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

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Overview

- Linear dynamic neural field
- One-layer nonlinear neural fields
- Applications

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Basic idea: spatial continuum limit

- Assume linear recurrent network with the dynamics:

$$\boxed{\tau \frac{\mathrm{d}\mathbf{u}}{\mathrm{d}t} = -\mathbf{u}(t) + \mathbf{M}\mathbf{u}(t) + \mathbf{s}(t)}$$

- Replace index n of the neurons by a continuous variable x.
- Summation over vector components goes over in integral.
- The last equation can then be rewritten:

$$\boxed{\tau \frac{\partial u(x,t)}{\partial t} = -u(x,t) + \int m(x,x')u(x',t)\,\mathrm{d}x' + s(x,t)}$$

neural field / neural mass model

- Simple example: Model for direction tuning; linear (partial) **integro-differential equation**.
- Often it is assumed that the **interaction kernel** is translation-invariant; this implies: $m(x, x') = m(x - x')$.

Example: direction tuning I

- Model: $$\boxed{\tau \frac{\partial u(\phi,t)}{\partial t} = -u(\phi,t) + \int_{-\pi}^{\pi} m(\phi-\phi')u(\phi',t)\,\mathrm{d}\phi' + s(\phi,t)}$$
- Input signal $s(\phi, t)$ specifies the activity of a direction-tuned feed-forward input (e.g. from direction-selective V1 cells).
- Assume: All functions periodic (here with 2π) in the variable ϕ.
- We assume in addition a symmetric translation-invariant interaction kernel $m(\phi, \phi') = m(\phi - \phi')$.

Example: direction tuning II

- The linear dynamic neural field equation can be easily solved using a **Fourier series expansion** with respect to the spatial/angle dependency, using:

$$\boxed{f(\phi) = \sum_{n=-\infty}^{\infty} \tilde{f}_n \exp(in\phi)}$$

$$\tilde{f}_n = \frac{1}{2\pi} \int_{-\pi}^{\pi} f(\phi) \exp(-in\phi)\, d\phi$$

Remark:

$$f(\phi) = \int_{-\pi}^{\pi} g(\phi - \phi')h(\phi')d\phi'$$

$$\Rightarrow \tilde{f}_n = 2\pi \tilde{g}_n \tilde{h}_n$$

- For the Fourier coefficients this implies the differential equation:

$$\boxed{\tau \frac{\mathrm{d}\tilde{u}_n}{\mathrm{d}t} = -\tilde{u}_n(t) + 2\pi \tilde{m}_n \tilde{u}_n(t) + \tilde{s}_n(t)}$$

(**Remark:** Convolution integral goes over in product in Fourier domain, see above)

Example: direction tuning III

- This specifies separate decoupled non-autonomous linear differential equations for each Fourier mode; each of them can be analytically solved (Lecture 6).
- The stationary solution follows for constant input with

$$\tilde{u}_n(\infty) = \frac{\tilde{s}_n}{1 - 2\pi\tilde{m}_n} \quad \Rightarrow \quad u(\phi, \infty) = \sum_{n=-\infty}^{\infty} \frac{\tilde{s}_n}{1 - 2\pi\tilde{m}_n} \exp(in\phi)$$

- From $s(\phi)$ is real follows $\tilde{s}_{-n} = (\tilde{s}_n)^*$, and since $m(x)$ is symmetric $\tilde{m}_n$ is real. The terms of the sum for n and $-n$ are thus conjugate complex and can be rewritten as a sum of a $\sin$ and $\cos$ functions (see Dayan & Abbott book).

Example: direction tuning IV

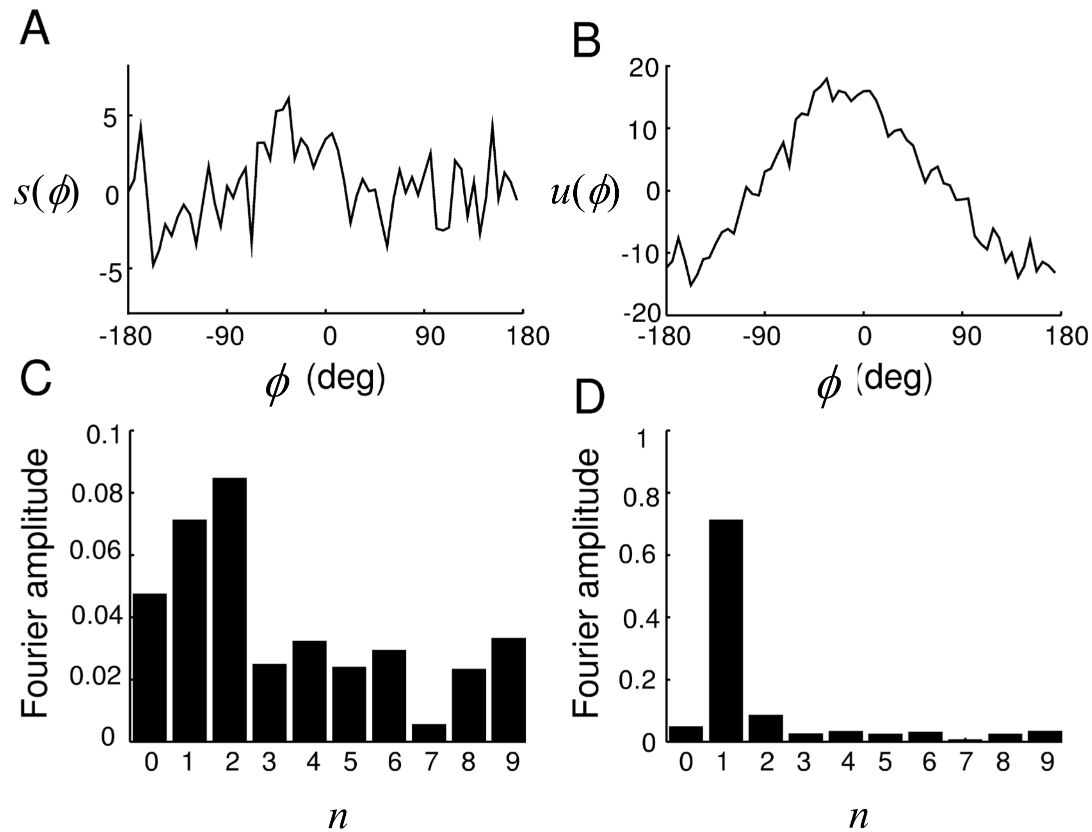
- Remark: **eigenfunctions** of the interaction kernel which are given by the integral equation:

$$\lambda_\mu e_\mu(\phi) = \int_{-\pi}^{\pi} m(\phi - \phi') e_\mu(\phi')\,\mathrm{d}\phi'$$
$$\Leftrightarrow \quad \lambda_\mu \tilde{e}_{\mu,n} = 2\pi\, \widetilde{m}_n \tilde{e}_{\mu,n}$$

- We conclude that the **eigen-values** λ_μ are proportional to the (real) Fourier coefficients of $m(\phi)$; the (orthogonal) eigenfunctions are simply given by the Fourier basis; the solution of the integro-differential equation is a superposition of them.
- Analogous to result form the system with a finite number of neurons in Lecture 6, where the solution was given by a superposition of the eigenvectors of the recurrent feedback matrix, here the solution is given by a superposition of the eigenfunctions of the interaction kernel.

Example: direction tuning V

- Example for $m(\phi) = (0.9/\pi)\cos\phi$; this implies $2\pi\widetilde{m}_{\pm 1} = 0.9$ (close to 1); the first harmonic is thus selectively amplified.
- Input is a cosine that peaks at 0 with strong noise (A).
- Plots show signal and amplitude of Fourier coefficients.
- Noise has been 'largely removed' in output signal $u(\phi, \infty)$ (see B).



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Model by Amari

S. Amari

- Simple **nonlinear** dynamic neural field model that allows to do some mathematical analysis.
- Equation (Amari, 1977):

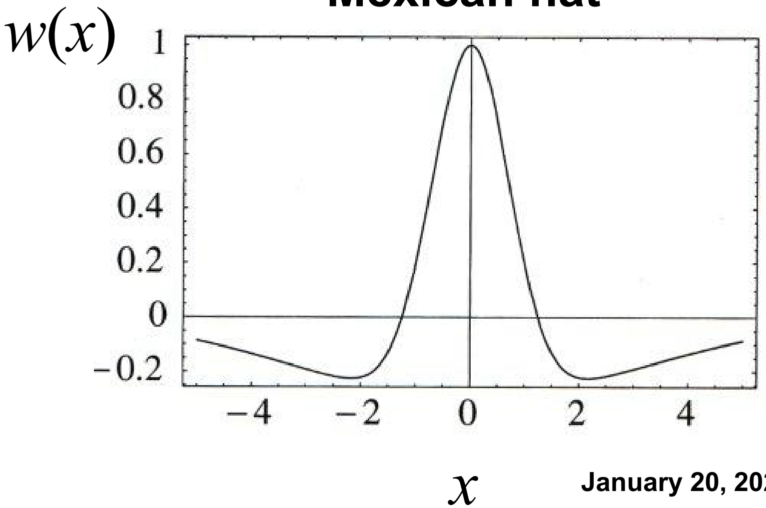
Resting level activity

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

Interaction kernel Threshold function

- Sigmoidal threshold; special case: step function $\theta(u) = 1(u)$.
- Often assumption of a sym-metric 'Mexican hat kernel'.

Mexican hat



Spatially homogeneous solutions I

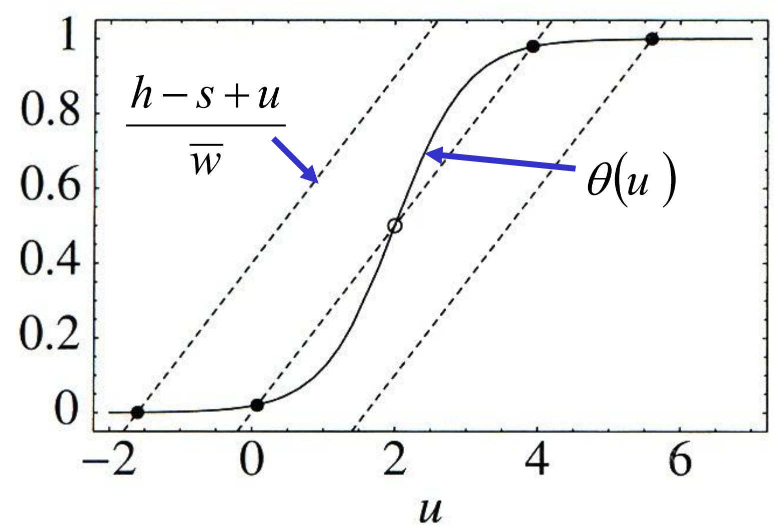
- No dependence on space: $u(x,\ t) \equiv u(t);\ s(x,\ t) \equiv s(t)$
- We assume (radially) symmetric kernel: $w(x) = w(|x|)$.
- Then field dynamics can be reduced to simple DEQ:

$$\boxed{\tau \frac{\mathrm{d}u(t)}{\mathrm{d}t} = -u(t) + \overline{w}\,\theta\big(u(t)\big) + s(t) - h \qquad \text{with} \quad \overline{w} = \int w(x)\,\mathrm{d}x}$$

- For a temporally constant input s we determine the fixedpoints u_0 using isoclines:

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = 0 \quad \Rightarrow \quad \frac{h - s + u}{\overline{w}} = \theta(u)$$

(nonlinear equation for u_0)



Spatially homogeneous solutions II

- Linearization of the dynamics about the fixedpoint u_0 results in the linearized dynamics:

  $$\tau \frac{\mathrm{d}u(t)}{\mathrm{d}t} = -u(t) + \bar{w}\,\theta'(u_0)u(t) \quad \text{with} \quad \bar{w} = \int w(x)\mathrm{d}x$$

  This implies for the eigenvalue:

  $$\lambda = -1 + \overline{w}\,\theta'(u_0)$$

- This implies stability for the condition: $\boxed{\overline{w}\,\theta'(u_0) < 1}$

(for a differentiable sigmoidal function)

Spatially homogeneous solutions III

- Remark: the analysis so far assumes spatially constant u. What happens for general perturbations of the homogeneous solution that violate this assumption?
- Behavior for a small perturbation $\delta u(x, t)$ about the stationary solution $u(x) \equiv u_0$ is given by linearization with $u(x, t) = u_0 + \delta u(x, t)$; this implies the **linearized dynamics**:

$$\boxed{\tau \frac{\partial \delta u(x,t)}{\partial t} = -\delta u(x,t) + \theta'(u_0) \int w(x - x')\, \delta u(x',t) \mathrm{d}x'}$$

- Solve by Fourier transformation w.r.t. space:

$$\delta u(x,t) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \delta\tilde{u}(k,t) e^{ikx} \mathrm{d}k \quad \Rightarrow$$

$$\tau \frac{\partial \delta\tilde{u}\,(k,t)}{\partial t} = -\delta\tilde{u}(k,t) + \theta'(u_0)\, \tilde{w}(k) \delta\tilde{u}(k,t) = (\theta'(u_0)\, \tilde{w}(k) - 1)\, \delta\tilde{u}(k,t)$$

Spatially homogeneous solutions IV

- The solutions for different *k* are independent:

$$\delta\tilde{u}(k,t) = \delta\tilde{u}(k,0)\, e^{\frac{\theta'(u_0)\tilde{w}(k)-1}{\tau}t}$$

- This implies stability if the following stability condition is fulfilled for all real k:

$$\boxed{\theta'(u_0)\,\tilde{w}(k) < 1}$$

Pattern formation I

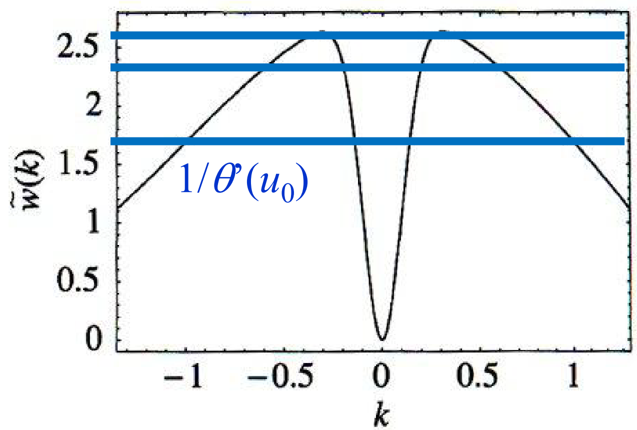
- Example 1: For purely excitatory coupling $w(x) = \exp(-ax^2)$ stability is guaranteed for:

$$\tilde{w}(k) \le \tilde{w}(0) = \int w(x)dx = \sqrt{\frac{\pi}{a}} < 1/\theta'(u_0)$$

($\tilde{w}(k) = \sqrt{\frac{\pi}{a}} e^{-\frac{k^2}{4a}}$ is also a Gaussian)

- The constant solution ($k = 0$) becomes unstable first. This result reflects that for purely excitatory networks no interesting pattern formation is occurring (constant solution).
- Example 2: Mexican hat $w(x) = A\exp(-ax^2) - B\exp(-bx^2)$. Fourier transform is a difference of Gaussians (all constants positive):

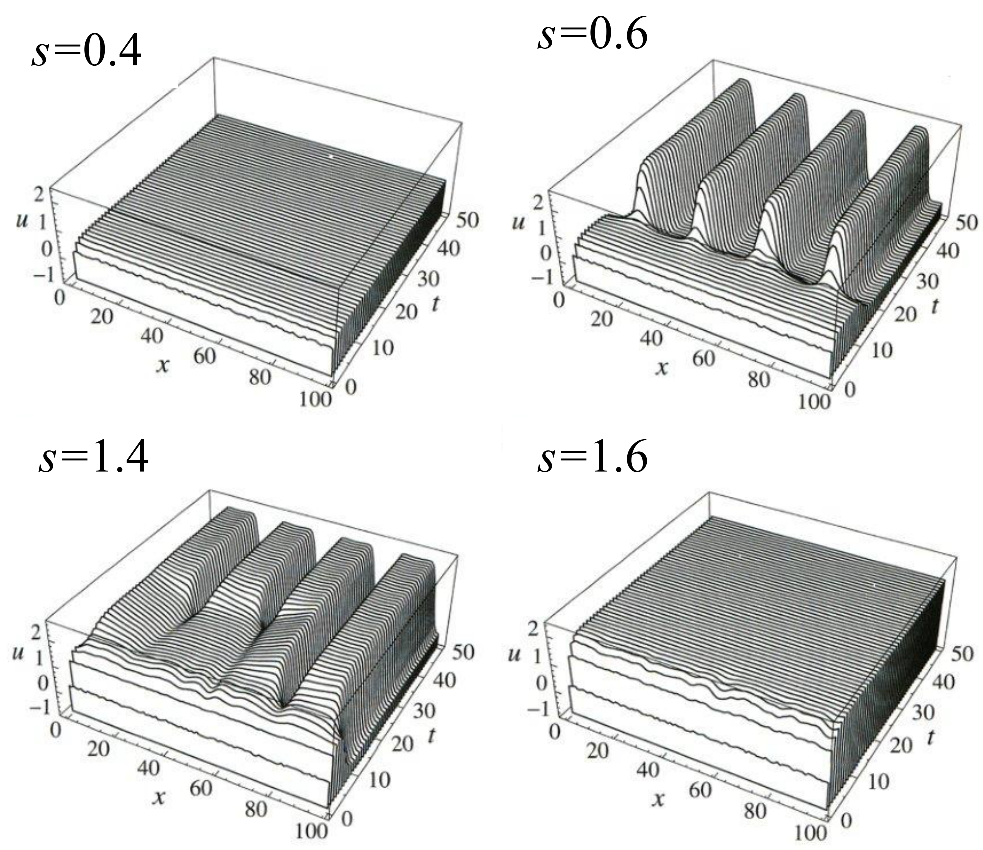
$$\tilde{w}(k) = A\sqrt{\frac{\pi}{a}} e^{-\frac{k^2}{4a}} - B\sqrt{\frac{\pi}{b}} e^{-\frac{k^2}{4b}} < 1/\theta'(u_0)$$



- Nonzero frequency component 'becomes unstable' first (if u_0 is varied).

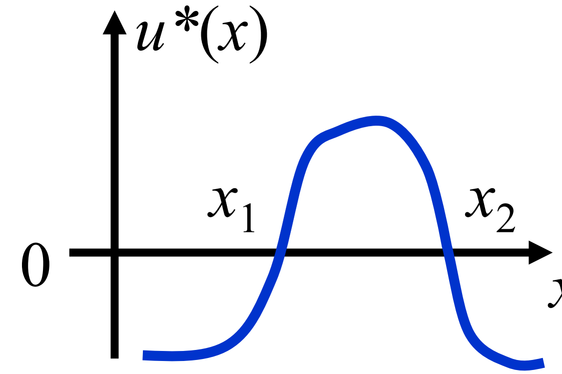
Pattern formation II

- If the last inequality is violated pattern formation occurs; small deviations from the homogeneous solution diverge with formation of periodic patterns.
- Pattern formation dependent on the constant input.
- Examples for signals s, with $\theta(u) = \dfrac{1}{1+\exp(5(u-1))}$.



Localized stationary solutions: activation peaks / blobs I

- Models with excitatory and inhibitory interactions can have stable localized spatially inhomogeneous solutions: $u(x, t) \equiv u^*(x)$. ('a solution')



- An example is a **local activation peak** with $u^*(x)\begin{cases} \geq 0 & \text{for } x_1 \leq x \leq x_2 \\ < 0 & \text{otherwise.} \end{cases}$
- For the case of a step threshold $\theta(u) = 1(u)$ the dynamics of the solution can be exactly solved (Amari, 1977).
- In this case the DNF equation for a temporally constant input $s(x)$ is given by:

$$\boxed{\tau \frac{\partial u(x,t)}{\partial t} = -u(x,t) + \int_{x_1(t)}^{x_2(t)} w(x-x')\,\mathrm{d}x' + s(x) - h}$$

Time-dependent boundaries of excited region

Localized stationary solutions: activation peaks / blobs II

- In the Advanced Computational Methods lecture we will prove the following two results (Amari, 1977).
- For a constant input signal $s(x,\ t) \equiv s$ we obtain a stationary local peak solution with a size of the excited region $a^* = x_2{}^* - x_1{}^*$ when the nonlinear equation $\boxed{W(a^*) + s - h = 0}$ with $W(x) = \int_0^x w(x')\,\mathrm{d}x'$ has a positive solution $a^* > 0$.

  *: stationary sol.

- This solution is stable if: $\boxed{\left.\frac{\mathrm{d}W}{\mathrm{d}a}\right|_{a^*} = w(a^*) < 0}$
- The position of the excited region is marginally stable. Its size a is asymptotically stable.

Localized stationary solutions: activation peaks / blobs III

- For weakly spatially varying input it can be shown by linearization about the solution with constant input (Amari, 1977):

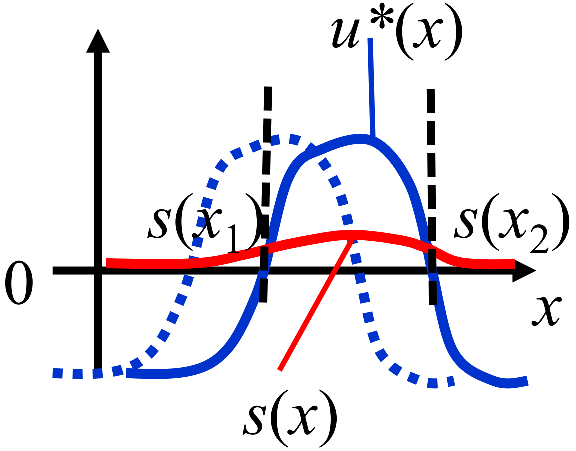
  ($\gamma_1 > 0$)

$$\boxed{\frac{\mathrm{d}x_{\mathrm{m}}}{\mathrm{d}t} = \frac{\mathrm{d}((x_1 + x_2)/2)}{\mathrm{d}t} = \frac{1}{\tau\gamma_1}\left(s(x_2) - s(x_1)\right)}$$

Center of the peak

  This implies that the activation peak moves towards the 'center' of the input peak.

- This property can be used, e.g. for maximum likelihood computation.



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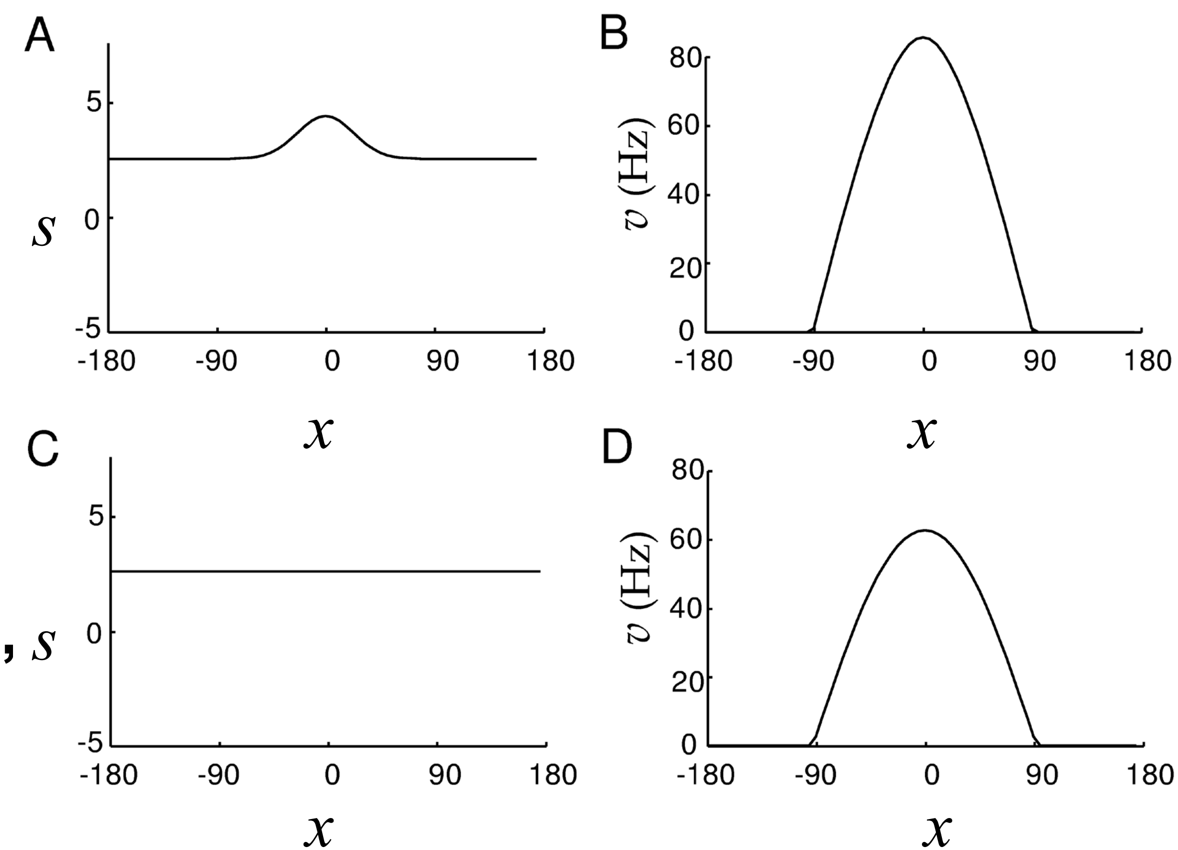
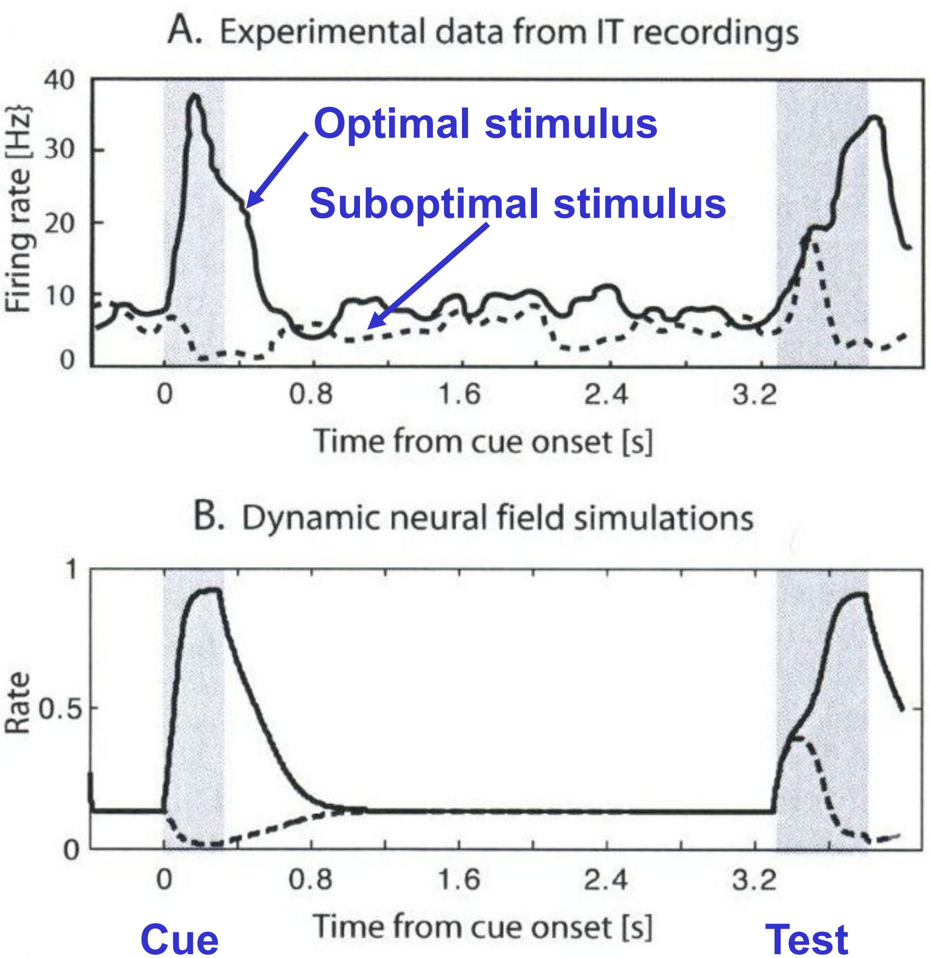
Example 1: Memory activity I

- Bistablility (of ϕ vs. a solution) can be used to model memory; once an activity peak is established it remains at the same position, even after the input peak vanishes.
- Example for a network with linear threshold function.
- Peak position marginally stable.
- New name: **'continuous/line-attractor network'**



Example 1: Memory activity II

- More serious example: model for the activity of IT neurons that are cued with an optimal or a sub-optimal stimulus, and tested with both stimuli (Chelazzi et al. 1993).
- Activation profiles qualitatively correctly reproduced by Amari-type model (Trappenberg, 2009).



Example 2: direction tuning I

- Like example for direction tuning before, but with linear threshold nonlinearity.
- Model:

Linear threshold function

$$\tau \frac{\partial u(\phi,t)}{\partial t} = -u(\phi,t) + \left[\int_{-\pi}^{\pi} m(\phi-\phi')u(\phi',t)\,\mathrm{d}\phi' + s(\phi,t) \right]_+$$

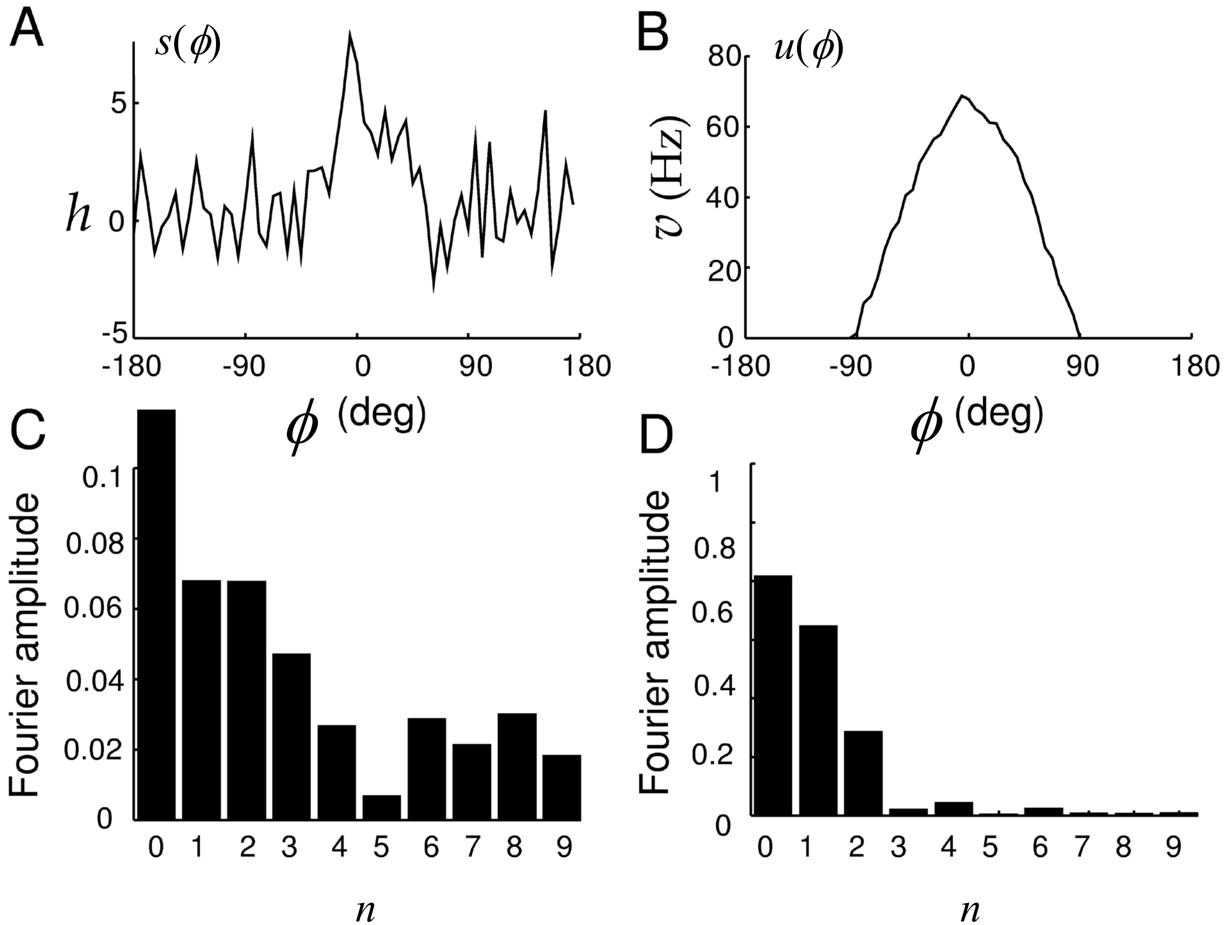
- Stable peak solution for periodic symmetric interaction kernel $m(\phi)$.
- Fourier analysis not meaningful because of non-linearity.

Example 2: direction tuning I

- Like example for direction tuning before, but with linear threshold nonlinearity.
- Model: $$\boxed{\tau \frac{\partial u(\phi,t)}{\partial t} = -u(\phi,t) + \underbrace{\left[\int_{-\pi}^{\pi} m(\phi-\phi')u(\phi',t)\,\mathrm{d}\phi' + s(\phi,t) \right]_+}_{\text{Linear threshold function}}}$$
- Stable peak solution for periodic symmetric interaction kernel $m(\phi)$.
- Fourier analysis not meaningful because of non-linearity.
- Stable localized activity peak for choice:
  $m(\phi) = (1.9 / \pi) \cos \phi$

Example 2: direction tuning II

- Plots show signal and amplitude of Fourier coefficients.
- Solution similar to linear field, but much smoother.
- Nonlinearity leads to narrowing of frequency spectrum; clipping of negative values by threshold.



Example 3: Model for simple cells I

- Related model for simple cells by Ben-Yishai, Bar-Or & Sompolinsky (1995): additional **global inhibition**.
- Consistent with anatomy, assumption that mainly recurrent connections cause orientation-selectivity.
- Model:

$$\boxed{\tau \frac{\partial u(\phi,t)}{\partial t} = -u(\phi,t) + \left[\int_{-\pi/2}^{\pi/2} m(\phi-\phi')\,u(\phi',t)\,\mathrm{d}\phi' + s(\phi,t) \right]_+}$$

with $m(\phi) = (-7.3 / \pi) + (11 / \pi) \cos 2\phi$ (interaction kernel)

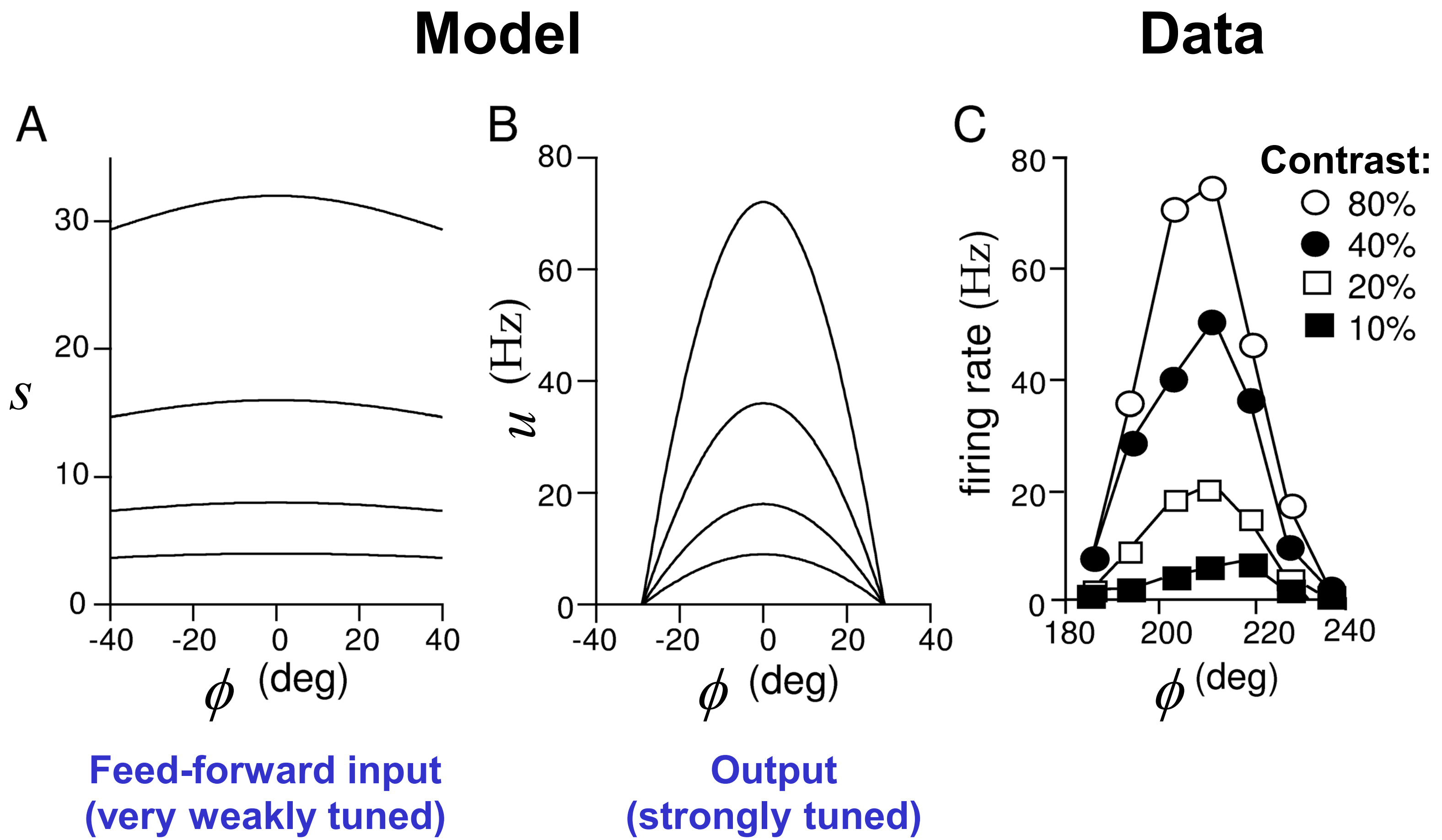
$s(\phi) = C \cdot 40\mathrm{Hz}\,(0.9 + 0.1 \cos 2\phi)$ (orientation-tuned LGN input

Stimulus contrast

Global inhibition

- Remark: orientation is π-periodic, explaining different integration interval.

Example 3: Model for simple cells II



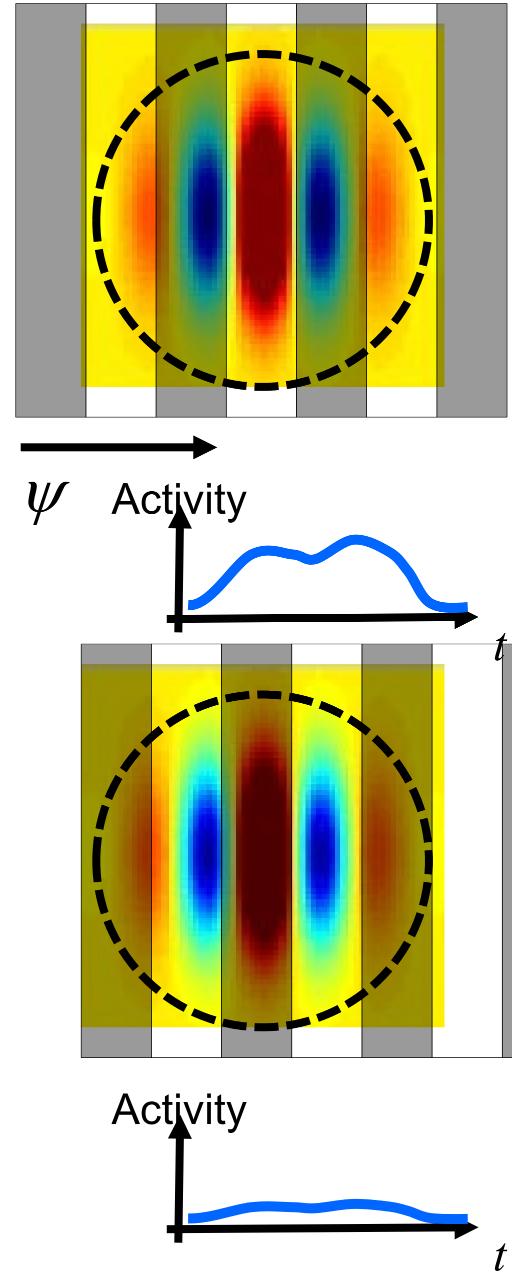
Example 4: Model for complex cells I

- Simple cells in primary visual cortex can be modeled by (Gabor) filters; their response is strongly dependent on the spatial phase ψ of input gratings (see figure).
- Opposed to simple cells, responses of **complex cells** are largely independent of the spatial phase ψ (‘phase invariance’!).
- Phase independence can be achieved by recurrent neural field with constant interaction kernel (Chance et al. 1999):

$$\boxed{\tau \frac{\partial u(\psi,t)}{\partial t} = -u(\psi,t) + \left[\frac{m}{2\pi} \int_{-\pi/2}^{\pi/2} u(\psi',t)\,\mathrm{d}\psi' + s(\psi,t) \right]_+}$$

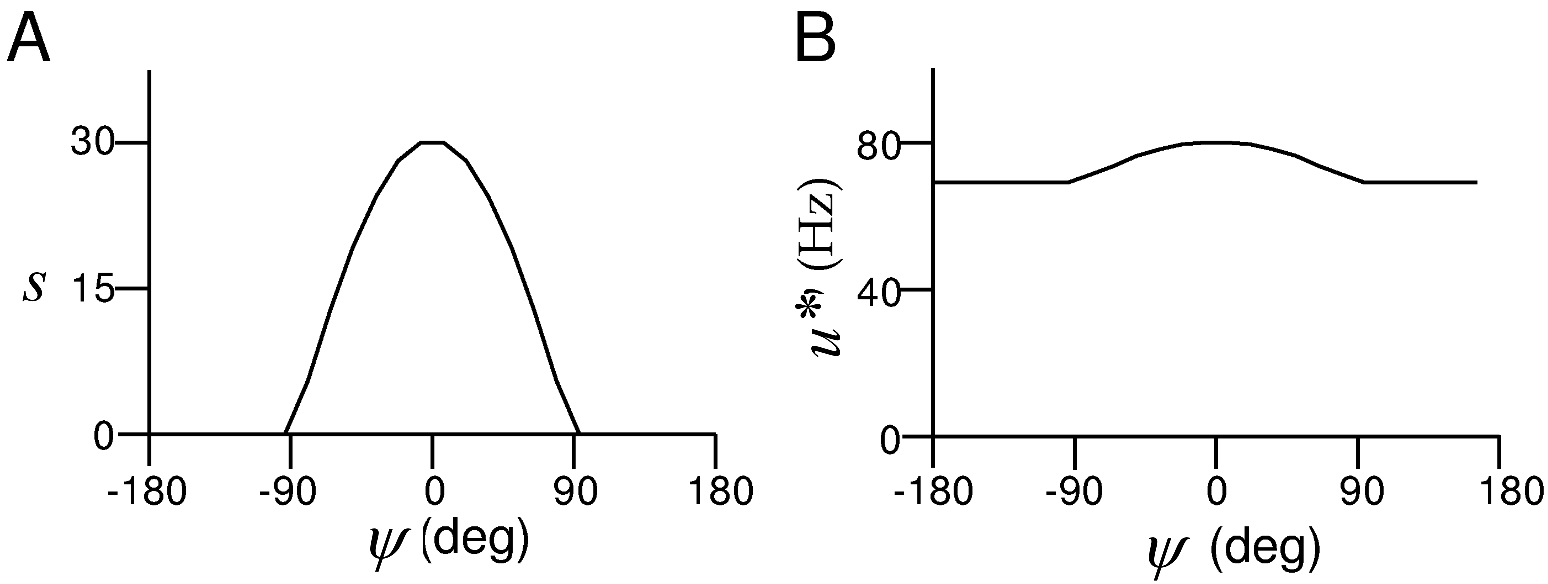
Phase-dependent input from simple cells

Gabor filter with b/w grating



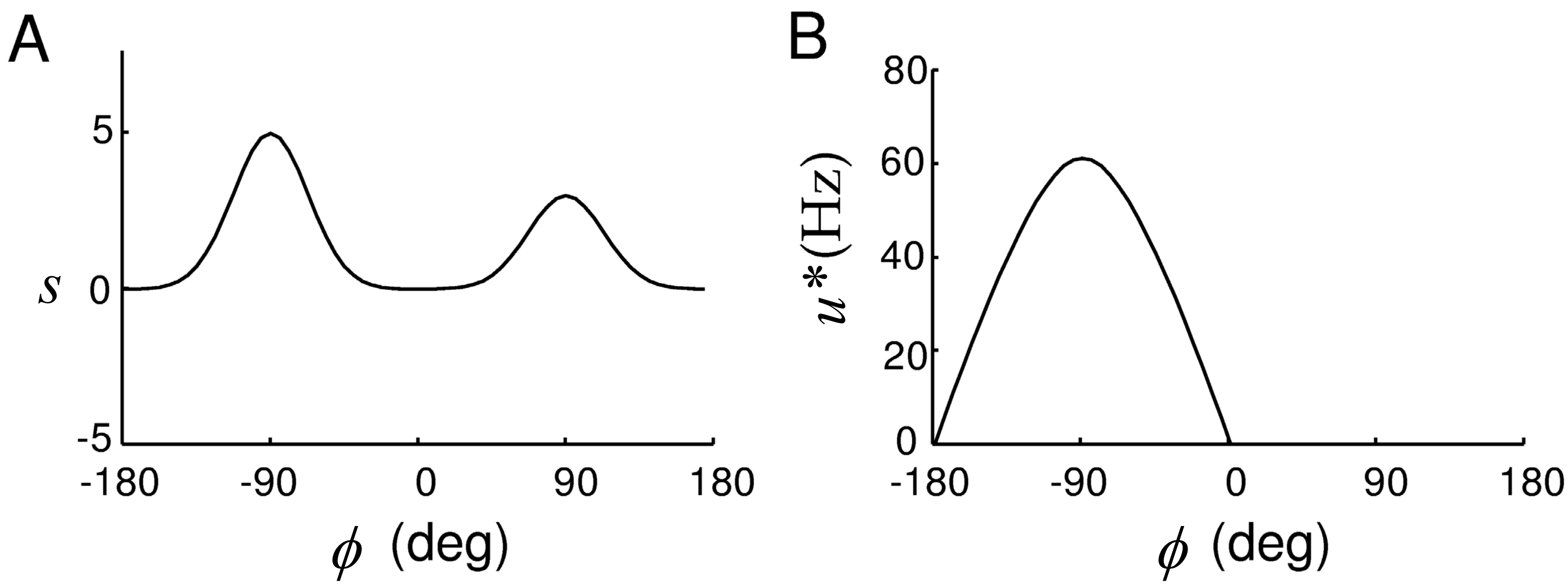
Example 4: Model for complex cells II

- For $m = 0$ follows $u^*(\psi) = u(\psi, \infty) = s(\psi)$ for nonnegative s.
- For m close to one we obtain an amplification of an eigenfunction that is close to the constant function. (Exact computation easy if nonlinearity is dropped. $\Rightarrow$ Fourier transform!)
- Simulation result with $m = 0.95$:



Example 5: Winner-takes-all input selection / 'decision'

- For multi-peaked input the network (for appropriate choice of the kernel and sufficient inhibition) tends to select a single input peak; with constant initial activation the selected peak corresponds to the highest input peak.



Example 6: Gain modulation I

- A nonlinear dynamic neural field of the previous form with Mexican hat kernel and appropriate choice of the parameters can realize multiplicative gain control (Salinas & Abbott, 1996).
- Additive shifts in the input result in approximately multiplicative changes of the output signal.
- Network dynamics (all constants positive):

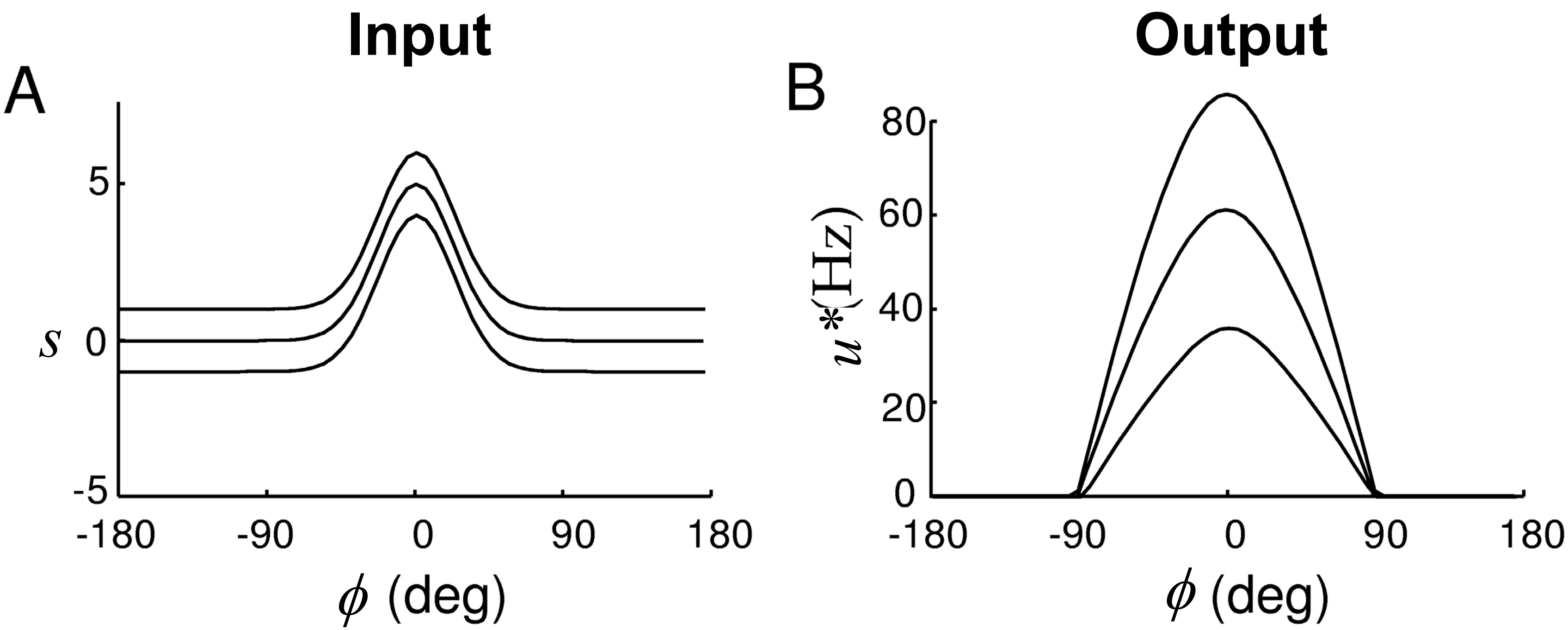
$$\boxed{\tau \frac{\partial u(\phi,t)}{\partial t} = -u(\phi,t) + \left[\int_{-\pi}^{\pi} m(\phi-\phi')u(\phi',t)\,\mathrm{d}\phi' + s(\phi,t) \right]_+}$$ where

$m(\phi) = A \exp(-a\phi^2) - B \exp(-b\phi^2)$ (Mexican hat)
$s(\phi) = C \cdot \exp(-c\phi^2) + g$ (Input with peak and const. part)

- Output: $\boxed{\max_{\phi} u(\phi) \sim C \cdot g}$

Example 6: Gain modulation II

- Simulation example:



Things to remember

- Spatial continuum limit leading to neural fields $\rightarrow$ 2)
- Computation of solutions and stability for step threshold $\rightarrow$ 1, 3)
- A variety of computational functions can be accomplished with excitatory-inhibitory fields $\rightarrow$ 2,4)

Literature (for this lecture)

1) Amari, S. (1977) Dynamic of pattern formation in lateral-inhibition type neural fields *Biological Cybernetics,* 27(2), 77-87

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

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

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

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