Natural selection in a population of automata

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1 Introduction

Although the theory of natural selection permeates much of modern biological thought, its logical and mathematical analysis is not yet available. The problem is in its great generality, which borders with unfalsifiability. There is a great number of possibilities to formulate a mathematical theory of natural selection and different formalizations lead to different and often opposite properties. Thus the evolutionary process based on a zero-sum game is quite different from that based on a game of partnership (Krka 1986). The elucidation of the dynamics of natural selection is the task of mathematics, but this is difficult both in full generality and in special cases. The fitness landscape obtained in evolutionary models is usually very irregular and rugged (see Schuster 1989 for discussion of this issue) and most mathematical techniques fail. Only populational genetics formulates a tractable theory of natural selection, but it is based on too simple model of gene expression and does not take into account complex gene interactions.

In the absence of a mathematical theory, there is a number of mathematical or computer models clarifying some aspects of natural selection. There are several evolutionary models, in which a population inhabits a fitness landscape and clusters around fitness maxima (Eigen and Schuster 1977, Niklas 1986, Dawkins 1986, Dewdney 1989, Galar 1989). The fitness in these models, however, is a property of an individual, rather than a property of its relation to the population, so the ecological dimension of natural selection is lost.

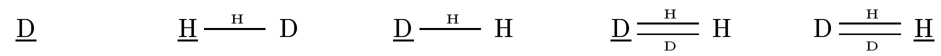
A simple model of interaction between individuals of a population provides the theory of games (Maynard-Smith 1982, Hofbauer and Sigmund 1984). A genotype describes strategy, which the individual adopts in encounters with other individuals. When there are enough strategies available, the resulting evolutionary models have rich behaviour with interesting features. This is the case in repeated matrix games, in which an individual chooses its moves on the base of past moves of the opponent (Krka 1986, Axelrod 1982, Miller 1989, Krka and Pavlk 1991).

Implicitly, these models are based on the metaphor of genetical information as computer program. This metaphor is rather widespread: It is the base of Dawkins's approach (Dawkins 1982, Dawkins 1986), and even Mayr (1982) relies on it considerably. Recently, it has been criticised by Atlan and Koppel (1990) on the grounds of Turing's Halting theorem: If the genetical information were really a program (i.e. a description of a Turing machine), then vast majority of mutations would be deleterious, and the evolution through random mutations would be unimaginable. It is significant, in the light of this criticism, that the evolutionary models so far proposed do not use the computer metaphor in this strong sense. Rather, these models use a recursive set of genotypes: Genotypes are vectors of integers or reals in Niklas 1986, Dawkins 1986, and Dewdney 1989, or recursive sets of strings of letters in Eigen and Schuster 1977, and Krka 1985. Because of recursiveness, it is possible to check the correctness of genotypes in advance, so that the majority of generated genotypes is viable. This fact can be counted as a support for Atlan and Koppel's thesis.

In the present contribution we reflect on the results of Krka and Pavlk (1991). We consider a population of finite automata, which play with each other the repeated Hawk-dove game. At each time step, an automaton chooses its move on the base of the previous moves of the partner. The game is played indefinitely and the pay-off of each player is the average of its pay-offs at single moves. The set of automata is infinite (though recursive), and there are many possibilities for both competition and cooperation between the partners. The automata reproduce and sometimes mutate. The lifespan of an automaton is inversely proportional to its fitness (mean pay-off obtained against other automata of the population).

In the repeated Hawk-dove game the natural selection leads to the establishment of an ecological network of mutually cooperating individuals. Two au-

Dove | Bully | Retaliator | Tit For Tat | Tat For Tit



Dove

	1
	D
D	1
H	1

Bully

	1	2
	H	D
D	1	2
H	2	2

Retaliator

	1	2
	D	H
D	1	2
H	2	2

Tit For Tat

	1	2
	D	H
D	1	1
H	2	2

Tat For Tit

	1	2
	D	H
D	1	1
H	2	2

Figure 1: Automata represented by graphs and tables

tomata may cooperate by alternating hawk and dove strategy and thus obtain more than two doves. When a nucleus of cooperating automata appears, it gets selective advantage, dominates the population, and then slowly evolves to ever increasing complexity, interdependence and variability. When such a community evolves, it is very stable. The participating individuals may change, but the cooperative pattern persists.

2 Genotypes

We consider the Hawk-dove game with strategies $S = \{D, H\}$ and a pay-off matrix $(A_{ij})_{i,j\in S}$

	D	H
D	2	0
H	6	-2

The game is played repeatedly by two partners, who independently choose either hawk or dove. Their choices are revealed simultaneously, and a player choosing strategy $i \in S$ obtains pay-off A_{ij} if its partner has chosen strategy j. We suppose that the game is played by finite automata. A finite automaton represents a model of rational behaviour. It is a device with finite set of inner states. At each time step it plays the strategy determined by its current inner state and switches to another state in dependence on its partner's move. We picture automata as labelled graphs. The vertices represent the inner states labelled by strategies, which the automaton outputs. The arrows are labelled by strategies too, and represent transitions, which the automaton undergoes upon communicating the partner's move. An unlabelled arrow means transition for both strategies. The initial state is specified with underlining.

The genotype of an automaton is a table with three rows and n columns, where n is the number of states, together with the specification of the initial state. First row represents outputs, and its entries are strategies. Second and third row represent the transition function and their entries are numbers from 1 to n. The initial state is again underlined. Some examples are in Fig. 1.

Thus Dove is an automaton which plays D, disregarding the moves of the opponent. Bully plays hawk so long as its partner plays dove, and switches to dove as soon as the partner plays at least once hawk. Conversely Retaliator plays dove so long as the partner plays dove and then switches to hawk. Tit For Tat plays at first dove and then the last move of the partner, while Tat For Tit differs only in playing at the beginninig hawk.

For example, when Bully plays against Tit For Tat, then its moves are $HHDDDD$... and those of Tit For Tat are $DHHDDD$.... We see that after three moves the games stabilize and both partners play dove. We neglect therefore the irregular beginning and set down both pay-offs as $A_{BT} = A_{TB} = 2$. Similarly the games of Tit For Tat against Tat For Tit are $DHDH$.... and $HDHD$.... respectively. Both sequences have period of length 2. We define the pay-offs as mean pay-offs obtained in this cycle. Thus the pay-offs of both Tit For Tat and Tat For Tit are $(6+0)/2 = 3$. In general, any game of two automata eventually reaches a cycle, whose length is at most the product of numbers of states of both automata. The pay-offs of the automata in question is defined as their mean pay-off in this cycle. In this way we obtain extended pay-off matrix for the whole (infinite) set of automata.

The pay-off of an automaton playing against itself is at most 2: in the repeated game only pairs of identical moves occur. On the other hand two different automata may alternately play dove and hawk against one another, so that they obtain mean pay-off 3. In this case we say that the automata cooperate. An example of cooperation is provided by six two-state automata in Fig. 2. The pay-offs of these automata against themselves ranges from -2 to 2, but any two of them cooperate and obtain pay-off 3. Other examples of cooperation are obtained when the second automaton is replaced by Tit For Tat, or when the last automaton is replaced by Tat For Tit.

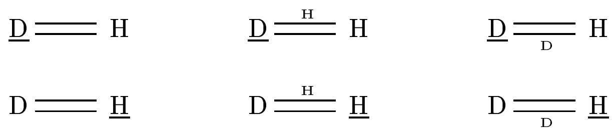


Figure 2: Cooperating automata

3 Mutations

According to the approach of genetical algorithms exposed in Holland 1975, we consider several genetic operators, which produce new automata by modifying the current ones. The genetical operators respect the "grammar of the genes", i.e. the syntactical constraints on the tables.

1. Point mutation: Another initial state is picked up or the value of either output or transition function is changed at one argument. This means that an entry of the table is changed.

2. Insertion: A new state is added and the transition and output functions are defined on it arbitrarily: A new column is added to the table. This is a neutral mutation, since the added state is not accessible from the initial one, and therefore the behaviour is not changed.

3. Deletion: A noninitial state is removed and the transitions leading to it are redirected: A column is removed from the table and the pointers are updated.

4. Conjunction: Two automata are united and a new initial state is added with transitions leading to the initial states of original automata: The tables are concatenated, new initial state is added and the pointers are updated.

We regard these mutations as errors in replication, which occur with certain probabilities. We suppose that each mutation of a given type is equally likely. However, the probabilities of insertion, deletion and conjunction depend on the number of states, so that the number of states would not grow without limit.

4 Selection

The selection process might be based either on game dynamics as in Krka 1985 and Krka 1986, on its stochastic version as in Krka and Pavlk 1991, or on a more complex computer algorithm as in Miller 1989. While game dynamics is more amenable to mathematical analysis, its stochastic version is closer to the spirit of natural selection. A genotype is typically present in a single copy at most, and there is a great genetical variability.

We have the set $\overline{S}$ of automata and for each automata $p, q \in \overline{S}$ their pay-offs A_{pq} and A_{qp}. The state of a population is given by a population vector $X = (X_p)_{p\in\overline{S}}$ of numbers of automata of each type. X_p are nonnegative integers, whose sum $N = \sum_{p\in\overline{S}} X_p$ is finite (population size). The phenotype of an individual p in a population X consists in its pay-offs against other individuals of X. We say that two individuals p, q are phenotypically equivalent ($p \overset{X}{\approx} q$) with respect to X if they have the same pay-off with individuals of X, i.e. if for each r for which $X_r > 0$ there is $A_{pr} = A_{qr}$, $A_{rp} = A_{rq}$. The phenotype of an individual determines its fitness, which is its average pay-off against other individuals except itself. (For this reason, A_{pp} is weighted by $X_p - 1$ instead of X_p.)

$$F_p(X) = (\sum_{q\in\overline{S}} A_{pq}X_q - A_{pp})/(\sum_{q\in\overline{S}} X_q - 1)$$

Note that the fitness of an individual depends on the whole population X.

To keep the population size constant, we suppose, that at each time step an individual reproduces and another dies. The rate of reproduction is uniform. An individual is chosen randomly and either reproduces without error or mutates to a slightly different one. New individual may also arise as a conjunction of two randomly chosen individuals. The choice of the automata to be reproduced or conjuncted is independent on its fitness. This yields greater variability in reproduced individuals with greater possibilities of successful mutations. The fitness determines the probability of death: the individuals with lesser fitness are more likely to die. These rules determine transition probabilities between population states. In this way the natural selection is conceived as a Markov process whose states are population vectors of given size.

5 Computer simulations

The result of a typical computer simulation is depicted in Fig. 3. Here population size is 25, the probability of error-free reproduction is 0.7 and that of point mutation is 0.21. The probabilities of insertion and mutation depend on the number of states and make together 0.09. (Conjunction is not used here: it does not significantly change the results.) We plot two rough characteristics of the population. The mean fitness ranges from -2 for a population of Hawks to 3 for a population of cooperating automata. The number of phenotypes, i.e. the number of phenotypically nonequivalent automata ranges from 1 to the population size.

At the beginning, all individuals are Doves and the mean fitness is 2. Soon a Hawk appears, the mean fitness slightly rises and then drops as the Hawks multiply. Further variants of hawk-like strategies appear, lowering the mean fitness bellow zero. This is a quasistable state, which persists usually for several thousands of simulation steps. Occasionally Retaliators succeed, drive out the Hawks, and establish a population of automata phenotypically equivalent to Doves. Such a population is more stable than that of pure doves, nevertheless, because of its phenotypical homogeneity, it is endangered by neutral mutations. The dove-like automata reappear and the population becomes vulnerable to hawk-like automata, which ultimately prevail, and lower again the mean fitness below zero. This development is reminiscent of the dynamics of doves, hawks, bullies and retaliators treated in Zeeman 1981.

Sooner or later, however, a group of two or three cooperating automata appears. For some time they coexist with Hawks and hawk-like automata, but three cooperating automata are already strong enough to drive the Hawks out. This process is enhanced by structural similarity of cooperating automata. Thus there are six two-state cooperating automata, which differ only slightly. As soon as two or three of them appear, the other follow quickly afterwards. Once a cooperative population appears, it is very stable. It may happen that a new mutant automaton outplays all individuals present and bring the cooperation to an end. With increasing number of phenotypes, however, such an event is very unlikely. More often a mutant automaton finds a new way of cooperation, i.e. it finds an unoccupied ecological niche. In this way the number of phenotypes grows, till it approaches the population size. Then the population slowly drifts through other modes of cooperation. From time to time a mutant appears and outplays a small number of automata, while cooperating with other ones. The outplayed individuals are driven out and new cooperating automata soon appear to replace them. This event is visible in a small, short-lived drop in mean fitness. The composition of population slowly changes, individuals once driven out reappear again, but the cooperation persists. The emergence of cooperative behaviour is a fairly regular event, occurring under nearly arbitrary initial conditions.

We can modify the model by dropping the assumption of constant population size. Let us suppose, that when the mean fitness is high enough, then reproduction is more likely than death, so that the population grows. With this assumption the number of phenotypes grows without limits. New strategies succeed only if they find a really novel way of cooperation. This means that their complexity and sophistication steadily increase.

6 Concluding remarks

The presented model illustrates some of the fundamental features of the theory of natural selection. The evolutionary process is a stochastic process taking place in the space of genotype distributions. There is infinity of genotypes, they have simple structure and determine a great variety of phenotypes. The process of gene expression, the translation of genotypes to phenotypes, is nevertheless complex and nontrivial. Similar genotypes may yield identical, similar or quite different phenotypes. There is a hierarchy of neutral mutations. Some mutations do not change the behaviour at all, other manifest themselves only under specific circumstances. Neutral mutations may be hidden for a long time and then manifest suddenly. Mutation is a random unpremeditated event with rather uniform distribution. The fitness of an individual depends on the whole population. Individuals with higher fitness have greater survival probability.

We have seen that in the repeated Hawk-dove game these assumptions lead to establishment of a cooperating ecosystem and its subsequent ramifications and self-organization. This is, however, not the neccessary consequence of natural selection alone. The structure of the underlying game is quite essential. There is no cooperation in a zero-sum game. As a result, the population of automata playing the rock-paper-scissors game, for example, remains forever on a rather primitive level. It is dominated by simplest automata and no ecosystem is established. When a more sophisticated strategy does appear, it is soon driven out by a simpler one (Krka 1987).

The current neodarwinian theory of evolution through natural selection postulates, that the fitness of an organism is determined by its genotype and environment, which includes genotypes of other organisms. The deciphering of this dependence is presumably the task of molecular biology. At present, however, this is not in sight. Without this law of gene expression, the theory of natural selection is incomplete und unfalsifiable. Different assumptions about the laws of gene expression lead to quite different patterns of evolutionary events. Moreover, any evolutionary event can be explained by natural selection. This is like classical mechanics, in which the Gravitation law would be replaced by the assumption, that some gravitation law exists. In such a theory, any trajectory could be explained, but no trajectory could be predicted.

It is therefore desirable to supplement the theory of natural selection with rules constraining gene expression. One possibility suggests the approach of Atlan and Koppel (1990). Another might come from non-equilibrium thermodynamics.

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