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A group-theoretic approach to rings of coupled biological oscillators

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Abstract. In this paper, a general approach for studying rings of coupled biological oscillators is presented. This approach, which is group-theoretic in nature, is based on the finding that symmetric ring networks of coupled non-linear oscillators possess generic patterns of phase-locked oscillations. The associated analysis is independent of the mathematical details of the oscillators' intrinsic dynamics and the nature of the coupling between them. The present approach thus provides a framework for distinguishing universal dynamic behaviour from that which depends upon further structure. In this study, the typical oscillation patterns for the general case of a symmetric ring of n coupled non-linear oscillators and the specific cases of three- and five-membered rings are considered. Transitions between different patterns of activity are modelled as symmetry-breaking bifurcations. The effects of one-way coupling in a ring network and the differences between discrete and continuous systems are discussed. The theoretical predictions for symmetric ring networks are compared with physiological observations and numerical simulations. This comparison is limited to two examples: neuronal networks and mammalian intestinal activity. The implications of the present approach for the development of physiologically meaningful oscillator models are discussed.

1 Introduction

Rhythmic oscillations abound in physiological systems and processes. They are involved, for example, in sleeping, locomotion, ventilation, circulation, mastication and digestion (Winfree 1980; Glass and Mackey 1988). Currently, there is considerable interest in understanding how these oscillations are generated and controlled. Many investigators have proposed that the associated neural and/or muscular mechanisms can be modelled as systems of coupled oscillators (e.g. Cohen et al. 1988). Theoretical and experimental studies have analysed a number of different network architectures with varying degrees of complexity. In this paper, we consider the general dynamics for a relatively simple geometric arrangement, namely that of a symmetric ring of coupled non-linear oscillators.

Ring geometries have been used extensively in physiological and biochemical modelling studies. In a seminal paper, Turing (1952) analysed rings of cells as models of morphogenesis and proposed that isolated rings could account for the tentacles of hydra and whorls of leaves of certain plants. Linkens et al. (1976) utilised rings of coupled van der Pol oscillators to simulate slow-wave activity in the mammalian intestine. A number of investigators have studied the emergent oscillatory dynamics of rings of three coupled model neurons (Dunin-Barkovskii 1970; Pozin and Shulpin 1970; Morishita and Yajima 1972). More recently, researchers have extended this work and analysed ring models in the context of neural network theory (Elias and Grossberg 1975; Tsutsumi and Matsumoto 1984a, b; Hoppensteadt 1986; Atiya and Baldi 1989). Others have considered rings of coupled neuronal oscillators as prototypes for simplified locomotor central pattern generators (Székely 1965; Gurfinkel and Shik 1973; Friesen and Stent 1977, 1978; Grillner and Wallén 1985; Bay and Hemami 1987). It has also been noted that ring architectures may be relevant to the development of patterns on certain animals' shells and to the function of other smooth muscle systems, such as the ureter (Ermentrout 1985).

From a physiological modelling standpoint, ring networks are important because they can serve as fundamental components of more complex oscillatory circuits (Atiya and Baldi 1989). From a mathematical standpoint, several approaches have been applied to the analysis of coupled oscillator rings. Linkens (1974), for instance, derived the analytical solution for a system of mutually coupled van der Pol oscillators using the method of harmonic balance, whereas Mori and colleagues (Endo and Mori 1978; Kouda and Mori 1981) used non-linear mode analysis to examine similar systems. Glass and Young (1979) represented ring networks of oscillatory neurons as asynchronous switching networks and

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analysed their dynamics using 'state transition diagrams'. Grasman and Jansen (1979) utilised asymptotic methods to obtain the synchronised solutions for a system of n identical oscillators coupled on a circle. Ermentrout (1985) studied rings of coupled oscillators using perturbation and numerical methods and determined the stability of the predicted waves of activity. Similarly, Alexander (1986) carried out numerical bifurcation computations for oscillator rings and was able to determine whether a bifurcating branch was subcritical or supercritical.

In this study, we approach the above problem from the perspective of group theory. This is a relatively new technique in connection with coupled oscillator systems. It works best for networks with some degree of symmetry, e.g. rings. The last decade has seen the emergence of a well-developed theory of dynamics in the presence of symmetry, founded on group-theoretic considerations. We survey and synthesise recent results from that theory which have substantial implications for systems of coupled biological oscillators and interpret them in that framework. Specifically, we consider the dynamics of ring networks of n symmetrically coupled, non-linear oscillators and explain how the symmetry of the respective systems leads to a general class of phase-locked oscillation patterns. Transitions between different patterns of activity are modelled as symmetry-breaking bifurcations (Golubitsky and Stewart 1985, 1986). Importantly, the symmetry-breaking analysis is independent of the details of the oscillators' intrinsic dynamics and the nature of the coupling between the oscillators. This symmetry approach thus enables one to distinguish model-independent features (due to symmetry alone) from model-dependent ones and represents an attempt to obtain 'generalizable formulations for simple networks' (Selverston 1988).

This paper is organised as follows. In Sect. 2, we present the general mathematical framework for studying symmetric systems of coupled non-linear oscillators. We review the background and major features of the symmetric Hopf bifurcation theorem of Golubitsky and Stewart (1985) and describe the typical phase-locked oscillation patterns for the general case of a symmetric ring of n coupled non-linear oscillators and the specific cases of three- and five-membered rings (Golubitsky and Stewart 1985). [The results for networks of two, four and six coupled oscillators are presented in the context of animal locomotion in earlier reports (Collins and Stewart 1992, 1993a, b).] We also discuss the effects of one-way coupling in a ring network and describe the differences between discrete and continuous systems. In Sect. 3, we compare the theoretical predictions given in Sect. 2 with experimental observations and numerical simulations. Finally, in Sect. 4, we discuss the implications of our approach for the development of physiologically meaningful oscillator models.

2 Mathematical analysis and results

In the following section, we outline the mathematical concepts underlying equivariant Hopf bifurcation in symmetric, non-linear dynamical systems and present the typical phase-locked oscillation patterns that arise in ring networks of symmetrically coupled, non-linear oscillators. Since our emphasis is on symmetry, we utilise the language and tools of group representation theory. This section is a summary of the mathematical analysis and results presented by Golubitsky and Stewart (1985, 1986) and Golubitsky et al. (1988). See the above works for more detailed accounts and formal treatments. Collins and Stewart (1993a) provide a more accessible introduction to dynamical systems theory, group theory and bifurcations in symmetric, coupled oscillator networks.

2.1 *Symmetric Hopf bifurcation*

If two identical oscillators are coupled symmetrically, then the most typical patterns of behaviour are perfect synchrony or perfect antisynchrony (in which the oscillators are half a period out of phase with each other). This is a symmetric dynamical system: its equations are unchanged – more technically, equivariant – if the two oscillators are permuted. It is also the simplest example of the effects of symmetry, and symmetry-breaking, on a system of coupled identical oscillators. The synchronous oscillation preserves the symmetry; the antisynchronous one breaks it, in a predictable and specific manner. Moreover, not all symmetry is lost: the antisynchronous solution is invariant under the operation that interchanges the two oscillators and shifts phase by half a period. There is a mixed spatiotemporal symmetry.

In order to provide a concrete image of the mathematical ideas, consider a network of four identical oscillators coupled together in a 'square' formation, all couplings being identical. If the state of oscillator i at time t is determined by a (vector) variable $u_i(t)$, then the state of the entire system is given by

$$u(t) = (u_1(t), u_2(t), u_3(t), u_4(t)). \tag{1}$$

The state $u(t)$ can possess two different types of symmetry: spatial and temporal. A 'spatial' symmetry occurs when two or more oscillators are behaving identically, i.e. they are synchronised. For example, suppose oscillators 1 and 2 are synchronised. Then

$$u_1(t) = u_2(t) \tag{2}$$

for all times t. Equivalently, the state $u(t)$ is unchanged if we permute coordinates 1 and 2, that is,

$$(u_1(t), u_2(t), u_3(t), u_4(t)) = (u_2(t), u_1(t), u_3(t), u_4(t)), \tag{3}$$

or, in more abstract notation,

$$u(t) = \pi \cdot u(t) \tag{4}$$

where the operator π permutes coordinates 1 and 2.

Temporal symmetries occur when some of the oscillators are phase-locked, for example, if oscillator 1 is half a period out of phase with (antisynchronous to) oscillator 2, and oscillator 3 is half a period out of phase with oscillator 4. Now

$$\begin{aligned} u_2(t) &= u_1(t + T/2) \\ u_4(t) &= u_3(t + T/2) \end{aligned} \tag{5}$$

where T is the period, or equivalently

$$u(t) = \rho \cdot u(t + T/2) \tag{6}$$

where ρ interchanges the pairs of oscillators (1,2) and (3,4). Notice that here the temporal symmetry (pure phase shift) occurs in combination with a spatial symmetry (interchange oscillators (1,2) and (3,4)). This is typical in such systems. In contrast, a purely temporal symmetry such as

$$u(t + T/2) = u(t) \tag{7}$$

implies that the period of each oscillator is $T/2$ rather than T, so such a symmetry indicates that a non-minimal period has been chosen.

The theory of dynamical systems with symmetry, and in particular that of Hopf bifurcation to periodic oscillations in such a system, is a far-reaching generalisation of this kind of effect. The behaviour of any dynamical system is typically governed by a parameter or set of parameters. As these parameters are varied, the qualitative nature of the system's dynamics can change. For certain situations, it is possible to have a limit cycle or periodic state arise from a stable steady state as some system parameter is varied. The conditions under which this occurs are classically prescribed by the standard Hopf bifurcation theorem (see Appendix 3 in Murray 1989). Hopf bifurcation has been successfully applied to the analysis of a number of different physical systems (e.g. Marsden and McCracken 1976; Hassard et al. 1981). It is one of the most common sources of periodic states in non-linear systems. Standard or ordinary Hopf bifurcation cannot be applied, however, to dynamical systems with symmetry, due to the fact that it may no longer be possible for simple imaginary eigenvalues to occur (Golubitsky et al. 1988)[1].

A general theory of spatiotemporal symmetries in Hopf bifurcation has been developed by Golubitsky and Stewart (1985). They provide abstract techniques, based on group theory, for predicting the occurrence of particular combinations of spatial and temporal symmetries when a symmetric network of non-linear oscillators undergoes Hopf bifurcation. Indeed, their analysis applies to any dynamical system with symmetry. Because of the abstract group-theoretic language – which is essential to the proper formulation of the mathematics but not widely familiar – we discuss the detailed features of the symmetric Hopf bifurcation theorem of Golubitsky and Stewart (1985) in the Appendix. In short, their theorem asserts that at a symmetric analogue of a Hopf bifurcation, one or more branches of periodic solutions, usually several, bifurcate. These oscillations may be distinguished by their spatiotemporal symmetry groups Σ, which are subgroups of $\Gamma \times S^1$. [Elements of Γ can be thought of as spatial symmetries and elements of S^1 as temporal symmetries (Golubitsky et al. 1988), where Γ is a compact Lie group and S^1 is the circle group R/Z.] The isotropy subgroups measure the amount of symmetry present in the branching solutions. The question of the existence of symmetry-breaking oscillations is thus reduced to purely group-theoretic calculations and depends only on the symmetry assumed in the system. The main point here is that typical oscillation patterns of the system can be predicted in terms of its symmetries, without investigating the detailed dynamical equations. The mathematical literature develops the consequences of this general theory for specific networks of oscillators, and we shall not enter into any technical discussion here. Instead, we discuss the results of the general theory in some specific cases that are important in the analysis of rings of coupled biological oscillators.

[1] When a system has symmetry, the eigenvalues may generically be forced to be multiple

2.2 Dynamics of symmetric ring networks

The symmetric Hopf bifurcation theorem (see Appendix) asserts the existence under appropriate conditions of a number of generic oscillation patterns in symmetric systems of coupled non-linear oscillators. In this section, we present the predicted results for three cases: (1) the general case of a symmetric ring of n coupled oscillators, (2) a symmetric ring of three coupled oscillators and (3) a symmetric ring of five coupled oscillators. The latter two are selected because of their popularity in previous physiological modelling studies (see above). We also discuss the effects of one-way coupling (versus two-way coupling) and describe the differences between discrete and continuous systems. The results given below summarise the original findings of Golubitsky and Stewart (1985, 1986) and Golubitsky et al. (1988). These results and the associated analysis, taken as a whole, form the basis for a general group-theoretic approach for studying rings of coupled biological oscillators.

Before presenting the theoretical results, we briefly describe some of the group representation symbols that will be used. For a ring of n coupled oscillators, there are three common types of symmetry (Golubitsky et al. 1988; Ashwin et al. 1990):

1. The symmetric group S_n, which involves all permutations of n objects. For this symmetry group, each oscillator in the ring is identically coupled to each of the other oscillators, i.e. a star configuration. Hadley et al. (1988) and Ashwin and Swift (1992) have investigated large systems of coupled oscillators with S_n symmetry. Such networks will not be considered in this paper.
2. The dihedral group D_n, which is the symmetry of a regular n-gon. For D_n symmetry, each oscillator in the ring is identically coupled to its two nearest neighbours (Fig. 1). This corresponds to two-way coupling (reflection symmetry). Note that for a three-membered ring (see Sect. 2.2.2 and Fig. 3a), S_3 and D_3 have the same symmetry.
3. The cyclic group Z_n, which is the symmetry of a directed n-gon. This symmetry group corresponds to one-way coupling about the ring, i.e. one direction is preferred (Fig. 3c,d).

For the results presented in Tables 1 and 2, A, B and C represent distinct oscillations,[2] and $A + \pi$ is waveform A phase-shifted by π, i.e. one-half the period of a 2π-periodic oscillation. The action of flip κ sends oscillator p to $-p$. For example, for the three-membered ring of Table 1 and Fig. 3a, the flip κ interchanges the states of oscillators 1 and 2 and leaves the state of oscillator 0 fixed.

2.2.1 General case: n-membered ring. We here consider the general case of a symmetric ring of n identical non-linear oscillators with symmetric (two-way) nearest-neighbour coupling (Fig. 1). The symmetry group for this system is the dihedral group D_n. Two points should be noted about the coupling between oscillators: (1) our analysis does not assume linearity of the coupling, and (2) the coupling need not be restricted to nearest-neighbour interaction, provided the appropriate symmetry is preserved.

In our analysis, it is assumed that D_n acts on the imaginary eigenspace in some, perhaps non-standard, representation. Oscillatory modes corresponding to different representations produce different – though often related – patterns (see Collins and Stewart (1993b) for exemplary results with a hexagonal ring network). From the existence of an action of D_n, we can predict possible periodic solutions which arise via Hopf bifurcation. We do not assert, however, that all periodic states for a ring network are obtained through Hopf bifurcation: of course, they may arise in other ways. However, if they can be continued – if necessary by introducing additional parameters – to merge into a branch of periodic solutions that arises by Hopf bifurcation, then they will have the same symmetries that Hopf bifurcation predicts. (By 'merge into' we mean that the branch may turn round at one or more fold points, but that no bifurcations to secondary branches occur.) This state of affairs is not unusual.

The equivariant Hopf theorem (see Appendix) shows that for ring systems with D_n symmetry, the purely imaginary eigenvalues associated with Hopf bifurcation are either simple or double. In the former case, standard Hopf bifurcation will always yield a unique branch of periodic solutions, in which all component oscillators have the same waveform and move in phase. In the double eigenvalue case, there are at least three symmetry-breaking branches of periodic solutions, corresponding to three conjugacy classes of isotropy subgroups of $D_n \times S^1$. Figure 2 shows the resulting generic oscillation patterns for a ring network with D_n symmetry. The exact form of the periodic solutions depends on whether n is odd, $n \equiv 2 (\mathrm{mod}\ 4)$, or $n \equiv 0 (\mathrm{mod}\ 4)$. In general, for each divisor m of n, the oscillators may group into n/m phase-locked sets of m equally spaced oscillators, interacting like a ring of n/m oscillators, i.e. the oscillators in each set behave identically. In all cases, the theory predicts that symmetry-breaking Hopf bifurcation produces rotating waves in a ring network of coupled oscillators (Fig. 2a).

[2] Though all waveforms are approximately sinusoidal close to the bifurcation point

Table 1. Generic oscillation patterns always produced by Hopf bifurcation in symmetric rings of three coupled identical oscillators

Representation	Isotropy	x_1	x_2	x_0	Comments
ρ_0	D_3	A	A	A	In-phase solution
ρ_1	$\tilde{Z}_3$	A	$A + \frac{2\pi}{3}$	$A + \frac{4\pi}{3}$	Rotating wave
	$Z_2(\kappa)$	A	A	B	
	$Z_2(\kappa, \pi)$	A	$A + \pi$	B	$B = B + \pi$: half-period

Moreover, the presence of symmetry in a system can force some oscillators to have twice the frequency of the others (Fig. 2b,c).

In non-linear dynamics, it is known that frequency-locked states commonly arise when two (or more) oscillators are coupled together. Such states occur because they are structurally stable, i.e. they persist despite small changes in the dynamics. The standard situation for such phenomena is that of a forced oscillator such as the 'kicked rotator' (see Arnold 1983; Thompson and Stewart 1986). This equation models an oscillator which, at discrete times, is given a fixed phase shift (or 'kick') and also advanced in phase by an amount that varies sinusoidally with time (the forcing). When the forcing amplitude is low, the oscillator typically acquires a period that is a rational multiple p/q of the forcing frequency. The regions of parameter space (amplitude of the forcing and size of the 'kick') in which a given rational number p/q occurs are called Arnold tongues. At higher forcing amplitudes, the dynamics becomes chaotic.

The 2:1 frequency-locking that we are referring to has a different mathematical origin and a different physical interpretation. It is a consequence of symmetry-breaking in an autonomous coupled system, not of forcing. Moreover, it is an integral feature of Hopf bifurcation in systems with appropriate symmetries. In other types of networks, symmetries can also be responsible for n:1 frequency-locking for integer n. For example, in a system of four oscillators with 'all-to-all coupling', that is S_4 symmetry, one class of solutions is necessarily 3:1 frequency-locked.

2.2.2 Three-membered ring. The results for a symmetric ring network of three coupled oscillators with two-way coupling (Fig. 3a) are shown in Table 1. For $n = 3$, there are two types of generic Hopf bifurcation. The first (ρ_0 representation) arises via standard Hopf bifurcation and preserves D_3 symmetry. In this case, all three oscillators have identical waveforms and move in phase (Table 1). The second type of bifurcation (ρ_1) involves three branches of symmetry-breaking oscillations, with isotropy subgroups $\tilde{Z}_3$, $Z_2(\kappa)$ and $Z_2(\kappa, \pi)$. For $\tilde{Z}_3$, the oscillators have identical waveforms but are phase-shifted by $2\pi/3$. This solution corresponds to a discrete rotating wave. For $Z_2(\kappa)$, two of the oscillators behave identically, i.e. they have the same waveform and move in

Table 2. Generic oscillation patterns always produced by Hopf bifurcation in symmetric rings of five coupled identical oscillators

Representation	Isotropy	x_1	x_2	x_3	x_4	x_0	Comments
ρ_0	D_5	A	A	A	A	A	In-phase solution
ρ_1	$\tilde{Z}_5$	A	$A+\frac{2\pi}{5}$	$A+\frac{4\pi}{5}$	$A+\frac{6\pi}{5}$	$A+\frac{8\pi}{5}$	Rotating wave
	$Z_2(\kappa)$	A	B	B	A	C	
	$Z_2(\kappa, \pi)$	A	B	$B+\pi$	$A+\pi$	C	$C = C + \pi$: half-period
ρ_2	$\tilde{Z}_5$	A	$A+\frac{4\pi}{5}$	$A+\frac{8\pi}{5}$	$A+\frac{2\pi}{5}$	$A+\frac{6\pi}{5}$	Phase lags $\pm\frac{4\pi}{5}$
	$Z_2(\kappa)$	A	B	B	A	C	
	$Z_2(\kappa, \pi)$	A	B	$B+\pi$	$A+\pi$	C	$C = C + \pi$: half-period

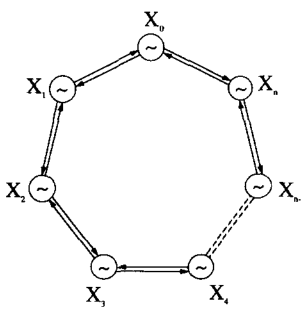

Fig. 1. Graphical representation of a symmetric ring of n coupled identical non-linear oscillators (adapted from Golubitsky and Stewart 1986). The system has D_n symmetry, which corresponds to identical two-way coupling

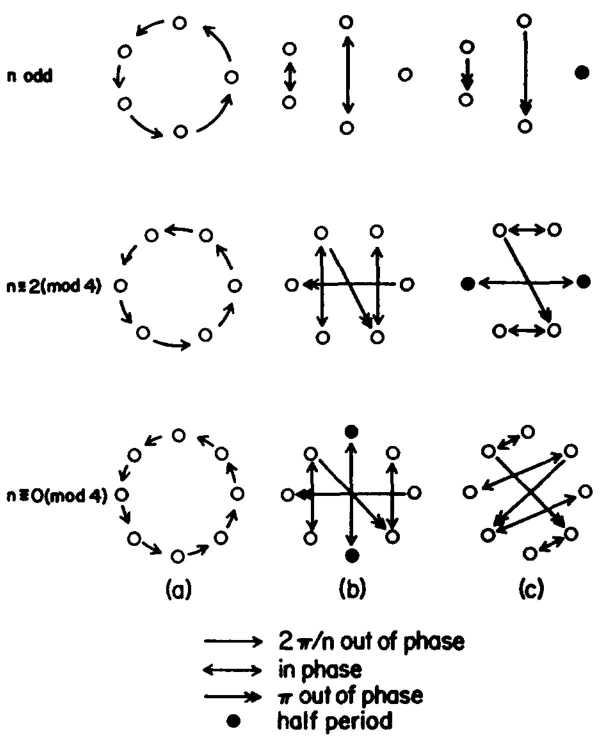

Fig. 2. Some of the generic patterns for a ring of n coupled identical non-linear oscillators that are produced by symmetric Hopf bifurcation (from Golubitsky et al. 1988). There are three distinct cases, depending on whether: (*top*) n is odd; (*middle*) $n \equiv 2 \pmod 4$; (*bottom*) $n \equiv 0 \pmod 4$

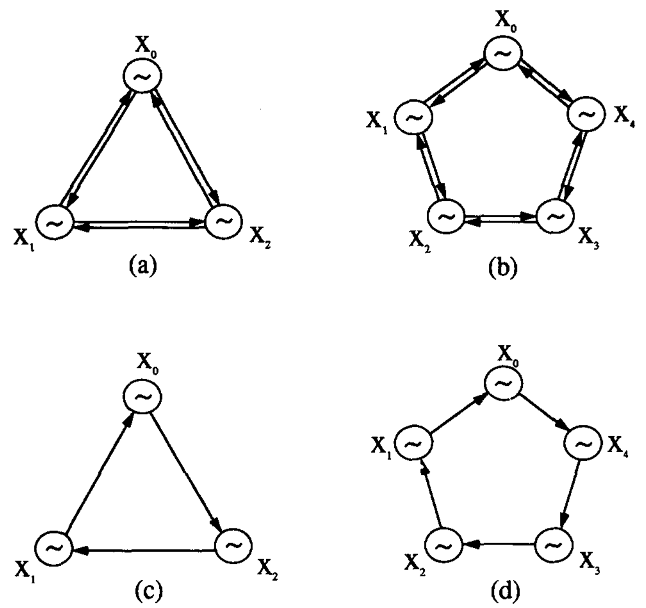

Fig. 3a–d. Graphical representation of symmetric rings of coupled identical non-linear oscillators. (**a**) Three-membered ring with two-way coupling (D_3 symmetry); (**b**) five-membered ring with two-way coupling (D_5 symmetry); (**c**) three-membered ring with one-way coupling (Z_3 symmetry); (**d**) five-membered ring with one-way coupling (Z_5 symmetry)

phase; the third oscillator has a different waveform. For $Z_2(\kappa, \pi)$, two of the oscillators have identical waveforms but are phase-shifted by π; the third oscillator has a different waveform and twice the frequency of the other two, i.e. it is 'π out of phase with itself'.

2.2.3 Five-membered ring. The results for a symmetric ring network of five coupled oscillators with two-way coupling (Fig. 3b) are shown in Table 2. For $n = 5$, there are three types of generic Hopf bifurcation. As above, the first case (ρ_0) corresponds to ordinary Hopf bifurcation in which D_5 symmetry is preserved. Thus, for this solution, all five oscillators have the same waveform and move in phase. In the other two cases (ρ_1 and ρ_2), there are three simultaneously bifurcating branches, with isotropy subgroups $\tilde{Z}_5$, $Z_2(\kappa)$ and $Z_2(\kappa, \pi)$. For ρ_1, $\tilde{Z}_5$ yields a pattern in which all five oscillators have identical waveforms, but nearest neighbours are $2\pi/5$ out of phase.

For ρ_2, $\tilde{Z}_5$ also corresponds to a periodic solution in which all five oscillators have the same waveform, but now nearest neighbours are phase-shifted by $4\pi/5$. For ρ_1 and ρ_2, the isotropy subgroups $Z_2(\kappa)$ and $Z_2(\kappa, \pi)$, respectively, yield the same patterns of oscillation (Table 2). For $Z_2(\kappa)$, oscillators 1 and 4 behave identically (same waveform A, same phase), oscillators 2 and 3 behave identically (same waveform B, same phase), and oscillator 0 has a distinct waveform, C. For $Z_2(\kappa, \pi)$, the oscillators in each pair, e.g. 1 and 4, are π out of phase with one another, and oscillator 0 is 'π out of phase with itself', i.e. it has half the period of the other four.

2.2.4 Effects of unidirectional coupling. As described above, ring networks with D_n symmetry have a rich bifurcation structure, which leads to various phase-locked oscillation patterns. This situation is simplified if the form of the coupling is changed from two-way to one-way interactions, but the cyclic symmetry is preserved, i.e. one direction is preferred. [This issue is important to consider given the prevalence of biological-oscillator models with unidirectional coupling (e.g. see Kling and Székely 1968; Friesen and Stent 1977, 1978).] Oscillator rings of this sort have Z_n symmetry (see Fig. 3c,d). For these network geometries, the general theory predicts Hopf bifurcation to a unique branch of rotating waves. The respective rotating-wave solutions correspond to each representation of Z_n. This result is not unexpected since Z_n is the subgroup of rotational symmetries for D_n-equivariant systems. However, whereas D_n rotating-wave solutions can have two distinct directions of rotation, only one sense of rotation will occur at any generic Z_n Hopf bifurcation. The interpretation of the term 'direction of rotation' depends upon the representation of Z_n that occurs.

2.2.5 Discrete vs. continuous systems. The model systems described above correspond to ring networks of coupled non-linear oscillators. Although these models are appropriate for analysing the behaviour of neuronal networks with discrete components, e.g. central pattern generators, they may not be as suitable for approximating the dynamics of rings of excitable tissue, e.g. cross-sections of intestinal smooth muscle. In such cases, it may be more physiologically relevant to consider continuous systems. Below we describe the generic oscillation patterns for continuous systems with circular $O(2)$ symmetry and compare them with those for discrete ring systems with D_n symmetry.

For equivariant Hopf bifurcation with $O(2)$ symmetry, there are two distinct symmetry-breaking branches of periodic solutions, with isotropy subgroups

$$\widetilde{SO}(2) = \{(\pi, \pi) \in O(2) \times S^1\}$$

and

$$Z_2 \oplus Z_2^c$$

where Z_2^c is generated by (π, π) in $O(2) \times S^1$.

For $\widetilde{SO}(2)$, the resulting oscillations correspond to rotating waves. These solutions, which involve spatiotemporal symmetries, can have two distinct senses of rotation, i.e. clockwise or counterclockwise. For $\mathbf{Z}_2 \oplus Z_2^c$, the periodic solutions correspond to standing waves, which possess purely spatial symmetries. In this case, the left and right oscillations are identical except for a π phase shift.

Thus, for the limiting case of D_n-equivariant systems, i.e. as $n \rightarrow \infty$, the number of distinct symmetry-breaking oscillations is reduced from three to two. This surprising result is due to the fact that the discrete-network solutions with isotropy subgroups $Z_2(\kappa)$ and $Z_2(\kappa, \pi)$ merge as $n \rightarrow \infty$. For large n, the differences between these solutions become negligible.

3 Physiological observations and previous modelling results

In this section, we compare the theoretical predictions for symmetric ring networks with physiological observations and numerical simulations. Our discussion will be limited to two examples: neuronal networks and mammalian intestinal activity. It should be emphasised, however, that the strength of our group-theoretic approach lies in the generality of its results and not in its application or relevance to a specific physiological or physical example.

3.1 Neuronal networks

Neuronal networks have been used widely to model oscillatory activity in the central nervous system. As noted in Sect. 1, a number of previous studies have analysed the dynamic behaviour of rings of three coupled model neurons (Dunin-Barkovskii 1970; Pozin and Shulpin 1970; Morishita and Yajima 1972; Friesen and Stent 1977, 1978). For three-cell systems with unidirectional coupling, the most common periodic solution is that of a rotating wave with $\tilde{Z}_3$ symmetry. This result, which is predicted by the above theory, has been generalised to n-membered ring models with one-way coupling (Kling and Székely 1968; Friesen and Stent, 1977, 1978). Golubitsky and Stewart (1985) carried out numerical experiments on a ring network of three non-linear oscillators with symmetric (two-way) coupling. The model oscillators were of van der Pol type, with additional terms for breaking the 'internal' odd-function symmetry of a conventional van der Pol oscillator. By varying the parameter values for the network, Golubitsky and Stewart were able to obtain phase-locked oscillation patterns with $\tilde{Z}_3$, $Z_2(\kappa)$ and $Z_2(\kappa, \pi)$ symmetry, respectively (as predicted by the symmetry analysis in Sect. 2.2.2).

3.2 Mammalian intestinal activity

Rhythmic oscillations play an important role in the functioning of the gastrointestinal tract. Waves of electrical and mechanical activity, for instance, propagate along the length of the intestines. These oscillations are produced by the circular bands of smooth muscle which make up the intestinal walls. A number of researchers have used rings of coupled relaxation oscillators to model cross-sectional slices of mammalian intestine (Linkens 1974, 1980; Linkens et al. 1976; Ermentrout 1985). Linkens et al. (1976), for example, considered a computer model of a ring network of four coupled van der Pol oscillators. By changing the initial conditions of the simulation or by applying an external stimulus to the model, they were able to obtain multiple phase-locked periodic solutions, i.e. patterns with 0°, 90° and 180° phase differences between nearest-neighbour oscillators. It has been reported that the basic electrical rhythm of the intestines propagates aborally as in-phase rings of activity, i.e. recordings from smooth muscle cells about the circumference of the bowel at any one point are all in phase (Bass et al. 1961). Such a pattern preserves D_n symmetry in a ring network. Others have noted that intestinal slow waves can also exhibit approximately 2:1 frequency-locking (Linkens 1976). In such cases, the higher frequency signals consistently have a smaller amplitude than the lower frequency signals. This finding agrees qualitatively with the numerical results obtained by Golubitsky and Stewart (1985) for a symmetric ring network of three coupled identical non-linear oscillators. Unfortunately, previous experimental studies were carried out in such a manner that their results do not allow us to decide whether the 180°-out-of-phase condition predicted by the symmetry analysis for 2:1 frequency-locked patterns is present in rings of intestinal smooth muscle cells.

4 Discussion

Our general approach for studying coupled biological oscillators is based on the finding that symmetric ring networks of coupled identical non-linear oscillators possess generic patterns of phase-locked oscillations. It is important to emphasise the fact that the associated abstract results are model-independent. By this, we mean that our analysis does not depend upon the mathematical details of the oscillators' intrinsic dynamics or the nature of the coupling between the component oscillators. The periodic states that arise via equivariant Hopf bifurcation are controlled primarily by the symmetries of the system. This approach, which is group-theoretic in nature, thus allows one to study the general behaviour of general classes of coupled oscillator systems. This provides a framework for distinguishing dynamic behaviour which is universal from that which depends upon further structure. We note that although the stability of the various oscillation patterns predicted by the general analysis depends upon the parameters of the system – and hence is not strictly model-independent – general criteria may be found that define the appropriate combinations of parameters whose signs must be checked to determine stability. Thus, stability is to some extent governed by general model-independent principles; however, the way those principles work out on a given model depends upon the precise parameter values.

General theories about general models can serve as useful starting points for investigations in mathematical biology. Often, it is not readily apparent what type or form of model should be used to approximate a particular physiological system. From the standpoint of oscillator networks, for instance, one can choose between several different types of 'biological' oscillators, e.g. van der Pol, Hodgkin-Huxley, FitzHugh-Nagumo, and various forms of coupling, e.g. synaptic, electrical. This problematic situation is compounded by the difficulties associated with estimating appropriate values for the model parameters[3] and determining which ones are important for the analysis. For many physiological models, the number of 'essential' parameters can be quite large. Bullock (1976), for example, listed over 40 different parameters or variables which could have an effect on the dynamics of neuronal networks. As described above, the presence of symmetry in a system imposes strong restrictions on its dynamics and thereby simplifies the theoretical analysis. One is thus enabled, in certain situations, to obtain robust principles for simple networks.

The theory of symmetry-breaking Hopf bifurcation predicts that oscillator ring networks with *invariant* structure can sustain *multiple* patterns of rhythmic activity. These results apply to both autonomous and forced oscillator systems. Spontaneous symmetry-breaking may thus enhance a neuronal network's ability to store/retrieve information (Cowan 1980, 1982) or to generate diverse cyclic behaviour. It may also play a role in the initiation of irregular rhythms in smooth muscle systems. From the standpoint of central pattern generators, this phenomenon counters the assertion that a network's architecture needs to be modulated in order to produce different oscillation patterns (e.g. Grillner and Wallén 1985; Selverston 1988).

Our analysis also considered the general differences between two-way and one-way coupling in ring oscillator networks. For bidirectional coupling, the theory predicts Hopf bifurcation to three branches of periodic oscillations. These solutions include rotating waves and 2:1 frequency-locked patterns. For unidirectional coupling, the situation is simplified: Hopf bifurcation yields a unique branch of rotating-wave solutions.

Ermentrout (1985) and Alexander (1986), using standard techniques, determined the stability of bifurcating periodic solutions in rings of coupled oscillators. In this study, we did not consider the stability of the respective branches of symmetry-breaking oscillations that arise in symmetric ring networks. However, such an analysis can be derived from the results of Golubitsky et al. (1988) provided that the ring systems have been put in Birkhoff normal form by a suitable change of variables. This method would make it possible to distinguish between additional classes of models.

The present group-theoretic approach could be extended to more complex, physiological model systems. Bardakjian and Sarna (1980), for example, represented the human colon as a tubular structure made up of 99 coupled oscillators. This model consisted of 33 symmetrically coupled rings, with each ring being made up of

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[3] In real physiological systems, the absolute values of many parameters can also change as a function of time

three bidirectionally coupled oscillators. The system was studied on a computer and used to simulate colonic electrical control activity. On a similar note, we have previously analysed the generic oscillation patterns for a 'mini-tube' system of coupled oscillators (Collins and Stewart 1993a). The model was made up of two symmetrically coupled rings of three non-linear oscillators. In principle, such a system could be expanded to include a larger number of coupled oscillator rings. It should be emphasised, however, that our symmetric approach is not appropriate for systems with significant asymmetries, e.g. the pacemaker unit of the pyloric network in lobster stomatogastric ganglion (Abbot et al. 1991). See Baesens et al. (1991) for a detailed treatment of the dynamics of coupled systems of three non-identical oscillators.

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Appendix
Symmetric Hopf bifurcation theorem

Consider a system of ordinary differential equations

$$\frac{dx}{dt} + f(x, \lambda) = 0 \tag{8}$$

where $x \in R^n$, f: $R^n \to R^n$, and $\lambda \in R$ is a parameter. In general, f is non-linear, and we assume that there is a trivial solution $f(0, \lambda) \equiv 0$ so that $x = 0$ is always a steady-state solution of (8). Let $(df)_{(x,\lambda)}$ be the Jacobian matrix $[\partial f_i/\partial x_j]$ evaluated at (x, λ). Suppose that f commutes with the action of a compact Lie group Γ on R^n. For Hopf bifurcation to occur, $(df)_{(x,\lambda)}$ must have purely imaginary eigenvalues $\pm i\omega$ at some value λ_0 of λ. Assume that the eigenvalues cross the imaginary axis with non-zero speed. Generically, the corresponding eigenspace of the derivative $L = (df)_{(x,\lambda_0)}$ is a Γ-simple representation; that is, it takes one of the two forms:

$V \oplus V$ where V is absolutely irreducible, or
W where W is non-absolutely irreducible.

Assume this generic hypothesis, and assume without loss of generality (via centre manifold or Liapunov-Schmidt reduction) that R^n is the real eigenspace of L for eigenvalues $\pm i\omega$. Define an action of the circle group $S^1 = R/Z$ on R^n by:

$$\theta \cdot x = e^{-2\pi\theta L}. \tag{9}$$

Define a second action on T-periodic solutions $x(t)$ of (8) by

$$(\gamma, \theta) \cdot x(t) = \gamma \cdot x(t + \theta T/2\pi). \tag{10}$$

Here Γ acts as before, but now S^1 acts by phase shift. The spatiotemporal symmetry group of a periodic solution $x(t)$ is the subgroup

$$\{(\gamma, \theta) \in \Gamma \times S^1 : \gamma \cdot x(t + \theta T/2\pi) = x(t)\}. \tag{11}$$

Similarly if $x \in R^n$, then its isotropy subgroup $\Sigma_x \subset \Gamma \times S^1$ is defined to be:

$$\Sigma_x = \{\gamma \in \Gamma \times S^1 | \gamma \cdot x = x\}. \tag{12}$$

If $\Sigma \subset \Gamma \times S^1$, then its fixed-point space is defined to be:

$$\mathrm{Fix}(\Sigma) = \{x \in R^n | \sigma \cdot x = x \text{ for all } \sigma \in \Sigma\} \tag{13}$$

With these assumptions, we have the following result of Golubitsky and Stewart (1985):

Symmetric Hopf bifurcation theorem
Let Σ be an isotropy subgroup of $\Gamma \times S^1$ such that dim $\mathrm{Fix}(\Sigma) = 2$. Then there exists a unique branch of small amplitude periodic solutions to (8) with period near $2\pi/\omega$, having Σ as their group of spatiotemporal symmetries, where S^1 acts on a periodic solution by phase shift.

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