

## Recent advances in symmetric and network dynamics

Martin Golubitsky<sup>1</sup> and Ian Stewart<sup>2</sup>

<sup>1</sup>*Mathematical Biosciences Institute, Ohio State University, Columbus, Ohio 43210, USA*

<sup>2</sup>*Mathematics Institute, University of Warwick, Coventry CV4 7AL, United Kingdom*

(Received 18 December 2014; accepted 16 March 2015; published online 20 April 2015)

We summarize some of the main results discovered over the past three decades concerning symmetric dynamical systems and networks of dynamical systems, with a focus on pattern formation. In both of these contexts, extra constraints on the dynamical system are imposed, and the generic phenomena can change. The main areas discussed are time-periodic states, mode interactions, and non-compact symmetry groups such as the Euclidean group. We consider both dynamics and bifurcations. We summarize applications of these ideas to pattern formation in a variety of physical and biological systems, and explain how the methods were motivated by transferring to new contexts René Thom's general viewpoint, one version of which became known as "catastrophe theory." We emphasize the role of symmetry-breaking in the creation of patterns. Topics include equivariant Hopf bifurcation, which gives conditions for a periodic state to bifurcate from an equilibrium, and the  $H/K$  theorem, which classifies the pairs of setwise and pointwise symmetries of periodic states in equivariant dynamics. We discuss mode interactions, which organize multiple bifurcations into a single degenerate bifurcation, and systems with non-compact symmetry groups, where new technical issues arise. We transfer many of the ideas to the context of networks of coupled dynamical systems, and interpret synchrony and phase relations in network dynamics as a type of pattern, in which space is discretized into finitely many nodes, while time remains continuous. We also describe a variety of applications including animal locomotion, Couette–Taylor flow, flames, the Belousov–Zhabotinskii reaction, binocular rivalry, and a nonlinear filter based on anomalous growth rates for the amplitude of periodic oscillations in a feed-forward network. © 2015 AIP Publishing LLC. [<http://dx.doi.org/10.1063/1.4918595>]

Symmetry is a feature of many systems of interest in applied science. Mathematically, a symmetry is a transformation that preserves structure; for example, a square looks unchanged if it is rotated through any multiple of a right angle, or reflected in a diagonal or a line joining the midpoints of opposite edges. These symmetries also appear in mathematical models of real-world systems, and their effect is often extensive. The last thirty to forty years has seen considerable advances in the mathematical understanding of the effects of symmetry on dynamical systems—systems of ordinary differential equations. In general, symmetry leads to pattern formation, via a mechanism called symmetry-breaking. For example, if a system with circular symmetry has a time-periodic state, repeating the same behavior indefinitely, then typically this state is either a standing wave or a rotating wave. This observation applies to the movement of a flexible hosepipe as water passes through it: in the standing wave, the hosepipe moves to and fro like a pendulum; in the rotating wave, it goes round and round with its end describing a circle. This observation also applies to how flame fronts move on a circular burner. We survey some basic mathematical ideas that have been developed to analyze effects of symmetry in dynamical systems, along with an extension of these techniques to networks of coupled dynamical systems. The underlying viewpoint goes back to ideas of René Thom on catastrophe theory which require models to be structurally stable; that is, predictions should not change significantly if the model is changed by a small amount, within an appropriate

context. Applications include the movements of animals, such as the walk/trot/gallop of a horse; pattern formation in fluid flow; the Belousov–Zhabotinskii chemical reaction, in which expanding circular patterns or rotating spiral patterns occur; and rivalry in human visual perception, in which different images are shown to each eye—and what is perceived may be neither of them.

### I. INTRODUCTION

A well-explored theme in nonlinear dynamics, over the past thirty years or so, has been symmetry. How does the symmetry of a system of differential equations affect generic dynamics and bifurcations? These questions have been studied for states ranging from equilibria to chaos.<sup>64,70,106</sup> The answers are central to questions about pattern formation, which arises via the mechanism of symmetry-breaking. Here, we focus on three main areas where significant progress has been made: time-periodic states, mode interactions, and non-compact symmetry groups. We also include brief discussions of equilibria when these illuminate more complex dynamics.

Limitations of space preclude descriptions of many other areas of symmetric dynamics where major advances have been made: examples include heteroclinic cycles, Hamiltonian systems, and time-reversal symmetries. We also make no attempt to survey the wide range of applications;

those discussed here are a representative sample, relevant to the topics selected.

Time-periodic states are classified by their spatio-temporal symmetries, which combine the symmetries of the equations and phase shifts on periodic states.<sup>41,61,70,104</sup> These symmetries provide some information about the patterns formed by these states. More detail comes from the linearized eigenfunctions.

Mode interactions occur in multiparameter bifurcations, where adjustment of an auxiliary parameter causes two generically distinct bifurcation points to coincide. Nonlinear interactions between primary bifurcations can produce additional secondary states. The mode interaction acts as an “organizing center,” which combines all of these states into a single coherent picture.

Many of the techniques developed in recent decades are based on group representation theory, and are often limited to compact Lie groups of symmetries. However, applications often involve non-compact groups. For example, spirals and target patterns in the Belousov–Zhabotinsky chemical reaction are typically modelled using a partial differential equation (PDE) whose domain is the plane, and the symmetry group is the Euclidean group  $\mathbb{E}(2)$ . Because this includes all translations, it is non-compact. Moreover, the relevant representations may be affine rather than linear. New techniques have been introduced to understand bifurcations in this context.

Over the past decade, analogous issues to those arising in the time-periodic case have also been investigated for networks of coupled dynamical systems.<sup>65,71,115</sup> Here, there is no assumption about the existence of a global group of symmetries. Instead, the network architecture (topology) plays a role analogous to symmetry. Moreover, the notion of symmetry can be generalized: as well as global symmetries, networks can possess “partial” symmetries, defined on subsets of nodes, in which different nodes have equivalent inputs. We summarize some of the main ideas involved.

One common theme is to understand how the constraints on the differential equation—symmetry or network architecture—affect the possible periodic states and their behavior. Another is the role that symmetry-breaking plays in pattern formation. The results we describe can be broadly categorized as classification, existence, and bifurcation of possible dynamical states with implications for pattern formation.

The main contents of the paper are as follows. Section II is a subjective survey of some key developments in nonlinear dynamics from about 1960 onwards, to put the paper in context. Section III introduces basic concepts of equivariant dynamics and discusses symmetries in space and symmetry-breaking. Section IV describes periodic solutions with spatio-temporal symmetries in applications. The first part of this section (Sec. IV A) discusses rotating and standing waves in laminar flames on a circular burner, flow through a flexible hosepipe, and Couette–Taylor flow. The second part of the section (Sec. IV B) discusses an example of three coupled FitzHugh–Nagumo systems, which motivates the phenomenon of a discrete rotating wave and exemplifies rigidity in phase relations. The basic existence results for periodic solutions with prescribed spatiotemporal symmetries (that is; Hopf bifurcation and the  $H/K$  theorem) are described in

Sec. V. The  $H/K$  Theorem characterizes the possible spatio-temporal symmetries of periodic states of an equivalent ODE, whether produced by Hopf bifurcation or not. Applications to animal locomotion are described in Sec. VB 1. Section VI is about mode interactions, when two generically distinct bifurcations occur at the same parameter values, with an application to Couette–Taylor flow. Section VII uses meandering of the spiral tip in the Belousov–Zhabotinskii chemical reaction to motivate the analysis of systems whose symmetry group is not compact; in particular, the Euclidean group in the plane. Section VIII transfers some of the general ideas of equivariant dynamics and bifurcation theory to a different context: coupled cell networks, which model coupled systems of ordinary differential equations (ODEs). An application to binocular rivalry is described in Sec. VIII B 1 and an  $H/K$  Theorem for rigid phase-shift synchrony in periodic solutions is given in Sec. VIIC. Section IX discusses the remarkable phenomenon of anomalous growth rates for Hopf bifurcation on a three-cell feed-forward network. The subjects of equivariant dynamics, network dynamics, and their applications are rich and extensive. It follows that any review must be limited, as indeed this one is. The last section (Sec. X) mentions a few areas that are not discussed in this review.

## II. HISTORICAL CONTEXT

One theme of the special issue in which this paper appears is the historical development of nonlinear dynamics over the past few decades. The technical aspects of equivariant dynamics, described below, tend to obscure the broader historical development. The influences that motivated new questions and guided their solutions emerged from the realization, in the 1960s, that a systematic theory of nonlinear dynamics might be feasible. The account that follows is necessarily subjective, and references are mostly omitted to keep the list within bounds.

### A. Nonlinearity and topological dynamics

By the early 20th century linear differential equations were relatively well understood. They had innumerable applications, but they also had their Dark Side. Often the application arose from a nonlinear model that was shoe-horned into the linear framework by *ad hoc* methods. Genuinely nonlinear equations were something of a mystery, with some honorable exceptions, mainly in Hamiltonian dynamics. Their study consisted of numerous specialized tricks, and the results did not reflect the true richness of the nonlinear world.

Three main factors drew new attention to nonlinear systems: the increasing demands of applied science, in which the limitations of linear models were becoming increasingly apparent; the development of computers rapid enough to integrate nonlinear equations numerically, making many strange phenomena obvious; and the appearance of new techniques, derived from areas of pure mathematics, that helped to explain those phenomena.

Paramount among these new approaches was the introduction of topological methods by Smale,<sup>111</sup> Arnold,<sup>2</sup> and others. This viewpoint had been pioneered in the 1880s by

Poincaré with his “qualitative” theory of differential equations, culminating in his discovery around 1890 of chaotic dynamics in the restricted three-body problem. Initially, this approach was mainly limited to ODEs in the plane, but Birkhoff began to understand how higher-dimensional topology can illuminate three-body chaos. This led Smale to discover his famous “horseshoe.” The remarkable consequence was that a key example of *deterministic* dynamics was rigorously proved to be equivalent, in a technical sense, to a *stochastic* system. This was strong evidence for what we now call “chaos.”

Previous isolated results on irregular dynamic behavior—such as the wartime work of Cartwright and Littlewood on nonlinear oscillators, Sharkovskii’s theorem on periodic points of maps, and numerical examples such as the Rikitake dynamo and the Lorenz attractor—now took their place as part of a bigger picture. The viewpoints introduced by Smale and Arnold led to an ambitious program to classify generic dynamics in any nonlinear system. Eventually, this objective proved too ambitious, because these systems become very complicated in higher dimensions, but it guided a long series of deep insights into the nature of nonlinear dynamical systems and their bifurcations.

## B. Catastrophe theory

A second major thread of nonlinear dynamics developed from the ideas of Thom,<sup>120</sup> which became known as “catastrophe theory.” Thom’s writing was rather obscure, but in one context, it motivated the seminal work of Mather on singularities of smooth mappings. The best known example is the classification of the “elementary catastrophes,” that is, singularities of real-valued functions. The techniques in this area, now known as “singularity theory,” were algebraic, highly abstract, and technically deep. A key idea was to reduce a singularity to a finite segment of its Taylor series by a smooth coordinate change, leading rigorously to a polynomial “normal form.”

Expositions of catastrophe theory aimed at a popular audience emphasized the elementary catastrophes because these were relatively accessible to non-specialists—much as popular accounts of fractals emphasize similarity dimension of self-similar fractals and avoid talking about Hausdorff-Besicovitch dimension. However, this emphasis had the side-effect of suggesting that Thom’s ideas were limited to the elementary catastrophes. Scientists attempting to apply these to their own research usually found that they were not appropriate, for reasons discussed below. In another direction, many of the early applications of elementary catastrophe theory surveyed in Zeeman<sup>128</sup> were not so much applications as hints at areas where elementary catastrophe theory might be useful. Together, this led to a widespread belief that “catastrophe theory” was a failure. This was never entirely true, even for the elementary catastrophes, as the surveys by Poston and Stewart<sup>101</sup> and Golubitsky<sup>50</sup> made clear at the time. Moreover, it has taken some time for the value of some of the less well-developed applications to be seen.

Here, we cite just one example. Cooke and Zeeman<sup>30</sup> applied the cusp catastrophe to the early development of the

spinal column in an embryo—the formation of a series of segments along its back, known as somites. They proposed that somites arise through a wave of chemical changes, coordinated by a molecular clock, calling this a “clock and wave-front” model.

Until recently, biologists preferred a different approach to the growth and form of the embryo: “positional information.” Here, an animal’s body was thought of as a map, with its DNA acting as an instruction book telling cells what to do at a given place and time. Coordinates on the map were believed to be supplied by chemical gradients. But in 2013, Lauschke *et al.*<sup>88</sup> used new molecular techniques to study the formation of segments in the spinal region of a mouse. Their main result was that the number and size of segments are controlled by a clock-and-wavefront process of the type proposed by Cooke and Zeeman.

In any case, the subtitle of Thom’s book made it clear that he had something much broader in mind. It was (in English translation) “an outline of a general theory of models.” He was not developing a theory: he was outlining a meta-theory. His key principle was that a meaningful model should remain valid if its equations are perturbed slightly, a property close to the concept of structural stability introduced by Andronov and Pontryagin in the 1930s and emphasised by Smale in the 1960s. However, Thom realized that a structurally unstable model can often be rendered structurally stable by embedding it in a parametrized family. For singularities, this family is the “universal unfolding.” It organizes the possible perturbations of a degenerate type of behavior by “unfolding” the degeneracy. The degenerate model then acts as an “organizing center” for the global structure of the unfolding. The number of parameters required to render a phenomenon generic is its “codimension.”

A simple example is Hopf bifurcation,<sup>78</sup> in which a stable equilibrium loses stability and throws off a periodic cycle. The dynamics at the Hopf bifurcation point is a degenerate equilibrium. Adding a single bifurcation parameter  $\lambda$  unfolds it into a 1-parameter family which (in the supercritical case) has a stable equilibrium for  $\lambda < 0$ , a limit cycle and an unstable equilibrium for  $\lambda > 0$ , and the degenerate behavior for  $\lambda = 0$ . So, Hopf bifurcation is a codimension-1 phenomenon.

One problem with Thom’s principle, as stated, is that it appears to imply that a Hamiltonian system is not an acceptable model. Perturb by adding a small amount of friction, and energy-conservation, not to mention the entire Hamiltonian structure, is lost. However, Hamiltonian dynamics is a marvelous model in areas where friction is not relevant, such as celestial mechanics. What was not clear at the time, and emerged only after later work, is that such examples do not destroy Thom’s approach. They merely imply that it has to be used *within an appropriate context*. The number of potential contexts is huge, and the formal implications of the Thomist philosophy have to be understood in whichever of these (if any) is relevant to a given problem.

When Golubitsky and Schaeffer tried to apply catastrophe theory to physical examples, it rapidly became clear that one such context is *symmetry*. Science is full of problems



about rectangles, cylinders, cubes, and spheres—all of which are symmetric. The elementary catastrophes do not take account of symmetry, so they do not apply to these systems. But, the sensible reaction is not to dismiss the Thomist approach: it is to work out its implications in the symmetric context. Another type of context also emerged from this class of problems. Bifurcation theory is about changes in the state of a system as a parameter is varied. An appropriate context must recognize the distinguished role of this parameter. The resulting theory<sup>61</sup> follows Mather's singularity-theoretic ideas, and uses many of his methods, but the detailed outcome is different. The same approach remains effective when symmetries are taken into account.<sup>70</sup> Indeed, the theorems needed for unfoldings and normal forms of most variants of singularity theory were proved in a general theorem of Damon.<sup>32</sup>

### C. Hopf bifurcation as an elementary catastrophe

In 1976, when reviewing Zeeman's collected papers<sup>128</sup> about catastrophe theory, Smale<sup>112</sup> pointed out what seemed to be a wide gulf between the behavior accessible using singularity theory, and more general (indeed, more *dynamic*) dynamics:

Catastrophe theorists often speak as if CT (or Thom's work) was the first important or systematic...study of discontinuous phenomena via calculus mathematics. My view is quite the contrary and in fact I feel the Hopf bifurcation (1942) for example, lies deeper than CT.

A lot here depends on what counts as discontinuous and what counts as being systematic, but we can ask whether the specific point about Hopf bifurcation is valid. The answer, surprisingly, is "no." One standard way to prove the Hopf bifurcation theorem, Hale,<sup>77</sup> is to reinterpret it as a nonlinear operator equation on an infinite-dimensional Banach space: "loop space," the space of all maps from the circle into the phase space of the associated ODE. The Implicit Function Theorem then reduces this equation to a finite-dimensional one (the method is well known as Liapunov–Schmidt reduction). The result is a 1-variable singularity. This would be an elementary catastrophe, except that the operator equation has circle group symmetry (phase shift on loops). Part of this symmetry remains in the reduced equation, which has to be an odd function of the variable. Using singularity theory, it can be proved that the reduced equation in the Hopf context is a pitchfork  $x^3 \pm \lambda x = 0$ . This is the symmetric section of the universal unfolding of the best-known elementary catastrophe of them all: the canonical cusp  $x^3 + ax + b = 0$ . The parameter  $b$  must be set to zero to make the equation odd in  $x$ .

The Implicit Function Theorem can hardly be considered "deep," so the Hopf theorem is *not* deeper than elementary catastrophe theory. In fact, somewhat ironically, it is a simple consequence of elementary catastrophe theory. This method also generalizes to classify certain *degenerate* Hopf bifurcations and their unfoldings.<sup>52</sup> The link with Hopf bifurcation also shows that singularity theory is not restricted to

the obvious case of steady-state "dynamics." It applies to any dynamic behavior that can be *reduced* to finding the zero-set of a smooth mapping.

Examples like this support the view that, contrary to common perceptions, "catastrophe theory won." That is, Thom's program, taken seriously and formalized in an appropriate context, has led to significant advances that have completely changed bifurcation theory.

The same philosophy has motivated most of the work reported in this survey, and we sketch the main developments in this area in historical order. Details and references are given in later sections.

### D. Symmetry

By the late 1970s, the beginnings of equivariant dynamics (that is, dynamics in systems with symmetry) was very much "in the air."<sup>106,107</sup> The need for such a theory was motivated by at least two distinct sources of symmetry.

The first was straightforward. Potential applications with physical symmetries were commonplace, such as the buckling of an elastic cube or spherical shell, and the flow of a fluid along a circular pipe or inside a rotating cylinder.

The second was subtler. The internal demands of dynamical systems theory also made symmetries unavoidable. In Hopf bifurcation, for example, phase shifts on periodic states lead to an action of the circle group  $S^1$ , whose influence has a significant effect on the structure of the bifurcation. Even when the original system has no symmetry, the *bifurcation* has  $S^1$  symmetry. So consideration of symmetries becomes unavoidable.

Symmetry introduces many technical obstacles. In the world of "general" systems, symmetric ones are by definition non-generic. Once again, Thom's philosophy comes to the rescue: work in a context in which they *are* generic, namely: the world of systems with a given symmetry group. Allowable perturbations to the model are those that preserve the symmetry of the equations. However, the type of behavior that is now generic can change.

For example, in the presence of symmetry, critical eigenvalues are generically multiple (except for trivial or cyclic  $\mathbb{Z}_m$  symmetry groups), so the hypotheses of the standard Hopf bifurcation theorem do not apply. However, it is possible to prove an analogous theorem for dynamical systems with symmetry, and for convenience, we also refer to the corresponding context as Hopf bifurcation (see Sec. V) Many examples of Hopf bifurcation for various physical systems with symmetry group  $O(2)$  independently found two types of oscillation: standing waves and rotating waves, Ruelle.<sup>104</sup> Building on this result, we obtained<sup>61</sup> a general existence theorem for Hopf bifurcation with any compact Lie group  $\Gamma$  of symmetries. The main criterion was that the spatio-temporal symmetry group of the bifurcating solution branch should have a 2-dimensional fixed point space. This condition was generalized by Fiedler<sup>41</sup> using topological arguments to include fixed point spaces of maximal isotropy subgroups.

The proof again used the loop space formulation of Hale,<sup>77</sup> which introduced an additional symmetry group  $S^1$  of phase shifts. Spatio-temporal symmetries are defined by

subgroups of  $\Gamma \times S^1$ . They specify how the overall  $\Gamma \times S^1$  symmetry of the model equations *breaks* to a smaller group of symmetries after bifurcation. This viewpoint contributed to a growing recognition that pattern formation can often be explained using symmetry-breaking. The theorem found a variety of applications in different areas of science. Among them were Couette–Taylor flow in a fluid and the dynamics of flames on a circular burner.

Experiments revealed the existence of other types of pattern in such systems, not present in generic Hopf bifurcation. Many of these additional patterns were traced to the occurrence of “mode interactions”—essentially, points in parameter space at which two distinct types of bifurcation coincided. The Thomist approach suggested treating a mode interaction as a degeneracy and unfolding it with additional parameters. This proved successful in many applications.

Among these was a network model of a plausible central pattern generator (CPG) for quadruped locomotion. States arising from mode interactions break symmetry in new ways, compared to generic Hopf bifurcation, which prompted a more general question. What is the catalog of all possible spatio-temporal symmetries of a periodic state of an ODE with given phase space? The answer, known as the *H/K Theorem*,<sup>17</sup> depends on the dimension of the phase space and the geometry of the group action, Sec. VB. Here, *K* refers to the pointwise “spatial” symmetries of the periodic orbit, and *H* describes the setwise symmetries, in which the orbit is invariant as a set but some symmetries induce phase shifts. The factor group *H/K* is always cyclic, and the periodic states are all discrete rotating waves, in which a spatial symmetry induces a corresponding phase shift. Crucially, these phase shifts are not arbitrary. They are specific fractions of the period, and they are *rigid*: the fraction concerned remains invariant under small symmetric perturbations of the model.

The methods developed at that time were restricted to compact Lie groups of symmetries, for technical reasons related to the representations of the group. However, many interesting problems have non-compact symmetry groups, whose representations behave differently. This, in particular, is the case for PDEs posed on unbounded domains such as  $\mathbb{R}^2$  or  $\mathbb{R}^3$ , with symmetry groups such as the Euclidean groups  $\mathbb{E}(2), \mathbb{E}(3)$ , Sec. VII. A key example is the Belousov–Zhabotinskii reaction, an oscillating chemical reaction that forms two basic patterns of chemical waves: expanding “target patterns” and rotating “spirals.” Understanding this system, and more complex states in which the tip of the rotating spiral meanders, led to effective techniques for analyzing systems with these non-compact symmetry groups.

## E. Networks

By the turn of the century, most of these ideas were well established, although unsolved problems remained (and still do). Many other aspects of equivariant dynamics fell into place as well. But the theory was about to branch out in a new and unexpected direction: networks, Sec. VIII. The vital role of networks in applied science, particularly in the bio

and life sciences, was becoming increasingly apparent: food webs in ecosystems, gene regulatory networks, cell signaling networks, neuronal networks, and so on. The equivariant theory applied without much modification to *symmetric* networks; in fact, examples of such systems (as “coupled oscillators”) had been widely studied. More general networks seemed out of reach, and if anything inappropriate for the point of view developed in equivariant dynamics.

That belief changed around 2002 with the discovery by Pivato of a 16-cell network which could be proved to have a periodic state in which the nodes were partitioned into four subsets, each containing four nodes. Within each subset, all nodes were in synchrony. Nodes in distinct subsets had identical dynamics except for a phase shift, which was a multiple of one quarter of the period. This was clearly a rotating wave related to  $\mathbb{Z}_4$  symmetry—except that the network *did not have*  $\mathbb{Z}_4$  symmetry. Further study led to two ideas. First: networks (with or without symmetry) may possess “balanced colorings” in which identically colored nodes have identically colored inputs. If so, there exists an invariant subspace of phase space, on which nodes with the same color have synchronous dynamics. Second: it is then possible to identify nodes with the same color to obtain a smaller “quotient” network. If the quotient has a cyclic group of symmetries, rotating wave states can then exist. So, the observed state is related to symmetry—but not of the original network.

Very recently, we have proved that (with suitable technical conditions) the only way to obtain rigid synchrony in network dynamics is via a balanced coloring and the only way to obtain rigid phase relations is via a cyclic symmetry group of the corresponding quotient network. In short, some features of network architecture can rigorously be inferred from features of the dynamics.

This initial insight has since been developed into a general formalism for network dynamics. The theory of these networks has been guided by analogies with equivariant dynamics, which suggests sensible questions such as “What does Hopf bifurcation look like in the world of network-preserving perturbations?” Equivariant dynamics seldom provides answers, but it is a very useful guide. Research in this formalism over the past decade has followed a Thomist program, working out what behavior is generic in the network context, and what conditions imply that it will occur.

The possibility that research into equivariant dynamics would lead to discoveries about the dynamics of asymmetric networks was not envisioned back in the 1980s. But with hindsight, this development was entirely natural. As with catastrophe theory, the way forward was not to try to apply existing methods “off the shelf,” but to develop new methods, appropriate to the new context. This was motivated by applying Thom’s general philosophy, which acted as a framework to organize the questions and concepts.

## III. SYMMETRIES IN SPACE

The symmetries of a mathematical system form a group consisting of transformations that preserve specific aspects of the structure of the system. Symmetries can take many physical forms—in particular, spatial symmetries, which

affect the geometry of states, and temporal symmetries (time translation or reversal) which occur in particular, for periodic states.

Many important PDEs in the plane are invariant under the Euclidean group  $\mathbb{E}(2)$  of all rigid motions of the plane, and PDEs on a circular domain are often invariant under the group  $\mathbb{O}(2)$  of all rotations and reflections of the domain. These groups are *Lie groups*, Adams,<sup>1</sup> Bröcker and tom Dieck,<sup>14</sup> Sattinger and Weaver.<sup>108</sup> Technically, finite (and some discrete) groups are Lie groups, but aside from these, every Lie group contains continuous families of transformations. For example,  $\mathbb{O}(2)$  contains the rotation group  $\mathbb{SO}(2)$ , parametrized by an angle  $\theta$ , which is a continuous variable.

At the other extreme are finite groups, such as the symmetry group of a square or an icosahedron. Permutation groups, which permute the members of some finite set, are an important class of finite groups. Both finite and continuous symmetry groups are important in applied science, but their implications often differ. Continuous groups often play a role in pattern formation on domains in the plane or space; patterns are formed when the symmetry “breaks,” so that individual states have less symmetry than the system itself. The Navier–Stokes equation describing motion of a fluid in a planar domain has an equilibrium of constant depth, which is symmetric under  $\mathbb{E}(2)$  and all time-translations. Parallel traveling waves break some of the translational symmetries, reducing these to a discrete subgroup, and also break temporal symmetry. However, they retain some symmetries, such as translations parallel to the waves and time translation through one period. More subtly, traveling waves have continuous spatio-temporal symmetry: translations perpendicular to the waves combined with suitable time translations.

Symmetry-breaking for finite groups also causes a form of pattern formation, but the interpretation of the “patterns” may not be geometric. We expand on this point in Sec. IV B; it is especially relevant to the dynamics of networks of coupled systems.

## A. Equivariant dynamics

Equivariant dynamics examines how the symmetries of a differential equation affect the behavior of its solutions—especially their symmetries. To describe the main results, we require some basic concepts. We focus on ODEs, although many ideas carry over to PDEs.

For simplicity, we assume that the phase space of the system is  $X = \mathbb{R}^n$ , and consider an ODE

$$\frac{dx}{dt} = f(x) \quad x \in X, \quad (3.1)$$

where  $f: X \rightarrow X$  is a smooth map (vector field). Symmetries enter the picture when a group of linear transformations  $\Gamma$  acts on  $X$ . We require all elements of  $\Gamma$  to map solutions of the ODE to solutions. This is equivalent to  $f$  being  $\Gamma$ -equivariant; that is

$$f(\gamma x) = \gamma f(x) \quad (3.2)$$

for all  $\gamma \in \Gamma, x \in X$ , and we call (3.1) a  $\Gamma$ -equivariant ODE.

Condition (3.2) captures the structure of ODEs that arise when modeling a symmetric real-world system. It states that the vector field inherits the symmetries, in the sense that symmetrically related points in phase space have symmetrically related vectors.

## B. Isotropy subgroups and fixed-point subspaces

Suppose that an equilibrium  $x_0$  is *unique*. Then  $\gamma x_0 = x_0$  for all  $\gamma \in \Gamma$ , so the solution is symmetric under  $\Gamma$ . In contrast, equilibria of a  $\Gamma$ -equivariant ODE need not be symmetric under the whole of  $\Gamma$ . This phenomenon, called (*spontaneous*) *symmetry-breaking*, is a general mechanism for *pattern formation*. For example, the equations for an elastic rod in the plane under a compressive load are symmetric under reflection in the rod. So is the rod when the load is low, but for higher loads the rod buckles—either upwards or downwards. Neither buckled state is symmetric under the reflection, but each is the reflection of the other.

To formalize “symmetry of a solution,” we introduce a key concept:

*Definition 3.1.* If  $x \in X$ , the *isotropy subgroup* of  $x$  is

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

This group consists of all  $\sigma$  that fix  $x$ . There is a “dual” notion. If  $\Sigma \subseteq \Gamma$  is a subgroup of  $\Gamma$ , its *fixed-point subspace* is

$$\text{Fix}(\Sigma) = \{x \in X : \sigma x = x \quad \forall \sigma \in \Sigma\}.$$

Clearly,  $\text{Fix}(\Sigma)$  comprises all points  $x \in X$  whose isotropy subgroup contains  $\Sigma$ . Fixed-point spaces provide a natural class of subspaces that are invariant for any  $\Gamma$ -equivariant map  $f$ :

*Proposition 3.2.* Let  $f: X \rightarrow X$  be a  $\Gamma$ -equivariant map, and let  $\Sigma$  be any subgroup of  $\Gamma$ . Then  $\text{Fix}(\Sigma)$  is an invariant subspace for  $f$ , and hence for the dynamics of (3.1).

The proof is trivial, but the proposition is very useful. We can interpret  $\text{Fix}(\Sigma)$  as the space of all states that have symmetry (at least)  $\Sigma$ . Then the restriction,

$$f|_{\text{Fix}(\Sigma)},$$

determines the dynamics of all such states. In particular, we can find states with a given isotropy subgroup  $\Sigma$  by considering the (generally) lower-dimensional system given by  $f|_{\text{Fix}(\Sigma)}$ .

If  $x \in X$  and  $\gamma \in \Gamma$ , the isotropy subgroup of  $\gamma x$  is conjugate to that of  $x$

$$\Sigma_{\gamma x} = \gamma \Sigma_x \gamma^{-1}.$$

Therefore, isotropy subgroups occur in conjugacy classes. For many purposes we can consider isotropy subgroups only up to conjugacy. The conjugacy classes of isotropy subgroups are ordered by inclusion (up to conjugacy). The resulting partially ordered set is called the lattice of isotropy subgroups,<sup>70</sup> although technically it need not be a lattice.

### C. Symmetry-breaking

Equilibria provide a useful starting-point, and there are useful analogies between equilibria and periodic states. We start with bifurcations.

Consider a 1-parameter family of maps  $f: \mathbb{R}^n \times \mathbb{R} \rightarrow \mathbb{R}^n$  satisfying the equivariance condition

$$f(\gamma x, \lambda) = \gamma f(x, \lambda), \quad (3.3)$$

for all  $x \in \mathbb{R}^n, \lambda \in \mathbb{R}$ . There is a corresponding family of ODEs

$$\frac{dx}{dt} = f(x, \lambda). \quad (3.4)$$

Suppose that  $(x(\lambda), \lambda)$  is a branch of equilibria parametrized continuously by  $\lambda$ .

A necessary condition for the occurrence of local bifurcation from a branch of equilibria at  $(x_0, \lambda_0)$  is that the Jacobian  $J = D_x f|_{(x_0, \lambda_0)}$  should have eigenvalues on the imaginary axis (including 0). A zero eigenvalue usually corresponds to steady-state bifurcation: typically, the number of equilibria changes near  $(x_0, \lambda_0)$ , and branches of equilibria may appear, disappear, merge, or split. The possibilities here can be organized, recognized, and classified using singularity theory.<sup>61</sup> A nonzero imaginary eigenvalue usually corresponds to Hopf bifurcation, Hassard *et al.*<sup>78</sup> Under suitable genericity conditions, this leads to time-periodic solutions whose amplitude (near the bifurcation point) is small. In either case, the corresponding eigenspace is said to be *critical*.

The basic general existence theorem for bifurcating symmetry-breaking equilibria is the Equivariant Branching Lemma. Its statement requires the concept of an *axial* subgroup of  $\Gamma$ . This is an isotropy subgroup  $\Sigma$  for which

$$\dim \text{Fix}(\Sigma) = 1.$$

The Equivariant Branching Lemma of Cicogna<sup>27</sup> and Vanderbauwhede<sup>122</sup> states that generically (that is, subject to technical conditions that typically are valid<sup>64,70</sup>) at a local steady-state bifurcation, for each axial subgroup  $\Sigma \subseteq \Gamma$ , there exists a branch of equilibria lying in  $\text{Fix}(\Sigma)$ . This result guarantees the existence of bifurcating branches of solutions with symmetry at least  $\Sigma$ . Other branches may also occur: the axial condition is sufficient but not necessary for a branch to exist.

There are representation-theoretic conditions on the critical eigenspace, which affects the catalogue of bifurcations.<sup>70</sup> In steady-state bifurcation, it is generically an absolutely irreducible representation of  $\Gamma$ .

### D. Continuous symmetries and patterns

Steady-state bifurcation in systems with symmetry is a common mechanism for the formation of equilibrium patterns, with many applications. Equivariant PDEs have been used to understand a wide range of pattern-forming experiments.

These bifurcations build on the fundamental observations of Turing<sup>121</sup> in reaction-diffusion equations and include Bénard convection,<sup>20,70,84</sup> the Belousov–Zhabotinskii reaction,<sup>51</sup> liquid crystals,<sup>21</sup> buckling plates,<sup>61</sup> cubes,<sup>61</sup> and hemispheres,<sup>46</sup> and the Faraday experiment.<sup>31,109,110</sup> They also include applications to biology in contexts as varied as the markings on big cats, giraffes, and zebras<sup>96</sup> to patterns of geometric visual hallucinations,<sup>13,40</sup> and central place theory in the formation of cities.<sup>80,95</sup> However, we shall not describe these applications here. Other applications that we will mention include flames and fluid flows—but, we will do this in the context of periodic solutions rather than steady-state solutions.

## IV. SPATIOTEMPORAL SYMMETRIES

In this section, we discuss spatiotemporal symmetries of periodic solutions in two contexts: circular  $\mathbb{O}(2)$  symmetry occurring in several fluid dynamics experiments (Sec. IV A) and permutation  $\mathbb{S}_3$  symmetry in networks (Sec. IV B).

### A. Experiments featuring rotating and standing waves

It is now well known that Hopf bifurcation in systems with circular symmetry can produce two distinct types of periodic solutions, as we now explain. We describe experiments with flames on a circular burner, oscillations of a circular hosepipe, and flow patterns in a fluid between two differentially rotating cylinders.

#### 1. Laminar premixed flames

During the 1990s, Gorman and co-workers performed a series of beautiful experiments on pattern formation in laminar premixed flames.<sup>72–75,99</sup> These experiments were performed on a circular burner and provided an excellent example of pattern formation obtained from steady-state and Hopf bifurcation in the world of circular  $\mathbb{O}(2)$  symmetry. The pattern in the flame front, as shown in the figures, is seen by looking down on the flame from a point directly above the center of the burner.

Specifically, generically,  $\mathbb{O}(2)$  steady-state bifurcation from a circularly symmetric state (Figure 1 (left)) leads to a state with  $k$ -fold symmetry (Figure 1 (center)). This kind of solution can be found in models using a simple application of the equivariant branching lemma. As we discuss in the next section, equivariant Hopf bifurcation leads to periodic solutions with certain spatiotemporal symmetries. In the case of  $\mathbb{O}(2)$  symmetry, these bifurcations lead to two types of time-periodic solutions: *rotating waves* (solutions where time evolution is the same as spatial rotation) and *standing waves* (solutions that have  $k$ -fold symmetry for all points in time). This theorem has been proved dozens of times in the applied mathematics literature in the context of specific examples, but it is helpful to realize that it is a special case of a Hopf bifurcation version of the equivariant branching lemma (see Ref. 61). One instant of time in a rotating wave solution is shown in Figure 1 (right).



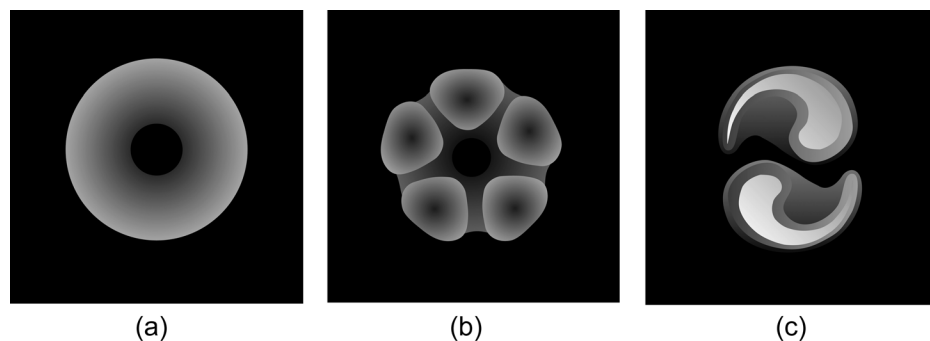


FIG. 1. Flames on a circular burner (schematic). (Left) Circularly symmetric flame. (Center) Steady flame with  $D_5$  symmetry. (Right) Rotating two-cell flame (Images courtesy of M. Gorman).

## 2. Flow through a hosepipe

A second experiment where rotating and standing waves are important is in flow induced oscillations in a hose. In the experiment, a circularly symmetric hose is hung vertically and water is sent through the hose at a constant speed  $v$ . When  $v$  is small the hose does not move, but when  $v$  is large, the hose itself oscillates. Bajaj and Sethna<sup>7</sup> show (both in experiments and in theory) that there is a critical value  $v_0$  when the oscillation commences. In models,  $v_0$  is a point of Hopf bifurcation. As noted, the  $O(2)$  symmetry of the model (and the experiments) forces two types of oscillation: in the rotating wave, the end of the hose moves in a circle; in the standing wave the hose oscillates back and forth in a plane. The general theory shows that generically only one of these two types of solutions is stable (near bifurcation)—which one depends on mechanical properties of the hose. This point might be important for firemen since a rotating fire hose would not move much when on the ground, whereas a standing wave oscillating fire hose might do a lot of damage while oscillating back and forth on the ground.

## 3. Flow between counterrotating coaxial circular cylinders

The Couette–Taylor experiment is one of the classic fluid dynamics pattern forming experiments. In this experiment, the flow of a fluid between two counterrotating

cylinders is tracked as the speed of the cylinders is varied. If the speed of the rotating cylinders are small, then the fluid flow is simple—fluid particles move in circles centered on the cylinder axis; such flow is called *Couette Flow* and is circularly  $SO(2)$  symmetric.

Rather surprisingly, the principal symmetry that drives pattern formation in the Couette–Taylor experiment is the symmetry of translation along the cylinder axis. Models (the Navier–Stokes equations for fluid flow coupled with appropriate boundary conditions) often assume periodic boundary conditions on the top and bottom of the cylinders. These boundary conditions lead to an additional  $O(2)$  symmetry generated by axial translation and up-down reflection.

In one of the standard Couette–Taylor experiments, the system begins with the outer cylinder rotating with a constant small speed and then continues by slowly ramping up the rotation speed of the inner cylinder in the direction opposite to that of the outer cylinder. The primary steady-state bifurcation from *Couette Flow* (Figure 2 (left)) leads to *Taylor Vortices* (Figure 2 (center)). Note that the azimuthal  $SO(2)$  symmetry is not broken in this bifurcation and *Taylor Vortices* are invariant under that symmetry.

If the experiment begins by rotating the outer cylinder at a larger speed, then the initial bifurcation is a Hopf bifurcation where the axial  $O(2)$  symmetry is broken. The new state that is usually observed in the rotating wave is called *Spiral Vortices* (see Figure 2 (right)). However, Demay and Iooss<sup>33</sup>

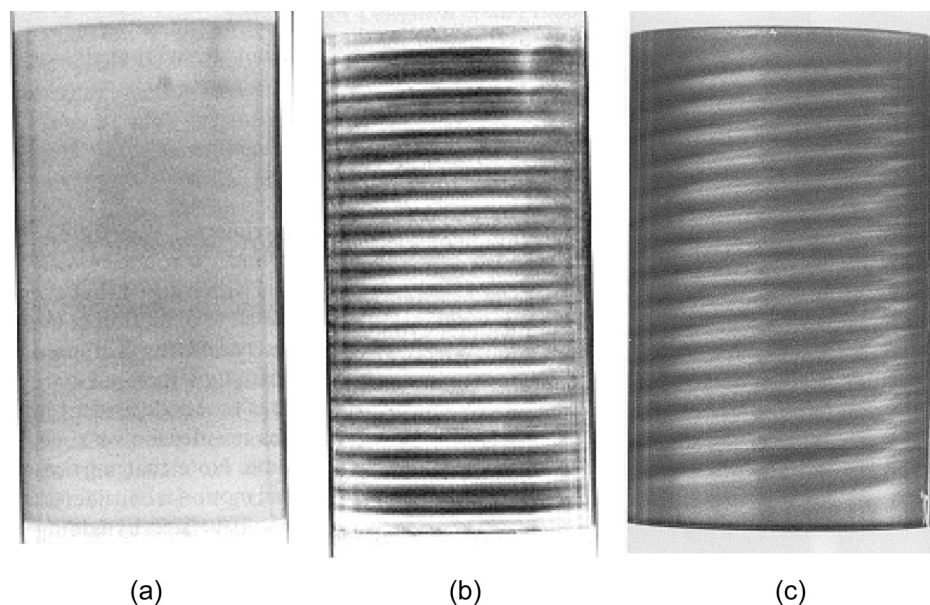


FIG. 2. Couette–Taylor experiment. (Left) *Couette Flow*. (Center) *Taylor Vortices*. (Right) *Spiral Vortices* (Images courtesy of H. L. Swinney).



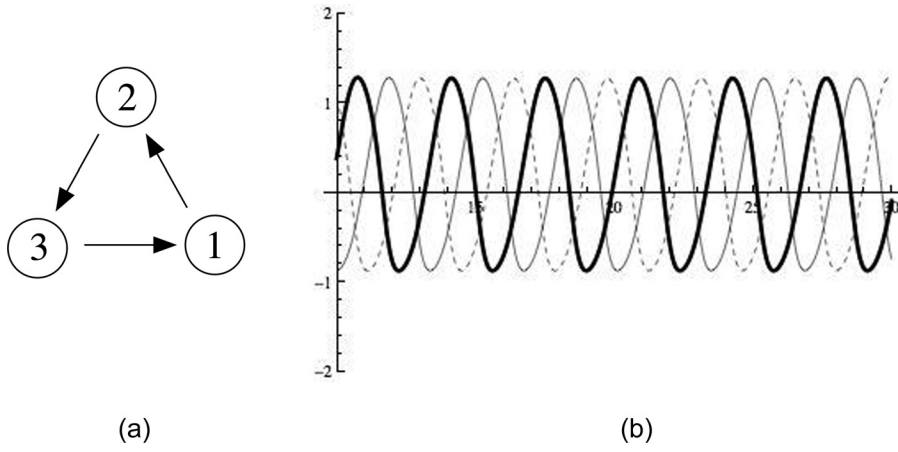


FIG. 3. *Left:* Ring of Fitzhugh–Nagumo neurons with unidirectional coupling. *Right:* Periodic oscillations of the 3-cell ring exhibiting a  $\frac{1}{3}$ -period out of phase periodic solution. Time series of  $v_1$  (thick solid),  $v_2$  (thin solid), and  $v_3$  (dashed).

computed the bifurcation from the Navier–Stokes equation and showed the unexpected result that the associated standing wave, which they called *Ribbons*, would be the stable state in a certain range of parameters. The prediction of *Ribbons* was confirmed in experiments of Tagg *et al.*<sup>118</sup> Other states of the Couette–Taylor system are discussed in Sec. VI on mode interactions.

## B. Symmetries of periodic states in networks

To discuss analogs of the above for periodic solutions in systems with a finite symmetry group, we begin with a simple example: three coupled Fitzhugh–Nagumo equations.<sup>48,98</sup> The Fitzhugh–Nagumo equation is widely used as a phenomenological model of a neuron.

### 1. A unidirectional ring of three coupled cells

The cells are coupled unidirectionally in a ring as in Figure 3 (left). Let  $v_i$  denote the membrane potential of cell  $i$ , let  $w_i$  be a surrogate for an ionic current, and suppose that  $a, b, \gamma$  are parameters with  $0 < a < 1$ ,  $b > 0$ ,  $\gamma > 0$ . We model the coupling by adding a voltage term to each cell equation

$$\begin{aligned} \dot{v}_1 &= v_1(a - v_1)(v_1 - 1) - w_1 - cv_2, \\ \dot{v}_2 &= v_2(a - v_2)(v_2 - 1) - w_2 - cv_3, \\ \dot{v}_3 &= v_3(a - v_3)(v_3 - 1) - w_3 - cv_1, \\ \dot{w}_1 &= bv_1 - \gamma w_1, \\ \dot{w}_2 &= bv_2 - \gamma w_2, \\ \dot{w}_3 &= bv_3 - \gamma w_3. \end{aligned} \quad (4.1)$$

The symmetry group is  $\mathbb{Z}_3$  generated by the 3-cycle (123) acting on pairs  $(v_j, w_j)$ .

When  $a = b = \gamma = 0.5$  and  $c = 0.8$ , the origin is a stable equilibrium for the full six-dimensional system. In this state, the cells are *synchronous*; that is, their time-series are identical. When  $a = b = \gamma = 0.5$  and  $c = 2$ , the system has a stable periodic state in which successive cells are one third of a period out of phase. See Figure 3 (right), which shows the pattern for the  $v_j$ ; the same pattern occurs for the  $w_j$ . This is an instance of “rosette phase locking,” Hoppensteadt.<sup>79</sup> Another term is *discrete rotating wave* and a third is *phase-shift synchrony*.

A discrete rotating wave occurs here because of the network’s  $\mathbb{Z}_3$  symmetry. Such a periodic state  $x(t) = (v(t), w(t))$  has *spatio-temporal* symmetry: it satisfies the phase relationships

$$x_2(t) = x_1(t - T/3) \quad x_3(t) = x_1(t - 2T/3).$$

So the solution  $x(t)$  is invariant if we permute the labels using the 3-cycle  $\rho = (123)$  and shift phase by  $T/3$ . That is,

$$\rho x(t + T/3) = x(t).$$

Thus,  $x(t)$  is fixed by the element  $(\rho, T/3) \in \Gamma \times \mathbb{S}^1$ , where  $\mathbb{S}^1$  is the circle group of phase shifts modulo the period.

The diagonal  $\Delta = \{(v_1, w_1, v_2, w_2, v_3, w_3) : v_1 = v_2 = v_3, w_1 = w_2 = w_3\}$  is a flow-invariant subspace. This is easy to verify directly; it also follows from Proposition 3.2 since  $\Delta = \text{Fix}(\mathbb{S}_3)$ . States in  $\Delta$  correspond to all three cells being synchronous. The invariance of  $\Delta$  implies that synchronous dynamics is common in  $\mathbb{Z}_3$ -symmetric three-cell systems. The rotating wave breaks the  $\mathbb{S}_3$  symmetry of the synchronous state.

### 2. Rigidity of phase shifts

An important feature of symmetry-induced phase shifts in periodic states is *rigidity*: if the vector field is slightly perturbed, the phase shifts remain unchanged (as a fraction of the period).<sup>64</sup> Rigidity is not typical of phase shifts in general dynamical systems.

To make this idea precise, we assume that the  $T$ -periodic orbit  $x(t)$  is *hyperbolic*: it has no Floquet exponent on the imaginary axis. Hyperbolicity implies that after a small perturbation of the vector field, there exists a unique  $\tilde{T}$ -periodic orbit  $\tilde{x}(t)$  near  $x(t)$  in the  $C^1$  topology, Katok and Hasselblatt,<sup>83</sup> and  $\tilde{T}$  is near  $T$ . Let the spatiotemporal symmetry group of  $x(t)$  be the subgroup  $H \subset \Gamma$  defined by

$$H = \{\gamma \in \Gamma : \gamma\{x(t)\} = \{x(t)\}\}, \quad (4.2)$$

that is,  $H$  is the subgroup of  $\Gamma$  that preserves the trajectory of  $x(t)$ . By definition, it follows that for each  $h \in H$ , there is  $0 \leq \theta < 1$  such that  $hx(0) = x(\theta T)$ . Uniqueness of solutions implies that  $hx(t) = x(t + \theta T)$ ; that is, the spatial symmetry  $h$

corresponds to a specific phase shift  $\theta$ . Moreover, since  $h^\ell = 1$  for some  $\ell$  (the order of  $h$ ), it follows that  $\theta = k/\ell$  for some integer  $k$ . Uniqueness of the perturbed solution  $\tilde{x}(t)$  implies that  $h\{\tilde{x}(t)\} = \{\tilde{x}(t)\}$ ; hence, by continuity, that the fractional phase-shift is the same for  $\tilde{x}(t)$ ; that is,  $h\tilde{x}(t) = \tilde{x}(t + \theta\tilde{T})$ .

Thus, we see that a natural consequence of symmetry is a form of phase-locking. For example, suppose that  $v(t)$  is a  $T$ -periodic solution to (4.1) and that  $\gamma$  is a symmetry. Then, either  $\gamma v(t)$  is a different periodic trajectory from  $v(t)$  or it is the same trajectory. In the latter case, the only difference is a time-translation; that is,  $\gamma v(t) = v(t + \theta)$  for all  $t$ . In the three-cell system where  $v = (x_1, x_2, x_3)$ , applying the permutation  $\rho = (123)$  three times implies that  $3\theta \equiv 0 \pmod{T}$ . Hence, either  $\theta = 0, \frac{T}{3}, \frac{2T}{3}$ . Therefore, when

- $\theta = 0$ ,  $x_3(t) = x_2(t) = x_1(t)$  (synchrony).
- $\theta = \frac{T}{3}$ ,  $x_2(t) = x_1(t + \frac{T}{3})$  and  $x_3(t) = x_1(t + \frac{2T}{3})$  (rotating wave).
- $\theta = \frac{2T}{3}$ ,  $x_2(t) = x_1(t + \frac{2T}{3})$  and  $x_3(t) = x_1(t + \frac{T}{3})$  (rotating wave in reverse direction).

Figure 4 shows the trajectory  $(v_1(t), v_2(t), v_3(t))$  in  $\mathbb{R}^3$ , viewed from a point very close to the main diagonal (to avoid confusing the perspective). The periodic cycle is shaped like a curved equilateral triangle, corresponding to the setwise  $\mathbb{Z}_3$  symmetry.

## V. THE HOPF BIFURCATION AND H/K THEOREMS

Two kinds of existence theorem for periodic solutions in equivariant systems have been developed over the past 30 years. Both are aimed at understanding the kinds of spatio-temporal symmetries of periodic solutions that can be expected in such systems.

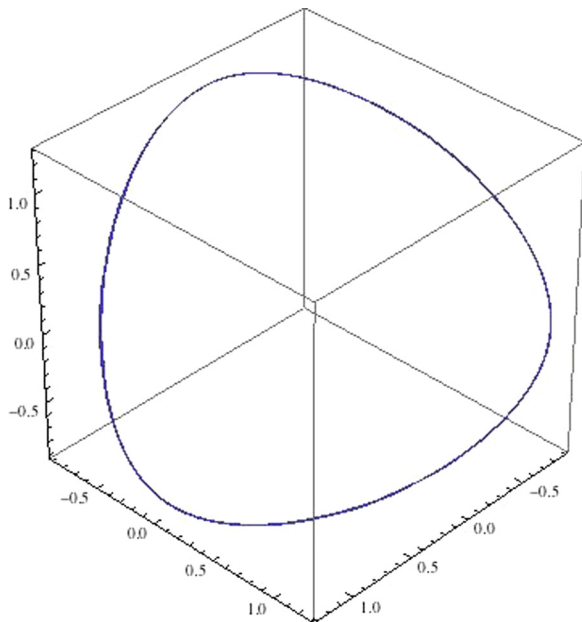


FIG. 4. Setwise  $\mathbb{Z}_3$  symmetry of periodic trajectory of three coupled Fitzhugh–Nagumo neurons.

## A. Equivariant Hopf theorem

A fundamental bifurcation process in general dynamical systems is Hopf bifurcation,<sup>76,78</sup> in which a stable equilibrium loses stability and throws off a limit cycle. The main condition for Hopf bifurcation is that the Jacobian  $D_x f$  has nonzero imaginary eigenvalues at some value  $\lambda = \lambda_0$ , referred to as *critical eigenvalues*. Some technical conditions are also needed: the critical eigenvalues must be simple, there should be no resonances, and the critical eigenvalues should cross the imaginary axis with nonzero speed.

These conditions are generic in dynamical systems without symmetry. Non-resonance (other than 1:1 resonance which arises for multiple eigenvalues) and the eigenvalue crossing condition are also generic in symmetric systems, but simplicity of the critical eigenvalues is usually not, so the standard Hopf theorem does not apply. However, there is a version adapted to symmetric systems, involving phase shift symmetries. A phase shift can be viewed as time translation modulo the period  $T$ , leading to an action of  $\mathbb{R}/T\mathbb{Z}$ , isomorphic to the *circle group*  $\mathbb{S}^1 = \mathbb{R}/\mathbb{Z}$ .

At a non-zero imaginary critical eigenvalue, the critical eigenspace  $E$  supports an action not just of  $\Gamma$ , but of  $\Gamma \times \mathbb{S}^1$ . The  $\mathbb{S}^1$ -action is related to, but different from, the phase shift action; it is determined by the exponential of the Jacobian  $J|_E$  on  $E$ . Specifically, if the imaginary eigenvalues are  $\pm i\omega$ , then  $\theta \in \mathbb{S}^1$  acts on  $E$  like the matrix  $\exp(\frac{2\pi\theta}{\omega} J|_E)$ .

The Equivariant Hopf Theorem is analogous to the Equivariant Branching Lemma, but the symmetry group  $\Gamma$  is replaced by  $\Gamma \times \mathbb{S}^1$ . A subgroup  $\Sigma \subset \Gamma \times \mathbb{S}^1$  is  $\mathbb{C}$ -axial if  $\Sigma$  is an isotropy subgroup of the action of  $\Gamma \times \mathbb{S}^1$  on  $E$  and  $\dim \text{Fix}(\Sigma) = 2$ . In Ref. 62 (see also Refs. 64 and 70), we proved.

**Theorem 5.1 (Equivariant Hopf Theorem).** *If the Jacobian has purely imaginary eigenvalues, then generically for any  $\mathbb{C}$ -axial subgroup  $\Sigma \subseteq \Gamma \times \mathbb{S}^1$  acting on the critical eigenspace, there exists a branch of periodic solutions with spatio-temporal symmetry group  $\Sigma$  (On solutions,  $\mathbb{S}^1$  acts by phase shifts.).*

The proof adapts an idea of Hale,<sup>77</sup> which reformulates Hopf bifurcation in terms of *loop space*, the space of all maps  $\mathbb{S}^1 \rightarrow X$ . The group  $\mathbb{S}^1$  acts on loop space by time translation (scaled by the period). Periodic solutions of an ODE correspond to zeros in loop space of an associated non-linear operator. The technique of Liapunov–Schmidt reduction<sup>61</sup> converts this problem into finding the zero-set of a *reduced function* on the critical eigenspace. If the original ODE has symmetry group  $\Gamma$ , the reduced function has symmetry group  $\Gamma \times \mathbb{S}^1$ .

Earlier, Golubitsky and Langford<sup>52</sup> used the same technique to reduce the analysis of *degenerate* Hopf bifurcations (not satisfying the eigenvalue-crossing condition) to the classification of  $\mathbb{Z}_2$ -equivariant singularities.

Again, there are representation-theoretic conditions on the critical eigenspace.<sup>70</sup> Generically, it is either non-absolutely irreducible, or a direct sum of two copies of the same absolutely irreducible representation.

### 1. Poincaré–Birkhoff normal form

Liapunov–Schmidt reduction does not preserve the stability conditions for a solution, but a closely related technique does. This is reduction to Poincaré–Birkhoff normal form, described for example, in Broer.<sup>15</sup> Write the ODE in the form

$$\frac{dx}{dt} = f(x) = Lx + f_2(x) + f_3(x) + \cdots,$$

where  $x \in \mathbb{R}^n$ , the first term  $Lx$  is the linearization, and  $f_k(x)$  is polynomial of degree  $k$ . Successive polynomial changes of coordinates can be chosen to simplify  $f_2$ , then  $f_3$ , and so on. These changes compose to give a coordinate change  $x \mapsto y$  and a transformed ODE

$$\frac{dy}{dt} = Ly + g_2(y) + g_3(y) + \cdots,$$

where the  $g_k(y)$  satisfy extra restrictions.

In particular, there is an important relation to symmetry. Namely, define the 1-parameter subgroup

$$\mathbb{S} = \overline{\exp(sL^T)} \subseteq \mathrm{GL}(n),$$

where the bar indicates closure. Suppose that  $f$  is  $\Gamma$ -equivariant. By analyzing the normal form reduction procedure, Elphick *et al.*<sup>39</sup> proved that  $\Gamma$ -equivariant coordinate changes can be chosen so that each  $g_k(y)$  is  $\Gamma \times \mathbb{S}$ -equivariant.

That is, the normal form, truncated at any given degree, acquires additional symmetries  $\mathbb{S}$ . The “tail” remaining after truncation is only  $\Gamma$ -equivariant, but for many purposes, it can be neglected if  $k$  is large enough. In general,  $\mathbb{S}$  is a torus group  $\mathbb{T}^m$  when  $L$  is semisimple, and  $\mathbb{T}^m \times \mathbb{R}$  if  $L$  has a non-trivial nilpotent part. So, here we see another example of a symmetry group induced by the bifurcation.

### B. $H/K$ theorem: Motivation and statement

The example in Sec. IV B 2 illustrates a general principle about periodic states. A periodic trajectory has *two* natural symmetry groups. One is the group  $H$  of transformations that fix the periodic orbit as a set, but change its time-parametrization. The other is the group  $K$  of transformations that fix each point in the periodic orbit, and thus leave its time-parametrization unchanged. The pairs of subgroups  $(H, K)$  of  $\Gamma$  that can arise as setwise and pointwise symmetries of a periodic state of a  $\Gamma$ -equivariant ODE are characterized by the  $H/K$  Theorem.<sup>17,64</sup>

**Theorem 5.2.** *If  $\Gamma$  is a finite group, there exists a  $\Gamma$ -equivariant ODE with a periodic state determining a pair of subgroups  $(H, K)$  if and only if:*

- (1)  $H/K$  is cyclic.
- (2)  $K$  is an isotropy subgroup of  $\Gamma$ .
- (3)  $\dim \mathrm{Fix}(K) \geq 2$ , and if the dimension equals 2 then either  $H = K$  or  $H$  is the normalizer of  $K$ .
- (4)  $H$  fixes a connected component of  $\mathrm{Fix}(K) \setminus \bigcup_{\gamma \notin K} \mathrm{Fix}(\gamma) \cap \mathrm{Fix}(K)$ .

Item (4) is a technical condition on the geometry of the action of  $\Gamma$  and will not be explained here, except to say, that it excludes certain obstacles created by the invariance of fixed-point spaces. The normalizer of a subgroup  $H$  of  $\Gamma$  is the largest subgroup  $\Delta$  such that  $H$  is a normal subgroup of  $\Delta$ .

The  $H/K$  Theorem shows that the pairs  $(H, K)$  associated with a periodic state are constrained in a precise manner, and can be classified group-theoretically for any representation of a finite group  $\Gamma$ . It does not imply the existence of such states for any given  $\Gamma$ -equivariant ODE, but it does provide an exhaustive catalogue of the possible pairs of pointwise and setwise symmetries of a periodic orbit. Knowing this, it becomes possible to carry out a systematic search for periodic states with given spatio-temporal symmetry in any specific ODE.

We call  $K$  the group of *spatial symmetries* of the periodic state, and  $H$  the group of *spatio-temporal symmetries*. The cyclic group  $H/K$  acts on the state by phase shifts. If its order is  $p$ , these are shifts by integer multiples of  $T/p$  where  $T$  is the period. For example, the discrete rotating wave in Figure 4 (right) has  $H = \mathbb{Z}_3, K = 1$ , so  $H/K \cong \mathbb{Z}_3$ , and the phase shifts are integer multiples of  $T/3$ .

### 1. Application: Animal gaits

The  $H/K$  Theorem was originally motivated by the classification of gait patterns in a model of quadruped locomotion.<sup>17</sup> Gaits are widely thought to be generated by a network of spinal neurons called a *central pattern generator* or CPG. The same network can produce more than one pattern when parameters (such as connection strengths or inputs from elsewhere) vary. Gaits can be characterized (in part) by the phases of the gait cycle at which a given leg hits the ground. Figure 5 (upper) shows these patterns for the gaits *walk*, *bound*, *pace*, and *trot*. Collins and Stewart<sup>28,29</sup> interpreted

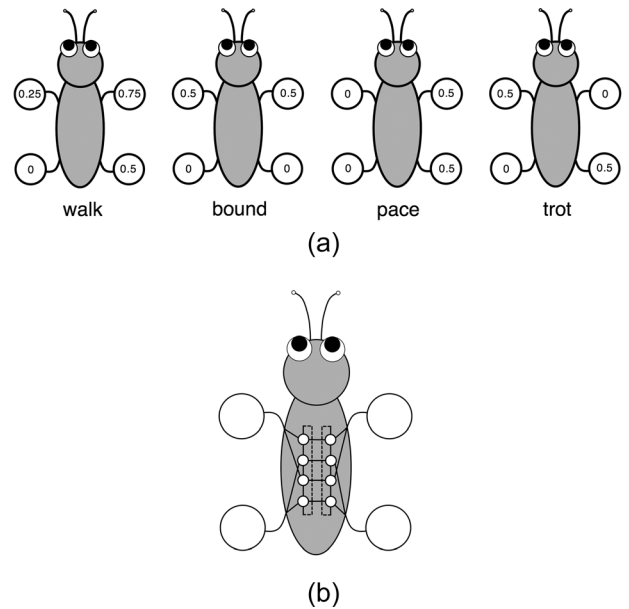


FIG. 5. Upper: Phase shifts (as fraction of gait cycle) for four standard quadruped gaits. Lower: Schematic representation of hypothetical 8-cell quadruped CPG showing assignment of cells to legs.



these phase relations as spatio-temporal symmetries and considered several CPG architectures.

The aim of Ref. 17 was to “reverse engineer” the schematic CPG architecture using the observed spatio-temporal symmetries of standard quadruped gaits. All fractions of the gait period  $T$  observed in the gaits in Figure 5 (upper) are integer multiples of  $T/4$ . More specifically, front-back phase shifts (between legs on the same side of the animal) are integer multiples of  $T/4$ , while left-right phase shifts (between corresponding legs on opposite sides) are integer multiples of  $T/2$ . The natural model for  $T/4$  phase shifts is a cyclic symmetry group  $\mathbb{Z}_4$ , and the natural model for  $T/2$  phase shifts is a cyclic symmetry group  $\mathbb{Z}_2$ . This suggests a CPG architecture with symmetry group  $\mathbb{Z}_4 \times \mathbb{Z}_2$ , because front-back and left-right symmetries act independently.

The simplest CPG of this kind, Figure 5 (lower), has eight cells. This figure is highly schematic. Each cell might represent a “module”: a small network of neurons. Also, not all potential connections are shown, because including them would create a complicated and confusing figure. The connections shown indicate the action of the symmetry group, *not* the neural connections in a hypothetical CPG. The only constraint is that if the CPG has a connection between some pair of cells, then all pairs of cells obtained by applying the  $\mathbb{Z}_4 \times \mathbb{Z}_2$  symmetry group must also be connected.

As well as being the simplest CPG with  $\mathbb{Z}_4 \times \mathbb{Z}_2$  symmetry, the 8-cell network is the smallest one that satisfies a specific set of conditions motivated by observed gaits. In Refs. 68 and 69, equivariant bifurcation theory was used to predict the possible occurrence of six distinct gaits (two occur as time-reversal pairs) arising by Hopf bifurcation. Five of these gaits (walk, trot, pace, bound, and pronk) are well known in animals. The sixth, the *jump*, can be seen in bucking broncos. It was known to Muybridge,<sup>97</sup> and has also been observed in the Siberian souslik and Norway rat, Gambaryan.<sup>49</sup>

The  $H/K$  Theorem predicts many other gaits, not arising by generic  $\mathbb{Z}_4 \times \mathbb{Z}_2$ -symmetric Hopf bifurcation from a group invariant equilibrium. These include “mixed-mode” gaits such as the transverse and rotary gallop, which can be obtained as secondary bifurcations from trot and pace, Buono.<sup>16</sup> It has also been applied to bipeds.<sup>100</sup>

## VI. MODE INTERACTIONS

A *mode interaction* occurs when two generically distinct local bifurcations occur in the same location in phase space and at the same parameter value. This is a codimension-2 phenomenon, whose generic occurrence requires at least two parameters: often a bifurcation parameter  $\lambda$  and an auxiliary parameter  $\alpha$ . Varying  $\alpha$  splits the bifurcations apart, so that they occur for nearby but distinct values of  $\lambda$ . In addition, the nonlinear interaction between the two modes often leads to new and surprising states. Thus, the mode interaction point acts as an “organizing center” at which the bifurcation is degenerate, but can be unfolded into a pair of generic bifurcations by varying  $\alpha$ .

Specifically, consider a parametrized family of  $\Gamma$ -equivariant bifurcation problems

$$\frac{dx}{dt} = f(x, \lambda, \alpha) \quad x \in \mathbb{R}^n, \lambda, \alpha \in \mathbb{R}.$$

A point  $(x_0, \lambda_0, \alpha_0)$  is a *mode interaction* if  $Df|_{(x_0, \lambda_0, \alpha_0)}$  has two distinct critical eigenspaces. These are “as generic as possible” subject to symmetry. There are thus three kinds of mode interaction: steady-state mode interaction (both eigenvalues zero); steady-state/Hopf mode interaction (one zero and one nonzero pair of imaginary eigenvalues); and Hopf/Hopf mode interaction (two distinct pairs of nonzero imaginary eigenvalues).

Generically, the real eigenspaces are absolutely irreducible for  $\Gamma$ , and the imaginary ones are  $\Gamma$ -simple. Also generically, varying  $\alpha$  splits the bifurcations into two generic steady-state or Hopf bifurcations.

The main dynamical implication of a mode interaction is that “secondary” states may occur generically. These states branch from the primary branches given by the two separate bifurcations, and sometimes link them. In Hopf/Hopf mode interactions, for example, quasiperiodic secondary branches sometimes occur.

When  $\Gamma = \mathbb{O}(2)$ , all three types of mode interaction have been classified using singularity theory in combination with phase-amplitude decomposition: see the summary in Ref. 70 and references therein.

### A. Couette–Taylor flow

We continue the discussion from Sec. IV A 3. Striking examples of mode interactions arise experimentally in the Couette–Taylor experiment, Andereck *et al.*<sup>3</sup> They can also be found numerically in the Navier–Stokes equations model of the experiment, DiPrima and Grannick,<sup>37</sup> Chossat *et al.*,<sup>22,26</sup> and Langford *et al.*<sup>87</sup> In this system, a wide variety of experimentally observed states can be predicted and understood using a reduction of the problem at parameter values (rotation speeds of the two cylinders) where mode interactions occur. See Chossat and Iooss<sup>25,26</sup> and Refs. 53, 63, and 64.

For example, the Hopf/steady-state model interaction leads to eight states: Couette flow, Taylor vortices, ribbons, spirals, twisted vortices, wavy vortices, plus two unknown states.<sup>63</sup> Golubitsky and Langford<sup>53</sup> used a numerical approach to Liapunov–Schmidt reduction to make quantitative predictions about which of these states occur, and are stable, for given parameter values near this mode interaction. Their analysis predicted stable wavy vortices, which had not been reported experimentally for those parameter values. The prediction was verified by Tagg *et al.*<sup>119</sup> Similarly, Chossat *et al.*<sup>22</sup> used a numerical approach based on center manifold reduction of Hopf/Hopf mode interactions to understand a variety of states including interpenetrating spirals.

### B. Other work on mode interactions

Mode interactions have been used to discuss secondary states in many classical fluid mechanics problems including the Faraday surface wave experiment, Crawford *et al.*,<sup>31</sup> Bénard convection between concentric spheres; spatially

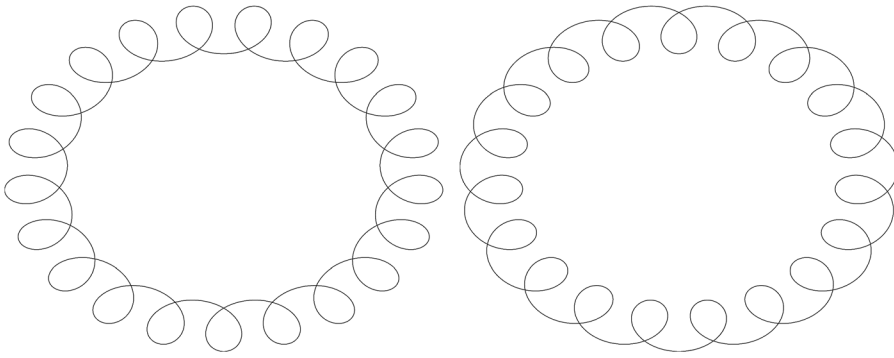


FIG. 6. Epicycle motion of spiral tip: outward and inward petals.

localized states, Burke and Knobloch;<sup>19</sup> and patterns in the heartbeat of the medicinal leech, Buono and Palacios.<sup>18</sup> The number of examples studied during the past two decades is extensive.

## VII. NON-COMPACT EUCLIDEAN SYMMETRY

Spiral waves are a commonly observed phenomenon in PDEs with planar Euclidean symmetry, such as reaction-diffusion equations. Such waves have been observed both in experiments<sup>89,126</sup> and in numerical simulations.<sup>11,81</sup> In suitable circumstances, the spiral can *meander*—its tip describes “epicyclic” paths in the plane, see Figure 6. Classically, such curves are called *epicycloids* or *hypocycloids*, depending on which way the “petals” point.

In more detail: planar spirals are rotating waves, so the tip of the spiral traces out a circle in the plane. When the tip meanders, it exhibits quasiperiodic two-frequency motion, which can be thought of as an epicyclic motion superimposed on the basic spiral wave circle. When the motion on the epicycle is in the same orientation as the motion on the circle (either clockwise or counterclockwise), then the petals of the flowers point in; when the motions have the opposite orientation, the petals point out. Winfree<sup>126</sup> observed both types of quasiperiodic motion and the possibility that the direction of the petals can change—we call this a change in *petality*—as a system parameter is varied.

However, in Barkley’s numerical simulation<sup>8</sup> and in experiments such as those by Li *et al.*,<sup>89</sup> a resonance phenomenon is observed. As the change in petality is approached, the amplitude of the second frequency grows unboundedly large, Figure 7. One of the exciting advances in equivariant bifurcation theory in the 1990s occurred when Barkley<sup>10</sup> discovered that meandering of the spiral tip and the resonant motion are both consequences of Hopf bifurcation with Euclidean symmetry and when Fiedler *et al.*<sup>42,127</sup> showed that this observation could be made rigorous for a class of reaction-diffusion systems. Our exposition follows Refs. 54 and 64.

### A. Heuristic description of unbounded tip motion

We can think of a planar rotating wave as a pattern that rotates at constant speed  $\omega_1$  about a fixed point. If the pattern has a distinctive marker, such as a tip, then that marker will move at constant speed on a circle. Moreover, if that pattern undergoes a Hopf bifurcation with Hopf frequency  $\omega_2$ , then

the epicyclic motion of the spiral tip can be written phenomenologically as

$$Q(t) = e^{i\omega_1 t}(z_1 + e^{-i\omega_2 t}z_2), \quad (7.1)$$

where  $z_1 \in \mathbb{R}$  and  $z_2 \in \mathbb{C}$ . In the epicyclic motion (7.1), the Hopf bifurcation point corresponds to the secondary amplitude  $z_2 = 0$ . In these coordinates, the change in petality occurs when  $\omega_1 = \omega_2$ . From the standard bifurcation-theoretic viewpoint, there is nothing significant about Hopf bifurcation at this critical parameter value.

Barkley<sup>10</sup> observed that Euclidean symmetry forces three critical zero eigenvalues (two for translation and one for rotation) in addition to the two critical Hopf eigenvalues. Assuming that some kind of “center manifold” exists, the time evolution of the meandering spiral tip can be described by a five-dimensional Euclidean-equivariant system of ODEs. Three variables represent the Euclidean group—the translation variable  $p \in \mathbb{R}^2 \cong \mathbb{C}$  and the rotation variable  $\varphi \in \mathbb{S}^1$ —and the variable  $q \in \mathbb{C}$  represents the amplitude of the eigenfunction of Hopf bifurcation. Along a solution,  $p(t)$  represents the translation of the spiral wave as a function of time. So, the motion of the spiral tip is unbounded if  $p(t)$  is unbounded. However, symmetry allows us to do this calculation.

In these variables Barkley<sup>10</sup> notes that translational symmetry and rotational symmetry act by

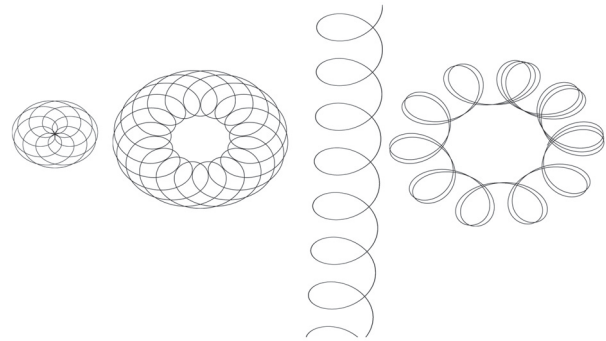


FIG. 7. Growth of flower near change in petality: path of  $\int_0^t Q(s)ds$ , where  $Q(t)$  is as in (7.1) with  $\omega_1 = 1$ ,  $z_1 = 1$ ,  $z_2 = 0.3$ , and  $\omega_2 = 0.61, 0.85, 1, 1.11$ .

$$T_x(p, \varphi, q) = (p + x, \varphi, q),$$

$$R_\theta(p, \varphi, q) = (e^{i\theta}p, \varphi, q).$$

Therefore, the ODE vector field is independent of  $p$ , and the  $(\varphi, q)$  equations decouple. That is, symmetry implies that the “center manifold” equations have the form

$$\begin{aligned}\dot{p} &= e^{i\varphi}f(q), \\ \dot{\varphi} &= g(q), \\ \dot{q} &= h(q).\end{aligned}\tag{7.2}$$

Heuristically, in Hopf bifurcation, we can assume the right hand side of the  $\dot{p}$  equation is (7.1). So, when  $\omega_1 = \omega_2$ , we can determine how the translation symmetry changes in  $t$  along the solution by just computing

$$\int_0^t Q(s)ds = \frac{1}{i\omega_1} e^{i\omega_1 t} z_1 + tz_2.$$

In particular, at the point of petality change, the spiral tip appears to drift off to infinity in a straight line, Figure 7. Thus, unbounded *growth* of the second frequency amplitude is a feature that is connected with change in petality.

## B. Reaction-diffusion systems

Barkley<sup>9</sup> performed a numerical linear stability analysis for the basic time-periodic spiral wave solution and showed that there is a Hopf bifurcation. In particular, a simple pair of eigenvalues crosses the imaginary axis while three neutral eigenvalues lie on the imaginary axis and the remainder of the spectrum is confined to the left half-plane. Starting from Barkley’s numerical calculation, Wulff<sup>127</sup> proved, using Liapunov–Schmidt reduction, that resonant unbounded growth occurs in Hopf bifurcation near the codimension-2 point where  $\omega_1 = \omega_2$ . Her proof is nontrivial because technical difficulties, such as small divisors and the nonsmoothness of the group action, must be overcome. Feidler *et al.*<sup>42,105</sup> (see also Ref. 54) have proved, under certain hypotheses, that a “center manifold” exists and the heuristic description is an accurate one.

The analysis of this bifurcation has led to a number of papers on the expected dynamics in Euclidean invariant systems. We mention issues surrounding hypermeandering.<sup>4–6,43</sup>

## VIII. NETWORKS

Over the past decade, we and others have introduced a formal framework for studying networks of coupled ODEs. They are called *coupled cell systems*, and the underlying network is a *coupled cell network*. More precisely, this is a directed graph whose nodes and edges are classified into “types.” Nodes “cells” represent the variables of a component ODE. Edges “arrows” between cells represent couplings from the tail cell to the head cell. Nodes of the same type have the same phase spaces (up to a canonical identification); edges “arrows” of the same type represent identical couplings.

Each network diagram (henceforth we omit “coupled cell”) encodes a space of *admissible vector fields*  $f$ , determining the *admissible ODEs*  $dx/dt = f(x)$ . Intuitively, these are the ODEs that correspond to the couplings specified by the network, and respect the types of nodes and edges. The precise formalism is not important here, so instead, we outline what it involves and give a typical example.

In order for a vector field  $f = (f_1, \dots, f_n)$  to be admissible, we require:

- (1) If  $i$  is a cell, the variables appearing in the corresponding component  $f_i$  of the vector field are those corresponding to cell  $i$  itself, and the tail cells of all input arrows.
- (2) If the sets of input arrows to cells  $i$  and  $j$  are isomorphic (the same number of arrows of each type), then components  $f_i$  and  $f_j$  are given by the same function, with an assignment of variables that respects the isomorphism.
- (3) Applying this condition when  $i = j$  yields a symmetry condition worth stating in its own right:
- (4) If cell  $i$  has several input arrows of the same type,  $f_i$  is invariant under permutations of the tail cells of those arrows.

Figure 8 shows a typical example, a network with five cells. There are two types of cell (square, circle) and three types of arrow (solid, dotted, wavy). Admissible ODEs have the form

$$\begin{aligned}\dot{x}_1 &= f(x_1, x_4), \\ \dot{x}_2 &= g(x_2, x_3, x_5), \\ \dot{x}_3 &= f(x_3, x_5), \\ \dot{x}_4 &= h(x_4, \overline{x_1, x_2}), \\ \dot{x}_5 &= h(x_5, \overline{x_2, x_3}),\end{aligned}$$

where the over line indicates that  $h$  is symmetric in its second and third arguments.

## A. Synchrony and phase relations

The main features of a dynamical system considered in modern nonlinear dynamics are those that are invariant under coordinate changes. It is natural to adopt the same philosophy for network dynamics, but it is important to recognize that coupled cell systems have extra structure, imposing constraints that restrict the permissible coordinate

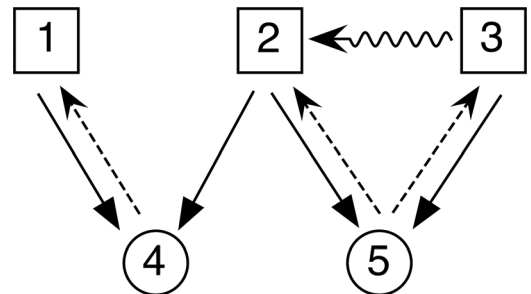


FIG. 8. A network with five cells.



changes. Such coordinate changes are characterized in Refs. 66 and 67.

These restrictions permit new phenomena that are not invariant for a general dynamical system. Two basic examples are:

- (1) *Synchrony*: If  $x(t) = (x_1(t), \dots, x_n(t))$  is a solution of an admissible ODE,  $i$  and  $j$  are cells, when is  $x_i(t) \equiv x_j(t)$  for all  $t \in \mathbb{R}$ ?
- (2) *Phase Relations*: If  $x(t)$  is a periodic solution of an admissible ODE, and  $i$  and  $j$  are cells, when does there exist a phase shift  $\theta_{ij} \in [0, 1)$  such that  $x_i(t) \equiv x_j(t + \theta_{ij}T)$  for all  $t \in \mathbb{R}$ ?

Synchrony and phase relations can be viewed as *patterns* in network dynamics, analogous to spatial and spatio-temporal patterns in the equivariant dynamics of PDEs. Here, the network architecture plays the role of space; in effect, a network is a discrete space, continuous time dynamical system. This is literally true for ODEs that are obtained as a spatial discretization of a PDE. The (global or partial) symmetries are now *permutations* of nodes and the associated arrows, so the technical setting is that of permutation representations. The three-cell FitzHugh–Nagumo model above is a typical illustration; here, the spatio-temporal pattern is “cycle the nodes and shift phase by  $\frac{1}{3}$  of the period.” Geometrically, the cycle rotates the network diagram.

There is a related phenomenon in which symmetry can force resonances among cells. For example, Figure 9 shows a 3-cell system with  $\mathbb{Z}_2$  symmetry, which interchanges cells 1 and 3 while fixing cell 2. This network supports a periodic state with a spatio-temporal symmetry that combines this interchange with a half-period phase shift. Now, cell 2 is “half a period out of phase with itself”; that is, it oscillates with half the overall period, creating a 1:2 resonance. We call such states *multirhythms*, and they can be considerably more complex. Section 3.6 of Ref. 64 gives an example of a 3:4:5 multirhythm in a 12-cell system. Filipinski and Golubitsky<sup>47</sup> analyze multirhythms in the context of Hopf bifurcation with a finite abelian symmetry group.

## B. Balanced colorings

In Sec. III B, we saw that in symmetric ODEs, there is a natural class of subspaces that are invariant under *any* equivariant map, namely, the fixed-point spaces of subgroups. These “universal” invariant subspaces impose significant constraints on dynamics. For networks, there is an analogous class of invariant subspaces for all admissible maps, but now these are determined by a combinatorial property known as “balance.”

*Definition 8.1.*



FIG. 9. A  $\mathbb{Z}_2$ -symmetric network supporting a multirhythm.

- (1) A *coloring* of the cells of a network assigns to each cell  $i$  a *color*  $k(i)$ , where  $k(i)$  belongs to some specified set  $K$ .

Formally,  $K$  corresponds to an equivalence relation “ $\sim$ ” on cells, in which  $i \sim j$  if and only if  $k(i) = k(j)$ . The colors are given by equivalence classes, so the choice of  $K$  is unimportant: what matters is when  $k(i) = k(j)$ .

- (2) The *synchrony subspace*  $\Delta_k$  determined by a coloring  $k$  is the subspace consisting of all points  $x = (x_1, \dots, x_n)$  for which  $k(i) = k(j) \Rightarrow x_i = x_j$ . That is, components of  $x$  for cells of the same color are synchronous (equal).
- (3) A coloring  $K$  is *balanced* if any two cells  $i, j$  of the same color have identically colored input sets (in the sense that corresponding tail cells of input arrows have the same colors, provided the correspondence is given by an input isomorphism).

Figure 10 (left) shows a balanced coloring of Figure 8.

Suppose that  $x(t)$  is a state of an admissible ODE of a network. The *pattern of synchrony* of  $x(t)$  is the coloring  $k$  given by

$$k(i) = k(j) \iff x_i(t) = x_j(t) \forall t \in \mathbb{R}.$$

By identifying cells with the same color, and associating to each such cluster the corresponding set of input arrows, we define a *quotient network*. The admissible maps for the quotient are precisely the admissible maps for the original network, but restricted to the corresponding synchrony space. Figure 10 (right) shows the quotient network for the balanced coloring of Figure 10 (left).

If a network has a global symmetry group of permutations, the fixed-point subspace of any subgroup  $\Sigma$  corresponds to a balanced coloring in which the colors correspond to orbits of  $\Sigma$ . So, equivariant and network dynamics come together in a consistent manner when networks have global symmetry groups. However, there are some subtleties in this context, mainly to do with possible differences between admissible and equivariant maps.<sup>56</sup>

We can now state three theorems relating synchrony on cells to balanced colorings, whose proofs become increasingly more difficult and technical. Say that a network is *path-connected*, or *transitive*, if any two cells are connected by a directed path of arrows.

### Theorem 8.2.

- (1) A synchrony space  $\Delta_k$  is invariant under all admissible maps if and only if the coloring  $k$  is balanced.

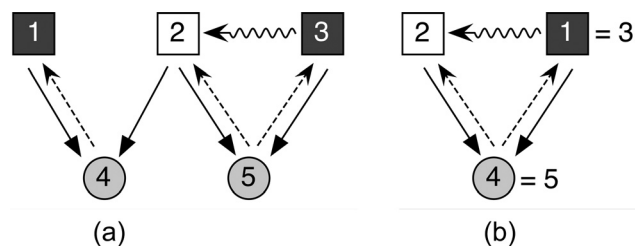


FIG. 10. Left: A balanced coloring of 5-cell network in Figure 8. Right: Corresponding quotient network.

- (2) In a path-connected network, an equilibrium state  $x$  has a rigid pattern of synchrony if and only if this pattern is balanced.
- (3) In a path-connected network, a periodic state  $x$  has a rigid pattern of synchrony if and only if this pattern is balanced.

*Proof.* (1) is proved in Ref. 115. (2) is proved in Ref. 71.

(3) is proved in Ref. 59.  $\square$

The main idea needed to prove (3) is the Rigid Synchrony Theorem, conjectured by Stewart and Parker.<sup>116</sup> This states that in a periodic state of a path-connected network, if two cells are rigidly synchronous, then their input cells, suitably associated, are also synchronous. A closely related result, the Full Oscillation Theorem, states that for a periodic state of a path-connected network, if at least one cell variable oscillates—that is, it is not in equilibrium—then after some arbitrarily small perturbation, all cells oscillate. Both theorems are proved in Ref. 59 by analyzing a specific class of admissible perturbations.

A generalization of the Rigid Synchrony Theorem, the Rigid Phase Theorem, states that in a periodic state of a path-connected network, if two cells are rigidly phase-related, then their input cells, suitably associated, are also phase-related, by the same fraction of the period. This theorem was also conjectured by Stewart and Parker,<sup>116</sup> and proved by Golubitsky *et al.*<sup>60</sup> Earlier, assuming this conjecture, Stewart and Parker<sup>117</sup> proved a basic structure theorem for path-connected networks with a rigid phase relation. Namely:

**Theorem 8.3.** *In a path-connected network, the quotient network obtained by identifying all rigidly synchronous cells has a global cyclic group of symmetries  $\mathbb{Z}_k$  for some  $k$ , and the phase difference concerned is an integer multiple of  $T/k$  where  $T$  is the period.*

Roughly speaking, this result proves that whenever a phase relation is observed in a periodic state of a path-connected network, and that relation is preserved by small perturbations of the model, then it must arise from a global cyclic symmetry of the quotient network defined by clusters of synchronous cells. This motivates the use of cyclically symmetric networks to model systems with this behavior; for example, animal gait patterns.

Different phase relations may correspond to different cyclic symmetry groups, as seen in the  $\mathbb{Z}_2 \times \mathbb{Z}_4$  network proposed for quadruped gaits.

## 1. Application: Rivalry

Wilson<sup>125</sup> proposes a neural network model for high-level decision-making in the brain, based on the phenomenon of binocular rivalry. Here, conflicting images are presented to the two eyes, and the visual system interprets this combination in sometimes surprising ways. Diekman *et al.*<sup>36</sup> observed that Wilson networks are useful for understanding rivalry itself. A Wilson network is trained on a set of signals or patterns, and its architecture is designed to detect these patterns and distinguish them from others. This architecture is achieved by setting up a list of *attributes*, which are features that differ between the patterns, such as color or

orientation. Each attribute can occur among a range of alternatives, called *levels*.

The monkey-text experiment of Kovács *et al.*<sup>85</sup> demonstrated a curious phenomenon in rivalry between the two images of Figure 11 (left). Subjects reported percepts that alternate, fairly randomly, between these two “mixed” images. However, some also reported an alternation between two “whole” images, neither of which occurred in the training set; see Figure 11 (right). Diekman *et al.*<sup>34,36</sup> considered a natural model using the Wilson network in Figure 12. This has two attributes, each with two levels, corresponding to which parts of the images appear in the “jigsaw” decomposition shown.

The behavior of the network is modeled by a system of admissible ODEs, employing a specific model of the neurophysiology known as a *rate model*.<sup>35,36</sup> Here, the state of each node is described by an *activity variable* and a *fatigue variable*. Nodes are coupled through a *gain function*.

The 4-cell network has  $\mathbb{Z}_2 \times \mathbb{Z}_2$  symmetry. Based on this symmetry, Diekman and Golubitsky<sup>34</sup> remark that equivariant Hopf bifurcation predicts four distinct periodic states. In two, cells in each column oscillate in synchrony. In the other two, cells in each column oscillate a half period out of phase.

The inhibitory connections in the model network suppress the states in which the nodes in a column are synchronous. The two remaining states are those with half-period phase shifts on diagonal pairs (the training set) or on left/right pairs (the other percepts reported in experiments). These *derived patterns* are predicted in many similar rivalry experiments.

Diekman *et al.*<sup>35</sup> have also applied quotient networks to a class of Wilson models of rivalry.

## C. Network H/K theorems

There are several contexts in which analogs of the *H/K* Theorem can be posed for hyperbolic periodic solutions on networks. First, determine the pairs  $H \supset K$  when the network has symmetry for equivariant vector fields or specifically for admissible vector fields. Second, for admissible vector fields, classify the  $H \subset K$  pairs or patterns of rigid phase shift synchrony. Third, the question can be investigated for several different cell phase spaces, with different answers.

For a symmetric network,  $H$  and  $K$  can be defined as the setwise and pointwise symmetry groups of the periodic state concerned. Josić and Török<sup>82</sup> considered the case when the cell phase spaces are  $\mathbb{R}^n$  for  $n \geq 2$ , where the result is essentially the same as the *H/K* Theorem for equivariant dynamics. They also observed that the answers change for cell phase spaces  $\mathbb{S}^1$  (phase oscillators).

For general path-connected networks, the Rigid Synchrony Theorem of Ref. 59 suggests that for a given periodic state, the role of  $K$  should be played by the balanced coloring determined by synchrony. By Stewart and Parker,<sup>117</sup> the corresponding quotient network (the contraction corresponding to “mod  $K$ ”) possesses global cyclic

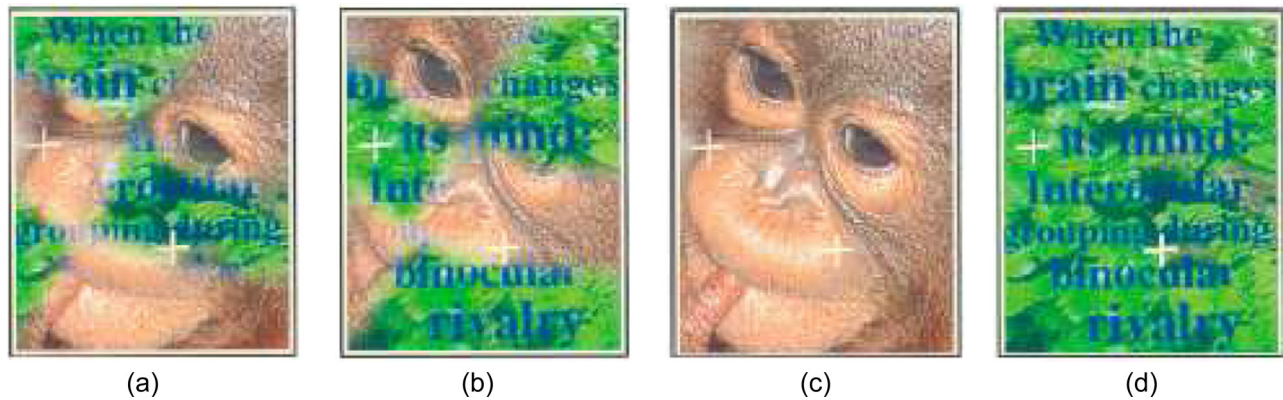


FIG. 11. Monkey-text experiment. Left: training set. Right: percepts reported by some subjects. Reproduced by permission from Kovács *et al.* Proc. Nat. Acad. Sci. U. S. A. **93**, 15508 (1996). Copyright 1996 by National Academy of Sciences of the United States of America.

group symmetry. This cyclic group plays the role of  $H$ , since it determines both the setwise symmetries of the periodic state, and the possible rigid phase shifts.

The relation between these various generalizations of the  $H/K$  Theorem are discussed in Ref. 55, but are not yet fully understood.

## IX. ANOMALOUS GROWTH IN NETWORK HOPF BIFURCATION

Network structure affects generic bifurcations as well as dynamics. Unexpected singularity-theoretic degeneracies can occur in steady-state bifurcation for some networks.<sup>113,114</sup> These lead to non-generic growth rates for bifurcating branches.

One of the examples of strange network phenomena discussed in Ref. 56 is Hopf bifurcation in a 3-cell feed-forward network, Figure 13. In a general dynamical system, generic Hopf bifurcation creates a bifurcating branch of equilibria whose amplitude grows like  $\lambda^{1/2}$  where  $\lambda$  is the bifurcation parameter. However, the growth rate is different for generic Hopf bifurcation in this 3-cell network.

The feed-forward architecture implies that the Jacobian has a nontrivial nilpotent part at Hopf bifurcation, and a non-rigorous analysis in Ref. 56 suggests the occurrence of an

anomalous growth rate. Elmhirst and Golubitsky<sup>38</sup> confirm this conjecture rigorously. They prove that under suitable generic conditions, there is a bifurcating branch of periodic states in which cell 1 is steady, the amplitude of the oscillation of cell 2 grows like  $\lambda^{1/2}$ , where  $\lambda$  is the bifurcation parameter, and the amplitude of the oscillation of cell 3 has an anomalous growth rate of  $\lambda^{1/6}$ . This increases more steeply than  $\lambda^{1/2}$  near the origin. An alternative treatment using center manifold theory is developed in Ref. 57. There is an analogous system with a feed-forward chain of  $m$  nodes. Synchrony-breaking Hopf bifurcation then leads to solutions that grow  $\lambda^{1/18}$  in the fourth node,  $\lambda^{1/54}$  in the fifth node, etc. For a proof see Rink and Sanders.<sup>102</sup>

A potential application of this behavior is to the design of a nonlinear filter which selects oscillations close to a specific frequency and amplifies them.<sup>58</sup> Experimental proof-of-concept can be found in McCullen *et al.*<sup>90</sup>

## X. OTHER CONTEXTS

In closing, it should be made clear that there are many other contexts in which periodic states arise in a nonlinear dynamical system and can be analyzed using a similarly Thomist approach. We mention a few for completeness.

The Takens–Bogdanov bifurcation is a codimension-2 bifurcation involving a periodic cycle and a homoclinic connection, associated with a zero critical eigenvalue in a nontrivial  $2 \times 2$  Jordan block (nonzero nilpotent part). Analogous bifurcations can be studied for symmetric ODEs.

Bifurcations from rotating waves and other relative equilibria have been studied for compact groups by Field,<sup>44</sup> Krupa,<sup>86</sup> and Vanderbauwhede *et al.*<sup>123</sup> The analysis involves a normal/tangential decomposition of the vector field in a tubular neighborhood of the relative equilibrium.

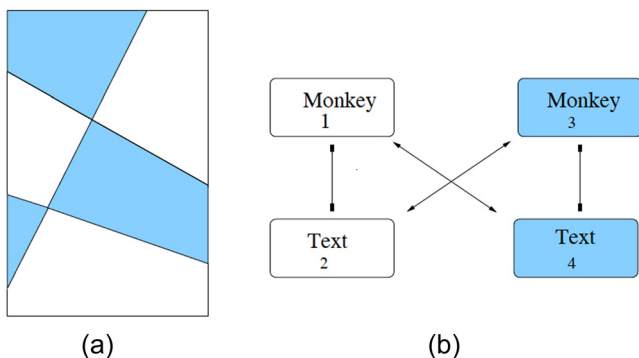


FIG. 12. Monkey-text experiment. Left: “jigsaw” decomposition of images. Right: Wilson network model. Vertical connections are inhibitory to create “winner takes all” choices. Diagonal connections are excitatory, to represent the training patterns.

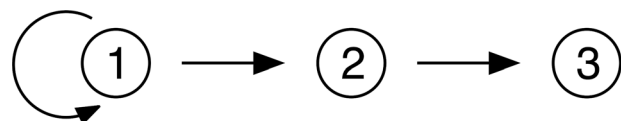


FIG. 13. A 3-cell feed-forward network.



The results of Barkley discussed in Sec. VII fit into this framework.

There are interesting similarities between periodic states in a Hamiltonian dynamical system, arising via the Liapunov Center Theorem and its generalization the Moser–Weinstein Theorem, and symmetric Hopf bifurcation. See Montaldi *et al.*<sup>91–94</sup>

Discrete time symmetric dynamics—iteration of equivariant mappings—can generate periodic orbits, along with more complex dynamics such as symmetric chaos, Chossat and Golubitsky<sup>23,24</sup> and Field and Golubitsky.<sup>45</sup>

Spatio-temporal symmetries of periodic states in forced symmetric systems have been studied in special cases, Ben-Tal.<sup>12</sup> The beginnings of a general theory can be found in Rosas.<sup>103</sup>

Finally, singularities in adaptive game theory<sup>124</sup> require yet another variant of Thom’s singularity theory, also covered by Damon’s general theory.<sup>32</sup>

## ACKNOWLEDGMENTS

The research of M.G. was supported in part by NSF Grant No. DMS-0931642 to the Mathematical Biosciences Institute.

- <sup>1</sup>J. F. Adams, *Lectures on Lie Groups* (University of Chicago Press, Chicago, 1969).
- <sup>2</sup>V. I. Arnold, “Proof of a theorem of A. N. Kolmogorov on the preservation of conditionally periodic motions under a small perturbation of the Hamiltonian,” *Usp. Mat. Nauk* **18**, 13–40 (1963).
- <sup>3</sup>D. C. D. Andereck, S. S. Liu, and H. L. Swinney, “Flow regimes in a circular Couette system with independently rotating cylinders,” *J. Fluid Mech.* **164**, 155–183 (1986).
- <sup>4</sup>P. Ashwin and I. Melbourne, “Noncompact drift for relative equilibria and relative periodic orbits,” *Nonlinearity* **10**, 595–616 (1997).
- <sup>5</sup>P. Ashwin, I. Melbourne, and M. Nicol, “Drift bifurcations of relative equilibria and transitions of spiral waves,” *Nonlinearity* **12**, 741–755 (1999).
- <sup>6</sup>P. Ashwin, I. Melbourne, and M. Nicol, “Hypermeander of spirals; local bifurcations and statistical properties,” *Physica D* **156**, 364–382 (2001).
- <sup>7</sup>A. K. Bajaj and P. R. Sethna, “Flow induced bifurcations to three dimensional oscillatory motions in continuous tubes,” *SIAM J. Appl. Math.* **44**, 270–286 (1984).
- <sup>8</sup>D. Barkley, “A model for fast computer-simulation of waves in excitable media,” *Physica D* **49**, 61–70 (1991).
- <sup>9</sup>D. Barkley, “Linear stability analysis of rotating spiral waves in excitable media,” *Phys. Rev. Lett.* **68**, 2090–2093 (1992).
- <sup>10</sup>D. Barkley, “Euclidean symmetry and the dynamics of rotating spiral waves,” *Phys. Rev. Lett.* **72**, 165–167 (1994).
- <sup>11</sup>D. Barkley, M. Kness, and L. S. Tuckerman, “Spiral-wave dynamics in a simple model of excitable media: The transition from simple to compound rotation,” *Phys. Rev. A* **42**, 2489–2492 (1990).
- <sup>12</sup>A. Ben-Tal, A study of symmetric forced oscillators, Ph.D. thesis, University of Auckland, 2001.
- <sup>13</sup>P. C. Bressloff, J. D. Cowan, M. Golubitsky, P. J. Thomas, and M. C. Wiener, “Geometric visual hallucinations, Euclidean symmetry, and the functional architecture of striate cortex,” *Philos. Trans. R. Soc. London B* **356**, 1–32 (2001).
- <sup>14</sup>T. Bröcker and T. Tom Dieck, *Representations of Compact Lie Groups* (Springer, New York 1985).
- <sup>15</sup>H. Broer, “Formal normal form theorems for vector fields and some consequences for bifurcations in the volume preserving case,” in *Dynamical Systems and Turbulence, Warwick 1980*, edited by D. A. Rand and L. S. Young, Lecture Notes in Mathematics Vol. 898 (Springer, New York, 1981), pp. 54–74.
- <sup>16</sup>P.-L. Buono, “Models of central pattern generators for quadruped locomotion II: Secondary gaits,” *J. Math. Biol.* **42**, 327–346 (2001).

- <sup>17</sup>P.-L. Buono and M. Golubitsky, “Models of central pattern generators for quadruped locomotion: I. primary gaits,” *J. Math. Biol.* **42**, 291–326 (2001).
- <sup>18</sup>P.-L. Buono and A. Palacios, “A mathematical model of motoneuron dynamics in the heartbeat of the leech,” *Physica D* **188**, 292–313 (2004).
- <sup>19</sup>J. Burke and E. Knobloch, “Homoclinic snaking: Structure and stability,” *Chaos* **17**, 037102 (2007).
- <sup>20</sup>E. Buzano and M. Golubitsky, “Bifurcation on the hexagonal lattice and the planar Bénard problem,” *Philos. Trans. R. Soc. London A* **308**, 617–667 (1983).
- <sup>21</sup>D. Chillingworth and M. Golubitsky, “Symmetry and pattern formation for a planar layer of nematic liquid crystal,” *J. Math. Phys.* **44**, 4201–4219 (2003).
- <sup>22</sup>P. Chossat, Y. Demay, and G. Iooss, “Interactions des modes azimuthaux dans le problème de Couette-Taylor,” *Arch. Ration. Mech. Anal.* **99**(3), 213–248 (1987).
- <sup>23</sup>P. Chossat and M. Golubitsky, “Symmetry increasing bifurcation of chaotic attractors,” *Physica D* **32**, 423–436 (1988).
- <sup>24</sup>P. Chossat and M. Golubitsky, “Iterates of maps with symmetry,” *SIAM J. Math. Anal.* **19**, 1259–1270 (1988).
- <sup>25</sup>P. Chossat and G. Iooss, “Primary and secondary bifurcations in the Couette-Taylor problem,” *Jpn. J. Appl. Math.* **2**, 37–68 (1985).
- <sup>26</sup>P. Chossat and G. Iooss, *The Couette-Taylor Problem, Applied Mathematical Science* (Springer, 1994), Vol. 102.
- <sup>27</sup>G. Cicogna, “Symmetry breakdown from bifurcations,” *Lett. Nuovo Cimento* **31**, 600–602 (1981).
- <sup>28</sup>J. J. Collins and I. Stewart, “Hexapodal gaits and coupled nonlinear oscillator models,” *Biol. Cybern.* **68**, 287–298 (1993).
- <sup>29</sup>J. J. Collins and I. Stewart, “Coupled nonlinear oscillators and the symmetries of animal gaits,” *J. Nonlinear Sci.* **3**, 349–392 (1993).
- <sup>30</sup>J. Cooke and E. C. Zeeman, “A clock and wavefront model for control of the number of repeated structures during animal morphogenesis,” *J. Theor. Biol.* **58**, 455–476 (1976).
- <sup>31</sup>J. D. Crawford, E. Knobloch, and H. Reicke, “Period-doubling mode interactions with circular symmetry,” *Physica D* **44**, 340–396 (1990).
- <sup>32</sup>J. Damon, *The Unfolding And Determinacy Theorems for Subgroups of A and K Memoirs* (A.M.S. Providence, 1984), Vol. 306.
- <sup>33</sup>Y. Demay and G. Iooss, “Calcul des solutions bifurquées pour le problème de Couette-Taylor avec les deux cylindres en rotation,” *J. Mech. Theor. Appl.*, 193–216 (1984).
- <sup>34</sup>C. Diekmann and M. Golubitsky, “Network symmetry and binocular rivalry experiments,” *J. Math. Neurosci.* **4**, 12 (2014).
- <sup>35</sup>C. Diekmann, M. Golubitsky, T. McMillen, and Y. Wang, “Reduction and dynamics of a generalized rivalry network with two learned patterns,” *SIAM J. Appl. Dyn. Syst.* **11**, 1270–1309 (2012).
- <sup>36</sup>C. Diekmann, M. Golubitsky, and Y. Wang, “Derived patterns in binocular rivalry networks,” *J. Math. Neurosci.* **3**, 6 (2013).
- <sup>37</sup>R. C. DiPrima and R. N. Grannick, “A nonlinear investigation of the stability of flow between counter-rotating cylinders,” in *Instability of Continuous Systems*, edited by H. Leipholz (Springer-Verlag, Berlin, 1971), 55–60.
- <sup>38</sup>T. Elmhirst and M. Golubitsky, “Nilpotent Hopf bifurcations in coupled cell systems,” *SIAM J. Appl. Dyn. Syst.* **5**, 205–251 (2006).
- <sup>39</sup>C. Elphick, E. Tirapegui, M. E. Brachet, P. Coulet, and G. Iooss, “A simple global characterization for normal forms of singular vector fields,” *Physica D* **29**, 95–127 (1987).
- <sup>40</sup>G. B. Ermentrout and J. D. Cowan, “A mathematical theory of visual hallucination patterns,” *Biol. Cybern.* **34**, 137–150 (1979).
- <sup>41</sup>B. Fiedler, *Global Bifurcation of Periodic Solutions with Symmetry*, Lecture Notes Mathematics (Springer, Heidelberg, 1988), p. 1309.
- <sup>42</sup>B. Fiedler, B. Sandstede, A. Scheel, and C. Wulff, “Bifurcation from relative equilibria of noncompact group actions: Skew products, meanders and drifts,” *Doc. Math.* **1**, 479–505 (1996).
- <sup>43</sup>B. Fiedler and D. V. Turaev, “Normal forms, resonances, and meandering tip motions near relative equilibria of Euclidean group actions,” *Arch. Ration. Mech. Anal.* **145**, 129–159 (1998).
- <sup>44</sup>M. J. Field, “Equivariant dynamical systems,” *Trans. Am. Math. Soc.* **259**, 185–205 (1980).
- <sup>45</sup>M. J. Field and M. Golubitsky, *Symmetry in Chaos* (Oxford University Press, Oxford, 1992).
- <sup>46</sup>M. J. Field, M. Golubitsky, and I. Stewart, “Bifurcation on hemispheres,” *J. Nonlinear Sci.* **1**, 201–223 (1991).
- <sup>47</sup>N. Filipitski and M. Golubitsky, “The abelian Hopf  $H \bmod K$  theorem,” *SIAM J. Appl. Dyn. Syst.* **9**, 283–291 (2010).

- <sup>48</sup>R. FitzHugh, "Impulses and physiological states in theoretical models of nerve membrane," *Biophys. J.* **1**, 445–466 (1961).
- <sup>49</sup>P. P. Gambaryan, *How Mammals Run: Anatomical Adaptations* (Wiley, New York, 1974).
- <sup>50</sup>M. Golubitsky, "An introduction to catastrophe theory and its applications," *SIAM Rev.* **20**(2), 352–387 (1978).
- <sup>51</sup>M. Golubitsky, E. Knobloch, and I. Stewart, "Target patterns and spirals in planar reaction-diffusion systems," *J. Nonlinear Sci.* **10**, 333–354 (2000).
- <sup>52</sup>M. Golubitsky and W. F. Langford, "Classification and unfoldings of degenerate Hopf bifurcation," *J. Differ. Equations* **41**, 375–415 (1981).
- <sup>53</sup>M. Golubitsky and W. F. Langford, "Pattern formation and bistability in flows between counterrotating cylinders," *Physica D* **32**, 362–392 (1988).
- <sup>54</sup>M. Golubitsky, V. G. LeBlanc, and I. Melbourne, "Meandering of the spiral tip: An alternative approach," *J. Nonlinear Sci.* **7**, 557–586 (1997).
- <sup>55</sup>M. Golubitsky, L. Matamba Messi, and L. Spardy (unpublished).
- <sup>56</sup>M. Golubitsky, M. Nicol, and I. Stewart, "Some curious phenomena in coupled cell systems," *J. Nonlinear Sci.* **14**, 207–236 (2004).
- <sup>57</sup>M. Golubitsky and C. Postlethwaite, "Feed-forward networks, center manifolds, and forcing," *Discrete Contin. Dyn. Syst. Ser. A* **32**, 2913–2935 (2012).
- <sup>58</sup>M. Golubitsky, C. Postlethwaite, L.-J. Shiau, and Y. Zhang, "The feed-forward chain as a filter amplifier motif," *Coherent Behavior in Neuronal Networks*, edited by K. Josić, M. Matias, R. Romo, and J. Rubin (Springer, New York, 2009), pp. 95–120.
- <sup>59</sup>M. Golubitsky, D. Romano, and Y. Wang, "Network periodic solutions: Full oscillation and rigid synchrony," *Nonlinearity* **23**, 3227–3243 (2010).
- <sup>60</sup>M. Golubitsky, D. Romano, and Y. Wang, "Network periodic solutions: Patterns of phase-shift synchrony," *Nonlinearity* **25**, 1045–1074 (2012).
- <sup>61</sup>M. Golubitsky and D. G. Schaeffer, *Singularities and Groups in Bifurcation Theory I*, Applied Mathematics Series (Springer, New York 1985), Vol. 51.
- <sup>62</sup>M. Golubitsky and I. Stewart, "Hopf bifurcation in the presence of symmetry," *Arch. Ration. Mech. Anal.* **87**, 107–165 (1985).
- <sup>63</sup>M. Golubitsky and I. N. Stewart, "Symmetry and stability in Taylor-Couette flow," *SIAM J. Math. Anal.* **17**(2), 249–288 (1986).
- <sup>64</sup>M. Golubitsky and I. Stewart, *The Symmetry Perspective* (Birkhäuser, Basel, 2002).
- <sup>65</sup>M. Golubitsky and I. Stewart, "Nonlinear dynamics of networks: The groupoid formalism," *Bull. Am. Math. Soc.* **43**, 305–364 (2006).
- <sup>66</sup>M. Golubitsky and I. Stewart, "Coordinate changes that preserve admissible maps for network dynamics" (unpublished).
- <sup>67</sup>M. Golubitsky and I. Stewart, "Homeostasis as a network invariant," (unpublished).
- <sup>68</sup>M. Golubitsky, I. Stewart, P.-L. Buono, and J. J. Collins, "A modular network for legged locomotion," *Physica D* **115**, 56–72 (1998).
- <sup>69</sup>M. Golubitsky, I. Stewart, P.-L. Buono, and J. J. Collins, "Symmetry in locomotor central pattern generators and animal gaits," *Nature* **401**, 693–695 (1999).
- <sup>70</sup>M. Golubitsky, I. Stewart, and D. G. Schaeffer, *Singularities and Groups in Bifurcation Theory II*, Applied Mathematics Series Vol. 69 (Springer, New York, 1988).
- <sup>71</sup>M. Golubitsky, I. Stewart, and A. Török, "Patterns of synchrony in coupled cell networks with multiple arrows," *SIAM J. Appl. Dyn. Syst.* **4**, 78–100 (2005).
- <sup>72</sup>M. Gorman, C. F. Hamill, M. el-Hamdi, and K. A. Robbins, "Rotating and modulated rotating states of cellular flames," *Combust. Sci. Technol.* **98**, 25–35 (1994).
- <sup>73</sup>M. Gorman, M. el-Hamdi, and K. A. Robbins, "Experimental observations of ordered states of cellular flames," *Combust. Sci. Technol.* **98**, 37–45 (1994).
- <sup>74</sup>M. Gorman, M. el-Hamdi, and K. A. Robbins, "Ratcheting motion of concentric rings in cellular flames," *Phys. Rev. Lett.* **76**, 228–231 (1996).
- <sup>75</sup>G. H. Gunaratne, M. el-Hamdi, M. Gorman, and K. A. Robbins, "Asymmetric cells and rotating rings in cellular flames," *Mod. Phys. Lett. B* **10**, 1379–1387 (1996).
- <sup>76</sup>J. Guckenheimer and P. Holmes, *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields* (Springer, New York, 1983).
- <sup>77</sup>J. K. Hale, *Infinite-Dimensional Dynamical Systems* (Springer, New York, 1993).
- <sup>78</sup>B. D. Hassard, N. D. Kazarinoff, and Y.-H. Wan, *Theory and Applications of Hopf Bifurcation*, London Mathematical Society Lecture Notes Vol. 41 (Cambridge University Press, Cambridge, 1981).
- <sup>79</sup>F. Hoppensteadt, *An Introduction to the Mathematics of Neurons* (Cambridge University Press, Cambridge, 1986).
- <sup>80</sup>K. Ikeda and K. Murota, *Bifurcation Theory for Hexagonal Agglomeration in Economic Geography* (Springer, Japan, 2014).
- <sup>81</sup>W. Jahnke, W. E. Skaggs, and A. T. Winfree, "Chemical vortex dynamics in the Belousov-Zhabotinsky reaction and in the two-variable Oregonator model," *J. Phys. Chem.* **93**, 740–749 (1989).
- <sup>82</sup>K. Josić and A. Török, "Network structure and spatiotemporally symmetric dynamics," *Physica D* **224**, 52–68 (2006).
- <sup>83</sup>A. Katok and B. Hasselblatt, *Introduction to the Modern Theory of Dynamical Systems* (Cambridge University Press, Cambridge, 1995).
- <sup>84</sup>K. Kirchgässner, "Exotische Lösungen Bénardschen problems," *Math. Methods Appl. Sci.* **1**, 453–467 (1979).
- <sup>85</sup>I. Kovács, T. V. Papathomas, M. Yang, and A. Fehér, "When the brain changes its mind: Interocular grouping during binocular rivalry," *Proc. Nat. Acad. Sci. U. S. A.* **93**, 15508–15511 (1996).
- <sup>86</sup>M. Krupa, "Bifurcations from relative equilibria," *SIAM J. Math. Anal.* **21**, 1453–1486 (1990).
- <sup>87</sup>W. F. Langford, R. Tagg, E. Kostelich, H. L. Swinney, and M. Golubitsky, "Primary instability and bicriticality in flow between counter-rotating cylinders," *Phys. Fluids* **31**, 776–785 (1987).
- <sup>88</sup>V. M. Lauschke, C. D. Tsiairis, P. François, and A. Aulehla, "Scaling of embryonic patterning based on phase-gradient encoding," *Nature* **493**, 101–105 (2013).
- <sup>89</sup>G. Li, Q. Ouyang, V. Petrov, and H. L. Swinney, "Transition from simple rotating chemical spirals to meandering and traveling spirals," *Phys. Rev. Lett.* **77**, 2105–2108 (1996).
- <sup>90</sup>N. J. McCullen, T. Mullin, and M. Golubitsky, "Sensitive signal detection using a feed-forward oscillator network," *Phys. Rev. Lett.* **98**, 254101 (2007).
- <sup>91</sup>J. Montaldi, R. M. Roberts, and I. Stewart, "Nonlinear normal modes of symmetric Hamiltonian systems," in *Structure Formation in Physics*, edited by G. Dangelmayr and W. Güttinger (Springer, Berlin, 1987), pp. 354–371.
- <sup>92</sup>J. Montaldi, R. M. Roberts, and I. Stewart, "Periodic solutions near equilibria of symmetric Hamiltonian systems," *Philos. Trans. R. Soc. London A* **325**, 237–293 (1988).
- <sup>93</sup>J. Montaldi, R. M. Roberts, and I. Stewart, "Existence of nonlinear normal modes of symmetric Hamiltonian systems," *Nonlinearity* **3**, 695–730 (1990).
- <sup>94</sup>J. Montaldi, R. M. Roberts, and I. Stewart, "Stability of nonlinear normal modes of symmetric Hamiltonian systems," *Nonlinearity* **3**, 731–772 (1990).
- <sup>95</sup>M. Munz and W. Weidlich, "Settlement formation—Part II: Numerical simulation," *Ann. Reg. Sci.* **24**, 177–196 (1990).
- <sup>96</sup>J. Murray, *Mathematical Biology* (Springer, Berlin, 1989).
- <sup>97</sup>E. Muybridge, *Muybridge's Complete Human and Animal Locomotion: All 781 Plates from the 1887 Animal Locomotion* (Dover, New York, 1979).
- <sup>98</sup>J. S. Nagumo, S. Arimoto, and S. Yoshizawa, "An active pulse transmission line simulating nerve axon," *Proc. IRE* **50**, 2061–2071 (1962).
- <sup>99</sup>A. Palacios, G. H. Gunaratne, M. Gorman, and K. A. Robbins, "Cellular pattern formation in circular domains," *Chaos* **7**, 463–475 (1997).
- <sup>100</sup>C. A. Pinto and M. Golubitsky, "Central pattern generators for bipedal locomotion," *J. Math. Biol.* **53**, 474–489 (2006).
- <sup>101</sup>T. Poston and I. Stewart, *Catastrophe Theory and Its Applications*, Surveys and Reference Works in Mathematical Vol. 2 (Pitman, London, 1978).
- <sup>102</sup>B. Rink and J. Sanders, "Coupled cell networks: Semigroups, Lie algebras and normal forms," *Trans. Am. Math. Soc.* **367**, 3509 (2014).
- <sup>103</sup>E. C. Rosas, "Local and global symmetries of networks of dynamical systems," Ph.D. thesis, University of Warwick, 2009.
- <sup>104</sup>D. Ruelle, "Bifurcations in the presence of a symmetry group," *Arch. Ration. Mech. Anal.* **51**, 136–152 (1973).
- <sup>105</sup>B. Sandstede, A. Scheel, and C. Wulff, "Center-manifold reduction for spiral waves," *C. R. Acad. Sci., Série I* **324**, 153–158 (1997).
- <sup>106</sup>D. H. Sattinger, "Group representation theory, bifurcation theory and pattern formation," *J. Funct. Anal.* **28**, 58–101 (1978).
- <sup>107</sup>D. H. Sattinger, *Group Theoretic Methods in Bifurcation Theory*, Lecture Notes in Mathematics Vol. 762 (Springer-Verlag, 1979).
- <sup>108</sup>D. H. Sattinger and O. L. Weaver, *Lie Groups and Algebras with Applications to Physics, Geometry, and Mechanics* (Springer, New York, 1986).

- <sup>109</sup>M. Silber, D. P. Tse, A. M. Rucklidge, and R. B. Hoyle, "Spatial period-multiplying instabilities of hexagonal Faraday waves," *Physical D* **146**, 367–387 (2000).
- <sup>110</sup>F. Simonelli and J. P. Gollub, "Surface wave mode interactions: Effects of symmetry and degeneracy," *J. Fluid Mech.* **199**, 471–494 (1989).
- <sup>111</sup>S. Smale, "Differentiable dynamical systems," *Bull. Amer. Math. Soc.* **73**, 747–817 (1967).
- <sup>112</sup>S. Smale, "Review of Catastrophe Theory: Selected Papers 1972–1977 by E. C. Zeeman," *Bull. Am. Math. Soc.* **84**, 1360–1368 (1978).
- <sup>113</sup>I. Stewart and M. Golubitsky, "Synchrony-breaking bifurcations at a simple real eigenvalue for regular networks 1: 1-dimensional cells," *SIAM J. Appl. Dyn. Syst.* **10**, 1404–1442 (2011).
- <sup>114</sup>I. Stewart, "Synchrony-breaking bifurcations at a simple real eigenvalue for regular networks 2: Higher-dimensional cells," *SIAM J. Appl. Dyn. Syst.* **13**, 129–156 (2014).
- <sup>115</sup>I. Stewart, M. Golubitsky, and M. Pivato, "Symmetry groupoids and patterns of synchrony in coupled cell networks," *SIAM J. Appl. Dyn. Syst.* **2**, 609–646 (2003).
- <sup>116</sup>I. Stewart and M. Parker, "Periodic dynamics of coupled cell networks I: Rigid patterns of synchrony and phase relations," *Dyn. Syst.* **22**, 389–450 (2007).
- <sup>117</sup>I. Stewart and M. Parker, "Periodic dynamics of coupled cell networks II: Cyclic symmetry," *Dyn. Syst.* **23**, 17–41 (2008).
- <sup>118</sup>R. Tagg, W. S. Edwards, H. L. Swinney, and P. S. Marcus, "Nonlinear standing waves in Couette-Taylor flow," *Phys Rev A* **39**(7), 3734–3738 (1989).
- <sup>119</sup>R. Tagg, D. Hirst, and H. L. Swinney, "Critical dynamics near the spiral-Taylor-vortex transition," unpublished report, University of Texas, Austin, 1988.
- <sup>120</sup>R. Thom, *Structural Stability and Morphogenesis* (Benjamin, Reading, MA, 1975).
- <sup>121</sup>A. M. Turing, "The chemical basis of morphogenesis," *Philos. Trans. R. Soc. London B* **237**, 32–72 (1952).
- <sup>122</sup>A. Vanderbauwhede, "Local bifurcation and symmetry," Habilitation thesis, Rijksuniversiteit Gent, 1980.
- <sup>123</sup>A. Vanderbauwhede, M. Krupa, and M. Golubitsky, "Secondary bifurcations in symmetric systems," in *Differential Equations*, edited by C. M. Dafermos, G. Ladas, and G. Papanicolaou, Lecture Notes Pure Applied Mathematics Vol. 118 (Dekker, New York, 1989), pp. 709–716.
- <sup>124</sup>A. Vutha and M. Golubitsky, "Normal forms and unfoldings of singular strategy functions," *Dyn. Games Appl.* (published online, 2014).
- <sup>125</sup>H. R. Wilson, "Requirements for conscious visual processing," in *Cortical Mechanisms of Vision*, edited by M. Jenkin and L. Harris (Cambridge University Press, Cambridge, 2009), pp. 399–417.
- <sup>126</sup>A. T. Winfree, "Scroll-shaped waves of chemical activity in three dimensions," *Science* **181**, 937–939 (1973).
- <sup>127</sup>C. Wulff, "Theory of meandering and drifting spiral waves in reaction-diffusion systems," Ph.D. thesis, Freie Universität Berlin, 1996.
- <sup>128</sup>E. C. Zeeman, *Catastrophe Theory: Selected Papers 1972–1977* (Addison-Wesley, London, 1977).