Week 15 – Integral Equation for population dynamics

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Biological Modeling of Neural Networks:

Week 15 – Population Dynamics:
The Integral –Equation Approach

Wulfram Gerstner

EPFL, Lausanne, Switzerland

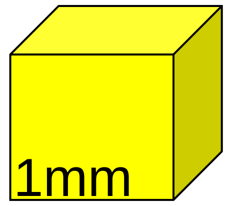
15.1 Populations of Neurons
- review: homogeneous population
- review: parameters of single neurons

15.2 Integral equation
- aim: population activity
- renewal assumption

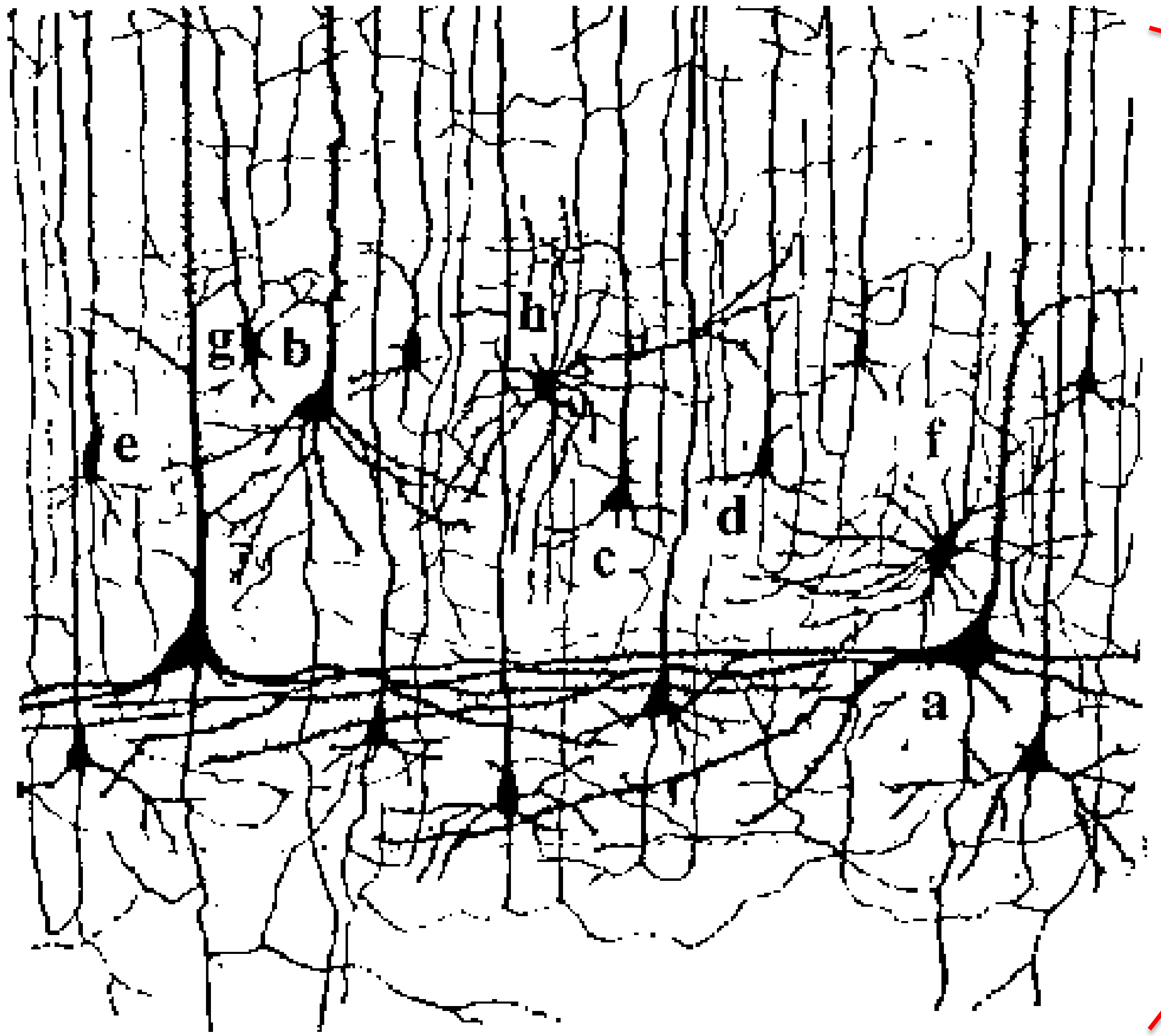
15.3 Populations with Adaptation
- Quasi-renewal theory

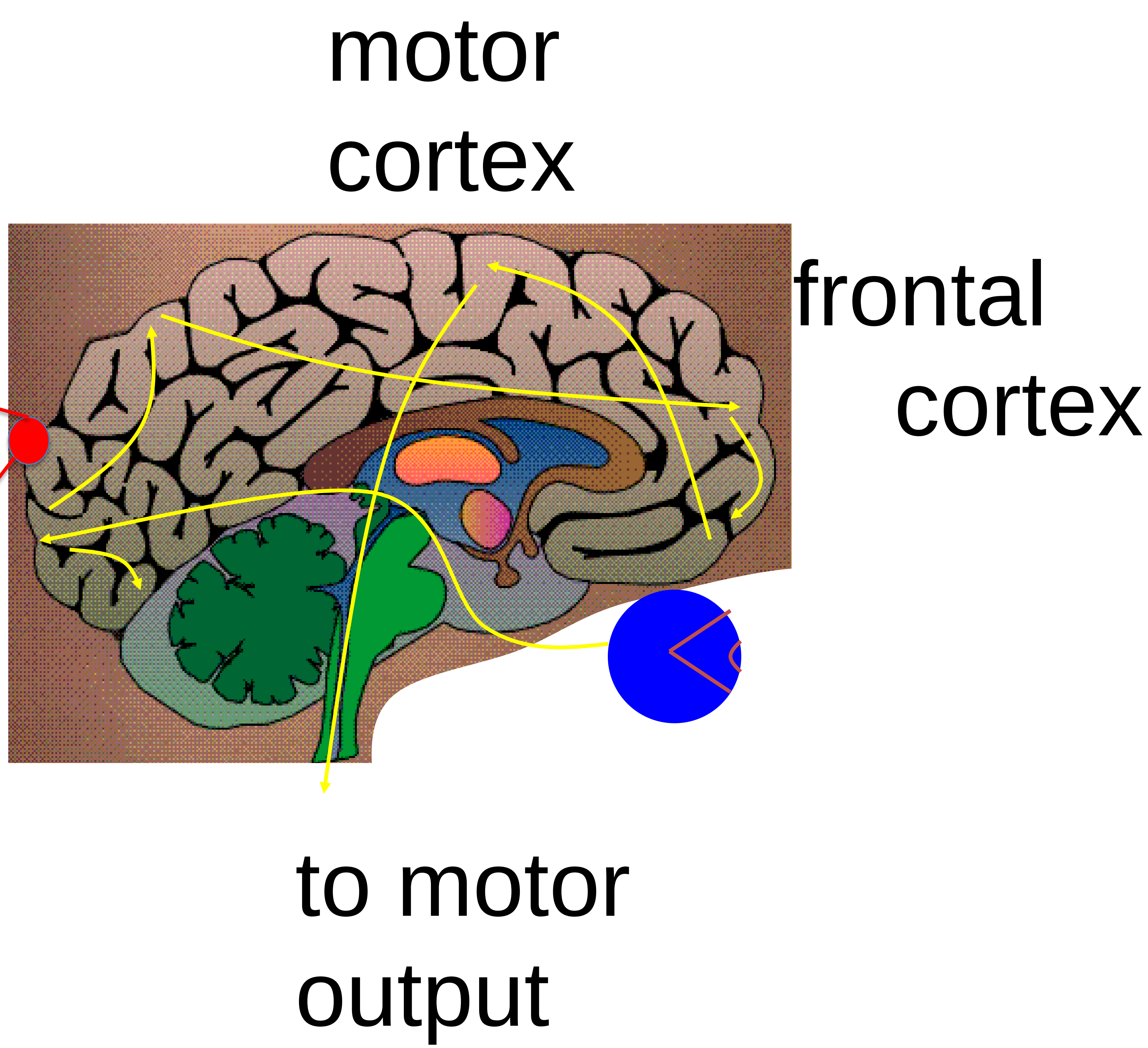
15.4. Coupled populations
- self-coupling
- coupling to other populations

Neuronal Dynamics – Brain dynamics is complex

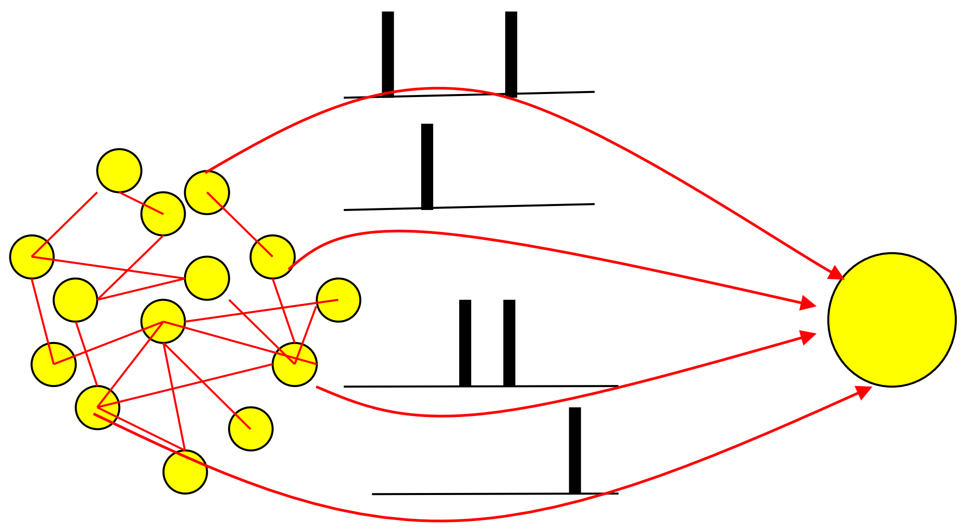


10 000 neurons
3 km of wire

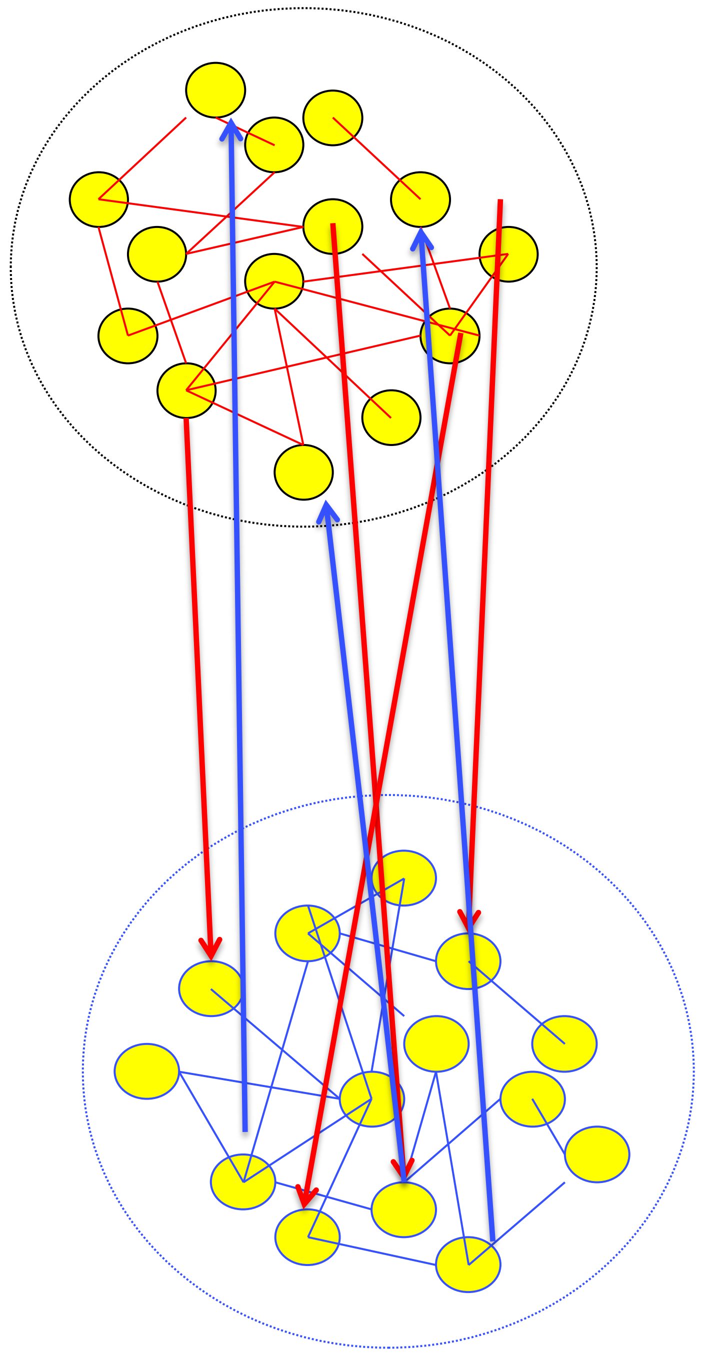




Week 15-part 1: Review: Homogeneous Population



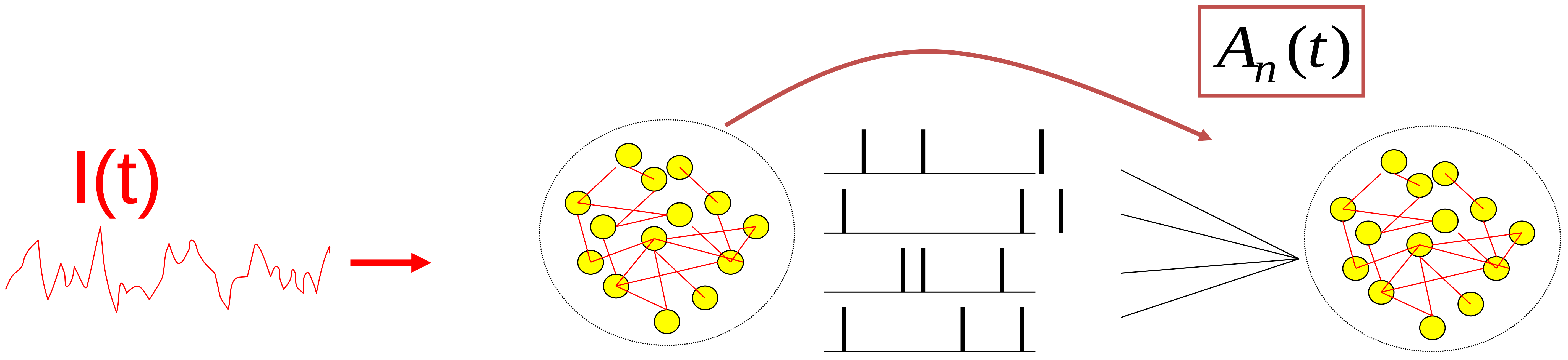
Example: 2 populations



Homogeneous population:

-each neuron receives input
from k neurons in the population
-each neuron receives the same
(mean) external input (could come from
other populations)
-each neuron in the population has roughly
the same parameters

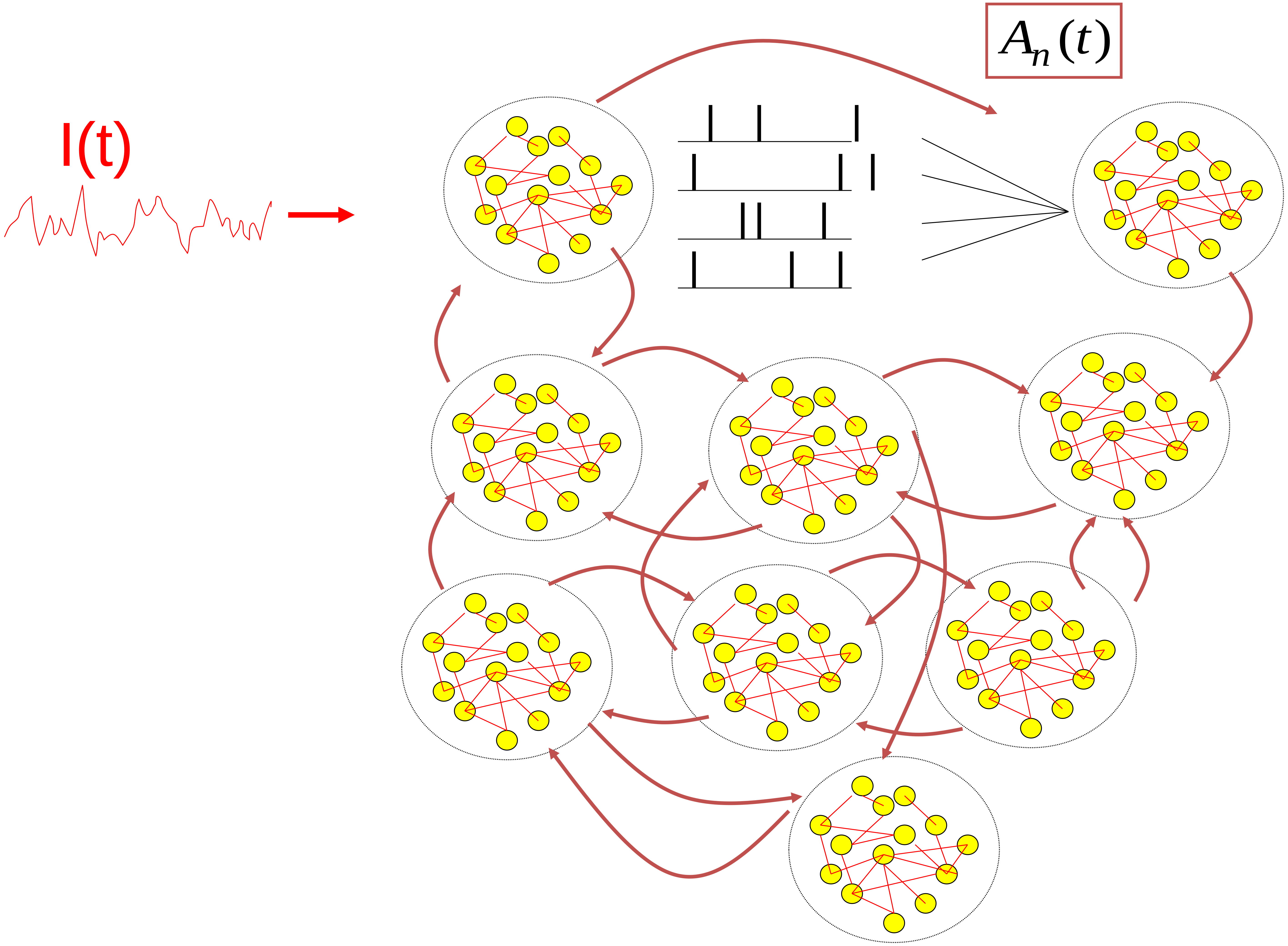
Week 15-part 1: Review: microscopic vs. macroscopic



microscopic:
-spikes are generated by individual neurons
-spikes are transmitted from neuron to neuron

macroscopic:
-Population activity $A_n(t)$
-Populations interact *via* $A_n(t)$

Week 15-part 1: Review: coupled populations



Week 15-part 1: Example: coupled populations in barrel cortex

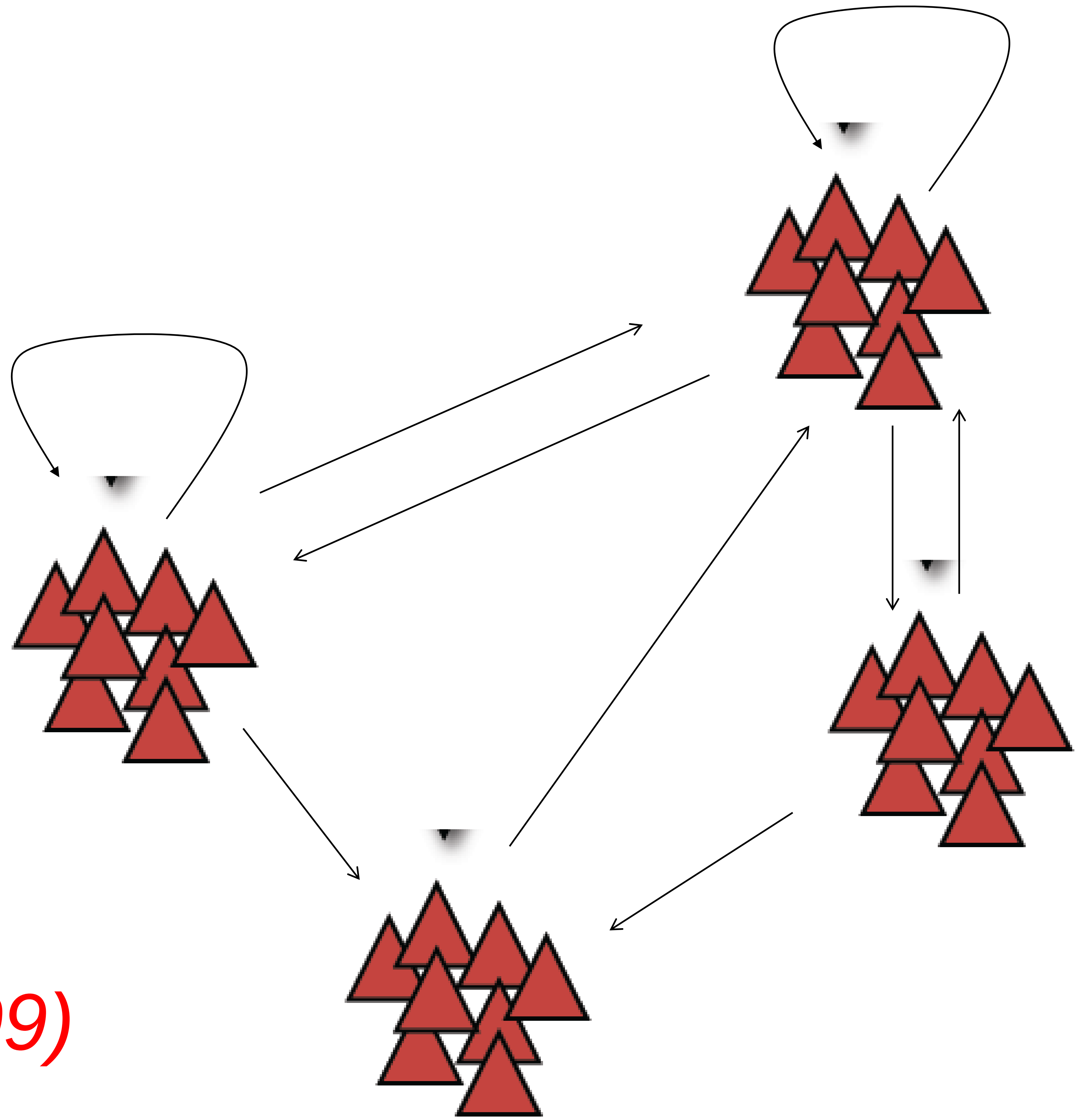
Neuronal Populations

= a homogeneous group of neurons
(more or less)

Populations:

- pyramidal neurons in layer 5 of barrel D1
- pyramidal neurons in layer 2/3 of barrel D1
- inhibitory neurons in layer 2/3 of barrel D1

100-2000 neurons
per group *(Lefort et al., NEURON, 2009)*



different barrels and layers, different neuron types → different populations

Week 15-part 1: Global aim and strategy

-Extract parameters for SINGLE neuron

(see NEURONAL DYNAMICS, Chs. 8-11; review now)

-Dynamics in one (homogeneous) population

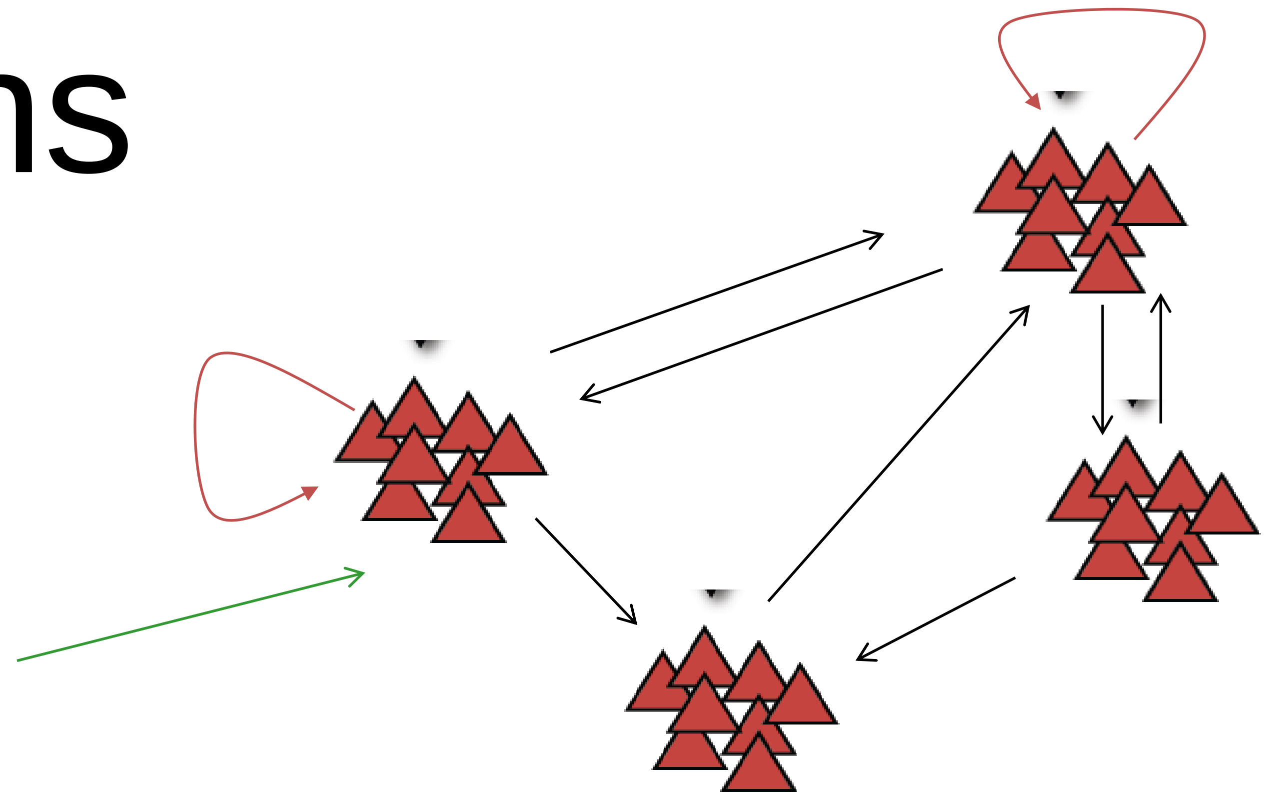
Today, parts 15.2 and 15.3!

-Dynamics in coupled populations

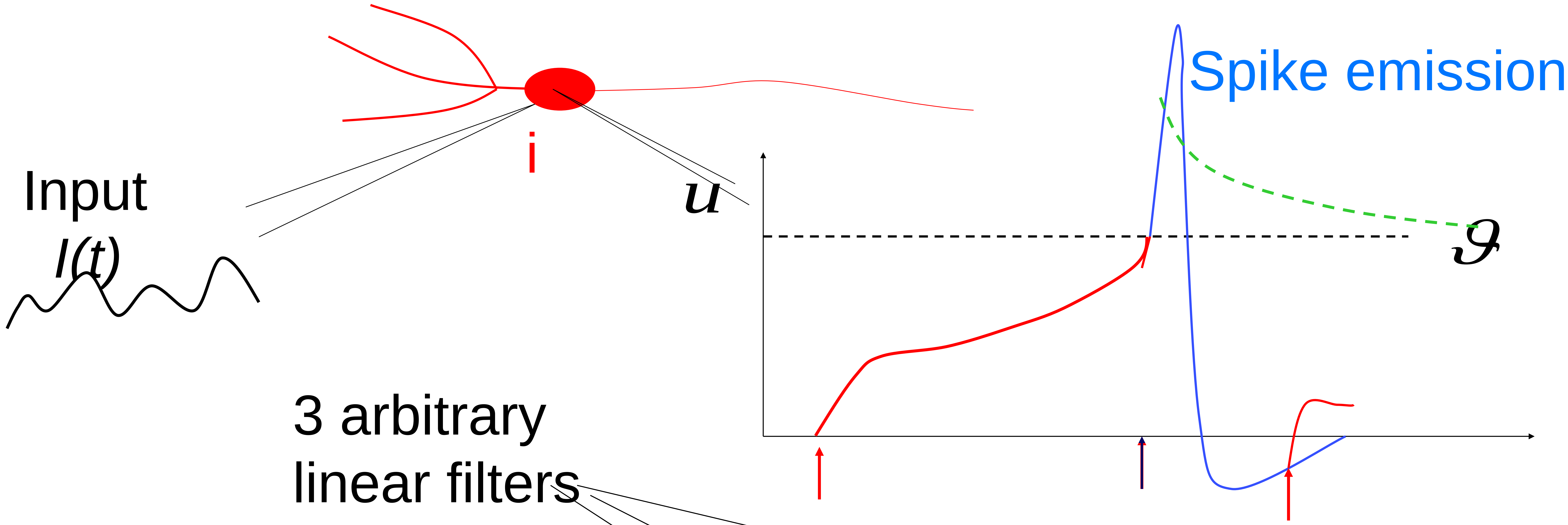
-Understand Coding in populations

-Understand Brain dynamics

Sensory input



Week 15-part 1: Review: Spike Response Mode (SRM)



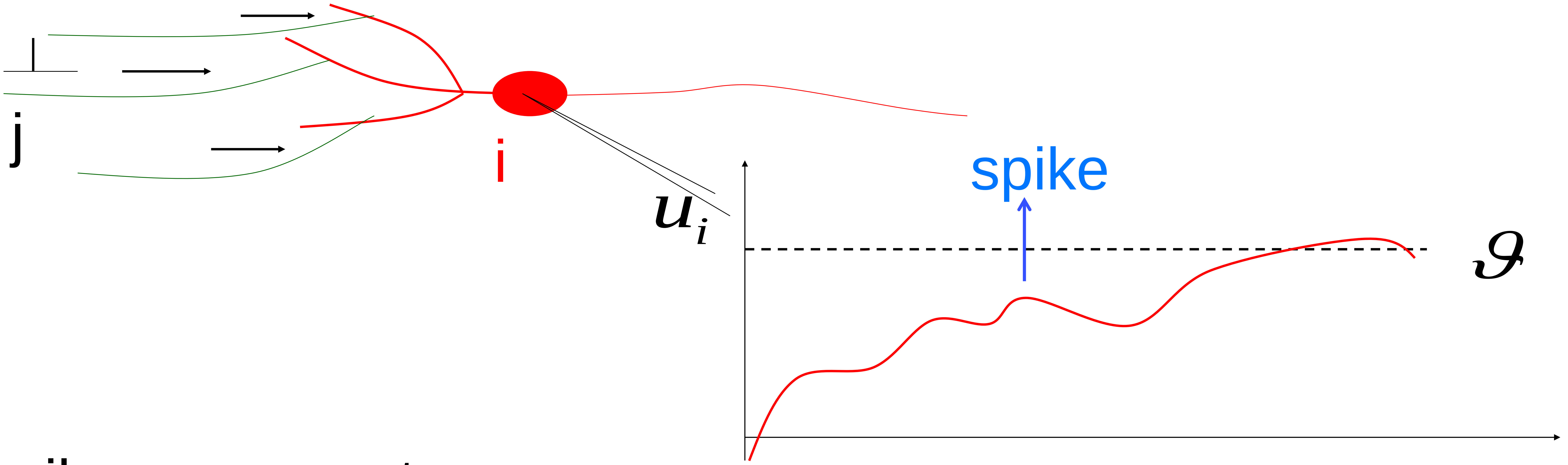
potential

$$u(t) = \sum_{\hat{t}} \eta(t-\hat{t}) + \int_0^\infty \varepsilon(s) I(t-s) ds + \dots$$

threshold

$$\vartheta(t) = \vartheta_0 + \sum_{t'} \theta(t-t')$$

SRM +escape noise = Generalized Linear Model (GLM)



-spikes are events

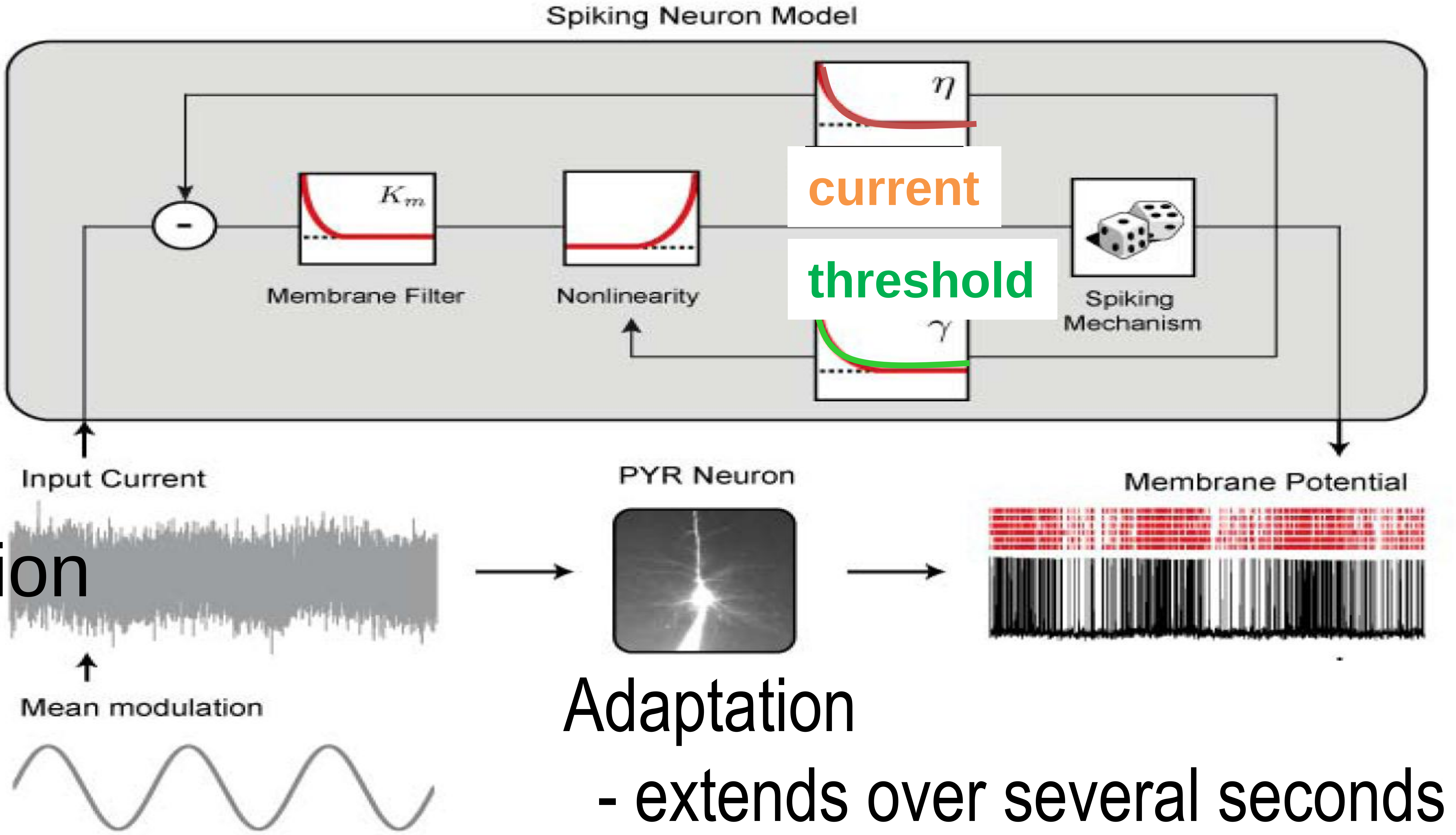
-spike leads to reset/adapt. currents/increased threshold

-strict threshold replaced by escape noise:

$$\Pr\{\ fire\ in [t; t+\Delta t]\} = \lambda(t)\Delta t = f[u(t) - \vartheta(t)]\Delta t$$

exp

Jolivet et al., J. Comput. NS, 2006

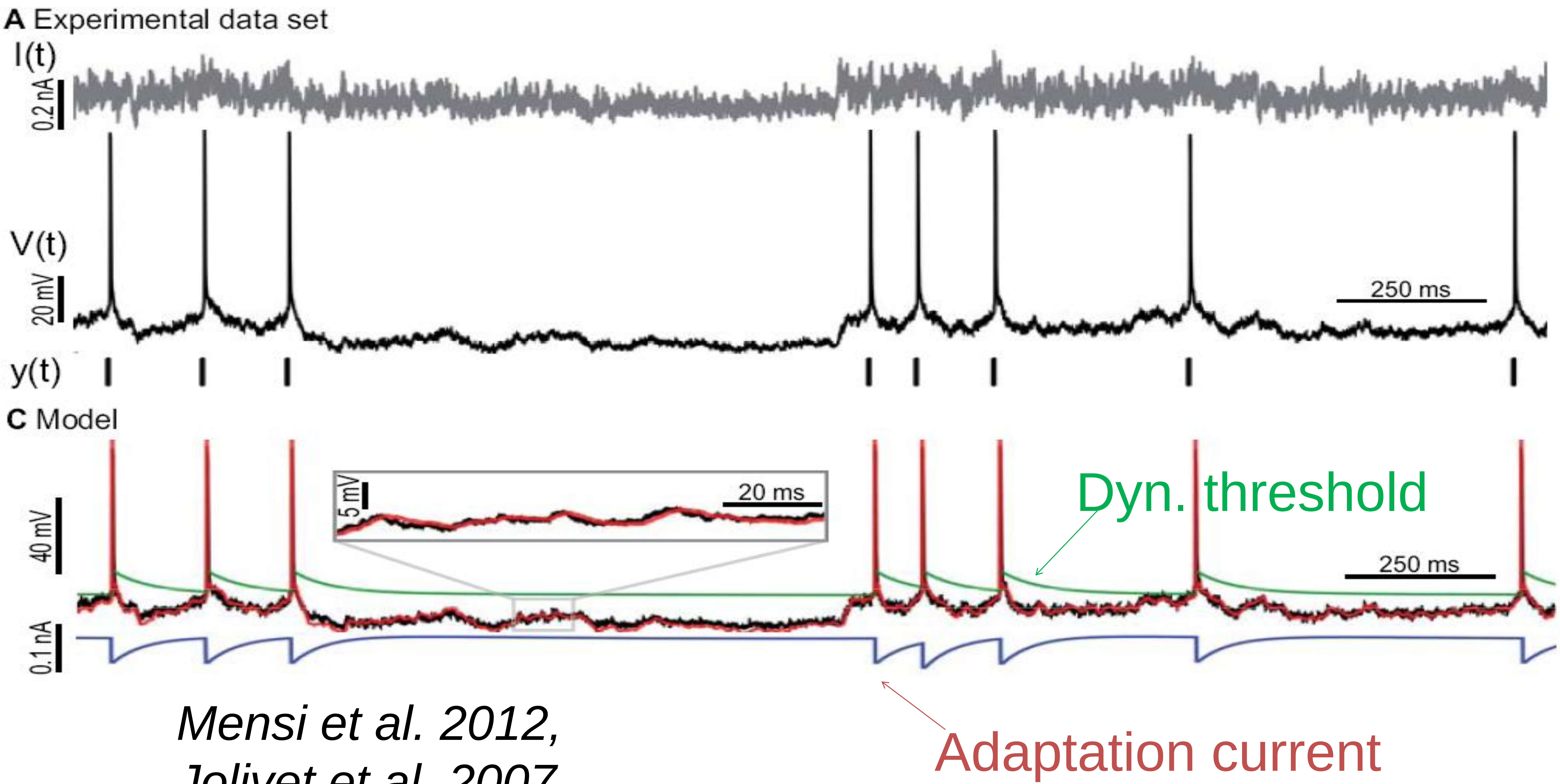


Input current:
-Slow modulation
-Fast signal

Adaptation
- extends over several seconds
- power law

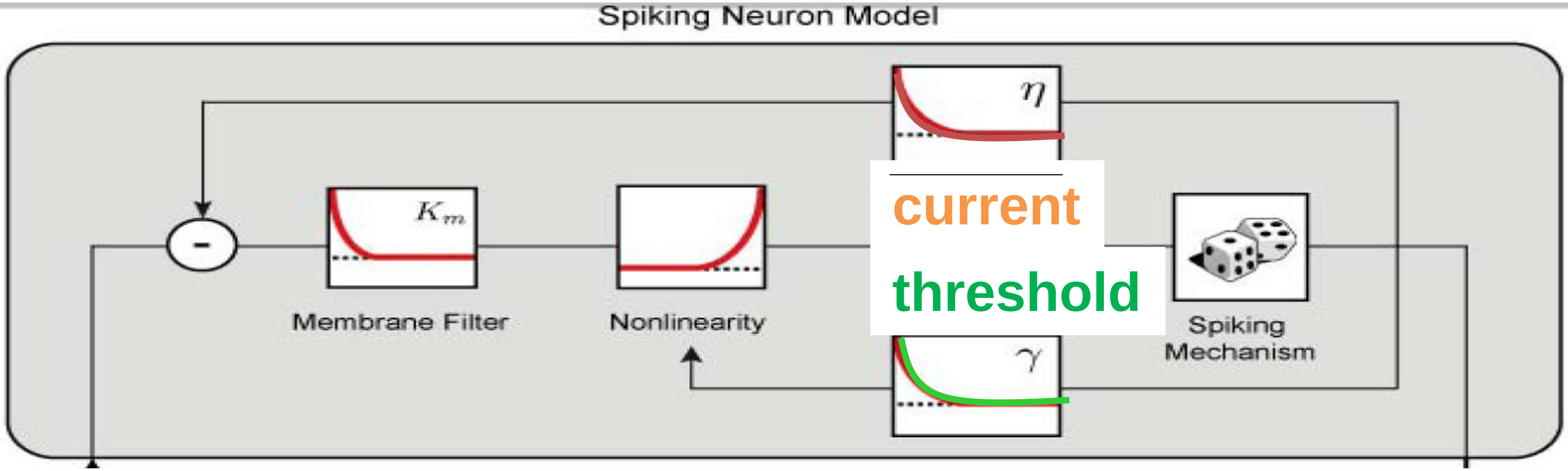
Pozzorini et al. Nat. Neuros, 2013

Week 15-part 1: Predict spike times + voltage with SRM/GLM



Mensi et al. 2012,
Jolivet et al. 2007

Week 15-part 1: Extract parameter for different neuron types



Mensi et al. 2011

Dynamic threshold

Pyramidal N.	Fast Spiking	Non-fast Spiking
Dyn. Threshold VERY IMPORTANT	*Dyn. Threshold unimportant*	***Dyn. Threshold important***

Different neuron types have different parameters

Week 15-part 1: Summary and aims

-We can extract parameters for SINGLE neuron

(see NEURONAL DYNAMICS, Chs. 8-11)

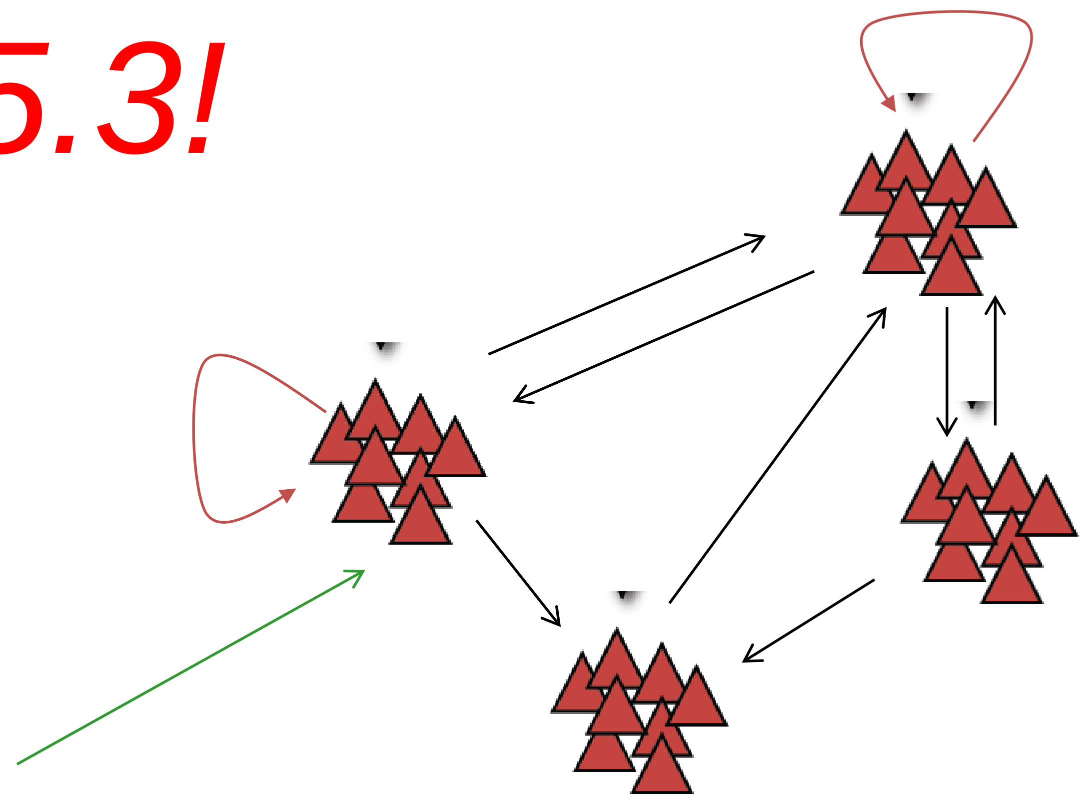
-Different neuron types have different parameters

→ Model Dynamics in one (homogeneous) population

Today, parts 15.2 and 15.3!

→ Couple different populations

Today, parts 15.4!



Sensory input

Eventually: Understand Coding and Brain dynamics

Week 15 – Integral Equation for population dynamics

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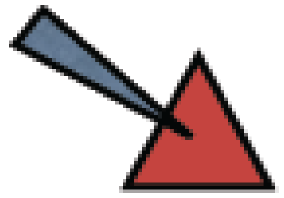
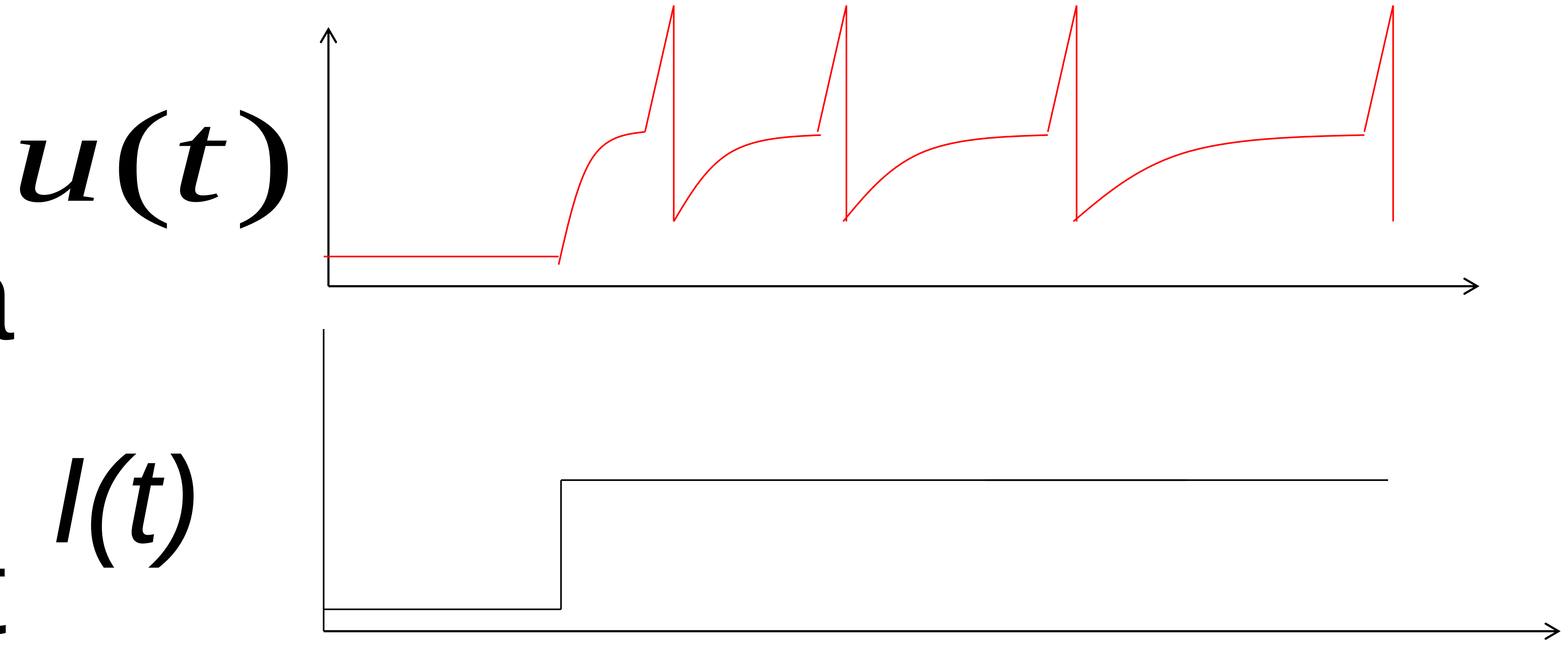
Week 15-part 2: Aim: from single neuron to population

Single neurons



- model exists
- parameters extract rom data
- works well for step rent
- works well for tim current

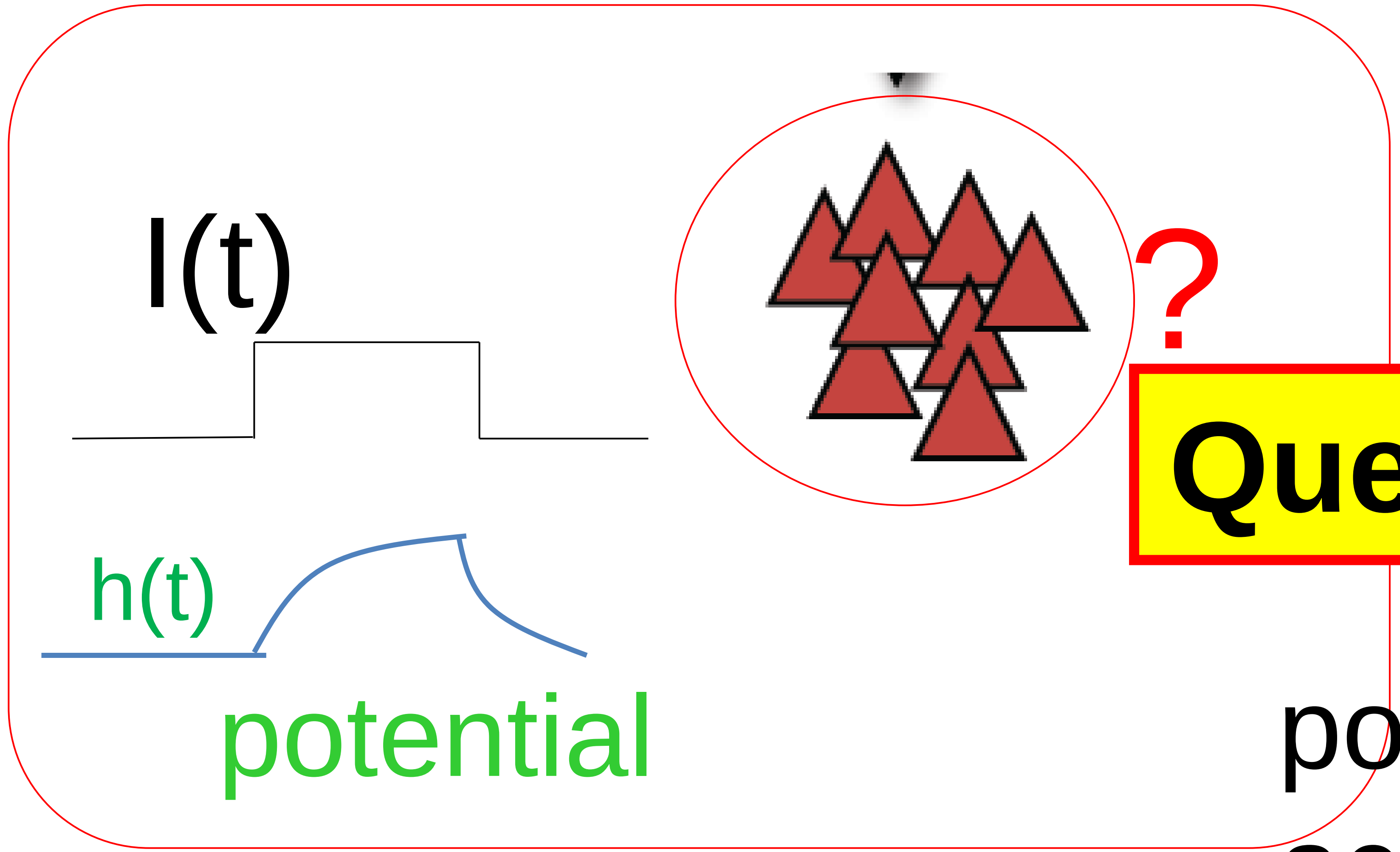


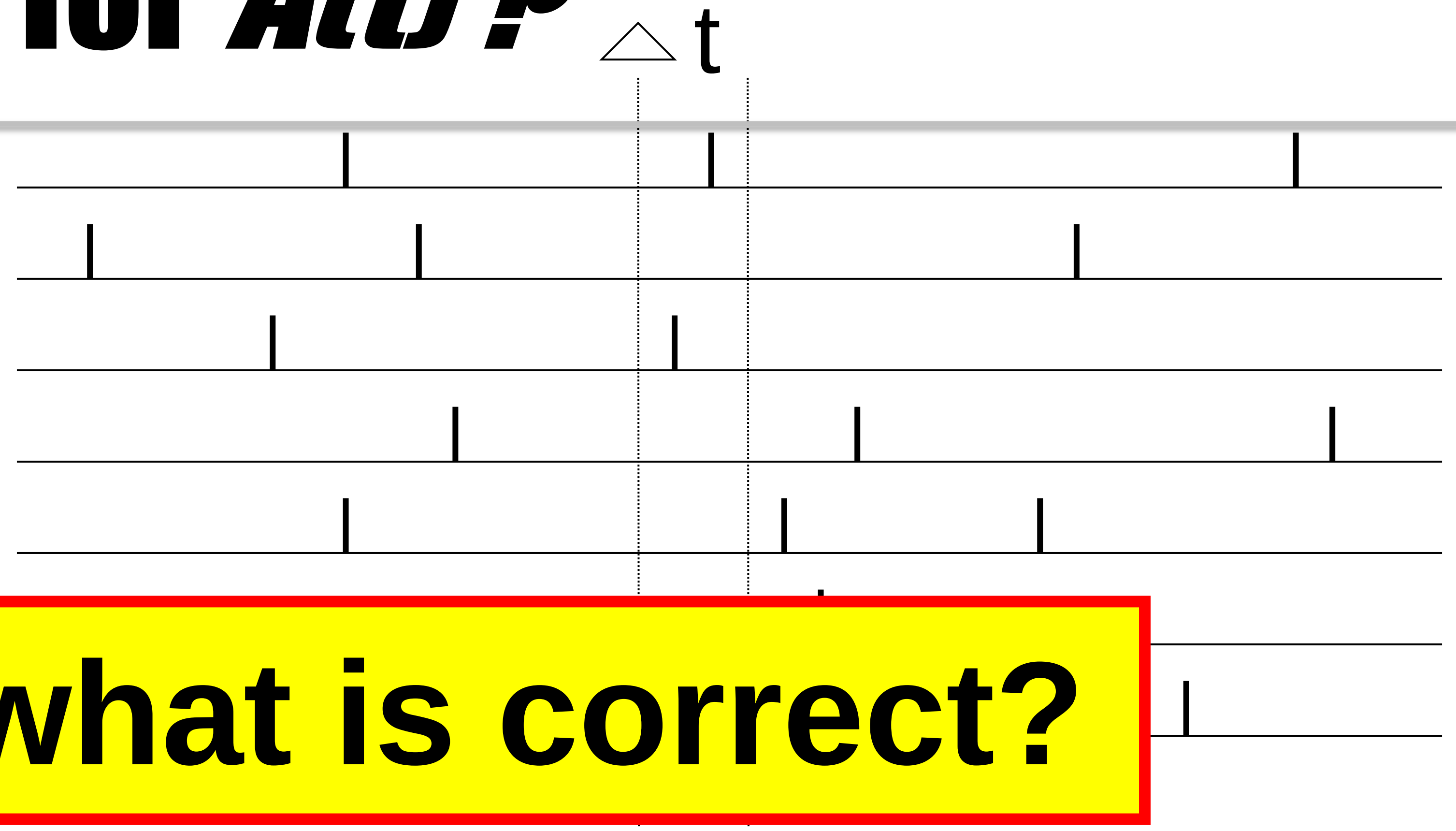
Population of Neurons?

Population equation for *A(t)*

-existing models
- integral equation

Week 15-part 2: population equation for *A(t)*?

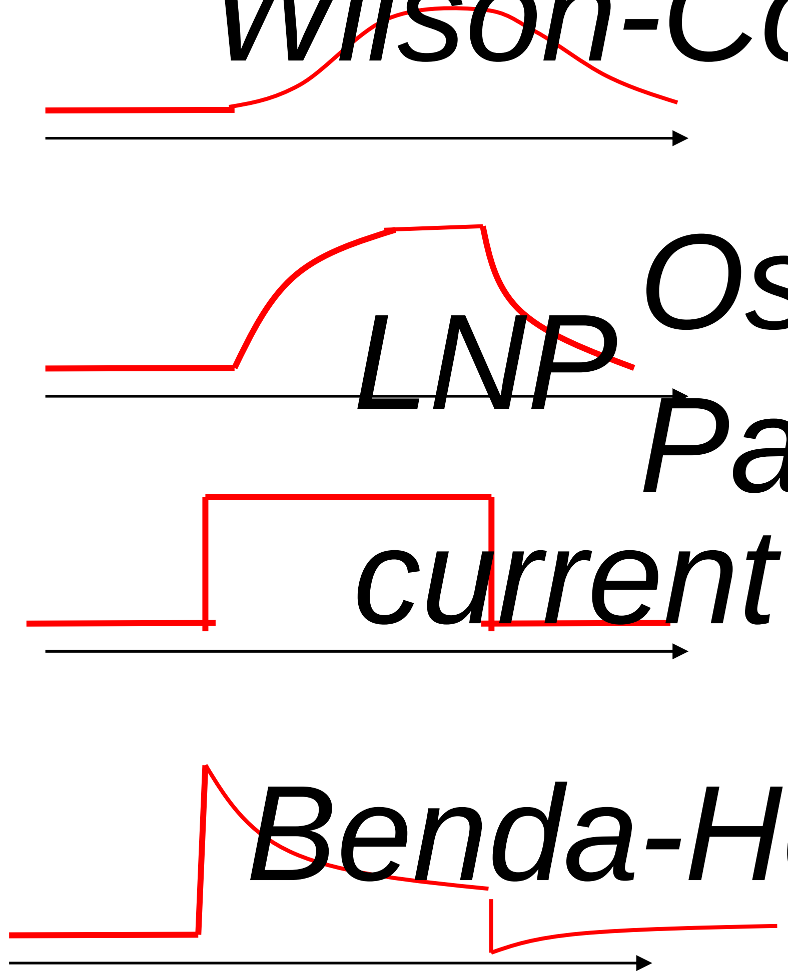




Question: – what is correct?

population activity

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



A(t) Wilson-Cowan $$\tau \frac{d}{dt} A(t) = -A(t) + f(h(t))$$

A(t) LNP Ostojic-Brunel, Paninski, Pillow $$A(t) = f(h(t)) = f\left(\int \varepsilon(s) I(t-s) ds\right)$$

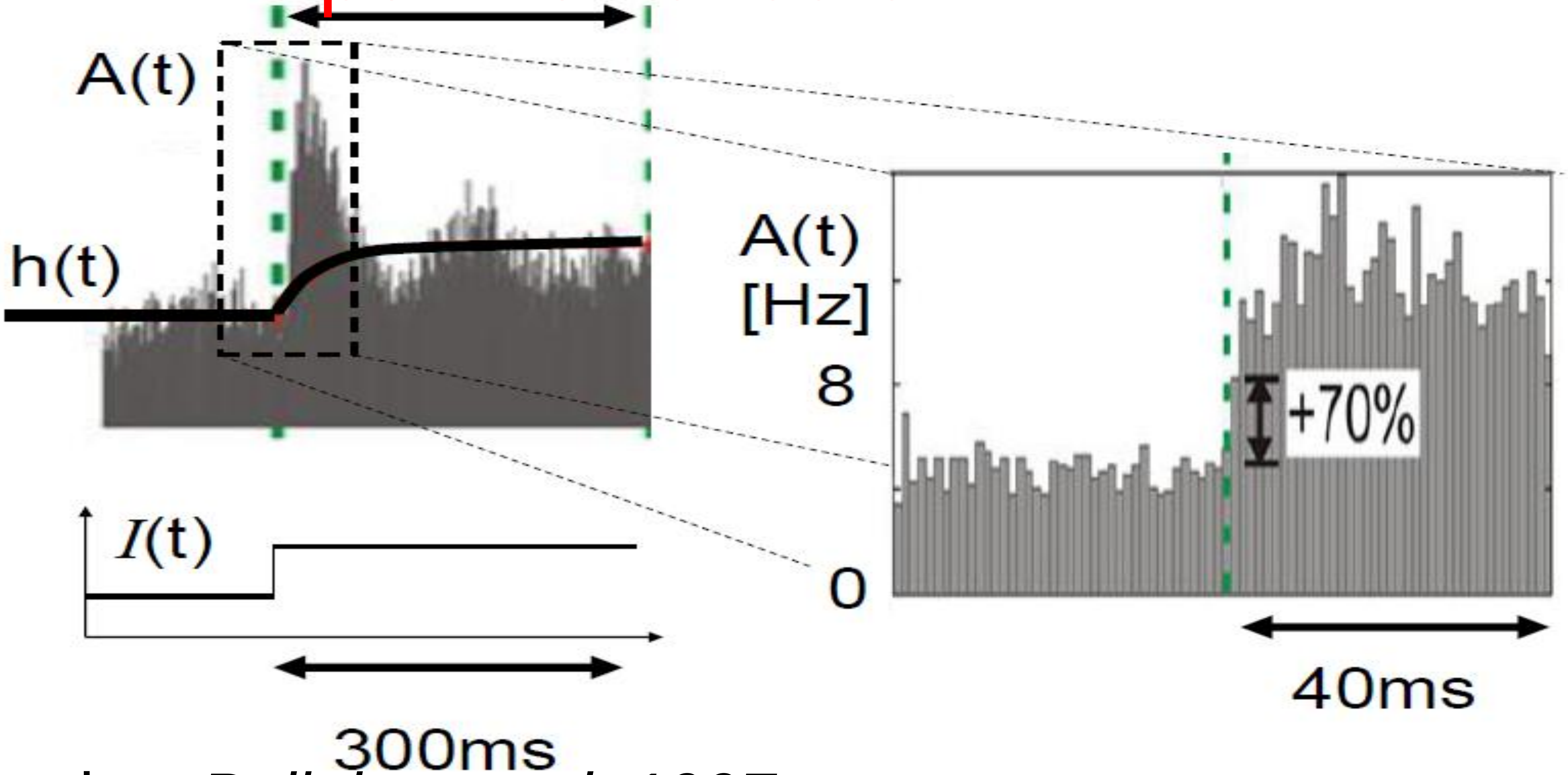
A(t) current $$A(t) = g(I(t))$$

Poll!!!

A(t) Benda-Herz $$A(t) = g\left(I(t) - \int G(s) A(t-s) ds\right)$$

Week 15-part 2: *A(t)* in experiments: step current, (*in vitro*)

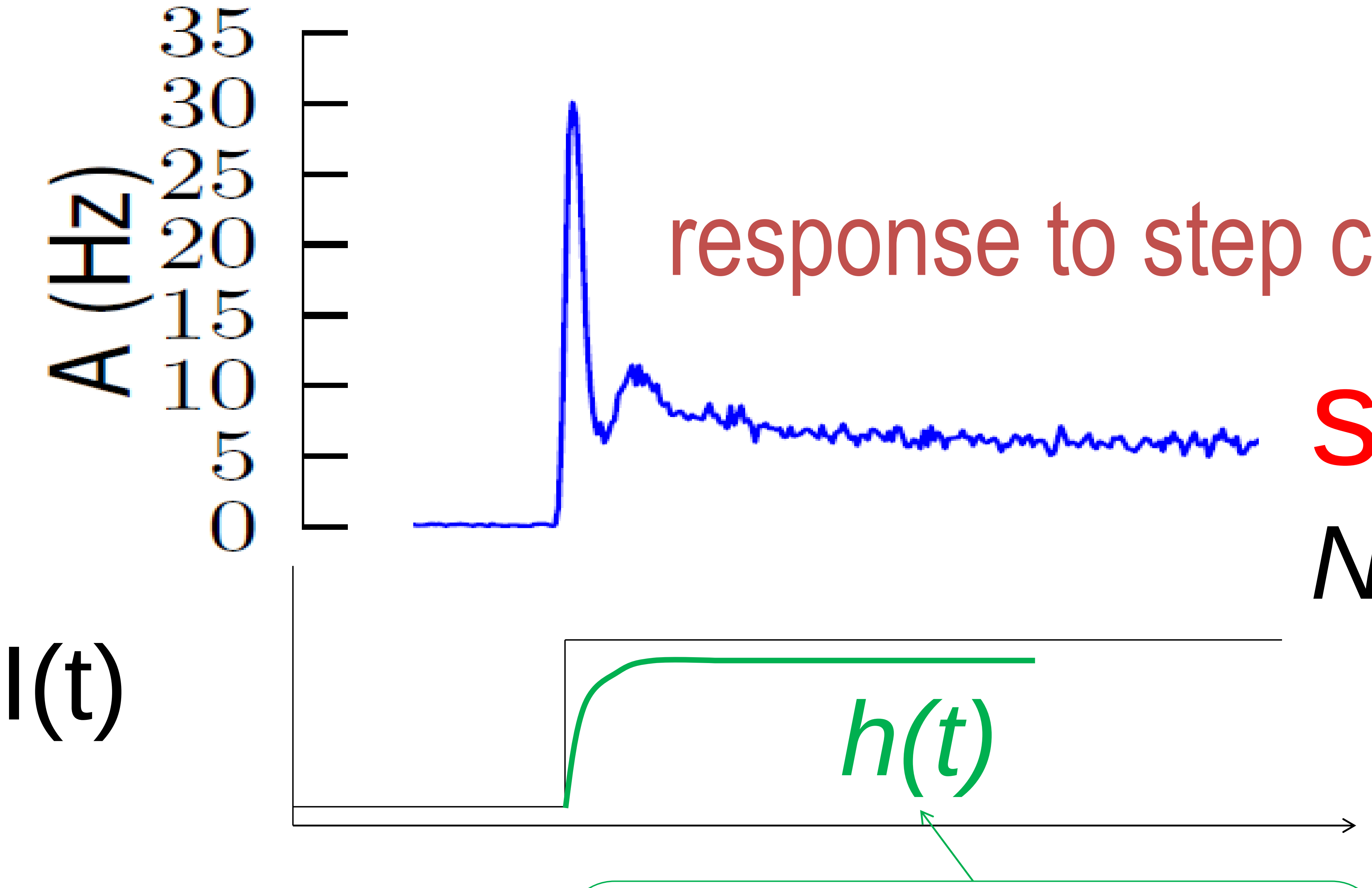
Experimental data: *Tchumatchenko et al. 2011*



See also: *Poliakov et al. 1997*

Week 15-part 2: *A(t)* in simulations : step current

25000 identical model neurons (GLM/SRM with escape noise)
parameters extracted from experimental data



simulation data:
Naud and Gerstner, 2012

potential

$$u(t) = \sum_{t'} \eta(t - t') + \int_0^\infty \varepsilon(s) I(t-s) ds + \ldots$$

Week 15-part 2: *A(t)* in theory: an equation?

Can we write down an equation for *A(t)* ?

Simplification: Renewal assumption

Potential (SRM/GLM) of one neuron

$$u(t) = \sum_{t'} \eta(t - t') + \int_0^\infty \varepsilon(s) I(t-s) ds$$

h(t)

~~Sum over all past spikes~~

Keep only last spike

→ time-dependent renewal theory

Week 15-part 2: Renewal theory (time dependent)

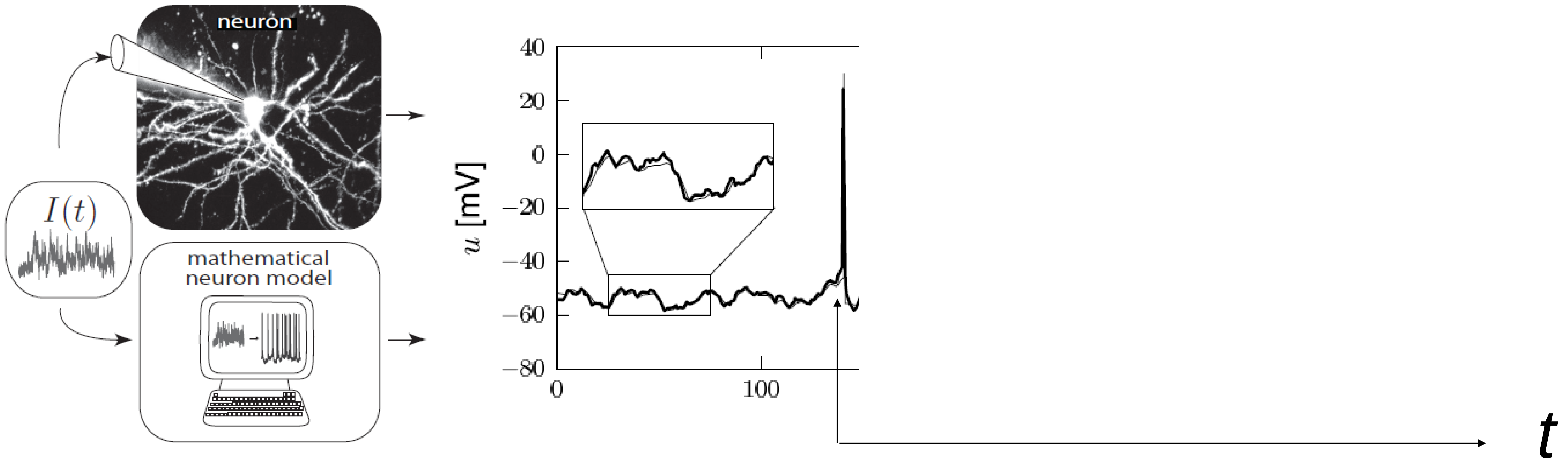
Keep only last spike → time-dependent renewal theory

Potential (SRM/GLM) of one neuron

$$u(t) = \eta(t - \hat{t}) + h(t)$$

last spike

Week 15-part 2: Renewal model –Example



deterministic part of input

$$I(t) \rightarrow u(t)$$

noisy part of input/intrinsic noise

→ *escape rate*

Example:
nonlinear integrate-and-fire model

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

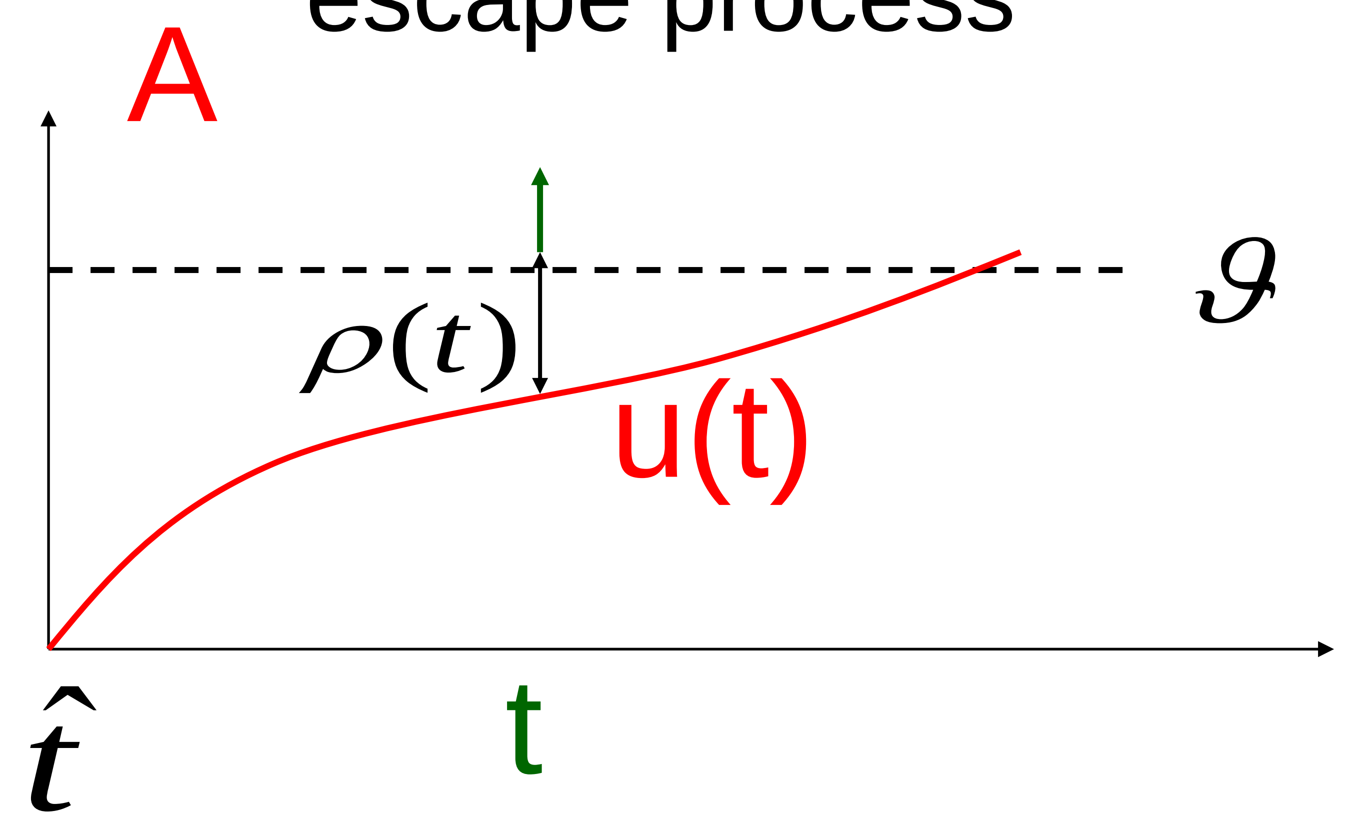
$$\text{if spike at } t^f \Rightarrow u\left(t^f + \delta\right) = u_r$$

Example:
exponential stochastic intensity

$$\rho(t) = f(u(t)) = \rho_\vartheta \exp(u(t) - \vartheta)$$

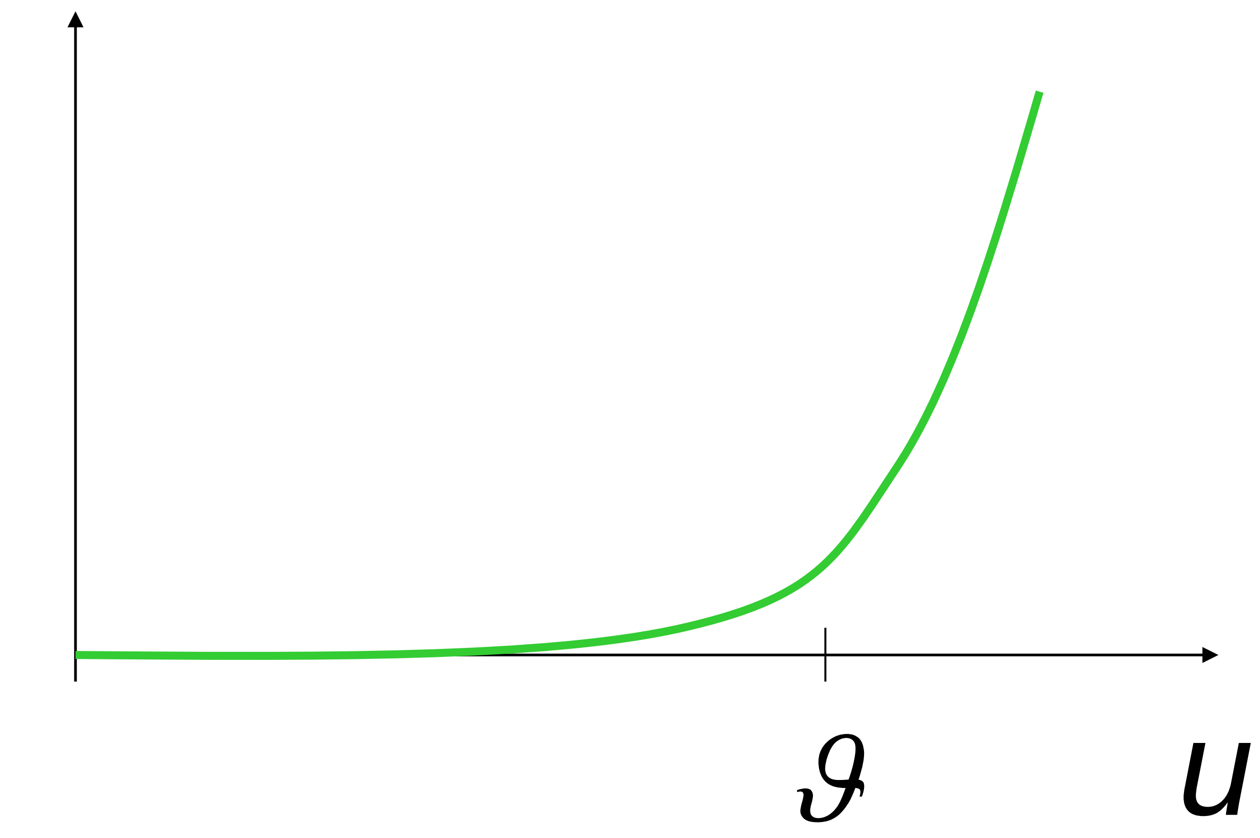
Week 15-part 2: Renewal model - Interspike Intervals

escape process



escape rate

$$\rho(t) = f(u(t) - \vartheta)$$



Survivor function

$$\frac{d}{dt} S_I(t|\hat{t}) = -\rho(t)\, S_I(t|\hat{t})$$

$$S_I(t|\hat{t}) = \exp\left(-\int_{\hat{t}}^{t} \rho(t')\,dt'\right)$$

Interval distribution

$$P_I(t|\hat{t}) = \rho(t) \cdot \exp\left(-\int_{\hat{t}}^{t} \rho(t')\,dt'\right)$$

escape rate

Survivor function

Week 15-part 2: Renewal model – Integral equation

population activity

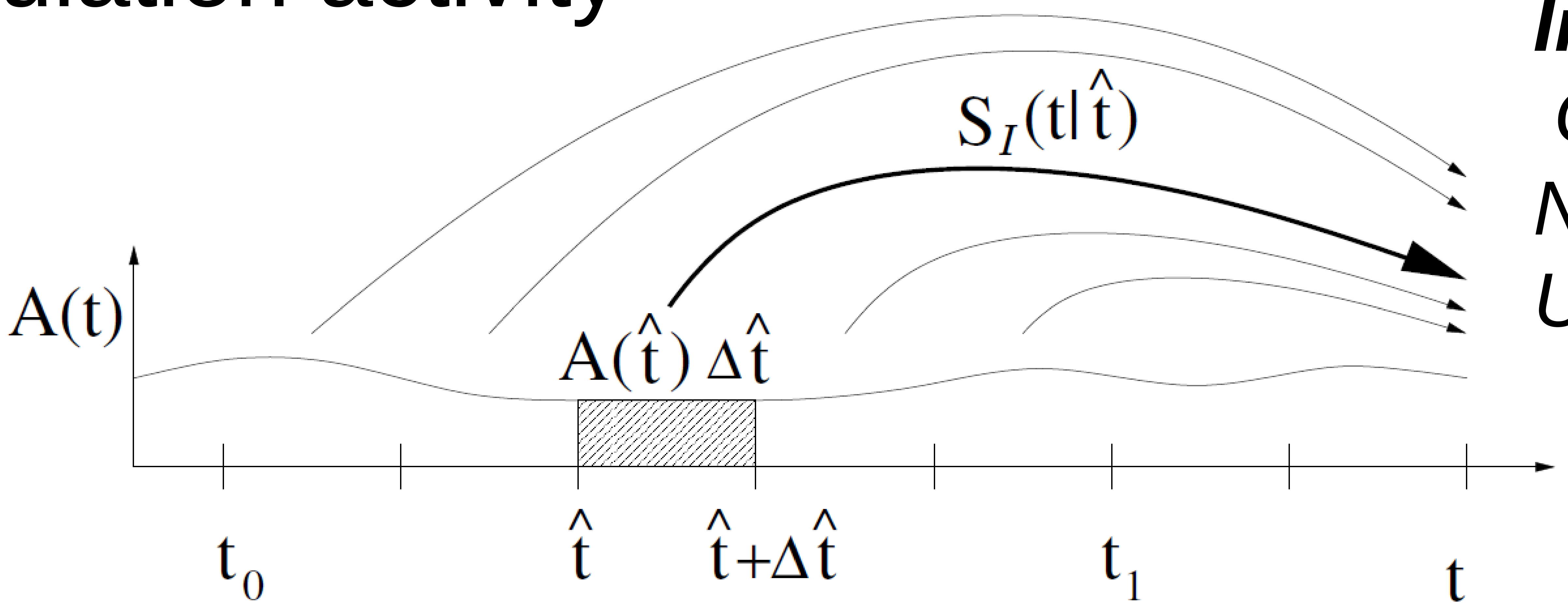


Image:
Gerstner et al., Neuronal Dynamics, Cambridge Univ. Press (2014)

Blackboard!

$$A(t) = \int_{-\infty}^{t} P_I(t|\hat{t})\, A(\hat{t})\, d\hat{t}$$

Interval distribution

$$P_I(t|\hat{t}) = \rho(t) \cdot \exp(-\int_{\hat{t}}^{t} \rho(t')dt')$$

escape rate

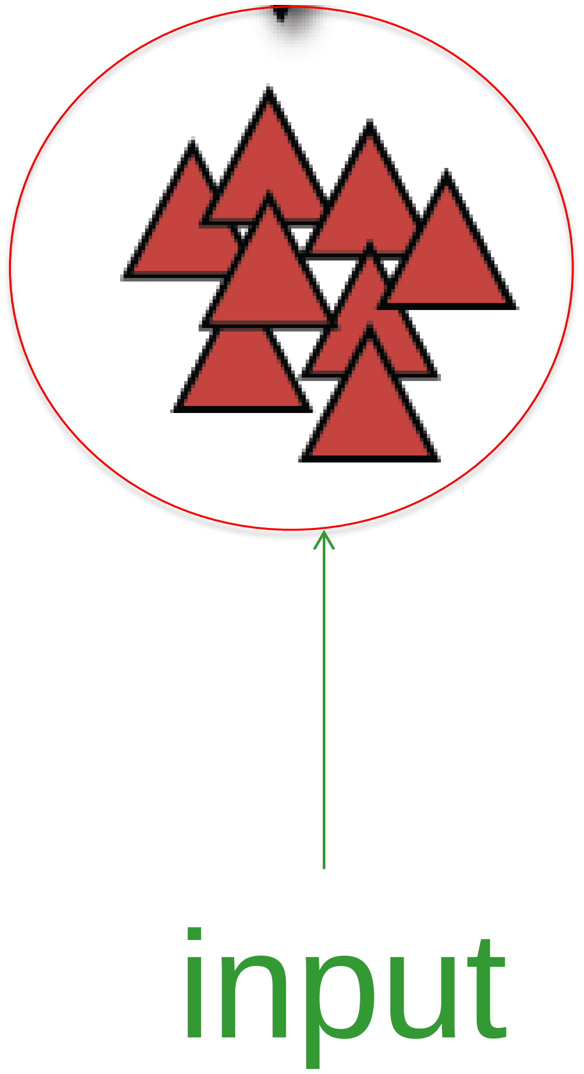
Survivor function

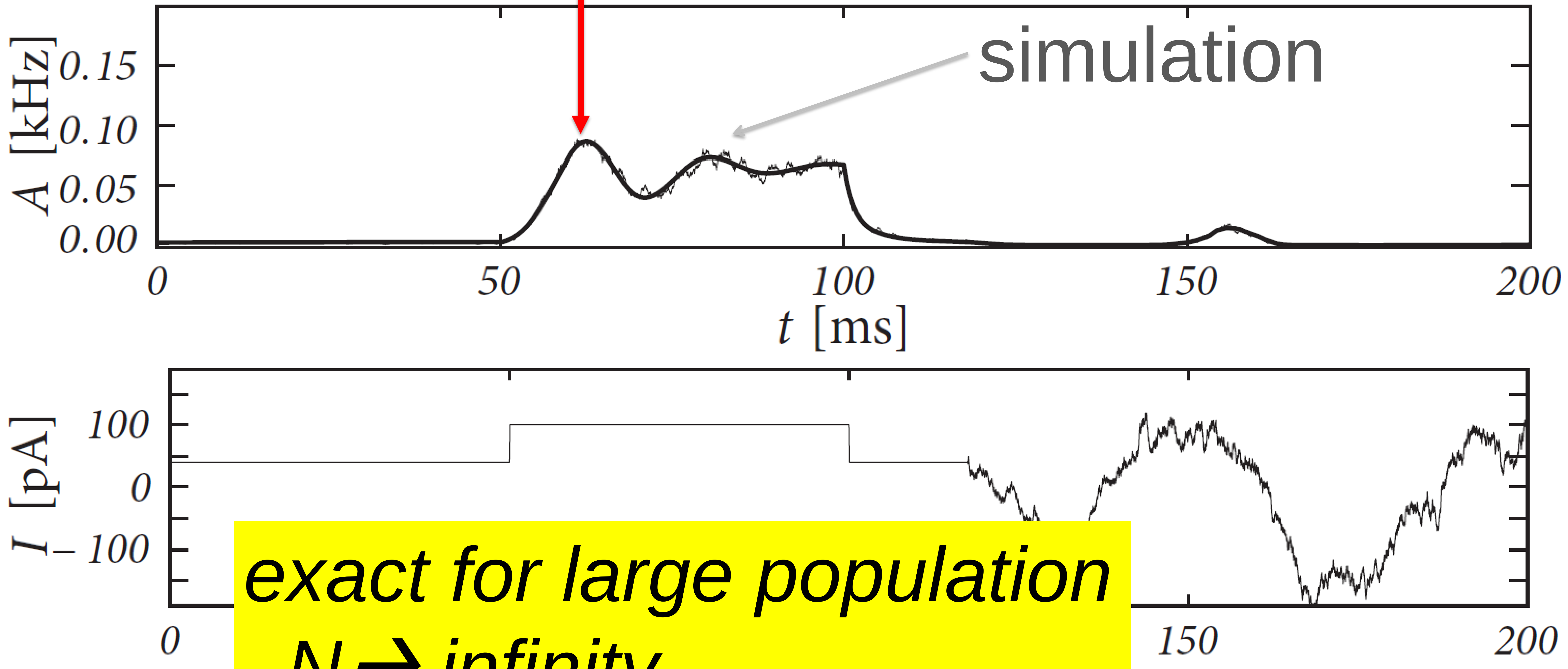
Gerstner 1995, 2000; Gerstner&Kistler 2002
See also: *Wilson&Cowan 1972*

Week 15-part 2: Integral equation – example: LIF

population of
leaky integrate-and-fire
neurons w. escape noise

$$A(t) = \int_{-\infty}^{t} P_I(t|\hat{t})\, A(\hat{t})\, d\hat{t}$$





exact for large population
N → infinity

Image: Gerstner et al., Neuronal Dynamics, Cambridge Univ. Press

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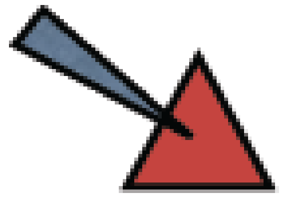
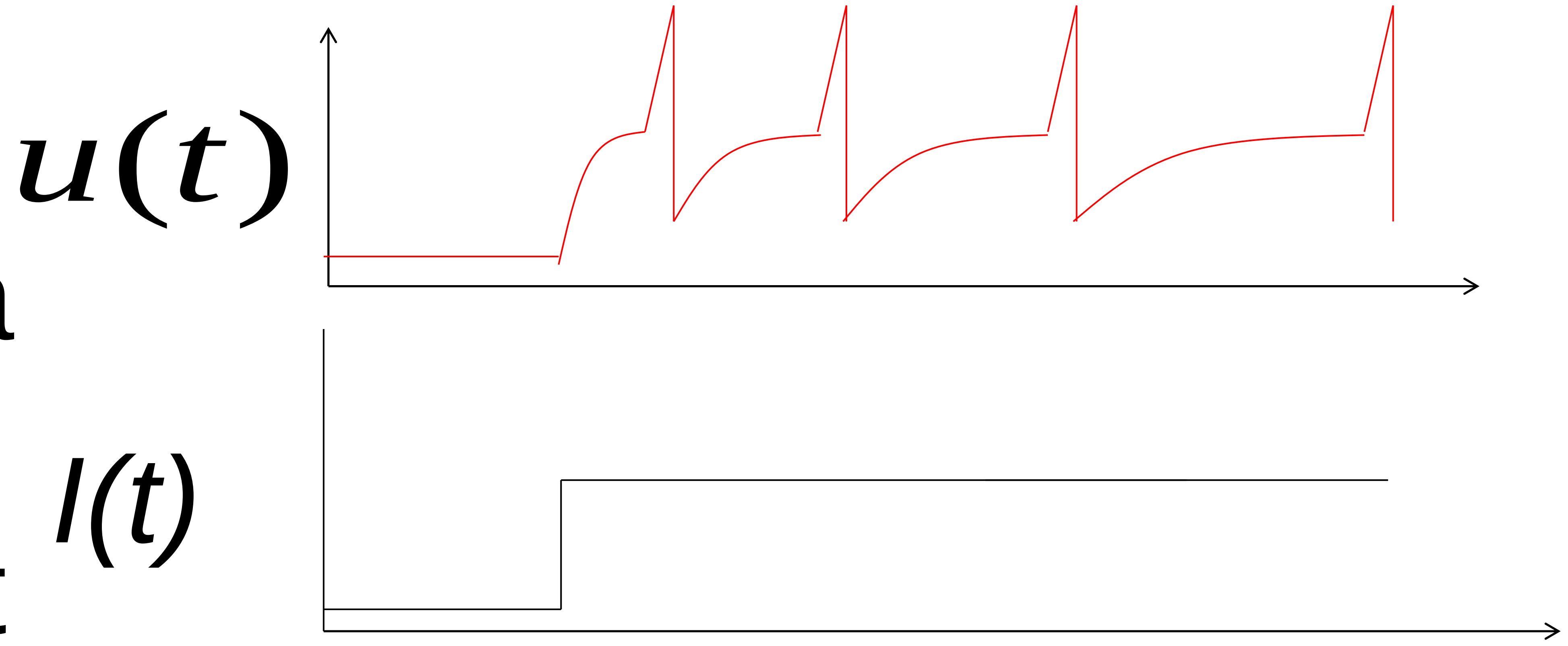
Week 15-part 3: Neurons with adapation

Real neurons show adapation on multipe time scales

Single neurons



- model exists
- parameters extract rom data
- works well for step rent
- works well for tim current

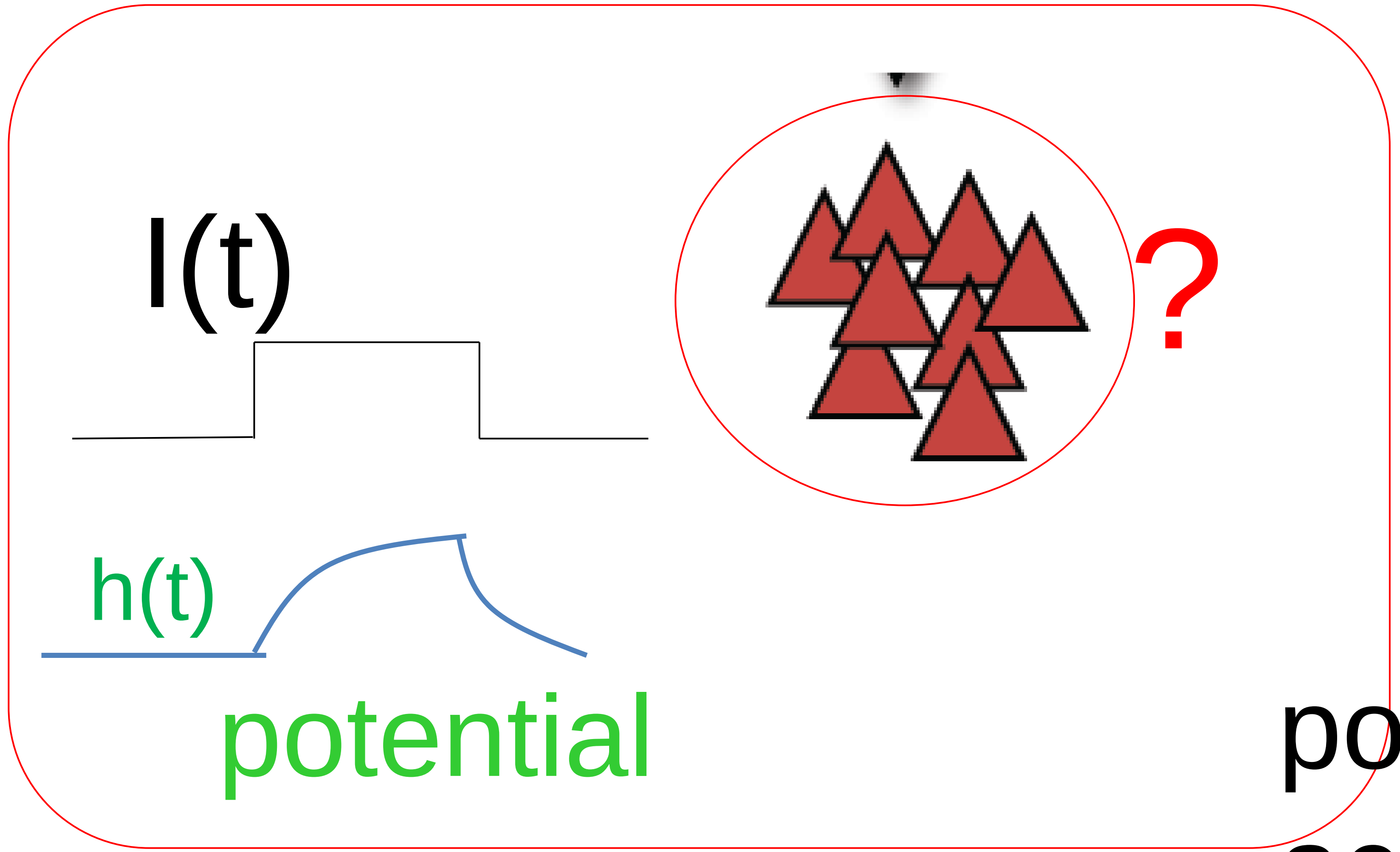


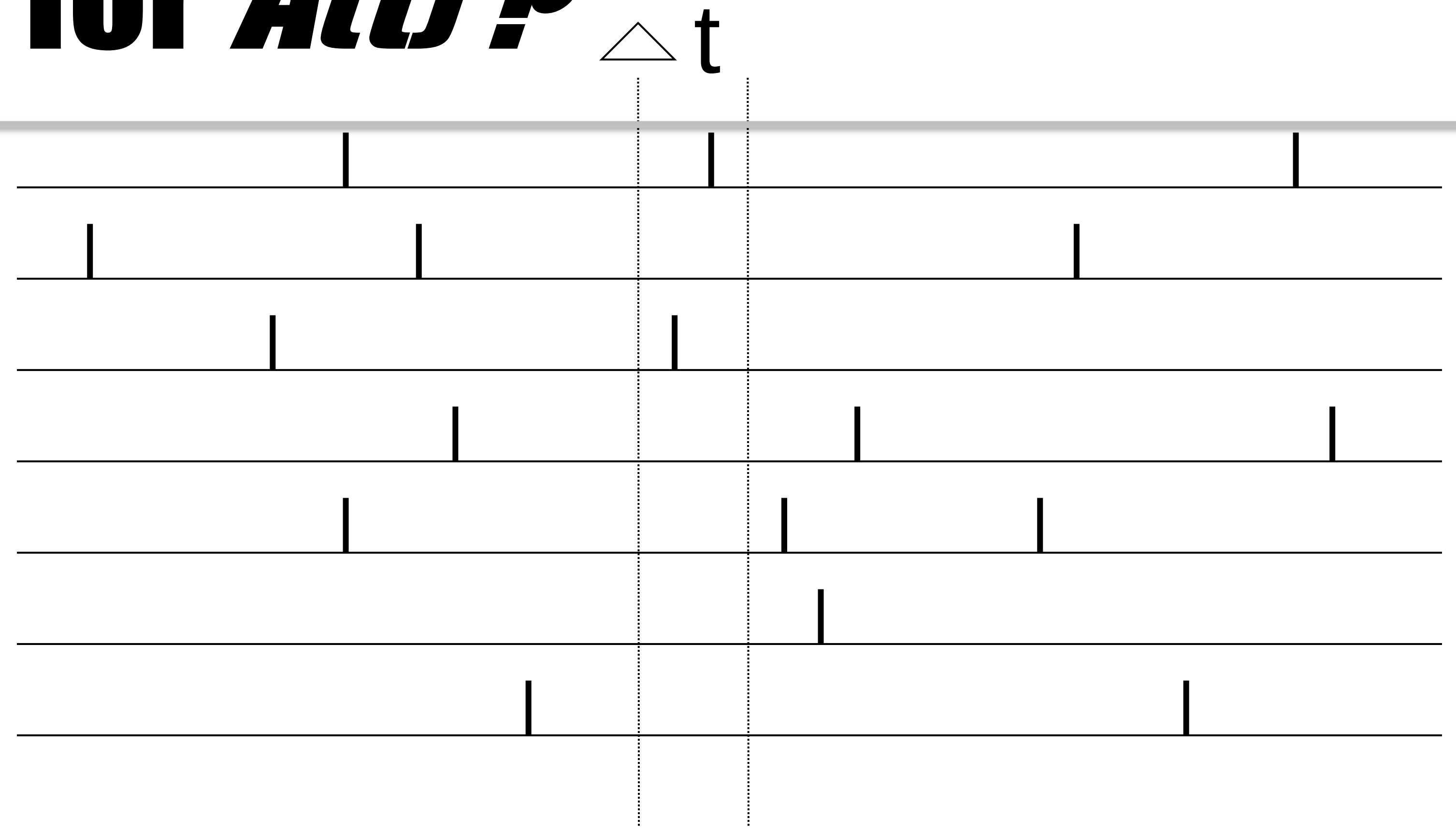
Population of adapting Neurons?

Population equation for *A(t)*

- existing modes
- integral equation

Week 15-part 3: population equation for *A(t)* ?





population activity

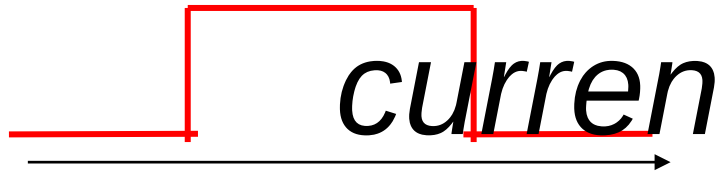
$$A(t) = \frac{n(t;t+\Delta t)}{N\Delta t}$$

A(t)  *Wilson-Cowan*

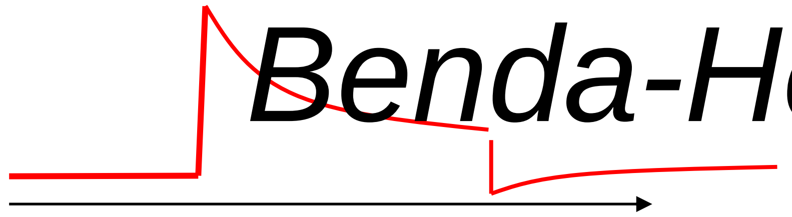
$$\tau \frac{d}{dt} A(t) = -A(t) + f(h(t))$$

A(t)  *LNP*

$$A(t) = f(h(t)) = f(\int \varepsilon(s) I(t-s) ds)$$

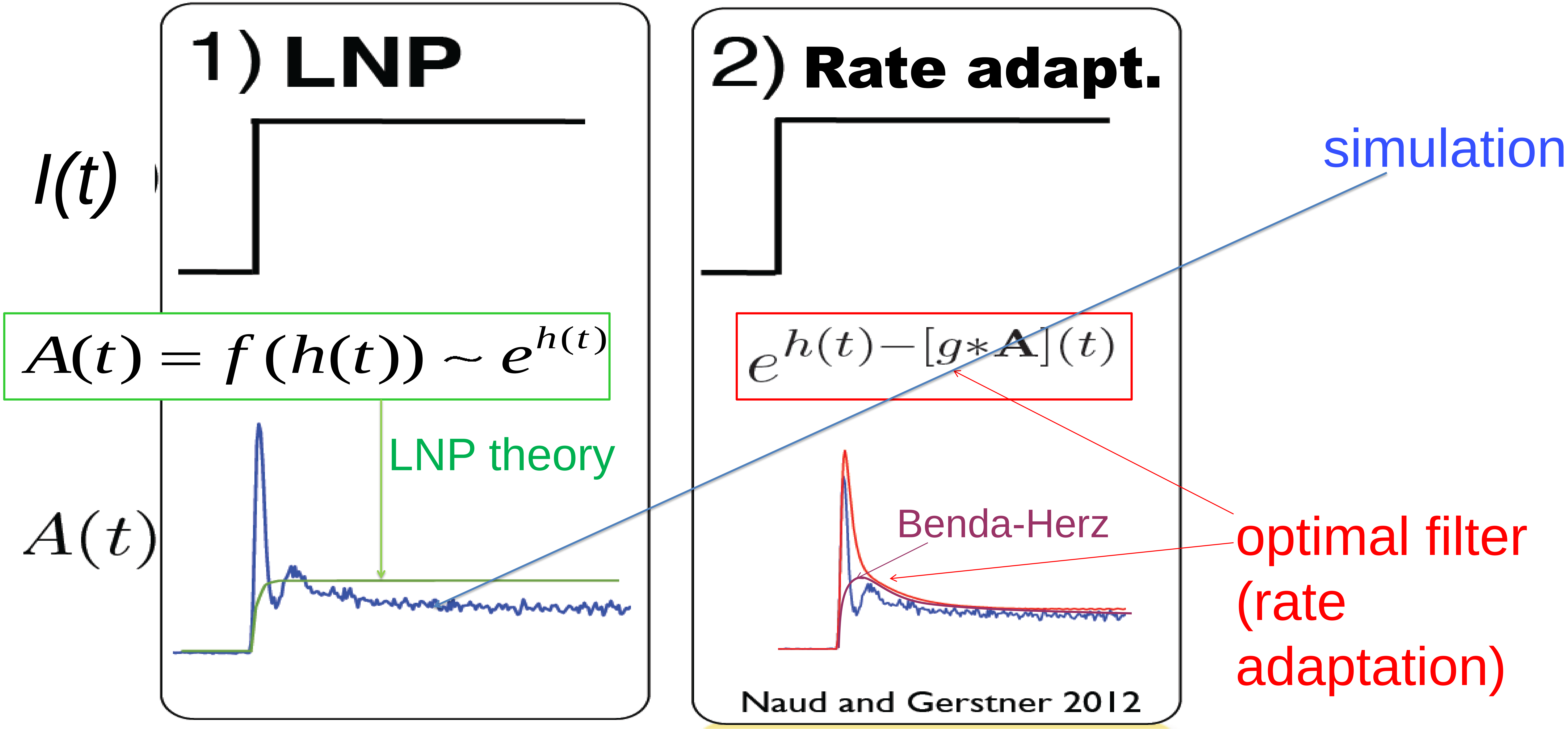
A(t)  *current*

$$A(t) = g(I(t))$$

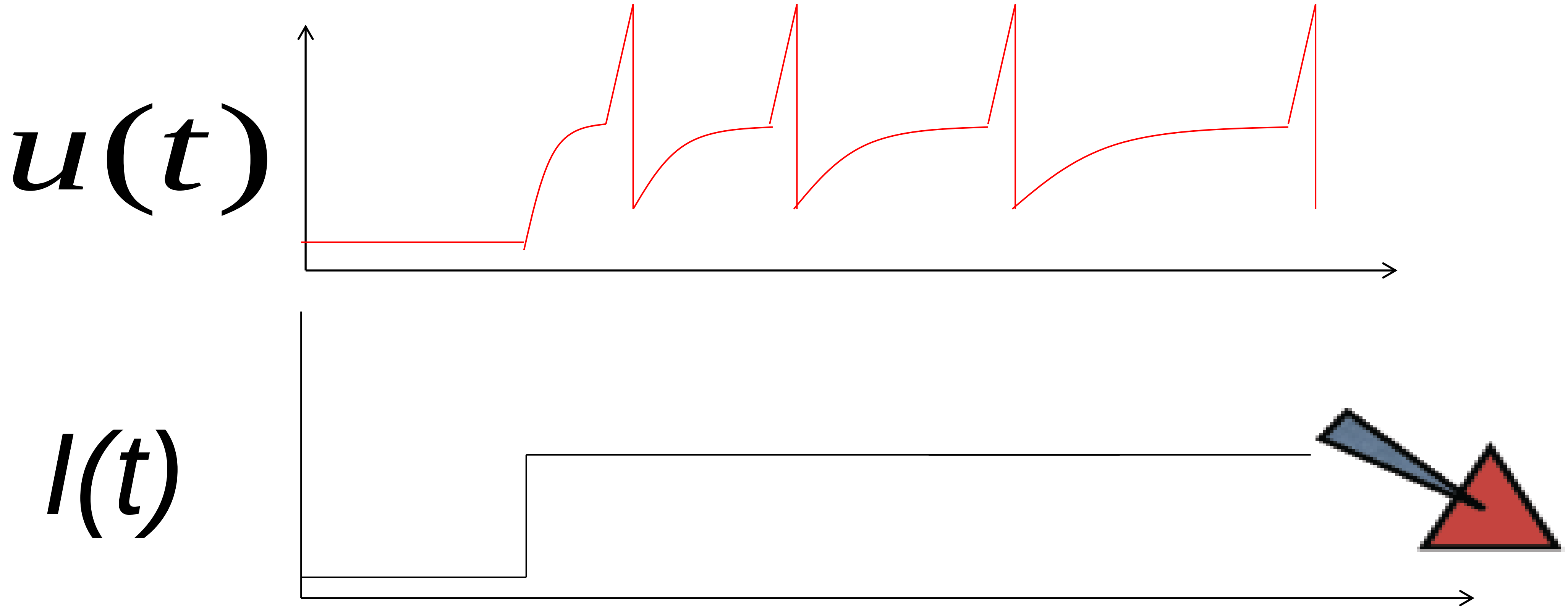
A(t)  *Benda-Herz*

$$A(t) = g(I(t) - \int G(s) A(t-s) ds)$$

Week 15-part 3: neurons with adaptation – *A(t)*?



Week 15-part 3: population equation for adapting neurons?



Population of
Adapting Neurons?

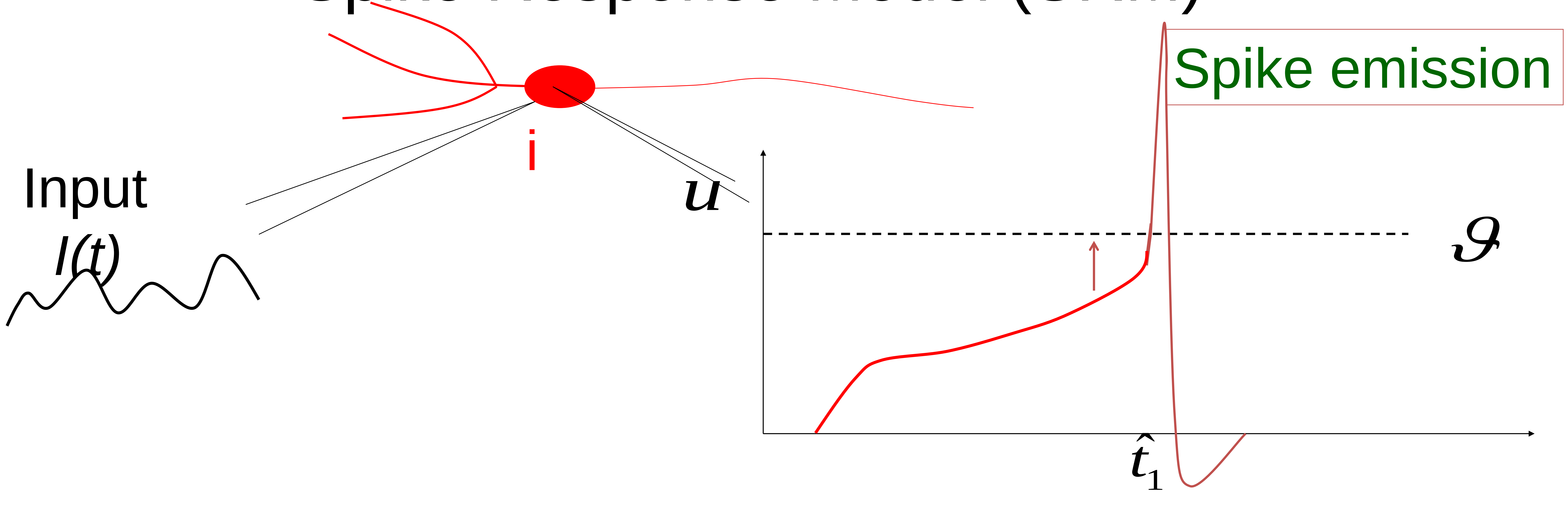
1) Linear-Nonlinear-Poisson (LNP): ***fails!***

2) Phenomenological rate adaptation: ***fails!***

3) Time-Dependent-Renewal Theory ?

→ Integral equation of previous section

Spike Response Model (SRM)



potential

$h(t)$

$$u(t) = \sum_{\hat{t}} \eta(t-\hat{t}) + \int_0^\infty \varepsilon(s) I(t-s) ds + \ldots$$

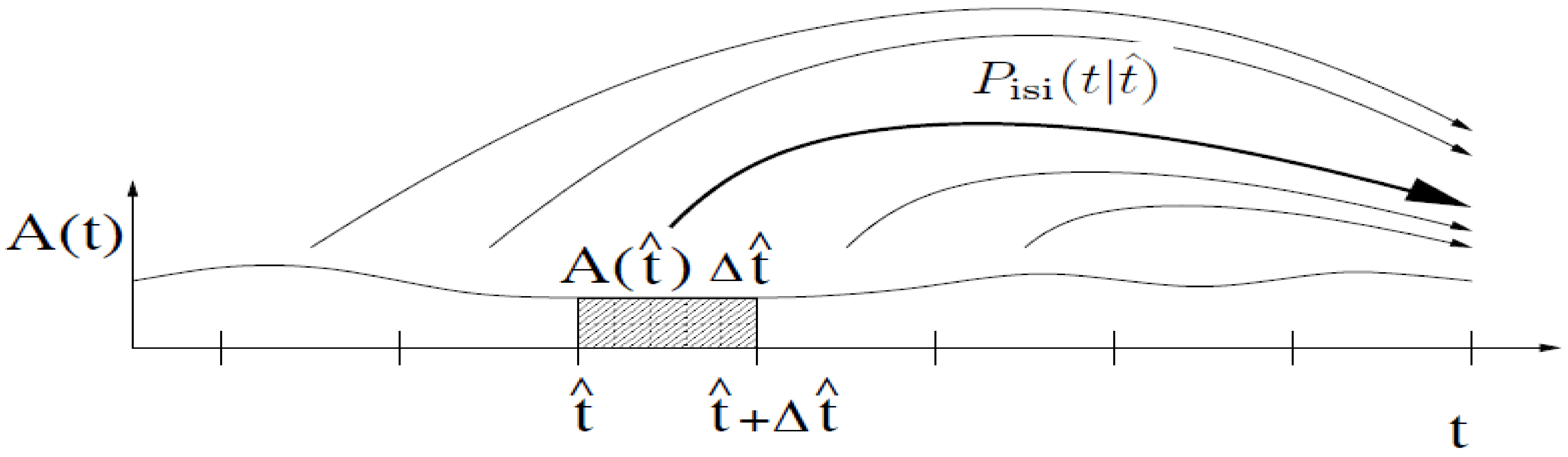
$$\Pr\{\, fire\, in [t; t+\Delta t]\} = \lambda(t)\Delta t = f[u(t) - \vartheta(t)]\Delta t$$

$$\lambda(t) = \lambda(t \mid h(t))$$

Time-dependent **Renewal** theory

Renewal assumption: $\lambda(t \mid h(t), \hat{t}_1, \hat{t}_2, \hat{t}_3, \ldots) \approx \lambda(t \mid h(t), \hat{t})$

last firing time



$$A(t) = \int P_{isi}(t \mid h, \hat{t})\, A(\hat{t})\, d\hat{t}$$

Gerstner 1995, 2000; Gerstner&Kistler 2002
See also: *Wilson&Cowan 1972*

interspike interval distribution

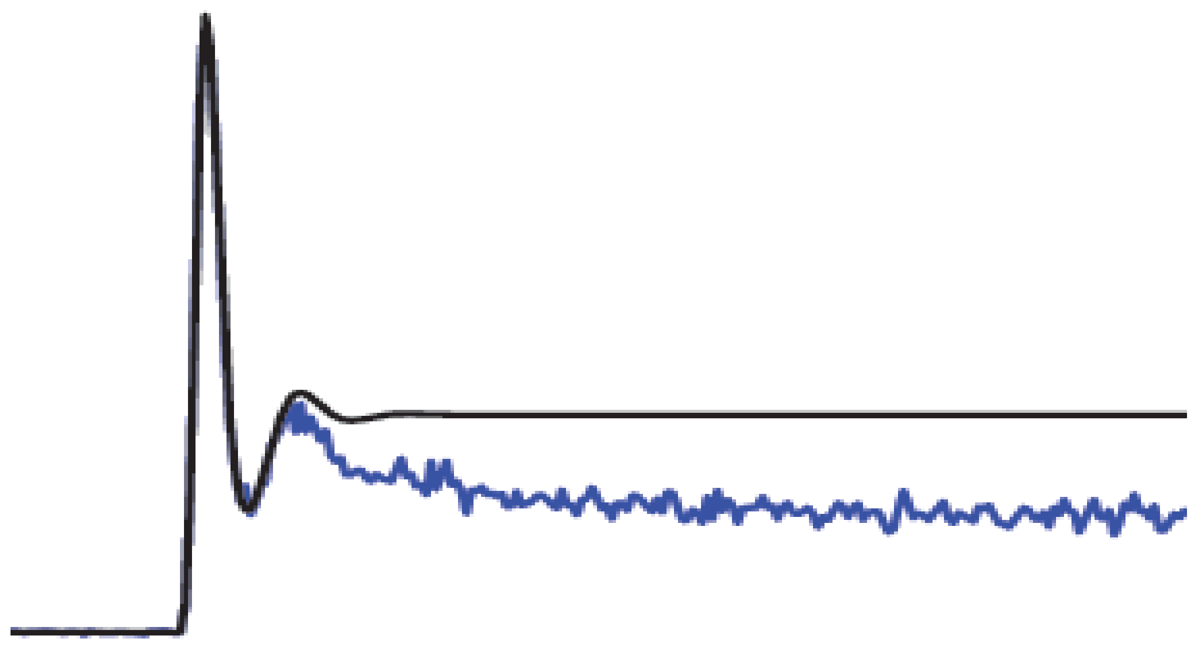
$$P_{\rm isi}(t|\hat{t}) = \lambda(t|\hat{t})\, e^{-\int_{\hat{t}}^{t} \lambda(x|\hat{t})\,dx}$$

Cox 1962

Week 15-part 3: population equation for adapting neurons?

3) Renewal

$$\int_{-\infty}^{t} A(t')\,P_{\mathrm{isi}}(t|t',\mathbf{h})\,dt'$$



Gerstner 1995

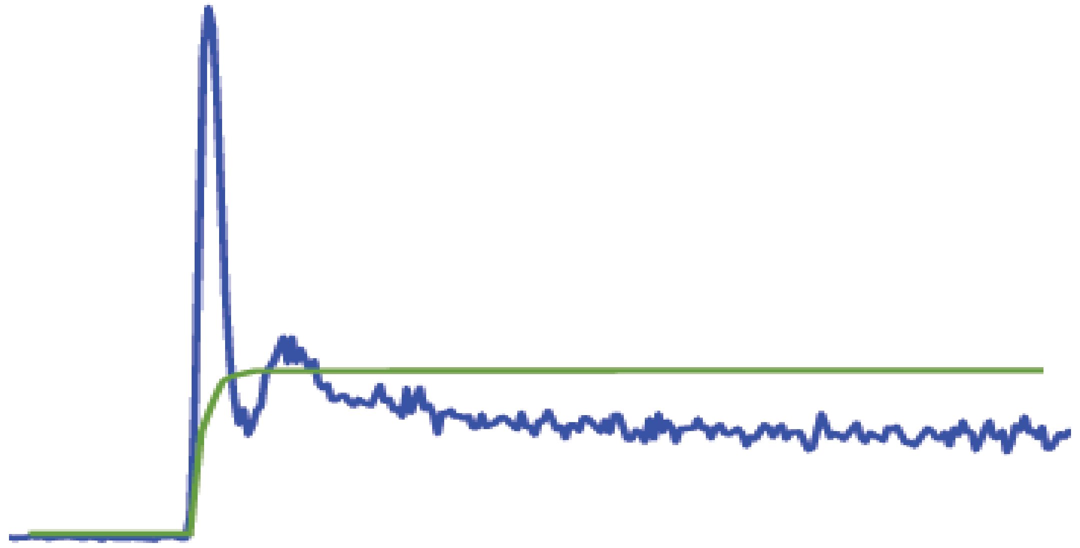
Week 15-part 3: population equation for adapting neurons?

1) LNP

$I(t)$

$A(t) \sim e^{h(t)}$

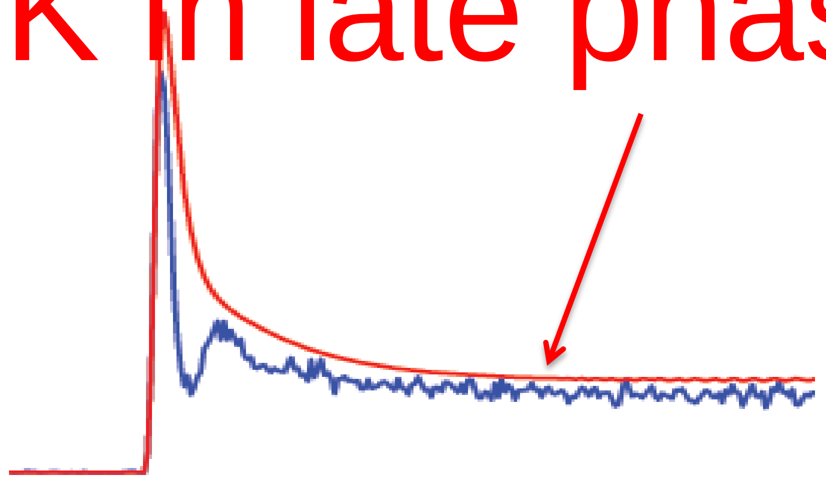
$A(t)$



2) Rate adapt.

$e^{h(t) - [g * \mathbf{A}](t)}$

OK in late phase

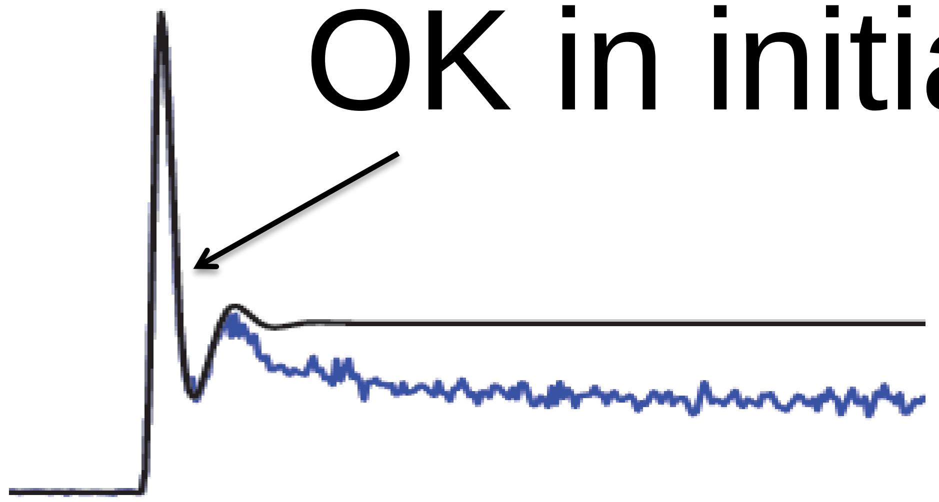


Benda and Herz 2003
Naud and Gerstner 2012

3) Renewal

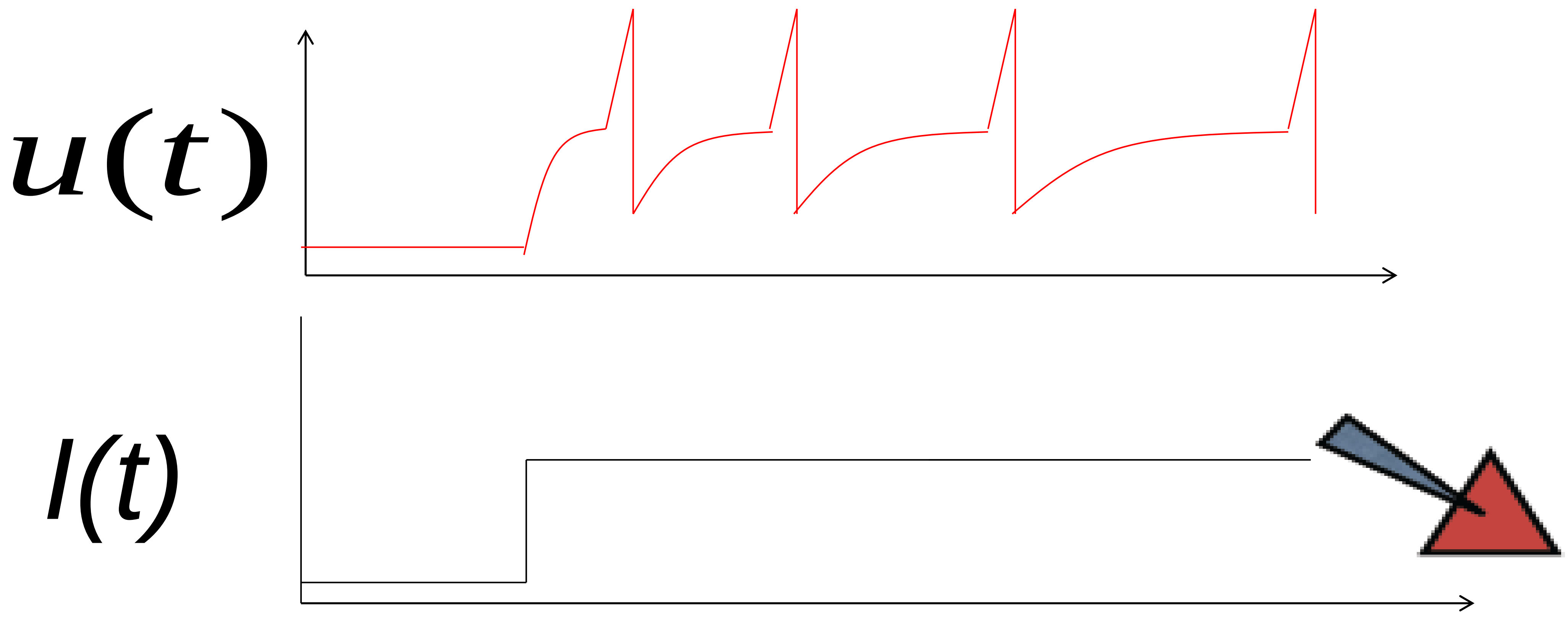
$\int_{-\infty}^{t} A(t') P_{\text{isi}}(t|t', \mathbf{h}) dt'$

OK in initial phase



Gerstner 1995

Week 15-part 3: population equation for adapting neurons



Population of Adapting Neurons

1) Linear-Nonlinear-Poisson (LNP): ***fails!***

2) Phenomenological rate adaptation: ***fails!***

3) Time-Dependent-Renewal Theory: ***fails!***

4) Quasi-Renewal Theory!!!

Week 15-part 3: Quasi-renewal theory

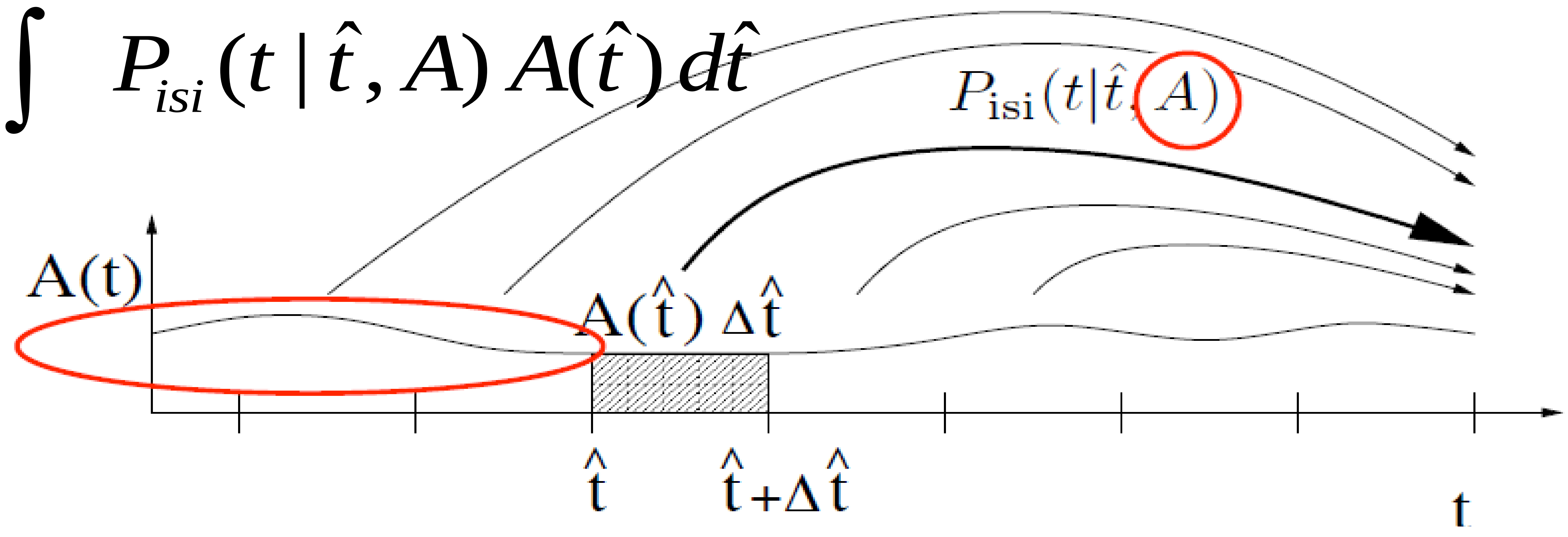
Quasi-Renewal assumption:

$$\lambda(t \mid h(t), \hat{t}_1, \hat{t}_2, \hat{t}_3, \ldots) \approx \lambda(t \mid \hat{t}, A)$$

and

h(t)

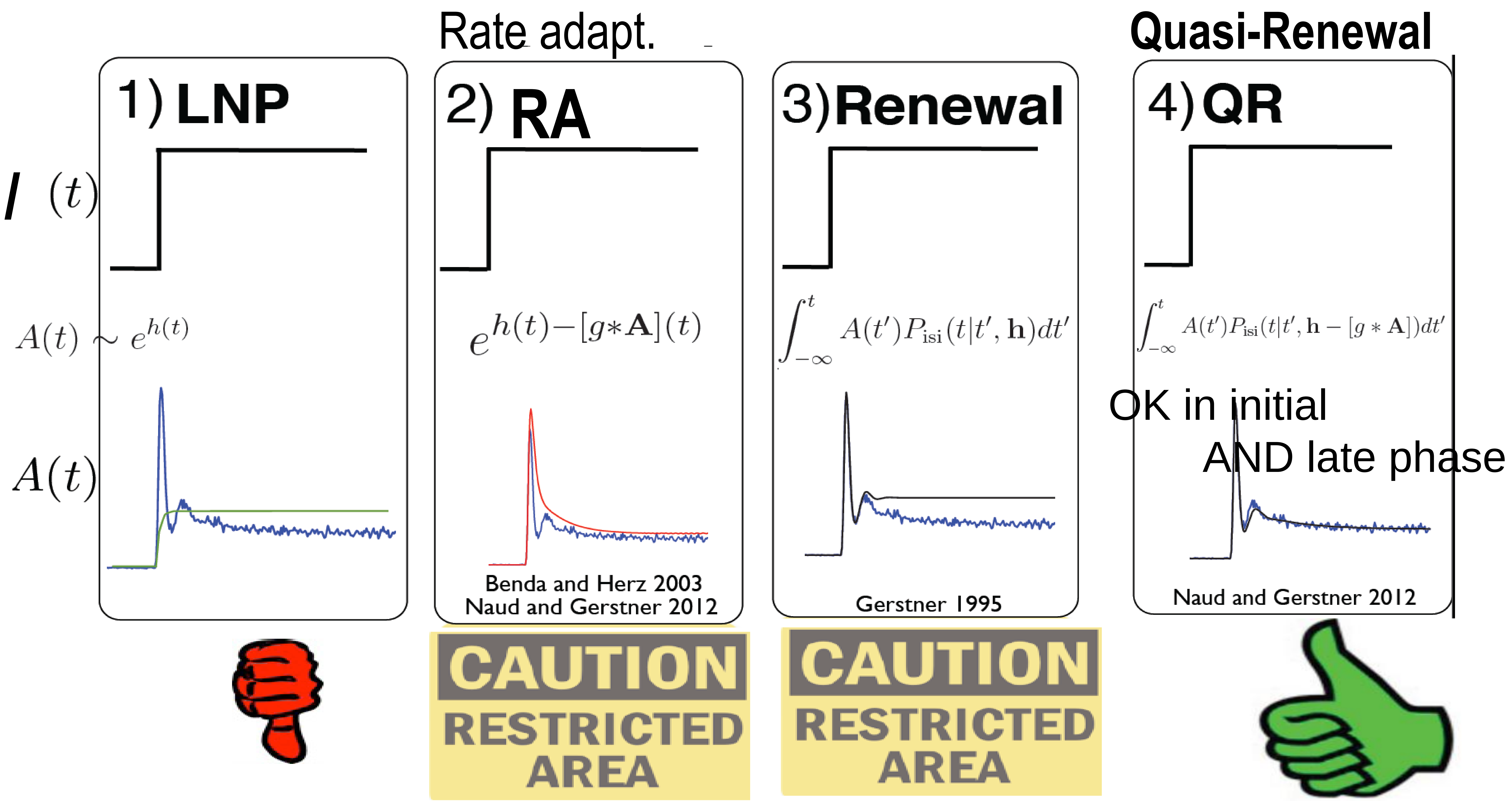
$$A(t) = \int P_{isi}(t \mid \hat{t}, A)\, A(\hat{t})\, d\hat{t}$$



Expand the moment generating functional

Blackboard!

$$\lambda(t|\hat{t}, A) = \lambda_0 e^{h(t)+\eta(t-\hat{t}) - \int_{-\infty}^{\hat{t}} \underbrace{(1-\exp(\eta(t-s)))}_{g(t-s)} A(s)ds}$$


Rate adapt.
Quasi-Renewal
1) LNP
2) RA
3) Renewal
4) QR
$I(t)$
$A(t) \sim e^{h(t)}$
$e^{h(t)-[g*\mathbf{A}](t)}$
$\int_{-\infty}^{t} A(t')P_{\mathrm{isi}}(t|t',\mathbf{h})dt'$
$\int_{-\infty}^{t} A(t')P_{\mathrm{isi}}(t|t',\mathbf{h}-[g*\mathbf{A}])dt'$
$A(t)$
OK in initial
AND late phase
Benda and Herz 2003
Naud and Gerstner 2012
Gerstner 1995
Naud and Gerstner 2012
CAUTION
RESTRICTED
AREA
CAUTION
RESTRICTED
AREA

Week 15-part 3: Quasi-renewal theory

$$\lambda(t\,|\,h(t),\hat{t}_1,\hat{t}_2,\hat{t}_3,\ldots) \approx \lambda(t\,|\,\hat{t},A) \longrightarrow A(t) = \int P_{isi}(t\,|\,\hat{t},A)\,A(\hat{t})\,d\hat{t}$$

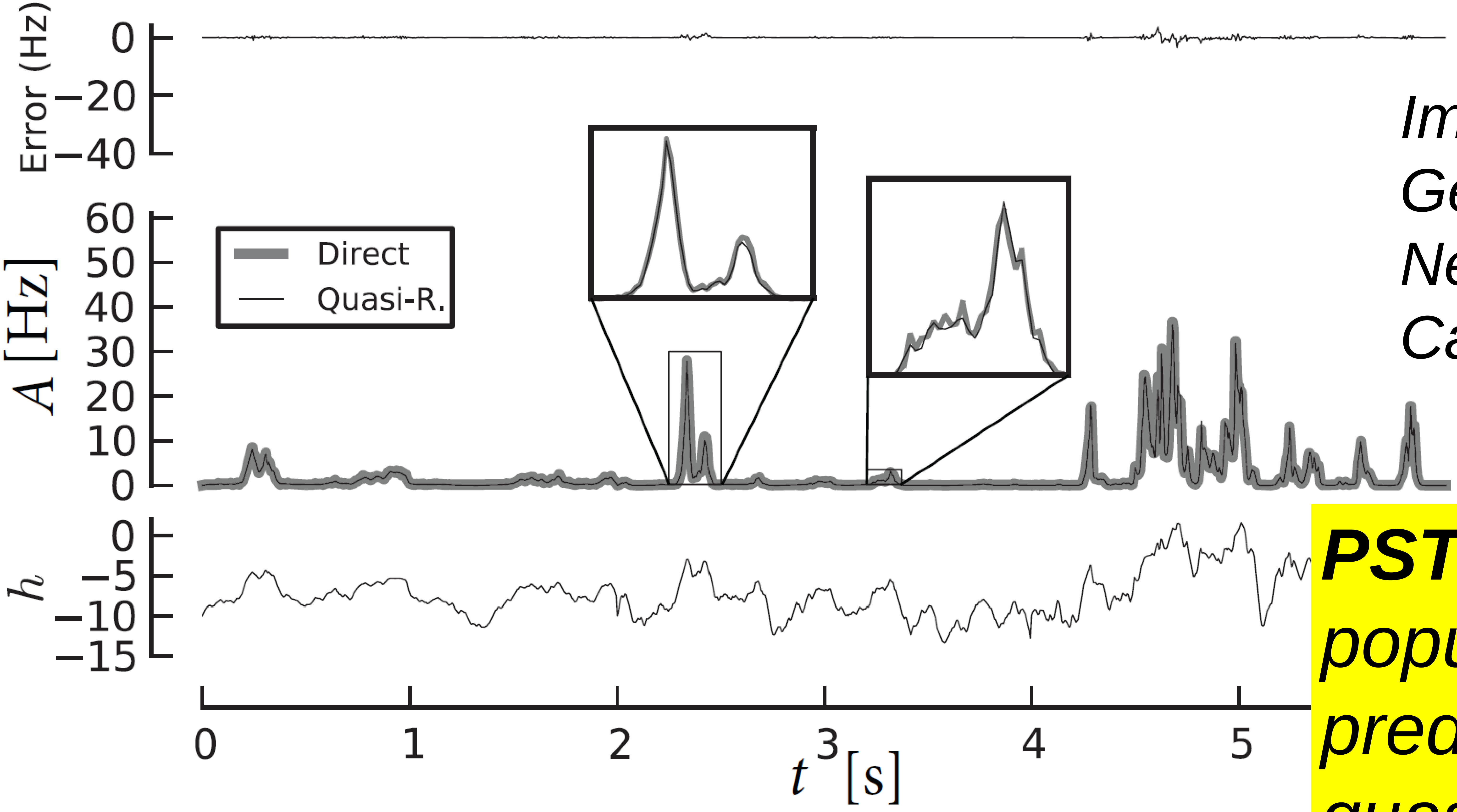
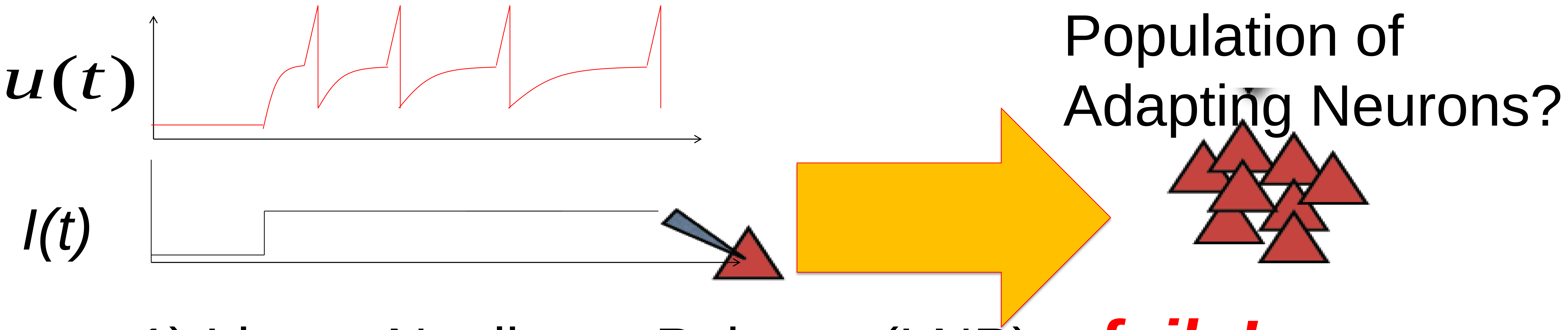


Image: Gerstner et al., Neuronal Dynamics, Cambridge Univ. Press

***PSTH** or population activity **A(t)** predicted by quasi-renewal theory*

Week 15-part 3: population equation for adapting neurons



1) Linear-Nonlinear-Poisson (LNP): ***fails!***

2) Phenomenological rate adaptation: ***fails!***

3) Time-Dependent-Renewal Theory: ***fails!***

4) Quasi-Renewal Theory: ***works!!!!***

Week 15 – Integral Equation for population dynamics

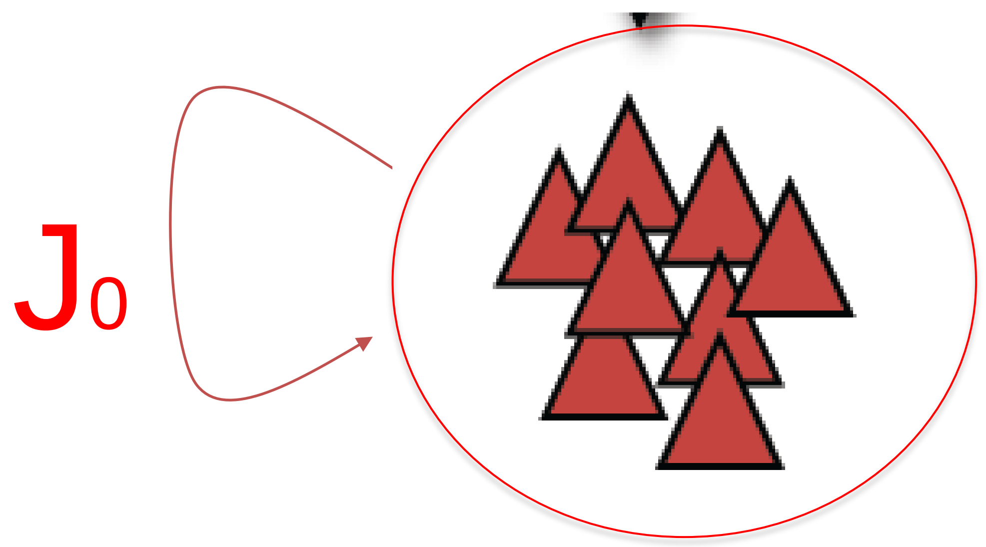
Biological Modeling of Neural Networks:

Week 15 – Population Dynamics: The Integral –Equation Approach

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Week 15-part 4: population with self-coupling



Same theory works
- Include the self-coupling in *h(t)*

Potential (SRM/GLM) of one neuron

$$u(t) = \sum_{t'} \eta(t-t') + \int_0^\infty \varepsilon(s) I(t-s) ds + J_0 \int_0^\infty \gamma(s) A(t-s) ds$$

h(t)

$$A(t) = \int P_{isi}(t \mid \hat{t}, A) A(\hat{t}) d\hat{t}$$

Week 15-part 4: population with self-coupling

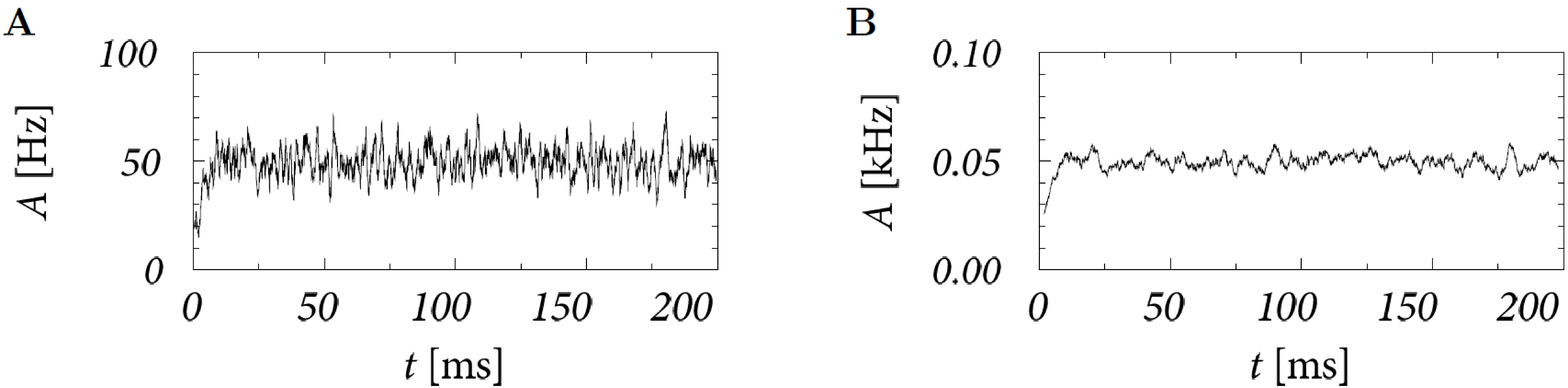


Fig. 14.5: Asynchronous firing. For a sufficient amount of noise, the population activity in a network of coupled spiking neurons with constant external input approaches a stationary value A_0. **A**. The population activity of 1000 neurons has been filtered with a time window of 1 ms duration. **B**. Same parameters as before, but the size of the population has been increased to $N = 4000$. Fluctuations decrease with N and approach the value of $A_0 = 50$ Hz predicted by theory.

Image: Gerstner et al.,
Neuronal Dynamics, Cambridge Univ. Press

Week 15-part 4: population with self-coupling

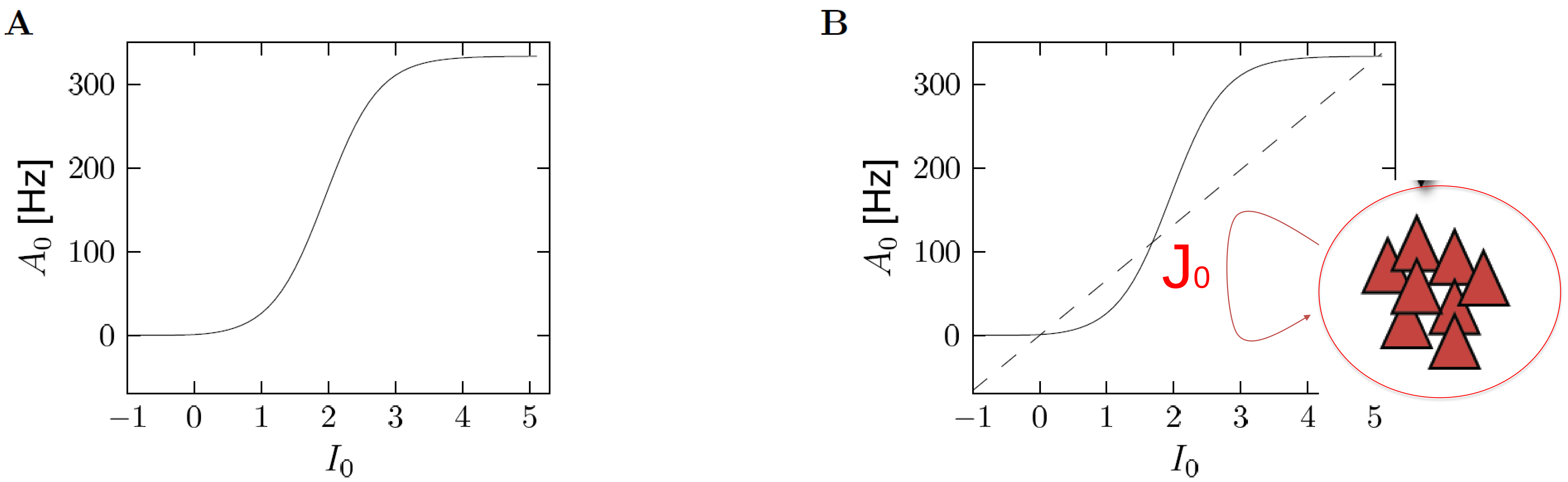
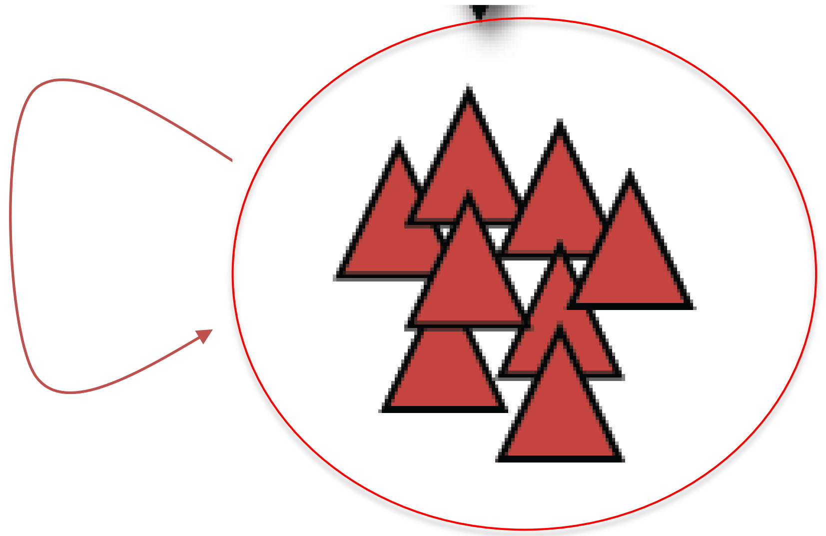


Fig. 14.6: Gain function and stationary activity in a population of SRM neurons with exponential escape noise. **A**. Gain function (single neuron firing frequency ν as a function of constant current I_0) for neurons with refractoriness given by Eq. (14.29). **B**. Self-consistent solution for the population activity $A(t) = A_0$ in a recurrent network of SRM neurons coupled to itself with strength J_0. Neurons are characterized by the same gain function as in part A of the figure.

Image: Gerstner et al.,
Neuronal Dynamics, Cambridge Univ. Press

Week 15-part 4: population with self-coupling

instabilities and oscillations



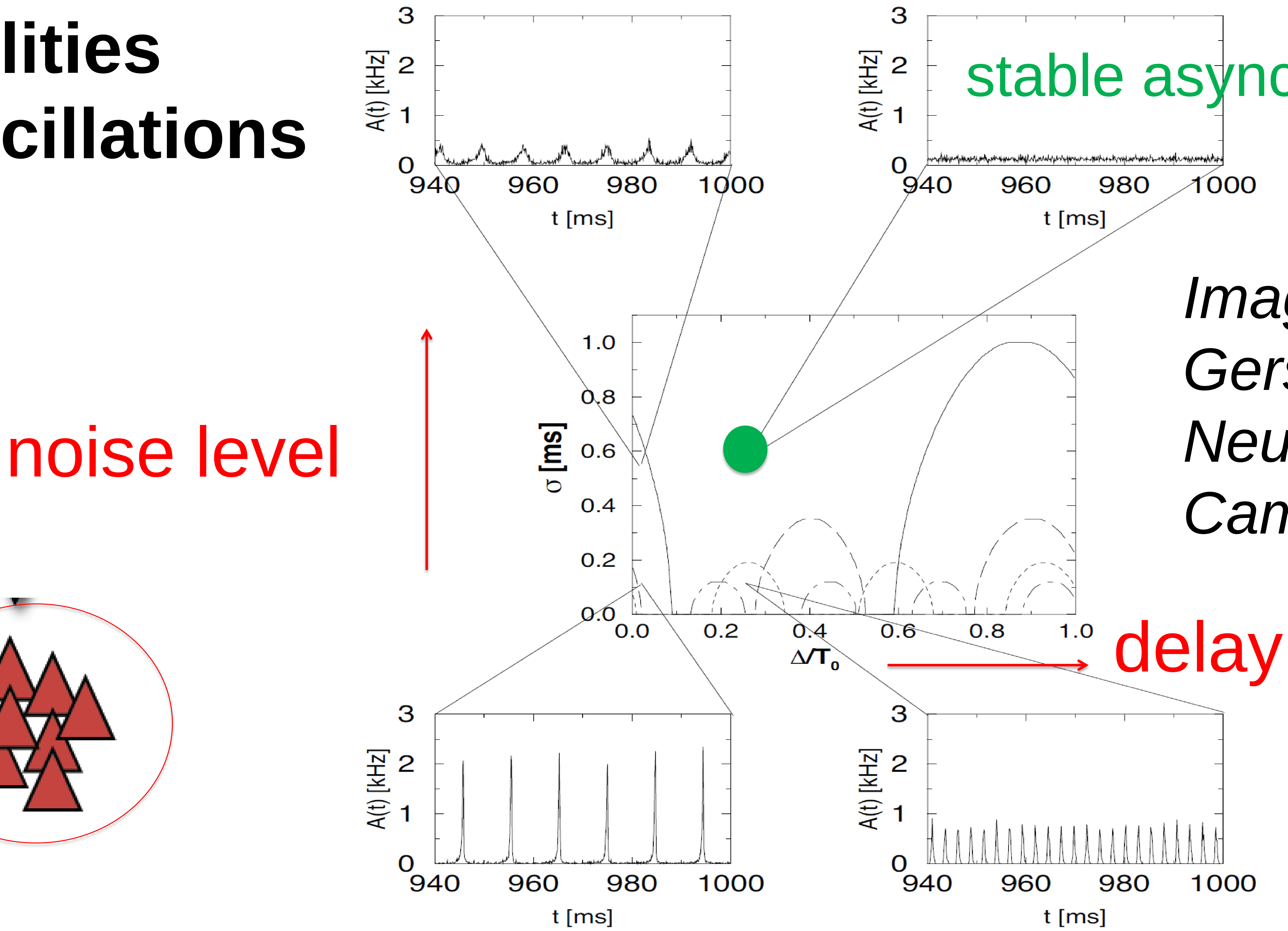
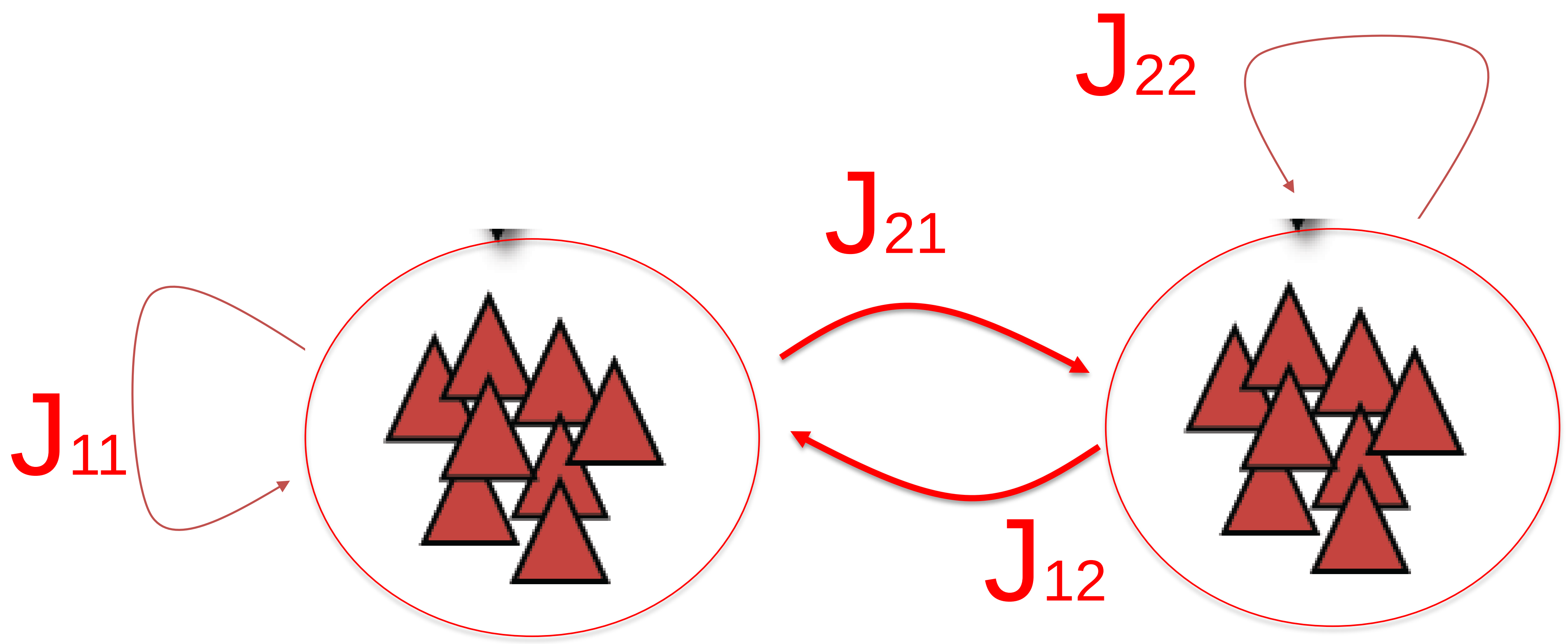


Image: Gerstner et al., Neuronal Dynamics, Cambridge Univ. Press

Week 15-part 4: multipe coupled populations



Same theory works

- Include the cross-coupling in *h(t)*

Potential (SRM/GLM) of one neuron in population *n*

$$u_n(t) = \sum_{t'} \eta(t-t') + \int_0^\infty \varepsilon_n(s) I_n(t-s)ds + \sum_k J_{nk} \int_0^\infty \gamma_k(s) A_k(t-s)ds$$

$h_n(t)$

$$A_n(t) = \int P_{isi}(t \mid \hat{t}, A_n) A_n(\hat{t}) d\hat{t}$$

Week 15-part 1: Summary and aims

-We can extract parameters for SINGLE neuron

(see NEURONAL DYNAMICS, Chs. 8-11)

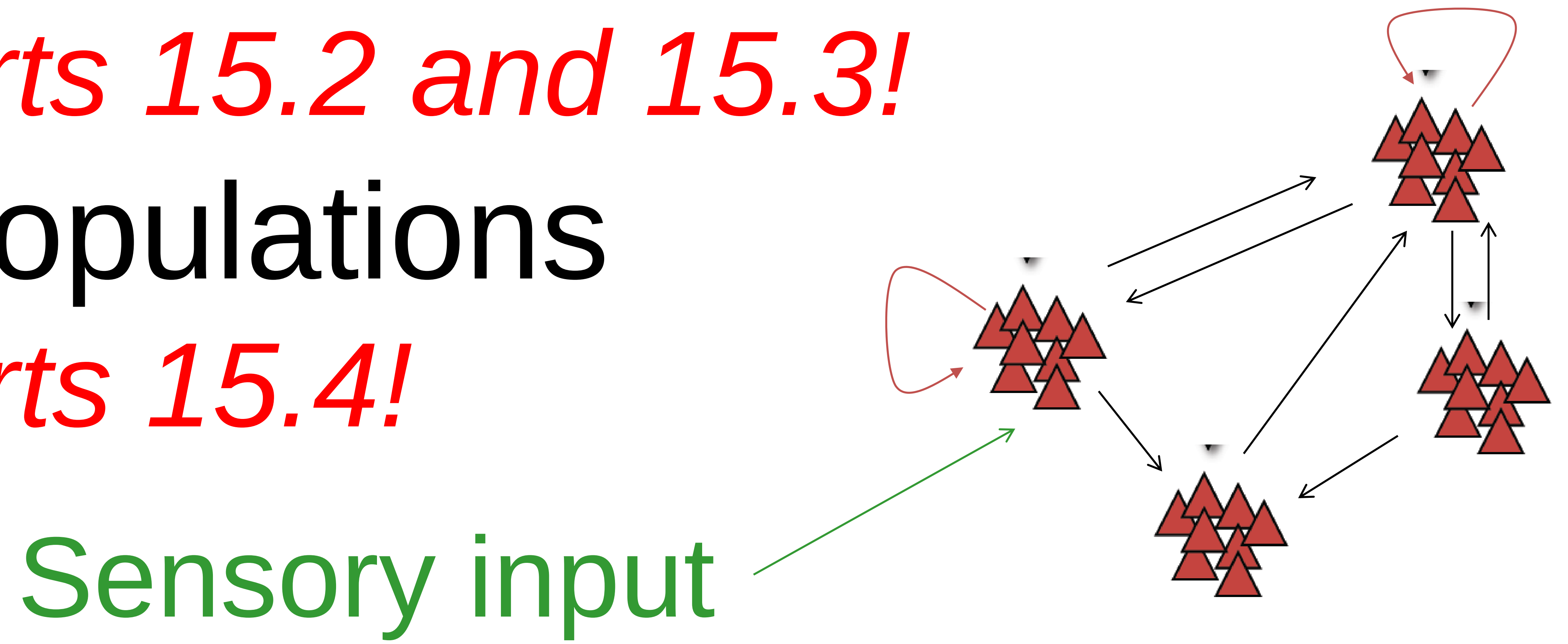
-Different neuron types have different parameters

→ Model Dynamics in one (homogeneous) population

Today, parts 15.2 and 15.3!

→ Couple different populations

Today, parts 15.4!



Eventually: Understand Coding and Brain dynamics

The end

Reading: Chapter 14 of
NEURONAL DYNAMICS,
Gerstner et al., Cambridge Univ. Press (2014)