Modeling Collective Animal Behavior --- From Ants to Human.

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Abstract   Understanding the collective behavior of large groups of animals is an interesting and challenging topic. Despite the diversity of animal species as well as the intrinsic complexity of individual animal, it has been shown that a wide range of collective behavior of the group can arise from much simpler behavior of the individuals. In this paper we will look into several typical examples of common types of collective behavior, arranging from ant trails to Fish schools and even humans, and introduce theoretical and computational model developed for these and other similar cases, in order to give a brief overview of the field's latest developments.

Introduction

Many species of animal display various types of collective behavior and self-organization. Ants and honeybees build sophisticated nets and perform well organized food searching, fish schools change swimming patterns and group size in response to different situation, migrating geese forming V-shaped flocks, even pedestrians walking on the side walk or consumers making their choices are just a few examples of behavioral patterns that became apparent only at the level of the group.

Efforts on understanding the principle behind complicated animal behavior dates back to as far as 1977. Through the pioneering works of Nicolis and Prigogine, Ashby, Weiner, von Bertalanffy and Deneubourg many others (see [1] for a brief review), it became clear that a wide variety of collective animal behavior can be viewed as a consequence of individuals following a set of simple behavior rules, and can thus be modeled by mathematical equations similar to physical and chemical approaches. This important notion has also inspired the idea of using computer simulation to model collective animal behavior similar to molecular dynamics simulation in condensed matter physics.

In this paper we will review several typical types of collective behavior, as well as some of the theoretical and experimental efforts trying to extract the essential laws behind. We intend to establish an overview of some of the late methods in the field, without going too much into the rich details of each case.

Attracting and Aligning ---- The SSP model:

One canonical and straightforward example of collective animal behavior is dynamic group motion of large number of animals, such as bird flocks, fish schools and even human crowds. The characteristic feature of such behavior is that the length scale of the group in uniform motion often far exceeds the possible interaction and communication range of single individual. For example, fish schools can spread over 700 m^2, and often consists of hundreds and thousands of individuals. [2] Therefore, groups of animals that are able to communicate through sound or chemical signals at distance comparable to group size do not fell into this category since they will have different mechanisms of generating group behavior.

A widely used class of model for simulating group motion of the animals is known as the Vicsek model, or the self-propelled particle (SSP) model. [3,4,5,6]

An example of basic SSP model can be found in [7], in which single animal are modeled as particle that behave according to the following set of rules:

1)   Avoid collision: individuals attempt to avoid collision by moving away from objects within a distance δ, which includes simulation boundaries and other individuals. In [7] this is implemented as:

$$\mathbf{d}_i(t + \Delta t) = -\sum_{j \neq i} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{\left|\mathbf{c}_j(t) - \mathbf{c}_i(t)\right|} - \frac{\mathbf{r}_B(t) - \mathbf{c}_i(t)}{\left|\mathbf{r}_B(t) - \mathbf{c}_i(t)\right|} \tag{1}$$

where $\mathbf{c}_i(t)$ is the position vector of the i'th particle and the summation is over all particles j within δ of particle i. $\mathbf{r}_B(t)$ is the position of the boundary. $\mathbf{d}_i(t)$ is the desired direction at time t.

2)   Attract and align: when no obstacle is within distance δ, individuals are attracted towards its neighbors within distance ρ. They will also try to align their moving direction to the direction of these neighbors $\mathbf{v}_k(t)$, i.e. :

$$\mathbf{d}_i(t + \Delta t) = 1/2 \left[\sum_{k=1} \frac{\mathbf{v}_k(t)}{\left|\mathbf{v}_k(t)\right|} + \sum_{k \neq i} \frac{\mathbf{c}_k(t) - \mathbf{c}_i(t)}{\left|\mathbf{c}_k(t) - \mathbf{c}_i(t)\right|} \right] \tag{2}$$

The first term in the parenthesis causes alignment and the second term is attraction. $\mathbf{v}_k(t)$ is the direction vector of each individual and $\mathbf{c}_k(t)$ is the position vector.

3)   There is a maximum turning angle of θ at each time step, and each turn is subjected to error.

While rules (1) and (3) can be viewed as general requirement for any simulation, rule (2) is unique to this model and could be thought of the origin of all the collective behavior that occur in computer simulations.

In [7], the model is used to simulate the group size change of banded killifish in response to different signals.

In lab experiment reported in the same paper, banded killifish form smaller groups or swim independently at the signal of food source. However, in the presence of crushed killifish skin, which mimics a predator attack signal, the fish form large schools as a means to protect themselves.

Computer simulation using SSP model reproduced the group size choice observed and suggests that it may simply be achieved by individuals adjusting the radius of attraction/alignment region ρ in response to different signals, as is shown in Fig.1.
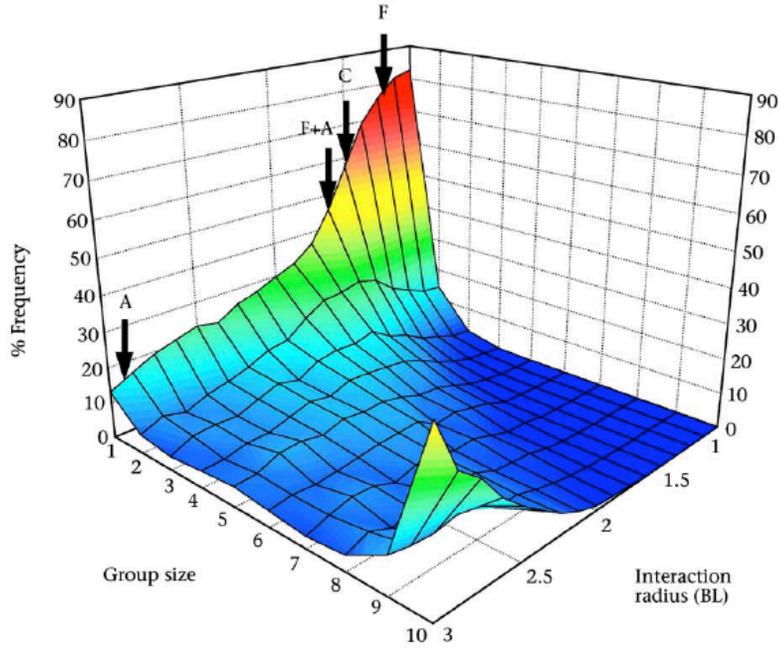

Figure 1. Simulated group size frequency with different Interaction radius. The interaction radius is expressed in terms of body length of single killifish (Figure from [7])

In both the lab experiments and computer simulations mentioned above, environmental signals are made to be almost equally accessible to each individual in the group, so that almost all members of the group adjust their motion spontaneously. However, the more natural situation would be that only a small fraction of animals in a group has sufficient information or experience to determine the direction of motion. This is especially true in the case of migrating groups of animals in which a limited number of experienced members of the group play the role of tour guide [cite in fish2]. It is interesting to ask how animal without means of long range communication can achieve effective leadership.

In [8], the authors tested the assumption that attraction and alignment behavior alone is able to achieve this goal at large group size. Their implementation of leadership based on the original SSP model   is as follows: A small number of 'informed

individuals' are assigned a preferred direction $\mathbf{g}_i$ with weight ω. This will bias their intended direction $\mathbf{d}_i(t + \Delta t)$ determined by methods mentioned above through:

$$\mathbf{d}_i'(t + \Delta t) = \frac{\mathbf{d}_i(t + \Delta t) + \omega\mathbf{g}_i}{\left|\mathbf{d}_i(t + \Delta t) + \omega\mathbf{g}_i\right|} \tag{3}$$

By introducing the above term and omitting the boundary term in (1) that are irrelevant for migration, the authors studied the effectiveness of leadership in several different situations. The effectiveness is represented by the accuracy of motion, which is defined by the normalized angular deviation[8] of the group direction around the preferred direction.

Fig.2 showed non-linear dependence of the accuracy to the portion of informed individual in the group, as well as to the number of informed individuals in the group. The accuracy of the group depends heavily on the absolute number of informed members, rather than on the proportion. This indicates that by adopting the attract-align behavior assumed in the SSP model, larger groups can be navigated by smaller portion of informed individuals.
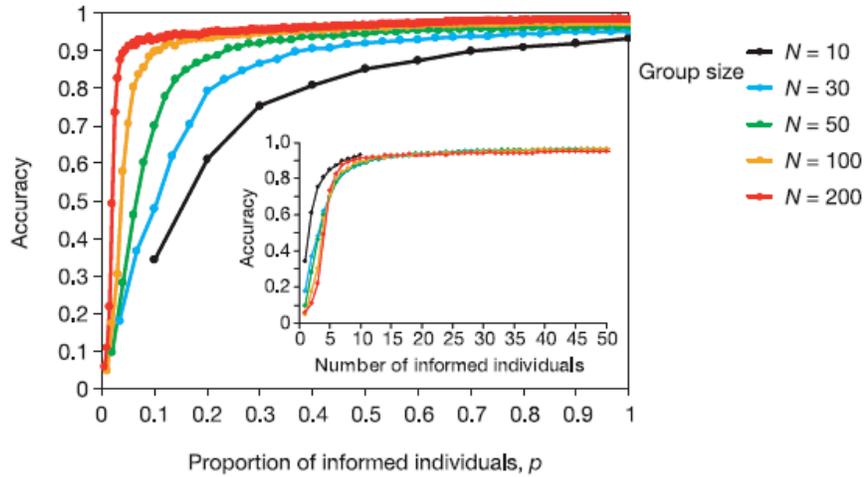

Figure 2. Group accuracy as a function of proportion of informed individual. Inset: Group accuracy as a function of absolute number of individuals. (Figure from [8])

When informed individuals differ in their choice of preferred direction, its very possible that this is caused by some of the 'guides' make wrong decision for various reasons. However, other group members have essentially no information as to the cause

of this disagreement. Therefore, the group can only judge from facts such as numbers of leaders in each direction or the quality of the information provided by the leaders.

Simulation using the SSP model showed that by adopting attract-align behavior, group of animals can be very sensitive to difference in the number of informed individuals moving in each direction, given that there is a sufficient difference in direction. (see Fig.3)

The group is also capable of choosing between low and high quality information, as is shown in Fig.4 . If one group of 'guides' are unsure of their directions, the group can automatically switch to another direction.
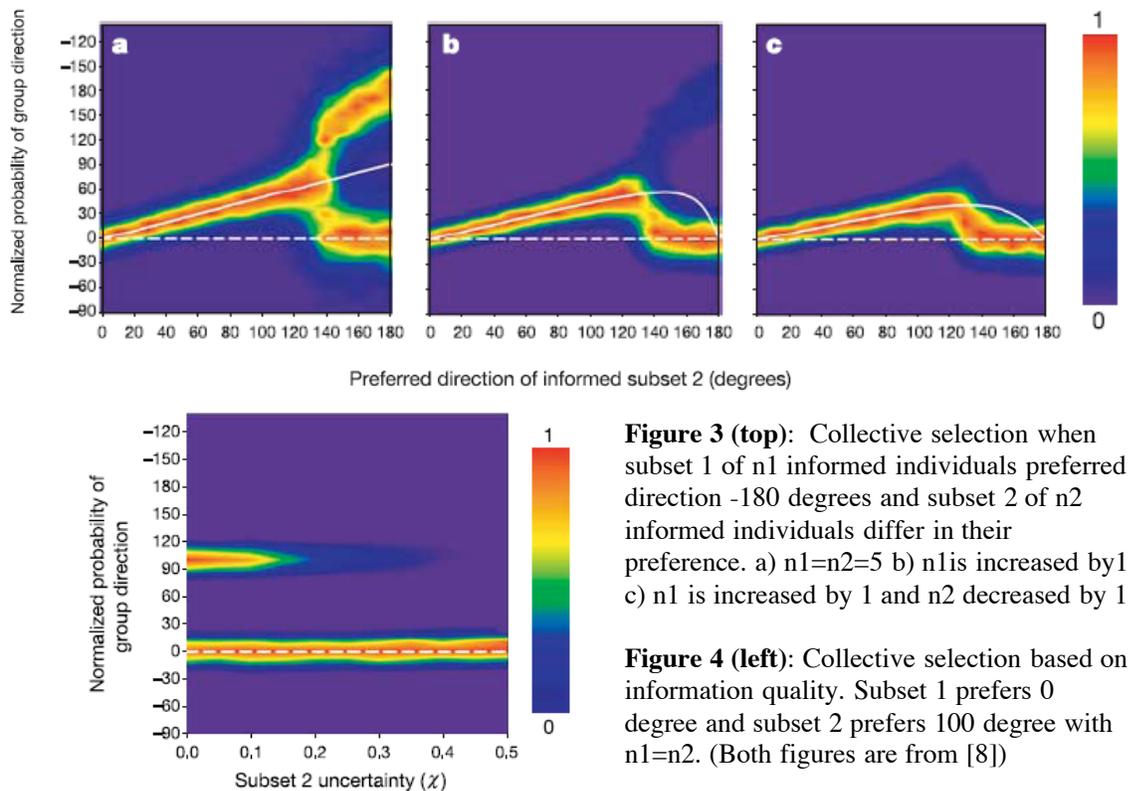

Figure 3 (top): Collective selection when subset 1 of n1 informed individuals preferred direction -180 degrees and subset 2 of n2 informed individuals differ in their preference. a) n1=n2=5 b) n1is increased by1 c) n1 is increased by 1 and n2 decreased by 1

Figure 4 (left): Collective selection based on information quality. Subset 1 prefers 0 degree and subset 2 prefers 100 degree with n1=n2. (Both figures are from [8])

Synchronization and coupled oscillators:

Synchronization is another class of common collective behavior that has been relatively well studied, and is likely the most common collective behavior found among human. Audiences clapping in theater often switch spontaneously between coherent and incoherent phases [9], female working or living together have synchronized menstrual cycles [10] and even consumers tend to synchronize their choice [11].

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In animals, the most well studied examples are probably fireflies' synchronized flashing [12] and activity pattern in ants [13,14]. For ants, the situation is further complicated by the fact of inhomogeneous distribution of population in nests. For example, in a nest of the ant *Leptothorax acervorum*, there are two spatially separated groups of ants, one is near the entrance of the nest and the other is near the brood pile which is in the center of the nest.[cite ant1] Ants within these groups synchronize their activation pattern through body contact into oscillation cycles with 20 minute period. The two groups are thought to couple their oscillation pattern in the absence of perturbation. However, in an ant colony, there are always a number of foraging ants leaving the nest and thus are decoupled from the oscillation pattern of the nest. When these ants return to the nest again, they present a perturbation to the oscillation pattern of the nest.

To study how the synchronized activity pattern depend on spatial distribution and external perturbation, Boi et al. [14] used a coupled oscillator model to simulate the activity circle in the ant nest. The coupled oscillator model consists of the following sets of differential equations:

$$\frac{dN_a}{dt} = g(E)f(N_a, B_a)N_i - (l-s)N_a + aF_a, \quad \frac{dB_a}{dt} = g_1(H)f_1(N_a, B_a)B_i - s_1 B_a,$$

$$\frac{dE}{dt} = N_a h(N_a, B_a) - wE, \quad \frac{dH}{dt} = B_a h_1(N_a, B_a) - zH.$$

$$\frac{dF_o}{dt} = 1 N_a - aF_a,$$

$$f(N_a, B_a) = [c + j(dB_a^2 + eB_a) + k(dN_a^2 + eN_a)],$$
$$f_1(N_a, B_a) = [c_1 + j_1(dB_a^2 + eB_a) + k_1(dN_a^2 + eN_a)],$$
$$g(x) = (b+x)^{-1},$$
$$h(N_a, B_a) = (mN_a + nB_a), \quad h_1(N_a, B_a) = (m_1 N_a + n_1 B_a).$$

Here, the number of active and inactive ants near and entrance or near the brood pile are indicated by N_a N_i B_a B_i respectively. The functions f and f_1 model the activation of inactive ants using experimentally evaluated constants, these functions couple activation both within a single group and in between the two groups. Functions g and g_1 and variables E and H measures the ants' reduced probability of activation having been active. In other words, these functions resemble a refractory period after activity.

Active ants become inactivated at rates s and s_1 respectively. The perturbation of foragers are incorporated using parameters l and a, which indicates the rate of ants leaving and reentering the nest respectively.
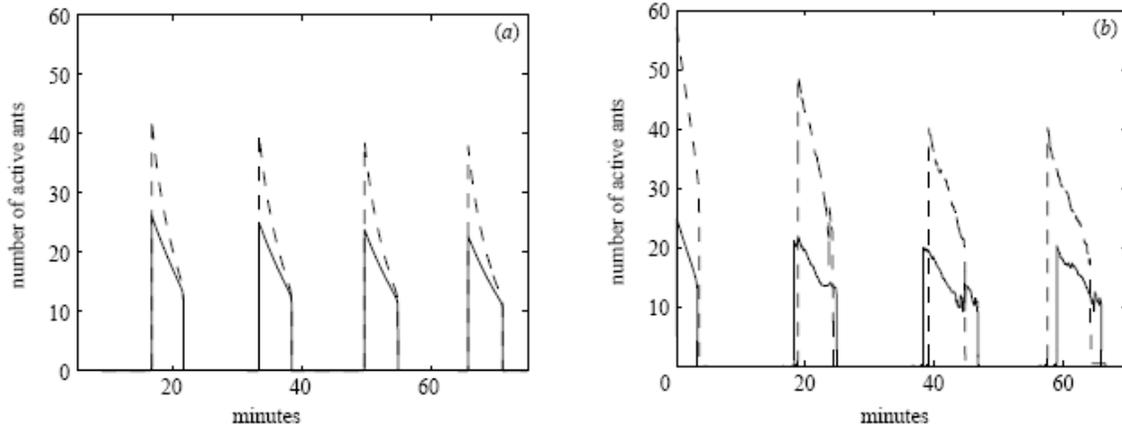

Figure 5 : Simulated oscillation pattern of ant activity. Dotted lines indicate entrance group and solid lines are brood pile group. Left, foraging ants are not allowed to reenter the net. Right, foraging ants are allowed to reenter. (Figure from [14])

To compare the results of simulation, the authors also used video camera to record ant behavior in laboratory environment.

Both simulation and experiment shows that when foraging ants are not allowed to return to the nest, the brood group and the entrance group are coupled to each other. When foraging ants are allowed to return to the nest, the perturbation mainly affects the entrance group and disturbs its oscillation pattern. (Fig.5)

Ant trails

Ants self-organizing by 'communicating' through pheromone signal is a typical example for collective behavior arising from communication and interaction at the length scale comparable to the group size.

Many species of ants leave signaling chemical substance, called pheromone, once they have found a food source and starts to return to their nest. Other ants can follow these pheromone trails to reach the food source and leave their own pheromone on the way to reinforce the signals. [15] Through this process, ant colonies can develop a network of pheromone trails linking to nearby food sources.
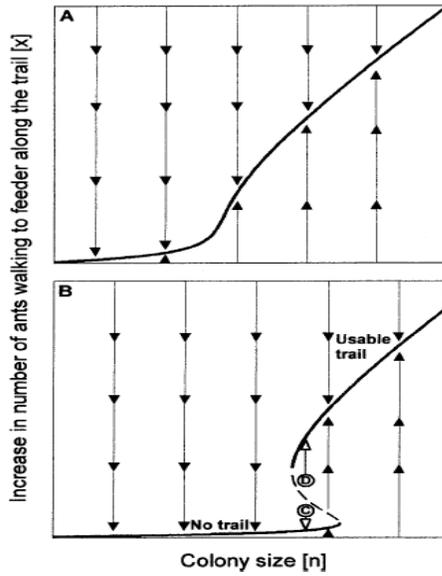
Figure 6 : phase transition behavior in ant pheromone trail. A: food source is frequently found B: food source is infrequently found. (Figure from [16])

The establishment and development of ant pheromone networks, or even single pheromone trail, is a result of group behavior of a considerable number of ants, and thus can display interesting formation patterns such as phase transitions due to memory effects.

In [16], the authors generated the following simple partial differential equation to study the establishment of an ant pheromone trail:

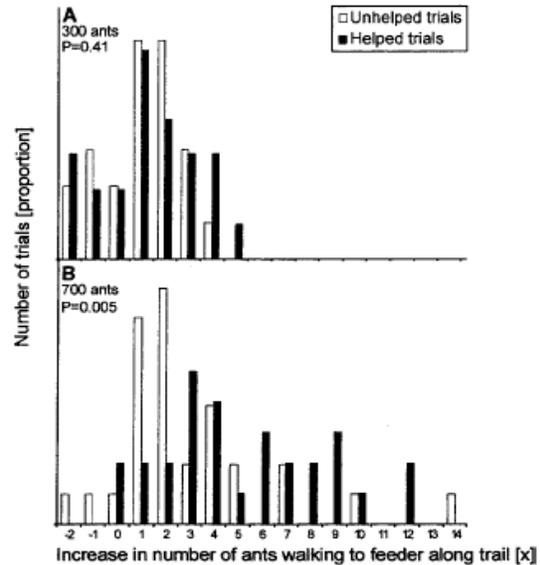$$\frac{dx}{dt} = (\alpha + \beta x)(n - x) - \frac{sx}{s + x} \qquad (4)$$

If the number of ants walking to the food source is x, then and βx determine respectively the rates at which a single ant finds a food source by independent searching or being led by pheromone signal reinforced by x other ants that were walking to the source before it. The size of the colony is n . The second term on the right hand side accounts for the deterioration of the pheromone signal in which s denotes a maximum rate at which ants lost the tail. The non-liner dependence of this term on x can be thought of as caused by deterioration of pheromone signal in time.

Figure 7: Increase in number of ants walking towards food source. A: colony of 300 B: colony of 700 (Figure from [16])

By solving the equation for x at $\frac{dx}{dt} = 0$, the authors observed phase transition phenomenon for small value of α, as shown in Fig.6b. It shows that for big enough ant colonies, pheromone trails can almost always be established. If the size of colony is too

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small, trails are hard to establish even if the food source was found by many ants at the beginning. Medium sized ant colony can also establish trails easily if α is large (Fig.6a), or the food source is easily found upon independent searching. However, if the food source is not found frequently enough, for a medium size ant colony the generation of pheromone trail is largely dependent on the initial condition. The trail will only establish if enough ants have found the food source at the beginning (Area D in Fig. 6b).

To test this prediction, the authors conducted experiments in which the food source is initially put close enough to the net so that individual foraging ants can easily find it. When a number of ants are feeding at the food source, the source is moved to a further distance. Previous experiments have shown that if placed at this distance in the beginning, ant colony of all sizes were not able to establish pheromone trails. The authors observed that when initially helped, colonies of 700 ants are usually able to establish pheromone trails while colony of 300 are not, in consistence with the prediction of the model. (See Fig. 7)

Collective behavior emerging from selfishness

A common feature in the examples introduced above is that collective behavior has always originated from individual animals' tendency to behave similarly to others in the group. No matter it is direct alignment in the case of fish school or indirect mimicking such as ants trying to follow the same track as others by sensing chemical signals. However, there are cases in which behavioral patterns can arise in the total absence of the tendency to 'mimic' others.

One extreme example is that collective behavior patter can arise from selfishness alone, as is in the case of human beings under escape panic. Helbing and Vicsek treated selfishness as 'psychological forces' in their dynamical model simulating behavior of escaping crowds. [17] In their equation of motion:

$$m_i \frac{dv}{dt} = m_i \frac{v_i^0(t)\mathbf{e}_i^0(t) - \mathbf{v}_i(t)}{\tau_i} + \sum_{j \neq i}\mathbf{f}_{ij} + \sum_{W}\mathbf{f}_{iW}$$

The second and third term on the right hand side are the repulsion and friction force between neighboring people and between people and walls respectively. The first term represents the tendency to reach a certain velocity $\mathbf{v}_i(t)$ within a desired time interval τ_i, this term can be interpreted as a 'selfish' term, which, in the case of this

study, caused disastrous blocking at narrow entrances when the desired velocity is high. (Fig. 8A)

It should be noted that beside the 'selfishness' effect, there is also a friction term tangential to the direction of motion present in $\mathbf{f}_{ij}$ which is critical to the clogging effect, and is unique to this model.

The authors also reported an unexpected result during simulation, that clogging can occur at widening of escape routes, as is shown in Fig. 8B, and can be avoided by placing asymmetrically columns in front of exits.
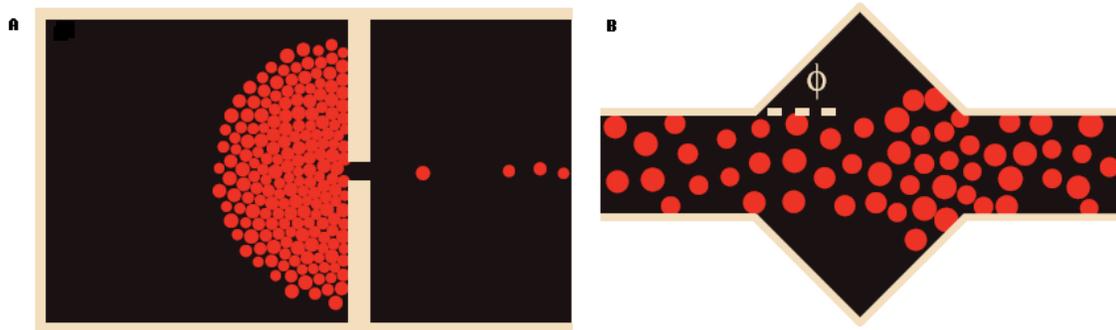

Figure 8 : Simulating human exist panic A) clogging due to narrowed exit. B) clogging due to sudden widening in escape routs. (Figure from [17])

Conclusion:

We have noted that a lot of parameters and details in the models are defined somewhat arbitrarily. This is partly due to the fact that experiments on collective behavior of large groups of animals are hard to implement, and we are left with insufficient data to fine tune these models. Details in the models can play a critical rule in the behavior of the model. For example, it is shown in [18] that difference in means of incorporating noise into the Vicsek model can cause different phase transition behavior. There also exist phase transition behavior when the attract-align radius is varied continually. Although a lot of rich behavior of mathematical model may not be biologically relevant, it is always interesting to ask why evolution has shaped animals to behave as we see.

Another point worth noticing is that although it is now safe to say that a wide variety of collective behavior is a result of individuals following SIMPLE rule, it is almost equally possible that certain collective behavior can arise from COMPLICATED

rules. [1] One should always keep in mind that animals are complicated entities themselves, and any modeling attempt involves a certain degree of simplification that might wipe out important details.

Lastly, one might notice that to this day, most of the efforts have been selectively using observed behavior of single animal to regenerate group behavior. It is interesting to ask if one could, by looking at group behavior of an animal group and make reasonable guesses as to what individual behavior rules might exist in behind which is previously unknown.

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