Mathematical Biology

Central pattern generators for bipedal locomotion

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Abstract Golubitsky, Stewart, Buono and Collins proposed two models for the achitecture of central pattern generators (CPGs): one for bipeds (which we call leg) and one for quadrupeds (which we call quad). In this paper we use symmetry techniques to classify the possible spatiotemporal symmetries of periodic solutions that can exist in leg (there are 10 nontrivial types) and we explore the possibility that coordinated arm/leg rhythms can be understood, on the CPG level, by a small breaking of the symmetry in quad, which leads to a third CPG architecture arm. Rhythms produced by leg correspond to the bipedal *gaits* of *walk*, *run*, *two-legged hop*, *two-legged jump*, *skip*, *gallop*, *asymmetric hop*, and *one-legged hop*. We show that breaking the symmetry between fore and hind limbs in quad, which yields the CPG arm, leads to periodic solution types whose associated leg rhythms correspond to seven of the eight leg gaits found in leg; the missing biped *gait* is the asymmetric hop. However, when arm/leg coordination rhythms are considered, we find the correct rhythms only for the biped gaits of *two-legged hop*, *run*, and *gallop*. In particular, the biped *gait walk*, along with its arm rhythms, cannot be obtained by a small breaking of symmetry of any quadruped gait supported by quad.

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1 Introduction

Vertebrate locomotion is often assumed to be controlled by a central pattern generator (CPG) capable of producing the rhythms associated to different gaits [10,9,31,21,28,40]. Moreover, CPGs are commonly modeled as networks of identical systems of differential equations, where the individual systems, which we call *cells*, model neurons, or more plausibly, collections of neurons. We remark that the existence of locomotor CPGs in mammals has not been established; nevertheless, many authors state that there is evidence for a CPG for human locomotion [7,20,16,6]. Although this issue is controversial, we assume here that locomotor CPGs do exist.

Golubitsky et al. [24,25] introduce two locomotor CPG models for the rhythms of leg movements: the eight-cell quadruped locomotor CPG model, which we call quad (see Fig. 1, left), and the analogous four-cell CPG model, which we call leg, for leg rhythms in bipeds. See Fig. 2. In this paper we introduce a third CPG arm (see Fig. 1, right) to explore interlimb coordination between arms and legs in biped gaits. The network arm is derived by breaking symmetry between the fore and hindlegs in quad.
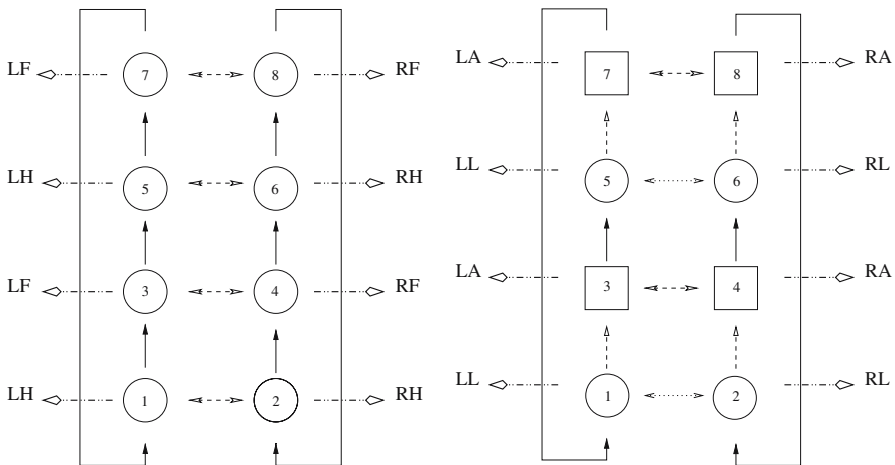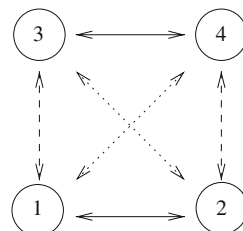

Fig. 1 Eight-cell CPGs: *(left)* quad; *(right)* arm. See text for explanation. *LF* left fore leg and *LH* left hind leg in quad and *LA* left arm and *LL* left leg in arm

Fig. 2 CPG network leg for the control of biped legs. Cells 1 and 3 send signals to the left leg, cells 2 and 4 send signals to the right leg

Each graph, the *network architecture*, corresponds to a class of systems of differential equations [27]. Each of these systems can be considered to be a model CPG. In this paper we use symmetry techniques to classify the types of periodic solutions, along with their associated limb rhythms, that systems from these classes can produce. Since exact CPG models are not known, indeed even the existence of CPGs in mammals is in question, a reasonable approach is to study the architectures that plausible CPG models may have.

Review of quad and leg

Collins and Stewart [11] observed that different gaits can be described by their spatiotemporal symmetries. They also showed, using equivariant Hopf bifurcation theory, that symmetries in a locomotor CPG network can be used to produce periodic solutions with the rhythms associated to given gaits. This approach builds on earlier work of Kopell and Ermentrout [34]. Collins and Stewart [11–13] and Kopell and Ermentrout [33] also observed that network symmetries can permit a given network of differential equations to have naturally occurring periodic solutions corresponding to several different gaits.

Golubitsky et al. [24,25,5,4] showed that it is possible to construct a (unique) eight-cell network quad that can produce periodic solutions corresponding to the common quadrupedal gaits of walk, trot, and pace. They also showed that no four-cell network can produce the rhythms associated to these gaits in a biologically reasonable way. The network quad has the striking property that each leg receives signals from two cells. Using this observation the eight-cell quadruped CPG model quad scales naturally to the four-cell biped CPG model leg.

As discussed in [25], a physiological interpretation can be given to the fact that locomotor quad models have two cells per limb. This point is most easily understood by considering the four-cell network leg. This four-cell model can produce two different types of periodic solutions, where in both types the signals to the left leg are a half-period out of phase with the signals to the right leg. In one solution type the two signals sent to the left leg are in phase and in the second solution type the two signals sent to the left leg are a half-period out of phase.

These two different solution types have a natural interpretation. It is well known that *walk* and *run* are two distinct biped gaits in which the leg motions are a half period out of phase. Mechanically, the legs move as pendula in the *walk* and in a pogo stick motion in the *run*. Using electromyographical recordings, Mann et al. [35,36] have shown that in a *run* the flexor and extensor muscles connected to the ankle joint are approximately in phase (thus holding the ankle joint rigid) and in a *walk* the two muscle groups fire out of phase (thus allowing the ankle joint to rotate). Thus we think of locomotor CPGs abstractly as controlling muscle groups rather than legs. Since most joints are controlled by two muscle groups, it makes sense that minimal locomotor CPG networks should have two cells for each leg. Moreover, it is a curious mathematical fact that a single minimal quadruped CPG model network can produce periodic solutions

corresponding to the rhythms of standard gaits only if that model allows two signals to be sent to each leg.

Systems and symmetries associated to quad, arm, and leg

The networks that we have drawn in Figs. 1 and 2 stand for classes of systems of differential equations. For example, the class of differential equations corresponding to quad is

$$
\begin{aligned}
&\dot{x}_1 = F(x_1, x_2, x_7), \quad \dot{x}_5 = F(x_5, x_6, x_3), \\
&\dot{x}_2 = F(x_2, x_1, x_8), \quad \dot{x}_6 = F(x_6, x_5, x_4), \\
&\dot{x}_3 = F(x_3, x_4, x_1), \quad \dot{x}_7 = F(x_7, x_8, x_5), \\
&\dot{x}_4 = F(x_4, x_3, x_2), \quad \dot{x}_8 = F(x_8, x_7, x_6),
\end{aligned}
\tag{1.1}
$$

where $x_i \in \mathbf{R}^k$ is the cell i variables, k is the dimension of the internal dynamics for each cell, and $F : (\mathbf{R}^k)^3 \to \mathbf{R}^k$ is an arbitrary mapping. The fact that the dynamics of each cell is governed by the same F indicates that the cells are assumed to be identical.

The symmetry breaking from quad to arm is made clear in Fig. 1 (right) by the use of two types of symbols (circles and squares) to represent cells, and three types of arrows (representing the coupling between cells). This network is motivated by the fact that all four limbs strike the ground in quadrupeds (hence the similarity between arms and legs is strong), whereas only two limbs (the legs) strike the ground in bipeds (hence the similarity between legs and arms is less strong). The class of ordinary differential equations (ODEs) associated to arm is

$$
\begin{aligned}
&\dot{x}_1 = F_1(x_1, x_2, x_7), \quad \dot{x}_5 = F_1(x_5, x_6, x_3), \\
&\dot{x}_2 = F_1(x_2, x_1, x_8), \quad \dot{x}_6 = F_1(x_6, x_5, x_4), \\
&\dot{x}_3 = F_2(x_3, x_4, x_1), \quad \dot{x}_7 = F_2(x_7, x_8, x_5), \\
&\dot{x}_4 = F_2(x_4, x_3, x_2), \quad \dot{x}_8 = F_2(x_8, x_7, x_6),
\end{aligned}
\tag{1.2}
$$

where $F_1 : (\mathbf{R}^k)^3 \to \mathbf{R}^k$ defines the dynamics corresponding to legs and $F_2 : (\mathbf{R}^k)^3 \to \mathbf{R}^k$ defines the dynamics corresponding to arms. The assumption that the symmetry breaking from quad to arm is small implies that $F_1 \approx F_2$.

Finally, the class of differential equations associated with the network leg is

$$
\begin{aligned}
&\dot{x}_1 = F(x_1, x_2, x_3, x_4), \\
&\dot{x}_2 = F(x_2, x_1, x_4, x_3), \\
&\dot{x}_3 = F(x_3, x_4, x_1, x_2), \\
&\dot{x}_4 = F(x_4, x_3, x_2, x_1),
\end{aligned}
\tag{1.3}
$$

where $x_i \in \mathbf{R}^k$ and $F : (\mathbf{R}^k)^4 \to \mathbf{R}^k$. Again all cells are assumed to be identical.

The network quad consists of two coupled four-cell unidirectional rings with two independent permutation symmetries: $\kappa = (1\ 2)(3\ 4)(5\ 6)(7\ 8)$

(the contralateral bilateral symmetry that interchanges the two rings) and $\omega = (1\ 3\ 5\ 7)(2\ 4\ 6\ 8)$ (the ipsilateral symmetry that cycles cells along the two rings). The group of symmetries of this network is the eight element group

$$\Gamma_{\mathsf{quad}} = \mathbf{Z}_4(\omega) \times \mathbf{Z}_2(\kappa), \tag{1.4}$$

where $\mathbf{Z}_k(\sigma)$ is the cyclic group of k elements generated by σ. Every element in Γ moves solutions of (1.1) to solutions.

The network leg consists of four cells, each one coupled to all other cells. The coupling allows two independent permutation symmetries: $\rho = (1\ 2)(3\ 4)$, which switches muscle groups between legs, and $\tau = (1\ 3)(2\ 4)$, which permutes muscle groups within each leg. The group of symmetries of leg is the four element group

$$\Gamma_{\mathsf{leg}} = \mathbf{Z}_2(\tau) \times \mathbf{Z}_2(\rho). \tag{1.5}$$

The symmetry group of arm is generated by ω^2 and κ. The contralateral symmetry κ of quad remains unchanged, however, the ipsilateral symmetry is reduced from ω to ω^2. This change allows cells that send signals to the same leg to be interchanged, but does not allow signals sent to legs and arms to be permuted. So the symmetry group is

$$\Gamma_{\mathsf{arm}} = \mathbf{Z}_2(\omega^2) \times \mathbf{Z}(\kappa). \tag{1.6}$$

Note that the symmetry groups Γ_{leg} and Γ_{arm} are isomorphic.

A review of spatiotemporal symmetries

In this section we review how spatiotemporal symmetries of periodic solutions may be associated with gait types and the H/K theory for finding periodic solutions with given spatiotemporal symmetries. As a first step, we discuss the rhythms associated with the common quadruped gaits of trot and pace. In the pace, the two left legs and the two right legs move synchronously, while the left leg pair and the right leg pair are a half-period out of phase. Similarly, in the trot diagonal pairs of legs move synchronously, while the two pairs are a half-period out of phase. The differences between these gaits can be understood in terms of two symmetry groups K and H, which we first describe in terms of leg permutations and then in terms of the model quad.

Let τ be the permutation that swaps the front legs with the hind legs. Applying τ to the pace does not change that gait since the left legs and the right legs are moving in unison. Applying τ to a trot does change the gait in the sense that the legs are now a half-period out of phase from where they were before applying τ. The permutation τ is called a *spatial* symmetry for the pace (the phase shift is zero) and is called a *spatiotemporal* symmetry for the trot. More precisely, $(\tau, \frac{1}{2})$ is a symmetry of the trot; that is, applying τ to a trot and then performing

a half-period phase shift does not change the trot gait. Collins and Stewart [11] observed that all of the common quadruped gaits can be distinguished by their leg permutation symmetries.

We define K to be the subgroup of all spatial symmetries and H to be the subgroup of all spatiotemporal symmetries. Clearly $K \subset H$. For systems of differential equations the subgroups H and K are defined in a mathematically more precise way. Let $x(t)$ be a periodic solution of a system of ODEs with symmetry group Γ. Then the subgroup K consists of symmetries that fix $x(t)$ pointwise, and the subgroup H consists of symmetries that preserve the periodic trajectory setwise. That is,

$$
\begin{aligned}
K &= \{\gamma \in \Gamma : \gamma x(t) = x(t) \text{ for all } t\}, \\
H &= \{\gamma \in \Gamma : \gamma \{x(t)\} = \{x(t)\} \text{ for all } t\}.
\end{aligned}
\tag{1.7}
$$

Note that if $\gamma \in H$, then $\gamma x(0) = x(\theta)$ for some θ. It follows from uniqueness of solutions for systems of differential equations with the same initial conditions that $\gamma x(t) = x(t + \theta)$ for all t; that is, θ is the temporal phase shift that corresponds to γ.

Next we discuss how symmetries of periodic solutions (H and K) in quad can correspond to gaits. For example, suppose that $H = \Gamma_{\text{quad}}$ and $K = \mathbf{Z}_4(\omega)$ and that $x(t) = (x_1(t), \ldots, x_8(t))$ is a 1-periodic solution with H and K symmetries. Since ω is a K symmetry the periodic solution must satisfy

$$
x_1(t) = x_3(t) = x_5(t) = x_7(t) \quad \text{and} \quad x_2(t) = x_4(t) = x_6(t) = x_8(t).
$$

Since κ is a spatiotemporal symmetry, $x_2(t) = x_1(t + \frac{1}{2})$. Thus

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

Note that the signals that go to both left legs are the same, the signals that go to both right legs are the same, and the signals that go to the left legs are a half-period out of phase with the signals that go to the right legs. Thus this rhythm is a pace. Similarly, $H = \Gamma_{\text{quad}}$ and $K = \mathbf{Z}_2(\omega\kappa)$ corresponds to a trot.

Golubitsky et al. [24] showed that there are six different gaits that have $H = \Gamma_{\text{quad}}$ and these are called *primary gaits*. The other four are walk, bound, pronk (all legs moving in synchrony) and jump (a surprising gait — but one that is actually observed — in which the left legs and right legs are synchronous and the hind legs lag the front legs by a quarter-period). Gaits that are not primary gaits are *secondary* gaits. Quadruped gallops are examples of secondary gaits.

Finally, we note that there is a mathematical theory that enables us to infer the CPG structure from the desired kinds of periodic solutions. The H/K Theorem [5] uses the symmetry group of a network to enumerate those pairs of spatiotemporal symmetry subgroups H and K that can correspond to periodic solutions of differential equations associated to the network. In particular, the

H/K Theorem is used in [5] to prove that quad is the only eight-cell network that can produce periodic solutions corresponding to walk, trot, and pace.

Structure of the paper

We address two main topics.

1. In Sect. 2, we classify the rhythms associated to periodic solutions that can be produced by a CPG network model for leg rhythms in bipeds, leg, and we relate these rhythms to known biped gaits.
2. We use, in Sect. 3, the CPG network model arm to discuss which of the biped gaits classified in 1, could have evolved directly from quadrupeds.

In Sect. 4 we discuss the insights gained with our CPG models and focus on that these are the simplest models for biped and quadruped locomotion.

2 Gaits in network leg

This section is divided into two parts. In Sect. 2.1 we use the H/K Theorem to classify the symmetry types of periodic solutions to (1.3), the systems of ODEs associated with network leg. Then, in Sect. 2.2, we discuss the relationship between these symmetry types and the rhythms of known biped gaits.

2.1 Symmetries of periodic solutions in (1.3)

Let H and K be the subgroups of spatiotemporal and spatial symmetries, as defined in (1.7). In order for (H, K) to correspond to symmetries of a periodic solution in a general Γ-equivariant system, certain algebraic conditions must be satisfied [5,26]. However, these conditions simplify for the coupled cell system (1.3).

Theorem 2.1 ([26]) *Consider the coupled cell system* (1.3) *where* $k \geq 2$. *Let* $H \supset K$ *be subgroups of* Γ_{leg}. *Then there is a periodic solution* $x(t)$ *to (1.3) for some function F if and only if H/K is cyclic.*

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

It is straightforward to enumerate all pairs of subgroups $K \subset H \subset \Gamma_{\text{leg}}$, defined in 1.5, such that H/K is cyclic. Nontrivial subgroups of Γ_{leg} are groups of order 2 (2 divides 4, the order of the group), and we have three such subgroups $\mathbf{Z}_2(\rho)$, $\mathbf{Z}_2(\tau)$, and $\mathbf{Z}_2(\rho\tau)$. There are 11 pairs of subgroups (H, K), and they are

$$(\Gamma_{\text{leg}}, \Gamma_{\text{leg}}), \quad (\Gamma_{\text{leg}}, \mathbf{Z}_2(\rho\tau)), \quad (\Gamma_{\text{leg}}, \mathbf{Z}_2(\rho)), \quad (\Gamma_{\text{leg}}, \mathbf{Z}_2(\tau)),$$
$$(\mathbf{Z}_2(\rho\tau), \mathbf{Z}_2(\rho\tau)), \quad (\mathbf{Z}_2(\rho\tau), \mathbf{1}), \quad (\mathbf{Z}_2(\rho), \mathbf{Z}_2(\rho)), \quad (\mathbf{Z}_2(\rho), \mathbf{1}), \quad (2.1)$$
$$(\mathbf{Z}_2(\tau), \mathbf{Z}_2(\tau)), \quad (\mathbf{Z}_2(\tau), \mathbf{1}), \quad (\mathbf{1}, \mathbf{1}).$$

In analogy with quad, we call gait types *primary* when $H = \Gamma_{\text{leg}}$ and *secondary* when $H \simeq \mathbf{Z}_2$. There are four primary gait types, which are distinguished by the property that all muscles in the two legs receive the same signal but perhaps with a half-period phase shift, and six secondary gait types distinguished by the fact that two types of signals are sent to muscle groups. The periodic solution types associated to these symmetries are given in Table 1. Numerical simulations of these solutions are given in [1]

2.2 Bipedal gaits associated to leg

We associate the four primary gait types that are produced by the four-cell network leg with the bipedal gaits *walk*, *run*, *two-legged hop*, and *two-legged jump*. We associate four of the six secondary gait types with the four bipedal gaits *skip*, *one-legged hop*, *asymmetric hop*, and *gallop*.

Primary gaits The bipedal gaits *walk* and *run* have the property that the left and right legs are a half-period out of phase. As discussed in [25] the flexor and extensor muscles of the ankle joint are in phase in the *run* and out of phase in the *walk* [35,36]. Biomechanically the legs move like pendula in the *walk* and like a pogo stick in the *run*. Moreover, in the *run*, the ankle joint is held rigid, whereas in the *walk*, ankle rotation is needed. It is this rotation that requires the flexors and extensors to be out of phase.

The differences between these gaits can be understood in terms of their respective (H, K) symmetry pairs. Indeed, in Table 1 we have identified the *run*

Table 1 Patterns of oscillation in leg

H	K	**Left leg**	**Right leg**	**Name**
Γ_{leg}	Γ_{leg}	$(x_1(t), x_1(t))$	$(x_1(t), x_1(t))$	*Two-legged hop*
Γ_{leg}	$\rho\tau$	$(x_1(t), x_1(t+\frac{1}{2}))$	$(x_1(t+\frac{1}{2}), x_1(t))$	*Walk*
Γ_{leg}	ρ	$(x_1(t), x_1(t+\frac{1}{2}))$	$(x_1(t), x_1(t+\frac{1}{2}))$	*Two-legged jump*
Γ_{leg}	τ	$(x_1(t), x_1(t))$	$(x_1(t+\frac{1}{2}), x_1(t+\frac{1}{2}))$	*Run*
$\rho\tau$	$\rho\tau$	$(x_1(t), x_2(t))$	$(x_2(t), x_1(t))$	*Asymmetric hop*
$\rho\tau$	$\mathbf{1}$	$(x_1(t), x_2(t+\frac{1}{2}))$	$(x_2(t), x_1(t+\frac{1}{2}))$	
ρ	ρ	$(x_1(t), x_2(t))$	$(x_1(t), x_2(t))$	
ρ	$\mathbf{1}$	$(x_1(t), x_2(t))$	$(x_1(t+\frac{1}{2}), x_2(t+\frac{1}{2}))$	*Skip*
τ	τ	$(x_1(t), x_1(t))$	$(x_2(t), x_2(t))$	*One-legged one*
τ	$\mathbf{1}$	$(x_1(t), x_1(t+\frac{1}{2}))$	$(x_2(t), x_2(t+\frac{1}{2}))$	*Gallop*
$\mathbf{1}$	$\mathbf{1}$	$(x_1(t), x_2(t))$	$(x_3(t), x_4(t))$	

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 ρ swaps the signals sent to identical muscle groups of the two legs; the symmetry τ swaps the two signals sent to muscle groups within each leg

as the gait where the two signals sent to one leg are in phase and the *walk* as the gait where the two signals sent to one leg are a half-period out of phase.

To understand these identifications more explicitly, observe that in the *walk*, $\rho\tau$ is a K symmetry, hence the periodic solution must have the form

$$X(t) = (x_1(t), x_2(t), x_2(t), x_1(t)).$$

Moreover, the spatiotemporal symmetry τ forces $x_2(t) = x_1(t + \frac{1}{2})$. Thus, the periodic solution has the form

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

Similarly, in the *run*, τ is a K symmetry, so the periodic solution has the form

$$X(t) = (x_1(t), x_2(t), x_1(t), x_2(t)).$$

Since τ is a spatiotemporal symmetry, $x_2(t) = x_1(t + \frac{1}{2})$, and

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

Left and right legs move synchronously in the bipedal gaits *two-legged hop* and *two-legged jump*. Farley et al. [22] discuss two different *hops*: high and low frequency. They suggest that the motion in high frequency hopping is similar to a spring-mass system, which we describe as pogo stick-like motion. The low frequency hopping, which we call a *two-legged jump*, is a different gait where ground contact is longer and appears to require ankle rotation, as in the *walk*. The network leg can produce two primary gaits in which the left and right legs receive the same pair of signals, and signals corresponding to muscle groups in one leg are either in phase (*two-legged hop*) or half-period out of phase (*two-legged jump*).

Secondary gaits Just two secondary gaits *skip* and *gallop* have been well studied in the literature, though two others, *one-legged hop* and *asymmetric hop*, can be identified. By contrast, leg can produce six different secondary gait types. We will discuss why we have identified the particular four types of rhythms with these four bipedal gaits. We have not identified the remaining two secondary periodic solution types with actual bipedal gaits.

The *skip* is a third gait in which interchanging the two legs leads to a half-period phase shift in the gait cycle. It differs from the *walk* because it has a significant flight phase, and from the *run* because it often has a double support period. *Skip* is also more demanding than *run* at the same speed [39]. A gait cycle of the *skip* (bilateral skipping in [39]) is characterized by each leg touching the ground twice before the opposite one does and is usually displayed by young children. The network leg predicts only one secondary gait that has

the property that interchanging legs lead to a half-period phase shift; namely, $(\mathbf{Z}_2(\rho), \mathbf{1})$. Thus, we identify this periodic solution with the *skip*.

The two gaits *gallop* [8,39,41,47,48] and *one-legged hop* have a common property: the existence of a lead leg in the gait cycle. 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* [8,47]. 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* [8]. The *gallop* is, like the *skip*, a prevalent gait in children's games. It is also commonly used by Lemur [32] and by small birds [30] for ground locomotion. Margaria and Cavagna [37] note that *generic jumping* (our *gallop*) could be the gait of choice under low gravity conditions such as those on the moon. The high metabolic cost of the *unilateral* skip [39], (our *gallop*), is overridden by the need for less work against gravity [39].

The fact that the bipedal *gallop* and the *one-legged hop* have lead legs, (that is, the motions of the two legs are different), suggests that the signals sent to the right and left legs are different. In two of our secondary gait types, the pair of signals sent to the left leg is different from the pair of signals sent to the right leg. For this reason we identify these periodic states with *one-legged hop* and *gallop*. These gaits differ from each other in that the two signals sent to one leg are either in phase or half-period out of phase. In analogy with the primary gaits of *two-legged hop* and *walk*, we call the in phase gait a *one-legged hop* (pogo stick-like motion) and the out of phase one a *gallop* (pendulum-like motion) [3,39].

Verstappen and Aerts [44] discuss an *asymmetric hop* in the black-billed magpie, where the two legs are nearly synchronous — one leg landing before the other. The individual leg motions seem to be like that in the *two-legged hop*. There is only one secondary gait predicted by leg where the signals sent to the two legs are different, but close enough so that the muscle groups in the two legs receive *almost* identical signals.

In phase space there are two (symmetry related) periodic solutions associated to each secondary gait. For the *gallop*, *one-legged hop*, and *asymmetric hop* these solutions correspond to interchanging the left and right legs (the symmetry is ρ). In the *gallop* and the *one-legged hop* these solutions correspond to a choice of lead leg; in the *asymmetric hop* the solutions correspond to whether the left or the right leg is the first to hit the ground. It is less clear how to interpret the differences between the two solutions in the *skip*. The symmetry that relates these solutions interchanges the two signals sent to a given leg.

3 Gaits in network arm

In this section, we discuss periodic solutions of the CPG network arm (Fig. 1, right) and attempt to associate those solutions with typical arm/leg coordination patterns that are observed in human gaits.

Table 2 Column 1 lists the primary and secondary gaits produced by quad.

Column 2 lists the associated rhythms of the hindlegs of these gaits, as they appear in leg. Column 3 lists the leg/arm rhythms in arm of solutions corresponding to a small symmetry-breaking perturbation of a quadruped gait type solution

Quad	Leg	Arm
Pronk	*Two-legged hop*	*Two-legged hop*
Bound	*Two-legged hop*	
Pace	*Run*	
Trot	*Run*	*Run*
Jump	*Two-legged jump*	
Walk	*Walk*	
Rotary jump	*Gallop*	
Transverse jump	*Gallop*	*Gallop*
Scuttle	*Skip*	
Loping trot	*One-legged hop*	
Rotary gallop	*One-legged hop*	
Loping pace	*One-legged hop*	
Transverse gallop	*One-legged hop*	

The idea is straightforward. We assume that the quadruped locomotor CPG has evolved to distinguish between arms and legs, and that this change is reflected in a small breaking of the symmetry in the quadruped CPG. Thus, the cells and couplings that correspond to arms differ from those that correspond to legs. These comments are reflected in arm.

Our results are summarized in Table 2. In the first column we list all primary and secondary quadrupedal gait rhythms that can be produced by quad (see [24]). Each of these quadrupedal gaits induces a rhythm on the hindlegs, and these rhythms correspond to biped gaits, as produced by leg. The results are listed in the second column. (Here one must take into account the phasing of the two signals that are sent to each leg.)

Finally, the solution types corresponding to quad perturb to solution types in arm, which could in principle correspond to arm/leg coordination patterns in biped gaits. We would expect this to be the case if biped gaits evolved directly from quadrupedal gaits. However, the correct arm/leg rhythms are found for only three biped gaits: *two-legged hop*, *run*, and *gallop*. In particular, the biped *walk* cannot be obtained by a small symmetry-breaking perturbation of any standard quadrupedal gait modeled by quad. We conclude that additional CPG changes were required for the human *walk* to have evolved, and this observation is in agreement with Schmidt [43]. See also [2, 29, 42].

The discussion of how periodic solutions of quad with certain spatiotemporal symmetries deform on symmetry breaking to solutions that maintain only those spatiotemporal symmetries that are consistent with arm is given in Sect. 3.1. A discussion of the leg/arm rhythms associated with these perturbed gaits is given in Sect. 3.2. This discussion completes column 3 in Table 2.

3.1 Rhythms produced by arm: a symmetry approach

Suppose that $X(t)$ is a hyperbolic periodic solution to quad corresponding to a gait with spatiotemporal symmetries H and spatial symmetries K, where $K \subset H \subset \Gamma_{\text{quad}}$. See Sect. 2.1. Suppose that we consider a small forced

symmetry-breaking of the equations so that $F_1 \approx F_2$ in (1.2). Hyperbolicity implies that $X(t)$ perturbs to a periodic solution of arm whose symmetry groups are $H' = H \cap \Gamma_{arm}$ and $K' = K \cap \Gamma_{arm}$. These points are verified as follows.

Uniqueness of the perturbed periodic solution implies that all symmetries in $K \cap \Gamma_{arm}$ fix the perturbed trajectory pointwise since the perturbed equations have Γ_{arm}-equivariance. So $K \cap \Gamma_{arm} \subset K'$. Conversely, any symmetry in $K' \subset \Gamma_{arm}$ must be in K again by the uniqueness of hyperbolic periodic solutions in a small neighborhood. An analogous argument is valid for H'.

In Table 3 we list the spatiotemporal symmetry types of primary and secondary quadrupedal gaits in quad computed in [24]. Given a periodic solution corresponding to one of these gait types, we break symmetry by a small perturbation in the associated system of differential equations and observe that the perturbed periodic solution has the symmetry groups in Γ_{arm} described above. Then, using these symmetry groups, we match the perturbed periodic solutions with leg rhythms in bipeds, see Table 3. Note that all of the spatiotemporal symmetry groups of leg rhythms in bipeds can be obtained as symmetry groups of perturbed symmetric solutions of quad. Finally, every symmetry type of periodic solution (corresponding to the biped gaits) in the four-cell biped model leg analyzed in Sect. 2.1 can be identified with a symmetry type corresponding to a gait in the arm. This identification uses the isomorphism between Γ_{leg} with Γ_{arm} given by identifying ρ with ω^2 and τ with κ.

3.2 Perturbed quadruped gaits vs biped gaits

We proceed with a discussion of the perturbed quadruped gaits and their identification with interlimb coordination patterns in bipeds. In particular, we explain

Table 3 Symmetry groups of standard gaits of the eight-cell CPGs.

Quadruped — quad			Bipeds — leg		
Name	H	K	**Name**	$H' = H \cap \Gamma_{arm}$	$K' = K \cap \Gamma_{arm}$
Pronk	Γ_{quad}	Γ_{quad}	*Two-legged hop*	Γ_{arm}	Γ_{arm}
Bound	Γ_{quad}	Γ_{arm}	*Two-legged hop*	Γ_{arm}	Γ_{arm}
Trot	Γ_{quad}	$\mathbf{Z}_4(\kappa\omega)$	*Run*	Γ_{arm}	$\mathbf{Z}_2(\omega^2)$
Pace	Γ_{quad}	$\mathbf{Z}_4(\omega)$	*Run*	Γ_{arm}	$\mathbf{Z}_2(\omega^2)$
Jump	Γ_{quad}	$\mathbf{Z}_2(\kappa)$	*Two-legged hop*	Γ_{arm}	$\mathbf{Z}_2(\kappa)$
Walk	Γ_{quad}	$\mathbf{Z}_2(\kappa\omega^2)$	*Walk*	Γ_{arm}	$\mathbf{Z}_2(\kappa\omega^2)$
Rotary jump	$\mathbf{Z}_4(\kappa\omega)$	1	*Gallop*	$\mathbf{Z}_2(\omega^2)$	1
Transverse jump	$\mathbf{Z}_4(\omega)$	1	*Gallop*	$\mathbf{Z}_2(\omega^2)$	1
Scuttle	$\mathbf{Z}_2(\kappa)$	1	*Skip*	$\mathbf{Z}_2(\kappa)$	1
Loping trot	$\mathbf{Z}_4(\kappa\omega)$	$\mathbf{Z}_4(\kappa\omega)$	*One-legged hop*	$\mathbf{Z}_2(\omega^2)$	$\mathbf{Z}_2(\omega^2)$
Rotary gallop	$\mathbf{Z}_4(\kappa\omega)$	$\mathbf{Z}_2(\omega^2)$	*One-legged hop*	$\mathbf{Z}_2(\omega^2)$	$\mathbf{Z}_2(\omega^2)$
Loping pace	$\mathbf{Z}_4(\omega)$	$\mathbf{Z}_4(\omega)$	*One-legged hop*	$\mathbf{Z}_2(\omega^2)$	$\mathbf{Z}_2(\omega^2)$
Transverse gallop	$\mathbf{Z}_4(\omega)$	$\mathbf{Z}_2(\omega^2)$	*One-legged hop*	$\mathbf{Z}_2(\omega^2)$	$\mathbf{Z}_2(\omega^2)$

Symmetry pairs (H, K) of standard quadrupeds gaits (quad) and symmetry pairs (H', K') of bipeds gaits (arm). The identification of bipedal gaits can be found in Sect. 2.1

how we can identify the biped gaits *two-legged hop*, *run*, and *gallop* with perturbed quadruped gaits in quad. We also explain why the biped *walk* cannot be thought of as a small symmetry-breaking perturbation of any standard quadruped gait in quad.

Perturbed pronk   The pronk has symmetry pair $(H, K) = (\Gamma_{\mathsf{quad}}, \Gamma_{\mathsf{quad}})$. After symmetry breaking, the perturbed pronk has symmetry pair $(H', K') = (\Gamma_{\mathsf{arm}}, \Gamma_{\mathsf{arm}})$. The pronk is a periodic solution in which equal signals are sent to all muscles; the perturbed pronk is a periodic solution in which the muscles in both the legs and the arms receive the same signal, and the signals sent to the arms are close to the signals sent to the legs. Thus, arms and legs move almost synchronously and this is similar to the *two-legged hop*, see Fig. 7 in [38].

Perturbed transverse jump   Both the rotary and the transverse jump perturb to a quadruped gait where the legs have the rhythms of a *gallop*. However, only the perturbed transverse jump produces periodic solutions with rhythms in interlimb coordination seen in the usual biped *gallop*.

In the typical biped *gallop* [48], the phases between the two arms are similar to their feet phasing and the arms and legs on the same side are close to synchrony. The two perturbed jumps, rotary and transverse, have an asymmetric arm pattern driven by leg phasing, nevertheless, only the later has arms and legs on the same side close to synchrony. Whitall et al. [48] also observe that in the *gallop* there can be much variability in the phasing between arms and legs. Indeed, in many subjects, the two arms are a half-period out of phase; this symmetric arm pattern is not a small perturbation of any quadruped gait.

Perturbed trot   In the biped *run* (see [47, Fig. 1]) the two arms and the two legs are a half period out of phase and the diagonal limbs are approximately synchronous. We have discussed previously that the two signals sent to (the muscle groups of the ankle joint of) a leg are approximately in-phase.

In arm the perturbed trot has symmetry pair $(H', K') = (\Gamma_{\mathsf{arm}}, \mathbf{Z}_2(\omega^2))$. In particular, ω^2 is a space symmetry so that the two signals sent to the same limb are synchronous. Since κ is a spatiotemporal symmetry, the two arms and the two legs are a half period out of phase. Since the arm solution is a perturbation of a trot in quad, pairs of diagonal limbs should be approximately synchronous. For these reasons we can identify a perturbed trot with a biped *run*.

The biped walk   As we discuss, the leg rhythms of a quadruped walk correspond to those in a biped *walk*. However, when one takes into account arm/leg coordination, the *walk* cannot be considered a small symmetry-breaking perturbation of the quadruped walk or indeed of any other quadruped gait. In general, at fast walking velocities, the left arm and the right leg are close to synchrony, and at slow walking velocities the arms move synchronously and twice as fast as the legs [18,17].

In our models the quadruped walk perturbs to a periodic solution in arm with symmetry pair $(H', K') = (\Gamma_{\mathsf{arm}}, \mathbf{Z}_2(\kappa\omega^2))$. Since ω^2 is a spatiotemporal symmetry the signals sent to muscle groups in the same limb are a half-period out of phase. Since κ is a spatiotemporal symmetry the signals sent to opposite limbs are also a half-period out of phase. These characterizations agree with those of a biped *walk*. However, if a periodic solution in quad is perturbed to

a periodic solution in arm, then the signals sent to an ipsilateral arm and leg will be approximately shifted by a quarter-period, which, as noted, does not agree with the interlimb coordination patterns of a biped *walk*. Moreover, as summarized in the second column of Table 2, the only quad gait that could correspond to a biped *walk* is the quadruped walk.

Our model arm suggests that transition from the quadruped walk to the biped *walk* is more complex than a small perturbation of a quadruped gait and this conclusion is in agreement with Schmidt [43], where it is suggested that evolution of bipedalism is a complicated process that cannot involve a simple transition between quadrupeds and bipeds. See also [29,42,2].

4 Conclusion

Following [24,25] we identify gait types in ODE CPG models with the spatiotemporal symmetries of possible periodic solutions. We discuss two issues concerning biped gaits. First, we show that the four-cell model leg introduced in [24,25] supports 10 different symmetry types of periodic solutions with nontrivial rhythms. Two of these rhythms were identified previously with the biped gaits *walk* and *run*. Here we identify six additional types of biped gaits: *two-legged hop*, *two-legged jump*, *skip*, *gallop*, *asymmetric hop*, and *one-legged hop*. We have not been able to identify the two remaining nontrivial rhythms with known bipedal gaits. See Table 1. This is also the case with quad, where certain periodic solution types have not been identified with known quadruped gaits.

Second, we discuss whether biped gait rhythms in CPGs could have evolved from quadruped gaits. At the simplest level, we observe that with one exception each known biped gait, as modeled in leg can be obtained by focusing on the hindleg rhythms in standard gaits found in quad. See Table 2. The exception is the *asymmetric hop*, which is curious because the only observation of this gait that we can find is in birds [44]. However, since it is well accepted that bipeds evolved from quadrupeds [29,42,43], it is much more interesting to ask whether or not the typical patterns of arm/leg coordination in bipeds can be obtained by small perturbations of quadruped gaits.

There is a large literature on the topic of arm/leg coordination [14,15,17–19, 23,45–48]. In particular, Schmidt [43] argues that several stages are needed to evolve from quadruped gaits to observed arm/leg coordination patterns in bipeds, and we offer evidence to support this conclusion. See also [29,42,2]. In particular, we show that perturbations of any standard quadruped gait modeled by quad do not lead to the correct arm/leg coordination pattern in the usual biped *walk*. On the positive side we find that small perturbations of the three quadruped gaits, pronk, trot, and transverse jump can be identified with the arm and leg rhythms in the biped gaits *two-legged hop*, *run*, and *gallop*. So, although arm by itself is inadequate to explain biped interlimb coordination, it may help us to understand how interlimb coordination in biped gaits evolved from quadruped gaits.

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