

SYNCHRONY VERSUS SYMMETRY IN COUPLED CELLS

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A coupled cell system is a network of dynamical systems, or ‘cells’, coupled together. Such systems are represented schematically by a directed graph whose nodes correspond to cells and whose edges represent couplings. Symmetry of coupled cell systems can lead to synchronized cells. We show that symmetry is not the only mechanism that can create such states in a coupled cell system. The first main result shows that robust synchrony is equivalent to the condition that an equivalence relation on cells is ‘balanced’. The second main result shows that admissible vector fields restricted to synchrony subspaces are themselves admissible vector fields for a new coupled cell network, the ‘quotient network’.

1. Introduction

Basic questions in the study of symmetric differential equations include:

- 1) What is meant by symmetry for a differential equation?
- 2) What kinds of symmetry can solutions to differential equations have?
- 3) How does the symmetry of solutions change as parameters are varied?

We limit the discussion to autonomous systems $\dot{x} = F(x)$, where $x \in \mathbf{R}^n$ and $F : \mathbf{R}^n \rightarrow \mathbf{R}^n$. A *symmetry* is a linear map $\gamma : \mathbf{R}^n \rightarrow \mathbf{R}^n$ that takes solutions to solutions; equivalently, γ satisfies the equivariance condition $F(\gamma x) = \gamma F(x)$. The set of symmetries forms a group Γ . Progress can be made on answering questions (2) and (3) only when the group Γ is specified first. That is, answers to these questions are found for the space of all Γ -equivariant differential equations.

There is a parallel theory for coupled systems of differential equations where ‘synchrony’ takes the role of symmetry. Indeed, we attempt to answer

the three questions with synchrony replacing symmetry and coupled cell systems replacing systems of differential equations.

In our discussion we use the term *cell* to indicate an autonomous system of ODEs. A *coupled cell system* is a set of cells with coupling. The salient feature of a coupled cell system is that the output from each cell is considered to be significant in its own right⁴. In particular, the output signals can be compared, and this observation leads to various notions of ‘synchrony’. A solution $x(t)$ has *synchrony* if there are (at least) two cells i and j that have identical outputs, that is, $x_i(t) = x_j(t)$ for all t . We are particularly interested in cell systems that exhibit *robust synchrony* — whenever a solution has synchronous initial conditions it exhibits synchrony for all time. For surveys on synchrony (which include a variety of definitions) see Boccaletti *et al.*¹ and Wang¹⁰.

In this paper we review recent work^{9,5,2} that addresses the question: What features of the typical dynamics in coupled cell systems are products of network architecture? By the *architecture* of a coupled cell system we mean: which cells influence which, which cells are ‘identical’, and which couplings are ‘identical’.

It is known^{3,4} that synchrony in coupled cell systems can be produced by network symmetry. However, the proper coding of system architecture is done in terms of the network’s symmetry groupoid^{9,5} and this structure leads to a much larger class of synchronous dynamics. We describe two theorems that follow from the groupoid formulation:

- Patterns of synchrony are determined by balanced equivalence relations on the set of cells.
- The restriction of a coupled cell vector field to a polysynchronous subspace is itself a coupled cell system, the *quotient system*, and every quotient system lifts to a system on the original network.

2. Coupled Cell Systems and Symmetry

Systems of two identical cells (with coordinates $x_1, x_2 \in \mathbf{R}^k$) have the form

$$\begin{aligned}\dot{x}_1 &= f(x_1, x_2) \\ \dot{x}_2 &= f(x_2, x_1)\end{aligned}\tag{2.1}$$

where the same function f governs the dynamics of both cells.

Informally, the ‘network’ of a coupled cell system is a finite directed graph whose nodes represent cells and whose edges represent couplings. Nodes are labeled to indicate ‘equivalent’ cells, which have the same phase

space; edges are labeled to indicate ‘equivalent’ couplings. The graph associated to (2.1) is given in Figure 1. Since cells 1 and 2 are the same and arrows $1 \rightarrow 2$ and $2 \rightarrow 1$ are the same, we can interchange cells 1 and 2 without changing the graph. We assume that the same is true for the system of differential equations and that the system has the form (2.1).

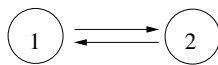


Figure 1. A two-cell network.

The permutation $\sigma(x_1, x_2) = (x_2, x_1)$ is a symmetry of (2.1). Indeed, every σ -equivariant system of differential equations on $\mathbf{R}^k \times \mathbf{R}^k$ has the form (2.1). Two consequences follow from this remark. First, synchrony in two-cell systems (solutions such that $x_1(t) = x_2(t)$ for all time t) is a robust phenomenon and should not be viewed as surprising. Second, time-periodic solutions can exhibit a kind of generalized synchrony in which the two cells oscillate a half-period out of phase.

The first consequence can be restated: the diagonal subspace $V = \{x_1 = x_2\} \subset \mathbf{R}^k \times \mathbf{R}^k$ is flow-invariant for every system (2.1). The second consequence is related to general theorems about spatio-temporal symmetries of time-periodic solutions to Γ -symmetric systems of ODEs^{3,4,6}. These theorems imply the existence of functions f having time-periodic solutions of period T satisfying

$$x_2(t) = x_1(t + T/2) \quad (2.2)$$

as long as the phase space of each cell has dimension $k \geq 2$.

A Three-Cell Network and Multifrequencies. The three-cell network in Figure 2 corresponds to systems of differential equations of the form

$$\begin{aligned} \dot{x}_1 &= f(x_1, x_2) \\ \dot{x}_2 &= g(x_2, x_1, x_3) \\ \dot{x}_3 &= f(x_3, x_2) \end{aligned} \quad (2.3)$$

where $g(x_2, x_1, x_3) = g(x_2, x_3, x_1)$, $x_1, x_3 \in \mathbf{R}^k$, and $x_2 \in \mathbf{R}^\ell$. Systems (2.3) are equivariant with respect to the permutation $\tau(x_1, x_2, x_3) = (x_3, x_2, x_1)$, and synchronous solutions (where $x_1(t) = x_3(t)$) occur robustly because the subspace $W = \{x : x_1 = x_3\}$ is flow-invariant for (2.3).

There are two differences between the networks in Figures 2 and 1. First, not all τ -equivariant systems on $\mathbf{R}^k \times \mathbf{R}^\ell \times \mathbf{R}^k$ have the form (2.3),

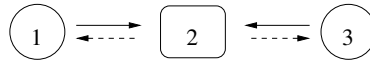


Figure 2. A three-cell network with transposition symmetry.

since in the general τ -equivariant system f can depend nontrivially on all x_j . So there is additional structure in coupled cell systems that does not correspond directly to symmetry. Second, the half-period out of phase periodic solutions satisfy $x_3(t) = x_1(t + T/2)$ and $x_2(t) = x_2(t + T/2)$. In particular, the oscillations in cell 2 are forced by symmetry to occur at twice the frequency of those in cells 1 and 3. So multirhythms³ can be forced by network architecture.

Another Three-Cell Network. Robust synchrony is possible in networks that have no symmetry. The network in Figure 3 has no symmetry, but the network structure still forces $Y = \{x : x_1 = x_2\}$ to be flow-invariant. To verify, observe that coupled cell systems associated with this network have the form

$$\begin{aligned} \dot{x}_1 &= f(x_1, x_2, x_3) \\ \dot{x}_2 &= f(x_2, x_1, x_3) \\ \dot{x}_3 &= g(x_3, x_1) \end{aligned} \quad (2.4)$$

where $x_1, x_2 \in \mathbf{R}^k$ and $x_3 \in \mathbf{R}^\ell$, and restrict (2.4) to Y .

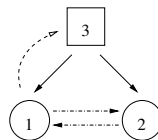


Figure 3. A three-cell network without symmetry.

There is a precise sense in which cells 1 and 2 are equivalent within this network. Define the ‘input set’ of a cell j to be cell j and all cells i that connect to cell j and all arrows from cells i to j . See Figure 4. Using input sets we can now see why Y is flow-invariant: the input sets of cells 1 and 2 are isomorphic via the permutation β that maps $(1\ 2\ 3) \rightarrow (2\ 1\ 3)$. The system (2.4) is *not* equivariant with respect to β , the third equation in (2.4) changes on application of β . However, the third equation *is* the same on the space Y ; so the restriction of (2.4) to Y is β -equivariant. This is enough to make Y flow-invariant.

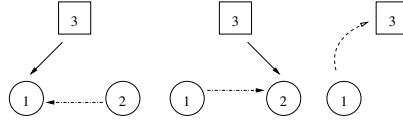


Figure 4. Input sets for three-cell network without symmetry.

3. Coupled Cell Networks

As in⁵ we define a class of coupled cell networks.

Definition 3.1. A coupled cell network \mathcal{G} consists of:

- A finite set $\mathcal{C} = \{1, \dots, N\}$ of nodes or cells.
- An equivalence relation $\sim_{\mathcal{C}}$ on cells in \mathcal{C} .
- Associated to each node c is a set of input terminals $I(c)$. Each $i \in I(c)$ is the receptacle for one edge $(\tau(i), i)$ that begins in tail cell $\tau(i)$ and ends in terminal i . Let \mathcal{E} denote the set of all arrows.
- An equivalence relation \sim_E on edges in \mathcal{E} .
- Equivalent edges have equivalent tails and heads — if $(\tau(i), i) \sim_E (\tau(j), j)$ where $i \in I(c), j \in I(d)$, then $\tau(i) \sim_{\mathcal{C}} \tau(j)$ and $c \sim_{\mathcal{C}} d$.

Observe that self-coupling ($\tau(i) = c$ for a terminal i in cell c) and multiple arrows ($\tau(i) = \tau(j)$ for two terminals in cell c) are permitted.

Definition 3.2. The relation \sim_I of input equivalence on \mathcal{C} is defined by $c \sim_I d$ if and only if there exists an arrow type preserving bijection $\beta : I(c) \rightarrow I(d)$. That is, for every input terminal $i \in I(c)$

$$(\tau(i), i) \sim_E (\tau(\beta(i)), \beta(i)) \quad (3.5)$$

Any such bijection β is called an input isomorphism from c to d .

The set $B(c, d)$ denotes the collection of all input isomorphisms from cell c to cell d . The set

$$\mathcal{B}_{\mathcal{G}} = \bigcup_{c, d \in \mathcal{C}} B(c, d)$$

of all input isomorphisms is a groupoid⁷, which is like a group, except that the product of two elements is not always defined. We call $\mathcal{B}_{\mathcal{G}}$ the *groupoid of the network*.

Remark 3.1. Suppose that a cell c has two input terminals $i, j \in I(c)$ whose receiving arrows $(\tau(i), i)$ and $(\tau(j), j)$ are \sim_E equivalent. Then the

transposition $\beta = (i j)$ is an input isomorphism in $B(c, c)$. Note that $B(c, c)$ is a group, called the *vertex group*.

Vector Fields on a Coupled Cell Network. We now define the class \mathcal{F}_G^P of vector fields corresponding to a given coupled cell network \mathcal{G} and that definition depends on a choice of ‘total phase space’ P . This class consists of all vector fields that are ‘symmetric’ under the groupoid \mathcal{B}_G .

For each cell c in \mathcal{C} let the *internal cell phase space* P_c be a finite-dimensional vector space of dimension ≥ 1 . We require that $P_c = P_d$ whenever $c \sim_C d$. The corresponding *total phase space* is $P = \prod_{c \in \mathcal{C}} P_c$; employ the coordinate system $x = (x_c)_{c \in \mathcal{C}}$ on P .

More generally, suppose that $\mathcal{D} = \{d_1, \dots, d_s\}$ is any finite ordered subset of cells in \mathcal{C} . In particular, the same cell can appear more than once in \mathcal{D} . Define $P_{\mathcal{D}} = P_{d_1} \times \dots \times P_{d_s}$ and write

$$x_{\mathcal{D}} = (x_{d_1}, \dots, x_{d_s})$$

where $x_{d_j} \in P_{d_j}$. Finally, suppose that $\mathcal{D}_1, \mathcal{D}_2 \subset \mathcal{C}$ are subsets, and that $\beta : \mathcal{D}_1 \rightarrow \mathcal{D}_2$ is a bijection such that $\beta(d) \sim_C d$ for all $d \in \mathcal{D}_1$. Define the *pullback* $\beta^* : P_{\mathcal{D}_2} \rightarrow P_{\mathcal{D}_1}$ by $(\beta^*(z))_j = z_{\beta(j)}$ for all $j \in \mathcal{D}_1$ and $z \in P_{\mathcal{D}_2}$.

We use pullbacks to relate different components of the vector field associated to a coupled cell network. For cell c the *coupling phase space* is

$$P_{\tau(I(c))} = P_{\tau(i_1)} \times \dots \times P_{\tau(i_s)}$$

Definition 3.3. A vector field f on P is \mathcal{G} -admissible if:

- (a) For all $c \in \mathcal{C}$ the component $f_c(x)$ depends only on the internal phase space variables x_c and the coupling phase space variables $x_{\tau(I(c))}$; that is, there exists $\hat{f}_c : P_c \times P_{\tau(I(c))} \rightarrow P_c$ such that

$$f_c(x) = \hat{f}_c(x_c, x_{\tau(I(c))}) \quad (3.6)$$

- (b) For all $c, d \in \mathcal{C}$, $\beta \in B(c, d)$, and $x \in P$

$$\hat{f}_d(x_d, x_{\tau(I(d))}) = \hat{f}_c(x_d, \beta^*(x_{\tau(I(d))})) \quad (3.7)$$

It follows that an admissible vector field is determined by one mapping f for each input equivalence class of cells, and each component f_c is invariant under the vertex group $B(c, c)$.

4. Balanced Relations and Quotient Networks

Suppose that \bowtie is an equivalence relation on cells that refines input equivalence. We visualize \bowtie by coloring all \bowtie -equivalent cells with the same

color. This equivalence relation is *balanced* if the sets of colors of input cells for two \bowtie -equivalent cells consist of the same colors with the same multiplicities. Theorem 6.5 of ⁹ states

Theorem 4.1. *The subspace*

$$\Delta_{\bowtie} = \{x \in P : x_i = x_j \text{ if } i \bowtie j\}$$

is flow-invariant for all \mathcal{G} -admissible f if and only if \bowtie is balanced.

A solution in Δ_{\bowtie} is *synchronous* in the strong sense that the time series from cells of the same color are identical; the synchrony is *robust* in the sense that it holds for any choice of f . We call Δ_{\bowtie} the *polysynchrony subspace* corresponding to \bowtie .

Definition 4.1. Given a coupled cell system $\mathcal{G} = (\mathcal{C}, \sim_C, \mathcal{E}, \sim_E)$ and a balanced equivalence relation \bowtie , define the *quotient cell system* $\mathcal{G}_{\bowtie} = (\mathcal{C}_{\bowtie}, \sim_{\mathcal{C}_{\bowtie}}, \mathcal{E}_{\bowtie}, \sim_{\mathcal{E}_{\bowtie}})$ as follows:

- (a) Let \bar{c} denote the \bowtie -equivalence class of $c \in \mathcal{C}$. Then $\mathcal{C}_{\bowtie} = \{\bar{c} : c \in \mathcal{C}\}$. Thus \mathcal{C}_{\bowtie} is the *quotient* \mathcal{C} / \bowtie .
- (b) Define $\bar{c} \sim_{\mathcal{C}_{\bowtie}} \bar{d} \iff c \sim_C d$. The relation $\sim_{\mathcal{C}_{\bowtie}}$ is well-defined since \bowtie refines \sim_C .
- (c) The edges in the quotient network are the projection of edges in the original network, that is,

$$\mathcal{E}_{\bowtie} = \{(\overline{\tau(i)}, i) : (\tau(i), i) \in \mathcal{E}\} \quad (4.8)$$

- (d) Two quotient edges are equivalent when the original edges are equivalent, that is,

$$(\overline{\tau(i_1)}, i_1) \sim_{\mathcal{E}_{\bowtie}} (\overline{\tau(i_2)}, i_2) \iff (\tau(i_1), i_1) \sim_E (\tau(i_2), i_2) \quad (4.9)$$

where i_j is a terminal head in cell c_j .

Note that input isomorphisms of \mathcal{G} project onto input isomorphisms of \mathcal{G}_{\bowtie} . The following is from ⁵.

Theorem 4.2. *Let \bowtie be a balanced relation on a coupled cell network \mathcal{G} . The restriction of a \mathcal{G} -admissible vector field to Δ_{\bowtie} is \mathcal{G}_{\bowtie} -admissible. Moreover, every \mathcal{G}_{\bowtie} -admissible vector field on Δ_{\bowtie} lifts to a \mathcal{G} -admissible vector field.*

Consider the five-cell network in Figure 5 (left). The phase space has the form $P = (\mathbf{R}^k)^5$ for some k . Since all cells are input-equivalent the diagonal

(x, x, x, x, x) is polysynchronous. There is another polysynchronous subspace Δ_{\bowtie} associated to the balanced relation in Figure 5 (center), namely,

$$\Delta_{\bowtie} = \{(x, y, x, y, z) : x, y, z \in \mathbf{R}^k\}$$

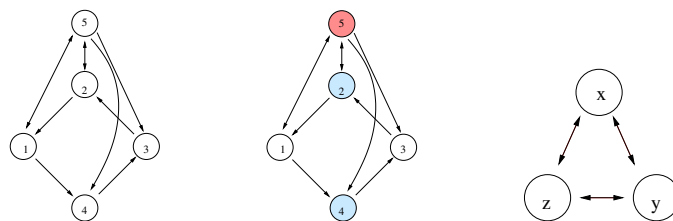


Figure 5. A five-cell network with a balanced relation leading to a quotient three-cell bidirectional ring with \mathbf{D}_3 -symmetry.

Observe that the quotient network \mathcal{G}_{\bowtie} has \mathbf{D}_3 symmetry even though the original network has none. It is known^{6,3} that \mathbf{D}_3 -equivariant vector fields can support solutions where two cells are out of phase while the third cell has twice the frequency of the other two when $k \geq 2$. Since all vector fields in the quotient lift, these solutions are also solutions to the original five-cell system. Typical simulations are shown in Figure 6.

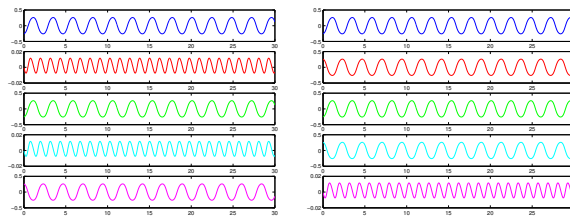


Figure 6. Simulations in five-cell network in Figure 5: (left) double frequency in cells 2 and 4; (right) double frequency in cell 5. The two solutions are symmetry related solutions on the quotient.

5. Synchrony-Breaking Bifurcations

The study of synchrony-breaking bifurcations is just beginning. We present two examples from ² that illustrate some of the intriguing possibilities.

A Three-Cell Feed-Forward Network. We consider the three-cell feed-forward network in Figure 7. We observe that one-parameter synchrony-breaking leads naturally to nilpotent normal forms in these networks and to solutions that are equilibria in cell 1 and periodic in cells 2 and 3. Surprisingly, the amplitude growth of the periodic signal in cell 3 is to the power $\frac{1}{6}$ rather than the expected $\frac{1}{2}$ power of amplitude growth with respect to the bifurcation parameter in Hopf bifurcation.

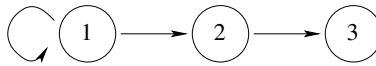


Figure 7. Three-cell linear feed-forward network.

This network has a new feature: the first cell is coupled (externally) to itself. The corresponding coupled cell systems have the form:

$$\begin{aligned}\dot{x}_1 &= f(x_1, x_1) \\ \dot{x}_2 &= f(x_2, x_1) \\ \dot{x}_3 &= f(x_3, x_2)\end{aligned}\tag{5.10}$$

Note that $x_1 = x_2 = x_3$ is a polysynchronous subspace and we consider a synchrony-breaking Hopf bifurcation from a synchronous equilibrium. We assume that the cell dynamics is two-dimensional and that $(0, 0, \lambda)$ is a stable equilibrium for cell 1.

The Jacobian at the equilibrium $(0, 0, 0)$ for (5.10) has the form

$$\begin{bmatrix} A + B & 0 & 0 \\ B & A & 0 \\ 0 & B & A \end{bmatrix}\tag{5.11}$$

where $A = D_u f(0, 0, \lambda)$ is the linearized internal cell dynamics and $B = D_v f(0, 0, \lambda)$ is the linearized coupling. We assume that $A + B$ has eigenvalues with negative real part and that there is a Hopf bifurcation for cell 2 at $\lambda = 0$. It follows from (5.11) that purely imaginary eigenvalues of A have multiplicity two as eigenvalues of the Jacobian. It is straightforward to arrange for the equation

$$\dot{x}_2 = f(x_2, 0, \lambda)$$

to have a unique stable limit cycle when $\lambda > 0$.

Next we assume that f is in ‘normal form’ in the following sense. Identify the two-dimensional phase space of each cell with \mathbf{C} , and assume

$$f(e^{i\theta}u, e^{i\theta}v) = e^{i\theta}f(u, v)\tag{5.12}$$

Note that this is a special assumption. It follows that

$$f(u, v, \lambda) = a(|v|^2, \bar{v}u, |u|^2, \lambda)u + b(|v|^2, v\bar{u}, |u|^2, \lambda)v \quad (5.13)$$

where a and b are complex-valued functions. For this f we have assumed above that $\text{Re}(a(0)) = 0$ and $\text{Re}(a_\lambda(0)) > 0$. In addition, we make the stability assumptions $\text{Re}(b(0)) < 0$ and $\text{Re}(a_3(0)) < 0$.

Proposition 5.1. *Under these assumptions, there is a unique asymptotically stable supercritical branch of bifurcating periodic solutions with cell 1 in equilibrium and the periods of cells 2 and 3 equal. The amplitude of the periodic state in cell 2 grows as $\lambda^{\frac{1}{2}}$; the amplitude of cell 3 grows as $\lambda^{\frac{1}{6}}$.*

A simple example is $f(u, v, \lambda) = (i + \lambda)u - |u|^2u - v$. The resulting periodic solution is shown in Figure 8.

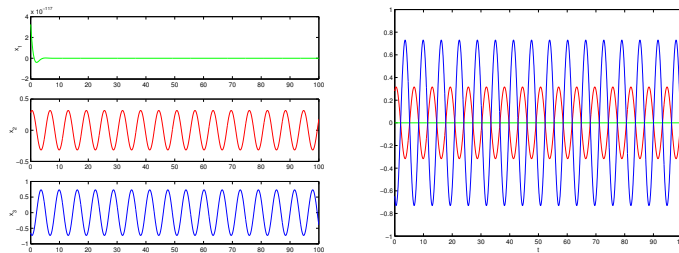


Figure 8. Time series from three-cell network with and $\lambda = 0.1$: (left) first coordinate time series of individual cells; (right) superimposed time series from all three cells. Note that $\sqrt{\lambda} = 0.32$ and $\lambda^{1/6} = 0.68$ and that these values are the approximate amplitudes of the periodic states in cells 2 and 3 respectively.

Two-Color Balanced Relations on Periodic Arrays. Consider a periodic $4n \times 4n$ array of cells, with bidirectional nearest-neighbor coupling. Figure 9 shows that patterned states may be found with two colors. The left figure is a 4-periodic balanced coloring with two colors: black and white. It is balanced because each cell receives two white and two black inputs. We show that balanced coloring predicts the existence of equilibria in codimension-one bifurcations with patterns of synchrony that have a certain kind of spatial randomness.

To generate new equilibria, choose any diagonal that slopes upward to the right, such as in Figure 9 (center). For cells on this diagonal interchange black and white. The new pattern is also balanced, Figure 9 (right).

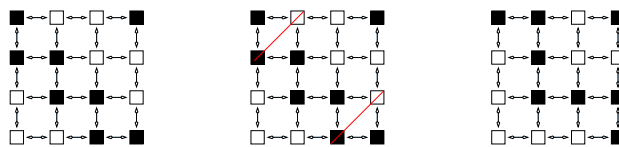


Figure 9. Two-coloring polysynchronous subspaces of a $4n \times 4n$ periodic array: (left) basic pattern; (center) specified diagonal; (right) new pattern.

The equations governing black x_B and white x_W cells in Figure 9 are

$$\begin{aligned} \dot{x}_B &= f(x_B, \overline{x_W, x_W, x_B, x_B}) \\ \dot{x}_W &= f(x_W, \overline{x_B, x_B, x_W, x_W}) \end{aligned} \quad (5.14)$$

where the overbar indicates invariant under permutation of the last four variables. These equations are identical for both Figure 9 (left) and (right). Hence solutions of the coupled system are taken to solutions by the parity swap. Wang and Golubitsky¹¹ enumerate all two-color patterns of synchrony for square arrays.

Parity swaps can generate ‘random’ spatial patterns in the sense that on any column there is a polysynchronous subspace that corresponds to an arbitrary sequence of black and white cells. See Figure 10.

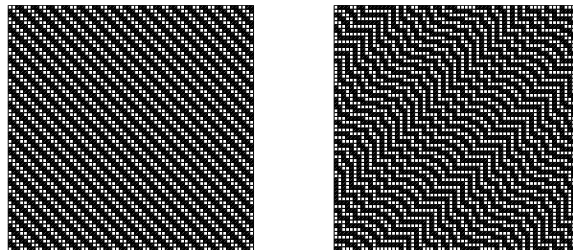


Figure 10. Polysynchronous subspaces of a 2-color 64×64 periodic array. (Left) The regular pattern. (Right) Dislocation pattern obtained by interchanging on a random selection of 25 diagonals.

Suppose that the phase space for each cell is one-dimensional. The synchronous subspace $x_B = x_W$ is flow-invariant, so the Jacobian of (5.14) has an eigenvector in the direction $(1, 1)^t$. By symmetry it also has one in the direction $(1, -1)^t$. It is straightforward to arrange that the eigenvalue associated with the symmetry-breaking eigendirection moves through zero with nonzero speed. Therefore a pitchfork bifurcation to the patterned solutions of Figure 9 can occur in a codimension-one bifurcation.

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