Gait transitions in a phase oscillator model of insect central pattern generators

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Introduction

Legged locomotion involves various gaits. It has been observed that fast running animals (cockroaches) employ a tripod gait (three legs lifted off the ground simultaneously) while slow walking animals (stick insects) use tetrapod gaits (two legs lifted off the ground simultaneously). In this work, we study the effect of stepping frequency on gait transition from tetrapod to tripod in a bursting neuron model.

CPG bursting neuron model

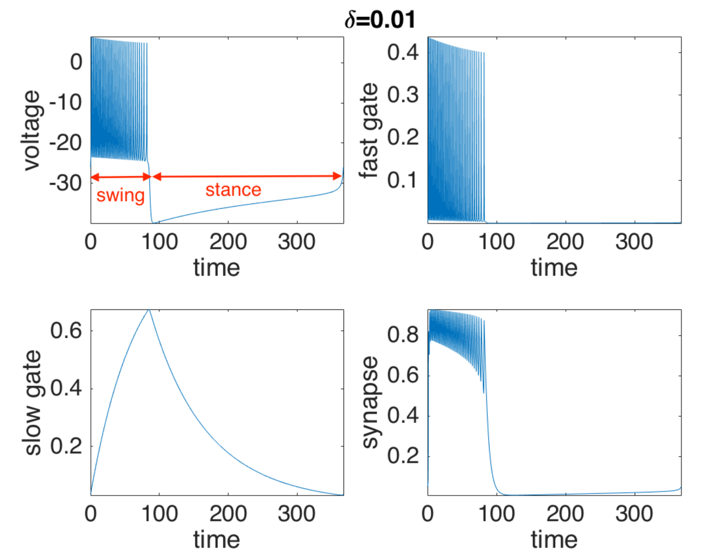
The system of equations for a bursting neuron model is [1]:

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

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

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

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



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

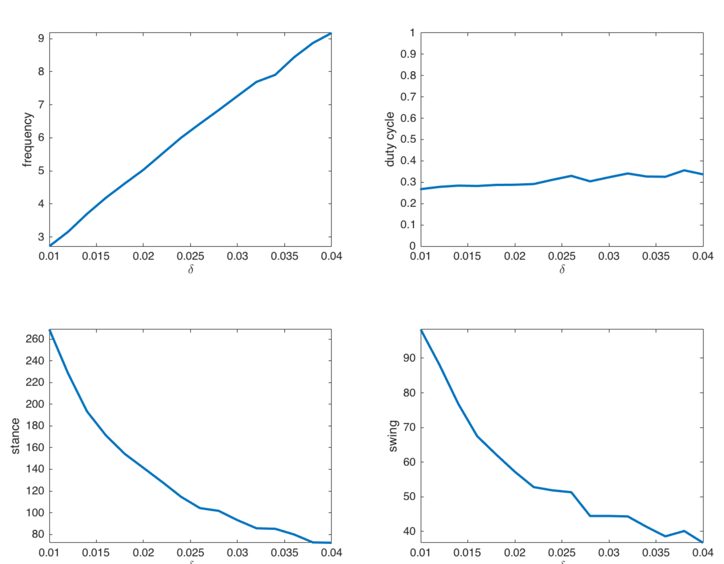
$$\begin{aligned} \tau_m(v) &= \operatorname{sech}(k_K(v - v_K)) \\ \tau_w(v) &= \operatorname{sech}(k_C(v - v_C)) \\ \tau_s &= \text{constant} \\ \delta &\ll \epsilon \ll 1/C \end{aligned}$$

The steady state gating variables are

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

The effect of δ on frequency, duty cycle, swing & stance

- T= the period of a cycle
- frequency = 1/T
- swing = the period of a burst
- stance = T - swing
- duty cycle = swing /T

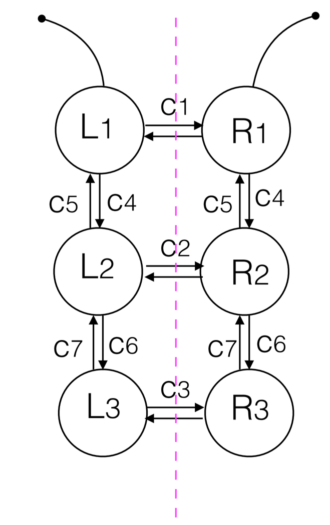


As δ increases from 0.01 to 0.04, the frequency increases by decreasing the stance and swing phases. Increasing I_{ext} has a similar effect on frequency, swing & stance phases, and the duty cycle. So both δ and I_{ext} can be considered as *speed* parameters. Here, we only study the effect of δ on gait transition [2].

Weakly interconnected neurons

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

- inhibitory coupling is achieved via synapses that produce negative postsynaptic currents
- contralateral symmetry
- include only nearest neighbor coupling (three contralateral coupling strengths c_1, c_2, c_3 and four ipsilateral coupling strengths c_4, c_5, c_6, and c_7)



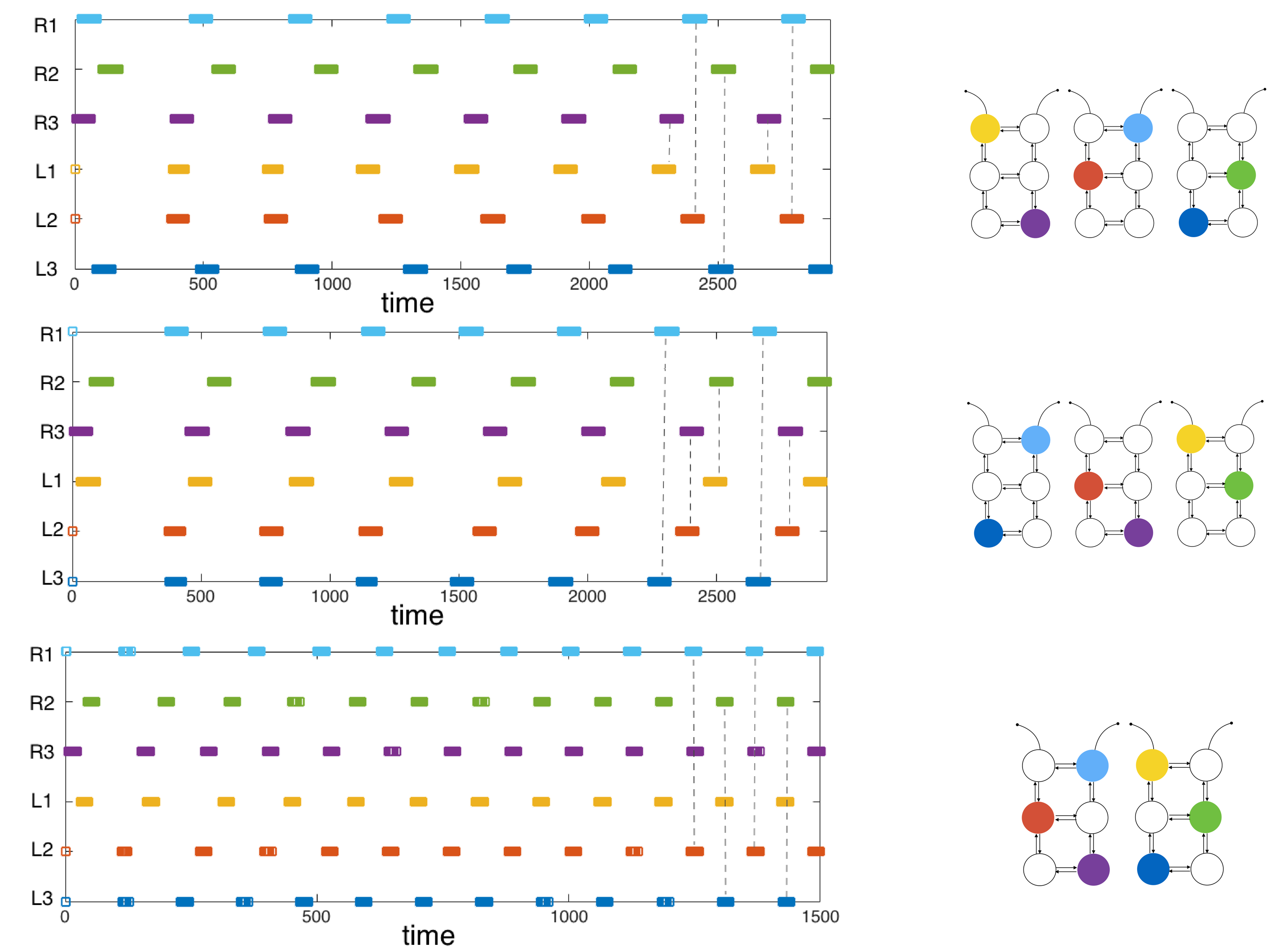
The synapse variable s enters the postsynaptic cell:

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

where

$$\mathbf{I_{syn}} = \mathbf{I_{syn}}(v,s) = -\bar{g}_{syn} s (v - E_s^{post}), \quad \bar{g}_{syn}: \text{synaptic strength}$$

The following figures show 3 different solutions of 24 equations (which describe 6 connected legs) with 3 arbitrary initial conditions and a fixed set of parameters, except for δ. The first two rows depict left & right tetrapod gaits, respectively, for low speed, $\delta = 0.01$, and the last row depicts a tripod gait for high speed, $\delta = 0.04$. In these simulations, $c_1 = c_2 = c_3$, and $c_5 = c_4 + c_7 = c_6$.



References

1. R. Ghighliazza and P. Holmes. Minimal models of bursting neurons: The effects of multiple currents and timescales. *SIAM J. Appl. Dyn. Syst.*, 3:636–670, 2004.
2. C. Mendes, I. Bartos, T. Akay, S. Márka, and R. Mann Quantification of gait parameters in freely walking wild type and sensory deprived *Drosophila melanogaster eLife*, 2:e00231, 2013.
3. E. Couzin-Fuchs, T. Kiemel, O. Gal, and A. Ayali, P. Holmes. Intersegmental coupling and recovery from perturbations in freely-running cockroaches. *Journal of Experimental Biology* 2(218): 285–297, 2015.

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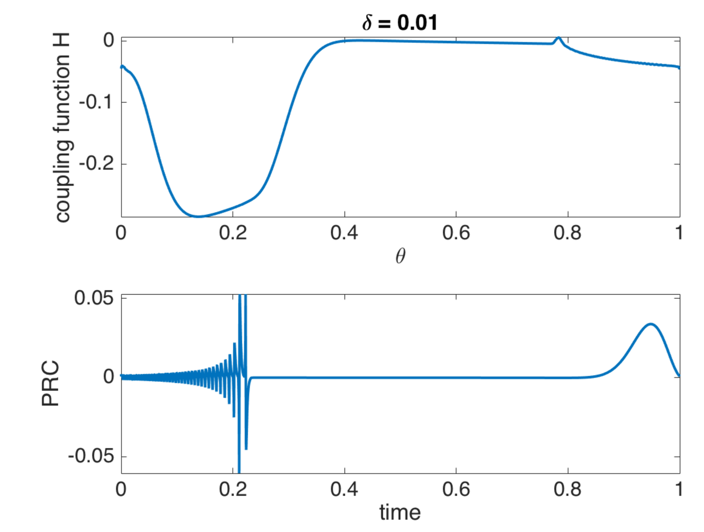
Phase equations for six weakly coupled neurons

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}).



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

Contralateral symmetry and phase difference of front-middle and hind-middle gives:

$$\begin{aligned} \dot{\theta}_1 &= (c_1 - c_2)H(0.5, \delta) + c_5 H(-\theta_1, \delta) - c_4 H(\theta_1, \delta) - c_7 H(\theta_2, \delta) \\ \dot{\theta}_2 &= (c_3 - c_2)H(0.5, \delta) + c_6 H(-\theta_2, \delta) - c_4 H(\theta_1, \delta) - c_7 H(\theta_2, \delta) \end{aligned} \quad (1)$$

Assuming $H(0.5, \delta) \neq 0$, $(0.5, 0.5)$ is a fixed point of Equation (1) if

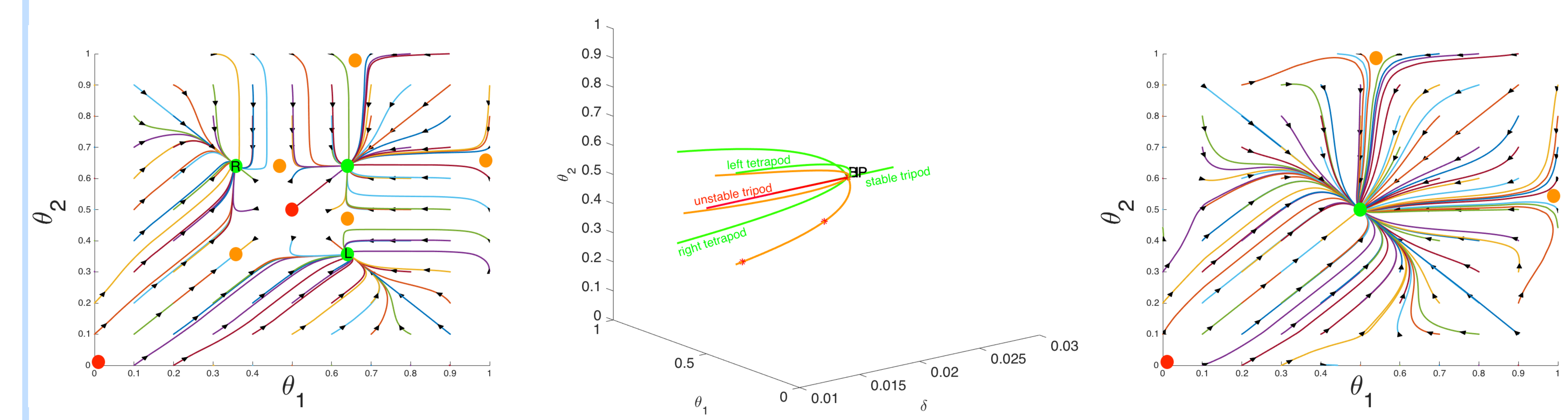
$$c_1 + c_5 = c_2 + c_4 + c_7 = c_3 + c_6. \quad \text{balance equation}$$

Also, $(0,0)$ is a fixed point if $c_1 = c_2 = c_3$. Letting $\alpha := \frac{c_4}{c_4 + c_7}$ $(0 < \alpha < 1)$, and making a change of time scale, Equation (1) becomes

$$\begin{aligned} \dot{\theta}_1 &= H(-\theta_1, \delta) - \alpha H(\theta_1, \delta) - (1-\alpha)H(\theta_2, \delta) \\ \dot{\theta}_2 &= H(-\theta_2, \delta) - \alpha H(\theta_1, \delta) - (1-\alpha)H(\theta_2, \delta) \end{aligned} \quad (2)$$

Phase planes of Equation (2) & bifurcation diagram

We can show that when δ increases, a gait transition from tetrapod to tripod occurs. We first study the phase plane and bifurcation diagram of Equation (2) for $\alpha = 0.5$ (the figures below) and then we generalize the result to any α, $0 < \alpha < 1$.



(Left) $\delta = 0.01$, 2 stable tetrapod (the letter R (L) corresponds to the right (left) tetrapod gait), 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 δ increases, a degenerate bifurcation occurs at approximately $\delta^* = 0.022$. Two tetrapod, one slow tripod, one unstable tripod, and three saddle points disappear and one stable tripod bifurcates. (Right) $\delta = 0.04$, 1 stable tripod, 1 unstable node, and 2 saddle points are observed.

Generalization to $\alpha \neq 0.5$. Calculations show that when $\alpha \neq 0.5$, the phase planes of Equation (2) are qualitatively similar to those when $\alpha = 0.5$, except when δ is very close to the bifurcation value. For δ is very close to the bifurcation value, one of the stable tetrapod gaits loses its stability (and the saddle point near the tetrapod gait becomes a stable node, i.e., a transcritical bifurcation occurs) while the other tetrapod gait remains stable.

Conclusion

We conclude that for any $0 < \alpha < 1$, when $\delta < \delta^*$ (bifurcation value), there exists at least one stable tetrapod gait and when $\delta > \delta^*$, there exists a unique stable tripod gait.

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