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INTRODUCTION

Collective motion in biological systems

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One of the conspicuous features of life is the persistent motion of creatures. Organisms move for many reasons; examples range from foraging through migration to escaping from a predator. Importantly in most of the cases, these organisms move together making use of the various advantages of staying close to each other. Thus, the spectrum of biological systems exhibiting group motion is wide and includes cases such as bacteria colonies, migrating locusts, schools of fish, flocks of birds, groups of mammals (including people) and so on. Each system has its specific features and motion patterns, but, as statistical physics teaches us, if a system is made of many similar, interacting units, then some relevant, universal behaviours are expected to take place as well, in this way bridging the gap between the aforementioned examples and making the studies of collective motion a sub-field (within collective behaviour) on its own right. What are these ‘universal’ features? It turns out that the motion of, for example, fish schools or flocking birds share a lot in common. These groups of animals produce collective motion ranging from orderly through turbulent to random.

Since group motion frequently results in spectacular motion patterns and these patterns are of great interest, during the past decade collective motion has been the subject of a quickly growing number of investigations. An important reason for the interest in collective motion is the appearance of new, extremely efficient and informative techniques to collect data about the details of motions within a collective of organisms. The present issue of Focus Interface collects a recent series of representative studies written by widely respected authors to make this flourishing topic closer to the general readership as well as to

specialists interested in the particular subject of the contributions. This issue is a very helpful addition to recent reviews of the field [1–3].

Before venturing into a concise overview of the content of the present issue, it would be useful to summarize the basics of collective motion as the Editors see it.

Throughout this issue, the notion of collective motion or flocking is used as a synonym of any kind of coherent motion of individual units. However, the notion of coherent motion needs some further elaboration since, as it turns out, it can be manifested in a number of specific ways. In any case, coherent or ordered motion is assumed to be a counterpart of disordered, random motion. In the various experiments and models on flocking, it emerges through a kind of transition (from disorder to order) as a function of the relevant parameter(s) of the models. Phase transitions have been a major topic in statistical physics, providing very useful tools for the interpretation of the characteristic features and changes and of motion patterns.

The main assumption behind the collective motion approach is that systems possessing the following set of properties are expected to exhibit flocking phenomena. Thus, if a system is made of units

- that are rather similar;
- moving with a nearly constant absolute velocity and are capable of changing their direction (gaining momentum from interaction with the environment);
- interacting within a specific interaction range by changing their direction of motion, in a way involving an effective alignment; and
- which are subject to a noise of a varying magnitude,

collective motion is bound to occur in almost all of the possible cases.

Furthermore, the number of units involved in flocking typically ranges from a few dozen to a few thousand (in rare cases tens of thousands), in contrast

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One contribution to a Theme Issue ‘Collective motion in biological systems: experimental approaches joint with particle and continuum models’.

with the systems treated by statistical mechanics. However, a simple transition from a disordered to an ordered state can take place even in cases when the number of units is in an intermediate scale between few and huge numbers. Thus, most of the real-life observations and the experiments involve this so-called ‘mesoscopic scale’.

Yet another specific feature of flocking is the role of leaders or ‘informed individuals’ having *a priori* preferences (e.g. a bird that knows which way to fly to find food or nest location). In the past few years, a number of exciting studies have appeared addressing the question of leadership versus followership relations.

As for the evaluation of the data, we point out that units which can be reached through neighbouring units belong to the same cluster, where ‘neighbouring’ stands for a predefined proximity criterion (e.g. based on Euclidian or topological distance). Consequently, the behaviour of units in the same cluster is usually highly correlated. In general, correlation functions represent a very useful tool to characterize the various possible aspects of the dependence of the motion of a single unit on the behaviour of its neighbours.

Collective motion in biological systems has been approached from two different angles. On the one hand, a large body of work in theoretical biology and statistical physics has been devoted to bridge the gap between individual and collective behaviour. These efforts yield an important collection of models reviewed in [1–3] and also in the paper by Lopez *et al.* [4]. The rationale behind these works was to understand the general mechanisms by which local rules lead to large-scale patterns, with the assumption that these mechanisms are rather independent of the detailed nature of the systems’ components. One of the simplest models exhibiting collective motion was introduced by Vicsek *et al.* [5]. In this model, self-propelled particles move at constant speed and choose, at discrete time-steps their new heading to be the average of that of their neighbours located within unit distance. This alignment rule competes with perturbations controlled by a noise term. This noise in the communication among individuals drives a phase transition between an ordered phase of collective motion and a disordered phase.

In the present issue, Baglietto *et al.* [6] review recent findings characterizing the phase transition in the standard Vicsek model and discuss the onset of ordering in connection with XY spin models [7,8]. The Vicsek model has then been extended by Grégoire *et al.* [9], who added an attraction–repulsion term so as to prevent the dissolving of flocks in open space. One important issue that has recently been discussed in the light of experiments on bird flocks concerns the choice of influential neighbours. Ballerini *et al.* [10] have shown in starling flocks that individuals interact mostly with neighbours determined by topological rules and not by metric criteria as assumed in most models. In their paper, Camperi *et al.* [11] compare the stability of metric versus topological self-propelled particle models in three dimensions. They show that topological models are much more stable against noise and external perturbations than metric ones. Previous models of fish schools assumed the existence of zones

around a focal individual in which the response to neighbours depends on their relative position to that individual. When the neighbours are too close, a repulsion zone elicits an avoidance behaviour, whereas neighbours within the attraction zone elicit an approach response; moreover, the focal individual attempts to align itself with the neighbours when they are located in the alignment zone [12–14]. Couzin *et al.* [14] have shown that a change in the radius of orientation caused sudden transitions at the school level in terms of collective behaviours (swarming, milling and schooling) characterized by different levels of polarization and structure. In their paper, Hemelrijk & Hildenbrandt [15] extend these zone models to account for speed variability and they review how these models have contributed to our understanding of the shape and the internal structure of travelling groups of fish and birds. In most existing zone models, individuals respond to instantaneous positions of neighbours. In his paper, Grunbaum [16] investigates the introduction of spatial memory effects on the distribution of individuals at the group level. We conclude this first line of research with a paper by Romanczuk & Schimansky-Geier [17] that investigates the onset of collective motion in a self-propelled particles model with only attractive and repulsive interactions. In their model, individuals react to their neighbours by moving away from others approaching them from behind and/or increasing their velocity towards those who are moving away in front of them. They show that for some parameter regime, large-scale collective motion emerges without any explicit velocity-alignment mechanism.

While all these models improved our understanding of collective motion, the proximate causes of these phenomena in most biological systems in which they have been described are still poorly understood. However, with the recent progress in video and GPS-tracking technologies, high-precision datasets on moving animal groups, from bacteria to pedestrians, are now available, thus discovering the way to a fine-scale analysis of individual behaviour [18–21]. An increasing number of works is opening a different and complementary approach to collective motion focusing on how individuals make behavioural choices when interacting with others or the role of physical interactions between each others when they occur [22–26]. Recent studies have explored new ways to infer interaction rules from experimental data such as the force mapping technique [27,28]. This is a powerful tool to investigate the behavioural responses of a focal individual as a function of the configuration of neighbouring individuals that also provides important information to build reliable models of collective motion. In their paper, Buhl *et al.* [29] compare the spatial distribution of locusts recorded in the field while they march collectively to the results of computer simulation models and use this information to infer the individuals’ interaction rules underlying locust mass movements. The paper by Sumpter *et al.* [30] reviews three modelling methodologies (theory-driven, data-driven and model selection) and discusses to what extent they can be used to describe plausible local interactions between individuals. A different bottom-up methodology was

recently introduced by Gautrais *et al.* [31] to build models for animal group motion from data gathered at the individual scale. This strategy is based on a step-by-step quantification of the spontaneous motion of a single individual and of the combined effects of local interactions with neighbours and obstacles on individuals' motion. At each step, each ingredient of the model is checked against experimental data. The parameters are determined using a dedicated inversion procedure and the numerical values of these parameters are kept unchanged in the following steps, yielding, in the end, a model without any free parameters. In their paper, Lopez *et al.* [4] show that this modelling framework can be used to emphasize a set of major and unknown behavioural components that are likely to play a crucial role in schooling. The characterization of interaction rules and behavioural mechanisms underlying collective motion also benefits from the study of mutants or transgenic individuals in which all the behavioural components can be selectively altered and their role in the coordination precisely evaluated. This approach is discussed by Starruß *et al.* [32]. In their paper, they report the spatial organization in three strains of *Myxobacteria* characterized by different motility systems and show in these microorganisms that cell density and the rod shape of the cells play an essential role in achieving collective motion. We conclude the present issue with a recently discovered phenomenon in a swarm of social bacteria, which is their ability to collectively transport biological cargo over long distances. In their paper, Shklarsh *et al.* [33] develop a new class of computer models to study cargo-carrying bacteria-inspired agents. They investigate how the features of agent-cargo bonds influence the collective motion and the transport of the cargo and they compare the simulation results to the experiments.

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