Introduction

CHARLOTTE K. HEMELRIJK
University of Groningen

This book contains a collection of studies of social behaviour that are mainly biologically oriented and are carried out from the perspective of emergent effects and of self-organisation. It brings together papers that show emergent aspects of social behaviour through interaction with the environment in the entire range of organisms (from single-celled organisms via slugs, insects, fish and primates to humans). This book treats the broadest range of organisms as regards self-organisation and social behaviour that has been treated so far in one book. It is only followed by the book by Camazine *et al.* (2001) in which mostly insect societies are emphasised. Most of the papers deal with the direct effect of self-organisation on patterns of social behaviour. We will treat them in increasing order of complexity from slime moulds to humans (Chapters 1–8). A few papers discuss the intricate relationship between evolution and self-organisation (Chapters 9 and 10).

Before treating each of the papers in turn, a few words about self-organisation and emergent effects by interaction with the environment are needed.

Emergent phenomena arise in social systems as a consequence of self-reinforcing effects and of 'locality' of interactions, as explained below. Self-reinforcing effects imply that if an event takes place, it increases the likelihood that it will happen again. An example is population growth. The larger a population gets, the more individuals it contains that can bear new offspring.

Other examples of self-reinforcing effects treated in this book are the cell-clustering mechanism coordinated through waves of cyclic AMP in the slime mould (Chapter 1), the marking and following of trails by ants (Chapter 2), the

Self-Organisation and Evolution of Social Systems, ed. Charlotte K. Hemelrijk.
Published by Cambridge University Press.

physiologically induced threshold changes for certain activities of honeybees (Chapter 3), the ‘winner/loser’ effect during competitive interactions (Chapter 5) and the usefulness of certain words compared to others (Chapter 7).

By the ‘locality of interactions’, we mean that individuals have information about, interact with, and change their environment only as far as it is nearby. This is due to the limitation of their sensory system and cognitive capacity. This locality leads to spatial patterns by self-organisation. For instance, it causes queens of honeybees to be able to suppress nearby workers better than those further off, and this influences their behavioural profiles (Chapter 3); it means that individuals that coordinate only with others nearby show flexible swarming behaviour (Chapter 4), it leads to a certain spatial distribution of individuals of different dominance ranks in groups of animals that compete (Chapter 5) and it leads to biases in voting systems with the majority rule (Chapter 8).

Self-organisation operates on any living organism, independent of its intelligence. However, biologists study self-organisation mainly in species with limited cognitive abilities, such as unicellular organisms (the slime mould) and social insects (ants, bees and wasps) and they are usually not aware of related work on humans by sociologists and linguists. However, that self-organisation is crucial among individuals with a more sophisticated cognition, such as humans, has already been shown in the studies by the economist Schelling in the 1970s (1969, 1971). He was puzzled by the strong segregation of races in certain quarters of a city, such as of New York. Using a cellular automaton, he showed that strong segregation may arise even where very little racism is involved. Related models have been published for the study of, for instance, ‘cultural transmission’ (Axelrod, 1997), the development of political borders (Cederman, 2002) and the emergence of language (for an overview, see Kirby, 2002). Because of the similarity in approach and since biologists may also learn from studies of human societies, we here publish also a few papers on aspects of societies of humans (Chapters 7 and 8).

As regards evolution, the main message is that because self-organisation produces new patterns of behaviour, it also supplies new characteristics on which selection may operate (Chapters 9 and 10).

The chapters

In the social system of one of the simplest organisms, the slime mould (*Dictyostelium discoideum*) self-organisation operates in the building of a complete organism. Cees Weijer gives an overview of empirical findings and of explanatory models for the occurrence of their aggregation, coordination and fusion

(Chapter 1). When food is plenty, amoebae are single-celled. When food is scarce, amoebae cluster together. This is coordinated through chemical communication. Hungry cells emit a chemical substance, called cyclic AMP. Amoebae are attracted to areas of higher concentration of this substance, and therefore the concentration of cyclic AMP increases more and more. During this aggregation cyclic AMP and cells form spiral waves. Subsequently, amoebae are absorbed into a single body (called a slug) that moves in a coordinated way. Behavioural traits of the slug (such as moving towards the light) arise from the interaction between physical and biological traits of the composing cells and are not separately coded genetically. In the last stage the slug develops a stalk that bears spores from which the next generation grows. Thus, these amazing facts show that self-organisation is a form of design in nature that is very 'cheap' (Pfeifer and Scheier, 1999).

Chemical substances are also important in the coordination of the foraging behaviour of ants. Ants mark their paths to and from food sources with pheromones. At a crossroad they choose the path that is marked the most strongly. Therefore, in the end they communally visit a single (or a few) food source(s) only. The collective 'decision' of the colony to visit a certain food source is an emergent effect of the interaction between ants and their physical environment; when there are two food sources of identical quality and size, by accident one path may be marked more strongly than another. As a consequence, more ants will be attracted to that path and thus, it will be marked more strongly again. In the end only one food source is 'selected' for exploitation. Deneubourg, Nicolis and Detrain (Chapter 2) explain further that the size of a colony affects the 'decision' whether a group exploits a single food source only or several food sources simultaneously. Larger colonies appear to be more likely to concentrate on a single food source than smaller ones, because the degree to which a path becomes marked is greater when the colony is larger (with more ants marking the path).

Intensity of marking and sensitivity is important in honeybees, where it functions in the social organisation of tasks. Moritz and Crewe (Chapter 3) explain that the queen suppresses others pheromonally. Therefore, workers that are further away from the queen suffer less suppression and consequently, they produce more 'queen pheromone'. This influences the tasks they perform (whether foraging or caring for the brood).

Coordination of movement arises not only through trail marking, however. Swarms of birds and fish are beautifully coordinated even without chemical trails and without a leader. Parrish and Viscido (Chapter 4) thoroughly review computer-based models that lead to swarming by self-organisation. They compare this to observational studies of fish.

Cambridge University Press
0521846552 - Self-Organisation and Evolution of Social Systems
Edited by Charlotte K. Hemelrijk
Excerpt
More information

Swarming consits of coordination of movement, but when a (food) source is reached, competition may prevail. From competitive interactions (dominance interactions) a dominance hierarchy arises. Both in animals and in humans, the effects of victory and defeat in competitive interactions are self-reinforcing: losing/winning an interaction (or match) increases the chance to lose/win the next one. This is called the winner/loser effect (Chase, 1974; Chase *et al.*, 1994). Hemelrijk (Chapter 5) shows in an agent-based model that the tendency to group in combination with such winner/loser effect leads to many emergent patterns of behaviour. For instance, at a high intensity of aggression, a steep hierarchy develops and also a spatial structure with dominant individuals in the centre and subordinates at the periphery. Both reinforce each other and lead to further emergent phenomena, which resemble those found in certain species of primates. It appears that increasing only one parameter in the model (intensity of aggression) causes a switch in the artificial society from characteristics typical of an egalitarian society to those of a despotic one as known from macaques. Thus, many different characteristics of societies may arise from a change in a single internal trait. It follows that, obviously, the genetic inheritance of a social system is then only partial and characteristics of the social system are largely formed through the interactions among the individuals.

In a similar line of thought, Thierry (Chapter 6) points out that not every trait is genetically inherited and shaped by natural selection; many traits are interconnected and may arise as side effects of other traits that are actually shaped by natural selection. He calls such effects pleiotropic. He illustrates them with certain kinds of behaviour of primates, such as infanticide, sexual intervention by youngsters and allo-mothering. Allo-mothering may be a natural tendency of females of all species. That it is not observed in all species may be due to its suppression in some of them. For instance, in societies where aggression is fierce, allo-mothering is impossible, because females restrict the movement of their offspring in order to protect them.

This view of partial genetic determination has also recently been applied to the language ability of humans. Although, traditionally, linguistic investigators considered the expression and understanding of language to be an innate ability, recently investigators have argued that the specifics of language emerge to a large extent from the interactions among individuals. De Boer, for instance, describes that reinforcement through communication causes a kind of vowel system to emerge among artificial agents that initially produce vowels at random (Chapter 7).

In order to make decisions, humans not only communicate directly, they have also invented voting systems (Chapter 8). Galam describes the hierarchical voting system that is based on majority rule and shows that it leads to very conservative decisions. Suppose individuals may either vote for or against a reform. If an equal number of opinions are pro and contra, the status quo is maintained. This creates a bias against reform. This bias (which operates only if group sizes are even) leads to extremely conservative politics. Consequently, an unexpectedly large initial majority of votes pro reform is needed for actual reform to take place. This is particularly true if the hierarchical voting system contains many layers and the subgroups in which the votes are taken are small.

The interplay of self-organisation and evolution of social behaviour is as yet little explored. We start with two chapters that address the great challenges for future research that are to be found in this area.

Whereas it has usually been believed that complexity restricts the potential evolutionary pathways, David Sloan Wilson emphasises that complexity may also enrich evolutionary potential (Chapter 9). He illustrates the relation between complexity and natural selection with three examples: evolution in fitness landscapes, selection at a group level and selection at the level of the community.

This is worked out in further detail in a highly innovative discussion by Paulien Hogeweg (Chapter 10). She indicates new ways in which self-organisation and natural selection may interact and this interaction may lead to new levels on which selection may act. For instance, interaction among individuals and their environment may lead to spiral waves (such as of chemical components in pre-biotic evolution: Boerlijst and Hogeweg, 1991; Boerlijst *et al*. 1993). Surprisingly, via selection at the level of the spiral wave, traits may evolve whose immediate effect is disadvantageous, such as slow growth and early death.

References

Axelrod, R. (1997). *The Complexity of Cooperation: Agent-Based Models of Competition and Collaboration*. Princeton, NJ: Princeton University Press.

Boerlijst, M. A. and Hogeweg, P. (1991). Spiral wave structure in pre-biotic evolution: hypercycles stable against parasites. *Physica D* **48**, 17–28.

Boerlijst, M. A., Lamers, M. E. and Hogeweg, P. (1993). Evolutionary consequences of spiral waves in a host–parasitoid system. *Proc. Roy. Soc. London B* **253**, 15–18.

Camazine, S., Deneubourg, J.-L., Franks, N. R. *et al.* (2001). *Self-Organisation in Biological Systems*. Princeton, NJ: Princeton University Press.

Cederman, L.-A. (2002). Endogenizing geopolitical boundaries with agent-based modeling. *Proc. Natl Acad. Sci. USA* **99**, 7296–7303.

Chase, I. D. (1974). Models of hierarchy formation in animal societies. *Behav. Sci.* **19**, 374–382.

Chase, I. D., Bartelomeo, C. and Dugatkin, L. A. (1994). Aggressive interactions and inter-contest interval: how long do winners keep on winning? *Anim. Behav.* **48**, 393–400.

Kirby, S. (2002). Natural language from artificial life. *Artif. Life* **8**, 185–215.

Pfeifer, R. and Scheier, C. (1999). *Understanding Intelligence*. Cambridge, MA: MIT Press.

Schelling, T. C. (1969). Models of segregation. *Am. Econ. Rev., Papers and Proceedings* **59**, 488–493.

(1971). Dynamic models of segregation. *J. Math. Sociol.* **1**, 143–186.

1

From unicellular to multicellular organisation in the social amoeba *Dictyostelium discoideum*

CORNELIS J. WEIJER
University of Dundee

The development of the social amoeba *Dictyostelium discoideum*

Development of a vertebrate embryo typically involves the generation of millions of cells that differentiate into hundreds of cell types to form a wide variety of different tissues and organs. Some cell types arise and differentiate *in situ* at the right position at the right time of development; however, many cell types have to migrate during development over considerable distances to reach their final destination. One of the best understood mechanisms guiding long-range cell movement is chemotaxis. Chemotactic cell movement is a key mechanism in the multicellular development of the social amoeba *Dictyostelium discoideum*. Its development is in many respects much simpler and more amenable to experimental analysis than that of vertebrates. The cells proliferate in the vegetative stage as single amoebae, which live in the soil and feed on bacteria. When the population size increases, the cells in the centre of the colony will start to starve, and starvation for amino acids acts as a signal for the cells to enter a multicellular developmental phase. Up to 10^5 cells aggregate to form a multicellular aggregate which transforms into a cylindrical slug. The slug migrates under the control of environmental signals such as light and temperature gradients to the soil surface, where low humidity and overhead light trigger the conversion of the slug into a fruiting body. The fruiting body consists of a stalk of dead cells supporting a mass of spores. The spores can under favourable conditions start new colonies, completing the life cycle (Fig. 1.1).

Self-Organisation and Evolution of Social Systems, ed. Charlotte K. Hemelrijk.
Published by Cambridge University Press.

Cambridge University Press
0521846552 - Self-Organisation and Evolution of Social Systems
Edited by Charlotte K. Hemelrijk
Excerpt
More information

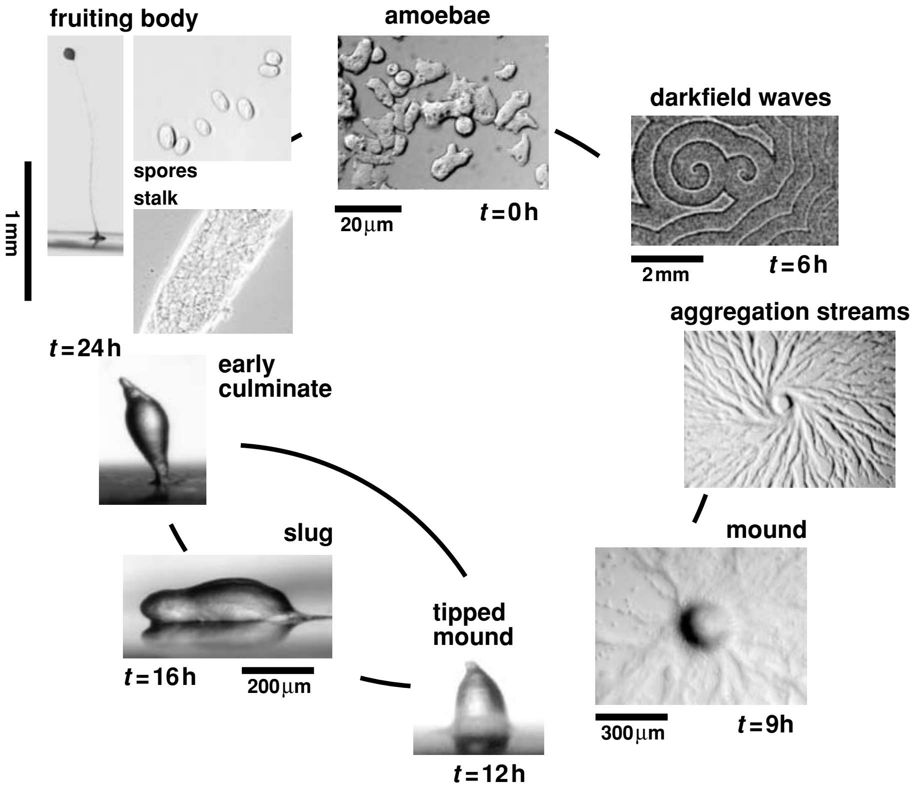

Figure 1.1 The *Dictyostelium discoideum* life cycle. Shown in a clockwise order starting at the top are: vegetative amoebae, darkfield waves as observed during aggregation (they reflect the cells in different phases of the movement cycle in response to cAMP waves), aggregation streams, a top view of a mound with incoming streams, a side view of a tipped mound, a side view of a migrating slug and an early culminate and a fruiting body with on its side high-magnification images of the stalk cells and spores. This developmental cycle is starvation-induced and takes 24 hours at room temperature.

During aggregation the cells start to differentiate into pre-stalk and pre-spore cells that are precursors of the stalk and spore cells in the fruiting body. The pre-spore and pre-stalk cells enter the aggregate in a random temporal order and are distributed in a salt-and-pepper pattern. Then a process of cell sorting takes place, in which the pre-stalk cells move to the top of the aggregate to form a distinct morphological structure, the tip, which guides the movement of all the other cells and is also involved in the control of the phototactic and thermotactic response (Kessin, 2001). Since the multicellular phase of the development occurs in the absence of food there is little cell division during development, and the number of cells doubles at most (Weeks and Weijer, 1994). Morphogenesis

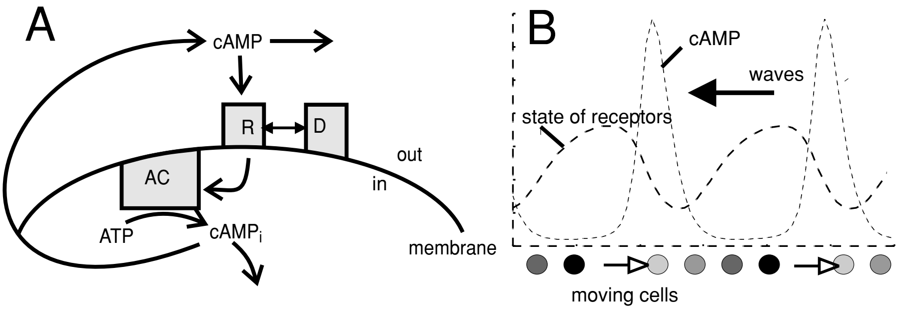

Figure 1.2 (A) Martiel–Goldbeter model for cAMP oscillations. cAMP binds to the receptor (R) and activates the adenylyl cyclase (AC) to produce cAMP in the cell (cAMP $_{i}$). Part of this cAMP is secreted to the outside (cAMP) where it binds to the receptor again, thus forming a positive feedback loop. Binding of cAMP to the receptor also uncouples the receptor from the adenylyl cyclase (D) resulting in a cessation of cAMP production. Extracellular and intracellular cAMP are being degraded all the time by extracellular and intracellular phosphodiesterase, thus allowing the system to return to a basal state where it be activated again resulting in cAMP oscillations. (B) Scheme showing wave propagation and cell movement. The cAMP wave profile and fraction of active receptors are shown as calculated from the model. Waves propagate from right to left, while cells (arrows and circles) move from left to right. Arrows represents moving cells, black circles resting cells, grey circles cells unable to move as a result of adaptation.

therefore is the result of the precisely orchestrated rearrangement of the differentiating pre-spore and pre-stalk cells in multicellular tissues to form aggregation streams, mounds, slugs and fruiting bodies.

Early aggregation

During development cells communicate over distances of several thousands of cell diameters, using a signal relay system that results in the formation of non-attenuated propagating waves of the chemo-attractant cAMP. Aggregation can be understood to result from three distinct cellular behaviours (Fig. 1.2):

(1) Periodic production and secretion of cAMP by cells in the aggregation centre.
(2) cAMP-induced synthesis and secretion of cAMP (cAMP relay) by surrounding cells, resulting in cAMP waves propagating outward, away from the aggregation centre.
(3) Chemotactic movement in the direction of increasing cAMP, resulting in movement directed towards the aggregation centre, the source of the waves.

Cyclic AMP wave initiation and propagation

A few hours after the initiation of starvation cells become sensitive to cAMP due to the expression of serpentine cell surface cAMP receptors. The cells are now able to synthesise and secrete cAMP in response to a cAMP stimulus, i.e. they become excitable. Binding of cAMP triggers two competing processes, excitation and adaptation. Binding of cAMP results in a fast autocatalytic cAMP-induced cAMP production, mediated by the aggregation stage adenylyl cyclase. Most cAMP is secreted in the extracellular medium, where it diffuses to neighbouring cells (Martiel and Goldbeter, 1987b; Devreotes, 1989). Binding of cAMP also triggers a slower adaptation process, which results in a block of the autocatalytic cAMP production. The cells are now refractory to further cAMP stimulation by signals of similar magnitude. Meanwhile cAMP is degraded continuously by an intracellular phosphodiesterase and a secreted extracellular phosphodiesterase (ePDE). This degradation of cAMP into inactive 5′AMP results in a decrease of the intra- and extracellular cAMP concentrations and the cells be come excitable again (Fig. 1.1). The molecular basis of the complex signalling pathways underlying these excitation and adaptation processes are being rapidly elucidated and are reviewed in detail elsewhere (Parent and Devreotes, 1996). The secreted cAMP diffuses away to activate neighbouring cells, which now in turn start to produce cAMP and stimulate their neighbours. These signals form initially small wave fragments that start to travel through the population of cells. Adaptation ensures the unidirectional propagation of cAMP waves, since cells that have just relayed are refractory to further stimulation by cAMP. The waves will interact and generally form spiral wave centres (Fig. 1.3). There also exists a strong feedback of the cAMP signal on the expression of the components necessary for signal detection and amplification, such as cAMP receptors and adenylylcyclase itself (Gerisch, 1987; Firtel, 1996). As a result the cells become more and more excitable and after a while all enter an oscillatory regime where they are being entrained by the fastest oscillating cells, which make up the aggregation centre.

Chemotactic movement

Cells move by extension of psuedopodia. Vegetative cells move by extending sequential pseudopodia in random directions resulting in a movement pattern resembling a random walk. Aggregation stage cells move up cAMP gradients, as long as the cAMP concentration is rising, by extending psuedopodia in the direction of the cAMP gradient and retracting their trailing rear end. Since the cells are small (~10 μm) compared to the wavelength of the cAMP waves