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An Investigation into the Evolution of Communication

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This article presents a theoretical criticism of current approaches to the study of the evolution of communication. In particular, two very common preconceptions about the subject are analyzed: the role of natural selection in the definition of the phenomenon of communication and the metaphor of communication as information exchange. An alternative characterization is presented in terms of autopoietic theory, which avoids the mentioned preconceptions. In support of this view, the evolution of coordinated activity is studied in a population of artificial agents playing an interactional game. Dynamical modeling of this evolutionary process based on game-theoretical considerations shows the existence of an evolutionarily stable strategy in the total lack of coordinated activity which, however, may be unreachable due to the presence of a periodic attractor. In a computational model of the same game, action coordination evolves even with individual costs against it, due to the presence of spatial structuring processes. A detailed explanation of this phenomenon, which does not require kin selection, is presented. In an extended game, recursive coordination evolves nontrivially when the participants share all the relevant information, demonstrating that the metaphor of information exchange can be misleading. It is shown that agents engaged in this sort of interaction are able to perform beyond their individual capabilities.

Key Words: evolution of communication; autopoiesis; action coordination; spatiotemporal constraints

Introduction

The variety of behaviors that we group under the label *communication* can range from the simplest iconic display to the most complex forms of human interaction. Not surprisingly, this subject has attracted the interest of a heterogenous group of disciplines, ranging from evolutionary biology and ethology to psychology, psychotherapy, sociology, philosophy of language, epistemology, and media studies, among others. This diversity suggests an immediate question about the actual degree of relatedness of similarly labeled corresponding subjects of these disciplines. It is apparent that the

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phenomenon of communication can be viewed from many angles so that the very existence of a constant underlying theme comes into question.

Given the biological nature of all known communicative phenomena, it could be argued that biology is in a privileged position for disclosing any such constant theme. However, current theoretical studies in the biology of communication have shown a tendency to move away from this target, partially because of the use as primitives of the same phenomena that they try to explain. Biologists have studied the interspecific and intraspecific signaling systems used by animals, their function and their evolution. These biologists have had a difficult time defining exactly what constitutes an act of communication, without borrowing primitive terms and concepts (e.g., *signal* and *information*) from other disciplines and contexts and using them within a functional framework. Consequently, the scope of their approach often is limited to classes of problems in which these terms can be used consensually, such as the problem of honesty in signaling systems.

The aim of this work is twofold. The first half of this article (sections 2 and 3) tackles some of the theoretical difficulties of defining communication by providing a critical analysis of the use of the beneficial-exchange-of-information metaphor. I will claim that this metaphor achieves very little in disclosing the basic nature of the phenomenon of communication. I also will introduce an alternative theoretical understanding of this subject based on the theory of autopoiesis (Maturana & Varela, 1980), an understanding whose roots can also be found in certain works on cybernetics, psychotherapy, pragmatic philosophy of language, and phenomenology.

To show the benefits arising from the adoption of this focus, the second half of this article (sections 4 through 6) presents an investigation into the evolution of nonrecursive coordination and coordination of recursive actions by proposing a mathematical and a computational model for the evolution of a population of agents playing an interactional game. The choice of this game is guided by the wish to maintain certain continuity of language and tools with more traditional approaches. An extended game-theoretical account of the problem will show that evolutionary dynamics do not necessarily reach an equilibrium that we may identify as a stable strategy, justifying, therefore, further modeling in order to consider more intervening factors, such as spatiality and asynchronicity. A good framework for this task will prove to be a direct computational modeling of the same process.

The results of these investigations will show that coordinated activity evolves in cases that cannot be accounted for in the traditional view but fall naturally within the alternative understanding of the phenomenon presented here. The relevance of these results for an investigation of the origin and evolution of natural communication is discussed in the last section of this article.

Preconceptions About Communication

In most studies of the evolution of communication (this article included), authors provide a new definition of the phenomenon or at least find it necessary to revise previous definitions. This fact alone can be considered as sufficient proof of how slippery the concept of communication can be. Depending on the aim of each study, it is not uncommon for concepts such as communication to suffer transformations in order to ensure the applicability of the research tools and methods available. In general, different views on the same subject reveal the origins of the research tradition in which they are embedded by the presence of different preconceptions. By *preconception*, I mean the unquestioned application to a new domain of theoretical constructs that have proved successful in some domains. It is important to notice that this transference of concepts is not usually done, as in the case of a working hypothesis wherein the possibility of revision exists, but rather as primitives that need no further questioning and are "accepted as such" (Stolzenberg, 1984). It would be, however, a mistake to think that any preconception is necessarily a *mis*conception. The latter has to do with how well our ideas fit into the world of our experience, whereas the former refers to an almost necessary consequence of any scientific activity.

Preconceptions have obvious repercussions for research. Not only do they shape the way in which specific questions are addressed, but they also constrain the range of questions that it is sensible to ask. We tend to rely blindly on them, and their very distinction demands an effort in self-reflective questioning of one's own methodology. It is my purpose in this section to analyze briefly two important preconceptions about the evolution of communication.

2.1   The role of selection

A preconception frequently found in definitions emerging from behavioral ecology is that communicative behavior is necessarily beneficial for some of the participants (at least probabilistically); otherwise, natural selection would not have favored it.

Wilson (1975) defines communication as the altering by one organism of the probability pattern of behavior in another organism in a manner adaptive to either one of them or to both. Lewis and Gower (1980, p. 2) define communication as "the transmission of signals between two or more organisms where selection has favoured both the production and reception of the signal(s)." Krebs and Davies (1993, p. 349) define it as the "process in which actors use specially designed signals or displays to modify the behaviour or a reactor." They later make clear that they understand "specially designed signals" as those that have been favored by natural selection (Krebs & Davies, 1993). Burghardt (1970; MacLennan & Burghardt, 1994, p. 163) defines it as a behavior that is "likely to influence the receiver in a way

that benefits, in a probabilistic manner, the signaller or some group of which it is a member." Maynard-Smith and Harper (1995, p. 306) define a signal "as an action or structure that increases the fitness of an individual by altering the behaviours of other organisms detecting it, and that has characteristics that have evolved because they have that effect."

All these definitions are questionable on simple methodological grounds: *They mix a characterization of the phenomenon with a possible (and, admittedly, plausible) explanation of it.* In other words, these definitions resolve a priori the problem of why communication has been established in animal societies, leaving little room for alternative or complementary elements in its explanation or their rebuttal, while at the same time providing a poor characterization of the phenomenon. Biologists have appealed to this kind of definition in order to rule out cases of behaviors that are intuitively not communicative and that fall within the characterization given by broader definitions such as "an exchange of signals." Their main concern is not whether their definitions of communication capture the essence of the phenomenon but rather whether communication, *as defined*, is subject to treatment in a variety of issues, such as honesty in aggressive signaling or quality advertisement and its relation to fitness costs and energy budgeting.

Unfortunately, the problem of poor characterization remains. Two questions may be asked about these definitions. First, is the notion of selective advantages enough to provide an understanding of what sort of behaviors can be considered communicative? Second, if alternative mechanisms were found to be playing a crucial role, in place of natural selection, in the evolution of behaviors that we believe to be communicative, should we provide a different definition for these phenomena?

Some biologists might respond to the first question by saying that everyone intuitively knows what a signal is and that we all agree on that. This would seem to contradict the succession of constant refinements to previous definitions that keep appearing in the biological literature. What are the logical consequences of the idea of communication as a self-benefitting activity? Is an organism that has developed a mimetic character emitting a signal in order to confuse a predator? Can we say that the predator acknowledges the signal by *not* receiving it? If we are strict enough, we should answer affirmatively (see Maynard-Smith & Harper, 1995). If, for instance, we saw a group of animals committing collective suicide after a call given by one of them, would not we still describe this as a case of communication? The fact that we rarely see such behaviors should perhaps be used to support selective *explanations* but not to provide an immediate definition of what goes on in communicative behaviors.

The second question might be answered by many biologists by arguing that there is no possible explanation for the existence of communication other than its being selected because of its benefits and so it is not really important whether the working

definitions leave room for alternative or complementary mechanisms. However, from a purely methodological point of view, this is not relevant. Even if one were a die-hard adaptationist, one would have to recognize that a description of a phenomenon and an (or the) explanation of it belong to different domains and, therefore, should not be mixed. We define wings structurally or functionally as appendages used by some organisms for aerial locomotion. We do not define them in terms of their selective advantages, even if we can explain their presence in those terms.

On the other hand, the assertion that traits—especially those with a strong interactive component, such as social coordination and communication—can be explained only in terms of their selective advantages to the individual that possesses them is constantly being challenged. This is not because natural selection plays no role but rather because the constraints imposed by neutrality and spatiotemporal structures (see sections 4 and 5) become elements of equal or greater importance in the explanation of those traits or behaviors. We may remain unaware even of the possibility of these other elements if we adopt a definition that stresses only one particular mechanism.

2.2   Signals and information

Another preconception about communication that often is found in the biology literature is that it involves operationally the transmission of information from a sender to a receiver. This is an understandably popular view in our age of mass media, fax machines, and computer networks. Information is a concept that has penetrated our understanding of developmental processes (Oyama, 1985) and, in general, of the mechanisms underlying the dynamics of complex systems. For some people, information should even have the same ontological status as matter, time, or space. This view of communication as informational exchange implies that there is "something" being transmitted through some channel, although few researchers specify what that something is. For instance, in Maynard-Smith and Harper (1995, p. 305), the term *information* is used to help define a taxonomy of signals, though from the outset these authors make it clear that they "mean information in the colloquial, rather than technical, sense."

An immediate criticism to this use of the term is simply that there is not such a *thing* as information. Information is not a quantity independent of the observer except in the formal sense of the term (and here only in virtue of a preagreement between sender and receiver). Theories such as Shannon's (Shannon & Weaver, 1949) are not really about our everyday idea of information; they are about the "reliable transmission of signals over unreliable channels" (von Foerster, 1980). These theories can account only for content-free, uncertainty-reducing mechanisms, as the authors themselves make clear. Information, as they present it, is a probabilistic

concept that has little to do with the kind of information that often is invoked when describing communicative behavior (Oyama, 1985). Though there have been interesting attempts to define our more colloquial understanding of information— such as the "difference that makes the difference" *to someone* (Bateson, 1972) or the *appearance* of dependency in otherwise independent systems in a given time frame (Holt, 1972; Pask, 1980)—these definitions have not made it into the mainstream treatment of the subject.

As these last definitions suggest, all an observer can say when witnessing an act of communication depends not only on the activity of the participants but on the observer himself or herself (particularly, on the observer's ability to draw inferences from his or her observations). There is no actual, observer-independent ground for identifying any informational content in the behavior identified as a signal. Information does not exist before the activity, and it cannot be separated from it. If anything, what we call *information* "in the colloquial sense" not only depends on but is, in fact, a *posterior* interpretation of the activity that generates it and, therefore, it cannot play any operational role in that activity. This is not to say that such functional interpretations are without scientific value. On the contrary, when systems become more and more complex, functional interpretations remain one of our main tools of research. It is when the functional and operational accounts become confused that methodological problems arise.

Understanding communication operationally as an exchange of information also implies that signals must denote something. They must refer to some feature of the world or stand for some state of affairs. Otherwise, they are meaningless and out of the scope of the explanatory mechanism of natural selection.[1] However, this certainly is not true. Reference and denotation are not necessary for communication to make a difference for those organisms that use it. Again, wings are not *about* anything, yet they are fundamental for animals that depend on them—*meaningful*, if we wish. Even if we can interpret a given communicative behavior as being *about* something, this "aboutness" is not necessarily a primitive feature of communication. In fact, this "aboutness" is more a feature of the interpretation rather than a feature of the behavior itself and, therefore, it "belongs" to the observer.

By inappropriately deriving operational features from functional conclusions, many researchers have assumed that a necessary condition for communication is that not all relevant aspects of the environment are known equally to all the participants. [It is interesting to see how this idea has influenced the computational approach to the problem; see, for instance, MacLennan and Burghardt (1994) and Werner and

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1 As the reader may have guessed, the preconceptions criticized here are not really independent; when *selection* is invoked at the definition level, *informational exchange* becomes almost necessary.

Dyer (1991).] If all the relevant *information* is readily available to everyone, why *should* communication arise? Thus, communication can be understood only if there is some relevant feature of the environment whose conspicuousness needs to be enhanced by a signal (such as a predator, or food) or if some internal state needs to be publicized. [This will be shown (in section 6) *not* to be the case.] Unfortunately, this assumption excludes as noncommunicative many interesting phenomena that involve the coordination of behaviors between organisms, even when they share all that there is to be aware of, behaviors that otherwise share a fundamental character with more "traditional" examples of communication, as we will see later. Examples of these are many behaviors in which a group of interacting organisms, as a consequence of mutual coregulation, collectively achieve results impossible to obtain at the individual level. Such is the case in the formation in wolf packs of hunting patterns for killing large prey. In these cases, all the relevant information is readily available to all the participants. Other examples can be found in most species of social mammals in which hierarchical social structures exist. In these societies, communication helps in the generation and maintenance of the social structure. A rebel member who is punished by the leader of the group is not being given a piece of information about who is boss (just in case this has been forgotten); the rebel member is being strongly oriented toward reintegrating into the social structure. Signals are used as actions rather than packages of information.

Communication as Social Coordinated Activity

Is it possible to *define* communication without appealing to concepts such as selective advantages or information? More importantly, can we work with such a definition? The view, presented in this section, of communication as a biological phenomenon is not new; similar aspects of it have been developed by different researchers in different, though related, fields. I will use here the language of autopoietic theory (Maturana & Varela, 1980), although similar ideas have been expressed, sometimes in different terms, in the field of cybernetics (von Foerster, 1980; Pask, 1976, 1980) and in certain branches of psychology and family therapy (Bateson, 1972; Watzlawick, Beavin, & Jackson, 1968) and sociocognitive development (Fogel, 1993). From a philosophical perspective, many otherwise different traditions, both pragmatical and phenomenological, converge into similar views (Austin, 1962; Dewey, 1958; Habermas, 1979; Heidegger, 1962; Wittgenstein, 1963). It is, however, far beyond the scope of this section to give a thorough introduction to autopoietic theory, and so the reader is referred to Maturana and Varela (1980, 1988) for a more complete account of this important field. Because certain concepts are necessary for the definition of communication that I wish to present, they will be briefly explained. This

is not an easy task, because concepts in this theory are linked by a very compelling logic and it is difficult to present isolated ideas without doing some injustice to the theory as a whole. I hope that readers knowledgeable in this area will understand this point, while others will refer to the aforementioned sources if they are looking for a deeper account.

3.1   Ontogeny and phylogeny in autopoietic systems

Autopoiesis is a theory of the organization of living organisms as composite, autonomous unities. An autopoietic system is a dynamic system whose organization is maintained as a consequence of its own operation. Autopoietic systems in a given space produce their own components and boundaries and, as a result of the network of processes (of production, transformation, and destruction) realized by the relations between these components, the organization that maintains them (both the components and their relations) is dynamically preserved. All living organisms are autopoietic systems that inhabit physical space. Autopoiesis is a property of the organization of the system; a given autopoietic organization is embodied in a particular *structure* or physical realization, and each state of such a system is determined *only* by that structure and a previous state. This is a fundamentally important point. It implies that any internal state of the system that we, as observers, can relate to a particular behavior of an organism is a direct result of the organism's own structure and of its history, and that successive states will be among those that allow the organization to be conserved, as long as the system remains autopoietic. Thus, autopoietic systems are a subset of the larger set of operationally closed systems,[2] which coincides, by hypothesis, with the set of autonomous systems (Varela, 1979).

Any autopoietic system exists in a medium with which it interacts and, as a result of that interaction, its trajectory in state-space (its history) changes, although its operation as a dynamic system remains closed. As a structure-determined system, its structure determines its *domain of perturbations*—that is, the possible trajectories that can be triggered by interactions with the medium, given a certain initial state, without destroying the system. If the system undergoes changes of state that result in plastic changes of structure and, therefore, in changes in its domain of future perturbations, and all this happens without disintegration or loss of its autopoiesis, then the system is said to undergo a process of *structural coupling* with the medium.

If the medium is also a structurally plastic system, then both systems may become structurally interlocked, mutually selecting their plastic changes and thus defining a history of plastic interactions that, for the organism, is its *ontogeny*. As long as autopoiesis is maintained during this history, the organism is said to be *adapted* to the

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2   *Closed* is used here in the mathematical sense (see Ashby, 1956; Varela, 1979).

medium. In slightly different terms, Ashby (1960, p. 58) arrives at a similar definition of adaptation in terms of stability and homeostasis: "...a form of behaviour is adaptive if it maintains the essential variables... within physiological limits."[3]

Structural coupling can account not only for changes in the individual during its lifetime but also for phylogenic changes during evolution. *Phylogeny* is the result of the history of structural coupling of a series of autopoietic unities connected sequentially by reproduction, during which adaptation is conserved. Selection acts negatively when, as a result of interactions with the medium, autopoiesis is lost, but it also acts through the process of structural coupling between medium and the organisms.

3.2 Communication in structure-determined, closed systems

An organism undergoing a process of structural coupling with the medium may act recursively over its own states if the plastic deformations of the medium have been triggered by the organism's previous actions and, at the same time, these deformations will provoke future perturbations in the organism. In the particular case in which the medium includes another autopoietic system, their individual ontogenies may become coupled. This condition is manifested when we observe that the activity of two or more organisms becomes coordinated while they are interacting. A domain of interlocked triggering of changes of state between the organisms participating in this network of co-ontogenies is established as long as the coupling subsists. This is called a *consensual domain*.

Behaviors in a consensual domain are mutually orienting behaviors. By means of their interaction, the activity of the agents (including actions not directly involved in the interaction itself) becomes coordinated. We define communication as *the behavioral coordination that we can observe as a result of the interactions that occur in a consensual domain* (Maturana & Varela, 1988). It is important to notice that all the activity in a consensual domain is, by nature, recursive in the sense that changes of state in an individual are built on previous changes of state in the same individual and other coparticipants. However, this is not to be confused with the idea of recursion on already existing coordinations. In this special case, the activity being coordinated is *itself* a coordination of actions, which must be understood as a different sort of recursion. This coordination of coordination of behaviors is identified as a defining characteristic of the phenomenon of "languaging" (Maturana, 1978), which will not be addressed in this work.

Through the history of structural coupling with the medium, a correspondence

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3 Related views can be found within the context of Aubin's viability theory (Aubin, 1991) and, in macroevolution, in the concept of "holey landscapes" (Gavrilets & Gravner, 1996), where fitness values are either 1 (viable) or 0 (nonviable).

can be identified by an observer between features or situations in the medium and the behaviors that are coordinated and oriented in their presence as a result of communication. In these cases, the observer may speak of certain actions as signals that denote or describe a certain state of affairs. However, it is a mistake to consider communication to be merely a set of descriptive interactions used by the organisms to pass on information in order to handle a particular situation. This concept ignores the fact that all interactions arise as a consequence of structural coupling between unities and that the relevant behaviors arise in each unity as a consequence of its own structure and are not prescribed by the perturbations that the unity suffers. Therefore, denotations and descriptions cannot be primitive operations in the consensual domain. They require the existence of previous agreement, which can be achieved only by preexisting communicative capabilities.

3.3   Consequences of the approach

The most obvious consequence of adopting this point of view about communication is a broadening of the scope of phenomena that can be considered communicative. As the idea of a composite autopoietic unity that interacts with its environment through a process of structural coupling does not favor an account of its behavior in terms of inputs and outputs, at first sight this account of communication will tend to be more complex than accounts that reduce the phenomenon to an informational exchange. What is gained, then, by adopting the former instead of the latter point of view?

Even though more behaviors are included by it, the definition presented in this work is not a loose one. On the contrary, it is more precise than most definitions of communication because it is based on operational, rather than functional, considerations. For our purposes, this is much preferred because such considerations may be used to constrain future operational descriptions or functional interpretations. (It is not, as is commonly thought, necessary for a nonfunctional account to be able to work out the last possible operational detail in order to be of any use.)

The focus on behavior, history, and structure (of both the organism and the medium) places communicative behaviors in their adequate context, permitting the formulation of questions about the relationships of these theoretical entities to one another and about how they affect the phenomenon itself. More traditional approaches tend to consider only simpler relationships (What is the cost of this behavior? How much is gained by it?), but the reality is that, though they may still have to be considered, these mechanisms' operation is embedded in a set of constraints that is simply ignored most of the time. In the autopoietic view, ignoring these relationships is much more difficult, as they play a fundamental role in the definition of the phenomenon, so that one is compelled to address them.

Yet another advantage of the autopoietic point of view is that it explicitly addresses the relevance of the observer, by pointing at things that arise only in the domain of interpretations, in contrast to features that are inherent to an operational description of the process. Hence, we are made aware of the need to be careful about the use of certain terms we take for granted.

As regards human communication and human language, many different perspectives coincide in an instrumental and pragmatic view similar to the one that can be derived from extension of the notion of communication as coordinated activity into the domain of human interaction. These perspectives differ from the predominant position that considers language as an object or a system of representations. For example, Dewey (1958, p. 168) expresses very strongly that language is a form of concerted action wherein the activity of each partner "is modified and regulated by partnership." Vygotsky (1978, p. 54) speaks of "semiotic tools of mediation," which also reminds us of Wittgenstein's "tool box" (Wittgenstein, 1963, p. 6e) and the early view of language by Heidegger (1962, p. H161) as available equipment instead of a collection of "word-things" which remain present-at-hand.

All these viewpoints coincide in interpreting language as a case of coordinated activity, generated in everyday use, of mutually tuned interactions, prior to anything else we may consider it to be. This is promising for our approach to communication, for it is the continuity that communication as recursive coordinated activity has into the realm of human language that makes this approach such an attractive position from which to study its evolution. Traditional views tend to place nonhuman communication and human language into two very different domains, creating by this action an insurpassable divide that, until very recently, has made the evolution of language a taboo subject and seemingly immune to a naturalizing process. By contrast, both human and nonhuman communication can be understood as recursive coordinated activity, although differences between the two remain evident and further operational considerations will be needed to account for them, as was mentioned earlier.

We can claim, therefore, that the position presented in this section establishes a good basic background for the understanding of communication in its widest scope.

Nonrecursive coordination: mathematical model

As a first step in studying the evolution of communication as just defined, we will address the case of nonrecursive coordination of actions between interacting agents. Let us consider the following game to be played by agents living in a shared environment. We will think of an *agent* as a unity that is able to act in the environment. As a consequence of its actions, an agent can receive certain payoff in a given currency

that we may call *energy*, which is used for self-maintenance. When a certain level of energy is reached, the agent is able to reproduce, and when this level falls below a certain minimum, the agent dies. Energy can be accessed by the agents if they perform a correct action on an energy container or *food source*, of which there can be various types, each of them requiring different actions to extract part or all of its energy. The total environmental energy contained in these sources is renewed at a fixed rate.

There are two "components" to each agent's actions: the *effective component*, on which the allocation of payoff is decided, and the *external manifestation* of the action, which is not directly relevant to the allocation of payoffs. This means that for an agent to receive a certain payoff, the effective component of its action must match the action required by the particular food source with which it is dealing. Behaviors that are required to obtain a certain amount of food in natural organisms (e.g., shaking the branch of a tree or digging the ground) can be thought of as the effective component, and the appearance to another organism of the movements implied in those behaviors can be considered an example of one possible external manifestation of that behavior. Others may be sounds, gestures, and the like. Whereas in real cases it may be difficult to decouple these two components in a single action, for simplicity's sake we will suppose that, in this model, any effective component can be found with any external manifestation.[4]

At each time step, agents are selected randomly to play the following game:

1. The selected agent, who will play the *first role* (A_1), selects at random another, different agent in its vicinity, who will play the *second role* (A_2).
2. A food source is selected randomly from A_1's vicinity.
3. A_1 perceives the type of the food source.
4. A_1 acts.
5. A_2 perceives the external manifestation of A_1's action but *not* the type of food.
6. A_2 acts.
7. The payoff is distributed. If both agents performed the correct action, the total amount of energy is equally distributed in halves. If only one of them performed the correct action, that agent receives a proportion c of the total energy $(0.5 \leq c \leq 1)$, the other receives no payoff, and the rest of the energy remains in the food source.

The game is played indefinitely or until the population becomes extinct. All agents

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4 This leaves, on one side, the possibility of studying how signals evolve out of existing body structures and dispositions, which will be the subject of future work.

have the same chance of being picked as A_1. The possibility exists that effective components and external manifestations of actions may become correlated in such a way that agents playing the second role may "use" the latter as a prompt to act correctly over the food source, even though they cannot perceive its type. However, this may be opposed to the immediate interest of the first player, who may receive a lesser payoff. For convenience, in the following paragraphs, I will speak of *signals* and *signaling* whenever I refer to the external manifestation of actions as orienting the behavior of an agent, without attempting to make this a strict definition.

An interesting feature of this game is the temporality that is introduced in the assignment of roles. This feature marks a difference between this game and others, such as the Prisoner's Dilemma (Axelrod, 1984), in which the role of players is not differentiated. Also, as we can see, this game includes the feature of hidden information, as the agent playing the second role is not able to see the food type with which it is dealing. I have criticized the assumption that this feature is required for communication to evolve, and in section 6 I will present a modified version of this game in which this feature is actually proved to be unnecessary.

The evolution of a population of players of this game can be analyzed with a simple mathematical model, provided that all interactions are assumed to occur globally. It will also be assumed that the effective component of the agent's action is always correct if the agent is able to perceive the food type. The dynamical model presented here has been built on purely game-theoretical considerations and simple energy-budgeting rules for time evolution. It has been proved (Zeeman, 1980) that if there is an evolutionarily stable strategy (ESS), this will be manifested as a fixed-point stable attractor in the system's state-space, and global convergence is assured if there are no other attractors. However, there may be attractors that are not ESSs.

Let P_i be the size of a population of identical players of the game sharing an environment with other such populations $(i = 1, \ldots, n)$. Let $N = \sum_i P_i$ be the total number of agents at a given time, and let E be the instantaneous amount of energy present in the environment that is being renewed with a constant rate R and is randomly distributed over F_Q food sources of different types. The amount of energy that will be consumed by the individuals in population i will depend on the frequencies of encounter per game with agents of the same and other populations. Because interactions do not depend on spatial relationships, we can suppose that any agent of any population can, with equal probability, play the first or second role in the game. Then the frequencies of encounter p_{ij} can be calculated:

$$p_{ij} = \begin{cases} \frac{P_i P_j}{N(N-1)} & \text{if } i \neq j \\[2mm] \frac{P_i(P_i-1)}{N(N-1)} & \text{otherwise} \end{cases}$$

Let $L_i = L_i(p_{ij}, F_Q)$ be the proportion of the available environmental energy E that is gained by the whole population i per unit of time. The general linear case is:

$$L_i = \frac{N_c}{F_Q} \left(\sum_j c_{ij}^i p_{ij} + \sum_j c_{ji}^i p_{ji} \right)$$

where c_{ij}^k is the payoff obtained by an agent of type k in a game $i \rightarrow j$. N_c is the number of contests per unit of time which, without loss of generality, we choose to be instantaneously equal to N so that there are as many contests as the total number of agents present at any given time.

If D is the energy spent per unit of time by an individual agent, and B is the number of individuals that are born per unit of net energy gained by the population, the quantity $B(EL_i - DP_i)$, if positive, expresses how many individuals are born into the population i per unit of time. If we suppose that individuals do not accumulate energy but that the energy gained by the whole population is used in its entirety to give birth to new individuals, then the same quantity, when negative, will express the number of individuals that will die due to loss of energy at the population level. The following distinction is made:

$$Q_i = \begin{cases} B(EL_i - DP_i), & \text{if } EL_i - DP_i \geq 0 \\ 0 & \text{otherwise} \end{cases}$$

$$M_i = \begin{cases} B(EL_i - DP_i), & \text{if } EL_i - DP_i < 0 \\ 0 & \text{otherwise} \end{cases}$$

And the following equations apply for $(i, j = 1, \ldots, n)$:

$$\frac{dE}{dt} = R - E \sum_i L_i$$

$$\frac{dP_i}{dt} = Q_i(1 - \mu_i) + M_i + \sum_{j \neq i} \mu_{ji} Q_j$$

where μ_{ij} is the rate of mutation of newborn individuals of kind i to a different kind j and $\mu_i = \sum_j \mu_{ij}$. B, D, and μ_{ij} are assumed to be constant for all populations and over time. These equations are similar to the so-called replicator or quasi-species equations, modified to account for energy flow.

For simplicity's sake, we will consider the case in which there are only two relevant actions (A and B) that the agents can perform in order to extract energy from a food

Table 1 Signals for actions A and B

Action	Type 1	Type 2	Type 3	Type 4
A	α	δ	δ	α
B	β	γ	γ	β

Table 2 Effective components (A, B) versus perceived signal

Signal	Type 1	Type 2	Type 3	Type 4
α	A	A	—	—
β	B	B	—	—
δ	—	—	A	A
γ	—	—	B	B

source. Agents playing the first role will emit one of two possible signals given the perceived food type. Accordingly, they may emit α or δ when the food source requires action A or they may emit β or γ when the food source requires action B. As a further constraint, α-emitters will also be β-emitters, and δ-emitters will also be γ-emitters. We will not consider mixed strategies. The agents playing the second role will act in accordance with the signal received and their own structure, some of them performing actions A or B when detecting α or β and a nonrelevant action in other cases, and some of them acting correspondingly when detecting δ or γ. Tables 1 and 2 show the behavior of the four possible types of agents in this scenario. In Table 1, we observe the external manifestation or signal corresponding to actions A and B, according to the type of agent. This table determines which signal accompanies the action of the agent playing the first role. The signal is interpreted by the second player according to Table 2, in which the long dash means a nonrelevant action.

Agents of types 1 and 3 may be called *coordinating* types. When confronted with individuals of the same type, these agents will emit signals that will prompt the second player to act correctly, consequently sharing the energy contained in the food source. Agents of types 2 and 4 behave deceptively toward agents of types 1 and 3, respectively. When they play the second role with agents of these types, they take advantage of their signals and act correctly but, when they play the first role, they emit different signals and agents of types 1 and 3 will therefore act incorrectly, so agents of types 2 and 4 will get a share c of energy that will be equal to or greater than 50 percent and the second player will get nothing. We may call these types *anticoordinating* because not only do they not coordinate actions with the same type but they also deceive a certain coordinating type.

However, anticoordinating agents are deceived as well. When confronted with the coordinating type that they do not specifically deceive (type 3 for type 2 and type

Table 3 Payoff matrix (c_{ij}^k)

$i \to j$	c^1	c^2	c^3	c^4
$1 \to 1$	1	—	—	—
$1 \to 2$	$\frac{1}{2}$	$\frac{1}{2}$	—	—
$1 \to 3$	c	—	0	—
$1 \to 4$	c	—	—	0
$2 \to 1$	0	c	—	—
$2 \to 2$	—	c	—	—
$2 \to 3$	—	$\frac{1}{2}$	$\frac{1}{2}$	—
$2 \to 4$	—	$\frac{1}{2}$	—	$\frac{1}{2}$
$3 \to 1$	0	—	c	—
$3 \to 2$	—	0	c	—
$3 \to 3$	—	—	1	—
$3 \to 4$	—	—	$\frac{1}{2}$	$\frac{1}{2}$
$4 \to 1$	$\frac{1}{2}$	—	—	$\frac{1}{2}$
$4 \to 2$	—	$\frac{1}{2}$	—	$\frac{1}{2}$
$4 \to 3$	—	—	0	c
$4 \to 4$	—	—	—	c

1 for type 4), their "deceiving" signals will be interpreted correctly and they will not get the extra payoff when they play the first role. Similarly, they will be prompted to act incorrectly when playing the second role. This creates an interesting circle of influences in the interplay of the four species, each one of them deceiving another and being deceived by a different one. (The situation can be viewed from the point of view of cooperation if we "reverse" the direction of the circle.) This feature is a consequence of using the simplest unbiased choice of possible behaviors.

With this information, we may calculate the c_{ij}^k for this game (Table 3).

To model the mutation matrix correctly, it is necessary to characterize the species with a genetic model. The simplest model is a two-gene haploid model in which the first locus indicates which pair of signals (α, β, or δ, γ) corresponds to the pair of relevant actions (A, B) and the second locus indicates how each pair of signals is interpreted (i.e., by producing the actions A and B correspondingly or by producing a nonrelevant action), with only two possible alleles in each case (p, P, and q, Q, respectively).[5] It is easy to see that, under these circumstances, μ_{ij} will be significantly greater between "neighboring" types than between "nonneighboring" types (type 1 and type 3 are nonneighboring types; both alleles would have to be

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5 Note that pq would correspond to type 1, Pq to type 2, PQ to type 3, and pQ to type 4.

changed to go from one to the other): μ_{ij}s will depend only on whether i and j are neighbors.

It is possible to prove that this system has a stable, fixed-point attractor[6]:

$$P_{1a} = P_{3a} = c \cong 0$$

$$P_{2a} = P_{4a} = N_a/2 - c \cong N_a/2$$

$$E_a = \frac{2RF_Q(N_a - 1)}{N_a(N_a(1 + c) - 2c)} \cong \frac{2RF_Q(N_a - 1)}{N_a^2(1 + c)}$$

where $N_a = R/D$, the carrying capacity of the environment. In this scenario, the whole population is divided between agents of types 2 and 4. This is equivalent to saying that a strategy in which agents behave half the time as anticoordinating agents of type 2 and half the time as anticoordinating agents of type 4 is a stable strategy.

Numerical resolution of the model's equations shows how the system evolves toward this asymptotic equilibrium when the initial conditions are symmetrical: $P_1 = P_3 = N_a/2 - x$, $P_2 = P_4 = x$, $(0 \leq x \leq N_a/2)$, and $E = E_0$. Unless otherwise stated, the values of the parameters used are: $F_Q = 10,000$, $R = 500$, $D = 0.25$, and μ_{ij} is 0 for nonneighboring types and 0.001 for neighboring types. (These figures were chosen to resemble analogous parameters in the computational implementation.) For $B = 0.01$ and $c = 0.6$, the invasion of an initially coordinating population ($x = 0$) is achieved in 2.5×10^7 time steps.

What happens with asymmetrical initial conditions? Figure 1 shows the behavior of P_1 and P_2 for the same parameters and for $E = 2500$, $P_1 = 600$, $P_2 = 200$, $P_3 = 400$, and $P_4 = 600$. The behavior is periodic, oscillating between periods of coordinating and anticoordinating prevalence. P_3 and P_4 show the same behavior as do P_1 and P_2, respectively, only with a half-period shift. The time scale for the same set of parameters also is significantly different; the period for the variation in population number is approximately 6.25×10^4 time steps.

This cyclical dynamic can be seen to follow many other initial conditions, and no other attractor has been observed. In Figure 2, we can see the shape of this periodic attractor in the space $P_1 - P_3 - P_4$. For this sort of cycle to occur, the number of possible strategies must be greater than two. Naturally occurring examples have recently been found in mating strategies in male side-blotched lizards (Sinervo & Lively, 1996).

These results lead to some important conclusions for the methodology of our work. As has already been said, in most (if not all) of the occasions in which the

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6 The equations present a discontinuity at the stable point where $B(EL_a - DP_a) = 0$, so we cannot provide analytical proof of stability. However, thorough numerical investigation in the vicinity of the attractor suggests that the fixed point is stable.
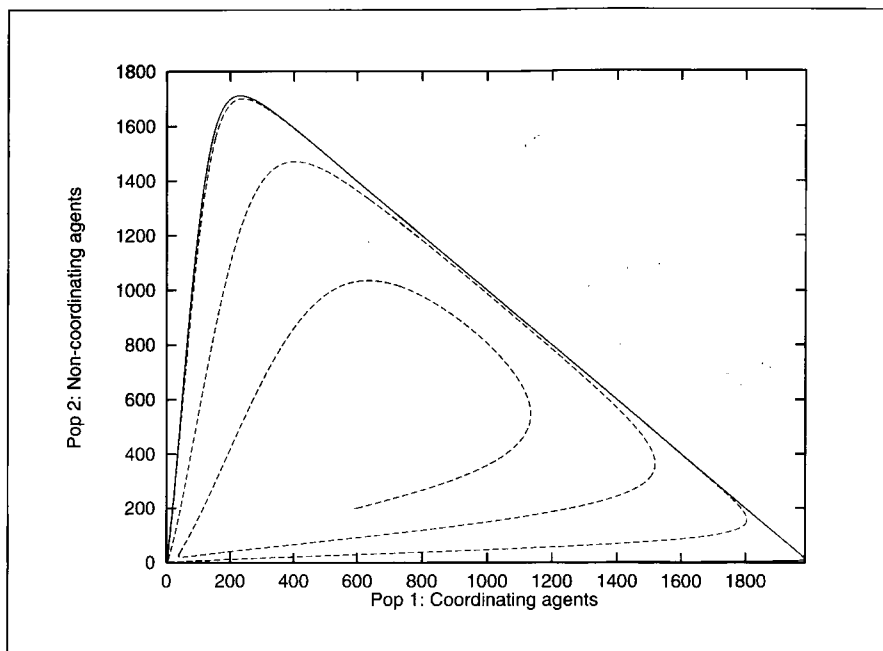
Figure 1

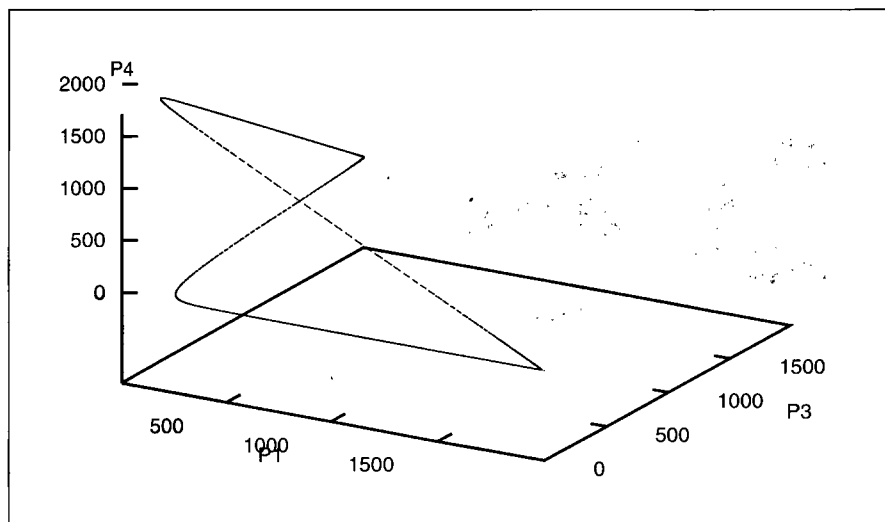Evolution of P_2 versus P_1 for nonsymmetrical initial conditions

Figure 2

Periodic attractor in the space $P_1 - P_3 - P_4$

game-theoretical machinery is applied, the aim is to obtain a first-order, static result such as a fixed-point solution. If sufficient "ingredients" in this process can be considered to be static, then many nonlinearities and dynamical effects are gracefully reduced and the game-theoretical approach is the best way to understand the problem. The question, "Is this the case for the evolution of coordinated action in this game?" was implicitly asked in this section. The answer is simply no. It has been found that whether the system reaches a stable equilibrium depends on initial conditions (i.e., on historical factors). Depending on such factors, the system may evolve into a periodic regimen of oscillations of very significant amplitude. Once within the regimen, the system will remain in it permanently; therefore, the ESS state will never be reached. This situation has been recognized as "an obvious weakness of the game-theoretic approach to evolution" (Maynard-Smith, 1982, p. 8).

More rigorous proofs of these conclusions for a general case can be found in Zeeman's work (1980), in which it is shown that global convergence to an ESS is assured only in the absence of other attractors, which may exist and may not themselves be ESSs.

Summing up for the general case:

- Whether an evolutionary system reaches an equilibrium state may be contingent on the history of the system.
- An ESS may be unreachable for a given population.
- An ESS may not exist (if no fixed-point attractor exists).

In the particular model presented here, both the first and second statements hold.

Important as they are, these conclusions do not seem to tell us much about our main problem. Is it to be expected that a society of interacting agents will fluctuate between periods of coordinated and noncoordinated behaviors? Many of the simplifying assumptions in this model may be difficult to justify in natural cases. I will mention some of the most evident:

- *Spatiality*: Global accessibility does not fairly represent interactions among real organisms. In real life, neighbors tend to remain neighbors, and the habitat of the offspring tends to be the same habitat of the parents. Uniforming factors can be expected to act locally, especially if reproduction is sexual instead of asexual.
- *Symmetry*: This model presents too high a degree of symmetry, partly as a consequence of panmictic interactions and partly owing to the nature of the different agent types. Any ordered, even permutation of indexes leaves the resulting dynamics unchanged for any set of initial conditions.
- *Synchronicity*: All interactions occur concurrently. Even in games without memory or voluntary choice of partners, such as this one,

synchronicity is a strong simplification, especially if spatial effects were to be taken into account. In such a case, a true differentiation between first and second roles may be manifested depending on different spatiotemporal constraints.

5 Nonrecursive Coordination: Computational Model

Instead of extending the mathematical model to relax the assumptions just listed, a direct computational approach is presented as the most practical choice.

5.1 The model

The dynamics of this model are very similar to those described in section 4. Agents live, interact, and die in a shared environment. The physical environment is represented as a toroidal grid of size X_{max} by Y_{max} (typically 100×100). Agents are situated in this environment in a position that does not change with time. A number, F_Q, of energy repositories, or food sources, also are distributed within the environment and remain fixed ($F_Q = X_{max}Y_{max}$, so that there is, on average, one food source per cell in the grid). Food source distribution can be uniform or random; this has proven not to be relevant to the results. These food sources are created at the beginning of the simulation run, and their position and associated food type remain unchanged. A food source cannot be created or destroyed during the rest of the simulation, but its energy content may run out. Food types are identified by numbers: F0, F1, and so on.

Neighborhoods are defined simply as squares of a fixed size (usually 10×10) centered around an agent. They represent the normal habitat of the agent during its lifetime. Agents can interact with other agents and access food sources only within their neighborhoods. Initially, agents are distributed randomly in the environment. Each agent possesses an internal energy counter that specifies the energy available for self-maintenance. Every time an agent is born, its energy level is set at a value chosen following a Gaussian distribution $\sigma(E_i, \Delta_e)$ centered on E_i. (Typical values are $E_i = 150$, $\Delta_e = 10$, negative values cut off.) Energy flow is strictly accounted for. The environment is subject to a constant energy flux R (500 per time step), which is manifested in a stochastic increase of the energy stored in the F_Q food sources. Agents derive their initial energy from their parents and, during their lifetime, from the food sources. This ensures energy conservation. Besides, agents spend a fixed amount of energy D (0.25 per time step) every time they are selected to act (independently of the outcome of the action), which does not return to the environmental resources, so as to ensure that the equivalent of the second law of thermodynamics is observed.

At each time step, a number of agents equal to the size of the current population is

selected randomly to perform the first role in the interactional game. The updating is performed asynchronously and, on average, each agent will always be selected for this role once per time step. A second player and a food source within the neighborhood of the first player are selected randomly. If no agent is found after a finite number of trials (approximately 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, regardless of the role it plays.

The payoffs will be assigned in the same way as described in the previous section: in equal parts when both of them act correctly and, when they do not, a proportion $c \geq 0.5$ (fixed for all agents during each simulation run) of the energy for the agent acting correctly and nothing for the other. When an agent has accumulated enough net energy, it is able to reproduce. The corresponding level of energy is selected according to the distribution $\sigma(2E_i, \Delta_e)$. Reproduction is sexual, and selection of a partner is based only on the locality condition, as is the location of the offspring, which occupies a randomly chosen position within the first parent's neighborhood. As neighborhoods do not overlap completely in the general case, gene flow is not prevented. The initial energy of the offspring is supplied by the parent, whose high energy level triggered the reproduction event in the first place.

Those agents unable to sustain their costs eventually will run out of energy and die. Costs are the same for all agents, with the exception of very "old" ones. After a certain age has been reached, costs are mildly incremented linearly with age. This is the only "developmental" feature included in this model, and it is done in order to avoid the presence of "immortals." This mechanism replaces the lack of a good model of developmental rules, with which it could be expected that typical life span would result from an interplay among population dynamics, availability of resources, and evolution of those rules.

The structure of agents is that of a stateless machine. The focus of this work will be on the global mechanisms that allow or constrain the evolution of coordinated activity as a first step toward an understanding of the evolution of coordinated activity. No claim will be made about the very important effects of ontogenic structural change during the coordination of actions with the medium. Agents will be seen as simple unities most of the time. This is a strong simplification for a model that is partly based on concepts derived from autopoietic theory; however, I maintain that the framework provided by this theory still is applicable for the design and understanding of the present study.

Actions depend on the perceived food type and on the perceived external manifestation of the partner in the game, when these are perceivable (an example of a behavioral matrix is shown in Table 4). Agents playing the second role will act according only to the perceived external manifestation of the actions of the first

Table 4 Example of behavioral matrix

	Perceived signal			
Food type	α	β	$\cdots$	ν
F0	B α	A α	$\cdots$	C δ
F1	C γ	D β	$\cdots$	A β
$\vdots$	$\vdots$	$\vdots$	$\ddots$	$\vdots$
Fn	B α	A α	$\cdots$	C δ

player and on the base hypothesis that the food is type F0 (this means their actions will be encoded in the first row of the matrix). Correspondingly, the actions of the first player will depend only on the perceived food type and on the base hypothesis that they perceive an external manifestation α (their actions will be encoded in the first column of the matrix). Although only one column and one row of the behavioral matrix are used, the matrix representation is retained for games involving more interactive steps (see section 6).

The behavioral matrix is encoded in a haploid genome, represented by a binary bitstring. Offspring receive their genome as the result of a uniform crossover operation on their parents' genotypes, plus certain probability of mutation μ per place.

This is a satisfying scheme in which selection acts negatively. There is no fitness function to optimize; likewise, there are no special rewards or punishments for behaving in a specific way apart from the rules of the game. A problem derived from the use of this scheme is the lack of obvious measures of evolution. Many variables were monitored—the size of the population, the amount of instantaneous environmental energy, the average number of offspring, and the like—but, for our purposes, the simplest way to monitor the evolution of action coordination is to look at changes in the average activity success of the first and second players and at the average success in coordinated activity and at correlations among all these.

5.2   Evolution of coordination

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, each food type had a different associated action and, in the other, a given action was correct for two food types and, therefore, only two actions were relevant (even when agents were able to perform more: For instance, action A corresponds to food types F0 and F1 and action B to F2 and F3, whereas actions C and D are not relevant). Because of space limitations, results will be reported only on this last set. Simulations with more food types and actions were also carried out, and the results were similar, though much more expensive to obtain and analyze.

In contrast to the mathematical model of section 4, agents are initialized totally at random. This means that they will also have to evolve an association between food types and the effective components of actions when they play the first role. (In section 4, we supposed that the first agent always acted correctly.) This task is consistently and very rapidly achieved in all the simulations, and its explanation in selective terms does not present too much of a problem, given that this action depends directly on the perceived food type only.

In all simulations the average size of the population stabilized at a value between 600 and 800 agents, after a short transient period. The instantaneous population size was characterized by regular "drops" of up to a 100 agents and, less regularly, by more catastrophic ones. Size and frequency correlations were studied, but evidence that these drops obeyed a power-law was found to be inconclusive.

A baseline case was run in order to understand what kind of activity emerged when agents were not able to perceive one another reliably. In these runs, the external manifestation of the first player's action was replaced with a random signal when perceived by the second player. The proportion of cases in which both players simultaneously acted correctly we may call the *coordination ratio*. This ratio stabilized at 50 percent for random signals. Because no food type is predominant, the best guess a second agent can make, given that there is no correlation between the "signal" it perceives and the particular type of food with which it is dealing, is to perform any of the two relevant (out of the four possible) actions. The achievement of these levels 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 3 shows the evolution of the success ratios for the whole population in a typical run. (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. $R1$ indicates the average proportion of successful actions for first players, which, as predicted, climbs steadily up to a level near 100 percent. (Perfect success is not necessarily achieved due to the effects of random mutations.) $R2$ shows the same quantity for second players, and $R12$ for both roles simultaneously (the coordination ratio). We see that both $R1$ and $R2$ start at a level of 25 percent, which corresponds to a random guessing behavior. Note that the correlation between $R2$ and $R12$ increases with time, and eventually they show the same behavior. Both ratios reach a higher-than-baseline level; coordinated activity evolves to a relatively steady state. This is very different from the two possibilities observed in the mathematical model (either oscillations or no coordination at all).

By observing the resulting behaviors once a relatively stable state has been achieved, it is possible to determine that signaling behaviors present a strong correlation with
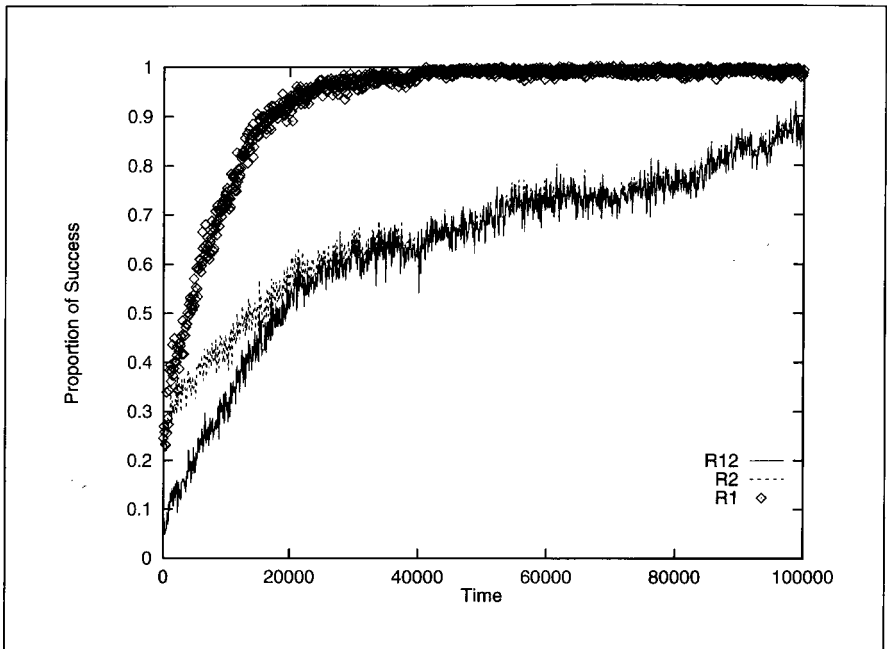
Figure 3
Proportional success in action for the first player (top line, *R1*), second agent (*R2*), and both simultaneously (*R12*)

actions and not with food types. Therefore, agents evolve a two-signal code for the two relevant actions that can be performed.

A study of the effect of parameter c on *R12* was performed in order to see how the extra payoff against coordination affected the level of simultaneous success. The intuitive expectation is that this level will decrease as c increases from 0.5 to 1.0. Figure 4 shows this effect on *R12* for different values of c.

We see that the proportion of coordinated activity for the whole population decreases as c is incremented from 0.5 to 0.7 and, for greater values, the baseline case is reproduced. This means that the level of coordination goes from almost perfect for $c = 0.5$ (neutral cost) to coordination by guessing when $c \cong 0.7$. The fact that for a certain range of costs *against* it, coordinated activity evolves anyway is in contradiction with the intuitions that can be gained from the mathematical model or from simplified selective arguments. Explanations for this phenomenon should be sought first in those assumptions that were made in the mathematical model but were unnecessary in the computational model.
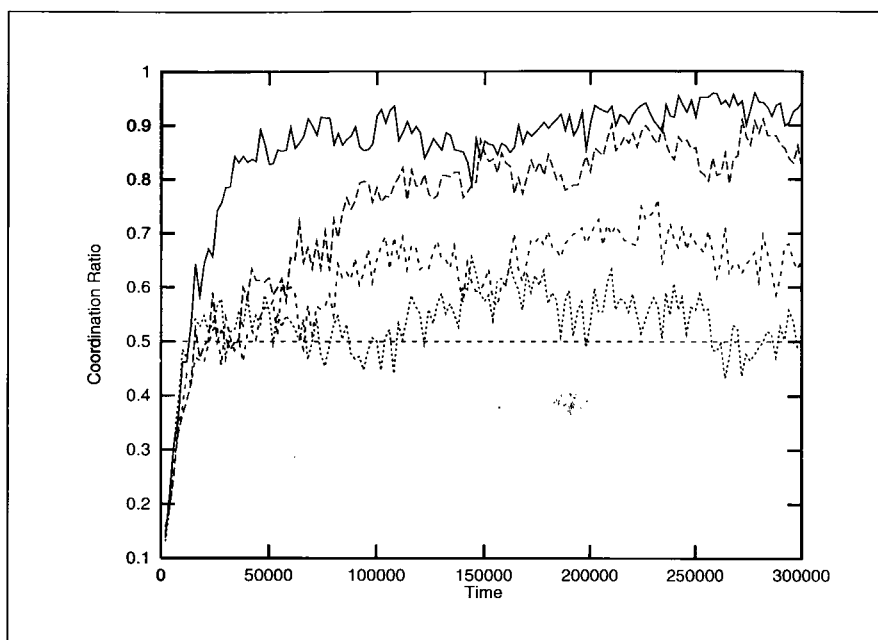
Figure 4
Whole-population coordination ratio ($R12$) for different values of c. The top (full) line between 90%
and 100% corresponds to $c = 0.5$—that is, no cost against communication; the line between 80% and
90% corresponds to $c = 0.55$; the one between 60% and 70% to $c = 0.6$; and the one between 50% and
60% to $c = 0.65$. Values of c equal to or greater than 0.7 result in a level of 50%, which is the baseline
case for this game.

5.3   Spatiotemporal structures

A simple inspection of the resulting data in all simulations shows that the individual
history of coordination success can differ significantly from agent to agent and from
the value of $R12$ at that time. For instance, groups of agents achieving 90 percent of
coordination success can coexist with other groups that achieve 60 percent, both in
a stable state during the same simulation run. Even though an individual historical
average is qualitatively different from an instantaneous population average, one would
expect the resulting numbers to differ little, especially if $R12$ has been stable for some
time. The results suggest that there may be some structure in the population that
prevents the homogenizing effects of sexual reproduction.

5.3.1   Cluster formation and stability   Figure 5 shows the first stages in the evolu-
tion of agent spatial distribution. Initially, agents are distributed randomly across the
whole of the environment (border effects have been avoided by the use of periodic
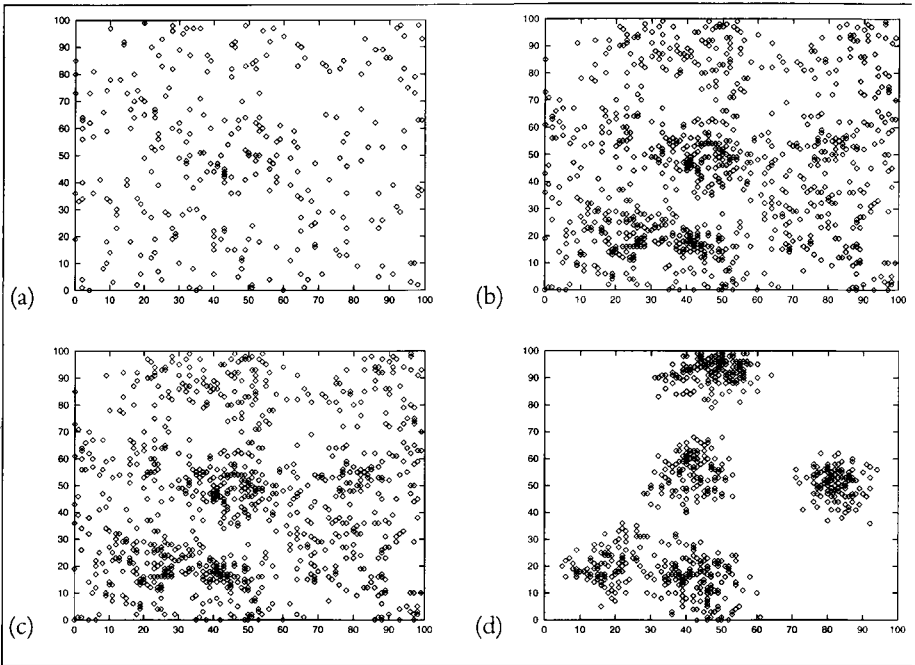
Figure 5 Formation of clusters. Each figure shows the distribution of agents in a 100 × 100 toroidal environment at different times (t) during the simulation: (a) $t = 0$; (b) $t = 2000$; (c) $t = 4000$; (d) $t = 16,000$. Neighborhood size: 10×10

boundary conditions). We can observe how this initial symmetry is broken rapidly and how agents show a tendency to aggregate into clusters. Symmetry breaking is caused by minor differences in the initial distribution in positions and also by the up-dating rules; so that some agents will be more successful than others just because they have a few more agents with which to interact or have been called to act a few more times and, therefore, have a slightly greater 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 interacting and will tend to die sooner, also contributing positively to an increase in the isolation of agents in similar positions.

Unfortunately, cluster formation mechanisms do not provide a satisfactory ex-planation of the reasons for clusters remaining more or less stable structures, as is generally observed. Why do they not expand or shrink or break or fuse? The fact is that these behaviors *have* been observed, but they are the exception rather than the rule, and they can be explained once an understanding of the general case of cluster quasistability is achieved.
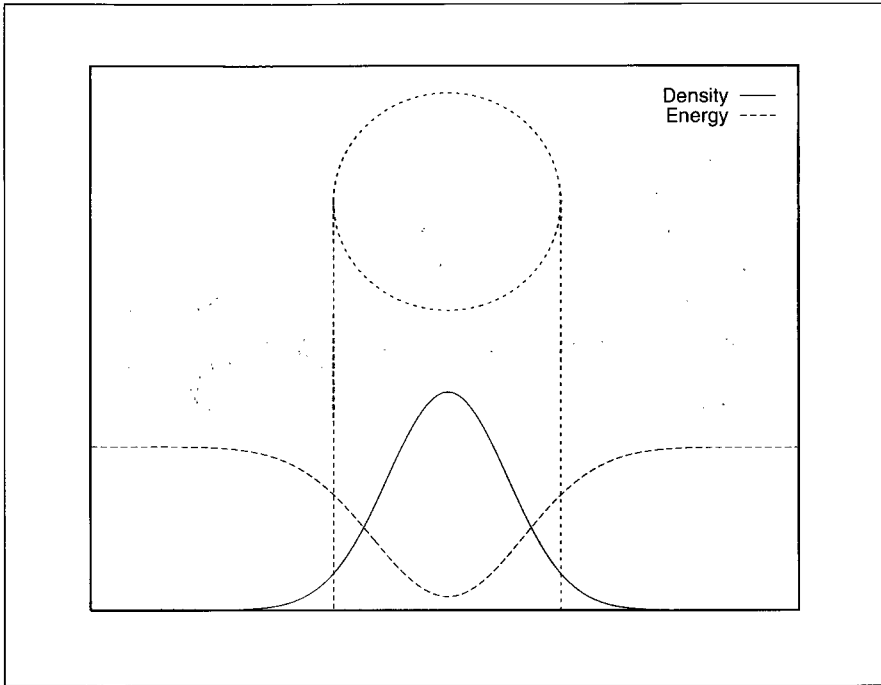
Figure 6
Energy and population distribution inside and around a cluster (circle)

Tendency to Expand Figure 6 shows a qualitative model of a typically observed distribution of environmental energy and density of agents inside and in the vicinity of a cluster. It is easy to see that resources will be more frequently used in more populated areas toward the center of the cluster than on peripheral areas in which the population is sparser, so that the amount of available energy will, on average, decrease toward the center, as is shown in the figure. Agents living in the periphery will have access to resources of greater quality, and the average energy gained per game played will be greater than that of agents in the center region. Hence, at first glance, peripheral agents would seem to be better off and to have a better chance of generating more offspring; therefore, the cluster would experience a tendency toward *expansion*.

Tendency to Collapse In contrast, though all agents have the same probability of being *chosen* to play the first role in the game, the frequency with which an agent *actually* plays the game depends on the surrounding population density. The more densely populated the area, the higher is the chance of finding a partner with which to play. For this reason, agents living near the center of a cluster will play the game

more frequently. Moreover, the probability of an agent playing the *second* role also depends on its position within the cluster. Given that certain regions of an agent's neighborhood will be more densely populated than others, second players will be chosen more frequently from those regions. As a result of the circular geometry of the cluster and of the increasing density of agents toward its center, agents in this particular region will benefit from this effect in a cumulative way and will, on average, play the second role more times than they play the first role. Conversely, agents living near the periphery will be chosen less frequently for playing the second role because their distribution is sparser and, therefore, they will, on average, play the first role more times than the second role. The ratio (frequency as second player/frequency as first player) has been observed to range from a minimum of 0.9 at the periphery to a maximum of 1.25 at the center of the cluster. In short, agents living in the populated areas near the center (1) will play the game more frequently than agents living in sparse areas and (2) will perform the second role more frequently than the first role. Therefore, in principle, they will stand a better chance of receiving (by coordination, or just by guessing) more energy per unit of time. This provides the cluster with a tendency to *collapse*.

Equilibrium The equilibrium of both these tendencies determines the size of the quasistable cluster. At a certain size, the extra energy gained by the peripheral subpopulation will match the energy lost by their being more sparsely distributed than the center subpopulation. Resulting clusters have been observed to have a typical radius of from one to three neighborhood sizes, with populations of between 30 and 200 agents. Other effects, such as effective energy transport from the outer regions of the cluster toward the center, have been identified, and they perform a stabilizing role in the attainment of equilibrium size.

5.3.2 Why action coordination evolves

The quasistability of clusters results from an interplay of two opposing tendencies in the spatiotemporal organization that arise from the fact that conditions differ at the center and at the periphery of the cluster. It must be remarked that this is a direct consequence of the activity of the evolving agents. The next obvious issue that must be examined is whether this difference of conditions has any effect on the evolution of coordinated activity.

Genetic Homogeneity Due to the nature of the cluster formation process and the homogenizing effect of sexual reproduction, clusters tend to be inhabited by agents which are very similar genetically. Spatial homogeneity will still be the case even when new mutations appear and become fixed. After a sufficiently long time (though, in practice, not very long), agents bearing this new mutation will be distributed across the entire cluster. This is due to the fact that cluster and neighborhood sizes are

of the same order of magnitude, as has consistently proven to be the case in all simulations. While agents within a cluster are genetically very similar, agents from different clusters may differ in general.

Conditions at the Periphery of a Cluster Agents are subject to two qualitatively different "microenvironments."[7] We saw how agents living in the periphery have access to resources of better quality (see Fig. 6) and how these agents tend to play the second role less often than they play the first role. They also tend to interact fewer times in absolute terms because of their sparse distribution. This means that, for these agents, to engage in coordinated activity is particularly costly because every time they do so they lose one of their few opportunities to obtain a greater absolute payoff compared to agents living in the center of the cluster. If we were asked what would be an ESS in such an environment, the answer would clearly be "not to coordinate."

Conditions at the Center of a Cluster Agents inhabiting the center of a cluster have access to poorer, much more frequently used, resources; therefore, the individual gain for not coordinating is not too high in absolute terms, though it still is positive. In contrast, these agents tend to play the second role more times than they play the first role, which means that there may be cases (depending on the value of c) in which they will have a positive *individual* gain if they *do* coordinate their actions, simply because they will be acting as second players more frequently, provided that c is not too high. While it may pay a little extra to be a "deceiver," the situation may be that once a deceiver lineage starts growing, it will pay more to break the deceiver agent's own code, rapidly reestablishing the level of coordinated activity.

Selection Ideally, this situation would be resolved by having two distinct subpopulations—one of (almost) total coordinating agents in the center of the cluster and one of total noncoordinating agents in the periphery—but this is not possible owing to the genetic homogeneity within a cluster. Given that the sizes of each subpopulation are comparable and that a newborn agent has comparable probabilities of being placed in either of the two regions, then there is no ground for selection to be very specific about which of the extreme behaviors to choose. Therefore, surviving agents will tend to be able to satisfy partially the conditions of both extreme environmental conditions and, consequently, they will necessarily possess the ability to coordinate their actions up to a certain level, which will depend on the parameter c.

Thus, the evolution of coordinated activity in this model can be explained by the interplay of spatiotemporal constraints and selective mechanisms. Figure 7 depicts

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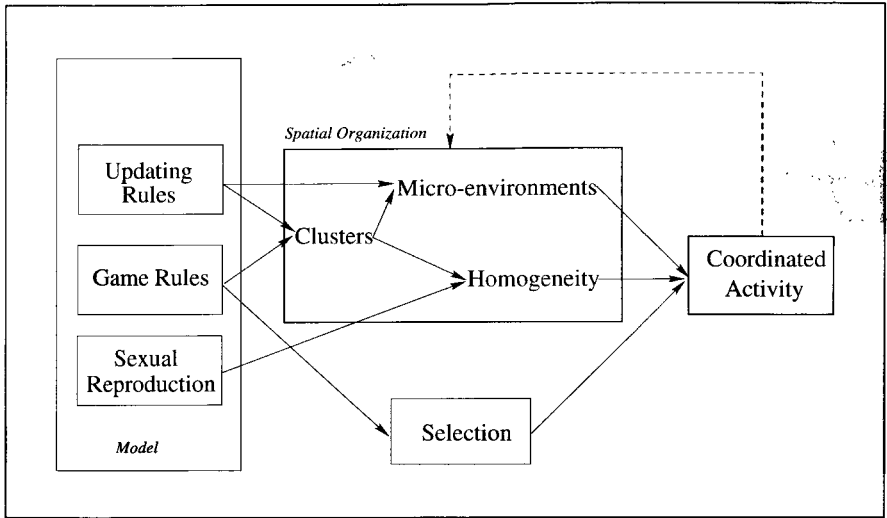7 Or, to be more precise, an environment presenting a continuum of variation.

Figure 7
Entities and mechanisms involved in explaining the evolution of coordination in the computational model. Features explicitly built into the model are shown in the box to the left. Other boxes indicate features that are implicit consequences of these. Arrows indicate explanatory relations.

the relation between the components of this explanation.

An alternative explanation could be attempted in terms of the mechanism of *kin selection* (Hamilton, 1964). For instance, to account for similar results, Ackley and Littman (1994) suggest that this mechanism is at work in their model: Given the relatedness of agents inhabiting the same cluster, and given that coordinated activity results in greater payoffs at the group (if not at the immediate individual) level, then it would make sense for an individual to coordinate actions with related individuals, thus spreading the benefits over a number of other agents carrying the same genes. Such an explanation, however, cannot account for the dependency of the level of coordination with the parameter c. It would be expected that, given that the group will always benefit from cooperative behavior, independently of c, if kin selection were at work, coordination should evolve always to the same level, something that, as shown in Figure 4, does not happen.

It has been observed that the level of coordinated activity may vary considerably from cluster to cluster in the same simulation run. Clusters can grow and, more rarely, shrink; these are interesting phenomena because they are related to the level of coordinated activity within them. The following correlation has been consistently observed: *Clusters with a high level of success in coordination are larger and more populated than are clusters with a lower level of success.* In general, the former can have a radius of

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up to three neighborhood sizes, whereas the latter have a radius of one neighborhood size or even less.

That a particular cluster is small with a low level of coordinated activity while another is big with a high level of coordination must mainly be attributed to contingencies in the clusters' respective histories. We cannot look for general reasons, because all agents evolve under the same general rules. All we can do is to describe, in terms of feedback mechanisms, certain tendencies that appear once a cluster has embarked in a particular historical path. This kind of explanation will focus mainly on the dashed line in Figure 7. The explanation is achieved by examining the effects on the distribution of environmental energy and, consequently, on the distribution of agents if coordinated activity in a cluster increases by a small amount. The same qualitative model that was presented in Figure 6 is used. Details are presented elsewhere (Di Paolo, 1996).

It must be remarked that these explanations are, in fact, simplifications of complex dynamical processes in which more ingredients than those mentioned may play an important part. For instance, I have followed a quasistatic approach, in which inertia has been unaccounted for. The complex effects arising from cluster interactions have also been ignored. The reason for such exclusions is that, interesting as these phenomena may be, they do not much further our understanding of how action coordination evolves due to spatiotemporal constraints and selection in this model.

Coordination of Recursive Actions

One-step action coordination, as presented in the previous model, does not reflect the idea of ongoing mutual orientation of behaviors that is implied by the view of communication as arising from the activity in a consensual domain. As the next logical step in this project, the previous model could be extended to approach a situation in which we may speak of such a consensual domain. Strictly speaking, this will not be possible as long as the structure of the agents remains nonplastic. However, the following modifications to the game can take us near this situation.

Instead of requiring a unique action, access to energy in the food sources requires the performance of a specific sequence of alternating actions by both agents. Energy is released partially depending on a correct action being taken at the required step of the sequence.

In this case, the actions of *both* players depend on the perceived food type and the perceived external manifestation of the coparticipant in the previous step. This means that the second agent also has access to information about the food type. If, for instance, food type F2 requires the sequence of actions A, B, C, D, Table 5 would show an example of two agents successfully coordinating their behaviors in

Table 5 Example of dialogical coordination

Time		Actions (F2)	
	$A_1(F2, \emptyset) \rightarrow (A, \alpha)$	A	
$\downarrow$		B	$(B, \beta) \leftarrow A_2(F2, \alpha)$
	$A_1(F2, \beta) \rightarrow (C, \delta)$	C	
		D	$(D, \gamma) \leftarrow A_2(F2, \delta)$

this game: A_i is the behavioral operator of each agent, the result of which is a pair (effective component, external manifestation); and $\emptyset$ is the initially assumed external manifestation for the first move.

This game has a more dialogical structure, and it resembles the kind of interaction described by von Foerster's eigen-behaviors (von Foerster, 1977, 1980). The problem is somehow more complicated than the simple action-response game, because not only must the external manifestations of one agent and effective components of the other become correlated, but also the external manifestations of both of them must become correlated through the whole sequence. Not only must the second player rely on the signal of the first player to act correctly, but this signal must also select in the second player another signal that, in turn, will select the correct behavior in the first player for the next step in the game. We see that this is a recursive task much more in accordance with the nature of communication as defined in section 3. We also see that a description of this task in terms of traditional notions of information is useless. If by *information* we mean information about features of the environment, these are equally accessible to both participants; if we mean information about the changing state or intention of the agents, they have none. In spite of this, the coordinating task that is required from the agents is not trivial.

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 in alternation with the second player, who must perform B, D, and the two other food types requiring the sequence C, D, A, B, which means that each agent must reverse the order of its own actions. Payoffs are allocated after the first two actions and then again after the last two actions, in the same manner as described in the previous game.

Figure 8 shows the evolution of the average instantaneous success in dialogue over time for two typical runs with different values of c. (Variations between runs with the same set of parameters were not qualitatively significant.) This quantity is similar to $R12$ in the previous section, the difference being that it is defined as the proportion of cases in which the *whole* sequence of actions is performed correctly in a given interaction.
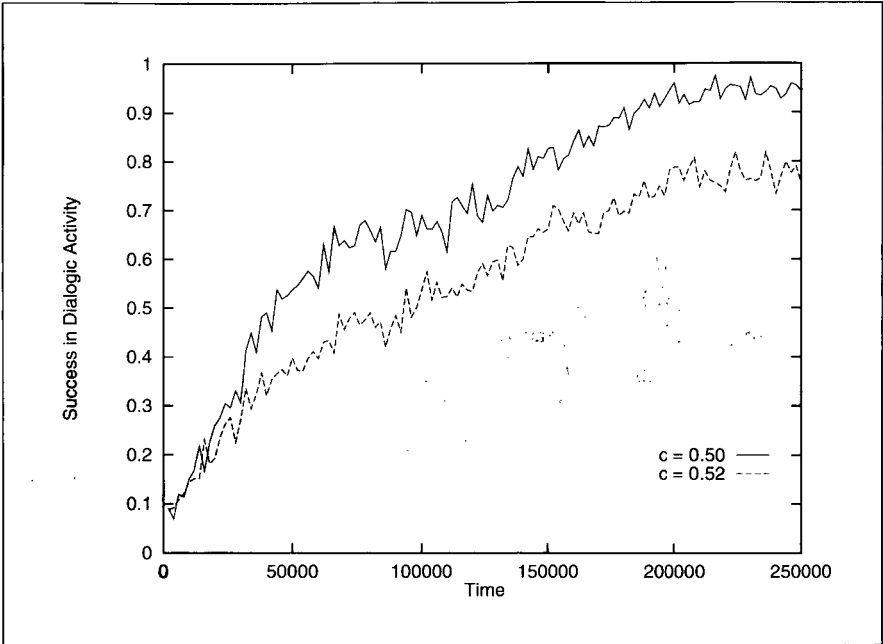
Figure 8
Evolution of dialogical coordinated activity for two values of c in two typical runs

Table 6 Evolved player in dialogical communication game

	Perceived signal			
Food type	α	β	δ	γ
F0	A γ	C α	B γ	C δ
F1	A δ	D γ	C γ	B β
F2	B β	D δ	A γ	C γ
F3	B δ	A γ	D α	C α

Analogous considerations mentioned for the previous game apply here as well. The level of dialogical success depends on the parameter c in a similar fashion as the level of coordinated activity did for the previous case; agents also form clusters, and these clusters can differ in their own levels of dialogical success.

We may observe the resulting behaviors by analyzing the evolved behavioral structures. For example, an evolved behavioral matrix within a highly successful cluster (greater than 90% of dialogical activity) is shown in Table 6.

Here, agents must produce the sequence A, B, C, D in the presence of food types F0 and F1 and the sequence B, A, D, C in the presence of food types F2 and F3.

The column corresponding to the signal α encodes the first action of the first agent ($\alpha = \emptyset$ in this case). As a contrast with the previous game, in this case the entire matrix is used and not just one column and one row. Assuming that this particular agent belongs to a rather homogeneous cluster, as it does, we can explore the result of the interaction with a structurally identical agent. It is easy to see that in such an interaction, the agent will achieve an average level of dialogical coordination of 93.75 percent (just by counting for each food type the success levels that this agent would achieve in a dialogue with itself). The actual level achieved by this agent was 96.2 percent, probably because other agents in its neighborhood are slightly different or because there is a relatively smaller number of food sources of type F0 surrounding it. (Success when the food is of type F0 is only 75%. Note in Table 6 that the effective component D is missing in the corresponding row, which prevents the production of the entire required sequence.)

These results show that agents coordinating their activity are able to perform tasks beyond their individual abilities. This particular game requires that both agents perform a sequence of different actions in the presence of an external environmental feature that remains unchanged over time. Given that agents are stateless machines, such a behavior is impossible for them to implement individually. However, pairs of interacting agents can achieve an important level of success in this task, each one taking advantage of the presence of the other, "using" their interactions as the internal states they lack. This feature provides an interesting metaphor for hypotheses that relate the evolution of cognition with the evolution of communicative behaviors and sociality.

7 Conclusions

The first part of this article was aimed at a methodological and conceptual criticism of the current approach to the question of the origins and evolution of communication. An analysis of the way the phenomenon is characterized in theoretical biology provided the necessary guidelines for identifying two important preconceptions prevalent in those studies—namely, the use of selective advantages, elsewhere used only in explanatory discourse, at the definition level, and the loose use of the idea of communication as an informational exchange. A different understanding of communication was considered as a way of characterizing the phenomenon which avoids some of the consequences identified with the inclusion of the previous preconceptions.

It could be said that, to this point, all I have done is to criticize theoretically a set of ideas, replacing it with another set that, surely, will meet with similar charges of preconceptions. However, I also showed that it is possible to work with such

ideas by addressing the problem of origins and evolution of coordinated activity, demonstrating the existence of phenomena that cannot be understood in purely selective terms (section 5) or as informational exchanges (section 6).

My critical stance did not compel me to ignore blindly the technical aspects of previous work in the area. Instead, my first step was to choose a game similar to those proposed in the theoretical biology literature on the evolution of communication, in which a common language, in terms of costs, payoffs, and so on, provided a continuity with these and the present works. Also, I did not ignore the tools, such as game-theory, used in these traditional approaches to understand conditions that allow equilibrium situations but rather showed that the benefit of their use was limited, even when modifications were introduced to account for dynamical effects as well.

The computational model has demonstrated that coordinated activity can evolve even in those cases in which the static and dynamical mathematical models showed it would not. The reason for this finding has been mainly the possibility provided by the computational model of studying selective mechanisms in the context of other phenomena such as spatiotemporal structures.

Of course, this increase in flexibility does not come without its own methodological problems. The question of the biases introduced by computational modeling in general is still an open issue in adaptive behavior research. We have explicitly tried to avoid common methodological pitfalls, such as the use of synchronous updating or (for our specific purpose) the use of explicit fitness functions. However, the possibilities may never be exhausted if we intend to make a detailed comparison between models and observed natural phenomena (for instance, not all the parameters that can be varied can be practically explored). For this reason, my approach has been one of comparing what can be achieved with some tools and what can be achieved with more complex tools, so that differences can be explicitly identified. The choice is a pragmatic one.

An explanation of the formation and quasistability of clusters was advanced in terms of a qualitative model of the observed distribution of population and environmental energy in the region occupied by a cluster. In exploring certain issues arising from this model, many of the observed phenomena (e.g., genetic homogeneity, differences of environmental conditions, and the evolution of action coordination even in the presence of individual costs against it) were able to be explained.

The role of spatiality in the evolution of cooperation has been identified previously (Axelrod, 1984; Ackley & Littman, 1994; Oliphant, 1994). Although the details of the respective models present important differences, the conclusions are very similar to those reached in this work. However, explanations for these similarities have relied, somewhat loosely, on the mechanism of kin selection (Ackley &

Littman, 1994). Though this mechanism may play an important role in other cases, it was proven that this is not so in the current case.

Similar conclusions have been arrived at in another context (Boerlijst & Hogeweg, 1991), which work looks at the role of spatial self-structuring occurring in the prebiotic evolution of catalytic cyclical ensembles (hypercycles). Mathematical models of these hypercycles are subject to the criticism of being unstable against the introduction of chemical parasites that take advantage of cooperative interactions without being cooperative themselves. Vulnerability to such parasites is, in fact, a consequence of studying the problem in a totally mixed medium. Once a spatial model is introduced, dynamical structures emerge that prove to be very robust against parasitic invasion.

A broad analogy can be drawn between the position of an agent within a cluster in the model presented in this article and the degree of participation in a social organization for a natural organism. For instance, animals spending more time in social activities as a consequence of their developmental stage or their social status will be analogous to agents living in the center of a cluster. Such an analogy would suggest that many answers to the question of natural communication could be sought in the nature of group structures or social hierarchies and the constraints they impose on the activity of individual organisms.

Interestingly, one of the relations found in this study—the positive correlation of cluster size and degree of coordinated activity—has a very suggestive parallel in primate societies: that of typical group size and relative neocortical size (Sawaguchi & Kudo, 1990; Dunbar, 1992). It has been suggested that language evolution has been deeply influenced by the growth in group size in humans as compared with other primates, and a functionalist explanation was advanced in terms of the role of language as a bonding mechanism in the maintenance of stability in large groups (Dunbar, 1993). The way that the analogous correlation was explained in the present study is rather different, more in terms of structural dynamics and feedback mechanisms than in terms of functional adaptations. Nevertheless, the parallel is worth noting.

The evolution of dialogical activity, such as the game presented in section 6, brings into question a very important aspect of communication as recursive coordination of actions that has not been explored in detail in this article: that of the relation of the evolution of communication and the evolution of cognitive abilities. Much could be said about this, but the present work cannot penetrate much farther into this area. These experiments can only be considered as a metaphor that suggests a possible way of understanding the evolution of cognition as rooted in social interactions. If social coordinated activity leads to more complex cognitive achievements, as we saw they can in a very simple model, a speculation could be forwarded about two possible

paths for cognitive evolution. One of them would lead roughly to highly structured societies of organisms in which the complexity of the social action involves the whole in such a way that individual behaviors have become more and more specialized, rigid, and subordinated to it (e.g., insect societies). The other would lead to a process of plastic or phylogenic assimilation of certain social modes of behavior in individual organisms, possibly leading, in turn, to higher complexity both in individual and social action. This latter path was very much discussed by Baldwin (1896) as a case of social heredity in gregarious animals. Interestingly enough, in the case of humans, this is how Vygotsky's theory of cognitive development (Vygotsky, 1978, 1988) accounts for experimental evidence in the development of higher cognitive functions in the child and the use of social modes of behavior in the self-regulation of individual activity. Evidently, any attempt at exploring the plausibility of such a process with a similar approach will have to take into account many of the features that were left out in the current model, such as an agent's bodyhood, autonomy, development, and plasticity.

Acknowledgments

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