

Hard-wired central pattern generators for quadrupedal locomotion

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Received: 17 September 1993/Accepted: 16 April 1994

Abstract. Animal locomotion is generated and controlled, in part, by a central pattern generator (CPG), which is an intraspinal network of neurons capable of producing rhythmic output. In the present work, it is demonstrated that a hard-wired CPG model, made up of four coupled nonlinear oscillators, can produce multiple phase-locked oscillation patterns that correspond to three common quadrupedal gaits – the walk, trot, and bound. Transitions between the different gaits are generated by varying the network's driving signal and/or by altering internal oscillator parameters. The above *in numero* results are obtained without changing the relative strengths or the polarities of the system's synaptic interconnections, i.e., the network maintains an invariant coupling architecture. It is also shown that the ability of the hard-wired CPG network to produce and switch between multiple gait patterns is a model-independent phenomenon, i.e., it does not depend upon the detailed dynamics of the component oscillators and/or the nature of the inter-oscillator coupling. Three different neuronal oscillator models – the Stein neuronal model, the Van der Pol oscillator, and the FitzHugh-Nagumo model – and two different coupling schemes are incorporated into the network without impeding its ability to produce the three quadrupedal gaits and the aforementioned gait transitions.

1 Introduction

Legged animals typically employ multiple gaits, i.e., phase-locked patterns of limb movements, for terrestrial locomotion. Quadrupeds, for example, commonly walk, trot, and bound (or gallop) (Dagg 1973; Gambaryan 1974; Hildebrand 1976, 1977). A number of experimental studies have demonstrated that animal locomotion is generated and controlled, in part, by a central pattern generator (CPG), which is an intraspinal network of neurons capable of producing rhythmic output (for reviews, see Grillner 1975, 1981, 1985; Shik and Orlovsky

1976; Stein 1978). Shik et al. (1966), for instance, showed that mesencephalic cats could exhibit a walking gait on a treadmill when an area of the midbrain was electrically stimulated. Moreover, they found that such preparations could switch from the walk to the trot to the gallop if either the strength of the stimulation or the speed of the treadmill was increased.

Although the aforementioned studies established the existence of rhythm-generating networks in the central nervous system (CNS), a vertebrate CPG for legged locomotion remains to be identified and/or isolated. As a result, little is known about the number or specific characteristics of the neurons or interconnections making up a locomotor CPG. Consequently, several researchers have resorted to using modelling techniques to gain insight into the possible functional organization of such networks. The most popular approach to date has involved the construction and analysis of systems of coupled nonlinear oscillators (Kopell 1988; Rand et al. 1988). Bay and Hemami (1987) and Taga et al. (1991), for example, utilized coupled-oscillator systems to control the movements of segmented bipeds. Many others have used networks of four coupled oscillators to represent quadrupedal locomotor CPGs (Willis 1980; Stafford and Barnwell 1985; Schöner et al. 1990; Yuasa and Ito 1990, 1992; Collins and Stewart 1992, 1993a; Jeka et al. 1993a).

Despite joint and independent efforts of experimentalists and theorists, the neural mechanisms underlying gait transitions in legged animals remain unclear.¹ In the aforementioned oscillator models, gait transitions are typically produced by selectively changing either the relative strength (Stafford and Barnwell 1985; Yuasa and Ito 1990) or the polarity (Bay and Hemami 1987) of the coupling that acts between the CPG oscillators. Within these modelling schemes, the locomotor CPG is essentially 'rewired' in order to produce different gait patterns. This work is aligned with the following statement of Grillner (1985, pp 147–148): 'In tetrapods the need to

¹ For discussions of the possible mechanical and metabolic factors that influence gait transitions, see the work of Taylor and colleagues (Taylor 1978; Hoyt and Taylor 1981; Farley and Taylor 1991). For a detailed review of previous neural-modelling studies that deal with gait transitions, see Collins (1995)

modify limb coordination with walking, trotting, and galloping *requires* [our italics] different sets of coordinating neurons to combine the limb CPG's in the different phase relations required for the particular type of gait.' Thus, according to this proposed control strategy, the trot-to-bound transition, for example, may be generated by switching from a set of mutually inhibiting coordinating neurons to another set that utilizes mutual excitation (Grillner and Wallén 1985).

Collins and Stewart (1992, 1993a,b), on the other hand, proposed that a 'hard-wired' CPG, i.e., one with fixed interconnections between its component oscillators, should be capable of generating multiple phase-locked oscillation patterns that correspond to different animal gaits. Their prediction was based on a group-theoretic analysis of various symmetric networks of coupled nonlinear oscillators. Specifically, Collins and Stewart utilized a symmetry-based approach to investigate the universal features of general classes of models for CPGs that could control bipedal, quadrupedal, and hexapodal locomotion. Gait transitions were modelled as symmetry-breaking bifurcations of various kinds. Within this modelling scheme, the respective coupled-oscillator networks could, in principle, be forced to switch between different phase-locked oscillation patterns (gaits) by varying certain system parameters, such as the amplitude of a command driving signal or the internal parameters of the individual CPG oscillators. It should also be noted that the above abstract results are model-independent, i.e., they do not depend upon the mathematical details of the oscillators' intrinsic dynamics or the nature of the inter-oscillator coupling.

Motivated by the aforementioned theoretical predictions of Collins and Stewart, we designed a series of computer experiments to test two hypotheses: (1) a hard-wired CPG can produce multiple phase-locked oscillation patterns that correspond to natural animal gaits; and (2) the production of multiple phase-locked oscillation patterns by a hard-wired CPG is a model-independent phenomenon. In order to address the former hypothesis, we modelled a quadrupedal locomotor CPG as a system of four coupled nonlinear oscillators and tested the ability of such a network to produce three common quadrupedal gaits – the walk, trot, and bound. We attempted to generate transitions between the different gaits by changing the network's driving signal and/or by altering the internal parameters of the component CPG oscillators. In order to address the latter hypothesis, we analyzed and compared the effects of using three different neuronal-oscillator models – the Stein neuronal model, the Van der Pol oscillator, and the FitzHugh-Nagumo model – as the unit oscillators for the aforementioned locomotor CPG.

2 Background and methods

2.1 Quadrupedal gaits

Quadrupeds can adopt a number of different gaits, depending upon their speed of locomotion and the terrain

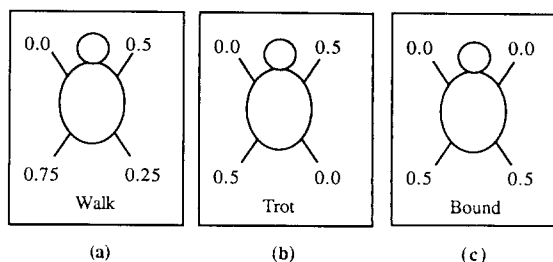


Fig. 1. Phase relations for three common quadrupedal gaits: (a) walk, (b) trot, and (c) bound

(Dagg 1973; Gambaryan 1974; Hildebrand 1976, 1977). In this study, we considered three of the more common quadrupedal gaits – the walk, trot, and bound. These gaits are shown schematically in Fig. 1. In the walk, which is a slow-speed gait, the limbs move a quarter period out of turn, in a figure-eight wave. In the trot, which is a medium-speed gait, diagonal limbs, e.g., right front and left hind, move together and in phase, and pairs of diagonal limbs move half a period out of phase with one another. (The pace is another medium-speed gait; in this case, ipsilateral limbs move together and in phase, and left and right limbs move 180° out of phase with each other.) The bound, which is a fast-speed gait, is similar to the trot, except that front and hind limbs, respectively, move together and in phase. (The gallop, which is also a fast-speed gait, resembles the bound, except the limbs of the front and hind pairs are slightly out of phase with each other.) Other quadrupedal gaits, such as the canter, pronk, and half-bound (Collins and Stewart 1993a), but they are less common and were not considered in this investigation.

In the present study, a CPG model was considered to be in a particular gait mode if the relative phases of the respective oscillator output signals were within 10% of a gait cycle of those expected for the ideal gait (Fig. 1). The above criterion was considered reasonable given the variability of natural animal gaits (e.g., Afelt et al. 1983; Alexander and Jayes 1983).

2.2 CPG network architecture

We modelled a quadrupedal locomotor CPG as a network of four coupled nonlinear oscillators. Each oscillator controlled the stepping movements of a single limb of a model animal (Arshavsky et al. 1965), e.g., when the output signal of a CPG oscillator reached its maximum value, the limb controlled by that oscillator initiated its next step. In the present study, we were not concerned with the patterns of muscle activity within each limb; we were only interested in interlimb coordination, i.e., the relative phases between the limbs (CPG oscillators) of the model quadruped. Interlimb coordination resulted from the coupling, and hence dynamic interactions, of the component CPG oscillators.

We considered the network shown in Fig. 2. Oscillators 1, 2, 3 and 4 control the timing of the left front (LF), left hind (LH), right hind (RH), and right front (RF)

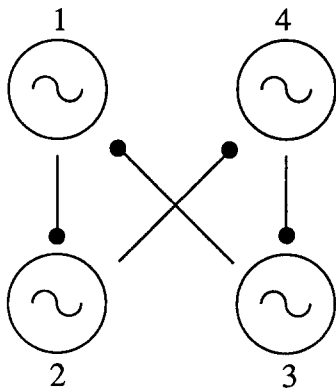


Fig. 2. Graphical representation of the locomotor central pattern generator (CPG) network of coupled nonlinear oscillators. Oscillators 1, 2, 3, and 4 control the timing for the left front, left hind, right hind, and right front limbs of a model quadruped, respectively. Solid lines between oscillators represent inhibitory coupling, with the filled circle next to the inhibited oscillator

limbs, respectively. Solid lines between oscillators represent inhibitory interconnections (Pearson 1993), with the filled circle next to the inhibited oscillator (Fig. 2), e.g., oscillator 1 inhibits oscillator 2. The CPG network of Fig. 2 is thus a ring network with Z_4 symmetry, i.e., the system has unidirectional coupling. This relatively simple coupling architecture was held fixed throughout the computer experiments, i.e., neither the polarity nor the relative strength of the respective synaptic interconnections was modified in order to generate the different gait patterns.

2.3 Neuronal-oscillator models

Here, we consider three different neuronal-oscillator models – the Stein neuronal model, the Van der Pol oscillator, and the FitzHugh-Nagumo model.

2.3.1 Stein neuronal model. The Stein neuronal model (Stein et al. 1974a), which is capable of producing oscillatory output, is defined by the following set of coupled differential equations:

$$\begin{aligned} \dot{x}_i &= a \cdot \left[-x_i + \frac{1}{1 + \exp(-f_{ci} - by_i + bz_i)} \right] \\ \dot{y}_i &= x_i - py_i \\ \dot{z}_i &= x_i - qz_i \end{aligned} \quad (1)$$

for $i = 1, 2, 3, 4$ where x_i represents the membrane potential (or the firing rate) of the i th neuronal oscillator, a is a rate constant affecting the frequency of the oscillations, f_{ci} is the driving signal for oscillator i , b allows the model to adapt to a change in stimulus, and p and q control the rate of this adaption (Stein et al. 1974a). Adaption, in this case, refers to the time-dependent decline in the firing rate of the model following the application of a step change in the driving stimulus (Stein et al. 1974a).

Inhibitory coupling between the CPG oscillators was achieved by decreasing the magnitude of the *inhibited* oscillator's driving signal by an amount proportional to the *inhibiting* oscillator's signal. [This method for implementing coupling was modified from Stein et al. (1974b).] The driving signal f_{ci} , which, in the present study, was assumed to have both a steady-state (tonic) component and a periodic (phasic) component, thus took the form:

$$f_{ci} = f \cdot \left[1 + k_1 \sin(k_2 t) + \sum_{j=1}^4 \lambda_{ji} \cdot x_j \right] \quad (2)$$

where f is an amplitude parameter, k_1 and k_2 control the amplitude and frequency, respectively, of the periodic component of the driving signal, λ_{ji} is a coupling term that represents the strength of oscillator j 's effect on oscillator i , and x_j is the membrane potential of oscillator j . The value of λ_{ji} was set to -0.2 if oscillator j inhibited oscillator i (see Fig. 2), and its value was set to 0.0 if oscillator j did not affect oscillator i . With the exception of the coupling term in (2), the driving signals to the respective CPG oscillators were identical.

2.3.2 Van der Pol oscillator. Van der Pol oscillators have been used extensively in physiological modelling studies (e.g., see Winfree 1990). The Van der Pol oscillators considered in the present investigation were defined by the following equation modified from Bay and Hemami (1987):²

$$\ddot{x}_i + \mu \cdot (x_{ai}^2 - p^2) \cdot \dot{x}_i + g^2 \cdot x_{ai} = q \cdot [1 + k_1 \sin(k_2 t)] \quad (3)$$

for $i = 1, 2, 3, 4$ where x_i is the output signal from oscillator i , x_{ai} is the same signal affected by the coupling [see (4) below], μ controls the degree of the nonlinearity of the oscillator (and thereby affects the shape of its waveform), p controls the amplitude of the oscillations, g influences the frequency of the oscillations, q is an amplitude parameter, and k_1 and k_2 control the amplitude and frequency, respectively, of the periodic component of the driving signal.

Coupling was introduced in the manner proposed by Bay and Hemami (1987), where:

$$x_{ai} = x_i + \sum_{j=1}^4 \lambda_{ji} \cdot x_j \quad (4)$$

where λ_{ji} is a coupling term that represents the strength of oscillator j 's effect on oscillator i , and x_j is the output signal from oscillator j . As with the Stein CPG model, the value of λ_{ji} was set to -0.2 if oscillator j inhibited oscillator i , and its value was set to 0.0 if oscillator j did not affect oscillator i . The synaptic interconnectivity for the Van der Pol CPG model had to be reversed from that shown in Fig. 2, e.g., oscillator 2 inhibited oscillator 1 in the Van der Pol CPG model. With the coupling arrangement of Fig. 2, the Van der Pol CPG model produced

² In the present study, the CPG driving signal was modified to include a steady-state component and a periodic component. Flaherty and Hoppensteadt (1978) offer a detailed treatment of periodically forced Van der Pol oscillators

a 'backwards' walk, i.e., the limbs of the model quadruped moved in the order LF, LH, RF, and RH, as opposed to the desired LF, RH, RF, and LH (Fig. 1). The Van der Pol CPG model could produce a 'forwards' walk (see Sect. 3.2.1) if the coupling interconnections were reversed. The need for this directional change, which did not alter the network's symmetry, was likely due to the different coupling method.

2.3.3 FitzHugh-Nagumo model. The FitzHugh-Nagumo model, which was developed and analyzed by FitzHugh (1961) and Nagumo et al. (1962), is defined by the following equations (Edelstein-Keshet 1988):

$$\dot{x}_i = c \cdot \left(y_i + x_i + \frac{x_i^3}{3} + f_{ci} \right) \quad (5)$$

$$\dot{y}_i = -(x_i - a + b \cdot y_i)/c$$

for $i = 1, 2, 3, 4$, where x_i is the membrane potential of the i th neuronal oscillator,³ f_{ci} is the driving signal for oscillator i , and a , b , and c are constants that do not correspond to any particular physiological parameters (FitzHugh 1961).

Inhibitory coupling was implemented in a manner similar to that for the Stein CPG model, i.e., the coupling served to decrease the driving signal acting on the inhibited oscillator. The driving signal f_{ci} , which, as with the Stein and Van der Pol CPG models, was assumed to have a tonic component and a periodic component,⁴ thus took the form:

$$f_{ci} = f_a + f_b \cdot \left[k_1 \sin(k_2 t) + \sum_{j=1}^4 \lambda_{ji} \cdot x_j \right] \quad (6)$$

where f_a is the steady-state value of the driving signal, f_b is an amplitude parameter that affects the magnitude of the variable component of the driving signal, k_1 and k_2 control the amplitude and frequency, respectively, of the periodic component of the driving signal, λ_{ji} is a coupling term that represents the strength of oscillator j 's effect on oscillator i , and x_j is the membrane potential of oscillator j . As with the other two CPG models, the value of λ_{ji} was set to -0.2 if oscillator j inhibited oscillator i , and its value was set to 0.0 if oscillator j did not affect oscillator i . The coupling arrangement of Fig. 2 was utilized in the FitzHugh-Nagumo CPG model.

2.4 Numerical analysis

The respective differential equations governing the Stein, Van der Pol, and FitzHugh-Nagumo CPG models were solved numerically using the fourth-order Runge-Kutta integration method with a stepsize equal to 0.005 s. Smaller stepsizes produced the same results for the respective CPG models; a stepsize of 0.005 s was thus used

Table 1. Representative parameter values for the walking, trotting, and bounding gaits of the three CPG models. For the Stein CPG model, p , b , and q were held fixed at values of 10.0 , -2000.0 , and 30.0 , respectively. For the Van der Pol CPG model, g^2 and μ were held constant at values of 20.0 and 1.0 , respectively. For the FitzHugh-Nagumo CPG model, a and b were held fixed at values of 0.1 and 0.5 , respectively

CPG model	Parameter	Walk	Trot	Bound
Stein	a	10.0	12.0	16.0
	f	40.0	40.0	50.0
	k_1	0.0	0.1	0.1
	k_2	0.0	57.0	59.0
Van der Pol	p^2	3.0	3.0	10.0
	q	0.0	-25.0	-25.0
	k_1	0.0	5.0	5.0
	k_2	0.0	7.5	7.5
FitzHugh-Nagumo	c	0.75	1.5	1.5
	f_a	0.0	0.0	1.0
	f_b	1.0	1.0	1.5
	k_1	0.0	2.0	2.0
	k_2	0.0	1.0	1.0

for reasons of computational efficiency. All testing was conducted on a 386 IBM-compatible personal computer.

3 Results

3.1 Stein CPG model

3.1.1 Production of multiple gait patterns. With a tonic driving signal, the Stein CPG model could produce either the walk or the bound from a random set of initial relative-phase conditions. The production of the respective gaits depended upon the specific values of the system parameters. For example, with the parameter values given in the first column of Table 1, the Stein CPG model generated the walking gait, whereas with larger values for parameter a , it produced the bounding gait (from a random set of initial relative-phase conditions). Moreover, the system could be switched from the walk to the bound simply by increasing the rate constant a (and thereby increasing the intrinsic frequency) of all four neuronal oscillators.⁵ (However, as noted in Sect. 3.1.2, the reverse transition, i.e., the bound-to-walk transition, could not be obtained by returning parameter a to its original value.)

If a periodic component was added to the system's driving signal, then the model could also move from the walk to the trot. Once in the trotting mode, the CPG model could be switched into the bound by increasing the value of the amplitude parameter (f) of the driving signal and/or by increasing the value of a . Thus, in short, the hard-wired Stein CPG model was capable of producing phase-locked oscillation signals corresponding to

³ As with the Stein neuronal model, the FitzHugh-Nagumo model is capable of exhibiting oscillatory behavior (Edelstein-Keshet 1988)

⁴ For a more extensive treatment of FitzHugh-Nagumo equations with periodic forcing, see Alexander et al. (1989)

⁵ In the computer experiments described in Sects. 3.1 and 3.2, the values of the respective parameters for each of the four component oscillators were changed in identical ways, e.g., the parameter values for an individual CPG oscillator were not selectively modified

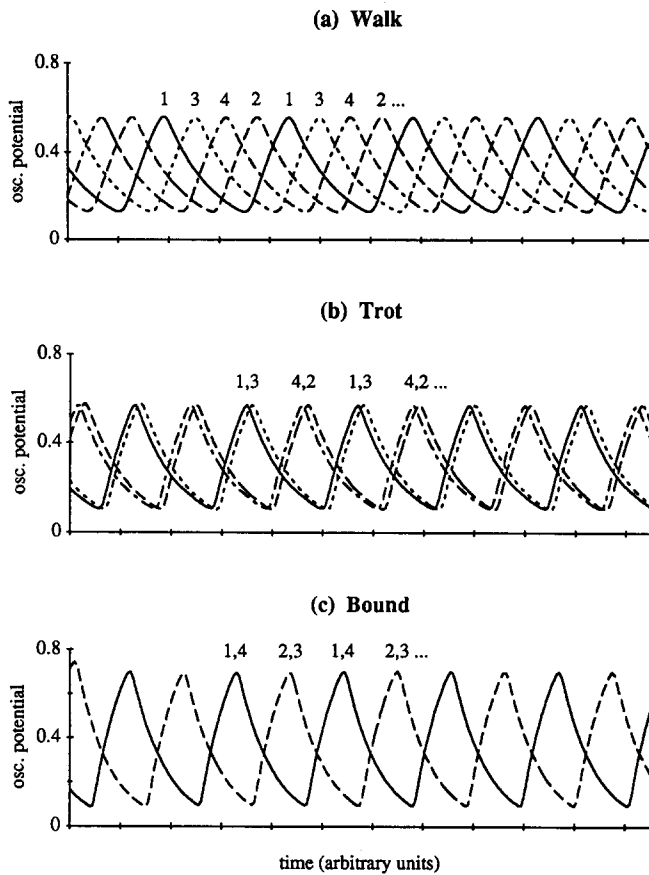


Fig. 3. Output patterns from the Stein CPG model corresponding to: (a) the walking gait, (b) the trotting gait, and (c) the bounding gait. These results were generated using the parameter values listed in Table 1

the walk, trot, and bound (Fig. 3).⁶ Table 1 provides a listing of the parameter values that were used to generate the results given in Fig. 3.

Since the value of a increased from the walk to the trot to the bound (Table 1), the oscillator's frequency, and thus the model animal's stepping frequency, increased as the Stein CPG model switched to 'faster' gaits. The parameter k_2 , which controlled the frequency of the sinusoidal component of the driving signal, also increased from the trot to the bound (Table 1), although this change was not needed to switch the system into the bounding gait. When a periodic component was present in the driving signal, the CPG oscillators became entrained to the sine wave such that they completed one cycle for every two driving-signal cycles. The values of 57 and 59 for k_2 were chosen for the trot and bound,

⁶ The output signals for the trot (Fig. 3b) did not correspond exactly to those expected for the ideal gait (Fig. 1): there were small phase differences (less than 10% of the gait cycle) between the output signals of diagonal oscillators. These slight phase differences, which were observed experimentally by Afelt et al. (1983) in trotting dogs, were likely due to the inhibition from oscillators 2 and 3 that acted on oscillators 4 and 1, respectively (Fig. 2)

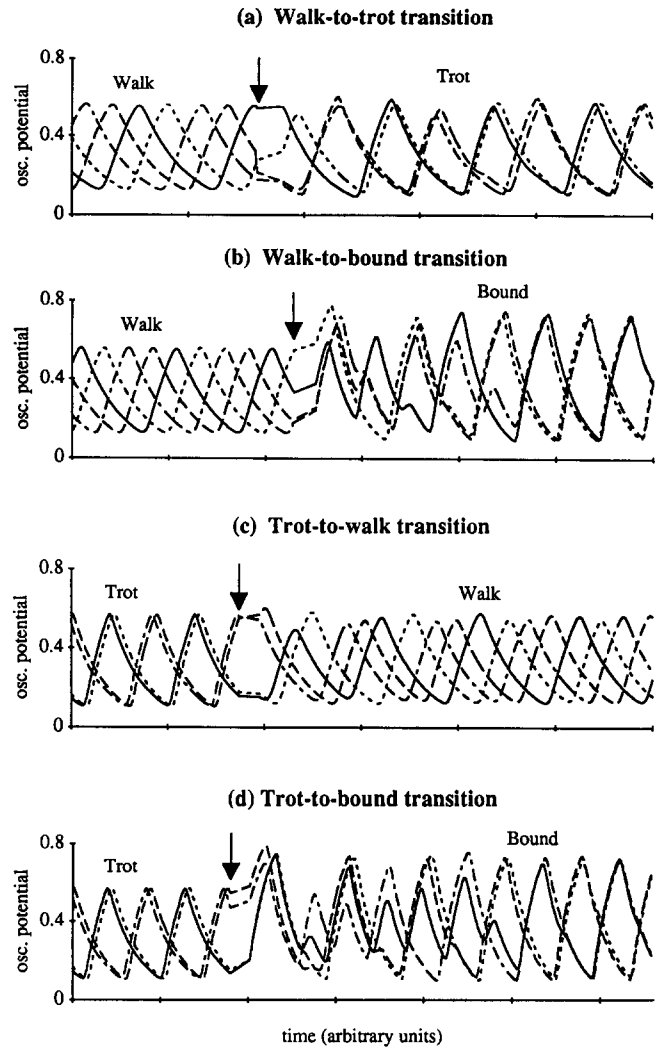


Fig. 4. Output patterns from Stein CPG model demonstrating: (a) the walk-to-trot transition, (b) the walk-to-bound transition, (c) the trot-to-walk transition, and (d) the trot-to-bound transition. Arrow in each plot indicates the point at which the system parameters were changed

respectively, because the resulting frequencies of the driving signal were close to twice the natural frequencies of the trotting and bounding CPG models (for the respective sets of representative parameter values given in Table 1).

3.1.2 Gait transitions. By changing the network's driving signal and/or by varying the internal parameters of the component oscillators (e.g., as indicated by the different sets of parameters listed in Table 1), four different gait transitions – the walk-to-trot, walk-to-bound, trot-to-walk, and trot-to-bound transitions – could be obtained with the Stein CPG model (Fig. 4). As observed in real animals (Jayes and Alexander 1978), transitions between the walk and trot could be either gradual or abrupt. With the CPG model, the nature of the transitions depended upon the nature of the parameter variation. For example, if the amplitude (k_1) of the periodic component of the driving signal was increased

slowly (gradually), then a gradual walk-to-trot transition was produced. If, on the other hand, k_1 was increased instantaneously, then the resulting walk-to-trot transition was completed within a single gait cycle.⁷

Transitions from the bound, however, could not be induced via parameter variation. Once the Stein CPG model was in the bounding gait, it maintained that gait even if the system parameters were returned to their original values for either the walk or the trot. Consequently, we explored other possible mechanisms for generating transitions from the bound; this work is described in Sect. 3.3.

3.2 Van der Pol and FitzHugh-Nagumo CPG models

3.2.1 Production of multiple gait patterns. As with the Stein CPG model, the walking, trotting, and bounding gaits could be produced with the hard-wired Van der Pol and FitzHugh-Nagumo CPG models. Representative output patterns from the two models are shown in Figs. 5 and 6, respectively. Table 1 lists the parameter values that were utilized to generate these patterns.

The representative parameter values for the walking gait of the Van der Pol CPG model (Table 1) were adapted from those used by Bay and Hemami (1987). Since Van der Pol oscillators are capable of self-sustained oscillations, an external input was not needed to generate and maintain the walk, i.e., q was set to 0.0. However, a driving signal was added to the system in order to move the CPG model from the walk to the trot (Table 1). (As with the Stein CPG model, the frequency of the periodic component of the driving signal was approximately twice the natural frequency of the model's trotting mode, as defined by the parameters given in Table 1.) The Van der Pol CPG model could then be switched from the trot to the bound by increasing parameter p . As the system moved to 'faster' gaits, its output frequency could be increased by increasing parameter g ; this change, however, was not needed to produce the different gait patterns.

The FitzHugh-Nagumo CPG model could be switched from the walk to the trot by increasing parameter c (which served to increase the stepping frequency of the model animal) and adding a periodic component to the driving signal. [As with the Stein and Van der Pol CPG models, the value of k_2 was chosen such that the frequency of the periodic component of the driving signal was approximately twice the oscillators' natural frequency for the representative set of trotting parameters (Table 1).] If the amplitude parameters for the steady-state (f_a) and variable (f_b) components of the driving signal were then increased (Table 1), the model could

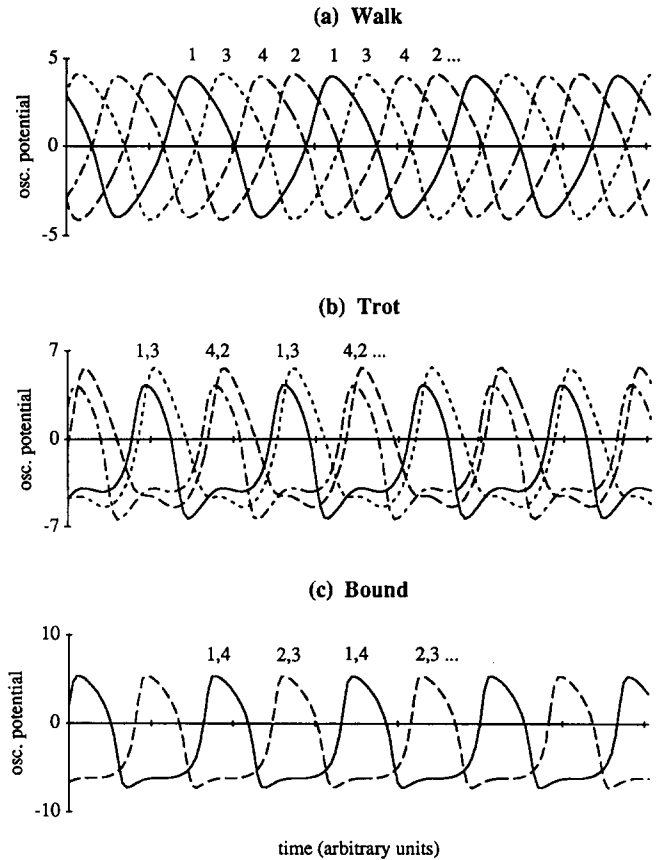


Fig. 5. Output patterns from the Van der Pol CPG model corresponding to: (a) the walking gait, (b) the trotting gait, and (c) the bounding gait. These results were generated using the parameter values listed in Table 1

move from the trot to the bound. As the system switched from the trot to the bound, its output frequency could be raised by increasing parameter c ; however, this change was not needed to produce the bounding gait.

The respective phase-locked oscillation patterns for the trotting gait of the Van der Pol (Fig. 5b) and FitzHugh-Nagumo (Fig. 6b) CPG models were neither identical nor exactly in-phase. However, given our assumptions that the present locomotor CPG networks only regulate the *relative timing* of the limbs of a model quadruped and that a step would be initiated when the output signal of a limb's CPG oscillator reached its maximum value (Sect. 2.1), these oscillation signals met our criterion for establishing a trotting gait. That is, the maximum values of the output signals of diagonal CPG oscillators were separated in time by less than 10% of a gait cycle.

3.2.2 Gait transitions. As with the Stein CPG model, four gait transitions – the walk-to-trot, walk-to-bound, trot-to-walk, and trot-to-bound transitions – could be obtained with the Van der Pol and FitzHugh-Nagumo CPG models by varying system parameters (e.g., between the respective sets of values given in Table 1). In each case, the above transitions could be generated by

⁷ A change in parameter a , as suggested by Table 1, was not necessary for the walk-to-trot and trot-to-walk transitions. Parameter a was increased from the walk to the trot in the set of representative parameter values (Table 1) only to ensure that the 'faster' gait had a higher stepping frequency. Similarly, an increase in the amplitude parameter f (Table 1) was not necessary for the walk-to-bound transition, although this change did facilitate the transition, e.g., it reduced the switching time

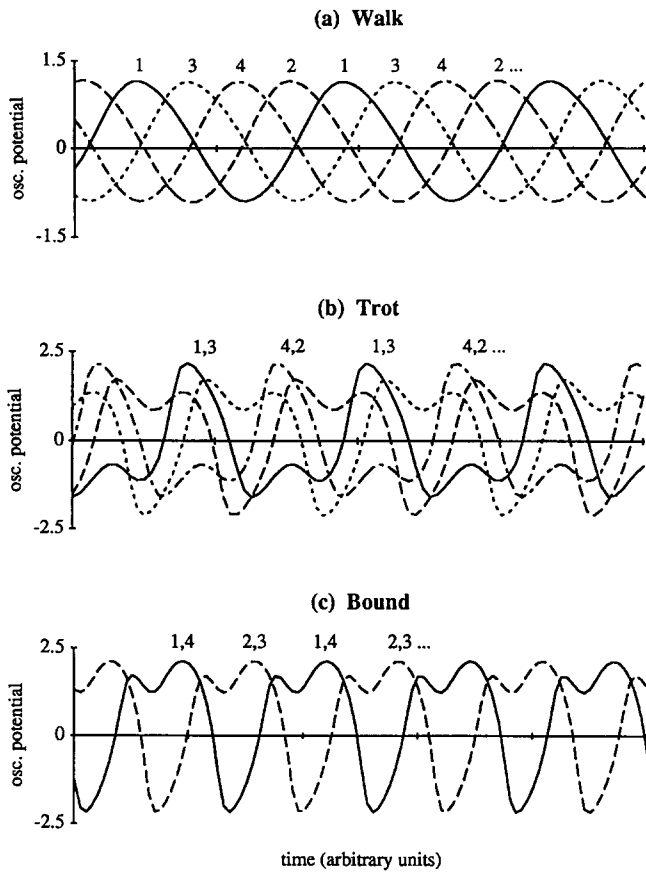


Fig. 6. Output patterns from the FitzHugh-Nagumo CPG model corresponding to: (a) the walking gait, (b) the trotting gait, and (c) the bounding gait. These results were generated using the parameter values listed in Table 1

changing the nature of the network's driving signal⁸ and/or by modifying the internal parameters of the component CPG oscillators. Moreover, as before, transitions from the bounding gait could not be induced via parameter variation.

3.3 Alternative gait-transition mechanisms

3.3.1 'Lead-leg' strategy. As discussed above, gait transitions from the bound via parameter variation were not possible with any of the three CPG models. In an attempt to generate the elusive bound-to-walk and bound-to-trot transitions, we developed a strategy whereby one of the four oscillators making up the network was selectively hyperstimulated. Specifically, we increased the amplitude parameter of the driving signal for one CPG oscillator by at least 100% for time periods ranging from 10% to 240% of a gait cycle. When the increased driving signal was returned to its original

value, the system parameters were then simultaneously switched from those of the bound to those of the desired gait, i.e., either the walk or the trot (Table 1). It was hoped that this approach, which we referred to as the 'lead-leg' strategy,⁹ would cause the CPG oscillators in the front and hind pairs, respectively, to shift from an in-phase state to an antiphase state.

However, when the 'lead-leg' strategy was applied to any one of the four neuronal oscillators making up the three CPG models, gait transitions from the bound were *never* obtained. In all cases, the unaffected pair of in-phase oscillators, i.e., either the front pair or the hind pair, forced the hyperstimulated oscillator and the fourth CPG oscillator back into phase with each other following the hyperstimulation period. Thus, the bounding gait could not be 'broken' by selectively stimulating only one of the CPG oscillators.

3.3.2 'Power-pair' strategy. The 'lead-leg' strategy failed to generate transitions from the bound largely because selective stimulation of a single CPG oscillator left a pair of in-phase oscillators essentially unaffected. Consequently, we implemented an alternate approach, which we referred to as the 'power-pair' strategy, whereby *two* of the component oscillators, i.e., a front-limb oscillator and a hind-limb oscillator, were subjected to an increased driving stimulus. As with the 'lead-leg' strategy, the amplitude parameters of the driving signals for the selected oscillators were increased by at least 100% for brief time periods; the increased driving signals were then returned to their original values, and the system parameters were simultaneously switched from those of the bound to those of either the walk or the trot (Table 1).

The 'power-pair' strategy was successful in generating the bound-to-walk and bound-to-trot transitions in all three CPG models¹⁰ (e.g., see Fig. 7). In most cases, the transitions were completed within one or two gait cycles. Similar results were obtained whether ipsilateral or diagonal pairs of oscillators were selectively hyperstimulated.

It was also found that the success of the 'power-pair' strategy in producing transitions from the bounding gait depended upon the relative values of the unaffected CPG oscillators at the time the increased driving signals were returned to their original values. Figure 8 presents results from a series of tests in which the right-limb oscillators (oscillators 3 and 4) of the Stein CPG model were hyperstimulated. In these tests, the CPG model consistently switched from the bound to the walk if the amplitude of the output signal of oscillator 1 was greater than that of oscillator 2 when the increased driving signals for oscillators 3 and 4 were returned to their original values

⁸ For the Van der Pol CPG model, the walk-to-trot transition was sensitive to the time in the gait cycle when the periodic component was added to the driving signal, i.e., under certain circumstances, the CPG model moved into the pace or the bound instead of the trot

⁹ This approach was motivated, in part, by the work of Deuel and Lawrence (1987), who documented a laterality or 'handedness' in the galloping gaits of horses. Given that a quadruped may favor one limb, we speculated that the favored limb (and its associated CPG oscillator) may be used to break the tight phase-locking of the bounding gait.

¹⁰ With the Van der Pol CPG model, the system parameters had to be switched (from those of the bounding gait to those of the desired gait) at the initiation, instead of the termination, of the hyperstimulation period

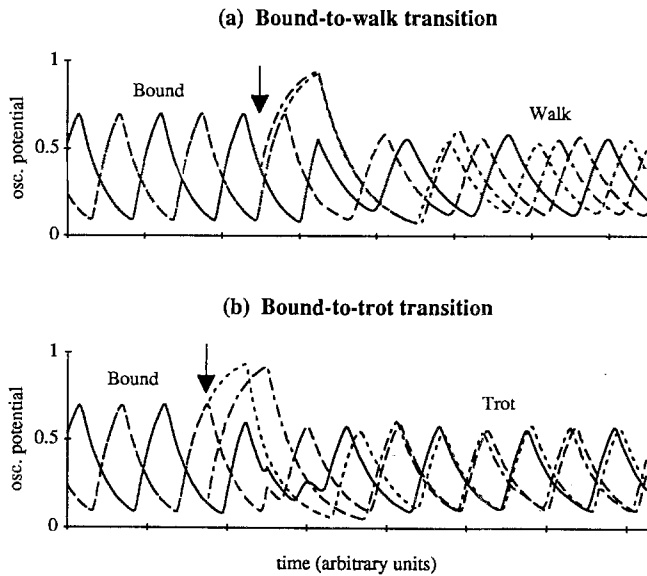


Fig. 7. Output patterns from the Stein CPG model demonstrating: (a) the bound-to-walk transition and (b) the bound-to-trot transition. These gait transitions were produced with the 'power-pair' strategy. Arrow in each plot indicates the point at which the hyperstimulation period was initiated

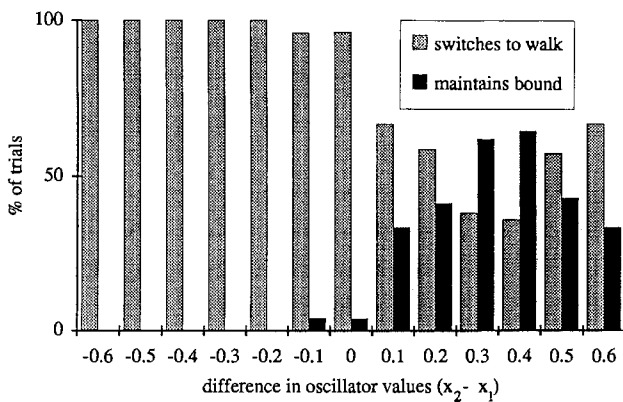


Fig. 8. The effects of the relative values of the unaffected CPG oscillators (at the termination of the hyperstimulation period) on the success of the 'power-pair' strategy in producing the bound-to-walk transition. These results were obtained from sets of multiple trials conducted with the Stein CPG model. In each trial, oscillators 3 and 4 were subjected to an increased driving signal; thus, oscillators 1 and 2 were the unaffected oscillators. Light bars indicate the percentage of trials for which the bound-to-walk transition was successful, whereas dark bars indicate the percentage of trials for which the transition was not successful, i.e., the CPG model remained in the bound

(Fig. 8). If, on the other hand, the amplitude of the output signal of oscillator 1 was less than that of oscillator 2 when the hyperstimulation period was terminated, then the CPG model sometimes remained in the bound (Fig. 8). Similar results were obtained with the bound-to-trot transition. Interestingly, the success of the 'power-pair' strategy did not depend upon the initiation time or the duration of the hyperstimulation period.

4 Discussion

We demonstrated that it was possible for a single, hard-wired CPG to produce multiple phase-locked oscillation patterns that correspond to three common quadrupedal gaits – the walk, trot, and bound. Transitions between the different gaits were generated by varying the driving signal and/or by altering oscillator parameters. Importantly, the above results were obtained without changing the relative strengths or the polarities of the system's synaptic interconnections, i.e., the network maintained an invariant coupling architecture.¹¹ We also showed that the ability of a hard-wired CPG to produce and switch between multiple gait patterns was a model-independent phenomenon, i.e., it did not depend upon the detailed dynamics of the component oscillators and/or the nature of the inter-oscillator coupling. (Instead, this general feature was likely due to the symmetry of the network itself.) Three different neuronal oscillator models – the Stein neuronal model, the Van der Pol oscillator, and the FitzHugh-Nagumo model – and two different coupling schemes (Sect. 2.3) were incorporated into the network without impeding its ability to produce the three quadrupedal gaits and the aforementioned gait transitions. These numerical results thus support the theoretical predictions of Collins and Stewart (1992, 1993a, b) and thereby demonstrate that abstract mathematical work can, in some cases, lead to testable hypotheses.

Although our work establishes the plausibility of utilizing a hard-wired CPG for quadrupedal locomotion, it obviously does not confirm the existence of such networks in the vertebrate CNS. Similarly, this investigation does not rule out the possibility that locomotor CPGs are reconfigured in order to produce different animal gaits, as suggested by Grillner (1981, 1985) and others. For instance, the notion that supraspinal centers may call upon functionally distinct sets of coordinating interneurons to generate different gait patterns is also plausible, although not yet experimentally established. In addition, from a slightly different but relevant perspective, it has been shown that rhythm-generating neuronal networks can be modulated, e.g., reconfigured, via the actions of neuroamines and peptides and thereby enabled to produce several different motor patterns (for reviews, see Harris-Warrick 1988; Getting 1989; Harris-Warrick and Marder 1991). This work, however, has largely been limited to invertebrate preparations. Thus, it is unclear whether similar neuromodulatory mechanisms are utilized in vertebrate motor systems.

¹¹ Earlier, Beer (1990) designed a hard-wired network for controlling hexapodal locomotion. In Beer's model, each leg of a model cockroach was controlled by a circuit made up of one pacemaker neuron, two sensory neurons, and three motor neurons. The pacemaker neurons of adjacent leg-controller circuits mutually inhibited one another. If the pacemaker neurons of the network were identical, then the model could generate the tripod gait. In order to produce metachronal-wave gaits, Beer varied the intrinsic frequencies of the component pacemaker neurons such that the natural frequency of the back-leg pacemakers was lower than that of the middle-leg pacemakers, which correspondingly was lower than that of the front-leg pacemakers. The present results were generated with a much simpler model made up of identical neuronal oscillators

From a physiological standpoint, the gait-transition mechanisms adopted in the present study are reasonable. Four of the six possible transitions – the walk-to-trot, walk-to-bound, trot-to-walk, and trot-to-bound transitions – could be produced by changing internal oscillator parameters and/or by varying the nature of the network's driving signal. The former mechanism, which largely amounted to modifying the excitability and/or intrinsic activity of the neuronal oscillators making up the rhythm-generating network, is supported by the fact that the excitability of a real neuron can be readily modified via changes to its membrane ion channels (Kaczmarek and Levitan 1987). The latter mechanism, on the other hand, is supported by several experimental studies which have shown that the output of a locomotor CPG can be modified via changes to its descending inputs. In particular, as noted in Sect. 1, Shik et al. (1966) demonstrated that decerebrate cats could be forced to switch from the walk to the trot to the gallop by increasing the strength of a midbrain stimulation signal. It should also be pointed out that the study by Afelt et al. (1983) provides experimental data which indirectly support the 'power-pair' strategy for generating gait transitions from the bound. Specifically, Afelt et al. found that the initiation of the gallop-to-trot transition in dogs was characterized by changes in the kinematics of a *single pair* of diagonal limbs. Moreover, as predicted by the 'power-pair' strategy, these changes always took place during a specific phase in the gait cycle. In general, further experimental studies are needed to document the relative-phase changes that characterize gait transitions in quadrupeds, e.g., see Kelso and Jeka (1992) and Jeka et al. (1993b) for experiments that deal with four-limb movements in humans. Work of this nature could shed additional insight into the neural mechanisms underlying gait transitions.

Further studies could also consider other mechanisms for generating the bound-to-walk and bound-to-trot transitions. The goal of such investigations could be to produce these transitions without selectively stimulating a limited number of the CPG oscillators (as was done with the 'power-pair' strategy). One possible strategy could consist of adding noise to various components of the network, e.g., the driving signal, coupling terms, etc. The addition of noise may serve to make the bound sufficiently unstable such that the CPG model could switch to the other gaits. (The presence of noise may also serve to reduce the switching times for these and other gait transitions.) A related study could consider the effects of replacing the periodic component of the system's driving signal with a pseudoperiodic component (Pecora and Carroll 1991). Again, such a modification may promote the 'elusive' bound-to-walk and bound-to-trot transitions in a homogeneously stimulated CPG model, e.g., by simplifying the overall shape of the bound's basin of attraction.¹²

¹² In a preliminary investigation, we were able to produce transitions from the bound with a pseudoperiodic component in the driving signal. However, the switching times for these transitions were unrealistically long, e.g., 20 gait cycles. This issue requires further study

In each of the present CPG models, the network driving signal had both a tonic component and a phasic component.¹³ However, the exact form of the driving signal(s) acting on a quadrupedal locomotor CPG is unknown. Similarly, it is unclear how externally applied stimulation signals are transmitted to locomotor CPGs, e.g., such signals may be significantly modified before reaching a CPG. For example, although the stimulation signal in the Shik study was amplitude modulated (in order to produce gait transitions), this does not necessarily mean that the resulting descending signals were also amplitude modulated. In addition, although the results obtained in the Shik study were largely independent of the stimulation frequency, there is some evidence that frequency-modulated stimulation signals can also modify the output of locomotor CPGs (Davis and Kennedy 1972; Lennard and Stein 1977). Lennard and Stein (1977), for instance, electrically stimulated the dorsolateral funiculus in spinal and intact turtles and found that an increase in the stimulus frequency resulted in an increased repetition rate of hindlimb swimming movements. (Interestingly, they also found that the frequency of hindlimb swimming movements could be increased by an increase in the stimulus amplitude.) Finally, along similar lines, it should be remarked that it is most likely erroneous to assume (as it has been in a number of previous CPG modelling studies) that the net driving signal of a locomotor CPG consists only of descending influences from supraspinal centers – it may also consist of afferent inputs from peripheral sensory organs (Delcomyn 1980; Bässler 1986).¹⁴ A number of recent experimental studies have shown, for example, that the locomotor rhythm in cats can become entrained to phasic afferent inputs (e.g., Andersson and Grillner 1983; Pearson et al. 1992). From the above discussion, it is clear that further work is needed to clarify the nature of the peripheral and central inputs that influence the output of a locomotor CPG.

The present *in numero* results could be tested and possibly validated in other experimental settings. For example, analogous electronic circuits of coupled nonlinear oscillators (e.g., Ashwin 1990) could be constructed and utilized to examine the possibility of generating transitions between different phase-locked oscillations signals with strategies that are functionally equivalent to those proposed in Sect. 3. Hard-wired circuits of this sort, if shown to be feasible, could eventually serve as valuable components in the control systems of walking robots (Beer et al. 1992; Chiel et al. 1992). In a more ambitious project, a network of four neurons could be constructed and analyzed *in vitro* (Kleinfeld et al. 1990; Syed et al. 1990; Sharp et al. 1992, 1993). The respective neurons

¹³ Each of the CPG models could, however, produce oscillatory output with only a tonic driving signal. Thus, it is possible that a more complex, hard-wired CPG model, e.g., one with non-identical coupling between ipsilateral and diagonal oscillators, may be able to produce the three quadrupedal gaits with only a tonic activation signal.

¹⁴ In the present CPG models, both scenarios are equivalent provided the resultant signals are distributed identically to the component neuronal oscillators

could be coupled via artificial, inhibitory synapses (Sharp et al. 1992, 1993), according to the arrangement of Fig. 2. It would be interesting to investigate such a network's capability for producing multiple phase-locked output patterns that correspond to different quadrupedal gaits.

Acknowledgements. We thank Laurel Carney, Carlo De Luca, Martin Golubitsky, Nancy Kopell, and Ian Stewart for helpful discussions and suggestions. S.A.R. was supported by the Patricia Roberts Harris Fellowship.

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