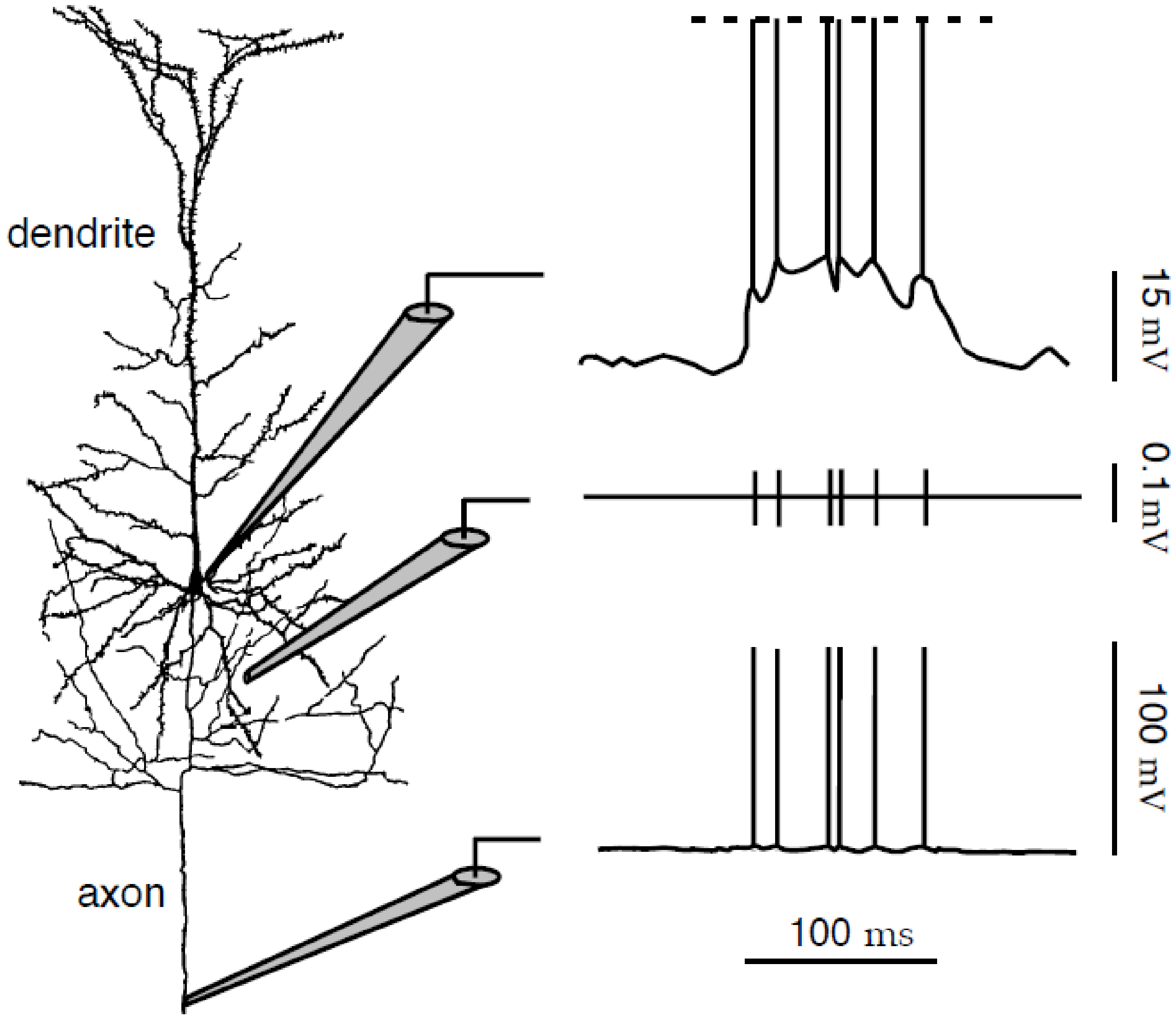
From networks to normal forms: using reduced models to understand network dynamics

Alex Roxin

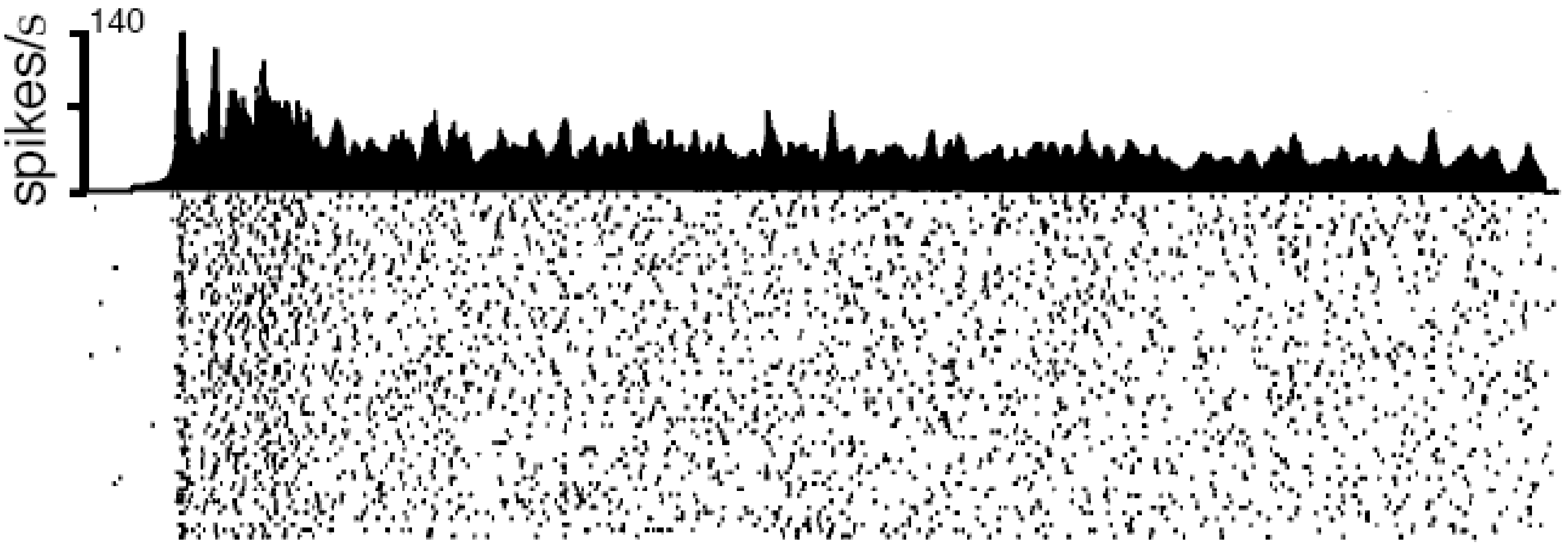
Institut d’Investigacions Biomediques August Pi i Sunyer, Barcelona

Mathematical Neuroscience 2011, Edinburgh.

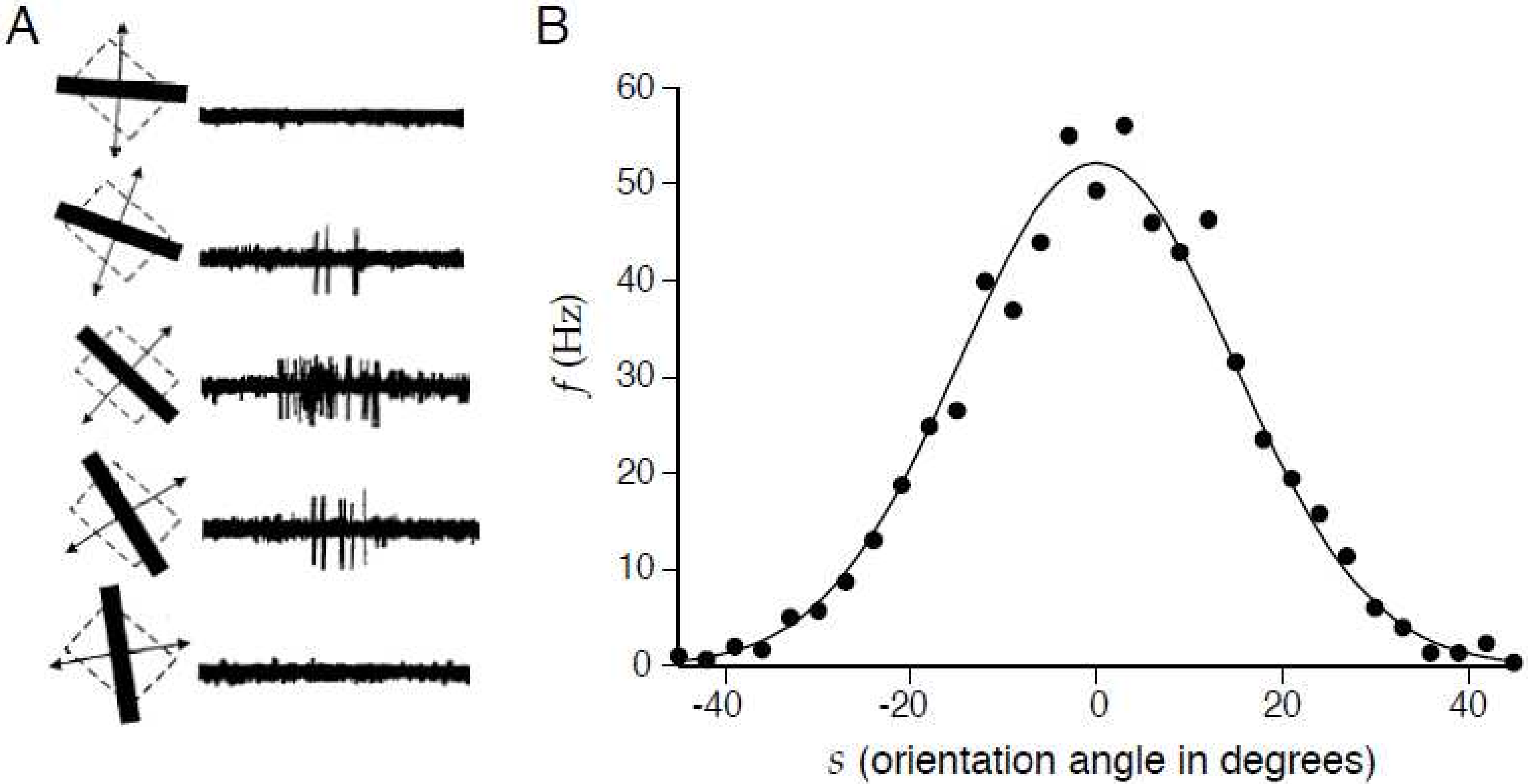


from Dayan and Abbott

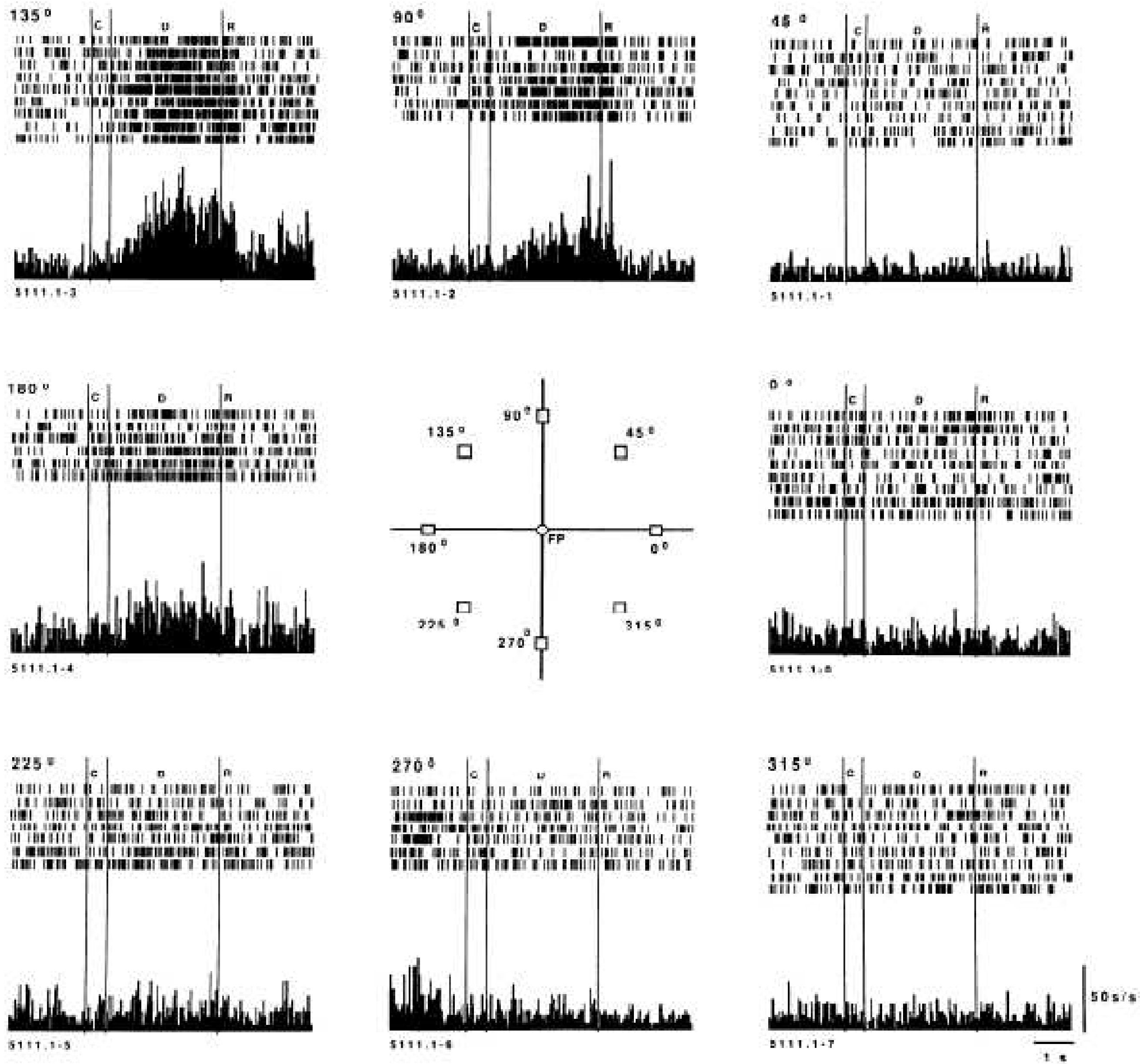
Spikes and Firing Rates



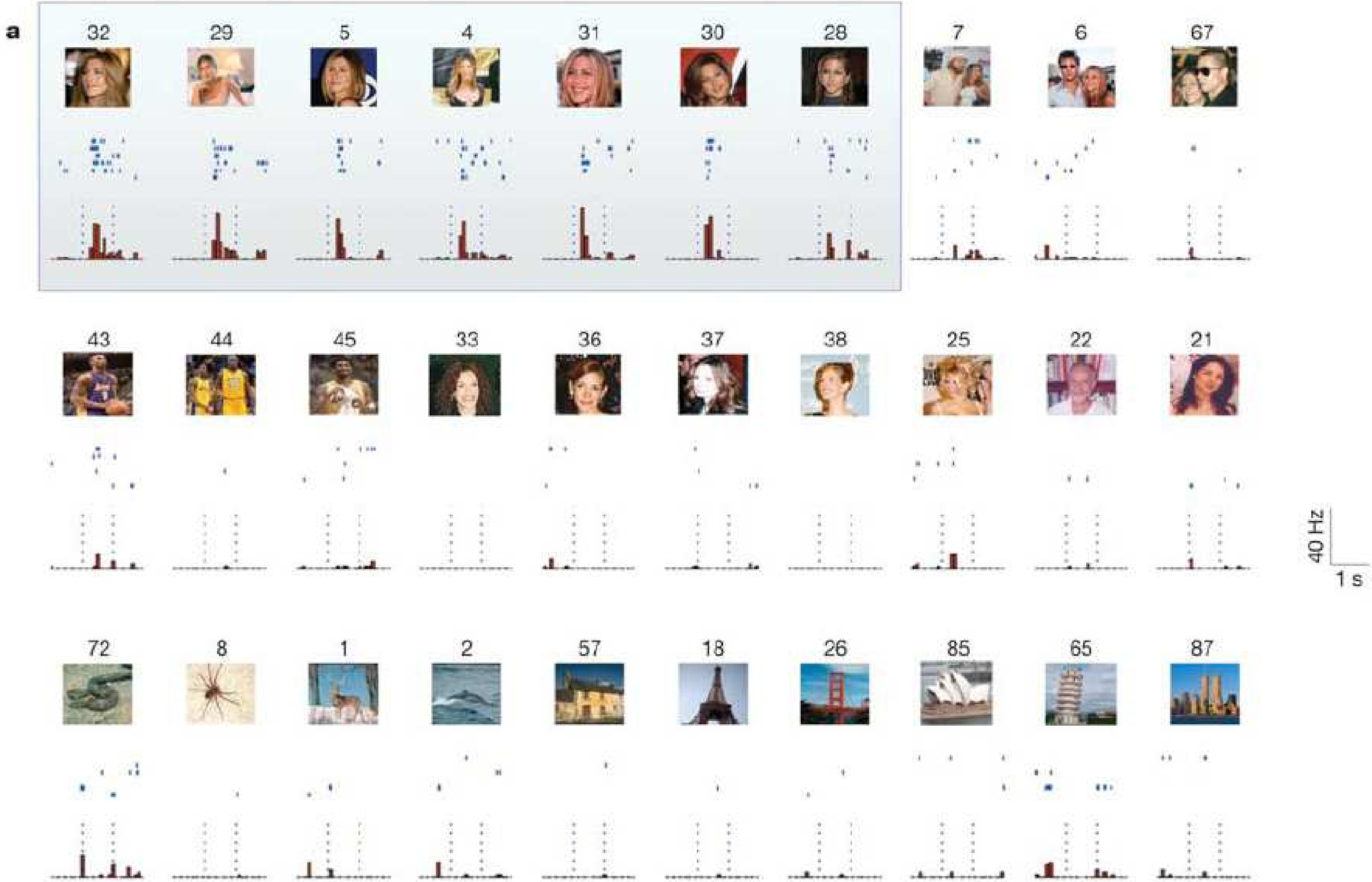
Raster plot of an MT cell.



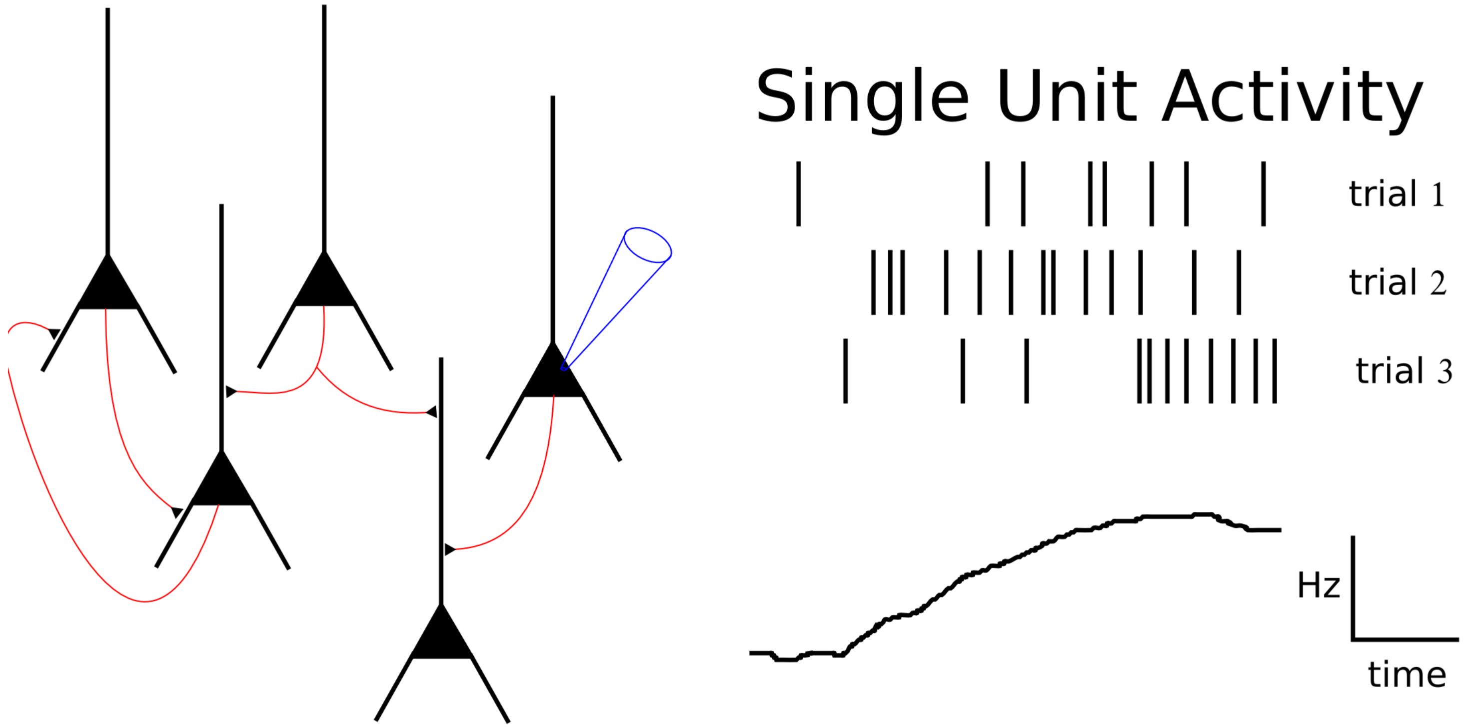
Orientation selectivity in V1. (Hubel and Wiesel 1968, Henry et al. 1974.)

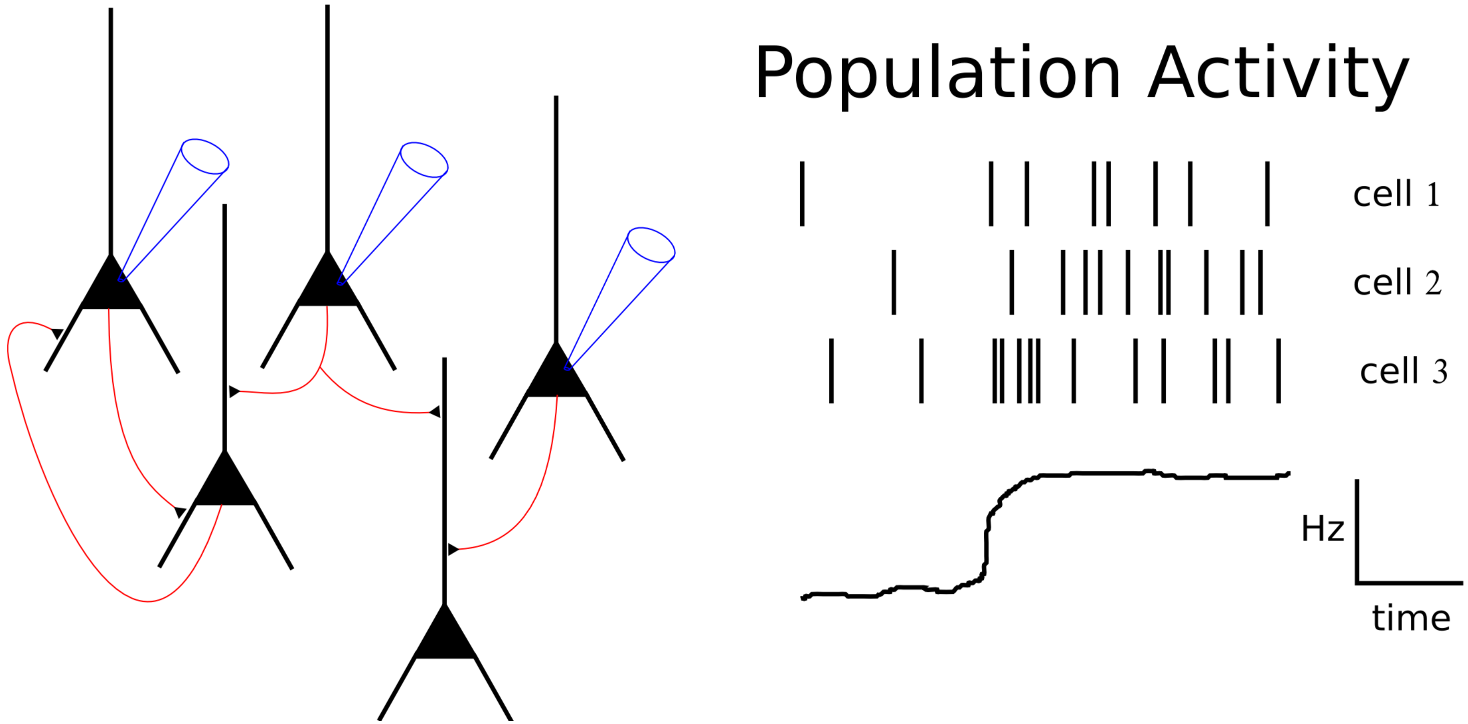


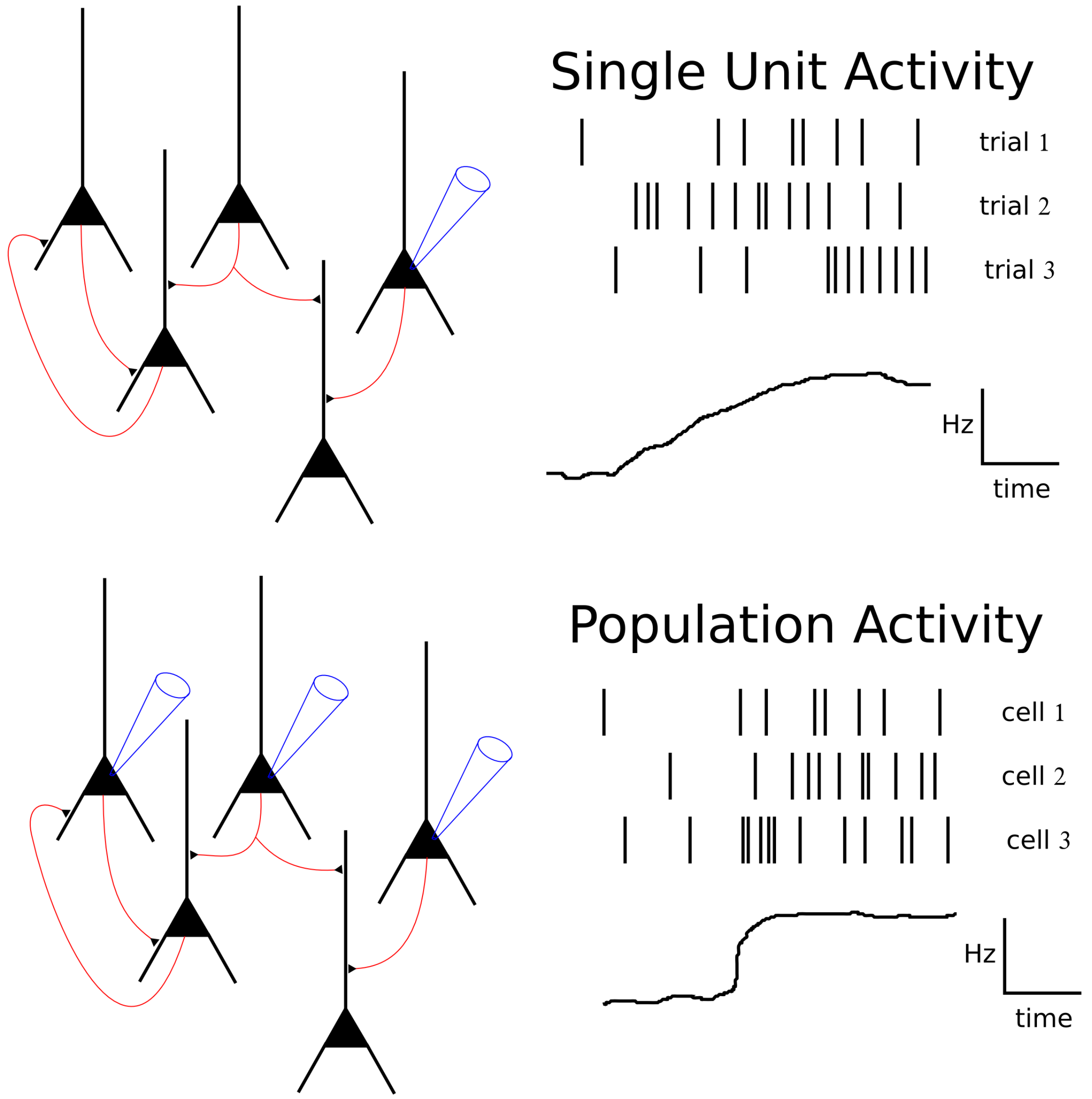
Spatial working memory in PFC. (Funahashi et al. 1989)



Jennifer Anniston cell in temporal lobe. (Quian Quiroga et al. 2005)


Single Unit Activity
trial 1
trial 2
trial 3
Hz
time

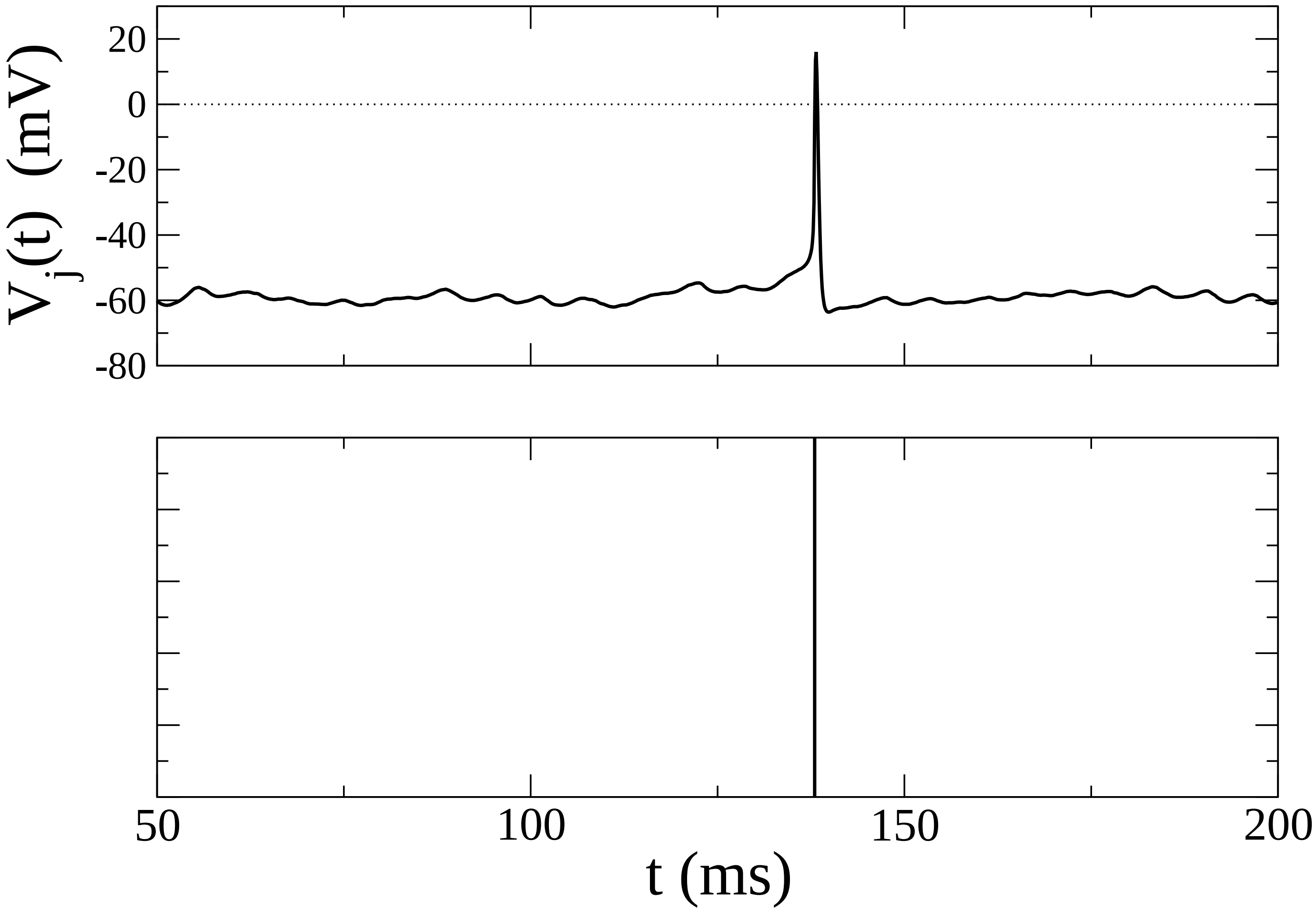

Population Activity
cell 1
cell 2
cell 3
Hz
time


Single Unit Activity
trial 1
trial 2
trial 3
Hz
time
Population Activity
cell 1
cell 2
cell 3
Hz
time

Consider a network of randomly connected neurons.

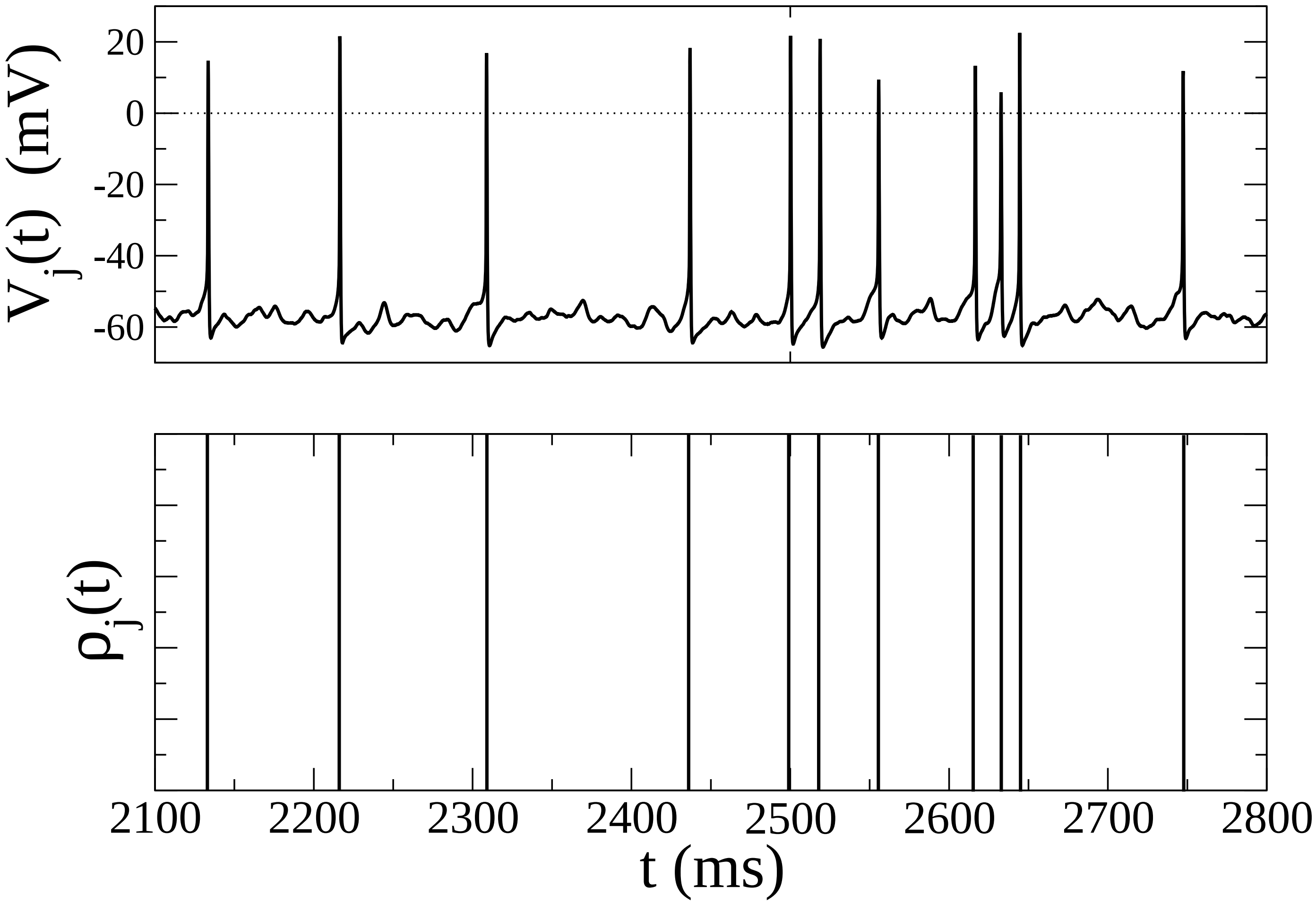
- What is the input to each cell?
- What is the output of each cell?
- They must be self-consistent at the network level.

A spike at time t_1 in cell j
$\delta(t - t_j^1)$



The neural response function of cell j

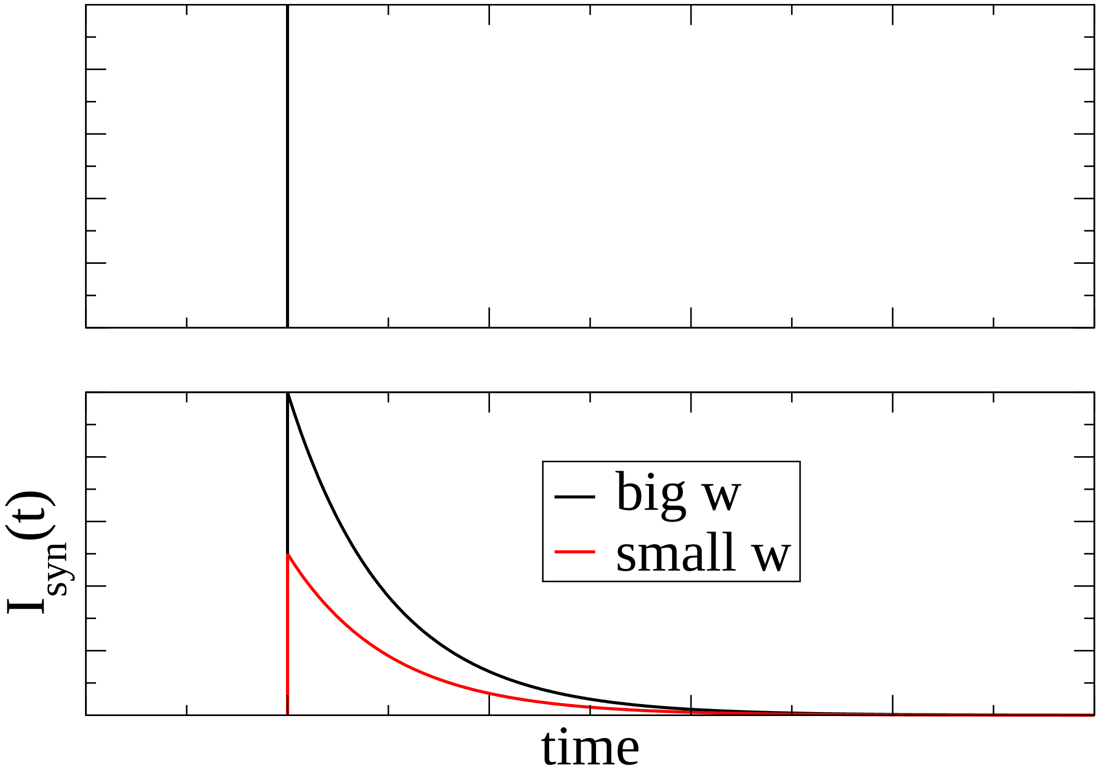
$$\rho_j(t) = \sum_l \delta(t - t_j^l)$$



The post-synaptic current

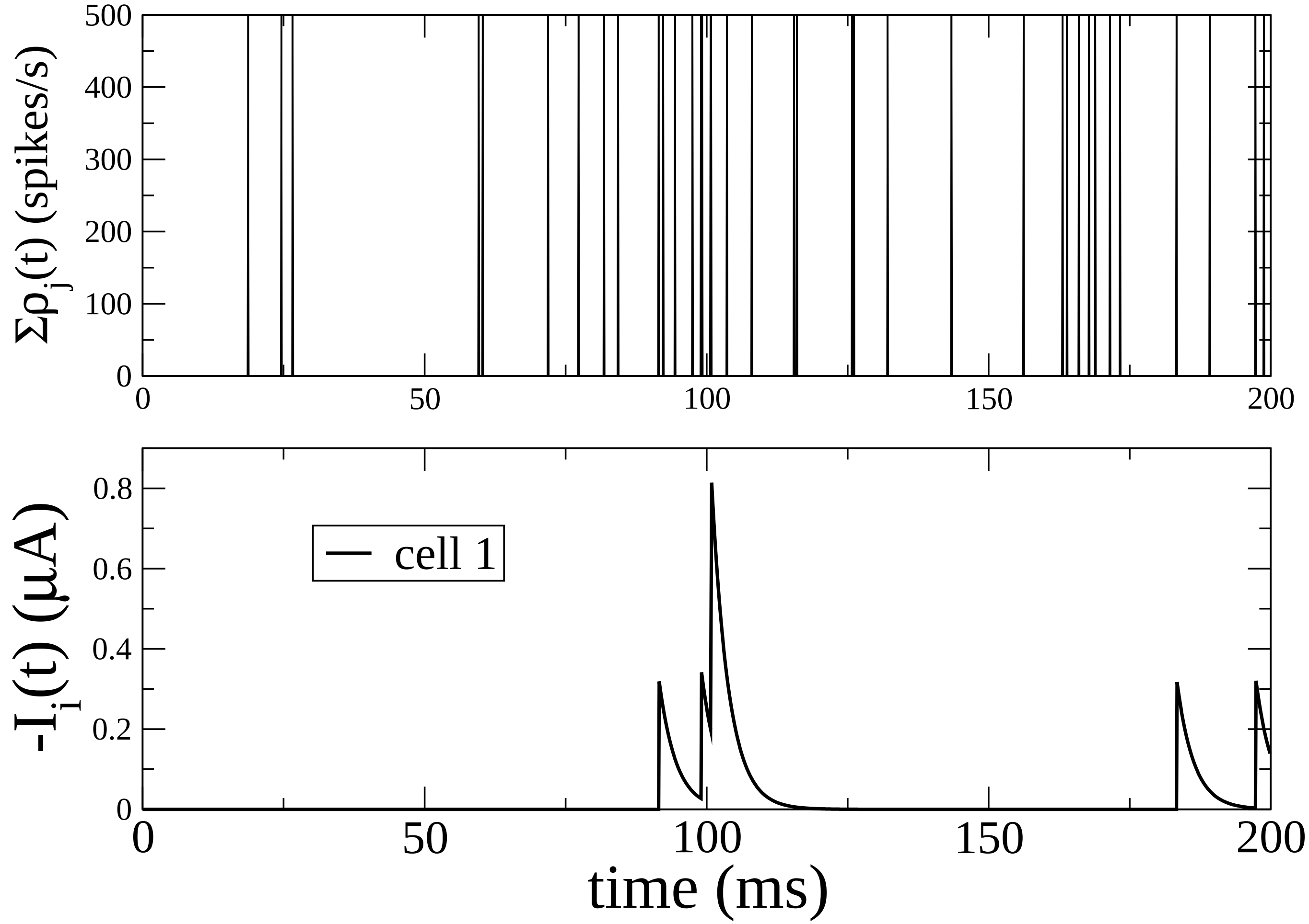
$$I_{syn,i}(t) = \int_{-\infty}^{t} d\tau K(t-\tau) \sum_{j=1}^{N} w_{ij}\rho_j(\tau)$$

$$K(t) = \frac{1}{\tau_s} e^{-t/\tau_s}$$



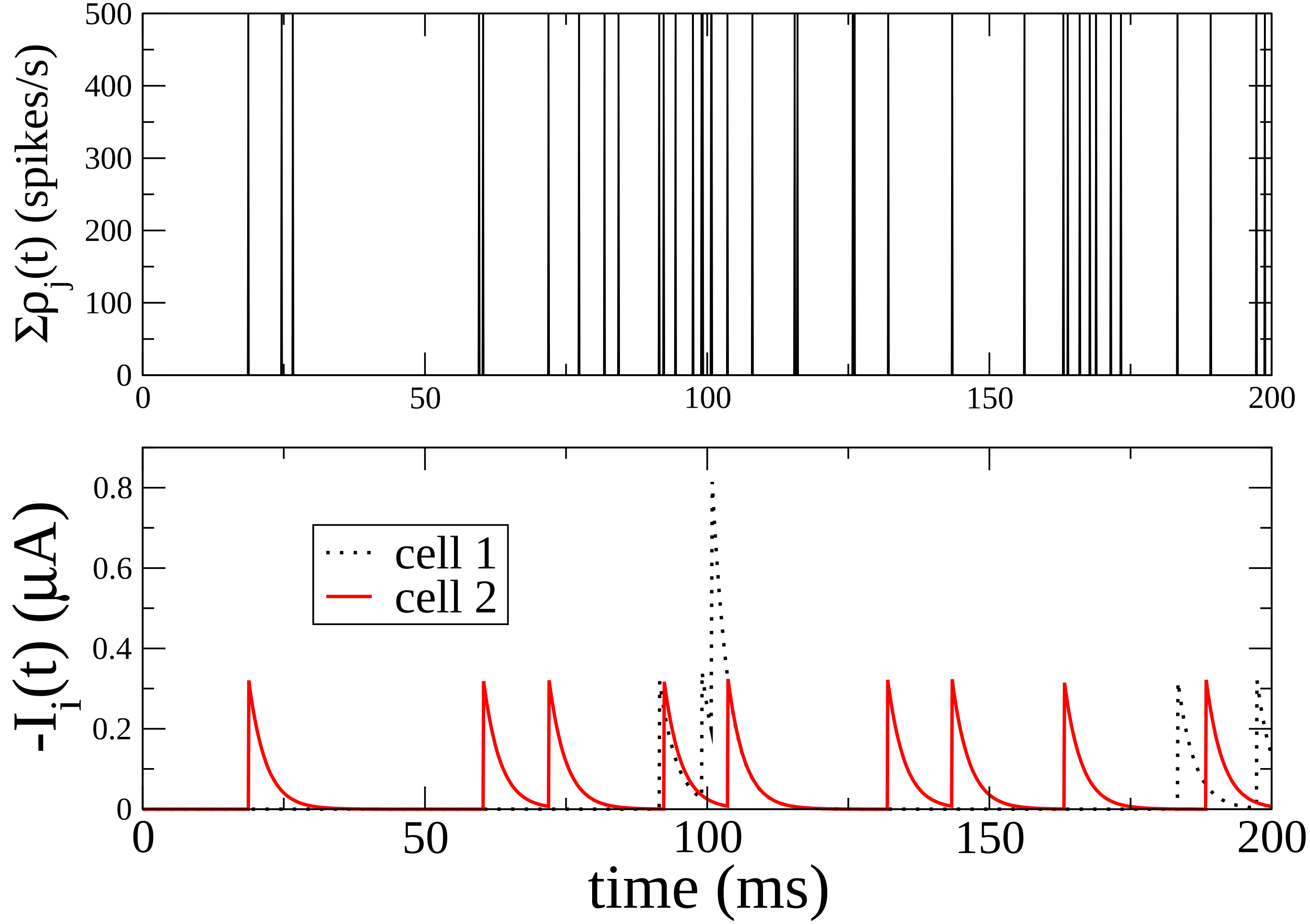
Network of 20 cells and 20% sparseness.

$$\frac{dI_{syn,i}}{dt} = -\frac{I_{syn,i}}{\tau_s} + \sum_j w_{ij}\rho_j$$



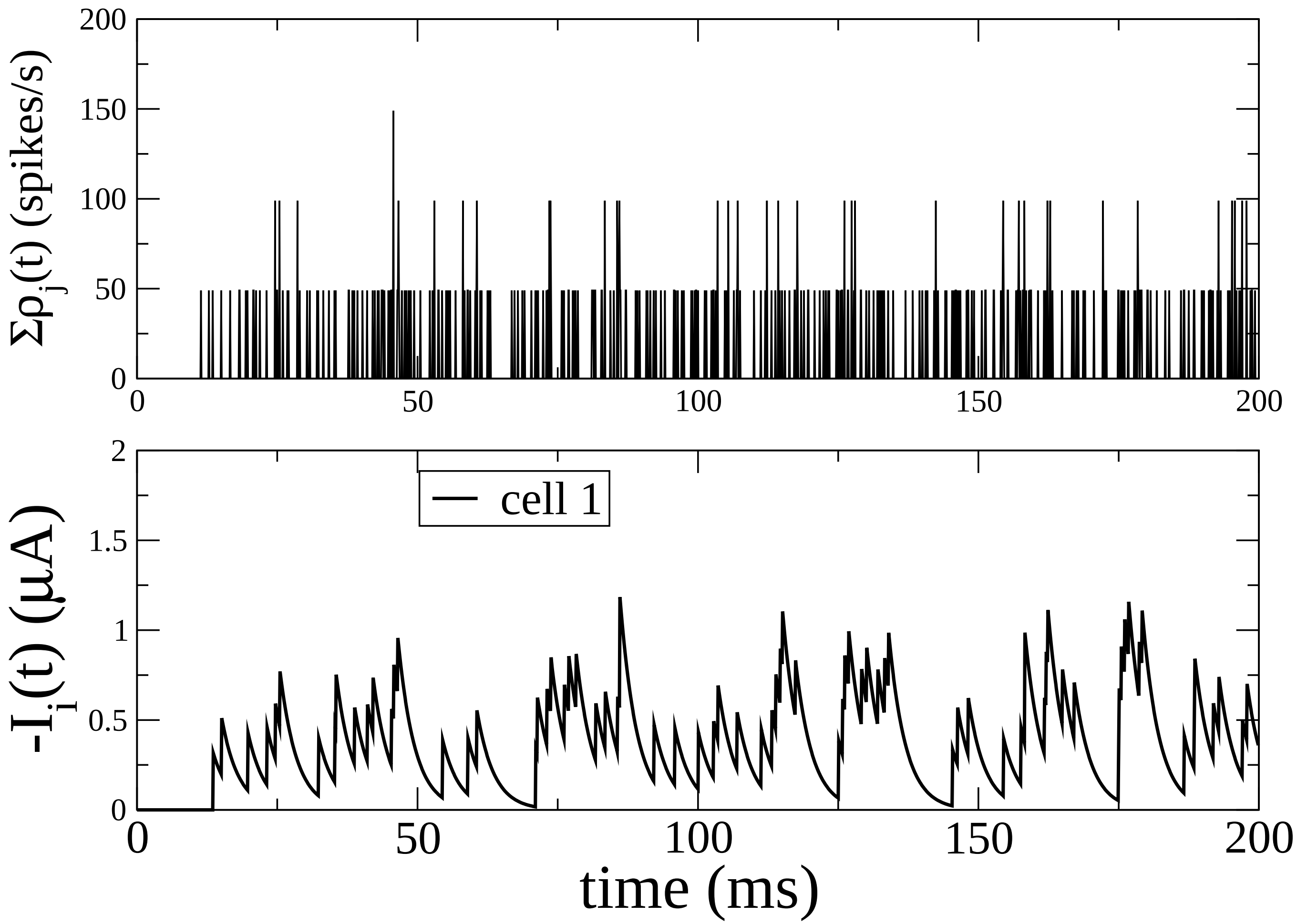
Network of 20 cells and 20% sparseness.

$$\frac{dI_{syn,i}}{dt} = -\frac{I_{syn,i}}{\tau_s} + \sum_j w_{ij}\rho_j$$



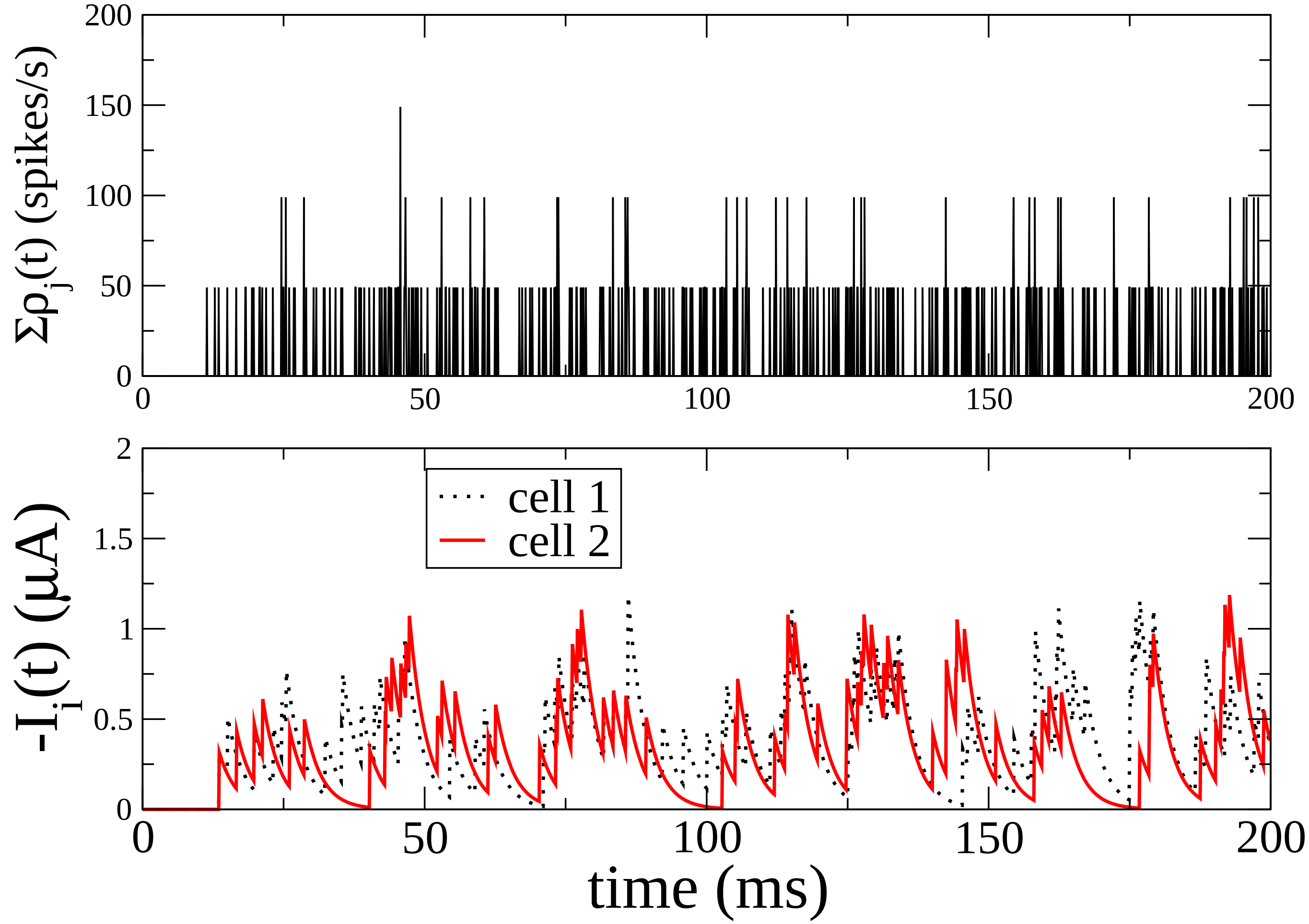
Network of 200 cells and 20% sparseness.

$$\frac{dI_{syn,i}}{dt} = -\frac{I_{syn,i}}{\tau_s} + \sum_j w_{ij}\rho_j$$



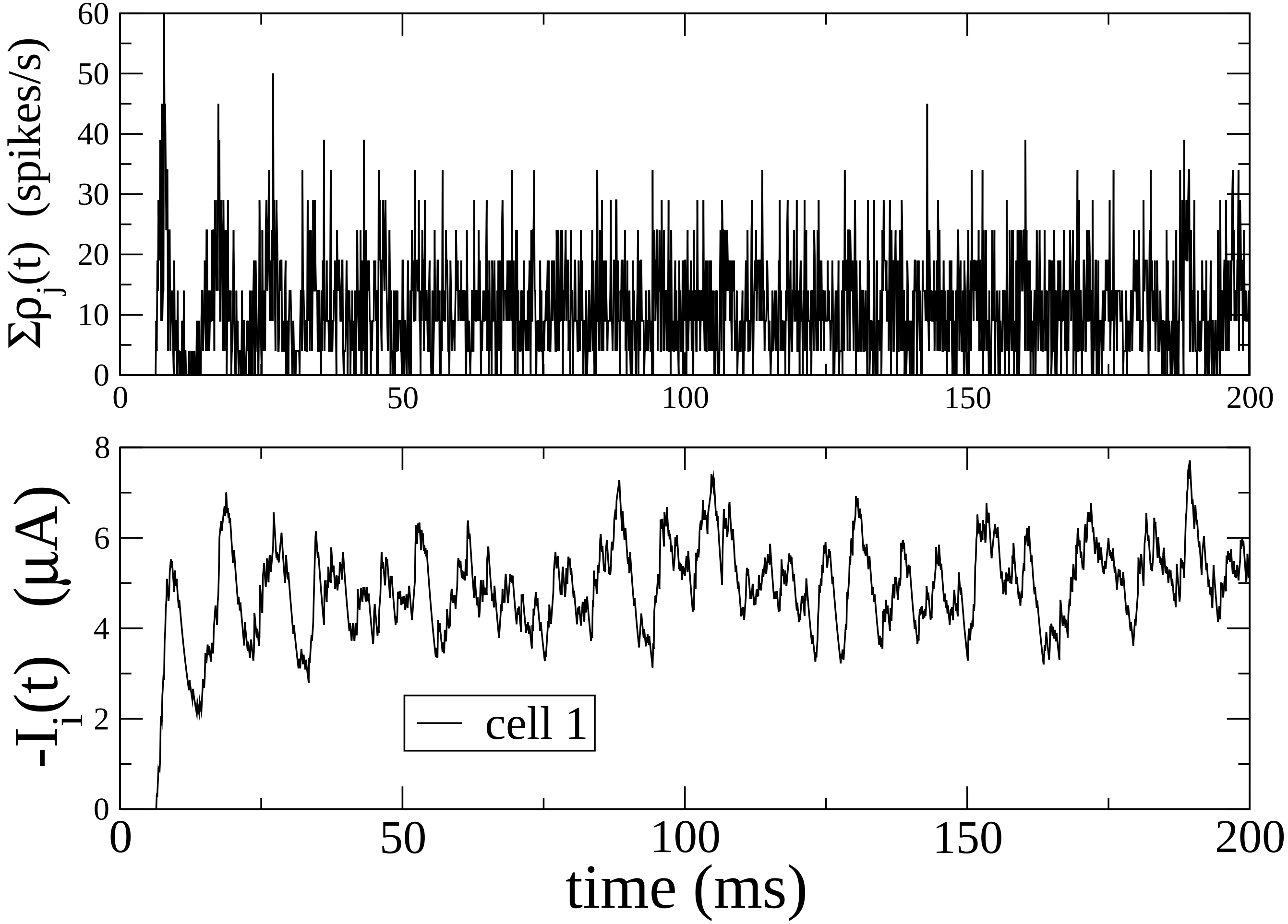
Network of 200 cells and 20% sparseness.

$$\frac{dI_{syn,i}}{dt} = -\frac{I_{syn,i}}{\tau_s} + \sum_j w_{ij}\rho_j$$



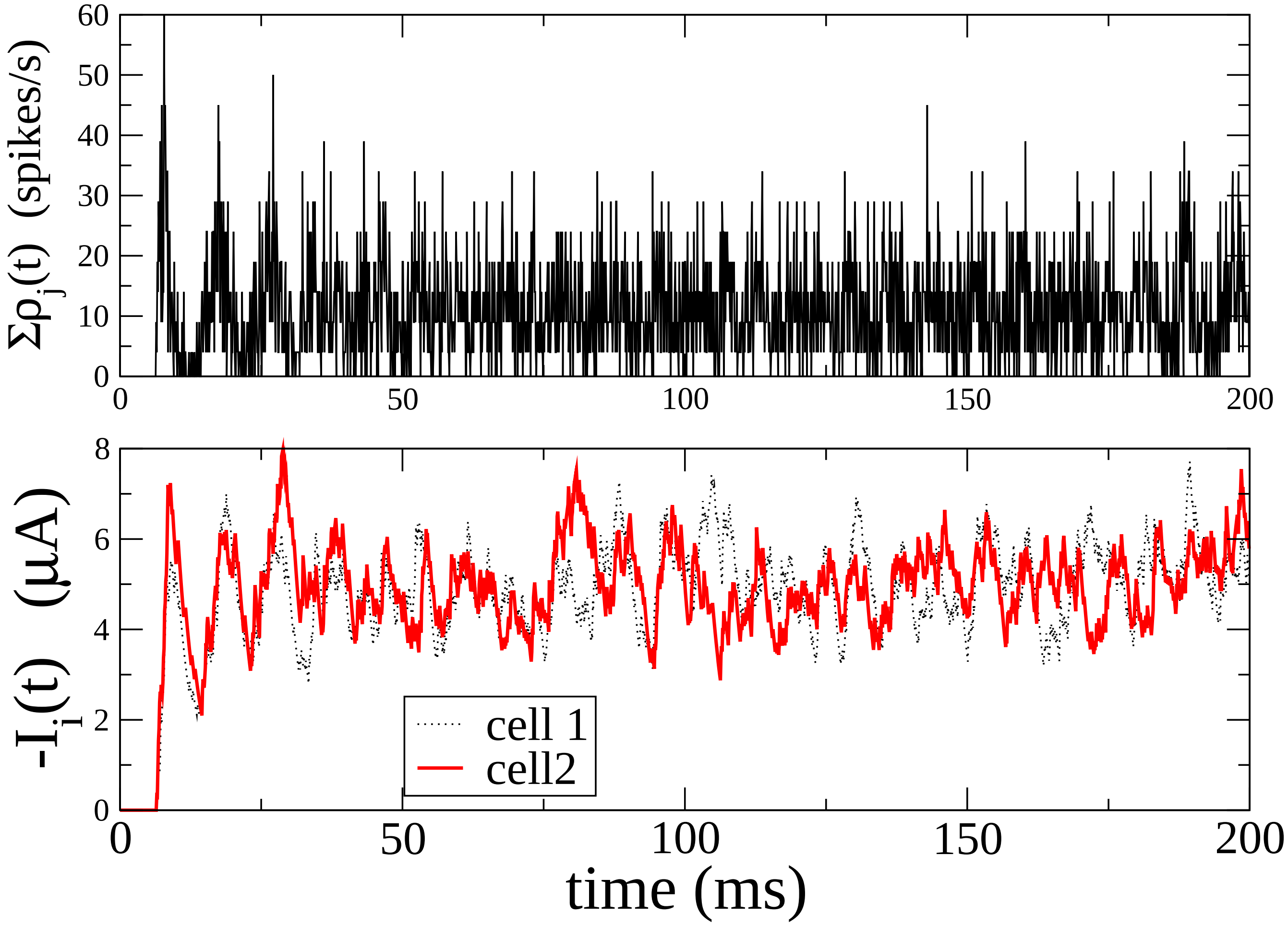
Network of 2000 cells and 20% sparseness.

$$\frac{dI_{syn,i}}{dt} = -\frac{I_{syn,i}}{\tau_s} + \sum_j w_{ij}\rho_j$$



Network of 2000 cells and 20% sparseness.

$$\frac{dI_{syn,i}}{dt} = -\frac{I_{syn,i}}{\tau_s} + \sum_j w_{ij}\rho_j$$



Rate model with Current

$$\tau_s \frac{dI}{dt} = -I + \bar{w} r(t)$$

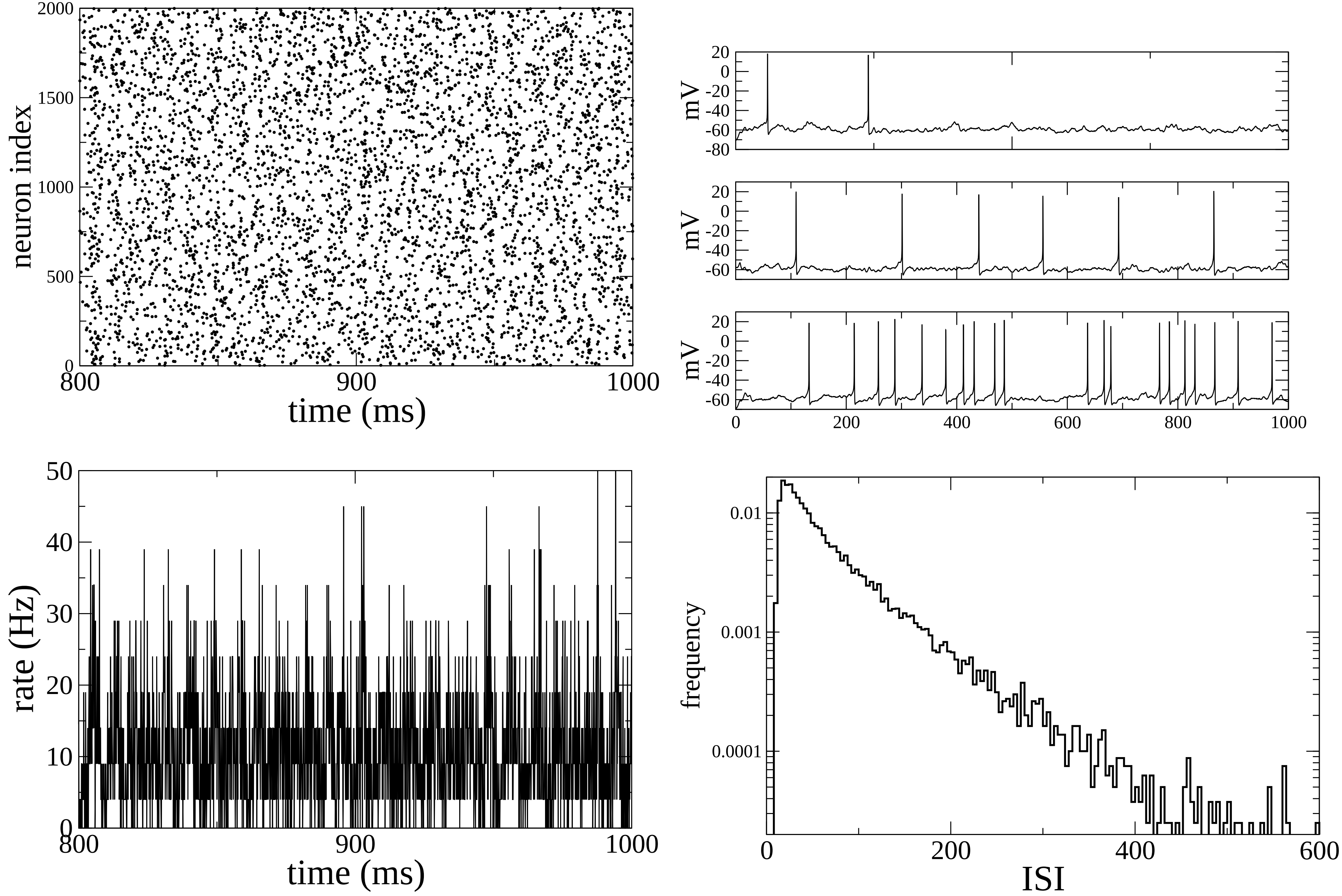
$$\tau_r \frac{dr}{dt} = -r + \phi(I)$$

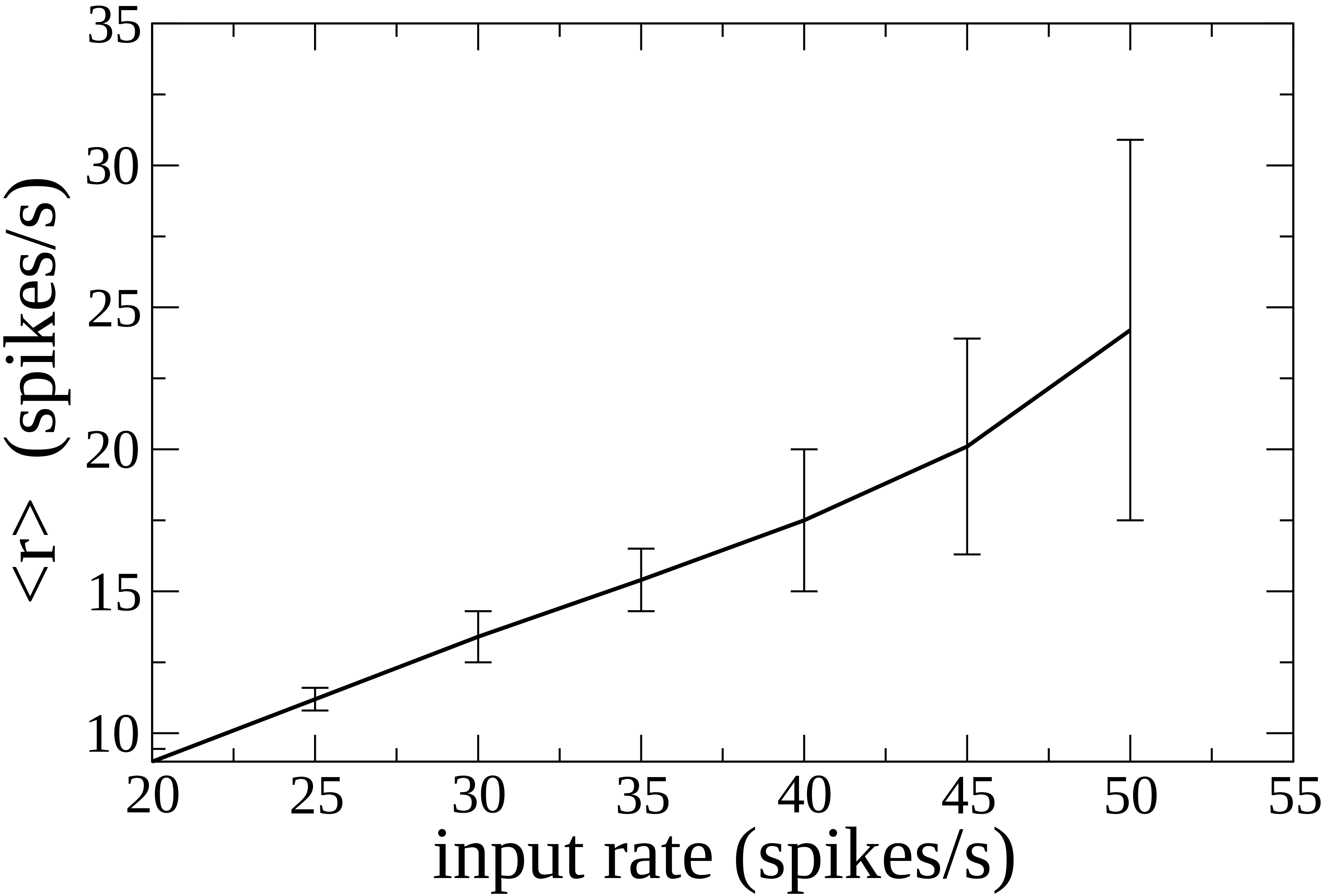
Rate Model for Inhibitory Network

$$\frac{dr}{dt} = -r + \phi(-wr + I)$$

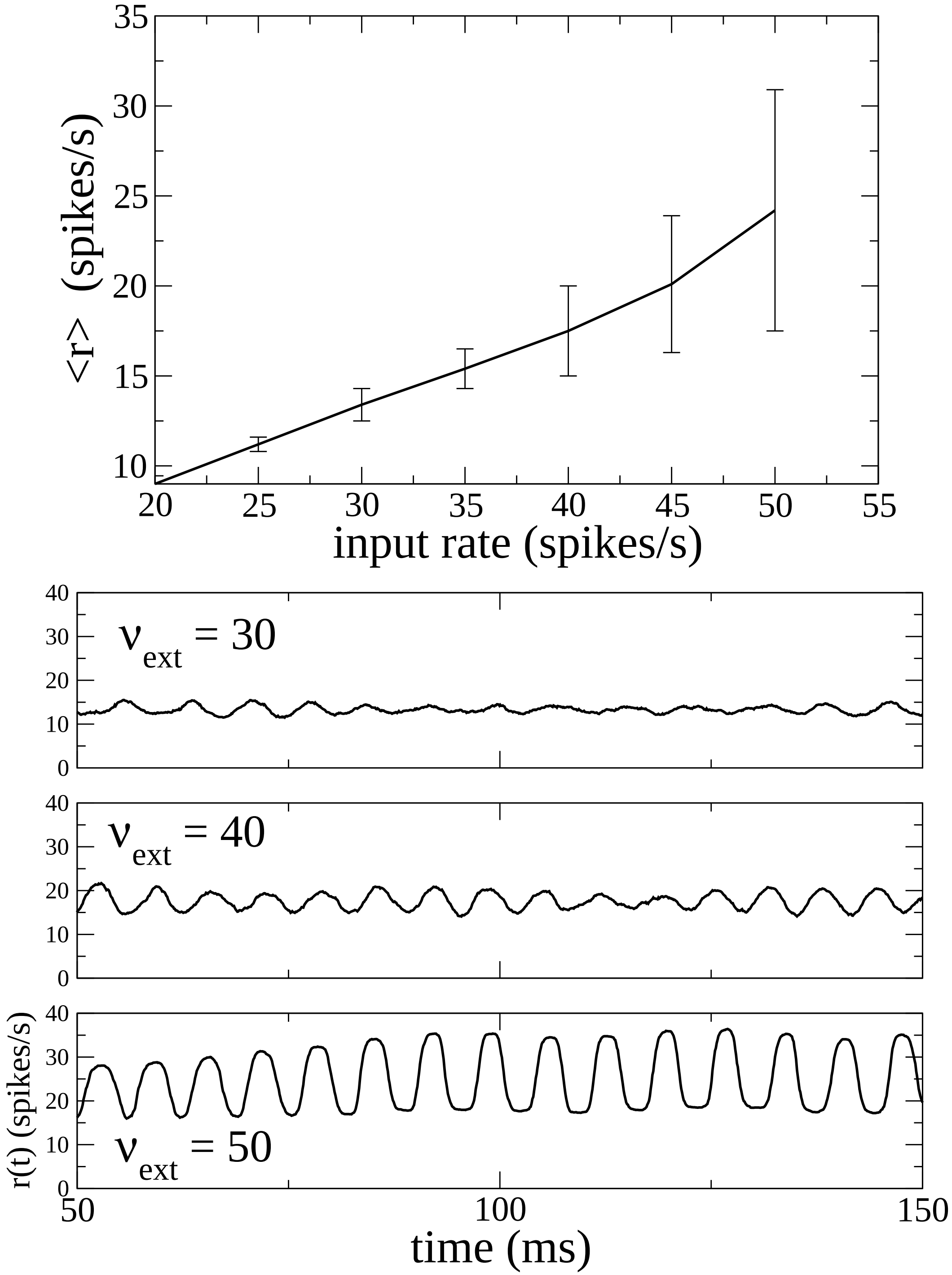
Network Simulations

- conductance based with K^+ and Na^+ (Wang & Buszaki, 1996)
- all inhibitory neurons
- exponential synaptic conductances
- sparse connectivity (20%)
- noisy external drive with rate ν_{ext}

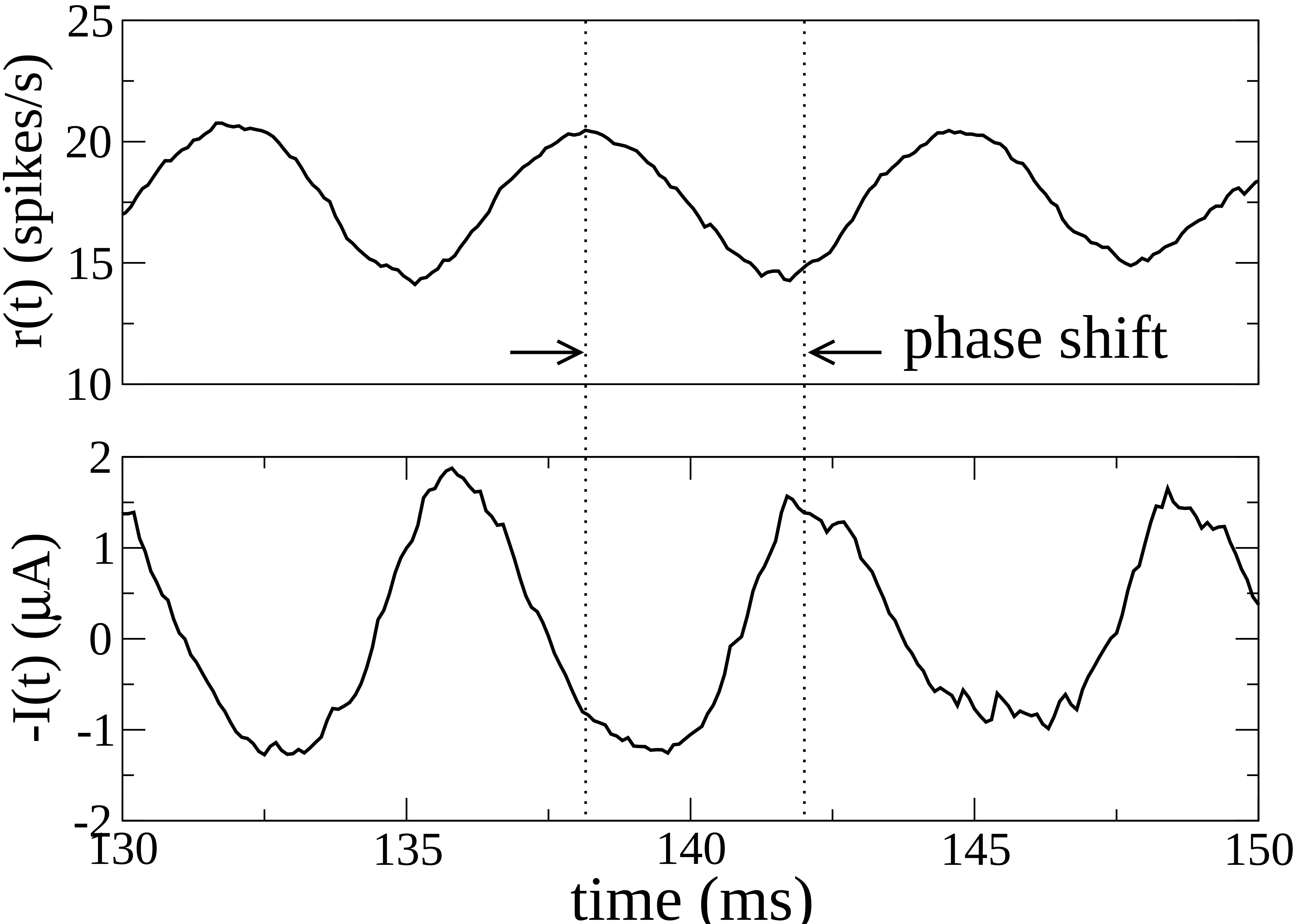

neuron index
time (ms)
mV
rate (Hz)
frequency
ISI



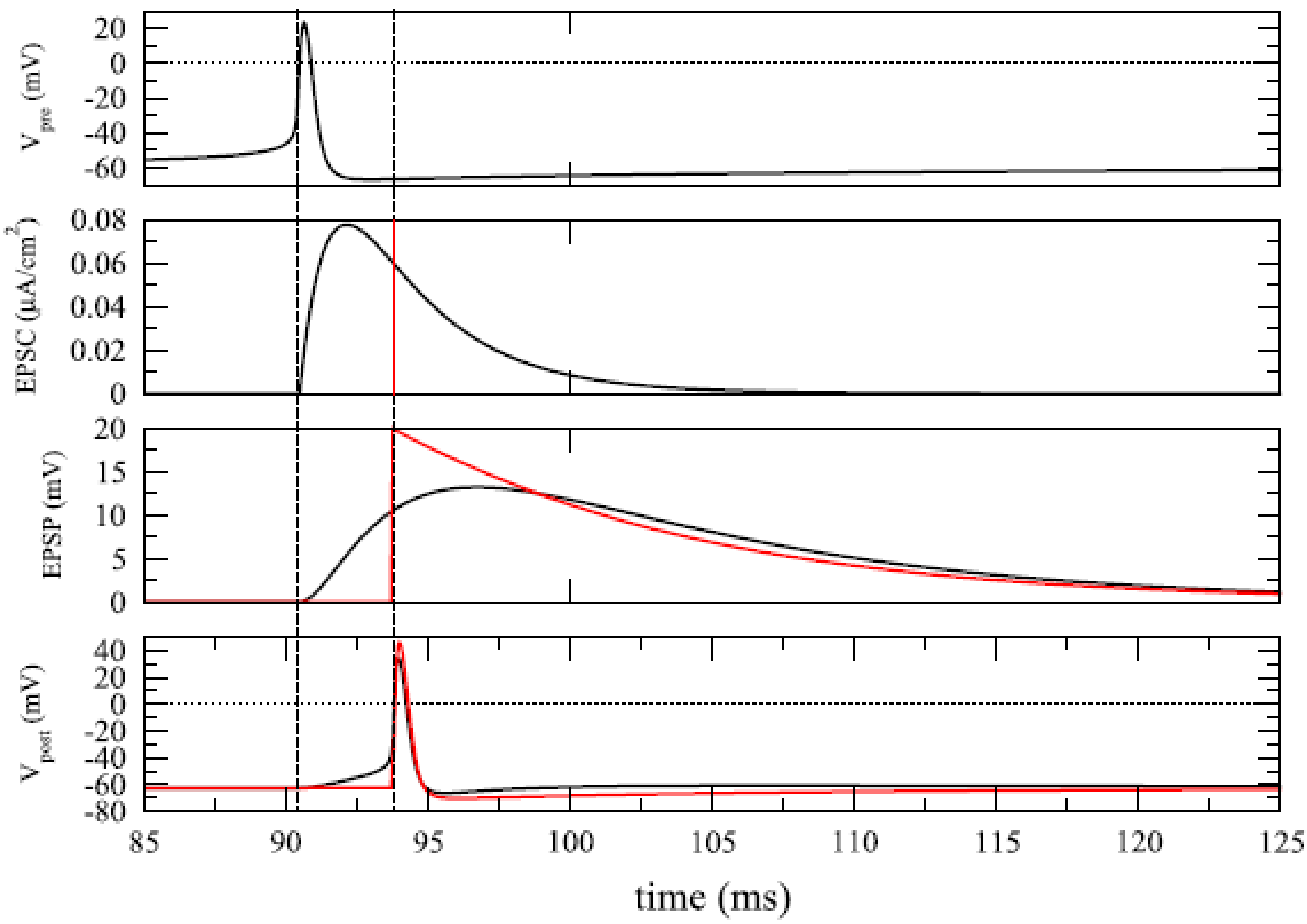
35
30
25
20
15
10
<r> (spikes/s)
20
25
30
35
40
45
50
55
input rate (spikes/s)



35
30
25
20
15
10
20
25
30
35
40
45
50
55
<r> (spikes/s)
input rate (spikes/s)
40
30
20
10
0
ν_{ext} = 30
ν_{ext} = 40
ν_{ext} = 50
r(t) (spikes/s)
50
100
150
time (ms)



25
20
15
10
r(t) (spikes/s)
phase shift
2
1
0
-1
-2
-I(t) (μA)
130
135
140
145
150
time (ms)

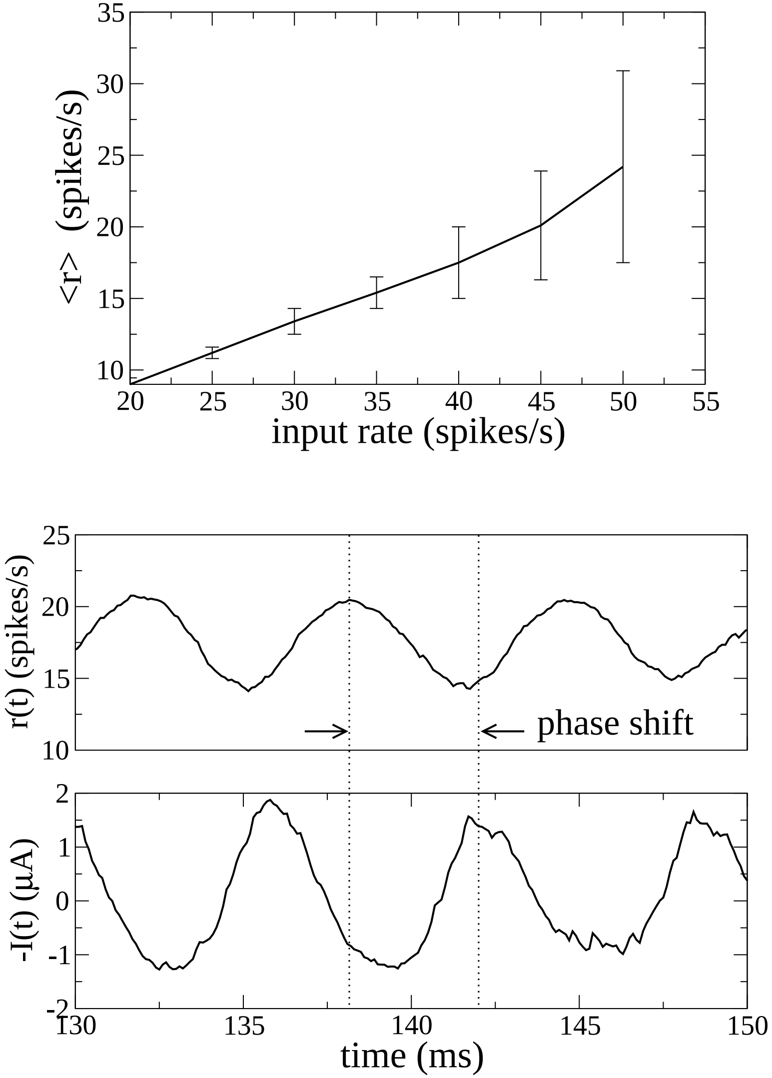


V_pre (mV)
20
0
-20
-40
-60
EPSC (μA/cm^2)
0.08
0.06
0.04
0.02
0
EPSP (mV)
20
15
10
5
0
V_post (mV)
40
20
0
-20
-40
-60
-80
85
90
95
100
105
110
115
120
125
time (ms)

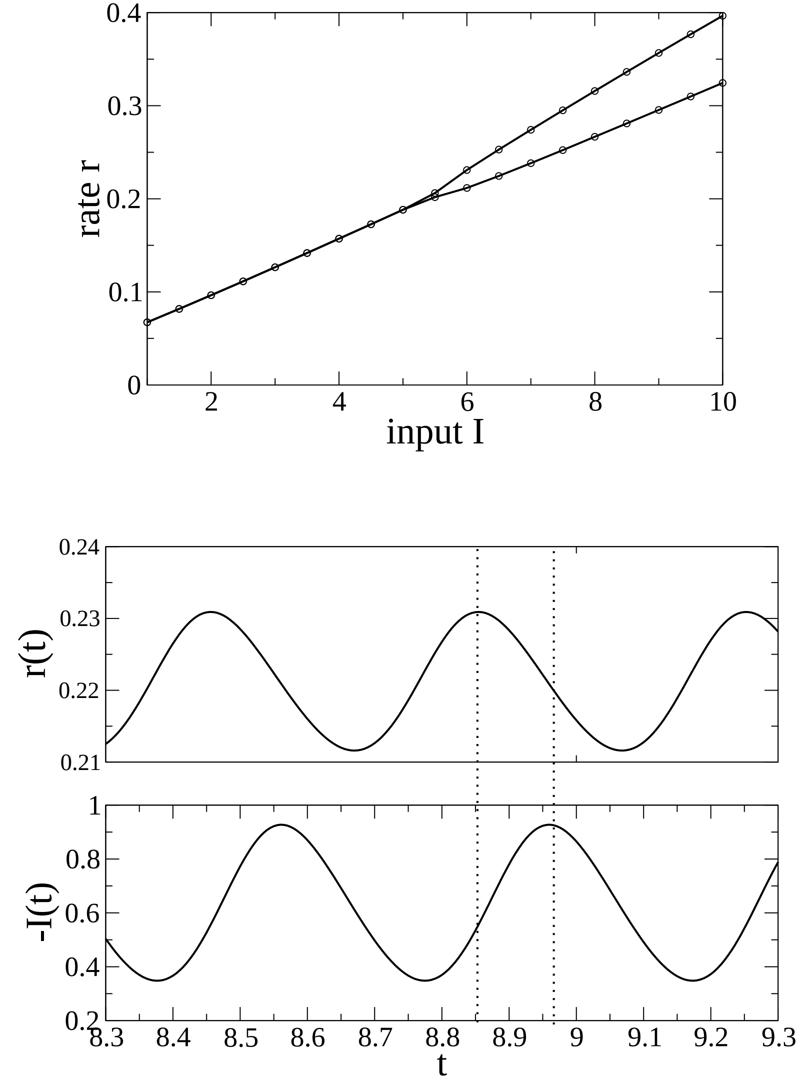
Inlcude fixed delay to account for phase shift.

$$\boxed{\frac{dr}{dt} = -r + \phi(-wr(t - D) + I)}$$

Network



Rate Model



Decision making at a pitchfork bifurcation.

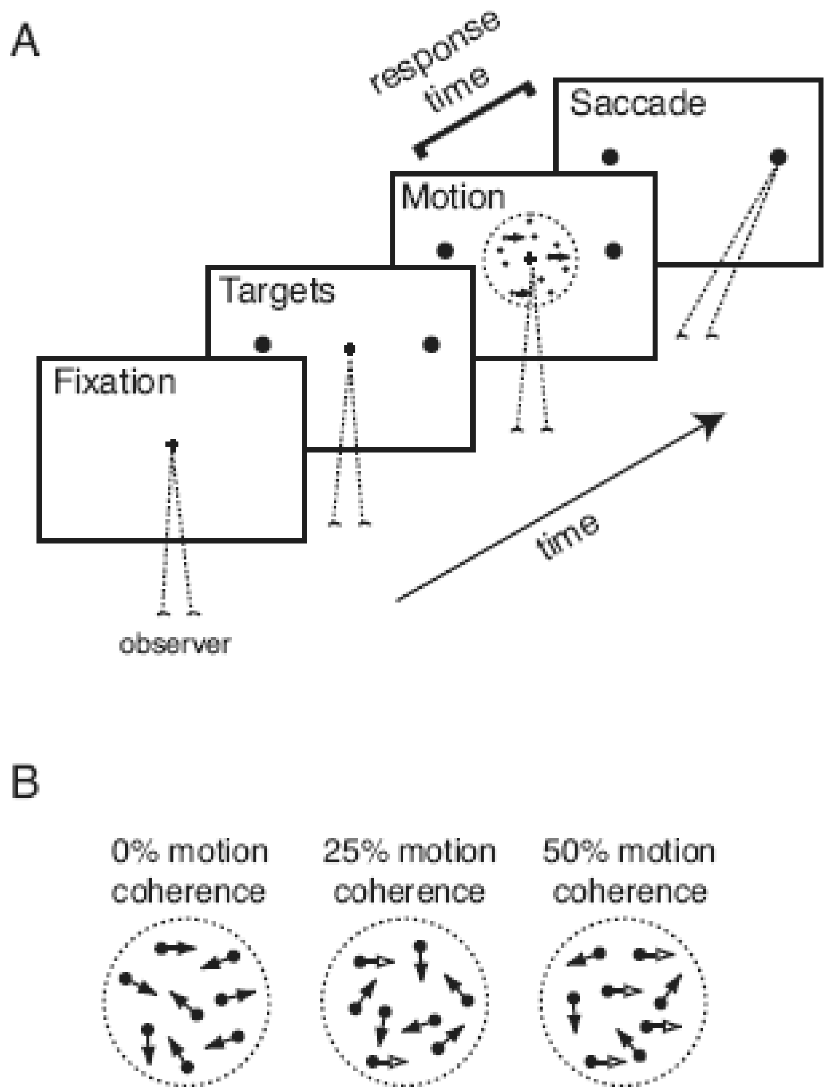


Figure 1: *Random Dot Task.* Palmer et al., J. Vision 2005.

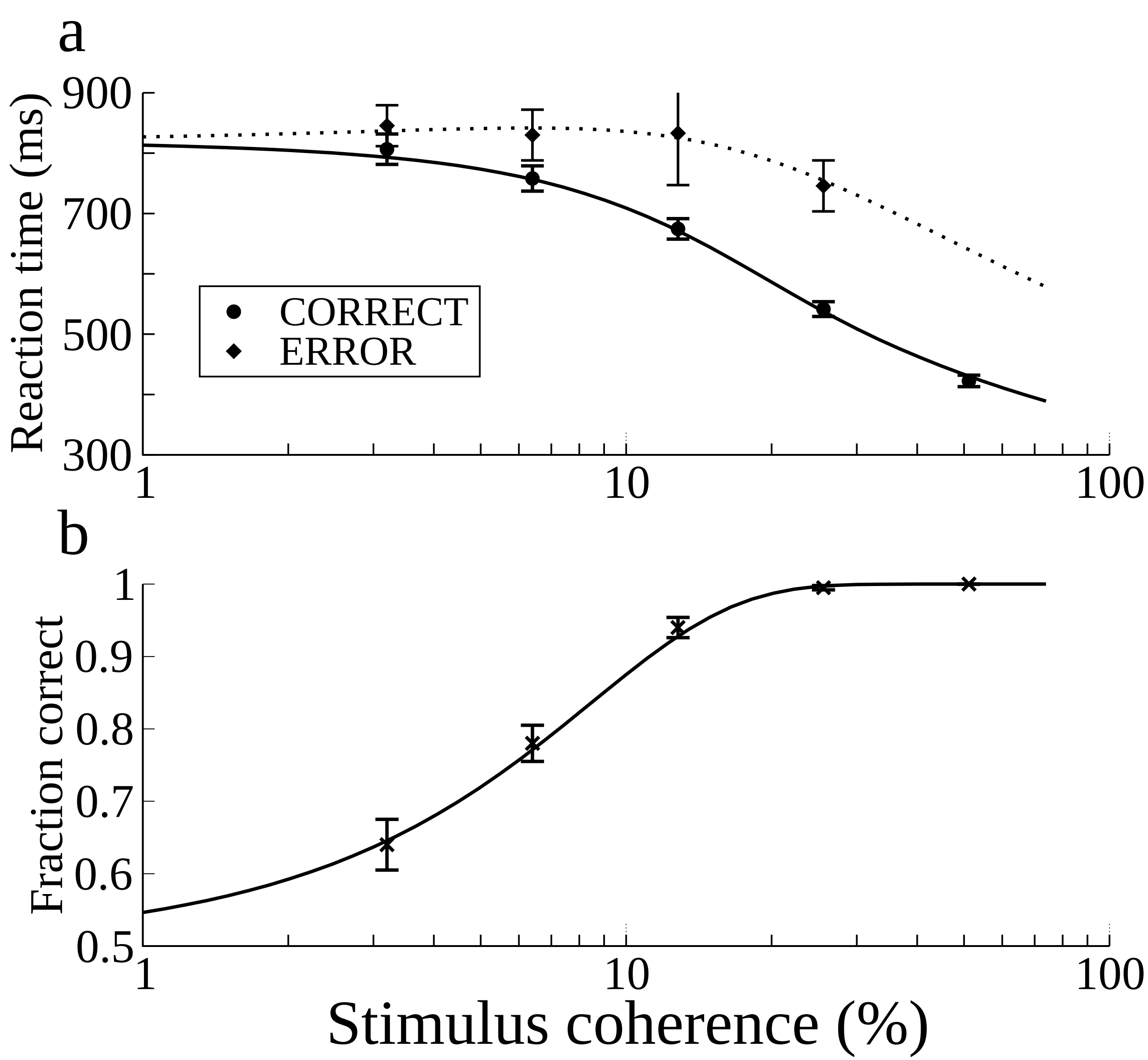


Figure 2: Behavior in monkeys for the moving dot task. From Roitman and Shadlen 2002.

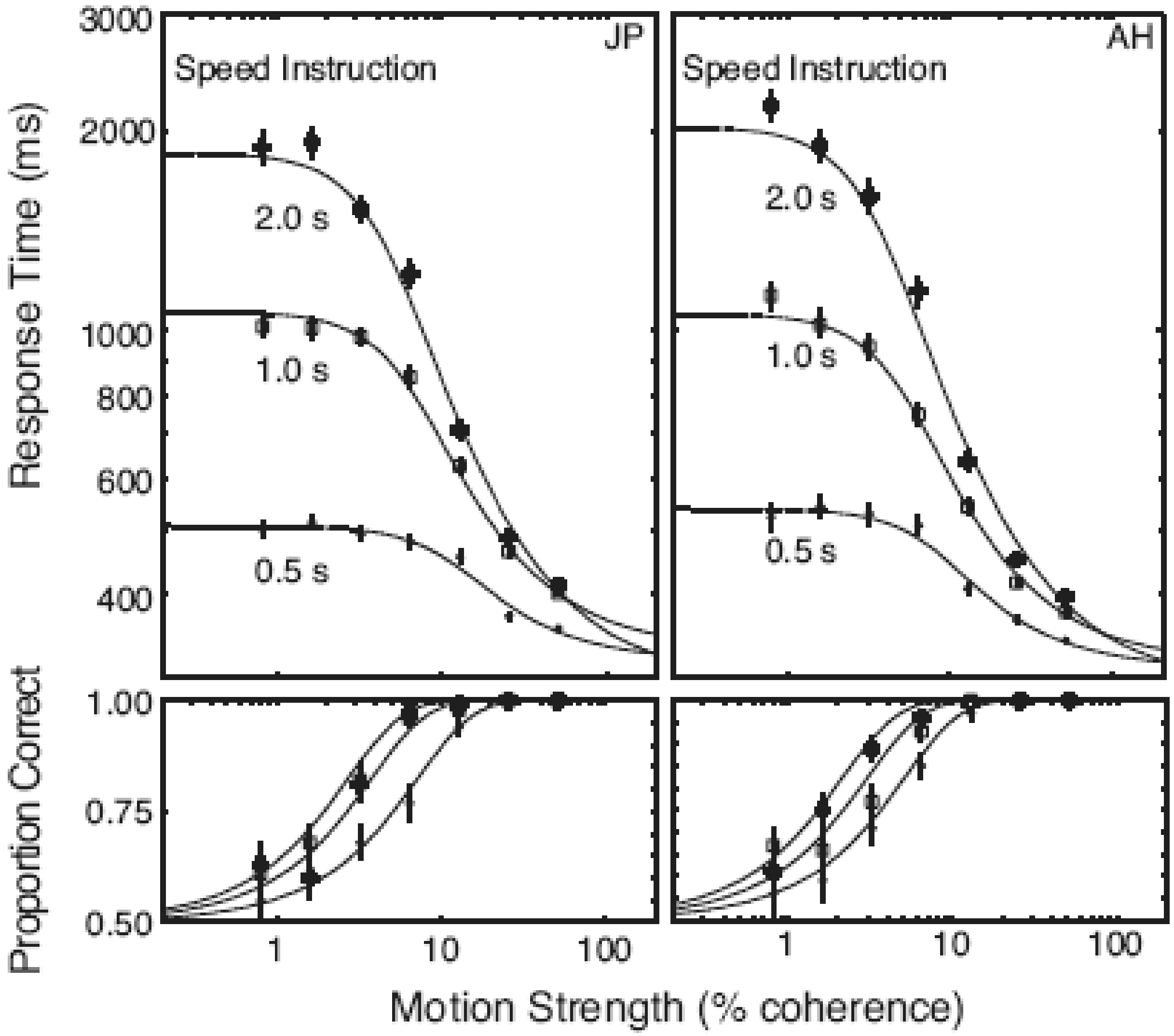
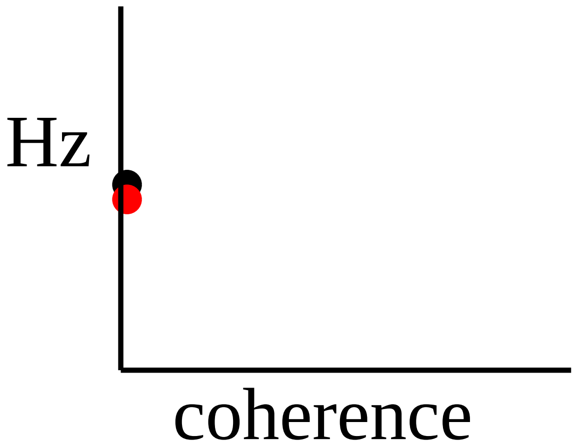
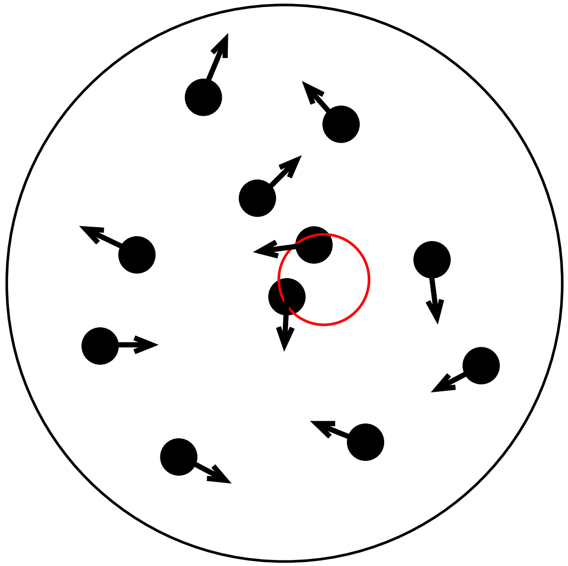


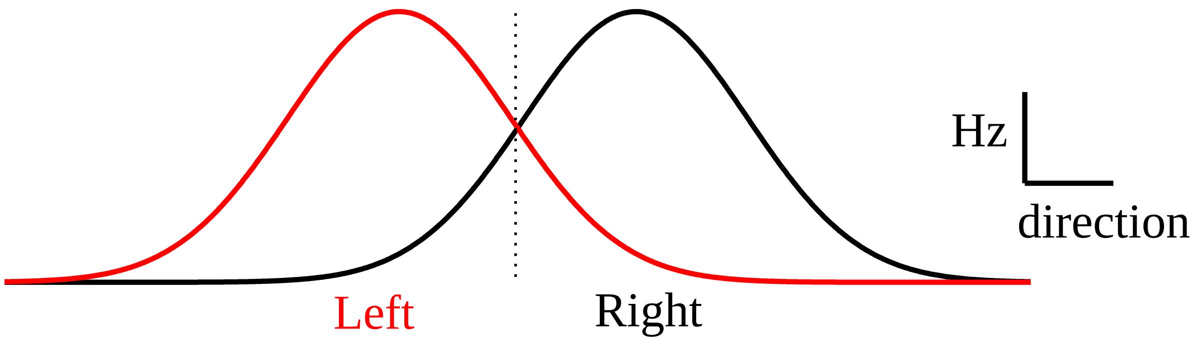
Figure 3: *The speed-accuracy trade-off in humans.* Palmer et al., J. Vision 2005.

How are sensory neurons encoding the stimulus?

0% Coherence

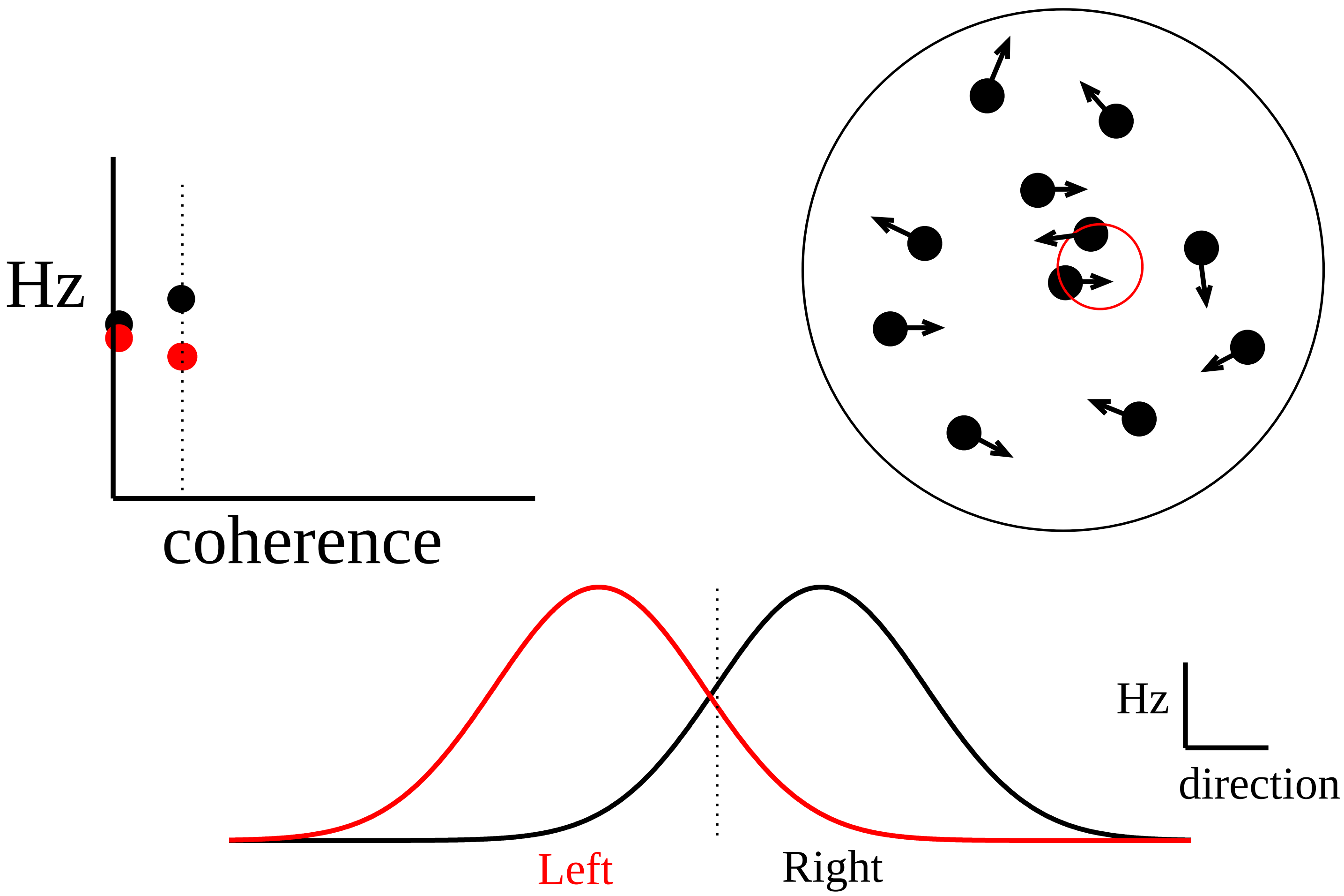






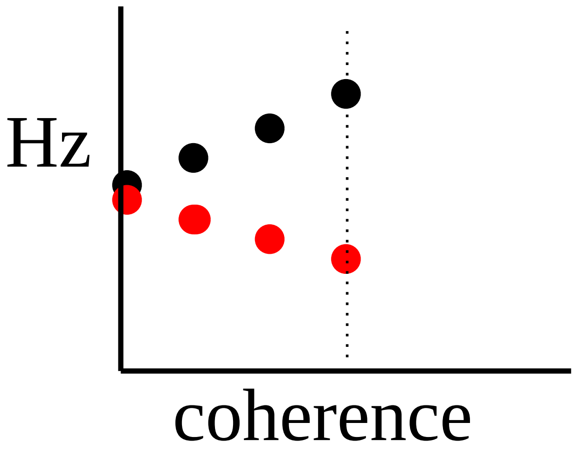
How are sensory neurons encoding the stimulus?

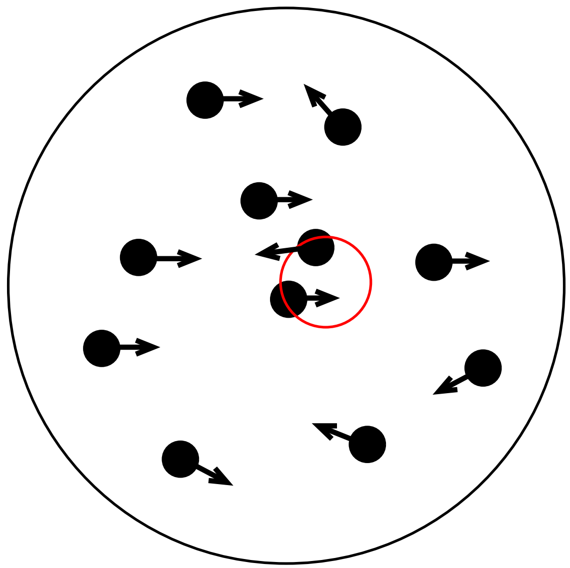
Non-zero Coherence

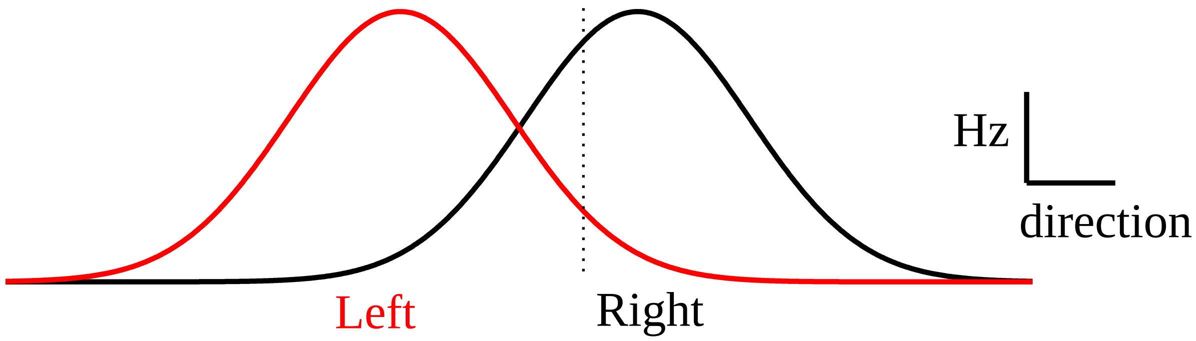


How are sensory neurons encoding the stimulus?

High Coherence

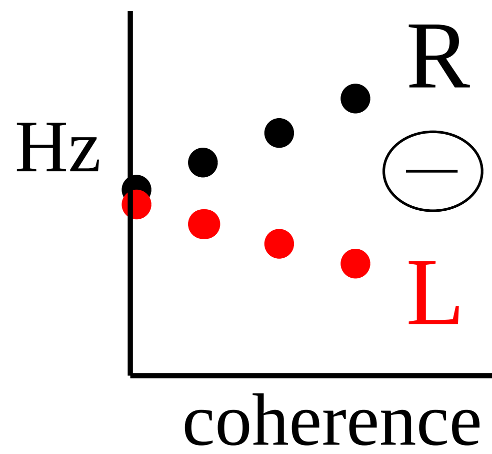




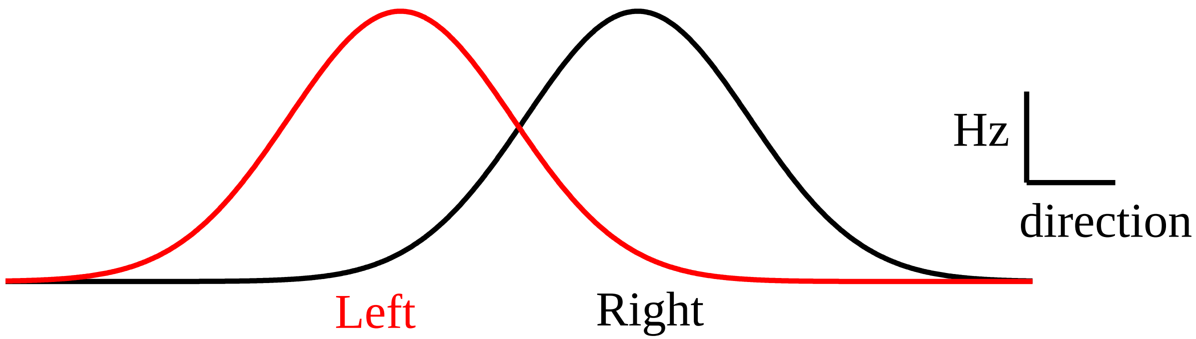


What's done with the sensory information?

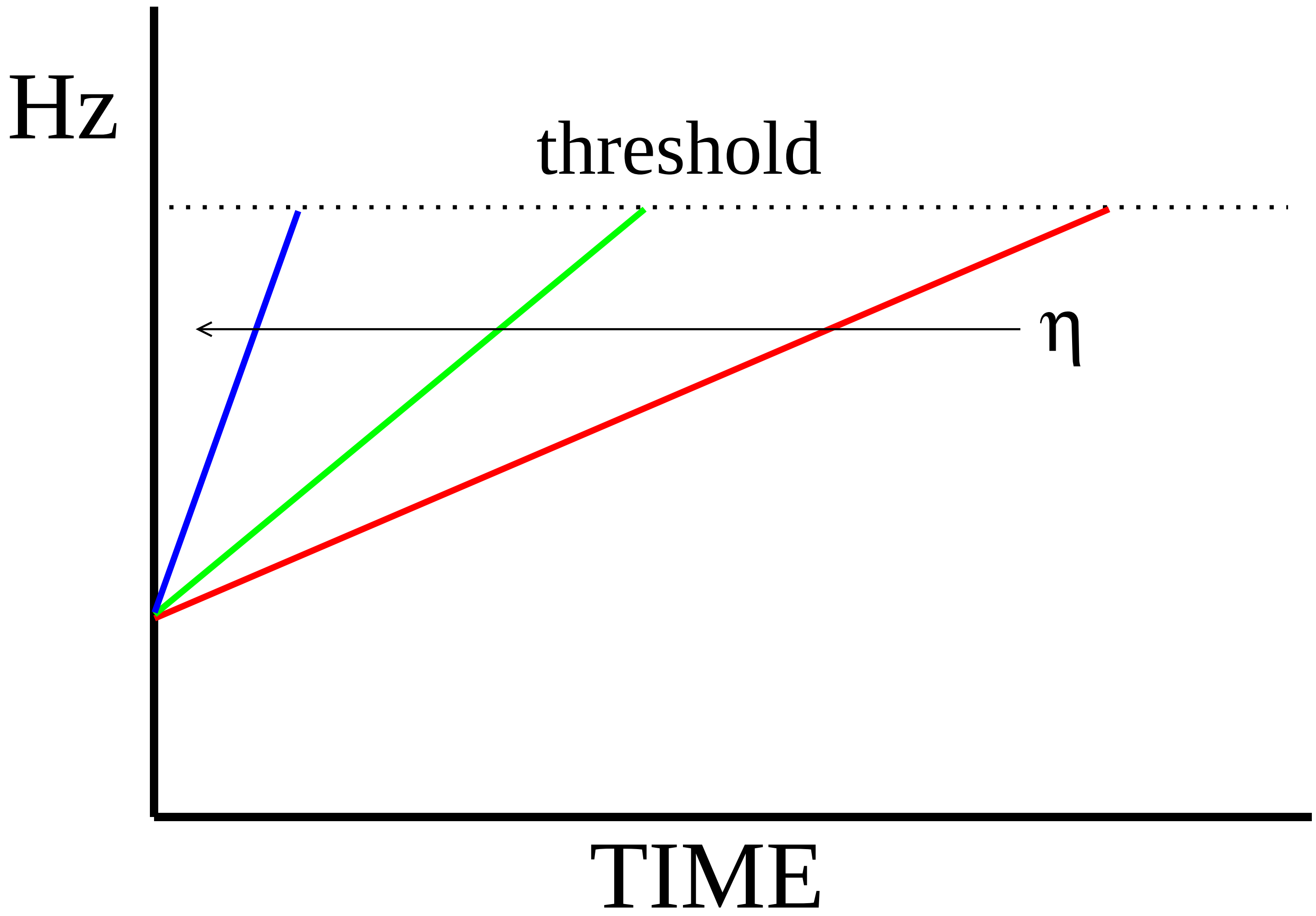
Integrate the Difference



$$= \eta+\sigma\xi(t)$$



What’s done with the sensory information?



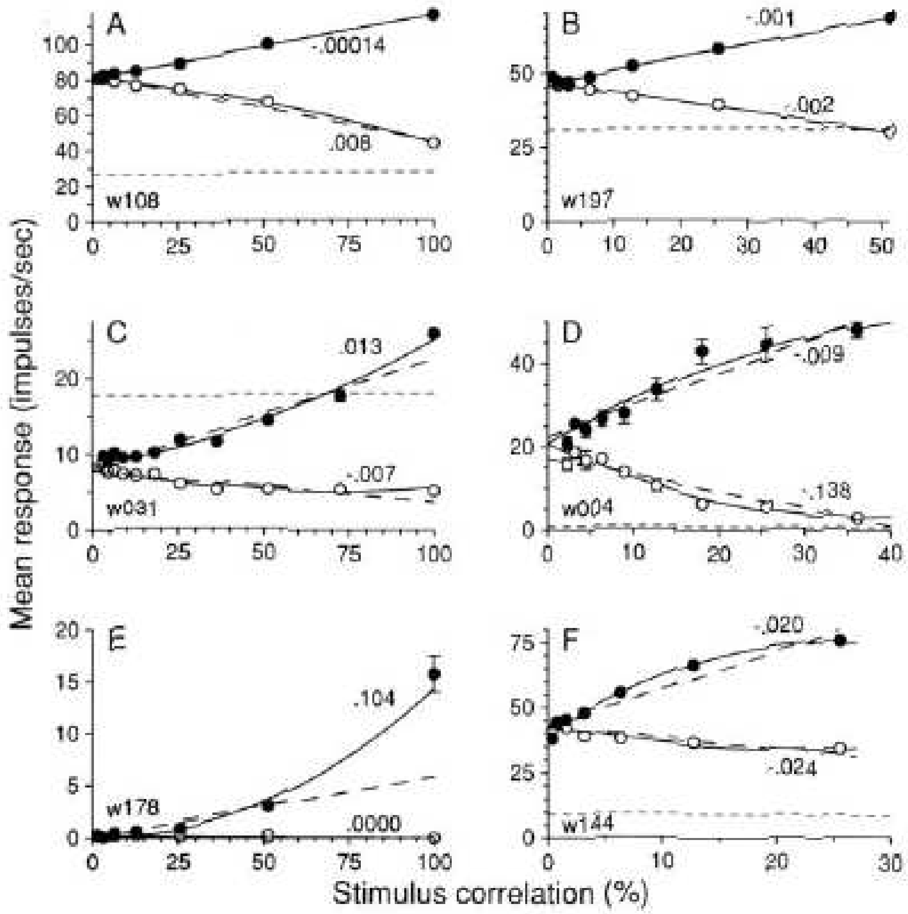


Figure 4: *Response of MT cells to randomly moving dots.* Britten et al. 1993.

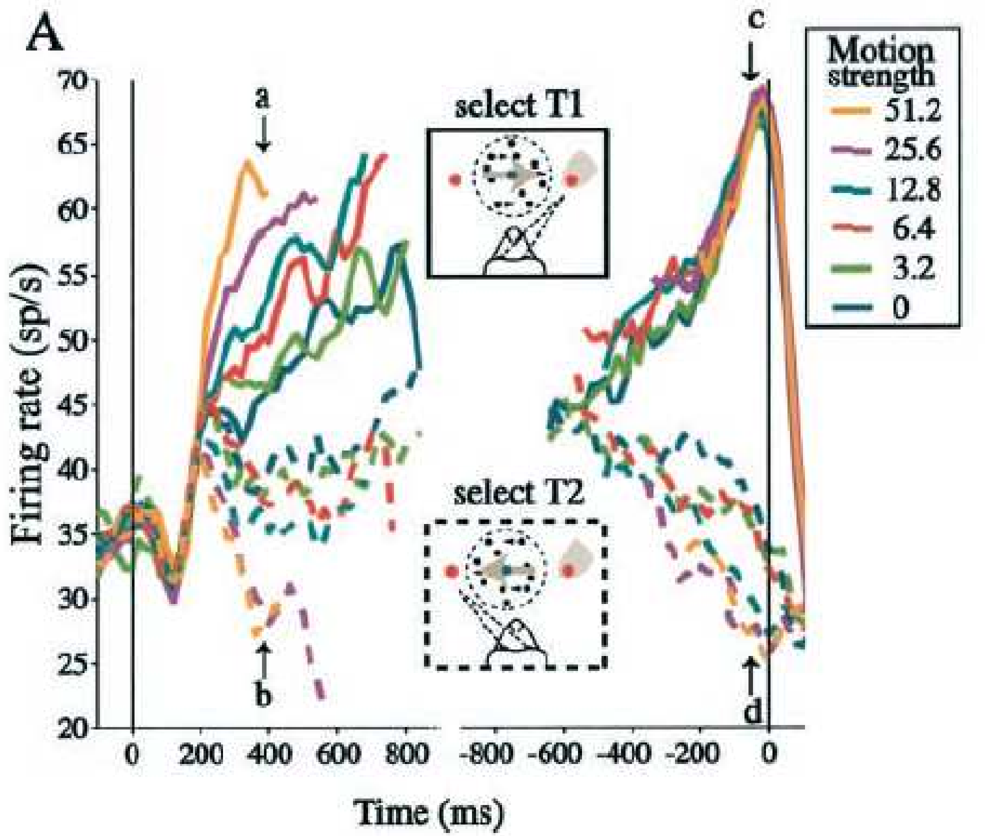


Figure 5: *Trial-averaged activity in LIP for the Reaction-time task.* Roitman and Shadlen 2002.

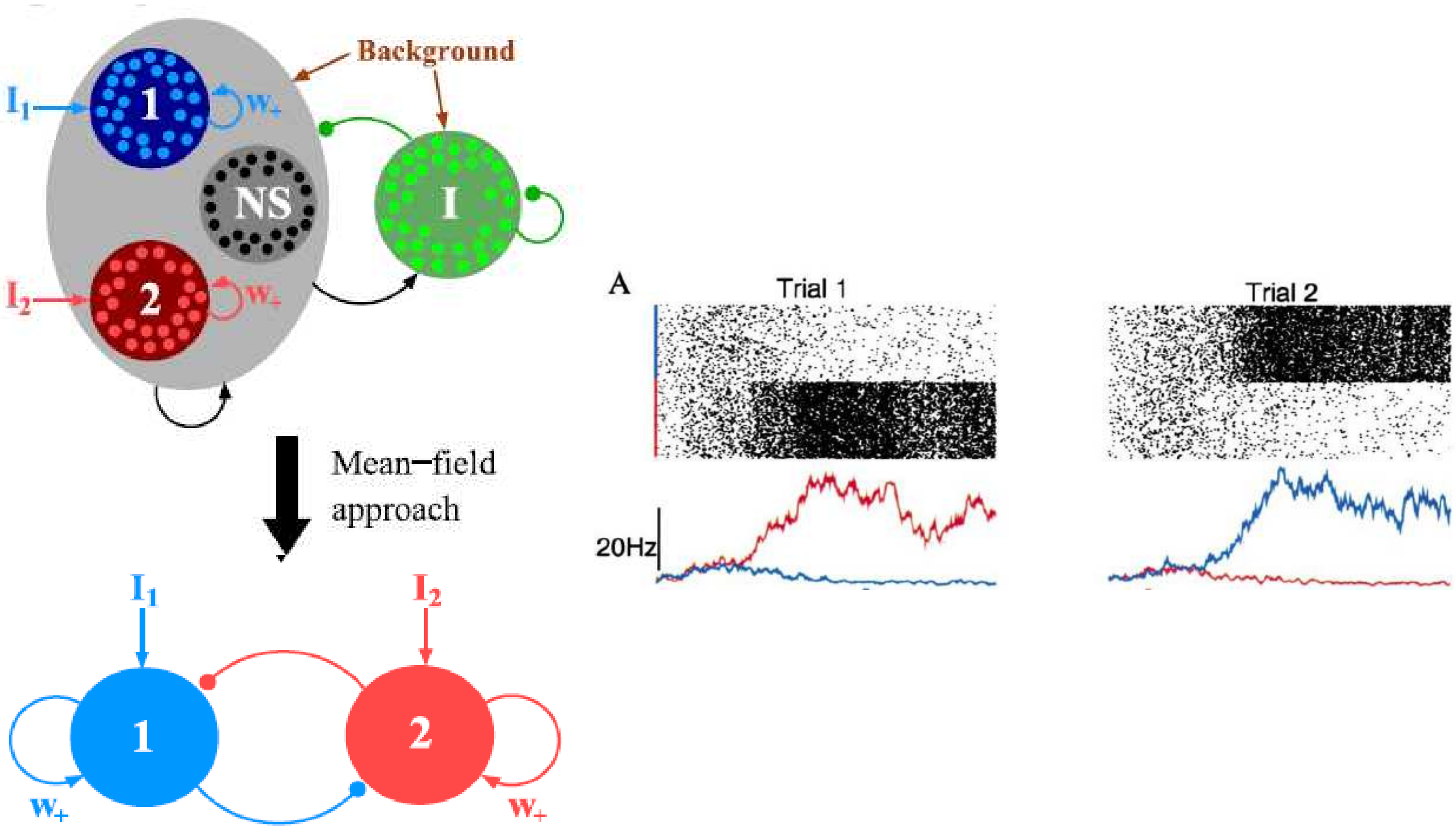


Figure 6: *Biophysically motivated 2-choice decision making network.* X.-J. Wang, Neuron 2002. Wong and X.-J. Wang, J. of Neurosci. 2006.

A simple rate model description.

$$\boxed{\begin{aligned}\dot{r}_1 &= -r_1 + \Phi\Big(sr_1 - cr_2 + \nu_1\Big)\\ \dot{r}_2 &= -r_2 + \Phi\Big(sr_2 - cr_1 + \nu_2\Big)\end{aligned}}$$

First consider symmetric case, $\nu_1 = \nu_2 = \nu$.

- Bifurcation for $c\Phi^{'}(\nu_{cr}) = 1 - s\Phi^{'}(\nu_{cr})$.
- Eigenvalues: $\lambda_c = 0$, $\lambda_s = -2(1 - s\Phi^{'}(\nu_{cr}))$.
- Eigenvectors: $r_c = (1, -1)$, $r_s = (1, 1)$.

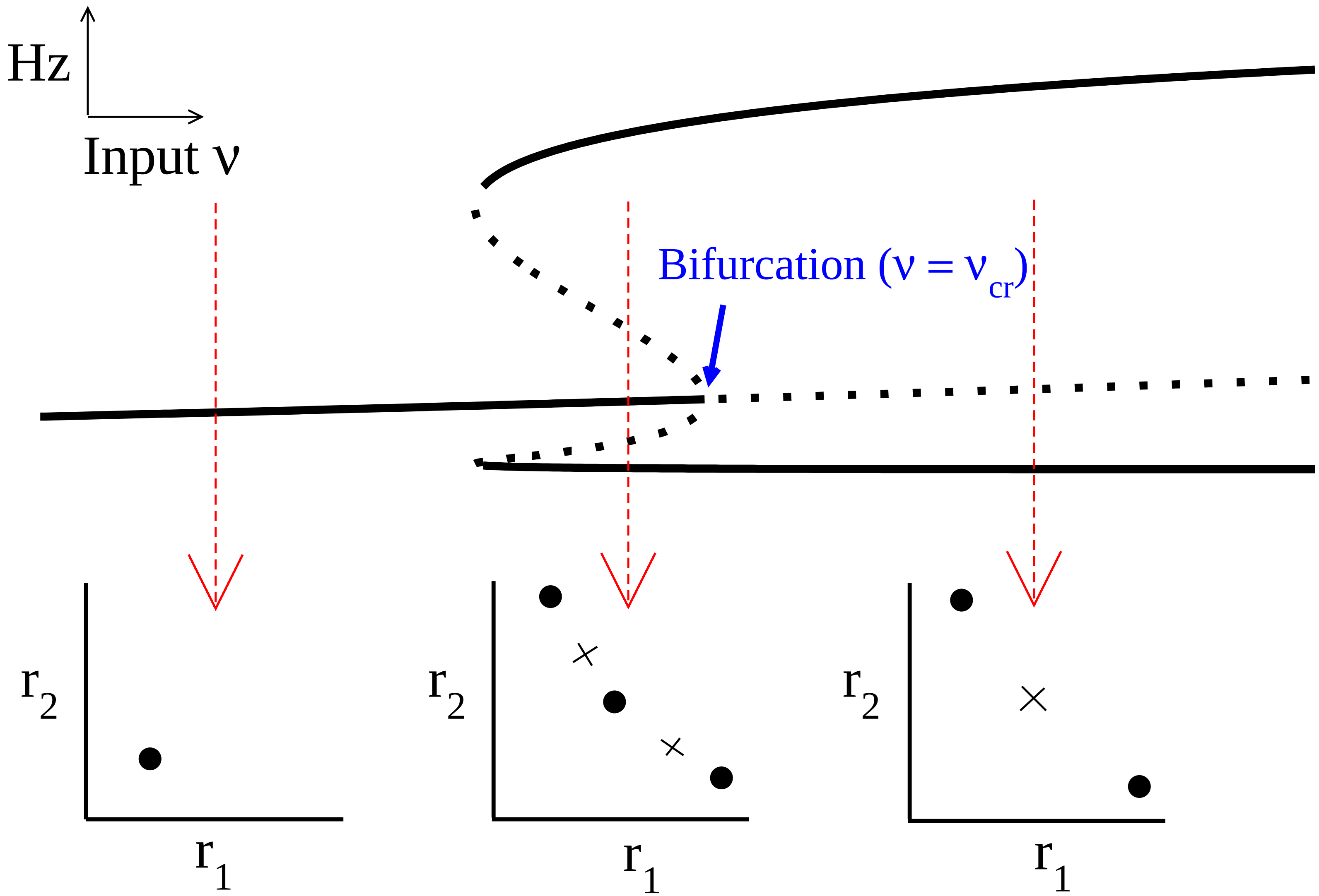
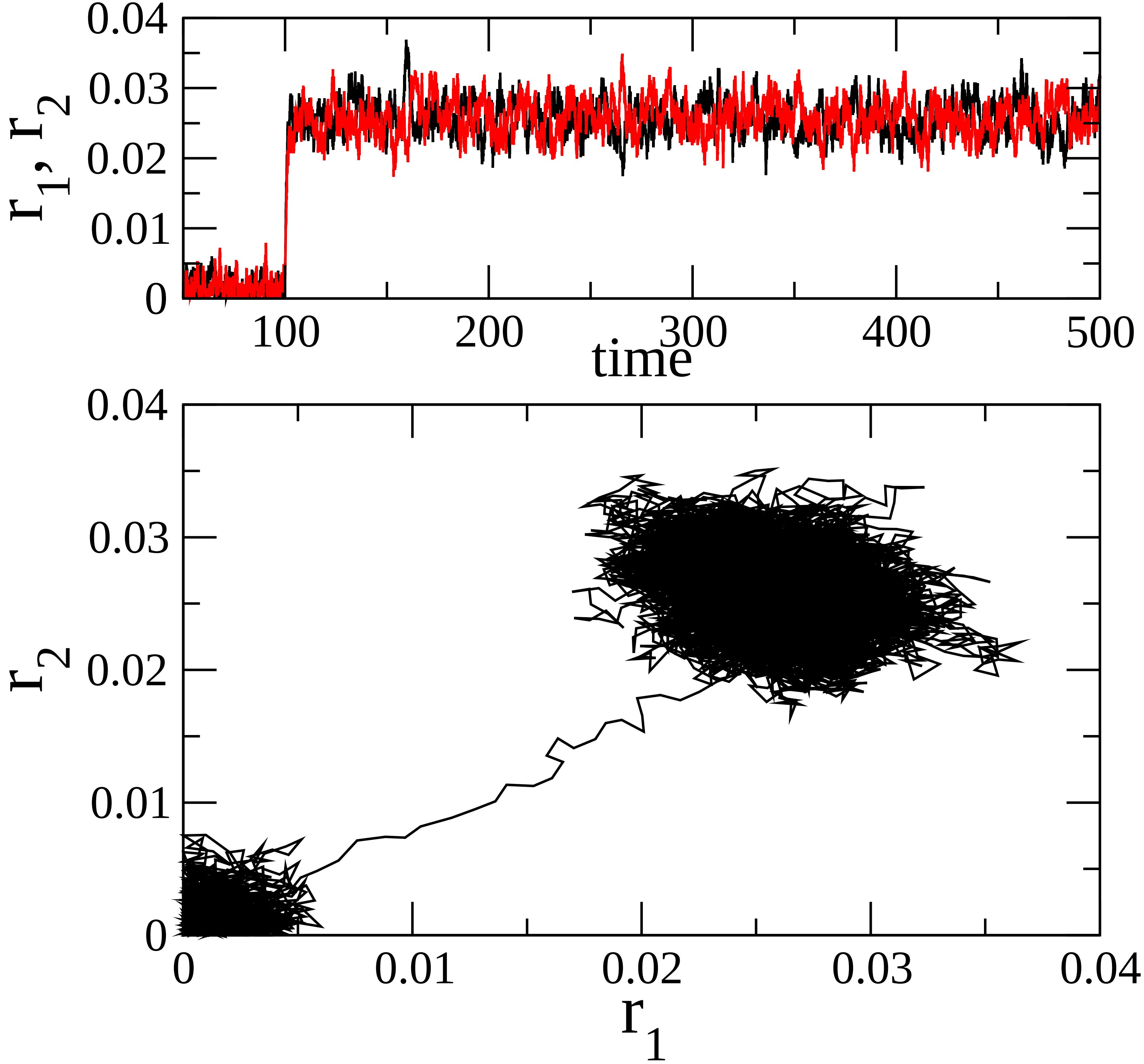
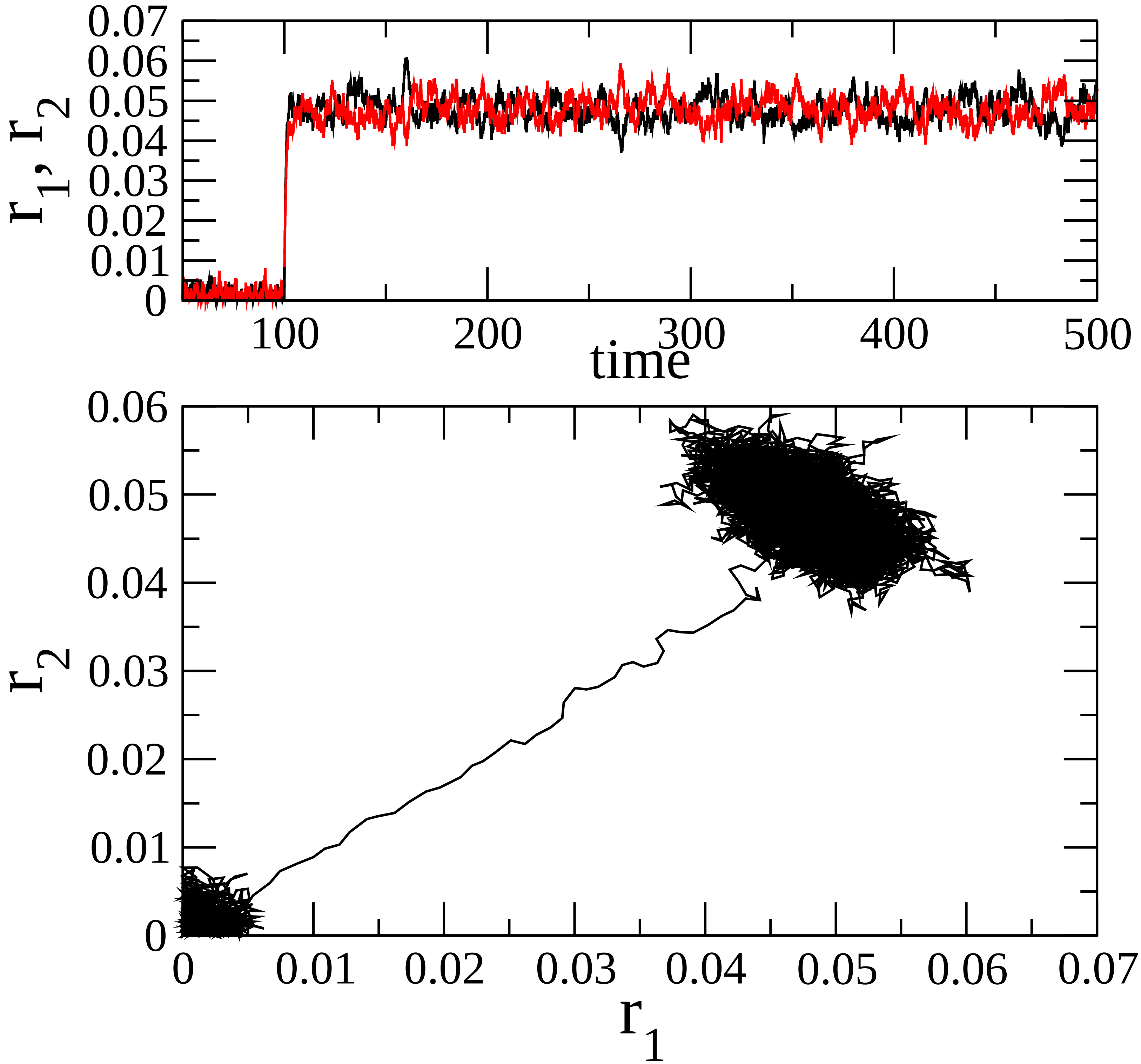


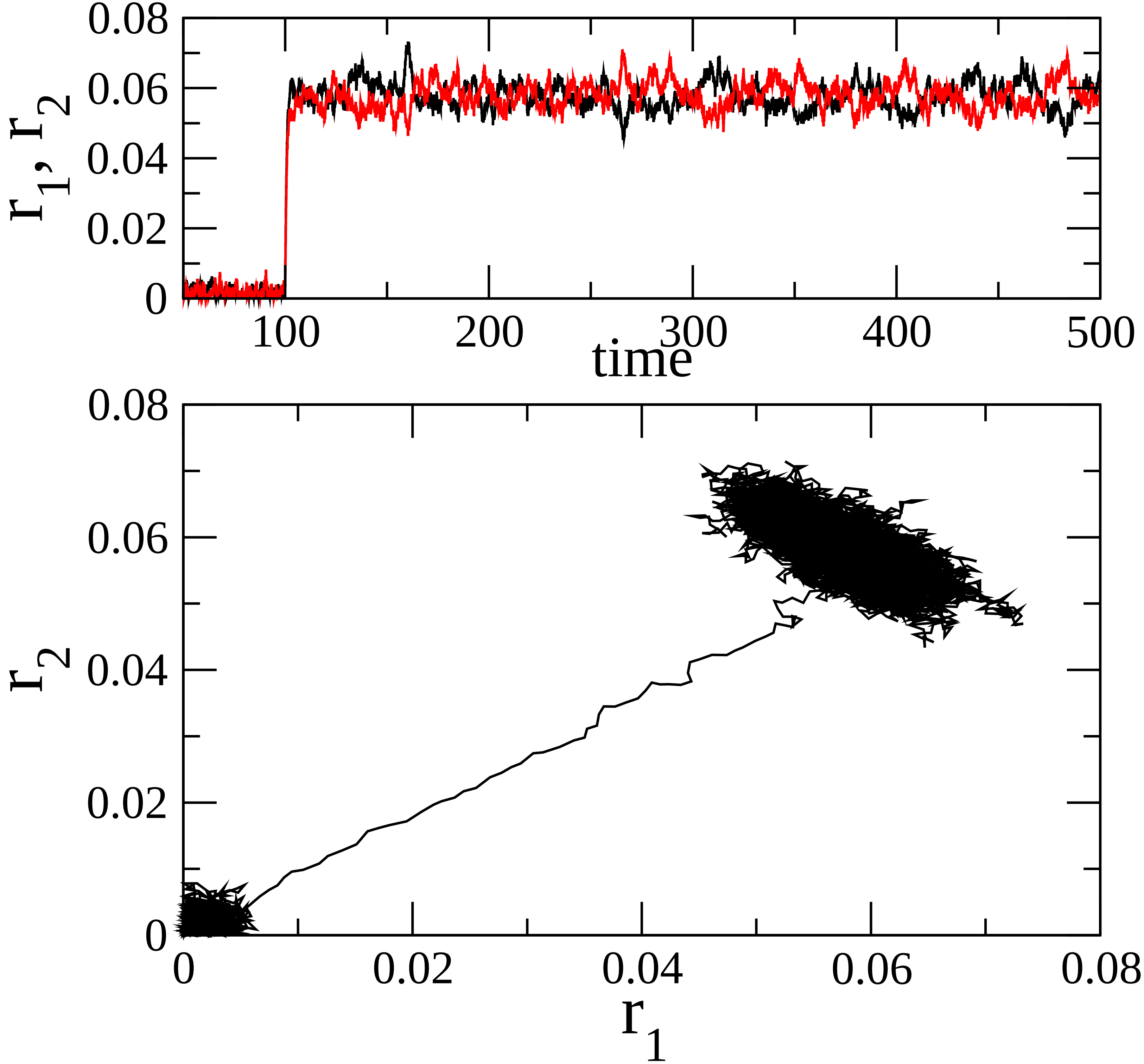
Figure 7: The bifurcation diagram for 2-choice decision-making networks.

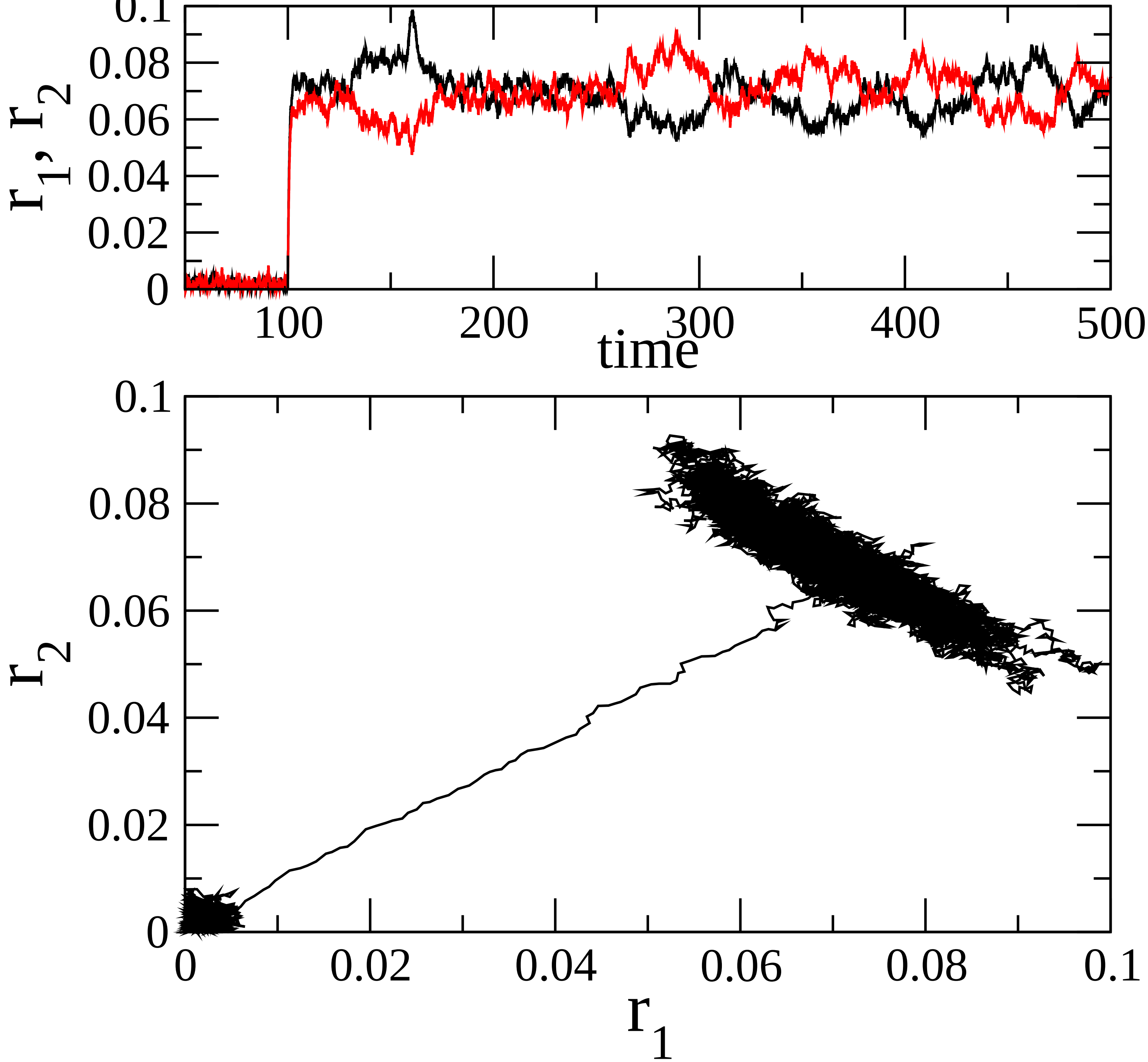


0.04
0.03
0.02
0.01
0
r1, r2
100
200
300
400
500
time
0.04
0.03
0.02
0.01
0
r2
0
0.01
0.02
0.03
0.04
r1

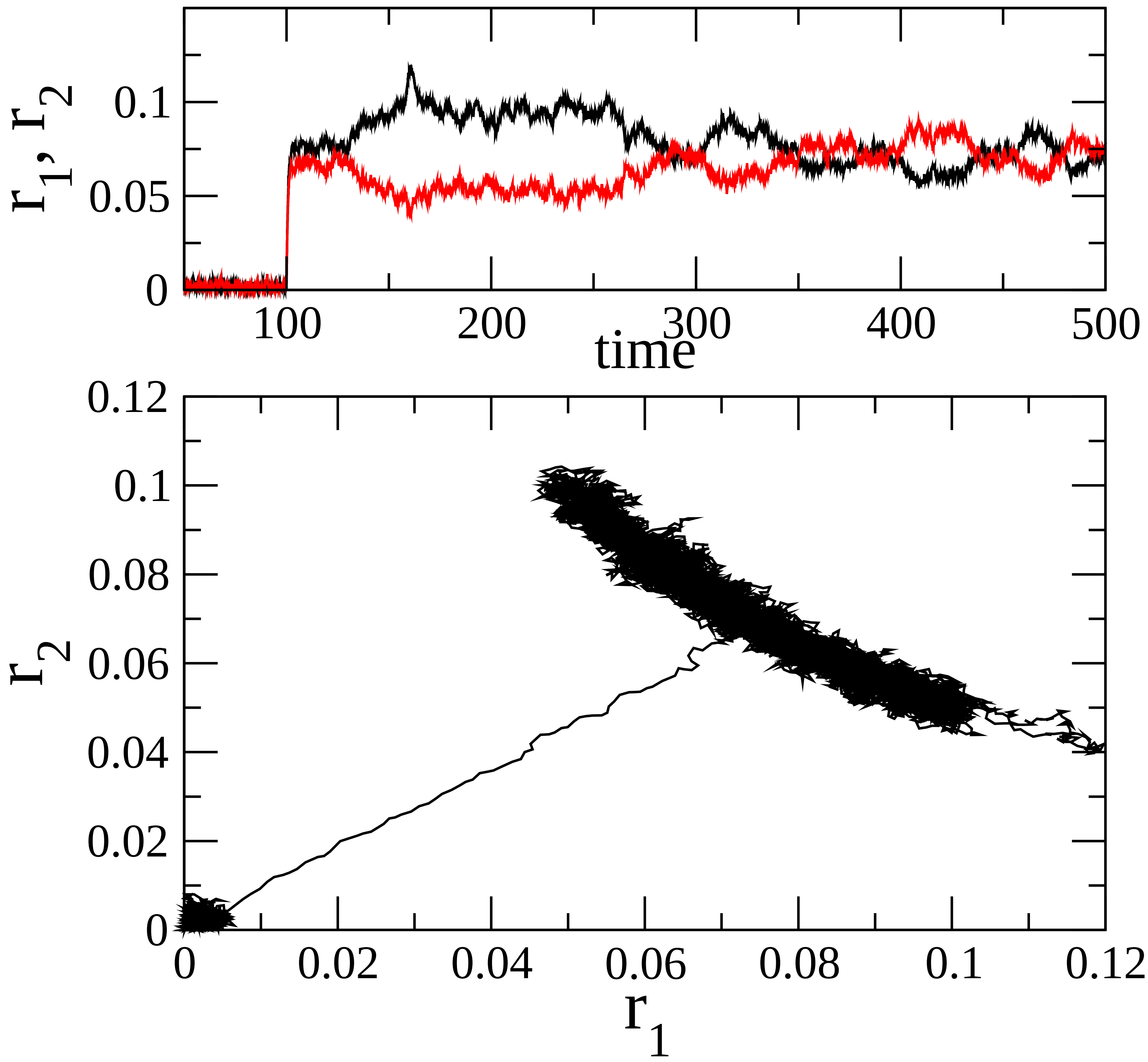


0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
r1, r2
100
200
300
400
500
time
0.06
0.05
0.04
0.03
0.02
0.01
0
r2
0
0.01
0.02
0.03
0.04
0.05
0.06
0.07
r1

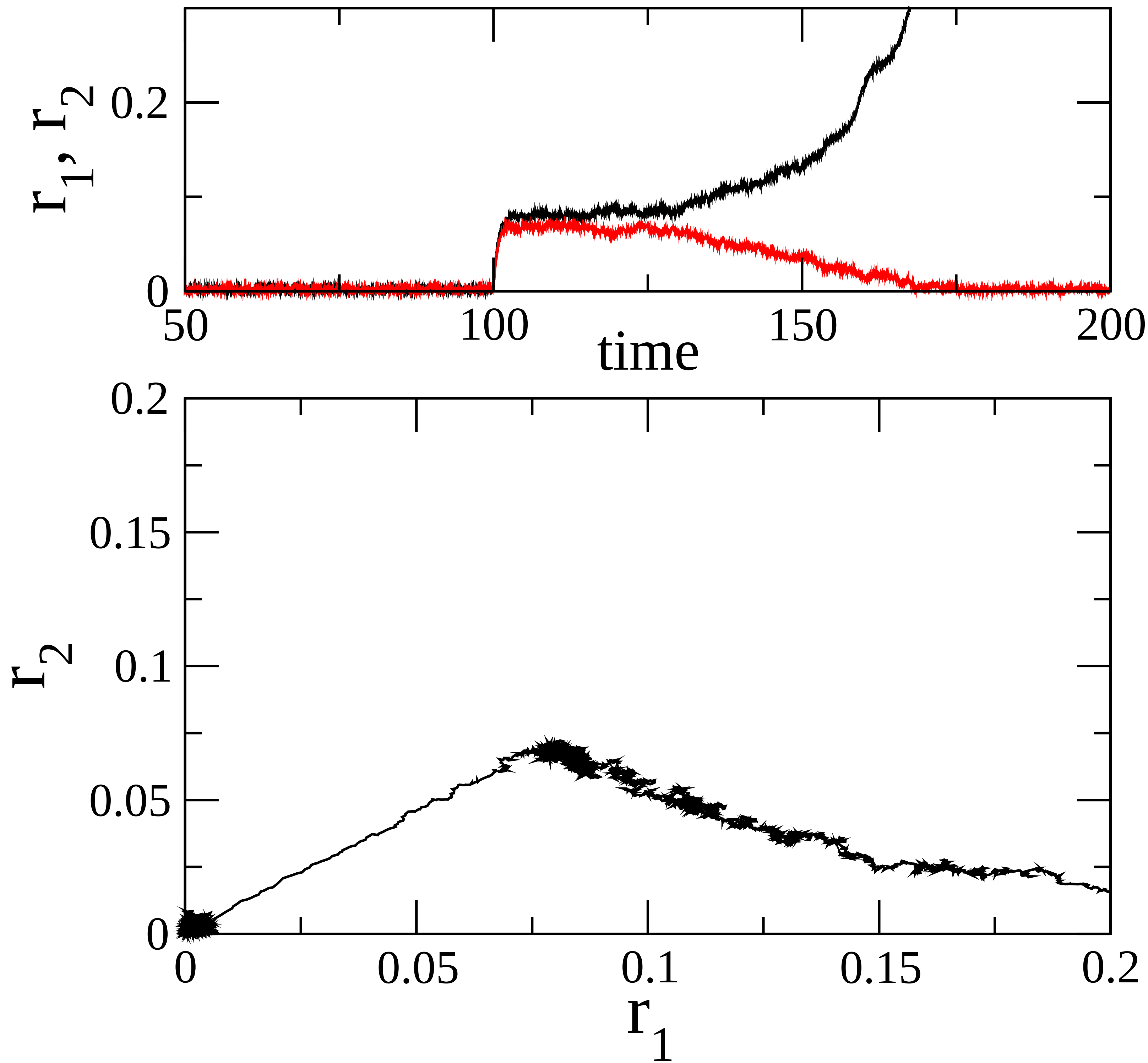

0.08
0.06
0.04
0.02
0
r 1 , r 2
100
200
300
400
500
time
0.08
0.06
0.04
0.02
0
r 2
0
0.02
0.04
0.06
0.08
r 1



0.1
0.08
0.06
0.04
0.02
0
100
200
300
400
500
time
r1, r2
0.1
0.08
0.06
0.04
0.02
0
0
0.02
0.04
0.06
0.08
0.1
r1
r2



r1, r2
0
0.05
0.1
100
200
300
400
500
time
r2
0
0.02
0.04
0.06
0.08
0.1
0.12
0
0.02
0.04
0.06
0.08
0.1
0.12
r1



r_1, r_2
0.2
0
50
100
150
200
time
0.2
0.15
r_2
0.1
0.05
0
0
0.05
0.1
0.15
0.2
r_1

How to derive the reduced model. An example.

$$\boxed{\begin{aligned}\dot{r}_1 &= -r_1 + \Phi\Big(sr_1 - cr_2 + \nu_1\Big) + \sigma\xi_1(t)\\ \dot{r}_2 &= -r_2 + \Phi\Big(sr_2 - cr_1 + \nu_2\Big) + \sigma\xi_2(t)\end{aligned}}$$

Now expand the equations about the bifurcation point with $\nu = \nu_{cr} + \bar{\nu}$, $r_1 = r_{cr} + \bar{r}_1$, $r_2 = r_{cr} + \bar{r}_2$. Treat $\bar{\nu}$ as a state variable.

$$\begin{aligned}\dot{\bar{\nu}} &= 0\\ \dot{\bar{r}}_1 &= -\bar{r}_1 + \Phi^{'}(s\bar{r}_1 - c\bar{r}_2 + \bar{\nu}) + \frac{1}{2}\Phi^{''}(s\bar{r}_1 - c\bar{r}_2 + \bar{\nu})^2 + ...\\ \dot{\bar{r}}_2 &= -\bar{r}_2 + \Phi^{'}(s\bar{r}_2 - c\bar{r}_1 + \bar{\nu}) + \frac{1}{2}\Phi^{''}(s\bar{r}_2 - c\bar{r}_1 + \bar{\nu})^2 + ...\end{aligned}$$

How to derive the reduced model. An example.

$$\boxed{\begin{aligned}\dot{r}_1 &= -r_1 + \Phi\Big(sr_1 - cr_2 + \nu_1\Big) + \sigma\xi_1(t)\\ \dot{r}_2 &= -r_2 + \Phi\Big(sr_2 - cr_1 + \nu_2\Big) + \sigma\xi_2(t)\end{aligned}}$$

Now rewrite in matrix form and separate into linear and nonlinear parts.

$\dot{\mathbf{r}} = \mathcal{L}\mathbf{r} + \mathcal{N}(\mathbf{r})$

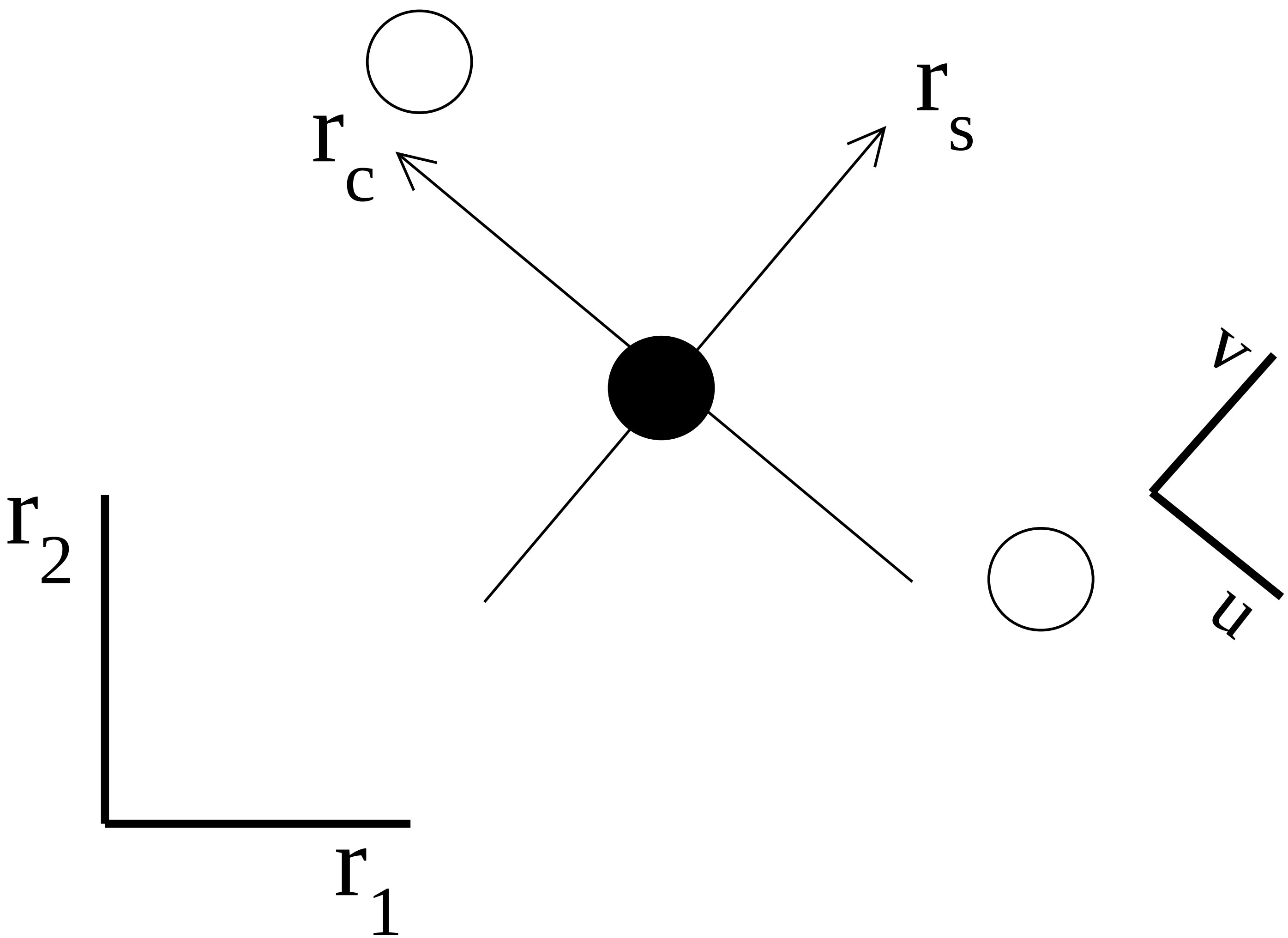
Diagonalize the linear operator and rotate the coordinates.

Diagonalize: $\dot{\mathbf{r}} = \mathcal{Q}\mathbf{\Lambda}\mathcal{Q}^{-1}\mathbf{r} + \mathcal{N}(\mathbf{r})$

Rotate: $\mathcal{Q}^{-1}\dot{\mathbf{r}} = \mathbf{\Lambda}\mathcal{Q}^{-1}\mathbf{r} + \mathcal{Q}^{-1}\mathcal{N}(\mathbf{r})$

Redefine: $\dot{\mathbf{X}} = \mathbf{\Lambda}\mathbf{X} + \mathcal{Q}^{-1}\mathcal{N}(\mathbf{r}(\mathbf{X}))$.

Linear Subspaces



How to derive the reduced model. An example.

$$\boxed{\begin{aligned}\dot{r}_1 &= -r_1 + \Phi\Big(sr_1 - cr_2 + \nu_1\Big) + \sigma\xi_1(t)\\ \dot{r}_2 &= -r_2 + \Phi\Big(sr_2 - cr_1 + \nu_2\Big) + \sigma\xi_2(t)\end{aligned}}$$

$$\dot{\mathbf{X}} = \mathbf{\Lambda}\mathbf{X} + \mathcal{Q}^{-1}\mathcal{N}(\mathbf{r}(\mathbf{X})).$$

$$\mathbf{\Lambda} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & -2c\Phi^{'} \end{pmatrix}, \mathcal{Q}^{-1} = \begin{pmatrix} 1/2c\Phi^{'} & 0 & 0 \\ 0 & 1/2 & -1/2 \\ -1/2c\Phi^{'} & 1/2 & 1/2 \end{pmatrix},$$

$$\mathbf{X} = \begin{pmatrix} \eta \\ X \\ Y \end{pmatrix} = \begin{pmatrix} \frac{\bar{\nu}}{2c} \\ \frac{\bar{r}_1 - \bar{r}_2}{2} \\ \frac{\bar{r}_1 + \bar{r}_2}{2} - \frac{\bar{\nu}}{2c} \end{pmatrix}.$$

How to derive the reduced model. An example.

$$\boxed{\begin{aligned} \dot{r}_1 &= -r_1 + \Phi\left(sr_1 - cr_2 + \nu_1\right) + \sigma\xi_1(t) \\ \dot{r}_2 &= -r_2 + \Phi\left(sr_2 - cr_1 + \nu_2\right) + \sigma\xi_2(t) \end{aligned}}$$

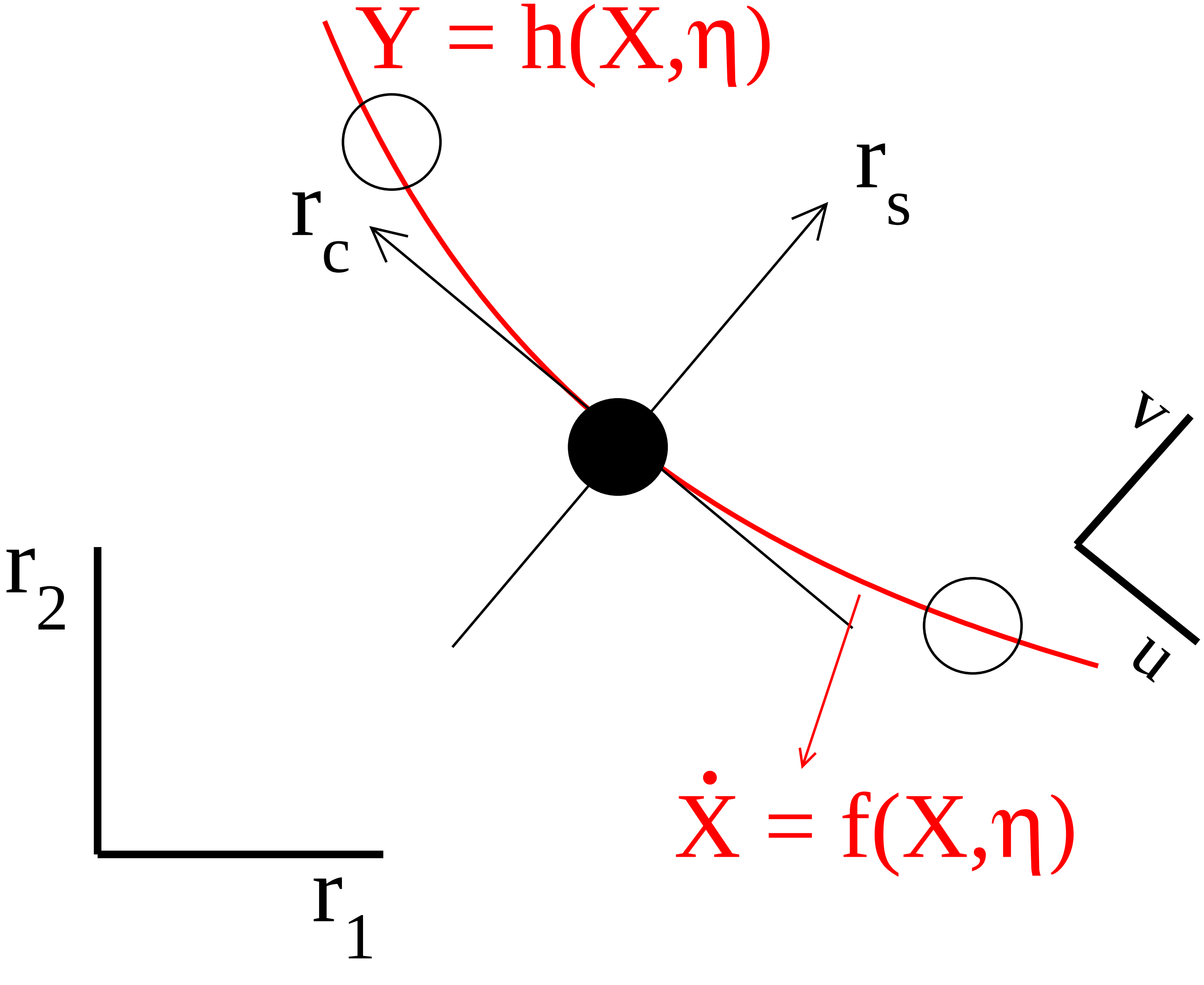
$$\dot{\mathbf{X}} = \mathbf{\Lambda X} + \mathcal{Q}^{-1}\mathcal{N}(\mathbf{r}(\mathbf{X})).$$

Express the 'fast' variables as a function of the 'critical' variables, $Y = h(\eta, X)$, where h is the center manifold. This is called Center Manifold Reduction (Crawford, 1993).

Plug in h for Y, expand, and find equation for X. Some algebra later...

$$\dot{X} = \Phi^{''}(s+c)\left(1 + \tfrac{s-c}{2c}\right)(\nu - \nu_{cr})X + \left(\tfrac{(\Phi^{''})^2(s+c)^2(s^2-c^2)}{4c\Phi^{'}} + \tfrac{(s+c)^3\Phi^{'''}}{6}\right)X^3.$$

Nonlinear Manifold



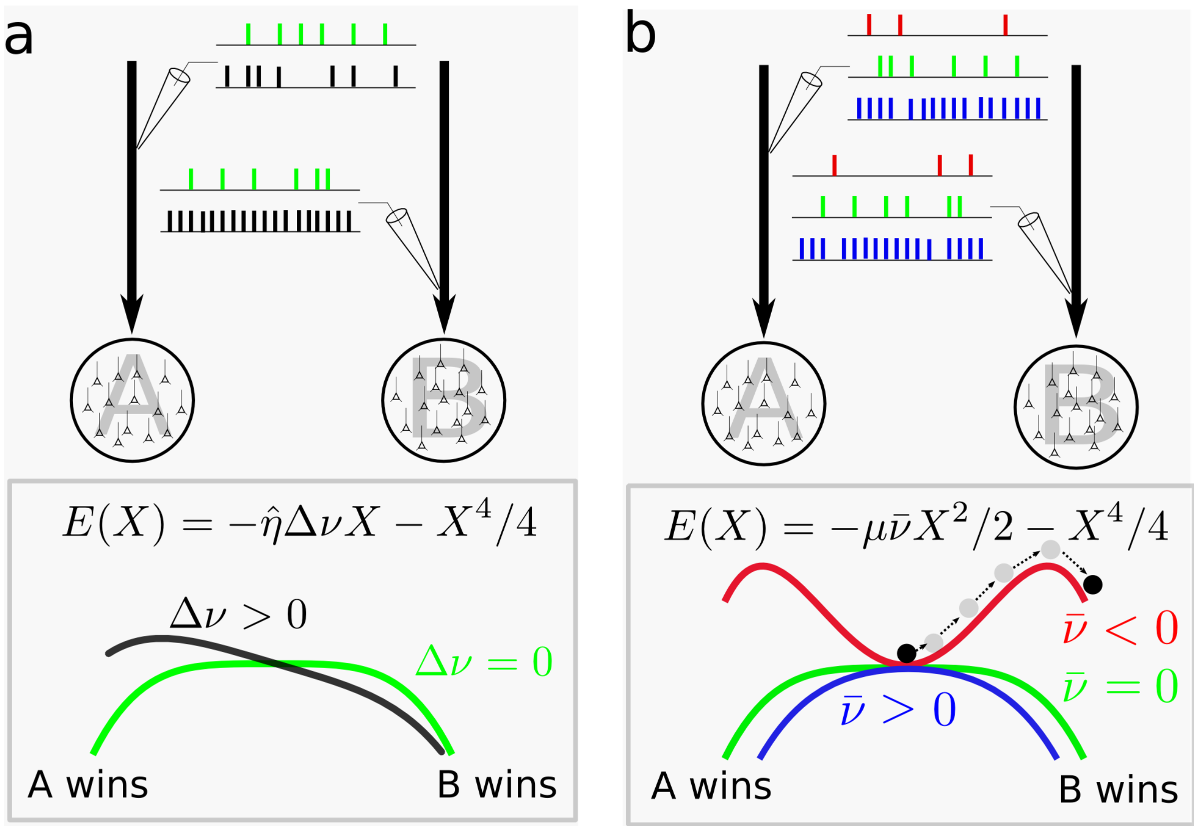
How to derive the reduced model. An example.

$$\boxed{\begin{aligned}\dot{r}_1 &= -r_1 + \Phi\Big(sr_1 - cr_2 + \nu_1\Big) + \sigma\xi_1(t)\\ \dot{r}_2 &= -r_2 + \Phi\Big(sr_2 - cr_1 + \nu_2\Big) + \sigma\xi_2(t)\end{aligned}}$$

Weakly non-symmetric inputs and noise can be accounted for with a simple linear transformation. This yields a nonlinear diffusion equation

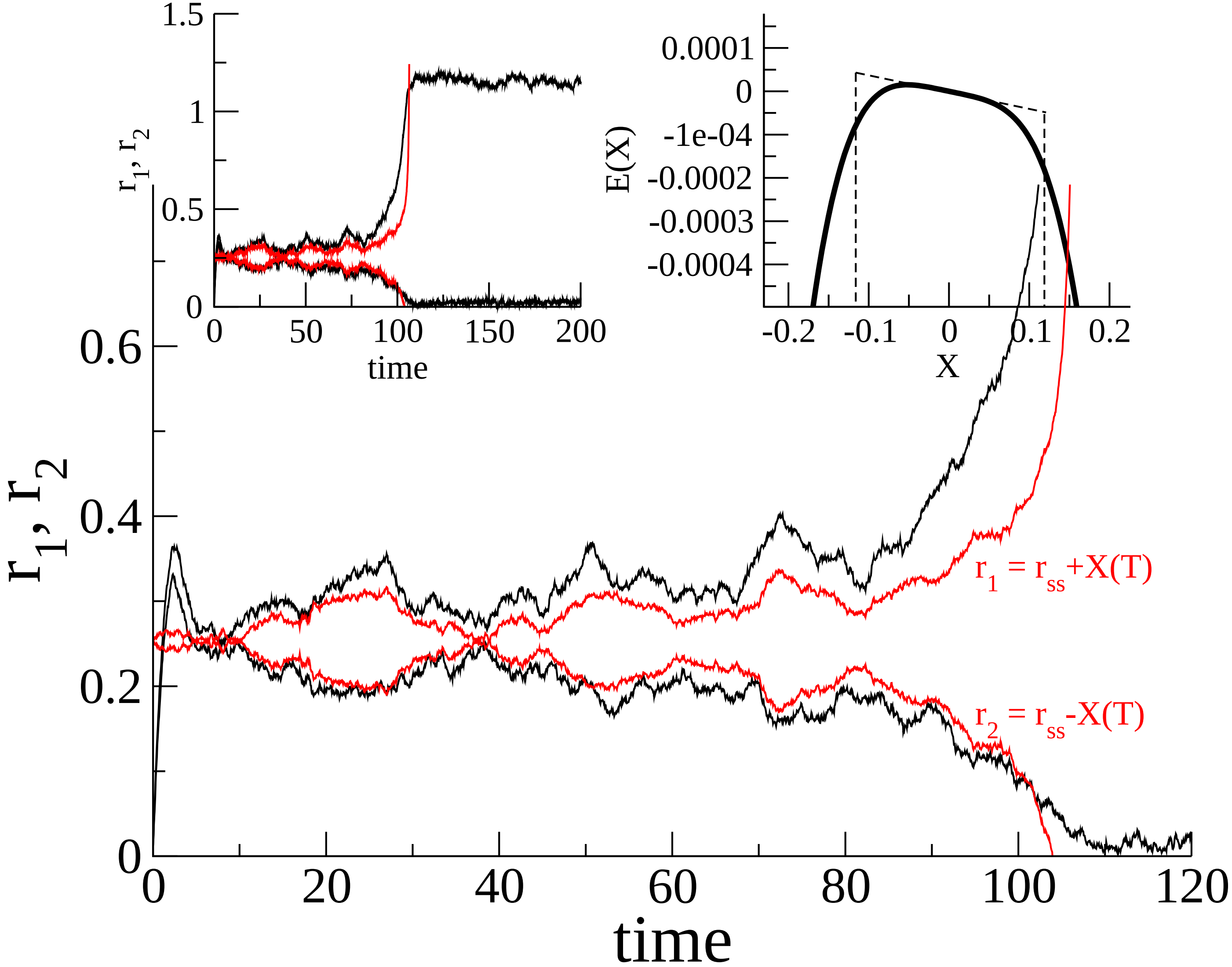
$$\dot{X} = \eta(\nu_1 - \nu_2) + \mu(\nu - \nu_{cr})X + \gamma X^3 + \sqrt{2}\sigma\xi(t).$$

Diffusion along an energy landscape.



$$\dot{X} = -\frac{dE(X)}{dX} + \sigma\xi(t)$$
$$E(X) = -\hat{\eta}\Delta\nu X - \frac{1}{2}\mu\bar{\nu}X^2 - \frac{1}{4}X^4$$

Sample dynamics.



The amplitude equation actually fits behavioral data.

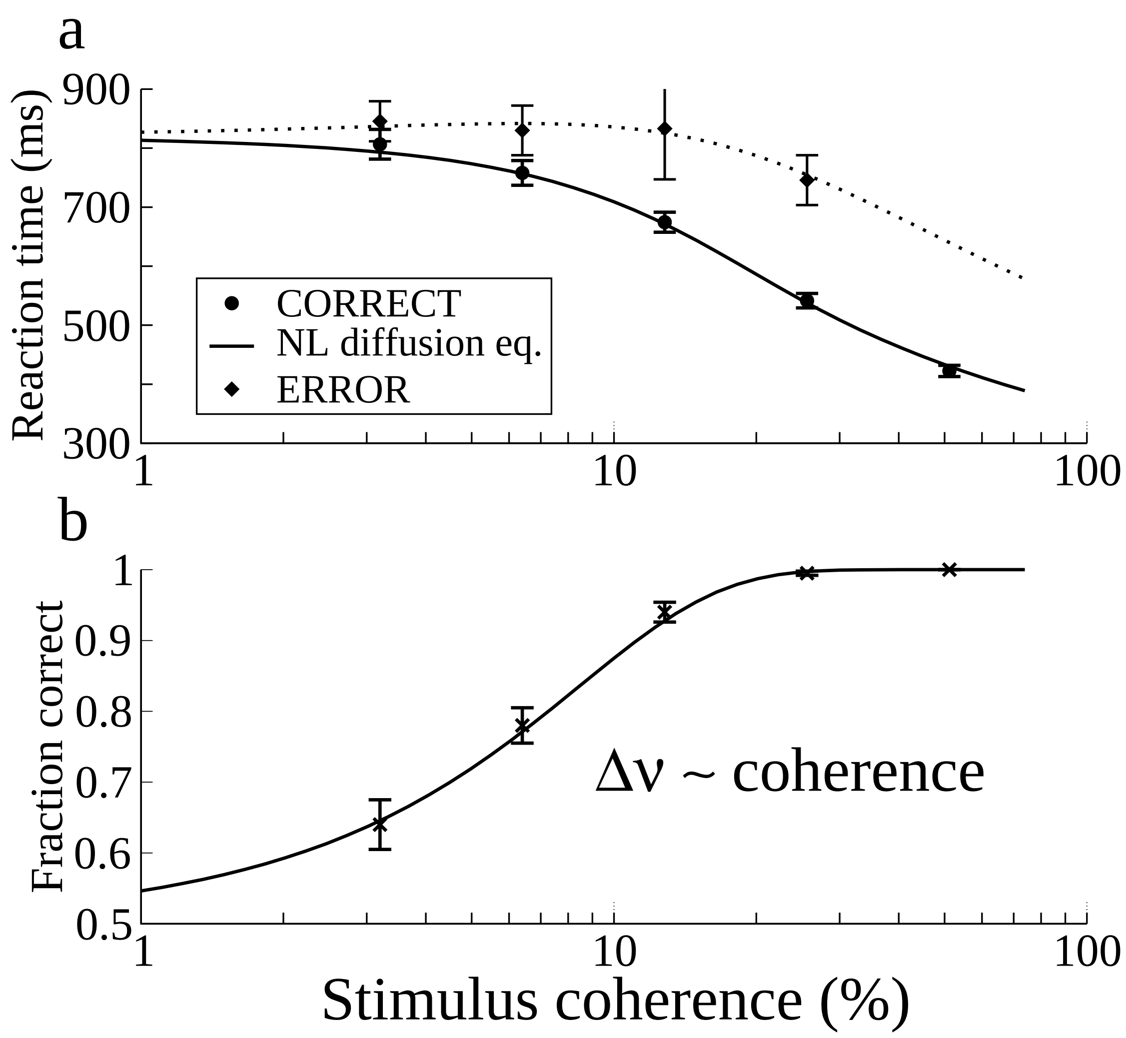


Figure 8: Data from Roitman and Shadlen 2002.

The amplitude equation actually fits behavioral data

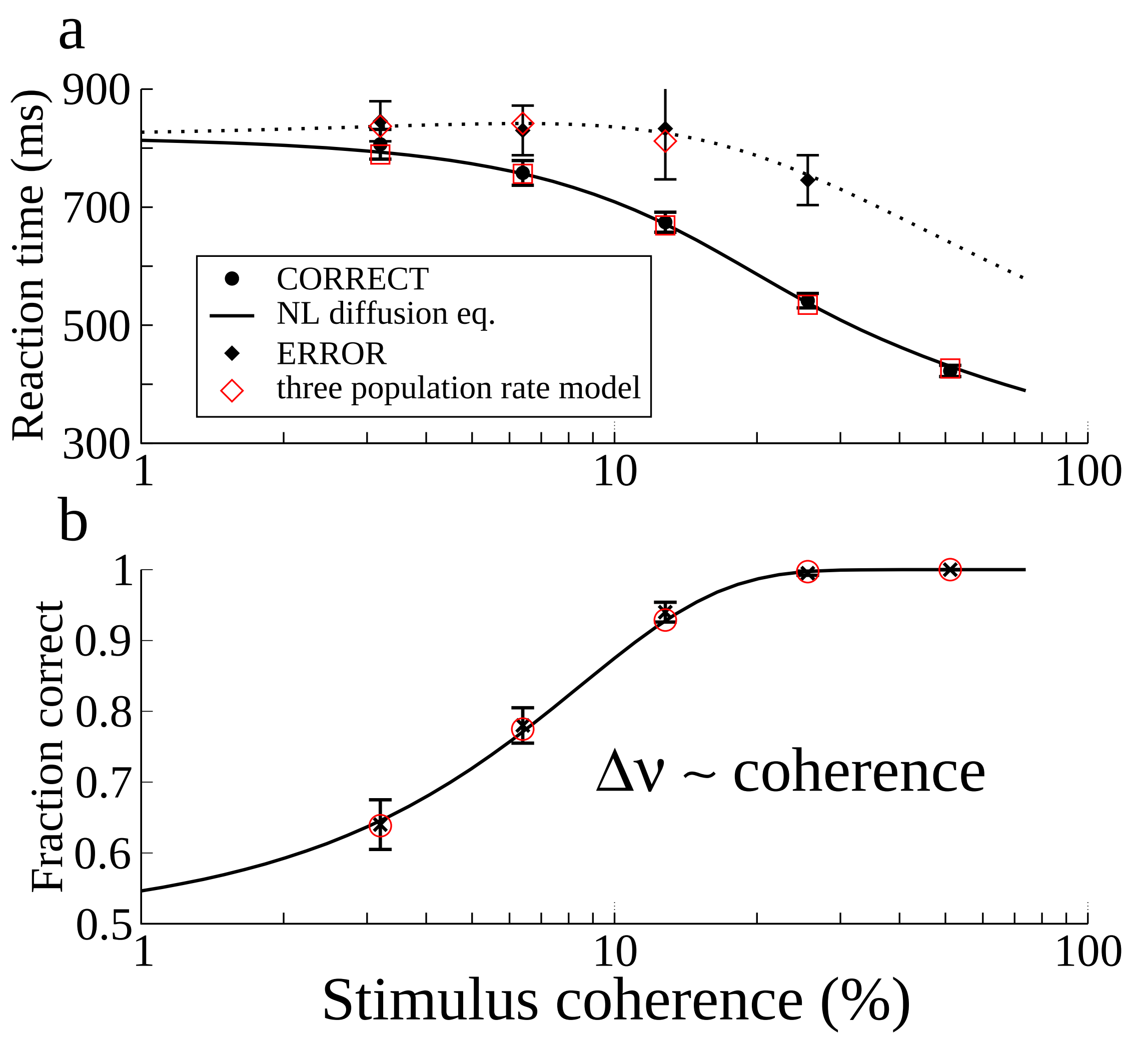


Figure 9: Data from Roitman and Shadlen 2002.

The amplitude equation actually fits behavioral data.

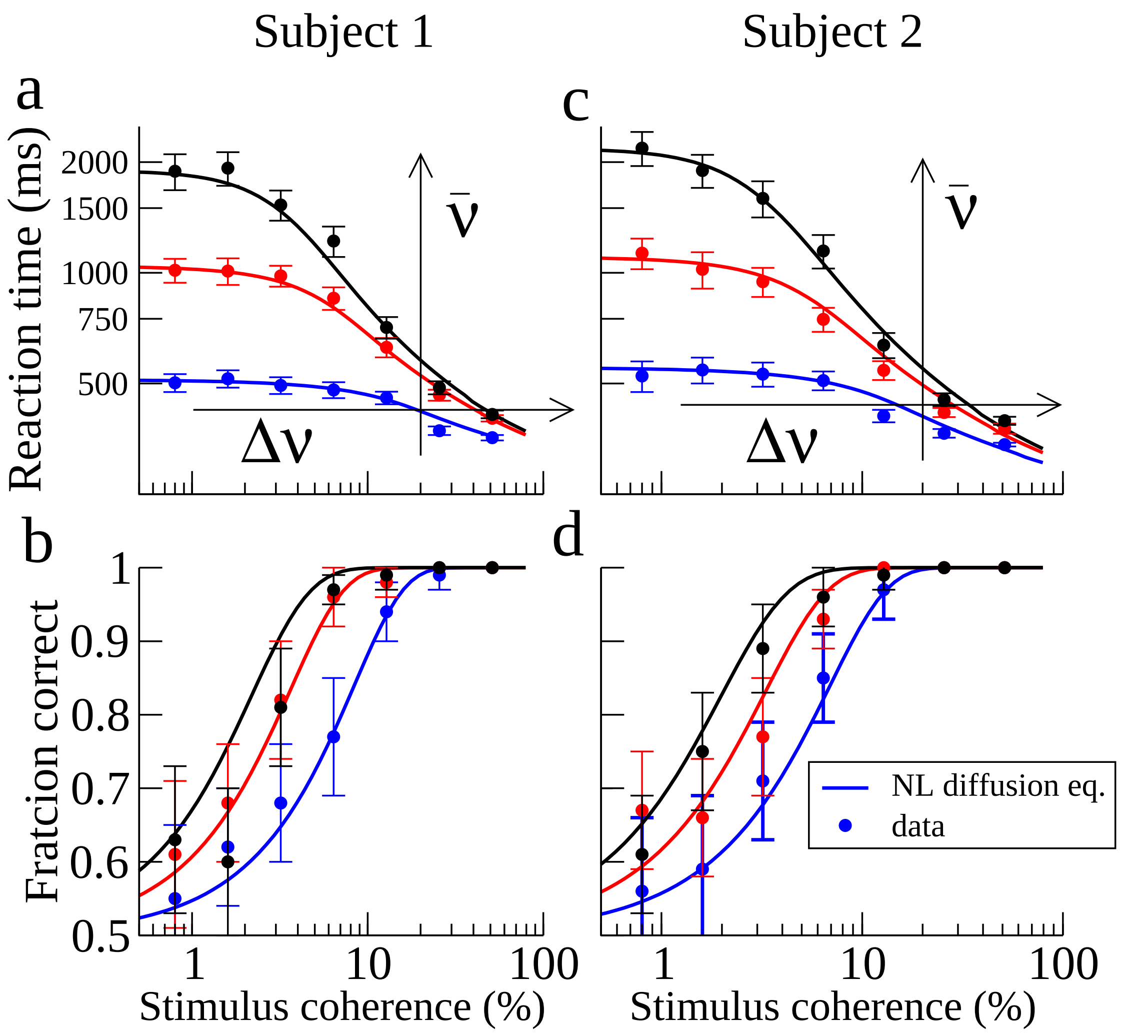


Figure 10: Data from Palmer et al., 2005.

The amplitude equation actually fits behavioral data.

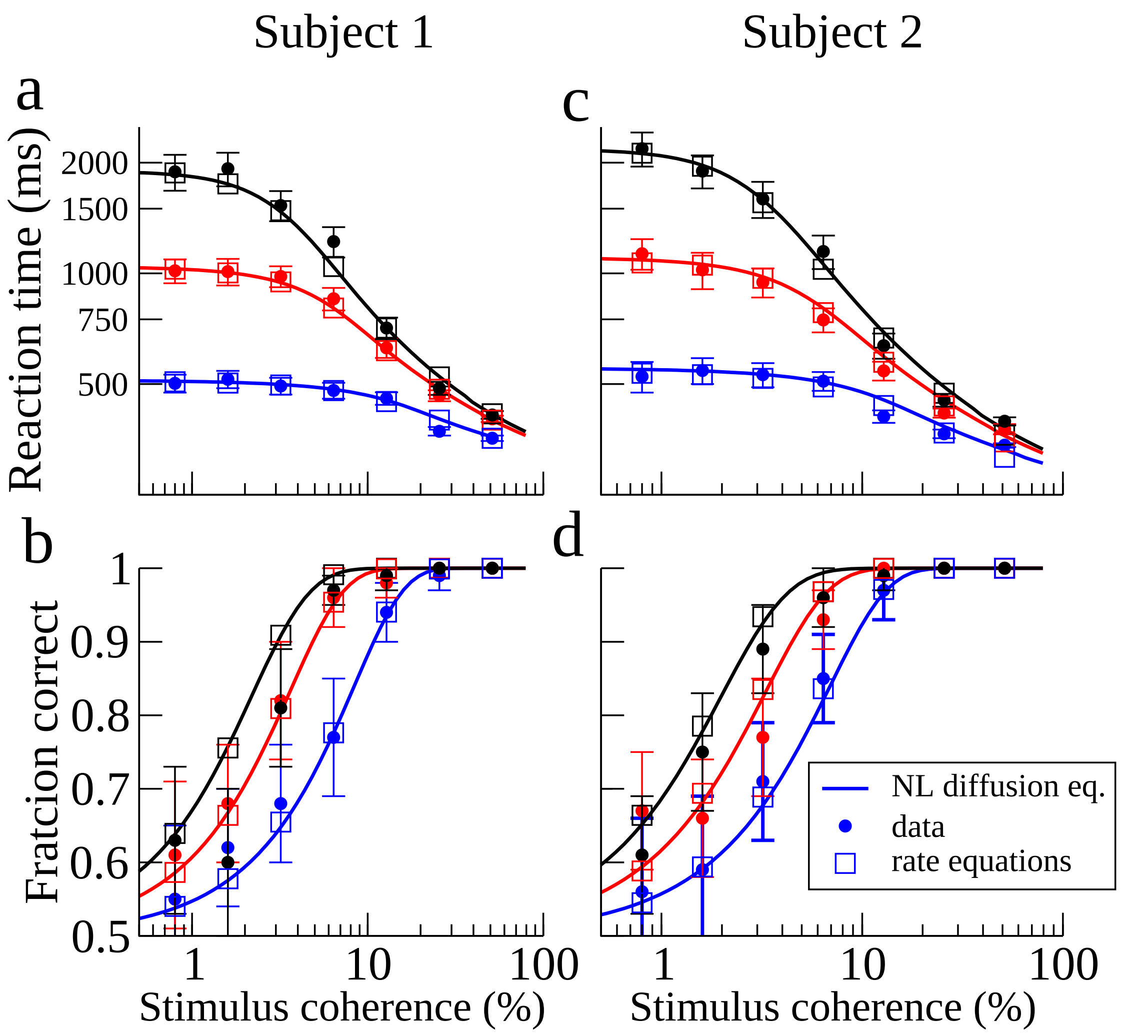


Figure 11: Data from Palmer et al., 2005.

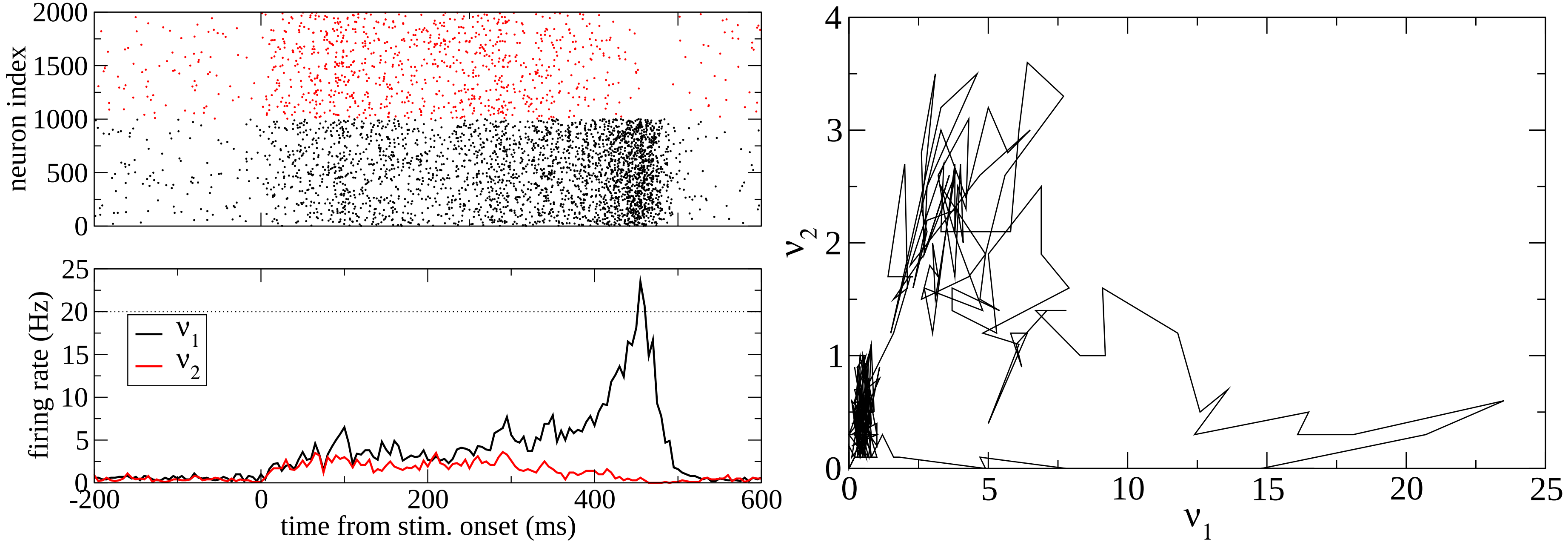
Spiking network.

I. Network of Integrate-and-fire neurons: Use multi-scaling following Brunel and Hakim 1999.

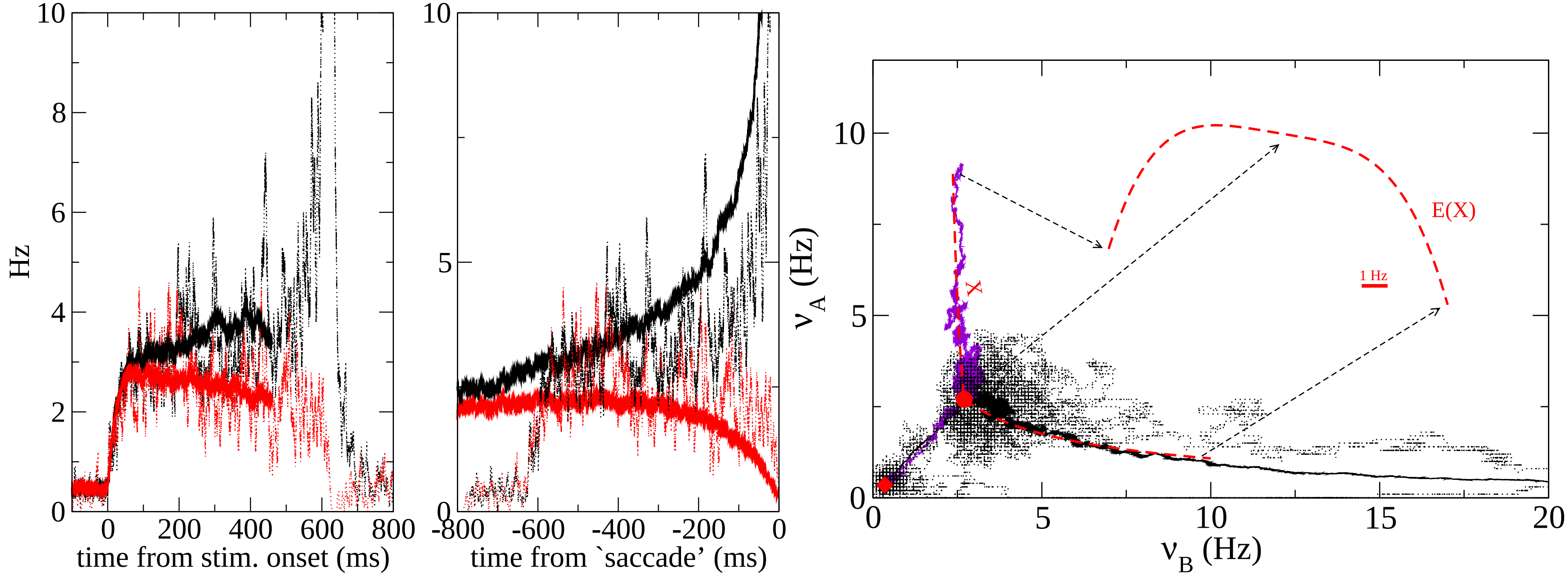
$$
\begin{aligned}
\tau \dot{V}_{A,i} &= -(V_{A,i} - E_e) + I_{AA,i} - I_{AI,i} + I_{Aext,i}, &(1)\\
\tau \dot{V}_{B,i} &= -(V_{B,i} - E_e) + I_{BB,i} - I_{BI,i} + I_{Bext,i}, &(2)\\
\hat{\tau} \dot{V}_{I,i} &= -(V_{I,i} - E_i) + I_{IA,i} + I_{IB,i} + I_{Iext,i}, &(3)\\
I_{XX,i} &= \tau \sum_j J_{ij}^{XX} \sum_k \delta(t - t_{X,j}^k - \delta_{E,ij}). &(4)
\end{aligned}
$$

- Difussion approximation $\longrightarrow$ coupled Fokker-Planck equations.
- Stability of stationary distributions.
- Weakly-nonlinear dynamics of “decision” mode.

Single-trial Activity



Trial-averaged Activity



Summary

- spiking networks and reduced models go hand in hand
- push simple models as far as possible