



Review Article (Invited)

Collective pattern formations of animals in active matter physics

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Active matter refers to systems composed of elements that are self-propelled by the dissipation of energy, in which dynamical patterns emerge, as is the case of flocks of birds and schools of fish. Some researchers in active matter physics seek to identify unified descriptions of such collective motions through interdisciplinary approaches by biologists and physicists. Through such collaborations, experimental studies pertaining to active matter physics have been developing recently, which allow us to verify the proposed mathematical models. Here, we review collective pattern formations and behaviors of animals from the perspective of active matter physics.

Key words: self-propelled particles, *C. elegans*

◀ Significance ▶

People, both non-scientists and scientists, are fascinated with collective pattern formations such as in flocks of birds and schools of fish. The research field to understand the mechanisms underlying such pattern formations is known as active matter physics. At the beginning of active matter research, these mechanisms have mainly been studied in the theoretical aspects. Then, experimental studies have recently been achieved along with methodological developments such as molecular biology and fluorescent imaging. Here, we introduce these experimental systems of active matter physics, focusing on animal collectives.

Introduction

How do locally interacting elements form a globally ordered pattern? Pattern formation by cells or individuals has fascinated us, and their underlying mechanisms have long been investigated in the field of biology. For example, developmental biologists have aimed to understand how each cell finds its own position to form tissue organs during morphogenesis. In the second half of the 20th century, morphogens, which are molecules that determine positional information by creating concentration gradients through diffusion, were identified, and attempts have been made to investigate morphogen-dependent molecular mechanisms. Furthermore, the mechanisms underlying skin pattern formation in fishes, such as the formation of stripe patterns, in terms of the reaction-diffusion system proposed by Turing, are widely studied in the field of mathematical biology [1].

In addition to transmitter-mediated pattern formation phenomena, there is a pattern formation phenomenon generated by elements that are self-propelled by the dissipation of energy, as observed in nonliving things, such as colloids and

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cytoskeletons, and living things such as biofilms of motile bacteria, flocks of birds, schools of fish, and crowds of humans [2]. Why do randomly moving particles collectively generate patterns without knowing their own positions in the entire structure? The research field that studies such pattern formation mechanisms is known as active matter physics. Active matter refers to systems composed of elements that are self-propelled by the dissipation of energy. The goal of active matter physics is to seek the universal laws underlying collective pattern formation. To achieve this purpose, both theoretical and experimental studies are required; a mathematical model proposed on the basis of theoretical research should be verified by the observation and perturbation of collective motions using living or nonliving things.

There are many good reviews summarizing pattern formations from non-living things, such as colloids and molecular motors to unicellular organisms [2–5], but it is in contrast with a smaller number of reviews for animals' pattern formations. Through the evolution of unicellular to multicellular organisms, animals have acquired complex brain functions such as memory, learning, and cognition. These brain functions enhance the efficiency of social behaviors represented by foraging, escaping from a predatory attack, and collective decision making. Thus, there are more examples of collective behaviors that have functional significance than those of non-living things and unicellular organisms. Therefore, it has been fascinating to consider which mechanisms underlie pattern formation by animal collectives, as observed in flocks of birds and schools of fish. Therefore, we here discuss the studies on animals' collective pattern formations through their behaviors. Finally, we discuss future directions for this research field.

Collective Pattern Formations by Non-Model Animals' Behaviors

The theory of active matter physics suggests that no matter how complex a collective motion is, a small number of simple rules govern it. The Vicsek model is one of the candidate unified descriptions of the collective motion of self-propelled particles [6]. This model predicts that only short-range alignment interactions of moving objects are needed to form a long-range ordered phase with fluctuations with a long-range correlation in two dimensions, as occurs in many collective motions. The model is controlled by two parameters: the density of the particles and the amplitude of the noise in the alignment. The ordered pattern appears with parameters of higher density or lower noise. Theoretical studies, including the work by Vicsek et al., were mainly conducted in the early phase of the active matter research field (until approximately 2000) [2]. Then, since the 2000s, theoretical and experimental studies have begun to come together.

Studies on animal collective behaviors have been performed using non-model or model animals; the definition of non-model and model animals is based on whether a versatile genetic method has been established. Since the collective behaviors of laboratory model animals have been less reported, non-model animals are often used in the studies. One of the main techniques for such studies are to record the trajectories of individual animals in collectives by putting small global positioning system (GPS) devices on them. Analyses of the acquired trajectory data have been combined with theoretical research.

Nagy et al. obtained the track logs of homing pigeons flying in flocks of up to 10 individuals using lightweight GPS devices and analyzed their velocity correlations [7]. These analyses show that most flights produce a robust hierarchical network in flocks containing leader-follower relationships; individuals occupying positions near the front of the flock tend to play leadership roles. They also suggest that leadership may be related to individual navigational performance; birds higher in the hierarchy demonstrated higher efficiency in a single solo homing test.

Iain Couzin's group proposed a model that determines the collective behaviors of fish groups resulting from local interactions based on the positions and orientations of individuals relative to one another [8]. They classified three interaction zones centered around each individual (Fig. 1). The innermost sphere is the zone of repulsion (Fig. 1a); if other individuals enter this zone, the individual moves away from them in the opposite direction. The interpretation of this zone is that it maintains a personal space and ensures the avoidance of collisions. The second area is the zone of orientation. If no mates are in the zone of repulsion, the individual aligns itself with neighbors in the zone of orientation region. The outermost area is the zone of attraction. This zone means that group-living individuals continually attempt to join a group and avoid being alone or on the periphery. This model reproduced the behavioral patterns of a fish group according to various parameter setups—swarm, torus, and parallel movement (Fig. 1b).

Regarding the collective behaviors of humans, the social force model introduced by Helbing and Molnar and its variants are well known to describe emergent dynamics in human crowds [9]. In this model, each pedestrian moves according to the equations of motion described by the sum of the driving force of a destination and the repulsive "social" force from other pedestrians and walls. This social force model allows us to simulate various crowd movements such as two pedestrian streams in opposite directions in a corridor and crowds exiting a metro station [10]. The control

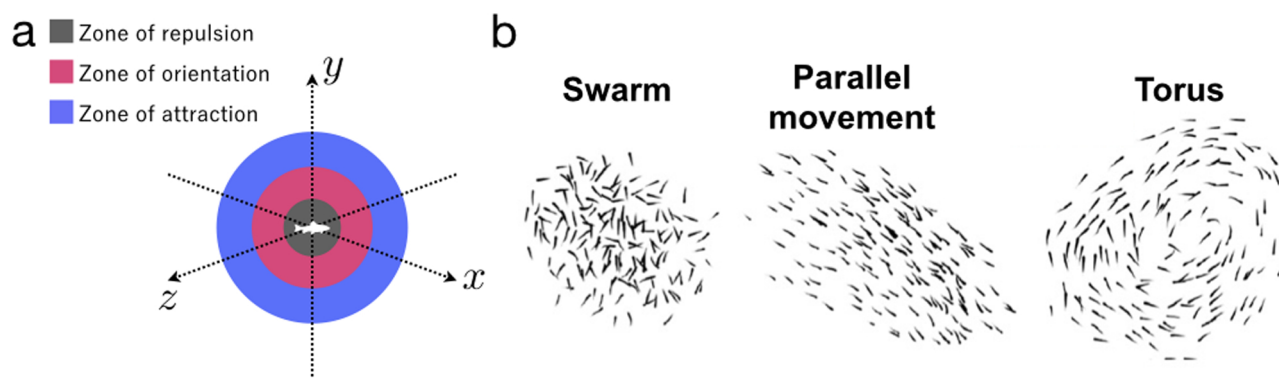


Figure 1 Representation of the zones around an individual centered at the origin and collective patterns in the model describing schooling fish. (a) The purple, magenta, and gray zones indicate zones of attraction, orientation, and repulsion, respectively. (b) Swarm, parallel movement, and torus patterns reproduced by a simulation based on the zone definition in (a).

of pedestrians' movement in a crowded environment and car traffic jams are important topics in traffic engineering and social psychology.

As described above, several models have been proposed for pattern formation by animal collectives. The widely accepted view is that local alignment interactions seem to have a significant influence on pattern formation, similar to molecules and cells. However, the difficulty of reproducing the collective behaviors of animals in the laboratory has hampered experimental verifications through changing environmental conditions and genetic perturbations for controlling the parameters of previously proposed mathematical models.

Collective Pattern Formations by the Nematode *C. elegans*

Although experimental studies pertaining to the physics of active matter are developing rapidly, experiments using animals are still challenging. In the News and Comment section in the journal *Nature*, Popkin noted that “Whereas the number of simulations was skyrocketing...the number of quantitative experiments was constant and very close to zero” [11]. Therefore, studies by researchers with a clear theoretical and experimental understanding of active matter are needed.

Some species of nematodes, particularly parasitic nematodes, have long been known to swarm in their habitats to survive desiccation for extended periods [12,13]. The free-living nematode *Caenorhabditis elegans* (Fig. 2a), a commonly used laboratory model animal [14], is genetically tractable and may offer an opportunity to experimentally examine the collective behaviors of animals under the control of a wide variety of parameters. However, it is difficult to prepare large numbers of worms on a solid surface in the standard cultivation protocol due to the decrease in its propagation speed as food becomes limited.

Interestingly, previous studies have proven that dog food agar medium, which contains sufficient nutrients, can be used as a food source to enable the propagation of a very large number of nematodes for a long time (>one month) [15]. We applied this method to *C. elegans* cultivation and found that large numbers of propagated worms collectively form a dynamical network pattern (Fig. 2b, c) [16]. This pattern comprises a large number of compartments surrounded by bundle-shaped worm aggregates and is dynamically remodeled over time by the repeated coalescence and division of compartments within approximately 100 s (Fig. 2d–g). This network pattern formation requires self-propelled activity, as no obvious self-organized pattern was observed for dead worms. The biological relevance of the emergence of this network pattern formation might be that swarming worms could keep more water than an isolated worm, which contributes to enhancement of desiccation tolerance.

Why do randomly moving worms form this network pattern without knowing their own locations in the entire structure? To elucidate the mechanism underlying this pattern formation, behavioral data of *C. elegans* were collected at the single-worm level. The sparsely isolated worms exhibited clockwise or anti-clockwise circular trajectories with gradual changes in the rotation rate (Fig. 3a–c). From the detailed trajectory analysis of 38 worms, the mean, the standard deviation, and the correlation time of the rotation rate were estimated to be $\omega_0=1.4\times 10^{-3}$ rad s^{-1} , $\sigma_\omega=0.155$ [rad/s], and $\tau=27$ [s], respectively. From $\tau\sigma_\omega=0.67\times 2\pi$ [rad], it is shown that worms tend to move halfway around with

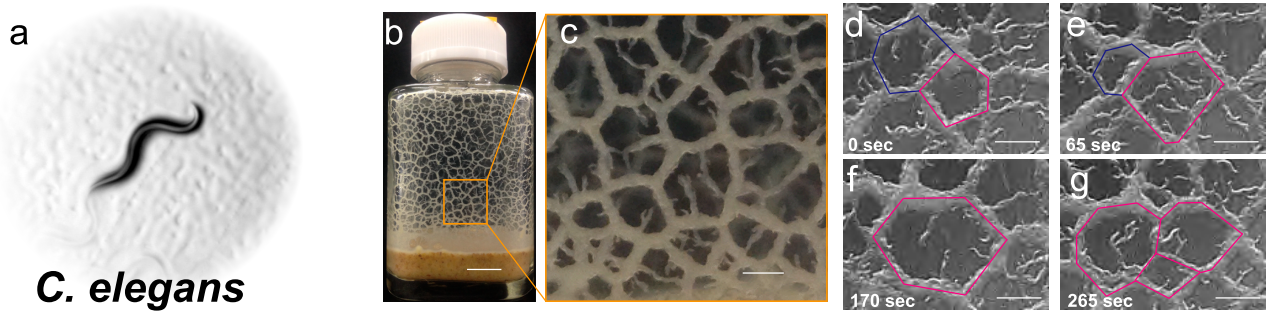


Figure 2 Individual *C. elegans* and its collective pattern formation. (a) Photo of an individual *C. elegans*. (b) Dynamical network formed by collective nematode behavior. Network pattern generated by a *C. elegans* population cultured in a glass bottle. The network was formed on the lateral surface of the glass bottle. Scale bar, 10 mm. (c) A magnified image of (b). Scale bar, 2 mm. (d–g) Remodeling of compartments. The shapes of the compartments were not fixed. Scale bar, 1 mm.

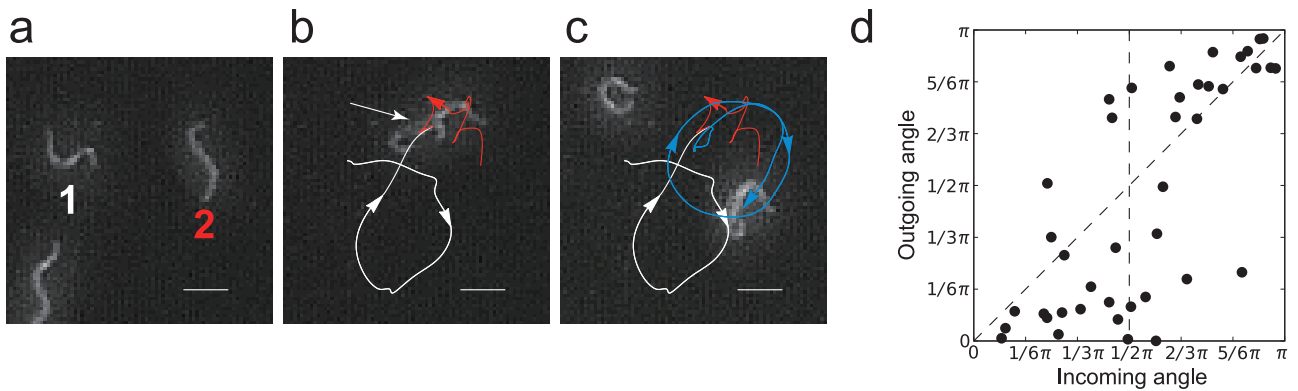


Figure 3 Nematic interactions between worms. (a–c) Representative trajectories of moving worms. The trajectories of two worms that moved separately for the first 105 s are indicated in white and red (a, b). Two worms collided at 105 s (b, arrow) and then moved together for at least 620 s (c, blue). Scale bar, 200 μm . (d) Incoming and outgoing angles of the collisions between worms. Forty-three collisions were analyzed.

an almost constant rotation rate.

We further analyzed the pair interactions of worms by observing that a large number of random collisions occurred between worms in close proximity. In 43 pair collision events, the outgoing angles were near 0 or π , irrespective of the value of the incoming angles (Fig. 3d). This result means that collisions induce the alignment or anti-alignment of worms. This type of alignment is nematic rather than polar order; in nematic order, it is known that both parallel and anti-parallel orientations of neighboring particles are observed like liquid crystals, whereas only either orientation is observed in polar order. Furthermore, the attachment of colliding worms was driven by the surface tension of the water around the worms, and this attractive force was strong enough to keep the worms in an aggregated state in opposition to the repulsive force exerted by their muscles. An increase in humidity strengthened the attraction.

These short-range nematic alignments and the smooth turning of *C. elegans* are reminiscent of microtubules driven by axonemal dynein *c* [17,18]. The hexagonal lattice of vortices formed by microtubules was reproduced by a simple agent-based model, in which the agents had a memory of the rotation rate. To confirm whether the collective pattern formation of *C. elegans* could be reproduced by the minimal model, we modified the model by adding two characteristics shown by the single-worm-level analysis: the attraction caused by surface tension (F_{ij}^a) and the repulsion due to the excluded volume of the worms (F_{ij}^r). The model is as follows:

$$\dot{\mathbf{r}}_i = \mathbf{e}_{\theta_i} + \sum_{i_j < r} \mathbf{F}_{ij}^r + \sum_{r < i_j < 1} \mathbf{F}_{ij}^a$$

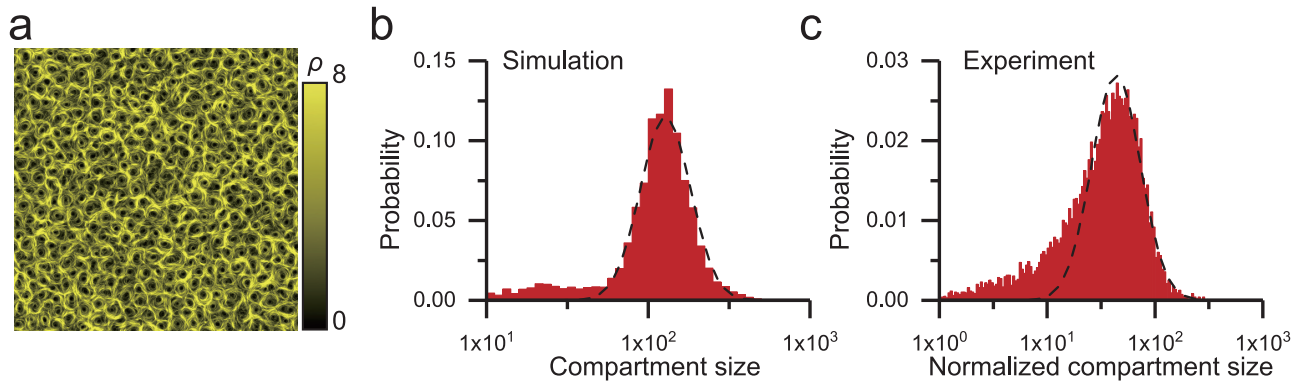


Figure 4 The dynamical network of *C. elegans* reproduced by the mathematical model and its characterizations. (a) Dynamical network of the model. The average number density was 4 per unit length square, $k^a=0.002$, in which k^a increase corresponds to humidity increase. The values of r^r and k^r were fixed to 0.2 and 10, respectively. The color shows the average local density over 10 time units. The images were constructed from the data after more than 1000 time units from random initial conditions. The area of simulation was 256 unit-length squares in (a) and 64 unit-length squares in (b, c). The boundary condition was periodic. (b, c) Distribution of the size of the compartments in the dynamical network of the model (b) and experiment (c). The dashed lines are the Gaussian curves fitted to the histograms. The size was normalized by the square of half the body length in (c). The shape of the distribution was a log-normal distribution in the large size range.

$$\dot{\theta}_i = \omega_i + \frac{1}{N_i} \sum_{r^r < r_{ij} < 1} \sin 2(\theta_j - \theta_i)$$

$$\dot{\omega}_i = -\frac{\omega_i - \omega_0}{\tau} + \sqrt{\frac{2}{\tau}} \sigma_\omega \xi_i$$

$$\mathbf{F}_{ij}^r = k^r (r_{ij} - r^r) \mathbf{e}_{ij}$$

$$\mathbf{F}_{ij}^a = \frac{k^a}{r_{ij}} \mathbf{e}_{ij}$$

\mathbf{r}_i , θ_i , and ω_i are the position, direction of motion, and rotation rate of particle i , respectively. \mathbf{e}_{θ_i} is the unit vector in the direction of θ_i , which indicates that isolated particles move with a speed of 1. The repulsive force \mathbf{F}_{ij}^r is exerted on particle i by particle j in a circle with a radius of r^r and a center at \mathbf{r}_j . The direction of \mathbf{F}_{ij}^r was the same as the unit vector from particle i to particle j , \mathbf{e}_{ij} . When $r^r < r_{ij} = |\mathbf{r}_i - \mathbf{r}_j| < 1$, an attractive force \mathbf{F}_{ij}^a is exerted by particle j . The inverse of the distance of the particles is chosen to represent the dependence of \mathbf{F}_{ij}^a on the distance from the neighbors, with reference to ref [19]. In the area where \mathbf{F}_{ij}^a applies, particle i aligns head-to-head or head-to-tail with particle j . The alignment interaction term is normalized by the number of interacting particles to avoid excessively strong interactions.

When the average ($\omega_0=0.0035$) and standard deviation ($\sigma_\omega=0.35$) of the rotation rate and the rotational correlation time ($\tau=10$) corresponding to the aforementioned estimated values are used, a collective network pattern is obtained in the simulation (Fig. 4a). To compare the dynamical networks of the model and the worms, we measured an area surrounded by thick bundles. In a large size range, the histogram of the logarithm of the compartment size has the form of a Gaussian distribution in both the experiment (Fig. 4b) and simulation (Fig. 4c), suggesting that the minimal model reproduces the collective network formation of the worms.

The *C. elegans* collective behavior system provides an opportunity for experimental verification of the above mathematical model by controlling a parameter of the model by changing the environmental conditions and genetic perturbations [20]. First, an analysis of density dependence showed that a large density was needed in both the experiment and simulation. Furthermore, the attraction force was controlled in both the experiment and simulation. In the experiment, we controlled the attraction force between the worms in a network formed on the lid of a plastic Petri plate by increasing the humidity inside the plate (Fig. 5a). As the humidity increased, the compartment sizes of the

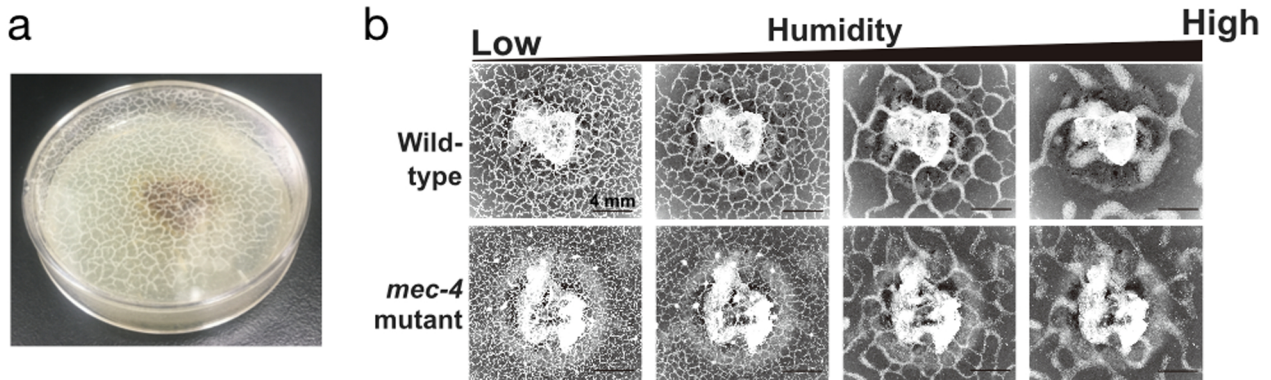


Figure 5 Dependence of the *C. elegans* network on the ambient humidity and movement curvature of isolated single worms. The *mec-4(e1611)* mutant (lower panel), which moves with a higher average curvature than the wild-type animal (upper panel), was used to vary the movement curvature. The average size of the compartments was 0.200 mm^2 at 0 min, 0.482 mm^2 at 5.7 min, and 8.878 mm^2 at 13.3 min in the upper row and was 0.090 mm^2 at 0 min, 0.241 mm^2 at 5.7 min, and 3.814 mm^2 at 13.3 min in the lower row. The object in the center is a lump of dog food on the agar, not on the lid. Scale bar, 4 mm.

network also increased (top four images in Fig. 5b). Eventually, the network collapsed, and many clusters of simple worm aggregates remained. In the case of the simulation, as the attraction force parameter k^a in the model became larger, the compartment sizes of the network also became larger, resulting in network collapse (top two images in Fig. 6). These similar experimental and simulation results verified the dependency of the model on the attraction force parameter.

The accumulated genetic resources and tools developed for *C. elegans* allowed us to control the parameters of the model. We therefore controlled the parameters ω_0 and σ_ω of the model in both the experiments and simulation. In the experiments, we observed the pattern formation of the *mec-4* mutant because this mutant moves along a circular trajectory with a higher curvature than that of the wild-type worm [21]. We found that the compartment sizes of the networks formed by the *mec-4* mutants were smaller than those of the wild-type worms (bottom four images in Fig. 5b). In the simulations, the particles traveling with higher ω_0 and σ_ω values formed smaller compartments, suggesting that the model also reproduces the experimental results (bottom four images in Fig. 6).

We further constructed an experimental system for optical manipulation of the network (Fig. 7a). This optogenetic system enables a transient perturbation to the worm aggregations by the optical activation of mechanosensory neurons. Blue light illumination has been known to competitively drive reversal, accelerate forward movements, and induce movement in halted worms [22]. Upon light illumination, the bundle started to collapse (Fig. 7b). Then, the bundles could recover the original shape as long as the duration of illumination was not long ($< 2 \text{ s}$). On the other hand, illumination with mild light intensity for a prolonged duration ($> 30 \text{ s}$) broke the bundle, and the worms formed different bundles after the light was turned off. In the simulations, to make the particles inactive, the terms e_{θ_i} in the first equation and ω_i in the second equation were multiplied by zero for 30% of the particles. The sudden change from the behavior of inactive particles to that of normal particles collapsed the network structure. Once the ratio of inactive particles returned

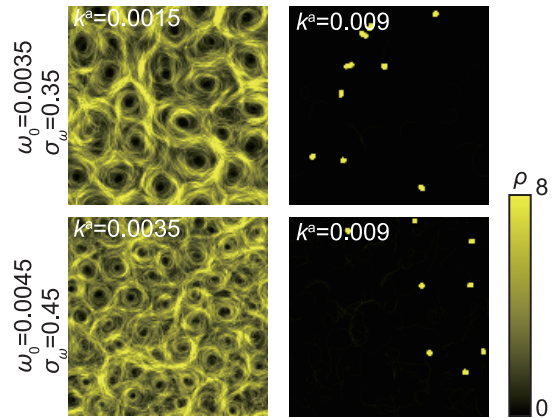


Figure 6 Collective motion dependence on k^a , ω_0 , and σ_ω . The average numerical density was 4 per unit-length square. In the upper row, $\omega_0=0.0035$ and $\sigma_\omega=0.35$, and in the lower row, $\omega_0=0.0045$ and $\sigma_\omega=0.45$. The average size of compartments larger than 30 unit-length squares was 133 unit-length squares for $k^a=0.0015$ and 57 unit-length squares for $k^a=0.0035$. Small spurious compartments inside the bundles were detected because point particles were used; therefore, the small size range was neglected in averaging the size.

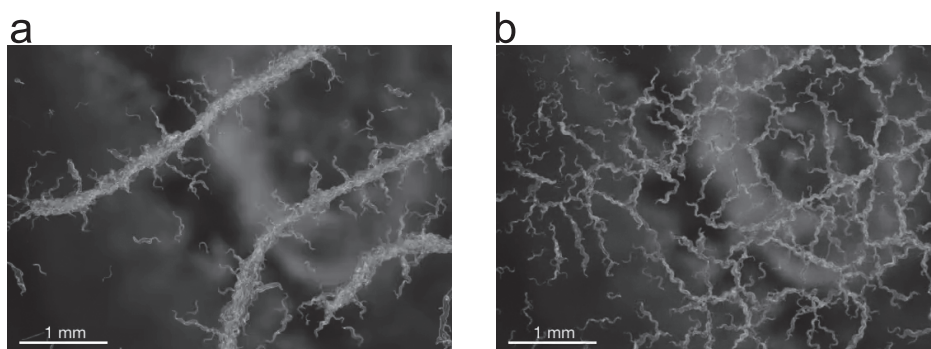


Figure 7 Optogenetic experiments with blue light exposure for approximately 30 s. Long-term light stimulation of worms expressing channel rhodopsin in the mechanosensory neurons was performed with mild light intensity (approximately $50 \mu\text{W mm}^{-2}$). Photos of worm collectives (a) before and (b) after light illumination. This activation initially caused the arborization and collapse of bundles.

to its initial value, the network reformed. Therefore, the results of the simulations were consistent with those of the optogenetic experiments. This optogenetic manipulation system will offer great opportunities for manipulating the collective patterns of *C. elegans*, which might provide clues to the development of algorithms for controlling self-propelled particles.

Taken together, the findings on collective pattern formation in *C. elegans* allowed for the experimental verification of the previously proposed model through parameter controls. This verification indicates that the local nematic alignment and smooth turning of worms underlie their collective network formation. In particular, experimental studies support the notion that local alignment interaction is generally one of the key factors in collective pattern formation by active matter.

Conclusion

Active matter physics began with the Vicsek's theoretical model, which shed light on the pattern formation by local alignment. This review introduced some real systems of pattern formation consisting of traveling animals. These animals showed diverse pattern formations that Vicsek model cannot deal with, e.g., the dynamical network structure by *C. elegans*. Each pattern can be explained by the complex theoretical model. Getting an agreement of a real system and model require to control the parameters in not only the model but animals. *C. elegans* is a good model animal that serves a lot of ways to control the inner parameters. Then, active matter physicists expect to be able to unify these models and develop the unified theoretical model that can reproduce a wide range of pattern formations which Vicsek model cannot.

However, there are still few experimental systems for controlling the parameters of mathematical models using animals. For such studies, the aforementioned Prof. Iain Couzin and his colleagues recently established a department of collective behaviour at the Max Planck Institute and the University of Konstanz. This department has attracted scientists from a wide range of disciplines, including not only biologists and physicists but also engineers studying the satellite tracking of animal behavior, data scientists with expertise in machine learning, and network scientists. They have focused on issues of the collective behavior and movement patterns of animals. In the domain of biology, ethologists have examined the collective behaviors of animals. The description based on observations has been the main tool in the research area. We anticipate more researchers who have interests in active matter physics will join the field of animal behavior in the future.

Collective pattern formation in animals can lead to the emergence of new functions that do not appear at the individual level. Since animals have a nervous system, they possess memory and learning abilities, and it is interesting to discover whether these neural functions are related to the physics of collective pattern formation. To date, it has been noted that collective pattern formation can improve the detection sensitivity of foreign organisms and prey and enhance the ability to make correct decisions [23–25]. *C. elegans* also has a nervous system consisting of 302 neurons and is known to have the ability to memorize the past cultivation temperature [26] and to move to a preferable humid place [27]. Therefore, it is interesting to examine the relationship between these neural functions and collective pattern formation in *C. elegans*.

In conclusion, active matter physics seeks to identify unified descriptions of collective pattern formations and needs more experimental verification of the proposed mathematical models through parameter controls. Additionally, the functional significance of each animal's collective pattern formation and its mechanical relevance to neural functions have been important open questions. Furthermore, considering the research field of 'soft robotics', one of whose purposes is the elaborate control of collectives of robots, we hope that an established algorithm can be applied in controlling the collective motions of soft robots.

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Conflict of Interest

All authors declare that they have no conflicts of interest.

Author Contributions

T.S., H.I., and K.H.N. wrote the manuscript and approved the final form.

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