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AUTOPOIESIS: THE ORGANIZATION OF LIVING SYSTEMS, ITS CHARACTERIZATION AND A MODEL

F.G. VARELA, H.R. MATURANA and R. URIBE

Facultad de Sciencias e Departamenta de Electricidad, University of Chile, Santiago, Chile

We formulate the organization of living organisms through the characterization of the class of autopoietic systems to which living things belong. This general characterization is seen at work in a computer simulated model of a minimal case satisfying the conditions for autopoietic organization.

1. Introduction

Notwithstanding their diversity, all living systems must share a common organization which we implicitly recognize by calling them "living". At present there is no formulation of this organization, mainly because the great developments of molecular, genetic and evolutionary notions in contemporary biology have led to the overemphasis of isolated components, e.g. to consider reproduction as a necessary feature of the living organization and, hence, not to ask about the organization which makes a living system a whole, autonomous unity that is alive regardless of whether it reproduces or not. As a result, processes that are history dependent (evolution, ontogenesis) and history independent (individual organization) have been confused in the attempt to provide a single mechanistic explanation for phenomena which, although related, are fundamentally distinct.

We assert that reproduction and evolution are not constitutive features of the living organization and that the properties of a unity cannot be accounted for only through accounting for the properties of its components. In contrast, we claim that the living organization can only be characterized unambiguously by specifying the network of interactions of components which constitute a living system as a whole, that is, as a "unity". We also claim that all biological phenomenology, including reproduction and evolution, is secondary to the establishment of this unitary organization. Thus, instead of asking "What are the necessary properties of the components that make a living system possible?" we ask "What is the necessary and sufficient organization for a given system to be a living unity?" In other words, instead of asking what makes a living system reproduce, we ask what is the organization reproduced when a living system gives origin to another living unity? In what follows we shall specify this organization.

2. Organization

Every unity can be treated either as an unanalyzable whole endowed with constitutive properties which define it as a unity, or else as a complex system that is realized as a unity through its components and their mutual relations. If the latter is the case, a complex system is defined as a unity by the relations between its components which realize the system as a whole, and its properties as a unity are determined by the way this unity is defined, and not by particular properties of its components. It is these relations which define a complex system as a unity and constitute its organization. Accordingly, the same organization may be realized in different systems with different kinds of components as long as these components have the properties which realize the required relations. It is obvious that with respect to their organization such systems are members of the same class, even though with respect to the nature of their components they may be distinct.

3. Autopoietic Organization

It is apparent that we may define classes of systems (classes of unities) whose organization is specifiable in terms of spatial relations between components. This is the case of crystals, different kinds of which are defined only by different matrices of spatial relations. It is also apparent that one may define other classes of systems whose organization is specifiable only in terms of relations between processes generated by the interactions of components, and not by spatial relations between these components. Such is the case of mechanistic systems in general, different kinds of which are defined by different concatenations (relations) of processes. In particular this is the case of living systems whose organization as a subclass of mechanistic systems we wish to specify.

The autopoietic organization is defined as a unity by a network of productions of components which (i) participate recursively in the same network of productions of components which produced these components, and (ii) realize the network of productions as a unity in the space in which the components exist. Consider for example the case of a cell: it is a network of chemical reactions which produce molecules such that (i) through their interactions generate and participate recursively in the same network of reactions which produced them, and (ii) realize the cell as a material unity. Thus the cell as a physical unity, topographically and operationally separable from the background, remains as such only insofar as this organization is continuously realized under permanent turnover of matter, regardless of its changes in form and specificity of its constitutive chemical reactions.

4. Autopoiesis and Allopoiesis

The class of systems that exhibit the autopoietic organization, we shall call autopoietic systems.

Autonomy is the distinctive phenomenology resulting from an autopoietic organization: the realization of the autopoietic organization is the product of its operation. As long as an autopoietic system exists, its organization is invariant; if the network of productions of components which define the organization is disrupted, the unity disintegrates. Thus an autopoietic system has a domain in which it can compensate for perturbations through the realization of its autopoiesis, and in this domain it remains a unity.

In contradistinction, mechanistic systems whose organization is such that they do not produce the components and processes which realize them as unities and, hence, mechanistic systems in which the product of their operation is different from themselves, we call allopoietic. The actual realization of these systems, therefore, is determined by processes which do not enter in their organization. For example, although the ribosome itself is partially composed of components produced by ribosomes, as a unity it is produced by processes other than those which constitute its operation. Allopoietic systems are by constitution non-autonomous insofar as their realization and permanence as unities is not related to their operation.

5. Autopoiesis: The Living Organization

The biological evidence available today clearly shows that living systems belong to the class of autopoietic systems. To prove that the autopoietic organization is the living organization, it is then sufficient to show, on the other hand, that an autopoietic system is a living system. This has been done by showing that for a system to have the phenomenology of a living system it suffices that its organization be autopoietic (Maturana and Varela, 1973).

Presently, however, it should be noticed that in this characterization, reproduction does not enter as a requisite feature of the living organization. In fact, for reproduction to take place there must be a unity to be reproduced: the establishment of the unity is logically and operationally antecedent to its reproduction. In living systems the organization reproduced is the autopoietic organization, and reproduction takes place in the process of autopoiesis; that is, the new unity arises in the realization of the autopoiesis of the old one. Reproduction in a living system is a process of *division* which consists, in principle, of a process of fragmentation of an autopoietic unity with distributed autopoiesis such that the cleavage separates fragments that carry the same autopoietic network of production of components that defined the original unity. Yet, although self-reproduction is not a requisite feature of the living organization, its occurrence in living systems as we know them is a necessary condition for the generation of a historical network of successively generated, not necessarily identical, autopoietic unities, that is, for evolution.

6. A Minimal Case: The Model

We wish to present a simple embodiment of the autopoietic organization. This model is significant in two respects: on the one hand, it permits the observation of the autopoietic organization at work in a system simpler than any known living system, as well as its spontaneous generation from components; on the other hand, it may permit the development of formal tools for the analysis and synthesis of autopoietic systems.

The model consists of a two-dimensional universe where numerous $\bigcirc$ elements ("substrate"), and a few $\star$ ("catalysts") move randomly in the spaces of a quadratic grid. These elements are endowed with specific properties which determine interactions that may result in the production of other elements $\boxtimes$ ("links") with properties of their own and also capable of interactions ("bonding"). Let the interactions and transformations be as follows:

SCHEMA I

[1] Composition: $\star + 2\bigcirc \rightarrow \star + \boxtimes$

[2] Concatenation (Bonding): $\underbrace{\boxtimes - \boxtimes - \ldots - \boxtimes}_{n} + \boxtimes \rightarrow \underbrace{\boxtimes - \boxtimes - \ldots - \boxtimes}_{n+1}$

$n = 1, 2, 3, \ldots$

[3] Disintegration: $\boxtimes \rightarrow 2\bigcirc$

Interaction [1] between the catalyst $\star$ and

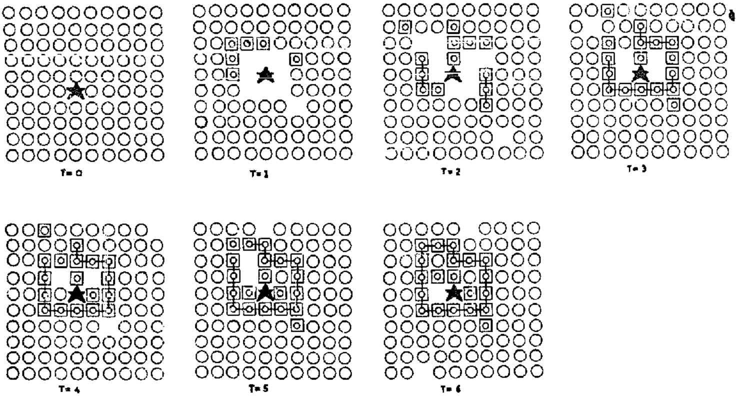

Fig. 1. The first seven instants (0→6) of one computer run, showing the spontaneous generation of an autopoietic unity. Interactions between substrate ○ and catalyst ★ produce chains of bonded links ⊡, which eventually enclose the catalyst, thus closing a network of interactions which constitutes an autopoietic unity within this universe.

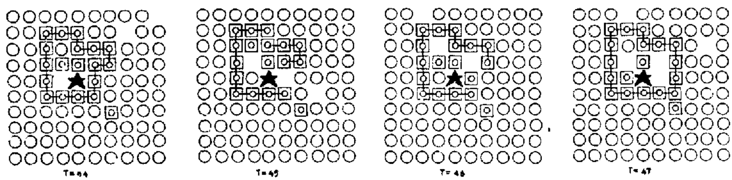

Fig. 2. Four successive instants (44–47) along the same computer run (Fig. 1), showing compensation in the boundary broken by spontaneous decay of links. Ongoing production of links re-establishes the unity under changes of form and turnover of components.

two substrate elements 2 ○ is responsible for the composition of an unbonded link ⊡. These links may be bonded through Interaction [2] which concatenates these bonded links to unbranched chains of ⊡. A chain so produced may close upon itself, forming an enclosure which we assume to be penetrable by the ○'s, but not for ★. Disintegration (Interaction [3]) is assumed to be independent of the state of links ⊡, i.e., whether they are free or bound, and can be viewed either as a spontaneous decay or as a result of a collision with a substrate element ○.

In order to visualize the dynamics of the system, we show two sequences (Figures 1 and 2) of successive stages of transformation as they were obtained from the print-out of a computer simulation of this system.*

If an ⧇-chain closes on itself enclosing an element ★ (Fig. 1), the ⧇'s produced within the enclosure by Interaction [1] can replace in the chain, via [2], the elements ⧇ that decay as a result of [3] (Fig. 2). In this manner, a unity is produced which constitutes a network of productions of components that generate and participate in the network of productions that produced these components by effectively realizing the network as a distinguishable entity in the universe where the elements exist. Within this universe these systems satisfy the autopoietic organization. In fact, element ★ and elements O produce element ⧇ in an enclosure formed by a bidimensional chain of ⧇'s; as a result the ⧇'s produced in the enclosure replace the decaying ⧇'s of the boundary, so that the enclosure remains closed for ★ under continuous turnover of elements, and under recursive generation of the network of productions which thus remains invariant (Figs. 1 and 2). This unity cannot be described in geometric terms because it is not defined by the spatial relations of its components. If one stops all the processes of the system at a moment in which ★ is enclosed by the ⧇-chain, so that spatial relations between the components become fixed, one indeed has a system definable in terms of spatial relations, that is, a crystal, but not an autopoietic unity.

It should be apparent from this model that the processes generated by the properties of the components (Schema I) can be concatenated in a number of ways. The autopoietic organization is but one of them, yet it is the one that by definition implies the realization of a dynamic unity. The same components can generate other, allopoietic organizations; for example, a chain which is defined as a sequence of ⧇'s, is clearly allopoietic since the production of the components that realize it as a unity do not enter into its definition as a unity. Thus, the autopoietic organization is neither represented nor embodied in Schema I, as in general no organization is represented or embodied in the properties that realize it.

* Details of computation are given in the Appendix. To facilitate appreciation of the developments, Fig. 1 and 2 are drawn from the print-outs with change of symbols used in the computations.

7. Tessellation and Molecules

In the case described, as in a broad spectrum of other studies that can generically be called tessellation automata (von Neumann, 1966; Gardner, 1971), the starting point is a generalization of the physical situation. In fact, one defines a space where spatially distinguishable components interact, thus embodying the concatenation of processes which lead to events among the components. This is of course what happens to the molecular domain, where autopoiesis as we know it takes place. For the purpose of explaining and studying the notion of autopoiesis, however, one may take a more general view as we have done here, and revert to the tessellation domain where physical space is replaced by any space (a two-dimensional one in the model), and molecules by entities endowed with some properties. The phenomenology is unchanged in all cases: the autonomous self-maintenance of a unity while its organization remains invariant in time.

It is apparent that in order to have autopoietic systems, the components cannot be simple in their properties. In the present case we required that the components have specificity of interactions, forms of linkage, mobility and decay. None of these properties are dispensable for the formation of this autopoietic system. The necessary feature is the presence of a boundary which is produced by a dynamics such that the boundary creates the conditions required for this dynamics. These properties should provide clues to the kind of molecules we should look for in order to produce an autopoietic system in the molecular domain. We believe that the synthesis of molecular autopoiesis can be attempted at present, as suggested by studies like those on microspheres and liposomes (Fox, 1965; Bangham, 1968) when analyzed in the present framework. For example: a liposome whose membrane lipidic components are produced and/or modified by reactions that take place between its components, only under the conditions of concentration produced within the liposome membrane, would constitute an autopoietic system. No experiments along these lines have been carried out, although they are potential keys for the origin of living systems.

8. Summary

We shall summarize the basic notions that have been developed in this paper:

A. There are mechanistic systems that are defined as unities by a particular organization which we call autopoietic. These systems are different from any other mechanistic system in that the product of their operation as systems thus defined is necessarily always the system itself. If the network of processes that constitutes the autopoietic system is disrupted, the system disintegrates.

B. The phenomenology of an autopoietic system is the phenomenology of autonomy: all changes of state (internal relations) in the system that take place without disintegration are changes in autopoiesis which perpetuate autopoiesis.

C. An autopoietic system arises spontaneously from the interaction of otherwise independent elements when these interactions constitute a spatially contiguous network of productions which manifests itself as a unity in the space of its elements.

D. The properties of the components of an autopoietic system *do not* determine its properties as a unity. The properties of an autopoietic system (as is the case for every system) are determined by the constitution of this unity, and are, in fact, the properties of the *network* created by, and creating, its components. Therefore, to ascribe a determinant value to any component, or to any of its properties, because they seem to be "essential", is a semantic artifice. In other words, all the components, and the components' properties, as well as the circumstances which permit their productive interactions, are necessary when they participate in the realization of an autopoietic network, and none is determinant of the constitution of the network or of its properties as a unity.

9. Key

The following is a six-point key for determining whether or not a given unity is autopoietic:

1. Determine, through interactions, if the unity has identifiable boundaries. If the boundaries can be determined, proceed to 2. If not, the entity is indescribable and we can say nothing.

2. Determine if there are constitutive elements of the unity, that is, components of the unity. If these components can be described, proceed to 3. If not, the unity is an unanalyzable whole and therefore not an autopoietic system.

3. Determine if the unity is a mechanistic system, that is, the component properties are capable of satisfying certain relations that determine in the unity the interactions and transformations of these components. If this

is the case, proceed to 4. If not, the unity is not an autopoietic system.

4. Determine if the components that constitute the boundaries of the unity constitute these boundaries through preferential neighborhood relations and interactions between themselves, as determined by their properties in the space of their interactions. If this is not the case, you do not have an autopoietic unity because you are determining its boundaries, not the unity itself. If 4 is the case, however, proceed to 5.

5. Determine if the components of the boundaries of the unity are produced by the interactions of the components of the unity, either by transformation of previously produced components, or by transformations and/or coupling of non-component elements that enter the unity through its boundaries. If not, you do not have an autopoietic unity; if yes, proceed to 6.

6. If all the other components of the unity are also produced by the interactions of its components as in 5, and if those which are not produced by the interactions of other components participate as necessary permanent constitutive components in the production of other components, *you have an autopoietic unity in the space in which its components exist.* If this is not the case and there are components in the unity not produced by components of the unity as in 5, or if there are components of the unity which do not participate in the production of other components, you do not have an autopoietic unity.

Acknowledgement

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APPENDIX

Conventions

We shall use the following alphanumeric symbols to designate the elements referred to earlier:

Substrate:	O → S
Catalyst:	* → K
Link:	⊡ → L
Bonded link:	-⊡- → BL

The algorithm has two principal phases concerned, respectively, with the motion of the components over the two dimensional array of positions, and with production and disintegration of the L components out of and back into the substrate S's. The rules by which L components bond to form a boundary complete the algorithm.

The "space" is a rectangular array of points, individually addressable by their row

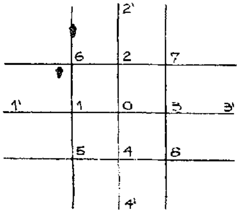

Fig. 3. Designation of coordinates of neighboring spaces with reference to a space with designation "0"

and column positions within the array. In its initial state this space contains one or more catalyst molecules K with *all* remaining positions containing substrate S.

In both the motion and production phases, it is necessary to make random selections among certain sets of positions neighboring the particular point in the space at which the algorithm is being applied. The numbering scheme of Figure 3 is then applied, with location 0 in the figure being identified with the point of application (of course, near the array boundaries, not all of the neighbor locations identified in the figure will actually be found).

Regarding motion, the components are ranked by increasing "mass" as S, L, K. The S's may not displace any other species, and thus are only able to move into "holes" or empty spaces in the grid, though they can pass through a *single* thickness of bonded link BL's to do so. On the other hand the L and K readily displace S's, pushing them into adjacent holes, if these exist, or else exchanging positions with them, thus passing freely through the substrate S. The most massive, K, can similarly displace free L links. However, neither of these can pass through a bonded link segment, and are thus effectively contained by a closed membrane. Concatenated L's, forming bonded link segments, are subject to no motions at all.

Regarding production, the initial state contains no bonded links at all; these appear only as the result of formation from substrate S's in the presence of the catalyst. This occurs whenever two adjacent neighboring positions of a catalyst are occupied by S's (e.g., 2 and 7, or 5 and 4 in Figure 3). Only one L is formed per time step, per catalyst, with multiple possibilities being resolved by random choice. Since two S's are combined to form one L, each such production leaves a new hole in the space, into which S's may diffuse.

The disintegration of L's is applied as a uniform probability of disintegration per time step for each L whether bonded or free, which results in a proportionality between failure rate and size of a chain structure. The sharply limited rate of "repair", which depends upon random motion of S's through the membrane, random production of new L's and random motion to the repair site, makes the disintegration a very powerful controller of the maximum size for a viable boundary structure. A disintegration probability of less than about .01 per time step is required in order to achieve any viable structure at all (these must contain roughtly ten L units at least to form a closed structure with any space inside).

Algorithm

1. Motion, first step
   1.1. Form a list of the coordinates of all holes h_i.
   1.2. For each h_i, make a random selection, n_i, in the range 1 through 4, specifying a neighboring location.
   1.3. For each h_i in turn, where possible, move occupant of selected neighboring location in h_i.
   1.31. If the neighbor is a hole or lies outside the space, take no action.

1.32. If the neighbor n_{ij} contains a bonded L, examine the location n'_i. If n'_i contains an S, move this S to h_i.

1.4. Bond any moved L, if possible (Rules, 6).

2. Motion, second step

2.1. Form a list of the coordinates of free L's, m_i.

2.2. For each m_i, make a random selection, n_i, in the range 1 through 4, specifying a neighboring location.

2.3. Where possible, move the L occupying the location m_i into the specified neighboring location.

2.31. If location specified by n_i contains another L, or a K, then take no action.

2.32. If location specified by n_i contains an S, the S will be displaced.

2.321. If there is a hole adjacent to the S, it will move into it. If more than one such hole, select randomly.

2.322. If the S can be moved into a hole by passing through bonded links, as in step 1, then it will do so.

2.323. If the S cannot be moved into a hole, it will exchange locations with the moving L.

2.33. If the location specified by n_i is a hole, then L simply moves into it.

2.4. Bond each moved L, if possible.

3. Motion, third step

3.1. Form a list of the coordinates of all K's, c_i.

3.2. For each c_i, make a random selection n_i, in the range 1 through 4 specifying a neighboring location.

3.3. Where possible, move the K into the selected neighboring location.

3.31. If the location specified by n_i contains a BL or another K, take no action.

3.32. If the location specified by n_i contains a free L, which may be displaced according to the rules of 2.3, then the L will be moved, and the K moved into its place. (Bond the moved L, if possible).

3.33. If the location specified by n_i contains an S, then move the S by the rules of 2.32.

3.34. If the location specified by n_i contains a free L, not movable by rules 2.3, exchange the positions of the K and the L. (Bond L if possible).

3.35. If the location specified by n_i is a hole, the K moves into it.

4. Production

4.1. For each catalyst c_i, form a list of the neighboring positions n_{ij}, which are occupied by S's.

4.11. Delete from the list of n_{ij} all positions for which neither adjacent neighbor position appears in the list (i.e., "1" must be deleted from the list of n_{ij}'s, if neither 5 nor 6 appears, and a "6" must be deleted if neither 1 nor 2 appears).

4.2. For each c_i with a non-null list of n_{ij}, choose randomly one of the n_{ij}, let its value be p_i, and at the corresponding location, replace the S by a free L.

4.21; If the list of n_{ij} contains only one which is adjacent to p_i, then remove the corrsponding S.

4.22. If the list of n_{ij} includes both locations adjacent to p_i, randomly select the S to be removed.

4.3. Bond each produced L, if possible.

5. Disintegration

5.1. For each L, bonded or unbonded, select a random real number, d, in the range (0,1).

5.11. If $d \leq Pd$ (Pd an adjustable parameter of the algorithm), then remove the corresponding L, attempt to re-bond (Rules, 7).

5.12. Otherwise proceed to next L.

6. Bonding

This step must be given the coordinates of a free L.

6.1. Form a list of the neighboring positions n_i, which contain free L's, and the neighboring positions m_i, which contain singly bonded L's.

6.2. Drop from the m_i any which would result in a bond angle less than 90°. (Bond angle is determined as in Figure 4).

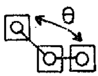

Fig. 4. Definition of "Bond-Angle" θ.

6.3. If there are two or more of the m_i, select two, form the corresponding bonds, and exit.

6.4. If there is exactly one m_i, form the corresponding bond.

6.41. Remove from the n_i any which would now result in a bond angle of less that 90°.

6.42. If there are no n_i, exit.

6.43. Select one of the n_i, form the bond, and exit.

6.5. If there are no n_i, exit.

6.6. Select one of the n_i, form the corresponding bond, and drop it from the list.

6.61. If the n_i list is non-null, execute steps 6.41 through 6.43.

6.62. Exit.

7. Rebond

7.1. Form a list of all neigbor positions m_i occupied by singly bonded L's.

7.2. Form a second list, p_{ij}, of pairs of the m_i which can be bonded.

7.3. If there are any p_{ij}, choose a maximal subset and form the bonds. Remove the L's involved from the list m_i.

7.4. Add to the bond m_i any neighbor locations occupied by free L's.

7.5. Execute steps 7.1 through 7.3, then exit.