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Physical constraints in biological collective behaviour

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Abstract

Many biological systems require the coordinated operation of a large number of agents linked together by complex interactions in order to achieve their function reliably. Because of the complex relationship between individual laws and system-level behaviour, theory is needed to assess which emergent phenomena result from fine-tuning or adaptation, and which follow from logical or physical constraints set by the system's design. Here we illustrate this crucial role of theory through recent examples from the collective motion of bird flocks. In some cases abstract theoretical laws explain the emergence of some apparently surprising traits, without the need to invoke new assumptions. Conversely, quantitative theoretical predictions sometimes show that general mathematical and physical laws are incompatible with otherwise mundane observations, forcing us to reconsider our assumptions and leading us to discover new principles.

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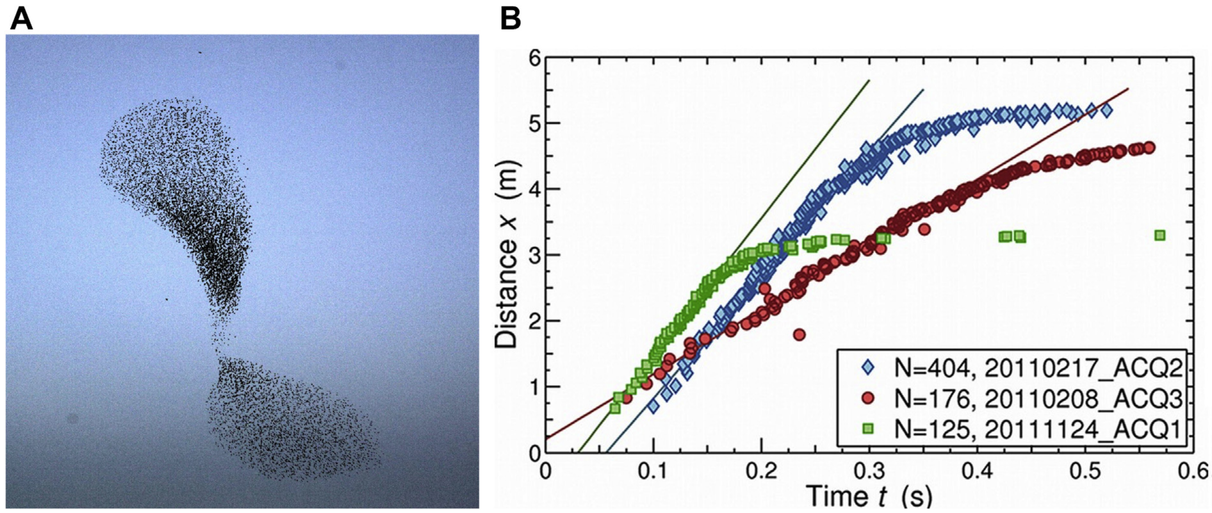
Living systems often display a finely orchestrated behaviour linking their many parts: the collective rearrangement of epithelial cells during wound healing [1], the coherent motion of large groups of birds when they come down to roost [2], the orchestrated action of our immune system to protect us against pathogens, or the complex programs of gene regulation and cell differentiation during development. The precision of cellular responses [3,4], the speed of information transmission, and the reproducibility of evolutionary paths on short timescales [5], all suggest a precise tuning of biological parameters to achieve these feats. Often, the collective nature of the biological function acts on effective parameters controlling the emergent behaviour of the system, rather than on individual biological parameters. It has been argued that this fine-tuning can lead the system into particular regions of the parameter space, similar to critical points or critical surfaces delineating phases in physics [6,7]. Yet sometimes a more careful examination of the phenomenon reveals that what we observe in nature is actually dictated by physical or logical constraints, rather than by resulting from making a particular set of adaptive choices. In certain cases, this realization comes directly from experimental facts: for instance, the reproducibility of protein evolution is explained by the fact that most evolutionary paths are forbidden as they include deleterious, often non-viable mutations [8,9]. In other cases, raw observations are not enough to reveal the underlying rules constraining the system, or to immediately deduce the range of behaviours implied by these constraints. Theory is then needed to decide whether the peculiar or intriguing biological phenomena we are confronted with is really the product of some biological optimization mechanism, or rather the consequence of general mathematical and physical principles. Conversely, theory may reveal that seemingly mundane observations actually put strong constraints on the class of models describing the phenomenon.

Collective behaviour holds many such examples of interesting dialogue between theory and observations, because of the complex relationship between the individual and collective levels, which require a thorough theoretical analysis. The concerted motion of large groups of animals, such as bird flocks (Figure 1A), fish schools and mammal herds [10–12], provides a visually stunning example of collective behaviour. Less visible, but resulting from similar forces and equally fascinating, is the rearrangement of cells in tissues that are driven to flow together [13–15]. In all of these cases, collective behaviour is *self-organized*, namely the group achieves its tasks by means of distributed control laws, without any leader. How these distributed laws result in complex collective motion is a rich field of investigation where theory has played an important role. Here we report and discuss some instructive cases from these systems in which theory helps us gauge the relative role of

Figure 1



A. A snapshot of a flock of European starlings (*Sturnus vulgaris*). **B.** Propagation law for starling flocks. During collective turns in flocks, a first individual starts turning and, one by one, all the others follow. The figure displays the distance from the initiator of the turning front as a function of time. Different colors correspond to different turning flocks. In all cases a linear regime is clearly identifiable where directional information propagates in a wave-like manner (black lines are linear fits). For each event, the speed of propagation is given by the slope of the curve in the linear regime. From Ref. [36].

biological, mathematical and physical principles in shaping the phenomenon at hand.

Phenomenological description and universality

Deriving collective behaviour from the dynamics of the individual units is, in general, a difficult task. This statement is especially true in the case of biological systems, where such units are living entities and interactions between them involve complex mechanical, chemical or cognitive processes. It is not *a priori* clear what is the level of detail needed in the description of individuals and in the way they coordinate with each other. Some important inspiration in this respect come from the statistical physics of condensed matter originally developed to describe non-animate materials, where collective phenomena have been studied to describe phenomena such as magnetization [16]. In this case advanced conceptual theoretical approaches, such as the Renormalization Group [17], and experimental findings show that in fact most of the microscopic details do not matter. Only a few fundamental features are relevant to describe the large scale behaviour: the nature of collective order, the dimensionality, symmetry properties and conservation laws. As a consequence many different physical systems exhibit the same large scale properties, i.e. there exists universal ‘classes’ of collective behaviour; and simple effective models can be formulated to describe the behaviour of an entire class.

This perspective has inspired the whole field of living active matter [18–20] and physics-based modelling of biological collectives [12,21]. Many results on active systems at the micro-scale (cell tissues, bacterial colonies, microtubules networks) support the value of this approach. It turns out that the same theory can equally well predict the large scale behaviour of living assemblies and inanimate active matter, which share the same fundamental properties [18–20]. Recent findings on bird flocks [22] and insect swarms [23] indicate that these animal groups satisfy static and dynamic scaling laws: the large scale properties of the system under different conditions (number of individuals, density, external parameters), once appropriately rescaled, can be described by a single master function. Laws of this kind are the phenomenological underpinning of universality in condensed matter materials, and suggest that the effective theoretical framework used for inanimate systems is also justified when looking at coherent animal groups at large scales. Clearly, at smaller scales, the specific nature of different groups matters, just as the type of chemical alloy used is important for a material.

The possibility of describing complex systems in terms of simple minimal models enormously helps their understanding. Such models are typically specified in terms of an interaction network, and very few control parameters. Comparison with classes of models sharing similar features can tell us whether the described collective behaviour is generic, i.e. we can expect it on the basis of the mechanistic structure of the dynamics, or rather requires some fine tuning of the parameters and/or some additional gauging principle.

Scale-free correlations

Bird flocks represent an archetypical example of collective behaviour in animal groups. The quantity that