

The statistical physics of biological systems

Technical information

Lectures: online (on Teams)

Monday 10:00 AM Sept, 14 - Oct 12 (first 5 lectures)

Anna Zafeiris / anna@hal.elte.hu /

- Dept. of Biological Physics, 3.92.
- Consultation time (online): Tuesday, 12:00 (on demand)
- Please write an email beforehand!

Máté Nagy / nagymate@hal.elte.hu /

- Dept. of Biological Physics, 3.91.

More materials from the previous years:

- http://hal.elte.hu/~vicsek/teaching/biologiai_rendszerek_statistikus_fizikaja/

Outline of the course

Part I Lecturer: Anna Zafeiris

- Collective motion (Sept 14, 2020)
- Hierarchy formation (Sept 21, 2020)
- Opinion dynamics (Sept 28, 2020)
- The geometry of bacteria colonies (Oct 5, 2020)
- Biological synchronization + discussion (Oct 12, 2020)

The material is available on Teams

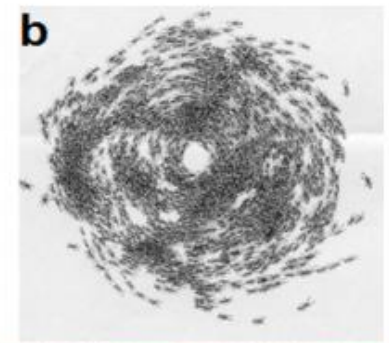
Collective motion



Sept 14, 2020

Examples

- Non-living systems (shaken rods, nano-swimmers, simple robots, boats, etc.)
 - Macromolecules
 - Bacteria colonies
 - Cells
 - Insects
 - Fish schools
 - Bird flocks
 - Mammals
 - Human crowds
-
- No leaders
 - Spontaneous ordering
 - What are the rules for self-organization?



Historical background – a new scientific field...

- One direction: computer graphics (end of 1980's)
- Statistical physics (1990's)*
 - Many more or less similar units
 - the concept of ***Self-propelled particles*** (SPP)
 - The assumption that the motion of the moving units are controlled by ***interactions with their neighbours***
 - Randomness (noise)
 - Spontaneous ordering
 - It was a very unconventional idea back in the 1990's to extend the concepts of statistical physics to these active, non-equilibrium systems
 - Actuality: Lars Onsager Price 2020

* T. Vicsek, A. Czirók, E. Ben-Jacob, I. Cohen and O. Shochet: Novel type of phase transition in system of self-driven particles. Physical review letters, 75(6), 1226. 1995

From a more broad point of view...

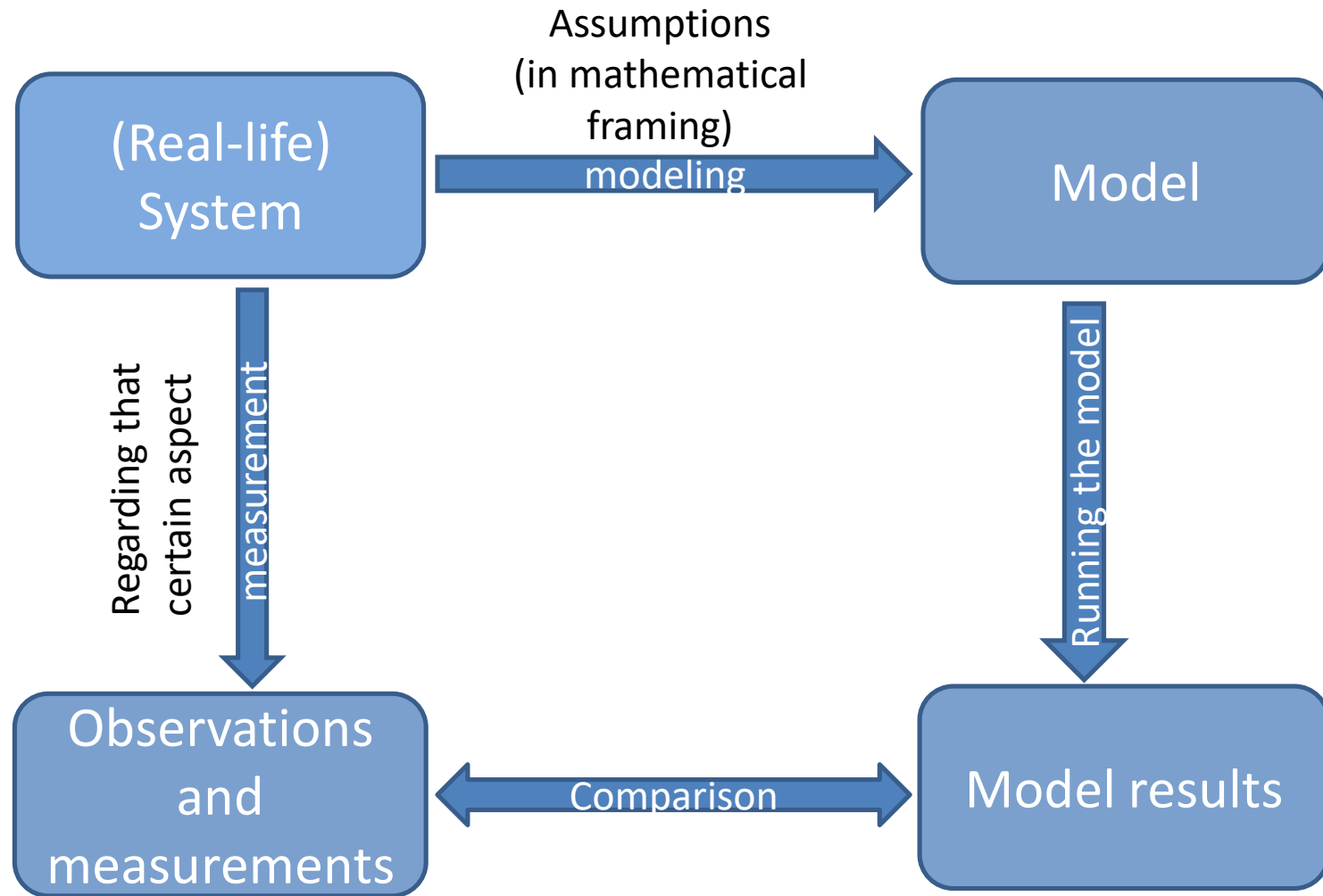
Collective motion is a form of *collective* behavior

- Strongly interdisciplinary fields
- Takes many forms. What is common:

The individual behavior is strongly effected by the behavior of other group members
(→ The units behave differently in a group and alone)

Many new branches, related fields appeared
(e.g: Collective decision making)

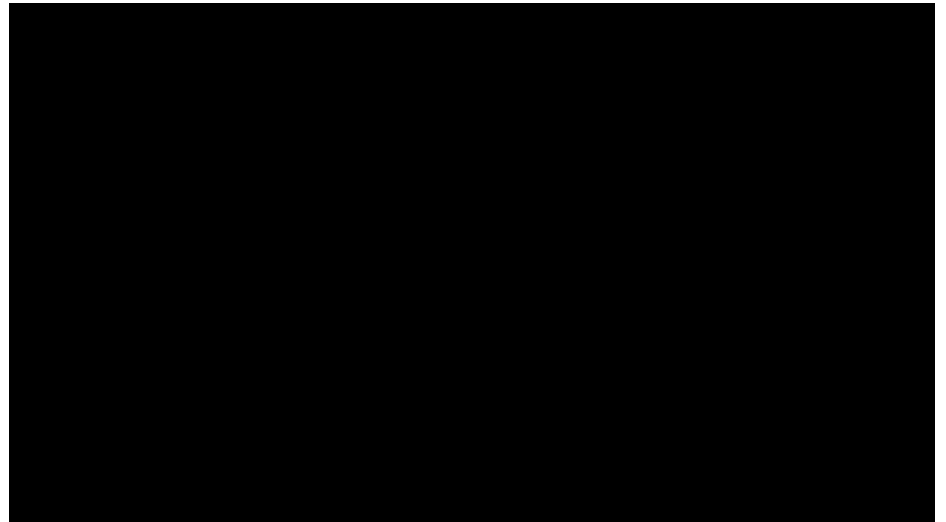
Modeling



Data collection techniques

- In order to yield data which is “good enough” to test model results, the individual trajectories of the group members have to be recorded.
- Sources of difficulties:
 - The number of units (individuals) is often high
 - They often look very much alike
 - They usually move fast

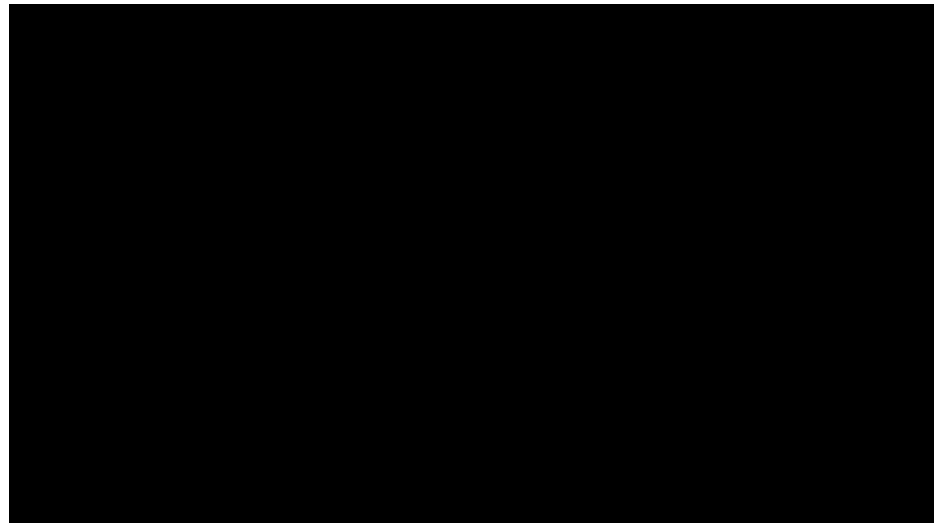
Starling video



Data collection techniques

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Starling video



Data collection techniques

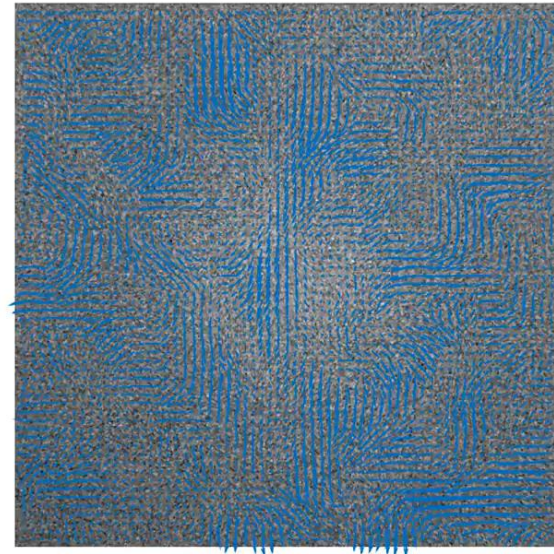
- The two main factors determining the applied technology:
 1. Size of the moving units
 2. Size and direction of the space in which the group can move(both can range through many scales)
- Different techniques allow for different types of results

Data collection technique(s) - bacteria

“Particle Image Velocimetry”, (PIV)

- Developed to visualize the motion of
 - small particles in
 - well-confined area

An optical technique used to produce the two dimensional instantaneous velocity vector field of fluids, by seeding the media with ‘*tracer particles*’. These particles are assumed to follow the flow dynamics accurately, and it is their motion that is then used to calculate velocity information.



Bacterial Collective Motion with PIV output overlaid

<https://www.youtube.com/watch?v=kCJekxCB9tM>

Data collection techniques – fish

- Various size of fish
- Confined or unconfined in space
- Confined space – aquarium
 - 2D (avoiding the difficulties of 3D data)
 - container which is “basically” two dimensional (very shallow): 40 cm × 30 cm × 2 cm.
 - Track fish with a single video recorder.
 - 3D : three orthogonally positioned video cameras
 - ID recognition has to be solved



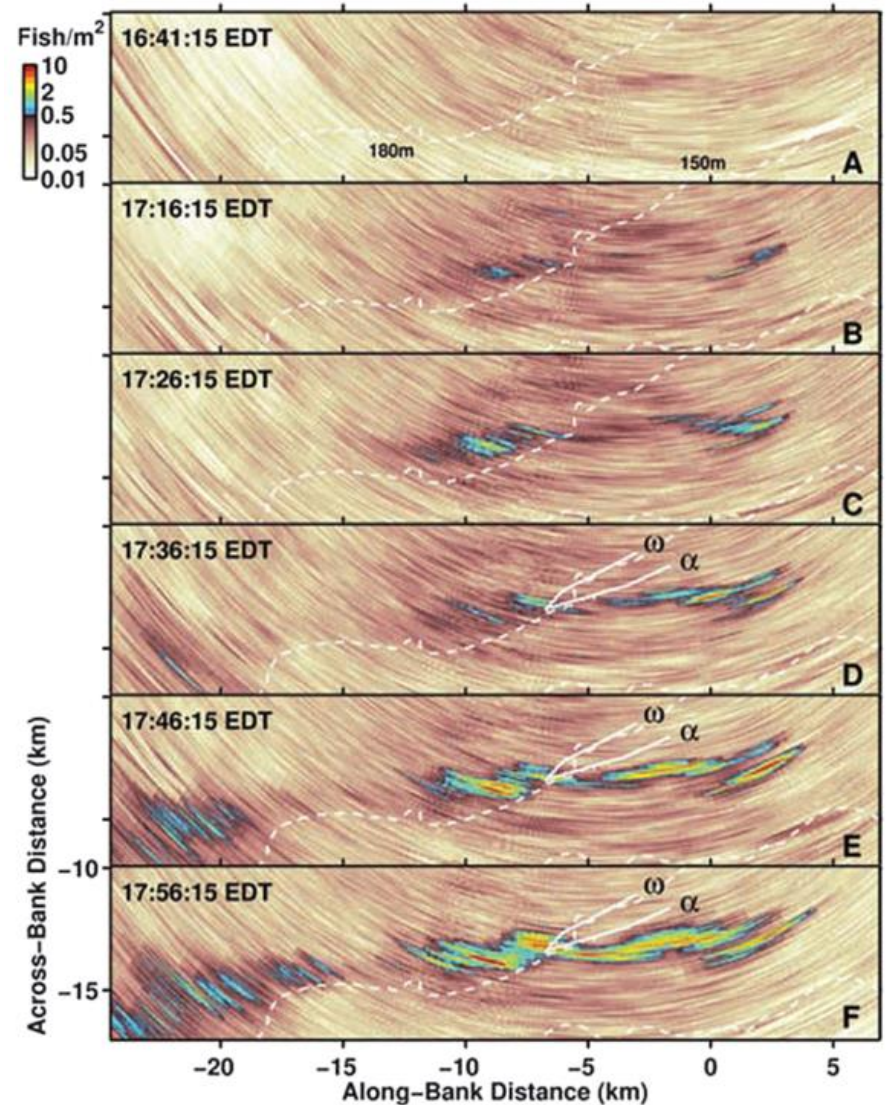
CDCL Tracking Fish Position and Pose II

The Collective Dynamics and Control Laboratory at the University of Maryland uses tools from projective geometry and Bayesian estimation to reconstruct the 3D position and pose of individual fish in a school.

<https://www.youtube.com/watch?v=QtqnMvWZfIY>

Data collection techniques – fish

- Unconfined space
 - OAWRS (“Ocean Acoustic Waveguide Remote Sensing”)
 - exploits the wave propagation properties of the ocean environment
 - Instantaneous, continuous monitoring of fish populations covering thousands of square kilometers
 - (no individual recognition)
 - Results:
 - rapid transition from disordered to highly synchronized behavior at a critical density
 - small set of leaders can significantly influence the actions of a much larger group

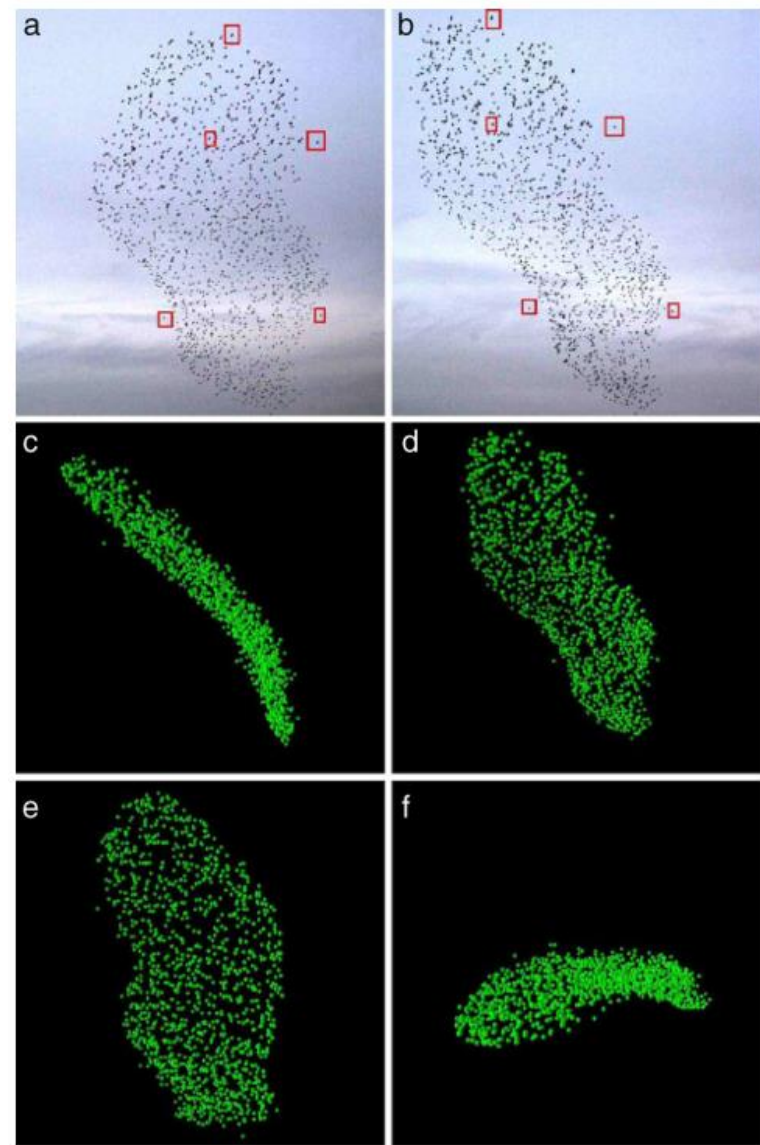


OAWRS snapshots showing the formation of vast herring shoals, consisting of millions of Atlantic herring, on the northern flank of Georges Bank (situated between the USA and Canada) on 3 October 2006. Source: Makris et al. (2009).

Data collection techniques – birds

Stereo photography technique

- Firstly: Major and Dill, 1978
- 3D positions of birds within flocks of European starlings and dunlins
- Ballerini et al. (2008) : 3D positions of up to 2,600 starlings in airborne flocks with high precision
- Pro: detailed and accurate analysis of nearest neighbor distances in large flocks
- Con: no trajectory reconstruction of the individual flock members
- Main observation: starlings in huge flocks interact with their 6–7 closest neighbors (“topological approach”) instead of those being within a given distance (“metrical approach”)



(a) and (b): stereometric photographs, taken from 25 meters apart. For reconstructing the flocks in 3D, each bird's image on the left had to be matched to its corresponding image on the right using and computer vision techniques. The small red squares indicate five of these matched pairs. (c–f) The 3D reconstructions of the analyzed flock from four different perspectives.

Source: From Ballerini et al. (2008).

Data collection techniques – birds - GPS

- Firstly: ~2006
- Record the trajectory of moving animal with high temporal resolution
- Unconfined region, natural environment
- Limits:
 - growing cost of the research with the growing number of tracked flock members
 - limited accuracy of the devices.



Data collection technique(s) – vertebrate flocks

- Bigger individuals
- Often unconfined space
- Mainly camera-based techniques
- First observations in the '70s
 - Aerial photos – 2D
 - African buffalo herds
- Later photos were replaced with videos
- New technologies, like GPS (dogs)
- Individual recognition:
 - By hand
 - Various computer algorithms
 - Color bar technique (rats, pigeons)
 - Colors fade
 - Individuals cover each other
 - Colors depend on the actual lighting conditions



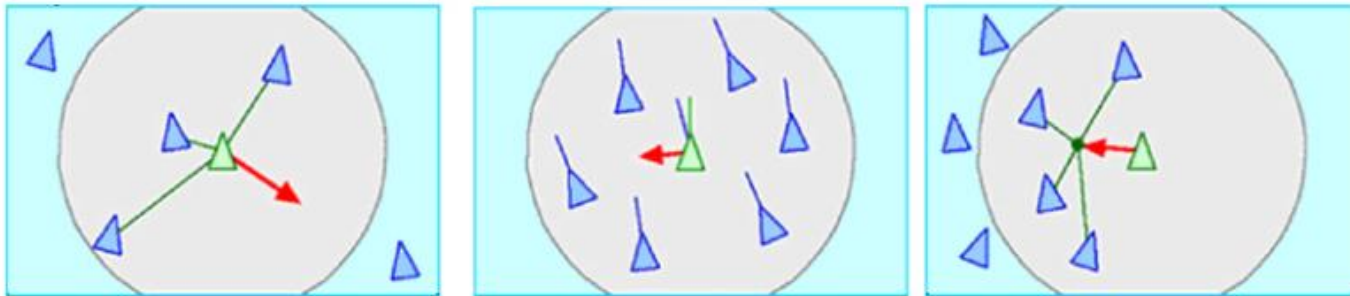
A snapshot of the processed video sequence, recording the feeding-queuing activity of a group of homing pigeons. Each bird is marked with a unique combination of three colors serving as an individual code for a computer program designed to identify the individuals automatically.

Circles divide the different activity regions:
central circle: feeding, blue: queuing, external circle: "not interested". Reproduced from Nagy et al. (2013)

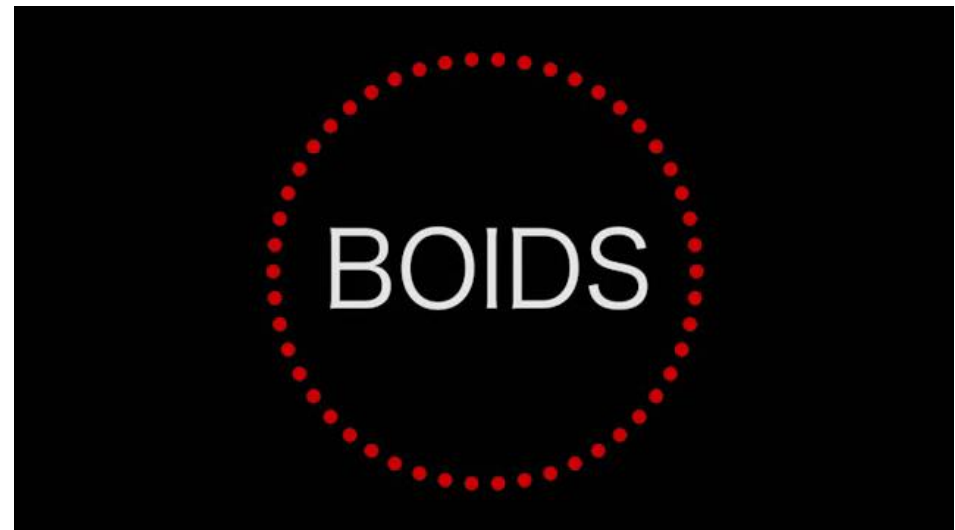
Basic assumptions in *collective motion* models :

- The units are
 - Rather similar
 - moving with a nearly constant absolute velocity
 - Capable of changing their direction (including active alignment)
 - interacting within a specific range
 - subject to a noise of a varying magnitude
- SPP: “*Self-propelled* particle”
(intrinsic source of motion)

The first models – Reynolds, 1987



- First well-known model. (Aoki)
- Main motivation: to simulate the visual appearance of a few dozen coherently moving objects, like birds or spaceships (computational graphics)
- “boid” - “bird-like object”
- 3 types of interactions:
 - *Separation*: Avoidance of collisions
 - *Alignment*: Heading in the direction of the neighbors
 - *Cohesion*: Staying close the center of mass of the flock
- “ROI” – range of interaction

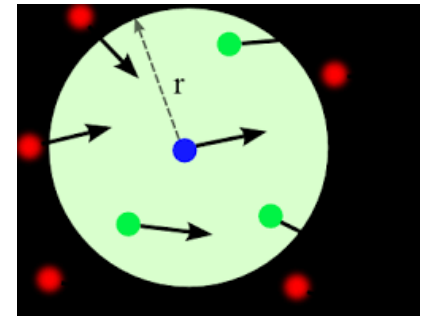


SVM – “Standard Vicsek Model”

- A Statistical physics type of approach
- The units
 - move with a fixed absolute velocity v_0
 - assume the average direction of others within a given distance R .
- Perturbations are taken into account by adding a random angle to the average direction.
- The equations determining the motion of particle i :

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

$$\vec{v}_i(t+1) = v_0 \frac{\langle \vec{v}_j(t) \rangle_R}{|\langle \vec{v}_j(t) \rangle_R|} + \text{perturbation}$$



Or, in other form:

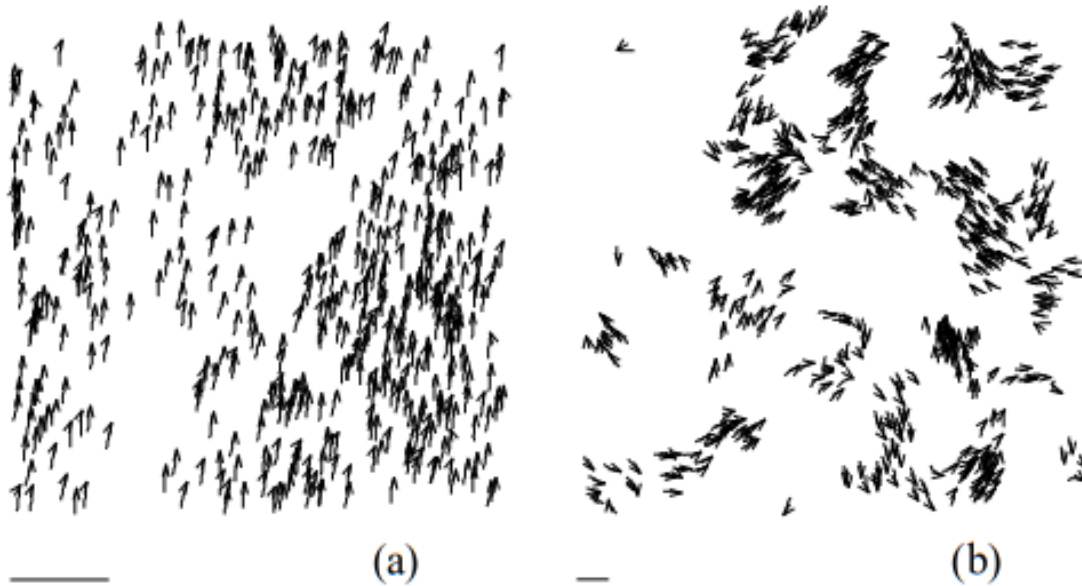
$$\vartheta_i(t+1) = \langle \vartheta(t) \rangle_{S(i)} + \xi$$

Where the noise ξ is a random variable with a uniform distribution in the interval $[-\eta/2, \eta/2]$.

"Novel Type of Phase Transition in a System of Self-Driven Particles". Physical Review Letters. 75 (6): 1226–1229. T. Vicsek , A. Czirók, E. Ben-Jacob, I. Cohen, O. Shochet (1995).

Parameters

- Density ρ (number of particles in a volume R^d , where d is the dimension) (or R , the interaction range)
- Velocity v_0 (fixed, same for all particles)
- Level of perturbation, η



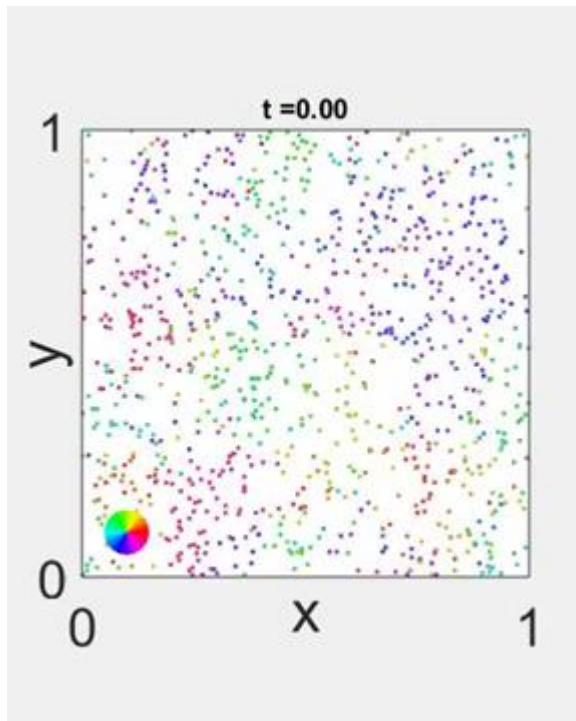
- Direction of the arrow: actual velocity
- Trajectory of the last 20 time-step: curve
- ROI: bar

Typical configurations of SPPs displayed for various values of density and noise. The actual velocity of a particle is indicated by a small arrow, while its trajectory for the last 20 time step is shown by a short continuous curve. For comparison, the radius of the interaction is displayed as a bar.

(a) At high densities and small noise ($N = 300$, $L = 5$ and $\eta = 0.1$) the motion becomes ordered.

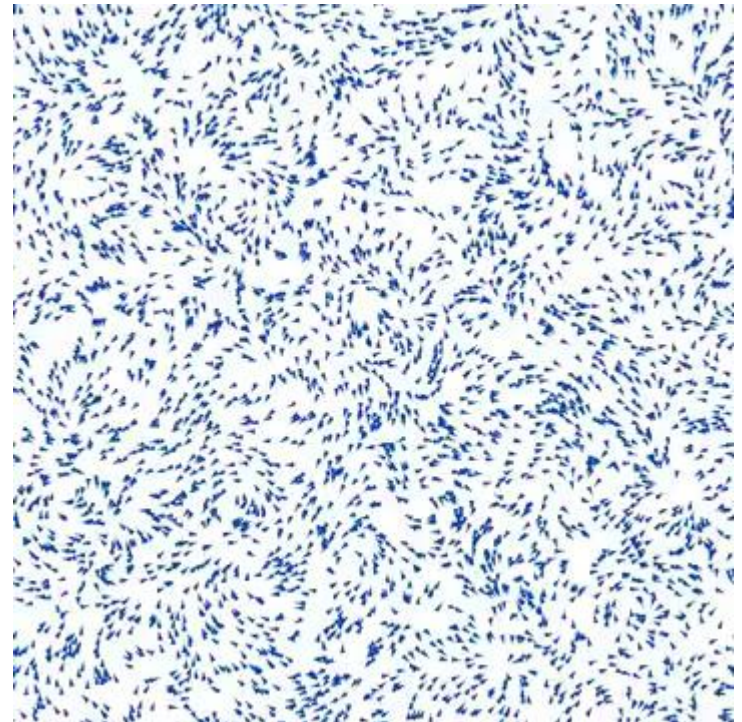
(b) For small densities and noise ($N = 300$, $L = 25$ and $\eta = 0.1$) the particles tend to form groups moving coherently in random directions.

Parameters in the SVM



Zero noise, $v_0 = 0.05$, $R = 0.1$

<https://www.youtube.com/watch?v=hOI7IhjDMQ8>

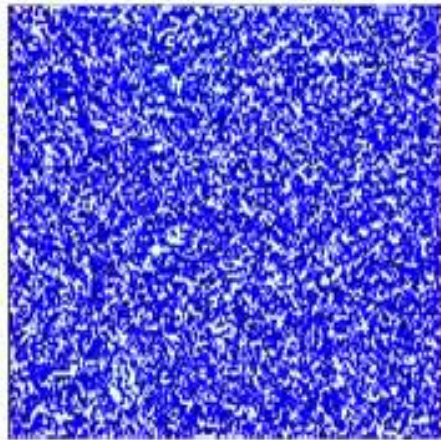


A system of 4.000 particles with a noise of $\eta = 0.5$.

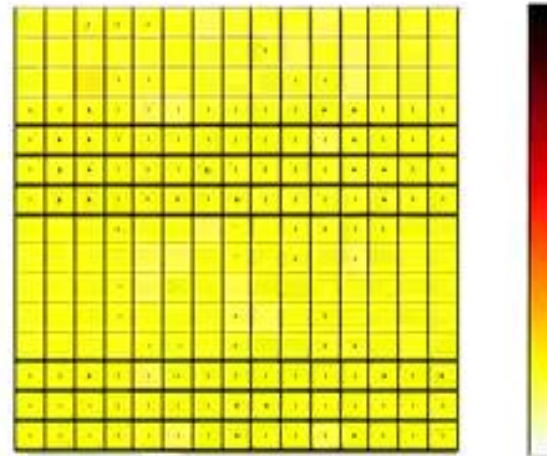
<https://www.youtube.com/watch?v=Oj9L70Fh9PM>

Simulation results

Particles at $t = 0.00$



Density and velocity at $t = 0.00$



Left panel: particle positions and velocities. Right panel: cell-averaged particle density (color coded) and momentum density (arrows).

Relation to the ferromagnetic model

Ferromagnets

SPP models

Analogies:

- Hamiltonian tending to align the spins
- Temperature
- aligning rule (regarding the direction of motion)
- Amplitude of the random perturbation

Differences:

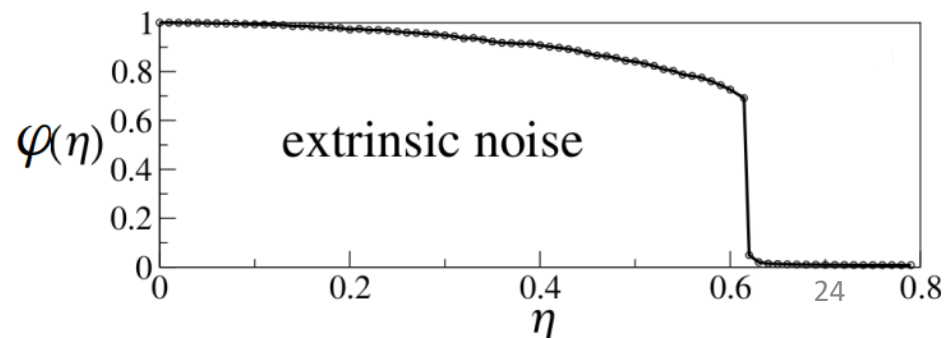
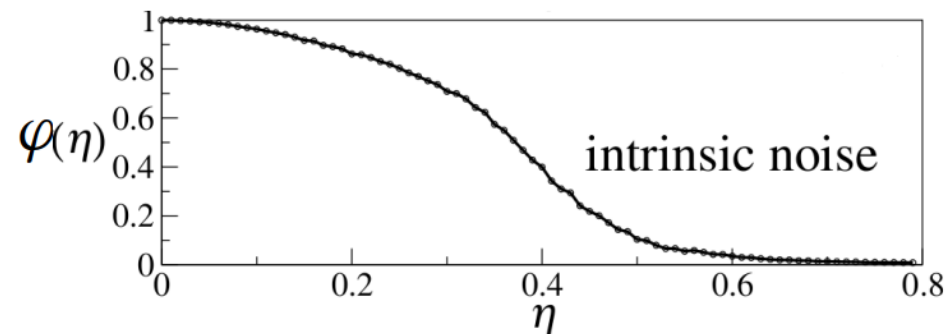
- Particles do not move
- There is no ordered phase in finite temperatures in 2D
- Particles move
- Ordered phase can exist at finite noise levels in 2D SPP models

The order of the phase transition

- Order parameter: normalized average velocity

$$\varphi \equiv \frac{1}{N \cdot v_0} \left| \sum_{i=1}^N \vec{v}_i \right|$$

- Non-zero in the ordered phase
- Zero in the disordered phase
- Long debate over the nature of the transition (1st or 2nd order)
- Result: it is the magnitude of the velocity and the way the noise is introduced into the system what plays the key role
- “Intrinsic noise”: the angle of the average velocity is computed and then a scalar noise is added to this angle
- “Extrinsic noise” / “Vectorial noise model”: a random vector is first added to the average of the velocities and the final direction is determined only after this. When the average velocity is small, this leads to a first-order type of transition.

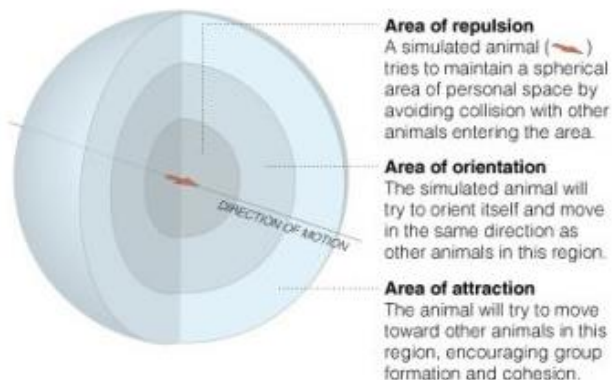


Moving in 3D (fish, bird) – the Couzin model

- Biologically realistic, yet still simple, individual based
- Individuals obey to the following basic rules:
 - (i) they continually attempt to maintain a certain distance among themselves and their mates,
 - (ii) if they are not performing an avoidance maneuver (described by rule i), then they are attracted towards their mates, and
 - (iii) they align their direction to their neighbors.
- Their perception zone (in which they interact with the others) is divided into three non-overlapping regions

Simulating Swarm Intelligence

Researchers created a model of swarm behavior by programming individuals to maintain personal space while turning and moving in the same direction as others.



Sources: Iain D. Couzin, *Journal of Theoretical Biology*

- Personal space – avoiding collision

- Orientation

- Cohesion; move forward the others

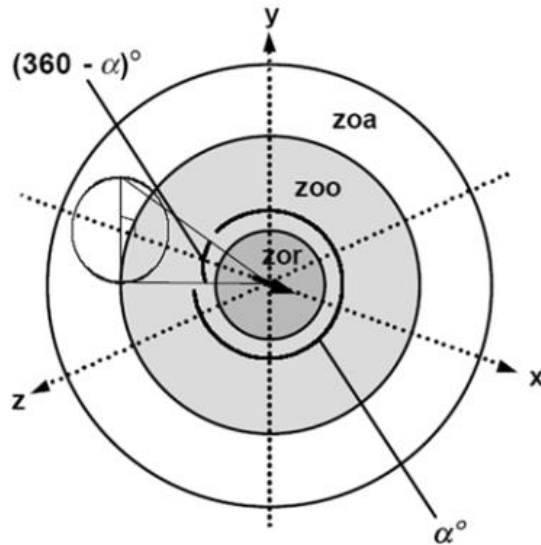
Moving in 3D (fish, bird) – the Couzin model

The interaction zones, centered around each individual.

- ZOR, the inner-most sphere with radius R_r , is the “Zone of Repulsion”

If others enter this zone, the individual will response by moving away from them into the opposite direction, that is, it will head towards $-\sum_{j \neq i} n_r \frac{\vec{r}_j - \vec{r}_i}{|\vec{r}_j - \vec{r}_i|}$, where n_r is the number of individuals being in the ZOR.

The interpretation of this zone is to maintain a personal space and to ensure the avoidance of collisions.



- ZOO: “Zone of Orientation”. If no mates are in the ZOR, the individual aligns itself with neighbors within this ZOO region.
- ZOA: “Zone of Attraction”.
The interpretation of this region is that group-living individuals continually attempt to join a group and to avoid being alone or in the periphery.
- α “Field of perception” (can be 360°)
- “Blind volume” behind the individual: a cone with interior angle $(360 - \alpha)^\circ$. Here neighbors are undetectable.

Couzin model – cont.

- System properties:

- Order parameter:

$$\varphi(t) = \frac{1}{N} \left| \sum_{i=1}^N \overrightarrow{v_i^u}(t) \right|$$

- (group) angular momentum:

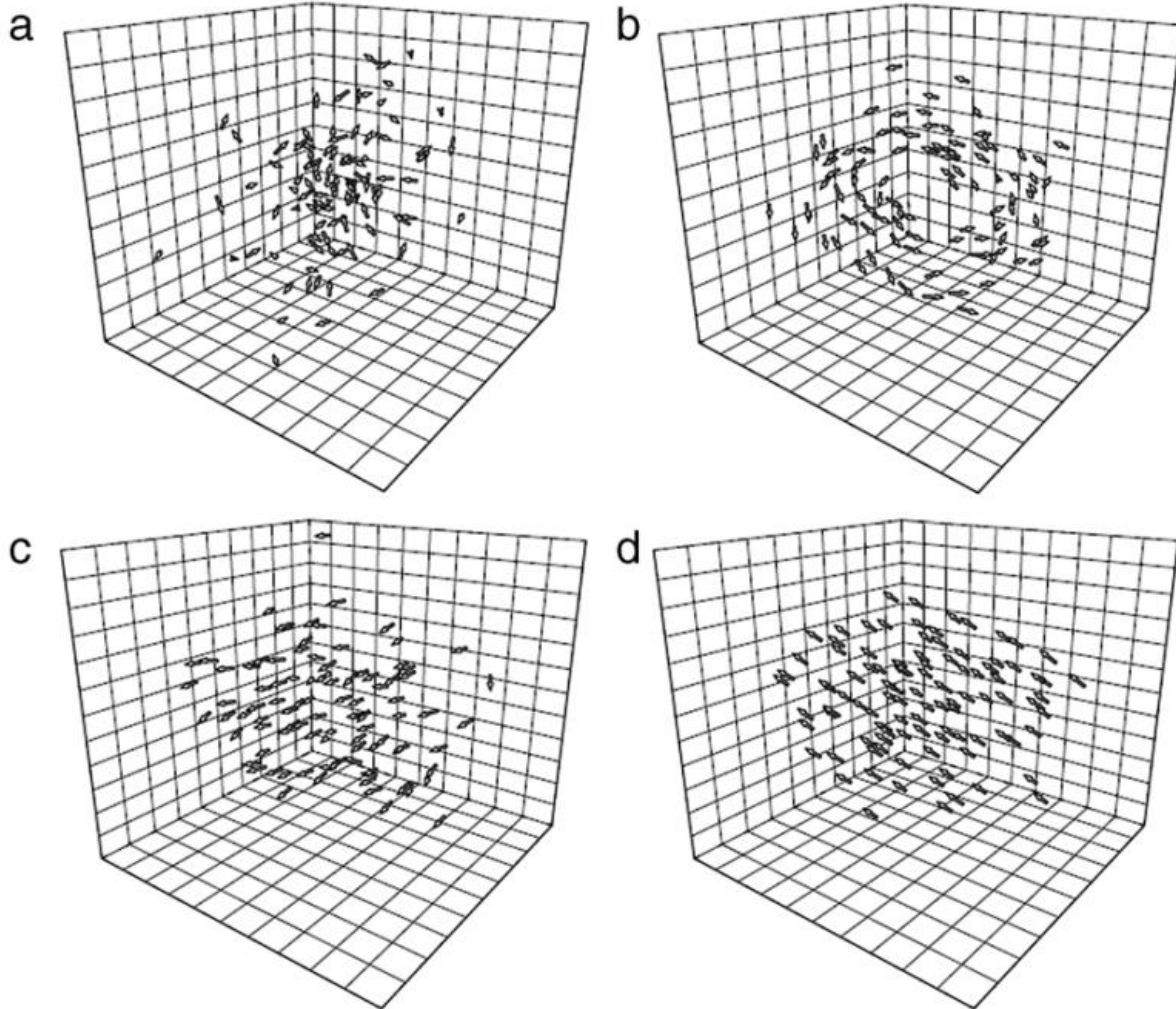
$$m_{Gr}(t) = \frac{1}{N} \left| \sum_{i=1}^N \vec{r}_{i-Gr}(t) \times \overrightarrow{v_i^u}(t) \right|$$

(average of the angular momenta of the group members around the center)

- $\overrightarrow{v_i^u}$ is *unit* direction vector of individual i , so
- φ (order param) is the same as in the SVM
- $\overrightarrow{r_{Gr}}$ position of the group center
- $\vec{r}_{i-Gr} = \vec{r}_i - \vec{r}_{Gr}$ vectorial difference of the position of individual i and the group center
- Group center:

$$\vec{r}_{Gr}(t) = \frac{1}{N} \sum_{i=1}^N \vec{r}_i(t)$$

Couzin model – Basic types



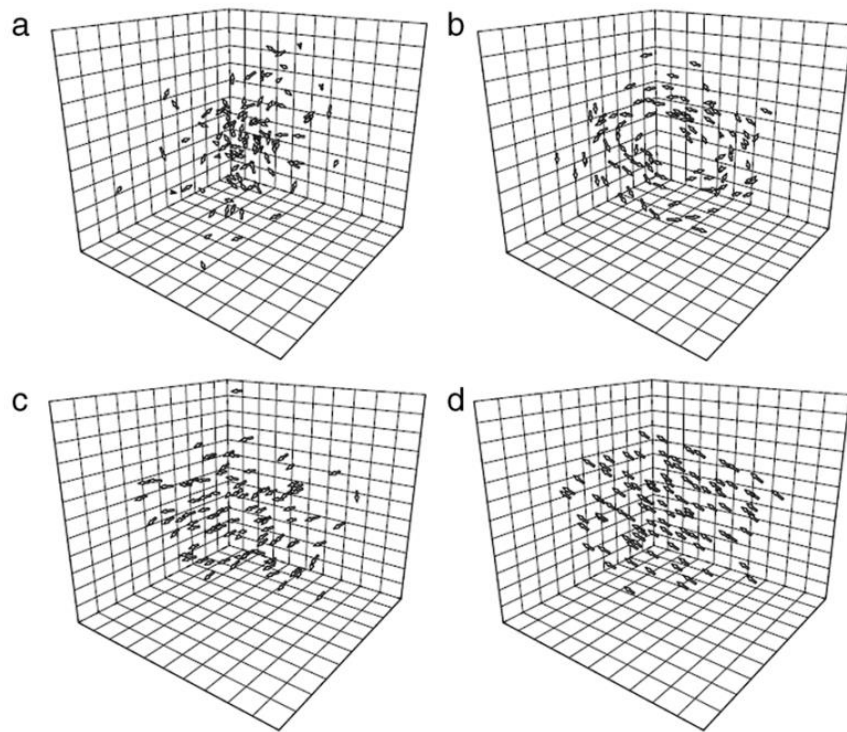
a) **Swarm**: Both the order parameter (ϕ) and the angular momentum (m_{Gr}) are small, which means little or no parallel orientation.

b) **Torus** or **milling**: Individuals rotate around an empty core with a randomly chosen direction. The order parameter (ϕ) is small, but the angular momentum (m_{Gr}) is big.

c) **Dynamic parallel group**: This formation is much more mobile than either of the previous ones. The order parameter (ϕ) is high but the angular momentum (m_{Gr}) is small.

d) **Highly parallel group**: a highly aligned formation characterized by very high order parameter (ϕ) and low angular momentum (m_{Gr}).

Basic types – parameter setting



a) **Swarm**

b) **Torus** or **milling**:

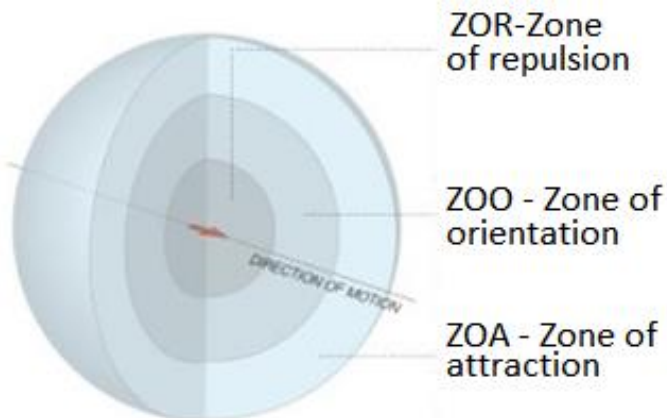
big ΔR_a (width of the Zone Of Attraction)
small ΔR_o (width of the Zone Of Orientation)

c) **Dynamic parallel group**:

intermediate to high ΔR_a (width of the Zone Of Attraction)
intermediate ΔR_o (width of the Zone Of Orientation)

d) **Highly parallel group**:

increasing ΔR_o further (width of the Zone Of Orientation)



ΔR_a : width of the ZOA

ΔR_o : width of the ZOO

Model variants

Two main directions:

1. Models with alignment rule

- Topological vs. metric neighbors
 - Differences in the models (dense to empty ROI)
 - Biological relevance
 - Systems with topological neighbors remain connected

2. Models without explicit alignment rule

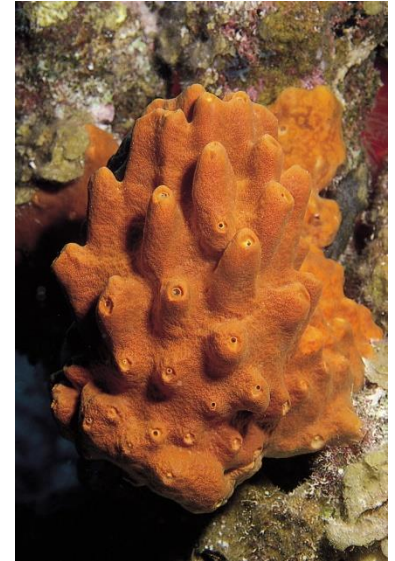
- The motion may become ordered
- Collisions between the particles
- Alignment is introduced by the collision in an indirect way by the local interaction rules

General (minimal) vs. system specific models

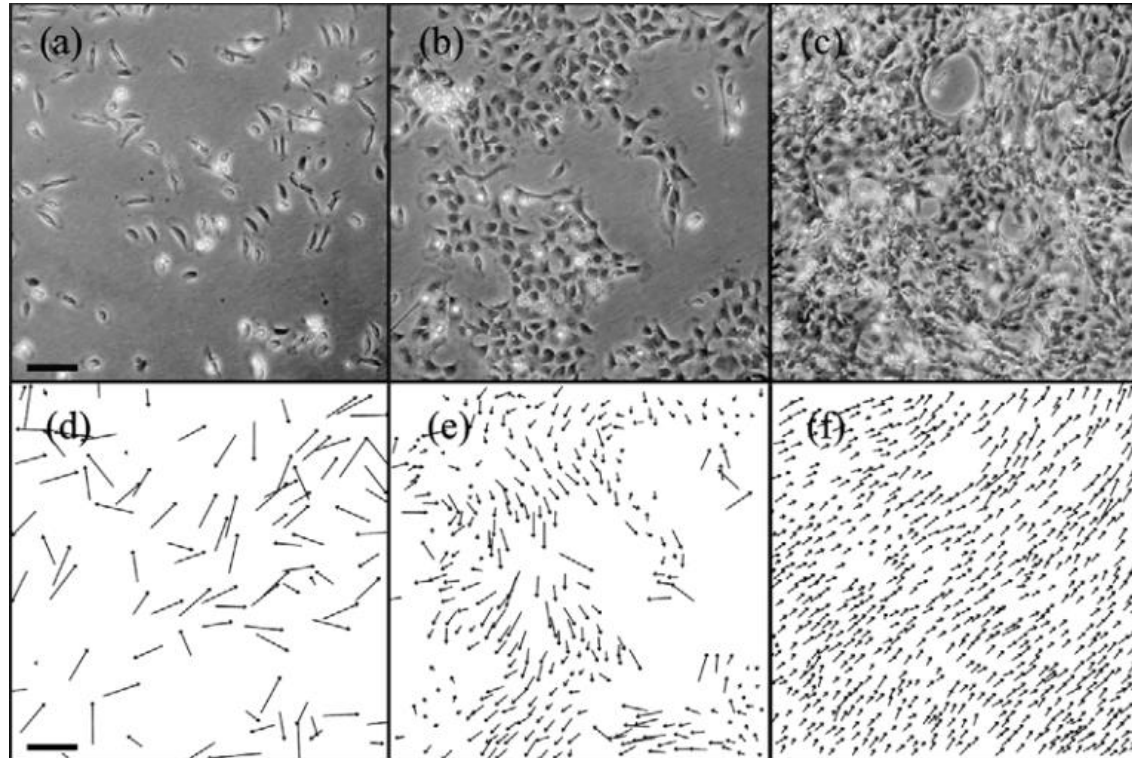
- General models: Few parameters, few assumptions (“minimal”), general results
- System specific models: include system-specific details
 - Individuals with different properties (segregating units)
 - Insect migration (e.g. locusts)
 - Predator-prey systems
 - Etc.
- Applications (among many):
 - Robotics / military applications
 - Traffic simulation
 - Vehicular traffic
 - Pedestrian motion (urban design, building design)
 - Panic

The role of adhesion

- Mechanism determining tissue movements?
 - Dates back to the beginning of the 20th century
 - 1907 Wilson discovered that sponge cells which have been previously squeezed through a mesh of fine bolting-cloth reunite again reconstituting themselves into a functioning sponge
 - Early studies
 - Cell sorting is a resultant of inhomogeneities in the immediate environment (for example of pressure)
 - Since then
 - the movements are due to intrinsic properties of the individual tissues themselves



Collective behavior of fish keratocytes



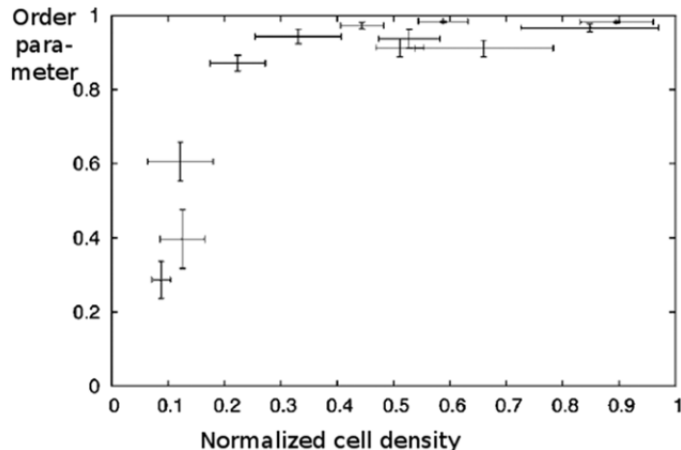
Observations / measurements

The collective behavior of fish keratocytes for three different densities. The normalized density, ρ^- is defined as $\rho^- = \rho/\rho_{\text{max}}$, where ρ_{max} is the maximal observed density, 25 cells/ $100 \times 100 \mu\text{m}^2$.

(a) $\rho = 1.8$ cells/ $100 \times 100 \mu\text{m}^2$ corresponding to $\rho^- = 0.072$

(b) $\rho = 5.3$ cells/ $100 \times 100 \mu\text{m}^2$ which is $\rho^- = 0.212$, and

(c) $\rho = 14.7$ cells/ $100 \times 100 \mu\text{m}^2$, $\rho^- = 0.588$. The scale bar indicates $200 \mu\text{m}$. As cell density increases cell motility undergoes to collective ordering. The speed of coherently moving cells is smaller than that of solitary cells. (d)–(f) on the bottom panel depicts the corresponding velocities of the cells.



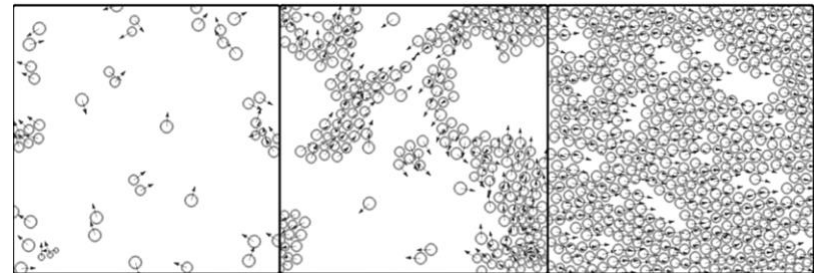
Order parameter versus the normalized cell density. The error bars show the standard error of the density and order parameter.

Source: Szabó, B., Szőllősi, G.J., Gönci, B., Jurányi, Zs., Selmeczi, D., Vicsek, T., 2006. Phase transition in the collective migration of tissue cells: experiment and models. Physical Review E 74, 061908.

Collective behavior of fish keratocytes – The model

- The model cells are self-propelled particles (SPP)
- Short-range attractive–repulsive inter-cellular forces account for the organization of the motile keratocyte cells into coherent groups.
- Direction of the cells: according to the net-force acting on them.
- 2D flocking model:
 - N SPPs move with a constant speed v_0 and
 - mobility μ
 - in the direction of the unit vector $\mathbf{n}_i(t)$ (can be described by $\vartheta_i^n(t)$ as well)
 - while the i and j particles experiences the inter-cellular force $\mathbf{F}(\mathbf{r}_i, \mathbf{r}_j)$.
 - The motion of cell $i (i \in 1, \dots, N)$ in the position $\mathbf{r}_i(t)$ is described by

$$\frac{d\vec{r}_i(t)}{dt} = v_0 \vec{n}_i(t) + \mu \sum_{j=1}^N \vec{F}(\vec{r}_i, \vec{r}_j)$$



Simulation results obtained by solving the equations with periodic boundary conditions.

The model exhibits a continuous phase transition from disordered to ordered phase.

Many authors put much emphasis on the actual *shape* and *plasticity* of the cells as well

Models with segregating units

- Special case: an originally heterogeneous mixture of units segregate into two (or more) homogeneous clusters without any kind of external field.
- 2D example:
 - Granular segregation
 - Cell sorting
 - development of organs in an embryo
 - regeneration after tissue dissociation

Granular segregation in a shallow container

Granular segregation in shallow container

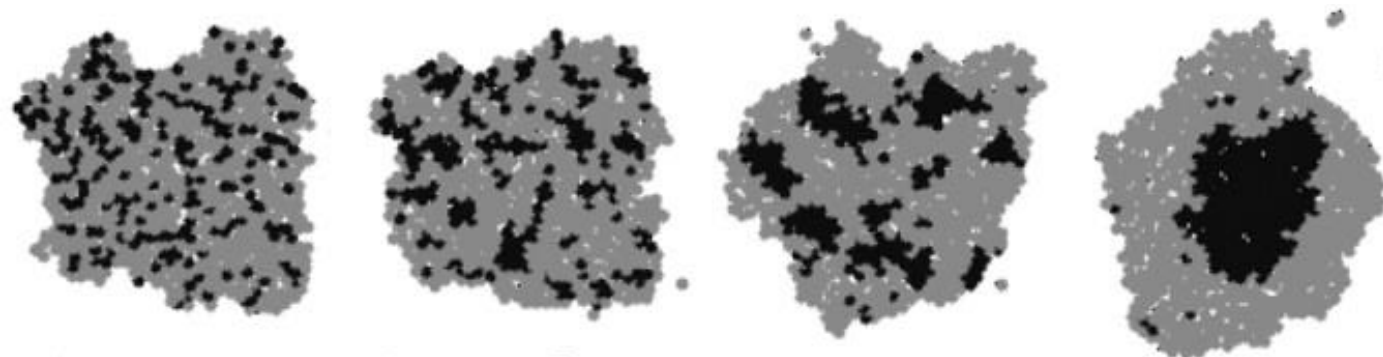
(Nicolás Rivas)

Perfect hard spheres inside a shallow, quasi-two-dimensional container, vibrated in the vertical direction. Two types of particles: blue ten times heavier than red ones (same size).

Periodic boundary conditions.

Paper: <http://iopscience.iop.org/1367-2630/1...>

<https://www.youtube.com/watch?v=I0Aea1EWcCI&t=5s>



- two kinds of cells, differing in their interaction intensities.
- 800 cells

Models with segregating units

- diverse particles (behavioral / motivational) exhibit sorting:
 - relative positional change, according to the actual inner state
 - *Relative* differences play a key role
 - If the individual variations are persistent then the group will reassemble to its' original state after perturbations
- “Swarm chemistry” – by Hiroki Sayama

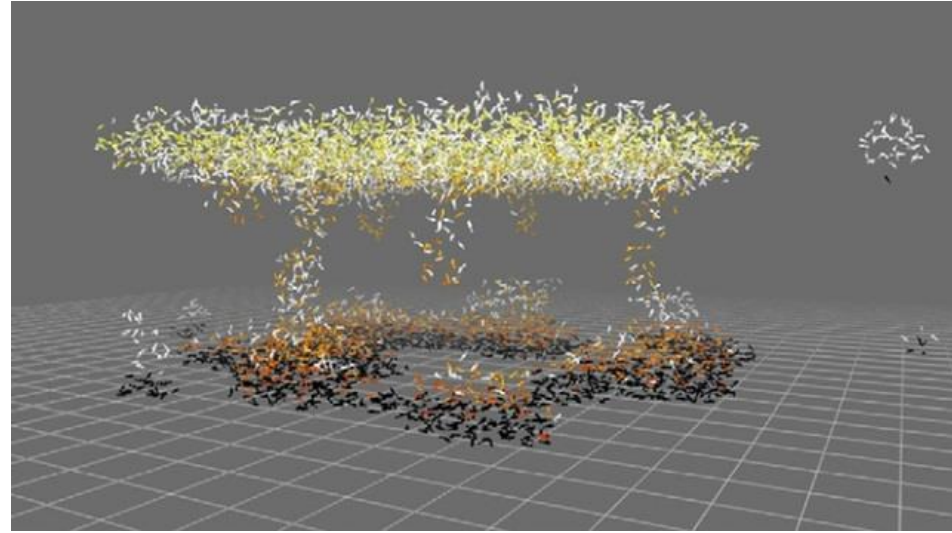
Homepage: <http://bingweb.binghamton.edu/~sayama/SwarmChemistry/>

- Emergent patterns in systems of particles with different kinetic parameters
 - Preferred speed, ROI, etc.
 - Infinite 2D space



Model: school of spawning herrings (Vabo & Skaret 2008)

- 3D individual-based model
- Units differed in their motivational level (controlled by a parameter)
- The motion of each individual:
 - (1) avoiding boundaries
 - (2) social attraction
 - (3) social repulsion
 - (4) moving towards the bottom to spawn
 - (5) avoiding predation



Results:

- Similar motivational levels results an integrated school, diverse inner states produce a system with frequent split-offs.
 - Intermediate degree of homogeneity: More complex structures, like layers connected with vertical cylindrical shaped schools
 - describing the observations (Axelsen et al., 2000) allowing ovulating herring to move across the layers
- the level of motivational synchronization among fish determines the unity of the school