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1. INTRODUCTION

Accumulation of information is a central issue in prebiotic evolution. Eigen and Schuster were the first to stress the existence of the information threshold; in a system containing self-replicative molecules, the length of the molecules is restricted by the accuracy of replication.

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Self-Structured and Selection: Spiral Waves as a Substrate for Prebiotic Evolution

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has great selective advantages. Each molecule in the hypercycle is still bound to the maximum string length, but the molecules can combine their information and thus cross the information threshold.

The selective properties of the hypercycle have been investigated by several authors by means of ordinary differential equations (ODE) model (see Appendix). In the ODE model, a hypercycle is not an evolutionary stable strategy because there is no positive selection for the giving of catalytic support to other molecule species; therefore, a “parasitic” mutant that gives no catalytic support but receives increased catalytic support is fatal to the hypercycle.

Recently we introduced a cellular automaton (CA) model for the hypercycle interactions. The introduction of a spatial dimension and incomplete mixing in this model has far-reaching consequences. In the CA model, the hypercycle interactions give rise to self-structuring into spiral waves. It turns out that by this self-structuring, the hypercycle becomes resistant to a large class of parasites.

In this paper we catalogue the changes in the selective properties of the hypercycle due to the spatial self-structuring. In the ODE model, the selection takes place at the level of the individual molecules; a mutant that produces more copies is always selected. We will show that many of the “self-evident” selective properties which are well known from the ODE model are not valid in the spatial CA model. This is caused by the fact that the CA model selection takes place between spirals.

2. THE MODEL

In order to simulate incomplete mixing, we use the model formalism of the cellular automaton. A cellular automaton is defined as a large tessellation of identical finite-state automata (cells). Each automaton is defined as a triplet: \((I, S, W)\), where \(I\) is the set of inputs, \(S\) is the set of states (both sets being finite and usually small), and \(W\) is the next-state function, defined on input-state pairs. The inputs are the states of “neighbor” cells, i.e., the adjacent cells in the tessellation. Cellular automata have proved to be a powerful tool in the study of spatial processes, for instance, fluid dynamics.

In our cellular automaton, the total space consists of \(300 \times 300\) cells in a square toroidal tessellation. The state of a cell refers either to its occupation by a molecule of a certain species or to its emptiness, i.e., a cell can contain one molecule or it can be empty. In the next-state function of the cells (see Table 1), we implement a representation of three processes:

1. Decay (see Figure 1(a)) can occur when a cell is occupied; after decay the cell becomes empty. The probability of decay is species (i.e., state) dependent.
2. Replication (see Figure 1(b)) is only possible in empty cells; a molecule in one of the four direct neighbor cells can replicate into the empty cell. The probability of replication is species dependent. There is also a probability that the cell will remain empty.
3. Catalysis (see Figure 1(c)) is related to replication; the probability that a molecule will replicate into an empty cell is increased when there are catalytic molecules in at least one of the four cells that lie adjacent to the direction of replication.

In addition to these three processes, diffusion is included in our model as a separate process, operating between “timesteps.” We use the diffusion algorithm of Toffoli and Margolus, which ensures particle conservation. In this algorithm, the space is divided into subfields of \(2 \times 2\) cells. At each diffusion step, the states of a subfield are rotated 90 degrees clockwise or anti-clockwise with equal probability. After a diffusion step, the subfields are shifted one cell diagonally.

![Figure 1](https://example.com/figure1.png)

**FIGURE 1** Three-state transitions of a cell in a cellular automaton in which hypercycles can be simulated. The next state \(t+1\) is drawn below the present state \(t\). \(X\) is a molecule of a certain species; \(\text{cat}X\) is a molecule that catalyzes molecule \(X\)’s replication. See text for further explanation.
3. RESULTS

3.1. EMERGENCE OF SPIRAL WAVES

In order to get a better understanding of the selective properties of the spatial model, we start with a section in which we will give a detailed description of the dynamical properties of the spirals.

3.1.1. DEVELOPMENT First we describe the spatial behavior of a set of molecules which are part of a pre-defined hypercycle. In plate 5A, the six members of the hypercycle are distributed at random in the space; 50% of the cells are empty. The six molecule species have identical replication and decay parameters (Table 1: \( \text{self}[1,6] = 1 \), \( \text{decay}[1,6] = 0.2 \)). Each species catalyzes one other member of the hypercycle; catalyzed replication is much stronger than non-catalyzed replication (Table 1: \( c[2,1] = c[3,2] = \ldots = c[1,6] = 100 \)). After each timestep, there are two diffusion steps.

Plate 5B shows the situation after 1000 timesteps. Spiral structures have developed containing all members of the hypercycle in catalytically ordered. Each species grows towards its catalytic supporter; species 1 (red) grows towards species 6 (blue), species 2 (orange) grows towards species 1, and so on. As a result of this directional growth, the spirals rotate. Most spirals occur in couples; a spiral rotating clockwise is close to a spiral rotating counter-clockwise.

Plate 5C shows the situation after 2000 timesteps. Some spirals have disappeared. This happens when two spirals rotating in the opposite direction come too close to one another. The number of molecules of a species between the two spirals is then reduced and, if, by chance, a species dies out, then temporarily the species that gives catalytic support to the extinct species takes over the complete region of the double spiral. Because this species now no longer gets catalytic support, the region formerly occupied by the double spiral is taken over by other nearby spirals.

After 2000 timesteps, the pattern remains stable: the centers of the spirals do not move and all spirals have the same rotation time.

3.1.2. GROWTH WITHIN A SPIRAL The middle of a spiral acts as a center of growth for the entire spiral. This is demonstrated in plates 6A-C (see color plates). In plate 6A the molecules in the middle and the periphery of the huge single spiral in the situation of plate 1C are labelled (only the labelled molecules are colored; each color represents three molecule species, which are adjacent in the hypercycle). In plate 6B, after 30 timesteps, the descendants of the labelled molecules in the periphery have reached the edge of the region of the spiral. The labelled molecules in the middle of the spiral have increased in number. After 200 timesteps (see plate 6C), the molecules from the middle have taken over the complete spiral region and the molecules from the periphery have disappeared. This direction of growth is caused by the catalytic waves that travel from the middle towards the periphery of the spiral. Note that, although the spirals rotate, growth is not rotational.

3.1.3. STABILITY The stability of spirals depends on the parameters of the molecules. We test this relation on a 150 x 150 field with empty boundaries (no torus). As a starting pattern we use the configuration in Figure 2. In this configuration, the molecules are already in catalytic order; normally only one spiral is formed, which rotates clockwise. At each run, we vary one parameter of species 1 (red); the default parameters of the other species are as in plate 5A.
In Figure 3 the stability results after 1000 timesteps for various parameters of species 1 are summarized. We distinguish three classes of stability:

1. **One stable spiral.** As long as the parameters of species 1 do not deviate too much from the default, a stable spiral is formed. The thickness of the spiral waves varies with the parameters; in plate 7A the situation after 1000 timesteps for $\text{decay[1]} = 0.06$ is shown: the waves of species 1 (red) and 2 (orange) are thick and the wave of species 6 (blue) is very thin.

2. **No spirals.** The spiral is unstable when a catalytic wave is too thin and becomes extinct. We give an example for $\text{decay[1]} = 0.03$; in plate 7B, after 1000 time steps, species 6 (blue) has vanished and five species remain. The remaining system is locally unstable, but the five species persist in a global dynamical equilibrium (see also subhead 3.2.3).

3. **Complex spirals.** Between the parameter regions of Class 1 and Class 2 there is always a zone of Class 3; in this zone, spirals are formed but they are not stable: there is a perpetual loss and reformation of spirals. An example is shown for $\text{decay[1]} = 0.05$ (plate 7C, see color plates, after 1000 timesteps): the catalytic wave of species 6 (blue) is thin and it has gaps: sometimes a gap is filled from the sides, and a new double spiral develops around the gap.

**3.1.4. Rotation Time.** The rotation time of a spiral varies with the parameters of the species. We measured the rotation time of the spirals in the stability experiments described above. The rotation time is measured by taking the situation after 500 time steps as a target pattern and matching it with subsequent patterns. A molecule is matched if there is a molecule of the same species somewhere in the nine-cell
species 2 has more trouble in replacing it. For self[1] > 12, the rotation time decreases sharply with increasing self-replication. In this parameter region, the self-replication of species 1 is so strong that the species from which it gets catalytic support (i.e., species 6) has almost vanished.

Figure 5(c) shows the rotation time for various catalysis parameters. Rotation time decreases asymptotically with increasing catalysis. With high catalysis, a molecule grows faster towards its catalytic supporter. For c[1,6] ≤ 20, (almost) all catalyzed replication claims are retracted and thus there is no further decrease in rotation time.

3.1.5. NUMBER OF SPECIES Not only the parameter values, but also the number of species in the hypercycle affects the stability and rotation time of the spirals. For hypercycles of 2 or 3 members (with default parameters), no spirals are formed (plate 8A; 3 members, \( t = 2000 \)), a hypercycle of four members is in the complex spiral region (plate 8B; 4 members, \( t = 2000 \)) and hypercycles of five or more members form stable spirals (plate 8C; 6 members, \( t = 2000 \)). The rotation time of the spirals increases linearly with increasing number of species (see Figure 5(d)).

If we compare these results with the ODE model, we see that hypercycles of five or more members form spatially stable spirals; whereas the ODE model has a limit cycle with extreme oscillations (such that extinction should be expected). For hypercycles of four or less members, the ODE model has a stable equilibrium. Such systems are spatially unstable in the CA model, although the frequency of the species is fairly constant.

3.2. PARAMETER MUTANTS

In this section we will investigate selection for mutants that differ in the strength of one parameter. We use the situation of plate 5C (see color plates) as a starting pattern. All molecules of species 1 in the center of the single spiral in the middle of the field are replaced by mutants, as shown in plate 9A (see color plates); mutants are black.

3.2.1. "DECAY" MUTANTS The ODE model predicts that mutants with slower decay will win and mutants with faster decay will lose. In Figure 6(a) the number of mutants and the number of molecules of species 1 are given 4000 timesteps after infection. The prediction of the ODE model is fulfilled for decay[mutant] ≤ 0.13 and decay[mutant] ≤ 0.53. However, for 0.14 ≤ decay[mutant] ≤ 0.5, the results contradict this prediction; the outcome of selection is reversed. How can this be explained?

It appears that, for decay[mutant] ≤ 0.13, the mutant decays so slowly that it can diffuse towards the center of the other spirals; the mutant is able to grow against the general direction of growth in the spirals (see subsection 3.1.2). Analogously, for decay[mutant] ≤ 0.55, species 1 is able to get into the center of the infected spiral and thus replace the mutant.
For $0.14 \leq \text{decay[mutant]} \leq 0.5$, the molecules are not able to grow towards the center of other spirals. Competition now takes place between spirals, and it turns out that rotation speed of the spiral is the decisive factor: a spiral that rotates faster expands towards a spiral that rotates slower.

In plate 9B the dynamical process of the competition between the spirals is shown; a one-dimensional horizontal section through the middle of the field ($y = 150$) is drawn for every fourth timestep. In this case the mutant decays slower than species 1 ($\text{decay[mutant]} = 0.15$; $\text{decay[1]} = 0.2$) and, therefore, the infected spiral expands. Plate 9C shows the situation after 4000 timesteps; there are still some mutants, but the infected spiral has lost most of its domain. The situation is stable in time; the mutants will not disappear but form a small cyst, because the infected spiral is reinforced by the other spirals.¹

Plate 9D shows the dynamics for $\text{decay[mutant]} = 0.4$. Now the infected spiral expands, because it rotates faster. After 4000 timesteps (plate 9E), the infected spiral has taken over almost the entire field, and some of the non-infected spirals have formed cysts.

3.2.2. "SELF-REPLICATION" MUTANTS According to the ODE model, a raised self-replication rate should be advantageous for a mutant. Figure 6(b) shows the number of mutants and the number of molecules of species 1, 4000 time steps after infection. For $\text{self[mutant]} \leq 7$, indeed, the mutant wins; it is able to get into the center of the other spirals. For $\text{self[mutant]} \leq 6$, there is competition between the spirals. For this parameter region, the rotation time increases with increasing self-replication (see Figure 5(b)).

3.2.3. "CATALYTIC SUPPORT" MUTANTS The ODE model makes a clear distinction between selection for getting catalytic support and selection for giving catalytic support; mutants that get more support are positively selected while selection for mutants that give more support is neutral. As mentioned, this renders hyperspecies vulnerable to "parasites." Figures 6(c) and 6D show the number of mutants and the number of molecules of species 1 after 4000 timesteps for both types of mutants. It appears that, in the CA model, selection for giving and getting catalytic support essentially follows the same pattern.

In both cases for $\text{c[mutant]} > 10$, selection is neutral, because there is no difference in the rotation time between the infected spiral and the other spirals (see Figure 9(c)). In this parameter region there is a slight increase in the number of

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1. The text references a superscript '1' which is not visible in the provided image.
mutants but this has to be explained by a thicker catalytic wave of the mutant for increasing catalytic support.

For $c_{\text{mutant}} \leq 10$, there is positive selection for both getting and giving catalytic support; the infected spiral in this case has a slower rotation time than the other spirals (see Figure 5(c)). A mutant for giving catalytic support forms a cyst, while a mutant for getting catalytic support is rejected completely. Note that these results imply that the hypercycle in the CA model is resistant to parasites.

### 3.3. CONNECTANCE MUTANTS

In this section we will examine selection for mutants that differ in their catalytic connections to other molecules. Again, as with the parameter mutants, we will start with replacing the molecules of species 1 with mutants in the center of a spiral.

**3.3.1. SHORT-CUT MUTANTS** Figure 7 shows the catalytic connections of a shortcut mutant in a hypercycle with five members. The shortcut mutant has the same connections as species 1, but it also gives catalytic support to species 3 and, therefore, enables a shorter hypercycle of four members. All catalytic connections are equally strong ($c = 100$) and the mutant has default decay and self-replication parameters.

Plate 10A (see color plates) shows the infection with the above-described shortcut mutant in a stable situation of a hypercycle with five members. Plate 10B shows the situation after 500 timesteps; in the infected spiral, species 2 (orange) has become (almost) extinct, so now the short hypercycle of length 4 dominates the former region of the infected spiral. However, this short hypercycle cannot form a stable spiral (see subhead 3.1.5) and it turns out that it cannot compete against the remaining spirals of length 5 which are stable; so after 3000 timesteps in plate 10C the mutant is rejected completely. This result holds for initial hypercycles of whatever length, infected by shortcut mutants for hypercycles of length 4 or less.

Something different happens when the shortcut hypercycle has length 6 or more, i.e., when it can form a stable spiral. Plate 11A shows the infection of a spiral is a stable situation of a hypercycle with seven members with a shortcut mutant for a hypercycle with six members. After 500 timesteps, in plate 11B, species 2 has become extinct in the infected spiral, and now there is competition between the two spirals of different length. From Figure 5(d), we know that the shorter hypercycle rotates faster, and, therefore, it will expand; after 2000 timesteps (see color plate 11C), the hypercycle of length 6 has taken over the complete field.

For shortcut mutants of length 5, the situation appears to be dramatic. A six member hypercycle is infected with a shortcut mutant for a hypercycle of length 5 (plate 12A, see color plates). Initially things develop as in the previous case; the short hypercycle expands, as shown after 2000 timesteps in plate 12B. However, in the end, as species 1 has become almost extinct, and species 2 is completely extinct, it turns out that a hypercycle of length 5 is vulnerable to parasites. With the extinction of species 2, species 1 no longer gives catalytic support to the hypercycle and thus it has become a "parasite" to the hypercycle. Plate 12C after 4000 timesteps shows that this parasite is deadly to the five-member hypercycle: it expands towards the spiral, and eventually all species, except for species 1, will become extinct.
3.3.2. DISJOINT HYPERCYCLES In the ODE model, the growth of a hypercycle is a nonlinear (approximately quadratic) function of its concentration. Therefore, an established hypercycle cannot be replaced by any newcomer, regardless of its parameters, because the latter has to start at low concentration. Thus, selection of a hypercycle is a "once forever" decision.

In the CA model, it is obvious that, as soon as the new hypercycle has formed a spiral, it can compete with the established hypercycle. In the situation of plate 5C (color plates), a new hypercycle was introduced at low concentration (25 molecules of each species), but in catalytic order. The new hypercycle has much higher parameters than the established hypercycle (decaynew = 1.6; decayold = 0.1; self[new] = 2.0; self[old] etc. = 200.0). It appears that the new hypercycle simply outgrows the established hypercycle. Thus once forever selection does not hold for this system.

3.3.3. RANDOM CONNECTIONS Preliminary experiments, in which the catalytic connections between molecules are chosen at random, indicate that sometimes there is selection for a hypercycle interaction structure. This occurs for a certain number of species and a certain number of connections. Much more often, interaction structures of short cycles with coupled parasites (an example is shown in Figure 8) arise. These structures would not persist in the ODE model; in the CA model, the system is locally unstable, but there is a dynamical global equilibrium.

In a future paper we will try to unravel the complex interaction pattern which evolves under various circumstances.

4. DISCUSSION AND CONCLUSIONS

4.1. MOLECULES WITH A HYPERCYCLIC INTERACTION STRUCTURE SHOW SPATIAL SELF-STRUCTURING; SPIRAL WAVES DEVELOP FOR A WIDE VARIETY OF PARAMETER VALUES

The spiral wave is a well-known pattern in excitable media which has been studied most thoroughly with respect to the Belousov-Zhabotinsky reaction, both experimentally and theoretically.11,14 Most theoretical models are formulated in terms of partial differential equations;17 spiral-wave solutions are found in cellular automata models as well.5,7,8,16 Spiral waves have been shown to play a role in cell-to-cell communication in Dictyostelium discoideum18 and in nervous tissue.19 Our analysis suggests a role for spiral waves in enabling the evolution of cooperation.

We tested our model extensively for robustness of the self-structuring property. It turns out that the precise definition of the cellular automaton does not affect the development of the spirals. We examined, for instance, asynchronous updating of the cells, a non-toroidal field, and other neighbor cells that can give catalytic support.

The individual molecule species in the hypercycle can, to some extent, differ in their parameters and still form stable spirals. However, when the difference is parameters is too large, the system becomes unstable and no spirals are formed. In between the parameter region of stable spirals and no spirals, there is always a zone of complex spirals; in this zone there is perpetual formation and degradation of spirals.

The number of species in the hypercycle affects the formation of spiral waves; it appears that (at least for the given default parameters) the hypercycle needs to consist of five members or more to form stable spirals. The hypercycle with four members is in the complex spiral zone and spirals of two or three members show no spiral formation at all.

For many of the parameters, we see a zone of complexity in between a dynamical (chaotic) zone and a spatially stable spiral pattern. This situation seems somewhat analogous to phase transitions.12

4.2. IN A SYSTEM WITH SPIRAL WAVES THERE IS SELECTION AT THE LEVEL OF THE SPIRALS; THIS SELECTION CAN CONTRADICT SELECTION AT THE LEVEL OF THE INDIVIDUAL MOLECULES

Within a spiral, there is a strikingly unequal distribution of long-term fitness: the molecules in the middle of a spiral generate the offspring of the entire spiral whereas the molecules in the periphery of a spiral disappear (as shown in color plate 6A-C). This direction of growth causes the spirals to act as independent entities in the selection process.

The following "rules of selection" can be formulated for the spiral wave system:

A. Molecules that are capable of growth toward the center of a spiral are always selected. An example of this rule is the situation for decay{mutant} ≤ 0.13 in Figure 6(a); the mutant decays so slowly that it is able to get in the center of all the spirals. Plate 12C also gives an example: species 1 (red) is coupled parasitically to the hypercycle and it is able to grow towards the center of the spirals. (Note that, in the latter case, species 1 will destroy the hypercycle, while in the first case, the mutant replaces species 1, but it does not destroy the hypercycle.)

B. If not A: molecules that can form a stable spiral are selected against molecules that cannot form a stable spiral. An example is the situation for the shortest mutant in plate 10A-C; the mutant selects for a hypercycle of four members, but this hypercycle does not form stable spirals and, therefore, is out-competed by the hypercycle with five members.

C. If not A or B: molecules whose spiral rotates faster will be selected against molecules with slower rotating spirals. The cases of plates 9A-E and 11A-C are examples of this rule. The process is analogous to the competition between pacemaker waves in the Belousov-Zhabotinsky reaction,21 where the wave with the highest frequency wins.
by the parasitical species 1. However, this result is not robust: if the five-member hypercycle has slow parameters (e.g., species 4 decays somewhat slower), it can be stable against species 1.

4.4. SPATIAL SELF-STRUCTURING CAN HAVE A MAJOR IMPACT ON THE OUTCOME OF SELECTION PROCESSES; THEREFORE, IT SHOULD BE TAKEN INTO ACCOUNT IN THE STUDY OF EVOLUTION

We have shown that spatial self-structuring into spiral waves alters almost all selective properties of the hypercycle. This is because selection no longer exclusively takes place at the level of the individual molecules, but also at the level of the spirals. The spatial self-structuring enables selection for all kinds of altruistic properties (e.g., selection for giving catalytic support and selection for decaying faster).

It seems plausible that the phenomenon of spatial self-structuring is not restricted to hypercycles. Farmer et al. propose a cyclic catalytic network of polymers. This network differs from the structure of a hypercycle in that the polymers are not self-replicative. However, the interactions in this network look very much like the interactions in the earlier mentioned Belousov-Zhabotinsky reaction, so the spiral structure may well emerge in this system, too. Whether cyclic interaction structures are likely to appear and out-compete other structures in networks with random interactions is a subject for further study.

Self-structuring is a well-known feature of cellular automata. Simple low-level transition rules can generate high-level spatial patterns. This spontaneous self-structuring has often been interpreted as a form of evolution. In this study we use a different approach; we consider self-structuring as a substrate for selection. The substrate has proved very fertile; an environment is created in which selection for altruistic features is possible.

We believe, therefore, that in the study of (prebiotic) evolution, it is important to look for self-structuring and examine its consequences.
APPENDIX THE ODE OF THE HYPERCYCLE

In the model, a self-replicative molecule species are linked cyclically by catalysis (see Figure 9). The total number of molecules C is kept constant by an output flux f. Erroneous mutants are not included in the model. For analytical proof and further discussion, see Eigen\(^5\) and Hofbauer.\(^5\)

\[
\begin{align*}
\text{(a)} & \quad \text{self-replication} \\
\text{(b)} & \quad i_i \xrightarrow{b_i} 2i_i \\
& \quad i_i \xrightarrow{d_i} \\
& \quad i_i \xrightarrow{k_i} i_{i-1} + 2i_{i+1} \\
& \quad f \\
\text{(c)} & \quad X_i = r_i X_i + k_i X_i X_{i+1} - d_i X_i \\
& \quad \sum_{i=1}^{n} X_i = C, \quad C \text{ being the total number of molecules} \\
& \quad f = \left( \sum_{i=1}^{n} (r_i X_i + k_i X_i X_{i+1}) \right) / C
\end{align*}
\]

FIGURE 9 (a) Schematic diagram of a hypercycle. The hypercycle consists of self-replicative molecule species \(i_i\); each species provides catalytic support for the subsequent species in the cycle. After Eigen.\(^5\) (b) Kinetic steps. (c) Differential equations.

FIGURE 10 A hypercycle with a self-replicative "parasitic" molecule species "par." The parasite gets catalytic support from species \(i_2\), but does not give catalytic support to any molecule species in the hypercycle. After Eigen.\(^5\)

FIGURE 11 Schematic diagram of two joint hypercycles. After Hofbauer.\(^5\)
Summary of dynamical and selectional properties

- Stability. The elementary hypercycle has only one attractor. At low dimensions \((n \leq 4)\), the attractor is an asymptotically stable fixed point, namely, a focus for \(n = 2\) and a spiral sink for \(n = 3\) and \(n = 4\). In systems of higher dimensions \((n \geq 5)\), "permanence" has been proven, i.e., no molecule species vanishes; numerical integration provides strong evidence for the existence of a stable limit cycle.

- Parasites. In Figure 10 a hypercycle with a so-called parasite is shown. The system appears to be competitive, i.e., the hypercycle and the parasite cannot co-exist. If the linear terms are neglected, the following relation holds: if \(k_{3}\) > \(k_{2}\), the parasite wins; if \(k_{3}\) < \(k_{2}\), the entire hypercycle (and the parasite) becomes extinct.

- Competition between joint hypercycles. In Figure 11, two joint hypercycles are shown. The two cycles exclude each other (again neglecting the linear terms): if \(k_{1}\) < \(k_{2}\), hypercycle \(\Gamma_2\) will out-compete \(\Gamma_1\); if \(k_{1}\) > \(k_{2}\), hypercycle \(\Gamma_1\) will out-compete \(\Gamma_2\).

- Competition between disjoint hypercycles. Selection of a hypercycle is a "once forever" decision. A hypercycle, once established, cannot easily be replaced by any newcomer, since new species always emerge as one copy; the growth rate of a hypercycle is nonlinear and therefore dependent on population size.

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REFERENCES


Plate 8. Development of a spiral wave pattern in a spatial hypercycle system. Colour molecule species: (1) red; (2) orange; (3) yellow; (4) green; (5) light blue; (6) blue. In order to increase contrast we do not show the state of a cell, but instead we show the majority molecule species in the 9-cell neighbourhood of the cell. If all 9 cells are empty the cell is white. A) $t=0$, random initialization; B) $t=1000$; C) $t=2000$, stable pattern.

Plate 9. Direction of growth within a spiral. Molecules in the middle and the periphery of a spiral are labelled. Plate 8C is used as a starting pattern; A) $t=0$, starting pattern with labelling; B) $t=30$; C) $t=200$.

Plate 10. Stability experiments. Figure 4 is used as a starting pattern. A) decay[1]=0.06; B) decay[1]=0.03; C) decay[1]=0.05.
Plate 11. Instability of short hypercycles. **A** 3 species; **B** 4 species.

Plate 12. Spiral selection. In plate **A** a spiral is infected with black mutants. **B,C** decay[mutant]=0.15; **B** timeplot of a one-dimensional horizontal section through the middle of the field; **C** situation at $t=4000$; **D,E** decay[mutant]=0.4; **D** timeplot of a one-dimensional horizontal section through the middle of the field; **E** situation at $t=4000$. 
Plate 13. Short-cut mutant "5 to 4". A) $t=0$, infection of a spiral; B) $t=500$; C) $t=3000$, the 5-cycle has won.

Plate 14. Short-cut mutant "7 to 6" (colour species 7: dark blue). A) $t=0$, infection of a spiral; B) $t=500$; C) $t=2000$, the 6-cycle has won.

Plate 15. Short-cut mutant "6 to 5". A) $t=0$, infection of a spiral; B) $t=2000$; C) $t=4000$, species 1 is a "deadly" parasite.