Fast oscillations in networks of noisy neurons: Mechanisms and spatial organization

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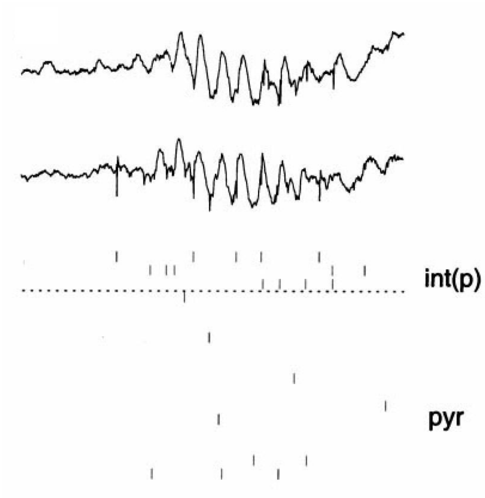
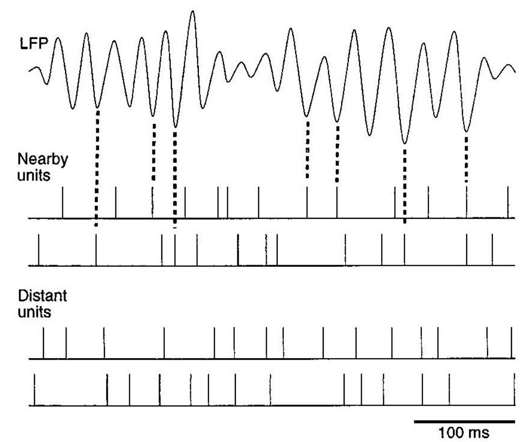
Nicolas Brunel

Fast oscillations

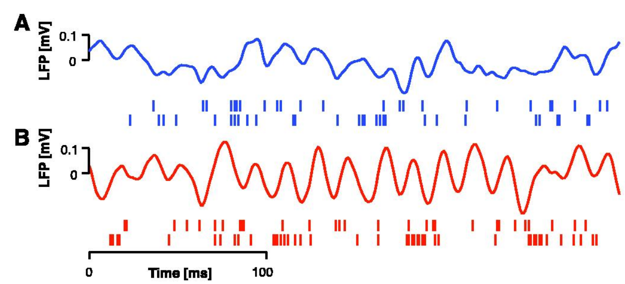
- Fast oscillations commonly seen in neurophysiological recordings (e.g. LFP)
- Typically, single cells fire very irregulary during such episodes
- In contrast with scenario considered by most modelling studies (i.e. coupled oscillators)
- What are the mechanisms of these oscillations?
- How are these oscillations spatially organized?



Csicsvari et al 1999

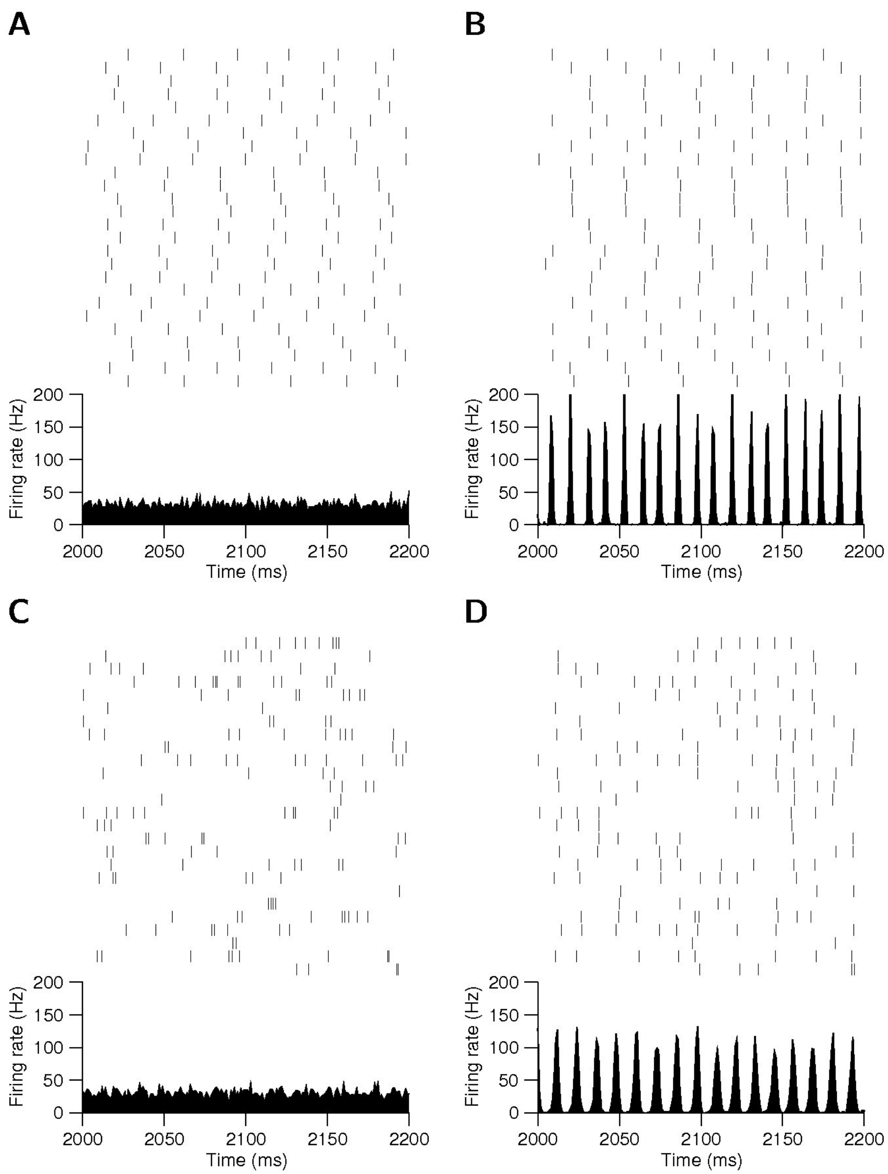


Destexhe et al 1999



Fries et al 2001

Oscillations in networks of inhibitory neurons



- Fully connected network of N inhibitory leaky integrate-and-fire LIF neurons
- Each neuron receives independent Gaussian white noise.
- Total input of a neuron i at time t

$$I_i(t) = \mu_{ext} + \frac{J}{N} \sum_j \sum_k S(t - t_j^k) + \sigma \sqrt{\tau_m} \eta_i(t)$$

where $S(t)$ describes time course of PSCs, t_j^k spike time of kth spike of neuron j.

How can we relate collective network properties with single cell/synapse properties?

Population density approach (Fokker-Planck equation)

- Network of LIF neurons characterized by p.d.f of voltage $P(V,t)$ and instantaneous firing rate $\nu(t)$;
- $P(V,t)$ given by Fokker-Planck equation

$$\tau_m \frac{\partial P}{\partial t} = \frac{\sigma^2}{2} \frac{\partial P}{\partial V^2} + \frac{\partial}{\partial V} \left[(V - \mu(t)) P \right],$$

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  - $\mu(t)$ deterministic time-dependent input (external $+$ recurrent)

$$\mu(t) = \mu_{ext} + J \int S(t - t')\nu(t')dt'$$

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- $\nu(t)$ and $P(V,t)$ coupled together through boundary conditions at threshold & reset;
- Normalization condition $\int dV\, P(V,t) = 1$

Linear stability of asynchronous state

1. Asynchronous state

$$P_0(V) = \frac{2\nu_0\tau_m}{\sigma} \exp\left(-\frac{(V-\mu_0)^2}{\sigma^2}\right) \int_{\frac{V-\mu_0}{\sigma}}^{\frac{V_t-\mu_0}{\sigma}} \exp(u^2)\Theta(u-V_r)du$$

$$\mu_0 = \mu_{ext} + J\nu_0\tau_m$$

$$\nu_0 = \frac{1}{\tau_m\sqrt{\pi}\int_{\frac{V_r-\mu_0}{\sigma}}^{\frac{V_t-\mu_0}{\sigma}} \exp(u^2)[1+\mathrm{erf}(u)]}$$

Linear stability of asynchronous state

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\end{aligned}
$$

2. Linear stability analysis

$$
\begin{aligned}
P(V,t) &= P_0(V) + \epsilon P_1(V,\lambda)\exp(\lambda t) \\
\nu_0(t) &= \nu_0 + \epsilon\nu_1(\lambda)\exp(\lambda t)
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$\Rightarrow$ obtain spectrum of eigenvalues by solving equation at first order in ϵ

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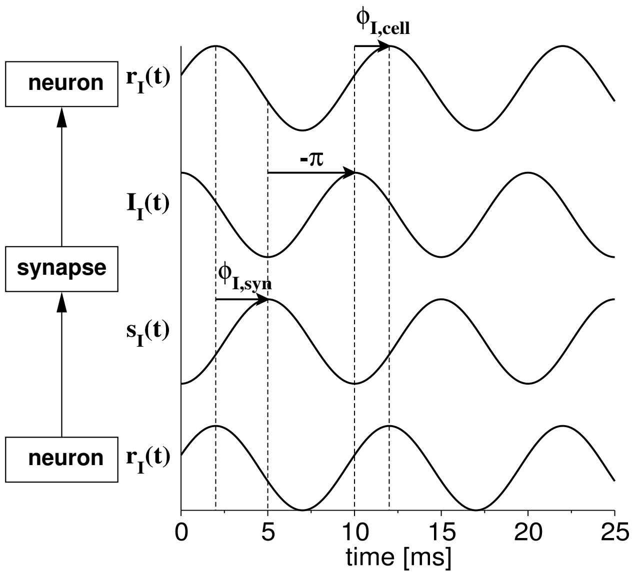
$\Rightarrow$ obtain spectrum of eigenvalues by solving equation at first order in ϵ

3. Instabilities of asynchronous state occur when the eigenvalue with largest real part $\Re(\lambda) = 0$, $\lambda = i\omega$

- Frequency ω given by

$$S(\omega) J N(\omega) = 1$$

  - $S(\omega) = A_S(\omega) \exp(i\Phi_S(\omega)) =$ synaptic filtering (how PSCs respond to oscillatory pre-synaptic rate)
  - $J =$ total synaptic strength
  - $N(\omega) = A_N(\omega) \exp(i\Phi_N(\omega)) =$ neuronal filtering: (how instantaneous firing rate of single cell responds to oscillatory input current)



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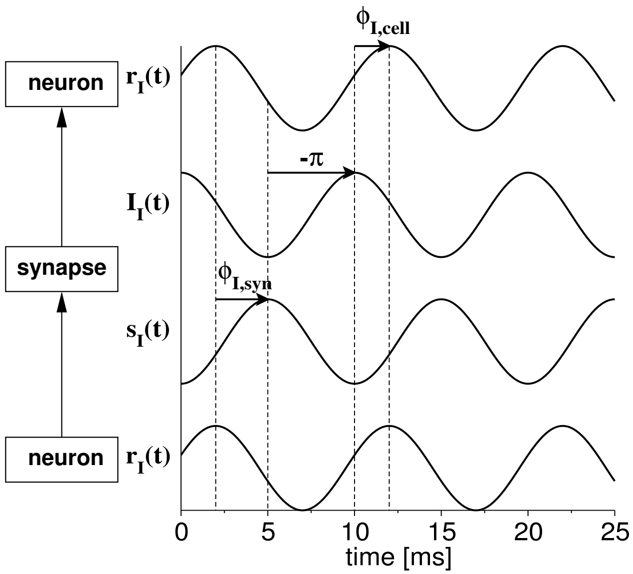

- Equation for phase $\Rightarrow$ frequency(ies) ω of instability (ies):

$$\Phi_N(\omega) + \Phi_S(\omega) = 2k\pi, \quad k = 0, 1, \ldots \quad \text{(excitatory network)}$$

$$\Phi_N(\omega) + \Phi_S(\omega) = (2k+1)\pi \quad k = 0, 1, \ldots \quad \text{(inhibitory network)}$$

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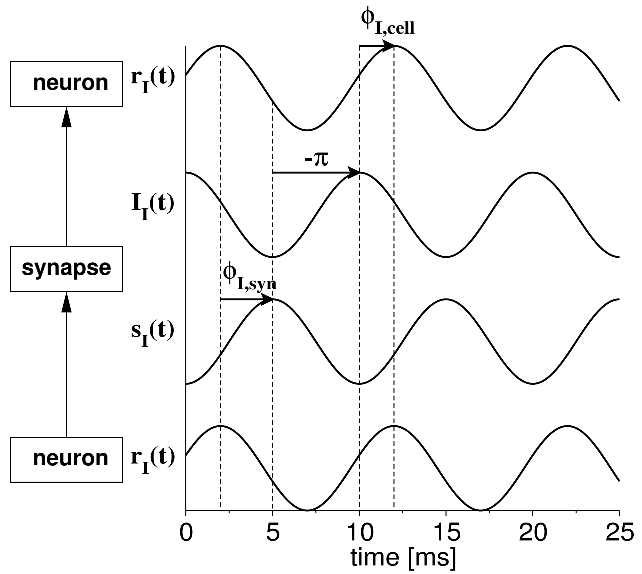

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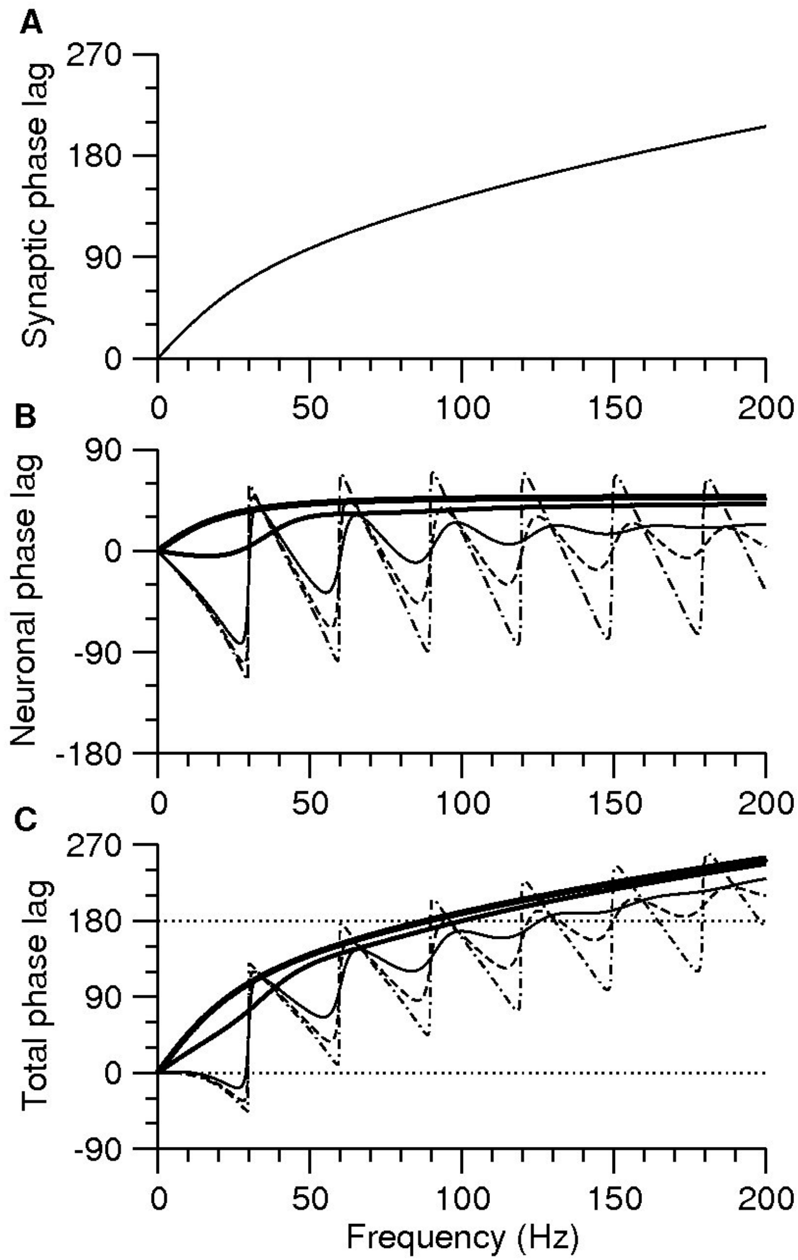
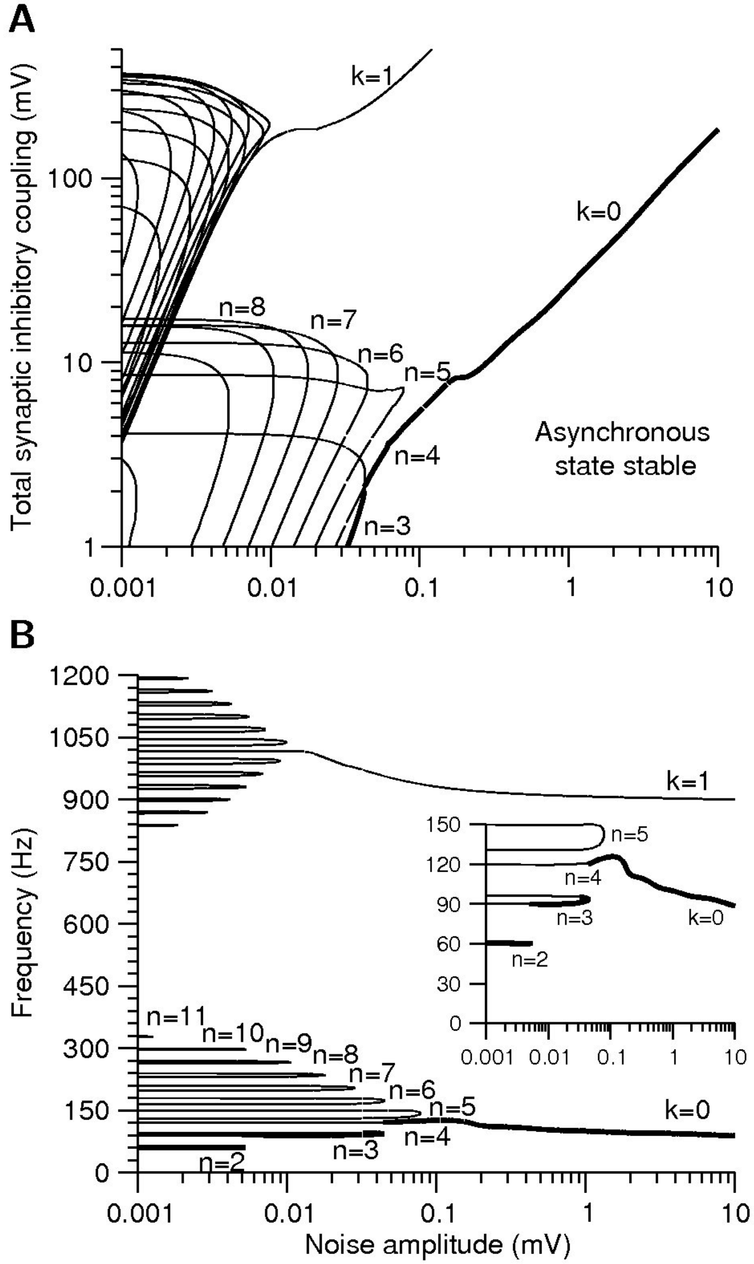
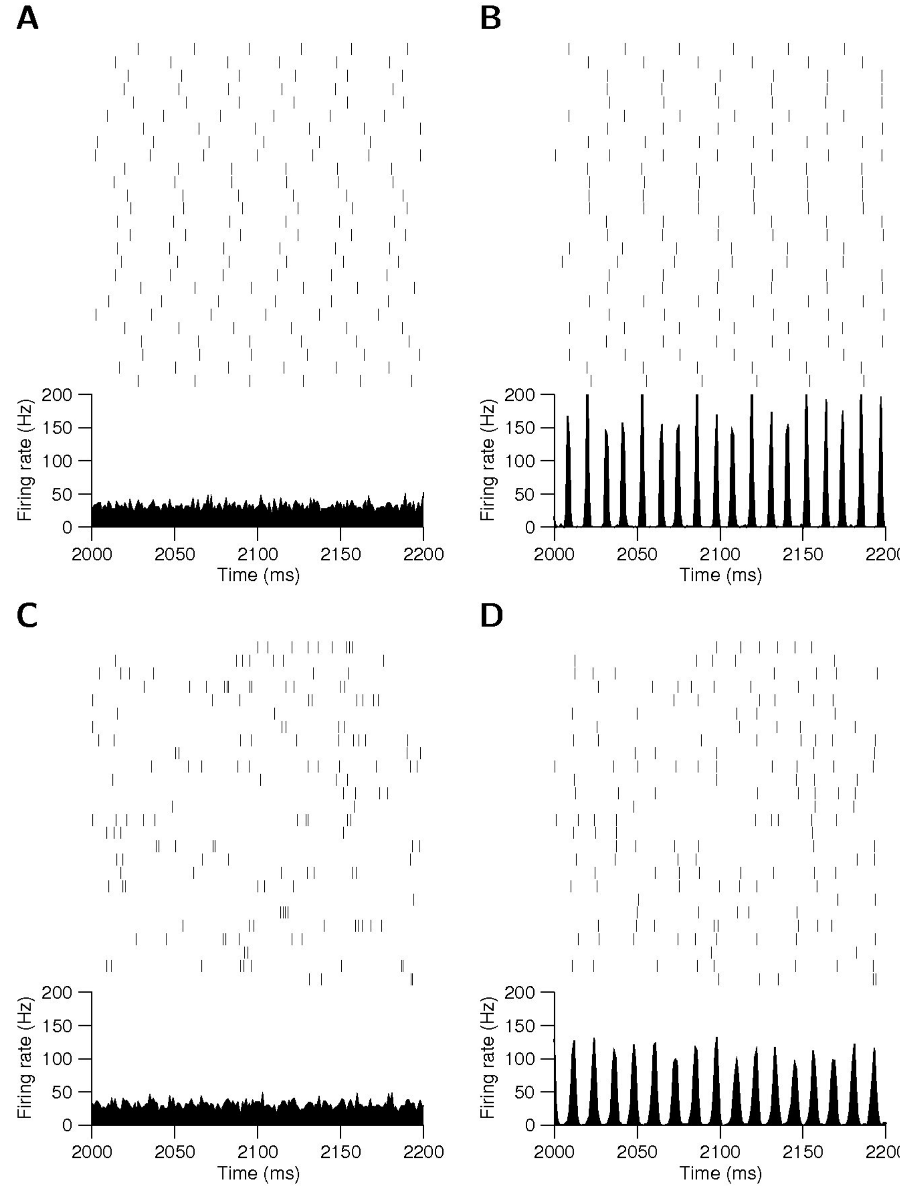
- Equation for amplitude $\Rightarrow$ associated critical coupling strength

$$|J| = \frac{1}{A_N(\omega) A_S(\omega)}$$


A
Synaptic phase lag
270
180
90
0
0
50
100
150
200
B
Neuronal phase lag
90
0
-90
-180
0
50
100
150
200
C
Total phase lag
270
180
90
0
-90
0
50
100
150
200
Frequency (Hz)


A
k=1
k=0
n=8
n=7
n=6
n=5
n=4
n=3
Asynchronous state stable
Total synaptic inhibitory coupling (mV)
100
10
1
0.001
0.01
0.1
1
10
B
1200
1050
900
750
600
450
300
150
0
Frequency (Hz)
k=1
n=5
n=4
n=3
n=2
k=0
n=11
n=10
n=9
n=8
n=7
n=6
n=5
n=4
n=3
n=2
k=0
Noise amplitude (mV)


A
B
C
D
Firing rate (Hz)
Time (ms)
2000
2050
2100
2150
2200

What determines the frequency of the oscillation?

- LIF neurons, strong (temporally correlated) noise: frequency depends on synaptic time constants only.

$$D\omega + \text{atan}(\tau_r \omega) + \text{atan}(\tau_d \omega) \sim \pi$$

- Frequency decreases when noise decreases;
- Introducing more realistic spike generation (Hodgkin-Huxley type sodium current) decreases network frequency.
- Excitation/inhibition loops tends to decrease frequency

Fast stochastic oscillations also occur in randomly sparsely connected networks

- Networks of inhibitory neurons: Brunel and Hakim 1999, Brunel and Wang 2003, Geisler et al 2005
- Excitatory/inhibitory networks: Brunel 2000, Brunel and Wang 2003, Geisler et al 2005
- Disorder in connectivity generates irregular single neuron activity even in absence of external noise

Conclusions I

- Noise moves the network in a qualitatively different synchronized state;
- Noise increases the network frequency (no longer constrained by single cell frequency)
- Frequencies up to 200Hz and more can be achieved
- ‘Stochastic’ oscillations captured qualitatively by a ‘rate model’ with delays

$$\tau \dot{m}(t) = -m(t) + \Phi \left[I(t) + J m(t - D) \right]$$

Spatial structure

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

- $\tau = 1$: 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);
- $I(x,t)$: external input
- $J(|x-y|)$: weight of synaptic connections between neurons at locations x and y;
- D: transmission delay

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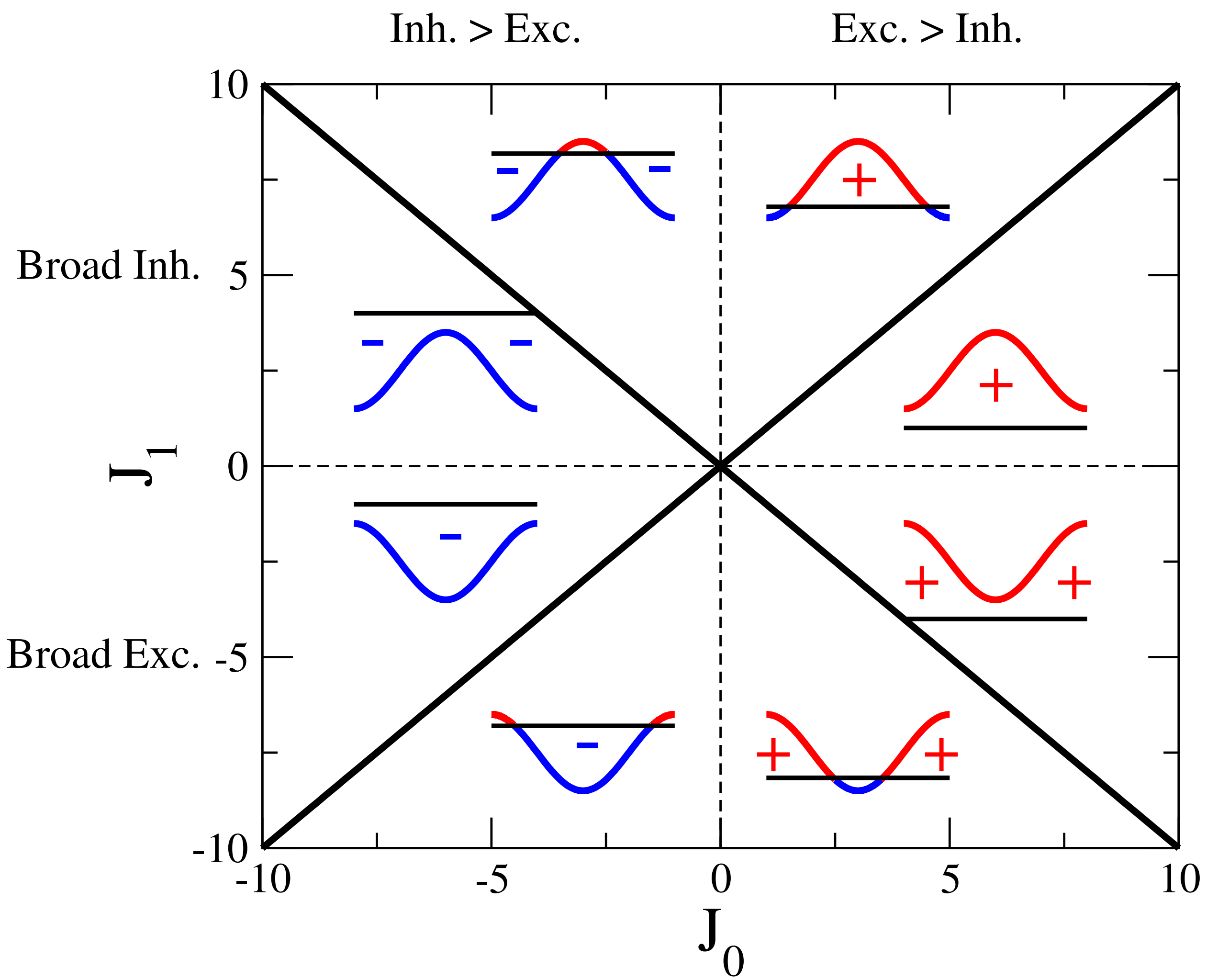
- D: transmission delay

Simplifying assumptions

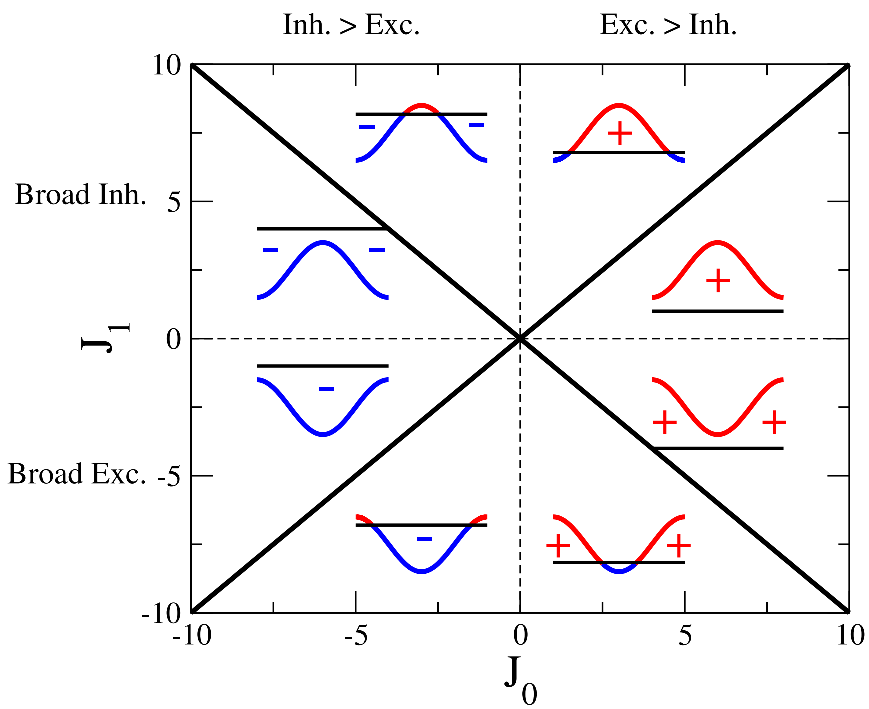
- 1 D space with ring topology: $x \in [-\pi, \pi]$
- Threshold-linear transfer function, $\Phi(I) = I$ if $I > 0$ and $\Phi(I) = 0$ otherwise
- External inputs are constant in space and time, $I(x,t) = I_0$
- Synaptic footprint: $J(|x-y|) = J_0 + J_1 \cos(x-y)$

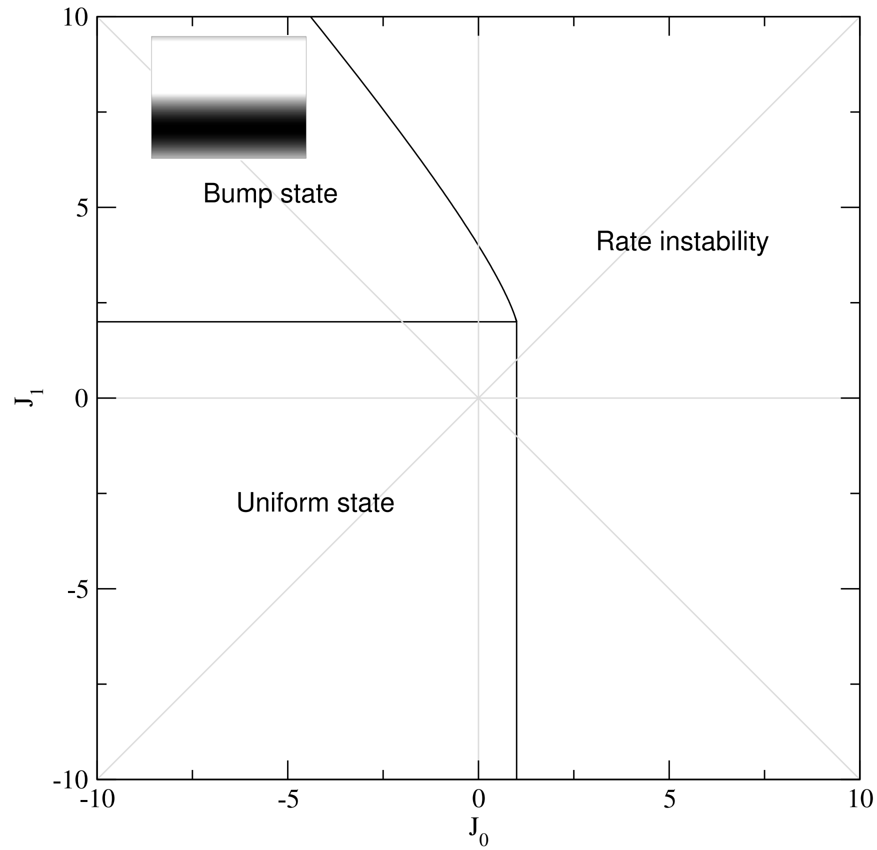
Connectivity profile in J_0-J_1 plane

$$J(|x-y|) = J_0 + J_1 \cos(x-y)$$



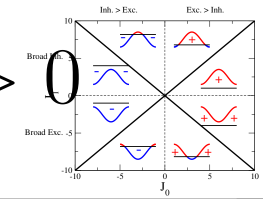
Phase diagram of the rate model for $D = 0$





Ben Yishai et al 1995, Hansel and Sompolinsky 1998

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



Four types of instabilities:

- Rate instability:

$$J_0 = 1$$

- Turing instability:

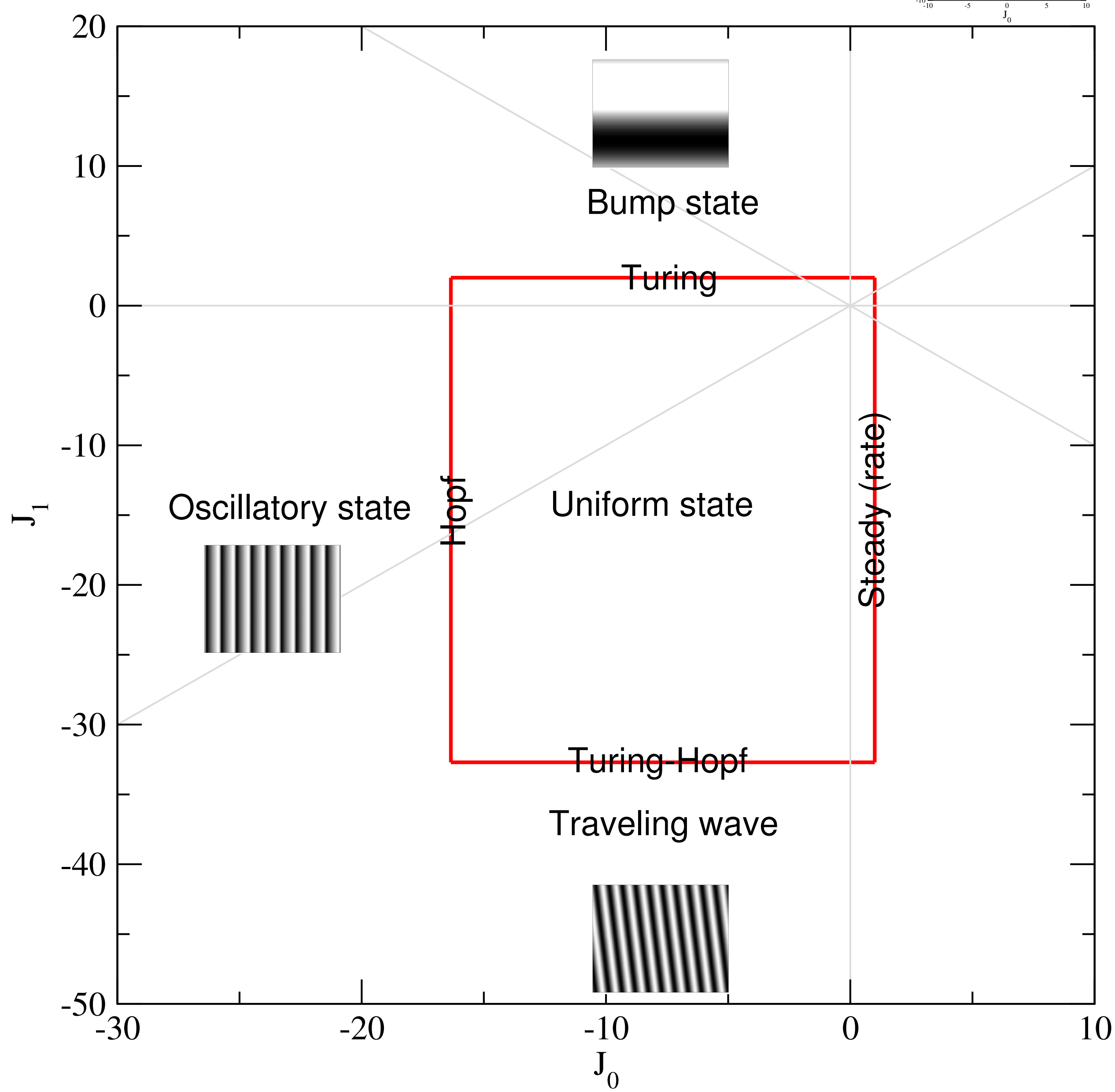
$$J_1 = 2$$

- Hopf instability:

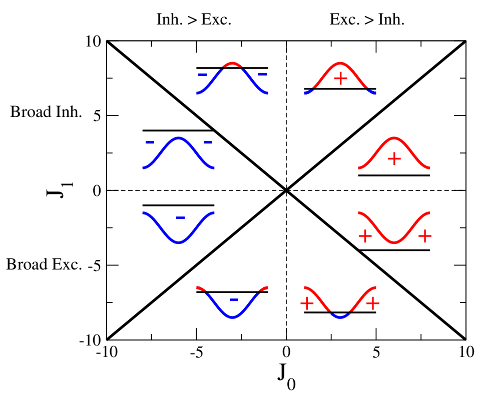
$$\begin{aligned} \omega &= -\tan(\omega D) \\ J_0 &= 1/\cos(\omega D) \end{aligned}$$

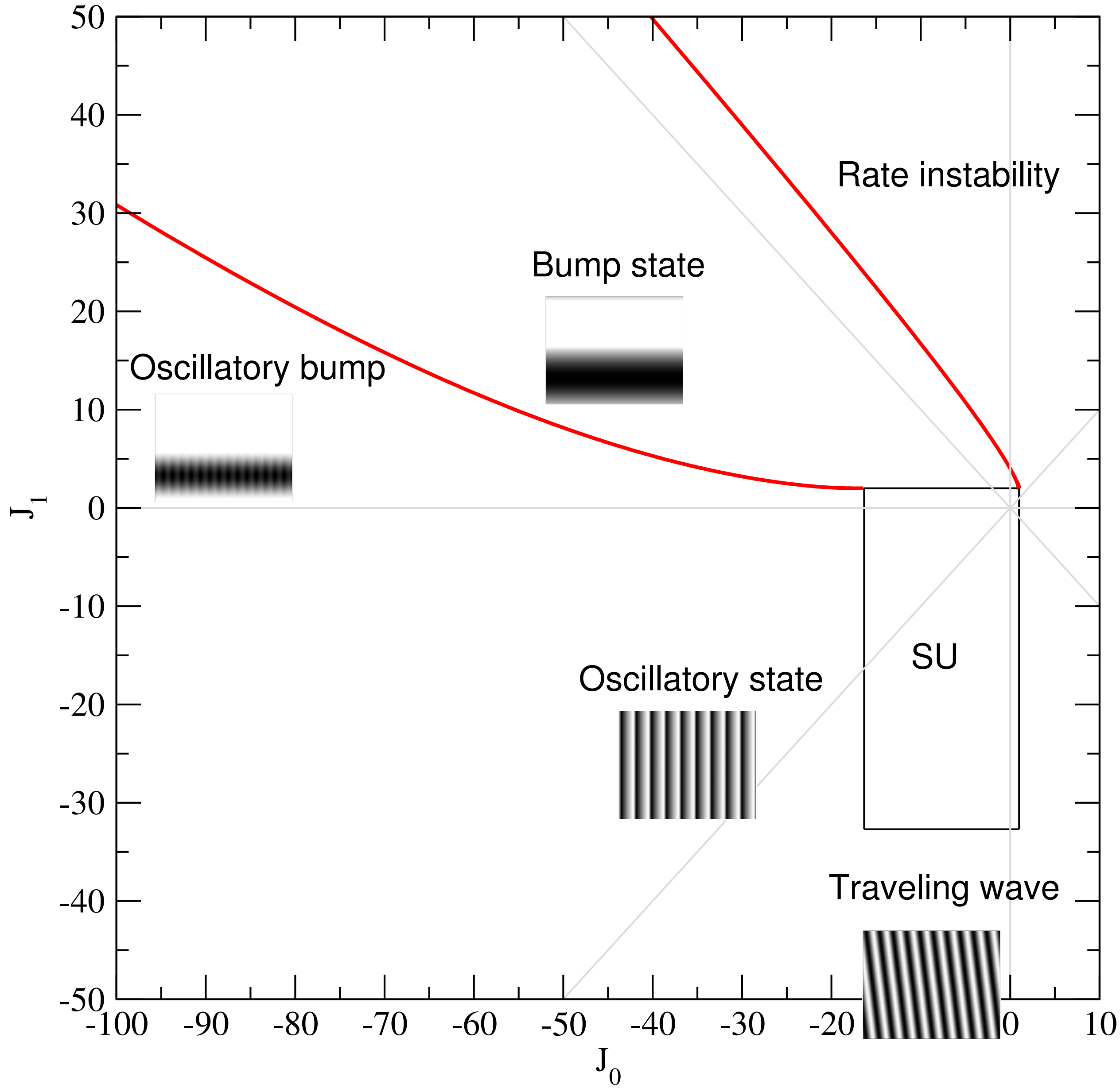
- Turing-Hopf instability:

$$\begin{aligned} \omega &= -\tan(\omega D) \\ J_1 &= 2/\cos(\omega D) \end{aligned}$$

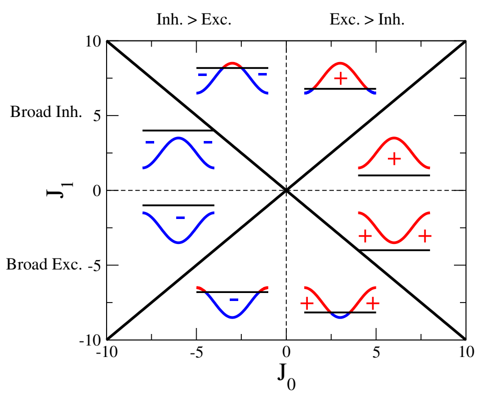


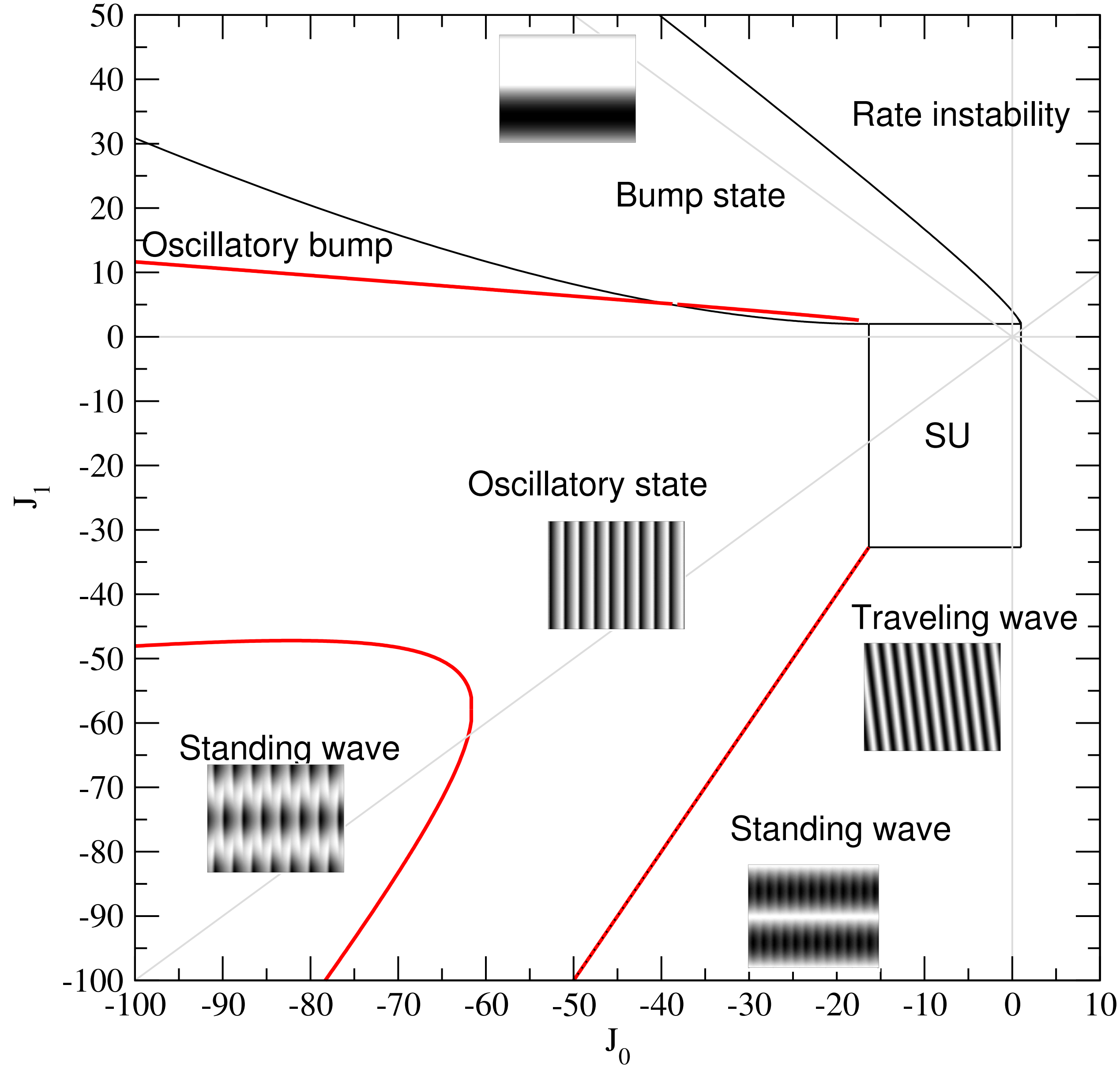
The mexican-hat region: stationary bump and its stability



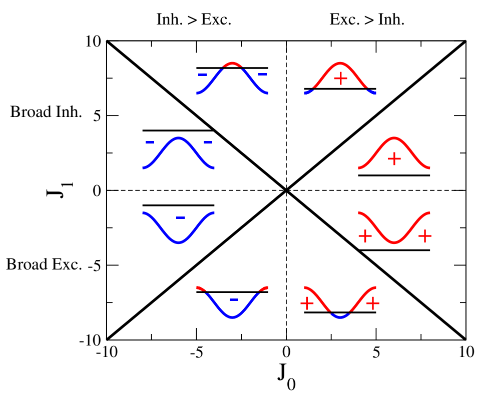


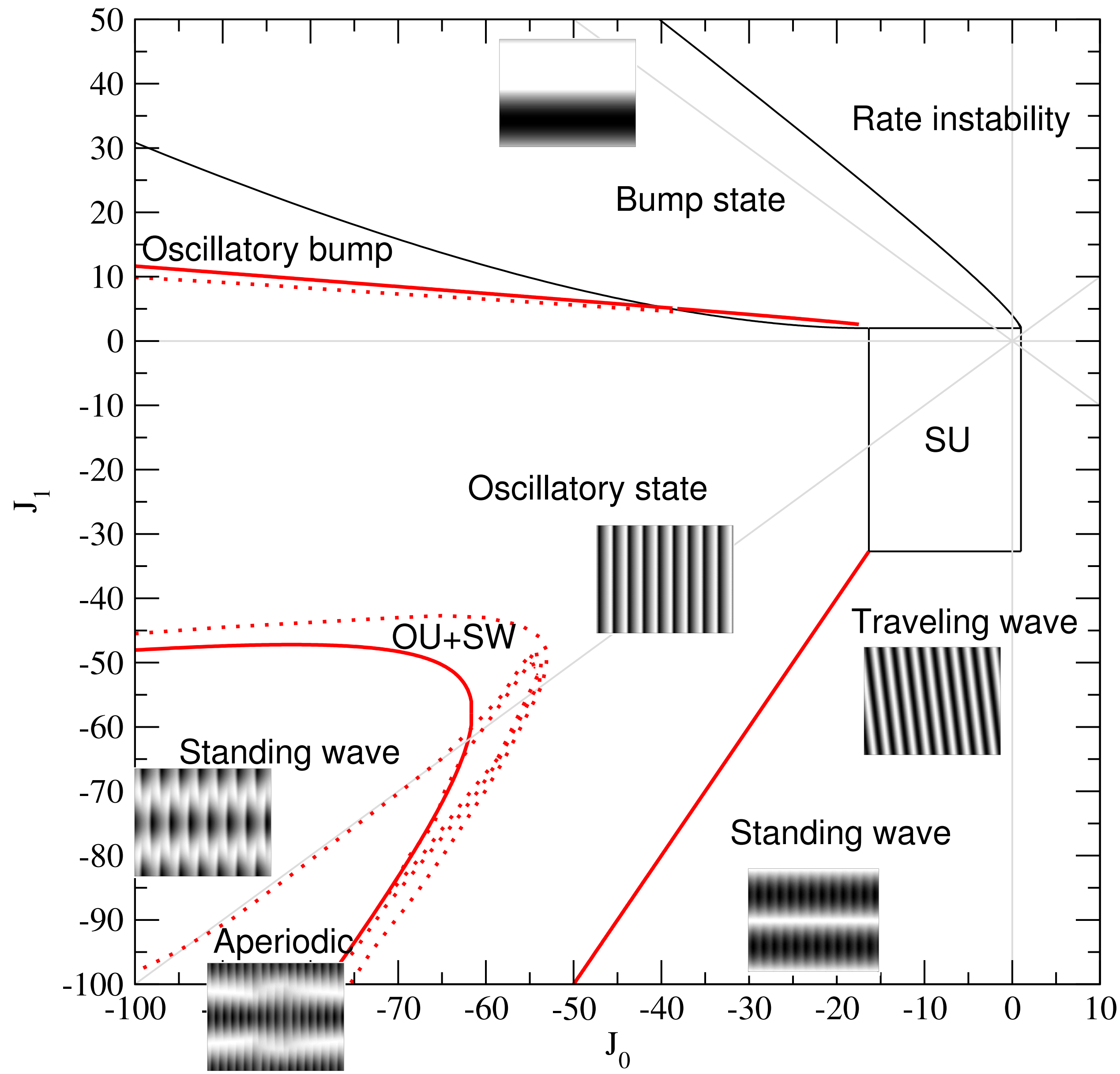
The strong inhibition region: oscillations and their stability



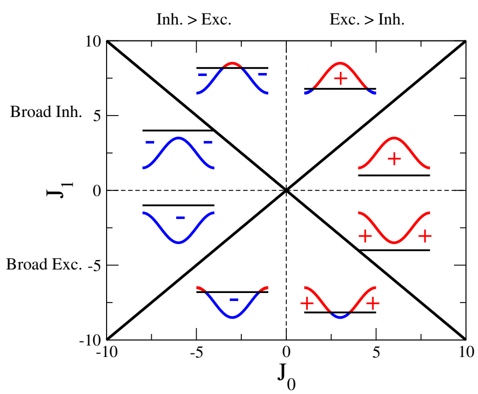


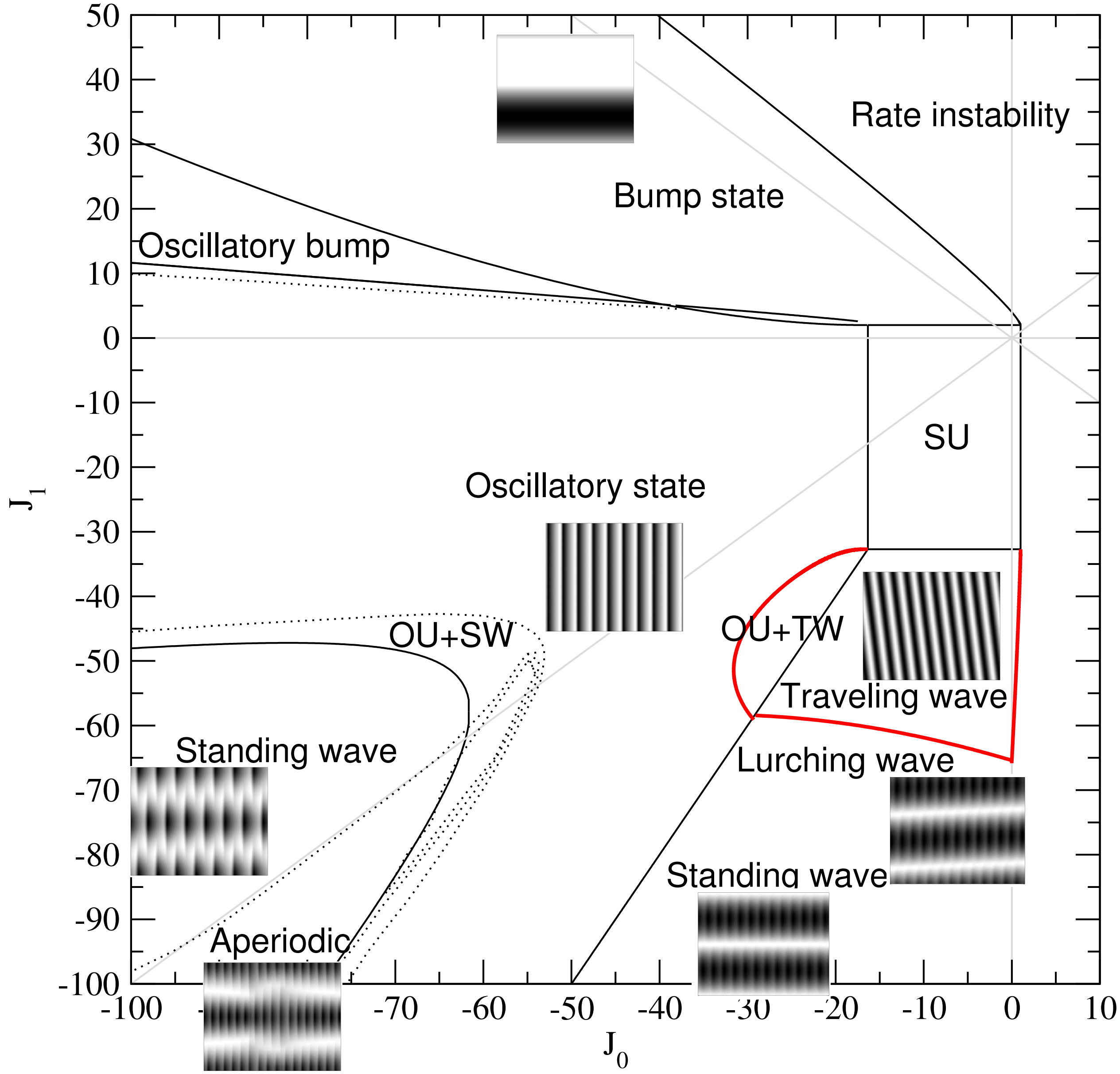
The strong inhibition region 2: more bifurcations





The reverse mexican-hat region: stability of TWs





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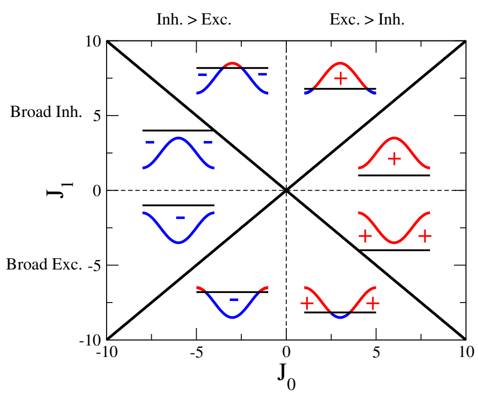
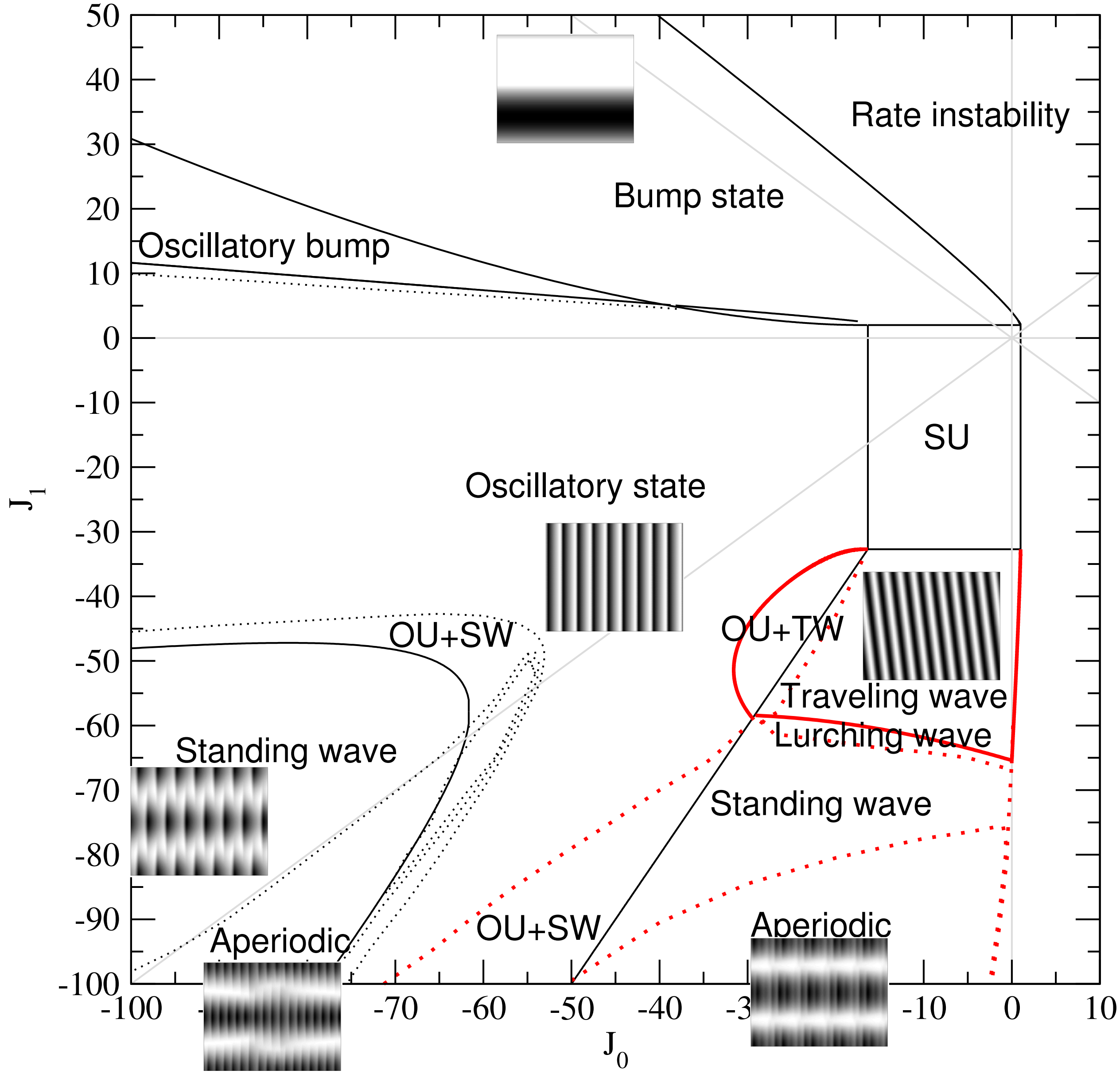
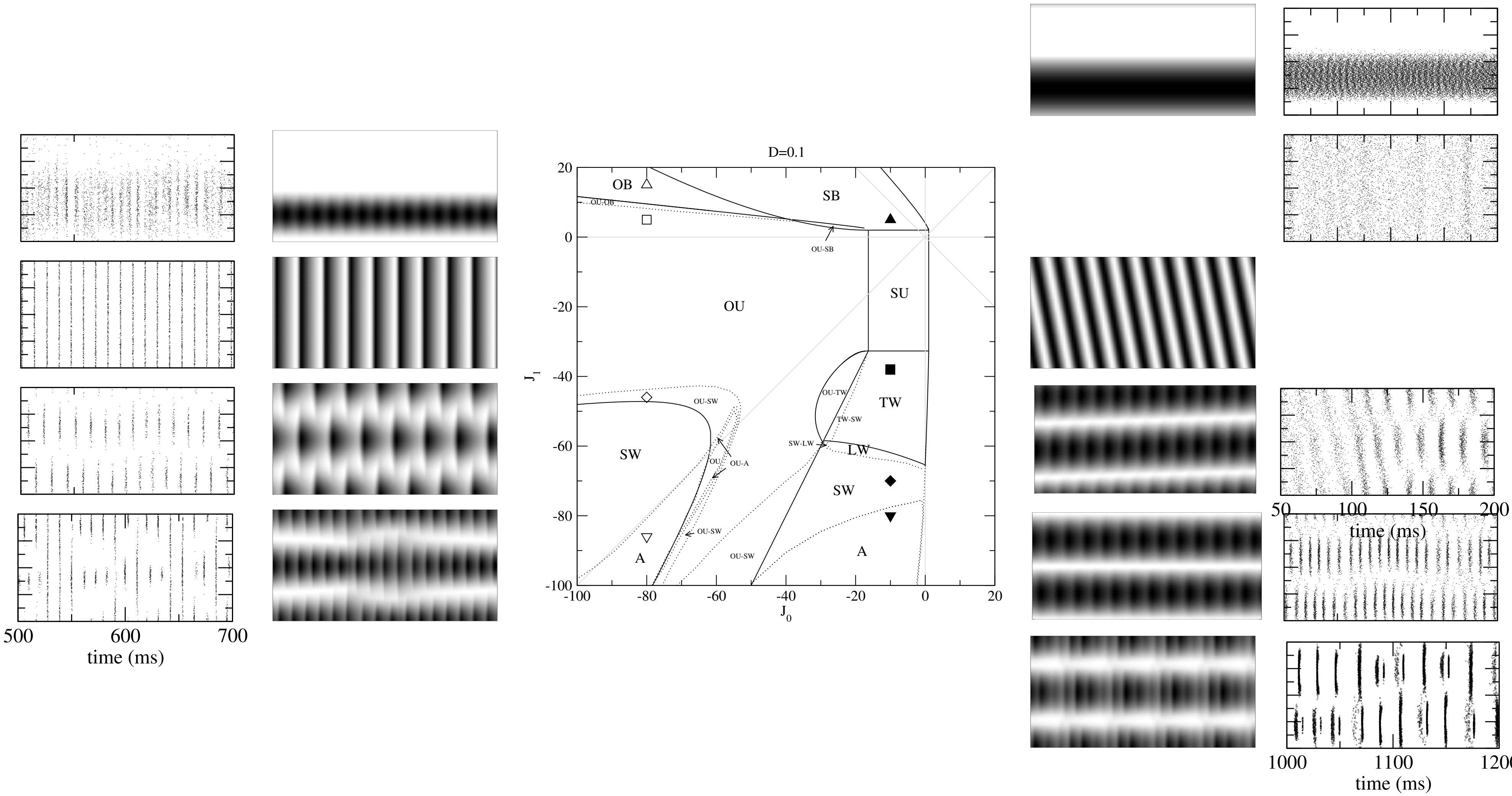


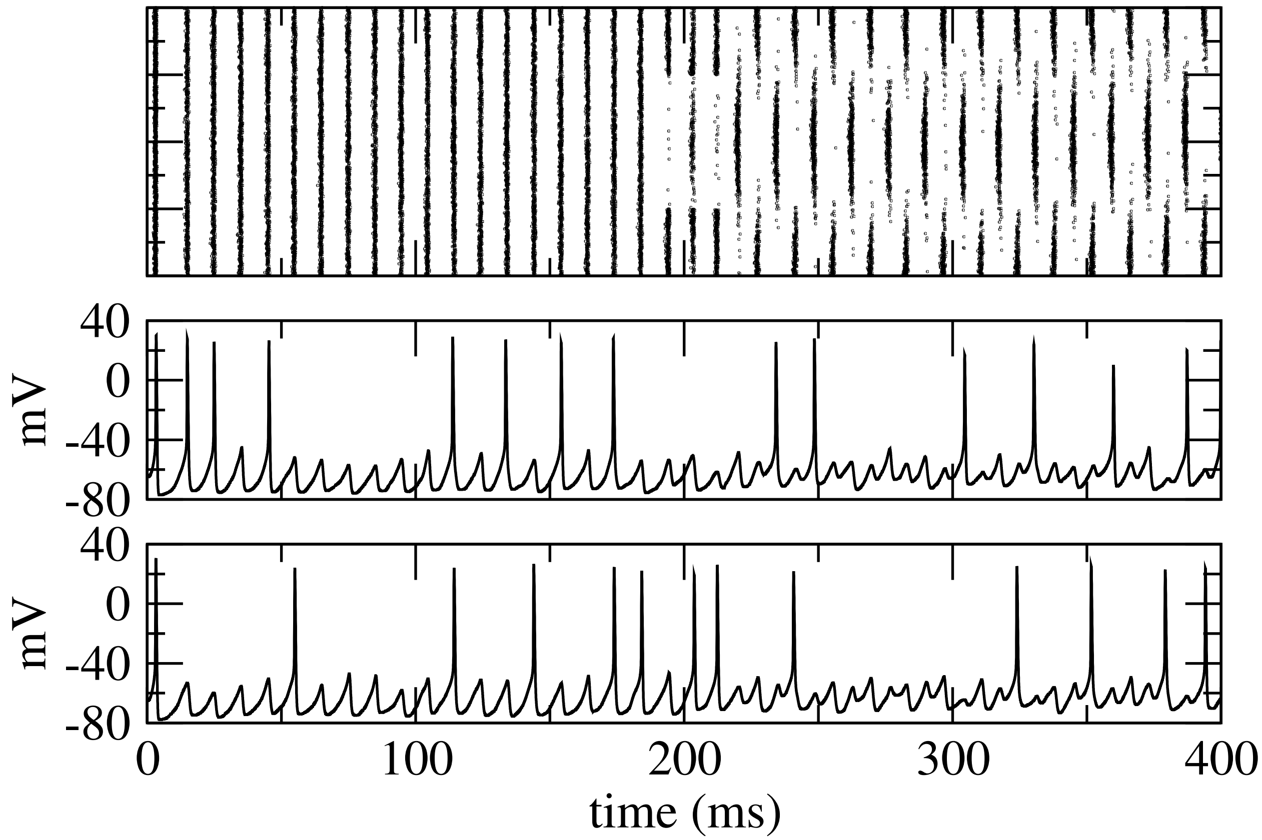


Rate model vs network of spiking neurons

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



Multistability in a network of inhibitory spiking neurons



Conclusions

- Rate model with delay describes qualitatively dynamics observed in networks of Hodgkin-Huxley-type neurons;
- Rate model can be analyzed mathematically in great detail, shows rich phase diagram
- New types of spatially modulated states in inhibition-dominated and inverted Mexican-hat regions;
- Many multistability regions in inhibition-dominated regions - both oscillatory uniform state and spatially modulated oscillatory states are stable;
- Could be used as a short-term memory

Roxin, Brunel, Hansel, Phys. Rev. Lett. (2005)

Thanks

- Fully connected networks: David Hansel (Paris)
- Sparsely connected networks: Vincent Hakim (Paris), Xiao-Jing Wang (Yale), Caroline Geisler (Rutgers)
- Networks with spatial structure: Alex Roxin (Barcelona), David Hansel (Paris)

From HH-type models to rate models via the exponential integrate-and-fire (EIF) model

Non-linear integrate-and-fire (NLIF) models

$$C\frac{dV}{dt} = -g_L(V - V_L) + \psi(V) + I_{syn}(t)$$

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When $\psi(V)$ supra-linear, divergence of V to infinity in finite time if the input current exceeds some threshold

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Examples

- **quadratic integrate-and-fire (QIF)**

$$\psi(V) = \frac{g_L}{2\Delta_T}(V - V_T)^2 + g_L(V - V_L) - I_T$$

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- **exponential integrate-and-fire (EIF)**

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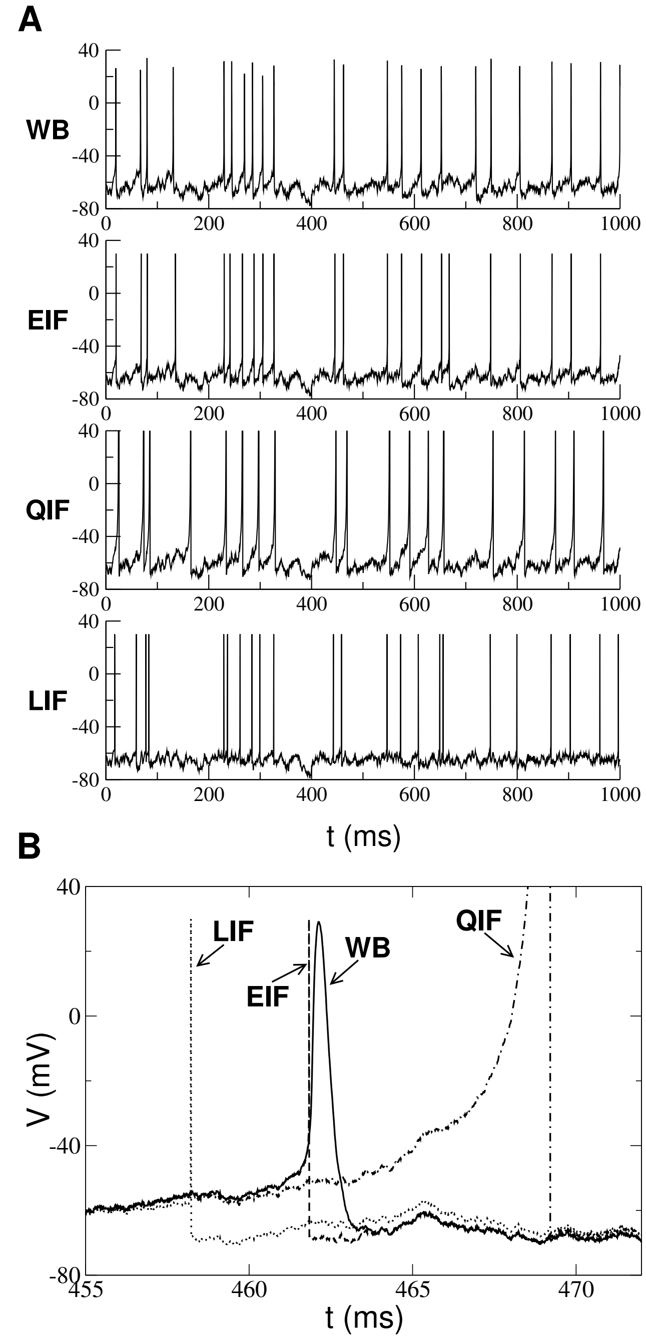
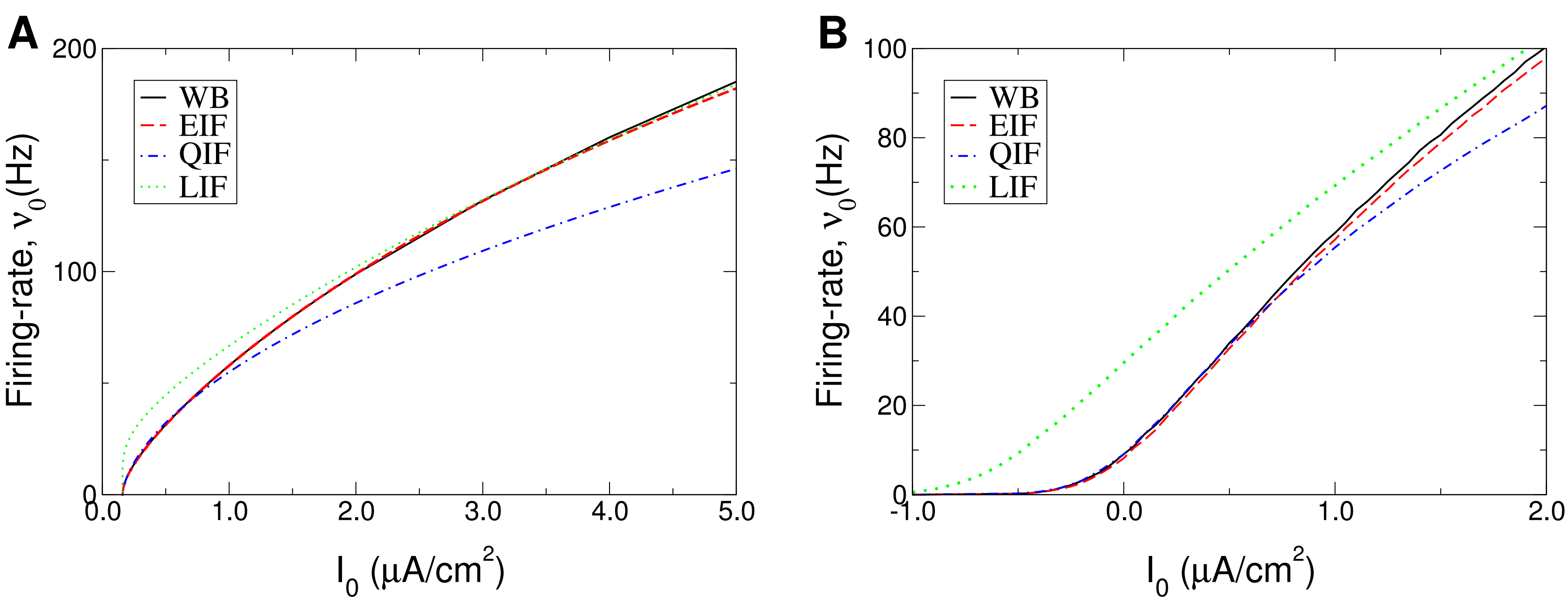


Steady state firing rate response (f-I curves)



Dynamical firing rate response (susceptibility)

$\nu_1(f) \sim 1/f^\alpha$

phase lag at high input frequency is $\alpha\pi/2$

Model	Exponent α	Phase lag $\phi(f \to \infty)$
LIF, colored noise	0	0
LIF, white noise	0.5	45°
EIF, all types of noise	1	90°
QIF, all types of noise	2	180°

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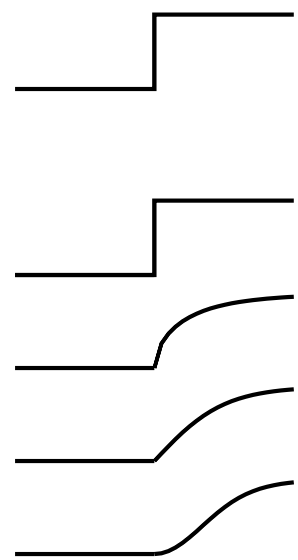
LIF, white noise	0.5	45°
EIF, all types of noise	1	90°
QIF, all types of noise	2	180°

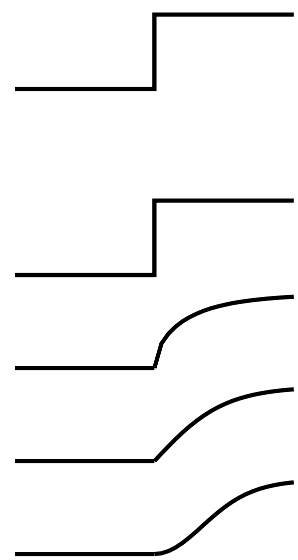


Dynamical firing rate response (susceptibility)

$\nu_1(f) \sim 1/f^{\alpha}$

phase lag at high input frequency is $\alpha\pi/2$

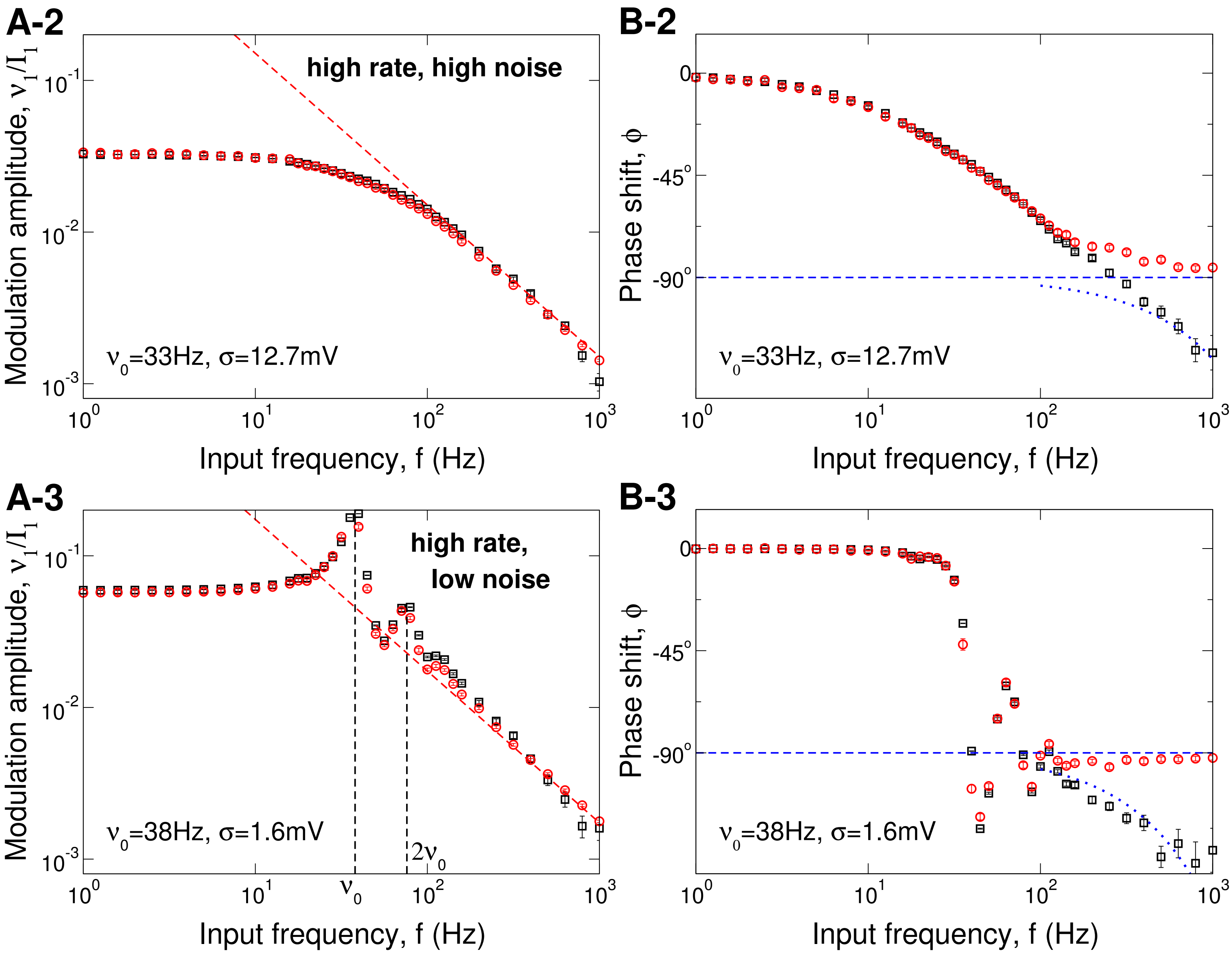
Model	Exponent α	Phase lag $\phi(f \to \infty)$
LIF, colored noise	0	0
LIF, white noise	0.5	45°
EIF, all types of noise	1	90°
QIF, all types of noise	2	180°



High frequency behavior of EIF consistent with HH-type models.

Other IF models fail to reproduce the behavior of the HH-type models.

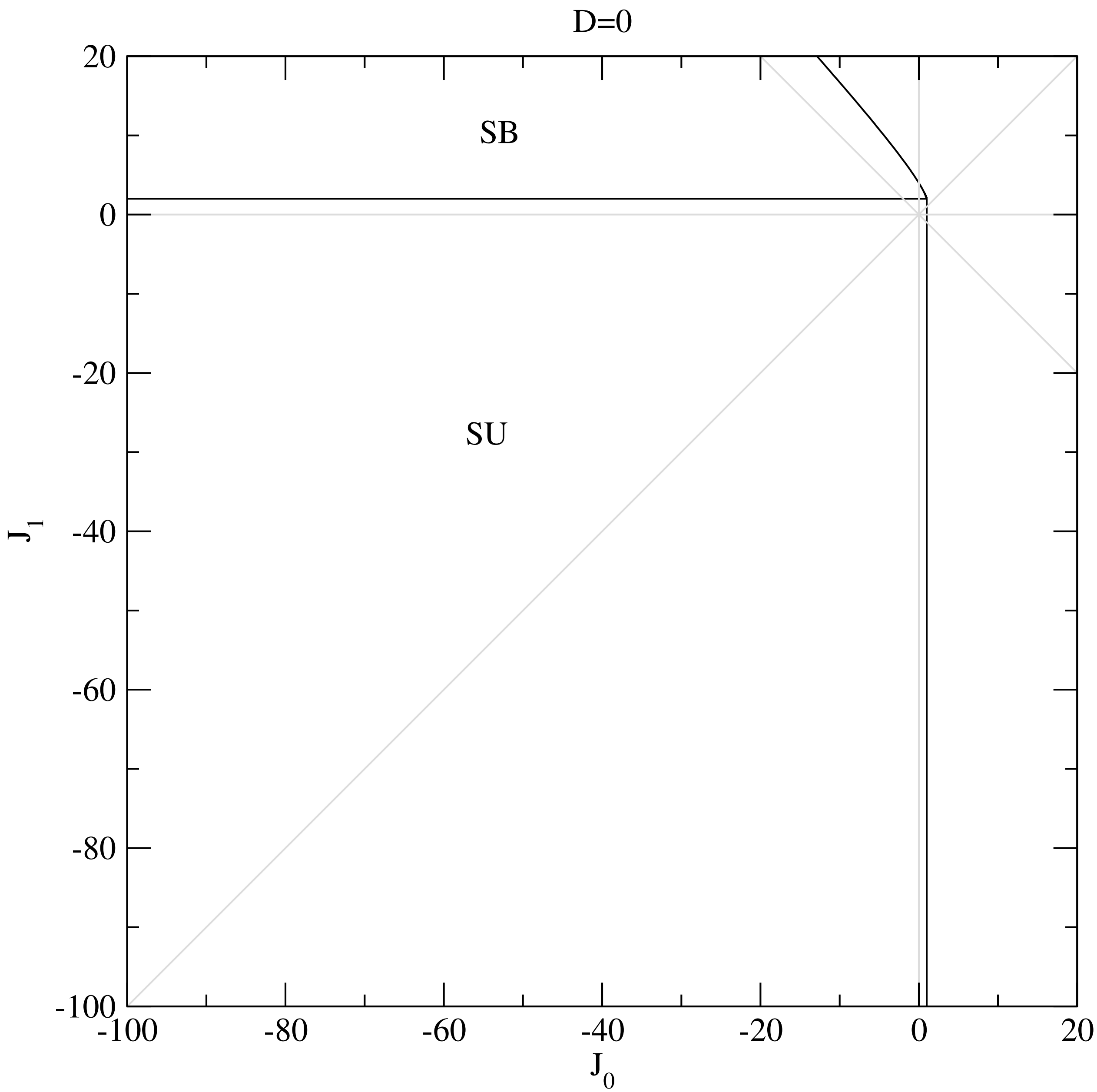
EIF vs conductance-based neuron (Wang-Buzsaki model)

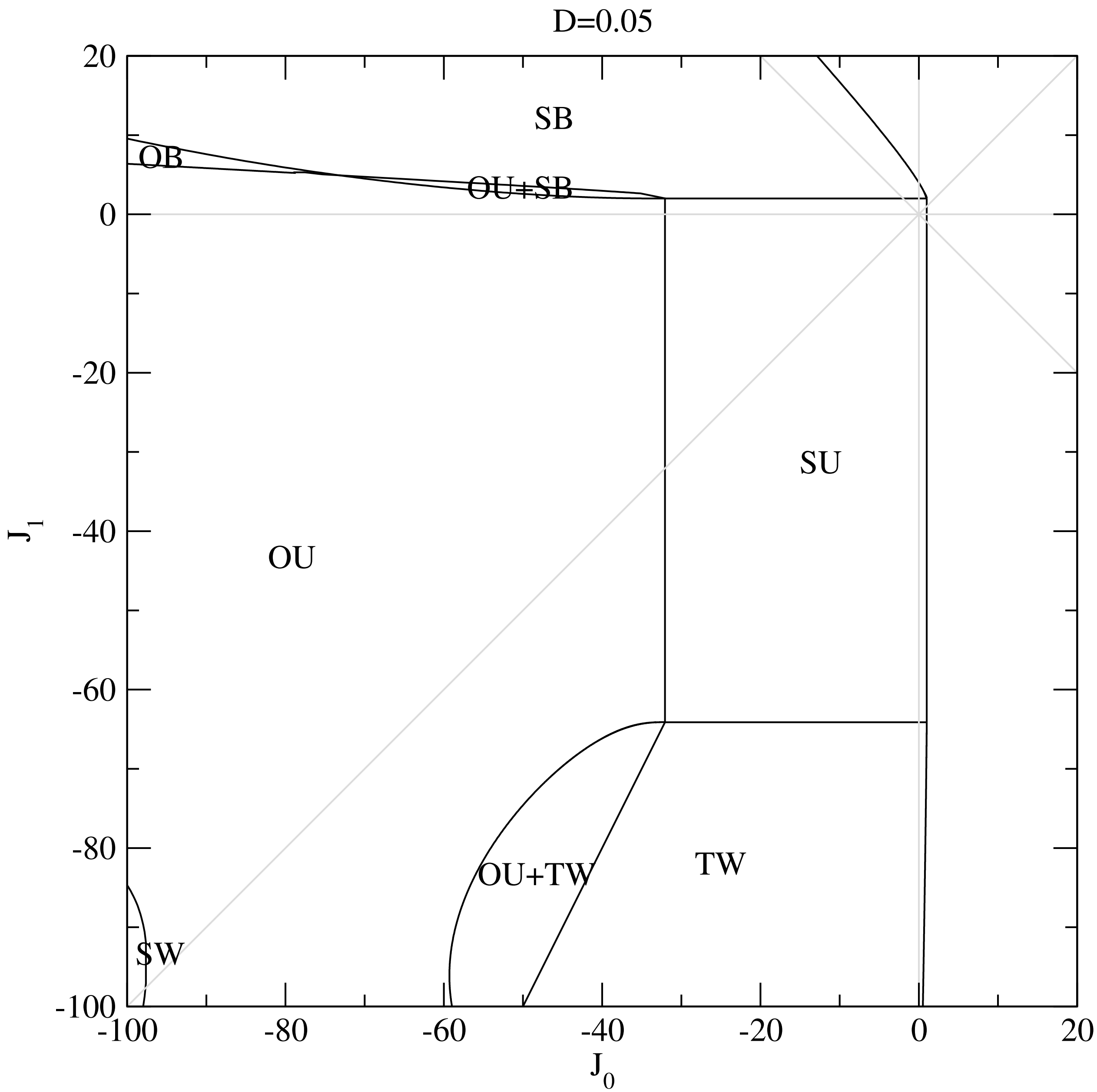


Thanks!

- Fast oscillations with noisy neurons: Vincent Hakim (Paris), David Hansel (Paris)
- Spatial organization of oscillations: Alex Roxin (Barcelona), David Hansel (Paris)
- EIF model: Nicolas-Fourcaud (Lyon), Carl van Vreeswijk (Paris), David Hansel (Paris)

Phase diagram vs delay





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SB
OB
OU+SB
SU
OU
OU+TW
TW
SW
J_1
J_0
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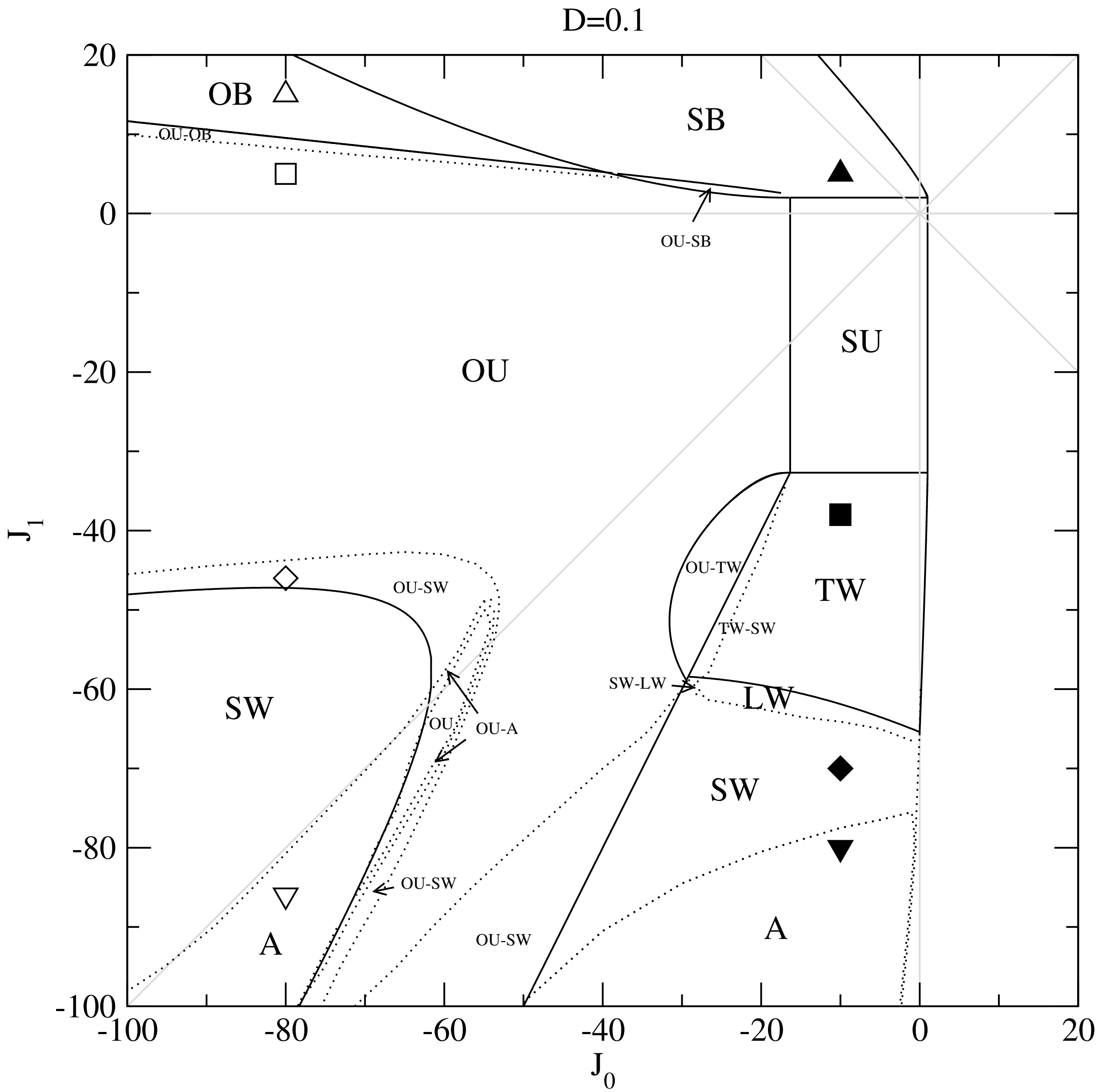
0
-20
-40
-60
-80
-100
-100
-80
-60
-40
-20
0
20



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OU-SB
SU
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TW
OU-TW
TW-SW
SW-LW
LW
SW
OU-SW
OU
OU-A
SW
A
OU-SW
OU-SW
A
J_1
J_0
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-40
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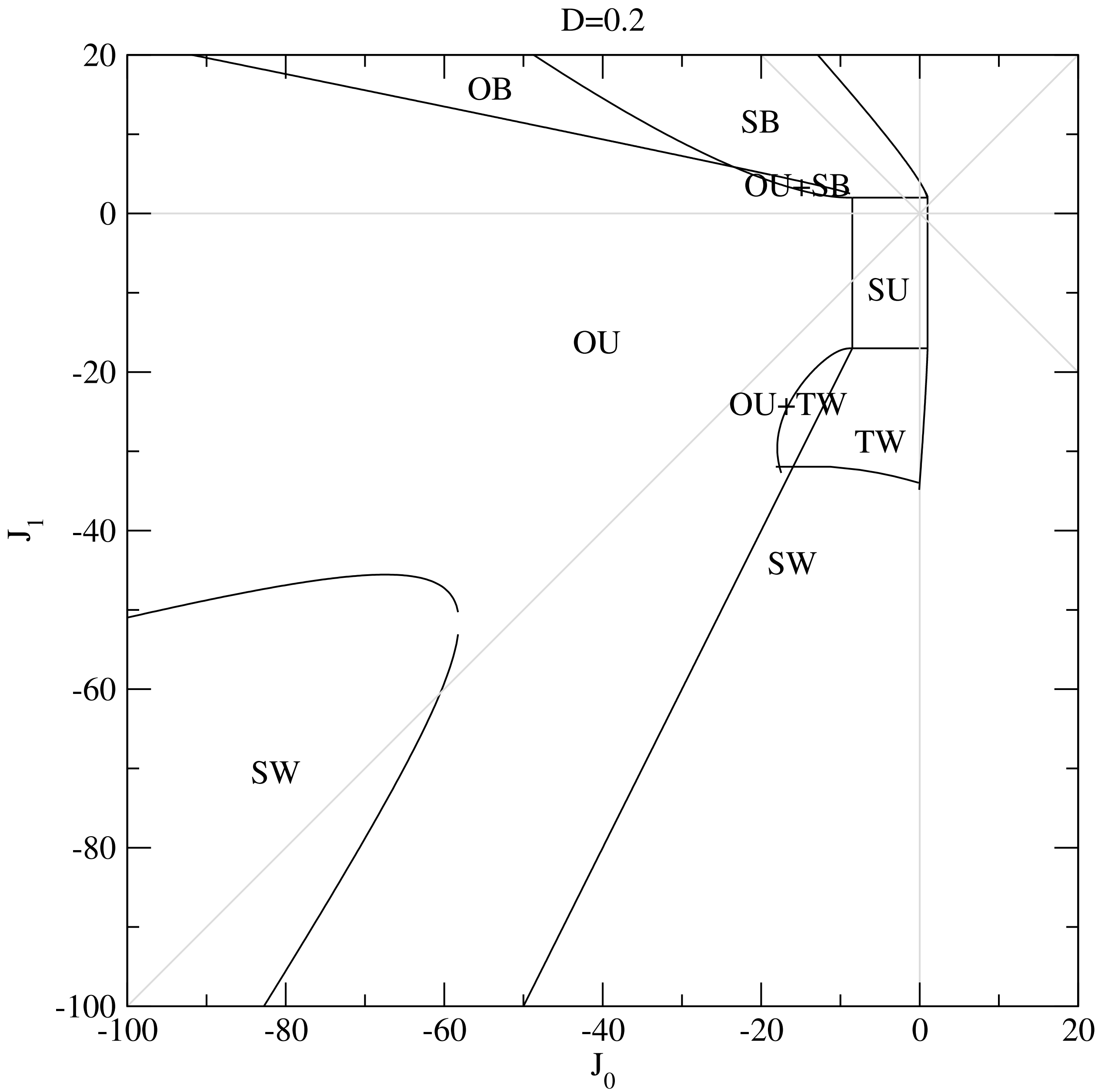
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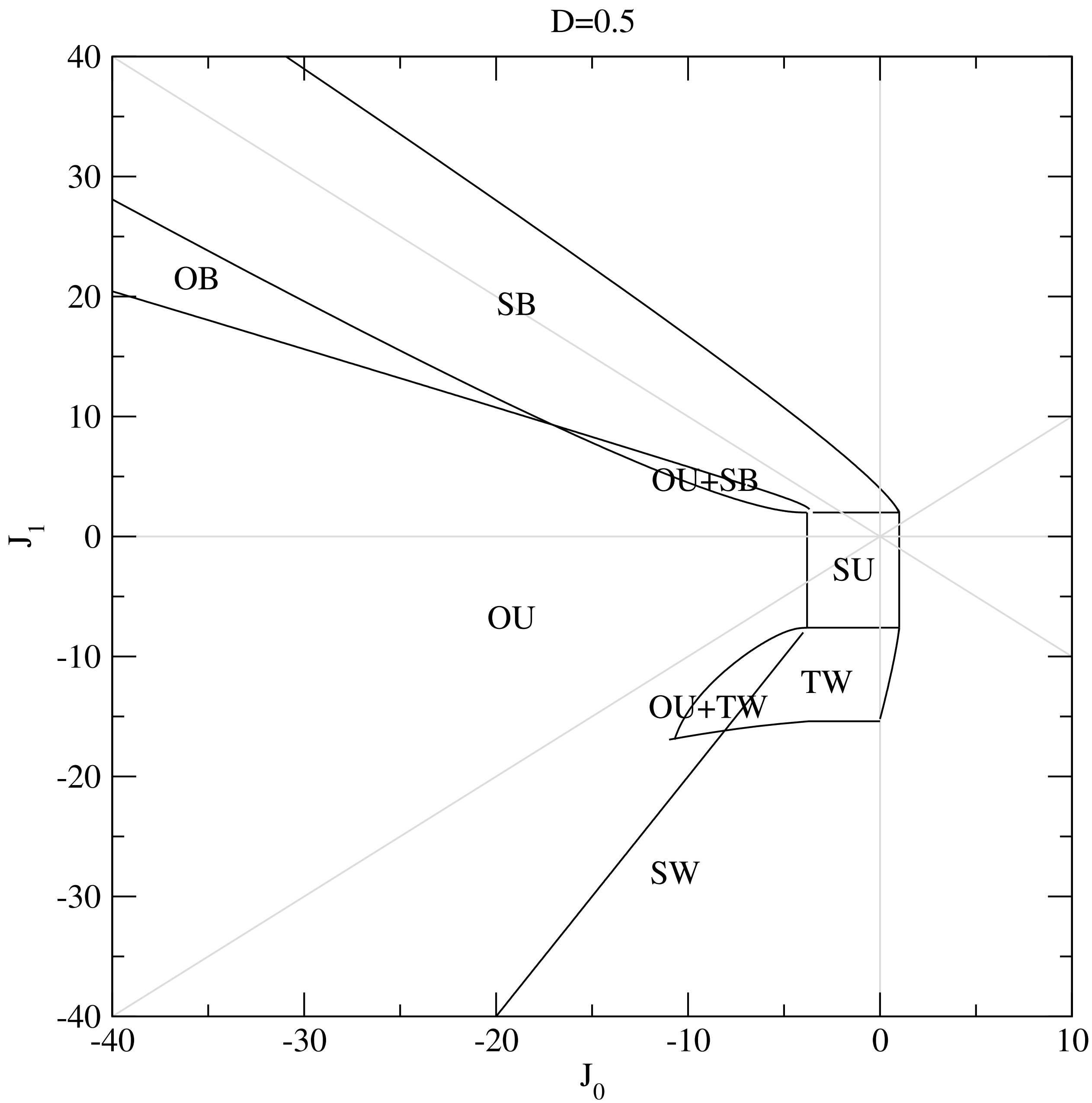
-80
-60
-40
-20
0
20
J1
J0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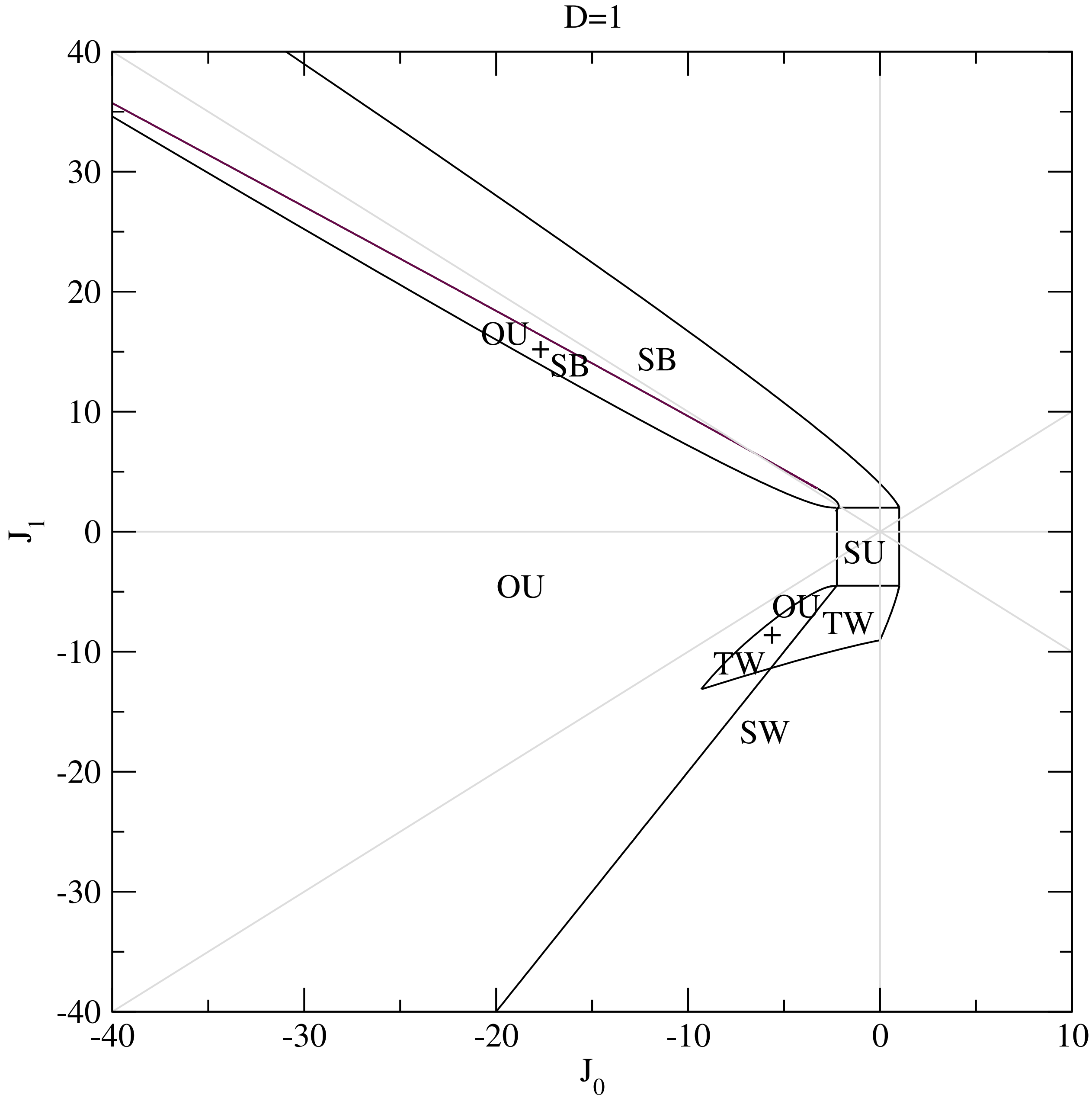
30
20
10
0
-10
-20
-30
-40
-40
-30
-20
-10
0
10
J_1
J_0
OB
SB
OU+SB
SU
OU
TW
OU+TW
SW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-20
-30
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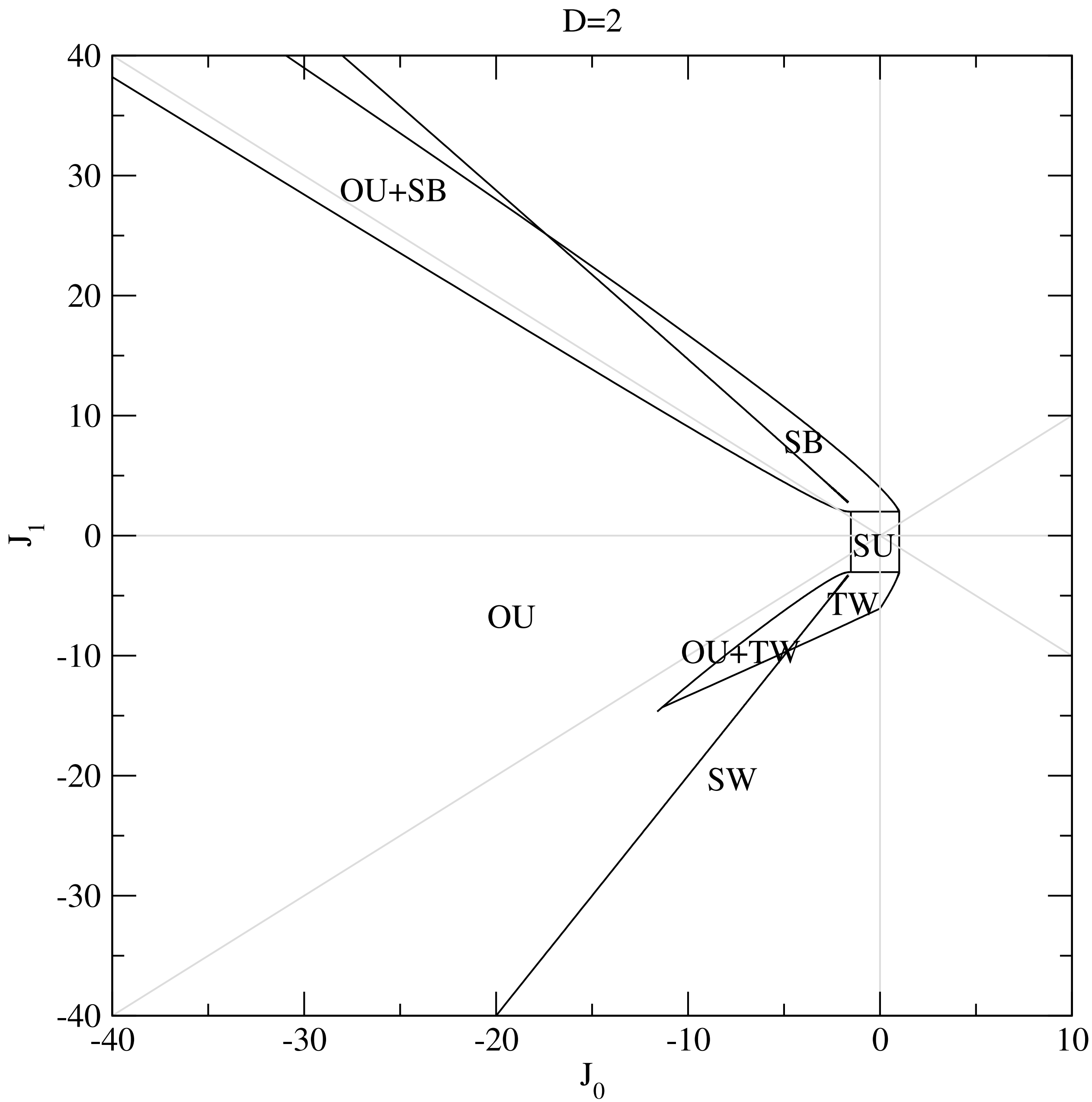
-20
-10
0
10
J_1
J_0
OU+SB
SB
SU
OU
OU+TW
TW
SW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SU
TW
OU
OU+TW
SW
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-40
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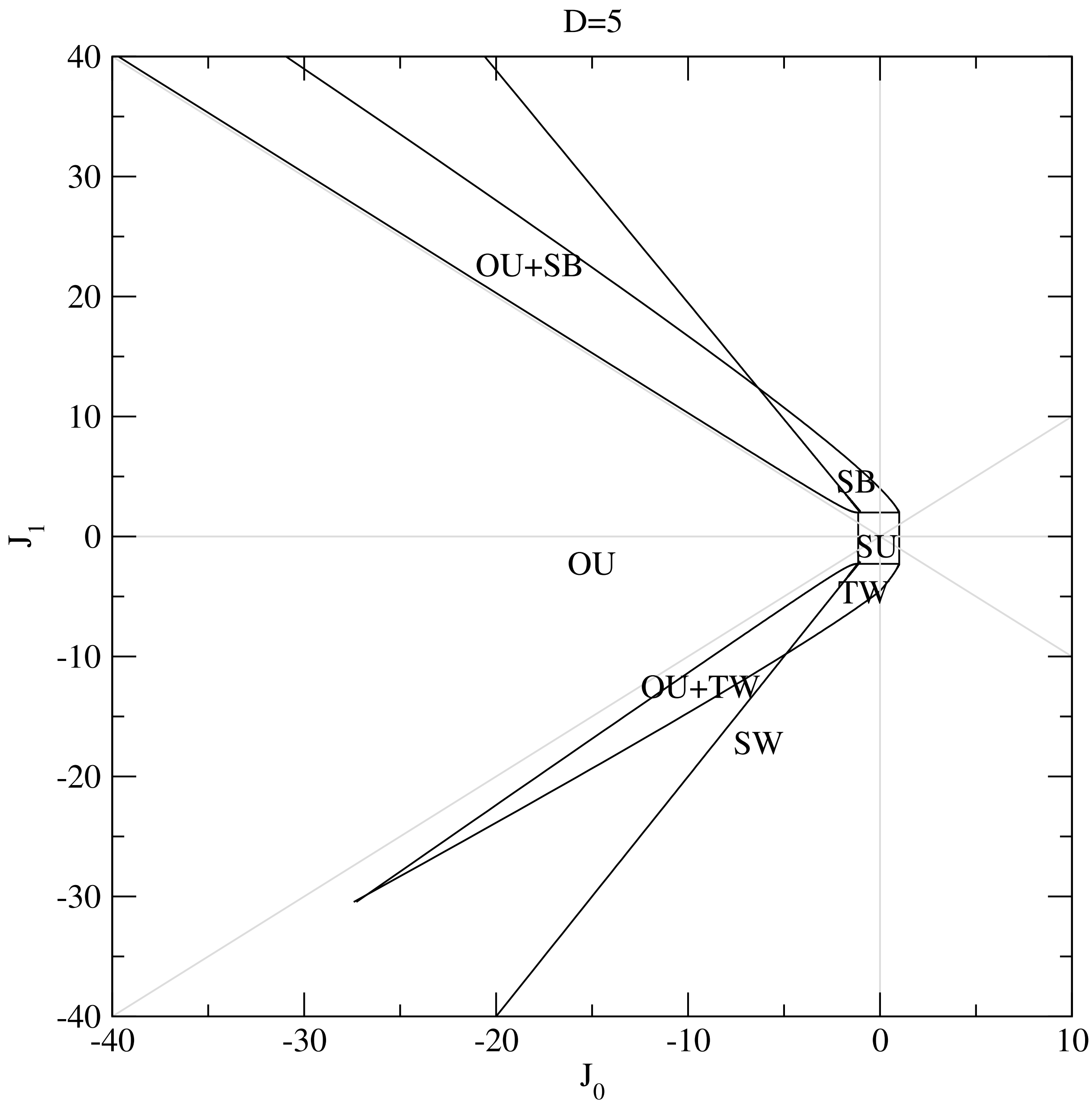
-20
-10
0
10
J_1
J_0



D=5
OU+SB
SB
SU
OU
TW
OU+TW
SW
J1
J0
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-40
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-20
-10
0
10