Propagation of information in turning flocks of starlings

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Cortona, May 2018

Flocks of starlings vs Physics

Typical flocking model:

attraction, repulsion, alignment

e.g.Vicsek et al. 1995

$$\vec{v}_i(t+1) = \vec{v}_i(t) + J\sum_{k\in i}\vec{v}_k(t) + \vec{\xi}_i$$

Langevin equation:

$$\frac{d\vec{v}_i}{dt} = -\frac{\partial H}{\partial \vec{v}_i} + \vec{\xi}_i$$

$$H = -J\sum_{<ij>}\vec{v}_i(t)\cdot\vec{v}_j(t)$$

Heisenberg ferromagnet

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Heisenberg ferromagnet

EMPIRICAL RESULTS ?

The first set of large-scale data on 3D animal aggregations:

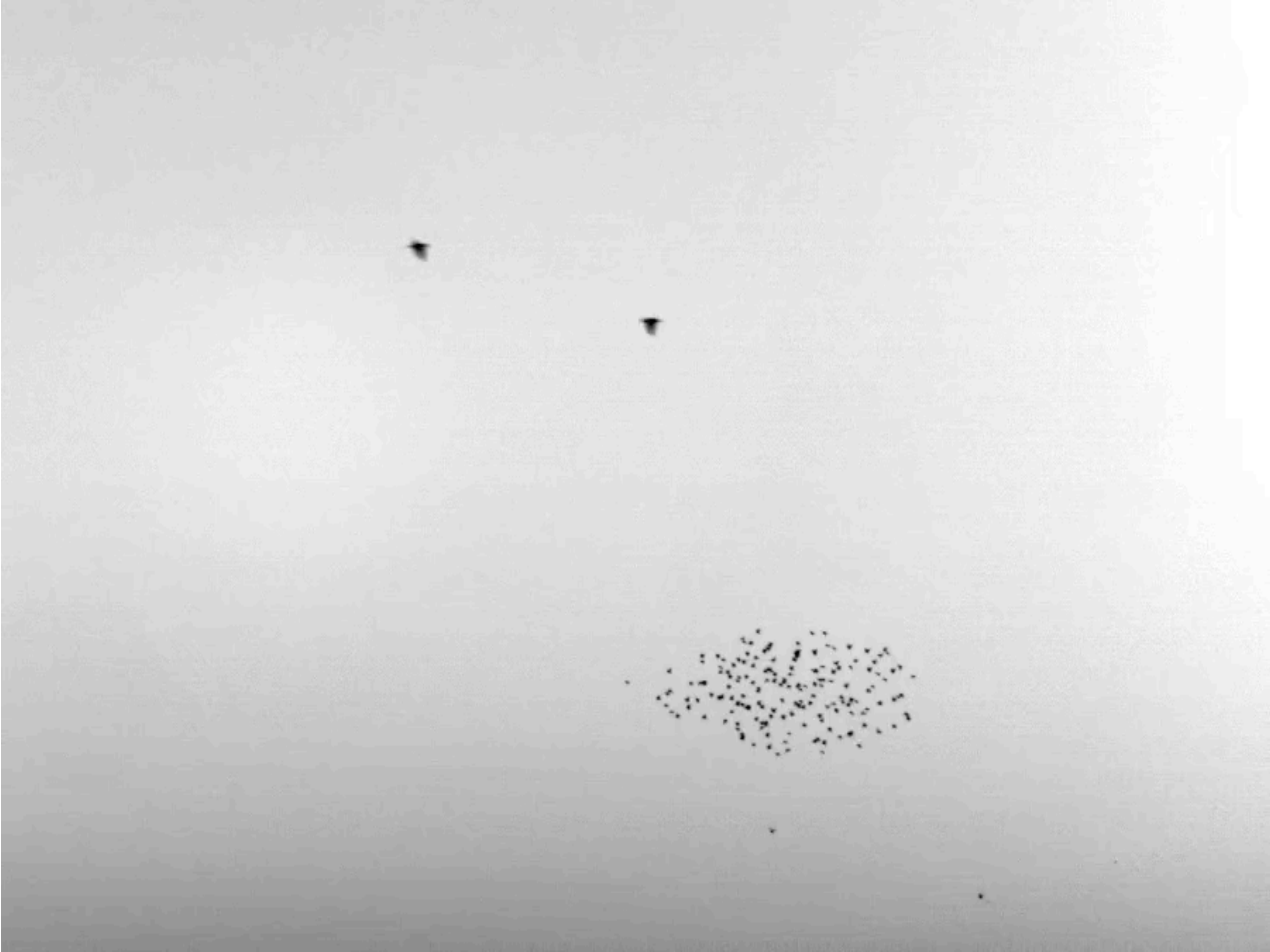
2008: Rome group **up to 2700 starlings** in the field

3D positions $\boldsymbol{r}_i$ and velocities $\boldsymbol{v}_i$ of all birds in a compact flock at *one moment of time* are obtained using stereoscopy

Static properties

Dynamics?

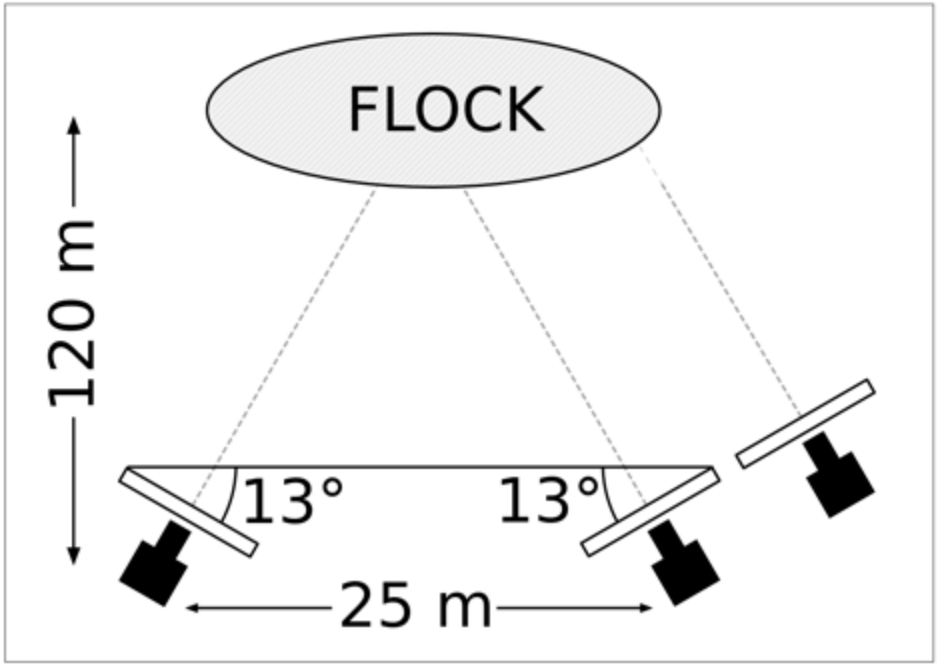
Synchronized and rapid changes of direction of the whole group?



Experiments

- Natural flocks of starlings making turns above a roosting place in Rome
- Experiments are performed using stereo photography with three different view points

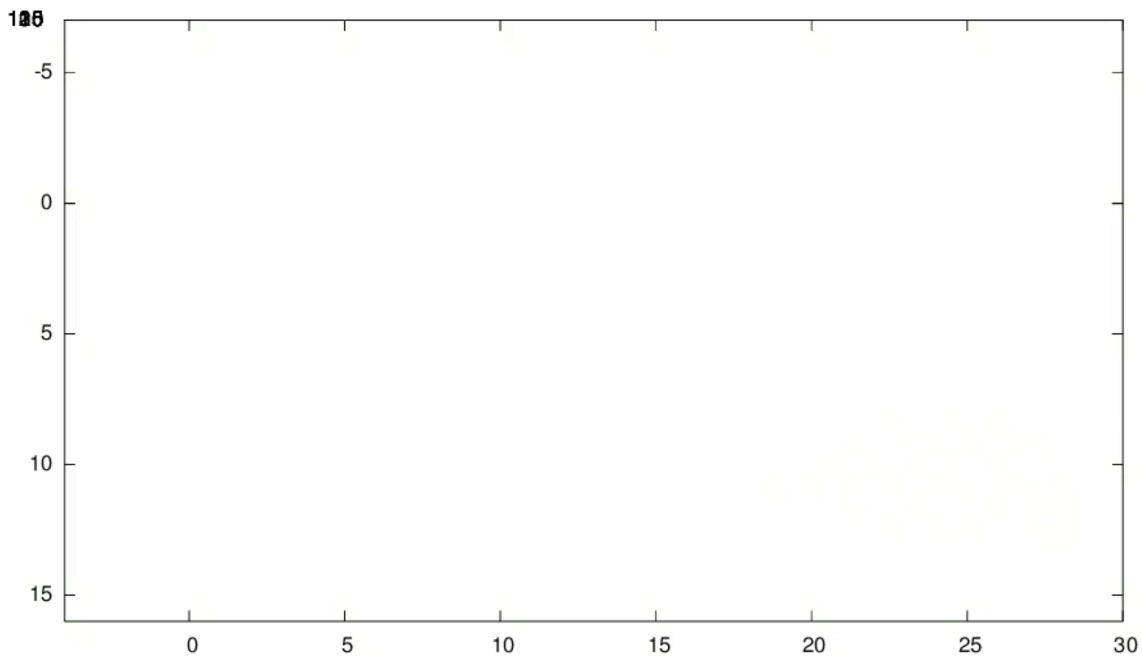
Experimental setup



3D trajectories of collective turns

- 12 turning flocks of 50 to 600 starlings above a roosting place in Rome
- 3D trajectories of individual birds for the entire duration of a turning event (>5s)

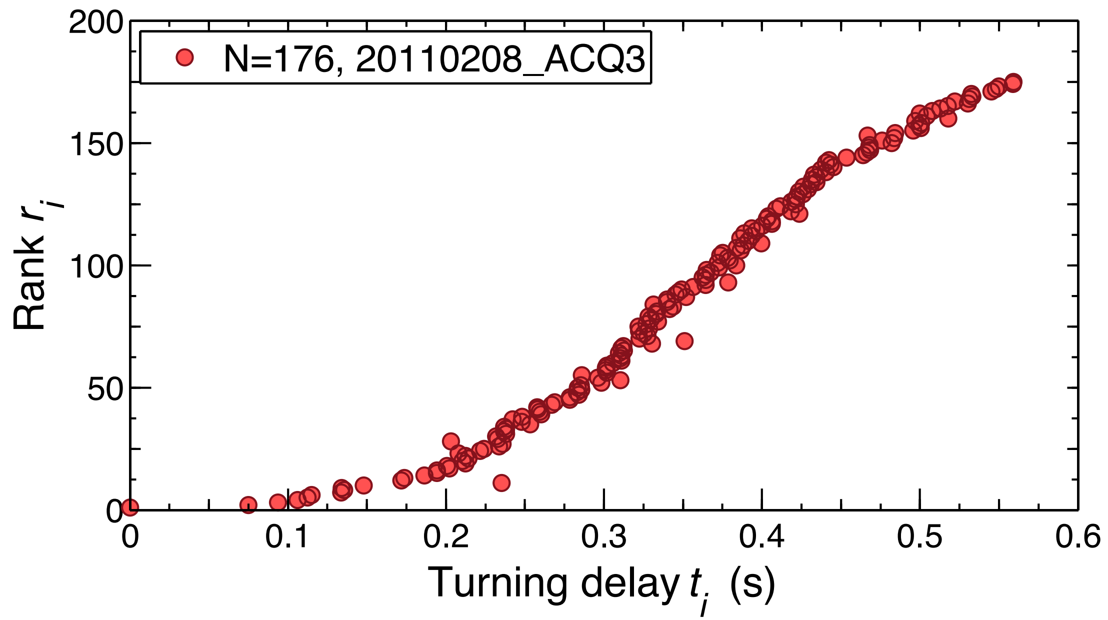
GReTA – tracking algorithm, IEEE trans. Pattern anal. Mach. Intell. (2015)



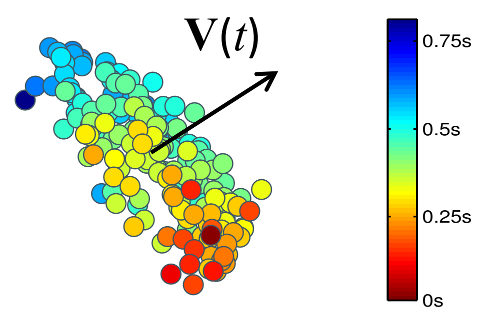
Birds ranking

Rank birds according to their mutual turning delays τ_{ij}

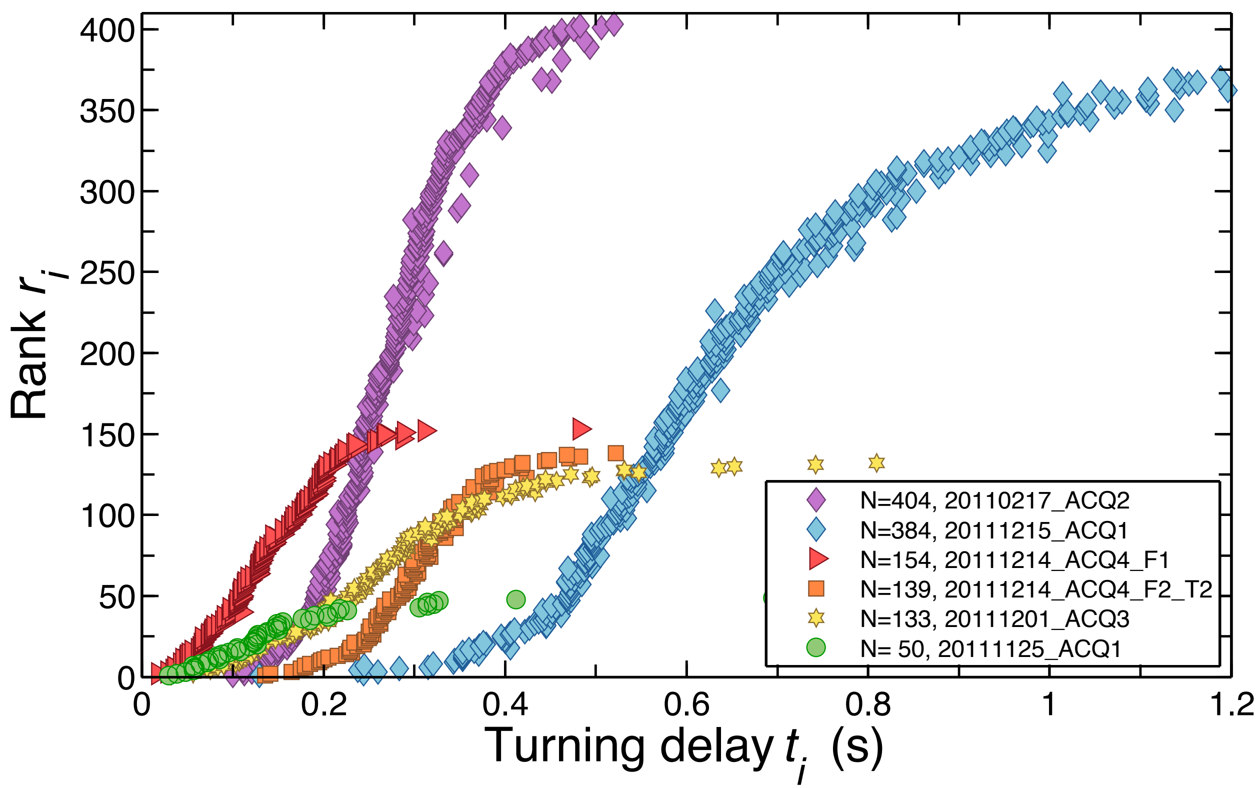
rank	delay
1	0 ms
2	35ms
3	44 ms
4	50 ms
5	52 ms
6	54 ms
7	63 ms
8	64 ms
9	68 ms
10	70 ms
11	71 ms
...	...



Turn starts localized and then it propagates across the flock



Ranking curves



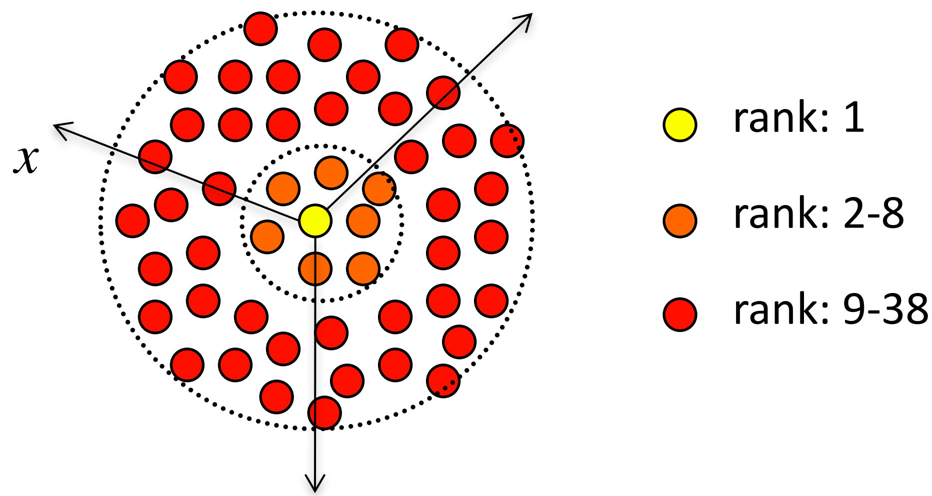
Ranking and propagation in space

(searching for dispersion law)

If the turn starts localized then:

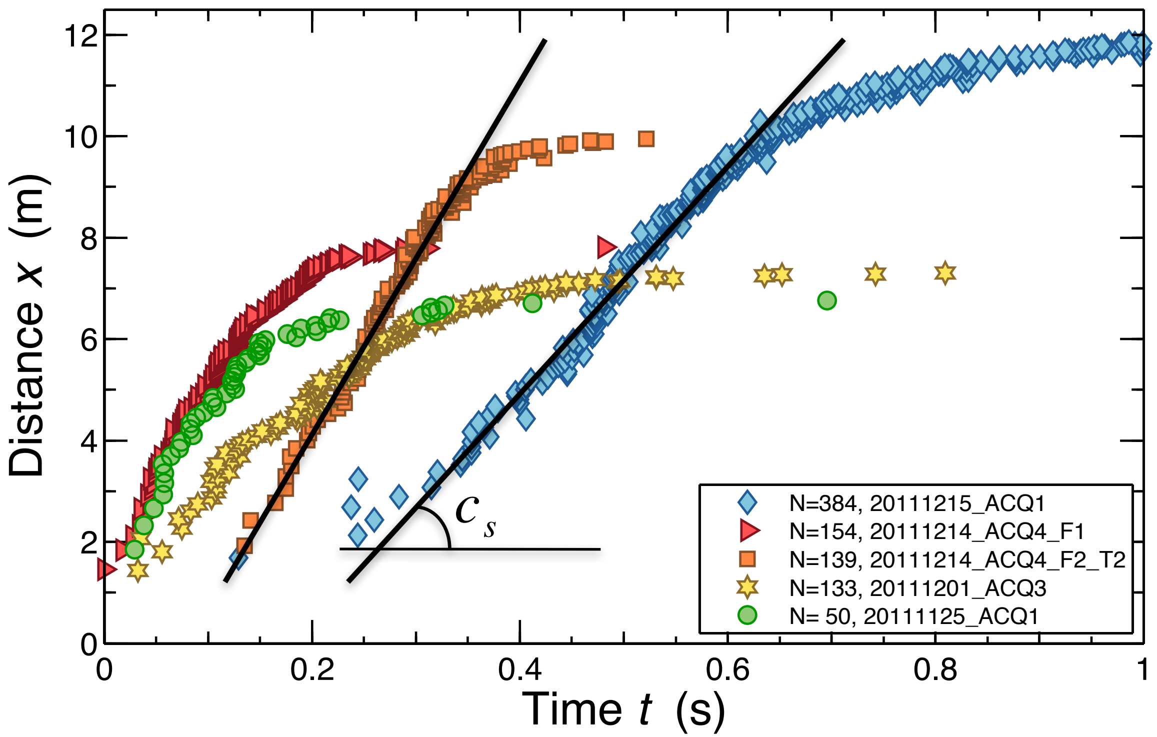
rank	delay
1	0 ms
2	35ms
3	44 ms
4	50 ms
5	52 ms
6	54 ms
7	63 ms
8	64 ms
9	68 ms
10	70 ms
11	71 ms
...	...

rank = *(density ρ)* x *(distance traveled by the turn x)* ^{3}



$$x(t) = \left[\frac{rank(t)}{\rho}\right]^{1/3}$$

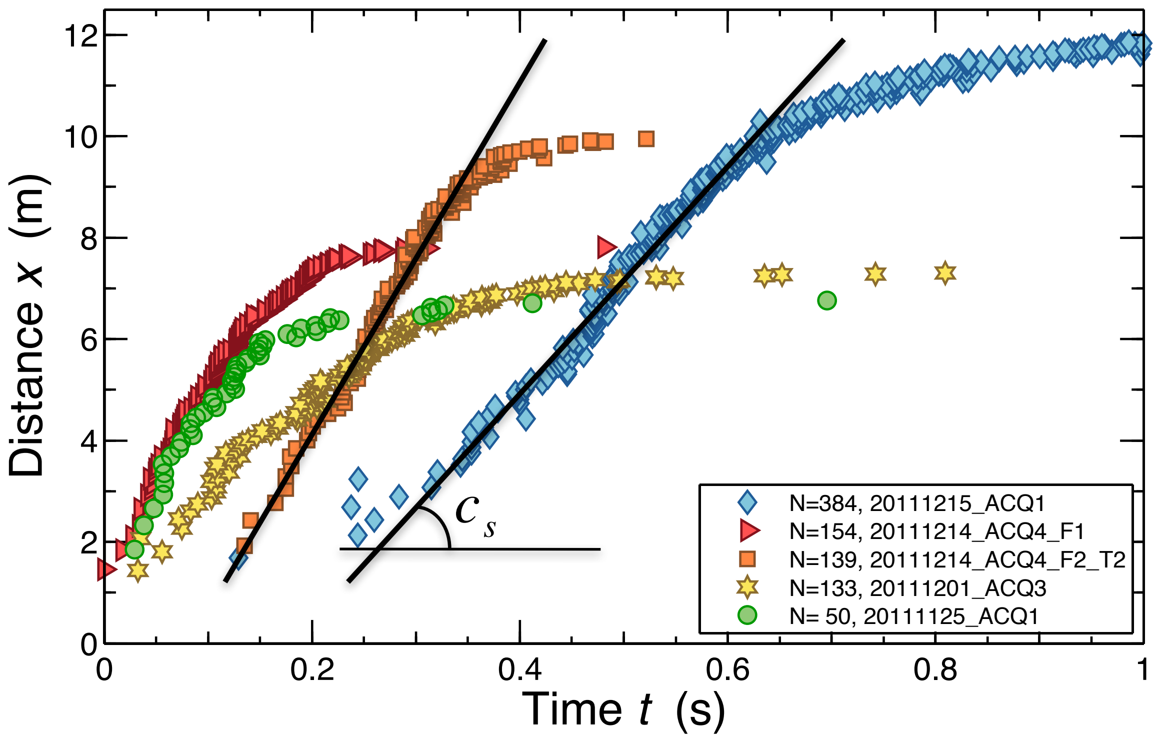
Dispersion law : linear propagation of the turn



$$x = c_s t$$

c_s = speed of propagation of the turn across the flock

Dispersion law : linear propagation of the turn



$$x = c_s t$$

c_s = speed of propagation of the turn across the flock

- Linear (sound-like) propagation of the turn (direction)
- Very weak attenuation of the turning signal (no damping)
- Variability of the speed of propagation c_S (20-40 ms^{-1})

Not explained by the standard theory of flocking!!

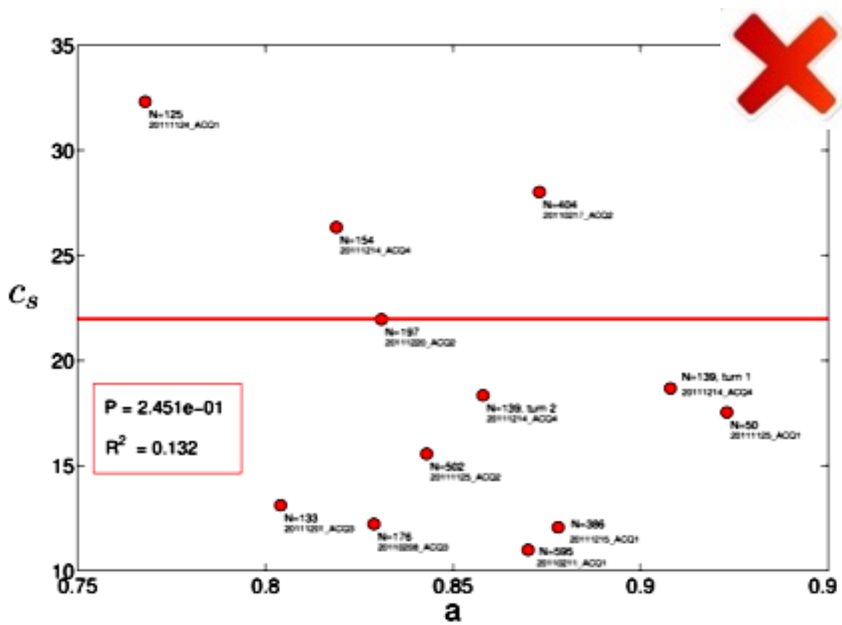
(predicts diffusive and damped spread of information)

Flock-to-flock variability of c_s

Making sense of the variability of c_s …

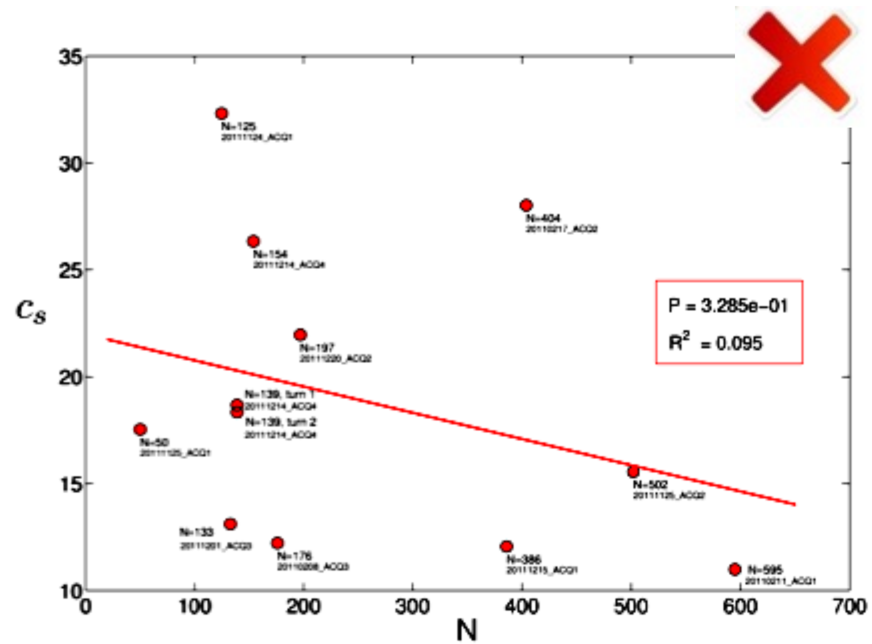
speed of turn propagation

attempt #1:



nearest neighbors distance
(density)

attempt #2:



number of birds in the flock

Standard theory of flocking

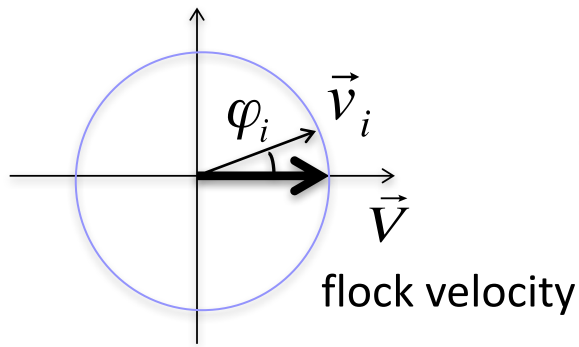
$$\vec{v}_i(t+1) = \vec{v}_i(t) + J\sum_{k\in i}\vec{v}_k(t) + \vec{\xi}_i$$

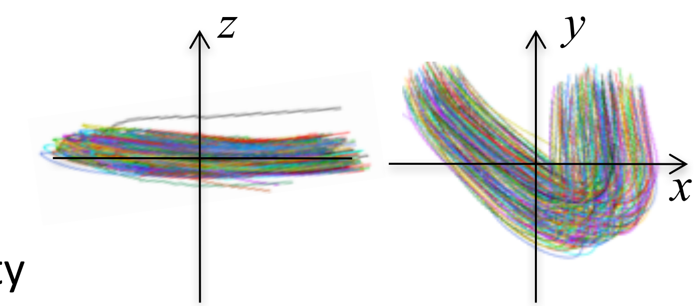
typical flocking model

$$\frac{d\vec{v}_i}{dt} = -\frac{\partial H}{\partial \vec{v}_i} + \vec{\xi}_i \qquad H = -J\sum_{<ij>}\vec{v}_i(t)\cdot\vec{v}_j(t)$$

- Planar order parameter:

$$v_i^x + i v_i^y = v\, e^{i\varphi_i}$$





- High polarization (low T) – spin wave expansion:

a = lattice spacing

$$\varphi \sim 0 \quad \Rightarrow \quad H = \frac{1}{2}J\sum_{<ij>}(\varphi_i - \varphi_j)^2 = \frac{1}{2a}J\int d^3x\left[\vec{\nabla}\varphi(x,t)\right]^2$$

equation for the orientation angle change during the turn

$$\frac{\partial\varphi}{\partial t} = -\frac{\delta H}{\delta\varphi} = a^2 J\,\nabla^2\varphi \quad \Rightarrow$$

$x \sim \sqrt{t}$ diffusive propagation ✗

$\omega = ik^2$ damping ✗

What is wrong?

1) Missing conservation law

Rotational symmetry of the Hamiltonian $\quad v_i = v\, e^{i\varphi_i} \qquad \varphi_i \to \varphi_i + d\varphi$

(all flight directions are equivalent)

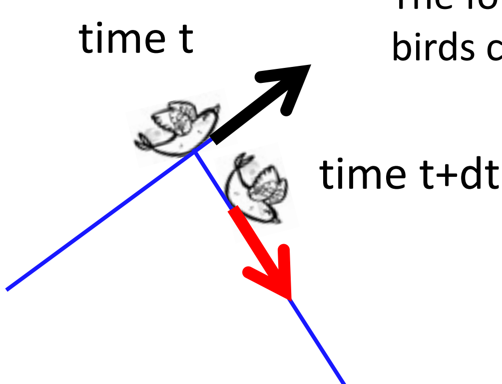
➡ Conservation law which affects the dynamics ! *(and dispersion law!)*

2) No inertia

- **Standard theory:**

$$\frac{\partial \varphi}{\partial t} = a^2 J \nabla^2 \varphi + \xi = -\frac{\delta H}{\delta \varphi} + \xi$$

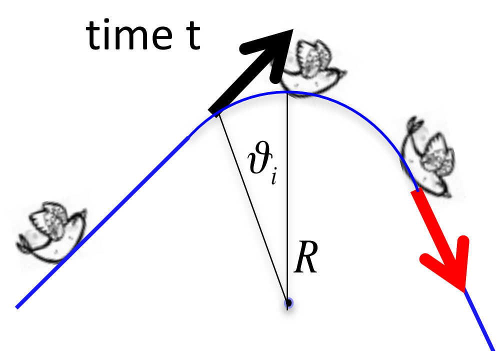
The force acts on velocity,
birds can turn instantaneously



but turns are smooth!

- **Real bird:**

To change direction, the bird has some constraints: mass, size, wings, etc.



New (superfluid) theory of flocking

$$H = \int \frac{d^3x}{a^3} \left\{ \frac{1}{2}\rho_S \left[\vec{\nabla}\varphi(x,t)\right]^2 + \frac{s_z^2(x,t)}{2\chi} \right\}$$

$\rho_S \equiv a^2 J$: rescaled alignment coupling

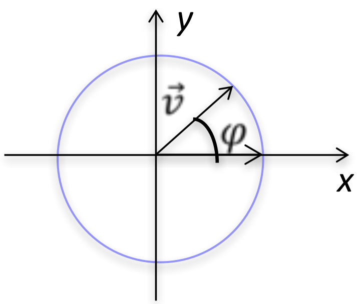
$\varphi(x,t)$ = parametrizes rotations of velocities

$s_z(x,t)$ = momentum conjugated to $\varphi(x,t)$, i.e. generator of the rotations around z-axis (SPIN)

χ = generalized moment of inertia

$$\vec{v} = v_x + i v_y = v e^{i\varphi}$$

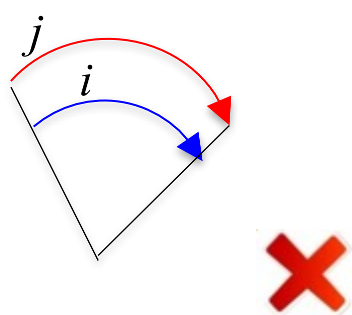
$$\{\vec{v}, s_z\} = \frac{\partial \vec{v}}{\partial \varphi} = i\vec{v}$$



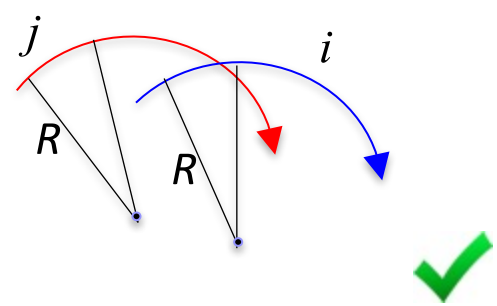
Biological motivation:

$R \approx \text{const.}$

$v \approx \text{const.}$



parallel paths trajectories



equal radius trajectories

Predictions of the superfluid theory

Equations of motion:

$$\begin{cases} \dfrac{\partial \varphi}{\partial t} = \dfrac{\delta H}{\delta s_z} = \dfrac{1}{\chi} s_z \\ \dfrac{\partial s_z}{\partial t} = -\dfrac{\delta H}{\delta \varphi} = \rho_s \nabla^2 \varphi \end{cases}$$

$$\frac{\partial^2 \varphi}{\partial t^2} - \frac{\rho_s}{\chi} \nabla^2 \varphi = 0$$

equation for the orientation angle change during the turn

$x = c_s t$	linear dispersion law	✓
$\omega = c_s k$	no damping	✓

Speed of propagation: $c_s = \sqrt{\dfrac{a^2 J}{\chi}}$

The alignment coupling J has been related to the polarization Φ

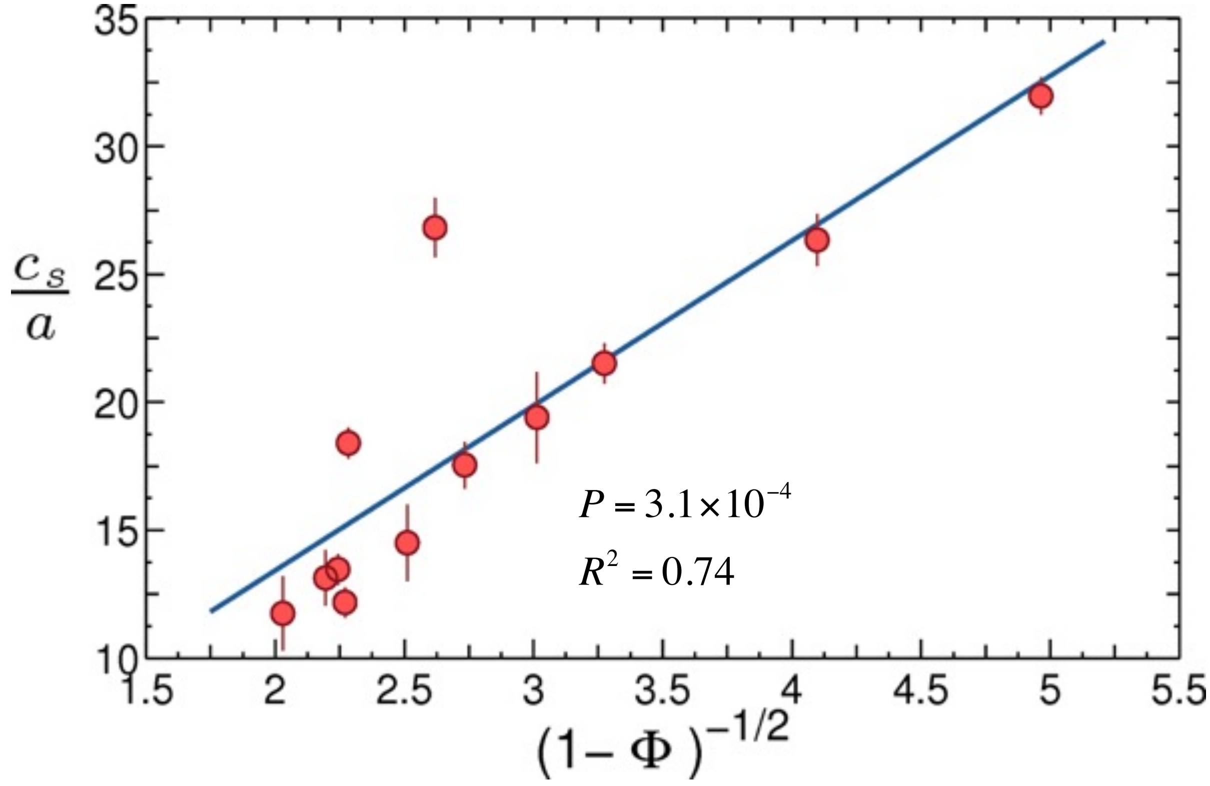
Bialek et al. PNAS (2012)

$J \propto \dfrac{1}{1-\Phi}$ And $\Phi = \left\| \dfrac{1}{N} \sum_i \dfrac{\vec{v}_i}{\|\vec{v}_i\|} \right\|$ is experimentally accessible!

$$c_s \propto \frac{1}{\sqrt{1-\Phi}}$$

the speed of propagation of the turn across the flock must be larger in more ordered flocks

Experimental test of the prediction

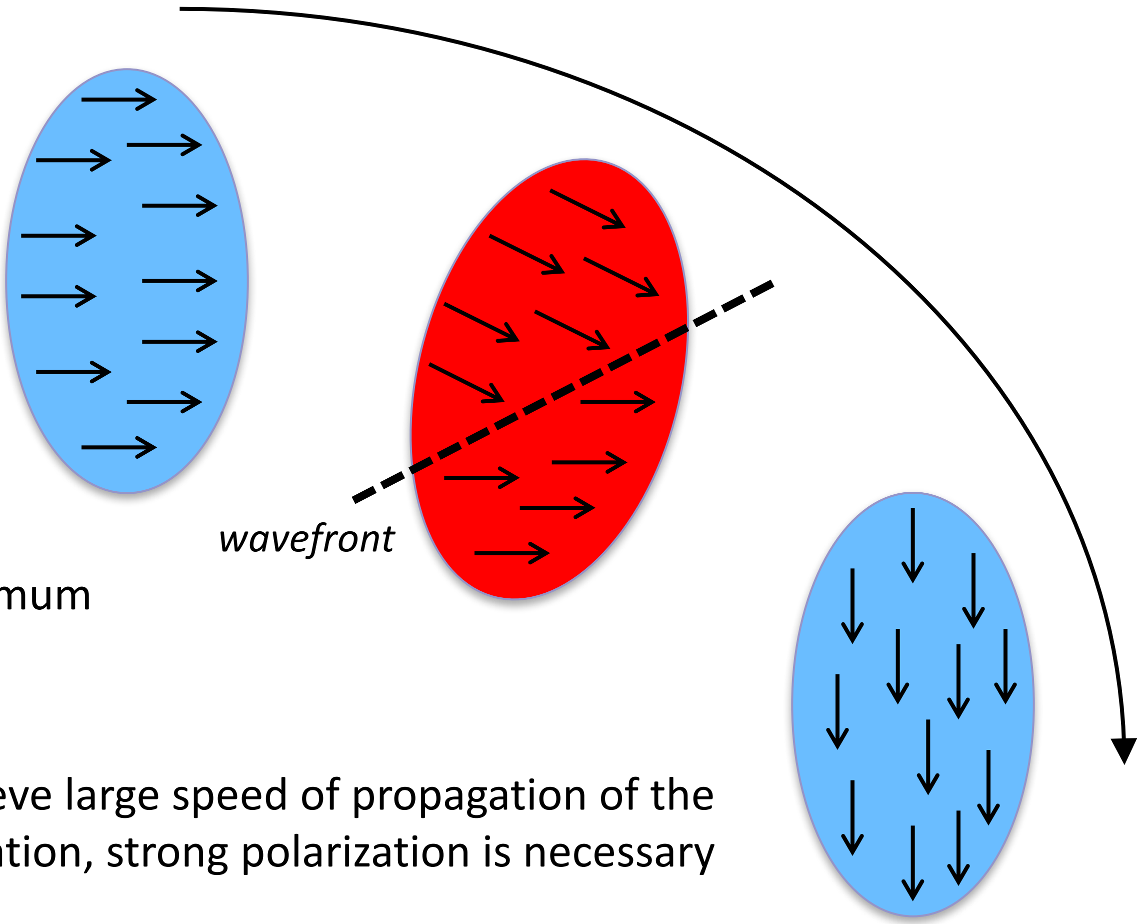


$$c_s \propto \frac{1}{\sqrt{1-\Phi}}$$ ✔

Nature Physics (2014)

Why natural groups are so polarized?

The group is fragile during the decision



fast information transfer keeps group's decoherence to a minimum

$$c_s \propto \frac{1}{\sqrt{1-\Phi}}$$

to achieve large speed of propagation of the information, strong polarization is necessary

The link between swift decision-making and large polarization may be the evolutionary drive behind the strong ordering observed in many living groups

The Inertial Spin Model

A new model for self-organized collective motion
(from phases to velocities, full 3D rotation)

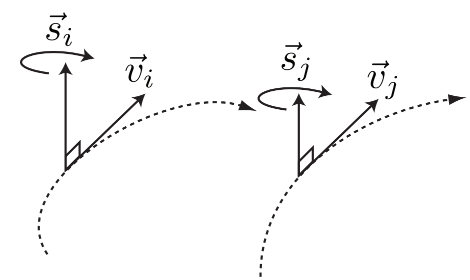
$$\frac{d\vec{v}_i}{dt} = \frac{1}{\chi}\vec{s}_i \times \vec{v}_i; \qquad \frac{d\vec{r}_i}{dt} = \vec{v}_i$$

$$\frac{d\vec{s}_i}{dt} = \vec{v}_i \times \left[\frac{J}{v_0^2}\sum_j n_{ij}\vec{v}_j - \frac{\eta}{v_0^2}\frac{d\vec{v}_i}{dt} + \frac{\vec{\xi}_i}{v_0}\right]$$

rotational dissipation

noise $\langle \vec{\xi}_i(t) \cdot \vec{\xi}_j(t') \rangle = 2d\eta T \delta_{ij}\delta(t-t')$

Model G



Connection between inertial terms and symmetry is automatically implemented giving correct information propagation

$$\chi\frac{d^2\vec{v}_i}{dt^2} + \chi\frac{\vec{v}_i}{v_0^2}\left(\frac{d\vec{v}_i}{dt}\right)^2 + \eta\frac{d\vec{v}_i}{dt} = J\left(\sum_j n_{ij}\vec{v}_j\right)^{\perp} + v_0\vec{\xi}_i^{\perp}$$

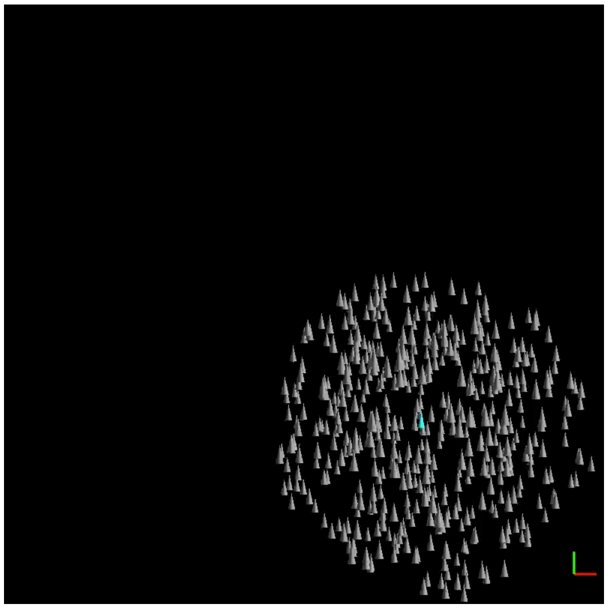
overdamped limit → Vicsek model

inertial term; centripetal term; dissipation; social force; noise

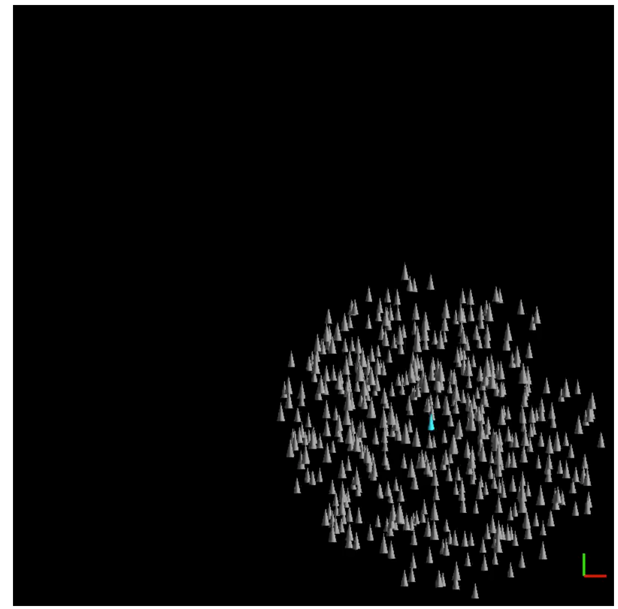
J. Stat. Phys. (2015)

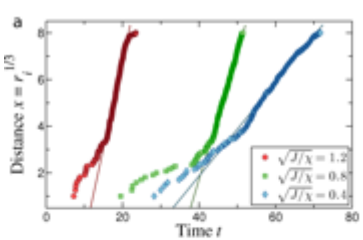
Inertial Spin Model - simulations

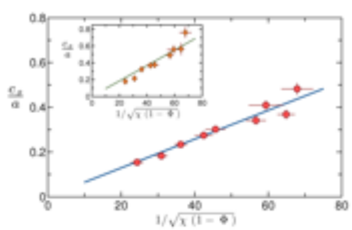
Underdamped regime



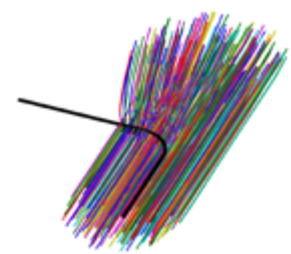
Overdamped regime







correct information propagation



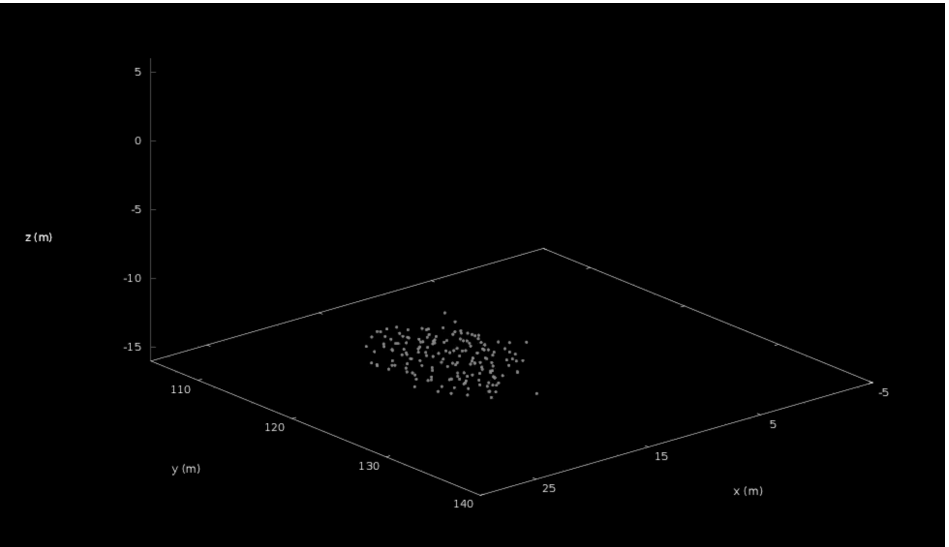
Vicsek model

Why and how did the turn start?

As a response to an external alarm cue? Not necessarily

- locusts - in the lab and in the field — Buhl et al. Science (2006)
- fish schools - collective evasion maneuvers (lab) — Rosenthal et al. PNAS (2015)
- starlings aerial display - flocks keep changing their direction of motion even in the absence of predators or obstacles

Collective directional switching can be triggered *spontaneously* without changes in the external environment

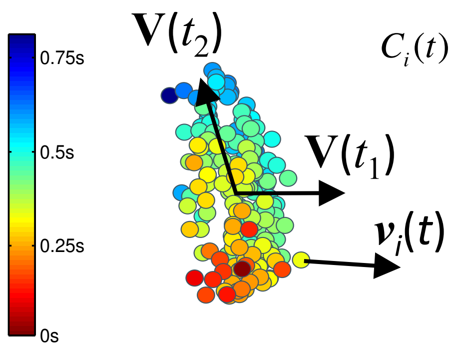


- Where it starts?
  individuals close to the border
- What triggers the turn?
  internal behavioural fluctuations

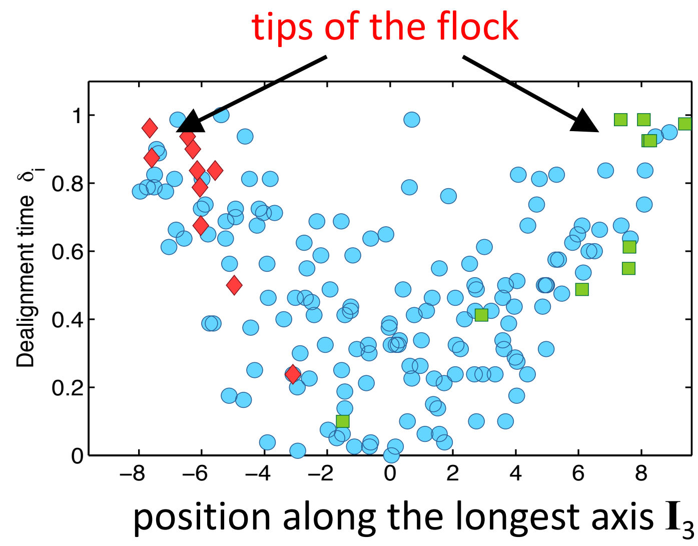
Roy. Soc. Interface (2015)

What triggers spontaneous turns?

Individual deviations from the global flock's direction of motion prior to the turn:



$$C_i(t) = \frac{\mathbf{v}_i(t)}{\|\mathbf{v}_i(t)\|} \cdot \frac{\mathbf{V}(t)}{\|\mathbf{V}(t)\|}$$



There is a correlation between the location of an individual in the flock and how persistently it deviates

Roy. Soc. Interface (2015)

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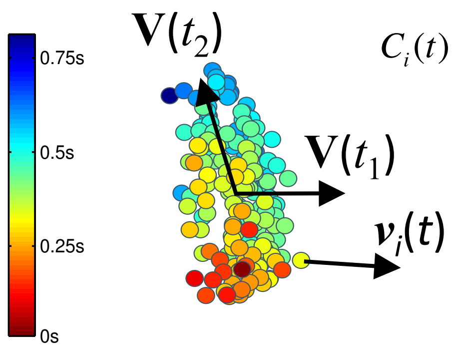
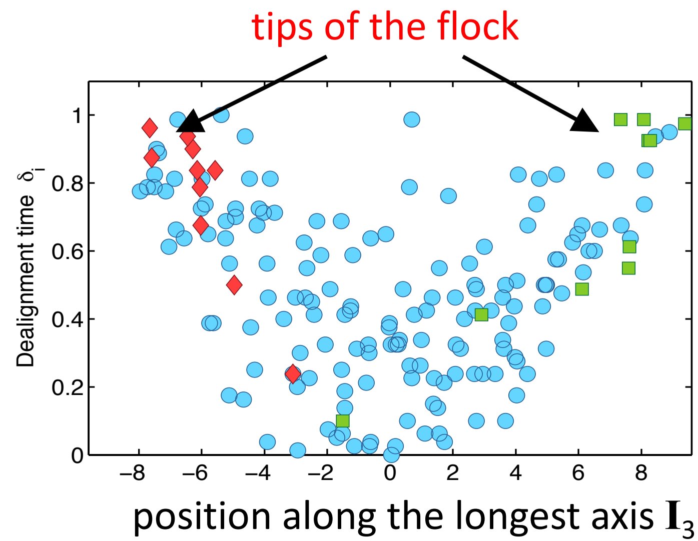
Individual deviations from the global flock's direction of motion prior to the turn:



$$C_i(t) = \frac{\mathbf{v}_i(t)}{\|\mathbf{v}_i(t)\|} \cdot \frac{\mathbf{V}(t)}{\|\mathbf{V}(t)\|}$$



Why turns occur spontaneously and often?

Standard Heisenberg model on a lattice: $\tau^{rel} \sim L^{d-2}$ the system changes global state on large scales

What is different in flocks?

the network is random
interactions are NOT symmetric

→ peripheral clusters are more sensitive to noise leading to collective changes to state

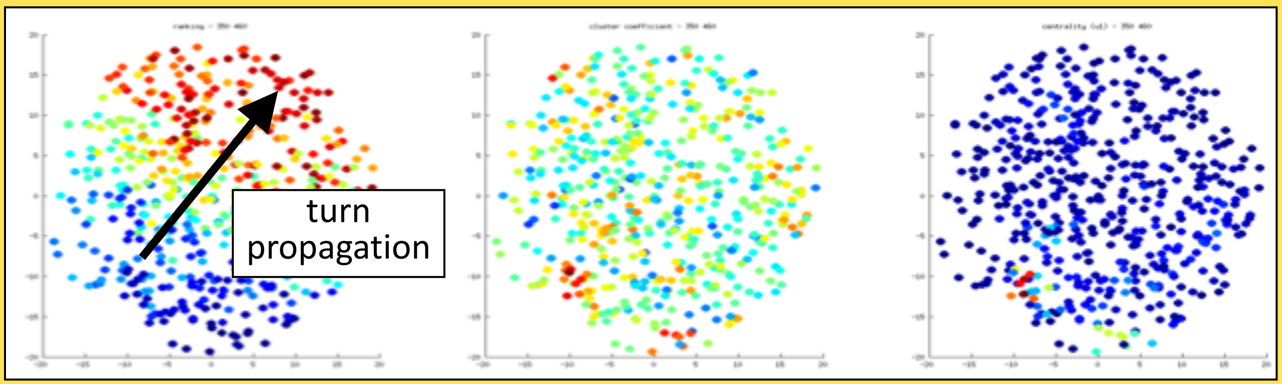
Phys. Rev. Lett. (2017)

Spontaneous turns determined by interaction network

Dynamics on a random Euclidean network?

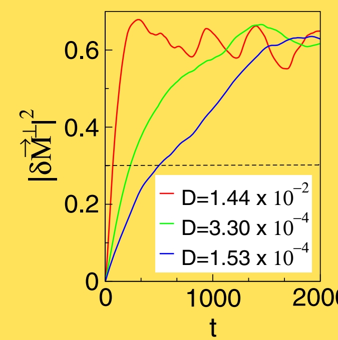
Phys. Rev. Lett. (2017)

- points drawn uniformly in Euclidean space instead on a regular lattice
- place the birds/spins and let them interact with their n_c nearest neighbours



ranking | clustering coefficient c_i | eigenvalue centrality u^0_i

turns start at the boundary where both c_i and u^0_i are large



Experimental confirmation:

✧ fish: large c_i of initiators of collective evasion waves in fish schools — Rosenthal et al. PNAS (2015)

✧ starlings: turns start from the tips;
initiators exhibit systematic fluctuations — Attanasi et al. Roy. Soc. Interface (2015)

Conclusions

- Turns start localized, then spread through the flock fast and accurate
    - linear propagation of orientational information, no damping
- New superfluid theory for turns
    - symmetries and conservation laws ideas work in biology too
- High order in the group grants a more efficient propagation of information
    - why natural groups are so polarized?
- Non-symmetric random interaction network and inertial dynamics can produce spontaneous changes of collective state on short scales

Based on

- ✧ Information transfer and behavioural inertia in starling flocks
  Nature Physics, 2014

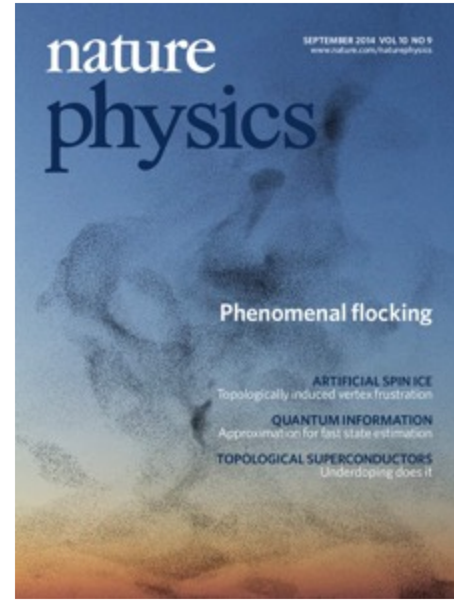
- ✧ GReTA -- a novel Global and Recursive Tracking Algorithm in three dimensions
  IEEE Trans. Pattern Anal. Mach. Intell., 2015

- ✧ Flocking and turning: a new model for self-organized collective motion
  J. Stat. Phys, 2015

- ✧ Silent flocks: : Constraints on Signal Propagation Across Biological Groups
  Phys.Rev.Lett., 2015

- ✧ Emergence of collective changes in travel direction of starling flocks from individual birds' fluctuations
  Roy.Soc. Interface, 2015

- ✧ Nonsymmetric Interactions Trigger Collective Swings in Globally Ordered Systems
  Phys.Rev.Lett., 2017



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Ed Shen
Edmondo Silvestri
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