

Course content

Topics (lectures):

1. Introduction (1)
2. **Structure** (2-5)
3. **Single molecule mechanics** (6-9)
4. **Collective/emergent properties** (10-12)
5. **Student presentations** (13-14)

Course structure:

1. Introduction to topic
2. Awardees (1-2 per week)
 - History, first-person, second-person accounts (C)
 - Article, analysis of scientific work (E)
3. Discussion of topic, outlook

Why is the course designed this way?

Explore the way science is done and who scientists are

Access resources beyond textbooks, to gain insights and experience

Lecture 10: Introduction to collective behavior

Today:

1. Quiz on single molecule mechanics
2. Emergent properties of a system of many units

- Basic questions
- Statistical mechanics basis
- Observations and experiments
- Basic models
- Modeling actual systems

.pdf “Collective Behavior”

Quiz: Single molecule mechanics

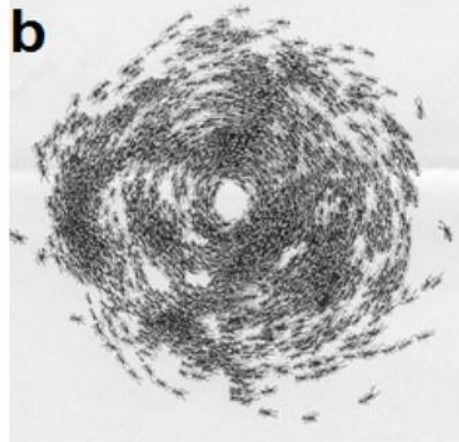
1. Name a main advantage of single-molecule techniques over ensemble measurements.
2. List three main methods used to measure single molecules. What are their respective strengths and limitations?
3. What is a typical output of a single-molecule mechanics experiment? What can this output reveal about the mechanical properties of biomolecules?
4. Describe one similarity and one difference between single molecule mechanics studies and protein folding studies.

Collective behavior: Basics

locusts



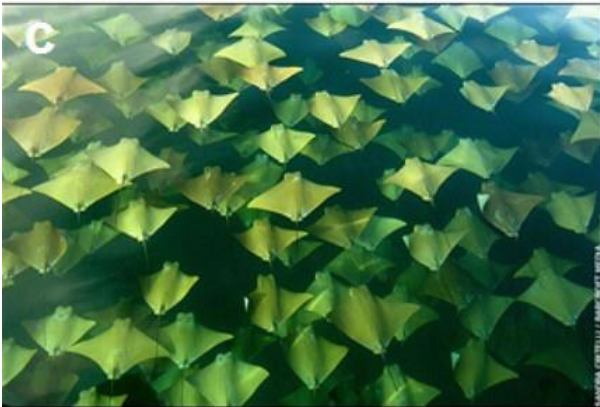
ants



starlings



zebra



rays



fish



people



sheep

Collective behavior: Basics

Common points:

- Systems of many similar units interacting in a well-defined manner
- Interactions: attraction/repulsion, or more complex combinations
- Behave differently than they would on their own
- Transitions can occur simultaneously, governed by the collective (critical phenomena)

Differences:

- Biological systems don't obey conservation laws (momentum, energy)
- Number of biological units is small (dozens to hundreds) compared to statistical ensembles
- In a confined geometry, jamming can occur
- Number fluctuations are larger: grow linearly with system size,

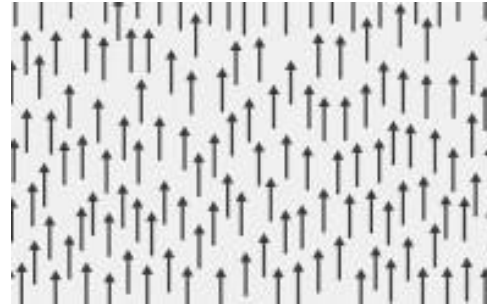
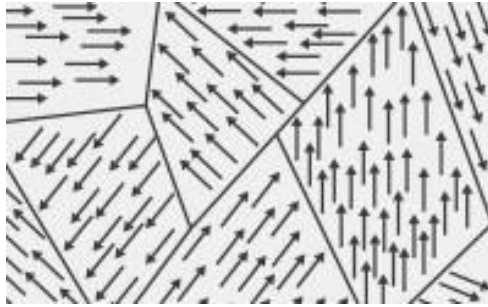
Goals:

- Explain patterns observed
- Exploit knowledge of patterns for control purposes

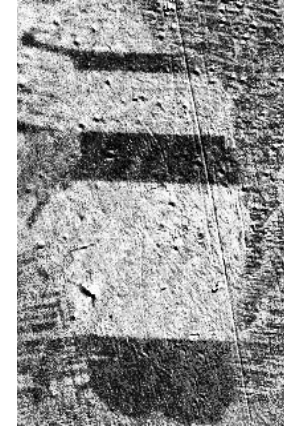
Statistical mechanics basis

1970s Renormalization group theory of **phase transitions**

magnetic dipole moments



change in order parameter



Flocking: coherent motion of individual units (in contrast to random)

- system of similar units
- moving with a nearly constant absolute velocity v
- interactions with neighbors change the direction of velocity
- subject to noise, η

Statistical mechanics basis

Critical behavior of order parameters

Order parameter: average normalized velocity
Takes on values $[0, 1]$

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

N number of units
 v_0 average absolute velocity

equilibrium

isothermal
compressibility of a liquid

$$\kappa_T \sim |T - T_c|^{-\gamma}$$

density difference
between liquid and gas

$$\rho_l - \rho_g \sim (T_c - T)^\beta$$

self-propelled

$\chi \sim (\eta - \eta_c)^{-\gamma}$ fluctuations in order parameter,
scaled by system size

$$\varphi \sim \begin{cases} (1 - \eta/\eta_c)^\beta & \text{for } \eta < \eta_c \\ 0 & \text{for } \eta > \eta_c \end{cases} \quad \text{for large system size, order parameter}$$

Statistical mechanics basis

Clusters and correlations

Units tend to form clusters with similar order parameters.

$$c_{vv}(t) = \frac{1}{N} \sum_{i=1}^N \frac{\langle \vec{v}_i(t) \cdot \vec{v}_i(0) \rangle}{\langle \vec{v}_i(0) \cdot \vec{v}_i(0) \rangle}$$

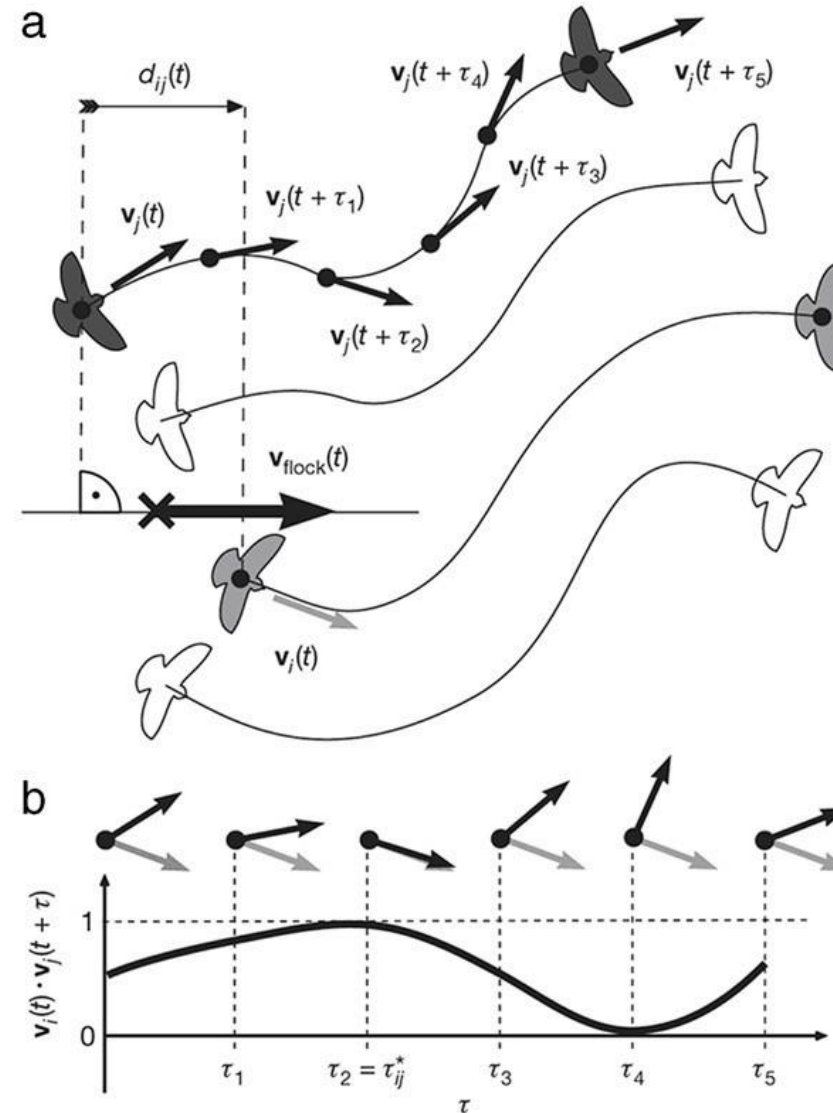
velocity-velocity correlation function

$$c_p(r) = \frac{V}{4\pi r^2 N^2} \left\langle \sum_i \sum_{j \neq i} \delta(r - r_{ij}) \right\rangle$$

pair correlation function

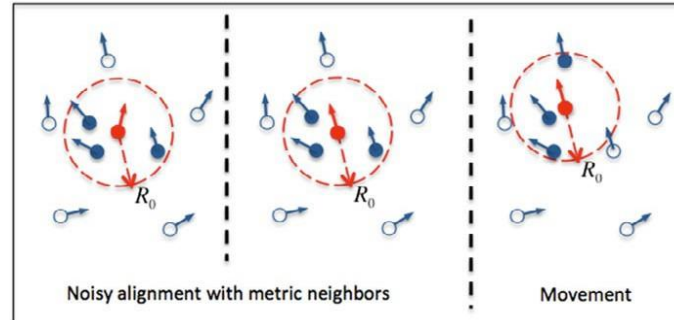
$$c_{ij}(\tau) = \langle \vec{v}_i(t) \cdot \vec{v}_j(t + \tau) \rangle$$

directional correlation function



Basic models

Standard Vicsek Model:



all units within R
have identical
interaction

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

velocity, standard magnitude
direction shared with neighbors within radius R

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

position

$$\arctan\left[\frac{\langle \vec{v}_j(t) \rangle_R}{|\langle \vec{v}_j(t) \rangle_R|}\right] = \vartheta_i(t)$$

unit vector pointing in average direction of
motion of neighbors within radius R

$$\vartheta_i(t+1) = \vartheta_i(t) + \Delta_i(t)$$

time evolution of direction
includes random component

Displays a second order phase transition from disordered to ordered as perturbation (noise) is decreased

Basic models

Cucker-Smale Model, exact model excluding noise (deterministic):

$$a_{ij} = \frac{1}{(1 + \|x_i - x_j\|^2)^\beta}$$

interaction between unit i and unit j
decays with distance, depends on exponent $\beta > 0$

$$v_i(t + h) - v_i(t) = h \sum_{j=1}^k a_{ij}(v_j - v_i)$$

velocity evolves with time

$$x(t + h) = x(t) + hv(t)$$

position evolves with time

Displays a second order phase transition from disordered to ordered as long as $\beta < \frac{1}{2}$.

All velocities tend toward a common value, v^*

Under some initial conditions, $\beta \geq \frac{1}{2}$ also leads to flocking.

Collective behavior: Observations

Iain Couzin (locusts) <https://www.youtube.com/watch?v=2R0rWJo6dK4> (16 min)

Nicholas Ouellette (humans, gnats) <https://www.sciencefriday.com/segments/the-physics-of-a-crowd/> (15 min)

Jennifer Zallen (cells in fruit fly) <https://www.ibiology.org/development-and-stem-cells/building-multicellular-structures-development-new-roles-toll-receptors/> (12 min)

Bonnie Bassler (bacteria) <https://www.ibiology.org/microbiology/chemical-communication/> (26 min)

Lectures 11, 12

- William Bialek: Fundamental physical limits on the performance of biological systems (2018)

"for the application of general theoretical principles of physics and information theory to help understand and predict how biological systems function across a variety of scales, from molecules and cells, to brains and animal collectives."

- Irene Giardina and Andrea Cavagna: Statistical physics of flocks and swarms (2021)

"For the incisive combination of observation, analysis, and theory to elucidate the beautiful statistical physics problems underlying collective behavior in natural flocks and swarms."