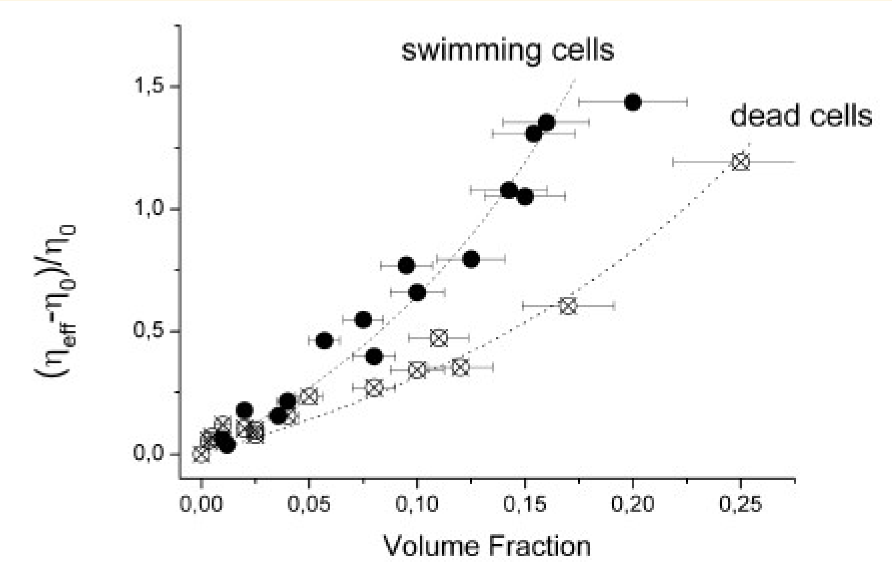
Swimming affects viscosity: theory



Base state isotropic
Shear aligns swimmers: built-in stresses → secondary flow
Contractile: opposes imposed flow; tensile: supports it
Hatwalne et al. PRL 2004

Swimming affects viscosity: experiments

Prediction (Hatwalne *et al.*, PRL 2004): bacteria lower viscosity, algae raise it
Confirmed: Rafai *et al.*, arXiv:0909.4193v1, Sokolov + Aranson PRL 2009



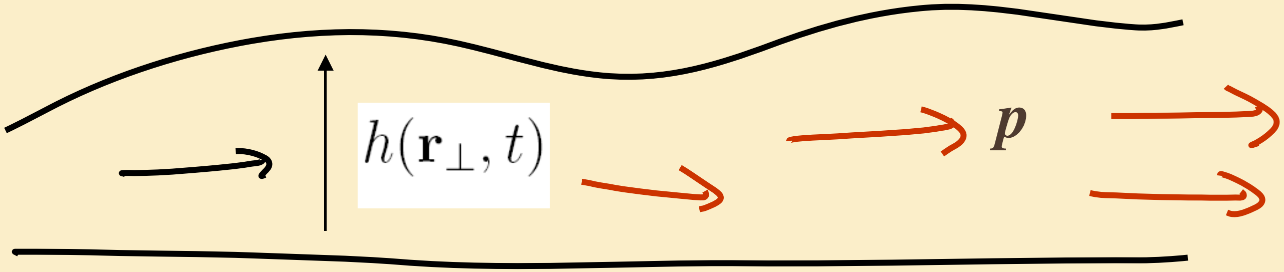
Compare viscosity
vs vol frac for living and dead
algal cells. Find living more viscous,
as theory (Hatwalne et al 2004)
predicts

S Rafai *et al.* 2009
arXiv:0909.4193v1

Instabilities of active ordered thin film

S Sankararaman + SR PRL 2009

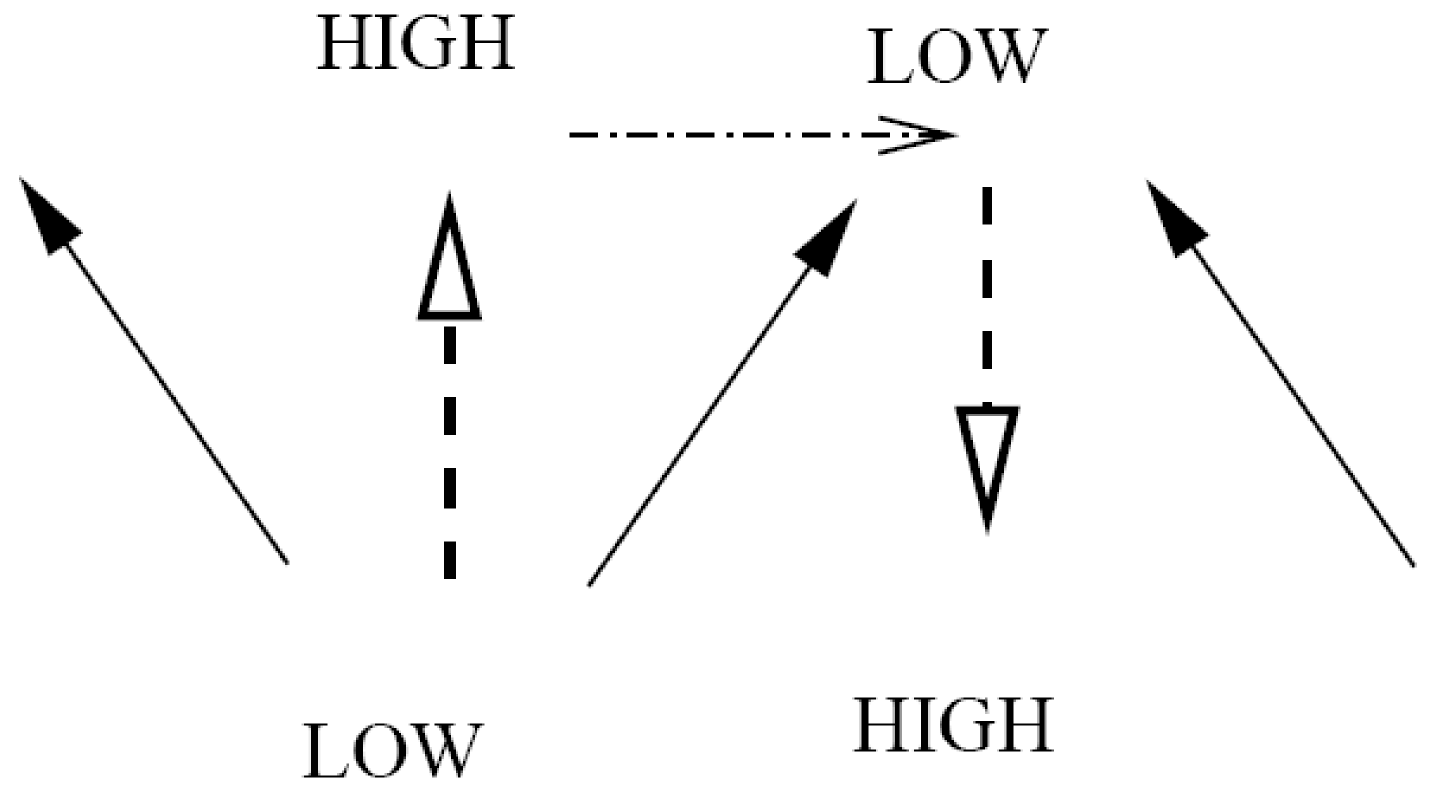
$$\partial_t h = -\nabla \cdot (h\mathbf{M} \cdot \boldsymbol{\nabla} \cdot \boldsymbol{\sigma})$$



Free surface: spontaneous splay; order parameter couples to tilt

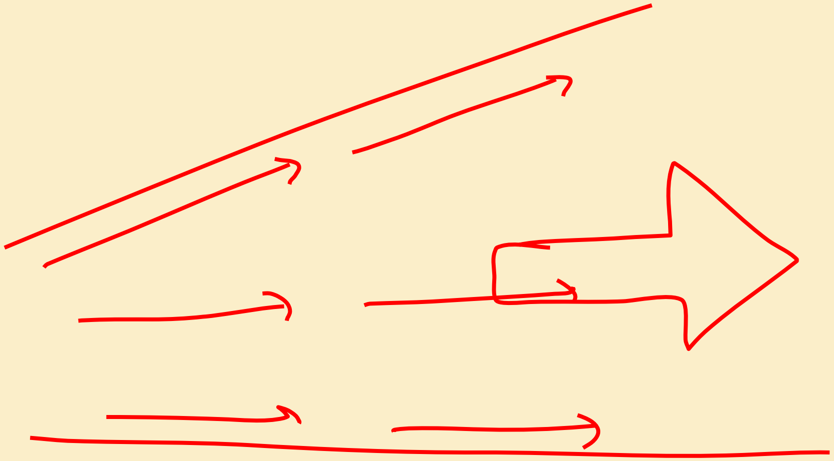
Get effective dynamics of
Thickness field h
Orientation field p
concentration c

Instability mechanism



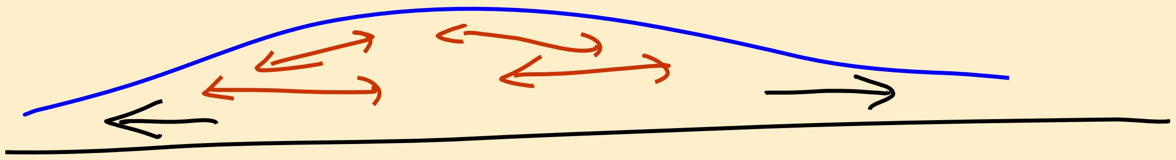
End result of these instabilities: turbulence at Re = 0
Saintillan and Shelley 2007-09; Wolgemuth 2008……

Another instability: tilt-induced pumping



Contractile filaments: splay → flow
Free surface unstable

And another: tensility lowers tension



Tensile active stresses: like anisotropic reduction of surface tension

Tabletop experiments

Testing flocking theories with dead particles

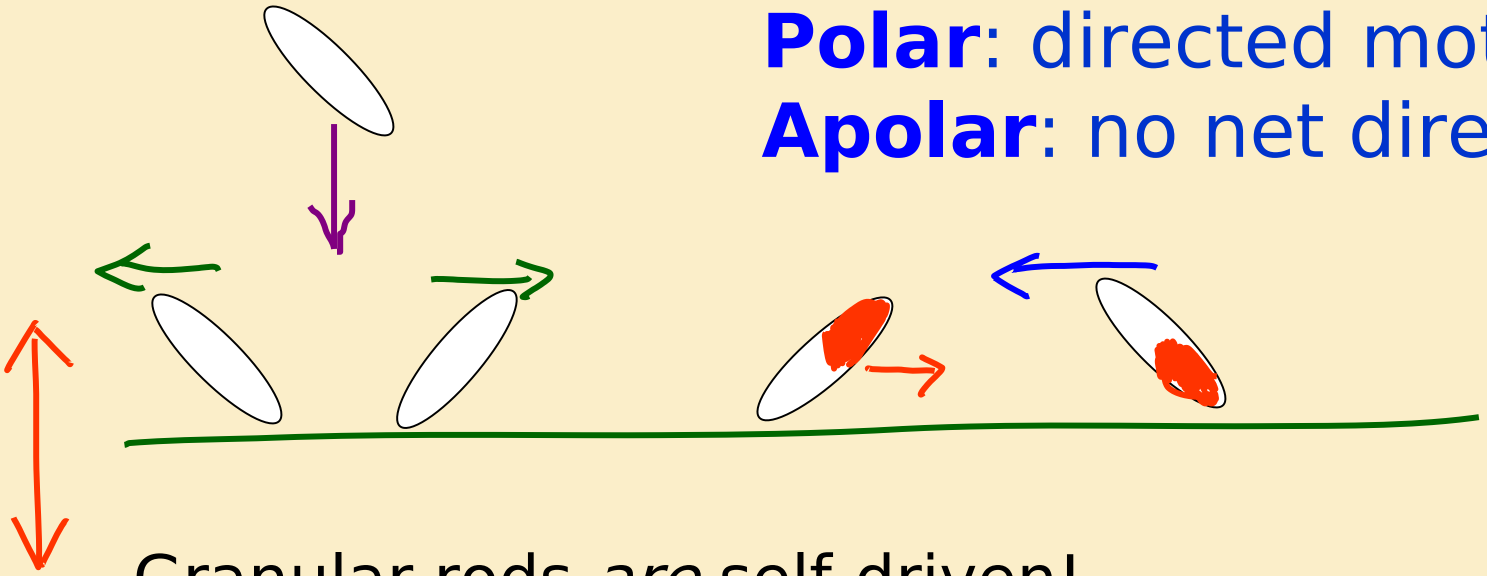
- vibrated granular matter:

  a model active system
- experiments

Dead active particles

Tilt = motor coordinate
Shaking = energy input to each particle

Polar: directed motion
Apolar: no net direction



Granular rods *are* self-driven!

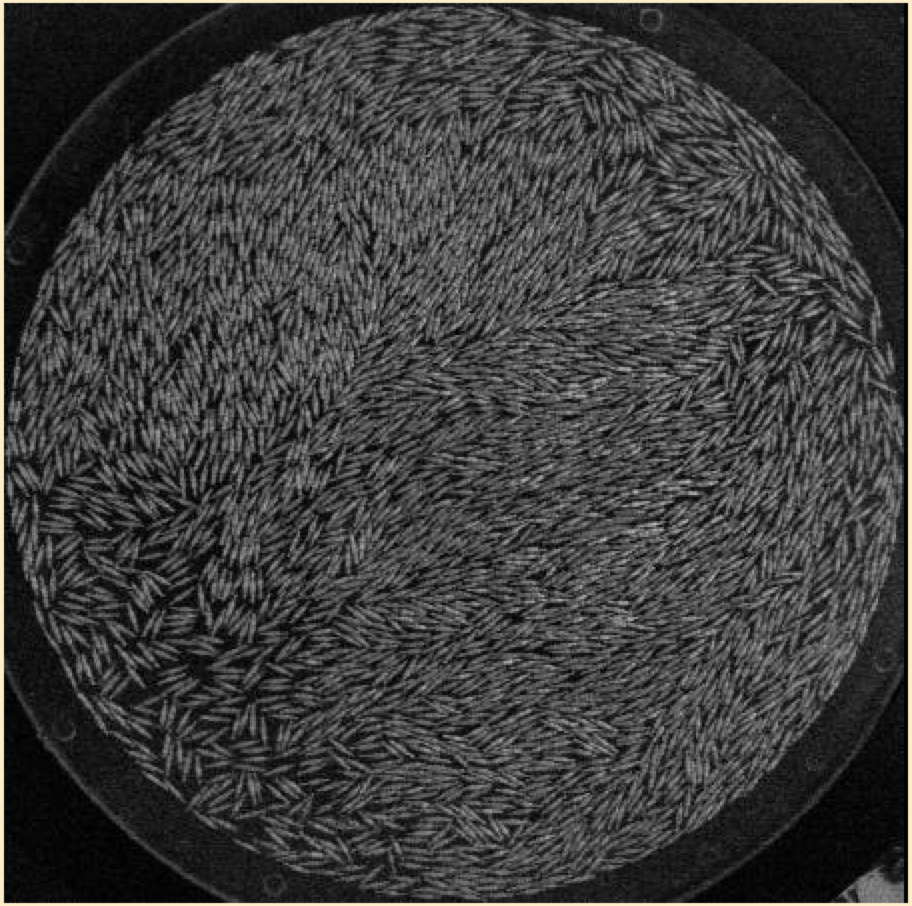
Yamada *et al.*, Kudrolli *et al.*

Active granular matter

- Granular systems: testing ground for active-matter theories
- Real-space imaging
  - Count all particles, measure all orientations
- Access to space-time data
  - Measure time-series, correlators
- SR, Simha, Toner predicted giant number fluctuations
  - Confirmed in Narayan *et al.* Science 2007

V. Narayan (IISc), N. Menon (UMass), SR:
JSTAT 2006, Science 2007

Swarming granular matter

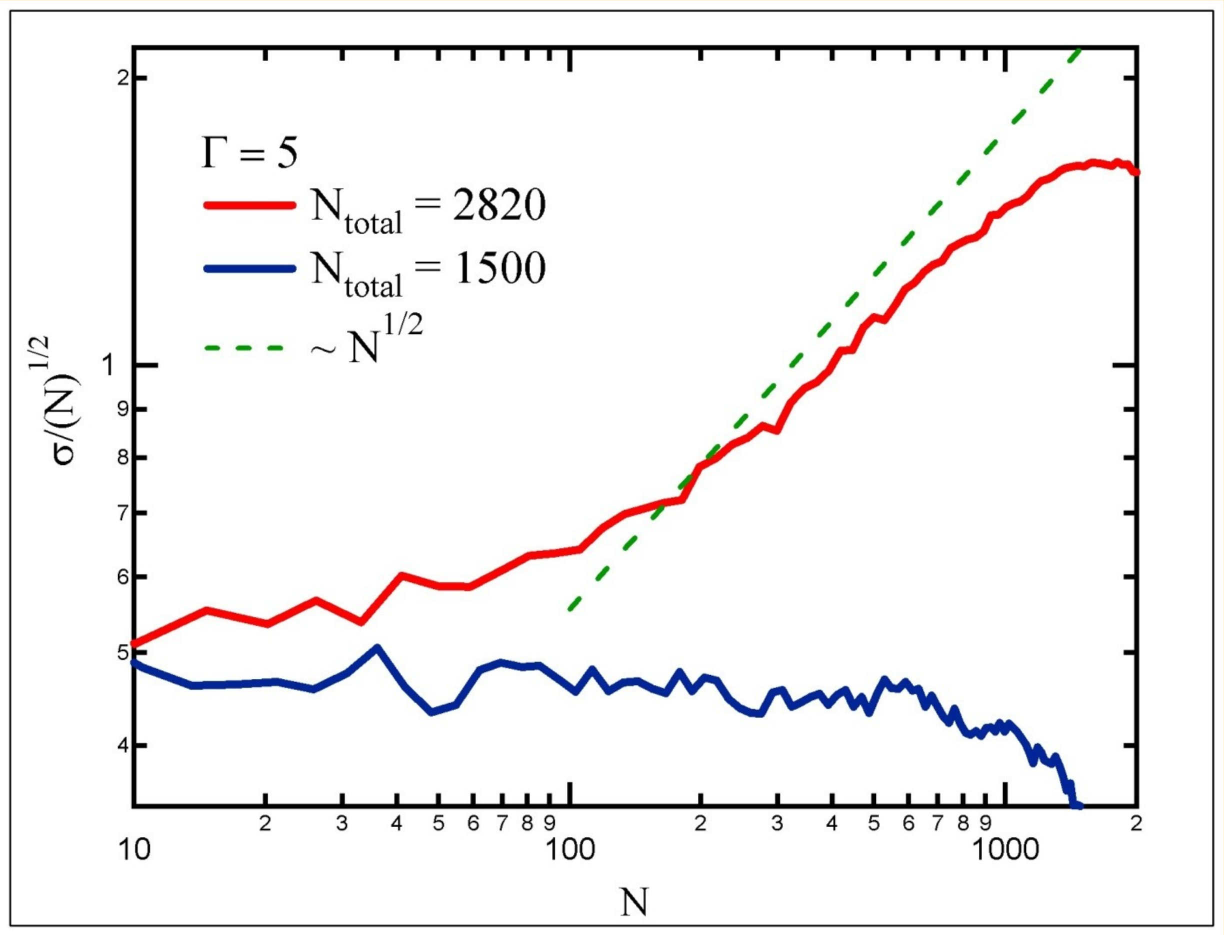


N = 2820

Γ = 5

Movie sped up 75x

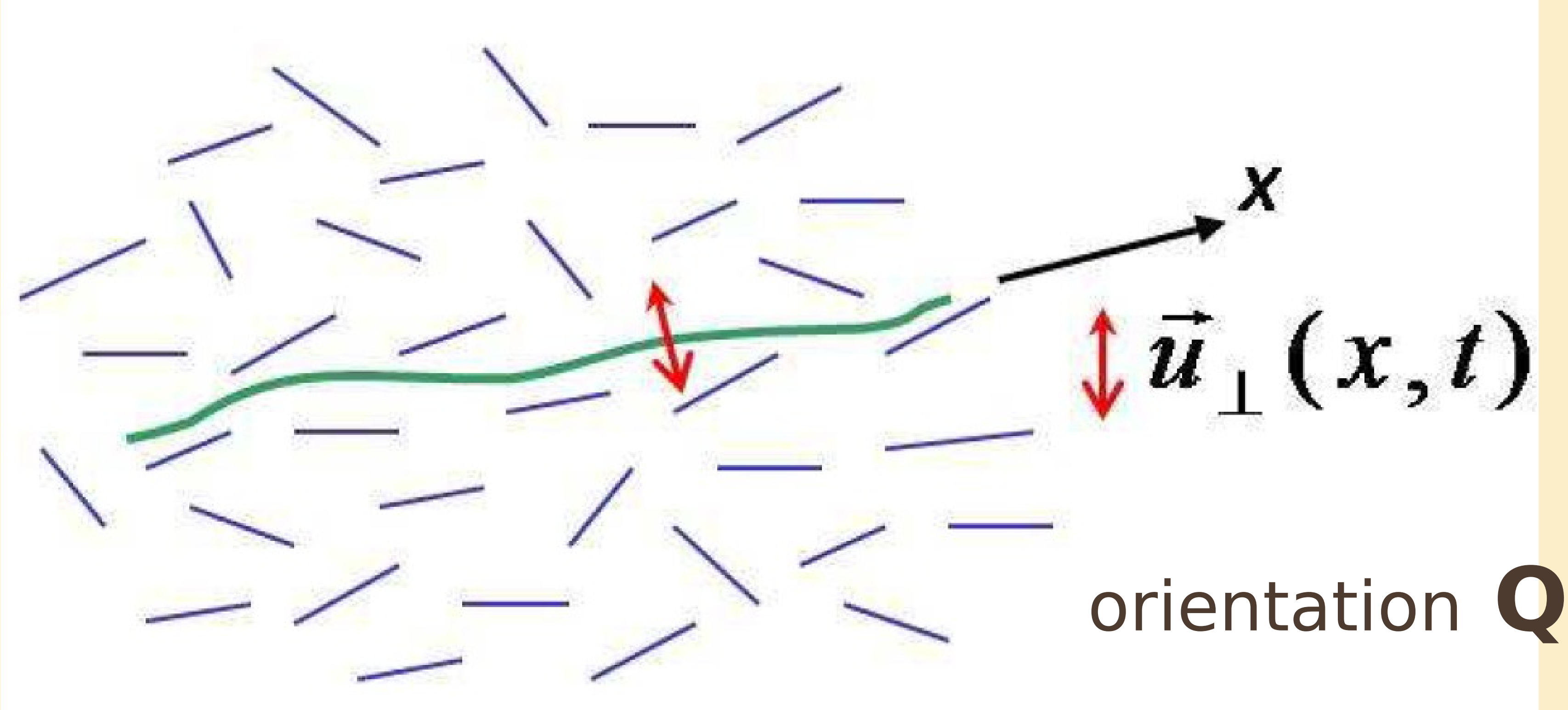
Fluctuation excess: Δ N/N$^{1/2}$ *vs* N



V Narayan *et al*
Science
317 (2007) 105

Get time series of number of particles in windows of various sizes, plot std dev vs mean

A filament among self-driven particles



What happens to a stiff filament surrounded by activity?
How does actin-myosin activity affect microtubules?

Kikuchi,,Ehrlicher,
Koch, Kaes,
Ramaswamy, Rao
arXiv:0901.4126

A simple model

$$\partial_t \mathbf{u}_\perp - \mathbf{v}_\perp(x, \mathbf{r}_\perp = \mathbf{0}, t) = -\frac{1}{\gamma}\delta F/\delta \mathbf{u}_\perp + \mathbf{f}_\perp$$

$$\partial_t \mathbf{Q} = -\frac{1}{\zeta}\delta F/\delta \mathbf{Q} + \boldsymbol{\eta},$$

$\mathbf{u}_\perp(x,t)$	transverse fluctuations
$\mathbf{v}$	hydrodynamic velocity field
$\mathbf{Q}$	nematic order parameter
$F[\mathbf{u}_\perp, \mathbf{Q}]$	free-energy functional

Free-energy: ordering, elasticity, anchoring

$$F[\mathbf{u}_\perp, \mathbf{Q}] = F_f[\mathbf{u}_\perp] + F_{LD}[\mathbf{Q}] + F_{anc}[\mathbf{u}_\perp, \mathbf{Q}]$$

$$F_f[\mathbf{u}_\perp] = \int_0^L dx[(\sigma/2)(\partial_x \mathbf{u}_\perp)^2 + (\kappa/2)(\partial_x^2 \mathbf{u}_\perp)^2]$$

$$F_{LD}[\mathbf{Q}] = \int dx \int d^2 r_\perp [(a/2)\mathbf{Q}^2 + (K/2)(\nabla \mathbf{Q})^2]$$

$F_{anc}[\mathbf{u}_\perp, \mathbf{Q}]$ Favours normal or parallel alignment of medium and filament

Where's activity?

$$\mathbf{v}_{\perp}(x, \mathbf{r}_{\perp}, t) = -(W c_0/\Gamma)\partial_x \mathbf{Q}_{x\perp}(x, \mathbf{r}_{\perp}, t)$$

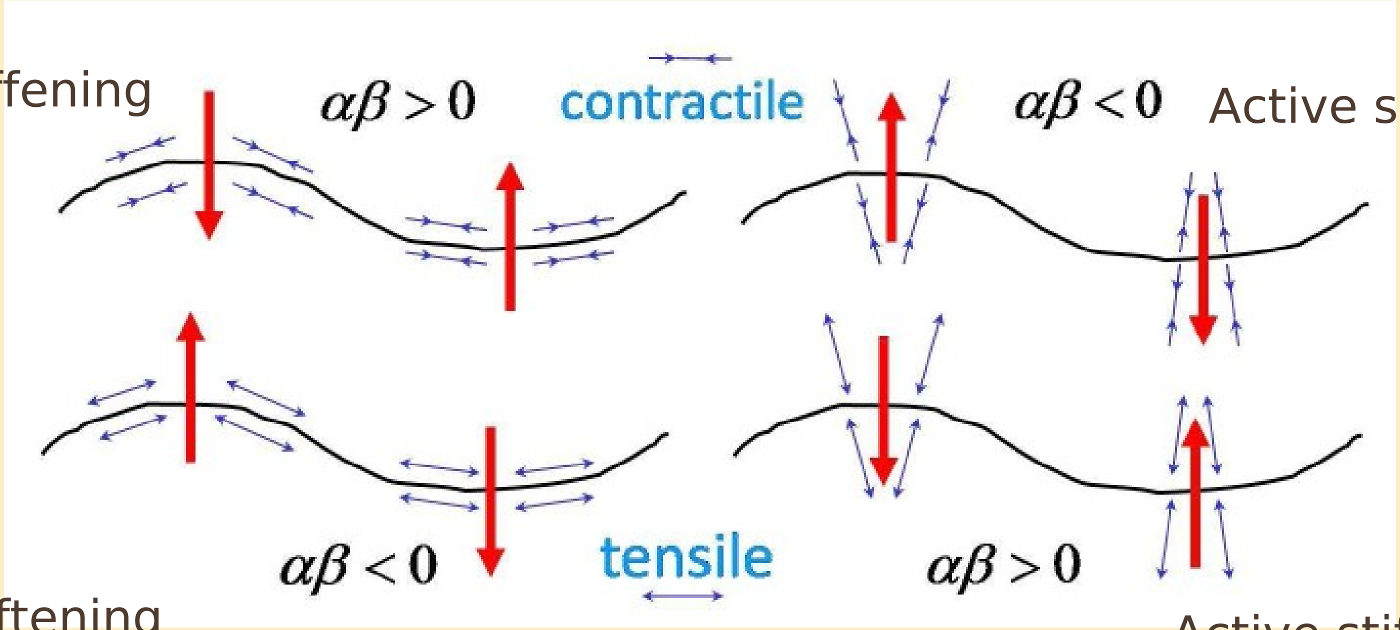
Force balance: friction against active stresses
"Rouse" approximation: local damping

Combine these elements

Interplay: anchoring and activity

Active stiffening

Active softening



Active softening

Active stiffening

- Stiffening: strictly nonequilibrium effect
- Buckling: provides basis for Brangwynne *et al*. 2008

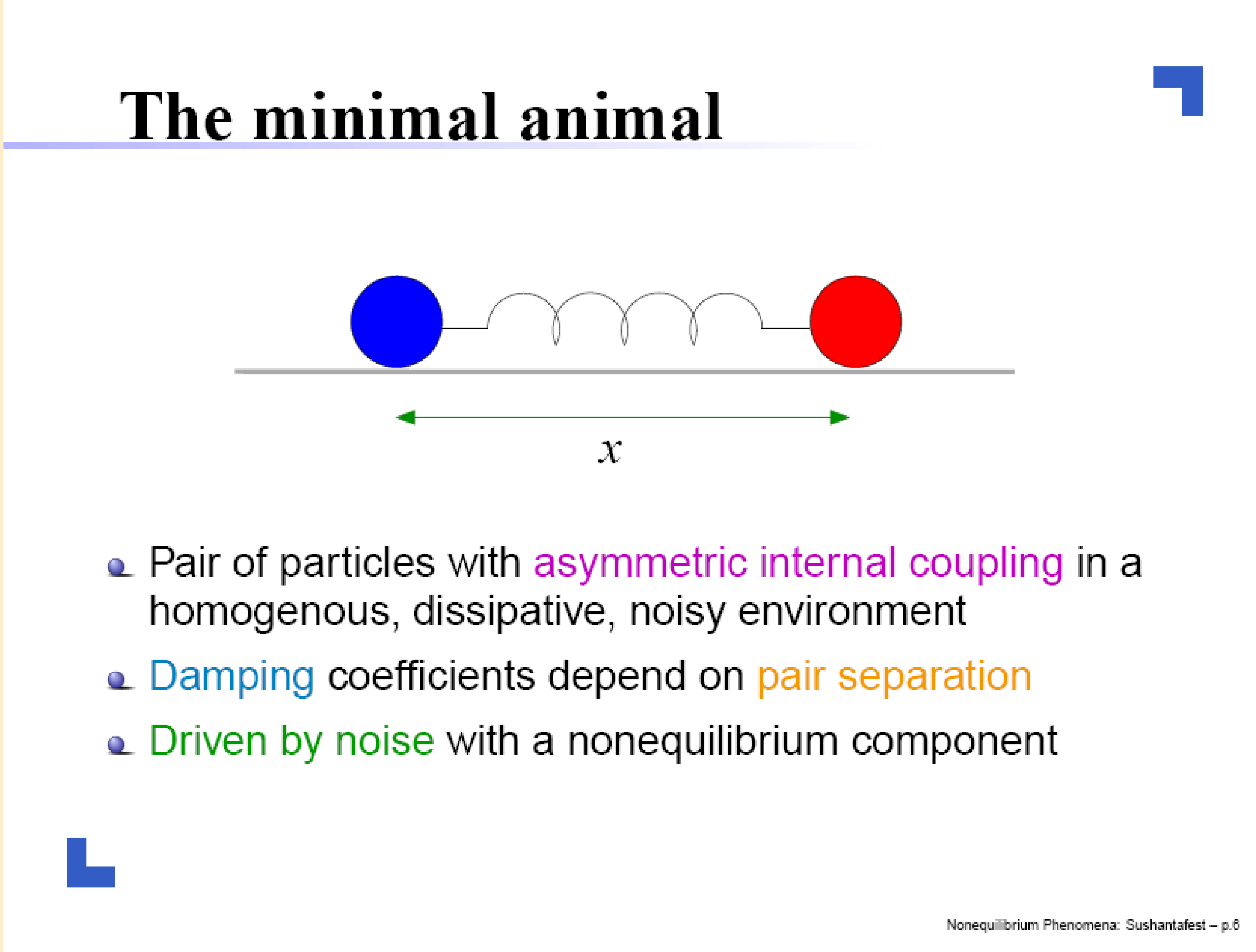
Fluctuation-dissipation ratio

$$R_{q_x \omega} = \frac{N_1 \gamma}{k_B T} \left[1 + \frac{\alpha \left(\alpha N_2 / N_1 + \beta \right) \left(\zeta / K \right)^2 q_x^2 \Sigma(q_\omega)}{1 - \alpha \beta (\zeta / K)^2 q_x^2 \Sigma(q_\omega)} \right]$$

Scaled ratio of correlation function and dynamic response

- A mess: should be unity if effective temperature
- Depends on activity through Σ
- Can turn negative at finite frequency
- Close analogy: Hudspeth *et al* PNAS ‘01 auditory hair cells

Self-propelled elastic dimer

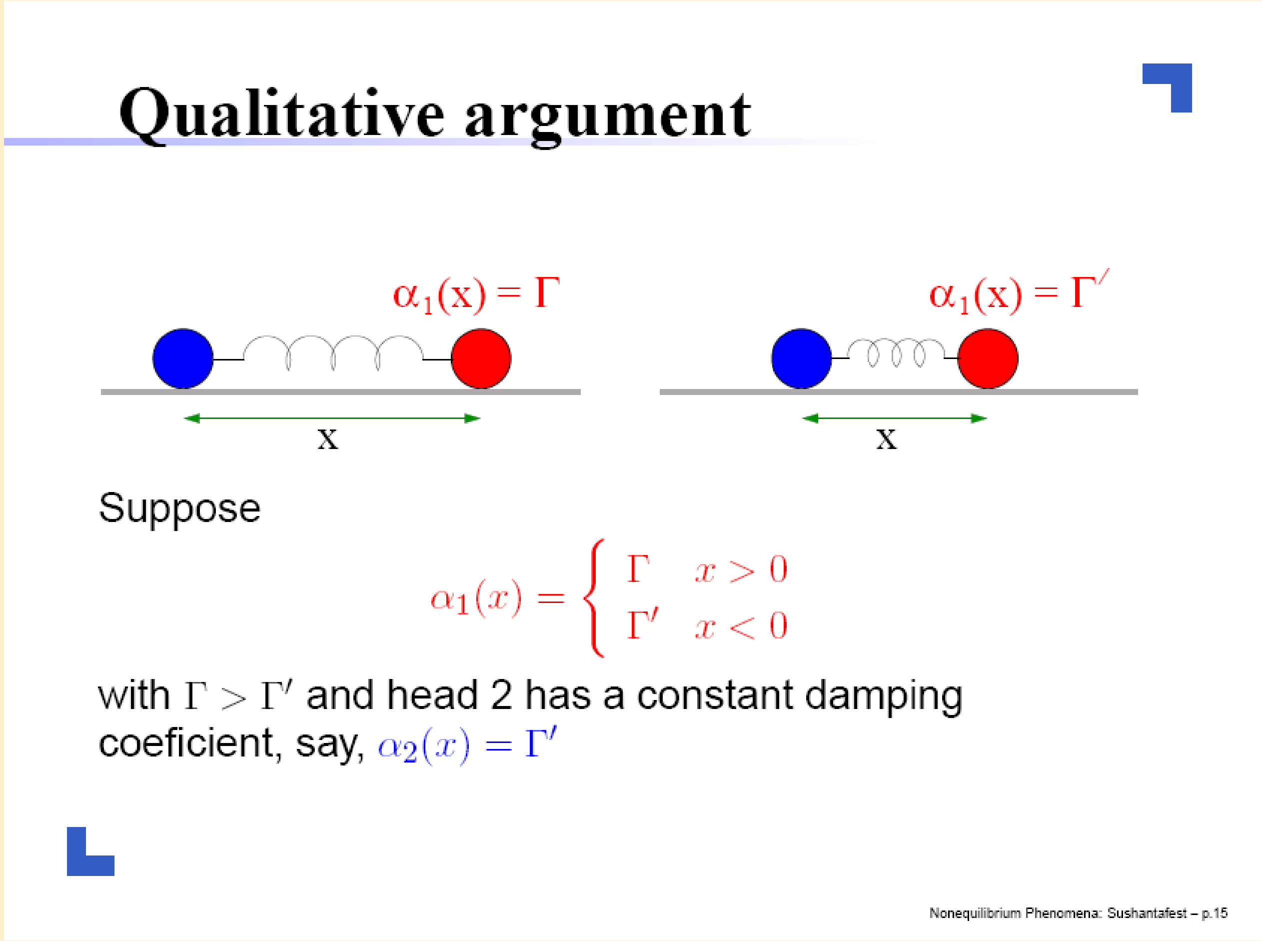


The minimal animal

- Pair of particles with asymmetric internal coupling in a homogenous, dissipative, noisy environment
- Damping coefficients depend on pair separation
- Driven by noise with a nonequilibrium component

Nonequilibrium Phenomena: Sushantafest – p.6

Self-propelled elastic dimer



Qualitative argument

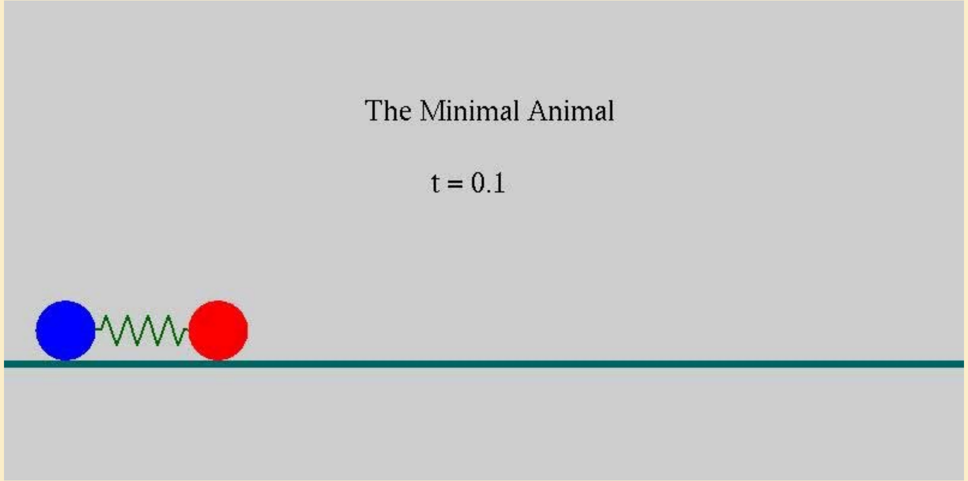
Suppose

$$\alpha_1(x) = \begin{cases} \Gamma & x > 0 \\ \Gamma' & x < 0 \end{cases}$$

with $\Gamma > \Gamma'$ and head 2 has a constant damping coeficient, say, $\alpha_2(x) = \Gamma'$

Nonequilibrium Phenomena: Sushantafest – p.15

Self-propelled elastic dimer



K Vijay Kumar *et al.*, Phys Rev E 2008

Prospect: where do we go from here?

- Achievements
- Quantitative experiments?
- Evolution?

Achievements

- Framework for mechanics of living matter
- Striking rheology, instabilities; new coarsening
- Activity → clumping: bio consequences?
- Thin-film instabilities – biofilms? Lamellipodium?
- Granular matter: great laboratory for active matter
- Many new directions to be explored

What’s missing?

Quantitative experiments?

- Most comparisons so far: qualitative
  - Picture in experiment looks like theory
  - Must do better
- Controlled experiments on model systems
  - Bacteria, cell extracts: motors, filaments, ATP
  - Collections of artificial swimmers?
  - Thin-film or confined geometries

Evolution?

- Guttal and Couzin 2010 (to be published) allow parameters in model to evolve, select those that yield success
- Find remarkable state space of Evolutionarily Stable Strategies

Thank you!