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A modular network for legged locomotion

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Abstract

In this paper we use symmetry methods to study networks of coupled cells, which are models for central pattern generators (CPGs). In these models the cells obey identical systems of differential equations and the network specifies how cells are coupled. Previously, Collins and Stewart showed that the phase relations of many of the standard gaits of quadrupeds and hexapods can be obtained naturally via Hopf bifurcation in small networks. For example, the networks they used to study quadrupeds all had four cells, with the understanding that each cell determined the phase of the motion of one leg. However, in their work it seemed necessary to employ several different four-oscillator networks to obtain all of the standard quadrupedal gaits.

We show that this difficulty with four-oscillator networks is unavoidable, but that the problems can be overcome by using a larger network. Specifically, we show that the standard gaits of a quadruped, including walk, trot and pace, cannot all be realized by a single four-cell network without introducing unwanted conjugacies between trot and pace – conjugacies that imply a dynamic equivalence between these gaits that seems inconsistent with observations. In this sense a single network with four cells cannot model the CPG of a quadruped. We also introduce a single eight-cell network that can model all of the primary gaits of quadrupeds without these unwanted conjugacies. Moreover, this network is modular in that it naturally generalizes to provide models of gaits in hexapods, centipedes, and millipedes. The analysis of models for many-legged animals shows that wave-like motions, similar to those obtained by Kopell and Ermentrout, can be expected. However, our network leads to a prediction that the wavelength of the wave motion will divide twice the length of the animal. Indeed, we reproduce illustrations of wave-like motions in centipedes where the animal is approximately one-and-a-half wavelength long – motions that are consistent with this prediction. We discuss the implications of these results for the development of modular control networks for adaptive legged robots. Copyright © 1998 Elsevier Science B.V.

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1. Introduction

The dynamics of networks of coupled identical cells has been studied in connection with the phase relationships observed in the gaits of legged animals [4–8,26,31,32] and creatures such as the lamprey [2,21–23,25] whose locomotion is effected by traveling waves of muscle contractions. Here we use the term ‘cell’ to indicate self-contained subcircuits of the network or, more mathematically, a system of ordinary differential equations. It is widely believed that animal locomotion is generated and controlled, in part, by a *central pattern generator* (CPG), which is a network of neurons in the central nervous system capable of producing rhythmic output. Current neurophysiological techniques are unable to isolate such circuits among the intricate neural connections of complex animals, but the indirect experimental evidence for their existence is strong (for reviews, see [17–19,24,27,29]). Irrespective of physiological considerations, CPG-like networks of coupled cells (e.g., electronic circuits) are an attractive option for the design and control of legged robots, because they produce a variety of phase relationships in a stable and natural manner.

Kopell and Ermentrout [21–23] have demonstrated that a linear network consisting of many coupled identical cells can generate traveling wave motions similar to those observed in the lamprey, and some biological predictions made by this model have been confirmed [30]. Although a lamprey has no legs, the phase relationships found in these wave patterns are similar to those that occur in animals such as centipedes and millipedes. As regards creatures with a small number of legs, Collins and Stewart [5–8] have shown that simple symmetric networks of coupled identical cells possess natural patterns of oscillation with the same phase relationships as many observed gaits in bipeds, quadrupeds, and hexapods. These oscillation patterns are determined by the periodic states that can arise by Hopf bifurcation from the trivial gait ‘stand’, and their existence and stability can be analyzed using the theory of symmetric Hopf bifurcation of Golubitsky and Stewart [14,16]. Since the assumption of symmetry is basic to our approach, we discuss the appropriateness of symmetry in animal gaits in some detail at the end of this section.

Because of the symmetry assumption, we shall throughout use the term ‘network’ to mean a fixed system of coupled *identical* cells (represented schematically by circles) with a fixed set of couplings (represented schematically by arrows). The couplings themselves divide into classes and all couplings in a class are assumed to be identical. (Different classes of couplings are represented by different arrow styles.) For example, the CPGs of bilaterally symmetric animals are usually modeled by bilaterally symmetric networks where the couplings connecting cells on the two sides of the CPG (contralateral coupling) are assumed to be identical and the couplings between nearest neighbor cells on the same side of the CPG (ipsilateral coupling) are assumed to be identical, but the couplings in these two classes are assumed to be different. Although it might be possible to arrange for the couplings in different classes to be the same, by arranging for certain coupling strengths to be equal, we view this equality as difficult to control and maintain, since the different classes of coupling represent different types of physical connections.

As a consequence, certain properties of the networks, such as the symmetries of the network, are fixed even though we do not specify at this level of abstraction the particular system of ODEs that represent a single cell or the exact form of the coupling terms between cells. Thus the specification of a particular network scheme for a CPG is a modeling assumption that fixes aspects of the network such as its symmetries.

With this view of networks in mind, Collins and Stewart show that suitable small networks can generate most of the phase relationships found in quadrupedal and hexapodal gaits. However, they do not describe any *single* network structure that is capable of generating *all* observed patterns. Moreover, in some of their networks, patterns corresponding to distinct gaits are ‘conjugate’ in the mathematical model – equivalent under a network symmetry – and hence must bifurcate together and possess the same stability characteristics. It is difficult to see why a corresponding CPG would preferentially select one of these conjugate patterns and suppress the other. For these reasons, it is necessary to seek a more satisfactory network.

In this paper we describe a simple network of coupled identical cells which can generate the full range of phase relationships observed in the gaits of $2n$ -legged animals, for all values of n . The same schematic structure also generates traveling waves of the kinds observed in legless animals such as eels, worms, snakes, and lamprey. Moreover, in this circuit there are no unwanted conjugacies, so patterns of oscillation that should be considered distinct in the animal are also distinct mathematically, and in particular can bifurcate at different parameter values from each other and can possess different stability characteristics. In addition, the structure of the network is modular: in a $2n$ -legged animal the network has one ‘head’ module, one ‘tail’ module, and $n - 2$ identical ‘body’ modules. Such a structure has obvious utility in robotics. Importantly, our network schematics can be realized in many different ways, and as long as the symmetry is preserved, the same basic range of phase relationships will in principle be generated.

The crucial observation is that in order for a symmetric network of identical cells to reproduce the phase relationships found in gaits of a $2n$ -legged animal, the number of cells should be (at least) $4n$, not $2n$ as proposed by Collins and Stewart. For instance, 8 cells are needed for a quadruped and 12 for a hexapod. This observation leads to predictions about wave numbers that potentially might distinguish such a network from linear chains, and there is evidence from centipede gaits to support those predictions, a point that will be discussed below. We note that Ermentrout and Kopell [12] consider cell networks with 8 and 12 cells that are similar to ours. However, the form of the coupling in their networks (and the resulting symmetries) are different from ours.

1.1. Rationale for symmetry

The assumption that a CPG has some degree of symmetry may seem rather arbitrary, but several different points of view suggest that it is both natural and reasonable. We provide a few comments to motivate the symmetry assumption. Bilateral symmetry is prevalent throughout the animal kingdom, so a bilaterally symmetric CPG seems virtually mandatory. Although the physiology of animal limbs differs according to the position of the limb – especially in quadrupeds, where front limbs typically differ in detail from back limbs – these differences need not extend to the underlying CPG. The role of the CPG is to provide timing signals to the limbs, with suitable phase shifts: there is nothing in the pattern of those phase shifts to indicate special timing differences between front and back. Indeed the observed phase shifts in many gaits are simple fractions of the gait period, for example $0, \frac{1}{4}, \frac{1}{2}, \frac{3}{4}$, in the quadruped walk and $0, \frac{1}{3}, \frac{2}{3}$ in the metachronal gait of a hexapod. Such phase relationships are common in symmetric networks but unexpected in asymmetric ones.

Indeed most oscillator network models of CPGs assume that the oscillators are identical, which is a tacit symmetry assumption. More crucial to our approach is the idea that the coupling patterns in the network also have some degree of symmetry. It is possible, for example, to use variable couplings designed to enforce particular phase relationships. We believe, however, that symmetry of the entire network is a more plausible mechanism, for several reasons. The first is that while it is of course possible to design coupling strengths that enforce any reasonable set of phase relationships, such models do not select particular phases as being in any way special. The same design principle could equally readily produce a walk with phase of, say, $0, 0.173, 0.628, 0.844$. Yet the phases actually observed are simple fractions of the period. It is hard to see why a design principle that can produce *any* phase relationships whatsoever should lead to the evolution of a CPG with simple fractional phases. In short, we wish to *explain* the observed phases, within some hypothetical framework, and not just *reproduce* them in a CPG circuit. Another argument is physiological. For creatures with six or more legs, there is often little overt difference between one pair of limbs and another pair. In most beetles, all six legs look fairly similar. This observation is even stronger for arthropods, whose evolutionary history rests on the trick of developing large numbers of more or less identical segments (which may later become specialized in some respects – especially at the head and tail). ‘Identical

segments' is a symmetry statement: it implies that (modulo the ends) the animal has a translational symmetry. It would therefore not be surprising to find that its CPG has similar (perhaps imperfect) translational symmetry.

We emphasize that the above considerations are introduced in order to *motivate* our symmetry assumptions. Our network could have useful potential in robotics even if it does not turn out to model animal CPGs. However, the case for symmetry – or approximate symmetry – in real CPGs seems to us to be plausible. It is important to recognize, however, that real systems, especially biological ones, are never perfectly symmetric. This does not have any serious effect on our analysis, for the following general reason. The dynamics of a system that is 'close to' symmetric – perturbed away from an ideal symmetric system – is in many respects very similar to that of the ideal system. The loss of perfect symmetry resulting from a perturbation may change fine details of the dynamics (for example states that were previously related by a symmetry may become distinct) but the broad pattern remains much the same (the differences between those states will usually be small). The dynamics of a system that is close to symmetry resembles that of the ideal symmetric system far more closely than it resembles the dynamics of a 'generic' asymmetric system.

For these reasons, we believe that symmetry is a reasonable modeling assumption, and our intention will be to pursue the consequences of making such an assumption. As will become apparent, the dynamics of a symmetric CPG is remarkably close to that observed in actual gaits – even for 'exotic' gaits such as gallops and the canter, where at first sight the symmetry properties of phase relationships are not especially apparent.

2. The obstruction of conjugate solutions

Let C_1, C_2, \dots, C_N be nominally identical cells, and let the state variables of C_i at time t be represented by a vector $x^i = (x_1^i, \dots, x_s^i) \in \mathbb{R}^s$, where \mathbb{R}^s is an s -dimensional Euclidean space. In the literature it is usual to refer to such a cell as an 'oscillator', but we prefer to avoid this terminology since such cells need not be capable of oscillating as individuals. They may nevertheless acquire the ability to oscillate when they are coupled in networks. An early example of this phenomenon is due to Smale [28]; other examples can be constructed using cell systems with $s = 1$.

We assume that each cell can be modeled by an ordinary differential equation (ODE) of the form

$$\frac{dx^i}{dt} = f(x^i, \lambda), \quad (1)$$

where $\lambda = (\lambda_1, \dots, \lambda_p)$ is a vector of p parameters and $f : \mathbb{R}^s \times \mathbb{R}^p \rightarrow \mathbb{R}^s$ is a smooth vector field. Since f is independent of i , each cell has the same dynamics as any other at given parameter values, and this is the sense in which they are 'identical'.

We further assume that these cells are coupled in a network, implying that the state of a given cell affects the states of all those to which it is coupled. For simplicity of description we model unidirectional coupling of C_j to C_i by a term $\alpha_{ij}h(x^j, x^i)$, where α_{ij} is the strength of the coupling from C_j to C_i . For example, diffusive coupling has the form $h(x^j, x^i) = x^j - x^i$. Notice that if $\alpha_{ij} = 0$, then cell C_j has no direct effect on cell C_i ; they are uncoupled. Bidirectional coupling will be represented as a combination of two equal and opposite unidirectional couplings ($\alpha_{ij} = \alpha_{ji}$). An alternative to diffusive coupling is synaptic (pulse) coupling. We stress that our results do not depend on the form of this coupling, but only upon the symmetries of the resulting system, so many other expressions for the coupling terms could be employed instead. In particular we could restrict the effect of the coupling to one or more components of x^i and x^j , for example to model voltage-coupled networks.

Graphically we represent such a network as a set of nodes joined by lines marked with arrows. Coupling from C_j to C_i is represented by a line of strength α_{ij} whose arrow points towards C_i , and couplings of strength

zero are suppressed. In practice, connections of differing strength are represented by arrows with different markings.

The network can thus be represented by a *coupling matrix* $A = (\alpha_{ij})$, where $1 \leq i, j \leq N$. The equations for the network become

$$\frac{dx^i}{dt} = f(x^i, \lambda) + \sum_{j \neq i} \alpha_{ij} h(x^j, x^i). \quad (2)$$

Now we are in a position to address the issue of spatio-temporal symmetries of such systems of ODEs. By a *spatial* symmetry we here mean a permutation of the cells, that is, a bijective mapping $\sigma : \{1, \dots, N\} \rightarrow \{1, \dots, N\}$, which preserves the coupling matrix. The permutation σ acts on $x = (x_1, \dots, x_N)$ by

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

Specifically, we let Γ be the group of permutations σ such that

$$\alpha_{\sigma(i), \sigma(j)} = \alpha_{ij} \quad \text{for all } i, j \in \{1, \dots, N\}. \quad (3)$$

If we now write Eqs. (2) in the abbreviated form

$$\frac{dx}{dt} = F(x, \lambda) + H(x) \equiv g(x, \lambda),$$

then the function g will be Γ -equivariant, that is, it will satisfy the condition

$$g(\sigma x, \lambda) = \sigma g(x, \lambda)$$

for all $\sigma \in \Gamma$. This implies that whenever $x(t)$ is a solution, so is $\sigma x(t)$. We call these *conjugate* solutions.

A *temporal* symmetry is a phase shift on a periodic solution of Eqs. (2). Specifically, if $x(t)$ is a periodic solution with period T , and $\varphi \in \mathbb{S}^1 \equiv \mathbb{R}/\mathbb{Z} \equiv [0, T)$ with 0 and T identified, then $x(t)$ has spatio-temporal symmetry $(\sigma, \varphi) \in \Gamma \times \mathbb{S}^1$ if

$$\sigma x(t + \varphi) = x(t) \quad (4)$$

for all t , or equivalently

$$\sigma x(t) = x(t - \varphi). \quad (5)$$

In other words, applying the spatial symmetry σ has the same effect as shifting phase by a fraction φ of a period.

The *symmetry group* or *isotropy group* of a periodic solution $x(t)$ is the group of all spatio-temporal symmetries of $x(t)$, considered as a subgroup of $\Gamma \times \mathbb{S}^1$. Conjugate solutions have conjugate symmetry groups.

The theory of symmetric Hopf bifurcation provides general conditions that guarantee the existence of primary bifurcations, from the trivial solution $x^i = 0$ for all i , to periodic oscillations with prescribed spatio-temporal symmetries. The symmetry groups of the resulting patterns are the subgroups of $\Gamma \times \mathbb{S}^1$ that have two-dimensional fixed point spaces, see [14,16]. More recently such subgroups have been called *C-axial* subgroups, see [9,10].

We are now in a position to sketch a group-theoretic argument showing that there is no single network composed of four identical cells in which symmetric Hopf bifurcation leads to all three quadrupedal gaits walk, trot, and pace, with trot and pace non-conjugate. (See Table 4, Collins and Stewart [6] and Gambaryan [13] for a description of these and other quadrupedal gaits.) Indeed, suppose that there is such a network, and let Γ be the group of spatial symmetries of the network. Then Γ contains \mathbb{Z}_4 and Γ is contained in \mathbb{S}_4 , so $|\Gamma| = 4, 8, 12$, or 24 . To support trot and pace, Γ must be larger than \mathbb{Z}_4 , so $|\Gamma| > 4$.

Now $|\Gamma| = 8$ implies $\Gamma = \mathbb{D}_4$, which conjugates trot and pace. If $|\Gamma| = 24$, then $\Gamma = \mathbb{S}_4$ and the same holds. So the only possibility is $|\Gamma| = 12$. However, there is no 12-element subgroup of \mathbb{S}_4 that contains \mathbb{Z}_4 , because the permutation (1234) is odd, so $|\Gamma|$ cannot be the alternating group \mathbb{A}_4 , which is the only subgroup of order 12.

Within the assumed context, this group-theoretic observation rules out all four-cell networks. Similar conjugacy obstructions arise when attempting to model $2n$ -legged gaits with $2n$ identical cells whenever $2n \geq 4$. However, for bipedal gaits there is no analogous argument that rules out a two-cell network.

3. The modular network

We now show that a network with $4n$ cells avoids the above difficulty, and appears to generate the appropriate kinds of gaits. The network is shown schematically in Fig. 1(a), with circles corresponding to the component cells (all assumed identical) and bonds corresponding to types of coupling between cells. We emphasize that this figure is not a ‘wiring diagram’, either for a CPG or for an electronic circuit controlling a robot: its sole intention is to show the requisite symmetries in the simplest manner. Each type of bond corresponds to a fixed type of coupling associated with a particular strength parameter (or parameters): arrows indicate unidirectional bonds and double lines bidirectional bonds.

The structure of this network is motivated by the observed gaits in quadrupeds, hexapods, and multi-legged animals such as centipedes. It respects the natural bilateral symmetry, and also possesses a $2n$ -fold cyclic ‘translational’ symmetry from back to front. The network consists of two cycles of $2n$ cells. For reference purposes the cells are numbered 1, 3, 5, ..., $4n - 1$ in one cycle and 2, 4, ..., $4n$ in the other. Unidirectional couplings, all assumed identical in form, run from cell i to cell $i + 2 \pmod{4n}$. Bidirectional couplings, again assumed identical (but

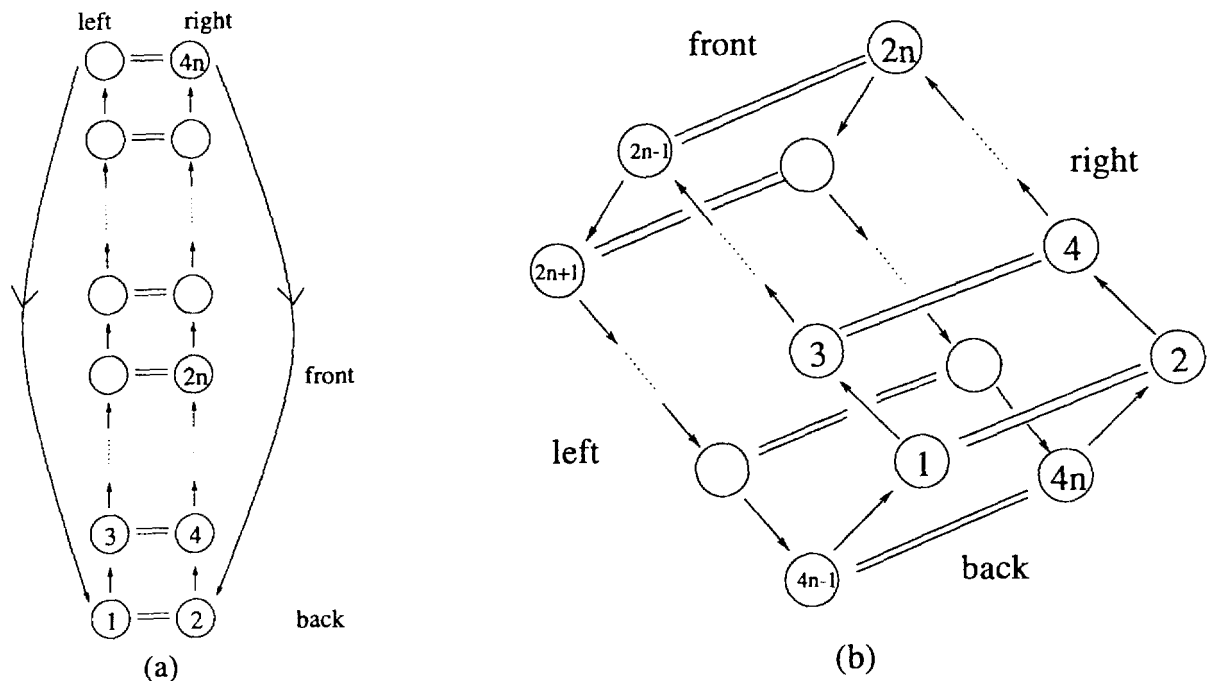


Fig. 1. (a) Schematic $4n$ -cell network for gaits in $2n$ -legged animals. Only cells 1, ..., $2n$ are connected to legs. (b) Folding up the network to eliminate long-range connections creates a structure with repeated modules, differing slightly at the two ends.

differing from the unidirectional ones) run between cells $2i - 1$ and $2i$. We shall later assume that signals to the limbs are generated only in the first half of the cells, numbers $1, \dots, 2n$. This assumption introduces a necessary asymmetry between the front and back of the animal, as well as distinguishing them from the section in between. Again this assumption is schematic for a wide range of alternatives with the same abstract structure: we expand on this point below.

Note that although the diagrams have been drawn with two unidirectional couplings that are longer than the others, this has merely been done for convenience in representing the structure on the page. One way to make all connections short in practice would be to fold the second part of the network, cells $2n + 1$ through $4n$, back over the first half, as illustrated in Fig. 1(b). This structure is advantageous in potential applications to robotics, because it permits a modular approach to circuit-building. While the absence of such long-range connections is also attractive biologically, we do not wish to draw any conclusions about the layout of animal locomotor CPGs at this stage.

From the point of view of equivariant bifurcation theory, the most important aspect of the network is its symmetry group. This is

$$\Gamma \cong \mathbb{Z}_{2n} \times \mathbb{Z}_2. \quad (6)$$

The subgroup \mathbb{Z}_{2n} cycles corresponding pairs of cells around their respective loops, and the subgroup \mathbb{Z}_2 interchanges left and right cells in corresponding positions. Specifically, in permutation notation, \mathbb{Z}_{2n} is generated by

$$\omega = (1\ 3\ 5 \dots 4n - 1)(2\ 4\ 6 \dots 4n) \quad (7)$$

and \mathbb{Z}_2 is generated by

$$\kappa = (1\ 2)(3\ 4) \dots (4n - 1\ 4n). \quad (8)$$

The group Γ is abelian (all elements commute); so there is no problem with spurious conjugacies. In fact, we shall see that if any periodic solution arising via Hopf bifurcation is transformed by an element of Γ , then the result is equivalent to a phase shift on that solution.

We now analyze the possible patterns of symmetry-breaking bifurcation that can occur in the network. We emphasize that these patterns are model-independent in the sense that the same patterns can in principle occur in any network with the symmetry group Γ . This is important for applications to robotics (or CPGs) in which a more complex network of connections would provide a broader range of parameters, which could simplify the practical problem of producing desired gait patterns as *stable* periodic cycles. By ‘with the same symmetries’ we mean that if the schematic is modified by introducing an additional connection, then all connections that are symmetrically related to it by Γ must also be introduced (and be identical in form). With this proviso, as many connections as desired may be added to the schematic. For an example where this option becomes important, see Section 6.

We apply the general theory of symmetric Hopf (and steady-state) bifurcation to read off the patterns of symmetry-breaking that can occur in any network with symmetry group Γ . This requires a little representation theory. Suppose as before that each cell has internal state space \mathbb{R}^s for some s . Then the coupled network has state space

$$U \cong \mathbb{R}^{4ns} \cong \underbrace{\mathbb{R}^s \times \dots \times \mathbb{R}^s}_{4n} \quad (9)$$

and Γ acts on this space by permuting the $4n$ components (each a vector of dimension s).

We first determine how the representation of Γ on U breaks up into real irreducible representations. As a first step complexify the space U to get $V \cong \mathbb{C}^{4ns}$. Since Γ is abelian, V is the sum of one-dimensional irreducible

subspaces (over \mathbb{C}); and these subspaces are V_{jk} , where $0 \leq j \leq 2n - 1$ and $k = 0, 1$. To define V_{jk} , let $\zeta = e^{i\pi/n}$ be a primitive $2n$ th root of unity. Then V_{jk} is spanned over \mathbb{C} by

$$v_{jk} = (1, (-1)^k; \zeta^j, (-1)^k \zeta^j; \zeta^{2j}, (-1)^k \zeta^{2j}; \dots; \zeta^{(2n-1)j}, (-1)^k \zeta^{(2n-1)j}). \quad (10)$$

Observe that

$$\omega v_{jk} = \zeta^j v_{jk}, \quad \kappa v_{jk} = (-1)^k v_{jk}$$

so that the subspace V_{jk} are indeed Γ -invariant.

The corresponding decomposition of U into irreducibles is into the representations U_{jk} where

$$U_{jk} = \begin{cases} \text{Re}(V_{jk}) & \text{if } j = 0, n, \\ \text{Re}(V_{jk} \oplus V_{2n-j,k}) & \text{if } 1 \leq j \leq n - 1. \end{cases} \quad (11)$$

See [16] for further details.

Local bifurcations from the trivial solution occur when the linearization (Jacobian matrix) has zero eigenvalues (steady-state bifurcation) or purely imaginary eigenvalues (Hopf bifurcation). Generically, the zero eigenspace is an absolutely irreducible representation for steady-state bifurcation, and is Γ -simple for Hopf bifurcation (either a direct sum of two isomorphic copies of an absolutely irreducible representation or a single nonabsolutely irreducible representation). That is, the network equations can undergo steady-state bifurcations corresponding to the subspaces $U_{00}, U_{n0}, U_{01}, U_{n1}$. The network can undergo Hopf bifurcation corresponding to any of the U_{jk} when $s > 1$, but when $s = 1$ the only Hopf bifurcations from the trivial branch are those corresponding to eigenspaces for which $j = 1, \dots, n - 1$. (The reason for this restriction is the condition of Γ -simplicity: imaginary eigenvalues cannot occur unless the representations of real type have multiplicity at least 2.) Our discussion in Section 6 treats the case $s = 2$. (Standard model equations for neurons have $s \geq 2$, see [3].)

The effect of the assumed bilateral symmetry of the network (the κ symmetry) can be detected immediately. Hopf bifurcations corresponding to the subspace U_{jk} lead to gaits in which (κ symmetric) pairs of legs are in phase when $k = 0$ and half a period out of phase when $k = 1$.

4. Primary bifurcations

4.1. Bipedal gaits

Recalling that n is the number of pairs of legs we see that the case $2n = 2$ refers to bipedal gaits. This case is exceptional because of its simplicity. For our proposed four-cell network the analysis of bipedal gaits leads to the same patterns as a two-cell network [6]: after a primary Hopf bifurcation the legs are either in phase or half a period out of phase.

We remark that other phase relationships, such as seen in the human gait ‘skip’, can occur via secondary period-doubling bifurcations. Recall that in such a bifurcation a periodic state $x(t)$ of period T makes a transition to a state of period $2T$, in effect by modifying two successive periods of $x(t)$ in two slightly different ways. Suppose that a bilaterally symmetric system has a T -periodic state $(x_1(t), x_2(t))$, where the symmetry permutes the indices 1 and 2. Then it is possible for such a state to undergo a period-doubling bifurcation to a state $(y_1(t), y_2(t))$ that has a spatio-temporal symmetry:

$$y_2(t) = y_1(t + T).$$

This symmetry is observed in (one form of) the skip, and is also in the ‘half-bound’ of small animals such as the jerboa, see [13].

4.2. Quadrupedal gaits

The difference between our $4n$ -cell model and $2n$ -cell models is evident when $2n = 4$, the case of quadrupeds: in this section we focus on that case. Each complex irreducible representation of Γ supports either one or two primary bifurcations to phase-locked patterns of oscillation, in which the phases are determined by the roots of unity in (10). Specifically, on the space U_{jk} the phase shift on cell C_m is:

$$\begin{aligned} \pm(m-1)\frac{j}{4n} & \quad \text{if } m \text{ is odd,} \\ \pm(m-2)\frac{j}{4n} + \frac{k}{2} & \quad \text{if } m \text{ is even,} \end{aligned} \tag{12}$$

where either the + or – sign is chosen throughout, and for $j = 0$ or $j = n$ only the + sign is used. (The reason for this restriction is that for phases of 0 or $\frac{1}{2}$ a sign change has no effect.)

We may now read off the corresponding patterns for the primary bifurcations. We denote them by an array of phase shifts corresponding to cells arranged in the form

$$\begin{array}{cc} 7 & 8 \\ 5 & 6 \\ 3 & 4 \\ 1 & 2 \end{array}$$

Recall that for purposes of interpretation, we assume that only cells 1–4 drive the legs, so that:

- cell 1 drives the left rear leg,
- cell 2 drives the right rear leg,
- cell 3 drives the left front leg,
- cell 4 drives the right front leg.

Thus the phases of cells 5–8 are ignored as far as the gait patterns are concerned: those cells are present in order to propagate the dynamics correctly. An alternative assumption with the same consequences for gait patterns is that the left rear leg is driven by some *asymmetric* function of the states of cells 1 and 5, and the same function of cells 2 and 6, 3 and 7, and 4 and 8 is used to drive the right rear, left front, and right front legs, respectively. The ‘wiring diagram’ for such a choice introduces long-range connections in a control network for multi-legged locomotion – this is not an obstacle in robotic applications, where long-range connections can be made effectively as rapid as short-range ones.

The primary patterns, in this notation, are found in Table 1.

4.3. Hexapodal gaits

When $2n = 6$ we have a 12-cell network, and in the same notation the primary Hopf bifurcations from the trivial state are listed in Table 2. From that table, we see that gaits U_{00} and U_{01} are the insect analog of *pronk* and *pace*, and gaits U_{31} and U_{11} are the standard *tripod* and *metachronal* gaits. (See [7] for a description of common hexapodal gaits.)

Gait U_{30} is a somewhat curious gait which we call the *lurch*. In gait U_{10} the animal (or robot) moves legs on left and right in synchrony in a wave that passes from back to front, and then appears to pause before continuing. This

Table 1
Quadrupedal gaits (in jump and walk choose either + or – throughout)

U_{00}	U_{01}	U_{10}	U_{11}	U_{20}	U_{21}
0 0	0 $\frac{1}{2}$	$\pm\frac{3}{4}$ $\pm\frac{3}{4}$	$\pm\frac{3}{4}$ $\pm\frac{1}{4}$	$\frac{1}{2}$ $\frac{1}{2}$	$\frac{1}{2}$ 0
0 0	0 $\frac{1}{2}$	$\frac{1}{2}$ $\frac{1}{2}$	$\frac{1}{2}$ 0	0 0	0 $\frac{1}{2}$
0 0	0 $\frac{1}{2}$	$\pm\frac{1}{4}$ $\pm\frac{1}{4}$	$\pm\frac{1}{4}$ $\pm\frac{3}{4}$	$\frac{1}{2}$ $\frac{1}{2}$	$\frac{1}{2}$ 0
0 0	0 $\frac{1}{2}$	0 0	0 $\frac{1}{2}$	0 0	0 $\frac{1}{2}$
Pronk	Pace	Jump $^{\pm}$	Walk $^{\pm}$	Bound	Trot

Table 2
Hexapodal gaits (choose + or – throughout in gaits where relevant)

U_{00}	U_{01}	U_{30}	U_{31}	U_{10}	U_{11}	U_{20}	U_{21}
0 0	0 $\frac{1}{2}$	$\frac{1}{2}$ $\frac{1}{2}$	$\frac{1}{2}$ 0	$\pm\frac{5}{6}$ $\pm\frac{5}{6}$	$\pm\frac{5}{6}$ $\pm\frac{1}{3}$	$\pm\frac{2}{3}$ $\pm\frac{2}{3}$	$\pm\frac{2}{3}$ $\pm\frac{1}{6}$
0 0	0 $\frac{1}{2}$	0 0	0 $\frac{1}{2}$	$\pm\frac{2}{3}$ $\pm\frac{2}{3}$	$\pm\frac{2}{3}$ $\pm\frac{1}{6}$	$\pm\frac{1}{3}$ $\pm\frac{1}{3}$	$\pm\frac{1}{3}$ $\pm\frac{5}{6}$
0 0	0 $\frac{1}{2}$	$\frac{1}{2}$ $\frac{1}{2}$	$\frac{1}{2}$ 0	$\frac{1}{2}$ $\frac{1}{2}$	$\frac{1}{2}$ 0	0 0	0 $\frac{1}{2}$
0 0	0 $\frac{1}{2}$	0 0	0 $\frac{1}{2}$	$\pm\frac{1}{3}$ $\pm\frac{1}{3}$	$\pm\frac{1}{3}$ $\pm\frac{5}{6}$	$\pm\frac{2}{3}$ $\pm\frac{2}{3}$	$\pm\frac{2}{3}$ $\pm\frac{1}{6}$
0 0	0 $\frac{1}{2}$	$\frac{1}{2}$ $\frac{1}{2}$	$\frac{1}{2}$ 0	$\pm\frac{1}{6}$ $\pm\frac{1}{6}$	$\pm\frac{1}{6}$ $\pm\frac{2}{3}$	$\pm\frac{1}{3}$ $\pm\frac{1}{3}$	$\pm\frac{1}{3}$ $\pm\frac{5}{6}$
0 0	0 $\frac{1}{2}$	0 0	0 $\frac{1}{2}$	0 0	0 $\frac{1}{2}$	0 0	0 $\frac{1}{2}$
Pronk	Pace	Lurch	Tripod	Inchworm $^{\pm}$	Metachronal $^{\pm}$	Caterpillar $^{\pm}$	Rolling tripod $^{\pm}$

we call the *inchworm* gait because it is reminiscent of the motion of that animal. Gait U_{20} is another gait in which the motion of left and right legs are in synchrony. We call it the *caterpillar* gait.

Finally, in gait U_{21} two waves travel from back to front, one third of a period out of phase, but left and right sides are half a period out of phase. So the order in which the legs move is back left, front right, middle left, back right, front right, middle right – at equally spaced interval. This is a kind of *rolling tripod*.

4.4. Many-legged gaits

A similar analysis applies to networks of the kind that might be associated with many-legged animals such as centipedes and millipedes – and also legless animals such as eels, snakes, and lamprey, in which ‘leg’ should be interpreted as ‘muscular unit’. The range of gait patterns is considerable, but they all have the same fundamental characteristics. First, select some divisor d of $2n$, the number of cells on one side of the network, but also equal to the total number of legs. Then group the cells on the left side into $2n/d$ clumps, each spaced d cells apart. The phase relationships along that side of the network are like those of a $(4n/d)$ -cell network of the same kind, but repeated d times in the ‘forward’ direction. The left–right pairs of cells either are in phase throughout the cycle, or half a period out of phase throughout the cycle. In centipedes, millipedes, and lamprey, the ‘half a period out of phase’ option is the one observed, so we focus on that example.

Similarly clumped traveling waves can be produced in linear chains of cells by forcing them at the end and imposing suitable boundary conditions at the free front end (the mathematically most tractable being periodic boundary conditions). The same goes for pairs of chains, cross-connected to impose a half-period phase shift. A model of this sort occurs in the work of Rand et al. [25]. In such a system there is no preferred ‘wave number’ for the traveling waves: they can be any integer, and are not related to the number of legs (or muscular units in cases such as the lamprey).

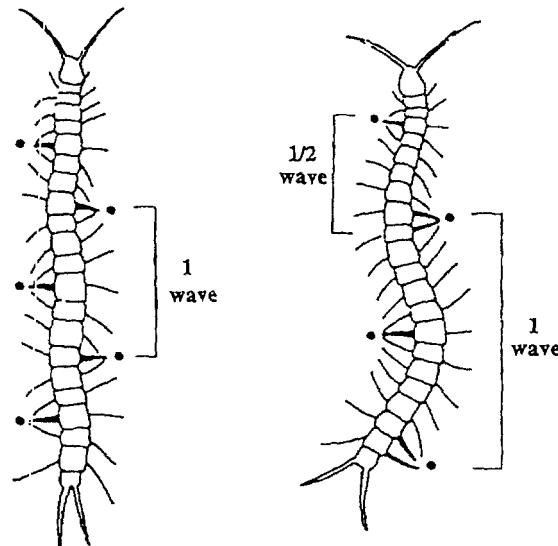


Fig. 2. Figure from [1]. Thick lines indicate legs in contact with the ground. (Left) The centipede has 3 waves. (Right) The centipede has $3/2$ waves.

This feature leads to a prediction that is specific to symmetry-based models of the type we are considering. Namely, that the wave number (the spatial period between synchronously moving legs, measured along the length of the animal) should always divide the *total* number of legs (or muscular units in cases such as the lamprey). For example in a 30-legged centipede ($n = 15$) the predicted wave numbers are 1, 2, 3, 5, 6, 10, 15. In a linear chain model, all numbers from 1 to 15 are possible; in a cyclic network model with $2n$ cells instead of $4n$, only divisors of n should appear – in this case 1, 3, 5, 15, excluding 2, 6, 10.

Another way to state this, which is less sensitive to imperfections in the network, is that the number of waves that fits into the ‘directly observable’ half of the network, cell 1 through $2n$, is either an integer or half-an-odd integer. The half-an-odd integer patterns are characteristic of ‘doubled’ networks such as that described in this paper (see [11]), and serve as an indirect indicator of the presence of the hidden half of the network. In the context of possible applications to CPGs, it may therefore be significant that Alexander [1] provides drawings of several gaits by a 40-legged centipede. In all cases the number of waves appears to be close either to an integer (4, 3, 2) or half-an-odd integer ($3/2$). In particular, the half-an-odd integer pattern does seem to occur. See Fig. 2. The number of legs depicted in the spatial period of the various traveling waves are not all exact divisors of 80: for example one picture shows 13 legs per wave. However, they are very close to exact divisors. For example 13 is very close to $80/6 = 20 \times 2/3$, where 20 is the number of legs along one side of the animal. So here the number of waves passing along the animal is very close to $3/2$.

Precise numerical agreement would be unlikely for several reasons: first, the symmetry of a real CPG will be only approximate; and second, an animal CPG, even if it is of the form we are studying here, might involve more cells than there are legs (for instance by assigning a chain of modules to each leg, which in this case would lead to a multiple of 80 cells). The prediction that half-an-odd integer waves can occur is robust under such changes.

The wavelike motion of the lamprey shown in [20] shows $5/2$ waves along the animal’s length, both in forward and backward motion: this is especially clear in the third and fifth images in the top figure on page 51. Again this relationship is consistent with our model but requires special explanation for linear chain models.

5. Secondary quadrupedal gaits

As discussed previously, periodic solutions $x(t)$ have spatio-temporal symmetries which form a subgroup $\Sigma \subset \Gamma \times \mathbb{S}^1$. So (σ, θ) is a symmetry of $x(t)$ if

$$\sigma x(t + \theta) = x(t), \quad (13)$$

and Σ consists of all pairs (σ, θ) satisfying (13). In our modular network for quadrupeds

$$x(t) = (x_1(t), x_2(t), \dots, x_8(t)),$$

where $x_j(t)$ describes the signal in cell j of the CPG. We then identified

$$(x_1(t), x_2(t), x_3(t), x_4(t))$$

as the signals from the CPG that drive the four legs of the quadruped.

In Section 4.2 we listed the primary gaits generated by the $\Gamma = \mathbb{Z}_4 \times \mathbb{Z}_2$ symmetry of our network. These gaits satisfy two properties:

- (a) The signals $x_j(t)$ all have identical waveforms (forced by symmetry) and differ only by phase shifts, and
- (b) Periodic solutions with these symmetries can be expected to appear in model equations by Hopf bifurcation from the trivial steady-state ‘stand’.

For simplicity we assume $x(t)$ has period 1. As an example, reconsider the walk. In our network, the symmetry group of a walk is generated by

$$\left(\omega, \frac{1}{4}\right) \quad \text{and} \quad \left(\kappa, \frac{1}{2}\right),$$

where

$$\omega = (1\ 3\ 5\ 7)(2\ 4\ 6\ 8) \quad \text{and} \quad \kappa = (1\ 2)(3\ 4)(5\ 6)(7\ 8).$$

The $(\sigma, \frac{1}{4})$ symmetry forces the components $x_j(t)$ to satisfy

$$x_3(t) = x_1\left(t + \frac{1}{4}\right) \quad \text{and} \quad x_4(t) = x_2\left(t + \frac{1}{4}\right),$$

$$x_5(t) = x_1\left(t + \frac{1}{2}\right) \quad \text{and} \quad x_6(t) = x_2\left(t + \frac{1}{2}\right),$$

$$x_7(t) = x_1\left(t + \frac{3}{4}\right) \quad \text{and} \quad x_8(t) = x_2\left(t + \frac{3}{4}\right).$$

The $(\kappa, \frac{1}{2})$ symmetry forces

$$x_2(t) = x_1\left(t + \frac{1}{2}\right).$$

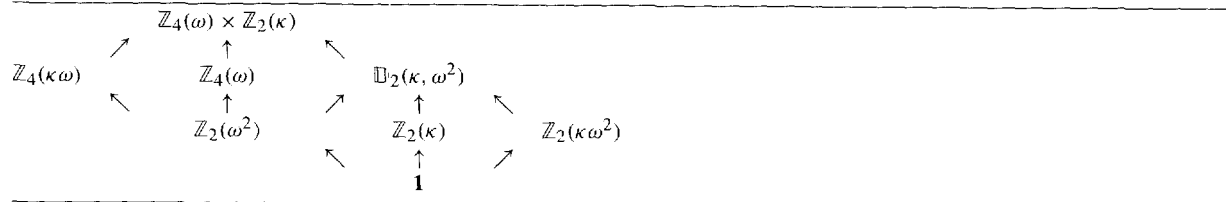
Consequently, the four signals sent by this CPG are

$$(x_1(t), x_2(t), x_3(t), x_4(t)) = (x_1(t), x_1\left(t + \frac{1}{2}\right), x_1\left(t + \frac{1}{4}\right), x_1\left(t + \frac{3}{4}\right)),$$

that is, the same waveform ($x_1(t)$) is sent to each leg – but with the characteristic phase shifts associated with a ‘walk’.

In this section we discuss all of the symmetries associated to periodic solutions in our modular network. By making this classification we will find secondary gaits that may be associated to rotary gallops, transverse gallops, and canters, as well as other possibilities. By the term *secondary gait* we mean that the CPG sends two different signals to two pairs of legs. Nevertheless, it is possible to associate a pattern of phase shifts for these gaits, as we explain below.

Table 3
Lattice of subgroups of $\Gamma = \mathbb{Z}_4 \times \mathbb{Z}_2$



5.1. Classification of isotropy subgroups

The strategy for classifying all isotropy subgroups of periodic solutions works as follows. Let $K = \Sigma \cap \Gamma$ be the subgroup of *space* symmetries that fix each periodic solution pointwise, that is $k \in K$ if $kx(t) = x(t)$ for all time t . For example, κ is a space symmetry of any gait where left and right legs move in unison, such as the pronk or bound. Let $K \subset \Gamma$ be the subgroup obtained from Σ by stripping off the phase shift, that is, if $(\sigma, \theta) \in \Sigma$, then $\sigma \in K$. It follows that K is a subgroup of H and H/K is a finite subgroup of \mathbb{S}^1 . Hence, H/K is cyclic. Our strategy divides into three parts:

1. Classify all subgroups L of $\Gamma = \mathbb{Z}_4 \times \mathbb{Z}_2$.
2. For each L classify all normal subgroups K such that H/K is cyclic.
3. For each of the admissible pairs H/K determine the constraints on the signal $x(t)$ to decide whether the associated gait is secondary.

The lattice of subgroups of $\mathbb{Z}_4 \times \mathbb{Z}_2$ is given in Table 3 where ω is the generator of \mathbb{Z}_4 and κ is the generator of \mathbb{Z}_2 .

The possible choices for H and K are listed in Table 4. In this table we indicate the restrictions on the signals from the network going to each leg. We assume that $x_1(t)$ is a given waveform and write, where appropriate, the restrictions of $x_2(t)$, $x_3(t)$, and $x_4(t)$. We do not indicate the restrictions on $x_5(t), \dots, x_8(t)$.

We define the *twist type* to be the order of the cyclic group H/K . The group elements in $H - K$ correspond to spatio-temporal symmetries. When the twist type is 2, the only phase shift is $\frac{1}{2}$. When the twist type is 4, there are two types of phase shift possible. The generator of H/K can be phase shifted by $\frac{1}{4}$ or $-\frac{1}{4}$. We indicate these possibilities by 4^+ and 4^- .

There are eight primary gaits – as we have discussed previously. The secondary gaits are those that have two independent wave form and we have indicated the 14 secondary gaits listed in this table by a^* .

5.2. Secondary gaits

Next we discuss the gait pattern that is associated with the secondary gaits of the previous subsection. We assume that the signals $x_j(t)$ produce approximately sinusoidal movement in the legs, that is, we assume for the purpose of identifying gaits that

$$x_j(t) \approx A_j \sin(2\pi(t + \varphi_j));$$

for some amplitude A_j and some phase shift φ_j .

For example, consider the secondary gaits that we have called rotary gallop, transverse gallop and canter. Assume after normalization of the phase shift and amplitude of $x_1(t)$ that

$$x_1(t) \approx \sin(2\pi t) \quad \text{and} \quad x_2(t) \approx A_2 \sin(2\pi(t + \varphi_2)).$$

Table 4
Pairs of H and K for quadrupeds

H	K	Name	Twist	$x_2(t)$	$x_3(t)$	$x_4(t)$
$\mathbb{Z}_4(\omega) \times \mathbb{Z}_2(\kappa)$	$\mathbb{Z}_4(\omega) \times \mathbb{Z}_2(\kappa)$	Pronk	0	$x_1(t)$	$x_1(t)$	$x_1(t)$
	$\mathbb{Z}_4(\omega)$	Rack	2	$x_1(t + \frac{1}{2})$	$x_1(t)$	$x_1(t + \frac{1}{2})$
	$\mathbb{D}_2(\kappa, \omega^2)$	Bound	2	$x_1(t)$	$x_1(t + \frac{1}{2})$	$x_1(t + \frac{1}{2})$
	$\mathbb{Z}_4(\kappa\omega)$	Trot	2	$x_1(t + \frac{1}{2})$	$x_1(t + \frac{1}{2})$	$x_1(t)$
	$\mathbb{Z}_2(\kappa)$		Jump	4^+	$x_1(t)$	$x_1(t + \frac{1}{4})$
4^-				$x_1(t)$	$x_1(t - \frac{1}{4})$	$x_1(t - \frac{1}{4})$
	$\mathbb{Z}_2(\kappa\omega^2)$	Walk	4^+	$x_1(t + \frac{1}{2})$	$x_1(t + \frac{1}{4})$	$x_1(t + \frac{3}{4})$
			4^-	$x_1(t - \frac{1}{2})$	$x_1(t - \frac{1}{4})$	$x_1(t - \frac{3}{4})$
$\mathbb{Z}_4(\kappa\omega)$	$\mathbb{Z}_4(\kappa\omega)^*$	Loping trot	0	$x_2(t)$	$x_2(t)$	$x_1(t)$
	$\mathbb{Z}_2(\omega^2)^*$	Rotary gallop	2	$x_2(t)$	$x_2(t + \frac{1}{2})$	$x_1(t + \frac{1}{2})$
	$\mathbf{1}^*$		Rotary canter	4^+	$x_2(t)$	$x_2(t + \frac{1}{4})$
4^-				$x_2(t)$	$x_2(t - \frac{1}{4})$	$x_1(t - \frac{1}{4})$
$\mathbb{Z}_4(\omega)$	$\mathbb{Z}_4(\omega)^*$	Loping rack	0	$x_2(t)$	$x_1(t)$	$x_2(t)$
	$\mathbb{Z}_2(\omega^2)^*$	Transverse gallop	2	$x_2(t)$	$x_1(t + \frac{1}{2})$	$x_2(t + \frac{1}{2})$
	$\mathbf{1}^*$		Canter	4^+	$x_2(t)$	$x_1(t + \frac{1}{4})$
4^-				$x_2(t)$	$x_1(t - \frac{1}{4})$	$x_2(t - \frac{1}{4})$
$\mathbb{D}_2(\kappa, \omega^2)$	$\mathbb{D}_2(\kappa, \omega^2)^*$	Loping bound	0	$x_1(t)$	$x_3(t)$	$x_3(t)$
	$\mathbb{Z}_2(\omega^2)^*$	Running walk	2	$x_1(t + \frac{1}{2})$	$x_3(t)$	$x_3(t + \frac{1}{2})$
	$\mathbb{Z}_2(\kappa\omega^2)^*$	Running walk	2	$x_1(t + \frac{1}{2})$	$x_3(t)$	$x_3(t + \frac{1}{2})$
	$\mathbb{Z}_2(\kappa)^*$	Loping bound	2	$x_1(t)$	$x_3(t)$	$x_3(t)$
$\mathbb{Z}_2(\omega^2)$	$\mathbb{Z}_2(\omega^2)$		0	$x_2(t)$	$x_3(t)$	$x_4(t)$
	$\mathbf{1}$		2	$x_2(t)$	$x_3(t)$	$x_4(t)$
$\mathbb{Z}_2(\kappa)$	$\mathbb{Z}_2(\kappa)^*$	Loping bound	0	$x_1(t)$	$x_3(t)$	$x_3(t)$
	$\mathbf{1}^*$	Running walk	2	$x_1(t + \frac{1}{2})$	$x_3(t)$	$x_3(t + \frac{1}{2})$
$\mathbb{Z}_2(\kappa\omega^2)$	$\mathbb{Z}_2(\kappa\omega^2)$		0	$x_2(t)$	$x_3(t)$	$x_4(t)$
	$\mathbf{1}$		2	$x_2(t)$	$x_3(t)$	$x_4(t)$
$\mathbf{1}$	$\mathbf{1}$		0	$x_2(t)$	$x_3(t)$	$x_4(t)$

The amplitude A_2 does not affect the determination of the time when a given leg strikes the ground. Assuming that these approximations are accurate, we can use the information in Table 4 to describe the order that the legs strike the ground and their relative phase. The signals to the legs are:

$$\begin{array}{cc|cc|cc}
 x_2(t + \frac{1}{2}) & x_1(t + \frac{1}{2}) & x_1(t + \frac{1}{2}) & x_2(t + \frac{1}{2}) & x_1(t + \frac{1}{4}) & x_2(t + \frac{1}{4}) \\
 x_1(t) & x_2(t) & x_1(t) & x_2(t) & x_1(t) & x_2(t) \\
 \text{rotary} & \text{gallop} & \text{transverse} & \text{gallop} & \text{canter} & \\
 \end{array}$$

This leads to relative phases:

$$\begin{array}{cc|cc|cc}
 \varphi + \frac{1}{2} & \frac{1}{2} & \frac{1}{2} & \varphi + \frac{1}{2} & \frac{1}{4} & \varphi + \frac{1}{4} \\
 0 & \varphi & 0 & \varphi & 0 & \varphi \\
 \text{rotary} & \text{gallop} & \text{transverse} & \text{gallop} & \text{canter} & \\
 \end{array}$$

Table 5
Parameter values where different gaits have been observed

Gait	c	α	β	γ	δ
Pronk	0.5	0.01	0.014	0.025	0.02
Pace	0.44	0.025	0.02	-0.01	-0.012
Bound	0.44	-0.01	-0.0102	0.025	0.02
Trot	0.44	-0.02	-0.002	-0.025	0.015
Jump	0.44	-0.02	0.01	0.025	0.015
Walk	0.44	-0.01	0.0102	-0.025	0.02

When φ is small in the first two gaits we obtain the standard phase description of the *rotary gallop* and the *transverse gallop*. In the third case, when $\varphi \approx \frac{1}{4}$, we have the standard phase description of the *canter*. There are several other phase relations possible from the other secondary gaits, but we do not enumerate them here.

6. Numerical results from model equations

In this section we consider the existence of the primary gaits in a specific system of differential equations. We are particularly interested in stable periodic solutions that are obtained in our network via Hopf bifurcation. To specify the network equations, we need to choose the differential equations modeling the internal dynamics and the precise form of coupling.

In order to have all Hopf bifurcations present in the network equations, the internal dynamics must be at least two-dimensional. We assume that the internal dynamics are exactly two-dimensional, and we choose specifically to work with the FitzHugh–Nagumo equations:

$$\dot{x} = c(x + y - \frac{1}{3}x^3) \equiv f_1(x, y), \quad \dot{y} = -\frac{1}{c}(x - a + by) \equiv f_2(x, y). \quad (14)$$

It follows that the eight-cell network is 16-dimensional.

In our model system we assume that all couplings are linear and diagonal, in a sense that we now make precise. Let (x_i, y_i) be the state variables of the i th cell. We assume that the contralateral coupling strength can be set at values different from the ipsilateral coupling strengths. That is, we assume that

$$\begin{aligned} \dot{x}_i &= f_1(x_i, y_i, \lambda) + \alpha(x_{i-2} - x_i) + \gamma(x_{i+\epsilon} - x_i), \\ \dot{y}_i &= f_2(x_i, y_i, \lambda) + \beta(y_{i-2} - y_i) + \delta(y_{i+\epsilon} - y_i), \end{aligned} \quad (15)$$

where $i = 1, \dots, 8$, the indices are taken modulo 8, and

$$\epsilon = \begin{cases} +1, & i \text{ odd,} \\ -1, & i \text{ even.} \end{cases}$$

Setting $a = 0.02$ and $b = 0.2$ in the FitzHugh–Nagumo equations we find that stable periodic solutions corresponding to each of the primary gaits occur at the parameter values given in Table 5. Each of these solutions can be found starting from the initial condition $(x_1, y_1) = (0.06, -0.04)$ and $(x_i, y_i) = (0, 0)$ for $2 \leq i \leq 8$. The simulations verifying these statements were performed using `dstool`.

It should be noted that each of these periodic solutions is found near a supercritical Hopf bifurcation of the appropriate type, as we now discuss.

Table 6
Block diagonalization of the linearization at the stand

Gait	Representation	Block diagonalization
Pronk	U_{00}	A
Pace	U_{01}	$A - 2C$
Bound	U_{20}	$A - 2B$
Trot	U_{21}	$A - 2B - 2C$
Jump	U_{10}	$\begin{pmatrix} A - B & -B \\ B & A - B \end{pmatrix}$
Walk	U_{11}	$\begin{pmatrix} A - B - 2C & -B \\ B & A - B - 2C \end{pmatrix}$

6.1. Hopf bifurcations

Suppose that $z_0 = (x_0, y_0)$ is an equilibrium of (14) so that setting the internal variables of all eight cells equal to z_0 is an equilibrium for (15). We call this equilibrium the *stand* and look for Hopf bifurcation from the stand. To find Hopf bifurcations, we must compute the linearization of (15) at the stand, find conditions when this linearization has purely imaginary eigenvalues, and determine when the representation of F on the eigenspace is of the type corresponding to each primary gait. From representation theory we know that this linearization is block diagonal with the blocks corresponding to the subspaces U_{jk} defined in (11).

Let

$$A = (dF)_{z_0, \lambda} = \begin{bmatrix} a & b \\ c & d \end{bmatrix}, \quad B = \begin{bmatrix} \alpha & 0 \\ 0 & \beta \end{bmatrix}, \quad C = \begin{bmatrix} \gamma & 0 \\ 0 & \delta \end{bmatrix}. \tag{16}$$

Then the diagonal blocks of the linearization are given in Table 6. Using this information one can check that in each case listed in Table 5, the periodic solution found is near a point of Hopf bifurcation.

7. Conclusions

We have applied the theory of symmetric Hopf bifurcation to infer a plausible class of CPG network architectures from the observed phase relationships of animal gaits. Previous attempts along similar lines have led to networks that either generate too limited a set of gaits, or suffer from the problem of unwanted conjugacies in which gaits that are expected to be distinct are related by a symmetry and hence have identical dynamical characteristics

We have shown that these problems are inescapable if the gaits of $2n$ -legged animals are modeled by symmetric CPGs composed of $2n$ identical cells. However, the proposed class of networks with $4n$ cells, which is characterized by $\mathbb{Z}_{2n} \times \mathbb{Z}_2$ symmetry, reproduces all of the standard quadrupedal gaits (including the canter and the transverse and rotary gallops), many of the standard hexapodal gaits, and the traveling-wave gaits/rhythms observed in centipedes, millipedes and lamprey. Because the symmetry group is abelian, there are no nontrivial conjugacies, hence no unwanted ones.

Whether the architectures of actual animal locomotor CPGs resemble the proposed networks requires further investigation. However, these networks have potential applications to the construction of legged robots. In particular, they permit a modular design in which the number of pairs of legs of a robot can be varied merely by plugging together or detaching the appropriate number of modules. This type of design suggests new ways to generate and control the motion of adaptive legged robots.

Acknowledgements

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