Effects of spatial connectivity and delays on spatio-temporal dynamics of cortical networks

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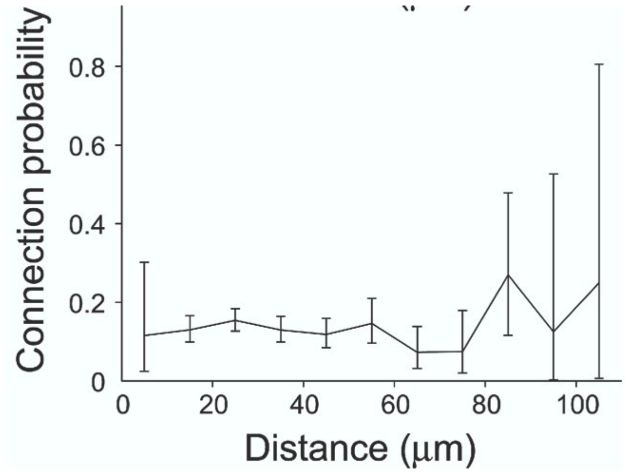
Alex Roxin, Nicolas Brunel, David Hansel

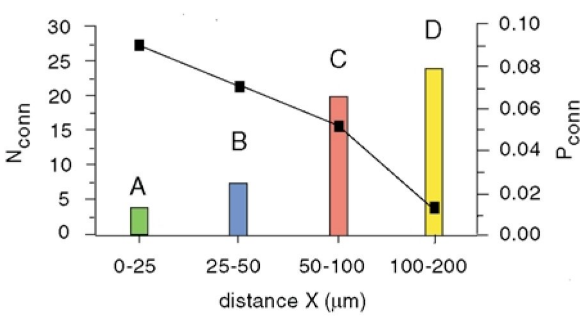
Spatial profile of connectivity in cortex

Connection probability between cells decays with distance

Paired recordings

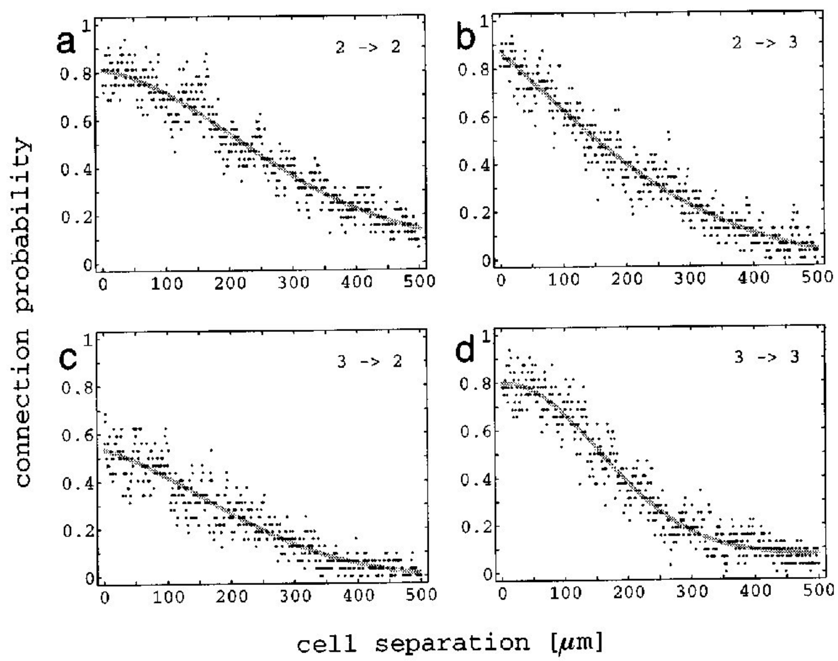


Song et al 2005 (L5)



Holmgen et al 2005 (L2/3)

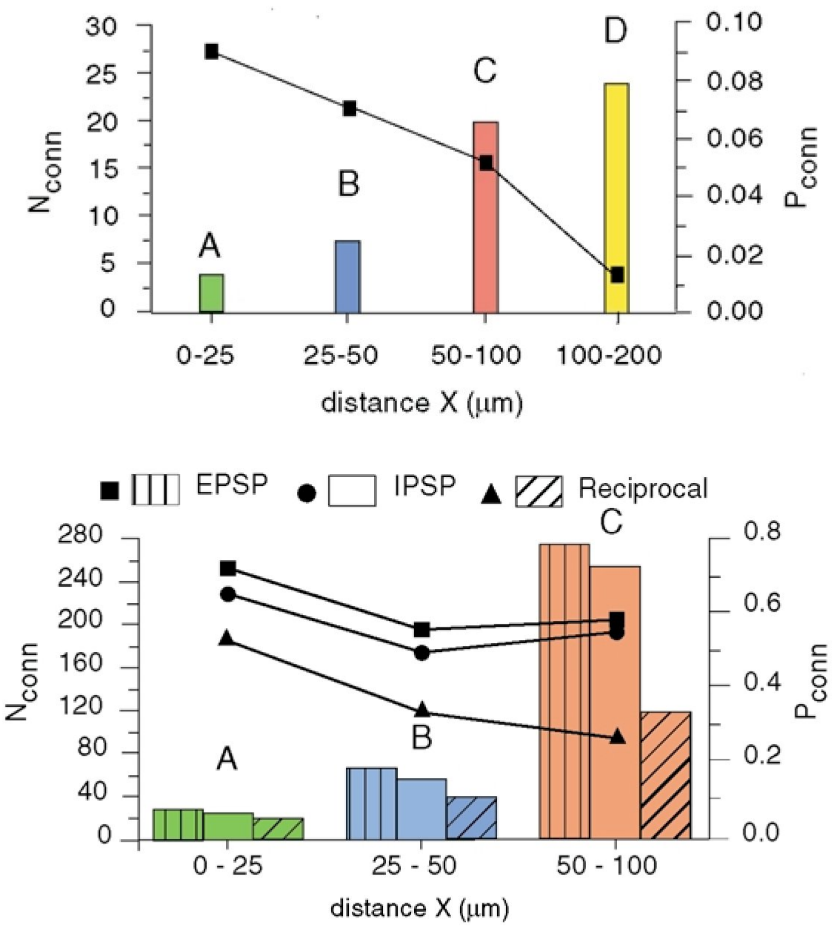
Reconstructed cells (L2/3)



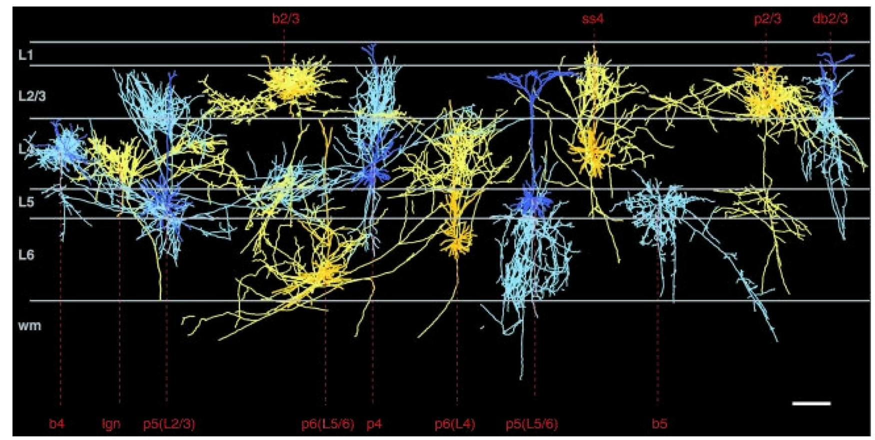
Hellwig 2000

Relative spatial scales of excitation and inhibition

Paired recordings (L2/3)



Reconstructed cells



Binzegger et al 2004

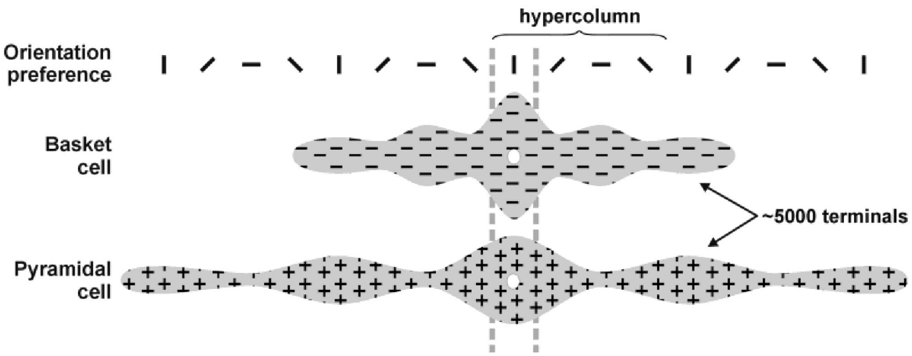
Holmgren et al 2003

Is excitation or inhibition more widespread? UNCLEAR!

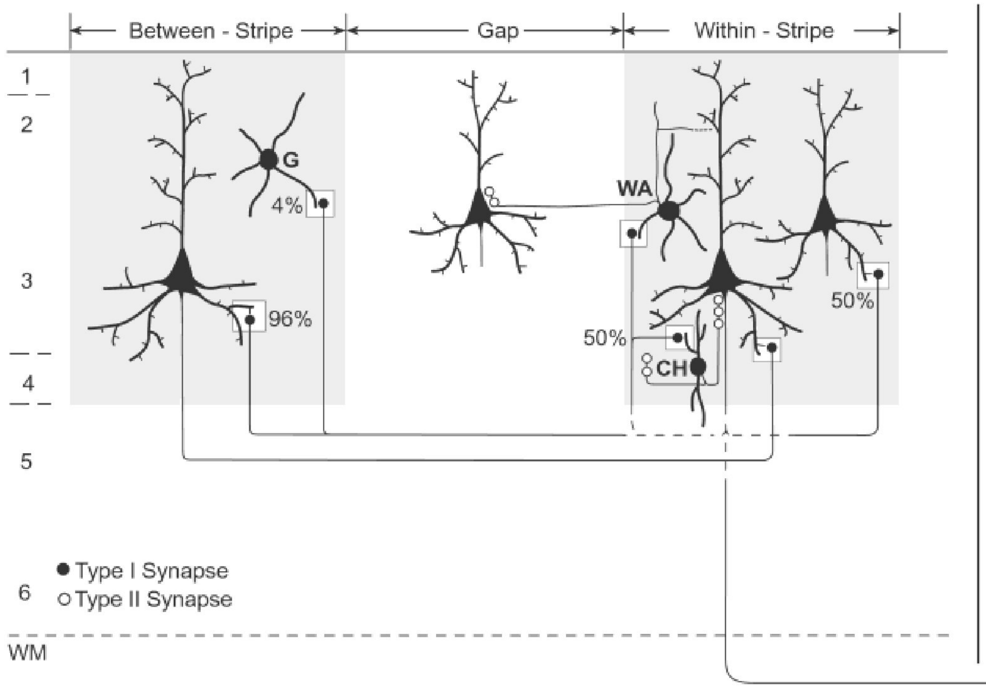
Longer range connectivity - prefrontal cortex

Prefrontal cortex

Visual cortex

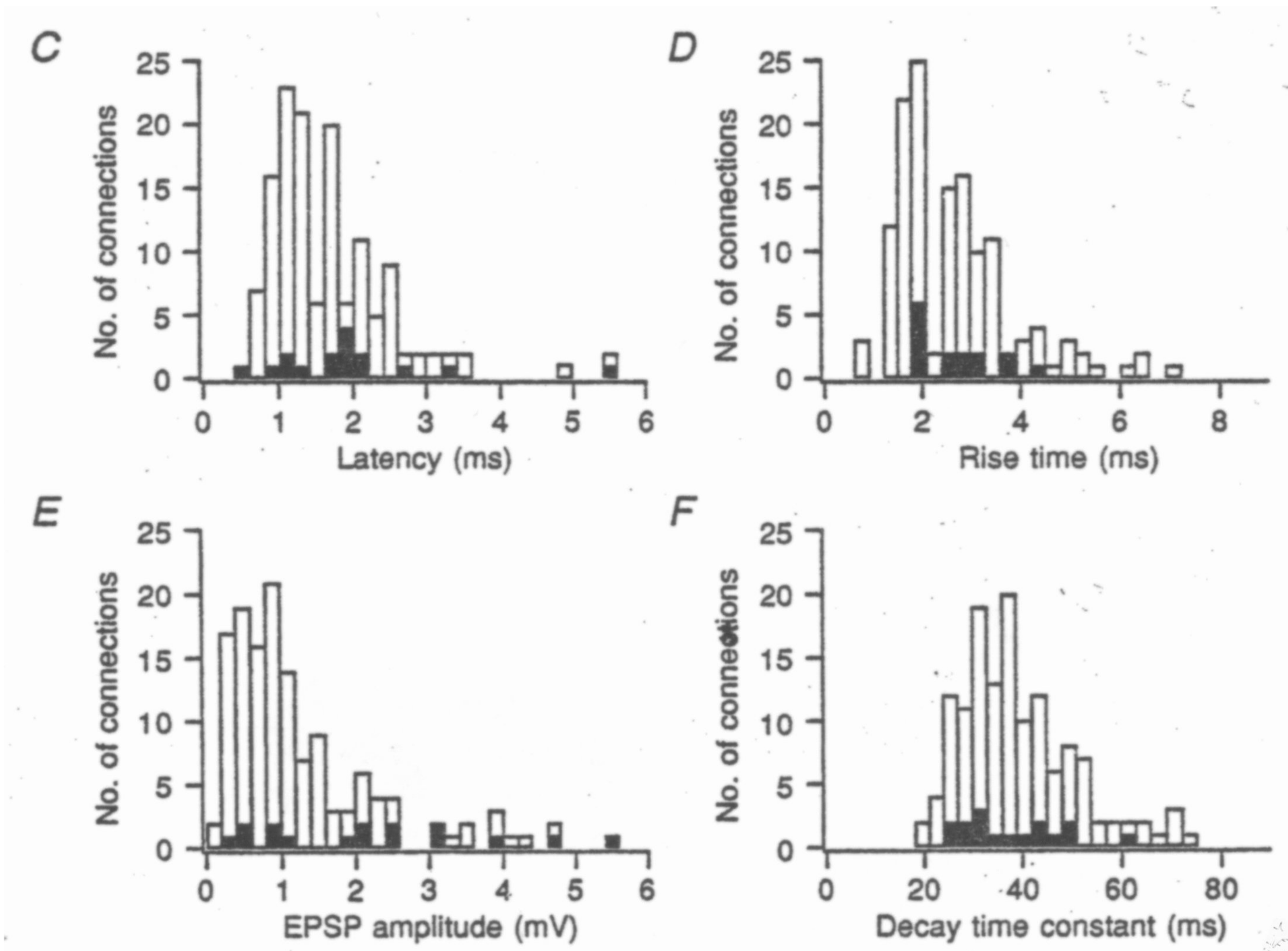


Buzas et al 2001



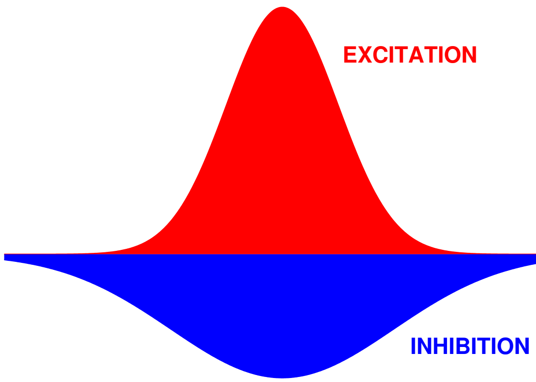
Gonzales-Burgos et al 2000, Melchitzky et al 2001

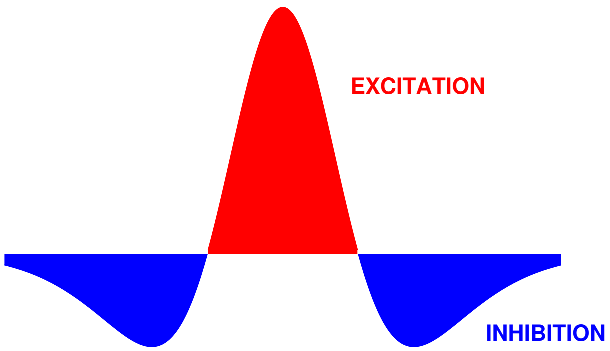
Temporal delays in cortex



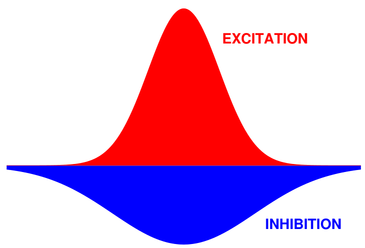
Markram et al 1997

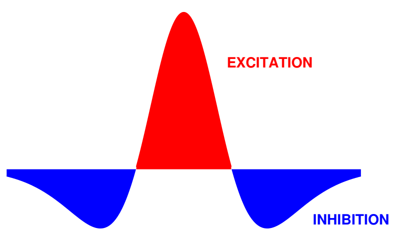
Models: mexican-hat type connectivity

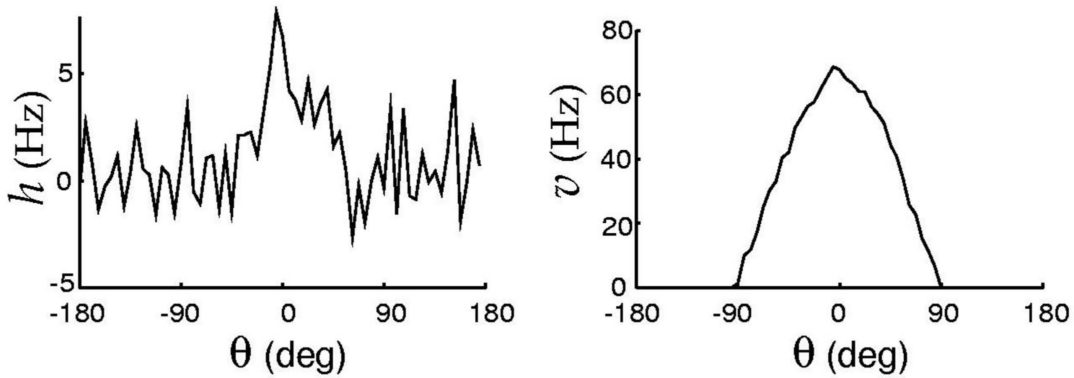


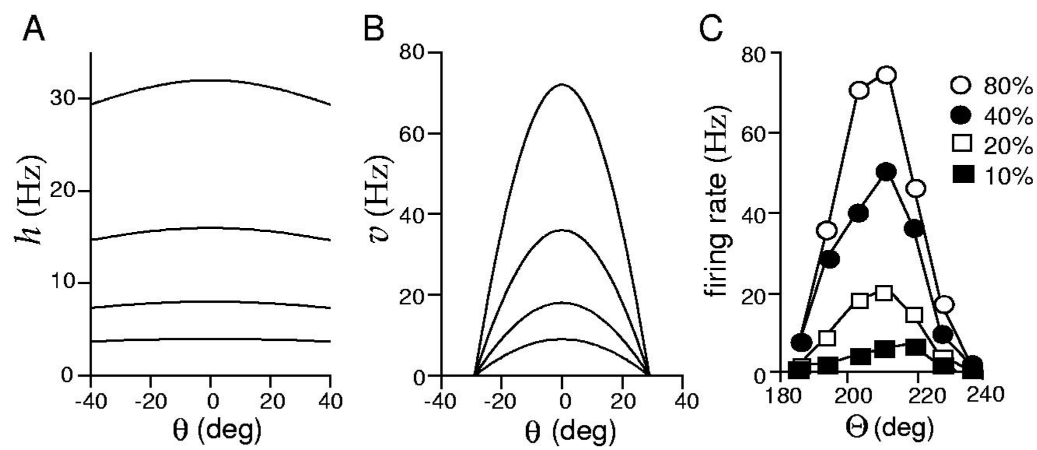


Amplification of selectivity (visual cortex)



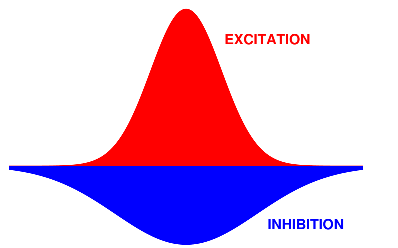


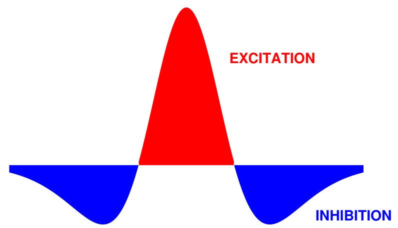


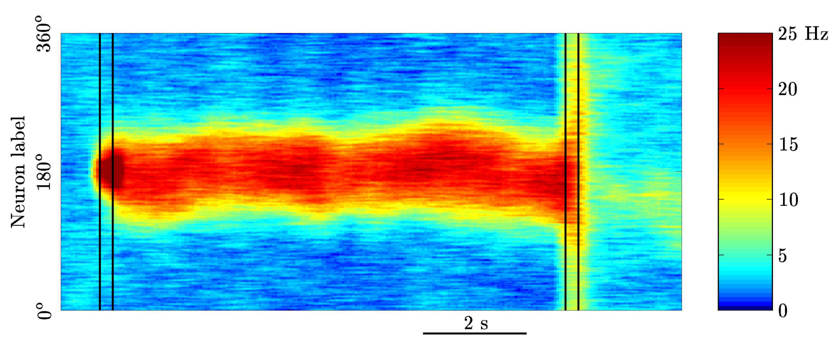


Somers et al 1995; Ben Yishai et al 1995; Hansel and Sompolinsky 1998

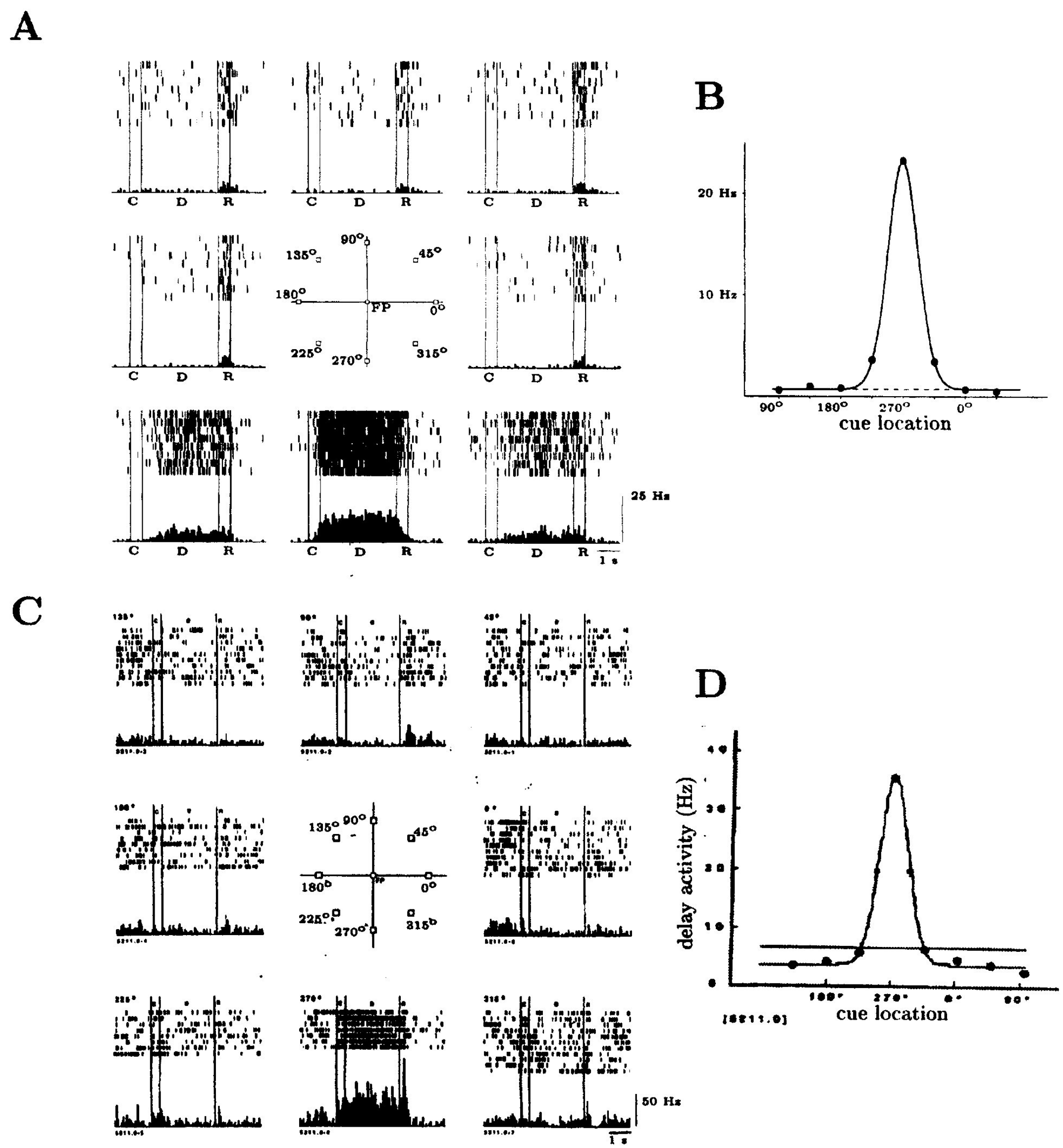
Multistability and spatial short-term memory (PFC)







Compte, Brunel, Wang, Goldman-Rakic 2000



Is connectivity in cortex mexican-hat type?

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No clear answer yet

Rate model

$$\tau \dot{m}(x,t) = -m(x,t) + \Phi\left(I(x,t) + \int dy J(|x-y|)m(y,t-D)\right)$$

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- $\tau = 1$: time constant of firing rate dynamics;
- $m(x,t)$: firing rate of neurons at location x at time t;
- $\Phi(.)$: static transfer function (f-I curve);
- $J(|x-y|)$: weight of synaptic connections between neurons at locations x and y;
- D: transmission delay

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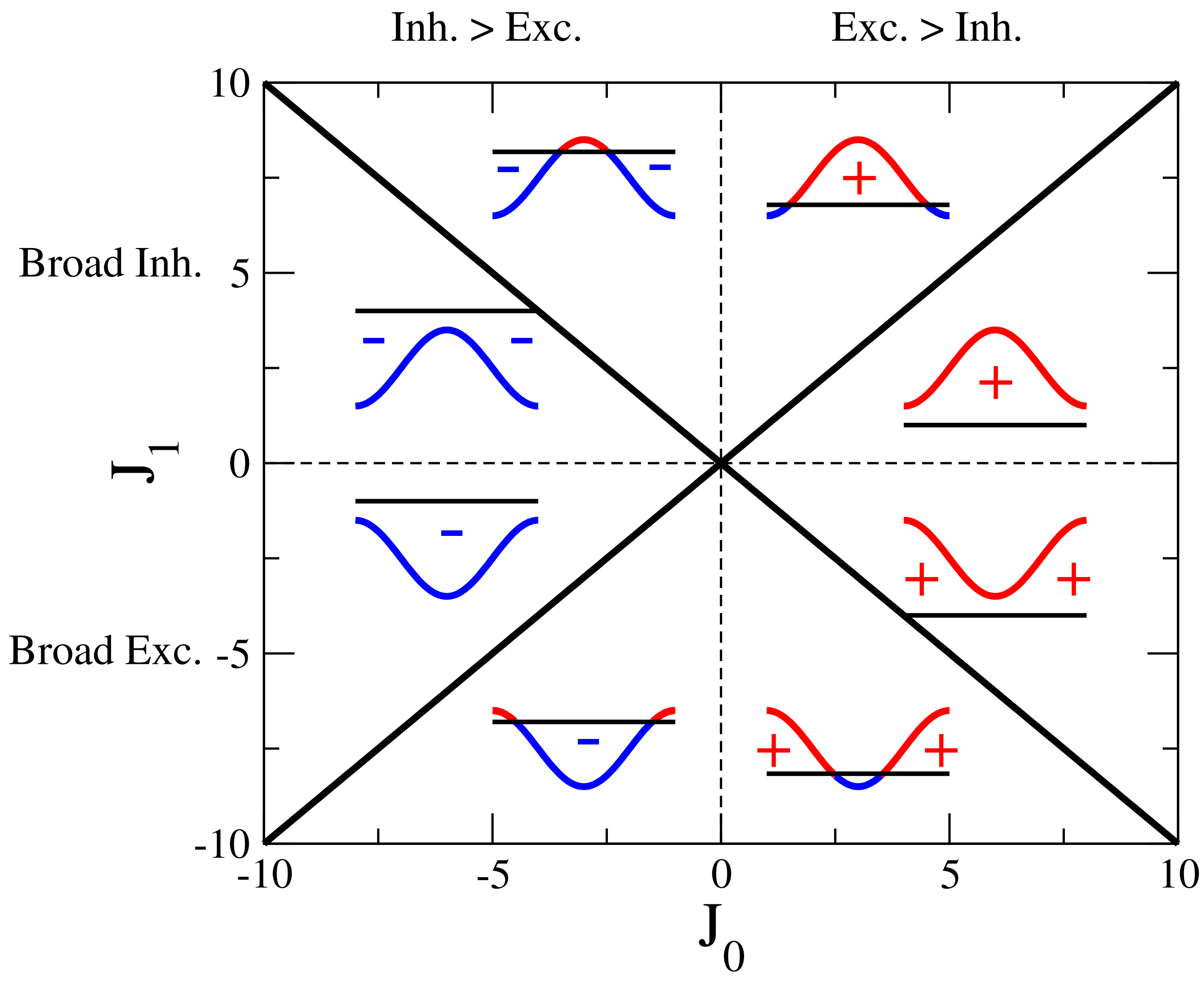
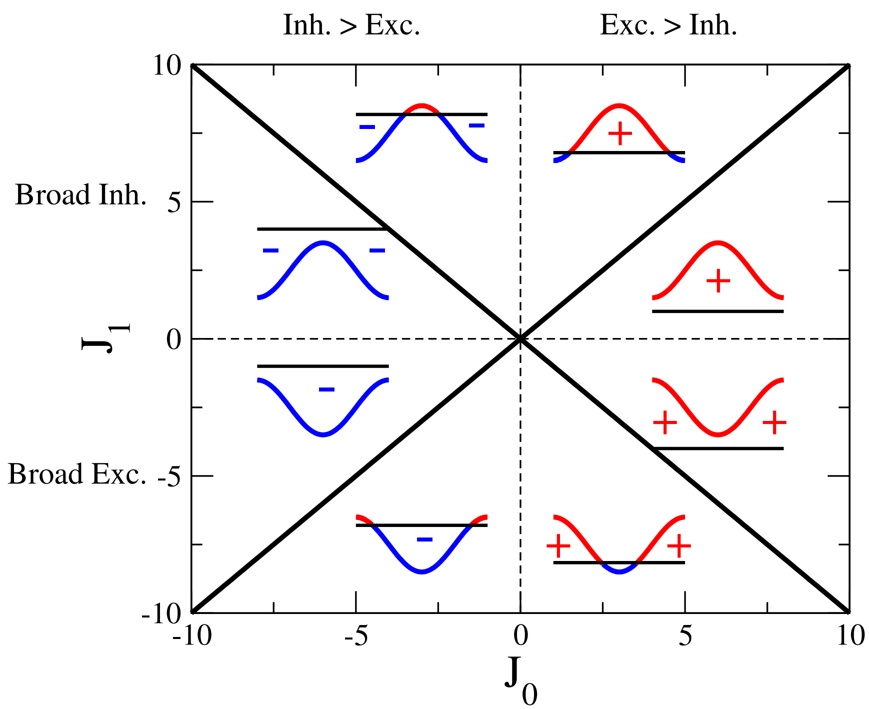
Simplifying assumptions

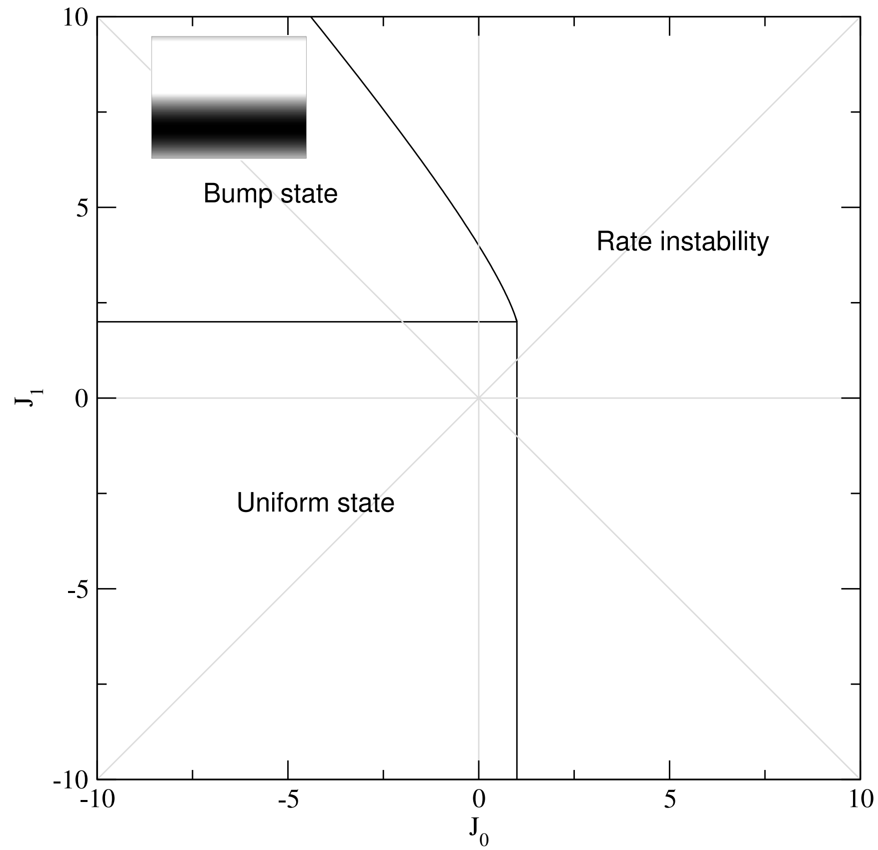
- 1 D space with ring topology: $x \in [-\pi, \pi]$
- Threshold-linear transfer function, $\Phi(I) = I$ if $I > 0$ and $\Phi(I) = 0$ otherwise
- Synaptic footprint: $J(|x-y|) = J_0 + J_1 \cos(x-y)$

The synaptic ‘footprint’



Phase diagram of the rate model for $D = 0$





Ben Yishai et al 1995, Hansel and Sompolinsky 1998

Analysis of the model

Thanks to the simplified transfer function and footprint, the dynamics can be written in terms of three order parameters m_0, m_1 and ψ defined by

$$
\begin{aligned}
m_0(t) &= \int \frac{dx}{2\pi} m(x,t) dx \\
m_1(t) &= \int \frac{dx}{2\pi} m(x,t) \cos(x - \psi(t)) dx \\
0 &= \int \frac{dx}{2\pi} m(x,t) \sin(x - \psi(t)) dx
\end{aligned}
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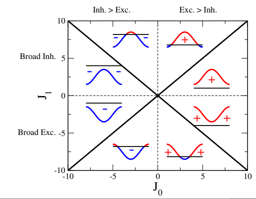
\end{aligned}
$$

These parameters evolve in time according to

$$
\begin{aligned}
\dot{m_0}(t) &= -m_0(t) + \int \frac{dx}{2\pi} I(x) \\
\dot{m_1}(t) &= -m_1(t) + \int \frac{dx}{2\pi} \cos(x - \psi(t)) I(x) \\
\dot{\psi}(t) m_1(t) &= \int \frac{dx}{2\pi} \sin(x - \psi(t)) I(x) \\
I(x) &= \left[I^{ext} + J_0 m_0(t-D) + J_1 \cos(x - \psi(t-D)) m_1(t-D) \right]_+
\end{aligned}
$$

The stationary uniform state and its stability for $D > 0$

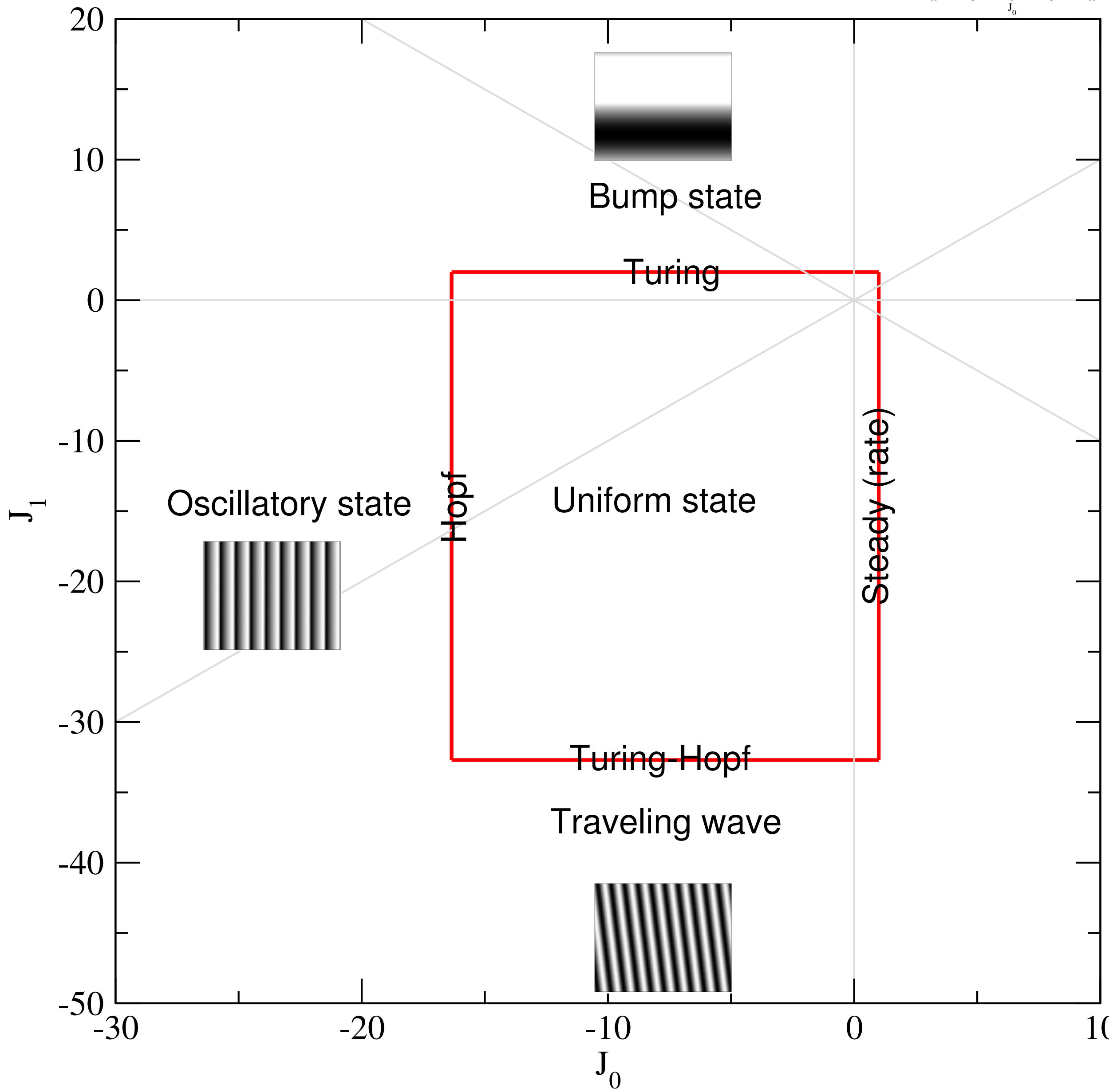


Stationary uniform state:

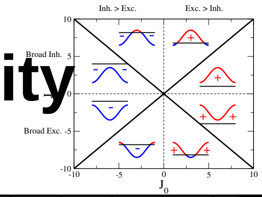
$$m_0(t) = M_0, \quad m_1 = \psi = 0.$$

Stability analysis yields four types of instabilities:

- Rate instability: $J_0 = 1$
- Turing instability: $J_1 = 2$
- Hopf instability:
  $\omega = -\tan(\omega D)$
  $J_0 = 1/\cos(\omega D)$
- Turing-Hopf instability:
  $\omega = -\tan(\omega D)$
  $J_1 = 2/\cos(\omega D)$



The mexican-hat region: stationary bump and its stability



Stationary bump:

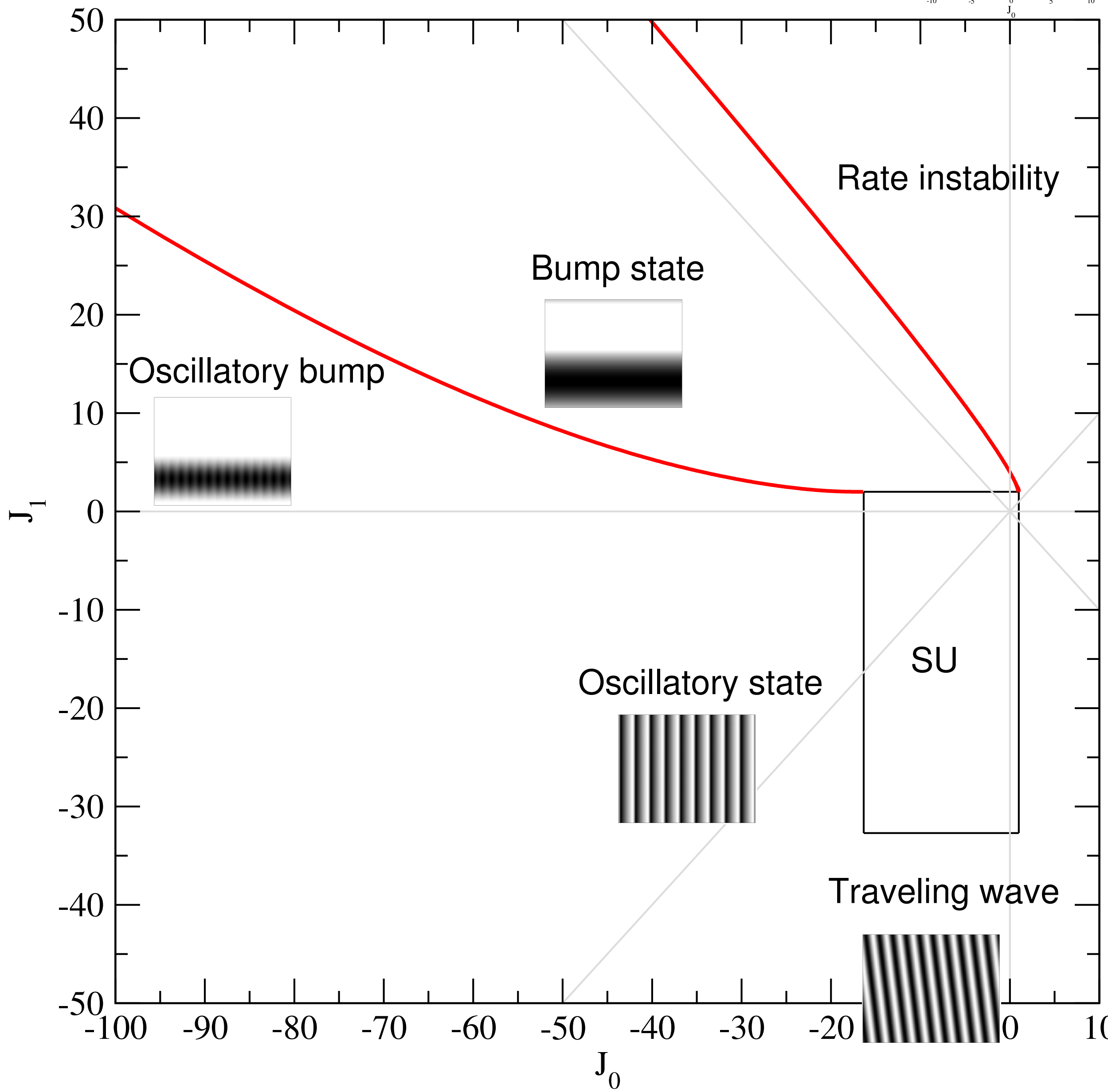
$$
\begin{aligned}
m_0(t) &= M_0, \\
m_1(t) &= M_1, \\
\psi &= 0
\end{aligned}
$$

The activity is non-zero in an interval $[x_0 - \theta, x_0 + \theta]$ where x_0 is arbitrary and θ is related to J_1 by

$$J_1 = 4\pi/(2\theta - \sin(2\theta)).$$

Stability analysis:

- Rate instability
- Hopf bifurcation



The strong inhibition region: oscillations and their stability

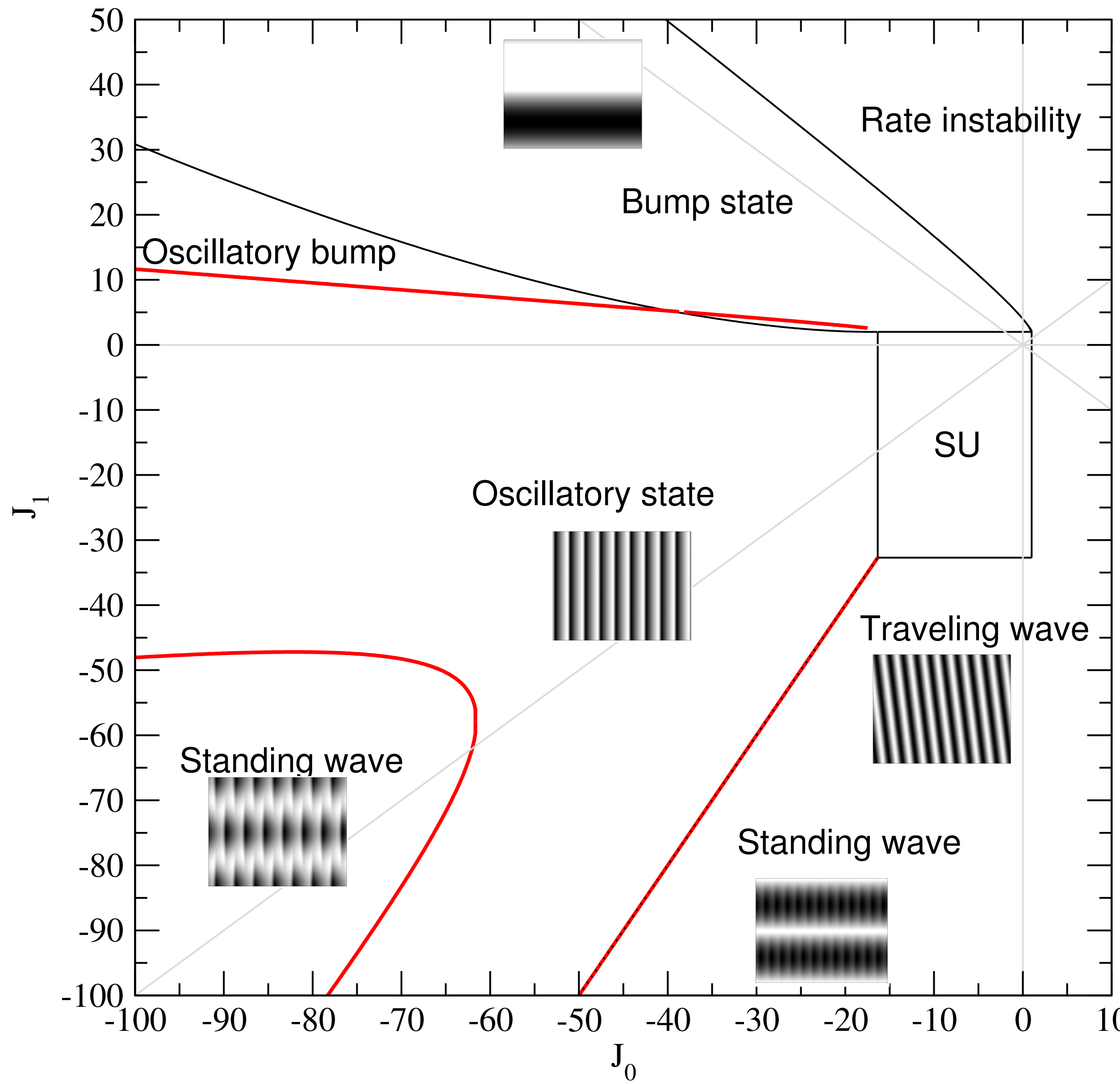
Limit cycle can be computed explicitly.

Stability analysis $\Rightarrow$ Floquet multipliers β_0 and β_1

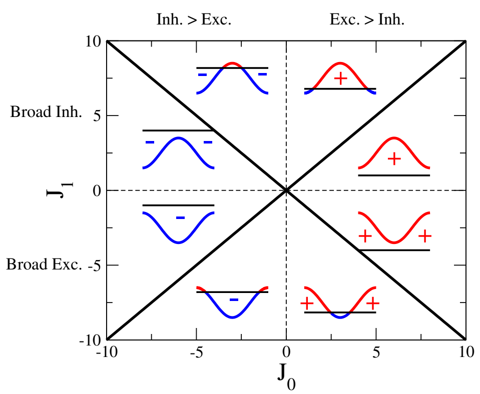
$$\delta m_0(T) = \delta m_0(0)\beta_0$$
$$\delta m_1(T) = \delta m_1(0)\beta_1$$

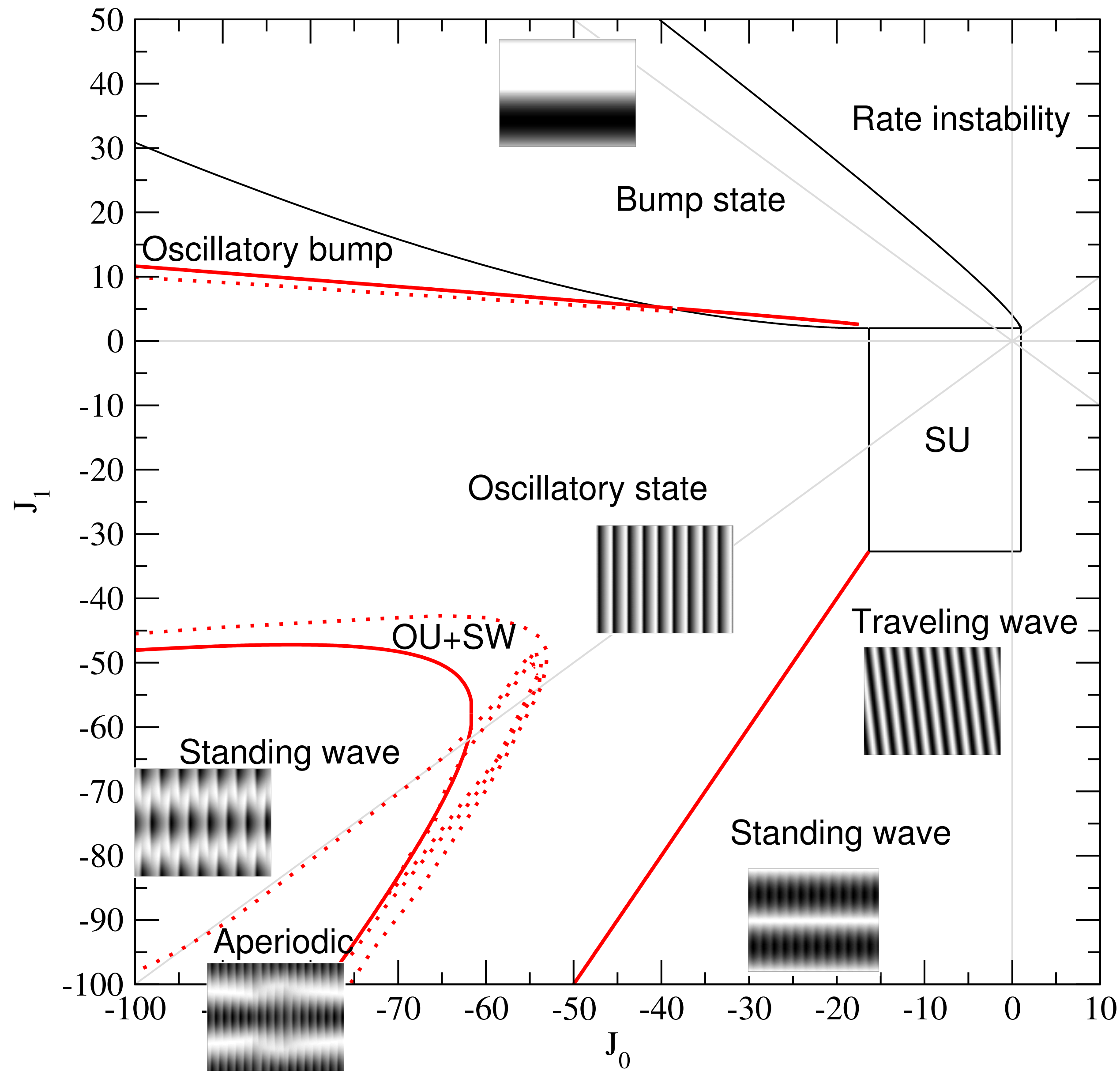
Two types of instabilities, both leading to spatially modulated states

- $\beta_1 = 1$
- $\beta_1 = -1$ (period-doubling bifurcation)

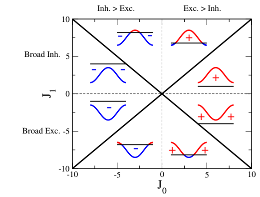


The strong inhibition region 2: nature of bifurcations





The reverse mexican-hat region: stability of TWs



Traveling waves:

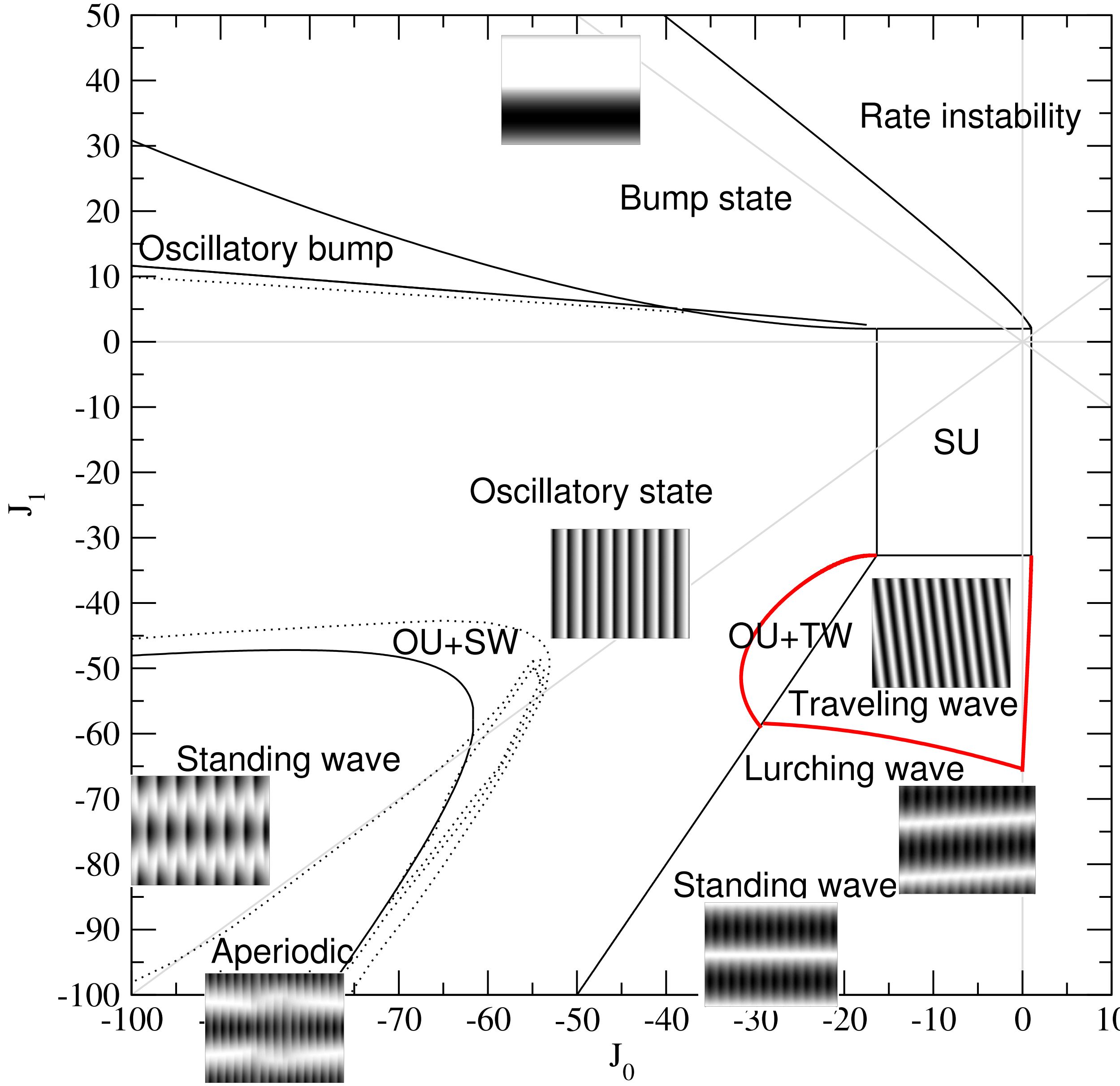
$$\begin{aligned} m_0 &= M_0, \\ m_1 &= M_1, \\ \psi(t) &= v \end{aligned}$$

Speed of the wave:

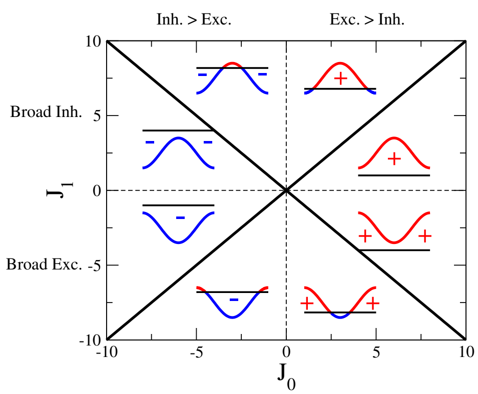
$$v = -\tan(vD)$$

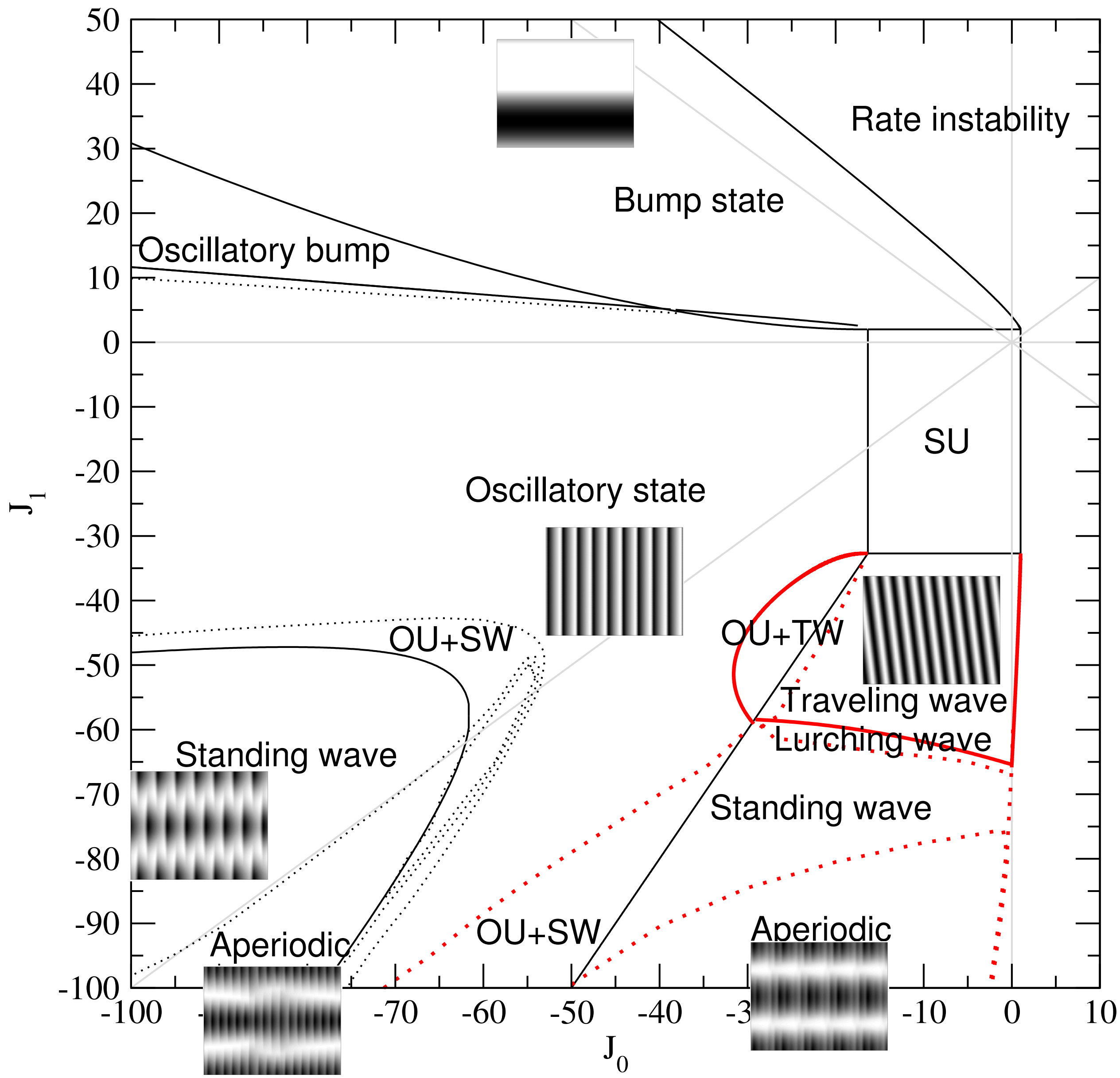
Stability analysis:

- rate instability
- Hopf bifurcations

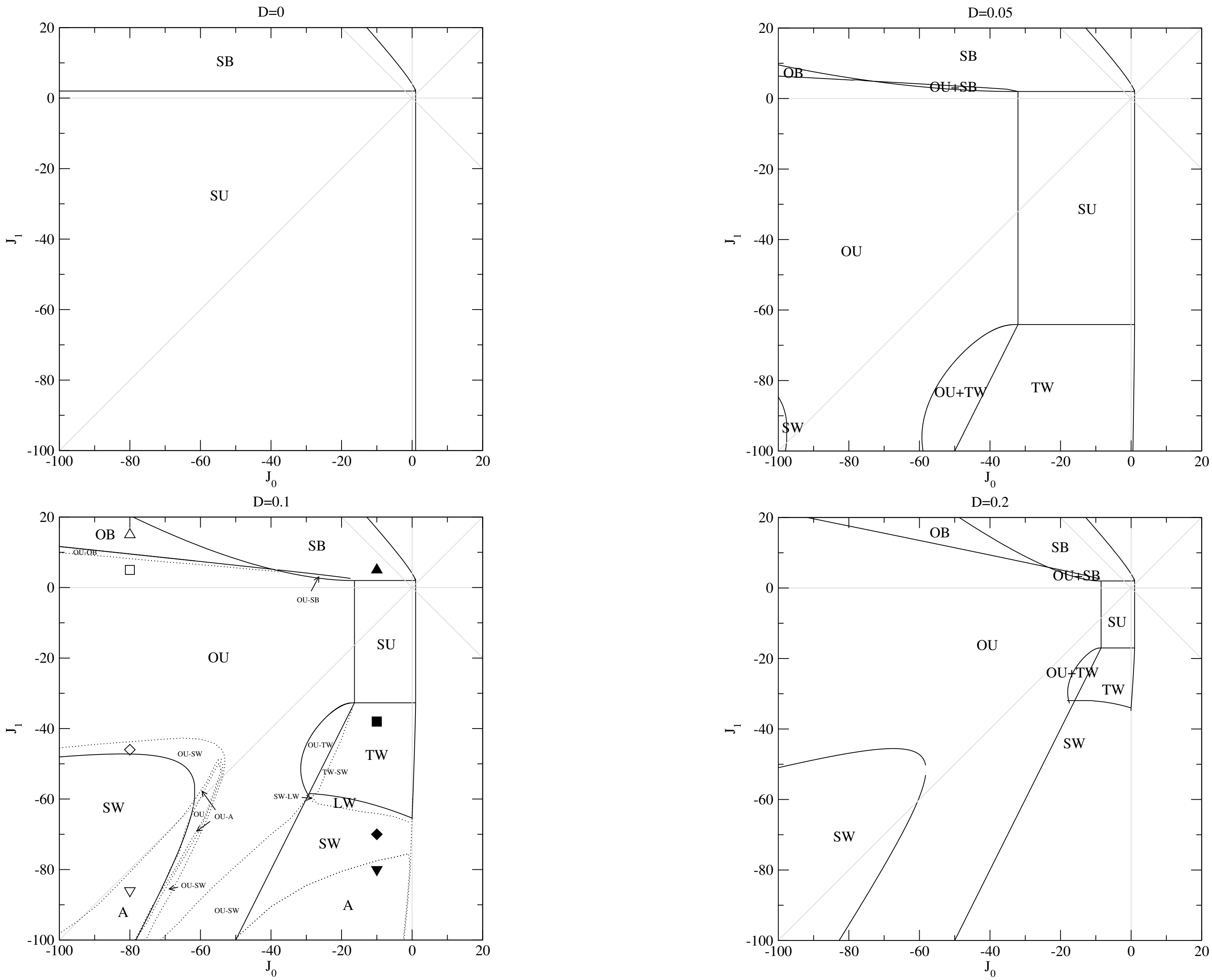


The reverse mexican-hat region II

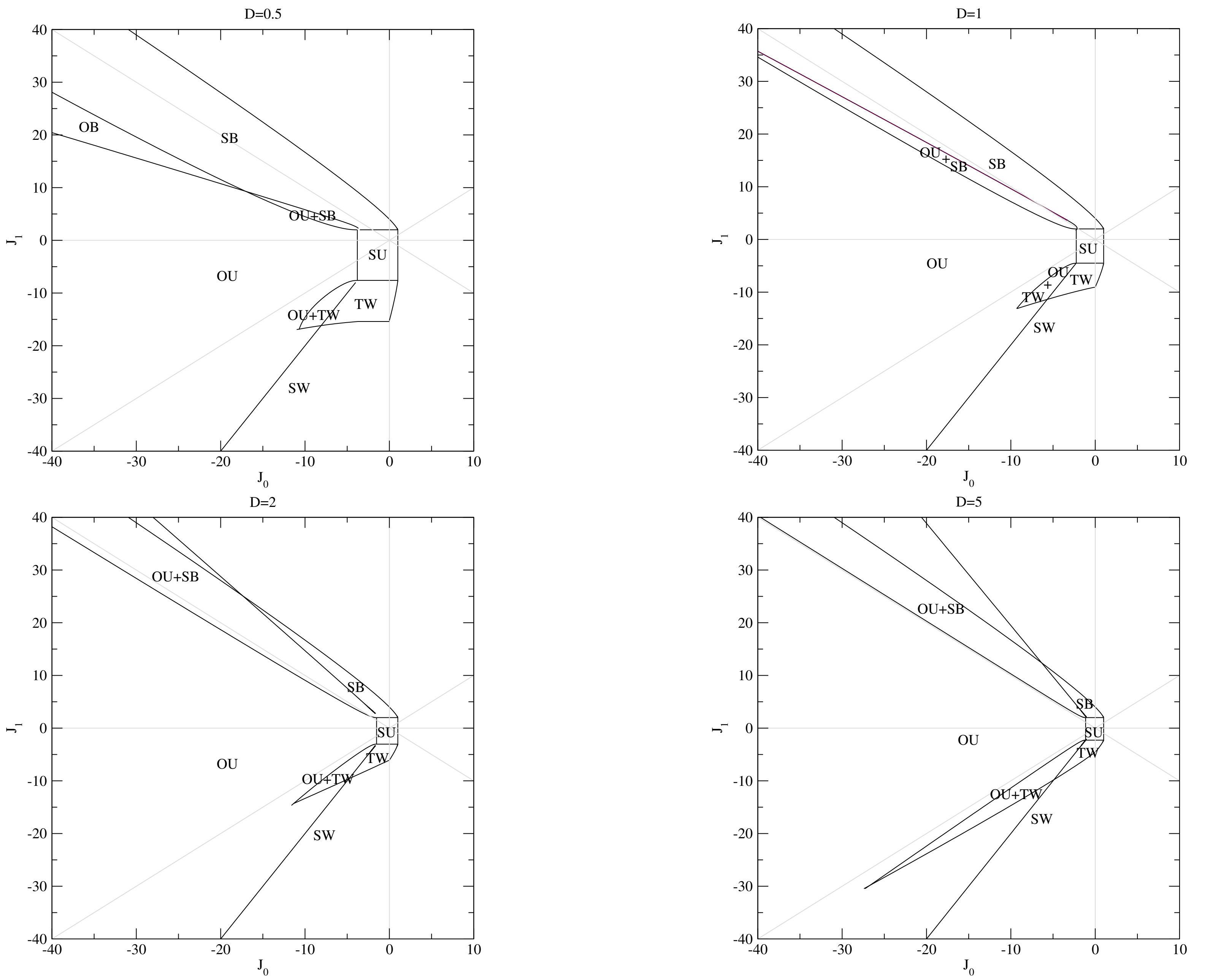




Phase diagram vs D



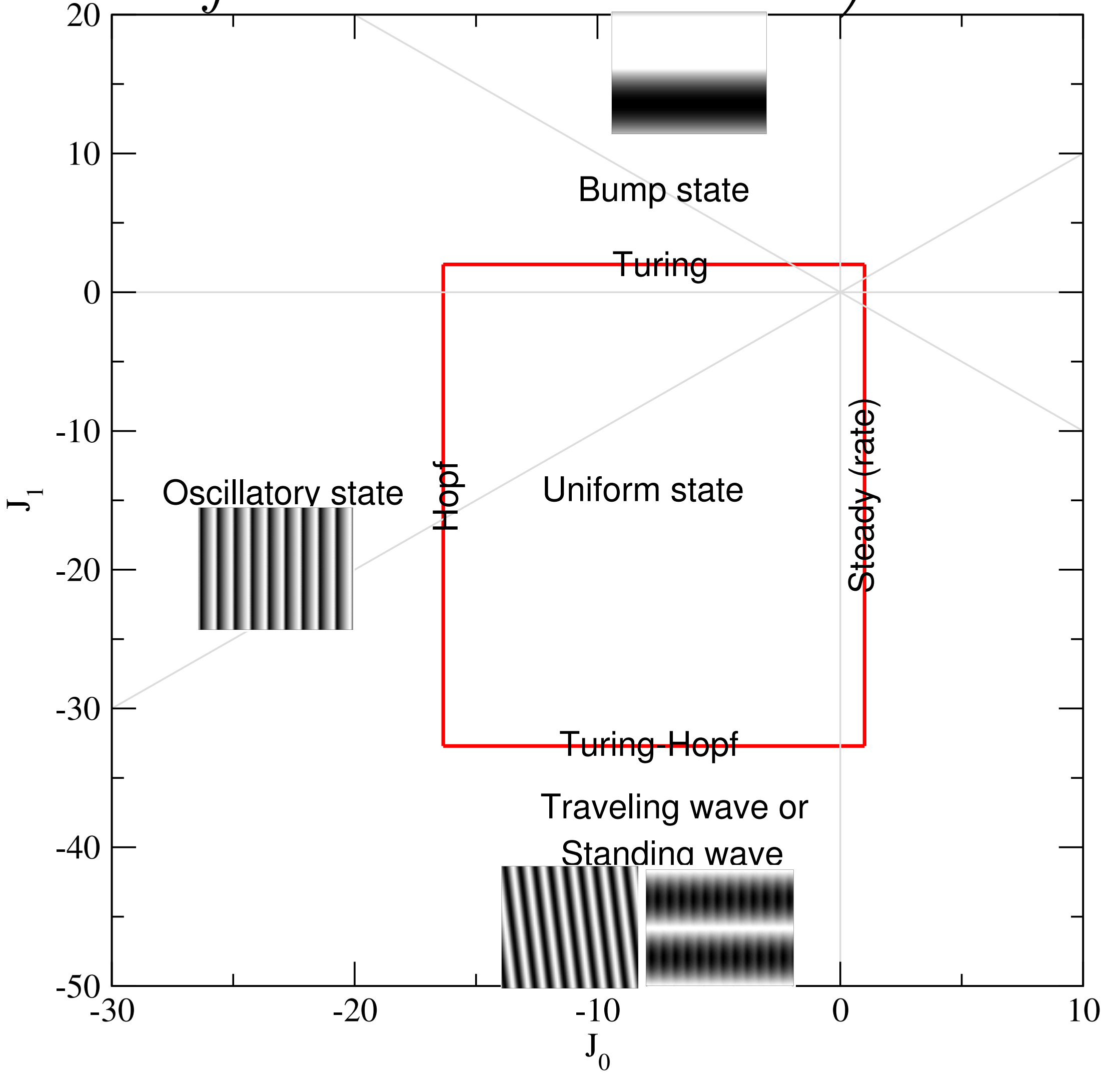
Phase diagram vs D, continued



Arbitrary f-I curves and spatial footprints

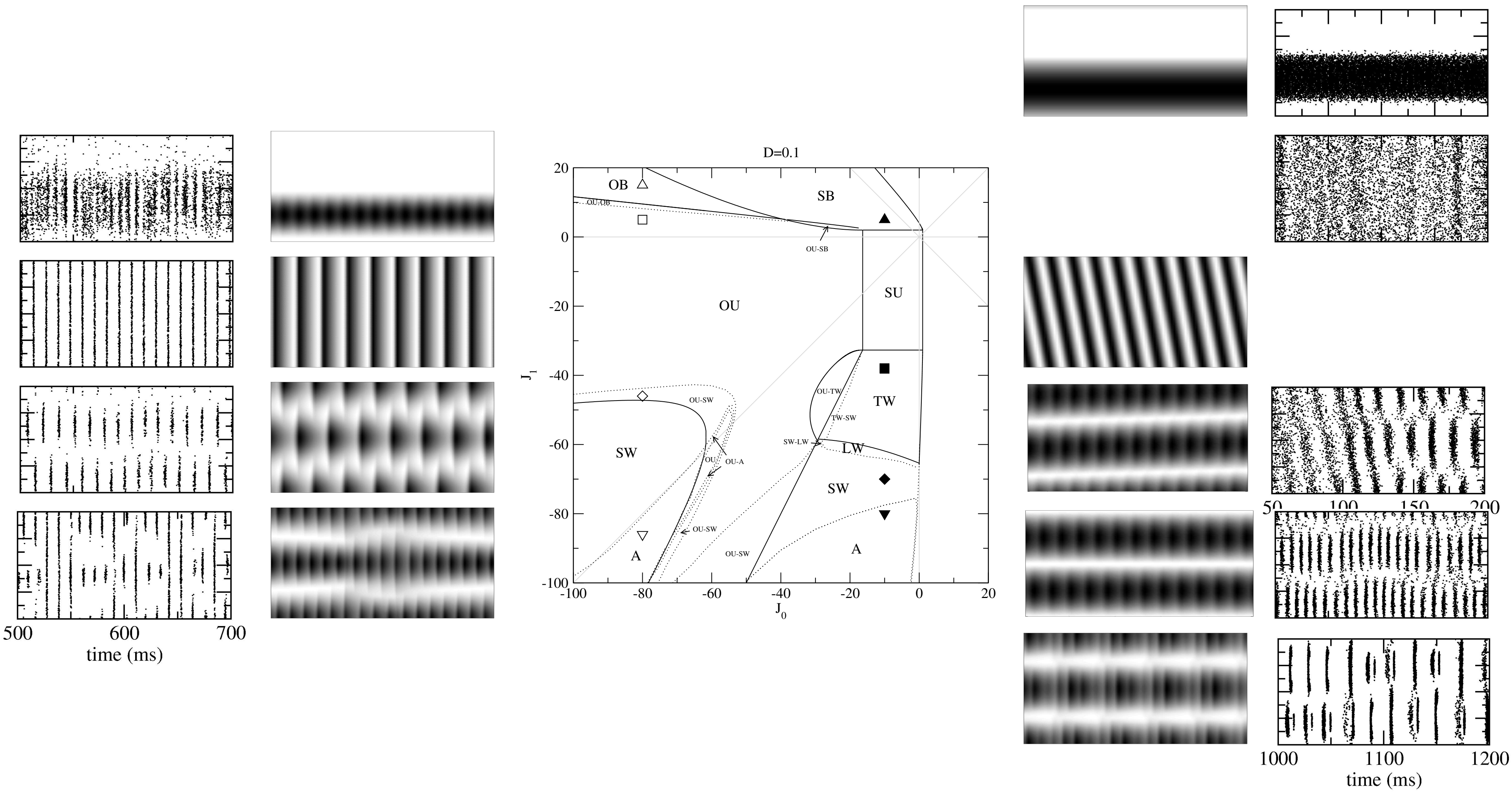
$$\tau \dot{m}(x,t) = -m(x,t) + \Phi\left(I(x,t) + \int dy J(|x-y|) m(y, t-D)\right)$$

1. Steady (rate) instability: trans-critical bifurcation
2. Turing: can be supercritical or subcritical depending on spatial footprint and f-I curve.
3. Hopf: for small D and quadratic transfer function, supercritical bifurcation
4. Turing-Hopf: for $J_0 < 0$, quadratic transfer function and small D, leads to standing waves in a supercritical bifurcation.

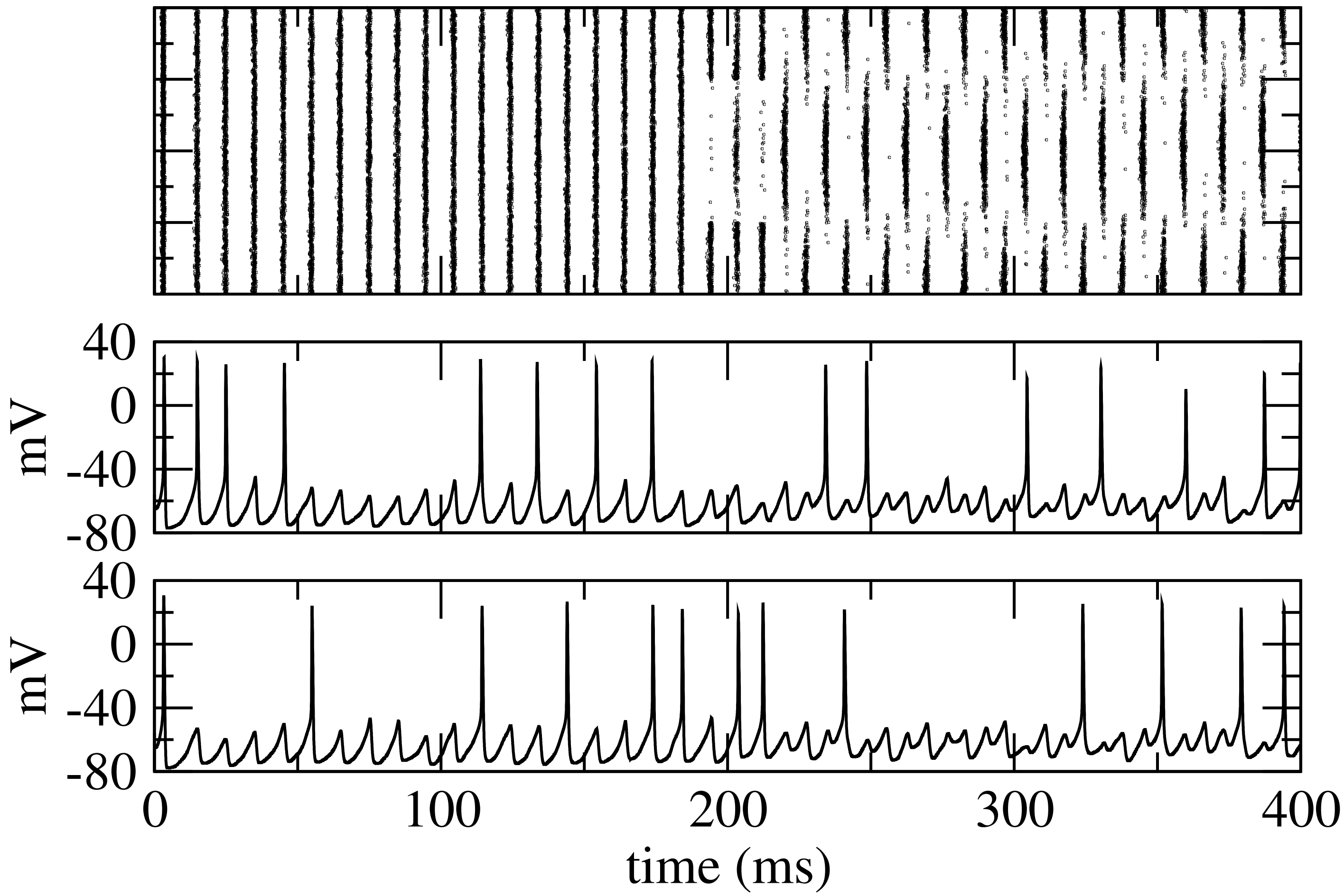


Networks of spiking neurons

Two populations of randomly connected excitatory and inhibitory Hodgkin-Huxley-type conductance-based neurons with noisy external inputs



Spatial working memory in a network of inhibitory spiking neurons



Conclusions I

Networks whose connectivity is not of the mexican hat type can maintain a spatial variable in short-term memory

Needs strong, spatially modulated, inhibition with temporal delays!

Oscillations are necessary for these states to emerge.

$\Rightarrow$ A computational role for oscillations?

Roxin, Brunel, Hansel, to appear in PRL (2005)