Self-organisation and Evolution of Social Systems
Charlotte Hemelrijk

Introduction
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This book is a broad collection of studies of social behaviour from the perspective of self-organisation and evolution from slime mould to humans (see Camazine et al. 2001 for another regarding insects).

Emergent phenomena arise in social systems as a consequence of self reinforcing effects and of 'locality' of interactions. Self-reinforcing effects imply that if an event takes place, it increases the likelihood that it will happen again. The locality of interactions is due to limitations of sensory systems and cognitive capabilities and this leads to spacial patterns of self-organisation. Because self-organisation produces new patterns of behaviour, it also supplies new characteristics on which evolutionary selection may operate. Self-organisation is a form of design in nature that is very 'cheap'. Swarming consists of coordination of movement but when a (food) source is reached, competition may prevail. From competitive interactions a dominance hierarchy arises – the more aggressive the interaction the more steep the hierarchy. The effects of victory and defeat are reinforcing. Each emergent trait can in turn cause subsequent effects so that changes to a single trait can have wide reaching results. Such partial determinism has also been applied to the development of language systems and voting systems which inherently support the status quo. Complexity may enrich evolutionary potential.

From unicellular to multicellular organisation in the social amoeba Dictyostelium discoideum
Cornelis Weijer.

Chemotactic cell movement is a key mechanism in the multicellular development of the social amoeba Dictyostelium discoideum. 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 105 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.

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. 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. Morphogenesis 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.

The development of Dictyostelium presents a prime example of the complex interactions and feedbacks that exist between signals generated by cells and their movement responses to these signals and how these interactions result in morphogenesis. A population of Dictyostelium cells behaves as a biological excitable medium, in which the cells communicate by propagating waves of cAMP. These waves interact with the dynamics of the medium on at least two time-scales. On a short time-scale they induce motion and rearrangement of the excitable elements, the cells. On a longer time-scale they control the gene expression of signalling molecules, which in turn changes the signalling and movement dynamics of the cells. Since many of these interactions are non-linear it is very difficult to imagine how they will affect development even qualitatively. These interactions are far more complex than those found in most physical or chemical excitable systems and in order to understand them it will be necessary to model these interactions. If we can successfully describe some of the key interactions, it will show that we understand the basic principles involved.

These elements can all be caught quite well by any model that describes cells as excitable units and requires the existence of at least two different cell populations which differ in their ability to move in response to a cAMP signal and furthermore differ in their ability to relay the signal. In an alternative modelling approach, cells are treated as cellular automata.

It seems most likely that Dictyostelium morphogenesis results from the propagation of waves of a chemo-attractant, cAMP, which coordinates a differential chemotactic movement response. The geometry of the signal controls the movement patterns of the cells and therefore the shape of the organism. The proposed mechanism of cell sorting and culmination needs to be further tested by investigation of wave propagation and cell movement patterns in various signalling and cell motility mutants. Integrating the cellular events leading to cell type proportioning and stabilisation of the cells types in the different stages of development will be the next major challenge.

Optimality of communication in self-organised social behaviour.
J. Deneubourg, S. Nicolis, C. Detrain.

Collective decisions can be made that, at the individual level, require only limited cognitive abilities and partial knowledge of the environment. Simple behavioural rules lead to behavioural flexibility of the society depending on its characteristics (e.g. demography, starvation and kinship) and on its environment (e.g. food distribution and presence of competitors).

Most self-organised decisions and patterns arise as a result of a competition between different sources of information that are amplified through different positive feedbacks. In contrast, negative feedbacks often arise 'automatically' as a result of the system's constraints (e.g. limits on the supply of food, the food reserve and the number of available workers). Amplifying communication is a characteristic of group-living animals

This paper presents a theoretical analysis of the role of some parameters involved in self-organised collective choices: the number of amplifications or competing resources, the intensity of the communication and the individual sensitivity to a signal. We will investigate how the communication can be optimised to generate the most efficient collective response and how these optimal values of communication depend on the characteristics of the society and of the environment. These questions will be addressed in the context of ants' recruitment by chemical means, known to be associated with foraging mostly but also with defence or nest-moving. A mathematical model of food recruitment applicable to trail-laying ants is used to perform this analysis.

$$\frac{dc_i}{dt} = \Phi q F_i - v c_i \quad where$$

$$F_i = \frac{(k+c_i)^l}{(k+c_1)^l + \ldots + (k+c_s)^l} \quad i=1,\ldots,s$$

- i is the number of food sources,
- c is the pheromonal concentration present,
- Φ is the flux of foragers from the nest,
- q is the quantity of pheromone deposited,
- k is a concentration threshold,
- l corresponds to deterministic behaviour,
- F sub i describes the relative attractiveness of trail i

Based on monte-carlo simulation, the plasticity in the pattern of choice between several food sources may result without any requirement for qualitative changes in the information exchanged between nest-mates nor any change in the individual behaviour of the ants, This plasticity has important consequences when direct competition frequently occurs between colonies. Indeed, the defence is a highly cooperative activity, meaning that the probability of winning a fight increases non-linearly with the number of workers. The model suggests that a large colony, able to fight efficiently and exclude competitors at a food site, will more often adopt a pattern where one source is preferentially exploited. A small colony unable in most cases to monopolise a source will tend to scatter the workers on several sources without trying to concentrate its whole foraging force on one site. By doing so, small colonies minimise antagonistic interactions and reduce the loss of workers.

Besides colony size, the quality of food sources also influences the pattern of food choice. Knowing that trail intensity increases with food quality, the model predicts that the selection and the monopolization of one source is automatically favoured when high quality food sources are discovered. At the evolutionary level, the value of the parameters will be selected depending in part upon whether there is a selective advantage in concentrating the colony's efforts on a single site or whether it is better to distribute one's workforce more widely.

The results above demonstrate that changes in the dynamics of information transfer, environmental and social parameters can be responsible for shifts between different collective responses. By increasing the number of sources in competition or by decreasing the number of workers, the colony shifts from a heterogeneous exploitation to an equal exploitation of all sources. The trail intensity (q) and the sensitivity to the trail (l) also act upon this shift with large values of both parameters favouring the heterogeneous exploitation of the environment.

The interplay of intracolonial genotypic variance and self-organisation of dominance hierarchies in honeybees
R. Moritz and R. Crewe

Reproduction of workers is an important aspect of the life history of the honeybee. The queen pheromones are a central signal in establishing worker reproductive hierarchies, but when the queen is lost, workers may use them too. The loss of the queen results in a predictable pattern of laying activity of workers. The few workers that develop into pseudo-queens are selected after a severe intra-colonial competition. Based on their individual inhibition threshold and the propensity to be attracted or repelled by queen pheromones, a reaction-diffusion-like mechanism as described in Fig. 3.2 can explain the development of worker reproduction. In such a model the reaction of the worker is the change of the individual suppression threshold to the queen substance concentration, which forms a cloud around the pheromone source. The workers change their own 9-0DA production thereby changing the local 9-0DA levels in the colony. The locally perceived pheromone concentration may cause two effects:
1. it enhances attraction or repellence to the pheromone source
2. it changes the suppression threshold level of the individual worker.

Both processes result in feedback loop systems tuning both the suppression threshold and the propensity for attraction towards pheromone sources by the worker. As a result, suppressed workers are attracted to strong pheromone sources, which further reduce the individual suppression threshold. This in turn raises the attraction of the worker towards the pheromone source. Consequently, they actively expose themselves to higher 9-0DA levels. Dominant workers avoid sources of royal mandibular gland pheromones. Because they are distant to the pheromone source, they experience a reduced 9-0DA level, which raises the individual suppression threshold levels, and increases the propensity for repellence to pheromone sources. These workers actively search for low 9-0DA concentration further increasing the suppression threshold. As a result one would expect two distinct types of workers: few pseudo-queens, because only those workers with the strongest 9-0DA signals and highest thresholds are not suppressed by others, and many sterile workers.

Genotypic variance is an important factor for division of labour in honeybee colonies but this does not mean that these workers carry specialist alleles at specific loci. It is likely that when an environmental cue exceeds an individual threshold, a specific behaviour will be released in that individual.

Polyandry, resulting in an unpredictable mix of genotypes in the colony, is nevertheless the base structure for establishing genetic reproductive hierarchies among the workers. We suggest that the genetically determined minute differences in individual threshold responses are enhanced by subsequent self-organised mechanisms. The final phenotype is thus not the direct effect of a specific gene for a certain trait, but rather the result of worker-worker interactions that are controlled by at least two feedback loops. The gene does not determine alone whether or not a specific worker develops into a pseudo-queen. The presence of a 'dominance' allele (e.g. for a high threshold or queen repellence) may enhance the probability of a worker becoming a pseudo-queen. In the end, however, the realised reproductive hierarchies will entirely depend on the other workers and the subfamily composition of the colony.

Traffic rules of fish schools: a review of agent-based approaches
J. Parrish and S. Viscido

Introduction.

The emergent behaviour of fish schools ranges from tens to millions, all aquatic environments, tropic levels, and phylogenetic groups.

Emergence versus epiphenomena.

Most studies ask *why* fish school with an underlying assumption that schooling is adaptive. The relationship between emergent pattern versus epiphemona has yet to be comprehensively explored by simulation or experimental work. This paper asks *how* fish school.

Agent-based Approaches.

Early models included agents acting locally based on neighbour distance to insert themselves between the two closest neighbours. Later "crystalline lattice models considered the regularity and architecture of packing, polarity, group shape, and activity synchronisation.

Agent based approaches have generally adopted the "sum-of-forces" approach, with varying numbers and functional forms of forces, depending on the model. Forces are generally applied according to zones of interaction, most commonly repulsion, alignment, attraction and search, as a function of distance from the agent of interest. In the aggregate, forces dictate either resultant direction or velocity. Additional forces, applied without reference to distance between agents, may include a random component of movement, a directed component of movement, and frictional drag. Finally, some models adopt a predetermined speed (i.e. fixed or randomly chosen from a normal distribution) to simplify the calculations. Most models have been restricted to two dimensions, a relatively small number of fish (2-20) and reduction to points (that is, the agents do not possess mass or volume).

Early work was concerned with the basic question: under what conditions will groups form and persist? Later the emphasis became more focussed on self-organising pattern within the group rather than on the existence of groups. Later still each fish behaved according to a different distance weighted social force functions. In this case it was found that the fish self-sorted by strategy and that even one fish with a different social-force function could substantially influence the movement patterns of the group, and that individual did not have to be on the periphery (i.e. leaders can be individuals that react differently),

and that groups could change from schooling to milling by altering group size. Transitions between schooling states (fragmented, swarm, torus, dynamically polarised, rigidly polarised) are abrupt. Also there is hysteresis in that both the current parameter states of in individuals and the architecture dictated by their precious parameter states are important in determining school configuration (i.e. the group possesses a structural memory).

Simple genetic algorithms have been used to select 'optimum' rules. However the results were unrealistic and show some of the difficulties of the evolutionary approach. These are that an optimal endpoint must be known, the optimum may not be a realistic result and optimality expresses a total lack of individuality.

Our results showed that group properties such as polarity, size and speed are strongly influenced by both population size and the number of influential neighbours (which themselves interact strongly).

There have also been other related and interesting but rarely cited results from Cellular Automata, physics, systems engineering, artificial life and animation literature as well.

What Actual Fish do.

Although the number of studies and size of the schools over which data are collected have both been small, several generalisations can be made. First, small groups appear to differ quantitatively from larger ones. However, even as the group becomes more three-dimensional, the envelope around each fish is not symmetrical, but resembles instead a flattened sphere; that is, fish are closer in z than in xy. Beyond some fairly small threshold, subgroups may appear. Within the school, fish pay most attention to their nearest neighbour followed by some sense of the entire group. Fish tend to match speed over position or heading. A definite school structure (measured as degree of polarisation) appears to be the base state, but is easily destroyed by the individual actions of school members.

What is probably important rule wise. Lots of stuff

Things that need exploring. Lots of stuff, but both simulations and experiments have indicated that groups composed of individuals with differing internal states can have significant effects on group size, structure and stability.

Conclusions.
There are pros and cons of both simulations and experiments. Neither identify the underlying cause.

A process-oriented approach to the social behaviour of primates
C. Hemelrijk

Introduction

The marked complexity of primate social behaviour is usually ascribed to the extraordinary intelligence of primates. The three main theories are:

1. **Kin Selection:** Altruism will spread evolutionarily if it is directed towards kin.
2. **Reciprocal Altruism:** Cooperative relationships.
3. **Sexual Selection:** Altruistic behaviour by males towards females to obtain preferential mating opportunities.

This paper demonstrates that empirical findings of sociopositive behaviour among chimpanzees cannot be explained by these traditional theories.

The dynamics of competitive interactions in an artificial society gives rise to certain self-organised patterns that appear to influence sociopositive behaviour as a side effect, in such a way that under some conditions patterns arise that do look like exchange, but which arise in a completely different way.

The traditional theories: exchange of sociopositive behaviour.

Three examples where the traditional theories are inadequate on closer inspection:

1. Male chimps cooperatively attack solitary males of neighbouring communities. Traditionally attributes to kinship but this is not supported by data.
2. Male chimps provide reciprocal support in conflicts amongst them selves. Traditionally attributed to reciprocal atruism by keeping a tally but it only happens in periods without a clear cut alpha-male and tallies are not supported by data. An alternative simpler explanation is that males join to attack common enemies in a wholly selfish manner.
3. Males render services to females but this does not result in additional reproduction. The services may simply reduce aggression in males and the tendency to flee in females

The introduction of context: sex ratio and philopatry.

An important feature of the social structure of primate societies is the identity of the migrating sex. Most often the males are the migrating sex and females remain in their native group for life.

In contrast to traditional models, analysis shows that reciprocation is independent of sex ration in female transfer species, and in female resident species females recipricate a a stronger reciprication of grooming at higher socionomic sex ratios. In additon, the degree of reciprocation was higher in single-male groups than in multi-male groups. This is purely the consequence of females applying one and the same set of rules, which leads to different results due the the variation in their opportunity to interact with males.

Modelling: complex social behaviour from simple rules.

In the artificial world (called DomWorld) reciprocation of support actually arises and does so in agents that are unable to keep records of acts, do not return debts and lack all motivation to help: all the same behaviour that looks like helping occurs whenever, by pure chance, agent C attacks another (A), who happens already to be involved in a fight with agent B. Furthermore, reciprocation occurs more often in loose than in cohesive groups.

This result does not preclude that selection may actually operate on such emergent patterns of cooperation.

The models also show that a dominance hierarchy and a social-spatial structure (with dominants in the centre, subordinates at the periphery) develop and mutually reinforce each other. These processes are accompanied by an automatic reduction of the frequency of interaction. Remarkably, it appears that frequency of aggression decreases in all three attack strategies, at least when groups are cohesive and the intensity of aggression is sufficiently high.

The model makes clear that changing the single parameter (aggression intensity) one may switch from an egalitarian to a despotic society.

In real primates the higher ranking individuals receive more grooming than others and most grooming takes place between individuals that are adjacent in rank. The model shows that competition leads to spacial centrality of dominants and this spacial arrangement in turn determines the grooming regime simply because the opportunity for grooming occurs more frequently between adjacent individuals.

Discussion and conclusion.
Although individual traits (such as grooming, food sharing and support in fights) may independently have been shaped by natural selection as is usually implicitly assumed, this is probably not always the case. Certain genetic differences between species may automatically imply a large number of side effects. It is not easy to imagine how and when side

effects arise, and here individual-based models, such as DomWorld, may be of help. For instance, increasing intensity of aggression in DomWorld has many consequences; it leads to a steeper hierarchy, reduced bidirectionality of aggression, a reduction of the frequency of aggression, an increase of the average distance among individuals, and spatial structure, etc.

Order and noise in primate societies.
B. Thierry

As students of animal societies, we claim we observe levels of organisation, networks of relationships, mating systems and demographic structures. We identify classes, matrilines and hierarchies. We consider things like parental investment, nepotistic patterns or dominance strategies. We try to explain the patterning of these behavioural characters by looking for their fitness.

I will advocate the heuristic value of the epigenetic stream in distinguishing noise and order in the social organisations of non-human primates.

Adaptive order or disorder?

Focusing on the individual's characters and strategies, leaves no mechanism to screen patterns that have no direct function. To illustrate this point, I will choose concrete examples from primate behaviour, namely infanticide, allo-mothering and interference in mating. Immature primates undergo a long period of dependency, allowing room for the intervention of conspecifics other than the mother during the developmental process. Conspecifics' behaviours may affect the fate of offspring positively or negatively. Since the main currency of evolution is the number of descendants left by individuals, behaviours related to reproduction and the survival of immature offspring cannot be disregarded as being of secondary importance.

Structural Order.

By focusing on individual reproducers, most evolutionary thinking points to the ordering action of natural selection. Exclusively focusing on individual strategies may be misleading. however. Any feature that is not a direct outcome of the selective process appears just as noise and disorder. The phenotype is not built only from genomic information. but also from self organisational rules that arise through the epigenetic process.

Macaque social organisations appear to belong to a finite set of possible forms. From the above behaviour patterns. macaques may be ordered along a four-grade scale going from species characterized by strict hierarchies on one side to others featured by more tolerant relationships on the other

The interconnection among variables indicate that natural selection acts on self-structuring rules rather than on social patterns.

Conclusion.

The search for universal laws without concern for specific developmental and evolutionary pathways may be misleading. If the role of individuals in evolution is stressed in an unbalanced way, behaviours become a mere expression of adaptive strategies, and sociodemographic forms appear as puzzles, the pieces of which are made of separate strategies. Acknowledging that structure and order are ascribed by the observer implies that a close examination of sociodemographic forms is necessary before resorting to selective processes.

For living beings meaning is cast upon nature by the observer and order cannot be defined in the same manner as in physics. The information encoded in the genes does not suffice to describe the whole phenotype. Once proteins have been fabricated, the epigenetic process starts, giving its shape to the phenotype through the enaction of local rules and multiple feedbacks. Specifying how important features of sociodemographic forms may be produced by constraints internal to organisations does not refute the role of natural selection. Rather, it shifts the main target of the selective process from complex patterns and strategies to individual characters and behaviours, a quite orthodox Darwinian stance by the way.

A number of patterns of macaque societies may be explained in a holistic manner. It may be expected that the role of epigenetic processes become all the more important as the distance from the level of expression of the genome increases. It is thus at the level of the social phenotype that we must expect to encounter the most powerful effects of self-organisation.

Self-organisation in language.
B. De Boer.

Definition of Self Organisation.

Self-organisation. according to this definition is '*The emergence of order on a global scale through interactions on a local scale*.' The definition assumes there is a system that has two main components: actors1 and interactions. There is a population of actors, and the interactions always entail a number of actors that is considerably smaller than the total number of actors in the population. This is what is meant by interaction on a local scale.

There are a number of notions that are sometimes used in conjunction with self-organising systems. These terms include the notions of chaos, bifurcations, emergence, attractors, catastrophes and (positive) feedback. A number of these terms have strict mathematical definitions and should therefore be used with care; as it is unlikely that all the conditions of the mathematical definition are fulfilled, such terms can only be used metaphorically in the context of language.

Computer modelling is crucial for investigating self-organisation in language.

An example

The model is based on a population of agents that can each produce, perceive and learn vowels in a realistic way. Each agent has a simple speech synthesiser that can generate all basic vowels, based on three inputs: the tongue height, tongue position and lip rounding needed to articulate the vowel. These three parameters are sufficient for generating all basic vowel qualities. Vowels are stored as 'prototypes'. For each vowel an agent knows, a point in both acoustic and articulatory space is stored that is most representative of that particular vowel. Perception is based on a cognitively plausible distance function that is based on properties of the sound spectrum of the vowels. For a given signal, its distance is calculated to all acoustic prototypes, and the one with the shortest distance is defined to be the vowel recognised. Agents start out with empty vowel repertoires, and add and remove vowels on the basis of the interactions with other agents. Agents can add random new vowels with low probability (1 % per game).

The agents interact in so-called imitation games. In each imitation game, two agents are chosen randomly from the population. One agent chooses a random vowel from its repertoire and produces this, while adding noise. The other agent analyses this

sound in terms of its prototypes, and picks the one that is closest to the signal. It then produces the corresponding sound in turn, also adding noise. The first agent then analyses this sound in terms of its prototypes, and checks whether the prototype it recognises is the one it originally used for producing the sound. If this is the case, the game is said to be successful. This is communicated to the other agents through 'non-verbal feedback'.

As a reaction on the imitation game, agents update their vowel system. They can add a vowel if necessary. Also, agents sometimes add random vowels, in order to create pressure to increase the size of their repertoires or to get imitation started when an agent's repertoire is empty and it has to produce a sound nevertheless. Vowels can also be discarded if it turns out that they are not successful for imitating other agents' vowels. This is evaluated on the basis of their past success or failure in imitation games. Vowels can also be merged if they come too close together in either acoustic or articulatory space. Finally, agents can shift vowels in their repertoire over a small distance in order to approximate more closely the signal heard in the imitation game.

All these actions and interactions lead to the emergence of realistic vowel systems. It turns out that these vowel systems are not only remarkably like the vowel systems found in human languages, but that the frequency with which different types of vowel systems occur agrees remarkably well with the frequency in which they occur in human languages.

Conclusion

This chapter has presented an overview of work on language as a self-organising system. It has been shown that viewing language in this way is extremely useful. Self-organisation is the emergence of global order through interactions on a local scale. It can happen (and has been investigated) in the human brain, but most work into self-organisation in language has focused on linguistic phenomena in a population of language-users.

Self-organisation provides a means by which diachronic linguistics (the description of how language changes) can be unified with synchronic linguistics (the description of grammars of human languages and the capacities that humans bring to bear on the tasks of learning and understanding language). Self-organisation can be used to gain insight in such diverse aspects of language as phonological universals of sound systems, the emergence of grammar, linguistic change or the way a population of language-users adopts new words.

All these approaches have in common that they view language as a dynamic system in which interactions between language-users is as important as the knowledge and capacities of those language-users. In this respect models of self-organisation attach equal importance to both De Saussure's 'langue' and 'parole', and Chomsky's 'performance' and 'competence'.

Dictatorship effect of majority rule in voting in hierarchical systems.
S. Galam.

In recent years statistical physics (Pathria, 1972; Ma, 1976) has been applied to a large spectrum of fields outside the scope of non-living matter (Bunde et al., 2002). While applications to social sciences are growing, they are still scarce (de Oliveira et al., 2000). In this chapter we analyse a basic ingredient of social organisations: the legitimacy of top leadership with respect to the distribution of support for various political trends present at the bottom of the organisation.

In hierarchical democratic systems each level is chosen from the one just below using a local majority rule. In principle this is supposed to yield 100% power to the larger trend. In the case of two competing trends, it means receiving more than 50% of the overall global support. This democratic ideal can seldom be satisfied, because the trend leading the organisation has several advantages. We show that accounting for such an asymmetry between the ruling trend and the challenging one may turn a democratic system into a drastic dictatorship.

This paradox is a consequence of the underlying dynamics associated with multi-level elections. It appears to obey a threshold-like dynamics, which can lead to democratic self-elimination of the huge majority against a minority trend which is in power (Galam, 1986). Indeed, repeated elections can drive the threshold for attaining power to a significant asymmetric value. For instance, it can be down to 23% for the group already in power and up to 77% for its challenging competitor.

Natural selection and complex systems: a complex interaction.
D. Sloan Wilson.

There is a view that complexity simply replaces natural selection as an explanatory principle rather than interacting with it. This chapter illustrates a more complex and synergistic relationship between natural selection and complex systems. The synergy occurs because complex systems have profound effects on phenotypic variation and heritability, the two basic ingredients of natural selection.

Case study 1: radical epistasis and the genotype phenotype fitness relationship

Many problems in evolutionary biology are represented by the metaphor of adaptive landscapes with natural selection as a hill-climbing process. It is difficult to see how a population can occupy more than one peak, because when individuals that occupy two peaks mate with each other, their progeny will be intermediate and will occupy valleys of low fitness. To make matters worse, the landscape is continually changes in response to the organisms.

Something quite remarkable happens when the genotype-phenotype relationship is made maximally epistatic. In this case, a subset of genotypes evolves that satisfies two criteria: (a) all genotypes occupy adaptive peaks, and (b) all genotypes give rise to each other by recombination. The progeny of two individuals, which are genetically intermediate by definition, need not be phenotypically intermediate, which makes it possible for the genetic system as a whole to occupy more than one peak while missing the valleys. Our model has the remarkable ability to mould itself to multi-peak adaptive landscapes and swiftly adapt to long-term recurrent changes in the environment. The reason is obvious, if only in retrospect: a radically epistatic system allows almost any combination of phenotypes to be produced by a randomly mating subset of genotypes, without the production of intermediate forms that has always made evolution in multi-peak adaptive landscapes seem problematic.

Case study 2: Group selection in humans and other animals.

Natural selection within a single group is insensitive to the welfare of the group. A solid citizen who behaves altruistically will decline in frequency if there is a private cost. Freeloaders are equally or more fit than solid citizens within groups. However, groups of solid citizens are more fit than groups of freeloaders and the solid citizens can evolve by group-level selection despite their selective disadvantage within groups. But, why should groups vary in their proportions of solid citizens and freeloaders?

Consider a model in which genes code for social transmission rules rather than directly for behaviours. The population has a binomial distribution of p solid citizens and (1 - p) freeloaders and they are placed randomly into many groups of size n. At first behavioural variation among groups follows the binomial distribution, but then the social transmission rule takes over and all groups become behaviourally uniform. Notice that the value of p has not changed in the total population because each group converges on one or the other behaviour at random, but the partitioning of the variation has changed dramatically. Initially most of the variation was within groups, whereas all of it becomes variation among groups.

The new partitioning of variation is maximally favourable for group selection and (with no exploitation within groups) the solid citizen groups do well and the frequency of solid citizens (P) increase in the global population. If the groups break up and the individuals (or their progeny) form new groups at random, the cycle repeats itself.

Evolution in randomly formed groups can evolve the psychological disposition to figure out what's good for the group and make sure that everyone does it.

Case study 3: Ecosystem selection.

The idea that entire ecosystems can evolve into adaptive units has been regarded as among the most extravagant claims of holistically minded biologists. Nevertheless, the same principles also apply to ecosystems consisting of multiple species interacting with each other and their abiotic environment.

Consider the community of microbes, fungi and invertebrates that inhabit the root zone of plants. Each plant and its associated fauna can be regarded as a local ecosystem, whose members interact primarily among themselves and with the physical environment in the immediate vicinity of the plant. These local ecosystems will surely vary in their species composition and in the genetic composition of the component species.

If the parameter space includes regions that (a) create the phenotype being selected and (b) are locally stable, then the process of ecosystem selection can 'find' these regions. There will be phenotypic variation at the ecosystem level and some of it will be heritable. Notice that ecosystem selection can take place purely by changing species

composition without any genetic changes in the component species. The local ecosystem has truly become the analogue of an organism and species have become the analogue of genes. However, the response to ecosystem selection can include genetic changes within species in addition to changes in species composition.

Interlocking of self-organisation and evolution. P. Hogeweg.

Organisms can cope with a variable environment in a which various actions are called for in a variety of ways.

- **'Red Queen' evolution.** Each individual performs the different types of actions with a preset frequency.
- **Frequency-dependent selection.** There are two or more sub-types in the population, each specialising in one or a subset of actions (i.e. Rover and sitter types in Drosophila).
- **TODO-based behaviour.** 'do what there is to do'. Stimulus response units are a powerful basis for self organising behaviour such as automatic adaption to the environment and 'division of labour'.
- **Self-reinforcing TODO.** Performing a certain action changes an internal state such that that action is more likely to be performed. (Age dependent polyethism in bees, social insects, primates .....)
- **Environmental Engineering.** Variation in the environment is controlled.

A small number of mutations in yeast can give rise to massive changes in gene expression by mediation of gene regulation networks – and therefore produce variants which phenotypically resemble alternate phenotypes produced by physiological adaption.

Mos research on behavioural adaption and differentiation is targeted at the different classes of mechanism in isolation. This is because the separation of time-scales appears to be appropriate and because there is a motivational desire to emphasise how either the properties of the basic organisms change over time or how the rules remain constant. This chapter endeavours to show that it is essential to study self-organisation and evolution in consort.

Interlocking ecological and evolutionary time-scales.
There is potential interlocking of evolutionary and ecological time-scales even when the prior defined time-scales of mutation and replication are very different (up to five orders of magnitude).

Self-organisation and multi-level evolution.

Classical population genetic theory has not tackled the intriguing question how an increase in complexity can evolve. Maynard Smith and Szathmary (1995) point out this fact, and conclude that major transitions have occurred which increased the complexity of living systems. These major transitions involve the generation of new levels of selection: replicators which are initially self-sufficient become part of coordinated larger units, which become new levels of selection. They document this process in early evolution, i.e. from self-replicating molecules to vesicles, and in later stages, e.g. the transition from prokaryotic to eukaryotic cells, from unicellular to multicellular organisms and from solitary insects to social insects.

Tackling the same problem from a different angle, in which we do not examine what did happen on earth, but what does happen in simple constructive models of eco-evolutionary dynamics, we found that new levels of selection occur automatically through self-organisation. The dynamics of the self-organised higher-level entities enslave the evolutionary fate of the basic entities that generate them.

Genomic self-organising and mutational 'priming'.
The repeated convergence to a similar set of very divergent phenotypes in short evolutionary time suggests that within these species these phenotypes are 'easy' to reach and only a few mutations apart.

Here we will discuss model studies, based solely on random mutations and selection, which, through genomic self-organisation, exhibit phenotypic bias of the outcome of the (random) mutations. The three studies we review tackle this question from different angles, namely from the viewpoint of the dynamics of metabolic/genetic networks, from the viewpoint of co-evolution, and from the viewpoint of morphogenesis.

The first model by Kaneko produces as a generic property a 'division of labour' which is environmentally induced and optimised the growth of the entire population (despite the fact that the perceived environment is identical for all cells). The system exhibits a 'phenotype first' scenario of speciation, within a strict Darwinian selection framework.

The second model contrasts 'behavioural versatility' with 'evolutionary versatility' by arranging for a cellular automaton (with evolving rules) to classify the density of the 'initial conditions' which also co-evolve. The outcome of te model depends on spacial pattern formation. In the case in which spacial pattern formation is prevented by global mixing between every time-step, 'mutational adaption' evolves. Without mixing, spacial pattern formation

occurs, and 'computational adaption' evolves.

The third is a model of morphogenesis, which is designed to study the effect of multi-level processes which consists of boolean gene regulation networks and cells which interact via cell adhesion and local cell signalling, which are defined by the state of the gene network. This evolving gene network incorporates more properties than meets the eye. Apart from the phenotype they produce, they organise themselves over evolutionary time so as to contain the potential for well defined alternatives which become apparent either through mutation or through regulation.