J. Nonlinear Sci. Vol. 3: pp. 349–392 (1993)

Journal of
Nonlinear
Science

Coupled Nonlinear Oscillators and the Symmetries of Animal Gaits

J. J. Collins[1] and I. N. Stewart[2]

[1] Oxford Orthopaedic Engineering Centre, Nuffield Orthopaedic Centre, University of Oxford, Headington, Oxford OX3 7LD, UK, and
NeuroMuscular Research Center and Department of Biomedical Engineering, Boston University, Boston, MA 02215, USA

[2] Nonlinear Systems Laboratory, Mathematics Institute, University of Warwick, Coventry CV4 7AL, UK

Received October 21, 1991; revised manuscript accepted for publication July 29, 1992
Communicated by James Murray

Summary. Animal locomotion typically employs several distinct periodic patterns of leg movements, known as gaits. It has long been observed that most gaits possess a degree of symmetry. Our aim is to draw attention to some remarkable parallels between the generalities of coupled nonlinear oscillators and the observed symmetries of gaits, and to describe how this observation might impose constraints on the general structure of the neural circuits, i.e. central pattern generators, that control locomotion. We compare the symmetries of gaits with the symmetry-breaking oscillation patterns that should be expected in various networks of symmetrically coupled nonlinear oscillators. We discuss the possibility that transitions between gaits may be modeled as symmetry-breaking bifurcations of such oscillator networks. The emphasis is on general model-independent features of such networks, rather than on specific models. Each type of network generates a characteristic set of gait symmetries, so our results may be interpreted as an analysis of the general structure required of a central pattern generator in order to produce the types of gait observed in the natural world. The approach leads to natural hierarchies of gaits, ordered by symmetry, and to natural sequences of gait bifurcations. We briefly discuss how the ideas could be extended to hexapodal gaits.

Key words. central pattern generators, locomotion, gait transitions, quadrupeds, bifurcation

1. Introduction

The past decade has witnessed considerable advances in the understanding of nonlinear effects in dynamics. In particular the behavior of systems of coupled nonlinear oscillators is relatively well understood provided either that the number of oscillators is small (namely two or three, see Baesens *et al.* (1991)), or that there is a high degree of symmetry (Golubitsky and Stewart, 1986; Golubitsky *et al.*, 1988; Ashwin, *et al.*, 1990; Ashwin, 1990; Ashwin and Swift, 1992). A number of phenomena are "universal" or "model-independent" in the sense that they arise in very general circumstances and are relatively insensitive to fine details of the mathematical model that is employed.

Multilegged animals utilize several distinct patterns of leg movements, known as *gaits* (Muybridge, 1899, 1901). For example, humans walk, run, or hop; horses walk, trot, canter, or gallop. A quotation from McGhee and Jain (1972) strikes an immediate chord for anyone familiar with nonlinear dynamics: "animals typically employ their limbs in a number of distinct periodic modes." Many of these modes possess some degree of symmetry (Hildebrand, 1965, 1966, 1968). For example, when an animal *bounds*, both front legs move together and both back legs move together, as in Figure 2g on page 356. This gait thus preserves the bilateral symmetry of the animal. Other symmetries are slightly more subtle: for example, the left half of an animal can follow the same sequence of movements as the right half, but half a period out of phase, as in Figure 1. This is an example of *symmetry-breaking* (Golubitsky *et al.*, 1988; Gaeta, 1990): the gait of a bilaterally symmetric animal can fail to be bilaterally symmetric. However, such a gait has its own symmetry: "interchange left and right sides *and* shift phase by half a period."

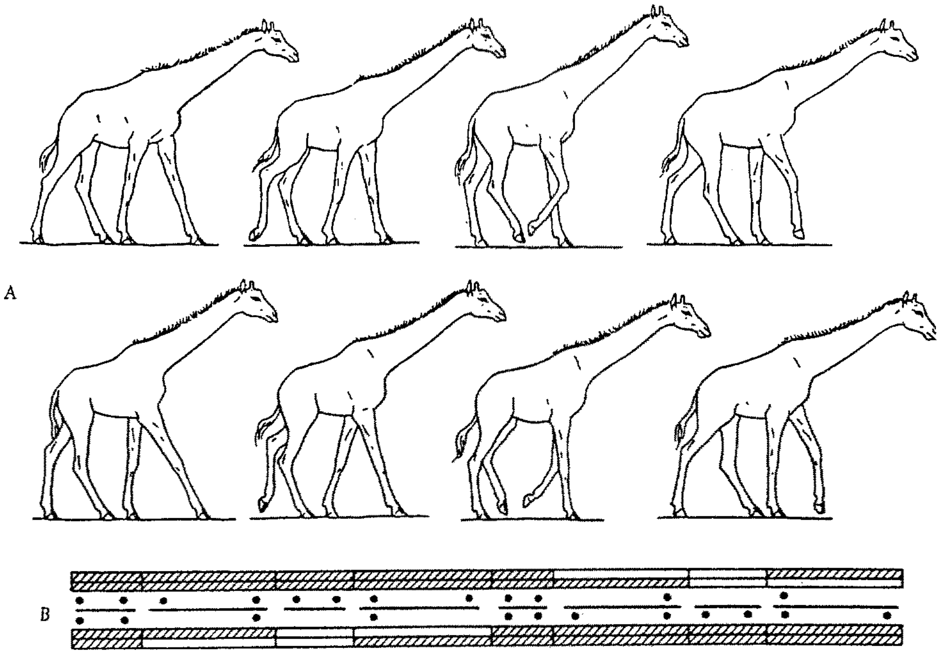

Fig. 1. Slow rack-like walk of giraffe is left-right reflected by a phase shift of half a period. The bars below are the *support graph* of the gait, and show when each foot is in contact with the ground. [From P. Gambaryan (1974), *How Mammals Run: Anatomical Adaptations.* Distributed by John Wiley & Sons, Inc., New York.]

Our aim in this paper is to draw attention to some remarkable parallels between the generalities of coupled nonlinear oscillators and the observed range of gait patterns in animal locomotion. It is widely held that locomotion might be controlled by a central pattern generator (CPG), which is a network of neurons capable of producing rhythmic output; see Sect. 3. One explanation of the observed parallel is that a locomotor CPG may have a degree of rectangular or square symmetry. If so, then our results may be interpreted as a symmetry classification of the general architecture of CPGs, describing which symmetry types of gaits can occur for each.

The traditional approach to CPG architecture has been to hypothesize specific neural circuitry and analyze its dynamics, either analytically for linear models or numerically for nonlinear ones. We approach this question from a different perspective, namely, that of nonlinear dynamics and local bifurcation theory. This approach makes the rigorous mathematical analysis of nonlinear systems more tractable, reveals general "universal" patterns and recognizable phenomena, and may be relevant to the neurophysiology of animals. These general results form a useful starting point for more detailed model-dependent analysis, and separate the questions to be answered into two types:

a. What are the general phenomena to be expected in symmetrically coupled systems of nonlinear neuronal oscillators?
b. What specific phenomena among these actually occur, and what does that imply about model-dependent features of the network architecture?

Here we answer some questions of type a. In particular we show that for each of a number of symmetry types of CPG, there is a natural "universal" hierarchy of symmetry-breaking oscillation patterns, many of which correspond to actual gaits. The patterns depend strongly on the architecture of the CPG network, but have a certain amount in common. Among quadrupedal gaits (Figures 2–4), the pace, trot, and bound (and also the rarer pronk) are highly symmetric, with relative phase lags of zero or half a period, and are very robust. The walk involves phase lags of a quarter of a period and also has a natural interpretation in terms of symmetry-breaking. The rotary and transverse gallops have less symmetry (but despite often being termed asymmetric, they retain *some* symmetry), are less robust, and involve somewhat arbitrary phase lags. They appear to correspond to networks of oscillators having an "odd" internal symmetry, a characteristic shared by pendulums and van der Pol oscillators. The canter is a more curious gait, rather fragile, with very little symmetry, and it remains mysterious. It is worth observing that it is often a "trained" gait.

Moreover, transitions between these gaits strongly resemble the typical types of symmetry-breaking bifurcation that can occur in the corresponding nonlinear dynamical systems. Varying parameters in a CPG, such as the coupling strengths between the component neuronal oscillators, may thus permit the *same* CPG to control a variety of distinct gaits, and to cause transitions from one to another.

The results of this paper complement those of Schöner *et al.* (1990), which approach the same problem from the point of view of synergetics rather than equivariant bifurcation theory. They describe the main observed gait symmetries group-theoretically, analyze the corresponding phase dynamics, and obtain gait transitions as phase transitions in model dynamical systems. In our approach all possible symmetries of gaits are derived as a natural consequence of generic symmetry-breaking in CPG dynamics, and gait transitions are viewed as generic symmetry-breaking bifurcations. Moreover, our main results (Sects. 7, 9 and Appendices 2, 3) are model-independent. Thus, Schöner *et al.* (1990) take symmetries of gaits as their starting point, and discuss their consequences for animal behavior; we concentrate on how such symmetries might arise from the dynamics of symmetric CPG networks.

The analogy between the general phenomenology of periodic oscillations of symmetric dynamical systems, and the various more-or-less symmetric gaits of animal locomotion, is thus quite striking. Below we investigate how far this analogy can be carried. We describe symmetric gaits and discuss how they can be classified. We present experimental evidence for nonlinear effects and symmetry-breaking in animal gaits and discuss the conclusions which can be drawn about the general nature of locomotion, without considering specific model equations for the dynamics.

2. Animal Gaits

Gait analysis is an ancient science. Aristotle (see references) described the walk of a horse in his treatise *De Incessu Animalium:* "The back legs move diagonally in relation to the front legs; for after the right fore leg animals move the left hind leg, then the left fore leg, and after it the right hind leg." However, he erroneously believed that the bound is impossible: "If they moved the fore legs at the same time and first, their progression would be interrupted or they would even stumble forward...For this reason, then, animals do not move separately with their front and back legs."

According to legend, modern gait analysis also originated with a horse: namely, a bet concerning the animal's gait (Taft, 1955). In the 1870s, Leland Stanford, former governor of the state of California, became involved in an argument with Frederick MacCrellish over the placement of the feet of a trotting horse. Stanford put $25,000 behind his belief that at times during the trot, a horse had all of its feet off the ground. To settle the wager, a local photographer, Eadweard Muybridge, was asked to photograph the different phases of the gait of a horse. As will be explained, Stanford was correct in his bold assertion.

Classification and Description of Gaits

Most gaits can be represented as symmetrical, cyclical patterns of leg movements. By convention, one gait cycle spans the interval from footstrike of some reference foot to consecutive footstrike by the same foot. The *duty factor* β of a foot is the fraction of the gait cycle for which it is in contact with the ground (McGhee, 1968). For each of the following gait descriptions, it is assumed that all feet (two or four) have the same duty factor. Walks have duty factors greater than 0.5; thus there are periods in bipedal walking gaits, called double-stance, when both feet are simultaneously on the ground. Runs have duty factors less than 0.5; therefore during running, there are periods, called ballistic or flight phases, when both feet of a pair are off the ground.

The *relative phase* φ_i of foot$_i$ is defined as the fraction of the gait cycle between ground contact of a reference foot (typically the left fore limb in quadrupeds) and ground contact of foot$_i$ (McGhee, 1968). The reference foot therefore has a relative phase of zero. The use of ground contact to standardize phases is convenient for most gaits, but can sometimes by unsatisfactory: see Sect. 7 and Figure 13. As far as considerations of symmetry are concerned, the relative phase is crucial, but the duty factor plays virtually no role.

Bipedal Gaits. The two limbs can be out of phase (walking and running) or in phase (hopping). Running and hopping involve flight phases separated by stance phases.

Quadrupedal Gaits. The gaits referred to below are illustrated in Figure 2 (except for the pronk, which is shown in Figure 3) as they occur in various animals, and schematically in Figure 4, following Alexander (1984).

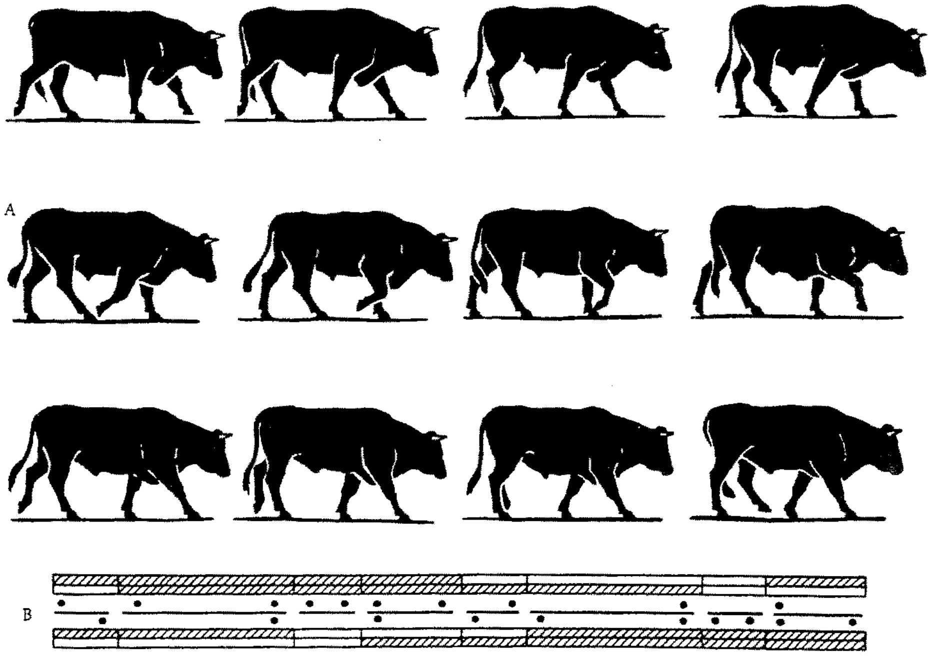

Fig. 2. Gaits of various quadrupedal animals. [From P. Gambaryan (1974), *How Mammals Run: Anatomical Adaptations*. Distributed by John Wiley & Sons, Inc. New York.] (a) Walk, ox.

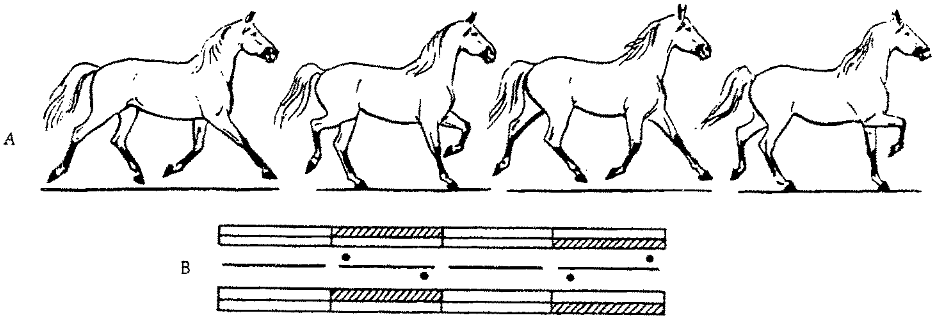

Fig. 2. (b) Trot, horse.

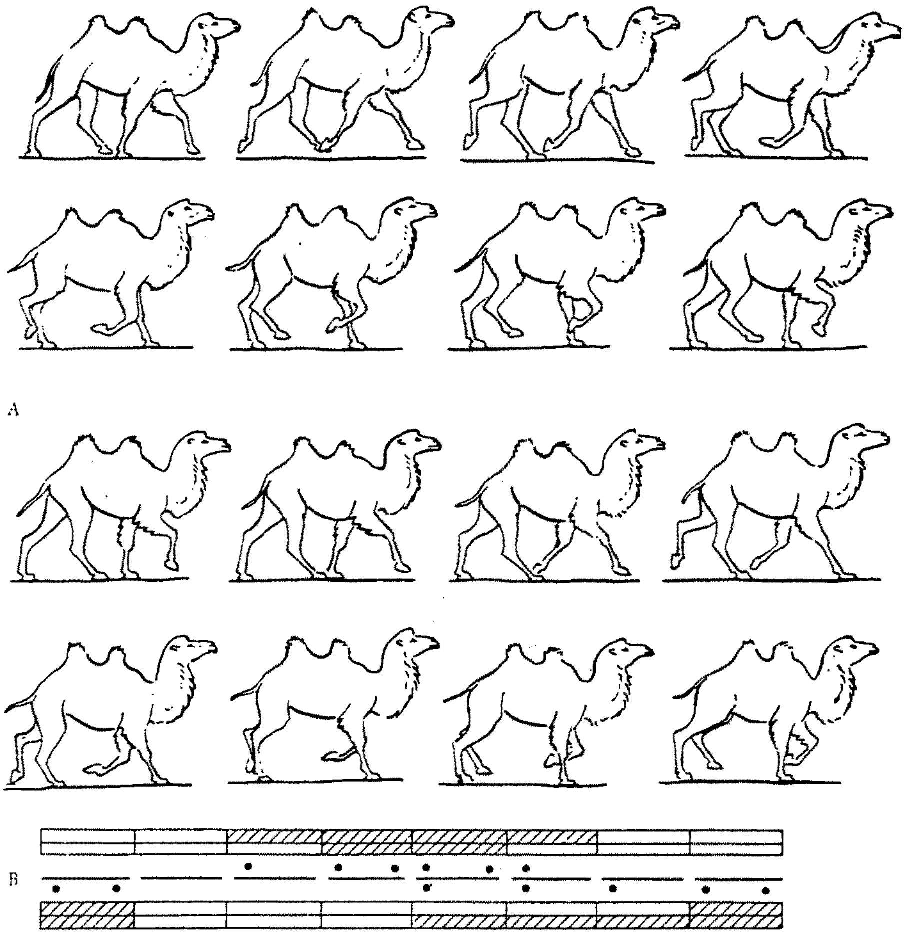

Fig. 2. (c) Pace, camel.

(a) ***Walk.*** The legs move a quarter period out of turn, in a figure-eight wave. The *amble* is the running form (lower duty factor) of this stepping sequence.

(b) ***Trot.*** Diagonal legs, i.e. left front/right back, move together and in phase. The right front and left back legs move together, half a period out of phase with the other pair. The trot is a running gait; therefore, the limbs of a trotting animal have duty factors less than 0.5.

(c) ***Pace (or Rack).*** Left/right pairing. The left legs move together and in phase. The right legs move together, half a period out of phase with the left legs.

(d) ***Canter.*** Right front/left back legs move together and in phase. The left front and right back legs move half a period out of phase with one another and out of phase

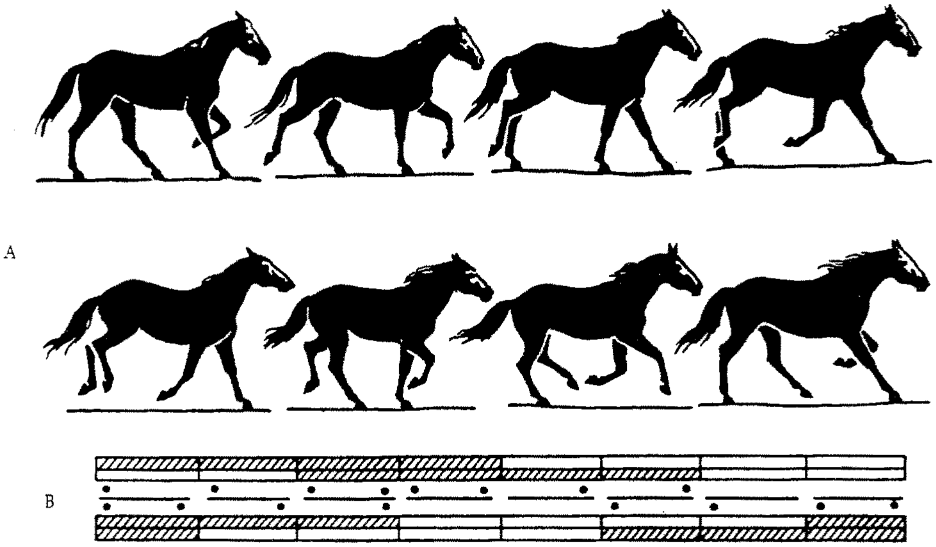

Fig. 2. (d) Canter, horse.

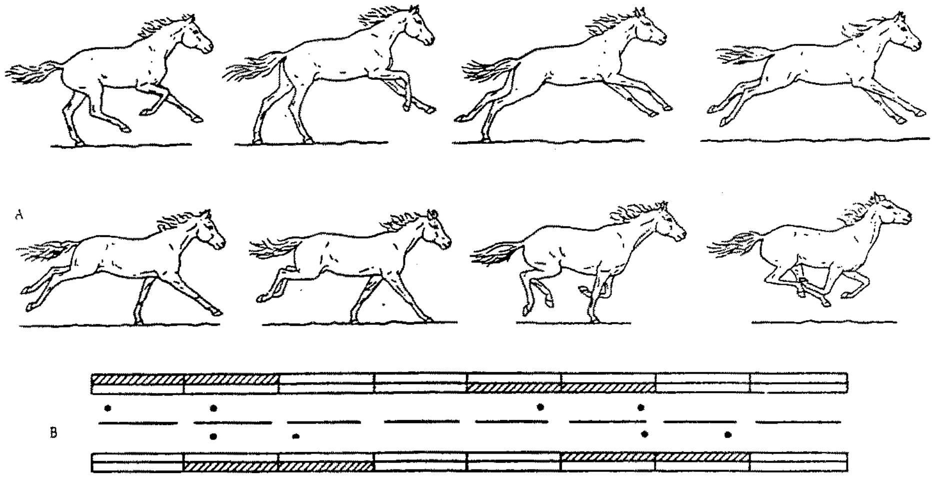

Fig. 2. (e) Transverse gallop, horse.

with the strongly coupled diagonal pair. With increasing speed, a horse will typically *walk–trot–canter–gallop*. The canter phase may be absent, and often has to be learned as a result of training.

(e) Transverse Gallop. This gait resembles the bound, but the feet of the front and back pairs are slightly out of phase with each other. The left back leg is half a period out of phase with the left front leg, and the right back leg is half a period out of phase with the right front leg.

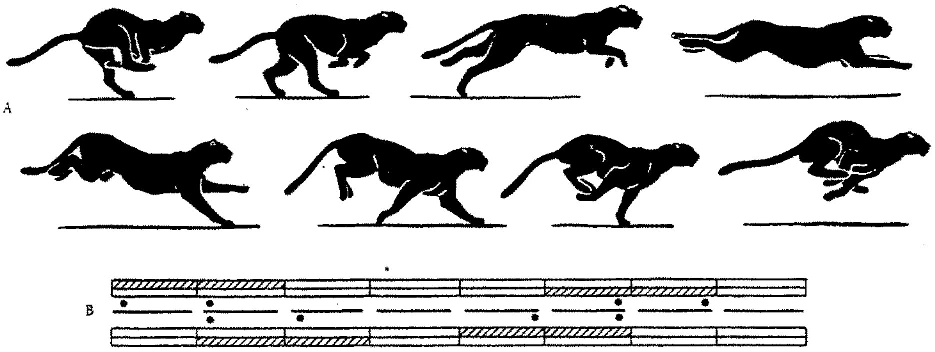

Fig. 2. (f) Rotary gallop, cheetah.

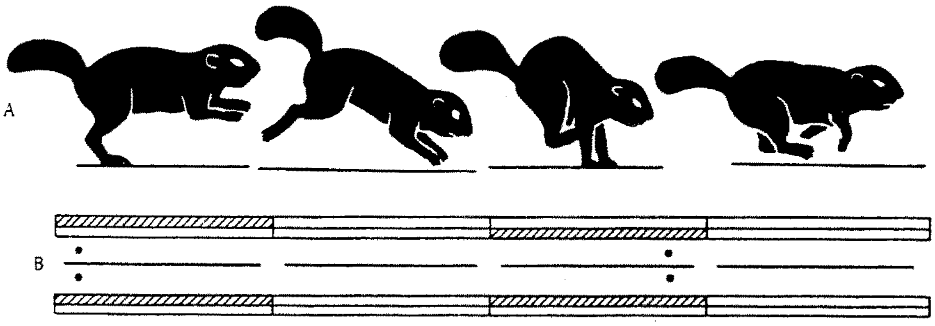

Fig. 2. (g) Bound, long-tailed Siberian souslik.

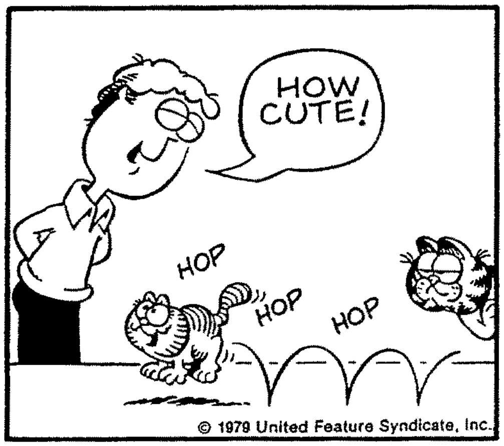

Fig. 3. The pronk, from Davis (1981).
[Reprinted with permission.]

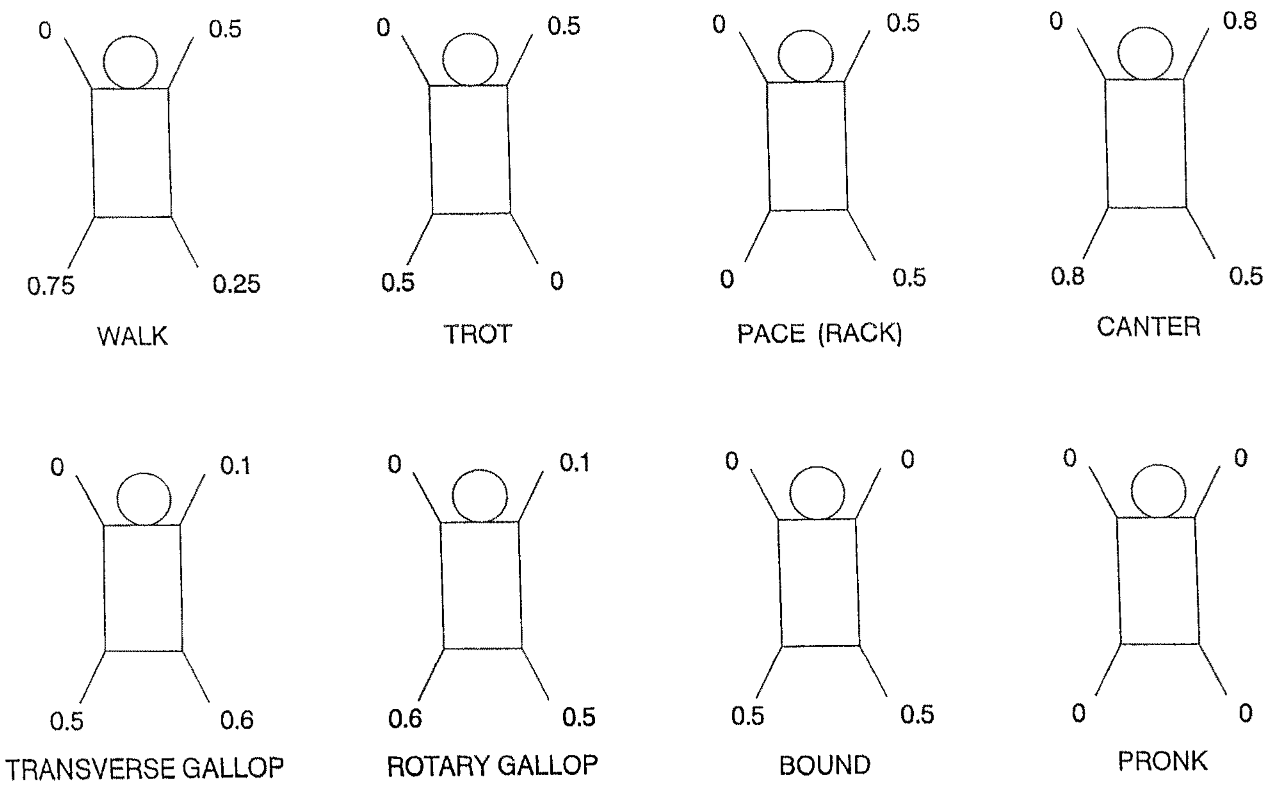

Fig. 4. Phase relations in animal gaits, corresponding to Figures 2 and 3. [Alexander R. McN., The gaits of bipedal and quadrupedal animals, Reprinted from *International Journal of Robotics Research*, vol. 3, No. 2, pp. 49–59, Figure 4, by permission of The MIT Press, Cambridge, Massachusetts, Copyright ©1984 The Massachussett Institute of Technology.]

(f) Rotary Gallop. Similar to the transverse gallop except left and right back legs have interchanged patterns. Diagonal legs are therefore half a period out of phase with one another.

(g) Bound. Front/back pairing. The front legs move together and in phase. The back legs move together, half a period out of phase with the front pair. At galloping speeds, some animals, e.g., squirrels, use the *half-bound* (Figure 5): the back legs move together and in phase, but the front legs are slightly out of phase with one another (similar to the front legs of a gallop).

(h) Pronk. All four legs move together and in phase. This gait is sometimes used by young animals and gazelles (Dagg, 1973).

3. Central Pattern Generators

Multilegged gaits require a high degree of coordination. It is generally believed that central pattern generators (CPGs)—networks of neurons in the central nervous system which produce cyclic patterns—play a significant role in the generation and control of locomotion and other rhythmic behaviors. This is not a new idea, for in 1879 T.H. Huxley (see Calabrese, 1980) compared the rhythmic motion of a crayfish to the melody played by a musical box: "It is in the ganglia that we must look for the analogue of the musical box. A single impulse conveyed by a sensory nerve to a ganglion, may

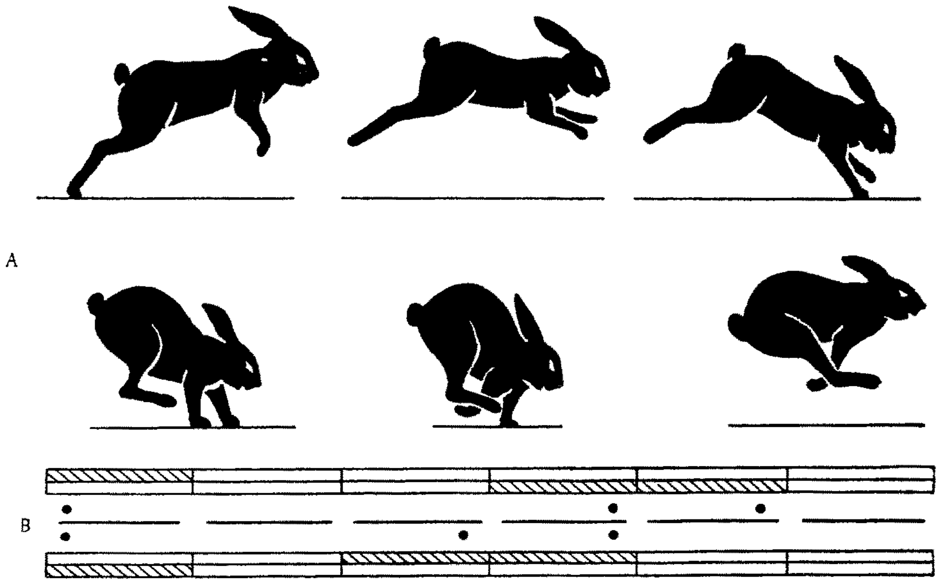

Fig. 5. Half-bound of the hare. [From P. Gambaryan (1974). *How Mammals Run: Anatomical Adaptations*. Distributed by John Wiley & Sons, Inc., New York.]

give rise to a single muscular contraction, but more commonly it originates in a series of such, combined to a definite end." Brown (1911) demonstrated that portions of a cat's spinal cord can elicit locomotor-like movements in the animal's hind limbs; he later proposed (Brown, 1914) a spinal rhythm generator model consisting of a pair of mutually inhibitory neurons ("half-centers"). Von Holst (1935, 1973) showed experimentally that an assembly of neurons in the spinal cord can coordinate fin movements in some fish, without any sensory feedback.

There is considerable evidence for the existence of locomotor rhythm generators or CPGs (Grillner, 1975, 1985; Herman *et al.*, 1976; Shik and Orlovsky, 1976; Stein, 1978; Delcomyn, 1980; Selverston, 1980; Grillner and Wallén, 1985). Quadrupedal locomotion may, for example, be controlled by four (or more) distinct but coupled neuronal oscillators (Grillner, 1975; Willis, 1980). These might be "central" in the sense that they occur in a small region of the central nervous system (CNS), or "distributed" about the CNS with longer neural interconnections. For the purposes of this paper, whenever we use the term CPG we include the distributed option as well as the central. Cohen *et al.* (1982), Rand *et al.* (1988), and Kopell (1988) consider linear arrays of identical oscillators, or of pairs of identical oscillators. Several previous studies analyze the behavior of rings of coupled oscillators (Glass and Young, 1979; Grasman and Jansen, 1979; Ermentrout, 1985; Alexander, 1986). The main aim of this paper is to study a number of different arrangements of four oscillators, either identical or identical in pairs, with the main emphasis being on symmetry and symmetry-breaking. For completeness and motivation we also treat the case of two identical oscillators (Sect. 7); and in Sect. 9 we make a few remarks about six-oscillator systems, appropriate to hexapodal gaits, and general systems of n coupled oscillators.

We shall consider five possible networks of four coupled oscillators, represented graphically in Figure 6. Here there are either one or two types of oscillator, and up to three distinct types of coupling between them. They are chosen bearing in mind two alternative interpretations: either as simple networks of neuronal oscillators in a CPG or as some coarse model of the morphological type of a quadruped. For convenience we shall not always distinguish between these two interpretations, making the same simplifying assumption as Cohen (1988): "that the motor patterns of intact animals more or less accurately reflect the organization of the CPGs which give rise to them." We are aware, as is Cohen, that this assumption need not always be valid. It is not essential to our discussion, but it lets us avoid interpreting every result in two distinct ways. One intriguing aspect of our results is that there are natural similarities between the two interpretations, perhaps suggesting a natural evolutionary route for the development of controlled locomotion. We return to this somewhat speculative point in Sect. 10.

4. Symmetries of Animal Gaits

The mathematical symbolism used to describe animal gaits is already extensive, including gait matrices (McGhee and Jain, 1972) and support graphs (Gambaryan, 1974). Some explanation should be given for introducing yet another. Our purpose is to focus on the symmetries of gaits, and this leads us to employ standard math-

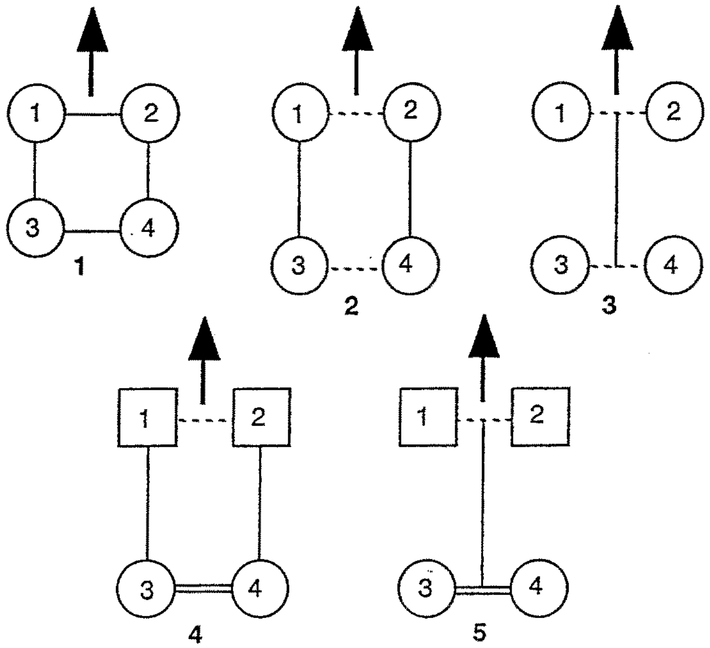

Fig. 6. Graphical representation of five distinct symmetric systems of coupled oscillators. Symbols ○ and □ indicate two distinct types of oscillator; lines ═, ---, and — indicate three distinct types of coupling. The arrow shows the direction in which the head of the animal is facing.

ematical notation for symmetries, which is group-theoretic in nature. Schöner *et al.* (1990) also employ group-theoretic methods to describe animal gaits. Our approach is similar, but is related more explicitly to the theory of periodic oscillations in systems with symmetry. The reader is not expected to know any group theory, although such knowledge is needed to follow the mathematical appendices.

We distinguish two types of symmetry in gaits. The first, *spatial* symmetry, refers to permutations of the oscillators (interpreted either as neuronal components in a CPG or as legs of an animal) in a coupled system. The second, *temporal* symmetry, involves patterns of phase-locking. The prime message from the mathematical theory of symmetric Hopf bifurcation (Golubitsky and Stewart, 1985; Golubitsky *et al.*, 1988) is that the symmetries of oscillating systems are either purely spatial or involve combinations of both spatial and temporal symmetries. We describe the two types of symmetry separately, before discussing their interaction.

Consider a system of n identical oscillators numbered $1, 2, \ldots, n$. At time t, oscillator O_i is in a state $x_i(t)$, which typically is a vector quantity. A *permutation* π is a mapping from the set $\{1, 2, \ldots, n\}$ to itself, associating to each number i between 1 and n a number $\pi(i) = i'$ between 1 and n, such that $i' = j'$ if and only if $i = j$. The permutation π also maps oscillator O_i to $O_{i'}$ and its state $x_i(t)$ to $x_{i'}(t)$. We say that the state of the system has *spatial* (or *permutational*) *symmetry* π if $x_i(t) = x_{i'}(t)$ for all times t and for all $i = 1, 2, \ldots, n$. That is, after applying the permutation π, all oscillators appear to behave exactly as before. For example, let the indices 1, 2, 3, and 4 refer to the left fore, right fore, left hind, and right hind limbs, respectively, of a quadruped. The *bound* gait is symmetric under the following permutations:

a. interchange $1 \longleftrightarrow 2$,
b. interchange $3 \longleftrightarrow 4$,
c. interchange $1 \longleftrightarrow 2$ and $3 \longleftrightarrow 4$, and (for mathematical completeness) under the *trivial* or *identity* permutation
d. leave 1, 2, 3, 4 unchanged.

That is, at any instant of time, limbs 1 and 2 are always in exactly the same state, and limbs 3 and 4 are in exactly the same state (though this generally differs from the state of limbs 1 and 2).

The permutations of $\{1, \ldots, n\}$ form a *group;* that is, if two permutations are *composed* by performing them in turn, the result is also a permutation. The composition of permutations ρ and σ, in that order, is usually written as $\sigma\rho$. The order is reversed in the notation so that $(\sigma\rho)(i) = \sigma(\rho(i))$.

There are two standard mathematical notations for a permutation. The first is cumbersome but explicit:

$$\pi = \begin{pmatrix} 1 & 2 & 3 & \ldots n \\ 1' & 2' & 3' & \ldots n' \end{pmatrix}.$$

That is, the top row lists the symbols $1, \ldots, n$ and the bottom row lists their images under π, so that i' lies directly below i. For example, when $n = 4$ the interchange $1 \longleftrightarrow 2$ is written as

$$\begin{pmatrix} 1 & 2 & 3 & 4 \\ 2 & 1 & 3 & 4 \end{pmatrix}. \tag{1}$$

The second notation is more compact but slightly less direct, and it has the advantage that the value of n can be left implicit. It is known as *cycle notation*, and we define it by examples to avoid complicated formalism. The cycle (123), for instance, represents the permutation in which $1' = 2$, $2' = 3$, and $3' = 1$, so that all symbols in the cycle "move one place on" with wrap-around to the back. In the two-rowed notation, again with $n = 4$, this permutation takes the form

$$\begin{pmatrix} 1 & 2 & 3 & 4 \\ 2 & 3 & 1 & 4 \end{pmatrix}.$$

The permutation in equation (1) is just (12) in cycle notation. Not all permutations are cycles, but all permutations can be obtained by composing cycles. As before we write the composition as a product; for example, if $n = 6$ then the cycle notation

$$(123)(45)$$

refers to the permutation

$$\begin{pmatrix} 1 & 2 & 3 & 4 & 5 & 6 \\ 2 & 3 & 1 & 5 & 4 & 6 \end{pmatrix}.$$

Greek letters $\alpha, \beta, \gamma \ldots$ are generally used to refer to individual permutations, and I to refer to the trivial permutation $I(i) = i$.

Temporal symmetries are simpler to describe. Suppose that $x(t) = (x_1(t), \ldots, x_n(t))$ is a time-dependent vector representing the states, at time t, of all n oscillators. (Again, each x_i may be a vector quantity.) We define the *phase shift* by φ of $x(t)$ to be

$$x(t - \varphi) = (x_1(t - \varphi), \ldots, x_n(t - \varphi)).$$

Then we say that the phase shift φ is a *temporal symmetry* of $x(t)$ if

$$x(t - \varphi) = x(t)$$

for all t, that is, if

$$x_i(t - \varphi) = x_i(t)$$

for all t and for all $i = 1, \ldots, n$. In words: φ is a temporal symmetry if each oscillator, phase-shifted by φ, looks the same.

Purely temporal symmetries (other than $\varphi = 0$) exist only if $x(t)$ is periodic. Suppose that T is the (minimal) period: then $x(t + T) = x(t)$ for all t, so that $x(t - mT) = x(t)$ for all integers m. That is, the purely temporal symmetries are the integer multiples of the period. Because the state is periodic, phase shifts by mT have no effect on the state. For this reason, phase shifts are considered *modulo* T, meaning that integer multiples of T may be discarded. In effect the set of phases is wrapped around into a circle so that 0 and T coincide. As a matter of convention, we normalize the period T to 1, so that phase shift by ϵT is denoted by ϵ; and ϵ is thus considered modulo 1.

Mixed spatio–temporal symmetries have a richer structure and are more common. If π is a permutation sending each i to i', and φ is a phase shift, then we say that the pair $[\pi, \varphi]$ is a *symmetry of the state* $x(t)$ if

$$x_i(t) = x_{i'}(t - \varphi)$$

for all t and for all $i = 1, \ldots, n$.

As an example, consider the trot (Figures 2b, 4). Here oscillators (in this case legs) 1 and 4 are identical; 2 and 3 are identical; and 2 is half a period out of phase with 1. If the gait period is T, this means that

$$x_2(t) = x_1(t + T/2), \quad x_3(t) = x_1(t + T/2), \quad x_4(t) = x_1(t).$$

The symmetries are:

a. The trivial permutation I; equivalently, the pair $[I, 0]$.
b. The cycle (14); equivalently, the pair $[(14), 0]$.

c. The cycle (23); equivalently, the pair [(23), 0].
d. The pair $[(12), \frac{1}{2}]$.

Note that to obtain consistent notation, purely spatial symmetries α are thought of as spatio–temporal pairs $[\alpha, 0]$ with zero phase shift. Spatio–temporal symmetries compose according to the rule

$$[\rho, \varphi][\sigma, \theta] = [\rho\sigma, \varphi + \theta],$$

and the set of *all* spatio–temporal symmetries of a given gait again forms a group; that is, composing two spatio–temporal symmetries produces another spatio–temporal symmetry. This set, together with its law of composition, is the *symmetry group* of the gait: it is the mathematical description of all of its possible symmetries. A vivid diagrammatic representation of mixed spatio–temporal symmetries may be found in Schöner *et al.* (1990).

The possible symmetry groups of gaits can be classified by purely group-theoretic arguments. By this we mean that a complete mathematical description of *all possible* groups of symmetries can be given. The approach of Schöner *et al.* (1990) is descriptive: it begins with the known gaits and determines their symmetry groups. We use group-theoretic methods to determine all possible mixed spatio–temporal symmetry groups for a given symmetry class of CPG networks, and only subsequently do we match these to observed gaits.

For simplicity we here consider only the "rectangularly symmetric" network 2 of Sect. 3 and Figure 6; see Appendix 2 for more details and a discussion of the general case. Table 1 lists all possible spatio–temporal symmetry groups for such a rectangular network. Table 2 lists the observed symmetries of various gaits in the same notation, together with the corresponding group. The symbols for the groups are chosen as

Table 1. Possible gait symmetries, type 2 (rectangular network). Let $\alpha = (12)(34)$ be left-right reflection, $\beta = (13)(24)$ be front-back reflection, and $\alpha\beta = (14)(23)$ be their composite, which geometrically is an interchange across diagonals, or equivalently a rotation through 180°.

Symbol	Symmetries				
$D_2 \times S^1$	$[I, \theta]$	$[\alpha, \theta]$	$[\beta, \theta]$	$[\alpha\beta, \theta]$	for all θ
D_2	$[I, 0]$	$[\alpha, 0]$	$[\beta, 0]$	$[\alpha\beta, 0]$	
Z_2^L	$[I, 0]$	$[\alpha, 0]$			
Z_2^F	$[I, 0]$	$[\beta, 0]$			
Z_2^D	$[I, 0]$	$[\alpha\beta, 0]$			
$\mathbf{1}$	$[I, 0]$				
$\tilde{D}_2^L$	$[I, 0]$	$[\alpha, 0]$	$[\beta, \frac{1}{2}]$	$[\alpha\beta, \frac{1}{2}]$	
$\tilde{D}_2^F$	$[I, 0]$	$[\alpha, \frac{1}{2}]$	$[\beta, 0]$	$[\alpha\beta, \frac{1}{2}]$	
$\tilde{D}_2^D$	$[I, 0]$	$[\alpha, \frac{1}{2}]$	$[\beta, \frac{1}{2}]$	$[\alpha\beta, 0]$	
$\tilde{Z}_2^L$	$[I, 0]$	$[\alpha, \frac{1}{2}]$			
$\tilde{Z}_2^F$	$[I, 0]$	$[\beta, \frac{1}{2}]$			
$\tilde{Z}_2^D$	$[I, 0]$	$[\alpha\beta, \frac{1}{2}]$			

Table 2. Observed gait symmetries in quadrupeds. Let $\alpha = (12)(34)$ be left-right reflection, $\beta = (13)(24)$ be front-back reflection, and $\alpha\beta = (14)(23)$ be their composite, rotation through 180°.

Gait	Symmetries					Group
Stand	$[I, \theta]$	$[\alpha, \theta]$	$[\beta, \theta]$	$[\alpha\beta, \theta]$	for all θ	$D_2 \times S^1$
Pronk	$[I, 0]$	$[\alpha, 0]$	$[\beta, 0]$	$[\alpha\beta, 0]$		D_2
Trot	$[I, 0]$	$[\alpha, \frac{1}{2}]$	$[\beta, \frac{1}{2}]$	$[\alpha\beta, 0]$		$\tilde{D}_2^D$
Bound	$[I, 0]$	$[\alpha, 0]$	$[\beta, \frac{1}{2}]$	$[\alpha\beta, \frac{1}{2}]$		$\tilde{D}_2^F$
Pace	$[I, 0]$	$[\alpha, \frac{1}{2}]$	$[\beta, 0]$	$[\alpha\beta, \frac{1}{2}]$		$\tilde{D}_2^L$
Transverse gallop	$[I, 0]$	$[\beta, \frac{1}{2}]$				$\tilde{Z}_2^L$
Rotary gallop	$[I, 0]$	$[\alpha\beta, \frac{1}{2}]$				$\tilde{Z}_2^F$
Canter	$[I, 0]$					1

follows: any group that involves all four permutations I, α, β, $\alpha\beta$ includes the symbol D_2; any group involving only I and one other permutation includes Z_2. Here D is the initial letter of "dihedral" and Z of the German "Zyklik" for "cyclic." The superscripts L, F, and D correspond to left-right reflection, front-back reflection, and diagonal interchange, respectively. For example, in Z_2^L the L means "no phase shift for interchange of left and right." A tilde ˜ indicates that phase-shift symmetries are involved. The symbol S^1 refers to the "circle group" of all phase shifts φ, taken modulo 1.

To avoid confusion we should add that in the gaits literature the term "symmetric gait" is often used to refer to the pace, bound, and trot (e.g., Gambaryan, 1974). As Schöner *et al.* (1990) remark, many other gaits possess nontrivial symmetries. Table 2 confirms this contention.

Observe that in Table 2 we have listed the canter as having trivial symmetry. This is because we have assumed a rectangular network of oscillators, type 2. In fact the canter has two spatio-temporal symmetries which in the above notation are [(23), 0] and [(14), $\frac{1}{2}$], but these do not arise in case 2. They do, however, arise in case 3, as shown in Appendix 2.

The above group-theoretic description may appear cumbersome, but it provides a precise framework for discussing symmetries of animal gaits and is used in the next section to analyze the possible patterns of broken symmetry, which are fundamental to our approach.

5. Symmetry-Breaking Bifurcations

In this section we discuss how a CPG network whose symmetry is fixed can generate patterns with different symmetries. Our contention is that changes in animal gaits fit neatly into the general pattern of symmetry-breaking bifurcation in dynamical systems. The likely role of bifurcation in physiological systems has been emphasized recently by many authors, such as Kopell (1988), Rand *et al.* (1988), and Alexander (1989). The possible role of symmetry-breaking has not received as much attention, but seems to be relevant to the issue of symmetry in gait patterns. Again our results complement those of Schöner *et al.* (1990): what they interpret as phase transitions in a synergetic system, we view as symmetry-breaking bifurcations.

We here describe a few basic phenomena of symmetry-breaking: for further details see Appendices 1–3 and Golubitsky *et al.* (1988). Consider a dynamical system

$$dx/dt = f(x, a), \tag{2}$$

where $x \in \mathbb{R}^n$, a is a parameter, and $f : \mathbb{R}^n \times \mathbb{R} \to \mathbb{R}^n$ is a smooth vector field. As the parameter a in (2) is varied, qualitative changes in the dynamical behavior may occur—typically at isolated values of a. Such a change is called a *bifurcation*, and a is therefore called a *bifurcation parameter.*

Let Γ be a compact Lie group acting orthogonally on $\mathbb{R}^n$. We say that f is Γ-*equivariant*, or that f *commutes with* Γ, if

$$f(\gamma x, a) = \gamma f(x, a)$$

for all $\gamma \in \Gamma$. Equivariant dynamical systems often arise as models of physical systems with a more or less "obvious" symmetry group Γ. For example, a system with circular symmetry will usually give rise to a dynamical system that is $O(2)$-equivariant, where $O(2)$ is the group of rotations and reflections in the plane that fix the origin; that is, the symmetry group of a circle.

Symmetry tends to cause violations of the hypotheses of theorems that give conditions for the occurrence of "generic" dynamical phenomena. For example, a common assumption on generic bifurcations is that the Jacobian $(df)_x = [\partial f_i/\partial x_j]$ should have simple eigenvalues. However, for equivariant f, its eigenvalues are usually multiple. In consequence, the symmetry must be "built into" the whole approach, and instead of "generic" behavior it is necessary to study behavior that is "generic among those systems that possess symmetry group Γ." A considerable body of technique now exists in this area.

One of the most fundamental phenomena in equivariant dynamics is *symmetry-breaking*. We measure the symmetry of a solution $x = x(t)$ of (2) by its *isotropy subgroup*

$$\Sigma_x = \{\sigma \in \Gamma \mid \sigma x(t) = x(t) \text{ for all } t\}.$$

If $\Sigma_x \neq \Gamma$ then we say that x *breaks* the symmetry from Γ to Σ_x. For example, the equations describing a spherical pendulum are equivariant under $O(2)$; but a pendulum that swings periodically in a vertical plane breaks the symmetry to a group Z_2 generated by reflection in that plane.

The simplest types of bifurcation are *steady-state bifurcation*, where the number of equilibria of the system changes, and *Hopf bifurcation*, where a stable equilibrium becomes unstable and creates a limit cycle. Our main concern in this paper is symmetry-breaking via Hopf bifurcation; and here the appropriate group is the collection of all spatio–temporal symmetries, which generalize those described in the previous section for permutations of oscillators. Namely, if (2) is Γ-equivariant, and $x \equiv x(t)$ is a periodic solution with period T, then $(\gamma, \varphi) \in \Gamma \times S^1$ is a *spatio–temporal symmetry* of x if

$$x(t) = \gamma x(t - \varphi)$$

for all t. Here S^1 is the circle group $\mathbb{R}/T\mathbb{Z}$. We discuss the general theory of symmetry-breaking Hopf bifurcations in Appendix 1.

We apply these ideas in the following manner. Any network N of identical oscillators possesses a "spatial" symmetry group Γ, consisting of all permutations of the nodes of the network that preserve the couplings. For example, a ring of n oscillators with identical nearest-neighbor couplings has spatial symmetry group D_n, the *dihedral group* of order $2n$, generated by cyclic permutations of the oscillators together with inversion:

$$\begin{pmatrix} 1 & 2 & 3\ldots n \\ n & n-1 & n-2\ldots 1 \end{pmatrix}.$$

Thus the spatio–temporal symmetry group is $D_n \times S^1$. Hopf bifurcation in this context has been analyzed, making essential use of the group-theoretic framework, by Golubitsky and Stewart (1986). For example, when $n = 3$ there are three types of bifurcating periodic oscillation: a rotating wave and two different standing waves. The possible types of symmetry-breaking Hopf bifurcation for the networks of oscillators employed in this paper are described in detail below, based upon the general theory.

For example, let us consider actual quadrupedal gaits, again using the model of rectangular symmetry, type 2 (Figure 6). From Tables 1 and 2 we can read off the possible patterns of symmetry-breaking, shown in the abstract in Figure 7 and for the corresponding gaits in Figure 8. We see the primary modes are the most symmetric gaits (pronk, pace, bound, trot) and the secondary "mixed" modes are the rotary and transverse gallops. Indeed the rotary gallop is a mixture of the pace and bound, and the transverse gallop is a mixture of the bound and trot. For other network types, see Appendix 2.

Primary bifurcations generally lead to states that possess a high degree of symmetry, and subsequent secondary and tertiary bifurcations lead to states with less and

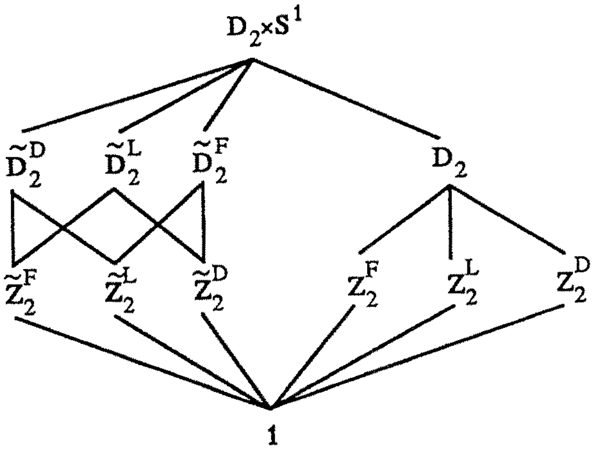

Fig. 7. Abstract patterns of symmetry-breaking for a rectangularly symmetric network (type 2 of Figure 6).

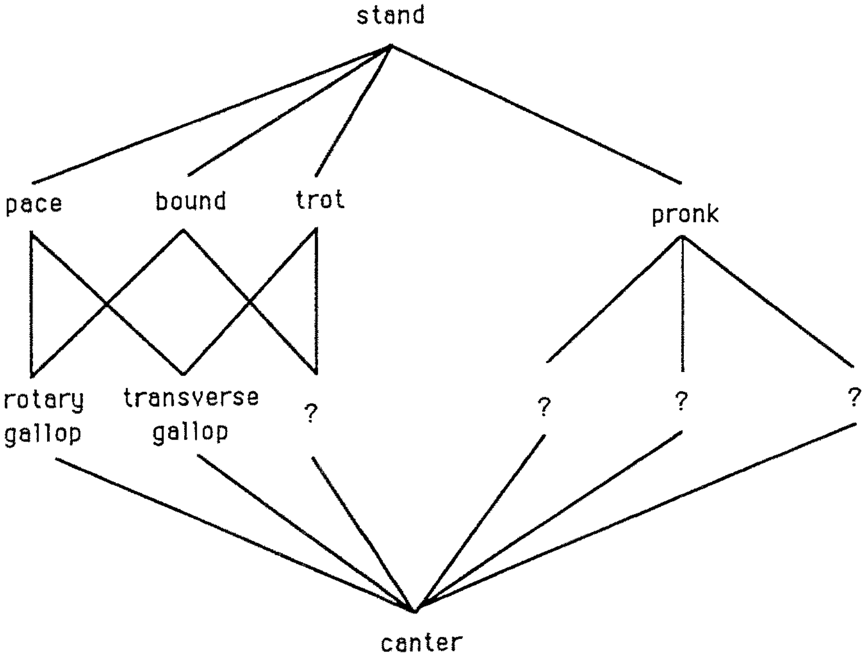

Fig. 8. Quadrupedal gaits corresponding to Figure 7.

less symmetry. In other words, successive bifurcations tend to break more and more symmetry, so the list of possible symmetry groups governs the broad pattern of the bifurcations that can occur. These statements are intended as a rough guide and should not be taken too literally, however. There are some known exceptions, and many points of fine detail are not captured by the list of possible symmetry groups (Golubitsky *et al.*, 1988, Chapter XIII, Sect. 10).

6. Evidence for Nonlinearity in Animal Gaits

The idea that nonlinearity is involved in the generation and regulation of animal movement is gaining recognition. The role of bifurcation, for example, is made explicit in Kelso and Schöner (1988), Kopell (1988), and Rand *et al.* (1988), and it plays a central role in Schöner *et al.* (1990). Alexander (1989) also offers extensive evidence for nonlinearity and bifurcation in animal gaits.

Striking experimental evidence that gait transitions in animals are related to the above types of bifurcations is given in Hoyt and Taylor (1981). In this study, horses were trained to walk, trot, and gallop on a treadmill. Hoyt and Taylor's observations of oxygen consumption as a function of speed are shown in Figure 9a. This type of diagram is precisely what one would expect from a nonlinear system bifurcating into one of several distinct modes. The overlap of the parabolic curves for the trot and gallop suggests the presence of hysteresis in the corresponding transition. The data are

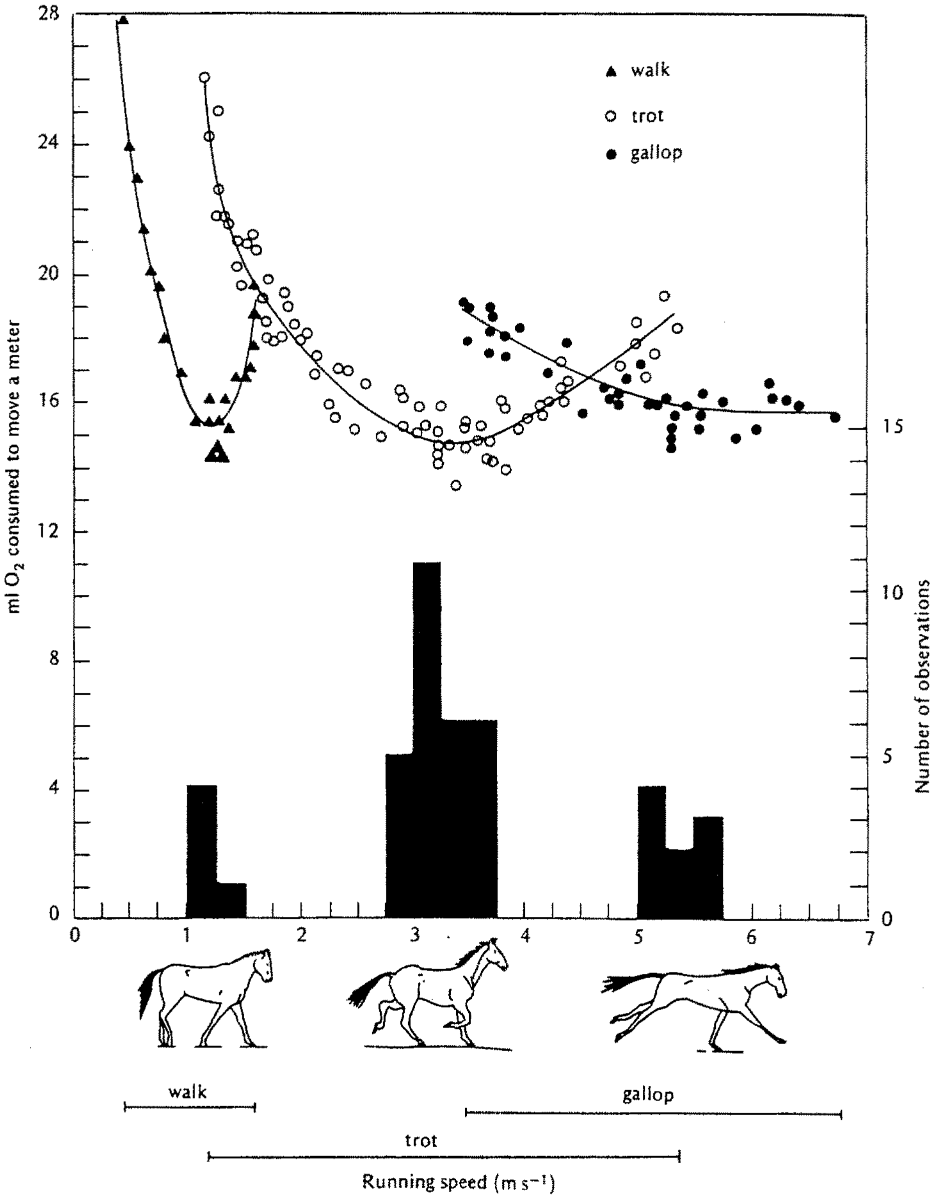

Fig. 9. (a) Graph of oxygen consumption versus speed for horses. [From Schmidt–Nielsen (1990), redrawn from Hoyt and Taylor (1981). Reprinted with permission from *Nature* (Gait and the energetics of locomotion in horses, *Nature* **292**, 239–240). Copyright 1981 Macmillan Magazines Limited, London.]

more equivocal for the walk/trot transition but support a smaller degree of hysteresis. The interpretation of these results in terms of a bifurcation diagram is shown in Figure 9b.

Alternative gait-transition conventions to bifurcation, such as optimization principles (Alexander, 1989), are attractive for several reasons: they reflect the plausible

(b)

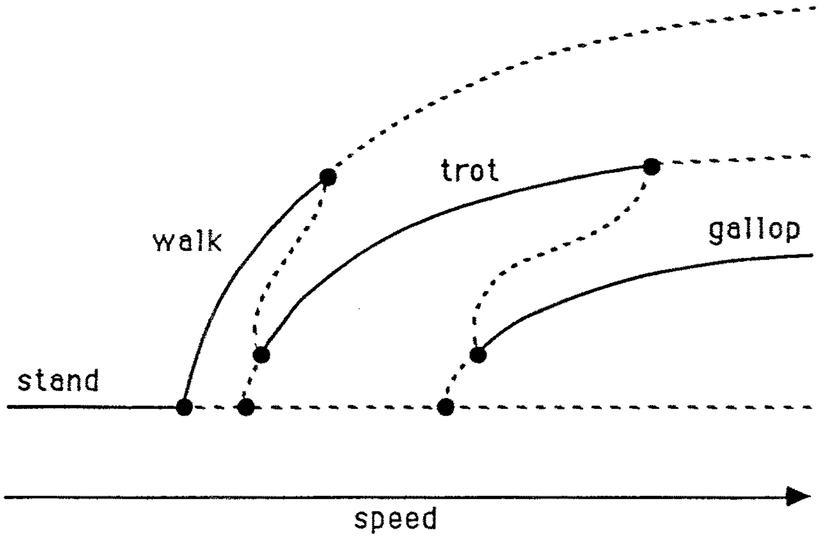

Fig. 9. (b) Interpretation as a bifurcation diagram.

hypothesis that gaits represent the effect of *controlled* rather than free-running dynamics, and are consistent with a great deal of experimental work. Thus Hoyt and Taylor (1981) observe (histograms in Figure 9a) that when the trained horses are permitted to select their own speeds, varying on the ground, they tend to minimize the oxygen consumption in each gait. They thus *select* discrete ranges of speeds from the continuous range available. One would not generally expect to find hysteresis if the gait transitions are determined by optimization principles. According to Taylor (private communication), dogs and horses do not exhibit any hysteresis at the trot/gallop transition in treadmill experiments for which the speed of the treadmill is changed slowly; however, they do exhibit hysteresis if the treadmill speed is changed rapidly.

7. Coupled Oscillators

We now describe the typical oscillation patterns of systems of two and four coupled nonlinear oscillators, where the oscillators are either identical or divided into two distinct groups. (By the use of the term "oscillator" here it is not intended to imply that the individual components are necessarily capable of oscillating on their own; for example, Smale (1974) reports a case where oscillation sets in only when the components are coupled.) We seek features that are independent of the detailed dynamics of the individual oscillators and of the nature of the coupling (other than its symmetry properties). This is similar in spirit to the approach of Kopell (1988), who states, "The idea is to develop a body of mathematics that can help decide, with minimal a priori guessing, which differences do indeed make a difference. Thus, the method is to work with robust classes of equations and, within these, to attempt to sort out which conclusions are essentially universal and which depend on further structure." Similarly Rand *et al.* (1988) emphasize "those aspects of the dynamical behavior of the models which should be shared by a rather general class of systems." This is not to deny the utility of specific models, such as those of Bay and Hemami (1987) or Yuasa and Ito (1990): its aim is to clarify which features of specific models are instances of more general phenomena.

Systems of Two Coupled Oscillators

If two identical oscillators are coupled together (Figure 10), then there are two typical oscillation patterns:

a. The *in-phase* pattern: both oscillators have the same waveform.
b. The *out-of-phase* pattern: both oscillators have the same waveform except for a phase difference of half a period.

These patterns are illustrated in Figure 11. The two patterns of phase-locking arise through a Hopf bifurcation, and typically they are the only patterns that occur.

These abstract results can be interpreted in the following ways. Firstly, the two oscillators could represent *identical* components of a central pattern generator, coupled neurally. Then the signals that they produce, either through "spontaneous" excitation or external stimulation by a *single* periodic signal (Kupfermann and Weiss, 1978), will possess the same pattern of phase-locking. Such signals could "drive" the musculature that controls a single leg or a pair of legs. Alternatively, the oscillators could represent the legs of a biped, coupled mechanically by the body of the animal. Again, the two natural oscillation patterns (for free or forced oscillations) will be the in-phase and out-of-phase oscillations. For the in-phase pattern, both legs will move together: that is, the animal will perform a two-legged hopping motion (Figure 12). The out-of-phase motion could resemble the normal human walking/running gait: both legs move with the same waveform, but half a period out of phase. A more exotic possibility with the same symmetry is shown in Figure 13. Observe that the figure shows only half a period: the "final" position is the mirror image of the initial one.

The gait in Figure 13 raises a problem concerning the usual definition of relative phase (see Sect. 2) because each foot hits the ground *twice* during a gait period. Only for one choice of ground contact is the relative phase equal to 0.5. The mathematical point behind this is that an oscillation does not of itself possess a phase: the notion of phase difference makes sense *only* for oscillation patterns that are identical except for time translation, as in Sect. 4. For such oscillations, *if* each foot hits the ground once

Fig. 10. Schematic of two identical coupled oscillators.

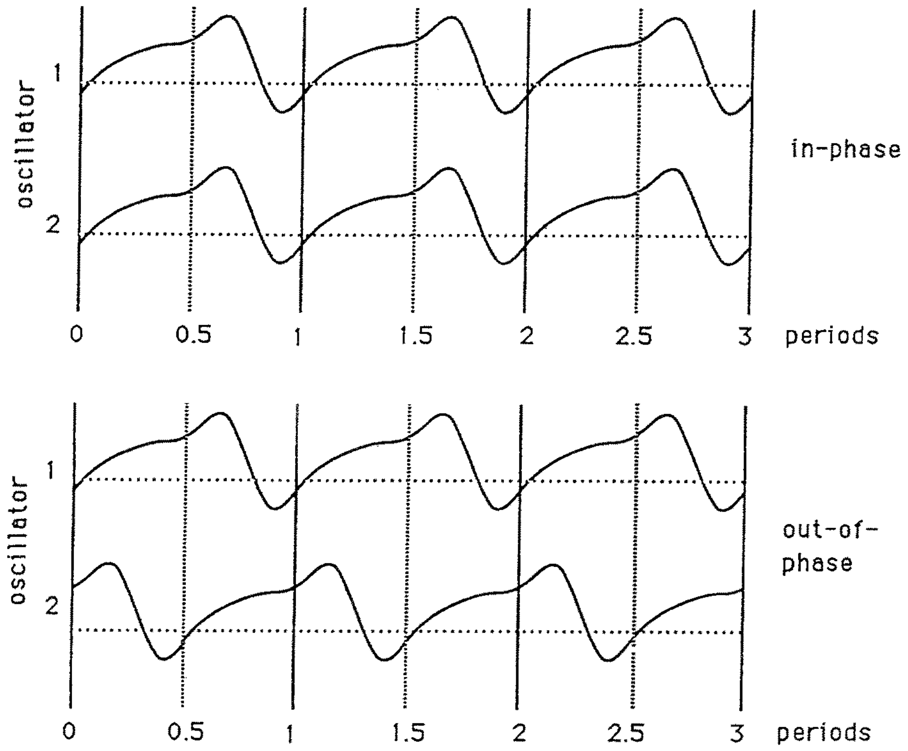

Fig. 11. Schematic of in-phase and out-of-phase motion for two identical coupled oscillators.

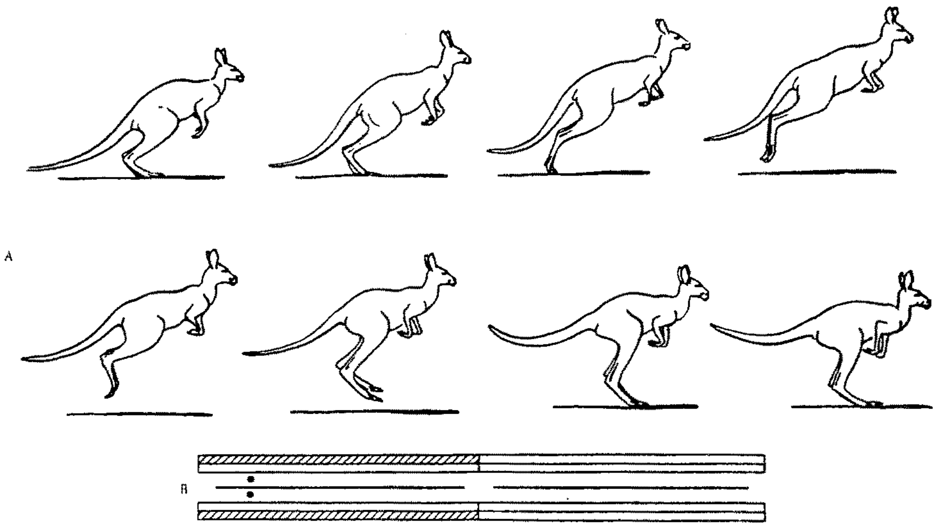

Fig. 12. Bound of kangaroo has in-phase left-right symmetry. [From P. Gambaryan (1974). *How Mammals Run: Anatomical Adaptations*. Distributed by John Wiley & Sons, Inc., New York.]

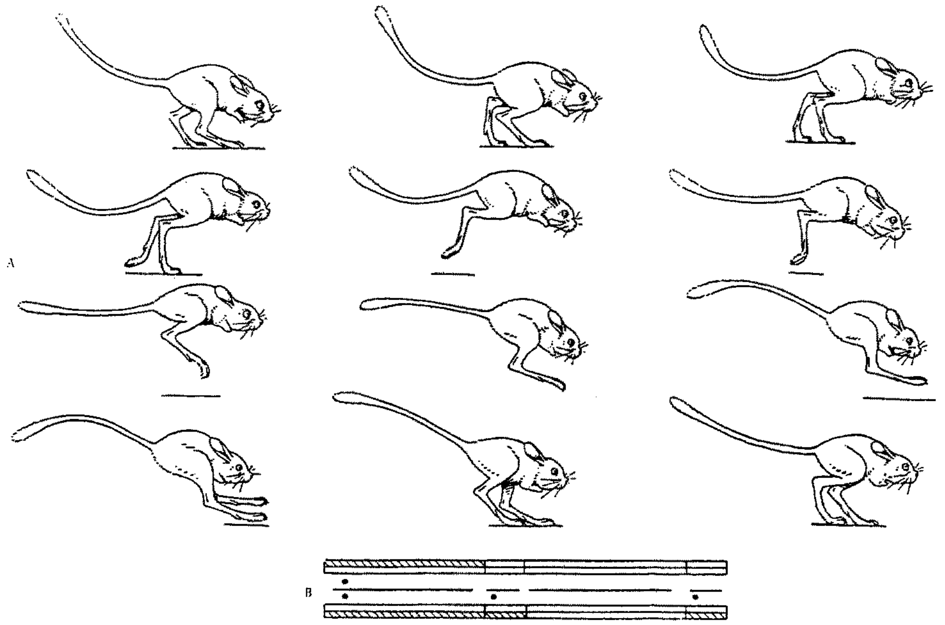

Fig. 13. Half-bound of Severtsov's jerboa has out-of-phase left-right symmetry. Note that each foot hits the ground twice per gait period. [From P. Gambaryan (1974). *How Mammals Run: Anatomical Adaptations.* Distributed by John Wiley & Sons, Inc., New York.]

per period, then ground contact provides a convenient reference point. Real gaits are not perfectly symmetric, so a degree of judgment is involved in deciding when to consider two oscillations as being "the same" except for time translation. Differences in such judgments could affect some details of our conclusions.

Systems of Four Coupled Oscillators

For four oscillators there are more types of pattern and more possible ways in which the oscillators might be coupled. In Sect. 3 we introduced five possible cases (Figure 6). We show in Appendix 3 that for these five coupled systems the typical symmetries of periodic oscillations which are *always* created by Hopf bifurcation are given in Table 3. In some systems there may be additional patterns, but the existence of those listed is model-independent. Several of these patterns can be observed in the results of Bay and Hemami (1987) for a specific model composed of van der Pol oscillators. In Sect. 8 we briefly describe the results of numerical experiments with two specific model systems.

The annotation BIFURCATE TOGETHER in Table 3 indicates states that occur together in a single Hopf bifurcation; that is, multiple branches of the bifurcation diagram which emerge from the same point. See Appendix 1 for further details.

Type 1 is an arrangement of four identical oscillators with square symmetry (Figure 6). We are not suggesting that there exist animals with square symmetry. If we

Table 3. Typical patterns for four coupled nonlinear oscillators.

System		LF (1)	RF (2)	LH (3)	RH (4)	Mathematical comments	Corresponding gait
1	a	A	A	A	A		pronk
	b	A	$A+\frac{1}{2}$	$A+\frac{1}{2}$	A		trot
	c	A	$A+\frac{1}{4}$	$A+\frac{3}{4}$	$A+\frac{1}{2}$		similar to rotary gallop
	d	A	$A+\frac{3}{4}$	$A+\frac{1}{4}$	$A+\frac{1}{2}$	BIFURCATE	similar to rotary gallop (opposite orientation)
	e	A	A	$A+\frac{1}{2}$	$A+\frac{1}{2}$	– TOGETHER	bound*
	f	A	$A+\frac{1}{2}$	A	$A+\frac{1}{2}$		pace
	g	A	B	$B+\frac{1}{2}$	A	$A = \frac{1}{2}$ period	
	h	A	B	B	$A+\frac{1}{2}$	$B = \frac{1}{2}$ period	canter?
2	a	A	A	A	A		pronk
	b	A	$A+\frac{1}{2}$	A	$A+\frac{1}{2}$		pace
	c	A	A	$A+\frac{1}{2}$	$A+\frac{1}{2}$		bound*
	d	A	$A+\frac{1}{2}$	$A+\frac{1}{2}$	A		trot
3	a	A	A	A	A		pronk
	b	A	A	$A+\frac{1}{2}$	$A+\frac{1}{2}$		bound*
	c	A	$A+\frac{1}{2}$	$A+\frac{3}{4}$	$A+\frac{1}{4}$		walk and amble
	d	A	$A+\frac{1}{2}$	$A+\frac{1}{4}$	$A+\frac{3}{4}$	BIFURCATE	
	e	A	$A+\frac{1}{2}$	$A+\frac{1}{2}$	A	– TOGETHER	trot
	f	A	$A+\frac{1}{2}$	A	$A+\frac{1}{2}$		pace
	g	A	A	B	$B+\frac{1}{2}$	$A = \frac{1}{2}$ period	
	h	A	$A+\frac{1}{2}$	B	B	$B = \frac{1}{2}$ period	
4	a	A	A	B	B		asymmetric bound*
	b	A	$A+\frac{1}{2}$	B	$B+\frac{1}{2}$		
5	a	A	A	B	B		asymmetric bound*
	b	A	$A+\frac{1}{2}$	B	B		
	c	A	A	B	$B+\frac{1}{2}$		

*Bound is close to transverse and rotary gallops.

are thinking of physical symmetries of the animal, then this arrangement would be appropriate for quadrupeds whose four legs are approximately the same and where the mechanical coupling between them is relatively similar. If we are thinking of locomotor central pattern generators then genuine square symmetry is reasonable.

Type 2 has rectangular symmetry, and is appropriate for animals whose fore limbs and hind limbs are fairly similar, but where the left/right coupling differs substantially from the front/rear. It might be argued that in animal limbs, exact front/back symmetry never occurs. In this case type 4 is more appropriate. However, approximate symmetry between front and back is common. Raibert (1986, 1988) notes that the rotary gallop of the cat is symmetric, apart from minor deviations, under time reversal and such a symmetry in particular interchanges front and back. Incidentally, front/back symmetry does *not* imply that the animal can move backwards as easily as forwards: this concept refers to the hypothetical interchange of front and back limbs, not to a reversal of direction. The oscillations of individual limbs can be "directional."

Type 3 preserves the differences in coupling of type 2 but has more symmetry. It treats the two front legs as a unit, coupled to an identical unit at the rear. Its symmetries are independent transpositions of oscillators (12) and (34), together with the interchange of front and rear. If, for example, the front and rear legs are mainly coupled through the spine, type 3 is appropriate. In the abstract, type 3 is isomorphic to type 1, which is why their lists of oscillation patterns (Table 3) are very similar. To be precise, if we renumber oscillators 1234 in type 3 as 1423 (so that front and back pairs in type 3 correspond to diagonal pairs in type 1), then the networks become identical. We distinguish the two cases because the labeling as limbs is not preserved by this isomorphism, but it means that we can read off the answers for type 3 directly from those for type 1. In the same way, networks 2 and 5 are isomorphic.

Types 4 and 5 are analogous to 2 and 3, but now the front pair of legs differs substantially from the back pair.

As Table 3 shows, each type of arrangement has its own particular set of "natural" oscillation patterns. The most symmetric gaits (pronk, trot, bound, pace, walk) correspond precisely to patterns that occur in the table. The final gait listed for type 1 has the correct phase relations for a canter, but a true canter does not involve the half-period property of waveform B. However, minor breaking of the square symmetry could destroy this property, leaving something closer to a canter.

The rotary and transverse gallops are not represented in our list, although type 1 has two conjugate patterns, 1c and 1d, that are similar to the rotary gallop. Among the twenty patterns listed for the first three networks (all oscillators identical), only four do not seem to correspond to gaits described in Sect. 2. All of these involve the half-period condition. This 2:1 frequency-locking effect and its relevance to animal locomotion are treated in greater detail in Collins and Stewart (1992).

The oscillation patterns for types 4 and 5 are plausible for animals whose front legs are significantly different from their rear legs. For example, pattern 5b corresponds to a two-legged walk on hind legs, while the front legs move together in phase; pattern 4b is essentially the normal bipedal human walking/running gait with A representing arm movements and B leg movements.

8. Numerical Simulations

In this section we describe some simple numerical simulations that show just how common, and how varied, symmetry-breaking oscillations are, in symmetric networks of identical oscillators. The model (see equations (3) below) consists of coupled oscillators of van der Pol type, with additional terms that break the "internal" odd-function symmetry of a conventional van der Pol oscillator. We are forced to add such terms because internal symmetries have a strong effect on the entire analysis. The equations describe four oscillators $O_j (j = 1, \ldots, 4)$, each of which involves two dynamic variables (x_j, y_j). There are five parameters α, β, γ, δ, ϵ, of which α, β, and ϵ affect the internal dynamics of each oscillator, and δ, γ are coupling constants. We have chosen a simple form of linear coupling. The model has no special physiological significance since it is presented only as evidence that the mathematical phenomena that we have described are easily observed in actual equations.

The model equations are

$$\begin{aligned}
\frac{dx_1}{dt} &= y_1 - \alpha x_1\left(\frac{x_1^2}{3} - 1\right) + \beta + \epsilon x_1^2 + \gamma(x_1 - x_2) + \delta(x_1 - x_4),\\
\frac{dx_2}{dt} &= y_2 - \alpha x_2\left(\frac{x_2^2}{3} - 1\right) + \beta + \epsilon x_2^2 + \gamma(x_2 - x_1) + \delta(x_2 - x_3),\\
\frac{dx_3}{dt} &= y_3 - \alpha x_3\left(\frac{x_3^2}{3} - 1\right) + \beta + \epsilon x_3^2 + \gamma(x_3 - x_4) + \delta(x_3 - x_2),\\
\frac{dx_4}{dt} &= y_4 - \alpha x_4\left(\frac{x_4^2}{3} - 1\right) + \beta + \epsilon x_4^2 + \gamma(x_4 - x_3) + \delta(x_4 - x_1), \qquad (3)\\
\frac{dy_1}{dt} &= -x_1, \qquad \frac{dy_2}{dt} = -x_2,\\
\frac{dy_3}{dt} &= -x_3, \qquad \frac{dy_4}{dt} = -x_4.
\end{aligned}$$

These correspond to networks of type 2 (Figure 6) when $\gamma \neq \delta$, and type 1 when $\gamma = \delta$. Since, as already explained, network 3 can abstractly be converted to network 1 by relabeling, the model covers the main three networks that we have discussed in the case of four identical oscillators.

Figures 14–20 show the results of some numerical experiments carried out on these equations using the package *kaos* developed by Guckenheimer and Kim (1990). We have not attempted a detailed exploration of this model, nor have we attempted to explain many additional dynamical phenomena that can be found numerically: we merely exhibit some of the symmetry-breaking dynamics that arise, without further comment.

We have not found the "exceptional" solution types 1g and 1h (Table 3) in (3). However, we have found them (Figure 21) in a related system with different coupling terms, where the first four equations of (3) are replaced by

$$\begin{aligned}
\frac{dx_1}{dt} &= y_1 - \alpha x_1\left(\frac{x_1^2}{3} - 1\right) + \beta + \epsilon x_1^2 + \gamma(2x_1 - x_2 - x_4),\\
\frac{dx_2}{dt} &= y_2 - \alpha x_2\left(\frac{x_2^2}{3} - 1\right) + \beta + \epsilon x_2^2 + \delta(2x_2 - x_1 - x_3), \qquad (4)\\
\frac{dx_3}{dt} &= y_3 - \alpha x_3\left(\frac{x_3^2}{3} - 1\right) + \beta + \epsilon x_3^2 + \gamma(2x_3 - x_2 - x_4),\\
\frac{dx_4}{dt} &= y_4 - \alpha x_4\left(\frac{x_4^2}{3} - 1\right) + \beta + \epsilon x_4^2 + \delta(2x_4 - x_3 - x_1).
\end{aligned}$$

The system (4) also has square symmetry, though of a slightly different kind.

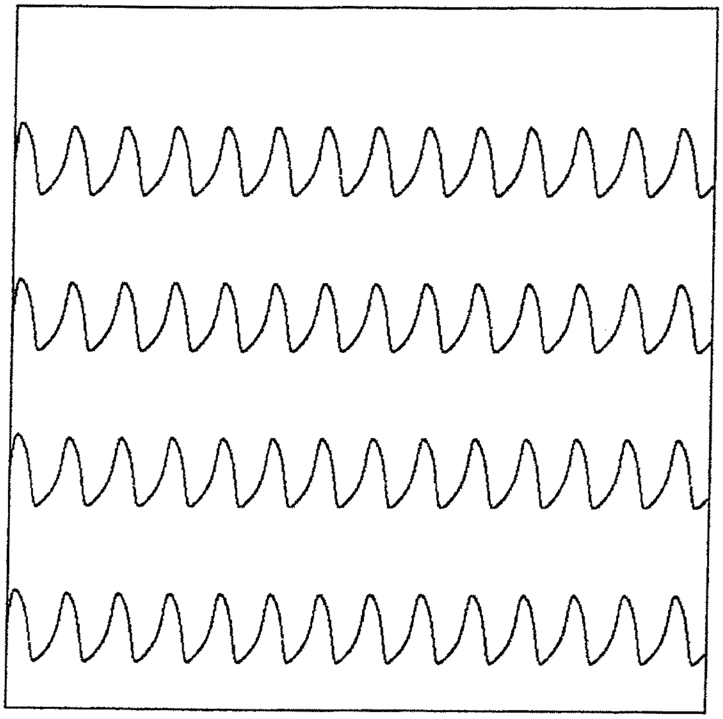

Fig. 14. Numerical solution of (3) when $\alpha = 1$, $\beta = 2$, $\gamma = -0.5$, $\delta = -0.5$, $\epsilon = 0.5$. Horizontal variable is time t (ranging from 0 to 100); vertical variables are x_4, x_3, x_2, x_1 reading from top to bottom. This solution illustrates the pronk gait 1a (Table 3), which does not break symmetry.

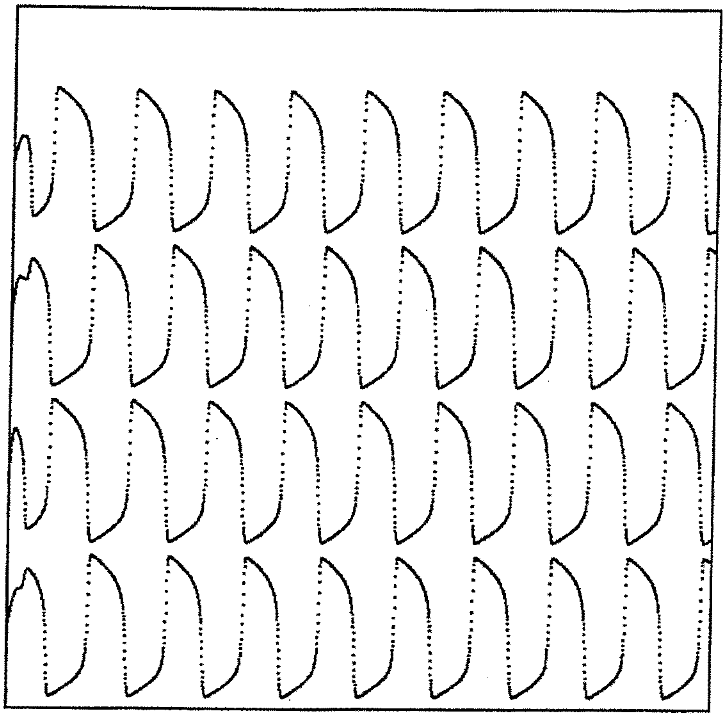

Fig. 15. Numerical solution of (3) when $\alpha = 1$, $\beta = 2$, $\gamma = 1$, $\delta = 1$, $\epsilon = 0.5$. Variables as in Figure 14. This solution illustrates the trot gait 1b (Table 3).

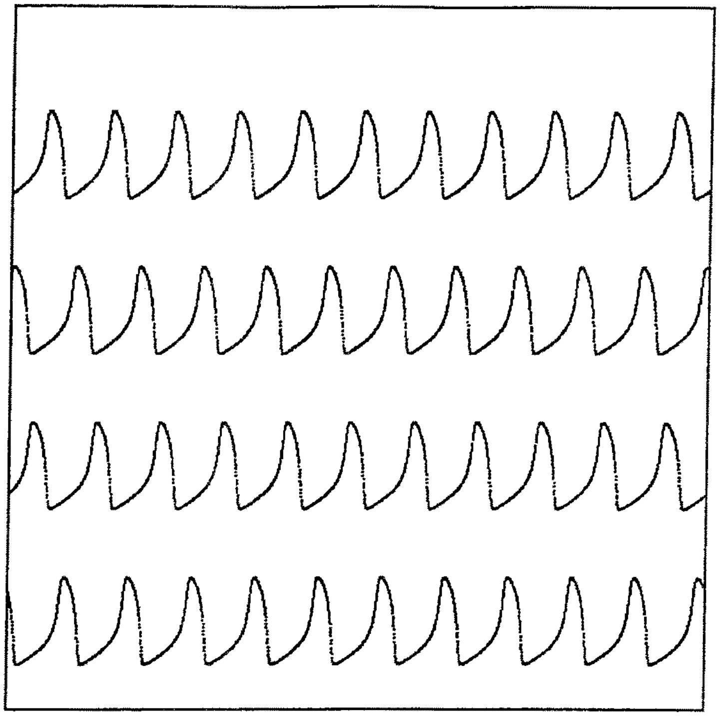

Fig. 16. Numerical solution of (3) when $\alpha = 1$, $\beta = 0$, $\gamma = 0.02$, $\delta = 0.02$, $\epsilon = 1$. Variables as in Figure 14. This solution illustrates the gallop-like gait 1c (Table 3); its conjugate 1d can be obtained by "rotating" the initial conditions through a right angle.

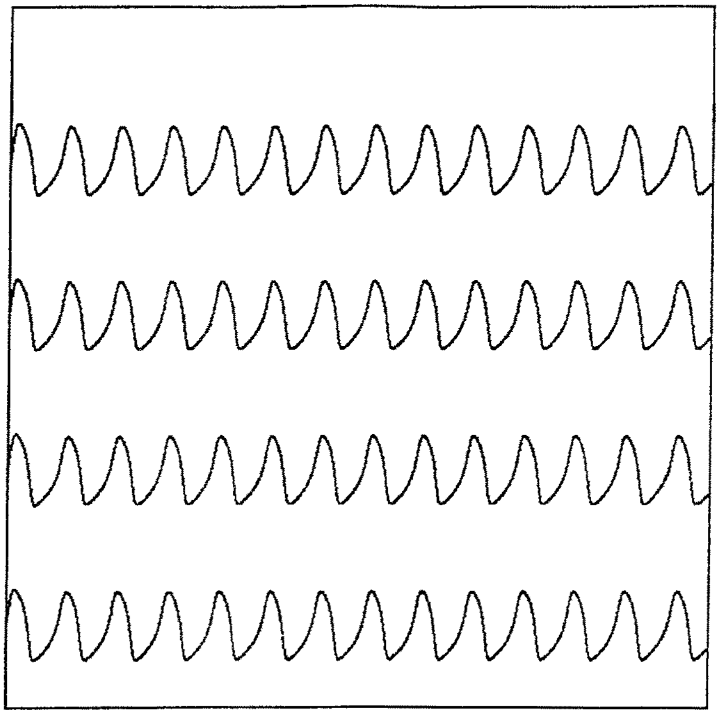

Fig. 17. Numerical solution of (3) when $\alpha = 1$, $\beta = 2$, $\gamma = -0.5$, $\delta = -0.7$, $\epsilon = 0.5$. Variables as in Figure 14. This solution illustrates the pronk gait 2a (Table 3).

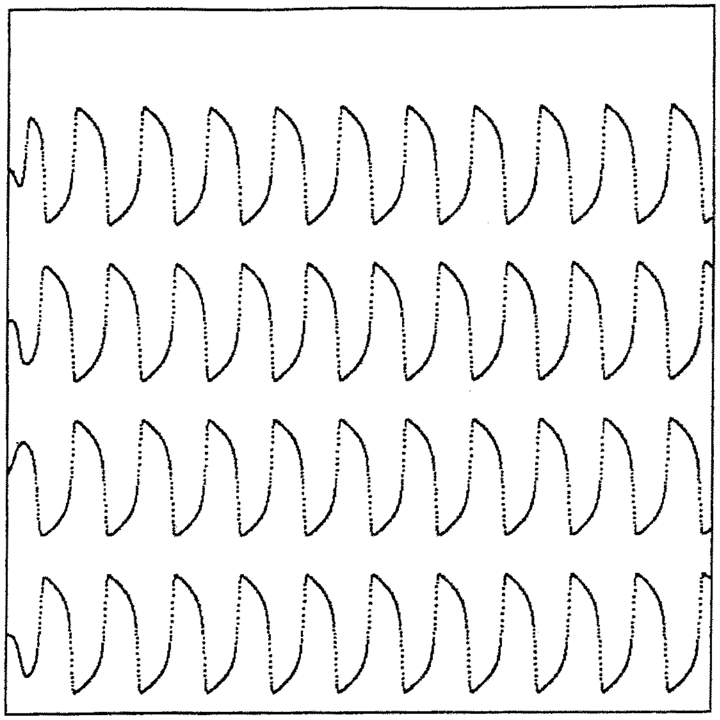

Fig. 18. Numerical solution of (3) when $\alpha = 1$, $\beta = 0$, $\gamma = 0.5$, $\delta = 0.7$, $\epsilon = 0.1$. Variables as in Figure 14. This solution illustrates the pace gait 2b (Table 3).

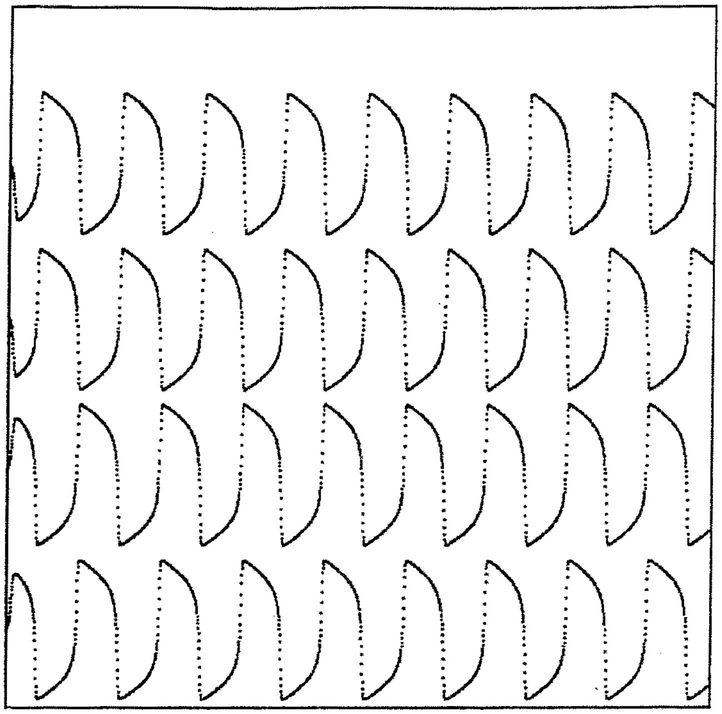

Fig. 19. Numerical solution of (3) when $\alpha = 1$, $\beta = 0$, $\gamma = 0.01$, $\delta = 2$, $\epsilon = 0.1$. Variables as in Figure 14. This solution illustrates the bound gait 2c (Table 3).

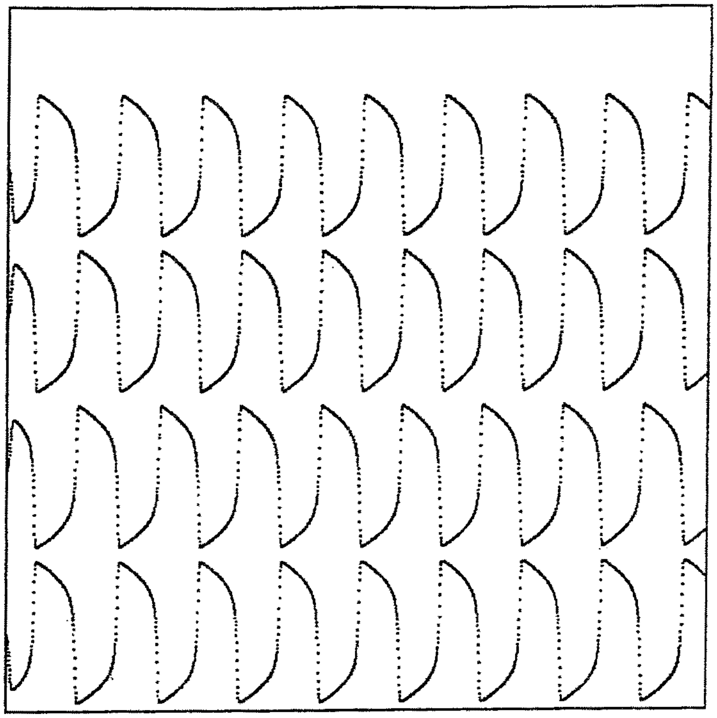

Fig. 20. Numerical solution of (3) when $\alpha = 1$, $\beta = 0$, $\gamma = 2$, $\delta = 0.01$, $\epsilon = 0.1$. Variables as in Figure 14. This solution illustrates the trot gait 2d (Table 3).

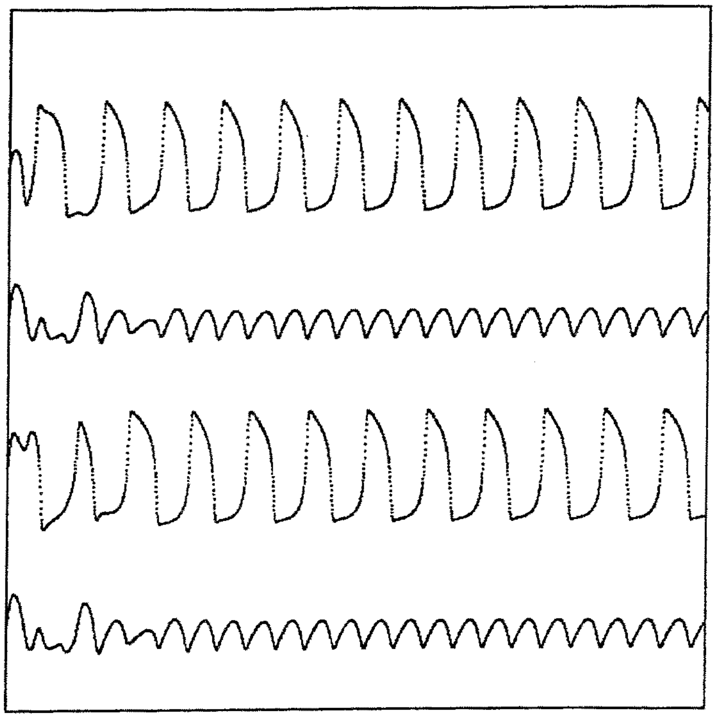

Fig. 21. Numerical solution of (4) when $\alpha = 1$, $\beta = 2$, $\gamma = -0.5$, $\delta = 1$, $\epsilon = 0.5$. Variables as in Figure 14. This solution has the same qualitative features as the "exceptional" gait 1g of Table 3 (and its conjugate 1h which occurs if the initial conditions are "rotated" through a right angle).

9. Hexapodal Gaits and Generalizations

We briefly indicate in this section an extension of the above group-theoretic approach to systems of more than four oscillators, beginning with six-oscillator models for hexapodal gaits. We consider only the arrangement of six identical oscillators shown in Figure 22, although many alternatives can be analyzed in a similar manner.

We impose spatial periodicity by assuming that the left oscillators are coupled to the right oscillators as shown by the dotted lines (Figure 22). An alternative method leading to the same result is to impose periodic boundary conditions at front and rear. [For a discussion of periodic boundary conditions, nonperiodic boundary conditions, and symmetry, see Crawford *et al.* (1991).] Then the symmetry group is generated by the permutations

$\alpha = (12)(34)(56)$	left-right reflection
$\beta = (135)(246)$	rearward rotation
$\gamma = (15)(26)$	front-rear reflection.

There are two classes of periodic pattern. In the first, the reflectional symmetry α is unbroken, and the patterns are given by the analysis of D_3-equivariant Hopf bifurcation in Golubitsky and Stewart (1986) or Golubitsky *et al.* (1988). In the other class, α produces a phase shift of half a period. The possibilities are listed in Table 4.

The common tripod gait of insects (in which the front and rear legs on one side, and the middle leg on the other, move together, followed by the remaining three legs

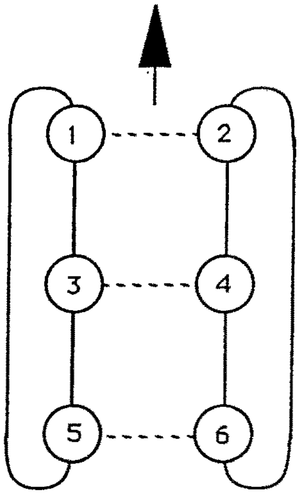

Fig. 22. Network of six identical oscillators modeling (some) hexpodal gaits.

Table 4. Typical patterns for six coupled nonlinear oscillators.

Ref.		LF (1)	RF (2)	LM (3)	RM (4)	LH (5)	RH (6)	Comments
1	a	A	A	A	A	A	A	
	b	A	$A+\frac{1}{2}$	A	$A+\frac{1}{2}$	A	$A+\frac{1}{2}$	
2	a	A	A	$A+\frac{1}{3}$	$A+\frac{1}{3}$	$A+\frac{2}{3}$	$A+\frac{2}{3}$	
	b	A	A	$A+\frac{2}{3}$	$A+\frac{2}{3}$	$A+\frac{1}{3}$	$A+\frac{1}{3}$	
3	a	A	A	A	A	A	A	
	b	A	A	B	B	A	A	
	c	B	B	A	A	A	A	
4	a	A	A	$A+\frac{1}{2}$	$A+\frac{1}{2}$	B	B	
	b	A	A	B	B	$A+\frac{1}{2}$	$A+\frac{1}{2}$	$B = \frac{1}{2}$ period
	c	B	B	A	A	$A+\frac{1}{2}$	$A+\frac{1}{2}$	$B = B+\frac{1}{2}$
5	a	A	$A+\frac{1}{2}$	$A+\frac{1}{3}$	$A+\frac{5}{6}$	$A+\frac{2}{3}$	$A+\frac{1}{6}$	
	b	A	$A+\frac{1}{2}$	$A+\frac{2}{3}$	$A+\frac{1}{6}$	$A+\frac{1}{3}$	$A+\frac{5}{6}$	
6	a	A	$A+\frac{1}{2}$	A	$A+\frac{1}{2}$	B	$B+\frac{1}{2}$	
	b	A	$A+\frac{1}{2}$	B	$B+\frac{1}{2}$	A	$A+\frac{1}{2}$	
	c	B	$B+\frac{1}{2}$	A	$A+\frac{1}{2}$	A	$A+\frac{1}{2}$	
7	a	A	$A+\frac{1}{2}$	$A+\frac{1}{2}$	A	B	B	
	b	A	$A+\frac{1}{2}$	B	B	$A+\frac{1}{2}$	A	$B = \frac{1}{2}$ period
	c	B	B	A	$A+\frac{1}{2}$	$A+\frac{1}{2}$	A	$B = B+\frac{1}{2}$

half a period later) does not occur in this network. However, it does occur naturally in a hexagonal network, as a mode in which alternate oscillators are phase-locked half a period apart, so that the oscillators group into two sets of three, effectively acting as a coupled pair of oscillating subsystems. Group-theoretically, this corresponds to the "threefold" mode in which the elements θ in $Z_3 \subset D_3$ act as rotation by 3θ. See Sect. 10 for an alternative possibility and Collins and Stewart (1993) for more extensive and detailed analyses.

By increasing the number of oscillators to $2n$, with a similar arrangement, we obtain models for multilegged animals such as centipedes. Among the symmetry types of solutions, there will typically occur traveling waves, sweeping along the chain of oscillators. We may also pass to the continuum limit and consider an interval composed of infinitely many, infinitely small oscillators. The periodic states for such a system include traveling waves and standing waves. Cohen (1988) reports that traveling waves occur in dogfish, whereas standing waves occur in salamanders (Figure 23). More detailed discussions of fish locomotion can be found in Gray (1968). Finally, we note that Epstein and Golubitsky (1992) have recently developed a "reflection" trick for converting problems posed for a linear string of n oscillators into rings of $2n$ oscillators. It is analogous to an idea developed for partial differential equations (Crawford *et al.*, 1991). It extends our symmetry methods to networks with very little symmetry. However, we shall not discuss this development further here.

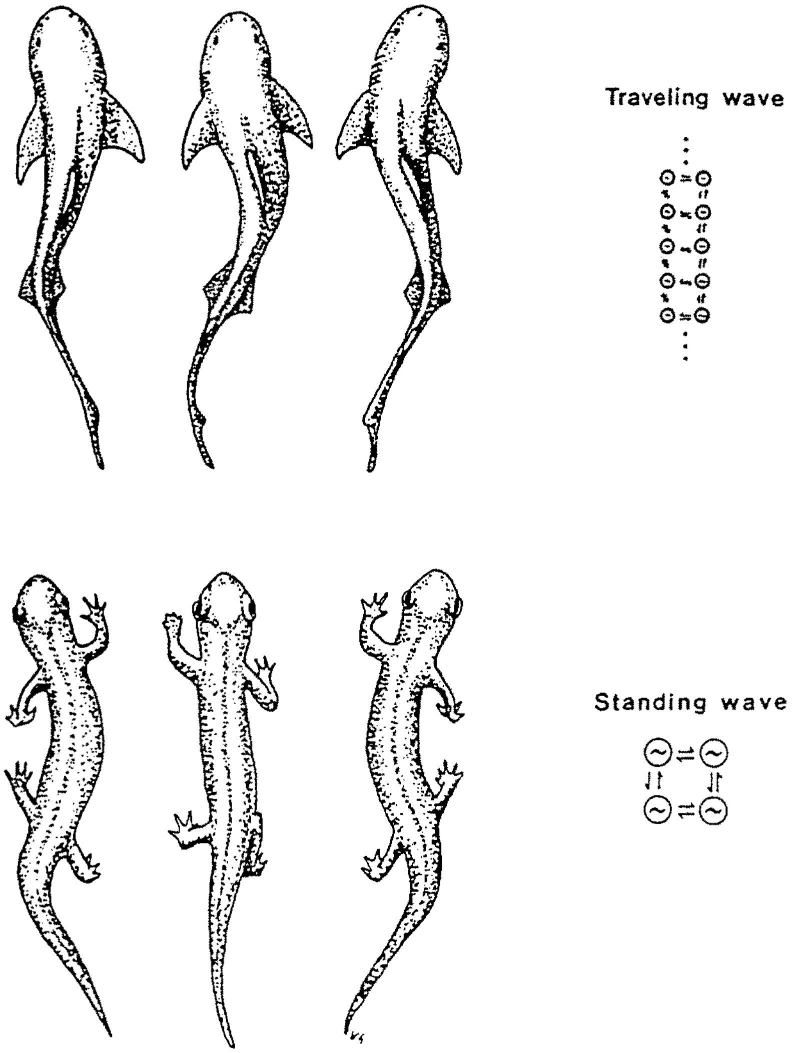

Fig. 23. Traveling wave in a dogfish. (b) Standing wave in a salamander. [Reprinted with permission of the publisher. From A.H. Cohen (1988). Evolution of the vertebrate central pattern generator for locomotion. In *Neural Control of Rhythmic Movements in Vertebrates* (Cohen, A.H., Rossignol, S., and Grillner, S., eds.), pp. 129–166. Copyright © 1988 John Wiley & Sons, Inc., New York. Reprinted by permission of John Wiley & Sons, Inc.]

10. Implications for the Neural Control of Locomotion

Using group-theoretic techniques, we have demonstrated that whole classes of models—namely networks of identical oscillators coupled in various more-or-less symmetric ways—possess "universal" patterns of phase-locked oscillations, many of which correspond to observed patterns of phase-locking in animal gaits. We have also shown that there are resemblances between the natural sequences of symmetry-breaking bifurcations that occur in symmetric systems, and the transitions observed in gaits. We have presented these patterns and transitions in two distinct interpretations: either as oscillation patterns of a central pattern generator controlling limb movement, or as the movements of the limbs themselves.

One way to develop these abstract results would be to build detailed physiological models, possessing the desired symmetries, and analyze the effects of various parameters, taking into account the known behavior of symmetric networks. The role of our results in such an investigation would be to organize what behavior should be looked for and suggest methods for finding it. These models would involve adjustable parameters for such quantities as the coupling between the component oscillators. The system will select possible patterns of oscillation from those available in general, according to the values of those parameters. This provides a natural mechanism for the control of gait transitions, and a natural mechanism for subsequent learning.

In a more speculative vein, we could attempt to combine our two distinct interpretations of CPG structure and animal morphology. Presumably locomotor ability, and its neural control, evolved together. The "universality" of oscillation patterns of symmetric systems with given symmetry provides a natural link between the signals that can be produced by a small network of neurons and certain "natural" oscillations of an animal's body. That is, some movements of an animal are naturally modeled by simple neuronal networks. Within a given symmetry class there is a "universal mapping" between possible CPG oscillations and possible gait patterns. It would thus be possible to select for efficient gaits by fine-tuning the parameters of both CPG and physiological development through the usual Darwinian mechanisms.

An important point to note about the correspondence between neuronal networks and gross physiology is that minor rerouting of a neuronal network could have a significant effect on the resulting gait. For example, we have observed that the six-oscillator network described in Sect. 9 does not exhibit the common tripod gait of insects. However, if the connections between the middle pair of oscillators (Figure 22) and the corresponding limbs are interchanged from left to right, then the relatively simple gait pattern 1b in Table 4 would become, precisely, the tripod gait.

Our analysis does not force any commitment on whether a CPG is a self-sustaining system, or whether it is a forced system, responding to an incoming signal. Neither does it imply that a CPG must necessarily be truly "central": its components might be distributed throughout the central nervous system. The patterns of symmetry-breaking are the same in all cases, provided only that the incoming signal is distributed identically to the component oscillators. Given the experimental evidence that at least some CPGs are located not in the brain but in the spinal cord, the picture which emerges is that of a forced oscillator-system, triggered by a signal from the brain: brain → CPG → limbs. The nature of symmetry-breaking implies that a single periodic signal from the brain (Kupfermann and Weiss, 1978) can stimulate different phase-locked oscillation patterns in the same CPG. Changes in animal gaits might thus depend on something as simple as the amplitude or frequency of this "driving" signal. They might also, as already mentioned, depend upon changing the strength or nature of the coupling within the CPG.

Central pattern generators are not easy to locate or analyze. Paying attention to the symmetries of animal gaits may provide information on the likely structure of CPGs, and on how the neural connections to limbs should be arranged to produce the observed gaits. Because varying parameters may produce different oscillation patterns in the same network architecture, the same locomotor central pattern generator may control a whole range of apparently very different gaits.

Appendix 1. Symmetric Hopf Bifurcation

In this appendix, we summarize the Hopf bifurcation theorem and its extension to symmetric dynamical systems. For the standard Hopf theorem see Appendix 3 in Murray (1989), and for full details on the symmetric generalization see Golubitsky and Stewart (1985) or Golubitsky *et al.* (1988). Consider the dynamical system

$$\frac{dx}{dt} = f(x, a). \tag{5}$$

where $x \in \mathbb{R}^n, f{:}\mathbb{R}^n \rightarrow \mathbb{R}^n$, and $a \in \mathbb{R}$ is a parameter. For convenience we assume that $f(0, a) \equiv 0$, so that $x = 0$ is always a steady-state solution of (5). Let $(df)_{(x,a)}$ be the Jacobian matrix evaluated at (x, a).

Suppose that f commutes with the action of a compact Lie group Γ on $\mathbb{R}^n$. For Hopf bifurcation to occur, the Jacobian $(df)_{(x,a)}$ must have purely imaginary eigenvalues $\pm i\omega$ at some value a_0 of a. Assume that the eigenvalues cross the imaginary axis with nonzero speed. Generically the corresponding real eigenspace of the derivative $L = (df)_{(x,a_0)}$ 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 nonabsolutely irreducible.

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

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

If $x \in \mathbb{R}^n$ then its *isotropy subgroup* $\Sigma_x \subset \Gamma \times S^1$ is defined to be

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

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

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

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

Symmetric Hopf Bifuraction Theorem

Let Σ be an isotropy subgroup of $\Gamma \times S^1$ such that dim (Fix Σ) $= 2$. Then there exists a branch of periodic solutions to (5) with period near $2\pi/\omega$, having Σ as their group of spatio–temporal symmetries, where S^1 acts on a periodic solution by phase shift.

Informally, this asserts that at a symmetric analogue of a Hopf bifurcation *several* branches of periodic solutions bifurcate, distinguished by their symmetry groups Σ. (Do not take "several" too literally: for some groups Γ—in particular any cyclic group—there will be only one branch, because only one subgroup Σ satisfies the condition $\dim(\mathrm{Fix}\ \Sigma) = 2$.)

Appendix 2. Space-Time Symmetry Classifications

With the notation of Appendix 1, we may ask what form an isotropy subgroup $\Sigma \subset \Gamma \times S^1$ can take. The answer (Golubitsky and Stewart, 1985; Golubitsky *et al.*, 1988, Chapter XVI, Sect. 7) is that it is a *twisted subgroup*

$$H^{\varphi} = \{(h, \varphi(h)) \mid \in H\}$$

for a closed subgroup H of Γ and a group homomorphism $\varphi{:}H \rightarrow S^1$. Not all such subgroups are isotropy subgroups, and whether one is depends upon the representation of Γ concerned. However, to obtain a list that includes all possible isotropy subgroups for all representations, it suffices to list all possible twisted subgroups. This we do by listing all closed subgroups H of Γ, and for each H finding all possible homomorphisms φ.

For the rectangularly symmetric network of Sect. 4 the group Γ is D_2, and the calculation just outlined is routine group theory. The possible subgroups H are shown (up to conjugacy) in Table 5, using the notation of Sect. 4. Case-by-case analysis of possible homomorphisms φ yields Table 1.

In Table 6 we also place on record the results for $\Gamma = D_4$, using the abstract presentation

$$< \alpha, \beta \,|\, \alpha^4 = I, \beta^2 = I, \beta\alpha\beta = \alpha^3 > .$$

We list the "untwisted" subgroups H of $D_4 \times S^1$ first.

The lattice of subgroup containments is shown in Figure 24. It determines the possible patterns of symmetry-breaking for network types 1 and 3, which as we have mentioned, abstractly have the same symmetries.

Table 5. Subgroups of D_2 (rectangular network 2). Here $\alpha = (12)(34)$ and $\beta = (13)(24)$.

Symbol	Elements
D_2	$I, \alpha, \beta, \alpha\beta$
Z_2^L	I, α
Z_2^F	I, β
Z_2^D	$I, \alpha\beta$
1	I

Table 6. Twisted subgroup of $D_4 \times S^1$(network types 1 and 3).

Symbol	Elements
D_4	$I, \alpha, \alpha^2, \alpha^3, \beta, \alpha\beta, \alpha^2\beta, \alpha^3\beta$
Z_4	$I, \alpha, \alpha^2, \alpha^3$
D_2^O	$I, \alpha^2, \beta, \alpha^2\beta$
D_2^Δ	$I, \alpha^2, \alpha\beta, \alpha^3\beta$
Z_2	I, α^2
Z_2^O	I, β
Z_2^Δ	$I, \alpha\beta$
1	I
$D_4 \times S^1$	$[I, \theta], [\alpha, \theta], [\alpha^2, \theta], [\alpha^3, \theta], [\beta, \theta], [\alpha\beta, \theta], [\alpha^2\beta, \theta], [\alpha^3\beta, \theta]$ for all θ
$\tilde{Z}_4$	$[I, 0], [\alpha, \frac{1}{4}], [\alpha^2, \frac{1}{2}], [\alpha^3, \frac{3}{4}]$
$\hat{Z}_4$	$[I, 0], [\alpha, \frac{1}{2}], [\alpha^2, 0], [\alpha^3, \frac{1}{2}]$
$\tilde{D}_2^{O1}$	$[I, 0], [\alpha^2, 0], [\beta, \frac{1}{2}], [\alpha\beta, \frac{1}{2}]$
$\tilde{D}_2^{O2}$	$[I, 0], [\alpha^2, \frac{1}{2}], [\beta, 0], [\alpha\beta, \frac{1}{2}]$
$\tilde{D}_2^{O3}$	$[I, 0], [\alpha^2, \frac{1}{2}], [\beta, \frac{1}{2}], [\alpha\beta, 0]$
$\tilde{D}_2^{\Delta 1}$	$[I, 0], [\alpha^2, 0], [\alpha\beta, \frac{1}{2}], [\alpha^3\beta, \frac{1}{2}]$
$\tilde{D}_2^{\Delta 2}$	$[I, 0], [\alpha^2, \frac{1}{2}], [\alpha\beta, 0], [\alpha^3\beta, \frac{1}{2}]$
$\tilde{D}_2^{\Delta 3}$	$[I, 0], [\alpha^2, \frac{1}{2}], [\alpha\beta, \frac{1}{2}], [\alpha^3\beta, 0]$
$\tilde{Z}_2$	$[I, 0], [\alpha^2, \frac{1}{2}]$
$\tilde{Z}_2^O$	$[I, 0], [\beta, \frac{1}{2}]$
$\tilde{Z}_2^\Delta$	$[I, 0], [\alpha\beta, \frac{1}{2}]$

Appendix 3. Generic Oscillation Patterns

The purpose of this appendix is to provide the mathematical justification for Table 3. It will assume familiarity with the techniques used to study Hopf bifurcation in symmetric systems, and with appropriate mathematical notation (Golubitsky and Stewart, 1985, 1986; Golubitsky *et al.*, 1988). Swift (1988) provides a more detailed analysis of four-oscillator systems.

Suppose that we have a system of ordinary differential equations

$$\frac{dx}{dt} + f(x, a) = 0,$$

where $x = (x_1, \ldots, x_n) \in \mathbb{R}^n$ and $a \in \mathbb{R}$ is a bifurcation parameter. Assume that f commutes with a linear action of a compact Lie group Γ on $\mathbb{R}^n$. If Hopf bifurcation occurs, then the Jacobian $(df)_x$ has purely imaginary eigenvalues $\pm i\omega$ at some value a_0 of a. Generically the corresponding real eigenspace of the derivative $(df)_x$ is a Γ-simple representation as in Appendix 1. Thus to find the possible range of generic Hopf bifurcations we decompose $\mathbb{R}^n$ into irreducibles and list all possible Γ-simple components, after which each component can be analyzed separately. In fact, for this paper, we need only the cases $\Gamma = D_4$ and Z_2, as we shall demonstrate.

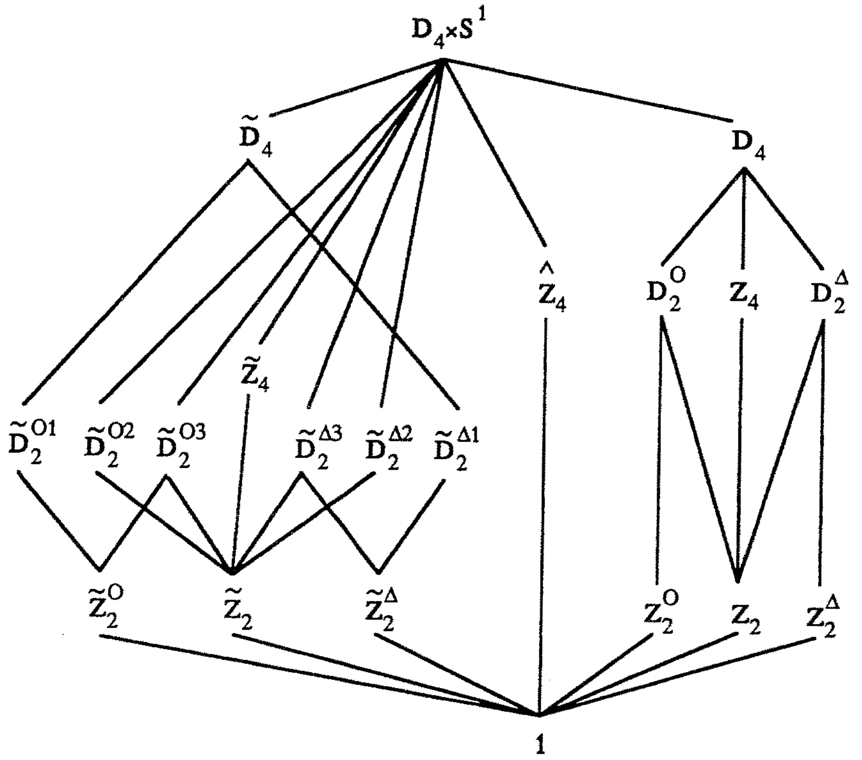

Fig. 24. Lattice of twisted subgroups of $D_4 \times S^1$.

Suppose we have a network N of oscillators. Let Γ be its *automorphism group*, the group of permutations of the oscillators that preserves

a. the type of oscillator, and
b. the type of coupling.

Then the associated dynamical system that describes the behavior of the network will be equivariant for Γ.

If we have k types of oscillators, $O_1, \ldots, O_k$, with n_i of each type O_i, and if the number of internal degrees of freedom in O_i is d_i, then the dynamical system is defined on the vector space

$$\bigoplus_{i=1}^{k} \mathbb{R}^{n_i} \otimes_{\mathbb{R}} \mathbb{R}^{d_i}$$

and the Γ-action is by permutation on $\mathbb{R}^{n_i}$ and is trivial on $\mathbb{R}^{d_i}$. It is this vector space that we must decompose into Γ-simple components. We consider network type 1 (Figure 6) as an example; the calculations in the other four cases are similar.

Type 1. This network has square symmetry D_4 generated by the permutations $\alpha = (1243)$ and $\beta = (12)(34)$. If there are d internal degrees of freedom, then $\mathbb{R}^n$ is of the form $\mathbb{R}^4 \oplus_{\mathbb{R}} \mathbb{R}^d$. Thus we first decompose $\mathbb{R}^4$. There are three distinct irreducible components:

$$\begin{array}{ll}
V_1 = \{(x, x, x, x)\} & \text{trivial action} \\
V_2 = \{(y, -y, -y, y)\} & \alpha : y \mapsto -y \\
 & \beta : y \mapsto -y \\
V_3 = \{(u, v, -v, -u)\} & \alpha : u \mapsto v \\
 & \alpha : v \mapsto -u \\
 & \beta : u \mapsto v \\
 & \beta : v \mapsto u.
\end{array}$$

Each representation is absolutely irreducible, so Hopf bifurcation requires $d \geq 2$; that is, there must be at least two internal degrees of freedom for the component oscillators. We have

$$\mathbb{R}^4 \otimes_{\mathbb{R}} \mathbb{R}^d \cong V_1 \otimes_{\mathbb{R}} \mathbb{R}^d \oplus V_2 \otimes_{\mathbb{R}} \mathbb{R}^d \oplus V_3 \otimes_{\mathbb{R}} \mathbb{R}^d$$

so the possible Γ-simple components are $V_1 \otimes_{\mathbb{R}} \mathbb{R}^2, V_2 \otimes_{\mathbb{R}} \mathbb{R}^2, V_3 \otimes_{\mathbb{R}} \mathbb{R}^2$. The first corresponds to ordinary Hopf bifurcation in which D_4 symmetry is preserved, so it implies that all four oscillators have the identical waveform. The second is equivalent to Z_2-equivariant Hopf bifurcation where the kernel $< \alpha^2, \alpha\beta >$ of the action is factored out and the Z_2-action is nontrivial. Here the symmetry is broken to a twisted Z_2 generated by $(\alpha, \frac{1}{2})$: that is, the effect of α or β on the oscillation pattern is to create a phase shift of $\frac{1}{2}$ (half a period). In other words, if oscillator 1 has waveform A then oscillator 2 $= \alpha(1)$ has waveform $A + \frac{1}{2}$; oscillator 4 $= \alpha(2)$ has waveform $A + \frac{1}{2} + \frac{1}{2} = A$; and oscillator 3 $= \alpha(4)$ has waveform $A + \frac{1}{2}$ again. Conjugates of the isotropy subgroup yield no new pattern.

The third case, V_3, is standard D_4 Hopf bifurcation (Golubitsky and Stewart, 1986; Golubitsky *et al.*, 1988). There are three simultaneously bifurcating branches, with isotropy subgroups conjugate to Σ:

$$\Sigma_1 = \tilde{Z}_4 = < (\alpha, \tfrac{1}{4}) >,$$

$$\Sigma_2 = Z_2^{\beta} \oplus Z_2^{(\pi,\pi)} = < \beta, (\alpha^2, \tfrac{1}{2}) >,$$

$$\Sigma_3 = Z_2^{\alpha\beta} \oplus Z_2^{(\pi,\pi)} = < \alpha\beta, (\alpha^2, \tfrac{1}{2}) > .$$

For Σ_1 we get the pattern

$$(A, A + \tfrac{3}{4}, A + \tfrac{1}{4}, A + \tfrac{1}{2}),$$

because the isotropy subgroup implies that oscillators related by a quarter turn (α) are a quarter of a period ($\frac{1}{4}$) out of phase. The conjugate solution is obtained by left-right reflection and is generated by $(\alpha^3, \frac{1}{4})$.

For Σ_2 we have the following isotropy: the system is unchanged by left-right reflection β, so oscillators 1 and 2 have the same pattern A, and 3 and 4 have the same pattern B. Also, the system is unchanged by rotation α^2 through angle π followed by phase shift of $\frac{1}{2}$, so $B = A + \frac{1}{2}$. Thus we have the pattern

$$(A, A, A + \tfrac{1}{2}, A + \tfrac{1}{2}),$$

and also its conjugate (front-back reflection instead of left-right)

$$(A, A + \tfrac{1}{2}, A, A + \tfrac{1}{2}).$$

For Σ_3 we find that the pattern is unchanged by reflection in the diagonal (1–4 or 2–3 depending on which conjugate we choose) and by rotation through 180° followed by $\frac{1}{2}$ phase shift. Consider the 2–3 diagonal: we have the same waveform A in oscillators 1 and 4, but 2 and 3 are arbitrary, say B and C respectively. Symmetry under the 180° rotation and $\frac{1}{2}$ phase shift implies that

$$B + \tfrac{1}{2} = C,$$

$$A + \tfrac{1}{2} = A.$$

The first determines C in terms of B; the second says that A is half a period out of phase with *itself*, that is *A has half the period of the overall system.* Therefore A oscillates at *twice* the frequency expected from linear analysis (determined by the imaginary eigenvalue $\pm i\omega$). This apparently paradoxical effect is actually quite natural, and an example is given in a three-oscillator system by Golubitsky and Stewart (1986) and Golubitsky *et al.* (1988). At any rate, we observe the patterns

$$(A, B, B + \tfrac{1}{2}, A) \quad [A = \text{half period}],$$

$$(A, B, B, A + \tfrac{1}{2}) \quad [B = \text{half period}].$$

This 2:1 frequency-locking phenomenon and its locomotor implications are treated in greater detail in Collins and Stewart (1992).

Acknowledgments

We are grateful to Peter Ashwin, Martin Golubitsky, and Greg King for helpful discussions. This work was carried out under the auspices of the Interdisciplinary Mathematical Research Programme of the University of Warwick. JJC was supported, in part, by a Rhodes Scholarship.

References

Alexander, J.C. (1986). Patterns at primary Hopf bifurcations of a plexus of identical oscillators. *SIAM J. Appl. Math.* **46**, 199–221.

Alexander, R. McN. (1984). The gaits of bipedal and quadrupedal animals. *Int. J. Robot. Res.* **3**(2), 49–59.

Alexander, R. McN. (1989). Optimization of gaits in the locomotion of vertebrates. *Physiol. Rev.* **69**, 1199–1227.

Aristotle. De Partibus Animalium, De Incessu Animalium, De Motu Animalium. In *Parts of Animals, Movement of Animals, Progression of Animals* (Peek, A.S., and Forster, E.S., translators). Cambridge, MA: Harvard University Press, 1936.

Ashwin, P. (1990). Symmetric chaos in systems of three and four forced oscillators. *Nonlinearity* **3**, 603–617.

Ashwin, P., King, G.P., and Swift, J.W. (1990). Three identical oscillators with symmetric coupling. *Nonlinearity* **3**, 585–601.

Ashwin, P. and Swift, J.W. (1992). The dynamics of n weakly coupled identical oscillators. *J. Nonlinear Sci.* **2**, 69–108.

Baesens, C., Guckenheimer, J., Kim, S., and MacKay, R.S. (1991). Three coupled oscillators: Mode-locking, global bifurcations, and toroidal chaos. *Physica D* **49**, 387–475.

Bay, J.S. and Hemami, H. (1987). Modeling of a neural pattern generator with coupled nonlinear oscillators. *IEEE Trans. Biomed. Eng.* **34**, 297–306.

Brown, T.G. (1911). The intrinsic factors in the act of progression in the mammal. *Proc. Roy. Soc. B* **84**, 308–319.

Brown, T.G. (1914). On the nature of the fundamental activity of the nervous centres; together with an analysis of the conditioning of rhythmic activity in progression, and a theory of the evolution of function in the nervous system. *J. Physiol. (Lond.)* **48**, 18–46.

Calabrese, R.L. (1980). Invertebrate central pattern generators: Modeling and complexity. *Behav. Brain Sci.* **3**, 542–543.

Cohen, A.H. (1988). Evolution of the vertebrate central pattern generator for locomotion. In *Neural Control of Rhythmic Movements in Vertebrates* (Cohen, A.H., Rossignol, S., and Grillner, S., eds.). New York: Wiley, 129–166.

Cohen, A.H., Holmes, P.J., and Rand, R.H. (1982). The nature of the coupling between segmental oscillators of the lamprey spinal generator for locomotion: A mathematical model. *J. Math. Biol.* **13,** 345–369.

Collins, J.J. and Stewart, I.N. (1992). Symmetry-breaking bifurcation: A possible mechansim for 2:1 frequency-locking in animal locomotion. *J. Math. Biol.* **30**, 827–838.

Collins, J.J. and Stewart, I. (1993). Hexapodal gaits and coupled nonlinear oscillator models. *Biol. Cybern* **68**, 287–298.

Crawford, J.D., Golubitsky, M., Gomes, M.G.M., Knoblach, E., and Stewart, I.N. (1991). Boundary conditions as symmetry constraints. In *Singularities, Bifurcations, and Dynamics: Proceedings of Symposium on Singularity Theory and Its Applications, Warwick 1989* (Roberts, M.R. and Stewart, I.N., eds.), vol. 2. Lecture Notes in Mathematics Series, Springer-Verlag, Heidelberg, 63–79.

Dagg, A.I. (1973). Gaits in mammals. *Mammal Rev.* **3**(4), 135–154.

Davis, J. (1981). *Garfield: Bigger than Life*. New York: Ballantine.

Delcomyn, F. (1980). Neural basis of rhythmic behavior in animals. *Science* **210**, 492–498.

Epstein, I. and Golubitsky, M. (1992). Linear arrays of coupled cells. Preprint, University of Houston.

Ermentrout, G.B. (1986). The behavior of rings of coupled oscillators. *J. Math. Biol.* **23**, 55–74.

Gaeta, G. (1990). Bifurcation and symmetry breaking. *Phys. Reports* **189,** 1–87.

Gambaryan, P. (1974). *How Mammals Run: Anatomical Adaptations*. New York: Wiley.

Glass, L. and Young, R. E. (1979). Structure and dynamics of neural network oscillators. *Brain Res.* **179,** 207–218.

Golubitsky, M. and Stewart, I.N. (1985). Hopf bifurcation in the presence of symmetry. *Arch. Rational Mech. Anal.* **87,** 107–165.

Golubitsky, M. and Stewart, I.N. (1986). Hopf bifurcation with dihedral group symmetry: Coupled nonlinear oscillators. In *Multiparameter Bifurcation Theory* (Golubitsky, M. and Guckenheimer, J., eds.). Contemporary Math. **56,** Amer. Math. Soc., Providence, 131–173.

Golubitsky, M., Stewart, I.N., and Schaeffer, D.G. (1988). *Singularities and Groups in Bifurcation Theory,* vol. II. New York: Springer.

Grasman, J. and Jansen, M.J.W. (1979). Mutually synchronized relaxation oscillators as prototypes of oscillating systems in biology. *J. Math. Biol.* **7,** 171–197.

Gray, J. (1968). *Animal Locomotion.* London: Weidenfeld and Nicolson.

Grillner, S. (1975). Locomotion in vertebrates: Central mechanisms and reflex interaction. *Physiol. Rev.* **55,** 247–304.

Grillner, S. (1985). Neurobiological bases for rhythmic motor acts in vertebrates. *Science* **228,** 143–149.

Grillner, S. and Wallén, P. (1985). Central pattern generators for locomotion, with special reference to vertebrates. *Ann. Rev. Neurosci.* **8,** 233–261.

Guckenheimer, J. and Kim, S. (1990). *kaos.* Mathematical Sciences Institute Technical Report, Cornell University, Ithaca, New York.

Herman, R.M., Grillner, S., Stein, P.S.G., and Stuart, D.G., eds. (1976). *Neural Control of Locomotion.* New York: Plenum Press.

Hildebrand, H. (1965). Symmetrical gaits of horses. *Science* **150,** 701–708.

Hildebrand, H. (1966). Analysis of the symmetrical gaits of tetrapods. *Folia Biotheoretica* **4,** 9–22.

Hildebrand, M. (1968). Symmetircal gaits of dogs in relation to body build. *J. Morphol.* **124,** 353–359.

von Holst, E. (1935). Erregungsbildung und Erregungsleitung im Fischrückenmark. *Pflügers Arch.* **235,** 345–359.

von Holst, E. (1973). *The Behavioral Physiology of Animals and Man.* Coral Gables, FL: University of Miami Press.

Hoyt, D.F. and Taylor, R.C. (1981). Gait and the energetics of locomotion in horses. *Nature* **292,** 239–240.

Kelso, J.A.S. and Schöner, G. (1988). Self-organization of coordinative movement patterns. *Human Movement Science* **7,** 27–46.

Kopell, N. (1988). Toward a theory of modelling central pattern generators. In *Neural Control of Rhythmic Movements in Vertebrates* (Cohen, A.H., Rossignol, S., and Grillner, S., eds.). New York: Wiley, 369–413.

Kupfermann, I. and Weiss, K.R. (1978). The command neuron concept. *Behav. Brain Sci.* **1,** 3–39.

McGhee, R.B. (1968). Some finite state aspects of legged locomotion. *Math. Biosci.* **2,** 67–84.

McGhee, R.B. and Jain, A.K. (1972). Some properties of regularly realizable gait matrices. *Math. Biosci.* **13,** 179–193.

Murray, J.D. (1989). *Mathematical Biology.* Biomathematics Texts 19. New York: Springer-Verlag.

Muybridge, E. (1899). *Animals in Motion.* London: Chapman and Hall. Republished Dover Publications, New York, 1957.

Muybridge, E. (1901). *The Human Figure in Motion.* London: Chapman and Hall. Republished Dover Publications, New York, 1955.

Raibert, M.H. (1986). Running with symmetry. *Int. J. Robot. Res.* **5,** 3–19.

Raibert, M.H. (1988). Balance and symmetry in running. In *Natural Computation* (Richards, W., ed.). Cambridge, MA: MIT Press, 487–503.

Rand, R., Cohen, A.H.,and Holmes, P.J. (1988). Systems of coupled oscillators as models of central pattern generators. In *Neural Control of Rhythmic Movements in Vertebrates* (Cohen, A.H., Rossignol, S., and Grillner, S., eds.). New York: Wiley, 333–367.

Schmidt-Nielsen, K. (1990). *Animal Physiology: Adaptation and Environment.* Cambridge: Cambridge University Press.

Schöner, G., Yiang, W. Y., and Kelso, J.A.S. (1990). A synergetic theory of quadrupedal gaits and gait transitions. *J. Theor. Biol.* **142,** 359–391.

Selverston, A.I. (1980). Are central pattern generators understandable? *Behav. Brain Sci.* **3,** 535–571.

Shik, M.L. and Orlovsky, G.N. (1976). Neurophysiology of locomotor automatism. *Physiol. Rev.* **56,** 465–501.

Smale, S. (1974). A mathematical model of two cells via Turing's equation. In *Some Mathematical Questions in Biology V* (Cowan, J.D., ed.). Amer. Math. Soc. Lecture Notes on Mathematics in the Life Sciences **6,** Providence, 15–26.

Stein, P.S.G. (1978). Motor systems, with specific reference to the control of locomotion. *Ann. Rev. Neurosci.* **1,** 61–81.

Swift, J.W. (1988). Hopf bifurcation with the symmetry of the square. *Nonlinearity* **1,** 333–377.

Taft, R. (1955). An introduction: Eadweard Muybridge and his work. In Muybridge, E. *The Human Figure in Motion*. New York: Dover Publications, vii–xiv.

Willis, J.B. (1980). On the interaction between spinal locomotor generators in quadrupeds. *Brain Res. Rev.* **2,** 171–204.

Yuasa, H. and Ito, M. (1990). Coordination of many oscillators and generation of locomotory patterns. *Biol. Cybern.* **63,** 177–184.