NEURAL FIELDS WITH REBOUND CURRENTS: NOVEL ROUTES TO PATTERNING

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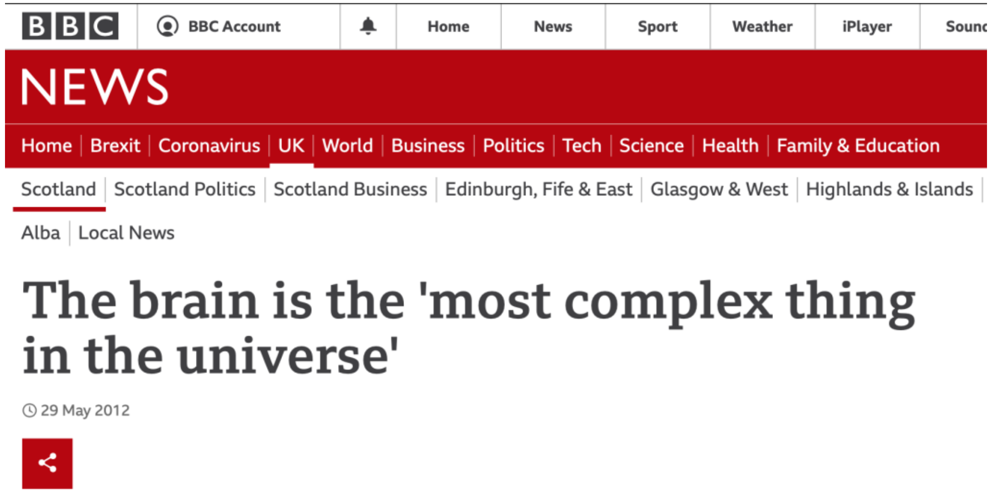
IN TODAY'S TALK

- Introduction
  - Brain modelling motivation
  - Neural field equation
- Thalamic model with a rebound current
  - Introducing the model
  - 2-D patterning
  - Spatial synchrony
  - Spatially periodic travelling waves
  - Continuation of solutions

BRAIN MODELLING?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The brain is the 'most complex thing in the universe'

29 May 2012

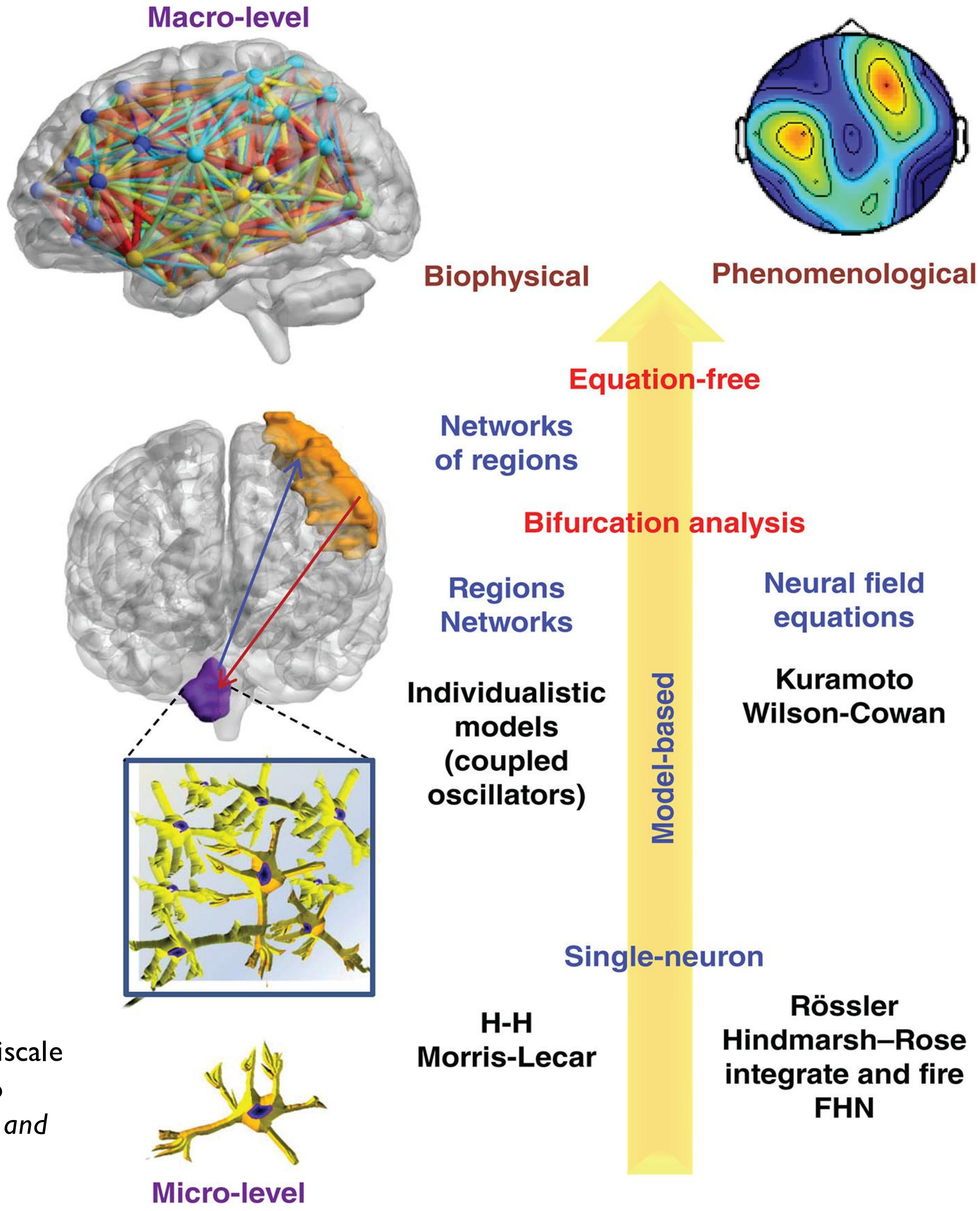
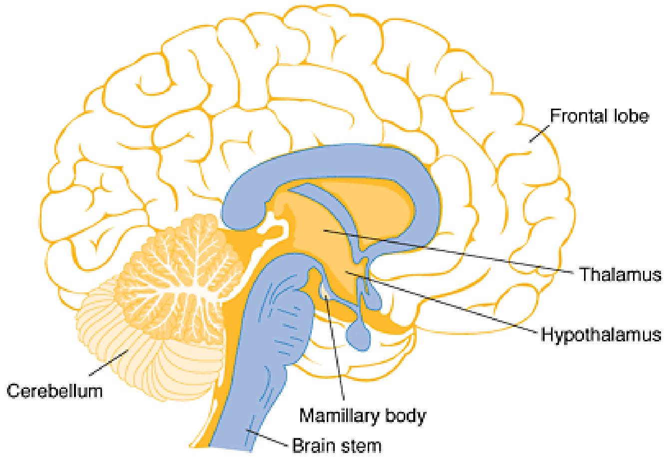


Figure adapted from Siettos, Constantinos, and Jens Starke. "Multiscale modeling of brain dynamics: from single neurons and networks to mathematical tools." *Wiley Interdisciplinary Reviews: Systems Biology and Medicine* 8.5 (2016): 438-458.

THE NEURAL FIELD EQUATION

$$\frac{1}{\alpha}\frac{\partial u}{\partial t}(x,t) = -u(x,t) + \int_{-\infty}^{\infty} w(y) f(u(x-y,t))\mathrm{d}y,$$

$$Qu = w \otimes f \circ u$$

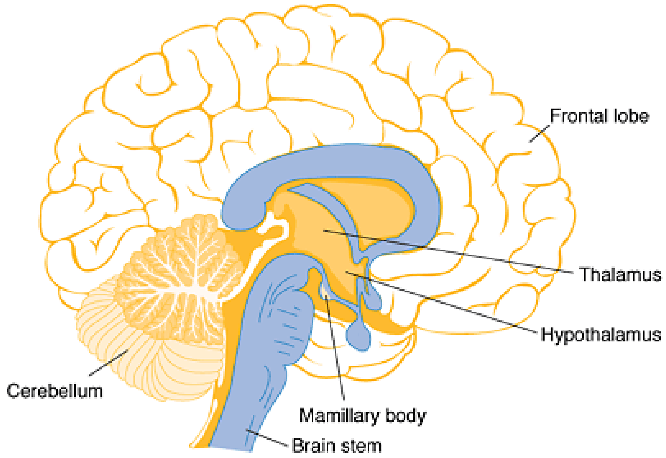


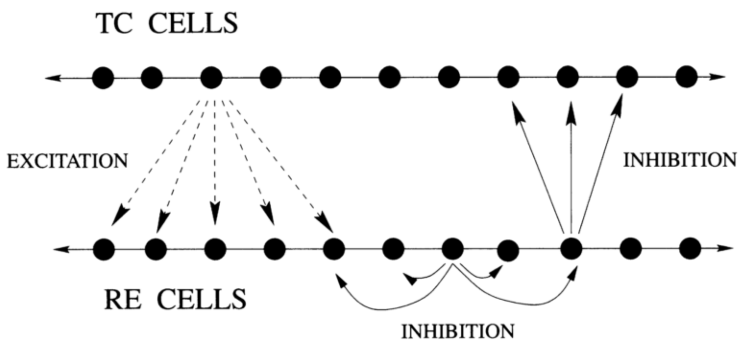
- Phenomenological model of "cortical activity", u
- Firing rate f typically sigmoidal
- Connectivity described by w

Amari, Shun-ichi. "Dynamics of pattern formation in lateral-inhibition type neural fields." *Biological cybernetics* 27.2 (1977): 77-87.

WHY STUDY THALAMOCORTICAL MODELS?

- The thalamus “relays” motor and sensory signals to the cortex
- Rebound currents (T-type calcium current) occur in the thalamus
- Rich dynamics in models





Yew, Alice C., D. H. Terman, and G. Bard Ermentrout. "Propagating activity patterns in thalamic neuronal networks." *SIAM Journal on Applied Mathematics* 61.5 (2001): 1578-1604.

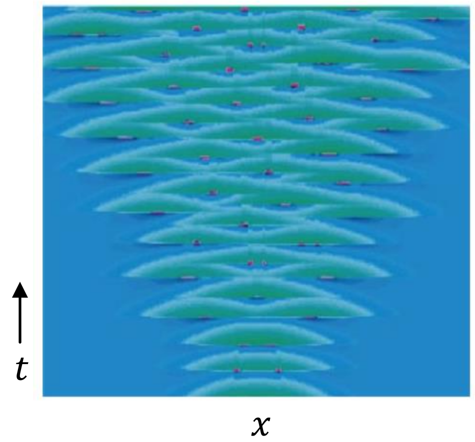
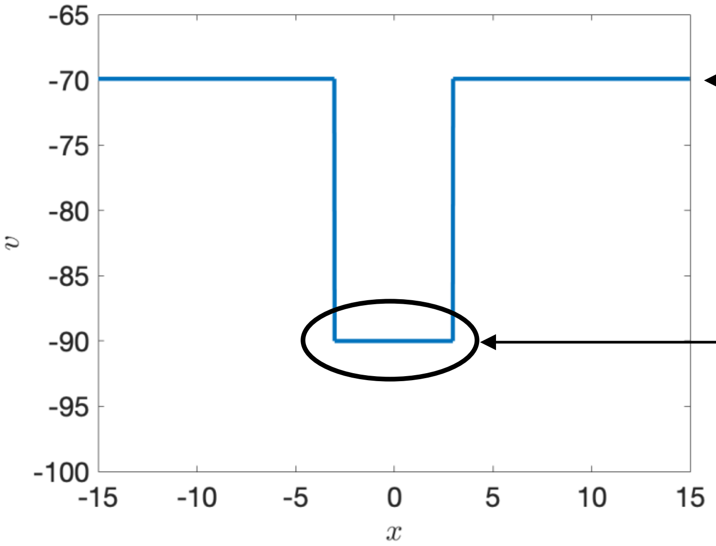
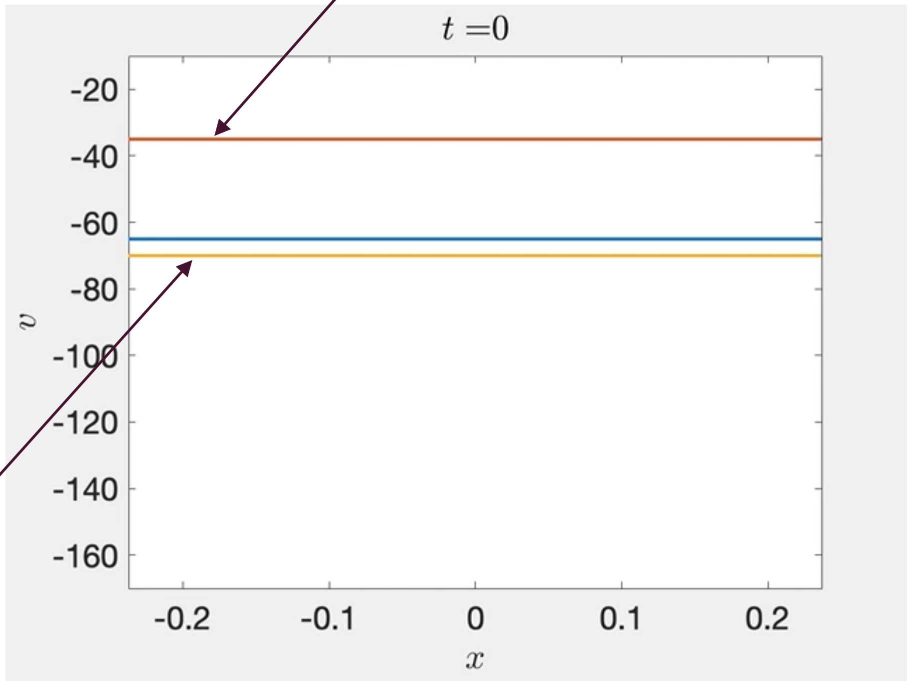


Figure adapted from Rinzel, J., et al. "Propagating activity patterns in large-scale inhibitory neuronal networks." *Science* 279.5355 (1998): 1351-1355.

WHAT IS A REBOUND CURRENT?

- Hyperpolarisation causes a firing event (*post-inhibitory rebound*)
- Hyperpolarisation removes the inactivation of the current
- When voltage reaches the rebound threshold, the rebound current activates
- This results in a large voltage depolarization





MODEL INGREDIENTS

- A voltage description including the relevant rebound current

$$C\frac{\partial}{\partial t}v = I_{\mathrm{L}} + I_{\mathrm{T}} + I_{\mathrm{syn}}$$

$$I_{\mathrm{T}} = -g_{\mathrm{T}} h m_{\infty}(v)(v - v_{\mathrm{T}})$$

$$\frac{\partial}{\partial t}h = \frac{h_{\infty}(v) - h}{\tau_{\mathrm{h}}(v)}$$

- Tissue connectivity

$$I_{\mathrm{syn}} = -g_{\mathrm{syn}} u(v - v_{\mathrm{syn}})$$

$$Qu = w \otimes f \circ v$$

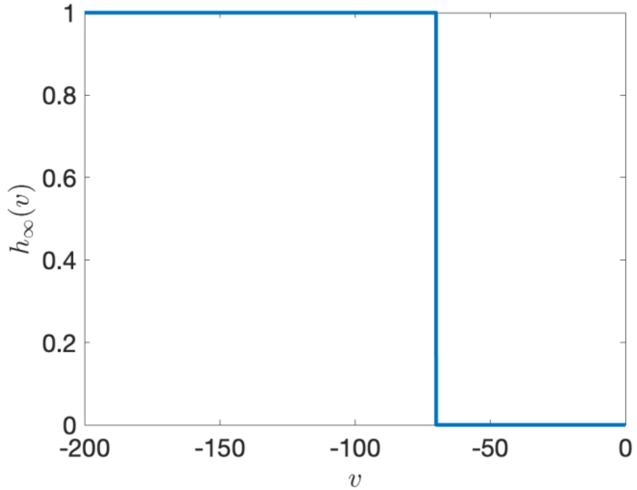
THE MODEL

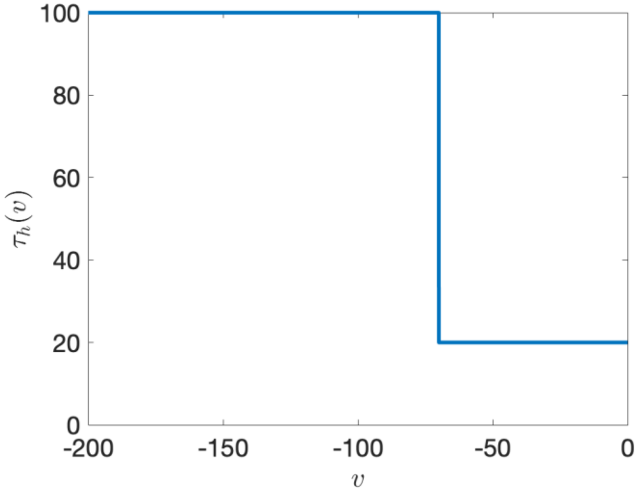
$$C\frac{\partial v}{\partial t} = \overbrace{-g_L(v-v_L)}^{\text{Leak current}} \overbrace{-\, g_T h \underbrace{H(v-v_h)}_{\substack{\text{Heaviside}\\ \text{step-function}}}(v-v_\mathrm{T})}^{\text{Rebound current}} \overbrace{-\, g_{\mathrm{syn}} u(v-v_{\mathrm{syn}})}^{\text{Synaptic current}},$$

$$\frac{\partial u}{\partial t} = \alpha(-u+r),$$

$$\frac{\partial r}{\partial t} = \alpha\Big(-r + \int_{\mathbb{R}^2} w(\mathbf{r},\mathbf{r}')f(v(\mathbf{r}',t))\mathrm{d}\mathbf{r}'\Big),$$

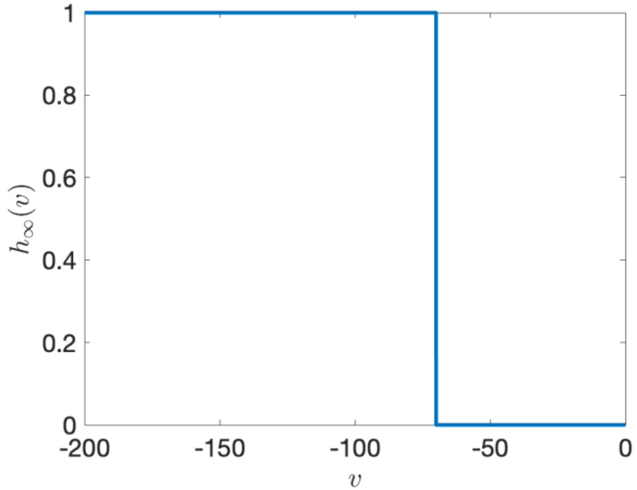
$$\frac{\partial h}{\partial t} = \frac{h_\infty(v)-h}{\tau_h(v)}.$$

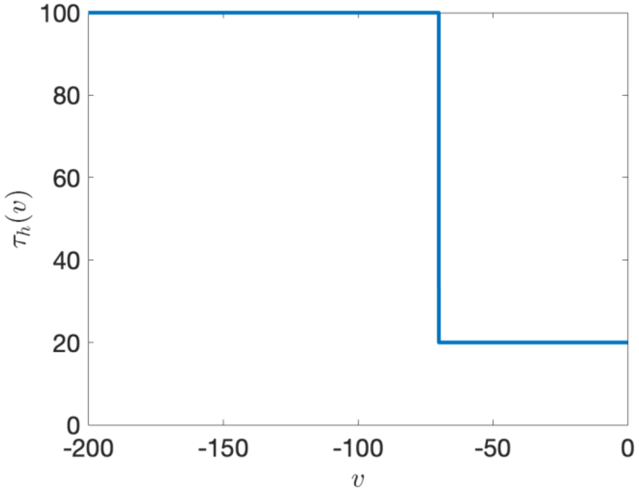




THE MODEL

$$
\begin{aligned}
C\frac{\partial v}{\partial t} &= -g_L(v-v_L) - g_T h \underbrace{H(v-v_h)}_{\substack{\text{Heaviside}\\ \text{step-function}}} - g_{\text{syn}} u,\\
\frac{\partial u}{\partial t} &= \alpha(-u+r),\\
\frac{\partial r}{\partial t} &= \alpha\Big(-r + \int_{\mathbb{R}^2} w(\mathbf{r},\mathbf{r}')f(v(\mathbf{r}',t))\mathrm{d}\mathbf{r}'\Big),\\
\frac{\partial h}{\partial t} &= \frac{h_\infty(v)-h}{\tau_h(v)}.
\end{aligned}
$$





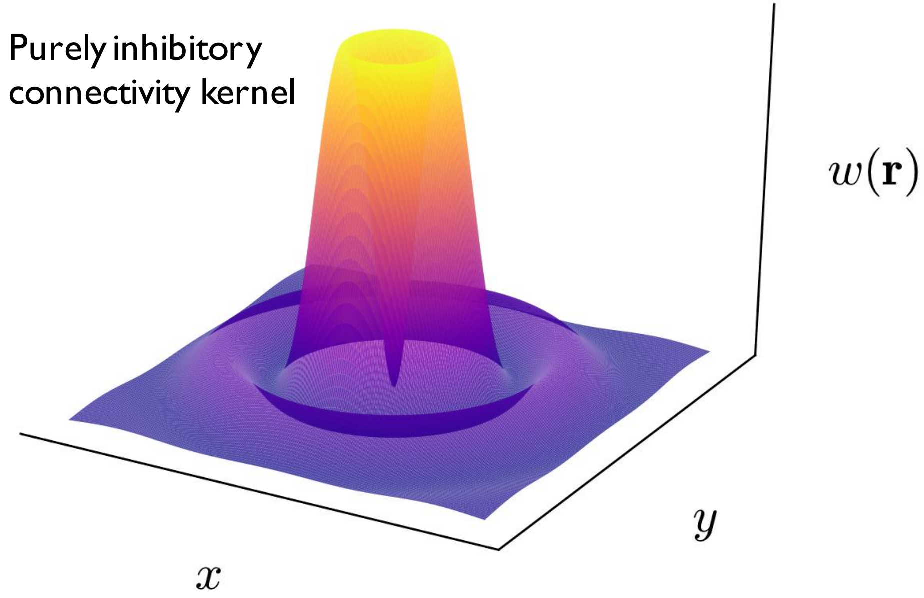
THE MODEL

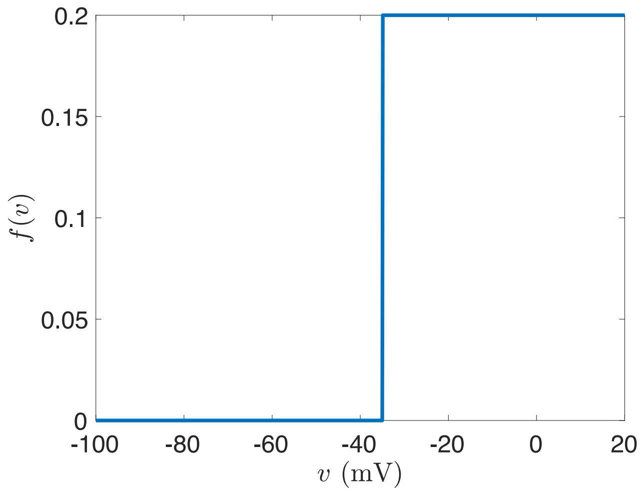
$$C\frac{\partial v}{\partial t} = -g_L(v - v_L) - g_T h \underbrace{H(v - v_h)}_{\text{Heaviside step-function}} - g_{\text{syn}} u,$$

$$\frac{\partial u}{\partial t} = \alpha(-u + r),$$

$$\frac{\partial r}{\partial t} = \alpha\left(-r + \int_{\mathbb{R}^2} w(\mathbf{r}, \mathbf{r}') f(v(\mathbf{r}', t)) \mathrm{d}\mathbf{r}'\right),$$

$$\frac{\partial h}{\partial t} = \frac{h_\infty(v) - h}{\tau_h(v)}.$$

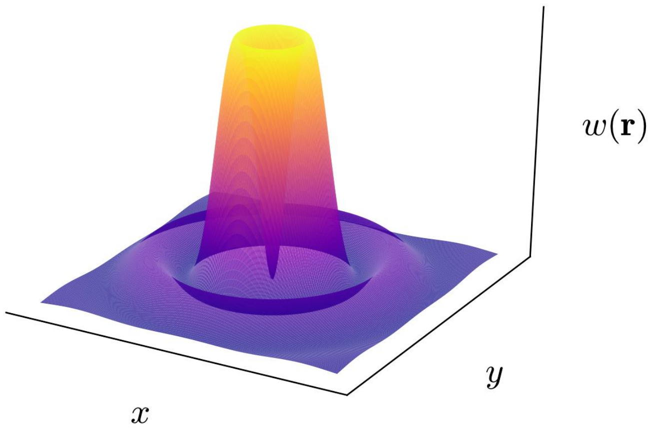


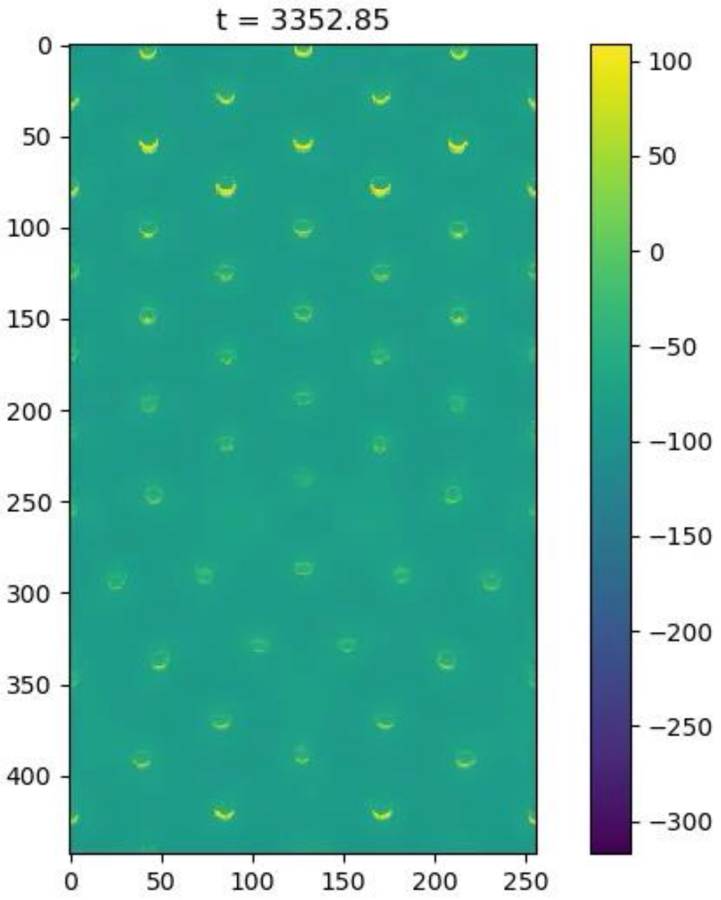


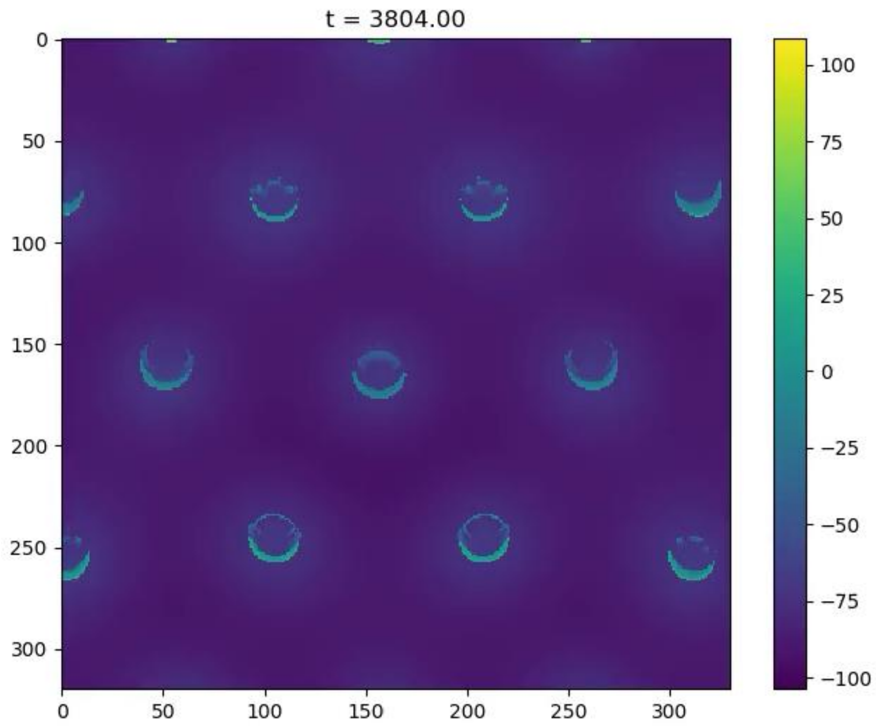
2-D PATTERNING

- Travelling patterns in two spatial dimensions

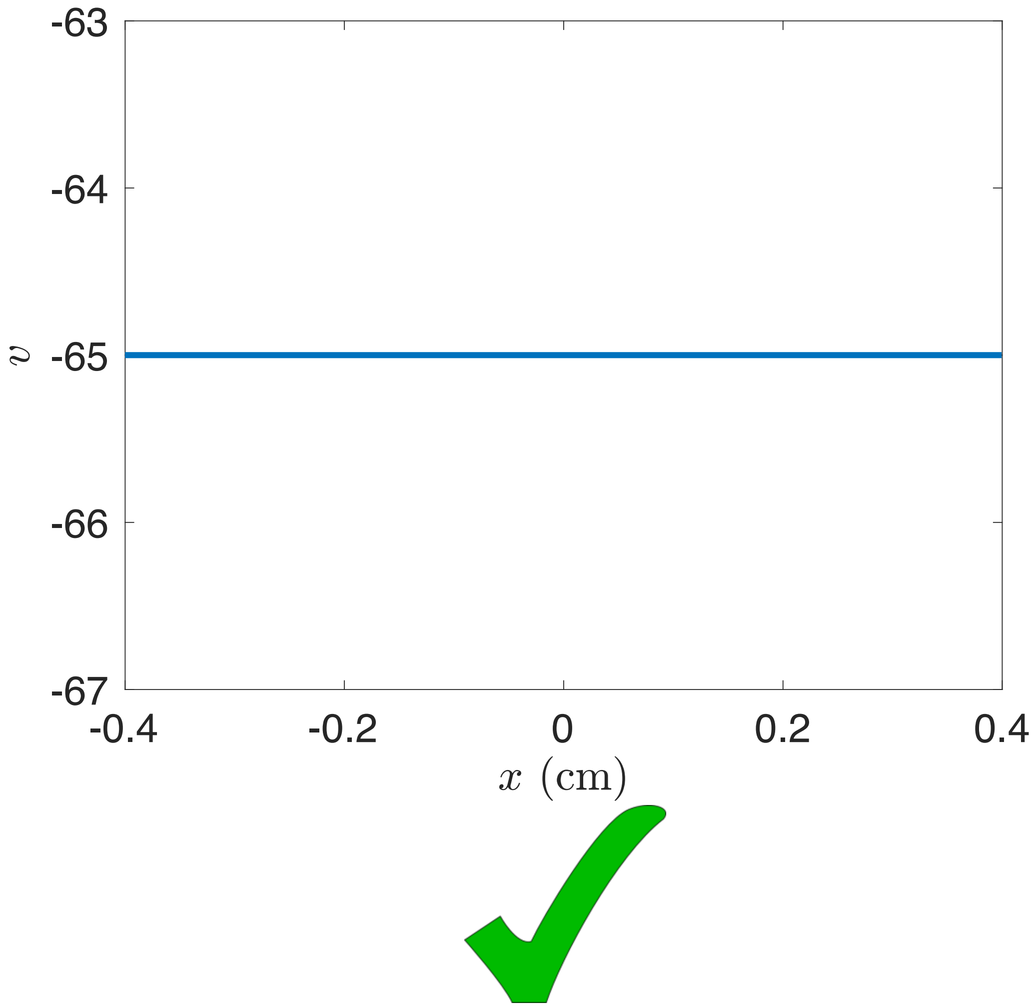
Purely inhibitory connectivity kernel

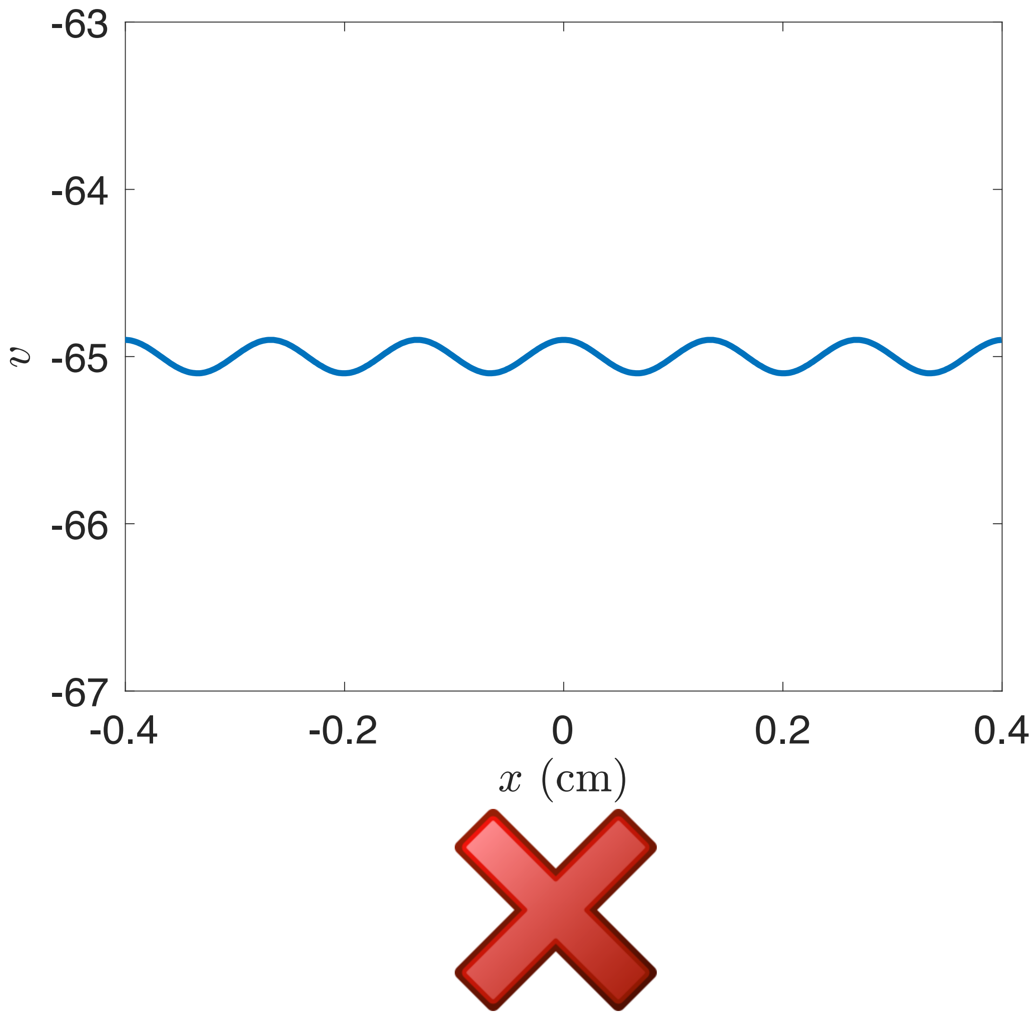






WHAT IS SPATIAL SYNCHRONY?



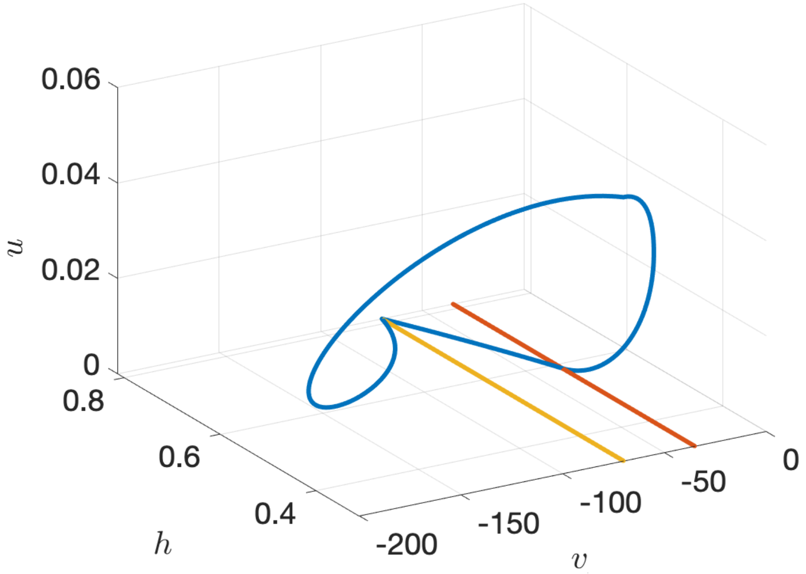


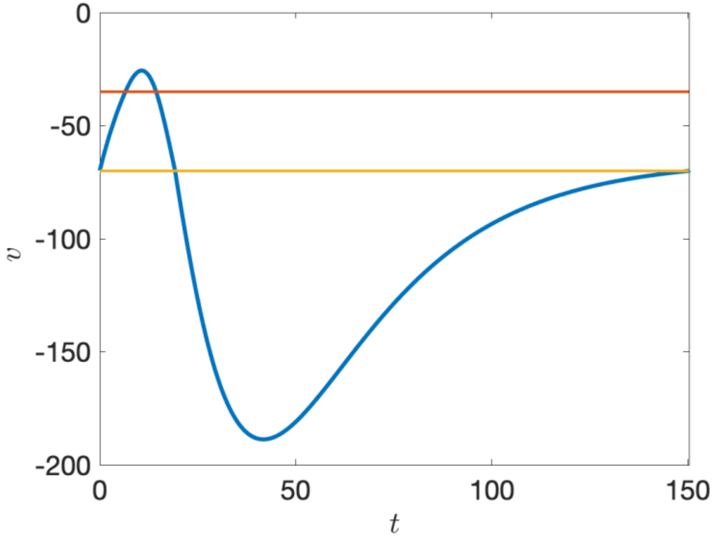
THE SYNCHRONOUS PERIODIC ORBIT

$$z(x,t) = z(t), \qquad \forall x \in \mathbb{R}$$

- The equations governing spatially independent solutions

$$C\frac{\mathrm{d}v}{\mathrm{d}t} = -g_L(v - v_L) - g_T h H(v - v_h) - g_{\mathrm{syn}} u,$$
$$\frac{\mathrm{d}u}{\mathrm{d}t} = \alpha(-u + r),$$
$$\frac{\mathrm{d}r}{\mathrm{d}t} = \alpha\left(-r + w_0 H(v - v_{\mathrm{th}})/\tau_R\right),$$
$$\frac{\mathrm{d}h}{\mathrm{d}t} = \frac{h_\infty(v) - h}{\tau_h(v)}.$$





THE SYNCHRONOUS PERIODIC ORBIT

- Phase space divided into three linear regions:

$$\text{(i) } v < v_{\mathrm{h}}, \text{ (ii) } v_{\mathrm{h}} < v < v_{\mathrm{th}} \text{ and (iii) } v > v_{\mathrm{th}}$$

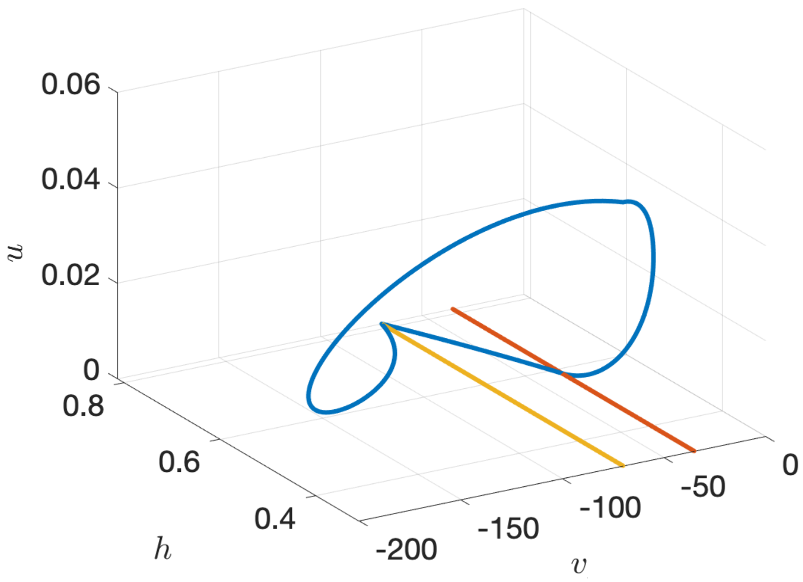
- The switching conditions and the periodicity conditions

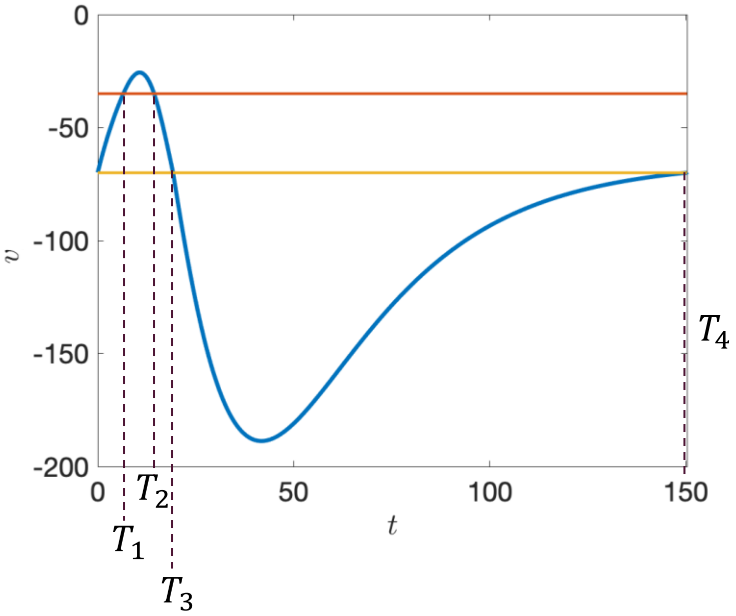
$$v(T_1) = v_{\mathrm{th}} \qquad u(T_4) = u_0$$

$$v(T_2) = v_{\mathrm{th}} \qquad r(T_4) = r_0$$

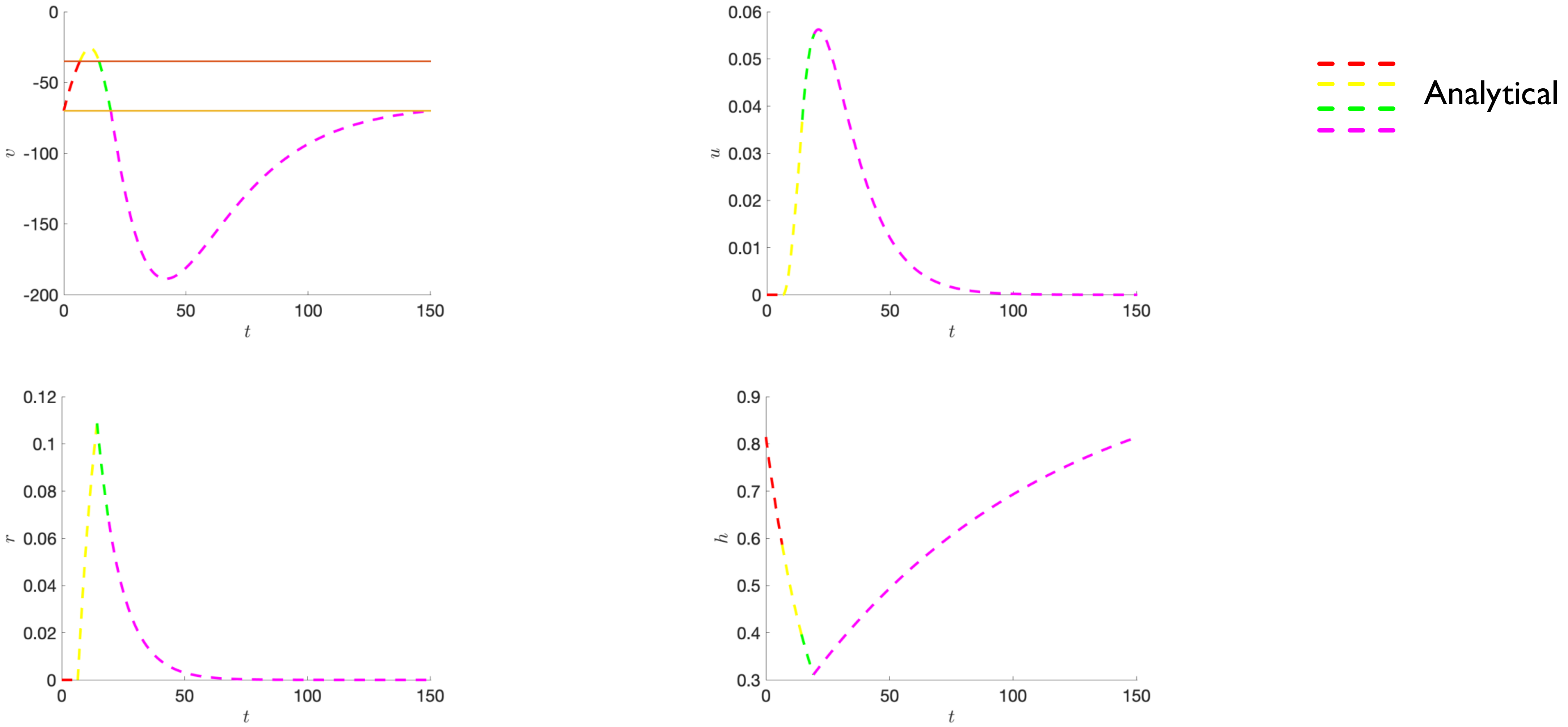
$$v(T_3) = v_{\mathrm{h}} \qquad h(T_4) = h_0$$

$$v(T_4) = v_{\mathrm{h}}$$





THE SYNCHRONOUS PERIODIC ORBIT – ANALYTICAL RESULTS



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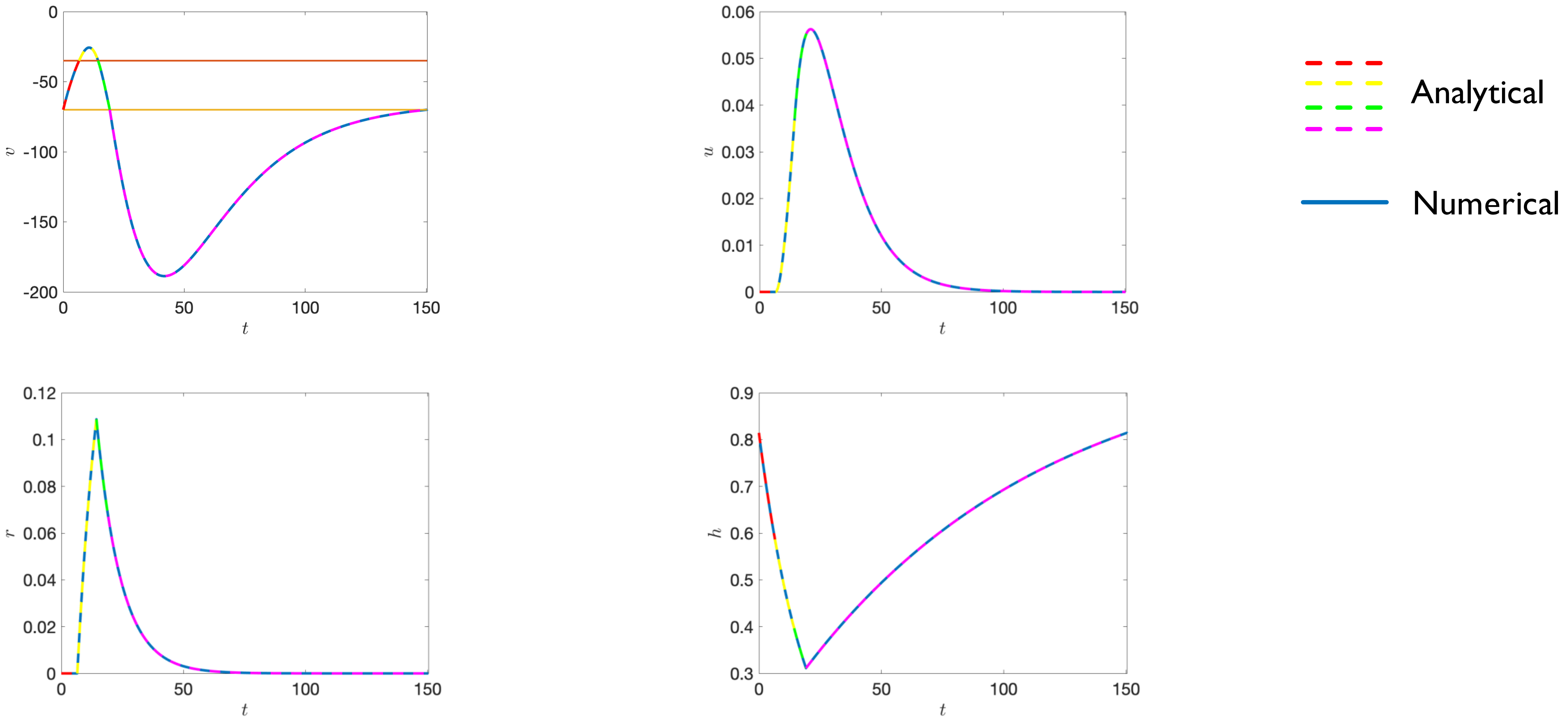
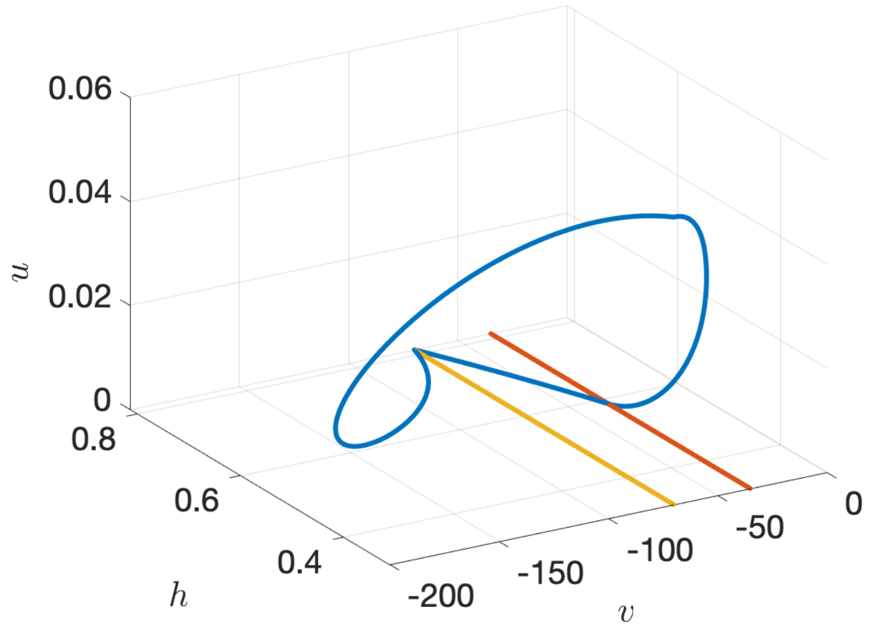
THE SYNCHRONOUS PERIODIC ORBIT – ANALYTICAL AND NUMERICAL COMPARISON



THE SYNCHRONOUS PERIODIC ORBIT – STABILITY ANALYSIS

$$z(x,t) = z(t) + \delta z(x,t),$$



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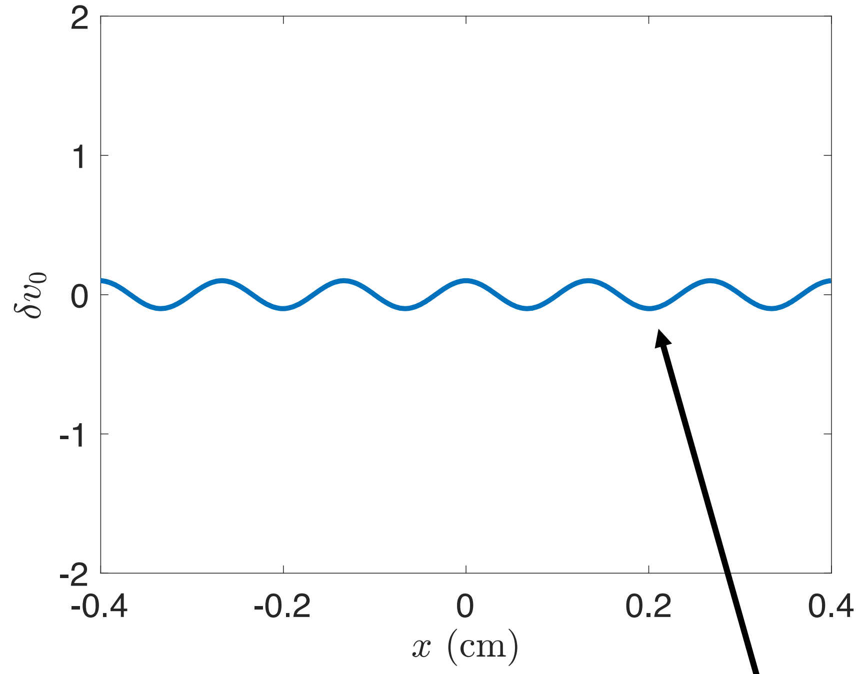


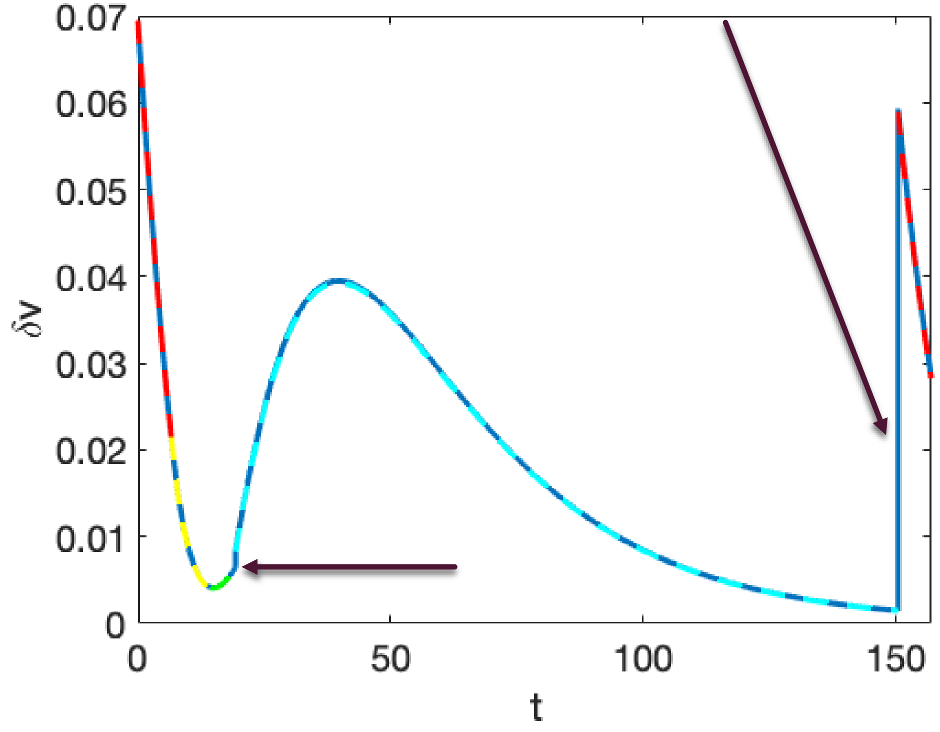
proportional to e^{ikx}

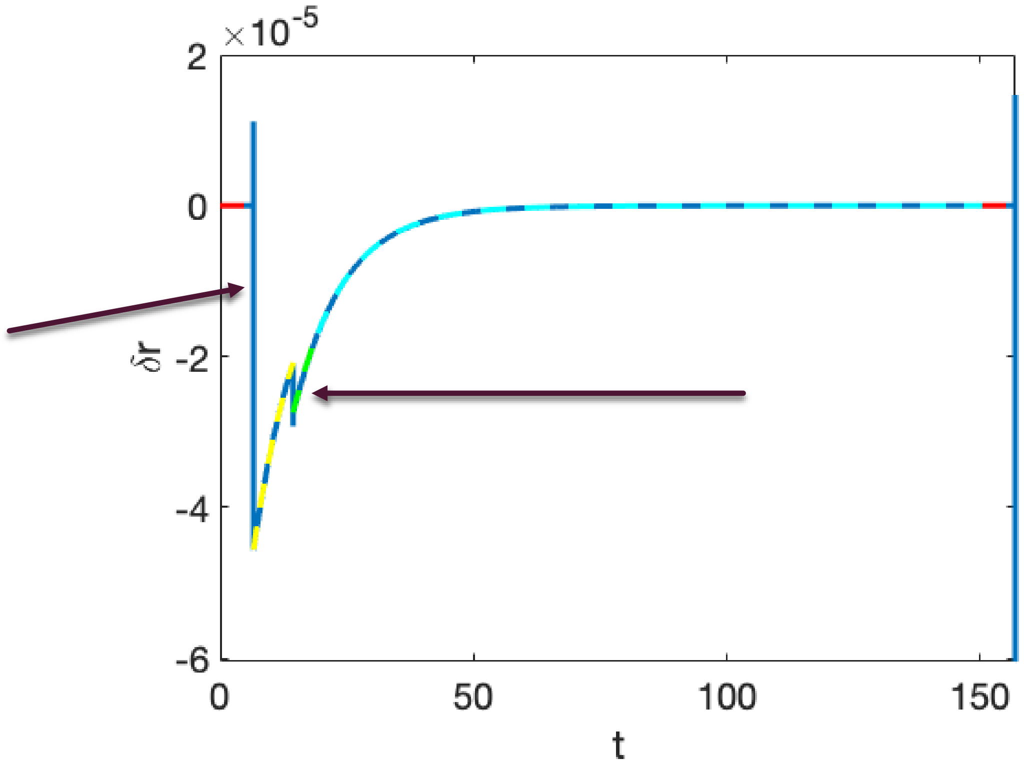
$$\delta z(x,\Delta) = \Psi \delta z(x,0)$$

THE SYNCHRONOUS PERIODIC ORBIT – STABILITY ANALYSIS

$$z(x,t) = z(t) + \delta z(x,t),$$

- Discontinuities in the vector field introduce discontinuities in the perturbations



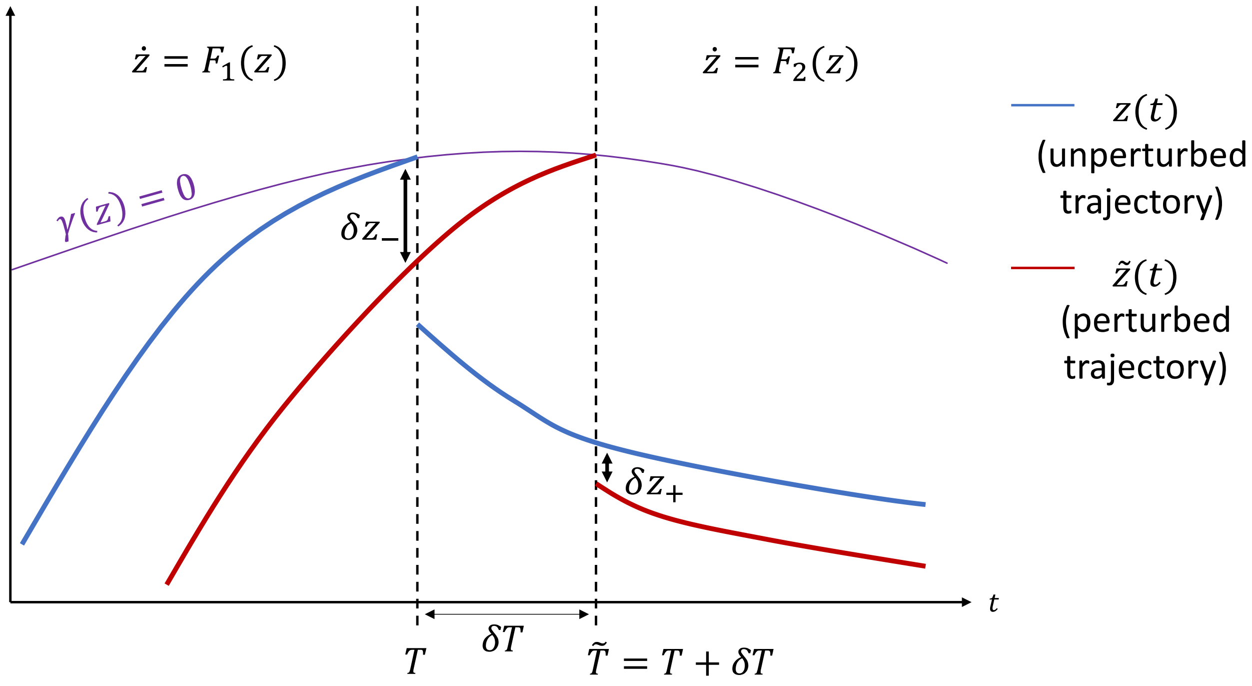


THE SYNCHRONOUS PERIODIC ORBIT – STABILITY ANALYSIS
SALTATION MATRICES – LOCAL ENTRIES

- For a time-dependent dynamical system

$$\frac{\mathrm{d}z}{\mathrm{d}t} = F(z), \qquad z \in \mathbb{R}^n,$$

with a switch in the dynamics at time $t = T$,



$$\delta z_+ = \underbrace{\boxed{\left[Dg(z(T^-)) - \frac{\{Dg(z(T^-))F_1(z(T^-)) - F_2(z(T^+))\}\, \nabla_z \gamma(z(T^-))^T}{\nabla_z \gamma(z(T^-)) \cdot F_1(z(T^-))} \right]}}_{K(T)} \delta z_-$$

Müller, Peter C. "Calculation of Lyapunov exponents for dynamic systems with discontinuities." *Chaos, Solitons & Fractals* 5.9 (1995): 1671-1681.

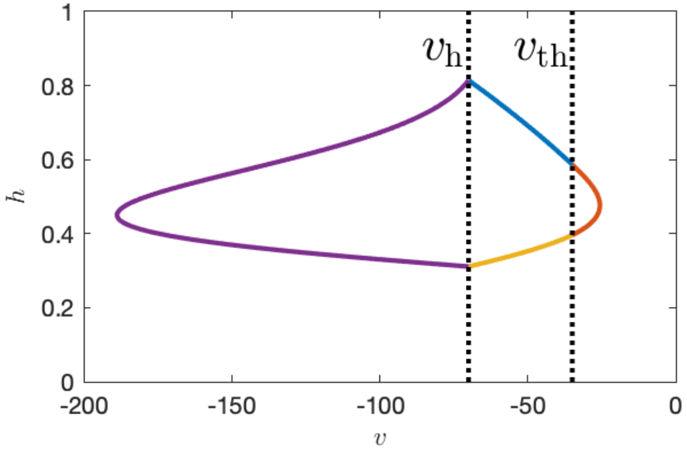
Nicks, Rachel, Lucie Chambon, and Stephen Coombes. "Clusters in nonsmooth oscillator networks." *Physical Review E* 97.3 (2018): 032213.

THE SYNCHRONOUS PERIODIC ORBIT – STABILITY ANALYSIS SALTATION MATRICES – LOCAL ENTRIES

$$\delta z(T^+) = K(T)\delta z(T^-)$$

- For the rebound model,

$$K(T) = I_4 - \frac{1}{\dot v(T^-)}\begin{pmatrix} \dot v(T^-) - \dot v(T^+) & 0 & 0 & 0 \\ \dot u(T^-) - \dot u(T^+) & 0 & 0 & 0 \\ \dot r(T^-) - \dot r(T^+) & 0 & 0 & 0 \\ \dot h(T^-) - \dot h(T^+) & 0 & 0 & 0 \end{pmatrix}$$



$$K(T) = I_4 + \begin{pmatrix} \checkmark & 0 & 0 & 0 \\ \checkmark & 0 & 0 & 0 \\ ? & 0 & 0 & 0 \\ \checkmark & 0 & 0 & 0 \end{pmatrix}$$

The Model Equations

$$C\frac{\partial v}{\partial t} = \underline{-g_L(v-v_L) - g_T h H(v-v_h) - g_{\text{syn}} u}$$

$$\frac{\partial u}{\partial t} = \underline{\alpha(-u+r)}$$

$$\frac{\partial r}{\partial t} = \alpha\left(\underline{-r} + \underline{\int_{-\infty}^{\infty} w(x,y) f(v(y,t))\,\mathrm{d}y}\right)$$

$$\frac{\partial h}{\partial t} = \underline{\frac{h_\infty(v) - h}{\tau_h(v)}}$$

Non-local

Local

THE SYNCHRONOUS PERIODIC ORBIT – STABILITY ANALYSIS SALTATION MATRICES – NON-LOCAL ENTRIES

- The non-local part is in

$$\frac{\partial}{\partial t} r(x,t) = \alpha \left(-r(x,t) + \int_{-\infty}^{\infty} w(x-y) f(v(y,t))\, \mathrm{d}y \right)$$

- Linearise and make the ansatz $\delta z(x,t) = \delta z(t) \mathrm{e}^{ikx}$ to obtain

$$\frac{\mathrm{d}}{\mathrm{d}t} \delta r(t) = \alpha \left(-\delta r(t) + \delta v(t) f'(v(t)) \int_{-\infty}^{\infty} w(y) \mathrm{e}^{-iky}\, \mathrm{d}y \right)$$

- Then use $f'(v(t)) = \delta(v(t) - v_{\mathrm{th}})/\tau_R$ to obtain

$$\frac{\mathrm{d}}{\mathrm{d}t} \delta r(t) = \alpha \left(-\delta r(t) + \frac{\delta v(t) \widehat{w}(k)}{\tau_R} \sum_{i=1}^{2} \frac{\delta(t - T_i)}{|\dot{v}(T_i)|} \right)$$

- The saltation rule relating perturbations before and after a switch is

$$\delta r(T_i^+) = \delta r(T_i^-) + \frac{\alpha \widehat{w}(k)}{\tau_R |\dot{v}(T_i)|} \delta v(T_i^-), \quad i = 1, 2$$

The Model Equations

$$C \frac{\partial v}{\partial t} = -g_L(v - v_L) - g_T h H(v - v_h) - g_{\mathrm{syn}} u$$

$$\frac{\partial u}{\partial t} = \alpha(-u + r)$$

$$\frac{\partial r}{\partial t} = \alpha \left(-r + \underline{\int_{-\infty}^{\infty} w(x,y) f(v(y,t))\, \mathrm{d}y} \right)$$

$$\frac{\partial h}{\partial t} = \frac{h_\infty(v) - h}{\tau_h(v)}$$

Non-local

THE SYNCHRONOUS PERIODIC ORBIT – STABILITY ANALYSIS SALTATION MATRICES – NON-LOCAL ENTRIES

$$\delta z(T^+) = K(T)\delta z(T^-)$$

- The saltation rule relating perturbations before and after a switch is

$$\delta r(T_i^+) = \delta r(T_i^-) + \boxed{\frac{\alpha \widehat{w}(k)}{\tau_R \left|\dot{v}(T_i)\right|}} \delta v(T_i^-), \quad i = 1, 2$$

$$K(T) = I_4 + \begin{pmatrix} \checkmark & 0 & 0 & 0 \\ \checkmark & 0 & 0 & 0 \\ \checkmark & 0 & 0 & 0 \\ \checkmark & 0 & 0 & 0 \end{pmatrix}$$

The Model Equations

$$C\frac{\partial v}{\partial t} = -g_L(v - v_L) - g_T h H(v - v_h) - g_{\text{syn}} u$$

$$\frac{\partial u}{\partial t} = \alpha(-u + r)$$

$$\frac{\partial r}{\partial t} = \alpha \left(-r + \underline{\int_{-\infty}^{\infty} w(x,y) f(v(y,t))\, \mathrm{d}y} \right)$$

$$\frac{\partial h}{\partial t} = \frac{h_\infty(v) - h}{\tau_h(v)}$$

Non-local

THE SYNCHRONOUS PERIODIC ORBIT – STABILITY ANALYSIS DETERMINING THE MONODROMY MATRIX

- The perturbation after a period, Δ, is given by

$$\delta z(x,\Delta) = \Psi \delta z(x,0)$$

where

$$\Psi(k) = K_4 \exp(J_4\Delta_4) K_3 \exp(J_3\Delta_3) K_2(k) \exp(J_2\Delta_2) K_1(k) \exp(J_1\Delta_1)$$

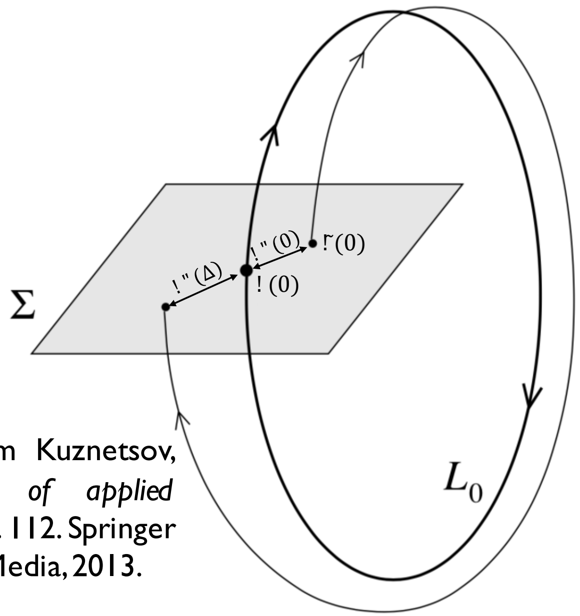
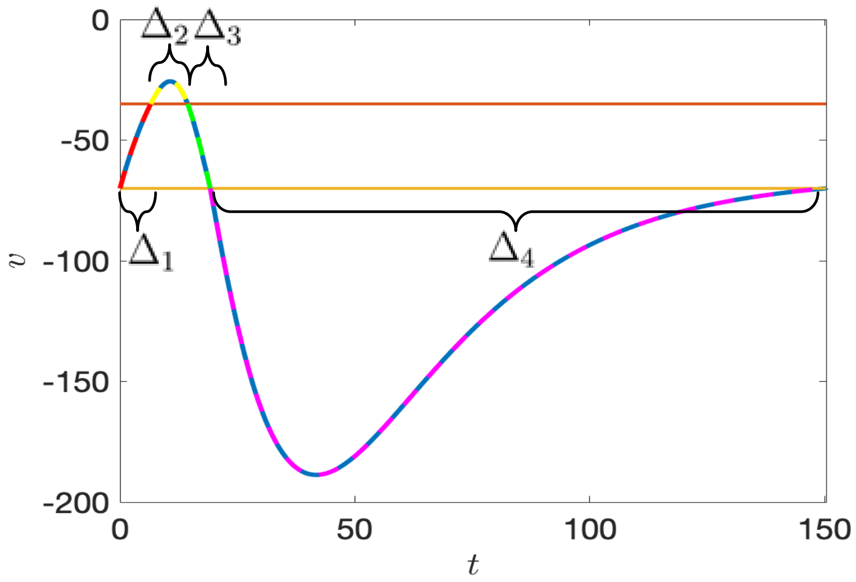


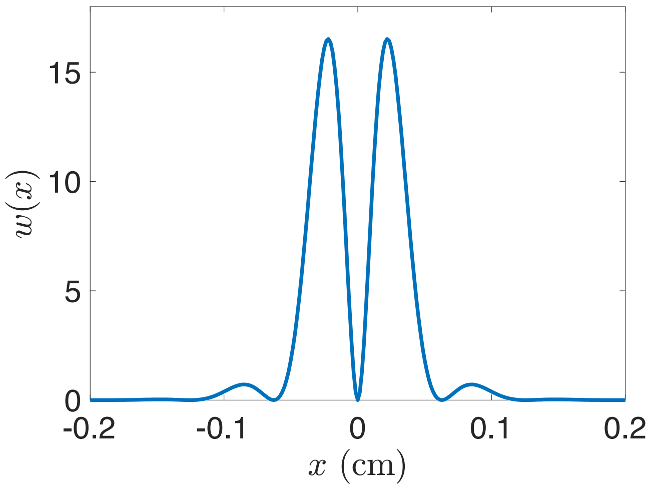
Figure adapted from Kuznetsov, Yuri A. *Elements of applied bifurcation theory*. Vol. 112. Springer Science & Business Media, 2013.

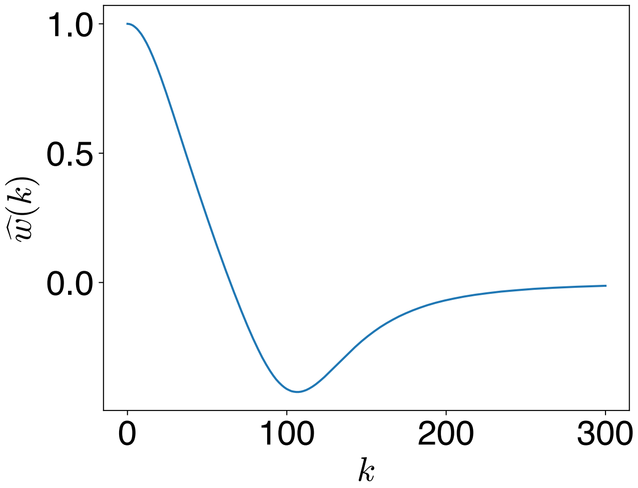


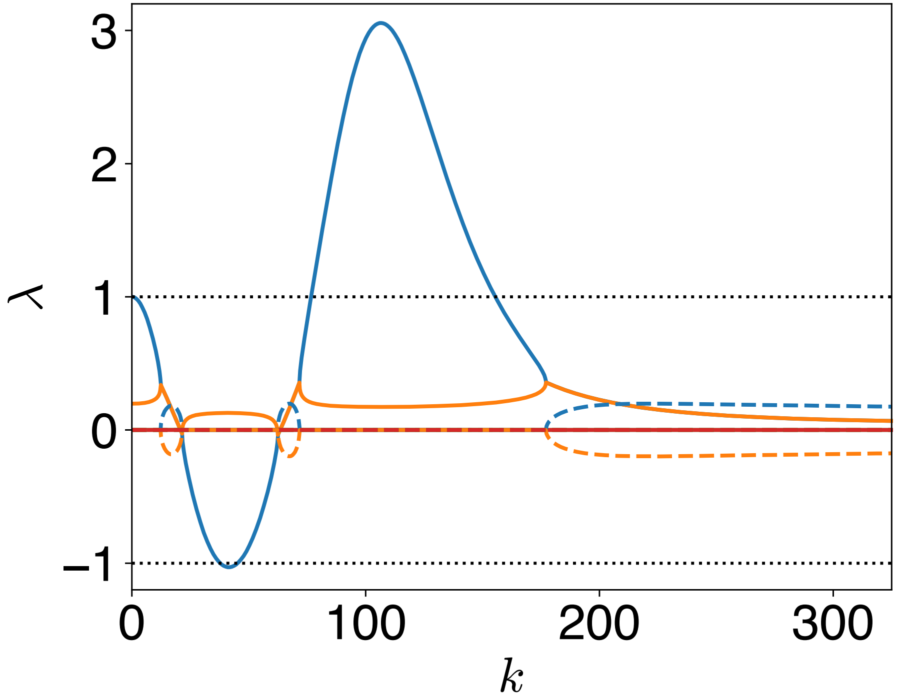
THE SYNCHRONOUS PERIODIC ORBIT – STABILITY ANALYSIS
AN UNSTABLE ORBIT

$$\Psi(k) = K_4 \exp(J_4\Delta_4) K_3 \exp(J_3\Delta_3) K_2(k) \exp(J_2\Delta_2) K_1(k) \exp(J_1\Delta_1)$$

- The eigenvalues of Ψ determine the stability of the orbit

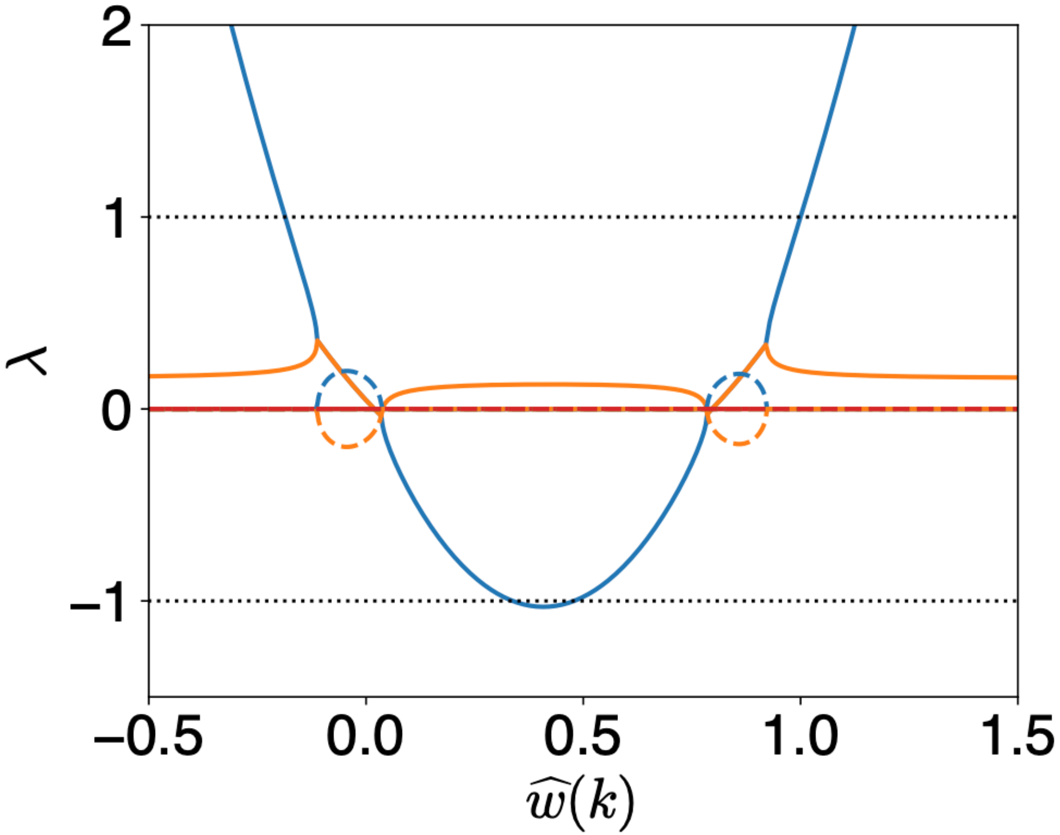




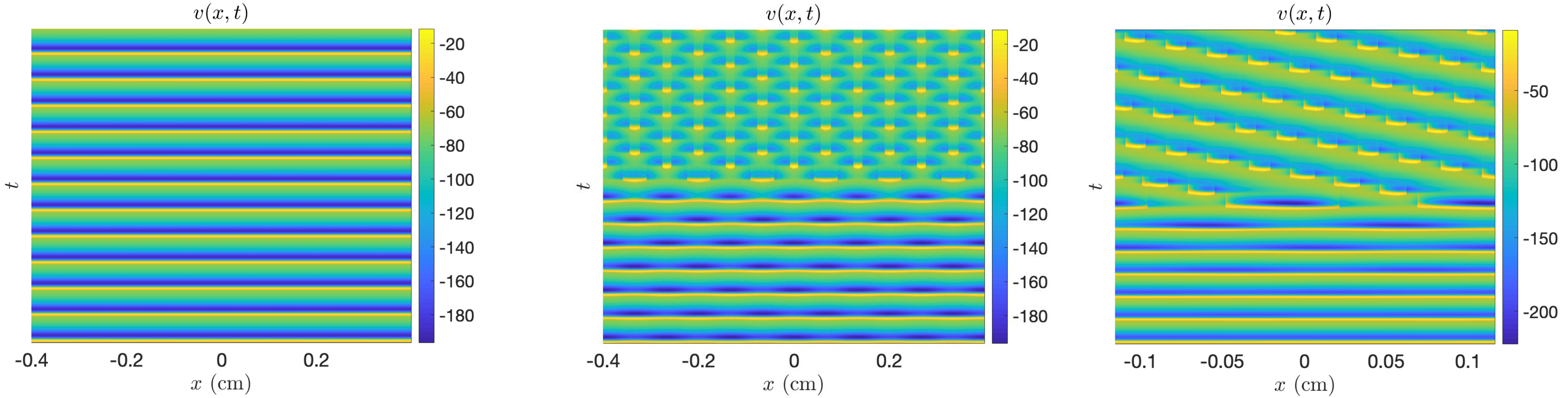


THE SYNCHRONOUS PERIODIC ORBIT – STABILITY ANALYSIS

$$\Psi(k) = K_4 \exp(J_4 \Delta_4) K_3 \exp(J_3 \Delta_3) K_2(k) \exp(J_2 \Delta_2) K_1(k) \exp(J_1 \Delta_1)$$



THE SYNCHRONOUS PERIODIC ORBIT NUMERICAL SIMULATION

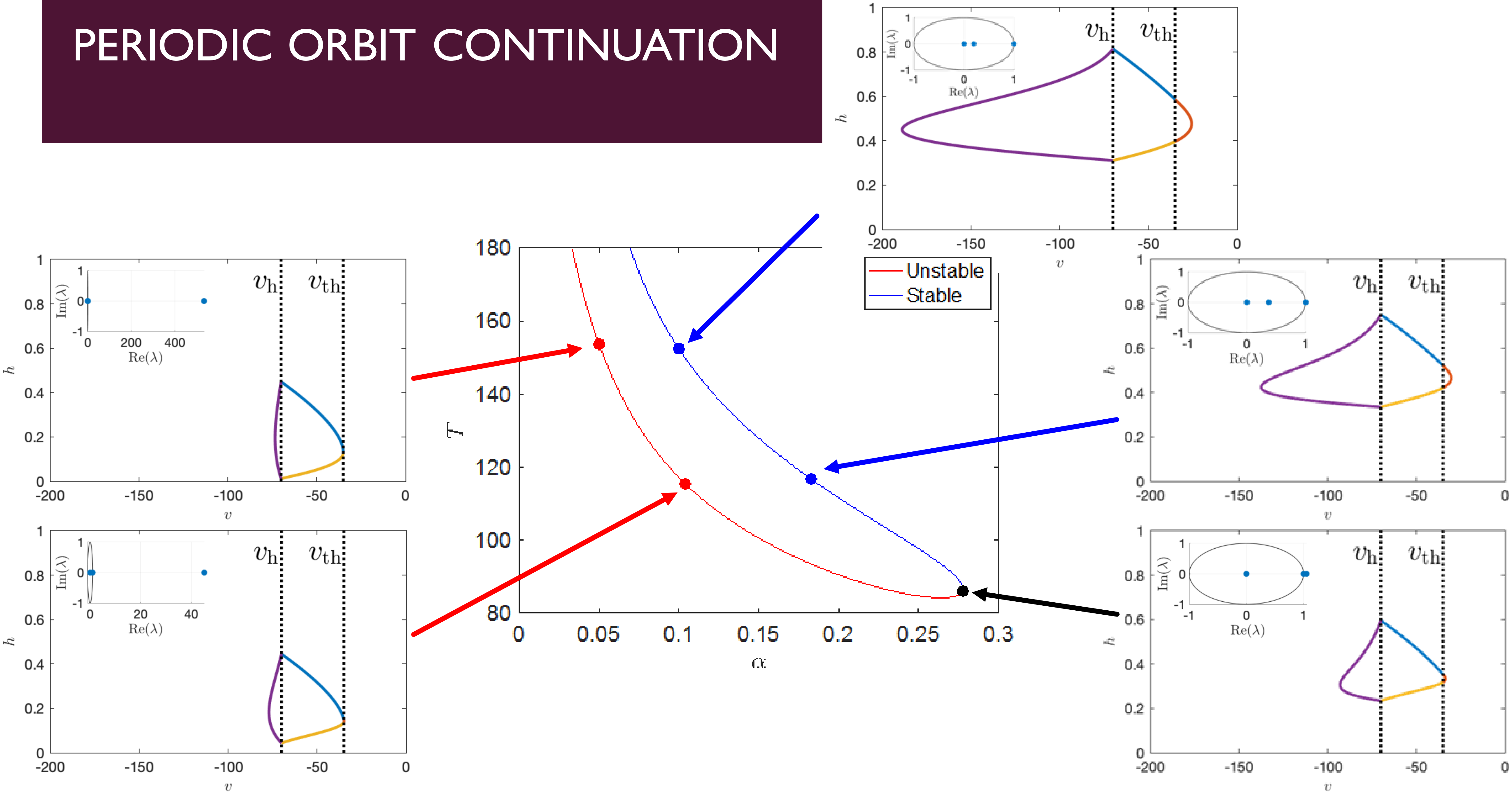


On-cycle initial conditions

Off-cycle initial conditions

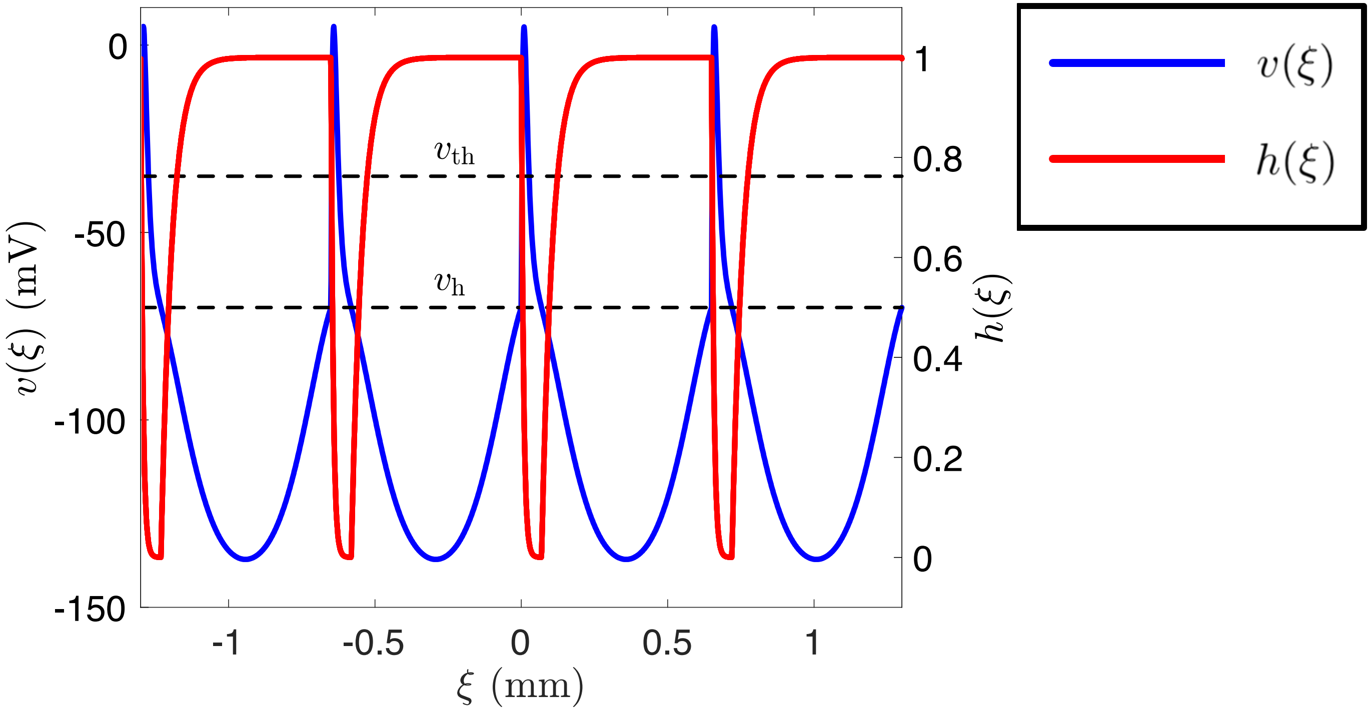
Rinzel, J., et al. "Propagating activity patterns in large-scale inhibitory neuronal networks." *Science* 279.5355 (1998): 1351-1355.

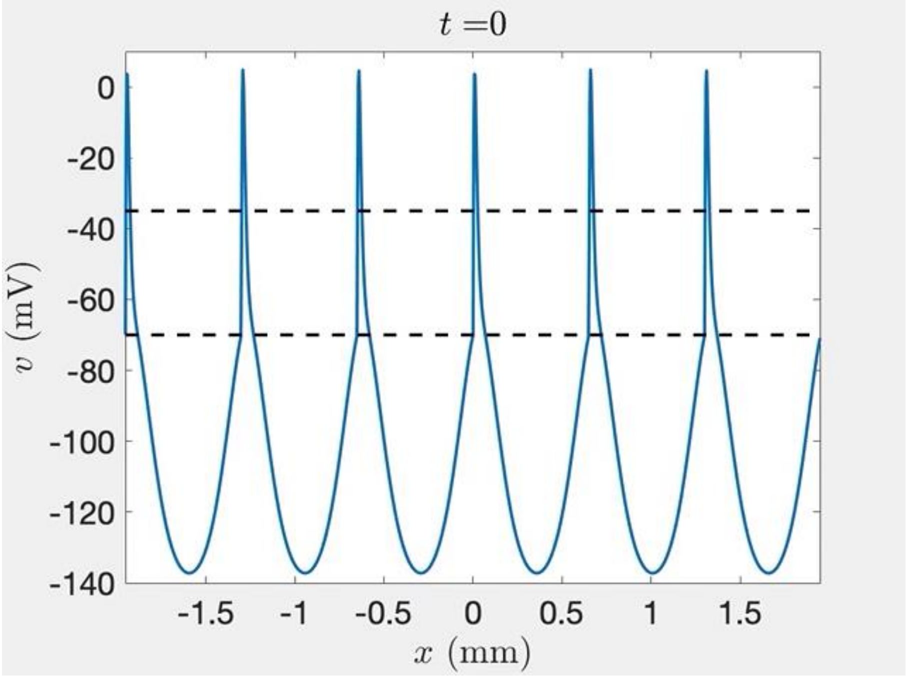
PERIODIC ORBIT CONTINUATION



SPATIALLY PERIODIC TRAVELLING WAVES

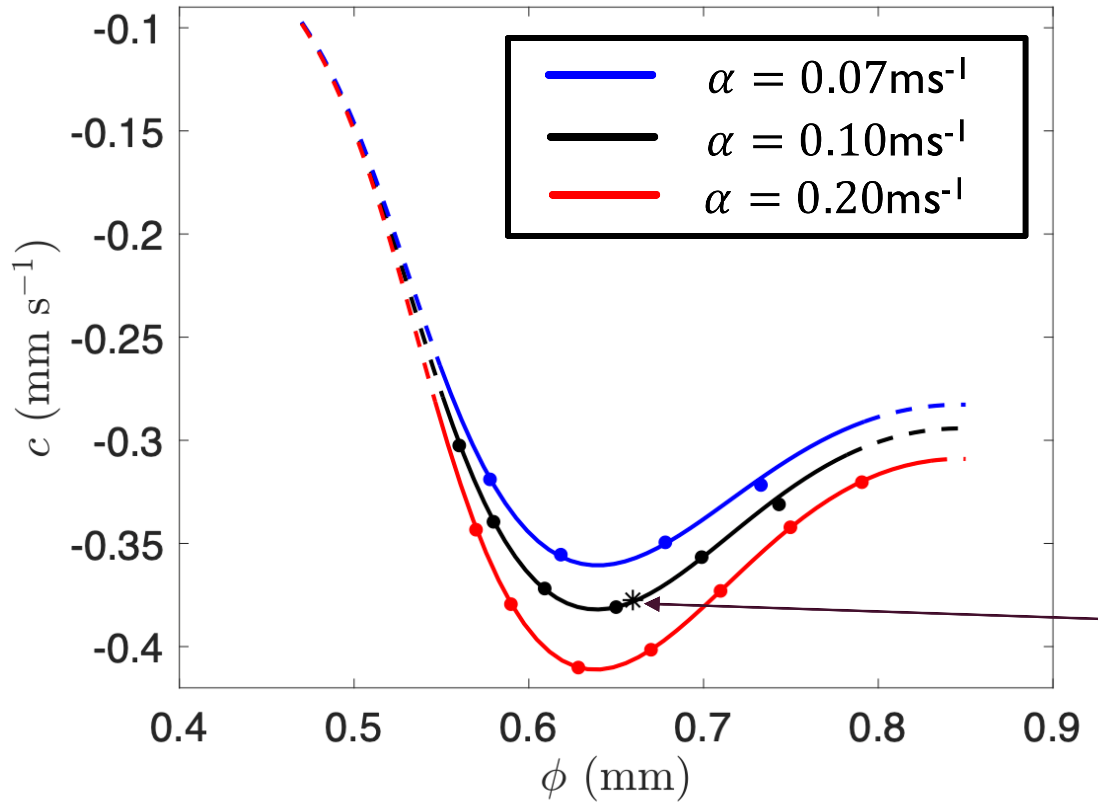
- The model supports travelling wave solutions
- Move to the co-moving frame, $\xi = x - ct$
- 4 switching events over a period ϕ, at $\xi = \xi_1, \xi_2, \xi_3, \phi$ topologically equivalent to $t = T_1, T_2, T_3, T_4$ for synchronous orbit

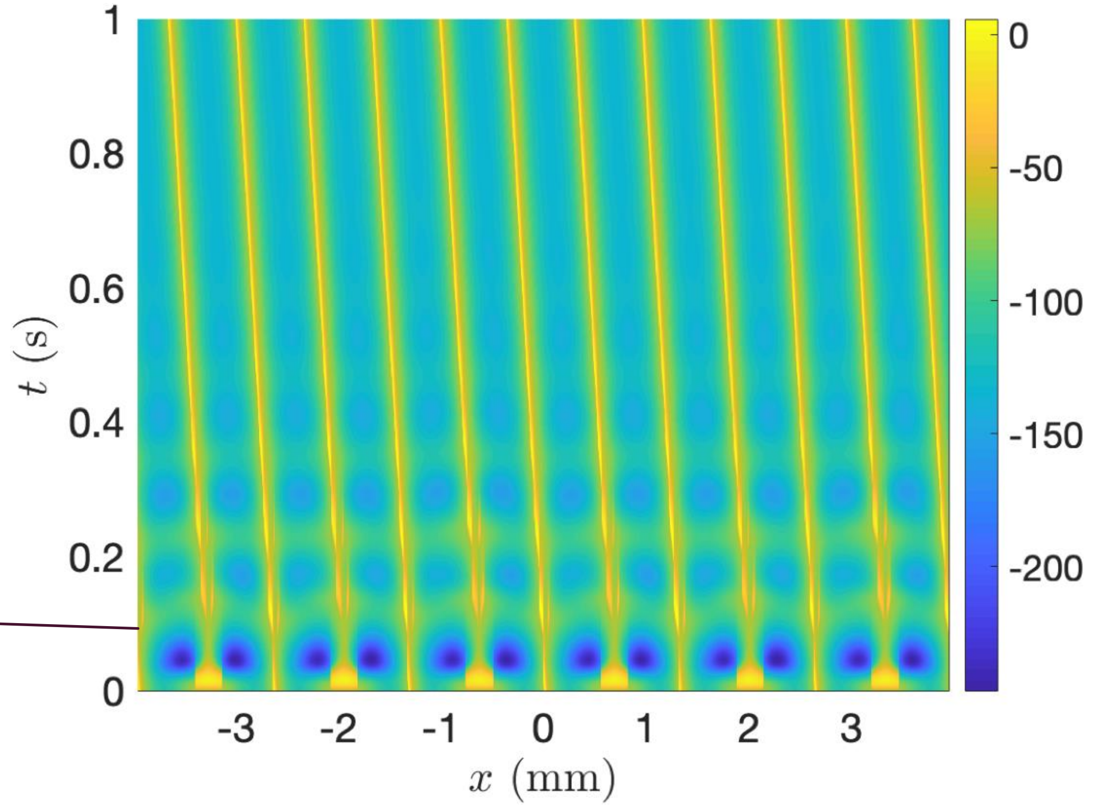




SPATIALLY PERIODIC TRAVELLING WAVES DISPERSION RELATION

- Dispersion curve, $c = c(\phi)$





SPATIALLY PERIODIC TRAVELLING WAVES – STABILITY FINDING THE EVANS FUNCTION

- Perturb the travelling waves

$$z(\xi, t) = z(\xi) + \delta z(\xi, t)$$

- Consider separable perturbations

$$\delta z(\xi, t) = e^{\lambda t} \delta z(\xi)$$

- Generate a linear system in the perturbations

$$(\Gamma(\lambda) - I_4)\boldsymbol{x} = \mathbf{0}$$

where $\boldsymbol{x} = (\delta v(\xi_1), \delta v(\xi_2), \delta v(\xi_3^-), \delta v(\phi^-))$ and demand non-trivial perturbations

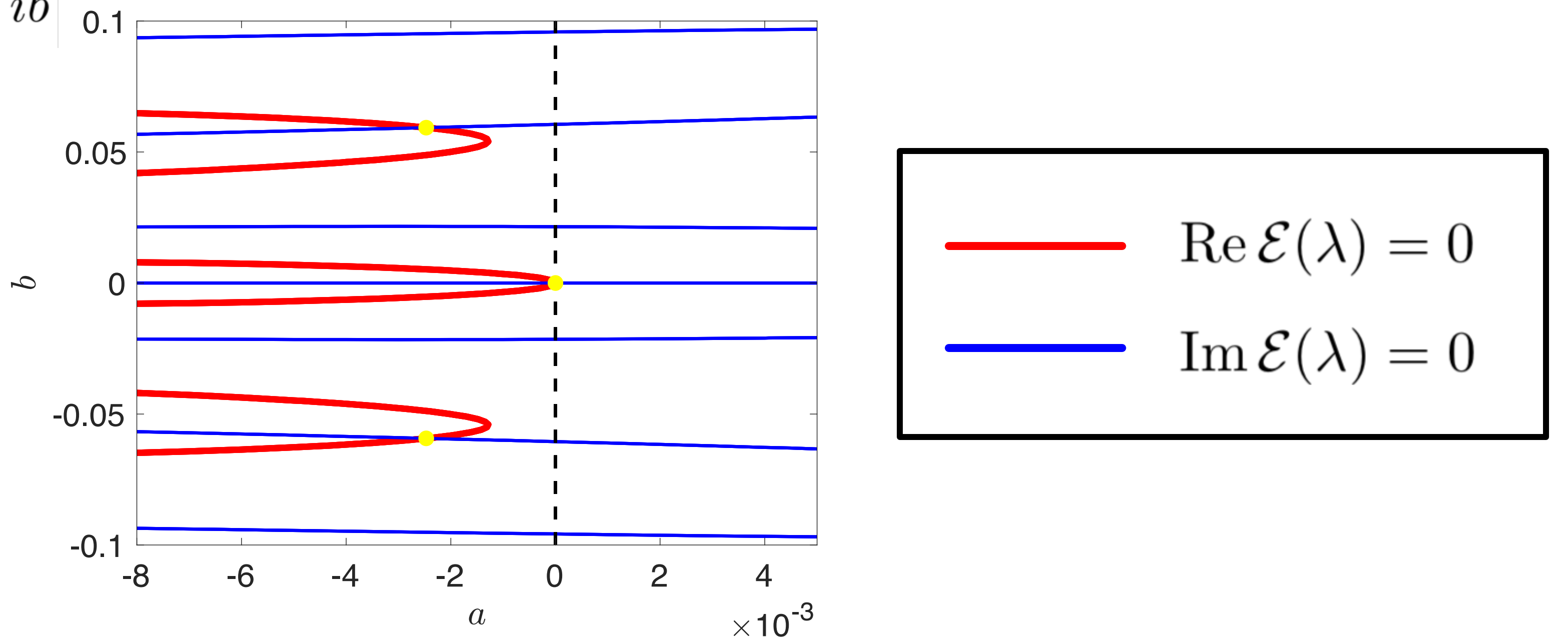
SPATIALLY PERIODIC TRAVELLING WAVES – STABILITY FINDING THE EVANS FUNCTION

- Then the Evans function is

Must vanish for non-trivial perturbations!

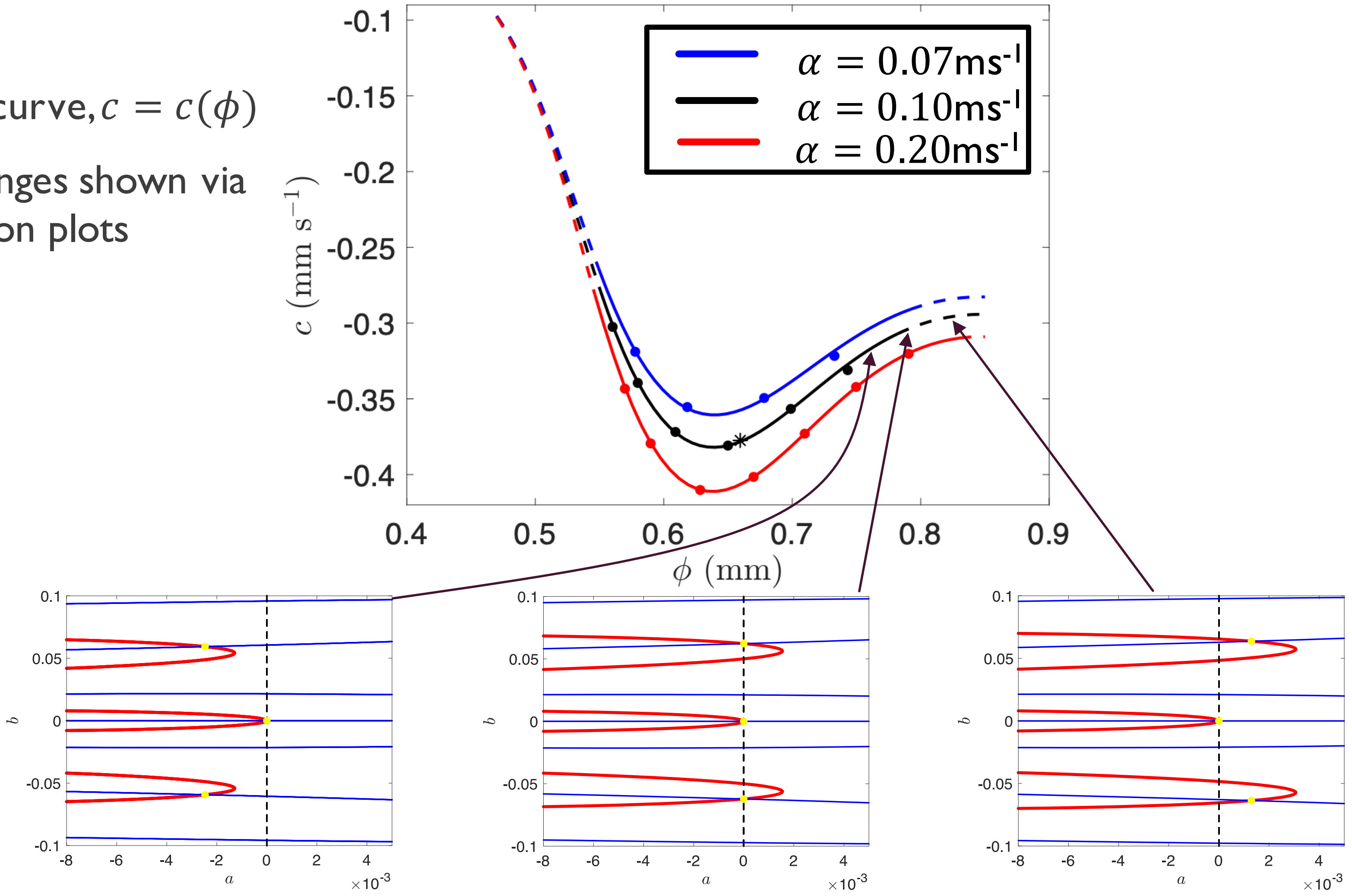
$$\mathcal{E}(\lambda) = \det(\Gamma(\lambda) - I_4)$$

- The zeros of the Evans function are the eigenvalues λ to the stability problem
- Decompose $\lambda = a + ib$



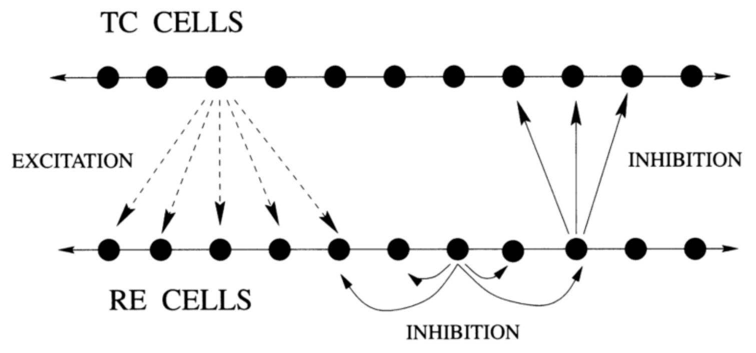
SPATIALLY PERIODIC TRAVELLING WAVES – STABILITY

- Dispersion curve, $c = c(\phi)$
- Stability changes shown via Evans function plots



CONCLUSIONS

- Augmented neural field-type model with ionic currents relevant at a sub-cortical scale
- Non-smooth, piecewise linear model
  - Allows for explicit construction of solutions
  - Facilitates analytical linear stability analysis
- Post-inhibitory rebound phenomenon seen biologically is successfully captured by the model
- Spatially synchronous periodic orbit
- Good agreement between theory and simulation
- Numerical continuation
- Periodic travelling waves
  - Construction
  - Dispersion curve, $c = c(\phi)$
  - Stability analysis via an Evans function approach

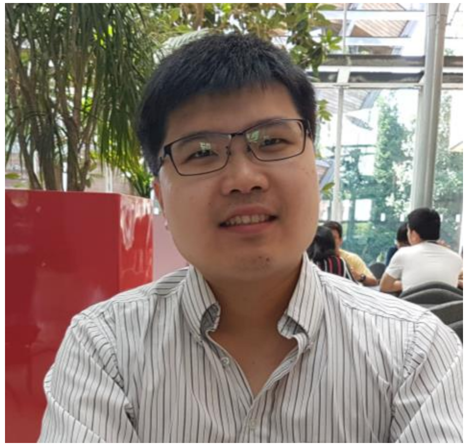


THANK YOU FOR LISTENING!

Me

Stephen Coombes

Rüdiger Thul



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