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Collective Movement and Collective Information Acquisition With Signaling

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We consider a population of mobile agents able to make noisy observations of the environment and communicate their observation by production and comprehension of signals. Individuals try to align their movement direction with their neighbors. Besides, they try to collectively find and travel towards an environmental direction. We show that, when the fraction of informed individuals is small, by increasing the noise in communication, similarly to the Vicsek model, the model shows a discontinuous order-disorder transition with strong finite-size effects. In contrast, for a large fraction of informed individuals, it is possible to go from the ordered phase to the disordered phase without passing any phase transition. The ordered phase is composed of two phases separated by a discontinuous transition. Informed collective motion, in which the population collectively infers the correct environmental direction, occurs for a high fraction of informed individuals. When the fraction of informed individuals is low, the misinformed collective motion, where the population fails to find the environmental direction, becomes stable as well. Besides, we show that an amount of noise in the production of signals is more detrimental for the inference capability of the population and increases temporal fluctuations, the density fluctuations, and the probability of group fragmentation, compared to the same amount of noise in the comprehension.

Keywords: collective movement, collective information acquisition, flocking, communication, signaling, comprehension-production asymmetry

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1 INTRODUCTION

Many species, from bacteria [1–3] and cells [4, 5] to insects [6, 7], large animals [8–11] and humans [12] show collective motion, an intriguing phenomena in which individuals in a population move in ordered groups, presumably due to local interactions [13]. Such a collective motion is suggested to endow many advantages, such as avoiding predators [14], or enhancing the information acquisition capability of the population in noisy environments [15, 16]. Besides the biological examples, similar phenomena and similar challenges to address these phenomena can arise in the collective motion of artificial agents [17–20].

Although the collective motion has been subject to intense study [3, 13, 21–31], an important point not considered in the relevant literature, is that in many cases, the information individuals reach from others in the population is provided through communication by exchanging signals [5, 32–36]. Besides, in many cases, collectively moving populations try to find and travel to a preferred goal, such as a nutrient source or a migration root [8, 12, 16, 24]. They may do so, while only a fraction of individuals have information about the preferred root and try to lead the group [8, 12, 16, 24]. These considerations raise the important question that how collective motion in a population of individuals who exchange their social information by production and comprehension of signals is formed, and how the noise inherent in the communication system affects the collective information acquisition capability of the moving population?

To answer this question, we consider a population of mobile agents trying to collectively find and travel towards an environmental direction. Individuals communicate information about their movement by production and comprehension of signals. Individuals can be uninformed or informed. Uninformed individuals make decisions over their direction of motion based on the information they receive from their neighboring individuals. Informed individuals, on the other hand, can make noisy observations of an environmental direction and make decisions over their direction of motion by combining this information with the information they receive from the direction of motion of their neighboring individuals. We show that an ordered phase, where individuals move towards the same direction, emerges for a low level of noise in communication, and a disordered phase, where individuals travel to different directions, emerges for high levels of noise. The ordered phase is composed of two phases. *Informed collective motion*, in which the population collectively moves towards the environmental direction, emerges if the noise in communication is low enough and the fraction of informed individuals is high enough. As the fraction of informed individuals decreases (for small communication noise), the model shows a discontinuous phase transition to a *misinformed collective motion* phase in which the population moves collectively, but towards a direction other than the environmental direction. The fraction of informed individuals needed for the population for collectively travel to the environmental direction is larger for higher noise levels.

By increasing the noise in communication, for a low fraction of informed individuals, the model shows a discontinuous phase transition to the disordered phase in which individuals move towards random directions. As is the case in Vicsek-like models [21–23], the order-disorder transition suffers from strong finite-size effects that make its discontinuous nature apparent only in large system sizes. On the other hand, when the fraction of informed individuals is high, such that the system is well into the informed collective motion phase, by increasing the communication noise, contrary to the Viscek-like models, the population moves gradually from the ordered phase to the disordered phase without any phase transition. This shows how the amount of information about the environment contained in the population can change the nature of the order-disorder transition observed in Vicsek-like models.

Finally, we show an amount of noise in the production of signals is more detrimental for the collective information acquisition capability of the population compared to the same amount of noise in the comprehension of signals. This result is in keeping with a recently found comprehension-production asymmetry in a model of collective decision making, where individuals residing on a network try to form a consensus about an environment that can be found in a finite number of possible states [37]. While Ref. [42] provides theoretical evidence for a comprehension-production asymmetry in a case where a population of immobile individuals has access to a Potts variable as their belief variable, our finding here provides evidence for a similar asymmetry in the case of collective motion, where agents can move on space and need to make decisions over their direction of motion. Besides, we show that the production noise increases the density fluctuations and the probability of group fragmentation, and temporal fluctuations compared to comprehension noise. Thus, in this regard, by extending results found in Ref. [37], our findings suggest asymmetry between signal comprehension and production is a fundamental characteristic of biological communication systems.

2 THE MODEL

A schematic representation of the model is provided in **Figure 1**. We consider a population of N mobile agents, moving with constant speed v_0 on a $L \times L$ two-dimensional surface with periodic boundaries. There is a favorable direction of motion ε, called the environmental direction. As a direction in two dimensions can be repressed with an angel, ε is an angle in a two-dimensional surface. In this manuscript, we measure angles with respect to the x-axis. Individuals try to find and travel towards ε. Individuals decide about their direction of motion based on their personal observation (if available) and social information. To model observation, each individual is equipped with a noisy information channel R, and to communicate, individuals are equipped with a signal production G, and signal comprehension channel C, which they use for exchanging signals. Below we describe these channels in turn.

Observation. Personal information is acquired by noisy observation of the environmental direction. We assume observation is made through a noisy channel $R(r|\epsilon)$, such that the result of an observation in environment ε is in the interval $[r - dr/2, r + dr/2]$ with probability $R(r|\epsilon)dr$. We take $R(r|\epsilon)$ to be uniformly distributed in the interval $[\epsilon - \eta_R, \epsilon + \eta_R]$. η_R can be thought of as the noise level in observation. To implement this, we simply set the result of an observation made by an individual according to $r = \epsilon + \xi_R$, where ξ_R is a uniformly distributed noise term drawn from the interval $[-\eta_R, \eta_R]$. We assume only a fraction h of the individuals, called informed individuals, are able to observe the environment.

Communication. Social information is acquired by production and comprehension of signals. To communicate its direction of motion b, each individual produces a signal σ, using its signal production channel $G(\sigma|r = b)$. That is a signal in the interval $[\sigma - d\sigma/2, \sigma + d\sigma/2]$ is produced when an individual intends to signal direction b with probability $G(\sigma|r = b)d\sigma$. Here, $d\sigma$ is a differential element, and b and σ, referring to a direction in two dimensions, satisfy $b, \sigma \in [0, 2\pi)$. We note that both b and σ are angles in two dimensions. We take $G(\sigma|b)$ to be uniformly distributed in the interval $[b - \eta_G, b + \eta_G]$. η_G is a measure of noise in signal production. This can be implemented by setting $\sigma = b + \xi_G$, where ξ_G is a uniformly distributed noise term drawn from the interval $[-\eta_G, \eta_G]$.

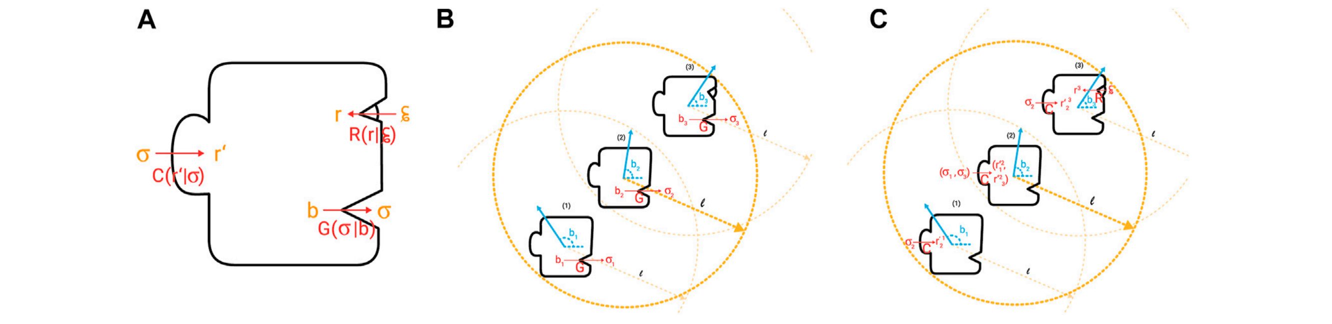

FIGURE 1 | Schematic representation of the model. **(A)**: Each agent is equipped with two information channels to communicate. Production channel $G(\sigma|b)$ is used for signal production, such that signal σ is produced for a direction b with probability $G(\sigma|b)$. In the same way, the Comprehension channel $C(r'|\sigma)$, is used for comprehension of the signals. In addition to these, a fraction q of the individuals are informed individuals, who are equipped with an observation channel $R(r|\epsilon)$. **(B)** and **(C)**: The dynamics of the model. Agents move on a two-dimensional space with constant speed v_0 and towards different directions b_i. In each time step, each agent i produces a signal σ_i based on its direction b_i to communicate its direction of motion **(B)**. The signal travels up to a distance l, such that all the agents up to a distance l from a transmitter receive its signal. Receivers comprehend signals using their comprehension channel **(C)**. Here, agents one and three receive a signal only from agent 2, but agent 2, having two individuals in its l-neighborhood, receive signals from both one and3. Besides, agent 3, who is an informed individual, makes an observation using its observation channel. Each agent i, makes a decision based on the information they receive from communication $\boldsymbol{r}'^i$, and the result of observation r^i (in the case of informed individuals), using the weighted averaging rule **Eq. 1**. Here, $\boldsymbol{r}'^1 = (r'^1_2)$, $\boldsymbol{r}'^2 = (r'^2_1, r'^2_3)$, $\boldsymbol{r}'^3 = (r'^3_2)$.

Signals are transmitted up to a distance l. That is all the individuals in a circle of radius l centered around the transmitter receive the signal. The receivers, comprehend a signal to refer to a direction of travel $r' \in [0, 2\pi)$, according to their comprehension channel $C(r'|\sigma)$. That is, signal σ is comprehended as referring to a direction in the interval $[r' - dr'/2, r' + dr'/2]$ with probability $C(r'|\sigma)dr'$. We take $C(r'|\sigma)$ to be uniformly distributed in the interval $[\sigma - \eta_C, \sigma + \eta_C]$. η_C is a measure of noise in signal comprehension. This can be implemented by setting $r' = \sigma + \xi_C$, where ξ_C is a uniformly distributed noise term drawn from the interval $[-\eta_C, \eta_C]$. In this way, we have taken the fact that signal production and comprehension are in general subject to noise [37–42] into account. This will allow us to study the effect of noise in communication on collective motion and collective information acquisition of the population.

Decision making. As a result of signals an individual receives, it reaches a set of representations $\boldsymbol{r}'$. We note that bold letters show a set, and thus, $\boldsymbol{r}'$ is a set. This set is composed of all the directions an individual receives by comprehending signals in its l-neighborhood. Besides, informed individuals make a personal observation, r. Each informed individual, α, makes a decision about its direction of motion b_α, based on its observation r_α and social information $\boldsymbol{r}'_\alpha$, by a weighted averaging rule. That is:

$$b_\alpha = \omega r_\alpha + (1 - \omega) \frac{\sum_{r' \in \boldsymbol{r}'_\alpha} r'}{|\boldsymbol{r}'_\alpha|}. \tag{1}$$

Here, $|\boldsymbol{r}'_\alpha|$ is the number of representations (directions) individual α has received, and ω is the self-confidence of individuals. Thus, $\frac{\sum_{r'_\alpha \in \boldsymbol{r}'_\alpha} r'}{|\boldsymbol{r}'_\alpha|}$ is the average direction of the motion of neighboring individuals of the individual α. ω lies between 0 and one and determines how individuals weigh their personal observation compared to their social information in decision making. We note that, here and in the following, to calculate summation over angles it is necessary to take periodicity into account. For this purpose, to average a set of angles $(\theta_1, .., \theta_n)$, we first decompose the angles into their x and y components, $(x_{\theta_1}, .., x_{\theta_n})$ and $(y_{\theta_1}, .., y_{\theta_n})$, and define the average angle based on its X and Y-components, $X = \sum_{i=1}^n x_{\theta_i}$ and $Y = \sum_{i=1}^n y_{\theta_i}$, as $\sum_{i=1}^n \theta_i / n = \arcsin\left(\frac{Y}{(X^2+Y^2)^{1/2}}\right)$. The same care is taken in calculating weighted average between two angles as in **Eq. 1**.

An uninformed individual, β, makes a decision about its direction of motion by simply averaging the social information it receives:

$$b_\beta = \frac{\sum_{r' \in \boldsymbol{r}'_\alpha} r'}{|\boldsymbol{r}'_\alpha|}. \tag{2}$$

As in the Vicsek model [21], the dynamic is synchronous. At each time step, informed individuals make an observation using $R(r|\epsilon)$, and all the individuals transmit a signal σ based on their direction of motion b using $G(\sigma|b)$. The signals are received by all the individuals up to a distance l of the transmitter. Receivers, comprehend the signals as referring to direction r' using $C(r'|\sigma)$. Finally, individuals make a decision about their direction of travel using their decision-making rule and update their direction accordingly. The simulations start with a random distribution of the position and direction of individuals. The base parameter values used in the simulations (unless otherwise stated) are $l = 1$, $L = 10$, $N = 100$, $v_0 = 0.1$, $\eta_R = 0.75$, $\omega = 0.25$. The density, ρ, is defined as $\rho = N/L^2$.

In the following we use two variables to distinguish different phases of the system. The absolute value of the normalized average velocity of the population is defined as $m = \left|\sum_{\alpha=1}^N \frac{\vec{v}_\alpha}{N v_0}\right|$. This variable is commonly used in the Viscek-like models to distinguish ordered from the disordered motion. As a second variable we define the angular deviation of the average population direction from the environmental direction as $\delta\theta = \sum_{\alpha=1}^N \frac{\theta_\alpha - \epsilon}{N}$. We will use this variable to distinguish informed collective motion

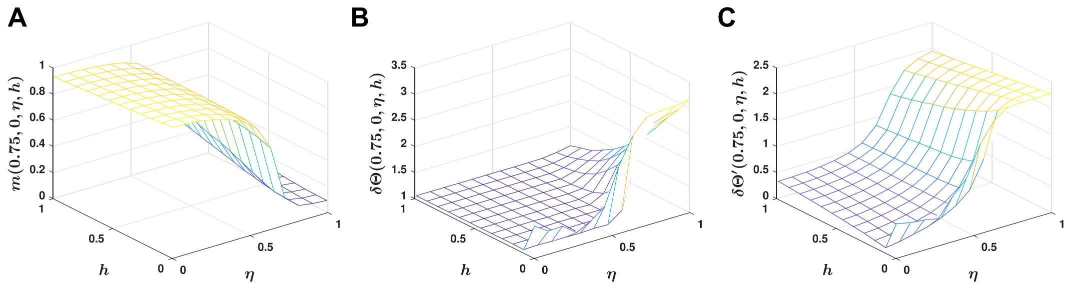

FIGURE 2 | Different phases of the system. From **(A)** to **(C)**, respectively, $m(0.75, 0, \eta, h)$, $\delta\Theta(0.75, 0, \eta, h)$, and $\delta\Theta'(0.75, 0, \eta, h)$ in the $\eta - h$ plane are plotted. For low communication noise η, collective motion emerges. As noise increases, the system settles in the disordered phase. The collective motion phase is composed of an *informed collective motion* phase, when the fraction of informed individuals h is large, and a *misinformed collective motion* phase, when h is small. Here, $L = 10$, $v_0 = 0.1$, $\omega = 0.25$, $\eta_R = 0.75$ and $\rho = 1$. The simulation is run for $T = 4000$ time steps, and an average over the last 2000 time steps and 24 runs is taken. ε taken equal to $\pi/3$.

from misinformed collective motion. Informed collective motion and misinformed collective motion can also be distinguished using average angular deviation of the direction of motion of individuals from the environmental direction, defined as $\delta\theta' = \sum_{\alpha=1}^{N} \frac{|\theta_\alpha - \epsilon|}{N}$. As we will see in the following $\delta\theta$ and $\delta\theta'$ lead to similar pictures. For a population with observation noise, production noise, and comprehension noise, equal respectively to, η_R, η_G and η_C, and with a fraction h of informed individuals, we show these variables by, $m(\eta_R, \eta_G, \eta_C, h)$, $\delta\theta(\eta_R, \eta_G, \eta_C, h)$, and $\delta\theta'(\eta_R, \eta_G, \eta_C, h)$.

3 RESULTS

3.1 Collective Motion Phases

We begin by studying the behavior of the system as a function of the noise level and the fraction of informed individuals. To do this, in **Figure 2A**, we plot the absolute value of the normalized average velocity of the population in the case that an amount of noise η is in the comprehension and production is noiseless, $m(0.75, 0, \eta, h)$. The case that the noise is in production is qualitatively similar. For low noise level, m is close to 1. This shows that collective motion emerges, and individuals travel in the same direction. By increasing the noise level, the model shows a transition to a disordered phase in which individuals fail to align their motion and travel in random directions. Thus, m takes a small value.

Interestingly, the ordered phase is composed of two distinct phases. To see this, in **Figure 2B**, we plot the angular deviation of the average direction of motion from the environmental direction, $\delta\theta(0.75, 0, \eta, h)$. In the ordered phase, for large h, the population possesses enough informed individuals to be able to collectively find the environmental direction. Consequently, $\delta\theta(0.75, 0, \eta, h)$ takes a value close to zero. We call this phase *informed collective motion* phase. On the other hand, for small h, misinformed collective motion, in which the population moves collectively in a wrong direction, becomes possible as well, and the system becomes bistable (see below). Consequently, $\delta\theta(0.75, 0, \eta_C, h)$ takes a large value. We call this phase *misinformed collective motion* phase.

In 2 (c), we plot average angular deviation of the direction of motion of individuals from the environmental direction $\delta\theta'(0.75, 0, \eta, h)$. This measure shows similar behavior to that of $\delta\Theta$ for small h. However, the two measures differ for large h and large noise levels. The reason is that, for large noise levels, ordered motion does not emerge. However, as long as h is large, individuals travel on average towards the environmental direction. Although, due to noise in observation, a large fluctuation around the environmental direction exists. For $\delta\Theta$, which gives the average direction of motion of the population, these fluctuations, being distributed symmetrically around ε cancel. On the other hand, in $\delta\Theta'$, which gives the average deviation of the individuals' direction of motion from the environmental direction, these fluctuations show up. Consequently, the two measures show different behavior for large h and large η.

3.2 Phase Transitions

The nature of the order-disorder transition in the Vicsek and related models has been the subject of intense research [13, 21–23]. It is well known that the order-disorder transition is discontinuous in many cases (depending on the parameter values and the way noise is implemented in the model) [13]. However, due to strong finite-size effects, the discontinuous nature of the transition shows up only in very large sizes [22]. Our model shows a similar phenomenology only for small h. However, the situation is different for large h. This can be seen in **Figure 3A** and **Figure 3B** for respectively, the production and comprehension noise, where the probability distribution of the order parameter for different noise levels and constant (large) h is plotted. Here, the distribution is derived from a single time series of the system of length $T = 50000$, after discarding the first 1,000 time steps. As can be seen, by increasing the noise level, the order parameter gradually decreases. This excludes a discontinuous transition. Besides, the distribution remains peaked at a single value and no broadening of the distribution resulting from large fluctuations characteristic of a continuous transition occurs [43]. This suggests it is possible to go from the informed collective motion phase to the disordered phase without passing any phase transition.

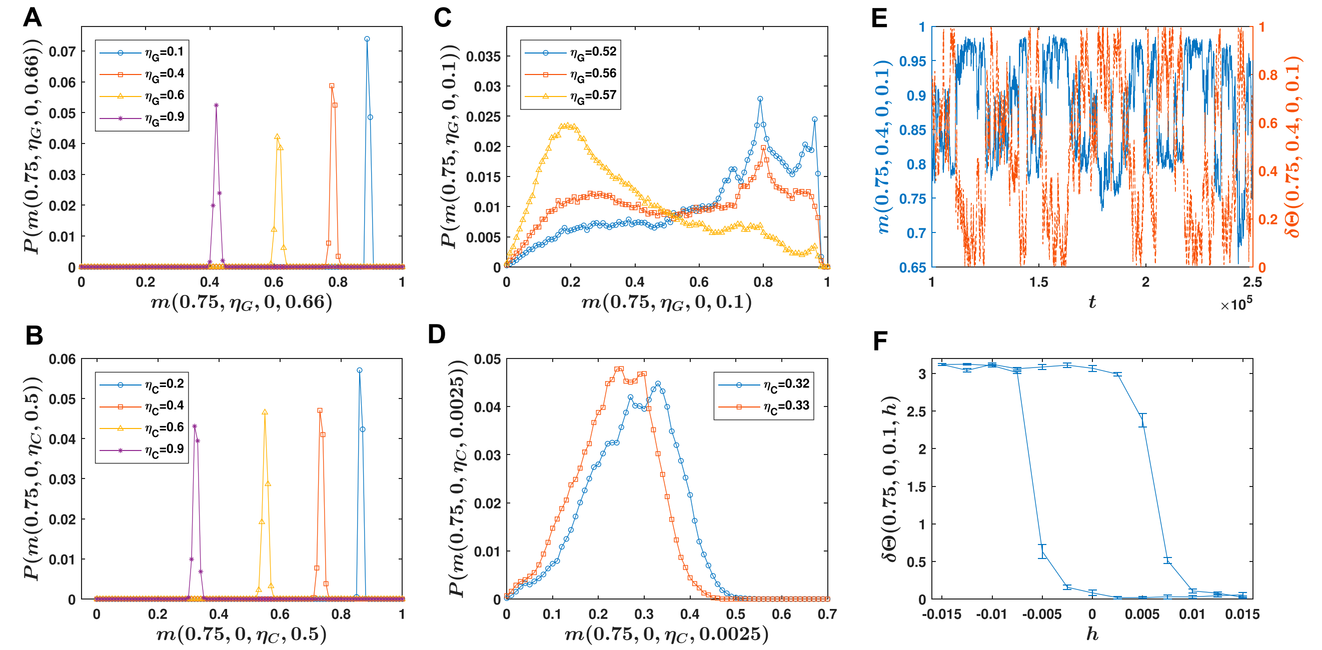

FIGURE 3 | Phase transitions. **(A)** and **(B)**: The probability distribution of the order parameter as a function of the order parameter for large fraction of informed individuals, h, is plotted. For large h, the order parameter decrease gradually as noise in communication increases, for both production **(A)** and comprehension **(B)** noise. Here $L = 300$, $v_0 = 0.6$, and $\rho = 0.1$. **(C)** and **(D)**: The probability distribution of the order parameter as a function of the order parameter for small fraction of informed individuals, h, is plotted. For small h, where misinformed collective motion is possible, the order-disorder transition is discontinuous for both production **(C)** and comprehension **(D)** noise. In **(C)** $L = 100$, $v_0 = 0.6$, and $\rho = 0.1$ and in (d) $L = 200$, $v_0 = 0.1$, and $\rho = 0.1$. (e): $m(0.75, 0.4, 0, 0.1)$ (blue solid lines) and $\delta\Theta(0.75, 0.4, 0, 0.1)$ (red dashed line) as a function of time. With production noise the population is decomposed into several dense independently moving groups. The evolution shows intermittency between the informed collective motion, where different groups move towards the environmental direction (high m low $\delta\Theta$) and misinformed collective motion where different groups head towards different directions (low m high $\delta\Theta$). Here, $L = 100$, $v_0 = 0.6$, and $\rho = 0.1$. **(F)**: Hysteresis loop shows the informed-misinformed collective motion transition is of first order. Here, $L = 20$, $v_0 = 0.1$, and $\rho = 1$. In all the simulations $\omega = 0.25$ and $\eta_R = 0.75$. ε taken equal to $\pi/2$.

In **Figure 3C** and **Figure 3D**, by plotting the distribution of the order parameter for fixed h and different noise levels, we study the discontinuous nature of the order-disorder transition for small h. In **Figure 3C** the case of production noise is considered. Here, $L = 100$, $v_0 = 0.6$, $\omega = 0.25$, $\eta_R = 0.75$ and the density $\rho = 0.1$. The distributions are derived from a single time series of the system of size $T = 1.2 \times 10^6$, after discarding the first 10^5 time steps. As can be seen, the distribution shows distinct peaks corresponding to the ordered and disordered phases. As the noise level increases, the peaks corresponding to the ordered phase decrease, while that corresponding to the disordered phase increases. This phenomenology is characteristic of a discontinuous transition [22, 44]. In **Figure 3D**, the case of comprehension noise is considered, where the same bi-modality which suggests a discontinuous transition is observed. Here, $L = 200$, $v_0 = 0.1$, $\omega = 0.25$, $\eta_R = 0.75$ and $\rho = 0.1$. We note that the finite-size effects are much stronger for comprehension noise compared to production noise, such that the discontinuous nature of the transition becomes apparent for larger population size in the former. Besides, for production noise, the finite-size effects are stronger for smaller velocities, while for comprehension noise, they are stronger for larger velocities. We have not been able to conclusively infer the discontinuous nature of the transition for large velocities when noise is in the comprehension.

Returning to **Figure 3C**, we see that for the case of production noise the distribution of the order parameter has two major peaks in the ordered phase. This happens only for small enough h, i.e., when the ordered phase is bistable, and the system can be found in both informed and misinformed collective motion phases. The two major peaks of m correspond to these two phases. This can be seen in **Figure 3E**, where m together with $\delta\Theta$, as a function of time, are plotted. As can be seen, m shows intermittency between two values corresponding to the two peaks of the ordered phase in **Figure 3C**. When m is very large, corresponding to the rightmost peak in **Figure 3C**, $\delta\Theta$ is very small, indicating that the average direction of motion coincides with the environmental direction. On the other hand, when m takes the smaller value, $\delta\Theta$ becomes large, indicating the average population direction differs from the environmental direction. The reason why the value of m in the misinformed collective motion phase is smaller than that in the informed collective motion phase is that when noise is in production (as is the case here), the probability of group fragmentation is high, such that in many times, the population is composed of different groups each collectively moving towards a different direction independently of others. Occasionally a group is decomposed into smaller groups, or different groups can merge to form a larger group (see the **Supplementary Video** for a visual manifestation). In the informed collective motion phase, all the groups head towards the

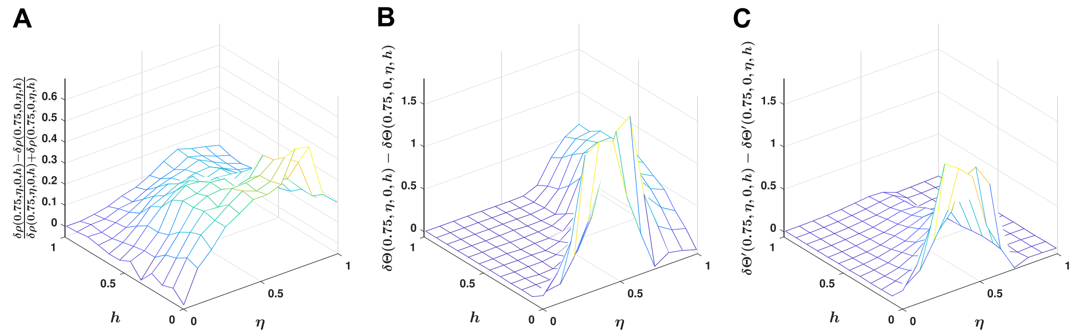

FIGURE 4 | Asymmetry between signal comprehension and production. Asymmetry in density fluctuations $\frac{\delta\rho(0.75,\eta,0,h)-\delta\rho(0.75,0,\eta,h)}{\delta\rho(0.75,\eta,0,h)+\delta\rho(0.75,0,\eta,h)}$ **(A)**, asymmetry in population average direction of motion from the environmental direction $\delta\Theta(0.75,\eta,0,h)-\delta\Theta(0.75,0,\eta,h)$, **(B)**, and asymmetry in average angular deviation of individuals from environmental direction $\delta\Theta'(0.75,\eta,0,h)-\delta\Theta'(0.75,0,\eta,h)$, **(C)**, in the $\eta-h$ plane are plotted. Production noise increases density fluctuations and deters the inference capability of the population. Here, $L=10$, $v_0=0.1$, $\omega=0.25$, $\eta_R=0.75$ and $\rho=1$. The simulation is run for $T=4000$ time steps, and an average over the last 2000 time steps and 24 runs is taken. ε taken equal to $\pi/3$.

environmental direction. Thus m takes the largest value. While in the misinformed phase, different groups can head in different directions. This decreases m as **Figure 3C** suggests.

For comprehension noise, m does not show a similar bi-modality that indicates intermittency between informed and misinformed collective motion. The reason is that, contrary to the production noise, with comprehension noise, the population rarely is decomposed into different dense groups with different directions of travel, and the strong fission-fusion dynamics observed for production noise is absent in the case of comprehension noise (see the **Supplementary Video**). We will shortly return to this difference between comprehension and production noise.

The bi-stability associated with a discontinuous transition results in hysteresis, which provides an alternative way to test the nature of the informed-misinformed phase transition [44]. This is shown in **Figure 3F**, where the hysteresis loop for the case of comprehension noise is shown. Production noise shows similar hysteresis effects. Here, we run a simulation beginning with $h=\frac{6}{400}$, which lies in the informed consensus phase. We gradually decrease h down to $h=-\frac{6}{400}$ (a negative h results from reversing the environmental direction) and then increase it back to the initial value. The resulting hysteresis loop results from the memory effects and indicates a discontinuous transition.

3.3 Noise in Signal Production Increases the Density Fluctuations, Temporal Fluctuations, and Degrades Collective Information Acquisition Capability

We have already seen that production noise increases the probability of group fragmentation and leads to a strong fission-fusion dynamic absent for the comprehension noise. This can be shown more quantitatively. For this purpose, we define the (relative) asymmetry in density fluctuations as $\frac{\delta\rho(\eta_R,\eta,0,h)-\delta\rho(\eta_R,0,\eta,h)}{\delta\rho(\eta_R,\eta,0,h)+\delta\rho(\eta_R,0,\eta,h)}$, where, the density fluctuation $\delta\rho$, is defined as the standard deviation of spatial density of the population. In a situation where the individuals are distributed uniformly in space, which is often the case for comprehension noise, this takes a small value. On the other hand, when the group is decomposed into independently traveling dense groups, as is often the case for the production noise, this takes a large value. Consequently, the asymmetry in density fluctuations is always positive, as can be seen in **Figure 4A**. This shows, compared to comprehension noise, the production noise increases the density fluctuations and the probability of group fragmentation.

There is another asymmetry between the comprehension and production of signals. This asymmetry arises in the collective information acquisition capability of the population. To see this, we define the asymmetry in the inference capability of the population as the difference between the angular deviation of the average population direction from the environmental direction when an amount of noise is in signal production compared to the case when the noise is in signal comprehension, $\delta\Theta(\eta_R,\eta,0,h)-\delta\Theta(\eta_R,0,\eta,h)$. To justify this choice, we note that in the case that production noise is more detrimental for the collective information acquisition of the population, it leads to a higher angular deviation compared to the case that the same amount of noise is in the comprehension. Consequently, this quantity becomes positive. The asymmetry in the inference capability of the population, $\delta\Theta(\eta_R,\eta,0,h)-\delta\Theta(\eta_R,0,\eta,h)$, for $\eta_R=0.75$, in the $\eta-h$ plane is plotted in **Figure 4B**.b. As can be seen, this quantity is always positive. This indicates that, compared to the same amount of error in the comprehension, an amount of error in production leads to a poor collective inference, and thus, a larger angular deviation from the environmental direction.

As a second measure of asymmetry in the inference capability of the population, we consider the difference between the average deviation of the individuals' direction of motion from the environmental direction, when an amount of noise is of production type compared to the case where the noise is of comprehension type $\delta\Theta(\eta_R,\eta,0,h)-\delta\Theta(\eta_R,0,\eta,h)$. This is plotted in **Figure 4C** in the $\eta-h$ plane. As can be, this

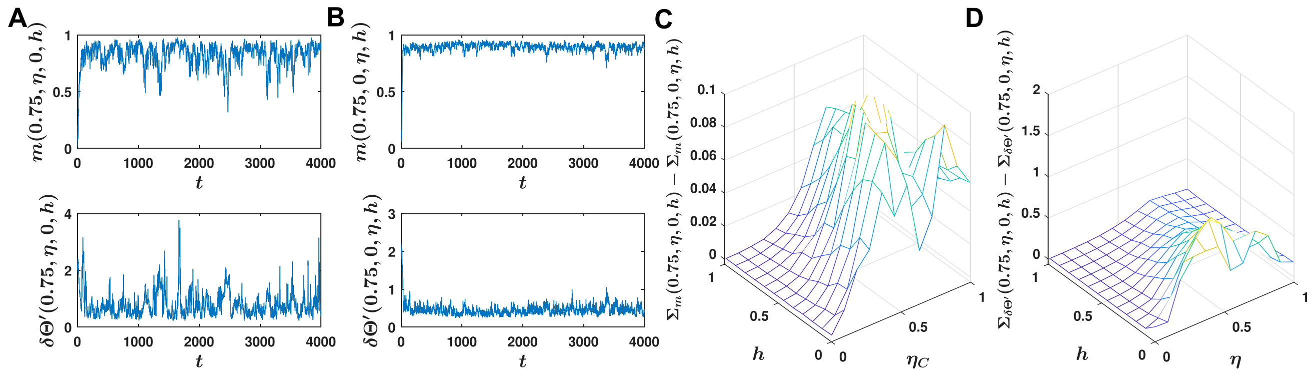

FIGURE 5 | Production noise increases temporal fluctuations. **(A)** and **(B)**: m **(top)** and $\delta\Theta'$ **(bottom)** for production noise **(A)** and comprehension noise (b) as a function of time. **(C)** and (d): Asymmetries in temporal fluctuations in m (c) and in $\delta\Theta'$ **(D)** in $\eta - h$ plane are plotted. Production noise increases temporal fluctuations. In **(A)** and **(B)** $\eta = 0.46$ and $h = 0.28$. In **(C)** and **(D)**, the simulations are run for $T = 4000$ time steps, and standard deviations are calculated based on the last 2000 time steps. An average over 24 runs is taken. Here, $L = 10$, $v_0 = 0.1$, $\omega = 0.25$, $\eta_R = 0.75$ and $\rho = 1$. ε is taken equal to $\pi/3$.

measure remains non-negative in the entire phase diagram. This suggests our results are robust with respect to the choice of the measure of asymmetry in collective information acquisition.

We note that the positivity of the measures of asymmetry in collective information acquisition results from two shifts in the phase transitions. First, production noise shifts the order-disorder transition to smaller noise levels. This shows production noise is more detrimental to the ordering of the population. Second, production noise shifts the monostable informed collective motion phase to larger values of h. This means with production noise, a larger fraction of informed individuals is necessary for the population to successfully infer the correct environmental direction. As shown in the **Supplementary Material**, both asymmetries in the density fluctuation and collective information acquisition are robust features of the model, valid for all the parameter values.

Finally, we note that noise in signal production also increases temporal fluctuations. To see this, in **Figures 5A,B**, we plot the normalized average velocity, m, and average angular deviation of the individuals from the environmental direction, $\delta\Theta'$, for, respectively, the cases where an amount of noise, η, is in signals production and signal comprehension. As can be seen, the same amount of noise is in signal production leads to higher temporal fluctuation in both m and $\delta\Theta'$. We note that the same picture holds for $\delta\Theta$. To see production noise leads to higher temporal fluctuation in the entire phase diagram, we calculate the standard deviation of the time series of m and $\delta\Theta'$, denoted respectively as Σ_m and $\Sigma_{\delta\Theta'}$. Subtracting the fluctuations in m when an amount of noise is in signal production from that when the same amount of noise is in signal comprehension, $\Sigma_m(0.75, \eta, 0, h) - \Sigma_m(0.75, 0, \eta, h)$, we arrive at a measure of asymmetry in temporal fluctuations when an amount of noise is of production type compared to a case where the same amount of noise is of comprehension type. Similarly, we define asymmetry in the temporal fluctuations of the average angular deviation of the direction of motion of individuals from the environmental direction, by first calculating the standard deviation of the time series of $\delta\Theta'(0.75, \eta, 0, h)$ and $\delta\Theta'(0.75, 0, \eta, h)$, denoted respectively as $\Sigma_{\delta\Theta}(0.75, \eta, 0, h)$ and $\Sigma_{\delta\Theta}(0.75, 0, \eta, h)$. Subtracting the first term from the second one, we arrive at a measure of asymmetry in the temporal fluctuation of the collective information acquisition capability when an amount of noise is of production type from that when the same amount of noise is of comprehension type. These two measures are plotted in **Figures 5C,D** in $\eta - h$ plane. As can be seen, both measures are non-negative in the entire $\eta - h$ plane. This shows that an amount of noise in signal production increases temporal fluctuations compared to the same amount of noise in signal comprehension.

4 DISCUSSION

We have introduced a model of collective movement in which individuals in a population try to collectively find and travel in a preferred direction. To do so, a fraction of individuals, informed individuals, can use private information provided by the noisy observation of the environment, and social information, provided by communication between individuals by exchanging signals. Others, uninformed individuals, can only use social information provided by communication. By analysis of the model, we showed that signal production noise not only decreases the inference capability of the population but also increases density fluctuations and the probability of group fragmentation. Besides, by identifying two different phases of collective motion (informed and misinformed) separated by a discontinuous transition, we have identified the mechanism by which a fraction of informed individuals able to only make noisy observations of the environment can lead the group. Finally, we have cast the much-studied order-disorder transition in Vicsek-like models into a broader context by showing that the nature of this transition depends on the amount of information about the environment available in the population, in other words, the fraction of informed individuals and the accuracy of their observation.

A similar comprehension-production asymmetry in the inference capability and similar phase transitions had been recently observed in a model of collective decision making in a population of immobile agents [37]. In this model, a population of agents who reside on a fixed communication network and live in an environment that can take one out of a finite number of possible states, try to collectively infer the environmental state [37, 45]. Similarly to the environmental state, in this model, individuals can take one out of a finite number of beliefs and are equipped with a production and a comprehension probability transition matrices to produce and comprehend a set of a finite number of signals. It is shown that such a model of collective decision making with signaling shows a similar comprehension-production asymmetry, according to which an amount of noise in signal production is more detrimental for the collective capability of the population to infer the environmental state, compared to the same amount of noise in signal production [37]. Our work here extends this study in different ways. In previous models of biological communication by production and comprehension of signals [37, 42, 45], or more generally, models of a proto-language [46–49], individuals try to communicate a finite number of states, which lack a distance measure. In other words, in that case, the state or belief variable is a categorical variable. In contrast, here, we have explored a case when individuals can form beliefs over a continuous space and produce and comprehend a continuous set of signals, which possesses a distance measure i.e., an ordinal variable. In this regard, in the limit of zero movement speed, our model reduces to a model of biological communication in a population of immobile agents, who can form beliefs and produce and comprehend signals over a continuous space of possible beliefs which possesses a distance measure. Second, by introducing movement into the model, we have been able to study collective movement in a communicating population. Our finding here shows that a similar asymmetry in the collective inference capability of biological populations is at work in this case as well. Furthermore, by showing that the production noise also increases temporal fluctuations, the density fluctuations, and the probability of group fragmentation, our analysis reveals new ways in which noise in signal production can be more detrimental than noise in the comprehension. This theoretical study thus strengthens the case for the existence of a comprehension production asymmetry and calls for empirical investigations to shed light on the question that whether such an asymmetry exists in biological populations.

Our study also provides insight on the question that how a fraction of informed individuals can lead the group on the move. Previous work has shown that enough fraction of informed individuals can indeed lead the collective movement of the group [24, 50]. Our study extends this line of research in two ways. First, our model introduces the more realistic possibility that informed individuals have only noisy and imperfect information of a preferred goal, such as a nutrient source. Second, our model studies how different types of noise in communication can affect the ability of the informed individuals to lead the group and the group's ability to find the preferred direction of motion. In this regard, our finding reveals that depending on the fraction of informed individuals and noise in observation and communication, a collectively moving population can be found in different ordered or disordered phases, separated by phase transitions. Besides, our analysis reveals that the fraction of informed individuals needed to successfully lead the group increases by increasing noise in communication. This can be interpreted to result from the fact that a higher noise level in communication disrupts the flow of information in the population, and thus, a higher fraction of informed individuals and a higher information flow from the environment to the population through informed individuals is necessary for finding the environmental direction.

Finally, we note that the similarity between the phenomenology of the two apparently different systems, that is, the model of collective movement introduced here and the model of collective decision making mentioned before [37, 45, 49], can be understood by noting that movement decision involves choosing a direction between a continuous set of possible directions. This observation highlights the similarity of collective movement with collective decision making, which can provide insights into the physics of collective movements such as the nature of the phase transitions observed in such models or the mechanisms by which such populations can optimize their information acquisition capabilities [45], which can be subject to future researches.

5 METHODS

5.1 The Simulations

All the simulations are started with a random distribution of positions and directions of motions. The parameter values used in the simulations differ for each figure and are given in the figure captions. To derive the hysteresis loop in **Figure 3.f**, we consider a population of size $N = 400$, with a fraction of informed individuals equal to $h = \frac{6}{400}$ (other parameter values are presented in the figure caption). Starting from random distribution of positions and directions of motion, the simulation is run for $T = 10000$ time steps, after which h is decreased by a value $\frac{1}{400}$, and the procedure is repeated until $h = -\frac{1}{400}$ is reached. As mentioned before, a negative h results from reversing the environmental direction (here $\epsilon = \pi/2$ is changed to $\epsilon = -\pi/2$). Then h is increased again in steps of $\delta h = \frac{1}{400}$, each time after performing the simulation for $T = 10000$ time steps, until h reaches its initial value of $h = \frac{6}{400}$. The angular deviation and its error bars for each value of h are calculated based on the last $T = 2000$ steps (after the system equilibrates) of the simulation for each h value.

5.2 Density Fluctuations

To calculate the density fluctuation, we first define the density field, $\rho(x, y)$ as the number of individuals per unit area. To define this quantity, we divide the space into square bins of linear size $l_0 = 1$. The density fluctuation is then defined as the standard deviation of this quantity $\delta\rho = [\langle[\rho(x,y) - \langle\rho(x,y)\rangle]^2\rangle]^{1/2}$. Where averages, $\langle . \rangle$, indicate an average over space.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

MS designed the research, SR contributed new reagents to the research, MS performed the research, MS wrote the paper. All the authors revised the manuscript.

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SUPPLEMENTARY MATERIAL

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