

Multi-level Selection and Immune Networks: Preliminary Discussion of an Abstract Model

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Abstract

An important gap in the relation between artificial evolutionary systems and their biological counterpart is the inability of artificial models to construct functional hierarchical structures in an emergent way. For composite structures to emerge and prosper in a biological hierarchical system, some form of selection is required at each level. In this paper we examine an abstract model of immune networks in terms of the selection dynamics present at the individual level and at the network level. In this context, a property of the individuals is examined in relation to its impact on the reproductive success on the individual and network level.

Introduction

In Biology, more and more evidence is discovered that selection operates on different levels and produces individuals whose properties (or traits) cause them to survive successfully at their focal level in a hierarchically organised environment. Moreover, these studies also show, that there is often conflict between these forces at the different levels, i.e. what is adaptive at one level can be maladaptive at another.

Multi-level Selection (MLS) and Evolutionary Transition (ET) theory are two relatively new theories which offer an explanation of why these individuals were able to evolve group-beneficial traits in a selfish environment. In order to discuss selection at multiple hierarchical levels, some prerequisites need to be in place in the system.

First, for Darwinian selection to occur at any level, certain properties need to be present at that level of selection in the biological hierarchy. These properties are 1) phenotypic variation, 2) heritability of phenotypic traits and 3) differential survival based on this phenotypic variation. Second, the selective forces at the different levels need to be linked in such a way that they can balance or counter each other. The combination of these two prerequisites results in a dynamical interplay where the quantitative ratio of group-beneficial traits versus individual traits changes over time. More info on MLS and ET and their products in Biology can be found in (Hogeweg 1994; Smith & Szathmary 1995;

Sober & Wilson 1998; Frank 1995; Keller 1999; Michod 2000).

In this paper we start with an examination of the relevance of MLS in the context of artificial evolutionary system using a simple problem of recognisers and target patterns based on an simplified abstract immune model. The goal of this paper is to get a better understanding of the forces which can be in place and not to deduce any conclusions about immune systems in general.

The Metaphor

The model used in this paper is a simplification in a number of ways of the immune network theory proposed by N.K. Jerne (Jerne 1973) and a model discussed by J.D. Farmer in the context of different connectionism examples (Farmer 1990). Our simplified model consists of a population of individuals which correspond to all the antibodies (free and surface antibodies) in the immune system and does not take into account the constant production of new B-cells by the bone-marrow as is the case in the immune system.

An individual in the population is represented by a couple (e, p) and e of one individual can interact with p of another. Each individual (e, p) consists of two strings of length l , where the string $p \in \{0, 1\}^l$ and the string $e \in \{0, 1, *\}^l$ ($*$ is the don't care symbol). Two individuals match when they are complementary and the specificity of the match is defined as the proportion of non- $*$ values in the e -part of the individual. Hence if $e = 001101$ and it matches with some p then the specificity is equal to 1. Otherwise if $e = *****$ then the specificity is 0. Note that the e -part will determine the type of the individual.

Hence it is assumed that there exist general locks (general e_j) which can be opened by many keys and specialised locks (specialised e_j) which can be opened by a unique key. This assumption can be made since match specificity (and in the case of the immune system, the binding specificity) does not determine the source of the matching value.

For more details on the immunological metaphor we refer to (Jerne 1973; Richter 1975; Hoffmann 1975; Hiernaux 1977; Farmer 1990)

Of Specialists and Generalists

An important property of the immune system is the ability of the B-cells and free antibodies to recognise foreign elements. In other words, it is an example of an abstract pattern matching algorithm.

Here, the example was selected to examine the impact of the selection scheme on the resulting individuals in the population. What kind of individuals (in terms of their properties) will evolve when using 1) a standard selection strategy or 2) a MLS strategy.

The general idea is that, on the one hand, in the standard strategy individuals will evolve which possess properties beneficial for the individuals themselves and not for the network (group) of interacting antibodies. On the other hand, in the MLS approach, it is expected that other properties which are beneficial for the group will emerge.

To summarise, it is assumed that an individual which has a specialised e has a cooperative behaviour. Alternatively, an individual which has general e is selfish in the sense that it tries to get as much stimulation as possible without reinforcing the rest of the individuals.

The Example Model

The dynamics of our simplified system can be summarised by:

$$\frac{db_i}{dt} = (c_1 f(s_i) - c_2 h_i - c_3) b_i \quad (1)$$

with

$$s_i = \sum_{j \in \{1 \dots N\}} m_{ij} (b_j/b) \quad (2)$$

$$h_i = \sum_{j \in \{1 \dots N\}} m_{ji} (b_j/b) \quad (3)$$

b_i represents the absolute number of an individual type (determined by e). The change in density of this particular type depends of the stimulation (s_i), the inhibition (h_i) and a damping effect (c_i). The values s_i and h_i are calculated in terms of the matching operation between the e_j -part and the p_i -part of the interacting individuals (given by the coefficient m_{ij} in equations 2 and 3). The function f describes the degree of stimulation and is expressed as a bell-shaped curve.

Hence, b_j benefits the production of b_i with an amount equal to m_{ij} , at a personal cost, m_{ji} . Furthermore this benefit and cost are frequency dependent since they are proportional to the frequency of other types in the population.

Selection Dynamics in a Population of Types

In order to understand the selection dynamics of the model, the replicator dynamics can be derived. Generally, the replicator dynamics is a mathematical description for the selection mechanism which specifies which

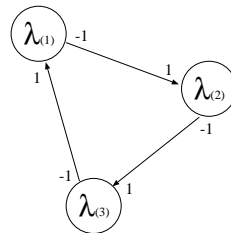


Figure 1: Three interacting individuals λ_1, λ_2 and λ_3 which maximally stimulate each other.

individual will be favoured over others. In other words it highlights the role of selection.

$$\dot{\lambda}_i = [\pi_i - \bar{\pi}] \lambda_i \quad (4)$$

Equation (4) is the replicator dynamics for our model described in equation (1) where $\pi_i = c_1 f(s_i) - c_2 h_i$ is the type's current fitness and $\bar{\pi} = c_1 f(s) - c_2 h$ is the current average success of the entire population. The entire state of the population is represented by the vector $\lambda = (\lambda_1, \lambda_2, \dots, \lambda_N)$.

For example, assume a population with N types and assume that the strength of stimulation (m_{ij}) and inhibition (m_{ji}) values are the same for all three types (Figure 1), then the dynamics of this system produces an asymptotically stable rest point with the same value for every λ_i .

The Dynamics of Individual Properties

The selection mechanism will promote individuals whose properties are beneficial for their reproductive success. Properties which give these individuals above average fitness compared to other members of the population. This fact can be expressed through an equation similar to the Price covariance equation (Price 1970; 1972; Frank 1995).

The same equation as presented by Price can easily be derived from starting from a discrete version of the replicator dynamic. The resulting equation will show how to determine if there exists a relation between the reproductive success of an individual and the fact that the individual possess the property z .

The average change of the property z in the population written into a covariance equation is:

$$\bar{\pi} \Delta \bar{z} = \text{COV}(\pi, z) + E[\pi \Delta z] \quad (5)$$

If the covariance is positive then the property z is beneficial for the reproductive success of the population. If it is negative, the property z makes the individuals bearing it less fit and if it is close to zero there is no relation between the property and the reproductive success of

the individual. The second term is negative if the property under investigation renders the individuals bearing it less fit.

Equation (5) can be simplified further to:

$$\bar{\pi}\Delta\bar{z} = \text{COV}(\pi, z) \quad (6)$$

This simplification holds as a very good approximation of equation (5) under certain circumstances which are fulfilled in the present case (for details see: (Price 1972))

In the example under investigation, we assume that the property z is the frequency of a certain type of individuals in the population. Thus for instance $\Delta\bar{z}$ can express the average change in the frequency of antibodies with very general e -parts. This would allow us to analyse whether the trait is beneficial under particular selection schemes.

Levels of Selection and the Price Covariance Equation

Equation (6) is a general selection mechanism which can be extended to model selection on different selection levels. This equation can be recursively expanded towards populations and groups of individuals. A derivation similar to the one by Price was performed here (Price 1972; Frank 1995; Gintis 2000).

A group G_j is defined, here, as a collection of types λ_i where all the λ_i in this collection form a network in which each member is stimulated and inhibited in some degree. The group G_j corresponds to the population state λ we defined in the previous section with the only difference that λ can consist of a collection of interacting networks and G_j does not contain any individuals which do not match with one of the individuals in the group. As a result, a group is defined as a collection of individuals which influence each other's fitness.

Assume a population P divided into M groups G_j . Λ_j is the frequency of individuals from P that are contained in G_j . Each group contains a distribution of the different individual types $G_j = (\lambda_{j1}, \dots, \lambda_{jN})$. In a MLS model, each group evolves in isolation and after one selection step, these groups are merged proportionally into a new population P' . Hence after one generation P' observes the new frequencies Λ'_j .

To make a distinction between the group and individual notation, the average fitness of one group is $\Pi_j = (\bar{\pi})_j$ and the frequency of individual that possess property z within the group $Z_j = (\bar{z})_j$. Hence, $\bar{\Pi}$ and \bar{Z} are respectively the average fitness of the total population ($\bar{\Pi} = \sum_j \Lambda_j \Pi_j$) and the average property value in the entire population ($\bar{Z} = \sum_j \Lambda_j Z_j$).

In the same way the covariance equation at individual level was derived, (5), the expression for the groups behaviour can be derived. In the following equation the subscript g identifies that the covariance and the expected value are taken relatively to the groups.

$$\bar{\Pi}\Delta\bar{Z} = \text{COV}_g(\Pi, Z) + E_g[\text{COV}(\pi, z)] \quad (7)$$

The first term of this equation represents selection between groups (intergroup selection). It shows the relation between the presence of a property in the groups and the fitness of the population. The second term on the right side of the equation expresses intra-group selection which is shown as the difference among the individuals within the group averaged over the different groups.

Discussion

In order to validate the model and to examine whether selection occurs at the higher-level, the three necessary properties for Darwinian selection need to be present at that higher level.

In order for selection to take place at the group level, groups have to differ in content. Sober and Wilson, in (Sober & Wilson 1998), describe clearly that, on the one hand, if there is much variation within the groups the chances are high that there will be little variation between the groups since each group will more or less contain similar elements. On the other hand, if there is little variation within each group, groups will differ more and as a result there will be more variation between the groups. For selection to occur at the group level, the latter case is required. In the first case, no variation means similar reproductive success and hence no observable selection at that level.

In the immune network example presented here, each group was defined as a collection of individual types which influence each others fitness and no individuals outside this group. It was concluded that each group contains a network of individuals which stimulate and inhibit each other with varying strengths. When comparing the different groups there should be variation since the members of the different groups respond to different ($e.p$) individuals. This indicates that under the assumptions of the previous sections, selection at a higher level can occur in this simple example. Based on this variation, groups which contain more individuals with above average fitness, will produce larger offspring groups and hence will contribute more to the population in next generation.

The phenotypic property (z) under investigation was the defining length of the e -part of the different individuals. At the individual level it was explained that for an individual it is better to possess an e -part with low defining length (general) since this results in a maximal stimulus and as a consequence in maximum fitness. At the level of the group or network the opposite is true. The network as a whole obtains its 'maximum' when all the members collaborate in an optimal manner. As a result it is better for the group's average phenotypic property Z to have individuals with high defining length

since these groups will contribute more to the next generation.

Inheritance is defined as the tendency of the offspring to resemble their parents. To know whether properties of the group are heritable, there has to be a relation between the properties of the group in this generation and the next.

In terms of the property z or Z this means that there has to be a relation between the average specificity of the individual/group in the current and next generation. In the model we investigate here, there were no mutation or any other reproduction operators. Only a cloning mechanism which produces a number of offspring based on the difference between stimulation and inhibition. Hence, the offspring of individuals always resemble their parents since no property change occurs. A similar argumentation holds for the groups. The only change that can occur is a shift in the number of individuals for a specific type in the group. Hence, the property z and Z are inheritable.

As a result of both previous properties and that the resources are finite, although the population can be large, differential survival and the clonal selection of these units will cause evolutionary change, leading to properties which are ‘fit’ for the environment. As discussed in the first paragraph, there is a conflict between the property which is considered to be fit for the individual and the network of individuals (the group). Hence, what will evolve will depend on the relative strengths between the two selective forces at the different levels.

Assume that selection at the higher level is the only force then those groups which possess collaborative individuals will perform better (in terms of reproductive success) than others. This occurs when there is strong difference between the different groups in their Z value.

Alternatively, assume that selection at the lower level is the only force, then all groups will contain on average the same kind of individuals in terms of the property and hence no clear variation exists and selection can not take place.

Conclusion

In this paper, a model of an abstract immune system was constructed to examine the difference between standard individuals selection and multi-level selection. The first step in building this model was to derive the selection dynamics which take place in an abstract immune network. As a second step, this selection dynamic was translated to a different selection model which expresses the relation between the properties of the individuals and the evolutionary success of these individuals. This second model has the property of being scalable to different levels. Hence as a third step this model was scaled to the level of a population of groups. To verify this model an argumentation in terms of the properties which

allow selection to occur was performed for both levels. From this argumentation it can be concluded that, in the model presented here, selection can occur at different levels and that both levels produce individual types which have different conflicting properties.

Further work on the computational model is currently conducted in order to verify the remaining arguments of this paper.

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