Patterns of Oscillation in Coupled Cell Systems

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Abstract

Coupled oscillators or coupled cell systems are used as models in a variety of physical and biological contexts. Each of these models includes assumptions about the internal dynamics of a cell (a pendulum or a neuron or a single laser) and assumptions about how the cells are coupled to each other.

In a primitive sense, coupled cell systems are just moderate sized systems of ODE; for example, an eight-cell system with four-dimensional internal dynamics (such as a Hodgkin-Huxley system) yields a 32-dimensional system of ODE. In a more sophisticated sense, coupled cell systems have additional structure; we want to be able to compare the dynamics in different cells (are they synchronous, or a half-period out of phase, or do they have a more complicated phase relation?).

In this paper we explore the extra structure that is associated with a coupled cell system. We argue that those permutations of the cells that are assumed to be symmetries of the cell system consititute a modelling assumption — one that in large measure dictates the kinds of equilibria and time periodic solutions that are expected in such models. We survey certain general results in the context of specific models, including locomotor central pattern generators for quadruped motion and coupled pendula. These results lead to a model for multirhythms.

Coupled cell dynamics are a worthwhile subject of study and we begin here to discuss some of the fascinating features of this area.

Contents

1 Introduction

Coupled oscillators or coupled cell systems have been much studied as models for certain physical or biological systems (Josephson junction arrays [Hadley, Beasley and Wiesenfeld, 1988], coupled lasers [Wang and Winful, 1988; Bracikowski and Roy, 1990], central pattern generators [Kopell and Ermentrout, 1986, 1988, 1990; Rand, Cohen and Holmes,1988], speciation [Cohen and Stewart, 1999], and so on). Many classical mechanical systems can be interpreted as coupled cell systems: for example chains of like rods [Synge and Griffith 1959 p. 270], normal mode vibrations of a loaded string [Fowles 1986 p. 301], linear motion of a triatomic molecule [Fowles 1986 p. 299], and n-body dynamics [Griffiths 1985 p. 132]. However, few attempts have been made to formalize the concept of a coupled cell system and develop a general, abstract theory. We begin that process in this paper.

An N-cell coupled cell system is often written in the form

$$\frac{dx_i}{dt} = f_i(x_i, \lambda) + \sum_{j \to i} h_{ij}(x_j, x_i) \qquad x_i \in \mathbf{R}^{k_i}; i = 1, \dots, N \tag{1.1}$$

where f_i is the *internal* dynamics of the ith cell, h_{ij} is the *coupling* from cell j to cell i, and λ is a vector of parameters. In these models the total coupling at cell i is just the sum of coupling contributions from those cells j that are actually connected to cell i (symbolized here as $j \to i$). This structure represents a rather special case of the general concept introduced in Section 3, but it serves as motivation.

In a coupled cell system we emphasize the comparative dynamics of all cells, as opposed to the dynamics of the whole system, and it is this comment that distinguishes the study of coupled cell systems from the study of systems of ordinary differential equations. Of course, the two points of view are intimately related, but they are not the same.

In particular, from the coupled-cell viewpoint the output signal from each cell is assumed to have its own significance. For example, in the context of time-periodic solutions two cells are often described as being 'a half-period out of phase'. In rings of cells, solutions may be described as forming 'discrete rotating waves'. Two cells i, j can be described as 'synchronous' — that is, satisfying the condition $x_i(t) = x_j(t)$ — even when the trajectory $x(t)$ is chaotic. For these reasons, we must consider a coupled cell system to be a system of ODE, equipped with a distinguished set of projections whose images are the individual cells. If we view each cell as representing a point in space, then coupled cell systems are discrete-space continuous-time systems. They therefore represent a fascinating compromise between ODE and PDE, without the technical complications typically associated with the latter.

We are intrigued by the structure implicit in coupled cell systems that permits patterned solutions to exist robustly, and ask: What structure in coupled cell systems allows specific cells to have identical time series, definite phase relations, or other identifiable spatio-temporal patterns? One answer is symmetry, and that is the one that we focus on here. In coupled cell systems symmetries appear naturally as permutations of the cells, and exist only when (subsets of) the cells are identical.

2 Model Cell Systems

As motivation for the concept of a coupled cell system we now introduce four coupled cell models, each having a different symmetry group: speciation, animal gaits, coupled pendula, and coupled hypercolumns in the visual cortex. Each example has an eight-cell version and it is curious to note that the symmetry groups corresponding to these four models $(\mathbf{S}_8, \mathbf{Z}_4 \times \mathbf{Z}_2, \mathbf{D}_8, \mathbf{D}_4)$ are all different. We return to these examples once we have developed appropriate general techniques for their analysis.

2.1 Speciation ($\mathbf{S}_N$)

Our first example arises in a model of speciation — the formation of new species — in evolutionary biology [Cohen and Stewart, 1999]. Examples include 'Darwin's finches' in The Galápagos Islands, where what was initially a single species of finch has diversified into 14 species over a period of about 5 million years. In fact, evolutionary changes in Darwin's finches can be observed today, over periods of just a few years [Ridley, 1996]. Speciation is usually discussed in terms of *genotype* — genetics. In contrast, we shall focus on the *phenotype* — the organism's form and behavior — because the dynamics of evolution is driven by natural selection, which acts on phenotypes. The principal role of genes is to make it possible for the phenotype to change. (For recent support for this approach, see [Pennisi, 2000], [Rundle, Nagel, Boughman, and Schluter, 2000], and [Huey, Gilchrist, Carlson, Berrigan, and Serra, 2000].)

Until recently, most explanations of speciation have invoked geographical or environmental discontinuities or non-uniformities. For example, the mechanism known as 'allopatry' involves an initial species being split into two geographically isolated groups — say by one group moving to new territory, later isolated from the original territory by floods or other geographical changes. Once separated, the two groups can evolve independently. See [Mayr 1963, 1970] for details.

Such theories are based on the belief that discontinuous or non-uniform effects must have discontinuous or non-uniform causes. The conventional wisdom was that if the organisms of two nascent species are not isolated, they will be able to interbreed, and 'gene-flow' will maintain them as a single species. Therefore gene-flow must be disrupted in some way, and the obvious possibility is geographical isolation.

However, it is now recognized that discontinuous or non-uniform effects can have continuous or uniform causes. Indeed, these are the phenomena addressed in bifurcation theory and symmetry-breaking. Towards the end of the 1990s evolutionary biologists increasingly began to consider mechanisms for 'sympatric' speciation. Here, organisms remain intermingled throughout the process of speciation. In sympatric speciation, gene-flow is disrupted by more subtle mechanisms than geographical isolation, in particular natural selection, which eliminates 'hybrid' offspring arising from matings between members of the two different speciating groups before the hybrids become breeding adults.

[Cohen and Stewart, 1999] developed a context in which sympatric speciation is explicitly represented as a form of spontaneous symmetry-breaking in a coupled cell system with all-to-all coupling ($\mathbf{S}_N$ symmetry). [Cohen, Stewart, and Elmhirst 2000] made numerical studies of such models. Since individual organisms can die or breed, their numbers can change, so it is unsatisfactory to model the system with a fixed number of immortal organisms. The cells of the system are therefore taken to be coarse-grained clusters of related organisms in phenotypic space; these clusters act as carriers for phenotypes. [Cohen and Stewart, 1999] refer to these cells as 'PODs' — Placeholders for Organism Dynamics.

The motivation behind the model is that a single species is invariant under all permutations of its organisms, whereas a mixture of species is invariant only under the smaller group of permutations that preserve each species. The appropriate symmetry group is therefore the symmetric group $\mathbf{S}_N$ of all permutations on N symbols, where N is the number of PODs in the model. (This number is a modelling choice, rather than being determined by biological considerations: typically something in the range 10-100 seems reasonable.) The model also assumes that the relevant phenotypes can be described by continuous characters, such as beak length for birds, and may therefore be inappropriate for characters that are determined by a single gene or a small gene-complex.

The model demonstrates that sympatric speciation can occur in a population where all organisms can potentially interbreed, and in an environment that is uniform at any instant but may change as time passes. A speciation event (bifurcation) is triggered if environmental changes render the uniform state (a single species) unstable, so that the symmetry of the uniform state breaks. Such an instability occurs if the organisms can survive more effectively by adopting different strategies, rather than by all adopting the same strategy (subject to genetic feasibility).

Consider a system of N PODs. The state of POD j is described by a vector x_j belonging to *phenotypic space* $\mathbf{R}^r$, where $1 \leq j \leq N$. A point in phenotypic space represents a phenotype. Each entry x_j^i in $x_j = (x_j^1, \dots, x_j^r)$ represents a phenotypic character. Throughout the following discussion, for simplicity, we focus on the case $r = 1$, so each cell is 1-dimensional.

Let $a = (a_1, \ldots, a_s)$ represent environmental influences (climate, food resources, other organisms, ...). Assume that on the appropriate time scale changes in phenotype can be described by a dynamical system

$$\frac{\mathrm{d}x_j}{\mathrm{d}t} = f_j(x_1, \ldots, x_N; a_1, \ldots, a_s) \tag{2.1}$$

for suitable functions $f_j : \mathbf{R}^N \times \mathbf{R}^s \to \mathbf{R}^N$.

The key observation is that the system should have $\mathbf{S}_N$-symmetry. Intuitively, this just means that the dynamical equations should treat all cells in the same way. Thus we assume that $F = (f_1, \ldots, f_N)$ is $\mathbf{S}_N$-equivariant. Figure 2.1 shows typical time-series of phenotypic variables (for a choice of F that we do not specify here): the split into two species is evident.

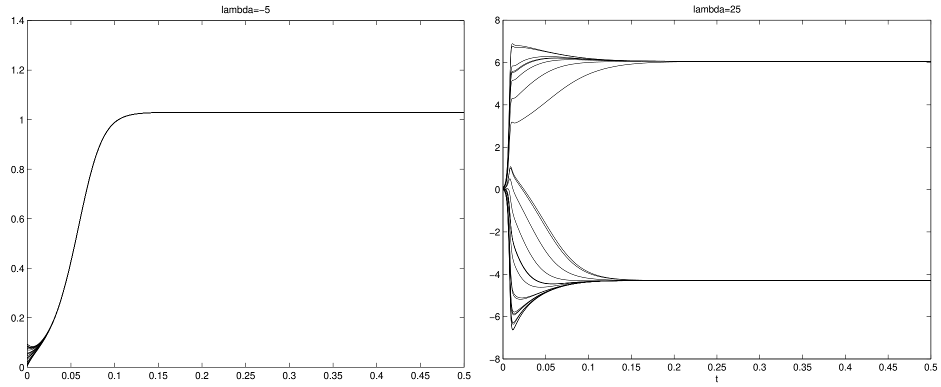

Figure 2.1: Bifurcation to two species in model with $N = 25$ PODs. Time series of all PODs are superimposed. (Left) one species; (right) two species (one with 9 PODs and one with 16 PODs).

2.2 Quadrupedal Gaits ($\mathbf{Z}_2 \times \mathbf{Z}_4$)

Quadrupedal gaits provide excellent examples of periodic states with spatio-temporal symmetries. In the pace, trot, and bound a four-legged animal partitions its legs into two pairs — the legs in each pair move in synchrony while legs in different pairs move with a half-period phase shift. The two pairs in a *bound* consist of the forelegs and the hind legs; the two pairs in a *pace* consist of the left legs and the right legs; and the two pairs in a *trot* consist of the the two diagonal pairs of legs. The quadruped *walk* has a more complicated cadence: each leg moves independently with a quarter-period phase shift in the order left hind, left fore, right hind, and right fore. As in the pace, the left legs move and then the right legs move — but the left legs and the right legs do not move in unison.

[Collins and Stewart, 1993b, 1994] pointed out that each of these gaits can be distinguished by symmetry in the following sense. Spatio-temporal symmetries are permutations of the legs coupled with phase shifts (translations of time). So interchanging the two fore legs and the two hind legs of a bounding animal does not change the gait, while interchanging the two left legs and the two right legs leads to a half-period phase shift. In a walk permuting the legs in the order left hind to left fore to right hind to right fore leads to a quarter-period phase shift. We list the spatio-temporal symmetries of each of these gaits in Table 2.1.

Gait	Symmetries (leg permutation, phase shift)		
pace	$((1\ 3)(2\ 4), 0)$	$((1\ 2)(3\ 4), \frac{1}{2})$	$((1\ 4)(2\ 3), \frac{1}{2})$
trot	$((1\ 3)(2\ 4), \frac{1}{2})$	$((1\ 2)(3\ 4), \frac{1}{2})$	$((1\ 4)(2\ 3), 0)$
bound	$((1\ 3)(2\ 4), \frac{1}{2})$	$((1\ 2)(3\ 4), 0)$	$((1\ 4)(2\ 3), \frac{1}{2})$
walk	$((1\ 3\ 2\ 4), \frac{1}{4})$	$((1\ 2)(3\ 4), \frac{1}{2})$	$((1\ 4\ 2\ 3), \frac{3}{4})$

Table 2.1: Gait symmetries: 1 = left hind leg; 2 = right hind leg; 3 = left foreleg; 4 = right foreleg.

Biologists often assume that animal nervous systems contain a variety of central pattern generators (CPGs) — each (partially) directing a specific function. For example, locomotor CPGs are suppose to control the rhythms associated to standard quadrupedal gaits. Locomotor CPGs are themselves often modelled by a coupled cell system where each cell is a cluster of neurons that is responsible for directing motion in a single leg. It is usually assumed that the various clusters are identical and coupled. The simplest such model consists of four cells — one for each leg.

[Golubitsky, Stewart, Buono, and Collins 1999, 2000] argue that, because of the spatio-temporal symmetries present in the gaits walk, trot, and pace, this four-cluster structure cannot be an appropriate model for quadrupedal gaits. The reason is that with four cells, symmetry forces the trot and pace gaits to correspond to conjugate solutions in the model — that is, these two solutions must exist simultaneously and be stable simultaneously. But many animals pace but do not trot (a camel for instance) and many animals trot but do not pace (a squirrel for instance). Although gait selection could in principle be accomplished by using different initial conditions, this option is not especially attractive and we seek something more robust.

These authors then show that there is a unique eight-cell model that can produce walk, trot, and pace, while avoiding the conjugacy problem. In this model the motion of each leg is directed by the output from two cells: see Figure 2.2. For purposes of visualization we may assume that only the first four cells send signals to the animal's four legs. Suppose that $x_j(t)$ is the time series associated to the jth cell. Then the gait 'pace' corresponds to a solution where

$$x_2(t) = x_1\left(t + \tfrac{1}{2}\right) \qquad x_3(t) = x_1(t) \qquad x_4(t) = x_1\left(t + \tfrac{1}{2}\right).$$

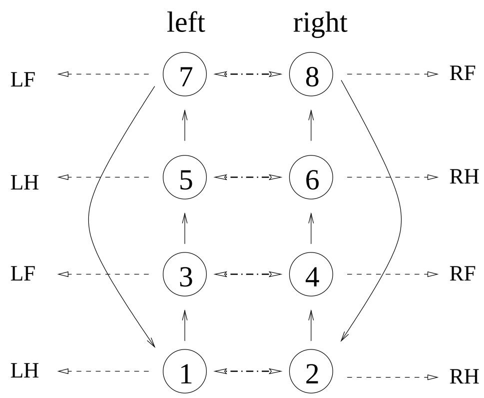

Figure 2.2: Eight-cell network for quadruped locomotor central pattern generator. The signals from cells 1 and 5 are sent to the left hind leg and the signals from cells 3 and 7 are sent to the left foreleg. Similar statements hold for the right side of the network. Ipsilateral coupling is indicated by solid lines and contralateral coupling is indicated by dashed lines.

Observe that this network consists of two unidirectional rings of four cells each. The coupling within a single ring is called *ipsilateral* and the coupling between rings is called *contralateral*. In the figure, different types of lines are used to represent each type of coupling. The symmetry group of the network is generated by two elements: the transposition κ that interchanges the left and right rings, and the four-cycle ω that permutes the cells in each ring simultaneously. Thus, the symmetry group of this network is $\Gamma = \mathbf{Z}_4(\omega) \times \mathbf{Z}_2(\kappa)$. Finally, this network can be generalized to a CPG model for myriapods with N pairs of legs by coupling two directed rings with $2N$ cells each leading to a network with $4N$ cells. The symmetry group of this network is $\mathbf{Z}_{2N}(\omega) \times \mathbf{Z}_2(\kappa)$.

2.3 Rings of Pendula Coupled by Torsion Springs ($\mathbf{D}_N$)

This example is one of the simplest nonlinear Hamiltonian coupled cell systems: it is perhaps best thought of as a chain of nonlinear oscillators with periodic boundary conditions, but we will think of it as a ring to keep the number of cells finite. Consider a ring of N identical simple pendula, coupled in nearest-neighbor fashion by torsion springs (Fig 2.3). The elastic force exerted by such a spring is proportional to the difference between the angular positions of its endpoints.

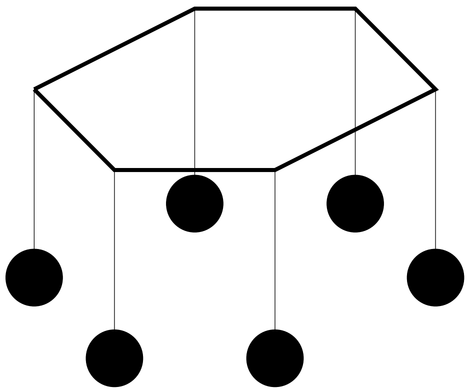

Figure 2.3: Ring of identical pendula coupled by torsion springs (bold lines). Each pendulum swings in a vertical plane through the center of a regular N-gon (here $N = 6$).

We can represent this as a coupled cell system, where each cell corresponds to a pendulum. There is a trivial equilibrium in which each pendulum is stationary and hangs vertically downwards. The problem we address here is the existence of small-amplitude time-periodic oscillations near that equilibrium. In §4 we classify possible spatio-temporal symmetries of periodic states of this system. In §5.4.1 we use symmetry methods and the coupled cell viewpoint to prove that generically (that is, for almost all values of the gravitational constant) there exist at least $\lfloor \frac{3N-1}{2} \rfloor$ distinct families of small-amplitude time-periodic oscillations, each parametrized by energy. The existence of these families of solutions depends on the fact that the coupled cell system has extra structure, namely, there is an internal cell symmetry due to the mechanical nature of the Hamiltonian system. See §4.3.1.

2.4 Coupled Hypercolumns ($\mathbf{D}_4$)

Neurons in the primary visual cortex V1 are known to be sensitive to the orientation of contours in the visual field. As discussed in [Bressloff, Cowan, Golubitsky, Thomas, and Wiener, 2000], the pattern of interconnection of these neurons has interesting symmetry properties, and these symmetries seem to be responsible in part for the types of geometric patterns that are reported in visual hallucinations. Using microelectrodes, voltage-sensitive dyes, and optical imaging, scientists have accumulated information about the distribution of orientation selective cells in V1, and about their pattern of interconnection. These studies can be interpreted to suggest that approximately every millimeter there is an *iso-orientation patch* with a given orientation preference and that a set of orientation patches covering the orientation domain $[0, \pi)$ (for each eye) occurs (in humans) in a millimeter square slab of V1. This slab was called a *hypercolumn* by [Hubel and Wiesel, 1974].

Thus there seem to be at least two length scales:

(a) *Local*: cells less than a millimeter apart tend to make inhibitory connections with most of their neighbors in a roughly isotropic fashion, and

(b) *Lateral*: cells make excitatory contact only every millimeter or so along their axons with cells in similar iso–orientation patches.

The experimental description of the local and lateral connections in V1 is illustrated in Figure 2.4. The neurons in each hypercolumn are all-to-all coupled while the connections between hypercolumns couple only those neurons that are sensitive to the same contour orientation. Moreover, if two hypercolumns lie in a direction ϕ from each other in V1, then only those neurons sensitive to contours oriented at angle ϕ are connected. Except for boundaries these connections are the same at every hypercolumn in V1.

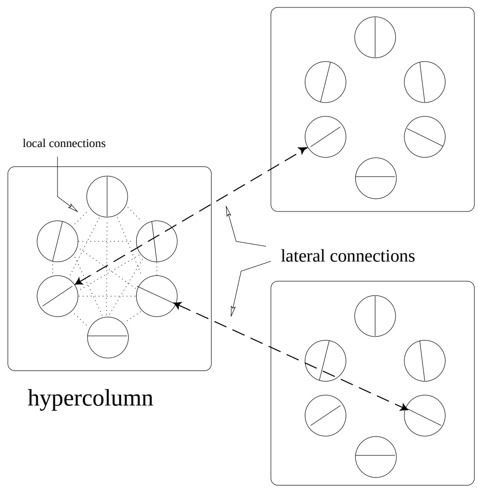

Figure 2.4: Illustration of isotropic local and anisotropic lateral connection patterns.

The simplest discrete model for orientation tuning in hypercolumns is a model system of four hypercolumns arranged in a square, as suggested by Nancy Kopell and shown in Figure 2.5 (left). In this model the jth hypercolumn consists of two cells:

one H_j is sensitive to horizontal contours and the other V_j is sensitive to vertical contours. As suggested by Figure 2.4, the connections between hypercolumns are restricted to connecting those cells that have like sensitivity — and then only when the cells are aligned along the line of their orientation preference. The result is shown in Figure 2.5 (left). This network has $\mathbf{D}_4$ symmetry, since it is the same network as the octagonal one shown in Figure 2.5 (right), where the $\mathbf{D}_4$ symmetry is transparent.

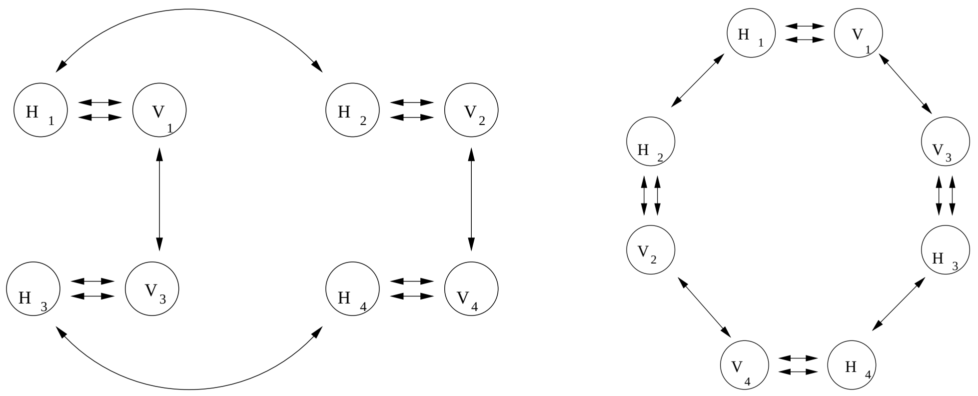

Figure 2.5: (Left) Schematic eight-cell network for orientation tuning model. (Right) Equivalent network.

3 A Formal Definition of a Coupled Cell System

With these examples in mind, we give a formal definition of a coupled cell system that is intimately related to its symmetries. Later we discuss the solution types that are consistent with and forced by symmetry. We also specialize the notion of a coupled cell system to the Hamiltonian context.

Let $\mathcal{N} = \{1, \ldots, N\}$ and let P_j be a manifold for $j \in \mathcal{N}$.

Definition 3.1 A *coupled cell system* is a dynamical system

$$\frac{dx}{dt} = F(x) \tag{3.1}$$

defined on the space

$$P = P_1 \times \cdots \times P_N$$

where the P_j are the *cells* of the system and the projections $\pi_j : P \to P_j$ are the *cell projections*. Let $x(t)$ be a trajectory of (3.1). Then the jth *cell trajectory* is $x_j(t) = \pi_j(x(t))$.

Abstractly, this completes the definition, but we need to be able to do two things: interpret a coupled cell system in terms of its individual cells and how they are coupled, and decompose the dynamical system into different levels of coupling. That is, we need to set up links between the abstract concept and the intuitive one employed in areas of application.

The basic idea is that F can be decomposed as a sum of terms, which correspond to various types of coupling. A formal definition is postponed to §6 to avoid complicating a relatively simple idea with technicalities: we summarize the basic ideas here.

The vector field F can be written (in an essentially unique way) as a sum of terms that depend on none of the x_j, on just one of them, on just two of them, and so on. Let Φ_k be the terms that depend on exactly k of the x_j. Each Φ_k can be further decomposed according to which x_j actually occur (that is, the value of $\Phi_k(x)$ is not independent of x_j). The constant part of F is Φ_0. We can write $\Phi_1 = f_1 + \cdots + f_N$ where f_j depends only on x_j. Then the ith component of f_i defines the internal dynamics of cell i. In a similar manner (the details require a little care) we can define the coupling from cell i to cell j. When the system has 'point to point' coupling, as in (1.1), this takes care of the whole of F, but in general there might be 'three-cell' coupling terms involving three different x_j, and so on. Such terms can also be given a canonical meaning.

Associated with a coupled cell system is a 'decorated directed graph' (more generally a labelled oriented simplicial complex) whose nodes correspond to the N cells of the system and whose edges (or higher-dimensional simplices) correspond to various types of coupling. An edge from node j to node i exists if and only if F_i contains terms that depend only on x_i and x_j, and so on. The resulting graph (or complex) provides a schematic description of which cells influence which— but not of what these influences actually are.

The key ingredient for this paper is *symmetry.* Suppose that a group $\Gamma \subset \mathbf{S}_N$ permutes the nodes in $\mathcal{N}$. Nodes are said to be *identical* (or to have the same *type*) if they lie in the same Γ-orbit. Edges are said to be *identical* (or to have the same *type*) if they lie in the same Γ-orbit, where Γ is now acting on pairs (i, j) with $i \neq j$. In practice we draw nodes of the same type with the same kind of symbol (circle, box...) and we draw edges of the same type with the same kind of arrow (single head, two heads, double shaft...).

Our four examples give four different examples of cell complexes: an N node simplex, two rings of four nodes each, a ring of N nodes, and a ring of eight nodes (with $\mathbf{D}_4$ symmetry). Note that the animal gaits model in Figure 2.2 and the coupled hypercolumn model in Figure 2.5(right) each have two different types of arrows in their definitions: the first case distinguishes between ipsilateral and contralateral coupling and the second case distinguishes between local and lateral coupling.

A symmetry $\gamma \in \Gamma$ acts on the phase space S by

$$\gamma(x_1, \ldots, x_N) = (x_{\gamma^{-1}(1)}, \ldots, x_{\gamma^{-1}(N)}). \tag{3.2}$$

Definition 3.2 The coupled cell system is *symmetric* under Γ if F is Γ-equivariant. By extension we also say that the coupled cell system is Γ-equivariant.

The equivariance assumption implies that the internal dynamics of nodes of the same type are identical. Similarly, coupling terms corresponding to edges of the same type are identical, and the same goes for multi-cell coupling terms. In particular:

Definition 3.3 A cell complex has *identical cells* if Γ acts transitively on the nodes.

Each of the systems in our four examples consists of identical cells.

3.1 Coupled Cell Systems with Additional Structure

There are three types of additional structure that are routinely placed on coupled cell systems of differential equations; in general, these structures change the kind of dynamics that one can expect from the coupled cell system. These structures are: restrictions on the type of coupling, Hamiltonian cells, and internal symmetries.

The cell system system (1.1) is restricted because the coupling at each node i is just the sum of couplings from all nodes connected to i — we call this *point-to-point* coupling. Other types of special coupling include diffusive, synaptic, nearest neighbor, dead cells stay dead, and linear. For example, the coupled pendula, animal gaits CPG, and simple hypercolumn models are all assumed to have nearest neighbor coupling, while the speciation model is an example of *all-to-all* coupling. Note that in the gaits model and the hypercolumn model, the couplings between nearest neighbor cells are not identical; indeed, generally we assume that couplings are identical only when that feature is forced by symmetry.

In some models the internal cell dynamics is restricted by extra structure. For example, Hamiltonian coupled cell systems are coupled cell systems where each cell is assumed to be Hamiltonian. In these models we assume that the permutation group of the cell complex acts symplectically, that is, the symplectic structure on the phase spaces of any two cells related by a permutation symmetry are identical. Coupled pendula provide an example of a Hamiltonian coupled cell system.

Another way that the internal cell dynamics may be restricted is through the existence of symmetry — in this case we refer to the permutation symmetries of the cells as *global* symmetries and the symmetries within each cell as *local* symmetries. As we shall see, the coupled pendula model has a transpositional $\mathbf{Z}_2$ symmetry related to the fact that it models a mechanical system; the total symmetry group of this coupled cell system is $\mathbf{D}_N \times \mathbf{Z}_2$. See [Dionne, Golubitsky, and Stewart, 1996] and [Dias, 1998] for a more detailed discussion of coupled cell systems with internal symmetries.

3.2 Symmetry and Modelling

Many times coupled cell systems are used as models in a schematic sense: the exact form that model equations may have is unknown. All that is known is which cells have equal influences on other cells. The examples on speciation, animal gaits, and hypercolumns all fall into this category. In these cases, it is the symmetry of the coupled cell system that is the important modelling assumption, not the detailed equations for the cells.

For example, in the animal gaits locomotor CPG model, the cells themselves may represent individual neurons or, as is more likely, collections of neurons. Should the internal dynamics of each cell be modelled by a single Hodgkin-Huxley system, or for simplicity by Morris-Lecar or Fitzhugh-Nagumo equations, or more realistically by a collection of Hodgkin-Huxley systems? Should the cell coupling be modelled by nearest-neighbor point-to-point coupling or more realistically by couplings that include dependence on all cells? In many cases, such issues are secondary because there is no well-established physical or biological reason to make any particular choice.

In this sense, the most important modelling assumption for the locomotor CPG model is the symmetry assumption; that is, the coupled cell system has $\Gamma = \mathbf{Z}_2 \times \mathbf{Z}_4$ symmetry. In these circumstances, the only *a priori* assumption on the form of the coupled cell system that we should make is Γ-equivariance. That is, we need to study Γ-symmetric coupled cell systems defined on the state space $(\mathbf{R}^k)^8$. We begin this process in Section 4.

4 Spatio-Temporal Patterns in Coupled Cell Systems

We begin this section by reviewing the definitions of spatial symmetries of equilibria and of spatio-temporal symmetries of time-periodic solutions of Γ-equivariant systems of ODE.

Suppose that

$$\dot{x} = f(x) \tag{4.1}$$

is a system of differential equations with $x \in \mathbf{R}^n$ and symmetry group Γ. The symmetry group of an equilibrium x_0 of (4.1) is just the isotropy subgroup of x_0, that is, the spatial symmetries $\gamma \in \Gamma$ that fix x_0.

For example, suppose $\Gamma = \mathbf{S}_N$, where $\mathbf{S}_N$ acts on $\mathbf{R}^N$ by permuting coordinates. It is a straightforward exercise to show that up to conjugacy the isotropy subgroups of this action of $\mathbf{S}_N$ all have the form

$$\mathbf{S}_{n_1} \times \cdots \times \mathbf{S}_{n_k} \tag{4.2}$$

where $n_1 + \cdots + n_k = N$. Thus, in the speciation model (2.1), equilibria correspond to decomposition of the population into k species, where $k \leq N$. See Figure 2.1 for an example where $N = 25$. The equilibrium on the left represents one species and has isotropy subgroup $\mathbf{S}_{25}$, while the one on the right represents two species and has isotropy subgroup $\mathbf{S}_9 \times \mathbf{S}_{16}$.

The symmetries of the time-periodic solutions are more complicated to describe than are the symmetries of equilibria. To begin, suppose that $x(t)$ is a T-periodic solution of (4.1). and that $\gamma \in \Gamma$. We discuss the ways in which γ can be a symmetry of $x(t)$; the main tool is the uniqueness theorem for solutions to the initial value problem for (4.1).

We know that $\gamma x(t)$ is another T-periodic solution of (4.1). Should the two trajectories intersect, then the common point of intersection would be the same initial point for the two solutions. Uniqueness of solutions implies that the trajectories of $\gamma x(t)$ and $x(t)$ would be identical. So either the two trajectories are identical or they do not intersect.

Suppose that the two trajectories are identical. Then uniqueness of solutions implies that there exists $\theta \in \mathbf{S}^1 = [0, T]$ such that $\gamma x(t) = x(t - \theta)$, or

$$\gamma x(t + \theta) = x(t). \tag{4.3}$$

We call $(\gamma, \theta) \in \Gamma \times \mathbf{S}^1$ a *spatio-temporal* symmetry of the solution $x(t)$. A spatio-temporal symmetry of $x(t)$ for which $\theta = 0$ is called a *spatial symmetry*, since it fixes the point $x(t)$ at every moment of time. The group of all spatio-temporal symmetries of $x(t)$ is denoted

$$\Sigma_{x(t)} \subset \Gamma \times \mathbf{S}^1.$$

Next we show how the symmetry group $\Sigma_{x(t)}$ can be identified with a pair of subgroups H and K of Γ and a homomorphism from H into $\mathbf{S}^1$ with kernel K. Define

$$\begin{array}{rcl} K & = & \{\gamma \in \Gamma : \gamma x(t) = x(t) \quad \forall t\} \\ H & = & \{\gamma \in \Gamma : \gamma\{x(t)\} = \{x(t)\}\}. \end{array} \tag{4.4}$$

The subgroup $K \subset \Sigma_{x(t)}$ is the group of *spatial symmetries* of $x(t)$ and the subgroup H consists of those symmetries that preserve the trajectory of $x(t)$ — in short, the spatial parts of spatio-temporal symmetries of $x(t)$. Indeed, the groups $H \subset \Gamma$ and $\Sigma_{x(t)} \subset \Gamma \times \mathbf{S}^1$ are isomorphic; the isomorphism is just the restriction to $\Sigma_{x(t)}$ of the projection of $\Gamma \times \mathbf{S}^1$ onto Γ.

4.1 A Classification Theorem for Spatio-Temporal Symmetries

There are three straightforward algebraic restrictions placed on the pair H and K defined in (4.4) in order for them to correspond to symmetries of a periodic solution. Recall that the *fixed-point subspace* of a subgroup $\Sigma \subset \Gamma$ is

$$\mathrm{Fix}(\Sigma) = \{x \in \mathbf{R}^n : \sigma x = x \quad \forall \sigma \in \Sigma\}$$

and that fixed-point subspaces are flow invariant, that is, $f : \mathrm{Fix}(\Sigma) \to \mathrm{Fix}(\Sigma)$.

Lemma 4.1 *Let $x(t)$ be a periodic solution of* (4.1) *and let H and K be the subgroups of Γ defined in* (4.4)*. Then*

(a) K is a normal subgroup of H and H/K is either cyclic or $\mathbf{S}^1$.

(b) K is an isotropy subgroup for the Γ-action.

(c) $\dim \mathrm{Fix}(K) \geq 2$.

Proof: For each $\gamma \in H$ there is a unique $\theta \in \mathbf{S}^1$ such that (γ, θ) is a spatio-temporal symmetry of $x(t)$. Uniqueness of solutions implies that the mapping $\Theta : H \to \mathbf{S}^1$ defined by $\Theta(\gamma) = \theta$ is a group homomorphism. By definition, the kernel of this homomorphism is K — thus verifying (a).

Let $x_0 = x(0)$ and suppose that $\sigma x_0 = x_0$. Then $\sigma x(t)$ is another (periodic) solution with initial condition x_0. If follows that $\sigma x(t) = x(t)$ and that $\sigma \in K$. Therefore, the isotropy subgroup of x_0 is in K. Conversely, by definition, $\sigma \in K$ fixes x_0 — and (b) is valid. Also by definition $x(t) \subset \mathrm{Fix}(K)$; so (c) must be valid.

Definition 4.2 *When $H/K \cong \mathbf{Z}_m$ the periodic solution $x(t)$ is called either a* standing wave *or (usually for $m \geq 3$) a* discrete rotating wave*; and when $H/K \cong \mathbf{S}^1$ it is called a* rotating wave.

In fact, the pair H and K must satisfy two restrictions in addition to those listed in Lemma 4.1. We discuss one of those in detail here. Let Γ be a finite group acting on $\mathbf{R}^n$ and let $x(t)$ be a periodic solution of a Γ-equivariant system of ODE. Define

$$L_K = \bigcup_{\gamma \notin K} \mathrm{Fix}(\gamma) \cap \mathrm{Fix}(K)$$

Since K is an isotropy subgroup (Lemma 4.1(a)), L_K is the union of proper subspaces of $\mathrm{Fix}(K)$. More precisely, suppose that $\mathrm{Fix}(\gamma) \supset \mathrm{Fix}(K)$. Then the isotropy subgroup of every point in $\mathrm{Fix}(K)$ contains both K and $\gamma \notin K$. Therefore, the isotropy subgroup of any point in $\mathrm{Fix}(K)$ is larger than K, and K is not an isotropy subgroup.

We claim that

$$H \text{ fixes a connected component of } \mathrm{Fix}(K) \sim L_K. \tag{4.5}$$

To verify (4.5) we first show that any δ in the normalizer $N(K)$ permutes connected components of $\mathbf{R}^n \sim L_K$. Observe that

$$\delta(\mathrm{Fix}(\gamma) \cap \mathrm{Fix}(K)) = \mathrm{Fix}(\delta\gamma\delta^{-1}) \cap \mathrm{Fix}(\delta K \delta^{-1}) = \mathrm{Fix}(\delta\gamma\delta^{-1}) \cap \mathrm{Fix}(K)$$

Moreover, $\delta\gamma\delta^{-1} \notin K$. (If it were, then γ would be in $\delta^{-1}K\delta = K$, which it is not.) Therefore $\delta : L_K \to L_K$. Since δ is invertible, $\delta : \mathbf{R}^n \sim L_K \to \mathbf{R}^n \sim L_K$ and δ permutes the connected components of $\mathbf{R}^n \sim L_K$. Since H/K is cyclic, we can choose an element $h \in H$ that projects onto a generator of H/K. We now show that h (and hence H) must fix one of the connected components of $\mathbf{R}^n \sim L_K$. Suppose that the trajectory of $x(t)$ intersects the flow-invariant subspace $\mathrm{Fix}(\gamma) \cap \mathrm{Fix}(K)$. Flow-invariance of $\mathrm{Fix}(\gamma)$ implies that γ is a spatial symmetry of the solution $x(t)$, and by definition $\gamma \in K$. Therefore the trajectory of $x(t)$ does not intersect L_K. Since h is a spatio-temporal symmetry of $x(t)$, it preserves the trajectory of $x(t)$. Therefore, h must map the connected component of $\mathbf{R}^n \sim L_K$ that contains the trajectory of $x(t)$ into itself, thus verifying (4.5).

The main theorem of this section is a characterization of the possible spatio-temporal symmetries of periodic solutions.

Theorem 4.3 (Buono and Golubitsky, 2000) *] Let Γ be a finite group acting on $\mathbf{R}^n$. There is a periodic solution to some Γ-equivariant system of ODE on $\mathbf{R}^n$ with spatial symmetries K and spatio-temporal symmetries H if and only if*

(a) H/K is cyclic.

(b) K is an isotropy subgroup.

(c) $\dim \mathrm{Fix}(K) \geq 2$. If $\dim \mathrm{Fix}(K) = 2$, then either $H = K$ or $H = N(K)$.

(d) H fixes a connected component of $\mathbf{R}^n \sim L_K$.

Moreover, when these conditions hold, there exists a smooth Γ-equivariant vector field with an asymptotically stable limit cycle with the desired symmetries.

Corollary 4.4 *For pairs (H, K) satisfying conditions (a)-(d) of Theorem 4.3, the property of having periodic solutions with spatial symmetries K and spatio-temporal symmetries H is robust in Γ-equivariant systems of ODE on $\mathbf{R}^n$.*

The case when the internal dynamics of a coupled cell system is $k \geq 2$ motivates the following corollary to Theorem 4.3.

Corollary 4.5 *Let Γ be a finite group acting on V and suppose that $W = V^k$ for some $k \geq 2$. Then there is a hyperbolic periodic solution to some Γ-equivariant system of ODE on $\mathbf{R}^n$ with spatial symmetries K and spatio-temporal symmetries H if and only if*

(a) H/K *is cyclic.*

(b) K *is an isotropy subgroup.*

(c) If $\dim \mathrm{Fix}(K) = 2$*, then either* $H = K$ *or* $H = N(K)$*.*

A Two-Cell Coupled Cell Example

Our first example of a coupled cell system is the simplest possible one — the two-cell system pictured in Figure 4.1.

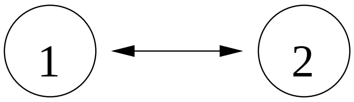

Figure 4.1: A two-cell coupled cell system.

The corresponding system of ODEs is

$$\begin{array}{rcl} \dot{x}_1 & = & f(x_1, x_2) \\ \dot{x}_2 & = & f(x_2, x_1) \end{array} \tag{4.6}$$

where $x_1, x_2 \in \mathbf{R}^k$. The symmetry group for the two-cell system is $\mathbf{Z}_2(\kappa)$ where $\kappa(x_1, x_2) = (x_2, x_1)$. According to symmetry there are three possible types of periodic solutions in this cell system and they correspond to: $(H, K) = (\mathbf{Z}_2, \mathbf{Z}_2)$, $(H, K) = (\mathbf{Z}_2, \mathbf{1})$, and $(H, K) = (\mathbf{1}, \mathbf{1})$. Suppose that $x(t) = (x_1(t), x_2(t))$ is a 1-periodic solution to (4.6).

- If $x(t)$ corresponds to $(H, K) = (\mathbf{Z}_2, \mathbf{Z}_2)$, then it is a *synchronous* solution where $x_2(t) = x_1(t)$.
- If $x(t)$ corresponds to $(H, K) = (\mathbf{Z}_2, \mathbf{1})$, then it is an *out of phase* solution where $x_2(t) = x_1\left(t + \frac{1}{2}\right)$.
- If $x(t)$ corresponds to $(H, K) = (\mathbf{1}, \mathbf{1})$, then $x(t)$ is asymmetric — but then $(x_2(t), x_1(t))$ is also a 1-periodic solution.

It follows from Corollary 4.5 that there are stable limit cycles with each of these symmetry types when $k \geq 2$ — indeed it is not too difficult to find examples of each type of periodic solution. When $k = 1$ Theorem 4.3 precludes the existence of both synchronous and out of phase periodic solutions. Note that $\mathrm{Fix}(\mathbf{Z}_2) = \{(x_1, x_1)\}$. So synchronous solutions cannot exist since $\dim \mathrm{Fix}(\mathbf{Z}_2) = 1$ and out of phase solutions cannot exist since κ does not fix a connected component of $\mathbf{R}^2 \sim L_{\mathbf{1}} = \mathbf{R}^2 \sim \mathrm{Fix}(\kappa)$. Asymmetric periodic solutions can exist when $k = 1$.

Three Cells in a Line

Consider the three-cell coupled cell system pictured in Figure 4.2.

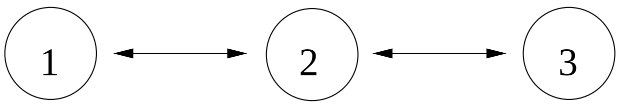

Figure 4.2: Three cells in a line.

The corresponding system of ODEs is

$$\begin{array}{rcl} \dot{x}_1 & = & f(x_1, x_2, x_3) \\ \dot{x}_2 & = & g(x_1, x_2, x_3) \\ \dot{x}_3 & = & f(x_3, x_2, x_1) \end{array} \tag{4.7}$$

where $x_1, x_2, x_3 \in \mathbf{R}^k$ and $g(x_3, x_2, x_1) = g(x_1, x_2, x_3)$. The symmetry group for this three-cell system is still $\mathbf{Z}_2(\kappa)$ where $\kappa(x_1, x_2, x_3) = (x_3, x_2, x_1)$ and there are still three types of possible periodic solutions: synchronous, out of phase, and asymmetric. Suppose that $x(t) = (x_1(t), x_2(t), x_3(t))$ is a 1-periodic solution to (4.7). Then

- If $x(t)$ is a *synchronous* solution, then $x_3(t) = x_1(t)$.
- If $x(t)$ is an *out of phase* solution, then $x_3(t) = x_1\left(t + \frac{1}{2}\right)$ and $x_2(t) = x_2\left(t + \frac{1}{2}\right)$. That is, the second cell oscillates with twice the frequency of the other cells.
- If $x(t)$ is asymmetric, then $(x_3(t), x_2(t), x_1(t))$ is a 1-periodic solution.

Again it follows from Corollary 4.5 that there are stable limit cycles with each of these symmetry types when $k \geq 2$. When $k = 1$ Theorem 4.3 precludes the existence of the out of phase periodic solutions.

4.2 Examples of Spatio-Temporal Symmetries

We now present two examples where spatio-temporal symmetries have important interpretations for the associated periodic solutions.

4.2.1 Animal Gaits

[Golubitsky, Buono, Collins and Stewart, 1998, 1999] argue that the eight-cell double-ring network pictured in Figure 2.2 is the simplest network that will produce periodic solutions having the rhythms of the quadruped gaits walk, trot, and pace. The symmetry group of this network is $\Gamma = \mathbf{Z}_4(\omega) \times \mathbf{Z}_2(\kappa)$.

We call a symmetry type (H, K) of a periodic solution *primary* when $H = \Gamma$. If the cell system consists of identical cells (that is, Γ acts transitively on the cells), then the signals emanating from each cell in a primary periodic solution are *identical* up to a phase shift. In this generalized sense signals sent from each cell in a primary periodic solutions are synchronous. It is a straightforward exercise to classify the primary periodic solution types in the network pictured in Figure 2.2; the results are listed in Table 4.2. Note that primary periodic solutions in this network also include models of the bound, the pronk, and an unusual gait called the jump (which has been seen in bucking broncos — as well as in gerbils and rats).

K	Γ/K	Spatio-Temporal	Phase Diagram	Gait
Γ	$\mathbf{1}$	—	$\begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}$	pronk
$< \omega >$	$\mathbf{Z}_2$	$(\kappa, \frac{1}{2})$	$\begin{pmatrix} 0 & \frac{1}{2} \\ 0 & \frac{1}{2} \end{pmatrix}$	pace
$< \kappa\omega >$	$\mathbf{Z}_2$	$(\kappa, \frac{1}{2})$	$\begin{pmatrix} \frac{1}{2} & 0 \\ 0 & \frac{1}{2} \end{pmatrix}$	trot
$< \kappa, \omega^2 >$	$\mathbf{Z}_2$	$(\omega, \frac{1}{2})$	$\begin{pmatrix} 0 & 0 \\ \frac{1}{2} & \frac{1}{2} \end{pmatrix}$	bound
$< \kappa\omega^2 >$	$\mathbf{Z}_4$	$(\omega, \frac{1}{4})$ $(\kappa, \frac{1}{2})$	$\begin{pmatrix} \pm\frac{1}{4} & \pm\frac{3}{4} \\ 0 & \frac{1}{2} \end{pmatrix}$	walk$^{\pm}$
$< \kappa >$	$\mathbf{Z}_4$	$(\omega, \frac{1}{4})$	$\begin{pmatrix} \pm\frac{1}{4} & \pm\frac{1}{4} \\ 0 & 0 \end{pmatrix}$	jump$^{\pm}$

Table 4.2: Symmetries of primary periodic solutions in a $\Gamma = \mathbf{Z}_4 \times \mathbf{Z}_2$ model.

4.2.2 Multirhythms

Coupled cell dynamics can lead to situations where different cells are forced by symmetry to oscillate at different frequencies [Golubitsky and Stewart, 1986; Golubitsky, Stewart, and Schaeffer, 1988; Armbruster and Chossat, 1999]. As we have seen, certain cells can be forced to oscillate at twice the frequency of other cells — but the range of possibilities is much more complicated.

The basic principle is simple (though combinatorial bells and whistles can be added). Let γ be an m-cycle that is a spatio-temporal symmetry of a coupled cell system having corresponding phase shift $\frac{1}{m}$. Suppose, in addition, that γ cyclicly permutes cells $1, \ldots, m$ and fixes cell $m+1$. Then cell $m+1$ must oscillate m times as quickly as cell 1 — with one caveat that we will return to in a moment. A simple example of a four-cell system that illustrates this point is given in Figure 4.3. In this coupled cell system a ponies on a merry-go-round solution $(\mathbf{Z}_3, \mathbf{1})$ will force cell 4 to oscillate at three times the frequencies of the other three cells.

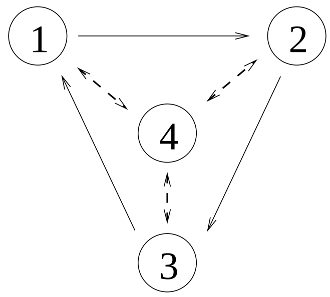

Figure 4.3: Unidirectional ring of three cells with a center cell.

We now return to the caveat: suppose two different cycles with nontrivial temporal symmetries exist. Then, they can force two different frequency relations between the cells — and it is quite curious how these two frequency restrictions are resolved into one relation, as we now show.

Consider a five-cell system consisting of two rings — one with three cells and one with two cells — as shown in Figure 4.4. The symmetry group of this system is $\Gamma = \mathbf{Z}_3 \times \mathbf{Z}_2 \cong \mathbf{Z}_6$. Note that the internal dynamics of cells 4 and 5 do not have to be the same as that of cells 1, 2, and 3 (indeed, they do not even have to have the same dimensions).

Suppose that a 1-periodic solution

$$X(t) = (x_1(t), x_2(t), x_3(t), y_1(t), y_2(t))$$

to this coupled cell system exists. Suppose that this solution has two spatio-temporal symmetries $((1\ 2\ 3), \frac{1}{3})$ and $(4\ 5), \frac{1}{2})$. The first symmetry forces the x_j to be in ponies

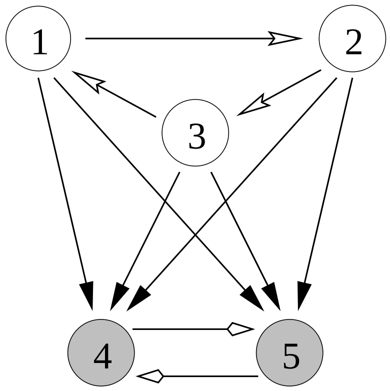

Figure 4.4: Five cell system made of a ring of three and a ring of two.

form with (nominally) the frequency of the y_i equal to three times the frequency of the x_j. The second symmetry forces the y_i to be a half period out-of-phase and the x_j to oscillate at twice the frequency of the y_i. This apparent nonsense is resolved as follows. The product of the two symmetries is

$$\gamma = ((1\ 2\ 3)(4\ 5), \tfrac{1}{6}),$$

explicitly exhibiting the isomorphism $\mathbf{Z}_3 \times \mathbf{Z}_2 \cong \mathbf{Z}_6$. Thus $X(t)$ actually has the form

$$X(t) = (x(t), x(t + \tfrac{1}{3}), x(t + \tfrac{2}{3}), y(t), y(t + \tfrac{1}{2})).$$

where three times the frequency of x is twice the frequency of y.

Does such a solution actually exist? Corollary 4.5 states that it does — at least if all nonlinearities consistent with $\mathbf{Z}_6$ symmetry are permitted to be present. The difficulty is to find a solution corresponding to the pair $(\mathbf{Z}_6, \mathbf{1})$ in the coupled cell system context.

The difficulty is compounded by the following fact that no such solution is supported by a primary Hopf bifurcation in this coupled-cell system. The reason is that in Hopf bifurcation the available representations of the symmetry group $\mathbf{Z}_6 \cong \mathbf{Z}_3 \times \mathbf{Z}_2$ are sums of irreducible components of the permutation representation on $\mathbf{R}^{5k}$, where k is the dimension of the state space of a single cell. However, there does exist a more complicated bifurcation scenario that contains such a representation: primary Hopf bifurcation to a $\mathbf{Z}_3$ discrete rotating wave, followed by a secondary Hopf bifurcation using the nontrivial $\mathbf{Z}_2$ representation. We therefore seek a 3:2 resonant solution arising from such a scenario. Let $x_1, x_2, x_3 \in \mathbf{R}$ be the state variables for the ring of three cells and let $y_1 = (y_1^1, y_2^1), y_2 = (y_1^2, y_2^2) \in \mathbf{R}^2$ be the state variables for the ring of two cells. Consider the system of ODE

$$\begin{array}{rcl} \dot{x}_1 & = & -x_1 - x_1^3 + 2(x_1 - x_2) + D(y_1 + y_2) + 3((y_2^1)^2 + (y_2^2)^2) \\ \dot{x}_2 & = & -x_2 - x_2^3 + 2(x_2 - x_3) + D(y_1 + y_2) + 3((y_2^1)^2 + (y_2^2)^2) \\ \dot{x}_3 & = & -x_3 - x_3^3 + 2(x_3 - x_1) + D(y_1 + y_2) + 3((y_2^1)^2 + (y_2^2)^2) \\ \dot{y}_1 & = & B_1 y_1 - |y_1|^2 y_1 + B_2 y_2 + 0.4(x_1^2 + x_2^2 + x_3^2)C \\ \dot{y}_2 & = & B_1 y_2 - |y_2|^2 y_2 + B_2 y_1 + 0.4(x_1^2 + x_2^2 + x_3^2)C \end{array} \tag{4.8}$$

where

$$B_1 = \begin{pmatrix} -\frac{1}{2} & 1 \\ -1 & -\frac{1}{2} \end{pmatrix} \quad B_1 = \begin{pmatrix} -1 & -1 \\ 1 & -1 \end{pmatrix} \quad D = (0.20, -0.11) \quad C = \begin{pmatrix} 0.10 \\ 0.22 \end{pmatrix}.$$

Starting at the initial condition

$$x_1^0 = 1.78 \quad x_2^0 = -0.85 \quad x_3^0 = -0.08 \quad y_1^0 = (-0.16, 0.79) \quad y_2^0 = (0.32, -0.47)$$

We obtain Figures 4.5 and 4.6.

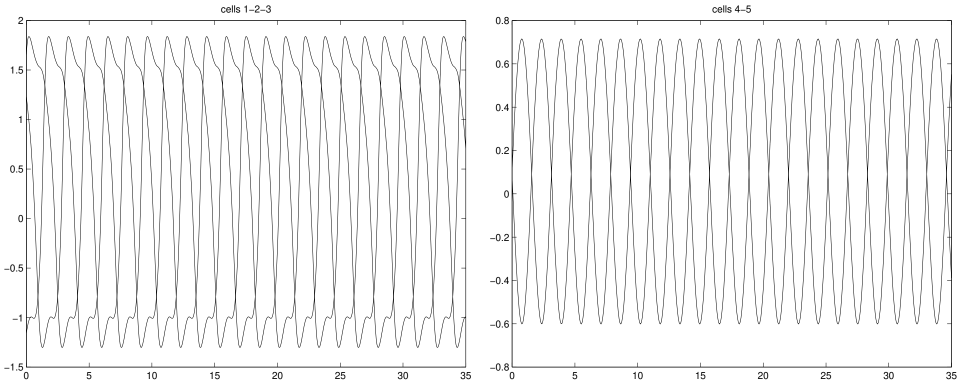

Figure 4.5: Integration of (4.8). (Left) Cells 1-2-3 out of phase by one-third period; (right) cells 4-5 out of phase by one-half period.

4.3 Spatio-Temporal Symmetries in Hamiltonian Systems

We now discuss the Hamiltonian version of Theorem 4.3. We begin by developing a theory of Hamiltonian coupled cell systems, by analogy with the dissipative case (the one described so far). We use standard concepts from Hamiltonian dynamics without further comment: see [Abraham and Marsden, 1978] and [Arrowsmith and Place, 1990]. In Hamiltonian systems the phase space is a symplectic manifold, and

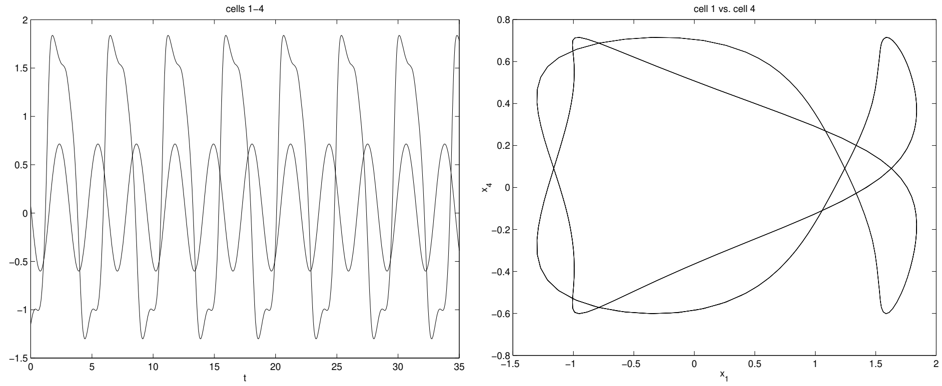

Figure 4.6: Integration of (4.8). (Left) Time series of cells 1 and 4 indicating that triple the frequency of cell 4 equals double the frequency of cell 1; (right) Plot of cell 1 versus cell 4 showing a closed curve that indicates a time-periodic solution.

for the purposes of local bifurcation theory it can be assumed to be a symplectic vector space $P = \mathbf{R}^{2n}$ with coordinates $(q, p) = (q_1, \ldots, q_n; p_1, \ldots, p_n)$ where q is position and p is velocity. The dynamics is determined by a *Hamiltonian*

$$\mathcal{H} : P \to \mathbf{R}$$

and we shall assume that $\mathcal{H} \in C^\infty$. *Hamilton's Equations* for the dynamics are:

$$\dot{q}_j = \frac{\partial \mathcal{H}}{\partial p_j} \quad \dot{p}_j = -\frac{\partial \mathcal{H}}{\partial q_j} \tag{4.9}$$

Because of the form of these equations, $\dot{\mathcal{H}} \equiv 0$, so the Hamiltonian is conserved by the flow. The level sets of $\mathcal{H}$, given by $\mathcal{H} = c$ for constant c, are called *energy levels.*

Let $\Gamma \subset \mathbf{O}(2n)$ be a finite group and let Ω be the symplectic 2-form on $\mathbf{R}^{2n}$. The group Γ acts symplectically if $\gamma^*\Omega = \Omega$ for all $\gamma \in \Gamma$. We recall that fixed-point subspaces of symplectic actions are symplectic, hence even-dimensional.

Theorem 4.6 *Let Γ be a finite group acting symplectically on $\mathbf{R}^{2n}$. There is a periodic solution to some Γ-equivariant Hamiltonian system of ODE on $\mathbf{R}^{2n}$ with spatial symmetries K and spatio-temporal symmetries H if and only if*

(a) H/K is cyclic.

(b) K is an isotropy subgroup.

(c) $\dim \mathrm{Fix}(K) \geq 2$. *If* $\dim \mathrm{Fix}(K) = 2$, *then either* $H = K$ *or* $H = N(K)$.

Moreover, when these conditions hold, there exists a smooth Γ*-equivariant Hamiltonian vector field having an elliptic periodic solution with the desired symmetries.*

The proof of this theorem is virtually identical to that of Theorem 4.3. As before, conditions (a)-(c) are necessary conditions. Note that condition (d) of Theorem 4.3 is superfluous in the Hamiltonian setting, since the symplectic structure implies that the codimension of $\mathrm{Fix}(\gamma) \cap \mathrm{Fix}(K)$ in $\mathrm{Fix}(K)$ is at least two; hence the complement of L_K is always connected.

Conversely, choose the closed curve $\mathcal{C}$ with the desired symmetry properties, as in the proof of Theorem 4.3. See [Buono and Golubitsky, 2000]. Then choose a nonnegative Hamiltonian in a small neighborhood of $\mathcal{C}$ whose zero set is $\mathcal{C}$. Extend the Hamiltonian to be Γ-invariant on all of $\mathbf{R}^{2n}$ in a way analogous to the construction of the vector field in the proof of Theorem 4.3. We can also assume that the Hamiltonian is chosen so that $\mathcal{C}$ is the trajectory of an elliptic periodic solution.

4.3.1 Coupled Pendula

In this subsection we discuss the spatio-temporal symmetries of periodic solutions to the ring of N identical simple pendula introduced in §2.3. Denote the position of pendulum j (taken modulo N) by q_j and its angular velocity by $p_j = \dot{q}_j$. Let the mass of each pendulum bob be m, normalize the length to 1, let gravity be g, and let the modulus of elasticity for each spring be α. Choose units so that $m = 1, g = 1$. Then the Hamiltonian is

$$H(q,p) = \tfrac{1}{2}p_j^2 - \cos q_j + \frac{\alpha}{2}((q_{j-1} - q_j)^2 + (q_{j+1} - q_j)^2) \tag{4.10}$$

The equations of motion are

$$\begin{array}{rcl} \dot{q}_j & = & p_j \\ \dot{p}_j & = & -\sin q_j + \alpha(q_{j-1} - 2q_j + q_{j+1}). \end{array} \tag{4.11}$$

Note that the coupling is this model is assumed to be nearest neighbor and diffusive.

In the pendulum system the symmetry group of the Hamiltonian is not $\mathbf{D}_N$ but $\mathbf{D}_N \times \mathbf{Z}_2$ where the extra symmetry is an internal one given by $(q,p) \mapsto (-q,-p)$. More precisely, the action of this group on $\mathbf{R}^N \oplus \mathbf{R}^N$ with coordinates (q,p) is:

$$\begin{array}{rcl} \sigma(q_0,\ldots,q_{N-1};p_0,\ldots,p_{N-1}) & = & (q_1,\ldots,q_{N-1},q_0;p_1,\ldots,p_{N-1},p_0) \\ \rho(q_0,\ldots,q_{N-1};p_0,\ldots,p_{N-1}) & = & (q_{N-1},\ldots,q_0;p_{N-1},\ldots,p_0) \\ \tau(q_0,\ldots,q_{N-1};p_0,\ldots,p_{N-1}) & = & (-q_0,\ldots,-q_{N-1};-p_0,\ldots,-p_{N-1}) \end{array} \tag{4.12}$$

Here $\mathbf{D}_N = \langle \sigma, \rho \rangle$ and $\mathbf{Z}_2 = \langle \tau \rangle$. Let $\Gamma = \mathbf{D}_N \times \mathbf{Z}_2$.

Next we ask: what kinds of periodic solution does Theorem 4.6 suggest may exist in the Hamiltonian system (4.11)? Theorem 4.6 states that we need to determine, up to conjugacy, all isotropy subgroups K having $\dim \mathrm{Fix}(K) \geq 2$ and all subgroups H for which H/K is cyclic. In general, this is a combinatorially difficult problem, but the enumeration simplifies when N is prime — which we now assume.

Note that the only isotropy subgroup that contains τ is Γ itself. Therefore, possible isotropy subgroups of Γ have one of two possible forms:

$$K = L \times \mathbf{1} \quad \text{and} \quad K = (L \times \mathbf{1}) \cup ((M \sim L) \times \{\tau\}), \tag{4.13}$$

where $L \subset M \subset \mathbf{D}_N$ and L has index two in M. When N is an odd prime there are only four subgroups of $\mathbf{D}_N$ up to conjugacy: $\mathbf{1}$, $\mathbf{Z}_2(\rho)$, $\mathbf{Z}_N$, and $\mathbf{D}_N$. It follows from (4.13) that there are just two additional possible isotropy subgroups: $\mathbf{Z}_2(\rho\tau)$ (from $\mathbf{1} \subset \mathbf{Z}_2(\rho)$) and $\widetilde{\mathbf{D}}_N$ (from $\mathbf{Z}_N \subset \mathbf{D}_N$). Of the seven possibilities only five

$$\mathbf{1} \qquad \mathbf{Z}_2(\rho) \qquad \mathbf{Z}_2(\rho\tau) \qquad \mathbf{D}_N \qquad \Gamma$$

are isotropy subgroups and they have fixed-point subspace dimension $2N$, $N+1$, $N-1$, 2, and 0, respectively. So $K = \Gamma$ is not possible. Finally, we enumerate the pairs $K \subset H$ for which H/K is cyclic. There are 13 such pairs:

$\mathbf{1} \subset \mathbf{1}$	$\mathbf{Z}_2(\rho) \subset \mathbf{Z}_2(\rho)$	$\mathbf{Z}_2(\rho\tau) \subset \mathbf{Z}_2(\rho\tau)$	$\mathbf{D}_N \subset \mathbf{D}_N$
$\mathbf{1} \subset \mathbf{Z}_2(\rho)$	$\mathbf{Z}_2(\rho) \subset \mathbf{Z}_2(\rho) \times \mathbf{Z}_2(\tau)$	$\mathbf{Z}_2(\rho\tau) \subset \mathbf{Z}_2(\rho) \times \mathbf{Z}_2(\tau)$	$\mathbf{D}_N \subset \Gamma$
$\mathbf{1} \subset \mathbf{Z}_2(\rho\tau)$	$\mathbf{Z}_2(\rho) \subset \mathbf{D}_N$	$\mathbf{Z}_2(\rho\tau) \subset \widetilde{\mathbf{D}}_N$	
$\mathbf{1} \subset \mathbf{Z}_2(\tau)$			
$\mathbf{1} \subset \mathbf{Z}_N$			

When N is not prime the number of isotropy subgroups increases substantially with the number of prime factors.

There is, however, another issue that needs to be discussed. In the models for speciation, animal gaits, and the visual cortex, specific equations for the internal dynamics and the coupling are not known; indeed, in a very real sense, they may never be known. In the coupled pendulum model, the Hamiltonian for the internal dynamics and the coupling are derivable from first principles. Therefore, for such systems, it is useful to have techniques that prove the existence of periodic solutions in the given model equation not just in all possible model systems having the same symmetries. In dissipative systems one method for finding periodic solutions of a given type in a fixed model is Hopf bifurcation. In Hamiltonian systems, the analogous method for finding periodic solutions is the Weinstein-Moser theorem. We present the equivariant versions of these techniques in the next chapter. Using this approach we will be able to prove that three of the 13 possibilities do appear in the Hamiltonian system (4.11). See §5.4.1 for further information.

5 Spontaneous Symmetry-Breaking

In Section 4 we discussed the symmetry types of stationary and periodic solutions that one can expect to find in equivariant systems of differential equations. We can apply these theorems only to the class of all equivariant systems — not to an individual system. Bifurcation theory is the traditional method by which solutions of a given symmetry type are proved to exist in a particular model system. Usually we start with a group-invariant equilibrium and ask what states bifurcate from that equilibrium as a parameter is varied. In general, almost anything can happen; but, generically, only rather specific types of bifurcations are possible. That comment follows from the well-developed theory of *spontaneous symmetry-breaking* and leads to a set of solutions that are 'likely to occur' in specific models. It is important to emphasize that the 'likely' solutions do not include all possible solutions. In this section we review some of equivariant bifurcation theory. See [Golubitsky, Stewart, and Schaeffer, 1988] for additional detail.

Let $f : \mathbf{R}^n \times \mathbf{R} \to \mathbf{R}^n$ be Γ-equivariant where $\Gamma \subset \mathbf{O}(n)$ is finite, that is,

$$f(\gamma x, \lambda) = \gamma f(x, \lambda).$$

Consider the Γ-invariant system of ODE

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

where λ is a bifurcation parameter. Suppose that $x = 0$ is a *trivial* group invariant equilibrium, that is,

$$f(0, \lambda) = 0.$$

Suppose, in addition, that there is a *bifurcation* at $\lambda = 0$; that is, there are eigenvalues of the linearization

$$L = (d_x f)_{(0,0)}$$

on the imaginary axis. By definition *steady-state* bifurcation occurs when L has a zero eigenvalue and *Hopf* bifurcation occurs when L has a complex conjugate pair of purely imaginary eigenvalues. Typically, either steady-state or Hopf bifurcation occurs — but not both — unless additional parameters are available in the model equations. For the moment we assume that only one parameter is present.

5.1 Linear Theory

It is easy to check that $\ker L$ is a Γ-invariant subspace of $\mathbf{R}^n$. It is proved in [Golubitsky, Stewart, and Schaeffer, 1988] that typically, at a steady-state bifurcation, the subspace $\ker L \subset \mathbf{R}^n$ is an absolutely irreducible representation of Γ. Recall that a real representation is absolutely irreducible if the only linear maps that commute with Γ are scalar multiples of the identity map. It is also shown that typically at a Hopf bifurcation the center subspace C of L is Γ-*simple*: either

(a) $C = V \oplus V$ where V is an absolutely irreducible representation of Γ, or

(b) C itself is irreducible but not absolutely irreducible.

One consequence of these two results is that there is a type of steady-state bifurcation for each absolutely irreducible representation of Γ and there is a type of Hopf bifurcation for each irreducible representation of Γ. Likely solutions are found by determining the new solutions that occur by symmetry-breaking bifurcation from each of these type of bifurcations.

5.2 Nonlinear Theory

There are two steps in analyzing symmetry-breaking bifurcations. First, either a Liapunov-Schmidt or center manifold reduction is used to reduce the question of finding new solutions to one of finding solutions to Γ-invariant systems of ODE

$$\dot{y} = g(y, \lambda)$$

where $y \in C$ and $g : C \times \mathbf{R} \to C$ is Γ-equivariant with respect to the action of Γ on C. These reductions can be performed to preserve symmetry and so that

$$g(0, \lambda) = 0.$$

The second step — analyzing the bifurcations of the implicitly defined system g — is generally quite difficult. There are, however, two theorems that simplify the search for generically occurring solutions — the Equivariant Branching Lemma and the Equivariant Hopf Theorem.

The symmetry group of an equilibrium $\Sigma \subset \Gamma$ is always an isotropy subgroup. An isotropy subgroup is *axial* if

$$\dim \mathrm{Fix}_{\ker L}(\Sigma) = 1.$$

Theorem 5.1 (Equivariant Branching Lemma) *Generically, for each axial subgroup $\Sigma \subset \Gamma$, there is a unique branch of equilibria having symmetry subgroup Σ.*

At a generic Hopf bifurcation $A = (d_y g)_{(0,0)}$ has one purely imaginary pair of complex conjugate eigenvalues each of multiplicity m where $\dim C = 2m$. It follows that e^{tA} induces an action of $\mathbf{S}^1$ on C that commutes with the action of Γ; hence there is a naturally defined action of $\Gamma \times \mathbf{S}^1$ on C. An isotropy subgroup $\Sigma \subset \Gamma \times \mathbf{S}^1$ is $\mathbf{C}$-*axial* if

$$\dim \mathrm{Fix}_C(\Sigma) = 2$$

If a periodic solution has symmetry subgroup $\Sigma \subset \Gamma \times \mathbf{S}^1$, then, as in Section 4, we can define $K = \Sigma \cap \Gamma$ and $H = \Pi(\Sigma)$ where $\Pi : \Gamma \times \mathbf{S}^1 \to \Gamma$ is projection.

Theorem 5.2 (Equivariant Hopf Theorem) *Generically, for each axial subgroup $\Sigma \subset \Gamma \times \mathbf{S}^1$, there is a unique branch of periodic solutions having symmetry subgroup Σ.*

The next two sections are devoted to applications of these bifurcation results to coupled cell systems. We then discuss genericity issues involving coupled cell systems and end the chapter with a discussion of the equivariant Moser-Weinstein theorem — the Hamiltonian analogue of the equivariant Hopf theorem.

5.2.1 $\mathbf{S}_N$ Steady-State Bifurcations and Speciation Revisited

In Section 1 we introduced a coupled cell model of speciation and exhibited a numerical simulation in which a single species splits into two. A number of general phenomena are associated with such models, independently of many details of the equations, and we now describe some of these. Specific models with a well-defined biological interpretation, such as simulations of speciation in bird populations, have been studied by [Elmhirst, 2000] and related to the general considerations stemming from symmetry.

Recall that the model deals with a set of N PODs (coarse-grained clumps of organisms) whose phenotypes are represented by $x = (x_1, \ldots, x_N) \in \mathbf{R}^N$. (To include more phenotypic variables, let the x_j be vectors in some $\mathbf{R}^k$. The discussion generalizes to this case.) We normalize all phenotypic variables to be zero prior to bifurcation: that is, we define them as deviations from the mean.

The subspaces

$$\begin{array}{rcl} V_0 & = & \mathbf{R}(1, 1, \ldots, 1) \\ V_1 & = & \{(x_1, \ldots, x_N) : x_1 + \cdots + x_N = 0\} \end{array} \tag{5.1}$$

are $\mathbf{S}_N$-invariant and $\mathbf{S}_N$-irreducible, and

$$\mathbf{R}^N = V_0 \oplus V_1$$

A symmetry-breaking bifurcation of equilibria occurs when the kernel of the linearization is V_1, and we can carry out a Liapunov-Schmidt reduction onto this space.

Consider the restriction of the action of $\mathbf{S}_N$ to V_1. Here, the isotropy subgroups are the same as for the action of $\mathbf{S}_N$ on $\mathbf{R}^N$, but the dimension of $\mathrm{Fix}(\Sigma)$ is reduced by 1. In particular $\dim \mathrm{Fix}(\Sigma) = 1$ when Σ is the isotropy group of a block $\{p, N-p\}$, where $p \leq \frac{N}{2}$.

The coupled cell system is modelled by an $\mathbf{S}_N$-equivariant ODE

$$\frac{\mathrm{d}x_j}{\mathrm{d}t} = f_j(x_1, \ldots, x_N; a_1, \ldots, a_s) \tag{5.2}$$

We can find symmetry-breaking equilibria by applying the Equivariant Branching Lemma. If there is a steady-state bifurcation with kernel V_1 then there exist branches of solutions for all axial isotropy subgroups. From §4 it is easy to check that the axial subgroups of $\mathbf{S}_N$ in this representation are, up to conjugacy, those of the form $\mathbf{S}_p \times \mathbf{S}_q$ where $p + q = N$ and $1 \leq p \leq [N/2]$. So there exist branches of solutions with these isotropy subgroups. Such solutions lie in fixed-point spaces of the form $(u, \ldots, u; v, \ldots, v)$, with exactly *two* distinct values u and v for phenotypic variables. These solution branches therefore correspond to a split of the population of N identical PODs into two distinct species consisting of p and q PODs respectively. One species has the phenotype u and the other species has the phenotype v . Note that $pu + qv = 0$ since $(u, \ldots, u; v, \ldots, v) \in V_1$.

We can also make an interesting universal *quantitative* prediction: on the above branches the mean value of the phenotypic variables changes smoothly during the bifurcation. The reason is that the fixed-point space of $\mathbf{S}_p \times \mathbf{S}_q$ is spanned by all vectors $(u, \ldots, u; v, \ldots, v)$ where there are $p\,u$'s and $q\,v$'s, and the mean phenotype is $pu + qv = 0$. Because we are using normalized phenotypic variables, all $x_i = 0$ prior to bifurcation. Thus the mean phenotype remains constant throughout the bifurcation. However, we are working with the Liapunov-Schmidt reduced problem, which involves a nonlinear change of variables. Therefore the mean varies *smoothly* in the original phenotypic variables, and is thus approximately constant.

Some studies reported in the literature are consistent with the above predictions. For example, a celebrated instance of polymorphism is the changes in beak size that occur among various species of Darwin's finches in the Galápagos Islands. The prediction of smoothly changing mean is consistent with observations of these finches. The evolution of the different finch species in the Galápagos Islands is thought to have occurred around five million years ago, and so cannot be observed (although small-scale evolution remains rapid enough that significant phenotypic changes can be observed from one year to the next). However, we can observe a surrogate for actual evolution: differences in the phenotype of a given species in allopatric and sympatric populations. The transition in phenotype from sympatric populations to allopatric ones should be just like the bifurcations in the speciation model: in particular, we expect to see approximately the same mean in either situation.

This is the case for the two species *Geospiza fortis* and *G. fuliginosa*, which occur in both sympatric and allopatric populations. *G. fortis* is allopatric on the island known as Daphne, and *G. fuliginosa* is allopatric on Crossman. The two species are sympatric on a number of islands which Lack placed in three groups for data analysis: Abingdon, Bindloe, James, Jervis; Albemarle, Indefatigable; and Charles, Chatham. Fig. 5.1, adapted from [Lack, 1968], shows the differences in beak size between these species on the cited groups of islands.

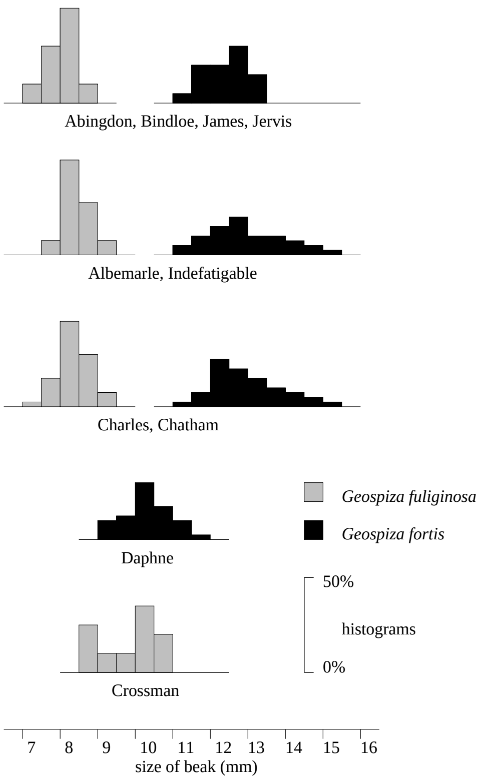

Figure 5.1: Beak sizes in allopatric and sympatric populations of *Geospiza* in the Galápagos Islands.

The mean beak sizes of both *G. fortis* and *G. fuliginosa* are approximately 10mm in allopatric populations. In all three (groups of) sympatric populations, the mean for *G. fortis* is about 12mm, while that for *G. fuliginosa* is about 8mm. These figures are consistent with the 'constant mean' prediction.

5.2.2 Animal Gaits and Multirhythms Revisited

We begin our discussion by recalling that if Γ is an abelian group, then its irreducible representations are either one-dimensional (and absolutely irreducible, since all linear maps are multiples of the identity) or two-dimensional (and nonabsolutely irreducible, since Γ commutes with $\mathbf{SO}(2)$). Thus, generically Hopf bifurcation in the presence of an abelian symmetry group reduces to standard Hopf bifurcation — a single pair of multiplicity one purely imaginary eigenvalues. Standard Hopf bifurcation, which is just a special case of the Equivariant Hopf Theorem, leads to a unique branch of periodic solutions.

The symmetry group pair $K \subset H$ of these solutions is simple to determine: K is the kernel of the action of Γ on C and $H = \Gamma$ (since the bifurcating periodic solution at any parameter value near 0 is unique up to phase shift). Thus, when Γ is abelian, bifurcating solutions are primary solutions.

Since $\Gamma = \mathbf{Z}_4 \times \mathbf{Z}_2$ in the animal gaits model, only primary gaits can be obtained by Hopf bifurcation from a trivial equilibrium. The second question that we ask is whether all primary gaits can, in principle, be obtained by Hopf bifurcation from a trivial equilibrium — and the answer is yes — at least when the dynamics in each cell is two dimensions or greater. First, for every subgroup $K \subset \Gamma$ for which Γ/K is cyclic, there is an irreducible representation of Γ with kernel K. Second, suppose that the internal dynamics of the cell system pictured in Figure 2.2 is one-dimensional. Then the state space is $\mathbf{R}^8$ and since $\mathbf{Z}_4 \times \mathbf{Z}_2$ has eight elements, $\mathbf{R}^8 = L^2(\mathbf{Z}_4 \times \mathbf{Z}_2)$. It is a standard theorem from representation theory that every irreducible representation appears at least once in $L^2(\mathbf{Z}_4 \times \mathbf{Z}_2)$ and hence at least twice when the internal dynamics in each cell is at least two-dimensional. It follows that in principle every primary gait can be obtained by Hopf bifurcation from a trivial equilibrium. Indeed, [Buono, 1998] shows that each of the primary gaits listed in Table 4.2 can be obtained by such a Hopf bifurcation. See also [Buono and Golubitsky, 2000].

The situation is different in the multirhythm example. In that case, see Figure 4.3, the cell system also has an abelian symmetry group $\Gamma = \mathbf{Z}_3 \times \mathbf{Z}_2 \cong \mathbf{Z}_6$. The multirhythm periodic solutions have a symmetry group pair $(H, K) = (\mathbf{Z}_6, \mathbf{1})$ but none of the irreducible representations occurring in the phase space of this cell system has trivial kernel — there are three different irreducible representations and their kernels are $\mathbf{Z}_2$, $\mathbf{Z}_3$, and $\mathbf{Z}_6$. So the multirhythm periodic solution cannot appear by a generic Hopf bifurcation from a trivial equilibrium. Indeed, we found ours by constructing a succession of two Hopf bifurcations with certain properties.

5.3 Genericity Questions in Coupled Cell Systems

In this subsection we comment on genericity questions concerning bifurcations in coupled cell systems. A simple example is instructive. Consider the two cell system pictured in Figure 4.1. The general system of differential equations for this cell system is given in (4.6). At a group invariant equilibrium (x_1, x_1), the Jacobian of the system is given in block form by

$$\begin{bmatrix} f_{x_1} & f_{x_2} \\ f_{x_2} & f_{x_1} \end{bmatrix}.$$

The eigenvalues of this matrix are the eigenvalues of the matrices

$$f_{x_1} + f_{x_2} \quad \text{or} \quad f_{x_1} - f_{x_2}.$$

Critical eigenvalues of the first matrix lead to bifurcations that preserve symmetry (the trivial representation of $\mathbf{Z}_2$), while critical eigenvalues of the second matrix lead to symmetry-breaking bifurcations (the nontrivial representation of $\mathbf{Z}_2$). Note that when the internal dynamics of each cell is one-dimensional, the eigenvalues are real — so Hopf bifurcation is not possible. However, when the internal dynamics of each cell are at least two-dimensional the eigenvalues of each matrix can be chosen arbitrarily. Thus, to achieve generic behavior of coupled cells systems, we may need to consider higher dimensional internal dynamics than is suggested just by the phase space of the coupled cell system. After all, when the internal dynamics are one-dimensional, the phase space is two-dimensional and Hopf bifurcation might have been possible.

A second example is given by a bidirectional ring of four cells with just nearest neighbor coupling. This coupled cell system has $\mathbf{D}_4$ symmetry. Suppose that the internal dynamics is k-dimensional. The differential equation in the first cell is denoted by

$$\dot{x}_1 = f(x_1, x_2, x_4),$$

where $f(x, y, z) = f(x, z, y)$. The Jacobian of the full $4k$-dimensional system at a group invariant equilibrium — all coordinates equal — is:

$$L = \begin{bmatrix} A & B & 0 & B \\ B & A & B & 0 \\ 0 & B & A & B \\ B & 0 & B & A \end{bmatrix}$$

where $A = d_{x_1} f$ and $B = d_{x_2} f$.

The eigenvalues of this matrix are determined in [Golubitsky, Stewart, and Schaeffer, 1988, p. 396], and it follows that the eigenvalues of L are the union of the eigenvalues of

$$A + 2B \qquad A - 2B \qquad A \text{ (twice)}.$$

There are three irreducible representations of $\mathbf{D}_4$ that occur in the ring system phase space: trivial one-dimensional, a nontrivial one-dimensional, and the standard two-dimensional. Critical eigenvalues of the three matrices correspond to bifurcations corresponding to each of these irreducible representations. As in the simple example, Hopf bifurcation cannot occur unless $k \geq 2$. We ask the following question: Can a stable symmetry-breaking $\mathbf{D}_4$ Hopf bifurcation occur when the internal dynamics is two-dimensional? The answer is basically no. Such bifurcations occur when $\mathrm{tr}(A) = 0$. It follows that the traces of the other two matrices are $\pm 2\mathrm{tr}(B)$. If $\mathrm{tr}(B) \neq 0$, then one of these matrices has a positive eigenvalue, and a stable Hopf bifurcation is not possible. If we need to require that $\mathrm{tr}(B) = 0$, then we have this bifurcation occurring with stable periodic solutions only in codimension two. In these models generic Hopf bifurcations to stable solutions can occur either when $k \geq 3$ or when next nearest neighbor coupling is also allowed.

It is clear that the determination of generic bifurcation behavior in coupled cell systems depend to some extent on the dimension of the internal dynamics allowed in each cell and on the ways in which coupling is restricted in the cell system.

5.4 The Equivariant Moser-Weinstein Theorem

The basic 'local bifurcation' existence theorem for periodic orbits in Hamiltonian dynamics is the Liapunov Center Theorem. Suppose that $\mathcal{H}$ is a Hamiltonian on $P = \mathbf{R}^{2n}$ and let $p \in P$ be an equilibrium, so that $(\mathrm{d}\mathcal{H})_p = 0$. Assume that p is a *nondegenerate* minimum of $\mathcal{H}$, that is $(\mathrm{d}\mathcal{H})|_p = 0$ and $(\mathrm{d}^2\mathcal{H})|_p$ is positive definite. Let L be the linearization of the Hamiltonian vector field at p and let the eigenvalues of L be the purely imaginary pairs $\{\pm\lambda_1, \ldots, \pm\lambda_n\}$. Liapunov proved that if the linearized flow at an equilibrium has a simple purely imaginary eigenvalue and some λ_i is *non-resonant* then there exists a smooth 2-dimensional submanifold of P, which passes through p and intersects every energy level near p in a periodic orbit, such that the period of that orbit approaches $2\pi/|\lambda_i|$ for orbits near p. By 'non-resonant' we mean that λ_j is not an integer multiple of λ_i for $j \neq i$.

Weinstein [1973] proved that even when there is resonance, there must exist at least $\frac{1}{2}\dim V_\lambda$ families of periodic solutions on each energy level near p. The proof was simplified by Moser [1976], and the result has come to be known as the Weinstein-Moser Theorem. However, Weinstein-Moser Theorem fails to predict all periodic solutions near equilibrium in the equivariant case. For instance, in the Hénon-Heiles system (Hénon and Heiles [1964]) the Weinstein-Moser Theorem predicts at least two (families of) periodic solutions near equilibrium, but actually there are eight. Even taking the symmetry into account, there are three group orbits of periodic solutions. The Equivariant Weinstein-Moser Theorem remedies this difficulty by exploiting the symmetry of the Hamiltonian.

Recall that a symplectic vector space over $\mathbf{R}$ is a vector space V over $\mathbf{R}$ equipped with a symplectic form. A *symplectic action* of a group Γ on a symplectic vector space V is an action that leaves the symplectic form invariant. The theory of group representations can be extended to symplectic representations [Montaldi, Roberts, and Stewart, 1988]: in particular any symplectic representation of a compact Lie group is a direct sum of irreducible symplectic representations, and there exists a unique isotypic decomposition. Moreover, the symplectic irreducibles for compact Γ are precisely what [Golubitsky, Stewart, and Schaeffer, 1988] call Γ-simple representations. These arise generically in symmetric Hopf bifurcation of dissipative systems.

Suppose that a compact Lie group Γ acts symplectically on P, let $p \in P$ be a fixed point for Γ, and suppose that the Hamiltonian H is Γ-invariant. This symmetry may force some of the λ_i to be equal, creating unavoidable resonances.

Let $u(t)$ be a periodic orbit of the flow of H having period T. Let $\mathbf{S}^1$ be the circle group, identified with $\mathbf{R}/2\pi\mathbf{Z}$, and consider the usual action of $\Gamma \times \mathbf{S}^1$ on the *loop space* $\mathcal{C}^k(T)$ of k-times differentiable T-periodic functions, as in equivariant Hopf bifurcation. That is, $\Gamma \times \mathbf{S}^1$ acts on $u = u(t)$ by

$$(\gamma, \theta).u(t) = \gamma u(t + T\theta/2\pi).$$

Define the *symmetry group* of $u \in \mathcal{C}^k(T)$ to be

$$\Sigma_u = \{(\gamma, \theta) \in \Gamma \times \mathbf{S}^1 : \gamma u(t + T\theta/2\pi) = u(t)\}.$$

Recall that when P is a vector space over $\mathbf{R}$ and G acts linearly, $\mathrm{Fix}(\Sigma)$ is a linear subspace. Analogously, if P is a symplectic vector space over $\mathbf{R}$ and G acts linearly and symplectically, then $\mathrm{Fix}(\Sigma)$ is a symplectic linear subspace.

Let X be the vector field of H, let L be the linearization of X at p. Define the *linearized flow* to be the flow generated by the ODE

$$\dot{x} + Lx = 0$$

on the tangent space $V = \mathrm{T}_pP$ to P at p. Let λ be a non-zero purely imaginary eigenvalue of L and define the *resonance space* $V_\lambda \subset V$ to be the (real part of the) sum of the generalized eigenspaces of L for eigenvalues $k\lambda$, where $k \in \mathbf{Z}$. Assume the following conditions on H:

1. $(d^2H)_p$ is a nondegenerate quadratic form.

2. $(d^2H)_p|_{V_\lambda}$ is positive definite.

Condition (1) is equivalent to L being nonsingular, and (2) implies that $L|_{V_\lambda}$ is semisimple (diagonalizable over $\mathbf{C}$).

Clearly L is Γ-equivariant, so V_λ is invariant under the action of Γ. It is also invariant under the linearized flow. Because $L|_{V_\lambda}$ is semisimple, the orbits of the linearized flow are all periodic with period $2\pi/|\lambda|$ and hence define an action of $\mathbf{S}^1$ on V_λ. Explicitly,

$$\theta.v = \exp\left(\frac{\theta}{|\lambda|}L\right)v.$$

This action commutes with the action of Γ, so together they define a $\Gamma \times \mathbf{S}^1$-action on V_λ.

We may now state:

Theorem 1 (Equivariant Weinstein-Moser Theorem) *Suppose that the Hamiltonian H satisfies* (1) *and* (2). *Then for every isotropy subgroup Σ of the $\Gamma \times \mathbf{S}^1$-action on V_λ, and for all sufficiently small ϵ, there exist at least $\frac{1}{2}\dim \mathrm{Fix}(\Sigma)$ periodic orbits of X with periods near $2\pi/|\lambda|$ and symmetry group containing Σ, on the energy surface $H(x) = H(p) + \epsilon^2$.*

For a proof see [Montaldi, Roberts, and Stewart, 1988]. A rather different approach to an equivariant Liapunov Center Theorem, using the 'constrained Liapunov-Schmidt procedure', can be found in [Golubitsky, Marsden, Stewart, and Dellnitz, 1995].

Because of the symplectic structure, $\dim \mathrm{Fix}(\Sigma)$ is always even. In practice — though it is more a rule of thumb than a provable theorem — the 'primary' isotropy subgroups Σ are those for which $\dim \mathrm{Fix}(\Sigma)$ is small. The most important isotropy subgroups, and the most tractable, of all are those for which $\dim \mathrm{Fix}(\Sigma)$ attains its minimum value, namely 2. These are what we have called $\mathbf{C}$-axial subgroups. So the Equivariant Weinstein-Moser theorem implies that under the usual hypotheses if Σ is $\mathbf{C}$-axial then there exists at least one family of periodic solutions with isotropy group *equal* to Σ.

The group theory involved in the $\Gamma \times \mathbf{S}^1$-action is identical to the action occurring in equivariant Hopf bifurcation. This is a consequence of the loop space technique employed in both contexts and the classification of symplectic irreducibles. We can use this relationship to import results from equivariant Hopf bifurcation into Hamiltonian dynamics. In particular, we can use the existing analysis of $\mathbf{D}_n$ Hopf bifurcation ([Golubitsky, Stewart, and Schaeffer, 1988], Golubitsky and Stewart, 1986]) to prove the existence of certain periodic solutions in Hamiltonian systems with $\mathbf{D}_n$ symmetry, such as the coupled pendulum system.

5.4.1 Coupled Pendula Revisited

In this subsection we apply the Equivariant Weinstein-Moser Theorem to the Hamiltonian system (4.11). The linearization of (4.11) is

$$L = \begin{bmatrix} 0 & I \\ M & 0 \end{bmatrix}$$

where I is the $N \times N$ identity matrix and M is the circulant matrix

$$M = \begin{bmatrix} -(1+2\alpha) & \alpha & 0 & \dots & 0 & \alpha \\ \alpha & -(1+2\alpha) & \alpha & 0 & \dots & 0 \\ 0 & \alpha & -(1+2\alpha) & \alpha & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \alpha & 0 & \dots & 0 & \alpha & -(1+2\alpha) \end{bmatrix}$$

First, we derive the eigenvectors and eigenvalues of L. Let $\omega = e^{2\pi i/N}$ and define

$$v_k = [1, \omega^k, \omega^{2k}, \dots, \omega^{(N-1)k}]^T$$

where $0 \leq k \leq N-1$. Let

$$\nu_k = \sqrt{\left| 2\alpha \left(\cos \frac{2\pi k}{N} - 1 \right) - 1 \right|}$$

and define $u_k^{\pm} = [v_k, \pm i\nu_k v_k]^T$. An easy calculation shows that the $u_k^{\pm}$ are eigenvectors of L with eigenvalues $\lambda_k^{\pm} = \pm i\nu_k$. The $\lambda_k^{\pm}$ are purely imaginary since $\mu_k < 0$. Generically (in α) these eigenvalues are non-resonant, and we henceforth assume that α has been chosen to avoid resonances.

The linearized flow on $\mathbf{R}^{2N}$ possesses periodic solutions corresponding to initial conditions $\mathrm{Re}(u_k^{\pm})$. The corresponding solutions take the form

$$\begin{aligned} q_j(t) &= \cos\left(\pm\nu_k t + \frac{2\pi j}{N} \right) \\ p_j(t) &= \pm\nu_k \sin\left(\pm\nu_k t + \frac{2\pi jk}{N} \right) \end{aligned}$$

which are discrete rotating waves of period $\frac{2\pi}{\nu_k}$ such that successive pendula are phase-shifted by $\frac{2\pi k}{N}$.

The general solution of the linearized equation is a superposition of such discrete rotating waves. When nonlinear terms are restored, some of these solutions persist as periodic solutions of the nonlinear equations— for example, the synchronous solutions ($k = 0$). The question is: which? The Equivariant Weinstein-Moser Theorem of [Montaldi, Roberts, and Stewart, 1987], stated in §5.4, provides a partial answer to this question, as we now describe.

First, we recall some useful results from representation theory. Assume that $\mathbf{D}_n = \langle\sigma, \rho\rangle$ where $\sigma^n = 1, \rho^2 = 1, \rho^{-1}\sigma\rho = \sigma^{-1}$. With two exceptions (when n is even) the irreducible representations of $\mathbf{D}_n$ over $\mathbf{R}$ are $\xi_0, \xi_1, \ldots, \xi_{[n/2]}$, defined as follows. ξ_0 is the trivial representation on $\mathbf{R}$. When n is even, $\xi_{n/2}$ is the representation on $\mathbf{R}$ in which σ acts trivially and ρ acts as -1. In all other cases, ξ_k is the representation on $\mathbf{R}^2 \equiv \mathbf{C}$ in which σ acts as multiplication by $\omega^k = e^{2\pi k/n}$ and ρ acts by complex conjugation $z \mapsto \overline{z}$. The exceptional cases when n is even arise because then $\mathbf{D}_n/\mathbf{Z}_n \cong \mathbf{D}_2$ which has four 1-dimensional irreducibles, which pull back to $\mathbf{D}_n$. Two of these give rise to $\xi_0, \xi_{n/2}$, but there are two others. All of these representations are absolutely irreducible.

The space $\mathbf{R}^N = \{q\}$ decomposes into Γ-irreducibles according to

$$\mathbf{R}^N = Q_0 \oplus \ldots \oplus Q_{[N/2]}$$

where the action of $\mathbf{D}_N$ on Q_k is isomorphic to ξ_k and the action of τ is by -1. Similarly $\mathbf{R}^N = \{p\}$ decomposes into Γ-irreducibles according to

$$\mathbf{R}^N = P_0 \oplus \ldots \oplus P_{[N/2]}$$

where the action of $\mathbf{D}_N$ on P_k is isomorphic to ξ_k and the action of τ is by -1. The symplectic Γ-irreducible components of R^{2N} are $Q_k \oplus P_k$ with actions $\xi_k \oplus \xi_k$. Moreover, these are the symplectic isotypic components. The action of τ on each component is by -1. The action of $\mathbf{S}^1$ can be written in the form

$$q + ip \mapsto e^{i\theta}(q + ip)$$

Therefore $\pi \in \mathbf{S}^1$ also acts by -1, so $(1, \tau, \pi) \in \mathbf{D}_N \times \mathbf{Z}_2 \times \mathbf{S}^1$ acts trivially. There is a homomorphism $\mathbf{D}_N \times \mathbf{Z}_2 \times \mathbf{S}^1 \to \mathbf{D}_N \times \mathbf{S}^1$ defined by

$$\begin{aligned} (\delta, 1, \theta) &\mapsto (\delta, \theta) \\ (\delta, \tau, \theta) &\mapsto (\delta, \theta + \pi) \end{aligned}$$

and the action factors through this homomorphism. So in effect we have a $\mathbf{D}_N \times \mathbf{S}^1$-action, modulo $K = \langle(1, \tau, \pi)\rangle$. In particular, the isotropy subgroups are generated by isotropy subgroups of the $\mathbf{D}_N \times \mathbf{S}^1$-action together with K. Physically, K represents the usual 'internal' symmetry of a simple pendulum: all periodic oscillations are invariant under reflection together with a half-period phase shift.

The problem therefore reduces to finding isotropy subgroups (more specifically, $\mathbf{C}$-axial subgroups) of $\mathbf{D}_N \times \mathbf{S}^1$ acting by ξ_k. To do this we use the results of [Golubitsky and Stewart, 1986], recorded in [Golubitsky, Stewart, and Schaeffer, 1988]. These apply to the *standard* action of $\mathbf{D}_N \times \mathbf{S}^1$. Here $\mathbf{D}_N$ acts as the direct sum of two copies of ξ_1. The representations with ξ_k in place of ξ_1 can be reduced to the standard case by use of the homomorphism $\alpha_k : \mathbf{D}_n \times \mathbf{S}^1 \to \mathbf{D}_n \times \mathbf{S}^1$ sending $\sigma \mapsto \sigma^k$: we omit the details of this reduction.

We next describe how to interpret the symmetries of the solutions given by the standard action. Denote the state of pendulum j at time t by $u_j(t)$, and let T be the overall period of the system of pendula. Then the standard representation leads to three conjugacy classes of $\mathbf{C}$-axial subgroups, whose interpretation is shown in Table 5.4.1.

Isotropy	Waveform Relationships
$N \equiv \pm 1 \pmod 4$	
$\tilde{\mathbf{Z}}_N$	$u_j(t) = u_0\left(t + \frac{jT}{N}\right)$
$\mathbf{Z}_2^\rho$	$u_j(t) = u_{-j}(t) \quad j \neq 0$
$\mathbf{Z}_2^{(\rho,\pi)}$	$u_j(t) = u_{-j}\left(t + \frac{T}{2}\right) \quad u_0(t)$ twice frequency
$N \equiv 2 \pmod 4$	
$\tilde{\mathbf{Z}}_N$	$u_j(t) = u_0\left(t + \frac{jT}{N}\right)$
$\mathbf{Z}_2^\rho \oplus \mathbf{Z}_2^c$	$u_j(t) = u_{-j}(t) = u_{N/2+j}\left(t + \frac{T}{2}\right)$ $= u_{N/2-j}\left(t + \frac{T}{2}\right) \quad 1 \leq j < \frac{N}{4} - 1$ $u_0(t) = u_{N/2}\left(t + \frac{T}{2}\right)$
$\mathbf{Z}_2^{(\rho,\pi)} \oplus \mathbf{Z}_2^c$	$u_j(t) = u_{-j}\left(t + \frac{T}{2}\right) = u_{N/2+j}\left(t + \frac{T}{2}\right)$ $= u_{N/2-j}(t) \quad 1 \leq j < \frac{N}{4} - 1$ $u_0(t) = u_{N/2}(t)$ twice frequency
$N \equiv 0 \pmod 4$	
$\tilde{\mathbf{Z}}_N$	$u_j(t) = u_0\left(t + \frac{jT}{N}\right)$
$\mathbf{Z}_2^\rho \oplus \mathbf{Z}_2^c$	$u_j(t) = u_{-j}(t) = u_{N/2+j}\left(t + \frac{T}{2}\right)$ $= u_{N/2-j}\left(t + \frac{T}{2}\right) \quad 1 \leq j < \frac{N}{4} - 1$ $u_0(t) = u_{N/2}\left(t + \frac{T}{2}\right)$ $u_{N/4}(t) = u_{-N/4}(t)$ twice frequency
$\mathbf{Z}_2^{\rho\sigma} \oplus \mathbf{Z}_2^c$	$u_j(t) = u_{1-j}(t) = u_{N/2+j}\left(t + \frac{T}{2}\right)$ $= u_{N/2+1-j}(t + \frac{T}{2}) \quad 0 \leq j \leq \frac{N}{4} - 1$

Table 5.3: Oscillatory wave patterns in $\mathbf{D}_N$-symmetric systems.

For illustrative purposes we show the 17 distinct (conjugacy classes of) **C**-axial solutions when $N = 12$, including the solutions arising from nonstandard actions. See Table 5.4.1. Here A, B, C, D are waveforms, $A + p$ indicates waveform A with a phase shift of $\frac{p}{12}$ of the overall period, a prime indicates a phase shift of half a period, and an asterisk indicates that the pendulum oscillates with twice the overall frequency of the system. Each of A, B, C, D must also have an 'internal' (τ, π) symmetry.

k	0	1	2	3	4	5	6	7	8	9	10	11
0	A	A	A	A	A	A	A	A	A	A	A	A
1	A	$A+1$	$A+2$	$A+3$	$A+4$	$A+5$	$A+6$	$A+7$	$A+8$	$A+9$	$A+10$	$A+11$
	A	B	C	D^*	C'	B'	A'	B'	C'	D^*	C	B
	A	B	C	C'	B'	A'	A'	B'	C'	C	B	A
2	A	$A+2$	$A+4$	$A+6$	$A+8$	$A+10$	A	$A+2$	$A+4$	$A+6$	$A+8$	$A+10$
	A	B	B'	A'	B'	B	A	B	B'	A'	B'	B
	A^*	B	B	A^*	B'	B'	A^*	B	B	A^*	B'	B'
3	A	$A+3$	$A+6$	$A+9$	A	$A+3$	$A+6$	$A+9$	A	$A+3$	$A+6$	$A+9$
	A	B^*	A'	B^*	A	B^*	A'	B^*	A	B^*	A'	B^*
	A^*	B	A^*	B'	A^*	B	A^*	B'	A^*	B	A^*	B'
4	A	$A+4$	$A+8$	A	$A+4$	$A+8$	A	$A+4$	$A+8$	A	$A+4$	$A+8$
	A	B	B	A	B	B	A	B	B	A	B	B
	A^*	B	B'	A^*	B	B'	A^*	B	B'	A^*	B	B'
5	A	$A+5$	$A+10$	$A+3$	$A+8$	$A+1$	$A+6$	$A+11$	$A+4$	$A+9$	$A+2$	$A+7$
	A	B	C	D^*	C'	B'	A'	B'	C'	D^*	C	B
	A	A'	B	C	C	B	A'	A	B'	C'	C'	B'
6	A	A'	A	A'	A	A'	A	A'	A	A'	A	A'

Table 5.4: The 17 **C**-axial solutions for a ring of 12 pendula.

As well as existence, we can ask about the linearized stabilities of these solutions. Methods for computing stability, based on Birkhoff normal form, can be found in [Montaldi, Roberts, and Stewart, 1990].

6 The Coupling Decomposition

Consider a cell system on N nodes, with symmetry group $\Gamma \subset \mathbf{S}_N$, where node i has phase space $P_i = \mathbf{R}^{k_i}$. The cell system dynamics is determined by a general Γ-equivariant vector field F on $P = P_1 \times \cdots \times P_N$. However, in interpretations of such models in applications, it is useful to consider specific 'terms' in the vector field as representing internal dynamics of one component cell, coupling between two specified cells, multi-cell couplings, and so on. Moreover, we may wish to determine whether such terms are linear or absent entirely (the cells are not coupled); and whether the structure of the system is Hamiltonian.

In order to give such terminology a precise basis, we develop a decomposition of F into vector fields that correspond to various forms of coupling. Refinements of this decomposition can also be introduced, but here we develop only the main idea. One aim of this decomposition is to provide a rigorous definition of 'point-to-point' coupling. See Definition 4.

As motivation, let $N = 3$, all $k_i = 1$, and define F by

$$F(x_1, x_2, x_3) = \begin{bmatrix} 2 + 3x_1^2 + 4x_1x_2 + 5x_2x_3^7 + 6x_1x_2^2x_3 \\ x_3 + 4x_1x_3^2 + x_1x_2x_3 - 2x_1x_2^2x_3^3 \\ 9 + x_1 - x_2 + 3x_3 + x_1^2 + x_2^2 + x_1x_3 + x_2x_3 - 11x_1^3x_2^3x_3 \end{bmatrix}$$

Given this explicit formula, we can decompose F directly into terms that depend on 0, 1, 2, or 3 of the variables:

$$F = \Phi_0 + \Phi_1 + \Phi_2 + \Phi_3$$

where

$$\begin{aligned}
\Phi_0(x_1, x_2, x_3) &= \begin{bmatrix} 2 \\ 0 \\ 9 \end{bmatrix} \\
\Phi_1(x_1, x_2, x_3) &= \begin{bmatrix} 3x_1^2 \\ x_3 \\ x_1 - x_2 + 3x_3 + x_1^2 + x_2^2 \end{bmatrix} \\
\Phi_2(x_1, x_2, x_3) &= \begin{bmatrix} 4x_1x_2 + 5x_2x_3^7 \\ 4x_1x_3^2 \\ x_1x_3 + x_2x_3 \end{bmatrix} \\
\Phi_3(x_1, x_2, x_3) &= \begin{bmatrix} 6x_1x_2^2x_3 \\ x_1x_2x_3 - 2x_1x_2^2x_3^3 \\ -11x_1^3x_2^3x_3 \end{bmatrix}
\end{aligned}$$

More importantly, we can obtain the same result with a more abstractly defined decomposition, as follows. Let $\mathcal{N} = \{1, \ldots, N\}$. For each $i \in \mathcal{N}$ choose a *base point* $b_i \in P_i$. In this paper we assume for simplicity that each P_i is a vector space and we let $b_i = 0$. When the P_i are manifolds technical issues concerning uniqueness arise, which we prefer to ignore here. For each subset $\mathcal{S} \subset \mathcal{N}$ define

$$F_{\mathcal{S}}(x) = F(y)$$

where

$$y_i = \begin{cases} x_i & \text{if } i \in \mathcal{S} \\ 0 & \text{if } i \notin \mathcal{S} \end{cases}$$

Then define the $\mathcal{S}$*-coupled part* of F to be

$$\Phi_{\mathcal{S}} = \sum_{\mathcal{T} \subset \mathcal{S}} (-1)^{|\mathcal{S} \setminus \mathcal{T}|} F_{\mathcal{T}},$$

where $\mathcal{S} \setminus \mathcal{T}$ is the set consisting of elements in $\mathcal{S}$ that are not in $\mathcal{T}$. Finally, define

$$\Phi_k = \sum_{\mathcal{S} \subset \mathcal{N},\ |\mathcal{S}|=k} \Phi_{\mathcal{S}}$$

We claim that F is the sum of the Φ_k, and that these components can sensibly be interpreted as the *k-node coupling terms*. First, we need to recall a standard result from combinatorics:

Lemma 2 *Let $\mathcal{Y}$ be a finite set. Then*

$$\sum_{\mathcal{X} \subset \mathcal{Y}} (-1)^{|\mathcal{X}|} = \begin{cases} 1 & \text{if } \mathcal{Y} = \emptyset \\ 0 & \text{if } \mathcal{Y} \neq \emptyset \end{cases}$$

Proof: Let $|\mathcal{Y}| = m$. If $m = 0$ the result is clear. Otherwise let $t_1, \ldots, t_m$ be indeterminates. Consider the identity

$$(1 + t_1) \cdots (1 + t_m) = \sum_{\mathcal{X} \subset \mathcal{Y}} \prod_{i \in \mathcal{X}} t_i$$

Now substitute $t_i = -1$ for all i.

Proposition 3 *With the above notation:*

1. $F = \Phi_0 + \cdots + \Phi_N$
2. *Suppose that $\mathcal{T} \subset \mathcal{N}$ and $|\mathcal{T}| = k > 0$. Then $\frac{\partial}{\partial x_i} \Phi_{\mathcal{T}} = 0$ for all $i \notin \mathcal{T}$.*
3. *Each Φ_k is Γ-equivariant.*

Proof: To prove the first statement, observe that

$$\begin{aligned} \Phi_0 + \cdots + \Phi_N &= \sum_{k=0}^{N} \sum_{|\mathcal{S}|=k} \sum_{\mathcal{T} \subset \mathcal{S}} (-1)^{|\mathcal{S} \setminus \mathcal{T}|} F_{\mathcal{T}} \\ &= \sum_{\mathcal{S}} \sum_{\mathcal{T} \subset \mathcal{S}} (-1)^{|\mathcal{S} \setminus \mathcal{T}|} F_{\mathcal{T}} \end{aligned}$$

The coefficient of $F_{\mathcal{T}}$ is

$$\sum_{\mathcal{S} \supseteq \mathcal{T}} (-1)^{|\mathcal{S} \setminus \mathcal{T}|} = \sum_{\mathcal{U}} (-1)^{|\mathcal{U}|}$$

where $\mathcal{U} = \mathcal{N} \setminus \mathcal{T}$. By Lemma 2 this coefficient is 0 unless $\mathcal{U} = \emptyset$, that is, unless $\mathcal{T} = \mathcal{N}$. Hence

$$\Phi_0 + \cdots + \Phi_N = F_{\mathcal{N}} = F$$

as claimed.

The second statement follows immediately from the definition of $\Phi_{\mathcal{S}}$. The third statement follows since Γ permutes the cells, F is Γ-equivariant, and Φ_k is defined as a sum over all subsets $\mathcal{S} \subset \mathcal{N}$ that contain k elements.

Definition 4 The cell system F has *point-to-point* coupling if $\Phi_k = 0$ for all $k \geq 3$. More generally, the *coupling degree* of F is the largest k for which $\Phi_k \neq 0$.

There is a Hamiltonian analogue of all this: decompose the Hamiltonian in the same way. The decomposition of the Hamiltonian induces the above decomposition on the Hamiltonian vector field.

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