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# Dynamics of Macrosystems

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# PREFACE

The history of the disciplines that led to the development of systems analysis is marked by a curious relationship between static and dynamic approaches. Although the importance of the dynamical element was recognized quite early on, the method chosen, more often than not, was a static equilibrium analysis.

One reason for this obviously lies in the mathematical intricacies of non-equilibrium situations. Although Poincaré and various other classical authors pointed out the amazing complexity of some mechanical problems, the general trend, as reflected in the standard textbooks, was to ignore such "subtleties" and concentrate on a handful of tractable equations and localized stability analysis. It is only in the last decade that the importance and universal nature of complicated asymptotic behavior has become more widely recognized. This shift in perspective is due to the development of new mathematical techniques, to the spread of computing facilities and, possibly, to the growing recognition of the limits of the human ability to handle, predict and control complex situations.

Other reasons for the dominating influence of equilibrium concepts in the history of systems analysis have a non-mathematical basis. In such diverse fields as physics, chemistry, ecology and economics, steady states were recognized, or at least postulated, as prime objects of study. It may be the fact that we are living today in a less stable world which has caused a shift in the focus of our interests "from being to becoming", to quote Prigogine. Irreversibility, oscillations and solitons, synergetic phenomena, phase transitions, turbulence and chaos have all forced themselves into the forefront of scientific investigation. Climacting ecosystems à la Clements or economic optima sensu Pareto now often seem too good to be true. The tremendous progress in the development of equilibrium theories and optimization techniques has forced the subject to level off, like a plane reaching the thinner layers of the atmosphere. By their very precision, mathematical investigations have restricted the domains in which we are prepared to expect stable equilibria. Their existence is something which has to be proved and can no longer be taken for granted.

We now know that the tacit assumption of tame and predictable dynamics traditionally made in the study of equilibria was naive. We are becoming aware of the important and pervasive role that instability and random, chaotic motion play in the dynamics of macrosystems.

Further research in this field should aim at providing useful tools, and therefore the motivation should come from important questions arising in specific macrosystems. Such systems include biochemical networks, genetic mechanisms, biological communities, neural networks, cognitive processes and economic structures. This list may seem excessively heterogeneous, but there are many similarities between evolution in the different fields. The prototype is biological evolution, of course, but the basic phenomenon – the interplay between increases in variability due to mutations (or errors, uncertainty, noise, chaotic behavior) and decreases in variability through selection mechanisms of one kind or another – is characteristic of evolution in fields ranging from chemistry and neural networks to economics and the social sciences. It is not surprising, therefore, that mathematical methods devised in one field can also be used to describe the dynamics in another.

The International Institute for Applied Systems Analysis (IIASA) is attempting to make some progress in this direction. With this aim in view, a Workshop on the Dynamics of Macrosystems was held at Laxenburg, Austria, over the period 3–7 September 1984. The Proceedings (contained in this volume) cover a broad canvas, ranging from specific biological and economic problems to general aspects of dynamical systems and evolutionary theory.

J.-P. Aubin
D. Saari
K. Sigmund

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# DYNAMICS OF THE CENTRAL NERVOUS SYSTEM

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## 1. INTRODUCTION

Describing a scene or object can be done at several different levels. Lower levels involve chiefly local features or attributes while at higher levels one tends to focus on relations between parts of the object. It is a major concern of today's cognitive sciences and artificial intelligence to devise frameworks for the representation of relational information.

Our Central Nervous System (hereafter CNS) is particularly well adapted for handling relational knowledge at different levels in a quite flexible way, and it is probably not an irrelevant fact in this context that connectivity within cortex is by several orders of magnitude richer than in the most sophisticated parallel machines. It is the big challenge of modern neurobiology to understand how this parallelism is exploited in the CNS.

Traditional neural network modelling strongly relies on the early ideas of McCulloch and Pitts (1943). Their formal neuron, computing a boolean function of binary inputs, is an essential component in many models. In a broader sense, most of current brain theory follows an algorithmic, or computational approach: the function of the brain is analyzed within a conceptual framework developed around the traditional von Neumann machine, where algorithms and data are by and large separate entities.

Such approaches have severe theoretical limitations. While they provide appropriate frameworks for studying the "processing" of attributive low-level information, they have, so far, proven to be largely inadequate for tackling higher-level problems where relational descriptions are crucial. Thus for instance, machines derived from the Perceptron of Rosenblatt (1961) immediately break down when confronted with the task of capturing in their most simplified form some of the high-order regularities in the environment which are vital to living beings: propositional calculus is clearly not the appropriate framework for this task.

There are today few alternatives to this approach. We shall refer several times in this paper to the recent models of Hopfield (1982) and of Hinton and

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The work described here has for the most been done in collaboration with Christoph von der Malsburg (Max-Planck Institute for Biophysical Chemistry, Göttingen, FRG), who in particular owns full credit for the underlying original ideas. The present paper is a preliminary account of this work. An extensive description, including both theoretical and technical aspects, will appear elsewhere.

Sejnowski (1983). These authors propose an attractive tool borrowed from statistical physics, to study the dynamical behaviour of neural networks in the spirit of the cell assembly model of Hebb (1949). In contrast with the philosophy of McCulloch and Pitts (1943), of Rosenblatt (1961), of Barlow (1972) and still many others, where the "psychon", or "semantic atom", or "carrier of meaning" is essentially the activity of an individual neuron (cardinal cell), meaning is now distributed over large populations of cells, exhibiting the required collective behaviour. The question of how to assemble pieces of knowledge into a consistent hierarchy is not directly addressed in these works. It is nevertheless fairly clear that here too, boolean logic is the answer.

The approach advocated by von der Malsburg (1981), and on which the present paper is based, moves us away from this boolean framework. The starting idea is simply that relational information can be represented on a faster time-scale than the one on which individual neuronal activity is usually measured and thought to play a role in CNS function. High flexibility can be achieved in this way: regardless of the average level of discharge of a given family of neurons (they may for instance all be firing at the same rate), their mutual correlations and higher-order statistics, evaluated on the faster time-scale, can take very different values depending on the circumstances.

Temporal correlations are however quite fluctuating, and should be complemented with a more robust physical support. This leads von der Malsburg to an original assumption: the efficacy of synaptic transmission between neurons in the CNS is subject to a type of modification which is somewhat reminiscent of the well-known hebbian modification (Hebb 1949), yet takes place on a much faster time-scale. A synapse may be activated or deactivated within a lapse of time as short as 100 msec or so. The dynamics of correlations and synaptic weights on this fast time-scale are coupled. They are essentially governed by a positive feed-back loop so that they eventually stabilize each other: high correlation in the discharge of neurons i and j increases the weight of the synapses from i to j or from j to i, which in turn tends to increase even more the correlation. The combined activity-connectivity variable thus reaches a stable state in a short period of time, and this state is the carrier of meaning.

The central notion in this model is thus the coupled dynamics of correlations and connections. It can be rephrased as a local principle of cooperation-competition (see §3.1). This principle has a far-reaching consequence at the global level, namely the organization of preferred brain states. Using an intuitive argument, von der Malsburg indeed conjectures that the dynamics leads to states of a particular type, characterized essentially by their topological properties (see §3). Accordingly, the hierarchical build-up of symbols obeys topological rules, which have little to do with the boolean logic of von Neumann machines.

The permanent connectivity in the CNS, laid down during development and learning, is the substrate on which different organized activity-connectivity states unfold in a sequence. On the global level, the different organization patterns follow each other rapidly, essentially at the pace of cognitive processes.

The contrast with the computational approach is a sharp one. CNS function is conceived of as self-organizational rather than (or maybe, in addition to) algorithmic. Consider for instance perception. Instead of passively processing, i.e., filtering, the incoming information according to wired algorithms, the brain generates, selects and combines inner patterns, according to its own criteria about organization, yet of course in constant interaction with the environment. This conception is very close to the selective, or darwinian approach to brain function, as exposed in particular

by Edelman (1978) and Changeux et al. (1984).

The main goals of the present paper are the following: (i) to make the notion of topological organization as clear as possible; (ii) to establish that such organization is achieved in a system obeying simple local interaction rules not inconsistent with what we know from the CNS; and (iii) to provide arguments in support of the claim that this type of organization is relevant to the representation and manipulation of natural, hierarchically structured, regularities.

Although our model proceeds from a very different approach, we shall follow Hopfield (1982) and use the statistical physics notion of a hamiltonian (or energy) function, from which we shall derive a particular type of "hamiltonian dynamics". In addition to being a very convenient and attractive mathematical tool, it provides us with a simple means of clarifying what in our approach differs from more conventional ones.

## 2. STATISTICAL MECHANICS FORMULATION

### 2.1. Notations and definitions

$\{1,\ldots,n\}$ : the set of neurons

$x_i \in [0,2\pi]$ : activity of neuron i, i=1,...,n

$w_{ij} \in \{0,1\}$ : synaptic weight, $i \neq j$, i,j= 1,...,n

$H_w(x) = -\sum_{ij} w_{ij}\cos(x_i - x_j)$ : the interaction energy, or Hamiltonian

$P_{w,T}(x) = (Z_{w,T})^{-1}\exp(-H_w(x)/T)$ : the Boltzmann distribution, with:

$$Z_{w,T} = \sum_{x'} \exp(-H_w(x')/T) \quad \text{(the partition function)}$$

### 2.2. Comments

All these definitions are quite standard in statistical mechanics. They are used in particular in the Ising model of magnetism. Throughout this paper, we shall emphasize the analogy between our model and the Ising model as much as possible. In an Ising model, the sites i=1,...,n are usually regularly spaced, e.g. at the nodes of a 2- or 3-dimensional square lattice. The variables $x_i$, called spins, represent local magnetic moments. They can be either discrete- or continuous-valued. The most extensively studied model uses "Ising spins", i.e., $\{-1,+1\}$-valued. Spins that take values on the circle as in the present paper are called X-Y spins, on the sphere Heisenberg spins. The link or interaction constant $w_{ij}$ determines the sign and magnitude of the interaction (see below) between the spins at i and j. In general, only neighbouring spins interact, i.e., $w_{ij}$ is 0 for all non-neighbouring pairs. (Neighbourhood can be defined in various ways.)

In our model, we assume that all neurons have same average activity, as evaluated on a "long" time-scale, i.e., of the order of a few seconds or dozen of seconds. Yet, the activities differ considerably in their fine temporal structure. We use the spin variable $x=(x_1,\ldots,x_n)$ to characterize the instantaneous deviation from mean activity (resolution time of the order of a few msec. or dozen of msec.) of each individual neuron.

The choice of the spin space, i.e., the degrees of freedom of $x_i$, is somewhat arbitrary. This space should be sufficiently rich for allowing a satisfactory representation of the degree of synchrony or asynchrony between neurons, i.e., of the second-order statistics of a multiple spike train. Clearly, the potential complexity of such a spike train cannot be compressed

into n X-Y spins, i.e., with values on the circle, unless the spike train is periodic and each neuron fires exactly once during each period. This is certainly not realized in general, yet for most of our purposes X-Y spins are sufficient. (Ising spins are definitely not: see end of §4.) This issue is discussed further in §6.

Regarding the links between neurons, an important difference between this model and most spin models is that in our case, no spatial order is given a priori: unless otherwise stated, all pairs (i,j) potentially interact, i.e., $w_{ij}$ can be equal to 1. The graph of intrinsic synaptic connections in neocortex is certainly far from being a complete graph, yet for our purposes, this assumption is not too unrealistic. For one thing, interpreting a link $w_{ij}$ as the union of all mono- di- or tri-synaptic pathways between i and j is very likely to yield a nearly complete graph. (We may ignore synaptic delays if the number of synapses in the pathway is small. However, see §6.) Thus, in a sense, all neurons are potentially quite "close" to each other. Moreover, assuming that only a fraction of links exist would not change the behaviour of the model in any important sense, provided the links are chosen at random.

In several other respects however, the model is oversimplified. First, no distinction is made between a synapse from i to j and a synapse from j to i: the matrix w is at all times symmetric, i.e., $w_{ij}=w_{ji}$ for all $i\neq j$. Also, diagonal elements are all 0. The assumption of symmetry has far-reaching consequences, as discussed in §6. Second, synaptic weights are discrete-valued. Finally, they are non-negative: only excitatory synapses are explicitly considered. Inhibitory synapses are however implicit in the model. They are assumed to be unmodifiable, but play an important role, namely preventing that all neurons become globally correlated. Global correlation corresponds to $x_i$ identical for all i. These trivial states are excluded by introducing a severe constraint on the family of allowed x's, i.e., the state (or "phase") space. The constraint on x is: $\sum_i x_i=0$. In an Ising model, this constraint means that total magnetization is 0. This type of constraint is also used in models of alloys which are formally very similar to models of magnetism using Ising spins, and where, obviously, the total number of atoms of each type is a constant. We shall moreover assume here that the $x_i$'s are at all times regularly distributed over the circle.

In the Ising model, a link of positive value $w_{ij}>0$ tends to align the spins at i and j in the same direction, i.e., bring $\cos(x_i-x_j)$ close to 1. Accordingly, the interaction energy, or Hamiltonian, is defined as the sum of many local contributions, one for each pair of interacting sites. The more the spins at i and j point in a common direction, the more negative the (i,j) contribution, $-w_{ij}\cos(x_i-x_j)$: as usual, the convention is that preferred states are the low-energy ones. Because of thermal noise however, strict minima in the phase space are seldom reached. The Boltzmann distribution relative to H says how likely each state x is to occur, given the connectivity state w, and the temperature T. The dependency of $P_{w,T}(x)$ upon $H_w(x)$ is a quite simple one: the lower the energy, the higher the probability of x. Specifically, the ratio between the probabilities of two states x and x' is $\exp((H_w(x')-H_w(x))/T)$. Thus, choosing T small enhances the peaks and troughs in the probability distribution, whereas choosing it large levels everything out: when T is high enough, all activity states are nearly equally likely.

In our model, the interaction term $\cos(x_i-x_j)$ measures synchrony of firing between cell i and cell j, corresponding to spin alignment in the Ising model. The effect on x of a positive $w_{ij}$ is analogous to its effect in the Ising model: an excitatory synapse between neurons i and j tends to synchronize their firings, for an action potential emitted by i at time t will increase the likelihood of j to discharge shortly after t. We thus use the

same formal Hamiltonian and Boltzmann distribution for neuronal activity states, as for spin configurations in the Ising model. Notice that T is now a mere control parameter, which measures the amount of noise present in the system. The words "temperature" and "energy" should by no means be taken literally in this model.

True noise may originate from a variety of sources: spontaneous transmitter release, threshold fluctuations, etc. Yet, "controlled" noise can also be actively injected into the network via a "non-specific" system of afferent fibres originating from any family of neurons distinct from the one under consideration. Such a device is of vital importance for regulating the dynamics of the system on a global level. In particular, it allows a very simple implementation, in a piece of neural tissue, of the "annealing" process to be described at the end of §2.3.

## 2.3. Dynamics of neuronal activity

Having at our disposal a hamiltonian function allows us to define "hamiltonian dynamics". A well-known example of hamiltonian dynamics is the Metropolis algorithm, originally devised by Metropolis et al. (1953) to study equilibrium properties, e.g. ensemble averages and low-temperature behaviour, in large systems of interacting elements such as gas, alloys, or spin systems. The $x_i$'s change only one at a time, moreover in random order. Once the site $i$ is chosen, a change of $x_i$ is attempted. The dynamics is specified by a formula or scheme (see below) that says how the decision to accept or reject an attempted change depends on the increment or decrement in H that will result from such a change. If the zero-magnetization constraint has to be satisfied, spin-exchange dynamics are used instead of "single-change". In any case, the philosophy is, roughly, the following: accept moves which lower H and reject the others, in order to eventually find low energy states.

More specifically, the algorithm says what the probability of any move is, as a function of the resulting change in energy, $\Delta H$, and of the control parameter T. The higher T, the more likely one is to accept a move which increases the energy instead of lowering it. On the other hand, if T=0, the dynamics is entirely deterministic, except for the sequence in which sites (or pairs of sites) are "visited" for tentative change: an attempted change is made if and only if it results in lowering H.

The following simple stochastic scheme is often used: if the energy change $\Delta H$ is negative, the move is always accepted, whereas if $\Delta H > 0$, the move is accepted with probability $\exp(-\Delta H/T)$. This is implemented on the computer by drawing a new random number for each tentative change; these random numbers should of course be statistically independent.

It is easily seen that under these conditions the Boltzmann distribution P is invariant under the dynamics, i.e., if at time t the probability of any state x is precisely $P_{w,T}(x)$, it remains so for all times. It follows from this that starting from any state or distribution of states at time t=0, the asymptotic distribution when time goes to infinity is precisely the Boltzmann distribution. When P is reached, the system is said to be in thermodynamic equilibrium.

Applications of the Metropolis algorithm, either in its original form or in various modified versions, are quite numerous and by no means confined to statistical physics proper. We shall only briefly mention here some recent works that bear direct relevance to our model.

Notice first that in a network of neurons obeying the dynamics described above with temperature T=0, each single cell behaves simply like the formal neuron of McCulloch and Pitts (1943). The system dynamics is, however, asynchronous. Hopfield (1982) investigates the behaviour of such a neural network, in which the connectivity w, hence the "energy landscape", have been

shaped by learning according to the principle of synaptic modification of Hebb (1949). During "recognition", or "retrieval", the state x of the system is seen to converge to one of the local energy minima in the phase space: since T=0, the state clearly cannot escape a local minimum of energy. This is the desired behaviour, since these local minima correspond to the various "memories" or associations, learned by the system. Thus, the system is capable of retrieving a stored pattern of activity, when given only a part or a noisy version of it.

A related work is the "Boltzmann Machine" (Hinton and Sejnowski 1983; Hinton et al. 1984). These authors formulate the problem in a slightly different way: after learning has taken place, the exchange parameters $w_{ij}$ should be such that $P_{w,T}$ is as close as possible to the probability distribution "of the world", as experienced by the system throughout the learning phase. In their work, positive temperature is used in the recognition step. Letting the system work at positive temperature is indeed a simple way to avoid being trapped in wrong minima, i.e., local minima of relatively high energy.

The idea of exploiting in a systematic manner positive temperature when looking for low-energy states, is proposed by Kirkpatrick et al. (1983) in the context of complex optimization problems. These authors deal in a quite general way with the family of combinatorial problems which lend themselves to a formulation in terms of minimizing a cost function f(x) made up of the sum of many "local" contributions. They propose to use the Metropolis algorithm, with f playing the role of the Hamiltonian, and with the control parameter T being very slowly brought to 0. This elegant process, termed simulated annealing, is a powerful computing tool that is now being used to solve a wide variety of complex problems in very different domains. The paper by Geman and Geman (1984), contains a short review, a proof of some convergence properties of the annealing algorithm, and an original application to image restoration. We shall see in §4 of the present paper another application of the annealing technique (to the problem of embedding a graph in $\mathbb{R}^2$).

## 2.4. Dynamics of neuronal connectivity

From now on, we shall depart from the classical Ising model, and treat the connections $w_{ij}$ as thermodynamic variables. This is also a fairly clear-cut demarcation line from conventional modelling in neurobiology. Connections are, surely enough, modifiable in all neural network models dealing with learning, starting from the Perceptron (Rosenblatt 1961), and ending with the Boltzmann Machine (Hinton et al. 1984). Yet modification of connectivity is generally associated in a strict way with learning or development. Function of the system, i.e., recognition, classification or retrieval of a memory, occurs at fixed connectivity. Following the proposition of von der Malsburg (1981), we now let the weights $w_{ij}$ evolve simultaneously with the $x_i$'s, in such a way that the two dynamics feed back on each other.

Two cases should be distinguished: a) fast connectivity changes; b) slow connectivity changes. We shall treat each case separately, presenting thus two different formal approaches, the extremes in each direction. We shall see that some important qualitative aspects of the behaviour are the same in the two cases. The relevance of the two formulations to various applications is discussed in §5-6. The application to function and perception involves of course relatively fast connectivity changes.

Fast connectivity dynamics. We assume here that the links $w_{ij}$ undergo modification on exactly the same time-scale as the activity variables $x_i$. The two types of variables are therefore treated on the same level. We shall thus consider a Hamiltonian H' which is a function of the composite

variable (x,w), and define a related Boltzmann distribution P' and hamiltonian dynamics, for the joint process (X,W):

$$H'(x,w) = H_w(x) + \alpha F(w) = -\sum_{ij} w_{ij}\cos(x_i - x_j) + \alpha F(w) \qquad (1)$$

with

$$F(w) = \sum_i \left(\sum_j w_{ij} - p\right)^2 \qquad (2)$$

The hamiltonian H' includes two terms. The first is the usual spin interaction energy, considered now as a function of x and w. It embodies in a simple way mutual positive feedback between synaptic weight and synchrony of firing. Assume indeed that for a given pair (i,j), $w_{ij}=1$: the (i,j) contribution is then minimal if $x_i=x_j$, i.e., if i and j are synchronous. This argument can now be reciprocated: if i and j are rather synchronous, i.e., $\cos(x_i-x_j)>0$, then the (i,j) contribution is negative if $w_{ij}=1$. Minimizing the first term in H' is thus equivalent to having the best possible match between active links and pairs of synchronous neurons.

The second term in H', $\alpha F(w)$, embodies a constraint on the number of active links per site. Clearly, this term is minimal if for all i, the number of j's such that $w_{ij}=1$ is exactly p. It is understood that $p<<n$. Thus, this term introduces local competition between links: each site has to choose a small number of links from the n available. A low-H' state is the result of a trade-off between two antagonistic drives, expressed by the two terms in H'.

Having fixed a temperature T, the dynamics for the joint process is defined as follows. A pair (i,j) is drawn at random, and one of the two possible moves is attempted: exchange the "spins" at i and j (whereby total magnetization is unaffected), or change the connection weight $w_{ij}$, from 0 to 1 or from 1 to 0 depending on its current value. In each case, the decision is made following the usual probabilistic scheme, which requires the evaluation of the change in H' resulting from the tentative move. Another pair of sites is then drawn at random, and the procedure is iterated. The decision as to what type of move is attempted at a given pair (i,j) is also made at random. (One can equally well alternate deterministically between the two.) This dynamics has as invariant distribution the Boltzmann distribution relative to the hamiltonian H', as a function of both x and w. (The partition function is of course obtained by summing over the (x,w) phase space.)

Slow connectivity dynamics. We now consider the other extreme case, namely w changes infinitely slowly with respect to x. This is formalized by assuming that after a move has been performed on w, x reaches thermodynamic equilibrium before one attempts the next move on w. Feedback will now occur between connections and correlations rather than connections and synchronies: given w, correlations are evaluated under the Boltzmann distribution $P_{w,T}(x)$, and these correlations are used in subsequent modification of w. We thus have two nested dynamics acting on different time-scales: a fast dynamics for x, which serves to evaluate correlations at fixed w, and a slow dynamics for w. This process can be described with the help of two hamiltonian functions instead of one. The first is $H_w(x)$, defined for any fixed w in §2.1. Having chosen a "temperature" T, we next define the Boltzmann distribution $P_{w,T}$ as in §2.1., and the correlations as follows:

$$s_{w,T}(i,j) = \langle\cos(x_i-x_j)\rangle_{w,T} = \sum_x \cos(x_i-x_j)P_{w,T}(x) \qquad (3)$$

Strictly speaking, correlations are ensemble averages. Such averages can not be computed and stored at the synapse. We shall therefore assume that they can be replaced by appropriate time averages with reasonable accuracy.

Finally, we define a Hamiltonian $H''_T(w)$, a function of w only:

$$H''_T(w) = - \sum_{ij} w_{ij} s_{w,T}(i,j) + \alpha F(w) \qquad (4)$$

Again, this Hamiltonian is made up of two terms. The first is minimized when the best possible match is achieved between links and correlations, whereas the second introduces competition between links. Notice that the first term is equal to the internal energy of the system (the spin interaction energy averaged under the distribution $P_{w,T}$).

The w-dynamics is the usual Metropolis algorithm, at a given temperature $T_c$ ($T_c$ may be different from T). w being fixed, the nxn matrix of correlations is computed. An attempt is then made to change w: the probability of the change depends in the usual way on $\Delta H''_T/T_c$.

## 3. CHARACTERIZATION OF LOW-ENERGY STATES

We now turn to the characterization of low-H' and low-H" states. This step is a crucial one: it establishes that the nature of organization is topological.

### 3.1. Intuitive characterization

Independently of whether we use H' or H", we should expect the following property in these states (when using H', we mean the w-part of the state): cycles and cliques of low order are more frequent than usual. A cycle of low order in w is for instance a triangle, i.e., a triplet (i,j,k) such that $w_{ij}=w_{jk}=w_{ki}=1$. A clique is a complete sub-graph, i.e., a subset $I \subset \{1,\ldots,n\}$ such that for all $i,j \in I$, $w_{ij}=1$. (Cycles and cliques are the same at order 3.) "More frequent than usual" means more frequent than in a random graph of same size and same number of connections per node.

This property results from the positive feedback between connectivity and correlation (or synchrony). Let i and j be given. If many short indirect pathways between i and j are "active", i.e., w=1 along these pathways, then $x_i$ and $x_j$ will tend to be synchronous (if H' is used) or correlated (if H" is used), for synchrony (resp. correlation) propagates along short pathways. This in turn will induce high likelihood of activating $w_{ij}$, since this edge will stand in competitive advantage with respect to other edges, both at i and at j. Because there are many short indirect pathways between i and j, activating $w_{ij}$ means closing many short cycles, and/or completing many small cliques. In summary then, edges belonging to small cliques or cycles cooperate with each other in the dynamics. It is the conjunction of local cooperation and competition which generates global organized states.

### 3.2. Formal characterization

We shall use three different properties of graphs to characterize topologically low energy connectivity states. For all three, random graphs are used as a reference. We will thus obtain three "criteria" for measuring the degree of topological organisation of w, each criterion consisting of the comparison of w to a random graph. Erdös and Rényi (1960) define random graphs by giving equal probability to all graphs of a given number of edges on a fixed set of nodes. Equivalently, a random graph is generated by connecting at random pairs of unconnected nodes until the desired number of edges is reached. In our case we need a slight correction to this definition, to account for the sharp constraining of the number of edges at each site, resulting from the term $\alpha F(w)$ in the Hamiltonian: we want to compare a low

energy w to a graph of same size which is random in all respects other than this constraint. This graph will be termed the corresponding random graph.

Erdös and Rényi (1960) investigate various properties of random graphs in the asymptotic limit when the size of the graph and the number of connections both tend to infinity. In particular, they study the number of cycles of a given order k, for any given k. They show that, as the size of the graph tends to infinity while the mean number of edges per vertex is kept constant and equal to c, the distribution of cycles of order k converges to a Poisson law of mean $c^k/2k$. In particular, the mean number of triangles (and of cycles of any given fixed order) is not an "extensive" variable: it does not increase with the size of the graph. This is not surprising: the disjoint union of two random graphs is all but a random graph!

The first criterion is the following:

Criterion 1 . For k small, e.g. k=3 or 4, compute the ratio of the number of cycles of order k in w to their average number in the corresponding random graph.

Next, we shall investigate the number $\varphi_w(i,k)$ of sites that stand within w-distance k from a given site i, as a function of k. The w-distance between i and j is the length (number of edges) of the shortest pathway in w which connects i to j. Let $f_w(k)$ be the average of $\varphi_w(i,k)$ over i. There are some particular w's for which the rate of growth of $f_w(k)$ for small k is easy to derive. If w is random, $f_w(k) \propto c^k$. If the vertices are thrown uniformly in a d-dimensional box and w is the resulting graph of connections between neighbours (however the concept of neighbourhood is defined), $f_w(k) \propto k^d$. Finally, if w is a disjoint union of cliques of order c+1, $f_w(k) \propto c$. In general then, slow growth of $f_w$ is associated with topological organization:

Criterion 2 . For small k, compute the ratio of $f_w(k)$ to the average value of f(k) in the corresponding random graph.

The first two criteria use local properties. The third and last one invokes a global property, related to the notion of the embedding of a graph in a euclidean space. Let the dimensionality dim(w) of the graph w be the least integer d such that there exists a sequence of n points $P_1,\ldots,P_n$ in the euclidean space $\mathbb{R}^d$, satisfying the following for each $i \neq j$: $w_{ij}=1$ if and only if $\|P_i-P_j\| < 1$. Low dimensionality is then associated with topological organization:

Criterion 3 . Compare dim(w) to the average dimensionality of the corresponding random graph.

## 4. NUMERICAL RESULTS

Activity-connectivity dynamics were numerically studied on small systems (n usually ranged between 30 and 60) using Metropolis algorithms with either one of the two Hamiltonians described in §2. Parameters such as the temperature(s), the optimal edge number p and the coefficient $\alpha$ in the second term of the Hamiltonian, were varied over broad ranges. In each case, initial connectivity was a random graph.

Simulation of slow connectivity dynamics (using H") is time-consuming, since the correlations $s_{w,T}(i,j)$ have to be computed at each step. The following "trick" is used to speed up the calculation of the correlation matrix s: instead of sampling over the entire phase space, only low-H x's, i.e., "valleys", are looked for. Indeed, since the distribution is exponential, only valleys contribute in a significant way to thermodynamic averages (when the temperature T is low). Also, in order to reach low-H" connectivity states faster, annealing techniques (see end of §2.3) are used rather than a Metropolis algorithm at $T_c=0$. It is worth stressing again that these computing tricks can also be implemented in a parallel system such

as a neural network, provided there is a control module in another part of the brain, which regulates the process on a global level.

We shall give here only a qualitative description of the results. The main observation is the following: low-H" states as well as (w-parts of) low-H' states are topologically organized using any of the three criteria of §3.2. For instance, the number of triangles in w, divided by their average number in the corresponding random graph, is seen to increase progressively in time, while H'(w,x) or H"(w) decreases. Starting close to 1, this ratio converges to an asymptotic limit which depends on the values of the various parameters in the dynamics, and the following relationship is generally observed: the lower the asymptotic energy, the higher the asymptotic frequency of triangles. Similar behavior is observed when rectangles are counted rather than triangles.

Criteria 1 and 2 are easy to deal with numerically. Criterion 3 however requires the solution to an embedding problem which is far from trivial. Given w and d, the "search space" for this problem is not even finite: it is in fact the high-dimensional euclidean space $\mathbb{R}^{nd}$. Neither is it clear how to obtain even rough estimates for the corresponding random graphs, as in Criteria 1 and 2.

The following strategy is therefore adopted: instead of seeking d such that a "perfect" embedding of the graph w in $\mathbb{R}^d$ is possible, i.e., an embedding in which any pair of connected nodes are closer to each other than any disconnected pair, one releases somewhat this constraint, and looks only for an "optimal" embedding of w in the space $\mathbb{R}^2$. The optimal embedding satisfies as closely as possible the following constraints: connected, respectively disconnected, nodes are close to, respectively distant from, each other. Yet some disconnected nodes may be closer to each other than some connected nodes. By comparing various optimally embedded graphs (asking for instance how often and how much the constraint is violated) one can get an idea of at least the relative dimensionalities of the graphs.

The optimization problem can be formulated using a cost function $C_w(r_1,\ldots r_n)$ to be minimized over r, where w is the given graph, and $r_1,\ldots,r_n$ are the positions of the n vertices in the unit square:

$$C_w(r_1,\ldots,r_n) = \sum_{ij} \|r_i-r_j\|^{-1} + k \sum_{ij} w_{ij}\|r_i-r_j\|^2 \qquad (5)$$

The first term embodies repulsion between all pairs of nodes, while the second is responsible for mutual attraction between pairs of connected nodes. The particular functional form of each term is quite arbitrary. Notice however the following simple physical interpretation. $C_w$ is the potential energy associated with pairwise interactions of two types: electrostatic repulsion (imagine that identical electric charges are attached to all nodes) and spring attraction (turn each edge in w into a perfect spring, with spring constant k).

Minimizing $C_w$ is easily achieved by simulated annealing: the cost function C(r) is now regarded as the "energy" of state r. A random initial r is first drawn, with all $r_i$'s in the unit square. Random changes of r are then attempted. One change consists in moving one randomly chosen $r_i$ to a random position in the unit square. The resulting change $\Delta C_w$ is calculated, and the move is accepted with probability 1 if $\Delta C_w<0$, and with probability $\exp(-\Delta C_w/T(t))$ if $\Delta C_w>0$. The temperature T(t) is a control parameter which decreases to 0 when the iteration step t goes to infinity. It is found that a fast annealing schedule, with T(t) decreasing exponentially, yields quite satisfactory results.

Here too, random graphs are used as a reference: one should compare an optimal embedding of a given graph to an optimal embedding of a corresponding random graph. Fig. 1a is an optimal embedding of a random graph $w_R$. Two

observations can be made regarding embeddings of random graphs. First, lengths of edges are quite non-uniform: even in optimal embeddings, it is impossible to avoid having a fair number of relatively long edges. In the physical interpretation of the optimization problem, this means that a fraction of the springs always remains stretched. Second, independent annealings of the same random graph yield very different optimal embeddings: nodes that are close in one embedding can be distant in another. Yet, all the annealed states have about the same energy $C_w$. Thus, the optimal embedding problem for random graphs is very "degenerate".

The existence of multiple "ground states" is indeed typical of large systems of local constraints, when the constraints are sufficiently random and mutually contradictory. Such systems are termed "frustrated" in solid state physics (Toulouse 1984). "Spin glasses" (for a review see Toulouse 1984) and "traveling salesman" problems (for a review see Garey and Johnson 1979) are probably the most extensively studied frustrated systems. The 2-dimensional embedding problem for a random graph is in a sense dual to the traveling salesman problem. (In the traveling salesman problem, positions of nodes in the square are given and one seeks the graph of minimal length under the constraints that the graph be connected and there be exactly two edges out of each node.)

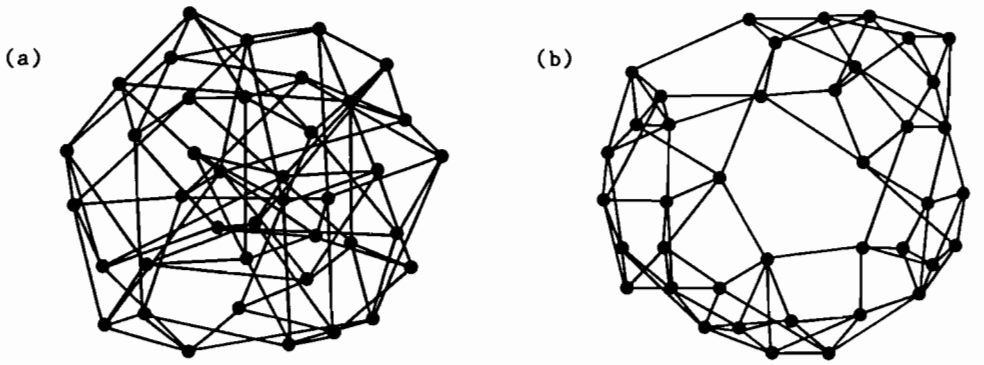


FIGURE 1. Optimal embeddings of graphs in $\mathbb{R}^2$. (a) Embedding of a random graph. (b) Embedding of a topologically organized graph.

Fig. 1b is an optimal embedding of a topologically organized graph $\mathcal{G}$. This graph was obtained with the fast connectivity dynamics (using H'). The slow dynamics (using H") yields similar graphs in almost all respects (see below). While $w_R$ and $\mathcal{G}$ have equal numbers of vertices (40) and of edges (100), there are five times as many triangles and three times as many rectangles in $\mathcal{G}$ as in $w_R$. It is also seen from fig. 1b that many pairs of vertices have $\mathcal{G}$-distances (Criterion 2) of 5 or 6, whereas distances in the graph $w_R$ do not very much exceed 3.

These are intrinsic properties of the two graphs, which do not depend on particular embeddings. If we now examine the embeddings proper, the most striking difference is that the edges in fig. 1b are of more uniform length, and shorter in the average, than in fig. 1a. Thus, although there is no "perfect" embedding of $\mathcal{G}$ in $\mathbb{R}^2$, hence $\dim(\mathcal{G})>2$, the optimal embedding of $\mathcal{G}$ is clearly more successful than the optimal embedding of $w_R$. It is quite likely that $\dim(\mathcal{G})<<\dim(w_R)$.

In fig. 1b, whenever two vertices i and j are connected they are located nearby each other and there generally exist several short indirect pathways between them, in addition to the direct connection $\mathcal{G}_{ij}$. If on the other

hand i and j are far from each other, there are only long pathways between them. As a result of this, the embedding problem for a topologically organized graph such as $\mathcal{G}$ is far less degenerate than for a random graph: proximity or remoteness of nodes is now an intrinsic property of the graph, hence nodes which are close neighbours in one embedding are very likely to be so in all others. In short, edges in $\mathcal{G}$ define a consistent set of neighbourhood relationships, that is, a topology on the set of nodes. In this particular case, the topology is, very roughly, that of a ring. We shall see below that this phenomenon is peculiar to connectivity graphs obtained with the fast dynamics. Notice that while a 2-dimensional embedding is adequate for revealing the topological organization of $\mathcal{G}$, it may not be so for larger graphs.

Topological organization, as illustrated in fig. 1b, is typical of connectivity states at intermediate temperatures (which are likely to be the relevant ones for brain function), when either H' or H" is used. If T and $T_c$ are further reduced, the observed states approach the very bottoms of the valleys, i.e., the energy minima. These minima are also the most organized states in all three criteria of §3.2. Yet they differ considerably depending on the hamiltonian that is used. The rest of this section deals with zero-temperature behaviour, that is, the characterization of the states that minimize globally H' or H".

1. Fast dynamics. The following is easily proved. The states $(\vec{x},\vec{w})$ which minimize H' satisfy: given i,j and k, if $\vec{w}_{ij}=1$ and $\cos(\vec{x}_i-\vec{x}_k)>\cos(\vec{x}_i-\vec{x}_j)$, then $\vec{w}_{ik}=1$. Thus, $\vec{w}$ connects sites which are neighbours in the circular topology induced by the spin configuration $\vec{x}$: minima of H' reproduce exactly the topology of the X-Y spin space. (The graph $\mathcal{G}$ of fig. 1b was produced by lowering the temperature just enough for the circular organization to appear. It still is far from an energy minimum $\vec{w}$.)

However, as far as the applications of the model are concerned, this particular type of organization is a mere "artefact", due to the arbitrary choice of the circle as spin space. If one uses Ising spins, i.e., the spin space is $\{-1,+1\}$, the characterization of minima of H' is even simpler: $(\vec{x},\vec{w})$ minimizes H' if and only if $\vec{w}$ minimizes $F(\vec{w})$ under the constraint $\vec{w}_{ij}=1 \Rightarrow \vec{x}_i=\vec{x}_j$. The graph is then made out of the disjoint union of two large subgraphs, each of which is random in our criteria (for minimizing F(w) yields a random graph). Thus, in the case of Ising spins, even the energy minima are rather poorly organized. This is already a good reason for not choosing Ising spins. The choice of spin space is further discussed in §6.

2. Slow dynamics. The form of the minima of H" is not derived as easily as for H', yet the simulations support the conjecture that the minima are disjoint unions of small cliques (completely connected subgraphs), of size slightly larger than p. Since $p<<n$, this is a quite strong type of organization, involving a high number of symmetry breakings. Such minima are approached only with the help of relatively long annealing schedules. In the case of H", the form of the minima seems to be independent of the choice of the spin space. Thus, at low temperature, the two systems behave very differently.

## 5. DYNAMICS OF PATTERNS

Preceding sections dealt with self-organization. It was shown that a simple cooperation-competition mechanism acting on connectivity graphs spontaneously produces topological structures. We now introduce the term pattern to designate graphs which are topologically organized according to the three criteria of §3: a pattern is the "skeleton" of a topology.

The notion of pattern is somewhat ill-defined: there is no strict boundary between patterns and non-patterns (random graphs). Accordingly, the present section is rather informal. It addresses the central issue of pattern dynamics: how does our dynamical system behave when presented with patterns, in various combinations? Patterns can be presented either as boundary conditions or as initial states in the dynamics. (We shall deal here only with the first case.) A system capable only of generating abstract internal patterns would indeed be of little help to us in understanding brain function. The system must be able to handle already existing patterns in an appropriate way.

We chiefly need to know how internal patterns interact with each other, and how they interact with external patterns, for our ultimate goal is a model of knowledge representation: the nervous system creates internal representations of external objects, and assembles them into a coherent representation of the world. We thus distinguish between two types of interaction, although it should be stressed here again that the boundary is drawn only for didactic purposes. In particular, "external" patterns include the case of patterns within the brain, yet in a region (or layer, or family of neurons) other than the one we currently consider. Various combinations of the two types of interaction are possible, and likely to occur.

We shall further restrict the discussion to the following two specific types of boundary conditions: Case a.- The "permanent" graph G of available synapses which undergo modification according to our dynamics is not a complete graph as in the preceding sections, but rather a superposition of several patterns. (G is the union of several graphs sharing a common set of vertices). Case b.- The graph G of modifying synapses forms a projection between two disjoint yet homeomorphic patterns.

Case a. As we shall later see, the available permanent synapses actually undergo modification, yet on a slower time-scale than the fast dynamics of §2.4. This slow modification, a combination of learning processes with the slow self-organization dynamics of §2.4, produces a superposition, in a single family of neurons, of patterns which are quite independent from one another.

We shall assume that the superposition is totally random, i.e., that the different topologies don't talk to each other. This condition can be formalized by using for instance Criterion 1 of §3. Let $\mathcal{A}$ and $\mathcal{A}'$ be two graphs on the same set of n vertices. We require that "pure" $\mathcal{A}$-triangles as well as pure $\mathcal{A}'$-triangles be more frequent than in random graphs (corresponding to $\mathcal{A}$ and $\mathcal{A}'$ respectively): $\mathcal{A}$ and $\mathcal{A}'$ are thus patterns. Yet we require that "mixed" triangles, e.g. triplets (i,j,k) such that $\mathcal{A}_{ij}=\mathcal{A}_{jk}=\mathcal{A}'_{ki}=1$, have "normal" frequency (the frequency of triangles in a random graph corresponding to this mixture). Such a random superposition can for instance be obtained by taking a pattern $\mathcal{A}$, and defining $\mathcal{A}'$ as follows: $\mathcal{A}'_{ij}=1 \iff \mathcal{A}_{p(i)p(j)}=1$, where p is a given random permutation of (1,..,n). The superposition G of $\mathcal{A}$ and $\mathcal{A}'$ is of course defined by $(i,j)\in G \iff \mathcal{A}_{ij}=1$ or $\mathcal{A}'_{ij}=1$.

We set the control parameters of the dynamics (essentially the parameter p in F(w) which regulates competition) so that at each node only half of the outgoing G-edges have a chance to survive. Locally then, edges belonging to the same pattern cooperate with each other (to form low-order cycles and cliques), while edges belonging to different patterns compete. Thus, there are exactly two global energy minima, $\mathcal{A}$ and $\mathcal{A}'$. Under this set of boundary conditions, the dynamics boils down to competition between patterns. Again, reaching a pure minimum may require careful and long annealing: in general, one obtains a mixture of the two, i.e., a "solution with defects", with a small number of coexisting pieces of each pattern. This unpleasant situation may be avoided with the help of further boundary (or initial) conditions,

which provide a selection mechanism (see below the application to invariant perception).

Case b. We are given two homeomorphic patterns $\mathcal{Q}$ and $\mathcal{Q}'$ on two disjoint sets of nodes N and N': we may for instance assume that card(N)=card(N') and that $\mathcal{Q}'$ is an identical replica of $\mathcal{Q}$. (The notion of a "homeomorphism" is of course legitimate in this context only inasmuch as we accept that of a pattern.) The graph G is the full projection between N and N': G=NxN'. Only synapses in G undergo modification: synapses within N or within N' are assumed to be fixed. Finally, the competition is set so that only a small number of edges shall survive at any node $i \in N \cup N'$.

It is not hard to guess the form of the energy minima under such boundary conditions. A state $\mathcal{Q}'' \subset NxN'$ is an energy minimum if it realizes a homeomorphism between N and N', with the topologies induced by $\mathcal{Q}$ and $\mathcal{Q}'$ respectively. Local cooperation between edges is then maximal (many triangles and rectangles are formed). By assumption, at least one such homeomorphism exists. There may however be more than one. Here too as in case (a), one may obtain a solution with defects (in this case a piecewise homeomorphic map).

Activating a homeomorphism between $\mathcal{Q}$ and $\mathcal{Q}'$ amounts exactly to creating a pattern on the larger set $N \cup N'$. The graph $\mathcal{Q}'''=\mathcal{Q} \cup \mathcal{Q}' \cup \mathcal{Q}''$ is indeed a pattern on $N \cup N'$. Think for instance of $\mathcal{Q}$ and $\mathcal{Q}'$ as 1-dimensional linear arrays of equal size. There are two obvious homeomorphisms between them, and let $\mathcal{Q}''$ be one of them. Clearly, the graph $\mathcal{Q}'''$ is a pattern according to all three criteria of §3.

This last remark relates to a key feature of the model. We have just seen that the property of being a pattern is preserved when two smaller graphs are assembled into a larger one. The notion of pattern is therefore a generic one: it applies uniformly throughout the hierarchical scale of symbols. Moreover, it can be seen that, in principle, the very same rule of cooperation-competition that forms the basis of connectivity dynamics at the lower level, i.e., that of synapses, "carries over" to the higher levels of pattern dynamics.

We shall not pursue this abstract discussion. Rather, we present now a simple illustration of pattern dynamics, in the form of a 3-layered network for invariant pattern recognition. The word "pattern" is taken here in its usual acceptation. Specifically, we think of a visual pattern, i.e., any contrasted stimulus impinging on a 2-dimensional retina. We shall however immediately turn it into a topological pattern, in the following way.

We introduce, in addition to the conventional activity variable for each retinal cell, the x-variable of §2-3. The former measures activity on a long time-scale (of the order of a second), whereas the latter relates to the fine temporal structure of the spike train. We shall assume that synchrony of firing of cells i and j, as expressed by the quantity $\cos(x_i-x_j)$, falls as a function of the retinal distance between i and j. Experimental evidence in support of this assumption exists in the goldfish retina (Arnett 1978) and the cat's retina (Mastronarde 1983). We thus obtain a 2-dimensional pattern in the x-variable (we have no connectivity so far), matching simply the 2-dimensional topology of the retina R.

This x-pattern is carried over to the next layer, which contain Local Feature Detectors. In this "LFD-layer", cells respond selectively to small elementary stimuli on the retina, such as oriented contours, colour, texture etc. There are m different types of elementary stimuli, hence, m LFD-cells at each location in this layer.

Finally, the third "FD-layer" contains Feature Detectors of the same m types as in LFD, yet without any selectivity for position on R: all cells of type k in LFD, irrespective of their locations, feed into all cells of type k in FD. The m types are hereafter called labels.

So far, if one disregards the x-variable, the model closely resembles one

of the original versions of the Perceptron (Rosenblatt 1961). The difficulties met by the Perceptron to achieve any kind of intelligent vision are well-known. In particular, position-invariant recognition according to this "algorithmic" approach (fixed connectivity) would require explicit wiring of the invariance (see e.g. Fukushima 1980), which makes generalization in any direction rather doubtful.

The solution offered by our dynamics is very different from the conventional algorithmic Perceptron-like approach. The system will now self-organize, i.e., select on a fast time scale the connectivity appropriate to the current recognition task. Two processes of synaptic modification are required. Learning concerns internal FD-connectivity only, while recognition is based on fast connectivity dynamics, in both the LFD-FD projection and the internal FD connections.

When a stimulus is presented on R, it elicits a pattern of activity in LFD. Competition deactivates most of the LFD-FD synapses: the resulting map is, say, one-to-one. If the stimulus was never experienced before, any such map is selected. The pattern is carried over to FD by this bijection, and stored there: connections between synchronous cells in FD are reinforced. Thus, a 2-dimensional pattern is now printed in the "permanent" connectivity of FD. (It is assumed that the available synapses in FD form a complete graph. In particular, they are not restricted to pairs of cells of same label.)

Presenting in sequence different stimuli on R results in the superposition of different patterns in the permanent FD-connectivity. All these patterns are homeomorphic images of the 2-dimensional R- and LFD-layers, or of parts of them, hence are roughly homeomorphic to each other. Yet they greatly differ as for the relative positions they affect to different labels. They are thus non homeomorphic as labelled patterns, if we define a homeomorphism between labelled patterns as a bijective map which preserves neighbourhood relationships and labels.

Recognition of an already experienced stimulus follows now in a straightforward way from the two rules of pattern dynamics discussed above. Several patterns are in competition in the FD-layer. The labelled pattern which is selected by the dynamics is the one which is homeomorphic to the labelled pattern currently activated in LFD.

This type of recognition is clearly homeomorphism-invariant. In particular, a pattern experienced earlier at a given position in R is recognized when presented at any other position. Invariance of size and under most usual distortions follows in the same way, provided the distortions don't interfere too much with the local features of the pattern.

Recognition is thus achieved when an appropriate pattern of activity-connectivity is selected. As discussed earlier, this pattern is of a generic form: it is ready to interact with, and actually be part of, concurrent mental processes, involving for instance associations with other sensory modalities, motor commands etc.

## 6. DISCUSSION

This paper gives an overview of a statistical mechanics formulation of the model of brain function originally proposed by von der Malsburg (1981). The formulation is simple, and provides a convenient frame for the comparison to other models, which do not assume short-term plasticity. On a formal level, the most closely related models are those of Hopfield (1982) and Hinton and Sejnowski (1983). Both were briefly discussed in §2.3. Schematically, the energy function in the present paper is almost the same as in these two works, yet it is minimized over both x and w, instead of over x alone.

This model thus rests on the hypothesis that "meaningful" brain states are activity-connectivity states, rather than pure activity states as is

always assumed. Physically, treating w as a variable is unconventional. (One should however mention the exception of lattice formulations of gauge field problems.) Moreover, it is the free energy which is minimized in physical systems, rather than the internal energy (the first component of H", see eq. 4). However, from a biological standpoint, the assumption of fast synaptic plasticity is not extravagant. Fast synaptic processes, which are quite difficult to study experimentally, have nevertheless been the subject of great interest in recent years.

The chief novelty in this model is not a mere change of format of knowledge representation, with a possible gain in storage capacity. More important is the specific constraint on brain states, which is associated with the dynamics: preferred (i.e., low energy) states, which were termed patterns, are topologically organized. Although this may seem paradoxical, it is precisely this constraint which gives the model its potential richness, namely pattern dynamics suited for flexible hierarchical build-up.

In conventional approaches, construction of higher-level symbols from lower-level ones is boolean. Consider for instance the cell assembly notion of Hebb (1949). If p cell assemblies are given, one may combine them in various ways, following essentially the rules of boolean logic. This is also very clear in Hopfield's modern formulation of Hebb's cell assembly model: the fundamental operation in memory storage is association.

Boolean logic certainly is an important aspect of brain function. Many recent advances in computational vision provide examples of successful use of the algorithmic approach, particularly in low-level vision. Yet we believe that this framework is in many cases insufficient: if an object is made out of p sub-objects, we often need to know how the p sub-objects relate to each other in the object. Devising an appropriate format for representing relational information is indispensable in a model which attempts to account for generalization, one of the most striking properties of our cognitive apparatus. The present model therefore offers an alternative way of combining sub-objects: sub-objects are assembled in topologically defined patterns. They may in fact be arranged according to many different topologies. In this sense, hierarchical build-up is more flexible here than in the boolean approach.

In our approach, pattern dynamics, briefly described in §5, is one of the fundamental operations in neocortex. This dynamics is used in many different forms in order to handle appropriately different types of patterns. In particular, the different modalities of interaction with the environment (vision, audition etc) impose different types of constraints on patterns. This requires the development (phylogenetic and ontogenetic) of dedicated modules with appropriate architectures, particularly at peripheral levels, as well as of control modules for regulating the different processes (switching on and off short-term plasticity, setting the parameters such as temperature, strength of competition etc).

We give an example of a problem involving simple representation of knowledge at the end of §5: a pattern has to be recognized from its local features, in an "invariant" way. Perceptron-like models, based on boolean combinatorics, behave very poorly in this task. The solution we propose, along the lines of our self-organizational approach, uses a strictly minimal architecture. It illustrates our claim that topological rules for assembling symbols can be more relevant than logical ones.

In §2, two alternative formulations of connectivity dynamics were proposed, based on two different Hamiltonians: H', corresponding to fast dynamics; and H", corresponding to slow dynamics. Both dynamics are important, and nature probably uses intermediate forms in most cases. Perception and other cognitive processes take place on a fast time-scale: reaction times typical of these processes are of the order of a second or slightly less.

It was however seen in §5 that minima of H' are less organized than

minima of H". This may at first sight have unpleasant consequences on pattern dynamics. For example, since the minima of H' have 1-dimensional circular connectivity, homeomorphisms between patterns can be produced in the pure fast dynamics only under the quite restrictive assumption that the patterns in question are 1-dimensional. This is of course not a real problem, since the form of H'-minima was shown to be an "artefact", linked to the spin space. X-Y spins were chosen here only for the sake of simplicity. In reality, the second-order statistics of a multiple spike train have many more degrees of freedom than a low-dimensional spin configuration, and these degrees of freedom can be fully exploited in the dynamics of patterns of dimension higher than 1.

H"-dynamics is necessary in order to shape, or prepare, the permanent connectivity on a slow time-scale, i.e., create in it patterns. It is vital that permanent connectivity be prepared for the interaction with the sensory information: the role of H"-dynamics is the creation, updating, and rearrangement of a repertoire (Edelman 1978) of patterns. In the fast dynamics, competition, which is set by the parameter p in F(w), is much stronger: fast pattern dynamics results in the selection of one pattern out of the competing superimposed stored patterns, according to the pattern selection rules of §5. Slow dynamics on the other hand tolerates the coexistence of many different patterns. Our model is thus clearly related to the selective or "darwinian" approach to brain function (Edelman 1978; Changeux et al. 1984). It relies on selection mechanisms on both the slow time scale (learning, shaping of patterns in the repertoire), and on the fast time-scale: perception, recognition, and in general any manipulation of "mental objects" (Changeux 1983).

Our model uses hamiltonian dynamics. A hamiltonian function is a convenient device: associated with it are the notions of thermodynamic equilibrium at finite temperature, and of asymptotic convergence to optimal states (minima of the Hamiltonian) at 0-temperature or using the annealing process (Kirkpatrick et al. 1983). It is important to stress that the assumption of symmetry of the synaptic interaction matrix w is an absolute prerequisite for being able to define a hamiltonian function. This assumption is of course very far from being realized in the CNS. In this sense, the model is a dramatic simplification. Yet it is reasonable to expect that more realistic non-hamiltonian dynamics would leave unaffected our main result, namely the topological character of organized connectivity states. Organization of activity should however be different: one should expect travelling activity waves, in the topology of the associated connectivity state, rather than standing correlation patterns. Incorporating synaptic delays in the model would then allow us considering temporal patterns, as well as sequential aspects in the handling of spatial patterns, which were ignored in the present paper.

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# NEURAL CONNECTIVITIES: BETWEEN DETERMINISM AND RANDOMNESS

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## 1. THE BRAIN AS A MACRODYNAMIC SYSTEM

When studying the structure and function of the brain using theoretical methods from macrodynamics it is necessary to emphasize two concepts: cooperation and hierarchy. It is often found that the properties of a system composed of many elements and subsystems are not those that would be expected from a simple superposition of the properties of the individual subsystems (at least according to the non-reductionist point of view). Interaction between the subsystems can lead to completely new characteristics and may produce temporal and spatial patterns on a macroscopic scale in an entirely self-organizing way (e.g., Haken, 1980).

Neural systems can be studied at different levels (e.g., molecular, membrane, cellular, synaptic, network or system levels). Mathematical models of the behavior over time of dynamical systems can be classified into two groups: single-level models and multi-level (hierarchical) models. The concept of the state space derived from the theory of mechanics and thermodynamics and generalized in mathematical systems theory (Kalman et al. 1969) can be useful in describing single-level phenomena. State-space concepts and the related single-level models are appropriate if all the information obtained by measurement and/or to be explained by the model refers to the same level of the morphological and functional hierarchy.

A brief classification of the different neural levels from the point of view of their dynamic behavior is given in Table 1.

Two types of dynamic models are commonly used:

1. When studying changes in the activity of the brain, the state of connectivities is usually considered to be constant.
2. Learning rules describing the influence of activity patterns are deduced from assumed changes in the organization of the neural network.

Technically speaking, the dynamical theory of neural systems represents a special chapter in the theory of dynamical systems. A number of models for neural dynamical phenomena have been proposed (e.g., Grossberg, 1980; Amari and Arbib, 1982; Levine, 1983), and certain particularly interesting phenomena (e.g., oscillatory behavior, chaos, travelling wave solutions, solitary waves, spatial pattern formation) have received considerable attention.

It is possible to take the view that neural connections are neither the result of some rigid deterministic mechanism, nor the eventual outcome of some random series of events. A possible resolution of the deterministic-

TABLE 1 Classification of the dynamical behavior of different neural levels.

| Levels | State variables | Dynamic laws |
|---|---|---|
| Molecular | Chemical composition | Reaction kinetics |
| Membrane | Membrane voltage<br>ionic conductance | Hodgkin-Huxley equations |
| Cellular | State of activity < "all-or-none" instantaneous spike frequency | McCulloch-Pitts<br>Equations for potential spreading |
| Synaptic | Strength or efficacy | Elementary learning rules |
| Network | State of connectivity < "all-or-none" synaptic strength | Learning rules |
| System | | Hierarchical models |

randomness dilemma will be provided by the principle described as "randomness in the small and structure in the large" (Anninos et al., 1970; Harth et al., 1970). The spirit of this principle accepts the existence of stochastic effects in the brain, but allows for "averaging out" of the fluctuations (e.g., Geman, 1980). More technically, the evolution equations at the population level are assumed to be deterministic, while the equations at the single-neuron level may have some random character (Holden, 1976).

From the point of macrodynamics, it is now clear that in certain situations (e.g., in the neighborhood of points of instability) the effects of fluctuations cannot be averaged out. On the contrary, they may be amplified and cause dramatic effects at even the macroscopic level. The point we want to emphasize in connection with the deterministic-stochastic question is that fluctuations (noises) superimposed on deterministic laws can have a crucial role in forming ordered structures. According to the theory of "noise-induced transitions" (Horsthemke and Lefevre, 1984), the fluctuations may operate as "organizing forces". In somewhat more technical terms, noises may cause the deterministic attractors to become unstable so that a stochastic model might exhibit properties which are qualitatively completely different from those of its deterministic counterpart.

Some general remarks on noise-induced ordering are given in Section 2., and problems in modeling the formation of ordered neural mappings are discussed in Section 3. Section 4. describes the framework of a model based on the idea of activity-dependent modifiable synapses and gives a short analysis of the model using simulation experiments. Finally, the main points of the discussion are summarized in Section 5.

## 2. NOISE-INDUCED ORDERING: GENERAL REMARKS

The state of many macroscopic systems can be characterized by a finite-dimensional vector $C(t)$ at a fixed time $t$. The behavior of such a system over time can be described by ordinary differential equations of the form

$$\dot{C}(t) = f(C(t),t,\lambda).$$

These equations may include explicit time-dependence. The function f also depends on a set of control parameters, and $\lambda$ is assumed to be a scalar quantity. Whatever our definition of the vague concept of "environment", it is plausible to postulate that it has a random character. More precisely, the influence of the fluctuating environment on the macroscopic properties of the system can be taken into account via the control parameter $\lambda$. The deterministic control parameter can be replaced by a stationary stochastic process. This means that the state variable and the evolution equation also assume a stochastic character (see Table 2).

TABLE 2 Comparison of deterministic and stochastic models.

| | Deterministic | Stochastic | Comments |
|---|---|---|---|
| State variable | $C(t)$ | $\hat{C}(\omega,t) \equiv C_t : (\Omega,A,P) \rightarrow (R,B)$ | Definition of random variable |
| Control parameter | $\lambda$ | $\lambda_t := \lambda + \sigma\xi_t$ | Gaussian white noise |
| Forcing function | $f(C(t),t,\lambda)$ | $h(C_t,t) + \lambda g(C_t,t)$ | f is linear in $\lambda$ |
| Evolution equation | $\dot{C}(t) = f(C(t),t,\lambda)$ | $\alpha C_t = \left[h(C_t,t) + \lambda g(C_t,t)\right]dt + \sigma g(C_t,t)\,d\omega_t$ | Derivation of stochastic differential equations |

The distribution function or probability density provides a characterization of the random variable which is sufficient for most practical purposes, while the shape of the probability density function provides a qualitative characterization of the system. If the effect of the environmental fluctuation depends on the state of the system, the qualitative properties (e.g., the modality) of the probability density function can be modified by increasing the environmental noise, as illustrated in Fig. 1 for the Verhulst model and the model of genic selection (Horsthemke and Lefevre, 1984).

These examples illustrate transitions corresponding to situations in which the system responds actively to the influence of fluctuations in the environment.

## 3. ONTOGENESIS OF ORDERED NEURAL CONNECTIONS: SOME DICHOTOMIES

Several alternative models of the formation of topographical mappings between different parts of the nervous system (e.g., the retina and tectum) have been proposed. These models could be summarized within the framework of a set of dichotomies (Érdi and Barna, 1984), which is summarized briefly below.

(a) "Pre-programmed" postsynaptic sheet versus fiber-induced mechanism. The classical work of Sperry (1943) proposes a point-to-point projection between retina and tectum. However, plasticity experiments suggest that the other extreme is at least worthy of theoretical consideration.

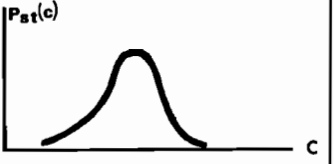
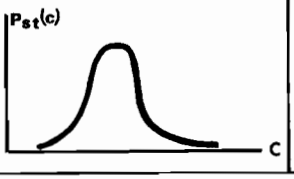
| MODEL | DETERMINISTIC | THE SHAPE OF THE PROBABILITY DENSITY FUNCTION FOR | |
|---|---|---|---|
| | | $\delta < \delta cr$ | $\delta > \delta cr$ |
| VERHULST | $C(t) = -C^2(t) + \lambda C(t)$ |   |   |
| GENIC SELECTION | $C(t) = \alpha - C(t) + + \lambda C(t)(1-C(t)); C \in [0,1]$ |   |   |

FIGURE 1 Noise-induced transitions for the Verhulst model and the model of genic selection.

(b) Genetically-specified versus environmentally-controlled wiring. The information content of the genome seems to be insufficient for topographical maps. It appears that the connections between specific cells are not preprogrammed, but a genetically-controlled algorithm selects the best system connections.

(c) Marker theories versus activity-dependent mechanisms. In the original version of Sperry's hypothesis, each retina cell was labelled with a unique chemical marker and the complementary marker on the tectal neuron identified by some "molecular recognition" mechanism. Alternatively, neural development, learning and conditioning could be explained in terms of modification of synapses by correlated activity at the pre- and postsynaptic cells.

(d) Decrease in synaptic strength due to global rule or to local selection mechanism. According to the global rule given by von der Malsburg (1973), the sum of the synaptic strengths exerted on a cell must always be constant. However, physiological experiments (Singer, 1979) suggest that some local mechanism is responsible for the decrease in synaptic strength. A "weakening rule" has been put forward (Hirai, 1980): the greater the contribution from the synapse to the output of the postsynaptic cell, the smaller the weakening of the synapse.

(e) Deterministic versus stochastic models. "Whenever he is looking at any piece of neural tissue, the investigator becomes immediately confronted with the choice between two conflicting issues: the question of how much of the intricate wiring of the neuropil is strictly predetermined by some genetically prescribed, and how much freedom is left to chance within some secondary mechanism of trial and error, or selecting connections according to necessities or the individual history of animal. Even on brief reflection one has to arrive at the conclusion that the case may not rest on their extreme..." (Szentágothai, 1978).

In the model presented in the next section a noise term is superimposed on the originally deterministic learning rule. The deterministic and stochastic models lead to qualitatively different structures.

(f) Set of discrete nerve cells versus continuous neural fields. Most models make the "discrete neural network" assumption which is convenient for digital simulation experiments. Although we acknowledge the mathematical superiority of the analytical approach, we recognize the necessity, at least for the time being, of simulation experiments.

(g) Positional information transmitted by concentration gradient or by wave. The general nature of the positional information is not known. The concept used in our model, i.e., "noise-induced ordering", does not need any artificial condition for obtaining correctly positioned connections, since the establishment and stabilization of ordered structures are direct consequences of the model.

## 4. FORMATION OF ORDERED NEURAL CONNECTIONS: A MODEL

We shall investigate the formation of an ordered mapping between two one-dimensional arrays of cells. Let k and l be the length of the presynaptic and postsynaptic chains, respectively and $m \in \mathbb{R}^k$ and $a \in \mathbb{R}^l$ denote the pre- and postsynaptic activity vectors. The activity of the presynaptic chain is determined by unstructured stimuli: a randomly selected element of the vector m takes the value $k_1$; all of the other elements are 0. The activity of the postsynaptic chain is described by a simple evolution equation; activity increases with the transfer of "presynaptic information" and decreases according to the first-order decay process

$$a_j(t+\Delta t) := a_j + k_2 \sum_{i=1}^{k} s_{ij}^{IV}(t) \cdot m_i(t) - k_3 \cdot a_j(t) \qquad j = 1,\ldots,l$$

where the asterisk denotes the previous time instant (the discrete time approach is used).

Synaptic strength can be modified in three different ways:

(i) Modification caused by activity patterns:

$$s_{ij}^{III} := s_{ij}^{II} + k_4 \cdot m_i \cdot a_j - k_5(m_i - s_{ij}^{IV} \cdot a_j).$$

This takes into account the Hebb rule (Hebb, 1949) as well as selective decreases.

(ii) Modification caused by the effects of immediate neighbors:

$$s_{ij}^{II} := s_{ij}^{III} + k_a((s_{i-1,j}^{III} + s_{i+1,j}^{III})/2 - s_{ij}^{III}); \qquad \begin{matrix} i=2,\ldots,k-1 \\ j=1,\ldots,l \end{matrix}$$

$$s_{ij}^{II} := s_{ij}^{III} + k_b((s_{i,j-1}^{III} + s_{i,j+1}^{III})/2 - s_{ij}^{III}); \qquad \begin{matrix} j=2,\ldots,l-1 \\ i=1,\ldots,k \end{matrix}$$

(The equations refer to a general element ij; boundary elements naturally have a different modification rule, which is neglected here for the sake of simplicity. Anisotropy ($k_a \neq k_b$) between rows and colums could also be taken into account.)

(iii) Modification as the result of normalization procedure

$$S^{I}_{ij} := \frac{S^{II}_{ij}}{(l/k)^{\frac{1}{2}} \sum_{n=1}^{k} S^{II}_{nj}}; \qquad \begin{matrix} i=1,\ldots,k \\ j=1,\ldots,l \end{matrix}$$

(for rows)

$$S^{I}_{ij} := \frac{S^{II}_{ij}}{(k/l)^{\frac{1}{2}} \sum_{n=1}^{l} S^{II}_{in}}; \qquad \begin{matrix} i=1,\ldots,l \\ j=1,\ldots,l \end{matrix}$$

(for columns).

Simulation experiments can be carried out with both deterministic and stochastic "learning rules". In the latter case superimposed noise is also taken into consideration:

$$S_{ij} := \max(0, S^{I}_{ij} + \xi \cdot k_6); \quad i=1,\ldots,k; \quad j=1,\ldots,l$$

(Note, however, that even in the case where $k_6 = 0$ the model is not completely deterministic since this presynaptic activity is inherently random in character.)

Both normal development and plastic rearrangement of the projections have been simulated by iterating the modification loop. "Deterministic" simulation experiments ($k_6 = 0$) suggest that the system has at least two locally stable attractors. Topographic order requires that the S matrix should be near-diagonal; Figures 2 and 3 illustrate the coexistence of local topographic and "antitopographic" order. The inclusion of noise implies the establishment of topographically ordered connections (Fig. 4).

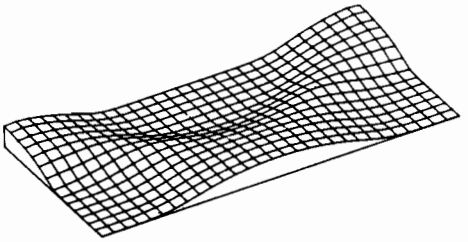


FIGURE 2 Attractors reflecting the coexistence of topographic and anti-topographic mappings.

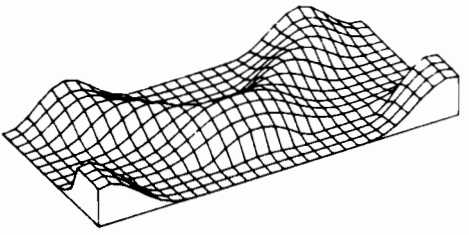


FIGURE 3 Attractors reflecting the coexistence of topographic and anti-topographic mappings.

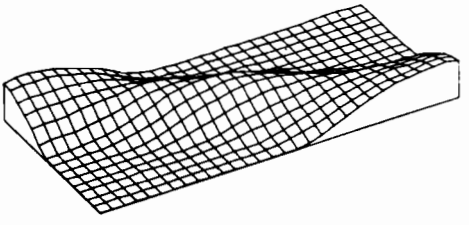


FIGURE 4 Representation of topographically observed corrections.

This model is also capable of describing the plasticity of the adult retinotectal connections. After partial retinal lesions the remaining optic axons can expand their area of termination in the tectum. Moreover, after partial tectal lesions the entire population of optic terminals can be compressed within the remaining tectal area (Udin, 1977).

## 5. DISCUSSION

This work was motivated by two ideas. Firstly, numerous neurobiological phenomena (such as synaptogenesis, the existence and relative stability of repetitive structures and ordered connections, the plasticity of the brain and its components, the dynamic behavior of neural nets) suggest that the brain could be considered as a self-organizing system (Szentágothai, 1984).

A rather new concept from theoretical physics, namely "noise-induced transition", provided the second motivation. Contrary to previous beliefs, it seems that noise might play an important constructive role in the organization of ordered structures. The superposition of noise might change the qualitative behavior of a deterministic system, in particular the nature of the attractors. In the light of results obtained in the theory of noise-induced transitions, the often used, but ill-defined, term "self-organization" might assume a more precise meaning. An improved theory of self-organizing systems would provide a useful theoretical framework for the interpretation of dynamic neural phenomena.

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# ON SOLITARY WAVES IN BIOLOGY

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## 1. INTRODUCTION

How do biological systems process information, and especially information of logical type (integers, yes/no decisions)? One small aspect of this general topic is the question of how biological systems deal with "long-distance" communication (from one end of the organism to the other). This is one of the functions of the nervous system: nerves are able to carry spikes for distances which are very large on the cellular scale (the axons on which "spikes" travel are the only known examples of such long cells or cell components).

Looking closely at these spikes, one sees that they are waves of a special type: they always have the same shape and speed. Of course, some fluctuations do exist, but these waves are very different from sound waves (for example), which can take any shape. This shows that the information transmitted by a spike must be of logical type: yes/no, "is there a spike or not?".

Waves of this type (which are restricted to a certain shape and can travel alone) are also found in some physical systems, where they are called *solitary waves*. The most well-known example is the Korteweg–de Vries solitary wave, which travels along water channels. However, it seems that most of the solitary waves found in physics behave differently to nerve impulse spikes, and there are good reasons to distinguish between the "hyperbolic" solitary waves which appear mainly in physics and the "parabolic" solitary waves which appear mainly in biology.

One of the purposes of this paper is to present some ideas which could justify this classification. In actual fact we do not yet have precise definitions of hyperbolic and parabolic solitary waves, but we hope to clarify what these definitions could be.

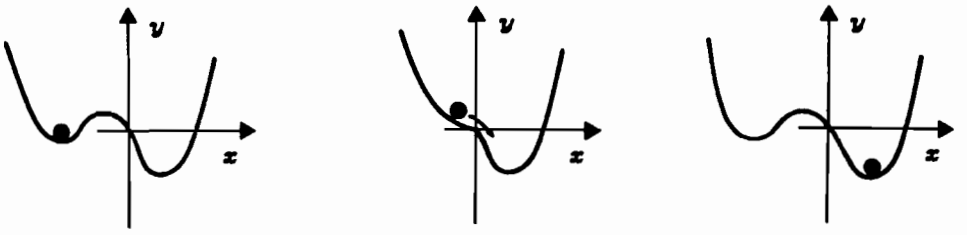
We shall first summarize the most important phenomenological differences between Korteweg–de Vries (KdV) solitary waves (which we shall take as a typical example of hyperbolic solitary waves) and nerve impulse spikes (which we shall consider as a typical example of parabolic solitary waves). The KdV can have *any* speed; the shape of the wave depends only on its speed; and two KdVs can cross with some interaction. By contrast, spikes have both a given speed and a given shape; two spikes travelling on the same axon in opposite directions destroy each other when they meet (although this can only happen in an experimental situation – in living organisms all spikes move along the axon in the same direction).

The mathematics of KdV solitary waves has received considerable attention; there has also been some work on the mathematics of spikes (e.g., the Hodgkin–Huxley equations [9], or the Fitzhugh–Nagumo simplified system [10]). What we wish to emphasize is the *epidemic* aspect of the propagation of parabolic solitary waves, i.e., the close connection that they seem to have with a special type of equilibrium which we shall call the *H-equilibrium* (where H stands for health).

## 2. H-EQUILIBRIUM AND EPIDEMIC PROPAGATION

### Equilibrium and memory: hysteresis

A quick review of simple logical memory theory leads to the greatly simplified hysteresis model (an elementary example from catastrophe theory) shown in Figure 1.




$-\lambda^* < \lambda < +\lambda^*$ $\lambda^* < \lambda$ $-\lambda^* < \lambda < +\lambda^*$

**Figure 1.** A simple hysteresis model of logical memory. Here the equation of the curve could be $y = x^4 - x^2 - \lambda x$ with $\lambda^* = (8/27)^{1/2}$.

The ball is assumed to move under gravity with a damped velocity. It therefore remains in a trough on either the left- or right-hand side as long as $\lambda$ lies in the interval $I = (-\lambda^*, +\lambda^*)$.

However, if the parameter $\lambda$ varies slowly, the ball will eventually move from one side to the other as $\lambda$ leaves $I$. Thus, if $\lambda$ lies in $I$ for most of the time, the ball acts as a memory: it stays on the side (left or right) where it came to rest after $\lambda$ last strayed outside $I$.

### H-equilibrium

The preceding example seems to use a minimal number of features to model memory: two stable equilibria (left and right) representing the states of the system, and the ability to move between them. This could give the impression that a more simple model could not be used for this purpose, although we shall show that this does not in fact seem to be the case. We shall now investigate a globally stable unique equilibrium situation which (as shown later in this section) seems to be the most elementary prime mover in parabolic wave propagation.

Let us first have a look at the concept of health and the dynamics associated with it. A greatly simplified description of health could be the following: $H$ (health) is a stable equilibrium; in the standard case death can only result from a high-level exogenous perturbation. However, the stability basin $B$ of $H$ has a peculiar feature: there is a surface $S$ which indicates the threshold of illness (see Figure 2). Starting near $H$ you always come back to $H$ quite soon; but if some exogenous perturbation forces you across $S$ then you become ill, and you start a long journey, the disease, which brings you back to $H$ only after some considerable time has elapsed (we shall not consider fatal diseases here).

The arrows in Figure 2 indicate trajectories (or parts of trajectories). The large circle represents the boundary of the stability basin; the small semicircle represents the illness threshold. Starting to the left of $S$ you come back to $H$ quickly, while starting to the right of $S$ you return to $H$ only after a long trip. At the beginning of this trip (i.e., at the beginning of the disease) things go badly (fever increases, etc.): this is because the trajectory is moving away from $H$. The trajectory does not move toward $H$ (i.e., recovery) until the trip nears its conclusion.

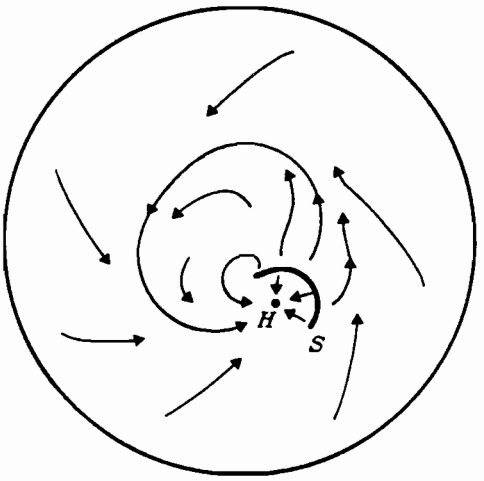



**Figure 2.** A simple model of health and disease.

We shall describe such a situation as an *H-equilibrium*: it is locally stable, globally stable, and "excitable", i.e., there is a threshold above which small perturbations start trajectories which move away from $H$ before returning to it.

**H-equilibrium and the saddle knot bifurcation**

A possible mathematical treatment of H-equilibrium comes from its similarity with the saddle knot bifurcation. Recall that this bifurcation (which is as generic as the *Hopf bifurcation*) consists in the mutual destruction (when some parameter changes) of a stable equilibrium by an unstable equilibrium (see Figure 3).

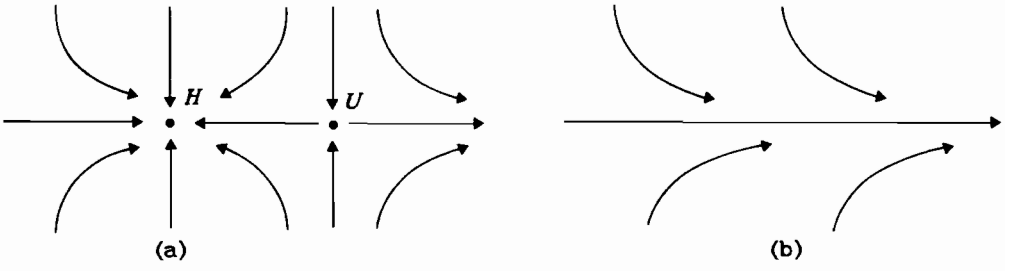



**Figure 3.** (a) $\lambda < \lambda^*$. In this case the knot $H$ is a stable equilibrium and the saddle $U$ is an unstable equilibrium. (b) $\lambda > \lambda^*$. In this case no equilibrium exists: $H$ and $U$ have destroyed each other.

An example of the situation illustrated in Figure 3 in two dimensions (the phenomenon can occur in any dimension) is given by the following:

$$\dot{x} = x^2 + \lambda$$

$$\dot{y} = -y$$

with $H = (-\sqrt{-\lambda}, 0)$, $u = (\sqrt{-\lambda}, 0)$ if $\lambda < \lambda^*$ and $\lambda^* = 0$.

Suppose now that this local bifurcation dynamics is contained in a domain $D$ which is the global stability domain for the equilibrium $H$: we then obtain the situation illustrated in Figure 2 (where the threshold surface corresponds to the

"vertical" trajectories converging to $U$ in Figure 3). An example of this in two dimensions is given below (using complex number notation):

$$z = \rho e^{i\vartheta}$$

$$\dot{z} = z\,(f(\rho) + ig(\vartheta)) \quad ,$$

where the given functions $f$ and $g$ have the shapes illustrated in Figure 4.

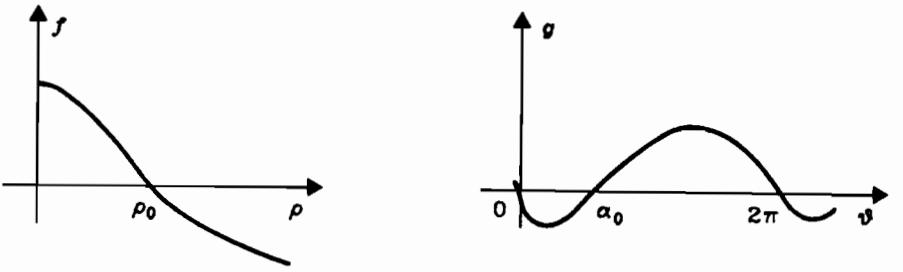



**Figure 4.** The shapes of the functions $f$ and $g$.

The resulting dynamics in the phase plane $\mathbf{R}^2 \cong \mathbf{C}$ are shown in Figure 5.

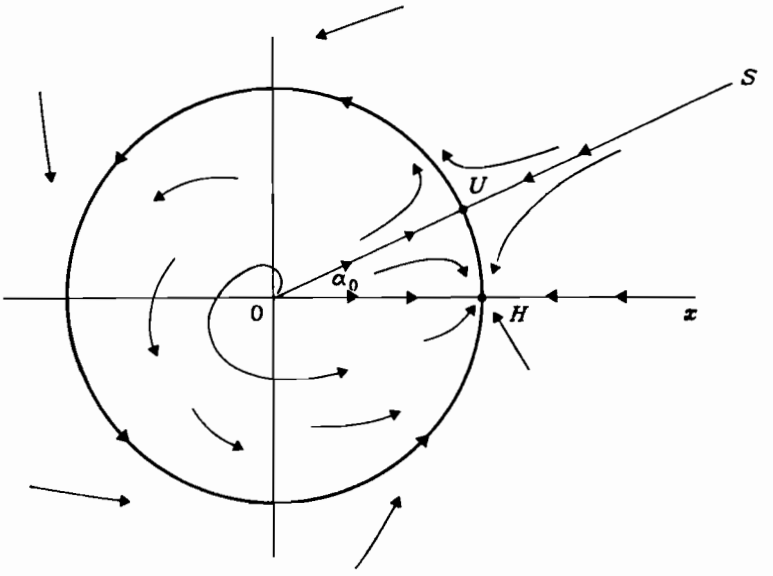



**Figure 5.** The dynamics in the phase plane $\mathbf{R}^2 \cong \mathbf{C}$.

The line $0S$ in Figure 5 plays the same role as the threshold surface $S$ in Figure 2. The angle between $0x$ and $0S$ is $\alpha_0$ (see $g$ in Figure 4). In this case the domain of stability of the equilibrium $H$ is the whole plane (ignoring the threshold line $0S$). The circle has radius $0H = \rho$ (see $f$ in Figure 4).

In this example it can be seen that if $\alpha_0$ goes to zero, $U$ and $H$ will destroy each other and a periodic trajectory will appear. This feature is not unique to this example, being present in any H-equilibrium – if $H$ moves to the threshold surface $S$ (see Figure 3), it is destroyed when it reaches $S$ and a periodic trajectory appears.

This provides an explanation of the appearance of oscillations which is different from the Hopf bifurcation: in this scheme the periodic trajectory is large when it first appears, while in Hopf bifurcation the periodic trajectory is initially small. These comments are due to P. Kepper and C. Lobry, and are developed and applied to chemistry in [4,6].

**Epidemic propagation**

Let us now combine many "individual" H-equilibria assuming (contiguous) spatial correlation between individual dynamics. To understand what comes out of this combination, we shall return to our first example of the H-equilibrium, namely health.

If some external perturbation starts an *infectious* disease, then at the beginning the disease "blows up" and the number of infectious germs grows by several orders of magnitude: this means that the sick person *can contaminate* others in his neighborhood. These may then contaminate other people in their neighborhoods and thus an epidemic can occur. However, the purpose of this is not to explain epidemics, but to use this example to understand what happens when we have an H-equilibrium plus neighborhood diffusion. Note that when the epidemic has passed, when individuals are healthy again, everything seems to be as it was before (we shall forget for the moment that after having the disease the victims are usually immune and therefore cannot have the same disease again). We can learn from this example that the epidemic travels like a solitary wave of parabolic type (see Section 1), i.e., two waves of the same disease disappear where they meet (destroy each other).

It seems to us that the above example is typical of the phenomena involved in parabolic solitary waves: for example, nerve impulse spikes propagate in the same way as an epidemic (on the part of the axons where there is no myelin) – the same is true of the contraction of the cardiac muscle. We will come back to the mathematical side of this question in the final section.

Note finally that individuals have some physical "memory" of their diseases: they usually cannot have the same disease twice. Hence they do not really return to the same equilibrium $H$ from which they set out: they go from $H_1$ to $H_2$, where the indices show that the state of health is not the same in the two cases. This leads us back to the first model in this section, which had two equilibria, i.e., memory (see Figure 1). Note that the individual dynamics shown in Figure 1 combined with diffusion (contamination) leads to a type of wave propagation which has been widely studied and appears to be closely connected to epidemic wave propagation – we will return to this point in the next section.

## 3. SOME RELATED PARTIAL DIFFERENTIAL EQUATIONS

We shall now give some partial differential equations and systems which provide a mathematical background to the arguments presented in Section 2.

**Wave front propagation**

The dynamics of the ball in Figure 1 could (for example) be described by

$$\dot{x} = f(x) \quad ,$$

where $f : \mathbf{R} \to \mathbf{R}$ is defined by

$$f(x) = -4x^3 + 2x + \lambda$$

and $\lambda$ is a fixed parameter (see Figure 6).

Let us now combine these dynamics with diffusion. We obtain the Kolmogorov equation:

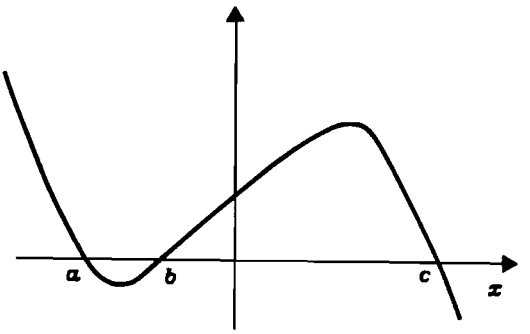



**Figure 6.** Graph of the function $f(x) = -4x^3 + 2x + \lambda$. Here $a$ and $c$ are the two stable equilibria and $b$ the unstable equilibrium (see Figure 1).

$$u_t = u_{zz} + f(u;\lambda) \quad , \tag{1}$$

where $u(t,z)$ is a real-valued function of a time variable $t$ and a space variable $z$ ($u_t = \partial u / \partial t$, $u_{zz} = \partial^2 u / \partial t^2$; recall that $u_t = u_{zz}$ is the heat diffusion equation and $u_t = f(u,\lambda)$ is the dynamics given above).

System (1) has been studied quite widely (see, for example, [11], and the bibliography therein). In particular, it has been shown that if the range of the space variable $z$ is the real line $\mathbf{R}$, there is a unique solution $u$ of (1) which is a travelling wave front:

$$u(t,z) = h(z - vt) \qquad \forall z,t \geq 0 \tag{2}$$

$$\text{with } h(-\infty) = c \ , \ h(+\infty) = a \quad ,$$

where the constant $v$ is the speed of the wave, and $h$ is the shape of the wave. A typical $h$ is shown in Figure 7.

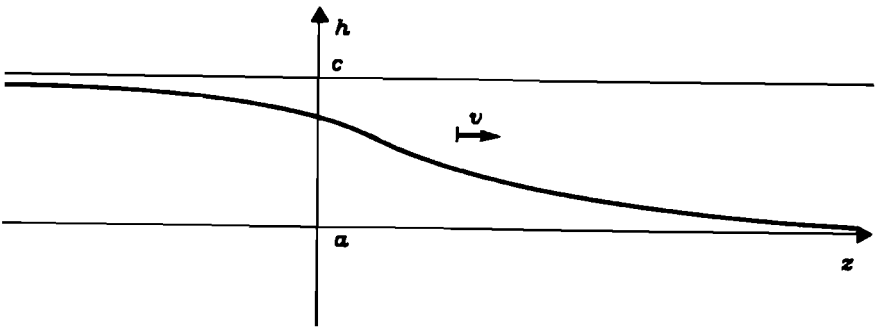



**Figure 7.** A typical $h$.

It can also be shown that for any initial data $u_0(z) = u(0,z)$ such that $u_0(-\infty) = c$, $u_0(+\infty) = a$, the solution $u$ of (1) will converge uniformly to the travelling motion $h(\cdot - vt - t_0)$ when $t \to +\infty$.

**Epidemic wave propagation**

Let us now replace the hysteresis dynamics by the H-equilibrium dynamics (combined with diffusion). We obtain (compare with (1))

$$y_t = y_{zz} + \varphi(y) \quad . \tag{3}$$

where $y$ is a function of time variable $t$ and of the space variable $z$ with *values* $y(t,z)$ in the two-dimensional plane $\mathbf{R}^2 \cong \mathbf{C}$ and where the function $\varphi$ from $\mathbf{R}^2$ into itself is (for example) the H-equilibrium dynamic given (in complex number notation) by:

$$\varphi(\rho e^{i\vartheta}) = \rho e^{i\vartheta}(f(\rho) + ig(\vartheta)) \tag{4}$$

(see Figure 4 for functions $f$ and $g$).

The mathematical behavior of the quasilinear parabolic system (3) with nonlinearity (4) is not at all well-understood.

The heuristic discussions on epidemic wave propagation in Section 2 lead to many natural conjectures about system (3–4). Some of these conjectures have been stated in [7], and some results proved by Barrow and Bates. However, many conjectures still remain open. We shall now give some typical examples.

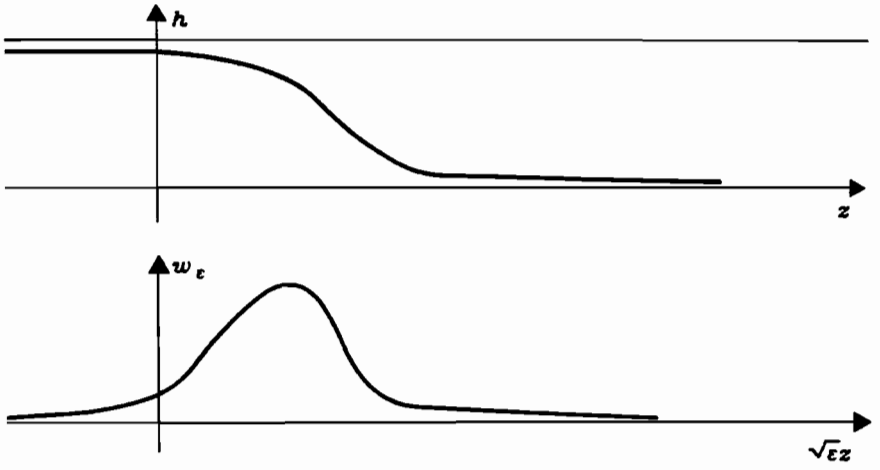



**Figure 8.** $u_\varepsilon$ has two coordinates, $v_\varepsilon$ and $w_\varepsilon$. From (5), we have $w_\varepsilon \cong \alpha \sin\vartheta + \beta$. If we take the travelling solution $h$ of the Kolmogorov equation (Figure 7) for $\vartheta$, the above forms are obtained.

Suppose that the functions $f$ and $g$ are as shown in Figure 4. Suppose also that the derivative $f'$ satisfies $f' \leq -1$, and that $|g'|$ is sufficiently small. Let the range of the space variable be the real line $\mathbf{R}$ and the initial data $u_0$ ($u_0(z) = u(0,z)$ $\forall z \in \mathbf{R}$) satisfy

$$u_0(-\infty) = u_0(+\infty) = H = (\rho_0, 0) \quad \text{(see Figure 5)}$$

$$|u_0(z_0)| = \rho_0 \quad \forall z \in \mathbf{R}$$

$$|du_0/dz| \text{ is sufficiently small} \quad .$$

Then there exists a function $h : \mathbf{R} \to \mathbf{R}$ and a constant $v$ such that $h(-\infty) = h(+\infty) = H$ and

$$u(t,z) \to h(z - vt) \text{ when } t \to +\infty$$

(uniform convergence); and such that $h$ and $u_0$ have the same index with respect to the origin in $\mathbf{R}^2$ (see Figure 5).

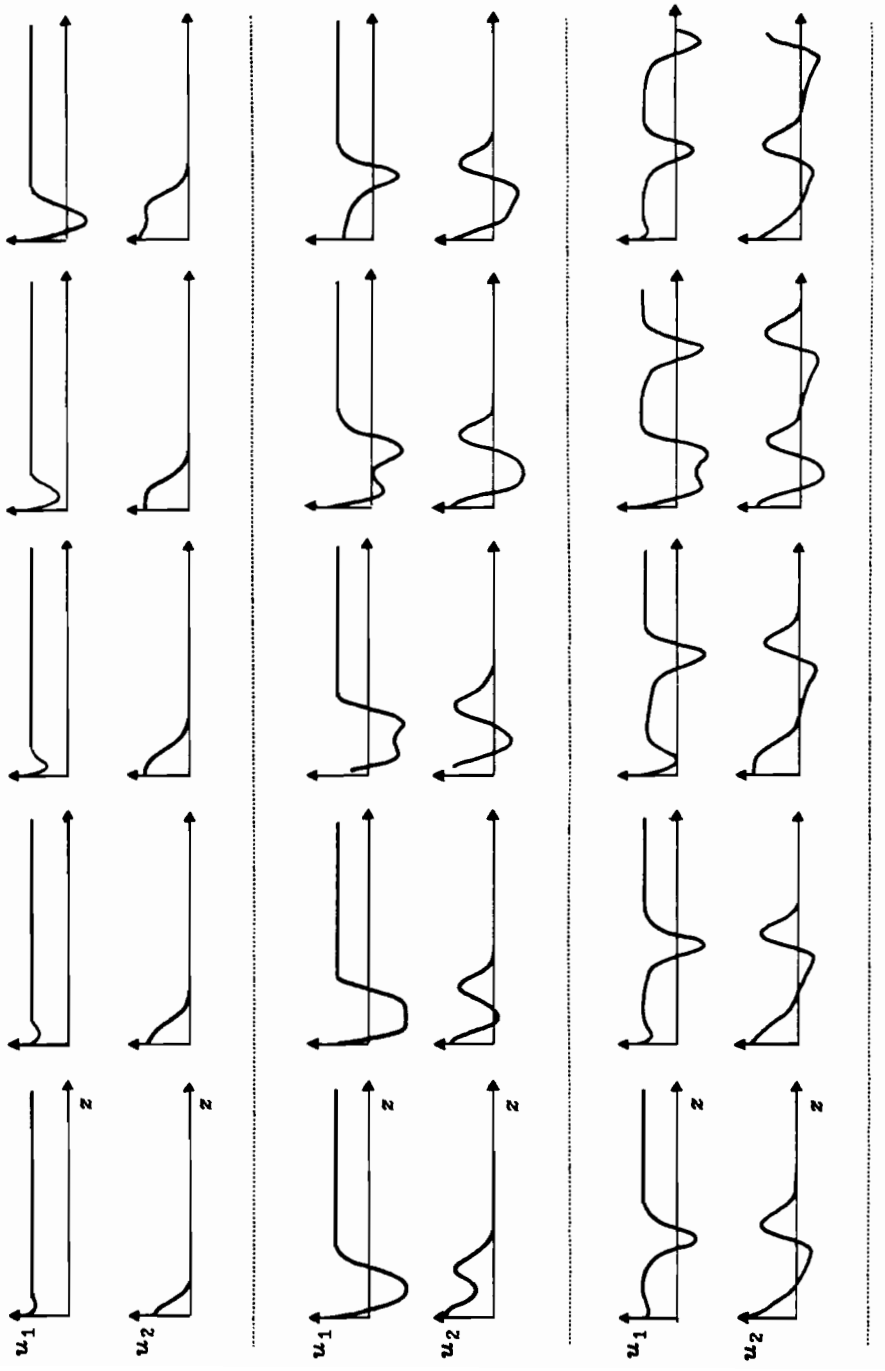



**Figure 9.** Results of the numerical simulation.

The function $h$ would represent the shape and $v$ the speed of the "epidemic" travelling wave.

Another conjecture is that, if we replace $\varphi$ in (4) by $\varphi_\varepsilon$,

$$\varphi_\varepsilon(\rho e^{i\vartheta}) = \rho e^{i\vartheta}(f(\rho) + i\varepsilon g(\vartheta))$$

and let $\varepsilon \to 0$, then $u_\varepsilon$ would be

$$u_\varepsilon(t,z) \cong c_1 e^{i\vartheta(\varepsilon t, \sqrt{\varepsilon} z)} + c_2 \quad , \tag{5}$$

where $\vartheta$ would be a solution of

$$\vartheta_t = \vartheta_{zz} + g(\vartheta) \quad . \tag{6}$$

Thus we are back to the Kolmogorov equation (1). This last conjecture connects the expected behavior of (3–4) with the well-known properties of (1): from (5), a solitary wave for (3) with small $g$ would behave as a sine or cosine of the wave front $h$ in Figure 7 (see Figure 8 and the simulation in Figure 9). These conjectures seem to be quite difficult to prove although they emerge naturally from the heuristic arguments of Section 2.

Numerical simulations give the expected results (see Figure 9). Discrete systems based on the same heuristic ideas can also be shown to exhibit the expected behavior.

## 4. SIMULATION

Figure 9 gives the results of a simulation of system (3–4) with space variable $z$ in the half line $[0,+\infty)$. The initial condition is $u_0(z) = H$ for all $z$ in $[0,+\infty)$. The boundary condition at $z = 0$ is $(\rho_0, 1)$ (which means that "excitation" is maintained for all $t$ at the point $z = 0$). Time increases from left to right along each row of graphs. Each pair of graphs gives the two coordinates of $u$ as functions of $z$ (at the same fixed time $t$). The first line of graphs shows the birth of one solitary wave; the last line shows the birth of a second.

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# II. ECOLOGICAL MODELS

# PERSISTENCE IN SYSTEMS WITH DIFFUSION

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## 1. INTRODUCTION

A great part of the literature in mathematical biology has been focussed on systems governed by autonomous ordinary differential equations. For systems of order greater than two, the dynamics may be extremely complex, and in most cases it is difficult to say much about the detailed behaviour of the system. However, from a biological point of view, the fine structure of the dynamics is often not of primary interest, and probably the most important question concerns the conditions under which the long term persistence of species, genotypes etc. is ensured. This is the question that is considered here.

Very frequently persistence has been tackled by an examination of the asymptotic stability of an interior equilibrium point, although sometimes (usually without great success) attempts have been made to discover whether global asymptotic stability holds. More recently it has become apparent that neither of these techniques is really appropriate, and that they are particularly misleading when the number of equations is large, large here meaning greater than two. There are at least two good reasons for this. The first is that even in rather special systems (for example in ecological problems governed by Lotka-Volterra equations), if there are three or more equations, in addition to an asymptotically stable interior equilibrium point, there can be other asymptotically stable equilibrium points on the boundary, so that persistence will depend on the initial values. The second is that it is quite easy to produce systems with a globally attractive limit cycle. The interior equilibrium will not then be asymptotically stable, but nonetheless the system leads to persistence in a realistic biological sense. Of course, even in three dimensions for Lotka-Volterra equations, more unpleasant behaviour such as a strange attractor may occur [Arneodo et al. 1980], and these remarks will apply with even greater force.

In order to take these points into account, a number of concepts of persistence have been discussed. One of these is the idea of permanent coexistence (also called permanence, cooperativeness, ecological stability) introduced by Schuster et al. (1979) and Hofbauer (1981). The system on $\mathbb{R}^+_n$

$$\dot{u}_i = u_i f_i(u) \quad (i = 1,\ldots,n) \tag{1}$$

with $u = (u_1,\ldots,u_n)$, is said to be <u>permanently coexistent</u> if there exists a compact set $M \subset \mathbb{R}^+_n$ with $d(M,\partial\mathbb{R}^+_n) > 0$ such that every semi-orbit with initial values in the interior of $\mathbb{R}^+_n$ is ultimately in M (that is eventually enters and remains within M). This idea appears to reflect well the intuitive

concept of 'persistence', for it is truly global, while completely general behaviour is allowed in M. From a mathematical point of view this idea is also attractive, for, since it is not necessary to know the detailed behaviour of the system, it is likely that permanent coexistence will be relatively easy to establish. Indeed there is a powerful technique available for tackling this question, see (Hofbauer 1981), and this has been applied in a number of examples, (Hutson and Vickers 1983b), (Hutson 1984a), (Amann and Hofbauer 1984), (Sigmund and Schuster 1983), which are intractable by other methods, and has been extended to difference equations where really unpleasant behaviour occurs even in one or two dimensions, see (Hutson and Moran 1982),(Hutson et al 1983a).

This technique gives no information concerning M itself, except that it is at a non-zero distance from the boundary. Of course it would be interesting to know more, in particular an actual value for $d(M,\partial\mathbb{R}^+_n)$, but in most examples this raises formidable difficulties. The technique is aimed at those (rather frequent) cases where further information concerning M is difficult to obtain.

Systems of ordinary differential equations do not of course provide anything like a realistic model of the complex interactions present in nature. Three obvious directions for investigation are the introduction of time delay, non-autonomous equations with at least periodic right hand sides, and systems with spatial diffusion, and it is the last that is considered here. Of course the dynamics are more complicated than for (1), and it is therefore of particular interest to enquire whether the idea of permanent coexistence can be taken over to this case. Conway et al (1978) have shown that if the diffusion parameters are large enough, solutions of reaction diffusion systems tend asymptotically to those of the corresponding kinetic system (1), when the previously discussed theory will be applicable. It is our purpose to show here that, even when this condition does not hold, permanent coexistence may often be established by an extension of the method for ordinary differential equations. Technically, in outline the idea is to translate Hofbauer's result into a theorem on dynamical systems on a compact metric space, and to prove that there is enough compactness around in the system of partial differential equations for the result to be applicable.

## 2. PERMANENT COEXISTENCE IN A REACTION-DIFFUSION MODEL

We study here the simplest model which includes spatial diffusion effects; its derivation is discussed, for example, by Okuba (1980) and Fife (1979). Let $D = (a,b)$ be a finite interval, and let $u_i(x,t)$ be the density of the i-th species (genotype) etc) at $x \in (a,b)$ at time t. We impose a homogeneous Neuman boundary condition, which implies that there is no migration across the spatial boundary. Consider then the initial/boundary value problem for the following system:

$$\frac{\partial u_i}{\partial t} = u_i f_i(u) + \mu_i \frac{\partial^2 u_i}{\partial x^2}, \tag{2}$$

$$\frac{\partial u_i}{\partial x}(a) = \frac{\partial u_i}{\partial x}(b) = 0,$$

$$u(x,0) = u_0(x),$$

where $1 \le i \le n$. The initial value $u_0$ is taken non-negative, and it is

assumed that all $\mu_i > 0$, $f_i \in C^1$, $u_0 \in C^0$.

$\|\cdot\|$ denotes the sup norm on $C^0$. Let

$Y$ = compact neighbourhood of the origin in $\mathbb{R}^+_n$.

$X_0 = \{u \in C^0: \ u(x) \in Y \text{ for all } x \in \bar{D}\}$

$S_0 = \{u \in X_0: \ u_i(x) = 0 \text{ (all } x \in \bar{D}) \text{ for some } i\}$

The following condition is assumed throughout.

(H) Global existence and uniqueness of classical solutions hold. Also $X_0$ is forward invariant, and given $u(x,0) \in C^0$, there exists $t_0$ such that the solution $u(\cdot,t) \in X_0$ for $t \geq t_0$.

This condition is usually ensured in ecological problems of interest by virtue of the existence of intraspecific competition, (Smoller 1983, ch. 14).

Definition. The system (2) is said to be permanently coexistent if and only if there exists an $\varepsilon > 0$ such that for any $u_0$ with no component identically zero, there is a $t_1$ (depending on $u_0$) such that

$$\min_{1\leq i\leq n} \int_a^b u_i(x,t)\, dx > \varepsilon \quad (t > t_1).$$

In view of (H) it is enough for the proof of permanent coexistence to restrict attention to initial values in $X_0$.

The solutions of (2) generate a dynamical system $(\pi, X_0, \mathbb{R}^+)$, but $X_0$ does not have the required compactness. However, the following strong a priori derivative estimate may be proved using the fundamental solution.

Lemma 1. If (H) holds, there exists $m < \infty$ such that for all $u_0 \in X_0$, solutions satisfy

$$\left\| \frac{\partial u}{\partial x}(\cdot,t) \right\| \leq m \quad (t \geq 1).$$

Define

$$X = \pi(X_0,[1,\infty)), \quad S = \pi(S_0,[1,\infty)).$$

$X$ thus consists of solutions after time $t = 1$ with initial values in $X_0$, and compactness is ensured by the lemma. $S$ is forward invariant from the form of the equations, and so is $X\backslash S$ by the maximum principle; indeed $u_i(x,t) > 0$ $(x \in \bar{D},\ t \geq 0)$ for $U \in X\backslash S$.

Lemma 2. $S$ is a compact subset of the compact metric space $X$, and $X\backslash S$ is dense in $X$. The system (2) generates a dynamical system $(\pi, X, \mathbb{R}^+)$, and $S$, $X\backslash S$ are forward invariant.

Let

$ut = \pi(u,t)$, $N[0,t] = \pi(N,[0,t])$ for a set $N \subset X$,

$\Omega(u) = \Omega$-limit set of $u$, $\Omega(N) = \bigcup_{u\in N} \Omega(u)$,

$\gamma^+(u)$ semi-orbit

Definition $\gamma^+(u)$ is said to be ultimately in M if and only if there is a $t_0 < \infty$ such that $ut \in M$ for $t \geq t_0$.

We consider a function $\phi$ which may be thought of as an 'average' or 'weak' Liapunov function. For $\phi: X\backslash S \to \mathbb{R}^+$ which is continuous, bounded and strictly positive, we define

$$\alpha(t,u) = \phi(ut)/\phi(u) \quad (u \in X\backslash S),$$

$$\alpha(t,u) = \liminf_{\substack{v \to u \\ v \in X\backslash S}} \phi(vt)/\phi(v) \quad (u \in S).$$

If $\alpha(t,u) > 1$ on S, it might be expected from a Liapunov function type argument that orbits will be repelled by S. The theorem below, (Hutson 1984b), shows that this is true in a rather strong sense even if $\alpha(t,u) > 1$ only for some t, and further that this need only hold on $\Omega(S)$. The point is that only a rather limited amount of information concerning the behaviour on S, rather than on the whole of X, is needed.

Theorem 3. With $\phi$, S, X as above, assume that

$$\sup_{t \geq 0} \alpha(t,u) > \begin{cases} 1 & (u \in \overline{\Omega(S)}), \\ 0 & (u \in S). \end{cases}$$

Then there is a compact forward invariant set M with $d(M,S) > 0$ which is such that every semi-orbit in $X\backslash S$ is ultimately in M.

We now show that in many cases when permanent coexistence may be proved for the kinetic system (1), it can also be established for the reaction-diffusion system (2). The key is of course the construction of an appropriate $\phi$; for illustration we make the choice here which has been most often useful. Set

$$\phi(u) = \exp\{\int_D \log P(u(x))dx\} \quad (u \in X\backslash S),$$

$$P(u) = \prod_1^n u_i^{\alpha_i} \quad (\alpha_i \geq 0).$$

From the partial differential equations (2) and an integration by parts, if $u \in X\backslash S$,

$$\alpha(t,u) = \phi(ut)/\phi(u)$$

$$= \exp\{\int_D \log[P(u(x,t))/P(u(x,0))]dx\}$$

$$= \exp\{\int_0^t ds \int_D \dot{P}(u(x,s))/(u(x,s))dx\}$$

$$= \exp\{\int_0^t ds \int_D \sum_1^n [\alpha_i f_i(u(x,s)) + \alpha_i \mu_i (u_i^{-1} \partial u_i/\partial x)^2]dx\}.$$

The second term is non-negative, so taking the lim inf we see that the condition of Theorem 3 will hold if

$$\sup_{t \geq 0} \int_0^t ds \int_D \sum \alpha_i f_i(u(x,s))dx > 0 \qquad (3)$$

for $u(x,0) \in \overline{\Omega(S)}$. Finally, to switch from $C^o$ to the integration condition is easy because of the derivative bound of Lemma 1, and we deduce the following

Theorem 4. Under condition (H), permanent coexistence holds for the system (2) if (3) is satisfied.

If $\Omega(S)$ consists only of spatially homogeneous equilibria, (3) will hold if $\sum_i \alpha_i f_i > 0$ at each of these equilibria.

## 3. PREDATOR MEDIATED COEXISTENCE WITH DIFFUSION

With $u_1$, $u_2$ prey densities and $u_3$ the predator density, consider the system

$$\partial u_1/\partial t = u_1(a_1 - \varepsilon_{11}u_1 - \varepsilon_{12}u_2 - \alpha_1 u_3) + \mu_1 \partial^2 u_1/\partial x^2,$$

$$\partial u_2/\partial t = u_2(a_2 - \varepsilon_{21}u_1 - \varepsilon_{22}u_2 - \alpha_2 u_3) + \mu_2 \partial^2 u_2/\partial x^2,$$

$$\partial u_3/\partial t = u_3(-c + \beta_1 u_1 + \beta_2 u_2 - \gamma u_3) + \mu_3 \partial^2 u_3/\partial x^2$$

where all constants are strictly positive. The corresponding kinetic system (1) has been extensively studied because of its relevance to the problem of predator mediated coexistence, that is the introduction of a predator may allow two prey to coexist which would not otherwise do so. Necessary and sufficient conditions for permanent coexistence are known for the kinetic system (Hutson and Vickers 1983b). For the system with diffusion, the technique is to show first by a Liapunov functional method, that in each of the three two-demensional subsystems (obtained by setting $u_1$, $u_2$, $u_3 = 0$ in turn), the $\Omega$-limit set consists just of equilibrium points. It then follows from Theorem 4 that:

Theorem 5. The above reaction diffusion system is permanently coexistent whenever the corresponding kinetic system has this property.

For the kinetic system there can be a limit cycle and at the same time permanent coexistence can hold. For the reaction diffusion system, of course the behaviour can be more complex, and it is known, for example, that (stable) patterns can exist, (Kishimoto 1982). A similar analysis can be carried out in many cases for three species, including for example when there is a switching predator, (Hutson (1984a), the system not being then of Lotka-Volterra type, and the technique should also be applicable to more general systems.

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# THERMODYNAMICS OF THE VOLTERRA MODEL

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## 1. INTRODUCTION

The following system of two coupled ordinary differential equations

$$\frac{du}{dt} = \lambda u(1 - v) \qquad \frac{dv}{dt} = -\mu v(1 - u) \tag{1}$$

was originally proposed by Lotka and Volterra [7] as a straightforward though quite rough description for the interaction of prey u and predator v. As is well known, this system exhibits neutrally stable oscillations. It is the goal of this note to give some results about the period and shape of these oscillations and to relate these statements to the behavior of the system treated as weakly interacting with a large background system in the sense of classical equilibrium thermodynamics.
By introducing new variables (p,q) via the transformation $u = e^p$, $v = e^q$, system (1) is converted into the Hamiltonian form

$$\frac{dp}{dt} = -\frac{\partial H}{\partial q}, \quad \frac{dq}{dt} = \frac{\partial H}{\partial p} \tag{2}$$

with the Hamiltonian $H(p,q) = \mu(e^p - p - 1) + \lambda(e^q - q - 1)$
The set of all solutions of this system is given by the function
$(p,q)\colon (t,E) \in R\times[0,\infty) \to (p,q) \in R^2$
satisfying equations (2) and the following conditions

$$\begin{aligned} &p(0,E) \geq 0\,, \quad q(0,E) = 0 \quad \text{for all } E \in [0,\infty) \\ &H(p(t,E),q(t,E)) = E \qquad \text{for all } (t,E) \in R\times[0,\infty) \end{aligned} \tag{3}$$

These solutions are periodic throughout with periods T(E). Hence

$$\begin{aligned} p(t+T(E),E) &= p(t,E) \\ q(t+T(E),E) &= q(t,E) \end{aligned} \qquad \text{for all } (t,E) \in R\times[0,\infty) \tag{4}$$

In the following we introduce the dependence on the parameters $\lambda$ and $\mu$ suppressed so far. We study the function $T = T(E,\lambda,\mu)$. To investigate the temporal structure of the orbit in more detail, we divide it into four parts in the four quadrants of the (p,q) - plane. By $T_{++}, T_{-+}, T_{--}$ and $T_{+-}$ we denote the time the orbit takes in the four quadrants $\{p>0,q>0\}$, $\{p<0,q>0\}$, $\{p<0,q<0\}$ and $\{p>0,q<0\}$, respectively.
Note that $T_{--}$ is the time for which both species are suppressed below their equilibrium value 1 whereas $T_{++}$ is the time for which both species are above equilibrium. It is quite clear that for large amplitude oscillations we have $T_{--}(E) \to \infty$ when $E \to \infty$. This is seen immediately from the (u,v) phase plane of system (1), because large amplitude trajectories get close to the saddle at (u,v) = (0,0). But (the mistake in [2]!) we get $T_{++}(E) \to 0$ for $E \to \infty$ as an effect of the quadratic terms in (1). This corresponds to the fact that prey and predator cannot coexist for a long time in a hard struggle. Nevertheless this struggle effects the long time behavior!

## 2. USE OF THERMODYNAMICS

In many situations, a system like (1) may be weakly coupled to a large system. As well known from the theory of heat, there are many cases where this coupling gives rise to a Boltzmann distribution in the (p,q) phase space of (2). The mathematical treatment of this situation, usually called "canonical ensemble", is managed by means of the partition function (see e.g. R. Becker [1] p.127). For inverse temperature $\beta \in (0,\infty)$ the partition function of any Hamiltonian system is

$$Z(\beta) = \int_0^\infty \exp(-\beta H(p,q))\, dpdq. \tag{5}$$

The point of view of the present note is rather modest though mathematically rigorous. We will not reason about validity of thermodynamics nor about ergodicity nor large Hamiltonian systems. (Some results in this direction were obtained by Kerner [4]). Instead we do the well-known calculations of thermodynamics and link them to the energy-period function $T = T(E,\lambda,\mu)$ from above.

We need some notation. Let $h(p) = e^p - p - 1$. For all $E \in (0,\infty)$ let $p_\pm$ be the positive and negative solution of $h(p_\pm) = E$. The functions $\tau_\pm$ and $\tau$: $E \in (0,\infty) \to \tau_\pm(E)$ and $\tau(E) \in (0,\infty)$ are given by setting

$$\begin{aligned} \tau_+(E) &= 1/h'(p_+) = 1/(e^{p+} - 1) \\ \tau_-(E) &= 1/|h'(p_-)| = 1/(1 - e^{p-}) \\ \tau(E) &= \tau_+(E) + \tau_-(E) \end{aligned} \tag{6}$$

Proposition 1
The Laplace transform of the energy-period function is the canonical partition function:

$$Z(\beta,\lambda,\mu) = \int_0^\infty e^{-\beta E} T(E,\lambda,\mu)\, dE \tag{7}$$

The partition function is explicitly

$$Z(\beta,\lambda,\mu) = z(\beta\lambda)z(\beta\mu) \quad \text{with} \quad z(s) = e^{s(1 - \log s)}\Gamma(s) \tag{8}$$

where the Euler $\Gamma$-function occurs (see e.g. [11] p. 243)
Furtheron

$$z(s) = \int_0^\infty e^{-sE} \tau(E)\, dE \tag{9}$$

The energy-period function T as well as the partial period functions $T_{\sigma\rho}$ with $\sigma\rho \in \{\pm\}$ are given by the convolutions

$$T(E,\lambda,\mu) = \frac{1}{\lambda\mu} \int_0^E \tau(a/\lambda)\tau((E-a)/\mu)\, dE \tag{10}$$

$$T_{\rho\sigma}(E,\lambda,\mu) = \frac{1}{\lambda\mu} \int_0^E \tau_\sigma(a/\lambda)\tau_\rho((E-a)/\mu)\, dE \tag{11}$$

## 3. INVERSION OF THE LAPLACE TRANSFORMS AND EXPANSIONS

The inversion of the Laplace transforms (9) and (7) are

$$\tau(E) = \frac{1}{2\pi i}\int_{-i\infty}^{i\infty} e^{sE} z(s)\, ds \tag{12}$$

$$T(E,\lambda,\mu) = \frac{1}{2\pi i}\int_{-i\infty}^{i\infty} e^{sE} z(s\lambda) z(s\mu)\, ds \tag{13}$$

The function $z = z(s)$ is analytic in the domain $C\setminus(-\infty,0]$ with a cut caused by the term $\log s$ along the axis $(-\infty,0]$ and poles (on all sheets of the Riemannian surface of $\log s$) at $s = -k$ with $k = 0,1,2,3\ldots$ . By deforming the path of integration to a path surrounding the cut along $(-\infty,0]$, the integrals in (12)(13) can be converted to real integrals. In case of (12) one gets an integral and a sum of residua. Furtheron, as shown in a forthcoming paper [6], these two parts coincide with $\tau_+(E)$ and $\tau_-(E)$, respectively. Hence one gets

$$\tau_+(E) = \int_0^\infty e^{-sE}(sz(s))^{-1}\, ds \tag{14}$$

$$\tau_-(E) = 1 + \sum_{k=1}^{\infty} e^{-kE}(kz(k))^{-1} \tag{15}$$

We turn to expansions in two limiting cases.
Small values of E correspond to low temperature and large s.
Large values of E correspond to high temperature and small s.
First turn to the low temperature case.
By Stirling's formula we get (see e.g.[3])

$$z(s) = \sqrt{\frac{2\pi}{s}}\left\{1 + \frac{1}{12s} + \frac{1}{288s^2} - \frac{139}{518400s^3} + O(s^{-4})\right\} \tag{16}$$

By a Theorem of Karamata (see Widder[10] p.192 Theorem 4.3) one can transform back this series term by term and gets series for $\tau(E)$ and $T(E,\lambda,\mu)$, where the residuals have the correct orders. Thus one gets (see [5])

$$\tau(E) = \sqrt{\frac{2}{E}}\left\{1 + \frac{E}{6} + \frac{E^2}{216} - \frac{139E^3}{97200} + O(E^4)\right\} \tag{17}$$

$$T(E,\lambda,\mu) = T(0) + T'(0)E + T''(0)\frac{E^2}{2} + T'''(0)\frac{E^3}{6} + O(E^4)$$

with

$$T(0) = \frac{2\pi}{\sqrt{\lambda\mu}}\,, \quad T'(0) = \frac{\pi}{6\sqrt{\lambda\mu}}\left(\frac{1}{\lambda}+\frac{1}{\mu}\right),$$

$$T''(0) = \frac{\pi}{144\sqrt{\lambda\mu}}\left(\frac{1}{\lambda}+\frac{1}{\mu}\right)^2 = \frac{T'(0)^2}{2T(0)} > 0 \quad \text{and}$$

$$T'''(0) = -\frac{139\pi}{25920\sqrt{\lambda\mu}}\left(\frac{1}{\lambda}+\frac{1}{\mu}\right)\left(\frac{1}{\lambda^2}+\frac{1}{\mu^2}-\frac{154}{139\lambda\mu}\right) < 0$$

Expansions for $\tau_{\pm}(E)$ can be given, too. To derive them, let $p = p(x)$ and $t = t(x)$ be analytic functions such that

$$e^{p(x)}-p(x)-1 = x^2/2\,, \quad p(x) > 0 \text{ iff } x > 0 \quad \text{and}$$
$$p'(x) = t(x) = x/(e^p-1) > 0. \tag{18}$$

Since a power series for $t = t(x)$ can be calculated and we have

$$t(x) = x\tau_+(x^2/2) \quad \text{for } x > 0 \quad \text{and}$$
$$t(x) = -x\tau_-(x^2/2) \quad \text{for } x < 0 \tag{19}$$

we get

$$\tau_{\pm}(E) = \frac{1}{\sqrt{2E}} \mp \frac{1}{3} + \frac{E}{6\sqrt{2E}} \mp \frac{4E}{135} + O(E^{3/2}) \tag{20}$$

By (11) this formula implies expansions for $T_{\pm\pm}$ as given below.
Now consider the high temperature limit.
The well-know power series for Euler's $\Gamma$-function implies

$$sz(s) = 1 + (1-C-\log s)s + O(s^2\log^2 s) \tag{21}$$

By the inversion formula (12) this implies an asymtotic formula for $\tau(E)$. Note that this formula does not give rise to a convergent expansion.

$$\tau(E) = 1 + \frac{1}{E} - \frac{\log E}{E^2} + O\left(\frac{\log^2 E}{E^3}\right) \tag{22}$$

By similar reasoning (13) implies

$$T(E,\lambda,\mu) = \frac{1}{\lambda\mu}\left\{E + (\lambda+\mu)(1+\log E) - (\lambda\log\lambda + \mu\log\mu)\right\} + O\left(\frac{\log^2 E}{E}\right) \tag{23}$$

Omitting further details we summarize the expansions in a table.

$$T_{++} = \frac{\pi}{2\sqrt{\lambda\mu}} - \left(\frac{1}{\lambda\sqrt{\mu}} + \frac{1}{\mu\sqrt{\lambda}}\right)\frac{\sqrt{2E}}{3} + \left(\frac{1}{9\lambda\mu} + \frac{\pi(\lambda+\mu)}{24\sqrt{\lambda\mu}\,\lambda\mu}\right)E + O(E^{3/2})$$

$$T_{--} = \frac{\pi}{2\sqrt{\lambda\mu}} + \left(\frac{1}{\lambda\sqrt{\mu}} + \frac{1}{\mu\sqrt{\lambda}}\right)\frac{\sqrt{2E}}{3} + \left(\frac{1}{9\lambda\mu} + \frac{(\lambda+\mu)}{24\sqrt{\lambda\mu}\,\lambda\mu}\right)E + O(E^{3/2})$$

$$T_{++} = \frac{2\log E - \log\lambda\mu + 2 - 2w}{E} + O\left(\frac{\log^2 E}{E^2}\right)$$

$$T_{--} = \frac{E}{\lambda\mu} + \frac{w(\lambda+\mu)}{\lambda\mu} + O(e^{-E/\lambda} + e^{-E/\mu})$$

$$T_{+-} = \frac{\pi}{2\sqrt{\lambda\mu}} + \left(\frac{1}{\lambda\sqrt{\mu}} - \frac{1}{\mu\sqrt{\lambda}}\right)\frac{\sqrt{2E}}{3} + \left(\frac{-1}{9\lambda\mu} + \frac{\pi(\lambda+\mu)}{24\sqrt{\lambda\mu}\,\lambda\mu}\right)E + O(E^{3/2})$$

$$T = \frac{2\pi}{\sqrt{\lambda\mu}} + \frac{\pi(\lambda+\mu)}{6\sqrt{\lambda\mu}\,\lambda\mu}E + \frac{T'(0)^2}{4T(0)}E^2 - O(E^3)$$

$$T_{+-} = \frac{\log E - \log\lambda + 1 - w}{\mu} + \frac{\lambda\log E - \lambda\log\lambda + w\mu + \lambda}{\mu E} + O\left(\frac{\log^2 E}{E^2}\right)$$

$$T = \frac{E}{\lambda\mu} + \frac{(\lambda+\mu)(1+\log E)}{\lambda\mu} - \frac{\lambda\log\lambda + \mu\log\mu}{\lambda\mu} + \frac{(\lambda+\mu)^2(1+\log E)}{\lambda\mu E} - \frac{(\lambda+\mu)(\lambda\log\lambda + \mu\log\mu)}{\lambda\mu E} + O\left(\frac{\log^2 E}{E^2}\right)$$

$$\tau_+ = \frac{1}{\sqrt{2E}} - \frac{1}{3} + \frac{\sqrt{E}}{6\sqrt{2}} - \frac{4E}{135} + O(E^{3/2})$$

$$\tau_- = \frac{1}{\sqrt{2E}} + \frac{1}{3} + \frac{\sqrt{E}}{6\sqrt{2}} + \frac{4E}{135} + O(E^{3/2})$$

$$\tau = \sqrt{\frac{2}{E}}\left\{1 + \frac{E}{6} + \frac{E^2}{216}\right\} - O(E^{5/2})$$

$$\tau_+ = \frac{1}{E} - \frac{\log E}{E^2} + O\left(\frac{\log^3 E}{E^3}\right)$$

$$\tau_- = 1 + \frac{1}{2e}e^{-E} + O(e^{-2E})$$

$$\tau = 1 + \frac{1}{E} - \frac{\log E}{E^2} + O\left(\frac{\log^3 E}{E^3}\right)$$

with $w = \sum_{k=1}^{\infty} \frac{k^k e^{-k}}{k!k}$

## 4. GLOBAL INEQUALITIES

We introduce new independent variables

$$x = \log(E/\mu) \quad \text{and} \quad y = \log(E/\lambda).$$

Since the function $(E,\lambda,\mu) \to ET(E,\lambda,\mu)$ is homogenous of degree zero (indeed, we did not scale time in order to retain more symmetry) we can define a function

$$t: (x,y) \in R^2 \to t(x,y) \in (0,\infty) \quad \text{by setting}$$
$$t(x,y) = ET(E,\lambda,\mu).$$

From the convolution formula (10) we get

$$t(x,y) = e^{x+y}\int_0^1 \tau(e^x s)\tau(e^y(1-s))\,ds. \tag{24}$$

We look for a convexity property which takes over from the function $\tau$ to the convolution (24).
To this end, note that for any smooth positive function $f = f(E)$ the following properties (i) and (ii) are equivalent:

(i) $\left(\frac{d}{dE}\right)^2 \log f(E) > 0$

(ii) $\left(\frac{d}{dE}\right)^2 e^{\alpha E} f(E) > 0 \quad$ for all $\alpha \in R$.

This follows from the identity

$$\left(\frac{d}{dE}\right)^2 [e^{\alpha E} f(E)] = e^{\alpha E} f\left\{\left(\alpha + \frac{d}{dE}\log f\right)^2 + \left(\frac{d}{dE}\right)^2 \log f(E)\right\}$$

As a simple consequence we get: If two functions f and g have property (i), then f + g as well as fg have property (i).
A further consequence is the following

**Lemma 2**

Let two smooth positive functions f and g satisfy

$$\left(\frac{d}{dz}\right)^2 \log f(e^z) > 0 \quad \text{for all } z \in R.$$

Then the convolution $(x,y) \in R^2 \to \log \int_0^1 f(e^x s) g(e^y(1-s))\,ds$ is convex on the whole plane.

Now we have to state the central estimates (see [8] for (a)):

Proposition 3

(a) The function $t = t(x)$ defined by (19) satisfies

$$\left(\frac{d}{dx}\right)^2 t(x) > 0 \quad \text{for all } x \in R.$$

(b) The function $\tau = \tau(E)$ is convex on double logarithmic scale:

$$\left(\frac{d}{dz}\right)^2 \log \tau(e^z) > 0 \quad \text{for all } z \in R.$$

Proof

(a) Some lengthy calculations show that the functions $p = p(x)$ and $t = t(x)$ given by (18) satisfy

$$\frac{dt}{dx} = 2e^p(e^p - 1)^{-3}(p - \operatorname{sh} p) < 0 \quad \text{and}$$

$$\frac{d^2t}{dx^2} = t\, e^p(e^p - 1)^{-4}(1 + 2e^p) \int_0^p 2(e^s - 1)^3(2e^s + 1)^{-2}\, ds.$$

Now the result is straightforward.

(b) First note that (20) and (14)(15)(22) imply

$$t(x) = 1 - x/3 + x^2/12 - \ldots \quad \text{and hence } t(0) = 1$$

and

$$\lim_{x \to \pm\infty} [t(x) - xt'(x)] = 0,$$

respectively. Thus the function $s(x) = [t(x) + t(-x)]/2$ satisfies for all $x \in R$

$$s'(x) > 0, \quad s''(x) > 0, \quad [s(x) - xs'(x)] \in (0,1].$$

Since $\tau(E) = \tau_+(E) + \tau_-(E) = s(\sqrt{2E})/\sqrt{2E}$ this implies

$$\left(\frac{d}{dz}\right)^2 \log \tau(e^z) = \frac{1}{4}\left(\frac{d}{du}\right)^2 \log s(e^u) =$$

$$= \frac{e^u}{4s}\left\{e^u s''(e^u) + \frac{s'}{s}(e^u)[s(e^u) - e^u s'(e^u)]\right\} \quad \text{with } u = \frac{z}{2} + \log 2$$

In the last formula all terms are positive which proves (b).

Remark. Since $\tau_\pm(E) \pm 1/3 = s_\pm(\sqrt{2E})/\sqrt{2E}$ with $s_\pm(x) = t(\pm x) \pm x/3$, the reasoning from above yields that for all $z \in R$

$$\left(\frac{d}{dz}\right)^2 \log[\tau_\pm(e^z) \pm 1/3] > 0 \quad \text{but} \quad \left(\frac{d}{dz}\right)^2 \log \tau_+(e^z) < 0.$$

Now we are able to apply Lemma 2 and Proposition 3 to the convolution formula (24). Together with some information from expansions this yields

Proposition 4

(a) The function $(x,y) \in R^2 \to \log t(x,y)$ is convex on the whole $R^2$.

(b) $\frac{1}{2} < \frac{\partial}{\partial x}\log t(x,y) < 1$ and $\frac{1}{2} < \frac{\partial}{\partial y}\log t(x,y) < 1$

for all $(x,y) \in R^2$. The lower- and upper bounds are assumed in the limit $x$ or $y \to -\infty$ and $x$ or $y \to \infty$, respectively.

(c) $\frac{1}{2} < \frac{\partial}{\partial y}\log t(x,y) < \frac{\partial}{\partial x}\log t(x,y) < 1 < 2\frac{\partial}{\partial y}\log t(x,y) < 2$

for all $(x,y) \in R^2$ with $x > y$.

(d) $t(\frac{x+y}{2},\frac{x+y}{2}) < t(x,y) < t(\frac{2x+y}{3},\frac{2x+y}{3})$

for all $(x,y) \in R^2$ with $x > y$.

Proof

(a) is a consequence of Lemma 2 and Proposition 3.

(b) The limits follow by the asymptotic expansions. Hence the inequality follows by monotonicity.

(c) Let the function $f = f(s)$ be defined by

$$f(s) = \log t(\frac{x+y}{2}+s,\frac{x+y}{2}-s).$$

Since $f'(0) = 0$, $\lim_{s\to\infty} f'(s) = 1/2$ and $f''(s) > 0$ for all $s \in R$, we get $0 < f'(s) < 1/2$ for all $s \in (0,\infty)$ and hence

$$0 < \left(\frac{\partial}{\partial x}-\frac{\partial}{\partial y}\right) \log t(x,y) < 1/2 \quad \text{for all } (x,y) \in R^2 \text{ with } x > y.$$

(d) For the function $f = f(s)$ defined in (c), we get $f(s) > f(0)$ for all $s \in R$, which implies the left-hand inequality in (d).

To prove the right-hand inequality, define the function $g(s) = \log t(\frac{2x+y}{3}+s,\frac{2x+y}{3}-2s)$. Since (c) implies $g'(s) < 0$ for all $s \in R$, we get $g(\frac{x-y}{2}) < g(0)$ for $x > y$ and hence the right-hand side of the inequality (d) follows.

Proposition 5

The energy-period function $T = T(E,\lambda,\mu)$ satisfies

(a) The function

$$(\log(E/\mu),\log(E/\lambda)) \in R^2 \to \log(ET)(E,\lambda,\mu)$$

is convex on the whole domain $R^2$.

(b) $$\frac{1}{2} < -\frac{\lambda\partial T}{T\partial\lambda} < -\frac{\mu\partial T}{T\partial\mu} < 1 < -2\frac{\lambda\partial T}{T\partial\lambda} < 2 \quad \text{for all } (E,\lambda,\mu) \in (0,\infty)^3 \text{ with } \lambda > \mu.$$

(c) $$0 < \frac{E\partial T}{T\partial E} < 1 \quad \text{for all } (E,\lambda,\mu)$$

(d) $$T(E,\sqrt{\lambda\mu},\sqrt{\lambda\mu}) < T(E,\lambda,\mu) < T(E,\lambda^{1/3}\mu^{2/3},\lambda^{1/3}\mu^{2/3})$$
for all $(E,\lambda,\mu) \in (0,\infty)^3$ with $\lambda > \mu$.

Proof

This follows from Proposition 4 by straightforward substitutions, noting

$$\frac{\partial}{\partial x}\log t = -\frac{\mu\partial T}{T\partial\mu}, \quad \frac{\partial}{\partial y}\log t = -\frac{\lambda\partial T}{T\partial\lambda} \quad \text{and}$$

$$\left(\frac{\partial}{\partial x}+\frac{\partial}{\partial y}\right)\log t = 1 + \frac{E\partial T}{T\partial E}.$$

Remarks

The very strong inequality in Proposition 3(a) was first obtained by Waldvogel [8] , who only derives monotonicity of the energy--period function from it. It is quite astonishing that only the weaker result in Proposition 3(b) gives so much new information.

It is worth while to look once more at the partial orbit times well hidden in Proposition 3 through 5. By the substitution $a = E\cos^2\varphi$, $E-a = E\sin^2\varphi$ in the convolution formulas (10)(11) we get

$$T(E,\lambda,\mu) = \frac{1}{\sqrt{\lambda\mu}}\int_0^{2\pi} t\left(\sqrt{\frac{2E}{\lambda}}\cos\varphi\right) t\left(\sqrt{\frac{2E}{\mu}}\sin\varphi\right)\, d\varphi \qquad (25)$$

and

$$T_{++} = \int_0^{\pi/2}, \quad T_{-+} = \int_{\pi/2}^{\pi}, \quad T_{--} = \int_{\pi}^{3\pi/2}, \quad T_{+-} = \int_{3\pi/2}^{2\pi}$$

with the same integrant.

On the other hand

$$T(E,\lambda,\mu) = \frac{1}{\sqrt{\lambda\mu}}\int_0^{\pi/2} s\left(\sqrt{\frac{2E}{\lambda}}\cos\varphi\right) s\left(\sqrt{\frac{2E}{\mu}}\sin\varphi\right)\, d\varphi \qquad (26)$$

where $s(x) = (t(x)+t(-x))/2$ is the symmetric part of $t$.

Since $t''(x) > 0$, $s''(x) > 0$ and $t'(x) < 0$ but $s'(x) > 0$ for all $x \in R$, formula (25)(26)imply that the functions $E \to T_{--}(E,\lambda,\mu)$ and $E \to T(E,\lambda,\mu)$ are increasing whereas the function $E \to T_{++}(E,\lambda,\mu)$ is decreasing for all $E \in (0,\infty)$.

## 5. INCLOSED AREA AND EQUIPARTITION THEOREM

The area $F(E,\lambda,\mu)$ enclosed by the orbit in the $(p,q)$-plane can be treated analogously to the energy-period function. Starting from the relation

$$\frac{\partial F}{\partial E} = T$$

and (7)(8)(9), one derives with the help of Laplace transforms the following convolution formulas:

$$F(E,\lambda,\mu) = \frac{1}{\sqrt{\lambda\mu}}\int_0^E \varphi(a/\lambda)\varphi((E-a)/\mu)\, da \qquad (27)$$

with

$$\varphi(E) = \int_0^E \tau(a)\sqrt{\frac{2}{E-a}}\, da\ .$$

Introducing again the variables $x = \log(E/\mu)$, $y = \log(E/\lambda)$ and exploiting that $F = F(E,\lambda,\mu)$ is homogeneous of degree zero, we define $f\colon (x,y) \in R^2 \to f(x,y)$ by setting

$$f(x,y) = F(E,\lambda,\mu).$$

Since the convolution formula (27) can be rewritten as

$$f(x,y) = e^{(x+y)/2}\int_0^1 \varphi(e^x s)\varphi(e^y(1-s))\, ds,$$

we can show that Proposition 4(a) through (d) are valid for the function $f = f(x,y)$ exactly as for the function $t = t(x,y)$. We have to transform to the original variables. Note that

$$\frac{\partial f}{\partial y} = -\lambda\frac{\partial F}{\partial \lambda} = \int_0^T \lambda(e^q - q - 1)\, dt =: TE_q\ ,$$

$$\frac{\partial f}{\partial x} = -\frac{\partial F}{\partial \mu} = \int_0^T \mu(e^p - p - 1)\, dt =: TE_p \quad \text{and}$$

$$\frac{\partial f}{\partial x} + \frac{\partial f}{\partial y} = E\frac{\partial F}{\partial E} = ET$$

with the solution $(p,q)(t,E)$ of system (2) inserted in the integrals.

Proposition 6

The area $F(E,\lambda,\mu)$ inclosed by the orbit in the $(p,q)$-plane has the following properties:

(a) The function $(\log(E/\mu),\log(E/\lambda)) \to \log F(E,\lambda,\mu)$ is convex on the whole domain $R^2$.

(b) $F/2 < TE_q < TE_p < F$ and hence $E_q < E_p < 2E_q$ for all $(E,\lambda,\mu) \in (0,\infty)^3$ with $\lambda > \mu$

This inequality may be interpretated as qualitative equipartition of the "energy" $E = E_p + E_q$ up to the factor of 2 even in situations where the parameters $\lambda$ and $\mu$ differ by orders of magnitude.

(c) $F(E,\sqrt{\lambda\mu},\sqrt{\lambda\mu}) < F(E,\lambda,\mu) < F(E,\lambda^{1/3}\mu^{2/3},\lambda^{1/3}\mu^{2/3})$ for all $(E,\lambda,\mu) \in (0,\infty)^3$ with $\lambda > \mu$

## 6. THE CANONICAL ENSEMBLE

The canonical ensemble is defined as the Boltzmann distribution in the $(p,q)$-phase space, which is

$$g(p,q) = z(\beta\lambda)^{-1} z(\beta\mu)^{-1} \exp[-\beta H(p,q)]$$

Table 2 summarizes the calculations for the symmetric case $\lambda = \mu = 1$, from which the general case is straightforward to obtain. For the entropy we get e.g.

$$\Sigma(\beta,\lambda,\mu) = [\Sigma_1(\beta\lambda) + \Sigma_1(\beta\mu)]/2.$$

Since by (9) $z = z(\beta)$ is the Laplace transform of $\tau = \tau(E)$, it is not hard to show that Proposition 3(b) implies

$$\left(\frac{d}{dx}\right)^2 \log z(e^x) > 0 \quad \text{for all } x \in R.$$

Hence the function $\beta \to \beta\langle E\rangle_g(\beta)$ is decreasing. Together with the expansions for small and large $\beta$ this implies

$$\beta^{-1} < \langle E\rangle_g(\beta,\lambda,\mu) < 2\beta^{-1} \quad \text{for all } \beta \in (0,\infty).$$

**Free energy**

$$\Phi_1(\beta) = -\frac{1}{\beta}\log z^2(\beta)$$

$$= 2\log\beta - 2 - \frac{1}{\beta}\log\Gamma(\beta)$$

$$= \frac{1}{\beta}\left\{\log\frac{\beta}{2\pi} - \int_0^\infty e^{-\beta t}\left(1-\frac{2}{t}+\frac{2}{e^t-1}\right)\frac{dt}{t}\right\}$$

**Mean value of energy**

$$\langle E\rangle_g(\beta) = -\frac{\partial}{\partial\beta}\log z^2(\beta)$$

$$= 2\log\beta - 2\psi(\beta)$$

$$= \frac{1}{\beta} + \int_0^\infty e^{-\beta t}\left(1-\frac{2}{t}+\frac{2}{e^t-1}\right)dt$$

Expansion for high temperature

$$\Phi_1(\beta) = \frac{2}{\beta}\log\beta + 2\log\beta - 2 + 2C - \frac{1}{\beta}\log\frac{\pi\beta}{\sin\pi\beta} + O(\beta^2)$$

$$\langle E\rangle_g(\beta) = \frac{2}{\beta} + 2\log\beta + 2C + \pi\operatorname{ctg}\pi\beta - \frac{1}{\beta} + O(\beta^2)$$

Expansion for low temperature

$$\Phi_1(\beta) = \beta^{-1}\log\frac{\beta}{2\pi} - \beta^{-3}/6 + \beta^{-5}/180 + O(\beta^{-7})$$

$$\langle E\rangle_g(\beta) = \beta^{-1} + \beta^{-2}/6 - \beta^{-4}/60 + O(\beta^{-6})$$

General case

$$\Phi(\beta,\lambda,\mu) = [\lambda\Phi_1(\beta\lambda) + \mu\Phi_1(\beta\mu)]/2$$

$$\langle E\rangle_g(\beta,\lambda,\mu) = [\lambda E_1(\beta\lambda) + \mu E_1(\beta\mu)]/2$$

**Entropy**

$$\Sigma_1(\beta) = \beta\langle E\rangle_g(\beta) - \beta\Phi(\beta)$$

$$= 2\beta - 2\beta\psi(\beta) + 2\log\Gamma(\beta)$$

$$= -\log\frac{\beta}{2\pi} + 1 + \int_0^\infty e^{-\beta t}\left(\beta+\frac{1}{t}\right)\left(1-\frac{2}{t}+\frac{2}{e^t-1}\right)dt$$

**Variance of energy**

$$\beta^2\operatorname{var}_g E = -\beta^2\frac{\partial E}{\partial\beta}$$

$$= -\frac{2}{\beta} + 2\psi'(\beta)$$

$$= 1 + \beta^2\int_0^\infty e^{-\beta t}t\left(1-\frac{2}{t}+\frac{2}{e^t-1}\right)dt$$

Expansion for high temperature

$$\Sigma_1(\beta) = 2\beta - 2\log\beta + 2 + \pi\beta\operatorname{ctg}\pi\beta - 1 + \log\frac{\pi\beta}{\sin\pi\beta} + O(\beta^2)$$

$$\beta^2\operatorname{var}_g E = 2 - 2\beta + \pi^2\beta^2\sin^{-2}\pi\beta - 1 + O(\beta^3)$$

Expansion for low temperature

$$\Sigma_1(\beta) = -\log\frac{\beta}{2\pi} + 1 + \beta^{-1}/3 - \beta^{-3}/45 + O(\beta^{-5})$$

$$\beta^2\operatorname{var}_g E = 1 + \beta^{-1}/3 - \beta^{-3}/15 + O(\beta^{-5})$$

Thus the mean thermal energy lies between the value for the harmonic oscillator and twice of it.

Note that in the table we have put $C = -\Gamma'(1) = 0.577...$ and $\psi(z) = \Gamma'(z)/\Gamma(z)$.

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# ON OPTIMIZATION PRINCIPLES IN PLANT ECOLOGY

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## 1. INTRODUCTION

Evolution seems to be governed by interactions of chance and necessity [14]. In the latter, optimization principles seem to enter biological systems very often in the process of selective adaption.

Here two examples from physiological plant ecology, looking at the dynamics of achieving an optimal relationship between biomass production and water loss, will be discussed:

a) at leaf level: the movement of stomata

b) at plant level: the partitioning of biomass production.

The hypothesis investigated in this article is, that these components of the plant's metabolism are regulated in accordance with principles of optimization. The consequences of this assumption are derived within the framework of optimal control theory and are compared with the observed dynamics in plants.

Although there is a growing number of publications using optimal control theory in a biological context, applications to the ecology of plants are quite rare. Some work like optimization of the yield in forests [ 1 ] or in greenhouse crops [ 6 ], including economic considerations, has been carried out at the level of plant populations.

## 2. MOVEMENT OF STOMATA

### 2.1. The biological background

In the epidermis (the outer surface-layer of a leaf) are embedded small pores, called stomata, which are capable of regulating their aperture. These stomata control two opposing gas flows, namly the flux of $CO_2$ from the atmosphere into the leaf for photosynthesis and the flux of water vapour from the water saturated leaf interior to the dry atmosphere [15]. The dynamics in stomatal aperature are due to a process allowing $CO_2$ uptake, while limiting the loss of water vapour to prevent leaf desiccation. We will investigate strategies minimizing the total daily loss of water, while the total amount of carbon uptake is fixed.

### 2.2. The model

In the following we review and extend the theory developed at [ 4 ], [ 2 ] in a mathematically rigorous way by using the framework of optimal

control theory.

The aim is to find a stomatal behavior, which reduces the average rate of water loss E as far as possible, relative to the average rate of assimilation A.

As A is a monotone increasing function of the stomatal aperture we can invert this functional relationship to express the evaporation E as a function of A. But the evaporation is still dependent on external physical parameters like light intensity, air temperature, wind speed, humidity etc. These factors are subsumed in the time variance of E(t,A(t)) (see figure 1).

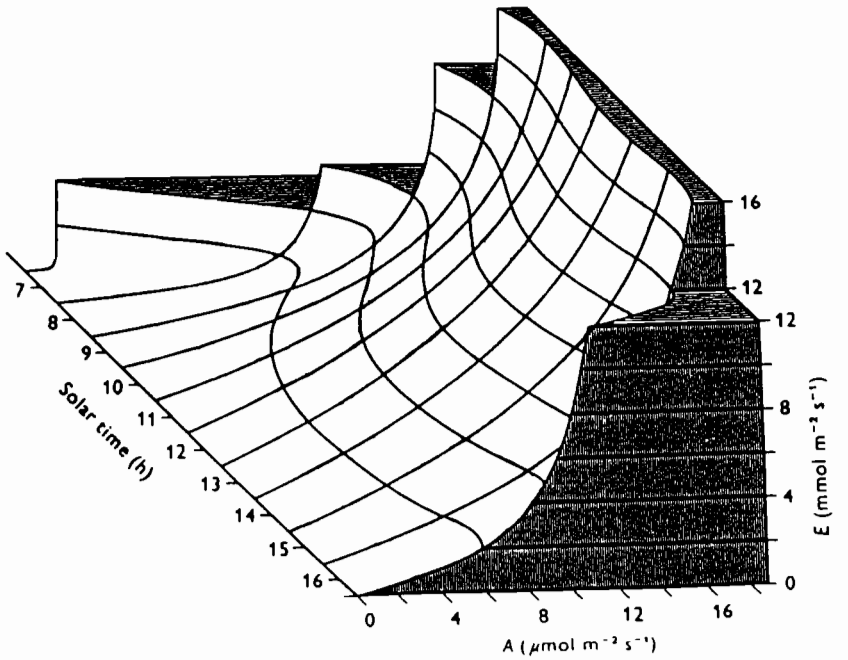



FIGURE 1 The function E(t,A) during the course of the day for a single leaf in an arid semi-tropical region. (Redrawn from [ 4 ])

In the following E is assumed to be partially differentiable twice with respect to A. So we can state this model now mathematically in the following form:

$$\underset{A(\cdot)}{\text{Min}} \int_0^T E(t,A(t))\ dt \tag{1}$$

$$\int_0^T A(t)\ dt = C \tag{2}$$

$$0 \leq A(t) \leq M,\ \forall\ t \in [0,T]. \tag{3}$$

It is assumed, that C is within a range, that will not cause water stress effects. If I take the amount of assimilates at time t as state variable,

(2) transforms to

$$\dot{x}(t) = A(t) \tag{2a}$$

$$x(T) = C \tag{2b}$$

$$x(0) = 0 \quad . \tag{2c}$$

This is a standard problem from control theory, which can be approached by applying the Pontryagyn Maximum Principle [ 8 ], giving a necessary condition for an optimal solution $(x_o(\cdot),A_o(\cdot))$. The Hamiltonian of this problem is given by

$$H(t,x,A,\lambda,\lambda_o) = \lambda A - \lambda_o E(t,A). \tag{4}$$

As the adjoint variable $\lambda(\cdot)$ satisfies

$$\dot{\lambda}(t) = \frac{\partial H}{\partial x}(t,x_o(t),A_o(t),\lambda(t),\lambda_o) = 0,$$

it follows that $\lambda(\cdot)$ is constant, i.e.

$$\lambda(t) = \lambda, \ \forall\, t \in [0,T], \ \lambda \in \mathbb{R}. \tag{5}$$

Further the Maximum Principle states that the Hamiltonian is maximized by the optimal $A_o(t)$, i.e.

$$\lambda u - \lambda_o E(t,u) \leqslant \lambda A_o(t) - \lambda_o E(t,A_o(t)), \ \forall\, M \geqslant u \geqslant 0, \ \forall'\, t \in [0,T]. \tag{6}$$

To interpret this biologically, a multiple of the benefit A minus the cost E has to be maximized.

## 2.3. The optimal solution and its biological relevance

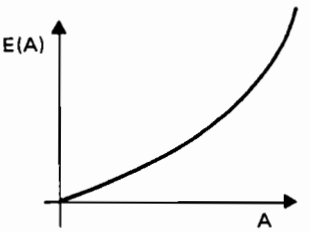
The degenerate case $\lambda_o = 0$ is biologically uninteresting, as only the two extreme strategies $A_o(\cdot) \equiv 0$ or $A_o(\cdot) \equiv M$ can result. So we set for the following $\lambda_o = 1$.

Now the dependence of optimal solutions on the shape of E(A) is discussed.

a) Convex case

The most important situation is

$$\frac{\partial^2 E}{\partial A^2}(t,u) > 0, \ \forall\, M \geqslant u \geqslant 0. \tag{7}$$



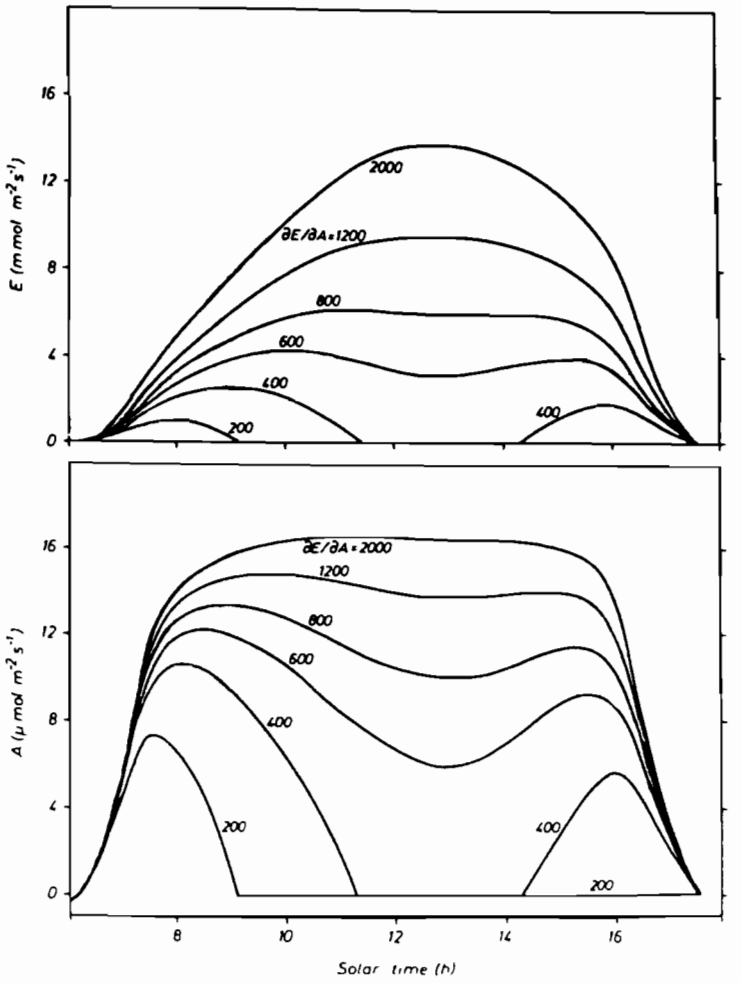

By the resulting monotony of $\frac{\partial H}{\partial A}$ the optimal solution $A_o(t)$, derived from (6), fulfills

$$\frac{\partial E}{\partial A}(t,A_o(t)) = \lambda \quad \text{if there exists a } u \in [0,M] \text{ with } \lambda - \frac{\partial E}{\partial A}(t,u) = 0, \tag{8}$$

$$A_o(t) = 0 \qquad \text{if } \lambda - \frac{\partial E}{\partial A}(t,u) < 0 \ \text{ for all } u \in [0,M],$$

$$A_o(t) = M \qquad \text{if } \lambda - \frac{\partial E}{\partial A}(t,u) > 0 \ \text{ for all } u \in [0,M]$$

and is uniquely determined for each value of $\lambda$. If (7) is valid for all $t \in [0,T]$, then by the necessary conditions the class of possible optimal controls is reduced to a family of curves depending on the parameter $\lambda \in \mathbb{R}$ (compare figures 2, 3). By taking (2) into account, $\lambda$ can be described as monotone increasing function of C (the total assimilation). This leads to selection of the particular optimal solution of (1) - (3).




FIGURES 2,3 The optimal trajectory A(•) and the resulting E(•) in dependancy of $\lambda$, resulting from the climate scenario summarized in figure 1. (Redrawn from [ 4 ])

For a small total assimilation C (respectively a small $\lambda$), the opening of stomata occurs in the morning and sometimes in the afternoon, while they remain closed around noon. Also as C increases the major openings occur in the morning and in the afternoon, with some small reduction around noon.

Several experimental works have already been published, confirming that $\frac{\partial E}{\partial E}$ is constant, as required in (8): [ 7 ], [ 5 ], [11]. In these experiments changes in humidity have always been imposed, while in figure 5 changes in temperature are also summarized.

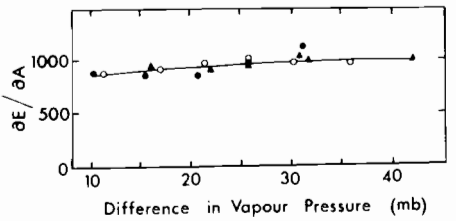
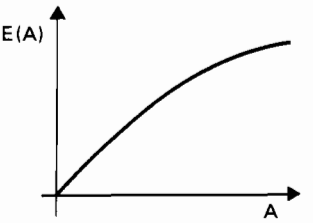



FIGURE 4 Quotient $\frac{\partial E}{\partial A}$ resulting from measurements with vigna unguiculata on the dependence on the difference between the leaf internal water pressure and the external water pressure at the leaf temperatures
● = 26°C, o = 30°C, ▲ = 34°C. (Redrawn from [ 7 ])

b) Concave case

By assuming

$$\frac{\partial^2 E}{\partial A^2}(t,u) < 0, \quad \forall\, u \in [0,M]$$

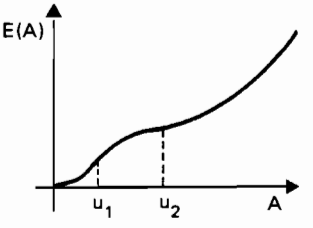



again from (6) it follows, that the optimal solution $A_o(t)$ only switches between 0 (completely closed stomata) and M (completely open stomata).

This characteristic "bang-bang"-behavior is discussed in [ 2 ], pp. 205-208, especially for the carbon fixation exhibited in $C_4$-plants.

c) Other cases

The only additional situation reported, is a function E(A) with positive curvature everywhere, exept for an interval with negative curvature:




$$\frac{\partial^2 E}{\partial A^2}(t,u) < 0, \quad \forall\, u \in ]u_1,u_2[$$

$$\frac{\partial^2 E}{\partial A^2}(t,u) > 0, \quad \forall\, u \in [0,M] \setminus [u_1,u_2]$$

$$0 \leqslant u_1 \leqslant u_2 \leqslant M$$

(6) states, that the optimal value of $A_o(t)$ is the maximum of the Hamiltonian either in $[0,u_1]$ or in $[u_2,M]$. In contrast to a) the solution may not be unique.

This type of E(A) is observed for example, if evaporation has a large cooling effect on the surface temperature of the leaves (i.e. at low wind, large leaves) or with nearly closed stomata, when evaporation through the cuticule becomes more important [10].

## 2.4. Discussion

By only focussing on an optimal relationship between E and A, the crucial influence of the curvature of E(A) becomes evident. The consequences of the optimization approach exhibit already characteristics of known plant behavior. The hint at the invariance of the crucial value $\lambda$ under different climatic regimes (as long as $\frac{\partial^2 E}{\partial A^2} > 0$ is conserved) has encouraged a series of experiments, cited in a).

For an extension of the short-term performance (timerange = 1 day) to a long-term-model (timerange = lifetime of the plant) the crucial step, under investigation, is the variation of the total daily amount of assimilation C (respectively $\lambda$), which changes during plant growth or according to the soil water content (also depending on the plants own activities).

# 3. PARTITIONING OF BIOMASS PRODUCTION

## 3.1. The biological background

Another problem, related to long-term-strategies, is the efficient allocation of the new biomass, gained through assimilation. Investment into new leaves will increase the capacity for further assimilation, while the enlargement of the root system will improve the plant water status. The aim is to find a balance, so that the biomass will be maximized, while the water status does not deteriorate.

## 3.2. The model

Following [16] an optimal allocation pattern will be developed, covering the time span from emergence at $t = 0$ till the end of growth at $t = T$.

The total biomass of the plant $B(t)$ at time $t$ consists of leaf biomass $F(t)$, stem biomass $S(t)$ and root biomass $R(t)$. As exhibited by measurements, $S$ is nearly proportional to $F$ in the considered period of growth (i.e. $S(t) = c \cdot F(t)$, $\forall\, t \in [0,T]$). So we obtain

$$B(t) = F(t) + S(t) + R(t) = (1+c)F(t) + R(t).$$

As the net production of the plant is the net carbon assimilation per leaf weight A (a measured plant characteristic) multiplied by the leaf biomass, we get

$$\frac{d}{dt} B(t) = A \cdot F(t).$$

And by defining $m(t)$ the proportion of carbohydrates assigned for the growth of new leaves, the dynamics of this system is described for $t \in [0,T]$ by

$$\frac{d}{dt} F(t) = m(t)\ A\ F(t) \quad , \quad F(0) = a_1 \tag{9}$$

$$\frac{d}{dt} R(t) = A\ F(t) - (1+c)\ m(t)\ A\ F(t), \quad R(0) = a_2 \tag{10}$$

$$0 \leqslant m(t) \leqslant \frac{1}{1+c}\ . \tag{11}$$

The required maintenance of the water balance gives an additional linkage

between F and R, as the uptake of water f(R) (which is an increasing concave function of R) must exceed the loss of water E·F (E is the rate of water loss per leaf weight, a measured plant characteristic):

$$f(R(t)) \geq E \cdot F(t) \qquad \forall\, t \in [0,T]. \tag{12}$$

The aim is now, to derive a control m(·) for the allocation process (9) - (12) such that during the given time interval [0,T] the total biomass is maximized, i.e.

$$\max_{m(\cdot)\in L_\infty[0,T]} B(T) = \max_{m(\cdot)\in L_\infty[0,T]} (1+c)F(T) + R(T). \tag{13}$$

### 3.3. The optimal solution and its biological relevance

This optimal control problem with state restrictions (9) - (13) can be treated by an extended version of the Maximum Principle (compare [16], Appendix). The only partitioning pattern fulfilling these necessary conditions is

$$m_0(t) = \begin{cases} \dfrac{1}{1+c} & \text{if } t \in [0,t^*[ \\ \dfrac{f'(R(t))}{E+(1+c)f'(R(t))} & \text{if } t \in [t^*,T] \end{cases}$$

$$\text{with } t^* = \frac{1+c}{A}\,(\ln f(a_2) - \ln E - \ln a_1).$$

This shows, that in [0,t*[ the root system is still large enough to compensate the water loss, so that the new biomass can be allocated completely into new leaves. During the succeeding phase for $t \geq t^*$ the system maintains the equality

$$f(R(t)) = E\,F(t)$$

in (12), which is fulfilled at $t = t^*$. Further development requires a decrease in m(·), the proportion invested in new leaves, so that the root system can be extended in order to maintain the plant water status.

Initial experiments with vigna unguiculata (an annual plant from semi-arid habitats) exhibit a high correlation with the computed patterns (see figures 5, 6).

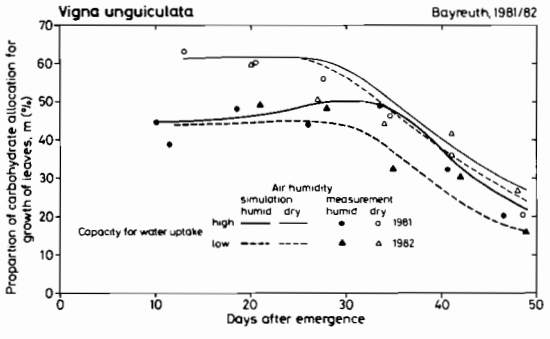



FIGURE 5 Comparison of computed (lines) and measured (dots) carbohydrate partioning patterns m(·). (Redrawn from [16])

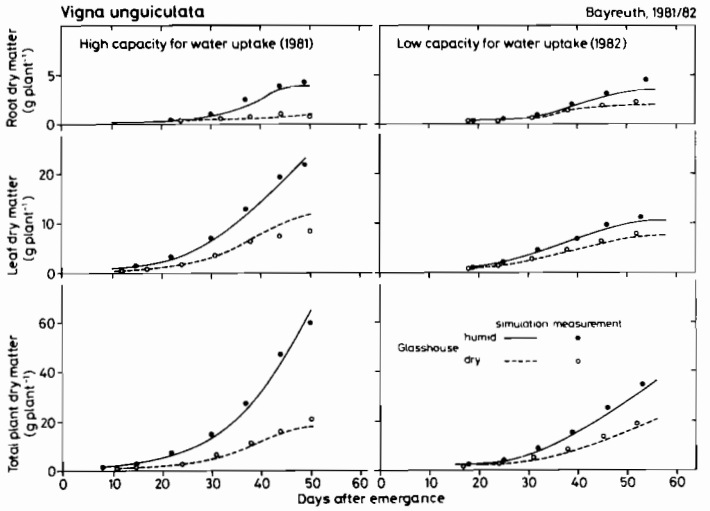



FIGURE 6 Comparison of computed (lines) and measured (dots) growth curves of root, leaf and total biomass at two different capacities for water uptake. (Redrawn from [16])

## 3.4. Discussion

Here the optimization principle in connection with the consideration of plant water status leads to predictions about the dynamics of growth, i.e. the often investigated root/shoot-behavior [13]. After an initial phase depending on the initial values $a_1, a_2$, the model illustrates the crucial influence of the nonlinearity of $f(R)$ for the succeeding phase of growth.

It would be desirable to extend this model now to the next phase, mainly determined by the reproduction process (flowering, crop production). This model can then be viewed as the first part of an extended model, giving the best starting condition for the reproduction phase. An interesting approach to this subject has been given in [ 9 ]. But this more implicit model requires some art in choosing a suitable function for the photosynthetic rate.

## 4. CONCLUSION

Here in two examples an approach is presented only using a very simple dynamical model and an optimization principle, based on very few physiological details. Nevertheless the crucial aspects of the plant's behavior could be summarized. It is to be hoped, that this models can provide suggestions for experiments, that may reveal the complex physiology causing this behavior. The optimization principles might also help to structure biological data and to improve our understanding by simple dynamical models.

## Acknowledgements

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# III. GENETIC SYSTEMS

# DYNAMICAL MODELS IN QUANTITATIVE GENETICS

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## 1. INTRODUCTION

The proposition of the theory of punctuated equilibria by Eldredge & Gould (1972) and others initiated a rather controversial debate on macroevolutionary phenomena and on the way how to explain them. One of the major points in this debate is the question whether the observed phylogenetic patterns are caused by natural selection and hence are due to adaptation or whether they are mainly due to physiological, developmental, architectural and other constraints acting on the phenotype. If the latter holds true then evolution cannot be viewed as a primarily adaptive process. Numerous contributions have been given to this subject. Let us only mention articles by Charlesworth, Lande & Slatkin (1982), Gould & Lewontin (1979), Maynard Smith (1983), Mayr (1983) and Riedl (1977).

To be able to investigate problems of macroevolution on a more quantitative and mathematical basis, it is necessary to have models that describe the evolutionary dynamics of phenotypic characters under the action of the various evolutionary and genetical mechanisms. Such a dynamical model has been proposed by Lande (1976, 1979, 1982). It is based on quantitative genetic theory and incorporates the selective forces acting on the phenotype and the pattern of variation and covariation of characters within the population. Lande's models have received a good deal of attention and have been used not only by himself (loc. cit, 1980, 1984) but by several authors to treat various topics from evolutionary theory analytically (e.g. Felsenstein 1979, Kirkpatrick 1982, Slatkin 1984, Wagner 1984 a,b). Other dynamical models for the evolution of quantitative characters have been introduced by Karlin (1979), Gimelfarb (1982) and others (see also Turelli 1984).

In a recent paper (Bürger, 1984) I used Lande's model to investigate the influence of genetic and phenotypic variance-covariance patterns for the evolution of functionally coupled quantitative characters.

In order to investigate the evolution of functionally coupled characters, I chose a fitness landscape that looked like a ridge. However, there is not only a single ridge in this landscape, there is in fact a saddle with the ridge and two hills adjacent to it. Evolution of a complex of functionally coupled characters then corresponds to moving uphill along the ridge. In order to make the analysis managable I assumed a particularly shaped ridge, which (following Rechenberg,1973) has been called a corridor. The result of a nonlinear analysis of the underlying dynamical system was that an unfavourable phenotypic and/or genotypic variance-covariance structure may prevent a population from moving uphill along the ridge, even if it starts at or very close to it.

Hence there exist population genetic constraints (in the intrinsic sense) restricting the directions of possible evolutionary change, although from the physiological point of view evolution into these directions is possible and even favourable. Moreover, it has been shown that in the corridor (or along the ridge) there exsits an optimal variance-covariance structure resulting in an optimal evolutionary rate. This adds to results of Rechenberg (1973) and Wagner (1984 a,b). It is the purpose of the present paper to investigate whether results similar to that derived in Bürger (1984) and described above can also be obtained by using a different class of corridor models.

## 2. THE MODEL

Let an infinite population with overlapping generations be given that is either monoecious or dioecious with the same pattern of selection on both sexes and no sexual dimorphism. To each individual we assign a vector $\underline{z} = (z_1,\ldots,z_n)^t$ where $z_i$, $1 \le i \le n$, is the value of the i-the character on some scale of measurement and $^t$ denotes transposition. The joint distribution of phenotypic characters is assumed to be multivariate normal, with mean $\bar{\underline{z}} = (\bar{z}_1,\ldots,\bar{z}_n)^t$ and covariance matrix $\underline{P}$. This can often be arranged by some simple scale transformations (Lande 1979, Falconer 1960). Moreover, $\underline{P}$ is split into additive genetic and environmental components $\underline{G}$ and $\underline{E}$. Assuming that the vectors of additive genetic effects $\underline{x}$ and of environmental effects $\underline{e}$ are also multivariate normal and mutually independent and supposing that $\bar{\underline{e}} = \underline{0}$, we can write $\underline{z} = \underline{x}+\underline{e}$, $\underline{P} = \underline{G}+\underline{E}$ and $\bar{\underline{z}} = \bar{\underline{x}}$. The density function is given by

$$\gamma(\underline{z},\bar{\underline{z}},\underline{P}) = (2\pi)^{-n/2} (\det \underline{P})^{-1/2} \exp\left(-\frac{1}{2} \langle \underline{P}^{-1}(\underline{z}-\bar{\underline{z}}), \underline{z}-\bar{\underline{z}}\rangle\right)$$

where $\langle \underline{v},\underline{w}\rangle = \sum_{i=1}^{n} v_i w_i$ denotes the usual inner product for vectors $\underline{v},\underline{w}$ in $\mathbb{R}^n$. Denoting Malthusian fitness of individuals with phenotype $\underline{z}$ by $m(\underline{z})$, the mean fitness of the population is

$$\bar{m}(\bar{\underline{z}},\underline{P}) = \int m(\underline{z})\gamma(\underline{z},\bar{\underline{z}},\underline{P})\,d\underline{z} \qquad (1)$$

where $\int \ldots d\underline{z}$ denotes integration over $\mathbb{R}^n$. The evolutionary dynamics of the vector $\bar{\underline{z}}$ is given by the following system of differential equations:

$$\dot{\bar{\underline{z}}} = \frac{d}{dt}\bar{\underline{z}} = \underline{G} \cdot (\mathrm{grad}_{\bar{\underline{z}}}\bar{m})(\bar{\underline{z}},\underline{P}) \qquad (2)$$

where $\mathrm{grad}_{\underline{z}} = \left(\frac{\partial}{\partial z_1},\ldots,\frac{\partial}{\partial z_n}\right)^t$ (Lande 1982). A discrete analogon has been derived by Lande (1976, 1979).

Lande (1982) has already shown that mean fitness $\bar{m}$ is always increasing, i.e. $\frac{d}{dt}\bar{m} = \dot{\bar{m}} \ge 0$ and $\dot{\bar{m}} = 0$ if and only if grad $\bar{m} = 0$. This implies that a population is always moving uphill in the fitness landscape (but not into the direction of steepest ascent, unless $\underline{G}$ is the identity matrix) and

therefore Lande's model provides an adaptive topography for phenotypes similar to Wright's (1932, 1969) adaptive topography for genotypes.

For investigating the evolution of functionally coupled phenotypic traits we have to specify our fitness landscape and assume that the fitness $m(\underline{z})$ of an individual with phenotype $\underline{z}$ is of the form

$$m(\underline{z}) = sz_1 \left[\exp(-\tfrac{1}{2} \langle \underline{A}\underline{u}, \underline{u}\rangle) - b\right]. \tag{3}$$

Here $\underline{u} = (z_2, \ldots, z_n)^t$ is a n-1 dimensional vector (hence $\underline{z}^t = (z_1, \underline{u}^t)$), $\underline{A}$ denotes a positive definite matrix of dimension n-1 and $s > 0$ and $0 < b < 1$ are constants. Thus we have directional selection along the $z_1$-axis and stabilizing selection perpendicular to it for positive values of $z_1$. In our adaptive landscape we have a saddle at the origin $\underline{z} = \underline{0}$ and a ridge (with edge $\underline{u} = \underline{0}$ and increasing fitness for increasing values of $z_1 > 0$) and two hills (with increasing fitness in directions where $z_1 \to -\infty$ and $\langle \underline{A}\underline{u}, \underline{u}\rangle \to \infty$) adjacent two it. These two hills are separated by a valley with bottom $\underline{u} = \underline{0}$ and $z_1 < 0$. For the two-dimensional case the isoclines of the fitness surface are shown in Fig. 1 for different values of b. To assume that directional selection acts along the $z_1$-axis is no restriction, since by applying a linear transformation $\underline{T}$ to the state space, the direction of the ridge can be chosen arbitrarily. Instead of $\underline{G}$ and $\underline{P}$ one has to take the matrices $\underline{T}\underline{G}\underline{T}^t$ and $\underline{T}\underline{P}\underline{T}^t$. According to Rechenberg (1973) we shall call this a corridor model as the phenotypic states that have positive fitness (given $z_1 \geq 0$) lie within a "corridor" given by the formula $\langle \underline{A}\underline{u}, \underline{u}\rangle \geq -2\ln b$. Rechenberg (1973) and Wagner (1984 a,b) used a somewhat related fitness landscape to investigate the existence of optimal variances and maximal evolutionary rates within the corridor. Wagner was the first who combined Rechenberg's theory with Lande's phenotypic model. In Bürger (1984) I investigated the evolutionary dynamics of a complex of functionally coupled characters using the fitness functions

$$m(\underline{z}) = sz_1(a_o - \langle \underline{A}\underline{u}, \underline{u}\rangle) \tag{4}$$

It is the purpose of the present note to investigate, how the results obtained there depend on the kind of fitness describing stabilizing selection along the ridge.

In order to deal with equation (2) we have to compute the population's mean fitness $\bar{m}$. To manage this we use the formula

$$\int \exp(-\tfrac{1}{2}\langle \underline{B}\underline{v}, \underline{v}\rangle + \langle \underline{v}, \underline{w}\rangle)\, d\underline{v} = (2\pi)^{n/2} (\det \underline{B})^{-1/2} \cdot \exp(\tfrac{1}{2}\langle \underline{B}^{-1}\underline{w}, \underline{w}\rangle)$$

(where $\underline{v}, \underline{w}$ in $\mathbb{R}^n$ and $\underline{B}$ is $n \times n$ matrix) and obtain, through integration by parts,

$$\begin{aligned}\bar{m}(\bar{\underline{z}}, \underline{P}) = s \cdot \det(\underline{I} + \underline{A}\underline{P}_1)^{-1/2} \left[\bar{z}_1 - p_{11}(p_{11} + \langle \underline{V}\underline{p}, \underline{p}\rangle)^{-1} \langle \underline{V}\underline{p}, \bar{\underline{u}}\rangle\right] \cdot \\ \cdot \exp(-\tfrac{1}{2}\langle \underline{V}\bar{\underline{u}}, \bar{\underline{u}}\rangle + \tfrac{1}{2}(p_{11} + \langle \underline{V}\underline{p}, \underline{p}\rangle)^{-1} \langle \underline{V}\underline{p}, \bar{\underline{u}}\rangle^2) - s\, b\, \bar{z}_1 .\end{aligned} \tag{1a}$$

Here $\underline{P} = \begin{bmatrix} p_{11} & \underline{p}^t \\ \underline{p} & \underline{P}_1 \end{bmatrix}$, $\underline{p} = (p_{12},\ldots,p_{1n})^t$ (the vector of covariances of character 1 and characters i, $i \geq 2$), $\underline{P}_1$ is the covariance matrix of characters 2,...,n. Furthermore,

$$\underline{Q} = \begin{bmatrix} q_{11} & \underline{q}^t \\ \underline{q} & \underline{Q}_1 \end{bmatrix} = \underline{P}^{-1},\ \underline{Q}_1^{-1} = \underline{P}_1 - \frac{1}{p_{11}}\ \underline{p} \otimes \underline{p}^t \text{ and } \underline{V} = \underline{Q}_1 - \underline{Q}_1(\underline{Q}_1+\underline{A})^{-1}\underline{Q}_1 = (\underline{Q}_1^{-1}+\underline{A}^{-1})^{-1}.$$

In the special case where character 1 is uncorrelated to the other characters, i.e. $\underline{p} = \underline{O}$, we obtain:

$$\bar{m}(\bar{\underline{z}},\underline{P}) = s.\det(\underline{I}+\underline{A}\underline{P}_1)^{-1/2}.\bar{z}_1.\exp(-\tfrac{1}{2}\langle\underline{V}\bar{\underline{u}},\bar{\underline{u}}\rangle) - s\,b\,\bar{z}_1 \qquad (1b)$$

with $\underline{V} = (\underline{P}_1 + \underline{A}^{-1})^{-1}$.

If we consider only two characters, we obtain (with $\underline{P} = \begin{bmatrix} p_{11} & p_{12} \\ p_{12} & p_{22} \end{bmatrix}$, and $\underline{A} = a$)

$$\bar{m}(\bar{\underline{z}},\underline{P}) = s\alpha^{-3/2}(\bar{z}_1\alpha - \bar{z}_2 a p_{12}).\exp(-a\bar{z}_2^2/2\alpha) - s\,b\,\bar{z}_1 \qquad (1c)$$

where $\alpha = 1+ap_{22}$ (and $\underline{V} = a/\alpha$). For the two dimensional case the isoclines of the population's fitness landscape are shown in Fig. 1.

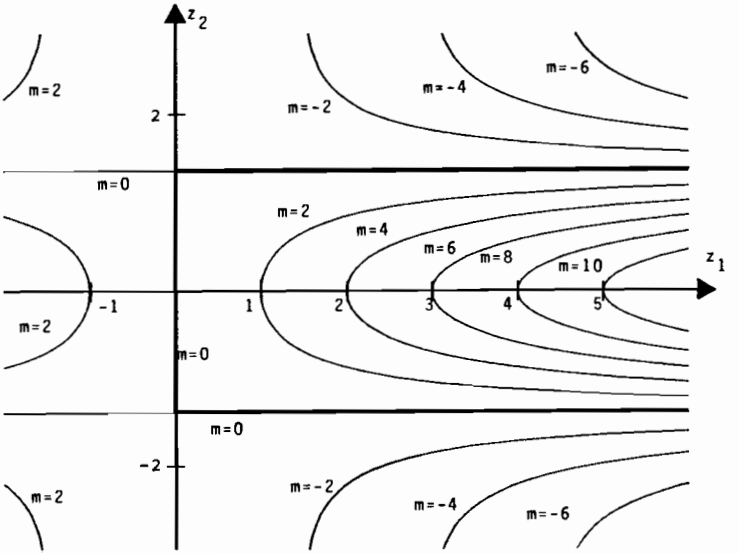


Figure 1a

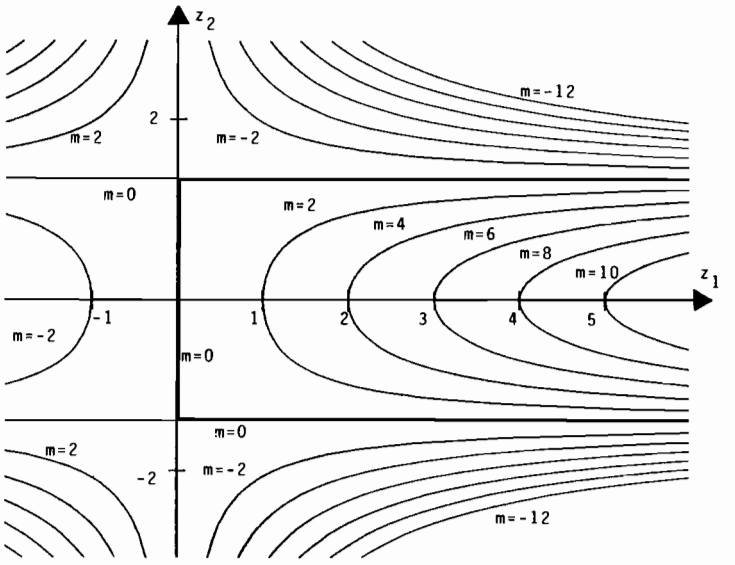


Figure 1b

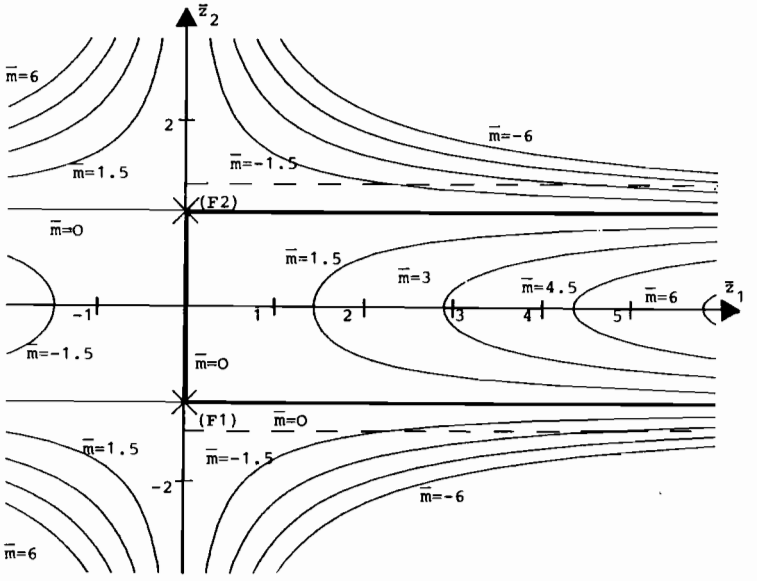


Figure 1c

Caption to Fig. 1: (1a) and (1b) show the contourlines of the individual fitness landscape according to formula (3) with b = 0.4 in (1a) and b = 0.9 in (1b). s and a are chosen such that in both cases the width of the individual's corridor is $BI = 2\sqrt{2}$ and the ascent is AJ = 2. Hence the main difference between these two parameter coices is the different selective disadvantage of individuals far away from the ridge.

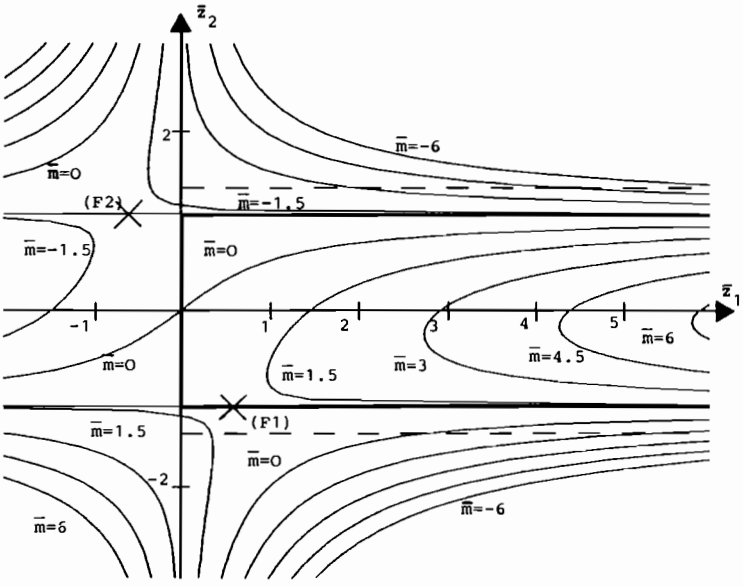


Figure 1d

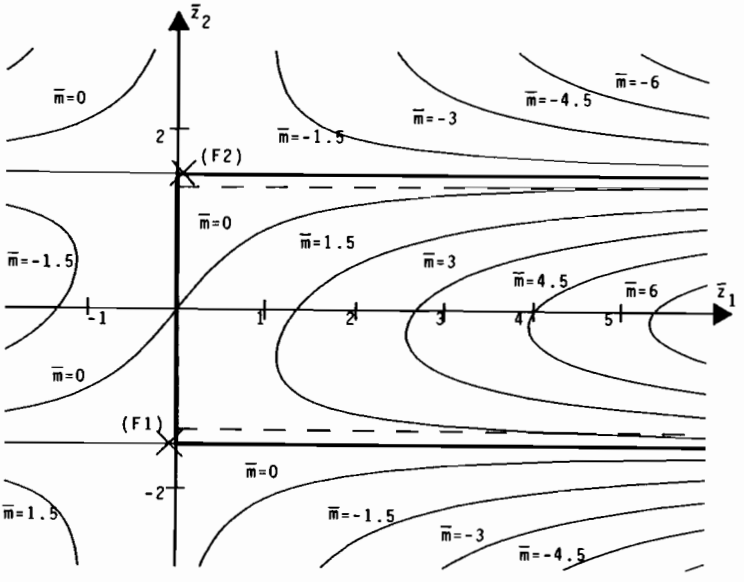


Figure 1e

Caption to Fig. 1 (continued): (1c) and (1d) show the contourlines of the population's fitness landscape corresponding to Fig.(1b) (see formula (1c)). In (1c) the phenotypic variances and covariances are $p_{11} = p_{22} = 1$ and $p_{12} = 0$, in (1d) they are $p_{11} = p_{22} = 1$ and $p_{12} = 0.75$. (1e) shows the contours of the population's fitness landscape corresponding to (1a) with $p_{11} = p_{22} = 1$ and $p_{12} = 0.75$. The dashed lines in (1c) - (1e) indicate the boundary of the individual's corridor, the bold lines that of the population's corridor.

## 3. ANALYSIS AND RESULTS

For simplicity in the sequel we will only consider the two-dimensional case, although most of the results may be derived for n-dimensions. But see Bürger (1985) for a more general treatment. From (1c) we obtain

$$\frac{\partial \bar{m}}{\partial \bar{z}_1} = s\alpha^{-1/2} \exp(-a\bar{z}_2^2/2\alpha) - sb$$
$$\frac{\partial \bar{m}}{\partial \bar{z}_2} = -s\alpha^{-3/2} a(p_{12} + \bar{z}_1\bar{z}_2 - \bar{z}_2^2 a\, p_{12}/\alpha)\exp(-a\bar{z}_2^2/2\alpha). \qquad (5)$$

Thus (2) reads

$$\dot{\bar{z}}_1 = g_{11}\, \partial\bar{m}/\partial\bar{z}_1 + g_{12}\, \partial\bar{m}/\partial\bar{z}_2$$
$$\dot{\bar{z}}_2 = g_{12}\, \partial\bar{m}/\partial\bar{z}_1 + g_{22}\, \partial\bar{m}/\partial\bar{z}_2 \qquad (2a)$$

with $\partial\bar{m}/\partial\bar{z}_i$ given above.

As the additive genetic covariance matrix $\underline{G}$ is assumed to be positive definite (and hence non-singular), the equilibrium points of system (2) must satisfy grad $\bar{m} = \underline{0}$. Together with (5) we obtain the following two equilibrium points:

$$(F\ 1)\quad Z_1 = -p_{12}(1 + 2\ln(b\alpha^{1/2}))/Z_2,\ Z_2 = -(-2\alpha\, \ln(b\alpha^{1/2})/a)^{1/2}$$
$$(F\ 2)\quad Z_1' = -Z_1,\ Z_2' = -Z_2$$

It can be shown easily that both equilibrium points have one positive and one negative eigenvalue and hence are saddle points.

As the adaptive landscape for the population, as given by $\bar{m}$, may considerably deviate from the adaptive landscape for individuals, as given by m, it is necessary to discern between an individual's corridor, defined as the region $\{(z_1,z_2)\colon z_1 \geq 0$ and $z_2^2 \leq (2\ln b)/a\}$, and a population's corridor, defined as $\{(\bar{z}_1,\bar{z}_2)\colon \bar{z}_1 \geq 0$ and $\bar{z}_2^2 \leq (-2\alpha/a)\ln b\alpha^{1/2}\}$. In the first case this is exactly the subregion of the right half plane where individual fitness is positive and in the second case this is the subregion of the right half plane where population fitness is positve, presupposed that the characters are uncorrelated. We denote by $AI = s(1-b)$, $AP = s(\alpha^{-1/2}-b)$, $BI = 2(-2(\ln b)/a)^{1/2}$ and $BP = 2((-2\alpha/a)\ln b\alpha^{1/2})^{1/2}$ resp. the ascent (along the axis) of the individual's and population's corridor and the width of the individual's and population's corridors. Note that AP is - up to the factor $g_{11}$ the evolutionary rate along the corridor axis if the characters are uncorrelated.

The first fact that should be noted is that a necessary and sufficient condition for the existence of a population's corridor (i.e. AP and BP are strictly positive) is that $b\alpha^{1/2} < 1$, or equivalently $p_{22} < (1-b^2)/ab^2$. Hence, a population can only move uphill along the ridge in our landscape if there is not too much variation in the character that is under stabilizing selection (i.e. $\dot{\bar{z}}_1 > 0$ close to the axis $z_2 = 0$). The same phenomenon, namely the existence of an upper bound of adaptivley reasonable phenotypic variance for the evolution of functionally coupled characters has already been observed in Bürger (1984) for the fitness function defined in (4).

However, in the present case where stabilizing selection is assumed to be Gaussian a new phenomenon arises. If $b < \exp(-\alpha \ln \alpha^{1/2}/ap_{22}) < 1$, which means that if the selective disadvantage of individuals being far away from the corridor is weak, then the population's corridor becomes wider than the individual's corridor. Furthermore, if $p_{22} < (1-b^2e)/ab^2e$ (e denotes Euler's constant), or equivalently $b\alpha^{1/2} < e^{-1/2}$, then for $p_{12} > 0$ the fixed point (F 1) lies in the left half plane and (F 2) in the right half plane, contrary to a quadratically deviating fitness function such as (4) or to the case of $b\alpha^{1/2} > e^{-1/2}$. See also Fig. 1.

Now lets turn to the dynamics of system (2a). Throughout we shall assume $b\alpha^{1/2} < 1$, i.e. there exists a population's corridor. If the two characters are genetically and phenotypically uncorrelated, so that $g_{12} = 0$ and $p_{12} = 0$ then

$$\frac{d}{dt}\bar{z}_2^2 = 2\bar{z}_2\dot{\bar{z}}_2 = -2s\alpha^{-3/2}a\, g_{22}\bar{z}_1\bar{z}_2^2 \exp(-a\bar{z}_2^2/2\alpha) \leq 0$$

if $\bar{z}_1 \geq 0$. As $b\alpha^{1/2} < 1$ we have

$$\dot{\bar{z}}_1 = g_{11}s(\alpha^{-1/2} \exp(-a\bar{z}_2^2/2\alpha) - b) \geq 0$$

for $\bar{z}_2^2 \leq BP^2/4$. Hence the population's corridor is positively invariant and each population starting within the corridor will converge to the axis and evolve along it. This result can be proved for much more general fitness functions, i.e. for functions of the form

$$m(\underline{z}) = m^0(z_1)m^1(\underline{u})$$

with $\partial m^0/\partial z_1 > 0$, $m^1(\underline{u}) = f(\langle \underline{Au}, \underline{u} \rangle)$ and $df/dx < 0$ (Bürger 1985).

Next let us drop the assumption $p_{12} = 0$ and assume $p_{12} > 0$ (if $p_{12} < 0$ symmetrical results are obtained). Thus the characters are still genetically uncorrelated but exhibit a positive phenotypic correlation. This gives also raise to a change in the adaptive landscape (see Fig. 1 and equ. (1c)) and therefore the dynamical behaviour of the population will change, although the fitness landscape for individuals remains the same. In particular, in order to be able to move uphill in the corridor it is not sufficient for a population to start within the population's corridor, since there exists a subregion from which no evolution in this direction is possible (see Fig. 2).

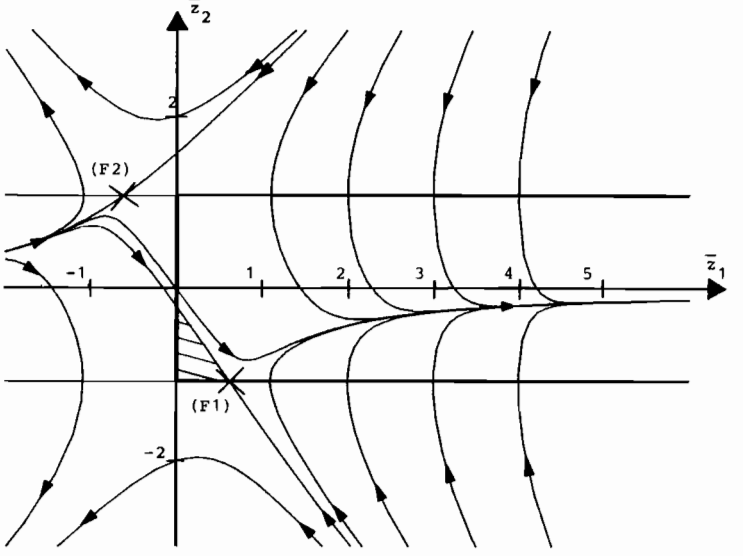


Figure 2a

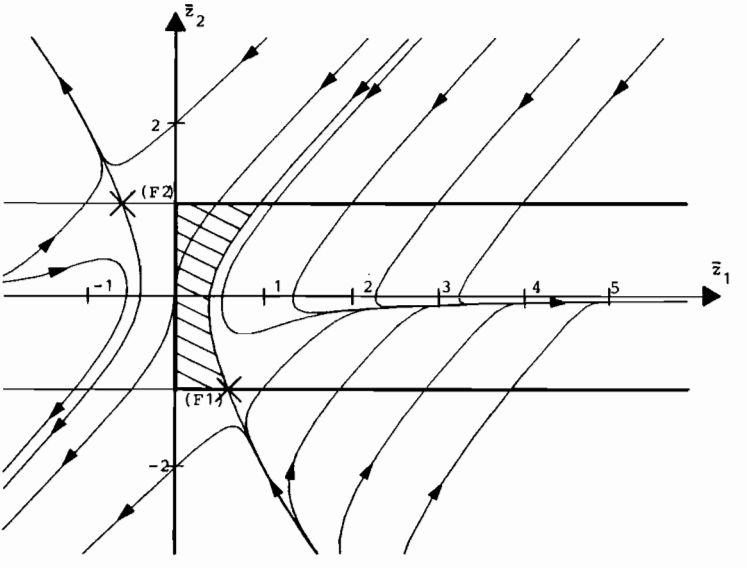


Figure 2b

Figures (2a) and (2b) show the trajectories of a population in the fitness landscape with contours as in Fig. (1d), i.e. $p_{11} = p_{22} = 1$, $p_{12} = 0.75$. The vast majority of individuals in the population has positive fitness, as the width of the individual's corridor is $2\sqrt{2}$. In (2a) the genetic covariance matrix is given by $g_{11} = g_{22} = 0.25$ and $g_{12} = 0$, in (2b) we have $g_{11} = g_{22} = 0.25$ and $g_{12} = 0.20$. The dashed area is the subregion of the corridor from which no evolution along the ridge can occur.

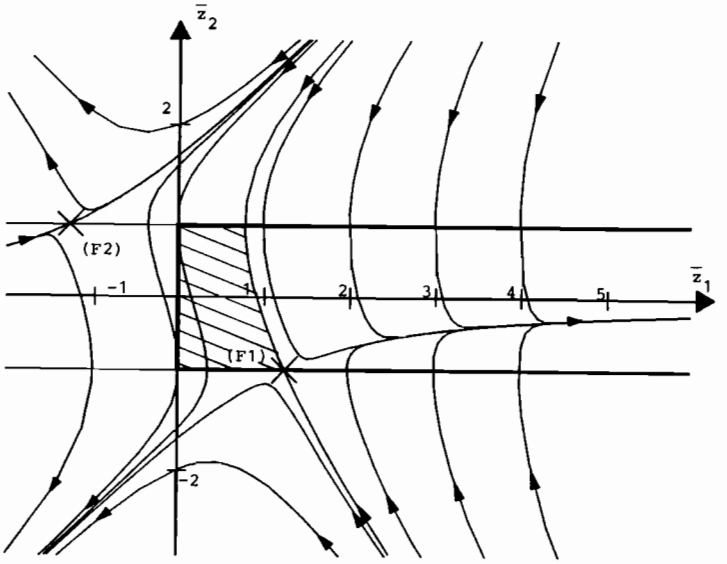


Figure 2c

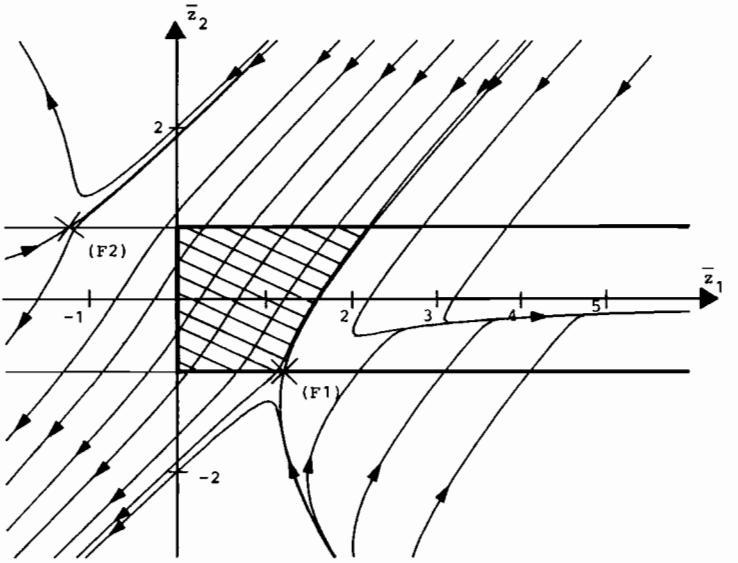


Figure 2d

Figures (2c) and (2d) show the trajectories of a population with parameters $p_{11} = p_{22} = 1.5$, $p_{12} = 1.125$, $g_{11} = g_{22} = 0.375$ and $g_{12} = 0$ (resp. $g_{12} = 0.30$) in (2c) (resp. (2d)). Thus relative to Fig. (2a) and (2b) the covariance matrices have been multiplied by a factor 1.5. Still about one half of the individuals has positive fitness. The subregion from which no evolution along the ridge can occur has been considerably increased by this change in the covariance matrices.

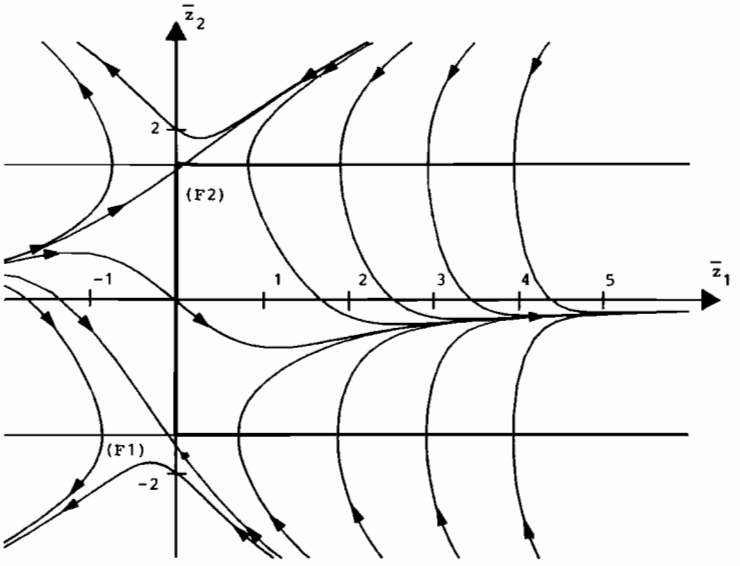


Figure 2e

Figure (2e) shows the trajectories of a population in the fitness landscape with contours as in Fig. (1e) with covariance matrices as in Fig. (2a). As in this case individuals which are far away from the corridor have only a slight selective disadvantage, no constraints for evolving along the ridge occur.

However, if the population is already sufficiently far uphill the ridge it will evolve along it. We can show analytically that convergence occurs if the population starts within the region

$$\{(\bar{z}_1,\bar{z}_2):\ \bar{z}_1 \geq |z_1| \quad \text{and} \quad \bar{z}_2^2 \leq z_2^2 = BP^2/4\}$$

First we already know that $\dot{\bar{z}}_1 \geq 0$ if $\bar{z}_2^2 \leq BP^2/4$. Moreover, we have

$$\frac{d}{dt}\bar{z}_2^2 = 2\bar{z}_2\dot{\bar{z}}_2 =$$

$$= -2s\alpha^{-3/2} a\, g_{22}\bar{z}_2(p_{12} + \bar{z}_1\bar{z}_2 - \bar{z}_2^2 a\, p_{12}/\alpha).\exp(-a\bar{z}_2^2/2\alpha)$$

which is negativ if and only if

$$\bar{z}_1\bar{z}_2^2 + p_{12}\,\bar{z}_2(1 - \bar{z}_2^2 a/\alpha) \geq 0.$$

From this it follows immediately that the subregion of the corridor where $\bar{z}_1 \geq |z_1|$ is positively invariant. Moreover, the above relation holds if

$$\bar{z}_2^2 \geq \frac{|p_{12}\,\bar{z}_2|}{|\bar{z}_1|}\,|\bar{z}_2^2(a/\alpha)-1|.$$

As we assume $|\bar{z}_2| \leq BP/2$, the right hand side tends to zero if $\bar{z}_1$ tends to infinity. Thus we have shown

$$\frac{d}{dt}\,\bar{z}_2^2 \leq 0 \text{ if } BP^2/4 \geq \bar{z}_2^2 \geq C(\bar{z}_1),$$

with $\lim C(\bar{z}_1) \to 0$, $\bar{z}_1 \to \infty$. Together with $\dot{\bar{z}}_1 > 0$ for $|\bar{z}_2| \leq BP/2$ this proves our assertion. An analogous result has been proved for fitness given by equ. (4) (Bürger 1984). To obtain an analytical estimate for the subregion of the corridor where no convergence along the ridge can occur seems to be rather difficult. The only thing that is obvious is, that such a region exists since $\frac{d}{dt}\,\bar{z}_2^2 > 0$ for $\bar{z}_1 < z_1$ with $\bar{z}_2 = z_2$ and for $\bar{z}_1 < z_1'$ with $\bar{z}_2 = z_2'$. Phase portraits are given in Fig. 2.

Of particular importance for the size of the region from which no evolution along the corridor axis is possible, is the ratio of a (describing the strength of stabilizing selection) and $p_{12}$ and $p_{22}$. If the individual's fitness landscape is held constant, and $p_{12}$ and $p_{22}$ are multiplied by some factor larger than 1, the population's corridor becomes narrower and the fixed point (F 1) shifts into direction of increasing $\bar{z}_1$ (and decreasing $|\bar{z}_2|$). Moreover, the rate of evolution $\dot{\bar{z}}_1$ along the ridge decreases significantly (see Fig. 2).

If part of the phenotypic covariance $p_{12}$ is due to genetic covariance, i.e. $g_{12} \neq 0$, it appears that it becomes more difficult to evolve along the ridge (see Fig. 2). However we have no analytical estimates.

Finally we shall investigate a phenomenon that has been discovered by Rechenberg (1973). Rechenberg assumed a fitness function of the form

$$m(\underline{z}) = \begin{cases} z_1, & |z_i| \leq C,\ i \geq 2 \\ 0, & \text{otherwise} \end{cases}$$

and proved the existence of an optimal amount of variance (the covariance was assumed to be zero and all variances to be equal) in the sense that this variance leads to a maximal evolutionary rate. Rechenberg's model, however, is based on optimization theory and not on population genetics. Wagner (1984 a,b) investigated this model in the framework of quantitative genetics on the basis of Lande's equations. He found that also in this context optimal variances and maximal evolutionary rates exist, but only if at least four characters are involved. For the fitness function (4) the same holds already for two characters. Subsequently we shall investigate this problem for the fitness function given by (3).

Instead of $\underline{P}$ and $\underline{G}$ we will consider $h\underline{P}$ and $h\underline{G}$ (where multiplication by h is componentwise) and look whether there exists an $h_o$ such that $\dot{\bar{z}}_1$ is maximal. For simplicity let us assume $g_{1i} = 0$, $i = 2,\ldots,n$. Denoting $\underline{V}_h = (h\underline{P}_1 + \underline{A}^{-1})^{-1}$, $\bar{m}_h = \bar{m}(\underline{\bar{z}}, h\underline{P})$ and $p(h) = \det(\underline{I} + h\,\underline{A}\,\underline{P}_1)$ we obtain:

$$\frac{\partial}{\partial h}\dot{\bar{z}}_1 = \frac{\partial}{\partial h}(hg_{11}\frac{\partial \bar{m}_h}{\partial \bar{z}_1}) = g_{11}\frac{\partial \bar{m}_h}{\partial \bar{z}_1} + hg_{11}\frac{\partial^2 \bar{m}_h}{\partial h \partial \bar{z}_1} =$$

$$= g_{11}s\, p(h)^{-1/2} \exp(-\frac{1}{2}\langle \underline{V}_h \underline{\bar{u}}, \underline{\bar{u}}\rangle)(1 - \frac{h}{2}\frac{p'(h)}{p(h)} + \frac{h}{2}\langle \underline{V}_h \underline{P}_1 \underline{V}_h \underline{\bar{u}}, \underline{\bar{u}}\rangle) - g_{11}sb.$$

If we write

$$p(h) = \det(\underline{I} + h\underline{A}\underline{P}_1) = h^{n-1}\det(h^{-1}\underline{I} + \underline{A}\underline{P}_1) = \sum_{k=0}^{n-1} a_k h^k$$

we see that $a_k$ is the (n-1-k)th coefficient of the characteristic polynomial of $\underline{A}\underline{P}_1$. As $\underline{A}\underline{P}_1^k$ is positive definite, $a_k > 0$, $k \geq 0$, and in particular $a_o = 1$.

It follows that $p(h)$ and $p(h)^{1/2}$ are monotonically increasing for $h \geq 0$. Moreover, $h \cdot \frac{p'(h)}{p(h)}$ increases monotonically ($h \geq 0$). To show this consider

$$h\cdot\frac{d}{dh}(h\frac{p'(h)}{p(h)}) = p(h)^{-2}(p(h)h(hp'(h))' - (hp'(h))^2) =$$

$$= p(h)^{-2}\Big(\sum_{k=0}^{n-1} a_k h^k \cdot \sum_{j=0}^{n-1} j^2 a_j h^j - \Big(\sum_{k=0}^{n-1} k\, a_k h^k\Big)^2\Big) =$$

$$= p(h)^{-2}\sum_{k,j=0}^{n-1} h^{k+j} a_k a_j j(j-k) =$$

$$= p(h)^{-2}\sum_{l=0}^{n-1} h^l \sum_{j=1}^{n} a_j a_{l-j}\, j(2j-l) > 0.$$

This shows that for $\underline{\bar{u}} = \underline{0}$

$$\frac{\partial}{\partial h}\dot{\bar{z}}_1 = g_{11}s\, p(h)^{-1/2}\,(1 - \frac{h}{2}\frac{p'(h)}{p(h)} - bp(h)^{1/2})$$

has a unique zero $h_o$ if $n \geq 2$ and $b > 0$ and $\dot{\bar{z}}_1$ has a unique maximum. This is qualitatively the same result as that for a fitness function of the form (4).

If $b = 0$ then such a $h_o$ only exists if $n \geq 4$, as $0 < \frac{h}{2}\cdot\frac{p'(h)}{p(h)} < \frac{n-1}{2}$ and $\lim_{h\to\infty} \frac{h}{2}\cdot\frac{p'(h)}{p(h)} = \frac{n-1}{2}$. This is the same as Wagner's (1984 a,b) result. It seems to be probable that a negative fitness outside the corridor, considered by Wagner, leads to the existence of an optimal evolutionary rate for $n \geq 2$. By a continuity argument it can be inferred that maximal evolutionary rates also exist near the corridor axis.

## 4. CONCLUSIONS

The present analysis shows that the pattern of variation and covariation in a population plays an important role for the evolution of functionally coupled characters in an adaptive landscape with multiple peaks. There are three main findings which are in best accordance with the results derived in Bürger (1984).

(i) There exists an upper bound for the adaptively reasonable amount of phenotypic variance of characters which are under stabilizing selection. If this bound is exceeded no evolution along the ridge is possible, although physiologically it is favourable. This bound depends on the shape and width of the corridor and on the fact that we have multiple peaks.

(ii) An 'unfavourable' covariance pattern yields constraints on the possible directions of evolutionary change. We proved that if the corridor axis is collinear with one of the axis of the state space then each population with zero phenotypic and genetic covariance starting within the corridor converges to the axis and evolves along it. Hence the population will develop the selectively favoured complex of functionally coupled characters. If the corridor is in arbitrary position the condition of zero phenotypic (resp. genetic) covariance has to be replaced by the condition that one eigenvector of the matrix $\underline{P}$ (resp. $\underline{G}$) points into direction of the corridor axis. If an deviation of $\underline{P}$ and/or $\underline{G}$ from this 'optimal' form occurs, there is a subregion of the corridor from which no evolution along the ridge is possible. Hence the complex of functionally coupled characters cannot evolve. For one and the same individual's fitness landscape this subregion increases in size if the deviation of the phenotypic and/or genetic covariances from their optimal values increases or if the phenotypic variances of the characters under stabilizing selection increase (see also (i)). In the latter case also the width of the corridor decreases. On the other hand if $\underline{P}$ and $\underline{G}$ as well as the width of the individual's corridor and the ascent along the ridge are held constant, the size of this subregion strongly depends (in the obvious way) on the parameter b, which measures the selective disadvantage of individuals being for away of the corridor.

(iii) There exists an optimal amount of overall variability resulting in a maximal evolutionary rate. To be precise, there is a positive number $h_o$ such that a population with covariance matrix $h_o\underline{P}$ evolves at an higher rate along the ridge than any population with covariance matrix $h\underline{P}$, $h \neq h_o$.

To sumarize, it has been shown that for the evolution of functionally coupled quantitative traits in a fitness landscape with multiple peaks there exists an optimal variance-covariance pattern of a population in a twofold sense. Any deviation from this pattern leads both to a restriction on the set of initial conditions enabling the population to adapt the selectively favoured configuration of characters as well as to a decrease in the rate adaptation. The constraints arising in this manner, namely the inability of a population to evolve into directions which are physiologically possilbe and even favourable, are population genetic constraints in the intrinsic sense as they are caused by the genetic structure of populations.

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# GRADIENTS VERSUS CYCLING IN GENETIC SELECTION MODELS

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We review the hierarchy of (continuous time) selection models starting with the classical Fisher's viability selection model, and its generalizations when allowing mutations, recombination, sex-dependent viabilities, fertility selection and different mortality rates. We analyse the question in which way Fisher's "Fundamental Theorem of Natural Selection" and Kimura's Maximum Principle can be extended to these more general situations. It turns out that in many cases this is principally impossible since the dynamics becomes cycling or even chaotic.

## 1. VIABILITY SELECTION

1.1. The basic selection model in population genetics was introduced by Fisher (1930). He considered one gene locus with n possible alleles $A_1,\dots,A_n$. Let $x_1,\dots,x_n$ be the frequencies of these alleles within the gene pool of the adult population. Assuming random mating, the frequency of the genotype $A_iA_j$ among the zygotes will be - according to the Hardy-Weinberg law - $2x_ix_j$ (if $i\neq j$) resp. $x_i^2$ (if $i = j$). Now assume that the individuals are not equally adapted to the environment and that a genotype $A_iA_j$ will survive until adult age only with probability $w_{ij}$. Then $w_{ij}\geq 0$, $w_{ij} = w_{ji}$ and $w_{ij}$ is also called the fitness of $A_iA_j$. The number of adults $A_iA_j$ in the next generation is therefore proportional to $w_{ij}x_ix_j$ and the frequency of the gene $A_i$ is then given by the recurrence relation

$$x_i' = x_i \sum_{j=1}^{n} w_{ij} x_j / \bar{w} \tag{1}$$

where

$$\bar{w} = \sum_{r,s=1}^{n} w_{rs}x_rx_s \tag{2}$$

the mean fitness of the whole population is needed as a normalization factor to guarantee $\Sigma x_i = \Sigma x_i' = 1$. Instead of assuming separate generations one may also consider overlapping generations, which leads to the differential

equation

$$\dot{x}_i = x_i\Big(\sum_{j=1}^{n} w_{ij}x_j - \bar{w}\Big) \tag{3}$$

which could also be obtained by a limiting argument from (1), since $x_i' - x_i = \dot{x}_i/\bar{w}$. The state space of both (1) and (3) is the probability simplex

$$S_n = \{x = (x_1,\ldots, x_n) : \Sigma x_i = 1,\ x_i \geq 0\}.$$

The selection equations (1) and (3) are rather well understood and their dynamics is characterized by two essential features:

1) FISHER's Fundamental Theorem of Natural Selection: The mean fitness $\bar{w}$ increases steadily along the orbits of both (1) and (3).

Mathematically speaking this means that mean fitness is a Lyapunov function:

$$\dot{\bar{w}}/2 = \Sigma\, w_{ij}\dot{x}_i x_j = \Sigma\, x_i w_i (w_i - \bar{w}) = \Sigma\, x_i (w_i^2 - \bar{w}^2) = \Sigma\, x_i (w_i - \bar{w})^2 \geq 0.$$

i.e. the change in mean fitness is twice the variance of fitness of the population. For (1) the proof is more technical (see e.g. EWENS (1979)). As a consequence all orbits of (1) and (3) will converge to the fixed points.

This picture of a population steadily climbing uphill in a fitness landscape is very attractive and satisfying and still very common among population genetists (despite the contrary results we will discuss below). Historically it was a justification of Darwinism on the basis of Mendelism, two (r)evolutionary theories which had been considered to be incompatible before.

2) KIMURA's Maximum Principle (1958) states that the change of the state of the population proceeds in such a way that the increase of mean fitness is the maximal possible. Mathematically this would mean that (3) is a gradient system: The orbits follow the steepest ascent on the fitness landcape $\bar{w}$, they are orthogonal to its contour lines. But this assertion is obviously wrong since e.g. the boundary of the state space $S_n$ would not be an invariant set.

But as often, when great men make "obviously wrong" statements, there is some truth behind it. It was Shahshahani (1979) who noticed that one needs only to redefine "orthogonality", i.e. to introduce a new Riemannian metric at every point of the simplex. This Shahshahani metric at $p \in S_n$ is simply given by

$$\langle x,y\rangle_p = \Sigma\, \frac{x_i y_i}{p_i} \qquad \text{for } x,y \in T_p S_n. \tag{4}$$

More generally it can be shown (see e.g. Sigmund(1984)), that

$$\dot{x}_i = x_i\,(f_i(x) - \bar{f}), \qquad \bar{f} = \Sigma\, x_i f_i \tag{5}$$

is a Shahshahani gradient on $S_n$, if $\dot{x}_i = f_i(x)$ is a usual gradient, i.e.

$f_i(x) = \partial V/\partial x_i$. For the selection equation (3) $f_i(x) = \Sigma\, w_{ij}x_j = \frac{1}{2}\frac{\partial \bar{w}}{\partial x_i}$ holds, since the fitness matrix $(w_{ij})$ is symmetric.

Another (equivalent) possibility to "save" Kimura's principle would be to make a change of coordinates: with $y_i = x_i^{1/2}$, (3) becomes a gradient system ( with respect to the usual Euclidean metric) on the sphere $\Sigma y_i^2 = 1$. (see Akin (1979)).

1.2. As a first generalization of this basic selection model we consider a model allowing mutations. Following Crow - Kimura (1970) or Hadeler (1981) mutations occur within the pool of newly produced genes, with probability $\varepsilon_{ij}$ from $A_j$ to $A_i$, after selection has changed the gene frequencies as before from $x_i$ to $x_i w_i/\bar{w}$ . So the action of selection and mutation is described by the recurrence equation

$$\bar{w}\, x_i' = \sum_j \varepsilon_{ij}x_j \sum_k w_{jk}x_k \tag{6}$$

which is usually replaced by the analogous differential equation

$$\dot{x}_i = \sum_{j,k} \varepsilon_{ij}x_j w_{jk}x_k - x_i\bar{w}. \tag{7}$$

Akin (1979) considers a different model, with simultaneous action of selection and mutation:

$$\dot{x}_i = x_i \Big( \sum_j w_{ij}x_j - \bar{w} \Big) + \sum_j \left( \varepsilon_{ij}x_j - \varepsilon_{ji}x_i \right) \tag{8}$$

Mathematically, Akin's uncoupled version can be obtained as limit case $\delta \to 0$ from (7), after the scaling

$$\varepsilon_{ij} \to \delta\varepsilon_{ij} \ (i \neq j), \quad w_{ij} \to 1 + \delta w_{ij}, \quad t \to t/\delta. \tag{9}$$

The special case of equal mutation rates, say

$$\varepsilon_{ij} = \varepsilon_i \quad (i \neq j), \tag{10}$$

deserves separate analysis. Hadeler (1981) studied in detail the case $\varepsilon_i = \varepsilon/n$, and after proving local stability, he posed the problem to find a Lyapunov function for (7) to globalize his results. This is now easily done: With his assumptions, (7) simplifies to (for the more general case (10) see Hofbauer (1984)):

$$\begin{aligned} \dot{x}_i &= x_i(w_i - \bar{w}) + \varepsilon(\bar{w}/n - x_i w_i) \\ &= x_i(f_i(x) - \bar{f})\,\bar{w} \end{aligned} \tag{11}$$

with

$$f_i(x) = (1-\varepsilon)\frac{w_i}{\bar{w}} + \frac{\varepsilon}{nx_i}, \qquad \bar{f} = \Sigma x_i f_i = 1.$$

Since the $f_j(x)$ fulfill the integrability conditions, Sigmund's result on (5) applies and (11) is a Shahshahani gradient with the potential function

$$V(x) = \frac{1-\varepsilon}{2} \log \bar{w} + \frac{\varepsilon}{n} \sum_{i=1}^{n} \log x_i . \qquad (12)$$

In particular one can take $\bar{w} \cdot (x_1 x_2 \ldots x_n)^{\alpha}$, $\alpha = 2\varepsilon/n(1-\varepsilon)$ as the Lyapunov function for the selection - mutation equation (7) under Hadeler's conditions which generalizes the mean fitness function $\bar{w}$ in Fisher's selection model. So in this special case all the results on gradient - like behaviour carry over. For Akin's equations (8) essentially the same result holds, but with a different potential:

$$V(x) = \frac{1}{2} \bar{w} + \frac{\varepsilon}{n} \sum_{i=1}^{n} \log x_i . \qquad (13)$$

Now suppose that the mutation rates are not equal. Thanks to Akin's geometric analysis we know now that then the situation is much more delicate: The mutation field $\dot{x}_i = \Sigma \varepsilon_{ij} x_j - x_i$ is then no longer a gradient with respect to the Shahshahani metric. And Akin (1979) proved that - given any mutation matrix $(\varepsilon_{ij})$ not of the form (10) - one can always find selection matrices $(w_{ij})$, such that the combined field (8) undergoes a Hopf bifurcation and periodic orbits occur. By the above approximation argument (9) this result carries over to Hadeler's equations (7). This shows that the picture of an adaptive topography (see e.g. Wright (1931)) is no longer reasonable for arbitrary interactions of selection and mutation. The dynamics is no longer gradient-like. The frequency distribution need no longer converge to a stationary equilibrium state, but may oscillate forever. And it is very likely that even chaotic motions should be possible for these differential equations.

1.3. One simplistic assumption in Fisher's selection model is to allow selective differences of alleles at one gene locus only. But even the most primitive species have thousands of different loci on their chromosomes. So let us consider at least the case of two loci A and B with possible alleles $A_i$ $(1 \leq i \leq n)$, $B_j$ $(1 \leq j \leq m)$. Then there are $nm$ different types of gametes $A_iB_j$, the frequency of which we denote by $x_{ij}$. Assuming random mating the proportion of $A_iB_j/A_kB_l$ individuals will change from $x_{ij}x_{kl}$ to $w_{ij,kl}x_{ij}x_{kl}$ from zygote to adult age by natural selection. When haploid gametes are produced during meiosis, besides the parental combinations $A_iB_j$ and $A_kB_l$ also "recombinants" $A_iB_l$ and $A_kB_j$ will appear due to cross-overs which happen with a certain probability r depending on the distance between the two loci. This recombination fraction r takes its maximum possible value 1/2 if the two loci are on different chromosomes. This leads to the following modification of the recurrence equations (1) for the gamete frequencies $x_{ij}$ (see e.g. Karlin (1978), Pollak (1979)):

$$\bar{w}\, x_{ij}' = (1-r)x_{ij} \sum_{k,l} w_{ij,kl}x_{kl} + r \sum_{k,l} w_{il,kj}x_{il}x_{kj}$$

$$= x_{ij} \sum_{k,l} w_{ij,kl}x_{kl} - r\, D_{ij} \qquad (14)$$

with

$$D_{ij} = \sum_{k,l} (w_{ij,kl}x_{ij}x_{kl} - w_{il,kj}x_{il}x_{kj}) \qquad (15)$$

The $D_{ij}$ are called linkage disequilibria. Since usually $w_{ij,kl} = w_{il,kj}$ holds (= no "position effects"), $D_{ij} = 0$ holds if the gamete frequencies $x_{ij}$ can be written as product of the gene frequencies $p_i = \sum_{j=1}^{m} x_{ij}$ of $A_i$ and $q_j = \sum_{i=1}^{n} x_{ij}$ of $B_j$, i.e. if linkage equilibrium holds. It is easy to see that for recombination without selection all $D_{ij}$ tend to 0 and $x_{ij} = p_i q_j$ holds in the limit. On the other hand, if $r = 0$ (= very tight linkage), (14) may be viewed as a selection equation for $nm$ "alleles" $A_iB_j$ and so the selection part is again a gradient with respect to Shahshahani's metric on $S_{nm}$. But the recombination field is not and Akin (1979) could again prove that the interaction of both fields may lead to cycling. For the simplest case of two alleles at each of the two loci (TLTA) he computed also the higher order terms which govern the stability of the cycles and showed that both stable and unstable limit cycles are possible (see Akin (1982,1983)). In this case the differential equation version of (14) simplifies to

$$\dot{x}_i = x_i \left( \sum_{j=1}^{4} w_{ij}x_j - \bar{w} \right) + \xi_i rbD, \qquad i = 1,2,3,4 \qquad (16)$$

where $x_1, x_2, x_3, x_4$ are now the frequencies of the gametes $A_1B_1$, $A_1B_2$, $A_2B_1$, $A_2B_2$ resp., $D = x_1x_4 - x_2x_3$ is the linkage disequilibrium (15), $\xi_1 = -\xi_2 = -\xi_3 = \xi_4 = -1$, and b is the birth rate of the double heterozygote.

1.4. One basic assumption in all our previous models is that there are no sex-differences, i.e. the population may be treated essentially to be monoecious. We will now briefly discuss the simplest possible way of allowing sex-differences in the basic viability model. Let there again be $n$ alleles $A_1, \ldots, A_n$ at one gene locus, let $x_i, y_i$ be their frequencies in the adult female and male population and let $f_{ij}$ ($m_{ij}$) be the fitness of an $A_iA_j$ female (male) individual. Now a gene $A_i$ in the female gene pool comes from females $A_iA_j$ which have frequency $x_iy_j + x_jy_i$ at time of conception (random mating) of which only a proportion of $f_{ij}$ will survive. Hence the equations read as (see e.g. Ewens (1979), Karlin (1972,1984), Roux (1977))

$$x_i' = \frac{1}{2}\left[ x_i \sum_j f_{ij}y_j + y_i \sum_j f_{ij}x_j \right] \Big/ \sum_{r,s} f_{rs}x_ry_s$$

$$y_i' = \frac{1}{2}\left[ y_i \sum_j m_{ij}x_j + x_i \sum_j m_{ij}y_j \right] \Big/ \sum_{r,s} m_{rs}x_ry_s \qquad (17)$$

The differential equations are obtained in the usual way. If $m_{ij} = f_{ij}$ the subspace $x_i = y_i$ of the state space $S_n \times S_n$ is invariant and globally attracting and so (17) reduces to (1). Interesting special cases of (17) are $f_{ij} = 1$, where selection acts only on one sex, or $m_{ij} = \alpha f_{ij} + b$, where selection acts in the same way in both sexes but at a different scale. Here $x_i = y_i$ holds at equilibria and all eigenvalues are real. So it is likely that these equations are gradients. For other cases, e.g. $m_{ij} + f_{ij} = 1$, which is used for sex-ratio models by Karlin (1984), nonsymmetric equilibria are also possible. In any case, no global results seem to be known for the two-sex equation (17), if $n \geq 3$. For two alleles see the next section.

## 2. FERTILITY SELECTION

2.1. In all selection models described in § 1 the two main assumptions were random mating to have the zygote population in Hardy-Weinberg proportions, and selection acting only by viability differences on the different genotypes. These assumptions are essential in order to deal with gene frequences $x_i$ of alleles $A_i$ only. In a more general selection model one has to consider genotype frequencies $x_{ii}$ of $A_iA_i$ - zygotes and $2x_{ij}$ of $A_iA_j$ - zygotes ($i \neq j$), so that $\sum_{i,j=1}^{n} x_{ij} = 1$. Now let $m_{ij}(f_{ij})$ be the viabilities for (fe)male genotypes $A_iA_j$ and let $h(ij,rs)$ be the probability for a mating of an $A_iA_j$ - male with an $A_rA_s$-female times the fecundity of this type of mating. An $A_iA_j$-zygote is issued either from an $A_iA_r \times A_jA_s$ or an $A_jA_s \times A_iA_r$ mating (with any r,s). This gives the frequencies of the next zygote generation (see e.g. Roux (1977)):

$$\Phi\, x_{ij}' = \sum_{r,s} \frac{1}{2} \left[h(ir,js)\, m_{ir} f_{js} + h(js,ir) m_{js} f_{ir}\right] x_{ir} x_{js}. \tag{18}$$

With

$$F(ij,rs) = h(ij,rs)\, m_{ij} f_{rs} \tag{19}$$

and

$$f(ij,rs) = (F(ij,rs) + F(rs,ij))/2 \tag{20}$$

we observe that mathematically a viability + fertility selection model is reduced to a pure fertility selection model (since we count zygotes here instead of adults):

$$\Phi\, x_{ij}' = \sum_{r,s} f(ir,js)\, x_{ir} x_{js} \tag{21}$$

with

$\Phi = \sum f(ij,kl)\, x_{ij} x_{kl}$ the mean fertility of the population.

The corresponding differential equation reads

$$\dot{x}_{ij} = \sum_{r,s} f(ir,js)\, x_{ir} x_{js} - x_{ij}\, \Phi \tag{22}$$

These equations define a dynamics on the $\frac{n(n+1)}{2}$ - simplex which is now forward invariant. Up to the special cases of additive and multiplicative fertilities which will be treated in 2.3, almost nothing is known for the fertility equation (22) if $n \geq 3$. Only the case of $n = 2$ alleles is well-studied and essentially completely analysed (Hadeler and Liberman (1975), Hadeler and Glas (1983), Koth (1984)). In this case the equations reduce to (with $x_{11} = x$, $x_{12} = y$, $x_{22} = z$, and numbering the genotypes $A_1A_1, A_1A_2, A_2A_2$ by 1,2,3 resp.):

$$\begin{aligned}
\dot{x} &= f_{11}x^2 + 2f_{12}xy + f_{22}y^2 - x\,\Phi \\
\dot{y} &= f_{22}y^2 + f_{12}xy + f_{23}yz + f_{13}xz - y\,\Phi \\
\dot{z} &= f_{33}z^2 + 2f_{23}yz + f_{22}y^2 - z\,\Phi
\end{aligned} \tag{23}$$

To get rid of the condition $x + 2y + z = 1$, (23) is best studied in the new variables $X = x/y$, $Y = z/y$, leading to

$$\begin{aligned}
\dot{X} &= f_{22} + (2f_{12} - f_{22})\,X + (f_{11} - f_{12})\,X^2 - f_{23}XY - f_{13}X^2Y \\
\dot{Y} &= f_{22} + (2f_{23} - f_{22})\,Y + (f_{33} - f_{23})Y^2 - f_{12}XY - f_{13}XY^2
\end{aligned} \tag{24}$$

The main problem when studying a two-dimensional system like (24) is whether it admits periodic orbits. This question was recently solved by Hadeler and Glas (1983), who observed that (24) is "quasimonotone", i.e. all off-diagonal terms of the Jacobian are negative on the whole state space. They have excluded the existence of exponentially stable limit cycles for such systems (in any dimension!) and the existence of periodic orbits in two dimensions. Similar results were obtained by Hirsch (1982) who called such systems "competitive". Now our equations are of a more special form

$$\begin{aligned}
\dot{X} &= a(X) - Y\,b(X) \\
\dot{Y} &= c(Y) - X\,d(Y)
\end{aligned} \tag{25}$$

with $b(X)$, $d(Y) > 0$ implying the "competitive" character. This leads to a more refined result: (24) is a gradient if we again choose a suitable Riemannian metric, or make a change of coordinates. The potential is given by

$$V(X,Y) = \int \frac{a(X)}{b(X)}\,dX - XY + \int \frac{c(Y)}{d(Y)}\,dY. \tag{26}$$

Then

$$\dot{V} = \left(\frac{a(X)}{b(X)} - Y\right)\dot{X} + \left(\frac{c(Y)}{d(Y)} - X\right)\dot{Y} \equiv b(X)^{-1}\,\dot{X}^2 + d(Y)^{-1}\,\dot{Y}^2 \geq 0$$

and so V is a Lyapunov function. The concrete form of V however is rather messy and it seems to be impossible to generalize this result to $n \geq 3$ alleles. In fact nothing concerning existence of Lyapunov functions or cycling is known for the general n-allelic fertility equation.

2.2. Now reconsidering the derivation of the fertility equation (22) - or any of the above differential equations - we see that it was obtained by a limit process or rather by analogy from the discrete time model (21), a point which has often been criticized, especially for the selection equation (3), see e.g. Ewens (1979). A true model for overlapping generations leading to a differential equation was first worked out by Nagylaki and Crow (1974), see also Ewens (1979), which can be roughly described as follows: the frequencies $x_{ij}(t)$ of $A_iA_j$ will increase in a small time interval $\Delta t$ due to births by $f(ir,js)x_{ir}x_{js}\,\Delta t$, with $f(ir,js)$ measuring again the fertility of a $A_iA_r \times A_jA_s$ mating, and decrease due to deaths by $d_{ij}\,x_{ij}\,\Delta t$, with $d_{ij}$ being the death rate of $A_iA_j$. This leads to

$$\dot{x}_{ij} = \sum_{r,s} f(ir,js)\, x_{ir}x_{js} - d_{ij}x_{ij} - x_{ij}\,\Phi \tag{27}$$

with

$$\Phi = \sum_{ijkl} f(ij,kl)\, x_{ij}x_{kl} - \sum_{ij} d_{ij}\, x_{ij}$$

denoting the mean fecundity minus the mean mortality, whose appearance in (27) ensures again that the relation $\sum_{i,j} x_{ij} = 1$ is kept invariant. So within a continuous time model, not only different fertility rates but also different mortality rates arise in a natural way. The continuous fertility-mortality equation is therefore more general than (22). Only in the case of equal mortality rates $d_{ij} \equiv d$, (27) is equivalent to (22).

With different mortality rates, (27) cannot be a gradient, even for $n = 2$, as was recently discovered by Koth (1984): Introducing the same coordinates X,Y which simplify (23) to (24), (27) transforms for $n = 2$ into the following generalization of (24):

$$\begin{aligned}
\dot{X} &= f_{22} + (2f_{12} - f_{22} + 2(d_2 - d_1))\, X + (f_{11} - f_{12} + d_2 - d_1)\, X^2 + \\
&\quad + (-f_{23} + d_2 - d_1)\, XY - f_{13}X^2Y \\
\dot{Y} &= f_{22} + (2f_{32} - f_{22} + 2(d_2 - d_3))\, Y + (f_{33} - f_{32} + d_2 - d_3)\, Y^2 + \\
&\quad + (-f_{12} + d_2 - d_3)\, XY - f_{13}\, XY^2
\end{aligned} \tag{28}$$

But now the coefficients of XY need no longer be negative and the system is not competitive in general. So the above argument does not work. And in fact Koth (1984) constructed examples where (28) has a fixed point with complex eigenvalues (so it cannot be a gradient), which - when varying some parameter - cross the imaginary axis. Hence Hopf bifurcations occur and periodic orbits are possible for (28). A more refined analysis of the higher order terms, using Marsden - Mc Cracken's (1976) formula, shows that both stable and unstable periodic orbits may occur. But it seems that these orbits are limited in size, they generally disappear very soon by a blue-sky ( = homoclinic) bifurcation.

2.3. We conclude with some remarks concerning the interrelationship of the fertility equation with other selection models, in order to obtain more insight into the logical hierarchy of selection models, as indicated in the diagram in 3.2.

The first observation is rather unexpected and surprising: the two-allelic fertility-mortality equation occurs as a subsystem of the TLTA-system (16). Akin (1983) proposed to study (16) equipped with some additional symmetry, e.g. that $A_1B_2$ and $A_2B_1$ should behave equally, i.e. $w_{2i} = w_{3i}$ for all $i$. Then the plane $x_2 = x_3$ is invariant and with $X = x_1/x_2$ and $Y = x_4/x_2$ the flow is there given by

$$\begin{aligned} \dot{X} &= X\{2(w_{12}-w_{22}) + (w_{11}-w_{12})X + (w_{14}-w_{24})Y\} + rb(1+X)(1-XY) \\ \dot{Y} &= Y\{2(w_{42}-w_{22}) + (w_{44}-w_{42})Y + (w_{14}-w_{21})X\} + rb(1+Y)(1-XY) \end{aligned} \tag{29}$$

Obviously these equations are identical with (28). So the limit cycles found for (28) carry over to (29) and one has at the same time given another (simpler) proof of Akin's result on cycling in TLTA.

Let us now consider the special case of (22) when the parents contribute <u>additively</u> to the fertility rates: $f(ij,kl) = m_{ij} + f_{kl}$. Then (22) reduces to

$$\dot{x}_{ij} = x_i F(j) + x_j F(i) - x_{ij}\,\Phi \tag{30}$$

with

$$F(i) = \frac{1}{2}\sum_{k=1}^{n}(m_{ik} + f_{ik})\,x_{ik} \quad \text{and} \quad \Phi = 2\sum_{i=1}^{n} F(i).$$

For the gene frequency $x_i = \sum_{k=1}^{n} x_{ik}$ of $A_i$ we obtain

$$\dot{x}_i = F(i) - x_i\,\Phi/2 \tag{31}$$

Then $(x_{ij} - x_i x_j)^{\cdot} = -(x_{ij} - x_i x_j)\,\Phi$ implies that in the limit $t \to +\infty$, $x_{ij} = x_i x_j$ holds, and the population is in Hardy - Weinberg equilibrium. But then (31) simplifies to Fisher's selection equation (3) with $w_{ij} = (m_{ij}+f_{ij})/2$. So the case of additive fertilities is essentially equivalent to the basic viability model.

Finally we consider the case of <u>multiplicative</u> contributions to the fertility rates: $F(ij,kl) = m_{ij}f_{kl}$. Then (21) reads as

$$x_{ij}' = \frac{M(i)F(j) + M(j)F(i)}{2\Phi} \tag{32}$$

with $M(i) = \sum_{k=1}^{n} m_{ik}x_k$, $F(i) = \sum_{k=1}^{n} f_{ik}x_k$, $M = \sum_{i=1}^{n} M(i)$, $F = \sum_{i=1}^{n} F(i)$, $\Phi = MF$. Then for the new variables $X_i = F(i)/F$ and $Y_i = M(i)/M$, (32) reduces exactly to the two-sex equation (17), as is also clear from the derivation of (18). A similar connection holds for the differential equations. In particular, if the male and female contributions are equal, $m_{ij} = f_{ij}$, (22) leads to

$$\dot{x}_{ij} = M(i)M(j) - x_{ij}M^2 \tag{33}$$

and

$$\dot{X}_i = X_i(\Sigma m_{ij}X_j - \bar{m})\ M \tag{34}$$

Hence the multiplicative fertility case with sex-independent contributions is also equivalent to Fisher's selection equation (1) resp. (3) and is therefore a gradient. The Hardy-Weinberg law however holds only for the discrete time model, but not for (33).

## 3. CONCLUDING REMARKS

3.1. In this paper I wanted to give some survey on the different selection models used in population genetics. The basic model is Fisher's viability selection model (1), (3) which behaves very nicely, since it is a gradient with mean fitness as a potential. This lead to the wide-spread view among population genetists that the evolution of gene (or genotype) frequencies within a population can be described by an "adaptive topography" and mean fitness or some suitable generalization of it will be optimized by evolution. However, research in the last years, mainly due to Akin, shows that this optimistic view cannot be maintained. Most of the generalizations of the basic model, allowing e.g.mutations, recombination, different fertility, and mortality rates etc. do not show gradient-like behaviour. The dynamics becomes much richer and more complicated: Oscillations (and probably also chaotic motions) occur.

Such periodic oscillations are well-known in other parts of biomathematics, the classical example being predator-prey interactions in population ecology. But population geneticists generally believed their equations to be free of such behaviour - maybe with the exception of frequency dependent selection. For a recent example of cycling in a frequency dependent TLTA system modelling the "battle of sexes" see Maynard Smith and Hofbauer (1984).

I confined myself to the dynamical behaviour of the differential equations. Now it is well-known that difference equations can play much worse things than correspomding differential equations. So it is not surprising that the results on cycling carry over to the discrete time models whenever they are found in the continuous time models. Mathematically this follows from a theorem in Hofbauer and Iooss (1984). For the basic selection model, which in continuous time is a gradient, the difference equation behaves equally well. Hopefully this can be extended to the selection-mutation equation with equal mutation rates. For the discrete version of the two-allelic fertility equation however, the function V from (26) cannot be a Lyapunov function, since stable periodic points of period 2 may arise by overshooting effects (see Hadeler and Liberman (1975)).

### 3.2. The hierarchy of genetic selection models

Figure 1 lists all selection models treated in this paper and shows the interrelations between them. The two dotted lines separate the models which lead to gradients from those which may produce cycles. For the intermediate region the problem is not yet solved.

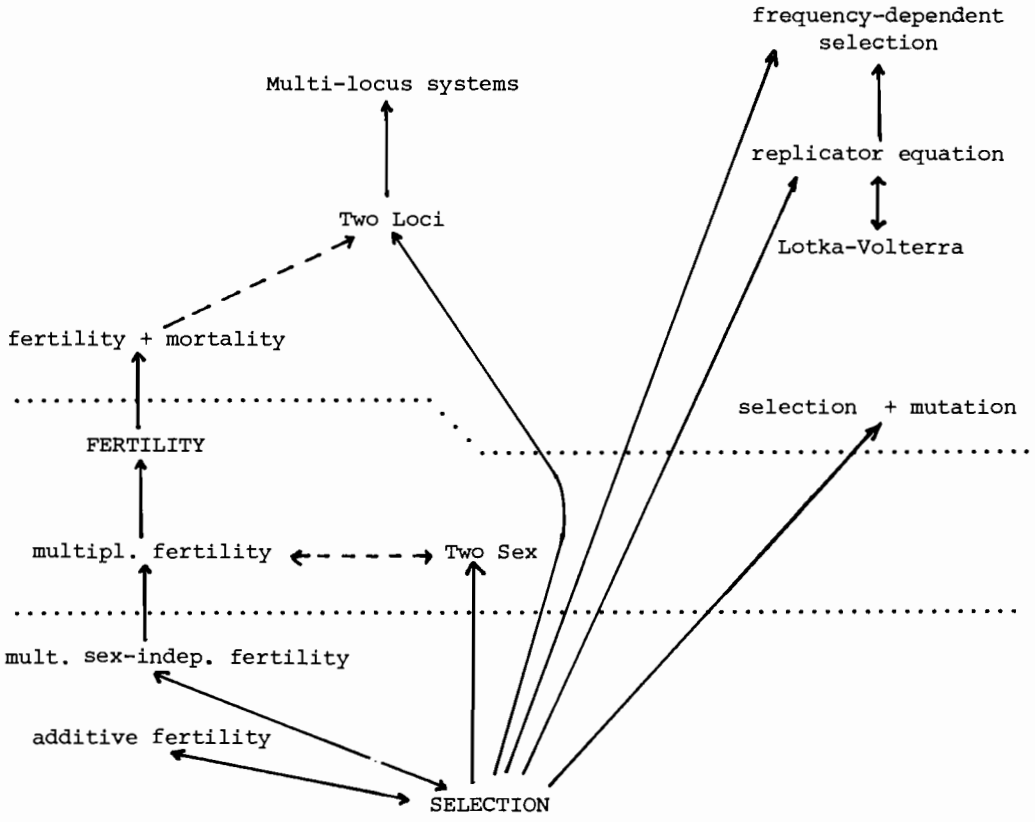


FIGURE 1 The selection models treated in this paper and the relationship between them.

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# EVOLUTION OF ASYMMETRY IN SEXUAL REPRODUCTION

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## 1. INTRODUCTION

Sexual reproduction is a widespread phenomenon. In most higher organisms it is the only mode of reproduction, while many lower organisms have the capacity to reproduce both asexually and sexually. There are few species in which sexual reproduction never has been observed. Sex can be characterized by the following three processes: fusion of two haploid sex cells (called gametes) into a (diploid) zygote, recombination of the genetic information from both gametes, and production of a new generation of haploid gametes. Although the processes involved are known into considerable detail, there is still no satisfactory functional explanation for the evolution of sex. In short, the problem is that it is difficult to explain the origin and maintenance of sex in terms of any benefit to individual fitness (fitness is a measure of the probability of survival and reproduction). The conclusion from theoretical analysis is that there should be strong selection pressure favouring the abandonment of sex by females, and the adoption of asexual reproduction instead. An extensive discussion of this matter can be found in Maynard Smith (1978).

There are a number of phenomena usually associated with sexual reproduction. Among these is the fact that (presumably) always the two gametes involved in producing a zygote show characteristic differences: in this sense sex is asymmetric. In anisogamous species the gametes differ either morphologically, the so-called male gametes being relatively small, while the so-called female gametes are relatively large, or they differ in behaviour, the male gametes being motile, and the female gametes not (or less) motile. In isogamous species the gametes cannot be distinguished morphologically, but they show physiological differences; in these cases the different types are called mating types, often designated as "plus" and "minus".

This paper will be concerned with the question why mating gametes are of different type. For anisogamous species this question is not too difficult to answer. In fact, two different explanations have been proposed (Parker (1978) and Hoekstra (1984)). Because of limited space, I will leave that case aside, and concentrate on the evolution of mating types in isogamous species. This problem is still unsolved, and is especially intriguing since at first sight the existence of mating types reduces considerably the probablility for a given gamete to find a suitable mating partner.

Three different models will be discussed, which aim to elucidate the effects of various selection forces that could be responsible for the evolution of mating types. In section 2 the evolution of asymmetry due to complementarity in gamete recognition is analysed. In section 3 the effect of a pheromonal gamete attraction mechanism on the evolution of mating types is investigated, while in section 4 the combined effects of parthenogenesis and segregation distortion are considered.

## 2. EVOLUTION OF UNIPOLAR COMPLEMENTARITY IN GAMETE RECOGNITION

In general, cell-cell recognition is brought about by complementary interacting macro-molecules in the cell surfaces. This complementarity can be unipolar of bipolar (Fig. 1).

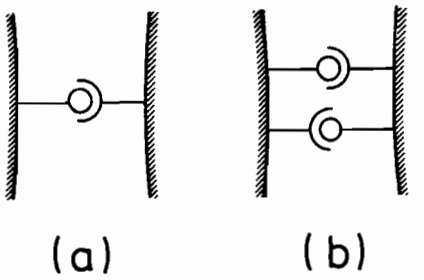



FIGURE 1 Complementarity in cell contact can be unipolar (a) or bipolar (b). (From Hoekstra, 1982).

There is good evidence that the specific recognition mechanism in microbial mating systems is of the unipolar type (Wiese, Williams & Baker, 1983; Musgrave & Van den Ende, pers.comm.). Bipolar complementarity is found, for example, in interactions between like cell-types during morphogenesis. Clearly, two mating types would quite naturally arise, if selection would favour a unipolar gamete recognition system. This possibility is analysed in the following model.

Consider a large population of vegetative haploid individuals living in water. Reproduction may be asexual, but under suitable conditions gametes are formed which fuse at random to form zygotes; these zygotes divide meiotically to form new vegetative individuals. (Many Algae have such a life cycle.) All gametes are assumed to have the same size, and there are no pre-existing mating types. There are two genetic loci $\underline{A}$ and $\underline{B}$, each coding for one of the two complementary recognition molecules. The alleles $\underline{A}_1$ and $\underline{B}_1$ cause the respective molecules to be present in the cell surfase, while the alternative alleles $\underline{A}_2$ and $\underline{B}_2$ suppress their formation. The precise relation between genotypes and phenotypes is depicted in Fig. 2, which also shows the various types of matings with their relative mating efficiency, which is assumed to be proportional to the number of successful matings.

The relative fitness of an $\underline{A}_1\underline{B}_1$ zygote is supposed to be lowered by a factor $1-\delta$ due to the fact that a certain fraction of these zygotes results from fusions within the same clone, which may cause "inbreeding depression". Furthermore, it is assumed that no fitness differences exist in asexual reproduction, and that $\underline{A}_2\underline{B}_2$ individuals cannot reproduce sexually. Using the notation shown in Fig. 2, and denoting the recombination fraction for the two loci by $\underline{R}$, the following recurrence equations connecting the genotype frequencies before and after sexual reproduction are obtained:

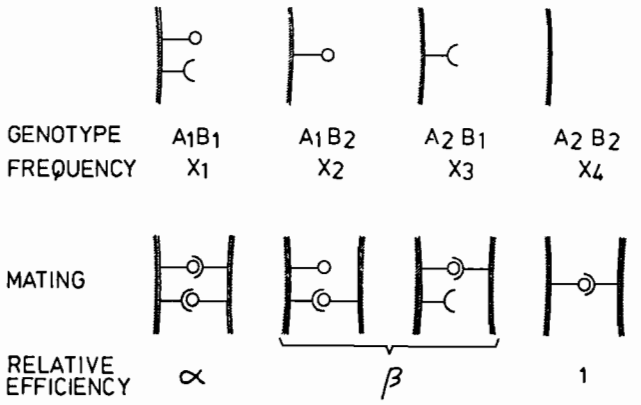



FIGURE 2 Specification of the genotypes of the various cell types and of the possible types of mating together with the notation used in the model of section 2. (From Hoekstra, 1982).

$$\begin{aligned}
\bar{W}x_1' &= x_1^2(1-\delta)\alpha + x_1(x_2+x_3)\beta + Rx_2x_3 \\
\bar{W}x_2' &= x_1x_2\beta + (1-R)x_2x_3 \\
\bar{W}x_3' &= x_1x_3\beta + (1-R)x_2x_3 \\
\bar{W}x_4' &= Rx_2x_3,
\end{aligned} \tag{1}$$

where $\bar{W} = x_1^2(1-\delta)\alpha + 2x_1(x_2+x_3)\beta + 2x_2x_3$.

Using standard methods, conditions for the existence and stability of boundary equilibria in (1) can be obtained without difficulties. This leads to the following results

(i) $\underline{A}_1\underline{B}_2$ individuals can establish themselves in an $\underline{A}_1\underline{B}_1$ population if

$$\beta > (1-\delta)\alpha \tag{2}$$

The same condition is necessary and sufficient for invasion of $\underline{A}_2\underline{B}_1$ into an $\underline{A}_1\underline{B}_1$ population.

(ii) In both these cases a globally stable non-trivial equilibrium between $\underline{A}_1\underline{B}_1$ and the other type results. When the third sexual type is introduced in low frequency into such an equilibrium population, it will increase in frequency if inequality (2) is satisfied.

(iii) The fate of $\underline{A}_1\underline{B}_1$ in the polymorphic population consisting of all genotypes depends on the recombination fraction $\underline{R}$: if $\underline{R} \neq 0$, $\underline{A}_1\underline{B}_1$ will be maintained for all parameter values; if $\underline{R} = 0$, $\underline{A}_1\underline{B}_1$ will be maintained

if

$$\beta > \tfrac{1}{2} \qquad (3)$$

How likely is a close linkage between the two loci $\underline{A}$ and $\underline{B}$ (implying $\underline{R} = 0$)? Since $\underline{R} = 0$ is a necessary condition for $\underline{A}_1\underline{B}_1$ to disappear from the population, it is of interest to investigate to what extent selection will favour a reduction in $\underline{R}$. There are various ways by which this can be achieved, for example by certain chromosomal rearrangements called "inversions", which suppress recombination in individuals heterozygous for the inversion. Suppose an inversion containing $\underline{A}_1\underline{B}_2$ is introduced at a low frequency $\underline{y}_2$ into a population, polymorphic for the three sexual types. The only effect of the inversion is supposed to be the suppression of recombination in heterozygotes. The recursion equations (1) are then modified as follows ($\underline{A}_2\underline{B}_2$ is left out of the equations since it is not influencing the dynamics of the model):

$$\begin{aligned}
\bar{W}x_1' &= x_1^2(1-\delta)\alpha + x_1(x_2+y_2+x_3)\beta + Rx_2x_3 \\
\bar{W}x_2' &= x_1x_2\beta + (1-R)x_2x_3 \\
\bar{W}x_3' &= x_1x_2\beta + (1-R)x_2x_3 + y_2x_3 \\
\bar{W}y_2' &= x_1y_2 + y_2x_3
\end{aligned} \qquad (4)$$

The mean fitness in the equilibrium population before the introduction of the inversion can be written as

$$\bar{\hat{W}} = \hat{x}_1\beta + (1-R)\hat{x}_3.$$

Therefore, if $y_2$ is sufficiently small we have

$$y_2' \simeq y_2(\hat{x}_1\beta+\hat{x}_3)/(\hat{x}_1\beta+(1-R)\hat{x}_3),$$

from which it follows that the inversion will always increase in frequency when rare. Furthermore,

$$\frac{y_2'}{x_2'} = \frac{y_2}{x_2}\left(\frac{x_1\beta + x_3}{x_1\beta+(1-R)x_3}\right),$$

which guarantees that the inversion will replace the original non-inverted type $\underline{A}_1\underline{B}_2$. This result implies that selection favours a reduction in recombination frequency $\underline{R}$, so that $\underline{R} = 0$ seems to be a likely situation.

The results of this section are summarized in Fig. 3. Evolution towards two mating types based on a unipolar complementarity in gamete recognition requires $\underline{R} = 0$, which seems plausible, but also $\beta < \frac{1}{2}$, which seems a very severe condition, since - albeit in totally different biological systems - bipolar cell interaction mechanisms do exist and function well. Finally, it is clear from the above analysis that inbreeding depression due to fusions between identical gametes cannot be responsible for the evolution of mating types.

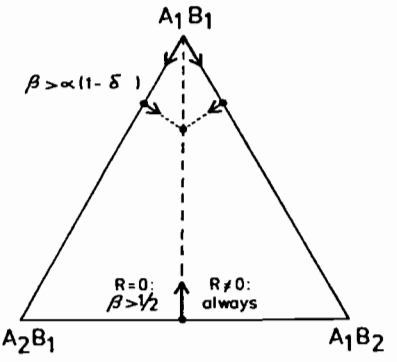
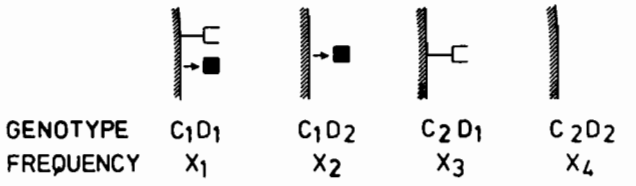



FIGURE 3 The results of the model of section 2 represented schematically in a de Finetti diagram (a particular population composition is represented by a point in the triangle, such that the relative frequencies of the three types are proportional to the lengths of the perpendiculars to the three sides). (From Hoekstra, 1982).

## 3. EVOLUTION OF GAMETE DIMORPHISM DUE TO PHEROMONAL ATTRACTION

The model analysed in the previous section shows that mating types can evolve due to unipolar complementarity of recognition molecules, but that the conditions for this to happen are not very likely to be satisfied. In this section a related model is analysed, in which one of the two complementary molecules is supposed to diffuse from the gamete into the surrounding water acting as a pheromone. The other type of molecule functions as a receptor on the cell surface, so that gametes can sense the presence of pheromones. It is assumed that once a gamete senses pheromone molecules, it will be able to adjust its swimming direction towards increasing pheromone concentrations and so to find the pheromone producing gamete.

The genetic model is as follows. Pheromone production is controlled by a locus $\underline{C}$ such that $\underline{C}_1$ individuals produce pheromone and $\underline{C}_2$ individuals do not. Locus $\underline{D}$ determines the response to pheromone: $\underline{D}_1$ individuals respond, while $\underline{D}_2$ individuals do not. Thus $\underline{C}_1\underline{D}_1$ gametes both produce pheromone and respond to it, $\underline{C}_1\underline{D}_2$ gametes only produce pheromone but cannot respond, $\underline{C}_2\underline{D}_1$ individuals only show a response, while $\underline{C}_2\underline{D}_2$ individuals do neither and consequently cannot participate in mating (see Fig. 4). Figure 4 also shows the relative mating efficiency (which is taken to be proportional to the number of successful matings) of the possible types of mating: $\underline{C}_1\underline{D}_1$ is impaired in its "male" function (chemotactic response) by a factor $\underline{m}$ relative to $\underline{C}_2\underline{D}_1$, and is impaired in its "female" function (pheromone production) by a factor $\underline{l}$ relative to $\underline{C}_1\underline{D}_2$. The assumption of an impaired "male" function is based on the idea that $\underline{C}_1\underline{D}_1$ individuals will to some extent have their receptor sites occupied with their own pheromone, thus diminishing their capacity for responding to pheromone of other gametes. The disadvantage of $\underline{C}_1\underline{D}_1$ in its "female" function could result from the same phenomenon, because part of the pheromone production is captured by its own receptors.




"♀"

| "♂" | | $C_1D_1$ | $C_1D_2$ |
|---|---|---|---|
| | $C_1D_1$ | ml | m |
| | $C_2D_1$ | l | 1 |

FIGURE 4 Specification of the genotypes of the various cell types and of the possible matings and their relative efficiencies together with the notation used in the model of section 3. (From Hoekstra, 1982).

Using again the symbol $R$ for the recombination fraction of the two loci, the following recurrence relations follow from the above assumptions:

$$\begin{aligned}
\bar{W}x_1' &= mlx_1^2 + \tfrac{1}{2}x_1(mx_2+lx_3) + \tfrac{1}{2}Rx_2x_3 \\
\bar{W}x_2' &= \tfrac{1}{2}mx_1x_2 + \tfrac{1}{2}(1-R)x_2x_3 \\
\bar{W}x_3' &= \tfrac{1}{2}lx_1x_3 + \tfrac{1}{2}(1-R)x_2x_3 \\
\bar{W}x_4' &= \tfrac{1}{2}Rx_2x_3,
\end{aligned} \tag{5}$$

where $\bar{W} = x_1(mlx_1+mx_2+lx_3) + x_2x_3$.

The following results are readily derived from stability analysis of the boundary equilibria of the system (5):

(i) Suppose originally the population consists exclusively of $\underline{C_1D_1}$ individuals. Then a mutant $\underline{C_1D_2}$ will increase in frequency if $\underline{l} < \frac{1}{2}$; similarly, a mutant $\underline{C_2D_1}$ will invade a $\underline{C_1D_1}$ population if $\underline{m} < \frac{1}{2}$. In both cases a globally stable non-trivial equilibrium will be established between the two types.

(ii) $\underline{C_2D_1}$ individuals can establish themselves in a population consisting of $\underline{C_1D_1}$ and $\underline{C_1D_2}$ if

$$(1-R)(1-2l) + l > m; \tag{6}$$

Similarly, $\underline{C}_1\underline{D}_2$ will invade a population consisting of $\underline{C}_1\underline{D}_1$ and $\underline{C}_2\underline{D}_1$ if

$$(1-R)(1-2m) + m > 1 \qquad (7)$$

(iii) In a polymorphic population with all genotypes present, $\underline{C}_1\underline{D}_1$ will be maintained (a) if $R \neq 0$ for all paramtere values, and (b) if $R = 0$, if

$$m + l > 1 \qquad (8)$$

(iv) Using a similar analysis as in the model of section 2, it can be shown that an "inversion" introduced into $\underline{C}_2\underline{D}_1$ which suppresses recombination between inverted and normal gametes will increase in frequency and replace the original "non-inverted" type $\underline{C}_2\underline{D}_1$. In general, a stable equilibrium with the "inversion" $\underline{C}_2\underline{D}_1$ and the genotypes $\underline{C}_1\underline{D}_1$ and $\underline{C}_1\underline{D}_2$ is not possible, so that one ends up with one of the following populations: (a) if $\underline{m} + \underline{l} > 1$, the population will consist of $\underline{C}_1\underline{D}_1$ and one of the other two types, depending on the values of $\underline{l}$ and $\underline{m}$; (b) if $\underline{m} + \underline{l} < 1$ (which is required anyway to get a polymorphic population with all three types when $\underline{R} = 0$), the population will finally consist of $\underline{C}_1\underline{D}_2$ and $\underline{C}_2\underline{D}_1$ in equal frequencies.

Thus, two mating types, based on dimorphism with respect to a pheromonal gamete attraction mechanism will evolve if $\underline{C}_1\underline{D}_1$ gametes are sufficiently impaired in their "male" and "female" function relative to gametes that are only "male" or only "female". Especially when $\underline{R} = 0$ (which is favoured by selection) the conditions are not unfavourable for the evolution of mating types, as argued in Hoekstra (1982). The results from analysis of the model in this section are summarized in Fig. 5.

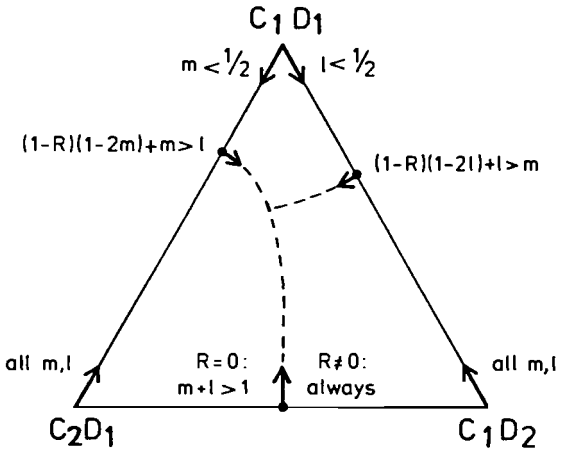



FIGURE 5 The results of the model of section 3 represented schematically in a de Finetti diagram.

## 4. THE EFFECT OF SEGREGATION DISTORTION COMBINED WITH PARTHENOGENESIS ON MATING TYPE EVOLUTION

The model discussed in the preceding section seems an attractive explanation for the existence of mating types in organisms with a pheromonal gamete attraction mechanism. There are, however, many isogamous species with mating types where pheromonal systems are absent. For example, among isogamous Algae only one case is known where possibly pheromones play a role in gamete attraction (Tsubo, 1961); on the other hand, almost all anisogamous Algae possess pheromonal gamete attraction. A possible explanation of this striking contrast is discussed in Hoekstra (1984). But it is clear that the model of the preceding section cannot explain mating types in isogamous Algae because these species have no sexual pheromones.

In this section a model will be formulated to explore the consequences of segregation distortion connected with the possibility of parthenogenesis for the evolution of mating types. Segregation distortion is the phenomenon that in a heterozygote a particular allele is favoured at meiosis at the expense of the alternative allele, which results in an $\underline{Aa}$ individual producing unequal numbers of $\underline{A}$ and $\underline{a}$ gametes. This may lead to a stable polymorphism if the allele which is favoured at segregation (say $\underline{A}$), is unfavourable in homozygote condition causing $\underline{AA}$ individuals to have a reduced fitness (Hiraizumi et al., 1960). Parthenogenesis is (in the present context) the asexual development of a gamete into a new vegetative individual. Parthenogenesis is known to occur in many isogamous Algae, if gametes fail to find a mating partner (Ettl et al., 1967). The intuitive idea of linking these two phenomena to the evolution of mating types is as follows. A distorting gene, if disadvantageous in homozygote condition, will lower the mean fitness of a sexual population. This will give a relative advantage to gametes reproducing asexually by parthenogenesis. Since gametes which are able to mate with any other gamete will have a higher probability to reproduce sexually than gametes which can only mate with a mating type different from their own mating type, there might be a selective advantage to the latter category of gametes. To analyse this situation more precisely, I consider the following model.

We have a population of organisms with the same life cycle as the model organism in the preceding sections of this paper. Since in the foregoing models it was shown that loci coding for different structures involved in the mating type tend to become very closely linked, it seems justified to assume the various mating types to be determined by alternative alleles at a single genetic locus. Specifically, assume that $\underline{M}_1$ gametes can mate with any type of gamete, while $\underline{M}_2$ and $\underline{M}_3$ gametes cannot mate with a gamete of their own type. (Thus $\underline{M}_1$ corresponds with the bipolar type $\underline{A}_1\underline{B}_1$ of the model of section 2, and $\underline{M}_2$ and $\underline{M}_3$ correspond with the two unipolar types). $\underline{M}_1\underline{M}_1$ homozygotes have a loss in fitness $\delta$ due to "inbreeding depression". At a second locus $\underline{S}$ there is segregation distortion in $\underline{S}_1\underline{S}_2$ heterozygotes, such that these heterozygotes produce $\underline{S}_1$ and $\underline{S}_2$ gametes in proportions $(1-\phi)$ and $\phi$ $(\frac{1}{2}<\phi<1)$. The relative fitness of $\underline{S}_2\underline{S}_2$ homozygotes is equal to $1-\delta$, while $\underline{S}_1\underline{S}_2$ and $\underline{S}_1\underline{S}_1$ zygotes have fitness 1. The probability that a gamete reproduces parthenogenetically is supposed to be proportional to the probability of finding an incompatible mating partner under the assumption of random mating. The fitness of individuals produced by parthenogenesis is $1-\theta$ relative to a fitness 1 of sexually produced offspring. Let the six different genotypes: $\underline{M}_1\underline{S}_1$, $\underline{M}_1\underline{S}_2$, $\underline{M}_2\underline{S}_1$, $\underline{M}_2\underline{S}_2$, $\underline{M}_3\underline{S}_1$ and $\underline{M}_3\underline{S}_2$ have respective relative frequencies

$\underline{x}_1$, $\underline{x}_2$, $\underline{x}_3$, $\underline{x}_4$, $\underline{x}_5$ and $\underline{x}_6$, and assume that the loci $\underline{M}$ and $\underline{S}$ are unlinked ($\underline{R} = \frac{1}{2}$). From all these assumptions we obtain the following system of recurrence relations:

$$\begin{aligned}
\bar{W}x_1' &= x_1\{x_1(1-\delta)+x_3+x_5\} + (1-\phi)\{2x_1x_2+x_2(x_3+x_5)+x_1(x_4+x_6)\} \\
\bar{W}x_2' &= x_2\{x_2(1-\delta)+x_4+x_6\}(1-\sigma) + \phi\{2x_1x_2+x_2(x_3+x_5)+x_1(x_4+x_6)\} \\
\bar{W}x_3' &= x_3\{x_1+x_5+(x_3+x_4)(1-\theta)\} + (1-\phi)\{x_4(x_1+x_5)+x_3(x_2+x_6)\} \\
\bar{W}x_4' &= x_4\{(x_2+x_6)(1-\sigma)+(x_3+x_4)(1-\theta)\} + \phi\{x_4(x_1+x_5)+x_3(x_2+x_6)\} \\
\bar{W}x_5' &= x_5\{x_1+x_3+(x_5+x_6)(1-\theta)\} + (1-\phi)\{x_6(x_1+x_3)+x_5(x_2+x_4)\} \\
\bar{W}x_6' &= x_6\{(x_2+x_4)(1-\sigma)+(x_5+x_6)(1-\theta)\} + \phi\{x_6(x_1+x_3)+x_5(x_2+x_4)\}
\end{aligned} \tag{9}$$

First consider the case when the driving gene $\underline{S}_2$ is absent. Then (9) reduces to

$$\begin{aligned}
\bar{W}x_1' &= x_1(1-\delta x_1) \\
\bar{W}x_3' &= x_3(1-\theta x_3) \\
\bar{W}x_5' &= x_5(1-\theta x_5)
\end{aligned} \tag{10}$$

It is easy to see that in this case a stable polymorphism will result if $\delta > 0$ and $\theta > 0$, and that $\underline{M}_1$ cannot be lost by selection.

I now turn to the general case given by equations (9). Of primary interest, of course, is the question under what conditions $\underline{M}_1$ genotypes will disappear from the population, thus giving rise to a population with two mating types. Since the model is symmetrical with respect to $\underline{M}_2$ and $\underline{M}_3$, it follows from (9) that in a population consisting solely of $\underline{M}_2$ and $\underline{M}_3$ types, there will be an equilibrium characterized by

$$\hat{x}_3 + \hat{x}_4 = \hat{x}_5 + \hat{x}_6 = \tfrac{1}{2}, \text{ and } \hat{x}_3 = \hat{x}_5,\ \hat{x}_4 = \hat{x}_6.$$

Furthermore, it can be deduced from (9) that

$$\hat{x}_3 = (1+\sigma-2\phi)/2\sigma;\ \hat{x}_4 = (2\phi-1)/2\sigma. \tag{11}$$

Thus there will be an equilibrium consisting of $\underline{M}_2\underline{S}_1$, $\underline{M}_2\underline{S}_2$, $\underline{M}_3\underline{S}_1$ and $\underline{M}_3\underline{S}_2$ in non-zero frequencies if

$$\tfrac{1}{2} < \phi < (1+\sigma)/2 \tag{12}$$

The question now is, whether this equilibrium is stable against invasion by $\underline{M}_1$ genotypes. The first two equations of (9) can be linearized for sufficiently small $\underline{x}_1$ and $\underline{x}_2$ to give

$$\begin{bmatrix} x_1' \\ x_2' \end{bmatrix} \simeq 1/\bar{W}\begin{bmatrix} 1-2\phi\hat{x}_4 & 2(1-\phi)\hat{x}_3 \\ 2\phi\hat{x}_4 & 2\phi\hat{x}_3 + 2(1-\sigma)\hat{x}_4 \end{bmatrix}\begin{bmatrix} x_1 \\ x_2 \end{bmatrix} \tag{13}$$

Stability of the equilibrium $\hat{x}_1 = 0$, $\hat{x}_2 = 0$ is ensured if the leading eigenvalue of the gradient matrix in (13) is smaller than unity in absolute value. After straightforward but tedious algebra this condition can be shown to be equivalent to

$$\theta < \phi \leq (1+\sigma)/2 \text{ and}$$
$$(1-\theta)(2\phi-\theta-1)/4 + (1-\sigma)\hat{x}_4\{1-\phi-(1-\sigma)\hat{x}_4\} - 4\phi(1-\phi)\hat{x}_3\hat{x}_4, \tag{14}$$

where $\hat{x}_3$ and $\hat{x}_4$ are given by (11).

If $\phi > (1+\sigma)/2$, then the segregation distorting gene $S_2$ is fixed in the population, and in that case $M_1$ will not increase in frequency when rare if

$$\phi > (1+\sigma)/2 \text{ and } 1-\theta > 1-\sigma. \tag{15}$$

A graphical representation of conditions (14) and (15) is shown in Fig. 6.

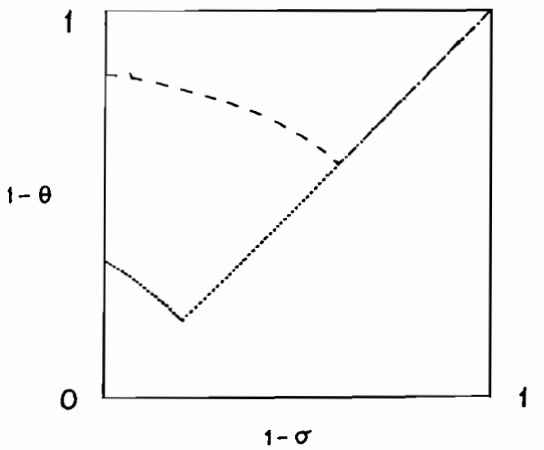



FIGURE 6 Gamete type $M_1$ (which can mate with any type of gamete including its own) will disappear from the population for parameter values above the curves. Dashed lines, $\phi = .7$; dotted lines, $\phi = .9$.

It is clear that, particularly with high values of $\phi$, that is with strong segregation distortion, evolution towards two mating types is not unlikely. With increasing values of $1-\sigma$, the disadvantage of $M_1$ increases because the frequency of the distorting gene $S_2$ is increasing. As soon as $S_2$ is fixed, however, the selective disadvantage of $M_1$ decreases again since the $S_2S_2$ zygotes get a higher fitness.

There is, however, a serious draw-back to this model. It appears that for those parameter values which give rise to the evolution of two mating

types, the mean fitness of a population in which there is only parthenogenesis is higher than the mean fitness of a population with both sexual reproduction and parthenogenesis. This implies that in fact this model leads to the prediction that when the $\underline{M}_1$ mating type is disadvantageous, the population will ultimately become asexual.

## 5. DISCUSSION

The evolution of mating types is not easy to understand. The only satisfactory model of those discussed in this paper is the model of section 3 which is applicable when pheromones are involved in gamete attraction. In many isogamous Algae however, gametes are moving at random and have no chemotaxis. The model of section 4 shows that segregation distortion combined with the possibility of asexual development of gametes into new individuals can lead to the existence of two mating types. The problem with this model is that segregation distortion makes sexual reproduction less advantageous than asexual reproduction because of the low fitness of zygotes homozygous for the distorting gene. This is precisely the reason why the "bipolar" mating type $\underline{M}_1$ is selected against in this model, since $\underline{M}_1$ gametes participate more in sexual fusions than the true mating types $\underline{M}_2$ and $\underline{M}_3$. It is however possible to modify this model by incorporating additional fitness differences analogous to those in the model of section 2. Preliminary analysis reveals that then the evolution of mating types can occur while sex is still advantageous.

Finally, all models discussed in this paper assume random gamete fusion. This implies that an "inbreeding depression" due to matings between identical gametes plays no role in the conditions for protection of the "bipolar" gamete type, since the linearised equations do not contain the parameter for this "inbreeding depression". For this reason exploration of models based on non-random mating is certainly worthwhile.

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# IV. ECONOMIC AND SOCIAL MACROSYSTEMS

# RANDOM BEHAVIOR IN NUMERICAL ANALYSIS, DECISION THEORY, AND MACROSYSTEMS: SOME IMPOSSIBILITY THEOREMS

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Abstract: For many topics, including decision analysis, policy making, and the normative study of certain macrosystems, tools of analysis are applied to determine the essence or the state of a problem. The one commonality among these tools is that we want them to be "reliable". For certain standard tools, it is shown that this goal of reliability may be impossible to attain. For some of these impossibility statements, alternative approaches are suggested.

## 1. Introduction

Certain basic tools are commonly used both with decision analysis and with macrosystems. Some of these tools are devices designed to be incorporated within the system in order to assist and to influence the subsequent dynamics. For instance, this includes any method used to facilitate the decision making within an organization. Here an obvious example would be voting methods used to aggregate individual differing rankings over several alternatives into one common group ranking. Other types of tools are the techniques used in systems analysis. On a theoretical level, this may be an algorithm designed to seek a zero of a smooth function - such a zero may correspond to an equilibrium or an optimal point for a system. Or, it may be an integer programming problem used to determine an efficient policy. It may be the statistical and probabilistic tools developed to understand and to interpret data - perhaps to aid in a decision analysis or a policy decision.

Central to the selection of any tool is the requirement that it is reliable. Here there are at least two criteria. First of all, the tool should apply for all of the situations within a class of interest; that is, we seek universal mechanisms. For instance, when we search for a zero or an equilibria of a function g, we prefer to use an algorithm which always will work as long as g is sufficiently smooth. Indeed, this is part of the historical attraction of the tatonnement story from economics; it has been viewed as being a universal mechanism where the market forces of supply and demand iteratively converge to a market equilbrium price.

A mechanism or tool is selected to achieve a specified goal. Consequently, a second crucial condition is that the tool doesn't lead to unexpected surprises, conclusions, or consequences which may violate or vitiate our objectives; we want the outcomes to consistently reflect these

objectives. For instance, in the choice of a voting method, we want the final result to accurately reflect the preferences of the electorate. As a hypothetical example, consider the problem of selecting a common beverage for lunch where a voting method is used to guide us in the decision process. Suppose a vote leads to the ordering wine > water > beer. Should wine be unavailable, we would expect to be able to replace it with the second ranked choice of water free of fear that a majority of the people really would have preferred beer.

An impossibility theorem arises when certain basic objectives are frustrated; when there doesn't exist a devise or a mechanism which satisfies the specified criteria. Therefore, the theme of this paper which is that impossibility theorems play an important role in the system sciences, is somewhat disturbing. Often such theorems arise because mechanisms violate conditions which are "intuitively obvious"; in this setting, an impossibility statement is called a "paradox".

In this paper, I'll consider several paradoxes and impossibility theorems with three goals in mind. The first is to introduce several new impossibility theorems related to the topics mentioned above. The second is to take these seemingly disparate results and to unify them by showing that they have a common explanation. (Although I will not develop the theme here, this approach relates these new results to several important paradoxes such as Arrow's Theorem, the Alabama paradox of apportionment, etc.) Finally, I'll briefly note some research, still in its infancy, which has the goal either to circumvent, or to handle the disturbing consequences of these impossibility results.

## 2.The source of the problem

All of the results to be discussed here are caused by the inverse image of certain functions being multivalued in a particular manner. To understand the basic idea, consider the function f represented in Figure 1.

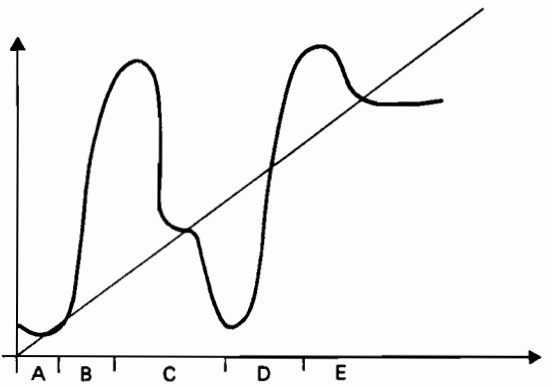


FIGURE 1

The inverse function, $f^{-1}$, clearly is multi-valued; indeed, in this figure, the intervals A, B, C, D, E designate those regions over which $f^{-1}$ is single valued. To see what mischief this multivalued property can create, consider the trajectories of the deterministic system

2.1) $\qquad x_{N+1} = f(x_N).$

This system admits five equilibria given by the intersection of the graph of $y=f(x)$ with the diagonal $y=x$; and the three asymptotically stable points are those equilibria in the regions A, C, E. (At these points $|f'|<1$.) But, there is much more interesting dynamics going on in the intervals B, C, and D than can be captured by any stability analysis. For instance, I contend that there exist trajectories of this deterministic system which are as "random" as you desire! By this I mean it is possible to specify in advance in which of these intervals the $N^{TH}$ iterate will land for all values of $N=0,1,...$ This selection can be made by any means desired, say a random process, and there will exist initial iterates with trajectories which will follow the specified pattern. For instance, choose the interval in which you wish the initial point, $x_0$, to be, say D. Then choose the interval in which you wish $x_1=f(x_0)$ to be, say B. Continuing in this fashion, specify the interval in which the $i^{TH}$ iterate should land. This defines a sequence of labelled intervals, say

2.2) $S = \{D, B, C, ...\}$

where the $k^{TH}$ symbol designates the interval in which $x_{K-1}$ should be. To establish the existence of a trajectory which will follow this designated future, a judicious choice of the multiple inverse images will be made. To do this, let $S_N$ denote the finite sequence consisting of the first N entries of S. Then, in an iterative fashion, we will determine all initial iterates for which at least the first (N-1) iterates do what they are supposed to do; they follow the pattern given by $S_N$. Let $K(S_N)$ be this set. For instance, for the above choice of S, $K(S_2)$ is the set of points in D which are mapped to B', the closure of B; i.e., $K(S_2) = f^{-1}(B')..D$. Because the image of f restricted to D, $f_D$, covers the set B', this is the closed subset $f^{-1}{}_D(B')$.

To determine $K(S_3)$, we first determine, as above, the set $K(\{B,C\}) = f^{-1}{}_B(C')$. This is a closed subset of the interval B. As a result, $K(S_3) = f^{-1}{}_D(K(\{B,C\})) = f^{-1}{}_D(f^{-1}{}_B(C'))$ is a closed subset of $K(S_2)$. Continuing in this fashion, it follows that $K(S_N)$ is a nonempty, closed subset of $K(S_{N-1})$. (It is nonempty because the image of $f_K$, K=B,C,D, covers the union of all three intervals.)

The sought after set is given by

2.3) $K(S) = \cap K(S_N)$.

This set is nonempty because it is given by the intersection of a nested, decreasing sequence of nonempty, compact sets. This establishes the existence of orbits with the behavior specified by S.

Some properties can be extracted immediately from this derivation. While most of them will not be explictly exploited in what follows, it should be clear that they provide additional information about the types of behavior of systems which we will be discussing.

1. Because there are an uncountable number of possible sequences S, there are an uncountable number of sets K(S). For an uncountable number of these sets, convergence to equilibria is impossible.

2. The system can exhibit sensitivitiy with respect to initial conditions. By using the figure to determine the set $K(\{D,B,C\})$, it is clear that these sets decrease in size quite rapidly. However, the initial points for any two trajectories which define the same $S_N$, but which differ quite radically after the $N^{TH}$ iterate, are in the same set $K(S_N)$. This means that near-by points may have radically different futures.

3. For any $S_N$, $K(S_N)$ contains a nonempty open set of points which converge to one of the equilibiria. This is because the image of f restricted to any of these three intervals meets A and E. Consequently, there are open sets of points where the first N-1 iterates obey the

specified pattern of $S_N$, and then the $N^{TH}$ iterates are either in A or in E. In either case, all subsequent iterates asymptotically tend to an equilibria. This has several implications:

a) The basin of attraction for an equilibrium can be extremely complex.
b) There has been about $10^{27}$ seconds of time since the "Big Bang". The fastest computers on the drawing boards are projected to do $10^{12}$ operations per second. Hence, for computational purposes, any stable point in $K(S_N)$, where $N \geq 10^{39}$ and where the last two entries of $S_N$ differ, are unstable for any practical purposes.

The above nested set construction, which depends upon the properties of the multivalued aspects of $f^{-1}$, and the accompanying properties listed above are the essential ideas behind the following impossilbity theorems. (For a comprehensive discussion of iterative dynamics, chaos, and random motion, I highly recommend [1,2].)

## 3. Applications

Based upon the discussion in Section 2, it is clear that iterative dynamics of deterministic systems can lead to random, unexpected behavior. This is particularly so should $f^{-1}$ be multivalued in a sense indicated above. As such, examples exhibiting this behavior are plentiful and easy to find. For instance, a macrosystem where all sorts of examples and applications of this type arise is the general area of biology; this type of random motion occurs in discrete preditor-prey models, in the Volterra equations adjusted for seasonal effects, in population genetics, etc. Other areas include the motion of a projectile entering the atmosphere (depending upon its angle of entry), and on and on.

It isn't as obvious that the same behavior is manifested in common tools of analysis. These are the topics I'll consider here.

### Numerical Analysis [3]

Consider the problem of determining a zero of a smooth function g. To be more specific, let

3.1) $G^K = \{ g \in C^{K+1}[0,1] \mid g(0)g(1) \leq 0 \}$.

(The product condition is imposed only to ensure that a function from $G^K$ has a zero. It can be replaced with a more restrictive condition such as $g(0)>0$, $g(1)<0$, or with a weaker condition that g has a zero in [0.1].) The goal is to find a universal algorithm; an algorithm which will determine a zero for any function g in $G^K$

Perhaps the best known algorithm is the Newtonian iterative scheme

$x_{N+1} = x_N - (g(x_N)/g'(x_N))$.

However, from the work of Barna [4] (also see [5,6,7]), we know that such a scheme isn't universal; there exist polynomials and initial points so that this scheme never converges. So, the issue becomes to determine what information we need in order to design an universal algorithm. A standard approach, which is in the spirit of Newton's method, is to seek this information in terms of the values of g, its first K derivatives, and the location of the initial iterates. (Actually, the goal is to find the class of all such universal algorithms so that an optimal choice, say in terms of computer costs or complexity, could be made.)

**Definition 1. A mechanism is given by (M,D) where M is a piecewise,**

smooth function from $R^{K+1}$ to R, and D is a subset of [0,1]. The mechanism defines the iterative scheme

3.2) $x_{N+1} = x_N + M(g(x_N),..,g^{(K)}(x_N))$

where $x_0$ is in the set D. The mechanism (M,D) is a <u>universal mechanism</u> if for any g in $G^K$, the sequence defined by Eq 3.2 converges to some zero of g.

For the Newton algorithm, $M(u,v,...) = -u/v$. The problem is to determine all choices of (M,D) which are universal mechanisms.

**Theorem 1.** There does not exist a universal algorithm for $G^K$ which is of the type specified in Eq. 3.2.

The basic idea for the proof of this theorem is that no matter how you choose M and D, there still exists an open set of functions in $G^K$ such that $(x+M)^{-1}$ is multivalued in a sense similar to that described in the previous section. As such, convergence will not occur.

A natural question is whether one could possibly design a more creative algorithm - based upon additional information - to overcome this negative statement. For instance, perhaps by incorporating a memory of the last "A" iterates, an algorithm could be designed to recognize earlier mistakes and to make the appropriate adjustments. In this case, the algorithm would assume the form

3.3) $x_{N+1}=x_N +M(g(x_N),.,g^{(K)}(x_N),.,g(x_{N-A}),.,g^{(K)}(x_{N-A}))$.

Again, the goal is to characterize the set of all (M,D)'s which are universal mechanisms; again an impossibility theorem results. In fact,

**Theorem 2.** For any (M,D) where M is of the type given in Eq 3.3 and for any integer s>A, there is an open set, B, of functions in $G^K$ so that if g is in B then the trajectories of Eq. 3.3 tend toward an attractive periodic orbit of period s.

In other words, for any such g, there is an open set of initial conditions where the trajectories oscillate with a periodicity just outside the limits of memeory of the algorithm; these iterates will never approach a small neighborhood of any of the zeros of g. These results suggest that to define an effective, universal algorithm, other techniques and approaches are required.

Recently, questions concerning the "complexity of algorithms" have been studied to determine whether one is better than another. Again, some of these concepts are stated from the viewpoint of "universality". Namely, these definitions are in terms of the "worse case" situations; in the worse case, how many iterates are needed to determine a zero of a function. A combination of the ideas in the proof of the above theorem and Comment 3 in the last section can be used to show that for any M of the type given in Eq. 3.3, (which includes Eq 3.2), there exists an open set of functions B in $G^K$ with the property that if g is in B, then there is an open set of "convergent" points for which convergence could never be discovered on any computer; the bounds on the number of required iterates to reach a small neighborhood of a zero can be made arbitrarily large.

Incidently, these theorems extend to functions from $R^N$ to $R^N$.

### Price Dynamics [3].

The standard tatonnement story from economics describes how the market forces of supply and demand adjust the prices so that the iterates converge to a price equilibrium where supply equals demand. One attraction of this story is that it describes a self-regulating universal mechanism which determines an equilibrium. But, is this story correct?

It is known from the work of H. Sonnenschein, G. Debreu, and others [8] that any function in the set $\{g \in C^k \mid g(0)>0, g(1)<0\}$ serves as the excess demand function for some standard, neo-classical economy. Thus, it follows from the above that the standard tatonnement story will not always work even for the highly restrictive setting of only 2 commodities! (The tatonnement story corresponds to the mechanism $M(g(x))=g(x)$.) Moreover, it also follows from the above that there doesn't exist a mechanism using the past history of market forces as captured by the excess demand function (which may be used to model speculation, anticipation, etc.) of the nature given in Eq 3.3 which will serve as a universal price mechanism. Consequently, the existence of such an universal mechanism, if one even exists, must depend upon a different form of information, and at this stage it isn't clear what it should be.

## 4. The tools of decision analysis

The iteration $x_{N+1}=f(x_N)$ can be expressed as $x_N=f(x_{N-1})=f(f(x_{N-2}))=\ldots=f^N(x_0)$; or $x_N=f^N(x_0)$. This means we are examining a specific sequence of functions $(f^N)$ (which happen to be obtained by composition), and analyzing the images as governed by a common domain point, $x_0$. A natural extension is to eliminate the restriction that these functions $(f^N)$ are derived in this special manner. Instead, let $(f_N)$ be any given sequence of functions where $f_N: B_0 \dashrightarrow B_N$.

The question is the same; for a specified sequence of behavior described in the different spaces $B_N$, does there exist a common point p in $B_0$ such that $f_N(p)$ will have the desired designated "random" future? This is the type of model I'll discuss in this section. (Traditionally, examples of the type I will be describing are analyzed in a "static" setting. An advantage of the "dynamic" approach advocated here is that it suggests the natural extensions of well-known paradoxes, and it suggests the approach to determine whether they exist.)

### Voting [9,10]

Consider the earlier hypothetical example concerning the choice of a luncheon beverage among wine (wi), water (wa), and beer (be). Assume there are 9 voters where 4 have the ranking wi>be>wa, 3 have the ranking wa>be>wi, and 2 have the ranking be>wi>wa. Using the customary plurality voting scheme where you vote for your first place alternative, the group ranking is wi>wa>be with the tally of 4,3,2.

For this voting model, $B_0$ is the space of all of the ways in which the 9 people could linearly rank the three alternatives in a linear, ordinal fashion. So, a point p in $B_0$ represents a specific choice of the individual rankings for the voters, $f_3(p)$ is the resulting ranking for the group, and $B_3$ is the set of all linear, ordinal rankings of the three alternatives. In general, if there are N alternatives, then $B_N$ corresponds to the N! ways in which these N alternatives can be linearly ordered. Note that in this setting, the spaces $B_N$ change with the value of $N=0,1,\ldots$

This example illustrates that plurality voting doesn't provide us with a desired consistency property. For instance, if wine isn't available, then the above ranking suggests that water would be the group's next choice. But is it? In fact, 2/3 of these people prefer beer to water. Indeed, a majority of them even prefer beer to wine! Thus, the outcome obtained by using this tool for decision making is inconsistent with majority sentiment over any of the possible pairwise comparisons!

In this example, the voting method is characterized by the vector $\underline{W}=(1,0,0)$. One source of the difficulty is the fact that lower level preferences aren't accounted for. A possible remedy would be to use a vector, such as $\underline{W}=(2,1,0)$. (Here, a first place alternative is assigned 2 points, a second place alternative is assigned 1 point and a third place alternative is assigned 0 points.) With this system, the group's ranking becomes be>wi>wa with a tally of 11, 10, 6. Notice that for this particular example, the resulting ranking <u>is</u> consistent with how a majority view each of the three possible pairwise comparisons.

In general, the problem becomes one of choosing a voting method $\underline{W}^N=(w_1,\ldots,w_N)$, $w_{K+1}\geq w_K$, $w_1>w_N$, where $w_K$ points are tallied for a voter's $K^{TH}$ place alternative. The objective is to choose a $\underline{W}^N$ to "avoid" surprises; to find a method which will preserve consistency in the group's rankings as alternatives are eliminated. However, a classical result due to K. Arrow [11] asserts the impossibility of choosing a $\underline{W}^N$, $N\geq 3$, without running into a phenomena of the type exhibited above -- for any voting method it is possible to find examples where the group's ordering ranks some one alternative over another even though a majority of the voters would have the opposite ranking for this particular pair.

The goal for social choice must be modified; the new goal isn't to find absolute consistency, but rather to find a set of vectors $\{\underline{W}^j\}$, $j=2,3,..,N$, which will preserve as <u>much</u> consistency in the different rankings of alternatives as possible. But, the following theorem shows that even should alternatives be eliminated (or added) in a simple monotonic fashion, there are serious obstacles in achieving this goal - for any choice of a voting method, no relationship whatsoever need be retained among the rankings of the different subsets of alternatives! Notice what this conclusion implies about "run-off elections" and other procedures such as the "Hare method".

**Theorem.** Let $N>2$ alternatives, $\{a_K\}$, $K=1,2,..,N$, be given. For $j=2,3,..,N$, let $S_j=\{a_1,..,a_j\}$. Let $Al_j$ be an arbitrary, linear, ordinal ranking of $S_j$; that is, $Al_j$ is some element of $B_j$. Let $\underline{W}_j$ be any voting vector used to rank $S_j$. Then, there exist examples of voters, each with a fixed, linear, ordinal ranking of the N alternatives, such that for each $j=2,..,N$, when these same voters rank the alternatives in $S_j$ by use of $\underline{W}^j$, the outcome is $Al_j$.

This result is an impossibility theorem asserting the inability ever to design voting (ballot) methods even with liberal allowances for inconsistencies suggested by this theorem; leave alone the stricter requirements imposed by Arrow. This result means that all sorts of counter-intuitive examples can be created; e.g., we can find examples where the outcome changes periodically with the number of alternatives. For instance, for N alternatives, there exist examples of voters' preferences (i.e., a point p in $B_0$) so that the outcome is $a_1>a_2>\ldots>a_j$ when j is even, but just the opposite whenever j is odd. Consequently, even though the voters vote in a consistent fashion, the group's outcomes oscillate as $a_1>a_2$ for $S_2$, $a_3>a_2>a_1$ for $S_3$,

$a_1 \succ a_2 \succ a_3 \succ a_4$ for $S_4$, ... In other words, Arrow's theorem, asserting the inconsistency of an outcome at the binary level was only the tip of this iceberg of possible inconsistencies!

Compare the statement of this theorem with that of the iterative example given in Section 2. In each setting, the image of $f_N$ is selected in a random fashion. In each case, $f^{-1}{}_N$ is multi-valued. (For instance, for $\underline{W}^3=(2,1,0)$, there are many choices of the rankings for the individuals which lead to the same ranking $be \succ wi \succ wa$.) Although the technical details differ significantly, the proof of this theorem can be viewed as being based on an intersection argument similar to that given in Section 2. (Incidently, a related argument will provide an alternative proof and extensions for the classical Arrow theorem.)

However, this goal of finding a proper choice of a voting system - a $\underline{W}^N$ which minimizes the number and the types of paradoxes and inconsistencies - still holds, and it can be answered. By increasing the number of subsets of the N alternatives which need to be ranked (e.g., by requiring that not just those subsets stated in the theorem must be ranked, but all possible subsets of the alternatives must be ranked), it turns out that the Borda method, $B^N=(N-1,N-2,..,0)$, is the unique "best choice" method to reduce the inconsistencies of voting. This will be described in a subsequent paper. (Also, see [9].)

## Probability and Statistics [9]

The tools of probability and statistics are not only indispensible for the analysis of data, but their concepts have become crucial in the development of several other areas. For instance, such basic ideas are fundamental for decision making (e.g., the Nash Baysian decision analysis which currently is popular in management science), in theoretical constructs (such as in the evolutional stable strategies in Biology), and in numereous other areas. But, are these tools reliable? Can they cause surprises and unexpected, undesired behavior?

That they can should be expected from the fact that the inverse image of standard probability constructs generally are multi-valued. A simple illustration of these unexpected inconsistencies can be obtained by identifying an important ranking problem from statistics with the voting discussion given above. Namely, consider the problem of determining which one of N firms produces the highest quality product, say a certain type of steel. An obvious approach to solve this problem would be to collect samples from the N firms; after the samples are compared, they are rank ordered. In this way, each sample describes a rank ordering of the firms, so a sample point can be identified with a voter who has a particular ordering of the N alternatives.

Before a decision is made, the problem is to aggregate the information embedded in several samples. But this problem is equivalent to the voting problem of aggregating voters' preferences. For instance, a natural approach would be to select the firm which has the top rating over most samples. This is equivalent to using the plurality voting method $\underline{W}^N=(1,0,..,0)$. Thus, this problem inherits all of the difficulties, inconsistencies, impossibility theorems, and complexities described above in the section on voting. (Moreover, the Borda Count is the unique set of weights to reduce the number of inconsistencies.)

Even more can occur; it turns out that pairwise comparisons of the firms can lead to any desired paradox. To see this, consider the process where from the samples we compare the quality of firm K with that of firm j, where firm j is better than firm K iff for a majority of the samples,

firm j had a better product than that of firm k. Now, for each of the N(N-1)/2 different choices of firms, designate (in a completely random fashion if you like) which firm is to be the better one. It turns out that there exist examples of data which will satisfy all of these (possibly inconsistent) rankings simultaneously! [9]

In both of these examples, the rankings are determined by "inequalities", thus the inverse image of the defining functions are, in general, multivalued. From this and an independence condition, the above conclusions follow, and they should be expected.

This difficulty for probability and statistics extends to other constructs for much the same reason. For instance, the concept of "conditional probability" has been used in all sorts of models of decision analysis ("do this if that occurs"), economic and political science models ("because we are in such a situation, we can expect ..."), etc. But, is there a consistency which is preserved as the conditions change - even if they change in a simple, monotonic fashion? The answer is no, not necessarily!

The easiest way to illustrate this is to consider the following game which involves a decision. There are two urns marked I and II; both contain a mixture of red and blue marbles. The game is for you to select one of the two urns, and then, at random, select a marble from this urn. Success is if you selected a red marble. The decision problem is, of course, to select the urn which maximizes your chance for success.

Now suppose there are two sets of urns labelled $(I'_j, II'_j)$, j=1,2, where it is known that from either set of urns it is more likely to select a red marble from the urn $I'_j$ than from the urn $II'_j$; i.e., $P(R|I'_j) > P(R|II'_j)$, j=1,2, where R is the random variable indicating that a red marble has been selected. For this setting, the decision analysis is trivial to resolve - select urn $I'_j$.

Suppose that the marbles from urns $I'_1$ and $I'_2$ are poured into an urn $I^0$, while those from $II'_1$ and $II'_2$ are poured into an urn $II^0$. You have the same decision problem, but now with these new urns. Which urn should you select? Presumably by now the reader has developed enough caution to avoid the "intuitively obvious" answer of urn $I^0$. This is fortunate because the same random behavior exists; for either choice of the sign of $P(R|I^0)-P(R|II^0)$, many examples illustrating this behavior can be found. (For the skeptic, consider the following allocation: $I'_1$ has 9 red out of 24 marbles, $II'_1$ has 2 red out of 6 marbles, $I'_2$ has 3 red out of 6 marbles, and $II'_2$ has 11 red out of 24 marbles. A simple computation shows that $P(R|I'_j) > P(R|II'_j)$, j=1,2, but $P(R|I^0) < P(R|II^0)$.)

This behavior is known as Simpson's paradox [12,13], and it can be extended in many directions [9]. For instance, the number of urns in each set can be more than two, the number can vary, etc. It can be extended to N levels, where initially there are $2^N$ sets of urns. Then, the marbles from urns $I^N_{2j-1}$ and $I^N_{2j}$ are poured into an urn labelled $I^{N-1}_j$, while those from $II^N_{2j-1}$ and $II^N_{2j}$ are poured into an urn $II^{N-1}_j$. This defines the contents of the $2^{N-1}$ sets of urns at the $(N-1)^{TH}$ level. This process is continued through the different levels, k=0,..,N. The problem concerns whether there needs to be any consistency in the signs of $P(R|II^k_s)-P(R|III^k_s)$, k=0,1,2,..,N, s=1,2,..,$2^k$. It turns out that there need not be; for each choice of the indices, you can choose the sign in an arbitrary fashion, and there exist initial apportionments of marbles so that all conclusions will be simultaneously satisfied! Again, the proof can be viewed as being based upon an "intersection argument", where $B_0$ is the space of initial allocations of marbles to the urns.

The implications of this result for decision making should be obvious. It points out that the component parts of a decision analysis can differ sharply from its aggregate. For instance, suppose the problem is comparing success rates of two different methods; say a comparison of the proposed cure of a disease with the standard method. In this setting, the urns $I^K_j$ correspond to pool of people being subjected to the new treatment, while $II^K_j$ corresponds to those receiving the standard treatments; the indices identify the locations where the experiments are being conducted and the level of aggregation of these figures. (If k=N, then the figures are the raw figures at the experimental locations. If k<N, then the figures correspond to a partial aggregration of the result at different locations.) If R corresponds to "regaining health", then the sign of $P(R|II^K_s)-P(R|III^K_s)$ indicates which treatment was more successful at that particular site and level of aggregation. The above indicates that the conclusions from such a study can be random and highly unexpected; local conclusions may differ from a global, or from a partially aggregated analysis.

This result impacts on decision analysis on the comparison of two (or more) strategies I and II, say in a military context or in an economic plan for a society. Here we see the existence of the apparent anomaly that, on the global level, strategy I is better than strategy II, $P(R|II^0)>P(R|III^0)$, even though this same strategy is <u>weaker</u> in each of the local situations, $P(R|II^K_j)<P(R|III^K_j)$ for all k>0 and j. (A phenomena of this type occurred at Berkely [14]. The objective was for the university to improve the percentage of women it hired in one year (I) over the preceeding year (II). The stategy to accomplish this was for each of the academic units to increase its hiring percentage of women $(P(R|II_j)>P(R|III_j)$. But, the aggregated results for the total university showed a reversal, $(P(R|II)<P(R|III))$!)

## 5. Summary

From this brief description, it should be clear that random, unexpected behavior can occur not only in deterministic dynamics, say the dynamics of decision theory or of macrosystems, but also in the basic tools employed to analyze them, and in the devises designed to be implanted within systems to facilitate certain processes (as price mechanisms in economics or voting in political science). In this survey, I've selectively described only standard tools - tools coming from numerical methods, voting, and probability - which are common and familiar to most readers. However, it is easy to demonstrate that the same phenomena extends to optimization problems [15] (such as optimal growth or overlapping generations problems), to integer programming problems (such as an apportionment problem of the type coming from the assignment of legislative seats or draft quotas to regions, or in the economics of decision making), and on and on. Indeed, <u>it probably is safe to speculate that such behavior is prevalent in the tools of decision making and in macrosystems</u>; such a speculative comment is based upon the fact that for most tools of analysis, inverse images of the key defining functions generally are multivalued!

But, if random, unexpected behavior is an inherient part of these tools -- a fact which reduces their reliability -- then we are faced with a serious problem. Decisions must be made, systems must be analyzed, certain tools must be used! This means that these systems must be analyzed to determine the root causes for this behavior; then this information must be used either to develop indicators which will warn when such

counterintuitive behavior is occurring, or to design different approaches which will eliminate these problems. The first approach is needed where a system is already specified, as in a gambling problem where the dice are given, as in the dynamics of evolution, as in a strategic situation where the laws of probability are already defined (an analysis of population data, strategic planning, gambling, etc.), or as in a voting situation where the type of ballot tally is designated by law. Here the issue becomes to develop the appropriate tools of information to ascertain, in advance, whether or not the random, unexpected behavior applies to the existing, current situation. This will warn us when an accompanying decision analysis need not be "monotone" - when the conclusions need not mean what we are assuming they mean - and we need to know this.

A different avenue is open for the "design" of tools; the design of algorithms to achieve a specified goal, the design of probabilistic techniques which avoid certain pitfalls, or the design of mechanisms which achieve a desired, self-enforcing status within a macrosystem such as in economics and in political science. Here the objective or the goal of the desired mechanism is stated; the design problem is to determine what type of information structures, communication rules, and decision approaches can be applied to implement these goals. On one hand, this may involve finding or designing a procedure which does minimal damage to these goals (as in the choice of a Borda count for voting). On the other hand, it may involve finding structures which eliminate the existence of these random behaviors. Here, following the lead of L. Hurwicz, some work at an initial stage has been done. [16].

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# DYNAMICS OF NEUMANN-TYPE ECONOMIC MACROSYSTEMS

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## 1. INTRODUCTION

Concepts from optimization theory are of fundamental importance in many macromodels of economic systems. It is assumed that these models describe the optimal (in some sense) functioning of the economy; the trajectory thus generated usually maximizes some objective functional which is exogenous (with respect to the system) and is defined on some family of trajectories of the system. But the very existence of such a functional in a real macroeconomic system is highly questionable. Therefore it is necessary to consider a wider family of models, namely models in which only an optimality principle is given. A principle of this type can be treated in a very broad sense as a formal description of some optimality concepts as in game theory. In some cases the optimality principle allows us to construct an objective functional, which may be optimized step-by-step under some constraints to realize the principle.

In the author's opinion, the study of different optimality principles and the corresponding trajectories is currently the main problem in the mathematical theory of the dynamics of economic macrosystems.

Each optimality principle can be interpreted in two ways: on the one hand it can imply that the controlling centre must make single-valued decisions, with the smallest deviation from this principle leading to a deterioration in the performance of the system. On the other hand the optimality principle can be viewed as a guideline: the centre, inspired by some considerations of an exogenous nature, is able to violate this principle at any time, although systematic violations result in some fundamental deterioration in the performance of the economy. In this case the state of the system obtained by following this principle is viewed as an ideal state which can be compared with the real state of the system and which is considered as the ultimate goal (assuming that the centre accepts the optimality principle).

The second approach seems more appropriate in the case of very rough macroeconomic models.

One mathematical tool useful in studying the second approach is provided by the so-called turnpike theorems (which describe the asymptotics of the trajectories). But in this case it is necessary to use more general results than usual to obtain the asymptotics of all trajectories, or at least some sufficiently large class of them.

This paper presents a short survey of the author's results concerning the dynamics of economic macrosystems of the Neumann type (Rubinov 1980, 1983). Two optimality principles are discussed:

(1) the efficiency principle; this is studied in multiproduct "classical" models of the Neumann type which describe systems with unbounded resources;

(2) the principle of fulfilling the potential of the economic mechanism; this principle is considered in single-product models with an exogenously determined labor force.

The following notation is used: $\mathbb{R}^n$ - n-dimensional coordinate space
$x^i$-the i-th coordinate of the vector $x \in \mathbb{R}^n$
$x \geq y \Leftrightarrow x^i \geq y^i \quad \forall i$
$x > y \Leftrightarrow x \geq y$ and $x \neq y$
$x \gg y \Leftrightarrow x^i > y^i \quad \forall i$

$$\mathbb{R}^n_+ = \{x \in \mathbb{R}^n \mid x \geq 0\}; \quad [u,v] = \Sigma u^i v^i$$

$\Pi(\Omega) = 2^{\Omega} \setminus \emptyset$ - the family of nonempty subsets of the set $\Omega$.

## 2. THE EFFICIENCY PRINCIPLE IN "CLASSICAL" MODELS OF THE NEUMANN TYPE

Superlinear mappings provide a very convenient means of studying Neumann-type models. A mapping $a: R^n_+ \to \Pi(R^m_+)$ is said to be superlinear if

$a(\lambda x) = \lambda a(x) \; \forall \lambda > 0$

$a(x+y) \supset a(x) + a(y)$

$a(0) = \{0\}$

$a(R^n_+) \cap \operatorname{int}(R^m_+) \neq \emptyset$

a is closed.

A mapping a is said to be normal if

$$(y \in a(x), \; 0 \leq y' \leq y) = y' \in a(x) \quad \forall x \in R^n_+.$$

The smallest normal mapping na containing a given mapping a is called the normal hull of a.

Remark. R.T. Rockafellar (1967, 1970) uses different terminology: he writes "convex processes" instead of "superlinear mappings" and "monotone processes of concave type" instead of "normal superlinear mappings".

The mapping a' dual to a superlinear mapping a is defined by the equality

$$a'(f) = \{g \geq 0 \mid [f,x] \geq [g,y], \; x \geq 0, \; y \in a(x)\} \quad \forall f \geq 0.$$

The mapping a' is superlinear. The following equality holds: $a' = na$.

In economic dynamics the graph $Z = \operatorname{gr} a$ of a superlinear mapping

$$a: R^n_+ \to \Pi(R^m_+)$$

is called a Neumann-Gale model. The Neumann rate of growth of this model $\alpha$ is defined by the equality

$$\alpha = \max \{\alpha(x,y) \mid (x,y) \in Z \setminus \{0\}\},$$

where

$$\alpha(x,y) = \max \{\alpha' | \alpha' x \leq y\}.$$

There exist vectors $\bar{x} > 0$ and $p > 0$ such that

$$\alpha\bar{x} \in a(\bar{x}), [p,y] \leq \alpha[p,x] \quad \forall (x,y) \in Z.$$

Vector p is called the Neumann price while vector $\bar{x}$ is called the Neumann equilibrium vector. If mapping a is normal then Z is called a normal Neumann-Gale model.

A Neumann-Gale type model $\mathfrak{M} = (a_t)$ is defined by a sequence of superlinear mappings

$$a_t : R_+^{n_t} \to \Pi(R_+^{n_{t+1}}),$$

where $n_t$ is a given sequence of natural numbers. A sequence $\chi = \{x_t\}$ is called a trajectory of model $\mathfrak{M}$ if

$$x_{t+1} \in a_t(x_t) \quad \forall t.$$

A finite sequence $\chi_T = \{x_t\}_{t=0}^{T}$ is called a T-step trajectory if

$$x_{t+1} \in a_t(x_t) \quad \forall t \in 0,\ldots,T-1.$$

In Neumann-Gale models the efficiency principle (a dynamic Pareto optimality principle) is generally used. A T-step trajectory $\chi_T = \{x_t\}_{t=0}^{T}$ of a model $\mathfrak{M}$ is said to be efficient if it is optimal with respect to some vector $f > 0$ i.e.,

$$\left[f,x_T\right] = \max \{[f,y] | y \in a_{T,0}(x_0)\},$$

where

$$a_{T,0} = a_{T-1} \circ \ldots \circ a_1 \circ a_0.$$

A trajectory $\chi = \{x_t\}$ is said to be efficient if all of its T-steps $\chi_T = \{x_t\}_{t=0}^{T}$ are efficient.

A sequence $\Phi = \{f_t\}$, where $f_t > 0$, is called the characteristic sequence of trajectory $\bar{\chi} = \{\bar{x}_t\}$ of model $\mathfrak{M}$ if for every trajectory $\chi = \{x_t\}$ of this model the sequence $\left[f_t,x_t\right]$ is decreasing, and $\left[f_t,\bar{x}_t\right] = \text{const} > 0$.

It is convenient to use dual models $\mathfrak{M}' = \{a_t'\}$ to study the characteristic sequences of trajectories of model $\mathfrak{M} = \{a_t\}$ since for every pair of trajectories $\chi = \{x_t\}$ of model $\mathfrak{M}$ and $\phi = \{f_t\}$ of model $\mathfrak{M}'$, the sequence $\left[f_t,x_t\right]$ is decreasing.

One new definition: A trajectory $\chi = \{x_t\}$ of model $\mathfrak{M}$ is said to be efficient with respect to ordering if there exists a trajectory $\phi = \{f_t\}$ of model $\mathfrak{M}'$ such that

$$\lim \left[f_t, x_t\right] > 0.$$

Theorem 1. Let $\chi = \{x_t\}$ be a trajectory of model $\mathfrak{M}$ and

$$A(\chi) = \bigcup_{t=1}^{\infty} (na_{t_o})^{-1} (x_t).$$

Then

(1) Trajectory $\chi$ is efficient if and only if $x_o$ is a lower-boundary element of set $A(\chi)$ i.e., $\lambda x_o \notin A(\chi) \quad \forall \lambda < 1$.

(2) Trajectory $\chi$ has a characteristic sequence if and only if the equality

$$\min_{y \in A(\chi)} \left[f,y\right] = \left[f,x_o\right] > 0$$

holds for some $f > 0$.

(3) Trajectory $\chi$ is efficient with respect to ordering if and only if the following relation holds for some $f > 0$:

$$\inf_{y \in A(\chi)} \left[f,y\right] > 0,$$

i.e., $\mathrm{cl}\left[A(\chi)\right] \neq R_+^n$.

We shall now consider the asymptotics of trajectories of Neumann-Gale models. Of special interest are trajectories with the Neumann growth rate, i.e., trajectories $\{x_t\}$ such that $\lim \alpha^{-t}\left[p,x_t\right] > 0$. Here $\alpha$ is the Neumann growth rate and p is the Neumann price. These trajectories are efficient with respect to ordering. Results concerned with asymptotics in this case are usually referred to as turnpike theorems. In the simplest case, a turnpike is a ray passing through the Neumann equilibrium vector. Turnpike theorems state that trajectories which have the Neumann rate of growth and efficient finite trajectories are in some sense close to the ray referred to above.

In the more general case the concept of a turnpike becomes more complicated. L.W. McKenzie (1963) (see also Makarov and Rubinov, 1977) suggested that the asymptotics of efficient finite trajectories could be studied by applying Neumann faces. But these faces are not convenient for a number of reasons; in particular, they do not belong to the state space of the model, they are very often too wide and therefore convergence to them provides no information about the trajectory.

We shall therefore consider another approach.

Let $\alpha$ be the Neumann growth rate of a normal Neumann-Gale model Z. A closed conical set $\tilde{M}$ belonging to $R_+^n$ is called a turnpike set if for any trajectory $\chi = \{x_t\}$ with the Neumann growth rate the following relation holds:

$$\rho\left(\frac{x_t}{\|x_t\|}, \tilde{M}\right)_t \to 0.$$

Recall that a set K is said to be conical if $\lambda K \subset K \ \forall \lambda > 0$. It is not required that K be convex.

The intersection M of all turnpike sets $\tilde{M}$ is called the turnpike and is itself a turnpike set. Here we discuss only the case in which Neumann prices $p \gg 0$ exist.

By $\varkappa$ we denote the set of vectors $x \geq 0$ such that for every scalar $\varepsilon > 0$ and vector $u \gg 0$ there exists a number t satisfying the inclusion

$$(1-\varepsilon)x \in \alpha^{-t} a^t(x+u).$$

A functional $s: R^n \to R_+$ is said to be in equilibrium if it is positively homogeneous, continuous, increasing and such that

$$s(y) \leq \alpha s(x) \quad \forall x \geq 0, \ y \in a(x).$$

If a functional s is in equilibrium then we can define

$$W_s = \{x \geq 0 \mid \alpha s(x) = \max_{y \in a(x)} s(y)\}$$

$$W = \bigcap \{W_s \mid s \text{ is in equilibrium}\}.$$

A trajectory $\chi = \{x_t\}$ of model Z is said to be universally optimal if the equality

$$s(x_0) = \alpha^{-1} s(x_1) = \ldots = \alpha^{-t} s(x_t) = \ldots$$

holds for every functional s which is in equilibrium.

Let $\tilde{W}$ denote the set of points lying on universally optimal trajectories ($x \in \tilde{W}$ if x lies on some universally optimal trajectory).

Theorem 2. Consider a model Z for which Neumann prices $p \gg 0$ exist. Then

(1) $M = \varkappa = W = \tilde{W}$;

(2) M is the smallest closed conical set such that $\rho(\alpha^{-t} x_t, M) \to 0$ for trajectory $\chi = \{x_t\}$ of model Z. Moreover, the trajectory does not have the Neumann growth rate if and only if $\alpha^{-t}\|x_t\| \to 0$.

Remark. Some of the ideas used to prove this theorem can also be used to study the asymptotics of trajectories of discrete dynamic systems (of a very general nature) defined by multivalued mappings.

Let Z be a normal Neumann-Gale model, $Z = gr\, a$ and $\xi$ be a compact set characteristic of mapping a, i.e., $a(\xi) = \beta\xi$ for some $\beta \geq 0$. Assume that the interior of $\xi$ is nonempty (in this case $\beta$ coincides with the Neumann growth rate $\alpha$). A trajectory $\chi = \{x_t\}$ of model Z is said to be $\xi$-optimal if the point $x_t$ belongs to the positive boundary of set $\alpha^t\xi$ for every $t = 0,1,\ldots$. The set of "starting points" of $\xi$-optimal trajectories is denoted by $\varkappa(\xi)$.

Proposition 1. The set $\bigcup_{\lambda \geq 0} \lambda\varkappa(\xi)$ is a turnpike set.

Theorem 3. (A strong turnpike theorem). Consider a normal superlinear mapping $a: R_+^n \to \mathbb{I}(R_+^n)$ which has a compact set $\xi$ with a nonempty interior and a point $x_0 > 0$ such that

$$\lim \alpha^{-t} a^t(x_0) = \xi,$$

where $\alpha$ is the Neumann growth rate of model $Z = gr\ a$. Then for every $\varepsilon > 0$ there exist natural numbers $L_1$ and $L_2$ such that for every finite efficient trajectory $\{x_t\}_{t=0}^T$, $T > L_1 + L_2$, starting at $x_0$ the following inequality holds:

$$\rho\left(\frac{x_t}{\|x_t\|_\xi}, \mathfrak{K}(\xi)\right) < \varepsilon \qquad \forall t \in [t_1, t_2].$$

Here

$$\|x\|_\xi = \inf \{\lambda > 0 \mid x \in \lambda\xi\}.$$

The Neumann growth rate $\alpha$ of model $Z = gr\ a$ is said to be strict if Neumann prices $p \gg 0$ exist and a turnpike M coincides with the ray $M = \{\lambda\bar{x} \mid \lambda \geq 0\}$.

If the growth rate is strict then every trajectory $\chi = \{x_t\}$ of model Z has a limit which is equal to $\lambda\bar{x}$ $(\lambda > 0)$. It follows from this property that the mapping a has a unique (to within a multiplier coefficient) characteristic compact set $\xi$. If, in addition, $\bar{x} \gg 0$, then for every point $x \gg 0$ the following limit exists:

$$\lim \alpha^{-t} a^t(x) = \lambda\xi.$$

Models with a strict growth rate are governed by a strong turnpike theorem (in this case $\mathfrak{K}(\xi) = \{\bar{x}\}$). Thus, the following result holds:

Proposition 2. If the infinite trajectories of a model tend to a ray then a strong turnpike theorem holds for finite efficient trajectories.

The asymptotics of all trajectories of a Neumann-Gale type model are described under the assumption that the model has a trajectory $\bar{\chi} = \{x_t\}$ with a strict characteristic sequence $\phi = \{f_t\}$. This means that $\phi$ is a characteristic sequence and

$$\max_{y \in a_t(x)} [f_{t+1}, y] < [f_t, x]$$

for all $x \gg 0$ which are not proportional to vector $\bar{x}_t$. It is possible to show that trajectory $\bar{\chi}$ plays the role of a turnpike ray: all other trajectories approach $\bar{\chi}$ (in some sense) or are growing "more slowly than $\bar{\chi}$".

In a Neumann-Gale model it is possible to describe goal functions which are consistent with the efficiency principle. A superlinear (i.e., concave positively homogeneous) continuous nonnegative functional q defined on $R_+^n$ and not identically equal to zero is said to be efficient if for some $\alpha > 0$ and for all $x \geq 0$ the equality

$$\alpha q(x) = \max_{y \in a(x)} q(y)$$

holds. The number $\alpha$ is called the efficiency index of q. A trajectory $\chi = \{x_t\}$ is said to be q-optimal if

$$q(x_o) = \alpha^{-1} q(x_1) = \ldots = \alpha^{-t} q(x_t) = \ldots .$$

If $q(x_o) > 0$ then a q-optimal trajectory is efficient, and to find it we must solve several convex programming problems; if the state $x_{t-1}$ is known then $x_t$ is defined as the solution of the problem

$$q(x) \to \max_{x \in a(x_{t-1})} .$$

Theorem 4. Let a Neumann-Gale model Z = gr a have Neumann prices p and a Neumann vector $\bar{x}$ such that $[p,\bar{x}] > 0$. Then this model has efficient functionals. Moreover, a superlinear functional q has an efficiency index $\alpha$ if and only if its superdifferential

$$\partial q = \{f \mid [f,x] \geq q(x) \quad \forall x \geq 0\}$$

is a characteristic set of the dual mapping $a^* = (a')^{-1}$ corresponding to the efficiency index $\alpha$ (i.e. $a^*(\partial a) = \alpha \partial q$).

If mapping a is not separable then the efficiency index of any efficient functional coincides with the Neumann growth rate of the model. Characteristic sequences of q-optimal trajectories can be constructed using the efficient functional $q^*$ of the model Z' = gr a', where

$$q^*(f) = \inf_{q(x)=1} [f,x].$$

Theorem 5. Let q be an efficient functional for a model Z, $x_o \gg 0$, and $\chi = \{x_t\}$ be a trajectory of the model Z which starts at $x_o$ and is q-optimal. Then any trajectory $\phi = \{f_t\}$ (of model Z') which starts at points belonging to $\partial q(x_o)$ and is $q^*$-optimal is a characteristic sequence of the trajectory $\chi$.

If model Z has a strict growth rate then there exists a unique (to within a multiplier coefficient) efficient functional q and, moreover, every efficient trajectory is q-optimal. Let P(x) be a bundle of trajectories starting at x. Let $\lambda(\chi)$ be defined by

$$\lim \alpha^{-t} x_t = \lambda(\chi)\bar{x},$$

where $\chi = \{x_t\}$ is a trajectory and $\bar{x}$ is the Neumann equilibrium vector. Then

$$q(x) = \max_{\chi \in P(x)} \lambda(\chi).$$

## 3. FULFILLING THE POTENTIAL OF THE ECONOMIC MECHANISM

The principle of fulfilling the potential of the economic mechanism can be used to study a number of models with bounded resources. In what follows this principle is applied to the simplest single-product model.

In this model ($M_1$) the vector $(K,L) \in R^2_+$ denotes the state of the economic system, where K represents capital and L labor.

A trajectory of the model is defined by

$$F_t(K,L) = I_{t+1} + w_{t+1},\ I_{t+1} > 0,\ w_{t+1} > 0;\ K_{t+1} = \nu_t K_t + I_{t+1};$$
$$w_{t+1} = \omega_{t+1} L_{t+1}.$$

Here $(K_t, L_1)$ is the state of the system at time t; $I_{t+1}$ is investment at t+1; and $w_{t+1}$ denotes funds which are intended to pay the labor force $L_{t+1}$, over the time interval $[t+1, t+2]$.

The number $\omega_t$ is the average wage at time t; $1-\nu_t$ is the coefficient of depreciation of capital during $[t,t+1]$; and $F_t$ is a production function. It is assumed that

$$F_t(\lambda K, \lambda L) = \lambda F_t(K,L) \qquad \forall \lambda > 0$$

$$F_t(0,1) = F_t(1,0) = 0.$$

The function $f_t(\eta) = F_t(\eta,1)$ is strictly concave and continuously differentiable for $\eta > 0$. The labor force in model $M_1$ is set exogenously, while the average wage is a control parameter. The controlling centre chooses $\omega_{t+1}$ at time t and defines the next point $(K_{t+1}, L_{t+1})$ on the trajectory. It is assumed that the information used in model $M_1$ is of two types. The first is information which the centre knows at some time t . Model $M_1$ has the important property that only information (about the parameters of the model) corresponding to times t and t+1 is known at time t. The second type of information is a list of hypotheses of a qualitative nature about the future behaviour of the economy. The main hypothesis is that the parameters which are most crucial for the development of the economy are slowly changing.

We shall now formulate the optimality principle.

We shall use the term economic mechanism to describe something which generates economic development in the framework of the controlled dynamical system represented by the model. For single-product models we take a set $(F,\nu,\omega)$, where F is a production function, $1-\nu$ is a depreciation coefficient, and $\omega$ is the average wage. We can treat this set as a superlinear mapping which generates a transition from state (K,L) to state (K',L') and for some $I' \geq 0$ satisfies the following relations:

$$I' + \omega L \leq F(K,L),\ K' \leq \nu K + I';\ K' \geq 0,\ L' \geq 0. \tag{1}$$

It is easy to check that the Neumann growth rate $\alpha$ of model $(F,\nu,\omega)$ satisfies the following equality:

$$\alpha = \max_{K,L \geq 0} \frac{\nu K + F(K,L)}{K + \omega L} = \max_{\eta > 0} \frac{\nu\eta + f(\eta)}{\eta + \omega}.$$

Here $f(\eta) = F(\eta,1)$, $\eta = \frac{K}{L}$, is the value of production corresponding to the state (K,L). The value $K + \omega L$ is the national wealth in the state (K,L); the value $\nu K + F(K,L)$ is the national wealth in states attainable in one step from (K,L) (assuming that the equality holds in (1)).

Thus, the Neumann growth rate $\alpha$ is the maximum possible rate of growth of national wealth. This growth rate will be referred to as the potential of the mechanism $(F,\nu,\omega)$. It is called a potential because it can be realized only in a state of $(\bar{K},\bar{L})$-Neumann equilibrium. The value

$\bar{\eta} = \frac{\bar{K}}{\bar{L}}$ corresponding to this state is said to be optimal.

The economic mechanism in model $M_1$ at time t is given by the set $(F_t, \nu_t, \omega_{t+1})$, which defines the next state $(K_{t+1}, L_{t+1})$ if the present state $(K_t, L_t)$ and labor $L_{t+1}$ are known. These states do not generally depend on the potential of the mechanism. Let us now consider the following auxiliary Neumann-type model $N_1$, which is defined as follows:

$$I_{t+1} + \omega_{t+1} L_{t+1} \leq F_t(K_t, L_t);\ I_{t+1} \geq 0,\ L_{t+1} \geq 0,\ K_{t+1} \leq \nu_t K_t + I_{t+1}.$$

In contrast to model $M_1$, the values of $\omega_t$ are assumed to be given while the size of the labor force $L_t$ is not fixed. It is also assumed that $N_1$ is a model with complete information, i.e., that sets $(F_t, \nu_t, \omega_{t+1})\ (t = 0,1,\ldots)$ are known from the beginning. The trajectories of model $N_1$ start at $t = 1$. It is possible to prove that any correct (i.e., such that $I_{t+1} = K_{t+1} - \nu_t K_t > 0\ \forall t$) efficient trajectory of model $N_1$ is proportional (for $t \geq 2$) to the trajectory

$$A_1(\bar{K}_1, \bar{L}_1), \ldots, A_t(\bar{K}_t, \bar{L}_t), \ldots, \qquad (2)$$

where $A_t = \alpha_0 \ldots \alpha_{t-1}$; $\alpha_0 = 1, \ldots, \alpha_t$ is the potential of the model $(F_t, \nu_t, \omega_t)$ $\forall\, t \geq 1$.

$(\bar{K}_t, \bar{L}_t)$ is the Neumann equilibrium vector of this model (normalized so that $\bar{K}_t + \omega_t \bar{L}_t = 1$). Trajectory (2) is said to be a standard trajectory. The economic mechanism of model $N_1$ at time t is a set $(F_t, \nu_t, \omega_t)$ which guarantees movement along a standard trajectory. The existence of a standard trajectory is equivalent to stating that inequalities

$$\alpha_t \bar{K}_{t+1} \geq \nu_t \bar{K}_t$$

hold for $t = 1, 2, \ldots$ .

If $\inf_t(\alpha_t - \nu_t) > 0$ then the validity of these inequalities can be viewed as a consequence of the fact that sets $(F_t, \nu_t, \omega_t)$ are "slowly changing" (as a function of time). If a standard trajectory exists then its state at time t does not depend on mechanisms $(F_\tau, \nu_\tau, \omega_\tau)$ for $\tau > t$.

Let us consider model $M_1$ once again. Assume that at time t the controlling centre knows the values of all the variables with index t as well as the values of $F_{t+1}, \nu_{t+1}, L_{t+1}$. By choosing the coefficient $\omega_{t+1}$, the centre defines the mechanism $(F_t, \nu_t, \omega_{t+1})$ of model $M_1$, the state $(K_{t+1}, L_{t+1})$ on the trajectory of the model and its value of production $\eta_{t+1}$. In model $N_1$ on the other hand the choice of $\omega_{t+1}$ defines the mechanism $(F_{t+1}, \nu_{t+1}, \omega_{t+1})$, its potential and the optimal value of production $\bar{\eta}_{t+1}$ which realizes the potential.

The principle of fulfilling the potential of the economic mechanism in the framework of model $M_1$ means in practice that the value of the control parameter $\omega_{t+1}$ must be chosen in such a way that the equality $\eta_{t+1} = \bar{\eta}_{t+1}$ is satisfied. Thus, the value of $\omega_{t+1}$ is in some senses adjusted to the given technology $F_{t+1}$, $\nu_{t+1}$ and labor force $L_{t+1}$ (and the choice does not depend on the future values of these parameters). Taking this principle as a guideline implies that the choice of coefficients $\omega_t$ must guarantee that

$$\eta_t - \bar{\eta}_t \to 0.$$

It is possible to show that if the hypothesis about a "slowly changing" mechanism and the condition $\inf_t (\alpha_t - \gamma_t) > 0$ are satisfied then the principle of fulfilling the potential can be realized. Under some additional assumptions, it is possible to prove that consistent violation of the principle is either impossible (the hypotheses are violated) or mechanisms will be constructed which use unbounded trajectories. A trajectory of model $M_1$ is not efficient in model $N_1$, even with respect to ordering.

The principle of fulfilling the potential of the economic mechanism can also be stated in the two-product model $M_1$. Its use is based on the decomposition of a two-product model into two single-product models, each of which describes the trajectories of one of the products.

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# V. VIABILITY THEORY AND MULTIVALUED DYNAMICS

# AN INTRODUCTION TO VIABILITY THEORY

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## 1. DEFINITION OF A VIABILITY PROBLEM

A viability problem for differential inclusions with memory may be formulated as follows.

The history of a trajectory $x(\cdot)$ up to time $t$ is described by a map $T(t)$ from the set of continuous mappings $C(]-\infty,t]\,;\,\mathbb{R}^n)$ into the set of continuous mappings $C_0 = C(]-\infty,0]\,;\,\mathbb{R}^n)$ defined by

$$[T(t)x](\zeta) = x(t+\zeta) \qquad \text{for all } \zeta \leqslant 0 \text{ and all } x(\cdot) \in C(]-\infty,t]\,;\,\mathbb{R}^n)\ .$$

A differential inclusion with memory is then defined through a set-valued map $F$ from $\mathbb{R} \times C_0$ into $\mathbb{R}^n$ wich associates the subset $F(t,T(t)x) \subset \mathbb{R}^n$ of feasible velocities with the history (up to time $t$) of a trajectory $x(\cdot)$.

We say that $x(\cdot) \in C(]-\infty,t_0+A\,]\,;\,\mathbb{R}^n)$, $A > 0$, is a solution of the differential inclusion with memory defined by $F(\cdot)$ if it satisfies under the initial condition $(t_0,\phi_0) \in \mathbb{R} \times C_0$:

$$\left\{\begin{array}{l} T(t_0)x = \phi_0 \\ (t,T(t)x) \in \text{Dom } F \qquad \text{for all } t \in [t_0,t_0+A] \\ x(\cdot) \text{ is absolutely continuous on } [t_0,t_0+A] \\ x'(t) \in F(t,T(t)x) \quad \text{for almost all } t \in [t_0,t_0+A]\,, \end{array}\right. \tag{$\star$}$$

where $\text{Dom } F = \{t,\phi) \in R \times C_0\ ,\ F(t,\phi) \neq \emptyset\}$.

We say that the solution is defined on $[t,+\infty[$ if it satisfies (★) for any $A > 0$ .

A viability problem can therefore be described as the particular problem of ensuring the existence of solutions of (★), solutions which in addition are asked to satisfy constraints of the form

$$T(t)x \in K(t) \qquad \text{for all} \quad t \geqslant t_0 \ ,$$

where sets $K(t) \subset C_0$ are defined for all $t \geqslant t_0$. These sets are called the viability sets associated with the problem.

Such a viability problem may be represented by the following system:

$$\begin{cases} x'(t) \in F(t,T(t)x) \\ T(t)x \in K(t) \quad . \end{cases} \tag{$i_1$}$$

The purpose of viability theory is thus to find conditions relating the dynamical system described by $F(\cdot)$ and the viability constraints described by $\{K(t)\}_{t \geqslant t_0}$ which ensure the existence of solutions to $(i_1)$ under any initial condition $(t_0,\phi_0)$ such that $\phi_0 \in K(t_0)$. Such solutions are called viable solutions.

This is a very general formulation of a viability problem. For example, if the viability constraints or the differential inclusion with memory were to take into account only a part of the history, it would still be possible to formulate the problem as in $(i_1)$.

Such a situation could , for example, be described by

$$\begin{cases} x'(t) \in G(t,(T(t)x)_a) \\ (T(t)x)_b \in K_b(t) \end{cases} \tag{$i_1'$}$$

where, for any $\phi \in C_0$ , $\phi_a$ and $\phi_b$ denote the restrictions of $\phi$ on $[-a,0]$ and $[-b,0]$ respectively, and a and b are positive real numbers, $G(\cdot)$ is a set-valued map from $\mathbb{R} \times C([-a,0]; \mathbb{R}^n)$ into $\mathbb{R}^n$ and $K_b(\cdot)$ is a set-valued map from $\mathbb{R}$ into $C([-b,0]; \mathbb{R}^n)$.

It is then sufficient to define

$$F(t,\phi) = G(t,\phi_a) \qquad \text{for any} \quad (t,\phi) \in \mathbb{R} \times C_0$$

and

$$K(t) = \{\phi \in C_0 \; ; \; \phi_b \in K_b(t)\}.$$

The ordinary case with no memory is obtained when $a=b=0$.

Historically the viability problem was introduced by Nagumo (1942), who considered ordinary differential equations and the case in which the viability set is a fixed nonempty compact subset of $\mathbb{R}^n$. Since then viability problems have been studied under a variety of assumptions [see, for example, Brézis (1970), Crandall (1972), Hartman (1972), Larrieu (1981), Martin (1973), Redheffer (1972) and Yorke (1967) for differential equations; Aubin,Cellina and Nohel (1977), Aubin and Clarke (1977), Castaing (1978), Gautier (1976), Haddad (1981), Methlouthi(1977) and Yarom (1982) for differential inclusions; Haddad (1981, 1984), Leela and Moauro (1978) and Seifert (1976) for differential equations(inclusions) with memory .

## 2. SOME MAJOR RESULTS OF VIABILITY THEORY

In this section we give some of the most important results of viability theory in the finite-dimensional case, most of which can be found in Aubin and Cellina (1984).

We shall begin with some definitions and properties. Let $\mathbb{R}^n$ be the finite n-dimensional real vector space with a norm denoted by $\|\cdot\|$. The closed unit ball in $R^n$ is defined by

$$B = \{x \in \mathbb{R}^n \; ; \; \|x\| \leqslant 1\}$$

If C is a nonempty subset of $\mathbb{R}^n$, then int C denotes its interior and for all $x \in \mathbb{R}^n$ we define $d_C(x) = \inf \{\|x-c\| \; ; \; c \in C\}$.

The graph of a set-valued map $F(\cdot)$ from X into Y is defined by

$$\text{Graph}(F) = \{(x,y) \in X \times Y \; ; \; y \in F(x)\} \quad .$$

Let X and Y be two metric spaces. Then a set-valued map $F(\cdot)$ from X into Y is said to be upper-semicontinuous (u.s.c.) on X if for any open subset $\Omega \subset Y$, the set $\{x \in X; \; F(x) \subset \Omega\}$ is an open subset of X.

The set-valued map $F(\cdot)$ is said to be lower-semicontinuous (l.s.c.) on X if for any open subset $\Omega \subset Y$, the set $\{x \in x; \; F(x) \cap \Omega \neq \emptyset \}$ is an open subset of X.

If $F(\cdot)$ is both u.s.c. and l.s.c. on $X$ it is said to be continuous on $X$.

Finally, let $I$ be any interval of $\mathbb{R}$. Then the topology of the space of continuous mappings $C(I,R^n)$ will be identical to the (metrizable) topology of uniform convergence on compact subsets of $I$.

Let us consider the viability problem defined in the first section

$$\begin{cases} x'(t) \in F(t,T(t)x) \\ T(t)x \in K(t) \end{cases} \qquad (i_1)$$

The fundamental tool of viability theory is given in the following definition :

Definition. For any $(t,\phi)$, $\phi \in K(t)$, we define $D_{K(t)}(\phi) \subset R^n$ by $v \in D_{K(t)}(\phi)$ if and only if, for any $\varepsilon > 0$, there exist $h \in ]0,\varepsilon]$ and $x_h \in C(]-\infty,t+h];\mathbb{R}^n)$ such that

$$\begin{cases} T(t)x_h = \phi \\ T(t+h)x_h \in K(t+h) \\ \dfrac{x_h(t+h) - x_h(t)}{h} \in v + \varepsilon B \end{cases} \qquad (1)$$

Then we have the following result (see Haddad, 1984).

THEOREM 1. Suppose that $K(\cdot)$ has a closed graph in $\mathbb{R} \times C_0$ and that all the elements of $K(t)$ are Lipschitzian with a constant independent of $t$.
Suppose that $F(\cdot)$ is u.s.c. on the graph of $K(\cdot)$ and takes nonempty convex compact values at every point in this set. Then the condition

$$F(t,\phi) \cap D_{K(t)}(\phi) \neq \emptyset \quad \text{for all} \quad (t,\phi) \in \text{Graph } K \qquad (c_1)$$

is necessary and sufficiennt for the existence under any initial condition $(t_0,\phi_0) \in$ Graph $K$ of an associated viable solution of $(i_1)$ defined on $[t_0,+\infty[$.

A concrete application of this theorem can be found in Haddad (1984), where the solutions are asked to satisfy

$$x(t) \in D\left[t, x(t+\theta_t^{(1)}), \ldots, x(t+\theta_t^{(p)})\right] \quad \text{for all} \quad t \geqslant t_0 .$$

Here $\theta_{(\cdot)}^{(1)}, \ldots, \theta_{(\cdot)}^{(p)}$ are given strictly negative real functions and $D(\cdot)$ is a given set-valued map from $\mathbb{R} \times (\mathbb{R}^n)^p$ into $\mathbb{R}^n$.

In this particular case the viability constraint appears to be directly related to decisions based on past information with some delay.

This reflects what happens in everyday life, where our information is never completely up-to-date for obvious reasons.

In another application, the solutions are asked to satisfy

$$x(t) = [x_1(t), \ldots, x_n(t)] \in E\left(t, \int_{-\infty}^{t+\theta_t} x_1(z)p_1(z)dz, \ldots, \int_{-\infty}^{t+\theta_t} x_n(z)p_n(z)dz\right)$$

for all $t \geqslant t_0$,

where $\theta(\cdot)$ is a given stictly negative real function, $p_1(\cdot), \ldots, p_n(\cdot)$ are given real functions and $E(\cdot)$ is a set-valued map from $\mathbb{R} \times \mathbb{R}^n$ into $\mathbb{R}^n$.

In this case the viability constraint appears to be directly related to decisions based on knowledge of the accumulated values

$$\int_{-\infty}^{t+\theta_t} x_1(z)p_1(z)dz, \ldots, \int_{-\infty}^{t+\theta_t} x_n(z)p_n(z)dz$$

of the trajectory up to the time $t + \theta_t < t$.

If no memory is required, i.e., we are considering a viability problem of the following type :

$$\begin{cases} x'(t) \in S(t, x(t)) \\ x(t) \in K(t) \end{cases} \qquad (i_2)$$

where $S(\cdot)$ is a set-valued map from $\mathbb{R} \times \mathbb{R}^n$ into $\mathbb{R}^n$ and $K(\cdot)$ is a set-valued map from $\mathbb{R}$ into $\mathbb{R}^n$, then an obvious adaptation shows that for any $x \in K(t)$ the set $D_{K(t)}(\phi)$ defined above may

be replaced by the set

$$D_{K(t)}(x) = \left\{ v \in \mathbb{R}^n \; ; \; \liminf_{h \to 0+} \frac{1}{h} d_{K(t+h)}(x+hv) \right\} = 0$$

This leads to the following result (see Haddad,1981):

THEOREM 2. Suppose that $K(\cdot)$ has a locally compact graph in $\mathbb{R} \times \mathbb{R}^n$ and that $S(\cdot)$ is u.s.c. on the graph of $K(\cdot)$ and takes nonempty convex compact values at every point in this set. Then the condition

$$S(t,x) \cap D_{K(t)}(x) \neq \emptyset \quad \text{for all} \quad (t,x) \in \text{Graph } K \qquad (c_2)$$

is necessary and sufficient for the existence under any initial condition $(t_0,x_0) \in \text{Graph } K$ of an associated viable solution of $(i_2)$.

Finally, it is easily verified that in the case where $K(t)$ does not depends on time, $K(t) = K \subset \mathbb{R}^n$ for all $t \in \mathbb{R}$, the fundamental tool is Bouligand's contigent cone (Bouligand,1982), which is defined for any $x \in K$ as follows:

$$D_K(x) = \left\{ v \in \mathbb{R}^n ; \; \liminf_{h \to 0+} \frac{1}{h} d_K(x+hv) = 0 \right\} .$$

Thus for the autonomous viability problem

$$\begin{cases} x'(t) \in S[x(t)] \\ x(t) \in K \end{cases} \qquad (i_2')$$

we have the following result, which is an extension of Nagumo's theorem:

COROLLARY. Let $K$ be a closed subset of $\mathbb{R}^n$ and $S(\cdot)$ a set-valued map from $\mathbb{R}^n$ into $\mathbb{R}^n$ which is u.s.c. on $K$ and takes nonempty convex compact values at every point in this set. Then the condition

$$S(x) \cap D_K(x) \neq \emptyset \quad \text{for all} \quad x \in K \qquad (c_2')$$

is necessary and sufficient for the existence under any initial

condition $(t_0,x_0)$ , $x_0 \in K$ , of an associated viable solution of $(i_2')$.

It is important to notice that if $K$ is an open subset of $\mathbb{R}^n$, then $D_K(x)=\mathbb{R}^n$ for all $x \in K$. Thus condition $(c_2')$ is automatically satisfied by any point in $K$. Corollary 2 therefore includes the standard local existence theorem (see Aubin and Cellina, 1984) for a differential inclusion defined on an open set when the set-valued map is u.s.c. with nonempty convex compact values.

Sufficient conditions for the existence of viable solutions of $(i_2')$ have also been given for the case in which the set-valued map $S(\cdot)$ is no longer assumed to take convex values. It is clear that the conditions have to be strengthened. We have the following result from Aubin and Clarke (1977) :

THEOREM 3. Let $K$ be a locally compact subset of $\mathbb{R}^n$ and $S(\cdot)$ a set-valued map from $\mathbb{R}^n$ into $\mathbb{R}^n$ which is continuous on $K$ and takes nonempty compact values at every point in this set. Then the condition :

$$S(x) \subset D_K(x) \quad \text{for all} \quad x \in K \qquad (C_3)$$

implies the existence under any initial condition $(t_0,x_0)$, $x_0 \in K$, of an associated viable solution of $(i_2')$.

Let us define Clarke's tangent cone (Clarke,1975) for any $x \in K$ as follows: ,

$$C_K(x) = \left\{ v \in \mathbb{R}^n ;\ \lim_{\substack{h \to 0+ \\ y \xrightarrow{} x \\ y \in K}} \frac{1}{h}\, d_K(y+hv) = 0 \right\} .$$

It is important to note that under the assumptions of Theorem 3 (and even if $S(\cdot)$ is only assumed to be l.s.c. on $K$), condition $(c_3)$ is equivalent to

$$S(x) \subset C_K(x) \quad \text{for all} \quad x \in K . \qquad (C_3')$$

However, based on the use of Clarke's tangent cone, we have the following different result from Yarom (1982) :

THEOREM 4. Let $K$ be a compact subset of $R^n$ and $S(\cdot)$ a set-valued map from $\mathbb{R}^n$ into $\mathbb{R}^n$ which is l.s.c. on $K$ and takes nonempty compact values at every point in this set. Then the condition

$$S(x) \cap \text{int } C_K(x) \neq \emptyset \quad \text{for all} \quad x \in K \qquad (c_4)$$

implies that under any initial condition $(t_0, x_0)$, $x_0 \in K$, and for any $v_0$ in the closure of $S(x_0) \cap \text{int } C_K(x_0)$, there exists an associated viable solution of $(i_2')$ which satisfies $x'(0) = v_0$.

An easy proof shows that Theorem 4 implies Bressan's local existence theorem (Bressan, 1980) for a differential inclusion defined on an open set in the case where the set-valued map is l.s.c. with nonempty compact values.

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# HEAVY VIABLE TRAJECTORIES OF CONTROLLED SYSTEMS

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ABSTRACT

We define and study the concept of heavy viable trajectories of a controlled system with feedbacks. Viable trajectories are trajectories satisfying at each instant given constraints on the state. The controls regulating viable trajectories evolve according a set-valued feedback map. Heavy viable trajectories are the ones which are associated to the controls in the feedback map whose velocity has at each instant the minimal norm. We construct the differential equation governing the evolution of the controls associated to heavy viable trajectories and we prove their existence. These results are applied to exchange economies for finding heavy trajectories of a dynamical decentralized allocation mechanism explaining the evolution of prices.

## 1. INTRODUCTION

When we study the evolution of macrosystems which arise in economics and the social sciences as well as in biological evolution, we should take into account not only :

(1) our ignorance of the future environment of the system

but also :

(2) the absence of determinism (including the impossibility of a comprehensive description of the dynamics of the system)

(3) our ignorance of the laws relating certain controls to the states of this system

(4) the variety of dynamics available to the system.

We propose to translate these requirements into mathematics by means of differential inclusions, which describe how the velocity depends in a multi-valued way upon the current state of the system. Another feature of such macrosystems is that the state of the system must obey given restrictions known as viability constraints, which determine the viability domain ; viable trajectories are those lying entirely within the viability domain. Finding viable trajectories of a differential inclusion provides a mechanism of selection of trajectories which, contrary to optimal control theory, does not assume implicitly

(1) the existence of a decision maker operating the controls of the system (there may be more than one decisionmaker in a game-theoretical setting)

(2) the availability of information (deterministic or stochastic) on the future of the system ; this is necessary to define the costs associated with the trajectories

(3) that decisions (even if they are conditional) are taken once and for all at the initial time.

Viability Theorems provide necessary and sufficient conditions for the existence of at least one viable trajectory starting from any viable initial state. It also provides the feedbacks (concealed in both the dynamics and the viability constraints) which relate the state of the system to the controls. These feedbacks are not necessarily deterministic : they are set-valued maps associating a subset of controls with each state of the system. We observe that the larger these subsets of controls are, the more flexible - and, thus, the more robust - the regulation of the system will be.

Finally the third feature shared by those macrosystems is the high inertia of the controls which change only when the viability of the system is at stake. Associated trajectories are called heavy viable trajectories : they minimize at each instant the norm of the velocity of the control. We shall provide a formal definition of heavy viable trajectories, which requires an adequate concept of derivative of the set-valued feedback map. We show that as long as the state of the system lies in the interior of the viability domain, any regulating control will work. Therefore, along a heavy trajectory, the system can maintain the control inherited from the past. (The regulatory control remains constant even though the state may evolve quite rapidly).

What happens when the state reaches the boundary of the viability domain ? If the chosen velocity is "inward" in the sense that it pushes the trajectory back into the domain, then we can still keep the same regulatory control.

However, if the chosen velocity is "outward", we are in a period of crisis and must find, as slowly as possible, another regulatory control such that the new associated velocity pushes the trajectory back into the viability domain.

When this strategy for "structural change" fail, the trajectory "dies" i.e., it is no longer viable (see Figure below).

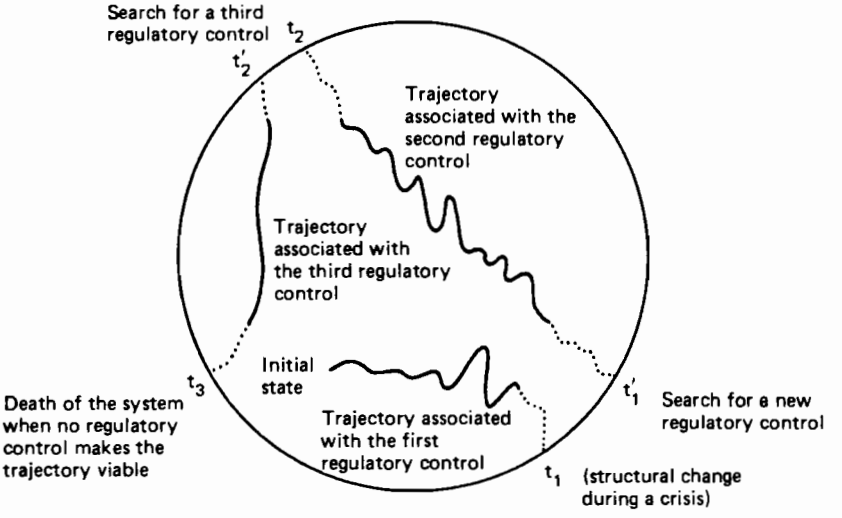


FIGURE 1 The viability domain

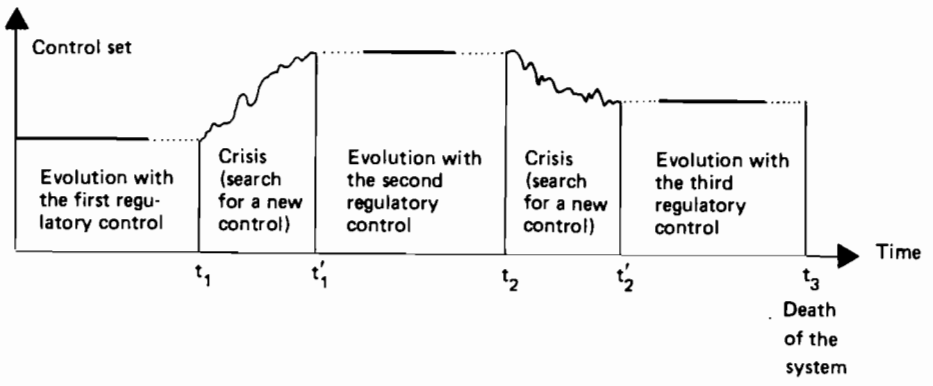


Figure 1 (continued)

The equations which govern the evolution of heavy viable trajectories also reveal a division of the viability domain into "cells" : each cell is the subset of viable states which can be regulated by a given control. To pass from one cell to another requires the control to be changed. The boundaries of these cells signal the need for structural change. We mentioned biological evolution as a motivation for studying heavy viable trajectories. Paleontological concepts such as punctuated equilibria proposed by Elredge and Gould are consistent with the concept of heavy viable trajectories.

Indeed, for the first time, excavations at Kenya's Lake Turkana have provided clear fossil evidence of evolution from one species to another. The rock strata there contain a series of fossils that show every small step of an evolutionary journey that seems to have proceeded in fits and starts. Williamson [ 1981 ] examined 3.300 fossils showing how thirteen species of molluscs changed over several million years. What the record indicated was that the animals stayed much the same for immensely long stretches of time. But twice, about 2 million years ago and then again 700.000 years ago, the pool of life seemed to explode - set off, apparently, by a drop in the lake's water level. In an instant of geologic time, as the changing lake environment allowed new types of molluscs to win the race for survival, all of the species evolved into varieties sharply different from their ancestors. That immediate forms appeared so quickly, with new species suddenly evolving in 5,000 to 50,000 years after millions of years of constancy , challenges the traditional theories of Darwin's disciples since the fossils of Lake Turkana don't record any gradual change ; rather, they seem to reflect eons of stasis interrupted by brief evolutionary "revolutions".

We shall also illustrate the behavior of heavy trajectories in the framework of an economic model : we conclude this introduction with the description of the most simple dynamical decentralized allocation mechanism of a good $w$ given in $\mathbb{R}^\ell$ among $n$ consumers. Knowing the price $p(t) \in \mathbb{R}^\ell$ and its consumption bundle $x_i(t)$ at time $t$ , consumer $i$ decides to change $x_i(t)$ according to the differential equation

$$x_i'(t) = (\gamma_i(x_i(t)) - \frac{1}{n} p(t) \quad , \quad x_i(0) = x_{oi} \tag{1.1}$$

in which the price $p(t)$ plays the role of a regulatory control.

Viable trajectories are the ones satisfying the scarcity constraint

$$\text{for all } t, \quad \sum_{i=1}^{n} x_i(t) \leqslant w \tag{1.2}$$

We denote by

$$K := \left\{x:=(x_1,\ldots,x_n) \in \mathbb{R}^{pn} \mid \sum_{i=1}^{n} x_i \leqslant w\right\}$$

the set of allocations of the resource $W$ among the $n$ consumers. We introduce a $C^1$-function $\varphi$ from a neighborhood of $K$ to the prices space $\mathbb{R}^{\ell}$ which represent the minimum price associated to an allocation $x$ set by the producers. It defines the set-valued feedback map $P$ by

$$P(x) := \{p \in \mathbb{R}^{\ell} \mid p \geqslant \varphi(x)\} \tag{1.3}$$

We define the set $H(x,p)$ of labels by

$$H(x,p) := \{h=1,\ldots,\ell : \varphi(x)_h = p_h\} \tag{1.4}$$

We shall assume that the following "compatibility" condition is satisfied

$$\left.\begin{aligned} &\forall\, h \in H_1(x) := \left\{h=1,\ldots,\ell \;;\; \sum_{i=1}^{n} x_{i_h} = w_h\right\}, \\ &\varphi(x)_h \geqslant \sum_{i=1}^{n} \gamma_i(x_i)_h \end{aligned}\right\} \tag{1.5}$$

The differential equation governing the evolution of prices associated with heavy trajectories is

$$\left.\begin{aligned} &\text{i)} \quad p_h'(t) = 0 \quad \text{if} \quad h \notin H(x(t),p(t)) \\ &\text{ii)} \quad p_h'(t) = \sum_{i=1}^{n} \left(\frac{\partial \varphi}{\partial x_i}(x(t))\right) \left(\gamma_i(x_i) - \frac{1}{n}\, p(t)\right)_h \\ &\qquad\qquad \text{if} \quad h \in H(x(t),p(t)) \end{aligned}\right\} \tag{1.6}$$

The price $p_h(t_o)$ is constant for $t \geqslant t_o$ as long as the $\varphi(x(t))_h$ is strictly less than $p_h(t_o)$. When $\varphi(x(t_1))_h = p_h(t_1)$, then the price $p_h(t)$ starts to evolve according to the differential equation (1.6)ii). (We shall deduce these differential equations from general results which are the pusposes of this work).

The outline of this paper is as follows. In section 2, we define the viability problem for controlled systems with feedbacks, which contain the usual controlled systems and the differential inclusions, and we recall Haddad's viability theorem. We proceed by introducing other tangent cones

and by defining contingent derivatives of set-valued maps which we need to define heavy viable trajectories. We define them in section 3 and state the existence theorem of heavy viable trajectories. We shall not give its proof here. Instead, we give explicit formulas in the smooth case in section 4. We conclude in section 5 with an economic application : we construct the differential equation governing the evolution of prices associated with heavy viable trajectories of a dynamical decentralized allocation mechanism in a general exchange economy.

## 2. BACKGROUND NOTES

We introduce a viability domain $K$ , a subset of a finite dimensional space $X$ , a finite dimensional control space $U$ , a set-valued map $F$ from $K$ to $U$ and a continuous function $f$ from graph$(F)$ to $X$ . We define the viability problem for a controlled system with feedbacks as follows : $\forall\ x_o \in K$ , find $T > 0$ and an absolutely continuous function $x(\cdot)$ satisfying

$$\left.\begin{array}{ll} \text{i)} & \text{for almost all } t \in [0,T] \ , \quad x'(t) = f(x(t),u(t)) \\ \text{ii)} & \text{for almost all } t \in [0,T] \ , \quad u(t) \in F(x(t)) \\ \text{iii)} & x(0) = x_o \end{array}\right\} \qquad (2.1)$$

which is viable on $[0,T]$ in the sense that

$$\text{for all } t \in [0,T] \ , \quad x(t) \in K \ . \qquad (2.2)$$

By taking $U = X$ , $f(x,u) = u$ , we obtain the particular case of a viability problem for a differential inclusion

$$x'(t) \in F(x(t)) \quad , \quad x(0) = x_o \qquad (2.3)$$

The viability requirement (2.2) involves naturally restrictions of the dynamical system at the boundary of $K$ . It happens that the best way to describe these conditions is to use the contingent cone to $K$ at $x$ (see Aubin-Cellina [1984], p. 176-179, for instance) defined by :

$$T_K(x) := \left\{ v \in X \mid \liminf_{h \to 0+} \frac{d_K(x+hv)}{h} = 0 \right\} \qquad (2.4)$$

We define the feedback map $R$ from $K$ to $U$ by

$$R(x) := \{u \in F(x) \mid f(x,u) \in T_K(x)\} \qquad (2.5)$$

We observe that any viable trajectory of the controlled system (2.1) is a solution to the "feedback" differential inclusion

$$\left.\begin{array}{ll} \text{i)} & \text{for almost all } t \in [0,T] \ , \quad x'(t) = f(x(t),u(t)) \\ \text{ii)} & \text{for almost all } t \in [0,T] \ , \quad u(t) \in R(x(t)) \\ \text{iii)} & x(0) = x_o \end{array}\right\} \tag{2.6}$$

(the initial set-valued map $F$ is replaced by the feedback map $R$ ).

The main viability theorem (see Haddad [1981], Aubin-Cellina [1984] p. 239-240) provides necessary and sufficient conditions for the existence of viable trajectories of (2.3).

Theorem 2.1

We assume that

$$\left.\begin{array}{ll} \text{i)} & K \text{ is locally compact} \\ \text{ii)} & F \text{ is upper semicontinuous with nonempty convex compact images} \\ \text{iii)} & f \text{ is continuous and is affine with respect to the control} \end{array}\right\} \tag{2.7}$$

Then the "first order" tangential condition

$$\forall\, x \in K \quad , \quad R(x) \neq \emptyset \tag{2.8}$$

is necessary and sufficient for the existence of a viable trajectory of the controlled system (2.1) for all $x_o \in K$ . ▲

Before defining heavy viable trajectories, we need to recall the following facts.

When $K$ is a subset of a finite dimensional $X$ , we can define other concepts of tangent cones, among which we mention

a) the tangent cone (introduced by Clarke [1975]) :

$$C_K(x) := \left\{ v \in X \;\middle|\; \lim_{\substack{h \to 0+ \\ y \to x \\ y \in K}} \frac{d_K(y+hv)}{h} = 0 \right\} \tag{2.9}$$

b) the Dubovickii-Miljutin [1963] cone :

$$D_K(x) := \{ v \in X \mid \exists\, \varepsilon > 0 \ , \ x + [0,\varepsilon](v+\varepsilon B) \subset K \} \tag{2.10}$$

We have the following relations (see Cornet [1981]; Penot [1981], Aubin-Ekeland [1984] p. 409).

$$C_K(x) = \liminf_{\substack{y \to x \\ y \in K}} T_K(y) \subset T_K(x) \tag{2.11}$$

and :

$$\text{Int } C_K(x) \subset D_K(x) \subset \text{Int } T_K(x) \tag{2.12}$$

The tangent cone is always convex. It coincides with the contingent cone when $K$ is a smooth manifold (tangent space) or when $K$ is convex or, more generally, when $K$ is soft in the sense that

$$x \to T_K(x) \quad \text{is lower semicontinuous} \tag{2.13}$$

(see Aubin-Clarke [ 1977 ]).

Consider now a set-valued map $R$ from $X$ to $U$ and a point $(x,u)$ of its graph. The contingent derivative $DR(x,u)$ is the set-valued map from $X$ to $U$ defined by

$$w \in DR(x,u)(v) \Leftrightarrow (v,w) \in T_{\text{Graph}(R)}(x,u) \tag{2.14}$$

It is equivalent to say that

$$\liminf_{\substack{h \to 0+ \\ v' \to v}} d\left(w, \frac{R(x+hv')-u}{h}\right) = 0 \tag{2.15}$$

The contingent derivative $DR(x,u)$ is a closed process (a map whose graph is a closed cone). We say that the map $F$ is soft if its graph is soft. Then $DR(x,u)$ is a closed convex process, because its graph is equal to the tangent cone to $\text{Graph}(R)$ at $(x,u)$). We shall say that $R$ is lower semicontinuously differentiable if

$$(x,u,v) \to DR(x,u)(v) \quad \text{is lower semicontinuous} \tag{2.16}$$

We observe that in this case $DR(x,u)$ is a closed convex process because property (2.16) implies that $(x,u) \to T_{\text{Graph}(R)}(x,u)$ is lower semicontinuous, and thus, $\text{Graph } DR(x,u)$ is a closed convex cone.

Finally, when $K$ is a closed subset of $X$, we denote by

$$m(K) := \left\{u \in K \mid \|u\| = \min_{v \in K} \|v\|\right\} = \pi_K(0) \tag{2.17}$$

the subset of elements of $K$ with minimal norm. If $F$ is a continuous set-valued map with closed convex images, the single-valued map $x \to m(F(x))$ is continuous. This is no longer the case when $F$ is only upper or lower semicontinuous (with closed convex images). However,

$$\left.\begin{array}{l}\text{if } F \text{ is lower semicontinuous with closed images,} \\ \text{then } x \to d(0,F(x)) \text{ is upper semicontinuous}\end{array}\right\} \tag{2.18}$$

We refer to Aubin [ 1983 ] and Aubin-Ekeland, [ 1984 ], Chapter 7, Clarke [ 1983 ] for a general presentation of nonsmooth analysis relevant to this study.

## 3. HEAVY VIABLE TRAJECTORIES

We consider the viability problem (2.1), (2.2) for controlled systems with feedbacks. We have seen that viable trajectories are solutions to the feedback differential inclusion (2.6). When the functions $x(\cdot)$ and $u(\cdot)$ are absolutely continuous, we can differentiate the "first order" feedback law

$$\forall\ t \in [0,T\ ],\quad u(t) \in R(x(t)) \tag{3.1}$$

and obtain the "second order" feedback law

$$\text{for almost all } t \in [0,T\ ],\ u'(t) \in DR(x(t),u(t))(f(x(t),u(t))) \tag{3.2}$$

We now propose to select among all regulatory controls satisfying (3.2) the ones whose velocity has a minimal norm : such trajectories seem to be present in the evolution of macrosystems arising in social, economic and biological sciences (which motivated viability theory in the first place).

Definition 3.1

We shall say that absolutely continuous functions $(x(\cdot),u(\cdot))$ form a heavy viable trajectory if it is a solution to the system of differential inclusions :

$$\left.\begin{array}{ll} \text{i)} & x' = f(x,u) \\ \text{ii)} & u' \in m(DR(x,u)(f(x,u))) \\ \text{iii)} & (x(0),u(0)) \quad \text{given in} \quad Graph(R) \end{array}\right\} \tag{3.3}$$

which are viable in the sense that

$$\forall\ t \in [0,T\ ],\quad x(t) \in K \ \text{ and } \ u(t) \in R(x(t)) \tag{3.4}$$

We shall say that the subsets

$$C(u) := \{x \in K \mid 0 \in DR(x,u)(f(x,u))\} \tag{3.5}$$

are the viability cells of the system. ▲

We observe that along a heavy viable trajectory, a system will keep the control $u(t_o)$ as long as the state $x(t)$ remains in the viability cell $C(u(t_o))$ for $t \geqslant t_o$, because in this case inclusion (3.3)ii) sates that $u'(t) = 0$. If not, when $x(t)$ leaves the viability cell $C(u(t_o))$ at time $\bar{t}_o$, the control starts to evolve at time $\bar{t}_o$ until the time $t_1$ when $x(t_1) \in C(u(t_1))$.

In the case of ordinary differential inclusions (when $U = X$ and $(f(x,u) = u)$, heavy viable trajectories can be written $x(t_o)+(t-t_o)x'(t_o)$ when $x(t_o) \in C(x'(t_o))$ as long as $x(t_o) + (t-t_o)x'(t_o)$ remains in

$\ddot{C}(x'(t_o))$ . In this case, the viability cells display areas of the viability domain where "linear quantitative growth" holds true.

We shall state now our main existence theorem.

For this we assume that

$$f \text{ is } C^1 \text{ in a neighborhood of } \text{graph}(F) \tag{3.6}$$

and that

$$\text{the maps } F \text{ and } T_K \text{ are soft} \tag{3.7}$$

We posit the following "transversality condition"

$$\left.\begin{array}{l} \forall\ (x,u) \in \text{Graph}(R)\ ,\ \forall\ (y,z) \in X \times X\ ,\quad v \in X \text{ satisfying} \\ z \in f'_x(x,u)v + f'_u(x,u)DF(x,u)(v) - DT_K(x,f(x,u))(v-y) \end{array}\right\} \tag{3.8}$$

Then the derivative of the feedback map $R$ can be written

$$\left.\begin{array}{l} DR(x,u)(v) = \\ DF(x,u)(v) \cap f'_u(x,u)^{-1}(DT_K(x,f(x,u))(v) - f'_x(x,u)v) \end{array}\right\} \tag{3.9}$$

Assume moreover that

$$\text{Graph}(F) \text{ is locally compact} \tag{3.10}$$

and that

$$\text{The feedback map } R \text{ is lower semicontinuously differentiable} \tag{3.11}$$

Theorem 3.2

Under the assumptions (3.6)-(3.8) and (3.10),(3.11), the "first order" condition

$$\forall\ x \in K\ ,\quad R(x) \neq \emptyset \tag{3.12}$$

and the "second order" condition

$$\forall\ (x,u) \in \text{Graph}(R)\ ,\quad f(x,u) \in \text{Dom } DF(x,u) \cap \text{Dom } T_K(x,f(x,u)) \tag{3.13}$$

imply the existence of heavy viable trajectories of the controlled system (2.1) for any initial state $x_o \in K$ and initial control $u_o \in R(x_o)$ if

$$\text{Graph}(T_K) \text{ is locally compact} \tag{3.14}$$

If the graph of $T_K$ is not locally compact, the initial control must satisfy

$$f(x_o,u_o) \in D_K(x_o) \tag{3.15}$$

▲

The proof of the above Theorem is quite long. We shall not give it here.

Several comments are in order. Theorem 3.2 should be compared to Theorem 2.1 Theorem 3.2 does not involve convexity requirements, but smoothness conditions (3.7) and (3.11) and second order condition (3.13) on top of the first order condition (3.12). The solutions are more regular (the control is absolutely continuous instead of being only measurable), but there exist the restriction (3.15) on the initial state when the graph of $T_K$ is not locally compact. Unfortunately, this happens whenever $K$ involves inequality constraints : Take for instance $K = \mathbb{R}_+$ . Then $Graph(T_K) = (\{0\} \times \mathbb{R}_+) \cup (]0,\infty[ \times \mathbb{R})$ is not locally compact. But the map $T_K$ is soft and even lower semicontinuously differentiable because

$$DT_K(x,u)(v) = \begin{cases} \mathbb{R} & \text{if } v \leq 0 \\ \emptyset & \text{otherwise} \end{cases} \tag{3.16}$$

This crucial example shows that assumption (3.7) is not unreasonable.

Since the maps $F$ and $T_K$ are soft, the derivative $DR(x,u)$ defined by (3.9) is a closed convex process and the differential inclusion (3.3)ii) governing the velocity of the control is actually the differential equation

$$u'(t) = m(DR(x(t),u(t))\ (f(x(t),u(t)))) \tag{3.17}$$

We can also provide sufficient conditions for the regularity assumption (3.11) to hold true. For instance, thanks to a theorem on the lower semicontinuity of the intersection of two lower semicontinuous maps (see Aubin-Cellina [ 1984 ] p. 49), conditions (3.7) and (3.11) follow from the following ones

$$\left.\begin{array}{ll} \text{i)} & \text{the set-valued maps } F \text{ and } T_K \text{ are lower semi-} \\ & \text{continuously differentiable} \\ \text{ii)} & (x,u) \to DF(x,u)(f(x,u)) \text{ is bounded on some neighborhood} \\ & \text{of each point } (x,u) \text{ of } Graph(R) \\ \text{iii)} & \forall\ (x,u) \in Graph(R)\ ,\ \exists\ \gamma > 0\ ,\exists\ \varepsilon > 0 \text{ such that} \\ & \forall\ (y,v) \in B_{Graph(R)}((x,u,\varepsilon)\ ,\ \forall\ z \in B(0,\gamma)\ ,\text{ we have} \\ & z \in f'_x(y,v)f(y,v) + f'_u(y,v)DF(y,v)(f(y,v)) \\ & \qquad - DT_K(y,f(y,v))(f(y,v)) \end{array}\right\} (3.18)$$

■

We can adapt Theorem 3.2 to viability domains $K$ which are the intersection of a subset $L$ whose tangent cone has a locally compact graph and another subset. Namely, consider the case of a viability domain of the form :

$$K = L \cap A^{-1}(M) \tag{3.19}$$

where $A$ is a $C^1$-map from $X$ to a finite dimensional space $Y$ . We also assume that :

$$T_K(x) = T_L(x) \cap T_{A^{-1}(M)}(x) \quad \text{and} \quad T_{A^{-1}(M)}(x) = A'(x)^{-1} T_M(Ax) \tag{3.20}$$

This holds true for instance when :

$$\left.\begin{array}{l} L \text{ and } M \text{ are closed convex subsets and } A \text{ is linear,} \\ \text{satisfying } 0 \in \text{Int}(A(L)-M) \end{array}\right\} \tag{3.21}$$

(see Aubin-Cellina [ 1984 ] p. 325) or when

$$\left.\begin{array}{l} L \text{ and } M \text{ are soft} \\ \text{and when } \forall\ x \in K\ ,\ A'(x)T_L(x) - T_M(Ax) = X \end{array}\right\} \tag{3.22}$$

(see Aubin-Ekeland [ 1984 ] p. 440).
In this case, the feedback map $R$ can be written

$$R(x) := \{u \in F(x) \mid f(x,u) \in T_L(x) \text{ and } A'(x)f(x,u) \in T_M(Ax)\} \tag{3.23}$$

Corollary 3.3.
Let us assume that (3.20) holds true and that the graphs of $F$ and $T_L$ are locally compact. We posit assumptions (3.7), (3.8), (3.11), (3.12) and (3.13).
Then for any $x_o \in K$ and any control $u_o \in F(x_o)$ satisfying

$$A'(x_o)\, f(x_o,u_o) \in D_M(Ax_o) \tag{3.24}$$

there exist $T > 0$ and a heavy viable trajectory of the controlled system (2.1) on $[0,T]$. ▲

Proof. We replace $F$ by $F \cap T_L$, whose graph is locally compact and we observe that $A'(x)D_M(Ax) \subset D_{A^{-1}(M)}(x)$. ■

Let us formulate Theorem 2 in the particular case of differential inclusions, when $U := X$ and $f(x,u) := u$.

Corollary 3.4.
Let us assume that the maps $F$ and $T_K$ are soft and satisfy the "transversality condition"

$$\left.\begin{array}{l} \forall\ (x,u) \in \text{Graph}(R)\ ,\ \forall\ (y,z) \in X \times X\ ,\quad v \in X \text{ such that} \\ z \in DF(x,u)(v) - DT_K(x-u)(v-y) \end{array}\right\} \tag{3.25}$$

Then

$$DR(x,u)(v) = DF(x,u)(v) \cap DT_K(x,u)(v)\ . \tag{3.26}$$

Assume that the graph of $F$ is locally compact and that the regularity condition (3.11) is satisfied. We posit the first and second order conditions

$$\left.\begin{array}{ll} \text{i)} & \forall\, x \in K\ ,\quad R(x) := F(x) \cap T_K(x) \neq \emptyset \\ \text{ii)} & \forall\, (x,u) \in \mathrm{Graph}(R)\ ,\quad u \in \mathrm{Dom}\ DF(x,u) \cap \mathrm{Dom}\ DT_K(x,u) \end{array}\right\} \tag{3.27}$$

Then, for any $x_o \in K$ and any $u_o \in F(x_o)$ satisfying either

$$u_o \in T_K(x_o) \quad \text{when the graph of } T_K \text{ is locally compact} \tag{3.28}$$

or

$$u_o \in D_K(x_o) \tag{3.29}$$

then there exist $T > 0$ and a $C^1$ heavy viable trajectory of $x' \in F(x)$, $x(0) = x_o$ and $x'(0) = u_o$, a solution to the second order differential equation

$$x''(t) = m(DR(x(t),x'(t))(x'(t)))\ ,\ x(0) = x_o\ ,\ x'(0) = u_o\ . \tag{3.30}$$

▲

## 4. EXAMPLE : THE SMOOTH CASE

We consider now the smooth case, when

$$K := \{x \in X \mid g(x) = 0\}$$

and when $F$ is the constant map equal to $U$.

Theorem 4.1.

Let us assume that $f$ is a $C^1$-function from $X \times U$ to $X$, $g$ is a $C^2$-function from $X$ to $Y$ and that, $\forall\, x \in K$, $g'(x) \in L(X,Y)$ is surjective. We suppose that

$$\forall\, x \in K\ ,\quad R(x) := \{u \in U \mid g'(x)\, f(x,u) = 0\} \neq \emptyset \tag{4.1}$$

and that

$$\forall\, (x,u) \in \mathrm{Graph}(R)\ ,\quad g'(x)\, f'_u(x,u) \in L(U,Y) \text{ is surjective} \tag{4.2}$$

Then, for any $x_o \in K$ and $u_o$ such that $g'(x_o)f(x_o,u_o) = 0$, there exists a heavy viable trajectory, a solution to the system of differential inclusions :

$$\left.\begin{array}{ll} \text{i)} & x' = f(x,u) \\ \text{ii)} & u' = -f'_u(x,u)^\star\, g'(x)^\star (g'(x) f'_u(x,u) f'_u(x,u)^\star g'(x)^\star)^{-1} \\ & \qquad [g'(x) f'_x(x,u) f(x,u) + g''(x)(f(x,u),f(x,u))] \\ \text{iii)} & (x(0),u(0)) = (x_o,u_o)\ . \end{array}\right\} \tag{4.3}$$

▲

Proof.

In this simple case, we can compute $m(DR(x,u))(v)$ explicitly. Indeed, since $T_K(x) = \mathrm{Ker}\ g'(x)$, then $R(x) = \{u \in U \mid g'(x)f(x,u) = 0\}$. By setting :

$$h(x,u) := (g(x) , g'(x)f(x,u)) \tag{4.4}$$

we observe that $\text{Graph}(R) = \{(x,u) \mid h(x,u) = 0\}$ . This function is $C^1$ and we check easily that

$$h'(x,u)(v,w) = (g'(x)v, g''(x)(f(x,u),v) + g'(x)f'_x(x,u)v + g'(x)f'_u(x,u)w)$$

Since both $g'(x)$ and $g'(x)f'_u(x,u)$ are surjective by assumption, then $h'(x,u)$ is surjective. Therefore, this contingent cone to $\text{Graph}(R)$ at $(x,u)$ - actually, its tangent space - is the set of pairs $(v,w)$ such that $h'(x,u)(v,w) = 0$ . Hence

$$\left.\begin{aligned} &DR(x,u)(v) = \\ &-f'_u(x,u)^{-1}g'(x)^{-1}\,[\,g''(x)(f(x,u),v) + g'(x)f'_x(x,u)v] \end{aligned}\right\} \tag{4.5}$$

Now we can compute explicitly the element of minimal norm $m(DR(x,u)(v))$, which minimize the norm $\|w\|$ under the linear constraint

$$g'(x)f'_u(x,u)w = -g'(x)f'_x(x,u)v - g''(x)(f(x,u),v))$$

Its solution is given explicitly by the right-hand side of (4.3)ii).

Example. Heavy viable trajectories on affine subspaces.

We consider the case when $K = \{x \in X \mid Gx = y\}$ where $G \in L(X,Y)$ is surjective. We assume that

$$\left.\begin{aligned} &\text{i)}\ \ \forall\, x \in K\ ,\quad u \in U \ \text{ such that } \ Gf(x,u) = 0 \\ &\text{ii)}\ \ \forall\, x \in K\ ,\ \forall\, u \in U \ \text{ such that } \ Gf(x,u) = 0\ ,\ \ Gf'(x,u) \\ &\quad\ \text{is surjective.} \end{aligned}\right\} \tag{4.6}$$

Then for any $x_o$ satisfying $Gx_o = y$ , $u_o$ satisfying $Gf(x_o,u_o) = 0$ , there exists a heavy viable trajectory, a solution to the system of differential equations

$$\left.\begin{aligned} &\text{i)}\ \ x' = f(x,u) \\ &\text{ii)}\ \ u' = -\,f'_u(x,u)^{\star}G^{\star}(Gf'_u(x,u)f'_u(x,u)^{\star}G^{\star})^{-1}Gf'_x(x,u)f(x,u) \end{aligned}\right\} \tag{4.7}$$

When $G = g \in X^{\star}$ $(Y = R)$ , assumptions (4.6) become

$$\left.\begin{aligned} &\text{i)}\ \ \forall\, x \in K\ ,\quad u \in U \ \text{ such that } \ \langle g, f(x,u)\rangle = 0 \\ &\text{ii)}\ \ \forall\, x \in K\ ,\ \forall\, u \in U \ \text{ such that } \ \langle g, f(x,u)\rangle = 0\ , \\ &\quad\ \text{then } \ f'_u(x,u)^{\star}g \neq 0 \end{aligned}\right\} \tag{4.8}$$

and equation (4.7)ii) becomes

$$u' = -\frac{f'_u(x,u)^\star g}{\|f'_u(x,u)^\star g\|^2} \langle g , f'_x(x,u)f(x,u)\rangle \tag{4.9}$$

Example. Heavy viable trajectories on the sphere.

Let $G$ be a symmetric positive definite linear operator from $X$ to $X^\star$ and we take

$$K := \{x \in X \mid \langle Gx,x\rangle = 1\} \tag{4.10}$$

We assume that

$$\left.\begin{array}{ll} \text{i)} & \forall\, x \in K\ ,\quad R(x) := \{u \in U \mid \langle Gx,f(x,u)\rangle = 0\} \neq \emptyset \\ \text{ii)} & \forall\, (x,u) \in \mathrm{Graph}(R)\ ,\quad f'_u(x,u)^\star Gx \neq 0 \end{array}\right\} \tag{4.11}$$

Then the heavy viable trajectories on the sphere are the solutions to the system of differential equations

$$\left.\begin{array}{ll} \text{i)} & x' = f(x,u) \\ \text{ii)} & u' = -\dfrac{f'_u(x,u)^\star Gx}{\|f'_u(x,u)^\star Gx\|^2}\ (\langle Gf(x,u),f(x,u)\rangle + \\ & \qquad\qquad + \langle Gx,f'_u(x,u)f(x,u)\rangle) \end{array}\right\} \tag{4.12}$$

■

Remark.

Consider the case when

$$K = \{x \in X \mid g(x) = 0\} \cap A^{-1}(M) \tag{4.13}$$

where $g$ is a $C^2$-map from $X$ to $Y$ and $A$ is a $C^1$-map from $X$ to $Z$, $Y$ and $Z$ being finite dimensional spaces. We assume that $y \to T_M(y)$ is lower semicontinuous, that

$$\forall\, x \in K\ ,\quad A'(x)\ \mathrm{Ker}\ g'(x) - T_M(Ax) = X \tag{4.14}$$

and that, $\forall\, y,z \in Z \times Z$, $\exists\, v$, a solution to the inclusion :

$$\left.\begin{array}{l} z = DT_M(Ax,A'f)(A'v-y) \cap [A'f'_x v + A''(f,v) \\ \qquad\qquad - A'g'^{-1}(g''(f,v) + g'f'_x v)] \end{array}\right\} \tag{4.15}$$

where we have set $f := f(x,u)$, $g' := g'(x)$, $A' = A'(x)$, $f'_x = f'_x(x,u)$, $f'_u := f'_u(x,u)$, $A''(u,v) = A''(x)(u,v)$, $g''(u,v) = g''(x)(u,v)$.

Assumption (4.14) implies that

$$R(x) = \{u \in U \mid g'(x)f(x,u) = 0 \ \text{ and } \ A'(x)f(x,u) \in T_M(Ax)\} \tag{4.16}$$

and assumption (4.15) implies that

$$\left.\begin{aligned} DR(x,u)(v) := &- (g'f'_u)^{-1}(g''(f,v)+g'f'_x v) \cap \\ &(A'f'_u)^{-1}(DT_M(A(x),A'f)(A'v)-A''(f,v)-A'f'_x v) \end{aligned}\right\} \tag{4.17}$$

## 5. HEAVY TRAJECTORIES OF DECENTRALIZED DYNAMICAL ALLOCATION MECHANISMS

We consider the decentralized dynamical allocation mechanism proposed in Aubin [ 1981 ]b) (see also Aubin-Cellina [ 1984 ], Section 5.5, 245-256 and Stacchetti, [ 1984 ]).

We interpret $Y := \mathbb{R}^\ell$ as a commodity space, its dual $Y^*$ as the price space.

The description of the exchange economy begins with

$$\text{the subset } M \subset Y \text{ of available commodities} \tag{5.1}$$

The problem is to devise decentralized mechanisms allowing to allocate an available commodity $y \in M$ among $n$ consumers $i=1,\ldots,n$.

Each consumer chooses a commodity in a consumption set $L_i \subset Y$. By setting

$$X := Y^n \quad , \quad L := \prod_{i=1}^n L_i \quad , \quad x = (x_1,\ldots,x_n) \in X$$

the set $K$ of allocations is defined by

$$K := \left\{ x \in L \mid \sum_{i=1}^n x_i \in M \right\} \tag{5.2}$$

Let $P \subset Y^*$ denote the subset of prices. We describe the behavior of each agent by change functions $c_i$ satisfying

$$\left.\begin{aligned} &\text{i) } \forall\, i=1,\ldots,n, \quad c_i : L_i \times P \to Y \text{ is } C^1 \text{ around } L_i \times P \\ &\text{ii) } \forall\, x \in L_i \,, \forall\, p \in P \,, \quad c_i(x,p) \in T_{L_i}(x) \end{aligned}\right\} \tag{5.3}$$

The decentralized dynamical allocation mechanism we study is described by a system of differential equations : Given $x_o = (x_{o1},\ldots,x_{on}) \in K$, find solutions $x_i(t)$ to the system of differential equations

$$\forall\, i=1,\ldots,n \,, \quad x_i'(t) = c_i(x_i(t),p(t)) \quad , \quad x_i(0) = x_{io} \tag{5.4}$$

controlled by prices $p(t) \in P$.

The viability condition requires that at each instant, $x(t) = (x_1(t),\ldots,x_n(t))$ is an allocation :

$$\forall\, t \geqslant 0 \,, \forall\, i=1,\ldots,n \,, \quad x_i(t) \in L_i \quad \text{and} \quad \sum_{i=1}^n x_i(t) \in M \tag{5.5}$$

In order to have an explicit description of the feedback map $R$, we posit the following assumptions :

$$\left.\begin{array}{l} \text{i) the subsets } L_i \text{, } M \text{ and } P \text{ are closed convex} \\ \text{ii) } 0 \in \operatorname{Int}\left(\sum_{i=1}^{n} L_i - M\right) \end{array}\right\} \tag{5.6}$$

which imply that

$$T_K(x) = \left\{ v \in \prod_{i=1}^{n} T_{L_i}(x_i) \mid \sum_{i=1}^{n} v_i \in T_M\left(\sum_{i=1}^{n} x_i\right)\right\}$$

(see Aubin-Cellina [ 1984 ] p. 241).

The feedback map $R$ is defined by

$$R(x) = \left\{ p \in P \mid \sum_{i=1}^{n} c_i(x_i,p) \in T_M\left(\sum_{i=1}^{n} x_i\right)\right\} \tag{5.7}$$

thanks to assumption (5.3)ii).

The first order condition requires that

$$\forall\, x \in K \quad , \quad R(x) \neq \emptyset \quad . \tag{5.8}$$

Remark.

We recall that when $P = S^{\ell}$, $M \subset M - \mathbb{R}^{\ell}_{+}$ and the change functions $c_i$ are affine with respect to $p$, then a sufficient condition for (5.8) is that the budgetary constraints

$$\forall\, p \in P \text{ , } \forall\, x \in L \text{ , } \quad \sum_{i=1}^{n} \langle p, c_i(x,p)\rangle \leqslant 0 \quad .$$

are satisfied. ∎

In order to express the second-order condition, we have to couch the derivative of the feedback map in terms of the derivatives of the change functions $c_i$ and the set-valued maps $T_{L_i}(\cdot)$, $T_p(\cdot)$ and $T_M(\cdot)$.

We posit assumptions (5.3) and (5.6). We assume that

$$\text{the set-valued map } T_M \text{ is soft} \tag{5.9}$$

and that for all $(x,p) \in \operatorname{Graph}(R)$, the following transversality property holds true :

$$\left.\begin{array}{l} \forall\, y,z \in Y \times Y \text{ , } \exists\, \pi \in T_p(p) \text{ , } \exists\, v_i \in T_{L_i}(x_i) \text{ such that} \\ z \in \sum_{i=1}^{n} \frac{\partial}{\partial x_i} c_i(x_i,p)v_i + \sum_{i=1}^{n} \frac{\partial}{\partial p} c_i(x_i,p)\pi \\ \qquad - DT_M\left(\sum_{i=1}^{n} x_i \text{ , } \sum_{i=1}^{n} c_i(x_i,p)\right)\left(\sum_{i=1}^{n} v_i - y\right) \end{array}\right\} \tag{5.10}$$

Then the derivative $DR(x,p)(v)$ of the feedback map $R$ is empty when $v_i$ does not belong to $T_{L_i}(x_i)$ for some $i$ and is equal to

$$DR(x,p)(v) = \left\{ T_P(p) \cap \left( \sum_{i=1}^n \frac{\partial}{\partial p} c_i(x_i,p) \right)^{-1} \left( DT_M\left( \sum_{i=1}^n x_i , \sum_{i=1}^n c_i(x_i,p) \right) \left( \sum_{i=1}^n v_i \right) - \sum_{i=1}^n \frac{\partial}{\partial x_i} c_i(x_i,p) v_i \right) \right\} \quad (5.11)$$

when $v_i \in T_{L_i}(x_i)$ for all $i=1,\ldots,n$ . ■

We then obtain the following theorem :

Theorem 5.1.

We posit assumptions (5.3), (5.6), (5.10). Assume moreover that

$$\left.\begin{array}{l} \text{the graphs of the set-valued maps } T_{L_i}(\cdot) \text{ and } T_P(\cdot) \\ \text{are locally compact} \end{array}\right\} \quad (5.12)$$

and

$$\text{the feedback map } R \text{ is lower semicontinuously differentiable} \quad (5.13)$$

Then, for all initial allocation $x_o \in K$ and all initial price $p_o$ satisfying

$$\sum_{i=1}^n c_i(x_{oi},p_o) \in T_M\left( \sum_{i=1}^n x_{oi} \right) \text{ if the graph of } T_M(\cdot) \text{ is locally compact or } \sum_{i=1}^n c_i(x_{oi},p_o) \in D_M\left( \sum_{i=1}^n x_{oi} \right) \text{ if not ,}$$

there exist $T > 0$ and a heavy viable trajectory of the decentralized dynamical allocation mechanism (5.4), a solution to the system of differential equations

$$\left.\begin{array}{ll} \text{i)} & x_i'(t) = c_i(x_i(t),p(t)) \ , \quad x_i(0) = x_{oi} \ , \quad i=1,\ldots,n \\ \text{ii)} & p'(t) = m(DR(x(t),p(t))(c(x(t),p(t)))) \ , \quad p(0) = p_o \end{array}\right\} \quad (5.14)$$

▲

We cannot have an explicit analytical expression of the element of minimal norm of $DR(x,p)(c(x,p))$ except in special situations. Assume for instance that we do not take into account the constraints on prices and individual consumptions. We take $P = Y^\star$ and $L_i = Y$ for all $i$ . Then, for all $x \in X$ ,

$$R(x) = \left\{ p \in Y^\star \mid \sum_{i=1}^n c_i(x_i,p) \in T_M\left( \sum_{i=1}^n x_i \right) \right\} \quad (5.15)$$

The surjectivity property

$$\forall\ (x,p) \in \text{Graph}(R) \ , \quad \sum_{i=1}^n \frac{\partial}{\partial p} c_i(x_i,p) \text{ is surjective} \quad (5.16)$$

implies that the transversality property (5.10) is satisfied. Then, if we assume that

$$\text{the set-valued map } T_M \text{ is soft ,} \tag{5.17}$$

we obtain

$$DR(x,p)(v) =$$

$$\left(\sum_{i=1}^{n} \frac{\partial}{\partial p} c_i(x_i,p)\right)^{-1} \left[DT_M\left(\sum_{i=1}^{n} x_i \ , \ \sum_{i=1}^{n} c_i(x_i,p)\right) \left(\sum_{i=1}^{n} v_i\right) - \sum_{i=1}^{n} \frac{\partial}{\partial x_i} c_i(x_i,p)\cdot v_i\right] \tag{5.18}$$

Let us set now

$$\varphi(x,p) := \left(\sum_{i=1}^{n} \frac{\partial}{\partial p} c_i(x_i,p)\right)^{-1} \left(\sum_{i=1}^{n} \frac{\partial}{\partial x_i} c_i(x_i,p) c_i(x_i,p)\right) \tag{5.19}$$

and

$$E(x,p) := \left(\sum_{i=1}^{n} \frac{\partial}{\partial p} c_i(x_i,p)\right)^{-1} DT_M\left(\sum_{i=1}^{n} x_i \ , \ \sum_{i=1}^{n} c_i(x_i,p)\right) \left(\sum_{i=1}^{n} c_i(x_i,p)\right) \tag{5.20}$$

Then the element with minimal norm can be written

$$m(DR(x,p)(c(x,p))) = (1 - \pi_{E(x,p)})\, \varphi(x,p) \tag{5.21}$$

We provide now a numerical example dealing with 3 consumers and 2 goods. We assume here that for $i = 1,2,3$

$$\gamma_i(x_i) = \begin{pmatrix} \alpha_i x_{i1}^{\alpha_i - 1} \cdot x_{i2}^{1-\alpha_i} & \\ & \\ (1-\alpha_i) x_{i1}^{\alpha_i} \cdot x_{i2}^{-\alpha_i} & \end{pmatrix}$$

$$\alpha = (\alpha_1,\alpha_2,\alpha_3) = (0.3,0.5,0.7)$$

The consumption level $w$ is fixed by

$$w = (1,1)$$

The initial conditions are

$$p(0) = (1.51,1.51) \ , \ x_1(0) = (0.7,0.3) \ , \ x_2(0) = x_3(0) = (0.14,0.3)$$

One can see from Fig. 2 that in this model the price of the first good is evolving in a heavy way. The initial conditions for the second good are such that the price can be kept constant on the time interval $[0,1]$.

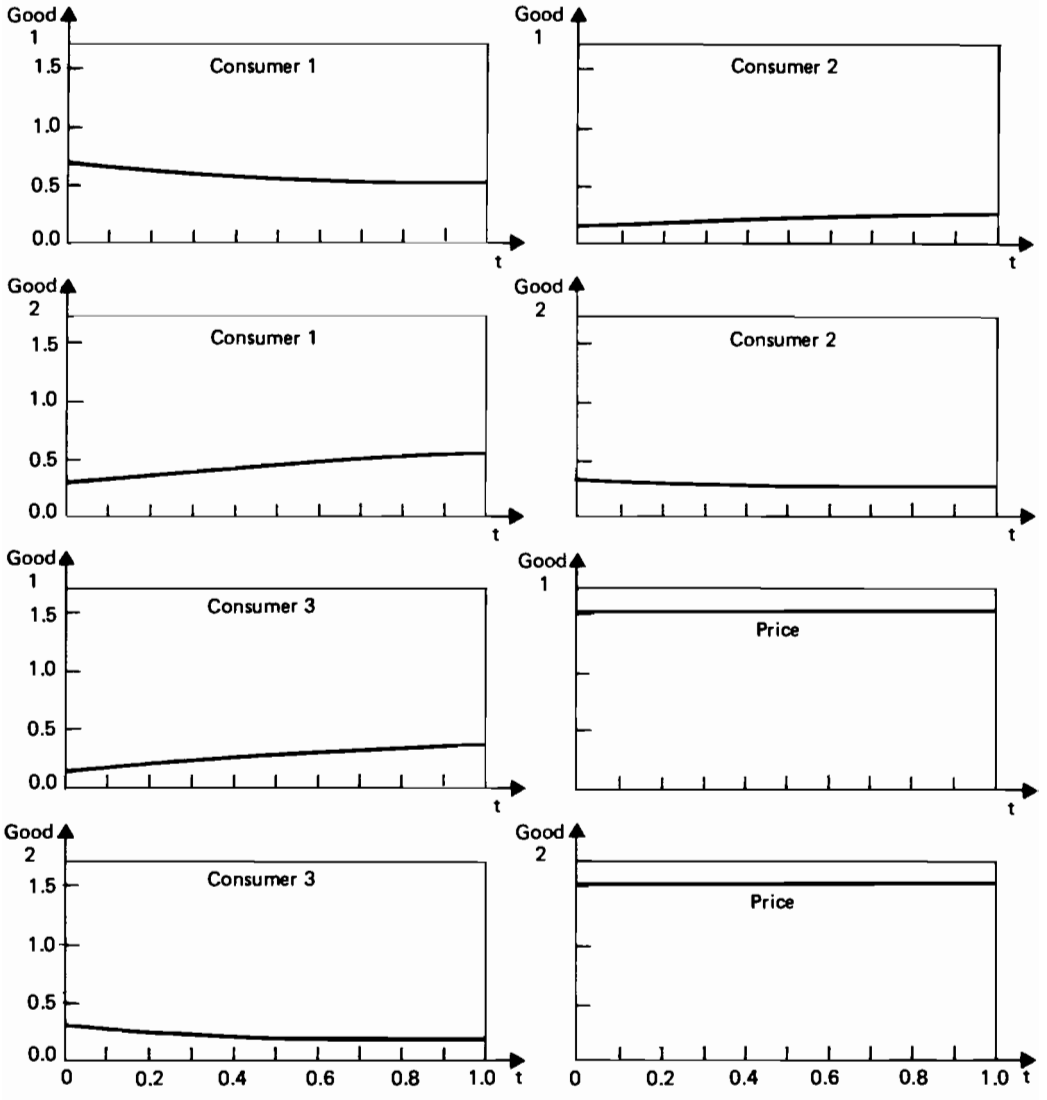


FIGURE 2 The results of the numerical simulation

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# SEMILINEAR PARABOLIC EQUATIONS WITH INFINITE DELAY

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## 1. INTRODUCTION

We shall deal with an abstract semilinear evolution equation

$$\dot{u}(t) + Au(t) = F(t,u_t),\ u_0 = \varphi\ , \qquad (1)$$

with infinite delay, i.e., $u_t$ denotes a function $u_t(s) = u(t+s)$ on the interval $(-\infty, 0]$. The motivation for the study of such equations comes partly from theoretical biology. For example, in his classical book Volterra introduced "historical action" into population growth models in the following form

$$\dot{u}(t) = au(t)[1-b\int_0^{+\infty} k(s)u(t-s)ds]\ .$$

The C.I.M.E. lectures of Cushing (1981) provide a very good review of such models. In addition, it is obvious that the effect of diffusion cannot be ignored on a microbial level. A similar situation occurs in epidemic, ecological and population genetics models (see, e.g., Capasso and Fortunato, 1980; Hadeler, 1981; Okubo, 1980). Introducing both effects, i.e. historical action and diffusion, we arrive at the following equation:

$$\frac{\partial u}{\partial t} = d\,\frac{\partial^2 u}{\partial x^2} + au\,[1-b\int_0^{+\infty} k(s)u(t-s,x)ds]\ . \qquad (2)$$

Existence and stability properties for such equations are given by Schiaffino (1979); the corresponding results for the predator-prey model are given by Pozio (1980).

Another motivation for the study of equation (1) comes from various papers on materials with memory. Coleman and Gurtin (1967) and Pipkin (1968) proposed a theory of heat conduction based on thermodynamics for such materials, which leads to a linear parabolic or hyperbolic equation with integral terms. A simple nonlinear version of these models, i.e. the equation

$$\frac{\partial u}{\partial t} - \frac{\partial^2 u}{\partial x^2} = \int_0^t a(t-s)\,\frac{\partial}{\partial x}\sigma\,(\frac{\partial u}{\partial x}\,(s,x))ds + f(t,x)\ , \qquad (3)$$

was studied by Crandall at al. (1978) using monotone operator methods and by Webb (1979), who adopted an approach similar to that described in this paper.

If we rewrite both equations (2) and (3) in the form (1), then the operator $-A$ is not only a generator of the $C_0$-semigroup $e^{-At}$ on some Banach space X but it is also sectorial, i.e., $e^{-At}$ is an analytic semigroup. This means that $R(e^{-At}) \subset \mathcal{D}(A)$ for $t > 0$ and $\| Ae^{-At} \| = O(t^{-1})$ for $t \to 0+$ (see Friedman 1969; Henry 1981). With regard to the right-hand side of (1), the

integral term in (3) shows that F depends not only on past values of u but also on its space derivatives. The very simple example $F(u) = 2Au$ implies that some special conditions have to be imposed on any nonlinear term F.

If a sectorial operator A satisfies the spectral condition

$$\inf \{\mathrm{Re}\ \lambda\ ;\ \lambda \in \sigma(A)\} > 0 \tag{4}$$

(e.g., A is the Laplace operator with Dirichlet data but not with Neumann conditions, or, more generally, A is a positive-definite self-adjoint operator in a Hilbert space), then fractional powers $A^\alpha$ of A are defined. Their domains with graph norms will be denoted by $X^\alpha$. These spaces can also be defined without condition (4) by means of an appropriate shift A + kI. Note that in the case where $X = L^2(0,1)$ and -A is the closure of the Laplace operator with Dirichlet conditions, we obtain $X^{1/2} = H_0^1$, $X^1 = H_0^1 \cap H^2$.

Further, we denote by $Y^\alpha(T)$ the Banach space of all bounded uniformly continuous maps of the interval $(-\infty, T)$ into the space $X^\alpha$ endowed with the sup norm.

We split any nonlinear term F into two parts:

$$F(t,u_t) = f(t,u_t) + \int_0^t g(t,s,u(s))ds\ ,$$

where we will make the following assumptions:

(Hf) There exist a $\beta > 0$ and an open subset $U_1$ of $[0, +\infty) \times Y^1(0)$ such that f is a continuous map of $U_1$ into $X^\beta$.

(Hg) There exists an open subset $U_2$ of $\{(t,s);\ 0 \leq s \leq t < \infty\} \times X^1$ such that g is a continuous map of $U_2$ into X and is locally Hölder continuous in the first variable and locally Lipschitz in the third.

Note that there are no smoothness conditions on f but the values of f are smoother with respect to the space variables (f maps into $X^\beta$, e.g., f does not depend on the second derivatives of u). On the other hand, the values of g need n be so good with respect to the space variables (e.g. g may depend on Δ but g satisfies some smoothness condition. Note that the conditions (Hf (Hg) are more general than those given by Webb (1979), Heard (1982) or Sc acher (1981).

## 2. EXISTENCE AND CONTINUOUS DEPENDENCE

The approach used to prove the existence of a solution to (1) is quite standard. Using a generalization of the variation of constants formulae, one proves the existence of a so-called "mild solution", i.e., a solution of the following integral equation:

$$u(t) = e^{-At}\varphi(0) + \int_0^t e^{-A(t-s)}f(s,u_s)ds + \tag{5}$$

$$+ \int_0^t e^{-A(t-s)} \int_0^s g(s,\sigma,u(\sigma))d\sigma\ ds\ ,$$

$$u_0 = \varphi\ ,$$

and then the regularity of a mild resolution is studied. Weak assumptions (Hf) , (Hg) make this approach rather difficult since it is not possible to use the contraction principle as f is not smooth. If A is assumed to have a compact resolvent (i.e., $e^{-At}$ is compact for $t > 0$), one can prove that the operator

$$\Phi_1(u)(t) := \begin{cases} 0 & \text{for } t \leq 0 \\ \int_0^t e^{-A(t-s)} f(s,u_s)\,ds & \text{for } t > 0 \end{cases}$$

is a compact continuous map of $Z(r) := \{u \in Y^1(T): u_0 = \varphi\ ,\ \| u(t) - \varphi(0)\|_1 \leq r \text{ for } t \in (0,T]\}$ into $Y^1(T)$ for sufficiently small positive r,T. We note that the assumption $\beta > 0$ in (Hf) is crucial in the proof. However, the third operator on the right-hand side of (5)

$$\Phi_2(u)(t) := \begin{cases} 0 \text{ for } t \leq 0 \\ \int_0^t e^{-A\,(t-s)} \int_0^s g(s,\sigma,u(\sigma))\,d\sigma\,ds \text{ for } t > 0 \end{cases}$$

is not compact on Z(r). Fortunately, it can be decomposed into the sum of a compact continuous operator and a contractive operator, so that use of the Darbo generalization of the Schauder fixed-point theorem (see Darbo, 1955) yields a solution to (5). The parabolic regularity is generally not too complicated and therefore the following theorem holds (for more details and applications see Milota and Petzeltova (1985a)).

Theorem 1. Let A be a sectorial operator with a compact resolvent and let assumptions (Hf), (Hg) be satisfied. Then for any $\varphi \in Y^1(\Omega)$ such that $(0,\varphi) \in U_1$, $(0,0,\varphi(0)) \in U_2$, there exist a $T > 0$ and a function $u \in Y^1(T)$ such that (i) A strong derivative (in X) $\dot{u}(t)$ exists for all $t \in (0,T)$ ;

(ii) u satisfies equation (1) at all points of the interval (0,T) ;

(iii) $u_0 = \varphi$.

Note here that the common continuation procedure yields maximal solutions. In what follows, when we use the word "solution" we always mean maximal solution.

As the assumption (Hf) does not ensure the uniqueness of a solution, the question of continuous dependence is more delicate. We shall make the following assumption:

(H) Let $U_1 = [0, +\infty) \times Y^1(0)$ , $U_2 = \{(t,s);\ 0 \leq s \leq t < \infty\} \times X^1$ in (Hf) and (Hg), respectively. Let f and g be bounded on any bounded subset and let g be Hölder continuous in the first variable and Lipschitz in the third variable on any bounded subset of $U_2$.

This assumption allows us to extend all solutions belonging to a fixed bounded set. This extension can be done uniformly, yielding a Kneser-type theorem:

Theorem 2. Let the assumptions of Theorem 1 be satisfied and (H) hold. Let all solutions to (1) be defined at least on the interval $[0,a]$. Then the set of these solutions is compact in the space $C([0,a],X^1)$.

Corollary. Under the assumptions of Theorem 2, there is a positive number $b$ such that all solutions are defined on the interval $[0,b)$ and at least one solution $u$ is not defined on any larger interval if $b < \infty$, i.e.,

$$\overline{\lim}_{t\to b-} \| u(t)\|_1 = \infty.$$

The last theorem is a major step towards a theorem of continuous dependence. For details of the proofs of both theorems see Milota and Petzeltova (1985b).

Theorem 3. Let a sequence of equations

$$\dot{u}(t) + Au(t) = f_n(t,u_t) + \int_0^t g_n(t,s,u(s))ds, \quad u_o = \varphi_n, \quad (6n)$$

be given, where $A$, $f_n$, $g_n$, $f$, $g$ satisfy the assumptions of Theorem 2. Assume that the following conditions are met:

(i) $\varphi_n \to \varphi$ in $Y^1(0)$;

(ii) Functions $f_n, g_n$ are locally uniformly bounded and the $g_n$ satisfy the Hölder and Lipschitz conditions both locally and uniformly (i.e., with the same constants and exponent);

(iii) If $t\in[0, +\infty)$, $\psi_n \to \psi$ in $Y^1(0)$, then $f_n(t,\psi_n) \to f(t,\psi)$ in $X^\beta$;

(iv) If $0\leq s\leq t<\infty$, $x_n \to x$ in $X^1$, then $g_n(t,s,x_n) \to g(t,s,x)$ in $X$.

Let $v_n$ be a solution to (6n) and let $b$ be given by the Corollary. Then for any $c \in [0,b)$ there exists a subsequence $v_{n_k}$ which converges to a solution of (1) in the space $C([0,c],X^1)$.

Now that we have a continuous dependence theorem we can try to use methods from dynamical systems theory to obtain some results concerning the asymptotic behavior of solutions, such as stability properties or the existence of periodic and almost periodic solutions. We postpone the question of periodic solutions to the next section and concentrate here on stability.

First, because of the non-uniqueness of solutions we have to use a dynamical theory for multivalued mappings which is not so well-developed as the theory for single-valued dynamical systems. We hope that at least some stochastic features of the real biological system can be reflected in the non-uniqueness of the solutions of deterministic models (see the notion of a trajectory discussed below) and therefore it is worth developing multivalued dynamics.

Let $S$ denote a phase space which is assumed to be a metric space and let $C : S\times\mathbb{R}\times\mathbb{R} \to \exp S$ represent a generalized dynamical system, i.e.,

(i) $C(\varphi,t_o,t)$ is a compact subset of $S$ for any $\psi\in S$, $t_o\in\mathbb{R}$ and $t\geq t_o$;

(ii) $C(\varphi,t_o,t_o) = \{\varphi\}$;

(iii) $C(\varphi,t_o,t_1) = \cup\{C(\psi,t,t_1);\ \psi\in C(\varphi,t_o,t)\}$ for any $t\in[t_o,t_1]$;

(iv) $C(\varphi,t_0,.)$ is a continuous map of the interval $[t_0, +\infty)$ into the space of compact subsets of S endowed with the Hausdorff metric;

(v) C is upper semicontinuous in initial conditions $(\varphi,t_0)$ and uniformly upper semicontinuous with respect to t from some compact interval.

In our example of equation (1) we put $S = Y^1(o)$, and if $C(\varphi,t_0,t)$ denotes the set of $u_t$ such that u is a solution of (1) with initial condition $u_{t_0} = \varphi$, then all these assumptions are satisfied with the exception of that concerning the domains of $C(\varphi,t_0,.)$. We note that it is sufficient to assume linear growth of F in $u_t$ to guarantee that all solutions are defined on the interval $[t_0, +\infty)$.

For a generalized system of this type a trajectory concept due to Barbashin (1949) can be introduced. A map $\omega:[t_1,t_2) \to S$ is said to be a trajectory of a system C if $\omega(\tau) \in C(\omega(t),t,\tau)$ for any $t_1 \leq t \leq \tau < t_2$. It can be proved that any trajectory is a continuous map and for each $\psi \in C(\varphi,t_1,t_2)$ there is a trajectory $\omega$ defined on $[t_1,t_2]$ such that $\omega(t_1) = \varphi, \omega(t_2) = \psi$. As trajectories need not be differentiable it is possible that they express the indeterminate nature of some biological factor. Using this notion of a trajectory, a weak positive invariant set can be defined. A closed set A is such a set iff for any $\varphi \in A$, $t_0 \in \mathbb{R}$ there is a trajectory $\omega$ such that $\omega(t_0) = \varphi$ and $\omega(t) \in A$ for all $t \geq t_0$. Further, $A \subset S$ is said to be a weakly stable set if for any $t_0 \in \mathbb{R}$, $\varepsilon > 0$, there is a $\delta > 0$ such that if $\operatorname{dist}(\varphi,A) < \delta$ then there exists a trajectory $\omega$ satisfying $\omega(t_0) = \varphi$ and $\operatorname{dist}(\omega(t),A) < \varepsilon$ for $t \geq t_0$.

A Ljapunov function method for weak stability was established by Roxin (1965) in connection with control systems. It can easily be seen that his assumptions of the local compactness of S and a backward continuation of C are not necessary in this case.

## 3. CAN HISTORY REPEAT ITSELF ?

In this section we shall use ideas from the proof of existence theorems to study the periodic solutions of equation (1). For the sake of simplicity we shall omit the integral term. We want to find out whether the periodic extension of a periodic initial condition $\varphi$ is a solution to (1). Suppose that $\varphi \in Y^1(0)$ is a T-periodic function and F is T-periodic in the first variable. If we put $u(t) = \varphi(t-nT)$ for $t \in [(n-1)T,nT)$, $n \in \mathbb{N}$, then u is a solution of equation (1) if and only if $\varphi$ solves the equation

$$\varphi(t) = e^{-A(t+T)}\varphi(0) + \int_{-T}^{t} e^{-A(t-s)}F(s,\varphi_s)ds \qquad (7)$$

on the interval [-T,0]. To investigate this equation we shall denote by Z the space of continuous mappings from the interval [-T,0] into $X^1$ which take the same values at the end points, and by $Z_0$ the space of continuous mappings which vanish at the point -T. We endow these spaces with the sup norm. The operators

$$\Phi\varphi(t) := \varphi(t) - e^{-A(t+T)}\varphi(0) ,$$

$$\Psi\varphi(t) := \int_{-T}^{t} e^{-A(t-s)}F(s,\varphi_s)ds$$

are defined on Z and map Z continuously into $Z_o$. Further, we have

$$\mathrm{Ker}\,\Phi = \{\varphi\in Z;\ \varphi(t) = e^{-A(t+T)}x,\ x\in\mathrm{Ker}(I-e^{-AT})\}$$

and

$$R(\Phi) = \{\psi\in Z_o;\ \psi(0)\in R(I-e^{-AT})\}.$$

Since, by assumption, $e^{-AT}$ is a compact operator, the subspaces Ker $\Phi$ and $R(\Phi)$ admit continuous projections. Therefore equation (7) is equivalent to the following pair of alternative equations (the so-called Ljapunov-Schmidt procedure):

$$\varphi = P\varphi + \Phi^{+}Q\Psi(\varphi) , \tag{8}$$

$$(I-Q)\Psi(\varphi) = 0 \tag{9}$$

where P is a projection onto Ker $\Phi$, Q is a projection onto $R(\Phi)$ and $\Phi^{+}$ is a continuous right inverse of $\Phi$ with $P\Phi^{+} = 0$.

If $f_1,\ldots,f_k$ is a base of $\mathrm{Ker}(I-e^{-AT})^*$ then the bifurcation equation (9) has the form

$$\int_{-T}^{0} f_i(e^{As}F(s,\varphi_s))ds = 0 , \quad i = 1,\ldots,k ,$$

and it does not seem easy to prove the existence of a solution. A simple calculation with the Fourier series of $e^{-At}x$, $x\in \mathrm{Ker}(I-e^{-AT})$, shows that

$$\mathrm{Ker}(I-e^{-AT}) = \sum_{n=0}^{N} \mathrm{Ker}(A^2 + (2\pi nT^{-1})^2 I)$$

for some finite N. If a sectoral operator A satisfies the spectral condition (4) then Ker $(I-e^{-AT})$ is trivial. Thus $\Phi$ has bounded inverse $\Phi^{-1}$ and equation (7) can be solved in the form

$$\varphi = \Phi^{-1}\Psi(\varphi),$$

i.e., by using the Schauder fixed-point theorem. In order to guarantee that $\Phi^{-1}\Psi$ maps a sufficiently large ball into itself we assume that

$$\lim_{r\to\infty} \frac{K(r)}{r} = 0 \tag{10}$$

holds for $K(r) := \sup\{\|F(s,\varphi_s)\|_\beta ;\ -T\le s\le 0,\ \|\varphi\|_{Y^1(0)} \le r\}$.

The other assumption of the Schauder theorem can be verified in the same way as in the existence theorem. This leads us to the following result:

Theorem 4. Let the function F satisfy assumptions (Hf) (10) and be T-periodic in the first variable. Let the sectoral operator A have a compact resolvent and satisfy assumption (4). Then there exists a T-periodic function $\varphi\in Y^1(0)$ such that its T-periodic prolongation is a solution of equation (1).

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# VI. STOCHASTIC MODELS FOR DYNAMICAL SYSTEMS

# A STOCHASTIC MIGRATION MODEL AND ITS APPLICATION TO CANADIAN DATA

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## 1. INTRODUCTION

The evolution of the society consists of a complex network of interacting processes on political, educational, social, economic and other levels. The migratory dynamics is only one of these partial processes embedded into others (W.Weidlich and G.Haag, 1983). Nevertheless migration theory is of particular interest for quantitative research because of the following reasons:

On one hand the underlying motivations for migrating are relatively well defined and specific and thus amenable to inquiry. On the other hand these motivations must always result in clear decisions to maintain or to change the location in a given interval of time. The number of relocations per unit of time of members of a population between a set of sites or areas can be counted. And the understanding of the dynamics of these changes and its relation to other socio-economic processes is the objective of a quantitative migration theory!

In this introduction we focus on a purely qualitative discussion of the inherent concepts of a quantitative migration theory and of their logical interrelation. The main elements of this description are summarized in a "Scheme of Model Building for Migration Processes" (Fig.1) at the end of the introduction. In order to facilitate their identification, the conceptional steps and the arrows of logical connection are enumerated with numbers in square [] or () brackets, respectively, and these numbers reappear in the text.

Let us begin our construction of the framework of the theory of migration with the discussion of some pre-dynamic concepts:

### Utilities [1]

Before a member of the population decides to change his location, he compare the utility of several regions, at least of the origin region and of the prospective destination region, with respect to his demands. In general many factors merge in this comparative estimation of utilities (A.Anas,1982). Some of these factors, like the climate, the landscape and the desire to remain in one's birthplace, are independent of the population density of the area considered. Other factors, like the offers for occupations and employment, the availability of schools, the cultural offers and options, the distance from home to working place etc. turn out to be roughly proportional to the population density of that area; and still other factors, like increasing rents or traffic congestion, will even be roughly proportional to the square of the population density. It is therefore suggestive to assume in a first approximation that the utility $u_i$ of region i is a polynomial in the population number $n_i$ of that region (Y.Y.Papageorgiou,

T.R.Smith, 1983). The coefficients of this polynomial which explicitly define the functional form of the utilities, will be denoted as trend parameters.

With respect to the application of the concept of "utility" to a dynamic theory of migration (G.Haag, D.S.Dendrinos, 1983), however, there arise difficulties which have to be overcome!

## Field Inquiry [2]

The first problem consists in the fact, that a direct field inquiry about comparative utilities of regions could at best lead to an ordered sequence of utilities, but not to the attribution of numerical values to regional utilities; in other words, direct inquiries lead (1) to an ordinal only, but not to a cardinal quantitative concept of utilities whereas we need numerical values of utilities to build up a fully quantitative dynamic theory!

The second drawback is, that even for cardinal utilities the conventional procedure of utility optimization - which is for instance widely used in economics for the theoretical description of market equilibrium states - is not useful for a dynamic theory, since it is a static concept.

We shall, however, simultaneously solve both problems; that means, we shall obtain empirically measurable and dynamically relevant numerical (cardinal) utility functions by attributing to the utilities a key role (2) in the next conceptional step, the decision process [3] which plays a basic role for the generation of the dynamics of migration.

## The Decision Process [3]

Let us now find an appropriate quantitative description of the decisions of the individuals potentially participating in the migration.

At first we have to exclude the idea of a completely deterministic description of these individual decisions. Such a description is not feasible, since it would overload the theory with too many details.

The way out of this difficulty is the transition to a probabilistic description of the individual decisions to migrate from region $i$ to region $j$. For this aim we introduce the concept of an individual transition probability per unit of time, $p_{ji}$, to migrate from $i$ to $j$. Applied to an ensemble of individuals in region i, the $p_{ji}$ gives the probable relative frequency of a transition from $i$ to $j$ within this ensemble per unit of time. As a consequence, one obtains the probable number of transitions from $i$ to $j$ per unit of time, $w_{ji}$, by multiplying $p_{ji}$ with the numer $n_i$ of people present in region $i$, that means $w_{ji} = p_{ji} \cdot n_i$. Simultaneously, $w_{ji}$ has another meaning: It is the probability per unit of time for the transition from the socioconfiguration $\{n_1,\ldots n_j \ldots n_i \ldots n_L\}$ to the socioconfiguration $\{n_1,\ldots(n_j+1),\ldots(n_i-1),\ldots n_L\}$ in an $L$-region model. This follows from the fact, that each of the $n_i$ members in region $i$ independently contributes his individual transition probability $p_{ji}$ to this change of configurations.

It is now a fundamental idea of our theory of migration to assume that the individual transition probabilites $p_{ji}$ are functions of the utilities and thus to link the concept of utilities with the dynamic concept of transition probabilities (G.Haag and W.Weidlich, 1984)!

The simplest and intuitively plausible assumption is to let $p_{ji}$ depend on the utility $u_j(n_j)$ and $u_i(n_i+1)$ of the origin and destination region $i$ and $j$, respectively (where $u_i^j$ and $u_j$ depend on the number of people

$n_i$ and $(n_j+1)$, respectively, present in $i$ and $j$ at the beginning and the anticipated end of the individual migration act). The form of this functional dependence of $p_{ji}$ on $u_i(n_i)$ and $u_j(n_j+1)$ is not arbitrary but has to fulfill the following requirements:

1. The transition probability $p_{ji}$ is positive by definition. Therefore $p_{ji}$ must be a positive definite function of $u_i$ and $u_j$ for arbitrary real values of $u_i$ and $u_j$.
2. The transition probability $p_{ji}$ from $i$ to $j$ must be larger than $p_{ij}$ for the inverse transition from $j$ to $i$, if $u_j$ exceeds $u_i$.
3. The transition probability $p_{ji}$ must be a monotonously increasing function of the difference $(u_j(n_j+1) - u_i(n_i))$, since on increasing utility difference between $j$ and $i$ induces a higher probability to migrate from $i$ to $j$.

The simplest form of $p_{ji}$ fulfilling 1. to 3. is an exponential dependence: $p_{ji} = \nu_{ji}\exp(u_j(n_j+1))$, which shall be used in all following models. By linking them in a definite way to measurable transition probabilities we have simultaneously made utilities cardinal measurable quantities, as we shall see later. The coefficients $\nu_{ji}$ are "mobilities" describing the time scale on which the transitions take place.

After the discussion of the basic decision process and its connection with utilities we have now to make use of the transition probabilities in the construction of a dynamic theory of the migration process (3). This theory decomposes into two main, though interrelated (5) tracks.

The first track [4] (4) [5] consists in the dynamics of population numbers, the central objective of migration theory. In this part of the theory we consider mobilities, utilities and their functional dependence on population numbers $n_i$ and trend parameters as already known, and proceed in setting up equations of motion for the evolution with time of the population numbers.

In order to make this first track theory operative and explicitly evaluable, however, we have to set up theoretical procedures, which allow of the determination of utilities and their functional composition by a regression analysis on empiric data and/or by a dynamic theory of trend parameters. This is done in the second track [6] (6) [7] (7) [8] (8) [9] (9) [10], which consists of different interconnected levels of a theory of utilities and mobilities. Let us begin with the first track, the dynamics of population numbers.

## The Stochastic Level [4]

Since we have started with a probabilistic description of the decision process via transition probabilities, we cannot expect a fully deterministic theory of the evolution of population numbers with time. Instead a stochastic theory of population evolution is adequate. The central concept of this stochastic theory is the probability distribution function $P(n_1, n_2, \ldots n_L; t)$ over the population numbers, which by definition describes the probability to find the configuration $\{n_1, n_2, \ldots, n_L\}$ at time $t$. For this distribution an equation of motion can be set up, which is denoted as master equation. The transition probabilities introduced above enter this equation in a natural way. The explicit form of this master equation will be written down in the following sections for different migration systems. Here we only give its intuitive meaning: The master equation namely can be interpreted as a probability rate equation: The change with time of the probability of the configuration $\{n_1 \ldots n_L\}$ (that is the time derivative of $P(n_1 \ldots n_L ; t)$) is according to this equation due to two counteractive effects, namely firstly

to the probability flux from all neighboring configurations into the configuration $\{n_1 \ldots n_L\}$, and secondly to the probability flux from the configuration considered into all neighboring configurations.

The solution of this equation [11], namely the time dependent distribution $P(n_1 \ldots n_L ; t)$ contains all informations about the migratory system at the most detailed level. In particular not only the meanvalues $n_i(t)$, but also their mean square deviations (due to fluctuations of the decision process) can easily be calculated, if $P(n_1 \ldots n_L ; t)$ is known. Correspondingly the amount of mathematics to solve the time-dependent master equation is considerable: If there exist c different configurations $\{n_1 \ldots n_L\}$, the master equation consist of c coupled linear differential equations for all $P(n_1 \ldots n_L ; t)$!

In most cases, however, the full information contained in the distribution $P(n_1 \ldots n_L ; t)$ cannot be exploited because of lack of sufficiently comprehensive empiric data. Therefore it is convenient to make a transition (4) to a less exhaustive description in terms of equations of motion for the meanvalues $n_i(t)$ only.

## The Deterministic Level [5]

The equations of motion for the meanvalues $\bar{n}_i(t)$ can be derived from the master equation in a straight forward manner. In their most useful, although approximate form they establish a selfcontained set of ordinary nonlinear coupled differential equations for the L meanvalues $\bar{n}_i(t)$ , $i = 1,2,\ldots,L$. Since the meanvalues by definition are averages over paths with fluctuating deviations, their evolution is described by deterministic equations. It must be expected, however, that the empiric values of the $n_i^e(t)$ show stochastic fluctuations around these meanvalues, even if the theory is completely correct. The meanvalue equations are the starting point of almost all empiric evaluations of the theory.

Let us now go over to the second track of the dynamic theory, the theory of utilities and trend parameters.

## Empiric Migratory Data and Determination of Utilities [6] [6] [7]

We have already stated, that the dynamic theory of population numbers, formulated as a master equation or as a set of meanvalue equations, is not yet operative, unless the main construction elements of these equations, the transition probabilities, are specified. Since the latter are functions of utilities (see [3]), we must determine their values.

This can be done, if empiric migratory data are available [6] namely the yearly area population numbers $n_i^e$ and the yearly migration matrix $w_{ji}^e$, where $w_{ji}^e$ counts the number of people who migrated from i to j in the year. Since we have seen, that on the other hand the theoretical expression $w_{ji} = n_i p_{ji}$, which are functions of the utilities $u_j$ and $u_i$ , have the meaning of the probable number of transitions from i to j per unit of time (i.e. per year), we can now match (6) the theoretical expressions $w_{ji}$ to the different $L(L-1)$ empirical matrix elements $w_{ji}^e$ whereas only L utilities $u_i, i = 1,2,..L$ are available, the determination of the utilities [7] amounts to an optimization procedure which minimizes the deviation of the theoretical from the empirical migration matrix.

After this determination of the values of the utilities (year by year) they may be inserted into the expressions for the transition probabilities - even extrapolating into the future, if they behave smoothly - thus making the dynamic equations for the population numbers explicit and operative (5).

Regression of Utilities on Empiric Socio-Economic Data [8] (8) [9]

As we have seen, the comparison of theoretical expressions with empiric migratory data leads to the determination of the numerical values of utilities and thus makes the theory of population numbers operative. In a second step we can now ask deeper questions: How can the form of $u_i$ as a polynomial ot the area population number $n_i$ be found? How is the value of $u_i$ - which is in general a function of time - linked to socio-economic data [8] like employment, education, rents, traffic etc.? In order to give answers to such questions the following approach is proposed: Take one or several socio-economic indicators $\Omega_l(t)$ of region i (eventually detrended and standardized) and correlate them (8) to the utility $u_i(t)$ found above (7) by assuming a linear relationship between $u_i(t)$ and the $\Omega_l(t)$ with as yet open influence coefficients. Among the $\Omega_l(t)$ can choose as special indicators the population number $n_i(t)$ itself and its powers. (We have denoted their influence coefficients as "trend parameters".) The influence coefficients thereupon can be determined by an optimization procedure [9]. If a high correlation between $u_i(t)$ and some indicator $\Omega_l(t)$ has been found, this may be considered as indicative of a causal relationship: The change of utility may have been causally effected by this indicator. In general, however, further inquiries are necessary to substantiate such an assumption.

Dynamic Theory of Utilities [10]

The last two steps consisted in the determination of the utilities $u_i$ and their functional form (including trend parameters) by making use of empirical migratory and socio-economic data. As a final step, however, a more ambitious approach is conceivable: A dynamic theory for the evolution of utilities! If the insight into the dynamic interdependence of utilities and socio-economic factors is deep enough (9), one can try to set up equations of motion for the utilities and/or their constitutive coefficients. The solution of such equations then yield the systematic evolution of utilities, if certain input data are available. These solutions may also be extrapolated into the future and give rise to forecasting methods (see [11] and [12]).

The significance of this approach is however limited by the following inherent problem: In general the equations of motion for the utilities (or its expansion coefficients) will not be selfcontained! This means, that they contain socio-economic factors with unknown time dependence. These factors require a further equation of their own, and so on. In this way there may arise a non-closed hierarchy of equations of motion, which is not practicable. The only way out of this difficulty is, to find - for special cases and situations - a small number of strongly interrelated dynamic quantities (the utilities among them) which satisfy a selfcontained set of equations without depending on further unknown time dependent quantities. If this is possible, one has converted the formerly exogenous time dependence of $u_i(t)$ into an endogenous dynamics of utilities and interrelated variables!

Solutions of the Equations of Motion; General Conclusions; Comparison with Real Migratory Processes [11][12][13]

If a dynamic theory of utilities exists according to [10], it is clear that the full set of coupled equations for utilities and population numbers (master equation or meanvalue equations) has to be solved simultaneously. In any case this can be done by numerical methods. Here, we focus on some

general remarks [12] about the dynamics of population numbers, if the utilities $u_i$ can be considered as given polynomials of $n_i$.

For constant trend parameters the master equation has a stationary solution $P_{st}(n_1, n_2, \ldots n_L)$, which can even be found analytically (see section 4), since for our model the transition probabilities fulfill the condition of detailed balance. The point (s) of maximal probability $\{\hat{u}_1, \hat{u}_2 \ldots \hat{u}_L\}$ can be determined. It depends on the numerical values of the trend parameters within the utility functions, whether the stationary solution is unimodal or multimodal. Furthermore it will be shown, that any time dependent solution $P(n_1, \ldots n_L ; t)$ approaches the stationary solution.

The meanvalue equations belonging to the master equation have one or several stationary states, which coincide with the maximum (the maxima) of the stationary distribution $P_{st}(n_1 \ldots n_L)$. All time dependent solutions approach for $t \to \infty$ one of these stationary states, but it depends on the initial conditions, which of the stationary states is approached. This means, that the migratory system may - depending on the values of the trend parameters - approach one unique, or one out of several possible, equilibrium state(s).

Let us now consider the case of trend parameters slowly varying with time. It does not matter, whether this time dependence is considered as an exogenous effect or as the result of an equation of motion for the utility or the trend parameter. Then it may happen, that the trend parameter passes a critical threshold for which one of the stationary equilibrium states of the system becomes unstable. If the actual migratory system was in this now unstable equilibrium, it will suddenly rush into a new stable equilibrium state. We denote this transition as a migratory phase transition in analogy to similar global system changes in physics.

After these general conclusions about the migratory dynamics [12] we shall now discuss the comparison with and forecasting of the real migratory process [13].

Retrospectively, the master equation and the meanvalue equations can of course be solved for all years in the past, for which the utilities, hence the transition probabilities, could be determined from empiric data. The solutions can be compared with the actual past migration data in order to get a measure for the degree of coincidence.

Furthermore, since the theoretical equilibrium values of population numbers for given utilities can be determined, one can also calculate the deviation between the actual population numbers and these virtual theoretical equilibrium values. This deviation - expressed in a correlation coefficient - is a measure of the "migratory stress". since it indicates the distance from the equilibrium, into which the system would like to relax for the presently given utilities.

Finally one can use the solutions of the meanvalue equations for forecasting purposes: If it turns out that the (empirically determined) utility functions are quasi-constant or smoothly evolving over the years in the past, it seems safe to extrapolate this smooth behaviour into the future, at least for some years. Inserting the extrapolated utilities into the transition probabilities and solving the equations of motion one obtains a forecast of the migratory evolution. This forecast may even be improved, if dynamic equations of utilities are known, which couple to the meanvalue equations. The solution of the total system of equations of motion describing an endogenous dynamics may then be prolonged into the future and compared with the forthcoming migratory (14) and socio-economic (15) data.

All steps described in the introduction are now summarized in the following scheme.

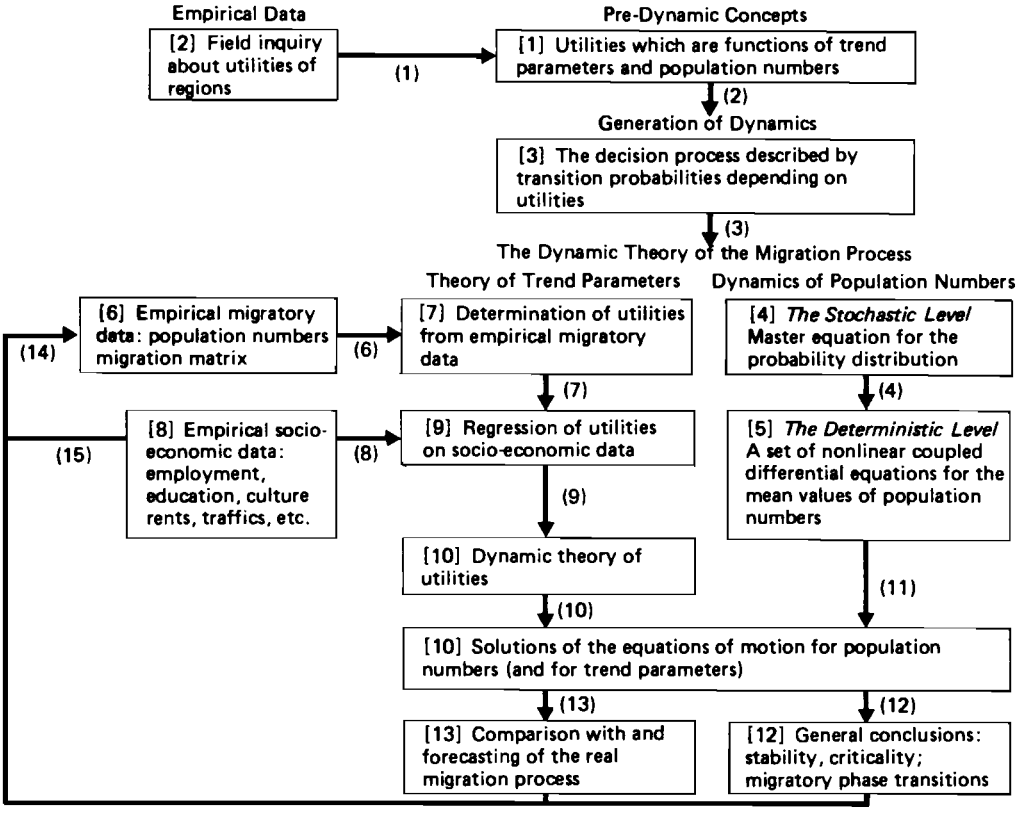


FIGURE 1 Scheme of model building for migration processes

## 2. INTER-REGIONAL MIGRATION

In this section we consider the migration of a population between L regions (G.Haag, W.Weidlich, 1984). These regions can for instance be the countries of a federal state or metropolitan areas. The difference in such applications will not be one of construction priciples, but of different choice of utility functions. (In inter-metropolitan migration for example the agglomeration parameter will play a more prominent role than in migration between countries.)

### 2.1 The Model

We consider one homogeneous population of N members migrating between L regions. The possible states of the migration system are then characterized by the "socio-configuration"

$$\underset{\sim}{n} = \{n_1, n_2, \ldots, n_L\} \tag{2.1}$$

with

$$\sum_{k=1}^{L} n_k = N, \tag{2.2}$$

where the integer $n_k$ is the number of members of the population in region k.

In order to provide for the description of the dynamics of the system we start from regional utility functions. Let the attractivity of region i for a member of the population be characterized by a utility function $u_i(n_i)$ depending on parameters specific of that region. These parameters include the number $n_i$ of its residents. A reasonable assumption of the functional form of $u_i(n_i)$ is

$$u_i(n_i) = \delta_i + \varkappa_i n_i + \rho_i n_i^2 \tag{2.3}$$

where the trend parameters $\{\delta_i , \varkappa_i , \rho_i\}$ according to their meaning are denoted as preference parameter $\delta_i$, agglomeration parameter $\varkappa_i$ and saturation parameter $\delta_i$. Obviously, $\delta_i$ comprizes contributions to $u_i$ independent of the population density, whereas $\varkappa_i n_i$ represents the contributions roughly proportional to $n_i$ , and $\rho_i n_i^2$ those proportional to $n_i^2$ , which include (for negative $\rho_i$) saturation effects.

Making use of the utilities (2.3) we can now construct individual transition probabilites for moves from region i to region j. In the introduction it has been explained that the form

$$P_{ji} = \nu_{ji} \exp[u_j(n_j+1)-u_i(n_i)] \tag{2.4}$$

fulfills all requirements to be posed for $p_{ji}$. Here, $\nu_{ji}$ are mobility parameters which may depend on the distance between i and j and which can be assumed symmetrical:

$$\nu_{ij} = \nu_{ji} \tag{2.5}$$

The plausible constraint (2.5) means, that the individual transition probability from i to j is equal to that from j to i, as soon as the utilities $u_i$ and $u_j$ are equal.

The transition probability for the transition between socio-configurations $\underset{\sim}{n} \equiv \{n_1 \ldots n_i \ldots n_j \ldots n_L\} \to \underset{\sim}{n}^{(ji)} \equiv \{n_1 \ldots (n_i + 1) \ldots (n_j - 1) \ldots n_L\}$ can now be easily constructed, since $n_i$ members in region i independently contribute their individual transition probability to this configuration change. Hence, we obtain for this change from $\underset{\sim}{n}$ to $\underset{\sim}{n}^{(ji)}$:

$$w_{ji}(n) = n_i P_{ji} = n_i \nu_{ji} \exp[u_j(n_j+1) - u_i(n_i)]. \tag{2.6}$$

## 2.2 The Master Equation and its Solutions

The equation of motion for the probability distribution $P(\underset{\sim}{n} ; t)$ has now to be set up. By definition $P(\underset{\sim}{n} ; t)$ is the probability to find the configuration $\underset{\sim}{n} = \{n_1 , n_2 \ldots, n_L\}$ at time t, and the master equation is its evolution equation, which can be interpreted as a probability rate equation: The change with time of the probability of configuration $\underset{\sim}{n}$ (l.h.s. of (2.7)) is due to two counteractive effects, namely firstly to the probability flux from all neighboring configurations $\underset{\sim}{n}^{(ji)}$ into $\underset{\sim}{n}$ (first term of r.h.s. of (2.7)), and secondly to the probability flux from n to all neighboring configurations $\underset{\sim}{n}^{(ji)}$ (second term of r.h.s. of (2.7)). Since the probability fluxes from $\underset{\sim}{n}$ to $\underset{\sim}{n}^{(ji)}$ and from $\underset{\sim}{n}^{(ji)}$ to $\underset{\sim}{n}$ are given by $w_{ji}(\underset{\sim}{n})P(\underset{\sim}{n} ; t)$ and $w_{ij}(\underset{\sim}{n}^{(ji)})P(\underset{\sim}{n}^{(ji)} ; t)$ , respectively (taking occupation probability of the

origin configuration times transition probability per unit of time from origin to destination configuration), we immediately obtain

$$\frac{dP(\underset{\sim}{n},t)}{dt} = \sum_{i,j=1}^{L} \{w_{ij}(\underset{\sim}{n}^{(ji)})P(\underset{\sim}{n}^{(ji)};t) - w_{ji}(\underset{\sim}{n})P(\underset{\sim}{n};t)\}. \tag{2.7}$$

Here the $w_{ij}(\underset{\sim}{n})$ according to (2.6) must be inserted.

Let us now consider the stationary solution $P_{st}(\underset{\sim}{n})$ of the master equation (2.7), which corresponds to a migratory system at equilibrium. The construction of $P_{st}(\underset{\sim}{n})$ is facilitated by the fact, that the transition probabilities (2.6) satisfy the condition of detailed balance:

$$w_{ij}(\underset{\sim}{n}^{(ji)})P_{st}(\underset{\sim}{n}^{(ji)}) = w_{ji}(\underset{\sim}{n})P_{st}(\underset{\sim}{n}), \tag{2.8}$$

which means, that the stationary flux from $\underset{\sim}{n}$ to $\underset{\sim}{n}^{(ji)}$ is equal to the inverse flux from $\underset{\sim}{n}^{(ji)}$ to $\underset{\sim}{n}$. The repeated application of (2.8) then leads to the following explicit result (for details see G.Haag, W.Weidlich, 1984):

$$P_{st}(n_1,n_2,\ldots,n_L) = \frac{Z^{-1}\,\delta(\sum_{i=1}^{L} n_i - N)}{n_1!n_2!\ldots n_L!} \exp\{2\sum_{i=1}^{L} F_i(n_i)\}, \tag{2.9}$$

where

$$F_i(n_i) = \sum_{\nu=1}^{n_i} u_i(\nu) \quad ; \quad F_i(0) = 0 \tag{2.10}$$

$$\delta(\sum_{i=1}^{L} n_i - N) = \begin{cases} 1 \text{ for } \sum_{i=1}^{L} n_i = N \\ 0 \text{ for } \sum_{i=1}^{L} n_i \neq N \end{cases} \tag{2.11}$$

and where the factor Z follows from the normalization condition for the probabilities $P_{st}(\underset{\sim}{n})$:

$$\sum_{\underset{\sim}{n}} P_{st}(\underset{\sim}{n}) = 1. \tag{2.12}$$

The sum in (2.12) extends over all socioconfigurations $\underset{\sim}{n}$. Using Stirling's formula for the factorials, $P_{st}(\underset{\sim}{n})$ can be written in the form

$$P_{st}(\underset{\sim}{n}) = \frac{\delta(\sum_{i=1}^{L} n_i - N)}{Z} \exp\{\sum_{i=1}^{L} \Phi_i(n_i)\} \tag{2.13}$$

with

$$\Phi_i(n_i) = 2F_i(n_i) - n_i(\ln(n_i) - 1) \tag{2.14}$$

The maxima $\{\hat{n}_1, \hat{n}_2 \ldots \hat{n}_L\}$ of $P_{st}(\underset{\sim}{n})$ can now be determined. They describe the equilibrium configuration (or configurations) of highest probability. The extrema of $P_{st}(\underset{\sim}{n})$ correspond to the extrema of $\sum \Phi_i(n_i)$ under constraint $\sum n_i = N$. Hence, $\underset{\sim}{\hat{n}}$ is found to satisfy

$$\hat{n}_i = \frac{N \exp[2u_i(\hat{n}_j)]}{\sum_{j=1}^{L} \exp[2u_j(\hat{n}_j)]} \quad ; \quad i = 1,2,\ldots,L \tag{2.15}$$

If this set of transcendental equations has one solution $\{\hat{n}_1 \ldots \hat{n}_L\}$ only, the distribution is unimodal, and the equilibrium is unique. If more than one solution exists, the distribution is multimodal with peaks at $\{\hat{n}_1^s \ldots \hat{n}_L^s\}$ corresponding to different possible equilibrium states of the migratory system. It can be proved, that any time-dependent solution (constant trend parameters presumed) must approach the stationary solution for $t \to \infty$. If, however, the trend parameters themselves - and hence the transition probabilities $w_{ji}$ - are time-dependent, the solution in general will not reach a stationary state at all.

As in the preceding sections we now proceed to the equations of motion for meanvalues $\bar{n}_i(t)$ of the regional population numbers which are often already sufficient for comparison with empiric data.
The definition of meanvalues is given by

$$\bar{n}_k(t) = \sum_{\underset{\sim}{n}} n_k P(\underset{\sim}{n};t) \tag{2.16}$$

where the sum extends over all possible socioconfigurations. Taking the time derivative of (2.16) and inserting the master equation (2.7) on the r.h.s. one obtains after a straight forward calculation (for details see G.Haag, W.Weidlich, 1984) for an essentially unimodal distribution,

$$\frac{d\bar{n}_k(t)}{dt} = \sum_{i=1}^{L} w_{ki}(\underset{\sim}{\bar{n}}) - \sum_{i=1}^{L} w_{ik}(\underset{\sim}{\bar{n}}) \quad , \; k = 1,2,\ldots,L. \tag{2.17a}$$

The explicit form of (2.17a) follows, if the transition probabilities (2.6) are inserted:

$$\begin{aligned} \frac{d\bar{n}_k(t)}{dt} = & \sum_{i=1}^{L} \bar{n}_i(t)\, \nu_{ki} \exp[u_k(\bar{n}_k(t)) - u_i(\bar{n}_i(t))] \\ & - \sum_{i=1}^{L} \bar{n}_k(t)\, \nu_{ik} \exp[u_i(\bar{n}_i(t)) - u_k(\bar{n}_k(t))]. \end{aligned} \tag{2.17b}$$

Evidently, (2.17) is a set of L coupled nonlinear first order differential equations for the $\bar{n}_k(t)$. We see that the stationary states $\bar{n}_k^{st}$ of the approximate meanvalue equations (2.17) coincide with the maximum (maxima)

$\hat{n}_k$ of the unimodal (multimodal) stationary probability distribution. This confirms the relation between the fully stochastic and the meanvalue approach.

In the further discussion we make use of the meanvalue equations (2.17) only.

Let us first consider the case of constant trend parameters. This means that the $\nu_{ki}$ are constants and the utility functions depend on time only via their dependence on the $\underset{\sim}{n}$. Some of the stationary points of (2.17) may be stable, others may be unstable. It can be shown that any time dependent solution of (2.17), wherever it starts will sooner or later be attracted by a stable focus and will finally end in this equilibrium state.

Second, we consider the case of slowly time dependent trend parameters in the utility functions. As a consequence, the situation of the foci will move slowly, too. Normally, however, the solutions of (2.17) will not change very much their global character: The foci will undergo small shifts and the solutions will approach the slowly moving stable foci. In certain cases however this picture changes dramatically: If some trend parameter passes a critical threshold it may happen, that an originally stable focus becomes unstable. If, so to say, the system was in this stable equilibrium, its situation has now become unstable and it makes a rather sudden transition into a neighboring still stable focus. We denote this phenomenon as a migratory phase transition. It turns out that this is a general phenomenon to be expected in migration dynamics:

In general the explicit solutions of (2.17) can only be found numerically. In simple model cases, however, a further analytical investigation of (2.17) is possible. For instance one finds (W.Weidlich, G.Haag, 1985) for the simple choice of parameters:

$$\nu_{ki} = \nu \; ; \quad u_k(\overline{n}_k) = \varkappa \overline{n}_k \quad ; \quad k = 1,2,\ldots,L$$

that the equipartition point

$$\underset{\sim}{\overline{n}}_0^{st} = \{\overline{n},\overline{n},\ldots,\overline{n}\} \; , \quad \text{with} \quad \overline{n} = N/L \tag{2.18}$$

is the only stable focus of the system, as long as $\varkappa$ is below a critical value $\varkappa_c$: $0<\varkappa<\varkappa_c$. If, however, $\varkappa$ exceeds $\varkappa_c$, it can be proved, by linear and nonlinear analysis that the equipartition point becomes unstable and that the only stable foci are now

$$\underset{\sim}{\overline{n}}_i^{st} = \{\overline{n}_1 = n_-,\ldots,\overline{n}_{i-1} = n_-,\overline{n}_i = n_+ \; , \; \overline{n}_{i+1} = n_-,\ldots,\overline{n}_L = n_-\} \tag{2.19}$$

with $\quad n_+ >> n_- \; ; \; i = 1,2,\ldots,L.$

The new stable foci describe - instead of equipartition of population over the regions - the arisal of one mega - metropole leaving (L-1) regions depleted. If the agglomeration parameter $\varkappa$ crosses $\varkappa_c$ from below, obviously in this model a phase transition from originally equally populated regions to the evolution of one mega-metropole takes place.

## 2.3 Determination of Utilities and Mobilities from Empirical Data

We are now determining the unknown terms in the transition probabilities $w_{ij}(\underset{\sim}{n})$, namely the mobility matrix $\nu_{ij} = \nu_{ji}$ and the utilities $u_i$ from empirical data. The migratory empirical data available year by year are listed in Table 1.

TABLE 1

| area | population size | Number of transitions per year from i to j | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 1 | $n_1^e(t)$ | | $w_{21}^e(t)$ | ... | ... | $w_{j1}^e(t)$ | ... | ... | $w_{L1}^e(t)$ |
| 2 | $n_2^e(t)$ | $w_{12}^e(t)$ | | ... | ... | $w_{j2}^e(t)$ | ... | ... | $w_{L2}^e(t)$ |
| . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . |
| i | $n_i^e(t)$ | $w_{1i}^e(t)$ | $w_{2i}^e(t)$ | ... | ... | $w_{ji}^e(t)$ | ... | ... | $w_{Li}^e(t)$ |
| . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . |
| L | $n_L^e(t)$ | $w_{1L}^e(t)$ | $w_{2L}^e(t)$ | ... | ... | $w_{jL}^e(t)$ | ... | ... | |

The theoretical migration matrix (2.6) has now to be matched to the empirical migration matrix $w_{ji}^e$ by an optimal estimation of the mobilities $\nu_{ij}$ and utilities $u_i$ , $i,j = 1,2,\ldots,L$.

The comparison of products yields year by year

$$w_{ji}(\underset{\sim}{n}) \cdot w_{ij}(\underset{\sim}{n}) = n_i^e n_j^e \nu_{ij}^2 = w_{ji}^e(t) w_{ij}^e(t)$$

or

$$\nu_{ij}(t) = \sqrt{\frac{w_{ji}^e(t) w_{ij}^e(t)}{n_i^e(t) n_j^e(t)}} = \nu_{ji}(t) \tag{2.20}$$

so that the mobilities are directly determined from the empirical data, independently of the values of the utilities. From (2.20) the global mobility parameter $\nu(t)$ can easily be constructed

$$\nu(t) = \frac{1}{L(L-1)} \sum_{\substack{i,j=1 \\ i \neq j}}^{L} \nu_{ij}(t). \tag{2.21}$$

On the other hand, the comparison of quotients yields:

$$\frac{w_{ij}(\underset{\sim}{n})}{w_{ji}(\underset{\sim}{n})} = \frac{n_j^e(t)}{n_i^e(t)} \exp[2(u_i - u_j)] = \frac{w_{ij}^e(t)}{w_{ji}^e(t)}$$

or, equivalently,

$$u_i(t) - u_j(t) = c_{ij}(t) \equiv \frac{1}{2} \ln \frac{w^e_{ij}(t) n^e_i(t)}{w^e_{ji}(t) n^e_j(t)} = - c_{ji}(t). \tag{2.22}$$

Since we have $(L^2-L)$ equations in (2.22), but only L unknown utilities to be determined, we can choose an optimal set of utilities by minimizing the sum of the square deviations, i.e. by requiring

$$F[u_1(t),\ldots,u_L(t)] = \sum_{\substack{i,j=1 \\ i\neq j}}^{L} [c_{ij}(t)-(u_i(t)-u_j(t))]^2 = \text{Min.!}$$

The standard procedure then yields the optimal utilities

$$u_i(t) = \frac{1}{L} \sum_{\substack{j=1 \\ j\neq i}}^{L} c_{ij}(t) + \sum_{j=1}^{L} u_j(t) \tag{2.23}$$

where the sum $\sum u_j(t)$ remains undetermined by the optimization. We can however put

$$\sum_{j=1}^{L} u_j(t) = 0$$

in (2.23) without changing the values $w_{ij}$ of the migration matrix (2.6). As an example we apply this theory to the Canadian interregional migration system for the years 1961-1982. We present only a few results. The further evaluation and interpretation of those results will be done in close cooperation with J.Ledent, Y.Y.Papageorgiou and K.L.Liaw.

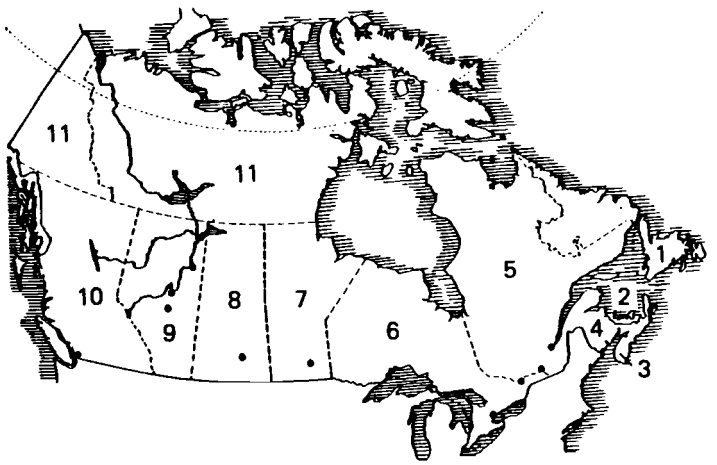


FIGURE 2 Map of Canada showing the regions studied.

Fig. 2 represents the map of Canada with eleven regions. These regions are:

| | | | |
|---|---|---|---|
| 1 | New Foundland | 7 | Manitoba |
| 2 | Prince Edward Island | 8 | Saskatchewa |
| 3 | Nova Scotia | 9 | Alberta |
| 4 | New Brunswick | 10 | British Columbia |
| 5 | Quebec | 11 | Yukon and Northwest Territories |
| 6 | Ontario | | |

In Fig. 3 we plotted using (2.23) the optimal utility functions $u_i(t)$ for the different Canadian regions. The robustness of all parameters (utilities, mobilities) with respect to data uncertainties could be established. Preferred regions are (5,6,9,10), more or less neutral regions (1,3,4,7,8) and not preferred regions (2,11)

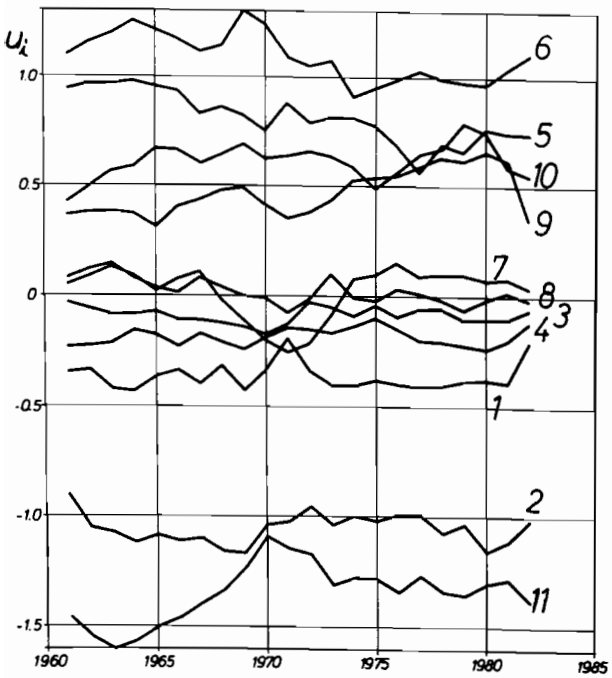


FIGURE 3 The optimal utility functions $u_i(t)$ for the different Canadian regions

In Fig. 4 the global mobility factor $\nu(t)$ after (2.21) is depicted. We observe a mean growth of $\approx$ 12% since 1961.

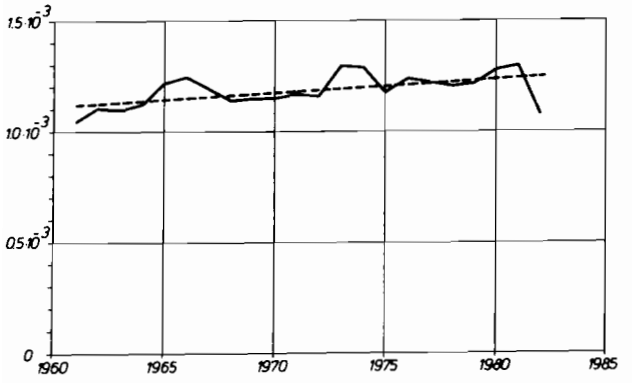


FIGURE 4 The global mobility $\nu(t)$ (solid line) and its trend (dashed line)

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# STATISTICAL METHODS FOR THE ANALYSIS OF DISEASE PROCESSES

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## 1. INTRODUCTION

This paper is concerned with three problems connected with the processing of clinical and laboratory data: (i) construction of a generalized index for the seriousness of a disease; (ii) estimation of the information content of biochemical indices and (iii) statistical estimation of the parameters of disease models. These problems arise both in clinical practice and during theoretical investigations of disease mechanisms: solutions would be of great value in the study of disease processes. Since the problems are concerned with the analysis of experimental data it seems natural to tackle them using probability methods. This paper gives a brief description of the approach to the above problems developed at the Department of Numerical Mathematics in Moscow.

## 2. A GENERALIZED INDEX FOR THE SERIOUSNESS OF A DISEASE

When trying to predict the course of a disease and prescribe the correct treatment it is very important to be able to form some reasonable estimate of the seriousness of the state of the diseased organism. Let the state of an organism be characterized by the vector $X = (x_1, x_2, \ldots, x_n)$. The components of X are clinical or laboratory indices, with values which depend on the state of the organism. The dimension of X is sufficiently high for the disease under consideration and components $x_i$, $i = 1, 2, \ldots, n$, have random deviations. This leads to some difficulties in the estimation of the seriousness of the disease. To avoid these difficulties in the investigation of hepatitis, Academician G.I.Marchuk (1983) proposed the use of a biochemical index (a scalar function of the vector X). In this section we shall consider how a general index of this type could be constructed. Let us consider X to be a continuous n-dimensional random value connected with a discrete random value $S = 0, 1, 2, \ldots, r$, which represents an estimate of the state of a diseased organism. The value of S is established by a physician on the basis of the value of the vector X, and has a specific meaning for each different disease.

Assume that a scale for the state estimate S is chosen, with the value $S = 0$ corresponding to perfect health. It is necessary to define a function $\varphi(X)$ (a general index) which predicts the value of S with the smallest possible error:

$$J = E(S - \varphi(X))^2 = \sum_S P_S E((S - \varphi(X))^2 | S) \to \min, \quad (1)$$

where $P_S$ is the probability of state S and $E(\cdot|S)$ is the conditional mathematical expectation given S. It is known that J is a minimum if

$$E(\varphi(X)|S) = S \quad (2)$$

for all S.

Let us make the assumption

$$E(x_k|S) = S,\ S = 0,1,\ldots,r,\ k = 1,2,\ldots,n. \qquad (3)$$

In this case a linear function of the vector X fulfills condition (2) because

$$E(\varphi(X)|S) = E\left(\sum_1^n \alpha_i x_i|S\right) = \sum_1^n \alpha_i E(x_i|S)$$

if $\sum_1^n \alpha_i = 1$.

The task is therefore reduced to defining the weight coefficients $\alpha_i$, $i = 1,2,\ldots,n$. To do this let us construct the Lagrange function:

$$L(\alpha,\lambda) = \sum_s P_s E\left(\left(\sum_1^n \alpha_i(x_i - S)\right)^2|S\right) + \lambda\left(\sum_1^n \alpha_i - 1\right).$$

Differentiating $L(\alpha,\lambda)$ with respect to $\alpha_i, i = 1,2,\ldots,n$ and $\lambda$, and setting the derivatives equal to zero, we obtain the following system of linear (in $\alpha$ and $\lambda$) algebraic equations:

$$\sum_1^n \alpha_i K_{ij} + \lambda = 0 \qquad j = 1,2,\ldots,n$$

$$\sum_1^n \alpha_i = 1,$$

where

$$K_{ij} = \sum_s P_s E((x_i - S)(x_j - S)|S).$$

The determinant of the system is equal to zero if and only if the values of the indices are linearly dependent.

If $K = (K_{ij}, i,j = 1,2,\ldots,n)$ is a diagonal matrix we have

$$\alpha_i = \left(\sum_k \prod_{j\neq k} K_{jj}\right)^{-1} \prod_{k\neq i} K_{kk},$$

$$\operatorname{var}\varphi(X) = E(\varphi(X) - S)^2 = \left(\sum_1^n 1/K_{ii}\right)^{-1}.$$

Since the diagonal elements $K_{ii}$, $i = 1,2,\ldots,n$ are positive and bounded, we have

$$\lim_{n\to\infty} \operatorname{var}\varphi(X) = 0.$$

Use of the general index $\varphi(X)$ thus provides us with a scalar characteristic of the state of the organism and reduces the possibility of an error in the estimate of the damage suffered by the organism. However, condition (3) is not always satisfied in practice. For this reason we shall introduce functions $f_i(x_i)$, $i = 1,2,\ldots,n$, defined in such a way that $E(f_i(x_i)|S) = S$.

These functions may take the form of polynomials

$$f_i(x_i) = C_{io} + C_{i1}x_i + C_{i2}x_i^2 + \ldots + C_{ir}x_i^r.$$

Since $f_i(x_i)$ must fulfill the condition $E(f_i(x_i)|S) = S$, the polynomial coefficients are defined by the system of equations

$$C_{io} + C_{i1}E(x_i|S) + C_{i2}E(x_i^2|S) + \ldots + C_{ir}E(x_i^r|S) = S,\ S = 0,1,\ldots,r.$$

The new variables $y_i = f_i(x_i)$ fulfill condition (3) and the above considerations allow us to construct a non-linear general index as a linear combination of polynomials of order $q_i \leq r$:

$$\varphi(X) = \sum_1^p \alpha_i y_i = \sum_1^p \alpha_i f_i(x_i).$$

It should be noted that the order $q_i$ of the polynomial may be chosen using well-known statistical criteria.

## 3. ESTIMATION OF THE INFORMATION CONTENT OF BIOCHEMICAL INDICES

Modern biochemical methods offer physicians a great number of indices with which to characterize the state of an organism. However, the great dimension n of vector X complicates this analysis in clinical practice. In general vector X includes indices which contain very little information about the state of the organism for the particular disease in question. This leads to the problem of how to select the most informative indices.

This problem can be treated in a number of different ways. We shall consider the approach based on the notion of entropy suggested by Professor I.B. Pogozhev et al.(1981).

Let $p(x|S = k)$ be the conditional distribution of the index when the seriousness of the state is $S = k$. We shall assume that $p(x|S)$ is known for all $S = 0,1,\ldots,r$. Let the unconditional distribution of x be

$$p(x) = \sum_s p_s p(x|S).$$

We shall set

$$H(x) = -\int_X p(x)\log p(x)dx,$$

$$H(x|s) = -\sum_s p_s \int_X p(x|S)\log p(x|S)dx.$$

The information about the seriousness of the state S of the organism obtained by measuring the index x is equal to the following:

$$I = H(S) - H(S|x) = H(x) - H(x|S).$$

From the second equation (i.e., S is a discrete value) we have

$$I = \Sigma p_s E\left(\log \frac{p(x|S)}{\Sigma_i p_i p(x|i)} \middle| S\right).$$

This formula allows us to calculate the information content of the index as an estimate of the mathematical expectation of the random value

$$z = \log\left(p(x|S)/\Sigma_i p_i p(x|i)\right).$$

It is convenient to use the relative information content

$$I_o = I/I_{max},\ I_{max} = \sum_s p_s \log p_s$$

with values on the interval [0,1].

To calculate the information content of an index using these formulae it is necessary to use the fact that the conditional density of the distribution of the logarithm of an index is generally Gaussian.

Methods and computer programs for analyzing the information content of indices based on this approach have been developed by Dr.M.G. Zaitsev.

## 4. ANALYSIS OF THE RECOVERY PROCESS

The general index described earlier is a numerical characteristic of the state of a diseased organism, and therefore its dynamics describe the recovery process of the organism. The mathematical description of the dynamics of

the general index is thus very important in the investigation of disease and allows us to define the parameters of the recovery process.

Analysis of the experimental data has shown that the average value of the index (calculated on the basis of data for a group of patients) can be described by the equation:

$$\frac{d}{dt}\bar{x}_t = -\lambda\bar{x}_t + \alpha,\ \bar{x}_0 > \alpha/\lambda,\ \alpha > 0,\ \lambda > 0, \qquad (4)$$

where $\bar{x}_t$ is the value of the index at time t. If $\alpha = 0$ this model describes the mathematical expectation of the general index; if $\alpha \neq 0$ this model can be used to describe the mean values of the components of vector X.

Since the real trajectories have short-term deviations with respect to the mean value (4), we shall describe them using the following stochastic model:

$$\dot{x}_t = -(\lambda + \delta_{t/\varepsilon})\, x_t + \alpha,\ x_0 = \bar{x}_0, \qquad (5)$$

where $\delta_t$ is a random process, $E\delta_t = 0$, and

$$\lim_{T\to\infty} \frac{1}{T} \int_0^T \int_0^T E\delta_t\delta_s dtds = \gamma < \infty .$$

The small parameter $\varepsilon > 0$ takes into account the fact that the random deviations in the trajectories are short-term.

Set

$$w_t^{\varepsilon} = \frac{1}{\sqrt{\varepsilon}} \int_0^t \delta_{s/\varepsilon}\, ds.$$

Then equation (5) may be rewritten in the form

$$\dot{x}_t^{\varepsilon} = -(\lambda + \sqrt{\varepsilon}\,\dot{w}_t^{\varepsilon})\, x_t + \alpha.$$

It is possible to show that as $\varepsilon \to 0$ the random process $w_t^{\varepsilon}$ converges in distribution on the interval [0,T] to the Wiener process $w_t^0$, where

$$E(w_t^0)^2 = \gamma t.$$

Since $\varepsilon$ is small we can assume that

$$\dot{x}_t = -(\lambda + Bw_t)x_t + \alpha,$$

where $B = \sqrt{\varepsilon\gamma}$ is a perturbation parameter and $w_t$ is a Wiener process,

$$Ew_t^2 = t.$$

In this case the Ito equation has the following form:

$$dx_t = (\alpha + (\frac{B^2}{2} - \lambda)\, x_t)dt + Bx_t dw_t. \qquad (6)$$

This model was suggested and investigated by Pogozhev et al.(1981) and Zuev (1982). The solution of this equation is asymptotically stable in the mean square when $\lambda > B^2$.

From the equations for the mathematical expectation $m_t$ and the variance $v_t$

$$\dot{m}_t = -(\lambda - 0.5B^2)m_t + \alpha$$

$$\dot{v}_t = -2(\lambda - B^2)v_t + B^2 m_t^2$$

it follows that the greater the value of $\lambda$ and the smaller the value of B, the better is the recovery process. Thus the parameters of equation (5) (calculated from observed data) can be used to characterize the dynamics of the recovery process.

The estimation of parameters from the set of index trajectories is based on the properties of the Wiener process $w_t$. For $\ln x_t$ we have

$$d \ln x_t = \left(\frac{\alpha}{x_t} - \lambda\right) dt + B dw_t. \qquad (7)$$

If $t_{i+1} > t_i$ and $\alpha = 0$ we can write a precise equation:

$$\ln x_{t_{i+1}} / x_{t_i} = -\lambda(t_{i+1} - t_i) + B(w_{t_{i+1}} - w_{t_i}); \qquad (8)$$

if $\alpha \neq 0$ we shall use the following approximation of (7):

$$\ln x_{t_{i+1}} / x_{t_i} = \left(\frac{\alpha}{x_{t_i}} - \lambda\right)(t_{i+1} - t_i) + B(w_{t_{i+1}} - w_{t_i}). \qquad (9)$$

Let $X = \{x_t^i, t \in \theta^i,\ i = 1,2,\ldots,N\}$ denote the set of experimentally observed index trajectories obtained from data about a group of N patients, and $\theta^i = \{t_{i0}, t_{i1}, \ldots, t_{in_i}\}$ denote the set of times at which the index of the i-th patient was measured. According to our stochastic model, we shall consider X as a contraction on $\theta^i$ of the set of outcomes of the random process which satisfy equations (8) or (9) (for the general index or indices). Then from (9) and the properties of the Wiener process it follows that the random values

$$Z_{ij}(\lambda,\alpha) = \frac{\ln x_j^i / x_{j-1}^i}{\sqrt{t_{ij} - t_{ij-1}}} - \left(\frac{\alpha}{x_{ij-1}} - \lambda\right)\sqrt{t_{ij} - t_{ij-1}}$$

$$i = 1,2,\ldots,N,\ j = 1,2,\ldots,n_i,\ x_j^i = x_{t_{ij}}^i$$

are independent and have a Gaussian distribution with zero mathematical expectation and variance $B^2$. This allows us to make use of the maximum likelihood principle to find parameter estimates $\hat{\alpha}, \hat{\lambda}, \hat{B}$, and to test the model against experimental data.

The maximum of the likelihood function is unique and corresponds to the following values:

$$\hat{\lambda} = (a_1 a_4 - a_2 a_3)/(a_3 a_5 - a_4^2),$$

$$\hat{\alpha} = (a_1 a_5 - a_2 a_4)/(a_3 a_5 - a_4^2),$$

$$\hat{B}^2 = B^2(\hat{\lambda},\hat{\alpha}) = \frac{1}{M} \sum_{i,j} Z_{ij}^2(\hat{\lambda},\hat{\alpha}),$$

where

$$a_1 = \sum_{i,j} (x_{j-1}^i)^{-1} \ln x_j^i / x_{j-1}^i, \quad a_2 = \sum_{i,j} \ln x_j^i / x_{j-1}^i,$$

$$a_3 = \sum_{i,j} (x_{j-1}^i)^{-2} (t_{ij} - t_{ij-1}), \quad a_4 = \sum_{i,j} (x_{j-1}^i)^{-1} (t_{ij} - t_{ij-1}),$$

$$a_5 = T = \sum_{i,j} (t_{ij} - t_{ij-1}), \quad M = \sum n_i,$$

$$i = 1,2,\ldots,N,\ j = 1,2,\ldots,n_i.$$

For the homogeneous equation we have

$$\hat{\lambda} = T^{-1} \sum_{i,j} \ln x_{j-1}^i / x_j^i,$$

$$\hat{B}^2 = \frac{1}{M} \sum_{i,j} Z_{ij}^2(\hat{\lambda},0).$$

The estimates of the parameters of the index dynamics can be used to compare different methods of treatment. This problem can be reduced to the comparison of parameter estimates based on data from groups of patients treated by different methods. This requires the calculation of confidence intervals for the parameters.

It is possible to show that for the homogeneous equation the random values

$$M\frac{\hat{B}^2}{B^2} \quad \text{and} \quad \frac{\hat{\lambda}-\lambda}{B}\sqrt{T}$$

have a $\chi^2_{M-1}$ distribution and a $S_{M-1}$ Student distribution, respectively.

Estimating the parameters of the non-homogeneous equation, the random values

$$M\frac{\hat{B}^2}{B^2}, \qquad \frac{(M-2)(B^2(\lambda,\alpha) - \hat{B}^2)}{2\hat{B}^2}$$

have a $\chi^2_{M-2}$ distribution and Fisher $F_{2,M-2}$ distribution, respectively.

This information allows us to calculate confidence intervals for the parameters. The approach discussed in this section may be generalized for the purpose of solving the identification problem for the more complex models which describe disease mechanisms.

## 5. STATISTICAL ESTIMATION OF THE PARAMETERS OF DISEASE MODELS

In this section we shall briefly describe the method suggested by Zuev (1983) for estimating the parameters of deterministic models from experimental data.

We shall consider the model described by the system of equations

$$\dot{x}_t = f(x_t,\alpha),\ x_o = q,\ t \in [0,T], \tag{10}$$

where $x_t(\alpha)$ is an n-dimensional vector of state variables and $\alpha$ is an $\ell$-dimensional vector of coefficients.

Let us assume that there is a unique solution of system (10) for each $\alpha \in D$. Experimental investigations yield a set of real trajectories $X_N = \{x^i_t,\ t \in \theta,\ i = 1,2,\ldots,N\}$, where $\theta = \{t_o,t_1,\ldots,t_N\}$, $x^i_t \in R^n$, and N is the number of trajectories.

We shall suppose that at $\alpha=\bar{\alpha}$ model (10) describes the interaction of the cellular populations that take part in the immune response. The sizes of these populations are the state variables of the model. The real trajectories of the chosen variables differ from the value $x_t(\bar{\alpha})$ determined from model (10) due to short-term random deviations of the trajectories from $x_t(\bar{\alpha})$. To describe the real trajectories within the framework of model (10) we shall assume that there exists a set of vector-functions $\{\delta^i_t,\ t \in [0,T], i=1,2,\ldots N\}$ that satisfy the following equalities:

$$x_t(\bar{\alpha} + \delta^i_t) = x^i_t,\ t \in [0,T],\ i = 1,2,\ldots,N.$$

Since the real trajectories have a stochastic character we can consider the functions $\{\delta^i_t,\ t \in [0,T],\ i = 1,2,\ldots,N\}$ to be the set of outcomes of a certain random process.

We shall therefore consider the set of real trajectories to be the contraction on $\theta$ of the set of outcomes of a random process $\{x_t, t \in [0,T]\}$ that satisfy the following equation:

$$\dot{x}_t = f(x_t, \bar{\alpha} + \delta_t),\ x_o = q,\ t \in [0,T], \tag{11}$$
$$E\delta_t = 0,\ E|\delta_t|^2 < \infty .$$

Now let us take into account the fact that the random deviations of state variables are short-term,i.e., the random variable $\delta_t$ changes faster than the state variable $x_t(\bar{\alpha})$. In this case we can reformulate the process $\delta_t$ as $\delta_t = \xi_{t/\varepsilon}$ , where random process $\xi_t$ takes values in $R^l$ such that $E\xi_t = 0$,

$$\lim_{T\to\infty} \frac{1}{T} \int_0^T \int_0^T E\, \xi_t^i \xi_s^j dtds = g^{ij}, \quad i,j = 1,2,\ldots,l,$$

and $\xi_t^i$ is the i-th component of the column vector $\xi_t$ .

We now have the following stochastic model describing the set of real trajectories:

$$\dot{x}_t = f(x_t, \bar{\alpha} + \xi_{t/\varepsilon}), \; x_0 = q, \; t \in [0,T]. \tag{12}$$

According to Venttsel and Freidlin (1979), it is possible to prove that as $\varepsilon \to 0$ the process

$$\zeta_t^\varepsilon = (x_t - x_t(\bar{\alpha}))/\sqrt{\varepsilon}$$

(where $x_t(\alpha)$ and $x_t$ satisfy (10) and (12)) converges on interval [0,T] to the Gauss-Markov process $\zeta_t^o$ which satisfies the following system of linear differential equations:

$$\dot{\zeta}_t^o = B(x_t(\bar{\alpha}))\zeta_t^o + w_t^o, \; \zeta_o^o = 0 \; . \tag{13}$$

Here $B(x)$ is an n x n matrix composed of elements $\partial f^i(x,\alpha)/\partial x^j$ and $w_t^o$ is a Gaussian process with independent increments, zero mathematical expectation and a covariance matrix $R_t$ given by

$$R_t^{ij} = E w_t^i w_t^j = \int_0^t A^{ij}(x_s(\bar{\alpha}))ds, \tag{14}$$

where

$$A^{ij}(x) = \lim_{T\to\infty} \frac{1}{T} \int_0^T \int_0^T A^{ij}(x,s,t)\, dsdt,$$

$$A^{ij}(x,s,t) = E(f^i(x,\xi_t) - Ef^i(x,\xi_t))(f^j(x,\xi_s) - Ef^j(x,\xi_s)).$$

If $\varepsilon > 0$ is sufficiently small we can consider that the deviations

$$x_t^i - x_t(\bar{\alpha}), \; t \in \Theta, \; i \in 1,2,\ldots,N$$

of the real trajectories from the solution $x_t(\bar{\alpha})$ are the outcomes of a Gauss-Markov process whose conditional moments may be deduced from model (13) and expression (14). These properties allow us to use a likelihood principle to estimate vector $\alpha$. This approach can be used to estimate the parameters in mathematical models of immune response.

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# VII. GENERAL SYSTEMS THEORY

# DYNAMICS IN HIERARCHICALLY ORGANIZED SYSTEMS

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## 1. INTRODUCTION

Hierarchical organization of macrosystems has been observed in many different fields of science. Roughly, one can distinguish the following levels of organization: particles, atoms, molecules, macromolecules, organelles, cells, organs, organisms, populations, ecosystems ...(see Weiss, 1971; Pattee, 1974; Voorhees, 1983; Toulouse and Bok, 1978). Each of these levels of organization is associated with a particular level of description. Indeed, many models have been developed at each level of organization and one can find large classes of models corresponding to the different levels. For instance, in ecology, there are three large classes of models corresponding to three levels of organization: individual, population, ecosystem levels. At the individual level, the models study the behaviour of animals and the distribution of animals in different activities such as resting, hiding, searching for food of different types... These dynamical models are concerned with the time dependence of the numbers of animals in the population occupied in each activity (Mackintosh et al., 1972; Auger, 1984a). At the population level, the models study the distribution of the animals according to age classes. These models are concerned with the time dependence of the age distribution (e.g., the Leslie model, see Leslie, 1945). At the ecosystem level, the models study the interactions between different species. These dynamical models are concerned with the time dependence of the numbers of individuals belonging to different species (e.g., the Lotka-Volterra models, see Volterra, 1931; Lotka, 1939; May, 1976).

Nevertheless, an ecosystem is composed of different species which are themselves composed of individuals of different ages and with constantly changing activities. Thus it seems necessary to develop a three-level model which at the same time deals with the individual, population and ecosystem levels. This is the purpose of this paper and continues work already begun in a previous article (Auger, 1983).

To do this, we must consider fundamental dynamical equations at the more microscopic level and also find methods allowing us to derive dynamical equations at more macroscopic levels. In Section 1, we present general methods for jumping from one level to the next. In Section 2, we apply the method to an ecological example, studying the connection between the individual and population levels. In this section, we use some of the results presented in a previous paper (Auger, 1983). In Section 3 we briefly consider the possibility of applying the method of Section 1 in other fields, such as the connection of the biochemical and cellular levels in biology. This has already been attempted by using the Kendall model at the cellular level

(Kendall, 1948; Auger, 1984b). Such methods could also be developed in economics, where hierarchical organization is important (Mesarovic et al., 1980; Roehner, 1982).

## 2. DYNAMICS IN A HIERARCHICALLY ORGANIZED SYSTEM

### 2.1. Linearization of the dynamical equations

Let us consider a system composed of a large number of elements. The elements can be in different states represented by equivalence classes. These equivalence classes are gathered into groups of classes, where $\alpha$ is an index representing the group, $\alpha \in [1,A]$. A is thus the total number of groups of classes.

Each group $\alpha$ contains equivalence classes. $i_\alpha$ is an index representing the equivalence classes belonging to group $\alpha$, $i_\alpha \in [1,N^\alpha]$. $N^\alpha$ is thus the number of equivalence classes in the group $\alpha$. The total number of classes in the whole system N is thus given by the following relation:

$$N = \sum_\alpha N^\alpha \quad . \tag{1}$$

The fundamental variables are the numbers of elements belonging to the $i_\alpha^{th}$ equivalence class of the group $\alpha$. We denote this population by $n_i^\alpha$ (for simplicity, we drop the index $\alpha$ from $i_\alpha$).

We have to choose fundamental dynamical equations governing the time dependence of the fundamental variables $n_i^\alpha$:

$$\frac{dn_i^\alpha}{dt} = \dot{n}_i^\alpha = f_i^\alpha \ (\underline{n}^1, \underline{n}^2, \ldots, \underline{n}^A) \quad , \tag{2}$$

where $\underline{n}^\alpha = (n_1^\alpha, n_2^\alpha, \ldots, n_{N^\alpha}^\alpha)$ are population vectors for each group. $f_i^\alpha$ are functions of the components of the population vectors $\underline{n}^\beta$. For the moment, we shall not make these functions explicit. Let $\hat{\underline{n}}^\alpha$ be the equilibrium populations which satisfy

$$\dot{n}_i^\alpha = f_i^\alpha(\hat{\underline{n}}^1, \hat{\underline{n}}^2, \ldots, \hat{\underline{n}}^A) = 0 \ . \tag{3}$$

We assume the existence of a steady-state point which has all its components positive. Let $\underline{u}^\alpha(t)$ be small variations in the population vectors around the equilibrium vectors:

$$\underline{u}^\alpha(t) = \underline{n}^\alpha(t) - \hat{\underline{n}}^\alpha \ . \tag{4}$$

Let us linearize system (2) around the chosen steady-state point. This leads to the following linearized system:

$$\dot{u}_i^\alpha = \sum_j \frac{\partial f_i^\alpha}{\partial n_j^\alpha} u_j^\alpha + \sum_{\beta \neq \alpha} \sum_k \frac{\partial f_i^\alpha}{\partial n_k^\beta} u_k^\beta \ . \tag{5}$$

We shall define matrices $A^\alpha$ and $A^{\alpha\beta}$ as follows:

$$\begin{cases} A^\alpha = [a_{ij}^\alpha] = [\dfrac{\partial f_i^\alpha}{\partial n_j^\alpha}] \ , \\ A^{\alpha\beta} = [a_{ij}^{\alpha\beta}] = [\dfrac{\partial f_i^\alpha}{\partial n_j^\beta}] \ . \end{cases} \tag{6}$$

Here the $A^\alpha$ are $(N^\alpha \times N^\alpha)$ matrices and the $A^{\alpha\beta}$ are $(N^\alpha \times N^\beta)$ matrices. Under these conditions, system (5) can be more simply written in the following form:

$$\underline{\dot{u}}^\alpha = A^\alpha \underline{u}^\alpha + \sum_{\beta \neq \alpha} A^{\alpha\beta} \underline{u}^\beta \ . \tag{7}$$

Matrices $A^\alpha$ correspond to intra-group transitions of elements while $A^{\alpha\beta}$ correspond to inter-group transitions. Terms $a_{ij}^\alpha$ represent transitions of elements from state j to state i in group $\alpha$. Terms $a_{ij}^{\alpha\beta}$ represent transitions of elements from state j in group $\beta$ to state i in another group $\alpha$.

Let $\underline{u}$ be a system population vector defined by:

$$\underline{u} = (\underline{u}^1, \underline{u}^2, \ldots, \underline{u}^A) \ . \tag{8}$$

The system of equations (7) can be rewritten in the following way:

$$\underline{\dot{u}} = A\underline{u} \ , \tag{9}$$

where

$$A = \begin{bmatrix} A^1 & A^{12} & & A^{1A} \\ A^{21} & A^2 & & \\ & & & \\ A^{A1} & & & A^A \end{bmatrix} \tag{10}$$

A is a $(\sum_\alpha N^\alpha)\times(\sum_\alpha N^\alpha)$ matrix and is a mosaic of the previous matrices $A^\alpha$ and $A^{\alpha\beta}$.

## 2.2. Hierarchy assumptions

We assume that intra-group transitions are much more frequent than intergroup transitions, i.e., for any $\alpha,\beta$, and $(i,j,k,l)$ we have:

$$|a^\alpha_{ij}| \gg |a^{\alpha\beta}_{kl}| \ . \tag{11}$$

The components of the matrices $A^\alpha$ are much larger than those of the matrices $A^{\alpha\beta}$. In the case of a total hierarchy, the inter-group matrices can be neglected in comparison to the intra-group matrices, i.e., $A^{\alpha\beta} = 0$, and system (7) simply becomes:

$$\dot{\underline{u}}^\alpha = A^\alpha \underline{u}^\alpha \ . \tag{12}$$

In this case of total hierarchy, the groups are independent of each other and the matrix A takes the form:

$$A = \begin{bmatrix} A^1 & 0 & & 0 & 0 \\ 0 & A^2 & & & 0 \\ & & \ddots & & \\ 0 & & & \ddots & 0 \\ 0 & 0 & & 0 & A^{\overline{A}} \end{bmatrix} \ . \tag{13}$$

In the hierarchical case the $A^{\alpha\beta}$ remain small with respect to $A^\alpha$ but are not equal to zero; the equivalence classes have been grouped in order to reflect a hierarchy in the transitions of the elements.

## 2.3. Dynamical equations for the populations of the groups

Let $u^\alpha(t)$ be the number of elements in group $\alpha$ at time t:

$$u^\alpha(t) = \sum_i u^\alpha_i(t) \ . \tag{14}$$

We are interested in the derivation of dynamical equations governing the time dependence of these collective variables $u^\alpha(t)$. The time derivatives of these variables are obtained using the following relation:

$$\dot{u}^{\alpha}(t) = \sum_i \dot{u}_i^{\alpha}(t) \ . \tag{15}$$

Let us substitute for $\dot{u}_i^{\alpha}(t)$ from (5) in (15):

$$\dot{u}^{\alpha}(t) = \sum_i \sum_j \frac{\partial f_i^{\alpha}}{\partial n_j^{\alpha}} u_j^{\alpha} + \sum_{\beta \neq \alpha} \sum_i \sum_k \frac{\partial f_i^{\alpha}}{\partial n_k^{\beta}} u_k^{\beta} \ , \tag{16}$$

or

$$\dot{u}^{\alpha}(t) = \sum_i \sum_j a_{ij}^{\alpha} u_j^{\alpha} + \sum_{\beta \neq \alpha} \sum_i \sum_k a_{ik}^{\alpha\beta} u_k^{\beta} \ . \tag{17}$$

In general, we can make the supplementary assumption:

$$\sum_i \sum_j a_{ij}^{\alpha} u_j^{\alpha}(t) = 0 \ . \tag{18}$$

This last assumption implies that only inter-group transitions are responsible for the time variation of the collective variables. Under these conditions, system (17) can be written more simply as:

$$\dot{u}^{\alpha}(t) = \sum_{\beta \neq \alpha} \sum_i \sum_j a_{ij}^{\alpha\beta} u_j^{\beta}(t) \ . \tag{19}$$

It can be shown (Auger, 1983), by comparing the relations (19) and (5) and using the hierarchy assumption (11), that the variables $u_i^{\alpha}(t)$ vary faster than the variables $u^{\alpha}(t)$. The hierarchy assumption for transitions, relation (11), is accompanied by a hierarchy assumption concerning time:

$$|\dot{u}^{\alpha}(t)| \ll |\dot{u}_i^{\alpha}(t)|, \text{ for all } t, \text{ for all } (\alpha,i) \ . \tag{20}$$

Let $\tilde{u}_i^{\alpha}(t)$ be relative variables defined as follows:

$$\tilde{u}_i^{\alpha}(t) = u_i^{\alpha}(t) - \frac{u^{\alpha}}{N^{\alpha}} \ . \tag{21}$$

Here $\tilde{u}_i^{\alpha}(t)$ represents the difference between the real number of elements in class i of group $\alpha$ and the average number of elements per class in group $\alpha$. Under these conditions, the variables $u_i^{\alpha}(t)$ can be described in the following way:

$$u_i^{\alpha}(t) = \frac{u^{\alpha}}{N^{\alpha}} + \tilde{u}_i^{\alpha}(t) \ . \tag{22}$$

Now let us substitute for $u_i^{\alpha}(t)$ from (22) in (19):

$$\dot{u}^{\alpha}(t) = \sum_{\beta \neq \alpha} a^{\alpha\beta} u^{\beta}(t) + \sum_{\beta \neq \alpha} \sum_{i} \sum_{k} a_{ik}^{\alpha\beta} \tilde{u}_k^{\beta}(t) \quad , \tag{23}$$

where

$$a^{\alpha\beta} = \sum_{i} \sum_{k} a_{ik}^{\alpha\beta} \quad . \tag{24}$$

The time hierarchy is very useful because the rapidly varying variables $\tilde{u}_i^{\alpha}(t)$ can be replaced by their time averages, denoted by $\langle \tilde{u}_i^{\alpha} \rangle$ . We shall not discuss the methods used to calculate the time averages here - thermodynamical treatments are given by Kerner (1972) and Goel et al.(1972). Finally, replacing the relative variables by their time averages, the system (23) becomes

$$\dot{u}^{\alpha}(t) = \sum_{\beta \neq \alpha} a^{\alpha\beta} u^{\beta}(t) + \sum_{\beta \neq \alpha} \sum_{i} \sum_{j} a_{ik}^{\alpha\beta} \langle \tilde{u}_k^{\beta} \rangle \quad . \tag{25}$$

## 3. AN ECOLOGICAL EXAMPLE: INTERACTIONS BETWEEN INDIVIDUAL AND POPULATION LEVELS

Consider a system in which the elements are animals belonging to the same species. These animals have different ages i and can be in different states s. These states correspond to different activities such as hiding, searching for food of different types, resting and so on (Mackintosh et al., 1972). $N^i$ is the number of possible states s for an animal of age i. Let $n_s^i$ be the number of animals of age i in state s. $E_s^i$ is the corresponding equivalence class and the $N^i$ classes $E_s^i$ constitute a group of classes which we call an age class. A is the number of age classes.

Let us choose fundamental dynamical equations for the variables $n_s^i$:

$$\dot{n}_s^i = f_s^i(\underline{n}^1, \underline{n}^2, \ldots, \underline{n}^A) . \tag{26}$$

By analogy with Section 1, we obtain a linearized system:

$$\dot{n}_s^i = \sum_{r} a_{sr}^{i} n_r^i + \sum_{j \neq i} \sum_{t} a_{st}^{ij} n_t^j \quad . \tag{27}$$

The terms $a_{st}^{ij}$ correspond to the ageing process, while the terms $a_{st}^{1j}$ represent births, i.e., animals of age j performing activity t (reproduction) give birth to young animals in age class 1. These terms can be assumed to

be independent of the index s, i.e., young animals are equally distributed over states s, and thus we can represent them more simply as $m_t^j$ (see Figure 1). Terms $a_{st}^{i,i-1}$ correspond to the ageing process. An animal of age i-1 in state t may survive to reach age class i. These terms can also be assumed to be independent of s but not of t because some activities are more dangerous than others. Let $b_t^{i-1}$ be the probability that an animal of age i-1 survives to reach age class i.

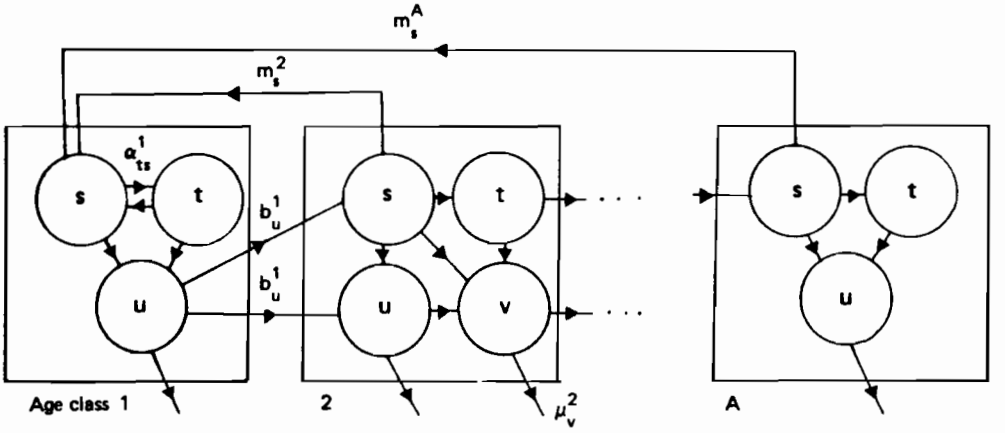


FIGURE 1. The arrows represent transitions between different activities grouped into age classes. The terms $m_s^i$ represent the birth process, the terms $b_s^i$ the ageing process and the terms $\mu_s^i$ the death process. All possible arrows are not represented - we only give some examples of possible transitions.

The term $\sum_r a_{sr}^i n_r^i$ must be written as a sum of three terms:

$$\sum_r a_{sr}^i n_r^i = \sum_r \alpha_{sr}^i n_r^i - \mu_s^i n_s^i - N^{i+1} b_s^i n_s^i \quad . \tag{28}$$

Here $\alpha_{sr}^i$ corresponds to the change of activities within age class i, $\mu_s^i$ represents the probability per unit time that an animal of age i in state s dies, and $N^{i+1} b_s^i$ corresponds to animals which leave age class i to survive in age class i+1. The factor $N^{i+1}$ corresponds to the number of states

available in class i+1. Using this new notation system (27) can be rewritten in the following way:

$$\begin{cases} i \neq 1, & \dot{n}_s^i = \sum_r \alpha_{sr}^i n_r^i - (\mu_s^i + N^{i+1} b_s^i) n_s^i + \sum_t b_t^{i-1} n_t^{i-1}, \\ i = 1, & \dot{n}_s^1 = \sum_r \alpha_{sr}^1 n_r^1 - (\mu_s^1 + N^2 b_s^1) n_s^1 + \sum_j \sum_t m_t^j n_t^i . \end{cases} \tag{29}$$

In this ecological example, the hierarchy assumption (11) implies that the animals often change their activity but relatively seldom change their age class. This signifies that the terms $\alpha_{rs}^i$ are much larger than the other terms:

$$|\alpha_{st}^i| \gg |\mu_s^i| \text{ or } |b_s^i| \text{ or } |m_s^i| \quad \text{for all } (i,s,t) .$$

The relation equivalent to (18) is

$$\sum_s \sum_r \alpha_{sr}^i n_r^i = 0 . \tag{30}$$

Indeed, the change in activities cannot affect the number of animals $n^i$ in age class i. Now let us obtain the time derivatives of the populations of the age classes, $n^i = \sum_s n_s^i$. To do this, we sum equations (29) over s and use relation (30):

$$\begin{cases} i \neq 1, & \dot{n}^i = -\sum_s (\mu_s^i + N^{i+1} b_s^i) n_s^i + N^i \sum_t b_t^{i-1} n_t^{i-1}, \\ i = 1, & \dot{n}^1 = -\sum_s (\mu_s^1 + N^2 b_s^1) n_s^1 + \sum_j \sum_t N^1 m_t^j n_t^j . \end{cases} \tag{31}$$

Following the method outlined in Section 1, we obtain:

$$\begin{cases} i \neq 1, & \dot{n}^i = -(\mu^i + b^i) n^i + \bar{b}^{i-1} n^{i-1} + \langle c^i \rangle , \\ i = 1, & \dot{n}^1 = -(\mu^1 + b^1) n^1 + \sum_j m^j n^j + \langle c^1 \rangle . \end{cases} \tag{32}$$

where

$$\begin{cases} \mu^i = \frac{1}{N^i} \sum_s \mu_s^i, \quad b^i = \frac{N^{i+1}}{N^i} \sum_s b_s^i , \\ m^j = \frac{N^1}{N^j} \sum_t m_t^j , \quad \bar{b}^{i-1} = \frac{N^i}{N^{i-1}} \sum_t b_t^{i-1}, \\ \langle c^i \rangle = -\sum_s (\mu_s^i + b_s^i N^{i+1}) \langle \tilde{n}_s^i \rangle + N^i \sum_t b_t^{i-1} \langle \tilde{n}_t^{i-1} \rangle . \end{cases} \tag{33}$$

$\langle \tilde{n}_s^i \rangle$ is the relative average number of animals of age i performing activity s. The distribution of animals between different activities can be obtained from experimental data (Mackintosh et al., 1972). Equations (33) establish the connection between individual and population levels; it is

clear that the equations governing the time dependence of the population variables $n_i$ also depend on the individual variables $\langle \overset{\sim}{n}{}^{i}_{s} \rangle$ .

## 4. DISCUSSION AND CONCLUSION

Hierarchy theory has recently undergone considerable development, in fields ranging from physics to biology, and a special conference on hierarchy theory was held in New York earlier this year. Many scientists are interested in hierarchy theory because it has been observed that complex systems often organize themselves in a hierarchical way. Some authors (e.g. Toulouse and Bok, 1978) explain this tendency towards hierarchical self-organization in terms of a principle of least resistance.

In Section 1 of this paper we proposed a general method which we applied to an ecological example in Section 2. However, the same method also has applications in fields other than ecology. For instance, one could try to connect the biochemical and cellular levels in biology.

At the biochemical level, one writes dynamical equations governing the time dependence of the concentrations of the different chemical species. These are chemical models for the metabolism (Weinberg and Zeigler, 1970). At the cellular level, one is interested in cell kinetics, i.e., in the time dependence of the numbers of cells of age i, as in the Kendall model (Kendall, 1948). In fact, in a population of cells, there are cells of different ages containing different chemical species and thus it is necessary to build a model including both biochemical and cellular levels. With some modifications, the general method presented in Section 1 could be used to develop such a two-level model (Auger, 1984b).

It would also be interesting to develop hierarchy theory in order to connect experimental data obtained at different levels. For instance, if we had the experimentally observed distribution of activities and probabilities of birth and death for the same population, we could use the model described above to study the interactions between the levels and compare it to the real system.

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# DYNAMICS OF INTERACTIVE MACROSYSTEMS

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## Introduction

Selected aspects of systems research programs and research practices are here chosen as a basis to suggest a general framework in support of an expanded search for an elucidation of the complex interaction of social and natural systems. This proposed framework is based on the recognition that complex interactions may be cast into the form of nonlinear dynamics. Indeed, selected characterizations of such methodologies have already emerged as part of the IIASA operational lexicon including concepts such as resilience, stability, connectivity, bifurcation, catastrophe, synergism, autonomy, and others.

In support of the framework proposed here, we will focus upon a universal generalization of interactions and then identify a particular mathematical structure. Our exposition will be predominantly conceptual and descriptive, but its relation to published formulations and applications will be emphasized.

In order to develop our theme, we first draw upon a particularly convenient characterization of common systems research programs to illustrate the existence of commonly used methodologies and their fundamental assumptions. Subsequently, we suggest a conceptual extension and provide an associated graphical generalization. Finally, we propose a comprehensive mathematical-analytical formulation and briefly discuss some of its properties and points of relevance.

## The Basic Pattern

We consider first human populations. One common issue of population analysis can be formulated as follows: given a set of initial conditions and evolving characterizations, what will be the population in region j at any time t of interest? If $P_j(t)$ is taken as the symbol for this quantity then this problem can be cast into the succinct mathematical form of

$$\frac{dP_j(t)}{dt} = f_P(\alpha, j, j', t) . \tag{1.a}$$

Here $f_p(\ )$ is a particular function with $\alpha$ a vector of parameters such as birthrates, deathrates, health care, nutrition, etc.; j' refers to any other j-region in order to account for in/out migration. The population of interest is then obtained by direct or indirect integration

$$P_j(t) = \int_0^t f_P(\alpha, j, j', t)dt + P_o \tag{1.b}$$

and yields a trajectory in (j,t) space as a graphical representation. The important consideration here is the form of the function $f_p(\ )$ and the determination of the several parameters; though extensive reconstructive methodologies are invariably drawn upon, the issue of dependence and independence of such information, the ad hoc nature of function construction and the skill of the analyst, are fundamental in such analyses and seldom fully treated.

Energy analysis involves issues relating to the amount of energy of type i produced/consumed in region j as a function of time t. We use the symbol $E_{ij}(t)$ for this with i typically coal, oil, geothermal, etc. and j a region or a country. The governing equation is now

$$\frac{dE_{ij}(t)}{dt} = f_E(\alpha,i,i',j,j',t)\,. \tag{2}$$

where the components of the vector $\alpha$ could be population, economic elasticity, resource capacity, etc. The problem is solved when one is able to determine $E_{ij}(t)$ which is then typically displayed as a trajectory in (i, j, t) space. IIASA's *Energy in a Finite World*[1] contains numerous such sets of graphs for i = 1,2,...,7 primary energy resources (gas, oil, nuclear, coal, synthetic fuels, hydro and solar) for j = 1,2,...,7 global regions (NA, SU/EE, WE/JANZ, LA, Af/SEA, ME/NAf, C/CPA), and for a time period up to the year 2030. An important property of this analysis is that population, $P_j(t)$, is taken as an independent function as are several other parameters; the important assumption here is that changes in energy do not intrinsically affect certain social or natural entities and when they do they are treated as points of qualification.

Food and agriculture research programs generally involve issues of quantities of food of type i for region j and for time t of interest. We use $F_{ij}(t)$ for this function and write again a differential equation

$$\frac{dF_{ij}(t)}{dt} = f_F(\alpha,i,i',j,j',t)\,, \tag{3}$$

where $\alpha$ is the parameter vector of soil fertility, climatic conditions, energy cost, accessibility to fertilizers, etc. Here both population and energy costs may appear as independent quantities extracted from other studies.

The quantity of a resource of type i (water, copper, forests, cattle....) in region j will similarly vary with time and one may write

$$\frac{dR_{ij}(t)}{dt} = f_R(\alpha,i,i',j,j',t)\,, \tag{4}$$

where $\alpha$ may include processing capability, market prices, labor costs, etc. Here also, functions which were the subjects of previous studies - population, energy, food, markets - may enter as independent parameters when, in fact, they are appropriately dependent parameters.

In a similar manner one might analyze environmental contaminants according to

$$\frac{dC_{ij}(t)}{dt} = f_C(\alpha,i,i',j,j',t)\,, \tag{5}$$

issues of industry-technology penetration using

$$\frac{dT_{ij}(t)}{dt} = f_T(\alpha, i, i', j, j', t), \tag{6}$$

and wildlife/animal populations by

$$\frac{dA_{ij}(t)}{dt} = f_A(\alpha, i, i', j, j', t), \tag{7}$$

Other density functions may similarly be specified and investigated.

Points of Observation

Several observations can be made on the above.

Dynamical systems describable by first order differential equations of the above type have long played a fundamental role in various sciences. In so-called "hard sciences" they are often found to be essentially exact because independent parameters can generally be well defined or controlled. Such precision has not yet been attained in all sciences because important interactions are insufficiently understood.

The next point we make is that each trajectory is associated with a particular function $f_N(\ )$. The specification of these functions is often viewed as an "art" and draws heavily upon the experience of the analyst and hence, unavoidably, on his personal perspective; this invariably leads to the undesireable feature of a model that is heavily influenced by the modeler. Additionally, limits of various resources impose rigid restrictions on the generality and extent of such studies. Plausibility arguments are important features in the rationalization of the specific functional methodology.

The results of the research themes suggested above can be graphically illustrated as trajectories in phase space (i, j, t), Fig. 1. Here, for each cell (i, j) one can associate a density trajectory in time t for a given set of assumptions as reflected in the parameter vector $\alpha$, and the associated functions employed from other studies. Numerous IIASA studies have been prepared on specific cells and their trajectories displayed (e.g., Water in Poland, Energy for the European Economic Community, Environmental Hazards for Obergurgl, etc. ...). Indeed, entire areas on the (i, j) plane have already been resarched while some other major areas are nearing completion.

The final point refers to the implicit use of functional information employed as independent contributions when, in fact, a definite dependent relationship may exist. We allude here to the importance of identifying a basic and comprehensive connectivity characterization which allows for a comprehensive and general coupling between the quantity associated with coordinate (i, j, t) and the quantities associated with all other relevant coordinates (i', j', t').

An Expanded Perspective

The various quantities of general systems interest -- population, coal, pollutants, water, etc. - will hereafter be interpreted as density functions denoted by $N_{ij}(t)$. That is, $N_{ij}(t)$ refers to some physical quantity of type i for region j and varying in magnitude with time t. We suggest this, as well as a generalization of categorizations, in Fig. 2.

The most critical issue is the general connection among the various density functions so that $N_{ij}(t)$ can be extrapolated in time with the influence of all relevant $N_{i'j'}(t')$ appropriately included. This is illustrated by typical questions; for example, how does the production of steel

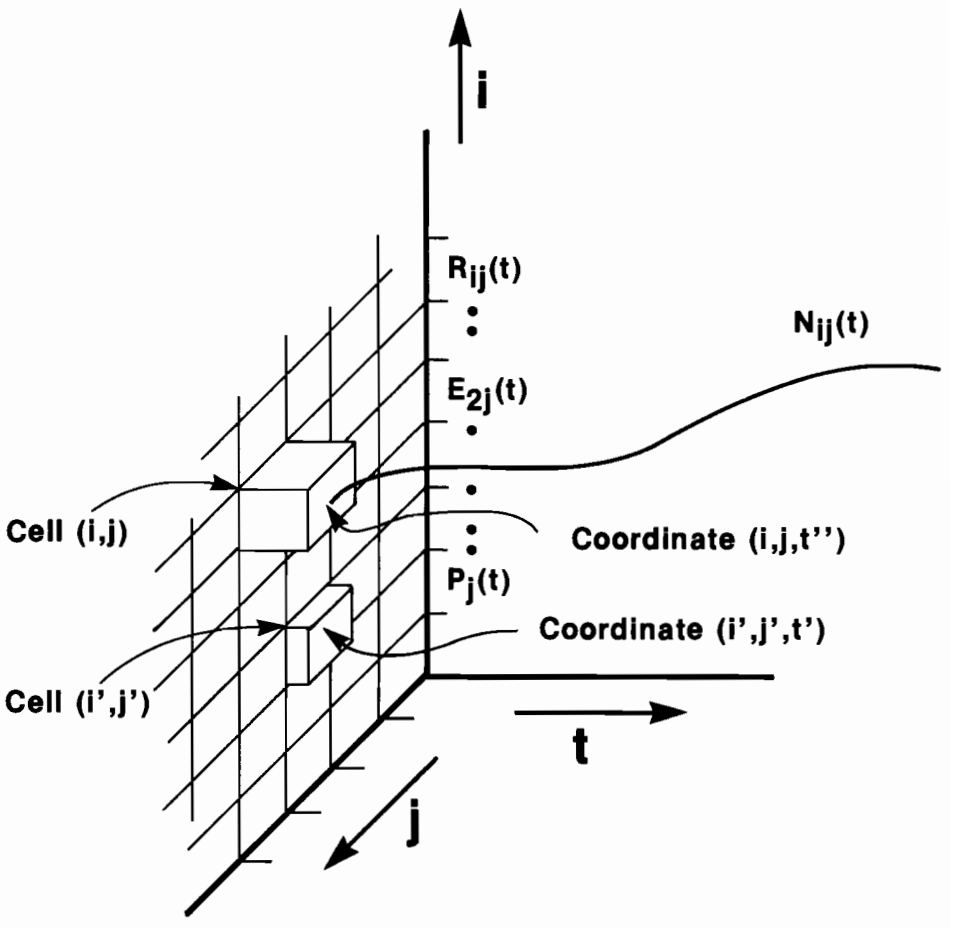


Fig. 1: Schematic depiction of various cells on a Cartesian (i,j,t) coordinate system. A hypothetical trajectory $N_{ij}(t)$ is suggested.

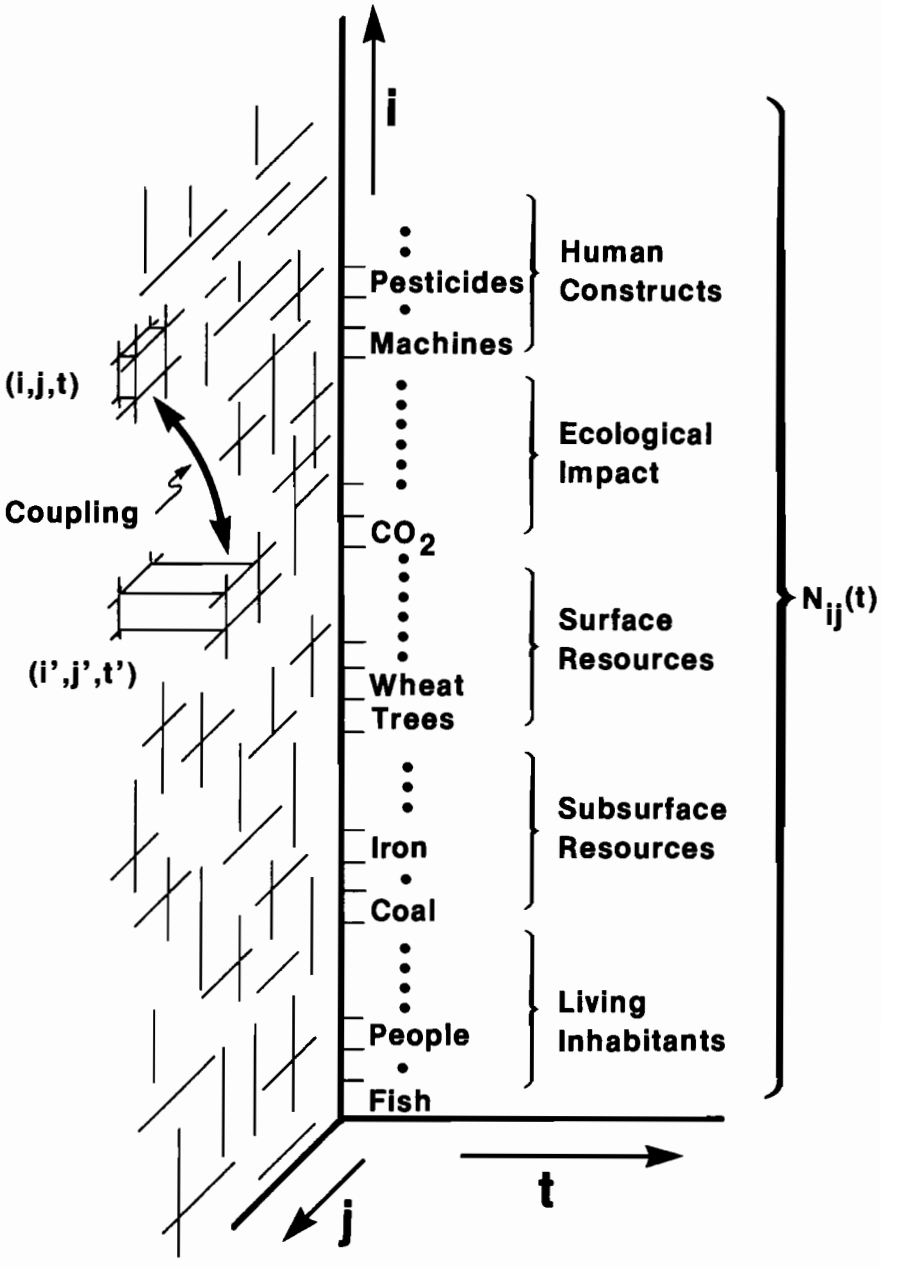


Fig. 2: Generalization and classification of densities Nij(t). Coupling between arbitrary coordinates (i,j,t) and (i',j',t') is depicted.

(=i) in Japan (=j) in 1990 (=t) depend upon the supply of oil (=i') in the OPEC region (=j') in the year before (=t'); or, how is the population (=i) of Nigeria (=j) in the year 2000 (=t) influenced by the available health care (=i') in Nigeria (=j) in the 1980's (=t')?

With $N_{ij}(t)$ a density function, its instantaneous variation with time is simply given by the balance condition

$$\frac{dN_{ij}(t)}{dt} = \left(\frac{dN_{ij}(t)}{dt}\right)_+ - \left(\frac{dN_{ij}(t)}{dt}\right)_- \tag{8}$$

Here, the left hand term refers to the instantaneous inventory change rate, the first term on the right to its gain rate and the last term to the loss rate; each term refers to the cell density $N_{ij}(t)$ at time t.

We can itemize several specific processes which may affect the density of $N_{ij}(t)$. Processes of decay, death, birth, depletion, degeneration or regeneration may be represented by

$$N_{ij}(t) \xrightarrow[\lambda_{(ij)'}]{} N_{i'j}(t)\,, \tag{9}$$

where $\lambda_{(ij)}$ is an extinction constant. We write, therefore, a change component for $N_{ij}(t)$ as

$$\left(\frac{dN_{ij}(t)}{dt}\right) = \lambda_{ij} N_{ij}(t)\,. \tag{10}$$

with the sign determined by the process.

In a similar vein, processes leading to multiplication or production of $N_{ij}(t)$ and involving densities of type i' and i" all in region j may be represented by

$$N_{i'j}(t) + N_{i''j}(t) \xrightarrow[K_{(ij)'}]{} v_{ij} N_{ij}(t) + \ldots \tag{11}$$

where $K_{(ij)}$, is the interaction rate parameter and $v_{ij}$ is a positive gain constant. The dynamical contribution of this process is given by

$$\left(\frac{dN_{ij}(t)}{dt}\right)_+ = K_{(ij)'} v_{ij} N_{i'j}(t) N_{i''j}(t) \tag{12}$$

Mutual self-destruction, neutralization or fusion in order to yield a loss in (i, j, t) and a gain in cell density (i', j ',t) may be represented by

$$N_{ij}(t) + N_{ij}(t) \xrightarrow[K_{(ij)'}]{} N_{i'j'}(t) + \ldots \tag{13}$$

and can be written as a rate equations

$$\left(\frac{dN_{ij}(t)}{dt}\right)_- = -K_{(ij)} N_{ij}^2(t) \tag{14}$$

Transport and extraction changes are given by

$$N_{ij}(t) \xrightarrow[C_{(ij)'}]{} N_{ij'}(t) \tag{15}$$

with their dynamic as

$$\left(\frac{dN_{ij}(t)}{dt}\right) = C_{ij'.} \tag{16}$$

With binary processes, as well as sequences of binary processes, as the fundamental phenomena, all generally typical processes of the type suggested above may be further characterised by a similar construction. The general, and comprehensive, formulation for the global analysis of the density function is then given by superposition leading to a Master Dynamical Equation of the form

$$\frac{dN_{ij}(t)}{dt} = \sum_{i'j'} \lambda_{i'j'} N_{i'j'}(t) + \sum_{i'j't'} \sum_{i''j''t''} K_{(ij)'v_{(ij)'}} N_{i'j'}(t') N_{i''j''}(t'') + \sum_{j'} C_{ij'} \tag{17}$$

with the summation over all relevant sets of indices. The coefficients possess units and magnitudes consistent with the transformations of the associated density function involved and with the sign specified accordingly. A random or pseudorandom component may be added if required for numerical, analytical or conceptual purposes.

The Nonlinear Dimension

The Master Dynamical Equation, Eq. (17), represents a system of first-order coupled quadratically nonlinear differential equations and, in the Synthesis proposed here, the function $N_{ij}(t)$ may represent general density functions of research interest in the context of applied systems analysis.

A degree of confidence in the general applicability of Eq. (17) can be acquired by its reduction to some known cases of relevance.

For example, an isolated homogeneous population ($i=j=1$) subject to birth/death processes will lead to the retention of only two terms from the first summation term of Eq. (17)

$$\frac{dN}{dt} = (\lambda_1 - \lambda_2)N, \tag{18}$$

with $\lambda_1$ and $\lambda_2$ as the birth and death rate-coefficient respectively. Thus, the population N (= people, animals, radioactive nuclei, chemical compounds) changes with time exponentially as determined by the competition between creation and destruction/consumption processes.

The case of environmentally limited carrying capacities introduces a negative squared term, from the second summation of Eq. (17), to give

$$\frac{dN}{dt} = \lambda N - KN^2, \tag{19}$$

and results in the well-known Verhulst Curve.

The conceptually important case of two interacting population species in infinite homogeneous space, the Lotka-Volterra predator-prey system, follows from Eq. (17) by a choice of $i = 1, 2$, retention of the appropriate terms and the proper assignment of sign to the coefficients:

$$\frac{dN_1}{dt} = \lambda_1 N_1 - K_1 N_1 N_2$$

$$\frac{dN_2}{dt} = -\lambda_2 N_2 + K_2 N_1 N_2 \tag{20}$$

Perhaps the more significant reason for confidence in Eq. (17) is that complex physically relevant nonlinear processes of recent interest can be deduced from this form. This applies in general to a large class of physical problems central to the work Prigogine[2] on self-organizing systems. We point out that some of the Prigogine formulations, for example the so-called Brusselator, contains cubic terms. This trimolecular component can however be eliminated in a manner consistent with chemical reaction processes[3] and hence only two-body interactions constitute the fundamental phenomena. Another example is the genetic-evolution hypercycle of Eigen[4]. Additionally, it is found that Eq. (17) also characterizes a large set of catalytic and regenerative nuclear reaction cycle[5].

Table I provides a summary listing of these nonlinear relationships for the case of spatially independent or point kinetics representations.

Table I
Listing of Nonlinear Systems in Point Kinetics Form

I. General Lotka-Volterra Population System:

$$\frac{dN_i}{dt} = b_i N_i + N_i \sum_{j \neq i} c_{ij} N_j,$$

II. Genetic Hypercycle ($\phi$ = dilution flux):

$$\frac{dN_i}{dt} = (b_i - \phi) N_i + N_i \sum_j c_{ij} N_j$$

III. Catalytic/Regenerative Nuclear Cycles:

$$\frac{dN_i}{dt} = \sum_j b_{ij} N_j + \sum_{k,l} c_{ikl} N_l N_k$$

IV. Master Dynamical Equation:

$$\frac{dN_i}{dt} = \sum_j b_{ij} N_j + \sum_j \sum_{k,l} c_{ikl} N_l N_k + C_i$$

The Essential Search

The availability of a mathematical-conceptual structure as represented by the Master Dynamical Equation, Eq. (17), next requires the determination of the various coefficients. This involves the specification of homogeneous and functionally consistent cells (i, j) for all t. Such coordinates have already been identified in numerous IIASA studies and hence constitute no major problem. The determination of the coefficients is more complex.

One may conceive of two approaches. At one extreme, one may "sweep" through all conceivable combination of coordinates seeking sufficiently strong correlations between the magnitudes of pairs $N_{ij}(t)$ and $N_{i'j'}(t')$ and compute $K_{(ij)}$ and $\nu_{(ij)}$; concurrently the coefficients $\lambda_{(ij)}$ should be calculated*. Issues of statistical significance, strength of correlation and dimensional specification, will arise but both the capacity of present computers and existing methods of statistical measures seem adequate for a meaningful effort in this area.

A more reduced and particularly manageable approach would consist of a judicious selection of density functions which intuitively suggest nonlinear couplings involving few equations. This approach will allow the development of a "feel" for nonlinear analyses and permit conceptual and numerical experimentation we cite two such examples.

As a first example we take Eq. (12) for $i=1, j=0$ and retain terms to give

$$\frac{dN}{dt} = aN + bN^2, \tag{21}$$

Further, we suppose

$$a = -b = \alpha > 0 \tag{22}$$

So that Eq. (21) becomes

$$\frac{dN}{dt} = \alpha N(1-N) \tag{23}$$

This is a special case of Riccati's equation variously referred to as the "logistics" formulation or "contagion" model. Marchetti and Nakicenovic[1,6] have found this representation to be very good agreement for the global energy market penetration of various primary energy sources.

As a second example, we tke Eq. (17) with $i=1.2, j=0$ to give

$$\frac{dN_1}{dt} = a_1N_1 + b_{12}N_1N_2 \quad , \quad a_1 \gtrless 0 \quad , b_{12} \gtrless 0$$

$$\frac{dN_2}{dt} = a_2N_2 + b_{21}N_2N_1 \quad , \quad a_2 \gtrless 0 \quad , b_{21} \gtrless 0 \tag{24}$$

An imposition on the range of the coeffcients -- $a_1>0$, $a_2<0$, $b_{12}<0$, $b_{21}>0$ -- leads to the well known Lotka-Volterra dynamic.

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* Evidently, $K_{(ij)}$ must essentially be composed of two dominant characterizations: one refering to the intrinsic physical consideration pertaining to the combination of the two constitutive densities and the other referring to non-physical circumstances which control the rate of transformation. The analogy to temperature and spectrum effects in chemical and nuclear processes as related to sociological influences and political controls may be relevant in this interpretation.

With $N_1$ and $N_2$ as national populations and per-capita-energy-consumption, the above coupled system of equations has been found to provide very good fits to historical data providing, additionally, a numerical-topological characterization of certain antional economic-developmental and resource states of some countries[7].

While the above provides very good description of a historical pattern, the issue of confidence is such models as a predictive tool -- in contrast to descriptive -- constitutes another and most vital issue.

The ultimate goal will be the extension of nonlinear relationships to encompass a large domain of social-natural systems components. Considerable demands regarding data sources and data management together with numerical testing will need to be faced. Additionally, theoretical-numerical analyses of equations of the form of the Master Dynamical Equation, Eq. (17), and refinements in the interpretation of the coefficients will need to be undertaken.

## Concluding Comment

The development and adaptation of the nonlinear dynamics methodology suggested here and applied to social and natural systems represents an emerging and challenging approach to systems analysis. In particular, its implementation would constitute an advance for the following reasons:

i) remove the ad hoc specification of functional relationships;

ii) minimize the influence of the modeler on the model;

iii) provide a basis for uncovering persistent social-natural patterns based on a common language and construction;

iv) permit a pioneer analysis of nonlinear dynamical analyses of local and global processes..

This proposed Synthesis may be viewed as an extension in the conceptualization and quantification of relevant interrelationships and their assessment and is thus fully in keeping with general objectives of systems research.

## Acknowledgement

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# MACROMODELS AND DYNAMICAL SYSTEMS

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## 1. INTRODUCTION

In this contribution we try to give a framework for macromodels and dynamical systems using an ecological pair of spectacles. The considerations have two sources, a methodological one and a 'philosophical' one.

The methodological source is based on the assumption that in nature the structural concept of chains and the fundamental concept of rate- coupling is met frequently. This leads on the one hand to the so- called 'evolon'- concept in growth dynamics and on the other hand to the Lotka- Volterra approach in system theory as a way for a deeper understanding of the character of interactions within the system.

The philosophical source is connected with the conviction that dialectics as a whole is of basic importance in system theory. Every system theory directed to generate models for real phenomena has to start with a system concept, with the determination of the framework in which every concrete model must be embedded.

To build up the corresponding specific framework a lot of dialectic dichotomies are of essential importance. A macromodel should have a system- concept as a compromise of the following dualisms resulting in the complex interaction structures:

- global- local behaviour
- static- dynamic behaviour
- continuous- discontinuous transactions
- random- deterministic behaviour
- cooperation- competition
- autonomous- controlled behaviour
- reliable forecast- strange and chaotic behaviour
- eigendynamics and eigenpreferences- control

This 'philosophical' source is discussed in more detail in Peschel et al., 1985 a, b. Our methodological and 'philosophical' approach can also be seen as 'simplest' nonlinear approach which takes care of the above mentioned phenomena, as 'umbrella of approximation' for several very complex approaches.

## 2. SIGNIFICANCE OF EVOLUTION AND GROWTH MODELS FOR MACROMODELS

Growth and structure- building are two phenomena in our real world which cannot be considered separately. In our formulation growth describes quanitative

changes and structure- building qualitative changes- and both penetrate each other.

Growth in objective reality takes place under the influence of complex interactions, and interaction is based on structure. Natural systems usually build up so- called cooperative structures to stimulate quick growth. These cooperative structures lead to driving forces which are able to generate explosive phenomena, the corresponding processes expose the tendency to approach infinite large values of their growth indicator in a finite time. In this extensive phase of growth structure is a precondition of growth.
On the other hand the cooperative structures which growth is based on will become senseless and even a brake under conditions where no longer large growth rates are possible because of constraints from restricted sources respective the existence of strong competitiors. In such a situation, the intensive phase of growth, the system exhibits a tendency to decouple and decompose its structure into smaller subsystems. These substructure elements can be used as bricks for the construction of new cooperative structures which could have a chance to stimulate a new growth trend after having identified a niche. In this intensive phase growth is a precondition for (new) structures.

Consequently we use a s- formed transition process representing the quantitative increase (or decrease) of a growth indicator during extensive and following intensive phase of growth and designate this process as 'evolon'. But we understand the notion 'evolon' not only as the phenomen expressed as trajectory over time but also as description of the whole background process of building up or decomposing structures. (For more details see Peschel et al., 1982, 1983 a, 1984, 1985 a). Figures 1 and 2 show schematically an evolon and the corresponding driving forces ('derivation' of the evolon), fig. 3 shows a global growth indicator which can be described by a serie of evolons.

As a functional concept for an evolon we propose the differential equation describing a hyperlogistic growth and saturation:

$$dx/dt = K.x^{k}.(B-x^{w})^{l} \qquad (1)$$

Ther x(t) can be seen for instance as growth indicator of biomass, number of populations, energy consumption,...
Equation (1) is a generalisation of the logistic growth law (k=w=l=1) which describes an isolated growing system without cooperative structures. In reality there exist these cooperative structures in the background resulting in a behaviour different from exponential growth and saturation: the parameters k, l, m 'measure' the complexity of the structure- building and - decomposing. Selforganizing systems which try to grow in the blue heaven are characterised by $k > 1$ ($l > 1$), systems with programmed growth (for instance living systems driven by a genetic code) by $k<1$ and $l<1$. The smaller these values are, the more complex is the organising system in the background which controls the growth by its program.

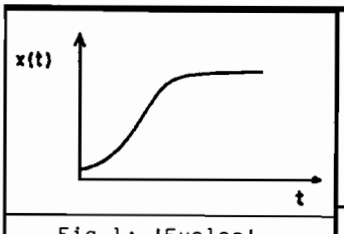



Fig.1: 'Evolon'

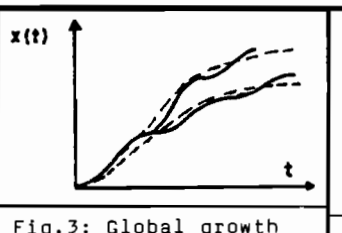



Fig.3: Global growth indicator - serie of evolons

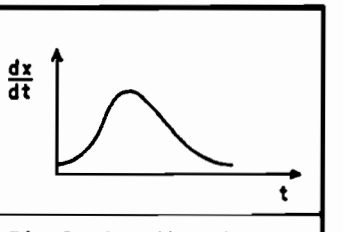



Fig.2: Growth rate (driving force) of evolon

In case of k>1 and l=0 we meet hyperbolic growth. In realitythis manner of growth occurs indeed:there exist a lot of systems which tend to infinity in a finite time- whether an explosion really takes place or not depends on external influences on the driving forces (see Peschel and Mende, 1982). Figure 3 shows that the evolon concept meets the dualism 'global- local behaviour': either one evolon represents a rough model for the growth indicator or a serie of evolon a more exact model.

The evolon concept works very well if one of the different states of a system can picked out as growth indicator with all necessary information. A possible generalisation (see Peschel and Breitenecker, 1983 d, 1984) is to pick out several states as growth indicators, to model them as evolons and to couple them in multiplicative or additive way. This leads, in general, to systems of "generalized" Volterra type (the exponents are different from one).

This concept can be imbedded into a general structure design principle characterised first by Mende and Peschel (1977) and introduced by Peschel et al., 1982, 1983 a, b, c, d, 1984. From experiences with studies of ecological systems we derive two demands for a system concept for structure and function for models of large scale (soft, highly aggregated) systems:

- The structure of the system is composed mainly of chains and cycles - chain with an overall feedback, note the relation to the hypercycles of Eigen and Schuster(1979)- with a relatively small number of internal feedbacks (weakly coupled substructures)
- The function of the system is frequently determined by elementary functions following the so- called rate- coupling principle, that means elementary modules obeying the functional equation Fx=K.y (y input, x output, K constant, F=dln/dt logarithmic differential operator) build up the function of the systems.

From these demands follows a very flexible concept for generating growth processes, the concept of so- called exponential towers (in analogue to Taylor series expansion, see Peschel and Mende, 1983 a):

$$Fx_i = K_i \cdot x_{i+1}, \quad i=0,1,2,\ldots$$

Of interest are special chains, namely finite chains with $x_n$=const. for some n and cycles and hypercycles with $x_n = x_m$ for m<n (fig. 4, see also Eigen and Schuster, 1979).

The idea of a continuous structure generating principle was now to model a system with coupled finite chains and (hyper-) cycles based on the fore- mentioned logarithmic differential operator F. The application of this principle is performed using fixed rules (Peschel et al., 1982, 1983 a, b). Applying the structure generating principle to system described by arbitrary complex differential equations leads to an astonishing result: the generated models are always system of differential equations of Lotka- Volterra type:

$$Fx_i = \sum_j G_{ij} \cdot x_j + \sum_s H_{is} \cdot y_s \qquad (2)$$

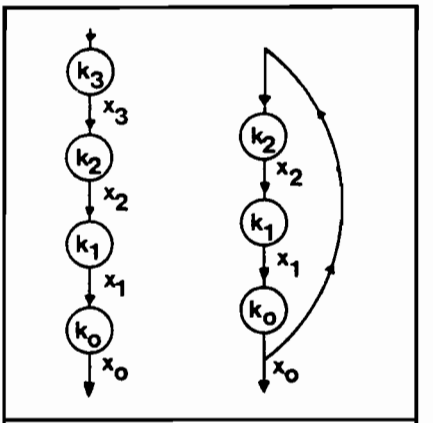



Fig.4: Chain and cycle

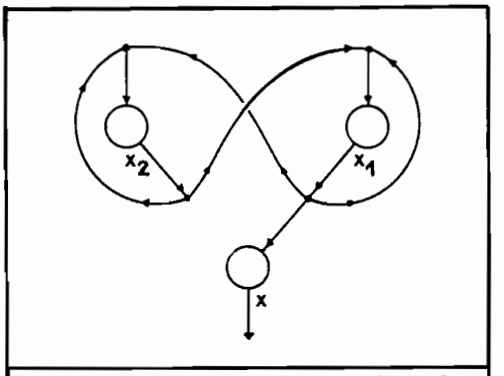



Fig.6: Volterra structure of evolon

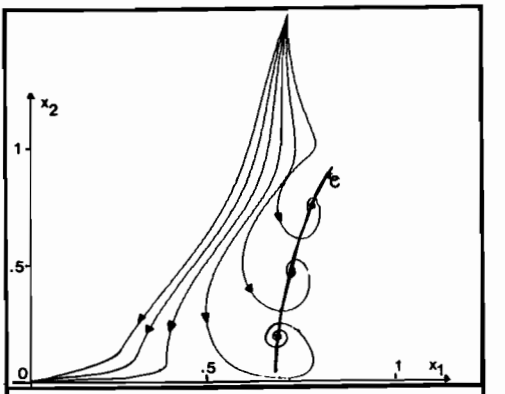



Fig.5: Phase diagram varying coupling parameters

This principle not only works for ecological systems, but also for mechanical systems, macroeconomic systems, reaction kinetics in chemistry, etc. For instance, also the linear- quadratic optimal control (regulator-) problem can be represented as Volterra system, where instead of states and costates of the regulator plant quotients of states and costates are used as (new) states of the Volterra system (Breitenecker, 1984 a,b).
The coefficients of the matrix G characterise the interactions between the species: cooperation and competition are the basic modules. Usually from the whole set of Lotka- Volterra equations (2) a structurisation of the corresponding system can be derived considering weakly and strongly coupled species (large or small absolute values of coefficients in G).
Consequently the application of the Lotka- Volterra approach on a given macromodel reduces a many- particle interaction to a set of weakly coupled two- particle interactions, to so-called predator- prey or Robinson- Friday relations. Because of this behaviour our concept meets the dualism cooperation-competition required in the 'philosophical' source.

Weakly coupled means that changing the coupling parameters in a given range does not influence the qualitative behaviour. Figure 5 gives an example: changing; coupling parameters shifts the equilibrium point along a curve C or let the zero point remain an equilibrium, otherwise the coupling is to be seen strong. The coupling of a predator- prey interaction with another one can also be seen as a control of the interactions in the sense of not unique feedbacks (viability) or in the sense of game theory (see Aubin, 1979 in case of economic systems).

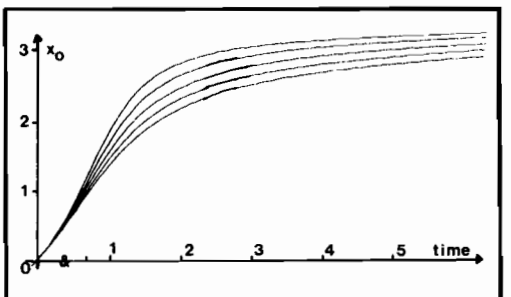



Fig.7: Evolons, varying k

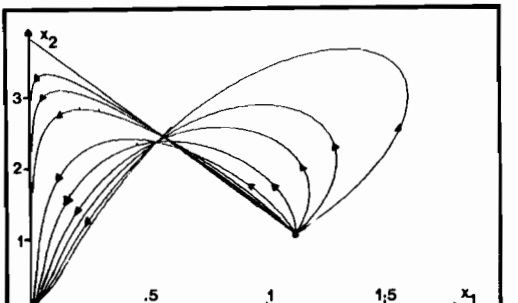



Fig.8: Driving forces of evolon (phase diagram), varying k

Applying the structure- building principle to the evolon- model (1) yields to the Volterra system ($\bar{k}$=k-1, $\bar{I}$=I-1, b=B-1)

$$Fx=Kb^{1}.x_1,\quad Fx_1=K\bar{k}b^{1}.x_1-Kw1b^{\bar{I}}.x_2,\quad Fx_2=Kb^{1}(\bar{k}+w).x_1-Kw\bar{1}b^{\bar{I}}.x_2 \qquad (3)$$

Figure 6 shows the structure of this Volterra system: the driving forces $x_1$ and $x_2$ (characterized by a hypercycle of order 2) build up a predator- prey interaction. Figure 7 shows the evolon for different values of k>1, fig. 8 the corresponding driving forces. In case of k=1 the phase diagram (fig. 8) degenerates to the straight line. For k>1 the driving forces are a curve which tends to zero for time to infinity. The 'difference' between curve and straight line may be seen as measure for the complexity responsible for structure building in the extensive phase and decomposing of structure in the intensive phase, resp.
In general, the approach using coupled evolons and the Lotka- Volterra approach can be seen equivalent: both are based on predator- prey interactions and build up the system behaviour by coupling weakly these basic modules.

## 3. QUALITATIVE ANALYSIS WITH EVOLON- AND VOLTERRA APPROACH

An advantage of the Volterra- approach is the fact, that well known results and new results on the qualitative behaviour of the solutions of Lotka- Volterra equations can be used. Because Volterra- systems show also strange and chaotic behaviour if no control is used, our concept meets the dualism 'reliable forecast' - strangem and chaotic behaviour. It is to be noted, that new results on qualitative behaviour deal with limit cycles and strange attractors (for instance Schuster, Sigmund et al., 1979, 1981 and Hofbauer, 1981). On the other hand it is to be noted, that for instance also in social systems models of Volterra type yield satisfactory results (Bartholomew, 1981).

The eigendynamics and eigenpreferences of the system (dualism with control) can be determined by means of so- called shift- cones. With the notations

$$Fx_i=\sum_j G_{ij}x_j,\quad z_i=\ln x_i,\quad \mathcal{H}\{G.j\}$$

where $\mathcal{H}$ is the convex hull of columns of G, then one has to distinguish between two cases: $\mathcal{O}\in\mathcal{H}$, $\mathcal{O}\notin\mathcal{H}$, $\mathcal{O}$ denoting the zero vector. In the first case it can be shown that there exist stationary solutions with vanishingly small driving forces around. If $\mathcal{O}\notin\mathcal{H}$ then the velocity dz/dt is directed into the direction $z(t)+\mathcal{K}$ where $\mathcal{K}$ is the convex cone spanned by $\mathcal{H}$, so that the eigenpreferences are evident; addionally follows that now no cyclic motion can exist (Peschel et a., 1983 a, d); fig. 9 shows this situation.

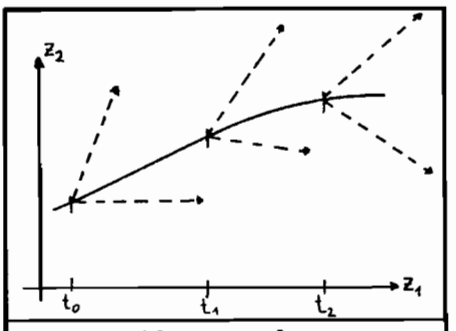


Fig.9: Shift-cones for eigenpreferences

Considering the flow S(t) and the total biomass V(t) of the Volterra system, i.e.

$$Fx_i=\sum_j G_{ij}x_{ij},\quad V(t)=\sum_i x_i,\quad S(t)=dV/dt$$

then one can derive the following relation for total biomass and flow:

$$V(t) > V^2(t_o)/(V(t_o)-S(t_o).t) \qquad (4)$$

Formula (4) can be shown by using the replicator form of the Volterra system; this replicator form (instead of 'absolute'

populations $x_i$ there dynamically normalised states $y_i=x_i/V(t)$ are considered) is very often used for deriving assertions on the qualitative behaviour of Volterra systems, see for instance Hofbauer, 1981 .
From (4) follows now:

- for $S(t)>0$ the biomass increases hyperbolically (and not proportionally!); consequently resources are used for structure building
- for $S(t)<0$ the biomass decreases less than hyperbolically; consequently new 'resources' are build up by decomposing structures.

The constant $S_o/V_o=S(t_o)/V(t_o)$ (pole of the hyperbola in (4)) can be seen as measure of complexity.
In case of the evolon these phenomena coincide with the behaviour required in the extensive and intensive phase resp. and using the Volterra representation (3) of the basic hyperlogistic growth module the complexity measure becomes

$$S_o/V_o = B.(2\bar{k}+w)/2+2-(k+lw)$$

Of interest is also the behaviour of the rate- coupled chains and cycles representing a (weakly coupled) Volterra system and of the evolon (as special basic module) under stochastic influences and disturbances.This was considered in detail by Albrecht et al., 1984 b. Disturbing the evolon with an additive noise in (1) and by adding stochastic variables $\xi$ to growth velocity K and saturation level B,

$$x = (K+\xi_1).x^k.((B+\xi_2)-x^w)^l + n$$

results in case of Gaussian white noise in closed analytical formulas for the stationary distributions. Within the extensive phase of the evolon the disturbances have almost no influence, in some sense they seem to "stabilize" the system behaviour, while within the intensive phase small disturbances result in instability, so that other saturation limits are reached (fig.10).

Thus, our concept meets also the required dualism random- deterministic behaviour.

This outlined phenomena of instability in the extensive phase 'supports' mutation, the emergence of new individuals, too.
Considering now the weakly coupled predator- prey systems for two species x,y than a mutant x of x entends the two dimensional system to a three dimensional one ('w.c.' means terms with weak couplings to 'neighbouring predator- prey systems).

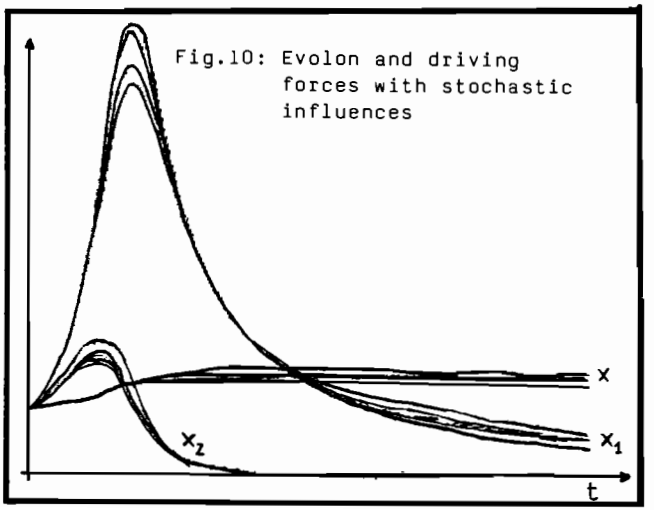



Fig.10: Evolon and driving forces with stochastic influences

$$Fx=ax+by+c+\tilde{a}\bar{x}+w.c$$
$$Fy=cx+dy+f+\tilde{c}\bar{x}+w.c$$
$$+$$
$$F\bar{x}=\tilde{a}x+\tilde{b}y+\tilde{e}+\tilde{a}\bar{x}+w.c$$

Following Allen, 1980 such a mutant $\bar{x}$ can occur (in a quasi-stationary state, for instance during approaching a saturation limit) only if the parameters obey the relation

$$\tilde{a}(bf-de)+\tilde{b}(ce-af) > \tilde{e}(bc-ad)$$

This relation has to be seen as 'condition for mutation' in

our concept which consequently is able to treat mutation:
It is to be noted, that also selection can be considered within our approach: a bifurcation with two evolons (see fig. 3) can be interpreted as selection and mutation.

Further qualitative analysis with the Volterra approach can be performed using a nonlinear transformation based on a Riccati differential equation. This 'Riccati'- transformation represents now the system (2) (in the homogenous and uncontrolled case ) as

$$\dot{u}_i=-g_{ii}\prod_{j\in A_i} u_j^{-g_{ij}/g_{jj}}\prod_{k\in\bar{A}} u_k^{g_{ik}},\ i\in A,\quad \dot{u}_i=u_i\prod_{j\in\bar{A}} u_j^{-g_{ij}/g_{jj}}\prod_{k\in A_i} u_k^{g_{ik}},\ i\in\bar{A} \qquad (5)$$

Where $j\in A$ if $g_{jj}\neq 0$ and $k\in\bar{A}$ if $g_{kk}=0$ with $A_i=A\setminus\{i\}$. The states $x_i$ and $u_i$ are related by $x_i=Fu_i$ if $i\in\bar{A}$ and $x_i=-Fu_i/g_{ii}$ if $i\in A$.

Applying this transformation e.g. on the Volterra system (3) of the evolon (1) yields to a system of differential equations of Cobb- Douglas production function- type:

$$\dot{u}=u.u_1^{1/\bar{k}},\ \dot{u}_1=K\bar{k}b^{\bar{l}}.u_2^{1/\bar{l}},\ \dot{u}_2=Kw\bar{l}b^{\bar{l}}u_1^{(\bar{k}+r)/\bar{k}} \qquad (6)$$

The representation (5) allows now again qualitative analysis. First it is to be noted that all relations in (5) are only multiplicative.
Following Peschel, 1982, 1983 a one can distinguish between five types of influences of a state $u_i$, which are determined by the sign of K and $G_{ii}$:

- quasi- hyperbolic growth leading to explosion
- quasi- hyperbolic decrease
- quasi- parabolic growth
- quasi- parabolic decrease leading to extinction
- quasi- logistic increase or decrease

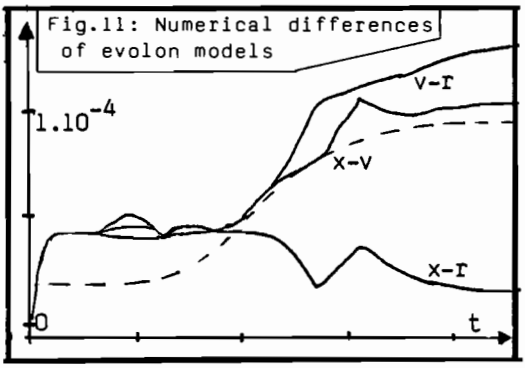
The last three influences are well known from the linear system theory: there the equivalent types of additive influences are determined e.g. by poles and zeros of the transfer function.

It is to be noted, that furthermore well known results for the Volterra system (2) can be used for considering the phenomena stability, structural stability, robustness, existence of limit cycles- phenomena which are essential phenomena of our approaches.

## 4. SIMULATION WITH EVOLON- AND VOLTERRA APPROACH

Simulation of macromodels requires the solution of the Volterra- representation (2) or of the Riccati- representation (5) on a computer. It is to be noted, that only 'integrators' with 'multiplying' inputs (or integrators with 'exponentiating' input) are necessary if e.g. simulation packages are used. It turns, that the Riccati representation is well suited for computer simulation. Figure 11 and table 1 show the differences of the solutions for the evolon, using the hyperlogistic growth law (1), denoted by 'x', the Volterra representation (3), denoted by 'v' and the Riccati representation (6), denoted by 'r'.

Simulation using the outlined concepts has proven successful for instance in case of the Lorentz attractor and of a model for a problem in virology with a delay time (Peschel et al., 1983 b).




| t | x - v | x - r | v - r |
|---|---|---|---|
| 0.0 | 0. | 0. | 0. |
| 0.1 | 8.975-05 | 2.705-05 | 1.845-04 |
| 0.5 | 1.109-04 | 9.430-06 | 1.203-04 |
| 1.0 | 1.133-04 | 7.722-06 | 1.210-04 |
| 1.5 | 1.142-04 | 7.385-06 | 1.216-04 |
| 2.0 | 1.147-04 | 7.251-06 | 1.219-04 |
| 2.5 | 1.150-04 | 7.180-06 | 1.221-04 |
| 3.0 | 1.152-04 | 7.136-06 | 1.223-04 |

Table 1:Numerical differences

The qualitative analysis outlined in section 3 can be implemented within a special software because of the common system description as system of 'population dynamics'. This 'automatic' analysis and simulation for systems of type (2) was implemented as interactive simulation package within the (hybrid) simulation HYBSYS (Solar et al., 1982). The software is able to perform the following actions:

- simulation of the trajectories with (graphic) documentation
- variation of parameters and initial values with (graphic) documentation
- calculation of equilibrium states
- local stability analysis by linearisation around the equilibrium or initial states
- global stability analysis by special investigations on the system
- global stability analysis by a graph- theoretic method stability
- analysis by stochastic methods

In the moment a 'Volterra'- compiler is in stage of designing which transforms an arbitrary system of differential equations into a Volterra system. This software package may be seen as first stage of an expert system for the outlined system concept (Breitenecker, 1983 b). Figure 12 shows a simulation of an evolon weakly coupled with a second evolon: the influences cause the process to leave the saturation limit (B) immediately and to approach another limit (B); it is to be noted, that also this three dimensional plot is a standard feature of the simulation software (language) HYBSYS.

Simulation in HYBSYS can be done by usual numerical integration or by hybrid (analog, parallel) integration. In the second case the integration is able to find out whether the model is 'structural' unstable because of the physical properties of the integration (Breitenecker, 1983 a).

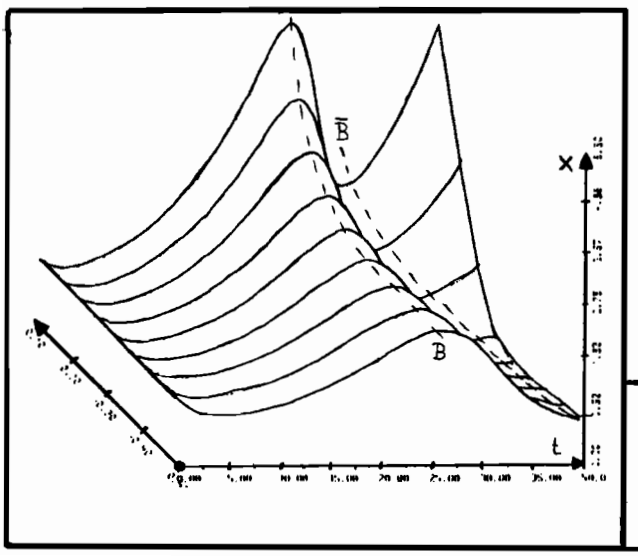



Fig.12: Coupled evolons - varying coupling parameters, simulation and documentation in HYBSYS

## 5. APPLICATION OF THE EVOLON CONCEPT ON SOCIOECONOMIC PROBLEMS

The outlined evolon- and Volterra- approach is also an appropriate and efficient tool for macromodels in socioeconomic processes.
Considering other approaches for modeling socioeconomic systems it turns out that our approach can be seen as 'common denominator' for a lot of approaches, as outlined in the following:
First of all, Volterra systems of low order are used as introducing models for socioeconomic processes because of the Robinson- Friday relations (Bartholomew, 1981; Allen, 1980).
Game theory is also a very often used tool (see Aubin, 1979). Predator- prey interactions can be seen as simplified games.
A very important tool (perhaps the most important up to now) for modeling socioeconomic processes is the stochastic method resulting e.g. in Markov chains (Bartholomew, 1981). Usually the stochastic model can be transformed into a deterministic one by deriving differential equations for the mean values which again have corresponding Volterra representations or are of Volterra type.
A possible compromise between deterministic and stochastic modeling is the fuzzy set approach (Zadeh, 1965). But again (due to Mende et al., 1977) fuzzy systems can be described by special Volterra systems where the cardinal numbers of the fuzzy sets become states.
A recent and very interesting approach is to use synergetics for socioeconomic processes (Haken, 1977). It is to be noted, that synergetics try to model first the structures and phenomena arising in the processes by comparing them with equivalent structures and phenomena e.g. technical processes and to reduce the number of dependent variables so that the remaining variables, the so called structure parameters are sufficient to describe the phenomena. It turns out, that a lot of the structures and phenomena in socio- economic processes correspond with equivalent structures and phenomena of Volterra equations, such as running into a stable steady state, into a periodic limit cycle, such as exploding or extincting behaviour of some variables. For instance, the global evolon can be seen as structure parameter.
In this context of interest is also the synergetic approach via 'fluctations' (Prigogine, 1980). There it is proposed to use the structures and phenomena of the thermodynamic theory as description for socio- economic processes. This idea is based on the fact that a process can be modelled either in space- time structure- as usual, or by describing the fluctuations between the essential states (structure parameters) of the process. So e.g. a dissipative structure in thermodynamics results in a (deterministic) system of differential equations for the mean values, which are again Volterra systems.

In the following we consider three applications of our system concept, where a 'global' evolon (1) resp. (3) and (6) is used.
The first application is the (projection of) world primary energy consumption and world population. Following Kriegel et al., 1983 these processes can be fitted by a global evolon with k=1 and w=1. The remaining parameters were identified with a special $\chi^2$- method. Figure 13 shows the results for the world primary energy consumption (with different 'time instants' of maximal growth rate, i.e. 1970, 1972, 1974) and fig. 14 for world population.
Remarkable in this analysis is the following fact:
First, the model was fitted with time series data up to the year 1913. Then the factor K(velocity of growth) was reduced to K-$\varepsilon$ for the period from 1914 to 1953 (period of the two World Wars and the restauration period after World War 2),in 1953 the model was continued with the parameters used before World Wars. Therefore, all model values beginning with 1953 must be considered as forecasts, which coincide very well with measured data from 1953 up to now. This is quite astonishing and proofs in our opinion the robustness of world

development against temporary disturbances, if large- scale soft systems are used.
Secondly a forecast for the future development was made, assuming that the maximum growth rate for world energy consumption and population is already behind us, namely in the years 1970 to 1974. With this assumption time series after the World War 2 were fitted in the evolon model.
Figure 13 and 14, resp. show the results of the both steps of fitting. Following Kriegel et al., 1983 the forecasts coincide very well with the forecasts made by IIASA in the energy project and with the forecasts of the 'Global 2000' report.

A third application was the population development of ten European towns from past century up to present time (Albrecht,1984a;fig.15 shows the results with an evolon model with k=1. It was shown, that the evolon model reflects the historical development very well.

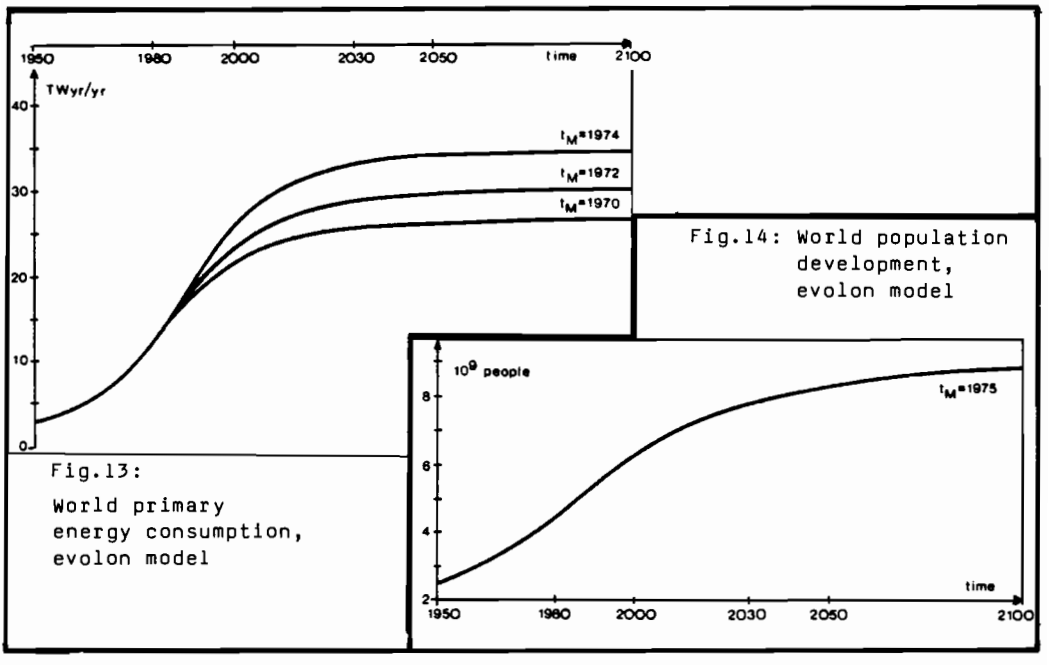



Fig.13:
World primary energy consumption, evolon model

Fig.14: World population development, evolon model

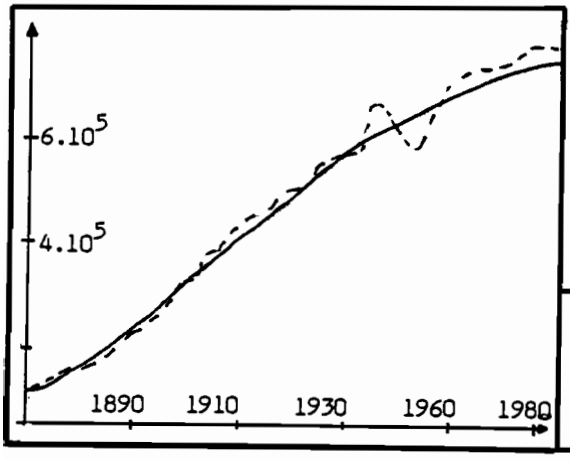
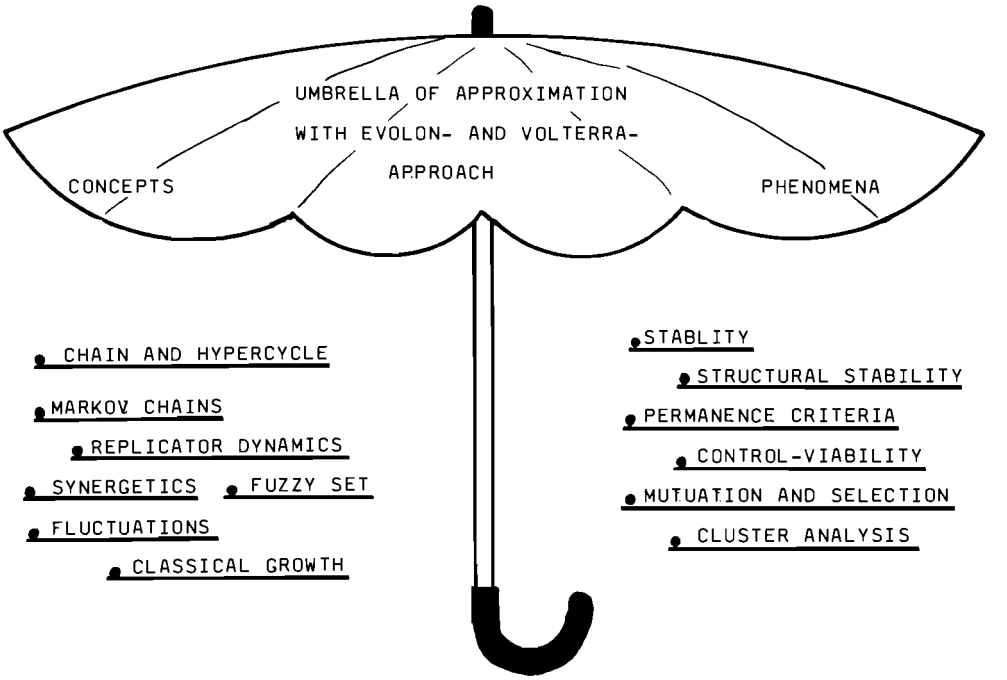



Fig.15:
Population development in an European town, evolon model

## 6. CONCLUSION

As already mentioned in the introduction, the evolon- and Volterra- approach to macro models can be seen as 'simplest' nonlinear approach which takes care of a lot of phenomena, as 'umbrella of approximation' for several complex and more accurate approaches. The following diagram summarizes our 'umbrella of approximation' using the evolon- and Volterra approach. It should be read in the sense, that approximations or simplifications of complex approaches coincide with our approach:

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# VIII. GENERAL ASPECTS OF EVOLUTION

# THE INTERFACE BETWEEN CHEMISTRY AND BIOLOGY – LAWS DETERMINING REGULARITIES IN EARLY EVOLUTION

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## 1. PRINCIPLES OF EARLY EVOLUTION

More than ten years ago Eigen (1971) started to develop a dynamical model of molecular self-organization which is based mainly on chemical kinetics and the presently known properties of biopolymers. Later on, this theoretical concept was extended (Eigen & Schuster, 1979,1982) and supported by experimental studies (Biebricher et al.,1981, 1982; Biebricher, 1983; for a popular review see Eigen et al.,1981). The model starts out from the simplest prerequisites : polynucleotides are present and activated monomers are available in sufficient amounts. Several principles of self-organization can be derived by straightforward analysis. We just enumerate them here.

### 1.1. Selection in systems of replicating molecules

The first principle is a consequence of self-enhancement through replication. Selection in the sense of Darwin's principle takes place in a solution of polynucleotides provided the environmental conditions sustain efficient replication. By "selection" we mean here that an originally heterogeneous mixture of different sequences becomes homogeneous after long enough time. (Homogeneous refers here to the distribution of sequences and characterizes systems in which exclusively one sequence is present). We distinguish two limiting cases, adaptive and random selection.

(1) Adaptive selection takes place in a system of polynucleotides with different kinetic constants. It represents a process modelling Darwin's "survival of the fittest" at the molecular level. Fitness is a measure of the number of descendants of a given sequence which enter the next replication cycle. In the molecular system fitness can be expressed in terms of rate constants (we neglect mutations for the moment and do not consider complementary replication explicitly). For a given sequence $I_i$ the fitness is simply

$$w_i = f_i - d_i \qquad (1)$$

Herein, $f_i$ is the rate constant of polynucleotide synthesis, i.e. the number of molecules of type $I_i$ which are synthesized on templates $I_i$ per unit time and unit concentration. Analogously, $d_i$ is the rate constant of degradation. It measures the number of molecules $I_i$ which are degraded per unit time and unit concentration. The criterion of selection is the net excess productivi-

ty (w), the difference between the rate of synthesis and the rate of degradation. The polynucleotide sequence with maximum fitness, the one which is characterized by the largest value of w, is selected, no matter what the initial distribution of sequences was, provided this fittest sequence was present. During the selection process we observe a steady increase of the mean excess productivity ($\bar{w}$). Thus, the total net production - synthesis minus degradation - of polynucleotides is optimized.

(2) In finite populations we observe another mechanism of selection which is entirely based on the stochasticity of the replication process. Heterogeneous initial distributions of sequences lead to homogeneous final states even in the absence of differences in the rate constants (Schuster & Sigmund, 1984). In this case of kinetic degeneracy we observe an example of "survival of the survivor". The sequence which is ultimately selected is chosen truly at random. Different runs starting from identical initial distributions give different results. The mean excess productivity ($\bar{w}$) of the population is constant (apart from irregular fluctuations) during random selection. In figure 1 we present a numerical example showing the statistics of disappearence of polynucleotide sequences.

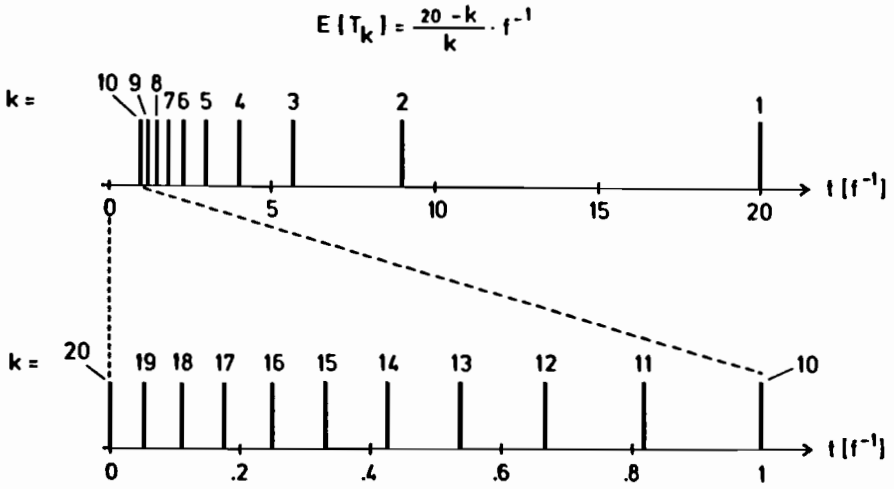


FIGURE 1 Statistics of random selection. By $E\{T_k\}$ we denote the mean value of the time after which we have k different sequences present. In our example we start from 20 replicating polynucleotides. Most sequences die out within the first time unit (We choose the reciprocal rate constant of replication, $f^{-1}$, as the unit of the time axis). Then, only few sequences remain and eventually the population becomes homogeneous.

## 1.2. Mutation and error threshold

No process in nature occurs with ultimate precision. The physics of base pairing, bond formation and bond cleavage sets limits to the accuracy of replication processes. The appearence of copies with replication errors, commonly called mutants, is unavoidable. How do mutations effect the process of selection? For the purpose of illustration we use a somewhat simplified description (Similar model considerations were recently presented by Maynard-Smith, 1983 in order to compare the error threshold relation with Muller's ratchet). We introduce a measure for the accuracy of replication by means of a quality factor Q which gives the fraction of correct replicas (figure 2).

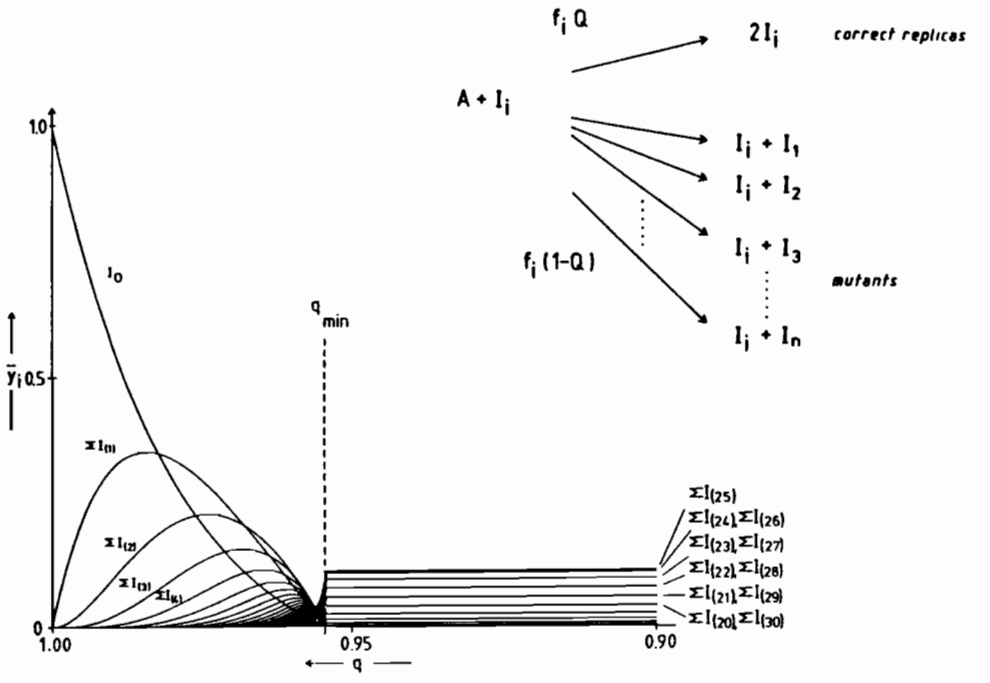


FIGURE 2 Replication with errors. The mechanism for template induced replication contains two classes of processes: correct replication occurring with frequency Q and mutations occuring in toto with the frequency 1-Q. We show the sequence distribution in the stable stationary state, the so called quasispecies. $I_o$ is the master sequence, $\Sigma I_{(1)}$ the sum of all one error mutants, $\Sigma I_{(2)}$, the sum of all two error mutants etc. The corresponding stationary concentrations are denoted by $[I_o] = \bar{y}_o$, $[\Sigma I_{(1)}] = \bar{y}_1$, $[\Sigma I_{(2)}] = \bar{y}_2$ etc. In the examples shown we have $\nu=50$ and $\sigma=10$ (see text). The single digit accuracy q is related to the total accuracy by the relation: $Q = q^\nu$. At q=1, the case of error free replication, we have a homogeneous stationary population consisting of the master sequence exclusively. The percentage of the master sequence at the stationary state decreases with decreasing single digit accuracy. Note the sharp break down of the quasispecies at the critical accuracy $q=q_{min}$. Below this critical value all sequences are present with equal probability. Accordingly, the 25-error mutants are most frequent because they have the highest statistical weight.

The frequency of mutations, hence, is 1-Q. The fitness function, then, has to be modified and reads now

$$w_i = f_i Q - d_i \qquad (2)$$

In the dynamics of replication we distinguish two scenarios:

(1) Replication is accurate enough to sustain inheritance. As in the error-free system we observe a selection process. The final state, however, is not homogeneous. Instead, it is a mutant distribution which we called "quasi-

species" and which consists of the "master sequence", the sequence with the largest w-value, together with a cloud of frequent mutants.

(2) The accuracy of replication is low, more precisely, too low to sustain a stable quasispecies. Then, the percentage of incorrect copies is simply too large and the mechanism of inheritance breaks down. The result derived from the conventional kinetic analysis is rather impressive: after long time the replicating ensemble approaches a stationary state at which all polynucleotide sequences are present in equal amount. The quasispecies distribution of mutants degenerates to equipartition of sequence frequencies. Let us examine this result more closely now: it is easy to convince oneself that the number of possible sequences is "hyperastronomical" and exceeds by far the number of molecules in a population. Consequently, equal frequencies of all possible sequences cannot be realized either in nature or in the laboratory: population sizes are much too small. We can really not have a fraction of a molecule in a given population. Most sequences, thus, will not be present and the ones which do exist in the population are there in a single copy or eventually in a few copies. New sequences appear at every instant due to copying errors and a certain percentage of the old sequences disappears as a consequence of degradation and dilution. In order to refer to an obvious analogy to random walk problems we called this scenario "random replication".

Next we consider a sequence of $\nu$ bases. In order to calculate the quality factor Q we define a "single digit accuracy" q. The value of q measures the incorporation of the correct base at the end of the newly synthesized growing strand[1]. It is characteristic for a given mechanism of replication. For the entire sequence we have $Q=q^{\nu}$. In figure 2 we present the dependence of the quasispecies on the single digit accuracy q for a small polynucleotide ($\nu$=50). The sharpness of the transition between scenario (1) and scenario (2) is remarkable. This transition characteristically called error catastrophy becomes sharper and sharper with increasing length of the polynucleotide ($\nu$): on the q-axis we observe a well-defined error threshold below which we have random replication. The value of q is determined by the machinery of replication. Hence, we can put it constant for a given system. Then, the error threshold defines a maximum chain length ($\nu_{max}$) for the existence of the quasispecies.

$$\nu_{max} = \frac{\ln\sigma}{1-q} \qquad (3)$$

This maximum chain length is a function of the single digit accuracy and the rate constants $f_i$ and $d_i$. The superiority of the master sequence, $\sigma$, is a factor weighting the excess productivity of the master sequence against the average excess productivity of the mutant distribution.

In some cases experimental data are available for single digit accuracies. The RNA replicating enzymes of some small RNA viruses like Qß or MS2 operate with single digit accuracies of $q \simeq 0.9997$. From the data on mutant distributions and replication kinetics one can estimate the maximum chain length of this system: $\nu_{max}(Q\beta) \simeq 4.600$ bases. Interestingly, the actual lengths of the genomes of this class of viruses comes very close to the calculated maximum: $\nu(Q\beta)$=4200 bases and $\nu$(MS2)=3500 bases. Replication errors, thus, seem to be the limiting factor for the transfer of genetic information in these viruses.

[1]This is, of course, a simplification since the accuracy of incorporation depends on the nature of the base G,A,C or U(T) and on the position. There are so called hot spots where mutations occur more frequently than in other parts of the genome. The single digit accuracy q, however, can be understood as the geometric mean of the individual single digit accuracies (Schuster, 1981)

The replication of DNA in bacteria is more sophisticated than bacteriophage RNA replication. This process is catalyzed by many enzymes, presumably more than ten. The major improvement compared to viral RNA replication consists in a proofreading mechanism which reduces the frequencies of errors by about three orders of magnitude. It seems that DNA replication in bacteria is subjected to an error propagation problem similar to that found with simple RNA phages, the error threshold lying around 10 million base pairs in this case.

Nature found a way to allow for still larger genomes by means of the replication mechanism of DNA in eukaryotic cells. This mechanism requires the extremly complicated machinery of mitotic (and meiotic) cell division which is not understood on the molecular level yet. At a first glance, however, it is evident that genomes at least three orders of magnitude longer than those of bacteria can be replicated without running into the error catastrophy.

The important take-home lesson is the existence of maximum chain lengths for stable polynucleotide replication. The accuracy of the replication process seems to provide a straightforward explanation for the differences in genome lengths of primitive organisms. Is there an optimum fraction of mutations in evolution? Clearly, the two extreme cases are disastrous: too few mutants freeze the system into a temporary optimum of selection which can be wiped out easily by forthcoming changes in the environment. Too many mutants cause the error catastrophy. An optimum thus is achieved when replication is accurate enough to avoid the error catastrophy but still not too perfect so that there is sufficient mutational flexibility in order to be able to compete successfully with a changing environment. Some organisms, like e.g. bacteria, have a molecular machinery which within some limits adapts the rate of mutation to the needs dictated by the environment.

## 1.3. Cooperation of competitors

Replication introduces competition and selection into an ensemble of replicating elements whatever they are, polynucleotides, viruses, bacteria, higher organisms etc. The properties which are relevant for multiplication are readily optimized by the mutation selection mechanism. In biology we find nevertheless examples of cooperation between species or between simple replicating elements. Such examples of "symbiosis" range from unlinked genes in some RNA viruses like influenza or reo to the complex regulation of behavioural traits in animal societies. We turn to general mechanisms which can suppress competition between replicating individuals.

The principle of cooperation we are searching for can be put into simple words: competition is suppressed by mutual dependece. Mutual dependence is introduced by catalytic action on replication. This catalytic action can be direct or, more likely,indirect via an intermediate. Inevitably, we have to deal with complex autocatalytic reaction networks. Most of these networks are unstable. The simplest stable reaction system consists of a closed positive feedback loop called a "hypercycle" (figure 3).

Hypercycles integrate their elements into a new dynamical unit: the elements lose their independence, the ensemble grows as an entity and exercises control on the relative abundance of its members. Hypercyclic coupling thus offers a possibility to increase the genetic information content of the system. the increase in coding capacity, in general, allows to acquire new properties at the level of the higher hierarchical unit which were not present in its elements.

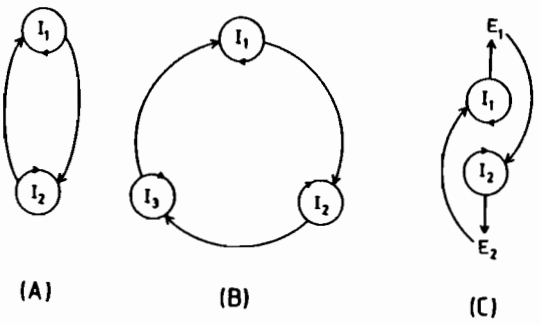


FIGURE 3 Examples of hypercycles. Hypercycles are dynamically organized ensembles of replicating elements which cooperate Competition is suppressed by means of mutual dependence. A: a two-membered hypercycle, $I_1$ catalyses the synthesis of $I_2$ and $I_2$ that of $I_1$. B: In the three-membered hypercycle we have cyclic catalytic dependence: $I_1$ favours $I_2$, $I_2$ favours $I_3$ and $I_3$ favours $I_1$. C: The catalytic effect is exerted by intermediates $E_1$ and $E_2$. These intermediates are produced under direct control of the replicating elements $I_1$ and $I_2$. In case $I_1$ and $I_2$ are polynucleotides and $E_1$ and $E_2$ proteins the entire functional unit is called hypercycle with translation (Eigen & Schuster, 1979).

Hypercycles have also other properties which are particularly interesting for evolution. The internal stabilization happens at the expense of the total rate of replication of the system. The regulated ensemble grows below optimum. Hypercycle formation, thus, pays off only if the integration of its elements is accompanied by a great evolutionary advantage. The evolution of hypercycles is different from Darwinian evolution in the sense that the optimization process is subjected to restrictions. Once a hypercycle has been selected it is not likely to be replaced by a more efficient mutant hypercycle but it can be enlarged by a mutation-incorporation mechanism (figure 4).

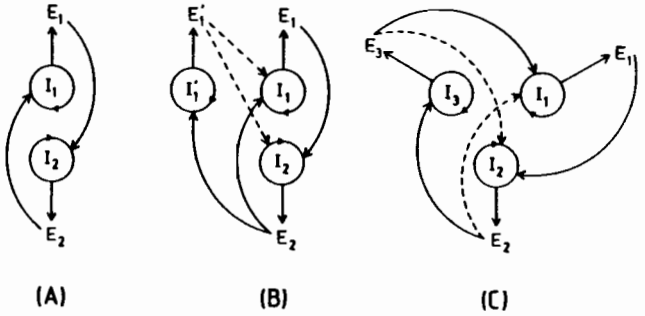


FIGURE 4 A mutation-incorporation mechanism for stepwise extension of hypercycles. A: A two-membered hypercycle with translation B: A mutant of $I_1$ denoted by $I_1'$ appears, it has certain catalytic effects on the replication of $I_1$ and $I_2$; C: Extension of the hypercycle occurs if the mutant has the following two properties: (1) $I_1'(=I_3)$ is recognized better and/or replicated more efficiently by $E_2$ than $I_1$ is and (2) the translation product of $I_1'$ $(=I_3)$, the protein $E_1'$ $(=E_3)$, is a better catalyst for the replication of $I_1$ than $E_2$ is. Then, we have mutual enhancement prevailing in the sequence $1 \rightarrow 2 \rightarrow 3 \rightarrow 1$ which is the condition for a three-membered hypercycle.

Evolutionary development through hypercyclic organization makes "once for ever decisions" and gives rise to "frozen accidents".

## 1.4. Spatial boundaries of organized ensembles

The molecular systems discussed so far were open to diffusion and free exchange with the environment. This property is definitely an advantage for primitive systems since it allows for metabolism without use of elaborate material transport systems through compartment boundaries. Later in development this advantage turns into a hindrance to efficient evolution. We illustrate the fourth principle of early evolution consisting in spatial isolation through compartment formation by means of a primitive replication-translation system in homogeneous solution (figure 5).

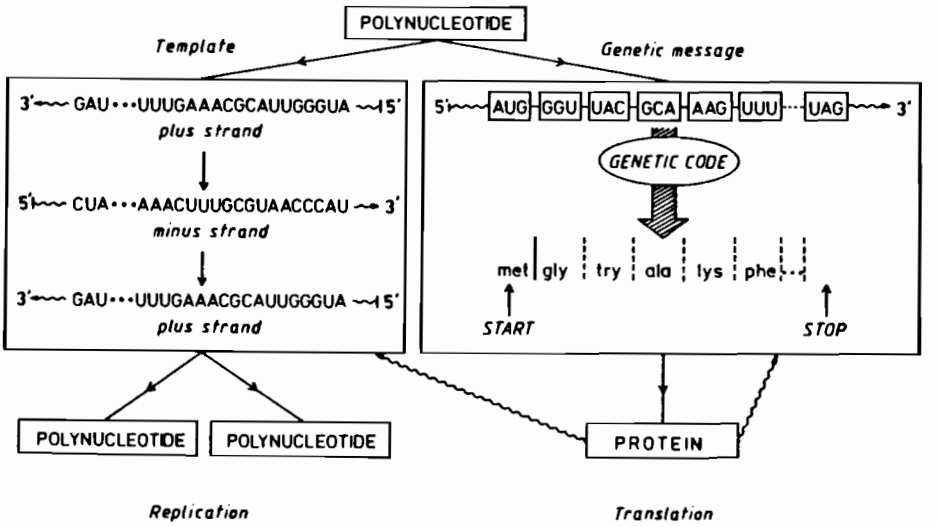


FIGURE 5 A replication-translation mechanism. The polynucleotide has a double function: it acts as a template for replication and as a genetic message for translation. In translation every base triplet has a uniquely defined meaning: the genetic code assigns either one of the 20 natural amino acids or a stop signal to a given triplet. Since we have 64 codons (these are the 64 three letter words built from the four letters G,A,C und U), and 21 meanings the code inevitably is redundant. Several codons may encode the same amino acid; there are three "stop" codons UGA, UAG, UAA. The start of the message is encoded by AUG, a triplet which internally codes for the amino acid methionine. An interesting detail, replication proceeds from the 3' end of the template towards the 5' end, translation in the opposite direction from 5' end to the 3' end of the message. Proteins assist as catalysts all steps in replication and translation. In the cell, translation is performed on the ribosome, a complex built from many proteins and a few RNA molecules. The connection between the genetic message and the amino acids is established by specific adaptors. These are small RNA molecules, the transfer RNA's.

In such a functional unit we can define two classes of somewhat idealized mutations which we call "phenotypic" and "genotypic" (figure 6).

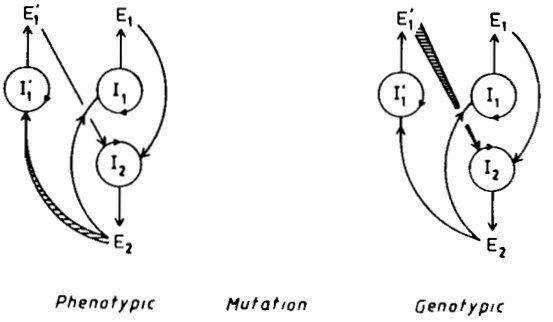


FIGURE 6 Two idealized classes of mutations in primitive replication translation systems. A "phenotypic" mutation leads to mutants ($I_1'$) which are better targets for the specific replicase ($E_2$) than the wild type ($I_1$) whereas the properties of their translation products ($E_1$ and $E_1'$) are almost the same. The "genotypic" mutation on the contrary, is characterized by a better translation product but roughly unchanged recognition by the replicase $E_2$.

A phenotypic mutation in a polynucleotide sequence causes a change in the tertiary structure of the molecule.Changes at the recognition sites of enzymes are of particular importance. In consequence of a phenotypic mutation the polynucleotide becomes a better or a worse target for replication. Selection sets in and, in general, the phenotypic properties are gradually improved until they attain an optimum. Phenotypic mutations play an important role in the evolution of viruses, particularly of RNA bacteriophages: specific recognition of viral RNA and the corresponding RNA-replicase is a conditio sine qua non for efficient RNA replication in the host cell. The role of phenotypic mutations in bacteria or higher organisms is not as clear. Presumably, most of the mutational changes in the tertiary structure of DNA are lethal. By definition, a phenotypic mutation has very little or no influence on the proteins which are synthesized through translation of the genetic information.

The consequences of genotypic mutations are just the opposite in this respect: they lead to changes in the translation products without substantial modification of the polynucleotide's tertiary structure. Selection for advantageous genotypic mutations is inefficient in homogeneous solution: the better translation product does not increase the fitness of the mutant which carries the information for it exclusively, but its presence is also to the benefit of less efficient variants as well as other non-integrated replicating elements in the environment.

Evolution is thus driven towards spatial isolation of the functional unit. This is achieved by the formation of a semi-permeable[2] boundary between the

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[2] "semi-permeable" we characterize the property to allow diffusion of small molecular weight compounds like nutrients and metabolites but to act as an impenetrable barrier for macromolecules like nucleic acids or globular proteins. In case of the ectoderm of higher organisms, obviously, cells play the role of nucleic acids.

functional unit and the environment. Such boundaries are commonly observed in nature: cell membranes and cell walls in prokaryotes, ectoderms or skins in higher, multicellular organisms may serve as examples. Compartment formation is accompanied by a number of structural and organizational problems which do not occur in homogeneous solution. They were discussed extensively in a previous review (Schuster, 1981) and, hence, we do not repeat them here.

Compartment formation is not the only mechanism leading to structural integration and spatial isolation although it is the most plausible one and the one we see realized everywhere in nature. Formation of tightly bound molecular complexes may serve as an example for an alternative.

### 1.5. Formation of higher hierarchical units

A combination of the four priciples presented here serves as a model for the formation of new hierarchical units. Initially, the replicating elements at the lower hierarchical level compete and properties relevant for replication are optimized by Darwinian evolution. The system runs into a temporary evolutionary "dead end" when the coding capacity is exhausted at the error threshold. We illustrate this dead end of evolution by means of a vicious circle: in order to construct a better phenotype we would need more coding capacity. In order to be able to replicate a higher number of digits we need a more accurate replication machinery. In order to build such an improved machinery we need more coding capacity. Hypercycle formation is a way out of this dilemma. Several information carriers can be present at the same stage of development because competition between them is suppressed. New abilities appear as a consequence of the enlarged, joint coding capacity. Evolution now follows special laws of restricted optimization. Finally, the new functional unit is coupled structurally by formation of a spatial boundary to the environment. Then, an ultimate stage of the integration is attained: the new unit replicates as a compact entity. The system is back to Darwinian evolution which operates now on the unit at the higher hierarchical level.

## 2. REGULARITIES AND RANDOMNESS

We need a conception of randomness in evolution which is different from that in algorithmic complexity theory. It is necessary to distinguish instructed and non-instructed synthesis of biopolymers. We shall use the term "instructed" in the narrow sense of template instructed, the template being the genetic information stored on a polynucleotide. Polynucleotide replication, to give an example, is instructed and so is also protein synthesis on the ribosome (Figure 5). Spontaneous, template free polymerization is a case for non-instructed synthesis. The formation of the first polymers in the primordial soup clearly was such a non-instructed process.

Non-instructed processes lead to regular or random sequences depending on the thermodynamics of neighbourhood relations and the detailed kinetics of the polymerization reaction. Examples of such regularities are well known in macromolecular chemistry: polymerization of mixtures of monomers sometimes lead to block polymers ..AA...ABB...BAA..., sometimes alternating sequences ...ABABAB... are the preferred products. Regularities were found also in the sequences of protenoids (Fox et al.,1982). Here, we are basically interested in instructed synthesis of biopolymers. Hence, we shall concentrate on these processes from now on and try to define randomness accordingly.

Instructed synthesis of biopolymers is regular in case it is error free. Replication and translation errors give rise to randomness. Replication errors in this respect are more critical than translation errors: a translation error gives rise to a modified protein, but it is like a solitary accident since it is not conserved. Replication errors, however, are transmitted as mutations to the next generation (provided they are not lethal).

The problem of error propagation has been discussed extensively in section 1.1. There we recognized two domains, one at high and one at low accuracy of replication, which are separated by a remarkably sharp transition region.

Perfect replication (q=1) is completely determined, completely non-random. The degree of randomness of the quasispecies increases with decreasing accuracy measured by q<1. Let us consider the structure of a quasispecies more closely: the frequency at which a given mutant sequence is present in the stationary distribution is a function of the probability of mutation and the fitness of the mutant. Thus, the mutant spectrum of a quasispecies has a regular structure which favours those mutants which are better adapted (for details see Swetina & Schuster, 1982; Eigen et al.,1984).

Beyond error threshold ($Q < Q_{min}$) we have random replication or, in other words, zero regularity. All sequences have equal probability no matter what their fitnesses are.

Efficient evolution as we see now requires both regularity and randomness. Regularity is warranted by conservation of sequences through correct replication, randomness by the appearence of mutations.

## 3. FROM EVOLUTION OF MOLECULES TO MOLECULAR EVOLUTION

The experimental approach to the evolution of molecules in the test tube was initiated by Spiegelman and coworkers (for a review see Spiegelman, 1971). They started with RNA from the simple bacteriophage Qβ and transferred it into a test-tube which contained a solution of the specific enzyme Qβ replicase and activated monomers, the nucleoside triphosphates GTP, ATP, CTP and UTP, in large excess. Instantaneously, RNA synthesis sets in. An open system is provided by serial transfer technique: after a given period of replication a small sample is transferred into fresh solution in the next test tube. This procedure is repeated many times - hundred times or more if necessary - until stationarity is attained. During such a serial transfer experiment the RNA is modified and the rate of RNA synthesis increases stepwise until it reaches an optimum value. More recently, these in vitro evolution experiments have been studied in great detail (for a review see Biebricher, 1983).

Evolution experiments in the test-tube have shown that a mixture of polynucleotide sequences fulfils the criteria of Darwinian evolution provided the necessary boundary conditions are granted. With respect to the capibility of optimizing fitness through mutation and selection there is no basic difference between these molecules ("naked" biopolymers), virus particles or bacterial cells. These studies on evolution of molecules provide an experimental test of the evolutionary principles presented in sections 1.1 and 1.2.

What about the other two principles? It would be extremely interesting to find a laboratory system in order to check the predictions of sections 1.3 and 1.4.

This, however, is not so simple. In vitro systems for replication and translation have not been developed so far although they seem to be within the range of present day technical possibilities. One major problem concerns messenger induced ribosomal protein synthesis in the test tube. Cellular extracts sustain translation for rather short times only.

A first step towards genetic engineering on the RNA level has been made recently (Miele et al.,1983): the enzyme recognition site of Qβ RNA is split off and "transplanted" onto another piece of RNA which is then multiplied by Qβ replicase. By means of the same technique it is possible to interchange the enzyme recognition sites of the RNA's from different viruses and thus design a first laboratory hypercycle.

Laboratory evolution experiments on replication in primitive compartments are even more sophisticated. The present stage of membrane assembly has been reviewed by Lodish & Rothman (1979). This process is extremely complex and we have to wait for future developments in this area.

The four principles of early evolution presented in section 1 were applied to questions of prebiotic evolution concerning the origin of translation and of the genetic code (Eigen & Schuster, 1982). Oligoribonucleotides with uniform stereochemistry, once formed in the primordial soup, will act as templates and instructed replication starts. Here, we assume implicitly that these oligomers had a tertiary structure which was sufficient to avoid double strand formation.

Then, Darwinian evolution of these small, replicating RNA molecules leads to chain elongation and adaption of the molecules's tertiary structures such that the fitness function becomes optimum under the conditions applied. From the experiments on enzyme free template induced RNA synthesis (Inoue & Orgel, 1983) we can estimate a mean single digit accuracy about $q \simeq 0.99$. Consequently, stable replication is limited to polynucleotides not larger than about $\nu_{max} \simeq 100$ bases. This is approximately the length of present day t-RNA molecules, the smallest RNA molecules found in present day cells.

An interesting detail concerns the pentose unit: attempts to use deoxyribonucleotides instead of ribonucleotides in enzyme free replication experiments failed to give significant amounts of oligomers so far. This finding together with the fact that the deoxyribose is particularly difficult to synthesize in enzyme free systems, suggest DNA being a latecomer in early evolution. The first replicating elements seemingly were polyribonucleotides.

What does such an early prebiotic scenario look like? Presumably we have t-RNA like molecules replicating when enough activated monomers are available, being degraded under conditions favouring hydrolysis. Soon, the optimum tertiary structure with a fitness function as large as possible is found and prevails together with its mutant distribution. Once in a while it is replaced eventually by a neutral mutant. A single master sequence of a maximum chain length of 100 bases does not provide enough coding capacity to develop a translation machinery. Several sequences are required.

We suggest the next step consists in the formation of a hypercycle out of several well adapted sequences. They might be members of the same quasispecies or they might be neutral mutants, accidentally present at the same time. Hypercycle formation in this model is accompanied by the origin of primitive translation using a primitive genetic code. We have to imagine a translation machinery which is by far less perfect than that used in present day cells which distinguishes as many as 20 amino acids with high precision. Assume that the code contained only few amino acids and that precision was low, just enough to allow instructed synthesis of polypeptides which were better catalysts than the other materials around.

How can we learn more about this important stage in our model of the origin of primitive organisms? Direct evolution experiments seem to be not practicable at present, ordinary fossils of this early period have not been found yet. Alternatively, we could search for "intellectual" fossils, for remnants of the early period which are still hidden in present day biochemistry. One tool in this direction is to be found in comparative sequence studies of biopolymers, nucleic acids and proteins, in different organisms which were applied successfully to the reconstruction of phylogenetic trees. This divi-

sion of biochemistry commonly called "molecular evolution" was extended also to the sequences of t-RNA molecules (for a recent review see Cedergren et al., 1981). Eigen & Winkler-Oswatitsch (1981) conclude from such sequence alignment studies that the t-RNA molecules originated from one or from a few closely related ancestor molecules. Their reconstruction of the early sequence is supported by other comparative studies of polynucleotides which revealed an interesting periodicity in the base distribution of period three (Sheperd, 1981). This periodicity is interpreted as a remnant of an ancient reading frame of primitive translation which is of the type RNY (R stands for a purine base, G or A, Y for a pyrimidine base C or U and N for any of the four bases). Putting together these results and the general demand of strong codon-anticodon interaction, which means as many GC pairs as possible, we obtain four primordial codons

GGC = gly (glycine)

GCC = ala (alanine)

GAC = asp (aspartic acid) and

GUC = val (valine).

It is interesting that the model suggests these four codons being the first which code for the four amino acids which are most abundant under prebiotic conditions. Later, more amino acids were incorporated into the primitive translation machinery (Eigen & Schuster, 1979; Eigen et al., 1981). Finally, an optimum was reached at the present number of 20 amino acids: the effort to extend the translation system further was no longer worth the improvement of the catalytic efficiency of the proteins.

The molecular mechanism of primordial compartment formation is even less clear. The following speculation is guided by the idea of a smooth transition of prebiotic reactions to present-day biochemistry. Much of our knowledge on the assembly of cell membranes is taken from studies on animal viruses (Lodish & Rothman, 1979). The virus particles are formed from the host cell membrane, which serves basically as a reservoir of lipids, viral RNA, viral proteins, viral glycoproteins, and a specific matrix protein which again is encoded by the viral RNA. Thus, by means of a few proteins a membrane coated particle is formed from the relatively large pool of lipids in the host cell membrane. Indeed, most proteins have other functions and eventually, the matrix protein is sufficient to initiate vesicle formation. Let us assume that lipids or related compounds were present in the primordial soup, which is very likely since similar molecules were isolated from meteorites. The replication-translation machinery might succeed to produce a polypeptide with similar properties as the matrix protein. Then, vesicle formation is induced and in a situation of proper statistics the whole machinery could itself be enclosed by the membrane. Further protein production may lead to growth of the membrane, eventually to division of the system which controls already in part the process of membrane formation. These compartments have already the characteristic features of individuals and can be considered as a kind of protocells.

In order to summarize the model of early evolution we present a sketch of critical stages in figure 7.

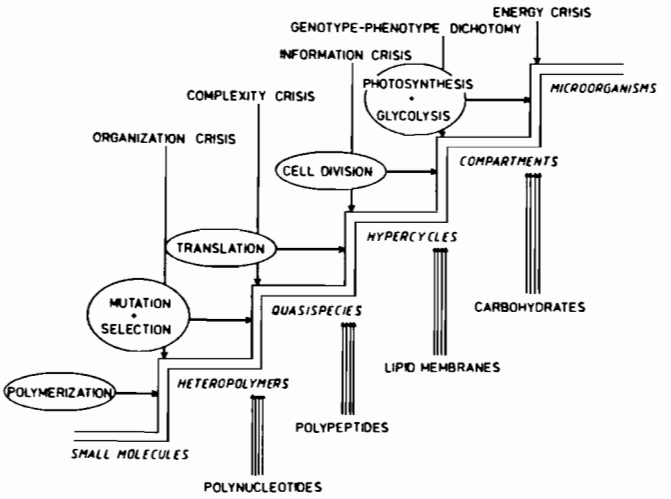


FIGURE 7 Five critical steps during evolution. On its way from small molecules to microorganisms the evolving system had to pass at least the five "crises" shown above. A "technical" innovation or new principle helped to get out of a dead end the system previously had run into. The new concepts are surrounded by ellipses in the sketch. Instruction is the basic concept of early evolution. The molecules becoming part of the instructed system are shown below; they flow into the main stream of evolution class by class at the individual steps.

The expression "crisis" is chosen to indicate that a new principle had to come into operation in order to get out of a "dead end" into which the previous development had run. The various crises represent a logical sequence of steps in prebiotic evolution from a mixture of small molecules to the first prototypes of procaryotic cells.Each of these steps requires the achievements of the previous ones, although two or even more have been taken at nearly the same time during the historical course of prebiotic evolution. It is necessary to stress one point in order to avoid misunderstanding: some of the critical steps incorporate new materials into the evolving system. For example, polypeptides came under control of the replicating system when the translation machinery started to operate, membranes when the first instructed compartments were formed. The utilization of sunlight became possible after the primordial energy crisis had been surmounted through the development of the photosynthetic machinery. Emphasis is laid on the formulation "came under control of the replicating system". We indicate thereby that polypeptides, lipids and membranes, energy rich compounds must have existed as necessary environmental factors and were used as resources before the replicated molecules "learned" to get control on these essential constituents of present day life. This control consists of the instruction of polypeptide synthesis through translation, of membrane synthesis and cell division, and of the development of various primitive metabolic pathways in order to utilize the environmental resources.

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# AUTOGENESIS: THE EVOLUTION OF SELF-ORGANIZING SYSTEMS

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## 1. INTRODUCTION

In order to study dynamic macrosystems like the biosphere, appropriate models are needed. Usually the mathematical models are most appreciated because of their unambiguous logic, relative structural simplicity and their well developed deductive verifiability. Nevertheless these elegant tools have some inherent drawbacks. They are not flexible enough, usually not suitable to describe really complex phenomena and they are not creative in a broader sense. Therefore the first step in model building is always to construct an intuitive model which, by its nature, is able to embody ambiguities, contradictions and descriptions on different levels. The intuitive model therefore might be appropriate to reflect a satisfactorily complex part of reality, securing the possibility of a further, more rigorous mathematical treatment. Theories of enormous influence such as behaviorism and the theory of evolution were nonmathematical and their impact far exceeded those occasional mathematical constructions which appeared later in their development and covered only particular aspects. It is also well known that logico-mathematical theories are tautological in the sense that they are derived analytically from a set of axioms and therefore they are unsuitable to prove the validity of an intuitive theory. In many cases the bright armor of mathematics only helps to delay the recognition of the inherent weakness of the intuitive theory. This does not mean at all that mathematical models are useless in biology, we only want to emphasize the basic primacy of the models of intuitive kinds in relation to mathematical ones which are only auxiliary tools and are not able to exceed the former.

## 2. PROBLEMS IN MODELLING LIVING SYSTEMS

The greatest achievement of the developing biological sciences is the realization of the system property of the living world. Nowadays it seems quite obvious that the problems of biology can be understood, can be solved only by treating the whole biosphere as a systemic unity. In spite of the wide perception of this evidence, a general theory of biology has yet to be born.

Four criteria can be formulated for such a general theory:

1. It has to explain the origin of the organizational levels from the genome to the level of ecosystems and the maintenance of the living systems.

2. It has to explain the history of the living system, that is, evolution.

3. It has to explain the direction of evolution in the past and in the future.

The traditional models developed by physiology, ecology and molecular biology solved some of the above mentioned problems but we still do not even have a general theory of the organism. The nature of the genetic code has been discovered, but the "text" written in the genome can not be read in spite of the spectacular advances of molecular biology. We have gained knowledge from the smaller part of the genome, mainly from structures coding proteins, but from the genetic process of the higher organisms we know almost nothing. Most of the genome is unknown. There are hints that the code is only a kind of alphabet and there must be a grammar of the genetic information, which rules expressed as special restrictions on the basic nucleotide sequences (Gatlin 1972, Rowe and Trainor 1983). This grammar resides at higher levels of control and regulation. The molecular level which once seemed to provide an excellent "atomic" basis for smooth extrapolation, now demands hierarchical interpretation itself.

The problem of the origin of life is a very actively studied field but production of life in the laboratory has not yet been achieved. It seems that the theories directing practical research are inappropriate. Eigen's model applying advanced mathematics, but principally operating with the simple conceptions of mutation and selection has not led to new discoveries (Eigen 1971).

Our knowledge is even more humble concerning the origin and extinction of the species. We cannot explain why certain families of species have an enormous diversity, while others have none (Willis 1940). Why do certain species live for hundreds of millions of years, a long time even in evolutionary sense, while others have become extinct in a relatively short period of some millions of years (Stanley 1975)? It is clear that regulatory forces are acting above the level of organisms and species but these are not reflected in our theories.

The Darwinian model of evolution is the basic theory in biology, the "general" model, but it was heatedly discussed by the biologists recently. Only minor corrections according to the recent development is needed by some (Maynard-Smith 1982), while an entirely new paradigm is advocated by others (Gould 1980, Eldredge 1979).

The modern neo-Darwinian theory operates by two basic postulates:

a. the variability of organism is caused by random mutations of the genome

b. the ensemble of mutants changes upon the forces of selection during geological times.

These are the assumed basic mechanisms of the origin of the species. Every regulatory factor of species evolution is supposed to act through mutation and selection. The evolutionary changes are always slow and gradual and most evolution occurs within established species.

Opponents of this view believe that punctuational change dominates the history of life. Evolution is concentrated in very rapid events of speciation. Most species do not change in any appreciable way (stasis) during their geological history (Gould and Eldredge 1977, Stanley 1979). It is firmly believed that mutation and selection are basic mechanisms of the living system, nevertheless they seem to be insufficient to solve the problems of evolution (Ho and Saunders 1979).

## 3. THE BIOLOGICAL SYSTEM, ITS PARTS AND THE PROBLEM OF REDUCTION

An appropriate model of a system has to contain representations of the system's components and algorithms which express the interactions of those components. There are many entities of very different organizations which are entitled to be components of the biological system. Species, populations, individual organisms or perhaps structures of organizational levels below the organism such as chromosomes, genes, nucleotides can be regarded as components. The choice of components can determine the domain of interactions encompassed by the model built upon them. If species are regarded as components then interactions among species and structures above them will dominate the model while by choosing nucleotide components the nature of interactions will be obviously molecular. Such a distinction in selecting the components was the basis of separation of various fields of biology, ecology, biochemical genetics etc.

Some of the contradictions in biology have just originated from various attempts to unite models of different organizational levels, for example the attempt to explain the origin of species by molecular interactions. Therefore it is not surprising that the most disturbing problems of current biology are connected with the problem of reduction. At the beginning, biology had been dominated by open or concealed vitalistic ideas, maintaining that there were particular laws governing biological phenomena and these laws were different in principle from the laws of physics and chemistry. Because of the many apparent weaknesses of the vitalistic ideas, a reductionist viewpoint has gained reign after a long and bitter fight. According to the reductionist view, all phenomena of biological systems can be ultimately reduced to chemical mechanisms in spite of their obvious hierarchical organization (Crick 1967). The spectacular boom of molecular biology was regarded as a proof of the reductionist view. Without diminishing the achievements of molecular biology that proof can be questioned. The problems of the Darwinian theory of evolution are rooted exactly in the problem of reduction. The simple explanation of the origin of species by nucleotide changes and selection has failed (Williamson 1981). The reductionist standpoint is more and more criticized. Besides mutation and selection at individual level, the random origin of species and particular mechanisms of species selection are assumed by Gould (1980) which can not be reduced to molecular level. This is in agreement with Stanley who emphasized the decoupling of the processes of micro- and macroevolution (Stanley 1975).

The antireductionist viewpoint was articulated most clearly by Polányi, writing that: "Mechanisms, whether manmade or morphological, are boundary conditions harnessing the laws of inanimate nature, being themselves irreducuble to those laws. The pattern of organic bases in DNA, which functions as a genetic code, is a boundary condition irreducible to physics and chemistry. Further controlling principles of life may be represented as a hierarchy of boundary conditions extending, in the case of man, to consciousness and responsibility" (Polányi 1968). This train of thought was also elaborated in detail by others (Rosen 1977, Primas 1977, Pattee 1967, Kampis 1984).

In our opinion, the algorithms describing the interrelationships of components according to the organizational levels are specific only at the given level. In a general model, in which all organizational levels are embodied, all effects computed by algorithms of the lower levels lead to random events in the event-space of the higher levels. The algorithms of the higher levels represent specific nonlogical constraints at the lower levels. Therefore models of biological systems are different by principle from models constructed for understanding phenomena of the physical world. In the following we shall illuminate the present use of the notion of algorithm.

## 4. BIOLOGICAL INFORMATION

The main problem with the reductionist standpoint is its ignorance of function, the basic concept in biology. The notion of function is in close connection with the level of organization. Function can be defined as constrains exerted by the ascending level's processes in the event-space of the descending level. The nucleotide triplets of, for example, the DNA, have functions: the direction of amino-acids into the protein structures. A given sequence of nucleotides in the DNA responsible for a protein structure is chemically not a particular set by all means. The sequence of this part of the DNA is not determined by the laws of the chemical affinity, but the function of the protein. Chemical affinity is only harnessed by this function in the same sense as it has been formulated by Polányi for the boundary conditions of the organizational levels. The appearance of functions is always the result of a decoupling process which decouples the interrelationships embodied in the function from the properties and relations of components of the lower level. The interpretation of function becomes possible only at ascending levels of the system. The function must always be formulated as an embodiment of description of constraints in the event space of the descending levels. Therefore the application of the concept of function in system models needs a proper informational theory. It was expressed very clearly by Rosen that a dynamic model of evolution cannot be constructed without the proper incorporation of the concept of function (Rosen 1973).

Pattee centered his argument around "traits" which were equivalents of functions and stated that the hereditary propagation of a trait involves a description or a code and therefore must involve a classification process and not simply the operation of inexorable physical laws of motion on a set of initial condition (Pattee 1967). Without accepting all of his conclusions we certainly agree in that the description of traits can be regarded as a kind of structural information. There are many attempts to introduce the concept of information into the models of biological systems. Quastler (1964) was the first to calculate the information content of various macro-

molecules at the advent of molecular biology but it only promoted the usage of information by others as a metaphore. Very attractive models of the living cells were built on the concept of information independently by Iberall and Libermann. The common property of both models is that the interactions among the components are regarded as a kind of grammar which emerges as the "mechanistic" linkages that can catalytically switch or evoke changed atomistic states in "soft" systems (Iberall 1983, Libermann 1979).

It is common in the various independently developed models that the function appears as a specific description, a kind of structural information, relevant only in the given system, not reducible to physical processes only harnessing them. The totality of the biological system and its functional components can be regarded as carriers of algorithms. Their interactions are computing processes prescribed by the algorithms. The question immediately arises: what the "meaning" of these algorithms would be? Later in this paper, we try to confirm our hypothesis that these algorithms are the algorithms of a selfreplicating process. A model representing biological systems must be constructed so that it represents the replication process of both the components and the whole system.

A new intuitive model, assumed to satisfy the above criteria, has been developed earlier (Csányi 1978, 1980, 1981, 1982). Discussion of the model in relation to others, especially to that of autopoiesis also has been published (Csányi and Kampis 1984).

In the following chapter we outline the essentials of the updated version of the model and discuss it from the point of relevance to problems of modelling the living systems.

## 5. THE REPLICATIVE MODEL

### Definitions and explanations

#### System

System is a finite physical space separated from the background by topological or organizational boundaries in which building blocks of physical components are present, components are assembled and disassembled and where there is an energy flux flowing through the system which is capable of exciting some of the building blocks. The number and types of building blocks present in the system, the energy flux etc. constitute the parameters of the system.

#### Zero-system

A system of components which have not yet developed functions is considered to be a 0-system.

#### Function

The ability of components to influence the probability of genesis or survival of other components of the system due to their relationships with the component producing or component-decaying processes.

Information

Information is a specific description of components on the basis of the arrangement of building blocks. Two main kinds of information are distinguished:

a. Parametric information

Components of a 0-systen are carrying a certain kind if structural information which is only a manifestation of the parameters in the system. This is called parametric information.

b. Functional information

Components endowed with function carry information to the system because their function is one of the determinants of the component-producing process; this information is in some way with the arrangement of building blocks in the respective components, i.e. it is a structural information. The structural information of components or part of a component bearing function is called functional information.

Replicative function, replicative information

In biological systems the most important function of the numerous possible ones is the replicative function. This term specifies an effect, owing to which the probability of genesis of the same component (or set of components) carrying the replicative function increases in the system. The structural arrangement of components which carry the replicative function is regarded as replicative information.

Organization

The network of interrelatedness of components and component-producing processes, i.e. the network of functions, constitutes the organization of the system:

Replication

Replication is understood as an imperfect copying process of the components, directed by information located either in the copied component itself or widely distributed in the whole system.

In the replicative process both the system and its components are produced.

In the copying process a constructor produces a copy (replica) of a component or the given system. The constructor needs a description, as the information necessary for this copying process. While the replication itself depends on the functional operation of this information, it is independent of the particular mechanisms of the storage and retrieval of this information.

In a replicative organization components are endowed with functions, which are expressed as functional information. In the component producing process regenerating the system, this information is also regenerated, and the process is guided by the very same information. Thus it is literally a self-copying process.

Two forms of replication are distinguished:

a. Temporal replication

Temporal replication is defined as the continuous renewal of the organism in time by the sequential and functional renewal of the components of the system while the unity and identity of the system is maintained.

b. Spatial replication

Spatial replication is identical to reproduction. The organism produces its own replica which becomes separated from it in space. From one unit, two units are formed.

In both temporal and spatial replication the same structural information is replicated. In temporal replication the structure of the system remains unchanged by the replication of components, in spatial replication the structure of the system is changing (duplicates) but in both the organization remains unchanged.

Fidelity of replication

Replicative processes are never error free. Replication can thus be characterized by its fidelity. If replication is precise by all parameters it is called identical replication. If fidelity can be expresses by a coefficient in (0,1) , replication is non-identical. In case of nonidentical replication either the structure of components or the component composition of the systen is different from the preceeding state.

Autogenetic system-precursor (AGSP)

AGSP is a minimal set of components which is able to replicate and which fulfills the following criteria:

a. It contains at least one cycle of component producing processes.

b. At least one of the components participating in this cycle can be excited by the energy flux flowing through the system.

## 6. OPERATION OF THE REPLICATIVE MODEL

In several articles it has been examined how the replicative model may operate (Csányi 1978, 1980, 1982). On the basis of various considerations and data collected from real biological systems it has been inferred that the functional content of a 0-system containing an appropriate AGSP will increase with the simultaneous decrease of the parametric information content. This process has been called autogenesis (Csányi and Kampis 1984). As time advances, an increasing part of the functional information becomes replicative information. This can appear only as an extension of AGSP, that is, additional replicative cycles appear which are interconnected with AGSP. These formations are termed hypercycles. As time passes, replicative coordination of hypercycles develops by increasing fidelity of replication. We can speak of some kind of functional differentiation and cooperation which results in the formation of communities of simultaneously replicating components, i.e. sub-systems called compartments form. The components of these are separated from others on the basis if their participation in co-replication. The emergence of compartments is accompanied

by the organizational, i.e. functional, closure of the network of component-producing processes and components having a replicative function. This succession of events is called the compartmentalization and convergence of replicative information.

Components and compartments embodying them may exist with different values of replicative fidelity. On a given level components may replicate with high accuracy, but the compartments formed by them with a low level of fidelity. As time passes the fidelity of the replication of both the components and compartments may increase and perhaps a next level of organization might be created, "compartments" of compartments are formed which also replicate with an increasing fidelity. A system may contain several different kinds of compartments, which are replicative units with diverse fidelity. Among these, interrelationships develop and, as a result, their replication becomes also coordinated. Gradually, the whole system will start replicating as a final replicative unity. In the autogenic process, the organization of the system (and of its parts) changes due to the function of existing components. Thus autogenesis is possible only if the state of identical replication has not yet been achieved. In that state, the system is functionally closed and its replication continues as long as the environment does not change. There are no further organizational changes initiated by organizational causes because new functions cannot originate. In the state of identical replication, the system is an autonomous, self-maintaining unity, a network of component producing processes which, through the functional interaction of components, produces exactly the same network which produced them. Its organization is almost closed and cyclic. Its input and output are subordinated to its replication, but, through them, its existence depends on the invariance of environment. The notion of function stresses that the end states of autogenic systems are not simply fixed points of some dynamic processes. Autogenesis is the evolution of active self-construction.

## 7. AUTOGENESIS AND EVOLUTION

A formal model of autogenesis was also formulated (Csányi and Kampis 1984) and probably it is suitable for a more rigorous mathematical treatment. But it was more important for us to collect data which demonstrates the practical value of this model in studying evolution. Our ideas and arguments were considered in the framework of a general theory of evolution (Csányi 1982). The main conception of that theory is the notion of replicative components which are both building blocks of a given organizational level and AGSP-s because they are able to take up energy and are members of replicative cycles. The evolution on earth began 3,5 - 4 billions of years ago when an evolutional 0-system containing molecules as components was formed. To the effects of various possible AGSP-s an autogenic process had started and the convergence and compartmentalization of replicative information commenced. As soon as the first compartmentalization takes place in the evolutionary system, the compartment becomes a new building block as a replicative unity. Replicative unities, commited inevitably to common material and energy resources, influence the probability of genesis of each other. They can be conceived as functional components in a new 0-system, where a new level of evolution starts exhibiting the demonstrated phases and phenomena of autogenesis. The autogenesis of different levels is interrelated, the functional information of the whole system (i.e. of all levels) is represented in the living unities. The constructive compartmentalization and formation of new levels continues until a unified macrosystem emerges that fills the entire available physical space and each component of which repli-

cates in perfect harmony, which identical probability to every other one. Thus the trend of the encompassing evolutionary process is toward the maximum of replicative information on a global scale. Then all autogenesis is at its end state.

Based on Csányi (1982), the levels of evolution on Earth are the following:

1. molecular
2. cellular — 2.a. neural
3. organismic — 3.a. cultural
4. ecological — 4.a. technical

On the level of molecular evolution, the convergence of replicative information gave rise to the cell as an autogenic compartment. The cell-compartment itself became the building block to form higher organisms on the organismic level of evolution. With the development of multicellular organism a further autogenetic unit appeared which was capable of absorbing energy as well as establishing interconnections between the individual components, i.e. forming higher organizations. Thereby a new evolutional level, a new 0-system emerged that led to the formation of ecosystems.The genesis of evolutional level does not, however, follow a linear trend: the interconnection of neurons, the excitable building blocks of the animal brain, may also result in more highly organized unities, i.e. conceptions. It is for this reason that the brain can also be regarded as an evolutional system with respect to the changes of its conception-components.This is what we regard as the level of neural evolution.Among the animals it is only man that is able to implant the almost identical replicas of conceptions formed in his brain into the brain of individuals of his own species. With the development of man the exchange, recombination and supra-individual replication of conception-components have also commenced. These supra-individual conception structures are called ideas and their evolution is considered to be the level of cultural evolution. In the society formed in the course of cultural evolution a "technical space" has come into being; this is a mechanism producing things, i.e. objects: its most important characteristic is replica-production. The production of objects is therefore regarded as a replicative process and the evolution of objects can be regarded as the technical level of evolution.

In the 0-system autogenesis spontaneously advances toward the increasing replicative information and it lasts until the whole system becomes one replicative unit. If the replicative unit thus evolved is smaller than the total physical space of the system, evolutional levels develop and the replicative information goes through a compartmentalization process. In the compartments the replicative information converges, and in the last phase of convergence the compartment itself becomes a replicative unit and a new level of evolution starts. This process continues until the extent of forces influencing the replicative processes reaches the dimensions of the whole system. In the early, molecular phase of evolution the appearance of functions capable of influencing the probability of genesis of molecules was the result of interactions of very weak forces. The effective range of these forces cannot be greater than a couple of centimeters. The dimension of the first compartment, the cell therefore does not exceed some cubic centimeters. Interactions, regulating connections between cells, are already effective at a distance of several meters, so the dimensions of the next, organismic compartment may reach several cubic meters. In the ecosystem

the dimensions of effects influencing the probability of genesis of the individual structures may extend to several hundreds of kilometers, thus the area occupied by individual ecosystems greatly increases (up to thousands or millions of square kilometers) but it has not yet reached the physical dimensions of the entire biosphere. Our analysis revealed that the autogenesis of the ecological compartment is in the late phase of non-identical replication. In side branches of evolution, specifically during the development of human society, have appeared those regulatory forces that have now reached or even exceeded the physical boundaries of the system. The appearance of regulatory forces like these will inevitably lead to the formation of a uniform global system. This uniform system includes the man-regulated biosphere, as well as human society itself.

## 8. ADVANTAGES OF THE REPLICATIVE MODEL

In chapter 2 the criteria for general models of living system were formulated. The evaluation of our replicative model follows accordingly.

### a. Origin of the organizational levels

The most important conception of the replicative model is the function which is usually avoided by biological theories (see the neodarwinian idea) or is expressed as a mere description in the various models based upon traditional physiology or molecular biology. The main problem with function is that it appears in different forms in each organizational level and actual domain of interactions. The usage of a common explanatory principle seemed to be impossible. In the replicative model such an explanatory principle was formulated. The general formula of function for all organizational levels is the replicative function. Advantages of the conception of the replicative function is that its general formulation permits an abstract treatment of all organizational levels and the same formula is suitable to express interactions on any actual level. Instead of avoiding it the function itself became the basis of the model.

Another great problem in biological modelling is the qualitative, "all or nothing" character of the biological function. We hope that by introduction the concept of fidelity of the replicative function this problem is diminished. The replicative function constrained by fidelity is suitable for both qualitative and quantitative expression of biological function and even it can reflect the integrability of the various effects, without becoming a mere tautology, like fitness in the neo-Darwinian theory.

The appearance of organizational levels in the replicative model followed unequivocally from the action of function. This shows again the advantage of the replicative model. Replicative function expresses interrelationships among components in a given organizational level and with the formation of a functional closure (convergence and compartmentalization of the replicative information) it creates new components for the next level, formulating a hierarchical structure by continuously acting factors of the same organizational logics.

In the replicative model all kinds of entities of actual biological systems can be represented. Molecule, cell, organism, ecosystem, hierarchy is formulated on the basis of a unified organizational principle.

We assume that when worked out in proper depth, the replicative model will be suitable both for modelling subsystems and serving as a general model of the total biosphere.

In most biological theories the connection of function and the lower levels of organization providing the action space for that function is always problematic as we discussed in chapter 3. In our opinion the replicative model, which treats function as information solved this problem. The function as an interrelationship influencing the probability of genesis of components of given organizational level is free from the condition of reductibility and any vitalistic notions.

Biological-information is treated as algorithmic in its nature by the replicative model. Each compartment of the system and the whole system itself carry the algorithms of selfreplication as structural information and its existence and actions are the computing process of this algorithm. In that way the general description of biological systems had been set free from the burden of the almost unlimited complexity characteristic of objects of the physical world (see the ontological and semiotic complexity of Bunge 1963) and only the description of the algorithmic complexity - a kind of semiotic complexity - will be its sole content. Cognition of this algorithmic complexity, cognition of the biological world based upon the notions above can be complete at last in principle. In this notion algorithm and information are not mere metaphores which somehow have to be reduced to chemical and physical laws but the way of existence of the biological system, which is independent from the physical world. There is no contradiction with the fact that if we are dealing with biological objects then of course we need to study the chemical and physical interaction occuring in these objects.

b. History

The early phase of biological modelling was ruled by the notion of environment-organism dichotomy. It was expressed in the broadest scale in the biological sciences: in the nature / nurture problem in psychology, in the problem of inherited / acquired mechanisms in genetics and especially important in the evolutional theory-Darwinian/Lamarckian mechanism.
In studying the various organisms, they were separated from the biological system and all remaining factors of that system were regarded as environment. But because both species and organisms are mere components of a higher system which operates with components and interactions, solving these problems, even understanding them were impossible. The replicative model clearly implies the fact, that for any given organism the presence of others is the most relevant environment factor. The evolutionary changes of an organism can be interpreted only in a system of positive feed-back loops. The replicative model contains this positive feed-back in the form of function. Of course abiogen factors of the environment are preconditions of its existence but are aspecific regarding its organization. The replicative model in that regard is very close to the niche theory developed to its modern form by Hutchinson (Hutchinson 1978). The niche is a region of a multidimensional niche space, the axes of which represent all the possible environmental variables. It is quite possible that the niche can be transformed into a construction of replicative information. The niche can be regarded as those parts of the replicative information of an organism which are outside of the organism in a distributed form.

The connection between the finely adaptive structures of the living organisms, like the eyes, and the chance variation of nucleotides of the

neodarwinian theory never has been clear and many biologists believe in its nonexistence. In the replicative model the information content of structures like that are carried not only by individual organisms but exist in a distributed form in the whole system - replicative information is highly redundant like a holographic code. The eye is originated as an algorithm solution of a given task for the organisms and later both as a solution and as a condition was able to influence other changes in the system. By the effects of its long range presence, the functional network of the whole system has changed and beside, the information of the adaptive structure as a structural information in the genome of the organism was represented also, like a mirror image in the network of functional information of the whole system. Most of the interrelationships of the animals are characterized by the concern to their visual ability. Such distributed and continuously acting information promotes the conservation of the given adaptive structure, or its reinvention in case of apparent loss. The conception of the "empty niche" of Hutchinson is very close to this comprehension of the adaptive process. The empty niche might be characterized by replicative information which is an active agent of evolution.

Creativity of the evolutionary process which always caused much worry to theoreticians can be explained by the interrelationships of the algorithmic information stored in the components of the replication system. Until the whole biological system has not reached the state of identical replication the possibility remains that new forms of interactions or new components arise and become stabilized in the subsequent replicative cycles. Therefore the replicative model is a creative model.

c. Origin

There is no accepted mechanism or even theory of the origin life. It is a general view that life originated spontaneously and the existence of a suitable set of chemical processes as the only condition for the initiation of life is assumed. Models are built upon the assumption that nucleic acid-protein complexes with the primitive but well recognizable ability to propagate themselves appear by mere chance, and the question of their subsequent evolution seems to be the only question worth of examination (Eigen 1971). This is certainly a naive assumption from the viewpoint of biological thinking because the really exciting question is just how this self-propagating system of the nucleoproteins came into existence. In a broader sense it is the question of the origin of the biological information. We can envisage how this information might propagate but we haven't yet known the answer to its origin. With some considerations the replicative model can be used for modelling the origin of life. The new aspect in this is the notion that the replicative model is a system model and doesn't serve the study of the origin of given components (molecules). The main question can be formulated as whether the conditions of the primeval Earth can satisfy the preconditions of an autogenic O-system and whether the presence of a spontaneously occured autogenetic system precursor can be proved.

The origin of the most primitive selforganizing system can be found not by studying the nucleoprotein systems which most probably appeared only in a later stage of the evolution of the O system but by examination of those chemical processes which were suitable to act as system precursors, that is, which were suitable for excitation by the radiaton of the Sun and were members of cyclic processes. Such chemical processes are quite well-known (Morowitz 1968).

Cycling energy transferring chemical processes contain a small amount of replicative information. Very minute, even seemingly negligible amounts of replicative information can be sufficient to start autogenesis according to our replicative model, at the level of nonidentical replication with a very low value of fidelity. During the convergence and compartmentalization of the replicative information those components as DNA, RNA appeared which carry most of the replicative information now.

d. Direction of changes

It was always perceived by biologists that evolution has some direction at least in the form of ever increasing complexity, but this feeling had never been supported by models with appropriate deductive power. Study of the details of the evolutionary process some times showed backward steps or branches and the existence of any direction has also been doubted. The nucleotid changes of the neo-Darwinian theory do not even hint at any directed process of the ascending levels of the organization. The replicative model, however, predicts well defined directions. The direction of changes leads to the maximalization of replicative information in the whole system by autogenesis. In the early 0-system with autogenesis started, replicative information rapidly approaches its maximum level and the system approaches, most probably via information of the cell compartment, the state of identical replication. The complexity of the system has reached now a fairly high level.

The established organization can be discontinued by two tendencies. One originates from inside the system. The replicative information which is converged in the cell compartment, i.e. the cell itself, represents a new system precursor. This system precursor, in turn, due to its probably higher replicative information content than the previously existing AGSP, starts a more rapid, more effective autogenesis at a new level, leading to the formation of the multicellular organismic compartment. Furthermore, according to the above discussion, the organism itself also forms a system-precursor and the autogenesis of ecosystems starts, in the course of which the rapid maximalization of replicative information leads to an ongoing "equilibrium" state, occasionally lasting as long as millions of years.

It is known from paleontological records that evolution has not preceeded so regularly and gradually. When the biosphere, being in a state of quasi-identical replication is subjected to a gigantic destructive effect (volcanic eruption, influence from space, drastic changes in climatic conditions, etc.), a part of its components, coordinated with respect to the replicative information, will be destroyed and the identity of the system disappears. If the interruption did not abolish the condition for life, then a new autogenetic process may commence. The less damaged parts of the biosphere will serve as AGSP and initiate the new autogenesis. The functions of the untouched components "search" the possibilities of rejoining the replicative chain and new cycles, a new type of organization will emerge. It is evident that the more complex the original biosphere, the more complex system-precursors will remain intact even after devastation damage. It follows that autogenesis following the damage elevates the system to a higher level of complexity, altough such an intervention itself probably cannot establish a new evolutional level. This accidental, yet quite often occuring external intervention might be the underlying reason for the high complexity of evolution on Earth. Our proposed mechanism is in agreement with the "punctuated equilibria" theory of evolution. The conception of stasis most probably reflects the phase of quasi-identical replication of

macro-evolution. In the course of stasis the individual species do not exhibit remarkable alterations. Sudden changes among stases are, in turn, the result of autogenesis - as suggested above. In the final shaping of complexity, however, both the external and the internal factors may play an important role. The inner factors of the system promote the increases of complexity until the dimensions of the regulatory forces of the system have reached the dimension of the physical space of the whole system. After the total system has reached the state of identical replication only outer factors can cause any perceived change in the system.

## 9. CONCLUSION

The replicative model was formulated on an intuitive level and its further development needs much refinement in that level. It has to be confronted with every other serious theory. We assume that the model perhaps in its present state is suitable for a rigorous mathematical formulation and then many assumptions of the model can be deductively tested. It would be also worth to try to apply the model to the simulation of concrete systems (cell, ecosystems, culture, etc.) to see whether its predictions may be used for practical purposes.


## Summary

Problems of modelling biological systems were analysed concerning formulation of a general theory of biology. Questions of systems theory, possibilities of reduction, origin of hierarchical levels of organization were discussed. An intuitive model based upon replication and functional information was presented. It has been examined whether this model satisfies the four criteria formulated for a general theory, namely serving as explanation for maintenance,history, origin, and the direction of changes in biological systems. The replicative model was compared with other models, first of all with the neo-Darwinian theory.


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# A COEVOLUTIONARY CIRCUIT MODEL FOR CULTURAL AND BIOLOGICAL EVOLUTION

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## INTRODUCTION

### Darwin, biological evolution and cultural evolution

"The concept of evolution has proved itself to be too fundamental and fruitful to be ignored indefinitely by anything calling itself a science. Evolutionism was therefore bound to return to cultural anthropology sooner or later." Leslie A. White (1960).

"It seems to me that what we need above all else in the study of society is theories which we can test. There is nothing easier, either in biology or in sociology, than to collect facts not previously known. Almost any facts about human beings have an intrinsic interest for us, but the mere collection of facts, however interesting or however true, does not constitute science. It is an essential feature of the scientific method that we should put forward theories or hypotheses which are in principle capable of being contradicted by observation, and that we should then perform experiments or collect facts to see whether they do not contradict our theories. If the drawing of analogies can help us to formulate such theories, then it is justified."
John Maynard Smith (1961).

The Darwinian theory of biological evolution explains the diversity of all living organisms; this theory says that existing organisms have evolved as a result of natural selection from earlier existing organisms. However,there is no similar theory which explains cultural history. That is, we have no theory which ties together available sociological, historical and anthropological data: there seems to be no theory that accounts for the development of culture in all its historical and spatial richness that is both detailed in explanations and predictions, and at the same time is widely acceptable. Even Marxist historical materialism - which indeed claims universal applicability - can, by its very nature, offer only the broadest outlines in the way of explanations.

The purpose of this essay is to discuss how such a cultural theory could be developed. More specifically, I present a theory for cultural evolution that is analogous to the Darwinian theory of biological evolution; in doing so I necessarily have to link biological and cultural evolution into a unified framework. I cannot claim to have developed a theory for cultural evolution based on assumptions that are necessarily true, as were Darwin's (1859) assumptions of multiplication, variation and heredity (see below). However, I hope I have been able to identify some of the

variables which such a theory must necessarily include, and to discuss how these variables may be related to one another.

Charles Darwin was himself interested in this topic. His books The Descent of Man and Selection in Relation to Sex (1871) and The Expression of the Emotions in Man and Animals (1872) demonstrate that Darwin was in fact the first sociobiologist. Hence, it is somewhat misleading to call E.O. Wilson the first sociobiologist. What Wilson did with the publication of his book Sociobiology: the New Synthesis (1975) was to make more people rediscover this part of Darwin's work. However, by christening the field "Sociobiology", Wilson certainly stimulated much discussion and detailed scientific work in this interdisciplinary field.

Sociologists and anthropologists tend to be sceptical about applying biological ideas to their subjects (Sahlins, 1977; Elster, 1979). Certainly their scepticism is easy to understand: a great deal of nonsense has been written on, for example, "Social Darwinism" and "Sociobiology", and many crimes justified by theories of racial superiority (e.g., the Nazis in the thirties and forties).

For this reason, it is important that I state my own view at the outset: I do not believe that biological evolution has been the only (or necessarily the major) cause of changes in man's social behaviour and culture during historical times. However, as a Darwinist, I do believe that biological evolution was the source of the specifically human characteristics that made human cultural history possible. Hence, I am sceptical about an uncritical application of "Human Sociobiology" (Wilson, 1978); i.e. the systematic study of the biological basis of man's social behaviour with the aim of interpreting man's social behaviour as a simple result of natural selection. Even though I think that some aspects of human behaviour may be explained mainly in biological terms, I believe that no theory attempting to explain the evolution of man's social behaviour and cultural system can dismiss purely social factors - or what I refer to below as cultural traits. This view is based on the fact that biological evolution must have occurred at a much slower rate than historical changes (e.g., Maynard Smith, 1961, 1975); that is, cultural traits are transmitted from person to person without there being any genetic relation between them, whereas in biological evolution traits can only be transmitted from parents to offspring. However, any theory attempting to explain the evolution of culture must necessarily consider the interaction between cultural and biological changes. For example, biological evolution of the human brain made man's advanced culture and civilization possible. On the other hand, this culture imposes an array of new selective pressures on man's biology. One possible example is concealed ovulation in humans, which may have been the outcome of a conflict between natural selection favouring higher fecundity and the conscious desire of women to avoid further pregnancies (Burley, 1979).

When discussing this topic, we should, of course, always be aware that any trait (cultural or behavioural) may be determined partly by biological and partly by cultural factors; the effect of each can, at least in principle, be determined theoretically by carrying out standard heredity studies (e.g., Falconer, 1960). Thus, rather than fighting over beliefs, we should collect the relevant data in order to make somewhat more objective decisions as to whether a trait is more dependent on biological or non-biological factors.

## The Lumsden-Wilson model

Due to the great scepticism of many social scientists and anthropologists about the usefulness of evolutionary ideas in their fields, the topic of human cultural evolution and the study of how cultural changes affect biological changes and vice versa have been a kind of a scientific no-man's land (Maynard Smith and Warren, 1982). However, recently Lumsden and Wilson (1981) have discussed several models in which biological and cultural evolution are linked together through individual development; as biologists they are optimistic (perhaps somewhat too optimistic), since they at least have a successful theory of biological evolution.

The most extensive of Lumsden and Wilson's models is their "coevolutionary circuit" model which allows for biological (i.e., genetic) effects on human behaviour and for behavioural effects on biological fitness and hence on gene frequencies. Finally, they allow for cultural transmission of behavioural traits. Lumsden and Wilson claim that this model produces some remarkable phenomena. It is, however, difficult to evaluate the validity of their conclusions (e.g., Maynard Smith and Warren, 1982): one of the main difficulties is the extreme complexity of the models considered. For this reason I offer here a more general and far more transparent model for cultural evolution. At the present stage of theoretical development, I believe it is far more profitable to analyze simple - and generalized - models before tackling very complex, detailed models. Like the study by Lumsden and Wilson, my model also yields some surprising results.

I offer this model in order to help us clarify our ideas about the various kinds of interactions between culture and biology that may be important in understanding cultural evolution. There is no guarantee that merely formulating the problem mathematically will produce a good theory of cultural evolution. But speculations without mathematics (which many social and biological scientists seem to favour) tend to leave the whole field looking rather muddled (see, e.g., Stenseth, 1984).

## THE IDEA OF EVOLUTION

Even though the idea of biological evolution is old, it was Darwin (1859) who made it acceptable to scientists. Besides presenting extensive evidence demonstrating that biological evolution has occurred, he put forward a hypothesis explaining how (and why) it occurred; i.e., he presented his theory of natural selection. Therefore, today the term "Darwinism" describes the theory which says that evolution is the result of natural selection. (Neo-Darwinism means this theory plus Mendel's laws plus a theory for how genes spread in a population, i.e., population genetics.) The acceptance of this theory revolutionized the study of biology. Today the Darwinian (or neo-Darwinian) theory of evolution represents the synthesis of all branches of modern biology. It is this theory which gives us a unified understanding of the bewildering phenomena observed in the living world - man included (see, e.g., Stenseth, 1985).

This Darwinian theory, which was originally suggested as an explanation of biological evolution (i.e., the evolution of living organisms after life had originated on earth) may be extended to explain other phenomena such as the origins of life and cultural evolution. Below I discuss how the Darwinian theory of biological evolution may suggest an analogous

theory for cultural evolution. However, I must first define the components of the Darwinian theory of evolution.

Any kind of evolution (biological or cultural) may be explained in terms of three properties: multiplication, heredity and variation. That is, any collection (e.g., a population) consisting of entities (e.g., individuals in biological evolution) that can multiply, so that more or less similar copies of themselves are produced, and where the coexisting entities vary with respect to their ability to produce copies of themselves, may undergo evolutionary changes. If the environment changes, evolution must take place. Notice that evolution is not a hypothesis if the entities in a collection are characterized by these three properties; in this case evolution is a logical consequence of these properties (see, e.g., Maynard Smith, 1978; Stenseth, 1985).

If some cultural entities could be defined so as to satisfy these three properties, then we would have some of the essentials for a theory of cultural evolution. To my knowledge, no-one has ever defined a theory of cultural evolution in exactly this way (but see Maynard Smith, 1961 and Alexander, 1979). The idea of cultural evolution is, however, not new. Well-known proponents of evolutionary thought in the social sciences and anthropology include Taylor (1871), Morgan (1907), Childe (1942), White (1949), Steward (1955, 1956), Sahlins and Service (1960) and Service (1971).

## AN ESSENTIAL DIFFERENCE BETWEEN BIOLOGY AND CULTURE

> "Culture, or civilization, ... is that complex whole which includes knowledge, belief, art, morals, customs, and many other capabilities and habits acquired by man as a member of society." Taylor (1871).

In the Darwinian theory of biological evolution there is no causal link between the occurrence of a new variety (or mutant) and the need for it. Lamarck (1809) believed that there was such a causal link. Darwin (1859) did not. Both assumed, however, that acquired characteristics (or traits) could be inherited by the offspring. Today we know that new biological traits do not arise as a result of some need, nor are acquired biological traits transmitted to future generations.

August Weismann (1892) was the first biologist to explicitly formulate a theory about how new varieties arise and how these are transferred to subsequent generations (see, e.g., Stenseth, 1985). He assumed that new varieties occur as a result of chance alone without any relation to the organism's need for particular adaptations. To use Monod's (1970) words in a slightly modified form, Darwinism is the theory of chance and necessity. The occurrence of a new variety (or mutant) is due to chance alone - if this variety improves the organism's adaptation, it is by necessity favoured by natural selection. This Weismannian version of Darwinism is consistent with Mendel's laws of heredity and with the "Central Dogma" of molecular biology [which says that information can only be transferred from DNA to proteins and not from proteins to DNA (Watson, 1965)].

In cultural evolution, the Weismannian assumption is no longer true. In cultural evolution, new (cultural) traits often arise as a result of need by the individuals. Furthermore, acquired characteristics are transmitted to the next generation (and to coexisting individuals). In other words,it is the Lamarckian assumption that applies in cultural evolution. [My idea of "cultural traits" of course resembles earlier concepts like "memes" (Dawkins, 1976) and "culture-genes" (see Lumsden and Wilson (1981) for a review).

However I feel that the term "cultural traits" is more general.]

This basic difference suggests a possible way of distinguishing biology from culture (or rather the biological and the cultural - or learned - components of a trait):

- Living - or biological - organisms consist of entities (i.e. individuals) with the three properties of multiplication, heredity and variation. In this case the Weismannian assumption applies.

- Cultural traits, on the other hand, may be defined as the collection of traits (i.e., knowledge, beliefs, art, morals, customs and behavioural patterns) satisfying the Lamarckian assumption of transmission from individual to individual; presumably any such cultural trait varies in its ability to be transferred to other members of society and in its ability to "stick" to individuals. Hence, the three properties necessary for evolution to occur are satisfied.

To me it seems reasonable to compare a cultural trait with a biological species; this is, however, inconsistent with the thinking of some social scientists (e.g., Harris, 1968). In biology, natural selection (within a particular species) operates on the individuals' ability to produce copies of themselves,thus forming future generations; this leads to (micro-) evolutionary changes altering the distribution of individual types within the species. In cultural evolution, I suggest that an analogue of natural selection operates on the trait's ability to be transmitted to coexisting individuals and the trait's ability to persist in the population.

By this definition I imply that a cultural trait is always associated with a repertoire of transmission and preservation. This is analogous to the fact that the individuals within a particular species are associated with a repertoire of reproduction and survival (see also Naess, 1982).

This definition of culture does not restrict culture to a particular species - man. In principle, any living species may have a culture. This view is consistent with Spencer (1898), Kroeber (1917) and Harris (1971). Mundinger (1980) gives a good general discussion of animal culture. Bonner (1979 , 1980) also gives a thorough discussion of the evolution and biological basis of culture in animals.

When attempting to formulate a model for cultural evolution, it is important to realize one essential difference between cultural and biological evolution (Futuyma, 1979): in cultural evolution, the changes refer to the traits (or behavioural patterns) themselves, not (as in biological evolution) to the individuals carrying (or practising) them. The gun, for example, replaced the spear and the Pill replaced other contraceptives.

## A MODEL FOR CULTURAL MICROEVOLUTION

By "cultural microevolution" I mean the change in the relative frequency of persons "applying" a particular cultural trait, given that the total number of different traits is constant (see, e.g., Mundinger, 1980). This is somewhat analogous to what biologists call microevolution. Cultural microevolution would then be the variation in frequency of particular traits. Cultural macroevolution, on the other hand, would be the change over time in the number of cultural traits in a population.

In the following I will consider only microevolution.

Genetic fitness

In biological evolution some genes are more easily transferred to subsequent generations than others. Those genes causing their carriers [or replicators (see Dawkins, 1976) or individuals] to give birth to more offspring than other individuals, and whose offspring survive better, will come to dominate the population. This we call individual selection. In an asexually reproducing population, natural selection operates by maximizing individual fitness, defined as

$$W = B \cdot s_1 + s_2 \qquad (1)$$

where B is the per capita birth rate, $s_1$ is the proportion of newborns surving to the time when reproduction next occurs (at which time they have matured) and $s_2$ is the adult survival rate.

Cultural fitness

Any particular cultural trait may be assumed to exist in many forms (differing with respect to their ability to be maintained in the human population by means of cultural transmission between individuals). With each of these forms, we may associate a particular cultural fitness.

As pointed out above, in cultural evolution some forms of a particular cultural trait are spread in the population by cultural transmission; i.e., traits are not only transferred from one individual to another through biological descent. Furthermore, new cultural traits appear as the result of a need. That is, cultural traits are inherited according to the Lamarckian assumption rather than the Darwinian assumption.

Cultural fitness - the capacity of a Lamarckian inherited trait (the $i^{th}$, for example) to spread in a population - may now be defined as

$$\gamma_i = \beta + c \qquad (2)$$

where $\beta$ is a measure of how easily a trait or habit (such as, for example, use of the Pill) is spread in the population, and c is a measure of how easily the trait is "preserved" in the population. Hence, in a stable population (with respect to density) the quantity $\gamma_i = N_{i,t+1}/N_{i,t}$, where $N_{i,t}$ is the number of individuals in the population carrying the $i^{th}$ trait at time t. Notice, however, that $\beta$ measures the transmission of a trait from the parent generation to the offspring as well as from one individual to another in the same generation. Effectively, $\beta$ measures how good individuals carrying a trait are at convincing others to adopt the trait, as well as how conservative they are in adhering to the trait themselves. Notice in particular that the equivalent to parental lineage - in effect - is established in this way.

The cultural fitness, $\gamma$, of a cultural trait can be changed by various cultural mutations; these mutations will, by definition, affect $\beta$ and c in eqn (2). For example, a new marketing strategy for the Pill will affect $\beta$ and c. Indoctrination is also a commonly used method of making people adopt and adhere to some political or religious idea; hence, indoctrination will affect $\beta$ as well as c.

Cultural lag load

The spreading of cultural traits can be likened to a Red Queen process (Van Valen, 1973; Maynard Smith, 1976; Stenseth, 1979). That is, an evolutionary advance made by one cultural trait (i.e., adoption by an increasing number of individuals in the population) will be "experienced" as a deterioration (or at least, a change) in the "condition" of the other traits. In a stable population of voters, for example, gains to one party are losses to the other parties. In the case of cultural lag load it is indeed likely that most of the time each trait is very close to its optimum in its particular environment. Thus cultural changes resulting in an increase in the fitness of one trait will be experienced as a deterioration in the "environmental conditions" of the other traits.

In order to formalize this, we can define the cultural lag load [analogous to Maynard Smith's (1976) biological lag load concept] as follows:

$$\lambda_i = \frac{\hat{\gamma}_i - \bar{\gamma}_i}{\hat{\gamma}_i} \qquad (3)$$

where $\bar{\gamma}_i$ is the average current cultural fitness of trait i, and $\hat{\gamma}_i$ is the best possible spreading and maintenance strategy of that trait in that particular environment. Notice that $\bar{\gamma}$ and $\hat{\gamma}$ both refer to the same trait, but with different transmission and maintenance strategies. A trait may therefore (as explained above) be compared with a species in a biological Red Queen model (see, e.g., Stenseth and Maynard Smith, 1984). "Cultural mutations", corresponding to biological mutations (or genotypes) as discussed by population geneticists, are the various new marketing and conservation strategies. To define the analogy in this way is, I believe, new, but presumably important in order to avoid muddled thinking.

By analogy to Stenseth and Maynard Smith (1984), I presume that new strategies for transmission and preservation are invented more frequently the larger the average cultural lag load, since in this case the need for new strategies is greatest. However, when the average lag is large, there will be extensive changes in the frequencies of the cultural traits; consequently, the rate of trait extinction will increase with increasing average cultural lag load.

Now consider a system consisting of the entire human population on earth and n traits. Notice that I assume a fixed number n of cultural traits in the entire human population; I therefore call it cultural microevolution. Let the cultural lag of the $i^{th}$ trait be $\lambda_i$. Then, by analogy to Maynard Smith (1976), the total change in $\lambda_i$ in unit time is given by

$$\delta\lambda_i = \delta_e\lambda_i - \delta_g\lambda_i \qquad (4)$$

where $\delta_e\lambda_i$ is the increase in the lag of the $i^{th}$ trait caused by evolutionary changes in other traits, and $\delta_g\lambda_i$ is the reduction in the cultural lag caused by changes in the $i^{th}$ trait itself. Hence,

$$\delta\lambda_i = \sum_j \alpha_{ij} \cdot \delta_g \lambda_j - \delta_g \lambda_i \qquad (5)$$

where $\alpha_{ij}$ is the increase in $\lambda_i$ due to unit change in $\lambda_j$; note that $\alpha_{ii} = 0$. Again by analogy to Stenseth and Maynard Smith (1984), changes in the average cultural load, $\bar{\lambda}$, would then follow the model

$$\frac{d\bar{\lambda}}{dt} = k \cdot (\Theta - 1) \cdot \bar{\lambda} \qquad (6)$$

where $\Theta$ is the leading eigenvalue of the matrix from eqn. (5). Since no genetic changes occur on this time scale, $\Theta$ is constant; notice in particular that $\Theta$ cannot be a function of $\bar{\lambda}$ since eigenvalues are never functions of the dynamic variables. However, k may be a function of $\bar{\lambda}$.

Then if $\Theta = 1$ (exactly), $\bar{\lambda}$ would settle down at an equilibrium value resulting in continuous cultural change (a typical social and cultural Red Queen analogue). If $\Theta > 1$, $\bar{\lambda}$ would continue to increase until some sort of social breakdown occurs; in this case, those traits having too large a lag load would become extinct. Finally, if $\Theta < 1$, $\bar{\lambda}$ would decrease to zero, after which no cultural change would occur - we would have reached a Utopia with complete harmony and where all ("surviving") traits would be at their cultural optimum.

## Cultural and biological interaction

As noted above, $\Theta$ is a constant when no biological change occurs. However, taking into account some biological change, $\Theta$ will in general change also; but $\Theta$ will usually change far more slowly than $\bar{\lambda}$. Hence, there will be an interaction between cultural and biological changes. The cultural coevolutionary circuit model of Lumsden and Wilson (1981) could then be given (as a linear approximation) by

$$\frac{d\bar{\lambda}}{dt} = k \cdot (\Theta - 1) \cdot \bar{\lambda}$$

$$\frac{d\Theta}{dt} = a + b \cdot \Theta + c \cdot \bar{\lambda}. \qquad (7)$$

As with eqn. (6), $k > 0$. Furthermore, $a > 0$ and (I presume!) $b < 0$: I assume $b < 0$ because there must be an upper level to the rate of genetic change ($d\Theta/dt$). Nothing, a priori, can be said about the sign of c. However, in the language of Lumsden and Wilson, I believe that $c < 0$ would correspond to the case in which cultural changes have "no catalytic effect" (i.e., the common-sense view that cultural influences usually slow down genetic changes). On the other hand, $c > 0$ corresponds to the "catalytic effect model" in which cultural changes accelerate genetic changes.

Analysis of eqn. (7) gives two phase diagrams (see Fig. 1).

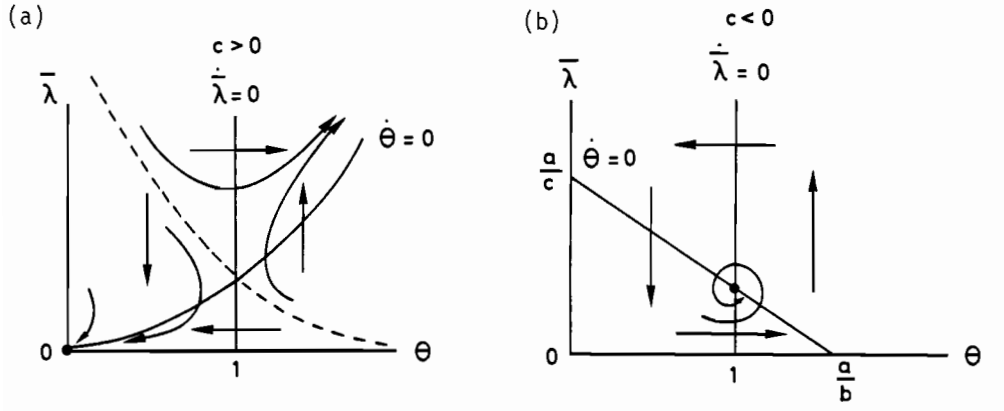


FIGURE 1 The dynamics of the cultural-biological coevolutionary process (a) assuming that cultural changes have a catalytic effect on biological changes (i.e., c>0); (b) assuming that cultural changes do not have a catalytic effect on biological changes (i.e., c<0). See the text for a discussion.

First, consider the diagram corresponding to the "catalytic effect model" of Lumsden and Wilson (Fig. 1a). Here we have two possible "solutions": either stagnation at Utopia (which can only be changed into another stable condition through some sort of revolution) or the Explosive Situation (this would correspond to the situation for which Lumsden and Wilson assume that "the catalytic effect might have contributed to the rapid evolutionary increase in human brain size associated with the onset of gene-culture coevolution"). Notice, however, that such an "explosion" cannot continue forever. Hence, the parameters in the model will, over time, change so as to satisfy the requirements of the other situation (see below). To my mind, it is interesting that both Utopia and the Explosive Situation are results of the "catalytic effect model" of Lumsden and Wilson. They did not seem to realize this. The other phase diagram corresponds to the common-sense view according to which cultural influences usually slow down genetic changes ( Fig. 1b). This model predicts a society where competition and non-revolutionary politics are most common. Even though this result seems intuitively obvious, no-one seems to have derived it formally before.

## DISCUSSION

An important empirical task would be to determine the signs of b and c. In particular, the various relations between biology and culture - and which patterns of cultural changes are produced under which conditions - could be tested on the basis of empirical data emerging from anthropological studies.

The model analyzed relates to the discussion of reductionism in biology and in sociology/anthropology: the basic assumption of Darwinian biology is that biology, in general, cannot be reduced to a theory consisting of only physical and chemical laws. In order to understand biological evolution, it is necessary to incorporate the principle of natural selection into our explanations of why the living world is as it is. It is therefore essential to understand the biological competition between different varieties. Physics and chemistry are not enough.

Similarly, I have assumed that cultural evolution cannot be understood without incorporating uniquely social and cultural processes. Many social scientists would, I presume, agree with this statement (for instance, Elster 1979). However, I think it is incorrect to conclude, as White (1949:xviii) did: "Culture may thus be considered as a self-contained, self-determined process; one that can be explained only in terms of itself." Therefore, I disagree with those social scientists who pretend that biological processes can be disregarded completely when studying social changes. Neither do I believe that the social sciences can be reduced to physical, chemical and biological laws [as Wilson (1975, 1978) seems to imply]. Rather I think, as do Lumsden and Wilson (1981), that in order to understand cultural evolution it is essential to study the interaction between culture and biology (and thereby physics and chemistry, among other things). In the earlier part of this paper I have suggested a framework for studying such interactions. It is, of course, only a start. Obviously much more theoretical and empirical work is necessary before we can say that we have developed a theory for cultural evolution comparable to the Darwinian theory of biological evolution. However, I do believe that the suggested framework is a possible basis. In particular, I think that social scientists ought to do something similar to what Darwin did in 1859; then sociology and anthropology might be more than just a collection of facts.

The model discussed earlier in this essay may also have interesting philosophical implications. My analysis does in fact strongly support Masters' (1982) contention:

> "Previous evolutionary explanations of human society have ... suggested diverse political conclusions. Indeed, if [evolutionary] models do have political implications, they could well challenge existing sociopolitical institutions rather than support them."

And that is indeed what is suggested by the fact that the patterns in Fig. 1 emerge from the same evolutionary model: the only difference is the parameter values determining how biology and culture interact - and that is an empirical issue.

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