1 Interpersonal coordination in biological systems

The emergence of collective locomotion

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Collective locomotion is a ubiquitous feature of the natural world, found in living systems great and small – from migrating skin cells to flocks of starlings. In humans, collective locomotion is one form of interpersonal coordination, a term that encompasses many of the social and cultural activities that define our species. Whereas studies of interpersonal coordination often focus on the synchronization of rhythmic movement, the domain also includes non-rhythmic coordination, which calls for other tools of analysis. In this introductory chapter our goal is to examine collective locomotion in bird flocks, fish schools and human crowds as a case study for understanding this broader range of interpersonal coordination. Despite vast differences across species – including morphology, neurophysiology, perception and cognition – these seemingly diverse phenomena obey common principles of self-organization and may share similar local mechanisms.

Introduction

Collective locomotion as self-organization

Herring swim together in schools ranging well into the millions of individuals (Misund, 1993), forming characteristic shapes (Partridge, Pitcher, Cullen, & Wilson, 1980) and responding effectively when attacked by predators (Nottestad & Axelsen, 1999). How can this be? How can such large-scale order emerge out of the behaviour of relatively simple animals, with limited perceptual and cognitive capabilities?

The most complete and compelling answer comes from the study of self-organization (Couzin & Krause, 2003; Haken, 2006). Camazine et al. (2001) describe self-organization as “a process in which the pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of a system. Moreover, the rules specifying interactions among the system’s components are executed using only local information, without reference to the global pattern”. Individual fish are perceptually coupled to their nearby neighbours and coordinate swimming with them; through a process of self-organization, these local interactions propagate and give rise to the global patterns of collective motion that characterize the school as a whole. The degree
of order in the global pattern is characterized by Haken (2006) as the order parameter. Variables that take the ensemble between ordered and disordered states are called control parameters.

**Levels of analysis**

Local interactions give rise to global patterns – this is the central claim of the self-organization approach to collective behaviour. Analyses can be conducted at the local or global level, but must ultimately characterize the links between them. Sumpter, Mann and Pernea (2012) outline a cogent framework for such a research programme. They characterize studies at each level and the links in both directions, from local to global and from global to local. Making sense of these distinctions is crucial to formulating research strategies to understand collective behaviour, so it will be useful to review them in depth.

At the local or ‘microscopic’ level of analysis, researchers focus on the behaviour of individual agents – be they birds, fish, particles or people. The goal is to understand and ultimately predict how an individual moves in response to its immediate environment, including steering to goals, avoiding obstacles and interacting with other nearby agents. Studies at this level can range from deciphering the perceptual information that guides key behaviours, such as optic flow in walking and flying (Srinivasan, Zhang, Lehrer & Collett, 1996; Warren, Kay, Zosh, Duchon & Sahuc, 2001) or pressure waves in swimming (Partridge & Pitcher, 1980), to the control of steering and obstacle avoidance (Warren & Fajen, 2008), or the social factors that bind two people together while having a conversation (Shockley, Richardson & Dale, 2009). To draw an analogy with physical systems, analysis at the local level is comparable to the study of classical mechanics, where the aim is to work out the kinematic equations of motion for bodies acted upon by a system of forces. Thus, individual agents in a collective occupy the same role as, say, particles in a gas.

The global or ‘macroscopic’ level, on the other hand, is concerned with the ensemble properties of the collective as a whole. Analysis at the global level is comparable to the study of classical thermodynamics, which deals with large-scale quantities such as temperature, pressure, entropy and energy that are defined over an entire system. The goal is to understand and ultimately predict how such collective variables change over time and react to changes in the environment. The local properties of individual agents are not considered. Global analyses often consist of analysing the overall collective motion pattern, which can range from disordered chaos in swarms of insects (Kelley & Ouellette, 2013) to organized translational and rotational flows in schools of fish (Couzin, 2009).

The key to self-organization lies in understanding how these local and global scales are related. The most common approach is local-to-global analysis, which seeks to understand how simple interactions between agents at the local level give rise to ordered collective phenomena at the global level. Continuing the physical analogy, local-to-global analyses resemble statistical mechanics, which relates macroscopic thermodynamic properties (e.g. heat) to microscopic properties of
interacting particles (e.g. velocity). This local-to-global approach often deploys multi-agent simulations of collective behaviour, in which the goal is to reproduce characteristic global patterns by modelling the behaviour of simple agents and their local interactions. By manipulating the “rules” or laws governing these interactions, such simulations can provide insight into the self-organization of collective locomotion, and help explain how complex behaviour emerges from seemingly simple agents. Ultimately, we seek general principles linking the local and global levels, analogous to physical equations that predict the velocity distribution of an ensemble from the equation of motion for individual particles.

A less common, but equally important, approach is global-to-local analysis. Here, the goal is to observe patterns at the global level and use them to infer properties of agents and their interactions at the local level. Regularities in the global patterns or their dynamics place constraints on the rules and models that characterize the local interactions. For example, a collective variable that indexes the degree of coordination between birds in a flock can provide clues about the local coupling, such as how many neighbours each bird responds to (Ballerini et al., 2008), how information about a predator propagates throughout the flock (Cavagna et al., 2010), or whether the coupling yields self-organized criticality in a flock (Bialek et al., 2013). However, due to the ‘degeneracy’ of large systems there are limitations to this approach: different local rules can give rise to identical global patterns (Vicsek & Zafeiris, 2012; Weitz et al., 2012). Specifying the rules thus requires experimental manipulations of individuals at the local level (Gautrais et al., 2012; Sumpter, Mann & Pernea, 2012).

Models of collective locomotion

The challenge of unraveling the complexity of collective locomotion has attracted an interdisciplinary community of scientists in fields as wide-ranging as biology, physics, mathematics, cognitive science, computer science, robotics, sociology, geography, architecture and evacuation planning. Since the 1970s computational modelling has served as a common platform for these efforts. Whether studying aggregations of particles, schools of fish, crowds of people or swarms of robots, there is a familiar arc: researchers propose a set of local rules governing individual locomotion, simulate interactions between individuals, and observe the resulting patterns of collective motion. However, the connections between the local rules or global patterns on the one hand and the observations of actual human or animal behaviour on the other are often tenuous. In this section, several landmark models will be described.

One of the most influential models of collective locomotion was introduced in computer animation by Craig Reynolds (1987), drawing from earlier models of fish schooling (Aoki, 1982; Breder, 1954). Reynolds’ Boids simulation is an example of agent-based modelling, in which a set of explicit rules defines how each “boid” (agent) behaves and interacts with other agents. His rules included: (1) repulsion – boids avoid collisions by moving away from nearby neighbours; (2) alignment – boids attempt to match the velocity (speed and heading direction)
of nearby neighbours; and (3) attraction – boids move toward the centroid of nearby neighbours. Along with some additional assumptions, these three simple rules produce realistic-looking animations of what Reynolds called “happy aimless flocking”. The boids form cohesive flocks, maintain a safe distance from each other, and avoid obstacles by splitting up and rejoining.

What accounts for the model’s behaviour? First, two of the rules are position-based (repulsion and attraction) and yield a preferred interpersonal distance between agents. This accounts for compact flocks that avoid collisions and reform after splitting around an obstacle. The third rule is velocity-based (alignment), which yields common motion among neighbouring agents. Crucially, collective phenomena emerge from purely local interactions: each boid responds only to neighbours within a fixed radius. Agent-based models thus exhibit self-organization: they demonstrate that global patterns characteristic of collective animal locomotion can, in principle, be reproduced by many locally-interacting agents.

Many subsequent models share these basic components, yielding what Schellink and White (2011) call the attraction-repulsion framework. Couzin, Krause, Ruxton and Franks (2002) showed that a model with three similar rules – repulsion from neighbours in a near zone, attraction to neighbours in a far zone and alignment with neighbours in an intermediate zone (see Huth & Wissel, 1992) – could generate qualitatively different global patterns (Figure 1.1). Specifically, varying the radii of the attraction and repulsion zones produces four distinct forms of aggregation: swarm (high cohesion, low alignment), torus (rotational motion about an empty centre), dynamic parallel (loosely aligned translational motion), and highly parallel (highly aligned translational motion).

This finding illustrates that different large-scale behaviours can result from relatively small changes in the parameters of local rules governing individual agents. Such parameter changes might account for discontinuous transitions observed in animal behaviour, such as a sudden rearrangement in response to the detection of a predator. The model also exhibits hysteresis effects; that is, the threshold of the parameter value for changing from one mode to another depends on the current mode. This is a characteristic property of nonlinear systems (Haken, 2006; Kelso, 1995).

From a physical perspective, Vicsek (1995; Czirok, Stanley, & Vicsek, 1997) proposed a stripped-down model of collective motion, the self-propelled particle (SPP) model, which only includes a velocity-based alignment rule. All particles are assumed to move at the same speed, and on every time step each particle adopts the mean direction of all neighbours within a fixed radius. Noise is introduced into the coupling by adding a random angle to this mean direction at each time step. Remarkably, this minimal heading-matching model is sufficient to generate a noise-induced phase transition from disordered to translational motion as the noise parameter is decreased. Canonical-dissipative models (Ebeling & Schimansky-Geier, 2008; Erdmann, Ebeling & Mikhailov, 2005) add dissipative terms, such as forcing and damping, to the SPP model. This enables
them to account for transients to attractor states, and to exhibit noise-induced phase transitions from a translational to a rotational mode, with hysteresis.

In contrast to these local or microscopic models, the earliest models of crowd behaviour focused at the global or macroscopic level, based on analogies with fluid dynamics (Henderson, 1974). A crowd of individuals is treated as a fluid, their interactions approximated by ensemble parameters such as viscosity, pressure and temperature, and collective behaviour is measured by aggregate quantities like density and velocity distributions. Crowd behaviour is characterized using continuum equations, such as variations on the Navier-Stokes equations (Hughes, 2003). However, these continuum models generally failed to capture the behaviour of individuals, and made little effort to link the global and local levels.

These results demonstrate the power of using simplified, idealized models to capture patterns of collective locomotion. However, more realistic biological models aim to explain the behaviour of particular classes or species of animals. At issue is the generality of a basic set of local rules, and whether small variations in the rules or their parameter values can account for the variety of species-typical behaviour.
Helbing and Molnár (1995) introduced the most influential agent-based model of human crowd behaviour, the social force model. A social force is not a physical force exerted on the pedestrian, like gravity or electromagnetism, but the “motivation to act”. Typical forces include attraction to goals, repulsion from obstacles and a preferred walking velocity. The net force on each person in a crowd is thus the sum of these forces. In addition, there is a noise term to account for random variation in pedestrian behaviour, and a maximum possible acceleration.

Helbing and Molnar (1995) used this framework to simulate a variety of qualitative and quantitative crowd phenomena. For example, lanes form in a corridor when pedestrian density exceeds a critical value, and the number of lanes scales linearly with the width of the corridor. Counterflow at bottlenecks arises when two groups of pedestrians try to pass through a constriction in opposite directions. Because of variability in preferred velocity and goal attraction, pedestrians are more or less motivated to move through the constriction. Several pedestrians from one side pass through at a time, until more highly-motivated pedestrians from the other side begin moving in the opposite direction, and the cycle continues until all pedestrians have cleared the bottleneck.

To model high-density crowds with tightly-packed pedestrians, Helbing, Farkas and Vicsek (2000) added physical forces to the social force model. These include a body force that resists compression from neighbours, and a sliding friction force that reduces speed due to physical contact with neighbours. Social force models have been criticized because, while they seem to produce characteristic patterns of crowd behaviour, “they tend to create simulations that look more like particle animation than human movement” (Pechano, Allbeck & Badler, 2007). In other words, behaviour may appear realistic at the global level, but individual motion is unrealistic at the local level.

Although the social force model continues to dominate the field of pedestrian and crowd modeling, alternative approaches have been proposed. Moussaid, Helbing and Theraulaz (2011) described a model based on what they call cognitive heuristics, featuring a “synthetic vision” component that uses information in each agent’s field of view. For all visual directions within the field of view, the model computes the distance to the first collision in that direction, taking into account the speed and motion direction of other objects. Two heuristics then drive behaviour. First, the agent steers in the direction that provides the most direct path to the goal without colliding with an obstacle. Second, if the time-to-collision in the current travel direction drops below some minimum value, the agent slows down or stops to prevent a collision.

Even though it is simpler than the social force model, the cognitive heuristics model can reproduce many of the same patterns of behaviour, such as lane formation and stop-and-go waves. By adopting a first-person viewpoint, it also simulates situations in which obstacles or other pedestrians are out of view, without additional components or assumptions. However, to deem the model “vision-based” or “cognitive” is problematic, for it makes a number of ungrounded assumptions about human vision. For example, the heuristics assume that the
current 3D positions and velocities of neighbours are accurately perceived, and that steering is based on their predicted future positions. These are empirical claims that must be tested before the model can properly be called cognitive.

**Grounding models in real behaviour**

Agent-based models and continuum approaches have yielded insights into collective locomotion, and provided an existence proof that global patterns can emerge from local interactions through a process of self-organization. However, nearly all such models are predicated on rather ad hoc rules and assumptions, and the resulting behaviour is seldom tested against empirical evidence. Researchers have long acknowledged that theoretical models of collective locomotion must ultimately be grounded in real behaviour. But what kind of data? And for what purposes?

A local-to-global approach begins with experimental data on individual locomotor behaviour, models the control laws that govern local interactions, and then simulates many interacting agents to predict emergent patterns. Reciprocally, a global-to-local approach collects observational data on real collective motion, analyses this data to derive properties of the local interactions, and uses it to test the simulations. We are taking precisely this dual approach to build a pedestrian model that can account for human locomotion and crowd behaviour. Fajen and Warren (2003; Warren, 2006) introduced the behavioural dynamics framework, which synthesizes Gibson’s (1979) approach to perception and the dynamical systems approach to action (Kelso, 1995; Kugler & Turvey, 1987). The aim is to understand how information about the environment modulates the dynamics of action to yield emergent, adaptive behaviour. At the individual level, Fajen and Warren (2003, 2007) decomposed the problem of locomotor control into four basic components – steering to a stationary or moving target, and avoiding a stationary or moving obstacle – modelling each as a second-order dynamical system. Combining these components can account for locomotor trajectories in more complex environments without the need for explicit path planning (Warren & Fajen, 2008).

The next step on the road from local to global is to consider interpersonal interactions between pairs of pedestrians (dyads). Cohen (2009) found that the steering dynamics model, originally developed for inanimate objects, could also account for pursuit and evasion of other pedestrians. The bridge to collective locomotion is to investigate interpersonal coordination: whether there are control laws governing pedestrian interactions analogous to the “rules” assumed in previous models. Do pedestrians adopt a common walking speed and heading direction (velocity-based alignment)? Is there a preferred interpersonal distance (position-based attraction/repulsion)? We are conducting a series of experiments to address these questions, building up from dyads (Figure 2) to pedestrian groups. Rio, Rhea and Warren (2014) found that a follower matches a leader’s speed in accordance with a simple dynamical model, and does so by nulling the leader’s optical expansion. Dachner and Warren (2014) found that a follower...
matches a leader’s walking direction in accordance with a very similar model. Thus there appears to be a human analogue of the alignment rule. On the other hand, we have seen little evidence of a preferred interpersonal distance, casting doubt on position-based attraction/repulsion rules. These findings provide basic control laws for multi-agent simulations of crowd dynamics (Bonneaud & Warren, 2014). To generate collective behaviour, all models assume that an individual agent interacts with multiple neighbours within some neighbourhood. However, the structure of a neighbourhood is unknown. To which neighbours is an agent visually coupled? Does coupling strength depend on distance and direction? How are the influences of multiple neighbours combined? Answering these questions requires experimental manipulation of neighbours and measurement of an agent’s response. One approach is the use of biomimetic robots to probe the behaviour of animal collectives, such as Faria et al.’s (2010) “Robofish” (see also Marras & Porfiri, 2012). A complementary approach, which can be used to probe an individual’s neighbourhood, is to manipulate multiple neighbours using virtual reality techniques.

We are investigating the neighbourhood of human pedestrians by immersing a walking participant in a virtual crowd. By perturbing the walking speed or direction of a subset of virtual neighbours, and recording the participant’s speed and heading adjustments, we can infer the local coupling to multiple neighbours (Rio & Warren, 2014). We find that the participant’s response increases linearly with the proportion of perturbed neighbours, but decreases with neighbour distance. The coupling can be modeled as a weighted average over the neighbourhood: a pedestrian is coupled to multiple neighbours, their influence is additive, and coupling strength decays with distance.

**Figure 1.2** Sample time series of two participants (solid) and a dynamical model (dashed) in a following task.

(a) Speed control: follower acceleration is highly correlated with leader acceleration (mean of 462 trials, \( r: 0.68 \)), with a slight visual-motor delay (\( M = 420 \) ms, \( SD = 373 \) ms). Speed-matching model captures follower acceleration (mean \( r: 0.67 \) m/s²). (b) Heading control: follower heading is highly correlated with leader heading (mean of 32 trials, \( r: 0.92 \)), with a long visual-motor delay (\( M = 985 \) ms, \( SD = 786 \) ms). Heading-matching model reproduces follower heading (mean \( r: 0.71 \) deg). From Rio, Rhea, & Warren (2014) and Dachner & Warren (2014), respectively.
Reciprocally, a global-to-local approach begins with observational data on collective locomotion. One of the most thorough observational studies to date used stereoscopic videography to record the 3D positions of thousands of starlings in a flock (Ballerini et al., 2008), allowing the authors to estimate the structure of a starling’s neighbourhood. Nearly all models assume a metric neighbourhood, such that an agent is coupled to all neighbours within a fixed radius (e.g. in metres), and coupling strength decreases with metric distance. In a topological neighbourhood, by contrast, an agent is coupled to a fixed number of nearest neighbours regardless of how far away they are, and the coupling strength decreases with ordinal distance. Ballerini et al. (2008) found that the “anisotropy factor”, a measure of the degree to which neighbours affect a given bird's behaviour, asymptoted at the sixth or seventh nearest neighbour. Crucially, this value remained constant despite changes in the flock’s density: a bird was coupled to its six or seven nearest neighbours regardless of how far away they were, consistent with the topological hypothesis. Young et al. (2013) subsequently showed that this number of neighbours was optimal for robust consensus within the flock. Cavagna et al. (2010; Bialek et al., 2013) found that starling flocks exhibit scale-free correlations; that is, the response of a given bird is affected by all other birds via propagation, regardless of flock size.

While a topological neighbourhood may be adaptive for bird flocks and fish schools that must maintain cohesion despite large variations in density, terrestrial species may have a different neighbourhood structure. Our preliminary results for a pedestrian in a virtual crowd suggest that the human neighbourhood is not topological (Rio & Warren, 2014). A participant’s response to a subset of perturbed neighbours decays to zero by a distance of 4m in a crowd, and depends significantly on crowd density, contrary to the topological hypothesis. However, the radius also appears somewhat flexible, since the participant responds to a ring of neighbours up to 8m away. We are currently pursuing this issue.

Quantifying global coordination

The signature of collective behaviour is the emergence of global order among individuals in the collective, which Haken (2006) characterized as the order parameter. It is thus important to develop a measure of the degree to which individuals are coordinated with one another. Changes in this measure can reveal the influence of control parameters that take the collective through a phase transition between ordered and disordered states, as well as the response to environmental conditions such as attacks from predators. Several measures of global coordination have been introduced.

Group polarization and group angular momentum purportedly capture the overall linear and circular alignment of a swarm’s heading and direction, respectively (Couzin et al., 2002). Both measures range from 0 to 1, with 0 representing no coordination and 1 representing perfect coordination. Group polarization ($P$) is essentially the vector sum of a unit velocity vector for each of $N$ individuals (i.e. the heading direction, with a magnitude of 1), divided by $N$. If
everyone’s heading is perfectly aligned, the result will be a vector in that direction with a magnitude of 1, the maximum polarization. However, the minimum value of 0 can be produced in multiple ways. If individual headings are randomly distributed, they will cancel each other out, on average. Alternatively, if there are two streams of pedestrians moving in opposite directions, they will also cancel; thus, the overall group polarization will be 0, even though there is a high degree of organization.

Group angular momentum \((M)\) measures the degree to which pedestrians orbit about the centre of mass of the group. Essentially, for each of \(N\) individuals, it computes a quantity proportional to the angle between the unit velocity vector and a unit vector pointing toward the crowd’s centre of mass; taking its sum and dividing by \(N\) yields a magnitude between 0 and 1. If all pedestrians are moving on a circle about the centre of mass, their velocity vectors will be tangent to the circle and perpendicular to their centre vectors, and the angular momentum will be the maximum value of 1. However, once again the minimum value of 0 can be produced in multiple ways, including random motion, rotation about the centre in opposite directions, or linear flow. In addition, this measure is somewhat unreliable because it is overly dependent on a closed circular motion.

The combination of polarization and angular momentum can describe a wide range of motion patterns. Couzin et al. (2002) used them to characterize the four types of motion shown in Figure 1. The ‘swarm’ pattern (Figure 1a), largely random motion, is characterized by low polarization and low angular momentum. The torus (Figure 1b), in which agents circle around an empty centre, is characterized by low polarization and high angular momentum. The dynamic parallel (Figure 1c) and highly parallel (Figure 1d) patterns are both characterized by relatively high polarization and low angular momentum, with polarization close to 1 for the latter. These measures have been applied to cases ranging from tissue cell migration (Szabo, Szöllösi, Gönci, Jurányi, Selmeczi & Vicsek, 2006) to human crowds (Río & Warren, 2013), indicating their general applicability. However, other measures based on the mean difference in heading between pairs of pedestrians may be more sensitive to the degree of organization within a group.

**Conclusion**

The purpose of this chapter was to introduce some of the key issues and approaches to research on collective behaviour, using collective locomotion as a case study. At this point, let us take a step back and consider some general conclusions that may apply to the study of interpersonal coordination more broadly.

First, the distinction between local and global levels of analysis is one that all researchers interested in interpersonal coordination must face, and this is especially true for interactions between many people. Consider the example of rowing. At the local level, it is important to understand the properties of individual rowers, as well as the local interactions between them. What is the preferred
frequency of each rower, the informational coupling between them, and how does each rower coordinate their behaviour with others? But it is also important to consider the global level. What are appropriate measures of the team's collective behaviour? How does this global behaviour depend on the properties of the local coupling? Most importantly, can we formulate general principles that link the local and global levels? Similar questions can be asked for any coordinated activity between people.

A second general point is that understanding collective behaviour and interpersonal coordination requires a delicate balance between theoretical and empirical approaches. Theoretical work, such as the formal modelling described above, is essential, because it gives the field a framework within which empirical results can be situated. Theory drives us to ask the relevant questions, and it guides the choice of which experiments to run and which variables to manipulate and measure. But analysing empirical data, both from experiments and observations, is equally critical. If our ultimate goal is to understand how people and other animals coordinate with one another, it is not enough to propose ways in which this could be done; eventually, we must determine how it is actually done in real systems.

A third general consideration is the importance of developing appropriate measures and analyses to quantify coordination between individuals. Interpersonal coordination involves both rhythmic and non-rhythmic behaviour, and applying the relevant analytic tools may reveal common principles underlying seemingly disparate phenomena. For example, relative phase may be the relevant order parameter and coupled-oscillator dynamics the relevant model for rhythmic behaviour, whereas polarization and statistical mechanics may be more relevant to collective locomotion. In each case, identifying the appropriate order parameter and analytic tools make it possible to determine how potential control parameters affect the degree of coordination, and may lead us to the fundamental mechanisms of coordination governing a system.

As the other chapters in this book demonstrate, interpersonal coordination is a complex, multifaceted and compelling problem. It is our hope that the diversity of phenomena can ultimately be understood within a framework of self-organized collective behaviour, by bringing the relevant concepts, analytic tools and theoretical models to bear on how people coordinate with one another.

References


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