

SYMMETRY AND PATTERN FORMATION IN COUPLED CELL NETWORKS

MARTIN GOLUBITSKY* AND IAN STEWART†

Abstract. We describe some basic concepts and techniques from symmetric bifurcation theory in the context of coupled systems of cells ('oscillator networks'). These include criteria for the existence of symmetry-breaking branches of steady and periodic states. We emphasize the role of symmetry as a general framework for such analyses. As well as overt symmetries of the network we discuss internal symmetries of the cells, 'hidden' symmetries related to Neumann boundary conditions, and spatio-temporal symmetries of periodic states. The methods are applied to a model central pattern generator for legged animal locomotion.

1. Introduction. The bifurcation theory of nonlinear dynamical systems with symmetry has grown extensively in recent years, and its impact has been felt in a variety of fields of applied science. In this survey we describe the role of symmetry and symmetry *breaking* in the context of networks of coupled *cells*, a useful halfway house between ODEs, whose structure is in essence purely temporal, and PDEs, which also possess spatial structure. Here a cell is a unit described by a system of ODEs. Many authors talk of coupled 'oscillators', but we prefer the neutral term 'cell' since the units can display many different kinds of dynamics, and even when the coupled network can oscillate periodically, the individual members may not be able to oscillate in isolation, see Smale [46]. For example, as an extreme case, the individual cells might have one-dimensional dynamics, so that they cannot oscillate as isolated individuals, but the coupled system might have oscillatory states.

A coupled cell network has discrete spatial structure but continuous temporal structure, and can be modelled as a structured system of ODEs. Our aim here is to interpret the theory of symmetry-breaking bifurcations in the context of coupled cell networks. We shall focus on the classical areas of steady-state and Hopf bifurcation, which deal with equilibria and periodic states. Our aim is to demonstrate how the explicit use of symmetry helps to organize the dynamics and the patterns of such networks. We avoid technicalities whenever possible, including proofs, and refer the reader to the literature for missing details. Applications to animal locomotion are included.

2. Coupled cells and ODEs. By a *cell* we just mean a system of ODEs defined on a Euclidean space. Interesting dynamical phenomena occur when cells are *coupled* by interactions between their state variables.

* Mathematics Department, University of Houston, Houston, TX 77204-3476, USA.

† Mathematics Institute, University of Warwick, Coventry CV4 7AL, UK.

A system of ODEs

$$(2.1) \quad \frac{dx}{dt} = F(x)$$

is a *system of identical coupled cells* if $x = (x_1, \dots, x_N)$ and

$$(2.2) \quad \frac{dx_j}{dt} = f(x_j) + h_j(x).$$

Here $x_j \in \mathbb{R}^k$, f governs the internal dynamics of the each cell, and h_j governs the coupling between cells. We call the h_j the *coupling terms*. Throughout all vector fields are assumed to be smooth (C^∞).

As in figures 1 and 2, we can represent the general structure of a coupled cell network by a graph on N nodes (one for each cell) by connecting cell i to cell j if h_j depends explicitly on x_i . To refine this schematic description we can use 'decorated' arrows to distinguish the different types of coupling term. (For example, the arrows may be drawn with light or bold lines, double or triple lines, fancy arrowheads, and so on.) It is this image that we have in mind when we speak of a 'network' of coupled cells.

EXAMPLE 2.1. Figure 1(a) shows a ring of N identical cells with unidirectional coupling, in the case $N = 4$. Here the governing equations are, say,

$$(2.3) \quad \frac{dx_j}{dt} = f(x_j) + h(x_{j-1}),$$

where indices j are taken modulo N .

EXAMPLE 2.2. Figure 1(b) shows N identical cells coupled in a bidirectional ring, again for $N = 4$. Here the governing equations are, say,

$$(2.4) \quad \frac{dx_j}{dt} = f(x_j) + h(x_{j-1}, x_{j+1}),$$

where indices j are taken modulo N and $h(u, v) = h(v, u)$. Note that the same coupling function h occurs for each cell, so the cells are identically coupled, or more properly symmetrically coupled.

EXAMPLE 2.3. Figure 2 shows two coupled rings of four identical cells with unidirectional coupling. Here the governing equations are, say for cells C_3 and C_4 ,

$$(2.5) \quad \frac{dx_3}{dt} = f(x_3) + h(x_1) + g(x_4) \quad \text{and} \quad \frac{dx_4}{dt} = f(x_4) + h(x_2) + g(x_3),$$

with similar equations for the other cells. This cell system may be used as a model for quadrupedal gaits; see section 4. Note that there are two types of coupling — the coupling around the rings and the coupling connecting the rings.



FIG. 1. Rings with four cells: (a) unidirectional and (b) bidirectional.

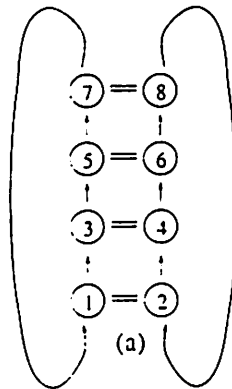


FIG. 2. Eight cell network used in animal gait model.

Many aspects of pattern formation in coupled cell systems are consequences of the symmetries of the system, and a systematic approach to pattern formation can be based upon explicit recognition and exploitation of the role of symmetry.

Several different types of symmetry can arise in coupled cell systems. Mathematically, all of these symmetries can be described within the same abstract framework, but they have distinct physical interpretations. In this survey we focus on three types of symmetry: Network symmetries, internal cell symmetries, and temporal phase-shift symmetries.

Network symmetries. These are permutations of the cells that preserve couplings — that is, automorphisms of the corresponding decorated graph. Specifically, a permutation σ of $\{1, \dots, N\}$ acts on the phase space $x = (x_1, \dots, x_N)$ by

$$\sigma x = (x_{\sigma^{-1}(1)}, \dots, x_{\sigma^{-1}(N)}).$$

The permutation σ is a *network symmetry* for (2.1) when

$$F(\sigma x) = \sigma F(x).$$

Since the cells are assumed identical, a permutation σ is a network symmetry if the coupling is symmetric, that is, in (2.2),

$$h_j(\sigma x) = h_{\sigma(j)}(x).$$

In other words, σ preserves the decoration of arrows in the graph. The *global* symmetry group \mathcal{G} is defined to consist of all network symmetries, and is a finite permutation group. For example, the global symmetry group in example 2.1 is \mathbf{Z}_N , the global symmetry group in example 2.2 is \mathbf{D}_N , and the global symmetry group in example 2.3 is $\mathbf{Z}_4 \times \mathbf{Z}_2$. Visually, a network symmetry permutes the cells while preserving the arrows.

Internal symmetries. An internal symmetry of cell C_j is an orthogonal matrix $\delta \in \mathbf{O}(\mathbf{R}^k)$ which satisfies

$$f(\delta x_j) = \delta f(x_j).$$

The group of all internal symmetries \mathcal{L} is called the *local* symmetry group. Whether local symmetries are symmetries of the coupled cell system depends on the type of coupling, as we discuss in §7.

Phase-shift symmetries. Suppose that $x(t)$ is a T -periodic solution and that γ is a symmetry of the cell system. Then $\gamma x(t)$ is also a periodic solution. If the sets $\{x(t)\}$ and $\{\gamma x(t)\}$ are identical, then uniqueness of solutions implies that there exists θ such that

$$\gamma x(t) = x(t + \theta),$$

and (γ, θ) is a *spatio-temporal* symmetry, with θ being the *phase-shift* symmetry.

3. Symmetric bifurcation theory. The general context for a symmetry-based analysis of pattern formation in coupled cell networks is symmetric (or equivariant) bifurcation theory. This is surveyed in Golubitsky *et al.* [32]. We briefly summarize the main ideas and state the simplest existence theorems. Bifurcations provide two of the simplest mechanisms for pattern formation: local steady-state and Hopf bifurcation. These lead, respectively, to the creation of equilibrium patterns and to time-periodic patterns, in both cases starting from a trivial 'homogeneous' or patternless state.

3.1. General strategy. Let Γ be a Lie group of linear transformations of \mathbf{R}^n . We say that f is Γ -equivariant if

$$(3.1) \quad f(\gamma x, \lambda) = \gamma f(x, \lambda)$$

for all $\gamma \in \Gamma$. Consider a Γ -equivariant ODE

$$(3.2) \quad \frac{dx}{dt} + f(x, \lambda) = 0$$

where $x \in \mathbb{R}^n$, $\lambda \in \mathbb{R}$. For simplicity, assume that $f(0, \lambda) \equiv 0$, so there exists a 'trivial branch' of solutions $x = 0$. The *linearization* of f is

$$L_\lambda = D_x f|_{0, \lambda}.$$

Local bifurcation at $\lambda = 0$ occurs when the trivial branch undergoes a change of linear stability, so that L_0 has eigenvalues on the imaginary axis (often called *critical eigenvalues*). There are two cases:

- Steady-state bifurcation: L_0 has a zero eigenvalue.
- Hopf bifurcation: L_0 has a complex conjugate pair of eigenvalues $\pm i\omega$.

To study such bifurcations, we look at the *critical eigenspace*: the real generalized eigenspace E for the critical eigenvalues. This is the kernel of $(L_0 + \omega^2 I)^n$, taking $\omega = 0$ in the steady-state case. By equivariance, E is a Γ -invariant subspace of \mathbb{R}^n .

1. Determine the generic possibilities for the action of Γ on E .
By 'generic' we mean 'unable to be destroyed by a small perturbation of f '.
 - For steady-state bifurcation, generically E is absolutely irreducible.
 - For Hopf bifurcation, generically E is Γ -simple. That is, either $E \cong X \oplus X$ where X is absolutely irreducible, or E is non-absolutely irreducible.
2. Use Liapunov-Schmidt or center manifold reduction to reduce the problem to one posed on the E . With sensible choices in the reduction procedure, the reduced problem is Γ -equivariant. See Golubitsky *et al.* [32].
3. In Hopf bifurcation, recognize the existence of an extra symmetry in the reduced problem, given by an action of the circle group. The reduced problem becomes $\Gamma \times S^1$ -equivariant.
4. Apply the equivariant branching lemma and the Equivariant Hopf theorem to show existence of symmetry-breaking solutions.
5. Study the stability of bifurcating solutions.

3.2. Basic existence theorems. Suppose that Γ acts on \mathbb{R}^n . If $x \in \mathbb{R}^n$, then the *orbit* of x under Γ is

$$\Gamma x = \{\gamma x : \gamma \in \Gamma\}.$$

If $f : V \rightarrow V$ is Γ -equivariant, then the zero-set of f is a union of Γ -orbits, for if $f(x) = 0$ then $f(\gamma x) = \gamma f(x) = \gamma 0 = 0$. It is convenient to consider solutions in the same Γ -orbit as being 'the same solution' up to symmetry.

The *isotropy subgroup* of $x \in V$ is

$$\Sigma_x = \{\sigma \in \Gamma : \sigma x = x\}.$$

Isotropy subgroups of points on the same orbit are conjugate. Indeed $\Sigma_{\gamma x} = \gamma \Sigma_x \gamma^{-1}$. We therefore tend not to distinguish between isotropy subgroups

and their conjugates. The *isotropy lattice* is the partially ordered set formed by all conjugacy classes of isotropy subgroups, with ordering induced by inclusion. It is a finite partially ordered set but, despite its name, it is not always a lattice in the strict algebraic sense.

If $H \subset \Gamma$ is any subgroup, we define the *fixed-point subspace*

$$\text{Fix}(H) = \{x \in V : \gamma x = x \ \forall \gamma \in H\}.$$

We have $\text{Fix}(\gamma H \gamma^{-1}) = \gamma \text{Fix}(H)$. A crucial feature of fixed-point subspaces is that they are dynamically invariant:

PROPOSITION 3.1. *If f is Γ -equivariant and $H \subset \Gamma$ then f leaves $\text{Fix}(H)$ invariant.*

Proof. Let $\gamma \in H$, $x \in \text{Fix}(H)$. Then $\gamma f(x) = f(\gamma x) = f(x)$ so $f(x) \in \text{Fix}(H)$. \square

Despite its trivial proof, the above fact is very useful. For suppose we are seeking a branch of solutions to a Γ -equivariant bifurcation problem $f(x, \lambda) = 0$, breaking symmetry to H . Then $x \in \text{Fix}(H)$, and it suffices to solve $f|_{\text{Fix}(H)} = 0$.

3.3. The equivariant branching lemma. An *axial* subgroup is an isotropy subgroup Σ for which $\dim \text{Fix}(\Sigma) = 1$. For such isotropy subgroups we have the following basic existence theorem of Vanderbauwhede [48] and Cicogna [7]:

THEOREM 3.2. (equivariant branching lemma). *Let $f(x, \lambda) = 0$ be a Γ -equivariant bifurcation problem where $\text{Fix}(\Gamma) = 0$. Let Σ be an axial subgroup. Then generically there exists a branch of solutions to $f(x, \lambda) = 0$ emanating from the origin with symmetry group Σ .*

3.4. The equivariant Hopf theorem. The situation for Hopf bifurcation is closely analogous to that for static bifurcation, but with the symmetry group Γ replaced by $\Gamma \times S^1$. The main hypothesis of the classical Hopf bifurcation theorem is that $Df|_{0,0}$ should have a pair of purely imaginary eigenvalues. In the equivariant case we may assume generically that the entire imaginary eigenspace is Γ -simple. By reduction methods, we can further assume, without loss of generality, that \mathbb{R}^n itself is Γ -simple. From now on we work in this context. We also scale time so that the imaginary eigenvalues are $\pm i$, and the period of oscillations is therefore near 2π .

The analogue for Hopf bifurcation of an axial subgroup is a *C-axial* subgroup, which is a subgroup of $\Gamma \times S^1$ acting on \mathbb{R}^n for which $\dim \text{Fix}(\Sigma) = 2$.

Unless a periodic state has nontrivial temporal symmetry, which means that its period is an integer divisor of the assumed period, its isotropy subgroup meets S^1 trivially. This implies that it must be a *twisted subgroup*, that is, a subgroup of the form

$$H^\rho = \{(h, \phi(h)) : h \in H\}$$

where H is a subgroup of Γ and $\phi : H \rightarrow S^1$ is a group homomorphism. The image of ϕ is either trivial, a nontrivial finite cyclic group, or the whole of S^1 . In these cases we say that the solution is, respectively, *purely spatial*, a *discrete rotating wave*, and a *rotating wave*. The rotating wave case cannot occur for finite Γ , hence cannot arise for network symmetries, but it may occur for internal symmetries of individual cells if the internal symmetry group is continuous.

THEOREM 3.3. (equivariant Hopf theorem [28]). *With the above notation, let Σ be a C -axial subgroup of $\Gamma \times S^1$. Then generically there exists a branch of periodic solutions to $\frac{dx}{dt} = f(x, \lambda)$, emanating from the origin, with spatio-temporal symmetry group Σ .*

Note that when *interpreting* the symmetries Σ for a given solution, we think of the S^1 -action as phase shift; but when *calculating* the dimension of the fixed-point subspace $\text{Fix}(\Sigma)$ we think of it as the action by $e^{-L\theta}$.

3.5. Unidirectional and bidirectional rings. As a warm-up problem, we apply the Equivariant branching lemma and the equivariant Hopf theorem to rings of four cells. There are two standard cases: unidirectional coupling and bidirectional coupling (figure 1). Everything that we describe here extends, with minor modifications, to rings with N cells, for all finite N .

Consider first the unidirectional case, and for simplicity assume that the internal dynamic of each cell is 1-dimensional, $k = 1$. (In fact by Liapunov-Schmidt reduction, general k reduces to this case.) The symmetry group is $Z_4 = \langle \rho \rangle$ acting on $\mathbb{R}^N = \mathbb{R}^4$, where $\rho x_j = x_{j+1}$, with subscripts taken mod 4 as usual. This action decomposes into three irreducible representations:

$$\mathbb{R}^4 = W_0 \oplus W_1 \oplus W_2$$

where W_0 is spanned by $[1, 1, 1, 1]$, W_1 is spanned by $[1, -1, 1, -1]$, and W_2 is spanned by $[1, 0, -1, 0]$ and $[0, 1, 0, -1]$. Of these, W_2 is non-absolutely irreducible (it is isomorphic to the standard action of Z_2 on $\mathbb{C} \equiv \mathbb{R}^2$ in which ρ acts as multiplication by i). Therefore W_2 does not occur as a critical eigenspace in generic steady-state bifurcation. The components W_0, W_1 are absolutely irreducible. Since the dimensions of these spaces are both 1, the equivariant branching lemma applies in both cases. For W_0 , the corresponding axial subgroup is the whole of Z_4 since the action is trivial, and on the bifurcating branch all four cells have identical states. For W_1 , however, the axial subgroup is $Z_2 = \langle \rho^2 \rangle$, so the states of cells are unchanged by ρ^2 . In other words, the states are of the form (A, B, A, B) , with an alternating pattern round the ring.

The analysis for the bidirectional cases follows similar lines, but leads to rather different results. This time the symmetry group is $D_4 = \langle \rho, \kappa \rangle$, where ρ acts as above and $\kappa x_i = x_{-i}$. The state space \mathbb{R}^4 again decomposes into the same three irreducibles W_j , but now all three are absolutely

irreducible (since κ acts on $W_2 \equiv \mathbb{C}$ as complex conjugation). Thus W_2 can occur in generic bifurcation, with a more interesting isotropy lattice which contains two non-conjugate axial subgroups $Z_2^\kappa = \langle \kappa \rangle$ and $Z_2^{\kappa\rho} = \langle \kappa\rho \rangle$. Solutions with isotropy Z_2^κ are invariant under reflection of the network graph in the diagonal line joining cells C_0 and C_2 , whereas solutions with isotropy $Z_2^{\kappa\rho}$ are invariant under reflection of the network graph in the horizontal line joining the midpoint of the arrow from C_0 to C_1 to the midpoint of the arrow from C_2 to C_3 . So states with isotropy Z_2^κ are of the form (A, B, C, B) , whereas states with isotropy $Z_2^{\kappa\rho}$ are of the form (A, A, B, B) . Note that both of these branches bifurcate simultaneously, but they may have different stabilities and branch in different directions, depending on the precise form of the vector field.

Table 3.5 summarizes these generic steady-state bifurcation patterns, and also includes patterns for Hopf bifurcation. The analysis of symmetric Hopf bifurcation in these two systems is similar to the above, but slightly more complicated, and can be found in Golubitsky and Stewart [29]. We omit the computations and merely state the results. In the table A, B, C are constant vectors, and $A(t), B(t)$ are T -periodic functions for some T .

The crucial point to observe is the occurrence of *patterns*, that is, the same dynamics may occur in more than one cell, possibly subject to a fixed phase shift that is a simple fraction of T .

Double frequency cell motions. One curious implication of spatio-temporal symmetry occurs in the solutions of the form $(A(t), B(t), A(t + T/2), B(t))$, namely, the frequency of $B(t)$ is double that of $A(t)$. We briefly explain how this fact is deduced from symmetry. The \mathbb{C} -axial subgroup corresponding to this solution is the subgroup of $D_4 \times S^1$ generated by $\langle (\kappa, 0), (\rho^2, \pi) \rangle$ where the period is 2π . Invariance under this subgroup implies that cells C_1 and C_3 are identical and that C_j is π out of phase with C_{j+2} . Therefore C_1 is identical to C_3 but also π out of phase with C_3 . This implies that C_3 is π out of phase with itself, which is equivalent to it having twice the frequency, that is, period π instead of 2π . This type of forced frequency-division is associated with any isotropy subgroup in which some cells are fixed by a spatial group element but their phase is shifted by a temporal element.

The interpretation of an isotropy subgroup depends upon the actual network, not just its symmetry type. For example, consider another \mathbb{C} -axial subgroup for the four-cell bidirectional ring, the twisted group $\tilde{Z}_4 = \langle (\rho, -T/4) \rangle$. This yields the pattern $(A(t), A(t + T/4), A(t + T/2), A(t + 3T/4))$ for the ring network. However, suppose there is a fifth cell at the center, coupled identically to the other four (figure 3.5). Then the symmetries are unchanged, but now the solution with isotropy \tilde{Z}_4 is of the form $(A(t), A(t + T/4), A(t + T/2), A(t + 3T/4), B(t))$ where B has four times the frequency of A .

TABLE I
Possible patterns in a four-cell ring. (*U* stands for unidirectional and *B* stands for bidirectional.)

Type	C_0	C_1	C_2	C_3	Ring Type
Steady	<i>A</i>	<i>A</i>	<i>A</i>	<i>A</i>	U or B
	<i>A</i>	<i>A</i>	<i>B</i>	<i>B</i>	B
	<i>A</i>	<i>B</i>	<i>C</i>	<i>B</i>	B
	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	U or B
Periodic	$A(t)$	$A(t)$	$A(t)$	$A(t)$	U or B
	$A(t)$	$A(t + T/4)$	$A(t + T/2)$	$A(t + 3T/4)$	U or B
	$A(t)$	$B(t)$	$A(t + T/2)$	$B(t)$	B
	$A(t)$	$A(t)$	$A(t + T/2)$	$A(t + T/2)$	B
	$A(t)$	$A(t + T/2)$	$A(t)$	$A(t + T/2)$	U or B

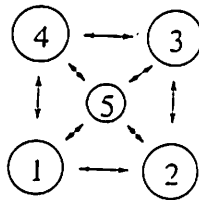


FIG. 3. Another network with D_4 symmetry.

4. Application to animal locomotion. In this section we apply the above techniques to a class of networks arising in the theory of central pattern generators for animal locomotion. For further details, both mathematical and biological, see [10, 11, 12, 13, 14, 44, 52, 53] for legged animals, and [8, 38, 39, 40, 42] for legless creatures such as the lamprey.

Collins and Stewart [11, 12, 13, 14] have shown that the phase relationships of many quadruped and hexapod gaits can be obtained naturally via Hopf bifurcation in small networks of identical cells. Golubitsky *et al.* [30] overcame certain difficulties in the results of Collins and Stewart by introducing a class of networks that models the gait of a $2n$ -legged organism with a network of $4n$ cells. This network is modular, in the sense that it naturally provides models of gaits in quadrupeds, hexapods, centipedes, and millipedes. The analysis of models for many-legged animals shows that wave-like motions, similar to those obtained by Kopell and Ermentrout [38, 39, 40] also arise. The network leads to a number of predictions

about the wavelength of the wave motion and about secondary gaits such as gallops and the canter.

It is now well established (Grillner [34, 35, 36], Shik and Orlovsky [45], Stein [47], and Pearson [41]) that animal locomotion is generated and controlled, in part, by a *central pattern generator* (CPG), which is a network of neurons in the central nervous system capable of producing rhythmic output. Kopell and Ermentrout [38, 39, 40] show that a linear network consisting of many coupled identical cells can generate traveling wave motions similar to those observed in the lamprey, and some biological predictions made by this model have been confirmed [49].

The crucial observation, explained in Golubitsky *et al.* [30], is that in order for a symmetric network of identical cells to reproduce the phase relationships found in gaits of a 4-legged animal, the number of cells should be (at least) eight. The network generalizes to a coupled cell CPG model for $2n$ -legged animals consisting of $4n$ cells, as is shown in figure 4.

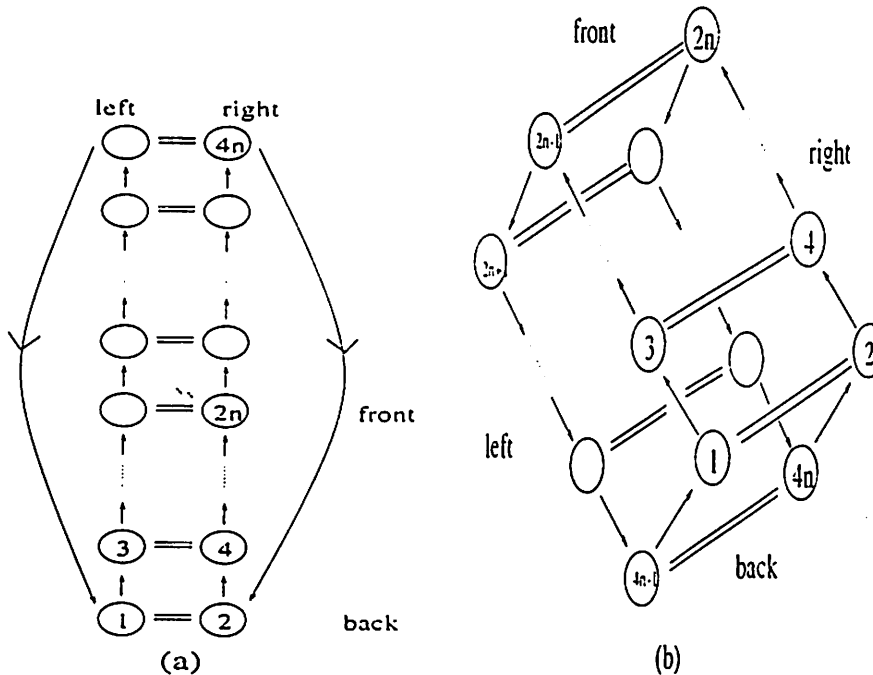


FIG. 4. (a) Schematic $4n$ -cell network for gaits in $2n$ -legged animals. Only cells $1, \dots, 2n$ are connected to legs. (b) Folding up the network to eliminate long-range connections creates a structure with repeated modules, differing slightly at the two ends.

The structure of this network respects the natural bilateral symmetry, and also possesses a $2n$ -fold cyclic 'translational' symmetry from back to front. The symmetry group of the network is $\Gamma \cong \mathbb{Z}_{2n} \times \mathbb{Z}_2$. The subgroup \mathbb{Z}_{2n} cycles corresponding pairs of cells around their respective loops, and

the subgroup Z_2 interchanges left and right cells in corresponding positions. The graph of this network is the 'direct product' of a unidirectional 4-cycle with a bidirectional 2-cycle, and the bifurcation analysis follows a very similar pattern. In each 4-cycle ring we find discrete travelling waves of various kinds, and the two rings are either synchronized or half a period out of phase with each other.

For quadrupedal gaits, we list the patterns for primary bifurcations, corresponding to C-axial subgroups. We denote them by an array of phase shifts corresponding to cells numbered in figure 2.3. For simplicity of exposition, we assume that only cells 1-4 drive the legs, so that C_1 drives the left rear leg, C_2 drives the right rear leg, C_3 drives the left front leg, and C_4 drives the right front leg. Thus in this exposition the phases of cells C_5-C_8 are ignored and are present in order to propagate the dynamics correctly. Collins and Stewart [13] obtain similar results for hexapodal gaits using a 12-cell network.

TABLE 2
Quadrupedal gaits. In jump and walk choose either + or - throughout.

pronk	pace	jump \pm	walk \pm	bound	trot
0 0	0 $\frac{1}{2}$	$\pm \frac{3}{4}$ $\pm \frac{3}{4}$	$\pm \frac{3}{4}$ $\pm \frac{1}{4}$	$\frac{1}{2}$ $\frac{1}{2}$	$\frac{1}{2}$ 0
0 0	0 $\frac{1}{2}$	$\frac{1}{2}$ $\frac{1}{2}$	$\frac{1}{2}$ 0	0 0	0 $\frac{1}{2}$
0 0	0 $\frac{1}{2}$	$\pm \frac{1}{4}$ $\pm \frac{1}{4}$	$\pm \frac{1}{4}$ $\pm \frac{3}{4}$	$\frac{1}{2}$ $\frac{1}{2}$	$\frac{1}{2}$ 0
0 0	0 $\frac{1}{2}$	0 0	0 $\frac{1}{2}$	0 0	0 $\frac{1}{2}$

A similar analysis applies to networks of the kind that might be associated with many-legged animals such as centipedes and millipedes — and also legless animals such as eels, snakes, and lamprey, for which 'leg' should be interpreted as 'muscular unit'. The range of primary gait patterns is considerable, but they all have the same fundamental characteristics. First, select some divisor d of $2n$; then group the cells on the left side into $\frac{2n}{d}$ clumps, each spaced d cells apart. The phase relationships along that side of the network are like those of a $\frac{4n}{d}$ -cell network of the same kind, but repeated d times in the 'forward' direction. The left-right pairs of cells either are in phase throughout the cycle, or half a period out of phase throughout the cycle.

Because the network has twice as many cells as the animal has legs, the analysis leads to the prediction that the number of waves that fits into the 'directly observable' half of the network, cells 1 through $2n$, is either an integer or half an odd integer. It may therefore be significant that Alexander [2] provides drawings of several gaits in a centipede. In all cases the number of waves appears to be very close either to an integer (4, 3, 2) or half an odd integer ($\frac{3}{2}$). In particular, the half odd integer pattern does

occur; for example, the popular tripod gait of hexapods is a $\frac{3}{2}$ gait.

It is possible to study secondary bifurcations in this network, analyzing 'mixed mode' solutions that are in a sense a nonlinear interaction between primary gaits. This framework provides an explanation of quadruped gaits such as rotary and transverse gallops; it also makes predictions about the transitions to secondary gaits. For details, see Golubitsky *et al.* [30] and Buono [5].

5. All-to-all coupling. A network of identical cells has *all-to-all* coupling if each cell is coupled in the same manner to every other cell. The symmetry group is then S_N , the symmetric group comprising all permutations of $\{1, \dots, N\}$.

Steady state bifurcation for S_N -equivariant systems is studied in Wood [50]. A dynamically more complex analogue, 'half way between' steady and Hopf bifurcation, is treated by Aronson *et al.* [3]: this is the period-doubling case. We shall not discuss period-doubling here, but there is a theory analogous to Hopf bifurcation in which the group S^1 is replaced by Z_2 . Indeed further generalizations are possible, see Brown [4].

Here we focus on Hopf bifurcation in all-to-all coupled cell networks. First we state the classification of the C -axial subgroups of the symmetric group S_N . The appropriate action of $S_N \times S^1$ is the 'natural' action on

$$C^{N,0} = \{(z_1, \dots, z_N) \in C^N \mid z_1 + \dots + z_N = 0\}.$$

in which $\sigma \in S_N$ acts by permutations of coordinates and $\theta \in S^1$ acts as multiplication by $e^{i\theta}$:

$$(5.1) \quad (\sigma, \theta)z = e^{i\theta}(z_{\sigma(1)}, \dots, z_{\sigma(N)}).$$

The permutation representation of S_N on $R^{N,0}$ is absolutely irreducible, and the representation (5.1) is isomorphic to $R^{N,0} \otimes C$ and is S_N -simple.

THEOREM 5.1. *Suppose that $N \geq 2$. Then the axes of $S_N \times S^1$ acting on $C^{N,0}$ have orbit representatives as follows:*

Type I:

Let $N = qk + p$ where $2 \leq k \leq N, q \geq 1, p \geq 0$. Let $\zeta = e^{2\pi i/k}$, and set

$$z = (\underbrace{1, \dots, 1}_q; \underbrace{\zeta, \dots, \zeta}_q; \underbrace{\zeta^2, \dots, \zeta^2}_q; \dots; \underbrace{\zeta^{k-1}, \dots, \zeta^{k-1}}_q; \underbrace{0, \dots, 0}_p).$$

Type II:

Let $N = q + p, 1 \leq q < \frac{N}{2}$, and set

$$z = (\underbrace{1, \dots, 1}_q; \underbrace{a, \dots, a}_p)$$

where $a = -q/p$.

Next we consider the corresponding isotropy subgroups. For type I we have

$$\Sigma_z = S_q \wr \widetilde{Z}_k \times S_p$$

where \wr denotes the wreath product and the tilde indicates that Z_k is twisted into S^1 . In more explicit terms, let $K = \ker(\theta) = S_q^1 \times \dots \times S_q^k \times S_p$, where S_q^j is the symmetric group on $B_j = \{(j-1)q+1, \dots, jq\}$ and S_p is the symmetric group on $B_0 = \{kq+1, \dots, N\}$. Define α to be the k -cycle

$$\alpha = (1, q+1, 2q+1, \dots, (k-1)q+1).$$

Then $\Sigma_z = \langle K, (\alpha, \zeta) \rangle$. The interpretation is that the solution comprises k clumps of q synchronized cells. The oscillations of the cells in distinct clumps are identical except for phase shifts by $\frac{mT}{k}$ where $m = 0, \dots, k-1$ and T is the period. Moreover, there is one further clump of p synchronized cells with period T/k .

In type II the isotropy subgroup is

$$\Sigma_z = S_q \times S_p$$

where the respective factors are the symmetric groups on $\{1, \dots, q\}$ and $\{q+1, \dots, N\}$. This corresponds to two clumps consisting of q and p synchronized cells.

6. Linear arrays of cells. Symmetry methods sometimes apply in circumstances where the appropriate symmetries are not immediately apparent. An instructive example occurs in linear arrays of cells, see Epstein and Golubitsky [23]. Consider a linear array of N identical cells, C_1, \dots, C_N , with bidirectional coupling between C_j and C_{j+1} for $j = 1, \dots, N-1$ as in figure 5(a). Then the model equations take the form

$$(6.1) \quad \begin{aligned} \frac{dx_1}{dt} &= f(x_1, x_1, x_2) \\ \frac{dx_j}{dt} &= f(x_{j-1}, x_j, x_{j+1}) \quad j = 2, \dots, N-1 \\ \frac{dx_N}{dt} &= f(x_{N-1}, x_N, x_N) \end{aligned}$$

where $f(x, y, z) = f(z, y, x)$ indicating bidirectional coupling. The form of the equations for x_1, x_N satisfies a discrete analogue of 'Neumann boundary conditions', and the subsequent analysis is based on methods that were originally developed for partial differential equations with symmetry (see Gomes *et al.* [33]).

The only symmetry evident in the network is the flip $x_j \mapsto x_{N+1-j}$. However, the equations can be extended to a ring of $2N$ identical cells, with

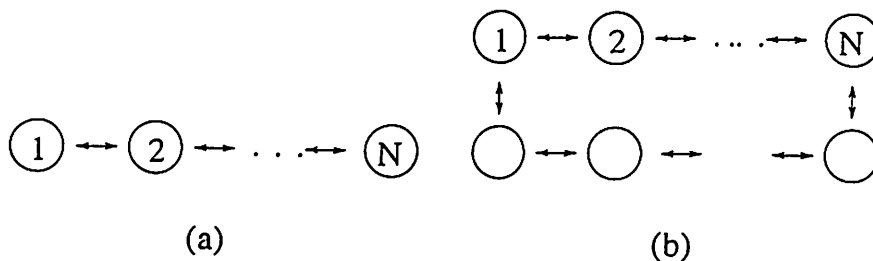


FIG. 5. (a) Bidirectional linear array; (b) doubled bidirectional array in a ring.

D_{2N} symmetry, by the 'reflection trick'. Introduce N new cells, labelled C_{-1}, \dots, C_N , arranged as in figure 5(b) and observe that any solution to (6.1) can be extended to the ring by setting $x_{-N} = x_N$. This is true in both the steady-state and the Hopf case. Such solutions lie in the fixed-point space of the flip $\kappa : x_N \mapsto x_{-N}$. In short: solutions for the equations of a linear array are in one-to-one correspondence with solutions for a D_{2N} -symmetric ring that lie in $\text{Fix}(\kappa)$.

Using these methods, Epstein and Golubitsky [23] classify steady-state and Hopf bifurcations in linear arrays. The results are nontrivial: for example in a 10-cell linear array the methods predict patterns of shape $ABCBAABCBA$ and $ABBAABBAAB$. They observe such patterns numerically in linear arrays of Brusselators.

These ideas have been developed further for square arrays of coupled cells by Gillis and Golubitsky [27]. Rectangular arrays could also be investigated by these methods.

There is also an analogue of Dirichlet boundary conditions if the oscillators have internal Z_2 symmetry whose fixed-point space comprises states that are identically zero. The reflection trick for PDEs can be extended to Dirichlet boundary conditions, see Castro [6], Gomes *et al.* [33], and it seems clear that a similar idea will work for linear or rectangular arrays of cells.

Finally, the reflection trick can no doubt be developed for cells that possess internal symmetries, see below. However, this has not yet been done.

7. Internal symmetries. We end this survey with a quick introduction to an area that is extremely rich both in algebraic structure and in dynamical behavior. This is the possibility of combining internal symmetries of individual cells with network symmetries of the coupled system. The theory developed for such systems currently concentrates on two types of coupling, known as *direct product* coupling and *wreath product* coupling. These names are taken from group theory and describe the structure of the associated symmetry groups. For full details see Golubitsky *et al.* [31] and Dionne *et al.* [21, 22].

We suppose that individual cells possess a local or internal symmetry group $\mathcal{L} \subset O(k)$. Here an element $\ell \in \mathcal{L}$ is an *internal symmetry* if

$$f(\ell x_j) = \ell f(x_j).$$

In other words, $\ell \in \mathcal{L}$ acts as a symmetry of cell j , ignoring all other cells and any coupling effects.

Whether such internal symmetries are symmetries of the whole coupled cell system depends on the coupling h . One reasonable requirement is that when ℓ acts simultaneously on each cell, then it is a symmetry of the entire coupled cell system. This boils down to the condition

$$(7.1) \quad h(\ell x_i, \ell x_j) = \ell h(x_i, x_j).$$

If we define

$$\ell x = (\ell x_1, \dots, \ell x_N),$$

then

$$F(\ell x) = \ell F(x)$$

and ℓ is a symmetry of (2.2). It follows that $\mathcal{L} \times \mathcal{G}$ are symmetries of (2.2) where \mathcal{L} is viewed as the diagonal subgroup of \mathcal{L}^N . In particular if the coupling h is diagonal and linear, that is,

$$h(x_i, x_j) = x_i - x_j,$$

then the *direct product* $\mathcal{L} \times \mathcal{G}$ is a symmetry group of (2.2).

However, we may also consider another natural case: systems for which the action of ℓ on each cell individually is a symmetry of the entire system (2.2). To achieve this, we suppose that

$$(7.2) \quad h(x_i, \ell x_j) = \ell h(x_i, x_j)$$

$$(7.3) \quad h(\ell x_i, x_j) = h(x_i, x_j).$$

Any two of equations (7.1,7.2,7.3) imply the third. In this case, the group \mathcal{L}^N is a symmetry group of (2.2); moreover, so is \mathcal{G} . The *wreath product* $\mathcal{L} \wr \mathcal{G}$ is the symmetry group generated by \mathcal{L}^N and \mathcal{G} . Under the above assumptions, $\mathcal{L} \wr \mathcal{G}$ is a symmetry group of (2.2). The algebraic structure of wreath products, which are perhaps less familiar than direct products, but equally natural both physically and algebraically, is discussed in [43]. If \mathcal{G} is nontrivial, then the wreath product $\mathcal{L} \wr \mathcal{G}$ is larger than the direct product $\mathcal{L} \times \mathcal{G}$. This implies that the system has *more* symmetry in the wreath product case, so that wreath product coupling is likely to be more tractable than direct product coupling, not less tractable. (The more symmetry there is, the tighter the constraints on the system, and therefore the more you can hope to prove about it.)

EXAMPLE 7.1. An example of wreath product coupling is given by

$$(7.4) \quad h(x_i, x_j) = |x_i|^2 x_j.$$

The exact form of such a system is:

$$\frac{dx_j}{dt} = f(x_j) + \sum_{i=1}^N C(i, j) |x_i|^2 x_j.$$

In summary: if \mathcal{L} denotes the internal symmetries and \mathcal{G} denotes the global symmetries, then there are (at least) two natural types of coupling leading to two different symmetry groups Γ . The first type of coupling leads to the *direct product* $\Gamma = \mathcal{L} \times \mathcal{G}$, whereas the second type of coupling leads to the *wreath product* $\Gamma = \mathcal{L} \wr \mathcal{G}$.

For information on stabilities in Hopf bifurcation for systems with $D_3 \times D_3$ symmetry see Dangelmayr *et al.* [15], and for an application to neural nets see Dangelmayr *et al.* [16]. For S_3^1 -symmetric systems with internal Z_2 symmetry in the direct product case see Wood [51]. Dionne *et al.* [22] classify Hopf bifurcations for $D_N \times O(2)$.

One characteristic feature of the wreath product case is that the cells may divide into active and quiescent clumps, see Dionne *et al.* [21]. Another characteristic feature of the dynamics in wreath product coupled cell systems is intermittency associated with heteroclinic cycles. See Field [25, 26, 17].

Motivation for both types of coupling, and examples where they are physically realized, are given in Golubitsky *et al.* [31]. Analyses of steady-state and Hopf bifurcation, setting up the necessary machinery for applying the equivariant branching lemma and the equivariant Hopf theorem, can be found in Dionne *et al.* [21] for wreath products, and in Dionne *et al.* [22] for direct products. An error in the classification of C-axial subgroups for wreath products is noted and corrected in Dias [18]. Information on stability calculations in the wreath product case can be found in Dias and Stewart [19], and observations on the associated invariant theory in Dias and Stewart [20].

REFERENCES

- [1] J. C. ALEXANDER, *Patterns at primary Hopf bifurcations of a plexus of identical oscillators*, SIAM J. Appl. Math., 46, (1986), 199-221.
- [2] R. MCN. ALEXANDER, *Terrestrial locomotion*, In: *Mechanics and Energetics of Animal Locomotion*, (R. McN. Alexander and J.M. Goldspink, eds), Chapman and Hall, London, (1977), 168-203.
- [3] D. G. ARONSON, M. GOLUBITSKY AND M. KRUPA, *Coupled arrays of Josephson junctions and bifurcation of maps with S_N symmetry*, Nonlinearity, 4, (1991), 861-902.
- [4] A. G. BROWN, *The Classification of Bifurcations in Maps with Symmetry*, PhD Thesis, Math. Inst., U. Warwick, 1992.

- [5] P.-L. BUONO, *Models of Central Pattern Generators Using Symmetrically Coupled Cell Systems*, PhD Thesis, Math. Dept., U. Houston, 1998.
- [6] S. B.S.D. CASTRO, *Symmetry and Bifurcation of Periodic Solutions in Neumann Boundary Value Problems*, MSc Thesis, Math. Inst., U. Warwick, 1990.
- [7] G. CICOGLA, *Symmetry breakdown from bifurcations*, *Lett. Nuovo Cimento*, **31**, (1981), 600-602.
- [8] A.H. COHEN, P.J. HOLMES AND R.H. RAND, *The nature of the coupling between segmental oscillators of the lamprey spinal generator for locomotion: a mathematical model*, *J. Math. Biol.*, **13**, (1982), 345-369.
- [9] J.J. COLLINS, C.C. CHOW, A.C. CAPELA AND T.T. IMHOFF, *Aperiodic stochastic resonance*, *Phys. Rev. E*, **54**, (1996), 5575-5584.
- [10] J.J. COLLINS AND S.A. RICHMOND, *Hard-wired central pattern generators for quadrupedal locomotion*, *Biol. Cybern.*, **71**, (1994), 375-385.
- [11] J.J. COLLINS AND I. STEWART, *Symmetry-breaking bifurcation: a possible mechanism for 2:1 frequency-locking in animal locomotion*, *J. Math. Biol.*, **30**, (1992), 827-838.
- [12] J.J. COLLINS AND I. STEWART, *Coupled nonlinear oscillators and the symmetries of animal gaits*, *J. Nonlin. Sci.*, **3**, (1993), 349-392.
- [13] J.J. COLLINS AND I. STEWART, *Hexapodal gaits and coupled nonlinear oscillator models*, *Biol. Cybern.*, **68**, (1993), 287-298.
- [14] J.J. COLLINS AND I. STEWART, *A group-theoretic approach to rings of coupled biological oscillators*, *Biol. Cybern.*, **71**, (1994), 95-103.
- [15] G. DANGELMAYR, W. GÜTTINGER, AND M. WEGELIN, *Hopf bifurcation with $D_3 \times D_3$ symmetry*, *Z. Angew. Math. Phys.*, **44**, (1993), 595-638.
- [16] G. DANGELMAYR, W. GÜTTINGER, J. OPPENLÄNDER, J. TOMES, AND M. WEGELIN, *Synchronized patterns in hierarchical networks of neuronal oscillators with $D_3 \times D_3$ symmetry*, *Belg. J. Math.*, to appear.
- [17] M. DELLNITZ, M. FIELD, M. GOLUBITSKY, A. HOHMANN AND J. MA, *Cycling chaos*, *Intern. J. Bifur. & Chaos*, **5** (4), (1995), 1243-1247.
- [18] A.P.S. DIAS, *Hopf bifurcation for wreath products*, *Nonlinearity*, **11**, (1998), 247-264.
- [19] A.P.S. DIAS AND I. STEWART, *Symmetry-breaking bifurcations of wreath product systems*, *J. Nonlin. Sci.*, to appear.
- [20] A.P.S. DIAS AND I. STEWART, *Invariant theory for wreath product groups*, preprint **36**, 1998, Math. Institute, Univ. of Warwick, 1998.
- [21] B. DIONNE, M. GOLUBITSKY AND I. STEWART, *Coupled cells with internal symmetry, Part I: wreath products*, *Nonlinearity*, **9**, (1996), 559-574.
- [22] B. DIONNE, M. GOLUBITSKY AND I. STEWART, *Coupled cells with internal symmetry, Part II: direct products*, *Nonlinearity*, **9**, (1996), 575-599.
- [23] I.R. EPSTEIN AND M. GOLUBITSKY, *Symmetric patterns in linear arrays of coupled cells*, *Chaos*, **3** (1), (1993), 1-5.
- [24] G.B. ERMENTROUT AND N. KOPELL, *Multiple pulse interactions and averaging in systems of coupled neural oscillators*, *J. Math. Biol.*, **29**, (1991), 195-217.
- [25] M.J. FIELD, *Heteroclinic cycles in symmetrically coupled cell systems*, This volume.
- [26] M.J. FIELD, *Lectures on Bifurcations, Dynamics and Symmetry*, Pitman Research Notes in Math., **356**, (1996).
- [27] D. GILLIS AND M. GOLUBITSKY, *Patterns in square arrays of coupled cells*, *JMAA.*, **208**, (1997), 487-509.
- [28] M. GOLUBITSKY AND I.N. STEWART, *Hopf bifurcation in the presence of symmetry*, *Arch. Rational Mech. Anal.*, **87**, (1985), 107-165.
- [29] M. GOLUBITSKY AND I.N. STEWART, *Hopf bifurcation with dihedral group symmetry: coupled nonlinear oscillators*, In: *Multiparameter Bifurcation Theory*, (M. Golubitsky and J. Guckenheimer, Eds), *Contemporary Math.*, **56**, (1986), 131-173.
- [30] M. GOLUBITSKY, I. STEWART, P.L. BUONO AND J.J. COLLINS, *A modular network*

- for legged locomotion, *Physica D*, **115**, (1998), 56–72.
- [31] M. GOLUBITSKY, I. STEWART AND B. DIONNE, *Coupled cells: wreath products and direct products*, In: *Dynamics, Bifurcation and Symmetry*, (P. Chossat, ed.), NATO ARW Series, Kluwer, Amsterdam, (1994), 127–138.
- [32] M. GOLUBITSKY, I.N. STEWART AND D. G. SCHAEFFER, *Singularities and Groups in Bifurcation Theory*, vol.II, *Appl. Math. Sci.*, **69**, Springer-Verlag, New York, (1988).
- [33] M.G.M. GOMES, I.S. LABOURIAU AND E.M. PINHO, *Spatial hidden symmetries in pattern formation*, This volume.
- [34] S. GRILLNER, *Locomotion in vertebrates: central mechanisms and reflex interaction*, *Physiol. Rev.*, **55**, (1975), 247–304.
- [35] S. GRILLNER, *Control of locomotion in bipeds, tetrapods and fish*, In: *Handbook of Physiology*, Sect. 1: The Nervous System, Vol. II: Motor Control, (V.B. Brooks, ed), Bethesda, American Physiological Society, (1981), 1179–1236.
- [36] S. GRILLNER, *Neurobiological bases of rhythmic motor acts in vertebrates*, *Science*, **228**, (1985), 143–149.
- [37] S. GRILLNER, *Neural networks for vertebrate locomotion*, *Scientific American*, **274**, No. 1, (1996), 48–53.
- [38] N. KOPELL AND G.B. ERMENTROUT, *Symmetry and phaselocking in chains of weakly coupled oscillators*, *Comm. Pure Appl. Math.*, **39**, (1986), 623–660.
- [39] N. KOPELL AND G.B. ERMENTROUT, *Coupled oscillators and the design of central pattern generators*, *Math. Biosci.*, **89**, (1988), 14–23.
- [40] N. KOPELL AND G.B. ERMENTROUT, *Phase transitions and other phenomena in chains of oscillators*, *SIAM J. Appl. Math.*, **50**, (1990), 1014–1052.
- [41] K.G. PEARSON, *Common principles of motor control in vertebrates and invertebrates*, *Annu. Rev. Neurosci.*, **16**, (1993), 265–297.
- [42] R.H. RAND, A.H. COHEN AND P.J. HOLMES, *Systems of coupled oscillators as models of central pattern generators*, In: *Neural Control of Rhythmic Movements in Vertebrates*, (A.H. Cohen, S. Rossignol and S. Grillner, eds), Wiley, New York, (1988), 333–367.
- [43] D.H. SATTINGER, *Branching in the presence of symmetry*, *CBMS-NSF Conference Notes*, **40**, SIAM, Philadelphia, (1983).
- [44] G. SCHÖNER, W.Y. JIANG AND J.A.S. KELSO, *A synergetic theory of quadrupedal gaits and gait transitions*, *J. Theor. Biol.*, **142**, (1990), 359–391.
- [45] M.L. SHIKH AND G.N. ORLOVSKY, *Neurophysiology of locomotor automatism*, *Physiol. Rev.*, **56**, (1976), 465–501.
- [46] S. SMALE, *A mathematical model of two cells via Turing's equation*, In: *Some Mathematical Questions in Biology V*, (J.D. Cowan, ed), *Amer. Math. Soc., Lecture Notes on Mathematics in the Life Sciences*, **6**, (1974), 15–26.
- [47] P.S.G. STEIN, *Motor systems, with specific reference to the control of locomotion*, *Annu. Rev. Neurosci.*, **1**, (1978), 61–81.
- [48] A. VANDERBAUWHEDE, *Local Bifurcation and Symmetry*, *Habilitation Thesis*, Rijksuniversiteit Gent, (1980).
- [49] T.L. WILLIAMS, K.A. SIGVARDT, N. KOPELL, G.B. ERMENTROUT AND M.P. REMER, *Forcing of coupled nonlinear oscillators: studies of intersegmental coordination in the lamprey locomotor central pattern generator*, *J. Neurophysiol.*, **64**, (1990), 862–871.
- [50] D. WOOD, *Coupled Oscillators with Internal Symmetries*, *PhD Thesis*, Math. Inst., U. Warwick, (1995).
- [51] D. WOOD, *Hopf bifurcations in three coupled oscillators with internal Z_2 symmetries*, *Dyn. Stab. Sys.*, **13**, (1998), 55–93.
- [52] H. YUASA AND M. ITO, *Coordination of many oscillators and generation of locomotory patterns*, *Biol. Cybern.*, **63**, (1990), 177–184.
- [53] H. YUASA AND M. ITO, *Generation of locomotive patterns and self-organization*, *J. Robot. Mechatron.*, **4**, (1992), 142–147.