Assessing the role of social development in the evolution of cooperation

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Abstract

The role of space-time structuring processes has recently come into focus as an important ingredient in the understanding of cooperative interactions in different contexts (Boerlijst and Hogeweg, 1991; Hemelrijk, 1997; Di Paolo, 1997; Di Paolo, 1998). This paper explores a similar role for a different sort of contextual process: phenotypical development under social conditions. A minimal ontogenetic, reaction-network model maps newborn phenotypes into adult ones according to genetic constitution and parental influence. In this way three coupled processes determine the distribution of behaviors within a population: selection, development and spatial organization. The presence of dynamic "developmental structures" is shown to play an important role in stabilizing cooperative coordination even when individual costs are against it. Resulting coordination levels prove to be much more stable than with spatial distribution alone. Some of the resulting self-promoting and self-regulating developmental structures are discussed.

1. Introduction

A tacit supposition in many evolutionary models is that those factors that remain outside the influence of natural selection are either fixed or vary at random. The evolution of a trait is often studied under the assumption that the relevant environmental factors change so slowly that they may be considered to be static (e.g. the distribution of food patches) or their variation is dependent upon so many contingencies that, for large populations, they may be considered to change randomly (for instance, mating opportunities). These are fruitful assumptions under which the evolution of the particular trait of interest becomes, as a dynamic process, decoupled from a myriad of other processes which, if considered, would make the treatment of the problem a very difficult task[1]. However, it is apparent that in many cases this is an oversimplification, even for the localized understanding that is intended to be obtained from such models. The distribution of food patches will partly depend on the efficiency of foraging strategies, and mating opportunities will depend, for instance, on space-time constraints.

This is a criticism that has been repeated many times (Bohm, 1969; Lewontin, 1982; Odling-Smee, 1988, among others) and should be taken seriously if an understanding of evolutionary processes in general is to be achieved. On the other hand, it is clearly impractical to model a whole ecosystem if we intend to understand the changes of a single trait in a particular species. If we are to find a compromise between accuracy, realizability and explanatory value, the relevance of those contextual factors which are not completely independent of the evolutionary process itself should be fully justified if we wish to include them in our models.

The aim of this paper is to accomplish such a justification in the particular case where the evolution of *cooperative social coordination* is coupled with a process of *social development*. Since, at this stage, we will only be interested in abstracting some basic dynamic features we can afford to ignore much of the complexities involved by using a rather simple but justifiable model.

2. Social coordination and dynamic structures

We are interested in the evolution of communicative behaviors. At first instance, and for reasons fully justified elsewhere (Di Paolo, 1998; Maturana and Varela, 1980), these will be better understood in terms of behavioral patterns of coordination rather than in terms of signals and information exchange. At a purely operational level, communication involves the interaction between two or more autonomous organisms, whose actions become mutually oriented as a result. In particular we will consider those cases of behavioral coordination that involve some sort of cooperation among participants with conflicting interests, since this sort of behavior has always been problematic when viewed from a neo-Darwinian framework.

From a game-theoretic perspective cooperative communication can only be understood if certain conditions are met regarding the distribution of cost-benefit relations among individuals differing in some quality and

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[1] In problems involving co-evolution assumptions like these are weakly relaxed so that the mutual influence of two or more "single" evolutionary processes can be accounted for.

degree of relatedness. The corresponding models are usually more sophisticated than simpler, "single trait" models, in that a distribution of possible strategies is assumed to exist and the beneficial properties of a given strategy are not independent of this particular distribution. In all other respects most of these models still assume either a static or a random variation of the rest of the relevant factors. For instance, they assume no structure in the interaction patterns of the individual organisms: *individuals play randomly with any partner in the population, and all individuals play all roles in the game with a fixed uniform frequency.*

Recently, the importance of a spatial distribution in the population of organisms that constrains both reproductive patterns and possible interactions has been put into focus. It is found in these cases that cooperation is stabilized even under circumstances where simpler models predict the contrary. This has been demonstrated both by mathematical considerations and computer models in the case of the Prisoner's Dilemma (Axelrod, 1984) and communication games (Ackley and Littman, 1994; Di Paolo, 1998). Depending on the particulars of the model there may be more than one possible explanation of this phenomenon. Axelrod argues that spatial clustering favours reciprocity if the playing strategy is cooperative (Axelrod, 1984, p. 65 - 69). Ackley and Litmann suggest, but fail to prove, that, since the areas where mating partners are chosen from and offspring allocated tend to coincide with areas where coparticipants are selected from, a process of kin-selection is responsible for stabilizing cooperation. In this way spatial distribution ensures that neighbours will be highly related so that cooperating with them will tend to increase inclusive fitness. Yet another possibility is *shown* to be at work in a model of an action-response game (Di Paolo, 1997; Di Paolo, 1998) and in a formally relevant model of distributed chemical catalytic interactions (Boerlijst and Hogeweg, 1991). In both these cases structured spatial entities and processes play a non-trivial role in the evolutionary process with which they are coupled. Di Paolo (1997; 1998) shows how agents playing an action-response game aggregate into structured clusters which influence the distribution of resources in the area occupied by them and modify the relative frequencies with which agents participate as players of the first role (action) and second role (response) in such a way that cooperative interactions result even for a range of individual costs against them.

These latter cases point to contextual processes or entities which are neither fixed nor randomly fluctuating, but depend either on the evolutionary process itself, or on some other non-decouplable aspect of the situatedness of organisms in their environment, (such as the distribution of resources). We may propose other processes or entities of this kind. In particular most gregarious animal species manifest some sort of social structure either in terms of phenotypical differentiation or behavioral patterns. The dynamics of such structures may constitute a very rich process in itself with far from obvious repercussions for the stabilization of cooperative interactions. For instance, Hemelrijk (1997) studies the effects on cooperative interactions of a self-reinforcing dominance hierarchy in spatially situated agents. A different sort of social process can be found when phenotypical development is affected by social influence. As an example we may think of parental imprinting of sexual preferences (Hess, 1973) and cultural processes in general. These processes will have an effect on the behavioral constitution of populations and consequently they will constrain the actual interaction patterns that become established within them. Since coordinated action is *not* an individual trait the relevance of these mechanisms should be evident.

The assertion that social structures can play an important role in the evolution of cooperative behavior is far from surprising. The point we wish to stress, though, is that the focus of attention should be on coupled dynamics, i.e. social structures not just as a static background against which organisms will try to optimize their behaviors, but as part of a generalized process in which organisms participate.

3. A model of social development

Our purpose is to make a *first order* assessment of the relevance that a socially influenced developmental process may have for understanding the evolution of cooperative action coordination, and also to try to identify what sort of dynamic constraints such a process may impose. This justifies the choice of an abstract, and indeed crude, model of development under social conditions. However, we will want our model to account for the following relevant aspects:

1. Phenotypes are the result of a dynamic process which is affected both by genetic constitution and coupling between the developing organism and its medium.
2. The nature of the process itself is not totally determined by genetic constitution nor by environmental coupling, (for instance, the number of possible attractors a developmental system may have depends on the specific transition dynamics and may not be easily changed during evolution).
3. In most natural cases of social development, the most relevant social coupling is between organism and parent(s).

The following scheme is an abstraction of these aspects. Let us suppose that an individual adult phenotype P_a^i is totally determined by its phenotype at birth P_b^i with the exception of certain minor changes which will depend both on P_b^i and the phenotypes of its parents $P_a^{p_1,p_2}$. P_b^i depends only on the genetic constitution of i. Parental influence is not arbitrary. We may define a *phenotypic metric* that, in principle, need not be the same as the genotypic metric in terms of Hamming distances, nor the same as a "behavioral" metric, but may take into account other traits besides those that are being studied. Under such a metric two phenotypes may be said to be close or apart. Parental influences will be taken into consideration only if the following condition holds:

$$\|P_b^i - P_a^{p_j}\| \leq D, j = 1 \text{ } or \text{ } 2,$$

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

$$P_a^i = Dev(P_b^i, P_a^{p_j}),$$

and

$$\|P_b^i - P_a^i\| \leq D.$$

This means that a social influence on development will be manifested when parents are not very distant from the offspring's phenotype at birth (so that genetic constitution does not become irrelevant), and it will be such that the resulting adult phenotype will remain within the same distance. If the above condition is not fulfilled then $P_a^i = P_b^i$.

4. Computer model

The abstract reaction-network model described above can be easily implemented in the context of an action-response game similar to those presented in (Di Paolo, 1997; Di Paolo, 1998). A population of agents are distributed in a two dimensional spatial environment. During its lifetime an individual agent does not leave its finite local habitat which is defined as a circle of radius R_0 around a fixed position with real-valued coordinates, and where all the interactions involving that agent take place. At each time step agents are chosen asynchronously with equal probability to play the first role in the game. An agent selected in this way will try to randomly locate a partner from its neighbourhood with a probability of success proportional to the local density of agents. At the same time a food repository will be randomly selected from those located in the neighbourhood. The first player performs an action A and the second player performs a response R. If A and R are complementary in the sense described below, the two players are said to be coordinating their behavior. In such a case both agents share equally the payoff which is an amount of energy extracted from the local repository. If they do not coordinate the first agent receives a proportion c of the energy in the repository, where $0.5 < c \leq 1$ and the other agent receives nothing.

In this simplified version A and R are fixed for all circumstances in a given individual: they do not depend on food types nor on a history of interactions. They are represented by two integer numbers between 0 and 15. The condition for A and R to be complementary is simply that $parity(A) = 1 - parity(R)$ where $parity(.)$ returns 1 for even numbers and 0 for odd numbers. From this it is possible to distinguish four possible behavioral types depending on the combination of parities for A and R.

Although all possible phenotypes will fall into one of the four possible behaviors (Figure 1), in order not to trivialize the issue of development, we have worked with the larger number of 256 behaviorally (but not developmentally) neutral phenotypes. These are encoded in an 8-loci binary haploid genome which defines P_b^i using binary encoding[2] where A is encoded in the top 4 bits and R in the lower 4 bits. The distance of allowed influence D was set to 2 (modulo 256).

Agents store the energy gained from the games they play and use it for self-maintenance (a fixed energy cost is discounted at each time step), and for reproducing once a certain amount has been accumulated. Selection of mating partner is based only on locality constraints, and offspring are placed within the neighborhood of the first parent. Neighborhoods do not overlap completely so that gene flow is not prevented. The offspring's genotype results from a uniform crossover operation on the genotypes of the parents plus random point mutations with a fixed probability μ per loci.

The adult phenotype of newborn agents is obtained as a function of P_b^i and $P_a^{p_1,p_2}$, observing the conditions discussed in the previous section. For each value of P_b^i its developmental function $Dev(.)$ is represented by an integer *symmetric* matrix M^{P_b} of $(2D+1) \times (2D+1)$ which is defined at the beginning of the simulation run. The elements of this matrix are integers randomly selected from the interval $I = [P_b^i - D, P_b^i + D]$. The indexes of the rows and columns correspond to the same interval, so that the first element of the first row will have indexes $(P_b^i - D, P_b^i - D)$. If the adult phenotypes of both parents fall within I the adult phenotype for the offspring will be:

$$P_a^i = M^{P_b}(P_a^{p_1}, P_a^{p_2}).$$

If only one of the parental phenotype falls within I the remaining index is taken to be equal to P_b^i:

$$P_a^i = M^{P_b}(P_a^{p_1}, P_b^i).$$

and if none of the parental phenotypes falls within I the adult phenotype is taken to be equal to the phenotype at birth. M^{P_b} defines a *constrained random reaction-network*. Table 1 shows an example of M^{P_b} for $P_b^i = 50$ and $D = 2$. For instance, if the parental adult phenotypes are 51 and 52, the resulting adult phenotype will be 49.

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[2] Tests performed using Gray encoding showed no significant difference in the results.

Table 1 Developmental matrix for $P_b^i = 50$.

	48	49	50	51	52
48	50	50	52	51	53
49	50	50	51	52	53
50	52	51	48	50	49
51	51	52	50	50	49
52	53	53	49	49	53

5. No development

How can we expect this model to behave? Based on previous experience and mathematical models we know how the model will behave if no social development is present, (for full details see Di Paolo, 1998):

No Space. Actions and responses may be odd (O) or even (E) so that there are four possible strategies related as shown in Figure 1, where arrows indicate a cooperative relationship between first player (arrow's starting point) and second player (arrow's end). Absent connections indicate non-cooperative relationships.

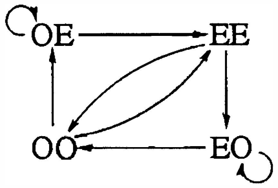

Figure 1 Cooperative relations between strategies. (EO) and (OE) are called "self-cooperating" or simply "cooperating" strategies.

Under these circumstances a dynamic game-theoretic analysis shows the presence of only two attractors. A fixed point stable attractor (ESS) where the population is divided equally between strategies (EE) and (OO) and so defining a baseline level of cooperation of 50 %, and also a limit cycle attractor, where each of the four types becomes dominant for a certain period, only to be followed by a different type in the order shown by the straight arrows in Figure 1. The basin of attraction for this second case is much larger than for the ESS. So, in the mixed medium situation the population will indefinitely oscillate between periods of cooperation and non-cooperation.

Space. When agents relate spatially results are different. In all cases a toroidal arena of 200 by 200 was used, the local neighbourhood radius R_0 was equal to 8 and the mutation rate to 0.002 per loci. 40,000 food resources were uniformly distributed across the arena, and energy related parameters were chosen so that population sizes varied between 700 and 1000 agents. The population tends to be distributed in relatively isolated, stable clusters. We do not find oscillations, and the resulting level of cooperation depends on parameter c, the payoff obtained by the first player in the case of non-coordination. For $c = 0.5$ (neutral cost) cooperation is established in the whole population (that is, the population becomes fixed at (OE) or (EO) or both of them, each in separated clusters). As c increases the level of cooperation decreases linearly until $c \cong 0.7$ where the baseline case of 50 % cooperation is reached. This shows that cooperation is stable even for some values of c greater that 0.5 (i.e. with individual costs against it), and that this level decreases gradually as c increases up to approximately 0.7. It has been observed that populations tend to be constituted largely by a mixture of strategy (EO) and a minor amount of (OO) or, conversely, by (OE) and a minor amount of (EE). Figure 2 shows an example of such a case, for a run of 1.5×10^5 time steps (roughly 400 generations). The population is rapidly invaded by a (self-)cooperating strategy (EO) and a small number of agents of type (OO) is maintained since they take advantage of the (EO) strategy, however the spatial dynamics prevents an invasion (other strategies disappeared early in the simulation). As c increases beyond 0.6 the constitution ceases to be stable and all strategies participate in a strong dynamics.

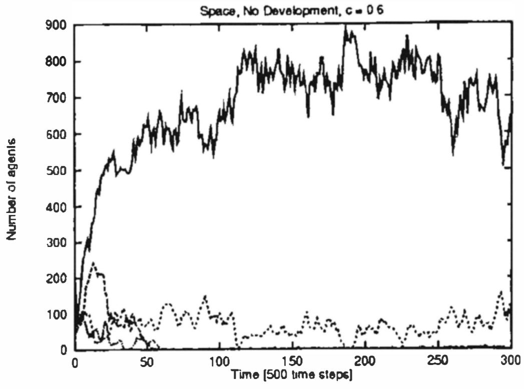

Figure 2 Population constitution for spatial game with no development, $c = 0.6$. Solid line: agents of type (EO), dotted line: agents of type (OO).

6. Results with social development

We find some interesting qualitative differences with the results discussed in the previous section when the evolutionary process incorporates development under social conditions. All simulations[3] were run using the same parameters and for various values of c between 0.6 and 0.95.

No Space. We mentioned that the imposition of spatial constraints changed the evolution of cooperation from an oscillatory pattern into a stable level. Here we

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[3] Data and code are available from: `http:\\www. ac.uk\users\ezequiel\dev\code.html`.

ask if a process of social development by itself could constrain the evolutionary dynamics in a similar way. The answer is no. The dynamics remain oscillatory, although qualitatively different in that strategies become phase-locked by pairs. The reason for this is not completely understood yet and further exploration is needed.

Space. Results are similar to the case of evolution with no development except that the range of c's where cooperation is stabilized is larger: $0.5 \leq c \leq 0.8$. More interestingly, almost for the totality of this interval, the population is constituted *purely* by a single cooperative strategy (either (OE) or (EO)), and only for $c \cong 0.8$ do mixed strategies appear. This means that the global level of cooperative coordination will not decrease smoothly as c increases, but will be maintained at near 100 % and then change rather abruptly for $c \cong 0.8$. Figure 3 shows a typical simulation run with $c = 0.6$.

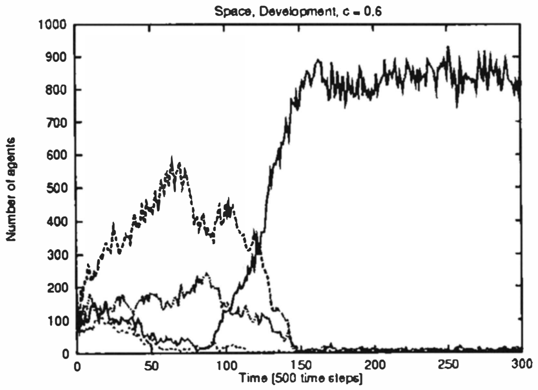

Figure 3 Population constitution for spatial game with development, $c = 0.6$. Each line represents one of the four strategies, solid line: (EO)

If we analyse the population constitution in detail we find that, within the range of c's where cooperation is stable, the population tends to be constituted mainly by a single phenotype either of type (EO) or (OE), with a developmental structure of the type shown in Figure 4.a. In this figure numbers in squares represent phenotypes at birth, numbers in ovals represent adult phenotypes, full arrows show a developmental relation and dashed arrows a parental influence on development. Figure 4.a shows that an agent i with $P_b^i = 238$ will develop into $P_a^i = 240$ if its parents happen to be $P_a^{p_j} = 240$.

By the term developmental structure we mean not only the logical relationship between offspring and parental phenotypes but the *actual* developmental relationship instantiated by the different types present in the population. The latter also depends on agent distribution and genetic relationships among other things.

As Figure 3 shows, there are no other strategies besides the main cooperating one (solid line). This marks a difference with the case without development (see Figure 2). This is due to the fact that the presence of a developmental structure promotes additional stability. While spatial organization seems to prevent an invasion by competing strategies, it cannot prevent their existence since they are just "one-mutation away" from the main component. With development the relationship between phenotypes of this main component and competing phenotypes is not so simple. It is not enough to be near in genetic space, but competing phenotypes must at the same time conform to the logic of the developmental space in such a way that the resulting behavioral relations still produce a competing interaction; a much more demanding constraint. As c increases there will be more pressure to meet this constraint. This is what we observe as we approach the limiting value of $c = 0.8$. Figure 5 shows the constitution of the population for such a value. Here we also see the main cooperating strategy constituting most of the population (solid line). The corresponding phenotype is also associated with the developmental structure shown in Figure 4.a. In addition, we observe that other strategies are not completely wiped out. By examining the population we discover that some agents relate through a more complex developmental structure (Figure 4.b).

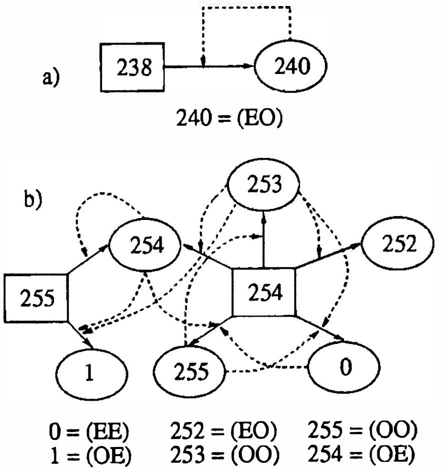

Figure 4 Developmental structures (see text) and corresponding behavioral types for a simulation with $c = 0.8$. a) Main self-promoting structure, b) secondary structure

The structures shown in Figure 4 originate from three different genotypes. The Hamming distance between '238' and '254', and between '254' and '255' is 1 meaning that uniform crossover will not be likely to introduce new genotypes. However, the two developmental structures are separate since developmental influences exist only if adult and newborn phenotypes differ in less that D[4]. From the behavioral perspective we see that two of the adult phenotypes produced in the second structure are of type (OO) which, under ideal circumstances,

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[4] Tests were run with values of D between 2 and 5, with similar results.

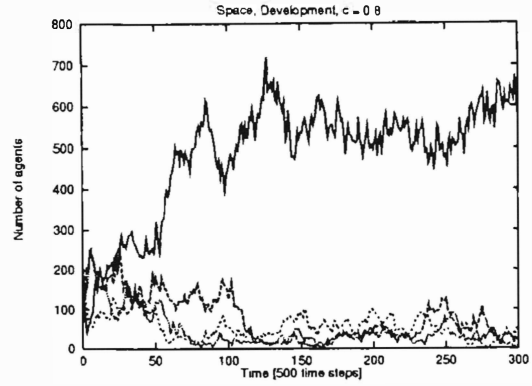

Figure 5 Population constitution for spatial game and development, $c = 0.8$

would invade a population constituted mainly of type (EO). However, as can be seen in Figure 4.b, these adult phenotypes are not "free" to grow but they are constrained by the amount of adult phenotypes that *favour* their development, some of which *compete* with them on the behavioral plane. In spite of what Figure 4.b may suggest all the phenotypes in this developmental structure remain bounded in number. In fact, if we study the time evolution of cooperating and non-cooperating phenotypes in this structure we find a very strong correlation in their variation ($\rho = 0.825$) as if the overall effect were behaviorally neutral which suggests that some complex self-regulation is taking place.

7. Discussion

As we said earlier our main purpose is purely exploratory, hence the abstractions made in this early model. The relevance of social development for understanding the evolution of cooperative coordination could well be supported independently by theoretical arguments. We chose to propose a minimal model where the nature of such influence could be explored.

We observe that in addition to the stabilization provided by spatial organization, cooperative coordination receives further stabilization by the presence of stable developmental structures which constrain the range of viable competing strategies. Further understanding of these structures could be obtained from other studies using reaction-networks. By the introduction of a chemical analogy, we may use notions such as catalysis, hypercycles, quasi-species, etc., (Eigen and Schuster, 1979), whereby developmental relations can be seen as favouring the production of certain group of phenotypes in a self-sustaining manner. But we must be careful, as the differences are also apparent, especially in terms of the other two "dimensions" in which these entities exist: the behavioral and the genetic.

We would like to emphasize that this study has looked at the issue of social development from an abstract perspective, that of an instantaneous process coupled with, but not completely governed by differential reproduction. This is a strong simplification of the issue of development under social conditions, especially if we are interested in its behavioral and dynamic aspects. Whatever the complexities of natural cases we can at least be certain that those features abstracted in our model have relevant consequences for the study of cooperative action coordination. We think this is enough justification for reconsidering the role played by natural selection as the main explanatory factor when social behaviors are involved.

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