Emergence in Collective Animal Behavior

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Abstract

Nature has presented us a wide variety of fascinating collective behaviors in animals – birds flying in flocks, fish swim in shoals and wild horses move in herds. A number of models are proposed in order to understand the origin of collective behavior and reveal the underlining physics. In this paper, two theoretical models are reviewed: the discrete SPP model and the continuum hydrodynamic model. Both model show that long-range ordering arise as a result of local interactions of the system. The results are compared with recent quantitative experimental data and the emergence of ordered collective motion is discussed.

In the evening sky of European countryside, thousands of starlings fly in a flock and move cohesively in one direction. The flock keep changing its direction every couples of minutes, and each individual bird flies with seemingly effortless skill to keep up the motion of the entire flock. While in the waters of Atlantic Ocean, the same trick is played by a school of herrings. Fish swim harmonically in the school as through they are programmed and know exactly what to do at any given time. We have all seen such amazing spectacles in real life or on television. Many words are used to describe the phenomenon: flocking, herding, schooling, swamping. These words are essentially the same, namely collective animal behavior.

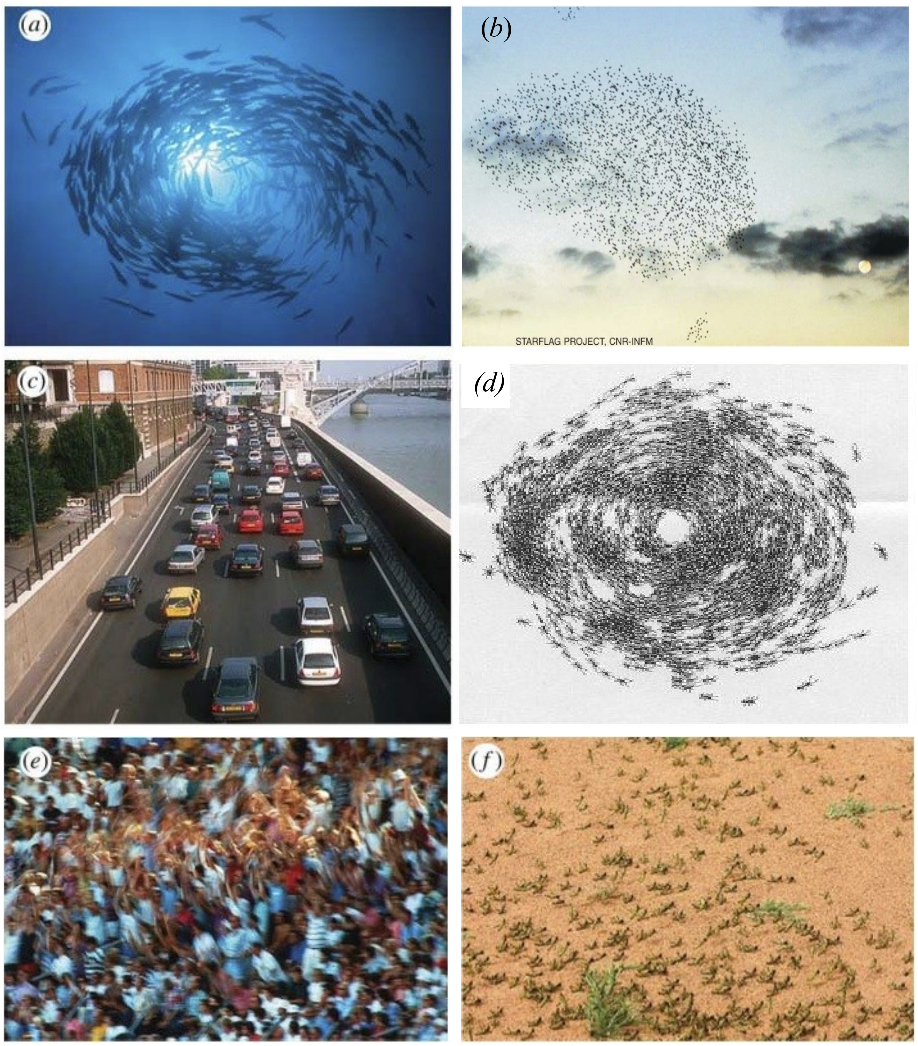

Figure 1: Images of collective behavior. (a) A typical fish school in the ocean [1]. (b) Starlings flocking in the dusk [2]. (c) Traffic flow in Paris [1]. (d) A swamp of fire ants [3]. (e) A Mexican wave in a football stadium [1]. (f) A group of marching locusts [1].

1. Introduction

Collective behavior is an emergent phenomenon, in which large numbers of individuals synchronize their movement in a group. It is observed in many living organisms (as shown in Fig. 1): birds, fish, mammals, insects, and bacteria, with scales ranging from a few micrometers to miles. Collective behavior occurs even in human society: pedestrian behavior, applause dynamics, and Mexican waves are a few examples.

The phenomenon of collective motion have posted a number of intriguing questions and attracted great attention of the scientific community. Questions like why do birds fly in flocks; how a fish among a crowded school synchronize its motion with the rest of the school; and what's the underlining rules of the collective animal behavior are asked by scientists from various disciplines.

From an evolutionary biological point of view, it is not hard to understand the reason why animals aggregate and move in groups. First of all, joining a flock protects an individual when encountering predators. Although fish at the edge of a school are easily attacked by predators, they are only a small fraction of the school. Majority of the fish are inside the school protected by a thick wall of peers, and are relatively safe. Secondly, searching for food as a flock is more effective than along. Thirdly, flocking is beneficial for the individuals in terms of social activities and mating [4].

Birds take great advantage of being a part of a flock, but how do they coordinate their motion as a whole? Although it appears that each individual adjusts its movement based on the knowledge of what the whole group is doing, biologists believe that individuals are only aware of what their neighbors are doing instead of seeing the whole picture of the flock. Animals interact with surroundings by their senses: vision, hearing and smelling. In a densely packed flock, they can only sense their close neighborhood. Just think of the experience of walk in a crowd, you have clear vision of your neighbors but you never know what is going on with the rest of the crowd. In a word, the interaction between individuals in the aggregation is short-range. And such local interaction is responsible for the emergence of the globe phenomenon [5].

To investigate the question of how birds fly together base on their local interactions, Reynolds first simulated the flocking of birds by computer animation in 1987 [4]. He established the following three simple rules for the artificial birds in his animation, namely boids. First, avoid collision. The boid must fly away from its neighbor when getting too close. Second, match velocity. The boid needs to fly with the average velocity of nearby peers. Third, flock centering. There are attraction between the boid to make them fly close. The model is able to generate flocking of the boids that closely resembles to the realistic bird flocks, which further confirms the collective motion originates from the local interactions.

The fact that long-range ordering arises from local interactions in animal groups has captured the attention of physicists. Viscek et al. first introduced the self-propelled particles (SPP) model to investigate the emergent phenomenon. In his model, particles are propelled with an intrinsic force and move with a constant speed. The only rule is that a particle aligns its direction of motion with its neighbors in a defined radius – at each time step, the particle sets its velocity to the average moving direction of the neighborhood plus a random noise. The simulation results of the model demonstrates long-range ordering phase exists in one-, two- and three-dimension.

Shortly after the proposal of the SPP model, a theoretical approach was attempted by Toner and Tu. Continuum hydrodynamics was applied to the SPP system by coarse-graining the velocity and density fields. In two dimensions, the hydrodynamic model showed the existence of an ordered phase, which is consistent with the SPP model. However, the model also predicts that there is no ordered phase in one dimension. To settle this discrepancy of the two models, Vicsek et al. derived continuum equations by integrating the master equation of the microscopic dynamics [6]. The linear stability analysis of the equations demonstrates the existence of ordered phase in one dimension when the noise is low.

Until recently, scientists had little empirical data to test their hypothesis and models. Biologists has collective data on schools consisting 20-40 fish in a tank [2]. These data includes only a small number of individual which are often loosely packed. To obtain empirical data on a large and closely packed group of animals and therefore understand the underlining rules for the collective animal motion, scientists set up a project named StarFlag in Italy [2]. They take images of flocks of starlings, and then precisely reconstruct the flocks in three dimensions. From analysis of these quantitative experimental data, the group reveals that the interaction of the birds is anisotropic and it depends on topological distance rather than metric distance as most models have assumed.

So far I have introduced the concept of collective animal behavior and presented a number of models proposed to study its origin. In section 2 of this paper, I will review the SPP model and hydrodynamic model in detail. In section 3, I will further describe the quantitative experimental approach by StarFlag. Section 4 is the conclusions and discussions.

2. Theoretical Models

2.1 The self-propelled particle model in two-dimension

To understand the complex behavior of non-equilibrium multi-particle system, Vicsek and Czirók proposed a model based on simple interactions of self-propelled particles (SPP) [7]. Self-propelled particles are particles with an intrinsic driving force, resembling organisms in biological systems. In the model, each particle is assigned a constant speed and is allowed to interact with its neighbors by aligning the direction of its motion with the average moving direction of nearby particles. By computer simulation, the model successfully demonstrates the transition from a disordered state to an ordered state.

N particle is confined on an L × L square shaped surface with periodic boundary conditions. Each particle has a velocity with a fixed magnitude v_0. At t = 0, particles are randomly distributed in the cell, and the direction of velocity θ is randomly assigned to each particle. At a later time t = Δt, the position and velocity are given by the following two equations:

$$\mathbf{x}_i (t + 1) = \mathbf{x}_i (t) + \mathbf{v}_i (t)\, \Delta t$$

The position and velocity vector of the ith particle at time t is denoted by $\mathbf{x}_i$ (t) and $\mathbf{v}_i$ (t) respectively. The time unit Δt = 1 denotes a time-step between updates of the position and velocity [7].

$$\theta_i (t + 1) = \langle \theta (t) \rangle_r + \Delta\theta$$

The direction of the ith particle is denoted by angle θ_i . The average of direction is taken over all the particles located in a radius r around the ith particle, including particle i itself. The noise comes in as Δθ, which is a random number taken from [-η/2 , η/2] with a uniform probability.

There are three control parameters in a given system: amplitude of the noise η, magnitude of the velocity v_0 and average density $\rho = N/L^2$. In the simulation, v_0 was kept constant, and various values of η, ρ where tested. Vicsek found that for low density, low noise, the particles aggregated into a number of small groups moving in detections randomly picked by their members. In each small group, the particles move cohesively as shown in Fig. 2 (b). While for high density, high noise, the velocities of the particles arbitrarily distributed in all directions (Fig. 2 (c)). However, figure 2 (d) indicates that for high density, low noise, the motion of all particles became ordered and move in the same direction.

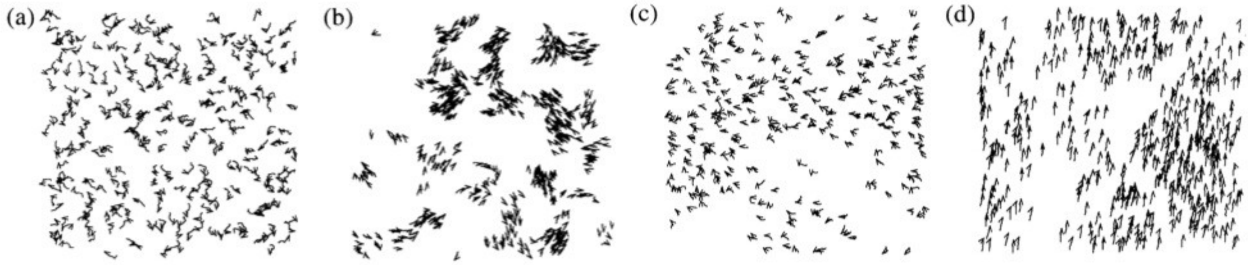

Figure 2: This figure shows the velocity field for different values of noise and density.

(a) Initial condition. (b) Low density, low noise. (c) High density, large noise. (d) High density, low noise

To understand the nature of this transition, the order parameter is chosen to be the magnitude of the average momentum of the particles :

$$\Phi = \frac{1}{N} \left| \sum_j \vec{v}_j \right|$$

When particles move in random directions, the sum of velocities is close to zero therefore Φ vanishes. Contrary, when particles move cohesively towards the same direction such as in Fig. 1 (d), Φ is close to 1. Collective behavior emerges when $\Phi > 0$. For an infinite size system, numerical results show that:

$$\Phi(\eta) \sim \left\{ \begin{matrix} \{[\eta_c(\rho) - \eta] / \eta_c(\rho)\}^{\beta} & for\, \eta < \eta_c(\rho) \\ 0 & for\, \eta > \eta_c(\rho) \end{matrix} \right\}$$

where η_c (ρ) denotes the critical noise amplitude and β is determined to be 0.42 ± 0.03 which is different from the mean-field theory value 0.5. The above equation describes the transition between the disordered phase above the critical noise and the ordered phase below.

2.2 Ordered phase in two-dimension

This model is a dynamic analogue of the ferromagnetic XY model [6]. The velocity of particles in the SPP model acts as the spin in the XY model, and the noise $\Delta\theta$ as the temperature [5]. Despite the resemblance of the two models, there is a remarkable difference: the SPP model describes a dynamic and non-equilibrium situation while the ferromagnetic XY model is based on the static equilibrium situation. Consequently, the SPP model has an ordered phase in 2D, while such ordered phase does not exist in the ferromagnetic XY model according to Mermin-Wagner theorem [6].

To further investigate this “discrepancy”, Vicsek et al set $v_0 = 0$, and observed the formation of Kosterlitz-Thouless vortices. At a non-zero velocity, for instance, $v_0 = 0.01$, the vortices vanishe after a certain relaxation time as shown in Fig. 3. Therefore, the Kosterlitz-Thouless vortices are unstable in the SPP model and long range order can form within the system.

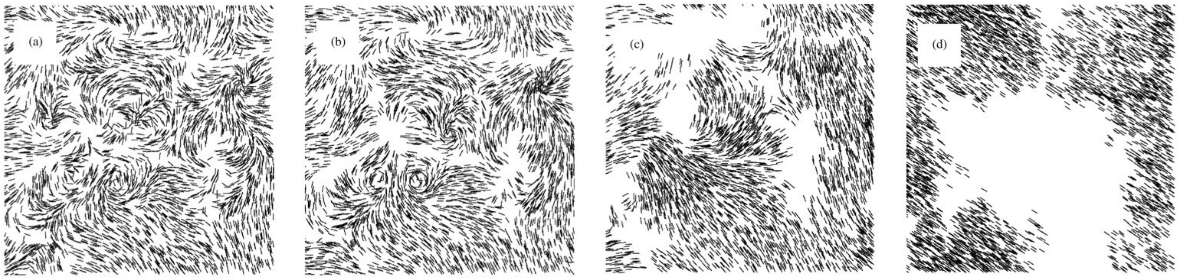

Figure 3: Time evolution of the velocity field with v_0 = 0.01. (a) is taken after 50 steps, (b) 100, (c) 400 and (d) 3000 steps.

2.3 The self-propelled particle model in one- and three-dimension

In 1D SPP model, the ordered phase was again observed with $\beta_{1d} = 0.6 \pm 0.05$, different from that of the 2D case and the mean-field value 0.5 [6]. The spontaneous symmetry breaking in 1D system well be further discussed in 2.4.

The behavior of the system in 3D case is generally the same as in 2D. The system exhibits long-range ordered phase for all densities for η (ρ) below the critical noise of the given density [6].

2.4 The continuum approaches

To investigate how the nonequilibrium aspects put a system into ordered phase even in 2D, Toner et al. proposed a continuum model based on hydrodynamics [8]. This approach is different from the SPP model - instead of working out the location and velocity of each particle and carefully define the interactions between the particles, it describes the behavior of the whole system by a set of continuum equations which involve only a few phenomenological parameters.

The continuum equations being used are Navier-Stokes equations. To apply these equations to a group of self-propelled organisms, one need to use the coarse-grained density and velocity fields which are obtained by averaging the number density and velocity fields over the coarse-grain characteristic volume. The basic equations for the fluid of SPPs are [9]:

$$\partial_t \rho + \nabla \cdot (\rho \vec{v}) = 0$$

$$P = P(\rho) = \sum_{n=1}^{\infty} \sigma_n (\rho - \rho_0)^n$$

$$\partial_t \vec{v} + \lambda_1 (\vec{v} \cdot \nabla) \vec{v} + \lambda_2 (\nabla \cdot \vec{v}) \vec{v} + \lambda_3 \nabla (|\vec{v}|^2) = \alpha \vec{v} - \beta |\vec{v}|^2 \vec{v} - \nabla P + D_B \nabla (\nabla \cdot \vec{v}) + D_T \nabla^2 \vec{v} + D_2 (\vec{v} \cdot \nabla)^2 \vec{v} + \vec{f}$$

The first equation is the conservation of mass. The second equation describes the pressure where ρ_0 is the average of the local number density and σ_n and $\rho(\vec{r})$ denotes coefficients in the pressure expansion. In the last equation ,the λ terms are convective derivative of the velocity field v, the coefficients λ_1, λ_2 and λ_3 are all non-zero because the system is not Galilean invariant [9]. The the coefficients α and β on the right hand side of the equation are connect to the symmetry breaking. The coefficients D_i are constants denoting the diffusion or viscosity of the SPP fluid. The term $\vec{f}$ is the random driving force from the noise. Interestingly, the equations introduce the viscous term, leading to the emergence of the elasticity in the SPP system: birds tend to align their velocities with their neighbors, which result in a long-range ordered phase within the flock.

In more than four dimensions, the model has the same behavior as the equilibrium model while in less than four dimensions, the two behave differently. The model works especial well in the 2D case where it demonstrated a stable long range ordered phase existing for the system and the scaling exponents is calculated. However, the model reveals that there is no ordering phase in 1D, which contradicts to the SPP model.

In order to settle the discrepancy between the two models, Vicsek et al. used a different approach by integration of the master equation of the microscopic dynamics and derived the following equations.

$$\partial_t = -v_0 \partial_x (\rho U) + D \partial_x^2 \rho$$

and

$$\partial_t U = f(U) + v^2 \partial_x^2 U + \alpha \frac{(\partial_x U)(\partial_x \rho)}{\rho} + \xi$$

where ρ and U are the coarse-grained density and velocity fields and ξ is the noise. The coefficients v_0, D, μ and α are phenomenological coefficients. The characteristic nonlinear term $\frac{(\partial_x U)(\partial_x \rho)}{\rho}$ slows down the particles when they encounter the particles coming from the opposite direction.

The results of this model reveals that the system become ordered when the noise is low and α is large which is consistent with the discrete 1D SPP model. Numerical results of the equations yield the same behavior of the system as the discrete 1D SPP model which further proves that continuum model and discrete model "belong to the same universal class" [5].

3. Experimental Methods

With a number of theories proposed for collective motion, experimental data become crucial to verify the assumptions and provide feedback to the existing models. Unfortunately, it is extremely hard for the experimentalists to collective 3D data on the collective motion of animals in nature and until recently there were only a few empirical data on groups composed of small numver of individuals. The experiment in studying the collective motion was far behind the theory [9].

To study the bird flocking behavior, and to understand the underlining nature of such phenomenon, a group of multidisciplinary scientists started a project in Italy named StarFlag. The project consists of physicists, biologists, computer scientists, and aims at determining the "fundamental laws of collective behavior and self-organization of animal aggregation in three dimensions" [2].

The group focuses on the flocking behavior of starlings which are common birds in Europe. They have a routine of flying in flocks and swirling around in the dusk before returning to their nests. A typical flock of starlings can range from hundreds to thousands of birds which move cohesively and put on a magnificent aerial display. To record the position of each bird at a certain time, stereophotography is used to take images of the flocks. Using the specific trifocal technique, with three different point of view, the group is able to identify the position of each bird with an error below 5% for both the relative and absolute distance [10].

Three cameras are used in order to generate a 3D image of the flock. One big problem is while reconstructing the 3D flock on the computer, it is hard to identify the same bird from images taken simultaneously by different cameras. First of all, the flock is densely packed. Second, it is difficult to tell the shape of a bird in the image since the flock is far away from the cameras. Consequently, one finds lots of small black dots densely distributed in the flock. To solve the problem, Cavagna et al. spent about two years to develop algorithms using statistical physics methods. The method does a great job with only < 5% mismatch of the targets[10].

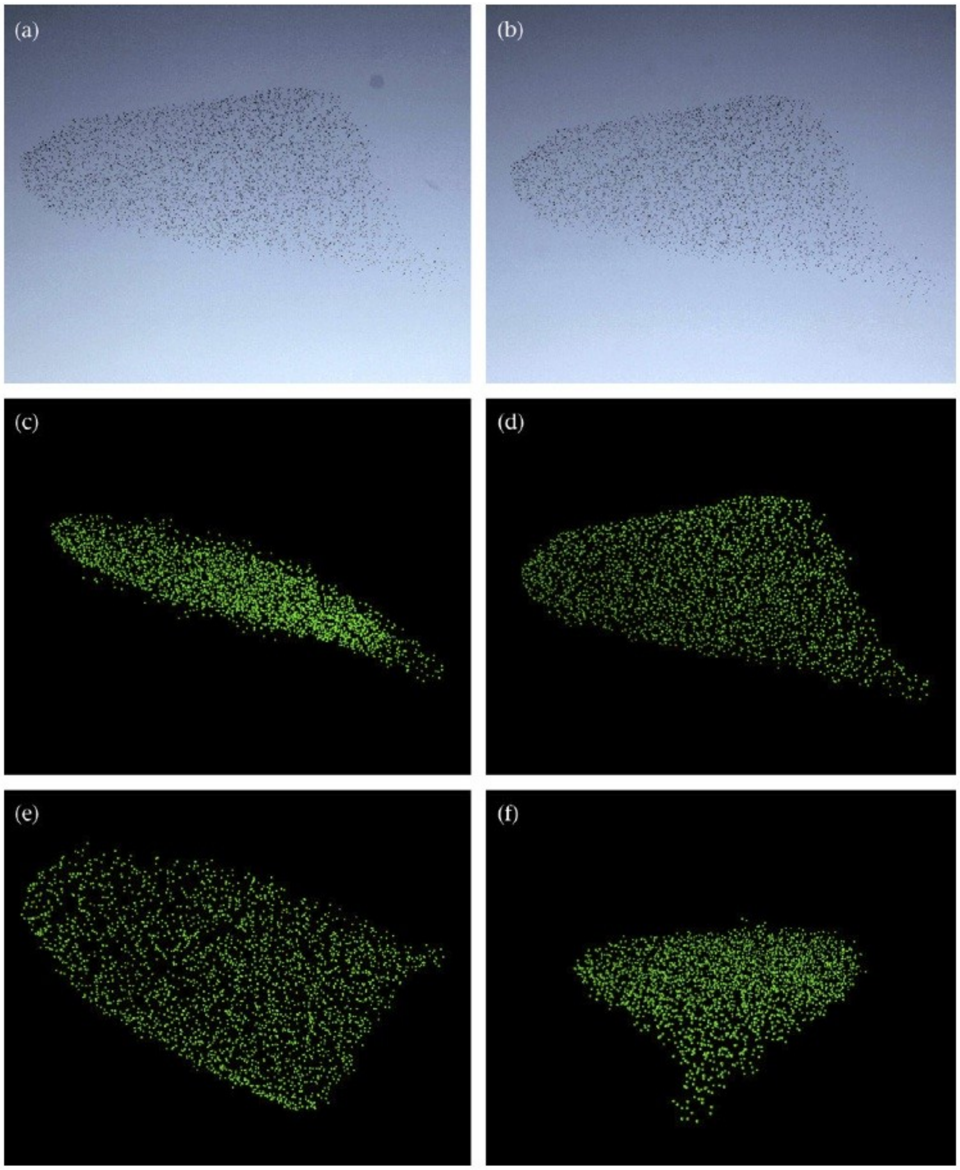

Figure 4: Images of a flock of starlings and its 3d reconstruction. The small black points are the images of birds [11]. To reconstruct the flock in 3D, each bird in the left-hand image has to match to the same bird in the right-hand image. (a) Left-hand image of the flock (b) right-hand image of the same flock taken simultaneously as (a). (c)-(f) 3D reconstruction of the flock from different point of view. (d) shows the same view point as in (b)

By studying the structure of starling flocks, the team reveals some interesting results:

1. All the previous models assumes isotropic interactions between the birds. From the reconstructed 3D flocks, StarFlag scientists found that the interaction is actually anisotropic in angular distribution. A bird in a flock tend to find its neighbors on the side

more easily than to find neighbors in front and behind it [2]. The anisotropy holds for about 6 to 7 neighbors before it decays where the spatial structure becomes isotropic. The anisotropy of the interaction is realistic if one think about the way birds see their surroundings which is never isotropic.

2. The team also found that the interactions between the birds depend on the topological distance of the neighbors instead of their metric distance and a bird only interacts with 6 to 7 nearest neighbors [10]. The metric distance is the actual distance between two birds. Most of the previous models have assumed interactions between birds as a function of physical distance, say 5 m. Topological distance is defined based on the numbers of individuals that separate the two birds. It fits the data better if one adopt the ideal that a bird interact with a fixed number of neighbors instead of with neighbors in a certain radius. When a flock is under attack by a predator, the flock split into two. The two sub groups will quickly merge once the predator passes. If the cohesive motion depended only on the interaction between birds within a distance of 5 m, then the two groups will never merge into one. On the other hand, if the interaction depends on topological distance, all this make sense. Further more, the advantage of topological interaction is that the flock can sustain stronger perturbations.

The StarFlag group has done extraordinary work to reconstruct 3D data for large and densely packed startling flocks. The data reveals some exciting results. This definitely provide precious feedbacks to the existing models. The teams are currently work on reconstructing trajectories of individual birds in the flock.

4. Results and Discussions

To investigate the nature of collective animal behavior and reveal the underlining physics, two theoretical models are discussed in this paper. The SPP model addresses the problem from a bottom-up manner while the hydrodynamic model used a top-down approach. Despite of the discrepancy in one dimensional systems, both models successfully demonstrate there exists a long-range ordering phase in two dimensions.

The SPP model is a simple but effective model. The particles driven with a constant speed follow only one rule: at each time step, a particle updates it direction of motion to the average direction of its neighborhood plus a random fluctuation. The model shows that with any value of the particle density, there are always a ordered phase in one- two- and three-dimension when the noise is sufficiently low. This conclusion seems to contradict the ferromagnetic XY model in 2D. Taking a closer look, however, one find that the SPP is a non-equilibrium system, and its dynamic features distinguishes it from the ferromagnetic case. By setting the particle speed to zero, with the formation of the Kosterlitz-Thouless vortices, the ordering phase vanish. This is a unstable state and if one increase the speed a little above zero, the ordering comes back.

One of the advantages of the SPP model is that it is based on simple rules, which makes calculation of the particle traces possible for a system as large as 10000 particles. And yet, it is very effective in showing the emergence of long-range order from local interactions. However, when dealing with much larger system on a longer time scale, the SPP model is not the optimized choice.

The continuum theory based on hydrodynamic equations is proposed to understand the large-scale, long-time dynamics of a flock [9]. Based on symmetry considerations, the hydrodynamic equations are derived for the coarse-grained velocity and number density fields. The complex self-propelled particle system is described by a couple of equations and several parameters which can be derived from microscopic models or obtained directly from experiments. The results of the dynamic renormalization group analysis indicate that system has long-range ordering in 2D.

The hydrodynamic model of provides a top-down view of the dynamic SPP system. The theoretical work explains the emergence of long-range order in 2D. Nevertheless, it predicts that there is no phase transition in 1D which contradicts the SPP model.

A different continuum theory is derived by Vicsek et al. in attempt to settle the above problem. The model is based on equations obtained from integration of the master equation of the microscopic dynamics. The numerical simulations demonstrates a ordering phase exists when the noise is low. The instability of the domains walls which separates particles moving in opposite direction is responsible for the emergence of the ordered state.

Quantitative experimental data is necessary to test the hypothesis and provide feedback to theoretical models. The StarFlag team in Italy has collected images of starling flocks and reconstructed the their structures in 3D. Careful investigations of these structures show that the interactions between birds are anisotropic and it depends on topological distance instead of metric distance.

The group modified the SPP model by replacing interacting metric radius with a topological radius in unit of bird. The numerical simulation indicates that this system has ordering at much stronger noise than the original SPP model. It will be very interesting to study the origin of this phenomenon.

In a word, great efforts have been made by scientists in exploring the collective animal behavior. Theories and models proposed to address the origin and principles of such behavior have not only benefited biological and physical science, but computer and social science as well. On one hand, more work is still needed to improve the experimental methods in order to provide quantitative data. On the other hand, theorists need to work closely with experimentalists to modify the existing models base on the empirical data.

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