Computational Neuroscience: Neuronal Dynamics

Lecture 12 – Membrane potential densities and Fokker-Planck

Wulfram Gerstner

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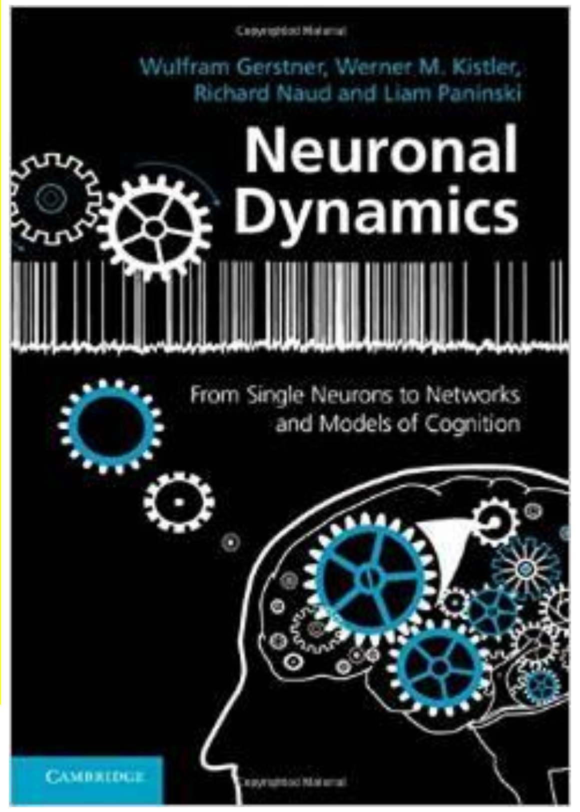
Reading for this Lecture:
NEURONAL DYNAMICS
Ch. 13.1-13.4



Cambridge Univ. Press

12.1 Review: Integrate-and-fire
- stochastic spike arrival

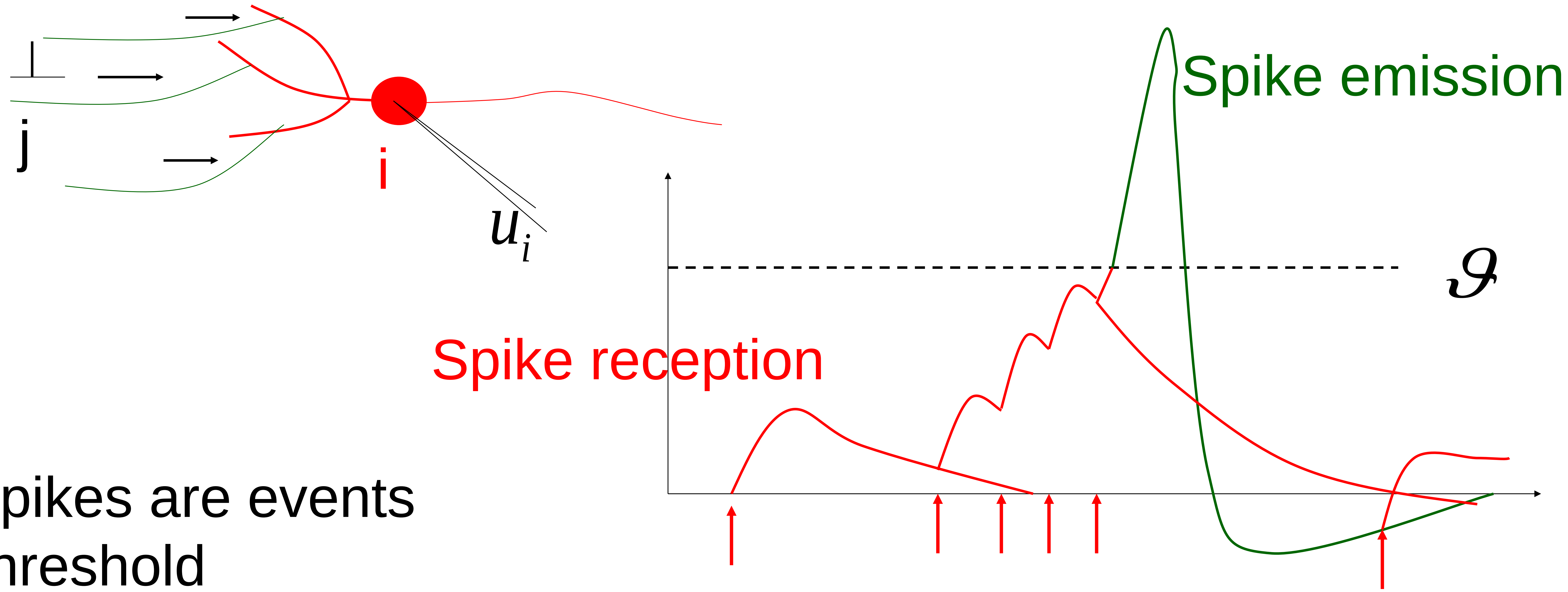
12.2 Density of membrane potential
- Continuity equation

12.3 Flux
- jump flux
- drift flux

12.4. Fokker –Planck Equation
- free solution

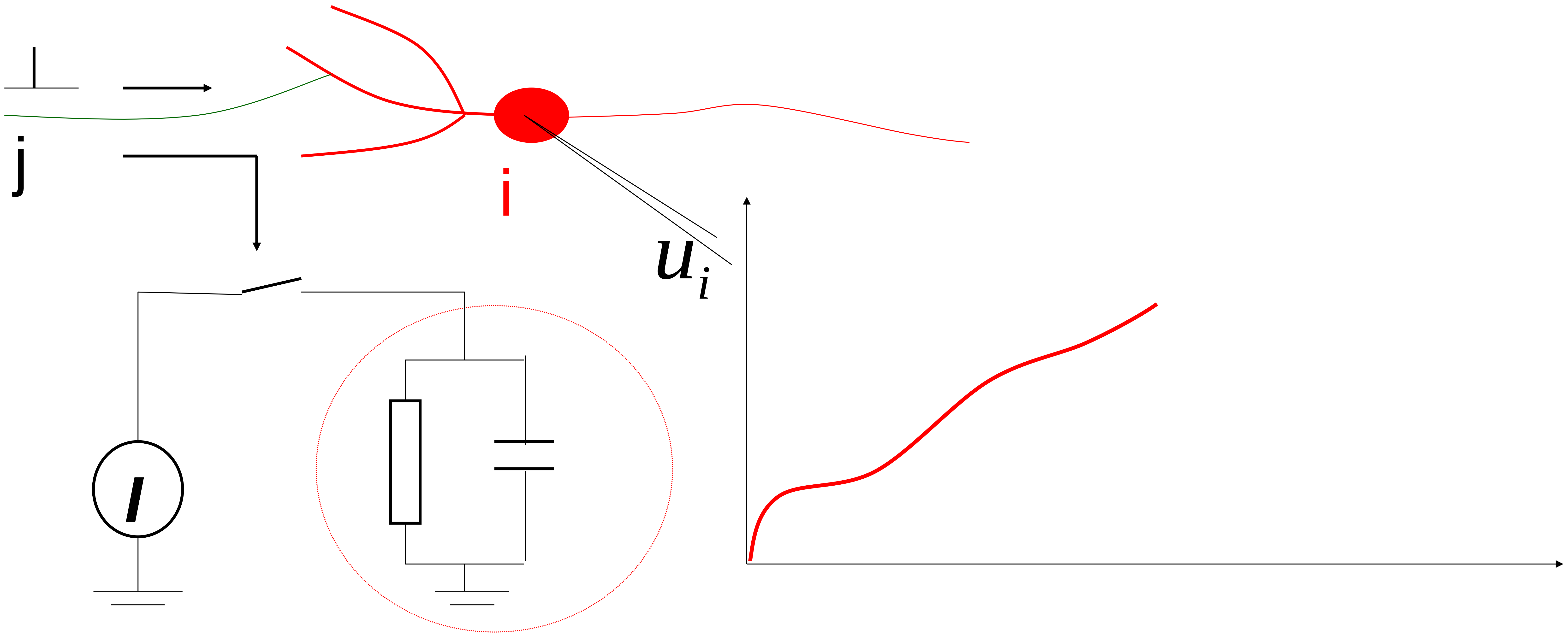
12.5. Threshold and reset
- time dependent activity
- network states

12. 1: Review: integrate-and-fire-type models



-spikes are events
-threshold
-spike/reset/refractoriness

12.1: Review: leaky integrate-and-fire model



$$\tau \cdot \frac{d}{dt} u = -(u - u_{eq}) + RI(t)$$

If $u = \vartheta$: firing: $u \rightarrow u_{reset}$

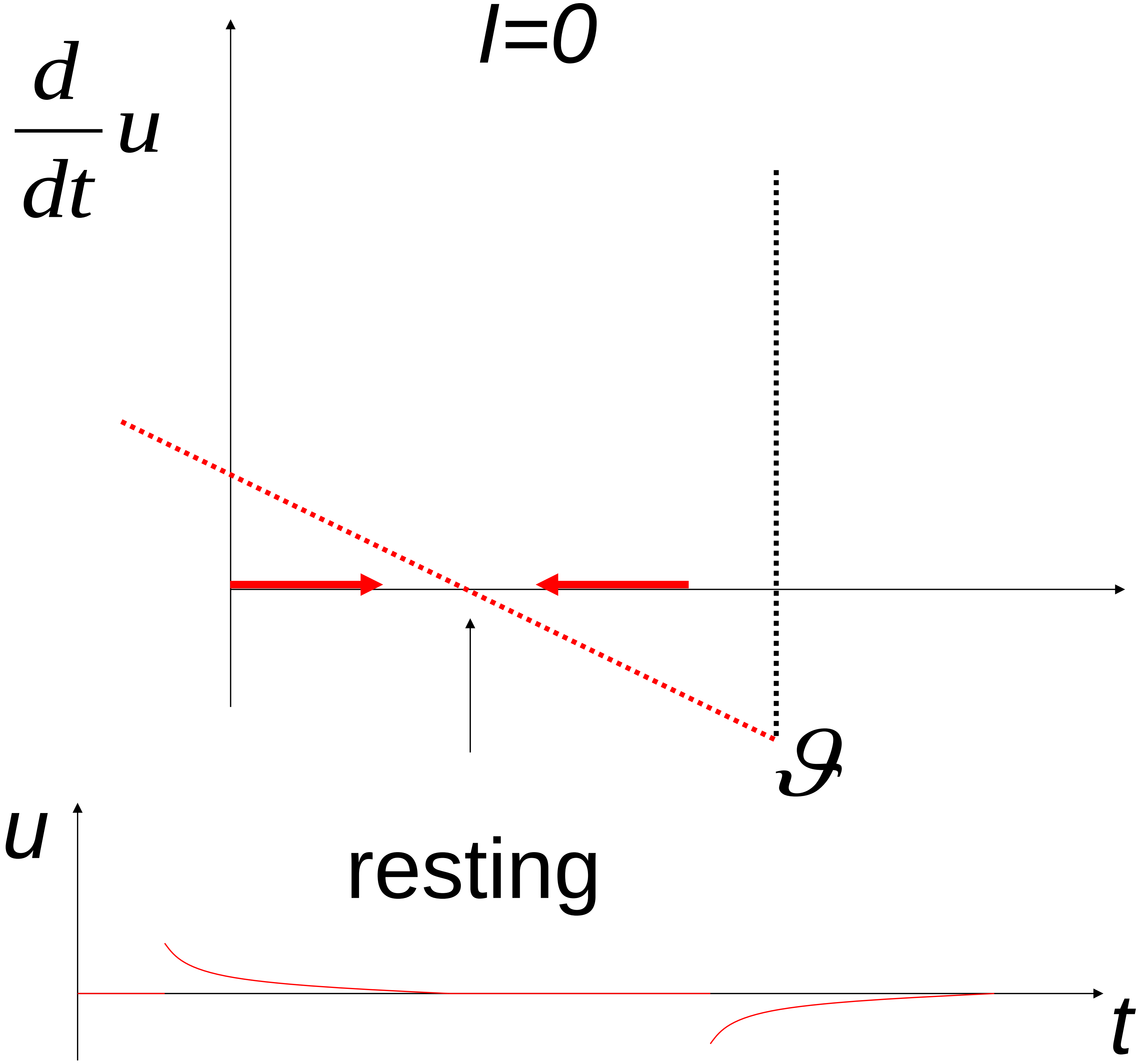
$$\tau \cdot \frac{d}{dt} V = -V + RI(t); \quad V = (u - u_{eq})$$

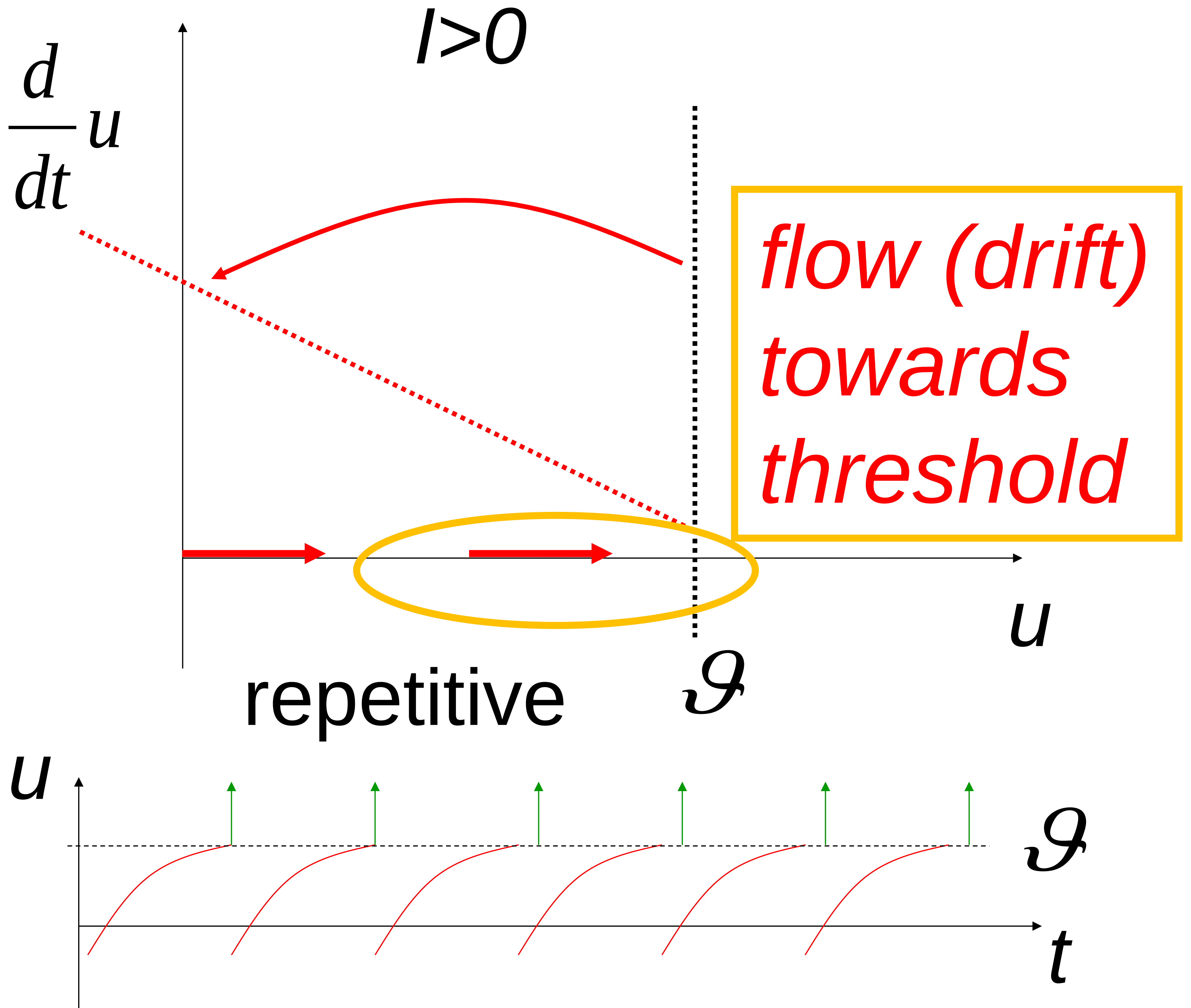
12.1: Review: leaky integrate-and-fire model

$$\tau \cdot \frac{d}{dt} u = -(u - u_{eq}) + RI(t)$$

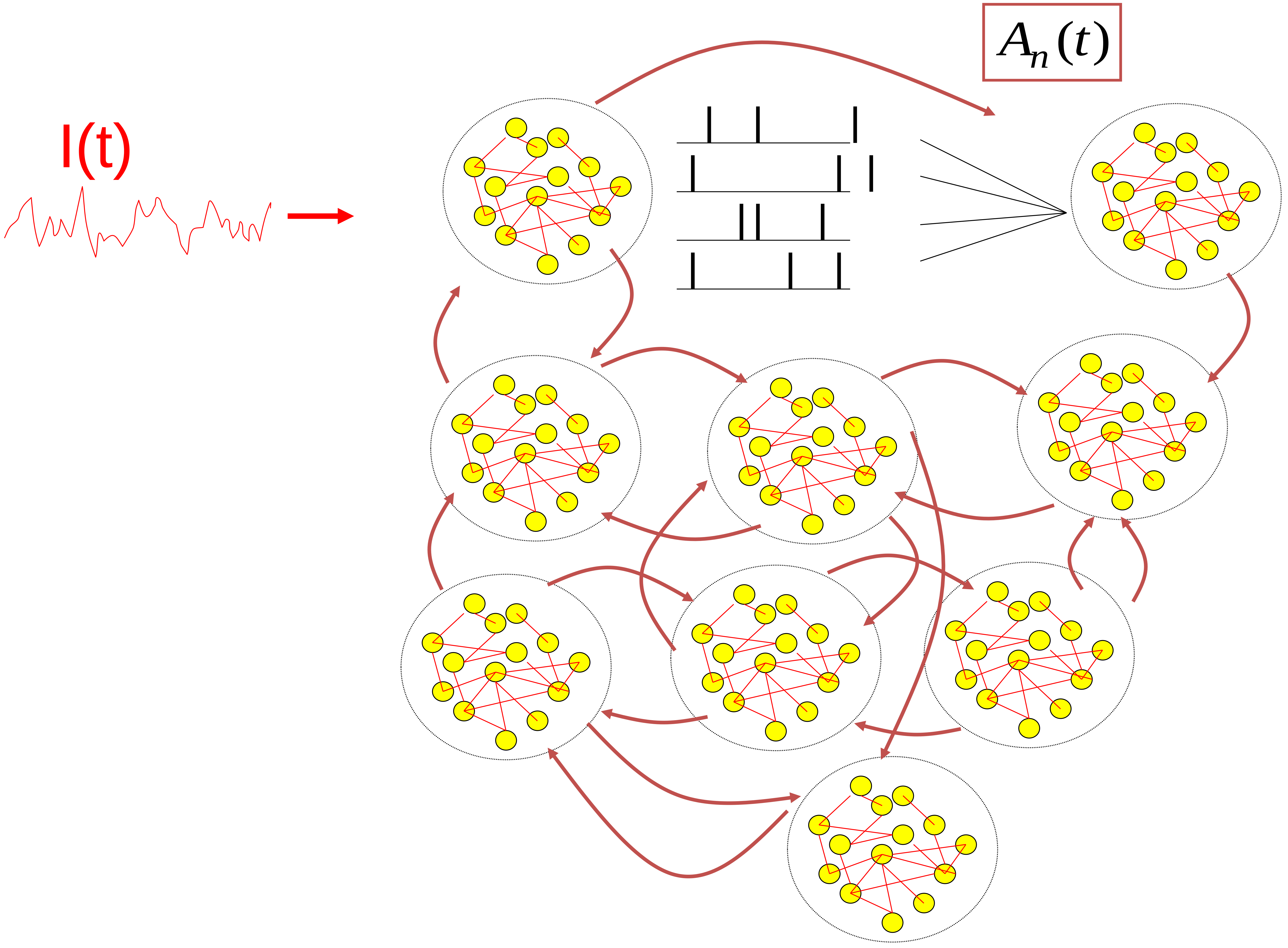
LIF

If firing: $u \rightarrow u_{reset}$

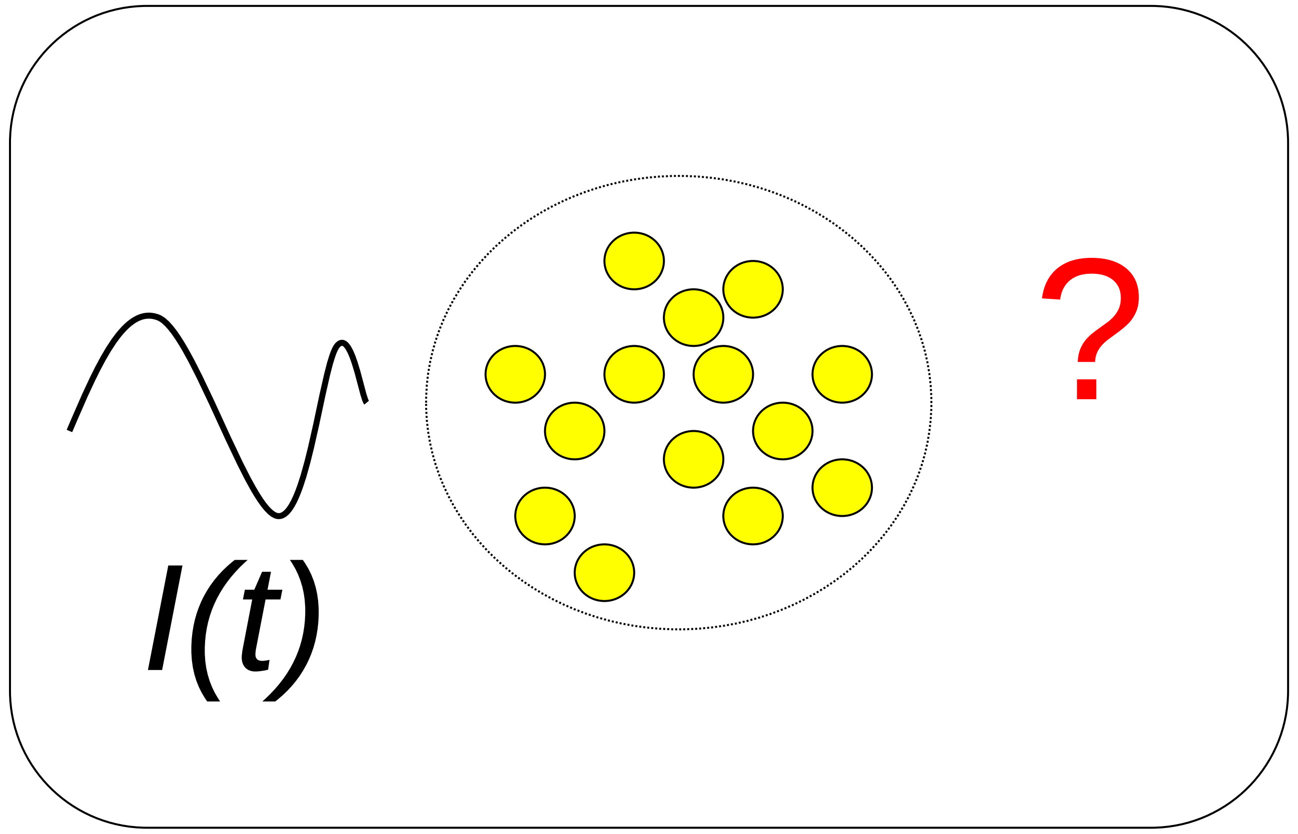


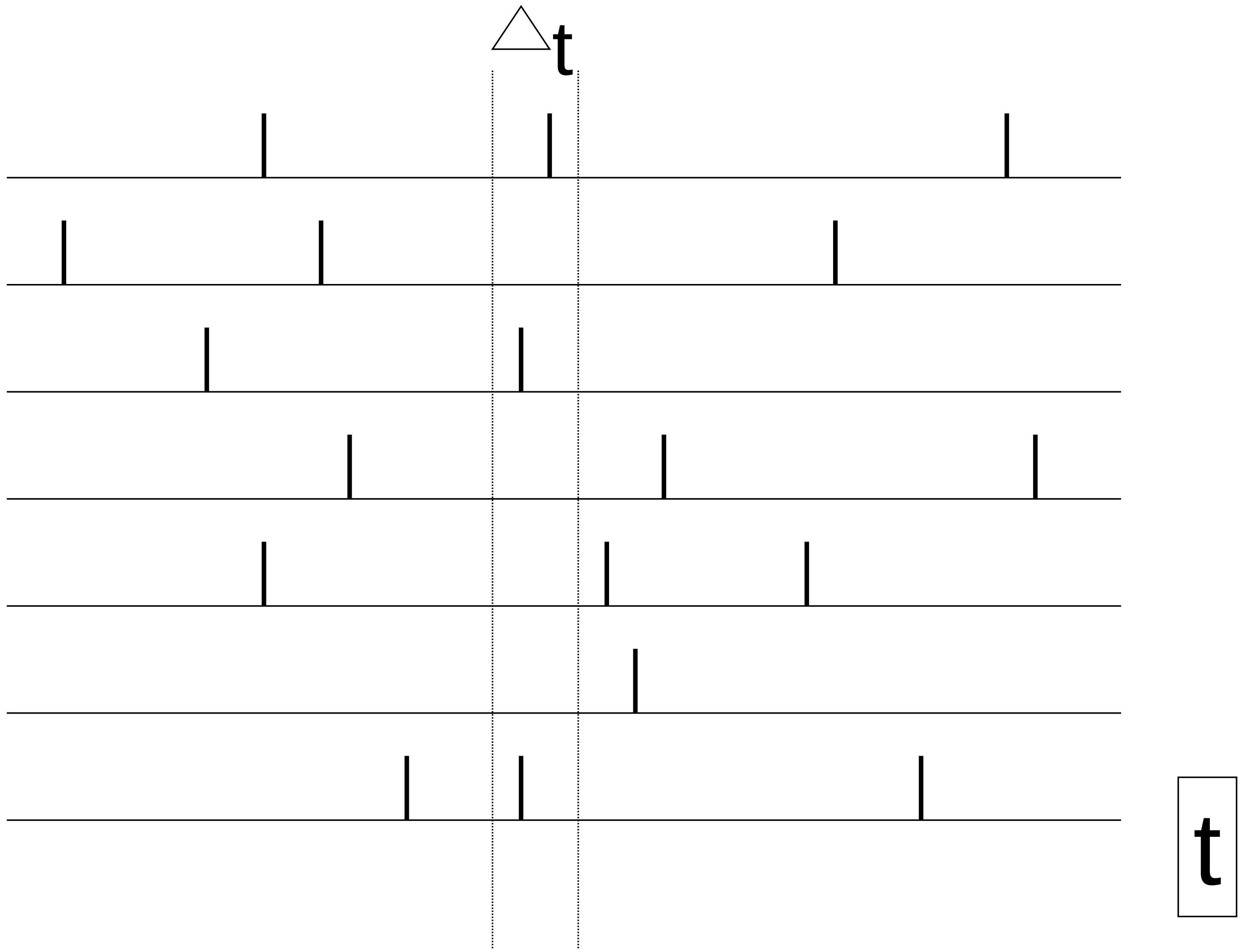


12.1: Review: microscopic vs. macroscopic



12.1: Review: homogeneous population





Homogeneous network:

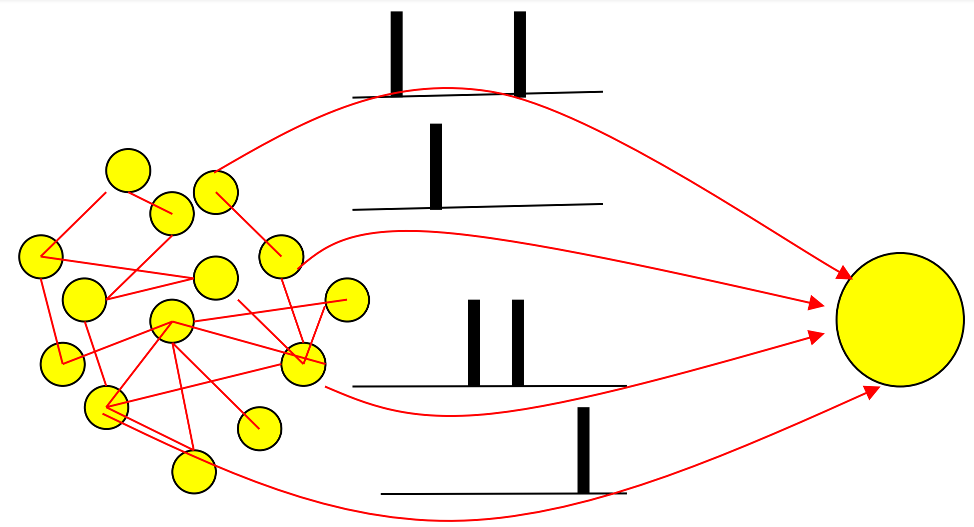
-each neuron receives input from k neurons in network

-each neuron receives the same (mean) external input

population activity

$$A(t) = \frac{n(t;t+\Delta t)}{N\Delta t}$$

12.1: Review: diffusive noise/stochastic spike arrival



Stochastic spike arrival:

excitation, total rate R_e

inhibition, total rate R_i

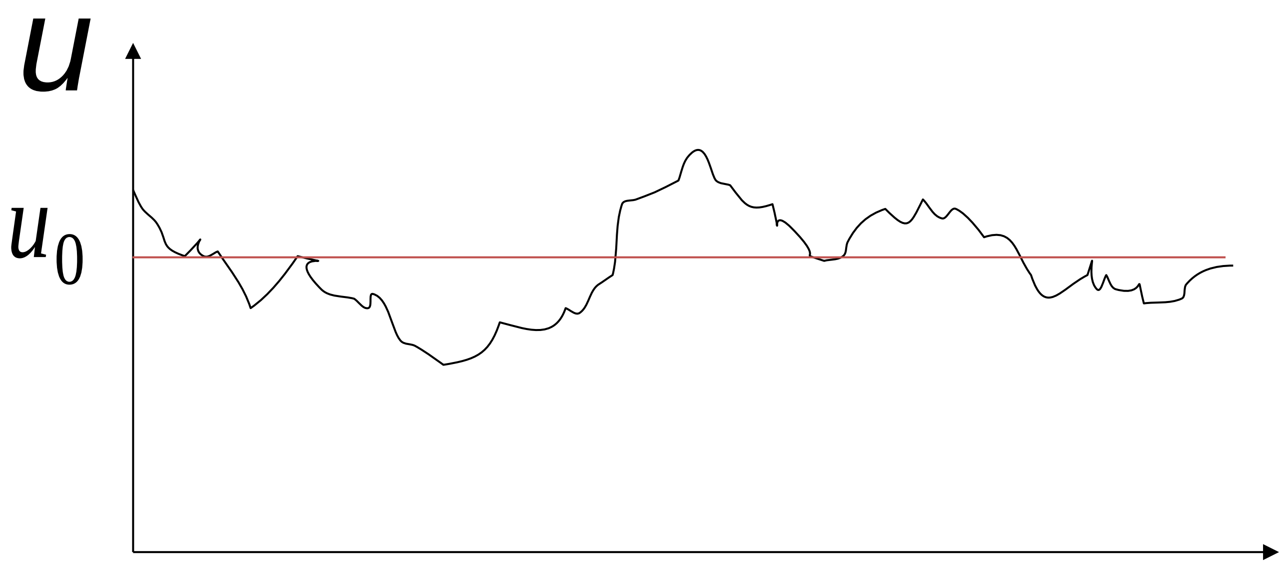
Synaptic current pulses

$$\tau \frac{d}{dt} u = -(u - u_{eq}) + R\left\{ \sum_{k,f} q_e \delta(t - t_k^f) - \sum_{k',f'} q_i \delta(t - t_{k'}^{f'}) \right\}$$

EPSC

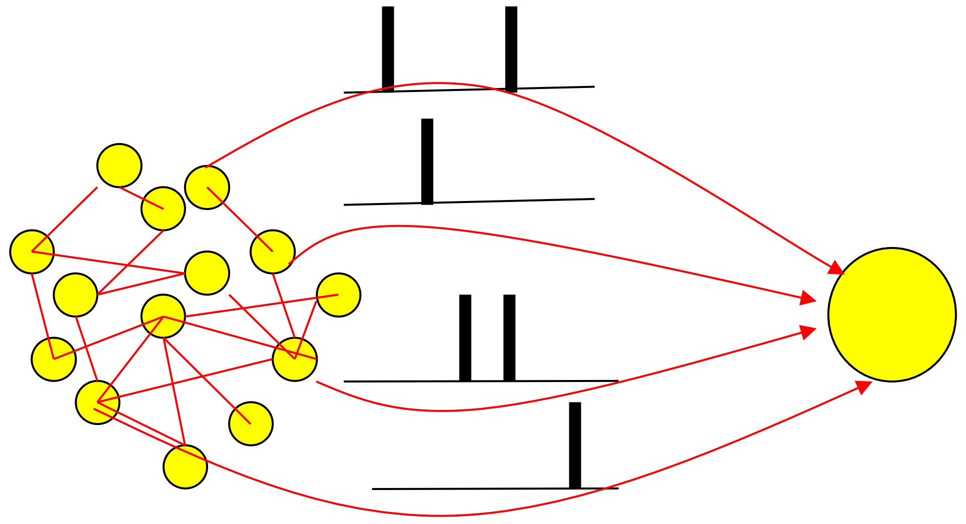
IPSC

$$\tau \frac{d}{dt} u = -(u - u_{eq}) + R\, I^{mean}(t) + \xi(t)$$



Langevin equation,
Ornstein Uhlenbeck process

12.1: Aim: Fokker-Planck-Equation for Population of neurons,



Distribution of membrane potential

Step 1: Continuity Equation/Transport Equation

$$\frac{d}{dt} p(u,t) = -\frac{d}{du} J(u,t)$$

Step 2: Fokker-Planck Equation

$$\tau \cdot \frac{\partial}{\partial t} p(u,t) = -\frac{\partial}{\partial u}[\gamma(u) p(u,t)] + \sigma^2 \frac{\partial^2}{\partial u^2} p(u,t)$$

Summary:

Describe dynamics for

- a homogeneous population of neurons,

- with stochastic spike arrival

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Lecture 12 – Membrane potential densities and Fokker-Planck

12.1 Review: Integrate-and-fire
- stochastic spike arrival

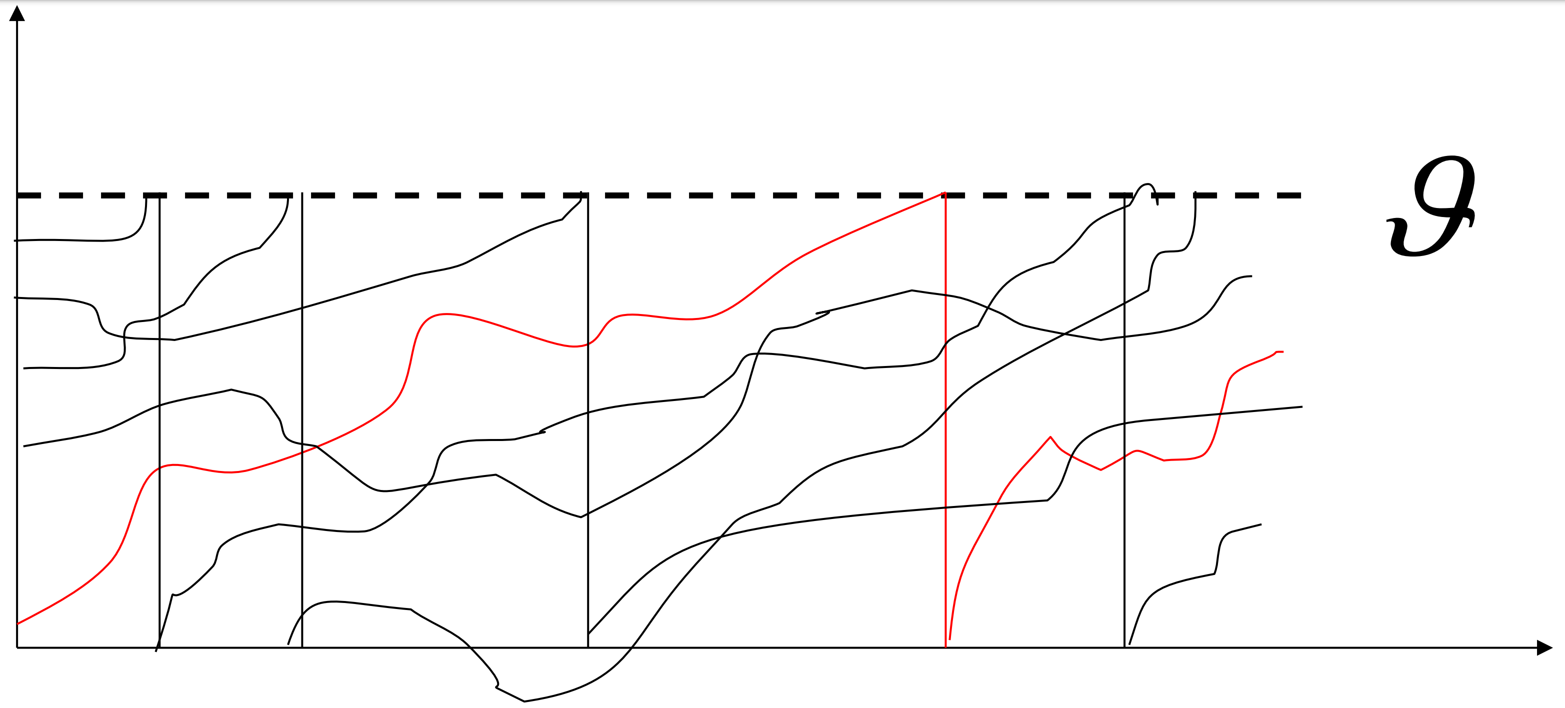
12.2 Density of membrane potential
- Continuity equation (Transport Equation)

12.3 Flux
- jump flux
- drift flux

12.4. Fokker –Planck Equation
- free solution

12.5. Threshold and reset
- time dependent activity
- network states

12.2: membrane potential density



For any arbitrary neuron in the population

$$\tau \frac{d}{dt} u = -u + R\Big(\sum_{k,f} q_e \delta(t - t_k^f) - \sum_{k',f'} q_i \delta(t - t_{k'}^{f'})\Big) \; + R I^{ext}(t)$$

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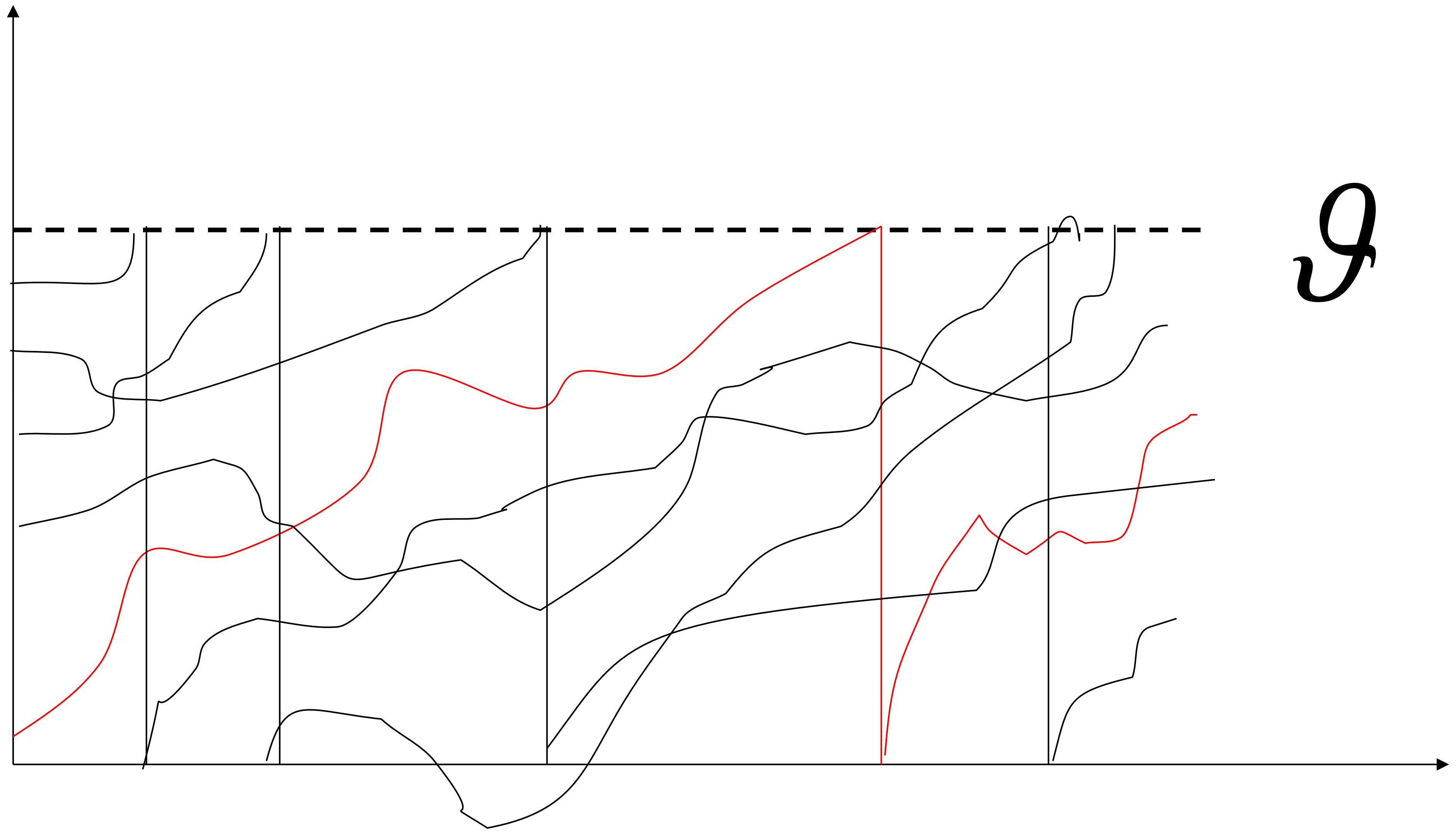
$$\frac{d}{dt} u = -\frac{u}{\tau} + \sum_{k,f} \frac{q_e}{C} \delta(t - t_k^f) + \frac{1}{C} I^{ext}(t)$$

excitatory input spikes

12.2: membrane potential density



12.2: continuity equation connects density and flux

$$\frac{d}{dt}p(u,t) = -\frac{d}{du}J(u,t)$$

$$\int_{-\infty}^{\vartheta} p(u,t)du = 1$$

The continuity equation is also called **transport equation.**
It is a **partial differential equation.**

It expresses that:
- the number of particles (neurons) does not change over time
  → trajectories are ‘continuous’ (not necessarily smooth: may contain ‘jumps’)
- the only way that the number of particles at location near u_0 changes (that the number of trajectories with voltage close to u_0 changes) is if a trajectory moves into the volume or out of the volume

$$\int_{u_0-\Delta u}^{u_0} p(u,t)du$$

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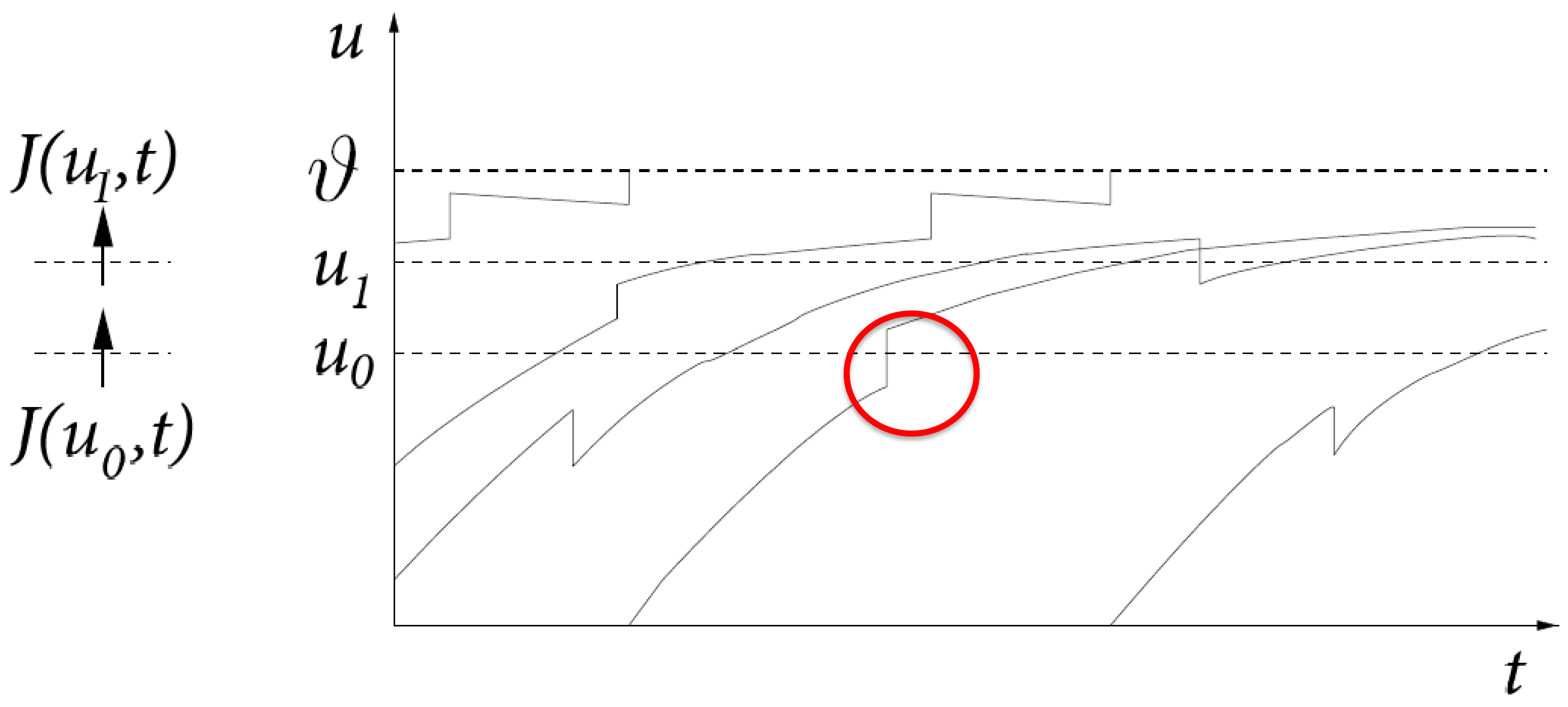
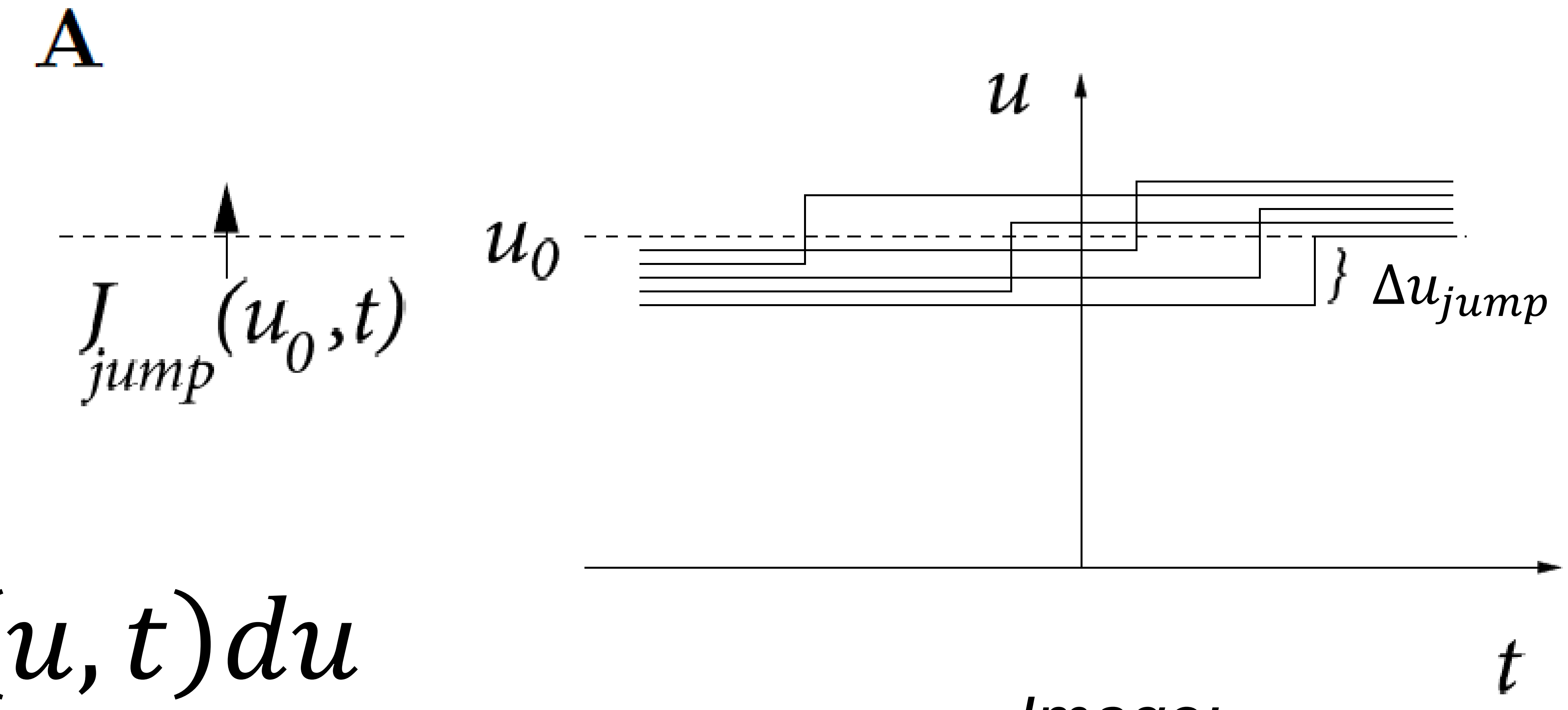
12.3: membrane potential density: flux by jumps



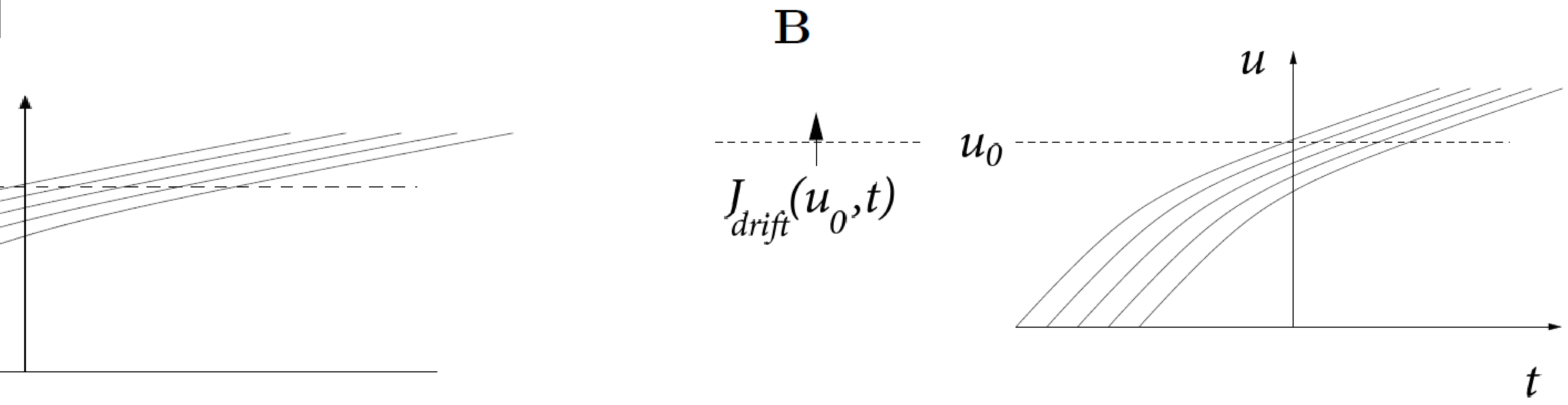
$$\int_{-\infty}^{\vartheta} p(u,t)du = 1$$



$$J_{jump}(u_0,t) = \nu \int_{u_0-\Delta u_{jump}}^{u_0} p(u,t)du$$

Image:
Gerstner et al. (2014),
Neuronal Dynamics

12.3: membrane potential density: flux by drift



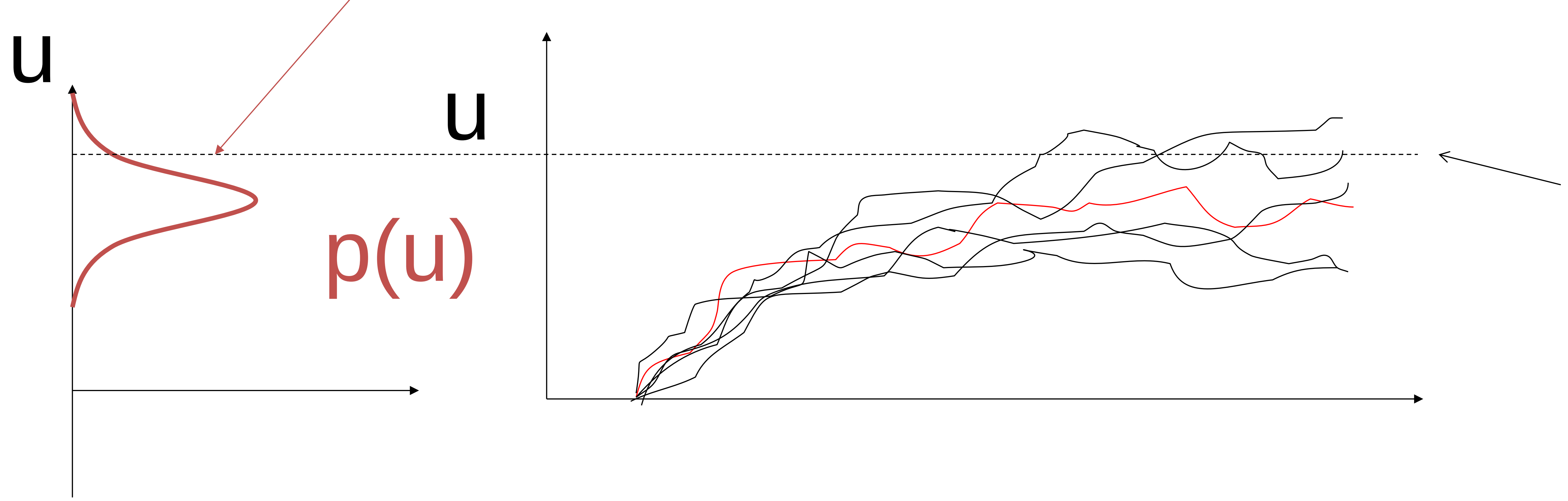
$$J_{drift}(u_0,t) = p(u_0,t) \cdot \frac{du}{dt}(u_0)$$

= ‘density’ · ′speed′

flux – two possibilities

$$\tau \frac{d}{dt}u = -(u-u_{eq}) + R\left\{I^{ext(t)} + \sum_f q_e \delta(t-t^f)\right\}$$

Membrane potential density



What is the flux across u_0?

Reference level u_0

Jumps caused at spike arrival rate ν

a) flux caused by jumps due to stochastic spike arrival

b) flux caused by systematic drift

Summary:

The flux has two components:

- Continuous component: The decay of the membrane potential in the absence of input or the increase of membrane potential in the presence of an external strong driving current.

- Discontinuous component: Small jumps in the presence of stochastic spike arrival from other neurons in the network

The flux $J(u,t)$ is defined for an arbitrary time and arbitrary value of membrane potential.

A particular important concept is the flux through the threshold. Hence we evaluate later J at the value of $u = \theta$.

Three important comments:

- We must take into account that the threshold can only be reached from below.
- The density $p(u,t)$ at threshold MUST be zero because if we imagine that a neuron has voltage just below threshold the next excitatory spike arrival will definitely remove it.
- The flux through the threshold causes spike emission and reset of the membrane potential. But before we add the threshold effects we study the 'free solution'.

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Lecture 12 – Membrane potential densities and Fokker-Planck

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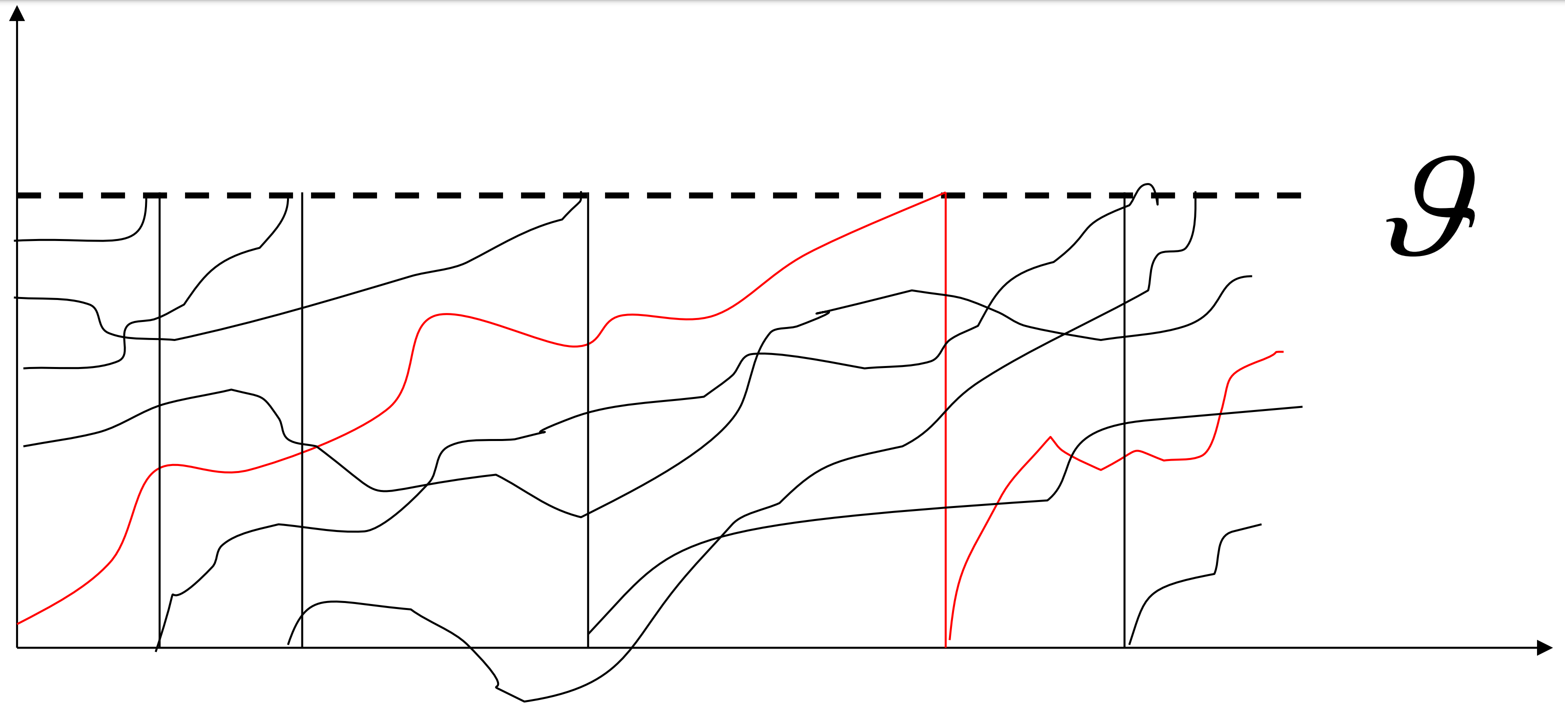
12.4: from continuity equation to Fokker-Planck



For any arbitrary neuron in the population

$$\frac{d}{dt}u = -\frac{u}{\tau} + \sum_{k,f} \frac{q_e}{C}\delta(t - t_k^f) - \sum_{k',f'} \frac{q_i}{C}\delta(t - t_{k'}^{f'}) + \frac{1}{C} I^{ext}(t)$$

EPSC

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external input

Continuity equation:

$$\frac{\partial}{\partial t} p(u,t) = -\frac{\partial}{\partial u} J(u,t)$$

Flux: - jump size! (spike arrival)

- drift! (slope of trajectory)

12.4: from continuity equation to Fokker-Planck

Continuity equation:

$$\frac{\partial}{\partial t} p(u,t) = -\frac{\partial}{\partial u} J(u,t)$$

Flux: - jump $J_{jump}(u_0, t) = \nu \int_{u_0 - \Delta u_{jump}}^{u_0} p(u,t) du$

- drift $J_{drift}(u_0, t) = p(u_0, t) \cdot \frac{du}{dt}(u_0)$

12.4: from continuity equation to Fokker-Planck

Continuity equation:

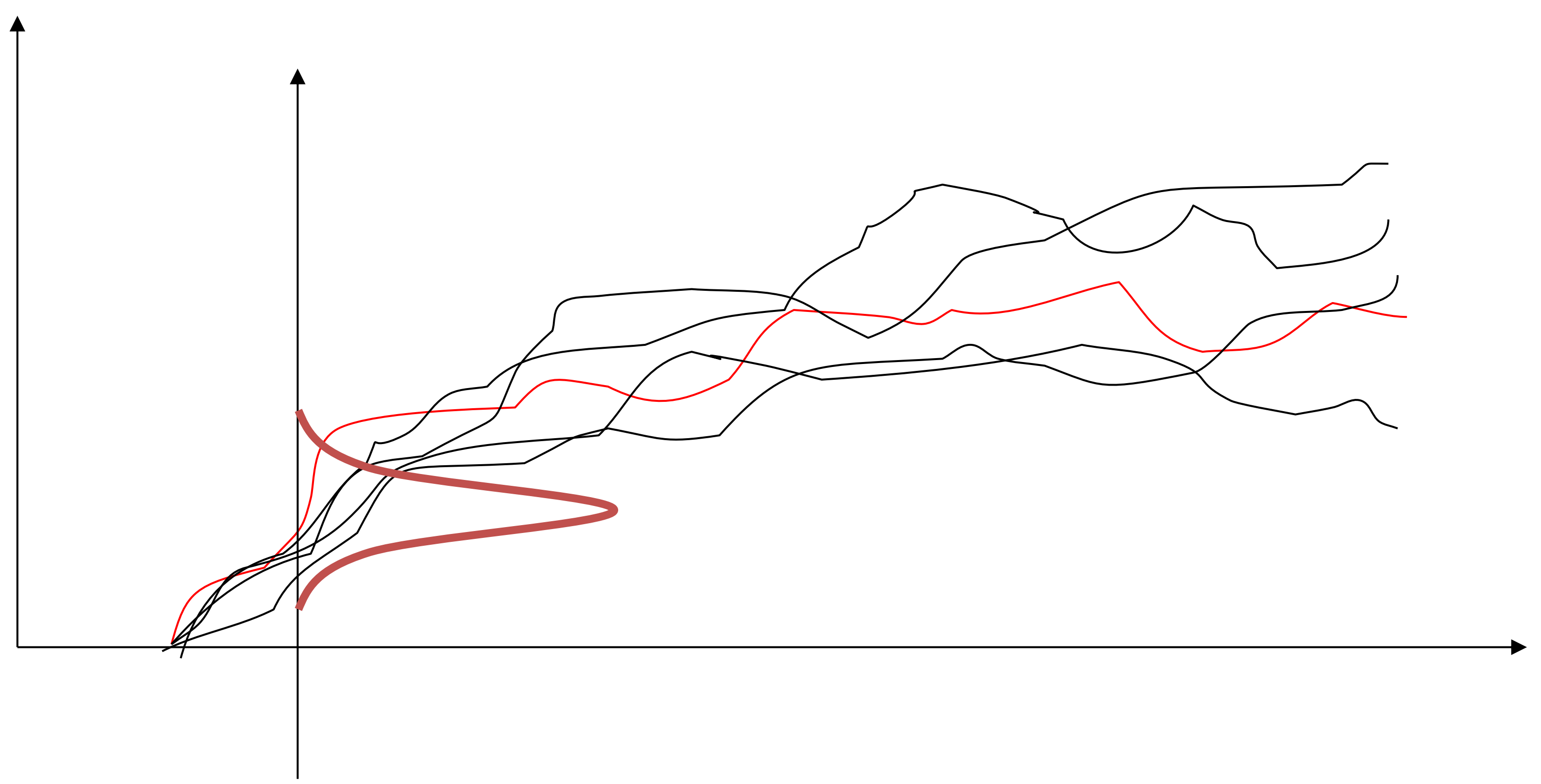
$$\frac{\partial}{\partial t} p(u,t) = -\frac{\partial}{\partial u} J(u,t)$$

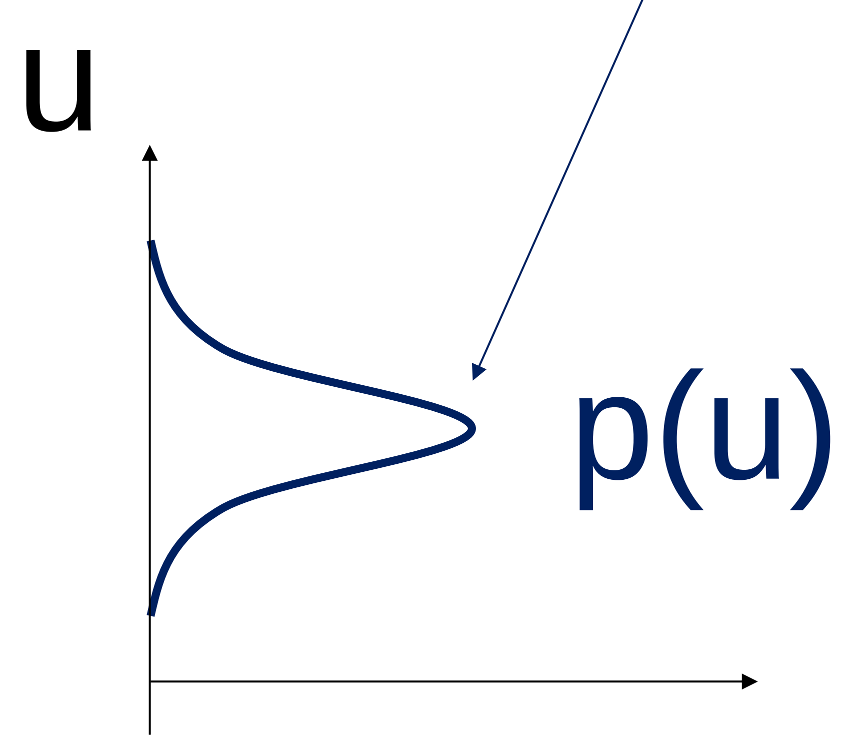
Flux: - jump $J_{jump}(u_0,t) = \nu \int_{u_0-\Delta u_{jump}}^{u_0} p(u,t)du$

- drift $J_{drift}(u_0,t) = p(u_0,t) \cdot \frac{du}{dt}(u_0)$

12.4: Fokker-Planck equation

Membrane potential density





Fokker-Planck

$$\tau \cdot \frac{\partial}{\partial t} p(u,t) = -\frac{\partial}{\partial u}[\gamma(u)\, p(u,t)] + \sigma^2 \frac{\partial^2}{\partial u^2} p(u,t)$$

drift

$$\gamma(u) = -u + \tau \sum_k \nu_k w_k$$

spike arrival rate

diffusion

$$\sigma^2 = \frac{1}{2}\tau \sum_k \nu_k w_k^2$$

Jump amplitude

$$w_{\mathrm{k}} = \Delta u_{jump,k}$$

D= diffusion constant

$$\sigma^2 = D/2$$

Summary:

In the absence of a threshold, the Fokker-Planck equation can always be solved.

The solution is a Gaussian distribution of membrane potential, with a mean that is located where the corresponding deterministic equation has its solution. The width of the membrane potential distribution is also time dependent. For example, in the absence of spike input the width decays back to zero.

In the presence of a threshold, we have an absorbing boundary at the threshold (where trajectories disappear) and a ‘source term’ at the reset potential (where trajectories reappear).

For the moment, however, we work in the absence of a threshold. This is called the ‘free solution’.

Quiz: stochastic spike arrival

$$\gamma(u) = -u + \tau \sum_k \nu_k w_k + RI(t) \qquad \sigma^2 = \frac{1}{2} \tau \sum_k \nu_k w_k^2$$

Suppose that we have a population of neurons that all receive excitatory input spikes arriving with Poisson frequency ν. There is no external input current.

Different neurons receive different realization of spike trains. Neurons do not have a firing threshold. Each spike causes a voltage jump by an amount w. We assume a system in stationary state.

[ ] Let us increase the Poisson spike arrival **frequency** by a factor of 2. Then the **mean** membrane potential <u> increases by a factor of 2 as well.

[ ] Let us increase the Poisson spike arrival **frequency** by a factor of 2. Then the **variance** of the membrane potential increases by a factor of 2 as well.

[ ] Let us increase the **parameter w** by a factor of 2. Then the **mean** membrane **potential <u>** increases by a factor of 2 as well.

[ ] Let us increase the **parameter w** by factor of 2. Then the **variance** increases by a factor of 2 as well.

[ ] Let us instead change the **parameter w** by a factor of (-2). Then the **variance** increases by a factor of 4.

[ ] If neurons receive two types of input, excitatory with frequency ν_+ and inhibitory with frequency ν_- , then it is possible to change the variance of the membrane potential without changing the firing rates

Hint:

assume weights

$$w_- = -w_+$$

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- free solution

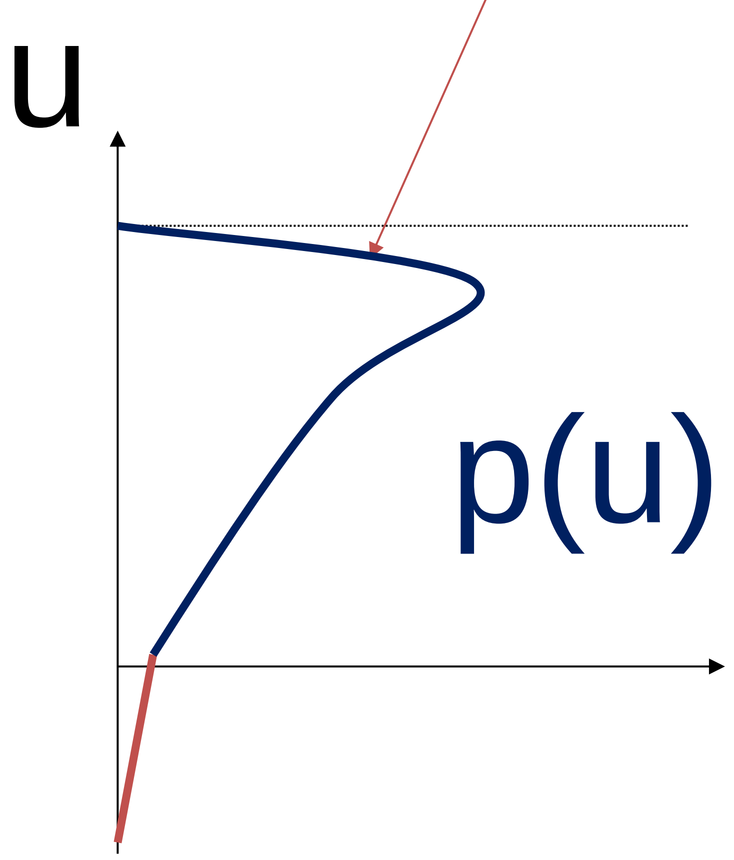
12.5. Threshold and reset
- constant asynchronous activity
- time dependent activity

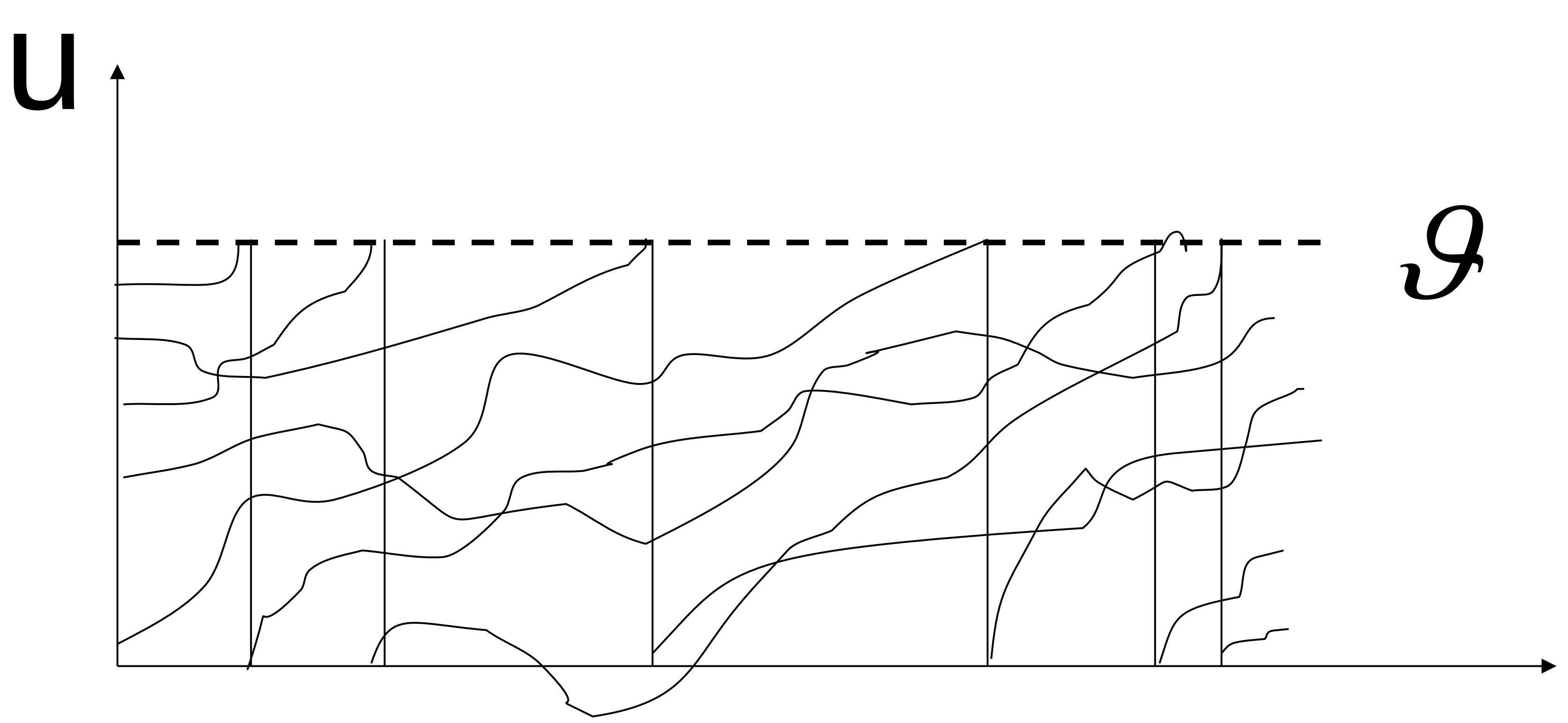
12. 6. Network states (Brunel net)

12.5: Threshold and reset (sink and source terms)

Membrane potential density

density at threshold





Fokker-Planck

$$\tau \cdot \frac{\partial}{\partial t} p(u,t) = -\frac{\partial}{\partial u}[\gamma(u)\, p(u,t)] + \sigma^2 \frac{\partial^2}{\partial u^2} p(u,t) + \tau A(t)\, \delta(u - u_{reset})$$

drift

$$\gamma(u) = -u + \tau \sum_k \nu_k w_k + RI$$

spike arrival rate

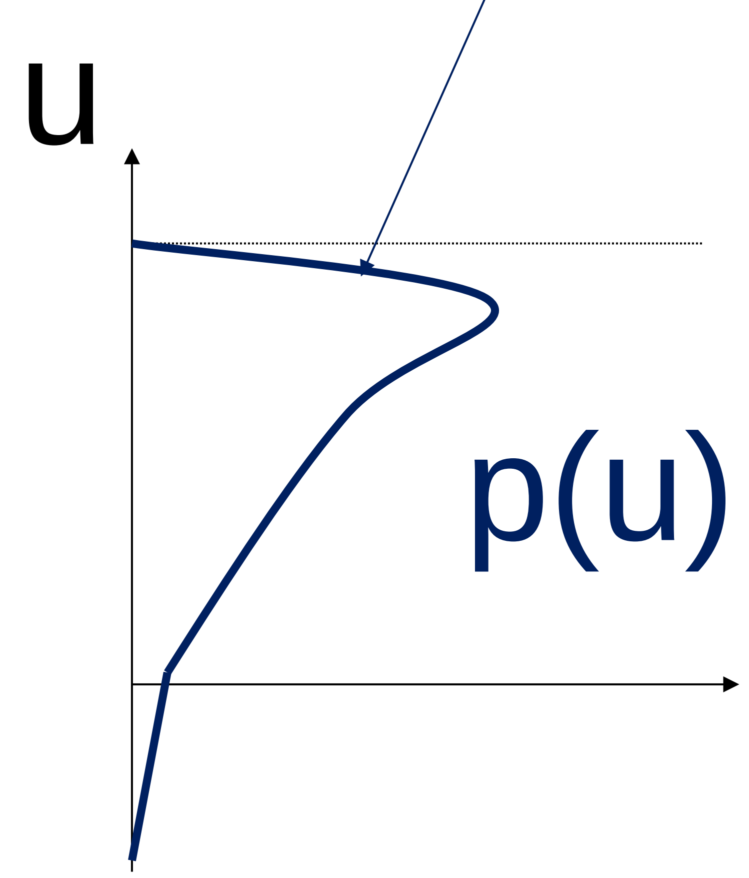
diffusion

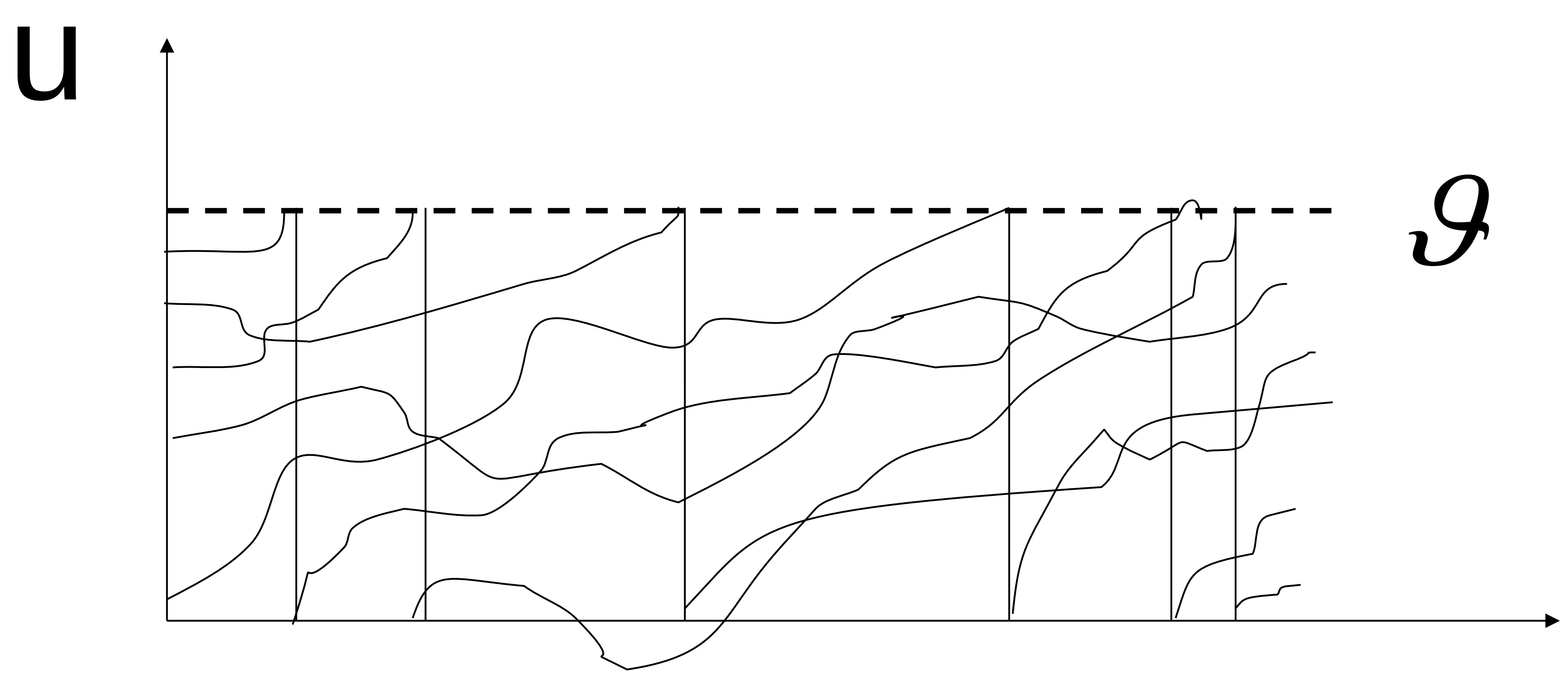
$$\sigma^2 = \frac{1}{2}\tau \sum_k \nu_k w_k^2$$

$$w_\mathrm{k} = \Delta u_{jump,k}$$

12.5: population firing rate A(t)

Membrane potential density





Population Firing rate *A(t):* flux at threshold

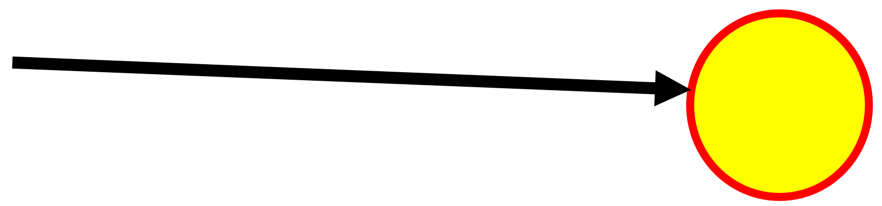
12.5: Applications of Fokker-Planck equation in Neuroscience

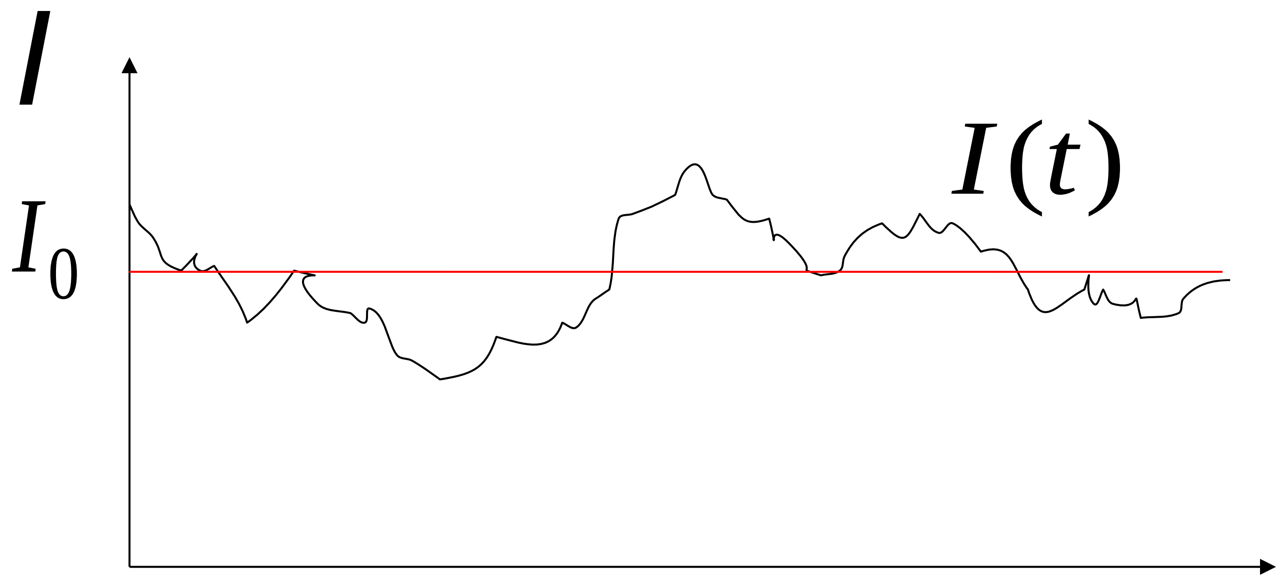
1) **Uncoupled network** of leaky integrate-and-fire neurons
- each neuron receives stationary stochastic input
- stationary state of asynchronous firing: $A(t)=A_0$
- firing rate of single neuron $\nu = A_0$ (analytical)

2) **Uncoupled network** of leaky integrate-and-fire neurons
- time-dependent input
- time-dependent population activity $A(t)$ (numerical)

3) **Coupled network** of leaky integrate-and-fire neurons:
- excitatory and inhibitory populations
- all neurons have same parameters ('Brunel network')
- network states (analytical and/or numerical)

12.5: population firing rate A(t) = single neuron rate





Synaptic current pulses

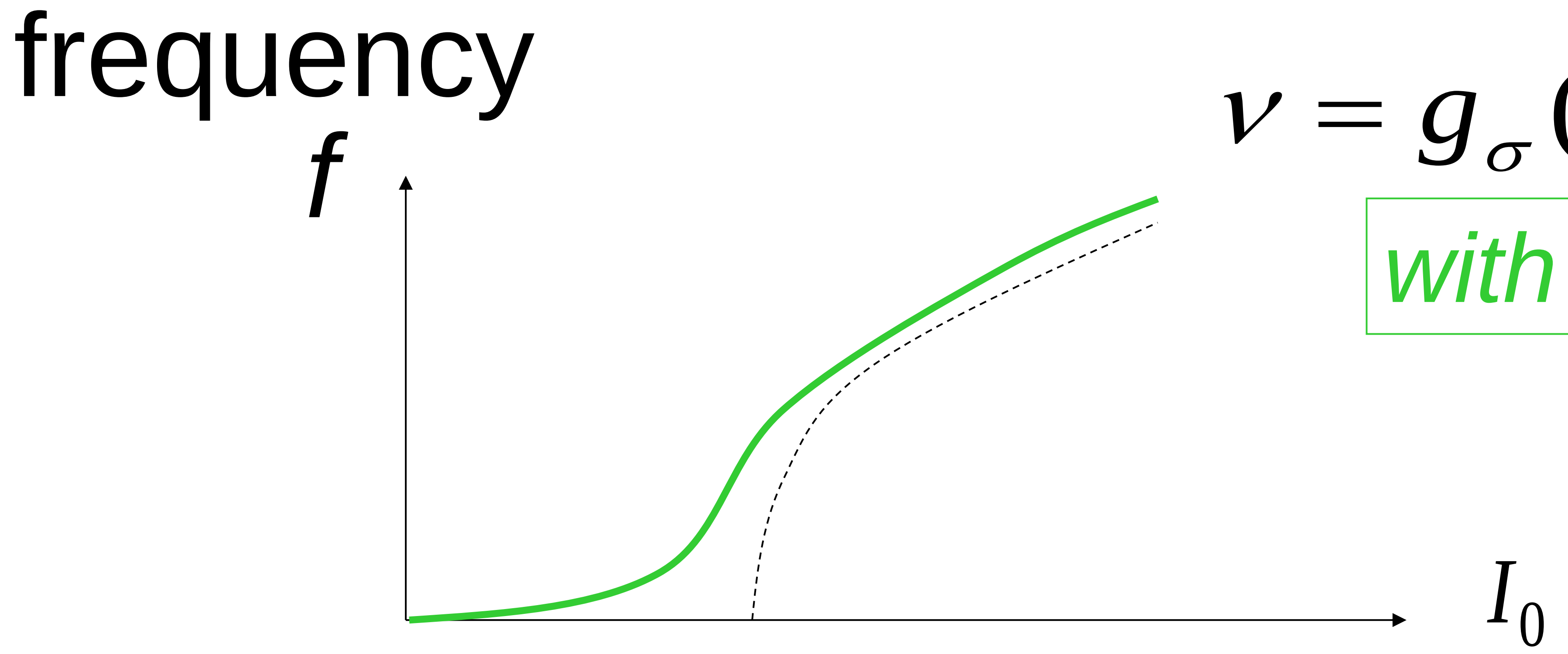
$$\tau \frac{d}{dt} u = -(u - u_{eq}) + R\{ \sum_{k,f} q_e \delta(t - t_k^f) - \sum_{k',f'} q_i \delta(t - t_{k'}^{f'}) \}$$

EPSC

IPSC

$$\tau \frac{d}{dt} u = -(u - u_{eq}) \quad + R I^{mean}(t) + \quad \xi(t)$$

$$\tau \frac{d}{dt} u = -(u - u_{eq}) \quad + R I(t)$$



$$\nu = g_\sigma(I)$$

with noise

$$I(t) = [I_o + I_{noise}]$$

effective noise current

12.5: membrane potential density (stationary state)

stochastic
spike arrival
$\nu_+ = \nu_- = 0.8kHz$

σ=0.2

firing rate/
population activity

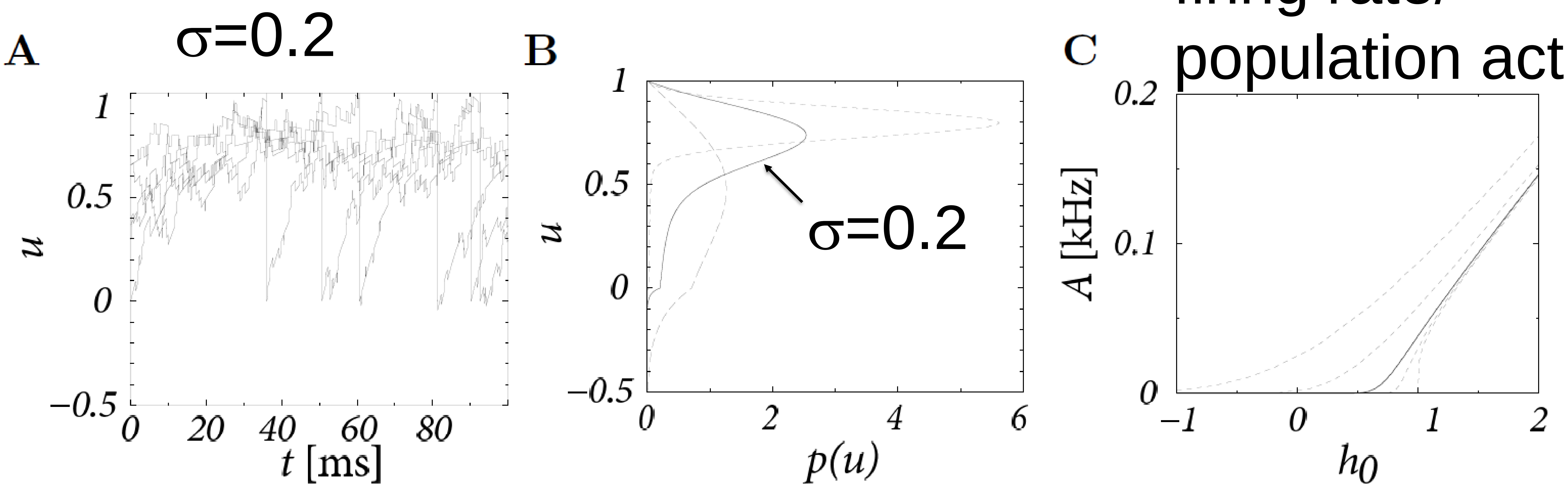


Fig. 13.5: **A**. Membrane potential trajectories of 5 neurons ($R = 1$ and $\tau_m = 10\,\text{ms}$) driven by a constant background current $I_0 = 0.8$ and stochastic background input with $\nu_+ = \nu_- = 0.8\,\text{kHz}$ and $w_\pm = \pm 0.05$. These parameters correspond to $h_0 = 0.8$ and $\sigma = 0.2$ in the diffusive noise model. **B**. Stationary membrane potential distribution in the diffusion limit for $\sigma = 0.2$ (solid line), $\sigma = 0.1$ (short-dashed line), and $\sigma = 0.5$ (long-dashed line). (Threshold $\vartheta = 1$). **C**. Mean activity of a population of integrate-and-fire

Image:
Gerstner et al. (2014),
Neuronal Dynamics

12.5: Applications of Fokker-Planck equation in Neuroscience

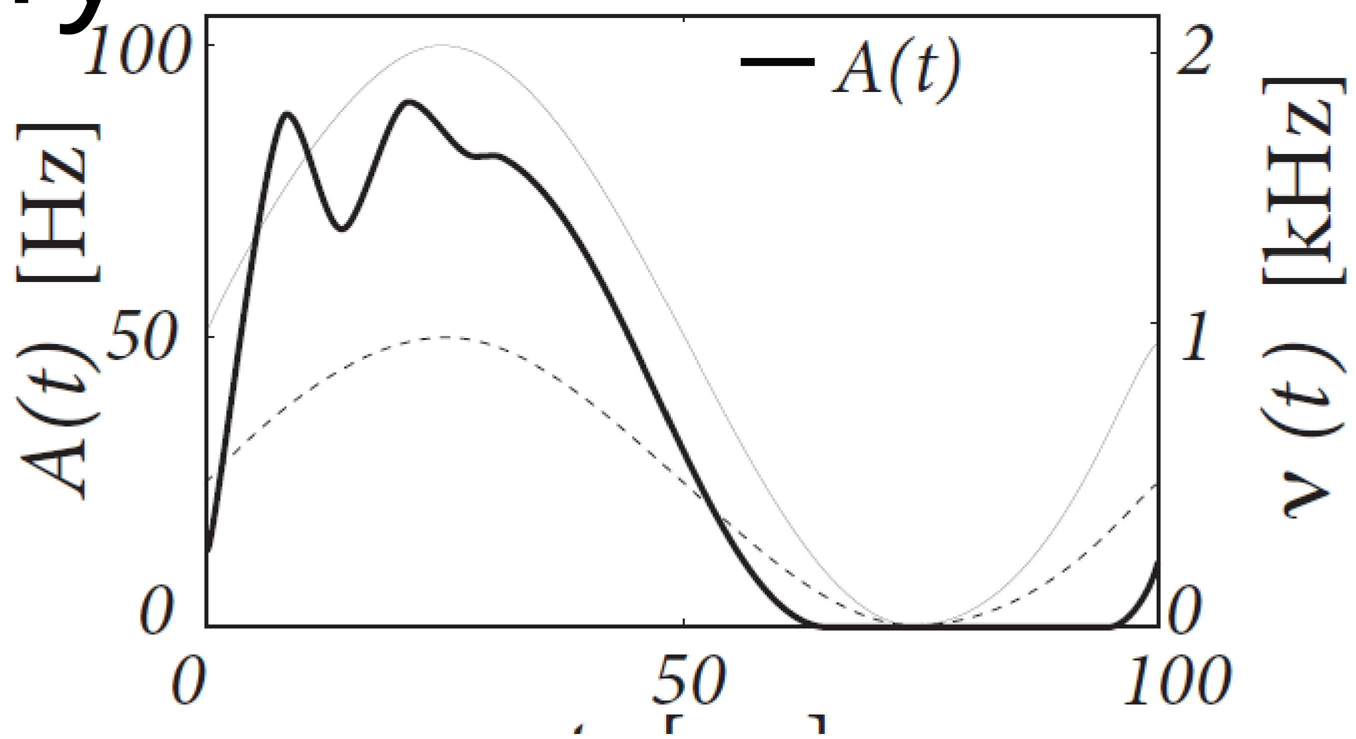
1) **Uncoupled network** of leaky integrate-and-fire neurons
- each neuron receives stochastic background input
- stationary state of asynchronous firing: $A(t)=A_0$
- firing rate of single neuron $\nu = A_0$ (analytical)

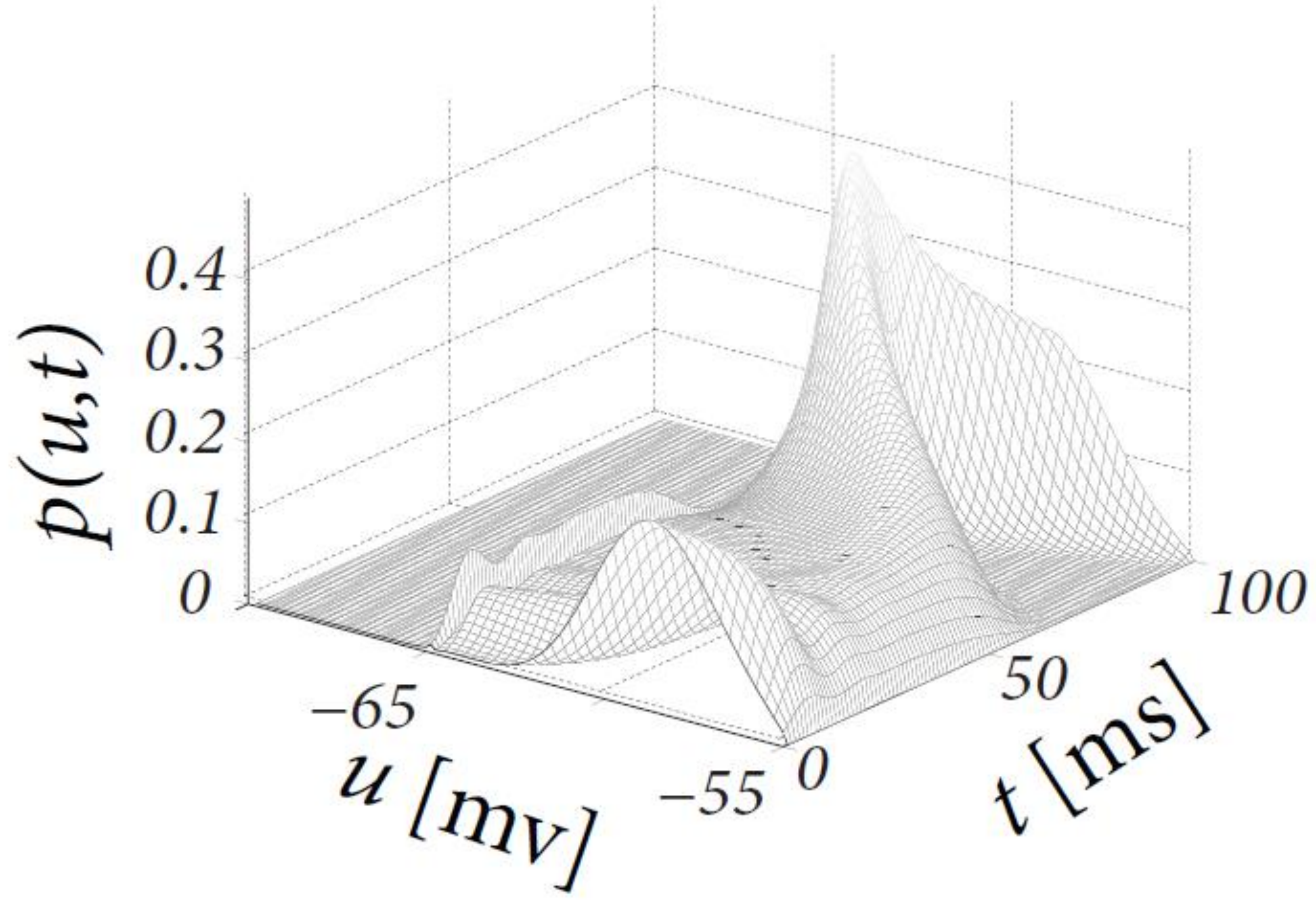
2) **Uncoupled network** of leaky integrate-and-fire neurons
- time-dependent input
- time-dependent population activity $A(t)$ (numerical)

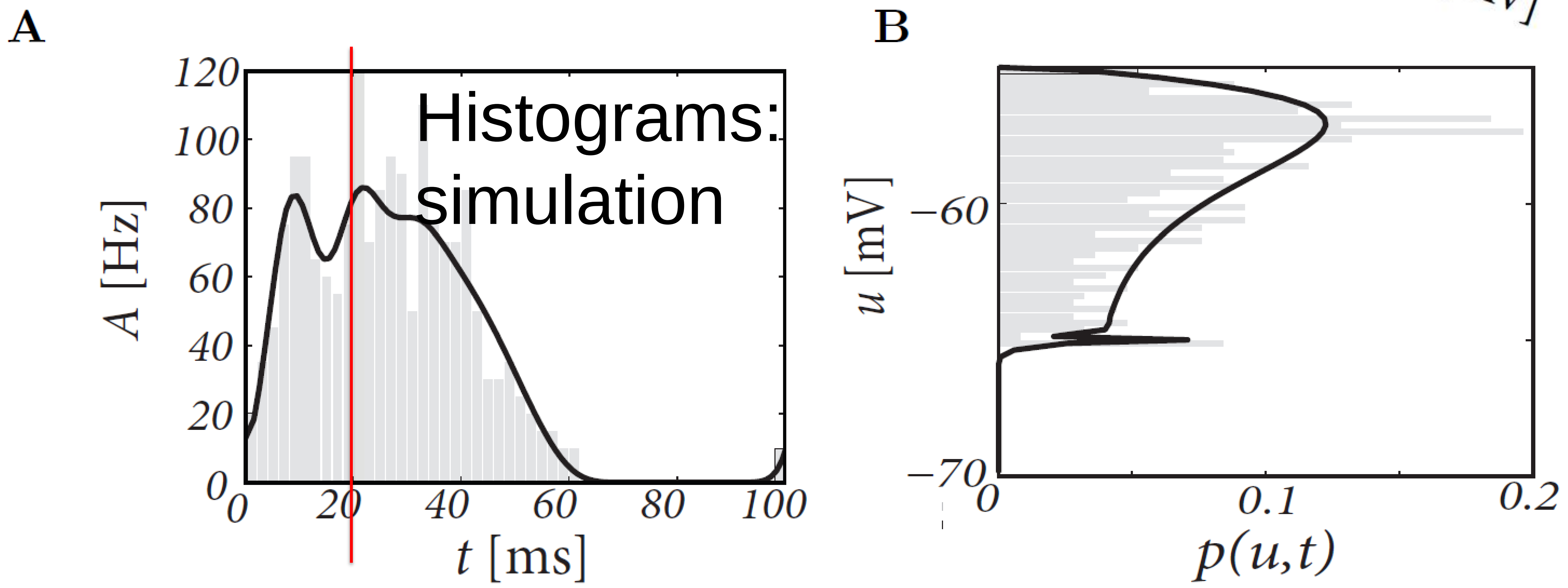
3) **Coupled network** of leaky integrate-and-fire neurons:
- excitatory and inhibitory populations
- all neurons have same parameters (‘Brunel network’)
- network states (analytical and/or numerical)

12.5: population activity, time-dependent

Theory







Nykamp+Tranchina, 2000

Fig. 13.4: Comparison of theory and simulation. **A**. Population firing rate $A(t)$ as a function of time in a simulation of 1 000 neurons (histogram bars) compared to the prediction

Image: Gerstner et al. (2014), Neuronal Dynamics

Summary:

In the absence of a threshold, the Fokker-Planck equation can always be solved.
In the presence of a threshold, the Fokker-Planck equation that corresponds to stochastic spike arrival needs special care.

The threshold acts as an absorbing boundary condition; hence the density at threshold must be zero (for stochastic spike arrivals that arrive infinitely often and cause infinitely small jumps).

For fixed spike arrival rate, the Fokker-Planck equation predicts that the membrane potential distribution converges to a stationary state. We can predict analytically the stationary distribution of membrane potentials and can compare it with simulations.
The stationary distribution is not Gaussian. It has a peak about one sigma below threshold.

For time dependent input we can numerically solve the Fokker-Planck equation and compare it to simulations of a large number of neurons. Again the simulations agree with the predictions if the number of neurons is sufficiently large.

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12.6. Random spiking network
- **Brunel network**: Random network of leaky integrate-and-fire neurons
- **Network states**

12.5: Applications of Fokker-Planck equation in Neuroscience

1) **Uncoupled network** of leaky integrate-and-fire neurons
- each neuron receives stochastic background input
- stationary state of asynchronous firing: $A(t)=A_0$
- firing rate of single neuron $\nu = A_0$ (analytical)

2) **Uncoupled network** of leaky integrate-and-fire neurons
- time-dependent input
- time-dependent population activity $A(t)$ (numerical)

3) **Coupled network** of leaky integrate-and-fire neurons:
- excitatory and inhibitory populations, random connections
- all neurons have same parameters ('Brunel network')
- network states (analytical and/or numerical)

Review/week 7: Random connectivity – fixed number of inputs

random: input connections K=500 fixed, weights chosen as $w_{ij} = \frac{w_0}{K}$

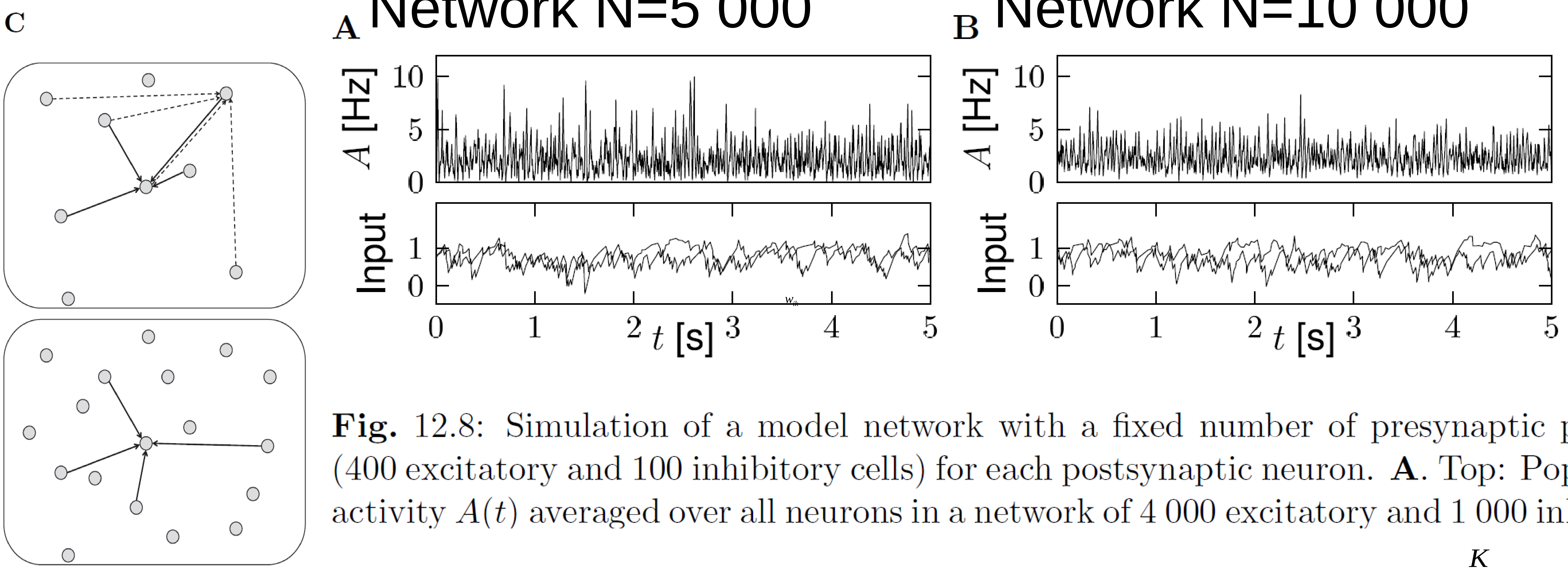


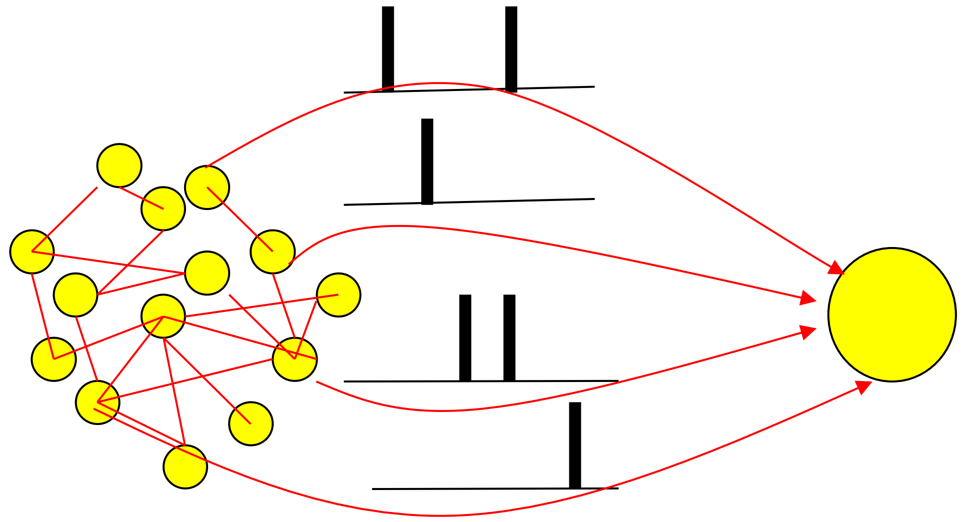
Fig. 12.8: Simulation of a model network with a fixed number of presynaptic partners (400 excitatory and 100 inhibitory cells) for each postsynaptic neuron. **A**. Top: Population activity $A(t)$ averaged over all neurons in a network of 4 000 excitatory and 1 000 inhibitory

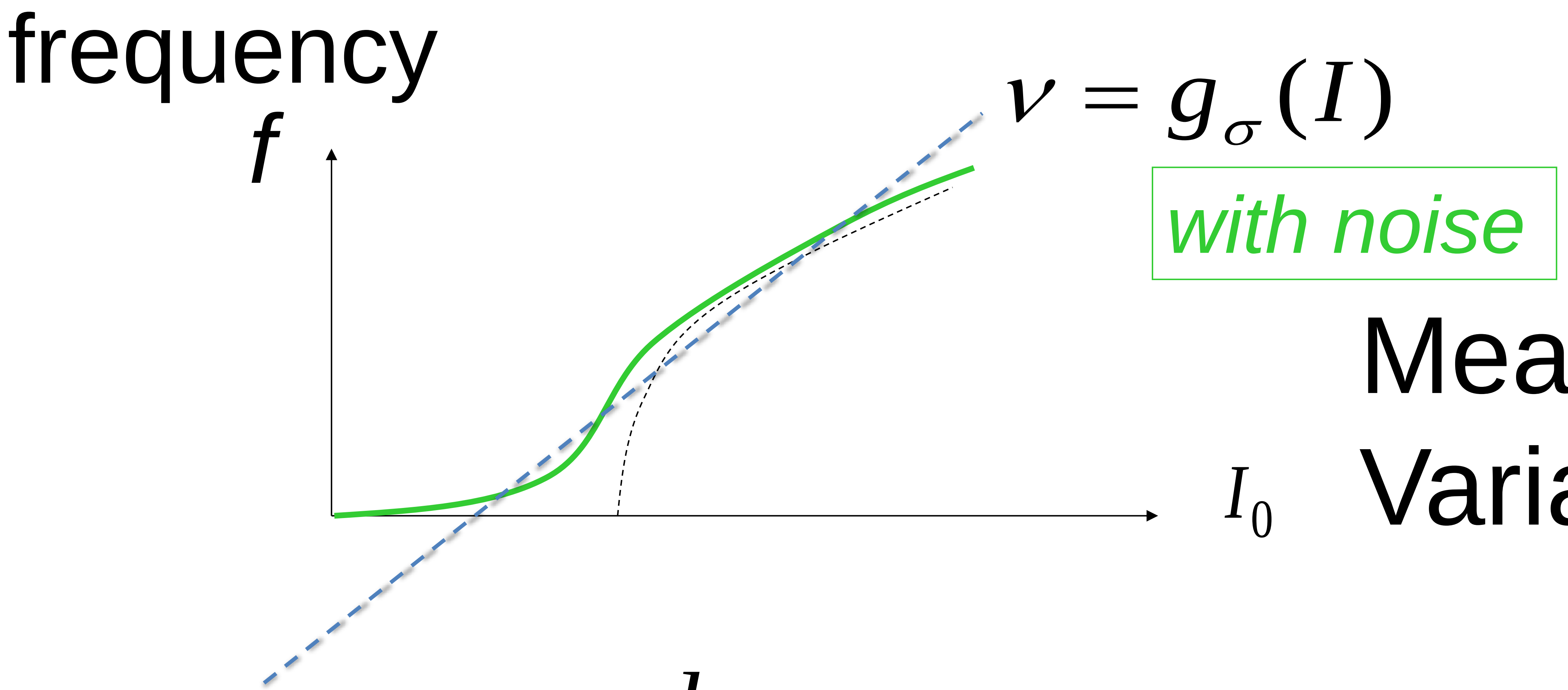
fluctations of *A* decrease, but
→ fluctations of *Input*
(and of u) remain

mean $\mu = RI(t) + \tau \sum_{k=1}^{K} \nu_k w_k$

diffusion $\sigma^2 = \frac{1}{2} \tau \sum_{k=1}^{K} \nu_k w_k^2$

12.5: network states: feedback from population activity





Mean current *I(t)* depends on state

Variance/noise depends on state

$$\tau \frac{d}{dt} u = -(u - u_{eq}) + R\{ \sum_{k,f} q_e \delta(t - t_k^f) - \sum_{k',f'} q_i \delta(t - t_{k'}^{f'}) \}$$

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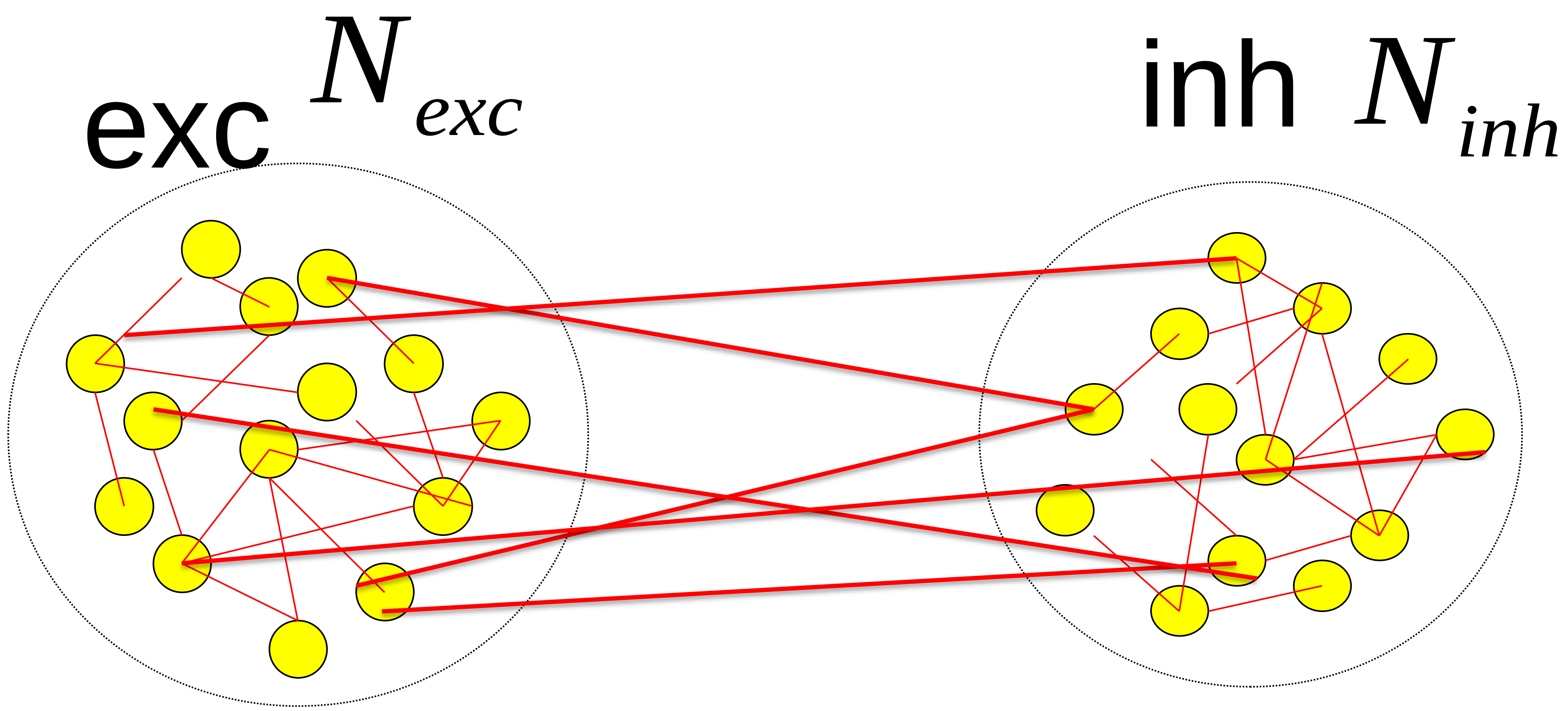
$$\tau \frac{d}{dt} u = -(u - u_{eq}) + R I^{mean}(t) + \sigma(t)\xi(t)$$

12.5: Connectivity scheme – Brunel network

$$N_{exc} >> K_{exc}$$

$$\frac{d}{dt} u_i = -(u/\tau) + \beta I_i$$

$$\beta I_i = \sum_{k,f} w_{ik}^{exc} \delta(t - t_k^f) - \sum_{k,f} w_{ik}^{inh} \delta(t - t_k^f)$$



$$4 N_{inh} = N_{exc}$$

$$w_{ij}^{exc} = w_0$$

$$w_{ij}^{inh} = g\, w_0$$

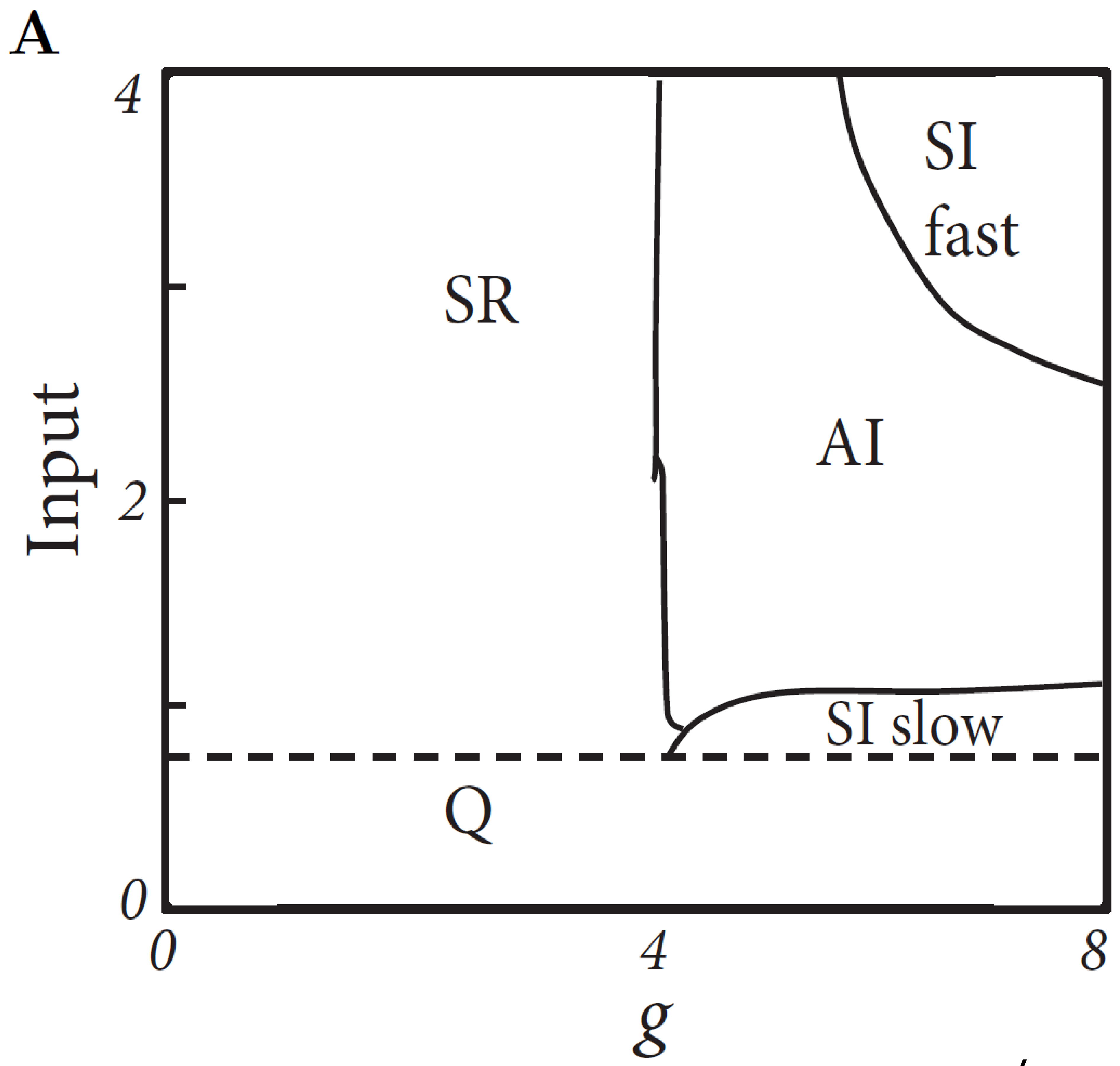
Each neuron receives K'_{exc} excitatory and $K_{exc}/4$ inhibitory synapses

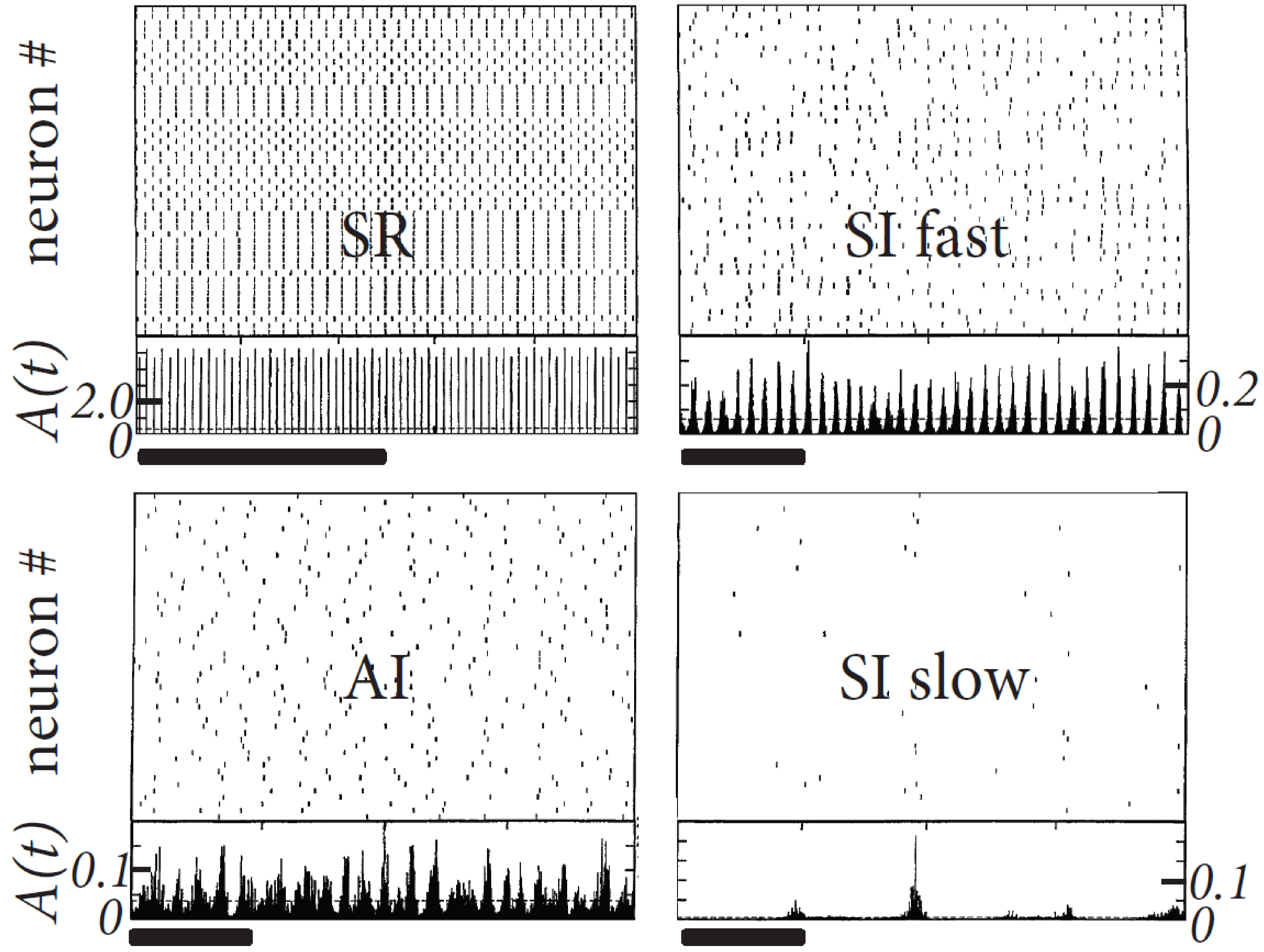
Mean and variance of membrane potential in Brunel network
→ Drift and diffusion in Fokker-Planck equation

12.5: network states: Brunel network

AI=Asynchronous Irregular

SR=Synchronous Regular





Q=Quiescent

$g = q_i / q_e$

Brunel 2000

12.5: Summary Fokker-Planck equation

$$\tau \cdot \frac{\partial}{\partial t} p(u,t) = -\frac{\partial}{\partial u}[\gamma(u)\, p(u,t)] + \sigma^2 \frac{\partial^2}{\partial u^2} p(u,t) + \tau A(t)\, \delta(u - u_{reset})$$

source term

drift

$$\gamma(u) = -u + \mu \quad = -u + RI(t) + \tau \sum_{k=1}^{K} \nu_k w_k$$

'target mean', see Ex. 2

$$\mu \quad = RI(t) + \tau \sum_{k=1}^{K} \nu_k w_k$$

diffusion parameter

$$\sigma^2 = \frac{1}{2} \tau \sum_{k=1}^{K} \nu_k w_k^2$$

Note: a sink term $-\tau A(t)\, \delta(u - \vartheta)$

is equivalent to an absorbing boundary condition

Summary:

The final step of this lecture is to consider two interconnected populations of neurons. The first one contains excitatory neurons, the second one inhibitory neurons.

To simplify the analysis we assume that all neurons are of the same type (same membrane time constant, same threshold).

Hence each neuron receives input from K_{exc} neurons in the excitatory population and from K_{inh} neurons in the inhibitory population. Therefore all neurons receive statistically the same input, but the actual inputs are different because each neurons receives inputs from a different subset of neurons. In the model it is assumed (based on experimental counts) that the excitory group is 4 times bigger than the inhibitory one.
An important parameter is the ratio $g = q_i / q_e$ of the jump size (charge) of excitatory versus inhibitory inputs.

The model can be solved by a combined analytical-numerical approach.
The solution shows different types of solutions:
AI = asynchronous irregular; Q=quiescent. SI – synchronous irregular. SR= synchronous regular.