Central Pattern Generators for Bipedal Locomotion

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Abstract

We use symmetry to study two central pattern generator (CPG) models for biped locomotion. The first one is a coupled four-cell network, proposed by Golubitsky, Stewart, Buono, and Collins, that models rhythms associated to legs. A classification based on symmetry shows that this network can produce periodic solutions with rhythms corresponding to the standard bipedal gaits of *run*, *walk*, *hop*, *gallop*, and *skip*, among others. Moreover, the four-cell model can produce two types of *hop*, two types of *gallop*, and three additional symmetry types of periodic solutions that have yet to be identified with the rhythms of known bipedal gaits. The second locomotor CPG network models interlimb coordination in bipeds (arms+legs). It is obtained by breaking the symmetry between fore and hind legs in an eight-cell CPG network for quadruped gaits, also proposed by Golubitsky et al. We match the rhythms of perturbed periodic solutions found in this eight-cell network with legs rhythms produced by the four-cell CPG model. We also compare patterns of oscillation of gaits of the eight-cell model with results on bipedal interlimb coordination in the literature, showing that the eight-cell model is a plausible network for modeling human interlimb coordination.

We show numerical simulations of periodic solutions corresponding to the bipedal gaits in the two CPG models. These simulations use clamped Hodgkin-Huxley equations to model cell internal dynamics and partial linear coupling (where only the electrical potentials of different cells are coupled). We use synaptic coupling in the four-cell model and diffusive coupling in the eight-cell model.

1 Introduction

Animal locomotion is controlled by a central pattern generator (CPG) capable of producing the rhythms associated to each gait. A CPG is commonly modeled as a network of identical systems of differential equations, also described as *neurons* or *cells*. We adopt the term *cells*. Golubitsky et al. [15, 16] use symmetry to infer plausible classes of CPG network architectures from observed patterns of animal gaits. Their CPG network has twice as many cells as the animal has legs. The physiological interpretation is that the motion of each leg is controlled by joints, and each joint is controlled by two muscle groups (flexors and extensors). Therefore, a locomotor CPG should be capable of independently controlling each muscle group.

In this paper, we consider two CPG models for bipeds. The first is a four-cell network proposed in [15, 16] that models leg rhythms. See Figure 1. The second is a CPG model for bipedal interlimb coordination (arms+legs) that is obtained from an eight-cell CPG network model for legs in quadrupeds, also proposed in [15, 16], by breaking symmetry between the fore and hind legs. See Figure 2 (right).

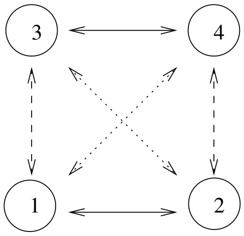
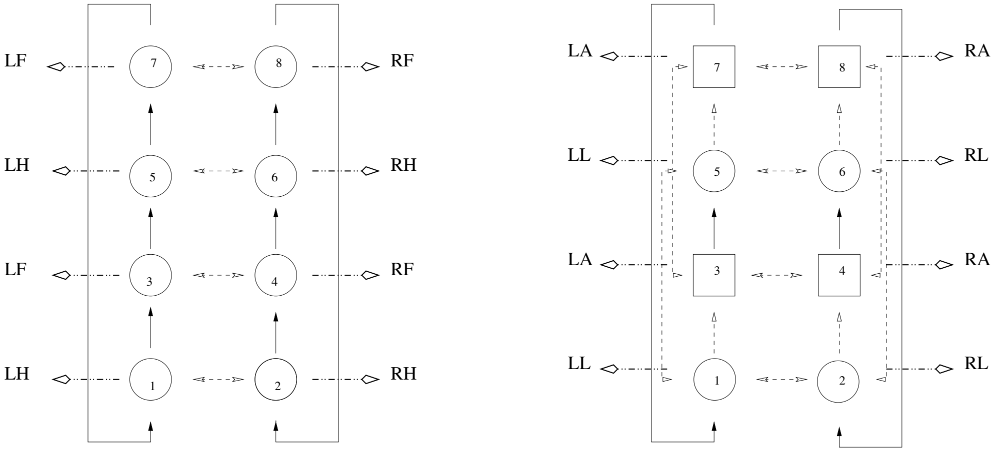


Figure 1: CPG network for bipeds controlling legs. Cells 1 and 3 send signals to the left leg, cells 2 and 4 send signals to the right leg.



CPG−Quad

CPG−Biped

Figure 2: Eight-cell CPGs. See text for explanation. Note: LF = left fore leg and LH = left hind leg in CPG-Quad and LA = left arm and LL = left leg in CPG-Biped.

In the four-cell model, the muscle groups in the left leg are controlled by cells 1 and 3 and those in the right leg by cells 2 and 4, with cells 1 and 2 controlling one type of muscle group and cells 3 and 4 the other muscle group. The four-cell model is capable of producing the rhythms of the standard bipedal gaits of *walk*, *run*, *hop*, *gallop*, and *skip*, among other gaits. Moreover, we have potentially two types of *hop*, two types of *gallop*, which we define as *gallop-walk* and *gallop-run*, and three additional symmetry types of periodic solutions not yet identified with known biped gaits.

Figure 2 shows two eight-cell CPG models. The one on the left is the CPG model for quadruped gaits (CPG-Quad) and the one on the right is the CPG model for biped interlimb coordination (CPG-Biped) obtained by breaking symmetry between fore and hind legs. It is argued in [15, 5] that the correspondence between signals from cells to limbs in CPG-Quad is the one given in Figure 2 (left). It follows that the correspondence between cells and limbs in CPG-Biped is the one given in Figure 2 (right).

CPG-Biped represents the attempt to include arm rhythms in our analysis of biped gaits. The reason for this attempt is an observed relationship between arm and leg movements in biped locomotion [11, 33, 34, 10]. We match periodic solutions of the eight-cell CPG-Biped with leg rhythms produced by the four-cell CPG model, and we compare patterns of oscillation of gaits of CPG-Biped with results in the literature concerning biped interlimb coordination. Interestingly, the biped *walk* is not found by perturbing any of the standard quadrupedal gaits in CPG-Quad and this observation is consistent with those of Schmidt [32].

There are three reasons why the assumption of symmetry in a locomotor CPG network is natural. First, there is clear evidence of bilateral symmetry in animals. Second, although the physiology of limbs may be different (say between fore and hind legs in a quadruped), these differences need not extend to the underlying CPG. Moreover, the physiological difference between pairs of limbs is negligible when considering arthropods with six or more legs. Indeed, the evolutionary history of these creatures relies on developing large numbers of more or less identical segments. Third, the role of CPGs is to send signals to limbs; so what we study are the signals sent to each limb and the phase relations between them. Exact phase relations are normal in symmetric networks and unusual in asymmetric ones. Finally, we note that the dynamics of a system that is close to symmetric often resembles that of an ideal symmetric system far more closely than it resembles the dynamics of a 'generic' asymmetric system. Thus, we consider symmetry to be a reasonable modeling assumption.

2 Central pattern generator for legs rhythms

The general system of ODEs corresponding to the four-cell CPG network in Figure 1 has the form:

$$\begin{array}{rcl} \dot{x}_1 & = & F(x_1, x_2, x_3, x_4) \\ \dot{x}_2 & = & F(x_2, x_1, x_4, x_3) \\ \dot{x}_3 & = & F(x_3, x_4, x_1, x_2) \\ \dot{x}_4 & = & F(x_4, x_3, x_2, x_1) \end{array} \tag{2.1}$$

where $x_i \in \mathbf{R}^k$ and $F : (\mathbf{R}^k)^4 \to \mathbf{R}^k$. The symmetry group of this four-cell CPG model is $\mathbf{D}_2$. It consists of the transpositions $\rho = (12)(34)$, $\tau = (13)(24)$, and $\rho\tau = (14)(23)$.

This section is divided into four parts. The classification of symmetry types of periodic solutions to equations (2.1) is given in the first part. In the second subsection we show periodic solutions for each of these symmetry types. These solutions were found using simulations with coupled Hodgkin-Huxley equations. The third subsection discusses the relationship between symmetry types and known bipedal gaits. The last subsection outlines the equivariant bifurcation theory of periodic solutions that provided the strategy for finding the different periodic solutions by numerical simulation.

2.1 Symmetries of periodic solutions in (2.1)

In this subsection we give a precise definition of spatio-temporal symmetries of time-periodic solutions and then, following [15, 16], we identify the symmetry types of periodic solutions to (2.1) with gait types. See [17, 18] for more details.

In general, let $\dot{x} = g(x)$ be a system of differential equations, where $x \in \mathbf{R}^n$. Assume g is Γ-equivariant, that is, $g(\gamma x) = \gamma g(x)$ for all $\gamma \in \Gamma$. Equivariance is equivalent to the statement that symmetries of differential equations take solutions to solutions. Suppose $x(t)$ is a periodic solution. Define

$$\begin{array}{rcl} K & = & \{\gamma \in \Gamma : \gamma x(t) = x(t)\} \\ H & = & \{\gamma \in \Gamma : \gamma\{x(t)\} = \{x(t)\}\} \end{array} \tag{2.2}$$

where H consists of symmetries that preserve the trajectory $x(t)$ setwise and K consists of symmetries that fix the trajectory pointwise. Symmetries in K are called *spatial* symmetries and symmetries in H are called *spatio-temporal* symmetries.

The uniqueness theorem for solutions of initial value problems is used to relate H symmetries to well-defined phase shifts and to justify the terminology. Let $h \in H$. Because of equivariance, $hx(t)$ is also a periodic solution of $\dot{x} = g(x)$. Uniqueness of solutions implies that there exists a phase shift $\theta \in \mathbf{S}^1$ such that $hx(t + \theta) = x(t)$. The pair $(h, \theta) \in H \times \mathbf{S}^1$ is also called a *spatio-temporal symmetry* of $x(t)$.

In order for (H, K) defined in (2.2) to correspond to symmetries of a periodic solution in a general Γ-equivariant system, some algebraic conditions must be satisfied. See [17]. However, these conditions simplify for the coupled cell system (2.1).

Theorem 2.1 ([17]) *Consider the coupled cell system (2.1) where $k \geq 2$. Let $H \supset K$ be subgroups of $\mathbf{D}_2$. Then there is a periodic solution $x(t)$ to (2.1) for some function F if and only if H/K is cyclic. Moreover, when such a periodic solution exists, F can be chosen so that $x(t)$ is asymptotically stable.*

Theorem 2.1 gives a method for classifying all possible symmetry types of periodic solutions to a given coupled cell network. This theorem does not assert that every coupled cell system has stable periodic solutions of symmetry type (H, K). In a given system, other methods, such as numerical simulation or Hopf bifurcation, must be used to verify the existence of periodic solutions with prescribed spatiotemporal symmetries.

It is a straightforward calculation to enumerate all pairs of subgroups $H \supset K$ of $\mathbf{D}_2$ that satisfy H/K is cyclic. There are ten such pairs of subgroups and they are

$$\begin{array}{cccc} (\mathbf{D}_2, \mathbf{D}_2) & (\mathbf{D}_2, \rho\tau) & (\mathbf{D}_2, \rho) & (\mathbf{D}_2, \tau) \\ (\rho\tau, \rho\tau) & (\rho\tau, \mathbf{1}) & (\rho, \rho) & (\rho, \mathbf{1}) \\ (\tau, \tau) & (\tau, \mathbf{1}) & & \end{array} \tag{2.3}$$

We call gait types *primary* when $H = \mathbf{D}_2$ and *secondary* when $H \simeq \mathbf{Z}_2$.

Let $X(t) = (x_1(t), x_2(t), x_3(t), x_4(t))$ be a periodic solution with period (normalized to) 1. Then these symmetries force the periodic solutions to have the form shown in Table 1. Note that primary gaits are ones whose signals to the legs are identical (up to phase-shift) and secondary gaits appear in conjugate pairs, where the conjugacy is given by a symmetry not in H. The conjugate pairs of *gallops* may be interpreted as a choice of lead leg. It is presently unclear how to interpret the conjugacy pairs in the other secondary gaits.

H	K	**Left leg**	**Right leg**	**Name**
$\mathbf{D}_2$	$\mathbf{D}_2$	(x_1, x_1)	(x_1, x_1)	*slow hop*
$\mathbf{D}_2$	$\rho\tau$	(x_1, x_1^S)	(x_1^S, x_1)	*walk*
$\mathbf{D}_2$	ρ	(x_1, x_1^S)	(x_1, x_1^S)	*fast hop*
$\mathbf{D}_2$	τ	(x_1, x_1)	(x_1^S, x_1^S)	*run*
$\rho\tau$	$\rho\tau$	(x_1, x_2)	(x_2, x_1)	
$\rho\tau$	$\mathbf{1}$	(x_1, x_2^S)	(x_2, x_1^S)	
ρ	ρ	(x_1, x_2)	(x_1, x_2)	
ρ	$\mathbf{1}$	(x_1, x_2)	(x_1^S, x_2^S)	*skip*
τ	τ	(x_1, x_1)	(x_2, x_2)	*gallop-run*
τ	$\mathbf{1}$	(x_1, x_1^S)	(x_2, x_2^S)	*gallop-walk*
$\mathbf{1}$	$\mathbf{1}$	(x_1, x_2)	(x_3, x_4)	

Table 1: Patterns of oscillation in the CPG for bipedal locomotion, where ^{S} indicates time shift by one-half period. The symmetry ρ swaps the signals sent to the two legs; the symmetry τ swaps the two signals sent to each leg.

2.2 Numerical simulations

The space-clamped Hodgkin-Huxley equations [20] are a system of four nonlinear ODEs that model the membrane potential of a cell v in the giant axon of a squid subjected to three ionic currents (sodium, potassium, and leakage). In our CPG model, we assume that the internal cell dynamics is the space-clamped HH equations and compute periodic solutions with the spatio-temporal symmetries given in Table 1. Numerical simulations of CPG (2.1) are done using Matlab. We plot only the first variable from the signal of each cell, $v_i(t)$, $i = 1, 2, 3, 4$.

In our simulations the coupling is linear synaptic and only membrane potentials in each cell are coupled.

The uncoupled system of ODEs is as follows:

$$\mathbf{HH} = \begin{cases} \dfrac{dv}{dt} & = \quad f(v,y) - I \\ \\ \dfrac{dy_j}{dt} & = \quad \Phi\left(\gamma_j(v) - y_j\right)\tau_j(v) \end{cases} \tag{2.4}$$

where v is the difference of electrical potential across the cell membrane, I is the intensity of an external current stimulus and $\Phi = 3^{\frac{T-6.3}{10}}$ is the temperature compensating factor. The function f is defined as

$$f(v,y) = -g_0(v - V_0) - \sum_{i=1}^{2} g_i\varphi_i(y)(v - V_i)$$

The functions $\tau_j(v)$ and $\gamma_j(v)$ are given by

$$\tau_j(v) = \alpha_j(v) + \beta_j(v)\gamma_j(v) = \frac{\alpha_j(v)}{\alpha_j(v) + \beta_j(v)}$$

Each term $g_i\varphi_i(y)(v - V_i)$ models an ionic channel that regulates the voltage along the membrane of the axon. The variables $y = (y_1, y_2, y_3)$ and the functions φ, with $\varphi_1 = y_1^3 y_3$, $\varphi_2 = y_2^4$, are considered probabilities and, when all $y_j \in [0,1]$, they assume values in the interval $[0,1]$.

The functions $\alpha(v)$ and $\beta(v)$ are defined by Hodgkin and Huxley in [20], to be:

$$\begin{array}{rclcrcl} \alpha_{y_1}(v) & = & \Psi(\frac{v+25}{10}) & \qquad & \beta_{y_1}(v) & = & 4\exp(\frac{v}{18}) \\ \\ \alpha_{y_2}(v) & = & 0.1\Psi(\frac{v+10}{10}) & & \beta_{y_2}(v) & = & \frac{1}{8}\exp(\frac{v}{80}) \\ \\ \alpha_{y_3}(v) & = & 0.07\exp(\frac{v}{20}) & & \beta_{y_3}(v) & = & (1 + \exp((v+30)/10))^{-1} \end{array}$$

where Ψ is the analytic function

$$\Psi(x) = \begin{cases} \dfrac{x}{\exp(x) - 1} & x \neq 0 \\ 1 & x = 0 \end{cases}$$

In this work we use the parameter values of [20], namely $V_0 = -10.599$, $V_1 = -115.0$, $V_2 = 12.0$, $g_0 = 0.3$, $g_1 = 120.0$, $g_2 = 36.0$.

Examples of periodic solutions with the ten different primary and secondary gait rhythms are given in Tables 2-4. The initial conditions for these examples are given in Table 5.

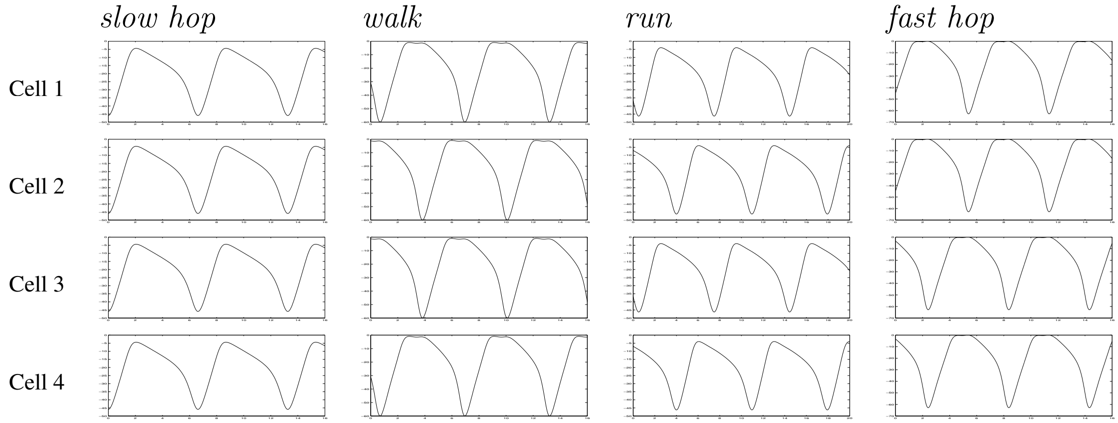


Table 2: Bipedal primary gaits.

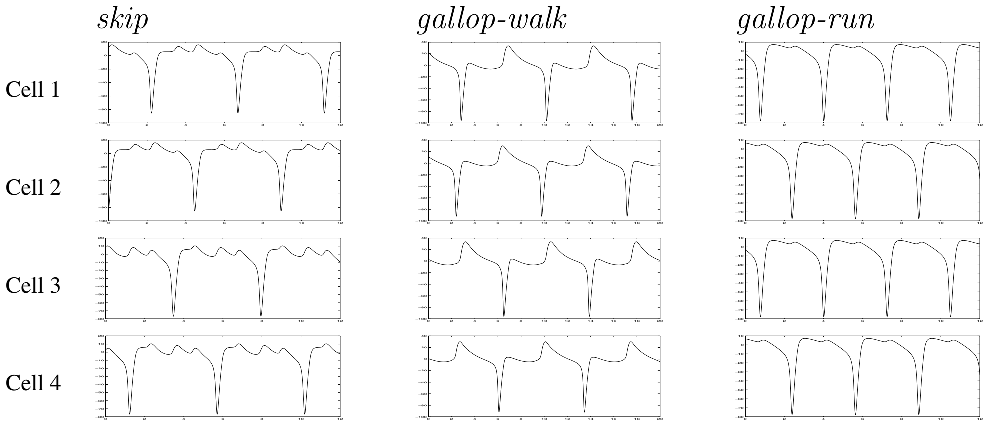


Table 3: Named bipedal secondary gaits.

2.3 Gaits: literature vs predictions by the model

In this subsection we compare bipedal gaits studied in the literature with the gait types predicted by the four-cell CPG model. *Walk*, *run*, *hop*, *skip*, and *gallop* are standard (human) bipedal gaits. The four-cell network CPG model for legs rhythms can produce the rhythms associated with *walk*, *run*, *skip*, two types of *hop*, and two types of *gallop*, in ways that we explain below. According to the four-cell network, bipedal gait types are either *primary* or *secondary*. Indeed, this model can produce four primary gait types (*walk*, *run*, *slow hop*, and *fast hop*) and six secondary gait types. Examples of secondary gaits are *skip* and *gallop*. Our discussion proceeds by category.

Primary gaits. Physiologically, *walk* and *run* share the symmetry property that swapping legs leads to a half-period phase shift in the gait cycle. Nevertheless, these are different gaits.

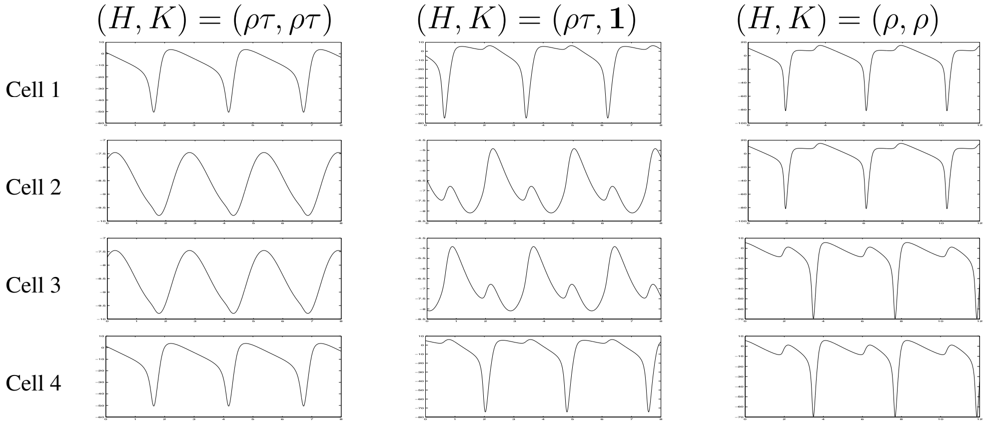


Table 4: The three unidentified bipedal secondary gaits.

Gait	Initial conditions	$T,\ I$	$k_1,\ k_2,\ k_3$
slow hop	$[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.8, 0.9, 0.9]$ $[1.0, 0.8, 0.9, 0.9]$, $[1.0, 0.1, 0.1, 0.9]$	$6.3,\ 100$	$0.4,\ 0.2,\ -0.8$
walk	$[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.8, 0.9, 0.9]$ $[1.0, 0.8, 0.9, 0.9]$, $[1.0, 0.1, 0.1, 0.9]$	$6.3,\ 100$	$1.4,\ -0.2,\ -0.8$
fast hop	$[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.1, 0.1, 0.9]$ $[1.0, 0.8, 0.9, 0.9]$, $[1.0, 0.8, 0.9, 0.9]$	$6.3,\ 100$	$0.4,\ 0.2,\ -0.8$
run	$[1.0, 0.5, 0.2, 0.8]$, $[-1.0, 0.9, 0.5, 0.1]$ $[1.0, 0.5, 0.2, 0.8]$, $[-1.0, 0.9, 0.5, 0.1]$	$6.3,\ 100$	$0.3,\ 0.2,\ -0.1$
	$[1.0, 0.5, 0.2, 0.8]$, $[-1.0, 0.9, 0.5, 0.1]$ $[-1.0, 0.9, 0.5, 0.1]$, $[1.0, 0.5, 0.2, 0.8]$	$26.0,\ 20$	$0.1,\ 0.0,\ -0.15$
	$[19.6, 0.001, 0.6, 0.3]$, $[0.8, 0.3, 0.7, 0.1]$ $[-66.4, 0.9, 0.7, 0.1]$, $[-12.6, 0.1, 0.5, 0.4]$	$26.0,\ 20$	$0.14,\ 0.6,\ 0.1$
	$[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.1, 0.1, 0.9]$ $[1.0, 0.8, 0.9, 0.9]$, $[1.0, 0.8, 0.9, 0.9]$	$26.0,\ 11$	$0.4,\ 0.2,\ -0.8$
skip	$[-13.9, 0.3, 0.6, 0.1]$, $[-20.2, 0.3, 0.6, 0.1]$ $[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.8, 0.9, 0.9]$	$26.0,\ 20$	$0.8,\ 0.6,\ 1.0$
gallop-run	$[1.0, 0.5, 0.2, 0.8]$, $[-1.0, 0.9, 0.5, 0.1]$ $[1.0, 0.5, 0.2, 0.8]$, $[-1.0, 0.9, 0.5, 0.1]$	$26.0,\ 11$	$-0.6,\ 0.5,\ -0.2$
gallop-walk	$[-0.2, 0.1, 0.7, 0.1]$, $[-54.1, 0.9, 0.7, 0.1]$ $[-17.3, 0.2, 0.6, 0.2]$, $[-4.3, 0.1, 0.6, 0.2]$	$22.0,\ 12$	$1.4,\ -0.1,\ -0.2$

Table 5: Initial conditions, temperature, intensity of external input, and coupling constants for figures in Tables 2-4.

To first order the legs move as pendula in the *walk* and in a pogo stick like motion in the *run*.

The difference between these gaits can be detected in electromyographic signals taken from the flexor and extensor muscles of the ankle joint, see Mann et al. [23, 24]. These muscle groups are coactivated in the *run* and not coactivated in the *walk*. The CPG network models the *run* by a primary periodic state in which the two signals sent to one leg are in phase and the *walk* by a state in which the two signals sent to one leg are a half-period out of phase.

The *walk-run* transition has been discussed by many authors. These authors often focus on either the energetics (for example, see Alexander [2, 1] and Minetti [29]) or the biomechanics of the two gaits (for example, see [7, 4, 5]). Diedrich et al. [8, 9] study locomotion through the time evolution of the relative phase of the segments within a limb. In their model gaits are viewed as attractors and the *walk-run* transition is seen as a transition between attractors. Transition from walking to running has also been studied in children as part of a developmental research on locomotor skills (see Whitall and Getchell [36] and Forrester et al. [12]).

Similarly, the four-cell CPG model can produce two primary gaits in which the signals corresponding to the same muscle groups in each leg are in phase; these gaits are called *slow hop* and *fast hop*. In the *fast hop* the signals sent to muscles in each leg are a half-period out of phase while in the *slow hop* they are in phase. In this sense, the *run* and the *slow hop* are *run-like* gaits, and the *walk* and the *fast hop* are *walk-like* gaits.

Secondary gaits. Just two secondary gaits *skip* and *gallop* have been well studied in the literature. By contrast, up to spatio-temporal symmetry, the four-cell model can produce six different secondary gait types.

Like *walk* and *run*, the *skip* is a gait in which interchanging the two legs leads to a half-period phase shift, see Minetti [28]. The *skip* differs from the *walk* because it has a significant flight phase, and from the *run* because it often has a double support period. The *skip* is displayed by young children; when adults perform the *skip*, a sense of high speed is perceived. In addition, the *skip* is performed by other bipeds, such as some birds [19] and lemurs [3]. The coupled four-cell model predicts only one gait that has the property that interchanging legs leads to a half-period phase shift. As noted previously, secondary gait types come in conjugate pairs. For the *skip* the conjugate is obtained by interchanging the two signals sent to the same leg. We call this pair of gait types a *skip*.

The *gallop* [31, 6, 33] is also a prevalent gait in children, readily reproduced by adults, and commonly used by Lemur for ground locomotion [21]. In the bipedal gallop there is a lead leg throughout the gait cycle, see Whitall [33]. The interlimb phasing of the gallop, measured as a portion of a limb cycle that has elapsed when the footstrike occurs on the contralateral limb, is approximately 0.66, as contrasted with 0.50 in the *walk* and *run*, see Caldwell and Whitall [6, 33]. Nevertheless the *gallop* displays aspects of both *run* and *walk*. Energetics of the lead leg closely resembles a *run*, whereas, the contrasting thrusts of the leading and trailing legs produce an anti-phase relation between the total body kinetic and potential energies similar to that of the *walk* [6]. The fact that the bipedal *gallop* has a lead leg (that is, the motions of the two legs are different), suggests that the signals to the left and right legs are different. In two of our secondary gait types, the pair of signals sent to the left leg is different from the pair sent to the right leg. For this reason we identify these periodic states with *gallops*. These *gallops* differ from each other in that the two signals sent to one leg are either in phase or a half-period out of phase. In analogy with the primary gaits we call the in phase gait a *gallop-run* and the out of phase one a *gallop-walk*. From our own observation, it seems that the *gallop-walk* is slower than the *gallop-run*. This observation is consistent with the fact that the *run* is a gait used when bipeds increase velocity, whereas the *walk* is used at lower velocities. In conjugate *gallops* the signals sent to the two legs are swapped. For this reason, we interpret the choice of lead leg in the *gallop* with conjugate solutions. Electromyographic data is needed to test the prediction that there are two types of *gallop*.

Margaria and Cavagna [25] note that *generic jumping* (our *gallop*) could be the gait of choice under low gravity conditions such as those on the moon. This observation is also made by Minetti [28] (under the name *unilateral skip*).

The four-cell CPG model predicts three other secondary gait types, see Table 1. In one of these, the pair of signals to the left leg is the same as the pair sent to the right leg. In the two remaining secondary gaits, the pair of signals sent to the left leg is the same (up to exact half-period phase shifts) as the ones sent to the right leg, but in reverse order. So far, we have not been able to associate these three secondary gait types to known bipedal gaits.

Predictions. We summarize our discussion of the relationship between the four-cell locomotor CPG model (2.1) and bipedal gaits by listing the several predictions made by this model. First, as noted previously in [16], this model predicts that there are two kinds of primary biped gaits in which the left and right legs are a half-period out of phase. These gaits were identified with *walk* and *run*. Similarly, the model also predicts two kinds of *hop* (*slow hop* and *fast hop*) and two kinds of *gallop* (*gallop-run* and *gallop-walk*). Second, this CPG model predicts that secondary gaits will appear in conjugate pairs and that there are two such gaits associated with the *skip*. Finally, the model suggests that there are three kinds of secondary gait types that have not yet been identified in biped locomotion.

2.4 Bifurcation of gaits

In Section 2.1 we used Theorem 2.1 to identify the primary and secondary gait types in the CPG model for legs rhythms. In this subsection we use bifurcation theory to explain how we found the examples of different gaits rhythms in (2.1) using coupled Hodgkin-Huxley equations. Primary gaits are obtained by bifurcation from a $\mathbf{D}_2$-invariant equilibrium, the *stand*, whereas secondary gaits are symmetry-breaking bifurcations of primary gaits.

Primary gaits. In order to study bifurcation and stability of primary gaits we need to compute the eigenvalues of the linearization L of (2.1) at an equilibrium $X = (x, x, x, x)$. The $\mathbf{D}_2$-equivariance of (2.1) implies that L commutes with $\mathbf{D}_2$ and hence simplifies the form of L.

We can decompose $(\mathbf{R}^k)^4$ into a direct sum of $\mathbf{D}_2$-irreducible subspaces. In general this decomposition is not unique, but if we use *isotypic components* that combine together all isomorphic $\mathbf{D}_2$-irreducible subspaces, we obtain a decomposition that is unique. Moreover, this decomposition is L-invariant. Let V_σ be the sum of all irreducible subspaces that are isomorphic to a representation σ of $\mathbf{D}_2$.

There are four distinct one-dimensional irreducible representations of $\mathbf{D}_2$. These representations are distinguished by their kernels and are denoted by such. See Table 6 for a list of the isotypic components. The isotypic decomposition can be used to block-diagonalize L, see Theorem 2.12 in [17]. Define the $k \times k$ matrices

$$A = \frac{\partial F}{\partial x_1}(X) \qquad B = \frac{\partial F}{\partial x_2}(X) \qquad C = \frac{\partial F}{\partial x_3}(X) \qquad D = \frac{\partial F}{\partial x_4}(X)$$

It follows from Table 6 that eigenvalues of L are the eigenvalues of the matrices

$$\begin{array}{lcl} L_{\mathbf{D}_2} & = & A+B+C+D \\ L_\tau & = & A+B-C-D \\ L_\rho & = & A-B+C-D \\ L_{\rho\tau} & = & A-B-C+D \end{array} \tag{2.5}$$

$\ker(\sigma)$	V_σ
$\mathbf{D}_2$	$\{(x,x,x,x) : x \in \mathbf{R}^k\}$
$\rho\tau$	$\{(x,-x,-x,x) : x \in \mathbf{R}^k\}$
ρ	$\{(x,-x,x,-x) : x \in \mathbf{R}^k\}$
τ	$\{(x,x,-x,-x) : x \in \mathbf{R}^k\}$

Table 6: Isotypic components of $(\mathbf{R}^k)^4$ for a CPG with $\mathbf{D}_2$ symmetry.

As $\mathbf{D}_2$ is an abelian group, generically Hopf bifurcation occurs with pairs of simple purely imaginary eigenvalues. Assuming this, we may compute Hopf bifurcation points for each matrix L_σ and stability of the corresponding periodic orbits. See Table 7 for the correspondence between periodic solutions obtained from L_σ and primary bipedal gaits. See also Example 2.2 .

Example 2.2 We consider Hodgkin-Huxley equations [20] as the internal dynamics in each cell in CPG 2.1 and give a preview of how to compute stability of primary gaits. For $i = 1, \ldots, 4$ let $x_i = (v_i, y^i)$ and define the function F in (2.1) by

$$F(x_1,x_2,x_3,x_4) = \left\{ \begin{array}{lcl} \frac{dv_1}{dt} & = & f(v_1,y^1) - I - k_1 v_3 - k_3 v_2 - k_2 v_4 \\ \\ \frac{dy_j^1}{dt} & = & \Phi\left(\gamma_j(v_1) - y_j^1\right)\tau_j(v_1) \end{array} \right. \tag{2.6}$$

L_σ	**Primary gait**
$L_{\mathbf{D}_2}$	*slow hop*
L_τ	*run*
L_ρ	*fast hop*
$L_{\rho\tau}$	*walk*

Table 7: Primary gaits

Let H be the matrix of the linearization of the uncoupled Hodgkin-Huxley equations and let

$$J = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}$$

Matrices (2.5) can be written in the following form

$$\begin{aligned} L_{\mathbf{D}_2} &= H - (k_3 + k_1 + k_2)J \\ L_\tau &= H - (k_3 - k_1 - k_2)J \\ L_\rho &= H - (-k_3 + k_1 - k_2)J \\ L_{\rho\tau} &= H - (-k_3 - k_1 + k_2)J \end{aligned} \tag{2.7}$$

where $A = H$, $B = -k_3 J$, $C = -k_1 J$ and $D = -k_2 J$.

The eigenvalues of $H - (k_i + k_j + k_l)$, $i \neq j \neq l$ have been computed in [22] for different values of I. This computation was used to obtain bifurcation to the four primary gaits. For instance, the *slow hop* appears when $k = k_1 + k_2 + k_3$ crosses a bifurcation value, whereas bifurcation into the *fast hop* is controlled by $k = k_1 - k_2 - k_3$.

Secondary gaits. In principle, smooth transitions in gaits can be associated with symmetry-breaking bifurcations from one stable periodic solution to another. In fact, in (2.1) secondary gaits are symmetry-breaking bifurcations of primary gaits. The four-cell CPG model produces the gait transitions shown in Table 8. For example, *gallop-walk* bifurcates from either *walk* or *fast hop*, and *skip* from either *walk* or *run*. We use properties of the Poincaré map to find symmetry-breaking bifurcations of the group $\mathbf{D}_2$. The list of possible symmetry-breaking bifurcations from primary gaits is found in Table 8. Note that *slow hop* has only spatial symmetries.

By Theorem 1 [4], each bifurcation listed in Table 8 can occur if the cell dynamics and coupling architecture are general enough. In particular, all secondary gaits may be obtained by symmetry-breaking bifurcation from primary gaits. In our numerical simulations we have found the secondary gait types by following primary gait branches until they lose stability at a symmetry-breaking bifurcation. We have shown that (2.1) with Hodgkin-Huxley equations as internal dynamics and linear coupling of the cells through the voltage variables provides a sufficiently general model to exhibit stable periodic solutions corresponding to all primary and secondary gaits.

K	**Primary Gait**	**Secondary Gait**	(H,K)
$\rho\tau$	*walk*	*gallop-walk*	$(\tau,\mathbf{1})$
		skip	$(\rho,\mathbf{1})$
τ	*run*	*skip*	$(\rho,\mathbf{1})$
			$(\rho\tau,\mathbf{1})$
ρ	*fast hop*	*gallop-walk*	$(\tau,\mathbf{1})$
			$(\rho\tau,\mathbf{1})$
$\mathbf{D}_2$	*slow hop*		(ρ,ρ)
		gallop-run	(τ,τ)
			$(\rho\tau,\rho\tau)$

Table 8: Possible bifurcations from primary to secondary bipedal gaits.

3 Central pattern generator for interlimb coordination

Relationships between arm and leg movements have been observed in bipeds [11, 33, 34, 10]; for this reason we attempt to include arm rhythms in a model CPG network for bipeds. CPG-Biped, our CPG model for biped interlimb coordination (arms+legs) pictured in Figure 2, is derived by breaking symmetry between fore and hind legs in CPG-Quad, the eight-cell quadruped locomotor CPG model studied in [15, 16, 5, 4].

The general system of ODEs associated to CPG-Biped has the form

$$\begin{array}{rcl}
\dot{x}_1 &=& F_1(x_1,x_2,x_7,x_5)\\
\dot{x}_2 &=& F_1(x_2,x_1,x_8,x_6)\\
\dot{x}_3 &=& F_2(x_3,x_4,x_1,x_7)\\
\dot{x}_4 &=& F_2(x_4,x_3,x_2,x_8)\\
\dot{x}_5 &=& F_1(x_5,x_6,x_3,x_1)\\
\dot{x}_6 &=& F_1(x_6,x_5,x_4,x_2)\\
\dot{x}_7 &=& F_2(x_7,x_8,x_5,x_3)\\
\dot{x}_8 &=& F_2(x_8,x_7,x_6,x_4)
\end{array} \qquad (3.1)$$

where $F_i : (\mathbf{R}^k)^4 \to \mathbf{R}^k$, $i = 1,2$. To derive this model we reason that quadrupeds have four limbs striking the ground during locomotion so the similarity between arms and legs is strong, whereas bipeds have only two limbs (the legs) striking the ground; so the similarity between legs and arms is less strong. Hence, we model the rhythms of the lower limbs (legs) by one function F_1 and the rhythms of the upper limbs (arms) by another function F_2.

CPG-Biped (3.1) is a perturbation of CPG-Quad, so we assume that $F_1 \approx F_2$. Since CPG-Biped is a symmetry-breaking perturbation of CPG-Quad, we must discuss how the symmetries of CPG-Biped are related to the symmetries of CPG-Quad. Observe that CPG-Quad has symmetry group $\Gamma_Q = \mathbf{Z}_4(w) \times \mathbf{Z}_2(\kappa)$, where w cyclicly permutes the four cells in both the left and right rings and κ interchanges cells on the left with cells on the right.

More precisely,

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

Note that CPG-Biped has symmetry group $\Gamma_B = \mathbf{D}_2(\kappa, w^2)$, where

$$w^2 = (1\ 5)(3\ 7)(2\ 6)(4\ 8)$$

permutes the muscle groups within a limb. Thus, the eight-cell network CPG-Biped has the same symmetry group as the four-cell network described in Section 2. This observation coupled with the assumption that $F_1 \approx F_2$ will enable us to speculate on how standard quadrupedal gait rhythms have evolved into bipedal gait rhythms. There is one surprise — when one takes into account the rhythms of both arms and legs, it appears that the bipedal walk cannot be obtained by a small perturbation of any of the standard quadrupedal gaits. This remark is consistent with Schmidt [32] who argues that bipedalism involves complex transitions originating with a compliant form of quadrupedalism.

In this section we will explore the relationships between gaits produced by the three different locomotor CPGs under discussion. In Subsection 3.1, we relate periodic solutions associated to standard rhythms of CPG-Quad with periodic solutions of CPG-Biped. We also interpret patterns of oscillation of gaits in the CPG-Biped model in terms of biped interlimb coordination. In Subsection 3.2 we explain why CPG-Biped is a plausible model for understanding human interlimb coordination. Finally, in Subsection 3.3 we show numerical simulations of CPG-Biped using Hodgkin-Huxley equations as internal cell dynamics.

3.1 Periodic solutions in CPG-Quad and CPG-Biped

CPG-Biped was introduced as a forced symmetry-breaking of CPG-Quad. We now show how the rhythms of periodic solutions, corresponding to standard quadruped gaits, in CPG-Quad perturb to standard bipedal leg rhythms (except the *skip*).

The basic idea is straightforward. Suppose that $X(t)$ is a hyperbolic periodic solution to CPG-Quad corresponding to a gait with spatio-temporal symmetries H and spatial symmetries K, where $K \subset H \subset \Gamma_Q$ are an admissible pair of subgroups. See Subsection 2.1. Suppose that we consider a small forced symmetry-breaking of the equations so that $F_1 \approx F_2$. Hyperbolicity implies that $X(t)$ perturbs to a periodic solution of CPG-Biped whose symmetry groups are $H' = H \cap \Gamma_B$ and $K' = K \cap \Gamma_B$. These points are verified as follows. Uniqueness of the perturbed periodic solution implies that all symmetries in $K \cap \Gamma_B$ fix the perturbed trajectory pointwise since the perturbed equations have Γ_B-equivariance. So $K \cap \Gamma_B \subset K'$. Conversely, any symmetry in $K' \subset \Gamma_B$ must be in K again by the uniqueness of hyperbolic periodic solutions in a small neighborhood. An analogous argument is valid for H'. So, the unperturbed periodic solutions with symmetry groups in Γ_Q and those solutions are perturbed to ones with symmetry groups in Γ_B.

In Table 9 we list the spatio-temporal symmetry types of standard quadrupedal gaits in CPG-Quad computed in [15]. Then, we perturb periodic solutions of quadrupeds to have symmetry groups in Γ_B and match the perturbed solutions with leg rhythms in bipeds, see Table 9. Note that all of the spatio-temporal symmetry groups of standard biped gait leg rhythms (except the *skip*) can be obtained as symmetry groups of perturbed symmetric solutions of CPG-Quad. In addition, every symmetry type of periodic solution (corresponding to the standard biped gaits, except the *skip*) in the four-cell biped model analyzed in Section 2.1 can be identified with a symmetry type corresponding to a gait in the CPG-Biped.

Quadrupeds — CPG-Quad			**Bipeds — CPG-Biped**		
Name	H	K	**Name**	$H' = H \cap \Gamma_B$	$K' = K \cap \Gamma_B$
pronk	Γ_Q	Γ_Q	*slow hop*	Γ_B	Γ_B
pace	Γ_Q	$\mathbf{Z}_4(w)$	*run*	Γ_B	$\mathbf{Z}_2(w^2)$
bound	Γ_Q	Γ_B	*slow hop*	Γ_B	Γ_B
trot	Γ_Q	$\mathbf{Z}_4(\kappa w^2)$	*run*	Γ_B	$\mathbf{Z}_2(w^2)$
jump	Γ_Q	$\mathbf{Z}_2(\kappa)$	*fast hop*	Γ_B	$\mathbf{Z}_2(\kappa)$
walk	Γ_Q	$\mathbf{Z}_2(\kappa w^2)$	*walk*	Γ_B	$\mathbf{Z}_2(\kappa w^2)$
rotary gallop	$\mathbf{Z}_4(\kappa w)$	$\mathbf{Z}_2(w^2)$	*gallop-run*	$\mathbf{Z}_2(w^2)$	$\mathbf{Z}_2(w^2)$
transverse gallop	$\mathbf{Z}_4(w)$	$\mathbf{Z}_2(w^2)$	*gallop-run*	$\mathbf{Z}_2(w^2)$	$\mathbf{Z}_2(w^2)$

Table 9: Symmetry groups of standard gaits of the eight-cell CPGs. Symmetry pairs (H, K) of standard quadrupeds gaits (CPG-Quad) and symmetry pairs (H', K') of bipeds gaits (CPG-Biped). The identification of bipedal gaits can be found in Section 2.1.

In Table 10 we show patterns of oscillation of gaits of the CPG-Biped model and compare our results with biped interlimb coordination results in the literature. In this derivation we use the perturbation assumption $F_1 \approx F_2$.

We begin with the *slow hop*. Observe there are two types of *slow hop* that appear from perturbed quadruped gaits: one from the pronk and the other from the bound. These two *slow hops* have the same symmetry type but differ in the rhythm patterns of the arms. The *slow hop* obtained from perturbing the pronk has limbs on each side *almost* in-phase, whereas the *slow hop* perturbed from the bound has each diagonal pair of limbs (for example, the left arm and right leg) *almost* in-phase. The human *slow hop* appears to be the perturbed pronk; see Figure 7 in [26].

Similarly there are two types of *run*. One is a perturbation of pace, which we call *in-phase march*, and the other is a perturbation from trot, which we call a *usual run*. These two *run*s differ again in the rhythms of the arms. In the *in-phase run* left (respectively right) limbs are *almost* in-phase while in the *usual run* diagonal limbs are *almost* in-phase. The human *run* appears to be the perturbed trot; see Figure 1 in [33].

The leg rhythm of a *fast hop* is a perturbed jump since both arms and legs are in-phase. However, there is an *approximate* quarter-period phase shift between corresponding muscle groups in ipsilateral arms and legs. This is not a usual phase-shift in humans, see Section 2.

The most surprisingly conclusion from CPG-Biped concerns the walk. Table 10 shows that the *leg rhythm* of the *walk* is a small perturbation from the quadrupedal walk. However,

Leg/Arm Rhythms of Gaits of CPG-Biped						
Quad Name	**Biped Name**	**Legs**		**Arms**		**Signals**
		Left	**Right**	**Left**	**Right**	
pronk bound	*slow hop*	(x_1, x_1)	(x_1, x_1)	(x_3, x_3)	(x_3, x_3)	$x_3 \approx x_1$ $x_3 \approx x_1^S$
pace	*in-phase march*	(x_1, x_1)	(x_1^S, x_1^S)	(x_3, x_3)	(x_3^S, x_3^S)	$x_3 \approx x_1$
trot	*usual run*	(x_1, x_1)	(x_1^S, x_1^S)	(x_3, x_3)	(x_3^S, x_3^S)	$x_3 \approx x_1^S$
jump	*fast hop*	(x_1, x_1^S)	(x_1, x_1^S)	(x_3, x_3^S)	(x_3, x_3^S)	$x_3 \approx x_1^{SS}$
walk	*walk*	(x_1, x_1^S)	(x_1^S, x_1)	(x_3, x_3^S)	(x_3^S, x_3)	$x_3 \approx x_1^{SS}$
rotary gallop	*gallop-run*	(x_1, x_1)	(x_2, x_2)	(x_3, x_3)	(x_4, x_4)	$x_3 \approx x_2^S$ $x_4 \approx x_1^S$
transverse gallop	*gallop-run*	(x_1, x_1)	(x_2, x_2)	(x_3, x_3)	(x_4, x_4)	$x_3 \approx x_1^S$ $x_4 \approx x_2^S$

Table 10: Patterns of oscillation for bipedal locomotion using both legs and arms where ^{S} indicates a time shift by one-half period and ^{SS} indicates a time shift of a quarter period.

in this case too, there is an *approximate* quarter-period phase shift between corresponding muscle groups in ipsilateral arms and legs. Like the *fast hop*, the quarter-period phase-shift is not usual in an adult *walk*. Indeed, none of the standard quadruped gaits (in CPG-Quad) evolve by small perturbations into a bipedal *walk*.

Finally, both rotary and transverse gallops perturb to a *gallop-run*. However, these perturbed gaits do differ in the arm rhythms. In the perturbed rotary gallop diagonal limbs (for example, left arm and right leg) are *approximately* one half-period out of phase. In the perturbed transverse gallop there is an *approximate* half-period phase shift between ipsilateral limbs. Whitall et al. [34] (Figure 2) suggest that the *gallop-run* is the perturbed transverse gallop, though they emphasize that for the *gallop* there is variability in the way subjects move their arms. That variability may be due to the lack of mechanical constraints on the arms as compared with the legs (which are in touch with the ground).

Whitall et al. analyzed data taken from subjects galloping by focusing on kinematic variables. We mention briefly their results on the temporal phasing relationships between feet and between arms. They found that the left foot hit the ground approximately two-thirds of the gait cycle after the right foot hit the ground. By contrast, the arm relationship was inconsistent. Many subjects performed an approximately symmetric pattern where the left arm reversal occurred approximately halfway through the gait cycle after the right arm reversal, whereas other subjects showed a definite asymmetric pattern similar to their feet phasing (see Muzzi et al. [30] for additional information).

Our CPG-Biped model predicts that a perturbed transverse gallop has an asymmetric arm pattern, since signals sent to ipsilateral limbs are almost a half period out-of-phase and signals sent to contralateral limbs are different.

The symmetric arm pattern is not a small perturbation of any standard quadruped gait. Subjects often choose this arm pattern because it is familiar to them in common gaits like *walk*, *run*, and *hop*. This choice involves cognition and may, from an evolutionary point of view, require a more complex set of transitions from a quadruped gait. Our CPG-Biped model suggests that bipeds first performed a gallop with asymmetric arm phasing.

3.2 CPG-Biped network: Is it plausible?

In this subsection we discuss results in the literature concerning biped interlimb coordination and evolution of human bipedalism, to explain why we believe that the CPG-Biped is a plausible network model for understanding human interlimb coordination.

From Subsection 3.1 we saw that there are three standard biped gaits that can be obtained by small perturbations from quadruped gaits; they are *slow hop* (perturbed pronk), *run* (perturbed trot), and *gallop-run* (perturbed transverse gallop). The two standard biped gaits, *fast hop* and *walk*, cannot be obtained by small perturbations of quadruped gaits because of the unusual quarter-period phase-shift. So, from the point of view of small perturbations, our CPG-Biped model seems inadequate to explain human interlimb coordination.

From an evolutionary point of view we ask: Could the two gaits of *walk* and *fast hop* have evolved from quadruped gaits using a sequence of perturbations? We try to give a possible answer of this question, using the perturbed quadruped walk as an example. When children learn to walk, they usually begin with the *crawl*. Crawling has been studied by many people. From a neuromuscular maturation point of view, Gesell [13] studies 22 stages of developmental crawling and McGraw [27] describes seven primary stages in the development of walking. From a dynamical systems point of view, Whitall *et al.* [35] study interlimb coordination patterns of human quadrupedal crawling. One of their main conclusions is that, when crawling forward on a treadmill, human adults adopt a lateral sequence of limb touchdowns: left foot, left hand, right foot, right hand. The relative phasing between ipsilateral limbs is $\simeq$ 20-30%. It seems the *approximate* quarter period phase shift (for the same muscle group) between left limbs (respectively, right limbs) is well accepted if a perturbed quadruped walk is a *crawl* and not a *walk*. So, a small perturbation of the quadruped walk occurs in an early developmental stage of the biped walk. In any case, CPG-Biped suggests that transition from the quadruped walk to *walk* is more complex than a small perturbation might suggest and this conclusion is in agreement with Schmidt [32]. Indeed, experimental data on humans and nonhuman primates suggest that the evolution of bipedalism is a complicated process that cannot involve a simple transition between quadrupeds and bipeds.

There is another point concerning *slow hop*, *run*, and *gallop-run* that we believe may be relevant to evolution theory. Table 10 shows that the perturbed bound (*slow hop*), the perturbed pace (*run*), and the perturbed rotary gallop (*gallop-run*) are not usual biped gaits. This fact may be due to the mechanical stability of these gaits in bipeds. It seems to us that a person performing any of these three gaits must work hard to keep his or her balance. This point could be worth studying.

3.3 Numerical results for CPG-Biped

Numerical simulations are done using the space-clamped Hodgkin-Huxley equations to model cells internal dynamics [20]. The coupling is linearly diffusive. The dynamics of the bipedal network for interlimb coordination is given by:

$$\begin{aligned} \dot{v}_i &= f(v_i, y^i) - I - k_3(v_i - v_{i+\epsilon_i}) - k_4(v_i - v_{i+4}) - K \\ \dot{y}^i_j &= \Phi\left(\gamma_j(v_i) - y^i_j\right)\tau_j(v_i) \end{aligned} \tag{3.2}$$

where $i = 1, \ldots, 8$, $j = 1, 2, 3$, addition of indices i is taken modulo 8, $\epsilon_i = (-1)^{i+1}$, $y_i = y(v_i)$, and

$$K = \begin{cases} k_1(v_i - v_{i-2}) & i = 3, 4, 7, 8 \\ k_2(v_i - v_{i+6}) & i = 1, 2, 5, 6 \end{cases}$$

In the figures, we only plot the membrane potential from the signal of each cell. See Figure 2 for the correspondence between signals and limbs.

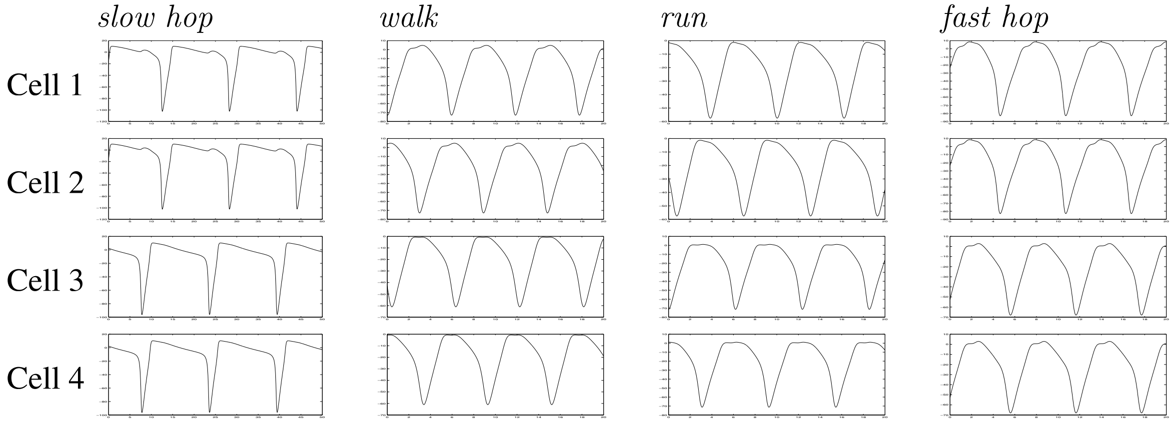


Table 11: Primary gaits of CPG-Biped (interlimb coordination).

4 Conclusions

We study two CPG models for biped locomotion. We use results by Golubitsky et al. [15, 16] to infer plausible classes of CPG architectures from the observed phase relationships of bipedal gaits. Symmetry is shown to perform a major role in this study of gaits.

We begin by studying a CPG model for legs rhythms. We use symmetry to classify the rhythms of periodic solutions that can be produced in this model and associate these rhythms with the *standard* bipedal gaits of *walk*, *run*, *hop*, *gallop*, and *skip*, and other gaits. We observe that there are potentially two types of *hop* and two types of *gallop*, one *skip* and three additional as yet unidentified symmetry types. We also observe that the secondary

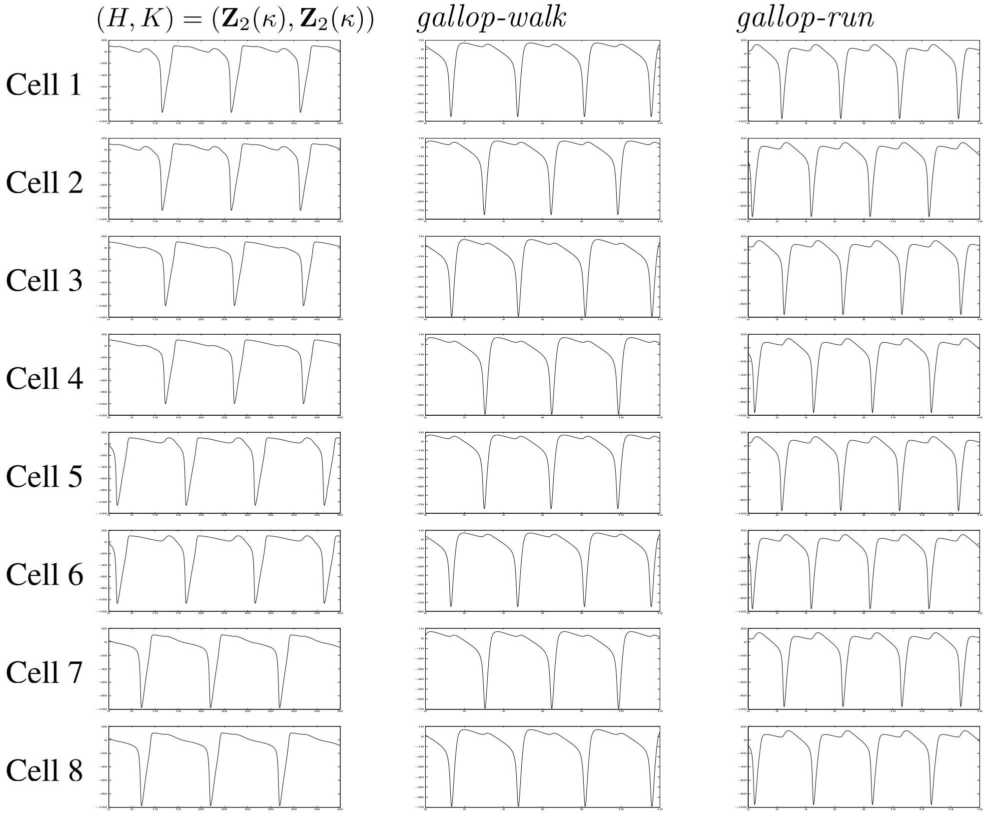


Table 12: Secondary gaits of CPG-Biped (interlimb coordination).

gaits appear in conjugate pairs, but we do not yet understand how this observation applies to the *skip*.

Our second (eight-cell) CPG model represents an attempt to include arm movements in bipedal locomotion. This model is obtained from a model for quadrupedal locomotion by breaking symmetry between the fore and hind legs. We discuss how standard bipedal gaits (except the *skip*) may be obtained by forced symmetry-breaking perturbations of standard quadrupedal gaits. Our results seem to be in accord with the literature on interlimb coordination and on evolution of human bipedalism. However, we emphasize that more study is needed to compare bipedal gaits to the periodic solutions produced by our theoretical model.

All numerical simulations have been done using Hodgkin-Huxley equations to model cell dynamics. We verify that the different types of periodic solutions do actually occur in these models.

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Gait	Initial conditions	$T,\ I$	$k_1,\ k_2,\ k_3,\ k_4$
slow hop	$[-13.9, 0.3, 0.6, 0.1]$, $[-20.2, 0.3, 0.6, 0.1]$ $[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.8, 0.9, 0.9]$ $[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.1, 0.1, 0.9]$ $[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.1, 0.1, 0.9]$	$6.3,\ 8.0$	$-0.1,\ -0.01$ $0.5,\ 3.5$
fast hop	$[8.57, 0.02, 0.63, 0.16]$, $[8.57, 0.02, 0.63, 0.16]$ $[0.57, 0.08, 0.67, 0.09]$, $[0.57, 0.08, 0.67, 0.09]$ $[-77.01, 0.96, 0.69, 0.12]$, $[-77.01, 0.96, 0.69, 0.12]$ $[-27.17, 0.34, 0.57, 0.18]$, $[-27.17, 0.34, 0.57, 0.18]$	$6.3,\ 100$	$-0.5,\ -0.15$ $3.5,\ -0.8$
walk	$[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.8, 0.9, 0.9]$ $[1.0, 0.8, 0.9, 0.9]$, $[1.0, 0.1, 0.1, 0.9]$ $[1.0, 0.5, 0.2, 0.8]$, $[-1.0, 0.9, 0.5, 0.1]$ $[-1.0, 0.9, 0.5, 0.1]$, $[1.0, 0.5, 0.2, 0.8]$	$6.3,\ 100$	$-0.5,\ 0.6$ $-0.8,\ 0.3$
run	$[1.0, 0.5, 0.2, 0.8]$, $[-1.0, 0.9, 0.5, 0.1]$ $[1.0, 0.5, 0.2, 0.8]$, $[-1.0, 0.9, 0.5, 0.1]$ $[-13.9, 0.3, 0.6, 0.1]$, $[-20.2, 0.3, 0.6, 0.1]$ $[-13.9, 0.3, 0.6, 0.1]$, $[-20.2, 0.3, 0.6, 0.1]$	$6.3,\ 100$	$-0.05,\ -0.5$ $-0.4,\ 1.0$
	$[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.1, 0.1, 0.9]$ $[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.1, 0.1, 0.9]$ $[1.0, 0.5, 0.2, 0.8]$, $[1.0, 0.5, 0.2, 0.8]$ $[1.0, 0.5, 0.2, 0.8]$, $[1.0, 0.5, 0.2, 0.8]$	$6.3,\ 8.0$	$-0.15,\ -0.01$ $2.0,\ -0.05$
gallop-walk	$[1.0, 0.5, 0.2, 0.8]$, $[-1.0, 0.9, 0.5, 0.1]$ $[1.0, 0.5, 0.2, 0.8]$, $[-1.0, 0.9, 0.5, 0.1]$ $[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.1, 0.1, 0.9]$ $[1.0, 0.8, 0.9, 0.9]$,$[1.0, 0.8, 0.9, 0.9]$	$26.0,\ 10.5$	$-0.1,\ 0.15$ $-0.1,\ -0.18$
gallop-run	$[1.0, 0.5, 0.2, 0.8]$, $[-1.0, 0.9, 0.5, 0.1]$ $[1.0, 0.5, 0.2, 0.8]$, $[-1.0, 0.9, 0.5, 0.1]$ $[1.0, 0.1, 0.1, 0.9]$, $[1.0, 0.8, 0.9, 0.9]$ $[1.0, 0.1, 0.1, 0.9]$,$[1.0, 0.8, 0.9, 0.9]$	$22.0,\ 12$	$-0.2,\ -0.15$ $-0.5,\ 0.6$

Table 13: Initial conditions, temperature, intensity of external input, coupling constants of Figures in Tables 11-12.

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