Neuromechanical Mechanisms of Locomotion in *C. elegans*: Relative Roles of Neural and Mechanical Coupling

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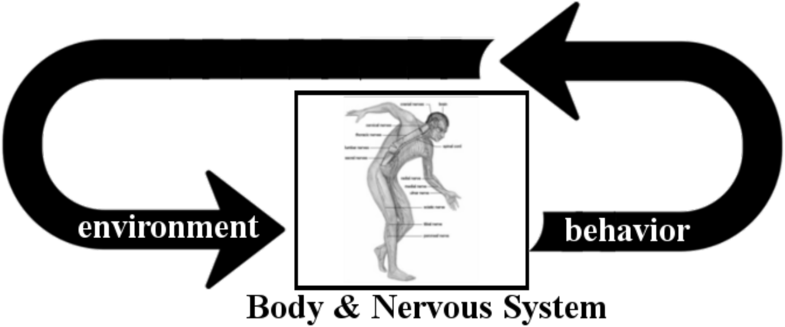
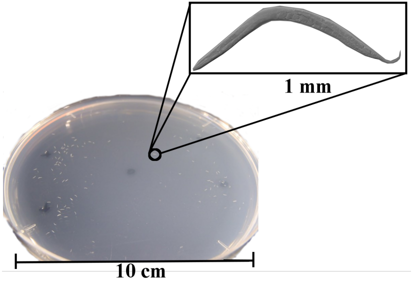
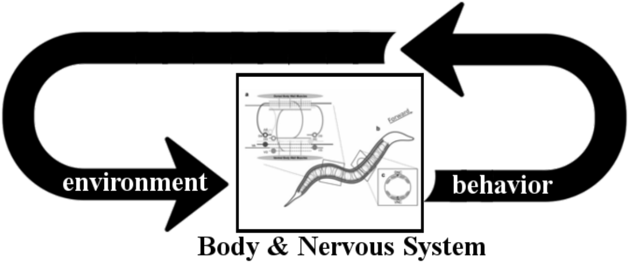
Neurolocomotion

How do the nervous system and body of an organism interact with its environment to produce behavior?

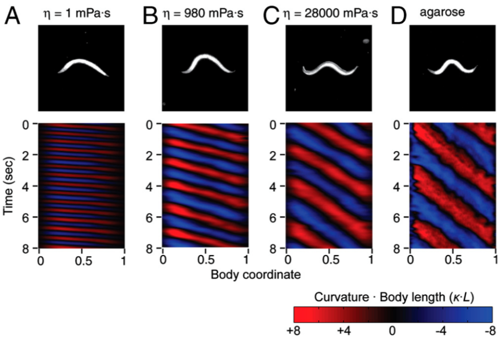


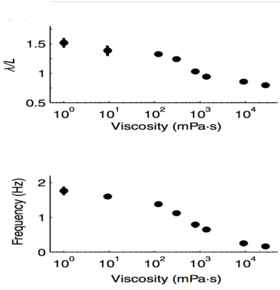
Neurolocomotion in *C. elegans*





C. elegans Gait Adaptation

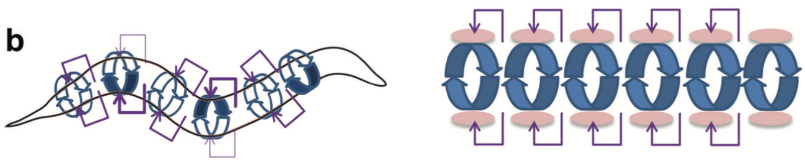




Figures: Fang-Yen et al., 2010 [2]

Similar conclusions: Berri et al., 2009, Sznitman et al., 2010 [7]

Motor Circuit has Oscillator-like Functional Units

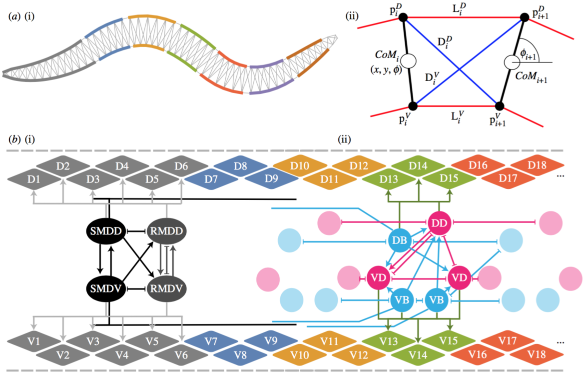


- Repeating circuit motifs - Haspel & O'Donovan, 2011 [5]
- Existence of more than one rhythm-generator - Fouad et al., 2018 [3]
- Proprioception is present in these circuits - Wen et al., 2012 [8]

(figure from Gjorgieva et al. 2014, [4])

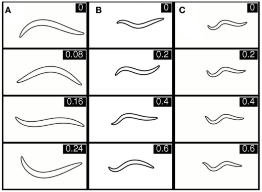
Previous Modeling Work

Boyle et al., 2012 [1], Izquierdo and Beer, 2018 [6] (figure)

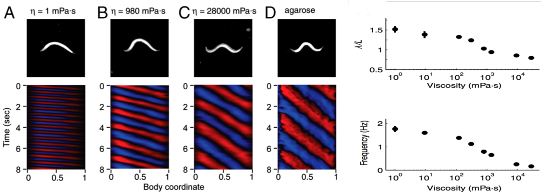


Main Questions

- What mechanisms underly the coordination seen in state-of-the-art Boyle-like models?



Boyle et al. 2012 model

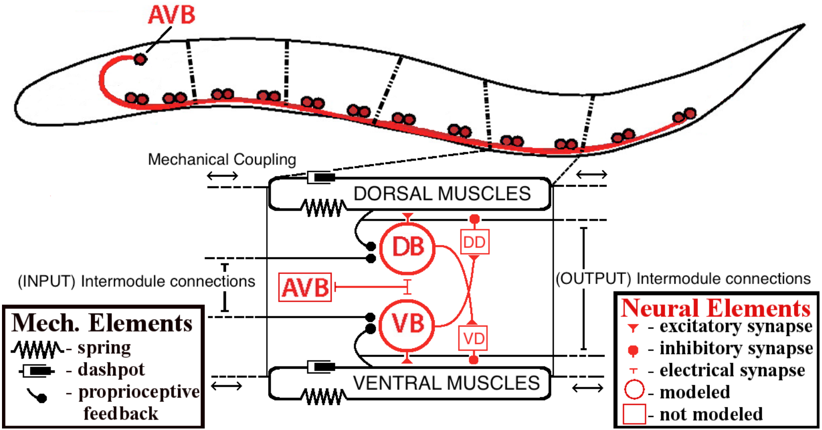


Fang-Yen et al. 2010 experiments

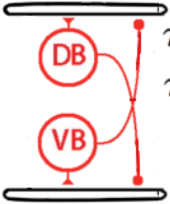
- How is the coordination of the neuromechanical oscillator modules achieved?

- What are the relative roles of passive, mechanical coupling and active, neural and proprioceptive coupling?

Neuromechanical Oscillator Model

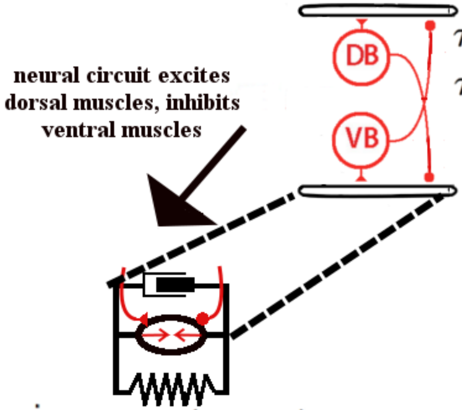


Single Neuromechanical Oscillator



$$\tau_n \dot{V}_D = F(V_D)$$
$$\tau_n \dot{V}_V = F(V_V)$$

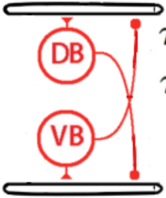
Single Neuromechanical Oscillator



$$\tau_n \dot{V}_D = F(V_D)$$
$$\tau_n \dot{V}_V = F(V_V)$$

$$\tau_m \dot{A}_D = -A_D + (V_D - V_V)$$
$$\tau_m \dot{A}_V = -A_V + (V_V - V_D)$$

Single Neuromechanical Oscillator

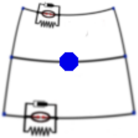


$$\tau_n \dot{V}_D = F(V_D)$$
$$\tau_n \dot{V}_V = F(V_V)$$

neural circuit excites dorsal muscles, inhibits ventral muscles

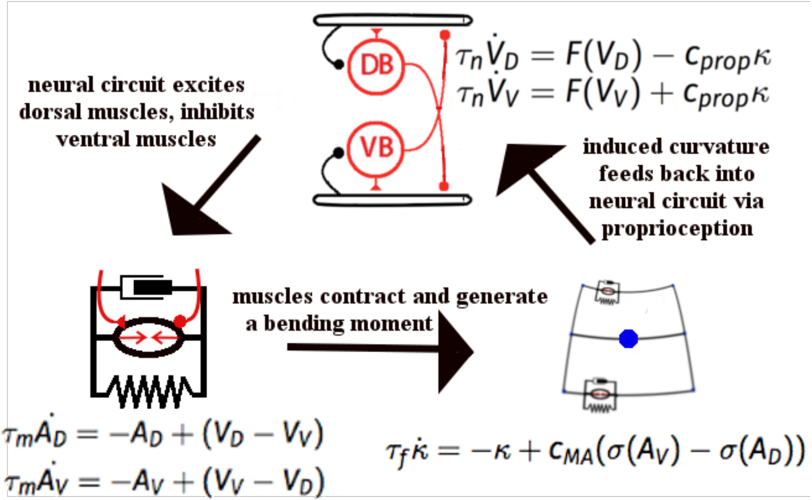
$$\tau_m \dot{A}_D = -A_D + (V_D - V_V)$$
$$\tau_m \dot{A}_V = -A_V + (V_V - V_D)$$

muscles contract and generate a bending moment

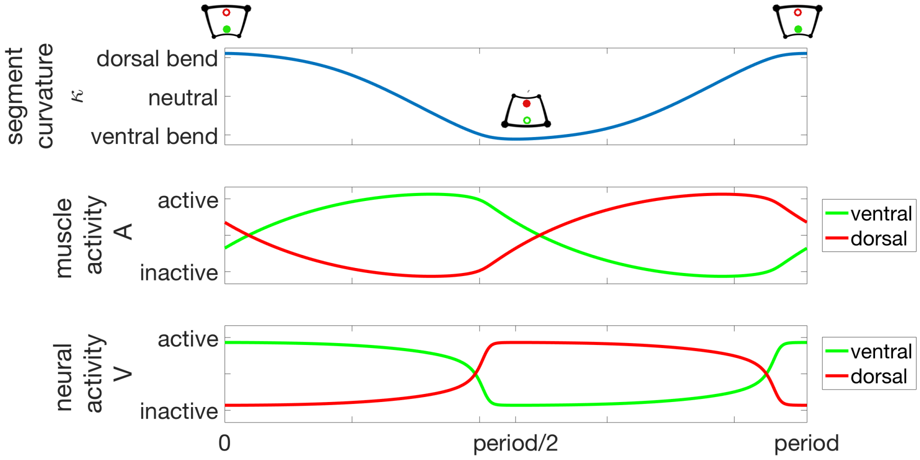


$$\tau_f \dot{\kappa} = -\kappa + c_{MA}(\sigma(A_V) - \sigma(A_D))$$

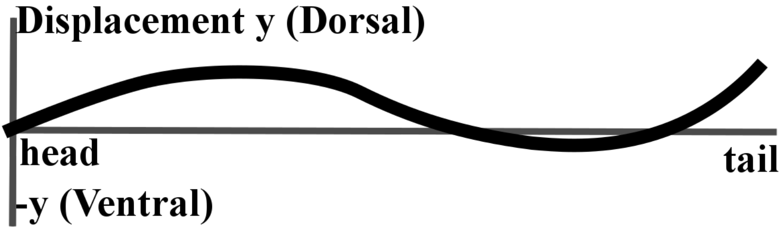
Single Neuromechanical Oscillator



Neuromechanical Oscillations



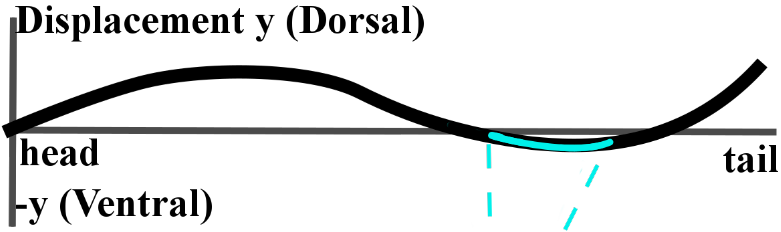
Mechanical Coupling



$$\kappa = y_{xx}$$

$$\implies \gamma y_t = K_b(\kappa + M)_{xx} - \mu \kappa_{txx}$$

Mechanical Coupling



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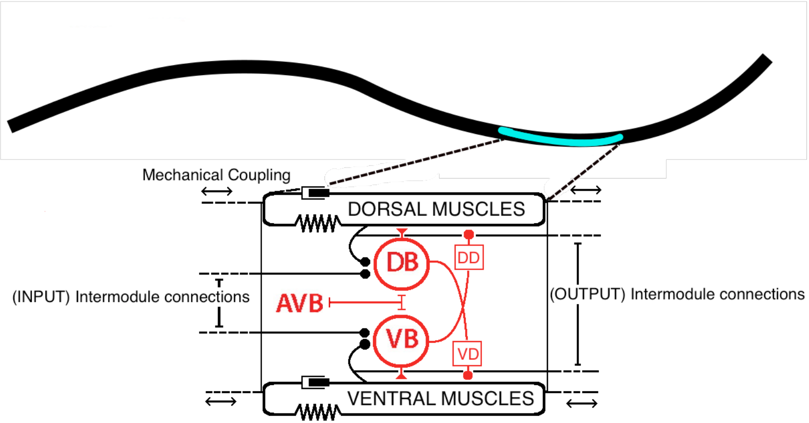
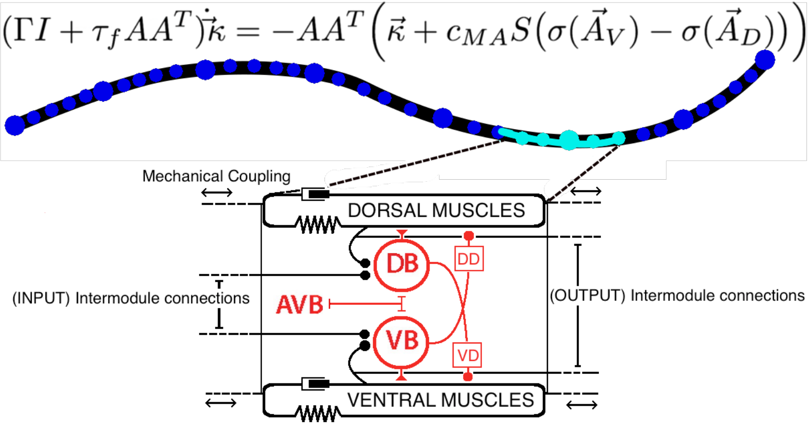
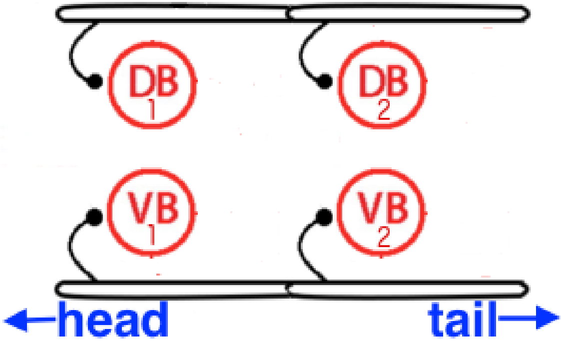


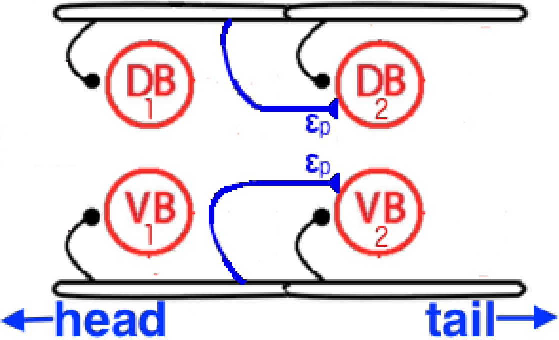
Mechanical Coupling



Neural Coupling



Neural Coupling



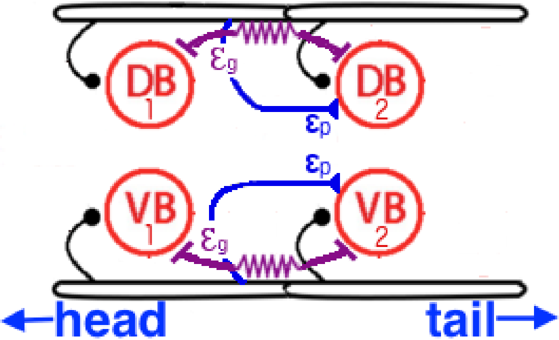
$$\dot{\vec{V_V}} = \vec{F}(\vec{V_V}) + \vec{\kappa} + W_p\vec{\kappa}$$

$$\dot{\vec{V_D}} = \vec{F}(\vec{V_D}) - \vec{\kappa} - W_p\vec{\kappa},$$

where

$$W_p(i-1, i) = -\varepsilon_p.$$

Neural Coupling



$$\dot{\vec{V_V}} = \vec{F}(\vec{V_V}) + \vec{\kappa} + W_p\vec{\kappa} + W_g\vec{V}_V$$

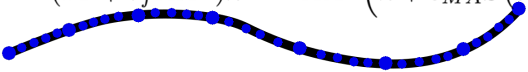
$$\dot{\vec{V_D}} = \vec{F}(\vec{V_D}) - \vec{\kappa} - W_p\vec{\kappa} + W_g\vec{V}_D$$

where

$$W_g(i-1,i) = W_g(i+1,i) = \varepsilon_g$$

Full, Coupled-Oscillators Model

$$(\Gamma I + \tau_f A A^T)\dot{\vec{\kappa}} = -AA^T\left(\vec{\kappa} + c_{MA} S\big(\sigma(\vec{A}_V) - \sigma(\vec{A}_D)\big)\right)$$



Full, Coupled-Oscillators Model

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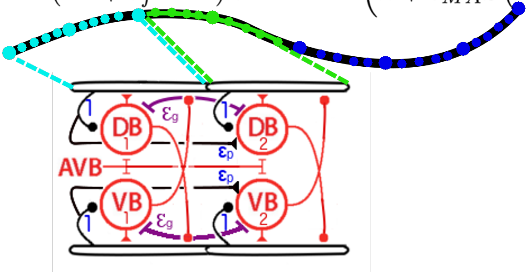

Full, Coupled-Oscillators Model

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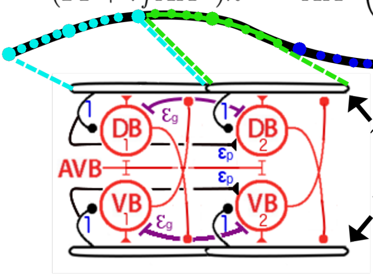
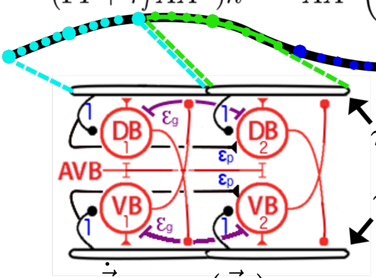


$$\tau_m \dot{\vec{A}}_D = -\vec{A}_D + \vec{V}_D - \vec{V}_V$$

$$\tau_m \dot{\vec{A}}_V = -\vec{A}_V + \vec{V}_V - \vec{V}_D$$

Full, Coupled-Oscillators Model

$$(\Gamma I + \tau_f A A^T)\dot{\vec{\kappa}} = -AA^T\left(\vec{\kappa} + c_{MA} S\big(\sigma(\vec{A}_V) - \sigma(\vec{A}_D)\big)\right)$$



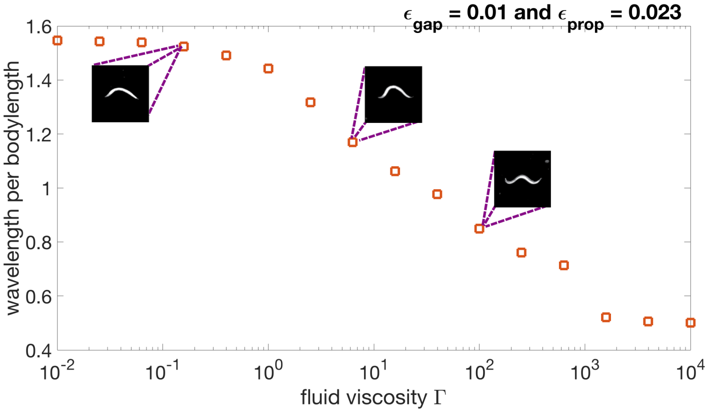
$$\tau_m \dot{\vec{A}}_D = -\vec{A}_D + \vec{V}_D - \vec{V}_V$$

$$\tau_m \dot{\vec{A}}_V = -\vec{A}_V + \vec{V}_V - \vec{V}_D$$

$$\tau_n \dot{\vec{V}}_D = F(\vec{V}_k) - c_{prop}(\vec{\kappa} + W_{prop}\vec{\kappa}) + W_{gap}\vec{V}_D$$

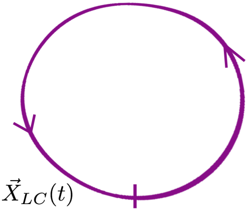
$$\tau_n \dot{\vec{V}}_V = F(\vec{V}_k) + c_{prop}(\vec{\kappa} + W_{prop}\vec{\kappa}) + W_{gap}\vec{V}_V$$

Full Model Captures Gait Adaptation



Reduction to Phase Model

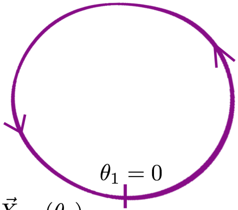
$$\frac{d\vec{X}_1}{dt} = F(\vec{X}_1)$$



$$\vec{X}_1(t) = \vec{X}_{LC}(t)$$

Reduction to Phase Model

$$\frac{d\vec{X}_1}{dt} = F(\vec{X}_1)$$

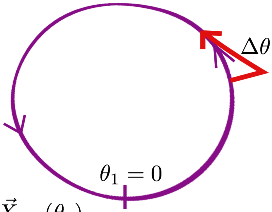


$$\vec{X}_1(t) = \vec{X}_{LC}(\theta_1)$$

$$\dot{\theta}_1 = \omega$$

Reduction to Phase Model

$$\frac{d\vec{X}_1}{dt} = F(\vec{X}_1)$$



$$\vec{X}_1(t) = \vec{X}_{LC}(\theta_1)$$

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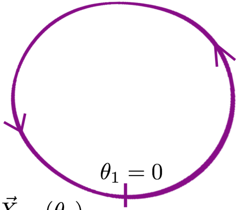
Reduction to Phase Model

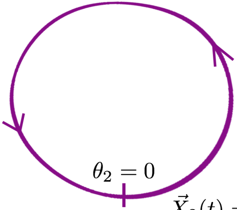
$$\frac{d\vec{X}_1}{dt} = F(\vec{X}_1)$$



$$\vec{X}_1(t) = \vec{X}_{LC}(\theta_1)$$

$$\dot{\theta}_1 = \omega$$

$$\frac{d\vec{X}_2}{dt} = F(\vec{X}_2)$$

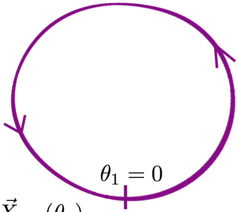


$$\vec{X}_2(t) = \vec{X}_{LC}(\theta_2)$$

$$\dot{\theta}_2 = \omega$$

Reduction to Phase Model

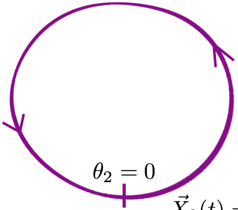
$$\frac{d\vec{X}_1}{dt} = F(\vec{X}_1) + \epsilon G(\vec{X}_1, \vec{X}_2)$$



$$\vec{X}_1(t) = \vec{X}_{LC}(\theta_1)$$

$$\dot{\theta}_1 = \omega$$

$$\frac{d\vec{X}_2}{dt} = F(\vec{X}_2) + \epsilon G(\vec{X}_2, \vec{X}_1)$$



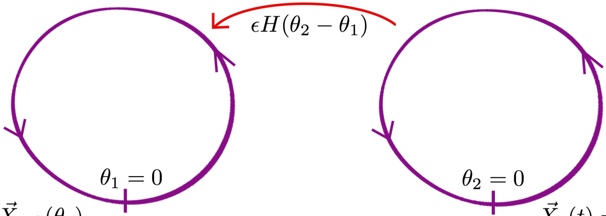
$$\vec{X}_2(t) = \vec{X}_{LC}(\theta_2)$$

$$\dot{\theta}_2 = \omega$$

Reduction to Phase Model

$$\frac{d\vec{X}_1}{dt} = F(\vec{X}_1) + \epsilon G(\vec{X}_1, \vec{X}_2)$$

$$\frac{d\vec{X}_2}{dt} = F(\vec{X}_2) + \epsilon G(\vec{X}_2, \vec{X}_1)$$



$$\vec{X}_1(t) = \vec{X}_{LC}(\theta_1)$$

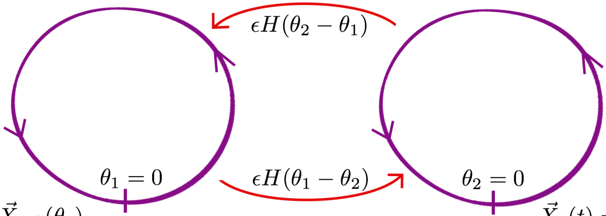
$$\vec{X}_2(t) = \vec{X}_{LC}(\theta_2)$$

$$\dot{\theta}_1 = \omega + \epsilon H(\theta_2 - \theta_1)$$

$$\dot{\theta}_2 = \omega$$

Reduction to Phase Model

$$\frac{d\vec{X}_1}{dt} = F(\vec{X}_1) + \epsilon G(\vec{X}_1, \vec{X}_2) \qquad \frac{d\vec{X}_2}{dt} = F(\vec{X}_2) + \epsilon G(\vec{X}_2, \vec{X}_1)$$



$$\vec{X}_1(t) = \vec{X}_{LC}(\theta_1) \qquad \vec{X}_2(t) = \vec{X}_{LC}(\theta_2)$$

$$\dot{\theta}_1 = \omega + \epsilon H(\theta_2 - \theta_1) \qquad \dot{\theta}_2 = \omega + \epsilon H(\theta_1 - \theta_2)$$

Reduction to Phase Model

$$
\begin{aligned}
\dot{\vec{\kappa}} &= -\frac{1}{\tau_f}\Big(\vec{\kappa} + c_{MA}\big(\sigma(\vec{A}_V) - \sigma(\vec{A}_D)\big)\Big) && -\frac{\Gamma}{\tau_f}\big(AA^T\big)^{-1}\dot{\vec{\kappa}} \\
\dot{\vec{A}}_k &= \frac{1}{\tau_m}\Big(-\vec{A}_k + \vec{V}_k - \vec{V}_{k'}\Big) && +0 \\
\dot{\vec{V}}_k &= \frac{1}{\tau_n}\Big(F(\vec{V}_k) \pm c_{prop}\vec{\kappa}\Big) && +\frac{1}{\tau_n}\Big(\pm c_{prop}W_{prop}\vec{\kappa} + W_{gap}\vec{V}_k\Big)
\end{aligned}
$$

Reduction to Phase Model

$$
\begin{aligned}
\dot{\vec{\kappa}} &= -\frac{1}{\tau_f}\left(\vec{\kappa} + c_{MA}\left(\sigma(\vec{A}_V) - \sigma(\vec{A}_D)\right)\right) & -\frac{\Gamma}{\tau_f}\left(AA^T\right)^{-1}\dot{\vec{\kappa}} \\
\dot{\vec{A}}_k &= \frac{1}{\tau_m}\left(-\vec{A}_k + \vec{V}_k - \vec{V}_{k'}\right) & +0 \\
\dot{\vec{V}}_k &= \frac{1}{\tau_n}\left(F(\vec{V}_k) \pm c_{prop}\vec{\kappa}\right) & +\frac{1}{\tau_n}\left(\pm c_{prop}W_{prop}\vec{\kappa} + W_{gap}\vec{V}_k\right)
\end{aligned}
$$

oscillator dynamics

weak coupling effects

Reduction to Phase Model

$$\dot{\vec{\kappa}} = -\frac{1}{\tau_f}\left(\vec{\kappa} + c_{MA}\left(\sigma(\vec{A}_V) - \sigma(\vec{A}_D)\right)\right) \quad -\frac{\Gamma}{\tau_f}\left(AA^T\right)^{-1}\dot{\vec{\kappa}}$$

$$\dot{\vec{A}}_k = \frac{1}{\tau_m}\left(-\vec{A}_k + \vec{V}_k - \vec{V}_{k'}\right) \quad +0$$

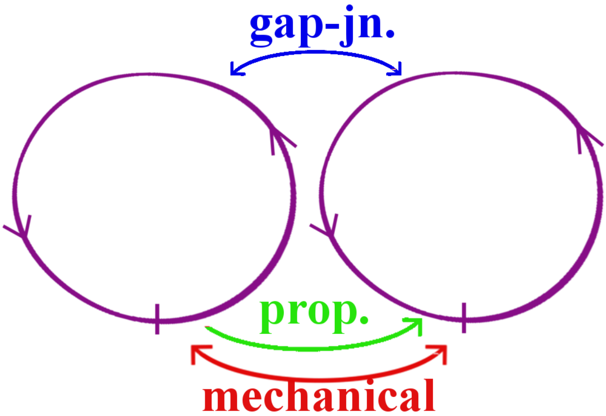
$$\dot{\vec{V}}_k = \frac{1}{\tau_n}\left(F(\vec{V}_k) \pm c_{prop}\vec{\kappa}\right) \quad +\frac{1}{\tau_n}\left(\pm c_{prop}W_{prop}\vec{\kappa} + W_{gap}\vec{V}_k\right)$$

oscillator dynamics

weak coupling effects

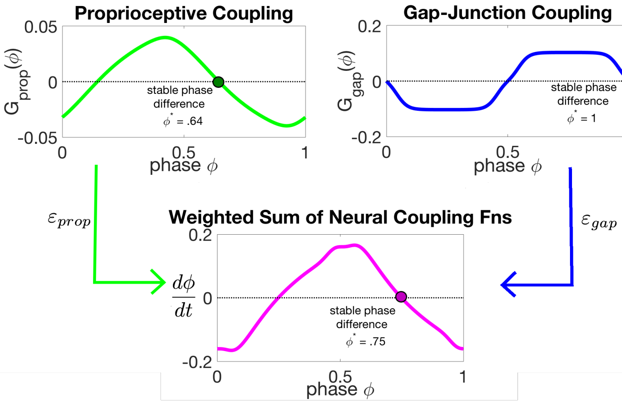
$$\dot{\vec{\theta}} = \omega + \quad H_{mech}(\theta) + H_{gap}(\theta) + H_{prop}(\theta)$$

Pair of Coupled Oscillators



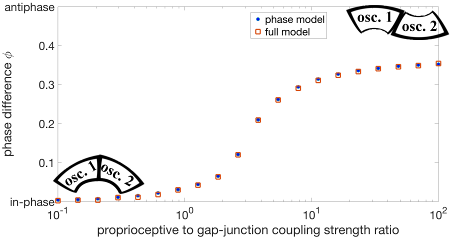
$$\frac{\mathrm{d}\phi}{\mathrm{d}t} = \frac{\mathrm{d}\theta_2}{\mathrm{d}t} - \frac{\mathrm{d}\theta_1}{\mathrm{d}t} = \epsilon_{prop} G_{prop}(\phi) + \epsilon_{gap} G_{gap}(\phi) + \Gamma G_{mech}(\phi)$$

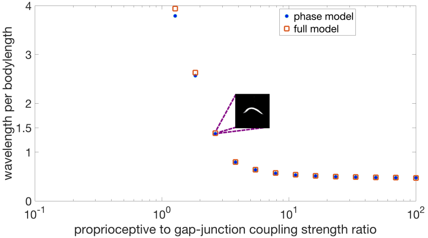
Neural Coupling sets the Long Wavelength



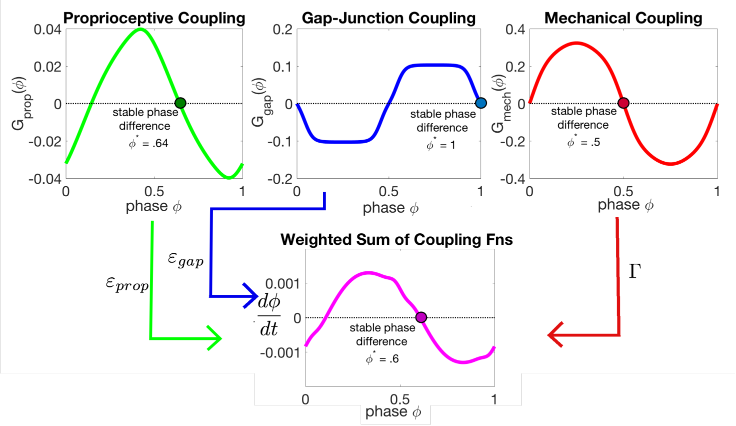
$$\frac{\mathrm{d}\phi}{\mathrm{d}t} = \varepsilon_{prop} G_{prop}(\phi) + \varepsilon_{gap} G_{gap}(\phi)$$

Neural Coupling sets the Long Wavelength



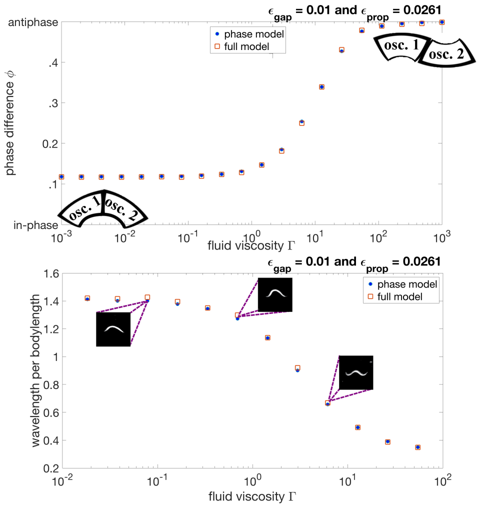


Effect of Mechanical Coupling

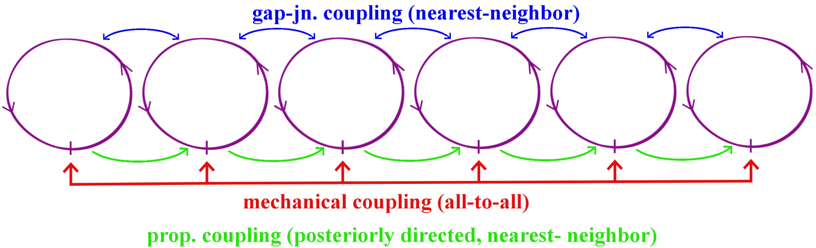


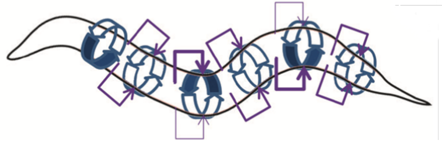
$$\frac{\mathrm{d}\phi}{\mathrm{d}t} = \varepsilon_{prop} G_{prop}(\phi) + \varepsilon_{gap} G_{gap}(\phi) + \Gamma G_{mech}(\phi)$$

Gait Adaptation in the Pair of Oscillators



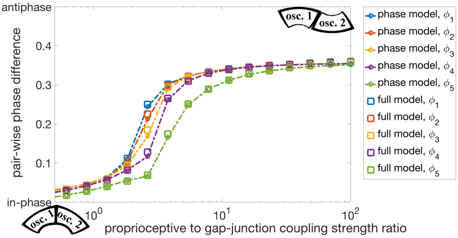
Full-Body Phase Model

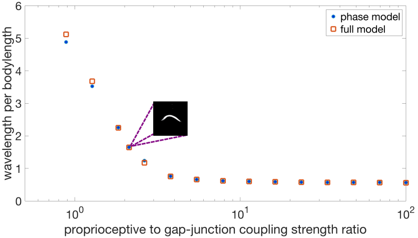




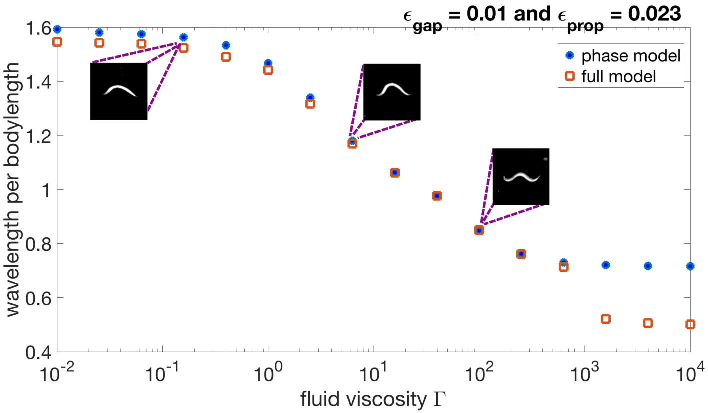
$$\frac{\mathrm{d}\vec{\phi}}{\mathrm{d}t} = \Gamma G_{mech}(\vec{\phi}) + \varepsilon_{gap} G_{gap}(\vec{\phi}) + \varepsilon_{prop} G_{prop}(\vec{\phi})$$

Neural Coupling sets the Long Wavelength



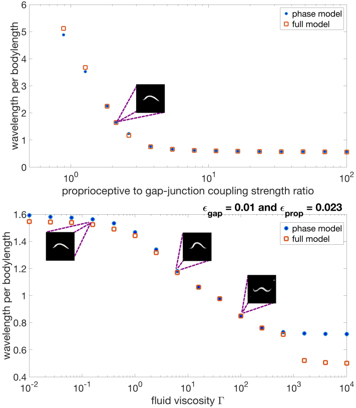


Gait Adaptation is the result of Competition between Neural & Mechanical Coupling



Summary

- Neural coupling sets the long wavelength
- Competition between mechanical and neural coupling provides a mechanism for gait adaptation



Gait & Frequency Adaptation