Bulletin of Mathematical Biology, Vol. 40, pp. 743–769
Pergamon Press Ltd. 1978. Printed in Great Britain

DYNAMICAL SYSTEMS UNDER CONSTANT ORGANIZATION I. TOPOLOGICAL ANALYSIS OF A FAMILY OF NON-LINEAR DIFFERENTIAL EQUATIONS —A MODEL FOR CATALYTIC HYPERCYCLES†

■ P. SCHUSTER, K. SIGMUND and R. WOLFF
Institute of Theoretical and
Radiation Chemistry, and
Mathematical Institute,
University of Vienna, Austria

The paper presents a qualitative analysis of the following systems of n differential equations: $\dot{x}_i = x_i x_j - x_i \sum_{r=1}^{n} x_r x_s$ ($j = i - 1 + n\delta_{i1}$ and $s = r - 1 + n\delta_{r1}$), which show cyclic symmetry. These dynamical systems are of particular interest in the theory of selforganization and biological evolution as well as for application to other fields.

1. Introduction. Selection and evolution of self-reproductive biological macromolecules can be described appropriately by systems of differential equations based on the formalism of deterministic chemical kinetics (Eigen, 1971). In the theory of Eigen a closed loop of autocatalytic reactions as shown in Figure 1 plays an essential role. It was found to be most likely that kinetic systems of this type were the only candidates which can develop a biochemical machinery for reduplication and translation of nucleic acids. Referring to their dynamical structure (Figure 1) these kinetic systems were called "hypercycles". The prerequisites of hypercycle formation, their physical properties and the relations between hypercycles and the origin of the genetic code have been discussed extensively in a recent paper (Eigen and Schuster, 1977). In the present paper we concentrate on some mathematical aspects, especially on the topological dynamics of the simplest class of differential equations comprising all important features of hypercycles:

†This work has been supported financially by the Austrian Fonds zur Förderung der Wissenschaftlichen Forschung, Project N. 2261.

$$\dot{y}_i = k_i y_i y_j - \frac{y_i}{c} \sum_{r=1}^{n} k_r y_r y_s; \qquad i = 1, 2 \ldots n \tag{1}$$

$$j = i - 1 + n\delta_{i1}, \quad s = r - 1 + n\delta_{r1} \quad \text{and} \quad c = \sum_{i=1}^{n} y_i.$$

y_i denote population or concentration variables for individual macromolecules, $y_i = [I_i]$. The indices j and s simply refer to the precursors of i and r in the catalytic cycle respectively. c represents the total concentration of polymers. In case c is constant, the system of equations (1) corresponds to the selection constraints of constant organization (Eigen, 1971).

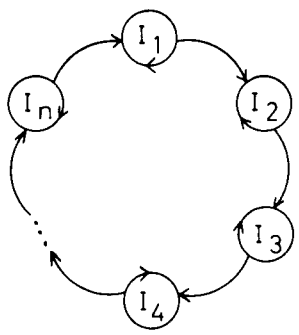


Figure 1. Catalytic hypercycle (closed cycles represent self-instructed replication, arrows pointing from one cycle to another correspond to the catalytic terms $x_i x_j$, $j = i - 1 + n\delta_{i1}$)

Superficially looking, the system of differential equations (1) could be understood as a special case of the continuous Fisher–Wright–Haldane model frequently used in population genetics (Hadeler, 1974; Crow and Kimura, 1970).

$$\dot{x}_i = \sum_j f_{ij} x_i x_j - x_i \sum_r \sum_s f_{rs} x_r x_s; \quad i = 1, 2 \ldots n \tag{2}$$

$$0 \leqslant x_i \leqslant 1, \quad \sum x_i = 1; f_{ij} = f_{ji}.$$

One basic assumption of this model for the evolution of gene distributions, however, is that the matrix of coefficients $\mathbf{F} = (f_{ij})$ is symmetric, whereas in

our case **F** shows a rather simple monomial but not symmetric form:

$$\mathbf{F} = \begin{vmatrix} 0 & 0 & 0 & \dots & 0 & k_1 \\ k_2 & 0 & 0 & \dots & 0 & 0 \\ 0 & k_3 & 0 & \dots & 0 & 0 \\ \vdots & & & & & \\ 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & k_n & 0 \end{vmatrix} \tag{3}$$

For equal rate constants, $k_1 = k_2 = \ldots = k_n = k$, *F becomes a cyclic permutation matrix*. Cyclic symmetry as we will show later is an essential feature of hypercycles and therefore, the solution curves of (2) do not resemble at all those of (1).

Recently, Jones (1977) made an attempt to find an analytically solvable system of differential equations which are related as closely as possible to (1). For this purpose he introduced logarithmic functions as catalytic coupling terms, i.e. he used terms $k_i y_i \ln y_j$ instead of $k_i y_i y_j$. Although the solutions obtained thereby have much in common with the solutions of our system of differential equations (1), the origin of logarithmic catalytic terms is hard to explain on the basis of physically meaningful kinetic mechanisms.

For a more convenient presentation dimensionless variables $x_i = y_i/c$ are introduced into (1). In order to simplify the following analysis the rate constants are assumed to be equal: $k_1 = k_2 = \ldots k_n = k$. The influence of variations in the distribution of rate constants will be discussed in a forthcoming paper. Finally, an appropriate choice of time and concentration scales enables us to set $k = c^{-1}$ and we obtain the following system of differential equations which shall be subjected to a detailed analysis:

$$\dot{x}_i = x_i x_j - x_i \sum_{r=1}^{n} x_r x_s; \quad i = 1, 2 \ldots n \tag{4}$$

$$j = i - 1 + n\delta_{i1} \quad \text{and} \quad s = r - 1 + n\delta_{r1}.$$

At fixed total concentrations c, the physically meaningful range of relative population variables, x_i, is represented by an n-simplex (S_n) which will be called "n-population simplex" here. Each actual composition of the system can be described by a state vector $\mathbf{x} = (x_1, x_2, \ldots, x_n) \in S_n$. S_n is defined

by:

$$S_n = \{\mathbf{x} \in \Re^n | x_i \geqq 0 \, \forall \, i, \sum x_i = 1\}. \tag{5}$$

For many purposes it will be useful to distinguish between pure states ($x_i = 1$, $x_{j \neq i} = 0$) which correspond to corners of the simplex, and mixed states. Clearly, the interior of the n-simplex is the set of mixed states for which no population variable is vanishing:

$$IS_n = \{\mathbf{x} \in \Re^n | x_i > 0 \, \forall \, i; \sum x_i = 1\}. \tag{6}$$

Thus, the whole n-simplex consists of two disjoint sets, the interior and the boundary, BS_n:

$$S_n = IS_n \cup BS_n \quad \text{and} \quad IS_n \cap BS_n = \varnothing. \tag{7}$$

In order to facilitate reading we shall split the analysis of (4) into three parts. At first general results which are valid for all dimensions n will be presented. Then we will describe the interiors (IS_n) of the n-simplices by means of complete phase portraits for systems with $n \leqq 4$. Examples of higher dimensional systems ($n \geqq 5$) are discussed with the aid of trajectories obtained by numerical integration. Finally, the boundaries (BS_n) of the n-simplices will be analysed in detail. A complete description is given for all types of dynamical systems occurring as restrictions of (4) to the simplices S_m with $m \leqq 4$ which belong to the boundaries BS_n ($n > m$).

2. *General Results*

2.1. The complete population simplex and its restrictions. The dynamical system of dimension n on S_n as it is defined in (4) will be denoted "complete simplex" since it contains all n population variables. For short we shall use the notation $\langle n \rangle$. These dynamical systems $\langle n \rangle$ have an important property:

$$x_i = 0 \Rightarrow \dot{x}_i = 0 \tag{8}$$

All simplices occurring in the boundaries BS_n, therefore, are (globally) invariant sets.

In general, there are several possibilities for restrictions of the dynamical systems $\langle n \rangle$ to S_m ($m < n$). Figure 2 shows the hierarchy of these restrictions of $\langle n \rangle$ with $n \leqq 8$. The individual types of dynamical systems will be denoted by $\langle mA \rangle$, $\langle mB \rangle$, $\langle mC \rangle$ etc. We shall describe all cases up to $m \leqq 4$

in Section 4. Here, we consider only one example ($m=2$) which we will need in the following discussion. There are three different types of dynamical systems on simplices of dimension two (S_2) which correspond to invariant sets or subsets of $\langle n \rangle$ (Figure 3):

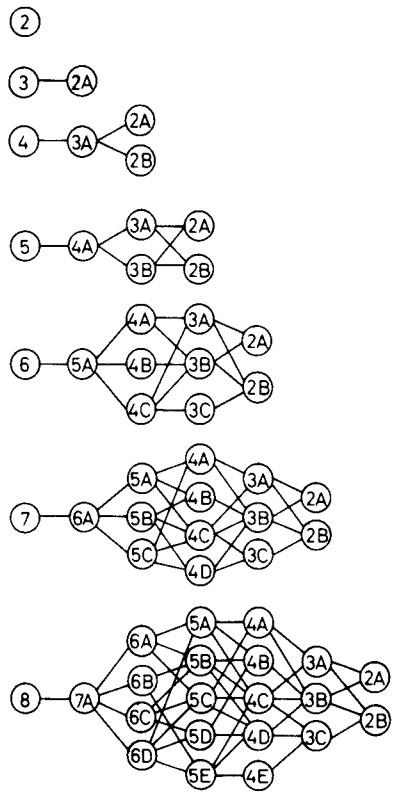


Figure 2. Restrictions of S_n to S_m, $n>m\geq 2$ (The general recursive algorithm for the diagrams is derived in Section 4.4)

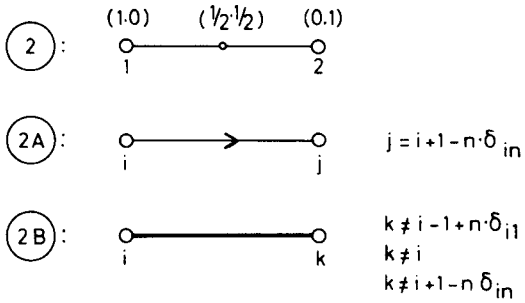


Figure 3. Schematic graphs for all simplices S_2 ($\langle 2 \rangle$ is the graph for the complete simplex S_2, $\langle 2A \rangle$ represents a flowing edge, and $\langle 2B \rangle$ a fixed point edge

(1) The complete simplex $\langle 2 \rangle$ which is characterized by three fixed points, two at the ends and one in the middle of the segment $\{(x_1, x_2) | x_1 \in [0, 1], x_1 + x_2 = 1\}$,

(2) the flowing edge $\langle 2A \rangle$ $\{(x_i, x_j) | x_i \in [0, 1], x_i + x_j = 1; j = i + 1 - n\delta_{in}\}$ with two fixed points, one on each end, and

(3) the fixed point edge $\langle 2B \rangle$ $\{(x_i, x_k) | x_i \in [0, 1], x_i + x_k = 1; k \neq i, k \neq i - 1 + n\delta_{i1}$ and $k \neq i + 1 - n\delta_{in}\}$. In the last case every point of the set is invariant.

2.2. Stability of points on the n-population simplex with respect to the neighbourhood in $\mathfrak{R}^n$.† Appropriately, we distinguish two different cases:

(1) Starting from any point $\mathbf{x}^0 \in \mathfrak{R}^n$ in the neighbourhood of IS_n with $c^0 = \sum x_i^0 \neq 1$ and $x_i^0 > 0 \, \forall \, i$ the total concentration will approach $c = 1$ asymptotically.

Proof. $$\dot{c} = \sum_{i=1}^{n} \dot{x}_i = r(1 - c) \tag{9}$$

wherein $$r = \sum_{i=1}^{n} x_i x_j, \; j = i - 1 + n\delta_{i:} \, . \tag{10}$$

From $x_i^0 > 0 \, \forall \, i$ follows $r^0 = \sum_i x_i^0 x_j^0 > 0$, which leads to

$$\dot{c} > 0 \quad \text{for} \quad c < 1 \quad \text{and}$$
$$\dot{c} < 0 \quad \text{for} \quad c > 1$$

thus proving asymptotic stability of the fixed point of (9) at $c = 1$.

The "neighbourhood" of a flowing edge $\langle 2A \rangle$ on BS_n shows the same dynamical behaviour as the neighbourhood of IS_n as long as the corners are excluded:

From $x_i^0 > 0$, $x_j^0 > 0$ with $j = i + 1 - n\delta_{in}$ follows $r^0 > 0$ as above.

(2) Approaching the neighbourhood of a pure state or of a fixed point edge $\langle 2B \rangle$ on BS_n the tangent vector along the c-axis vanishes and hence the fixed point at $c = \sum x_i = 1$ is not a sink.

†For the sake of brevity we use "neighbourhood" for the set theoretic difference between the neighbourhood of S_n and S_n restricted to the cone of non negative vectors $\mathbf{x}$.

Proof. $\mathbf{x}^0 \in \Re^n$;

(a) $x_i^0 > 0$; $x_j^0 = 0 \, \forall j \neq i$

$r^0 = 0 \Rightarrow \dot{c} = 0$ or

(b) $x_i^0 > 0, x_k^0 > 0$; $x_j^0 = 0 \, \forall j \neq i, k$ *and* $k \neq i$, $i-1+n\delta_{i1}$ or $i+1-n\delta_{in}$

$r^0 = 0 \Rightarrow \dot{c} = 0$.

2.3. Fixed points of the dynamical systems $\langle n \rangle$. All dynamical systems of type $\langle n \rangle$ have one fixed point in IS_n. According to our choice of equal rate constants this fixed point coincides with the center of the simplex:

$$\bar{\mathbf{x}}_0 = \left(\frac{1}{n}, \frac{1}{n}, .., \frac{1}{n}\right). \tag{11}$$

Furthermore, there are fixed points in BS_n which for convenience can be grouped into several classes.

(1) All corners of the simplices $\langle n \rangle$ represent fixed points

$$\bar{\mathbf{x}}_i : (x_i = 1, \; x_j = 0 \, \forall j = 1, 2 \ldots n, j \neq i). \tag{12}$$

(2) Fixed point edges $\langle 2B \rangle$ connecting two non consecutive corners $(i, j$; $j \neq i$, $j \neq i-1+n\delta_{i1}$ and $j \neq i+1-n\delta_{in})$ are one-dimensional manifolds of fixed points. According to Figure 2 they occur in BS_n with $n \geqq 4$.

(3) Two-dimensional manifolds of fixed points are represented by the triangles (S_3) of type $\langle 3C \rangle$. They are spanned by three pairwise non consecutive corners and consequently are found in BS_n with $n \geqq 6$.

(4) Three-dimensional manifolds of fixed points occur in BS_n with $n \geqq 8$ and are shown in Figure 2 as tetrahedra of type $\langle 4E \rangle$.

This sequence may be continued easily up to higher dimensions.

2.4. Normal modes and eigenvectors of the fixed points in IS_n. General results—valid for all n—can be obtained by linearization of the dynamical system (4) around the central fixed point $\bar{\mathbf{x}}_0$:

$$\dot{\mathbf{z}} = \mathbf{A}\mathbf{z} + o(\|\mathbf{z}\|) \quad \text{with} \quad \mathbf{z} = \mathbf{x} - \bar{\mathbf{x}}_0. \tag{13}$$

The Jacobian matrix at the central fixed point $\bar{\mathbf{x}}_0$

$$\mathbf{A} = \left\{ A_{ij} = \left(\frac{\partial \dot{x}_i}{\partial x_j}\right)\bigg|_{\mathbf{x} = \bar{\mathbf{x}}_0} \right\}$$

becomes very simple as a consequence of our initial assumption of equal rate constants:

$$\mathbf{A}=\begin{vmatrix} -\frac{2}{n} & -\frac{2}{n} & -\frac{2}{n} & \cdots & -\frac{2}{n} & 1-\frac{2}{n} \\ 1-\frac{2}{n} & -\frac{2}{n} & -\frac{2}{n} & \cdots & -\frac{2}{n} & -\frac{2}{n} \\ -\frac{2}{n} & 1-\frac{2}{n} & -\frac{2}{n} & \cdots & -\frac{2}{n} & -\frac{2}{n} \\ & & & & & \\ -\frac{2}{n} & -\frac{2}{n} & -\frac{2}{n} & & -\frac{2}{n} & -\frac{2}{n} \\ -\frac{2}{n} & -\frac{2}{n} & -\frac{2}{n} & & 1-\frac{2}{n} & -\frac{2}{n} \end{vmatrix} \tag{14}$$

Due to cyclic symmetry of $\mathbf{A}$ the eigenvalues $\omega_0^{(i)}$, $i=1,\ldots,n$ and the corresponding eigenvectors $\xi_0^{(i)}$, $i=1,\ldots,n$ can be calculated easily:

$$\omega_0^{(1)}=-1; \quad \xi_0^{(1)}=(1,1\ldots1). \tag{15a}$$

$$\omega_0^{(j)}=\exp\left\{\frac{2\pi i}{n}(j-1)\right\}=\lambda_j; \quad j=2,3,\ldots,n;$$

$$\xi_0^{(j)}=(1,\lambda_j^{-1},\lambda_j^{-2},\ldots,\lambda_j^{-n+1})=(1,\lambda_j^{n-1},\lambda_j^{n-2},\ldots,\lambda_j). \tag{15b}$$

Depending on whether n is odd or even we find one or two real eigenvalues respectively and $[(n-1)/2]$ complex conjugate pairs of eigenvalues. For two- and three-dimensional systems $(n=2,3)$ all eigenvalues have negative real parts. The central fixed point therefore is asymptotically stable. In the case of $n=3$ we obtain one pair of eigenvalues with non zero imaginary parts indicating the existence of a rotational component. Trajectories therefore will spiral into the central sink.

The four dimensional system $(n=4)$ represents a special case since we find two purely imaginary eigenvalues $\omega_0^{(2)}=i$ and $\omega_0^{(4)}=-i$ besides the two additional degenerate modes $\omega_0^{(1)}=\omega_0^{(3)}=-1$. The linearized system with $n=4$ thus contains a center $\mathbf{x}_0\in IS_n$. Centers are inherently instable

systems and in contrast to sinks or sources may change into spiral sinks or sources when non-linear terms are included (Coddington and Levinson, 1955; see also Section 3).

The central point in IS_n, $n \geqq 5$, represents an unstable equilibrium point since there is at least one pair of complexes conjugate eigenvalues with positive real parts.

Turning now to the eigenvectors we find that $\xi_0^{(1)}$, the vector belonging to $\omega_0^{(1)}$, corresponds to simultaneous and equal changes in all variables x_i.† Thus $\xi_0^{(1)}$ points in a direction perpendicular to the simplex S_n. $\omega_0^{(1)}$ is negative and real in agreement with asymptotic stability derived for $\dot{c} = \Sigma \dot{x}_i$ at the point $c = 1$ (see Section 2.2).

The four dimensional system ($n = 4$) will be of some interest in Section 3 and therefore we will now describe the corresponding eigenvectors of the linearized system in some detail. The eigenvector $\xi_0^{(1)} = (1, 1, 1, 1)$, perpendicular to S_4, need not be considered any further. For the other three we find:

$$\omega_0^{(2)} = i,\ \xi_0^{(2)} = (1, -i, -1, i)$$
$$\omega_0^{(3)} = -1,\ \xi_0^{(3)} = (1, -1, 1, -1)$$
$$\omega_0^{(4)} = -i,\ \xi_0^{(4)} = (1, i, -1, -i).$$

$\xi_0^{(3)}$ points from the center of the simplex towards the middle of the fixed point edges of type $\langle 2B \rangle$ $\overline{13}$ or $\overline{24}$. According to the eigenvalue $\omega_0^{(3)} = -1$ trajectories approach asymptotically the plane through x_0 perpendicular to $\xi_0^{(3)}$. This plane is spanned by the remaining two eigenvectors $\xi_0^{(2)}$ and $\xi_0^{(4)}$ and contains the purely rotational component of the center in the linearized system; thus the trajectories in the plane spanned by $\xi_0^{(2)}$ and $\xi_0^{(4)}$ form a set of closed orbits surrounding the midpoint of S_4.

2.5. Normal modes and eigenvectors of some fixed points in BS_n. Normal mode analysis in the linearized dynamical systems around the fixed points in BS_n is less straightforward than the previous examples. We will restrict ourselves to the fixed points at the corners of S_n. In this case the Jacobian matrix $\mathbf{A}$ is almost completely filled with zeroes. For the fixed point $\bar{\mathbf{x}}_i = (x_i$

†In case n is an even number the eigenvalue $\omega_0^{(1)} = \omega_0^{(n/2+1)} = -1$ is twofold degenerate. Without loss of generality we can always choose the eigenvectors in such a way that $\xi_0^{(1)} = (1, 1, \ldots, 1)$, see (15a, b).

$=1,\ x_j=0\,\forall j\neq i)$ we find:

$$\mathbf{A}=\begin{array}{c} \\ \\ i \\ j \\ \\ \end{array}\begin{array}{c} \begin{array}{cccccc} & & i & j & & \end{array} \\ \left|\begin{array}{cccccc} 0 & \dots & 0 & 0 & \dots & 0 \\ 0 & \dots & 0 & -1 & \dots & 0 \\ 0 & \dots & 0 & 1 & \dots & 0 \\ 0 & \dots & 0 & 0 & \dots & 0 \end{array}\right| \end{array};\ j=i+1-n\delta_{in}. \tag{16}$$

The matrix $\mathbf{A}$ has only one nonzero eigenvalue $\omega_i=1$ with $\xi_i=(x_i=-1,\ x_j=1;\ \ x_k=0\,\forall k\neq i,j)=(0,0,\dots,-1,+1,\dots,0,0)$ as the corresponding eigenvector. ξ_i thus points from the corner $x_i=1$ in the direction of the outgoing flowing edge towards the next fixed point $\bar{\mathbf{x}}_j: x_j=1,\ j=i+1-n\delta_{in}$. The eigenvalue $\omega_j=1$ indicates that the corners of S_n are unstable. Since there are $n-1$ zero eigenvalues an analysis of the linearized system provides only very limited information on the behaviour of the corresponding non linear dynamical system (4) around the fixed points $\bar{\mathbf{x}}_i$ (see Section 4).

2.6. Lemma. In the next section it will be useful to introduce a function u defined in (17) which has the following properties:

$$u=-x_1x_2,\dots,x_n \tag{17}$$

(I) $\dot{u}=-u(1-nr)$ (18)

(II) $u=0$ in BS_n (19)

(III) $\dot{u}=0$ in BS_n and at $\bar{\mathbf{x}}_0$, the center of S_n (20)

(IV) $u=\min$ in IS_n at $\bar{\mathbf{x}}_0$. (21)

Proof. (I) Making use of the previously defined function (see (10))

$$r=\sum_{i=1}^{n} x_ix_j,\ j=i-n\delta_{i1},$$

it is easy to verify that

$$\dot{u}=-u\sum_{i=1}^{n}\left(x_i-\sum_{k=1}^{n} x_kx_l\right)=-u(1-nr),\qquad l=k-1+n\delta_{k1}.$$

(II) In BS_n there is at least one vanishing variable,

$$x_i = 0 \Rightarrow u = 0 \; \forall \, i = 1, 2, \ldots, n.$$

(III) From (I) and (II) follows $u = 0 \Rightarrow \dot{u} = 0$ in BS_n;

$$\bar{\mathbf{x}}_0 = \left(\frac{1}{n}, \frac{1}{n}, \ldots, \frac{1}{n}\right) \Rightarrow r = \frac{1}{n} \Rightarrow (1 - nr) = 0 \Rightarrow \dot{u} = 0.$$

(IV) $\delta u = \sum_{i=1}^{n} \left(\frac{\partial u}{\partial x_i}\right) \delta x_i = u \sum_{i=1}^{n} \delta \ln x_i$

in IS_n: $\sum_{i=1}^{n} \delta x_i = 0$

at $\bar{\mathbf{x}}_0$: $\sum_{i=1}^{n} \delta \ln x_i = \sum_{i=1}^{n} \frac{\delta x_i}{x_i} = n \sum_{i=1}^{n} \delta x_i = 0 \Rightarrow \delta u = 0$

$$\delta^2 u = 2u \sum_{i<j}\sum \delta \ln x_i \delta \ln x_j, \text{ since } \left(\frac{\partial^2 u}{\partial x_i^2}\right) = 0 \; \forall \, i = 1, 2, \ldots, n$$

in IS_n: $\sum_{i=1}^{n} \delta x_i \cdot \sum_{k=1}^{n} \delta x_k = \sum_{i=1}^{n} (\delta x_i)^2 + 2 \sum_{i<k}\sum \delta x_i \delta x_k = 0$

$$\sum_{i<k}\sum \delta x_i \delta x_k = -\tfrac{1}{2} \sum_i (\delta x_i)^2$$

at $\bar{\mathbf{x}}_0$: $\delta^2 u = -\frac{u}{n^2} \sum_i (\delta x_i)^2 = \left(\frac{1}{n}\right)^{n+2} \sum_i (\delta x_i)^2 > 0 \Rightarrow u = \min$

3. *The Interior of the n-Population Simplex*

3.1. Dimension 1 ($n = 2$). Putting $x = x_1$ in (4) (for $n = 2$) one obtains the Abelian differential equation $x' = 2x^3 - x^2$ on $[0, 1]$.

Since $r = 2x_1(1 - x_1) \leqq 1/2$ (with equality iff $x_1 = x_2 = 1/2$), one has by Lemma (2.6) $\dot{u} \leqq 0$, with equality iff $x_1 = x_2 = 1/2$. Hence u is a Ljapunov function for the stable attractor $x_1 = x_2 = 1/2$. The phase portrait consists of three fixed points on S_2 and two nonsingular orbits having $x_1 = 1$, resp. $x_2 = 1$ as α-limits and $x_1 = x_2 = 1/2$ as ω-limit.

3.2. Dimension 2 ($n=3$). Again, $\dot{u} \leqq 0$ with equality iff $x_1=x_2=x_3=1/3$, u is a Ljapunov function and the center of the simplex is a stable attractor whose basin of attraction is the interior of S_3. This can be pictured in another way by noting that $\dot{x}_i=0$ iff $x_{i-1}^2=x_i x_{i+1}$ ($i=1, 2, 3$, $x_0=x_3$ and $x_4=x_1$). It is easy to see that this condition is fulfilled by a circle through the center which is tangent to the edge $x_{i-1}=0$ at the point $x_{i+1}=1$ and to the edge $x_{i+1}=0$ at the point $x_{i-1}=1$. Hence the edges of a hexagon as shown in Figure 4a are crossed from the outside to the inside. This shows that the points in the interior of S_3 have the center as ω-limit and the loop 1–2–3–1 as α-limit. An example of an orbit obtained by numerical integration is shown in Figure 5.

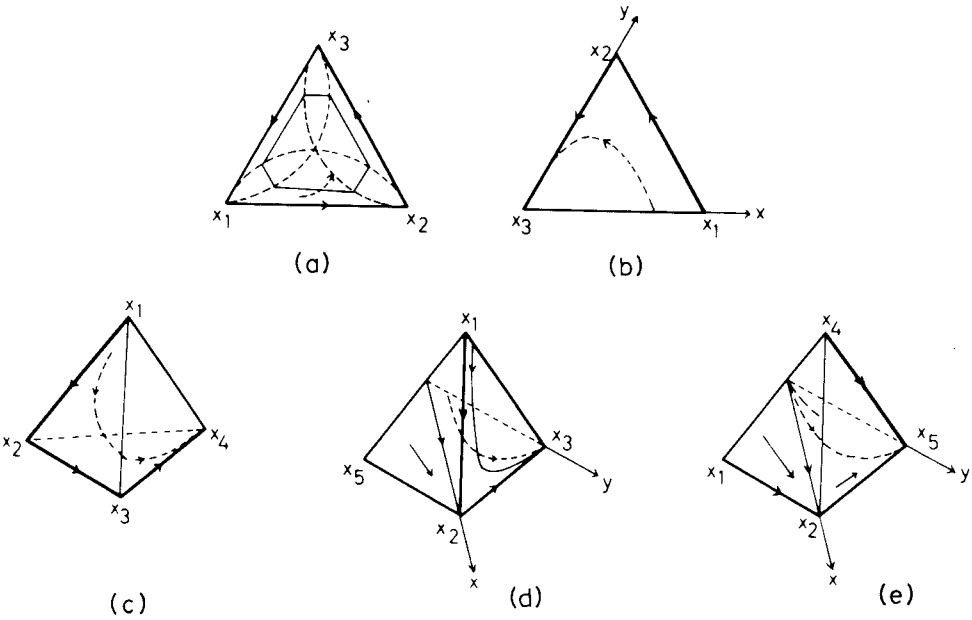


Figure 4. Dynamical systems on some simplices S_3 and S_4 (a=the complete simplex $\langle 3\rangle$, $b=\langle 3A\rangle$, $c=\langle 4A\rangle$, $d=\langle 4C\rangle$, and $e=\langle 4B\rangle$

3.3. Dimension 3 ($n=4$). By the change of coordinates $x=x_1$, $y=x_2$, $z=x_3$, and elimination of the fourth linearly dependent variable, (4) becomes

$$\dot{x}=x(1-x-y-z-\bar{r})$$

$$\dot{y}=y(x-\bar{r})$$

$$\dot{z}=z(y-\bar{r})$$

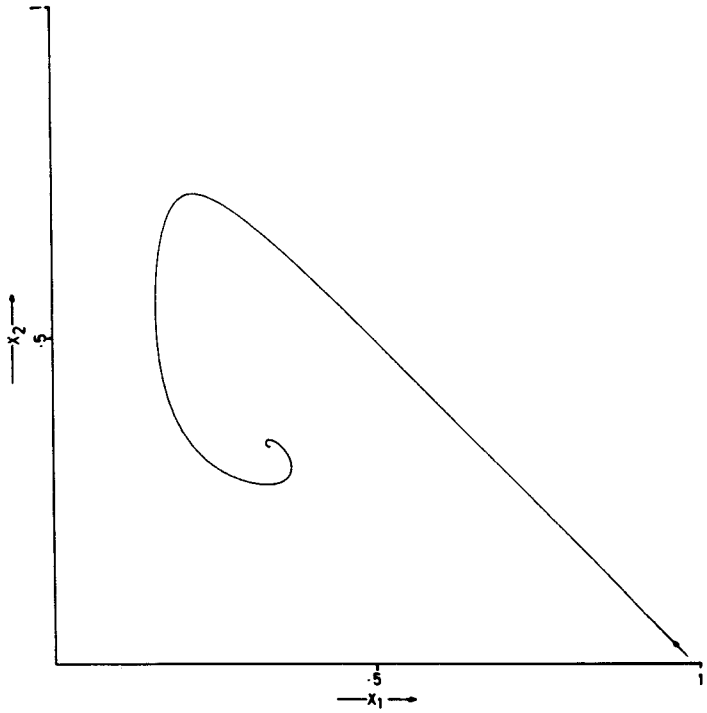


Figure 5. Phase portrait of ⟨3⟩

(with $\bar{r}=(x+z)(1-x-z)$). Another change of coordinates

$$\begin{bmatrix} x \\ y \\ z \end{bmatrix} \to \begin{vmatrix} 0 & -2 & -2 \\ 2 & 2 & 0 \\ 2 & 0 & 2 \end{vmatrix} \begin{bmatrix} x \\ y \\ z \end{bmatrix} + \begin{bmatrix} 1 \\ -1 \\ -1 \end{bmatrix}$$

puts the origin into the center of S_4 and the x-, y-, and z-axes through the midpoints of the edges $\overline{23}$, $\overline{34}$ and $\overline{13}$ respectively. The system then becomes

$$\begin{aligned} \dot{x} &= -(1+z)(y-xz) \\ \dot{y} &= (1-z)(x-yz) \\ \dot{z} &= z^3 - z + x^2 - y^2 . \end{aligned}$$

Note that the equation is invariant for the transformation $z \to -z$, $x \to -y$, $y \to x$. The eigenvalue -1 of the Jacobian at the origin corresponds to a

F

contraction along the z-axis. On the plane $z=0$ (which corresponds to the condition $x_1+x_3=1/2$) the previous system reduces to

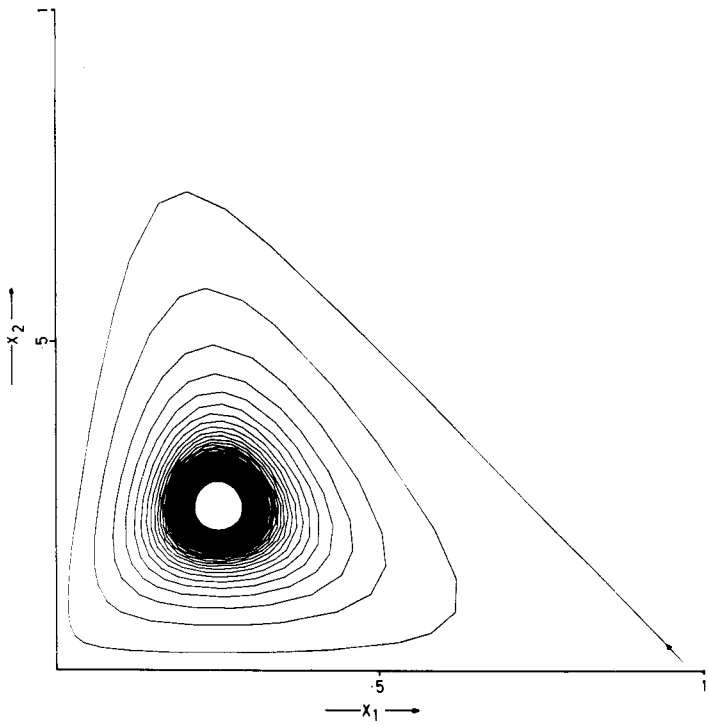
$$\dot{x}=-y,\ \dot{y}=x,\ \dot{z}=x^2-y^2.$$

Since $\dot{z}=0$ iff $x=\pm y$, one sees that apart from the fixed point in the center there are no orbits on the plane $x_1+x_3=1/2$. The first two equations show that the system has a strong rotational component around the z-axis. Introducing cylinder coordinates $z=z$, $x=r\cos\theta$, $y=r\sin\theta$ one sees that

$$\dot{\theta}=1-\sqrt{2}z\sin(2\theta+\pi/4)$$

is independent of r and always positive if $|z|<1/2$.

This strong rotational component is also shown in the numerical solutions (see Figures 6a, b) and tends to suggest that there might be closed orbits around the z-axis, lying on the center manifold corresponding to the eigenvalues $\pm i$ of the Jacobian at the fixed point $\mathbf{x}_0$. This evidence is misleading, however.



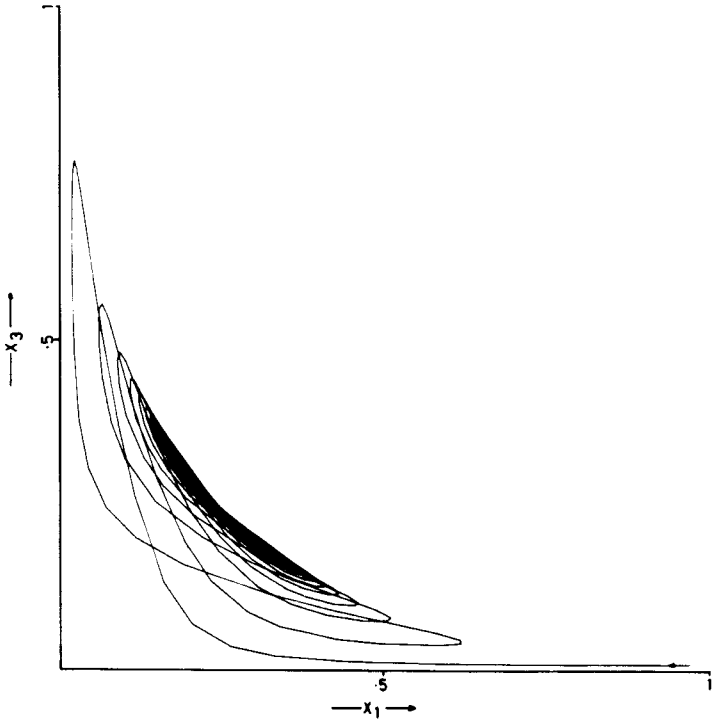


Figure 6. Phase portrait of ⟨4⟩. (a) projection onto the plane (x_1, x_2); (b) projection onto the plane (x_1, x_3)

Note, indeed, that

$$r = x_1x_2 + x_2x_3 + x_3x_4 + x_4x_1 = (x_1 + x_3)(x_2 + x_4) = s(1 - s)$$

with $s = x_1 + x_3$. Clearly $0 \leqq r \leqq 1/4$, with $r = 1/4$ iff $s = 1/2$, i.e. iff $x_1 + x_3 = 1/2$. Thus $\dot{u} = u(1 - 4r) \leqq 0$ in the interior of S_4 with equality iff $x_1 + x_3 = 1/2$. However, as we have seen above, there are no orbits on this plane; more precisely, the set $\{t \in \Re : x_1(t) + x_3(t) = 1/2\}$ is at most countable for every orbit $x(t)$ except the one corresponding to the fixed point in the center. Thus $t \to u(x(t))$ is monotonically decreasing, u is a Ljapunov function, and the center of the simplex is a stable attractor whose basin of attraction is the interior of S_4. This is in contrast to the behaviour of the linearized system described in 2.4.

3.4. Dimension $n \geqq 5$. For $n \geqq 5$ the central point is a saddle point—the Jacobian has eigenvalues with positive and negative real parts—and is certainly no longer an attractor. There is strong numerical evidence (see

Figure 7a, b) that there exists a closed orbit which is a stable attractor. We are unable, however, to present a proof of this conjecture.

4. *The m-Dimensional Boundaries of the n-Population Simplex*

4.1. The case $m=2$. Apart from the complete 2-population simplex, there are two possible cases:

(1) Flowing edge $\langle 2A \rangle$: This system occurs as edge between two consecutive states of the n-hypercycle, $n \geqq 3$. For example, if $x_3=0$ in the three population simplex, one obtains the differential equations

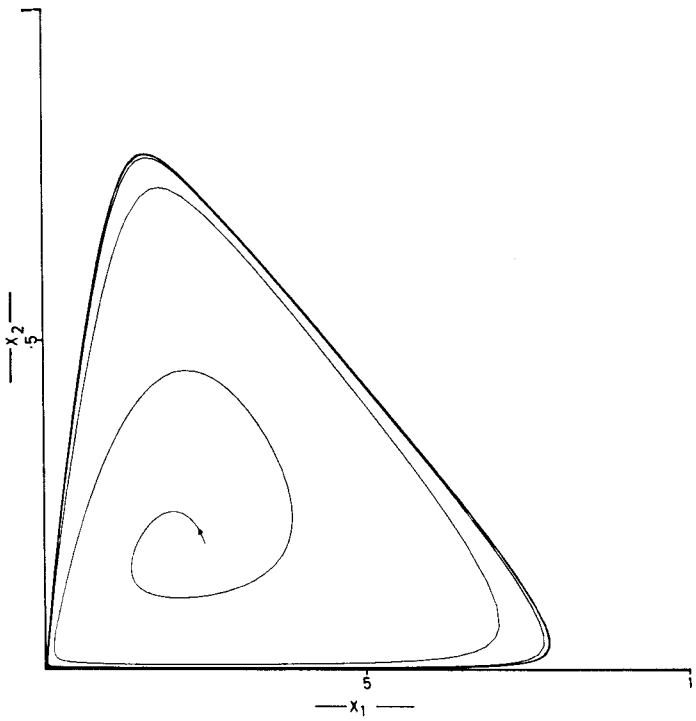
$$\dot{x}_1 = x_1(-r)$$

$$\dot{x}_2 = x_2(x_1 - r) \tag{22}$$

(with $r = x_1 x_2$), on the simplex S_2. Putting $x = x_1$, this reduces to the Abelian differential equation

$$\dot{x} = x^3 - x^2 \tag{23}$$

on the interval $[0, 1]$.



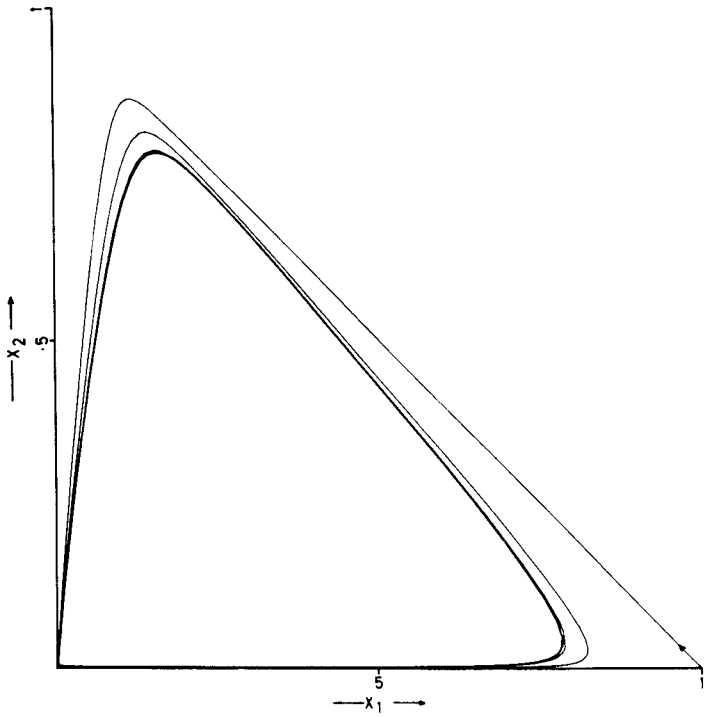


Figure 7. Phase portrait of $\langle 5 \rangle$ projected onto the plane (x_1, x_2). (a) = starting from a point near the center of S_5; (b) = starting from a point near the corner $(1-\delta: \delta/4, \delta/4, \delta/4, \delta/4)$, $\delta = 10^{-4}$

The interior of S_2 consists of a single orbit with the point $x_1 = 1$ as α-limit and the point $x_2 = 1$ as ω-limit. Note that the eigenvalue of the Jacobian, i.e. the $\partial/\partial x$ derivative of the right hand side of (23), is 0 for $x = 0$ and 1 for $x = 1$. Thus the system is not symmetric under time reversal.

(2) Fixed point edge $\langle 2B \rangle$. This system occurs as the edge between two nonconsecutive pure states of the n-hypercycle, $n \geqq 4$. For example, if $x_2 = x_4 = 0$ in the 4-population simplex, one obtains $\dot{x}_1 = \dot{x}_2 = \dot{x}_3 = \dot{x}_4 = 0$. Thus all points on such an edge are invariant.

4.2. The case $m = 3$. Apart from the complete 3-population simplex, there are three cases:

(1) Two flowing edges $\langle 3A \rangle$: This system occurs on the boundary of the n population simplex for $n \geqq 4$. For example, if $x_4 = 0$ in the 4-population

simplex, one obtains the system

$$\begin{aligned}\dot{x}_1 &= x_1(-r)\\ \dot{x}_2 &= x_2(x_1 - r)\\ \dot{x}_3 &= x_3(x_2 - r)\end{aligned} \tag{24}$$

(with $r = x_1x_2 + x_2x_3$)$^{\cdot}$ on the simplex S_3. The edge $\overline{13}$ is fixed, the other two are flowing. Since $(x_1 + x_2)^{\cdot} = -x_2^2x_3 \leqq 0$, $x_1 + x_2$ is a Ljapunov function for the interior of S_3, and thus the point $x_3 = 1$ is a stable attractor for every point in the interior. By a change of coordinates $x = x_1$, $y = x_2$ one obtains

$$\begin{aligned}\dot{x} &= xy(y-1)\\ \dot{y} &= y(x - y - y^2).\end{aligned} \tag{25}$$

The Jacobian at the point $y = 0$, $x = d$ has eigenvalues 0 and d $(0 \leqq d \leqq 1)$. Introducing polar coordinates, $r = \sqrt{x^2 + y^2}$ and $\psi = \operatorname{arctg}(y/x)$, one obtains

$$\dot{\psi} = r\cos^2\psi \sin\psi, \dot{r} = r^2 \sin\psi\,[r\sin\psi - 1 + \sin\psi\cos\psi].$$

Thus we find

$$\lim_{r\to 0} \frac{r\dot{\psi}}{\dot{r}} = \frac{\cos^2\psi}{\sin\psi\cos\psi - 1} \text{ for } r \to 0.$$

This result shows that $\psi = \pi/2$ is the only critical direction (cf. Nemytskii and Stepanov, 1960). Thus the orbits become tangent to the edge $\overline{23}$ as they approach the ω-limit $x_3 = 1$. On the other hand, since $r\dot{\psi}/\dot{r} = -1$ for $\psi = 0$, the orbits become parallel to the edge $\overline{12}$ near their α-limits on the edge $\overline{13}$. The phase portrait is drawn in Figure 4b.

(2) One flowing edge $\langle 3B \rangle$: This system occurs on the boundary of the n-population simplex for $n \geqq 5$. For example, if $x_3 = x_5 = 0$ in the 5-population simplex, one obtains the system:

$$\begin{aligned}\dot{x}_1 &= -x_1 r\\ \dot{x}_2 &= (x_1 + x_4)r\\ \dot{x}_4 &= -x_4 r\end{aligned} \tag{26}$$

(with $r=x_1x_2$). The only flowing edge is $\overline{12}$. It is easy to see that in the interior, x_1/x_4 is constant while x_1/x_2 and x_4/x_2 are decreasing. Thus the orbits point straight towards $x_2=1$. All points in the interior have $x_2=1$ as ω-limit and some point on the fixed edge $\overline{14}$ as α-limit.

(3) No flowing edge $\langle 3C\rangle$: This system occurs on the boundary of the n-population simplex for $n\geqq 6$. For example if $x_2=x_4=x_6=0$ in the 6-population simplex, the 3-simplex (x_1, x_3, x_5) consists entirely of fixed points.

4.3. The case $m=4$. Apart from the complete 4-population simplex, there are five cases:

(1) Three flowing edges $\langle 4A\rangle$: This system occurs on the boundary of the n-population simplex for $n\geqq 5$. For example, if $x_5=0$ in the 5-population simplex, one obtains:

$$\begin{aligned}\dot{x}_2&=x_1(-r)\\ \dot{x}_2&=x_2(x_1-r)\\ \dot{x}_3&=x_3(x_2-r)\\ \dot{x}_4&=x_4(x_3-r)\end{aligned}\tag{27}$$

(with $r=x_1x_2+x_2x_3+x_3x_4$). Two of the faces of this simplex (namely $x_1=0$ and $x_4=0$) are of type $\langle 3A\rangle$, the other two of type $\langle 3B\rangle$. Three of the edges are flowing and three are fixed. Since $\dot{x}_1<0$ in the interior of S_4, there are no fixed points or closed orbits. The ratio x_3/x_1 is increasing, since

$$\left(\frac{x_3}{x_1}\right)^{\cdot}=\frac{x_2x_3}{x_1}\geqq 0$$

Thus the orbits through the planes $x_3/x_1=\text{const.}$ (which contain the edge $\overline{24}$) are directed towards the plane $x_1=0$. Once x_3/x_1 is larger than 1, the ratio x_4/x_2 is increasing

$$\left(\frac{x_4}{x_2}\right)^{\cdot}=\frac{x_4x_1}{x_2}\left(\frac{x_3}{x_1}-1\right).$$

The orbits approach the flowing edge $\overline{34}$. The point $x_4=1$ is the ω-limit of all points in the interior of S_4 (see Figure 4c).

(2) Two consecutive flowing edges $\langle 4C\rangle$: This system occurs on the

boundary of the n-population simplex, $n \geqq 6$. For example if $x_4 = x_6 = 0$ on the 6-population simplex, one obtains:

$$\begin{aligned} \dot{x}_1 &= x_1(-r) \\ \dot{x}_2 &= x_2(x_1 - r) \\ \dot{x}_3 &= x_3(x_2 - r) \\ \dot{x}_5 &= x_5(-r) \end{aligned} \tag{28}$$

with $r = x_1x_2 + x_2x_3$. The boundary has two faces of type $\langle 3B \rangle$, one of type $\langle 3A \rangle$ and one of type $\langle 3C \rangle$. The edges $\overline{12}$ and $\overline{23}$ are flowing, the others are fixed. The planes $x_5/x_1 = \text{const.}$ are invariant. Putting a coordinate system (x, y) on such a plane, with $(1, 0)$ corresponding to $x_2 = 1$, $(0, 1)$ corresponding to $x_3 = 1$ and $(0, 0)$ corresponding to some point on the edge $\overline{15}$, one obtains

$$\begin{aligned} \dot{x} &= x[-xy + d(1 - x - y)(1 - x)] \\ \dot{y} &= xy[(1 - d)(1 - y) + dx] \end{aligned}$$

with $0 \leqq d \leqq 1$ given by $x_5/x_1 = (1 - d)/d$.

Since $\dot{y} \geqq 0$, the point $(0, 1)$ is an attractor for all the points (x, y) belonging to the interior of S_4. The phase portrait is shown in Figure 4d: every point in the interior of S_4 has $x_3 = 1$ as ω-limit and some point on the face $x_2 = 0$ as α-limit. x_2 increases for a time, then decreases to 0.

(3) Two non-consecutive flowing edges $\langle 4B \rangle$: This system occurs on the boundary of the n-population simplex for $n \geqq 6$. For example, if $x_3 = x_6 = 0$ on the 6-population simplex we obtain:

$$\begin{aligned} \dot{x}_1 &= x_1(-r) \\ \dot{x}_2 &= x_2(x_1 - r) \\ \dot{x}_4 &= x_4(-r) \\ \dot{x}_5 &= x_5(x_4 - r) \end{aligned} \tag{29}$$

(with $r = x_1x_2 + x_4x_5$). The four faces of this simplex are all of type $\langle 3B \rangle$. The two edges $\overline{12}$ and $\overline{14}$ are flowing, the others are fixed. Again we find invariant planes $x_1/x_4 = \text{const.}$ Putting a coordinate system (x, y) on such a plane, with $(1, 0)$ corresponding to $x_2 = 1$, $(0, 1)$ corresponding to $x_5 = 1$

and (0,0) corresponding to some point on the edge $\overline{14}$, one obtains

$$\dot{x} = x(1-x-y)[(1-d)-x(1-d)-yd]$$
$$\dot{y} = y(1-x-y)[d-x(1-d)-yd]$$

with $0 \leqq d \leqq 1$ given by $x_1/x_4 = (1-d)/d$. Interchanging d and $1-d$ has the same effect as permuting x and y. The origin is a source with eigenvalues d and $1-d$. For $d > 1/2$ one has $\dot{y} > 0$ and the point (0, 1) is an attractor for all the points (x, y) belonging to the interior of S_4. For $d < 1/2$ the situation is symmetric. For $d = 1/2$, the orbits point straight away from the origin. The phase portrait is shown in Figure 4e. The α-limit of any point in the interior of S_4 is some point on the edge $\overline{14}$. The ω-limit is $x_5 = 1$ in the "half simplex" $x_4 > x_1$, $x_2 = 1$ for $x_4 < x_1$ and some point on the edge $\overline{25}$ for $x_4 = x_1$.

(4) One flowing edge $\langle 4D \rangle$: This system occurs on the boundary of the n-population simplex for $n \geqq 7$. For example, if $x_3 = x_5 = x_7 = 0$ on the 7-population simplex, one obtains

$$\begin{aligned} \dot{x}_1 &= x_1(-r) \\ \dot{x}_2 &= (x_1 + x_4 + x_6)r \\ \dot{x}_4 &= x_4(-r) \\ \dot{x}_6 &= x_6(-r) \end{aligned} \tag{30}$$

(with $r = x_1 x_2$). Two faces are of type $\langle 3B \rangle$ and two of type $\langle 3C \rangle$. Only the edge $\overline{12}$ is flowing. Since $x_4/x_1, x_6/x_1$ and x_6/x_4 are constant and $\dot{x}_2 > 0$, one sees that all orbits point straight towards $x_2 = 1$. The points in the interior of S_4 have $x_2 = 1$ as ω-limit and some point on the face $x_2 = 0$ as α-limit.

(5) No flowing edge $\langle 4E \rangle$: This system occurs on the boundary of the n-population simplex for $n \geqq 8$. For example, if $n = 8$ and if $x_1 = x_3 = x_5 = x_7 = 0$, one obtains $\dot{x}_2 = \dot{x}_4 = \dot{x}_6 = \dot{x}_8 = 0$. Thus the simplex S_4 consists entirely of fixed points.

4.4. Recurrence relations between S_m and S_{m-1}. Denoting a simplex S_m as $M(a, b, c, \ldots, z)$ we shall understand by M the total number of edges and by a, b, c the number of adjacent flowing edges following each fixed point edge; a zero has to be put in places where two fixed point edges touch each other.

Thus 6(2, 1, 0) describes a simplex S_6 containing two adjacent flowing

edges and one such edge separated from the former by one and two fixed point edges on each side respectively. Note that the simplex is left invariant under cyclic permutation and under reflection of the indices. Applying the following recurrence relations to all indices "i" of a simplex S_m, one obtains all restrictions of S_m to S_{m-1}

$$
\begin{array}{lcl}
S_m & \Rightarrow & S_{m-1} \\
M(\ldots,i,\ldots): i=0 & & M-1(\ldots,\hat{i},\ldots) \\
M(\ldots,i,\ldots): i=1 & & M-1(\ldots,0,\ldots) \\
M(\ldots,i,\ldots): i\geqq 2 & & M-1(\ldots,0,i-2,\ldots) \\
 & & \oplus M-1(\ldots,1,i-3,\ldots) \\
 & & \vdots \\
 & & \oplus M-1(\ldots,i-2,0,\ldots)
\end{array}
$$

5. *Discussion*

5.1. Stability of hypercycles. One of the most important results obtained here concerns the existence of an attractor in IS_n. This attractor is a stable equilibrium point in systems with $n=2$, 3 and 4 and a stable limit cycle for $n\geqq 5$. In the three systems of lower dimension we were able to derive an analytical proof for asymptotic stability of the dynamical systems which converge to the fixed point $\bar{\mathbf{x}}_0=(1/n, 1/n, \ldots, 1/n)$. For dynamical systems with $n\geqq 5$ $\bar{\mathbf{x}}_0$ was found to be a saddle point. There is strong numerical evidence for the existence of a stable closed orbit in these systems ($n\geqq 5$). Thus there is no point in IS_n, which has an ω-limit on BS_n.

As a consequence of the existence of an attractor in IS_n no population variable vanishes along a trajectory starting from any point in IS_n. Hence no component of an intact or complete hypercycle of type (4) will be extinguished within the frame of the deterministic approach of chemical kinetics.†

5.2. Time average of population variables. All sets of solution curves for the system of differential equations in (4) have a common characteristic and physically important property: The time averages of the relative (or normalized) population variables, $w_i(t)$

$$w_i(t)=\frac{1}{t-t_0}\int_{t_0}^{t} x_i(\tau)\mathrm{d}\tau \tag{31}$$

$$\bar{w}_i=\lim_{t\to\infty} w_i(t)=\lim_{t\to\infty}\frac{1}{t-t_0}\int_{t_0}^{t} x_i(\tau)\mathrm{d}\tau \tag{32}$$

†A rigorous proof for this statement is given in Schuster *et al.*, 1978.

converges very fast. In systems with stable fixed points in IS_n ($n=2$, 3 and 4), of course, $\bar{w}_i=\bar{x}_i=1/n$. Systems with limit cycles in IS_n ($n\geqq 5$) converge to the same values $\bar{w}_i=1/n$ obtained by integration over a whole period. Again we find fast convergence of $w_i(t)$. In Figures 8a,b $x_i(t)$ and $w_i(t)$ are compared for two examples with oscillating solutions ($n=4, 5$). After a few rotations the time averages for all population variables remain constant for practical purposes; $w_i(t)$ exhibits strongly damped oscillations. We might call this approach towards stationary or oscillatory states "internal equilibration". Complicated dynamical systems consisting of hypercyclic units or subunits can be studied appropriately under the simplifying assumption of established internal equilibrium (Eigen and Schuster, 1977). This approximation can be well justified only for rapidly equilibrating systems like those considered here.

5.3. Regulation of population variables. As we have shown in Section 5.2 all time averaged population variables $w_i(t)$ converge to $\bar{w}_i=1/n$. The equal values for all variables are just a consequence of the assumption of equal rate constants $k_1=k_2=\ldots=k_n=k$. In the more general case one would have obtained:

$$\bar{w}_i=k_j^{-1}\Big/\sum_{l=1}^{n} k_l^{-1}\,;j=i+1-n\delta_{in}\,. \tag{33}$$

Accordingly, relative values of time averaged population variables are automatically controlled by the dynamical system. This property unites the set of components to an organized system. In case of total populations, $c=c(t)$, growing slowly enough to guarantee established internal equilibrium, the time averaged relative population variables remain constant for practical purposes and the hypercycle is growing as a stable entity.

5.4. ω-limits of points in BS_n. Let us assume that a hypercycle has reached BS_n by some catastrophic or stochastic event which led to extinction of one component: $x_i=0$. In this situation, which can be understood properly as a break in the catalytic hypercycle the residual dynamical system represents an open chain of catalytic reactions involving autocatalysts. Such chains are not stable. A chain resulting from a cleavage between the components k and l ($k=i-1+n\delta_{i1}$, $l=i+1-n\delta_{in}$; $x_i=0$) of a hypercycle will converge to the pure state lying just before the break: $x_k=1$. For more details see Section 2 in Schuster *et al.*, 1978.

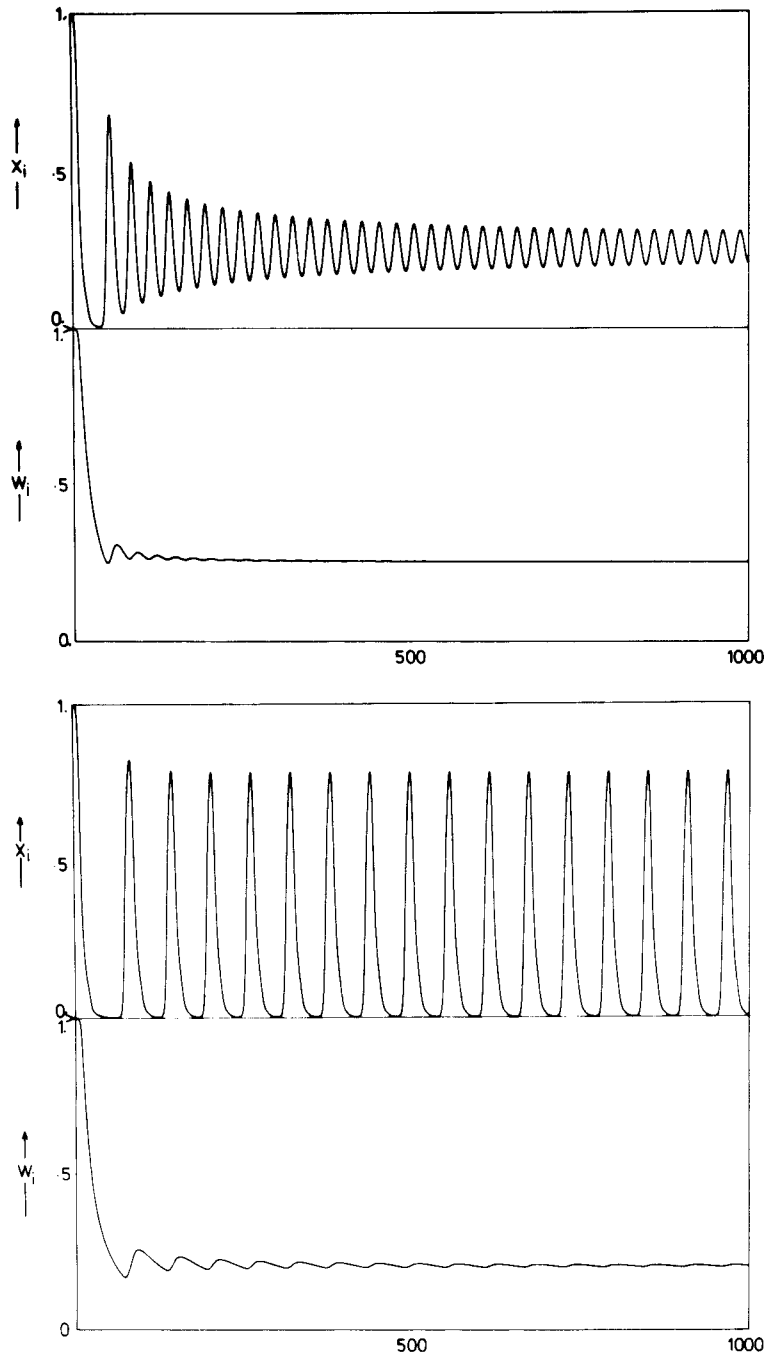


Figure 8. Solution curves $x_i(t)$ and their time averages $w_i(t)$. (a) a typical curve of $\langle 4 \rangle$ on S_4; (b) a typical curve of $\langle 5 \rangle$ on S_5, abscissa = time axis, full range = 1000 time units

5.5. Asymmetry of flows and pure states. Turning now to more mathematical aspects of the dynamical system (4) on S_n we realize an interesting local asymmetry around pure states, $x_i = 1$. The state is unstable against fluctuations of x_k: $\delta x_k > 0$, $k = i + 1 - n\delta_{in}$. In case such a fluctuation occurs, the state vector leaves with initially strongly increasing speed and flows along the edge $\overline{ik}$ towards the next pure state $x_k = 1$. Fluctuations in the opposite direction with respect to the cycle shown in Figure 1: $\delta x_j > 0$, $j = i - 1 + n\delta_{i1}$, on the other hand, are not enhanced and will slowly fade out. This asymmetry at the corners of the concentration simplex reflects the cyclic symmetry of the dynamical system and the complete irreversibility of catalytic actions presumed in our model.

5.6. Relations between the eigenvectors of the dynamical systems linearized around $\bar{\mathbf{x}}_0$ *and the cyclic groups* $\mathfrak{C}_n$. It seems interesting to relate the symmetry properties of our dynamical systems (4) to group theory. The analysis can be performed in a straightforward way by linearizing the set of differential equations around the central fixed point $\bar{\mathbf{x}}_0$. For that purpose we define the permutation

$$P_n = \begin{pmatrix} 1234 \ldots . n \\ n123 \ldots . n-1 \end{pmatrix}$$

as an element of the group Γ_n. It is easy to verify that the set $(E, P_n, P_n^2, \ldots, P_n^{n-1})$ fulfils the group postulates. Furthermore Γ_n is isomorphic to the cyclic group $\mathfrak{C}_n$. The operation P_n is equivalent to the rotation C_n. Additionally, we find that the eigenvectors $\xi_0^{(j)}$ are also solutions of the following eigenvalue equation:

$$P_n \xi_0^{(j)} = \xi_0^{(j)} \cdot \lambda_j \,. \tag{34}$$

Thus, λ_j represents the character χ_j of the corresponding one dimensional irreducible representations or the character of one dimensional components of two dimensional representations.† Finally, we realize that the eigenvectors $\xi_0^{(j)}$ can be assigned to the irreducible representations of $\mathfrak{C}_n$ in a one to one relation (Table I).

5.7. Structural and Ljapunov stability. The dynamical system (4) is certainly not structurally stable since the fixed points in the corners have

†In the cyclic groups $\mathfrak{C}_n$ there are one- and two-dimensional irreducible representations. The two-dimensional representations however, can be split into two one-dimensional components, provided complex numbers are admitted as characters.

TABLE I
Eigenvectors $\xi_0^{(j)}$ and Irreducible Representations of $\mathfrak{C}_n$ (McWeeny, 1963).

n: odd integer		n: even integer	
$\Gamma(\mathfrak{C}_n)$	$j(\xi_0^{(j)})$	$\Gamma(\mathfrak{C}_n)$	$j(\xi_0^{(j)})$
A	1	A	1
E_1	$\begin{cases} 2 \\ n \end{cases}$	B	$\frac{n}{2}+1$
E_2	$\begin{cases} 3 \\ n-1 \end{cases}$	E_1	$\begin{cases} 2 \\ n \end{cases}$
E_3	$\begin{cases} 4 \\ n-2 \end{cases}$	E_2	$\begin{cases} 3 \\ n-1 \end{cases}$
$\vdots$	$\vdots$	$\vdots$	$\vdots$

zero eigenvalues. Thus there exist arbitrarily small perturbations of the differential equations which lead to completely different phase portraits. On the other hand, (4) is Ljapunov stable in IS_n, i.e. small changes in the initial conditions produce only small changes in the solutions. This holds also for most of the restrictions of (4) to the interior of the subfaces S_m of S_n.

5.8. Comparison with Hopf bifurcation. The equations (4) seem to exhibit a phenomenon somewhat reminding of Hopf bifurcation (Marsden and McCracken, 1976): for $n \leqq 4$, the fixed point in the center is a sink and an attractor for IS_n, while for $n > 4$, it is a saddle point and the attractor of the system is a closed orbit. In contrast to the ordinary Hopf bifurcation, however, the critical parameter in our dynamical systems is a discrete quantity, namely the dimension of the system, n.

The authors want to express their gratitude to Prof. Dr. Manfred Eigen for numerous stimulating discussions and his continuous encouraging interest in this subject. Financial support by the Austrian "Fonds zur Förderung der Wissenschaftlichen Forschung" and generous supply of computer time by the "Interuniversitäres Rechenzentrum, Wien" and by the "Institut für technische Mathematik, Technische Universität Wien" is gratefully acknowledged. We are indebted to Prof. Schnabl, Dr, Vogl. Dr. Hörtlehner, Dr. Rattay and Dr. Fuchs for helpful conversation.

LITERATURE

Coddington, E. A. and N. Levinson. 1955. *Theory of Ordinary Differential Equations*, pp. 371–388. New York: McGraw-Hill.

Crow, J. F. and M. Kimura. 1970. *An Introduction to Population Genetics Theory*. Harper & Row.

Eigen, M. 1971. "Selforganization of Matter and the Evolution of Biological Macromolecules." *Die Naturwissenschaften*, **58**, 465–523.

Eigen, M. and P. Schuster. 1977. "The Catalytic Hypercycle—a Principle of Precellular Organization." *Die Naturwissenschaften*, **64**, 541–565.

Hadeler, K. P. 1974. *Mathematik für Biologen*, pp. 96–97, 147–149. Berlin: Springer.

Jones, B. L. 1977. "A Solvable Selfproductive Hypercycle Model for the Selection of Biological Molecules." *J. Math. Biol.*, **4**, 187–193.

Marsden, J. E. and M. McCracken. 1976. "The Hopf Bifurcation and its Applications." *Springer Series in Applied Mathematical Sciences* **19**. New York: Springer.

McWeeny, R. 1963. *Symmetry*: pp. 96–100. Oxford: Pergamon Press.

Nemytskii, V. V. and V. V. Stepanov. 1960. "Qualitative Theory of Differential Equations." *Princeton Mathematical Series* **22**. Princeton University Press.

Schuster, P., K. Sigmund and R. Wolff. 1978. "Dynamical Systems Under Constant Organization III: Cooperative and Competitive Behaviour of Hypercycles." Submitted for publication.

RECEIVED 5-10-77
REVISED 9-14-77