Dynamics of Neural Systems
Dynamic neural fields: Excitatory and inhibitory networks II

Martin A. Giese

Martin.giese@uni-tuebingen.de

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Hertie-Institut
für klinische Hirnforschung

CIN
Werner Reichardt
Centre for Integrative Neuroscience

Overview

- Wilson-Cowan model
- Travelling waves

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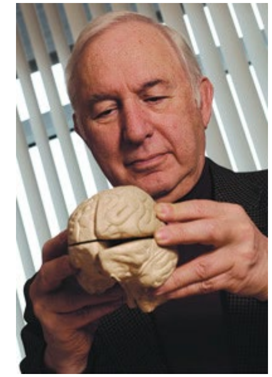
Wilson-Cowan model I

H. Wilson



J. Cowan

- First neural field model (1972).
- Separate equations for **excitation** and **inhibition**:

$$\tau \frac{\partial u(x,t)}{\partial t} = -u(x,t) + \theta\left(\int w_{\mathrm{EE}}(x-x')\, u(x',t)\,\mathrm{d}x' + \int w_{\mathrm{IE}}(x-y')\, v(y',t)\,\mathrm{d}y' + s_{\mathrm{E}}(x,t)\right)$$
$$\tau \frac{\partial v(y,t)}{\partial t} = -v(y,t) + \theta\left(\int w_{\mathrm{II}}(y-y')\, v(y',t)\,\mathrm{d}y' + \int w_{\mathrm{EI}}(y-x')\, u(x',t)\,\mathrm{d}x' + s_{\mathrm{I}}(y,t)\right)$$

- Again, assumption of Naka Rushton threshold function θ in the following: $\theta(x) = \left[\theta_{\max} x^2 / (K^2 + x^2)\right]_+$
- In this case $u^*(x) \equiv v^*(x) \equiv 0$ is an asymptotically stable solution without input ($s_i(x) \equiv 0$).

Wilson-Cowan model II

(i,j: E or I)

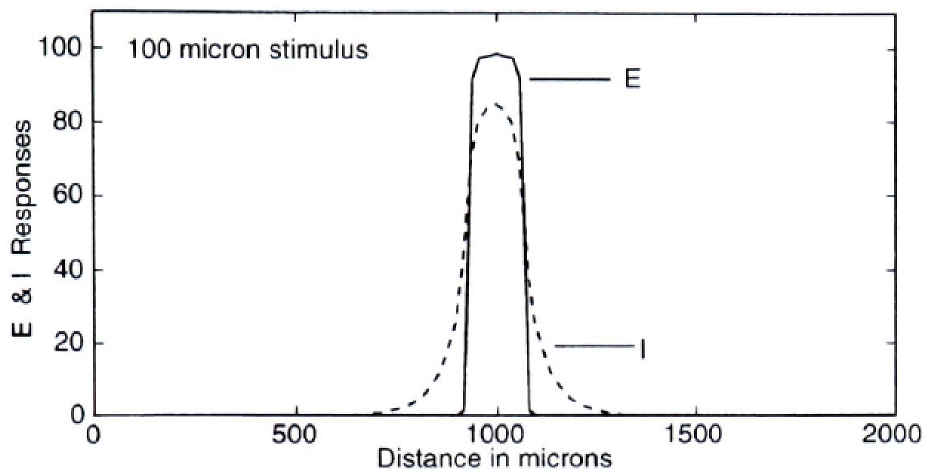
- Exponential interaction kernels; typically, inhibition kernels wider than excitation kernels: $w_{ij}(x) = A_{ij}\exp(-|x|/\sigma_{ij})$
- The spatially uniform solution becomes unstable, so that 'interesting' patterns emerge if (see Wilson book):

$$\boxed{\begin{aligned}&\theta_{\max}(A_{\mathrm{EE}}\sigma_{\mathrm{EE}} - A_{\mathrm{IE}}\sigma_{\mathrm{IE}}) < K_{\mathrm{E}}/2\\&\theta_{\max}(A_{\mathrm{EI}}\sigma_{\mathrm{EI}} - A_{\mathrm{II}}\sigma_{\mathrm{II}}) > K_{\mathrm{I}}/2\end{aligned}}$$

- Dependent on parameters, different types of solutions can emerge.
- Basic stability analysis by perturbation around the constant solution like for Amari field (see Appendix).

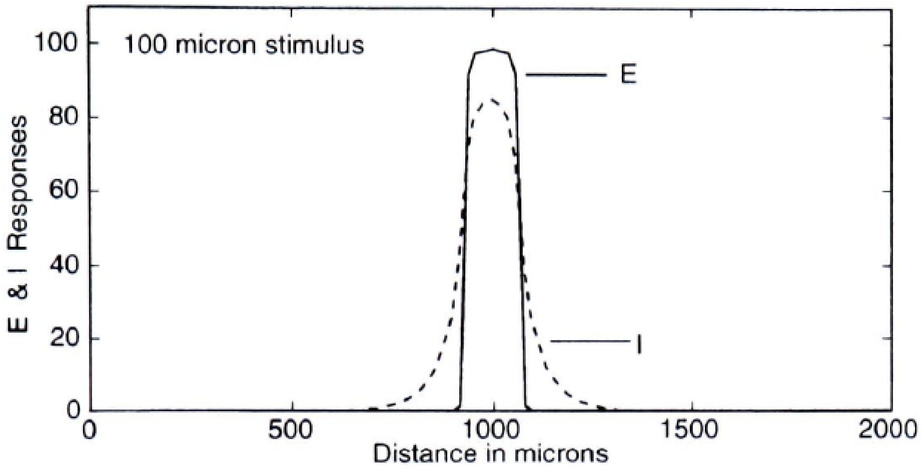
Memory solution

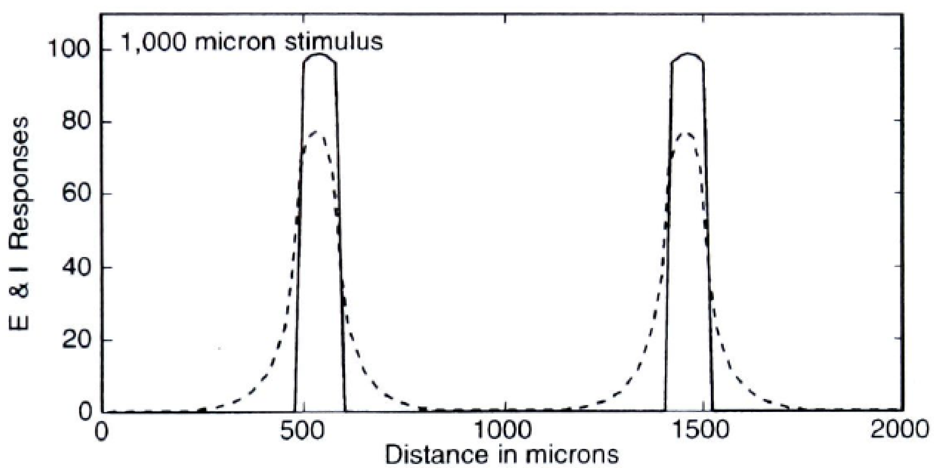
- Self-sustained activity peak after 10 ms of stimulation with a local excitatory peak.



Memory solution

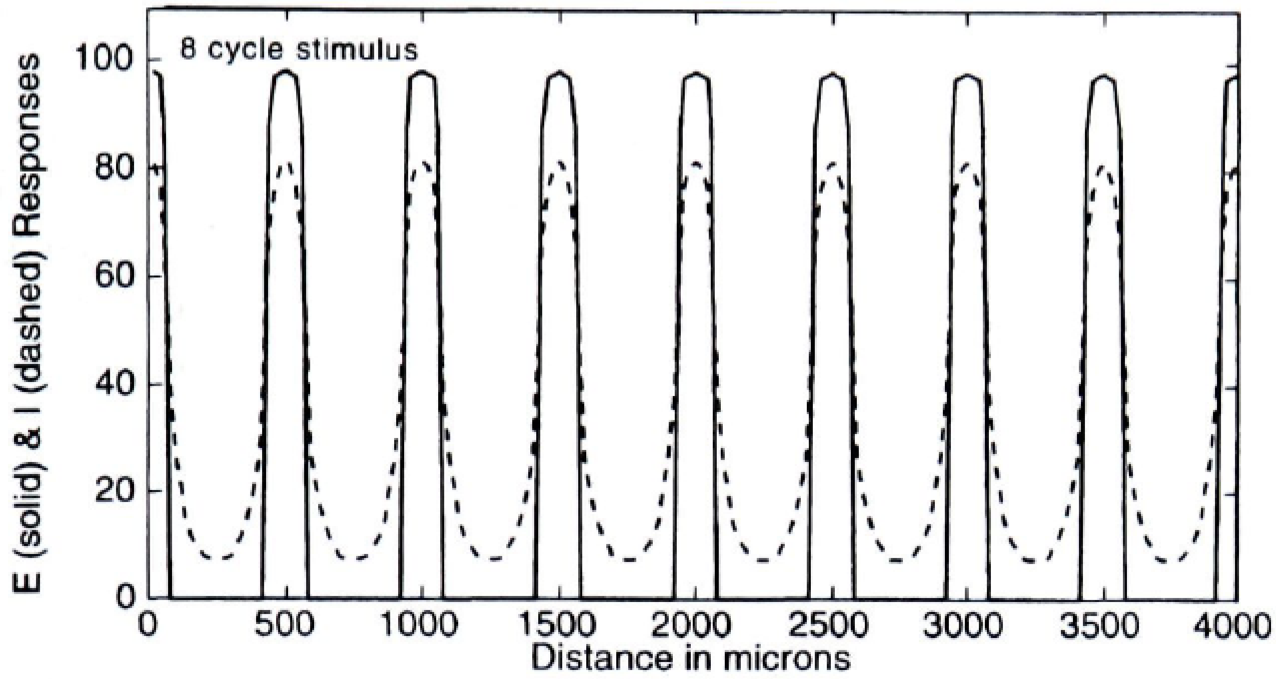
- Self-sustained activity peak after 10 ms of stimulation with a local excitatory peak.
- Multiple peaks can be stored if width of interact-ion kernels is much smaller than length of the field since then activation decays to resting level between the peaks (no interaction between peaks).





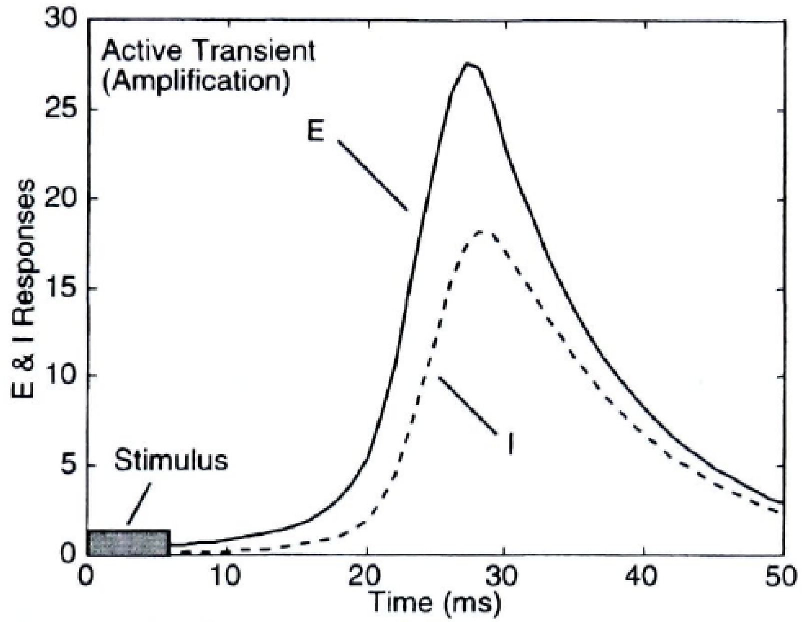
Other solution types

- Non-moving spatially periodic solutions (see Appendix).

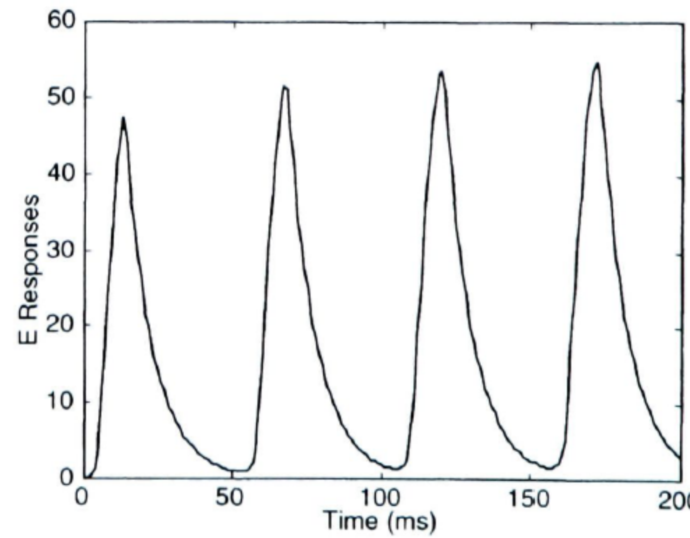


Other solution types

- Transient amplification: short stimulus strongly amplified for a short time.



- Spatially localized oscillatory solution.



- Travelling waves.

Overview

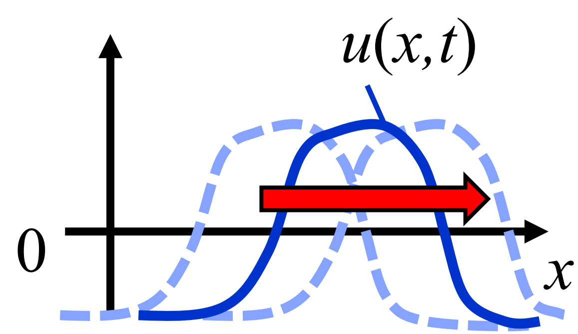
- Wilson-Cowan model
- Travelling waves

Asymmetric interaction kernel

- What happens if the interaction kernel $w(x)$ in an Amari field is asymmetric?
- We assume constant input $s(x, t) \equiv s$.
- Special case: $w(x) = a(x) + \gamma a'(x)$ with $a(x) = a(-x)$ (symmetric part). Implies: $a'(x) = -a'(-x)$ ('antisymmetric')
- In this case (for appropriate parameters) the field has a stable inhomogenous propagating solution (**travelling wave / pulse**).
- This solution has a stable form but propagates with constant velocity v along the field
- Mathematically this implies:

$$\boxed{u(x, t) = U(x - v\,t)}$$

Stable shape



Travelling wave solution I

- Introducing new ‘travelling coordinate system’, we can define the function: $\boxed{U(x-vt,t):=u(x,t)}$; if the system has converged to the travelling pulse solution we have:

$$U(x,t)\equiv U^*(x)$$

- Introducing this in the neural field equation yields:

s constant

$$\tau\frac{\partial U(x,t)}{\partial t}-\tau v\frac{\partial U(x,t)}{\partial x}=-U(x,t)+\int w(x-x')\,\theta\big(U(x',t)\big)\mathrm{d}x'+s-h$$

- For the stationary travelling pulse solution this implies:

$$\boxed{-\tau vU'^*(x)=-U^*(x)+\int w(x-x')\,\theta\big(U^*(x')\big)\mathrm{d}x'+s-h}$$

- Assume that $U_0(x)$ is a stable localized solution of the dynamic field equation with symmetric kernel; that is:

$$U_0(x)=\int a(x-x')\,\theta\big(U_0(x')\big)\mathrm{d}x'+s-h$$

Travelling wave solution II

- This implies: $U_0'(x) = \int a'(x - x')\,\theta\big(U_0(x')\big)\mathrm{d}x'$
- Weighted summation of the last two equations implies:

$$U_0(x) - \tau v U_0'(x) = \int \underbrace{\left(a(x - x') - \tau v a'(x - x')\right)}_{w(x\text{-}x')}\theta\big(U_0(x')\big)\mathrm{d}x' + s - h$$

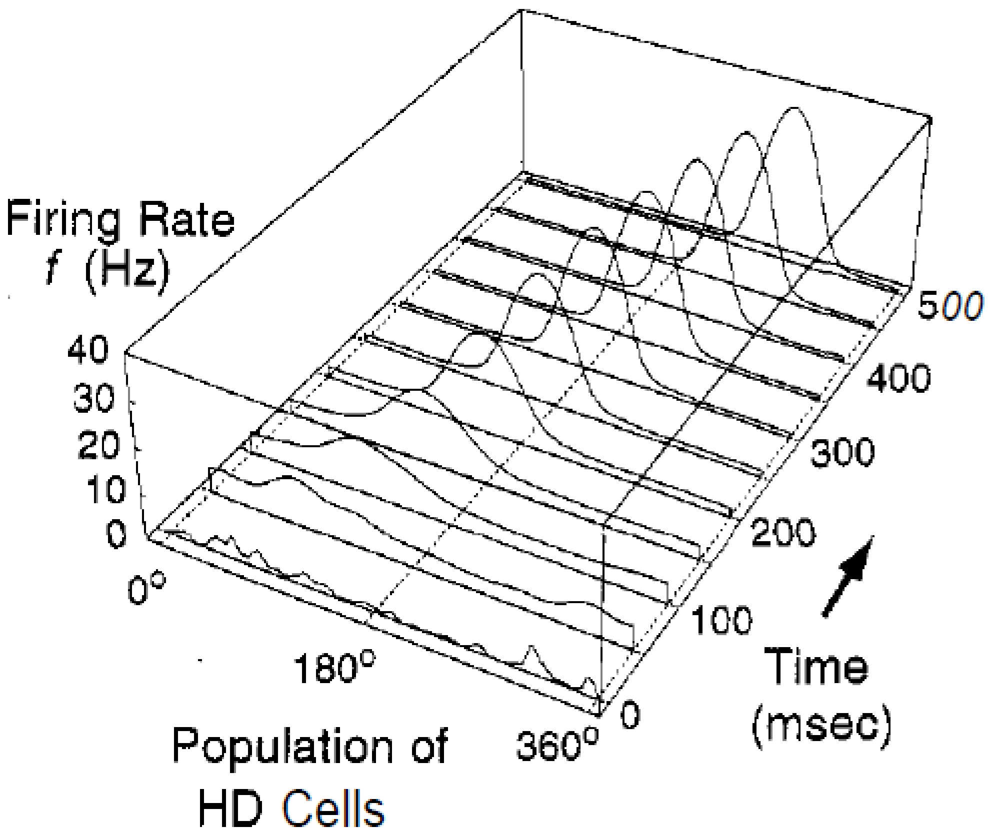
- This proves the following **Theorem** (Zhang, 1996):

$\boxed{\text{}}$

Assume that the interaction kernel has the form: $w(x) = a(x) + \gamma\, a'(x)$ with $a(x) = a(-x)$ and that the function $U(x)$ is a stable peak solution of the dynamic neural field equation with the symmetric interaction kernel $a(x)$, then the field with the kernel $w(x)$ has a **traveling pulse solution** with the same shape that propagates with the constant velocity $v = -\gamma / \tau$.

Travelling wave solution III

- Example simulation (Zhang, 1996):



Diffusion-reaction equation I

- Similar phenomena can also arise along **excitable membranes**, for example for an axon.
- Nonlinear extension of cable equation (with $E_{\mathrm{m}} = 0$ and $\tau = r_{\mathrm{m}} c_{\mathrm{m}}$ and $D^2 = {}^{r_{\mathrm{m}}}\!/_{r_{\mathrm{a}}}$; no external current):

$$\boxed{\tau \frac{\partial V(x,t)}{\partial t} = D^2 \frac{\partial^2 V(x,t)}{\partial x^2} + F\big(V(x,t)\big)}$$

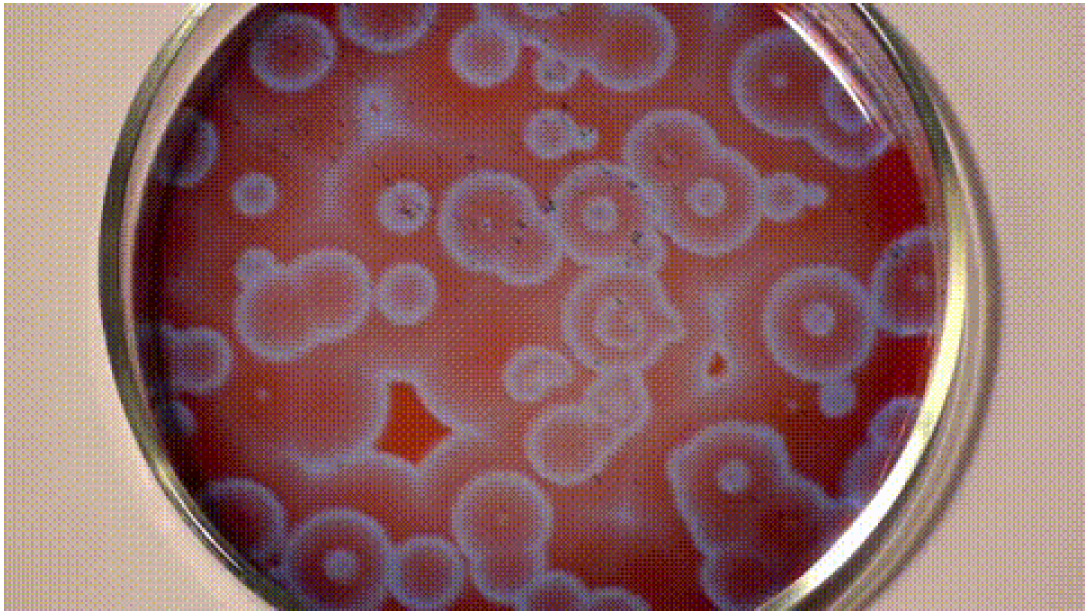
- The function F is **nonlinear**; for the choice $F(V) = -V$ the standard linear cable equation results.
- The resulting equation is called a **diffusion-reaction equation**, because such equations emerge in physical chemistry for diffusing substances that react with each other.

*Lenin award, 1980

B. Belousov*

Diffusion-reaction equation II

- Example: **Belousov*-Zhabotinsky reaction** (discovered 1950).
- ‘Chemical oscillator’; spontaneous pattern formation.



- System of coupled reactions:

I	$2\,Br^- + BrO_3^- + 3\,H^+ + 3$ "H_2Mal"	$\rightarrow$	3 "HBrMal" $+ 3\,H_2O$
II	$BrO_3^- + 4\,Ferroin^{2+} +$ "H_2Mal" $+ 5\,H^+$	$\rightarrow$	$4\,Feriin^{3+} +$ "HBrMal" $+ 3\,H_2O$
III	$4\,Feriin^{3+} +$ "HBrMal" $+ 2\,H_2O$	$\rightarrow$	$4\,Ferroin^{2+} + HCOOH + 2CO_2 + 5\,H^+ + Br^-$

Diffusion reaction equation IV

- Introducing this in the original equation results in the regular second-order DEQ: :

$$-v\tau \frac{\mathrm{d}V_0(z)}{\mathrm{d}z} = D^2 \frac{\mathrm{d}^2 V_0(z)}{\mathrm{d}z^2} + F\big(V_0(z)\big)$$

- This equation can be rewritten in standard form:

$$\boxed{\begin{aligned}\frac{\mathrm{d}V_0(z)}{\mathrm{d}z} &= W_0(z)\\ \frac{\mathrm{d}W_0(z)}{\mathrm{d}z} &= -\frac{1}{D^2}\Big(v\tau W_0(z) + F\big(V_0(z)\big)\Big)\end{aligned}}$$

- The problem reduces to the solution of a second-order nonlinear differential equation in the variable z.

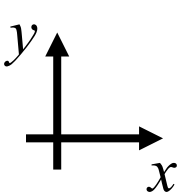
Diffusion reaction equation V

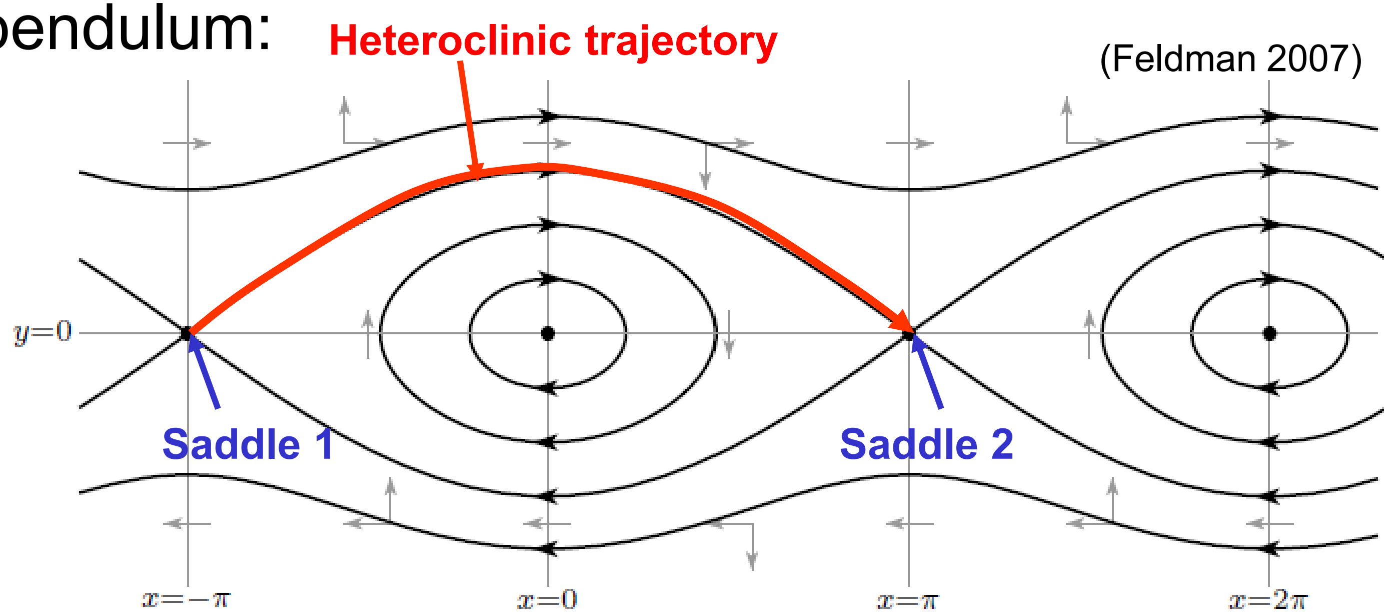
- For something ‘interesting’ to happen we need to find invariant solutions that vary as a function of z. (A stable fixed point would lead to a constant solution.) It can be shown that such solutions are **heteroclinic trajectories** that link different fixed points that are approached for $z \to \pm\infty$.

Diffusion reaction equation V

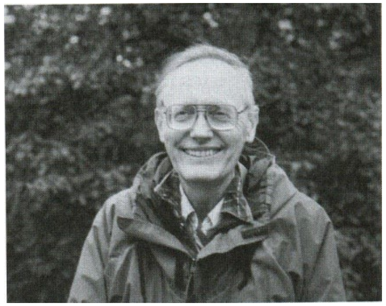
- For something ‘interesting’ to happen we need to find invariant solutions that vary as a function of z. (A stable fixed point would lead to a constant solution.) It can be shown that such solutions are **heteroclinic trajectories** that link different fixed points that are approached for $z \to \pm\infty$.
- Example: undamped nonlinear pendulum:

$$\boxed{\begin{aligned}\dot{x} &= y \\ \dot{y} &= -\sin x\end{aligned}}$$





FitzHugh-Nagumo model I



R. FitzHugh

- Direct mathematical analysis of the HH equations too difficult.
- FitzHugh and Nagumo (1969) proposed the following simplified model:

$$\boxed{\begin{aligned}&\tau \frac{\partial V}{\partial t} = D^2 \frac{\partial^2 V}{\partial x^2} - \left(a_0 + a_1 V + a_2 V^2\right)(V - a_4) - b_0 R (V + b_1)\\&\tau_1 \frac{\partial R}{\partial t} = -R + c_1 V + c_0\end{aligned}}$$

- Assuming very slow variation of R, compared to V this system has the discussed from; standard form:

$$\frac{\mathrm{d}V_0}{\mathrm{d}z} = W_0$$

assumed to be constant (equilibrium value)

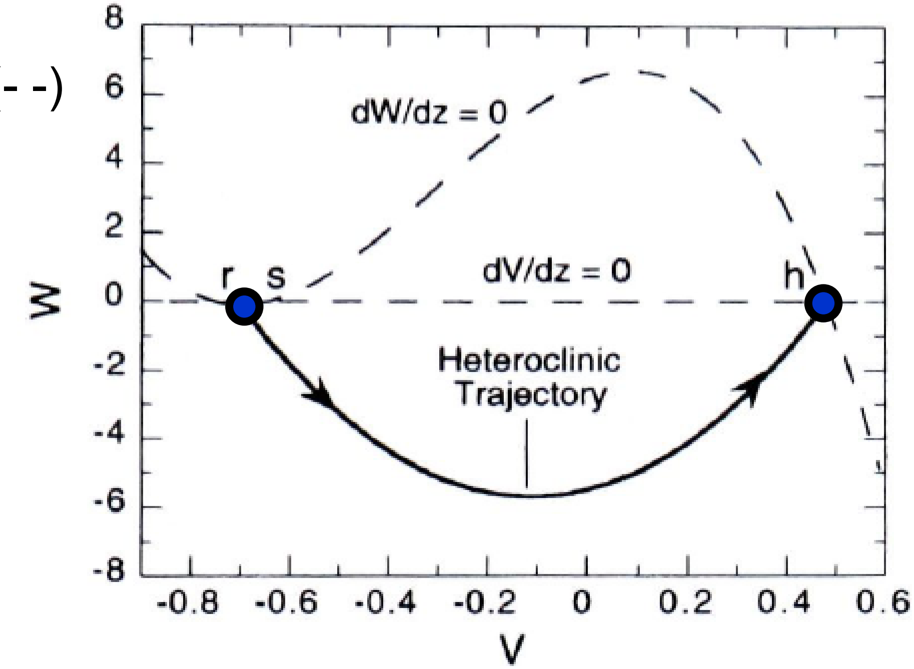
$$\frac{\mathrm{d}W_0(z)}{\mathrm{d}z} = \frac{1}{D^2}\left(-v\tau W_0 + \left(a_0 + a_1 V_0 + a_2 V_0^2\right)(V_0 - a_4) + b_0 R^*(V_0 + b_1)\right)$$

FitzHugh-Nagumo model II

- This system has two unstable saddle points and a stable spiral point; the heteroclinic trajectory that connects the saddles defines the relevant travelling wave solution.

Isoclines (- -)

Isoclines



FitzHugh-Nagumo model III

- The form of this trajectory is obtained by 'division' of the dynamic equations:

$$\frac{\mathrm{d}W_0}{\mathrm{d}V_0} = \frac{1}{D^2 W_0}\Big(\underbrace{\left(a_0 + a_1 V_0 + a_2 V_0^2\right)(V_0 - a_4) + b_0 R^*(V_0 + b_1)}_{\text{3rd order polynomial in } V_0}\Big) - \frac{v\tau}{D^2}$$

- A solution of this equation is given by:

$$W_0(V_0) = -K(V_0 - V^1)(V_0 - V^3)$$

Roots of the 3rd order polynomial

- The amplitude K depends on the wave velocity v; both constants follow from nonlinear equation system (see Wilson book).

FitzHugh-Nagumo model IV

- This implies the differential equation for V_0:

$$W_0(V_0) = \frac{\mathrm{d}V_0}{\mathrm{d}z} = -K(V_0 - V^1)(V_0 - V^3)$$

- This differential equation has the solution (separation of variables):

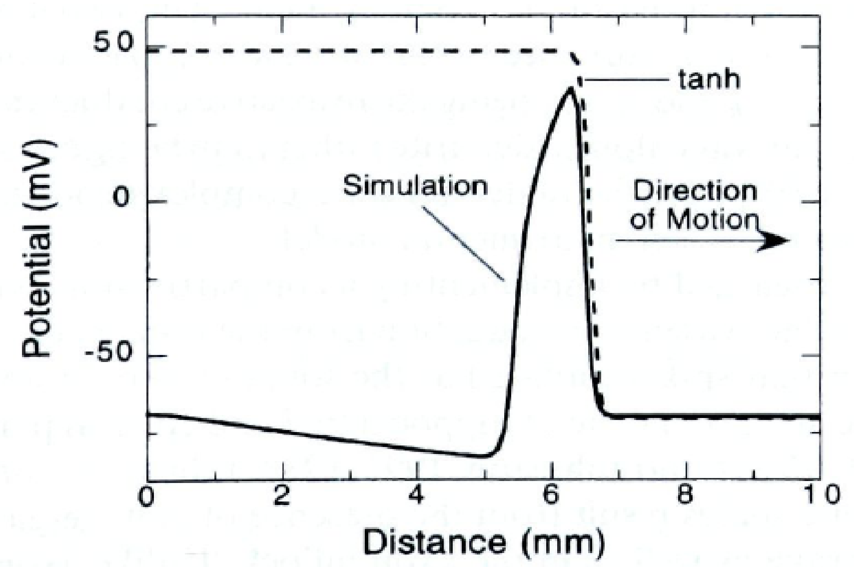
$$-\int \frac{\mathrm{d}V_0}{K(V_0(z') - V^1)(V_0(z') - V^3)} = \int \mathrm{d}z + \text{const.}$$

$$\Rightarrow V_0(z) = V^1 + \frac{V^3 - V^1}{2} \tanh\left(\frac{K(V^3 - V^1)z}{2}\right)$$

$$= V^1 + \frac{V^3 - V^1}{2} \tanh\left(\frac{K(V^3 - V^1)(x - vt)}{2}\right)$$

FitzHugh-Nagumo model V

- Analytical travelling solution in comparison with simulation of the full FitzHugh-Nagumo model:



- Travelling flank at the front of the action potential (AP) well-modeled; decay of the signal on the back of the AP is not captured by the model.

Things to remember

- Wilson-Cowan model $\rightarrow$ 4)
- Solution types of WC model $\rightarrow$ 4)
- Travelling wave $\rightarrow$ 2,4)
- Heteroclinic trajectory $\rightarrow$ 4)
- FitzHugh-Nagumo model $\rightarrow$ 4)

Literature (for this lecture)

1) Dayan, P. & Abbott, L.F. (2001 / 2005) *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems.* MIT Press, Cambridge MA, USA. Chapter 7.

2) Gerstner, W. & Kistler, W. (2002) *Spiking Neuron Models - Single Neurons, Populations, Plasticity.* Cambridge University Press, UK. Chapter 9.

3) Trappenberg, T.P. (2010) *Fundamentals of Computational Neuroscience*. Oxford University Press, UK. Chapter 7.

4) Wilson, H.R. (1999) *Spikes, Decisions, and Actions.* Oxford University Press, UK. Chapters 7 +15.

Appendix: Stability analysis and solutions of the Wilson-Cowan model (Not relevant for exam!)

Spatially periodic solution I

- Linearization of the solution about a spatially homogeneous stationary state (u_0, v_0) results in the linear integro-differential equations:

$$u_0 = \theta(\breve{u}_0)$$
$$v_0 = \theta(\breve{v}_0)$$

$$\boxed{\begin{aligned}\tau\frac{\partial\delta u(x,t)}{\partial t} &= -\delta u(x,t) + \theta'(\breve{u}_0)\left(\int w_{\mathrm{EE}}(x-x')\,\delta u(x',t)\mathrm{d}x' + \int w_{\mathrm{IE}}(x-y')\,\delta v(y',t)\mathrm{d}y'\right)\\ \tau\frac{\partial\delta v(x,t)}{\partial t} &= -\delta v(x,t) + \theta'(\breve{v}_0)\left(\int w_{\mathrm{II}}(y-y')\,\delta v(y',t)\mathrm{d}y' + \int w_{\mathrm{EI}}(y-x')\,\delta u(x',t)\mathrm{d}x'\right)\end{aligned}}$$

- These can be solved by Fourier transformation w.r.t. the spatial variables resulting in separate differential equations for different spatial modes (spatial frequency k):

$$\boxed{\begin{aligned}\tau\frac{\mathrm{d}\delta\tilde{u}(k,t)}{\mathrm{d}t} &= \delta\tilde{u}(k,t)(\theta'(\breve{u}_0)\tilde{w}_{\mathrm{EE}}(k)-1) + \delta\tilde{v}(k,t)(\theta'(\breve{u}_0)\tilde{w}_{\mathrm{IE}}(k))\\ \tau\frac{\mathrm{d}\delta\tilde{v}(k,t)}{\mathrm{d}t} &= \delta\tilde{v}(k,t)(\theta'(\breve{v}_0)\tilde{w}_{\mathrm{II}}(k)-1) + \delta\tilde{u}(k,t)(\theta'(\breve{v}_0)\tilde{w}_{\mathrm{EI}}(k))\end{aligned}}$$

Spatially periodic solution II

- This dynamics is stable if the frequency-dependent system matrix

$$\boxed{\mathbf{A}(k)=\begin{bmatrix}(\theta'(\breve{u}_0)\tilde{w}_{\mathrm{EE}}(k)-1) & \theta'(\breve{u}_0)\tilde{w}_{\mathrm{IE}}(k)\\ \theta'(\breve{v}_0)\tilde{w}_{\mathrm{EI}}(k) & (\theta'(\breve{v}_0)\tilde{w}_{\mathrm{II}}(k)-1)\end{bmatrix}}$$

has only eigenvalues with negative real part for all k. Otherwise, spatial oscillations emerge.