Life as a process of open-ended becoming: Analysis of a minimal model

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Abstract

We argue that the phenomenon of life is best understood as a process of open-ended becoming and that this potentiality for continuous change is expressed over a variety of timescales, in particular in the form of metabolism, behavior, development, and evolution. We make use of a minimal synthetic approach that attempts to model this potentiality of life in terms of simpler dissipative structures, using reaction-diffusion systems to produce models that exhibit these characteristics. An analysis of the models shows that its structures exhibit some instances of relevant changes, but we do not consider them open-ended enough to be called alive. Still, the models shed light on current debates about the origins of life, especially by highlighting the potential role of motility in metabolism-first evolution.

Introduction – The standard view

In the field of synthetic biology there is a widespread optimism that the creation of an entire living cell from scratch is imminent (e.g. Zimmer, 2009; Deamer, 2005; Szostak, et al. 2001). It is hoped that this bio-engineering approach will help to resolve one of the outstanding mysteries of science, namely the origin of life on earth. The mainstream consensus is that the crucial element in the transition from non-living to living matter is the appearance of evolution. Many of the researchers in the field of artificial life, who are studying the origin of life, also share this guiding idea. Their work is thus focused on the question of how best to simulate or chemically engineer the emergence of self-replicating structures (e.g. Rasmussen, et al. 2004; Solé, 2009). Within this general direction of research we can distinguish two relatively distinct traditions in terms of whether they assume the replication of information or the replication of metabolism to be the first factor in evolution.

The *information-first* (a.k.a. 'replicator-first')[1] view of life claims that there was *genetic evolution* right at the start of life itself. An extreme version of this view is known as the "RNA world", which holds that "the first stage of evolution proceeds […] by RNA molecules performing the catalytic activities necessary to assemble themselves from a nucleotide soup" (Gilbert, 1986, p. 618). However, it is now recognized that this RNA-only view is incomplete, and that the appearance of Darwinian evolution also requires the compartmentalization of replicating nucleic acids to ensure the segregation of genomes from one another. The field has therefore turned toward the task of incorporating suitable information-carrying molecules into the right kind of vesicle in a way that ensures the reproduction of both (e.g. Hanzcyc, et al. 2003), and in a way that allows for competition and differential success (e.g. Chen, et al. 2004). On this updated information-first view, the role of metabolism in the origin of the first living cell is at most a secondary aspect, and perhaps even completely absent. Rather, the essence of life consists of only two components: "fundamentally, a cell consists of a genome, which carries information, and a membrane, which separates the genome from the external environment" (Chen, 2006: 1558).

The *metabolism-first* view of life, on the other hand, claims that the main driving force at the origin of life was *epigenetic evolution*. A radical version of this view holds that the origin of life coincided with the emergence of autocatalytic systems (e.g. Kauffman, 1986), and that under certain conditions some selective pressures could have already been effective at this chemical level (e.g. Fernando and Rowe, 2007; Meléndez-Hevia, et al. 2008). It has also been claimed that "Darwinian competitive exclusion is rooted in the chemical competitive exclusion of metabolism" (Morowitz and Smith, 2007: 58), and that metabolism has played a bigger role than replication in making novelties appear in evolution (Pulselli, et al. 2009).

Similar to the updated information-first view, many of the metabolism-first researchers also argue for the essential role of some kind of spatial separation. It is said that autocatalysis by itself is not sufficient for life, and that these processes must necessarily be part of the constitution of a spatially localized individual (Maturana and Varela, 1980). Some researchers have gone further in claiming that the network of autocatalytic processes must necessarily be enclosed within a bounding membrane (e.g. Luisi and Varela, 1989).

Modeling studies along these lines have tended to assume that a physical membrane is essential, because it prevents the autocatalytic processes from diffusing into the environment (e.g. Bourgine and Stewart, 2004; Varela, et al. 1974), and allows the regulation of molecular intake (e.g. Bitbol and Luisi, 2004). Research in prebiotic chemistry has shown that it is possible to engineer the emergence of membrane-bounded micelles that provide the autocatalysis for their own replication (e.g. Walde, et al. 1994; Bachmann, et al. 1992; see also the model by Ono and Ikegami, 2000). In addition, recent models have demonstrated that under some conditions the growth and division of membrane-bounded autocatalytic

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[1] We call the 'replicator-first' tradition 'information-first' here in to avoid the misleading impression that the 'metabolism-first' tradition does not involve replication. The core of the dispute is not about replication versus emergence as such, but rather about what kind of replication was primary, namely informational versus metabolic or compositional.

systems can lead to differential replicative success (e.g. Ono, 2005; Ono, et al. 2008). On this view, which is sometimes identified with the "autopoietic" approach (e.g. Maturana and Varela, 1980; Varela, et al. 1974), the essence of life consists in a membrane-bounded, self-producing system.

It is important to notice that, although the two mainstream traditions may differ in emphasis, they do not hold mutually exclusive theories about the essence of life. In fact, they both accept the general claim that a biological individual is defined by the physical boundary that is imposed by its membrane, although they have different primary reasons for doing so (i.e. unit of selection versus unit of self-production). And they also both accept that life is essentially about stability and survival, and that the driving force of instability and biological change is primarily located outside of the individual, in the external environment and in evolutionary changes. They only disagree on the details of this account (i.e. is survival primarily about other generation or self re-generation, and is the beginning of evolution genetic or epigenetic). In general, the underlying assumption of the mainstream view is that the first form of life is essentially structurally isolated and behaviorally passive.

In this paper we will challenge this assumption. We follow Virgo (2011) in arguing that dissipative structures whose self-production is spatiotemporally localized, but not necessarily membrane-bound, have much in common with living beings. Even very simple examples of these structures are capable of motility, adaptive behavior, structural change, and epigenetic evolution. Consequently we regard such systems as worthy of study in the context of the origins of life.

Living without doing? An alternative view

Despite some outstanding disagreements, the two mainstream traditions are united by a theoretical view of life that is centered on a combination of the spatiotemporal conservation of the individual with an evolutionary realization of biological change. Accordingly, there are promising attempts to bring these two traditions together, such that life is viewed as essentially consisting of three distinct and yet functionally interrelated components: an informational system, a metabolic system, and a compartment (e.g. Rasmussen, et al. 2003; Ganti, 1975). And given this convergence of the two main traditions, and considering the recent experimental successes in realizing this view via synthetic biology, it seems that the optimism pervading the field is well founded. The creation of all kinds of useful artificial life forms appears to be within our grasp, and the final mysteries of the origin and evolution of life on earth seem tantalizingly close to being resolved.

However, the confident promises of synthetic biology will sound all too familiar to those of us who know the history of synthetic psychology – an approach better known as artificial intelligence. Indeed, around half a century ago there was a similar optimism prevalent in the scientific community that the creation of artificial minds and conscious robots was just around the corner. The driving force of that optimism, which in hindsight looks hopelessly naïve and deeply misguided, was a digital-information-centered science of the mind that resonated with advances in engineering and technology.

Today the view that cognitive science can be reduced to computer science is no longer in fashion, although the alternative still remains to be properly worked out (Froese 2010). How ironic it is, then, that at the moment in which cognitive science is undergoing a major theoretical makeover, namely toward a view of the mind as essentially embodied, embedded, and enactive (e.g. Gallagher 2005; Clark 2008; Thompson 2007), the science of life is at the same time extoling the virtues of trying to reduce the complexities of cellular biology to the abstract linearity of "logic circuits" (Nurse 2008) and "computer programming" (Balazs & Epstein 2009). History, it seems, is repeating itself.

But the purported reduction of life to logic is not as straightforward as the recent advances in biotechnology may seem to indicate. In particular, we note that, in a crucial sense, the life of the individual organism is completely absent from the mainstream framework outlined above. On the one hand we have structural self-maintenance, and on other hand we have informational self-replication. However, we know the former from the general class of dissipative structures, and the latter from the case of viruses – and neither of these two phenomena is typically considered as being alive. What they are missing is the autonomous expression of goal-directed behavior at the level of the individual, namely forms of translational movement and transformational change, which can be studied in terms of ethology and ontogeny.

We propose that all of these aspects of life, i.e. metabolism, behavior, development, and evolution, are integrated into one coherent process of open-ended becoming. On this view, the possibility of distinguishing between these different aspects is simply due to the fact that the process of living is expressed in terms of activities on a variety of timescales. All known forms of life are embedded within four broad categories of change:

<u>Metabolism:</u> the events on this timescale are taking place continuously in the chemical domain. They are foundational in that they realize the concrete, spatiotemporally localized, existence of the individual living being in an autonomous manner via self-production (Barandiaran and Moreno, 2008).

<u>Behavior:</u> the events on this timescale are unfolding in the relational domain of the individual-environment interaction in a moment-to-moment manner. The relational changes can be more or less tightly coupled to metabolic changes (Egbert, et al. 2010), but they are a non-reducible emergent property of the interaction that cannot be conceptualized non-relationally.

<u>Development:</u> events on this timescale make an individual become a structurally qualitatively different kind of individual within its lifetime. Examples are learning and morphogenesis.

<u>Evolution:</u> structurally qualitative changes in the historical lineage of generations of individuals take place on even larger timescales. Examples are genetic, compositional genetic, and epigenetic forms of evolution that are shaped by natural selection, sexual selection, and/or natural drift.

Of course, the differentiation of the changes exhibited by living beings into these four distinct timescales should not be misunderstood in any absolute sense. Our starting point is to treat life as a unified phenomenon, and these distinctions do not reflect strict boundaries between the distinct timescales of becoming. While each of these timescales can be addressed in relative isolation, as demonstrated by their respective fields of scientific study: molecular biology, ethology, developmental biology, and evolutionary biology, a complete understanding of life must be able to show how these different aspects are expressions of one and the same unified phenomenon. They are mutually interdependent and yet non-reducible.

We suggest that one way of approaching this issue is by introducing the intermediate timescales, namely behavior and development, into the current debates surrounding the origin of life. We need to consider that the living 'self' referred to by the notions of self-maintenance and self-replication is a center of activity, i.e. an agent (Ruiz-Mirazo, et al. 2010). And at the same time this additional complexity requires a model that is simple enough so that it can still be understood in a complete manner. To be sure, it may be that the most minimal form of life that satisfies our timescale criteria would actually have to be a membrane-bound single-celled organism that is already capable of information-based genetic evolution by means of natural selection. This is, of course, the hope that is harbored by those in synthetic biology who are trying to create life by combining bounded self-maintenance with self-replication.

On the other hand, we know from work in artificial life that some life-like behaviors can already be found in protocells and prebiotic chemistry. For instance, it has been shown that metabolic self-production can easily lead to movement as well as adaptive gradient following, i.e. chemotaxis, in minimal models of protocells (e.g. Suzuki and Ikegami, 2009; Egbert, et al. 2010). Similarly, it has been demonstrated that some of the chemicals typically favored for the synthesis of artificial cells can spontaneously form oil droplets that exhibit self-sustained motility and a type of chemotaxis (e.g. Hanczyc, et al. 2007; Toyota, et al. 2009). It is in this context that there have been calls for the establishment of a new field of study, variously labeled as "homeodynamics" (Ikegami and Suzuki, 2008), "chemo-ethology" (Egbert and Di Paolo, 2009), and "chemical cognition" (Hanczyc and Ikegami, 2010). In what follows we make a novel contribution to this endeavor.

The primacy of movement

Let us conclude this introduction by outlining our motivation for the rest of this paper. It has been argued that the 'RNA world' hypothesis faces considerable difficulties when confronted with the constraints of prebiotic Earth (Shapiro, 2000). One promising response is to reject the requirement of a *digital* genetic system for open-ended evolution, and to relax the distinction between genotype and phenotype. It is possible that these two features may not have been present at the origin of life, but developed in later stages. We therefore assume that a primordial protocell's chemical mixture itself can serve as a kind of "compositional genome" (Segré, et al. 2000), which remains relatively well preserved during protocell division; or alternatively that heredity can be achieved through multiple attractors in the autocatalytic reaction network's dynamics, as in the model of Fernando and Rowe (2007).

We could also assume the existence of a self-organizing membrane structure to protect the consistency of the chemical mixture from adverse environmental influences, e.g. a lipid vesicle (Luisi, et al. 1999). This is the main alternative "Lipid world" scenario of the origin of life (Segré, et al. 2001). However, through this additional step the scenario inherits the major underlying assumptions of the standard view, namely that the origin of life gave rise to an essentially structurally *isolated* and behaviorally *passive* entity. The living individual is enclosed in an interactionally inert compartment. And yet all life as we know it today is an active process of organism-environment interaction and its adaptive regulation (Di Paolo, 2009), and the membrane of cellular organisms is an active interface in this process (Hanczyc and Ikegami, 2010). It is precisely by means of this active self-other interface that a cell regulates its metabolism and behavior through chemical and sensorimotor coupling (Bitbol and Luisi, 2004).

This dilemma leaves us with two possibilities: either we continue to assume that life began enclosed in a compartment and try to explain how this boundary later developed an active role, or we relax the traditional requirement of a compartment as the first step in biological organization (Tanford, 1978). It may seem that only a structural compartment can ensure the individuality of a protocell as an entity that is distinct from its environment, but this is not always the case. This assumption confuses the organizational limits of the organism with its spatial boundaries (Virgo, et al. 2011). It is possible that chemical gradients are sufficient for the self-maintenance of a coherent systemic identity, as we will argue below.

While it is true that such a flexible 'boundary' makes it more challenging to survive in unfavorable environmental conditions, it is also the case that some adverse effects of the environment can be mitigated by rapid multiplication and, especially, by motility and directed exploration – a possibility that has not yet been sufficiently considered by the standard view. Here we see the importance of distinguishing between different timescales. In other words, in evolutionary terms it does not matter if these individuals are more prone to die from environmental events, as long as they can replicate and move to different areas quickly enough. The whole population must be sufficiently distributed in space such that some of them always remain alive. It is therefore conceivable that at the origin of life a capacity for adaptive self-motility came before the development of a more solid self-boundary. The model described in the next section is intended as a minimal proof of concept of this possibility.

Toward a Minimal Model of Life

One of us (Virgo, 2011) has argued that many of the properties of living organisms are shared by simple dissipative structures of the kind that form in reaction-diffusion systems. Prigogine (1955) coined the phrase "dissipative structure" to denote a structure within a physical system that is actively maintained by a flow of energy and/or matter, rather than being an inert structure that is merely resistant to decay. Prigogine observed that living organisms are dissipative structures in this sense; however there are many other examples.

Given what has been argued above, a suitable starting point for our model would be a self-sustaining chemical processes that is a spatiotemporally coherent individual, and yet is non-compartmentalized. These criteria are met by a special class of dissipative structures, which Virgo (2011, Chap. 5) has called *precarious, individuated dissipative structures*. In addition to being dissipative structures, organisms have the properties of being *precarious*, in the sense that if their structure is sufficiently disrupted it will stop being maintained (i.e. death); and *individuated*, in the sense that organisms are spatially localized, and this localization is a result of the dissipative processes that make up the organism, rather than being imposed from outside (see also Di Paolo, 2009).

Virgo points out that certain other dissipative structures share these properties with living organisms. One non-living example of this type is a hurricane (McGregor and Virgo, 2009). It is dissipative in that it 'feeds' off a temperature gradient between the sea surface in the upper atmosphere; it is precarious in that if an important component is removed it can blow out (as will eventually occur if it passes over land); and it is individuated in that it is the cause of its own spatial localization. Not all dissipative structures are precarious or individuated, and not all precarious, individuated dissipative structures share all properties of living systems. Nevertheless, as Virgo argues, studying such structures provides a useful methodology for modeling some of life's basic properties.

A simple and easy-to-study system that exhibits precarious, individuated dissipative structures is the Gray-Scott reaction-diffusion system, which was first studied in a two-dimensional context by Pearson (1993). This is a simple model of chemical reactions taking place on a surface. The reaction modeled is a simple autocatalytic one, $A + 2B \rightarrow 3B$, meaning that when two molecules of *B* collide with one of *A*, they react to produce a third molecule of *B*. A second reaction, $B \rightarrow P$, represents the decay of the autocatalyst into an inert product that leaves the system. The molecules *A* and *B* have a separate concentration at each point on a 2-D surface, represented by *a* and *b* (the concentration of *P* is not modeled). In addition, the 'food' molecule *B* is fed into every point at a rate proportional to 1-*a*. This can be thought of as due to the surface being immersed in a solution of *A* at a constant concentration of 1.

Finally, in addition to reacting and being added to the system, the two chemical species can diffuse across the surface. Overall this gives rise to the equations

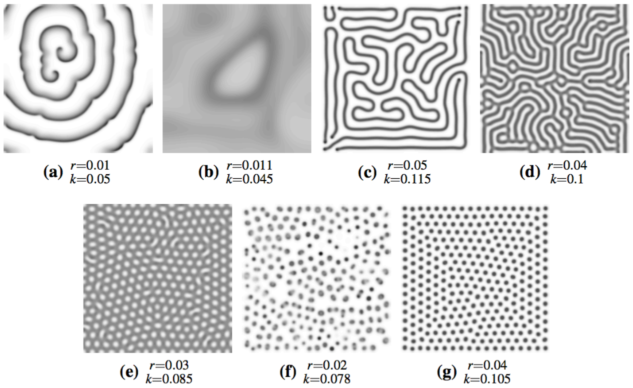
$$\frac{\partial a}{\partial t} = D_A \nabla^2 a - ab^2 + r(1-a); \tag{1}$$

$$\frac{\partial b}{\partial t} = D_B \nabla^2 b + ab^2 - kb, \tag{2}$$

where *a* and *b* are functions of space as well as time, *r* and *k* are parameters determined by the rates of the two reactions and the feed process (the rate of the autocatalytic reaction has been set to 1 without loss of generality), and D_A and D_B are the rates at which the species diffuse across the surface. These equations can be solved numerically using a method that is akin to a cellular automaton, except that each cell contains a continually variable amount of the two chemical species.

Pearson observed that, depending on the choice of initial parameters, this system can form a variety of patterns, some of which are shown in Figure 1. Of particular interest are the spot patterns in Figure 1(f) and 1(g), since the spots have the properties of being individuated and precarious (Virgo 2011).

Finally, we know that many kinds of dissipative structures that are formed by reaction-diffusion systems are also capable of sustained movement and even replication. This kind of self-organized motility has been investigated experimentally (e.g. Lee and Swinney, 1995; Lee, et al. 1993; 1994) and modeled mathematically (e.g. Varea, et al. 2007; Krischer and Mikhailov, 1994; Pearson 1993). The dynamics of replicating reaction-diffusion patterns have also been studied (e.g. Reynolds, et al. 1994; 1997). In the dissipative structures of the Gray-Scott model we find cases of motility and replication as well, and this includes some kinds of spots. We thus have all the basic requirements to begin our investigation of these spots as a potential minimal model of life as a form of open-ended becoming, as it is expressed on the four timescales of metabolism, behavior, development, and evolution.


(a) r=0.01 k=0.05 **(b)** r=0.011 k=0.045 **(c)** r=0.05 k=0.115 **(d)** r=0.04 k=0.1

(e) r=0.03 k=0.085 **(f)** r=0.02 k=0.078 **(g)** r=0.04 k=0.105

Figure 1. Examples showing the range of patterns exhibited by the Gray-Scott reaction-diffusion system with various parameters ($D_A = 2 \times 10^{-5}$ and $D_B = 10^{-5}$ in each). The integration method and initial conditions are similar to those used by Pearson (1993). Patterns are chosen as exemplars of various phenomena; see Pearson (1993) for a more systematic classification. (a) A spiral pattern; (b) A chaotic pattern of travelling waves; (c) A line pattern. Lines grow at the ends and then bend to fill space in a process reminiscent of a river meandering; (d) A labyrinth pattern; (e) A hole pattern; (f) A pattern of unstable spots, whose population is maintained by a balance between reproduction and natural disintegration; (g) A stable spot pattern. Spots reproduce to fill the space and then slowly migrate into the more-or-less organized pattern shown (with a different choice of parameters, spots can be produced that are stable but cannot reproduce).

Metabolism

A reaction-diffusion spot can spontaneously emerge under appropriate conditions, and once it exists, it can self-maintain its precarious existence by means of a continuous turnover of chemical reactions. As a self-producing network of chemical processes it satisfies the requirements of the first timescale. It also provides the reference point of a spatiotemporal entity against which changes on other timescales can be measured.

It is interesting to note in this regard that the spatiotemporal boundaries of a spot are intrinsically fuzzy. It is just as impossible to pinpoint the precise moment in time when the spot begins or ceases to exist, as the precise point in space where the spot ends and the environment begins. This is because the spot is a self-organizing phenomenon that is both continuous in time (temporal ambiguity) and continuous in space (spatial ambiguity). Nevertheless, an intuitive grasp of what constitutes an individual spot is possible; we either see an individual spot on the surface or we do not.

Once an individual spot has spontaneously formed, it will continue to exist even when it encounters a limited range of conditions that would not have enabled its original emergence. The fact that spots can exist outside of their original range of emergence is an indication that they are actively re-producing the viability conditions required for their existence, which can be considered as a strong criterion for autopoietic autonomy

(Froese and Stewart, 2010). It is no different in the case of living beings: although they must have first emerged when the environmental conditions were right, they must now actively produce their own conditions of existence in order to persist.

Behavior

We define the concept of behavior broadly as any change in the individual-environment relationship, which is induced by an instability or tension in that relationship. A behavior ceases when that tension is resolved or transformed into a different kind of tension, which elicits a different kind of behavior. In this paper we take the view that all behavior is characterized by an essential asymmetry centered on the individual (Barandiaran, et al. 2009). The tension that triggers a behavior may originate in the environment, but the fact that there is a response at all is an achievement of the self-constitution of the individual. In this sense their behavior is intrinsically active.

The term ‘behavior’ covers a huge variety of changes in all kinds of entity-environment relations, so some distinctions are in order. One important distinction in biology and psychology is between *reactive behavior*, namely behavior that is triggered by events in the environment, and *active*, or *intrinsic behavior*, namely behavior that is initiated by the individual. Again, the distinction is not an absolute one since, on the one hand, all biological systems have internal state and their reactive behavior is therefore always also a function of their history, and, on the other hand, the expression of active behavior always takes place in the context of environmental events. Nevertheless, a behavior can be more or less driven by autonomous and environmental conditions. Let us consider these two kinds of behaviors in the case of the spots.

Reactive behavior. The spots exhibit a clear type of reactive behavior with respect to differences in chemical gradients in their surroundings. We can describe this behavior in terms of approach and avoidance: the spots are capable of following chemical gradients that increase the concentration of their constituents, i.e. chemotaxis, and they are also capable of avoiding chemical gradients that decrease the concentration of their constituents. For example, when we remove constituents from nearby a spot by using a virtual pipette, the spot will tend to move away from the pipette. In this way it is possible to chase spots around the surface. If the pipette is too fast and gets too close to a spot, it destabilizes the spot in such a way that it is no longer sustainable and dies.

If there are several spots in the environment, then these approach and avoidance behaviors will make them interact in certain ways. This is because a spot consumes the food in its proximity, thereby surrounding itself with a negative gradient that keeps other spots away. If the spots did not tend to move away from one another then they would merge rather than remaining separate; these approach and avoidance behaviors therefore form an important part of the individuation process.

Note that although these behaviors are reactive in the sense that they do not occur except in the presence of an appropriate environmental trigger, they are the result of an active growth process. The spot moves because the autocatalyst grows faster on the side where the food concentration is higher. This behavior could thus be said to be reactive in the behavioral domain, but active in the metabolic domain. In order for the spot to move even in the absence of environmental triggers it must create its own instabilities. Of course, the whole spot is already in a far-from-equilibrium state, but what is needed is an asymmetrical distribution in the general field of individual-environment relationships (Matsuno, et al. 2007).

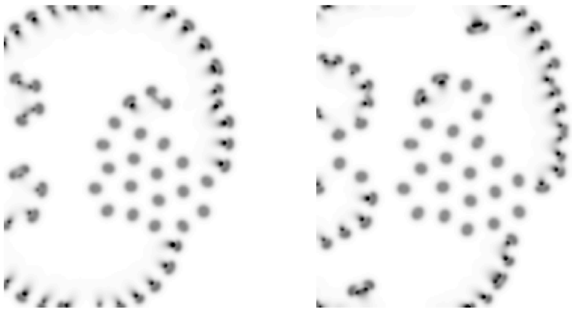

(a) $t = 9060$ (b) $t = 9949$

Figure 2. Two snapshots of the system resulting from Equations (4)-(6), integrated on a surface of 2 by 2 units, with the parameters $D_A = 2 \times 10^{-5}$, $D_B = 10^{-5}$, $D_C = 10^{-6}$, $r = 0.0347$, $k_1 = 0.2$, $k_2 = 0.8$ and $k_3 = 0.005$. The colors are adjusted so that the secondary autocatalyst C appears as a darker shade of gray than the primary autocatalyst B. A group of spots with tails can be seen on the mid-left side of plot (a), and after duplication in plot (b) in the same place. Some tail-less spots can be seen as well, their tails having been lost in the process (hence, this is limited heredity with variation). The spots with tails move constantly in the direction facing away from their tails at a rate of approximately 4×10^{-4} distance units per time unit, which results in their colonizing the empty part of space more rapidly than the tail-less spots. However, with this choice of parameters, the tailed spots cannot invade areas occupied by tail-less spots, and they are eventually crowded out and become extinct.

Intrinsic behavior. One way of achieving active motion is by modifying the original Gray-Scott reaction-diffusion system by introducing a second autocatalyst to the system, which feeds not on the ‘food’ molecule but on the other autocatalyst (see Virgo, 2011). That is, the reactions $B + 2C \rightarrow 3C$ and $C \rightarrow P$ are added to the system, so that Equations 1 and 2 are extended to Equations 4-6, where D_C is the rate of diffusion of C, and k_1, k_2 and k_3 are the rate constants for the reactions $B \rightarrow P$, $B + 2C \rightarrow 3C$ and $C \rightarrow P$, respectively.

$$\frac{\partial a}{\partial t} = D_A \nabla^2 a - ab^2 + r(1-a); \tag{4}$$

$$\frac{\partial b}{\partial t} = D_B \nabla^2 b + ab^2 - k_1 b - k_2 bc^2; \tag{5}$$

$$\frac{\partial a}{\partial t} = D_C \nabla^2 c + k_2 bc^2 - k_3 c, \tag{6}$$

With an appropriate choice of parameters, the effect of this is to produce spots of the primary autocatalyst, which are accompanied by a region of the secondary autocatalyst. Since the secondary autocatalyst feeds on the primary one, the spot of primary autocatalyst tends to avoid it by moving away, while the secondary spot follows. This gives the secondary autocatalyst the appearance of being attached as a ‘tail’ behind the primary spot (see Figure 2.) The spot-tail system as a whole moves around spontaneously even in a homogeneous environment. In the sense that this motility depends on the internal constitution of the whole spot-tail system itself, we can characterize it as intrinsic rather than as reactive.

Although this spot-tail system is not strictly speaking an autocatalytic "hypercycle" (Eigen 1971), because the catalytic dependency is not mutual, it nevertheless can be considered as symbiotic to some extent (see Lee, et al. 1997). While the tail is somewhat parasitic on the primary spot (since it contributes nothing to it metabolically), their jointly induced movements can be adaptive in some environments. Thus, in contrast to the standard view that parasitic reactions are a significant problem for the metabolism-first approach because of their detrimental metabolic effects (and hence, the necessity of a compartment, see Takeuchi and Hogeweg, 2009), we argue that this is not always the case. With certain parameter settings, the spot-tail systems can reproduce more rapidly than spots without tails, and their movement also tends to make them colonize new areas more rapidly. This highlights once more the importance of distinguishing between different timescales: what may be detrimental on the metabolic timescale (parasitic reaction), can induce changes on the behavioral timescale (exploratory behavior), which are adaptive on the evolutionary timescale. Figure 3 shows an example of a scenario where over longer timescales spots with tails are better adapted than tail-less spots. The parasite-enabled exploratory behavior helps to prevent the occasional localized extinction events from killing the population. We will return to this finding later.

Development

We conceive of the notion of development in a broad way so as to include any structural changes induced by the organism, which turn it into a qualitatively different kind of being in its own lifetime. These structural changes can include (in order of increasing temporal scale) growth, habituation, learning, adaptation, and ontogeny. Not all forms of life will exhibit all of these variations of becoming to the same extent, but all will display some capacity for developmental change.

We find lifetime dependent structural changes in the case of the spots as well. These changes typically proceed via the incorporation of external elements rather than the internal differentiation that is familiar from modern cells, but we can perhaps still think of this as a kind of proto-development. The emergence of spot-tail systems that was described above is one example. Virgo (2011) also observed a second, related kind of process in a reaction-diffusion system (with a different set of equations), whereby two nearby spots consisting of mutually complementary catalytic reactions join together to form a multi-spot system, thus forming a proper hypercycle (Eigen, 1971). In some respects, development can be seen in single spots as well. When they exhibit directional movement, they do it because they grow toward the increasing gradient, and die back on the other side. They are like plants in that growth and behavior are not always readily separable.

Evolution

We have already observed that there is a heritable difference between a spot with a tail and a spot without tail (see Figure 2). However they are clearly lacking a digital genetic system with which to encode these differences. In our analysis of the evolutionary capacity of the reaction-diffusion systems we therefore focus only on the possibilities of epigenetic evolution and of evolution with a compositional genome.

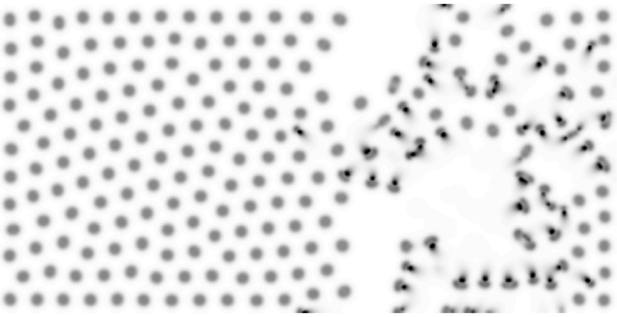


Figure 3. A snapshot from the same system shown in Figure 2, with the same parameters, except that randomly chosen areas in the right-hand side of the surface are occasionally cleared by an externally induced cataclysm (e.g. the food concentration in a random 0.5-by-0.5 area is set to zero every 1000 time units). The spots with tails are able to persist in this region due to their ability to colonize the cleared areas more rapidly than the spots without tails. But in the left-hand side of the figure they are out-competed.

Epigenetic evolution. It is well known that one of the main epigenetic factors of inheritance is the particular time-space configuration in which an individual is born. A famous case is the beaver's dam, which, once constructed, provides a home for subsequent generations. This kind of inheritance can also occur in the case of reaction-diffusion spots. For instance, the offspring of those spots, which happened to divide because of a high concentration of nutrients, will also find themselves in a situation with high concentration of nutrients.

Composition-genomic evolution. We have noted above that the chemical composition of spot can be considered as both its phenotype and genotype combined. The idea is that this kind of 'compositional genome' could have enabled protocellular evolution by means of natural selection even in the absence of a digital information-carrying component such as RNA and DNA (Segre and Lancet 2000). For instance, Virgo (2011) has observed spots undergoing a Lamarckian form of evolution, whereby traits that have been acquired during an individual's lifetime are passed along to the offspring. This is the case for spots with tails. Once a spot has acquired a tail (perhaps by passing near to another tailed spot), it will divide in a way that typically results in offspring that have tails.

We also find a difference in selective pressure since in some environments the spots with tails are more viable than the single spots on their own (see Figure 3). This is because their combination results in an internal instability that makes the spot system move around even in the absence of chemical gradients, and they are thereby able to minimize the impact of catastrophic events. Greater spatial distribution lessens overall risk to the population. In this scenario the original single-spot constituents may therefore die out eventually, while the spot-tail variant persists. Here we therefore have all the elements of evolution as it is standardly conceived, namely reproduction, variance, and selection, but with limited rather than unlimited heredity (*sensu* Szathmary and Maynard Smith, 1997).

Discussion

The model has served as a proof of concept that even simple reaction-diffusion spots can exhibit many essential life-like characteristics, where life is conceived as a process of open-ended becoming. We have focused on the importance of self-organized motility and behavior in the context of current debates on the origin of life. In this discussion we would like to draw attention to the shortcomings of the current model, and to consider possible ways of overcoming them.

The spots satisfied the basic requirements of metabolism (self-creation) and movement (self-motility). In fact, they are even capable of adaptive behavior that resembles the foraging behavior of actual bacteria (nutrient gradient following). The spots are also capable of some proto-development through the incorporation of new external elements, and these lifetime changes are inheritable over generations. Taken together these findings suggest that the spots meet the criteria of undergoing changes within the four major timescales characteristic of life, namely metabolism, behavior, development, and evolution.

But are these spots a model of the phenomenon of life? We characterized life as an open-ended process of becoming, and it is precisely in relation to open-endedness that the limitations of the model are most apparent. How far can this approach be scaled up? Are compositional genomes capable of "unlimited heredity" (Szathmary and Maynard Smith, 1997) as suggested by the work of Segre and Lancet? Is it possible to set up the environmental conditions such that a more complex network of dissipative structures emerges? By which mechanism could such a network learn? How could it reproduce itself?

One issue that would need to be tackled in future models of this kind is how to introduce the possibility of solidity. In the current model the spots are fully transparent to environmental interactions, although chemical gradients may constitute some boundaries. This extreme openness effectively turns the whole spot into an interface with its environment. In order to enable a more open-ended increase of complexity it may eventually become necessary for the system to localize these interfaces at its spatial boundaries. Some researchers have argued that internal differentiation between the constitutive elements that are responsible for self-creation and those that are needed for interaction is a first step toward more behavioral autonomy (Barandiaran and Moreno, 2008). Internal differentiation may enable further specialization of these elements, since they no longer need to do both tasks at the same time.

Relatedly, it is possible that at some point a differentiation between phenotype and genotype may become necessary in order for further evolutionary transformations to become a stable possibility. And even during the organism's lifetime the internal mediation between phenotype and genotype entails a certain lack of self-coincidence in the being of the organism that could facilitate open-ended becoming. The organism's being is then no longer simply a product of its own doing, as it is in the case of the spots, but also of its own genetic self-interpretation. This is because the same DNA can give rise to different expressions in the context of a different phenotype. It is of general interest to further determine to what extent DNA is necessary for the phenomenon of life. One way to address this issue, and which we have pursued in this paper, is to see how far it is possible to get without DNA or any other genetic system. By following this approach some constraints may become apparent for which a dedicated digital genetic system is an essential part of the solution.

Conclusion

We have argued that the phenomenon of life is a process of open-ended becoming, and that contemporary debates about the origins of life should take the role of self-organized motility and behavior into account. We revisited Virgo's (2011) arguments concerning simple dissipative structures in reaction-diffusion systems from this theoretical perspective, and discussed the potential of some of these structures as a minimal model of life. We conclude that the current model is able to partially satisfy the proposed view by exhibiting some changes on the temporal scales of metabolism, behavior, development, and evolution. The model also demonstrated the importance of distinguishing between the organizational limits of the organism and its spatial boundaries, as well as between its various timescales. Future work should try to determine to what extent this approach is able to scale up to more complex phenomena, including individuals that have the potential for a greater variety of becoming.

Acknowledgments. Tom Froese's research is funded by the Japanese Society for the Promotion of Science (JSPS) and is financially supported by their Grant-in-Aid program.

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