

SIGNAL PROPAGATION AND DYNAMICAL CORRELATION IN BIOLOGICAL ACTIVE MATTER

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Introduction

The aim of this PhD thesis is to investigate the mechanisms underlying information propagation within a biological group. Collective phenomena in animal groups have attracted much attention in the last years, becoming one of the most attractive topics in biology. However, in most of the studies on animal collective behavior it has been tried to understand how a globally ordered state may emerge from simple behavioral rules, less effort has been devoted to the understanding of the way in which information propagates within an animal group. The study of this phenomenon derives its importance from the fact that it is the "conditio sine qua non" for collective response: the way the group as a whole reacts to its environment. Collective response in biological systems require all individuals in the group to go through a behavioral change of state. In order to avoid a loss of cohesion by the group it is important that during this transition the transfer of information is rapid and robust. The mechanism by which such robustness is achieved, however, is not clear yet [1].

In carrying out this study I will use multiple approaches that can be basically divided into three parts: theoretical analysis, experimental data analysis and numerical simulation.

Collective Behavior

Collective behavior includes all those phenomena for which the emergent properties of a group cannot be reduced to the individual constituents, but they depend crucially on the interaction between the various components of the group [1, 2, 3]. From a general perspective, collective behavior is a key concept in many different area of science, including physics. In the last 50 years theoretical and experimental physics has studied in depth the mechanisms underlying ordering phenomena and phase transitions. In this context, the origin and emergence of collective behavior have been understood in great detail. In physical systems there are at least two facts that have been recognized as fundamental, which suggests that they may be relevant to other disciplines: (i) locality of interactions: a system of individual units (particles, magnetic moments, etc.) that interact locally in space can generate, under appropriate conditions, an ordered state with collective global properties; (ii) universality: the large scale features of many order-disorder transitions do not depend on the details of the local interaction but only on some general characteristics of the system (the dimensionality of the space, the nature of the order parameter, symmetries, etc.). These two properties, though only strictly valid in physics, yet provide an inspiring paradigm also in other fields [1].

In biology the individual units are much more complex than in physics, as a product of evolution they have cognitive abilities and are diversified among species. Moreover one has to do with a great diversity of size scales and complexity. Collective behavior is indeed a widespread phenomenon in biological systems: bird flocks, fish schools, swarms of insects, trails of ants, herds of mammals, etc. Nevertheless there are experimental evidence providing good opportunity that the mechanism of group formation is more general and transcends the detailed nature of its components. The working hypothesis

is to trace back the global behavior of all these systems from simple individual and local rules. Therefore it seems reasonable to believe that the individual complexity is less essential in determining the collective properties and only a few characteristics are necessary to explain group formation. Following this line of reasoning we can describe local interactions with simple models, taking into account only the fundamental traits of the individual complexity, so as to insert the collective behavior into a universal framework that unites all of these phenomena [1, 2, 3].

Previous theoretical models

The Vicsek model (VM) represents the starting point of many collective motion models. In the VM the particles move with a constant absolute velocity v_0 and at each time step the direction of motion, which in $d = 2$ is just an angle or a phase φ , is calculated from the previous directions of all particles within an interaction range r_c with some random perturbation ξ added:

$$\vec{r}_i(t + dt) = \vec{r}_i(t) + \vec{v}_i(t)dt \quad (1)$$

$$\vec{v}_i(t) = v_0 e^{i\varphi_i(t)} \quad (2)$$

$$\varphi_i(t + dt) = \sum_j n_{ij}(t) \varphi_j(t) + \xi_i(t) \quad (3)$$

$$n_{ij}(t) = \begin{cases} 0 & \text{if } |\vec{r}_j(t) - \vec{r}_i(t)| > r_c \\ 1 & \text{if } |\vec{r}_j(t) - \vec{r}_i(t)| \leq r_c \end{cases} \quad (4)$$

$\vec{r}_i(t)$ is the position at time t of the i th particle, $\vec{v}_i(t)$ is its velocity and $\varphi_i(t)$ its direction of motion; $n_{ij}(t)$ is the adjacency matrix and tells us which are the j particles found at time t in the neighborhood of radius r_c of the particle i ; $\xi(t)$ is a random number chosen with a uniform probability from the interval $[-\eta/2, \eta/2]$. This model became famous because, varying either the noise strength η or the particle density $\rho = N/L^2$ in periodic domains of linear size L , it shows a phase transition when the density is large and the noise is small, in which the motion becomes ordered on a macroscopic scale and all of the particles tend to move in the same spontaneously selected direction [4, 5].

Regarding the motion of birds in a flock, a study of 2008 shows that the interactions do not depend on the metric distance, but rather on the topological distance: each bird interacts on average with a fixed number of neighbors (six to seven), rather than with all neighbors within a fixed metric distance. Let's suppose that each individual interacts with its first n_c neighbors, then this consideration is mathematically reflected in a modification of the adjacency matrix:

$$n_{ij}(t) = \begin{cases} 1 & \text{if } j \text{ at time } t \text{ is within the } n_c \text{ neighbors of bird } i, (j \in n_c^i) \\ 0 & \text{otherwise} \end{cases} \quad (5)$$

A topological interaction is indispensable to maintain a flock's cohesion against the large density changes caused by external perturbations [6].

A crucial feature of bird flocks is that the interaction network $n_{ij}(t)$ is not fixed in time, as each individual moves and continuously changes its neighbors and because of this the adjacency matrix depends on time. The possibility to exchange neighbors strongly enhances the stability of global ordering [7]. However, even though neighbor reshuffling definitely occurs, it is not a very fast process. Moreover information transfer is a transient, a very quick process that takes place on small scales of time and length. Any kind of update of the internal state of motion of a bird happens on a time-scale much faster than it takes to change even just half of its neighbors. This indicates that neighbor permanence is rather high and that in formalizing signal propagation in bird flocks it is possible to consider the adjacency matrix constant over time $n_{ij}(t) \sim \text{const.} = n_{ij}$ [8].

A quantitative microscopic theory for directional ordering in a flock can be derived directly from field data. Using the maximum entropy method (MEM) it is possible to build the minimally structured model consistent with experimental measured correlations in large flocks between the velocities, $C_{ij} = \langle \vec{v}_i \cdot \vec{v}_j \rangle$. The minimally structured distribution $P(\{\vec{v}_i\})$ consistent with the measured correlations is mathematically identical to the Heisenberg model [9]. We can use this identity between MEM distributions and Boltzmann distribution for system in thermal equilibrium to define a cost function or

pseudo-Hamiltonian on the space of birds' velocities:

$$H(\{\vec{v}_i\}) = -\frac{J}{2} \sum_{ij} n_{ij} \vec{v}_i \cdot \vec{v}_j \quad (6)$$

where J represents the interaction strength. Since the trajectories of birds during a turn lie approximately on a plane, to simplify the algebra, let's assume a $2d$ order parameter, $\vec{v}_i = (v_i^x, v_i^y) = v_0 e^{i\varphi_i}$, where the phase φ_i is the angle between the direction of motion of i and that of the flock [10]. In the highly ordered regime the phases of the velocity are small and it is possible to write an Hamiltonian for the phase:

$$H(\{\varphi_i\}) = \frac{J}{2} \sum_{ij} n_{ij} (\varphi_i - \varphi_j)^2 \quad (7)$$

If phase variations are smooth and we look at distances larger than the typical distance a between interacting neighbors, we can consider the continuum limit in space $\varphi_i(t) \rightarrow \varphi(\vec{x}, t)$ and the Hamiltonian can be conveniently approximated by:

$$H(\{\varphi(\vec{x}, t)\}) = \frac{1}{2} a^2 J n_c \int \frac{d^3x}{a^3} [\nabla\varphi(\vec{x}, t)]^2 \quad (8)$$

where $n_c = \frac{1}{N} \sum_{ij} n_{ij}$ is the average number of interacting neighbors. Once we know the Hamiltonian there is a plausible dynamics that allows the system to relax toward equilibrium, the Langevin dynamics:

$$\frac{\partial\varphi_i}{\partial t} = -\frac{\delta H}{\delta\varphi_i} + \xi_i(t) = \sum_{j=1}^N J_{ij} \varphi_j + \xi_i(t) \quad \rightarrow \quad \frac{\partial\varphi(\vec{x}, t)}{\partial t} = a^2 J n_c \nabla^2 \varphi(\vec{x}, t) + \xi(\vec{x}, t) \quad (9)$$

$$\vec{v}_i(t) = v_0 e^{i\varphi_i(t)} \quad \frac{d\vec{r}_i}{dt} = \vec{v}_i(t) \quad (10)$$

This equation of motion leads to diffusive dispersion law for the phase. In the case of birds the dispersion law tells us how local disturbances in flight direction of a particle affect the rest of the flock. In this Vicsek-like model the frequency ω obtained by computing the propagator in Fourier space is purely imaginary with a quadratic diffusive dispersion law $\omega \sim ik^2$. Therefore there is no propagation in this case [11].

However experimental studies of starling flock performing turns find that information about direction changes propagates across the flock with a linear dispersion law ($\omega = ck$) and negligible attenuation, minimizing group decoherence. In order to account for this the Inertial Spin Model (ISM) was developed [10, 11]. A new inertial term was introduced by adding a generalized kinetic term in the Hamiltonian for the phase φ of the velocity in order to restore the rotational symmetries and conservation laws of the problem:

$$H = \int \frac{d^3x}{a^3} \left\{ \frac{1}{2} a^2 J n_c [\nabla\varphi(\vec{x}, t)]^2 + \frac{s^2(\vec{x}, t)}{2\chi} \right\} \quad (11)$$

Since φ is the parameter of the rotation in the internal space of velocity, the generator of this rotation is the internal angular momentum, the spin s , while χ is a generalized moment of inertia quantifying the resistance of a bird to a change of its spin. The equations of motions are:

$$\frac{\partial\varphi}{\partial t} = \frac{\delta H}{\delta s} = \frac{s}{\chi} \quad (12a)$$

$$\frac{\partial s}{\partial t} = -\frac{\delta H}{\delta\varphi} - \eta \frac{\partial\varphi}{\partial t} + \xi = a^2 J n_c \nabla^2 \varphi - \eta \frac{\partial\varphi}{\partial t} + \xi \quad (12b)$$

where it was added noise ξ and dissipation ($\eta \frac{\partial\varphi}{\partial t}$) to the "conservative" forces $F = -\frac{\delta H}{\delta\varphi}$. Finally we can write:

$$\frac{\partial\varphi^2}{\partial t^2} + 2\gamma \frac{\partial\varphi}{\partial t} - c_s^2 \nabla^2 \varphi = \xi \quad (\gamma = \eta/2\chi, c_s^2 = a^2 J n_c / \chi) \quad (13)$$

In the appropriate overdamped limit ($\chi/\eta^2 \rightarrow 0$) the ISM recovers the Vicsek model. In particular it is possible to appreciate that the large scale $k \rightarrow 0$ behavior is well accounted for by the VM overdamped case and therefore by hydrodynamic

theories of flocking. In this region of large times scales ($t \gg \tau = 1/\gamma = 2\chi/\eta$) the inertia becomes irrelevant and therefore also the second order terms of the microscopic dynamics, while becomes relevant the movement of individuals. As a consequence orientational fluctuations couple with fluctuations in density giving rise to hybridized sound modes transporting both directional and density disturbances [7, 11].

This new theory not only explains the data, but also predicts that information transfer must be faster the stronger the group's orientational order, a prediction accurately verified by the data [10].

My Project

An inertial model for the speed

The models considered up to now have the modulus of the velocity v_0 fixed. However apart from the existence of turning waves it is also well known the existence of density waves. Indeed it was found that birds under predation, attempting to escape, give rise to self-organized density waves that propagates linearly on the flock [12]. The existence of density waves is a phenomenon that has been theoretically deeply understood and studied using a hydrodynamic approach [7, 13, 14]. However the "hydrodynamic density waves" (hdw) are very different from those that have been observed experimentally in [12]. This substantial difference is mainly based on three facts. The first relates to the essence of the hydrodynamic approach: this approach considers the limit $k \rightarrow 0$ $L, t \rightarrow \infty$, while we know that natural systems are often far from these limits and exhibit important collective phenomena over medium scales. The second is that the hdw have an anisotropic propagation which is not observed in the data: the hdw that has significant speed in the reference frame of the flock propagates only in the orthogonal direction to the motion of the flock (the longitudinal modes are suppressed); however experiments show that natural density waves also propagates longitudinally [15]. Third since the speed v_0 of each individual is fixed, in hydrodynamic theory the density waves are derived from the orientational fluctuations of the system particles and are in fact coupled to these [7, 13, 14, 15].

However one can expect that in real flock density waves can also be associated to fluctuation of the individual speed. The idea is to consider density waves as a byproduct of speed waves. In particular my PhD thesis work has the aim of building an inertial model also for the speed, or better for the speed fluctuations $u(\vec{x}, t) = |\vec{v}_i(\vec{x}, t)| - v_0$, and then possibly develop an inertial model for the full velocity vector in agreement with the observed data. At the beginning I made an hypothesis over the possible form of the speed Hamiltonian.

$$H = \int \frac{d^3x}{a^3} \left\{ \frac{1}{2} a^2 J n_c [\nabla u(\vec{x}, t)]^2 + \frac{g}{2} u^2(\vec{x}, t) + \frac{w^2(\vec{x}, t)}{2\mu} \right\} \quad (14)$$

The first term describes the tendency of the individual speeds to have the same value as that of their neighbors. The second term forces the speed to have, on average, the physiological value v_0 . Larger J means a tighter connection to the neighbors, a larger g means a tighter individual control over speed. Finally the third term represents a generalized kinetic term: $w(\vec{x}, t)$ is the momentum field conjugated to $u(\vec{x}, t)$ (as it is s for φ), it is the generator of the boost of which the speed u is the parameter. This transformation is related to the symmetry of being able to vary the speed, i.e. the so-called Galilean invariance. The term g breaks explicitly this symmetry, while in the case $g = 0$ there would be actually Galilean invariance. Finally μ is a generalized moment of inertia quantifying the resistance of a bird to a change of its internal boost. This model predicts that:

$$\langle u(\vec{x}) u(\vec{x}') \rangle \propto e^{-\frac{|\vec{x} - \vec{x}'|}{\xi_{\text{bulk}}}} \quad (15)$$

where the bulk correlation length is given by:

$$\xi_{\text{bulk}} \sim a \sqrt{\frac{J n_c}{g}} \quad (16)$$

the subscript bulk means that we are treating the flock as a bulk material, with no boundaries.

Experimental data collected for the study of birds in flocks of starlings showed that besides orientational fluctuations even the fluctuations around the mean velocity are scale-free [16]. Local interactions can produce long-ranged correlations basically in two ways. In the case of the orientations the choice of a particular direction corresponds to the breaking of the

rotational symmetry. When the system spontaneously breaks a continuous symmetry then the fluctuations are dominated by Goldstone modes that do not decay on any fixed length scale. However choosing a speed does not correspond to breaking any plausible symmetry of the system, then, in order for the system to generate scale-free correlations, the parameters must be tuned to a critical point. The correlation length ξ_{bulk} becomes infinite at the critical point $g = 0$. However g cannot be exactly zero, otherwise there is nothing to fix the mean speed of the flock. Nevertheless for small enough values of g the system is effectively critical due to the finite size effects ($\xi \propto L$) [16].

From the previous Hamiltonian descend the following equations of motion:

$$\mu \frac{\partial^2 u(\vec{x}, t)}{\partial t^2} + \eta \frac{\partial u(\vec{x}, t)}{\partial t} + gu(\vec{x}, t) - a^2 Jn_c \nabla^2 u(\vec{x}, t) = \xi(\vec{x}, t) \quad (17)$$

where I add a friction term η , while ξ is a white noise $\langle \xi(\vec{x}, t) \xi(\vec{x}', t') \rangle = 2\eta T \delta(\vec{x} - \vec{x}') \delta(t - t')$. We can rewrite the equation in the following way:

$$\frac{\partial^2 u(\vec{x}, t)}{\partial t^2} + 2\gamma \frac{\partial u(\vec{x}, t)}{\partial t} + \omega_0^2 u(\vec{x}, t) - c^2 \nabla^2 u(\vec{x}, t) = \xi(\vec{x}, t) \quad (18)$$

where $c^2 = a^2 Jn_c / \mu$, $\gamma = \eta / 2\mu$ and $\omega_0^2 = g / \mu$. This equation turns out to be a well-know equation in the literature: the telegraph equation [18, 19]. We can simplify this by introducing a new field $u'(x, t) = e^{-\gamma t} u(x, t)$ in such a way that the terms containing $\partial u' / \partial t$ fall out in the equation for u' . Then for the homogeneous equation we get:

$$\frac{\partial^2 u'}{\partial t^2} = c^2 \nabla^2 u' + \varepsilon^2 u' \quad (19)$$

where $\varepsilon^2 = \gamma^2 - \omega_0^2$. It appears immediately the fact that the equation, for a "critical" value of the parameters, $\varepsilon^2 = \eta^2 / 4\mu - g / \mu = 0$, takes the form of the classical wave equation. This case in which the physical constants could be adjusted to eliminate the dispersion corresponds in literature to the "lossless transmission line" [18]. In our case, though, one has more freedom as the critical parameter is not constrained to be positive (as in the standard telegraph equation), but can also be negative, resulting in a richer phenomenology. The dispersion relation (1) for the frequency of propagation of the speed $u(\vec{x}, t)$:

$$\omega = i\gamma \pm \sqrt{c^2 k^2 - \varepsilon^2} \quad (20)$$

it's possible to appreciate even more the decisive role of ε in determining the type of propagation. If $\varepsilon^2 < 0$ we are in the underdamped zone and there is propagation even for $k = 0$. For small value of k the dispersion is quadratic, while for large values we recover the linear dispersion law. On the other side if $\varepsilon^2 > 0$ the system is overdamped and there is propagation only from a certain k on, $k > k_0 = \varepsilon / c$. Also here for large values of k we have linear dispersion. Finally if $\varepsilon^2 = 0$ there is always linear propagation, for every value of k .

This picture has a strong connection with what happens in a single harmonic oscillator and that's the reason why I defined the point $\varepsilon^2 = 0$ as "critical damping point". In the case of the single harmonic oscillator the system is said to be critically damped when the damping ratio $\zeta = \omega_0 / \gamma = 1$ and so there is a double root for the parameter α of the solution $x(t) = e^{\alpha t}$, which is real. A critically damped system converges to the equilibrium position as fast as possible without oscillating [20].

To verify that also in this case the critical damping actually corresponds to the minimum return time I performed a preliminary study of the solution of the telegraph equation in $d = 1$ (2). The general solution for the initial condition of a disturbance at $x = 0$, $u(x, 0) = u_0 \delta(x)$ and $\frac{\partial u(x, 0)}{\partial t} = 0$, for $\varepsilon^2 \geq 0$ is given by:

$$u(x, t) = u_0 e^{-\gamma t} \left\{ \frac{\delta(x - ct) + \delta(x + ct)}{2} + \left[\frac{\gamma}{c} I_0 \left(\frac{\varepsilon}{c} \sqrt{c^2 t^2 - x^2} \right) + \frac{\varepsilon t}{2} \frac{I_1 \left(\frac{\varepsilon}{c} \sqrt{c^2 t^2 - x^2} \right)}{\sqrt{c^2 t^2 - x^2}} \right] \theta(|x| - ct) \right\} \quad (21)$$

where I_0 and I_1 are modified Bessel function of the first kind. In the case $\varepsilon^2 < 0$ the modified Bessel function are replaced by Bessel functions of the first kind J_0 and J_1 of argument $\frac{\text{Im}(\varepsilon)}{c} \sqrt{c^2 t^2 - x^2}$. First I gave a definition of return time τ as the time it takes for the solution to reach a certain value $u(x, \tau) = 1/q$, which represents the root mean square value due to fluctuations. Clearly, this definition is valid only in the event that there are no oscillations, and then for $\varepsilon^2 \geq 0$. In the oscillating case I assume that the return time is $\tau = -t_0 + 1/\gamma$, where $t_0 = \frac{x^*}{c}$, i.e. the time it takes the signal to reach a certain position x^* . On the critical line $\varepsilon^2 = 0$ we have:

$$\tau_0 = -t_0 + \frac{1}{\gamma} \log(u_0 q \gamma / c) \quad (22)$$

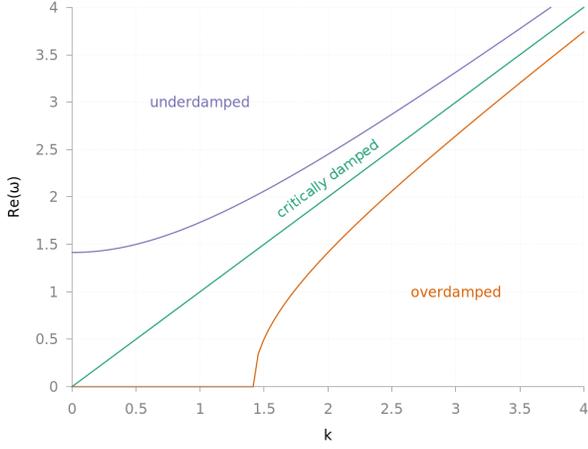


Figure 1: Sketch of the dispersion law: if $\varepsilon^2 < 0$ (lilac line) we are in the underdamped zone and there is propagation for every value of k ; if $\varepsilon^2 > 0$ (orange line) the system is overdamped and there is propagation only for $k > k_0 = \frac{\varepsilon}{c}$; if $\varepsilon^2 = 0$ (teal line) we are at the critical damping and there is always linear propagation.

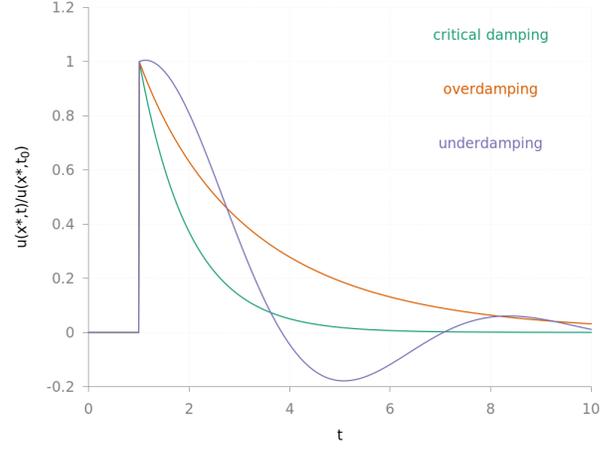


Figure 2: Different solutions of the telegraphic equation in $d = 1$. Depending on the value of ε the solution will go to zero differently: at the critical damping point $\varepsilon = 0$ (teal line) it reaches the zero as fast as possible, without oscillating; in the overdamped regime (orange line), $\varepsilon > 0$ the solution goes to zero more slowly while in the underdamped (lilac line) case the solution shows oscillations.

Looking at τ as a function of γ we can note that depending on the parameters you can have two areas in which the return time is zero. The first one is for small values of γ , as being no dissipation the restoring force instantly returns the system to the equilibrium position. The second is, instead, for large values of γ and it is due to the fact that since there is strong dissipation ($\gamma \gg 1/t_0$) the signal does not get anywhere because traveling below the noise threshold. If we place ourselves close to the critical line we can develop the Bessel functions for small argument value and by solving recursively we get in the end that:

$$\tau_\varepsilon = \tau_0 + \frac{\varepsilon^2}{2\gamma^2} \left(\frac{t_0}{2} + \frac{\tau_0}{2} + \gamma t_0 \tau_0 + \gamma \frac{\tau_0^2}{2} \right) \quad (23)$$

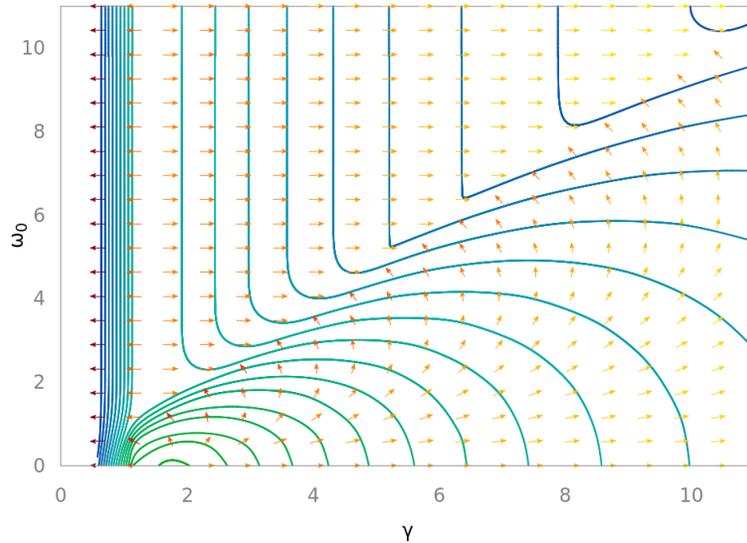


Figure 3: Level lines of $\tau(\gamma, \omega_0)$ are drawn with colors from blue for lower values, to green for the higher ones. In the same figure there is the vector field given by the negative gradient of the function, also here the color is the intensity of the field, ranging from yellow for lower values to dark red for the highest ones.

Finally watching the trend of τ in the (γ, ω_0) plane (3) you can appreciate how the critical line in fact represents an attractor for a steepest descent dynamic of τ .

To verify that the natural system is actually on this critical line seems to be crucial: for a biological system it is important to minimize the return time in order to have a minimum energy waste.

Experimental data analysis

There are essentially two ways to analyze the propagation of a signal. The first involves direct observation of the disturbance that propagates in space and time within a system from which, for example, it is possible to measure the speed propagation and the relaxation time. The other consists in the analysis of the spontaneous fluctuations of the system through which it is possible to trace back the equations of motion. In this PhD thesis it will be used the second method to conduct the experimental analysis. In particular we are interested to see how the system propagates the disturbance generated by noise. In fact, given an equation of motion:

$$\mathcal{D}_t \psi(\vec{x}, t) + \mathcal{D}_x \psi(\vec{x}, t) = \xi(\vec{x}, t) \quad (24a)$$

$$\mathcal{O}(\vec{x}, t) \psi(\vec{x}, t) = \xi(\vec{x}, t) \quad (24b)$$

where \mathcal{D}_t and \mathcal{D}_x respectively represent generic derivative in space and time and ξ is a Gaussian white noise. It is possible to use the Green's function method (the propagator) to find the solution of the problem:

$$\mathcal{O}(\vec{x}, t) G(\vec{x}, t) = \delta^3(\vec{x}) \delta(t) \quad (25)$$

$$\psi(\vec{x}, t) = \int d^3 x' dt' G(\vec{x} - \vec{x}', t - t') \xi(\vec{x}', t') \quad (26)$$

So if you know the propagator in fact you also get the solution. In Fourier space the propagator will be a polynomial of k and ω :

$$\mathcal{O}(\vec{x}, t) \int d^3 k d\omega e^{i(\vec{k} \cdot \vec{x} + \omega t)} G(\vec{k}, \omega) = \int d^3 k d\omega e^{i(\vec{k} \cdot \vec{x} + \omega t)} p(\vec{k}, \omega) G(\vec{k}, \omega) = \int d^3 k d\omega e^{i(\vec{k} \cdot \vec{x} + \omega t)} = \delta^3(\vec{x}) \delta(t) \quad (27)$$

it follows that $G(\vec{k}, \omega) = 1/p(\vec{k}, \omega)$ and one has $\psi(\vec{k}, \omega) = G(\vec{k}, \omega) \xi(\vec{k}, \omega)$. The zeros of this polynomial ω_{\pm} are the fundamental frequencies of the system. In particular the dynamical correlation function of the system in Fourier space is given by:

$$C(\vec{k}, \omega) = \langle \psi(\vec{k}, \omega) \psi(-\vec{k}, -\omega) \rangle_{\xi} = G(\vec{k}, \omega) G(-\vec{k}, -\omega) \langle \xi(\vec{k}, \omega) \xi(-\vec{k}, -\omega) \rangle \quad (28)$$

Therefore in order to have firmer support from the data for the inertial model of the speed I have to inspect the dynamical correlation function, or dynamic structure function, since it contains important information about the dispersion law [21]:

$$C(k, \omega) \propto G(k, \omega) G(-k, -\omega) \sim \frac{1}{(\omega^2 - \omega_+^2)(\omega^2 - \omega_-^2)} \quad (29)$$

where the dependence now is only on the modulus k of the vector \vec{k} due to the presence of the Laplacian in the equation of motion. In general it is easier to study the so-called intermediate scattering function $C(k, t)$:

$$C(k, t) = \int dt e^{i\omega t} C(k, \omega) = \int dr e^{-ikr} C(r, t) = \int dr e^{-ikr} \langle \delta u(0, 0) \delta u(r, t) \rangle \quad (30)$$

Depending on the type of dynamics, Langevin or inertial, $C(k, t)$ will have a different shape. In the Langevin case $C(k, t)$ will have the form:

$$C(k, t) = \frac{2T e^{-(Ja^2 n_c k^2 + g)t}}{Ja^2 n_c k^2 + g} \quad (31)$$

where T is the generalized temperature, while for inertial dynamics it will be:

$$C(k, t) = \frac{\eta T e^{-\gamma t}}{\left(\frac{Ja^2 n_c k^2}{\mu} + \omega_0^2\right)} \left\{ \frac{\sin\left(\sqrt{\frac{Ja^2 n_c k^2}{\mu} - \varepsilon^2} t\right)}{\sqrt{\frac{Ja^2 n_c k^2}{\mu} - \varepsilon^2}} + \frac{\cos\left(\sqrt{\frac{Ja^2 n_c k^2}{\mu} - \varepsilon^2} t\right)}{\gamma} \right\} \quad (32)$$

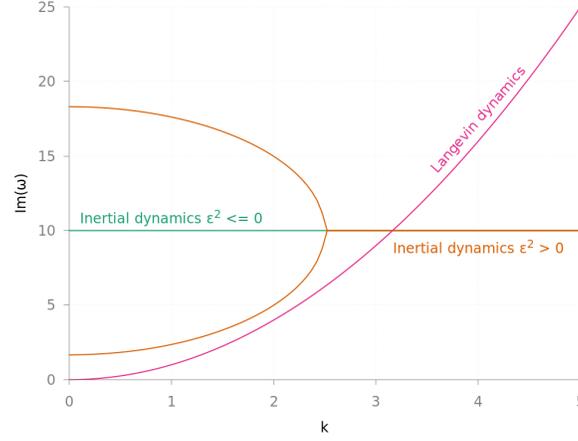


Figure 4: $(\text{Im}(\omega), k)$ plane: the magenta line represent Langevin dynamics that grows with k^2 ; teal line represent the underdamped and critically damped situations in which $\text{Im}(\omega)$ is constant; the orange line represent the overdamped regime in which the $\text{Im}(\omega)$ is constant only for $k > k_0$ and grows quadratically with k for small values of k .

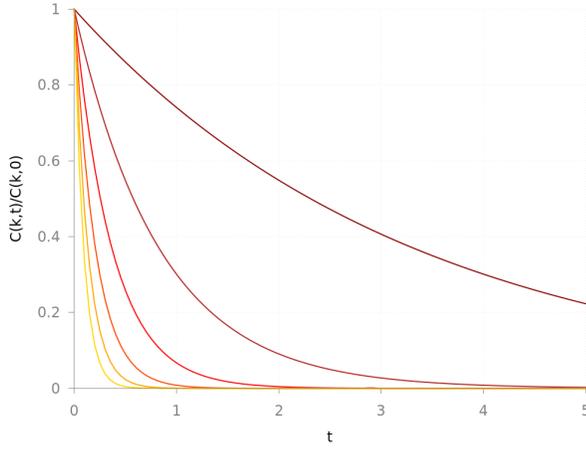


Figure 5: $C_k(t)$ in the overdamped regime ($\varepsilon^2 > 0$) of the inertial dynamics for $k < k_0$ and for every value of k in the Langevin dynamics. The colors represent different values of k , ranging from dark red for small values of k , to yellow for high k . We noticed that $(\tau \propto 1/k^2)$.

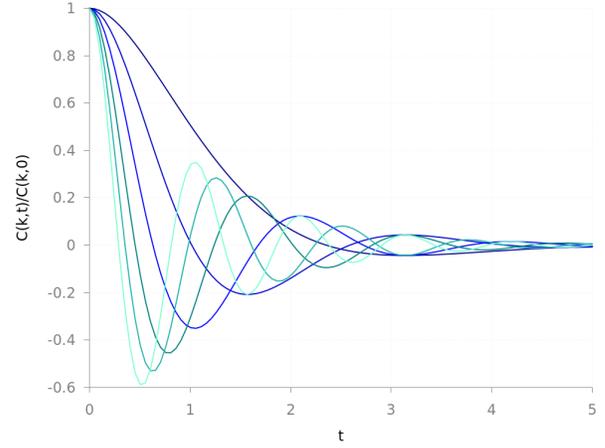


Figure 6: $C_k(t)$ in the inertial case for every value of k if $\varepsilon^2 \leq 0$ and only for $k > k_0$ if $\varepsilon^2 > 0$. The colors represent different values of k , ranging from dark blue for small values of k , to aquamarine for high k . We notice that $\tau = 1/\gamma = \text{const.}$, while frequency of oscillations increases roughly linearly in k .

This expression is certainly valid if $\varepsilon^2 < 0$, while in the overdamped regime $k < k_0, \varepsilon^2 > 0$ the trigonometric functions are replaced by the respective hyperbolic functions having argument $\sqrt{\varepsilon^2 - \frac{Ja^2 n_c k^2}{\mu}} t$.

First of all taking a look at what happens in the (k, ω) plane (4) it can be seen that the two theories have completely different implications. In the case of diffusive equation (Langevin dynamics) there is only the imaginary part of ω which grows with k^2 . On the other hand, if there is linear propagation (inertial dynamics) there are three different situations depending on the value of ε . In all cases, though, it exists a range of values of large k ($k > k_0$) for which $\text{Im}(\omega)$ is constant while $\text{Re}(\omega)$ is linear in k . In light of this $C(k, t)$ will be a function decreasing exponentially in time that goes to zero more rapidly with increasing k (5) in the Langevin case ($\tau = 1/\text{Im}(\omega) = 1/k^2$), whereas it is an oscillating function that decreases in time in the inertial case (6). Besides, since the damping is constant in k ($\tau = 1/\gamma = \text{const.}$), only the frequency of the oscillations increases [22]. Since on orientations there are already solid evidence of the presence of the inertia, this analysis will be first carried out for the phase correlations so as to have at once an important check of this method, also providing a further potential confirmation of previous studies. Finally I will study the behavior of the experimental correlation function of the speed.

To check that for the available data $C(k, t)$ is in agreement with the theoretical results, I have to solve a series of problems. First of all the very definition of the experimental correlation function is itself a nontrivial problem. Besides since I will focus on the large k region I must take care of the noise which increases with increasing k . Finally each bird has a proper frequency

due to wings beating (flapping time) which generates oscillations present at every value of k . So I must take extra care in the analysis of the oscillations.

Numerical simulation

Since we deal with active matter we have to face a lot of problem of implementation of classical physics tools. In fact many physical aspects are not well-defined: we are not on lattice since particles move, the theory is not truly Hamiltonian because there is dissipation and energy injection, etc. [23]. Given the non-standard nature of the experimental data it is essential to test the tools developed on an under control simulational data. In this part of the work I will concentrate on the development of a C++ program for the numerical simulation of some well-known models of collective behavior (e.g. Vicsek model). Once verified that the instruments I developed for the study of $C(k, t)$ produce the correct results for this known model, I will finally simulate the inertial model for the speed in order to fully study the phenomenology and compare it with the experimental findings.

References

- [1] I. Giardina *Collective behavior in animal groups: theoretical models and empirical studies*. (2008) HFSP journal 2.4: 205-219.
- [2] D. J. T. Sumpter *The principles of collective animal behaviour* Philosophical Transactions of the Royal Society of London B: Biological Sciences 361.1465 (2006): 5-22.
- [3] S. Camazine *Self-organization in biological systems*. (2003) Princeton University Press.
- [4] T. Vicsek, A. Czirók, E. Ben-Jacob, I. Cohen, O. Shochet *Novel type of phase transition in a system of self-driven particles*. (1995) Physical review letters 75 (6), 1226
- [5] G. Grégoire, H. Chaté. *Onset of collective and cohesive motion*. (2004) Physical review letters 92.2: 025702.
- [6] M. Ballerini, N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini, M. Viale and V. Zdravkovic. *Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study*. (2008) Proceedings of the national academy of sciences, 105(4), 1232-1237.
- [7] J. Toner, J.,Y. Tu *Flocks, herds, and schools: A quantitative theory of flocking*. (1998) Physical review E, 58(4), 4828.
- [8] A. Cavagna, S.D. Queirós, I. Giardina, F. Stefanini, M. Viale. *Diffusion of individual birds in starling flocks*. (2013) Proceedings of the Royal Society of London B: Biological Sciences, 280(1756), 20122484.
- [9] W. Bialek, A. Cavagna, I. Giardina, T. Mora, E. Silvestri, M. Viale, A.M. Walczak. *Statistical mechanics for natural flocks of birds*. (2012) Proceedings of the National Academy of Sciences, 109(13), 4786-4791.
- [10] A. Attanasi, A. Cavagna, L. Del Castello, I. Giardina, T. S. Grigera, A. Jelić, S. Melillo, L. Parisi, O. Pohl, E. Shen, M. Viale *Information transfer and behavioural inertia in starling flocks*. Nature Physics 10 (9), 691-696
- [11] A. Cavagna, L. Del Castello, I. Giardina, T. Grigera, A. Jelic, S. Melillo, T. Mora, L. Parisi, E. Silvestri, M. Viale, A. M. Walczak *Flocking and turning: a new model for self-organized collective motion*. Journal of Statistical Physics 158, 601-627
- [12] A. Procaccini, A. Orlandi, A. Cavagna, I. Giardina, F. Zoratto, D. Santucci, F. Chiarotti, C. K Hemelrijk, E. Alleva, G. Parisi, C. Carere *Propagating waves in starling (*Sturnus vulgaris*) flocks under predation*. Animal behaviour 82 (4), 759-765
- [13] J. Toner, Y. Tu *Long-range order in a two-dimensional dynamical XY model: how birds fly together*. (1995) Physical Review Letters, 75(23), 4326.

- [14] J. Toner, Y. Tu, M. Ulm *Sound Waves and the Absence of Galilean Invariance in Flocks*. (1998) Physical Review Letters, 80(21), 4819-4822.
- [15] A. Cavagna, I. Giardina, T.S. Grigera, A. Jelic, D. Levine, S. Ramaswamy, M. Viale *Silent flocks: constraints on signal propagation across biological groups*. (2015) Physical review letters, 114(21), 218101.
- [16] A. Cavagna, A. Cimorelli, I. Giardina, G. Parisi, R. Santagati, F. Stefanini, M. Viale *Scale-free correlations in starling flocks*. (2010) Proceedings of the National Academy of Sciences, 107(26), 11865-11870.
- [17] W. Bialek, A. Cavagna, I. Giardina, T. Mora, O. Pohl, E. Silvestri, A.M. Walczak *Social interactions dominate speed control in poising natural flocks near criticality*. (2014) Proceedings of the National Academy of Sciences, 111(20), 7212-7217.
- [18] Magnusson, Weisshaar, Tripathi and Alexander *Transmission lines and wave propagation*. (2000) CRC Press.
- [19] Vladimir Smirnov *A Course in Higher Mathematics, Vol. II* (1964) Adiwes International Series in Mathematics
- [20] J.R. Taylor *Classical mechanics*. (2005) University Science Books.
- [21] J.P. Hansen, I.R. McDonald *Theory of Simple Liquids* (1990) Elsevier.
- [22] R. Zwanzig *Nonequilibrium statistical mechanics*. (2001) Oxford University Press, USA
- [23] S. Ramaswamy *The mechanics and statistics of active matter*. (2010) Annu. Rev. Condens. Matter Phys., 1.