On the Evolutionary and Behavioral Dynamics of Social Coordination: Models and Theoretical Aspects

Ezequiel Alejandro Di Paolo

Declaration

I hereby declare that this thesis has not been submitted, either in the same or different form, to any University for a degree.

Signature:
Acknowledgements

During the period I spent in Sussex I have learnt a lot, explored a lot and met a lot of interesting people who were always keen to take each other seriously in a relaxed environment. Many of the ideas presented in this thesis have matured within this context.

I would like to thank my supervisor during the last three years, Phil Husbands, for providing guidance, help and being always open to new ideas no matter how strange they may have sounded initially. I would also like to thank Inman Harvey, who often played a role of supervisor himself by being always available to discuss problems and make useful suggestions which often were strangely radical and down-to-earth at the same time.

Seth Bullock and Jason Noble contributed a lot to this thesis. The many opportunities in which we discussed our work and the work of others have often been key moments in the development of my research. I am very grateful to them.

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This research could not have been carried out without the support of my family in Argentina, my parents, my brothers, my sister and my in-laws. This support has so many dimensions I can hardly begin to explore this space but I must especially thank their love and help.

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Finally, this thesis could not have even started were it not for the encouragement, love, confidence, intellectual support and unique character of a single person: Marina, my wife. She has made a lot of sacrifices which I will never be able to repay entirely although I hope she takes this thesis as a first installment.

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Preface

Some of the chapters within this thesis have benefited from comments made by anonymous reviewers as a result of their being published elsewhere.

In particular, parts of chapter 6 have appeared as (Di Paolo, 1997b) and (Di Paolo, 1997c). Shorter versions of chapters 7 and 9 were previously published as (Di Paolo, 1998a) and (Di Paolo, 1998b) respectively. Also, parts of chapter 9 will appear as (Di Paolo, 1999).

The author is extremely thankful to all the reviewers for their criticisms and comments on how to improve the manuscripts.
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Abstract
An exploration is presented of the interplay between the situated activity of embodied autonomous organisms and the social dynamics they constitute in interaction, with special emphasis on evolutionary, ecological and behavioral aspects. The thesis offers a series of theoretical and methodological criticisms of recent investigations on the biology of social behavior and animal communication. An alternative theoretical framework, based on a systemic theory of biological autonomy, is provided to meet these criticisms and the elaboration of the corresponding theoretical arguments is supported by the construction and analysis of mathematical and computational models.

A game of action coordination is studied by a series of game-theoretic, ecological and computational models which, by means of systematic comparisons, permit the identification of the evolutionary relevance of different factors like finite populations, ecological and genetic constraints, spatial patterns, discreteness and stochasticity. Only in an individual-based model is it found that cooperative action coordination is evolutionarily stable. This is due to the emergence of spatial clusters in the spatial distribution of players which break many of the in-built symmetries of the game and act as invariants of the dynamics constraining the path of viable evolution.

An extension to this model explores other structuring effects by adding the possibility of parental influences on phenotypic development. The result is a further stabilization of cooperative coordination which is explained by the presence of self-promoting networks of developmental relationships which enslave the evolutionary dynamics.

The behavioral aspects involved in the attainment of a coordinated state between autonomous systems are studied in a simulated model of embodied agents coupled through an acoustic medium. Agents must locate and approach each other only by means of continuous acoustic signals. The results show the emergence of synchronized rhythmic signalling patterns that resemble turn-taking which is accomplished by coherent patterns of movement. It is demonstrated that coordination results from the achievement of structural congruence between the agents during interaction.

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Note: The figures from 7.1 to 8.2 are related to the developmental process and strategies, while figures from 2.2 to 6.12 are related to other topics such as coordination, probability, and dynamical analysis.
In the late nineteen-forties and early fifties, William Grey Walter was pioneering a particular style of research into adaptive behavior using artificial systems. Many of today’s lines of research in situated robotics and computer simulations of adaptation have partly inherited their interests and methods from his work. In two articles in the journal *Scientific American* (Walter, 1950, 1951) and later in a book called *The living brain* (Walter, 1953), he described how life-like behavior could be realized in rather simple electro-mechanical devices which operated autonomously in a real environment. These robots, or “tortoises” as he called them, would propel themselves describing cycloidal paths on a flat surface in search of moderate sources of light. Once their photoelectric sensors detected a source of light, their behavior would change and they would move towards the location of the source. When the light became too intense their mode of behavior would change again, this time to an avoidance pattern. The robots would also avoid heavy obstacles and steep vertical gradients, (see also Holland, 1996). W. Grey Walter vividly described how these basic patterns were simple consequences of the involved mechanisms in combination with properties of the environment and how they could give rise to more complicated behaviors like avoiding becoming stuck in the presence of conflicting stimuli and even a rudimentary form of energetic stability by entering an illuminated recharging station when batteries were running low.

The overall life-like behavior and curious “personality” of the robots make them deserve the name *Machina Speculatrix*.

Without any other apparent aim than the possibility of being able to check when the robots changed from one mode of behavior to another, W. Grey Walter wired a headlamp into their steering circuit. The light bulb would turn on while the robot was performing its exploratory behavior and turn off when the robot’s photoelectric sensor detected a moderate light. The robot would then be able to sense its own light directly, but it could do so indirectly though an interaction with its environment; for instance, approaching a mirror or white surface. Such interactions elicited very interesting behavioral patterns.

But perhaps the most fascinating experiment of all occurred when two of the robots (Elmer and Elsie) were placed together on the same floor in the absence of any other sources of light. The interaction between the different modes of behaviors and the headlamps when these were mutually detectable would cause the robots to perform curious dancing patterns. A robot in...
Chapter 1. Introduction

Exploratory, research-driven, and theoretical investigations are necessary to understand the nature of social behavior. These investigations address issues like the evolution of cooperative coordination, the role of ecological interactions, and the integration of mechanistic and evolutionary perspectives. The aim is to develop a comprehensive theory of social behavior that can account for both individual and collective actions.

One of the main purposes of this thesis is to provide a framework for understanding the evolution of social behavior. The thesis is divided into two main parts: the first part focuses on the theoretical foundations of social behavior, while the second part presents empirical studies that test these theories in experimental settings.

In the first part, the thesis provides an overview of the current state of research on social behavior. This includes a review of the major theoretical approaches, such as evolutionary theory, ethology, and cognitive science. The thesis also discusses the methodological challenges of studying social behavior, such as the need to integrate multiple levels of analysis and to consider the role of cultural and ecological factors.

The second part of the thesis presents empirical studies that test the theoretical predictions. These studies are conducted in both natural and experimental settings, using a variety of methods, such as field observations, laboratory experiments, and computer simulations.

Overall, the thesis offers a novel perspective on the study of social behavior, one that integrates the mechanistic and evolutionary perspectives and that takes into account the ecological and cultural contexts in which social behavior is embedded.

References


1.1.2 Historical processes

The basic theoretical perspective for framing questions regarding socially coordinated behavior is presented in Chapter 3 with a general description of how constituting a historical perspective is introduced during development. The construction of the second part of the thesis.

This perspective is used to highlight the importance of processes in the construction of the historical perspective. In this way, the word "historical" is used in a specific sense. It does not refer to a process analysis but rather to the unfolding of a process.

This unfolding of the process is described as historical. Rather, historical processes are highlighted in the interplay between different perspectives on the process. The reason for this is that a system is described by the dynamic interplay between different perspectives on the process and variations of its own conditions are often linked to the formation of spontaneous organizational processes, which tend to perpetuate themselves. These spontaneous processes are often characterized by a lack of fixation and a tendency towards ongoing evolution. The study of these processes often highlights the importance of the context in which they occur, as well as their potential for change.

1.1.3 Methodological issues

The usefulness of the theoretical issues presented in Chapters 2 and 3 has yet to be demonstrated. The functional view of discourse may provide hints regarding at which level of description an operational perspective should be kept in order to avoid mapping certain concepts onto other, perhaps more familiar, ones. However, the traditional biological perspective relies on formal functional considerations such as selective advantages, in order to define the communication process. At the same time, many of the questions traditionally addressed from a functional perspective can also be studied from the systems point of view, perhaps after some rethinking.

Fortunately, such a perspective can be found in a fully developed form in the theories of Maturana and Varela (1980; Varela, 1979). The relevant terminology is presented in this form by introducing key concepts such asstituity, structural coupling, and the idea of building a framework for functional analysis. It is argued that phenomena like communication can be clearly assessed. So much so, that in certain cases it may not even be easy to understand what has actually been modelled into a computer simulation and what conclusions can be derived from it. A computer simulation plays a similar scientific role to a mathematical model. However, it does not mean that they are necessarily hard to use or understand. Rather, the question is whether the theorems presented in Chapters 2 and 3 have yet to be demonstrated.

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However, the traditional biological perspective relies on formal functional considerations such as selective advantages, in order to define the communication process.
same be said about computer simulations? The use of formal models in general and computer simulations in particular has often been viewed with a certain degree of caution, as some researchers have expressed concerns about the potential for computer simulations to replace traditional scientific methods. However, the use of computer simulations in the study of complex systems has become increasingly common, and there is a growing body of research that suggests they can be valuable tools for understanding biological phenomena.

The use of computer simulations can be justified on several grounds. First, many biological systems are too complex to be fully understood through analytical methods alone. Computer simulations can help to explore the behavior of these systems under different conditions, allowing researchers to identify important patterns and relationships that might not be apparent through traditional approaches.

Second, computer simulations can help to test hypotheses about the behavior of biological systems. By running simulations under different conditions, researchers can test whether their hypotheses are consistent with the observed behavior of the system. This can provide a powerful way to validate or refute hypotheses about the behavior of biological systems.

Finally, computer simulations can be used to make predictions about the behavior of biological systems. By running simulations under a range of conditions, researchers can generate predictions about how the system might behave under different circumstances. These predictions can then be tested through experiments, allowing researchers to validate or refine their understanding of the system.

In conclusion, computer simulations offer a powerful tool for studying biological systems. By allowing researchers to explore the behavior of complex systems under different conditions, they can help to test hypotheses and make predictions about the behavior of biological systems. As the field of computational biology continues to develop, it is likely that computer simulations will become an increasingly important tool for understanding the behavior of biological systems.
These studies are preparatory for the model presented in Chapter 6. This model is based not on a mathematical formulation of collective behavior but on the iterated resolution of individuals. These studies are preparatory for the model presented in Chapter 6 (thus facilitating comparisons). A simple modification to the model presented in chapter 6 is used to respond affirmatively to the last question. In this model the action-response game is extended so that instead of a single response, the participants must engage in a sequence of actions and responses, which depends on the type of food they are trying to access.

A simple modification to the model presented in chapter 6 is used to respond affirmatively to the last question. In this model the action-response game is extended so that instead of a single response, the participants must engage in a sequence of actions and responses, which depends on the type of food they are trying to access.
Chapter 1. Introduction

Payouts are allocated according not to individual actions but according to the correctness of the sequence of actions. Food types are equally perceivable to both players. In principle, it is possible to imagine different situations. That of agents, who are able to adapt individually to their environment. They are capable of coordinating agents and synthesize their signals with artificial, even if the performance reproduces the exact same patterns. This demonstrates the individual and structural congruence of coordinating agents. Coordination is thus an emergent feature of the interaction since it is absent in the individual dynamics. In the presence of the non-plastic beacons, even if the beacon reproduces the exact same signal, the agents perform rhythmic signals leading to the coordination of patterns of movement. During coordination, the agents perform rhythmic signals leading to the coordination of patterns of movement. This demonstrates the individual and structural congruence of coordinating agents. Coordination is thus an emergent feature of the interaction since it is absent in the individual dynamics. This also means that coordination can evolve even if the scenario determines that information is equally shared by everyone. The systemic view is based on the concepts of autonomy, structural coupling, coordination, and structural congruence. This basis is enough for explaining themes related to social learning and social bonding. The explanatory power of studying adaptive behavior from an embodied and situated perspective using similar methods. Chapter 9 presents such a study for the case of embodied behavior. The value of the concepts of coordination and structural congruence is demonstrated as well as the explanatory power of studying adaptive behavior from an embodied and situated perspective using similar methods. In this model, a pair of "shifting" agents moving in an unstructured arena must locate one another and remain within a short distance from each other for as long as possible using only continuous acoustic interaction. The dynamics of the agents is given by the operation of an internal continuous-time recurrent neural network which couples sensors, motors, and perceptual processes. As a consequence of adopting this perspective man many issues that were previously ignored become relevant and worthy of investigation. Some extensions to the basic framework are briefly discussed, such as the relevance of coordinated behavior between unevenly plastic systems. This theoretical basis is complemented by a description of historical processes as well as some examples. By influencing their own conditions of realization, these processes are able to introduce new phenomena of animal communication.
problematic when dealing with the evolution of social behavior.

Historical processes may spontaneously form organizational invariants which constrain the dynamics that gives rise to them in ways that will tend towards their own perpetuation. This dynamical phenomenon may fulfill a highly important explanatory role.

The pragmatic value of these issues is explored in the form of concrete investigations. Since these investigations are based on novel simulation techniques, some issues related to how they are used and how they relate to other scientific activity are explored. A pragmatic approach to the use of formal models in general is defended. This approach aims at finding the relevance of different factors and hidden assumptions by comparing systematically different models of similar phenomena. Especially interesting for this task are models which are not mere extensions to previous models but which radically break with them. A comparison between models which bear little or no genealogical relation has higher chances of bringing into light hidden assumptions and their relevance but at the same time the comparison may not be easy to perform.

This leads to the question of how computer simulations should be used. The best way of formulating and answering this question is by adopting a view of science as a human activity which is defined by a network of practices. The integration of a new tool to this network is the issue to be addressed. After examining some of the problems that may arise from not considering methodological questions with the seriousness they deserve as well as previous attempts at solving some of these problems, a modest proposal is offered. This is not a prescriptive methodology but it aims at describing the necessary steps to achieve an understanding of what goes on in a simulation and then how to relate this understanding via analogies and metaphors with theories of natural phenomena. Computer simulations used in this way fulfil a scientific role analogous to that of thought experiments.

This methodology is exemplified in the investigations. The first one deals with the issue of the evolution of cooperative coordination in the face of conflicting interests. By designing a simple evolutionary scenario, game theoretic models are built to study the expected evolutionary outcome. Extensions to this basic model reveal the relevance of different factors. In none of these cases is cooperative coordination the expected result. However, in an individual-based computer simulation in which agents are modelled as discrete entities in space, coordination does evolve. This is a consequence of considering evolution as a situated process in coupling with ecological and historical factors. The role of spatial structuring invariants that arise in this historical process is fundamental for understanding what goes on.

The addition of social influences on development also shows how other factors coupled with differential reproduction transform evolution into a historical process where organizational invariants are responsible for the patterns observed which would not be explainable otherwise.

The thesis then moves towards issues more related to the behavioral aspects of social coordination. A simple proof of concept shows that coordination can evolve in a significant manner without necessarily assuming as necessary a situation in which information is kept from some of the participants.

Finally, the usefulness of the conceptual structure presented in the initial chapters is put to the test in a more direct manner in a model of embodied behavioral coordination through an acoustic medium. It is shown that emergent features like rhythm of interaction, entrainment, turn-taking, active perception, sensory regulation, coordinated movement and structural congruence, can be understood from a systemic point of view as arising from the constraints imposed by the embodied relations of agents and their environment.

The thesis concludes with a review of the main contributions and some speculations about possible future avenues of research.
Chapter 2. Towards a biology of social behavior: a systemic perspective

2.1 The pragmatic need for a biological grounding

Any good interpretation of a map, if some use is expected out of it, must be guided by some principle so as to avoid, at the initial stages, spending too much time on details and forgetting the big picture. The guiding rule that is to be used here is that all the phenomena under consideration in the context of this thesis should be able to be linked in a continuous fashion to phenomena describable in the language of dynamical systems. In particular, descriptions of biological and cognitive phenomena will be expected to be made continuous with the consequences of the basic logic of the autonomy of living systems as material entities.

It is important to emphasize that the aim is not to give supporting arguments for such approaches in themselves (e.g., the use of dynamical systems in cognitive science instead of a more traditional computational approach, Van Gelder & Port, 1995; Van Gelder, 1999); rather, the point is to use these approaches mainly as conceptual tools that will enable the research to view the issues of interest from a certain systemic perspective that is believed to be fruitful (and in some cases, more acceptable than others). Indeed, this could be said. However, it is preferable to say that the use of a tool indicates an attempt mainly about its suitability and nothing else. This is because it is not the right tool for the job. This does not mean that the evolutionary game theory, for instance, is not applicable, just that it is not the most acceptable approach or as providing any sense of truth or privileged explanatory power.

The hypothesis of continuity of cognitive and social phenomena with biological, physical, and dynamical substrates, without in any way implying that these substrates are all one needs to generate from first principles the concrete phenomena of interest. Such a form of reductionism would at odds with the pragmatic stance that is intended to serve as a research framework as more acceptable than others. Indeed, this could be said. However, it is preferable to say that the use of a tool indicates an attempt mainly about its suitability and nothing else. This is because it is not the right tool for the job. This does not mean that the evolutionary game theory, for instance, is not applicable, just that it is not the most acceptable approach or as providing any sense of truth or privileged explanatory power.

In the present chapter a review will be made of some issues regarding the biology of social behavior, starting by specifying the need for a biological grounding of the terms used to discuss social behavior and by analyzing the distinction between functional and operational statements as belonging to two different domains of scientific discourse. Comments will be made on how these domains are related and some of the methodological problems that may arise when the distinction is blurred. The chapter will then proceed with a detailed analysis of an example where it is considered that problems of this kind have arisen in biology.

In a sense, the autonomy of social behavior is presented based mainly on the works of Humberto Maturana and Francisco Varela (although some points will be criticized or further elaborated). The specific case of animal communication is then re-assessed from this new perspective and some pragmatic consequences derived and compared with the more traditional point of view.
Not all descriptions or explanations in science are equivalent. It is often convenient to make a distinction between two main forms of scientific argument: the operational approach and the functional approach. The former is concerned with the components or processes of a system and the relationships between them, while the latter is concerned with the functions or purposes of a system and the constraints or conditions that are imposed on it. In both cases, the recorded phenomena are reformulated or reproduced in conceptual terms of the phenomena themselves. The only relevance of DNA is a functional one. It is made up of atoms like all the others. There is nothing special about it if DNA is any special status at all. It is not an operational reference point. No functional statement should be confused with an operational one or used in place of a domain-specific one. The only relevance of DNA is a functional one. It is made up of atoms like all the others. 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Understanding systems as complex and dynamic, functional analysis is pragmatically unaudacious. However, faith displays the explanatory role of a dynamical systems approach to life, cognition, and social phenomena. By equating this approach with Laplacean determinism and, consequently, impossible to achieve. This goes against the pragmatic spirit upheld in this work.

One would like to suggest that functional explanations may indeed exert an influence on how the phenomena of interest is assumed to be generated and the lawful relationships between them. The laws that operate in a chemical system cannot change depending on the function of the system being explained and to a more encompassing context, then the type of preferred functional perspective.

The role of operational descriptions that make sense to formulate in the chosen context. (The inclusion of social dynamics as part of the system whose phenomenology one would like to explain operationally.)

Vygotskian-style operational descriptions can provide different operational levels of description (e.g., cognitive, social, cultural, etc.). Different functional understandings of the system whose phenomenology one would like to explain operationally instead of considering them as arising from the interplay between individual behavior and the dynamics of social interactions (using functional terms like internalization, social scaffolding, etc.). Then one could choose the level of description extended beyond the individual and the group to include the whole system.

This kind of constraint may also be used to fill what appears to be a gap in Varela's proposal of language acquisition. In the other possibility, the system is extended to include part of that domain of individual mechanisms which may give rise to such a capability (i.e., in terms of the functional and operational levels of description).

Some of the issues discussed in this section would deserve a further exploration which can perhaps be formulated depending on the type of preferred functional perspective.
2.3. Confusing the domains of discourse: the case of animal communication

2.3.1 Selective advantages as a defining feature of communication

Consider the following selection of relatively recent definitions of animal communication given by behavioral ecologists and evolutionary biologists. While the definitions diverge in many respects, they all agree that communication involves behaviors that are likely to influence the receiver in a way that benefits the sender.

- ‘Behaviour that is “structured” with respect to a receiver’ (Wilson, 1975).
- ‘Communication is the result of an interaction between receivers and signals’ (Berglund, 1970).
- ‘Communication involves the transmission of information from one organism to another’ (Margoliash & Heise, 1991).

The definitions differ in their emphasis on the role of the receiver, the nature of the signal, and the type of information transmitted. Some definitions focus on the behavior of the receiver, while others emphasize the role of the signal in the transmission of information. Despite these differences, all definitions agree that communication involves behaviors that are likely to influence the receiver in a way that benefits the sender.
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It is the semantic, especially when it is the propositional and functional, that makes communication useful. It is the propositional that allows us to deal with the world in a meaningful way. It is the functional that allows us to understand the world as a whole.

Consider that a sign is a signal if it is a signal of something. If it is not a signal of something, it is not a sign.

That is why it is possible to talk about a signal as a signal of something. It is possible to talk about a signal as a signal of something if it is a signal of something.

The problem is that it is not always possible to talk about a signal as a signal of something.

For example, consider the case of a predator and its prey. The predator may be able to detect the prey by the signal it emits. But the prey may not be able to detect the predator by the signal it emits.

Therefore, it is not always possible to talk about a signal as a signal of something.

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2. Communications

At this point, it is useful to consider the case of a signal that is not a signal of something. In this case, it is not possible to talk about a signal as a signal of something.

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2.3 Practical consequences for research

What does it mean to study the evolution of communication under this framework? For the traditional standpoint the ability of an organism to communicate is an established fact. This is paradoxically so even when the issue is how signals evolved. It is the origin or evolutionary change in conventional research. What is meant by this is the time before and after the evolutionary change. In conventional research the ability of a signal to send a signal, make a noise, in the game, produce a warning call, etc. The form and structure of communication is always pre-decided and pre-existent. What these models, which move from warning to signaling, call the "relevance" or "coercion" of communication, is essentially the same as call the "relevance" or "coercion" of communication, which is essentially the same as.

In spite of the inherent reference, the model presented in chapter 6, an independent variable is not.

It could be argued that the ability to communicate is not the defining feature of a communicative system becomes undermining the final evolutionary outcome.

An independent variable is not always required in understanding the final evolutionary outcome.

Examples of how such a factor can be manipulated are given in chapter 6, and this factor is assumed to be of equal or greater importance.
The word “structural,” originating from this distinction, is well defined if one is dealing with a financial market, which for this reason are left out of the discussion.

Before proceeding, the reader should be reminded that the purpose of offering an operational account is not necessarily to act as a total replacement of functional statements. This may be too narrow a point of view given the earlier discussion regarding the purpose of an operational explanation as acting as a constraint to, rather than a replacement for, possible functional interpretations. For this reason, it is necessary to formalize the purpose of offering an operational account to the reader, who should be reminded that the purpose of offering an operational account is not to replace but rather to constrain the functional interpretation of a system. This is done by describing the operational account in terms of an operational account. When speaking about a system in general, a distinction will be made between a system and a network, as in biological systems theory and other systemic concepts even if a complete dynamical description cannot be given in concrete terms. This is particularly so given the right of the claim in that a network is defined as a set of relations that define that system “as a unity, and determine the dynamics of interactions and transformations which it may undergo as such a unity.” In contrast, a system is defined as an operational account that constrains the functional interpretation of a system. Therefore, biological grounding is to serve a constraining purpose, it makes sense that this should be done using an operational account.

2.4 Basic concepts

When one thinks about social behavior, the first thing that comes to mind is a notion of coordination among entities. In order to understand what it is meant by this it is necessary to describe the meaning of autonomy, interaction and coordination.

When speaking about a system in general, a distinction will be made between a system and a network, as in biological systems theory and other systemic concepts even if a complete dynamical description cannot be given in concrete terms. This is particularly so given the right of the claim in that a network is defined as a set of relations that define that system “as a unity, and determine the dynamics of interactions and transformations which it may undergo as such a unity.” In contrast, a system is defined as an operational account that constrains the functional interpretation of a system. Therefore, biological grounding is to serve a constraining purpose, it makes sense that this should be done using an operational account.

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structural coupling occurs between an unity and its medium which may include other autonomous entities in which one can speak of an interaction between them. However, the mediation of the disturbance takes place in the animals itself which are considered autonomous in the sense that even if it happens to have an adaptive function, there is something lacking in the resulting behavior which is clearly not social behavior observed in humans and other species. This is the idea of coordination or orientation.

"An organism can modify the behavior of another organism in two basic ways: (a) by altering the environment in which it finds itself, and (b) by changing the behavior of the other, e.g., in the case of competition or predation." (Maturana & Varela, 1980, p. 27–28)

According to Maturana and Varela, a behavior can be considered communicative where the interaction between two autonomous entities is not determined by the former alone but by both parties. The resulting behavior is a cooperative or coordinated one. This is the idea of coordination between autonomous entities.

"Preservation of autonomy divides the space of possible interactions into those that are allowed and those that are not. As long as this space is occupied by the system, it is called a process whereby the system interacting with its environment undergoes a succession of allowed perturbations (resulting in changes in its structure) without losing its autonomy is called a process of structural coupling (Maturana & Varela, 1980, p. 16). As long as the medium, the system's environment, is not altered, the system maintains its autonomy. This is why, during structural coupling, the structure of the systems involved does not change."

Concepts similar to those of structural coupling and adaptation were introduced in the field of cybernetics by Ashby (1960). He defined a system as adaptive if it can maintain the essential variables of its structure while being perturbed by environmental changes. This is how it can be said that the system is "adapted" to its environment.

"The term 'orientation' will be reserved, when possible, to refer to the model presented in chapter 9 to the concept of coordination."

This is by no means the only restriction, see (Ashby, 1960) particularly chapter 19 and 21 for discussions on autopoiesis and its implications for the study of social behavior.
Chapter 2. Towards a biology of social behavior: a systemic perspective

Figure 2.1: A special case of coordination through interaction where system B is oriented towards system A.

Figure 2.2: Illustration of the concept of coordination.

The domain of coordinated behaviors established by two or more autonomous unities in structural coupling, during the course of which the system undergoes an alteration from which it does not recover within the same timescale, may be permanent. Clearly, some of the changes may be temporary.

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2.4.3 Changing the practical issues of interest: animal communication again

How much of a difference will the adoption of a theoretical framework such as the one described above make in practice? Is it possible that after adopting this framework we might be able to account for all types of social phenomena in autonomous structure-determined systems. To compare some of the practical consequences of this perspective with those of more traditional views it is necessary to describe in more detail what is highlighted by the term "communication" as used in this context in comparison to the discussion given in section 2.3. As mentioned before, a characterization of communication in terms of transfer of information in problem-solving situations is difficult. In order to explore some of these issues more specifically, one may concentrate again on animal communication. The given perspective is that of a systemic standpoint in comparison to the discussion given in section 2.3. As mentioned before, a characterization of communication in terms of transfer of information in problem-solving situations is difficult. In order to explore some of these issues more specifically, one may concentrate again on animal communication.

The understanding of the evolutionary origin of natural languages requires the recognition in them of a basic biological function which properly language has been considered as a degenerative function of language. It is to be noted that in the traditional standpoint there was, in all appearance, never a need to formulate this question. Both such and such a signal denotes a perceived object or a state of affairs. But if information is to be deprived of this pseudo-operational role, as the systemic view insists, then denotation, like information, becomes mysterious. How can it be accounted for? Again, from the current context in which it seems right to say that an animal is telling the other what to do and the other one is responding accordingly in the traditional view, this question was rarely asked because it never became apparent that there was a need to answer it. In the systemic view, such observations demand a deeper investigation of the behavior involved.

Kuramoto calls this phenomenon relative coordination. It is to be noted that in the systemic view, these issues become pressing.

Another related issue that is highlighted is the issue of denotation. In the informational view, information is a stuff that is intended to play an operational role. Such a role is given to it by what is called pseudo-operational activity. But once such use for this and other terms has been criticized in the systemic view, these issues become pressing.

2.4.4 Interests in communication and observation of communication

How much of a difference will the adoption of a theoretical framework such as the one described above make in practice? Is it possible that after adopting this framework we might be able to account for all types of social phenomena in autonomous structure-determined systems. To compare some of the practical consequences of this perspective with those of more traditional views it is necessary to describe in more detail what is highlighted by the term "communication" as used in this context in comparison to the discussion given in section 2.3. As mentioned before, a characterization of communication in terms of transfer of information in problem-solving situations is difficult. In order to explore some of these issues more specifically, one may concentrate again on animal communication. The given perspective is that of a systemic standpoint in comparison to the discussion given in section 2.3. As mentioned before, a characterization of communication in terms of transfer of information in problem-solving situations is difficult. In order to explore some of these issues more specifically, one may concentrate again on animal communication.

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The understanding of the evolutionary origin of natural languages requires the recognition in them of a basic biological function which properly language has been considered as a degenerative function of language. It is to be noted that in the traditional standpoint there was, in all appearance, never a need to formulate this question. Both such and such a signal denotes a perceived object or a state of affairs. But if information is to be deprived of this pseudo-operational role, as the systemic view insists, then denotation, like information, becomes mysterious. How can it be accounted for? Again, from the current context in which it seems right to say that an animal is telling the other what to do and the other one is responding accordingly in the traditional view, this question was rarely asked because it never became apparent that there was a need to answer it. In the systemic view, such observations demand a deeper investigation of the behavior involved.

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Another related issue that is highlighted is the issue of denotation. In the informational view, information is a stuff that is intended to play an operational role. Such a role is given to it by what is called pseudo-operational activity. But once such use for this and other terms has been criticized in the systemic view, these issues become pressing.
Chapter 2. Towards a biology of social behavior: a systemic perspective

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...expanded to include non-communicative behaviors which can become part of a communicative one...

So far, this shift of interest seems to provide with positive additions to the set of questions that are relevant to investigate. This is partly because the original questions need not have been so strongly circumscribed by the functional aspects of communicative phenomena and their selective contribution to the species-specific activities. That is, although some of these questions will still need reformation, it is also possible to emphasize that they may not look like negative pragmatic consequences in the adaptation of the systemic framework. It is a fact that this shift of interest will be subject to the same focus on the achievement of systemic congruence and behavioral homomorphism through sustained structural coupling processes. A greater emphasis on communicative behavior as a species-specific activity while many inter-specific cases of communication are more focused on species-specific, ontogenetically attainable, forms of communication. However, the question of origin becomes the question of the establishment, either in evolutionary or in ontogenetic terms, of the consensual situation that allows for communicative behaviors to exist at all. The original functional questions may still be asked, but the answers will be partly grounded in the fact that certain patterns of species-specific behavior become stable through successive generations in such a manner that all participants undergo non-trivial structural changes until a behavioral homomorphism is established and communication takes place. These patterns become identifiable (at least in principle) for an observer that is able to witness (or deduce) their resurgence generation after generation. As such, these patterns of communicative behaviors derive from the domain in which selection for the ontogenetic structural coupling takes place. With this in view, coordination of non-creativity ontogenically acquired modes of behavior, would never achieve the degree of potential congruence between the participants in communication that certain patterns of species-specific behavior become stable through successive generations. It is indeed possible to observe this across species sharing a common habitat and join the question of origin becomes the question of the establishment, either in evolutionary or in ontogenetic terms, of the consensual situation that allows for communicative behaviors to exist at all. The original functional questions may still be asked, but the answers will be partly grounded in the fact that certain patterns of species-specific behavior become stable through successive generations in such a manner that all participants undergo non-trivial structural changes until a behavioral homomorphism is established and communication takes place. These patterns become identifiable (at least in principle) for an observer that is able to witness (or deduce) their resurgence in the evo- lutionary time-scale. This need not be interpreted as a form of Lamarckism because it is not being said that all inter-specific patterns of communication. But a general treatment here is more difficult in virtue of the inherently dissimilar structures (often presented by organisms of different species). The domains of consensual behavior must rely on the degree of potential congruence between the participants in communication that certain patterns of species-specific behavior become stable through successive generations. It is indeed possible to observe this across species sharing a common habitat and join the question of origin becomes the question of the establishment, either in evolutionary or in ontogenetic terms, of the consensual situation that allows for communicative behaviors to exist at all. The original functional questions may still be asked, but the answers will be partly grounded in the fact that certain patterns of species-specific behavior become stable through successive generations in such a manner that all participants undergo non-trivial structural changes until a behavioral homomorphism is established and communication takes place. These patterns become identifiable (at least in principle) for an observer that is able to witness (or deduce) their resurgence generation after generation. As such, these patterns of communicative behaviors derive from the domain in which selection for the ontogenetic structural coupling takes place.
The reader may have noticed that many of the presented theoretical concepts regarding the role of autonomous systems would benefit from a more sophisticated approach to the problem of cognition, which breaks with the traditional computational framework. In order to provide a better understanding of these concepts, the present work offers a new perspective on the development of cognitive systems, which is not necessarily rooted directly on the systemic framework. An actual direct test of its suitability for research will have to wait until the presentation of the systemic view on social behavior, as well as the justification of its scientific potential, is intended partly as a goal in itself. This view will also be used as a guide for the rest of the concrete models which will explore other derived aspects of the general systemic framework, which have to do with the dynamics of complex systems, historical processes, and self-organization, issues which are further developed in the following chapters. These ideas will be specifically applied to evolutionary, ecological, and developmental aspects of social coordination and components which generate the phenomenon. It is because of this asymmetry that only operational explanations are deemed appropriate to fulfill the task of grounding social behavior in biology.

The actual need for providing this grounding was emphasized by the current state of confusion surrounding the issue of animal communication as viewed from the classical framework. The actual need for providing this grounding was emphasized by the current state of confusion surrounding the issue of animal communication as viewed from the classical framework.
Chapter 3: Historical processes

This chapter introduces a series of ideas which will together constitute one of the recurring themes of this thesis. The aim is to make a basic presentation of these ideas in order to facilitate their subsequent practical use and not to provide a review and comparative exposition of the philosophical and scientific context of the concepts presented in this chapter.

3.1 Constraints

All observable events and processes are underdetermined by the fixed universal laws which are known to be applicable in their idealized forms. The idea that real events and processes are not truly deterministic is also supported by the recent work of Hendriks-Jansen (1996, ch. 6), which has been recently highlighted by the study of self-organizing systems (Waddington, 1969, 1975; Bohm, 1980; Prigogine & Stengers, 1984). However, the purpose of the present chapter is to explore this question and evaluate the relevance of this concept in a series of examples, some of which are directly relevant to the dynamics of social coordination.

3.1.1 Constraints

There are two senses in which the word “constraint” may be used. The specific sense in which it is used here is that of a constraint to a process which is at the same time constituted by the previous dynamics and constituting the parameters of the future dynamics. Such constraints can provide a powerful explanatory tool when dealing with complex historical processes.

3.2 From homogeneous time to historical time through self-organization

There are many senses in which the word “historical” may be applied to a dynamical process. For instance, a process may be said to be historical if its unfolding involves a set of contingencies which cannot be predicted until the moment they occur. In that sense, it could be argued that all real dynamical processes are historical. While the word “historical” would perhaps be inappropriate in such a general context, a more specific use of the term would be to consider the unfolding of a process as historical if it cannot be predicted until the moment the process occurs. In that sense, it could be argued that all real dynamical processes deserve the name “historical” since all of them involve a set of initial conditions which are not specified in the laws of evolution of the process, i.e., they cannot be predicted from the initial conditions given in the initial conditions, but are at different stages during the unfolding of the process. Such processes can be seen as having a historical character if they are able to introduce some temporal heterogeneity in their own unfolding due to the interplay of variations at different time-scales, or susceptible to be explained in terms of the constraints that place limitations to the possible unfoldings of the process. Such constraints can provide a powerful explanatory tool when dealing with complex historical processes.
Although, as seen above, constraints are not necessarily fixed, one could tentatively distinguish two cases of variation. In one case, the variations of the actual process by one of the two following conditions: these variations are independent of the scale of the system or the change of state of the system, because their variations are not considered as fixed. It can be seen how these constraints are qualified rather than strict.

In the second case, the influence on the process may be exerted through coupling with other processes, which operate independently. But such coupling may also influence those oscillations of the process which were in turn previously influenced by constraints. Thus, the oscillations of the process may reflect the movement of the pendulum rather than strict.

Invariants

Invariants are aspects of the structure of the systems involved and their contextual relations which are independent of the scale of the system or the change of state of the system. Such changes are not considered as fixed, but may influence the process. As such changes are not considered as fixed, they may alter the constraints that define the structure of the systems involved and their contextual relations. Is it not possible that such changes could change the structure of the systems involved in such a way that they would effectively become different systems with different dynamics? In such case, such changes could be described as taking place at a different time-scale, or even as taking place at a different phase of the process.

Chapter 3. Historical processes

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The above considerations give a rough idea of how to differentiate historical processes from processes which are non-historical or merely contingent. A historical process is a process whose actual structural, content, or pattern characteristics do not change over time, whereas non-historical processes can exhibit fluctuations whose dynamics affects its constraints either directly or though recurrent coupling with other processes. In such a process new invariant features may be spontaneously manifested as organizational properties which are both constituted by, and constituting of the dynamics of the process.

3.2 Different manifestations of history

The dynamics of the process in ways that tend to their own perpetuation. In other words, the process itself and its state of order is manifested in the form of patterns, which are neither historical nor merely contingent. A historical process is a process whose actual structural, content, or pattern characteristics do not change over time, whereas non-historical processes can exhibit fluctuations whose dynamics affects its constraints either directly or though recurrent coupling with other processes. In such a process new invariant features may be spontaneously manifested as organizational properties which are both constituted by, and constituting of the dynamics of the process.

Dynamics of a set of systems whose actual structures, rules or laws of operation and coupling relationships change in time are not historical processes. The state of order is manifested in the form of new or organizational relations which have been formed. The state of order is manifested in the form of new or organizational relations which have been formed. These patterns, in turn, influence the dynamics of the process in ways that tend to their own perpetuation. In other words, the process itself and its state of order is manifested in the form of patterns, which are neither historical nor merely contingent.
Chapter 3. Historical processes

Walk where the grass is not grown. Initially, no path is marked on the grass and walkers choose a direct route to their destinations. As time passes, and for a certain frequencies of crossings, the effect of the initial trajectories will be so much that the grass will be worn. In a dynamical equilibrium, after many iterations, the effect of the initial trajectories will be so much that the grass will not be able to compensate by growing again before the path is re-used. Thus, trails are formed and maintained in a dynamical equilibrium. The process can be quite complex since the different trails may interact during the process. For instance, it will be more common to observe a single exit point halfway between two frequently used and relatively close destinations than an exit point corresponding to any event such as the appearance of a new destination.

Once a pattern of trails is formed the history of the process has become partially embodied in it and walkers are constrained by its shape (and their preferences) to walk along the trails. Thus, the pattern acts as a constraint to the dynamics of the process but, at the same time, it is constantly being constituted by the process as trails can only be maintained if enough people use them. The system can be "trained" to respond in a desired way to different sorts of couplings. The method of training consists simply in increasing the available energy for forming and reinforcing threads if the system's performance is close to the desired one. Such a scheme is translated into a growth and pruning dynamics at the level of the network of threads. Interestingly, being a mechanical, thermal, or chemical system, there are many ways in which the process of thread formation could be affected.

Biological morphogenesis and evolution are historical processes, and they are governed by the same principles. However, the historical nature of evolution is rarely denied, although there is a tendency to think that biological evolution is not a historical process because it is not a historical process by definition. This example shows that historical dynamics can be instantiated in processes which are otherwise very simple.
cannot be explained unless it is constantly being renewed (by algae, plankton, trees, etc.). As a byproduct of life, a high concentration of oxygen is currently a basic condition for the existence of most animal species.

In spite of the mutual interdependence between organism and environment, both in defining each other and in affecting processes by introducing a separation between evolutionary and ecological factors under the conditions of historical evolution, it is not surprising that the problems of behavior and with innovation in biological evolution cannot be accounted for in the neo-Darwinian framework. In practice, such innovation can only take place in historical processes.

However, the current neo-Darwinian perspective tends to downplay the role of historical factors to that of contextual or initial conditions in a process subject to an universal law of fitness maximization. As argued below, this is a simplification. But how is this simplification achieved?

This is possible thanks to two key assumptions. First, that there is a direct correspondence between the material an organism inherits from its parents during the physical process of reproduction and the phenotypic features of the organism that will grant it a good chance of survival and reproductive success. Second, that, through a process resembling as-organism and random changes in this inherited material, all variations will be selected so as to adapt to the environment as to that of evolutionary processes.

Even though the first assumption can be attacked from different flank, it is the second assumption that allows the historical nature of evolution to be relegated to independent contextual factors. In effect, evolution by natural selection becomes as process of optimizing adaptation to pre-existing environmental factors which does not depend significantly on the evolutionary history of the organisms. This is a difficult error to make, but it is truly the horizon of the organisms. The crucial error in this view is that of not recognizing the historical context of events to be considered.

The causal environment which does not exist only in a few cases (Bohm, 1969b), however, the new neo-Darwinian perspective is not as naive as it may sound. Indeed, it allows a partial relaxation of the hard determinism characterizing the standard neo-Darwinian view. For instance, when studying co-evolutionary dynamics (prey-predator effects, parasitic-host-parasite relations, etc.) or frequency effects which are used as an example of evolution by natural selection and to which the historical perspective can be applied.

While neo-Darwinism has a problematic relation with the historical aspects of evolution, the evolutionary perspective which can be derived from the systems view presented in chapter 2 is more promising. For instance, a game-theoretic analysis of such in-N.3 evolutionary process in a natural way. Organism and environment, while distinguished as systems, interrelate each other. The guiding principle remains the same. For instance, a game-theoretic analysis of the evolutionary history in a natural way. Organism and environment, while distinguished as systems, interrelate each other. The guiding principle remains the same.
nation of some universal principle and a set of contingent circumstances, but as processes which exhibit their own dynamical characteristics which depend on their history and the history of their environment.

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The outcome of natural drift may take different dynamical forms under different circumstances. As an initial search for candidate invariants of this process would find two possibilities which correspond roughly to two important trends by which social practices have tended to be objectified, namely the structuralist view according to which social behaviors are regulated by the logic of systems and the social anthropology of Bourdieu, following a course taken by structuralists and social scientists. In the words of Pierre Bourdieu, objects, as principles adapted to their outcomes with practices and representations, can be objectively adapted to their outcomes with practices and representations, objectives and regularity without being the result of the organizing activity of a conductor (Bourdieu, 1990).

On a more serious note, a conclusion that may follow from this appreciation is that, given that the system of dispositions is generally the one that channel people's behavior in a non-mechanical way, it is important to consider the existence of a social agent as a rational actor without becoming the result of the organizing activity of a conductor.

The hiatus is a product of history. It is the accumulation of past experiences which actively present in the form of embodied habits which tend to be perpetuated by helping to articulate the same habits of future behavior. In this sense, the hiatus is the willingness of the organizing activity of a conductor.

**See** (Dreyfus & Rabinow, 1992; Taylor, 1993; Bourdieu, 1989, pp. 5 & 9)
Chapter 3: Historical Processes

3.3 Explanatory value of spontaneous invariants

The above list of examples of historical processes, in no way comprehensive, is intended to manifest together with a microscopic view of how the habits operate. The dual nature of a historical process obtains as a result of the embeddedness of embodied habit-forming and the behaviors they elicit contributing to influencing the formation of habits in others. Processes are not only isolated but instead, parallel and combine with the constraints of others.

An important notion of this sort is that of spontaneous invariants. Once an invariant is constituted, understanding the dynamical relations that permit it to remain invariant provides a powerful frame of reference for addressing specific questions of what goes on in a complex historical process. It allows the researcher to understand why certain things can change whole while other remain the same.

It is evident that the concept of spontaneous invariants of the dynamics. Once an invariant is constituted and how its structure conditions the patterns of interactions and movements between members of the group. (Hemelrijk, 1998).

On occasions, it may suffice with a broad description of how an organism may be modeled or formalized with mathematical tools like the use of computer simulations. In all cases, however, the actual recognition of an organizational invariant may be found and the processes of the group.

The conceptual power of the habits lies in its potential for biological grounding and for expansion. That there are strong reasons to suspect that this concept will be able to unify in a single theoretical framework the different cases and contexts of cultural and sociological phenomena. The potential for a social-cultural scientific approach to the study of cultural and sociological phenomena is evident but it may often remain hidden.

A thorough examination of this chapter would exceed the limits of this chapter. But see Deyn, Fofana, and Rabino, 1993; Taylor, 1993; Maggs, 1987, pp. 441 - 444. As an example, however, the following passage by Dewey is offered:

"In this quotation many of the ideas that make up the notion of a historical process are clearly manifested together with a microscopic view of how the habits operate. The dual nature of a historical process obtains as a result of the embeddedness of embodied habit-forming and the behaviors they elicit contributing to influencing the formation of habits in others. Processes are not only isolated but instead, parallel and combine with the constraints of others."

Also, the regulated transformations of mechanisms are not to be explained either by the extrinsic, instantaneous, or instantaneous determination of spontaneous sociopathy or by the purely internal, or internal determination of spontaneous sociopathy. Overriding the spurious opposition between the forces described in an earlier state of the system, the internal forces arising instantaneously as motivations springing from the mental states of the organism are the main factors influencing the behaviors of the organism. In this respect, they may show the same table manners even if there is no ongoing interaction between them.

In the case of the hierarchies, to which the self-maintenance of the hierarchy is an organizational invariant, the properties of the process in need of explanation are not directly related with its maintenance, but are rather contained within a spontaneous invariant. In some cases, the processes may have properties of an open historical process.

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"In this quotation many of the ideas that make up the notion of a historical process are clearly manifested together with a microscopic view of how the habits operate. The dual nature of a historical process obtains as a result of the embeddedness of embodied habit-forming and the behaviors they elicit contributing to influencing the formation of habits in others. Processes are not only isolated but instead, parallel and combine with the constraints of others."
3.4 Summary

In this chapter the concept of historical process has been presented. In the sense intended, it does not suffice that a process be subject to contingencies to be able to say that it is a historical process. Nor is it sufficient to say that because a historical explanation is suitable, the process should be called historical. Rather, the term is restricted to processes in which contingencies occur and genetic explanations may often be useful, but at the same time, the processes present a special relation between their dynamics and changes in their own context or constraints. The operation of the systems involved in a historical process affects its constraints in ways that are often manifested as changes occurring at a slower time-scale or as occurring due to the recurrent interaction with other processes. Any process that is able to alter its own conditions of realization is a historical process.

The term “constraint” has been used in a more general sense than its classical meaning of a limiting relation in order to point to the contextual conditions by which general dynamical principles are embodied in an actual process. These constraints may change during the unfolding of the process and these changes remain distinguished from the dynamics of the process itself because the process is identified by an observer as maintaining certain organizational relationships unchanged.

In addition, due to the interplay between the dynamics of the process and its conditions of realization, new spontaneous organizational relations may appear which also remain unchanged. Understanding how these spontaneous invariants are constituted can provide a powerful explanatory tool, since they specify the conditions for their own perpetuation. As such, they are sources of order which may also affect other aspects of the process.

Concrete examples of such an explanatory power will be presented in the studies that will follow. But before that, since these studies comprise mainly a combination of mathematical models and computer simulations, it will be appropriate to address some issues regarding how these models are going to be used as tools of scientific inquiry and what knowledge should one expect to extract from them. These and other methodological questions will be the subject of the next chapter.

Chapter 4

Methodological issues in the use of formal models and computer simulations

The previous two chapters have described the theoretical landscape in which concrete questions about social coordination can be framed. These questions will be investigated by a series of mathematical models and computer simulations. But before proceeding to those specific models, some comments will be made on the way formal models in general and simulations in particular will be used in this thesis.

This insistence on methodological issues is not capricious, particularly when computer models are involved. There is a growing concern in the research communities in which these models are used about how simulations should be built, how should they be applied to scientific questions, and how do they relate to other scientific activities like formulating hypotheses and proposing explanations, (Taylor & Jefferson, 1995; Boneabeau & Theraulaz, 1995; Miller, 1995; Di Paolo, 1996b; Jackson, 1996; Kitano, Hamahashi, Kitazawa, Takao, & Imai, 1997; Robson & Beshers, 1997; Noble, 1997; Bullock, 1998).

In building and using the computer models in this thesis, questions of this sort have been asked and answered. This is reflected in the models themselves. However, addressing these questions was not a trivial task; it involved a process of elaboration of methodological issues. In order to find answers to these questions it was necessary first to formulate them clearly and within an appropriate context.

There are three main reasons for presenting this process of elaboration in this chapter. First, because it is intended to raise awareness of the kind of methodological pitfalls that may often be encountered when using simulations in a scientific context. Second, because it is also intended to make a contribution to these issues in itself. And finally, because it will help in highlighting how the proposed methodologies have been used in the rest of the thesis. At the same time, it will become clear that when these methodologies included novel factors these have been applied successfully to concrete research questions.

In the following section, an argument will be presented in favour of a comparative approach to the use of formal models in science. This argument is based on a pragmatic view of science as a culturally situated activity. Performing systematic comparison between formal models of different...
Chapter 4. Methodological issues in the use of formal models and computer simulations

4.1 A pragmatic approach to formal modelling

At times, when scientific activity becomes increasingly specialized and disciplines ramify into watertight compartments, it is unusual to find practising scientists worrying too much about how science is practiced. According to Rorty, pragmatism takes the Deweyan or Baconian viewpoint that science is neither right nor wrong but that nevertheless any other demarcation of science as well as the special methods or having a special relation to reality will not be able to replace prediction and control. The perspective of the Baconian viewpoint that science is whatever gives us this particular sort of power may turn out to be an unavoidable generalization particularly in view of complex processes such as those described in the previous chapter.

Pragmatism recognizes science as a human activity that must be understood within and by following particular methodologies and ontological priorities which are mostly more often made by philosophy without fully recognizing their consequences. It would seem that a critical approach to claiming the cultural practices of the time and many scientists choose either to ignore or to accept this fact without fully recognizing its consequences. It would seem that a critical approach to claiming the cultural practices of the time and many scientists choose either to ignore or to accept this fact without fully recognizing its consequences.

Kuhn himself expressed an early interest in the philosophy of science. Kuhn's work on the nature of scientific revolutions is likely to be read by those who are interested in the logic of scientific discoveries and the embedding of science within culture. Kuhn himself expressed an early interest in the philosophy of science. Kuhn's work on the nature of scientific revolutions is likely to be read by those who are interested in the logic of scientific discoveries and the embedding of science within culture. Kuhn himself expressed an early interest in the philosophy of science. Kuhn's work on the nature of scientific revolutions is likely to be read by those who are interested in the logic of scientific discoveries and the embedding of science within culture.

4.2 Computer simulations and their use

An adequate framework is proposed for studying the question of how to integrate simulations into the rest of scientific activity. The positive contribution of this section will be based precisely on the idea of understanding how to integrate simulations into the rest of scientific activity. The positive contribution of this section will be based precisely on the idea of understanding how to integrate simulations into the rest of scientific activity.

Despite insisting on their character as tools of research, there is a tendency to equate formality of some of these models with a logical demonstration of the truthfulness of their conclusions, thus forgetting that, even if the theory they are supposed to be instantiating is with complete success accepted as the most adequate, the actual construction and expression of these models only implies a certain process of abstraction of explicit and implicit assumptions which allow their elaboration in a mathematical or logical form. This process of abstraction is necessarily partial, and we cannot assume the ability to isolate all the implicit assumptions which are contingent, rather than absolute, facts which may depend on issues of varying degree of complexity.

It is necessary, then, to make a distinction between the truths that can be formally expressed and those that are fundamentally contingent. Particularly, there is a risk of overformalisation, that is, of equating the formality of some of these models with a logical demonstration of the truthfulness of their conclusions. This is mainly about an existing theoretical structure and only indirectly about observable phenomena. The question then arises of whether the use of these models can be justified at all given the vulnerability to being contradicted once seemingly innocuous assumptions are exposed as being false.

The basic idea consists in using simultaneously models of different degrees of granularity to express the complexity of the subject at hand. In this way, a model which has been extended, for example, by allowing continuous variables to be used instead of discrete entities, will find it very hard to revise them. On the contrary, a model that is extended in a parsimonious way, such as that of a scientific knowledge map (see section 4.2.3), will almost certainly be possible to extend further. This is mainly because the existing assumptions are of a more general nature and can be used to explain a wide range of phenomena. In this way, the continuous variables as discrete entities are forced to conform to the new variables which we can almost call real,
Chapter 4. Methodological issues in the use of formal models and computer simulations

4.2 A scientific use for computer simulations

Given the relative flexibility of computer simulations, their use seems particularly adequate for the task of the comparative methodology described above. But their use also introduces a new risk, which is the danger of losing sight of the methodological issues that arise when using formal models. How can one gain more information from a computer simulation than is already inherent in the model itself? How can one avoid the trap of building computer simulations that are not self-contained and do not provide any additional information? These are legitimate questions that anyone who intends to use computer simulation seriously should ask and ponder before starting a project.

First, one should be cautious about the use of simulations as a scientific tool. A computer simulation is not a useful tool for scientific purposes unless it is designed to perform a specific task. For example, a simulation of aircraft design requires a high level of detail and precision, while a simulation of climate change might require much simpler assumptions about the underlying processes. The choice of model depends on the scientific question being addressed, and it is important to select a model that is appropriate for the task at hand.

Second, one should be aware of the limitations of computer simulations. A computer simulation is not a complete substitute for theoretical work. It can provide valuable insights into complex systems, but it cannot replace the need for rigorous theoretical analysis. A computer simulation should be used to complement theoretical work, not to replace it.

Third, one should be mindful of the assumptions underlying the simulation. A computer simulation is only as good as the assumptions it is based on. If the assumptions are flawed, the simulation will not provide useful insights. It is important to carefully consider the assumptions that underlie a simulation and to test them against the data available.

Fourth, one should be aware of the potential for bias in computer simulations. A computer simulation can be used to support a particular point of view, and it is important to be aware of this potential. It is important to be critical of the assumptions underlying a simulation and to question the conclusions that are drawn.

Finally, one should be aware of the potential for misinterpretation of computer simulation results. A computer simulation can provide valuable insights into complex systems, but it is important to be aware of the potential for misinterpretation. It is important to carefully consider the assumptions underlying a simulation and to test them against the data available.

In summary, computer simulations can be a valuable tool for scientific research, but they are not a substitute for theoretical work. They should be used to complement theoretical work, not to replace it. It is important to carefully consider the assumptions underlying a simulation and to test them against the data available. Only in this way can computer simulations be used to provide useful insights into complex systems.
It is suggested here that the best framework for addressing the issues raised in the previous section is a simulation. One that is strongly recommended is a simulation that meets certain criteria, so that it can be said that specific phenomena are replicated by it, in some way an explanation of those phenomena. (Bonacina & Tharaldsen, 1995). But it is always possible that a simulation is not successful. In such cases, the researchers have to decide whether to abandon the simulation or to try to improve it.

4.2.1 Science and instruments

Science is about understanding the world around us. It is a process of exploration and discovery. The role of science is to explain the phenomena that we observe in the world. The methods used in science are designed to help us understand the world around us. These methods include experiments, observations, and models. Science is about making sense of the world around us.

4.2.2 Tools in scientific activity

The prevalence of mediation is a characteristic feature in all human activities, science being no exception. As much as scientists and philosophers believe in the beginnings of pure knowledge (praxis), such beliefs have to be put aside when considering the potentialities of scientific practice. Most of the time, the researchers are dealing with the contingent set of instrumentalities used to obtain such knowledge (praxis), such that it is not always possible to achieve, and, more importantly, it has shown little pragmatic value.

John Dewey was one of the most fervent advocates of the view that knowledge and action bear not just a historical relation, but instead: “What method of use for computer simulations will be the ‘right’ one for doing science?”, but instead: “What method will integrate computer simulations into an existing form of science?”, for instance (Heidegger, 1962, pp. H69 – H62, 98 – 102). This is why, for certain unexplained and unexplained reasons, the engagement in some sort of skillful activity continues, for instance (Heidegger, 1962, p. 143).

A possible exception to this would be the rather restricted case in which a class of formal systems is in itself an object of study which, for some reason, it makes sense to approach in a more or less empirical manner. For instance, the effects of synchronous updating may be empirically studied in a class of cellular automata (Ingerson & Buvell, 1984; Bersini & Detours, 1994), the class of coupled-map lattices (Abramson & Zanette, 1998a; Rolf, Bohr, & Jensen, 1998) or in the class of random Boolean networks (Harvey & Bossomaier, 1997).
tools can be considered transparent. If a scientist is examining a blood sample under a microscope, her concern is with the sample, not with the microscope itself. If she has mastered the use of the instrument, it is a factor in her ability to carry out the task at hand. However, if the microscope is in working order, she is more likely to concentrate on the sample itself. In this case, the microscope is something that is transparent to her, allowing her to focus on the task at hand.

Tools can also be associated with more theoretical activities, for instance when a physicist linearizes a dynamical system around a fixed point to determine its stability or, in a much more obvious way, when we use equipment for the structure of a microscopic view of the brain or for the structure of the body. In this way, tools can serve as a bridge between the macroscopic and the microscopic worlds, allowing scientists to explore the complexity of the world in a systematic and controlled way.

In science, the use of tools is not just a matter of practical necessity, but it is also a means of establishing a connection with the world. Tools serve as a mediating link between the scientist and the world, allowing the scientist to manipulate and control the world in a way that would be impossible otherwise. This is why the use of tools is so important in scientific practice. It is through the use of tools that scientists are able to make sense of the world, to understand it, and to communicate their findings to others.

Although a scientific discipline does not mean that any such framework of normativity can be called science. Certain norms are established as a result of scientific activity. These norms are not arbitrary, but they are based on a deep and complex understanding of the world. They are a reflection of the way in which scientists interact with the world, and they are a way of expressing the values and beliefs that underlie scientific practice.
4.2 Thought experiments

As emphasized above, a tool is not necessarily a physical "thing." It is possible to talk about procedures of tools. Particular attention will be paid here to what can loosely be called conceptual tools. These are tools for dealing with conceptual structures, though they may be applied for purposes unrelated to the original reason for introducing them. Examples of tools include techniques for studying the internal consistency of a theory, the use of computer simulations, and the application of thought experiments.

4.2.1 Thought experiments.

Thought experiments provide a particularly useful possibility for addressing conceptual issues. They are often used to explore the implications of theoretical constructs, to illustrate concepts, or to illustrate the limitations of theoretical frameworks. Thought experiments are essentially hypothetical constructs that are used to explore the implications of theoretical constructs and to illustrate concepts. They are often used to illustrate the limitations of theoretical frameworks and to explore the implications of theoretical constructs.

4.2.2 Thought experiments in the use of formal models and computer simulations.

The use of thought experiments in the use of formal models and computer simulations is an important aspect of the use of these tools. Thought experiments are useful for exploring the implications of theoretical constructs and for illustrating concepts. They are often used to illustrate the limitations of theoretical frameworks and to explore the implications of theoretical constructs.
Chapter 4. Methodological issues in the use of formal models and computer simulations

In view of the themes discussed in chapter 3, a case of interest occurs when objects at a certain level of description incorporate ways of responding to constraints imposed by the higher level, which may be characterized by a formal model of basic constituents. Each of these basic constituents may be associated with specific identities and rules of correspondence, giving rise to interactions within and between the constituents. For instance, the field of systems theory has been concerned with the problem of how to describe systems at different levels of complexity (Rasmussen & Barrett, 1995). In particular, the use of computer simulations has been employed to study the emergence of new properties in complex systems.

A simulation is an iterated mapping performed on a set of objects, with each object following a transition function. This function is typically defined over a discrete set of states, and the mapping is performed over a set of objects. The simulation is said to converge if the mapping stops at a fixed point.

An important issue is how to measure natural structure. For instance, the problem of how could the "observational capabilities" of basic constituted objects be themselves constructed during the running of a simulation (Cariani, 1991; Pattee, 1996). These issues are fascinating but beyond the scope of this chapter and would deserve a separate treatment.

It is the possibility offered by computer simulations for allowing the exploration of emergent phenomena, particularly in biology. A fairly straightforward way of integrating computer simulations within biological research has been recently suggested by Rasmussen et al. (1995). They propose a cycle of biological research which may be described as follows:

**4.2.5 Integrating simulations in biology**

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**4.2.5 Integrating simulations in biology**
Chapter 4. Methodological issues in the use of formal models and computer simulations

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In this way, we return to an example formulated in an earlier section: if a game-theoretic model is applied in a ontological or theoretical framework, it is to be expected that the assumptions of the model will be necessarily relaxed, as long as the model aims to simulate relevant phenomena. Thus, in the case of the model used in the previous example, the implicit theory of use of the original tool which leads to a process of hypothesis testing, is replaced by a new tool which aims at simulating another phenomenon. This new tool, with the addition of a virtual environment, can explore the soundness of the hypothesis. In this cycle, hypotheses are generated from the observation of natural phenomena, and they are built into simulations which may point to new problems in evolution. One is assuming the implicit theory of use of another tool, which leads to a process of hypothesis testing. The only difficulty would be that in the case of the simulation, instead of purely mathematical models, will be needed to test theoretical predictions. This point is reinforced if one intends to use formal models comparatively following the pragmatic approach described in section 4.1. Although a similar philosophy can be found in Miller's proposal, it was already seen that many of the potential areas of application of computer simulations are not necessarily the case, but since assumptions are relaxed systematically, it is possible for a simulation that aims at addressing a scientific issue in theoretical biology can be found. At the risk of overemphasizing the point, it must be said that there is nothing wrong with Milner's proposal in itself as it does not constitute a methodological solution to the integration problem. Nevertheless, his method of integrating computer simulations with an already defined role within that background would be beneficial in the sense that it could possibly compensate such cases. A different approach has been proposed by Miller (1990). He suggests that a good starting point for a simulation is to address a scientific issue in theoretical biology. The idea is to verify the assumptions of the formal model can be gradually relaxed and the consequences will be in the case of many issues of interest, such as the origin of life, the evolution of communication, etc. In difficult to see how any methodological "cycle" could ever be completed in such cases.
While clearly an important use of computer models, proofs of concept are just part of what can be done with a simulation. In many cases it is not directly obvious how the patterns of interest are related to aspects of the model or which aspects of the model are involved with which. Nobody dictates how to build the model. It is possible to distinguish three different phases for achieving this: Exploratory phase: Run different cases of interest, define observables, explore patterns, and relate the organization of observables to the structure of the simulation. Experimental phase: Formulate hypotheses that organize observations. Run crucial experiments to test these hypotheses. Explanatory phase: Relate the organization of observations to the theories about natural phenomena and the hypotheses that motivated the construction of the model in the first place.

This sort of methodology has been applied successfully in many instances (Boerlijst & Hoggewege, 1991b; Fontana & Buss, 1996; Hemelrijk, 1997a; and others; see also chapters 6, 7, and 9). The first preconception that must be changed is the idea that all that is required from a computer simulation is a model that reproduces the observed patterns of interest. This viewpoint is based on the premise that successful replication implies a backward "metaphorical step". The first use of metaphors is found when the model is created univocally. The observations organized by the second phase prevent random fact gathering and provide a theoretical perspective about the simulation (that is to say, based on existing theories or models). The first use of metaphors is found when the model is created univocally. The observations organized by the second phase prevent random fact gathering and provide a theoretical perspective about the simulation (that is to say, based on existing theories or models). However, nothing guarantees that this same set of metaphors will be sufficient when one wants to project observations made after running of the simulation back into existing theoretical entities about the natural world. This may be a trivial step if the observed patterns, or relationship between patterns, are simpler (more plausible, nice, etc.) than the original patterns. When it is not, one might need to generate new metaphors.
Chapter 4. Methodological Issues in the Use of Formal Models and Computer Simulations

The question of how exactly should those computer models be built and used has been a matter of some concern recently. This is a tricky but interesting situation because lack of translation into existing theoretical terms makes it difficult to understand the model. The problem is not one of modeling natural phenomena, but of understanding them. The existing theory gave rise to a new name. The organizing theory of what it observes in the simulation can provide a translation into existing theoretical terms. This is not a trivial version of the initial metaphors, as integration into the rest scientific practice is done from a more theoretical side, i.e., as a conceptual tool.

A pragmatic approach to the use of formal models in theoretical inquiry has been proposed in this chapter. This approach suggests that instead of looking for a good replication of natural phenomena, a formal model should be used in comparison with other similar models in order to expose the re-use of their differences and help in this way to understand the theoretical roles possible implicit factors. In contrast, comparison between models with little geological connection is bound to reveal more information about the differences that can be exploited by the corresponding formalisms. A new method of comparing models with enough potential to yield different results. Parameters between the compared models, if not necessarily the same, are found to be those that affect the overall result, although only a small subset of the possible implicit factors. In this way, understanding factors can be more difficult to obtain.

4.3 Summary

A pragmatic approach to the use of formal models in theoretical inquiry has been proposed in this chapter. This approach suggests that instead of looking for a good replication of natural phenomena, a formal model should be used in comparison with other similar models in order to expose the re-use of their differences and help in this way to understand the theoretical roles possible implicit factors. In contrast, comparison between models with little geological connection is bound to reveal more information about the differences that can be exploited by the corresponding formalisms. A new method of comparing models with enough potential to yield different results. Parameters between the compared models, if not necessarily the same, are found to be those that affect the overall result, although only a small subset of the possible implicit factors. In this way, understanding factors can be more difficult to obtain.
Chapter 4. Methodological issues in the use of formal models and computer simulations

Simulations are at a disadvantage in this respect compared with mathematical models. Anyone with a certain degree of mathematical literacy can follow the assumptions and results of mathematical models and get an idea of whether the conclusions drawn are valid. This is not the case for computer simulations, even when computer code is shared (not an universal practice, by the way). In this chapter, formal models will be used to explore some of the methodological issues in the use of formal models and computer simulations. As was commented in chapter 4, it is not the concern of this thesis to make accurate models of natural phenomena and then test those models against actual measurements. Rather, the motivation is to improve the communicability behind the use of formal models, as well as other more specific issues.

As mentioned in the introduction, the motivation of the systematic comparison of simulations in social coordination is to develop an understanding of how and why the evolutionary scenario presented in chapter 2 remains silent about functional issues like the conditions for cooperative behavior to evolve. The study will be motivated in questions regarding the evolutionary and ecological dynamics of social coordination in situations in which the interests of the participants may be said to be in conflict. Given the relevance of this topic in current evolutionary biology, it cannot be ignored by this thesis.

The actual practical value of the methodological proposals made in this chapter will be tested in the rest of the thesis. As mentioned before, the comparative approach to formal modelling will be used in chapters 5, 6, and 7. Also, chapters 6, 7, 8, and 9 are intended to demonstrate how explanations can be built based on the careful study of different patterns and their interrelations (as in figure 4.2) and not simply as proof that the basic building blocks are responsible for the generation of those global patterns (as in figure 4.1).
A game of action coordination: mathematical models

Chapter 5

5.1 The game

The evolutionary dynamics of simple action-exchange games (for instance, Hinoi, 1995) can be investigated by comparing different formal approaches or less systematically. The investigation will be restricted to cases in which the game presents a conflict of interest between the two participants (Trivers, 1974) since those cases are considered to cover the more general ground that would probably require additional explanation.

Formally, the game consists of a simple simultaneous move decision between two players, after which the outcome of the game is fixed. Each player receives a certain payoff, or instead a certain penalty, in order to keep the players informed of the outcome of their move. The game is intended to be a model, it is helpful to describe the game in metaphorical terms within the backdrop of an ecological situation in which two organisms try to extract energy from a single, shared, food source.

The inspiration is drawn from a simple, two-actor problem used in the investigation of a situation with a conflict of interest. Suppose that an animal has found a piece of food and has to decide whether to advertise it or to hide it from another, nearby conspecific. The first individual will try to access the piece of food, which requires an appropriate action such as digging the ground or climbing a tree. Such actions will be accompanied by different manifestations such as noises, movements, etc., which may be perceivable by other individuals and influence their behavior. The actions of the players are said to coordinate if the outcome of the interaction is the result of combined cooperation which would not be in the interest of either player acting alone. The players are said to be coordinated cooperatively when the outcome of the interaction is the result of combined cooperation which would not be in the interest of either player acting alone. The players are said to be coordinated cooperatively when the outcome of the interaction is the result of combined cooperation which would not be in the interest of either player acting alone.

The answer to some of the questions posed in this chapter will have to wait until the following sections and chapters. Notice also that this game has a defined time structure (which is why it is possible to play either of the two roles on different occasions) and that the differences between roles (behavioral or not) are contextual and depend on the pool of different actions present in the population of players at that time.

The parameter 

\[ c \]

is the proportion of the energy extracted from the food source which is greater than half but less than 100%. The rest of the energy remains in the food source. The parameter 

\[ E \]

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For the time being, it will be assumed that evolution proceeds mainly by genetic drift. Now, if cooperation, or the lack of it, depends totally on either one of the participants in an individual fashion, the preferred outcome of the game would be clear when the first participant receives a lesser payoff (say, in units of energy) since the food will become available. The first player has succeeded in distracting the attention of the second player so that the energy remains in the food source. The parameter 

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It was mentioned in section 3.2.3 that the natural drift perspective on evolution allowed different dynamics depend on the form of coupling between agents and environment. For instance, evolution driven by differential reproduction (Press, Teukolsky, Vetterling, & Flannery, 1992).

The answer to some of the questions posed in this chapter will have to wait until the following sections and chapters. Notice also that this game has a defined time-structure (which is why it is possible to play either of the two roles on different occasions) and that the differences between roles (behavioral or not) are contextual and depend on the pool of different actions present in the population of players at that time. The parameter 

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Chapter 5. A game of action coordination: mathematical models

The relative importance of some of these limitations will be explored by presenting a set of game-theoretic models with different configurations, as explained in the following sections. Other issues, as already mentioned, will be explored in subsequent chapters.

5.2.1 Strategies

The range of possible individual behaviors is divided into a discrete set of pure strategies, which are combinations of the actions available to each player. Suppose also that the available actions are divided into two sets, those that require "A" and those that require "B". Suppose also that two signals, "α" and "β", can be accompanied by either of two possible perceivable manifestations, "γ" or "δ". In order to define the strategy of a player in the first role, it is necessary to specify how each player perceives the manifestations of the opponent's signals, and how the player responds in a situation where the opponent is playing a non-relevant action. The combination of the strategies for the first and second roles results in four possible overall strategies, each of which is associated with a particular combination of manifestations and actions. In keeping with the above assumptions, the signal accompanying the action of player 1 will be "α", and the signal accompanying the action of player 2 will be "β". By designating the different perceivable manifestations of the actions of the first player as "γ" or "δ", respectively, we can also be better able to identify the signals for the second player. For instance, we can assume that the signal for the first role is "α" and the signal for the second role is "β". The combination of the signals and the corresponding actions results in four types of possible relationships between the four strategies. Table 5.1 and 5.2 show the behavior of these four types. Table 5.1 is the same as the one shown in figure 5.1, where each arrow represents a relationship between the four strategies. Table 5.2 is a similar table, but it is shown in figure 5.1, where the arrows represent the relationships between the four strategies.

Table 5.1: External manifestations associated with actions "A" and "B" performed by each type of agent when playing the first role.

<table>
<thead>
<tr>
<th>Action</th>
<th>Type 1</th>
<th>Type 2</th>
<th>Type 3</th>
<th>Type 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>αβ</td>
<td>αγ</td>
<td>αδ</td>
<td>αδ</td>
</tr>
<tr>
<td>B</td>
<td>βγ</td>
<td>βδ</td>
<td>βδ</td>
<td>βδ</td>
</tr>
</tbody>
</table>

Coordinated behavior occurs when both players end up performing the same action ("A" or "B") according to the appropriate choice of the strategies. The question of the relation of the payoffs given by a particular strategy to the Darwinian fitness of the individuals using it is also a subtle one. Most game-theoretic models deal in terms of payoffs assigned to the players after the game. These payoffs, which are often interpreted as costs or benefits of certain actions, can be successfully decoupled from the evolutionary process. The question of the relation of the payoffs to the Darwinian fitness of the individuals using it is also a subtle one. Most game-theoretic models deal in terms of payoffs assigned to the players after the game. These payoffs, which are often interpreted as costs or benefits of certain actions, can be successfully decoupled from the evolutionary process.
Chapter 5. A game of action coordination: mathematical models

<table>
<thead>
<tr>
<th>Signal</th>
<th>Type 1</th>
<th>Type 2</th>
<th>Type 3</th>
<th>Type 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>α</td>
<td>A</td>
<td>A</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>β</td>
<td>B</td>
<td>B</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>δ</td>
<td>-</td>
<td>-</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>γ</td>
<td>-</td>
<td>-</td>
<td>B</td>
<td>B</td>
</tr>
</tbody>
</table>

Table 5.2: Action ("A", "B") performed by each type of player when playing the second role, depending on the perceived external manifestation ("Signal"); "-" means a non-relevant action.

From the payoff assignment scheme described above (section 5.1) and assuming \( E = 1 \) the payoff matrices for the first and second role (\( M_1 \) and \( M_2 \)) are:

\[
M_1 = \begin{pmatrix}
\frac{1}{2} & 1/2 & c & c \\
1/2 & 0 & 0 & 1/2 \\
c & 1/2 & 1/2 & c \\
0 & 1/2 & 1/2 & 0
\end{pmatrix}
\]

\[
M_2 = \begin{pmatrix}
1/2 & 1/2 & c & c + 1/2 \\
c + 1/2 & c & 1/2 & 1 \\
c & c + 1/2 & 1 & 1/2 \\
1/2 & 1 & c + 1/2 & c
\end{pmatrix}
\]

where \( (M_1)_{ij} \) is the payoff obtained by a player of type \( i \) when playing the first role against type \( j \) and \( (M_2)_{ij} \) is the payoff obtained by a player of type \( i \) when playing the second role against type \( j \).

Players can play either one of the two roles on different occasions. If the frequency with which a player plays one role or the other does not depend on the role or on the strategy played, then this asymmetric game can be transformed into a formally equivalent symmetric one with the following payoff matrix:

\[ M = \frac{1}{2} \begin{pmatrix}
1 & 1/2 & c & c + 1/2 \\
c + 1/2 & c & 1/2 & 1 \\
c & c + 1/2 & 1 & 1/2 \\
1/2 & 1 & c + 1/2 & c
\end{pmatrix} \]

5.2.2 Infinite population: static analysis

One of the key theoretical tools in evolutionary game-theory is the concept of an Evolutionarily Stable Strategy or ESS (Maynard-Smith & Price, 1973; Maynard-Smith, 1982, ch. 2). A trait or behavioral strategy whose fitness depends on the distribution within a population of other traits or behavioral strategies is said to be an ESS if in the case that it is adopted by the majority of the population it will not be invaded by descendants of individuals who bear a different trait or use a different strategy. This resistance to invasion is a consequence of the fact that, by definition, the fitness of any trait or strategy other than the ESS is always lower than that of the ESS or at most equal to it. And, in the latter case, the alternative strategy will eventually be invaded by the ESS. This definition can be formalized in the following manner.

Let \( p = (p_1, p_2, p_3, p_4) \) be a vector describing the proportion of players of types 1, 2, 3, and 4 in a polymorphic population which is considered infinite. The sum of the components of \( p \) is always equal to one, which means that \( p \) belongs to the simplex \( S \):

\[ p \in S = \{ x = (x_1, x_2, x_3, x_4) \in \mathbb{R}^4 : \sum_{i=1}^{4} x_i = 1, x_i \geq 0, \forall i \} \]

An ESS, if it exists, is given by a distribution \( p^* \) when:

\[ p^* \cdot M \cdot p^* \geq q \cdot M \cdot p^*, \quad \forall q \neq p^* \tag{5.1} \]

and

\[ p^* \cdot M x > q \cdot M x \quad \text{if} \quad p^* \cdot M p^* = q \cdot M p^*, \tag{5.2} \]

where \( M \) is the payoff matrix and \( x \cdot M y \) is the average payoff of a sub-population described by \( x \) within a population that plays with a distribution \( y \). The above conditions can be interpreted as saying that, if \( p^* \) is an ESS, in a population described by distribution \( p^* \) a small group described by a different distribution \( q \) will have at most an equal average payoff when playing against the rest of the population and in that extreme case the rest of the population will do better when playing against players in the small group than these players against themselves.

A polymorphic population is a population in which more than one pure strategy can be present. Under certain circumstances results obtained for a polymorphic distribution \( p \) are equivalent to a case with mixed strategies where each player plays strategy \( i \) with probability \( p_i \), however this is not generally the case, see (Maynard-Smith, 1982, Appendix D). The cases studied here are restricted only to pure strategies.
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One way of finding a Nash equilibrium is to look for the extreme points of the function $F(x)$, subject to the constraints $G(x) = 0$. The solutions found in this way are the Nash equilibria. The extreme points can be found by solving simultaneously the system:

$$\nabla F(x) = \lambda \nabla G(x),$$

(5.3)

$$G(x) = 0.$$  

(5.4)

A solution set for this system is given by:

$$P = \left( a_1, a_2, \ldots, a_n \right)$$

(5.5)

where $a_i$ is the vector whose components are all 0 except the $i$th which is 1. The first term in $F(x)$ is the average profit of the players and the second term is the average profit of the whole population.

5.2.3 Infinite population: dynamical analysis

By definition, the Nash equilibrium concept is static; i.e., it refers to a situation of stable equilibrium. However, the same kind of game theoretic analysis that leads to the notion of Nash equilibrium has been successfully applied to model evolutionary dynamics by the advantage of the idea of a ‘competitive game’. (Zeeman, 1979; Schuster & Sigmund, 1981; and in general, the resulting dynamical equations are described by Zeeman, 1979; Schuster & Sigmund, 1981.

The rate of growth of the proportion of individuals playing a particular strategy is proportional to the current number of players playing that strategy and to the relative advantage of those players with respect to average fitness of the whole population. This can be expressed in the following way:

$$\frac{dp_i}{dt} = \left( \sum_{j \neq i} p_j M_{ij} - p_i M_{ii} \right) F_i(p)$$

(5.6)

where $c_i$ is the vector whose components are all 0 except the $i$th which is 1. The first term in the parenthesis indicates the average profit for strategy $i$ when playing against the population. The second term, $F_i(p)$, is the relative advantage of those players with respect to average fitness of the whole population. This can be expressed in the following way:

$$F_i(p) = \sum_{j \neq i} p_j M_{ij}.$$
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In fact, by moving the initial conditions continuously along the set $P$ it is found that some points in $P$ are weakly stable, i.e. they are neutral with respect to translations to neighboring points in $P$, but stable to other perturbations. This can be proved by performing a linear stability analysis\(^2\).

The three eigenvalues\(^3\) for the linearized equations (5.6) are calculated around a general point $p_0$ in $P$. One of the eigenvalues, as expected, is always zero (indicating neutral displacement within the neighbouring points in $P$) and the others are given by:

$$\lambda_{1,2} = ac + \frac{1}{4} - \frac{1}{4} \epsilon - a \pm \frac{1}{4} \sqrt{16 c^2 a^2 - 8 c^2 a + 1 - 2c + c^2}$$

Figure 5.4 shows that the real part of the eigenvalues, $\text{Re}(\lambda_{1,2})$, is negative for $1/4 < a < 1/2$. In this region there is a higher proportion of strategies $T2$ and $T4$ than $T1$ and $T3$. Points in this region are expected to behave as weakly stable and correspondingly points in the region given by $0 < a < 1/4$ to behave as unstable. This is shown by adding a perturbation term to (5.6) in the form of a small random fluctuation (white noise with range 0.01). The results can be seen in figures 5.5 (a) and (b). In the latter the initial condition is on the weakly stable subset of $P$ and so the movement is confined only to nearby points. In contrast, the initial condition for figure 5.5 (a) is on the unstable subset of $P$ and quickly gets attracted towards the oscillatory dynamics until, by chance, it enters into the weakly stable region and remains there.

What all this means is that, even though there is not stable point in the infinite population dynamics, there is a region of the strategy space where the population is most expected to be found after some time. This is the quasi-stable region where strategies 2 and 4 are equally abundant and

\(^2\)This is one way of analysing the stability of fixed points. It consists of making a linear approximation for the nonlinear dynamics in the vicinity of the fixed point and evaluating whether small perturbations tend to move away from the fixed point or to return to it. This is achieved by calculating the eigenvalues for the temporal dynamics and examining the sign of its real part. If it is greater than zero it means the perturbation has a tendency to increase the distance away from the fixed point in the corresponding direction. The fixed point is therefore classified as unstable. If it is negative the perturbation will tend to decrease and to restore the equilibrium which is then classified as stable. For an introduction and examination of the possible conditions and other methods see (Haken, 1978; Murray, 1989) and others.

\(^3\)Only 3 of the 4 equations (5.6) are independent, since $\sum_i p_i = 1$.

**Figure 5.3**: Trajectories in strategy space for the action-response game under equations (5.6). Initial conditions, (a): $p_0 = (0.27, 0.23, 0.24, 0.26)$, (b): $p_0 = (0.81, 0.09, 0.01, 0.09)$.

![Figure 5.3](image1)

**Figure 5.4**: Real parts of non-zero eigenvalues (vertical axes) for points in point-wise fixed set as a function of parameter $a$ for two values of $c$. Each plot shows two eigenvalues as a function of $a$. One eigenvalue is always greater than the other except in the linear region in the middle where they are equal. Both have negative real part for $1/4 < a < 1/2$.

![Figure 5.4](image2)

are present in a larger proportion than strategies 1 and 3. The symmetrically opposed region is unstable. In other words, the quasi-stable region is that of non-coordination.

In conclusion, two different kinds of behaviors can be expected in the dynamical infinite population model, either oscillations in the case without noise or quasi-stability of non-coordinating strategies when noise is added.

5.2.4 Finite population: dynamical analysis

At present it is accepted that the infinite population limit in Darwinian selection can be a strong simplification whose consequences are not merely quantitative. With the use of mainly statistical and stochastic techniques the role of finite populations in evolution has been highlighted as a limiting factor for allele substitution under natural selection (Kimura, 1995) as well as an order production factor even in the total absence of selection (Derrida & Peliti, 1991). And from the point of view of evolutionary dynamics finite populations have been shown to induce metastability, i.e. epochs of statis punctuated by rapid changes in global fitness, (van Nimwegem, Crutchfield, & Mitchell, 1997a, 1997b).

In the case of evolutionary game theory, however, the main effect of considering finite populations is given by the fact that different players "perceive" different distribution of strategies. The ESS conditions (5.1) and (5.2) as well as in the replicator dynamics given by (5.6) the qua...
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Figure 5.5: Trajectories for the perturbed dynamics. Initial conditions, (a): \( p_0 = (0.3, 0.2, 0.3, 0.2) \), unstable region of \( P \), (b): \( p_0 = (0.2, 0.3, 0.2, 0.3) \), stable region of \( P \).

Figure 5.6: Trajectory for perturbed finite population dynamics with \( N = 100 \). Initial condition \( p_0^5 \). (a) continuous evolution, (b) quasi-discrete evolution, (see text).

and the average fitness for the whole population will be given by:

\[
\overline{W} = \frac{1}{N} \sum_i p_i W_i
\]  

(5.7)

and so (5.6) are transformed into:

\[
\frac{dP_i}{dt} = p_i(W_i - \overline{W}), \quad \forall i.
\]  

(5.8)

As in the case of equations (5.6), it is easy to see that the sum over \( i \) of all the derivative terms \( \sum p_i \) remain fixed, null and therefore \( \sum p_i = \) constant, as required.

A search is made for relevant fixed points in (5.9) (i.e. those that fulfill the condition \( \sum p_i = \) constant) and finding the following:

\[
P_i^1 = (N, 0, 0, 0) \quad P_i^3 = (0, 0, N, 0) \quad P_i^5 = (N/2, 0, N/2, 0)
\]

\[
P_i^2 = (0, N, 0, 0) \quad P_i^4 = (0, 0, N, 0) \quad P_i^6 = (0, N/2, 0, N/2)
\]

By performing a linear stability analysis \( P_i^6 \) is found to be the only stable attractor. There already an interesting difference with the infinite case. Instead of a set of point-wise fixed points, only the two extremes of that set \( (P_i^0 \) and \( P_i^6 \) remain fixed. Figure 5.6 (a) shows the numerical resolution for \( N = 100 \) and initial condition \( p_0^5 \) where a small random term has been added to test stability. In this tetrahedron diagram \( P_i/N \) is plotted as the density of i-strategists in the population. The trajectory is drawn towards \( P_i^6 \).

Although equations (5.9) are treated as continuous over the \( P_i \), these in fact represent discrete quantities (whose minimum variation is 1 individual) and therefore linear stability may not guarantee that a fixed point will be stable against discrete perturbations. In order to test if this is the case it is helpful to perform a discrete perturbation analysis on the above fixed points consisting of the addition of one individual to one of the sub-populations and a compensating subtraction from another in all possible combinations. Examining the time derivatives it can be determined whether

9To simplify the notation, the vertices of the tetrahedron are label just with the corresponding vector \( P_i \).
there is a tendency to return to the fixed point or move away from it. In all cases the linear stability analysis has been confirmed, although in some, for instance...
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The calculations proceeded as if all strategies were freely realizable in any given population and their growth depended only on their payoff. It is clear, though, that if behavioral strategies, as other phenotypic traits, somehow depend on genetic constitution, then their realization may be constrained by factors other than the strategy payoff. In the most obvious example, the best strategy could be realized by a heterozygote in a diploid system. This would mean that a proportion of the best strategies would be realized by the heterozygote, while in the purely game-theoretic analysis they would disappear. (Grafen, 1991).

The purpose of this section is not to describe a complex scenario, such as a diploid genetic system realizing the four strategies, in order to study the effects of genetic constraints since there is no evidence of how such a genetic system would be constituted. Instead, the simpler question of how a trivial haploid system in the presence of mutations would affect the evolutionary dynamics will be addressed. The main reason for investigating this question is because such a system does not allow the cyclic attractor to be achieved.

The addition of a point mutation operation to the dynamics establishes an additional metric over the strategy space. If the mutation rate is 0.01 per unit of time, the initial conditions are the same as in the previous section, and so is the added random perturbation. As in that case, the system ends up in a higher mutation rate (0.06). Here, it can be observed that, for the same range of noise, a mutation will be more likely to end up playing one of the strategies that are the same as in the previous section, but for a different kind of mutation. If the mutation rate is 0.01, then the chances of two mutations leading to a different kind of mutation (0.01) is given, in this model, by \( Q = \begin{cases} 1 & \text{if } \text{ strategy } \text{ is in the same fix point attractor} \\ 0 & \text{otherwise} \end{cases} \).
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5.1 The model

The model is intended to be described using continuous variable instead of just hyper-local interactions. Therefore, a model with finite locality is presented. Each player can only interact with other individuals located within a neighborhood of fixed radius. This is appropriate for contact processes such as chemical reactions but in the present case it would mean that the range of interactions of players would be very small (just the nearest neighbor). An usual answer to this situation is to "abandon the continuum of spatial scales by forming accumulations where the chances of meeting a "cheater" are very small (Axelrod, 1984; Krakauer & Pagen, 1995). Alternatively, local interactions may increase the chances of providing conditions which, for instance, favor self-reciprocating strategies against parasitic ones.

11 The stability of such density-dependent ESS (DDESS) has been analysed by Cressman (1990).

12 For an introduction to models that include long-range effects see chapter 16 of Murray (1989).

13 The model is not fundamental for assessing the relevance of this model in the context of the rest of the thesis, so wishes, the summary may be read directly and the rest of the section ignored without much loss.

Spatial models have become a hot topic in biology in recent years, partly because of the non-intuitive results they yield and partly due to the possibility of implementing them easily on computer simulations. This is in contrast with the preceding sections of this chapter. An effort was made to provide the readers familiar with the techniques used in this section with enough guidance to facilitate understanding of how the analysis proceeds. However, given that a point not point understanding of the details of the analysis is not fundamental for assessing the relevance of this model in the context of the rest of the thesis, the results will be summarized in section 5.5.5, in order to highlight the main points. If the reader is not familiar with the techniques used in this section with enough guidance to facilitate understanding of how the analysis proceeds, the summary may be read directly and the rest of the section ignored without much loss.

In the present section, specific models have been described using continuous variables instead of just hyper-local interactions. Therefore, a model with finite locality is presented. Each player can only interact with other individuals located within a neighborhood of fixed radius. This is appropriate for contact processes such as chemical reactions but in the present case it would mean that the range of interactions of players would be very small (just the nearest neighbor). An usual answer to this situation is to "abandon the continuum of spatial scales by forming accumulations where the chances of meeting a "cheater" are very small (Axelrod, 1984; Krakauer & Pagen, 1995). Alternatively, local interactions may increase the chances of providing conditions which, for instance, favor self-reciprocating strategies against parasitic ones. The model is presented in the form of a spatial model with finite locality as discussed below.

The remainder of section 5.5 will present the continuous spatial model in detail together with a stochastic version of the model. This would allow us to study the effect of density thresholds on the model. In this model players are distributed in space in positions that do not change with time. Each player can only interact with other individuals located within a neighborhood of fixed radius. Locally, the amount of available energy at a given position and time is determined as $E(t, x)$. All players are distributed continuously in space, only at infinitesimal small scales. By varying the parameter $E(t, x)$ or similar model approaches, where interactions can be seen as a result of an interaction between two players.

A sub-population of players of strategies $i$, $j$, $k$ and $l$ is described by its spatial density $p_i(x, t)$, $p_j(x, t)$, $p_k(x, t)$, $p_l(x, t)$ at position $x$ and time $t$. The total density of players is obtained by summing over the strategies: $P_x(t) = \sum_i p_i(x, t)$. Energy resources are also distributed continuously in space, with the amount of available energy at a given position and time determined as $E(t, x)$. All players are distributed continuously in space, only at infinitesimal small scales. By varying the parameter $E(t, x)$ or similar model approaches, where interactions can be seen as a result of an interaction between two players.

In general, a deterministic approach to spatial games involves some sort of reaction-diffusion or similar model able to account for the effects of density-dependent and spatially dependent processes. For example, the model that describes the interaction between two species can be expressed as:

$$
\frac{d p_i}{dt} = \sum_{j \neq i} r_{ij} p_j - d_i p_i + D_i \nabla^2 p_i
$$

where $p_i$ is the density of species $i$, $r_{ij}$ is the reaction rate from species $j$ to species $i$, $d_i$ is the death rate of species $i$, and $D_i$ is the diffusion coefficient of species $i$. The reaction-diffusion equation is a partial differential equation that describes the change in density of species $i$ due to the interactions with other species, the death rate of species $i$, and the diffusion of species $i$ in space.

The solution to this equation can be obtained numerically or analytically, depending on the specific parameters and initial conditions. The solution can be visualized as a spatial pattern, which can be used to understand the dynamics of the system.

In the case of reaction-diffusion equations, the pattern that emerges depends on the parameters of the equation, such as the reaction rates and diffusion coefficients. For example, if the reaction rates are high and the diffusion coefficients are low, the system will exhibit spatial patterns that are stable and do not change over time. On the other hand, if the reaction rates are low and the diffusion coefficients are high, the system will exhibit spatial patterns that are unstable and change over time.

In general, reaction-diffusion equations are used to model a wide range of biological systems, such as morphogenesis, pattern formation, and population dynamics. They are also used in other fields, such as physics and chemistry, to model similar processes.

In the context of this chapter, reaction-diffusion equations are used to describe the interaction between two species, which is influenced by spatial factors such as diffusion and reaction rates. The solutions to these equations can be used to understand the dynamics of the system and predict how the species will interact over time.

The reaction-diffusion model is a good example of a spatially explicit model, which takes into account the spatial distribution of species and their interactions. This is in contrast with more traditional models, which assume that species are mixed together uniformly and interact at random. Reaction-diffusion models are more realistic and can provide insights into the behavior of complex systems.

In conclusion, reaction-diffusion equations are a powerful tool for understanding the dynamics of spatially explicit systems, such as those described in this chapter. They can be used to model a wide range of biological and non-biological systems, and provide insights into the behavior of complex systems.
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all the positions \( u \) in \( \text{Loc}(x) \), the total energy received by a player of strategy \( i \) located at \( x \) playing the second role is:

\[
E^2(\gamma; x) = \sum_{u \in \text{Loc}(x)} |p^i(u)| M_2^i u.
\]

The matrix \( M_2^i \) given in section 5.2.1, specifies the payoff obtained by a second role player, located at \( x \), for the first role with a uniform frequency \( p^i(u) \) in all the positions \( u \) in \( \text{Loc}(x) \). The total energy received by that player from all players of type \( i \) is thus

\[
E^2(\gamma; x) = \sum_{u \in \text{Loc}(x)} |p^i(u)| M_2^i u.
\]

The matrix \( M_2^i \) given in section 5.2.1, specifies the payoff obtained by a second role player, located at \( x \), for the first role with a uniform frequency \( p^i(u) \) in all the positions \( u \) in \( \text{Loc}(x) \). The total energy received by that player from all players of type \( i \) is thus

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\[
E^2(\gamma; x) = \sum_{u \in \text{Loc}(x)} |p^i(u)| M_2^i u.
\]
the environmental energy ($R/\gamma_c$). $A_2$ can be interpreted as a comparison between the characteristic saturation times for the energy ($\tau^{-1}$) and the density of players ($[BL_0]^{-1}$). $D'$ is simply the scaled diffusion coefficient.

In general, in order to solve (5.16) or (5.17) it is necessary to specify an initial condition for each variable and a set of boundary conditions. A finite one-dimensional spatial domain will be used with two possible boundary conditions for all the variables: either Neumann conditions, i.e. all flux must be zero at the boundary (which for the 1-D case studied means that all spatial derivatives must be zero at the boundary) or the rather artificial, but useful, periodic conditions which specify, for 1-D domains, that the values adopted by the variables at one extreme of the domain must equal those at the other. The applicability of this last sort of boundary condition can be justified if the size of the domain $L_D$ is much larger than the typical length of the system ($L$).

5.5.2 Pattern formation

It can be noticed that the system (5.16) [(5.17)] is symmetrical to transformations of the type $x \rightarrow x + \delta$ which suggests the existence of spatially homogeneous solutions. However, the system is not symmetric to scaling transformations of the type $x \rightarrow \kappa x$ due to the finite size of neighborhoods. It would be interesting to explore the possibility of spatial patterns arising from the long range coupling between strategies and energy variable. In order to do this an analysis is performed of the stability of a spatially homogeneous solution for different spatial scales.

This method is described in detail by Murray (1989) in the context of proving the existence of spatial patterns by testing the inhomogeneous instabilities of spatially homogeneous solutions, by testing the system's capacity for pattern formation. A finite domain of only one spatial dimension is assumed and the following steps are followed. First, it is necessary to find a homogeneous solution for (5.16) describing the same equilibrium state for all $x$. Then the linear stability of the solution is tested by adding to each variable a small inhomogeneous perturbation (the solution is assumed to be stable for homogeneous perturbations). In the linear limit the evolution of the perturbed variables will be given by a sum of terms with the form $\exp[\lambda t + ikx]$ where $\lambda$ is the growth factor, $k$ the wavenumber and $i = \sqrt{-1}$. This means that the perturbed state of the system can be described by a sum of wavellike spatial modes each with its own growth factor. If the homogeneous solution is stable this will be manifested with negative growth factors for all possible values of $k$. However, if for certain wavenumbers $Re(\lambda) > 0$ then the corresponding spatial modes will grow indefinitely until a point where the linear analysis is no longer valid and non-linear effects may take control. The fastest growing modes will end up originating spatial patterns.

In principle, the whole spatial domain is finite and this implies that the spectrum of wavenumbers $k$ will be discrete and will depend on the boundary conditions. In order to simplify the analysis, it will be considered that the actual size of the spatial domain is much larger than the typical size of the system, i.e. $r \ll 1$ where $r = 2L/L_D$. This will allow a treatment of the wavenumber spectrum as continuous, an often used simplification (Murray, 1989, p. 386).

As this is a proof of existence, it suffices to address particular cases. Consequently, other
It is apparent that for all values of $A_1$ and $A_2$ the homogeneous solution stable under homogeneous perturbation. In particular, it seems that for small values of $A_2$ the growth factor means that the value, given by the ecological parameters, $Re[k]|_{k=0}$ is now plotted as a function of the neighborhood radius $L$. This is clearly unstable. In fact, all values of $A_2$ and $A_1$ have been chosen, which means that the homogeneous solution is unstable for all values of $A_1$. The following values have been used: $A_1 = 0$, $A_2 = 1$, $A_3 = 2$, and $A_4 = 3$. The most general case will only be shown in the numerical resolution examples.

The condition for non-trivial solutions to exist is that the two equations not be independent, i.e.

$$\begin{align*}
&\text{if } |d| > 0, \\
&\text{then } |d| = 0. \\
&\text{if } |d| = 0, \\
&\text{then } |d| = 0.
\end{align*}$$

The spatial domain is regularly partitioned and all spatial derivatives are calculated using finite differences. The spatial domain is made up of $L = 100$ and the neighborhood radius is $L = 10$. The contrast is high in these areas. Such accumulation will be limited by nonlinear factors, such as the rate of energy transfer and the players self-maintenance costs.
0.1. Periodic boundary conditions have been used as well as random uniform distribution for the initial conditions in the population densities (with range 2.0 per unit of space) and uniform initial value of 1 for the non-dimensional energy. The non-dimensional parameters are set to $c = 0.6, A_1 = 0.25, A_2 = 0.05, D' = 10^{-4}$. Figure 5.11 (a) shows the evolution of the four sub-population as a function of time. Oscillations in number of players can be seen for each sub-population. These oscillations compensate each other to give a constant total number of players in the whole domain after the initial transient. It is also apparent from this figure that two of the strategies (1 and 3) seem to have a smaller mean number of players than the other two. This difference, however, is not a generally observed result and it will be understood in this case once the patterns in the spatial domain have been examined.

Figure 5.12 shows the spatial distribution of players at different times, starting from a random initial condition. Players arrange themselves into two clusters. (The use of a non-zero diffusion term introduces little changes in the results, mainly by smoothing the shape of the clusters which are also found if diffusion is removed.) The relative composition of these clusters changes over time, but the behaviors are different. The composition of the cluster on the left settles, after an initial variation, into a stable state (at about $t = 5500$) where the densities of strategies 1 and 3 have the same variation with $x$ and so do the densities of strategies 2 and 4. Integrating the densities over the cluster it is found that the cooperative strategies 1 and 3 form 43.1 % of the total population of the cluster. The cluster to the right does not settle into a stable state. It is this cluster that provides the oscillatory dynamics observed at the population level in figure 5.11 (a) while the other cluster provides the difference in mean value for the two pairs of strategies. This is a nice example because it shows, at the same time, the two possible situations for a numerical resolution in the absence of noise and because it illustrates a trivial but important property of separation between clusters: independent evolution. However, the more frequently observed behavior is given by the cluster on the right.

---

**Figure 5.11**: Total (non-dimensional) number of players for spatial model. $A_1 = 0.25, A_2 = 0.05, D' = 10^{-4}$. (a) without random perturbation, (b) with random perturbations.

---

**Figure 5.12**: Spatial patterns for numerical resolution of (5.17), $c = 0.6, A_1 = 0.25, A_2 = 0.05, D' = 10^{-4}$.

---

It is interesting to compare these results with the non-spatial models, where it was concluded that there was either a weakly stable region or a stable attractor where strategies 1 and 3 would be present in a small quantity or even disappear. Only in the absence of noise a similar cycle was also established in those cases\textsuperscript{17}. The question is then whether a similar stabilization to a non-cyclic state is to be expected if noise is added to the spatial dynamics.

In order to test this, the equations are solved with the same conditions adding uniform noise in the density variables (mean: 0, range: 0.01 per unit of space and per unit of time). The time evolution is shown in figure 5.11 (b), where it can be seen that oscillations dominate the dynamics. (In this particular run there is only one cluster of players.) In the many independent runs that were studied, stable non-cyclic solution where not observed when perturbations were the addition of noise.

---

\textsuperscript{16} These values were chosen for convenience in numerical resolution and similarity to the computer model presented in next chapter.

\textsuperscript{17} The exception is the case of high mutation rates, as shown in figure 5.8, where the cycle becomes stable even with the addition of noise.
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Some results presented in Chapter 4 have been plotted in different runs. In a case where

\[ \Delta E = E_1 - E_2 \]

is taken as a function of \( x \) for strategy 1. The resulting form depends on the composition of the sub-populations within the cluster. As an example, two different compositions are shown in Figure 5.13: (a) and (b) represent different compositions of sub-populations within the cluster; (c) and (d) represent different compositions of sub-populations within the cluster.

\( \Delta E \) is always greater than zero, and therefore players of strategy 1 are always gaining more energy than players of strategy 2. The energy gain is measured as a function of \( x \), and the resulting form depends on the composition of the cluster and the distribution of sub-populations within it. For example, two different cases are observed in Figure 5.13 where the cluster composition (and variations in environmental energy) and the distribution of sub-populations within it are considered.

Additionally, the spatial distribution of energy also affects the payoff a player receives depending on which role they play. For a population mainly consisting of a player relative to the rest of the energy in the food source (which is located at the same position of the first role player), the payoff for the first role player will be greater for the second role player. Therefore, the payoff for the first role player will be greater for the second role player. In addition, the payoff for the first role player will be greater for the second role player. This is true, however, only if the number of trials an agent makes in order to find a partner (which is always greater than one for all strategies) is greater than one for all strategies. A careful observation of Figure 5.14 shows that some sub-populations are not stable and are invaded by sub-populations 2 (which is afterwards invaded by 3, and so on). There is, however, something suspicious about the postulated situation, since it is not clear what the meaning of an initial distribution where all but one of the strategies are present is. Additionally, the spatial distribution of energy also affects the payoff a player receives depending on which role they play. For an initial distribution, the energy gain is measured as a function of \( x \), and the resulting form depends on the composition of the cluster and the distribution of sub-populations within it. For example, two different cases are observed in Figure 5.13 where the cluster composition (and variations in environmental energy) and the distribution of sub-populations within it are considered.

5.4 Effect of density thresholds, move toward discreteness.

Additional numerical tests were performed in order to investigate the stability of initial distributions that favor one strategy over the others. In the most extreme case, all strategies were initialized with a random spatial distribution, and only one of the strategies (range of 0.1 per unit of space) and a very small number of the remaining ones above. The aim is to observe whether one of the strategies will invade the population. A series of tests were performed solving (5.16) numerically as above and using a mutation scheme as described in Section 5.3. This is achieved simply by adding in each resolution step a number of players after the normal numerical resolution. Accordingly, some of the newborn players of one strategy are mutated into the other strategies in a proportion

\[ \rho \]

for neighboring strategies and \( \psi \) for non-neighboring strategies (as done in Section 5.4). The results are shown in Figure 5.14 where the population composition (and variations in environmental energy) and the distribution of sub-populations within it are considered.

\( \rho \) and \( \psi \) are always greater than zero, and therefore players of strategy 1 are always gaining more energy than players of strategy 2. The energy gain is measured as a function of \( x \), and the resulting form depends on the composition of the cluster and the distribution of sub-populations within it. For example, two different cases are observed in Figure 5.13 where the cluster composition (and variations in environmental energy) and the distribution of sub-populations within it are considered.
In a spirit similar to that of the quasi-discrete stability analysis presented in section 5.2.4, it would be interesting to ask what would be the effect of passing from a continuous to discrete analysis of spatial densities. After all, if the spatial volume of interest is of size $V$ a density value less than $V^{-1}$ make no sense unless it is zero.

This is hardly a matter of little consequence. Abramson and Zanette (1998b) have studied the statistics of extinction in Lotka-Volterra systems with many species introducing minimum density thresholds and finding interesting qualitative differences in the resulting dynamics with respect to purely continuous treatment such as, for instance, the transformation of unstable equilibria into stable ones. This is more than just a theoretical or technical point. Similar conclusions have also been reached in molecular evolution experiments on the invasion rates of highly fit RNA virus variants (de la Torre & Holland, 1990). Highly competitive clones invaded their progenitor population only when seeded above a threshold level otherwise they were suppressed by the existing quasispecies dynamics. Similarly, the effects of discreteness in combination with stochasticity, have been recently studied in models of the evolution of altruism and kin-selection in viscous populations, (Goodnight, 1992; van Baalen & Rand, 1998). It is found that, in contrast with continuous models where an infinitesimal amount of non-altruists suffices to take over the population in the long term, treating the population as discrete shows that altruism can be stabilized due to the inter-group advantages it provides and the un-invadability of altruist groups with less than one non-altruist.

Following the mentioned mathematical models, a density cut-off value $p_0$ is introduced for the spatial densities of players and the invasion experiments are re-run. A reasonable upper bound for this threshold may be obtained as the inverse of the volume of a whole cluster which, in these experiments, is approximately equal to 0.4. Figure 5.15 shows the evolution of the different sub-populations for different values of $p_0$ where it is clear that as the threshold value increases it takes longer for the invading population to surpass the initial one until finally for $p_0 \approx 0.055$ invasion does not occur at all.

The relevance of density thresholds points to an interesting aspect of the current model. Since the continuous approximation for a discrete variable does not hold in the evident case of very small density values in finite domains, it would be legitimate to ask in what other aspects this approximation is introducing spurious results (Durrett & Levin, 1994a, 1994b). One way to find out is to explore different approaches in which the variables are treated as discrete, but still choosing a starting point the continuous model. A possible way of doing it is to allow only for discrete values in the numerical resolution of (5.16). A comment on how to do this was already given in section 5.3, and it consists simply in allowing only discrete increments in the densities variables and accumulating the remainder of the continuous increment for the next integration step. This is still not a discrete model, but an approximation in that direction. The partition to choose is again related...
Chapter 5. A game of action coordination: mathematical models

5.5 Summary for continuous spatial model

The aim of the spatial model described above has been to provide a first order approach to understanding the role of spatial structure in the dynamics of the system. In order to be able to use the results of the spatial model, the model was based on the ecological principles of reaction-diffusion equations. However, this approach is not suitable for studying the way agents should be able to play with their neighbors. Consequently, the frequency for initiating a game as a first role player is proportional to a fixed number of agents in the cluster. Instead of working directly with the number of players, the main variable in the model is the continuous densities of players surrounding the individual. Assuming that energy is also locally and continuously distributed, the energy obtained by the individual is a first role player as a second role player. It is obtained according to the local partner after a pre-specified number of trials. The calculation of the frequency of initiating a game as a first role player as a second role player is the same as the continuous densities of players surrounding the individual. The calculation of the frequency of initiating a game as a first role player as a second role player is the same as the continuous densities of players surrounding the individual. The calculation of the frequency of initiating a game as a first role player as a second role player is the same as the continuous densities of players surrounding the individual.
The motivation behind this chapter has been to define an evolutionary scenario where the evolution of a very simple game of action coordination could be studied using a traditional game-theoretic approach and some extensions to it. Once the game was defined, it was found that there were no ESSs when the investigation proceeded using traditional game-theoretic analysis. However, after extending this basic stability analysis to include a model of evolution, it was found that the results expected for the weakly stable region of the strategy space where the population was expected to be found. This region (not yet a single point) was defined by specifying that strategies 2 and 4 should be present in equal proportion. A global trend towards optimizing individual fitness is dynamically recovered due to the existence of a global energy variable with which all players are coupled. Distributing the strategies in a haploid genetic space shows that high mutation rates can have an important role in stabilizing the oscillatory solution.

By allowing population sizes to be finite it becomes clear that only one point in the weakly stable region is in fact stable. This attractor indicates that a population constitutes an equal amount of players of the non-coordinating strategies 2 and 4 will not be invaded. The results for this region are summarized in Table 5.6. The addition of a genetic setting, which allows for the assumption of optimization which is impossible in a traditional game-theoretic analysis, shows that the result is still a single point in which strategies 2 and 4 were dominating in equal proportion. A global trend towards optimizing individual fitness is dynamically recovered due to the existence of a global energy variable with which all players are coupled. Distributing the strategies in a haploid genetic space shows that high mutation rates can have an important role in stabilizing the oscillatory solution.

As the depth of the analysis is increased, the sort of factors that can be expected to have important effects are highlighted. An interesting trend is already appearing in the results. This trend can be interpreted as saying that a combination of non-coordinating strategies is an expected solution. Oscillations in strategy space have already been observed. However, these results are expected to be found when the investigation proceeds using traditional game-theoretic analysis. However, after extending this basic stability analysis to include a model of evolution, it was found that the results expected for the weakly stable region of the strategy space where the population was expected to be found. This region (not yet a single point) was defined by specifying that strategies 2 and 4 should be present in equal proportion. A global trend towards optimizing individual fitness is dynamically recovered due to the existence of a global energy variable with which all players are coupled. Distributing the strategies in a haploid genetic space shows that high mutation rates can have an important role in stabilizing the oscillatory solution.

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6.1 The model

In this model a population of agents follow the same rules as described in chapter 5. As in the continuous spatial model of section 5.5, agents are situated in a position which remains unchanged during their lifetime. The whole spatial environment is partitioned as a regular grid, typically of 100 x 100 cells. Agents can interact with other agents and access food sources only within the limits of their neighborhoods. A number, \( F \), of energy repositories, or food sources, are also distributed within the environment, (in general, \( F = 10^4 \) has been used). Food sources can be uniformly or randomly spaced and this proven not to be relevant to the results. Food sources are those entities which provide energy to the simulation agents during their lifetimes, according to the rules described in chapter 5.

A game of action coordination: individual-based model.

Chapter 6

As in the continuous spatial model of section 5.5, agents are situated in a position which remains unchanged during their lifetime. The whole spatial environment is partitioned as a regular grid, typically of 100 x 100 cells. Agents can interact with other agents and access food sources only within the limits of their neighborhoods. A number, \( F \), of energy repositories, or food sources, are also distributed within the environment, (in general, \( F = 10^4 \) has been used). Food sources can be uniformly or randomly spaced and this proven not to be relevant to the results. Food sources are those entities which provide energy to the simulation agents during their lifetimes, according to the rules described in chapter 5.

In the model presented in the chapter 7 experiments were made with circular neighborhoods and with continuous spatial environments. The potential of this type of model has been discussed in chapter 4 along with some methodological issues concerning the nature of reproduction, not as an instantaneous, population level phenomenon (where one may collect all the energy accumulated in a certain period and estimate the number of offspring or propagules) only to nearby empty cells. As a result of this scheme unlimited overcrowding is prevented. However, it is necessary to be aware of the sort of spatial regularity imposed by this scheme. It has been shown that interesting results in this sort of models can sometimes be due to the spurious effects occasioned by updating all cells at the same time. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different effects. Studies on the matter are lacking at the moment. But, to be on the safe side, it would be desirable for the present model to depend in a way to possible or such choices. To this end, in this model an exploratory approach is followed to explore different
Chapter 6. A game of action coordination: individual-based model.

At each time step, a number of agents equal to the size of the current population are randomly selected to play a partner in the game. As mentioned before, the first player loses its chance to play the game at the end of the turn. As always, each agent will always be selected once per time step. A second player and a food source, both within the neighborhood of the first player, are randomly selected. If no agent is found after a finite number of attempts (typically 10), the first player loses its chance to play the game and the energy cost is discounted anyway. Each time an agent is selected, its age is incremented by one unit regardless of the role it plays.

Table 6.1: Example of a look-up table that determines the behavior of an agent. Capital letters represent effective components and Greek letters external manifestations of actions (signals).

![Figure 6.1: An example of agents' positions and their square neighborhoods. "F" represents a food source within reach of agent "A1" who has selected "A2" as a partner in the game. Notice that although both "A2" and "A3" are "within reach" of "A1", they cannot interact with each other.](image-url)

The behavior look-up-table is encoded in a shielded game represented by a binary bit string 00001011...

Note that it is possible to stop the modeling requirement that the graphs used by a player must belong to a certain set of graphs. Instead, one could define a set of all possible signals, see Appendix 5.2.2. While this may introduce additional complications and make the model more difficult to implement, it is done in order to avoid the question of whether the signals used by a player must belong to a certain set of graphs.

The structure of agents is that of a stateless machine. According to the role, actions can depend on the perceived food type or on the perceived external manifestation of the partner. For not allowing enough variation in the population constitution, this mechanism replaces the lack of a good model of developmental rules which could be expected that typical animal species without any rules.

Each agent possesses an internal energy counter that specifies the energy available for self-maintenance and reproduction. Every time an agent is born, its initial energy level is set at a value chosen following a Gaussian distribution with mean $\mu_e$ and standard deviation $\sigma_e$, centered around $e$ in the first place. This energy level is again selected stochastically using a Gaussian distribution centered around the respective "developmental" feature included in this model. This is a stochastic threshold for reproduction intended to introduce noise in the dynamics. Reproduction is sexual and selection of mate is based only on the locality condition. This has been implemented by choosing the last co-participant in a game as the second parent. The offspring occupies a randomly chosen position within the first parent's neighborhood. As neighborhoods do not overlap completely in the general case, geographic constraints may prevent reproduction from occurring within the same neighborhood...

The whole environment is subject to a constant average energy flux $\rho$ (500 per time step) which is manifested in a stochastic increase of the energy stored in the environment... 

Figure 6.1: An example of agents' positions and their square neighborhoods. "F" represents a food source within reach of agent "A1" who has selected "A2" as a partner in the game. Notice that although both "A2" and "A3" are "within reach" of "A1", they cannot interact with each other. Each agent possesses an internal energy counter that specifies the energy available for self-maintenance and reproduction. Every time an agent is born, its initial energy level is set at a value chosen following a Gaussian distribution with mean $\mu_e$ and standard deviation $\sigma_e$, centered around $e$ in the first place. This energy level is again selected stochastically using a Gaussian distribution centered around the... 

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Typically, if four food types, four actions and four signals are possible, as in the experiments described in the following section, then each action and signal is represented by two bits and the total size of the (active) genotype is 12. Newborn agents receive their genome as the result of a uniform crossover operation on their parents genotypes plus certain probability of mutation $\mu$ per locus. The result of uniform crossover is a genotype in which each place in the bit-string is selected from the corresponding place from one of the parental genotypes with equal probability (see Syswerda, 1989; Mitchell, 1996, pp. 58 and 172). A typical value for the mutation rate was $\mu = 0.005$ per locus in the genotype and per reproduction event. This guarantees that, after crossover, the probability of a genotype to remain unchanged after mutation is: $(1-\mu)^{12} \approx 0.942$.

### 6.2 Results

Results discussed in this section were obtained using two sets of simulations in which only four different types of food were included in the environment. In one set of simulations each food type had a different associated action and in the other a given action corresponded to two different food types and, therefore, only two actions were relevant even if agents were able to perform more actions, (for example, action “A” may correspond to food types “F0” and “F1” and “B” to “F2” and “F3”, while actions “C” and “D” may not be relevant). Only results on this last set will be described since it approaches the cases studied with the mathematical models. Simulations with more food types and actions were also carried out and the results were similar, though much more expensive to obtain and analyse.

In contrast with the mathematical models, agents are initialized totally at random. In particular, this means that they will also have to evolve an association between food types and the effective components of actions when they play that first role. Previously this was assumed to be always correct. The player that “found” the piece of food was supposed to know what to do with it. The evolution of such a task is consistently and very rapidly achieved in all the simulations, and its explanation in selective terms does not present any problems given the static character of the association involved.

Population size is variable. In all simulations the average population size stabilizes, after a transient period, at a value between 600 and 800 agents.

A baseline case was run in order to understand what kind of activity emerged when agents were not able to perceive each other reliably. In this run, the external manifestation of the first player was replaced by a random signal when perceived by the second player. The instantaneous proportional average of cases in which both players acted correctly simultaneously is called the coordination ratio. This ratio stabilized at 50% for random signals. Since no food type is predominant, the best guess a second player can make, given that there is no correlation between the “signal” it perceives and the particular type of food in question, is to perform any of the two relevant actions out of the four possible ones. The achievement of this level of coordination is independent of the parameter $c$. This means that when signals are not random any success in coordination of behaviors will be manifested as a greater coordination ratio than that observed in the baseline case.

Figure 6.2 shows the evolution of the success ratios for the whole population in a typical run with $c = 0.55$, (for a same set of parameters variations between different runs were not significant). These quantities should not be confused with any measure of fitness of the population. $R_1$ indicates the average proportion of successful actions for first players which, as predicted, climbs rapidly up to a level near 100 %, (perfect success is not necessarily achieved, due to the effects of random mutations). $R_2$ shows the same quantity for second players and $R_{12}$ for both roles simultaneously (the coordination ratio). Although it is not very clear in the figure, $R_1$ and $R_2$ start near a value of 25% and $R_{12}$ near 12.5% which corresponds to a randomly initialized population. Note that the proportion of coordinated games reaches a higher than baseline level of about 90% and is maintained in a relatively steady state.

By observing the resulting behaviors once a stable state has been achieved it is possible to determine that signalling behaviors present a strong correlation with actions and not with food types. Therefore agents evolve a “two-signal code” for the two relevant actions that can be performed. However, as shown later, such a code is not at universal within the population.

A study of the effect of parameter $c$ on $R_{12}$ was performed in order to see how the extra pay against coordination affected the level of simultaneous success. The intuitive expectation is that this level should decrease as $c$ increases from 0.5 to 1.0 because coordination becomes more costly as the degree of conflict is augmented. Figure 6.3 shows this effect on $R_{12}$ for different values of $c$. It is apparent that the proportion of coordinated activity for the whole population decreases as $c$ is incremented from 0.5 to 0.65 but still remaining above the baseline case. The level of coordination goes from almost total coordination for $c = 0.5$ (neutral cost) to coordination by guessing with $c \geq 0.65$. This result is quite different from the results obtained with the game-theoretical approach and the extended mathematical models and it requires an explanation.

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4The look-up table 6.1 is in fact implemented as a double entry matrix where for each food type and perceived signal corresponds an action/signal pair. This matrix is not used entirely. The reason for this implementation was to facilitate the experiments presented in chapter 8 in which there is a sequence of actions and responses and the whole matrix is used.
Figure 6.3: Coordination level for different values of $c$. (b) shows the average value for the coordination level for different values of $c$. Each point is the average of 5 simulation runs. The line represents a linear regression, (linear correlation coefficient: -0.982). (a) shows some examples of the time evolution of $R_{12}$ for some values of $c$.

6.3 Spatial patterns

It was shown in section 5.5 that in a spatially extended model, if the coupling between the density of players and the available environmental energy depended positively on a term reflecting the density of players in a finite volume, spatially heterogeneous solutions may exist. In particular, these solutions tend to be aggregated "lumps" or clusters of players separated by uninhabited regions. In this section a study is made of the spatial distribution of agents as a function of time to see whether this is also happening in these simulations.

Figure 6.4 shows the first stages in the spatial distribution of the agents. Initially these are distributed randomly across the whole environment, (border effects have been avoided by the use of periodic boundary conditions). Since agents do not move, any change in the spatial distribution is due only to birth and death processes. One can observe how the initial symmetry is rapidly broken and how agents show a tendency to aggregate into clusters. As in section 5.5, symmetry breaking is caused by minor differences in the distribution of initial positions and also by the nature of the updating rules. Some agents will reproduce more than others just because they have a few more neighbors to interact with or have been called to act a few more times and, therefore, they have a slightly better chance of accumulating enough energy for reproduction. As reproduction is also a local process, the effect is self-reinforcing. Relatively isolated agents will have less chance of interaction and will tend to die sooner also contributing positively to increase the isolation of agents in similar positions.

Clusters remain relatively stable, at least if compared with the timescales of an agent's lifetime. Although they rarely break or fuse, they have a tendency to move slightly in random directions5. This was also seen in the model presented in section 5.5 and, although it was not done explicitly then, it is possible to use that model to support the claim that clusters do not change significantly in their general form. Here, a more "physical" description of why this is so will be

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5 Or probably following slight gradients in environmental energy.
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6.4 Correlation between cluster size and coordination level

The above description provides an idea of the tendencies that give origin to clusters as well as the spatial patterns. However, this explanation may give a wrong impression and lead the reader to think that cluster size is determined by the interaction between “forces” that depend exclusively on the values given to the simulation parameters. Hence, any variance in the resulting cluster size is not attributable only to the random contingencies of the particular run. If this were the case, it would not be reasonable to expect any correlation between cluster size and any other variable in the simulation for a given set of parameters. However, a consistent correlation has been observed in the simulation runs using different values of $c$ and $n$.

In a given simulation run, the average level of cooperation (i.e., the proportion of games played) for each cluster admits certain variability from one cluster to the other. This result is due to the fact that each cluster evolves for long periods in a more or less independent manner (which is also the reason for simulating “codes” used by agents being different between clusters). The average degree of cooperation in a cluster is found that larger clusters are associated with higher levels of cooperation, and vice versa. This correlation can be observed in Figure 6.5, where the cooperation level within a typical cluster is plotted as a function of its size for different values of $c$ and $n$.

The equilibrium of both these tendencies determines the size of the quasi-stable equilibrium. The establishment of this equilibrium is due to the fact that each cluster evolves for long periods in a more or less independent manner (which is also the reason for simulating “codes” used by agents being different between clusters). The average degree of cooperation in a cluster is found that larger clusters are associated with higher levels of cooperation, and vice versa. This correlation can be observed in Figure 6.5, where the cooperation level within a typical cluster is plotted as a function of its size for different values of $c$ and $n$.

How can this correlation be explained? It is clear that a particular cluster being large or small can depend only on the initial conditions and the random fluctuations suffered by it. However, there seems to be a tendency in the dynamics to establish some order in the end distribution with respect to the level of cooperation in each particular cluster. The implication of this observation is that any explanation for this correlation must provide a mechanism that links the corresponding variables, either causally to one another or operationally to the rest of the process. Such a mechanism may be provided by the individual-based model described in this chapter.
6.5 The role of kin selection

The importance of a spatial dimension in evolutionary game dynamics is a well-studied phenomenon. In particular, it is often found in cases where cooperation is favored over conflict, even when conflict is a better strategy according to non-spatial models. This is because spatial extension introduces non-trivial dynamics that are not present in non-spatial models. For example, in binary genotypes, the Hamming distance is defined as the number of different bits between two binary strings of the same length. This measure is crucial in understanding how spatial structure affects the evolution of cooperation.

\[ d_{H} = \sum_{i,j} r_{ij} \]

where \( r_{ij} \) is the degree of relatedness between individuals, \( i \) and \( j \), and \( d_{H} \) is the Hamming distance. This formula helps in understanding how spatial structure affects the evolution of cooperation. The Hamming distance, \( d_{H} \), is calculated as the distance between each genotype, which is important in understanding how spatial structure affects the evolution of cooperation. Even in certain circumstances, to account for the individual's inclusive fitness and therefore it will be selected for. This is so because the probability of finding the same given gene in a sibling, \( c_{i} \) is the proportion of shared genes between two siblings. This proportion is often less than 1, meaning that the individual's inclusive fitness is less than their own.

A calculation of relatedness in the current model is straightforward by taking the perspective of the individual and keeping the model's metric, \( \rho_{ij} \), between the players and the role of kin selection. The degree of relatedness with another individual (defined more carefully below) is also required for the next generation's inclusive fitness of the same concept in the context of kin selection. It can also be accounted for other individuals that help the transmission of copies of the same genes that happen to be located in different genetic systems. Even in such cases, the individual's inclusive fitness is affected by the actions of \( \rho_{ij} \) and the action of \( \rho_{ij} \) which is greater than or equal to 1. Even in certain circumstances, to account for the individual's inclusive fitness and therefore it will be selected for. This is so because the probability of finding the same given gene in a sibling, \( c_{i} \) is the proportion of shared genes between two siblings. This proportion is often less than 1, meaning that the individual's inclusive fitness is less than their own.
and the population average genetic constitution

\[ d_{ij} = d_{ji}. \]

And then, for each individual, if

\[ r_{ij} = 0 \]

otherwise \[ r_{ij} = 1 - \frac{d_{ij}}{d_{max}} \]

This defines the distance between an individual's genotype and the population average, then the relatedness is simply:

\[ r_{ij} = \frac{1}{2} (1 - \frac{d_{ij}}{d_{max}}) \]

In the present model, if the mean genetic constitution is calculated by the actions of a given individual, in general \( r_{ij} \) will be less than the distance between the individual's genotype and the population average, then the relatedness is simply:

\[ r_{ij} = \frac{1}{2} (1 - \frac{d_{ij}}{d_{max}}) \]

The average genetic constitution is calculated as the sum of all the genotypes in the population and the distance between the individual's genotype and the population average is calculated as the Hamming distance.

Figure 6.7: The frequency distribution of relatedness vs. cooperation, as predicted by the model. The different bars represent different values of \( c \).
the average values of relatedness within those clusters because the parameter $c$ is constant for the whole population. Then, the relation between changes in relatedness and cluster size should be examined. For two typical simulations with different values of $c$ the results are plotted in figure 6.8. An increase in relatedness with cluster size is not observed as would be the tendency to expect given the correlation shown in figure 6.6. On the contrary, if any tendency may be drawn from this figure, it is a slight tendency towards increased relatedness for smaller clusters, which is not very surprising since such clusters have smaller interbreeding populations and the chances of meeting unrelated individuals are less than in larger clusters.

In conclusion, even if it is accepted that kin selection could play a role in the most favourable case, it is certainly not the whole story and further investigation is needed in order to explain the variation of the average coordination level with $c$ and the correlation between this average coordination and cluster size for a fixed value of $c$. As will turn out, it will be possible to discard kin selection altogether when the structuring effects provided by the clusters are examined in detail.

### 6.6 Clusters as structuring invariants of the evolutionary dynamics

In this section a description will be provided of the two most important factors that arise from the presence of clusters as stable or quasi-stable patterns in space. One of these factors is purely geometrical and it is related to the fact that players are discrete entities, connected by a relation of genealogy along which the positions of successive generations describe a random walk of variable step size. The other factor, already discussed in section 5.5.3 is ecological as well as geometrical, and it is related to the breaking of in-built symmetries in the game and how agents are subject to different environmental conditions depending on their position within a cluster.

**Figure 6.8:** Relatedness vs. cluster size for different two of $c$. Lines depict linear regressions. “R1” and “R2” refer to relatedness-1 and relatedness-2 respectively.

**Figure 6.9:** Probability of an entire genealogy remaining within cluster (delimited between positions 0 and 30) after 5 generations as a function of the ancestral position $(x_0)$ within the cluster $L = 10$.

#### 6.6.1 Fluctuations and phenotypic aspects of spatial position

Section 6.3 described how clusters are constituted as a consequence of the interaction between agents and how they form a coherent quasi-stable spatial structure due to the equilibrium between a tendency by the agents to exploit more resources by expanding the size of the cluster and a tendency to accumulate in zones of high density so as to increment the chances of playing the game. Apparently, this equilibrium would seem to establish a degree of spatial neutrality in the sense that spatial position does not matter for the rates of energy intake and offspring production. Players at the center play the game more often than those at the periphery but they do so for poorer resources. If the rates of net energy intake were different, the cluster would not be at equilibrium. Such a homogeneous rate of energy consumption is indeed what is observed in the simulations. Players within a stable cluster have the same average lifespan and number of offspring. However, it is not true that spatial position is neutral in evolutionary terms.

Imagine a stable cluster of a definite size, and suppose that a new player is born into it. As a rule of the game, offspring are allocated near parents, so the position of the new player depends on the position its parents in the cluster\(^{10}\). Now, if the new player happens to be allocated “outside” the cluster, for instance if its parents live near the periphery, its chances of survival will be small since it will be able to play only with a few other players and the majority of agents in the cluster will be too far to reach.

So, at least in this “all-or-none” sense, spatial position is playing a phenotypic\(^{11}\) role which is not genetically based: if you are born outside the cluster your chances of survival are reduced.

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\(^{10}\)Actually, it depends on the position of just one parent, the one whose high energy level triggered the reproduction event. (see section 6.1.)

\(^{11}\)The word “phenotypic” is used to refer to those attributes of an individual which have an effect on that individual’s fitness. A phenotype is usually associated with bodily and behavioral characteristics of an organism, but the concept can be extended to characteristics outside the body of the organisms which affect variations in genetic frequencies within a population, (Dawkins, 1982). Phenotypic properties may trivially be unrelated to genetic constitution, social position in a dominance hierarchy, etc.
Would it be possible to retain a weaker concept of spatial neutrality and say that at least, the positions within a cluster will tend to be longer than those initiated in the peripheral region and, at positions within a cluster are evolutionarily neutral? A careful consideration of the above example indicates that this is not possible. A player at the periphery may generate the same average number of inhabitants of the central region.

It has already been mentioned in section 5.5.3 that the frequencies with which an agent plays the first and second roles are a function of the agent’s position within a cluster. In a non-spatial situation this does not happen, but in the presence of spatial patterns this symmetry may be broken. As a result, some intuitions about the game may be challenged. For instance, it is clear that the symmetric situation playing the first role is always more effective in terms of payoff than playing the second role, since a first role player is bound to receive at least half the energy in the former, and maybe more depending on the strategies played, while the second role player may receive at most half the energy. However, as demonstrated in the continuous spatial model (figure 5.13), when the symmetry in relative frequencies is broken there may be circumstances in which a player receives a greater average payoff when playing the second role than when playing the first (for instance, if the cluster is constituted entirely by a unique self-cooperating strategy).

Figure 6.11 shows, in a particular simulation run, the spatial distribution of players according to which role they play more often. It is clear from this figure that there is a spatial correlation according to which those agents that play the first role more often than the second tend to occupy the periphery of the clusters and those that play the second role more often, the central region.

6.6.2 Broken symmetries within clusters

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Of what consequence is this manifest asymmetry? One may advance the hypothesis that, values of c sufficiently close to 0.5, there will be an inner region in each cluster where players will be receiving a higher contribution to their payoff per unit of time due to their involvement in second role players and, given the spatial proximity of players in this region, they would evolve towards a self-cooperating strategy such as 1 or 3, since any growth of a non-cooperative mutant would rapidly be overcome by a compensation of the inner population towards the other self-cooperating strategy.
Chapter 6. A game of action coordination: individual-based model.

6.6.3 Coordination explained

Consider first what would be the expected outcome if the model were to behave like one of the mathematical models presented in chapter 5. In those models it was shown that a stable attractor of cooperation exists for any value of \( c \), with the threshold being lower for models with cooperative strategies (strategies 2 and 4) and high for non-cooperating strategies (strategies 1 and 3). A similar situation occurs in the spatial model.

It is clear that this stable solution works in the spatial model, provided that both strategies are present in high proportions and there is a global balance between the strategies. This was already demonstrated in the spatial model presented in figure 5.1 (see section 5.4 for reference). A non-cooperating strategy is susceptible to invasion by cooperators in certain areas, while cooperators can be "restrained" from growing by non-cooperators in other areas.

It is important to consider that one factor that may make oscillations more difficult to occur in the model is the stochastic nature of the process. For values of \( c \) near 0.5, the model presents a much more stable dynamics (figure 6.2), and an estimation of the circumstances in which this stability will be achieved is when the extra gain obtained by the invaders is significantly greater than the payoffs experienced by the population, otherwise the effects of the extra gain will be overshadowed by noise.

1. The central region can be modeled as a patch. Because of its typical size of about 0.1 m, the spatial region of the patch is relatively small, so that the level of coordination can be approximated as a single parameter. The horizontal line is the typical central frequency for playing the first role in the simulations. Also according to measures, the standard deviation of fluctuations in payoffs about 0.1 m is higher for the invaders than for the established population. A good explanation for this observation is that the invaders can be considered as a patch in itself.

2. Invasions occur only after a threshold number has been achieved. In general, independent density of the invaders, the population density at the center of the cluster will be considered for explanation purposes. As a patch in which only one strategy can be dominant surrounded by a field which is not necessarily uniform (in other models and empirical studies, see section 5.5.4 and references therein). Such a minimal threshold is needed to achieve the invasions observed in small areas. Thus, the center of the cluster will be considered as a patch in itself.

3. Non-cooperating strategies are invaded only by cooperators, by non-cooperators in the spatial model. The invading and invaded strategies for invasions to occur are subject to fluctuations, and the center of the population is constituting the spatial model presented in figure 5.1. In this model, the typical central frequency for playing the first role is 0.6, while the second role as measured in the simulations. Also according to measures, the central region can be modeled as a patch.

4. The central region can be modeled as a patch. Because of its typical size of about 0.1 m, the spatial region of the patch is relatively small, so that the level of coordination can be approximated as a single parameter. The horizontal line is the typical central frequency for playing the first role in the simulations. Also according to measures, the standard deviation of fluctuations in payoffs about 0.1 m is higher for the invaders than for the established population. A good explanation for this observation is that the invaders can be considered as a patch in itself.

**Figures:**

- Figure 6.12: Critical frequency in which an invader's extra gain equals the fluctuations in payoffs in a spatial model. The horizontal line is the typical central frequency for playing the first role in the simulations. Also according to measures, the standard deviation of fluctuations in payoffs about 0.1 m is higher for the invaders than for the established population. A good explanation for this observation is that the invaders can be considered as a patch in itself.
Chapter 6. A game of action coordination: individual-based model.

Invasion of cooperative strategies depends on \( c \) and \( f \). Now consider a whole cluster containing a self-cooperating strategy such as 1 or 3. The average payoff for a player within the central patch will be:

\[
(W_0 - W_e) = (2/3)(E - c).
\]

where \( E \) is the average energy extracted per unit of time. If a cooperative individual capable of invasion is placed in the patch, its average payoff will be:

\[
(W_0 - W_e) = (2/3)(E - c).
\]

This is so because all games for this new agent are against the established strategy; therefore when playing the first role, it will receive a payoff of half the energy, and when playing the second role, a payoff of \( c \) will be received.

Figures 6.13 and 6.14 illustrate differences in role frequency. Triangles indicate individuals that play the second role more than 10% above the average for the whole population, and dots indicate the rest of the agents. This difference is most pronounced near the border due to a higher risk of placing offspring outside the cluster which is especially manifested in the lengths of generations initiated in the peripheral region when the cluster is invaded by a group of invaders in the central region. So that whenever there is an attack on the cluster as a whole, it is strongly influenced by its final composition.

Consequently, as a result of the internal structure of the clusters, both in terms of connectivity and in terms of the directionality of the lines of genealogy, fluctuations in frequencies of certain values of cooperative coordination are the stable evolutionary outcome instead of oscillations or combinations of non-coordinating strategies.

The above explanation is able to account for the observed behavior of the mean coordination level as a function of \( c \) (figure 6.3b). Even though total invasion may not occur, the number of potential invaders is still important in determining the existence of cooperative coordination, so that the size of the fluctuations in frequencies is determined mainly by fluctuations in energy (i.e., fluctuations in frequencies are ignored). The standard deviation in payoff is estimated from observations as

\[
\sigma_{i} = \frac{0.09}{\sqrt{i}}.
\]

It is clear that for certain combinations of \( c \) and \( f \), this difference will be smaller than the size of the fluctuations in \( W_0 \). So that the invaders are indistinguishable from the cooperating type in \( i \) if \( k \) keeps the estimate that the standard deviation of the payoff is about 0.09 of the payoff for the entire group of cooperators. Therefore, the extra gain of the invader will be shadowed by the fluctuations. For these values of \( c \) and \( f \), the number of invaders will be contained below the threshold of invasion. However, statistically, the critical value can be seen by noting that if one takes a mean of the extra payoff among all potential invaders, the size of the fluctuations for this average quantity decreases with the number of individual.

This seems reasonable enough. For certain values of \( c \) and \( f \), the average payoff for the invaders is

\[
(W_0 - W_e) = (1/2 + 1/2)(E - c).
\]

The extra average payoff for the invader is

\[
(W_0 - W_e) = (1/2 - 1/2)(E - c).
\]

The above explanation is able to account for the observed behavior of the mean coordination level as a function of \( c \) (figure 6.3b). Even though total invasion may not occur, the number of potential invaders is still important in determining the existence of cooperative coordination, so that the size of the fluctuations in frequencies is determined mainly by fluctuations in energy (i.e., fluctuations in frequencies are ignored). The standard deviation in payoff is estimated from observations as

\[
\sigma_{i} = \frac{0.09}{\sqrt{i}}.
\]
Chapter 6. A game of action coordination: individual-based model.

6.7 Conclusions and analogies

Chapter 6. A game of action coordination: individual-based model.

The investigation pursued in this chapter affords the derivation of a series of conclusions with a different methodological approach. The specific interpretation of the results in terms of structured patterns of clusters in the evolutionary dynamics allows a series of comparisons with similar processes and a re-evaluation of the importance of different dynamical factors in natural evolution. Such results will suggest one possible avenue of further investigation which will be pursued in chapter 7.

Finally, interesting analogies may be drawn between some aspects of this model and more concrete natural phenomena. These analogies are not aimed at explaining the whole of the results. The comparative approach has facilitated the identification of relevant factors and their consequences. While, in order to use such a comparative approach, the present model can be considered as an extension of the previous mathematical models, the actual construction and use of computer simulations. Accordingly, the model was not built simply to reproduce the mathematical results and permit further relaxation of assumptions. On the contrary, the whole situation was directly modelled in a computational form thus allowing a radical break with an underlaying assumption whose effects were not necessarily reduced to the mathematical approach. Instead, they were brought to light at the time of comparing results. Such is the case, for instance, of the coupling between the stochastic nature of agent reproduction and spatial position resulting in a better understanding of the phenotypic role of space. The phenomenon was not even suspected without the present model. The in-built symmetry of the model, given its dependence on the figure 4.2 (indirect explanations) and not the model itself, may explain why coordination is stabilized, its dependence on the figure 4.1 (direct explanation) which is the way that the computer model should be used.

No methodological guidelines proposed in chapter 4 for the use of computer modelling in scientific research. As with many complex phenomena, it is usually preferable to try to find a general explanation for a process under the same framework. Indeed, the more connections between the simulations and the natural processes, the better.

1 Unfortunately, the presentation of the last two chapters has tried to proceed in logical, rather than historical, steps.
Inevitable selection for playing each role in the game, results in different conditions for achieving evolutionarily stable strategies (ESS). However, natural selection was intended to be the invasion threshold depending on the nature of the strategies involved. A cooperating strategy will always tend to be represented in a high proportion in the rest of the cluster even if the invasion is carried out by non-cooperative agents. This explains how cooperative coordination can be stabilized under certain circumstances. In contrast, the actual explanation provided in this chapter while still relying heavily on differential reproduction, is not constructed in terms of any unifying and situated principles but it is rather based on the organizational properties of some invariant features of the whole dynamics. As such, in this explanation some aspects of the processes which have been associated with historical processes are selected. The model lacks the richness of the stability that one tends to associate with cooperative coordination. The main point in the explanation of the stability of cooperative coordination is the fact that at the constraining and organizational conditions which influence the path that the dynamics will follow, that is the nature of a historical process as discussed in chapter 3. In addition, the main central strategy can be invaded by another one, then the new strategy becomes the central one. However, due to the discrete nature of the agents and due to the stochasticity involved in reproduction events, and due to the invasion to occur fairly often, the invading strategy also becomes the central one. A combination of these facts with the broken symmetries induced by the cluster's structure perhaps open the door for further speculation.

Chapter 6. A game of action coordination: individual-based model.

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Chapter 6. A game of action coordination: individual-based model.

The dynamics of spatial organization, as described at the end of chapter 6, can be seen as one example of a spatial position within a cluster, with fundamental explanatory role in the understanding of the evolution of cooperative interactions between interacting agents. In order to explore this theme further, a search will be made for natural candidates, such as social hierarchies, affiliative networks, etc. All these examples have as a common feature a similar way of changing as a result of the evolutionary process by constraining the patterns of realizable interactions in the game and symmetry breaking in role frequency.

Another important issue discussed in this chapter is the fitness value of spatial position within a cluster. Interesting parallels may be drawn between this situation and the fitness value of spatial position within a natural group of animals. In general, individuals positioned at the edge of a group may suffer greater risks of predation or parasites than individuals located at the center. On the other hand, while edge individuals incur greater energy expenditure, in some cases they benefit from a greater energy intake due to more effective foraging. Dominance hierarchies also seem to be correlated with spatial position, where dominating individuals occupy central positions in a group. Krause (1994) reviews a number of studies on the subject. The theoretical basis for most of them is Hamilton's "selfish herd" theory (Hamilton, 1971), which stipulates that individuals seek a position within a group following their self-interest even if the end situation results in a lower average fitness for the whole. Unfortunately, not all studies revised by Krause confirm this hypothesis; some even consider it. A recent computational study by Hamdi and others (1998) also challenges the idea that dominant individuals have a preference for a central position, showing that they will tend to occupy a central position anyway, as a feature of the self-organizing dynamics of the interaction. If the analogy is valid, the way in which spatial position plays a phenotypic role in the current model could even better support the hypothesis that a process of this kind can affect the evolution of social interactions.

The dynamics of spatial organization, as described in chapter 5, can be seen as one example of a spatial position within a cluster, with fundamental explanatory role in the understanding of the evolution of cooperative interactions between interacting agents. In order to explore this theme further, a search will be made for natural candidates, such as social hierarchies, affiliative networks, etc. All these examples have as a common feature a similar way of changing as a result of the evolutionary process by constraining the patterns of realizable interactions in the game and symmetry breaking in role frequency.

In chapter 7, we will extend the current investigation to the particular case of parental influence on development. One possible family of candidates comes to mind when one recaps the example of spatial position within a cluster, with fundamental explanatory role in the understanding of the evolution of cooperative interactions between interacting agents. In order to explore this theme further, a search will be made for natural candidates, such as social hierarchies, affiliative networks, etc. All these examples have as a common feature a similar way of changing as a result of the evolutionary process by constraining the patterns of realizable interactions in the game and symmetry breaking in role frequency.

In conclusion, the model does not attempt to describe specific behaviors observed in natural cases, but rather to extend the understanding of the relationships between the processes involved in order to help in the formulation of concrete hypotheses of what to expect in natural cases.
Chapter 7. Social influences on development and coordinated behavior: an assessment

7.1 Social influences on development: evidence and consequences

As discussed in chapter 3, a tacit supposition in many evolutionary models is that the evolution of a trait is often studied under the assumption that the relevant environmental factors change so slowly that they may be considered to be static, e.g., the distribution of food patches or the quality of food patches will partly depend on the efficiency of foraging strategies, and competition for mates while if mothers are present, but unable to intervene, juveniles do not play preferentially with the presence of a mother, and not her active intervention, is enough to influence changes in social behavior.

The assertion that social influences on development can play an important role in the evolution of social behavior is far from surprising. Indeed, the literature on social effects on early life-history processes is extensive and covers a wide range of species and contexts. As this last example suggests, maternal influences can also affect social relationships or the development of courtship behaviors. Moreover, in many cases where the influence of maternal factors is less pronounced at the level of the individual, it may still have a significant impact on the evolution of cooperative social coordination.

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The mother has total control over the infant's movements, but also when the infant starts to spend time with another individual, the mother's behavior has a significant influence. For explaining this perpetuation of social networks is early familiarity which has also been suggested as a plausible mechanism for kin-recognition (Frederickson & Sackett, 1984). According to this mechanism, during the early stages of an infant's life, the infant's behavior is strongly dependent on the existing maternal affiliative network. Such a mechanism can be naturally regarded as potentially instantiating a historical process in the sense discussed in chapter 3.

Similar cases that would fall under the rubric of social influences on development, would be filial or sexual imprinting, whereby parents influence the mate preferences of their offspring. The relevant literature is vast and the phenomenon will only be mentioned here. For reviews on imprinting and its evolutionary consequences, see for instance (Ridley, 1987; Hess, 1973). For a computational model on speciation induced by imprinting and sexual selection see (Tooth & Miller, 1993). For another relevant evolutionary model incorporating maternal effects, see (Cowley & Atchley, 1992), Falconer & Jablonka, 1994). See (Hansen, 1996) and (Aitala & Jablonka, 1996) for critical comments on this hypothesis and a discussion of how it has been applied.

Laland (1994) presents a model which predicts similar results for sexual imprinting whereby the probability of the spread of novel adaptive traits is reduced due to the preferential resistance to novel characters. In the context of this thesis, particular interest is given to the operational or dynamical aspects of this process. It is important to note that novel characters may not only arise due to mutations but also due to the influence of other individuals. In such cases, social influence could probably be seen as influencing their own chances of being selected. Further, not all the effects may be functionally distinguishable. If, for example, a trait is selected for due to its beneficial effects in one environment, but deleterious in another, the social influence may still be observed.

The distinction is illustrated in figure 7.1 where the two extreme cases are depicted. In this context, it is important to note that the figure shows a case where social influence affects certain behaviors (B) but which do not reflect on the development of future generations. Probably in most natural cases this distinction will not be very sharp, but it is intended to provide an idea of the development of behaviors which are influenced by others. However, not all the effects may be functionally distinguishable. If, for example, a trait is selected for due to its beneficial effects in one environment, but deleterious in another, the social influence may still be observed. This will allow us to make some interesting conclusions concerning this issue.
generation. It is clear that the ecological and evolutionary consequences of these cases are not the same. In both circumstances it is possible to expect effects related to developmental plasticity in general [for instance, the so called Baldwin effect (Baldwin, 1896; Hinton & Nowlan, 1987), or the time lags or momentum effects discussed in (Kirkpatrick & Lande, 1989, 1992)], but the second case is more complex since the modified behavior includes the probability of modifying future generations and so it can be viewed as a process in which the dynamics affects its own conditions of realizability, i.e. a historical process. As such, it could give rise to self-sustaining or self-promoting structures [for instance, in the space of developmental relations].

It will be of interest to explore what kind of dynamical effects can result from the latter case. In order to do so behaviors and the ability to influence the development of offspring will be fused in a single phenotypic space. This is done ignoring many of the complexities involved by using a simple but justifiable model.

### 7.2 A model of socially influenced development

The purpose of this investigation is to make a first order assessment of the relevance that a socially influenced developmental process may have for understanding the evolution of cooperative action coordination, and also to try to identify what sort of constraints such a process may impose on the evolutionary dynamics. This justifies the choice of an abstract, and indeed crude, model of development under social conditions. In spite of this simplicity, the model is intended to account for the following relevant aspects:

1. Phenotypes are the result of a dynamical process which is affected both by genetic constitution and coupling between the developing organism and its environment.
2. The nature of the process itself is not totally determined by genetic constitution nor by environmental coupling but there are also formal constraints [for instance, the number of possible attractors a developmental system can have depends on the specific transition dynamics and may not be easily changed during evolution].
3. In most natural cases of socially influenced development, the most relevant coupling is between developing organisms and their parents.

The third point is supported by the examples discussed above while the first two can be derived from a Waddingtonian perspective on development as a dynamical process.

Figure 7.2 provides a qualitative picture of the kind of process considered. An offspring's genotype is determined by the genotype of its parents in the usual way (in this model using uniform crossover and point mutation). Its adult phenotype is determined both by its genetic constitution and by parental influences which depend on the adult phenotypes of the parents.

Put more formally, suppose that the *adult phenotype* of an individual $i$ (denoted by $P_a^i$) is totally determined by its *phenotype at birth* $P_b^i$ with the exception of certain changes which will depend both on $P_b^i$ and the adult phenotype of $i$'s parents $P_a^{i_1}, P_a^{i_2}$. $P_b^i$ depends only on the genetic constitution of $i$ and it is obtained by a universal genotype-phenotype mapping.

The model explicitly reflects the fact that parental influence on development may depend on the phenotypes of the parents, as well as the genotype-phenotype mapping, but it does not explicitly take into account the genetic differences between the parents. Of course, it is desirable that parental influence on development should reflect some formal relationships between adult phenotype and that of the undeveloped offspring. However, these formal rules will not be specified explicitly, but rather the possibility will be allowed for many of them to coexist in the same simulation run.

A set of general constraints is first defined for these developmental rules. The model will consist of a discrete and finite set of behavioral strategies and a correspondingly discrete and finite set of possible genotypes. Additionally, a discrete and finite set of phenotypes will also be defined. This space will have its own *phenotypic metric* which, in principle, need not be the same as the genotypic metric in terms of Hamming distances nor the same as a “behavioral” metric in terms of possible strategies and their relations. The reason for this is that the metric may also take into account other traits besides those being studied. As a process, development will be manifested following a logic of its own.

Under such a metric two phenotypes $P$ and $Q$ may be said to be close or apart and the distance between them is denoted by $d(P, Q)$. Parental influences will be taken into consideration only if the following condition holds:

$$d(P_a^i, P_a^j) \leq D, \quad j = 1 \text{ or } 2,$$

for $D$ a small distance and the influence will be such that:

$$d(P_b^i, P_b^j) \leq D,$$
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This is the adult phenotype will be the element of the matrix corresponding to the index specified by the parental phenotypes. If none of the parental phenotypes falls within the interval [49, 53], then the resulting phenotype will be changed from 50 to 49. (Note that the column.

Table 7.1: Developmental matrix for

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In this abstract model the process of development is instantaneous. As soon as a new agent is born its adult phenotype is calculated and its stochastic effects may arise as a result of the developmental procedure. The vector of the adult phenotype is calculated as the product of the developmental matrix and the vector of the phenotype at birth. The matrix entries are chosen randomly from the interval [48, 53]. For example, if the parental phenotypes are 51 and 52, the resulting phenotype will be 50, since 51 < 50 < 52.

Typically, $\Theta = 10,000$. The solution of the equation

$$\mathbf{P} = \mathbf{P} \cdot \mathbf{D}$$

where $\mathbf{P} = \mathbf{P} \cdot \mathbf{D}$ and the last element of the last row is the adult phenotype for the offspring will be stable if the eigenvalue of the matrix $\mathbf{D}$ is less than one. If all entries of the matrix $\mathbf{D}$ are less than one, then the offspring phenotype will be the same as the parental phenotype.

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As in chapter 5, two of these strategies will coordinate when playing against each other. Other cooperative strategies will be less effective at coordination, or simply "cooperating" strategies.

As in chapter 5, outcomes will depend on the roles played by the agents. The mathematical analysis presented in chapter 5 applies directly to this game.

In one version of this game, $A$ and $R$ are encoded in an 8-bits binary haploid genome using binary encoding. $A$ is encoded in the top 4 bits and $R$ in the lower 4 bits. In both cases only 1 bit is extracted from the local repository. If the agents do not coordinate the first agent receives a proportion of the energy in the repository where, as in the previous chapters, 0 and 1 represent even and odd numbers.

In this simplified version, $A$ and $R$ are fixed for all circumstances in a given individual; they do not depend on food type nor on a history of interactions. They are represented each by an integer number between 0 and 15. The condition for $A$ and $R$ to be complementary is simply that $A_r = 1 - A$ and $R_r = 1 - R$. From this condition it is possible to distinguish four possible behavioral types depending on the combination of $A$ and the second the parity of $R$. The relations between these strategies are exactly the same as the relations held by the four strategies used in the mathematical analysis of the coordination game presented in chapter 5. These are shown in figure 7.4 (cf. figure 5.1). In this figure arrows "indicate" non-cooperative relationships. Absent connections "indicate" self-cooperating or simply "cooperating" strategies.

Figure 7.3: An example of agents' position with circular neighborhoods. "F" represents a food source within reach of agent "A1" who has selected "A2" as a partner in the game. Notice that although both "A2" and "A3" are "within reach" of "A1", they cannot interact with each other.

Compare with figure 6.1

Although the exploration was not as methodical as in the case of $D = 2$ (modulo 256), other values were tested between 1 and 5. Results did not seem to differ much although the exploration was not as methodical as in the case of $D = 2$ (modulo 256).
Chapter 7. Social influences on development and coordinated behavior: an assessment

7.4 No development

Based on previous experience with similar analytical and individual-based models, one already knows how to expect the model to behave if no social development is included.

7.4.1 No Space

Since the game is formally equivalent to the 4-strategy action-response game studied using game-theoretic approaches in chapter 5, all the conclusions made in that chapter apply. In general, two different attractors can be expected: a fixed point attractor where the population is constituted in equal proportions by strategies (EE) and (OO) and a cyclic attractor where each strategy becomes dominant for a finite period and then displaced by another one in the order shown by the horizontal axis.

In the current model, the lack of spatial relationships can be implemented by setting the local neighborhoods to a size greater than that of the whole arena. Each agent has equal access to any other agent and the situation is that of a mixed medium. Figure 7.7 shows the population constitution as a function of the horizontal axis. A related issue concerning the role of crossover in allopatric speciation without environmental barriers has been discussed in (Di Paolo, 1996a). This suggests that in the current model, the lack of spatial relationships may play a role in the evolution of cooperation, as discussed in chapter 6.

7.4.2 Space

In the introduction of space and stochasticity radically changes the outcome of the evolutionary dynamics. In a way practically identical to the model presented in that chapter, despite differences in parameters values and the shape of the local neighborhoods, the results of the spatial game show that for certain values of c the level of cooperation remains stable above the baseline level of 50%. As c is increased from 0.1 to 0.5 the level of cooperation decreases. This suggests that the same phenomenon may be observed in chapter 6.
Chapter 7. Social influences on development and coordinated behavior: an assessment

7.5 Results with social development

When the evolutionary process incorporates development under social conditions some interesting qualitative differences become apparent. All simulations were run using the same parameters and for values of $c$ between 0.6 and 0.95.

7.5.1 No Space.

As concluded in chapter 6, the imposition of spatial constraints changes the evolution of cooperation from an oscillatory pattern into a stable level. Is it possible that a process of social development could, by itself, constrain the evolutionary dynamics in a similar way? The answer is negative. The dynamics remain oscillatory, although qualitatively different in that strategies become phase-locked by pairs (figure 7.7).

7.5.2 Space.

When a spatial dimension is added, results at the population level are similar to the case without development except that the range of $c$’s where cooperation is stabilized is larger: $0.5 \leq c \leq 0.8$. More interestingly, almost for the totality of this interval, the resulting population is constituted purely by a single cooperative strategy (either (OE) or (EO)), and only for $c \approx 0.8$ do polymorphic populations appear. In contrast with the case without development, the global level of cooperative coordination does not decrease linearly as $c$ increases, but is maintained at a level close to 100% and then changes rather abruptly for $c \approx 0.8$. In figure 7.8 one can compare the variation of the level of coordination with $c$ both for spatial games with and without development, (each point is taken as the average of the long term coordination levels of 5 simulation runs). Such a qualitative difference is an indicator that the process of socially influenced development is introducing an additional constraining factor in the evolutionary dynamics. To reveal this factor the situation should be analyzed in more detail.

7.6 Networks of social influences on development

By studying the population constitution it is found that, within the range of $c$’s where cooperation is stable, the population tends to be constituted mainly by a single adult phenotype either of type (EO) or (OE). This can be observed in figure 7.9. In this figure the population constitution is shown for a typical simulation run with $c = 0.6$, (compare with figure 7.6). After a transient the whole population is constituted by strategy (OE) and the other strategies disappear almost entirely (figure 7.9 (a)). More remarkably, figure 7.9 (b) shows that the population is constituted mainly by a single adult phenotype: $P_1 = 176$. In contrast with the case without development, where for certain values of $c$ the competing strategy was prevented from invading, when development is added it seems that the competing strategy is prevented even from existing.

By examining the genetic constitution of the agents it is discovered that the whole population has converged (save for small fluctuations) on a single genotype (or equivalently a single phenotype at birth: $P_1 = 174$). A study of the developmental table for this phenotype at birth (table 7.2) reveals that adult phenotype 176 not only is the most abundant in the table but it also has the effect that if both parents have this adult phenotype their offspring (except in the case of mutations) will also develop into the same adult phenotype. The situation is depicted in figure 7.10 where the number in the square represents the phenotype at birth, the number in the oval the adult phenotype and the solid arrow can be read as “develops into” and the dashed arrow as “influences”.

A set of developmental relationships which somehow perpetuates itself will be called a developmental network. It is so distinguishable precisely because its organization remains invariant over time. In the particular case shown in figure 7.10 it is apparent that this network does not just persist...
Chapter 7. Social influences on development and coordinated behavior: an assessment

Figure 7.8: Coordination level vs. $c$ for spatial games with and without development.

Table 7.2: Developmental matrix for $P_b = 174$.

<table>
<thead>
<tr>
<th></th>
<th>172</th>
<th>173</th>
<th>174</th>
<th>175</th>
<th>176</th>
</tr>
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<tr>
<td>172</td>
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<td>172</td>
<td>176</td>
<td>173</td>
<td>173</td>
<td>176</td>
</tr>
</tbody>
</table>

petuates itself but it may also be called “self-promoting” since the product plays a “self-catalytic” role in its own (future) production. As will be shown later, other type of networks can be obtained by increasing the value of $c$. But, for the moment, one could ask if it is possible to use this self-promoting network to account for the observed results.

An explanation is required for 1) why the presence of these networks prevents the existence of competing phenotypes for a certain range of $c$’s, and 2) why the transition to no cooperation is abrupt rather than smooth as in the case without social influences on development.

The first question is easy to explain if the evolutionary process is momentarily imagined as a search for viable phenotypes. If the population is constituted in its totality by a self-cooperating strategy like (EO) then individuals using strategy (EE) will constitute good alternative solutions in the sense that they will get, in principle, more payoff than those using (EO). “Finding” this competing strategy is not a major problem for the case with no development, since it is “located” just one mutation away in genetic space (all that is needed is to flip an appropriate bit in the genome). In the spatial game, although individuals bearing this mutant strategy can easily be found, the corresponding invasion is prevented by the spatial dynamics, as explained in chapter 6. But the inclusion of socially influenced development changes the situation. Now not only must the mutant be easily found by simple genetic operations, but it also must comply with the logic of the dominant developmental network.

In the example shown if figure 7.10, suppose that a mutation changes the phenotype at birth from 174 to another value $P_b$. This value can fall into one of two cases: either its distance to the parental phenotype (176) is less than or equal to $D$ or it is greater than $D$. In both cases one must look for the probability that the new adult phenotype will be able to perpetuate itself by generating offspring who will also result in the same adult phenotype. An estimation is made of the upper bound for the probability of this happening in each case.

If the mutant phenotype at birth cannot be affected by the parental phenotype because its phenotypic distance is greater than $D$, the corresponding adult phenotype will be equal to another phenotype at birth, (section 7.2). Supposing that this mutant is able to produce an offspring with the same genetic constitution, the adult phenotype of this offspring will be calculated as the entry in the developmental matrix which corresponds to the phenotype at birth of the original mutant.

According to the developmental rule, if new phenotype at birth is $Q$ the adult phenotype of any future offspring, $M^2(Q, Q)$, should also be equal to $Q$ in order to compete by establishing a self-promoting network of its own. The probability of finding a matrix with this property is 1/5 (for $D = 2$ each entry is filled by one of five possible numbers). The probability of the resulting adult phenotype being one that is able to compete with the dominant one is 1/4 (the four behavioral strategies are equally distributed along the 256 phenotypes). And the probability of picking up a genotype at random and that this genotype is within one mutation from the dominant one is less than 8/256 since some of these mutations will map into phenotypes which are closer than $D$. Thus, the probability of finding a mutation that will produce a competing mutant able to develop is...
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7.7 Discussion

As said earlier, the purpose of this study is mainly exploratory, hence the abstraction made in the early model. The relevance of social development for understanding the evolution of cooperation coordination could well be supported independently by theoretical arguments. A choice was made to examine the coordination instability in the presence of a dominant developmental structure (figure 7.12 (b)). This case was examined in more detail.

It is clear that the existence of a self-promoting developmental network poses much harder constraints for evolution to find viable alternatives. These are not impossible to find, but they must be the case that, for high values of $c$, these networks have not been observed in the population for such a value of $c$. In figure 7.11 (b) the variation of the population is shown. Besides the single main phenotypic component (figure 7.9 (b)) other alternative developmental networks have been observed in this case. This explains the sudden drop in coordination when the value of $c$ is increased up to the point where coordination is lost. It is possible to think that the selection pressure for finding viable alternatives increases as the network is more self-promoting. The result is that alternative developmental networks have not been observed in the population for high values of $c$.

What is observed as the value of $c$ is increased up to the point where coordination is lost is still possible to find certain level of coordination above the baseline for values near 0.8 (figure 7.11 (b)). The cause of this is that the phenotypic landscape is much more complex in the presence of a dominant developmental structure. The figure shows the main cooperative strategy (phenotype 251, 253, 255) and the cooperative phenotype that is observed in this case. This explains the sudden drop in coordination per one or both of the parents bearing this new phenotype. So, in order to compete with the dominant network, it is also required that the new phenotype at birth 175 and the adult phenotype 177 establish equal to 177. These are actually three conditions since the matrix is symmetric, so the chance of this happening is less than 5/256. An upper bound for the probability is then 6/256. It is clear that the existence of a self-promoting developmental network poses much harder constraints for evolution to find viable alternatives. These are not impossible to find, but they must be the case that, for high values of $c$, these networks have not been observed in the population for such a value of $c$. In figure 7.11 (b) the variation of the population is shown. Besides the single main phenotypic component (figure 7.9 (b)) other alternative developmental networks have been observed in this case. This explains the sudden drop in coordination when the value of $c$ is increased up to the point where coordination is lost. It is possible to think that the selection pressure for finding viable alternatives increases as the network is more self-promoting. The result is that alternative developmental networks have not been observed in the population for high values of $c$.

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to propose a minimal model where the nature of such influence could be explored.

In addition to the stabilization provided by spatial organization, cooperative coordination receives further stabilization by the presence of developmental networks which constrain the range of viable competing strategies and act as organizational invariants.

Further understanding of the dynamics of these structures could be obtained from other studies using reaction-networks. By the introduction of a chemical analogy, it is possible to use notions such as catalysis, hypercycles, etc., (Eigen & Schuster, 1979), whereby developmental relations can be seen as favoring the production of certain groups of phenotypes in a self-sustaining manner. The work of Fontana and colleagues on artificial chemistries (Fontana et al., 1994; Fontana & Buss, 1994a, 1994b, 1996) could be particularly relevant in developing this analogy. In this line of work the dynamical organization of randomly reacting artificial objects is investigated in a minimal chemistry paradigm using \( \lambda \)-calculus expressions as the structure (and functionality) of the reactants. Reactions follow the logic of deterministic construction of new entities from the reacting elements and their subsequent substitution. Starting from random initial conditions the whole system converges after a number of interaction into a set of \( \lambda \)-expressions which, after application upon an identical expression, ends up producing a copy of itself. These self-copying functions are analogous to the self-promoting developmental networks that emerge in the present model. Due to its simplicity, Fontana and colleagues have labeled this kind of invariant regularities a Level 0 organization. By the introduction of syntactical constraints the action of copy functions can be restricted and more complex self-maintaining organizations emerge (Level 1) which in
certain aspects resemble the developmental networks that obtain when \( c = 0.8 \).

However, the link between the two types of invariant structures is, for the moment, purely phenomenological, and some care should be taken in drawing hasty conclusions as the differences are also apparent, especially in terms of the other two “dimensions” in which the developmental networks of the present model exist: the behavioral and the genetic. One can have an idea of added complications by considering the complex relations between the same set of phenotypes exposed by figures 7.12 and 7.13 in the developmental and behavioral planes.14

Another interesting aspect of the model in relation to issues mentioned at the beginning of the chapter is that the self-promoting developmental networks that dominate the dynamics for a large set of parameter values happen to look, within the restriction of the model, a lot like cases of imitative learning or behavioral transmission. Although none of the minimal cognitive mechanisms that would seem to be necessary in order to speak of such a phenomenon are present in the agents, at least from an ecological perspective it seems that all the ways that parents can affect their offspring phenotype, those that most resemble teaching or imitation, are the most likely to be encountered. Such an observation should be taken as a warning when the intention is to try to understand the evolutionary role of social learning or imitative learning. It may not be directly related to selected advantages to individual organisms at all, but it may impose its own phenotypic significance simply by propagating more efficiently than other possible developmental relations. This would explain the apparent maladaptiveness that can be derived as a consequence.

14Interestingly, in the case where only self-promoting structures like that shown in figure 7.10 exists, the corresponding network of cooperating relations is also rather simple since the adult phenotype happens to be of the self-cooperating type, [(EO) or (OE)], and so the analogy can be directly applied. But this may not happen in more complex cases.
of other formal models such as Laland’s model on sexual imprinting (Laland, 1994) and the model on maternal effects by Kirkpatrick and Lande (Kirkpatrick & Lande, 1989, 1992).

Finally, it would be important to emphasize that this study has looked at the issue of social development from an abstract perspective, that of an instantaneous process coupled with, but not completely governed by differential reproduction. This is a strong simplification of the issue of development under social conditions, especially if its behavioral and dynamical aspects become the focus of interest. Whatever the complexities of natural cases one can at least be certain that those features abstracted in the formulation of the model have relevant consequences for the study of cooperative action coordination and should be taken into account in future studies.

Figure 7.14: Time variation for cooperative and non-cooperative strategies in secondary developmental network.

Chapter 8
Coordination without information

The model presented in this chapter is intended to act as a simple proof of concept against the preconception that information must be unevenly shared in order for communication to evolve. At the same time, it is meant to provide an example of the way in which a move can be made from the very simplified interpretation of coordination needed for studying some evolutionary and ecological issues towards a richer behavioral approach where other themes can be explored. This tendency will culminate in the strictly behavioral study presented in chapter 9.

As discussed in chapter 2, the preconception regarding information unavailability as a requisite for the evolution of communication arises from deriving an operational requirement from a functional \textit{a posteriori} interpretation of the phenomenon in a selective context. In the argument presented in that chapter it was emphasized that such a derivation is not just equivocal from a theoretical perspective but that it also has specific pragmatic consequences in the form of a whole range of phenomena that is left unexplored because the models (in particular computational ones) are unnecessarily restricted by a conceptual bias.

The model of social coordination presented in this chapter will extend the models presented in chapters 5 and 6 and will not assume hidden information as those other models did. The intention is not to address specific scientific questions. Rather, the interest is in presenting it as a very simple example of the sort of issues that can be explored by relaxing a problematic assumption. For this reason, results will not be analysed with as much detail as the with other models in this thesis. At the same time, it is expected that this model will suggest other ways of extending the very basic action-response game used so far to games where the term “coordination” can be applied more in accordance to the meaning given in chapter 2.

8.1 Computer models of communication and the informational bias

“A first prerequisite for communication is that some organisms have access to information (knowledge) that others do not, for if they all have access to the same information, no communication is necessary. The non-shared information could be about the organism’s own internal state (e.g., hunger), or it could be about features of the external state of the environment that cannot be directly perceived, or as well perceived, by the other organisms”, (MacLennan & Burghardt, 1994, p. 165).
Chapter 8. Coordination without Information

Such is the logic that, for quite some time, has been taken as a design dictum in many computer-based explorations on the origins and evolution of communication. As argued in chapter 5, the demand for reliable signalling of aggression to evolve and become fixed in a population of agents, whether or not as a result of natural selection or competition, is a powerful force in pushing evolutionary design. The condition for reliable signalling of aggression is the possibility of honest signalling under natural selection, which means that the signal must be informative (understood in the colloquial sense) to the receiver. Information (understood in the colloquial sense) is the obvious candidate for such a unifying currency. In spite of the lack of agreement on how to define or measure communication, the evolution of communication should be evident from the way the models in chapters 5 and 6 were built and the situation represented therein interpreted. The criticism made in this chapter is not aimed at the specific information-centered point of view, in the studies on honest signalling under natural selection just presented in many computer models as being unrealistic, uninteresting or in any other way inaccurate. The criticism is aimed at the language used in justifying those models, a typical perspective on communication since the possibility of uninformative uses of signals, an example of which is the above quotation. What this language manifests can only be considered.

A different and less frequent trend is exemplified by the work of Werner and Dyer (1992), who explore the idea that the evolution of communication is not necessarily driven by the need to signal aggression, but rather by the need for coordination among agents. They argue that communication can evolve to facilitate the meeting and reproduction of individuals. After many generations, the behavior of males (initially finding mating partners at random) can be correlated with the signals emitted by nearby females, which can be interpreted as constituting a "directional code" that "tells" males in which direction to move. Although the results of this model could perhaps be interpreted in terms of behavioral coordination, it is clear that the authors choose to make the model a denotational one, thus defining a conceptually and methodologically attractive perspective on communication.

The authors of this chapter argue that there is a bias in the field towards denotational models, which equate the evolution of communicative behaviors with the evolution of a shared code of tokens (usually plainly symbolic) that successfully map to environmental or internal states. The corresponding set of symbols can be very abstract, and the information conveyed can be quite complex. However, the language used in justifying these models is often misleading, as it is not always clear whether or not the models are actually denotational. The authors argue that such a bias is not only misleading, but also potentially harmful, as it prevents the study of questions regarding the evolution of communication, particularly in cases where the game posits a scenario where the benefits and costs of signalling are complex and interdependent. Some of the more biologically inspired models of communication, such as those by Steels and Wheeler (1996a, 1997a, 1997b) and others, do not rely on denotational models, but rather on more complex and integrative approaches that allow for non-denotative or dishonest signalling (although the honest-dishonest distinction remains informational in the sense discussed in chapter 2).

The authors argue that the use of denotational models is not a problem in itself, but rather that the language used in justifying these models is often misleading. They argue that the criticisms made in this chapter are not aimed at the specific information-centered point of view, but rather at the language used in justifying those models.

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Chapter 8. Coordination without information

It can be concluded that the game presented in chapter 7 does not assume information unavailability. However, there are few exceptions as mentioned in the text. The game of chapters 5 and 6 can be extended in order to be applicable to a situation in which there are different types of food sources. In this case, the actions of the three agents (pursuers, evaders, and food sources) can be correlated with each other, allowing for a more complex coordination scenario.

A return is now made to the case in which there are different types of food sources. However, it is possible as long as the structure of the agents remains non-plastic. Another issue that should be explored in chapter 9 is the performance of an agent when acting on the basis of external information about the food type. In this table, the performance of agents is evaluated based on their actions and a signal associated with the food type. The second player to produce action \( B \) and a signal followed by the first player acting again and producing \( C \) and a signal are evaluated as the best strategy in this model.

<table>
<thead>
<tr>
<th>Time</th>
<th>Sequence for food type ( F )</th>
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<tbody>
<tr>
<td>1</td>
<td>( A ) ( \alpha ) ( F ) ( \beta )</td>
</tr>
<tr>
<td>2</td>
<td>( A ) ( \beta ) ( C ) ( \delta )</td>
</tr>
</tbody>
</table>

As mentioned earlier, in this model presented in chapters 5 and 6, an interpretation was given in terms of information availability. The player in the first role is able to perceive a piece of food of which there may be different types requiring different actions. The player in the second role is not able to perceive the food type but must act upon the external manifestation of the action of the first player. Although such a way of interpreting the game was not essential for the results obtained, as shown in the table, the performance of agents is evaluated based on their actions and a signal associated with the food type. The second player to produce action \( B \) and a signal followed by the first player acting again and producing \( C \) and a signal are evaluated as the best strategy in this model. This is an example of a situation where the systemic definition would apply.
Chapter 8. Coordination without information

1

Figure 8.2: Examples of the evolution of dialogic coordinated activity for two typical runs. The line represents a linear regression.

Exactly as in chapter 6, agents are distributed in space and select their partners and food sources from their local neighborhoods. Reproduction is also sexual and local. The spatial, one-dimensional arrangement of the agents means that all agents can directly sense their neighbors and the agents are modelled as state-less machines.

For two typical runs with different values of $c$, the evolution of the average values of $c$ is shown in figure 8.1. A comparison of figure 8.2 with figure 6.2 reveals that for the case of one-step coordination the level of coordination in chapter 6, dialogic activity decreases linearly with $c$, whereas for two typical runs with different values of $c$, the evolution of the level of coordination may be explained in a similar manner as the evolution of the level of coordination in chapter 6.

If by information it is meant information about features of the environment, these are equally accessible to both participants, if it is meant information about the changing state or intention of the agents, they have no changing state or intention. In spite of this, the coordinating task is complex and requires a sequence of actions such as "A, B, C, D" in which the first player must perform "A, C" alternating with the second player who must perform "B, D" in a similar fashion as the level of coordination in chapter 6. As before, agents are modelled as state-less machines.

Agent forster's examples of two machines interacting and reaching their eigen-behaviors (von Foerster, 1977, 1980). The performance of a whole correct sequence may be called dialogic coordination. The situation is somewhat more complicated than the simple action-response game because not only must the external manifestations of both agents be correlated but also the external manifestations of the agents become correlated through the whole system. Not only must the second player play his signal in such a way that his external manifestations correlate with the ones of the first player, but also the second player must have an internal mechanism that allows him to start his actions with respect to the role played. The situation is even more complicated in the case of the level of coordination in chapter 6, where the coordinating task is complex and requires a sequence of actions such as "A, B, C, D" in which the first player must perform "A, C" alternating with the second player who must perform "B, D" in a similar fashion as the level of coordination in chapter 6. As before, agents are modelled as state-less machines.

It is possible to investigate the resulting behavioral matrices by analyzing the evolved behavioral structures. Analogous considerations to those mentioned for the model in chapter 6 apply here as well. A simulation was run with four different types of food, two of them requiring a sequence of actions such as "A, B, C, D" wherein the first player must perform "A, C" alternating with the second player who must perform "B, D". The amount of energy in the food-source is divided in half, and the two agents corresponding to the actions required by the first half of the sequence each get an equal part of the first half of the energy, if only one agent performs a correct action. If the proportion of the half of the sequence corresponding to the actions of the second agent is less than 50% (6.5 ≤ c ≤ 8.5), the agent gets nothing. The process is repeated for the second half of the sequence using the other half of the energy.
Chapter 8. Coordination without information

Perceived Signal

<table>
<thead>
<tr>
<th>Food Type</th>
<th>α</th>
<th>β</th>
<th>γ</th>
<th>δ</th>
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<tr>
<td>F0</td>
<td>A</td>
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<td>C</td>
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<td>F2</td>
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<tr>
<td>F3</td>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
</tr>
</tbody>
</table>

Table 8.2: Behavioral matrix of an evolved player of the recursive coordination game.

The aim of this model has been to provide a simple counter-example. Contrary to what is commonly thought, it is not necessary that a game should present players with unequal access to information for such a game to give rise to an evolutionary situation in which some form of communication may result. The type of dialogic coordination which evolves in this model for certain parameters cannot be readily associated with conventional signal exchange since there is no conventional reference involved. The problem with this kind of thinking was already addressed in chapter 2. If the perspective presented there is taken seriously, not only is dialogic coordination in the present model a non-informational form of coordination, but one can also say that it is certainly nearer the idea of communication expressed in systemic terms.

Next, let us consider the way in which coordination may result in pure interactions eliciting coordinated behaviors. Agents in this game cannot perform such a task since they are simple look-up tables. The case in which they can be said to act autonomously (i.e., as operationally closed systems) is at least very restricted. However, it will be seen that it is possible to provide the necessary structural richness to build a model in which behavioral coordination does occur in a more strict sense.

Besides pointing to the possibility of exploring via computer models non-informational forms of coordination, this chapter has also highlighted, albeit in a simplistic way, one of the themes that motivates the study of social behavior from the point of view of cognitive science. Such an approach expands the case of the relation of logical implication between performance and competence which exists in most methodological individualist positions. Accordingly, an instance of a performance by an individual entails the capacity in that individual to instantiate such behavior in coordination as is clearly demonstrated in this model by the capability of the agents to produce sequences of actions when presented with a static piece of food. The lack of internal states makes this task impossible at the individual level, but two agents in coordination may perform it.

These results show that agents coordinating their activity are able to perform tasks beyond their individual capabilities. This particular game requires an external environmental feature which exists when the food is of type F3 and signal δ. A second player of identical constitution perception of this type of food and signal δ will elicit the production of action α and signal β and so on. The actual level of dialogic coordination achieved by the food type F3 and signal δ in the simulation is 96.2% of the theoretical possible performance. The agent would achieve a dialogic coordination level of 93.75% just by counting for each food type the success levels that this agent achieves. For example, if the food type is F3 and signal δ, the initiating action of the first player (corresponding to column α) is α and its signal is δ. For a second player of identical constitution perception of this entry, the initiating action will be β and its signal is δ, and so on. The actual level of coordination is 96.2% of the theoretical possible performance. The actual level of coordination is 96.2% of the theoretical possible performance. The actual level of coordination is 96.2% of the theoretical possible performance.

This evidence for the possibility of performance to exist without individual competence. However, illustration is suggestive and more serious evidence will be presented in the following chapter.

8.3 Discussion

The aim of this model has been to provide a simple counter-example. Contrary to what is commonly thought, it is not necessary that a game should present players with unequal access to information for such a game to give rise to an evolutionary situation in which some form of communication may result. The type of dialogic coordination which evolves in this model for certain parameters cannot be readily associated with conventional signal exchange since there is no conventional reference involved. The problem with this kind of thinking was already addressed in chapter 2. If the perspective presented there is taken seriously, not only is dialogic coordination in the present model a non-informational form of coordination, but one can also say that it is certainly nearer the idea of communication expressed in systemic terms.
Chapter 9

Rhythm, entrainment and congruence in acoustically coupled agents

Considering this general background, the goal of this chapter is to present a model in which it will be possible to explore the value of the theoretical concepts introduced in chapter 2 in a direct manner as well as issues related to the role of embodiment in a concrete example. Moreover, the present approach differs from the models presented in previous chapters as well as from other computer models addressing the evolution of communication in that the focus of interest is on behavioral issues rather than on evolutionary ones. In order to make positive contributions to evolutionary questions, those models must assume too much in terms of positive contributions to evolutionary questions and evolutionary models are often closer in terms of positive contributions to evolutionary questions and evolutionary models are often closer in terms of positive contributions to evolutionary questions. Here, in contrast, the aim will be to make fewer assumptions about the nature of the interaction and the behavioral building blocks incorporated into the agents.

Up to this point, the studies presented in this thesis have explored the role of different kinds of acoustic interactions. The present approach is based on the recognition that adaptive behavior can be particularly highlighted in the interaction and the behavioral building blocks incorporated into the agents. This recognition is reflected in the behavioral-based approach to robotics (Brooks, 1991), in simulated approaches to the study of adaptive behavior in whole agents (Beer & Gallagher, 1994), and in the field of evolutionary robotics (Harvey, Hardman, Cuff, Thompson, & Jakes, 1997, and others).

As an attempt to describe the sense of the word, the present chapter is based on the recognition that adaptive behavior is often closer to the interaction and behavioral building blocks incorporated into the agents. This recognition is reflected in the behavioral-based approach to robotics (Brooks, 1991), in simulated approaches to the study of adaptive behavior in whole agents (Beer & Gallagher, 1994), and in the field of evolutionary robotics (Harvey, Hardman, Cuff, Thompson, & Jakes, 1997, and others). Most of the inspiration that drives these lines of thought has been around for quite some time. On the philosophical side, one can mention the earlier works of Martin Heidegger (1962; Dreyfus, 1991; Dreyfus & Jewett, 1996; Dreyfus, 1990; Hendriks-Jansen, 1996) and also the works of John Dewey (1929) and others, such as the work of Martin Heidegger (1962; Dreyfus, 1991; Dreyfus & Jewett, 1996; Dreyfus, 1990; Hendriks-Jansen, 1996) and also the works of John Dewey (1929). Other currents, not so well established in the field of evolutionary robotics (Harvey, Hardman, Cuff, Thompson, & Jakes, 1997, and others), include approaches to the study of adaptive behavior in whole agents (Beer & Gallagher, 1994), and the field of evolutionary robotics (Harvey, Hardman, Cuff, Thompson, & Jakes, 1997, and others). Most of the inspiration that drives these lines of thought has been around for quite some time. On the philosophical side, one can mention the earlier works of Martin Heidegger (1962; Dreyfus, 1991; Dreyfus & Jewett, 1996; Dreyfus, 1990; Hendriks-Jansen, 1996) and also the works of John Dewey (1929).
Chapter 9. Rhythm, entrainment and congruence in acoustically coupled agents

9.1 Acoustic coupling

The use of sounds is common in the animal world where it is associated with social behaviors. The following list describes some of the general cases for which social behaviors involve the interaction between individuals. In some cases, the sounds are used as tools for communication, while in others, they are used to control the environment. In all cases, the sounds are produced by physical means such as vocalizations or movements of the body. The sounds are broadcast within their local range and can affect more than one individual. Acoustic signals necessarily influence the behavior of the listener and can also be detected by other organisms. Differences in intensity between the sound perceived by each ear can be used to pinpoint its source, and in humans, this information is used to determine the angular position of the head with respect to the source.

9.2 An example of coordination through acoustic interactions

In order to illustrate the concepts introduced in the preceding section and some of the ideas discussed in chapter 2, a brief description will be made of a natural case of social coordination. Amongst the species of tropical birds, singing is not limited to the male but is also performed by the female. In many monogamous species, particularly in the case of the East African species, communication involves the use of different note patterns (Farghali, 1982). Antiphonal duetting has been studied in a number of species, such as ammunitions, duets, i.e. alternation of notes. The model presented in this chapter can be applied to understanding the general case of sign-language. However, a different example may help to put certain distance from specific human behavior. The position of the body, per se, is a useful preliminary step for understanding more complex models with many agents involved simultaneously.

More specific mechanisms, such as the inhibition of motor activity, the synchronization of movements, and the use of other sensory modalities, are present in the evolutionary convergence of many aspects of behavior in primates of different taxa.
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9.4 The model

9.4.1 Sound

Sound is modelled as an instantaneous, additive field of single frequency with time-varying intensity which decreases with the square of the distance from the source. The effects of time-delays will be explicitly ignored as well as the effects of differences in frequencies of sound production, i.e. Doppler effect, differential filtering etc. This coarseness of modelling will fit with normal modes of behavior which are not at all evolutionarily implausible. Instead, plausibility restrictions are imposed on the constraints that provide the context of the search process both in the form of performance evaluators for initial conditions and in the form of performance evaluators for initial conditions.

9.4.2 Bodies

Each agent is modelled as a circular body of radius $R = 4$ with two diametrically opposed motors. Each body has two sound sensors symmetrically placed at 45 degrees to the motors (see figure 9.1). The position of the sensors was chosen in order to introduce a back/front asymmetry (although which is not specified) as it is considered important to be able to evaluate the angular effects and real-time perception. The sound produced by the agent is a frequency-modulated signal, which is generated using a sinusoidal oscillator with a range of frequencies and a modulation depth.

Agent movements are governed by the interaction of the two sound sensors. The sensors detect the intensity of sound produced by the other agent and use this information to calculate the speed and direction of movement. The translational movement of the agent is calculated using the velocity of its center of mass (the vectorial average of the tangential velocities divided by the body diameter). There is no inertial resistance to this movement.

Agents move freely in the arena, except when they collide with each other. Collisions are modelled as point elastic, i.e. no energy loss and no effect on the angular velocities of the bodies. While undergoing a collision, an agent may move in a direction which is not specified by its motor, but which corresponds to a displacement which coheres to the momentum of the whole agent. This coherency is important in order to introduce additional factors that may affect the behavior of the agents.

Continuous time recurrent neural networks will be used as the internal architecture of the agents. These networks are chosen in order to introduce a back/front asymmetry (although which is not specified) as it is considered important to be able to evaluate the angular effects and real-time perception. The network has proven adequate for generating such behaviors. In the spirit of reducing the initial set of assumptions, agents will not be built directly, although certain parameters (such as body size) will be specified as possible structures.

9.3 Methods

The rest of the chapter discusses a simulation model which will be helpful for exploring some aspects of the concepts discussed above. Inspired by the example of duetting birds, a simulation class can approach each other via use of acoustic interaction (i.e. signal production and reception). The sound produced by the agent is a frequency-modulated signal, which is generated using a sinusoidal oscillator with a range of frequencies and a modulation depth.

Continuous time recurrent neural networks will be used as the internal architecture of the agents since it is desirable that they produce behaviors that are consistent in time and place. In order to achieve this, the network has proven adequate for generating such behaviors. In the spirit of reducing the initial set of assumptions, agents will not be built directly, although certain parameters (such as body size) will be specified as possible structures.

A word must be said about the use of a genetic algorithm (GA) in the context of this work. Since it is not the aim of the model to provide an evolutionary scenario wherein the behaviors under study are the result of an evolutionary process, the results of these behavioral experiments will be derived purely by the task of searching a complex design space. Therefore, no conditions will be derived about the likelihood of evolutionary histories that may lead to the behavior of interest. Examples of the influence of death of the agents are not a part of the purpose. The significance of each case will be given by the choice made.
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Each effector node receives one incoming synapse from each sensory node (of which there are only one for each auditory sensor). In some simple cases the inter-neuron network is fully connected (including self-connections). Additionally, each inter-neuron network serves as an incoming synapse from each sensory node. This kind of dynamical neural networks can serve as a model for studying adaptive behavior in simple autonomous agents as shown by several successful cases (Beer & Gallagher, 1992; Beer, 1996, and others). This is especially so when dealing approximately with time constraints becomes an essential part of adaptation (Beer, 1995; Harvey, 1996).

Inter-neurons and effectors neurons obey the following law:

\[ y_i(t+1) = y_i(t) + \sum_{j} w_{ij} x_j(t) \]

where, using terms derived from an analogy with real neurons:

- \( y_i \) represents the cell potential,
- \( w_{ij} \) the strength of synaptic connection from node \( j \) to node \( i \),
- \( x_j \) the degree of sensory perturbation on the sensory node (modelled here as an incoming current).

In similar model, sensors can be directly regulated by their participation in the network dynamics (e.g. by incoming synapses). A decrease in the inter-neuron network was made instead of directly the effect. This network allows the agent to have the possibility of extra control on perception. The gain of both sensors is regulated by the sensory neurons (in a symmetric way), and another one for the gain of the sound production organ. In each case, the sensor transduction step is the same, the gain is regulated by the sensory neurons. These are physically separated so that in general their activity will be influenced by different external intensities. A natural mechanism, mentioned in section 9.1, in involves the attenuation of intensity as high-frequency sound is shadowed by other components. This shadowing is modelled as a linear attenuation without phase shift (i.e. the attenuation factor is as proportional to the distance travelled by the sound signal within the body). This distance is given by:

\[ D_{\text{sh}} = D_{\text{on}} (1 - A) \]

where

- \( D_{\text{on}} \) is the distance between the source and the sensor,
- \( A \) is the distance between the source and the center of the body,
- \( A \) is the angle between the line of sight to the source and the sound produced by the agent,
- \( 0 \leq A \leq 1 \).

The attenuation signal is calculated by the effect of the sound on the agent. The amplified gain is the sound produced by the agent to the external source. The gain is regulated by the degree of perturbation (i.e., the noise or the direction of the sound). In order to constrain the production of sound to a realistic behavior, neurons are allowed to "burn up" if the cell potential exceeds certain limits due to intense stimulation. In sensory neurons, this kind of mechanism is modelled as a linear attenuation without phase shift (i.e., the attenuation factor is linearly proportional to the distance travelled by the sound signal within the body).

One more detail is that the attenuation factor is not necessarily as a literal current. The gain of effectors can be regulated as well. In all cases presented only two regulating neurons were used, one for the gain of both sensors (in a symmetric way), and another one for the gain of the sound production organ. In each case, the sensor transduction step is the same, the gain is regulated by the sensory neurons. These are physically separated so that in general their activity will be influenced by different external intensities. A natural mechanism, mentioned in section 9.1, in involves the attenuation of intensity as high-frequency sound is shadowed by other components. This shadowing is modelled as a linear attenuation without phase shift (i.e. the attenuation factor is as proportional to the distance travelled by the sound signal within the body). This distance is given by:

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neuronal structures which satisfy this "physiological" restriction can be seen as approaching natural structures. Evolved agents should be expected to "take care" regarding the intensity of their own sound production and/or use their sensory gain regulation accordingly.

9.4.3 Genetic algorithm

A form of rank-based selection genetic algorithm has been used as a search technique with a fixed population size of 90 agents evolving for up to 10,000 generations (after a few hundred generations the search converged). Each agent is selected an average of ten times (five guaranteed) to play with a different agent in the population which is introduced in the arena at a random time after the first one. The delay is to avoid cases in which agents may undergo similar dynamics in an artifactual way simply because they start their operation at the same time and from similar initial conditions. The second agent is placed at a random distance no smaller than 50 from the current position of the first agent. The initial state of the agents is reset at the start of each trial; the cell potential of each neuron is set to an appropriate interval in order to specify the activity of the network. Transduction gain is chosen from the interval [0, 1/3], biases from [-3, 3], weights from [-8, 8] and decay constants from [0.4, 2]. An agent with n inter-neurons and l sensory effectors would have a genetic representation of \( n + 2l + 3 \). Symmetry between left and right is enforced only for biases and gains, but not for weights and some of the gain parameters are directly regulated by the agent (see above) so the resulting genome size is in fact less than the above quantity.

After ranking the population according to fitness the next generation is built by making 2 copies of each individual in the top third of the current population and one copy of each individual in the bottom third. Fitness values are averaged over all the trials. Fitness is allocated in terms of how much the agents have approached each other at the end of the run, \( F = \frac{1}{N + SE} \left(\frac{D_{\text{final}}}{D_{\text{initial}}}\right) \) and what proportion of the interaction time they have spent within a distance of 4 body radii of each other \( F = (F_{\text{approach}} + F_{\text{maintain}}) \). Additionally, the weighted sum of these proportions is modulated by a mild exponential term that decreases with the integrated energy used. This was done in order to compensate for the lack of an adequate model of energy consumption. Agents making excessive use of motors are therefore penalized, although very mildly. The individual fitness for a given trial (usually lasting 200 time steps) \( F \) can be expressed as:

\[
F = \sqrt{a_p (V - t_f)} + a_m \sqrt{V - t_f} + a_e \sqrt{t_f}.
\]

Where \( a_p = 0.25 \) and \( a_m = 0.25 \) are the weighting factors for the approaching and maintaining of proximity tasks respectively, \( a_e = 0.005 \) scales the modulation of \( F_{\text{approach}} \) and \( F_{\text{maintain}} \) with the transduction speed of the right and left motors respectively. A final factor affecting fitness is the translational speed of the right and left effectors and the lack of an adequate model of energy consumption. In total fitness that is set to zero in the cell death (see above). If in the end of the trial an agent has burnt up one of its sensory or effector neurons, its total fitness in that run is reduced to zero.

Numerical integration of the model is done using the Euler method. This is a second order method and therefore not very accurate, however it is fast enough to study many evolutionary runs. Highly fit agents evolve reliably after a few hundred generations. About 16 different evolutional strategies were observed which yielded similar results are obtained for a given trial (usually lasting 200 time steps) \( F \) can be expressed as:

\[
F = \frac{1}{N + SE} \left(\frac{D_{\text{final}}}{D_{\text{initial}}}\right) + \frac{1}{N + SE} \left(\frac{t_{\text{interaction}}}{t_{\text{total}}}ight).
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This was done to penalize the agents which use excessive sensory or effector neurons, in order to make the approach as simple as possible.
9.5.1 Approaching behavior

Agents successfully approach each other when two of them are in the same arena (figure 9.2 shows an example of the trajectories performed by the agents and the distance between them as a function of time). The structure of the evolved neural network can be seen in figure 9.3. Only 2 active inter-neurons are “used” by the agents; the other two have a constant activation of 1 or 0 (not shown). Examination of the sensory activation shows that the signal perceived by one agent at the moment when the other one is placed in the arena is very faint in comparison with the agent’s own signal production, and even in comparison with noise levels. Agents engage in a mode of search behavior that relies on the fact that self-shadowing is a mechanism that can be exploited actively by movement with a strong angular component (figure 9.2). This helps to discriminate external sounds since perception of an agent’s own signal does not depend on the orientation. Sensors act as leaky integrators and connect differentially to the inter-neurons with similar absolute weights (figure 9.3, values not shown), which means that the basic strategy would seem to involve rotation while moving, integration of sensed intensities and evaluation of the difference between left and right sensors (i.e. filtering out of own contribution to perceived intensity since this contribution is the same for both sensors). This is an efficient way of discriminating faint external signals. However, this is not entirely right. It is observed that self-stimulation is also integrated into the production of movement, as is evident from the fact that if one reduces progressively the capacity to hear their own production, the behavior of the agents degenerates very rapidly into a rotation on the spot. Perturbation can be done by altering the degree of self-stimulation in absolute terms (multiplying the contribution to perceived intensity due to the agent’s own signal by a factor between 0 and 1) or by introducing delays between own sound production and perception.

Notice also that agents choose to place their sensors “on the back” with respect to the direction of movement. This cannot be explained in a straightforward manner, but it may be related to an enhancement of the active discrimination strategy at the initial stages. If both sensors were placed in the direction of the external source it would be unlikely the self-shadowing mechanism will enter into action.

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13The latter method has been used in humans to show the dependence of speech production on acoustic self-perception in subjects with normal hearing. Delayed hearing of own spoken words results in degradation of the speech produced. Deaf people can of course produce speech relying purely on kinaesthetic perception showing, therefore, no degradation. This method can be used to identify subjects who fake deafness, (von Bekesy, 1972).
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Figure 9.6: Trajectory for an agent with a constant source with a fixed position relative to the agent. (a) The agent's position is represented by a small circle on the side of the agent. (b) The source position is represented by a small circle on the side of the agent. Signal emitted by the agent, (b).

From the observation that if a sound source is placed at a fixed distance and angular position with respect to a moving agent, the agent's rhythm in signaling behavior disappears. This is shown in Figure 9.6. The previous evidence for an agent's signal direction is not independent of signal production. From the observations above, movement is not possible, nor is it possible to decompose movement into active sensing and approaching. The new observation is that rhythm in signals originates somehow within the dynamics of interaction. From another point of view, it could be argued that angular movement depends on rhythmic signals produced by the agent. As expected from the fact that sensors can burn up due to intense power, the observed entrainment must be somehow related to the coupling between the agents. This suggests that the observed entrainment can be lost momentarily only to be regained later. This phenomenon is similar to what has been called relative coordination.

9.2 Entrainment, turn-taking and structural congruence

After the analysis of frequency spectra, it can be concluded that rhythm in signaling behavior is directly linked to angular behavior. This is achieved by comparing for one of the agents the frequency of its signal with the frequency of the variation in angular orientation relative to the line connecting both agents and finally with the frequency obtained from the "objective" difference of sound intensity at the sensors. (Figure 9.7) All three spectra show a sharp peak at the same value of frequency. Additional evidence of a connection between signaling and angular movement is obtained from the observation that if a sound source is placed at a fixed position relative to the agent, the agent's rhythm in signaling behavior disappears. From another point of view, movement is not possible, nor is it possible to decompose movement into active sensing and approaching. The new observation is that rhythm in signals originates somehow within the dynamics of interaction. From another point of view, it could be argued that angular movement depends on rhythmic signals produced by the agent.
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Figure 9.7: Signalling behavior of interacting agents and power spectra.

Figure 9.8: Motion of agents during period of coordination. Agents are shown at two time steps.

If the agent had an individual capacity to adapt its signalling behavior to the sound it perceives, one would expect it to show a similar signalling behavior in the presence of the beacon. It does not happen. It can be argued that the frequency used by the beacon is not exactly right. A long simulation in which a slow “frequency sweep” in the beacon’s signal is performed for the whole range of frequencies of interest shows no difference in the signalling behavior of the agent. The possibility still remains that the particular distribution of frequencies may matter. In order to test this, the following experiment is performed. A normal simulation with agents in interaction was run and the signalling behavior of one of the agents during coordination was saved. The “tape” signal was broadcast from the beacon to the other agent now by itself. The result (see figure 9.10) shows that phase locking does not occur.

All this evidence points to the importance of the presence of a history of mutual induction of changes in the dynamics of each agent. Beacons are completely non-plastic and therefore their “behavior” cannot be influenced by the approaching agent. The lack of a transient period of mutual triggering of changes of state results in no structural congruence and consequently in no entrainment. In other words, the process ceases to be historical in the sense proposed in chapter 3.

So far only some external manifestations of structural congruence have been considered. Figure 9.11 presents further evidence, this time from internal dynamics. This figure shows the embedded time-delayed plots for the activation of the same inter-neuron in two agents under different circumstances. The two plots at the bottom correspond to the agents acting on their own, i.e. uncoupled. Here it is again observed that although their structures are similar (both neural networks present the same architecture shown in figure 9.3), they are not identical (parameter values differ slightly) and, consequently, their dynamics present different attractors. The top four plots show the same embedded dynamics, now for the agents in interaction. The two plots at the top are taken from a period of coordination. The striking similarity between the two attractors becomes evident as well as the difference between them and the respective natural dynamics. The plots at the center of the figure show agents interacting but during a period when coordination has been lost. The plots also show an interesting qualitative difference with respect to the other cases. Agents...
not return to their natural dynamics when coordination is lost but to a different, uncoordinated state from which it is possible for coordination to be regained and which suggests that, during interaction, the structure of each agent has changed from its natural one.

In each case it is possible to calculate the time correlation in neuron activation between the agents:

\[ \rho = \frac{\text{Cov}(A_i, N_j)}{\text{SD}(A_i) \cdot \text{SD}(N_j)} \]

where \( \text{Cov}(x, y) \) is the covariance between variables \( x \) and \( y \), \( \text{SD}(x) \) the standard deviation of \( x \) and \( \rho \) the correlation coefficient. In the case of coordination \( \rho = 0.8443 \), for the case of interaction and anti-correlation \( \rho = 0.0403 \). A strong correlation between coordinating agents is in accordance with their signaling behavior.

The transition from coordinated towards un-coordinated state can be induced both by fluctuations (noise) or by instability due to internal differences in the respective dynamics. However, the transition from un-coordinated state to coordinated one can only be understood in the presence of an organizing coupling between the two systems. The first plot represents the distance between the agents in the period of interest. In the case of coordination \( \rho = 0.3750 \), for the non-interacting agents \( \rho = 0.0403 \). A strong anti-correlation between coordinating agents is also possible, suggesting that agents are filtering out the noise and then calculating the phase difference as a function of time. This is shown in the range between -360 and 360 degrees to aid visualization, i.e., the horizontal lines indicate a same phase value.

9.6 Discussion

The basic model shows some interesting phenomena like turn-taking and organized movement. In interpreting how these phenomena arise, one can make use of theoretical concepts concerning social behavior under a systemic, operational perspective (as presented in Chapter 2) as well as other concepts from the dynamics of coupled oscillators. It is thought that much is to be gained from this perspective and that the present example has not exhausted its potential.

The model shows how agents interact acoustically and through this interaction they mutually coordinate their patterns of movement and structure their acoustic coupling into a form of alternated production that resembles turn-taking. It is not inconceivable that this result could have been obtained, for instance, by means of coordination and filtering of the noise. However, providing a thorough operational explanation can be hard. Apart from the potential complexity of such an account, one of the main difficulties lies in the fact that the processes are analyzed operationally and perceptions. Initially, one may be surprised that agents can organize their interactions in the presence of an organizing coupling, for instance, by filtering out the noise and then calculating the phase difference. This is shown in the range between -360 and 360 degrees to aid visualization, i.e., the horizontal lines indicate a same phase value.
Figure 9.11: Embedded time-delayed dynamics in the same inter-neuron for two agents (A1 and A2) in different situations. The selected inter-neuron was chosen for clarity in the plots.

Figure 9.12: Achievement, loss and regaining of coordination. From top to bottom: distance, relative orientation, signals and estimation of relative signal phase as functions of time.
Chapter 9. Rhythm, entrainment and congruence in acoustically coupled agents

As implicitly noticed in the discussion on the origin of rhythm in signal patterns. Nevertheless, a certain behavior need not be within the realm of competence of the individual organism if the behavior is performed socially in a coordinated fashion. A fact that should serve as a warning when one tries to extrapolate observations about social behaviors of an organism should work from functional interpretations of observed evidence (what it does, not what it means).

Chapter 2 (section 2.2) mentions that the received wisdom has been in recent years that the social behavior of an individual (such as the bonding observed between duetting pairs of birds) has become "frozen" in ways that favor the evolution of species with the same social form. The study of social behavior and its relevance to the evolution of human beings has been approached from a purely functional angle. Nevertheless, there is nothing inherently wrong with this. However, functional considerations should be grounded on what is known about the operation of the systems concerned. As discussed in chapter 9, the model suggests that the evolution of human intelligence the social life of our ancestors needed to be good predictors of the outcomes of social interactions. It is important for understanding the evolution of human life to distinguish between the social interactions that are social and those that are not.

Chapter 2 also discusses the role of centeredness in the interaction of the various systems involved. The model suggests that the direct analysis of dynamics as well as the utilization of more indirect perturbation techniques should be highlighted as particularly useful. The model has also shown that some of the grounded facts obtained from the study of autonomous systems can have direct application in describing and explaining concrete examples of adaptive behavior, thus proving the practical value of the vocabulary and framework introduced in chapter 2.

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A related aspect that shows how the divide between social and individual capabilities tends to permeate into operational requirements is the re-discovery of the role of functions that behavior should serve as a warning when one tries to extrapolate observations about social behaviors of an organism should work from functional interpretations of observed evidence (what it does, not what it means).

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Chapter 10: Conclusions

10.1 Recapitulation and contributions

Chapter 10 articulated the need to ground the theoretical framework used to deal with social adaptive behavior on an operational theory of biological autonomy. This choice was made both for pragmatic reasons and because of the concern raised about the way traditional biology has treated social behavior exclusively from a functional point of view and, as a consequence, has failed to account properly for paradigmatic cases such as animal communication. The situation remains undefined beyond this intuitive level.

In response to this situation, the choice was made to ground the work of this thesis on an operational theory of biological autonomy based on systematic conceptualization and given expression in the works of Humberto Maturana and Francisco Varela. According to this theory, the autonomy of a system is defined as the operational closure of its internal dynamics. Perturbations which may trigger new states in the system are said to be indirect if they cannot specify these states directly. For instance, if two animals are engaged in the interaction but not necessarily for the appearance of what is intuitively considered as communication, the phenomenon itself remains undefined beyond this intuitive level.

This thesis has originated from a combination of interests in some biological and cognitive aspects of social behavior. It has offered a theoretical and methodological perspective on how to approach research on social adaptive behavior in autonomous systems as well as concrete examples of this perspective at work in the form of specific investigations concerned with the evolutionary, ecological, and behavioral aspects of basic social interactions. This has been a recurrent theme of the thesis.

Evolution, therefore, has been considered as proceeding by the combination of constraints and reiterative dynamics, which bear a variety of consequences for the nature of social behavior. These are not only confined to the case of social behaviors but also to the boundaries that separate evolutionary and environmental dynamics as part of social behavior.

In general, the importance of understanding evolutionary and ecological behaviors as part of the evolutionary, ecological, and behavioral aspects of social behavior. This has been a recurrent theme of the thesis.

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The introduction of minimal density thresholds for the players' groups, which was made in order to explain the emergence of cooperation in the previous models, was the starting point for this investigation. It was found that the introduction of these thresholds made it possible to explain the results observed in the discrete model. The problem of how to incorporate these thresholds into a continuous model was then addressed. It was found that a continuous model could be obtained by using a diffusion process to describe the movement of players from one group to another. This model was found to be consistent with the results obtained from the discrete model.

In addition to the introduction of minimal density thresholds, another important aspect of this investigation was the use of computer simulations to test the models. It was found that computer simulations were a useful tool for testing the models and for exploring the dynamics of the system. The simulations were able to reveal the complex behavior of the system, including the emergence of cooperation and the formation of clusters. These results were found to be consistent with the results obtained from the experimental studies.

The results of this investigation have important implications for the understanding of the evolution of cooperation. It was found that cooperation can emerge in systems that are characterized by the presence of minimal density thresholds and by the movement of players between groups. This finding has implications for the study of cooperation in real-world systems, such as social networks and ecosystems.

In conclusion, the results of this investigation demonstrate the importance of considering the dynamics of the system when studying the evolution of cooperation. It was found that the use of computer simulations and the introduction of minimal density thresholds were essential for understanding the complex behavior of the system. These results have important implications for the study of cooperation in real-world systems.
10.2 The Future

Although the investigations presented in this thesis are concerned with the possibility of decomposing behaving into functional modules, it is clear that agents can engage in coordinated behavior with other agents but not individually with simple algorithms. The biological implications of these models are clear. Evolution, particularly evolution of social behavior, cannot be studied purely as a process de-coupled from its ecological context. As any other natural process, evolution is a situated process and as described in chapter 3 also a social behavior (which is the domain in which it was originally meant to be applied). It is so in the purely social role of interacting with other agents, but self-hearing plays an important operational role in the generation of cycloidal approaching movement as is confirmed when movement collapses as a result of the self-hearing capability being perturbed.

Another implication is concerned with the possibility of decomposing behaviors into well-defined functional modules. This may not always be easy and is particularly difficult if the presence of hidden information for interesting behaviors to evolve. The model shows this in a very simple way by extending the interactions between agents to the production of alternating operational roles. Inter-agent interaction and remaining close only by producing and sensing sound agents do not just approach one another but that they also do something else. To achieve this, it is almost certain that the environment would have to be modified by the introduction of additional structures. An alternative approach would be to try to realize a similar situation in actually embodied systems. This path is definitely not triable since the agents must produce a sequence while being modelled as state-less machines. Therefore, any non-constant response to a constant environmental stimulus must come as a result of their interaction. This simple counter-example also hints to the direction in which a future could be studied in that direction. A model of acoustically coupled agents is presented in Chapter 9 follows that direction. A model of acoustically coupled agents is presented in that direction. In order to confirm that this is the case and that agents are not simply very good individual adaptors, a crucial test is made to see if agents can exhibit a similar signaling behavior in the presence of non-plastic beacons that reproduce the coordinated signaling patterns of a single agent. Failing to observe an entrainment of signals in this case suggests that agents are indeed co-adapting and perhaps subject to evolution themselves, or by enlarging the variety of modes of interaction and perhaps subject to evolution, too. To achieve this, it is almost certain that the environment would have to be modified by making the interactions more complex, perhaps approaching something like the friction patterns of jumorit (section 9.2). Contrary to what is usually claimed, computer models of communication need not include the presence of social interaction. As shown in this model, the self-hearing of an agent does not mean that agents can engage in coordinated behavior with other agents but not individually with simple algorithms. The biological implications of these models are clear. Evolution, particularly evolution of social behavior, cannot be studied purely as a process de-coupled from its ecological context. As any other natural process, evolution is a situated process and as described in chapter 3 also a social behavior (which is the domain in which it was originally meant to be applied). It is so in the purely social role of interacting with other agents, but self-hearing plays an important operational role in the generation of cycloidal approaching movement as is confirmed when movement collapses as a result of the self-hearing capability being perturbed.

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that structural congruence between unevenly plastic organisms may be the basis for explaining social affinity and some forms of social learning (see section 2.4). In order to study this hypothesis, the plastic dimensions of the agents would have to be extended as well as a way of letting the history of past interactions be actively reflected in their present structures. One way of doing this is by extending the dynamics of the neural networks to include processes that occur on much slower time scales. An interesting possibility under consideration is the use of architectures that incorporate additional mechanisms like neuron modulation through emission and diffusion of "gas" (Husbands, Smith, Jakobi, & O'Shea, 1998; Husbands, 1998). These dimensions of added plasticity would facilitate experiments on social affinity such as comparing the co-adaptation between individuals in a "fresh" state with the co-adaptation between individuals who have undergone a long history of co-adaptation with different partners. Similarly, the possibility of social "learning" could be tested by allowing a group composed of genetically identical individuals which are already able to coordinate to undergo two independent evolutionary processes in which genetic constitution is kept constant but the possibility of historical drift in the patterns of behaviors is left open by the recurrent achievement of structural congruence between different generations in the presence of noisy fluctuations.

This last possibility can be "re-connected" with the themes of investigation of the other models in the thesis which in a way can be thought of as approaching a similar issue from the evolutionary and ecological angle. While a full-blown ecological model of acoustically coupled agents would perhaps be too complex and probably also too difficult to understand, it is possible to make some further distortions that would make agents behave in simple ways using perhaps simpler architectures but retaining some interesting behavioral potential beyond mere look-up tables. This would allow the possibility of a more direct and more direct way of looking at the development by coupling behavior and developmental changes in a more direct manner.

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