How can birds and bacteria move together without a leader?

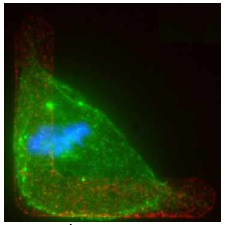
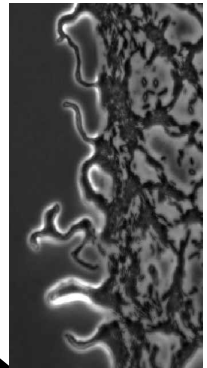
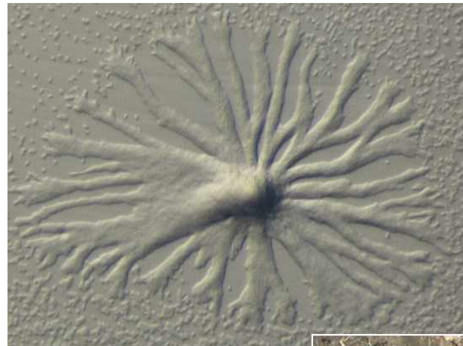
An introduction to collective motion in biology

Fernando Peruani

In collaboration with:
M. Bär, H. Chaté, A. Deutsch, F. Ginelli, V. Jakovlievic, L. Søgaard-Andersen, and J. Starruß

Summer Solstice Conference - Nancy – 2010

Motivation: Examples of collective motion in biology


Molecular motors

bacteria

~10^{-6} m

eukaryote cells

social insects

~10^{-2} m

bird and fish

~10^{-1} m

Mammals

~10^{0} m

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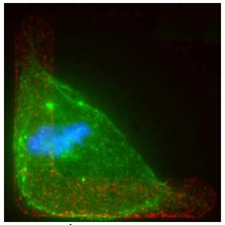
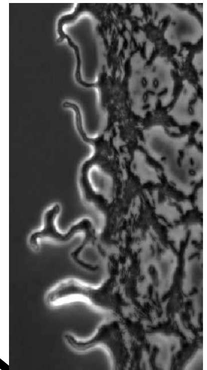
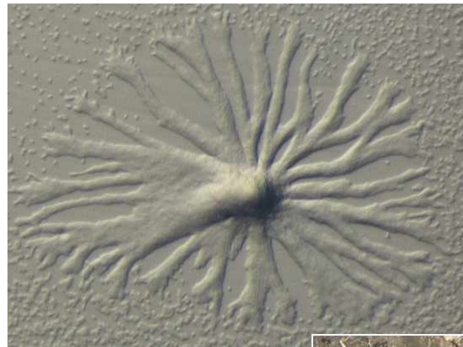
Motivation: Examples of collective motion in biology


Molecular motors

bacteria

$\sim 10^{-6}$ m

eukaryote cells

social insects

$\sim 10^{-2}$ m

Large-scale patterns of millions of individuals emerge without a central control system!

Coherent moving structures that emerge from local rules and short range interactions – i.e., without global knowledge of the system!

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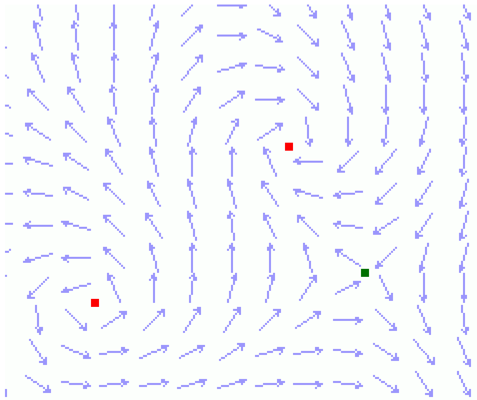
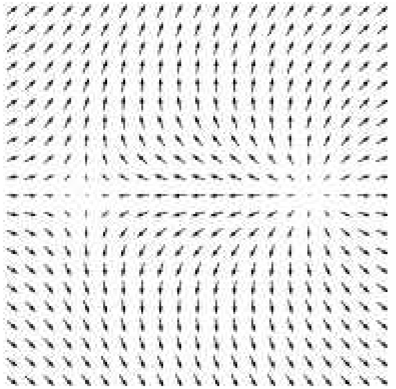
Motivation: collective motion as a theoretical challenge

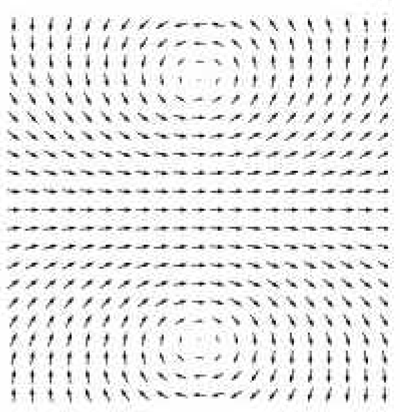
Imperfect flow of information leads to defects, and defects set the limit to the size/scale of the patterns we can observe

Some classical results from statistical mechanics:

- The Kosterlitz-Thouless transition: $E_{ij} = -J\,(\mathbf{s}_i \mathbf{s}_j) = -J\cos(\varphi_i - \varphi_j)$







- The Mermin-Wagner theorem:

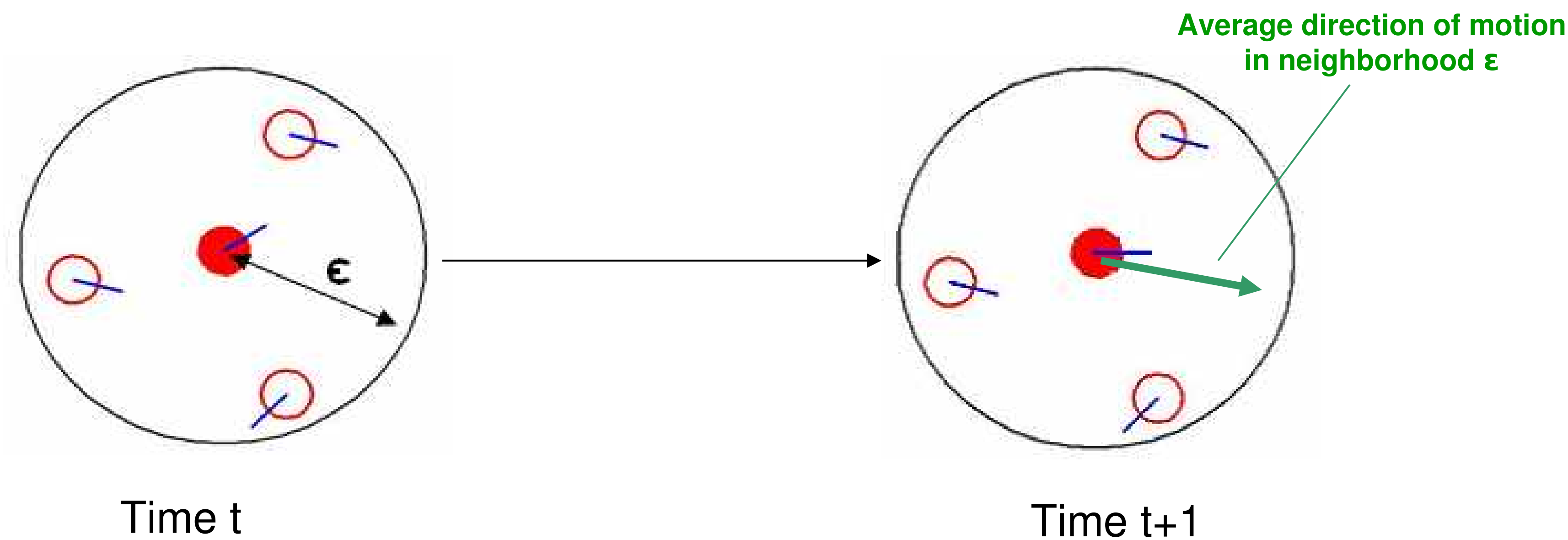
In equilibrium systems with SU2 symmetry, long-range order out of short-range interactions cannot emerge in 1D or 2D!

[Ref.: Peruani, Nicola, Morelli, http://arxiv.org/abs/1003.4253 (2010)]

Collective motion in a simple model

The Vicsek model

[T. Vicsek *et al.*, Phys. Rev. Lett. 75, 1226 (1995)]



Motion in space

$$\mathbf{x}_i(t+1) = \mathbf{x}_i(t) + \mathbf{v}_i(t)\Delta t$$

Change of the direction of motion

$$\theta(t+1) = \langle\theta(t)\rangle_r + \Delta\theta$$

Average direction of motion at time t

Angular noise !!!

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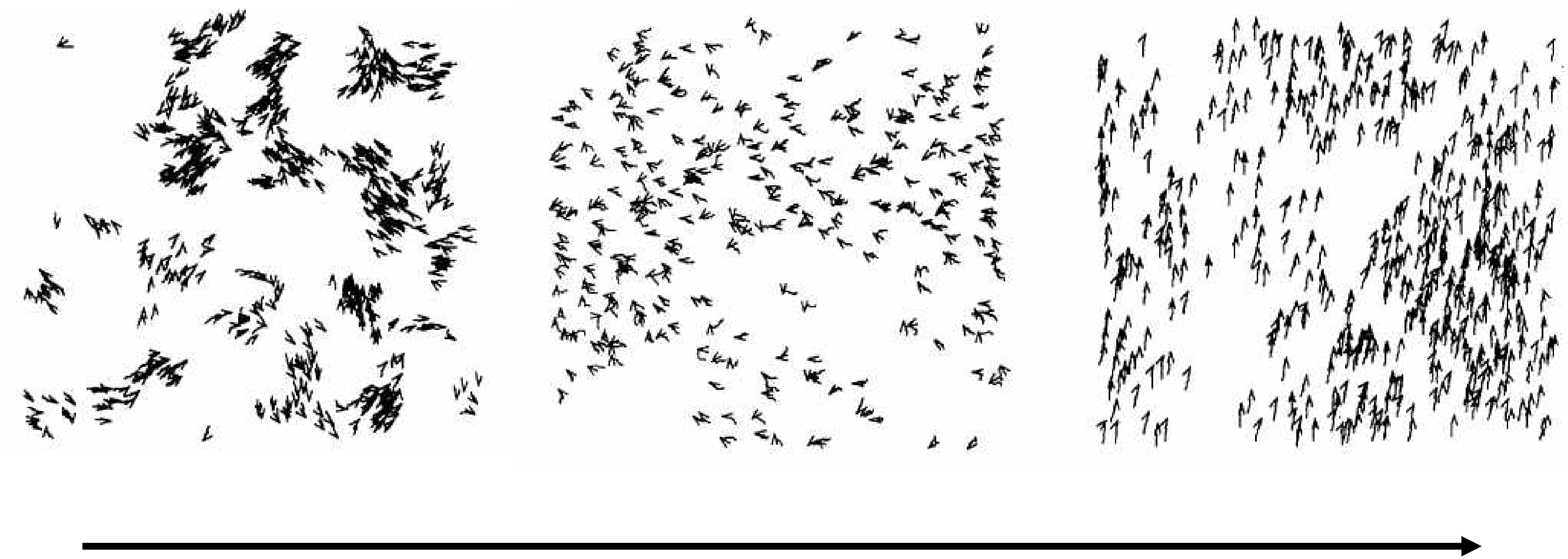
Collective motion in a simple model

The Vicsek model



Decreasing noise values

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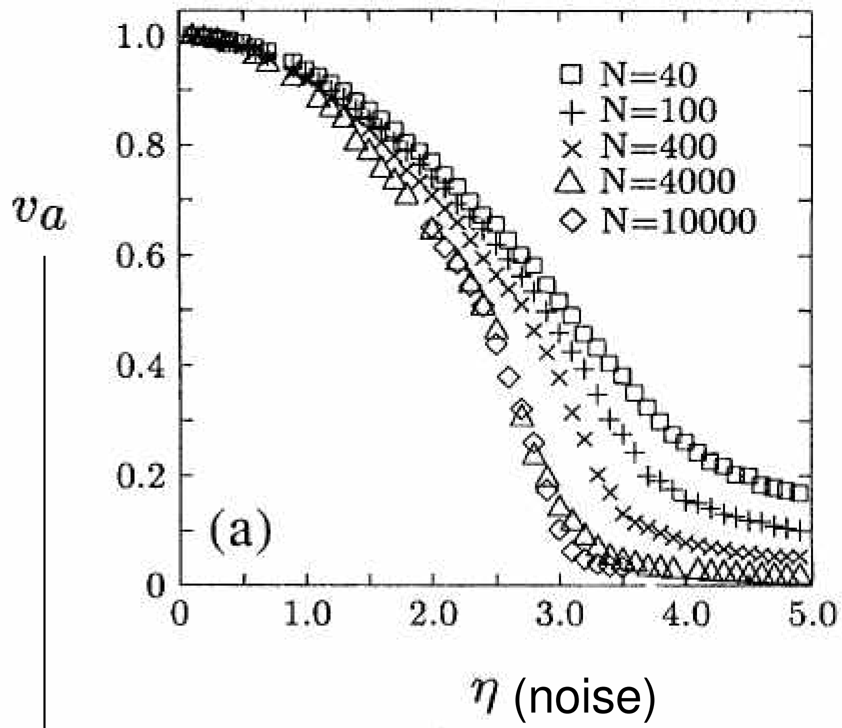
Collective motion in a simple model

The Vicsek model



$$v_a = \frac{1}{Nv} \left| \sum_{i=1}^{N} \mathbf{v}_i \right|$$

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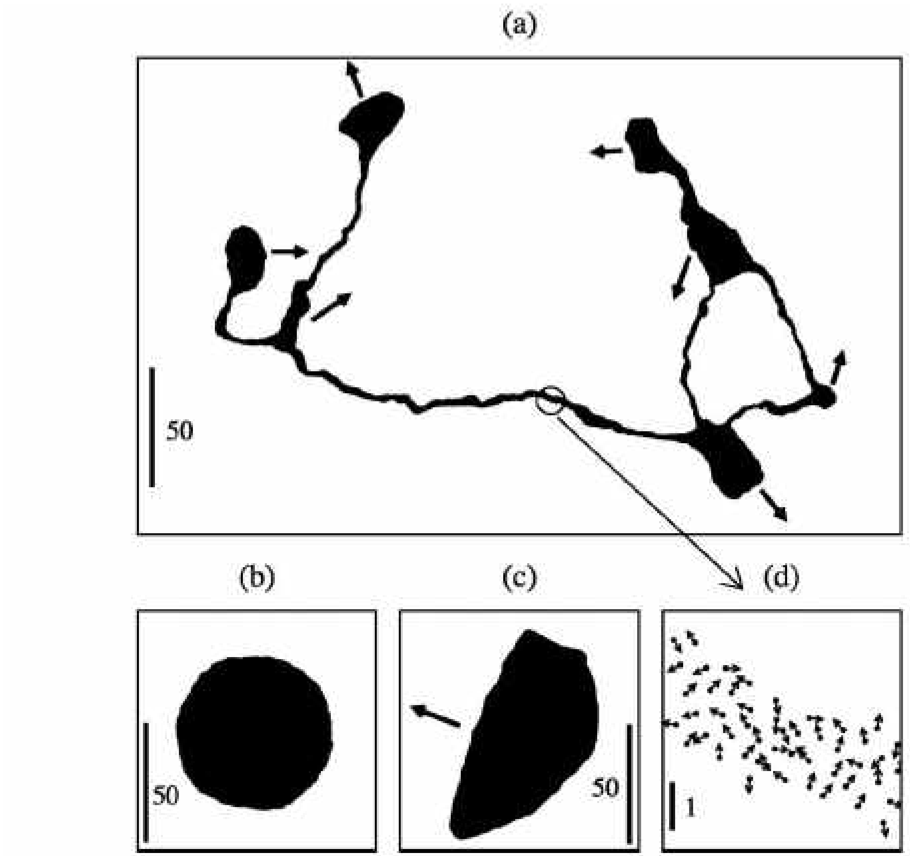
Collective motion in a simple model

<u>Need of cohesion to sustain a flock in open space</u>

[G. Grégoire and H. Chaté, Phys. Rev. Lett. 92, 025702 (2004)]



$$\theta_j^{t+1} = \arg\left[\alpha \sum_{k\sim j} e^{i\theta_k^t} + \beta \sum_{k\sim j} f^t_{jk} e^{i\theta^t_{jk}} + \eta n_j^t e^{i\xi_j^t} \right],$$

where,

$$f_{jk} = \begin{cases} -\infty & \text{if } r_{jk} < r_c \\ \frac{1}{4}\frac{r_{jk}-r_e}{r_a-r_e} & \text{if } r_c < r_{jk} < r_a \\ 1 & \text{if } r_a < r_{jk} < r_0, \end{cases}$$

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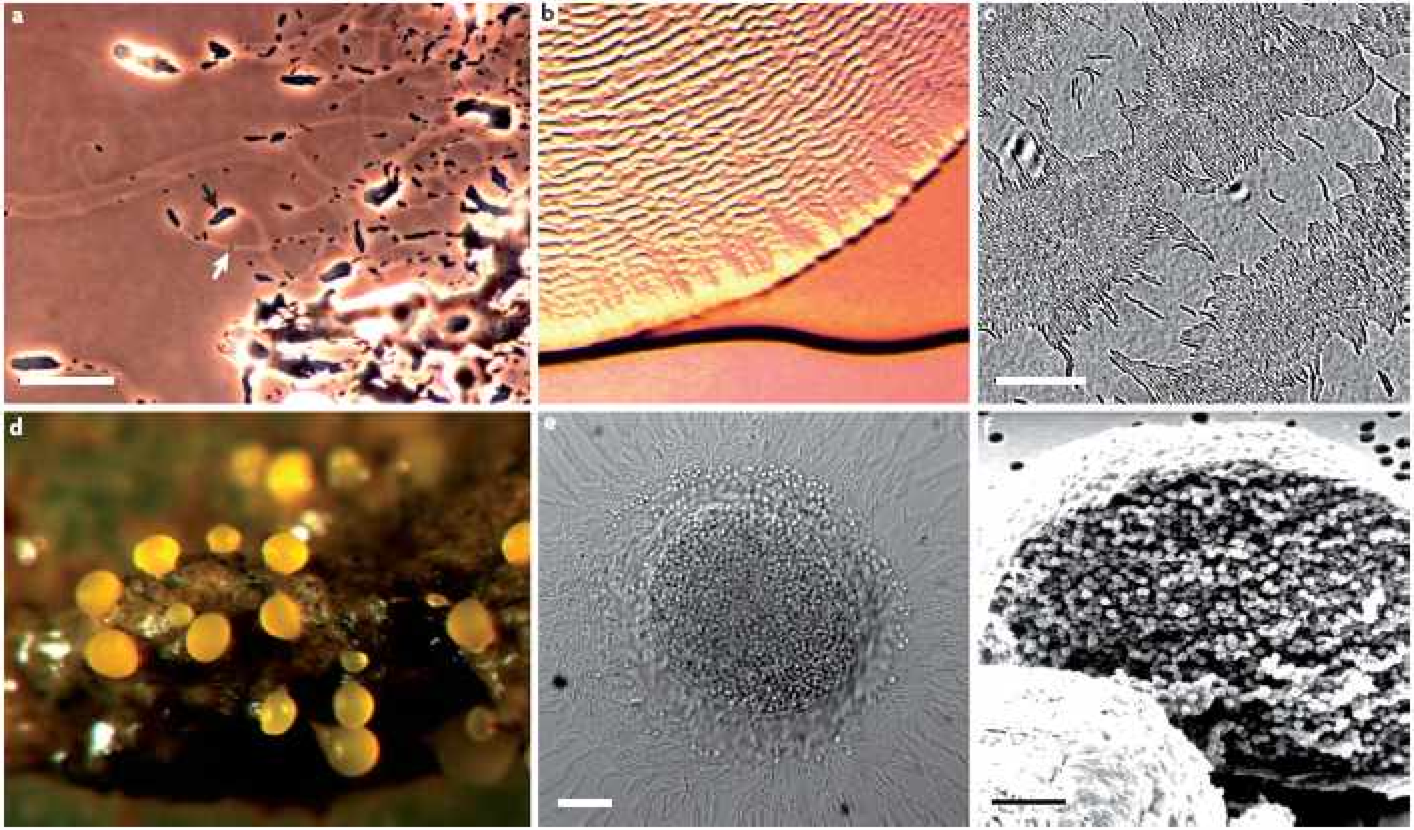
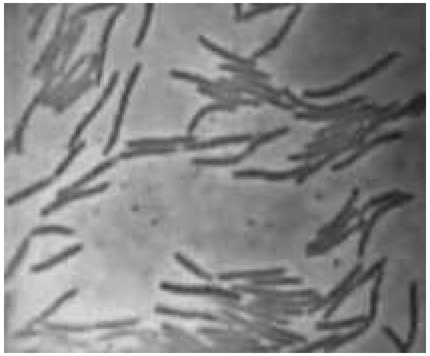
A specific example: collective motion in myxobacteria

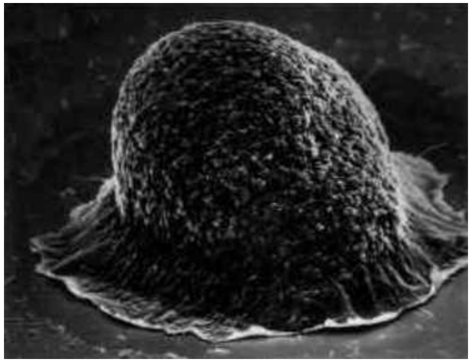
Myxococcus xanthus

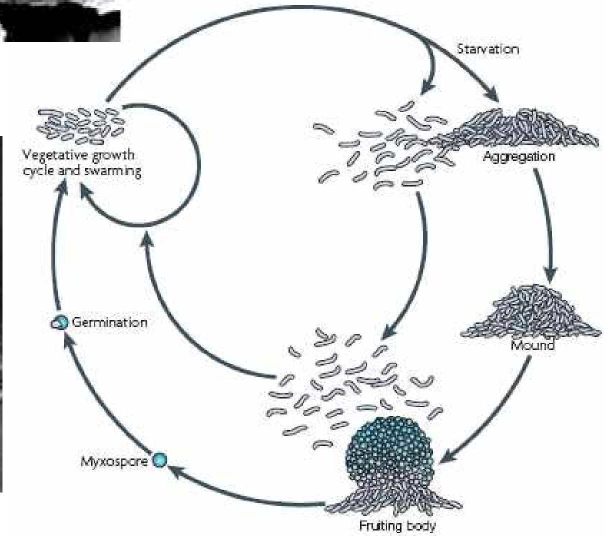


Zusman 2007

Reichenbach 1965







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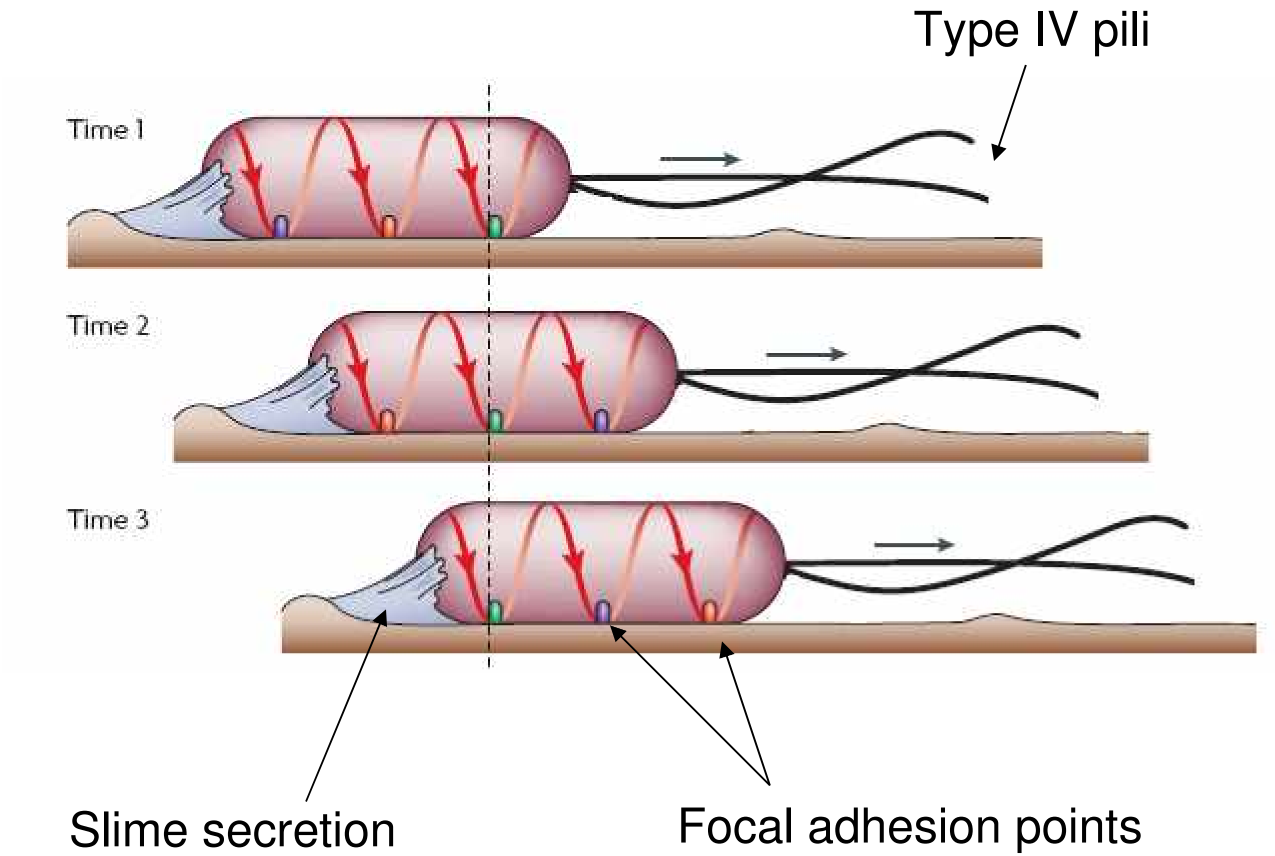
A specific example: collective motion in myxobacteria

- **<u>Motility engines in M. xanthus:</u>**



Pelling 05

Myxobacteria (speed = 0.025 to 0.1 μm/s)
Cyanobacteria (speed =10 μm/s)
Cytophaga-Flavobacterium (speed = 2 to 4 μm/s)

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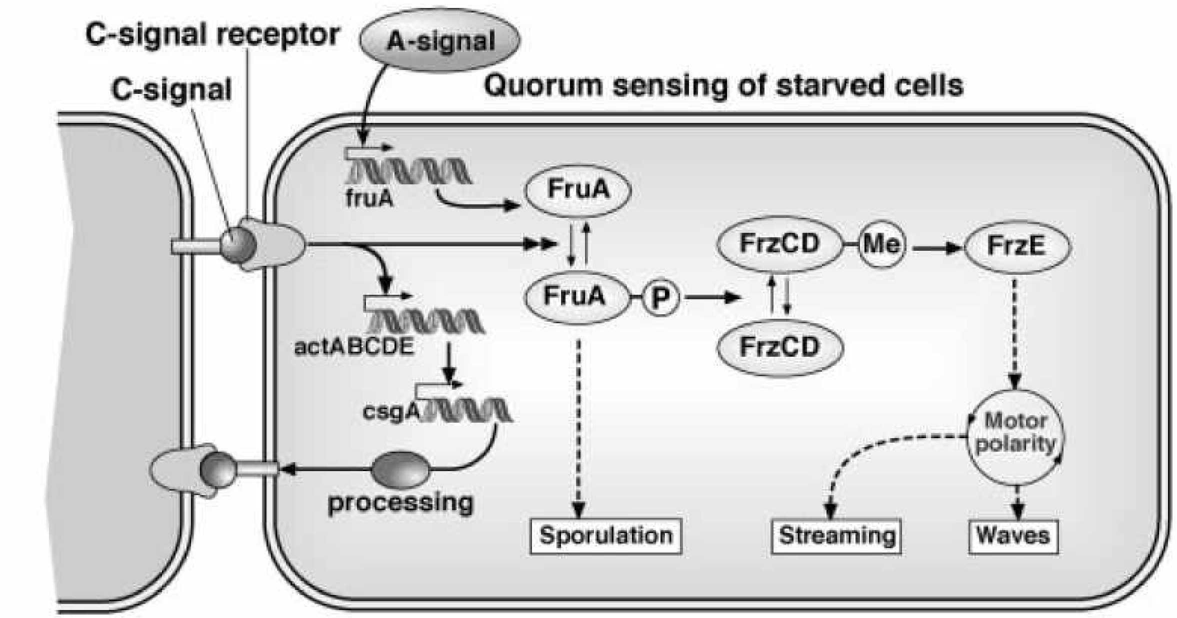
A specific example: collective motion in myxobacteria

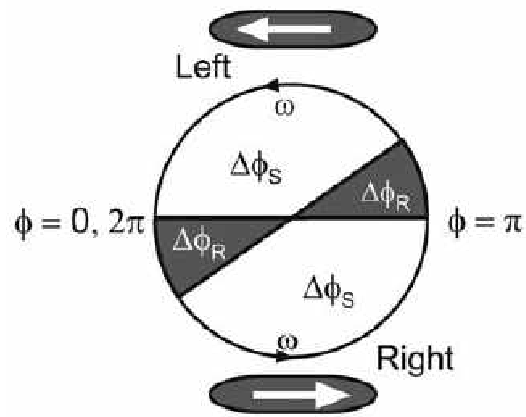
- **How do M. xanthus cells communicate?**

  - A quorum sensing diffusive mechanism to trigger the life cycle.
  - There is no evidence of a guiding chemotactic signals involved in collective motion.
  - Cells exchange C-signal which controls cell reversal (it requires cell-cell contact).

- **Cell reversal and C-signal:**



Igoshin & Oster 2003



Internal clock

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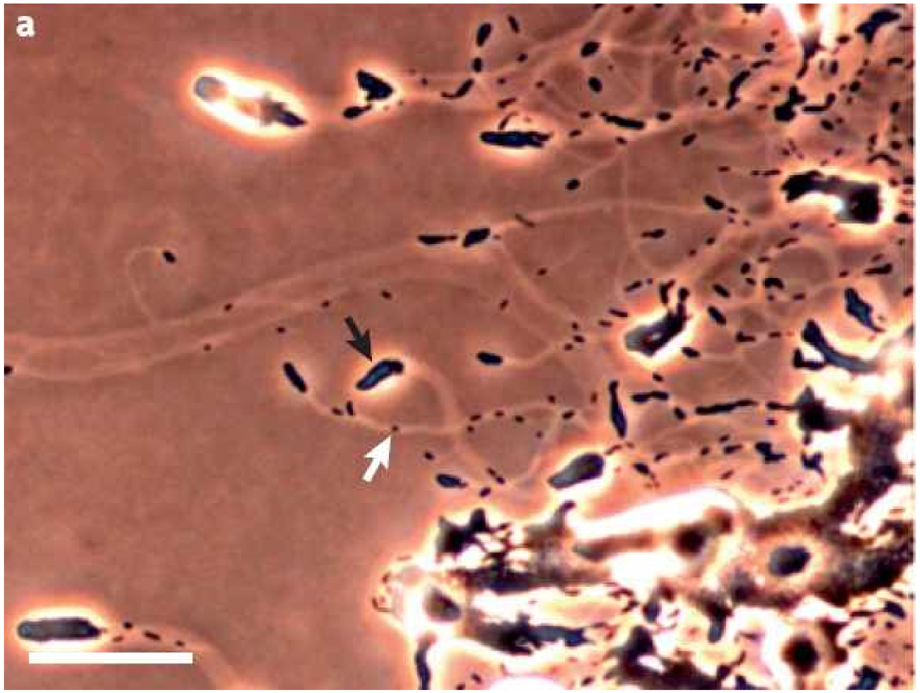
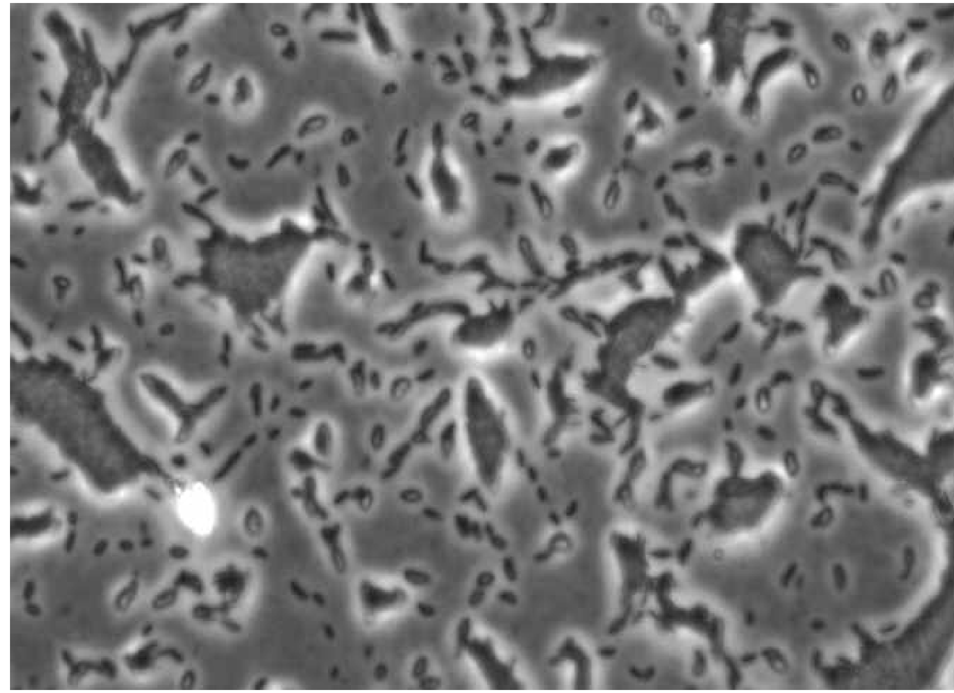
A specific example: collective motion in myxobacteria

Which mechanism is used by the cells to coordinate their motion?





(Collective motion and clustering in the wild type during the vegetative growth)

- Is there a hidden guiding chemotactic signal?
- Can slime trail following cause these effects?
- Is there a cell-density sensing mechanism that controls cell speed causing of these effects?
- What is the minimal mechanism that can produce these effects?

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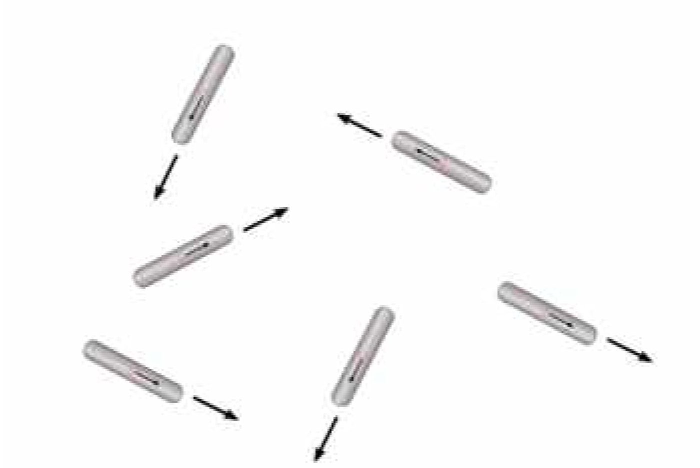
A specific example: collective motion in myxobacteria

Self-propulsion of bacteria + elongated shape

= collective behavior ?

What macroscopic effects can we expect

in a system of self-propelled rods ?



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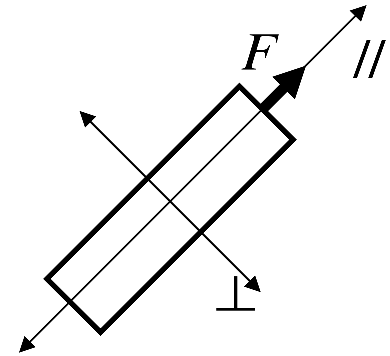
A specific example: collective motion in myxobacteria

A simple model for self-propelled rods

[F. Peruani, A. Deutsch, and M. Bär, Phys. Rev. E *74, 030904* (2006)]

We consider the over-damped situation in which we have:

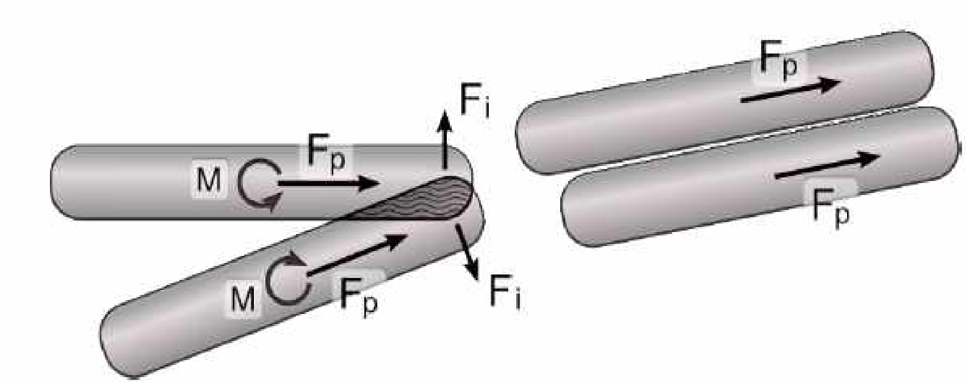


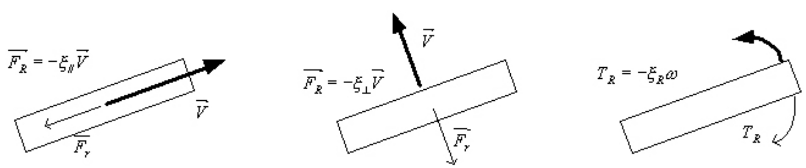
Self-Propelling force

$$\begin{cases} (v_{//}, v_{\perp}) = \left(\frac{1}{\zeta_{//}} \left(R_{//}(t) + F + F_{Inter_{//}} \right), \frac{1}{\zeta_{\perp}} \left(R_{\perp}(t) + F_{Inter_{\perp}} \right) \right) \\ \frac{d\theta}{dt} = \frac{1}{\zeta_R} \left(\tilde{R}(t) + M_{Inter} \right) \end{cases}$$

Interactions

$R_{//}, R_{\perp}, \tilde{R}$ **are white noises!**





Interactions are due to overlapping of particles :

$$V(\vec{x}, \theta, \vec{x}', \theta) = \tilde{C} \left\{ \frac{1}{\left(\gamma - a(\vec{x}, \theta, \vec{x}', \theta) \right)^{\beta}} - \frac{1}{\gamma^{\beta}} \right\}$$

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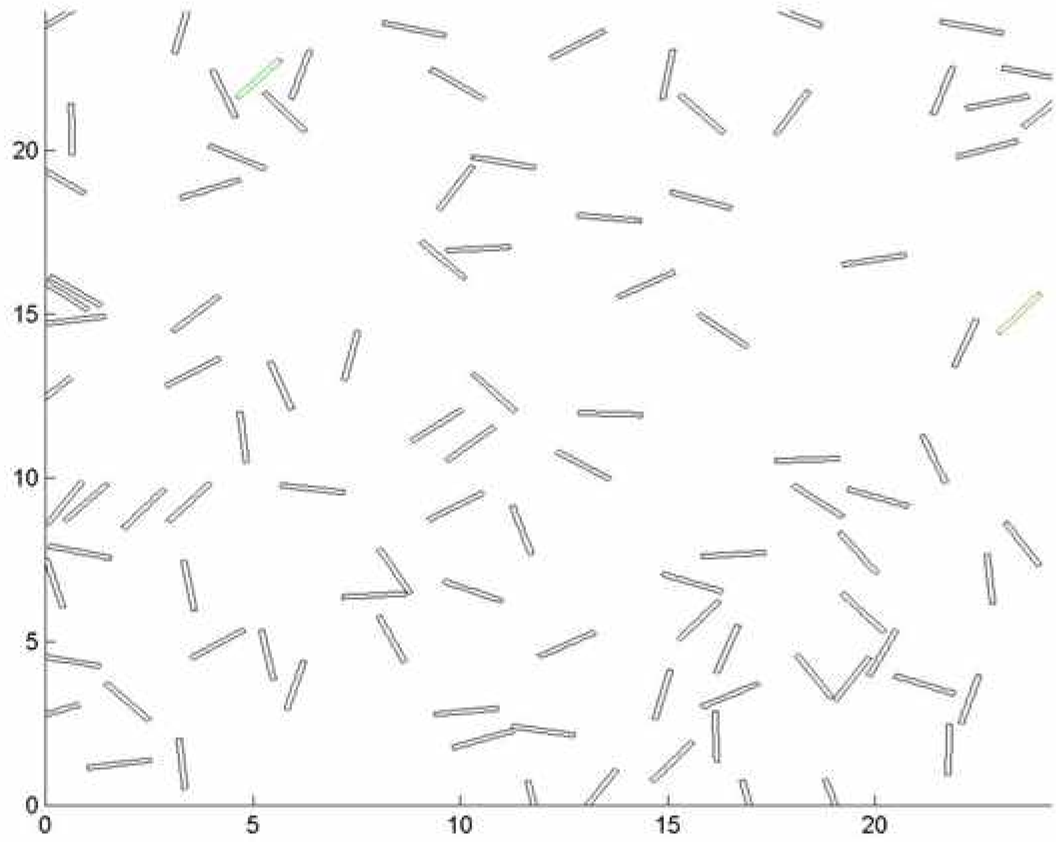
A specific example: collective motion in myxobacteria

- **<u>Putting the model in the computer</u>**- simulations w/ periodic boundary conditions!



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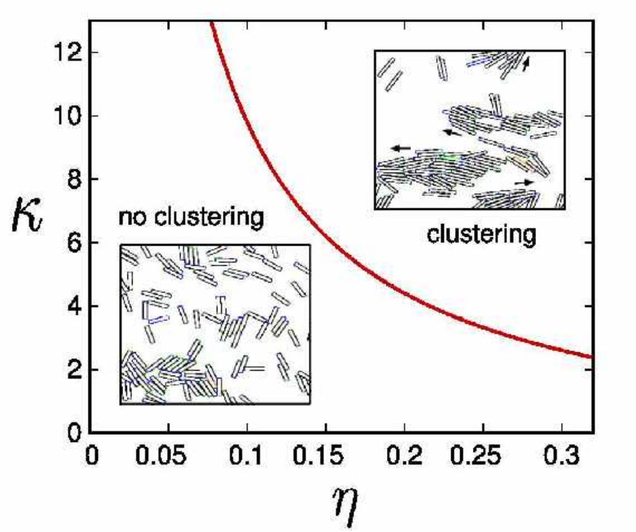
A specific example: collective motion in myxobacteria

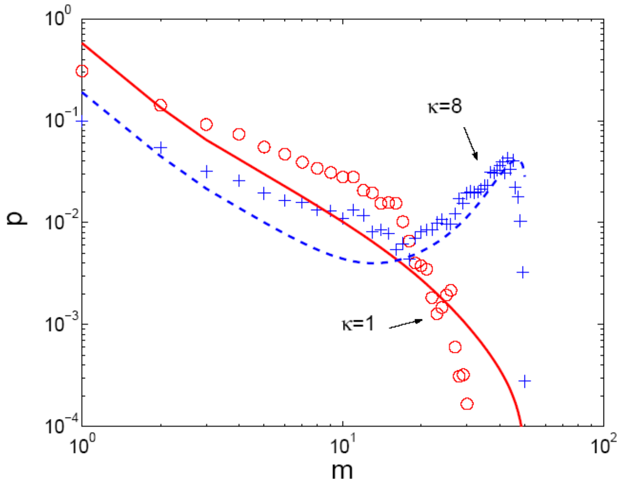
How can we characterize the macroscopic collective behavior of myxobacteria/self-propelled rods?

↓

What can we measure here?

By looking at the clustering properties we can differentiate between individual and collective behavior





Peruani, Deutsch, and Bär, PRE (2006)

There is a dramatic change in the clustering properties of the system when either the density or the aspect ratio of the particles is changed!

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A specific example: collective motion in myxobacteria

The evolution equation for the cluster size distribution → $\{n_j(t)\}_{j=1}^{\infty}$

$$\dot{n}_1 = 2B_2 n_2 + \sum_{k=3}^{N} B_k n_k - \sum_{k=1}^{N-1} A_{k,1} n_k n_1,$$

$$\dot{n}_j = B_{j+1} n_{j+1} - B_j n_j - \sum_{k=1}^{N-j} A_{k,j} n_k n_j + \frac{1}{2}\sum_{k=1}^{j-1} A_{k,j-k} n_k n_{j-k} \quad \text{for } j = 2, \ldots, N-1$$

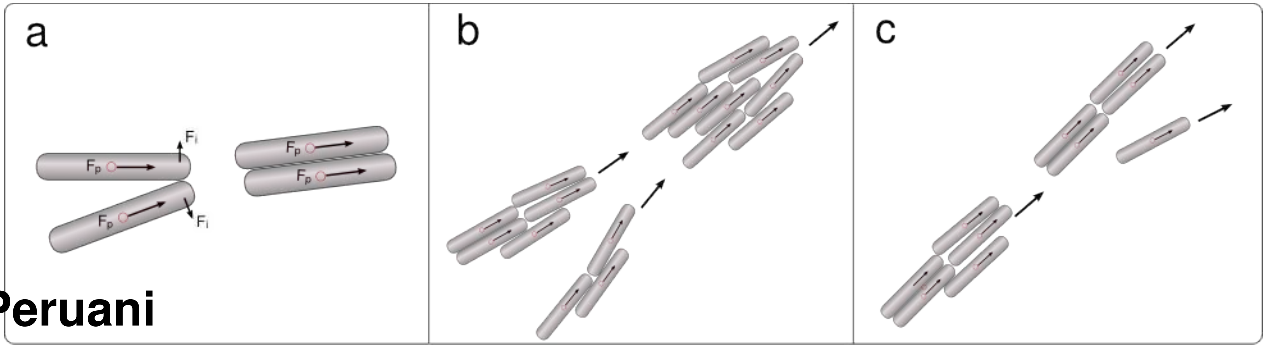
$$\dot{n}_N = -B_N n_N + \frac{1}{2}\sum_{k=1}^{N-1} A_{k,N-k} n_k n_{N-k},$$

collision kernel

$$A_{j,k} = (\tilde{v}\sigma_0/A)(\sqrt{j}+\sqrt{k})$$

fragmentation kernel

$$B_j = (\tilde{v}/L)\sqrt{j}$$



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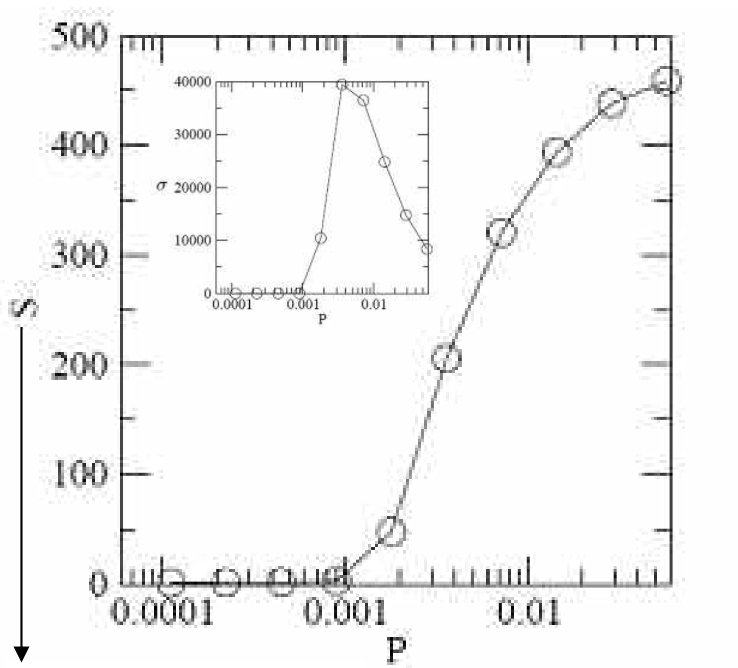
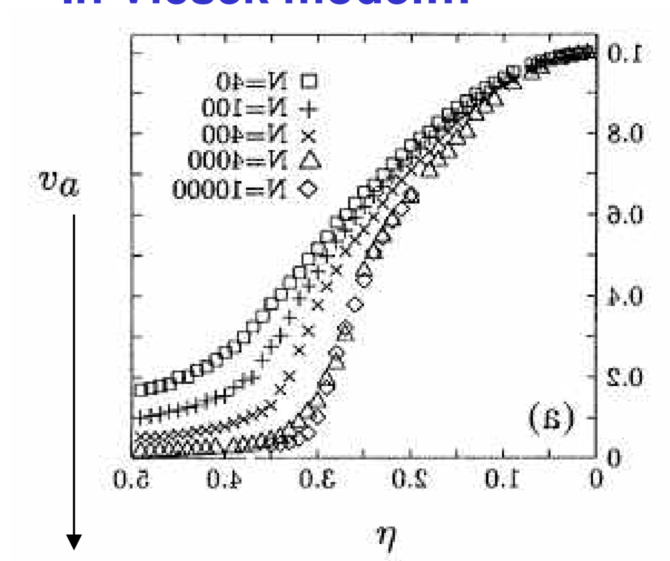
The system exhibits a phase transition to an aggregation phase



$$S = \sum_{k=1}^{N} k p_k$$

In Vicsek model…



$$v_a = \frac{1}{Nv} \left| \sum_{i=1}^{N} \mathbf{v}_i \right|$$

Three types of distributions/phases:

- Exponential (P<Pc) – [monodisperse phase w/ characteristic cluster size]
- Power-law (P=Pc) – [at the transition point, scale-free distribution]
- Peak for large m (P>Pc) – [aggregation phase!]

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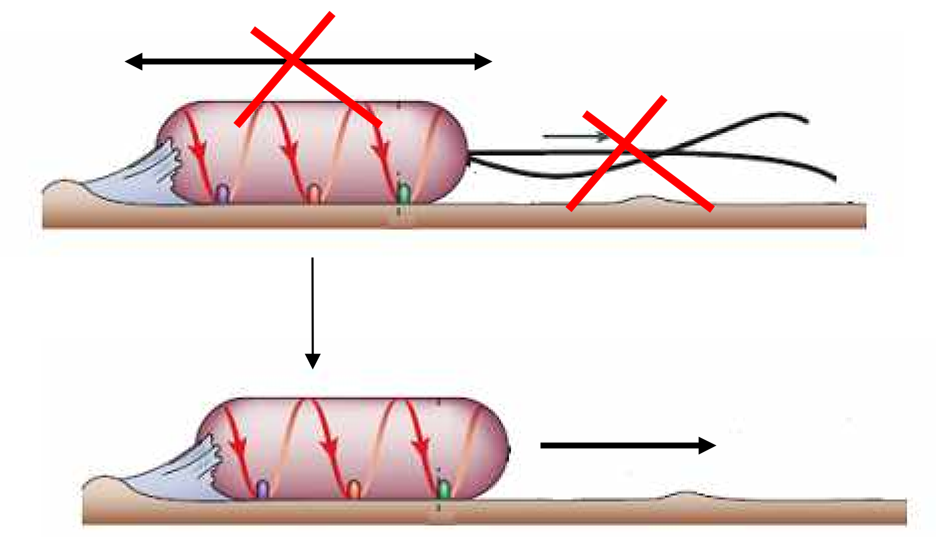
A specific example: collective motion in myxobacteria

What about collective motion and clustering in real myxobacteria ?

• **<u>Experiments with A+S-Frz- Myxococcus xanthus mutant</u>**

In collaboration with:
M. Bär, A. Deutsch, V. Jakovlievic, L. Søgaard-Andersen, and J. Starruß



***Adventurous* mutant:**

• **Cells do not reverse**

• **Social motility engine – off**

• **Advent. motility engine - on**

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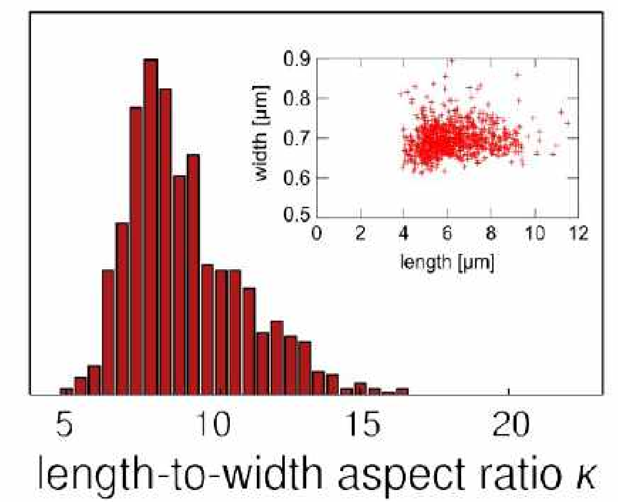
A specific example: collective motion in myxobacteria

• Clustering in the A+S-Frz- mutant

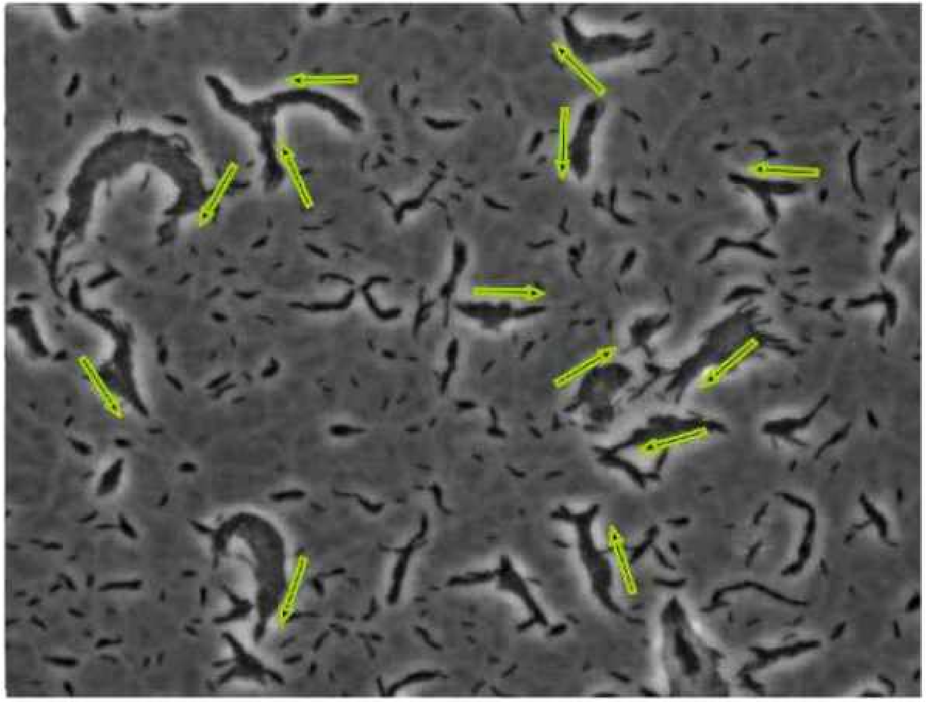


• Gliding speed = 3.10 ± 0.35 µm/min

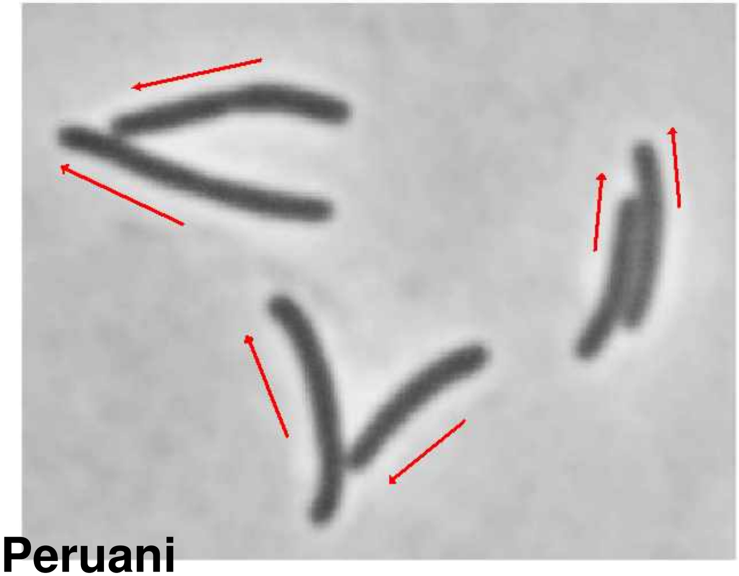
• W=0.7 µm, L=6.3 µm, a=4.4 µm^2

• κ=8.9 ± 1.95

Moving clusters of bacteria are formed:



Cell collision leads to alignment:



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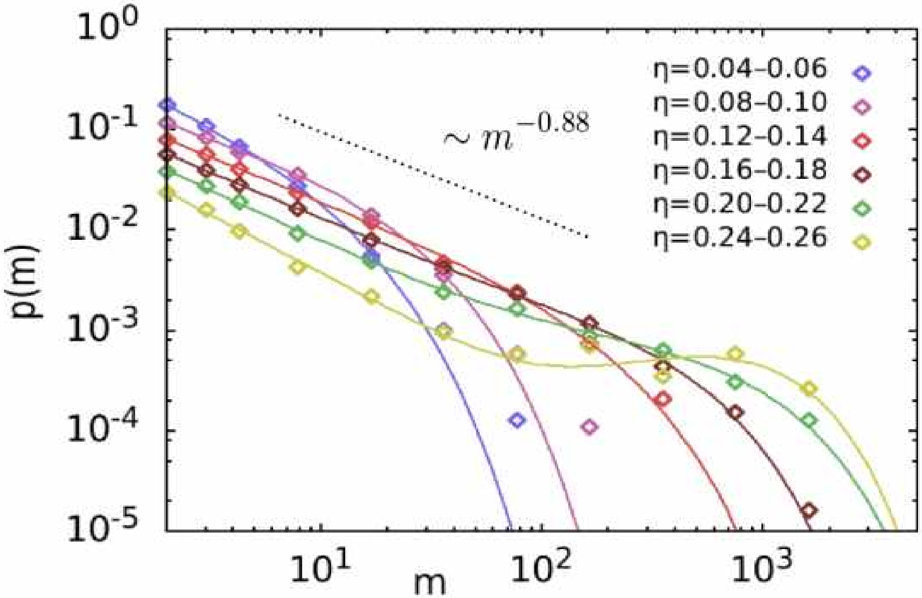
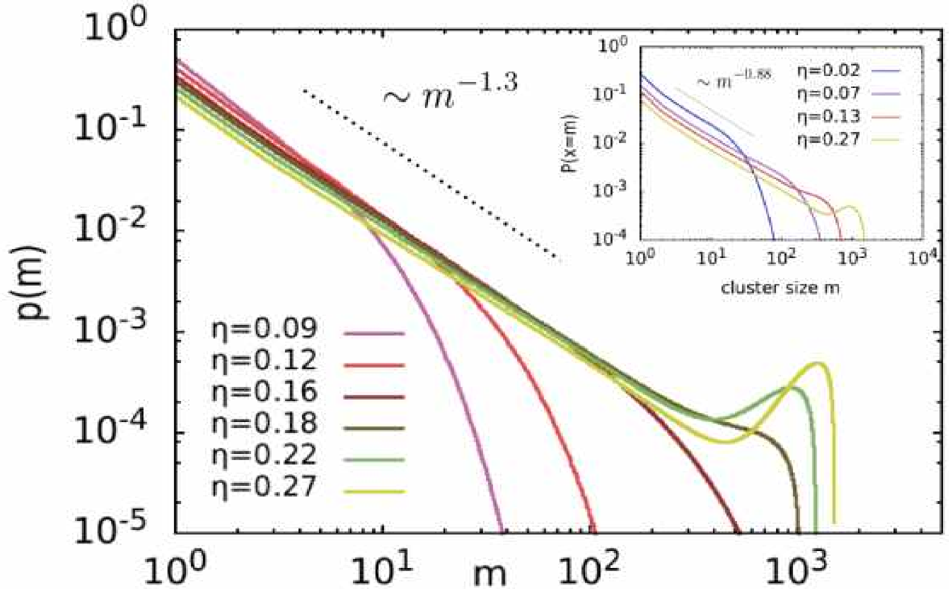
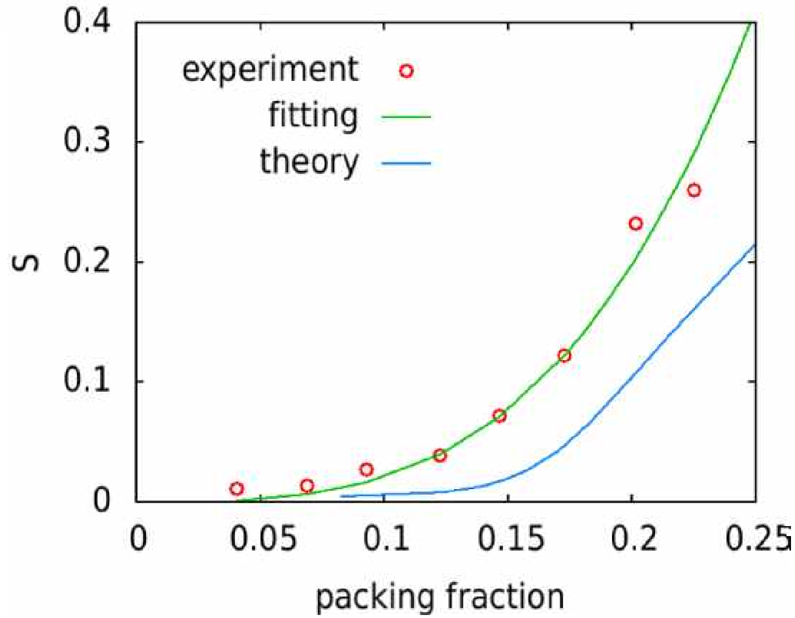
A specific example: collective motion in myxobacteria

- **Comparison: theory and experiments**







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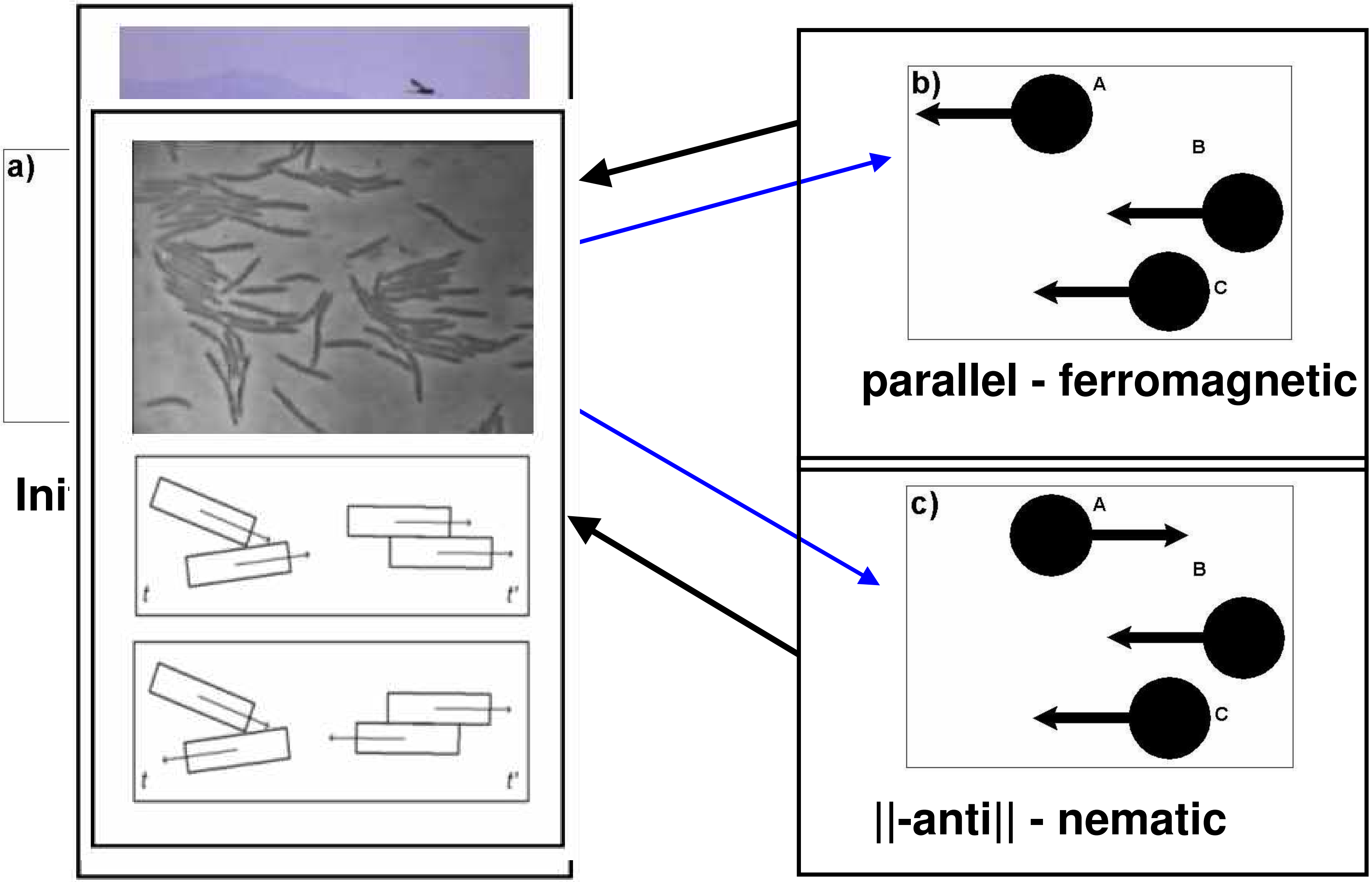
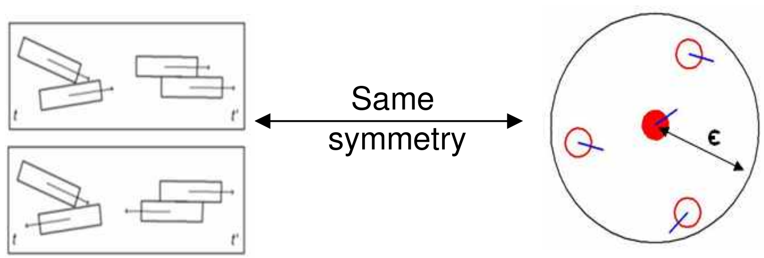
Symmetries!



Symmetries!

A simple model for self-propelled rods (e.g., bacteria)

[F. Peruani, A. Deutsch, and M. Bär, Eur. Phys. J. Special Topics 157, 111 (2008)]



$$\mathbf{x}_i^{t+\Delta t} = \mathbf{x}_i^t + v_0 \mathbf{v}\left(\theta_i^t\right)\Delta t$$

$$\theta_i^{t+\Delta t} = \arg\left(\sum_{\left|\mathbf{x}_i^t - \mathbf{x}_j^t\right| \le \epsilon} \mathbf{f}\left(\mathbf{v}(\theta_j^t), \mathbf{v}(\theta_i^t)\right)\right) + \eta_i^t$$

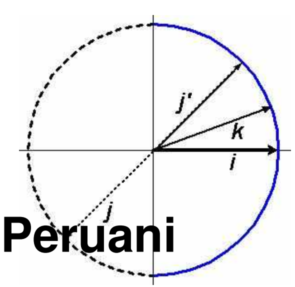
Particles move in the direction given by:

$$\mathbf{v}(\theta_i) = (\cos(\theta_i), \sin(\theta_i))$$

Update of the moving direction

Alignment

Additive noise



$$f\left(\mathbf{v}_j, \mathbf{v}_i\right) = \begin{cases} \mathbf{v}_j & if \quad \mathbf{v}_i . \mathbf{v}_j \ge 0 \\ -\mathbf{v}_j & if \quad \mathbf{v}_i . \mathbf{v}_j < 0 \end{cases}$$

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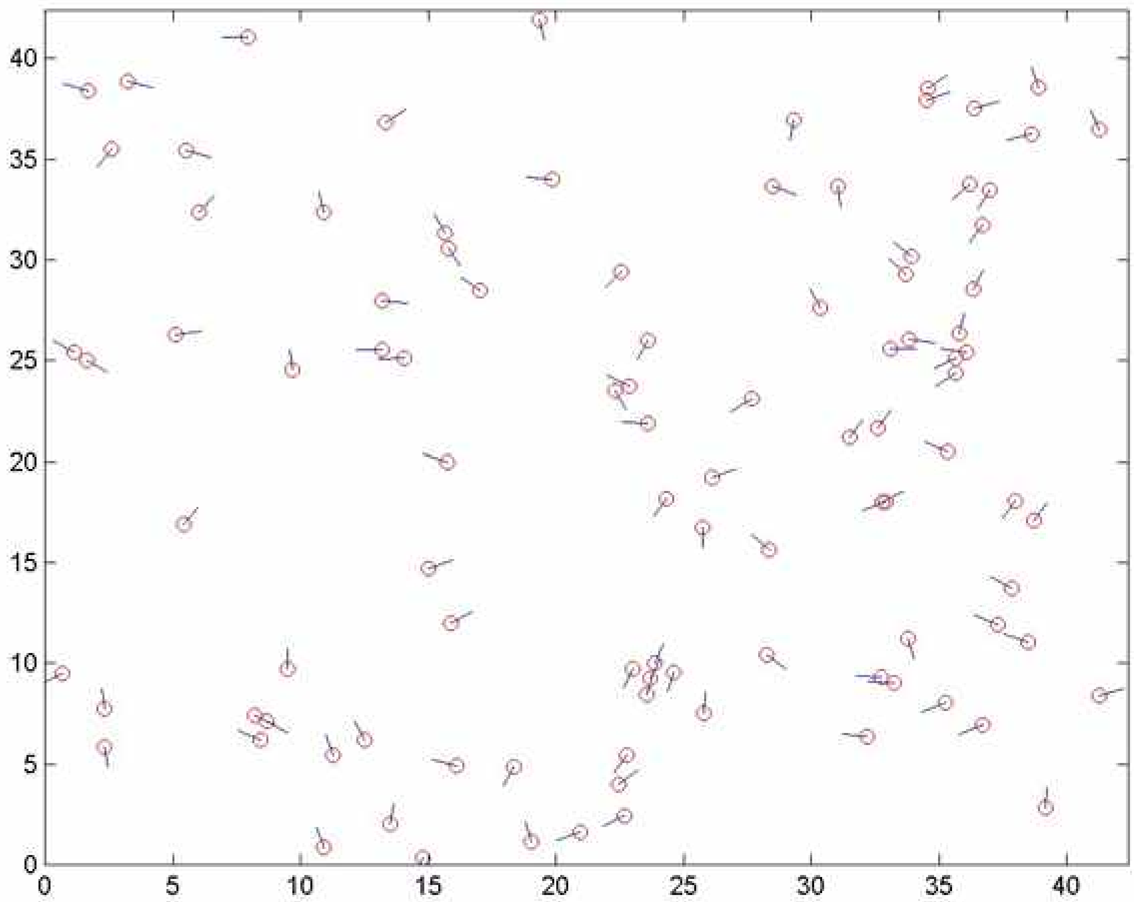
Symmetries!



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Symmetries!

The symmetry of the alignment determines the type of macroscopic order

[F. Peruani, A. Deutsch, and M. Bär, Eur. Phys. J. Special Topics 157, 111 (2008)]

- **A mean-field approach to understand collective motion**

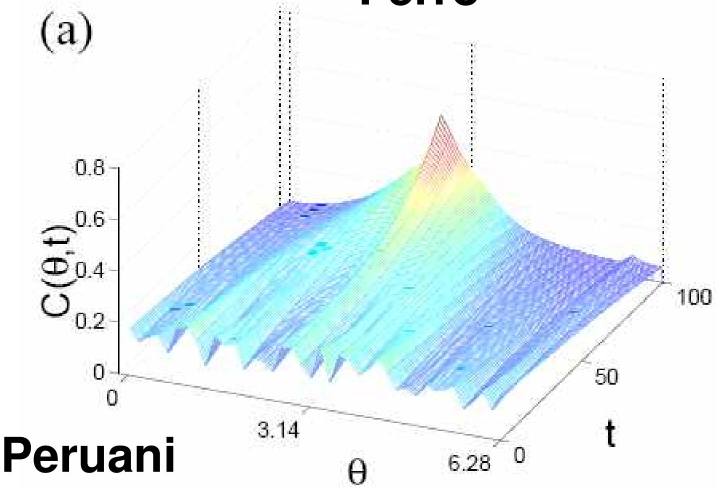
$$\partial_t C = \underbrace{D_\theta \partial_{\theta\theta} C}_{\text{noise}} + \gamma(\rho)\partial_\theta \left[\underbrace{\partial_\theta \left(\int_0^{2\pi} d\theta' C(\theta', t)\, U(\theta, \theta') \right) C(\theta, t)}_{\text{alignment}} \right]$$

noise alignment

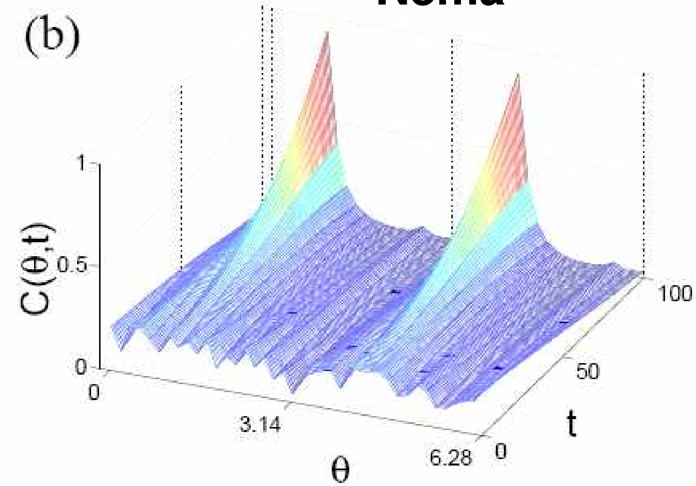
Ferromagnetic alignment → $U(\theta, \theta') = -\cos(\theta - \theta')$

Nematic alignment → $U(\theta, \theta') = -\cos^2(\theta - \theta')$

Ferro



Nema



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noise — alignment

Ferromagnetic alignment → $U(\theta, \theta') = -\cos(\theta - \theta')$

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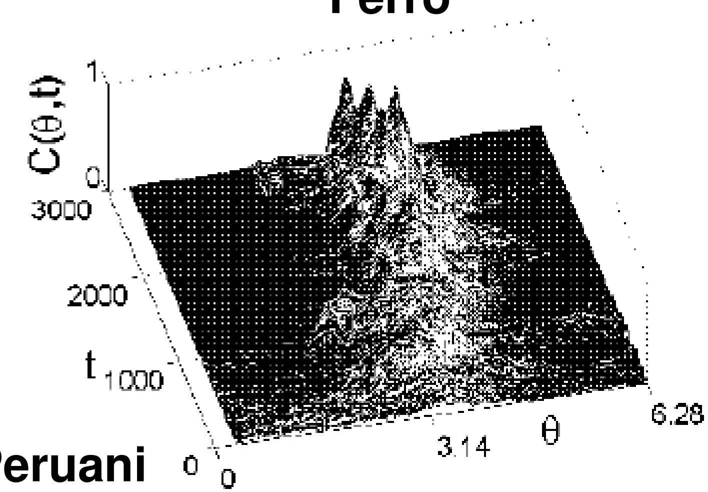
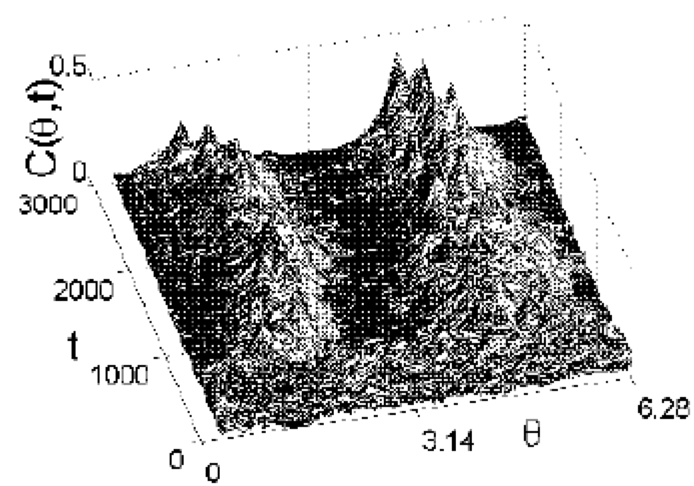
Ferro



Nema



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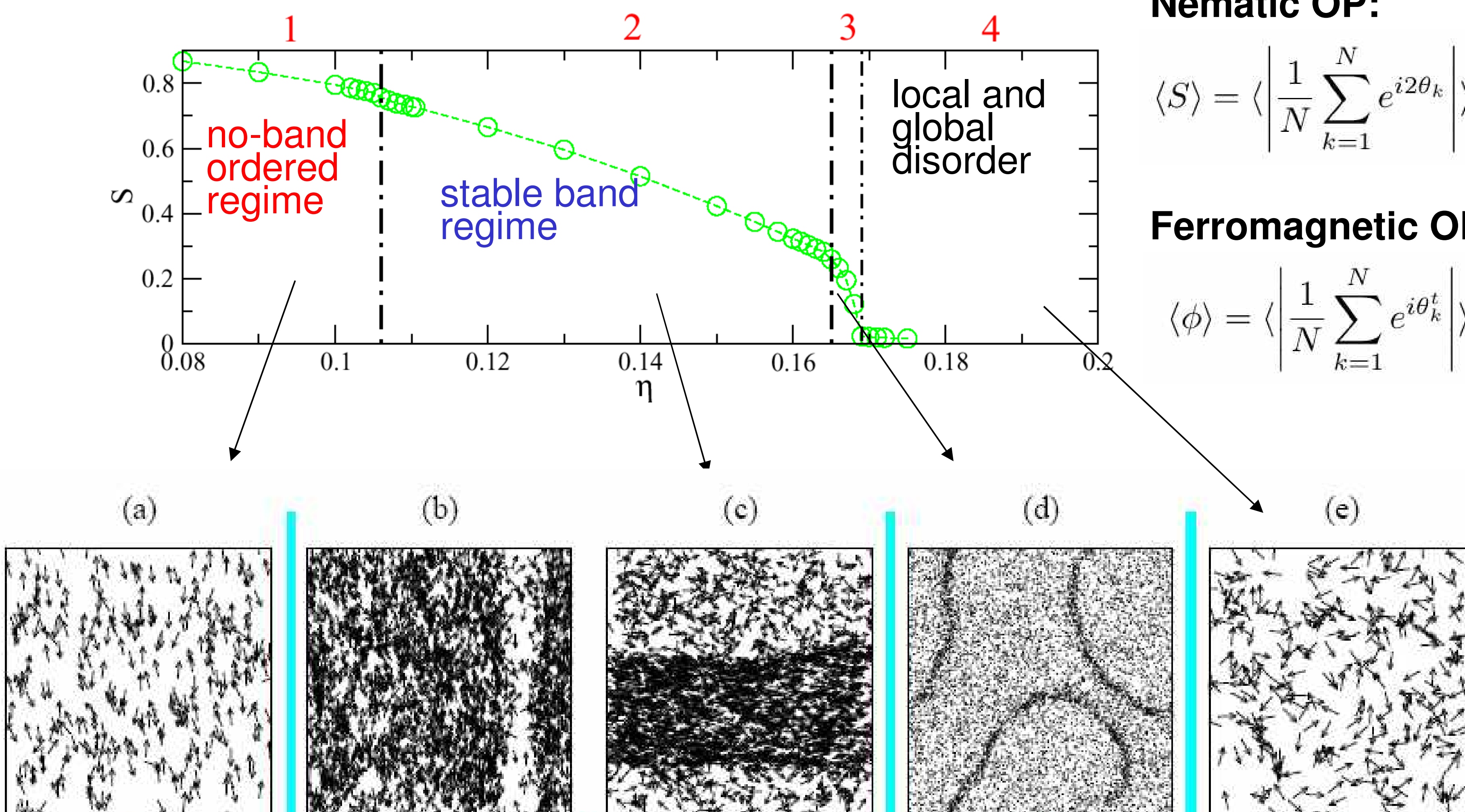
Symmetries!

The symmetry of the alignment plays a crucial role in pattern formation

[F. Ginelli, F. Peruani, M. Bär, and H. Chaté, Phys. Rev. Lett. 104, 184502 (2010)]



Nematic OP:

$$\langle S\rangle = \left\langle \left| \frac{1}{N}\sum_{k=1}^{N} e^{i2\theta_k} \right| \right\rangle_t$$

Ferromagnetic OP:

$$\langle \phi\rangle = \left\langle \left| \frac{1}{N}\sum_{k=1}^{N} e^{i\theta_k^t} \right| \right\rangle_t$$

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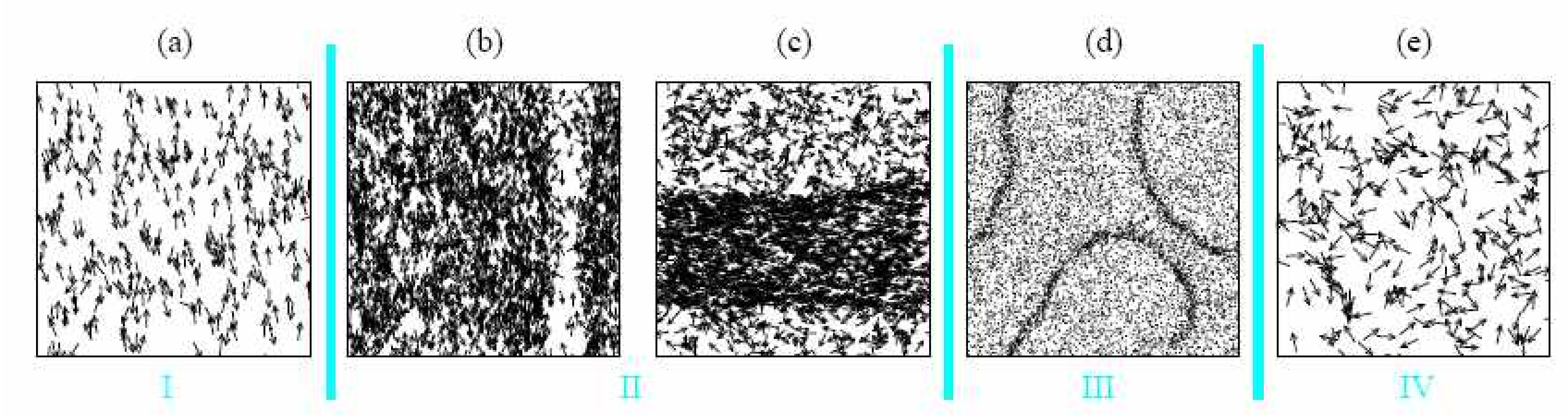

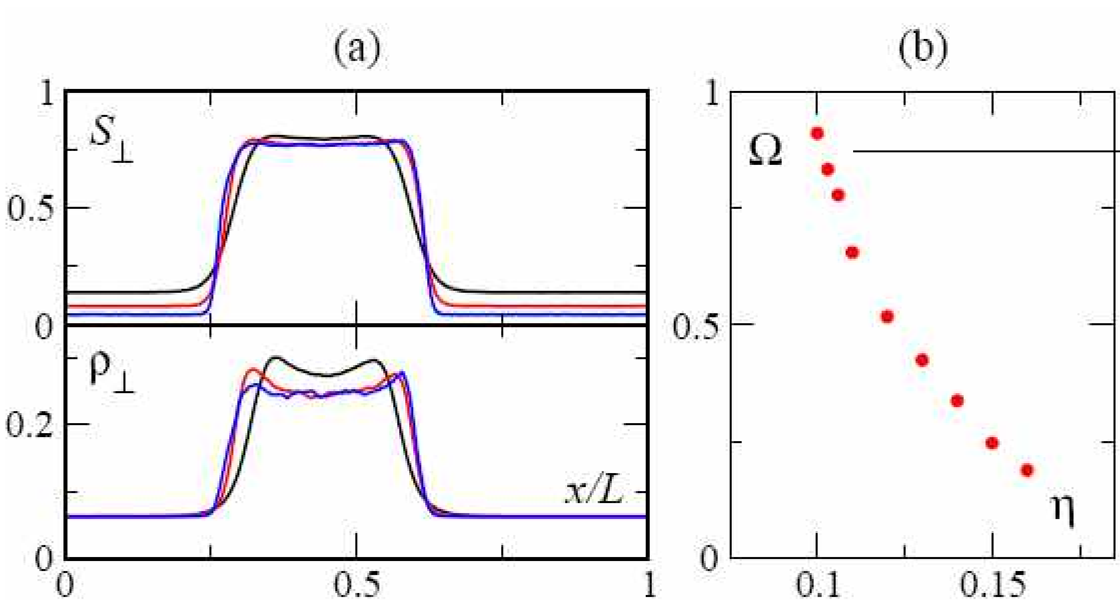

Fraction of the area occupied by the band

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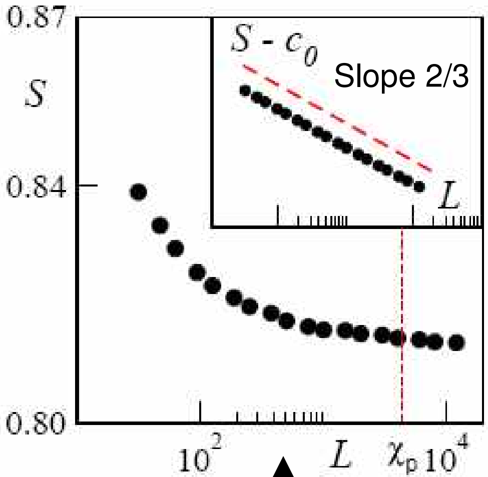
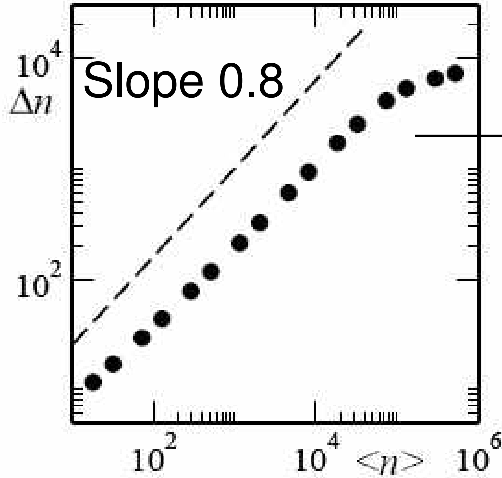
Symmetries!

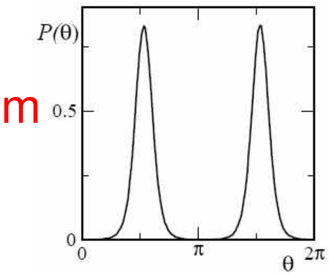


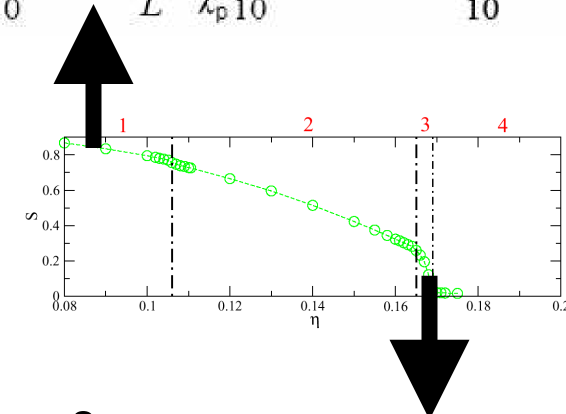


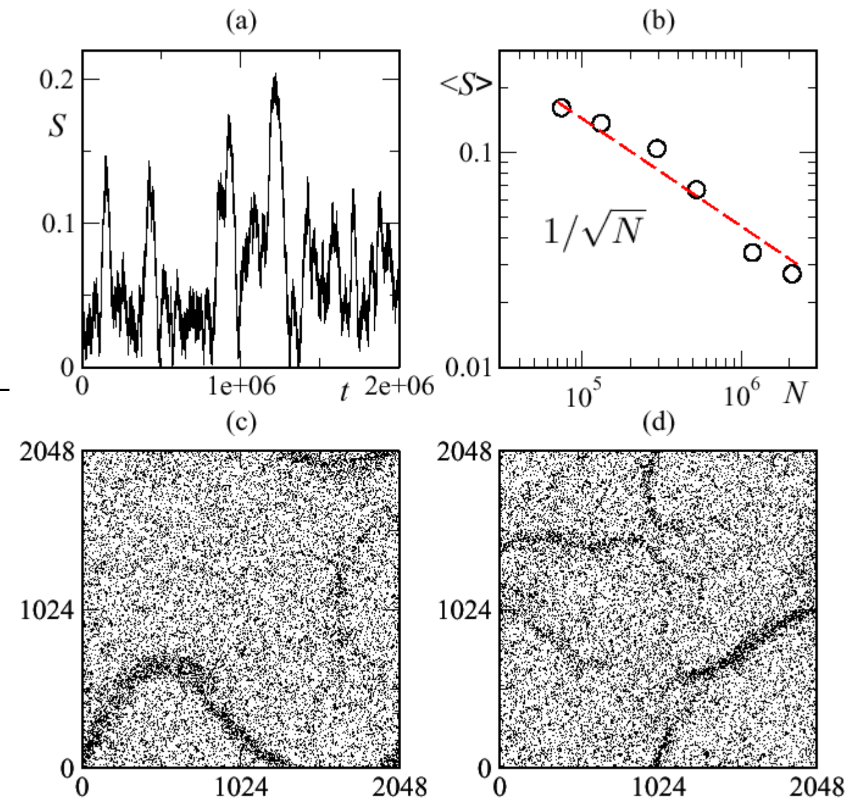
In regime 1:

- True Long-Range Order (LRO)
- Giant fluctuations

Mermin Wagner Theorem (for equilibrium syst.) does not allow for LRO!







In regime 3:

- There is no LRO
- Unstable macroscopic structures (bands!)

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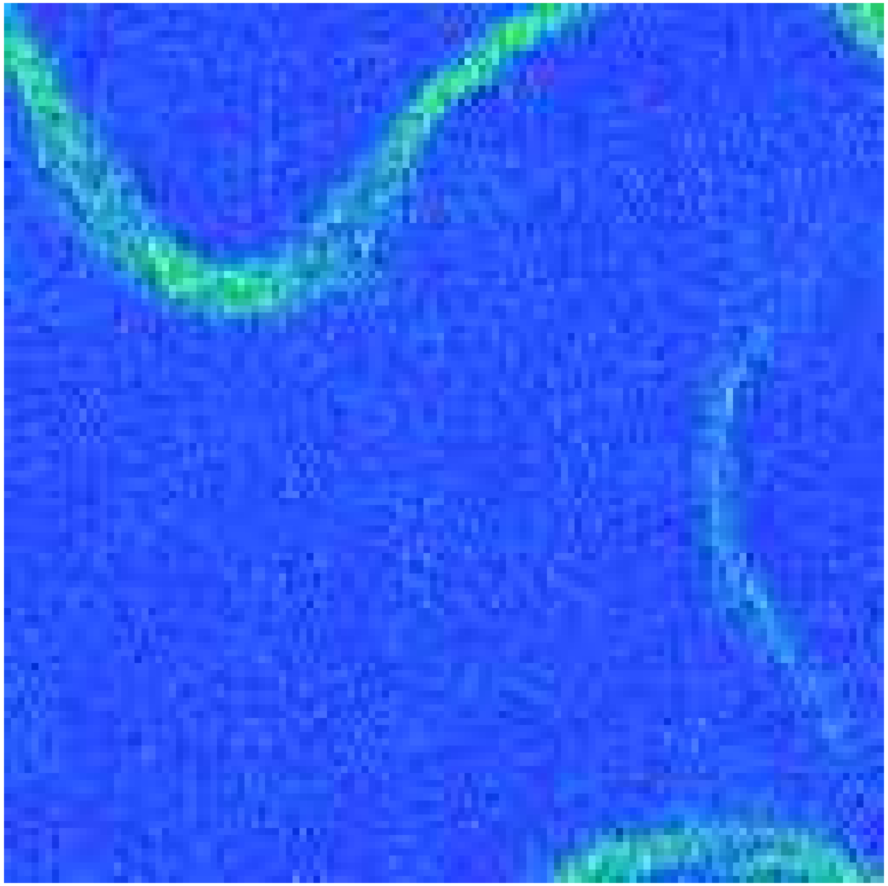
The symmetry of the alignment plays a crucial role in pattern formation



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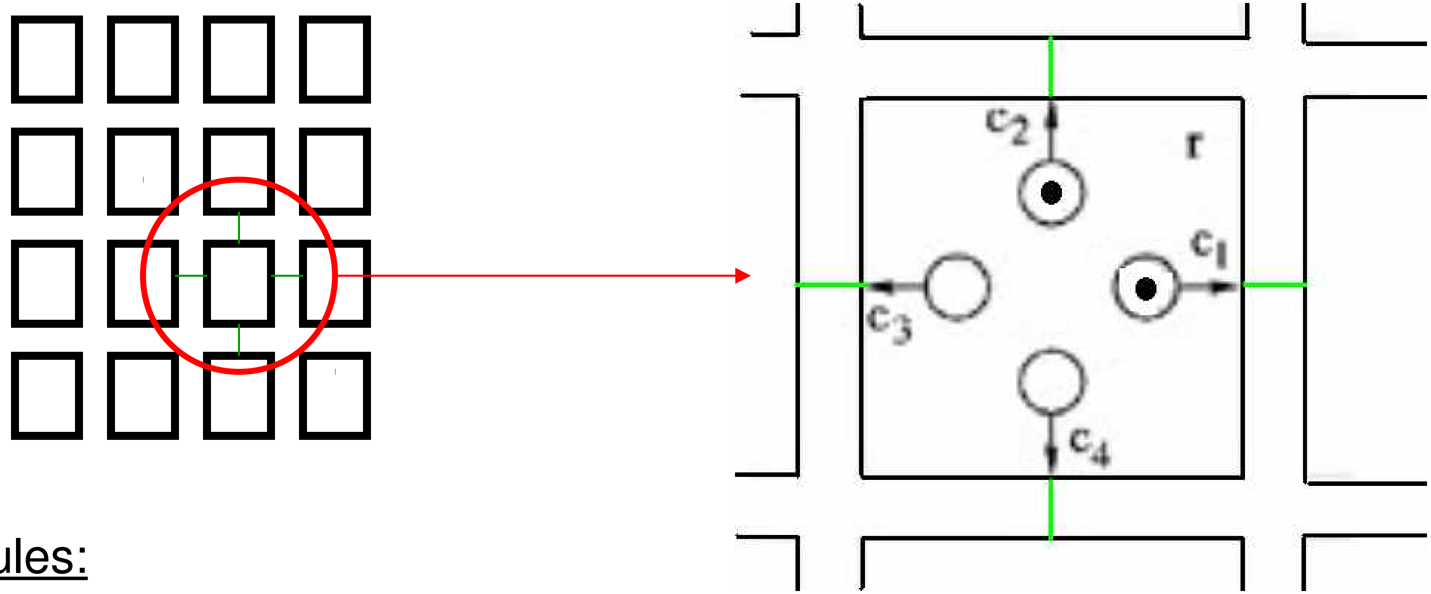
Collective motion on the lattice

Collective motion in a simple cellular automaton model

[H.J. Bussemaker, A. Deutsch, and E. Geigant, Phys. Rev. Lett. 78, 5018 (1997)]



Rules:

1) Migration to next neighbor (according to channel direction)

2) Reorientation (i.e., velocity change) according to the following rule:

$$A[s \rightarrow \sigma \mid \mathbf{D}] = \frac{1}{Z}\,\delta[\rho(\sigma), \rho(s)]\exp[\beta \mathbf{D} \cdot \mathbf{J}(\sigma)]$$

Mean local velocity:

Where Z defined such that $\sum_{\sigma} A[s \rightarrow \sigma \mid \mathbf{D}] = 1$ and $\mathbf{D}(\mathbf{r}, t) = \sum_{p=1}^{4} \sum_{i=1}^{4} \mathbf{c}_i s_i(\mathbf{r} + \mathbf{c}_p, t)$

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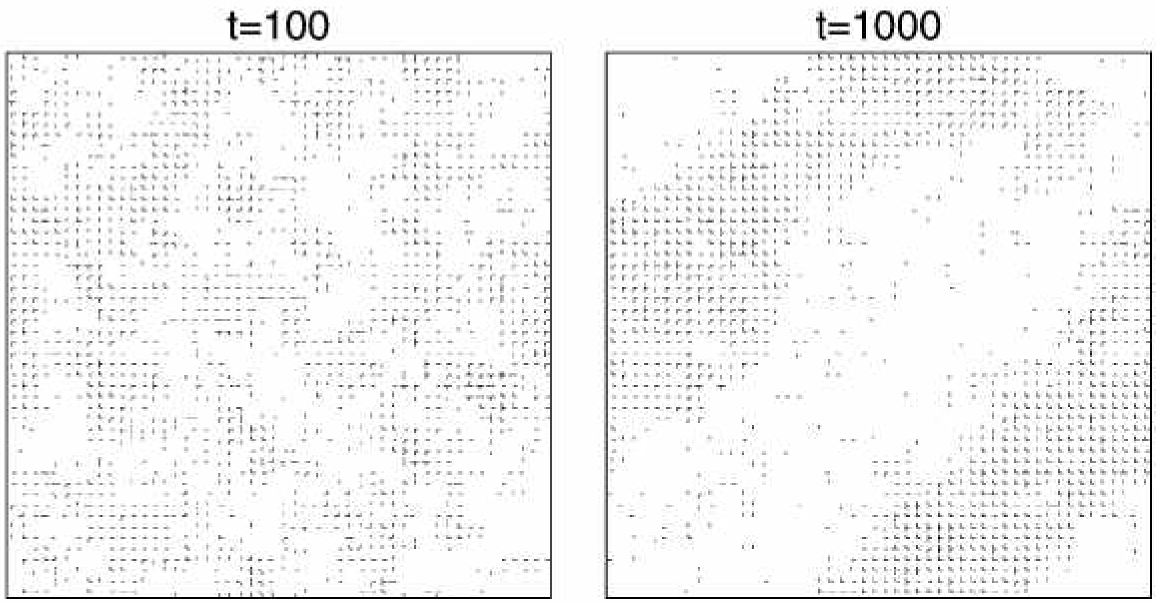
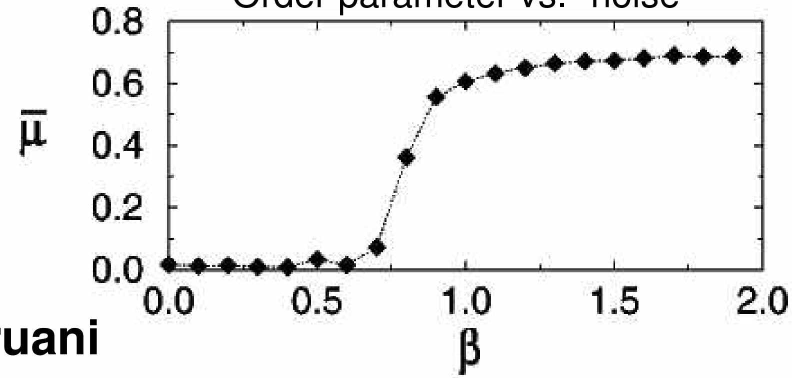


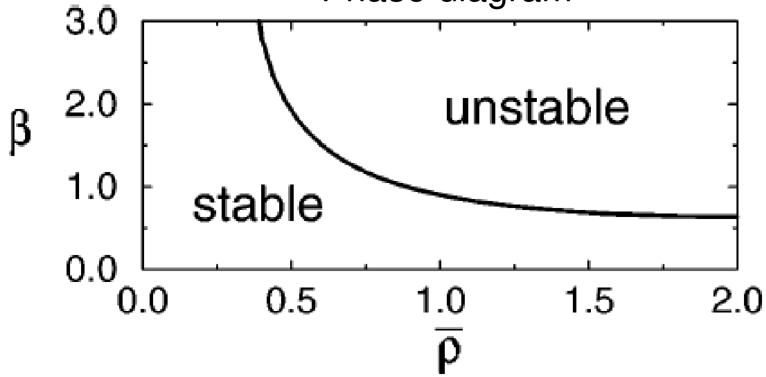
Parameters: L=50, ß=1.5, ρ=0.8 (N ~ 2000)

Order parameter vs. “noise”



Mean velocity

Phase diagram



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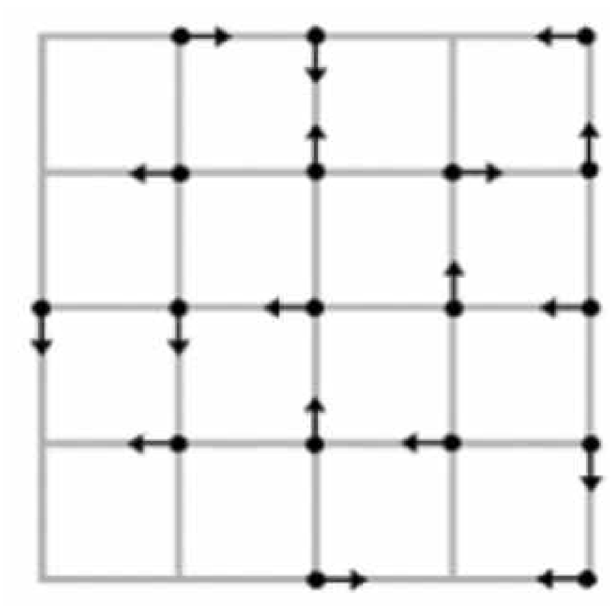
Collective motion on the lattice

First- and second order phase transition in a lattice model for swarming

In collaboration with:
T. Klauß, A. Deutsch, and A. Voß-Böhme



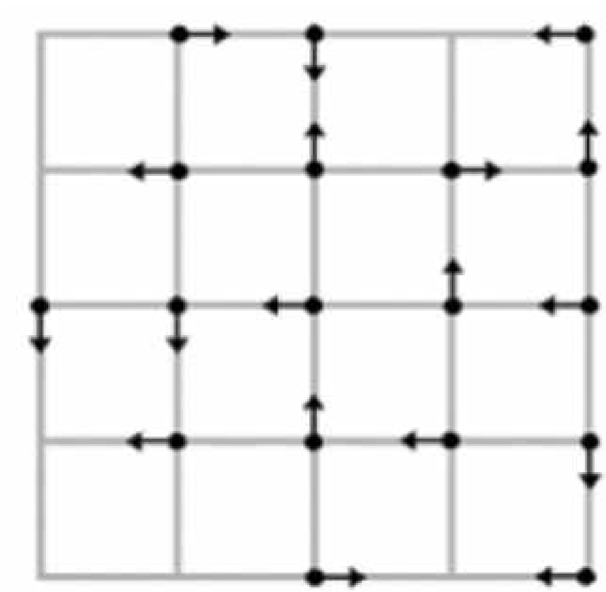
Possible velocities for a particle:

$$\left\{ \downarrow, \uparrow, \leftarrow, \rightarrow \right\}$$

Possible states of a node:

1) Empty
2) Occupied

First- and second order phase transition in a lattice model for swarming



The "stochastic rules", defined in continuum time:

Each particle can perform two actions:

1) Migrate according to its velocity direction

2) Reorient its velocity direction

Associated to each action,
there is a transition probability (per unit time):

$$T_M\left((\mathbf{x},\mathbf{v}) \to (\mathbf{y}=\mathbf{x}+\mathbf{v},\mathbf{v})\right) = \begin{cases} m & \text{if node } \mathbf{y} \text{ is empty} \\ 0 & \text{if node } \mathbf{y} \text{ is occupied} \end{cases}$$

2) Reorient its velocity direction

$$T_R\left((\mathbf{x},\mathbf{v}) \to (\mathbf{x},\mathbf{w})\right) = \exp\Big(g \sum_{\mathbf{y}\in A(\mathbf{x})} \langle \mathbf{w}|\mathbf{V}(\mathbf{y})\rangle\Big)$$

This defines a ferromagnetic alignment rule!

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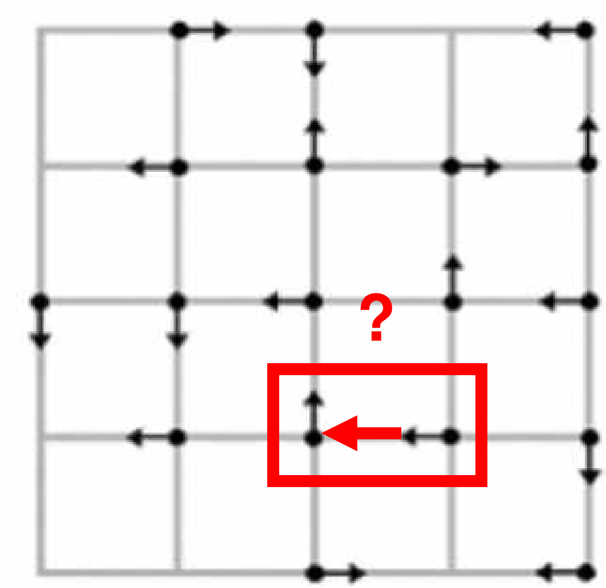
First- and second order phase transition in a lattice model for swarming



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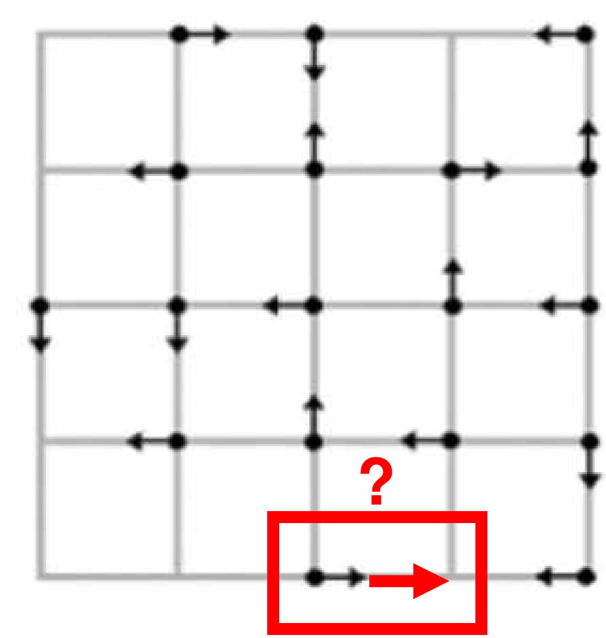

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Collective motion on the lattice

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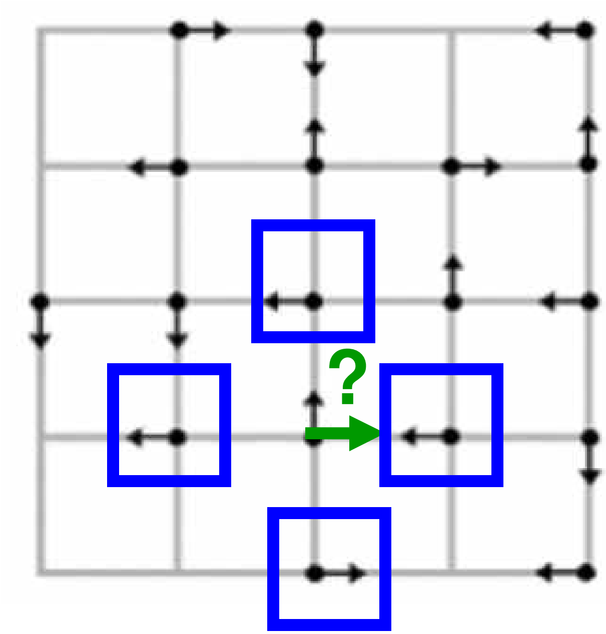

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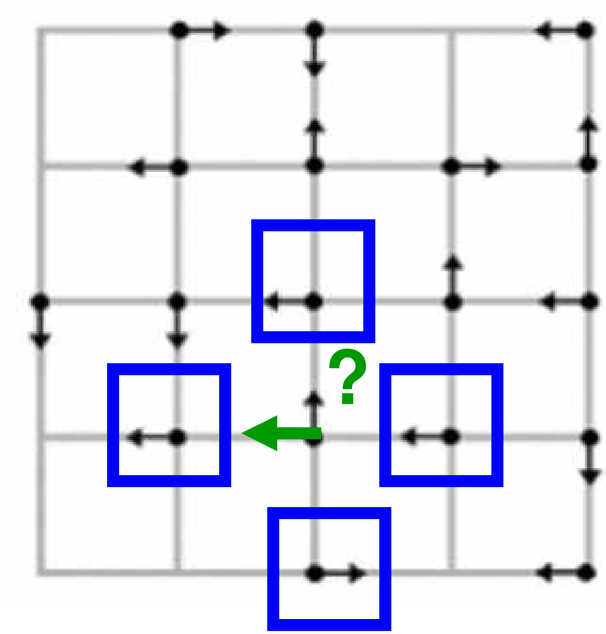

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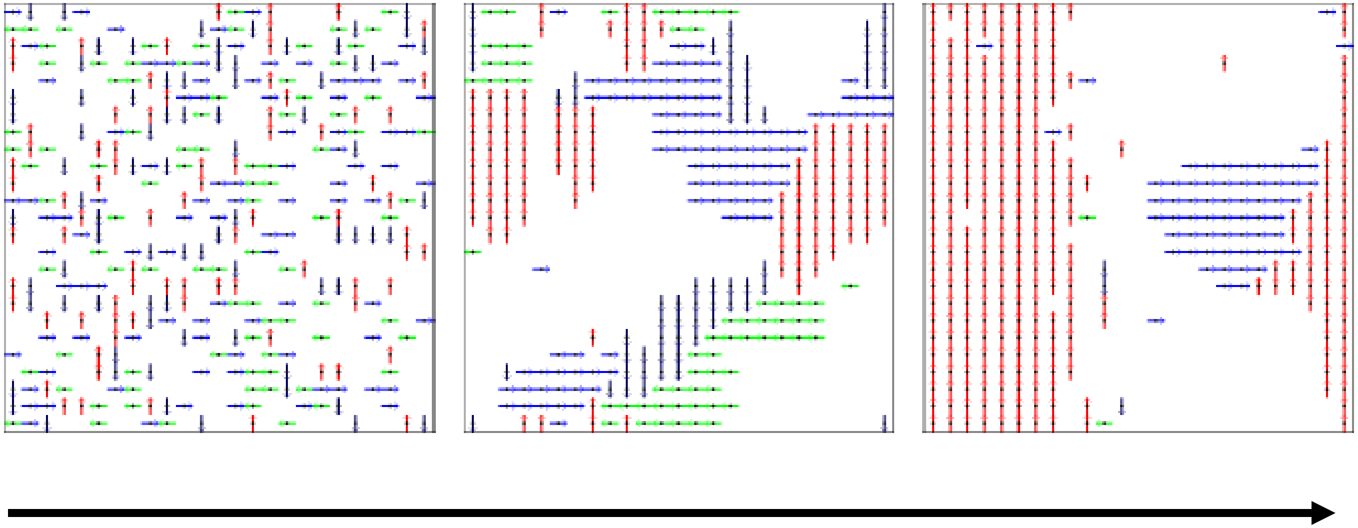
First- and second order phase transition in a lattice model for swarming

Results at "low" density



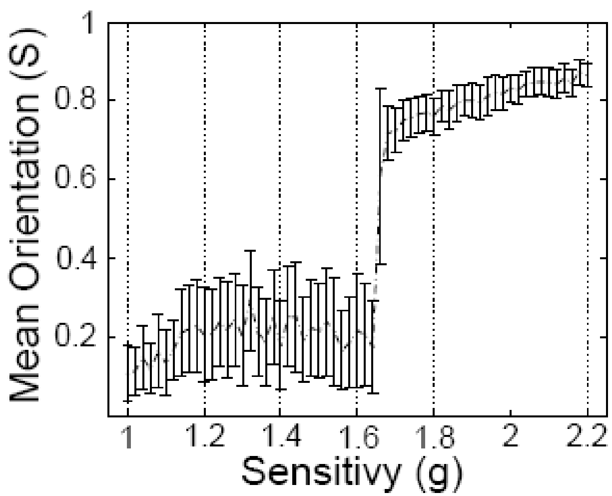
time

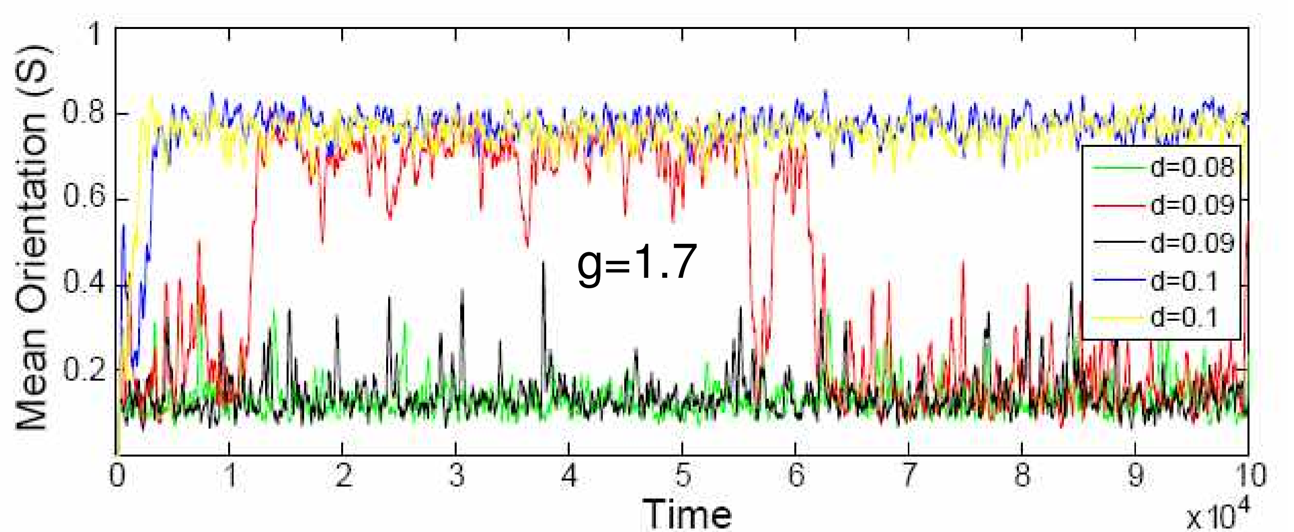
Parameters: L=25, d=0.5, g=1.7, m=100

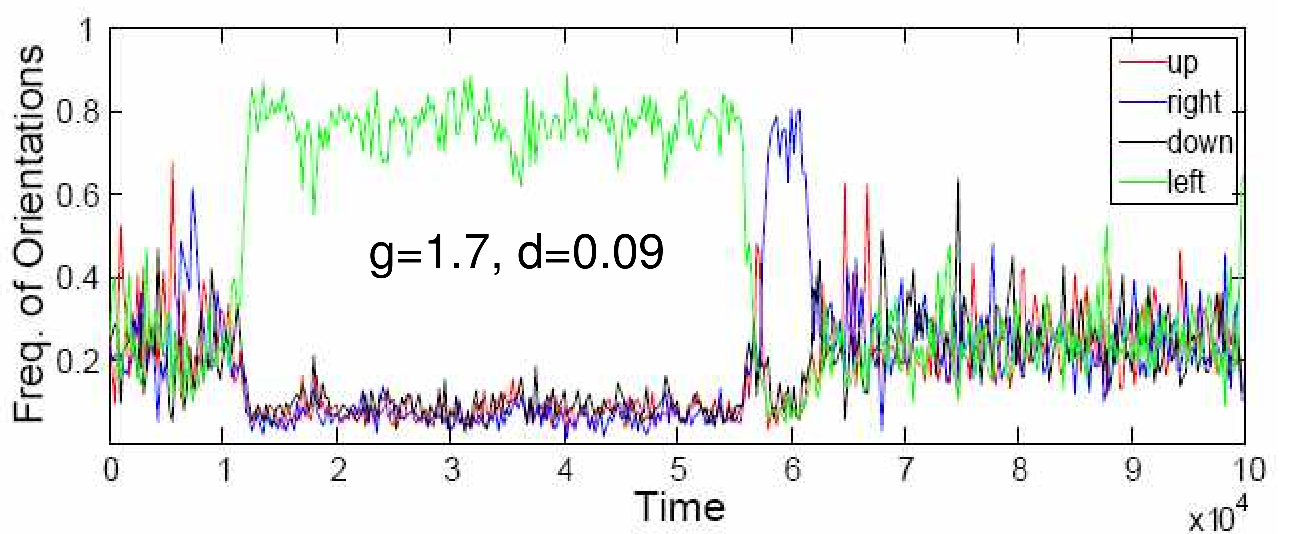
Collective motion on the lattice

First- and second order phase transition in a lattice model for swarming

Results at "low" density (L=50, m=100)







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Collective motion on the lattice

First- and second order phase transition in a lattice model for swarming

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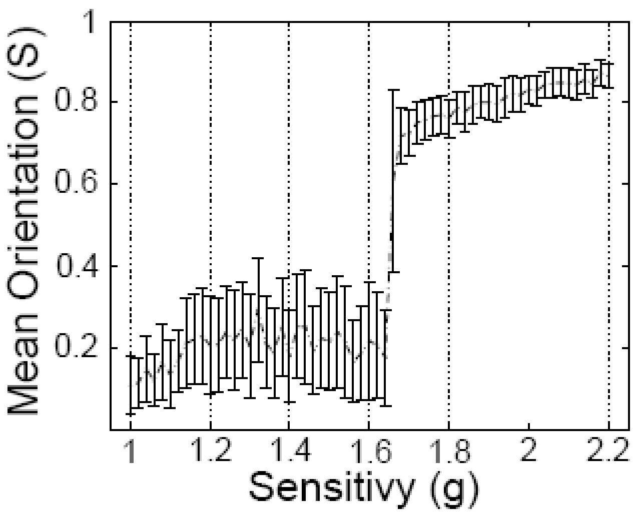

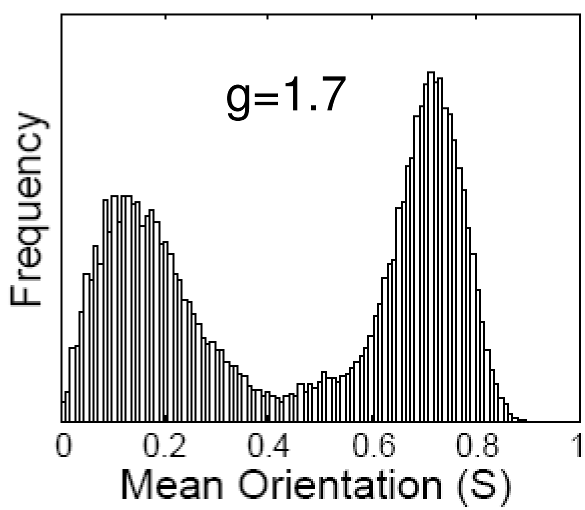

At "low" density the numerical evidence points towards a dynamical **first order** transition

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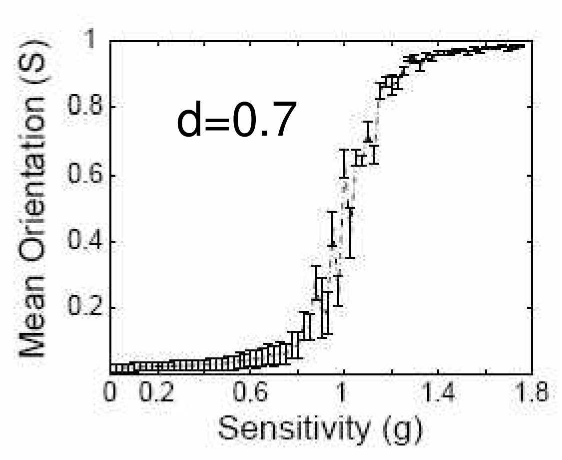
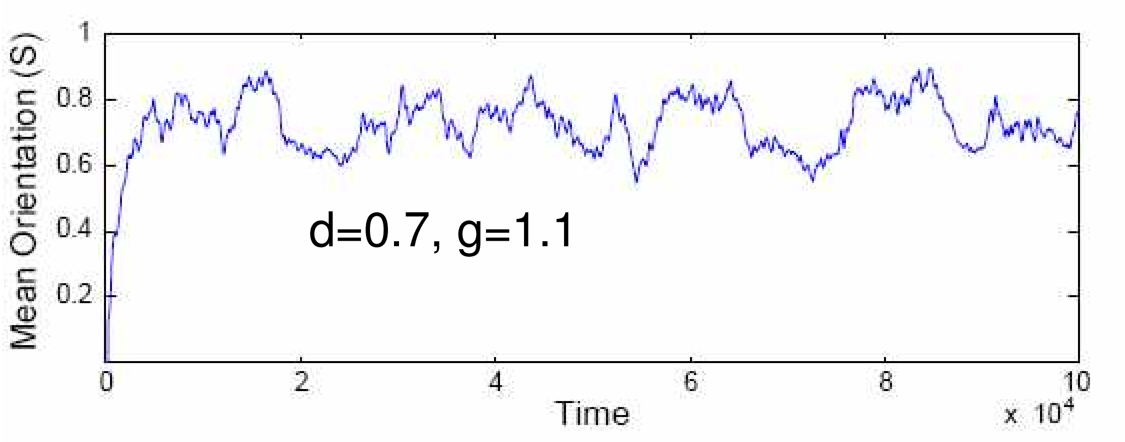
First- and second order phase transition in a lattice model for swarming

Results at “high” (=full occupancy) density

- The problem with full occupancy can be mapped to the 4-Potts model
- The 4-Potts model exhibits a second order phase transition
- Then, our model exhibits a **second order** transition at **d=1** !

Results at “intermediate” density





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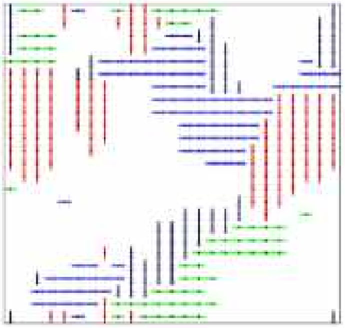
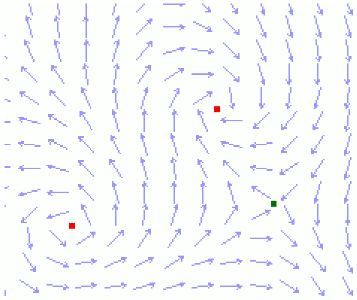
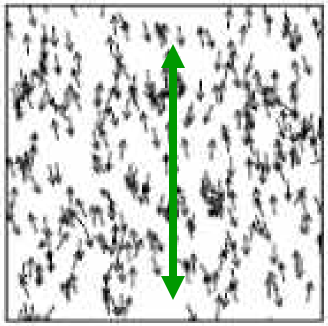
Summary

• Models for collective motion can be either continuum (off-lattice) or discrete (on-lattice)



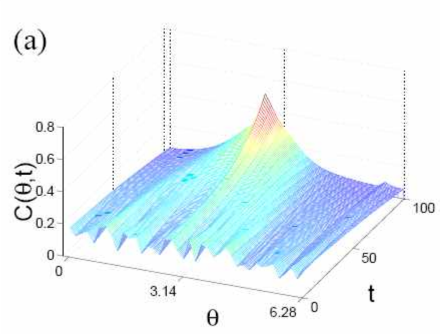
• Collective motion models are intrinsically (thermodynamically) non-equilibrium systems

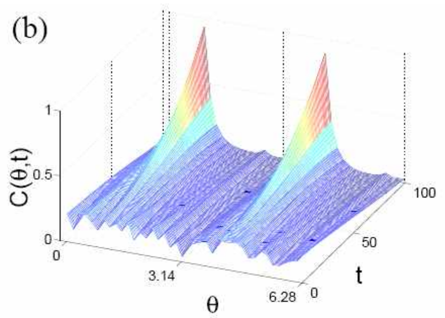




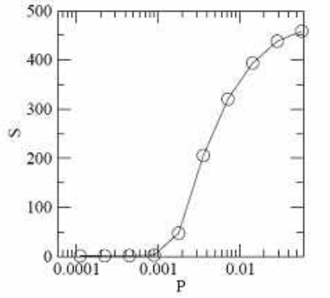
Summary

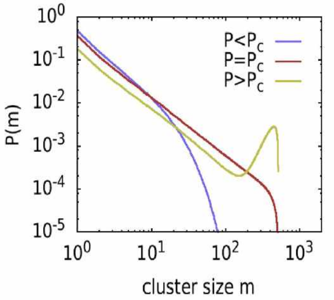
• The symmetry of the interaction determines the kind of order: either polar or nematic





• Collective motion can be characterized as a transition to aggregation (link to pattern formation)





• Collective motion modeling applies to **animal behavior** (fish, birds, sheeps, ants, etc) as well as **developmental biology** (aggregation patterns in bacteria, tissue formation, cancer, etc)

F.Peruani

Thanks for you attention!

Some references:

FP, Deutsch, and Bär, PRE (2006)
FP, Morelli, PRL (2007)
FP, Deutsch, and Bär, EPJ-ST (2008)
Ginelli, FP, Bär, Chaté, PRL (2010)
FP, Nicola, Morelli, arXiv (2010)