Self-Ordered Motion within Biological Systems

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This essay explores the emergence of collective motion within biological systems by modeling them as swarms of identical self-propelled particles with biological motivation. The results show that it is indeed possible to simulate cohesive, collective motion similar to that of existing life forms.

In nature, the aggregation of organisms in large groups is very common. This phenomenon can be seen in numerous life forms ranging from bacteria to bison. Group movement is evolutionarily derived and can benefit an organism in two ways. First, it can aid in locating food. A large group provides a large number of food sensors. For example, bacteria use chemotaxis, a mechanism that directs motion toward higher nutrient gradient, to direct a large group towards food. Swarms not only have numerous food sensors they also have many predator sensors. Safety is the second function of swarming since early detection of a predator can help save the entire group from danger. If a predator attacks, an individual has a lower probability of being caught in a group as compared to if the individual were alone. Additionally, when dealing with the higher mammals it is often very dangerous for a predator to attack a swarm due to the risk of life threatening collisions. For example, when wildebeest herds cross the a river, crocodiles are weary to stay out of their way to avoid getting trampled and only prey upon those that are in the periphery of the herd. Finally, swarming can be used to protect those in the group of the greatest value such as infants. Zebras will often travel in herds with the young located at the center where it is the most difficult for predators to access.

Of course there are some drawbacks to swarming, which is why the behavior is not seen in all species. More organisms means more mouths to feed and can be less efficient than spreading out in the search for food. Also, a large group is far easier to spot by predators than an individual, which can make them less safe than traveling alone.

The phenomenon of group motion has recently been studied using mathematical models. A researcher can follow one of two different approaches [1]. The first of these approaches is a spatial approach, which considers the size of the environment. There are two types of spatial approaches. The first is an individual based model which generally considers the equation of motion for each individual with in the swarm. Attractive and repulsive forces are factored into the Lagrangian framework from each particle. The second approach is the continuum model which looks at the swarm as a whole rather than at the members that it is composed of. This model focuses on the population density. The advection-diffusion-reaction equation is often used to model the population dynamics for these types of problems.

Nonspatial approaches analyze swarming by simply analyzing the fission and fusion of groups through statistics. Group dynamics, and environmental conditions are just a few of the variables considered. The main disadvantage of nonspatial techniques is that makes assumptions about how groups split and merge and do not consider the size of environment being used. This paper will solely focus on spatial approaches to the study of swarming.

Clearly this topic is of interest to biologists who study the behavior of the organisms that display this type of swarming behavior. One of the early biologists to study this problem was Breeder who used simple math to model the movements of schools of fish [2]. Inspired by Coulomb's law, he created a constant attraction term and a constant repulsion term between the fish. He then varied these parameters to best fit the schooling behavior of four different

species of fish. Another interesting biological study aimed to model the movement of herding animals in two dimensions [3]. The model proposes a hierarchal algorithm, where an individual in the group gathers information on its neighbors and will move away from neighbors too close and near distant ones. This model ensures cohesion of the group if all members have a homogeneous velocity. The paper also explores heterogeneous groups where the faster members often become leaders. The results find that herding animals will have a 'neutral zone' or an optimal distance from one another. This type of 'neutral zone' is then observed confirmed to exist in herding animals. Although the methods are very crude, this model shows the potential for individual based models to accurately reflect the motion of organisms in swarms.

From a physics standpoint, swarming is of great interest since it is an emergent phenomenon of organism alignment and motion without the presence of any one leader. It is fascinating how extremely complex life forms focused on self preservation are capable of such massive group movements when they are only capable of considering stimuli within a limited distance. This is indeed one of the more impressive products of evolution. I am personally attracted to the topic due to its potential implications within my own field of research. I study molecular motors which do work through their movement within cells. These motors must perform tasks that require group effort and group movements. Can this type of collective movement be modeled and can it even be compared to the large scale movements performed by swarms of animals?

One of the first physicists to investigate this emergence of self-ordered motion within systems of self-propelled particles was Tamas Vicsek [4]. In his paper he uses a spatial, individual based framework to model the motion of N objects constrained to move in a square shaped cell (side length of L) with periodic boundary conditions. All of the particles are moving at a constant velocity such that each moves a distance v during each timestamp (Δt). The density ρ is simply defined as N / L^2. At time equals zero each particles is randomly placed in the cell and its velocity vector is then randomly orientated at an angle of θ_i where i represents the particle number. If this were all there was to the model, each particle would move in random straight lined paths. To introduce interaction amongst the particles with surrounding particles, the velocity vector is determined by averaging the velocity vectors of the nearby particles within a certain set radius. Finally the model factors in a certain amount of noise. In the end $\theta_i (t+1) = <\theta(t)>_r + \Delta\theta$ represents the angle of the velocity vector of particle i at time t+1. Here $\Delta\theta$ represents the noise term and it is chosen with uniform probability from the interval $[-\eta/2, \eta/2]$.

If v goes to infinity, the particles become completely mixed between two states, similar to the mean-field behavior of a ferromagnet. Looking at the other extreme of v equaling zero, the particles are stationary. Figure 1 shows different scenarios of particle movement varying only L and η and keeping all other variables constant. Here we can see that at high density and high noise (a) the particles move in a seemly random manner. After time, we begin to see some slight correlation in the movement as shown in c. For low density and low noise (b) group movements emerge. Finally, high density and low noise (d) show

correlated movements between particles. It is this phase transition to ordered movement on a macroscopic scale that this paper is interested in identifying.
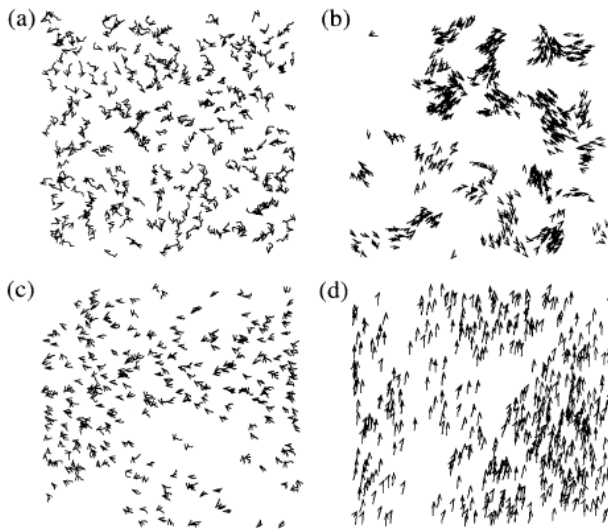

Figure 1. Here the arrow head represents the direction of the velocity vector, and the trajectory of the particles over the last 20 steps is shown by the short continuous curve. For these simulations N = 300 and the density is varied along with the noise level. (a) High density and high noise. (b) Low density and low noise. (c) High density and high noise after a lot of time has passed. (d) High density and low noise.

To better understand this transition the average normalized velocity of all the particles (v_a) was calculated to determine net motion of the population. For motion with low density and high noise this velocity is around zero, while for high density and low noise the average normalized velocity should be approximately one. Figure 2 shows how this average velocity is affected by changes in noise and density. To analyze this, Vicsek draws upon the similarities between v_a and the order parameter of equilibrium systems near the critical point. Therefore he aims to solve for β and δ in the following relations:

$$v_a \sim [\eta_c(\rho) - \eta]^{\beta} \qquad\qquad v_a \sim [\rho - \rho_c(\eta)]^{\delta}$$

Here, $\eta_c(\rho)$, and $\rho_c(\eta)$ are the critical values for the noise and density when L approaches infinity. To determine β and δ scaling plots were produced for $\ln(v_a)$ vs. $\ln([\eta_c(L) - \eta]/\eta_c(L))$ and $\ln(v_a)$ vs. $\ln([\rho - \rho_c(L)]/\rho_c(L))$ as shown in Figure 3. Values for η and ρ were fixed in a reasonable range while manipulating $\eta_c(L)$ and $\rho_c(L)$ to make the plots as linear as possible. The slopes represent β and δ. From this form of analysis, β and δ vales were found to be 0.45 ± 0.07 and 0.35 ± 0.06 respectively. These are fairly conservative estimates since the scaling plots used are especially sensitive to the choice for the critical noise and density values. We might expect that η_c and ρ are analogous to temperature and density of spins for a ferromagnet, but for this case we would then expect that β and δ would be equal. Vicsek does not rule out the possibility that this is indeed the case for simulations at the thermodynamic limit. Clearly, there are flaws in this particular model, although it is successful in demonstrating the transition from disordered motion to cooperative motion using very simple rules and mathematics.
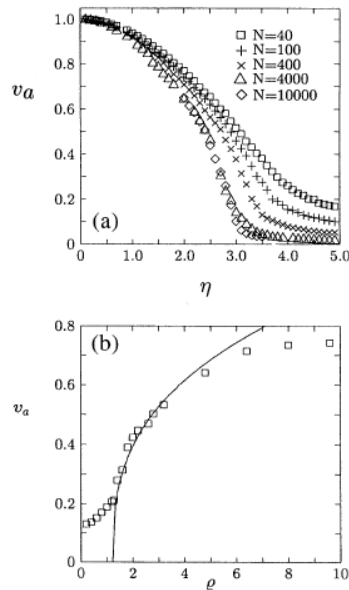
Figure 2. (a) The absolute value of the average group velocity vs. noise. Here the density is kept constant while the cell size and number of particles are manipulated. (b) The absolute value of the average group velocity vs. density. Here the noise and cell size are kept constant.
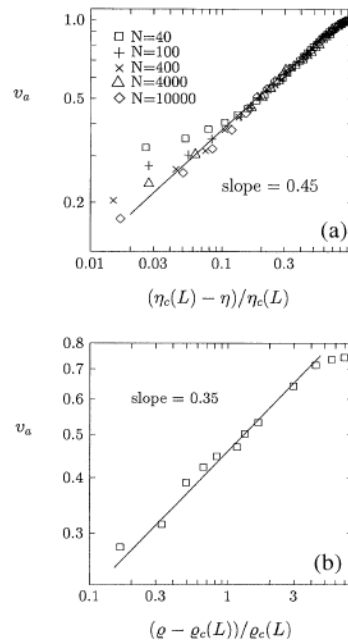
Figure 3. Logarithmic scaling plots. (a) The slope of this graph represents the exponent β. Here density is kept constant. (b) The slope of this graph represents the exponent δ. The cell size and noise are held constant.

Shortly after this research, Vicsek released yet another paper on the topic [5]. In this paper, he uses a few of the same basic principles from his previous work, but adds many more complications to the picture. He tries to model bacteria movement using the lattice gas model. First off, instead of using a continuum square environment with periodic boundary conditions, he uses a triangular lattice with periodic boundary conditions. Particles are constrained to move along the edges of the lattice, which makes it possible to move in one of six directions (q = 6) during each timestamp. Additionally it is possible for more than one particle to occupy a cell at a given time. In this case, one of the particles, or the 'lowest' one, is randomly selected. This particle will then move in a completely random direction during the next time step. All the particles in the cell that are not the 'lowest one' have their directions determined by a Boltzman distribution which factors in the velocity vectors of all nearby particles from the previous time step. Another major difference is the introduction of a 'temperature' term. Since Vicsek is primarily concerned with modeling for bacteria, the 'temperature' term is an effective value which takes environmental factors such as food concentration and humidity into consideration. In these simulations density and temperature are varied, much like noise and density

were varied in his previous paper. Figure 4 shows snapshots of a system regulated by these rules for different temperatures and densities.
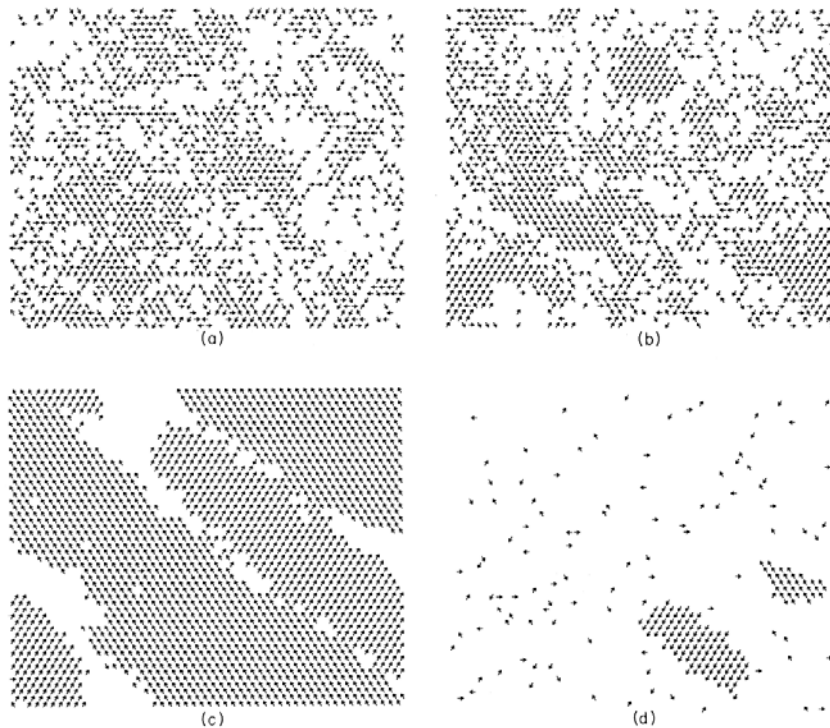

Figure 4. Snapshots of the triangular lattice system at different 'temperatures' and densities. (a) High temperature. (b) Intermediate temperature. (c) Low temperature. (d) Intermediate temperature and low density.

Ultimately Vicsek once again wants to find values for β and δ and calculates them to be approximately .27 and .5 respectively. These values for the lattice differ from the continuum model. Additionally, they differ from the q = 6 Potts model. The Potts model is a model for interacting spins in crystal lattice. This difference is reasonable since the Potts model is concerned with particles with stationary spin in a lattice while here the particles are constantly moving, occupying new sites in the lattice. Although very interesting, this particular bit of research seems to impose restraints upon particle motion which do not exist in nature.

Vicsek's first continuum model describes interactions among particles that are in close proximity and do not need to stay together as a collective whole. For example, it is accurate in describing the movement of bacteria [6]. Experimental confirmation of this involved a film of E. Coli which were labeled with polystyrene beads. These beads were then tracked as the bacteria swim about. The superdiffusive motion observed can be seen as collective motion with features similar to those predicted in Vicsek's model.

Not surprisingly, Vicsek's model breaks down when considering the cohesion of the population. For example, if it were applied to a school of fish,

which exists in open space, the fish along the edge of the school would constantly break away and scatter. After enough time the entire school will have dispersed into open space and no longer have any collective motion. To model these types of systems it is important for there to not only be directional similarities between the particles, but also cohesive forces along with repulsive forces. For example, our fish must feel attraction to the group so as not to be separated from it, but the fish must also feel repulsive forces from the fish rubbing up against it in close proximity.

A model that takes all this into consideration is proposed in a paper by Gregoire et. al. [7]. They start under the following assumptions: the group lacks a leader, the environment is very noisy, interactions are only local, and the population is not confined. Gregoire expands upon Vicsek's model through the addition of a Lennard-Jones-type body force (attraction and repulsive force) acting between all particles within a certain radius. Additionally, the velocity vectors are still influenced by a noise term and a term averaging the velocity vectors within a certain radius. Finally, the Voronoi tessellation is calculated for each particle so that particles are only influenced by the action of the first layer of particles surrounding it. This means that for the high density situation particles that are shielded by another yet are still within the critical radius of particle i have no influence upon its motion of particle i treating the particles more like cells. This is a huge improvement upon Vicsek since in biological situations an organism's senses can be shielded by the presence of another. In this model α is the coefficient controlling the strength the directional influence of nearby particles while β controls the strength of attraction/repulsion between particles. As shown in figure 5, when you vary α and β the group behavior changes drastically. Higher values of α cause for group movement in one direction, while higher values of β increases the cohesiveness of the group. N is defined as the total population and n is the size of the largest cluster.
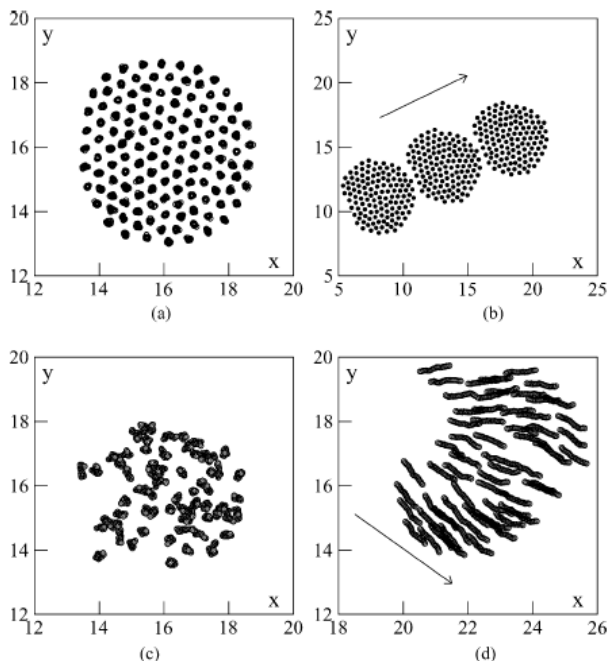

Figure 5. Groups of particles traveling with different values of α and β. (a) Small α and large β for 20 timesteps. (b) Large α and large β in 3 snapshots separated by 120 timesteps. (c) Small α and small β for 20 timesteps. (d) Large α and small β for 20 timesteps.

The paper views group movement as being in one of three phases. These phases are referred to gas, liquid, and solid in analogy with chemical phase transitions. The gas to liquid phase transition is defined as when the n/N is equal to ½. The liquid to solid transition takes place at high β values when there is strong cohesion in the flock. To truly define this transition a variable referred to as the relative diffusion or Δ is calculated for the entire population. Low values of Δ indicate limited diffusion between adjacent molecules, or a large amount of cohesion. For liquids Δ ~ 1, while for a solid Δ ~ 0. Therefore there fairly arbitrarily define the liquid to solid transition as when Δ = ½. Clearly the relative diffusion varies depending upon where in the swarm you are observing. Because of this, the authors decide to divide the group into 4 'sectors'. These are referred to as the core, head, tail, and sides.

Next the paper aims to define 'collective motion'. Here the average velocity of the group is the variable V. If α, or the coefficient controlling the impact of the velocity vector of nearby particles on particle i, is very large, V ~ 1, while when α is small, V ~ 0. Collective motion is defined as when $V = v_o/2$ where v_o is the magnitude of the velocity of each particle. Using this system, phase diagrams are produced to illustrate these transitions. These diagrams of β vs. α are shown in figure 6. This figure is for a fixed system size with a set density. The goal is to better understand what occurs in infinite system size, zero density limit. Unfortunately, this type of calculation far exceeded the research groups computing power. Instead several different methods of calculations were performed and showed that indeed, cohesive and collective motion is possible in these regimes. One of these methods involved double limit of an arbitrarily large flock evolving into infinite space.
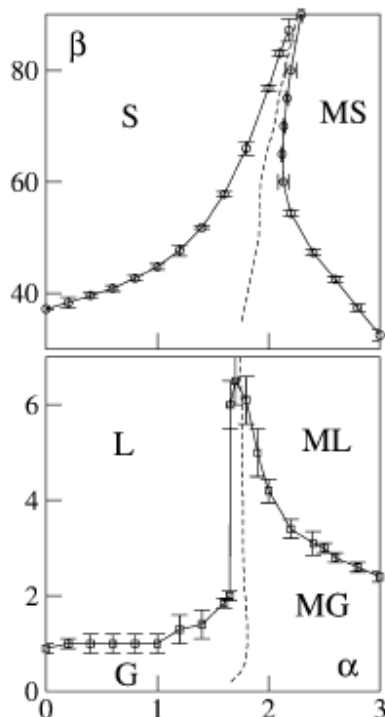

Figure 6. Phase diagram of β vs. α showing the transitions between solid (S), moving solid (MS), liquid (L), moving liquid (ML), gas (G), and moving gas (MG). Here density and cell size are held constant.

Certainly this paper is a vast improvement upon Viscek's paper when analyzing group motion in open space. It shows that cohesive and collective motion is possible and categorizes the state of group cohesion into three phases. Unfortunately, these transitions seem to be based upon arbitrary boundaries. Still, the evolution from disordered motion to cohesive, collective motion has been well demonstrated using this model.

Clearly, it is impossible to accurately model the group movements of complex organisms. There are far too many variables and environmental factors affecting the motion of each individual thus changing the motion of the group as a whole. Despite this impossible barrier, the models proposed above are capable of producing seemingly reasonable group behavior. Although simplified, they consider many of the major factors that might influence the motion of an organism buried within a large aggregation of similar organisms. Not only did these models mimic group behavior, they were used to explore the transition from disordered motion to collective motion. The research presented in this paper reflects huge advancements in understanding the motion of swarms, yet there is still much to be done theoretically.   Additionally, experimental research of biological organisms in groups is deficient and more research is necessary to truly test the validity of the theoretical models produced and the assumptions each one makes. Unfortunately, phase transitions from disordered to collective motion are essentially impossible to observe in nature and can only be done through computer simulations. Regardless, the data presented seems to reflect many of the group behaviors seen in the many organisms that depend upon aggregation for survival.

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