PhD Project – Vito Volterra School in Physics - XXX Cycle

Signal propagation and dynamical correlation in biological active matter

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Introduction

Collective behavior in biological active matter includes all those phenomena for which the emergent properties of a group cannot be reduced to the individual elements that make it up, but, rather, are critically dependent on the coordination between the various components and the interaction between them. From a very general point of view the mechanisms underlying the collective behavior do not differ much from the typical topics of statistical mechanics: in both cases one has to understand how the properties of a global system, consisting of a large number of components, can derive from what happens at the microscopic level [1, 2]. The collective phenomena occurring in biological active matter have attracted much attention in the scientific community over the last years, making it one of the most discussed topics in biology.

The world of collective behavior is very wide: from fish schools in the ocean to swarms of insects, from ant lines to herds of mammals and flocks of birds in flight. Therefore one has to do with a great variety of size scales and complexity. However the global behavior of all these systems can be traced back to simple rules that are both individual and local. This common and fundamental feature suggests the possibility of formalizing local interactions with simple models, taking only the fundamental characteristics of the complexity and individual peculiarities, so as to insert the collective behavior in a universal context that unites all of these phenomena [1].

My PhD thesis will study how information propagates within a biological system. In particular I will focus on the collective motion of birds in a flock. The work will be made up of multiple approaches that can be basically divided into three parts: theory, experimental data analysis and numerical simulation.

Theory

Many models of collective motion are based on Vicsek model for self-driven particles. In this model the particles are driven with a constant absolute velocity and at each time step assume the average direction of motion of the particles in their neighborhood with some random perturbation added [3]. This model shows a phase transition in which the motion becomes ordered on a macroscopic scale and all of the particle tend to move in the same spontaneously selected direction. Vicsek model has equations of motion that lead to diffusive dispersion law for the velocity (1).

$$\eta \frac{dv_i(t)}{dt} = J\left(\sum_j n_{ij}\vec{v_j}\right)^{\perp} \tag{1}$$

In the case of birds the dispersion law tells us how local disturbances in the flight direction of a particle affect the rest of the flock. In Vicsek model the frequency ω obtained by computing the propagator in Fourier space is purely imaginary with a quadratic diffusive dispersion law $\omega \sim ik^2$ [4]. Therefore there is no propagation in the Vicsek case.

However experimental studies of starling flock performing turns find that information about direction changes propagates across the flock with a linear dispersion law and negligible attenuation, minimizing group decoherence [5]. In order to account for this a new model, the Inertial Spin Model (ISM), was developed. They introduce a new inertial term by adding a 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 (2).

$$H = \int \frac{d^3x}{a}\frac{J}{2}\left[\nabla\phi(x,t)\right]^2 \qquad \longrightarrow \qquad H = \int \frac{d^3x}{a^3}\left(\frac{a^2 J}{2}\left[\nabla\phi(x,t)\right]^2 + \frac{s_z^2(x,t)}{2\chi}\right) \tag{2}$$

In the appropriate overdamped limit the ISM recovers the Vicsek model. The 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[4, 5]. Besides turning waves there are also evidences of density waves that can be derived from speed waves (the modulo of the velocity). In fact it was found that birds under predation, attempting to escape, give rise to self-organized density waves that propagates linearly on the flock $\omega = ck$ [6].

My PhD thesis work has the aim of building an inertial model also for the speed and then possibly develop a full inertial model for the velocity in agreement with the observed data. At the beginning, I made an assumption about the possible evolution equation of the speed u that takes into account the experimental evidences and the considerations previously made on the phase. This equation (3) containing the inertial term μ, the friction η and an anchoring term g turns out to be a well-known equation in the literature: the telegraph equation [8].

$$\left(\mu\frac{\partial^2}{\partial t} + \eta\frac{\partial}{\partial t} + g - J\nabla^2\right)u(x,t) = 0 \tag{3}$$

I studied the solution and the relative dispersion law of this equation. It is of particular interest the fact that the equation, for a particular (critical) value of the parameters $\epsilon = \frac{\eta^2}{4\mu^2} - \frac{g}{\mu}$, 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" [7]. In our case, though, one has more freedom as the critical parameter is not constrained to be positive, but can also be negative, resulting in a richer phenomenology. I defined this point as "critical damping point" in analogy with what happens in a single harmonic oscillator. The critical damping condition gives the fastest return of the system to its equilibrium position. I am studying the solution both analytically and numerically to verify that indeed also in the case of a chain of harmonic oscillator the critical damping actually corresponds to the minimum return time. This seems to be crucial: for a biological system it is important to minimize the relaxing time in order to have a minimum energy waste.

Experimental data analysis

In order to have firmer support for the inertial speed model in the data I have to inspect the dynamical correlation function (dynamic structure factor) of the system (4).

$$C(k,w) = \frac{1}{2\pi}\int dt\, e^{i\omega t} C_k(t) = \frac{1}{2\pi}\int dt\, e^{i\omega t}\int d^3x\, e^{-i\vec{k}\cdot\vec{x}}\left\langle \frac{1}{N}\int d^3x'\, u(x' \vec{+} x, t)u(\vec{x'}, 0)\right\rangle \tag{4}$$

In particular I am studying the so called intermediate scattering function $C_k(t)$ that contains important information about the dispersion law [9]. In fact, depending on the type of dynamics, Langevin or inertial, $C_k(t)$ will have a different shape. In the case of diffusive equation (Langevin dynamics) $C_k(t)$ will be a function decreasing exponentially in time that goes to zero more rapidly with increasing k. On the other hand if there is linear propagation (inertial dynamics) it definitely exists a range of values of large k ($k > k_0$) for which the correlation is an oscillating function that decreases in time. However, since the damping is constant in k, only the frequency of the oscillations increases [10].

In this thesis I will check that for the available data $C_k(t)$ is in agreement with the theoretical results. To do this 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 I must take care of the noise and the fact that each bird has a proper frequency due to wings beating (flapping time). I will first make these checks on the orientations (the phase of the velocities), on which some results are already known, also providing a further potential confirmation of previous studies. Finally I will study the behavior of the experimental correlation function of the speed.

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 strictly on lattice since particles move, the theory is not truly Hamiltonian because there is dissipation and energy injection, ecc. Given the non-standard nature of the experimental data it is essential to test the tools developed on an under control simulational data. I will devote this part of the work to test that the instruments I developed for the study of $C_k(t)$ produce the correct results for the Vicsek model [3], investigating the behavior for both large and small k. Finally, once developed the general model for the speed in which there is propagation of phase and speed waves, I will simulate this completely inertial model for the velocity creating and running a C program in order to fully study the phenomenology and compare it with the experimental findings.

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