Some Remarks on Autocatalysis and Autopoiesis

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Abstract

The notions of collective autocatalysis and of autopoiesis are clearly related; equally clearly, they are not quite the same. The purpose of this paper is to try to clarify the relationship. Specifically I suggest that autopoiesis can be at least roughly characterized as "collective autocatalysis *plus* spatial individuation". While some mechanism of spatial confinement or concentration is probably necessary to the effective operation of *any* collectively autocatalytic reaction network, autopoiesis requires, in addition, that the mechanism for maintaining this confinement should itself be a product of the reaction network—and should thus (?) be capable of separating or individuating otherwise identically organized networks.

I suggest an informal heuristic test to discriminate the (merely) collectively autocatalytic from the (properly?) autopoietic. Finally, in the light of this, I review a variety of published *abstract* or *model* systems (Alchemy, α -universes, Tierra, SCL).

Keys: Autopoiesis, Collective Autocatalysis, Individuality, Artificial Life.

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1 Introduction

The concept of *autopoiesis* was originally formulated by the Chilean biologists Francisco Varela and Humberto Maturana as being "necessary and sufficient to characterize the organization of living systems" (Maturana and Varela, 1973, p. 82). They conceived of autopoiesis as specifying an organization which might be realizable with a variety of material components—not just the specific biochemical molecular species that happen to be characteristic of life on Earth. Indeed, to illustrate this, they described a model system, implemented as a computer program, where autopoietic organization could be realized with just three distinct kinds of component (Varela et al., 1974).¹

The notion of autopoiesis has been extended and applied in a wide variety of domains, including linguistics, social organization, and family therapy. However, my own interest in the theory is strictly concerned with its original "molecular" formulation, as a description of the characteristic autonomy of even the simplest living organisms, conceived as a special category of essentially *chemical* system. The discussion here will be strictly limited to this "molecular" or "chemical" autopoiesis.

To the extent that autopoiesis correctly captures something like a minimum condition for living phenomenology, it has an obvious connection to discussions of the *origin* of life. Indeed, in the autopoietic framework, the origin of life is essentially identical with the origin of molecular autopoiesis (Maturana and Varela, 1973, pp. 93–95).

Much more recently, the concept of a "collectively autocatalysis" has been presented by Stuart Kauffman as being critically involved in, if not identical with, the origin of life (Kauffman, 1993). However, Kauffman makes no explicit reference to autopoiesis.

My purpose here then is primarily to attempt such an explicit comparison between the notions of autopoiesis and collective autocatalysis.

2 Autopoiesis

An autopoietic machine is a machine organized (defined as a unity) as a network of processes of production (transformation and destruction) of components that produces the components which:

- (i) through their interactions and transformations continuously regenerate and realize the network of processes (relations) that produced them; and
- (ii) constitute it (the machine) as a concrete entity in the the space in which they (the components) exist by specifying the topological domain of its realization as such a network.

Maturana and Varela (1973, pp. 78–79)

This is the canonical definition of autopoiesis offered by Maturana and Varela. In the specific case of molecular autopoiesis, it seems clear that the "components" should be interpreted as individual molecules, and the "processes of production" are essentially chemical reactions. It is not quite so clear what it means for these molecules to "continuously regenerate and realize the network of processes that produced them". Elsewhere, the following qualification is offered:

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.

Varela et al. (1974, p. 188)

Still, it is not clear what is the force of the phrase "generate and participate recursively". Specifically, is "generating" a chemical reaction a distinct thing from "participating" in one?

Having reference to the (highly schematic) computer model presented by Varela et al. (1974), it seems plausible to interpret "participating" in a reaction as meaning simply to be a reactant; whereas "generating" a reaction might mean to *catalyse* it. Catalysts are also, of course "reactants"; but their special property is that they emerge unchanged from the catalysed reaction, while drastically increasing the reaction rate. In the limiting case, the uncatalysed reaction may occur with negligible rate, whereas, in the presence of catalyst, it may occur at a rate which has significant manifestations in the system. In such a case, it seems reasonable to say that the catalyst "generates" the reaction (given the availability of the other reactants).

¹It has recently become clear that the original published description of this model had a significant technical defect; but that does not affect the current discussion, and in any case, has now been corrected (McMullin and Varela, 1997).

So the first condition for molecular autopoiesis is that the reaction network which characterizes the organization of the system must produce all the species of molecular component which are considered to materially constitute the system, *and* these components must themselves *generate* the reaction network, in the sense of catalysing some (or all?) of the reactions (which would otherwise occur at negligible rate).

There are still some significant ambiguities here. How, for example, do we determine which components materially "constitute" the system? In the computer model of molecular autopoiesis there is one component, performing a specifically catalytic function, which is *not* itself produced by any reaction in the network—so should it not be regarded as a material component of the system? There are also "substrate" particles which are not-or at least, not necessarily—produced through the constituent reactions of the system (i.e., they may be produced by the reaction network, but may alternatively "drift" in from the external ambience). Also in this model there are two reactions ("concatenation" and "disintegration") which are not catalysed at all—and thus arguably not "generated" by the system.

I should note that Varela et al. (1974) do present a 6-point "key" for determining whether or not a specific system should be regarded as autopoietic. This seems to suggest, for example, that it is acceptable for some of the components not to be produced by reactions in the system, provided that they "participate as necessary permanent constitutive components in the production of other components". This may account for the case of the catalytic component in the model system—though I would suggest that the meaning is still less than precise.

In any case, let us now move on to the second defining condition for autopoiesis. This is that the system itself must specify "the topological domain of its realization". The essential idea here seems to be that the same network of chemical processes which is used to identify the system as such, must also have the effect of locating or demarcating the system in space. The system must, in other words, establish some sort of boundary between "itself" and the rest of the universe in which it is embedded.

In the specific case of biological cells, this boundary is manifested in the external membrane of the cell. In the simplified computer model (which exists in a two dimensional universe), this boundary consists of a closed linear chain of molecules. It seems that, in the case of molecular autopoiesis, the boundary performs at least the function of limiting or controlling the spatial diffusion of the molecules constituting the system. This is presumably necessary because, in the absence of such control on diffusion, the reactant concentrations may dilute to the point where one or more of the defining reactions effectively ceases to operate, and the whole self-sustaining reaction network then breaks down.

3 Collective Autocatalysis

The basic notion of an "autocatalyst" is a molecular species which, in the presence of suitable reaction substrates, catalyses a reaction in which one or more molecules of that same catalyst molecular species are among the reaction products—over and above the original catalyst molecule itself. Note carefully the distinction here between the *original* catalyst molecule which—by definition—emerges unchanged from the catalysed reaction; and the one or more *additional* catalyst molecules which are among the reaction products.

If we assume that the uncatalysed reaction occurs at negligible rate then, in the absence of any catalyst molecules, the substrates will remain unreactive; but if the medium is seeded or innoculated with one or more catalyst molecules this would then trigger production of more catalyst so that the reaction would actually proceed at an *accelerating* rate until limited by the availability of the substrate. If the reaction takes place in a flow reactor, where substrate is continuously provided, and the reaction product removed, then the reaction could evidently sustain itself indefinitely.

Autocatalytic molecules may also be termed "selfreplicating" in a reasonable sense. This has an obvious biological relevance in the exploitation of such molecules as genetic information carriers. This usage depends on the existence of a large set of distinct molecules (which can thus carry "information" via their distinctions) but which are all individually autocatalytic, thus allowing for the generation of informational "copies" for distribution to offspring.

The autocatalytic molecules which play this role, in modern organisms at least, are the nucleic acids. Note, however, that nucleic acids are themselves rather complex; and require complex substrates (nucleotides) and additional catalysts (replicases) in order to manifest their autocatalytic activity. So while autocatalytic molecules, per se, can be very useful and play a key role in modern organisms, it is doubtful whether such molecules could participate in the spontaneous emergence or *origin* of life.

In response to this, Stuart Kauffman has proposed that, while individually autocatalytic molecules might be rather unlikely to arise (or even sustain themselves) spontaneously, the same is *not* necessarily true for *sets* of molecular species which mutually catalyse each others production. The idea here is to consider sets of molecular species such that none of them need be individually autocatalytic (which may be an unfeasible requirement), but where production of every element of the set is effectively catalysed by at least one other member of the same set. In such a situation the whole set is said to be *collectively* autocatalytic.

In just the same way as sketched out for an individually autocatalytic molecular species, we can imagine seeding a flow reactor with a collectively autocatalytic set of species (at least one molecule from each member of the set). Again, provided we maintain a flow of some basic substrate molecules (the "exogenous food set" in Kauffman's terms) there should now be the possibility of an indefinitely sustained, self-reinforcing, reaction network, continuously producing more molecules of all the species in the set.

4 Comparison?

It is clear that the notion of an autocatalytic set is closely related to the *first* element of the definition of autopoiesis. Both involve the idea of a "closed" reaction network which may therefore be able to dynamically sustain itself indefinitely-subject to the availability of some basic "substrate" materials and the overall reaction kinetics etc. The definition of autopoiesis is, admittedly, somewhat ambiguous about the role of *catalytic* activity as such; but the computer model certainly explicitly involves at least one catalysed reaction, without which the putative reaction *network* could not be closed. Conversely, while the reaction networks posited for collective autocatalysis seem to be technically limited to include only catalysed reactions, there doesn't seem to be any particular difficulty about allowing some uncatalysed reactions to participate also; if anything, this possibility should slightly improve the prospects for the spontaneous emergence of such sets.

In trying to isolate more precisely what it is that both the notions of autopoiesis and collectively autocatalytic sets seem to share, I suggest it may be useful to think about the following more concrete scenario. Suppose we have a flow reactor, with a flow of some specified "substrate" or "food set" materials through it. There may be some reactions which occur spontaneously, at significant rates, among these, but we essentially discount such reactions (or assume they run to equilibrium etc.). Now suppose it is the case that this reactor can be seeded with some set of further molecular species, such that a reaction network is then established *which sustains* the presence of these same molecular species under flow conditions. This new network may involve some uncatalysed reactions (which did not previously occur because the relevant reactants did not arise); but it must necessarily involve at least one reaction which must be catalysed, and such that the catalyst species itself gets produced (directly or indirectly) only if this catalysed reaction takes place.

Let me call any reaction network with this property "collectively self-sustaining".

I suggest that this notion is at once both somewhat stronger and somewhat weaker that Kauffman's "collectively autocatalytic set". It is weaker because it allows the inclusion of some uncatalysed reactions. If anything, this relaxation should make it easier for such networks to arise, and would thus strengthen Kauffman's claims for the spontaneous emergence of such networks. However, it is stronger than Kauffman's notion in that it explicitly asks for the reaction network to be selfsustaining in practice—under some specific reaction conditions, and associated reaction kinetics; the collectively autocatalytic property, on the other hand, is a purely topological characteristic of a reaction network graph—indicating only the *possibility* of a self-sustaining network under some otherwise unspecified conditions. Of course, as a practical matter in the origin of life, only reaction networks which are actually self-sustaining under some reasonably feasible conditions can play any significant role.

The relationship between the idea of a selfsustaining network and autopoiesis is somewhat more obscure. Certainly, autopoiesis shares the requirement for actual (as opposed to "potential") self-maintenance, and would seem to have a similar requirement for some sort of (catalytic?) "closure". Yet, it also seems that autopoiesis does not promise a reaction network that would sustain itself under "open" flow conditions. In particular, as already mentioned, in the simplified computer model the molecular species termed "catalyst" does not get produced by any reaction in the network. Under flow conditions either catalyst would flow out without replacement and the reaction network would break down, or catalyst would have to be continuously supplied as a component of the "food set"; but in the latter case the "autopoietic" reaction network would be immediately and unconditionally instantiated, rather than being contingent on seeding. On the face of it this suggests that autopoiesis is a significantly weaker notion than that of self-sustaining network, even to the point of being too weak to be of any interest.

But of course, autopoiesis was not intended to deal with an "open" flow reaction condition; instead it is concerned with very special flow conditions. Special firstly in that they can be (or must be?) *selective*—in the sense of something like a semipermeable membrane; but special secondly in the requirement that the constraints on flow should themselves be a result or consequence of the autopoietic reaction network. It is this requirement for the reaction network to exhibit these two different kinds of closure—closure of the reaction network together with *spatial* closure—that critically demarcates autopoiesis per se, and makes it a significantly stronger and more interesting idea than a self-sustaining reaction network alone.

Maturana and Varela themselves have been clear from their earliest descriptions of autopoiesis that this spatial or topological separation is a critical distinction between their concept and autocatalysis per se:

Autocatalytic processes do not constitute autopoietic systems because among other things, they do not determine their topology. Their topology is determined by a container that is part of the specification of the system, but which is independent of the operation of the autocatalysis. Processes of this or similar kind are abundant in the physical space.

> Maturana and Varela (1973, p. 94, emphasis added)

I suggest that we might interpret Kauffman's work on the emergence of collective autocatalysis as, in significant part, a more formal and rigorous demonstration of the rather bold assertion at the end of this quotation. It should be noted that Kauffman is certainly well aware that spatial enclosure is a significant issue in this area. For example, he stipulates explicitly that, for the reactions of a putatively autocatalytic set to occur "effectively" then the reactants "must be confined to a sufficiently small volume" (Kauffman, 1993, p. 298). However, while he goes on to consider some candidate mechanisms for providing such confinement (e.g., coascervates, proteinoid microspheres, liposomes) it is not clear to me whether he attaches any particular importance to the idea that these containment devices should themselves be produced and maintained as products of the contained reaction network-which seems to be the decisive extra constraint involved in autopoiesis.

5 A Heuristic Test

I have suggested that (molecular) autopoiesis and collective autocatalysis are closely related ideas. Both involve something like a self-sustaining reaction network, and both require some mechanism of spatial localization or confinement for effective operation. The critical distinction is that autopoiesis specifically requires that this confinement should itself be in some sense a product of the confined reaction network, whereas collective autocatalysis is assumed to rely on some independent confinement mechanism.

This seems to me clear enough as far as it goes; but I still have some difficulty in deciding whether the full requirement of autopoiesis is met in particular cases. Specifically, consider the computer model system offered by Varela et al. (1974). It is true that, in this case, there is a cleavage of the space which confines the reaction network, and which is maintained as a specific consequence of the reaction network. However, it is also true that, as an integral aspect of the ongoing behaviour of this autopoietic system, the spatial boundary or membrane is regularly *ruptured*. The membrane is subsequently repaired again—and, indeed, this is arguably the chief phenomenon of interest in this system. Nonetheless, the fact that the spatial localization is regularly interrupted in this way makes it more difficult to be clear what exactly the "topological" autopoietic requirement or criterion is.

So I would like to suggest the following informal and heuristic test. Consider two instances of the same collectively self sustaining reaction network. For the moment I suppose that we do not know whether these should qualify as autopoietic or (merely) collectively autocatalytic. They are considered as instances of the same reaction network in the sense that the same set of molecular species is present in both cases; but they are separate instances in the sense that each is constituted (instantaneously) by distinct collections of individual molecules. Specifically I assume that, initially, they have been prepared or instantiated in separate reaction "vessels" (in the manner of the independent confinement mechanism already posited to support the continued operation of a collectively autocatalytic set). Now consider the situation if the contents of both vessels are "mixed" together. I assume that there will be continued availability of any necessary food set materials etc., so that the selfsustaining behaviour of the network(s) can continue unchanged. The key question now is whether there will still meaningfully be two instances of the reaction network or just one. That is, in the absence of any imposed spatial separation mechanism, do the networks themselves maintain their individuality? I would suggest that, if they do, then this reaction network may reasonably be classified as meeting the autopoietic criterion "for specifying the topological domain of its realization"; whereas if not, then the network should be regarded only as collectively autocatalytic.

6 Some Cases

6.1 Alchemy

The Alchemy system was formulated by Walter Fontana and Leo Buss in an explicit attempt to examine the *abstract* problem of the emergence of biological organization (Fontana and Buss, 1994a, b).

An Alchemy universe or reactor embodies the abstract notion of molecular species, with internal, compositional, structure, and characteristic reactions between instances of these species. All reactions may be characterized as "catalytic" in the sense that the original reactants are preserved, unchanged. (This is possible because, in this abstract system, there is no "conservation of matter" so that reaction products can be created without any consumption of reactants.) There is no notion of "space"—any reactant can potentially react with any other (this is also referred to as a "well-stirred" reactor).

Reactions are deliberately specified to occur under flow conditions—so that particular sets of molecular species can continue to inhabit the reactor on an ongoing basis only if they (collectively) regenerate themselves. Thus, by definition, *only* collectively autocatalytic sets can persist for extended periods in the Alchemy system.

Several different experimental arrangements and outcomes have been described. Briefly, if the possibility of *individually* autocatalytic molecules is allowed (the "Level 0" experiments) then reactors quickly become dominated either by one such species, or a co-operative network of such species. The latter connects these results with the Hypercycles of Eigen and Schuster (1979). Such networks are found to be unstable under perturbation and collapse to single autocatalytic species. If individual autocatalysis is dis-allowed (the "Level 1" experiments), then the spontaneous emergence and persistence of *collectively* autocatalytic reactions networks is reliably observed. This is consistent with Kauffman's analyses. Unlike the previous case, these networks tend to be rather stable under perturbation.

A further set of experiments ("Level 2") considers the results of "mixing together", in one reactor, collectively autocatalytic sets that have first emerged in independent reactors. This is clearly related to my heuristic test for autopoiesis; but it differs critically in that the networks being brought together are *different*, rather than distinct instances of the same network. The results of these experiments are interesting in their own right, but do not relate to my concerns here. On the contrary, it seems clear that, because Alchemy deliberately eschews any notion of spatial structure in a reactor, there is no mechanism for spatial separation or containment. Therefore, even in the absence of any specific experiment, it seems that, if two instances of the same network are placed in a single reactor then they instantly lose all individuality, and become just a single instance.

Thus, although Fontana and Buss refer to Alchemy as being related to work on autopoiesis (as, indeed, it certainly is), I think that the collectively autocatalytic reaction networks exhibited should certainly *not* be considered as autopoietic; and given the deliberate elimination of spatial notions from the model, it seems that autopoietic organization *cannot* emerge, or be embedded, in such systems.

6.2 α -universes

The α -universes are a category of abstract or model systems devised by John Holland over 20 years ago (Holland, 1976). They were loosely inspired by notions of basic biochemical organization, and were devised specifically to consider some issues in the spontaneous emergence of life. The systems are, broadly speaking, "artificial chemistries", with notions of atoms, molecules, and reactions between them (both catalysed and uncatalysed). There is an explicit notion of *space*, albeit only one-dimensional.

Holland discussed one particular α -universe in detail. In this case, while (by design) no single molecular species would be autocatalytic, it is trivially the case that an infinite class of *collectively* autocatalytic networks can be instantiated. This fact can be interpreted—in retrospect—as a specific example of the results presented by Kauffman regarding the relatively weak conditions which are needed for such a phenomenon. Of course, Holland's results significantly predate Kauffman's more general results, and are expressed in a different vocabulary.

Holland's particular interest with this model system was to assess the expected emergence time of instances of such collectively autocatalytic networks. As it turns out, these results are of limited value. Although the reaction networks he cites are abstractly—collectively autocatalytic, they are not in fact capable of sustaining themselves under the conditions envisaged by Holland (McMullin, 1992b). This is at least in part due to the specific dynamics of the system, including diffusion, and the occurrence of unanticipated "side-reactions" which were not allowed for in Holland's analysis. There is also a significant effect due to rapid depletion of the initial "food set".

It is possible (though, to my knowledge, no specific experiments have been carried out) that at least some of the α -universe reaction networks might be successfully self-sustaining if the system were organized in the form of a flow reactor (i.e., with a continuing inflow of food set materials). However, regardless of that, this system actually does not provide any mechanism for spatial localization or containment which could be caused as a result of *any* reactions instantiated in the system. Therefore we can say that, even if it *could* be made to host a viable, self sustaining, reaction network, multiple instances of the same network would *not* be able to maintain their separation, but would inevitably merge together and become indistinguishable.

Therefore the α -universes are not capable of exhibiting autopoietic agents, according to my heuristic test.

6.3 Tierra

Tierra is a class of model system invented by Tom Ray specifically to investigate *evolution* in an abstract framework (Ray, 1992). The inspiration or metaphor for the system is that of the Cambrian explosion. That is, the primitive entities are intended to be analogous to biological (rather than molecular) species; and the dynamics are supposedly ecological and evolutionary rather than chemical. However, I shall suggest that a chemical metaphor may be at least equally applicable, and perhaps illuminating.

In practice, Tierra can viewed as a development of an earlier line of systems, including Core Wars (Dewdney, 1987) and Coreworld (Rasmussen et al., 1990), with, indeed, some strong similarities to the α -universes already discussed. These all involve some sort of one dimensional or linear spatial system, similar to a conventional computer memory (the "core") in which are embedded patterns that can effectively act as information processors or (concurrent) computer *programs*. More technically, each concurrently executing program is termed a separate *process*. Given this general structure, one can immediately envisage circumstances in which processes can interact, can create new processes, and can be destroyed. On a chemical metaphor this means taking individual processes as molecules (with their programs defining their molecular *species*), and their interactions as chemical reactions. The conventional possibilities already raised here for self sustaining systems thus arise afresh in this context.

Ray's experiments can be briefly summarized—in the chemical metaphor—as follows. It is possible, in the basic Tierra system, to construct individually autocatalytic molecules. These are moderately complex, and not capable of spontaneous emergence. However, if the system is manually seeded with such a molecule, it reacts rapidly to fill the reactor. Experiments are conducted under flow conditions (there is an outflow of molecules and an inflow of the "food set"—unallocated core memory in this case). A single individually autocatalytic species can persist in the reactor for an extended period in these circumstances. However, over time, more "efficient" individually autocatalytic species tend to successively emerge and displace each other. Efficiency here essentially means reaction speed. More complex dynamics then ensue. "Parasites" emerge, which are not individually autocatalytic in isolation but have an autocatalytic pathway which can be catalysed by fully autocatalytic "host" species, which are already present. These parasites and their hosts thus form—in my terms—a somewhat degenerate kind of collectively autocatalytic set; degenerate because some of the species are still individually autocatalytic. At later stages Ray reports the emergence of what he terms "sociality", meaning entities which "can only replicate when they occur in aggregations". In my terms, it seems that these should be regarded as "properly" collectively autocatalytic, in that there are no longer any individually autocatalvtic components.

In these terms, **Tierra** can be regarded as again independently corroborating Kauffman's results on the likely spontaneous emergence of collectively autocatalytic reaction networks—though with the addition of some significant and interesting results on the subsequent development and even elaboration of such networks. Ray himself does not make this explicit connection, but that is presumably due, in part at least, to his perspective of an ecological/evolutionary rather than molecular metaphor.

However: again, as with the previous systems, **Tierra** seems to lack any mechanism for spatial localization or containment of collectively autocatalytic reaction networks. Note carefully that this is true despite the fact that Ray variously refers to "organisms", "creatures" and "individuals" in the system; but what he means in each case is a single Tierra *process*—i.e., the entity which, in my terms, is analogous to a single *molecule* rather than a self sustaining system. In particular, although these primitive entities each have a specific, bounded, spatial extent in the Tierra core, there is no sense in which they produce or maintain this spatial boundary though their own operations. On the contrary, Tierra enforces a notion of "memory allocation" whereby some outside agency allocates or reserves spatial segments of core to individual processes, and this cannot be subverted by other processes. If we consider the application of my heuristic test for autopoiesis it again seems clear that multiple instances of the same reaction network, inserted into the same Tierra reactor, would *not* be able to maintain their separation; and thus, Tierra is not capable of supporting fully autopoietic organization.

6.4 SCL

Finally, let me turn to the SCL (Substrate-Catalyst-Link) system (McMullin and Varela, 1997), which is a recent re-implementation of the original computer model of autopoiesis (Varela et al., 1974). It specifically corrected a defect in the original published description of the model, establishing that a previously undocumented interaction (chain inhibition) was in fact essential to the autopoietic phenomenology of the model. In any case, the experiments reported both in the original paper and in this re-implementation were confined strictly to examination of a single putatively autopoietic system, spatially separated from any other. In this case, such an entity can indeed exhibit a self-sustaining network, with a clearly recognizable spatial structure or boundary which is both maintained by, and in turn confines, the reaction network.

It is then interesting to enquire how this behaviour is affected if two such entities are placed in close spatial proximity, as envisaged in the heuristic test described above. (Since the SCL system is deliberately simplified there is, in fact, only one possible self sustaining reaction network; therefore the multiple instances are necessarily instances of the same network).

Some (unpublished) experiments have been conducted along these lines. The outcome is, at best, inconclusive. The details are quite technical and only an outline will be presented here.

It should first be noted that the self sustaining agents in this system are quite unstable, even in isolation (see the example runs in McMullin and Varela 1997), which makes any interpretation of results quite difficult. However, this instability does *seem* to be exacerbated when multiple agents are in close proximity. In particular, the chain inhibition interaction, mentioned earlier as crucial to the operation of an isolated agent, turns out to also have an unintended side effect of inhibiting maintenance of the bounding membrane when two membranes are adjacent to each other. This means that, if anything, adjacent agents tend positively to *merge* rather than to maintain their individuality.

On balance then, I would say that the self sustaining agents in the SCL system do *not* pass my suggested heuristic test for "full" autopoiesis. This must be considered at least a little controversial given that the model was designed explicitly to *illustrate* autopoietic organization (albeit in minimal form).

7 Conclusion

The primary purpose here has been to review and contrast the notions of autopoiesis and collective autocatalysis. This has resulted in a focus on the autopoietic requirement for spatial localization or confinement to itself be a product of the reaction network. I have attempted to make this criterion as clear as possible by proposing a specific heuristic test. In essence this says that the critical test should not merely involve the ability of an entity to discriminate or demarcate itself from some sort of relatively disorganized background. Rather, it should require the ability for an agent to discriminate itself from other, spatially adjacent, but organizationally identical, agents. In particular, although it is not an integral element of the autopoietic concept, it seems to me that for agents to serve as actors in a Darwinian selective process, it is essential that they should be capable of this minimal "individuation".

In reviewing a number of abstract models of biological organization, I have tried to bring out the fact that—as envisaged by Kauffman—the emergence of collective autocatalysis seems to be relatively easy or robust. Systems with wildly different underlying architectures seem to exhibit this phenomenon, corroborating the claim that the conditions for its appearance are relatively weak. On the other hand, it seems that *none* of these systems should qualify as exhibiting properly autopoietic organization—including even the SCL system which was specifically concepted as an exemplar of autopoiesis.

It is not clear to me whether this is merely because these systems have not (with the obvious exception of SCL) been designed with this end in mind; or because autopoietic organization is, in fact, a *fundamentally* more elusive phenomenon than collective autocatalysis. I would welcome discussion on the question.

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