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
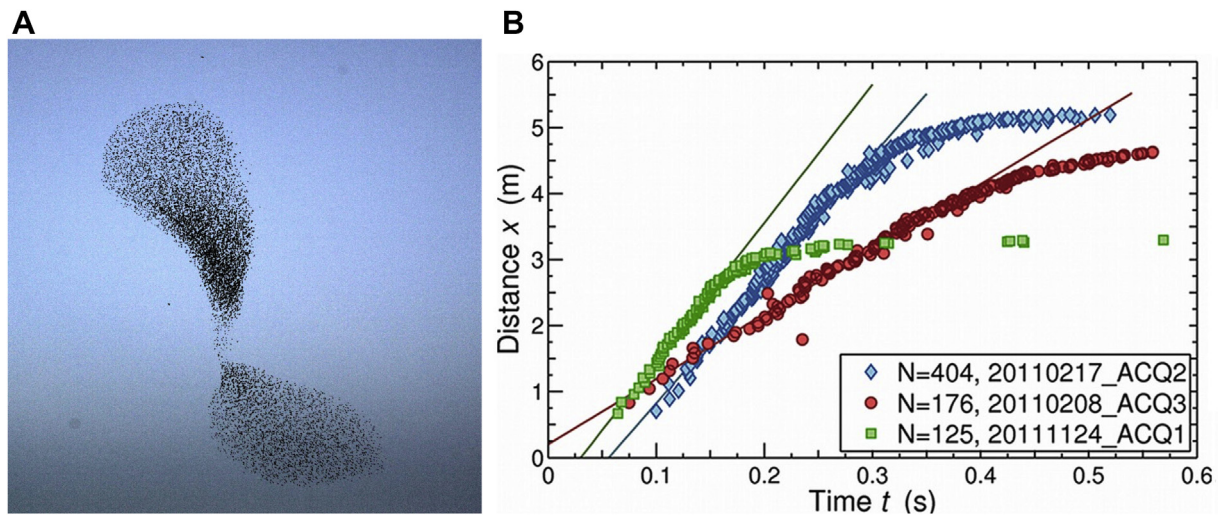
A. A snapshot of a flock of European starlings (*Sturnus vulgaris*). **B.** Propagation law for starling flocks. During collective turns in flocks, a first individual starts turning and, one by one, all the others follow. The figure displays the distance from the initiator of the turning front as a function 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

best characterizes the degree of collective behaviour in an interacting system is the correlation function between the fluctuations of the relevant degrees of freedom [21,24]. In the case of animal groups on the move, this amounts to measure the correlation between the changes in velocity of different individuals separated by a certain distance. In bird flocks, whose linear dimension ranges from ∼10m up to ∼100m, the spatial span of this correlation has been found to be as large as the group itself; more precisely, one says that the correlation length scales linearly with the flock size [22]. This kind of scaling is a signature of the lack of a characteristic length scale of the problem — there is no natural scale for the birds to communicate over. A similar situation arises in natural swarms of insects, where again experiments find that the scale of correlation of the groups grows with its size [25]. The scale-free nature of self-organized groups is very important, as it implies that the behavioural changes of different individuals can influence each other (statistically) over very large scales. It is therefore interesting to understand how generic this feature is, and whether it tells us something unexpected about the systems under investigation.

Collective motion can be described theoretically in terms of interacting agents that locally decide their direction of motion based on that of their local neighbours [26,27]. The dynamical rules for the movement of the individual agent are of the kind:

$$\mathbf{v}_i(t+1) = \sum_j J_{ij}\mathbf{v}_j(t) + \mathbf{f}_{cn} + \boldsymbol{\xi}_i(t), \qquad (1)$$

$$\mathbf{r}_i(t+1) = \mathbf{r}_i(t) + \mathbf{v}_i(t), \qquad (2)$$

where $\mathbf{r}_i(t)$ and $\mathbf{v}_i(t)$ are the position and velocity of agent i. The first term at the r.h.s. of Eq. (1) is a social force aligning the agent's flight direction to a weighted average of the neighbours' velocities (including agent i), where J_{ij} specifies the interaction network and is different from zero only for neighbours in a well defined interaction range. The function $\mathbf{f}_{cn}$ is a constraint fixing the speed $|\mathbf{v}_i|$ to its cruising value, and mathematically implements the active nature of the constituents, i.e. the fact that agents have an internal source of energy that they convert into motion (as opposed to 'passive' particles in physics). Finally, $\boldsymbol{\xi}_i$ is a noise term translating errors in the alignment process.

Several variations of this model have been investigated in the literature [28−32], but all of them share some very general features: the system is endowed with a continuous symmetry (a rotation of all velocities leaves the equations invariant), interactions are local and based on mutual alignment, speed is constrained. When the noise in the system is low enough, this kind of interaction gives rise to a global net motion of the group, as is observed for flocks. However, if no factors favour one direction over another, i.e. if the system is *symmetric*, the flock has the freedom to arbitrarily choose a specific flight direction out of all the equally probable ones. This arbitrary global choice is known theoretically as the spontaneous breaking of a continuous symmetry (the rotational one, in this case), a very general phenomenon that is ripe with deep mathematical consequences, the most conspicuous of which being the fact that the system develops long-range correlations. To grasp the generality of this mechanism, known as the Goldstone theorem [33], it is worth mentioning that it holds for ferromagnetic systems in condensed matter [34], and that the exact same mathematics is at the core of the existence of the celebrated Higgs boson.

Hence, scale-free correlations of the flight orientations in a flock do *not* rely on any biological fine-tuning, no matter how relevant these correlations are to achieve global coordination; in fact, we should have expected them from the symmetry properties of the dynamical equations.

On the other hand, the modulus of the velocity, i.e. speed, is not a symmetry-broken degree of freedom: there is no arbitrariness for a bird in choosing its own speed, as this is fixed by sharp physiological and aerodynamic factors (encoded is the constraint $\mathbf{f}_{cn}$ in Eq. (1)). For this reason, from a theoretical standpoint we would expect the modulus of the velocity to be correlated only over short distances. Yet, experiments show that speed fluctuations too are correlated over long distances in flocks [22]. To explain this phenomenon, the value of some effective parameter must sit near a particular value, called a critical point by analogy with phase transitions in physics [35] and reaching that particular place in parameter space *does* requires a biological tuning principle. Insect swarms do not globally move: no arbitrary direction of motion of the group has been selected, and therefore math does not require scale-free modes to emerge. Hence, again one needs a *bona fide* biological principle to explain the scale-free correlations empirically observed in swarms [25]. These examples emphasize that, although scale-free correlation may seem equally striking in the distinct contexts of orientation and speed fluctuations, in flocks and swarms, a closer look under the lens of theory tells us that it is far more demanding in some cases than in others. This distinction, which has clear and important biological implications, comes in this case from modelling and theoretical physics.

Information transfer and memory
Up to now we have seen how theory sometimes modifies our preliminary expectations, and therefore stops our search for new biological principles, by providing general mathematical and physical laws able to explain the salient traits of the phenomenon at hand. Some other

times, the opposite happens: our intuition suggests that what we observe is not particularly noteworthy, hence inviting us to deal with more exciting phenomena, while a more careful theoretical analysis indicates that in fact we should investigate further what we have found. An instructive example is that of information transfer across bird flocks. Experiments [36] show that the information about a collective change of direction propagates across a flock in a "ballistic" manner, i.e. linearly in time, just like an ordinary wave (Figure 1B). This may seem a rather mundane observation, as waves are part of our ordinary experience both in the physical and in the biological world [37−39]. A sub-linear propagation law would seem inadequate to transfer information across large biological groups. In this case simulations show that as the propagation front crosses the flock, it divides it into two parts that fly in different directions, risking splitting the group [40]. A swift mechanism of information propagation thus seems paramount to keeping the group's cohesion.

Theory tells a different story. The traditional description of interacting agents (see Eqs. (1) and (2)), which we invoked to make sense of long-range correlations in flocks, fails to predict the wave-like propagation of information [54]. Our common physical experience with waves is light and sound. In light, what propagates are perturbations of the electric and magnetic fields. In sound, it is fluctuations of the density and displacement speed of the medium. In both cases propagation is mathematically ruled by D'Alembert's wave equation, a second order partial differential equation in both time and space, which ensures linear propagation. The equation's structure results from the reciprocal coupling of two conjugate quantities: the electric and magnetic fields in light; the density and velocity fields in sound. In general, identifying conjugate variables, such as time and frequency in acoustics, that are coupled through a mathematical transformation, often helps to describe signal propagation.

However, what propagates in a flock is the direction of motion of the birds, which is not coupled to an experimentally identified conjugate field, such as density in standard sound. Classic flocking theories thus describe the fluctuations of the direction of motion through a first-order equation in time (Eqs. (1) and (2)). The analysis of the model reveals that this seemingly innocuous assumption leads to a wrong prediction—the diffusive transmission of information, meaning that the distance covered by information grows with the square root of time, rather than linearly, in clear contradiction with the data.

Here, the theoretical analysis compels us to re-discuss the structure of models like Eqs. (1) and (2), and calls for a new principle [40]. Within the new theory, linear information propagation is a direct result of the same global rotational symmetry mentioned earlier, which suggests to define a conserved quantity that is conjugate to the direction of flight. This new variable, a continuous internal angular momentum, is connected to the behavioural inertia of birds in changing their heading direction. It describes a dynamics where birds do not immediately adapt their flight direction to the external forces but integrate past information, i.e. they have memory (technically, birds are non-Markovian). This new biological ingredient leads to modified second order equations of motion that are mathematically equivalent to light and sound propagation, in agreement with the data [36,40]. The new conserved field, which has interesting formal ties with the *spin* of quantum particles [40] has an entirely biological role. It implements the memory kernel of the velocity update and also has a direct kinematic interpretation: it represents the radius of curvature of the birds' trajectories. This abstract theoretical detour leads to concrete experimental predictions. It implies that information transfer must be faster the stronger the group's orientational order, as accurately verified by the data [36]. The fact that there exists a conserved quantity also results in a specific way of turning, where individuals follow equal radius paths, as observed experimentally in natural flocks [36,41,42].

The role of memory to describe collective patterns in living assemblies—initially overlooked in the literature of active particles—has been recently considered in several works. Models of collective motion with memory, even though of a different kind and symmetry properties than the one discussed above, have been considered to describe coordinated behaviour in fish schools [43], the emergence of vortex-like structures of biofilaments in motility assays [44], and collective oscillations in dense bacterial suspensions [45].

Asymmetric interactions
Another example where theory and physics-based modelling helps us understand the specificity of biological collective behaviour is the role of fluctuations on the stability of collective order. It is empirically observed that during aerial display, large flocks of birds perform frequent collective turns, even in absence of predation [42]. Similarly, spontaneous evasion manoeuvres have been measured in fish schools [46]. It therefore seems that endogenous fluctuations can have an important role in the group dynamics, as they are able to produce relevant changes in the collective state of the system (the group's global direction of motion). A model like Eqs. (1) and (2) is not able to explain this kind of behaviour. If groups are large enough, this model predicts that global order is stable in time in absence of perturbations. When reconsidering this model in light of experimental observations, one realizes that some features present in animal groups must be taken into

consideration. One standard assumption in this model, as in many other agent based models in active matter, is that interactions between individuals are reciprocal. This assumption is natural in physics, where all forces between particles depend on distance and are therefore necessarily symmetric. However, when considering local coordination rules in living groups, this is not generally true. For example, interactions between birds in a flock are topological rather than metric [30,47], meaning that each individual coordinates with a given number of closest neighbours independently of their distance. These interactions are therefore non-symmetric. Similarly, the visual and perceptual field of many animals is not fully isotropic, which again implies a non-symmetric interaction network—if I see you, you might not see me [48,49]. Considering directed (i.e. non-symmetric) interaction graphs can have relevant effects on the role of fluctuations and order stability, and can explain why large finite groups change their collective state on finite time-scales [50]. When interactions are symmetric, each individual is influenced and influences others in a balanced way. As a consequence, local errors (i.e. noise) are spread through the whole network and only cause negligible fluctuations of global order. On the contrary, this does not always happen for asymmetric interactions: fluctuations can get locally enhanced before propagating through the system, causing a finite change in the collective state of the group. Even though asymmetric interactions have been considered in the past in models of collective motion (zone models with blind angles, see e.g. Refs. [28,51]), their connection to fluctuations and stability of long-range order is not fully understood. Recent studies have also investigated the destabilizing role of fore-aft asymmetries in Vicsek-like models [52,53], showing how asymmetries can qualitatively change the behavior of active matter systems on the large scale.

Conclusions

The examples we discussed in the context of collective animal motion show how a theoretical framework helps us to gauge our expectations, by distinguishing cases where an intriguing observation requires invoking some new underlying biological principle, from cases where the same observation is already expected, with no additional assumption. Conversely, as was the case with information propagation and spontaneous large-scale changes in flocks, sometimes predictions of existing theories do not agree with seemingly mundane observations; when this happens, our understanding of the phenomenon is wrong or at best incomplete, and we must look for a new theory to make genuine biological predictions and progress. These are of course the most exciting cases: while living systems must function within the known laws of physics and mathematics, they may also hide some new laws, whose existence may only be revealed by the theoretical analysis, but whose rationale lies entirely within the boundaries of biology. In absence of a theoretical perspective, though, we risk to be looking for biological tuning principles aimed at explaining what we do not expect, when there is actually no need for them. Using the above examples we tried to show that a detour into abstract theoretical, and possibly oversimplified theories, is not always only a theoretical exercise but may lead to new insights with direct experimental and biological consequences. Constantly confronting theory with quantitative experimental measurements pushes our understanding of living systems at all scales into new directions.

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