

# Gait transition in a central pattern generator for bipeds<sup>★</sup>

A.P. Santos<sup>\*</sup> C.M.A. Pinto<sup>\*\*</sup>

<sup>\*</sup> Faculty of Sciences, Department of Mathematics  
University of Porto, Rua do Campo Alegre 687  
4169-007 Porto, PORTUGAL  
(email: xana\_psantos@hotmail.com)

<sup>\*\*</sup> Center of Mathematics of the University of Porto  
and Instituto Superior de Engenharia do Porto  
Rua Dr António Bernardino de Almeida, 431  
4200-072 Porto, PORTUGAL  
(email: cpinto@fc.up.pt)

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**Abstract**In this paper we study gait transition in a central pattern generator (CPG) model for bipedal locomotion. This model is proposed by Golubitsky, Stewart, Buono and Collins (14; 15) and is studied further by Pinto and Golubitsky (28). It is a network of four coupled identical cells, with  $D_2$  symmetry. Each cell is modeled by a system of ordinary differential equations.

We briefly review the work done in (28). We revisit the symmetry arguments that allow us to enumerate the periodic solutions predicted by the CPG model, identified with primary and secondary gait types. Using bifurcation theory, we list the bifurcations between these two types of gaits.

We compute gait transition in the 4-cell CPG model for bipeds. We use the Morris-Lecar equations (26; 34) as the internal dynamics for each cell. We consider two types of coupling between the cells: diffusive and synaptic. We obtain the secondary gait *skip* by bifurcation of the primary gaits *walk* and *run*. The secondary gait *gallop* is obtained by bifurcation of the primary gait *walk*.

**Keywords:** Gait transition, Central Pattern Generator, Bifurcation Theory, Symmetry.

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## 1. INTRODUCTION

Animal locomotion is an interesting research issue for scientists in distinct areas of science. Every animal has its own form of locomotion, however, there are symmetries in the locomotor patterns that are common in different species. For example, the *pronk* of quadrupeds is “symmetrically” identical to the *two-legged hop* of bipeds, in the sense that in both quadrupeds and bipeds, all legs perform the same movement at the same time.

Locomotion is a complex mechanism, involving the neural bases that are behind animal locomotion.

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In vertebrates goal-directed locomotion involves the central pattern generators, the brainstem command systems for locomotion, the control systems for steering and control of body orientation, and the neural structures responsible for the selection of motor primitives. In this paper, we focus in the neural networks that send signals to the muscle groups in each joint, the so-called CPGs. We give numerical evidence of gait transition in a CPG model for legs rhythms in bipeds, supporting analytical results.

We note that there are still controversial issues concerning the existence of locomotor CPGs in mammals. Despite this, we assume here their existence, based on the work of many authors (5; 8; 9).

CPGs are located somewhere in the nervous system (6; 7; 14; 15; 17; 18). Mathematically, CPGs are modeled by networks of systems of ordinary differential

equations (ODE's), where each system models one neuron (or collections of neurons) and it is assumed that all neurons (or cells) are identical. Identical cells are defined as cells which are modeled by the same system of ODE's. CPG models are capable of producing the locomotor rhythms of animals, such as walking, jumping, running, galloping, among others.

Investigators in many areas have been interested in animal locomotion (2; 3; 4; 14; 15; 19; 20; 21; 28). Calabrese and Marder (4) discuss the generation of rhythmic movements by central pattern-generating networks in both invertebrates and vertebrates nervous systems using cellular, circuit and computational analyses. Kopell and Ermentrout (19; 20; 21) show that networks of coupled oscillators with a given symmetry, can be used to model the locomotor patterns of animals, in particular the lamprey. Golubitsky, Stewart, Buono and Collins (14; 15) propose a CPG model for locomotion patterns of animals with  $2n$  legs (see Figure 1). This model is based on the assumption that each leg receives signals from two cells. This is an analogy with what happens in animals joints, where two muscles groups, flexors and extensors, control most movements.

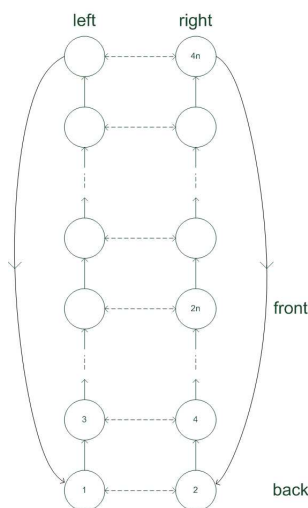


Figure 1. CPG model for the locomotor patterns of animals with  $2n$  legs (14).

Golubitsky *et al* (14; 15) propose a CPG model for the locomotor rhythms of bipeds legs (see Figure 2). This model is studied further by Pinto and Golubitsky in (28). Pinto *et al* (28) identify four primary gaits: *two-legged hop*, *two-legged jump*, *walk* and *run* and four secondary gaits: *asymmetric hop*, *skip*, *one-legged hop* and *gallop*. Later, another secondary gait, the *hesitation-walk*, is identified [Personal communication of Pinto in January 2009]. Primary and secondary gait types are distinguished by the signals

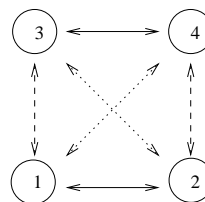


Figure 2. 4-cell CPG model for the rhythms of bipedal locomotion (28). Cells 1 and 3 send signals to two muscle groups in the left leg and cells 2 and 4 send signals to the homologous muscle groups in the right leg.

sent to the muscle groups. In primary gaits the muscle groups receive the same signal, whereas in secondary gaits there are two signals sent to the muscle groups. Buono and Golubitsky study the model for quadruped locomotor patterns (2; 3). In this model, Buono and Golubitsky identify six primary gaits: *pronk*, *pace*, *bound*, *trot*, *walk* and *jump*, and twelve secondary gaits: *loping pace*, *running walk*, *rotary gallop*, *loping trot*, *transverse gallop*, *canter*, *tertiary gait*, *loping bound*, *rotary canter*, *double bound*, *double canter* and *double loping bound*. Pinto and Golubitsky (28) also study a CPG model for arm/leg coordination in bipeds. Their model is derived from the CPG model for quadrupeds, by breaking the symmetry between front and hind legs. This translates the morphological and functional differences between arms and legs in bipeds. These authors identify the patterns exhibited by legs and arms in biped gaits of *two-legged hop*, *run* and *gallop* as symmetry-breaking bifurcations of the quadrupeds gaits *pronk*, *trot* and *transverse jump*, respectively.

In Robotics, CPG models are used to control robots' movements (1; 22; 23; 31; 32; 33; 36). CPGs are capable of independently produce rhythmic patterns which makes them extraordinarily important in this area. Other interesting properties of these CPG models are robustness against small perturbations, limit cycle behaviour and smooth online modulation of trajectories, by changes in parameter values of the equations (24; 25; 30). Righetti and Ijspeert (32) present a programmable CPG used to generate periodic trajectories and apply it in the control of bipedal locomotion of a simulated Hoap-2 robot.

The study of CPG models in Robotics has contributed for significant advances in Physical Medicine and Rehabilitation. Nandi *et al* (27) developed an Adaptive Module Active Leg (AMAL), which consists on an active prosthetic leg with initial gait patterns. The AMAL is capable of adaptation, which means that it changes the patterns recorded, adapting them to the amputee patterns. Studies in this way

can be useful to make the prosthetics more efficient and less expensive than the actual.

In this paper we compute gait transition occurring in the 4-cell CPG model in Figure 2. We consider as the internal cells' dynamics the Morris-Lecar equations (26; 34). We assume two types of coupling between the cells: diffusive and synaptic. We find that the secondary gait *skip* is obtained numerically by bifurcation of the primary gaits *walk* and *run*, and the secondary gait *gallop* is obtained by bifurcation of the primary gait *walk*. This is in accordance with analytical results.

### 1.1 Framework of the paper

In Section 2 we briefly review the work done by Pinto and Golubitsky (28). We revisit the symmetry arguments that allow us to enumerate the periodic solutions predicted by the CPG model, identified with primary and secondary gait types. Using bifurcation theory, we list the bifurcations between these two types of gaits. In Section 3 we present the numerical simulations showing gait transitions. We consider the dimensionless Morris-Lecar equations (26; 34) as cell dynamics and we assume both diffuse and synaptic couplings. In Section 4 we state the conclusions.

## 2. THE 4-CELL CPG MODEL

In this section we review the 4-cell CPG model for biped rhythms in Figure 2. In Subsection 2.1 we give a brief introduction on coupled cell networks theory. In Subsection 2.2 we present the general class of ordinary differential equations (ODE's) associated with the 4-cell CPG model. In Subsection 2.3 we discuss the symmetries of the model. In Subsection 2.4 we list the bipedal gaits predicted by the 4-cell CPG model. The  $H/K$  theorem (12) is used to enumerate all pairs of spatial-temporal and spatial symmetries of each periodic solution predicted by the coupled cells system (2.1). These periodic solutions are then identified with bipedal gaits. In Subsection 2.5 we review arguments from bifurcation theory that enable us to compute the bifurcations of the primary gaits to secondary gaits.

### 2.1 Coupled cells networks

Recently, a new framework for the theory of coupled cell networks has been developed. See Stewart, Golubitsky and Pivato (11; 35), Golubitsky, Nicol and Stewart (10) and Golubitsky, Stewart and Török (16). For a survey, overview and examples, see Golubitsky and Stewart (13). Here, we use a simplified version of the 'multiarrow formalism' of

Golubitsky, Stewart and Török (16), the 'single arrow formalism'.

A network of  $n$ -coupled cells is represented by a graph whose nodes are identified with cells (or dynamical systems) and whose arrows represent the coupling between cells. Different nodes indicate distinct internal dynamics and different arrows represent different couplings between the cells.

Consider a  $n$ -coupled cell network with a finite number of cells  $C = \{c_1, \dots, c_n\}$  and a finite number of arrows. Each cell  $c_j$  has an internal phase space, which will be denoted by  $P_j$ . Cells represented by the same nodes have identical internal phase space. We consider the total phase space of the network to be the direct product of internal phase spaces of each cell,  $P = \prod_{i=1}^n P_i$ . On  $P_j$  we denote the coordinates by  $x_j$  and on  $P$  we denote by  $(x_1, \dots, x_n)$ . At a time  $t$  we represent the state of the system by  $(x_1(t), \dots, x_n(t))$ , where  $x_j(t) \in P_j$  is the state of the cell  $c_j$  at time  $t$ .

The group symmetry of a coupled cell system is a subgroup of the permutation group  $S_n$  consisting of all the permutations that preserve the coupling between the cells.

In the graph of Figure 2, we have a network of four cells. As all nodes are represented by the same symbol, this means that all cells are considered to be identical, i.e., all have the same internal dynamics. The arrows are of three distinct types, representing three different types of couplings between the cells. This network has  $\mathbf{D}_2$  symmetry. At time  $t$ , the state of this system is given by  $(x_1(t), x_2(t), x_3(t), x_4(t))$ .

### 2.2 The equations

The derivation of the model assumes that each leg receives signals from two cells (see Section 1). The joint muscles of the left leg receive signals from cells  $c_1$  and  $c_3$  and similarly the right leg joint muscles receive the signals from cells  $c_2$  and  $c_4$ . The existence of four cells is justified by the fact that *run* and *walk* are two distinct gaits. In both primary gaits *walk* and *run* the left and right legs are half-period out of phase. Nevertheless, in the *run* both flexor and extensor muscles of the ankle joints are in phase, whereas in the *walk* they are out of phase. This is reflected in the rigidity of the ankle joint in the *run* and in the ankle rotation in the *walk*. The differences between these two gaits are translated by their respective  $(H, K)$  symmetry pairs (Table 1).

The internal dynamics of each cell is modeled by a system of ODE's. The general class of ODE's associated with the 4-cell model is given by:

$$\begin{cases} \dot{x}_1 = F(x_1, x_2, x_3, x_4) \\ \dot{x}_2 = F(x_2, x_1, x_4, x_3) \\ \dot{x}_3 = F(x_3, x_4, x_1, x_2) \\ \dot{x}_4 = F(x_4, x_3, x_2, x_1) \end{cases} \quad (2.1)$$

where  $x_i \in \mathbb{R}^k$  is the state of cell  $c_i$ ,  $i \in \{1, 2, 3, 4\}$ ,  $k$  is the dimension of the internal dynamics for each cell and  $F : (\mathbb{R}^k)^4 \rightarrow \mathbb{R}^k$  is a function that models the internal dynamics of the four cells.

### 2.3 Symmetry of the model

In the graph of Figure 2 we can see three distinct types of arrows, which represent three distinct types of couplings between the cells. The arrows in bold indicate us that the signals sent to cells  $c_1$  and  $c_2$  may be interchanged, if the signals sent to cells  $c_3$  and  $c_4$  also interchange. Mathematically, it corresponds to the permutation (12)(34), which we label  $\rho$ . The dashed arrows are associated to the permutation (13)(24), which will be called  $\tau$ . In this case, the signals sent to cells  $c_1$  and  $c_3$  may be switched if the signals sent to cells  $c_2$  and  $c_4$  are also switched. Finally, the dotted arrows indicate that the signals sent to cells  $c_1$  and  $c_4$  can be interchanged if the signals sent to cells  $c_2$  and  $c_3$  are also interchanged. This last symmetry is associated with the permutation  $\rho\tau = (14)(23)$ . Note that (14)(23) = (12)(34)  $\circ$  (13)(24). Together with the *Identity*, these permutations form the abelian group  $\mathbf{D}_2$ . We have  $\mathbf{D}_2 = \langle \rho, \tau \rangle$ .  $\mathbf{D}_2$  is a symmetry group of order 4. This is the group of symmetries associated with the model.

### 2.4 Bipedal Gaits

We use  $H/K$  theorem (12) to identify all spatial-temporal and spatial symmetry associated with periodic solutions produced by the system (2.1). Let  $K \subset H \subset \mathbf{D}_2$  such that a given periodic solution  $x(t)$  has the pair of symmetries  $(H, K)$ .  $K$  is the set of spatial symmetries  $k$ , i.e.,  $kx(t) = x(t)$ .  $H$  is the set of spatial-temporal symmetries  $h$ , i.e.,  $hx(t + \theta) = x(t)$ , where  $\theta$  is the value of the phase-shift. We distinguish two types of gaits: primary and secondary. Primary gaits have spatial-temporal symmetry group equal to  $\mathbf{D}_2$  and the secondary gaits have spatial-temporal symmetry group isomorphic to  $\mathbb{Z}_2$ . In the primary gaits, the muscles groups receive the same signal, whereas in secondary gaits there are two different signals sent to these muscles.

*Theorem 2.1.* (28) 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.

Theorem 2.1 allows us to identify 11 pairs of symmetries  $(H, K)$  such that  $H/K$  is cyclic, given below:

$(\mathbf{D}_2, \mathbf{D}_2)$ ,  $(\mathbf{D}_2, \rho\tau)$ ,  $(\mathbf{D}_2, \rho)$ ,  $(\mathbf{D}_2, \tau)$ ,  $(\rho\tau, \rho\tau)$ ,  $(\rho\tau, Id)$ ,  $(\rho, \rho)$ ,  $(\rho, Id)$ ,  $(\tau, \tau)$ ,  $(\tau, Id)$ ,  $(Id, Id)$  where *Id* represents the *Identity*.

The periodic solutions with symmetry pairs  $(H, K)$  and corresponding biped rhythms are shown in Table 1.

$H$	$K$	Periodic solution	Gait
$\mathbf{D}_2$	$\mathbf{D}_2$	$(x_1(t), x_1(t), x_1(t), x_1(t))$	<i>two-legged hop</i>
$\mathbf{D}_2$	$\rho\tau$	$(x_1(t), x_1(t + \frac{1}{2}), x_1(t + \frac{1}{2}), x_1(t))$	<i>walk</i>
$\mathbf{D}_2$	$\rho$	$(x_1(t), x_1(t), x_1(t + \frac{1}{2}), x_1(t + \frac{1}{2}))$	<i>two-legged jump</i>
$\mathbf{D}_2$	$\tau$	$(x_1(t), x_1(t + \frac{1}{2}), x_1(t), x_1(t + \frac{1}{2}))$	<i>run</i>
$\rho\tau$	$\rho\tau$	$(x_1(t), x_2(t), x_2(t), x_1(t))$	<i>asymmetric hop</i>
$\rho\tau$	$Id$	$(x_1(t), x_2(t), x_2(t + \frac{1}{2}), x_1(t + \frac{1}{2}))$	<i>hesitation-walk</i>
$\rho$	$\rho$	$(x_1(t), x_1(t), x_2(t), x_2(t))$	
$\rho$	$Id$	$(x_1(t), x_1(t + \frac{1}{2}), x_2(t), x_2(t + \frac{1}{2}))$	<i>skip</i>
$\tau$	$\tau$	$(x_1(t), x_2(t), x_1(t), x_2(t))$	<i>one-legged hop</i>
$\tau$	$Id$	$(x_1(t), x_2(t), x_1(t + \frac{1}{2}), x_2(t + \frac{1}{2}))$	<i>gallop</i>
$Id$	$Id$	$(x_1(t), x_2(t), x_3(t), x_4(t))$	

Table 1. Periodic solutions and corresponding biped gaits predicted by the 4-cell CPG model. Let  $X(t) = (x_1(t), x_2(t), x_3(t), x_4(t))$  be a periodic solution with period normalized to 1. The symmetry  $\tau$  switches the signals sent to identical muscle groups of the two legs; the symmetry  $\rho$  switches the two signals sent to muscle groups within each leg.

### 2.5 Bifurcation of gaits

In this subsection it is summarized, using arguments of bifurcation theory, the classification of primary and secondary gaits produced by the 4-cell CPG model (12; 29). The primary gaits are bifurcations of a  $\mathbf{D}_2$ -invariant equilibrium,  $X = (x, x, x, x)$ . The secondary gaits are symmetry breaking bifurcations of the primary gaits.

Let  $L$  be the matrix of linearization of the system 2.1, around the equilibrium  $X$ . The system 2.1 is  $\mathbf{D}_2$ -equivariant, i.e.,  $F(\gamma \cdot x) = \gamma \cdot F(x)$ , for all  $\gamma \in \mathbf{D}_2$ . This feature translates into good properties in the matrix  $L$ .

To determine the bifurcations and stability of the primary gaits, it is necessary to compute the eigenvalues of the matrix  $L$  in the equilibrium  $X$ . This task is easier if the decomposition in isotypic components of the subspace  $(\mathbf{R}^k)^4$  is used.  $(\mathbf{R}^k)^4$  can be decomposed in a direct sum of  $\mathbf{D}_2$ -irreducible subspaces, in such a way that it is unique and invariant under  $L$ .

Let  $V_\sigma$  be the sum of all irreducible subspaces isomorphic to a representation  $\sigma$  of  $\mathbf{D}_2$ , i.e.,  $V_\sigma$  is the isotypic

component of  $(\mathbf{R}^k)^4$  corresponding to  $\sigma$ . There are four irreducible representations of  $\mathbf{D}_2$ . These representations are described in Table 2.

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

Table 2. Isotypic components of  $(\mathbf{R}^k)^4$  for the 4-cell CPG model.

The isotypic decomposition (see (12), Theorem 2.12) can be used to block diagonalize the matrix  $L$ . Thus, the task of computing its eigenvalues is done with little effort. We define the following matrices  $k \times k$ :

$$\begin{aligned} A &= \frac{\delta F}{\delta x_1}(X) \\ B &= \frac{\delta F}{\delta x_2}(X) \\ C &= \frac{\delta F}{\delta x_3}(X) \\ D &= \frac{\delta F}{\delta x_4}(X) \end{aligned}$$

It follows from Table 2 that the eigenvalues of  $L$  are the eigenvalues of the following matrices:

$$\begin{aligned} L_{\mathbf{D}_2} &= A + B + C + D \\ L_{\tau} &= A + B - C - D \\ L_{\rho} &= A - B + C - D \\ L_{\rho\tau} &= A - B - C + D \end{aligned}$$

As  $\mathbf{D}_2$  is an abelian group, Hopf bifurcations occur for a unique pair of imaginary eigenvalues. Thus, Hopf bifurcation points can be computed for each matrix  $L_\sigma$  as well as the stability of its periodic orbits can be calculated. Table 3 establishes the correspondence between the periodic solutions obtained from  $L_\sigma$  and the primary gaits.

$L_\sigma$	Primary Gait
$L_{\mathbf{D}_2}$	<i>two-legged hop</i>
$L_\tau$	<i>run</i>
$L_\rho$	<i>two-legged jump</i>
$L_{\rho\tau}$	<i>walk</i>

Table 3. Primary Gaits.

In order to classify secondary gaits we need to compute symmetry breaking bifurcations of the primary gaits. This is done using properties of the Poincaré Maps. See more details in (29). In Table 4 we present all the symmetry breaking bifurcations of primary gaits predicted by the 4-cell CPG model. In the *two-legged hop* there is an additional bifurcation to a secondary gait, with  $(H, K) = (\rho, \rho)$  symmetry pair. This solution is not yet identified with a bipedal gait.

Primary Gait	Secondary Gaits
<i>walk</i>	<i>gallop</i> <i>skip</i>
<i>run</i>	<i>skip</i> <i>hesitation-walk</i>
<i>two-legged jump</i>	<i>hesitation-walk</i> <i>gallop</i>
<i>two-legged hop</i>	<i>asymmetric hop</i> <i>one-legged hop</i>

Table 4. Secondary gaits obtained by symmetry breaking bifurcations of primary gaits, in the 4-cell CPG model.

### 3. NUMERICAL SIMULATIONS

In this section, we present numerical simulations of the 4-cell CPG model for bipeds. We consider, as internal dynamics of each cell, the dimensionless Morris-Lecar (26; 34) equations, given by:

$$\begin{cases} \dot{v} = -g_{Ca}m(v)(v-1) - g_l(v-v_l) - g_kw(v-v_k) + I \equiv f_1(v, w) \\ \dot{w} = \phi\tau(v)(n(v)-w) \equiv f_2(v, w) \end{cases} \quad (3.2)$$

where  $m(v) = \frac{1}{2}(1 + \tanh(\frac{v-v_1}{v_2}))$ ,  $n(v) = \frac{1}{2}(1 + \tanh(\frac{v-v_3}{v_4}))$ ,  $\tau(v) = \cosh(\frac{v-v_3}{2v_4})$ . The parameter values used in the simulations are  $v_1 = 0.2$ ,  $v_2 = 0.4$ ,  $v_3 = 0.3$ ,  $v_4 = 0.2$ ,  $g_l = 0.6$ ,  $g_k = 1.8$ ,  $v_l = -1.8$ ,  $v_k = -0.8$  and  $I = 1$ .

We consider two types of coupling: diffusive and synaptic. Let  $h(x_i, x_j)$  be the function that represents the coupling between the cells  $c_i$  and  $c_j$ . The coupling is called diffusive if  $h(x_i, x_j) = x_i - x_j$  and synaptic if  $h(x_i, x_j) = x_j$ .

The internal dynamics of the cell  $c_i$  is given by:

$$\begin{aligned} \dot{x}_{i1} &= F(x_i, x_j, x_k, x_l) = f_1(x_{i1}, x_{i2}) - \\ &\alpha_a h(x_{i1}, x_{j1}) - \beta_b h(x_{i1}, x_{k1}) - \gamma_c h(x_{i1}, x_{l1}) \\ \dot{x}_{i2} &= F(x_i, x_j, x_k, x_l) = f_2(x_{i1}, x_{i2}) \end{aligned}$$

where  $\alpha_a$ ,  $\beta_b$  and  $\gamma_c$  are the coupling constants associated to the arrows directed from cells  $c_j$ ,  $c_k$  and  $c_l$  to cell  $c_i$ , respectively (see Figure 3).

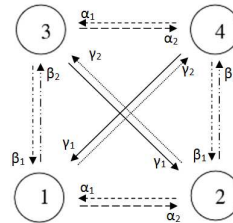


Figure 3. Coupling constants.

The secondary gait *skip* is numerically obtained by bifurcation of the primary gaits *walk* and *run*. *Gallop* is a bifurcation of *walk*.

In the following tables we present the values of the initial conditions, the coupling constants and bifurcation parameters used to obtain both primary and secondary gaits. We also plot the periodic solutions.

Gait	Init. Cond.
<i>walk</i>	(0.180, 0.277) (0.097, 0.159) (0.097, 0.159) (0.180, 0.277)
<i>run</i>	(0.004, 0.110) (0.195, 0.117) (0.004, 0.110) (0.195, 0.117)
<i>two-legged jump</i>	(-0.046, 0.298) (-0.046, 0.298) (0.527, 0.253) (0.527, 0.253)

Table 5. Values of the initial conditions of the periodic solutions of the 4-cell CPG model, obtained with the Morris-Lecar equations and diffusive coupling in the first component of the internal dynamics of each cell,  $i = 1, 2$ .

Gait	$g_{Ca}$	$\phi$	$\alpha_i$	$\beta_i$	$\gamma_i$
<i>walk</i>	1.500	0.200	-0.300	0.100	0.200
<i>run</i>	1.000	0.500	-0.300	0.200	-0.100
<i>two-legged jump</i>	2.000	0.200	0.100	-0.100	-0.200

Table 6. Values of the parameters and coupling constants, of the periodic solutions of the 4-cell CPG model, obtained with the Morris-Lecar equations and diffusive coupling in the first component of the internal dynamics of each cell,  $i = 1, 2$ .

#### 4. CONCLUSIONS

In this paper we study the CPG model for locomotor patterns in bipeds, proposed by Golubitsky *et al* (14; 15) and studied by Pinto *et al* (28). The bipedal rhythms predicted by the CPG model identified with the gaits *two-legged hop*, *walk*, *two-legged jump*, *run*, *hesitation-walk*, *asymmetric hop*, *skip*, *one-legged hop* and *gallop* are reviewed.

Prim. gait	Sec. gait	Init. Cond.	Bif. Param.
<i>walk</i>	<i>gallop</i>	(0.176, 0.225) (0.176, 0.225) (0.176, 0.176) (176, 0.225)	$\alpha_1 = -0.281$
<i>walk</i>	<i>skip</i>	(0.176, 0.225) (0.176, 0.225) (0.176, 0.225) (0.176, 0.225)	$\beta_1 = 0.119$
<i>run</i>	<i>skip</i>	(0.033, 0.118) (0.163, 0.093) (0.013, 0.122) (0.139, 0.057)	$\gamma_2 = -0.228$

Table 7. Values of the initial conditions and bifurcation parameter associated to the bifurcations of primary gaits *walk* and *run* in Tables 5-6.

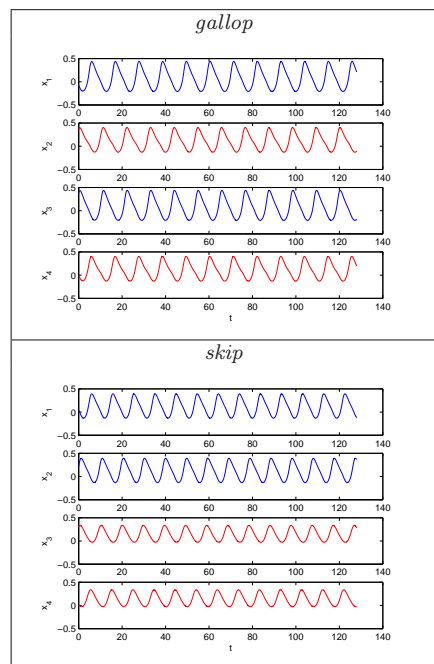


Table 8. Periodic solutions of the 4-cell CPG model identified with the secondary gaits in Table 7, obtained by bifurcation of the *walk*.

We numerically simulate the primary and secondary gaits predicted by the model in Figure 2, using XPP and MATLAB. The secondary gaits are obtained from bifurcations of the primary gaits, when the dimensionless Morris-Lecar (26; 34) equations are considered as internal dynamics of each cell in both diffusive and synaptic coupling. We show numerical evidence of gait transition in bipeds.

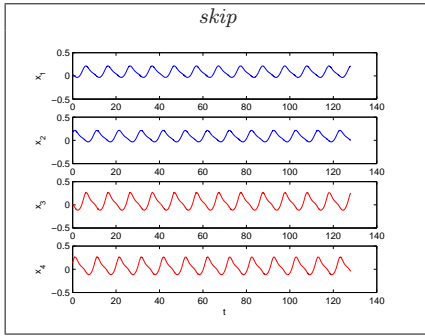


Table 9. Periodic solution of the 4-cell CPG model identified with the secondary gait in Table 7, obtained by bifurcation of the *run*.

Gait	Init. Cond.
<i>walk</i>	(0.329, 0.413)
	(-0.282, 0.125)
	(-0.282, 0.125)
	(0.329, 0.413)
<i>run</i>	(0.230, 0.453)
	(-0.260, 0.002)
	(0.230, 0.453)
	(-0.260, 0.002)
<i>two-legged jump</i>	(0.315, 0.182)
	(0.315, 0.182)
	(-0.017, 0.177)
	(-0.017, 0.177)

Table 10. Values of the initial conditions of the periodic solutions of the 4-cell CPG model, obtained with the Morris-Lecar equations and synaptic coupling in the first component of the internal dynamics of each cell,  $i = 1, 2$ .

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Gait	$gCa$	$\phi$	$\alpha_i$	$\beta_i$	$\gamma_i$
<i>walk</i>	2.000	0.200	0.100	0.300	-0.100
<i>run</i>	2.000	0.300	0.400	0.000	0.400
<i>two-legged jump</i>	1.500	0.400	-0.100	0.300	0.200

Table 11. Values of the parameters and coupling constants, of the periodic solutions of the 4-cell CPG model, obtained with the Morris-Lecar equations and synaptic coupling in the first component of the internal dynamics of each cell,  $i = 1, 2$ .

Prim. gait	Sec. gait	Init. Cond.	Bif. Param.
<i>walk</i>	<i>gallop</i>	(0.241, 0.320)	$\alpha_1 = -0.014$
		(0.156, 0.277)	
		(0.193, 0.296)	
		(0.258, 0.315)	
<i>walk</i>	<i>skip</i>	(0.100, 0.270)	$\gamma_1 = 0.160$
		(0.287, 0.264)	
		(0.332, 0.289)	
		(0.088, 0.293)	
<i>run</i>	<i>skip</i>	(0.115, 0.083)	$\gamma_1 = 0.199$
		(0.202, 0.380)	
		(-0.330, 0.020)	
		(0.214, 0.446)	

Table 12. Values of the initial conditions and bifurcation parameter associated to the bifurcations of primary gaits *walk* and *run* in Tables 10–11.

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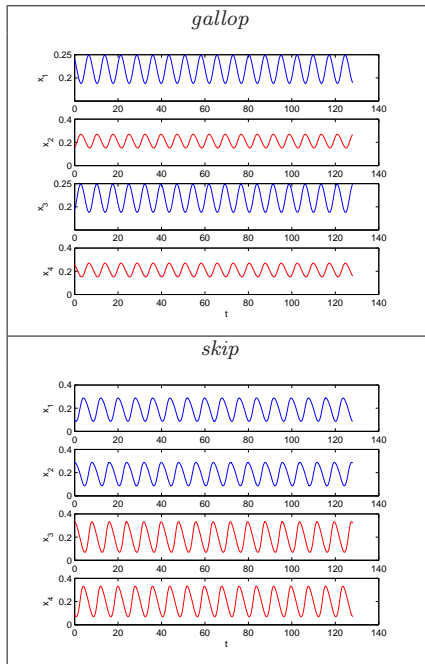


Table 13. Periodic solutions of the 4-cell CPG model identified with the secondary gaits in Table 12, obtained by bifurcation of the walk.

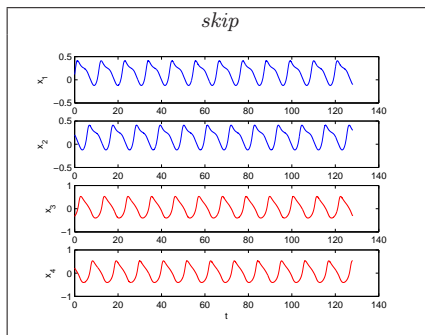


Table 14. Periodic solution of the 4-cell CPG model identified with the secondary gait in Table 12, obtained by bifurcation of the run.

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