Oscillations in the bistable regime of neuronal networks.

Alex Roxin (with Daniel Jercog, Jaime de la Rocha and Albert Compte)

Institut d'Investigacions Biomèdiques August Pi i Sunyer, Barcelona

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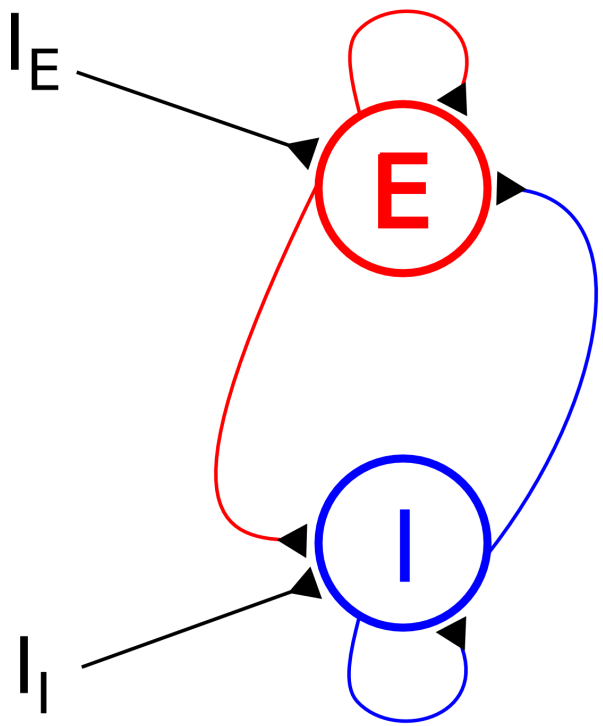
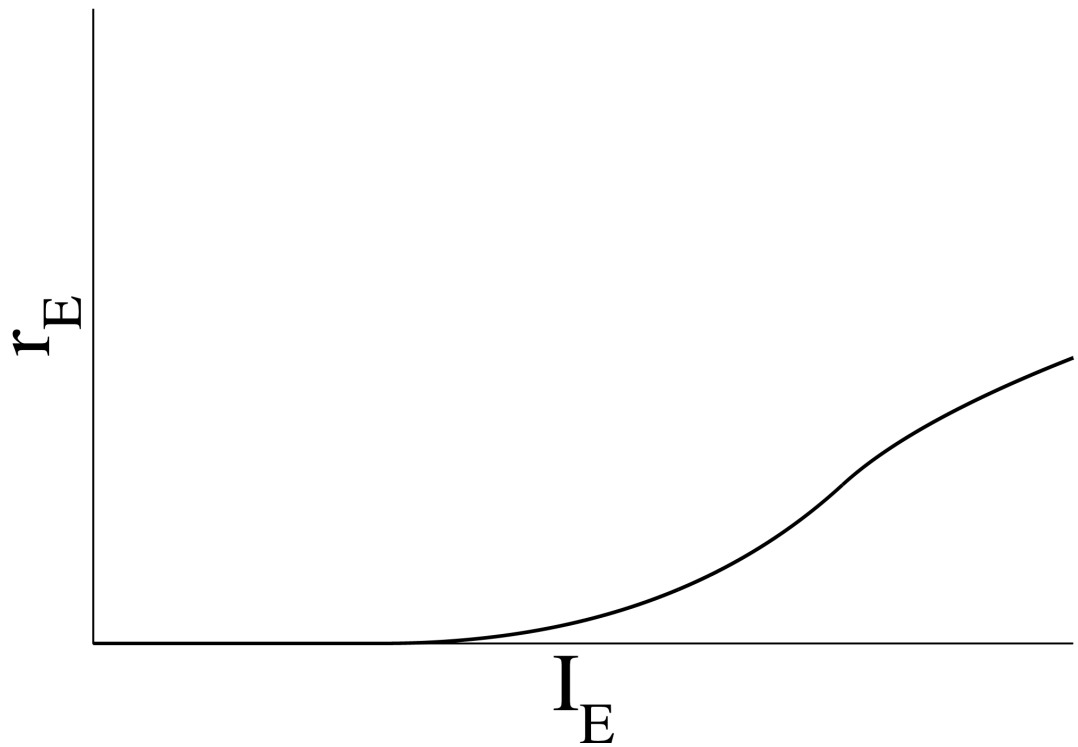
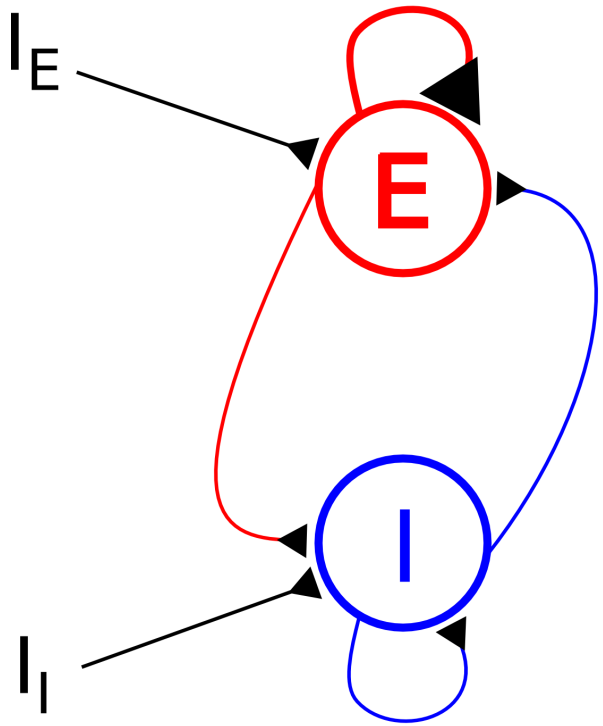
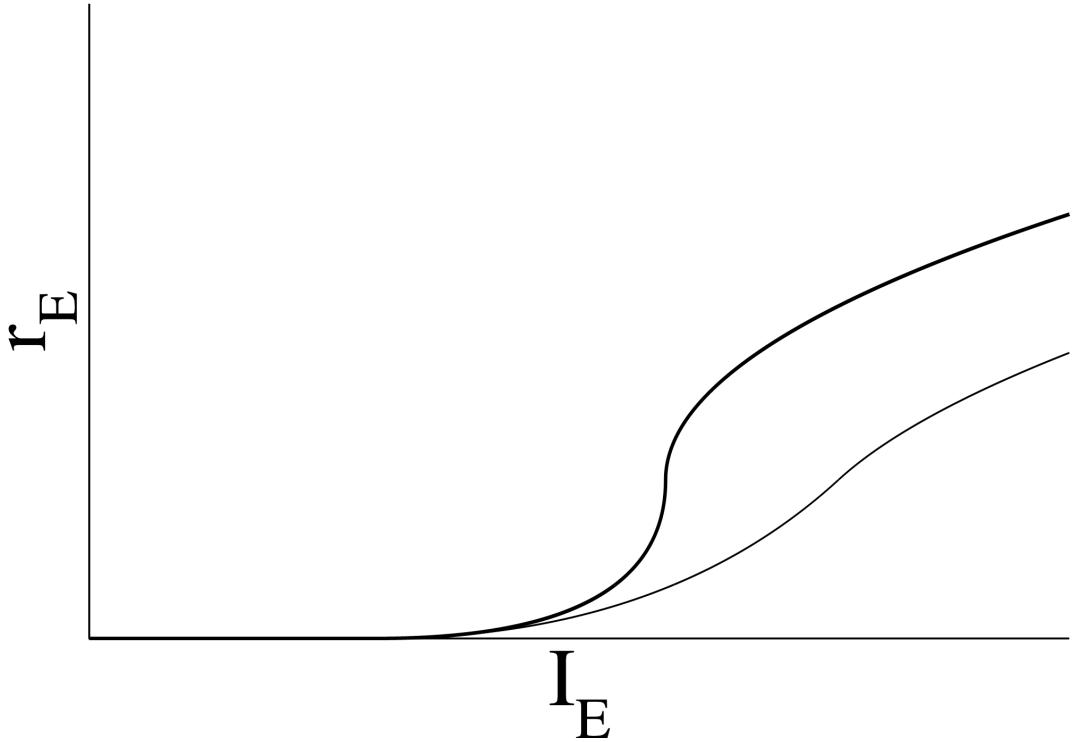
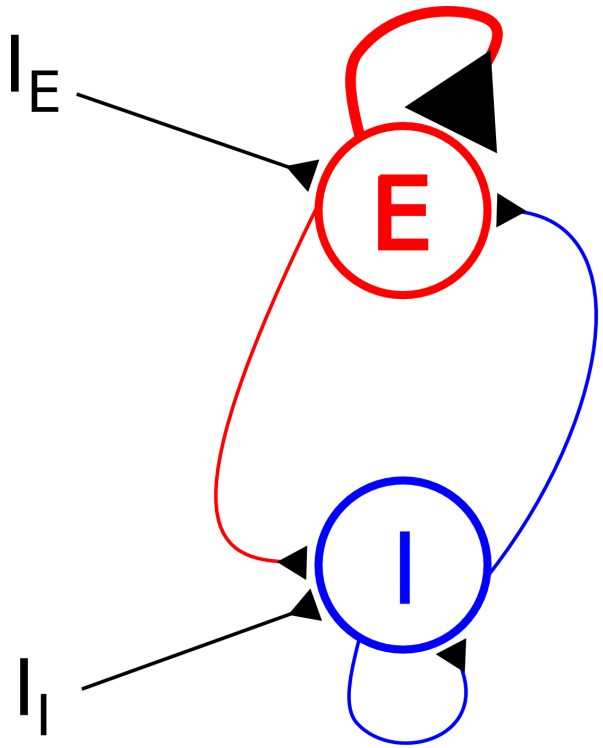
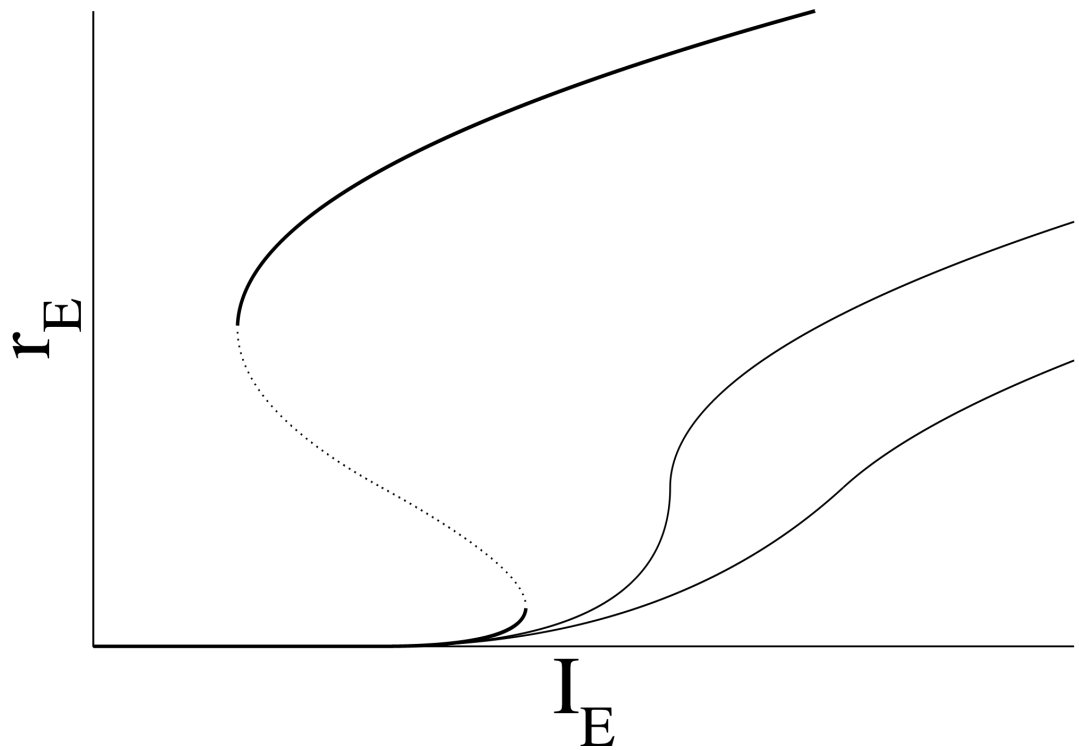

I_E
E
I
I_I

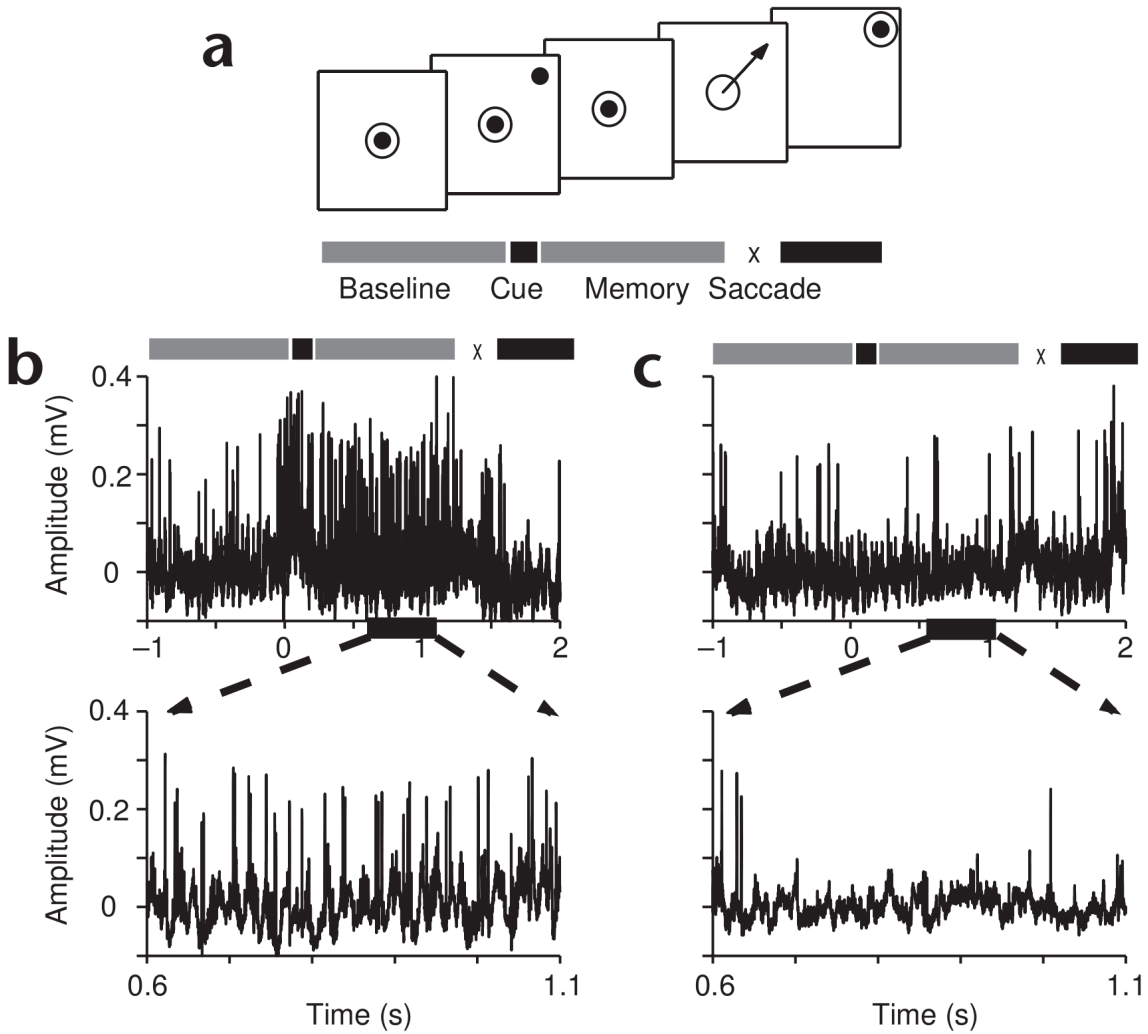

r_E
I_E


I_E
E
I
I_I

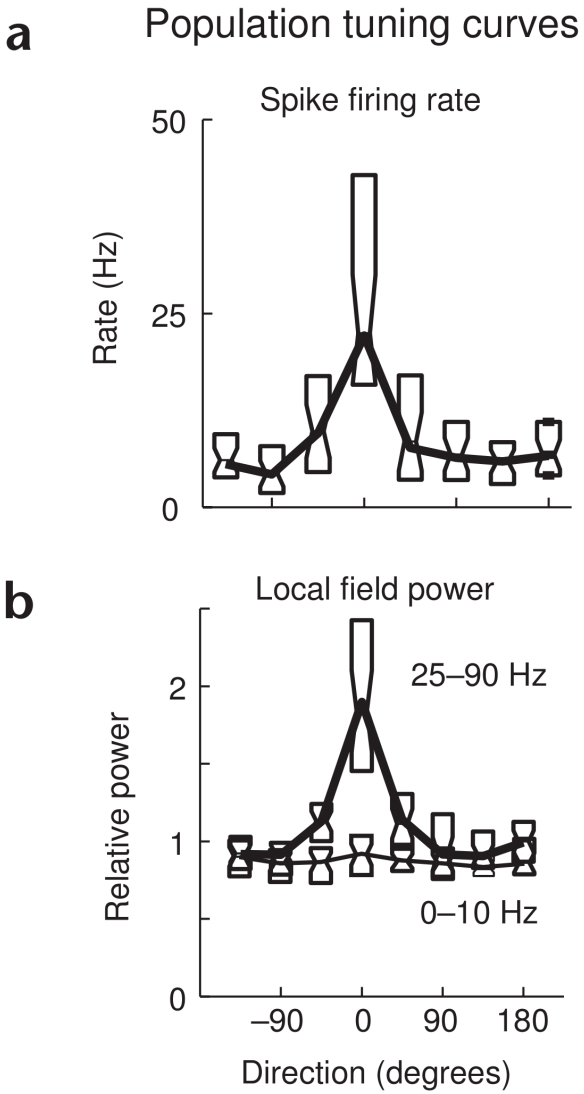

r_E
I_E

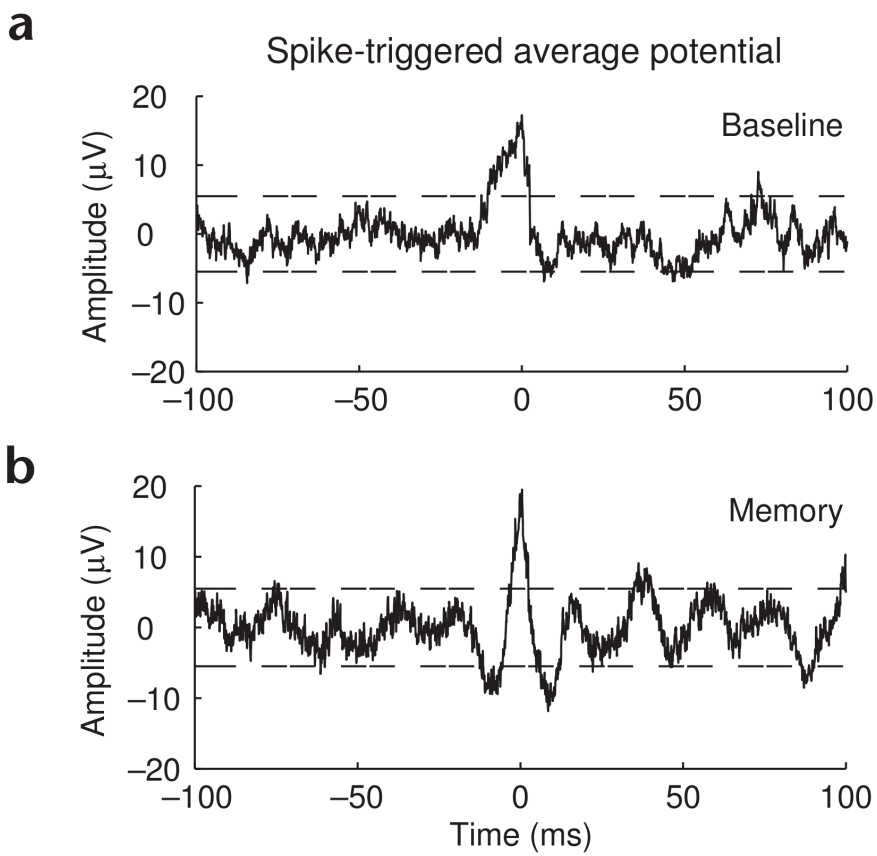

I_E
E
I
I_I


r_E
I_E

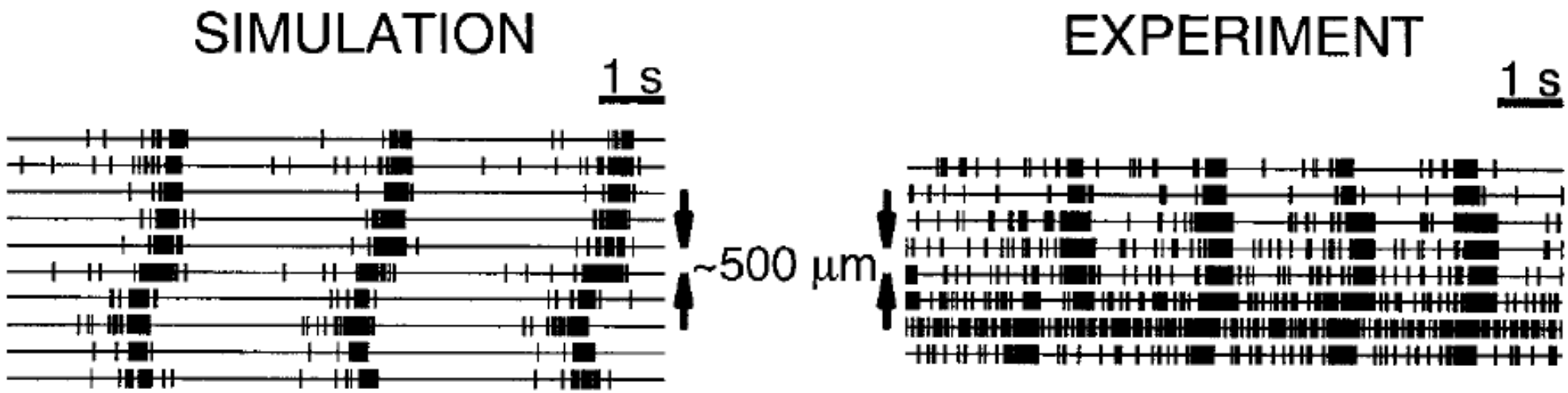


Pesaran et al. Nat. Neurosci. 2002

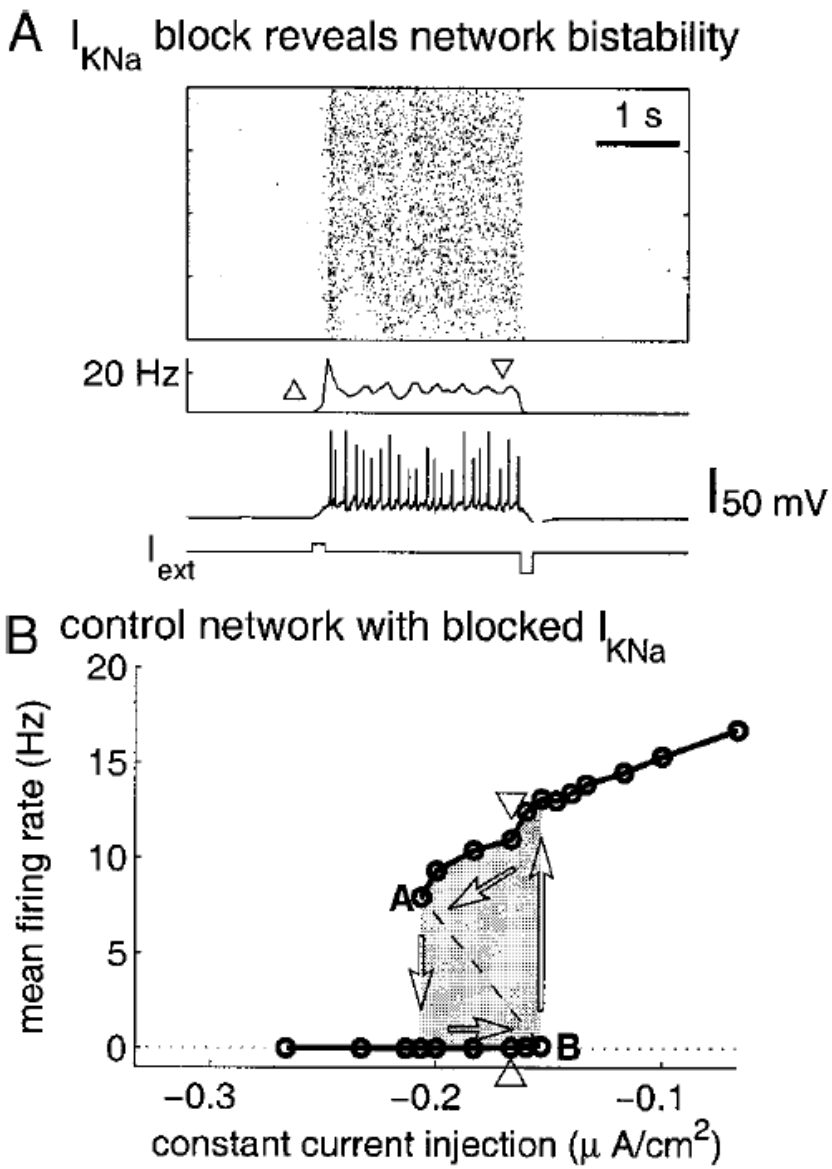




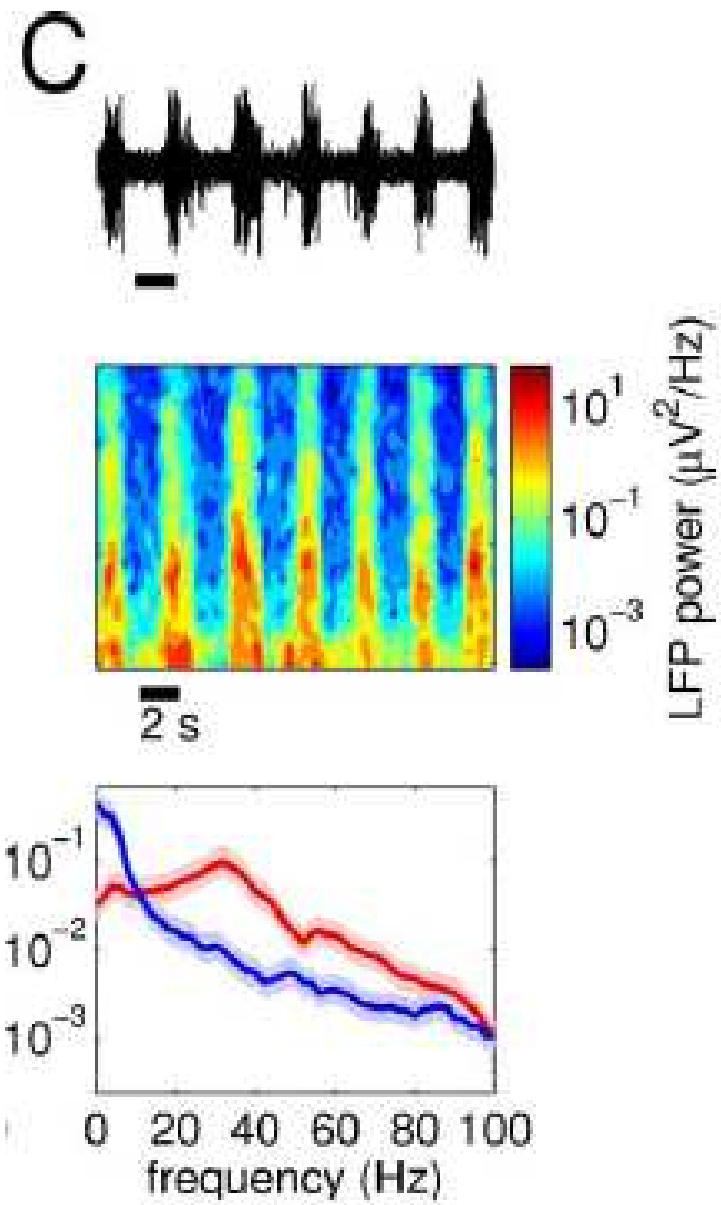
Pesaran et al. Nat. Neurosci. 2002



Compte et al. J. Neurophysiol. 2003

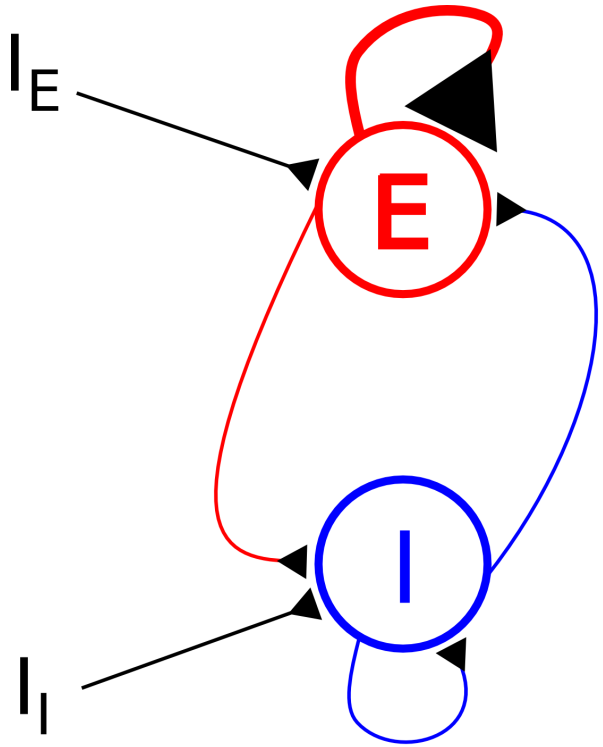


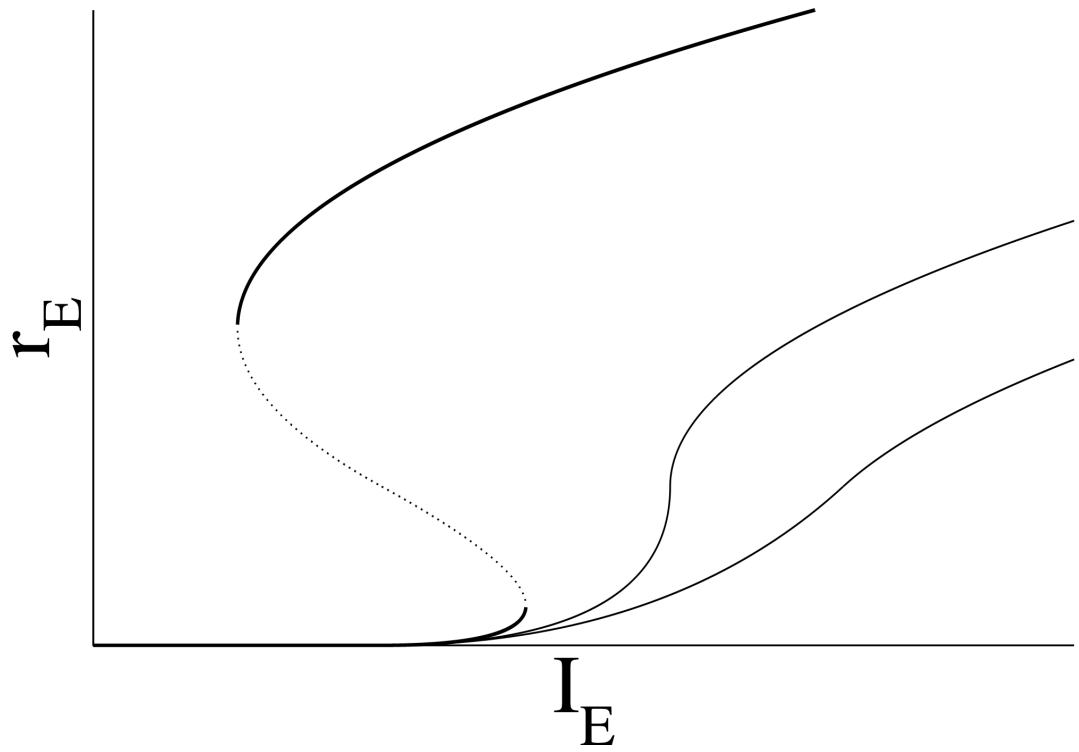
Compte et al. J. Neurophysiol. 2003



Compte et al. J. Neurosci. 2008

... and oscillations?





Two types of firing rate synchrony in E-I networks

(Brunel and Wang 2003)

1. Strong inhibition: “fast” oscillations. Frequency set by synaptic kinetics.
2. Strong excitation, slow inhibition: “slow” oscillations. Frequency an emergent property.

In the bistable regime:

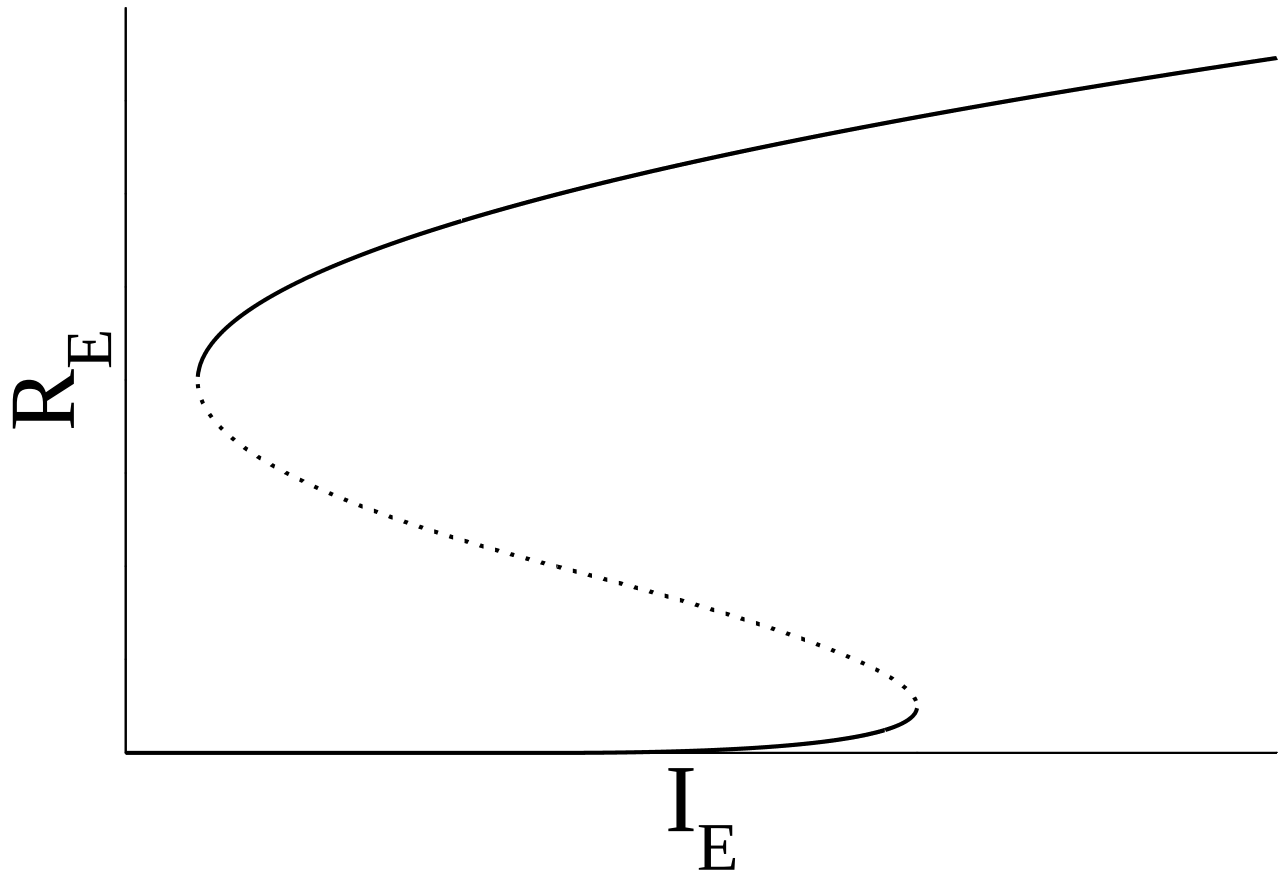
- Slow oscillations dominate
- Oscillations arise via a Takens-Bogdanov bifurcation (Hoppensteadt and Izhikevich 1997, Hansel and Mato 2003)

Outline:

1. Study firing rate model (Wilson-Cowan equation)
2. Confirm results in network simulation of LIF neurons
3. Look at slow-wave data from anesthetized rat

Takens Bogdanov in the Firing Rate Model

$$
\begin{aligned}
\dot{r}_E &= -r_E + \Phi_E(g_{EE} \cdot r_E - g_{EI} \cdot r_I + I_E), \\
\tau \cdot \dot{r}_I &= -r_I + \Phi_I(g_{IE} \cdot r_E - g_{II} \cdot r_I + I_I).
\end{aligned}
$$



$$(r_E, r_I) = (R_E, R_I) + (\delta r_E, \delta r_I)e^{\lambda t}$$

$$\boxed{\begin{aligned}\dot{r}_E &= -r_E + \Phi_E\Big(g_{EE}\cdot r_E - g_{EI}\cdot r_I + I_E\Big),\\ \tau\cdot\dot{r}_I &= -r_I + \Phi_I\Big(g_{IE}\cdot r_E - g_{II}\cdot r_I + I_I\Big).\end{aligned}}$$

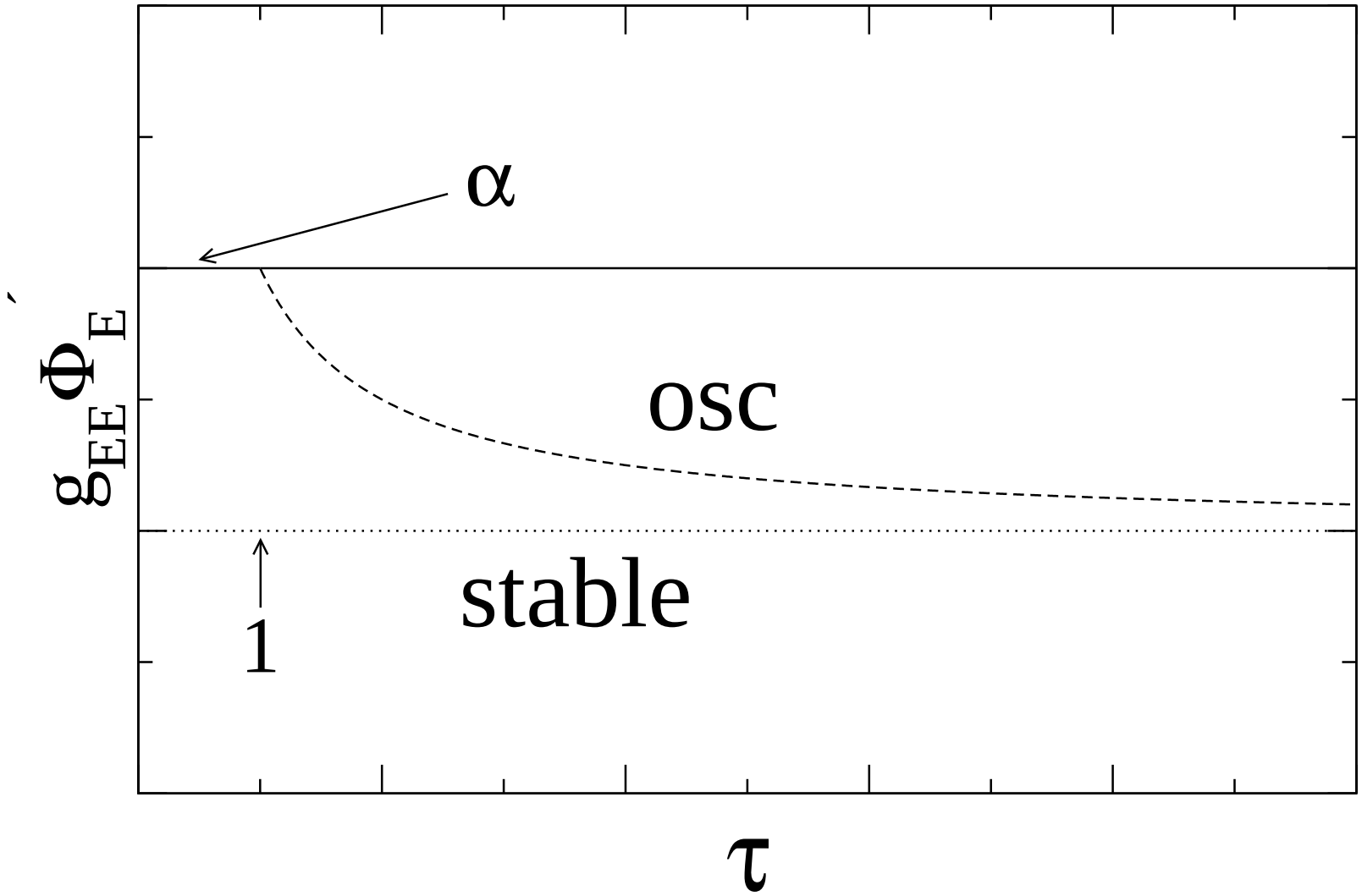
Take: $\lambda = i\omega$, i.e. on the stability boundary

$$-\tau\omega^2 + i\omega\Big(1 + g_{II}\Phi_I^{'} + \tau(1 - g_{EE}\Phi_E^{'})\Big)$$
$$+(1 + g_{II}\Phi_I^{'})(1 - g_{EE}\Phi_E^{'}) + g_{EI}g_{IE}\Phi_I^{'}\Phi_E^{'} = 0$$

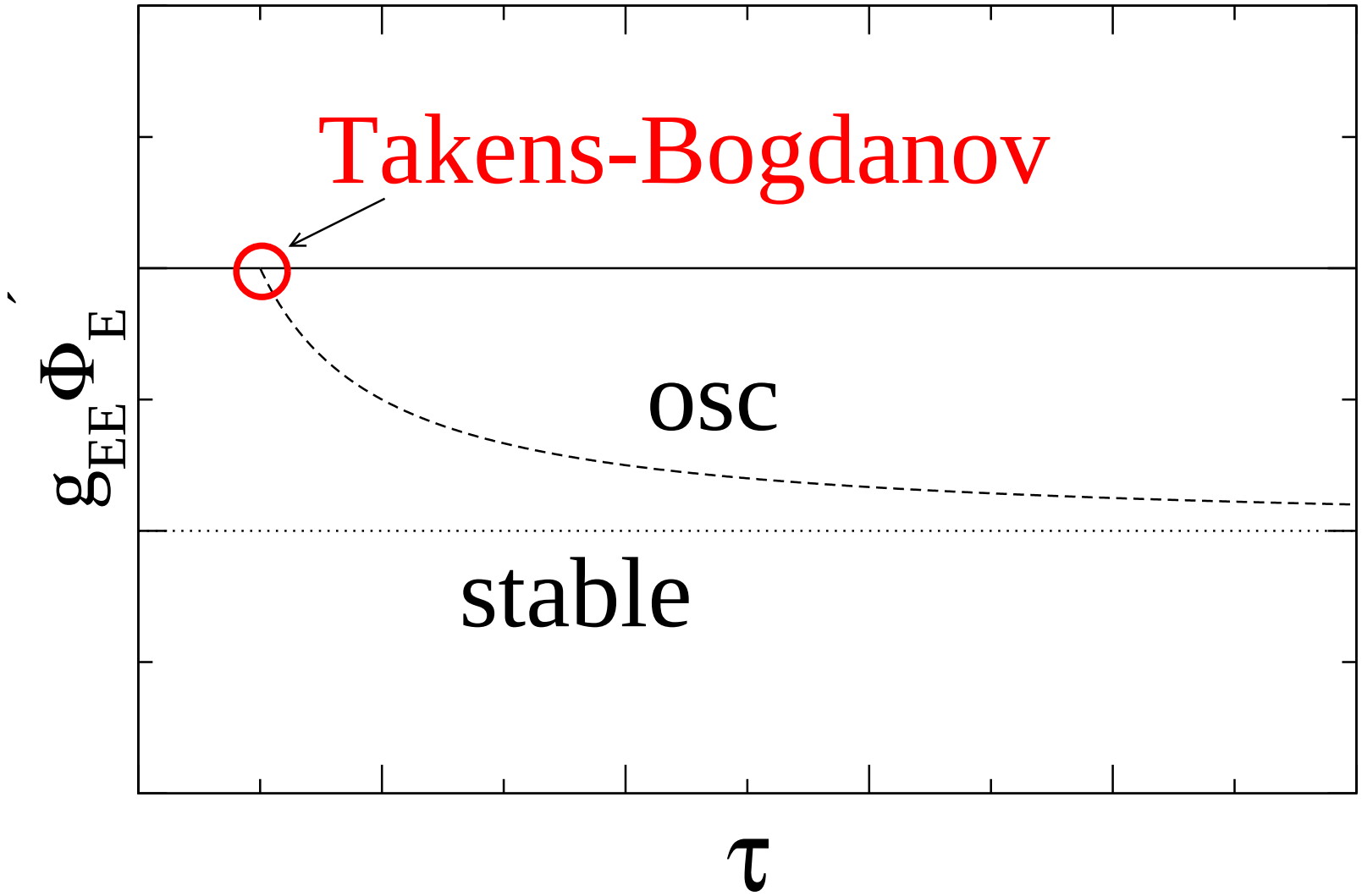
1. Steady Instability: $\omega = 0$
2. Oscillatory Instability: $\omega \neq 0$

Wilson and Cowan 1972, Ermentrout and Cowan 1979

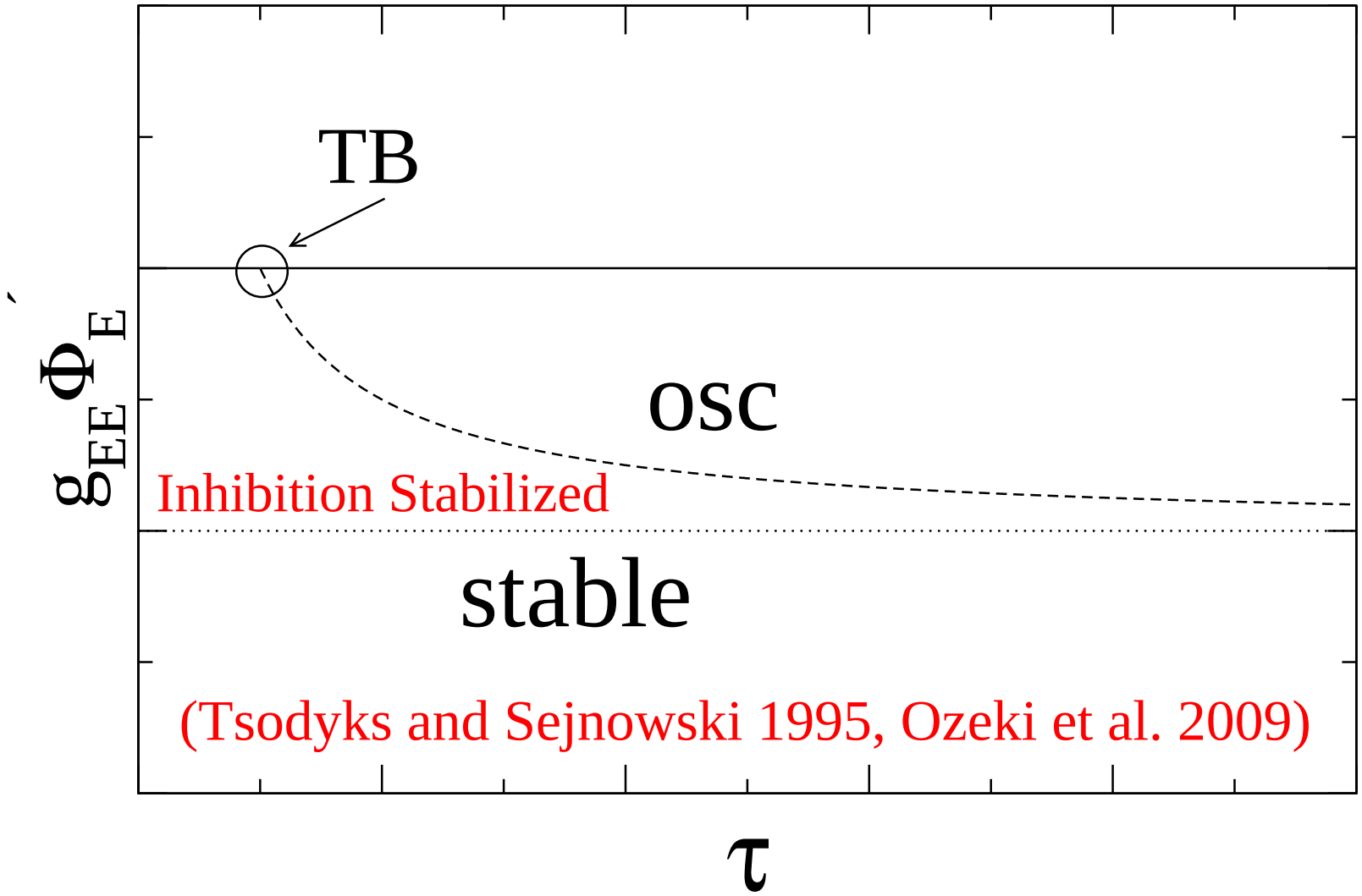
λ **= 0:**	λ **=** $\pm i\omega$**:**
$g_{EE}\Phi_E^{'} = \alpha$	$g_{EE}\Phi_E^{'} = 1 + \beta/\tau, \tau\omega^2 = \alpha - g_{EE}\Phi_E^{'}$



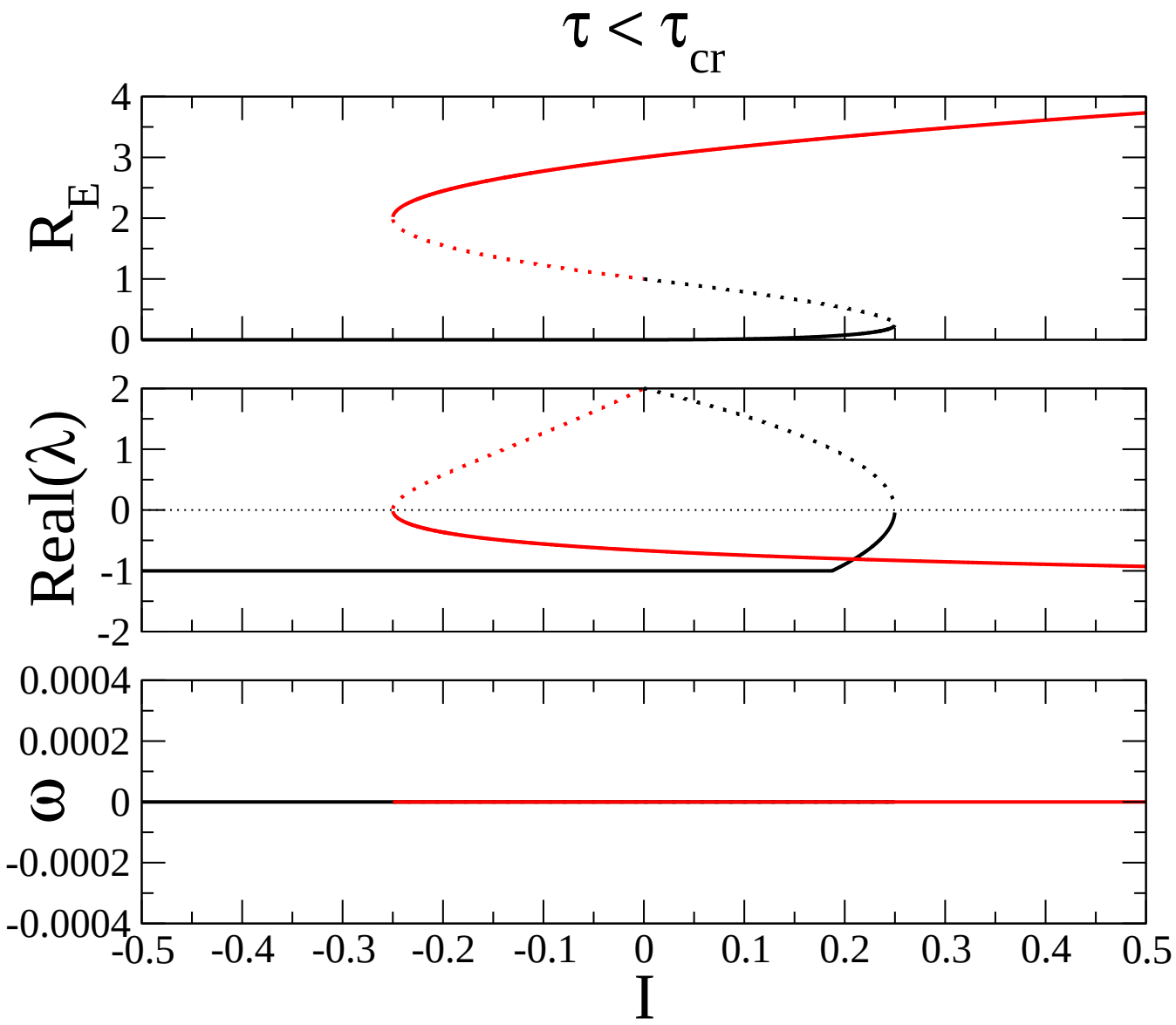
λ = 0:	$\lambda = \pm i\omega$:
$\Phi'_E = \alpha$	$\tau\omega^2 = 0$

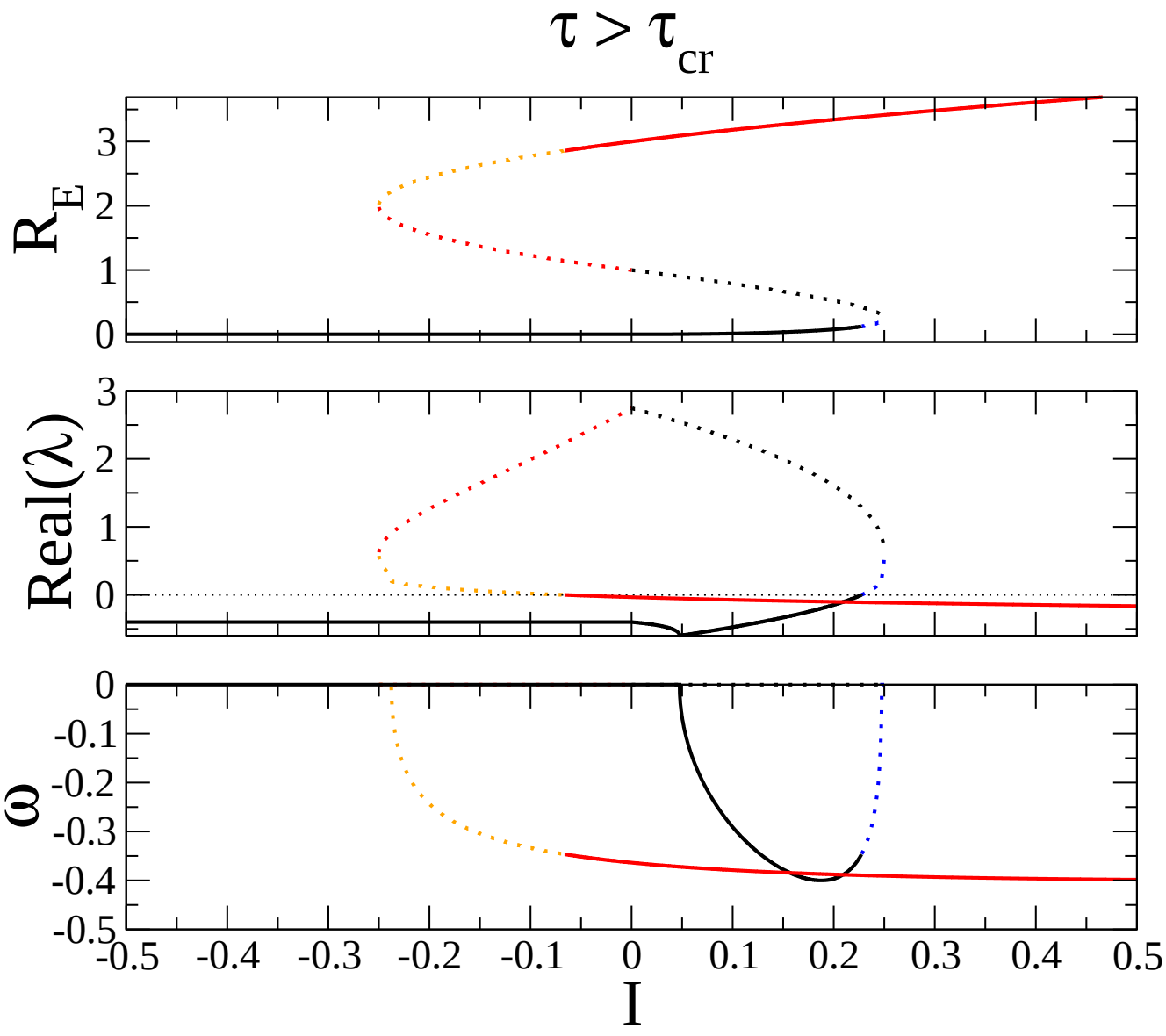


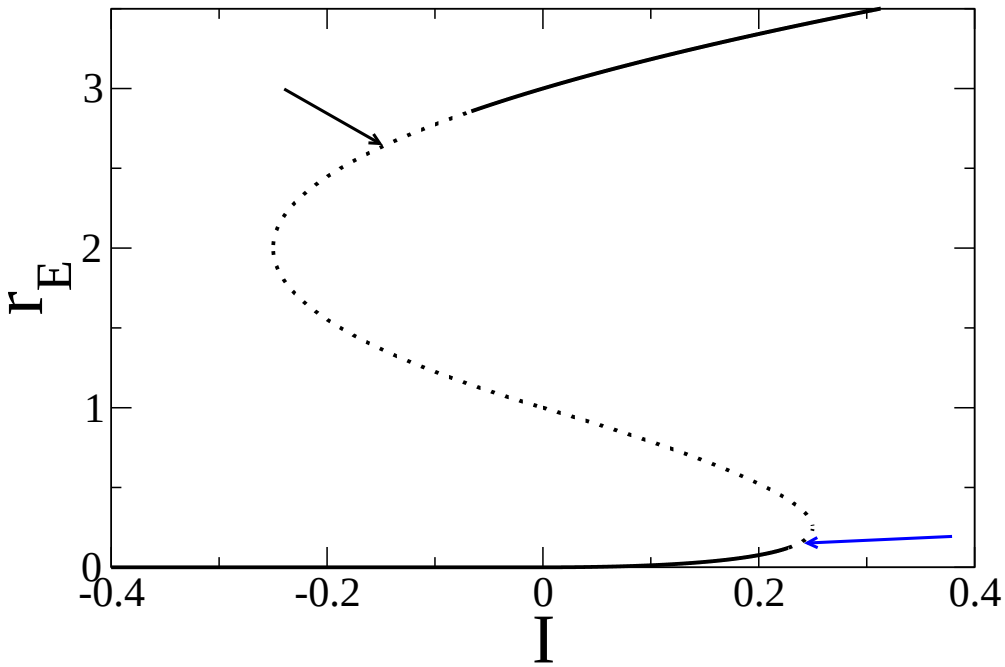
λ = 0:	$\lambda = \pm i\omega$:
$\Phi'_E = \alpha$	$\tau\omega^2 = 0$

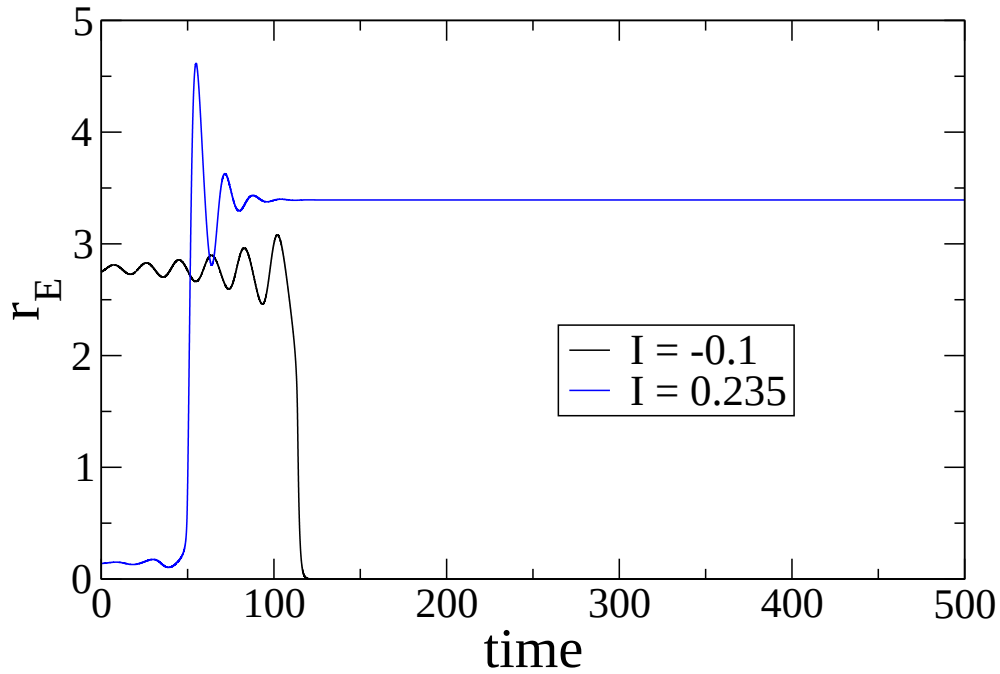


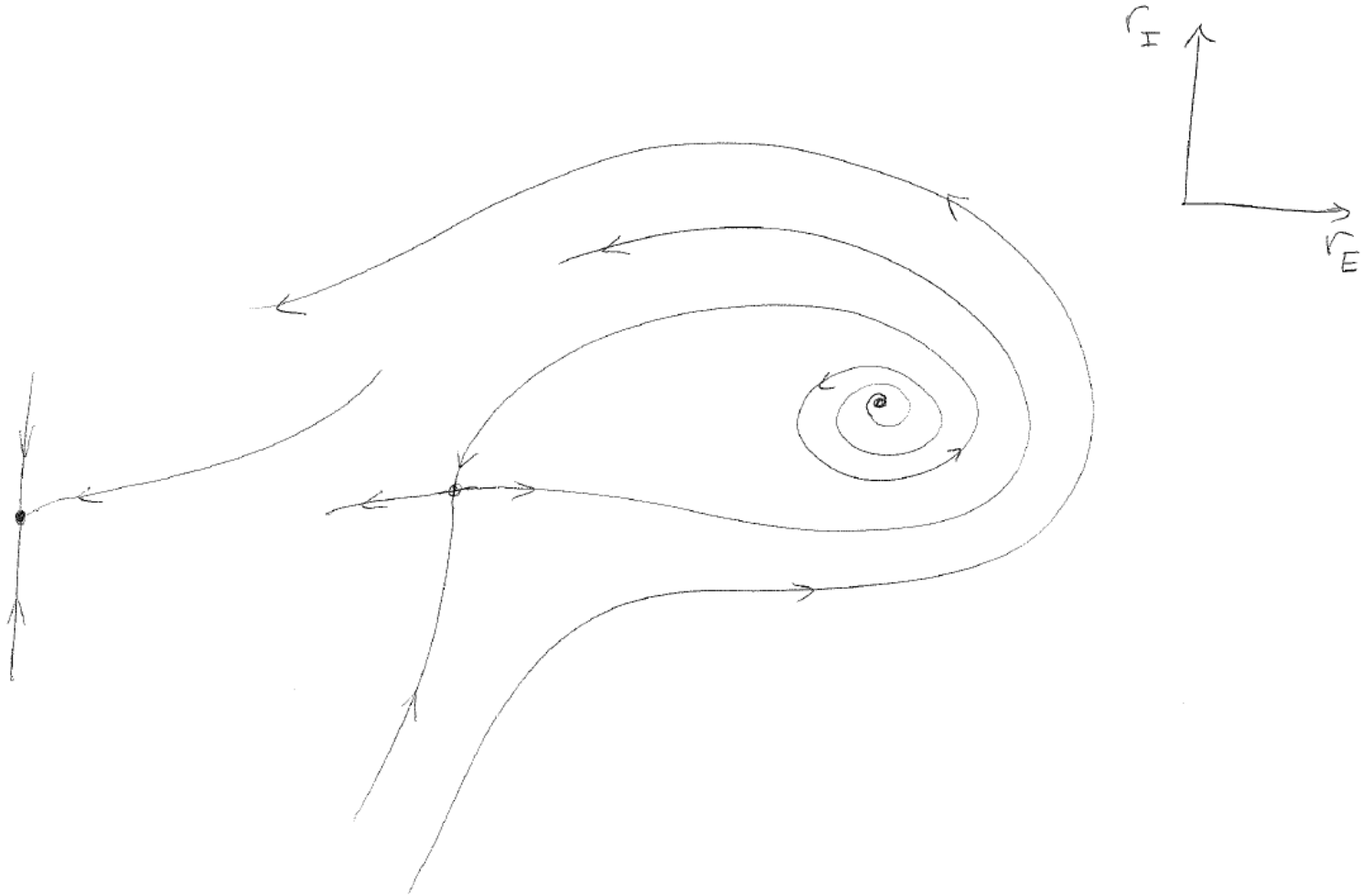
(Tsodyks and Sejnowski 1995, Ozeki et al. 2009)

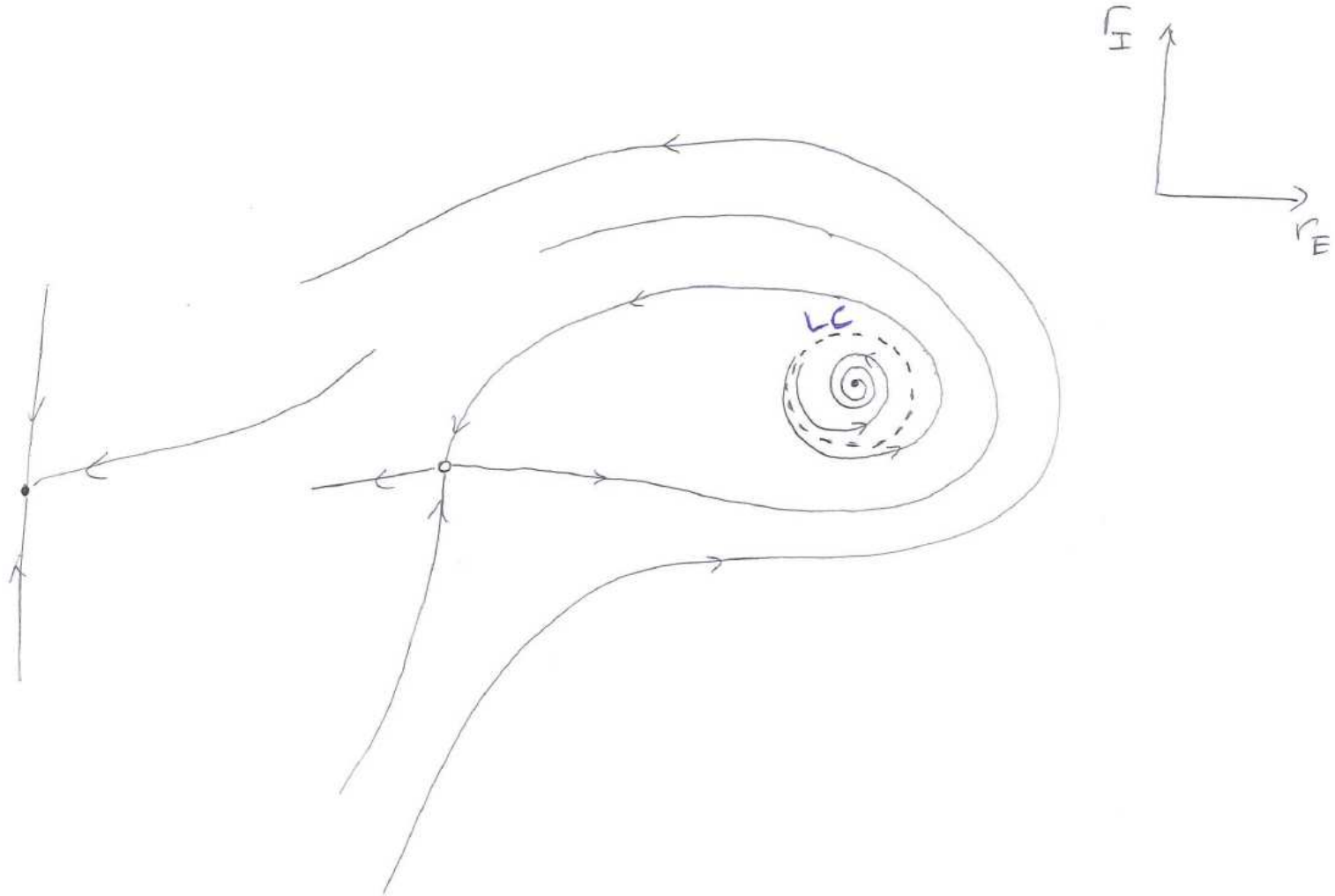

τ < τcr
RE
Real(λ)
ω
I
4
3
2
1
0
2
1
0
-1
-2
0.0004
0.0002
0
-0.0002
-0.0004
-0.5
-0.4
-0.3
-0.2
-0.1
0
0.1
0.2
0.3
0.4
0.5

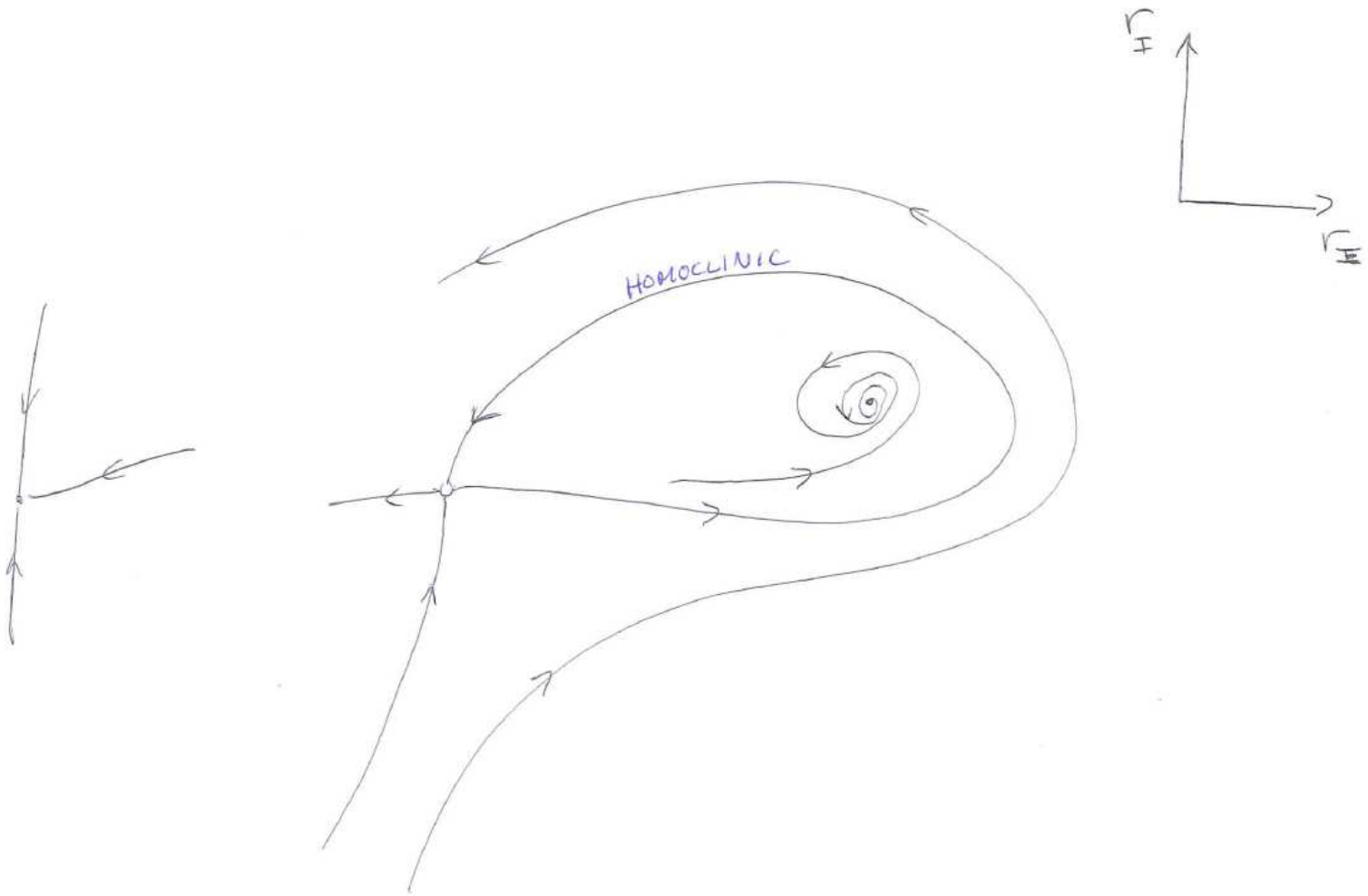

τ > τcr
RE
Real(λ)
ω
I
3
2
1
0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.5
-0.4
-0.3
-0.2
-0.1
0
0.1
0.2
0.3
0.4
0.5

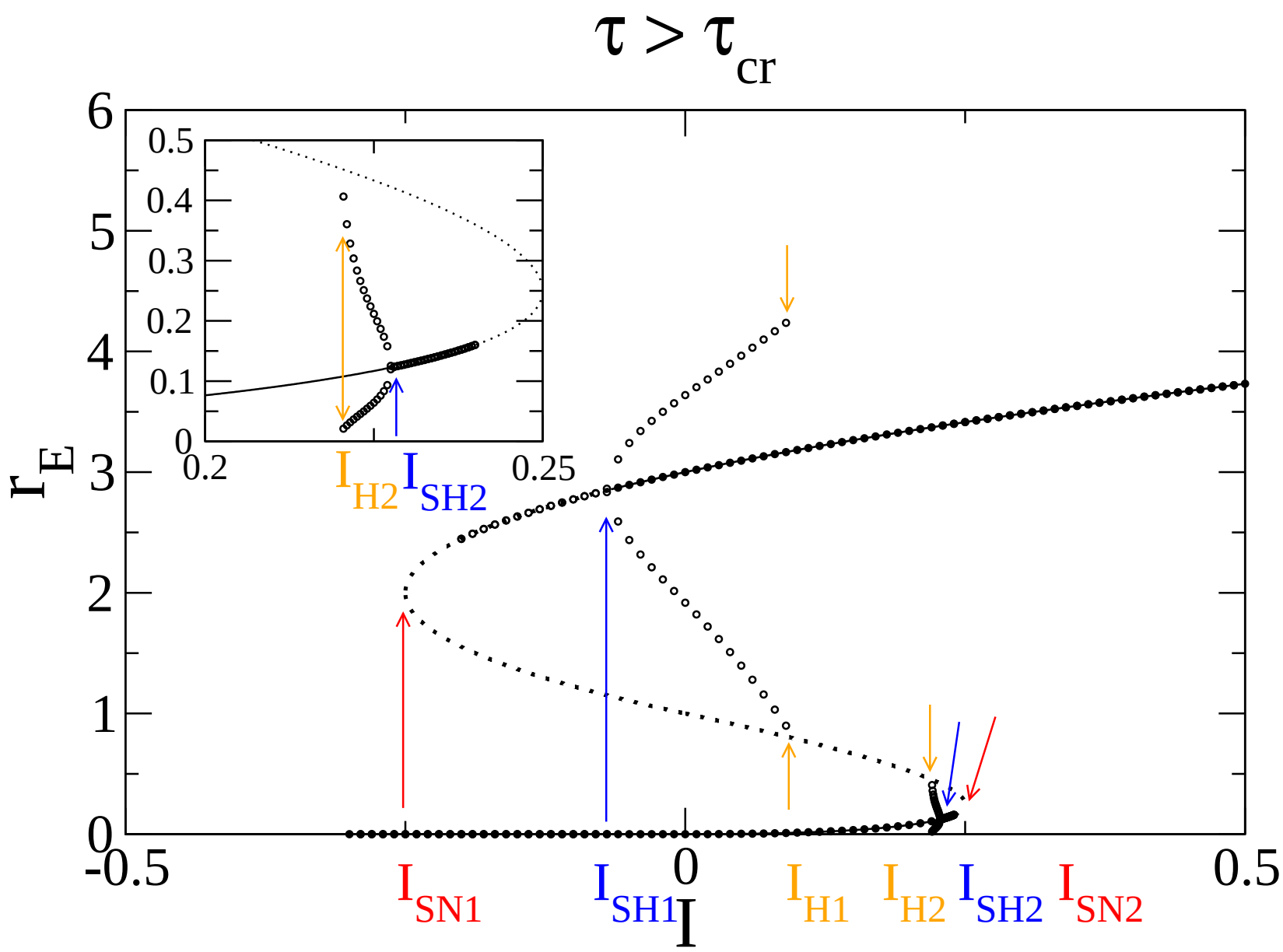

3
2
1
0
-0.4
-0.2
0
0.2
0.4
I
r_E


5
4
3
2
1
0
0
100
200
300
400
500
time
r_E
I = -0.1
I = 0.235


r_I
r_E


r_I
r_E
LC


r_I
r_E
HOMOCLINIC

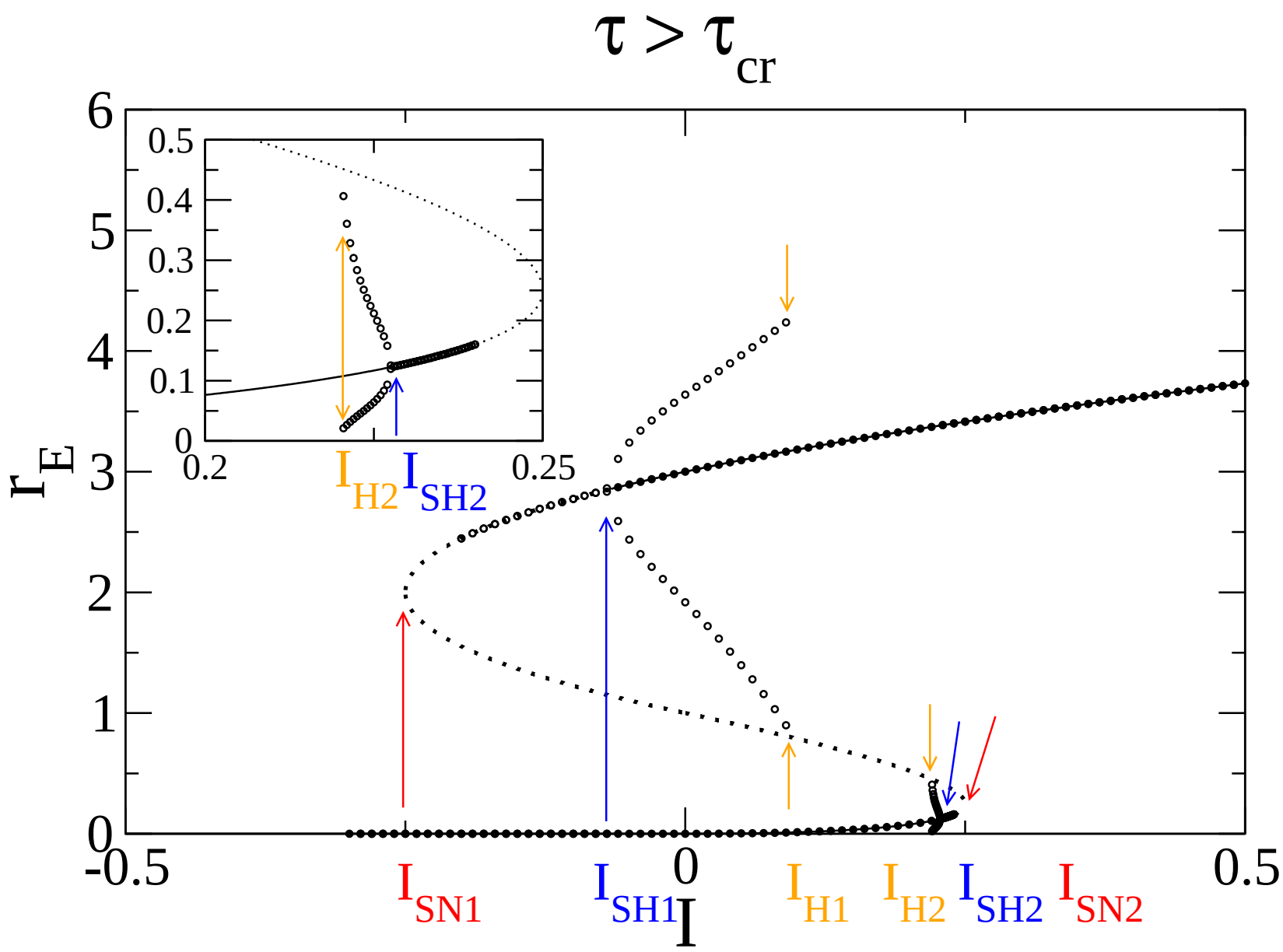

τ > τcr
rE
I
6
5
4
3
2
1
0
-0.5
0
0.5
ISN1
ISH1
IH1
IH2
ISH2
ISN2
0.5
0.4
0.3
0.2
0.1
0
0.2
0.25
IH2
ISH2

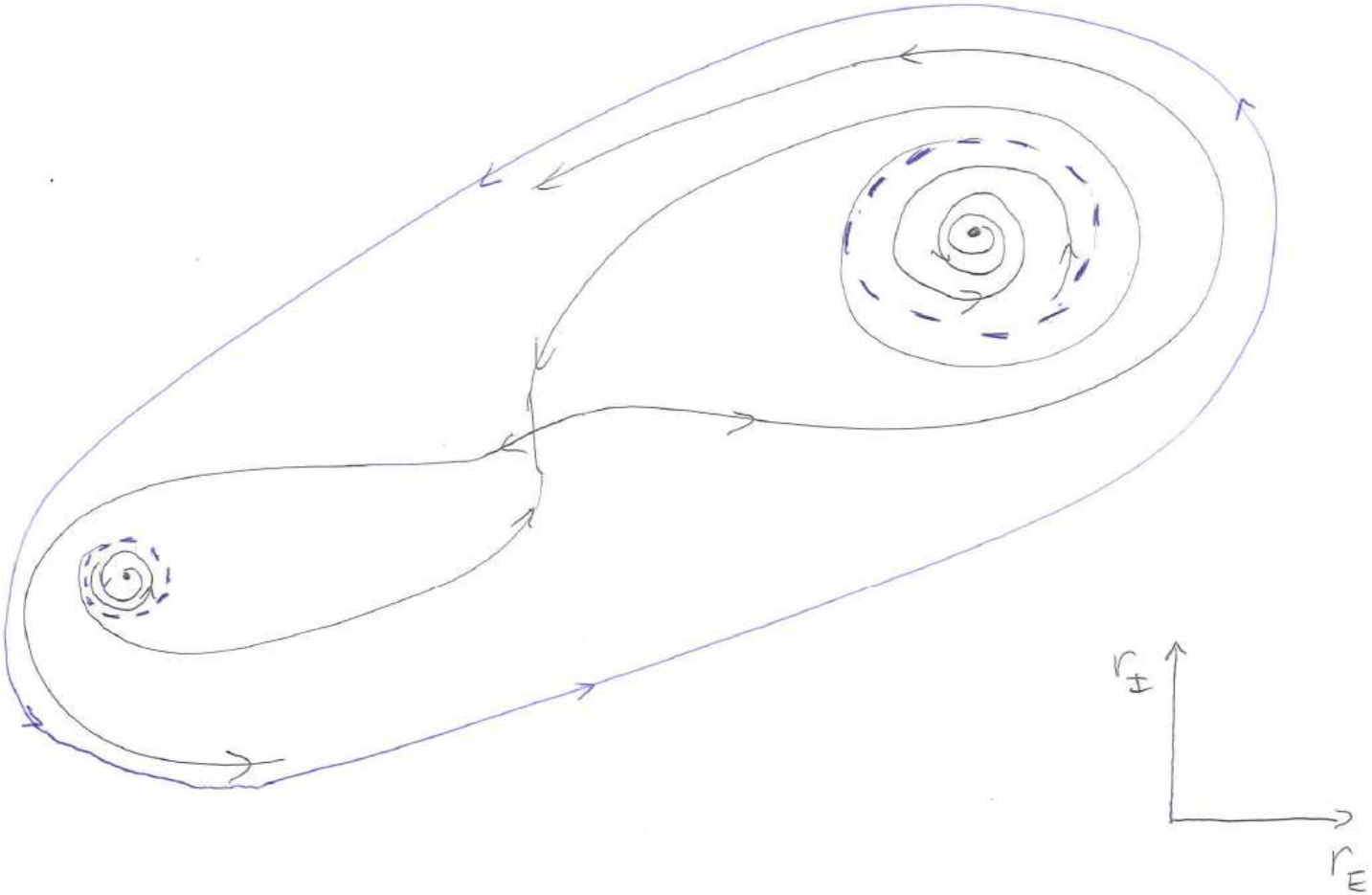
Can determine bifurcation structure analytically

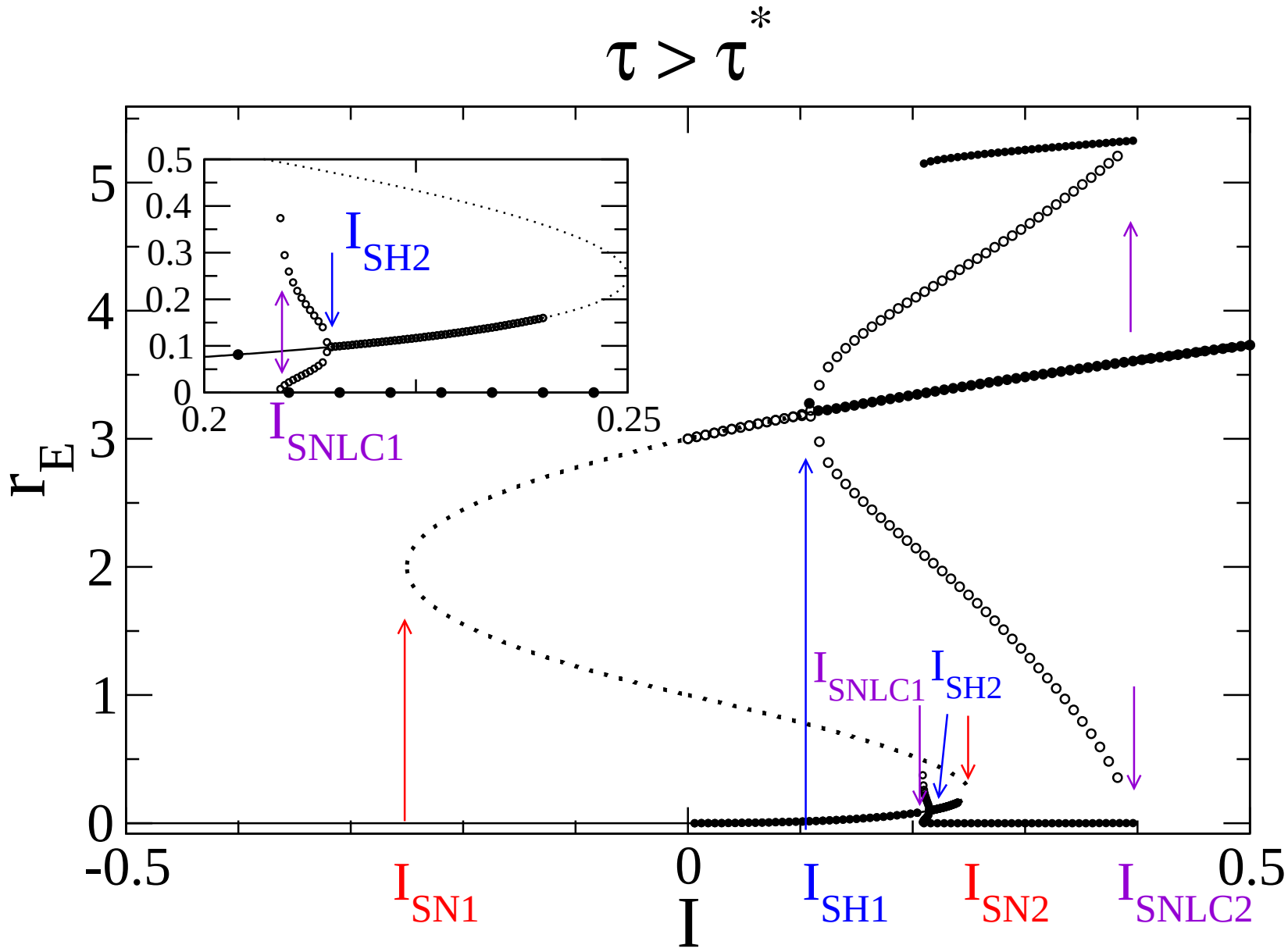
(Guckenheimer and Holmes)

$$(r_E, r_I) = (R_E, R_I) + X(T) \cdot \phi + Y(T) \cdot \psi + ...$$

$$\begin{aligned} \partial_T X &= Y, \\ \partial_T Y &= \mu_1 + \mu_2 Y + a_1 X^2 + a_2 XY \end{aligned}$$


τ > τcr
rE
I
6
5
4
3
2
1
0
-0.5
0
0.5
ISN1
ISH1
IH1
IH2
ISH2
ISN2
0.5
0.4
0.3
0.2
0.1
0
0.2
0.25
IH2
ISH2


r_I
r_E


τ > τ*
r_E
I
-0.5
0
0.5
0
1
2
3
4
5
I_SN1
I_SH1
I_SN2
I_SNLC2
I_SNLC1
I_SH2
0.2
0.25
0.1
0.2
0.3
0.4
0.5

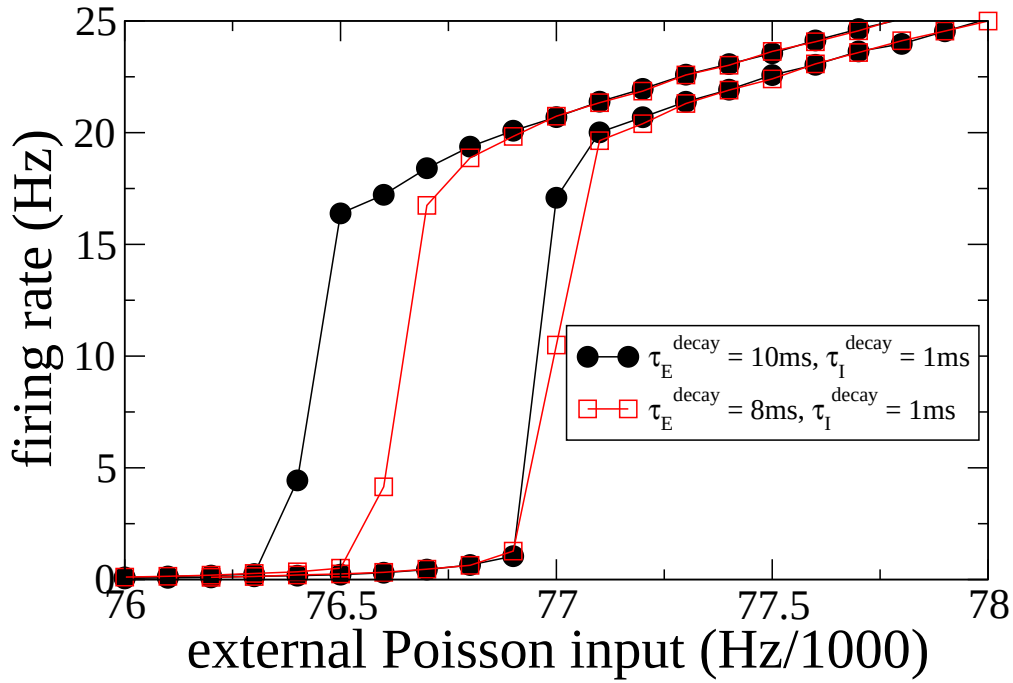
Indirect evidence of TB in network simulations

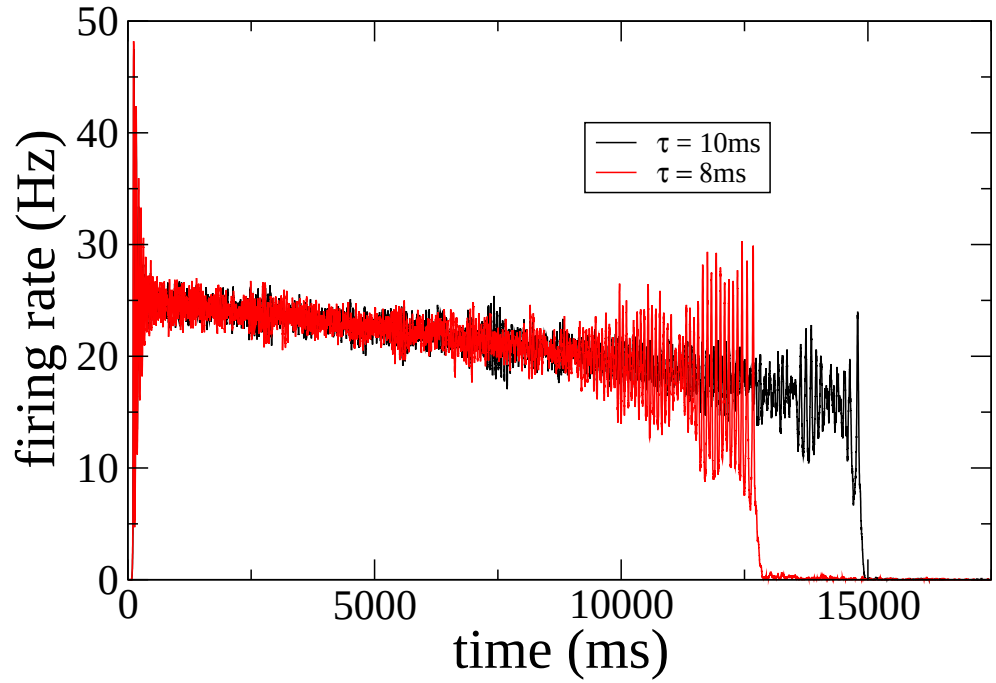
Once in bistable regime, make inhibition slower, and should find:

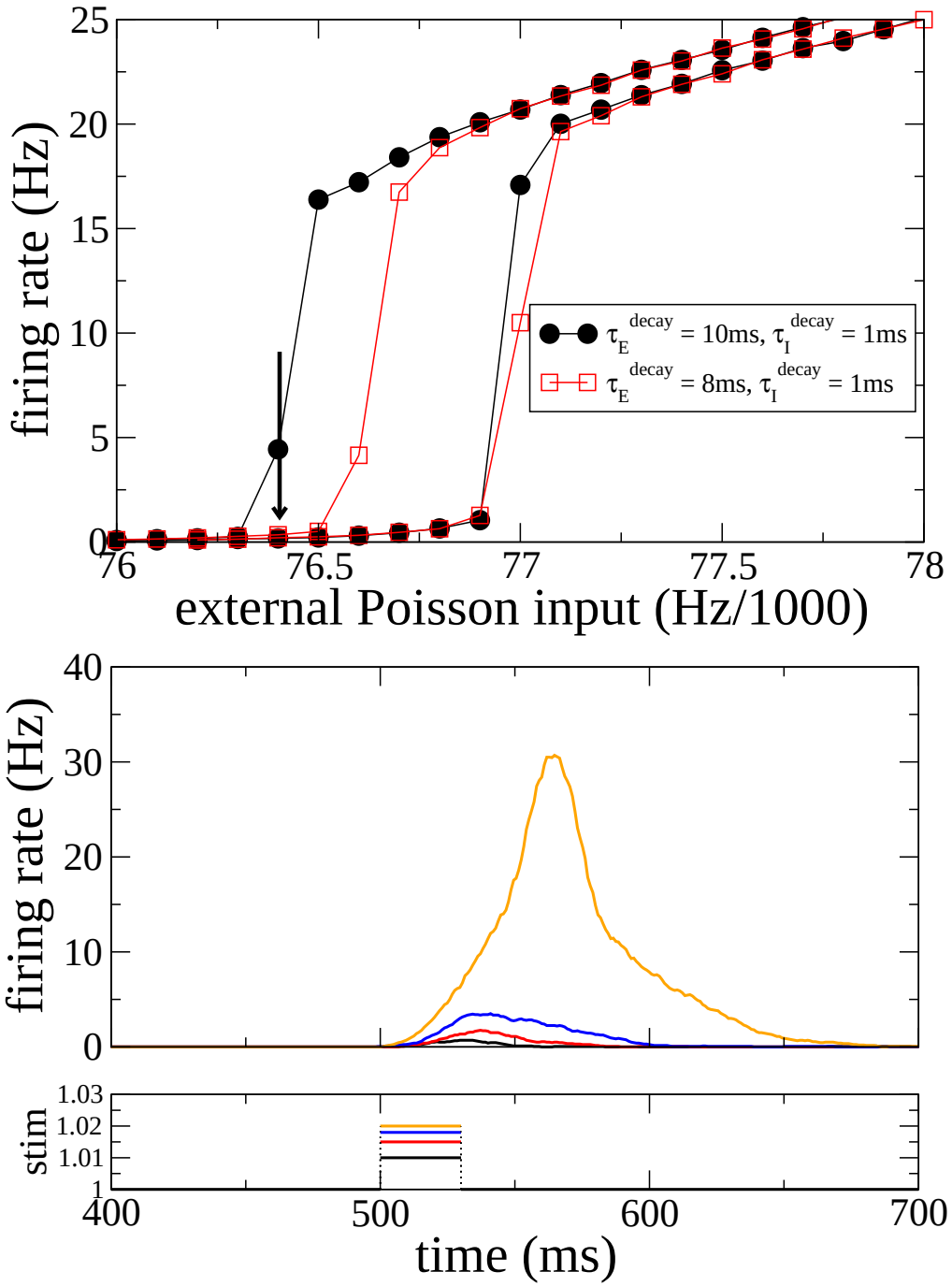
- Population spikes to left of bistable regime.
- Oscillations arise in bistable regime.
- Oscillation amplitude neg. correlated with firing rate.
- Oscillation frequency pos. correlated with firing rate.
- Large amplitude LC for slow enough inhibition.

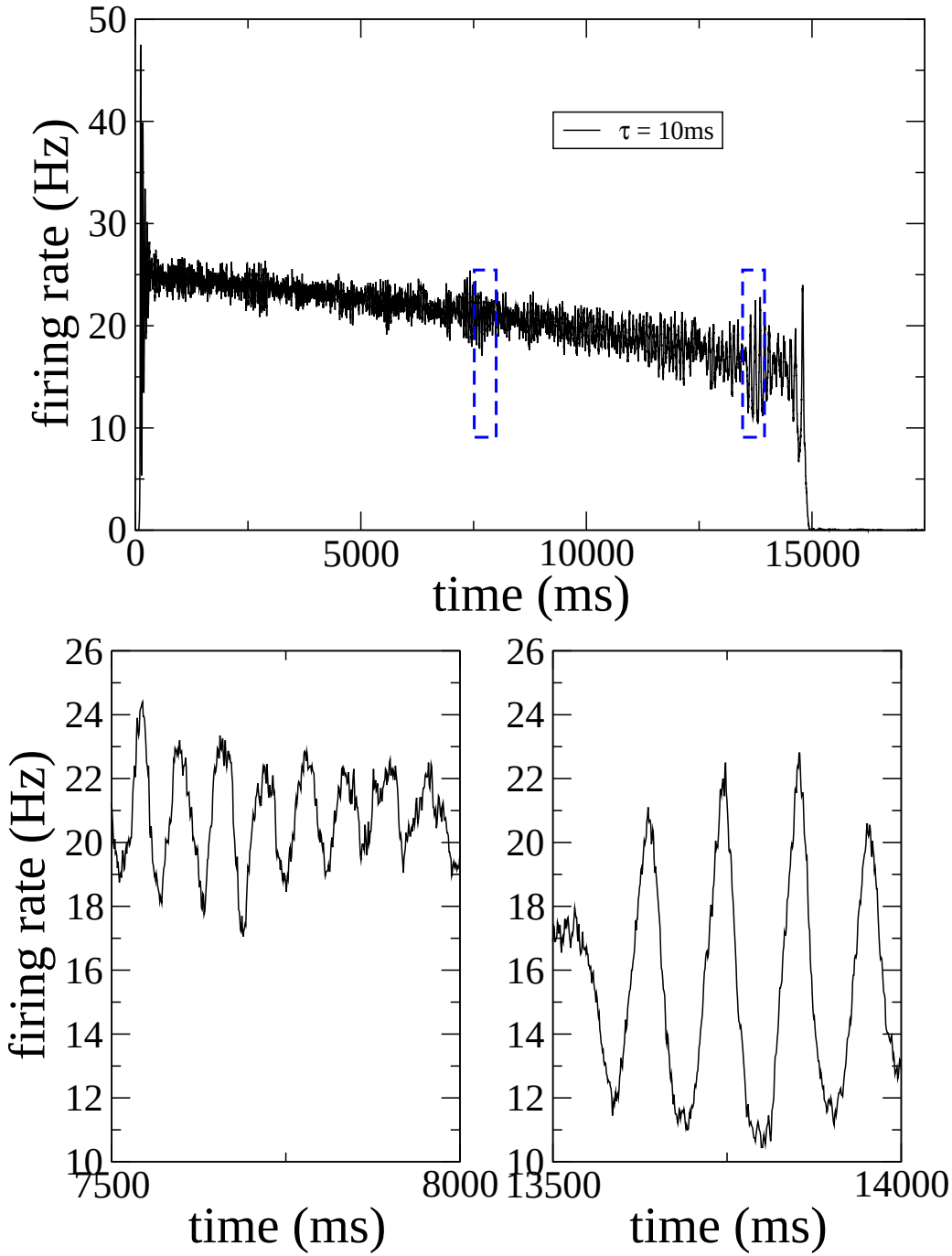
Network Simulations

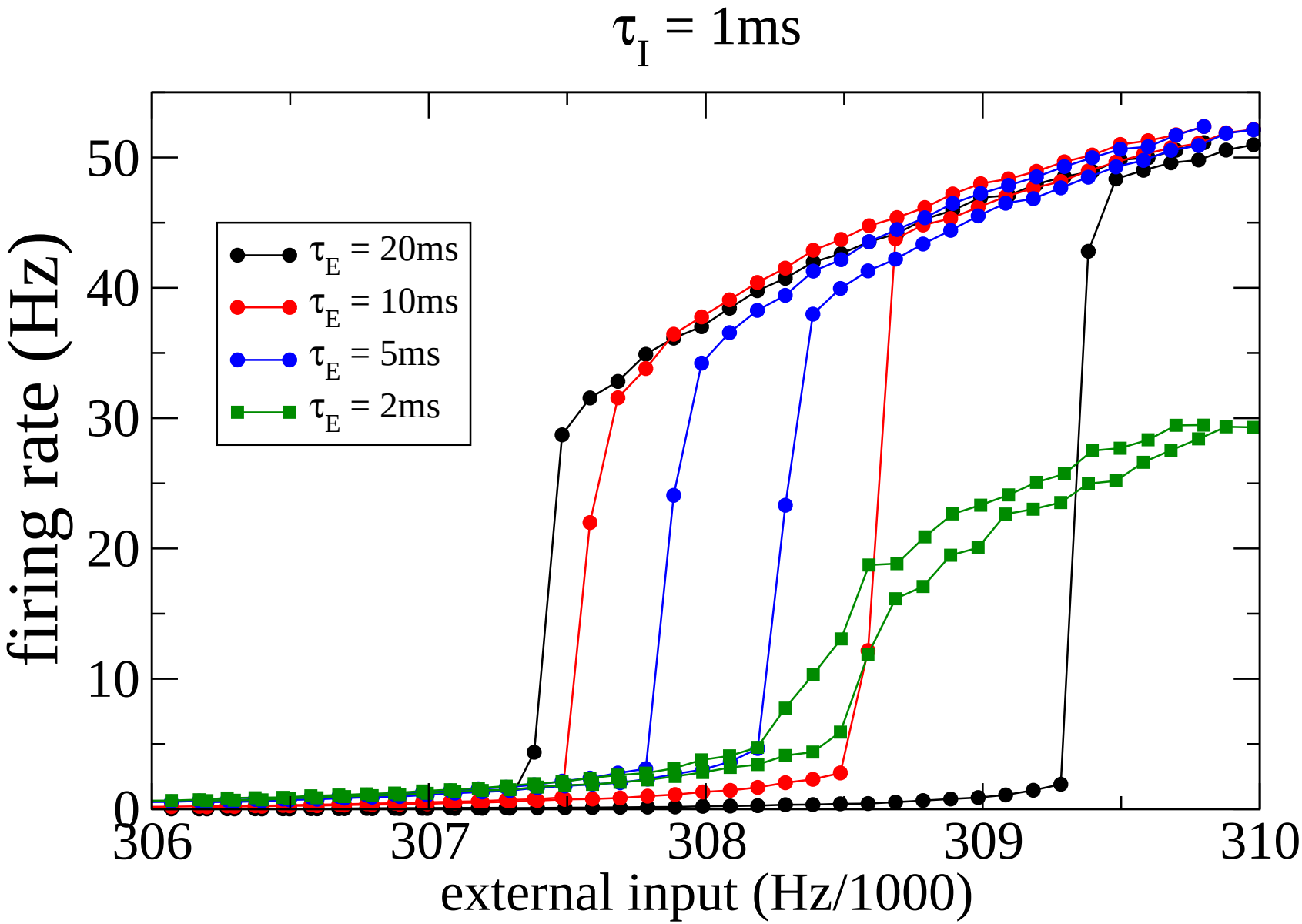
- LIF neurons: 4000 E and 1000 I
- current-based synapses
- all synapses difference-of-exponential
- independent external Poisson synapses for each neuron

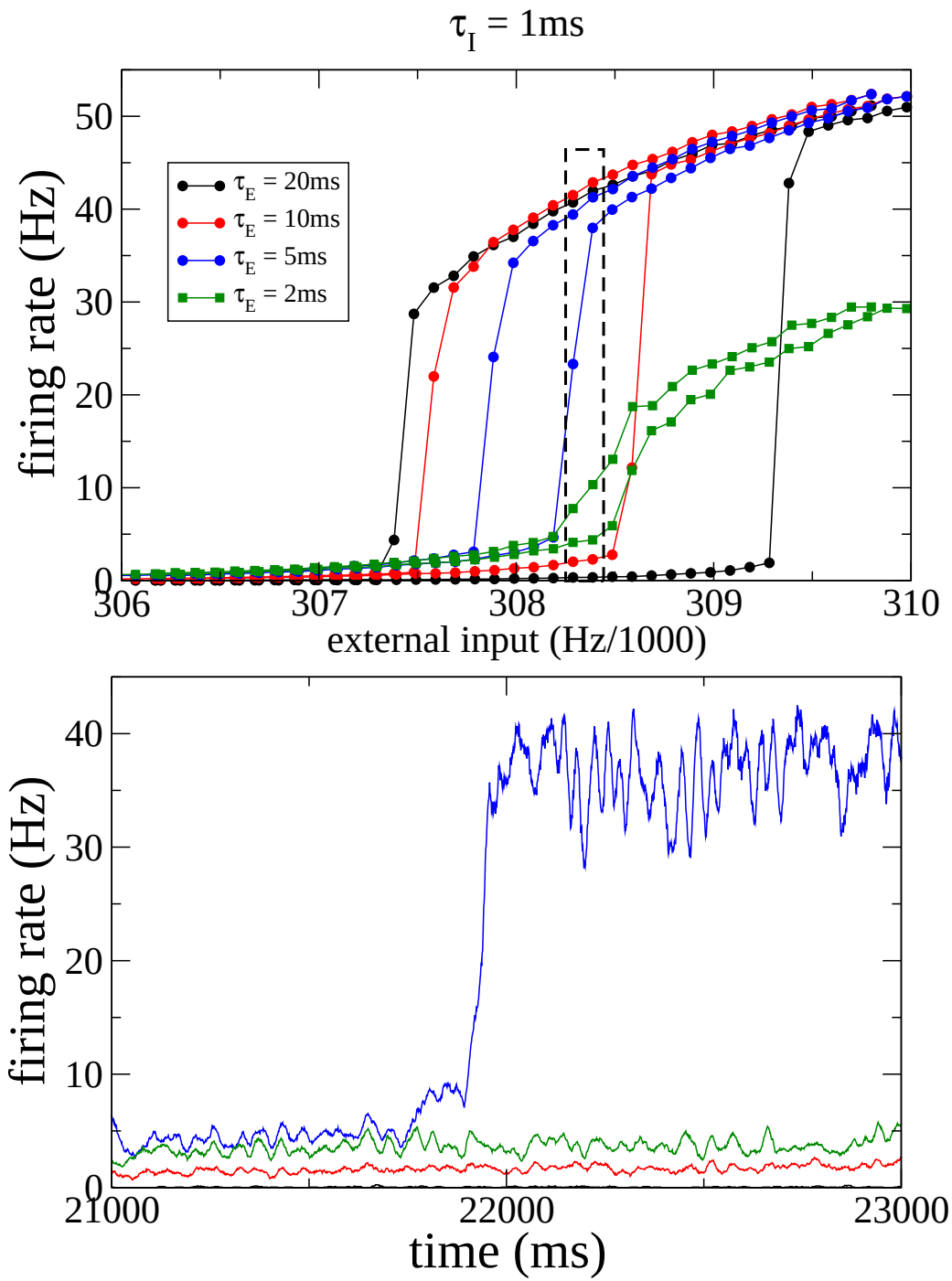

25
20
15
10
5
0
76
76.5
77
77.5
78
firing rate (Hz)
external Poisson input (Hz/1000)
τ_E^{decay} = 10ms, τ_I^{decay} = 1ms
τ_E^{decay} = 8ms, τ_I^{decay} = 1ms

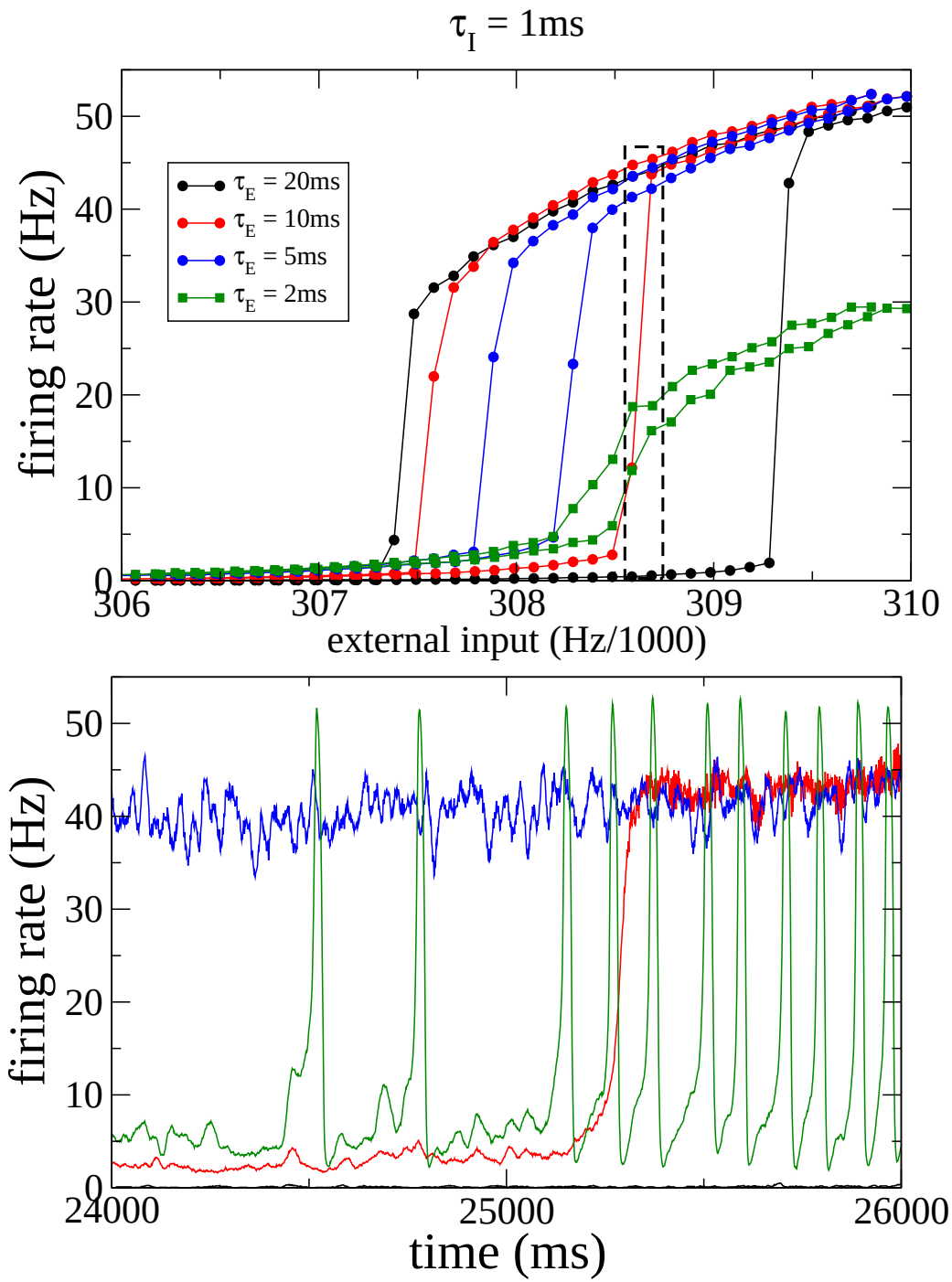

50
40
30
20
10
0
0
5000
10000
15000
firing rate (Hz)
time (ms)
τ = 10ms
τ = 8ms


25
20
15
10
5
0
76
76.5
77
77.5
78
firing rate (Hz)
external Poisson input (Hz/1000)
τ_E^{decay} = 10ms, τ_I^{decay} = 1ms
τ_E^{decay} = 8ms, τ_I^{decay} = 1ms
40
30
20
10
0
firing rate (Hz)
1.03
1.02
1.01
1
stim
400
500
600
700
time (ms)

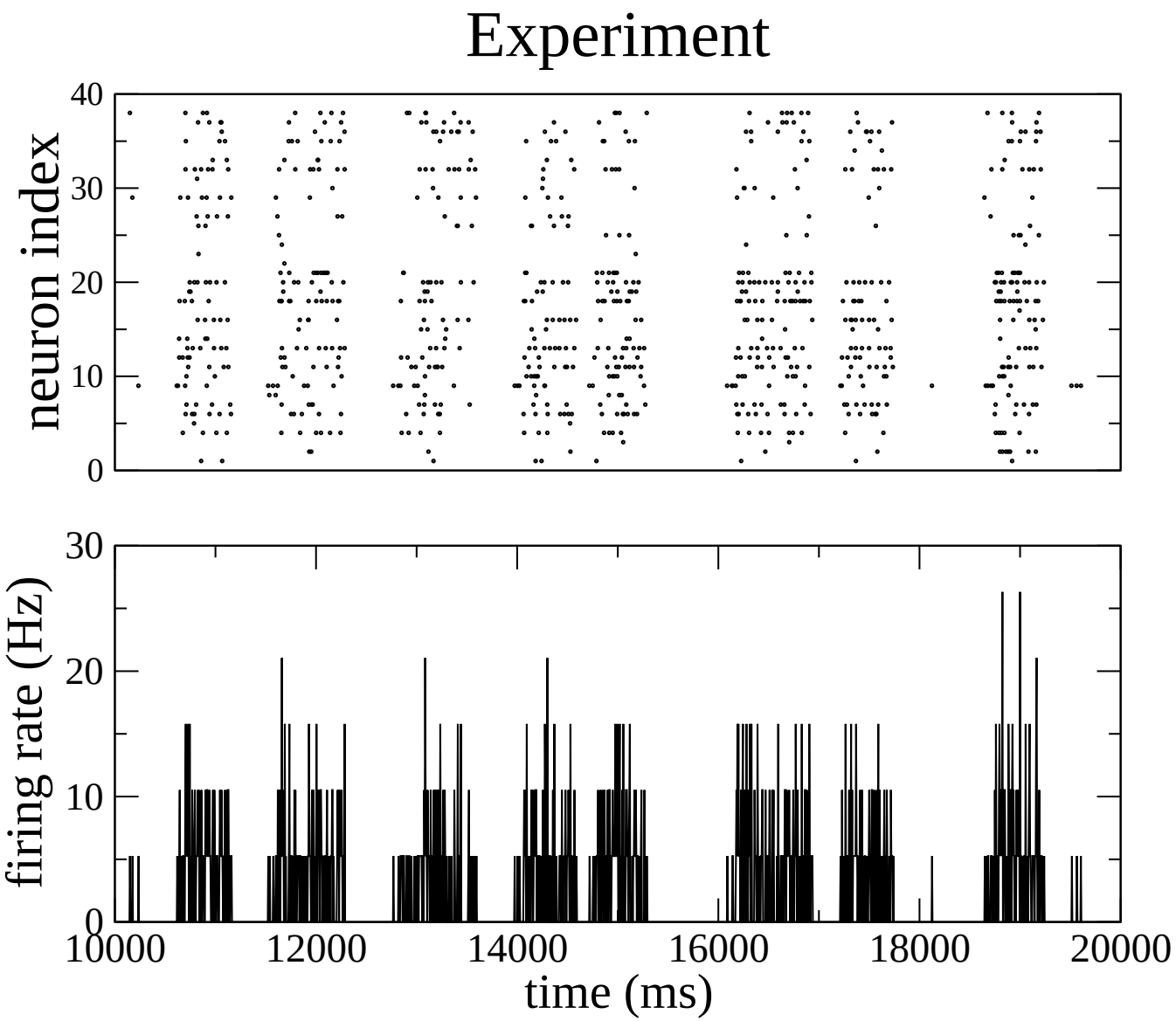

τ = 10ms
firing rate (Hz)
time (ms)
0
10
20
30
40
50
0
5000
10000
15000
firing rate (Hz)
time (ms)
7500
8000
13500
14000
26
24
22
20
18
16
14
12
10

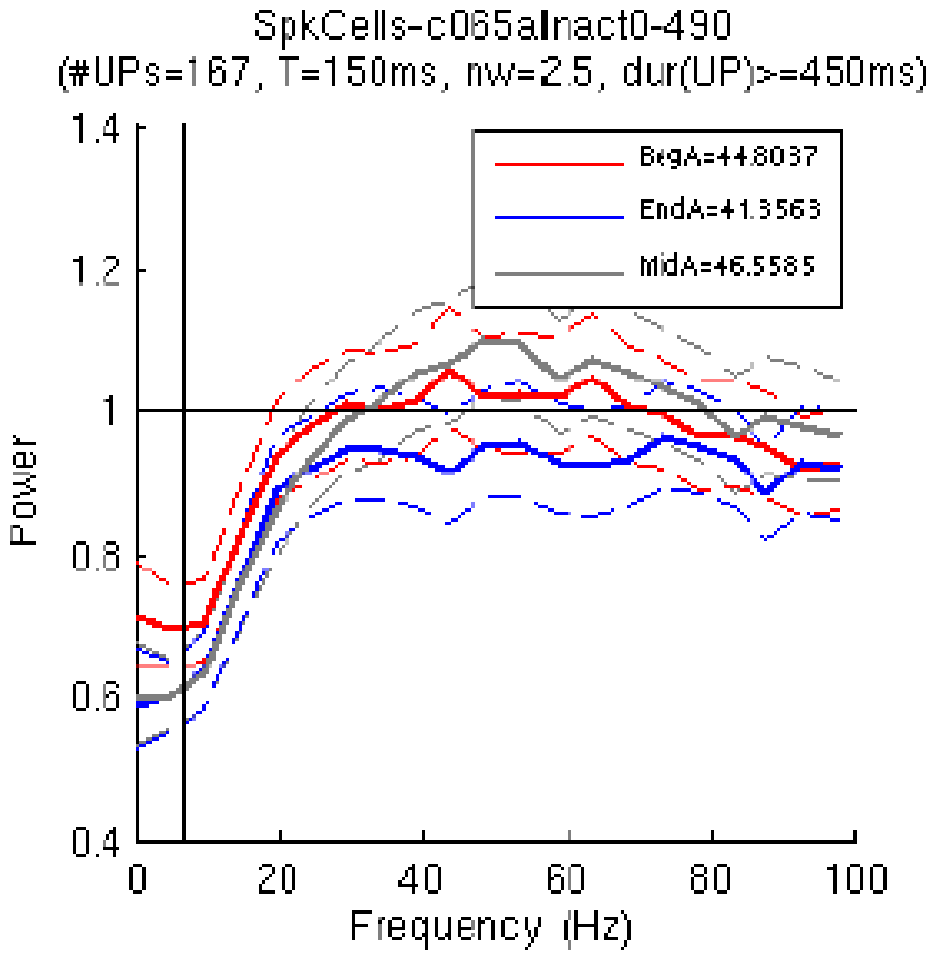

τI = 1ms
τE = 20ms
τE = 10ms
τE = 5ms
τE = 2ms
firing rate (Hz)
external input (Hz/1000)
0
10
20
30
40
50
306
307
308
309
310


τI = 1ms
τE = 20ms
τE = 10ms
τE = 5ms
τE = 2ms
firing rate (Hz)
external input (Hz/1000)
0
10
20
30
40
50
306
307
308
309
310
firing rate (Hz)
time (ms)
0
10
20
30
40
21000
22000
23000


τI = 1ms
τE = 20ms
τE = 10ms
τE = 5ms
τE = 2ms
firing rate (Hz)
external input (Hz/1000)
0
10
20
30
40
50
306
307
308
309
310
firing rate (Hz)
time (ms)
24000
25000
26000

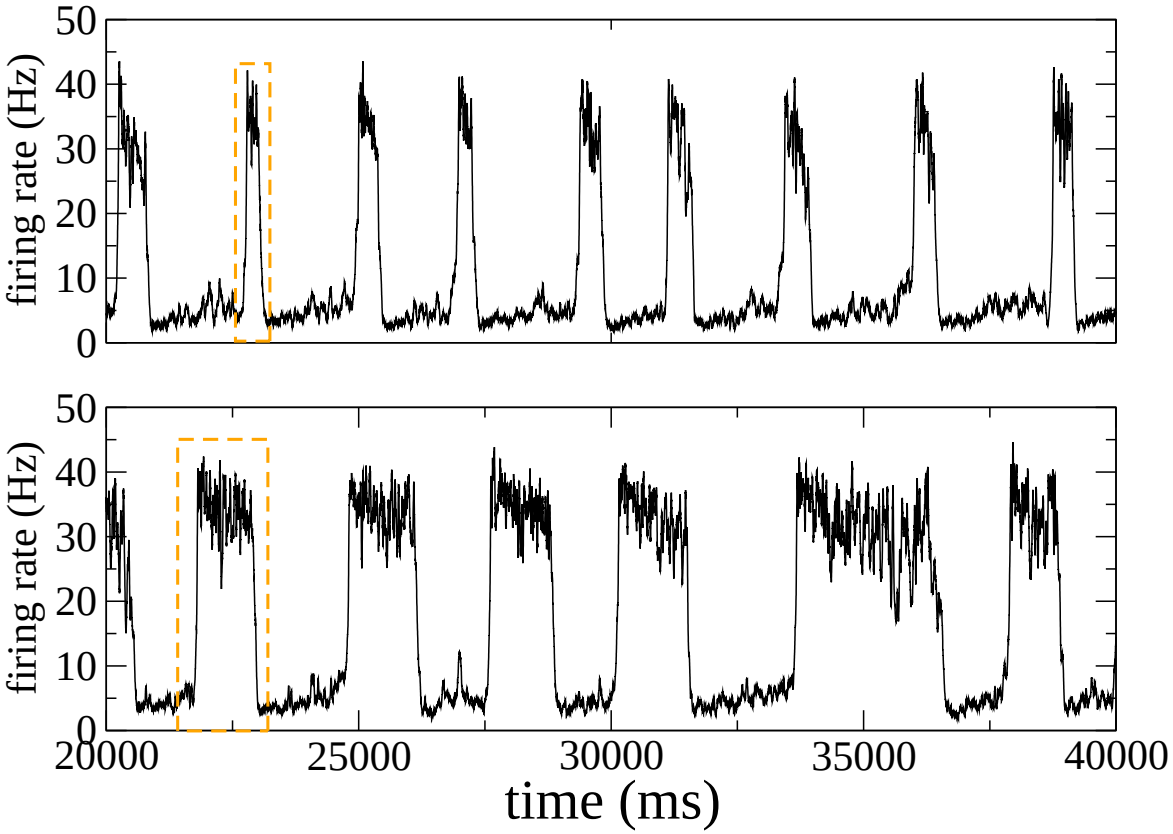
Slow-wave activity in anesthetized rat


Experiment
neuron index
40
30
20
10
0
firing rate (Hz)
30
20
10
0
10000
12000
14000
16000
18000
20000
time (ms)


SpkCells-c065aInact0-490
(#UPs=167, T=150ms, nw=2.5, dur(UP)>=450ms)
BegA=44.8037
EndA=41.3563
MidA=46.5585
Power
Frequency (Hz)
1.4
1.2
1
0.8
0.6
0.4
0
20
40
60
80
100

Network of LIF neurons with adaptation

$$
\begin{aligned}
C\dot{V}_i &= -g_L(V_i - E) + I_{ext,i} + I_{syn,i} - I_{A,i}, \\
\tau_A \dot{I}_{A,i} &= -I_{A,i} + \alpha \sum_j \delta(t - t_i^j)
\end{aligned}
$$



Network of LIF neurons with adaptation

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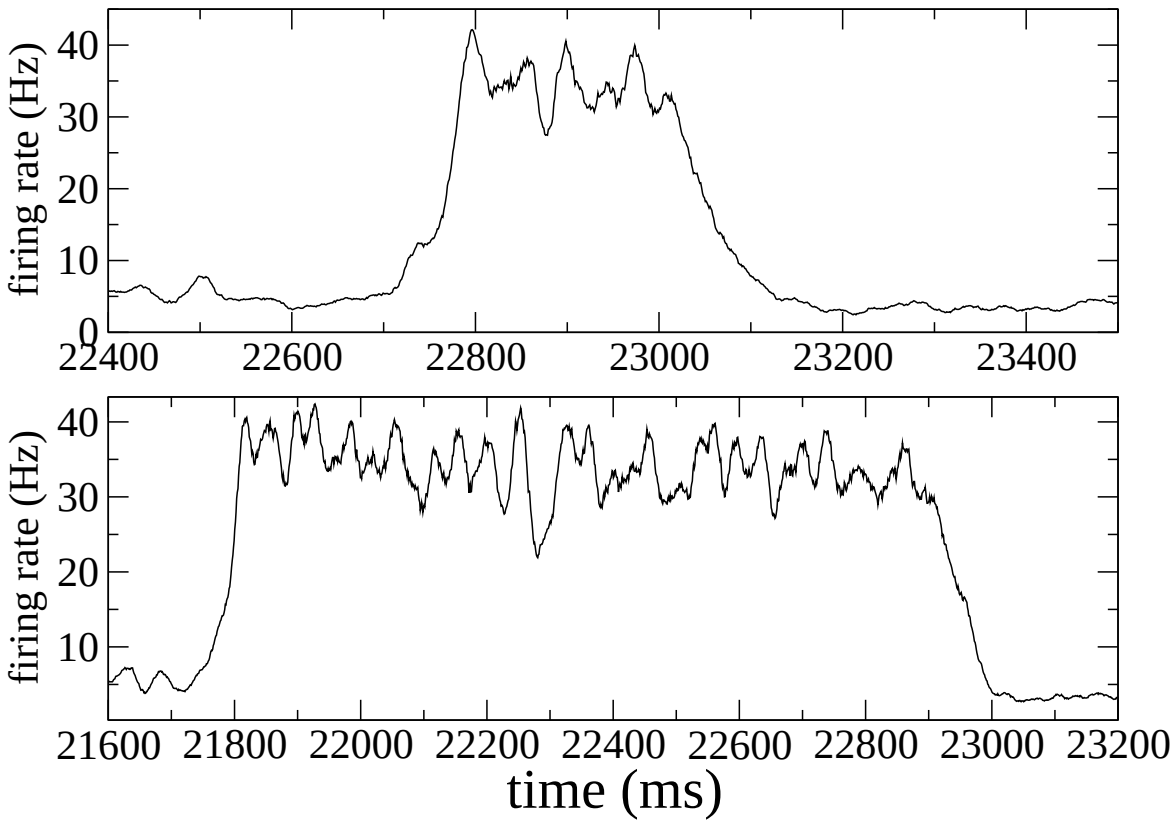
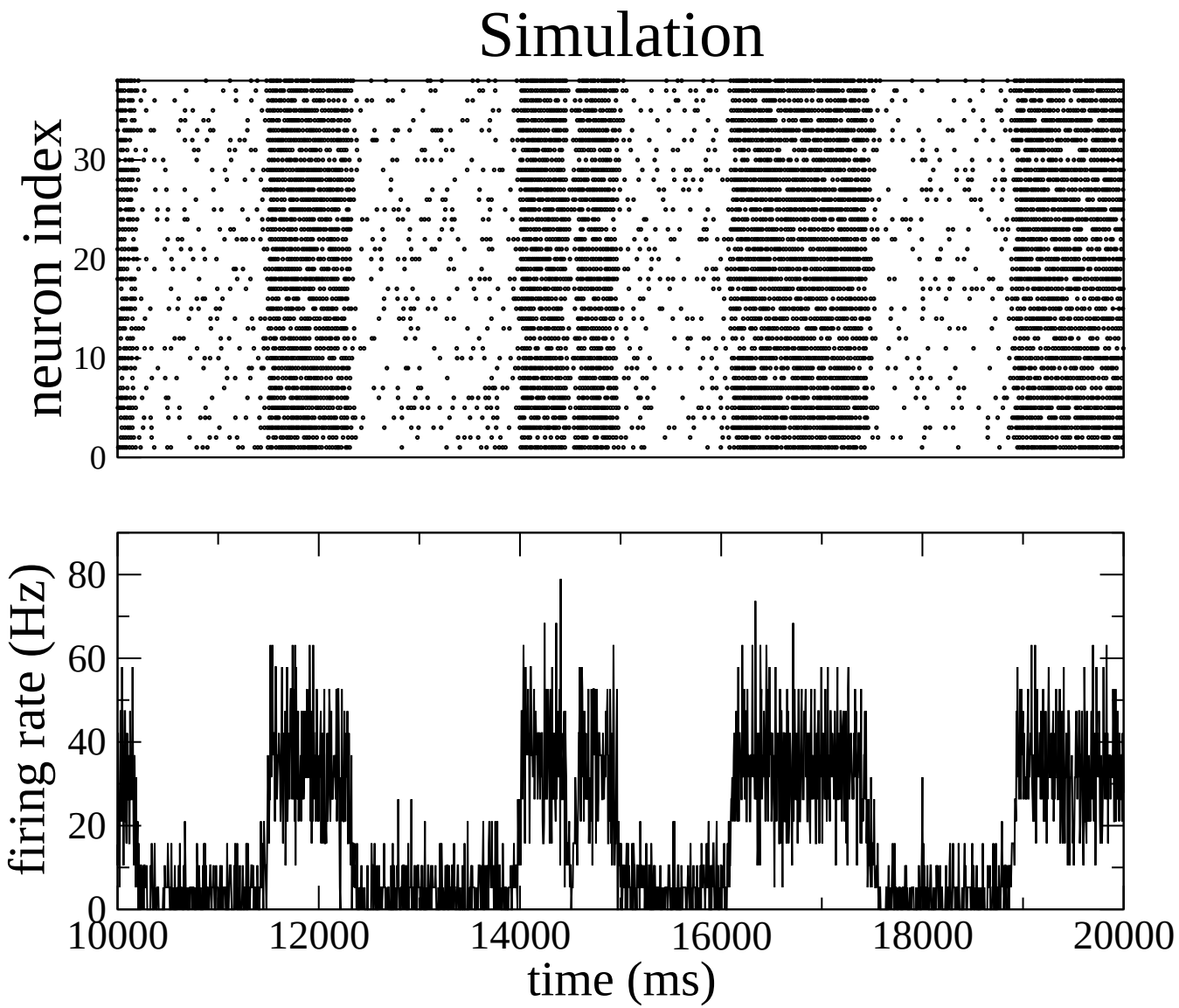
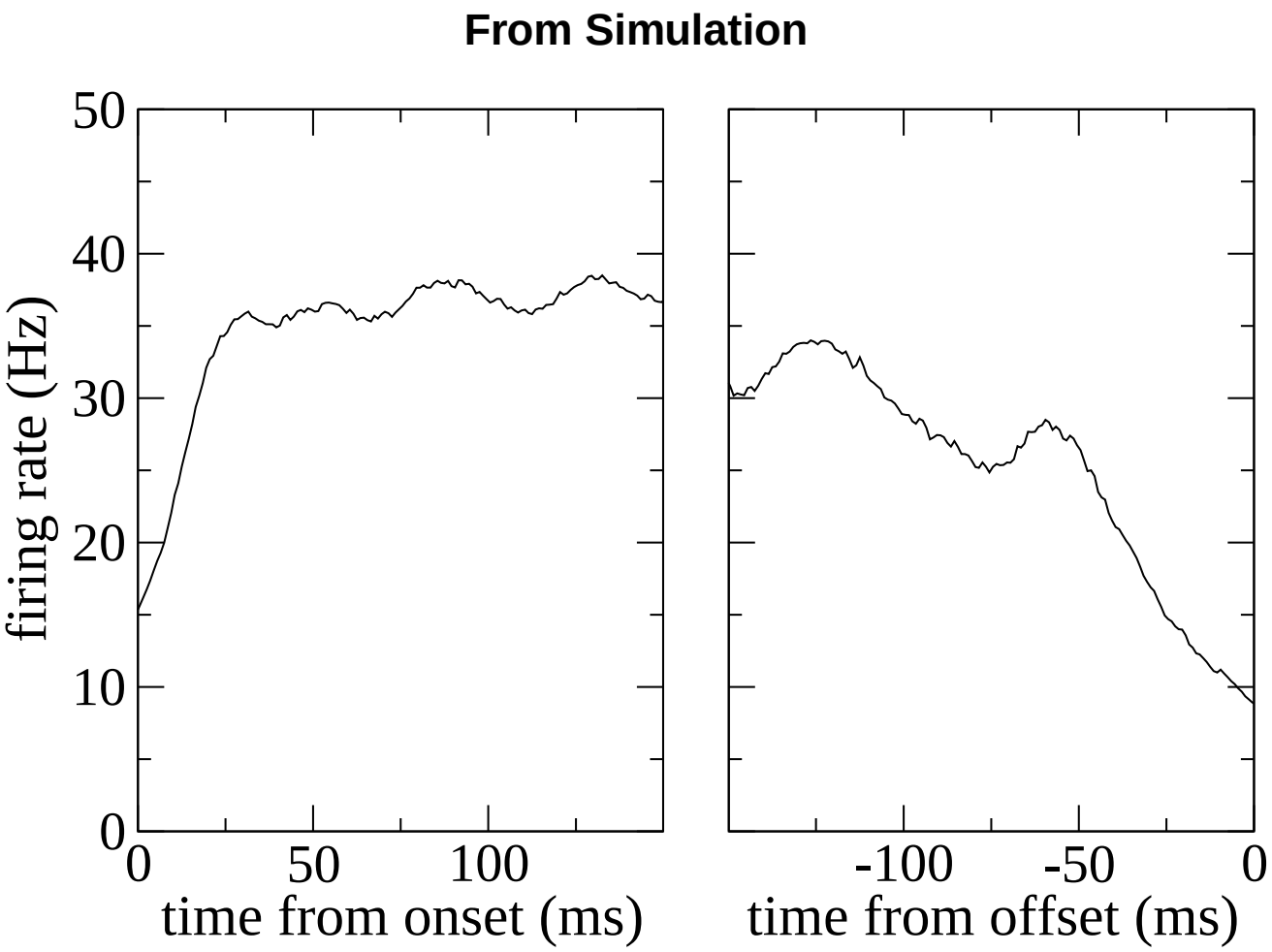
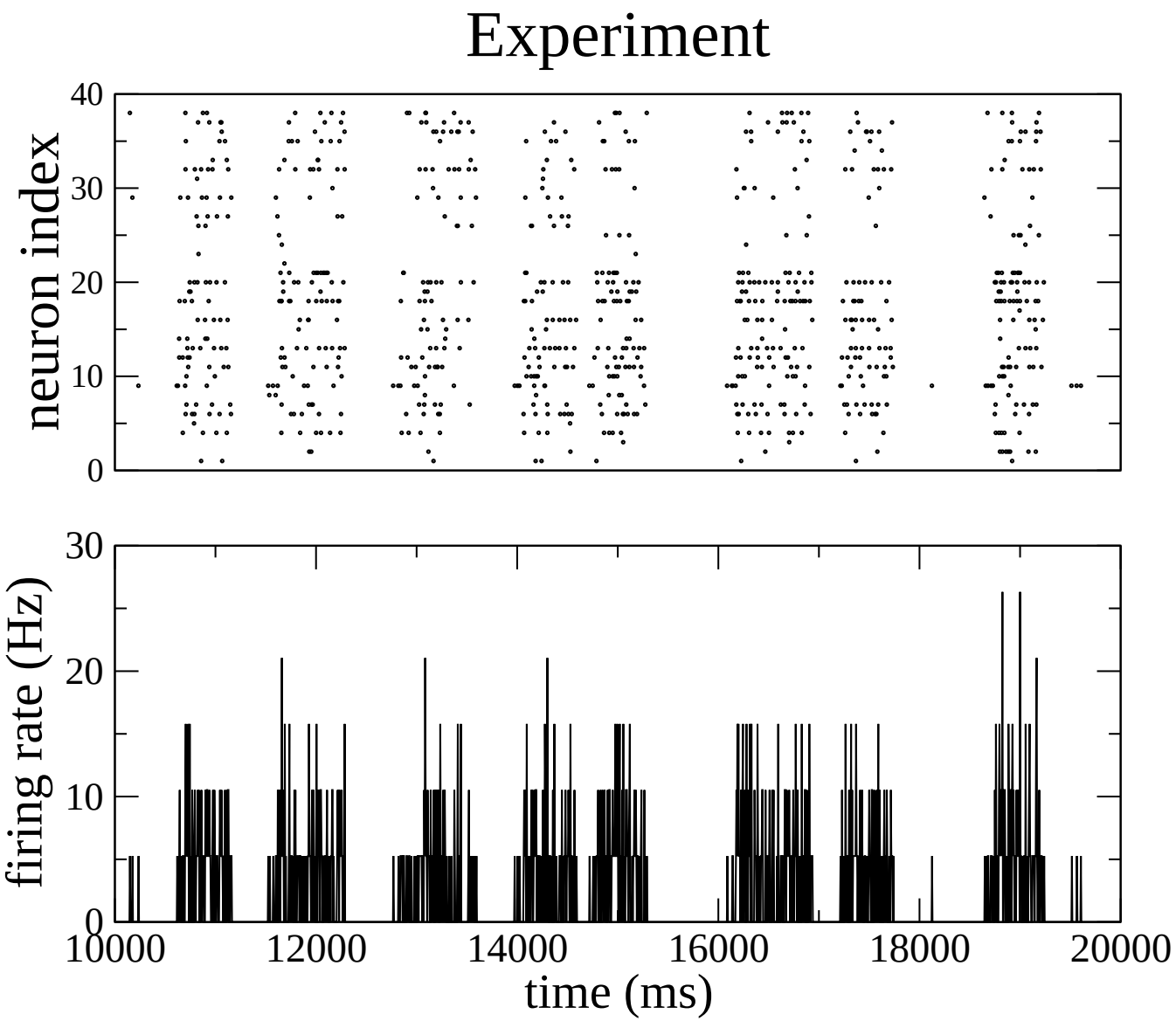
\tau_A \dot{I}_{A,i} &= -I_{A,i} + \alpha \sum_j \delta(t - t_i^j)
\end{aligned}
$$

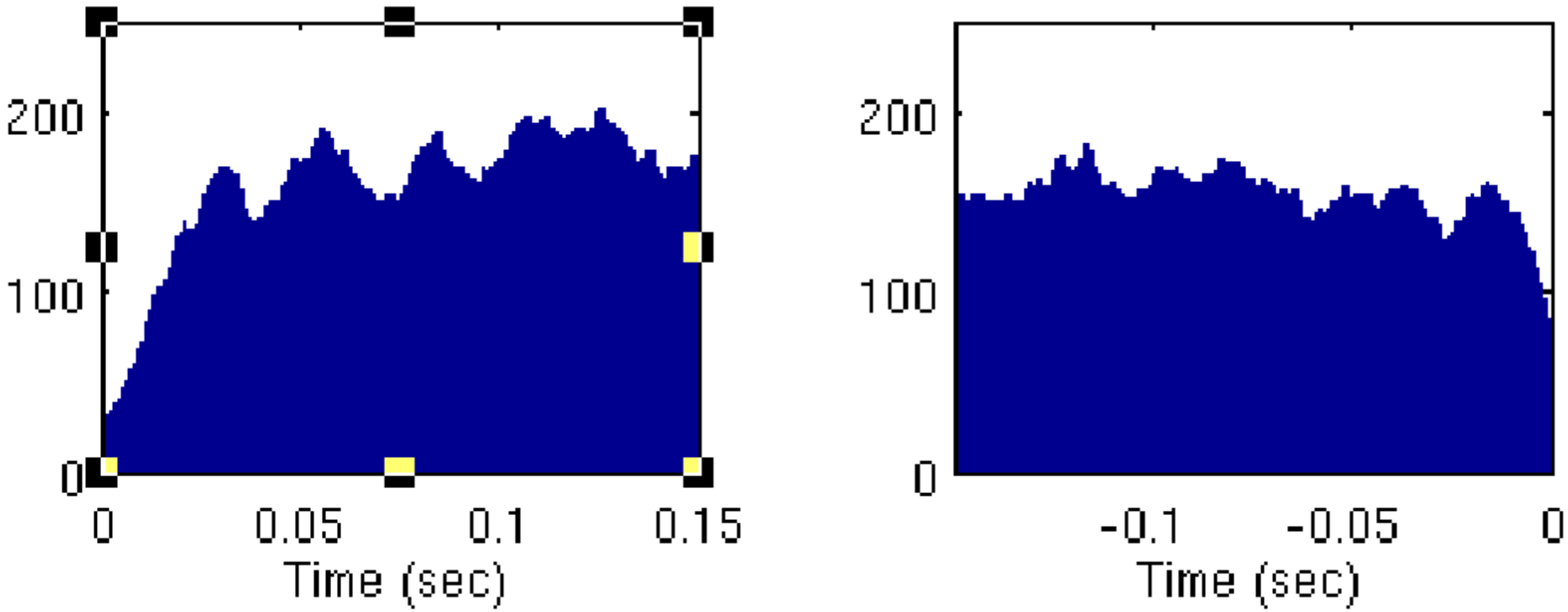


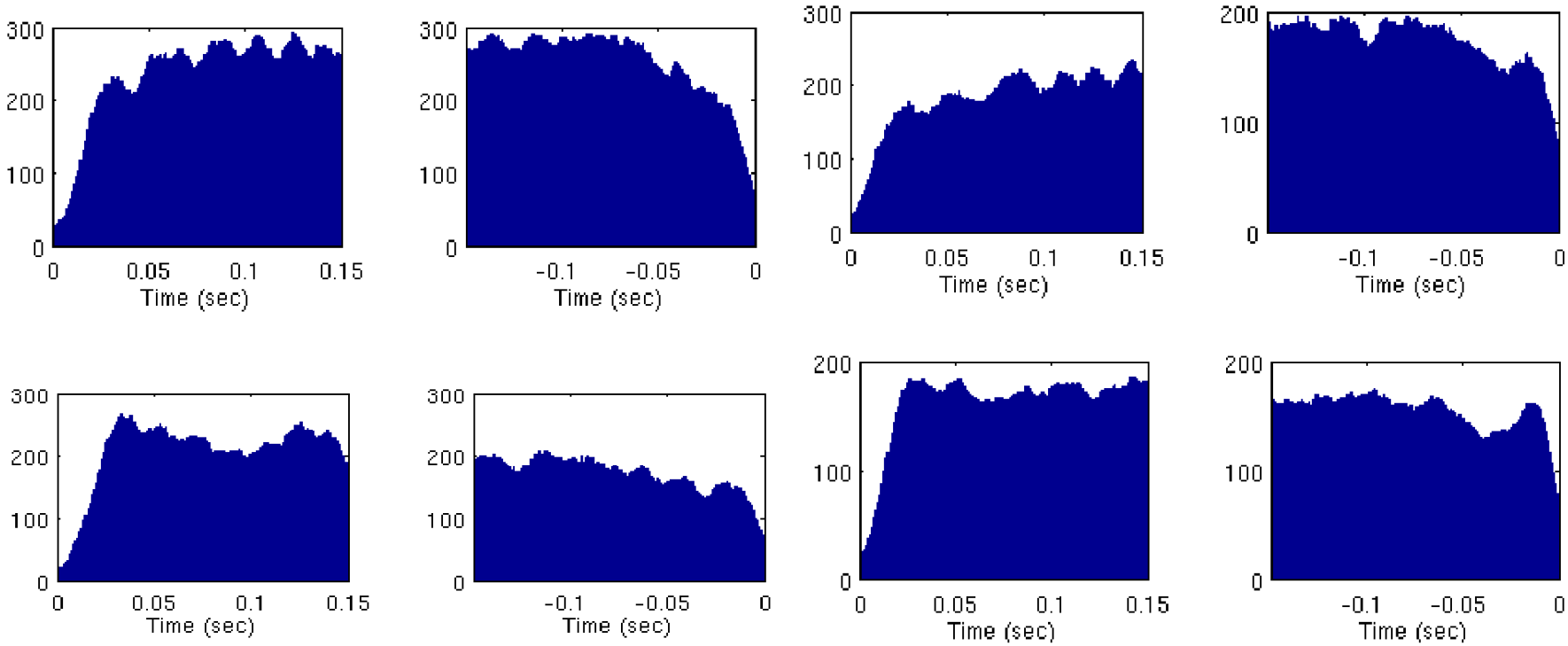

Simulation
neuron index
0
10
20
30
firing rate (Hz)
0
20
40
60
80
10000
12000
14000
16000
18000
20000
time (ms)


From Simulation
50
40
30
20
10
0
firing rate (Hz)
0
50
100
time from onset (ms)
-100
-50
0
time from offset (ms)


Experiment
neuron index
40
30
20
10
0
firing rate (Hz)
30
20
10
0
10000
12000
14000
16000
18000
20000
time (ms)

From Experiment

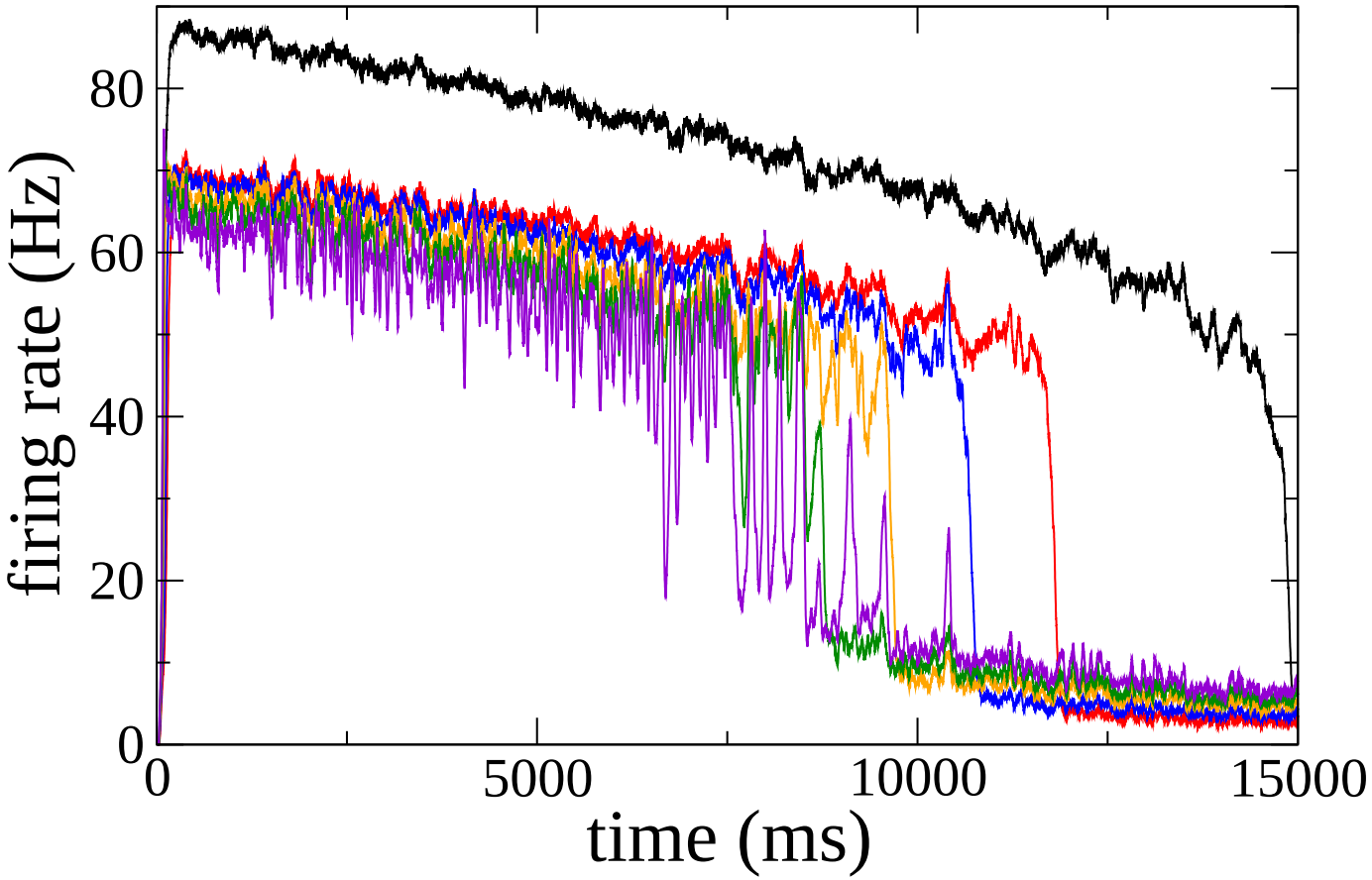


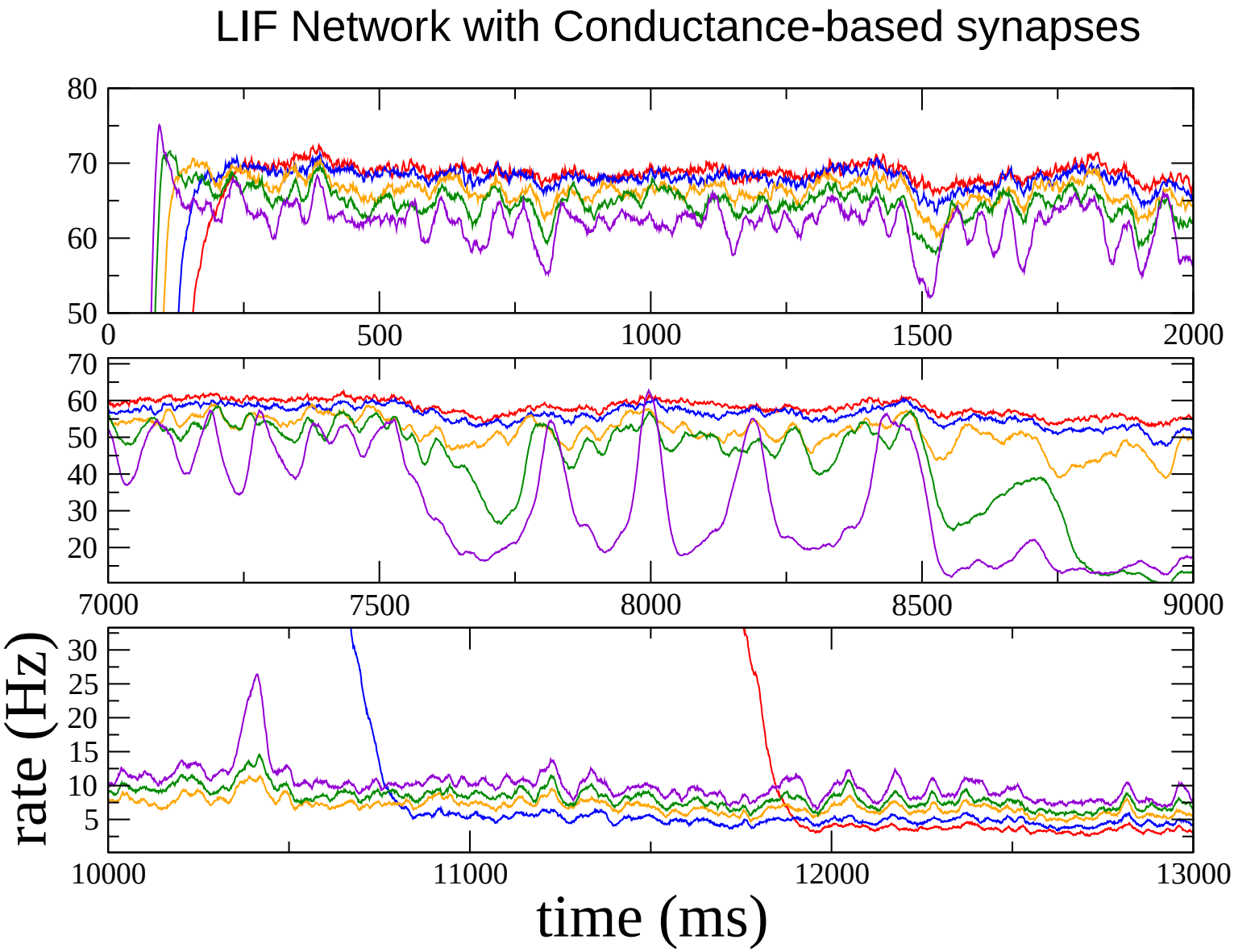

300
200
100
0
0
0.05
0.1
0.15
Time (sec)
300
200
100
0
-0.1
-0.05
0
Time (sec)
300
200
100
0
0
0.05
0.1
0.15
Time (sec)
200
100
0
-0.1
-0.05
0
Time (sec)
300
200
100
0
0
0.05
0.1
0.15
Time (sec)
300
200
100
0
-0.1
-0.05
0
Time (sec)
200
100
0
0
0.05
0.1
0.15
Time (sec)
200
100
0
-0.1
-0.05
0
Time (sec)

Conclusions

- Oscillations in bistable regime in E-I networks through TB
- TB very robust in spiking networks
- Oscillations (beta and low gamma) during SW activity in anesthetized rat

LIF Network with Conductance-based synapses




LIF Network with Conductance-based synapses
80
70
60
50
0
500
1000
1500
2000
70
60
50
40
30
20
7000
7500
8000
8500
9000
30
25
20
15
10
5
10000
11000
12000
13000
rate (Hz)
time (ms)