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Towards a Formal Understanding of Bateson's Rule: Chromatic Symmetry in Cyclic Boolean Networks and its Relationship to Organism Growth and Cell Differentiation

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Abstract

There has been considerable prior research on the biological processes of morphogenesis and cellular differentiation, and the manner by which these processes give rise to symmetries in biological structures. Here we extend our previous work on thermal robustness and attractor density in cyclic formal Boolean dynamical systems, introducing a new form of spectral analysis on digital organisms at the cellular level. We interpret the phenomena of radial and bilateral symmetry in terms of spatial periodicities in the color sequences, as manifested by an organism while it orbits in its attractors. We provide new results on the influence of various organism properties on its emergent color symmetries—providing initial insights toward an eventual formal understanding of metamerism and Bateson's Rule.

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Keywords: Boolean networks; dynamical systems; chromatic, symmetry

1. Introduction

Since the seminal work of Von Neumann [1], the subject of cellular automata has received considerable and continued attention (see [2, 3] for brief surveys). Understanding how the structure of a cellular network impacts its behavior as a dynamical system is crucial to determining how networks should be built, how they evolve over time, and how they can be made to grow while still exhibiting desired dynamical properties. Biological networks (e.g. neural networks) are subject to preferential selection processes, which drive evolution over long time scales. It is reasonable to expect that this selection process will be sensitive to not only the structural properties [4] of networks, but to their dynamical properties as well [5]. Previous researchers have considered measures such as landscape ruggedness [6, 7] and redundancy [8] in evaluating dynamical systems. In this paper, we extend our previous work on attractor dynamics [16] to describe *the manner in which the requirement to maintain rotational chromatic symmetries in an organism's attractor dynamics might serve to structure its growth trajectory*.

In addition to evolution over long time scales, biological networks exhibit cellular differentiation over short

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time scales, particularly during morphogenesis when changes in cellular structure frequently arise from symmetry breaking during growth. One striking example of this occurs in the inner cell mass of a blastocyst that goes on to form the diverse and specialized tissues of the human body. Additionally, in this paper we explore *the impact of cell differentiation on the emergence of bilateral chromatic symmetries in an organism's attractor dynamics*.

Throughout this investigation we consider a theoretical synthetic biology, using Boolean networks as a formal basis. These networks consist of cells whose instantaneous state is always either 0 or 1, and are the subject of considerable research since their introduction by Kauffman [9] as plausible models of genetic regulatory networks. Although Boolean networks are typically considered in terms of potentially dense random Boolean "NK" networks [10], here we consider the more restricted class of cyclic networks (K=2). Such one-dimensional automata have themselves received considerable attention [11], and are known to exhibit many of the phenomena seen in their more general *NK* counterparts [12]. We assume that the dynamic evolution in our networks is given by synchronous deterministic rules; this is not a significant limitation, since it is well-known that asynchronous behavior with small temporal tolerances can be translated into equivalent synchronous models [13].

Our approach differs from previous approaches in 3 key respects: (i) Rather than considering the instantaneous state of an organism (wherein each cell is either 0 or 1), we consider the state of *each cell over unbounded time*, examining the periodicity of its binary oscillations while the organism orbits in an attractor; (ii) Rather than considering fixed size organisms, we explore symmetry *invariants* across organism sizes, which might inhibit or promote particular growth patterns; (iii) Rather than considering an organism in which cell states evolve according to unchanging logic, we consider (in Section 3.2) the impact of cell differentiation.

The results presented here are the outcome of large-scale computational experiments based on simulations grounded in a formal mathematical model that builds upon existing research in the area of synchronous Boolean networks and cellular automata. Determining network dynamics is a computationally intensive endeavor, and data collected from the somewhat more accessible class of synchronous, cyclic, Boolean networks is used here to make inferences about broader relationships between rotational chromatic symmetry and growth and the role of cell differentiation on the emergence of bilateral chromatic symmetry.

2. Mathematical Preliminaries

This paper considers the interplay of four broad aspects of complex adaptive systems. First, at the base is the well-studied area of cellular automata. Second, within this area we introduce a chromatic characterization of the oscillations manifested by individual cells while an organism is trapped in an attractor. Third, we consider the prevalence of rotational symmetries in the chromatic representations of organisms and explore possible connections between such symmetries and the growth of the size of organisms. Lastly, we evaluate the possibility of environmental noise that can perturb the functioning of an organism through the emergence of bilateral symmetry.

2.1. Organism structure, state, and dynamics

We model the *microstructure* of synthetic organisms as cyclic cellular automata, each of which is represented as an undirected cyclic graph $C = (V, E)$ of size n whose vertices $v_0, v_1, \ldots v_{n-1}$ are **cells** within an organism. Each cell v_i in V is connected to two neighbors in this cyclic ordering, so $E = \{(v_i, v_{i+1 \bmod n}) \mid i = 0, \ldots n-1\}$. The microscopic behavior of cells is modeled by fixing a function $f: V \to V$ that assigns to each cell $v_i \in V$, a function $f(v_i)$ from the set of all binary Boolean functions F.

$s(v_{i-1 \bmod n}, t)$	$s(v_{i+1 \bmod n}, t)$	$s(v_i, t+1)$
0	0	b_0
0	1	b_1
1	0	b_2
1	1	b_3

The truth table for $f(v_i)$ maps the value of $v_{i-1 \bmod n}$ and $v_{i+1 \bmod n}$ at time t to the value of v_i at time $t+1$. Often, we denote $f(v_i)$ by the 4-bit binary number $b_3 b_2 b_1 b_0$; for example the XOR function is referred to as function 0110_2=6, AND is 1000_2=8, OR is 1110_2=14, etc. In this paper, we primarily consider homogeneous organisms, where $|Im(f)| = 1$; that is, all cells evolve over time according to a uniform binary Boolean function.

The instantaneous Boolean *state* of the organism is specifiable as a function $V \to \{0,1\}$. The organism's constituent cells evolve according to the rule specified by a Boolean function operating at each cell, together with the instantaneous state of its two adjacent neighbors. The organism's trajectory evolves over (discrete) time and is given by $s: V \times \mathbb{N} \to \{0,1\}$, where at time t, cell $v_i \in V$ is in state $s(v_i, t)$ defined inductively by

$$s(v_i, t+1) = f(v)(\, s(v_{i-1 \bmod n}, t), s(v_{i+1 \bmod n}, t)\,) \qquad (1)$$

for each $i = 0, \ldots n-1$ and $t \geq 0$. We denote $s^+(t) = \{v_i \mid s(v_i, t) = 1\} \subseteq V$, the vertices that are "on" at time t. The macroscopic *dynamics* of the organism are represented as a directed graph $S = (2^V, D)$ on the power set of V, whose edge set $D = \{(X, Y) \mid s^+(t) = X \;\&\; s^+(t+1) = Y\}$. The directed graph S is the organism's phase space, in which the edge (X, Y) indicates that whenever the organism is in state X at time t, it is necessarily in state Y at $t+1$. For a pair of states $X, Z \subseteq V$ we write $X \to Z$ if there is a directed path from X to Z in S—that is, a sequence of $k > 0$ states $Y_o, Y_1, \ldots, Y_k$ in V satisfying $Y_o = X, Y_k = Z$ and $(Y_i, Y_{i+1}) \in D$ for $i = 0, \ldots k-1$. A state $X \subseteq V$ is said to be on an **attractor** if $X \to X$. The set of states that are on an attractor are denoted $A \subseteq 2^V$; the remaining states in $2^V \setminus A$ are tributaries forming basins into attractors. Considering A modulo the equivalence relation $\approx_R$ gives rise to quotient $[A] = A/R$, wherein $c \in [A]$ is the attractor with states cR; the **length** of the attractor is taken to be the number of states in $|cR|$. Given a state $X \in A$, the corresponding attractor is denoted $[X]$. We define $X \approx_R Z$ whenever both $X \to Z$ and $Z \to X$, i.e. both X and Z are on the same attractor [X]=[Z] [16].

The computational platform. Our program samples the state space by picking random start states and computing the attractor in the dynamics that the start state leads to. For our experiments we used 100,000 random start states for each organism from which we identify and store each attractor discovered, the length of the attractor, the number of times a random start state has lead to this attractor, and the periodicity of each cell state across an attractor. Using the periodicity for each cell across an attractor we build a table of symmetry in the coloring of an organism for each attractor, where the color for each cell is the periodicity for that cell on that attractor. The number of attractors discovered at each interval of exploration is used in capture-recapture techniques to estimate the number of attractors at a given organism size while the number of start states that lead to an attractor can be used to estimate the size of the basin of the attractor.

Figure 1 shows the decomposition of the dynamics graph of a size n=12 homogeneous organism where every cell uses the function 6 (XOR) to determine its' Boolean state. The complete dynamics graph of this organism has 6 attractors of length 2 as in Figure 1 (left), 60 attractors of length 4 as in Figure 1 (center), and 4 attractors of length 1 as in Figure 1 (right). The nodes are labeled with the Boolean of the organism's cells' states. The directed edges lead from a state X at time t to state Y at time $t+1$; black edges are tributaries while blue edges are in attractors.

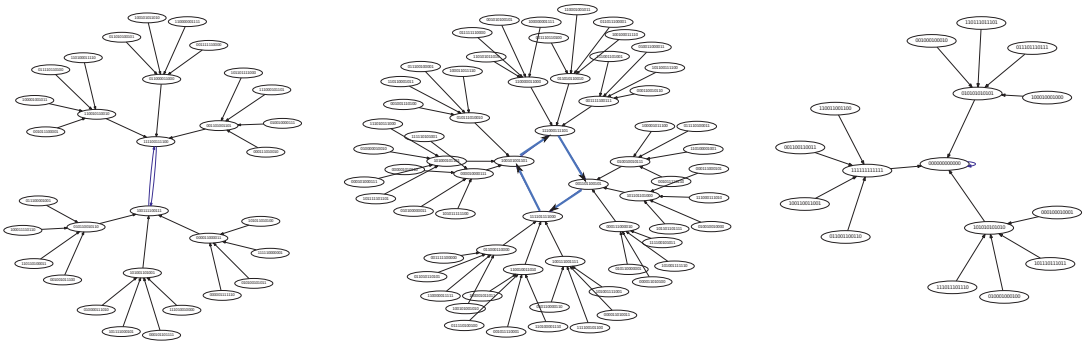


Figure 1. The 4096 vertex dynamics graph of a size n=12 homogeneous organism in which all cells operate function 6 (XOR).

2.2. Chromatic representations of organisms in attractors

Within each attractor $c \in [A]$, each cell $v_i \in V$ oscillates among the binary states 0 and 1, producing an infinitely repeating binary sequence whose periodicity $\lambda(v_i, c)$ necessarily divides the attractor length $|c|$. The **color** of cell v_i relative to attractor c is defined to be $\chi(v_i, c) = \lambda(v_i, c)/|c|$, a rational number in the interval $[0,1]$. It may

not be obvious at first glance, that a homogeneous organism in which all cells are operating according to the same function can be polychromatic. For example, Figure 2 (left) shows the length 4 attractor from Figure 1 (center) in the state space of a function 6 (XOR) organism of size n=12; in the middle figure, we see the corresponding infinite binary sequences experienced at each of the 12 cells; finally, the right figure shows the periodicity $\lambda(v_i, c)$ of each cell—a range of multiple periodicities (1,2,4) implies a range of colors (1, 0.5, 0.25). Because of this, we say that the organism in this attractor is polychromatic. Next we turn to the question of symmetries in the coloring.

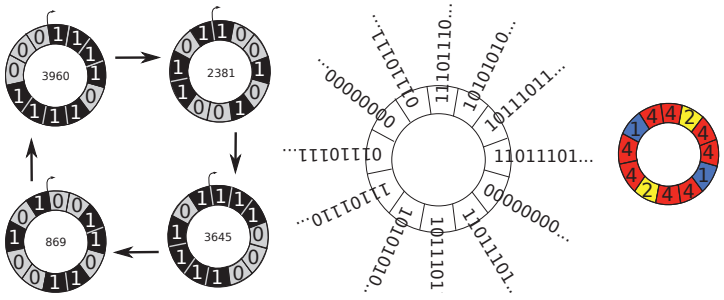


Figure 2. Attractor of size 4 in the n=12 homogeneous organism with function 6 (XOR)

An organism has a non-trivial **rotational chromatic symmetry** within attractor c if for some segment size $0 < L < n$, we have $\chi(v_i, c) = \chi(v_{i+L \bmod n}, c)$ for all $i = 0, \ldots n-1$. The maximal such segment size L_{max} defines the **foldedness** n/L_{max} of the organism within attractor c. For example, relative to the length 4 attractor in Figure 2, the size n=12 function 6 (XOR) organism exhibits 2-fold rotational symmetry with segment size $L_{max} = 6$.

An organism is said to exhibit **bilateral chromatic symmetry** in attractor c if for some phase offset $0 \le P \le n-1$, we have $\chi(v_i, c) = \chi(v_{P+i \bmod n}, c) = \chi(v_{P-i \bmod n}, c)$ for all $i = 0, \ldots \lfloor n/2 \rfloor$. It is easy to verify that relative to the length 4 attractor in Figure 2, the size n=12 function 6 (XOR) organism exhibits bilateral symmetry.

3. Results

To begin, we consider the question "What colors can arise?" in the chromatic representation of an organism. Since the color of a cell is the periodicity of its binary state, it must necessarily divide the length of the attractor. Towards understanding the range of colors possible, the left graph in Figure 3 shows the sizes of attractors observed, as the organism size increases; all 16 homogeneous organism types were considered by sampling at least 1000 random start states for each; the attractor sizes for function 6 (XOR) are shown in red. The y-axis for organism attractor length is a logarithmic scale and it is clear from this graph that the homogeneous function 6 (XOR) organism exhibits explosive growth in attractor sizes, and hence in the potential colors which may arise in chromatic renderings of the organism.

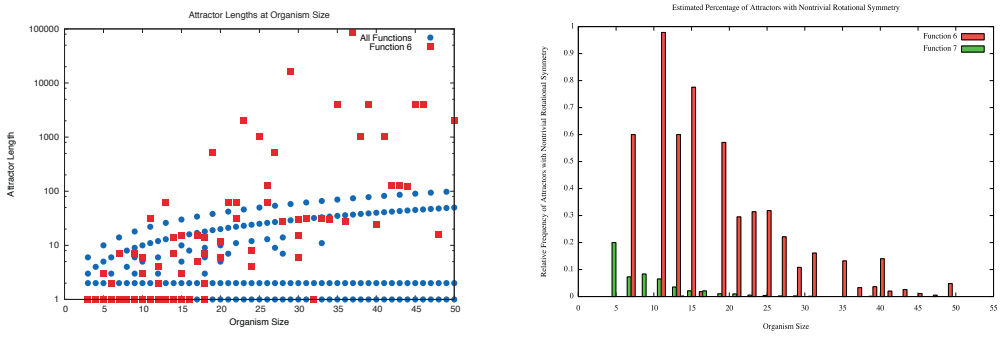


Figure 3. Sizes of attractors (left) percentage that are rotationally symmetric (right).

The next question we consider, is just how rare are rotational chromatic symmetries? The right graph in Figure 3 shows the relative frequency of attractors as organism size increases; after an initial sampling of 1000 darts only functions 6 (XOR) and 7 (NAND) exhibit attractors with nontrivial rotational symmetries in the organism coloring. The graph shows that as organism grows in size the relative frequency of attractors with nontrivial rotational symmetry decreases. For NAND the relative frequency goes toward 0 at size 30. However, we see that XOR is distinguished in that it shows positive probability for rotational color symmetries to be present even for larger organisms. This is significant because existence of chromatic symmetry at larger sizes is necessary if there is a relationship between symmetry and growth.

3.1. Chromatic rotational symmetry and organism growth

In the previous section, we saw the homogeneous function 6 (XOR) organism continues to exhibit polychromatic rotational symmetry even as the organism size is allowed to increase. Here we explore two hypothetical requirements for rotational chromatic symmetry invariance and see how such requirements conflict or align with the organism's impetus to grow. Towards this, we postulate two competing hypothetical requirements:

Hypothesis 1, "Growth occurs by segment reduplication": If there is a rotationally symmetric organism of size n, having segment size L, then there is a rotationally symmetric organism of size n+L, also with segment size L. This would suggest that a k-fold symmetric organism can grow by retaining its segment size, transforming into a larger (k+1)-fold symmetric organism.

Hypothesis 2, "Growth occurs by segment elongation": If there is a rotationally symmetric organism of size n, having segment size L, then there is a rotationally symmetric organism of size n+(n/L), with segment size L+1. This would suggest that a k-fold symmetric organism can grow by retaining its k-foldedness but transforming its segment size to L+1.

The two hypotheses are depicted in Figure 4. On the left, we see an attractor of the size 10 homogeneous function 6 organism as the "If" precondition for hypothesis 1 and 2. This attractor has length 6 with rotation segment size L=5, exhibiting k=2-fold chromatic rotational symmetry. Figure 4 (right-top) shows symmetry preserving growth to size 15 by way of Hypothesis 1, occurring by the addition of a segment of size 5; the post-condition for Hypothesis 1 is indeed satisfied by the provided attractor of length 3 which has segment size L=5 in the size n=15 homogeneous function 6 organism (k=3-fold chromatic rotational symmetry). Figure 4 (right-bottom) growth to size n=12 by way of Hypothesis 2, wherein a cell is added in each segment; the post-condition for Hypothesis 2 is satisfied by the provided attractor of length 4 which has segment size L=6 in the size n=12 homogeneous function 6 organism (k=2-fold chromatic rotational symmetry). This example is part of data aggregated in row 2 of Table 2.

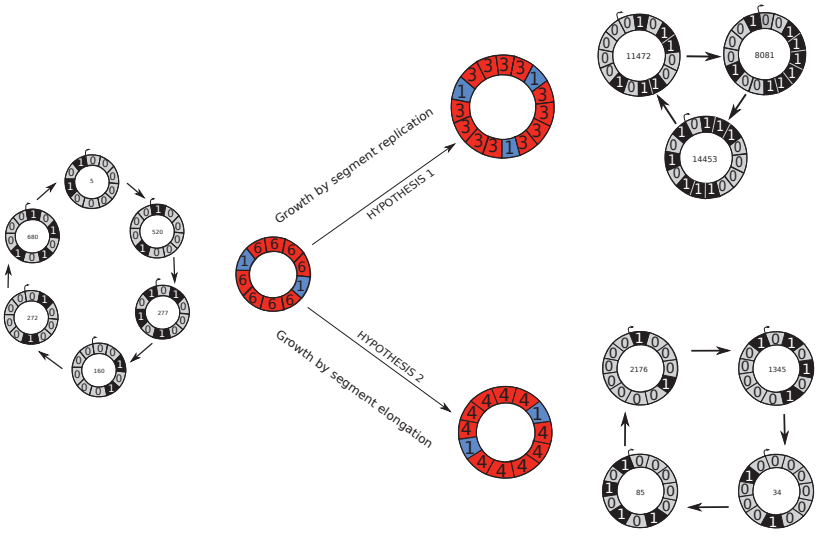


Figure 4. Maintaining chromatic symmetry invariants during growth, two competing hypotheses.

Table 2 shows the results of testing the pre and post conditions for Hypothesis 1 and Hypothesis 2 on the attractors discovered by sampling random starting states in organism. The first column is the organism size n where non-trivial rotational symmetry segment sizes L were found; column 2 is the segment size L; column 3 is the total number of attractors discovered at size n by sampling randomly; column 4 is the percentage of attractors which were found to have rotational symmetry with segment size L; column 4 is the organism size n+L that is referenced in the post-condition of Hypothesis 1; column 5 is the percent of attractors with segment size L discovered in the state space for the organism size n+L; column 6 is the organism size n+n/L for the post-condition of Hypothesis 2; column 7 is the percent of attractors with segment size L+1 discovered in the state space for organism size n+n/L.

Precondition				Hypothesis 1		Hypothesis 2	
n	L	#c	% Sym w Seg=L	n+L	% Sym w Seg=L	n+(n/L)	% Sym w Seg=L+1
6	3	10	60	9	0	8	0
10	5	46	98	15	1.8	12	34
12	6	70	34	18	0	14	78
12	3	70	0.26	15	0	16	0
14	7	298	0.78	21	0	16	0
15	5	1112	0.019	20	17	18	0
18	9	4707	0.57	27	0	20	12
18	3	4707	0.0011	21	0	24	0
20	10	932	0.12	30	0	22	31
20	5	932	0.17	25	0	24	15
22	11	974	0.31	33	0	24	15
24	12	930	0.15	36	0	26	22
24	6	930	0.15	30	0	28	9
24	3	930	0.022	27	0	32	0
26	13	998	0.22	39	14	28	1.8
28	7	1000	0.09	35	0	32	0
28	14	1000	0.01	42	0	30	1.6

From Table 2 we can verify that both Hypothesis 1 and Hypothesis 2 have non-zero percentages for size 10 and 26 suggesting that both the relationship of growth to symmetry might fit both hypotheses. However, it is clear from the table that Hypothesis 2 has a higher percent of matching post-conditions for more sizes. This suggests that *if there is a requirement to maintain rotational chromatic symmetries in an organism's attractor dynamics during growth—then growth is more feasible by way of segment elongation (Hypothesis 2) than by segment reduplication (Hypothesis 1).* In the presence of symmetry invariants, an organism's impetus to grow is better aligned with the Hypothesis 2 strategy that adds a single cell to each segment producing a larger organism of size n+n/L with the same k-folded nontrivial rotational symmetry. An organism whose impetus to grow follows the Hypothesis 1 strategy of segment reduplication cannot grow indefinitely. In other words, if nontrivial rotational symmetry segment size is a desired property to be maintained throughout growth, then a constant foldedness of the chromatic rotational symmetry will be selected for.

3.2. From rotational to bilateral chromatic symmetry

In "Steps to an Ecology of Mind" [15], Gregory Bateson wrote: "An unfertilized frog's egg is radially symmetrical, with animal and vegetal poles but no differentiation of its equatorial radii. Such an egg develops into a bilaterally symmetrical embryo, but how does it select one meridian to be the plane of bilateral symmetry of that embryo? The answer is known—that, in fact, the frog's egg receives information *from the outside*." Here we interpret his assertion in the synthetic formal biology. The next hypothesis makes our interpretation precise.

Hypothesis 3, "Cellular differentiation leads to bilateral symmetry": If we start in an attractor with nontrivial rotational symmetry segment size in the dynamics of a homogeneous function 6 (XOR) organism and one

of its' cells is mutated to function 9 (NXOR), then the attractor state will lead to an attractor that is bilaterally symmetric in the dynamics of the mutated organism.

In Table 3, we compare the percentage of single-cell mutations in each attractor which lead to a bilaterally symmetric attractor in settings where nontrivial rotational symmetry is both present and absent. Column 1 is organism size where attractors with nontrivial rotational symmetry segment sizes have been discovered by sampling; column 2 is the number of attractors with nontrivial chromatic rotational symmetry; column 3 is the percent of bilaterally symmetric attractors reached from attractor states in column 3 by mutating a single cell from function 6 (XOR) to function 9 (NXOR) in the original organism; column 4 is the number of attractors without nontrivial chromatic rotational symmetry; column 5 is the percent of bilaterally symmetric attractors reached from the attractor states in column 4 by mutating a single cell from function 6 (XOR) to function 9 (NXOR) in the original organism.

	Rotationally Symmetric Attractors		Non-Rotationally Symmetric Attractors	
Org Size	#	% become bilateral	#	% become bilateral
6	6	100	4	100
10	45	90	1	100
12	42	100	28	100
14	231	100	67	100
15	20	47	20	33
18	1000	94	1000	89
20	606	100	606	95
22	893	100	893	100
24	1000	100	1000	100
26	654	100	654	100
28	270	100	270	100
30	998	100	446	90

Table 3 shows that there is a high probability after cellular mutation an attractor state will lead to a bilaterally symmetric attractor in the dynamics of the mutated organism. However, the probability of the attractor state leading to a bilaterally symmetric attractor is higher if the initial attractor state has a nontrivial chromatic rotational symmetry.

4. Conclusions and Future Work

In this paper we consider the impact of cellular growth on symmetry as well as how symmetry might drive growth, and the impact of cellular mutations on symmetry. We focus on homogeneous organisms where every cell determines its' state using the function XOR. Our experimental approach computes estimates by sampling the state space to explore larger organisms where completely exploring the entire state space is computationally intractable.

If rotational symmetry is to be preserved in an attractor, growth must occur either by an entire arm segment or by a cell in each arm. Experimentally we identify the non-trivial rotationally symmetric segment sizes of attractors for an organism size and then searched for matching rotational symmetric segment sizes in attractors at the corresponding larger grown organism. The results of our experimental approach match observed growth in biological organisms and suggest that if symmetry drives organism growth then the growth would occur by segment elongation (Hypothesis 2) rather then by segment reduplication (Hypothesis 1).

Our results also suggest outside information in the dynamics of a rotationally symmetric attractor will lead to a bilateral symmetry attractor which also matches observed development in biological organisms: In "A Re-examination of "Bateson's Rule", Gregory Bateson asserts the necessary role of outside information on homogenous organisms impacting the symmetrical development to result in bilateral symmetry [15]. Since our organisms are closed and the only input comes from neighboring cells, we simulate the outside information through cellular mutation and look at the resulting possible dynamics that arise from the initial state.

Future work includes developing formal proofs from the experimental results for the homogeneous

function 6 organism and expanding the random sampling to include non-homogeneous organisms. The experimental data from the much larger set of non-homogeneous organisms should lead to a better understanding of cellular differentiation, symmetry, and morphogenesis.

Acknowledgements

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