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Abstract

A four–channel neural pattern generator is described in which both the frequency and the relative phase of oscillations are controlled by a scalar arousal or GO signal. The generator is used to simulate quadruped gaits; in particular, rapid transitions are simulated in the order – walk, trot, pace, and gallop – that occurs in the cat. Precise switching control is achieved by using an arousal dependent modulation of the model's inhibitory interactions. This modulation generates a different functional connectivity in a single network at different arousal levels.

1 A Neural Pattern Generator

This article describes a neural pattern generator that is capable of triggering the primary gaits and gait transitions that are observed in quadrupeds as emergent properties of network dynamics. Phase transitions from one gait to the next are triggered by a descending scalar control signal, called the GO signal, that realizes a form of network arousal. An analysis of quadruped gait transitions leads to propose that the GO signal modulates the functional connectivity of the controlling neural pattern generator. Task-specific modulation of the functional connectivity of neural pattern generators has been experimentally observed; for example, in the stomatogastric ganglion of the crab [3]. The present model predicts a pattern of arousal-dependent modulation that permits *only* the naturally occurring quadruped gait transitions to be generated by a single model circuit, in some parameter ranges, as its GO signal is parametrically increased. We therefore call such a model a GO Gait Generator, or G^3 model. The G^3 model an extension of the Ellias–Grossberg nonlinear cooperative-competitive feedback network [2]. This model extends to the quadruped case earlier modeling of these generators that was summarized in Cohen, Grossberg and Pribe [1]. The G^3 model is defined by the equations

$$\dot{x}_i = -Ax_i + (B - x_i)[f(x_i) + I_i] - (C + x_i)[\sum D_{ij}h_{ij}(I)g(y_j)] \tag{1}$$

$$\dot{y}_i = E[(1 - y_i)[x_i]^+ - y_i], \tag{2}$$

where

$$[\omega]^+ = max(\omega, 0), \tag{3}$$

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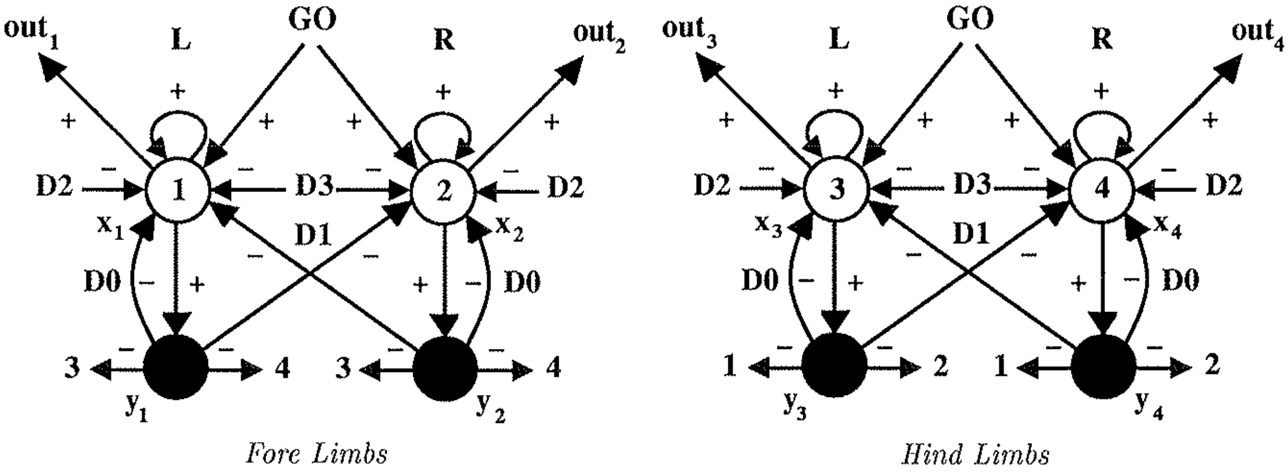


Figure 1: Each limb is represented by an (x, y) pair. Each x_i receives the same arousal or *GO* and each is self-excitatory. Oscillations are generated by a slow inhibitory interneuron, y_i. Inhibition in the neural pattern generator; each arrow represents an inhibitory connection from one channel's y to another channel's x. See text for inhibitory coefficient labels, $D0$, $D1$, $D2$, and $D3$.

$$f(\omega) = \frac{F_1([\omega]^+)^2}{F_2 + ([\omega]^+)^2}, \quad g(\omega) = \frac{G_1([\omega]^+)^2}{G_2 + ([\omega]^+)^2}, \tag{4}$$

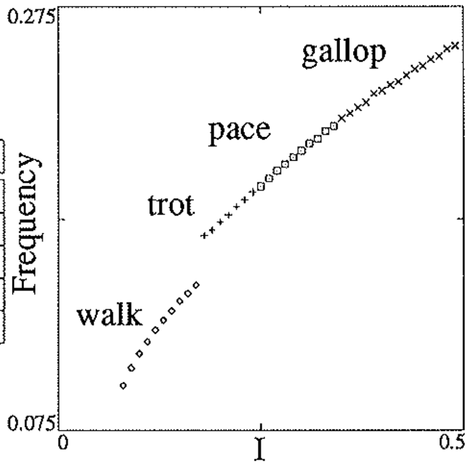
and $i = \{1, 2, 3, 4\}$. Here x_i is the activity, or potential of a fast excitatory neuron or population, and y_i is the activity of a slow inhibitory interneuron or population. The excitatory and inhibitory activities obey a shunting membrane equation [4]. A single arousal source controls a scalar input, I, to each x_i. Arousal, I, performs two functions in the G^3 model: it modulates the inhibition and it provides the activation that triggers the oscillations via the inputs I_i. Inhibitory modulation is performed via the function $h_{ij}(I)$ in (1). A table of the inhibitory coefficient values at various arousal levels is shown in Figure 2*A*. Although, each x_i receives the same arousal or *GO* signal, symmetry is broken in the oscillator by allowing changes in arousal to arrive via the input I_i at each x_i at slightly different times. The time lag in the arrival of arousal between the sides, that is x_1 and x_3 versus x_2 and x_4, is called the *sidelag* and is set to .0001 for the simulations in this paper. The time lag between the fore and aft, that is x_1 and x_2 versus x_3 and x_4, is called the *cordlag* and is set to .00025 for the simulations in this paper.

To simplify notation, the following abbreviations are used to define the parameters of the four channels whose outputs control the quadruped gaits: the self-inhibitory coefficients D_{ii} are called D0. The reciprocal fore → fore and aft → aft contralateral inhibitory coefficients are all called $D1$. The fore → aft and aft → fore ipsilateral inhibitory coefficients are called $D2$. The fore → aft and aft → fore contralateral (transverse) inhibitory coefficients are called $D3$. For a key to the inhibitory connections see Figure 1.

2 Simulation Results

The G^3 model produces the cat gait transitions in the order observed *in vivo* [5]. The temporal asymmetry helps provide rapid initiation of and switching between gaits. We have found that,

I	$I \leq .17$	$.17 < I \leq .25$	$.25 < I \leq .35$	$.35 < I$
$D1$	0.3	0.3	0.3	0.55
$D2$ aft → fore	0.0	0.3	0.55	0.3
$D2$ fore → aft	0.3	0.3	0.55	0.3
$D3$ aft → fore	0.3	0.55	0.3	0.3
$D3$ fore → aft	0.0	0.55	0.3	0.3



(A)

(B)

Figure 2: *(A)*: The values of the modulated inhibitory coefficients for increasing arousal levels, I. The self-inhibition, $D0$, is not modulated and, so, is not listed here. *(B)*: Frequency plot for the four-channel generator with arousal dependent inhibitory modulation. The initial conditions were reset at each I increment. The frequencies were sampled at arousal increments of .01.

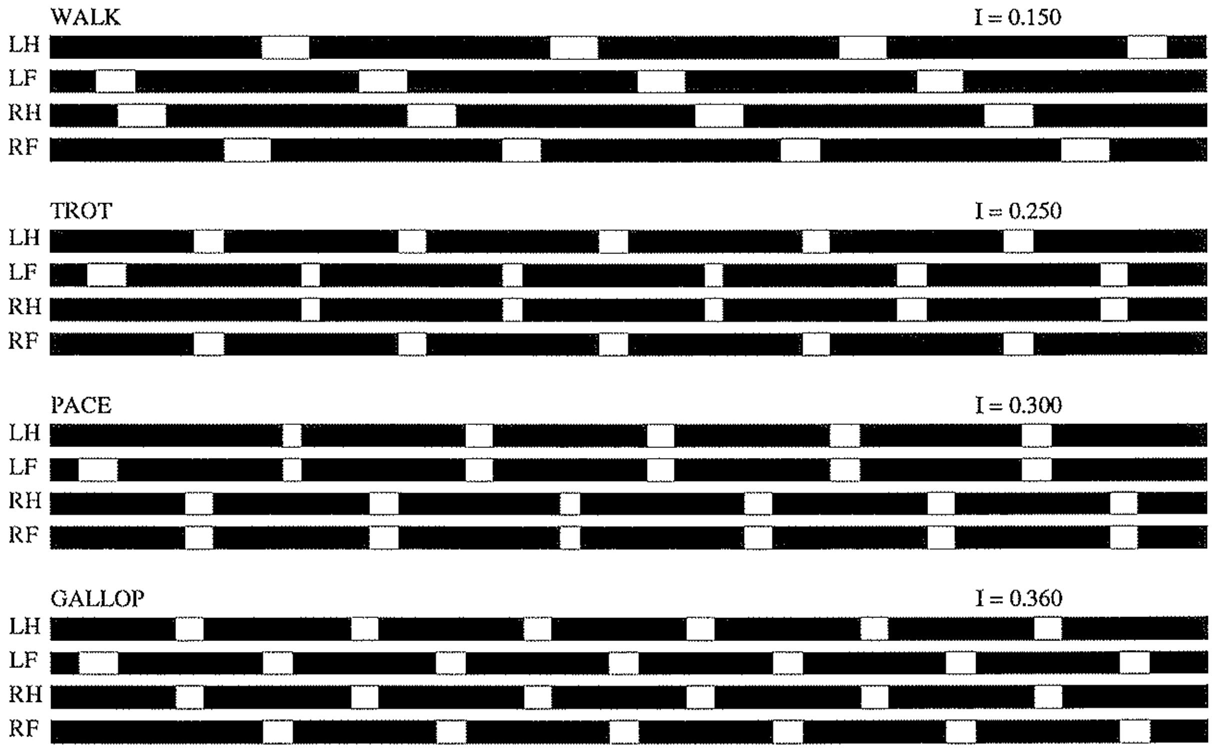


Figure 3: Using the arousal dependent modulation of the inhibitory coefficients yields all four gaits. There is a small asyncrony in the arrival time of any change in arousal to the channels. $A = 1.0$, $B = 1.05$, $C = 2.5$, $D0 = 1.0$, $D1$, $D2$, and $D3$ are as specified in Figure 2A. $E = 1.5$, $F_1 = 9.8$, $G_1 = 3.9$, $F_2 = 0.5$, $G_2 = 0.5$. cordlag $= 0.00025$, sidelag $= 0.0001$, $t_{max} = 30.0$, and $\Delta t = 0.25$. The initial conditions were reset to zero before each run. Notice the clean gait initiations.

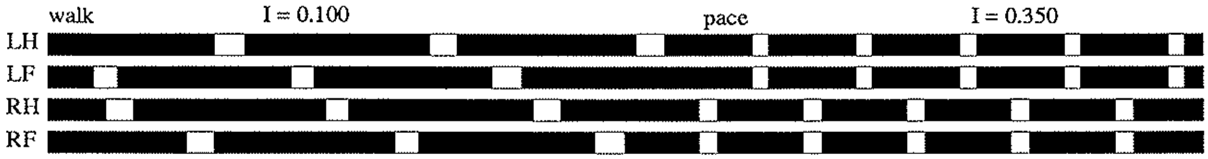


Figure 4: Initiating a walk from a still position, then generating a transition to a pace. The arousal is instantaneously switched from $I = 0.1$ to $I = 0.35$ at $t = 25.0$. The initial conditions were set to zero at $t = 0.0$ and were not changed thereafter. $t_{max} = 50.0$, $\Delta t = 0.25$, and other parameters are as in Figure 3.

without modulation of the inhibitory coefficients, the anatomically symmetric version of the model with asymmetries in the arousal signal is capable of producing correctly ordered cat gaits. However, it is sensitive to changes in initial conditions and parameters and did not always uniquely specify the gait at a given arousal level.

With arousal–dependent modulation of inhibitory coefficients, the model reliably produces the gaits in the experimentally observed order (Figure 3) and with clean transitions (Figure 4). The frequency plot of the limbs for the walk, trot, pace, and gallop, (see Figure $2B$) shows an appropriate monotone increase in frequency of oscillations as a function of the GO signal.

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