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Making noise: Emergent stochasticity in collective motion

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ABSTRACT

Individual-based models of self-propelled particles (SPPs) are a popular and promising approach to explain features of the collective motion of animal aggregations. Many models that capture some features of group motion have been suggested but a common framework has yet to emerge. Key to all of these models is the inclusion of "noise" or stochastic errors in the individual behaviour of the SPPs. Here, we present a fully stochastic SPP model in one dimension that demonstrates a new way of introducing noise into SPP models whilst preserving emergent behaviours of previous models such as coherent groups and spontaneous direction switching. This purely individual-to-individual, local model is related to previous models in the literature and can easily be extended to higher dimensions. Its coarse-grained behaviour qualitatively reproduces recently reported locust movement data. We suggest that our approach offers an alternative to current reasoning about model construction and has the potential to offer mechanistic explanations for emergent properties of animal groups in nature.

1. Introduction

Modelling the collective motion of animals remains a tantalising problem for scientists of a host of different disciplines. Both visually attractive and scientifically challenging, the concept remains useful because of its applicability to both animation (Reynolds, 1987) and control systems (Liu et al., 2003; Tanner et al., 2007) as well as the fundamental ecological understanding it brings (Sumpter, 2006). Many individual-based models have emerged in the last few decades that exploit advances in computational power to describe features seen in collective animal motion including group decision making (Couzin et al., 2005; Conradt and Roper, 2007), information flow (Sumpter et al., 2008) and response to predation (Wood and Ackland, 2007). This article focuses on the development of 1D models that seek to describe some of the simplest observed features in collective motion. Such models are now known collectively as 1D self-propelled particle (SPP) models.

In recent years the biological relevance of these models has been demonstrated as a result of the development of novel, approximately 1D, experimental systems. By constraining marching bands of locust nymphs to a specially constructed annular arena Buhl et al. (2006), and more recently Yates et al. (2009), have shown that these insects do indeed behave in a manner that is qualitatively comparable to 1D SPP models. In particular this work demonstrated that SPP models capture the spontaneous turns of the locust bands, where the entire group reverses its direction of motion without external input. It is believed that the origin of these observations lies in internal, or intrinsic, stochastic effects or "noise" which may or may not correspond to inaccuracy of the individual movements (e.g Buhl et al., 2006; Couzin et al., 2005).

Recently, the coarse-grained behaviour of 1D SPP models has been compared to locust movement in a more systematic way. From their study Yates et al. (2009) suggested that the insects respond to a decrease of group alignment by increasing the noise in their movement. The importance of this finding is that the addition of simple noise terms is not necessarily sufficient to describe and explain collective motion in animals. However, despite its great importance the origin of this stochasticity is far from clear.

In this research we focus exclusively on a simple 1D SPP model, and show how a combination of an asynchronous updating scheme and a novel implementation of particle interactions can produce a coarse-grained behaviour which reproduces findings by Yates et al. (2009) in locust movement data. The novelty of our research lies in the fact that all noise in the system emerges from the algorithmic implementation of our model rather than being added to the movement of particles. We therefore work towards explaining the origin of stochasticity in animal collective motion using our modelling approach.

First we give an overview of selected 1D SPP models described in previous work and the results that they give. Second we

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introduce our modelling approach. We then show that our model can produce stable groups and spontaneous direction switching and study the coarse-grained behaviour of our model via an equation-free approach using numerical simulations. We conclude by commenting on the potential of our modelling approach for integrating individual-level characteristics and describing motion in dimensions greater than one.

2. SPP models

The first 1D SPP model simulated particles with a local aligning behaviour on a continuous line with periodic boundary conditions (Czirók et al., 1999). In this model the individual and continuous velocities and positions are updated sequentially and simultaneously for all individuals. Particles tend to align with the average velocity of all particles within a fixed distance from them. This alignment is subject to a stochastic error in the form of uniformly distributed noise which is explicitly added to the particles' response to the average local velocity. An antisymmetric function G is applied to the preferred velocity of individuals and introduces both propulsion and friction to the system. The individual velocities $u_i(t)$ are therefore updated as

$$u_i(t+1) = G(\langle u(t) \rangle_i) + \xi_i, \tag{1}$$

where $\langle u \rangle_i$ is the local average velocity for particle i and ξ_i is a random variable with uniform probability distribution over a finite interval $[-\eta/2, \eta/2]$ (Czirók et al., 1999). The function $G(z)$ is given by

$$G(z) = \frac{1}{2}(z + \mathrm{sgn}(z)), \tag{2}$$

which sets the average of the individual speeds in the absence of particle interactions to magnitude 1 (Czirók et al., 1999). Analysis of the model has indicated that the average velocity of all particles undergoes a phase transition from an ordered state to a disordered state when the amplitude of the noise (η) or the particle density is varied (Czirók et al., 1999). Such phase transitions have also been observed for SPP models in two and three dimensions which suggests that some features of higher-dimensional systems are preserved in 1D models (Vicsek et al., 1995; Grégoire and Chaté, 2004; Chaté et al., 2008). For certain parameter values the model exhibits a fascinating direction switching behaviour—the average velocity of all particles in the system changes sign spontaneously and on a short time-scale compared to longer intervals of sustained high absolute values of the average velocity. Several variants of this scheme to introduce noise have been published (Chaté et al., 2008).

Another approach has been to implement SPP models on a 1D lattice with periodic boundary conditions over which particles move with velocities +1 or -1 (O'Loan and Evans, 1999; Raymond and Evans, 2006). In the first model of this type particles align with the velocity of the majority of particles around them with a given probability (O'Loan and Evans, 1999). The magnitude of this probability is the first source of noise in the model. The second source of noise and an important aspect of the model related to this research is its asynchronous updating scheme. In each step only the position and velocity of one, randomly chosen particle, are updated. Simulations of the model showed a phase transition from high to low average particle velocities for increasing sizes of the aligning probability. This is qualitatively similar to the phase transition exhibited by the model of Czirók et al. (1999).

This asynchronous 1D SPP lattice model was subsequently extended significantly by the inclusion of repulsion and attraction into the individual behaviour of the particles and the modification of the alignment behaviour (Raymond and Evans, 2006). The authors justified their implementation of the different behaviours by showing that they correspond qualitatively to taking random samples of neighbours (Raymond and Evans, 2006). This implementation results in two separate parameters which control the size of the error or noise in the reaction of individuals to their surrounding neighbours. One parameter controls the error arising from stochastically sampling the local group to determine the particle's preferred direction and the other parameter introduces uncorrelated errors (Raymond and Evans, 2006).

In summary, 1D SPP models show a wealth of emergent behaviours which have increasingly been compared to real collective animal motion. The way stochastic errors have been included into such models can roughly be divided into three categories. First, adding a random variable to the preferred direction of individuals (Czirók et al., 1999). Second, asynchronous and probabilistic updates (O'Loan and Evans, 1999; Raymond and Evans, 2006). Third, varying the probability and accuracy with which individuals execute their behavioural rules (O'Loan and Evans, 1999; Raymond and Evans, 2006). In the next section we will introduce our model which takes inspiration from the second and third approaches.

3. Modelling approach

In our model N individuals are represented by points on a continuous line and not by points on a lattice as in some of the models discussed above. The individuals, indexed i, are characterised by their position x_i and instantaneous velocity θ_i and they react to their "neighbours" which are less than a distance r_A away from them. We assume that each individual reacts with an identical stochastic rate to its surroundings. This defines an implicit master equation that in principle could be solved with a stochastic simulation algorithm (Gillespie, 1976). Instead, we exploit the identical rates and a simple particle picking approach to simulate the system (O'Loan and Evans, 1999). The algorithmic implementation of our model is as follows:

1. Choose individual i at random, where $i = 1, \ldots, N$ (equal probabilities, with replacement).
2. If i has neighbours, choose a neighbour k of i at random (equal probabilities for all individuals within less than r_A of i).
3. Update x_i and θ_i (based on the interaction between k and i or on previous θ_i if i has no neighbours).

N realisations of steps (1)–(3) constitute one update step of length Δt time-steps (see also Fig. 1). The duration of this update step corresponds to the reciprocal value of the algorithmic rate at which individuals update. Small values of Δt imply rapid updates, while large values of Δt imply slow updates. The output of the model is obtained by recording the positions and velocities of all individuals every $T = \lambda \Delta t$ time-steps, where $\lambda \geq 1$. This is analogous to how data of animal motion are obtained empirically where individual positions and orientations are sampled according to the frame rate of video recordings (Aoki, 1980; Buhl et al., 2006). In our simulations we keep T fixed and only vary Δt and therefore also λ.

Suppose individual i and a neighbour k of i have been chosen in the algorithm described above. The interaction between i and k depends on the distance d between the two individuals. If $d \leq r_O < r_A$, i attempts to align with k and has desired velocity,

$$\theta_i^{desired} = G(\theta_k). \tag{3}$$

If $r_O < d < r_A$ individual i gets attracted to k and has desired velocity,

$$\theta_i^{desired} = G\left(\mathrm{sgn}(x_k - x_i)\left(\frac{d - r_O}{r_A - r_O} + 1\right)\right), \tag{4}$$