Mathematical analysis of the spinal cord neural circuit for locomotion in lamprey (fish).

Presentation at Mathematics in Neuroscience Symposium, June 10, 2008,
Ecole nationale superieure de chimie de Paris (ENSCP).

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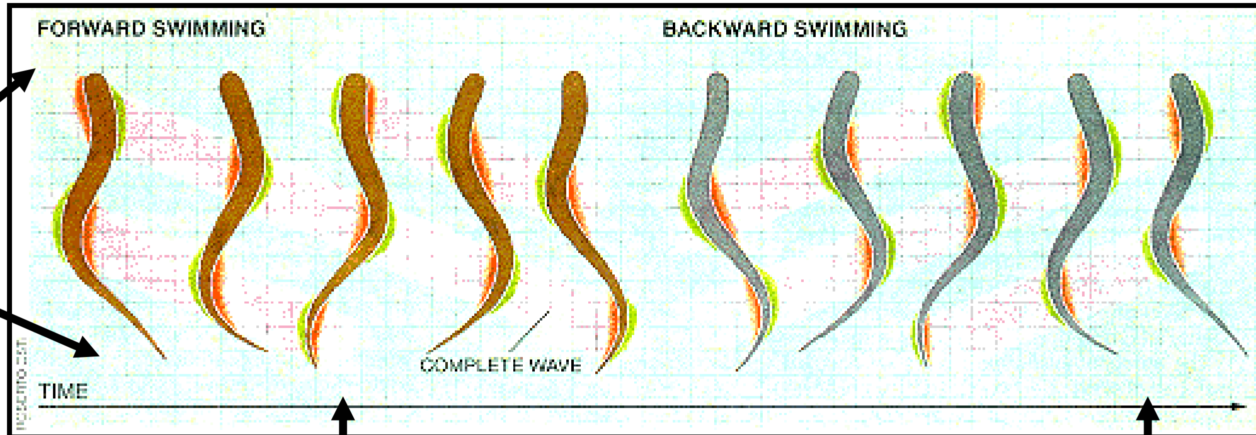
Silvia Scarpetta

Details in Zhaoping et al, Physical Review Letters, 2004,
www.cs.ucl.ac.uk/staff/Zhaoping.Li/

Lamprey, locomotion (swimming)

One wave length over
about 100 body segments



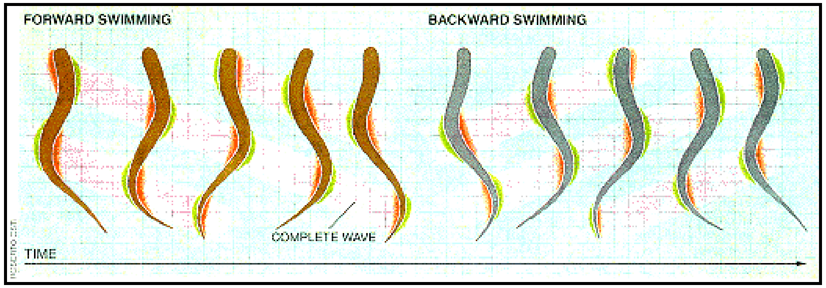
Head oscillation leads tail
forward swimming

Head oscillation lags tail
backward swimming

Spatially organized oscillatory neural activities in the spinal neural circuit generate oscillatory muscle action for swimming.

The nervous system survives under in vitro conditions for days for well controlled experimental study: fictive swimming.

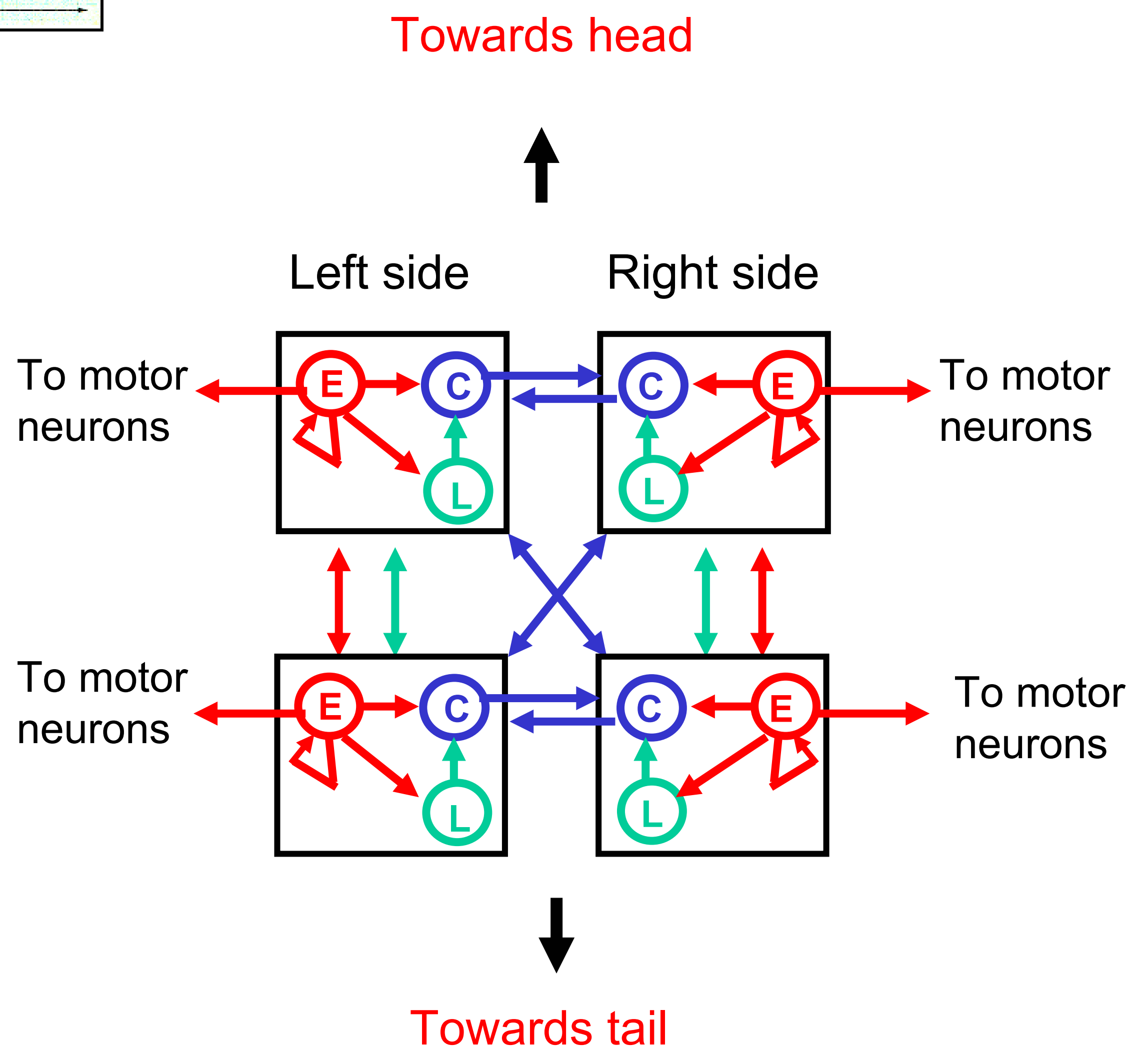
A textbook model system to study motor control,
neural circuit (network), and central pattern generator (CPG).



Two segments in the spinal cord neural circuit (the CPG):

Three types of neurons:

E (excitatory),
C (cross-caudal inhibitory),
L (inhibitory)



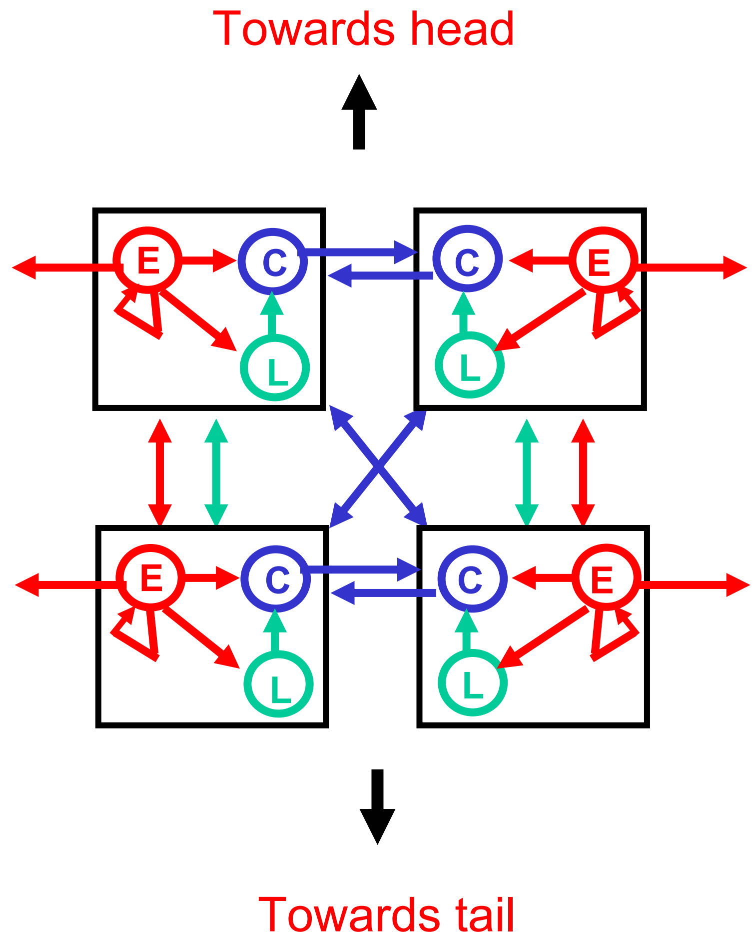
Experimental data in literature:

Spontaneous oscillations occur in decapitated sections with a minimum of 2-3 segments, from anywhere along the body.

E and C neurons: shorter range connections (a few segments), L: longer connections. Approx. 100 segments for whole body

Head-to-tail (rostral-to-caudal) descending connections dominate

E and L oscillate in phase, C phase leads.



Representative Previous works

More biological details

Grillner, Lansner, Hellgren, Kozlov, Brodin, Ekeberg, Wallen, etc:
Simulation of CPG with detailed cellular properties.

Our Work: analytical study of the neural circuit.

- How do oscillations emerge when single segment does not oscillate? --- {no previous studies}

- How are inter-segment phase lags determined by connections --- {not yet fully understood in previous works}

- How can the same network do both forward and backward swimming? how is it controlled?

More abstract

Kopell, Ermentrout, Cohen, Holmes, etc: Mathematical model of CPG simplified as a chain of coupled abstract phase oscillators.

$$d/dt\, \theta_i = \omega_i + \Sigma_j f_{ij} (\theta_i, \theta_j)$$

Neurons modeled as leaky integrators

$$\frac{d}{dt}\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} = -\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} + \begin{pmatrix} J & 0 & -K \\ W & 0 & -A \\ Q & -H & -B \end{pmatrix}\begin{pmatrix} g(E_L) \\ g(L_L) \\ g(C_R) \end{pmatrix}$$

+ external inputs from outside CPG

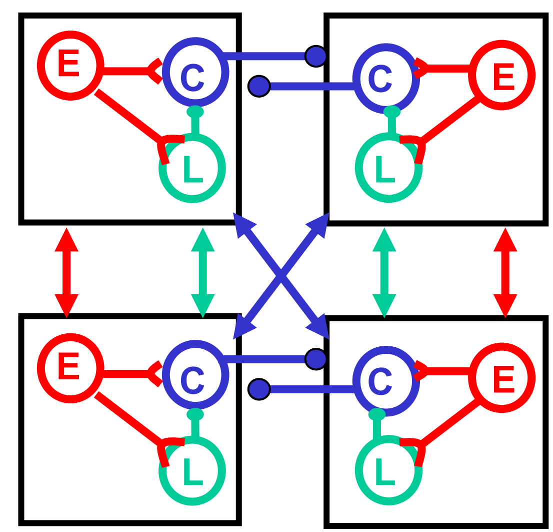
Membrane potentials

Decay (leaky) term

Connection strengths

Firing rates

Inputs from other neurons within CPG



Neurons modeled as leaky integrators

$$\frac{d}{dt}\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} = -\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} + \begin{pmatrix} J & 0 & -K \\ W & 0 & -A \\ Q & -H & -B \end{pmatrix}\begin{pmatrix} g(E_L) \\ g(L_L) \\ g(C_R) \end{pmatrix} + \text{external inputs}$$

Membrane potentials

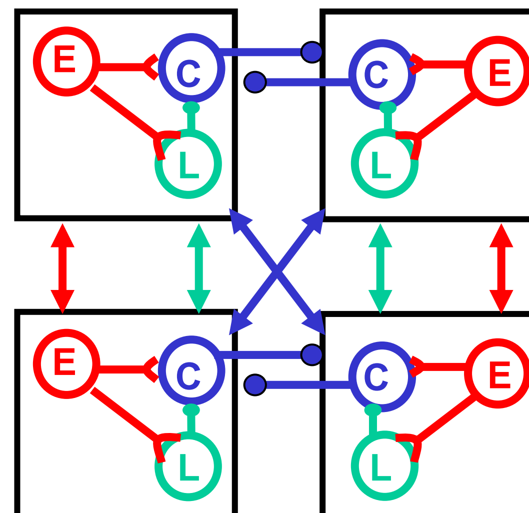
Decay (leaky) term

Connection strengths

Firing rates

Contra-lateral connections from C neurons

Left-right symmetry in connections



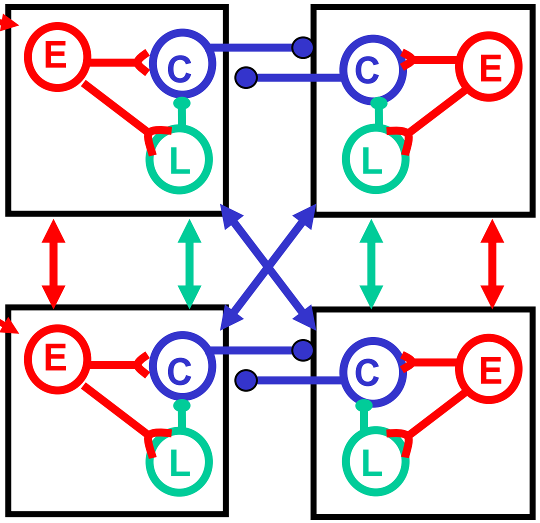
Neurons modeled as leaky integrators

$$\frac{d}{dt}\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} = -\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} + \begin{pmatrix} J & 0 & -K \\ W & 0 & -A \\ Q & -H & -B \end{pmatrix}\begin{pmatrix} g(E_L) \\ g(L_L) \\ g(C_R) \end{pmatrix} + \text{external inputs}$$

Membrane potentials

Connection strengths

E,L,C are 100 component vectors: $E_L = \begin{pmatrix} E^1_L \\ E^2_L \\ E^3_L \\ \vdots \end{pmatrix}$



$\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix}$ is an 300 component vector

Neurons modeled as leaky integrators

$$\frac{d}{dt}\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} = -\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} + \begin{pmatrix} J & 0 & -K \\ W & 0 & -A \\ Q & -H & -B \end{pmatrix}\begin{pmatrix} g(E_L) \\ g(L_L) \\ g(C_R) \end{pmatrix} + \text{external inputs}$$

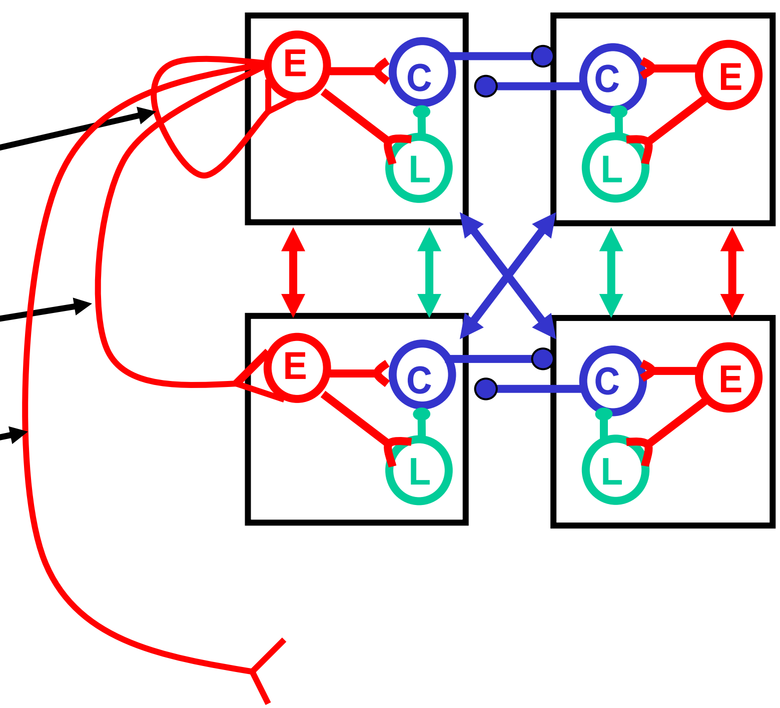
Membrane potentials

Connection strengths

J,K,etc are 100x100 matrices:

$$J = \begin{pmatrix} J_{11} & J_{12} & J_{13} & \cdot \\ J_{21} & J_{22} & \cdot & \cdot \\ J_{31} & \cdot & \cdot & \cdot \end{pmatrix}$$

Near-diagonal matrix



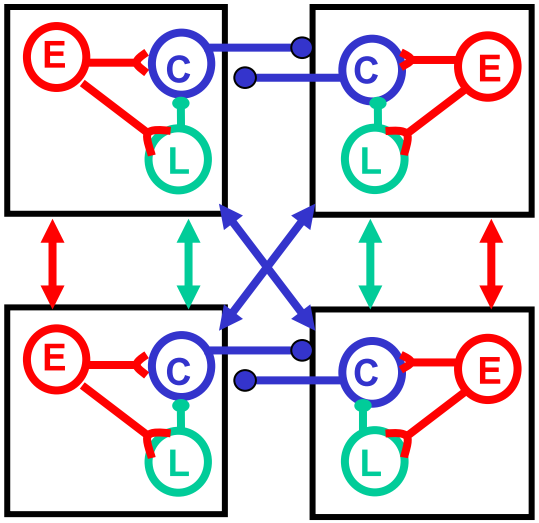
Neurons modeled as leaky integrators

$$\frac{d}{dt}\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} = -\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} + \begin{pmatrix} J & 0 & -K \\ W & 0 & -A \\ Q & -H & -B \end{pmatrix}\begin{pmatrix} g(E_L) \\ g(L_L) \\ g(C_R) \end{pmatrix} + \text{external inputs}$$

Membrane potentials

Connection strengths

This is a 300 x 300 matrix



Equations still too complex, Need simplification!!!

Methods used in the simplification/analysis:

1. Linear approximation
   to reduce to a low-dimensional system (mode)
   using various real and approximated symmetries.

2. Using physiological data to arrive at another additional simplification to a 2-dim system

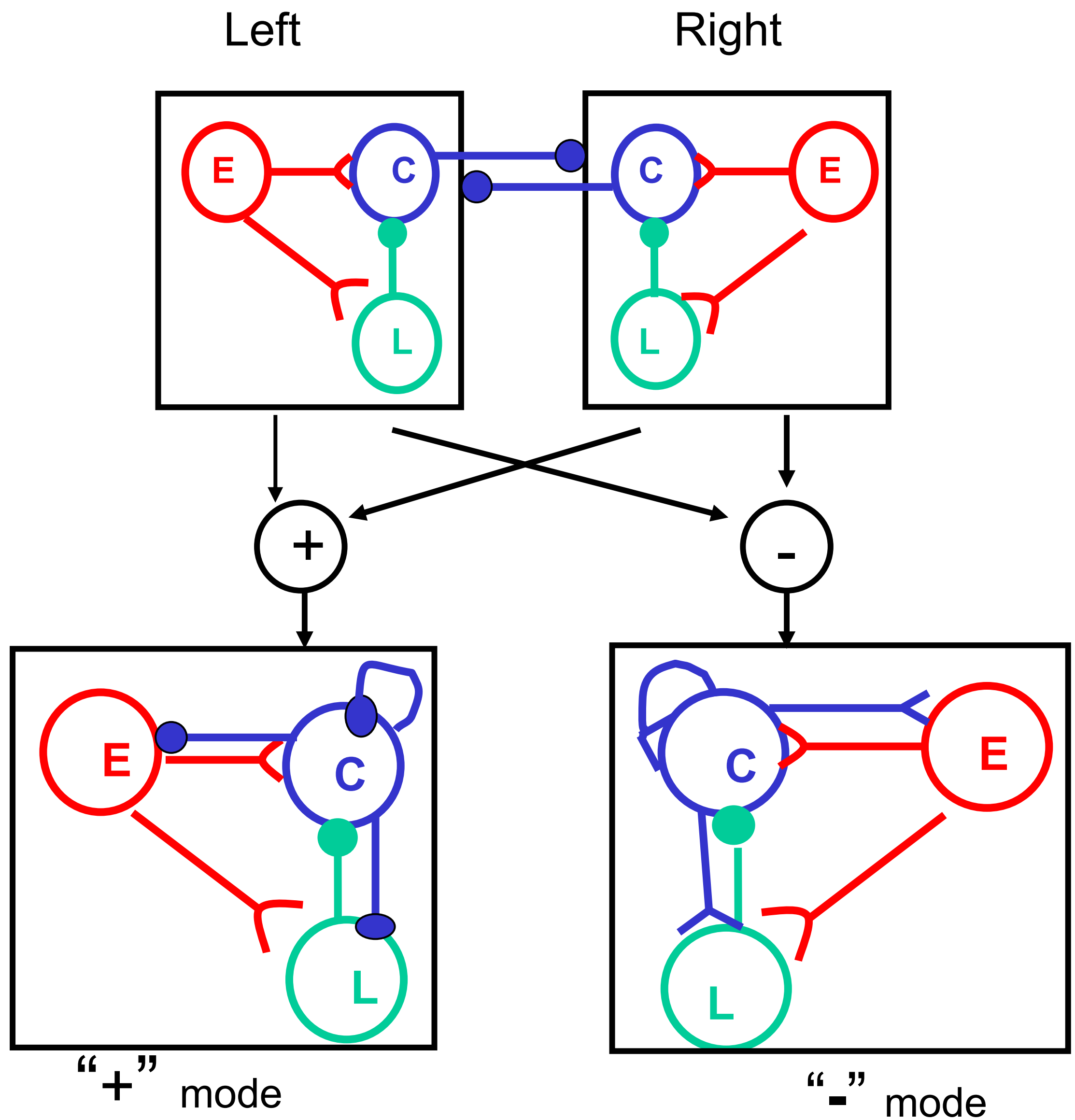
3. Computer simulation confirming the validity of the approximation

4. Nonlinear analysis --- to study coupling between modes and stability

5. Coupled oscillator analysis for boundary conditions

Left and right sides are coupled

$$\begin{pmatrix} E_+ \\ L_+ \\ C_+ \end{pmatrix} = \begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} + \begin{pmatrix} E_R \\ L_R \\ C_R \end{pmatrix}$$



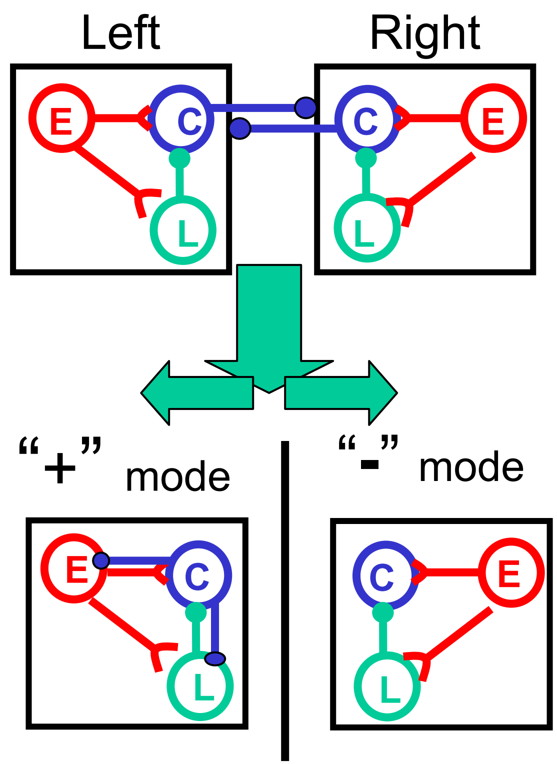
$$\begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix} = \begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} - \begin{pmatrix} E_R \\ L_R \\ C_R \end{pmatrix}$$

The swimming mode !!

Now decoupled!

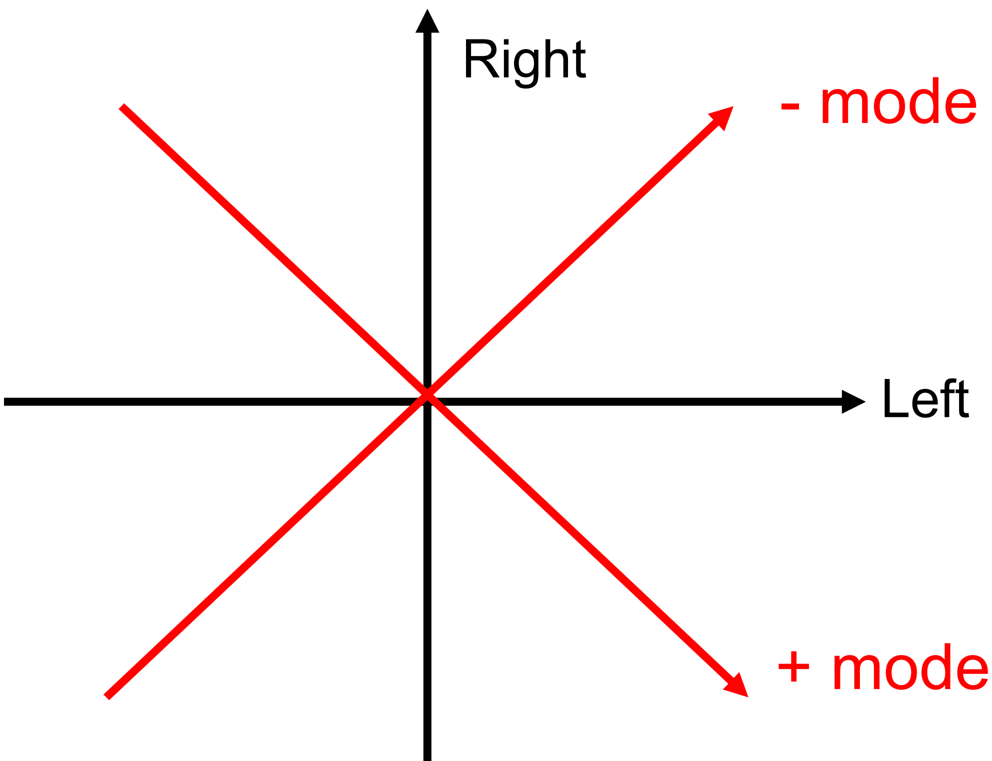
Mathematically:

$$\frac{d}{dt}\begin{pmatrix}E_L\\ L_L\\ C_L\end{pmatrix} = -\begin{pmatrix}E_L\\ L_L\\ C_L\end{pmatrix} + \begin{pmatrix}J & 0 & -K\\ W & 0 & -A\\ Q & -H & -B\end{pmatrix}\begin{pmatrix}g(E_L)\\ g(L_L)\\ g(C_R)\end{pmatrix} + \text{external inputs}$$



Linear approximation leads to decoupling

$$\begin{pmatrix}E_\pm\\ L_\pm\\ C_\pm\end{pmatrix} = \begin{pmatrix}E_L\\ L_L\\ C_L\end{pmatrix} \pm \begin{pmatrix}E_R\\ L_R\\ C_R\end{pmatrix}$$



Mathematically:

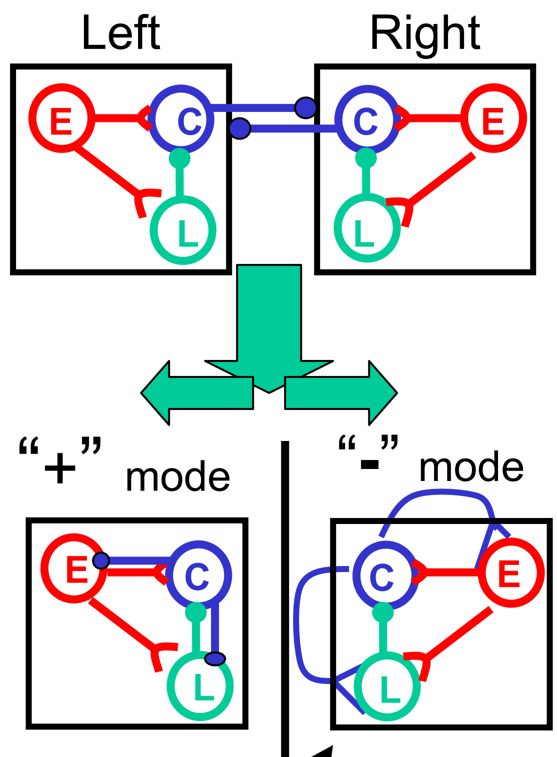
$$\frac{d}{dt}\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} = -\begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} + \begin{pmatrix} J & 0 & -K \\ W & 0 & -A \\ Q & -H & -B \end{pmatrix}\begin{pmatrix} g(E_L) \\ g(L_L) \\ g(C_R) \end{pmatrix} + \text{external inputs}$$

Linear approximation leads to decoupling

$$\begin{pmatrix} E_\pm \\ L_\pm \\ C_\pm \end{pmatrix} = \begin{pmatrix} E_L \\ L_L \\ C_L \end{pmatrix} \pm \begin{pmatrix} E_R \\ L_R \\ C_R \end{pmatrix}$$

$$\frac{d}{dt}\begin{pmatrix} E_+ \\ L_+ \\ C_+ \end{pmatrix} = -\begin{pmatrix} E_+ \\ L_+ \\ C_+ \end{pmatrix} + \begin{pmatrix} J & 0 & -K \\ W & 0 & -A \\ Q & -H & -B \end{pmatrix}\begin{pmatrix} E_+ \\ L_+ \\ C_+ \end{pmatrix} + \text{external inputs}$$

$$\frac{d}{dt}\begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix} = -\begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix} + \begin{pmatrix} J & 0 & +K \\ W & 0 & +A \\ Q & -H & +B \end{pmatrix}\begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix}$$



The connections scaled by the gain g'(.) in g(.), controlled by external inputs.

Swimming mode
C_- becomes **excitatory.**

Swimming mode always dominant!

Dynamics for the left-right antiphase (swimming) mode

$$\frac{d}{dt}\begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix} = -\begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix} + \begin{pmatrix} J & 0 & +K \\ W & 0 & +A \\ Q & -H & +B \end{pmatrix}\begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix}$$

All connections J, W, Q, H, K, A,B are approximately that, e.g., connections J_{ij} depend only on segment difference

$x = i - j.$

Fourier Transform

$k=2\pi m/N$

So $J_{ij} \longrightarrow J(x) \longrightarrow \mathcal{J}(k)$

$E_1, E_2, E_3 \ldots \longrightarrow E(x) \longrightarrow \mathcal{E}(k)$

Amplitude of spatial waves $E(x) = \cos(kx+\varphi)$

$J_{ij} E_j \longrightarrow J(x-x')E(x') \longrightarrow \mathcal{J}(k)\, \mathcal{E}(k)$

Different waves k decouple from each other:

Fourier Connections

$$\frac{d}{dt}\begin{pmatrix} E(k) \\ L(k) \\ C(k) \end{pmatrix} = -\begin{pmatrix} E(k) \\ L(k) \\ C(k) \end{pmatrix} + \begin{pmatrix} J(k) & 0 & K(k) \\ W(k) & 0 & A(k) \\ Q(k) & -H(k) & B(k) \end{pmatrix}\begin{pmatrix} E(k) \\ L(k) \\ C(k) \end{pmatrix}$$

Solution:

$$\begin{pmatrix} E(k) \\ L(k) \\ C(k) \end{pmatrix} \exp[-t + \lambda(k) t]$$

eigenvector

Eigenvalue of

Fourier Connections

$$\begin{pmatrix} J(k) & 0 & K(k) \\ W(k) & 0 & A(k) \\ Q(k) & -H(k) & B(k) \end{pmatrix}$$

$-\mathrm{Im}(\lambda)$

$$\begin{pmatrix} E(k) \\ L(k) \\ C(k) \end{pmatrix} \exp[-t + \mathrm{Re}(\lambda)\, t - i\, \omega\, t]$$

Spatial waves, oscillating

at fr

Connection structure decides which wave k has **Re(λ(k)) > 1**

ding

Oscillation phase

$$E \sim \exp[-t + \mathrm{Re}(\lambda)\, t - i\,(\omega t - k x + \Phi_E)]$$

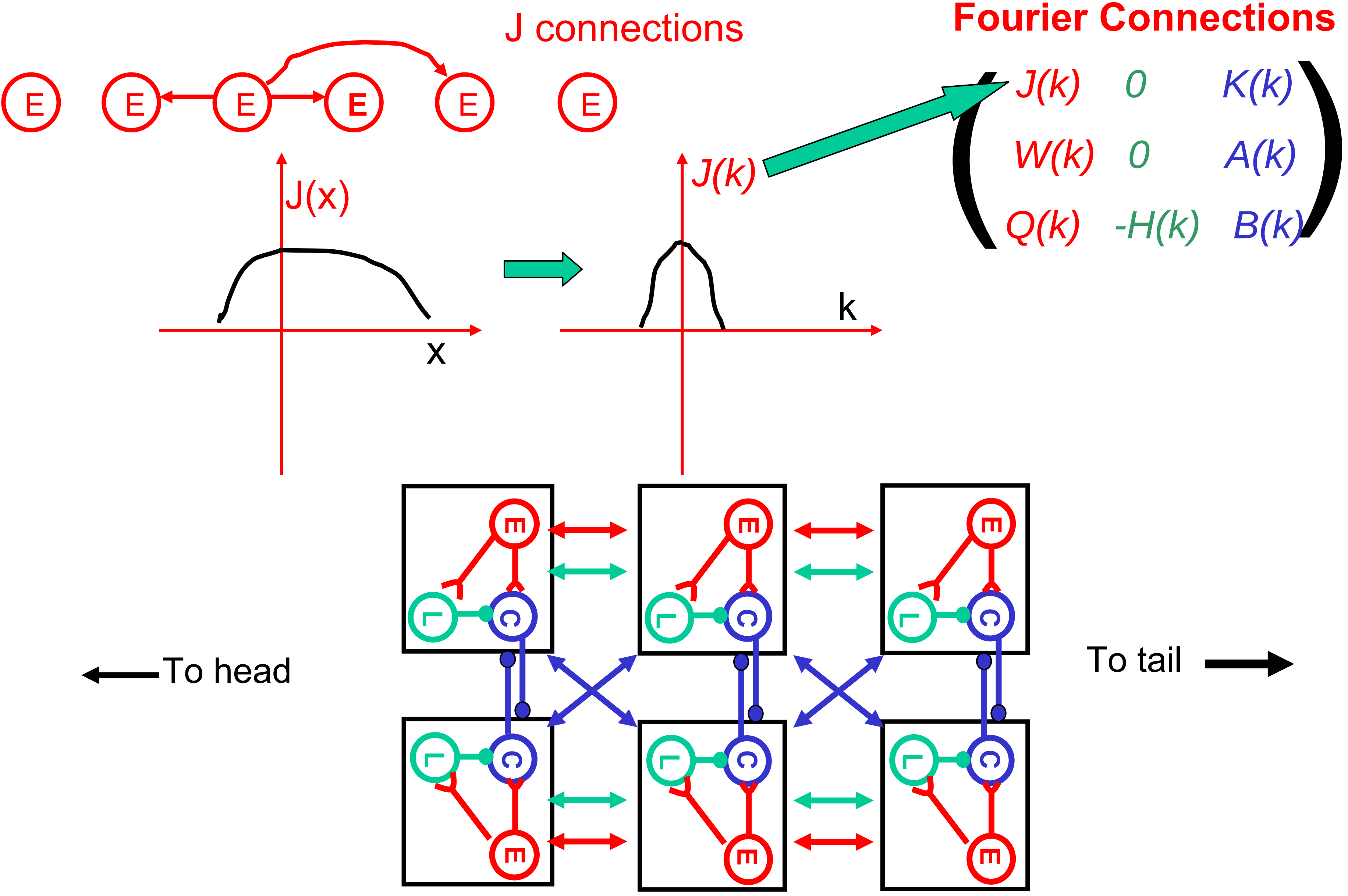
$$L \sim \exp[-t + \mathrm{Re}(\lambda)\, t - i\,(\omega t - k x + \Phi_L)]$$

$$C \sim \exp[-t + \mathrm{Re}(\lambda)\, t - i\,(\omega t - k x + \Phi_C)]$$

k<0, phase descending from head to tail

Wave unsustainable unless Re(λ) > 1

In a nutshell:



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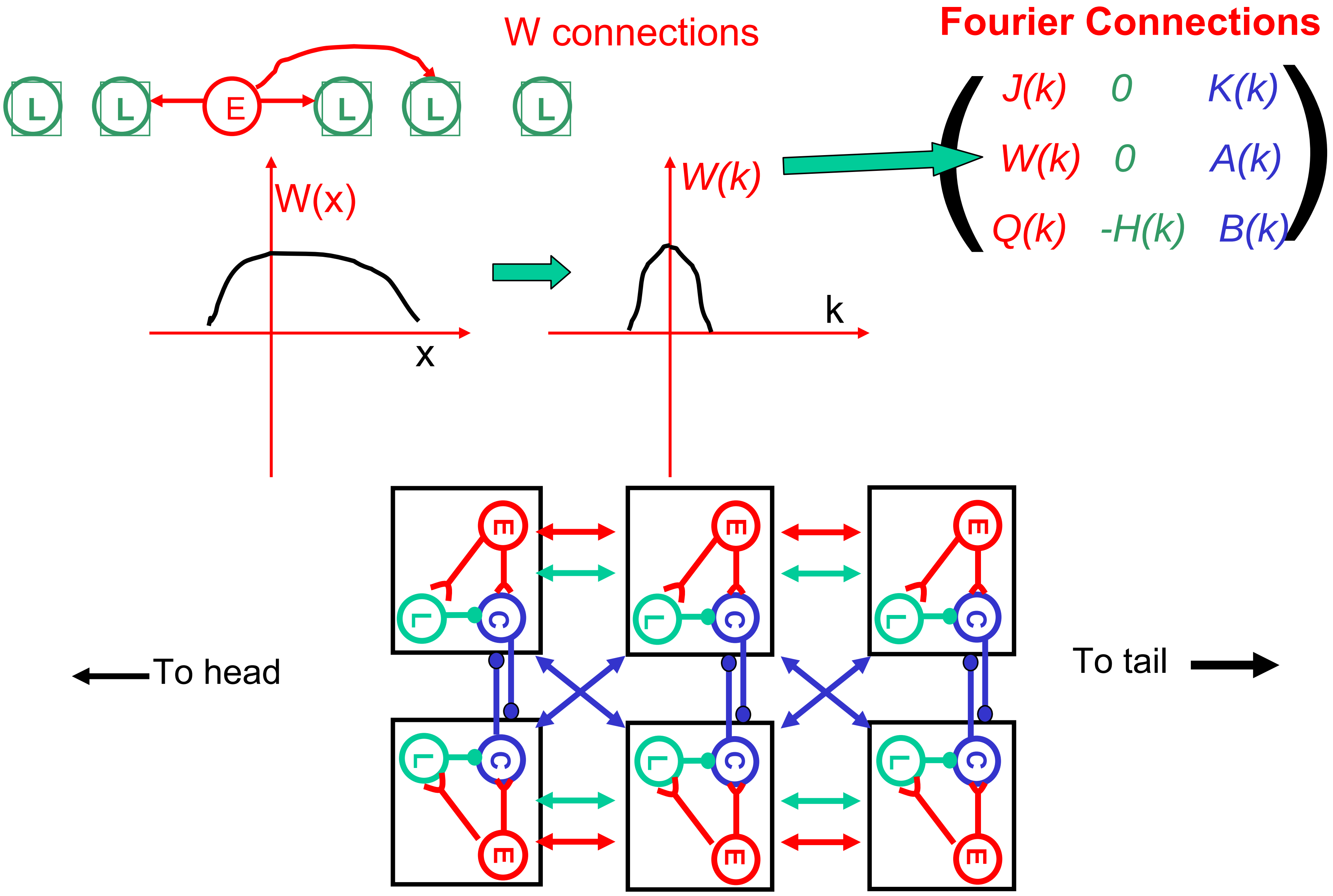

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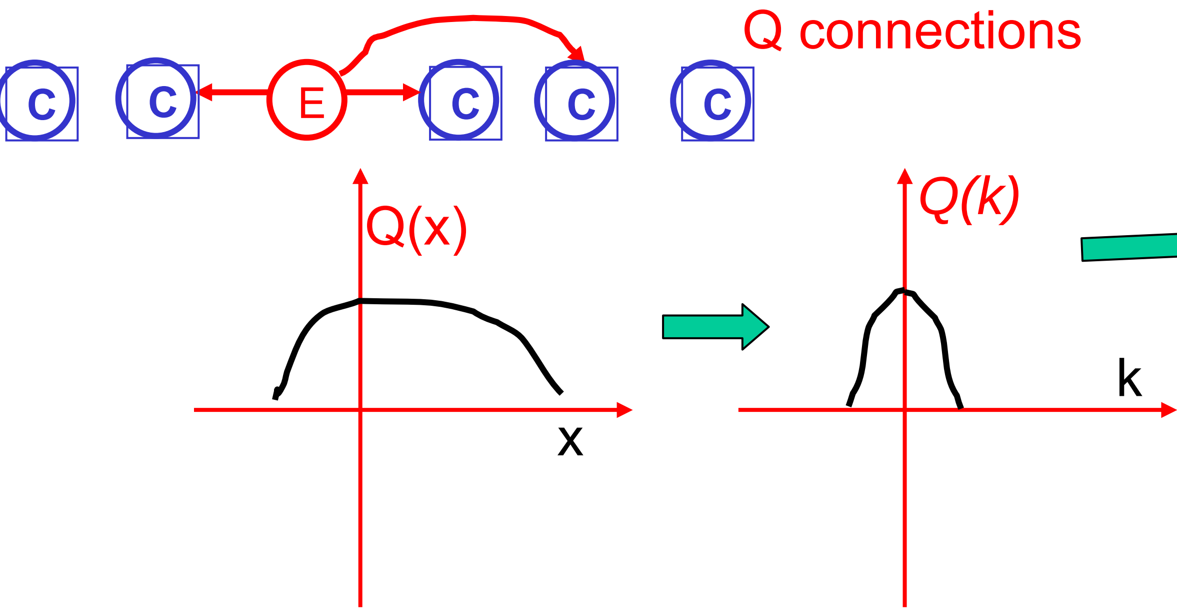
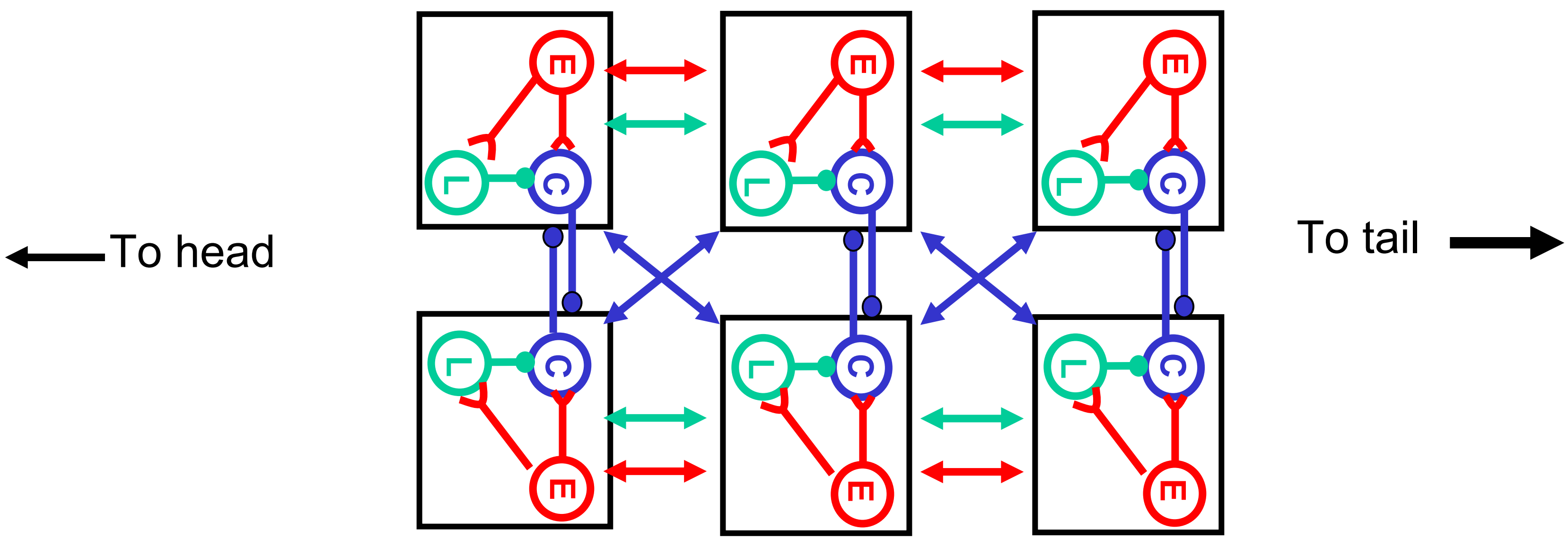


Fourier Connections

$$\begin{pmatrix} J(k) & 0 & K(k) \\ W(k) & 0 & A(k) \\ Q(k) & -H(k) & B(k) \end{pmatrix}$$



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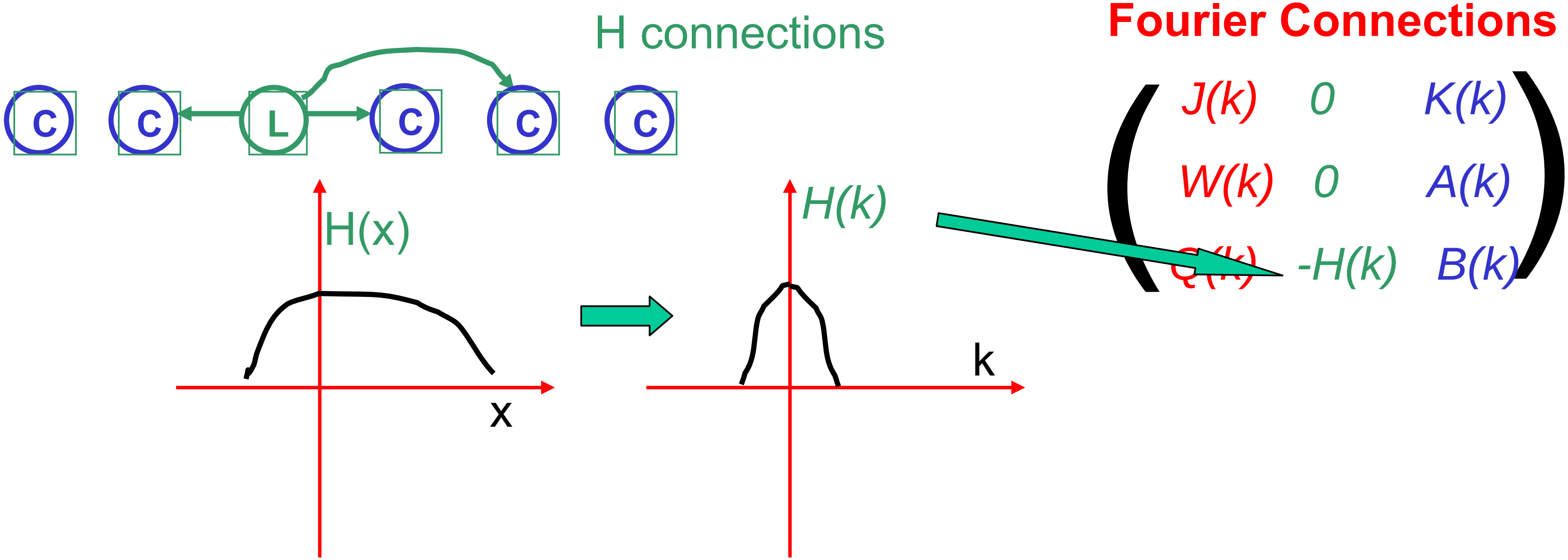
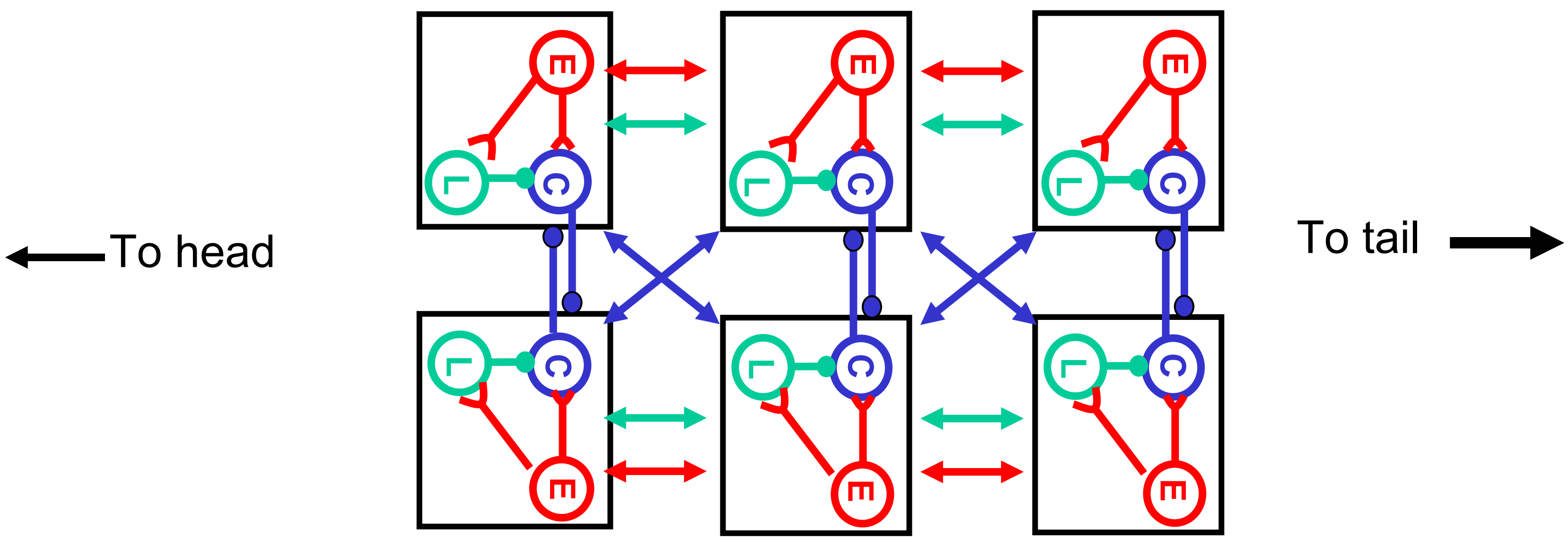


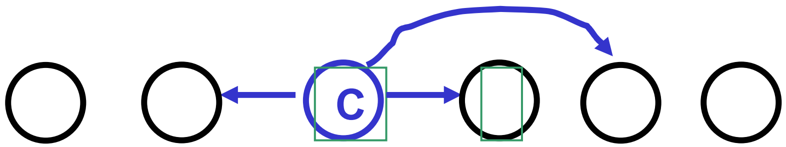


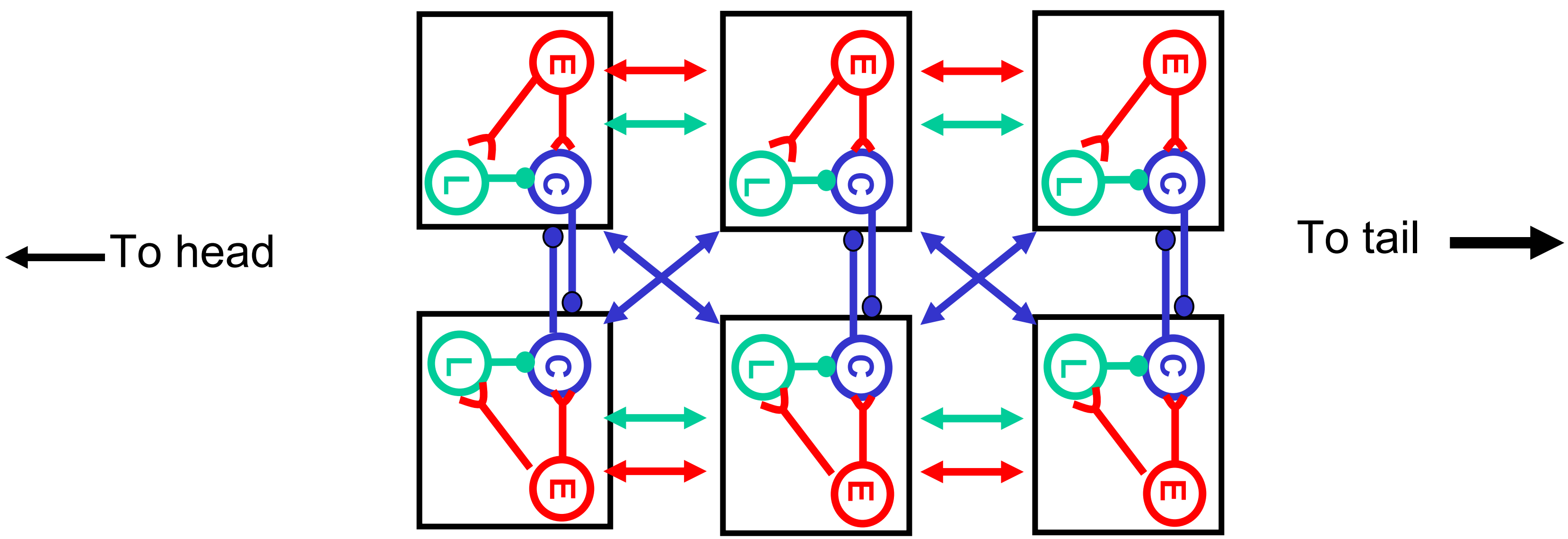
In a nutshell:

Fourier Connections

Similarly, connections from C cells

$$\begin{pmatrix} J(k) & 0 & K(k) \\ W(k) & 0 & A(k) \\ Q(k) & -H(k) & B(k) \end{pmatrix}$$





The connections are such that,

Fourier Connections

$$\begin{pmatrix} J(k) & 0 & K(k) \\ W(k) & 0 & A(k) \\ Q(k) & -H(k) & B(k) \end{pmatrix}$$

Re(λ(k)) largest for **wave k** corresponding to the swimming mode, when k corresponds to wavelength of a whole body length, and

In default situations, **swimming forward, k>0**

Connection structure decides which wave k has **Re(λ(k)) > 1**

$$E \sim \exp[\,-t + \mathrm{Re}(\lambda)\,t \;-\; i\,(\omega\, t - k\, x + \Phi_E)]$$

$$L \sim \exp[\,-t + \mathrm{Re}(\lambda)\,t \;-\; i\,(\omega\, t - k\, x + \Phi_L)]$$

$$C \sim \exp[\,-t + \mathrm{Re}(\lambda)\,t \;-\; i\,(\omega\, t - k\, x + \Phi_C)]$$

Wave unsustainable unless Re(λ) > 1

The swimming mode

$$\frac{d}{dt}\begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix} = -\begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix} + \begin{pmatrix} J & 0 & K \\ W & 0 & A \\ Q & -H & B \end{pmatrix}\begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix}$$

Experimental data show E &L synchronize, C phase leads by quarter cycle

$$\frac{d}{dt}(E_- - L_-) = -(E_- - L_-) + (J-W)E_- + (K-A)C_-$$

$E_- = L_-$ → $(J-W)E_- + (K-A)C_- = 0$

$(J-W) \sim E_-$, $(K-A) \sim C_-$

Since J, W, K, A all near diagonal

→ Simplification : E=L, J=W, K=A

$$\frac{d}{dt}\begin{pmatrix} E_- \\ C_- \end{pmatrix} = \begin{pmatrix} J\text{-}1 & K \\ Q\text{-}H & B\text{-}1 \end{pmatrix}\begin{pmatrix} E_- \\ C_- \end{pmatrix}$$

Prediction 1: H>Q, i.e., L inhibits C more than E excites C, needed for oscillations!

Compare with harmonic oscillator

$$\frac{d}{dt}x = \omega y$$
$$\frac{d}{dt}y = -\omega x$$

The swimming mode

$$d/dt \begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix} = - \begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix} + \begin{pmatrix} J & 0 & K \\ W & 0 & A \\ Q & -H & B \end{pmatrix} \begin{pmatrix} E_- \\ L_- \\ C_- \end{pmatrix}$$

Experimental data show E &L synchronize, C phase leads by quarter cycle

$$d/dt\,(E_- - L_-) = -(E_- - L_-) + (J-W)\,E_- + (K-A)C_-$$

$$E_- = L_- \longrightarrow (J-W)\,E_- + (K-A)C_- = 0$$

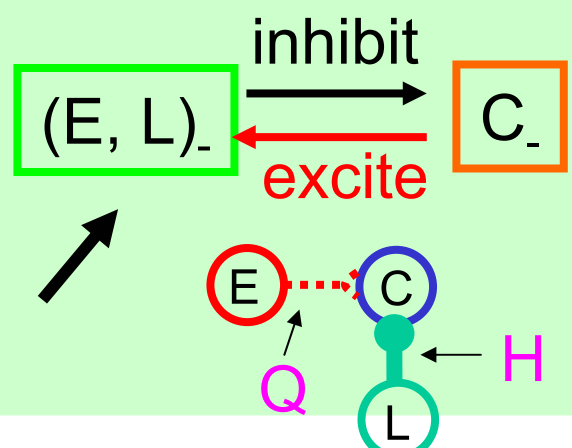
$(J-W)\,E_- \downarrow \sim E_-$; $(K-A)C_- \downarrow \sim C_-$

Since J, W, K, A all near diagonal

$\longrightarrow$ Simplification : E=L, J=W, K=A

$$d/dt \begin{pmatrix} E_- \\ C_- \end{pmatrix} = \begin{pmatrix} J\mathbf{-1} & K \\ Q\,-H & B\mathbf{-1} \end{pmatrix} \begin{pmatrix} E_- \\ C_- \end{pmatrix}$$

Prediction 1: H>Q, i.e., L inhibits C more than E excites C, needed for oscillations!



The swimming mode

$$\frac{d}{dt}\begin{pmatrix} E_- \\ C_- \end{pmatrix} = \begin{pmatrix} J-1 & K \\ Q-H & B-1 \end{pmatrix}\begin{pmatrix} E_- \\ C_- \end{pmatrix}$$

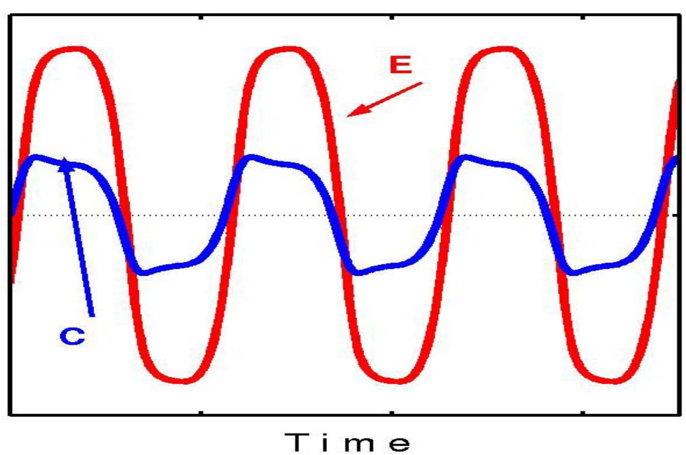
Oscillator equation:

$$d^2/dt^2\, E + (2-J-B)\; d/dt\, E + [(1-J)(1-B) + K(H-Q)]\, E = 0$$

Damping ↑ (2-J-B)

Restoration force ↑ K(H-Q)

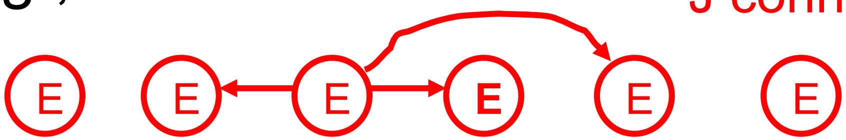
Simulation

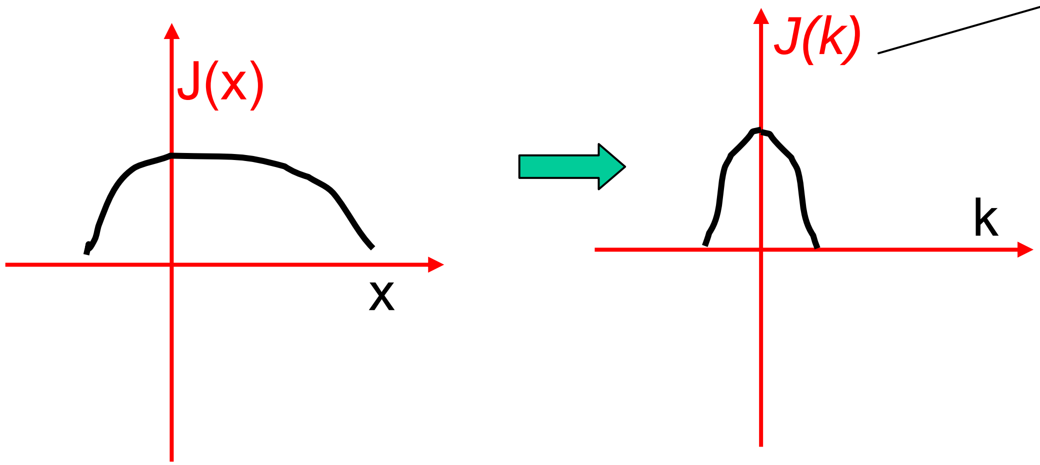


The swimming mode's wave number k

$$\frac{d}{dt}\begin{pmatrix} E_- \\ C_- \end{pmatrix} = \begin{pmatrix} J-1 & K \\ Q-H & B-1 \end{pmatrix}\begin{pmatrix} E_- \\ C_- \end{pmatrix}$$

e.g.,





expand in small k<< 1:

$J(k) = j_0 - ikj_1 - k^2 j_2 + O(k^3)$

where $j_n = \Sigma_x J(x)\, x^n/n!$

etc

moment

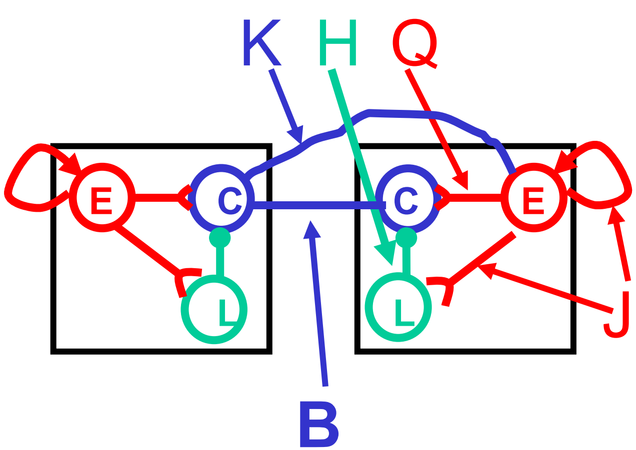
$$\frac{d}{dt}\begin{pmatrix} E_- \\ C_- \end{pmatrix} = \begin{pmatrix} J-1 & K \\ Q-H & B-1 \end{pmatrix}\begin{pmatrix} E_- \\ C_- \end{pmatrix} \xrightarrow{\text{Eigenvector solution}} \begin{pmatrix} E_- \\ C_- \end{pmatrix} e^{\lambda t+ikx} \sim e^{-i(\omega t-kx)}$$

The dominant eigenvector k determines the global phase gradient (wave number) k

For small k, $Re(\lambda) = const - k \cdot a$,

where $a \propto$ first moment of $(K(H-Q) - (B-J)^2)$

Eg. Head-to-tail B tends to increase the head-to-tail phase lag (k>0); while head-to-tail H tends to reduce or reverse it (k<0).



Prediction 2: swimming direction could be controlled by scaling connections H, (less easily also Q (K, B, J)), e.g., through external inputs (via recruiting more neurons or via gain g'(.) in the sigmoid function)

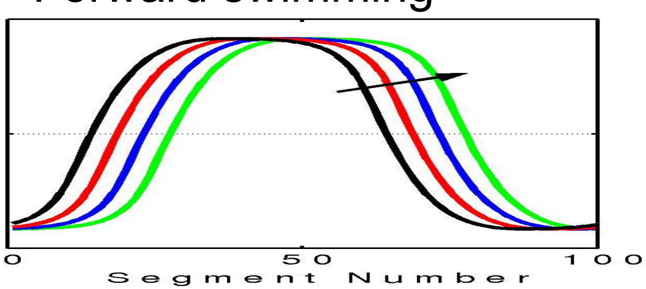
$$\frac{d}{dt}\begin{pmatrix} E_- \\ C_- \end{pmatrix} = \begin{pmatrix} J-1 & K \\ Q-H & B-1 \end{pmatrix} \begin{pmatrix} E_- \\ C_- \end{pmatrix} \xrightarrow{\text{Eigenvector solution}} \begin{pmatrix} E_- \\ C_- \end{pmatrix} e^{\lambda t + ikx} \sim e^{-i(\omega t - kx)}$$

The dominant eigenvector k determines the global phase gradient (wave number) k

So, e.g, increasing H (e.g, via input to L neurons) → Backward Swimming

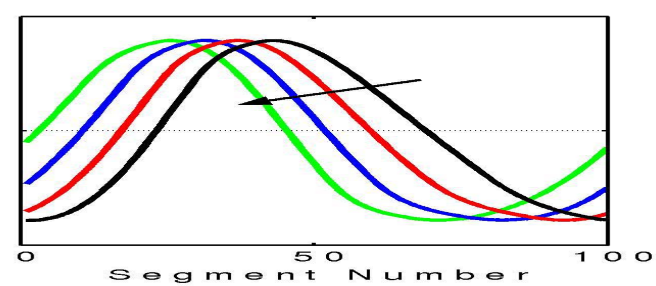
Simulation results:

Forward swimming



Scaling H & Q →

backward swimming



More intuitively,

See the system as a group of coupled oscillators

Oscillator equation: $d^2/dt^2 E + (2-J-B)\, d/dt\, E + [(1-J)(1-B) + K(H-Q)]\, E = 0$

Unlike previous models:

Damped single segment → $2 > J_{ii} + B_{ii}$ Self excitation does not overcome damping

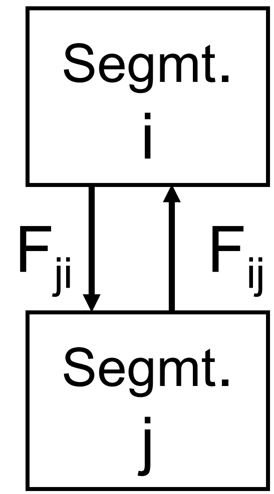
Inter-segment interaction:

$$d^2/dt^2 E_i + \alpha\, d/dt\, E_i + \omega_o^2 E_i = \Sigma_j F_{ij}$$

i^{th} damped oscillator segment of frequency ω_o

Driving force from other segments.

When driving forces feed energy from one oscillator to another, global spontaneous oscillation emerges.



Coupling: $F_{ij} = (J_{ij} + B_{ij})\, d/dt\, E_j \quad + [B+J]_{ij}\, E_j \quad - [BJ + K(H-Q)]_{ij} E_j$

Feeds energy when E_i & E_j synchronize

Feeds energy when E_i lags E_j

Feeds energy when E_i leads E_j

Balance between them controls phase lag and direction !

Feeding energy by coupling

Coupling: $F_{ij} = (J_{ij} + B_{ij})\, d/dt\, E_j \quad +[B+J]_{ij}\, E_j \quad -[BJ+K(H-Q)]_{ij} E_j$

Feeds energy when E_i & E_j synchronize

Feeds energy when E_i lags E_j

Feeds energy when E_i leads E_j

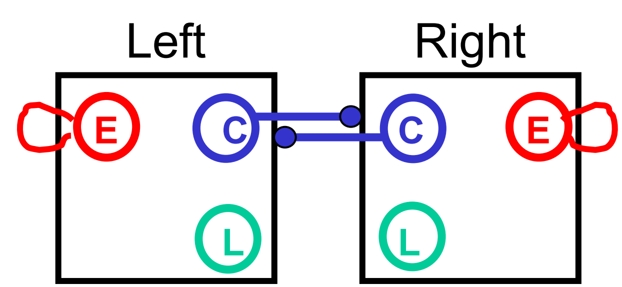
Dominant term is above, since phase gradient is small

The relevant connections for oscillations are thus

J E to E connections

B C to C connections

this as more dominating



Controlling swimming directions

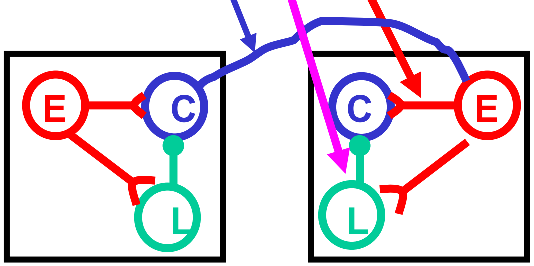
Coupling: $F_{ij} = (J_{ij} + B_{ij})\ d/dt\ E_j \quad +[B+J]_{ij}\ E_j \quad -[BJ+K(H-Q)]_{ij} E_j$

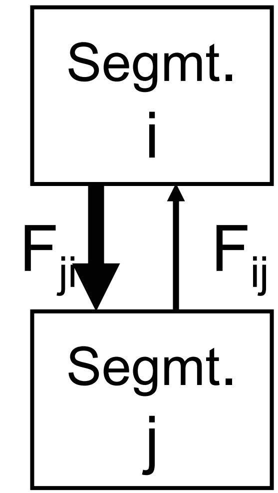
- Feeds energy when E_i & E_j synchronize
- Feeds energy when E_i lags E_j
- Feeds energy when E_i leads E_j

Given $F_{ji} > F_{ij}$, (ascending connections dominate)

$B+J > BJ+K(H-Q)$ → Forward swimming (head phase leads tail)

$B+J < BJ+K(H-Q)$ → Backward swimming (head phase lags tail)

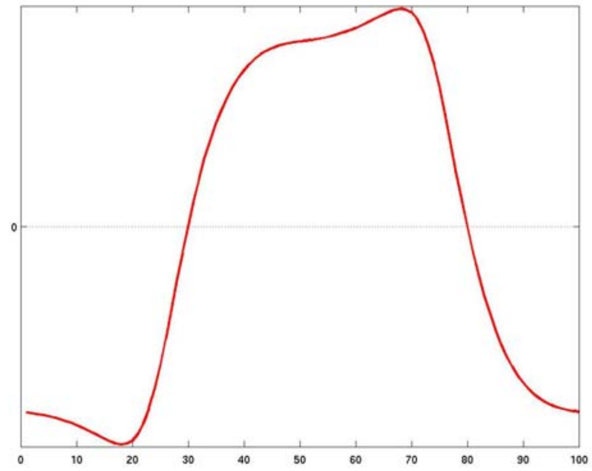




SIMULATIONS

Forward swimming:

$E_- = E_L - E_R$

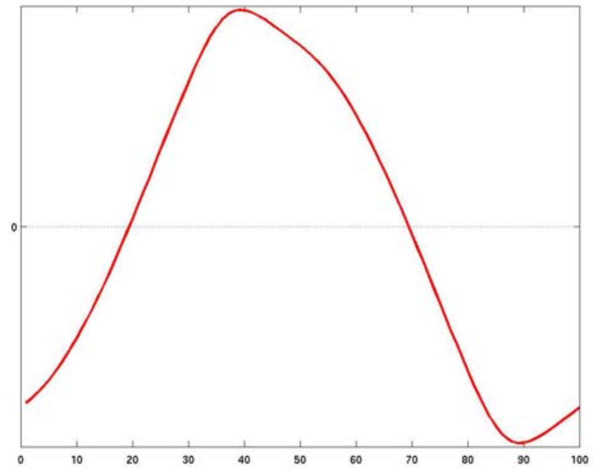


Segment no.

SIMULATIONS

Backward swimming:

$E_{-} = E_{L} - E_{R}$



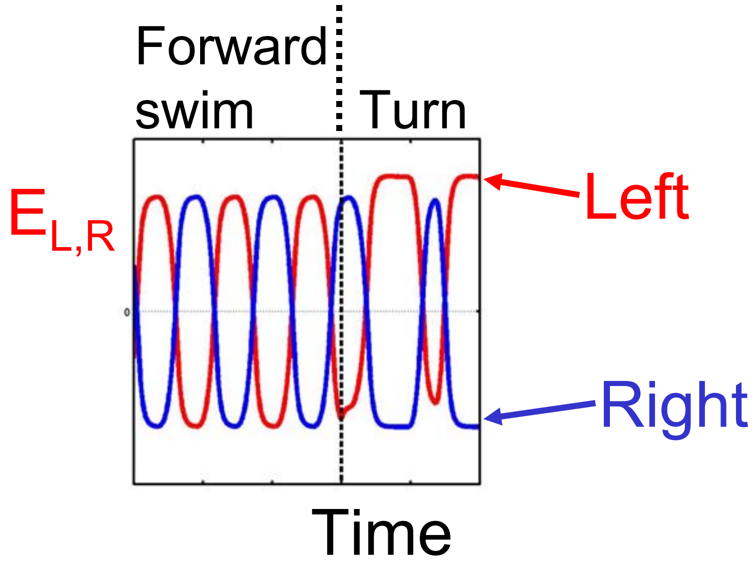
Segment no.

Turning

Amplitude of oscillations is increased on one side of the body.

Achieved by increasing the tonic input to one side only (see also Kozlov et al., Biol. Cybern. 2002)

Simulation



Linearized equations:

Eigenvector solution

$$\frac{d}{dt}\begin{pmatrix} E_- \\ C_- \end{pmatrix} = \begin{pmatrix} J\mathbf{-1} & K \\ Q\,\text{-}H & B\mathbf{-1} \end{pmatrix}\begin{pmatrix} E_- \\ C_- \end{pmatrix} \longrightarrow \begin{pmatrix} E_- \\ C_- \end{pmatrix} e^{\lambda t+ikx} \sim e^{-i(\omega t-kx)}$$

The dominant eigenvector k determines the global phase gradient (wave number) k

When there are more than one mode with Re(λ) >0, nonlinear coupling between modes exist.

Nonlinear analysis (for simplicity in g(C) only)

$$\dot{\mathbf{E}}_{\pm} = -\mathbf{E}_{\pm} \mp \mathsf{K}^0 g_{\pm}(\mathbf{C}) + \mathsf{J}\mathbf{E}_{\pm},$$

$$\dot{\mathbf{L}}_{\pm} = -\mathbf{L}_{\pm} \mp \mathsf{A}^0 g_{\pm}(\mathbf{C}) + \mathsf{W}\mathbf{E}_{\pm}, \qquad (6)$$

$$\dot{\mathbf{C}}_{\pm} = -\mathbf{C}_{\pm} \mp \mathsf{B}^0 g_{\pm}(\mathbf{C}) + \mathsf{Q}\mathbf{E}_{\pm} - \mathsf{H}\mathbf{L}_{\pm},$$

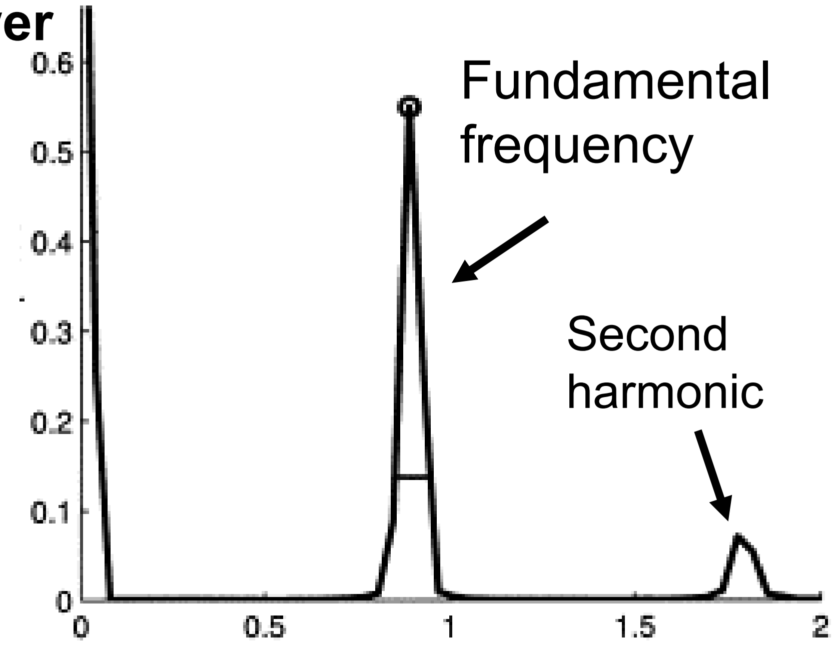
where $g_{\pm}(\mathbf{C}) = [g_C(\mathbf{C}_l) - g_c(\bar{\mathbf{C}})] \pm [g_C(\mathbf{C}_r) - g_c(\bar{\mathbf{C}})]$. If the nonlinearity is of the form $g_C(x + \bar{\mathbf{C}}) - g_C(\bar{\mathbf{C}}) = x + ax^2 - bx^3 + \mathcal{O}(x^4)$, we have

$$g_-(C) \approx C_- + aC_+C_- - bC_-^3/4 - 3bC_-C_+^2/4,$$

$$g_+(C) \approx C_+ + aC_+^2/2 + aC_-^2/2 - bC_+^3/4 - 3bC_+C_-^2/4.$$

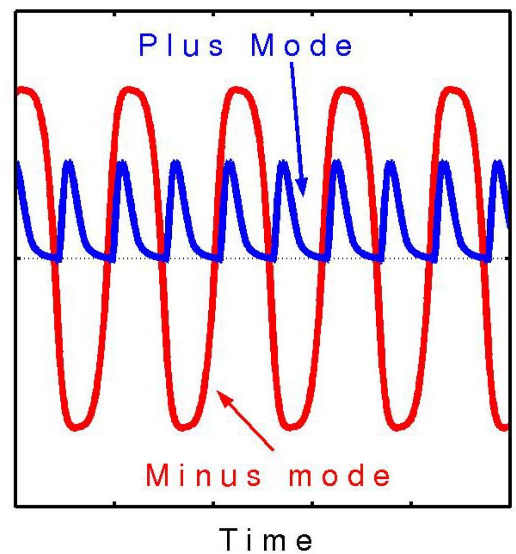
Miller & Sigvardt (1998) measured power spectrum of lamprey oscillations

neural oscillation power



Frequency

Simulation results



Nonlinear analysis of model equations

Prediction 3: second harmonic exists in "+" mode only (ie. left-right synchronous)

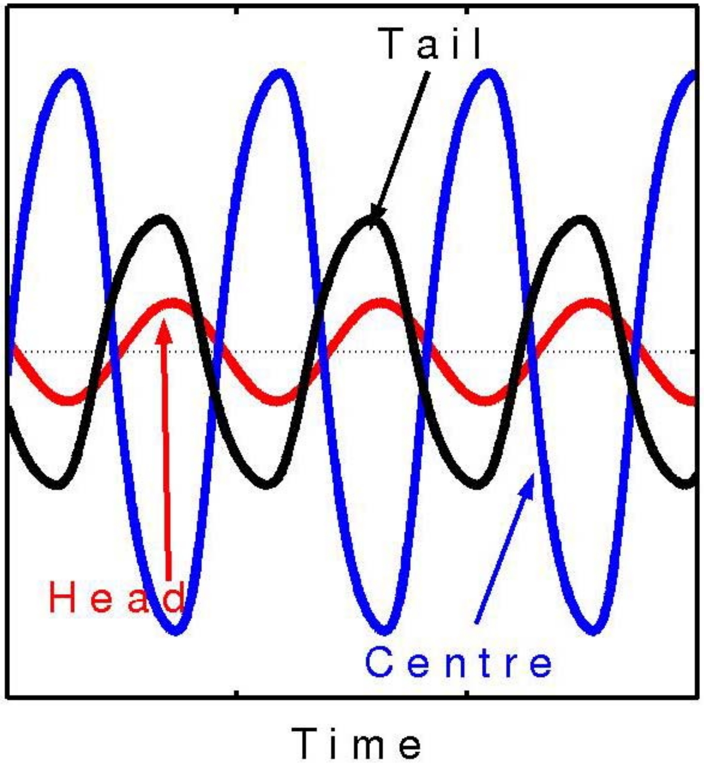
Easily testable

Other conclusions from the nonlinear analysis:

•the swimming cycle, if its linear mode is dominant, is stable against perturbations of another linear, unstable, but less dominant mode.

•If two modes, forward and backward swimming modes, are dominant, swimming direction could be selected by initial conditions, though experimental data indicates that this is less likely.

Boundary conditions: reduced amplitudes at head and tail can be understood



No translation invariance approximations, simply analyze oscillation coupling

$$\frac{d^2}{dt^2} E_i + \alpha \frac{d}{dt} E_i + \omega_o^2 E_i = \Sigma_j F_{ij}$$

Summary 1:

100x3x2 coupled neurons in a neural circuit of spinal cord

↓ Left-right symmetry

100x3 coupled units in the swimming mode only

↓ Translation symmetry

3 coupled units

↓ Experimental data on phase pattern allow simplification

2 coupled units related to harmonic oscillator

Nonlinearity allows dominance of a single mode.

Selected mode controlled by neural connection patterns and external input --- testable predictions

Summary

Analytical study of a CPG model of suitable complexity
gives **new insights**

How coupling can enable global oscillation from damped oscillators

How each connection type affects phase relationships

How and which connections enable swimming direction control
--- can be tested experimentally.

Further work:

Include synaptic temporal complexities in model → Control of swimming speed (oscillation frequency) over a larger range