A bursting neuron CPG model: phase reduction, dynamical mechanisms, and gait transitions

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Summary

Insects use various gaits. Fast running insects employ tripod gaits with 3 legs up in swing and 3 down in stance. Slower insects use tetrapod gaits with 2 legs in swing and 4 in stance. Fruit flies use both gaits with a transition from tetrapod to tripod at intermediate speeds. We study the effect of stepping frequency on transitions between these gaits in an ion-channel bursting neuron model in which each cell represents a hemi-segmental thoracic circuit of the central pattern generator (CPG). Employing phase reduction and dynamical systems methods, we show the existence and stability of tetrapod, tripod and transition gaits.

CPG bursting neuron model

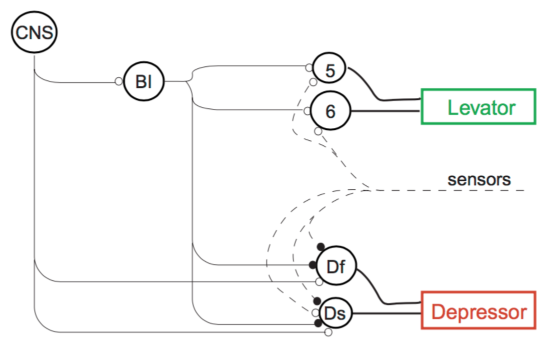
The system of equations for a single bursting neuron model is [1]:

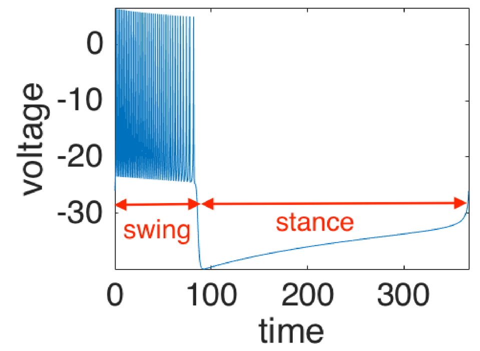
$$C\dot{v} = -\{I_{Ca} + I_K + I_{KS} + I_L\} + I_{ext}$$

$$\dot{m} = \frac{\epsilon}{\tau_m(v)}[m_\infty(v) - m]$$

$$\dot{w} = \frac{\delta}{\tau_w(v)}[w_\infty(v) - w]$$

$$\dot{s} = \frac{1}{\tau_s}[s_\infty(v)(1-s) - s] \quad \text{(synapse)}$$





The currents take the forms

$$\begin{aligned} I_{Ca}(v) &= \bar{g}_{Ca} n_\infty(v)(v - E_{Ca}) \\ I_K(v,m) &= \bar{g}_K\, m\,(v - E_K) \\ I_{KS}(v,w) &= \bar{g}_{K_{Ca}} w\,(v - E_K) \\ I_L(v) &= \bar{g}_L(v - E_L) \\ I_{ext} &= \text{constant} \end{aligned}$$

The time scales take the forms

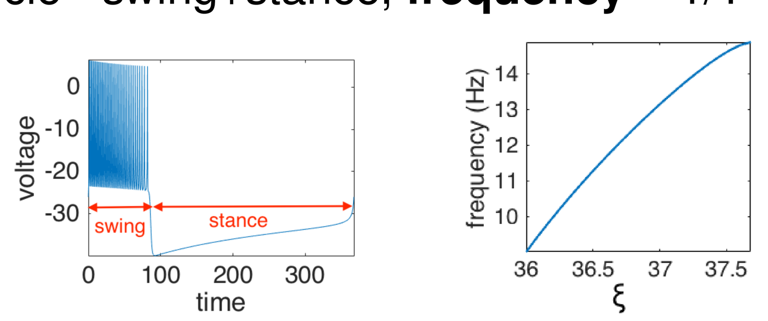
$$\begin{aligned} \tau_m(v) &= \operatorname{sech}(k_K(v - v_K)) \\ \tau_w(v) &= \operatorname{sech}(k_C(v - v_C)) \\ \tau_s &= \text{constant} \end{aligned}$$

The steady state gating variables are

$$\begin{aligned} m_\infty(v) &= \frac{1}{1+e^{-2k_K(v-v_K)}} \\ w_\infty(v) &= \frac{1}{1+e^{-2k_C(v-v_C)}} \\ n_\infty(v) &= \frac{1}{1+e^{-2k_{Ca}(v-v_{Ca})}} \\ s_\infty(v) &= \frac{a}{1+e^{-2k_s(v-E_s^{pre})}} \end{aligned}$$

Effect of I_{ext} & δ on frequency of limit cycle

T = period of a cycle= swing+stance, **frequency** = 1/T

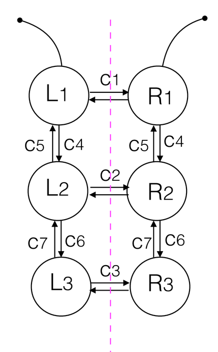


As I_{ext} or δ increases, the frequency increases. So both I_{ext} and δ can be considered as *speed* parameters (ξ).

Weakly interconnected neurons

For a network of six mutually inhibiting units, assume [3]:

- Inhibitory coupling via negative postsynaptic currents.
- Contralateral symmetry (3 contralateral (c_1, c_2, c_3) and 4 ipsilateral (c_4, c_5, c_6, c_7) coupling strengths).
- Nearest neighbor connections with identical coupling functions.



Synapses

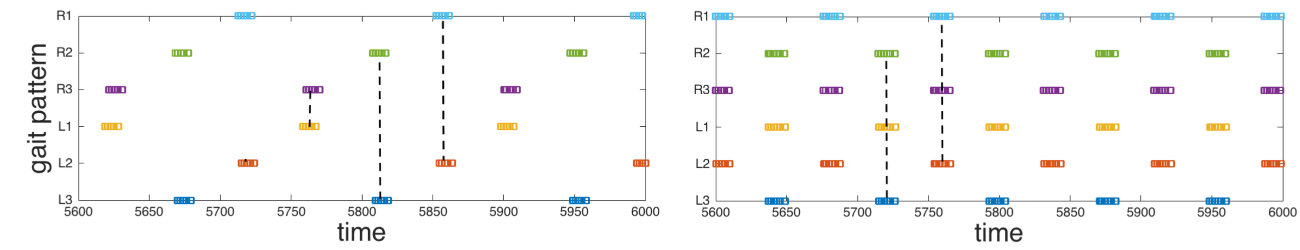
The synapse variable s enters the postsynaptic cell:

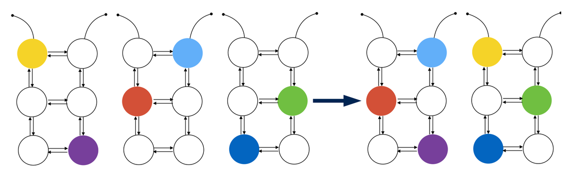
$$C\dot{v} = -\{I_{Ca} + I_K + I_{KS} + I_L\} + I_{ext} + \mathbf{I_{syn}}$$

where $\mathbf{I_{syn}} = \mathbf{I_{syn}}(v,s) = -\bar{g}_{syn}\, s(t)\, \left(v - E_s^{post}\right)$, $\bar{g}_{syn}$: synaptic strength

Gait transition

The following figures show gait transitions from tetrapod to tripod as ξ increases in the network of 6-coupled bursting neurons represented by 24 ODEs. Each bar represents the swing phase of one leg. Note the transitional gaits with partial overlap of swing phases in the middle row. In these simulations, $c_1 = c_2 = c_3$, and $c_5 = c_4 + c_7 = c_6$.

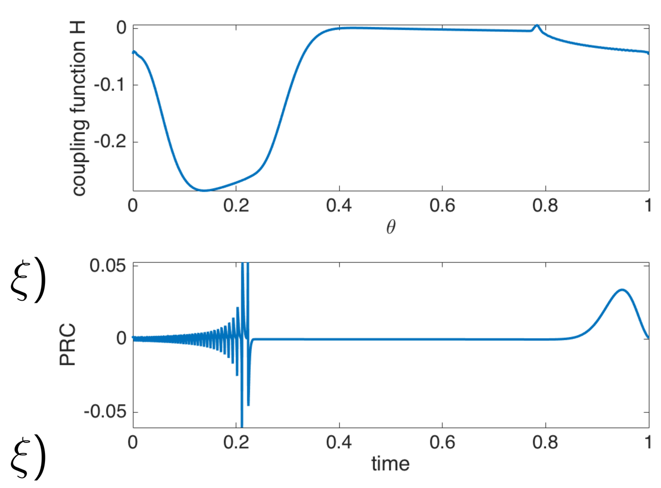




Goal: To justify the observed gait transitions mathematically. To this end, we first reduce the 24 ODEs to 6 phase equations:

Phase equations for six weakly coupled neurons

Phase reduction theory yields a single equation for each bursting neuron. The coupling function is computed by convolving the phase response curve (PRC) with the synaptic current (I_{syn}).

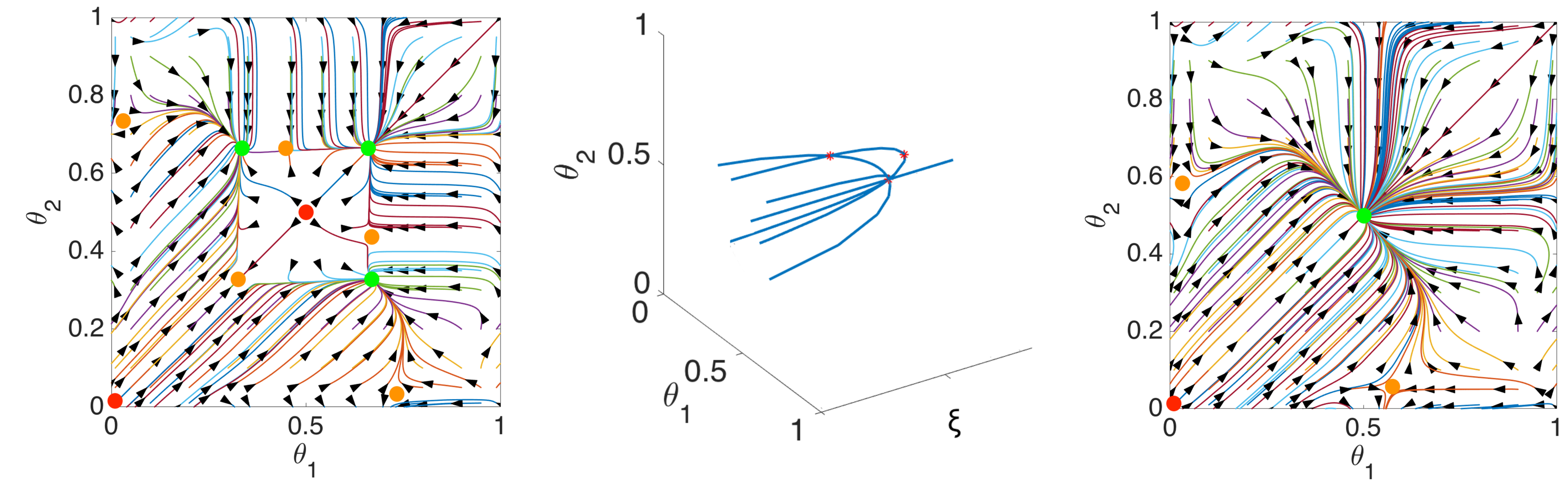


$$\begin{aligned} \dot{\phi}_1 &= \omega_0 + c_1 H(\phi_4 - \phi_1, \xi) + c_5 H(\phi_2 - \phi_1, \xi) \\ \dot{\phi}_2 &= \omega_0 + c_2 H(\phi_5 - \phi_2, \xi) + c_4 H(\phi_1 - \phi_2, \xi) + c_7 H(\phi_3 - \phi_2, \xi) \\ \dot{\phi}_3 &= \omega_0 + c_3 H(\phi_6 - \phi_3, \xi) + c_6 H(\phi_2 - \phi_3, \xi) \\ \dot{\phi}_4 &= \omega_0 + c_1 H(\phi_1 - \phi_4, \xi) + c_5 H(\phi_5 - \phi_4, \xi) \\ \dot{\phi}_5 &= \omega_0 + c_2 H(\phi_2 - \phi_5, \xi) + c_4 H(\phi_4 - \phi_5, \xi) + c_7 H(\phi_6 - \phi_5, \xi) \\ \dot{\phi}_6 &= \omega_0 + c_3 H(\phi_3 - \phi_6, \xi) + c_6 H(\phi_5 - \phi_6, \xi) \end{aligned}$$

- There exists a unique $\eta = \eta(\xi)$, $0 \le \eta \le 1/6$, such that
$$H(2/3 - \eta, \xi) = H(1/3 + \eta, \xi).$$
- We assume constant contralateral symmetry between the left and right legs:
$$\phi_{i+3} - \phi_i = 2/3 - \eta.$$
- Phase difference of front-middle and hind-middle gives two equations on a torus:
$$\begin{aligned} \dot{\theta}_1 &= (c_1 - c_2)H(2/3 - \eta, \xi) + c_5 H(-\theta_1, \xi) - c_4 H(\theta_1, \xi) - c_7 H(\theta_2, \xi) \\ \dot{\theta}_2 &= (c_3 - c_2)H(2/3 - \eta, \xi) + c_6 H(-\theta_2, \xi) - c_4 H(\theta_1, \xi) - c_7 H(\theta_2, \xi) \end{aligned} \qquad (1)$$
- Assumption: $(1/3 + \eta, 2/3 - \eta), 0 \le \eta \le 1/6$ is a fixed point of Equation (1).
($\eta = 0 \sim$ tetrapod and $\eta = 1/6 \sim$ tripod)
This assumption gives the following relations among c_i's:
$$c_1 + c_5 = c_2 + c_4 + c_7 = c_3 + c_6 \quad \text{(balance equation)}$$
- Special case (motivated by data): $c_1 = c_2 = c_3$.
Letting $\alpha := \frac{c_4}{c_4 + c_7}$ $(0 < \alpha < 1)$, and making a change of time scale, Equation (1) becomes
$$\begin{aligned} \dot{\theta}_1 &= H(-\theta_1, \delta) - \alpha H(\theta_1, \delta) - (1-\alpha)H(\theta_2, \delta) \\ \dot{\theta}_2 &= H(-\theta_2, \delta) - \alpha H(\theta_1, \delta) - (1-\alpha)H(\theta_2, \delta) \end{aligned} \qquad (2)$$

Phase planes of Equation (2) & bifurcation diagram

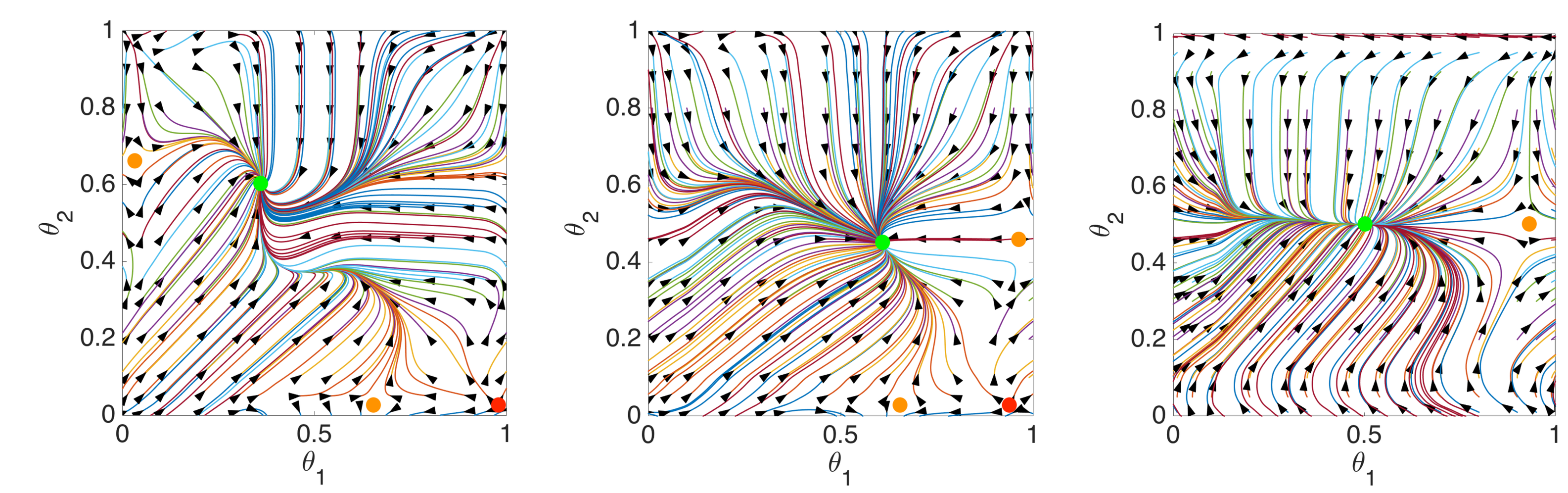
We show that when ξ increases, a gait transition from tetrapod to tripod occurs.



(Left) Small ξ, 2 stable tetrapod (corresponding to back-to-front and front-to-back waves of stance movements), 1 stable "slow" tripod (green dots), 1 unstable tripod (corresponding to point (0.5,0.5)), 1 unstable node (corresponding to point (0,0)) (red dots), and 5 saddle points (orange dots) are observed.
(Middle) As ξ increases, a degenerate bifurcation and a saddle node bifurcation occur. Through these bifurcations, two tetrapod, one slow tripod, one unstable tripod, and three saddle points disappear and one stable tripod bifurcates.
(Right) Large ξ, 1 stable tripod, 1 unstable node, and 2 saddle points are observed.

Gaits deduced from fruit fly data fitting

	$\hat{\omega}$	c_1	c_2	c_3	c_4	c_5	c_6	c_7
slow	9.92	0.3614	0.1478	0.1780	0.1837	0.2509	0.3409	0.1495
medium	12.48	0.2225	0.6255	0.4715	0.1436	0.3895	0.7921	0.2964
fast	15.52	0.0580	0.8608	0.6726	0.0470	0.4294	1.1498	0.8500



tetrapod gait | transition | tripod gait

Conclusion

We conclude that when $\xi < \xi^*$ (some bifurcation value for the speed parameter), there exists at least one stable tetrapod gait and when $\xi > \xi^*$, there exists a unique stable tripod gait.

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