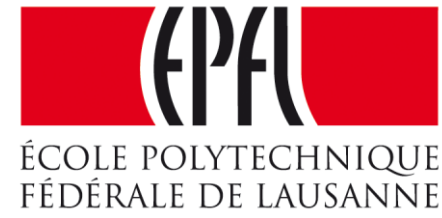


Week 4 – part : Type I and Type II Neuron Models



Neuronal Dynamics: Computational Neuroscience of Single Neurons

Week 4 – Reducing detail:

Two-dimensional neuron models

Wulfram Gerstner

EPFL, Lausanne, Switzerland

✓ 4.1 From Hodgkin-Huxley to 2D

✓ 4.2 Phase Plane Analysis

✓ 4.3 Analysis of a 2D Neuron Model

4.4 Type I and II Neuron Models

- where is the firing threshold?
- separation of time scales

4.5. Nonlinear Integrate-and-fire

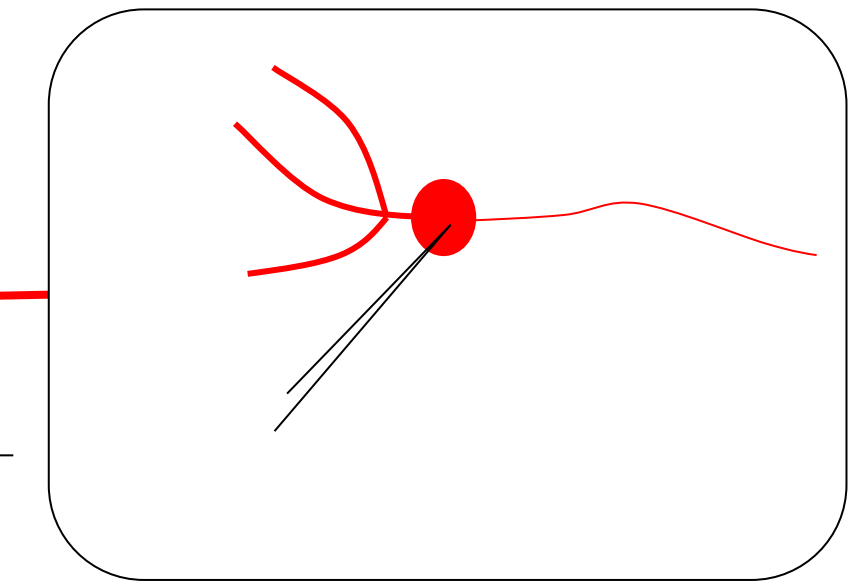
- from two to one dimension

Neuronal Dynamics – 4.4. Type I and II Neuron Models

ramp input/
constant input

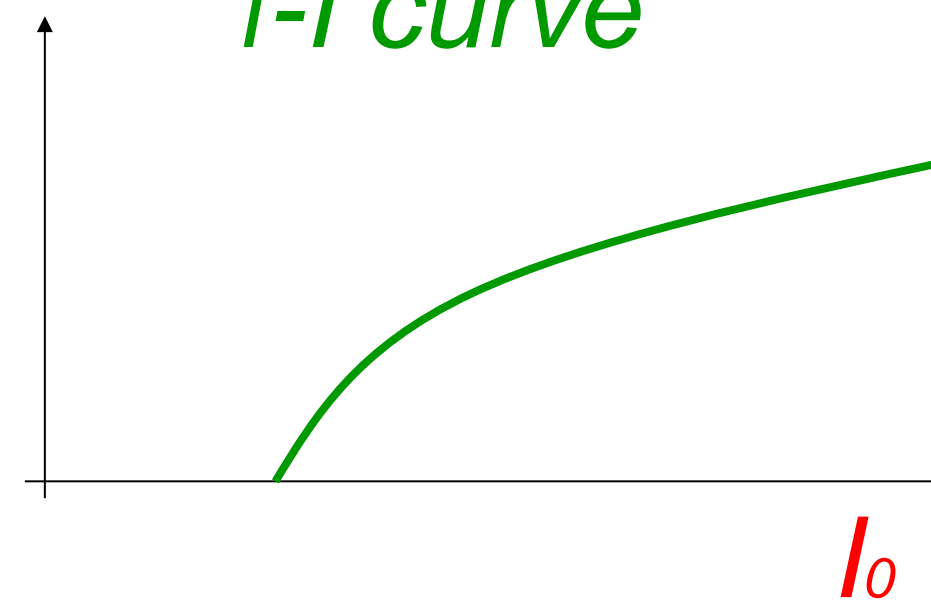


neuron

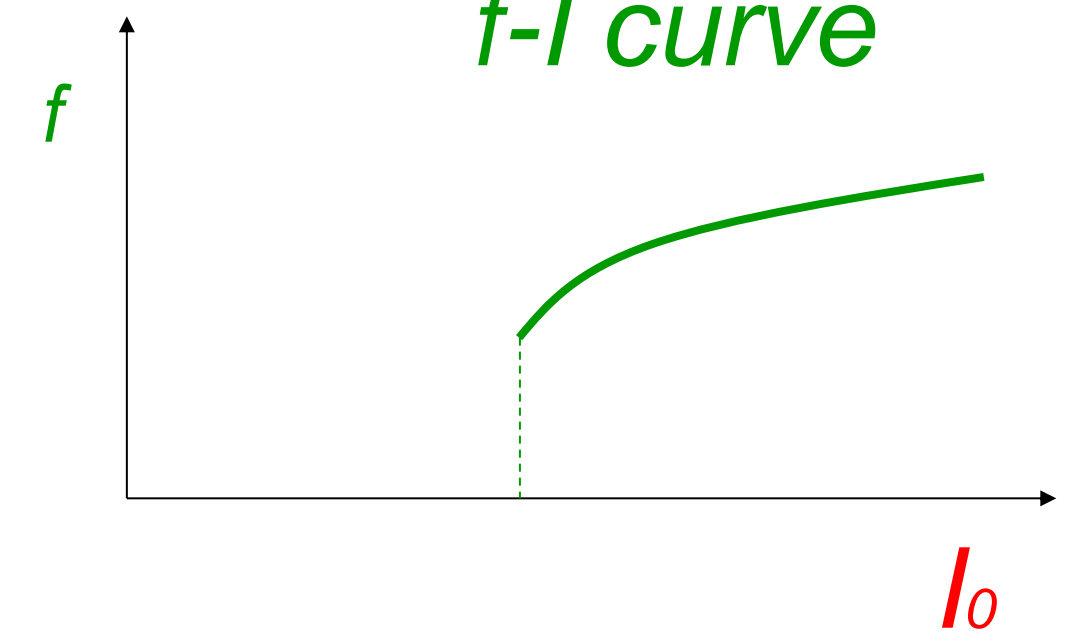


Type I and type II models

f-I curve



f-I curve



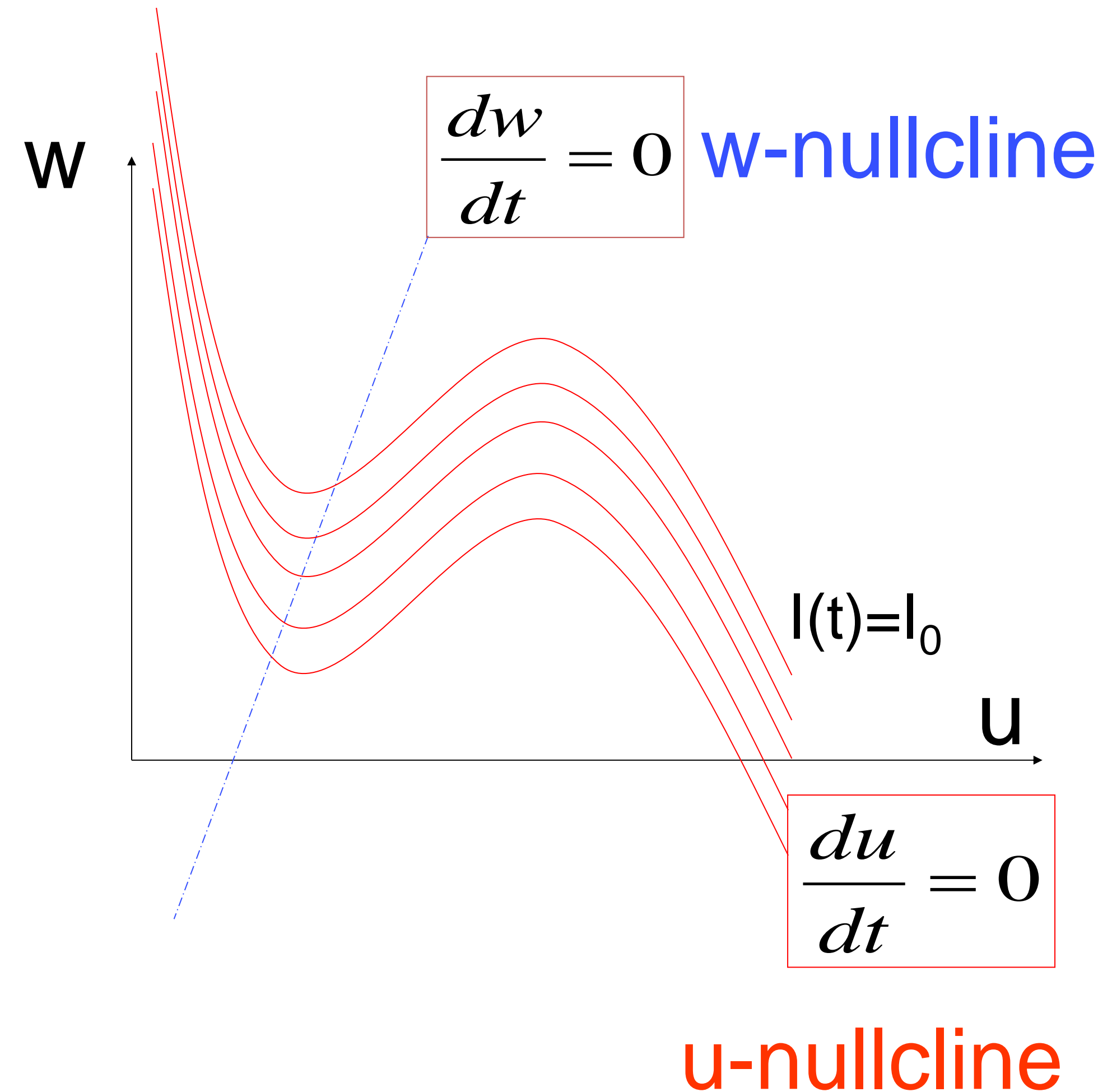
2 dimensional Neuron Models

$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

stimulus
↓

$$\tau_w \frac{dw}{dt} = G(u, w)$$

apply constant stimulus I_0

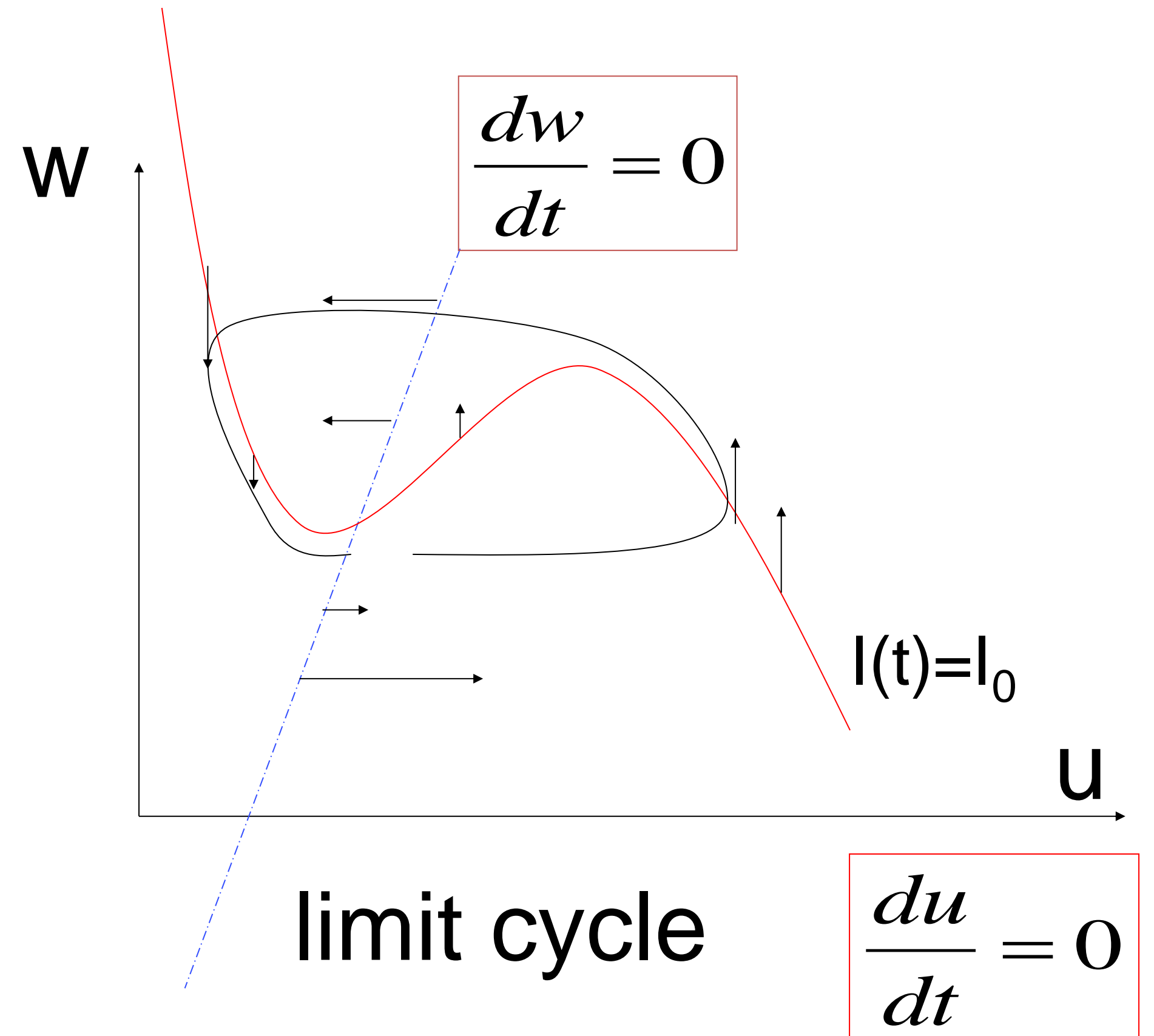


FitzHugh Nagumo Model – limit cycle

$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

- unstable fixed point
 - closed boundary
with arrows pointing inside
- limit cycle

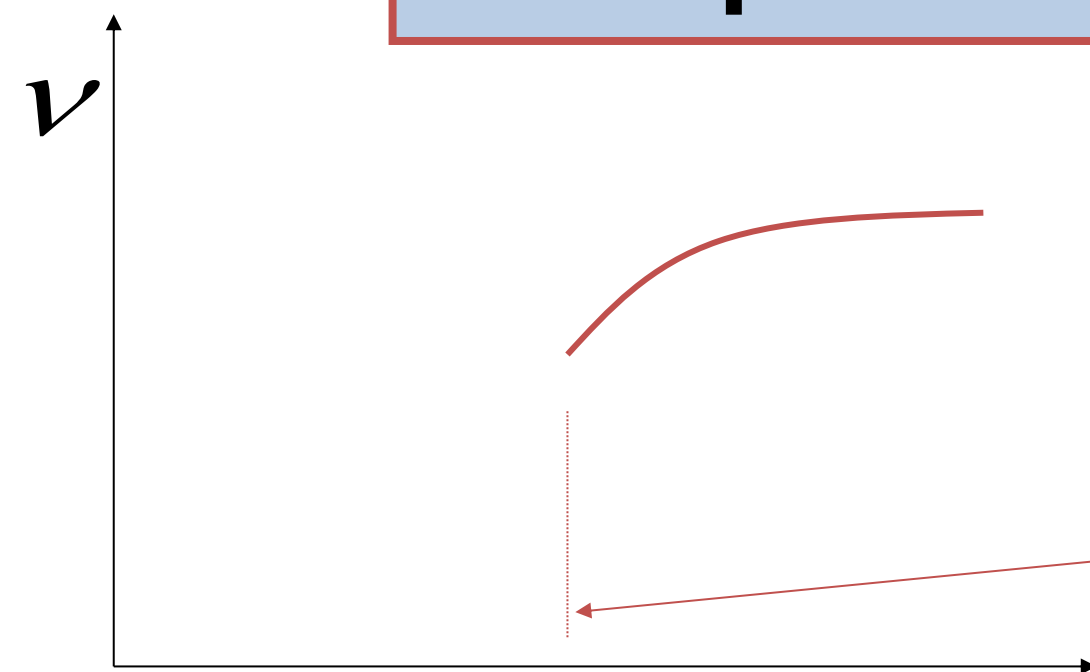


Type II Model constant input

$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

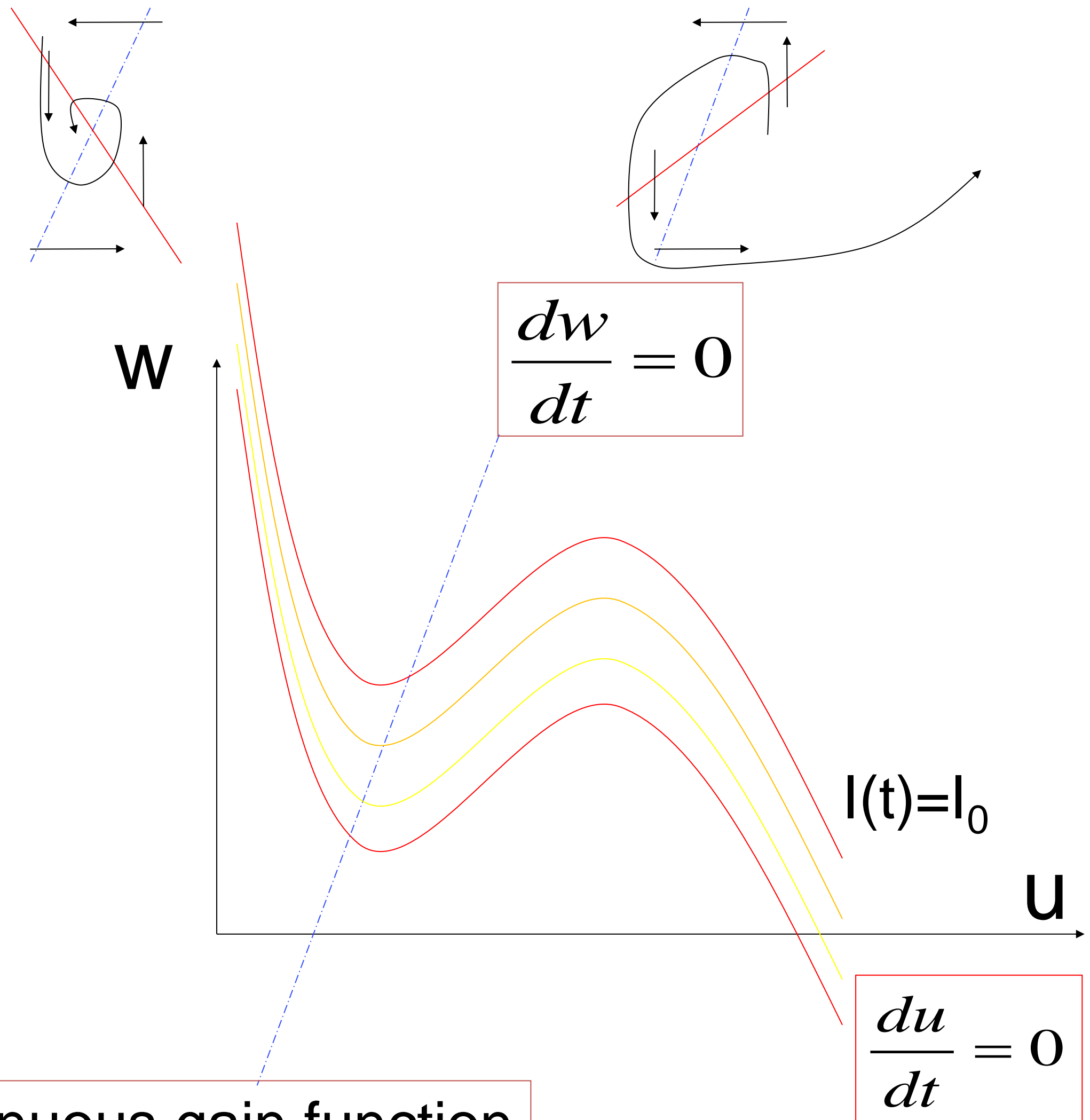
Hopf bifurcation



Discontinuous gain function

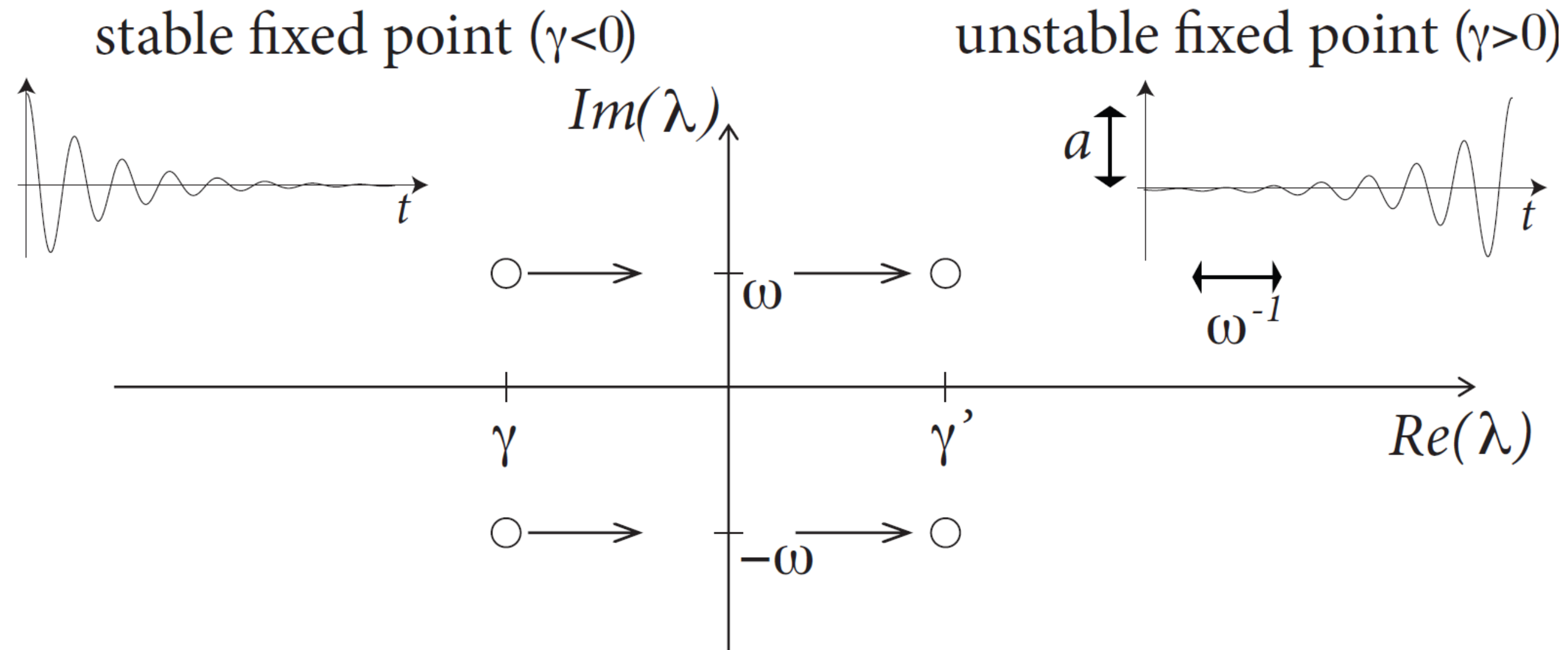
Stability lost \rightarrow oscillation with finite frequency

stimulus

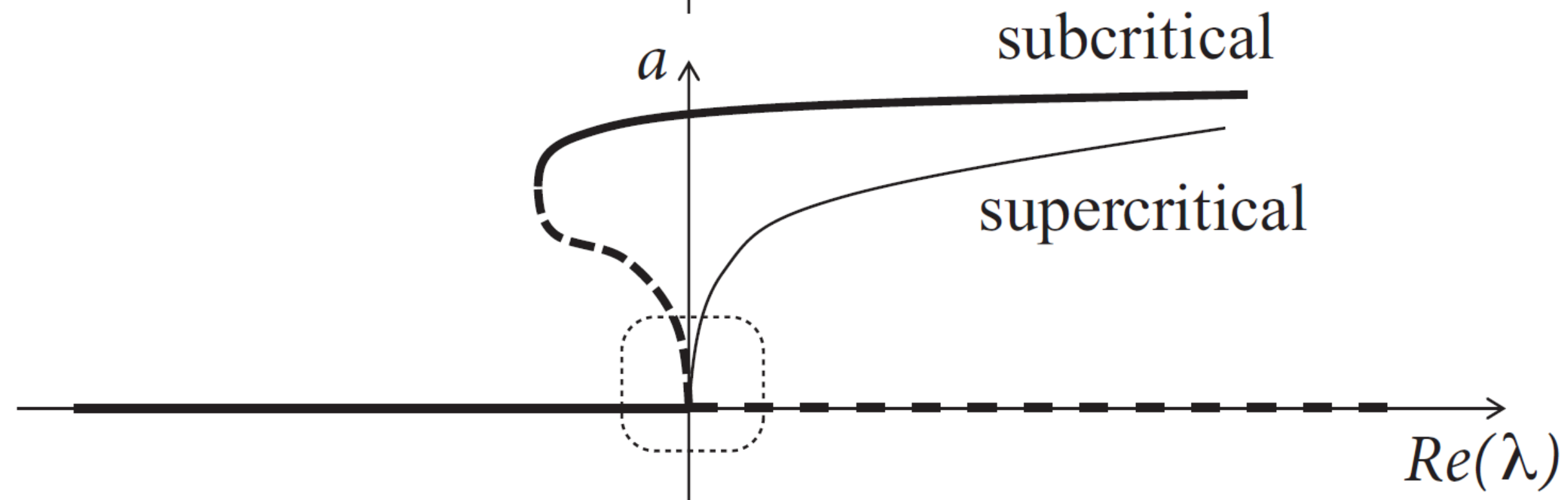
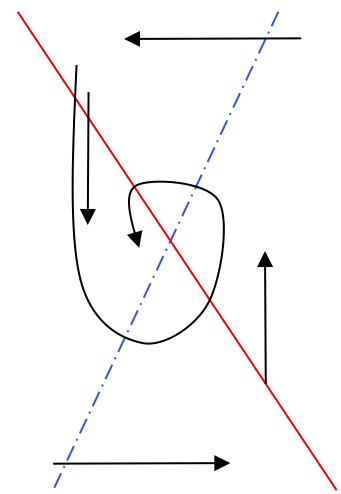


Neuronal Dynamics – 4.4. Hopf bifurcation

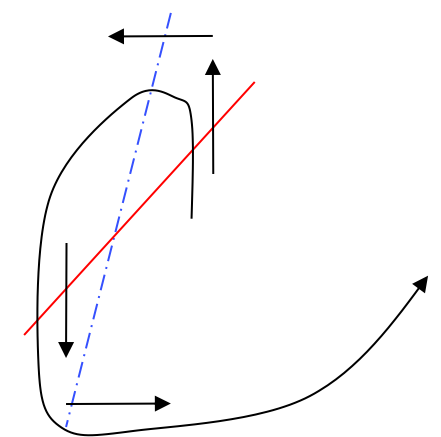
$$\lambda = \gamma + i\omega$$



$$\gamma < 0$$

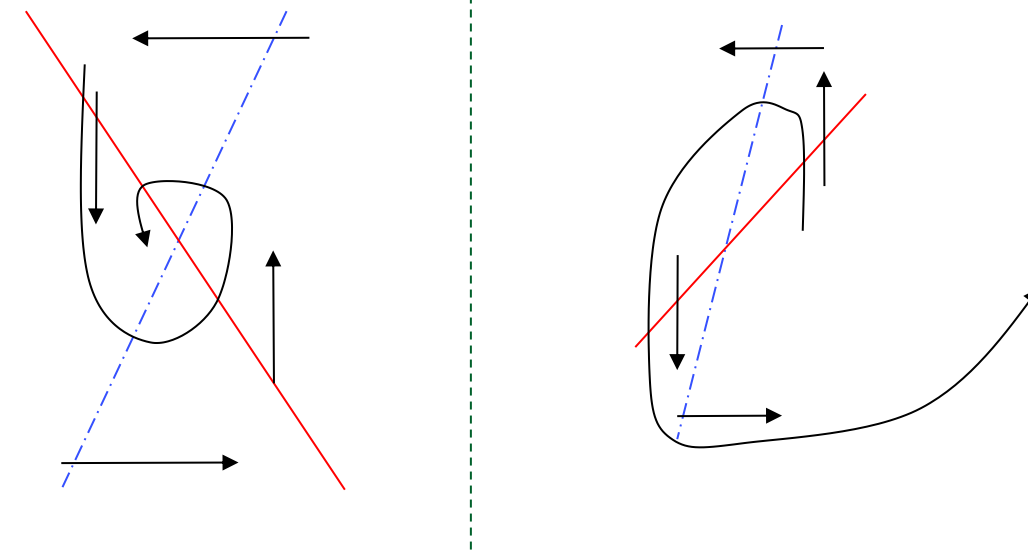
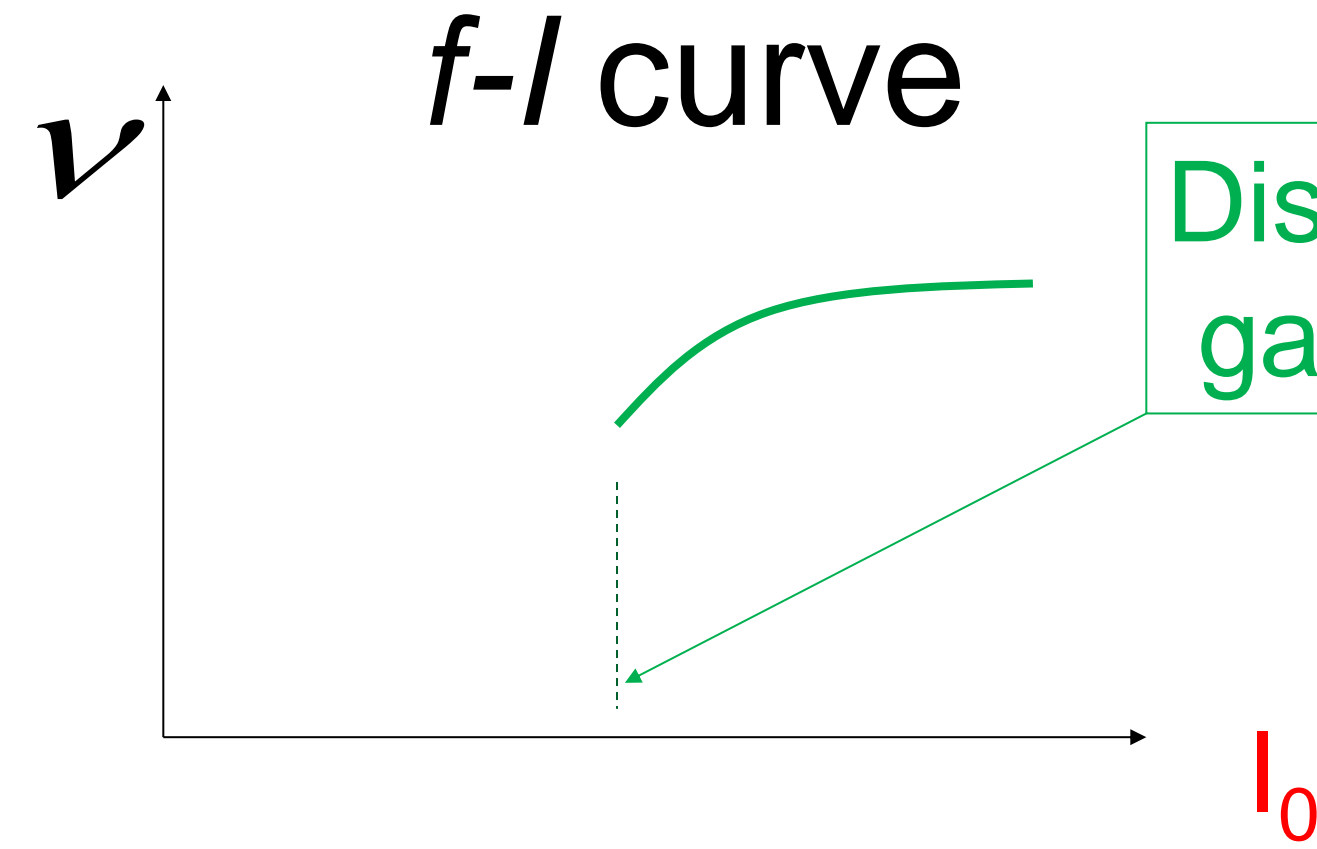
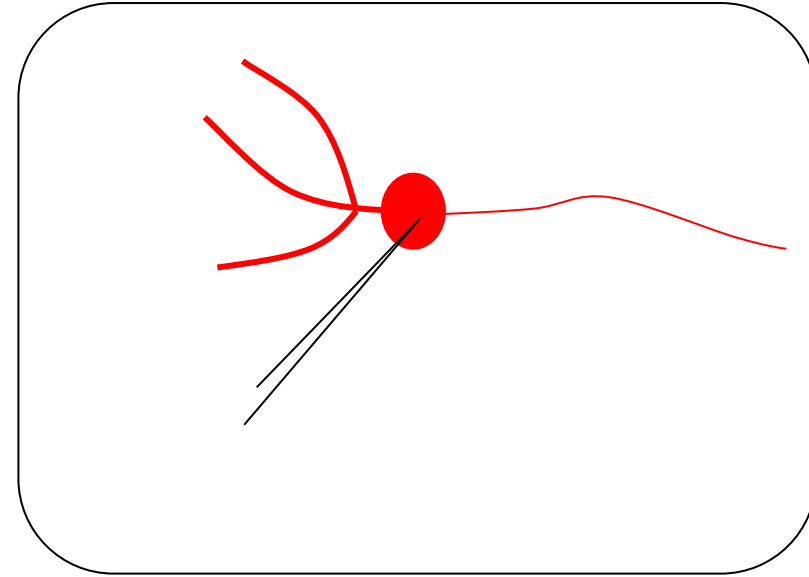
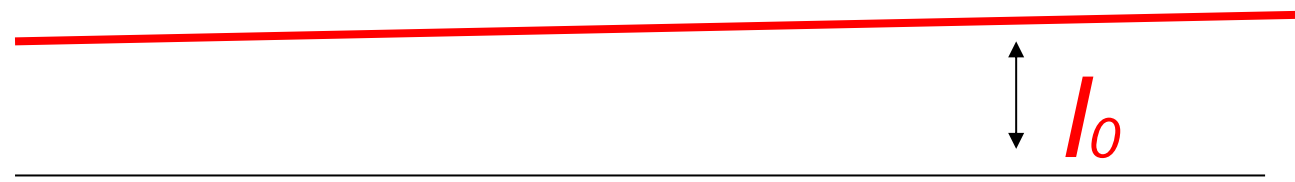


$$\gamma > 0$$



Neuronal Dynamics – 4.4. Hopf bifurcation: *f*-*I*-curve

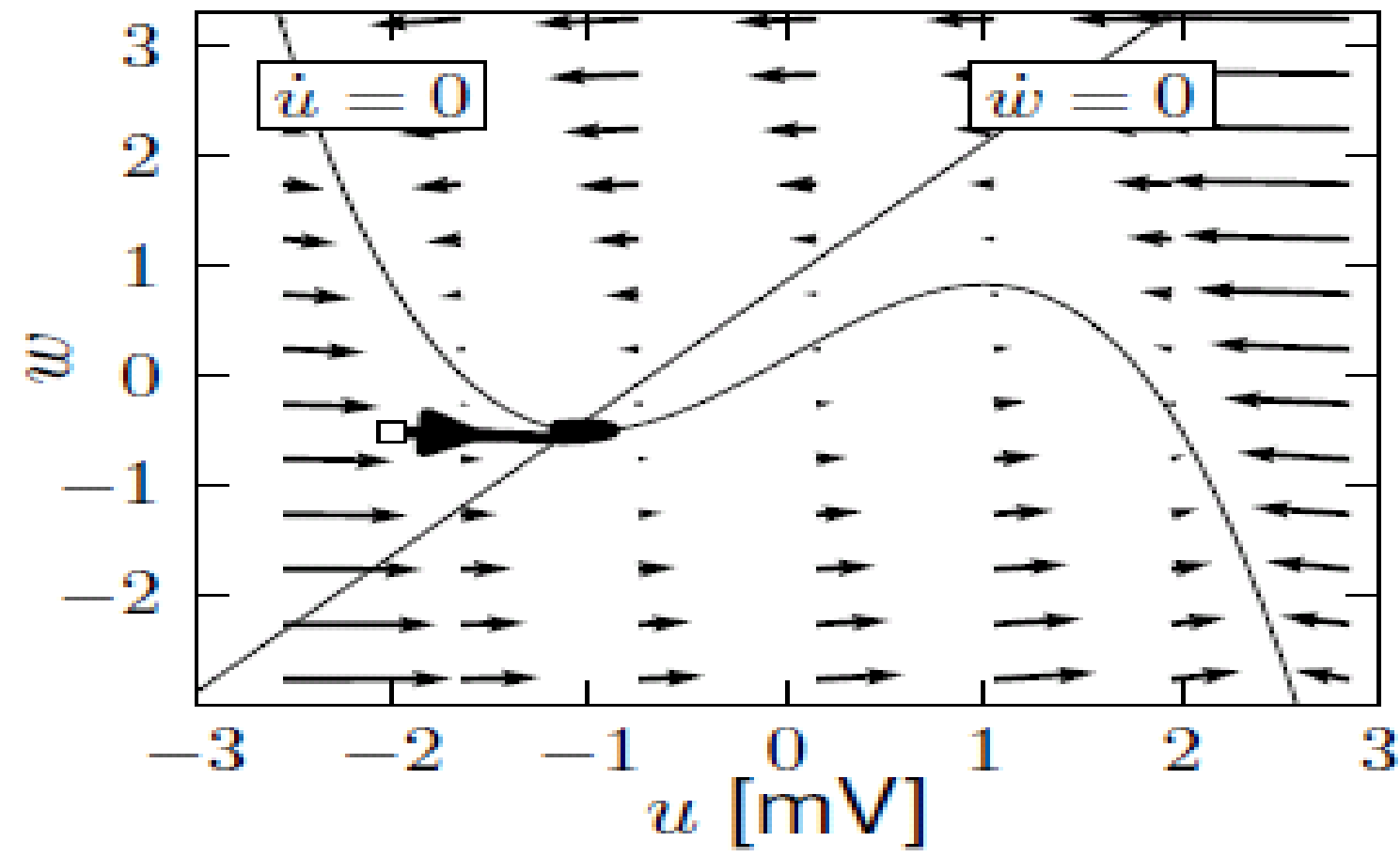
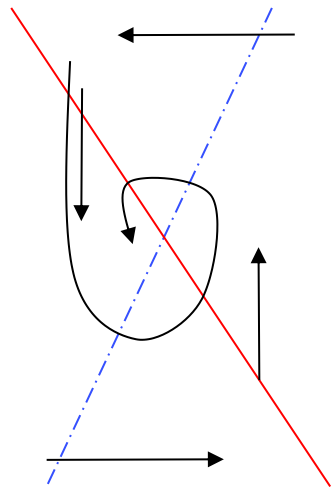
ramp input/
constant input



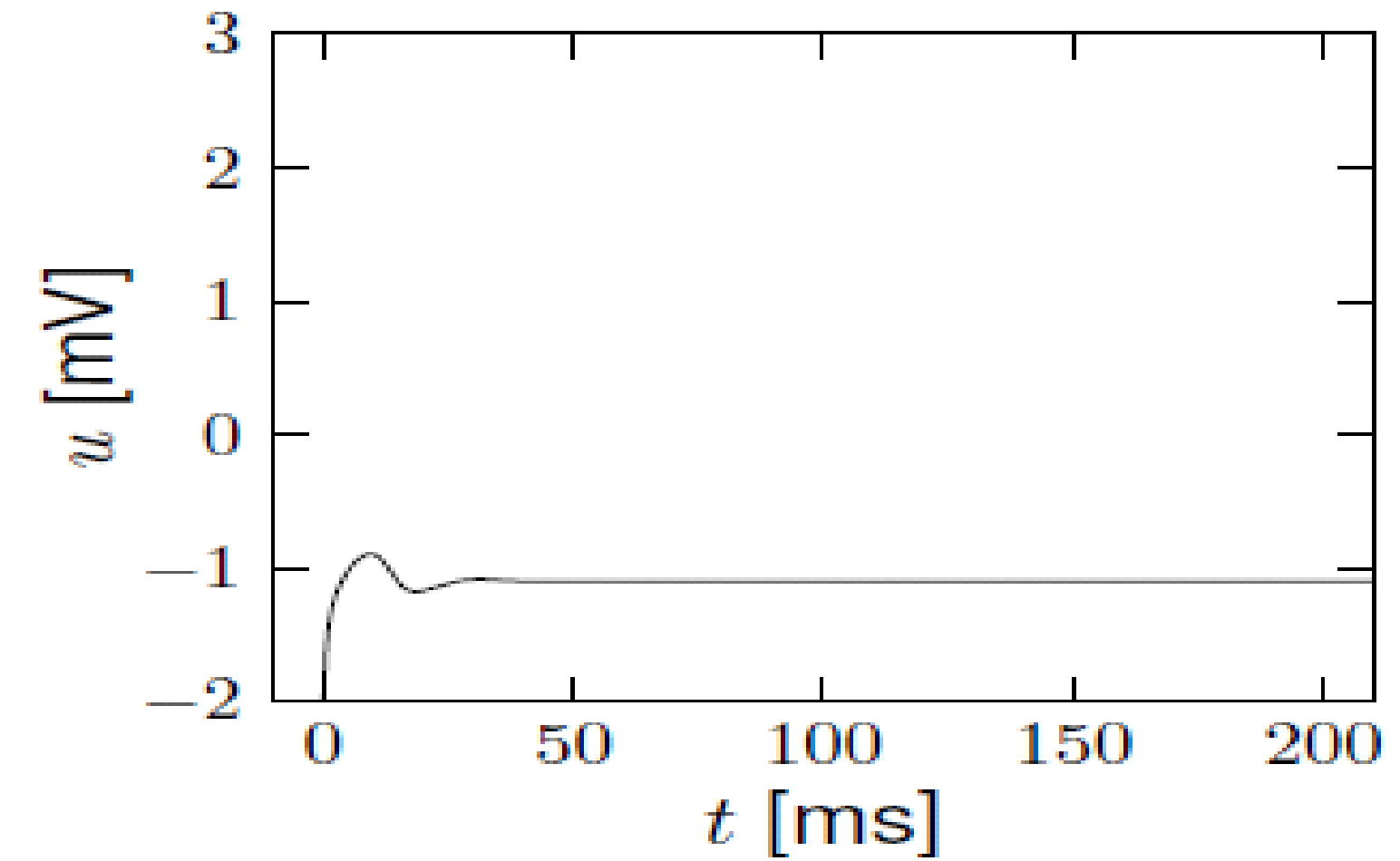
Stability lost → oscillation with finite frequency

FitzHugh-Nagumo: type II Model – Hopf bifurcation

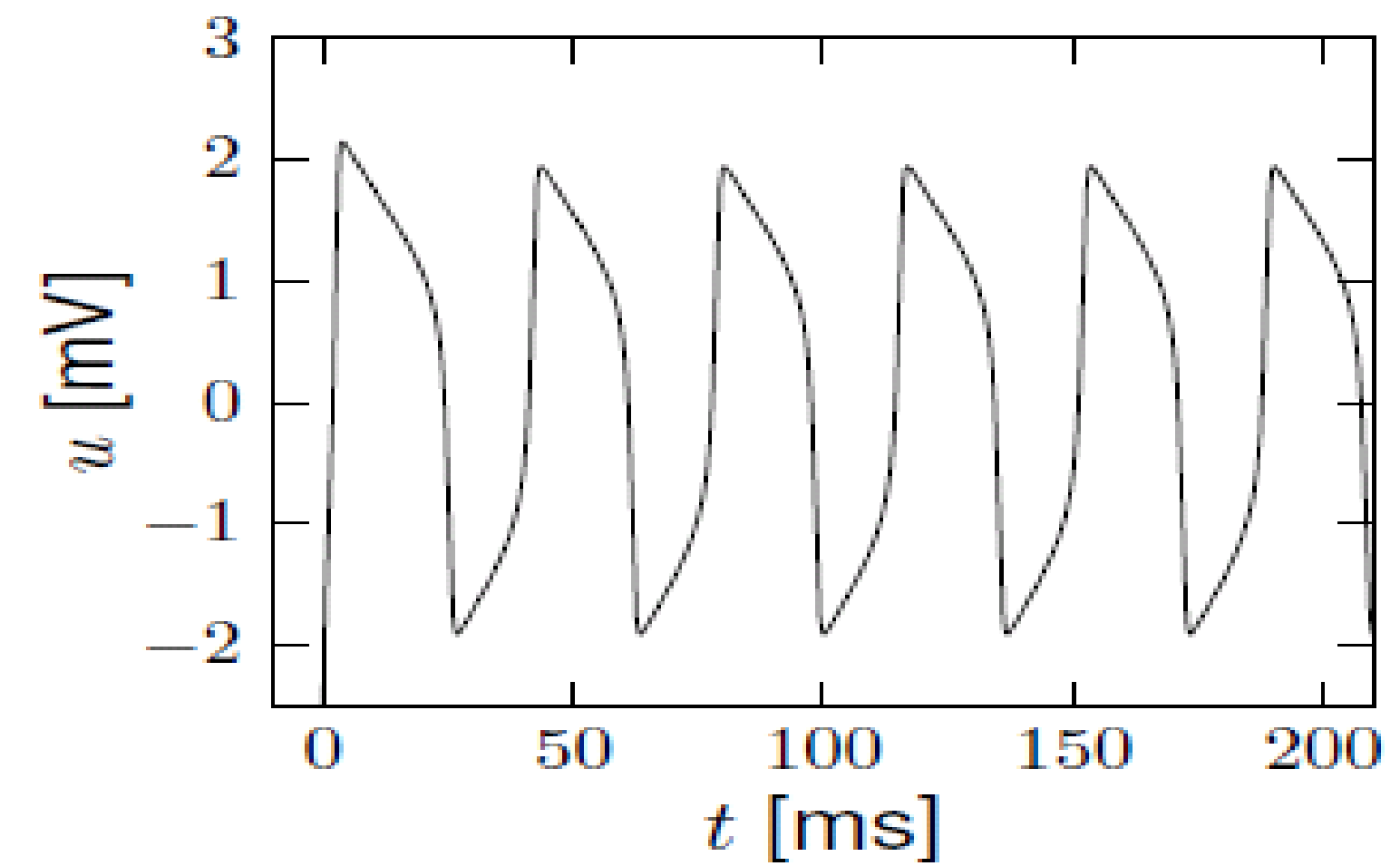
$I=0$



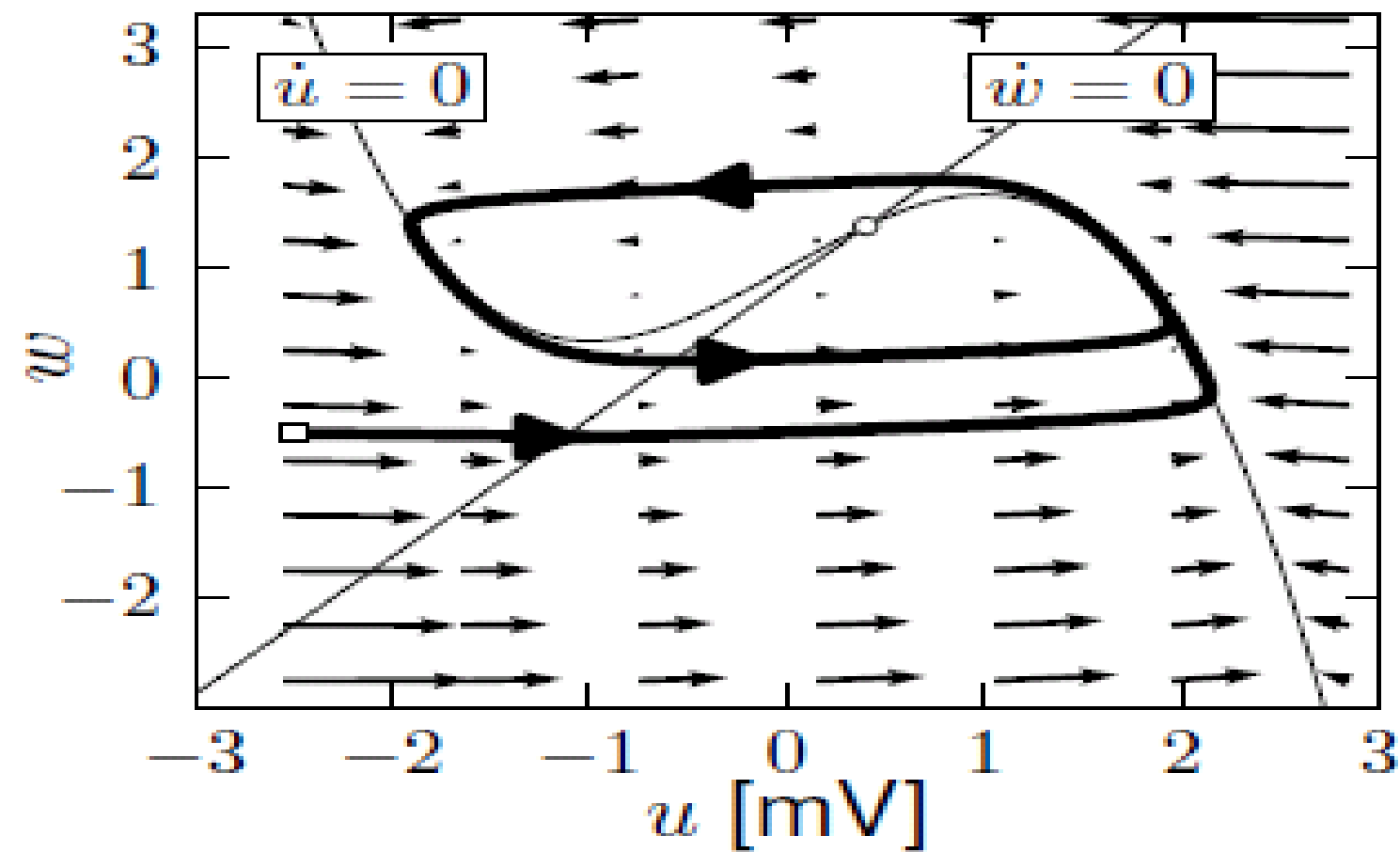
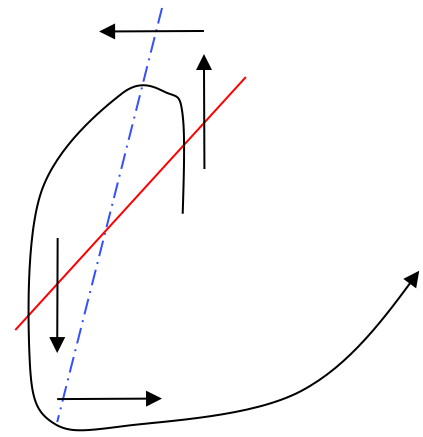
B



D

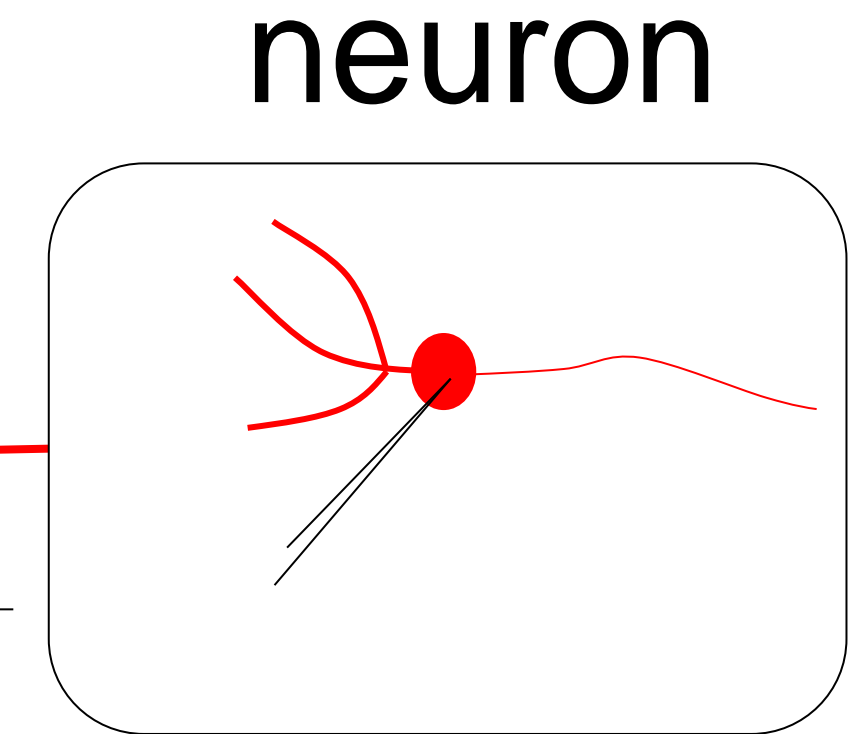


$I > I_c$

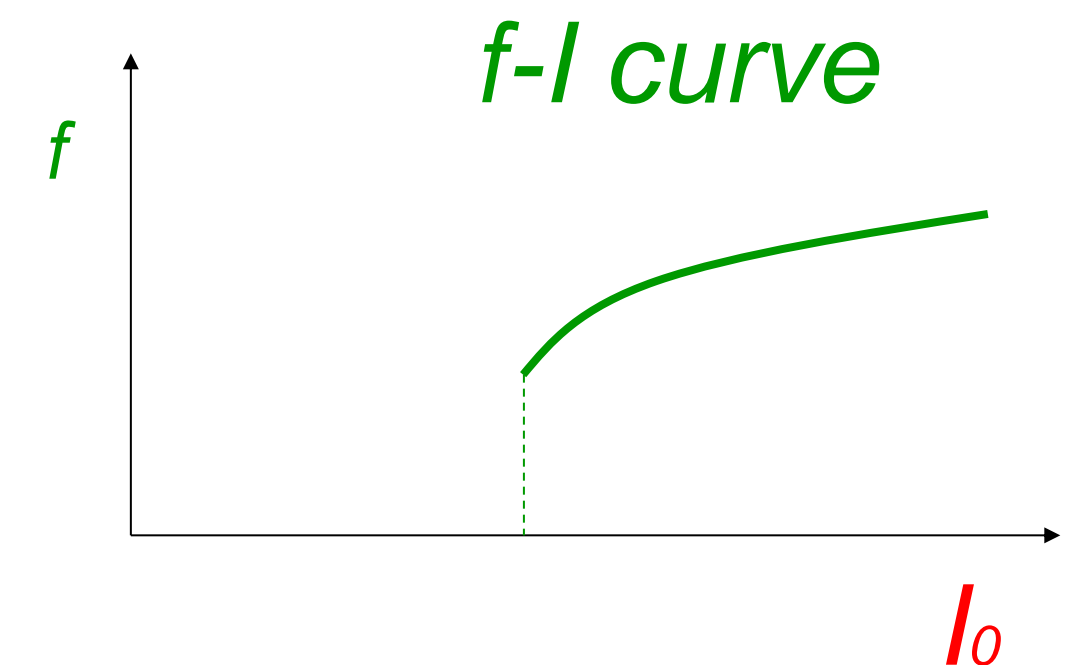
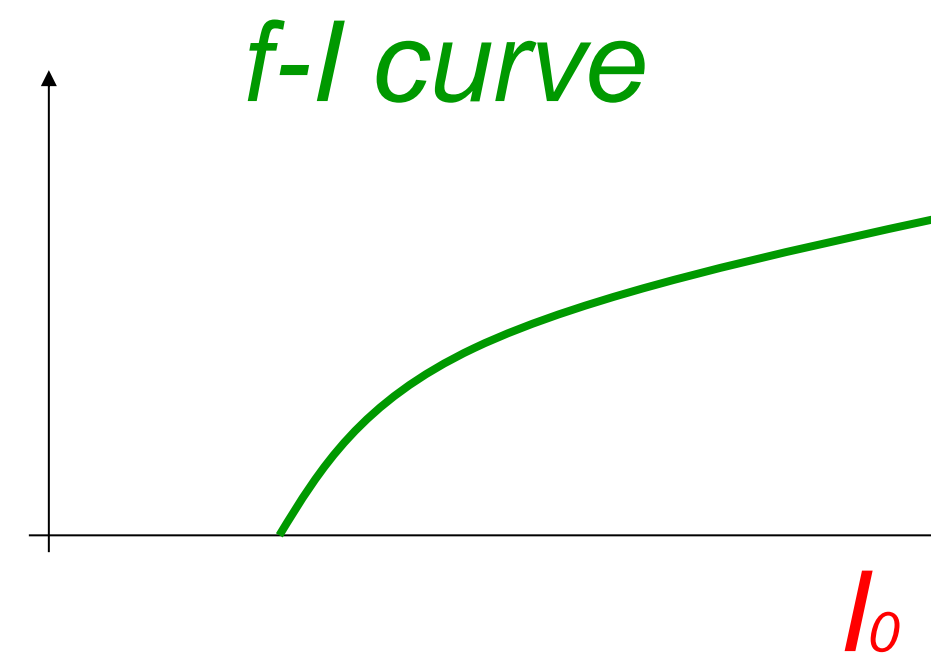


Neuronal Dynamics – 4.4. Type I and II Neuron Models

ramp input/
constant input



Type I and type II models



Neuronal Dynamics – 4.4. Type I and II Neuron Models

type I Model: 3 fixed points

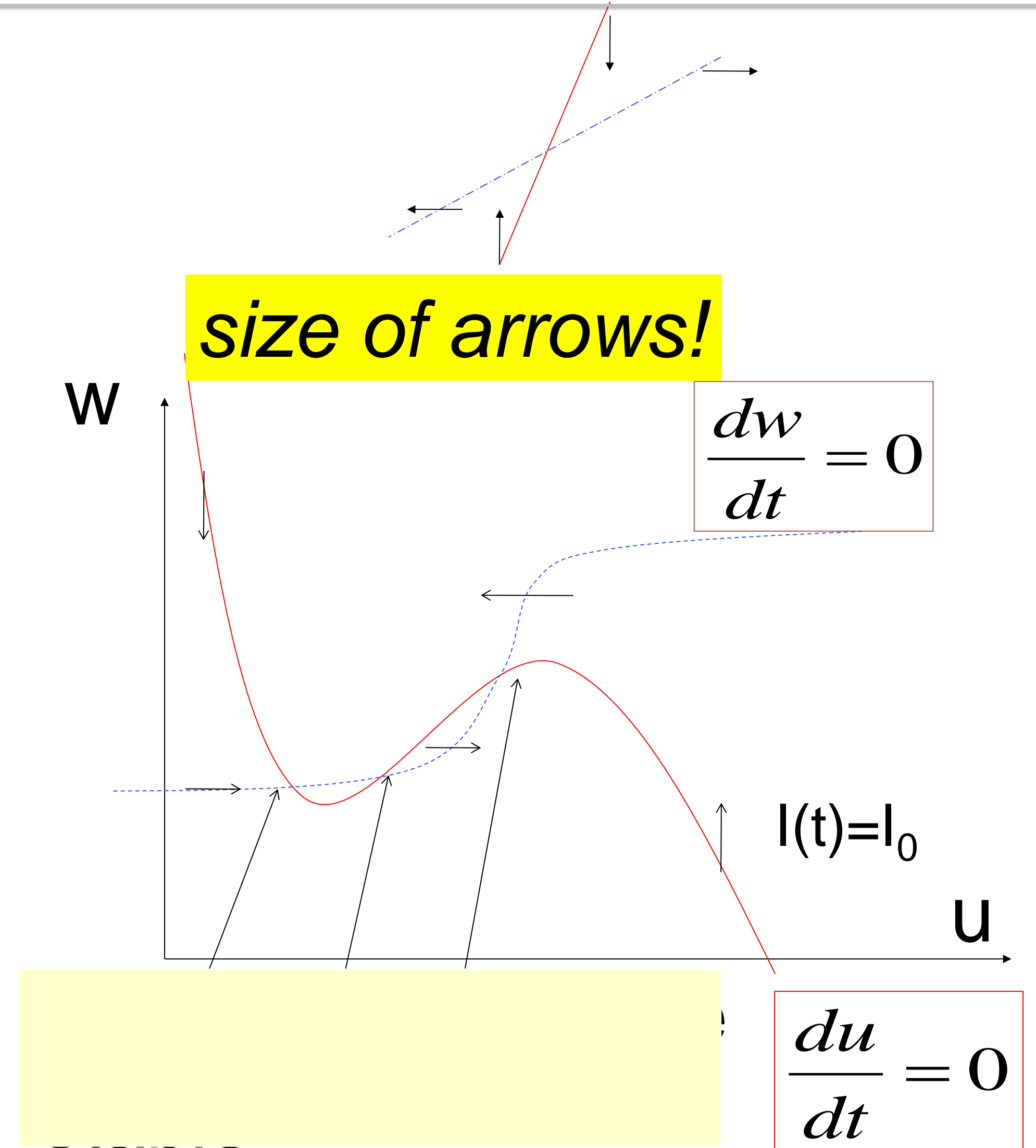
stimulus

$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

apply constant stimulus I_0

Saddle-node bifurcation



Saddle-node bifurcation

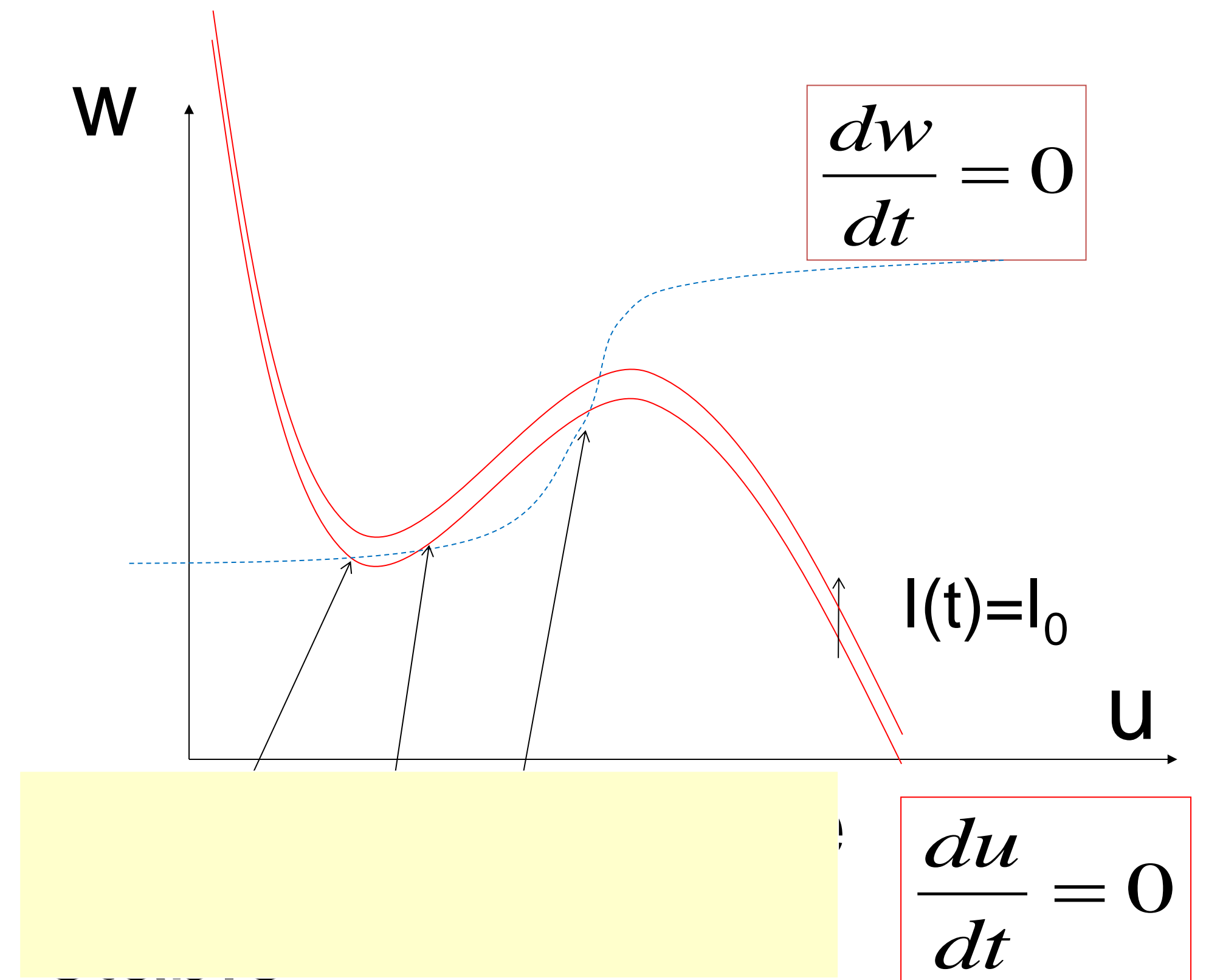
stimulus



$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

flow arrows

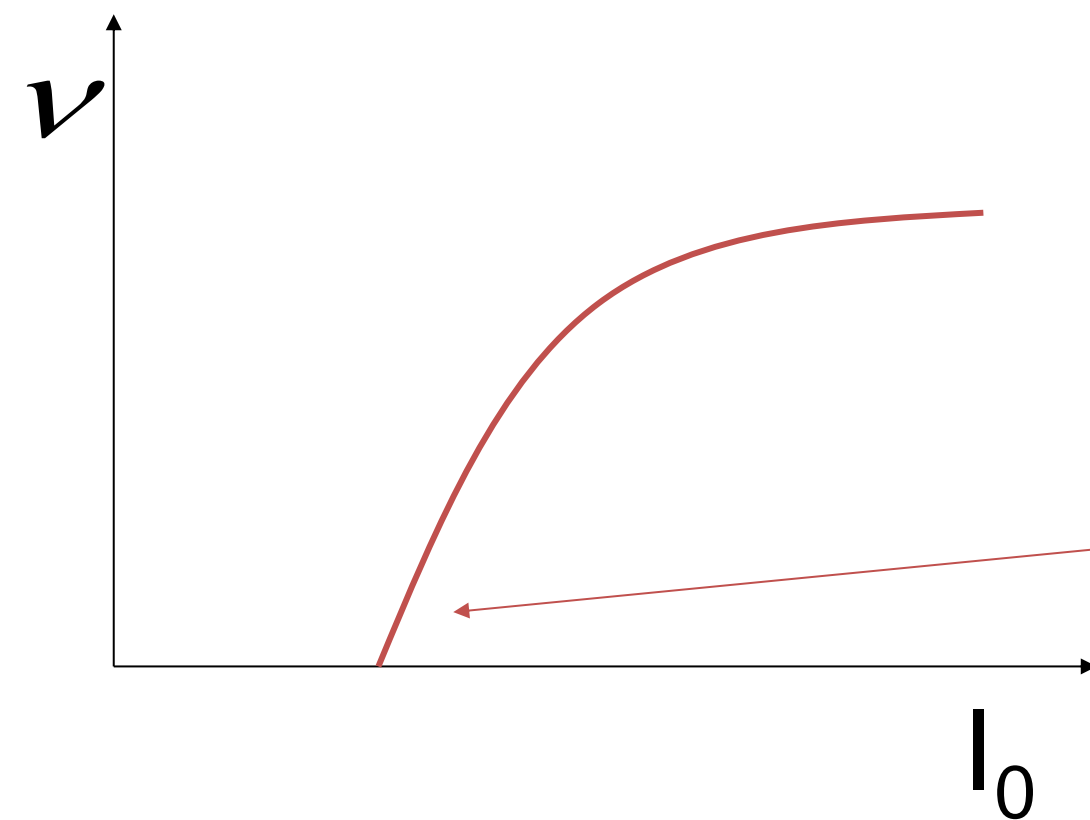


type I Model – constant input

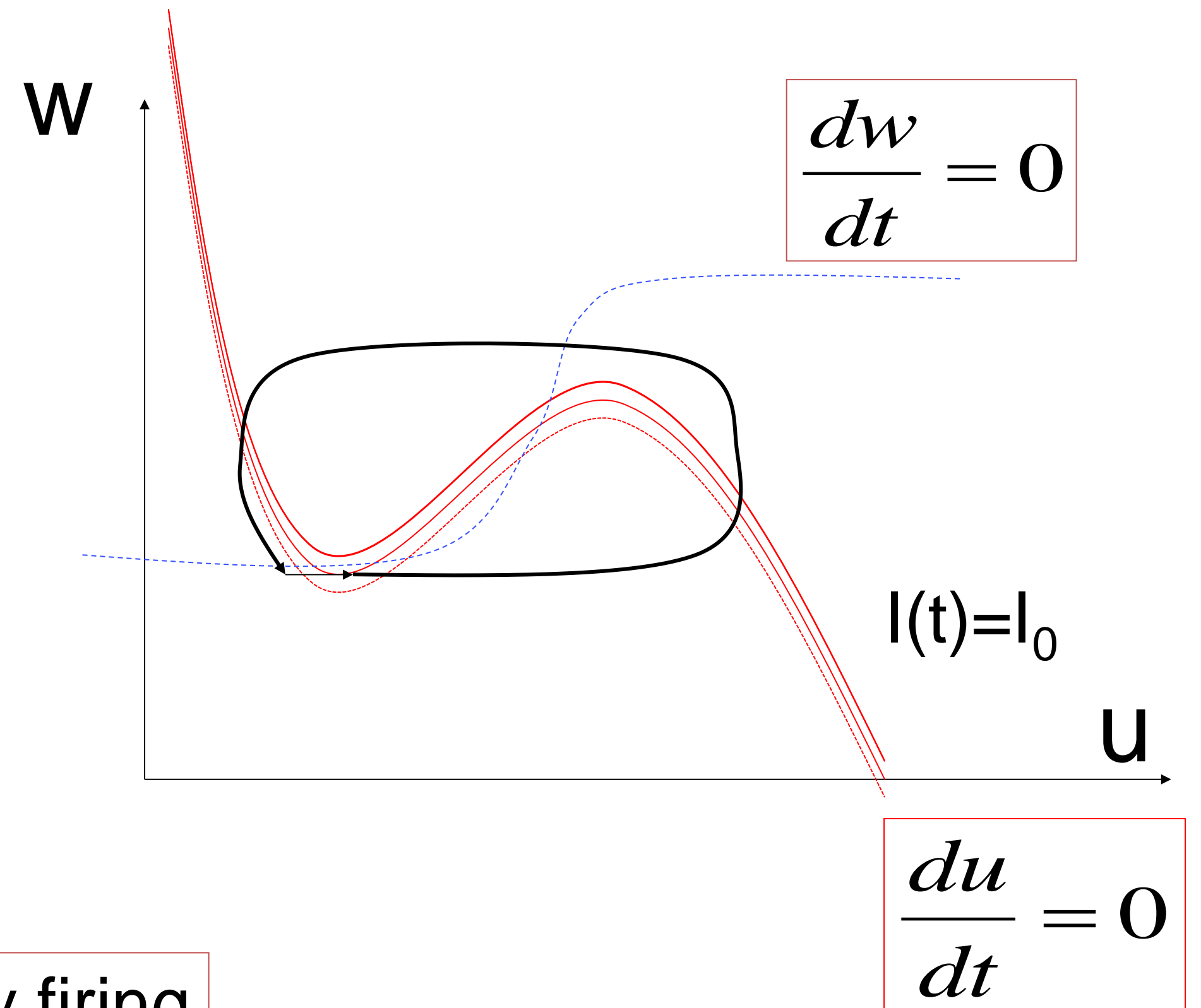
$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

stimulus
↓

$$\tau_w \frac{dw}{dt} = G(u, w)$$

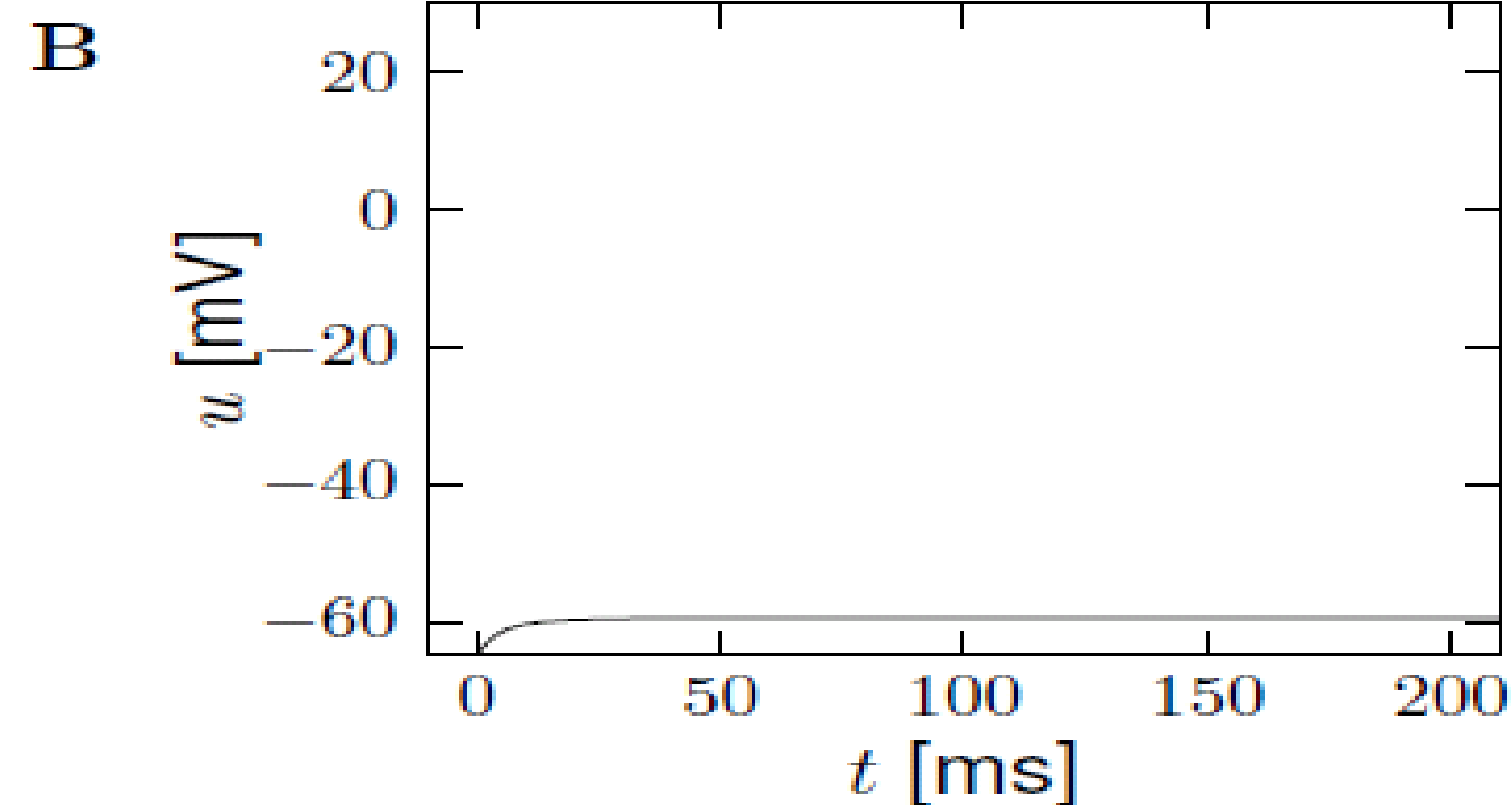
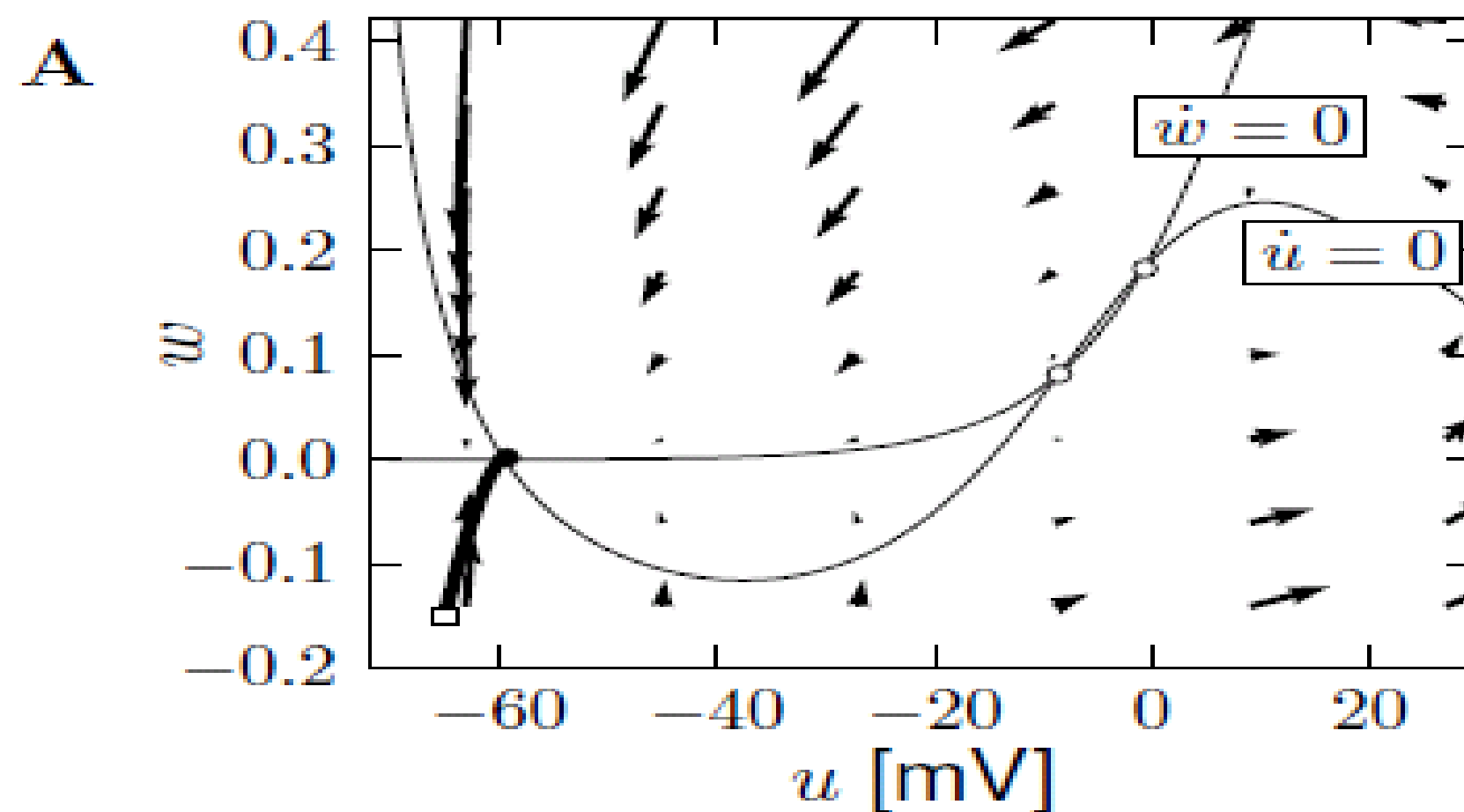


Low-frequency firing

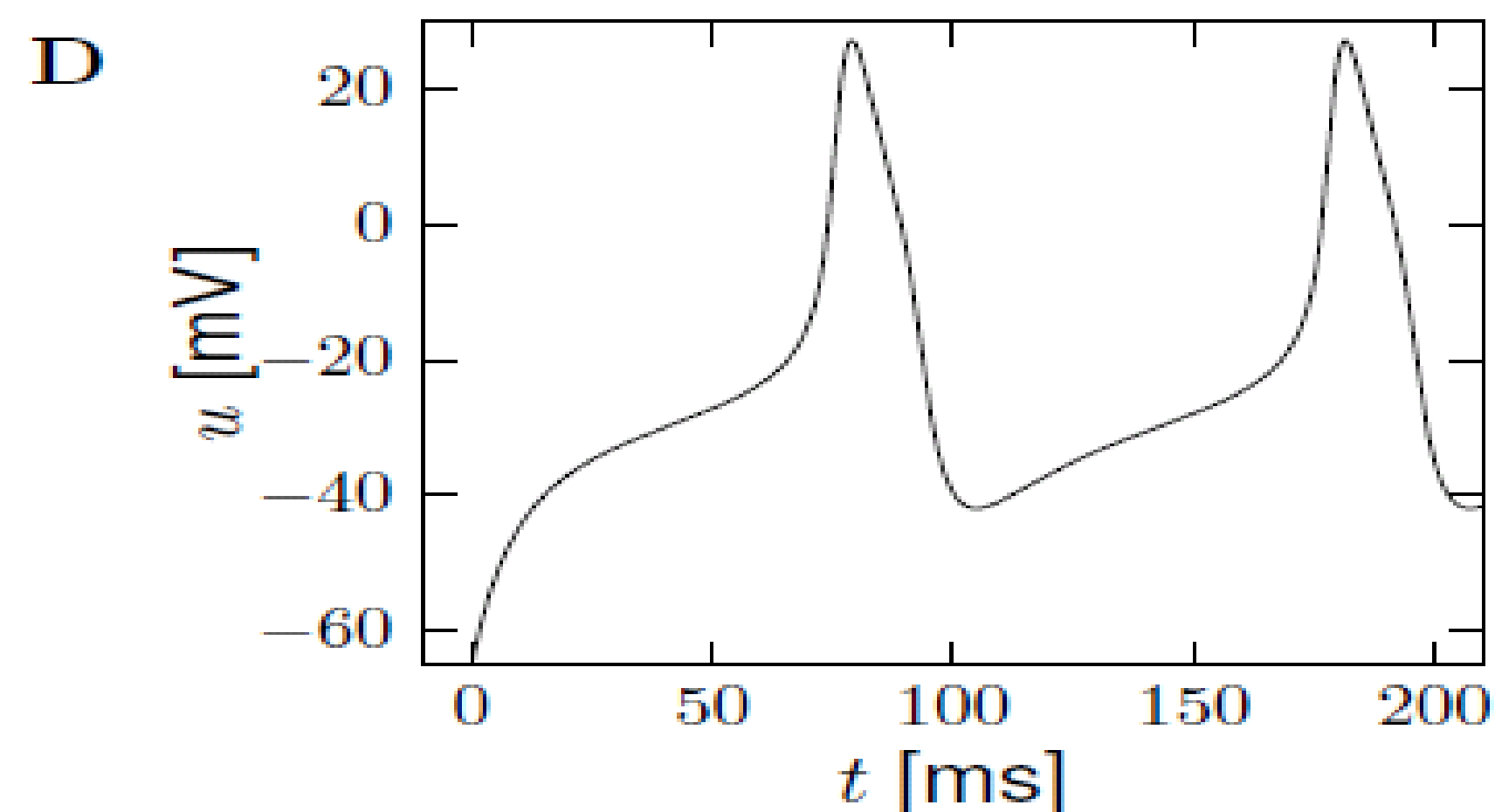
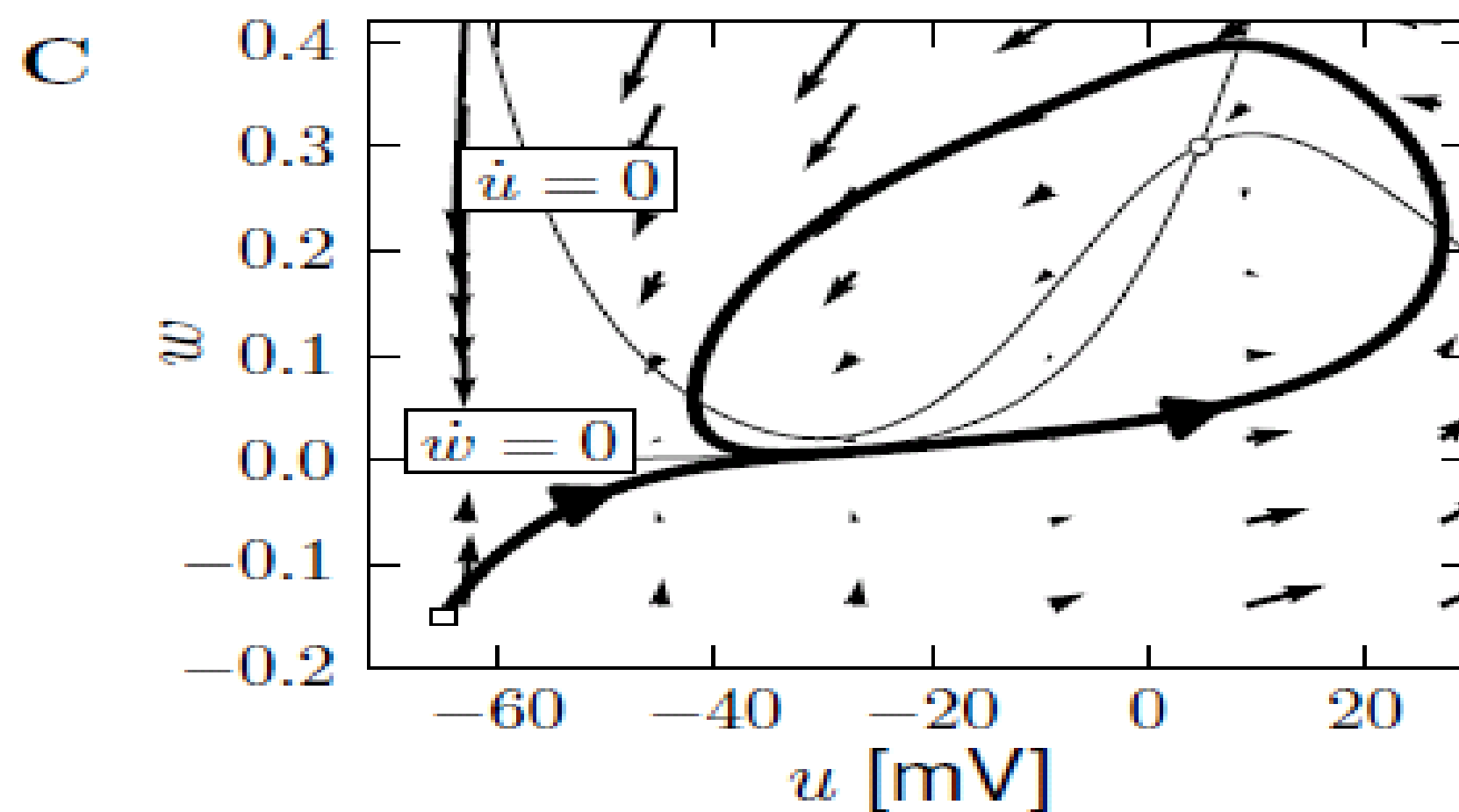


Morris-Lecar, type I Model – constant input

$I=0$



$I > I_c$



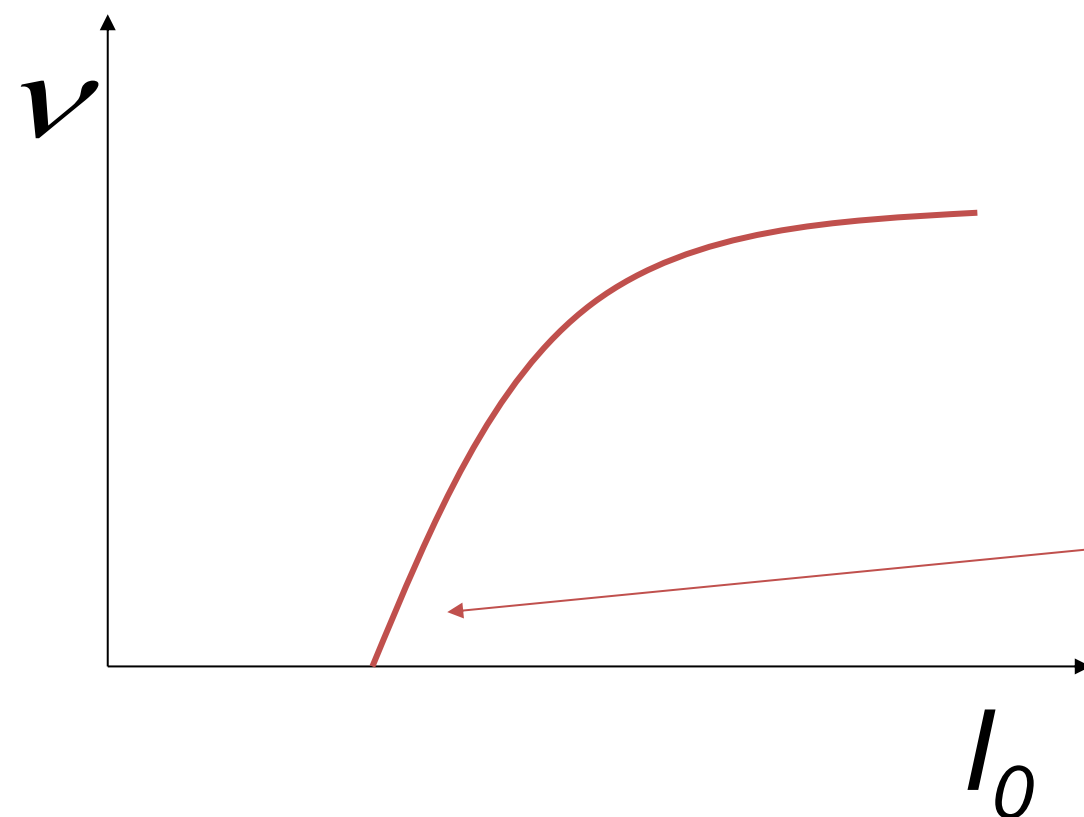
type I Model – constant input

stimulus

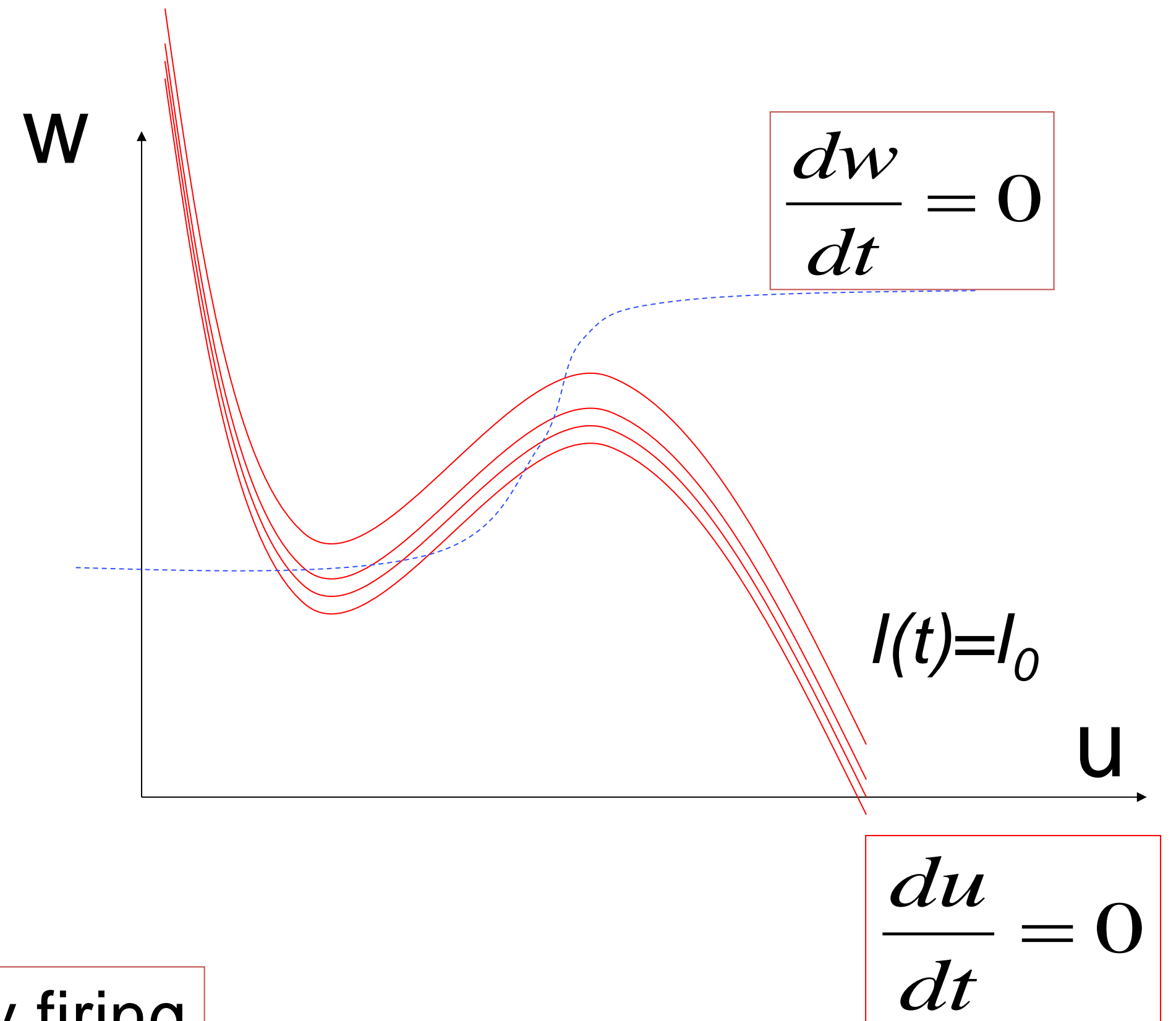
$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

$$\frac{dw}{dt} = -\frac{w - w_0(u)}{\tau_{eff}(u)}$$

$$w_0(u) = 0.5[1 + \tanh(\frac{u - \theta}{d})]$$



Low-frequency firing



Type I and type II models

Response at firing threshold?

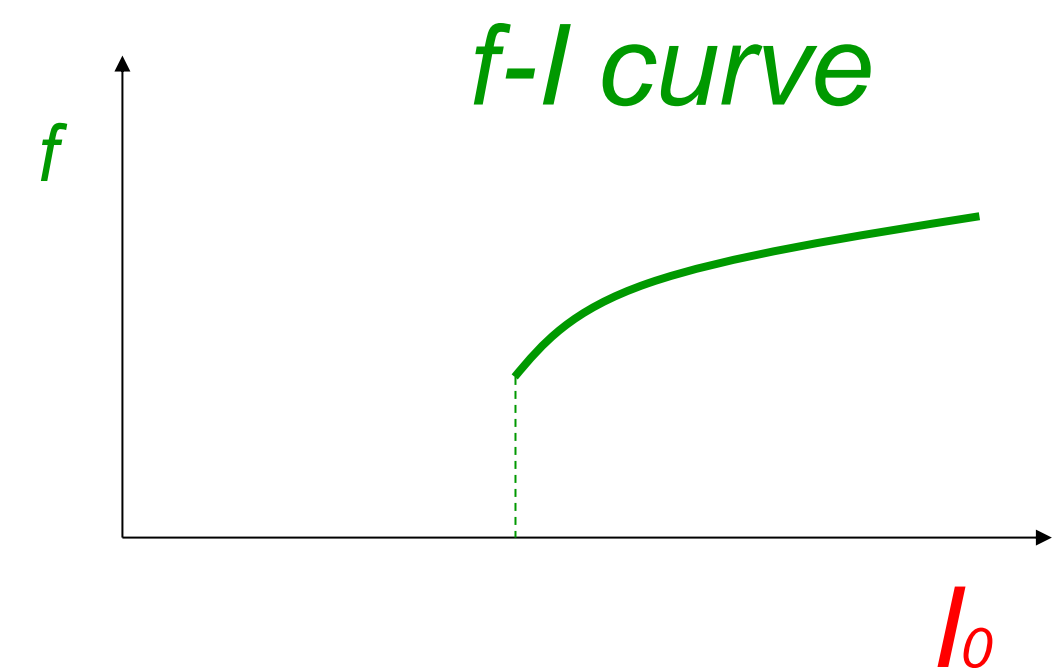
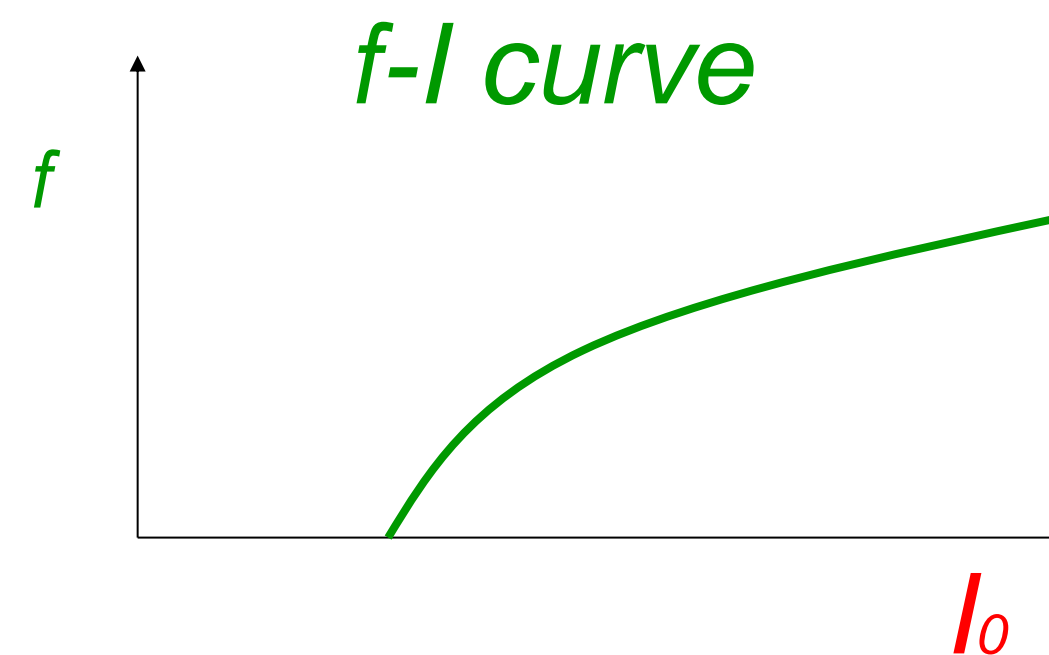
Type I

type II

Saddle-Node
Onto limit cycle

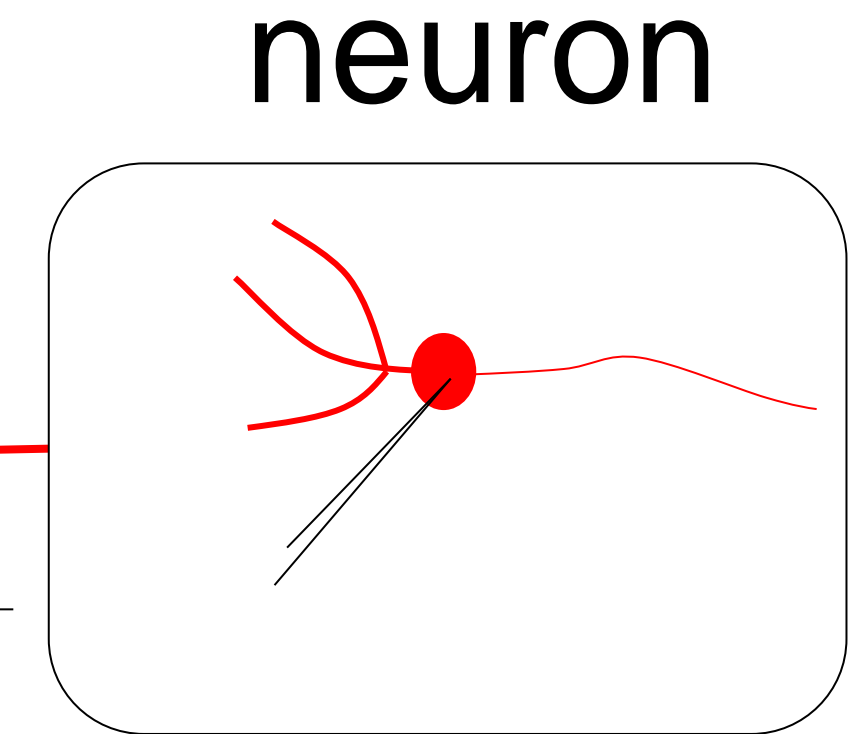
For example:
Subcritical Hopf

ramp input/
constant input

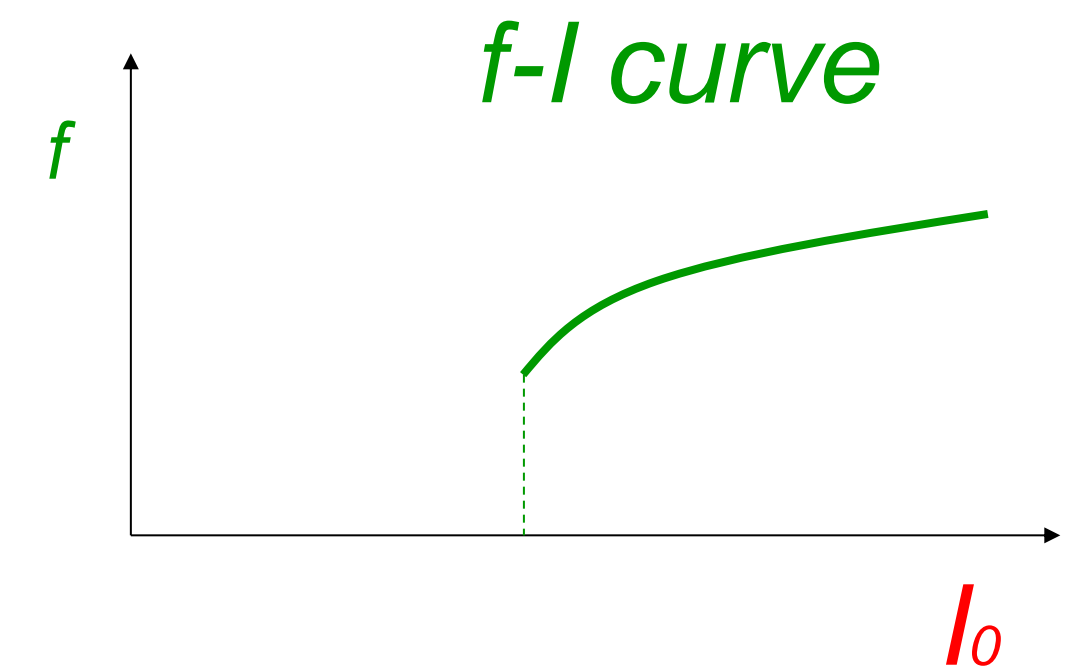
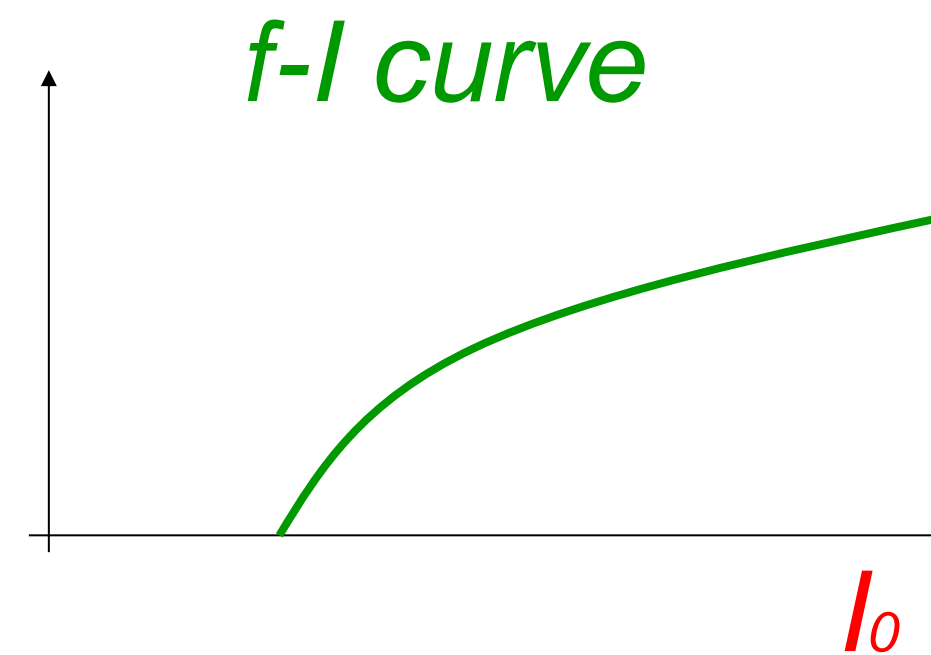


Neuronal Dynamics – 4.4. Type I and II Neuron Models

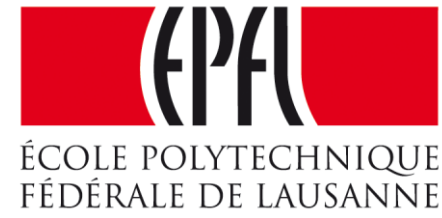
ramp input/
constant input



Type I and type II models



Week 4 – part 4b : Firing threshold in 2D models



Neuronal Dynamics: Computational Neuroscience of Single Neurons

Week 4 – Reducing detail: Two-dimensional neuron models

Wulfram Gerstner

EPFL, Lausanne, Switzerland

✓ 4.1 From Hodgkin-Huxley to 2D

✓ 4.2 Phase Plane Analysis

✓ 4.3 Analysis of a 2D Neuron Model

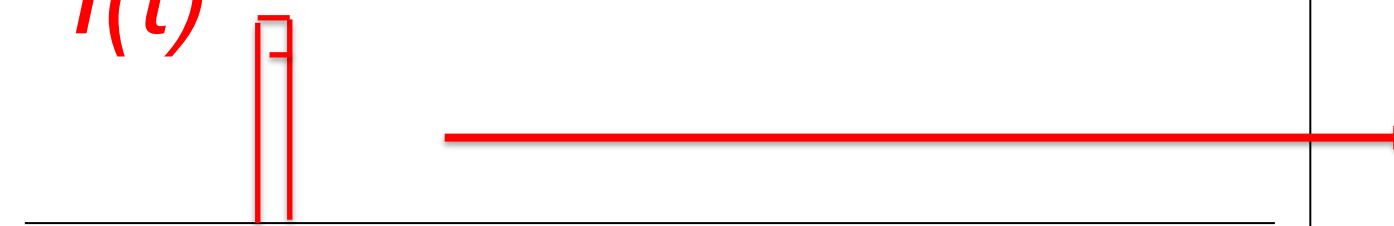
✓ 4.4 Type I and II Neuron Models
- where is the firing threshold?

4.5. Nonlinear Integrate-and-fire
- from two to one dimension

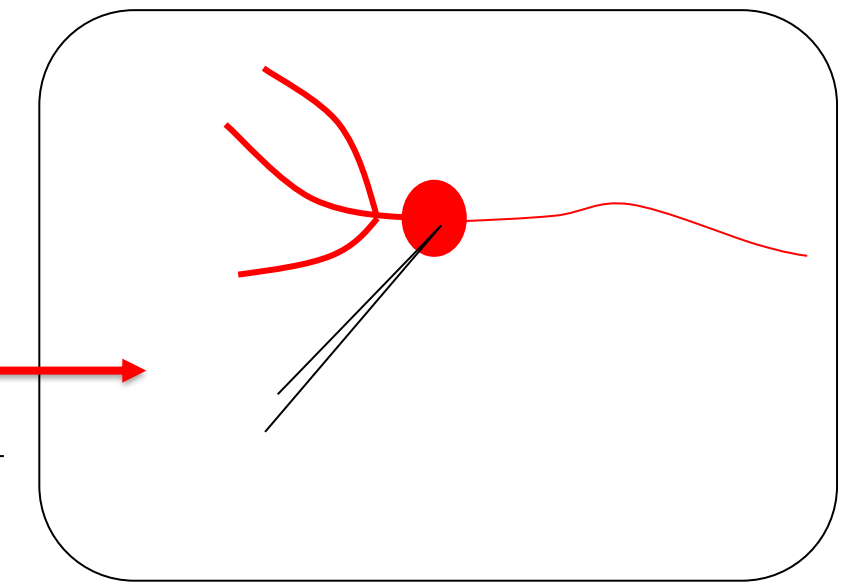
Neuronal Dynamics – 4.4b Threshold in 2dim. Neuron Models

pulse input

$I(t)$

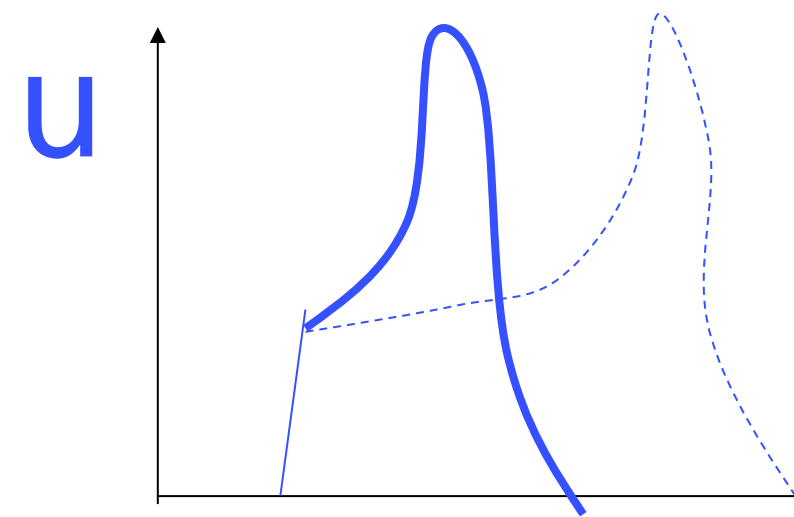


neuron



Delayed spike

Reduced amplitude



Neuronal Dynamics – 4.4 Bifurcations, simplifications

Bifurcations in neural modeling,
Type I/II neuron models,
Canonical simplified models

*Nancy Koppell,
Bart Ermentrout,
John Rinzel,
Eugene Izhikevich
and many others*

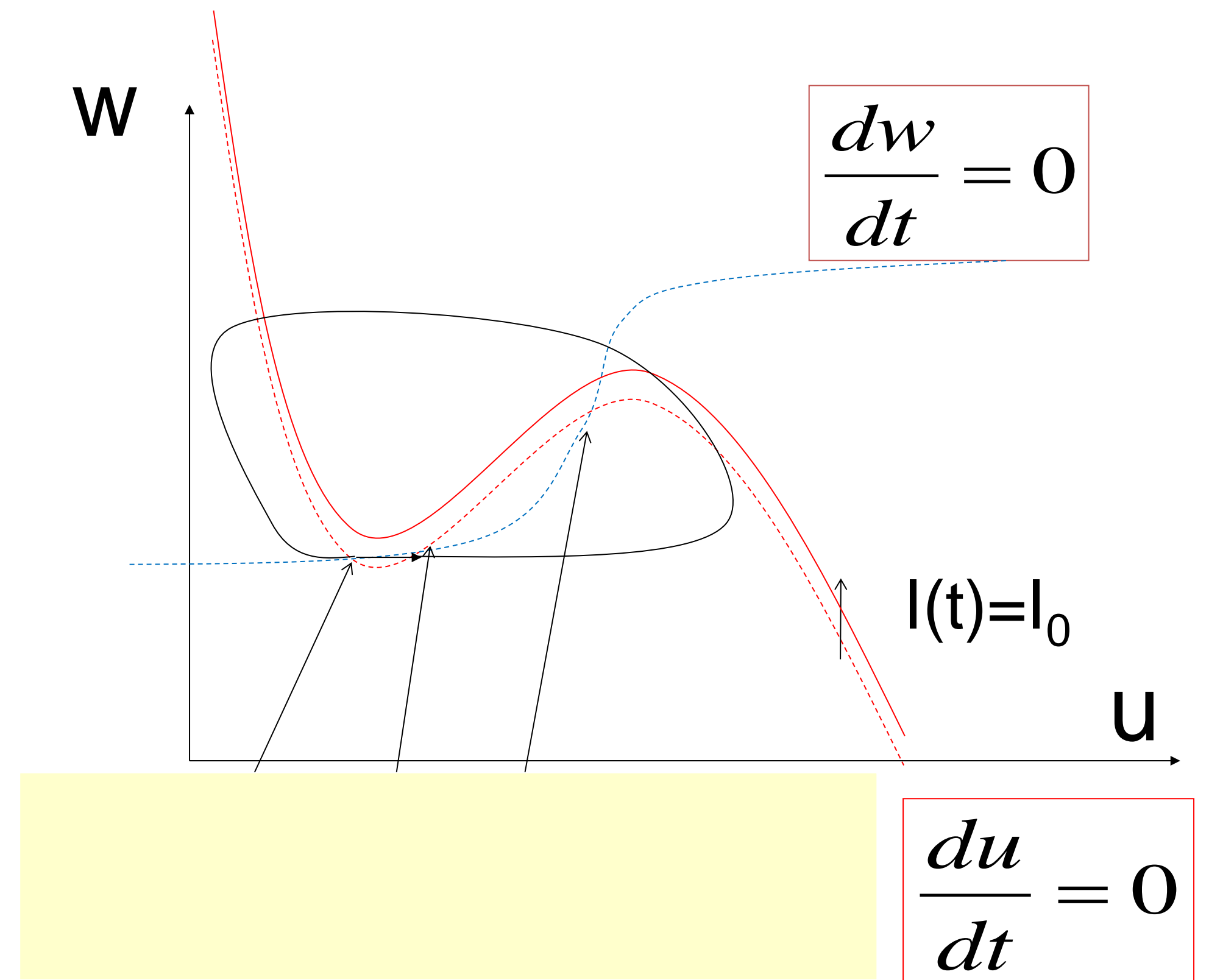
Saddle-node onto limit cycle bifurcation

stimulus



$$\tau \frac{du}{dt} = F(u, w) + RI(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$



Neuronal Dynamics – 4.4b Pulse input

stimulus

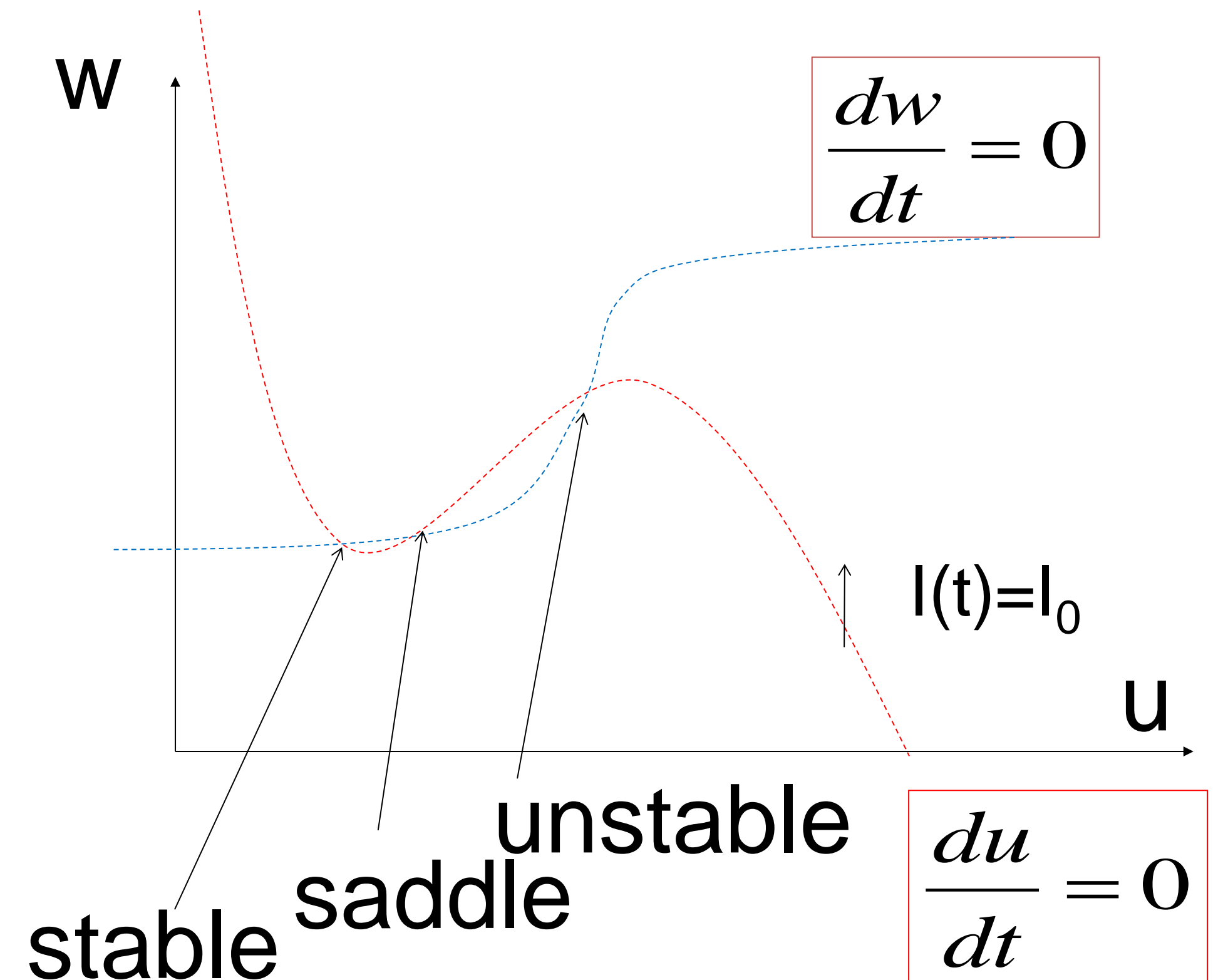
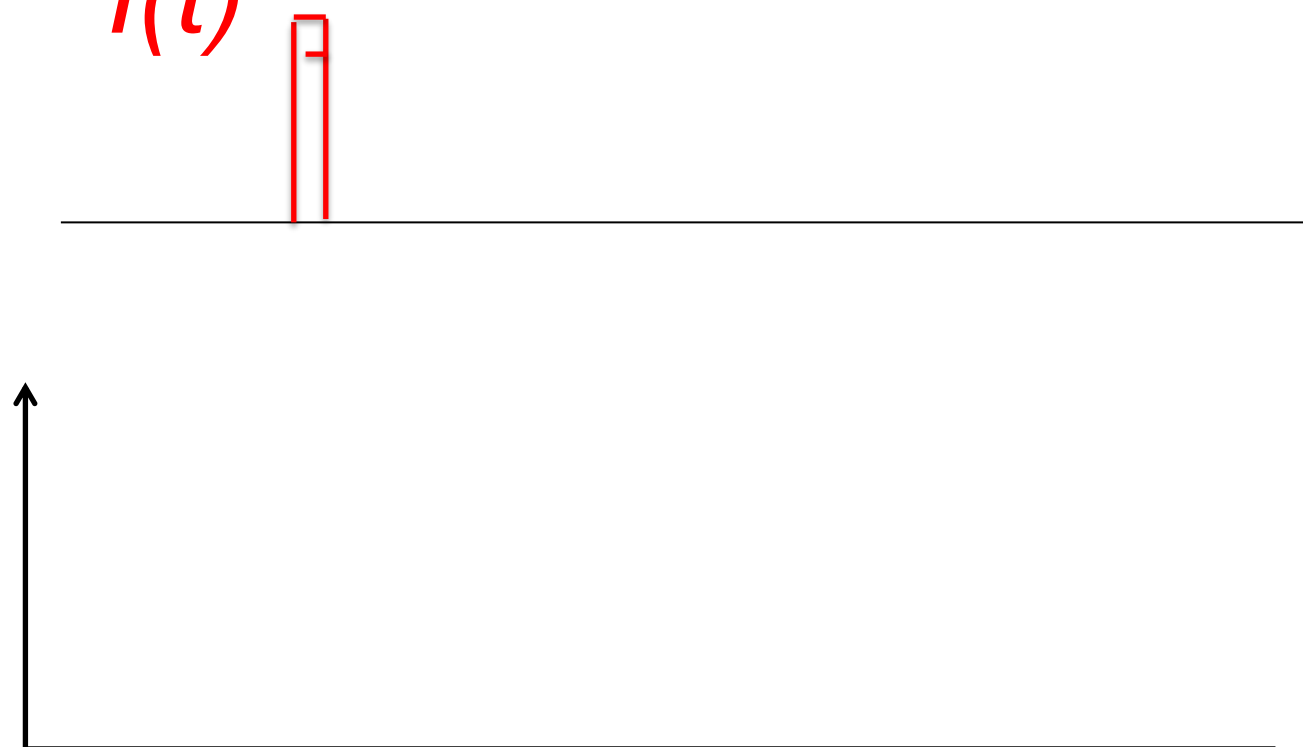


$$\tau \frac{du}{dt} = F(u, w) + RI(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

pulse input

$I(t)$

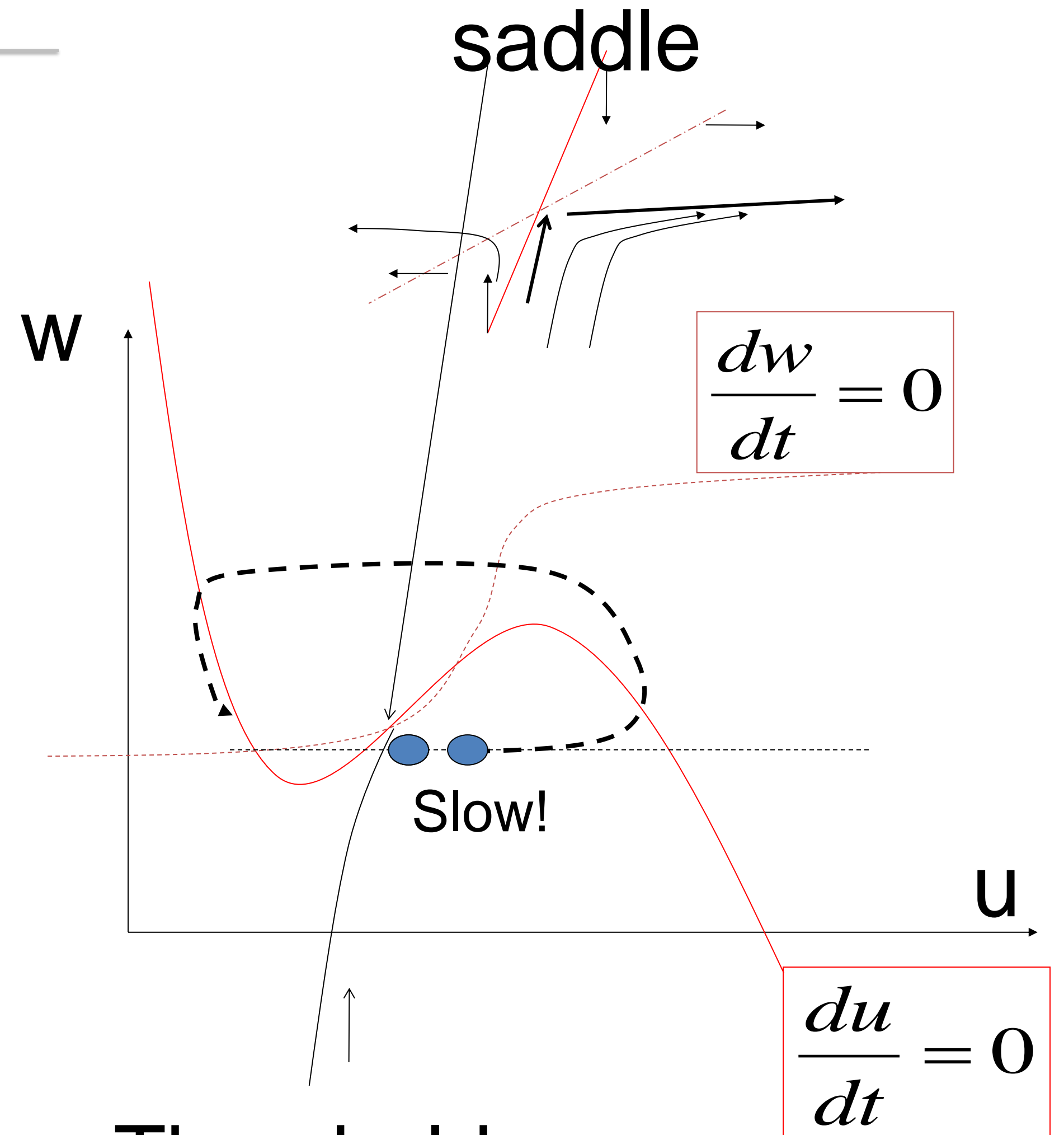
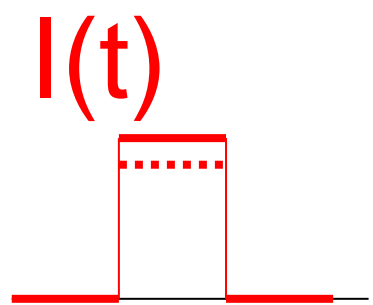


4.4b Type I model: Pulse input

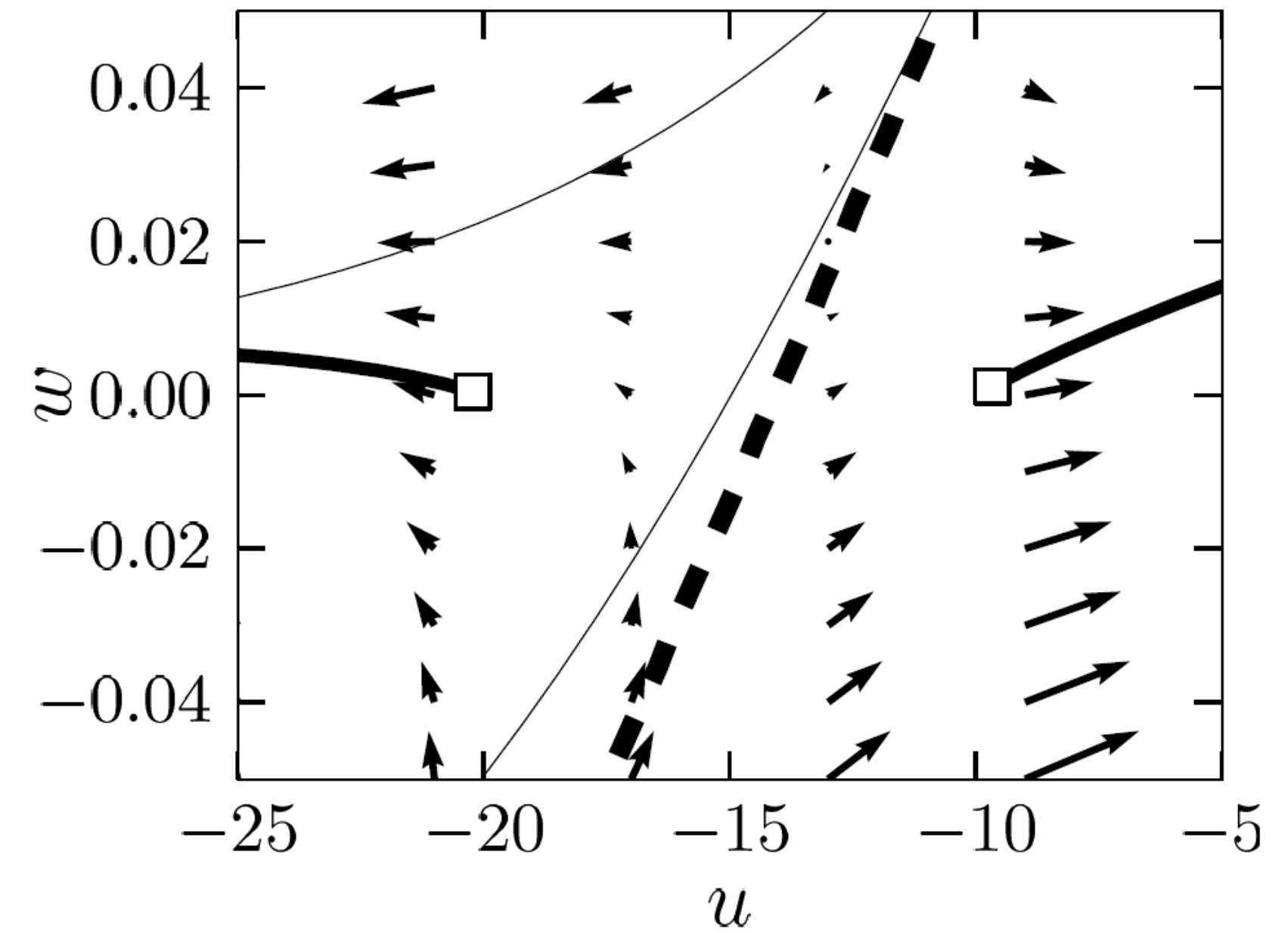
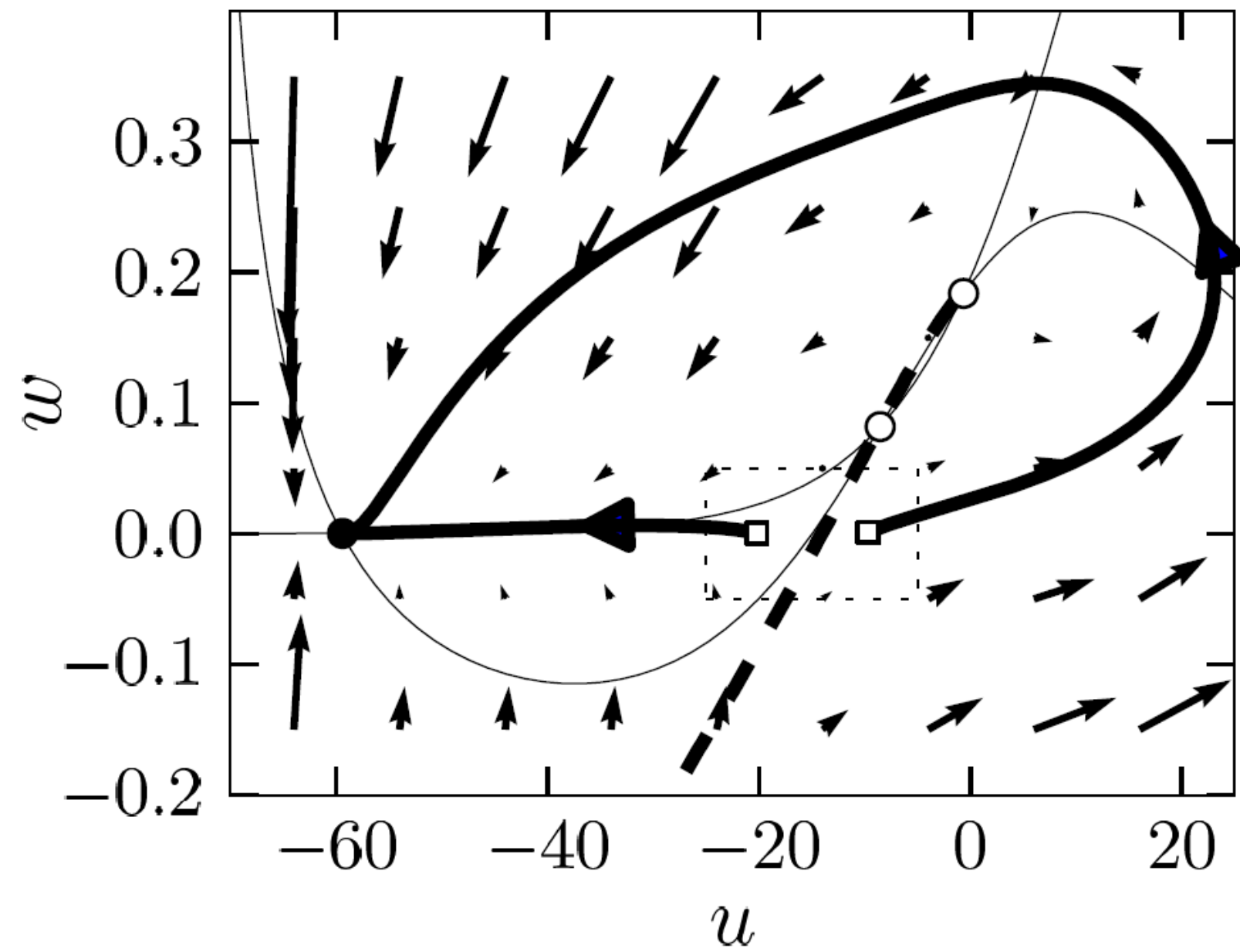
$$\tau \frac{du}{dt} = F(u, w) + \overset{\text{stimulus}}{\downarrow} RI(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

pulse input



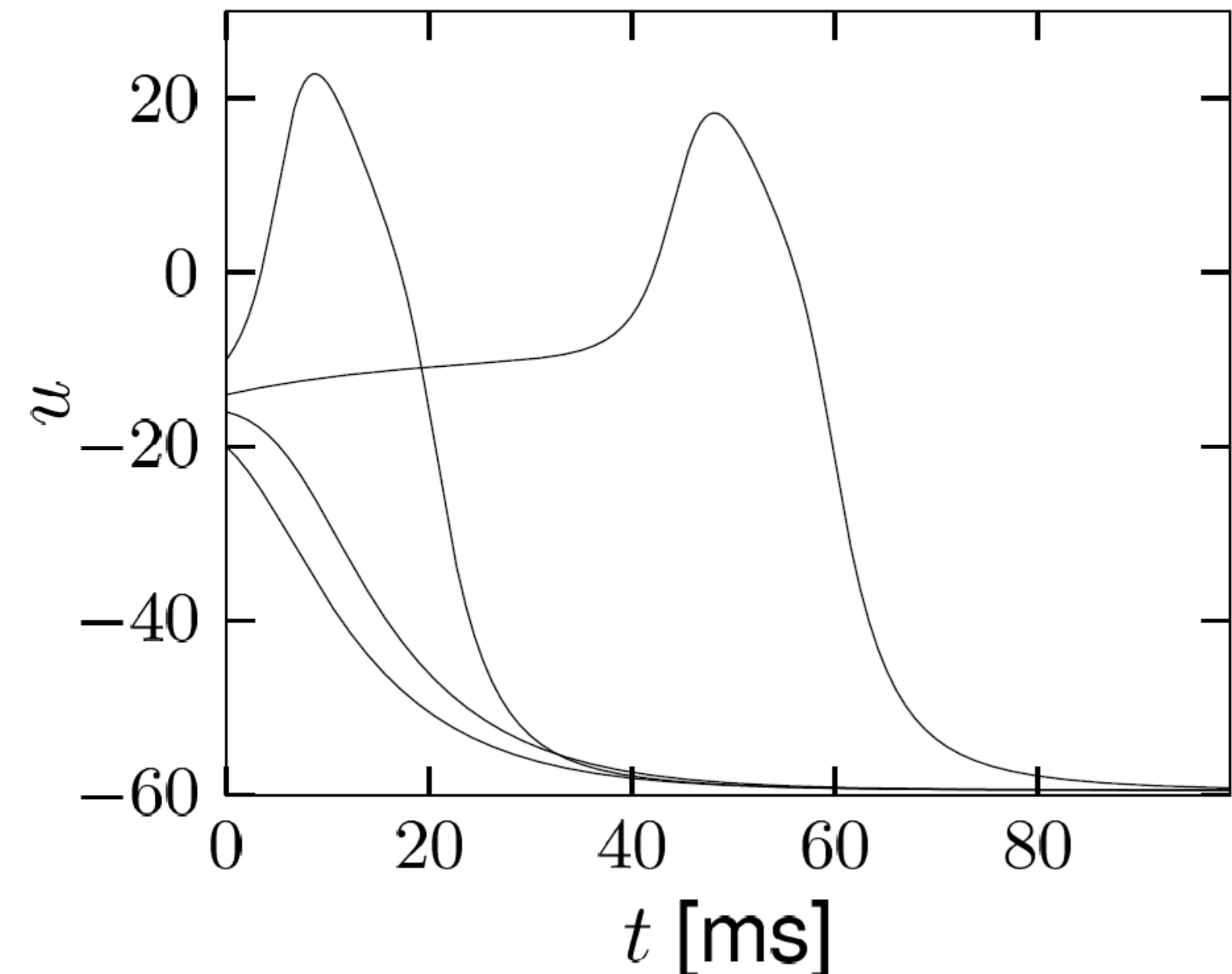
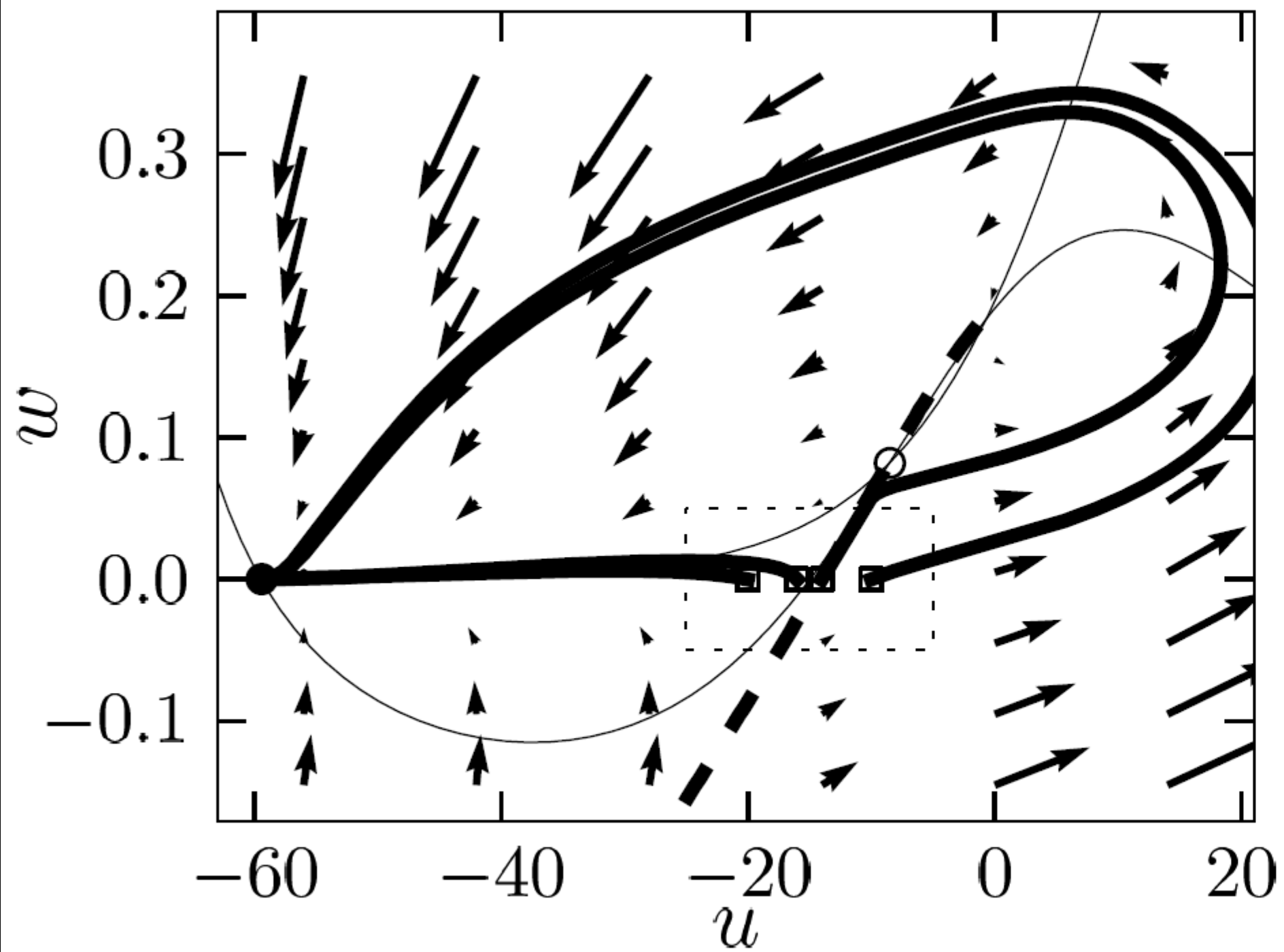
4.4b Type I model: Threshold for Pulse input



Stable manifold plays role of
'Threshold' (for pulse input)

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

4.4b Type I model: Delayed spike initiation for Pulse input

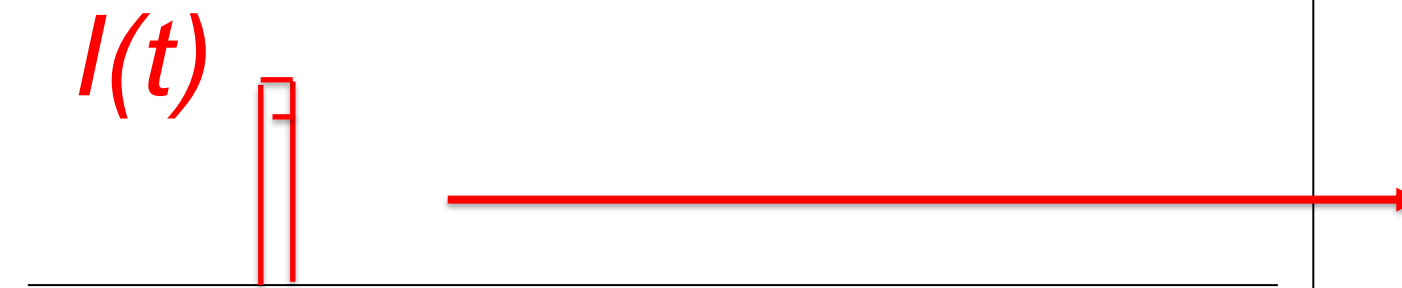


Delayed spike initiation close to
'Threshold' (for pulse input)

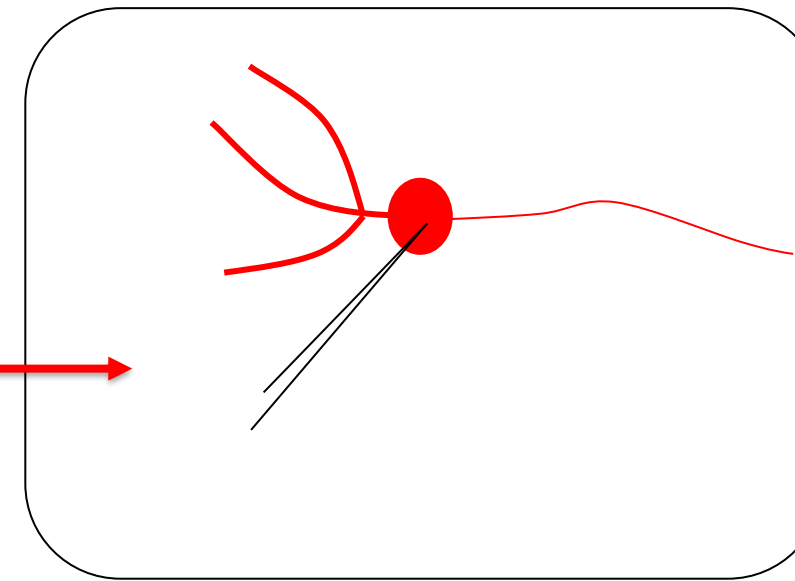
*Image: Neuronal Dynamics,
Gerstner et al.,
Cambridge Univ. Press (2014)*

Neuronal Dynamics – 4.4b Threshold in 2dim. Neuron Models

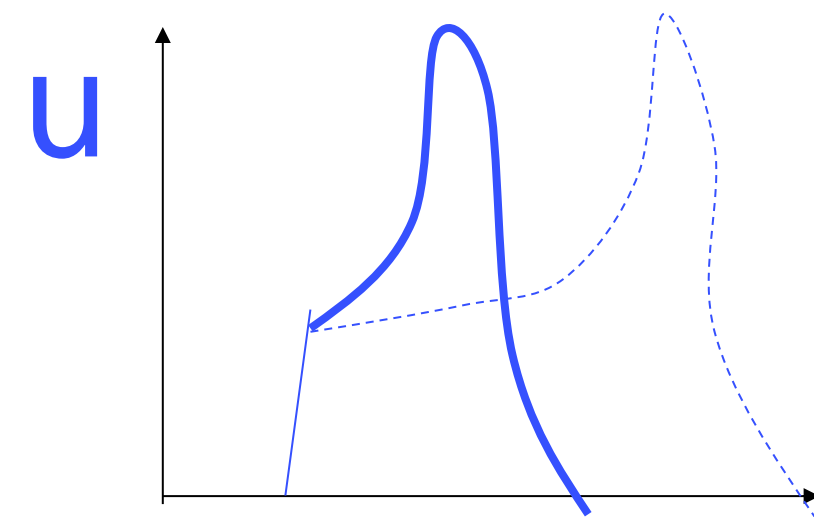
pulse input



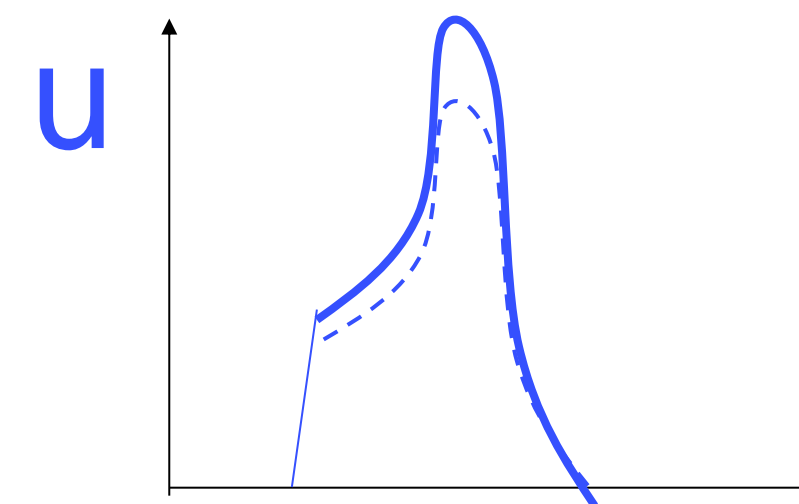
neuron



Delayed spike



Reduced amplitude



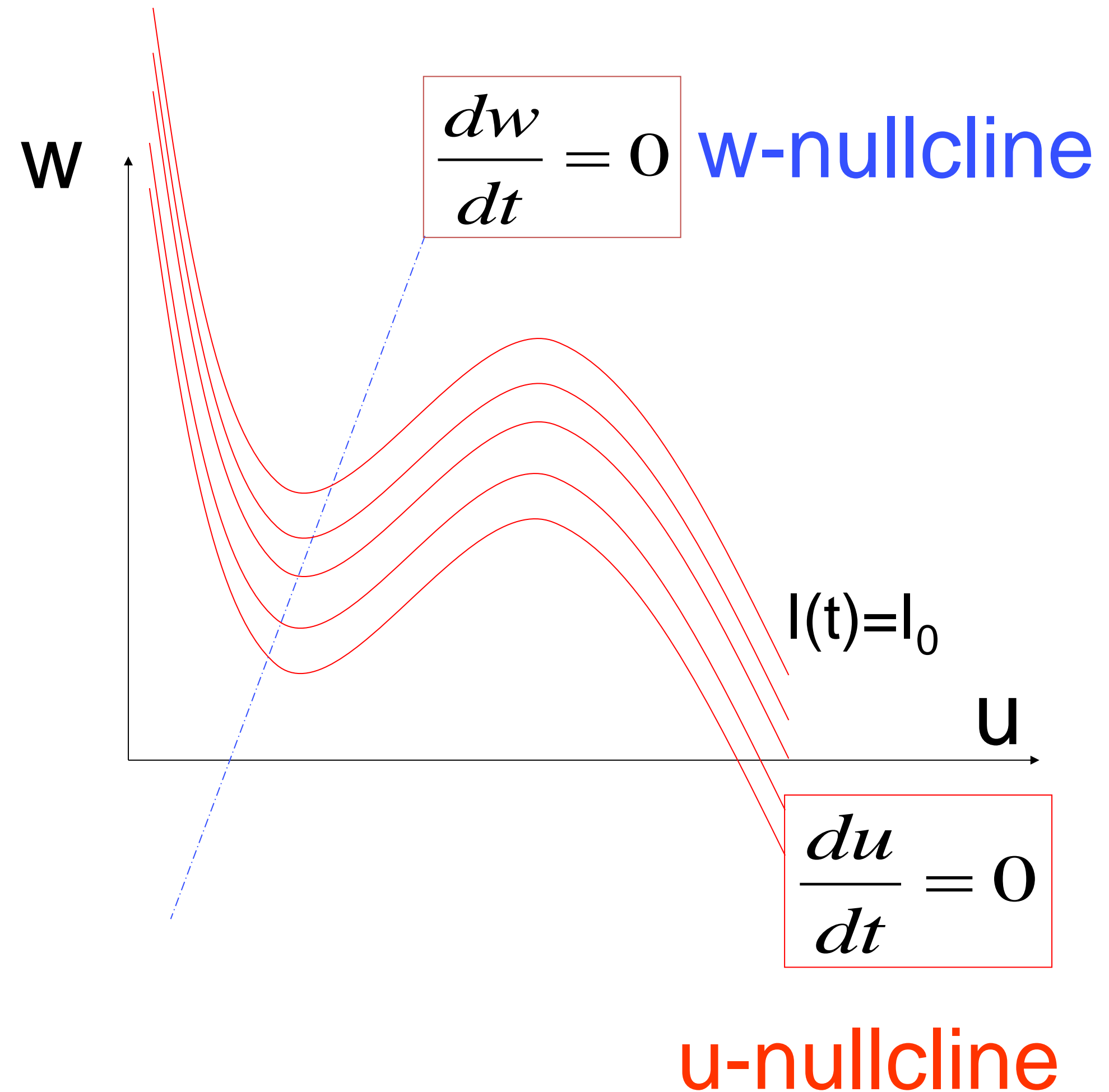
FitzHugh-Nagumo Model: Hopf bifurcation

$$\tau \frac{du}{dt} = F(u, w) + RI(t)$$

stimulus
↓

$$\tau_w \frac{dw}{dt} = G(u, w)$$

apply constant stimulus I_0

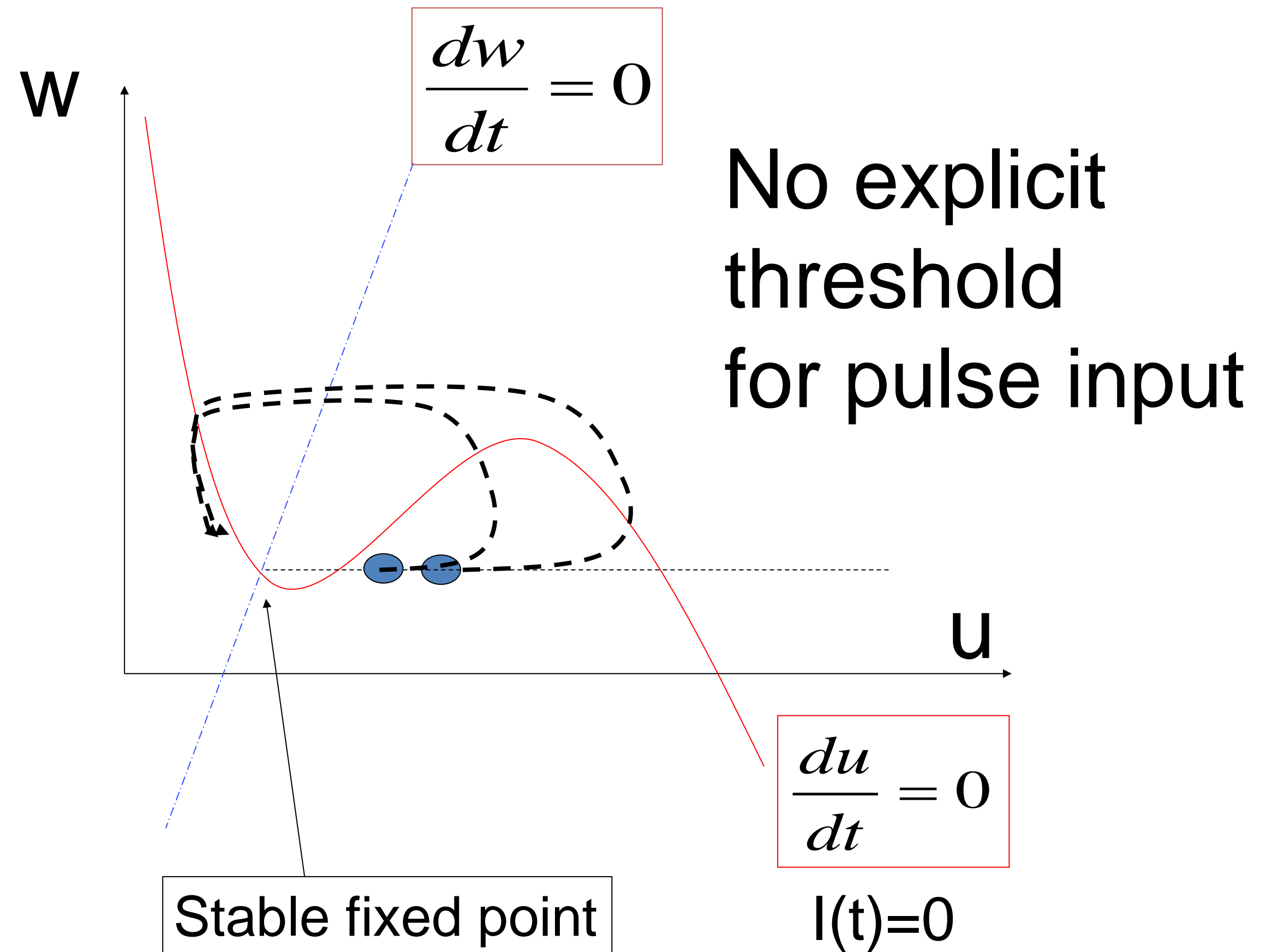
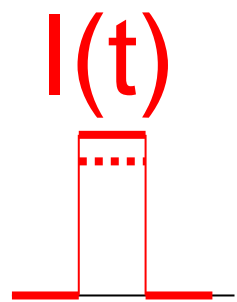


FitzHugh-Nagumo Model - pulse input

$$\tau \frac{du}{dt} = F(u, w) + \overset{\text{stimulus}}{RI(t)}$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

pulse input



FitzHugh-Nagumo Model - pulse input threshold?

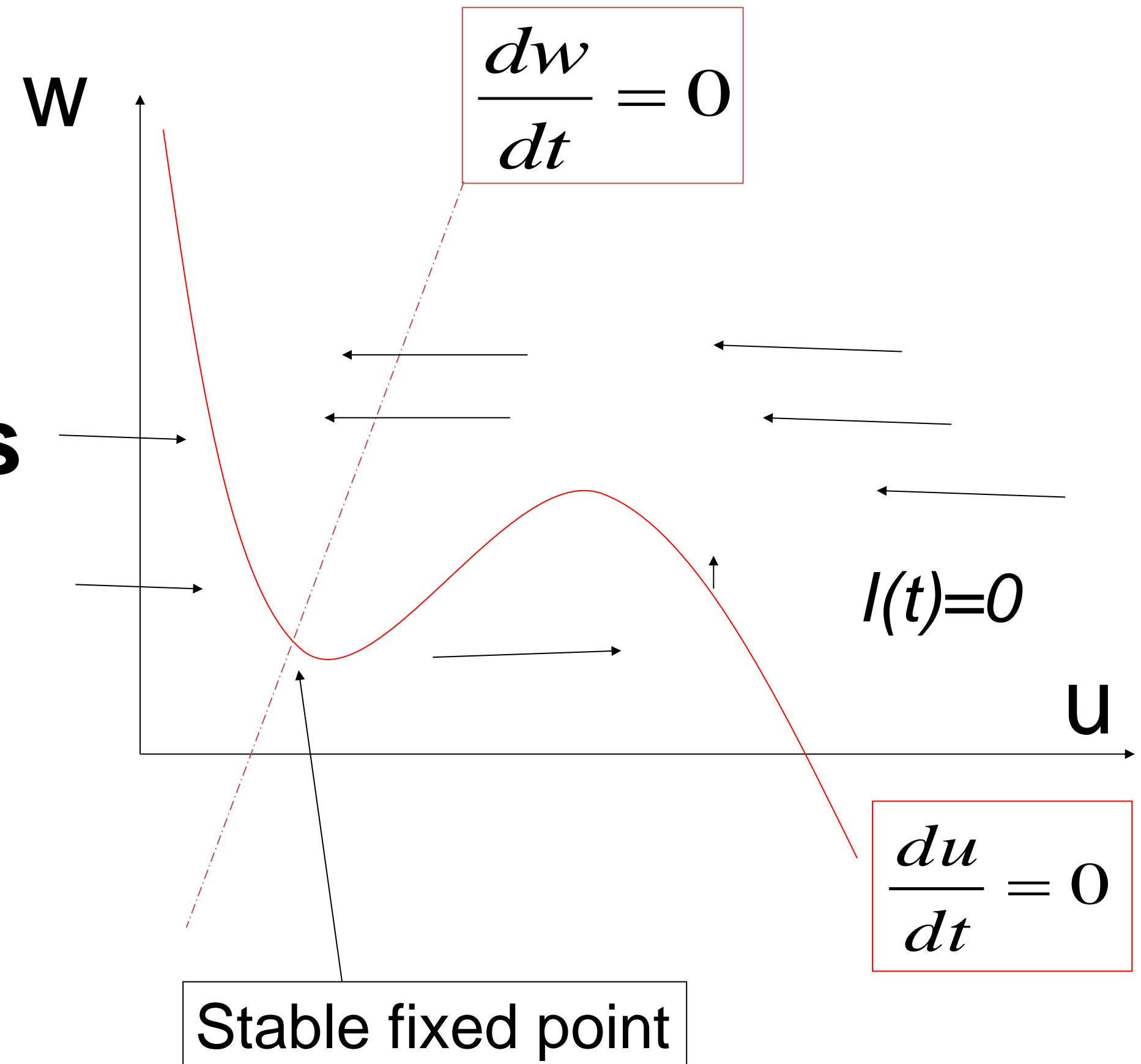
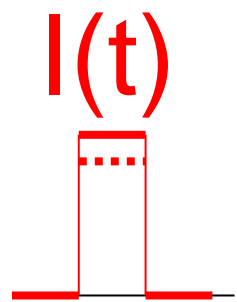
$$\tau \frac{du}{dt} = F(u, w) + \overset{\text{stimulus}}{\downarrow} RI(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

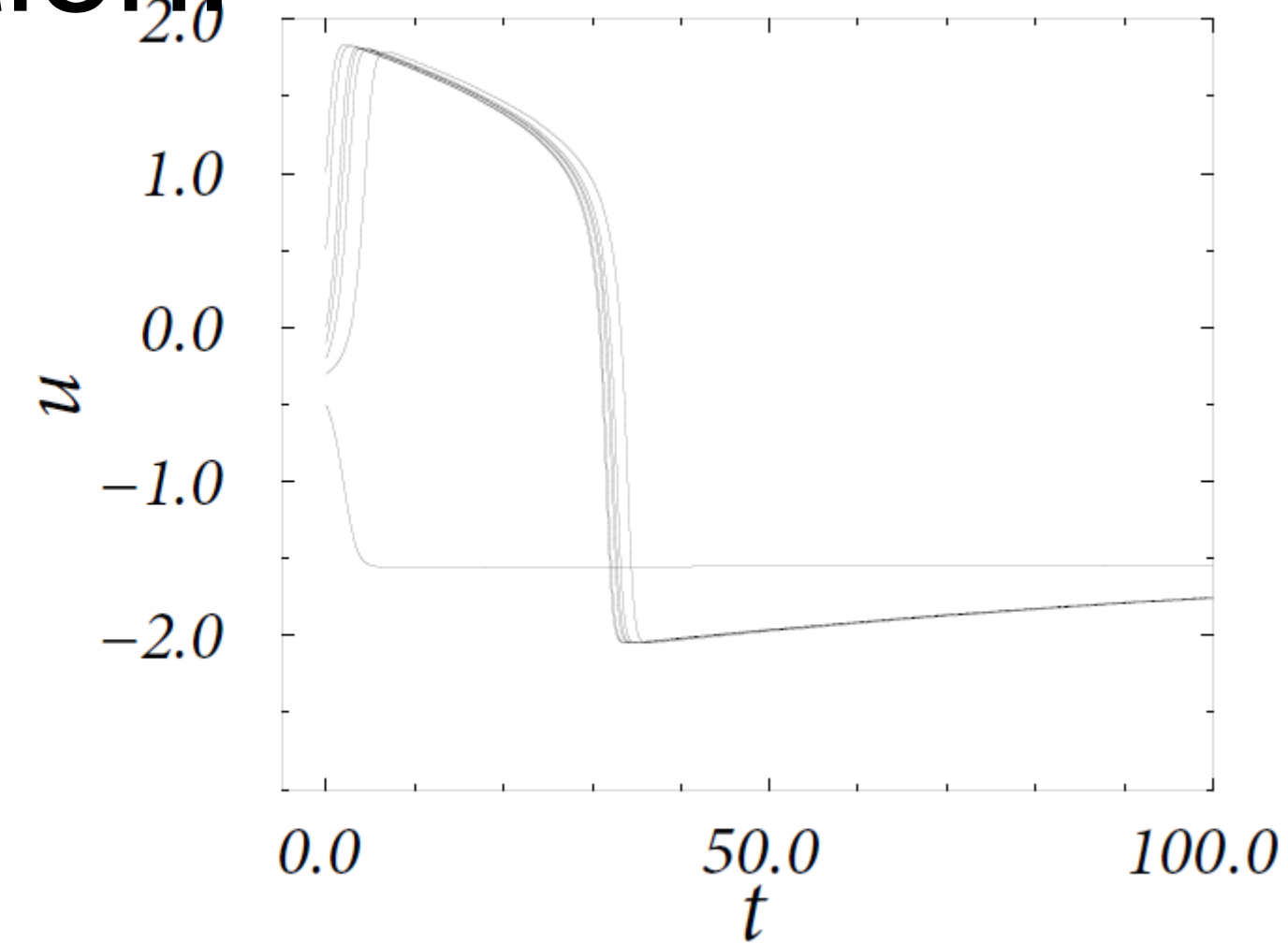
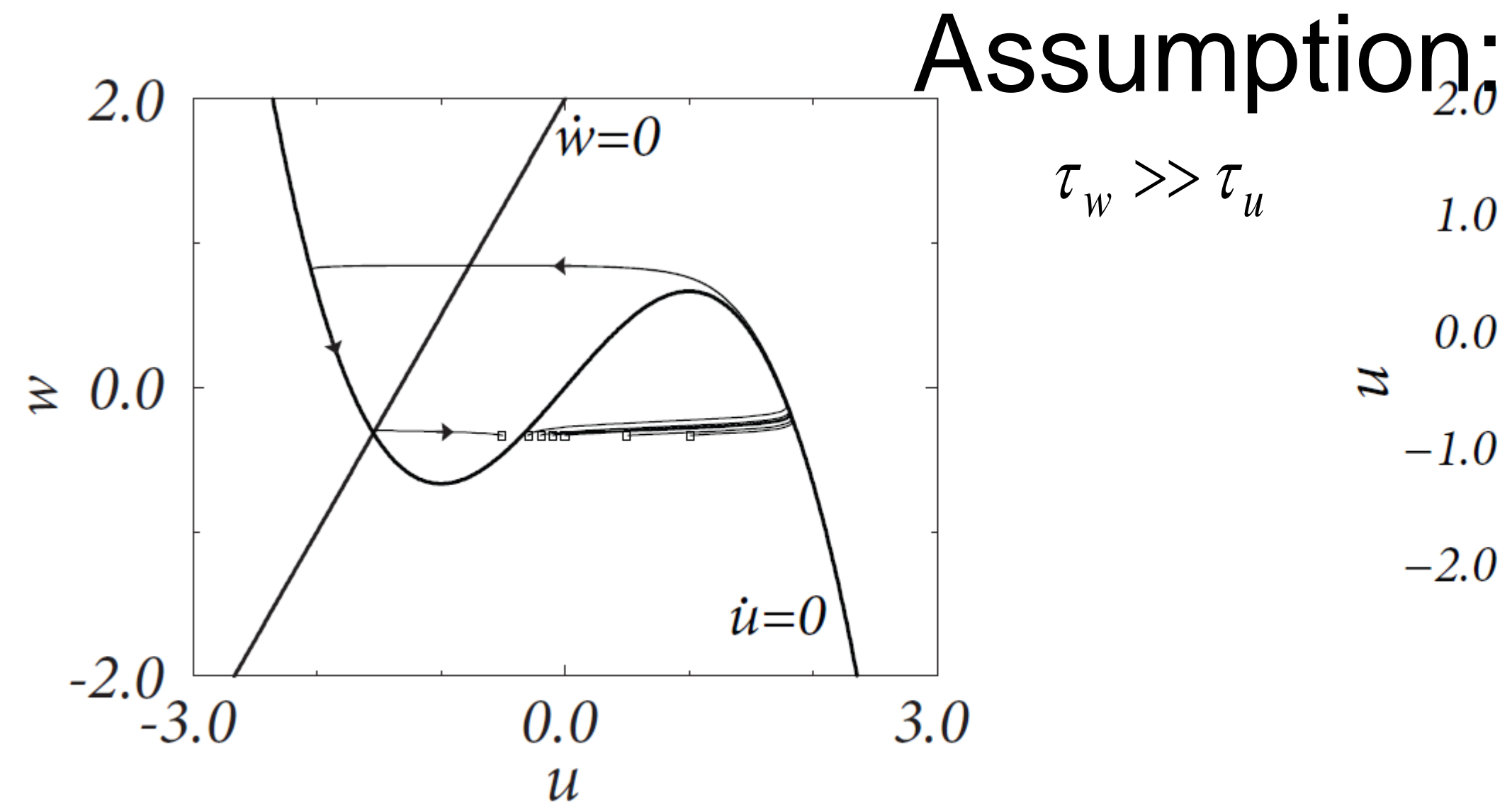
Separation of time scales

pulse input

$$\tau_w \gg \tau_u$$



4.4b FitzHugh-Nagumo model: Threshold for Pulse input



Middle branch of u -nullcline
plays role of
'Threshold' (for pulse input)

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

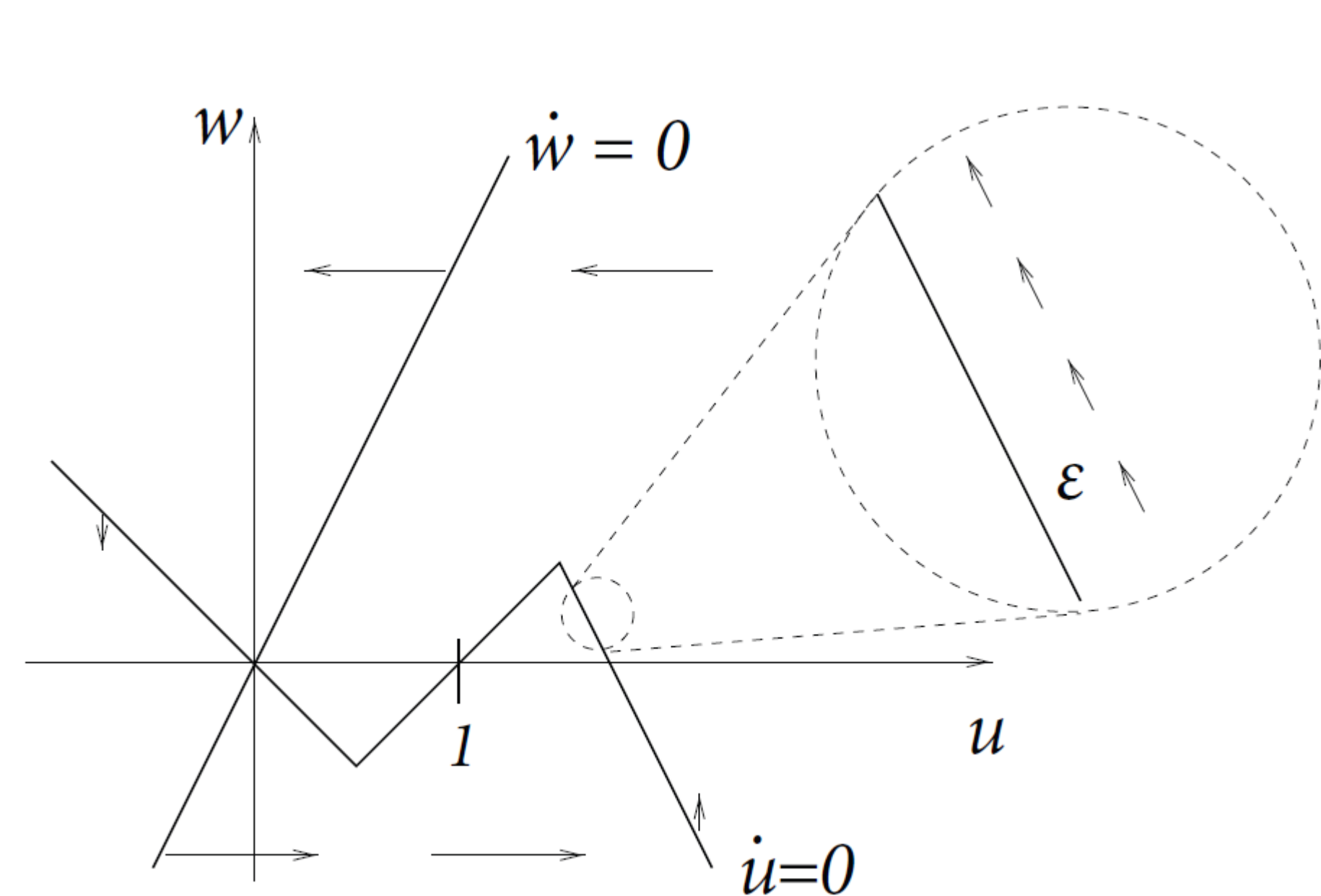
4.4b Detour: Separation of time scales in 2dim models

$$\tau \frac{du}{dt} = F(u, w) + \overset{\text{stimulus}}{\downarrow} RI(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

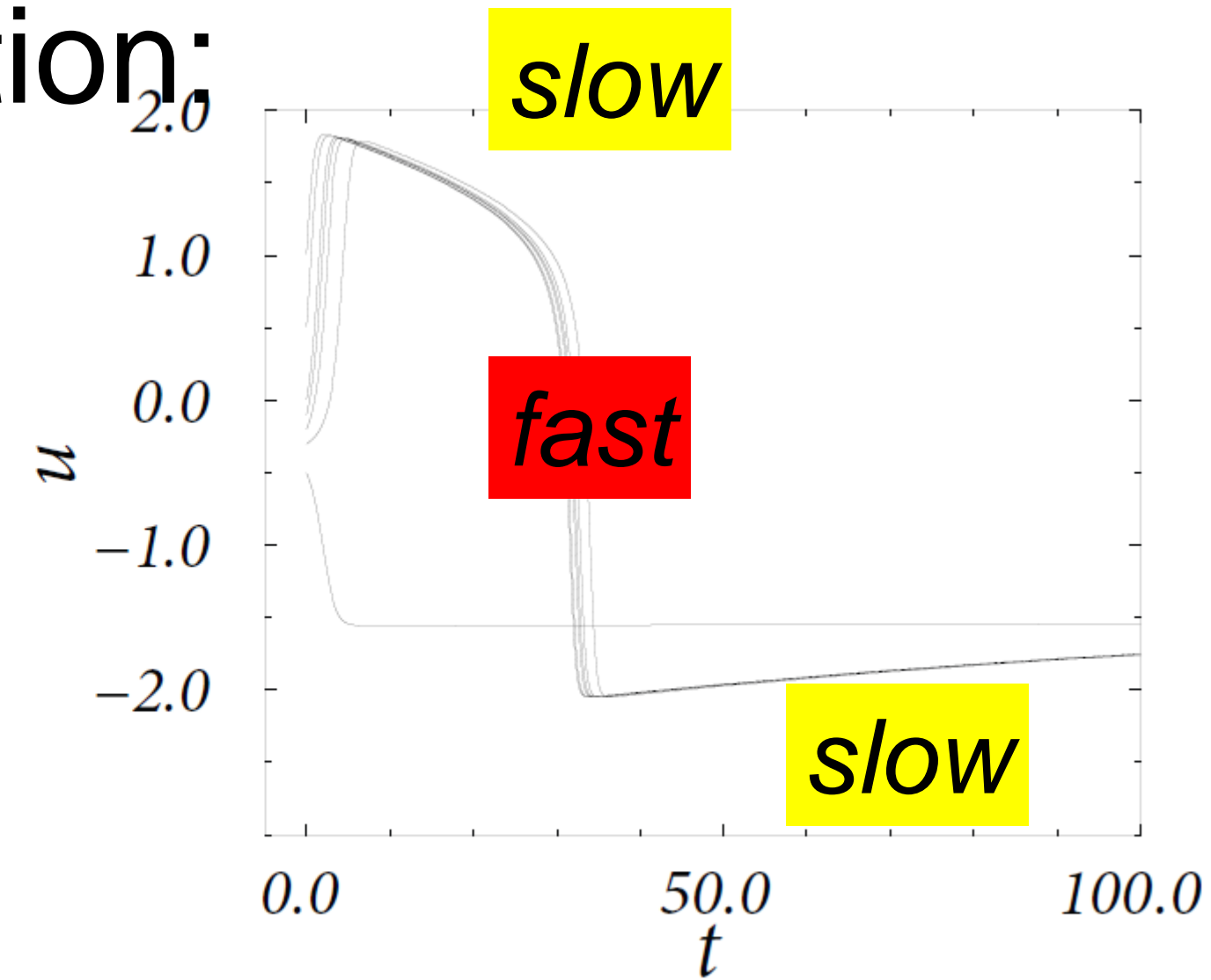
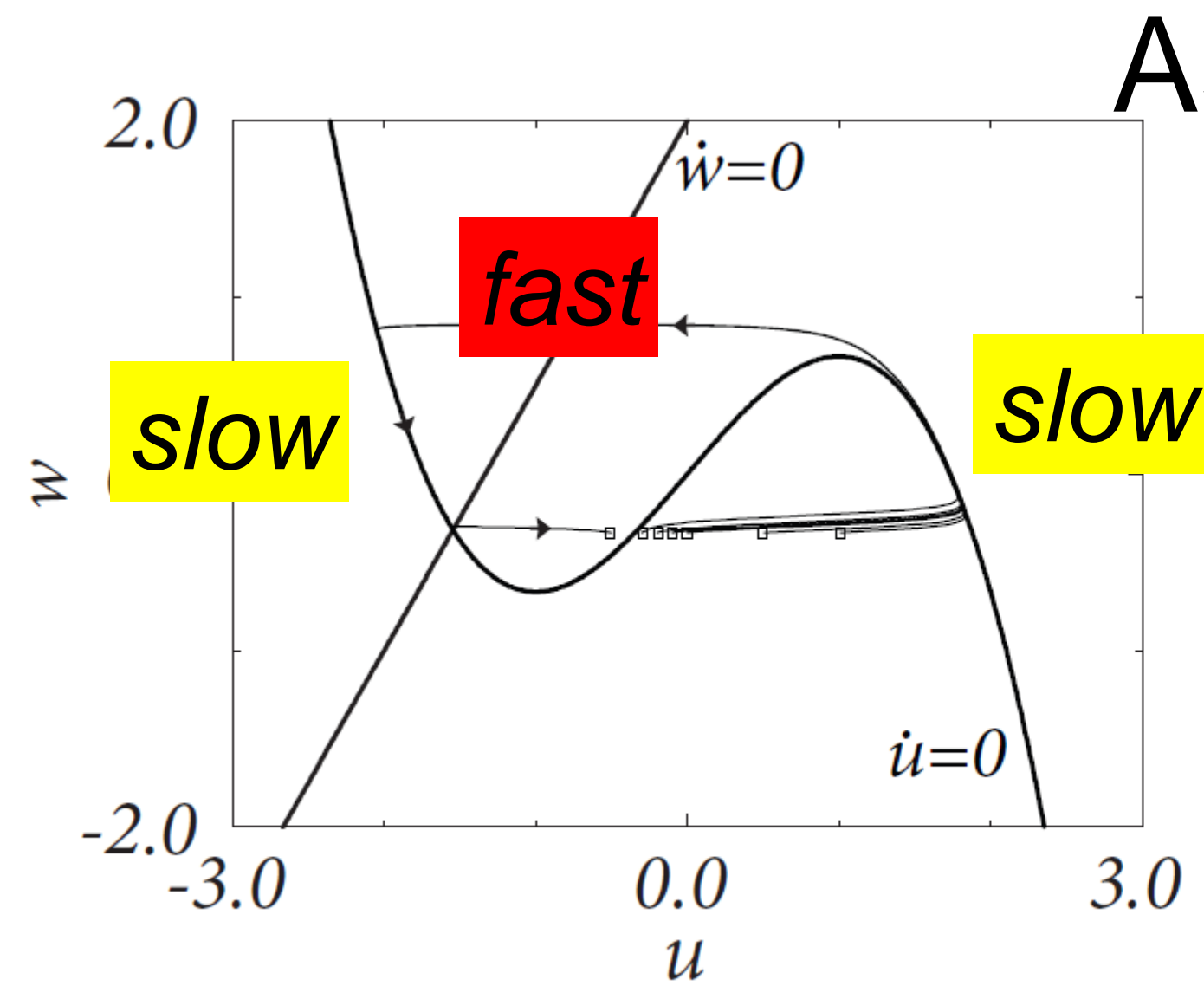
Assumption:

$$\tau_w \gg \tau_u$$



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

4.4b FitzHugh-Nagumo model: Threshold for Pulse input



trajectory

-follows u -nullcline: **slow**

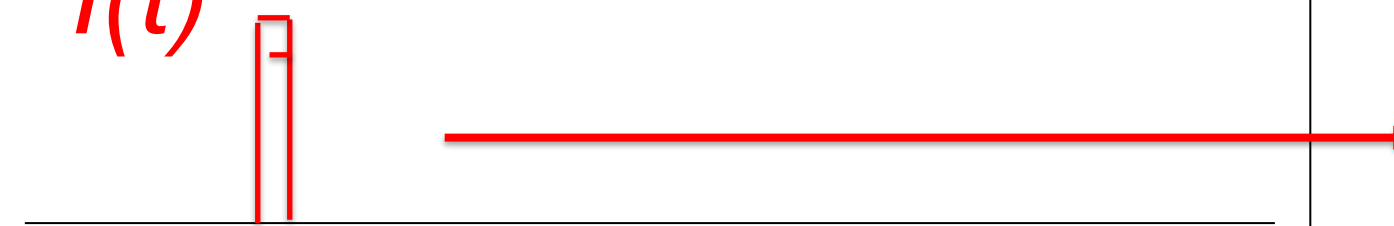
-jumps between branches: **fast**

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

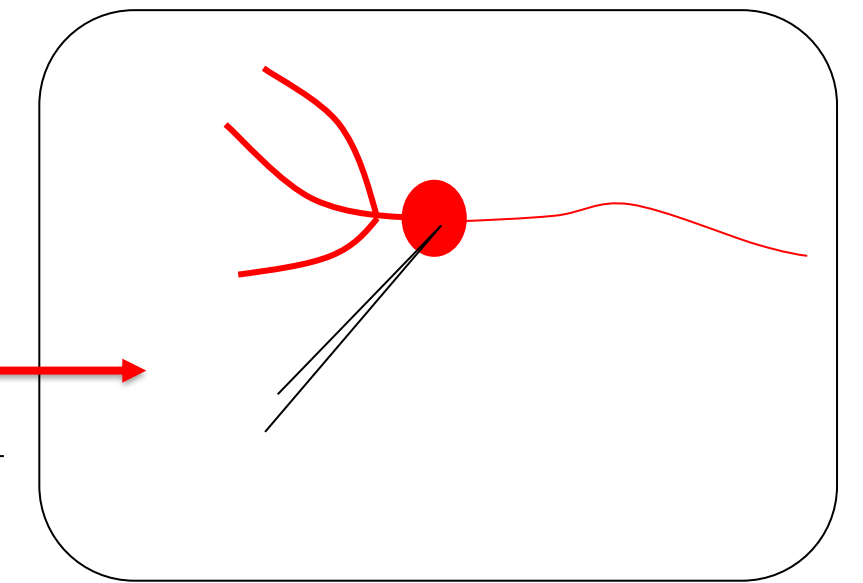
Neuronal Dynamics – 4.4b Threshold in 2dim. Neuron Models

pulse input

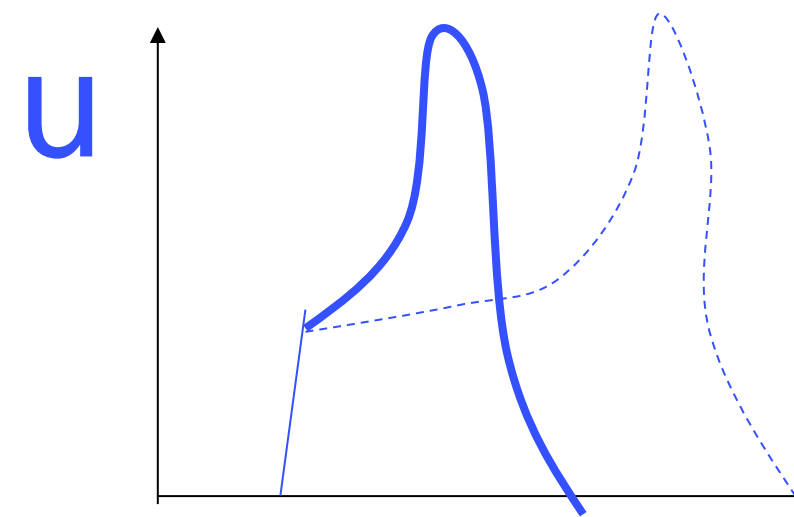
$I(t)$



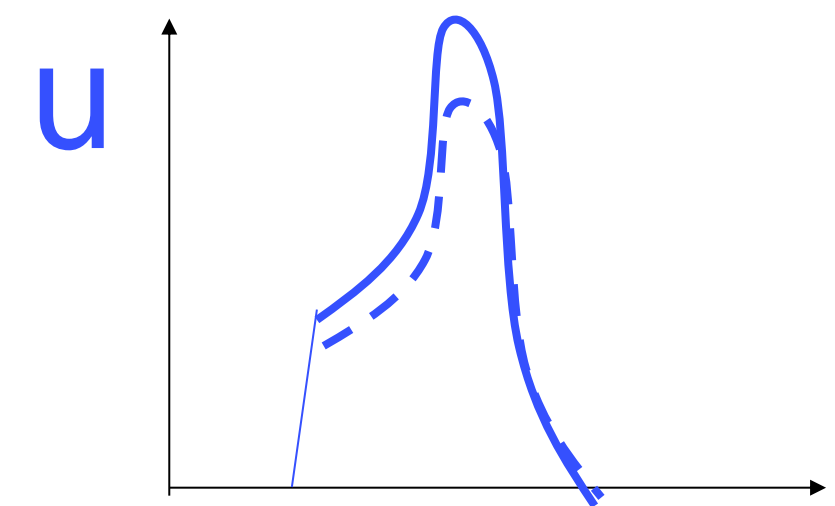
neuron



Delayed spike



Reduced amplitude



Neuronal Dynamics – 4.4 Literature

Reading: W. Gerstner, W.M. Kistler, R. Naud and L. Paninski,

Neuronal Dynamics: from single neurons to networks and

models of cognition. Chapter 4: *Introduction*. Cambridge Univ. Press, 2014

OR W. Gerstner and W.M. Kistler, *Spiking Neuron Models*, Ch.3. Cambridge 2002

OR J. Rinzel and G.B. Ermentrout, (1989). Analysis of neuronal excitability and oscillations.

In Koch, C. Segev, I., editors, *Methods in neuronal modeling*. MIT Press, Cambridge, MA.

Selected references.

-Ermentrout, G. B. (1996). *Type I membranes, phase resetting curves, and synchrony*.

Neural Computation, 8(5):979-1001.

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Biological Cybernetics, 99(4-5):361-370.

- E.M. Izhikevich, *Dynamical Systems in Neuroscience*, MIT Press (2007)

Neuronal Dynamics – Quiz 4.6.

A. Threshold in a 2-dimensional neuron model with saddle-node bifurcation

- ☐ The voltage threshold for repetitive firing is always the same as the voltage threshold for pulse input.
- ☐ in the regime below the saddle-node bifurcation, the voltage threshold for repetitive firing is given by the stable manifold of the saddle.
- ☐ in the regime below the saddle-node bifurcation, the voltage threshold for repetitive firing is given by the middle branch of the u-nullcline.
- ☐ in the regime below the saddle-node bifurcation, the voltage threshold for action potential firing in response to a short pulse input is given by the middle branch of the u-nullcline.
- ☐ in the regime below the saddle-node bifurcation, the voltage threshold for action potential firing in response to a short pulse input is given by the stable manifold of the saddle point.

B. Threshold in a 2-dimensional neuron model with subcritical Hopf bifurcation

- ☐ in the regime below the bifurcation, the voltage threshold for action potential firing in response to a short pulse input is given by the stable manifold of the saddle point.
- ☐ in the regime below the bifurcation, a voltage threshold for action potential firing in response to a short pulse input exists only if $\tau_w \gg \tau_u$

Week 4 – part 4b : Firing threshold in 2D models



Neuronal Dynamics: Computational Neuroscience of Single Neurons

Week 4 – Reducing detail: Two-dimensional neuron models

Wulfram Gerstner

EPFL, Lausanne, Switzerland

✓ 4.1 From Hodgkin-Huxley to 2D

✓ 4.2 Phase Plane Analysis


✓ 4.3 Analysis of a 2D Neuron Model

✓ 4.4 Type I and II Neuron Models
- where is the firing threshold?

4.5. Nonlinear Integrate-and-fire
- from two to one dimension

Neuronal Dynamics – 4.5. Further reduction to 1 dimension

2-dimensional equation stimulus

$$\tau \frac{du}{dt} = F(u, w) + RI(t)$$


$$\tau_w \frac{dw}{dt} = G(u, w)$$

slow!

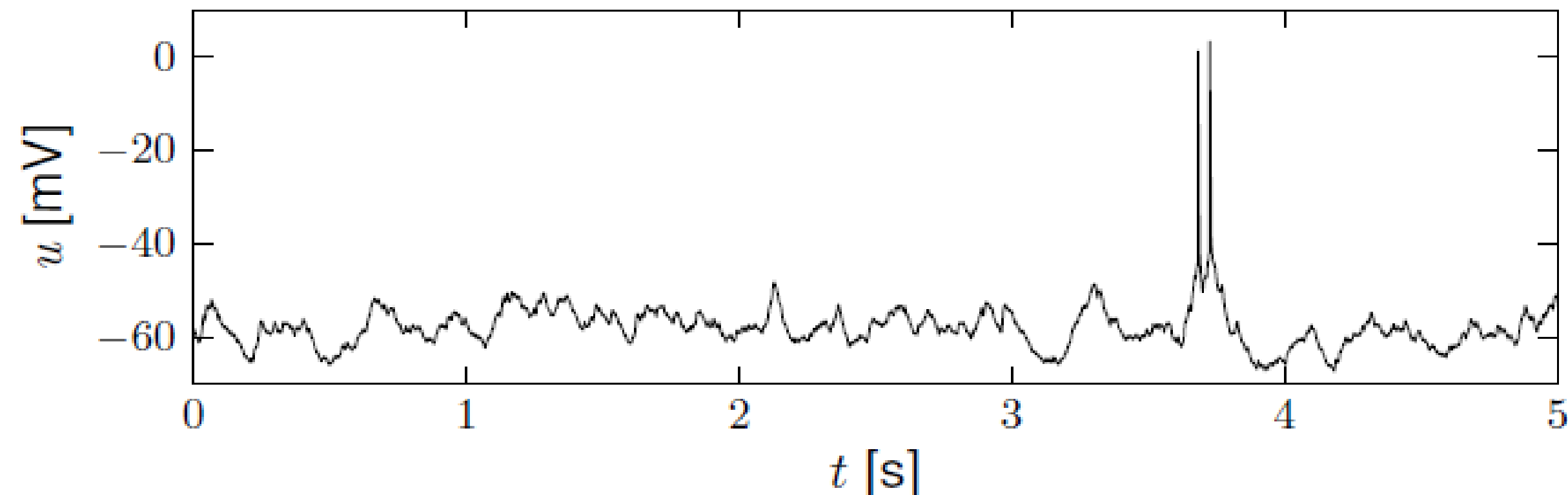
Separation of time scales

**-w is nearly constant
(most of the time)**

Neuronal Dynamics – 4.2 sparse activity in vivo

Spontaneous activity *in vivo*

awake mouse, cortex, freely whisking,



-spikes are rare events

Crochet et al., 2011

-membrane potential fluctuates around 'rest'

Aims of Modeling:

- predict spike initiation times
- predict subthreshold voltage

Neuronal Dynamics – 4.5. Further reduction to 1 dimension

stimulus



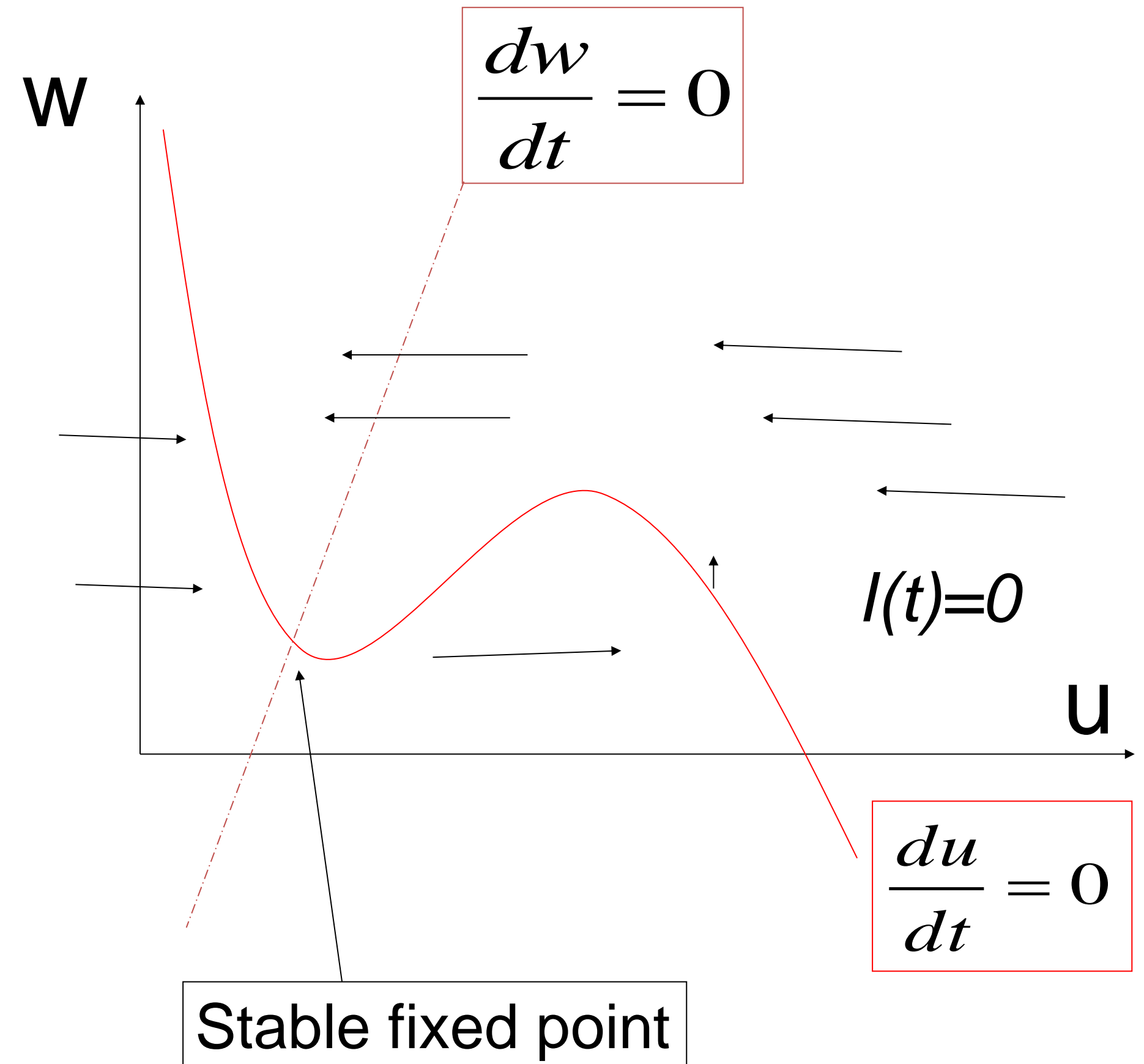
$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

Separation of time scales

$$\tau_w \gg \tau_u$$

→ Flux nearly horizontal



Neuronal Dynamics – 4.2. Further reduction to 1 dimension

Hodgkin-Huxley reduced to 2dim

$$\frac{dw}{dt} = 0$$

$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

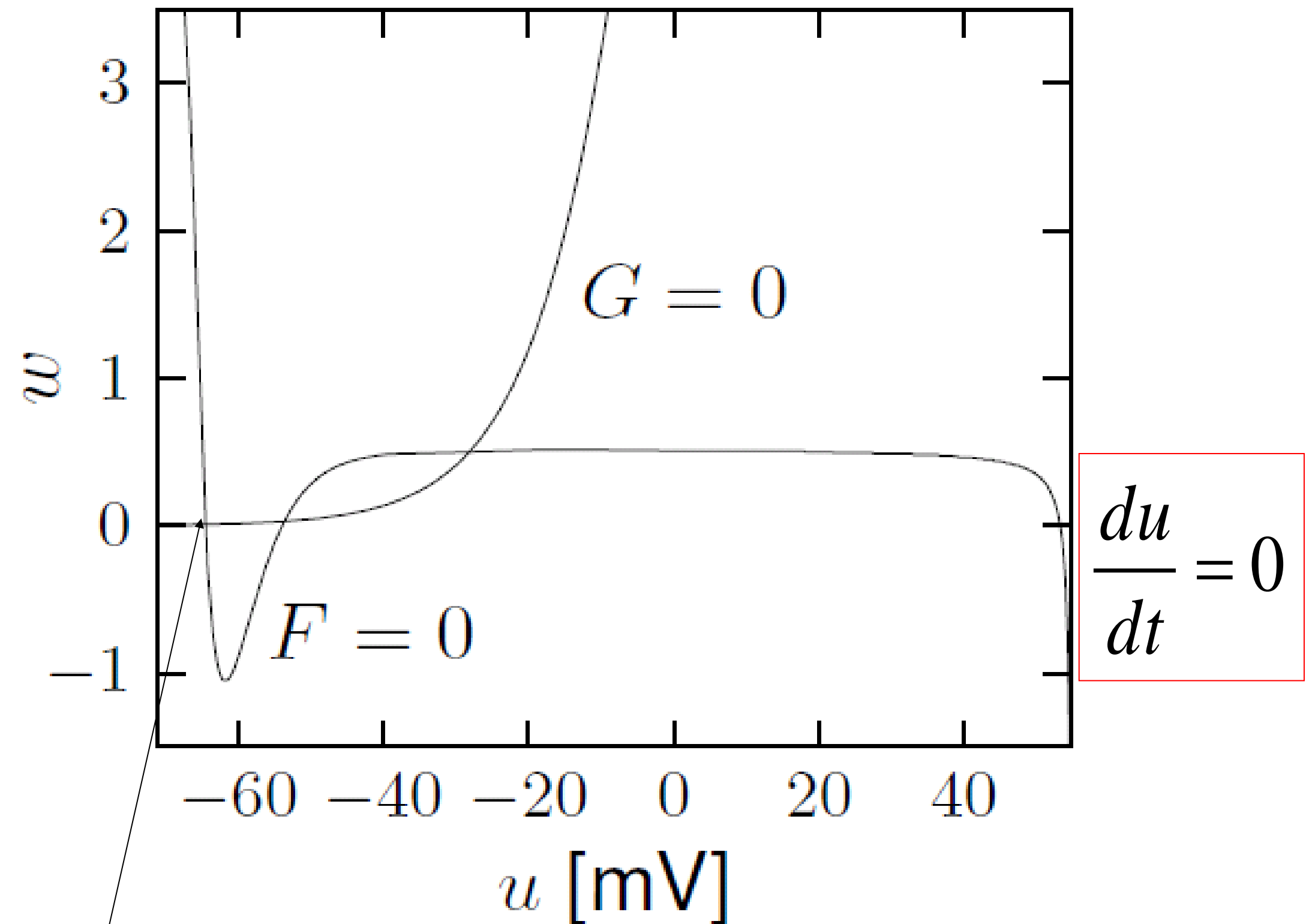
$$\tau_w \frac{dw}{dt} = G(u, w)$$

Separation of time scales

$$\tau_w \gg \tau_u$$

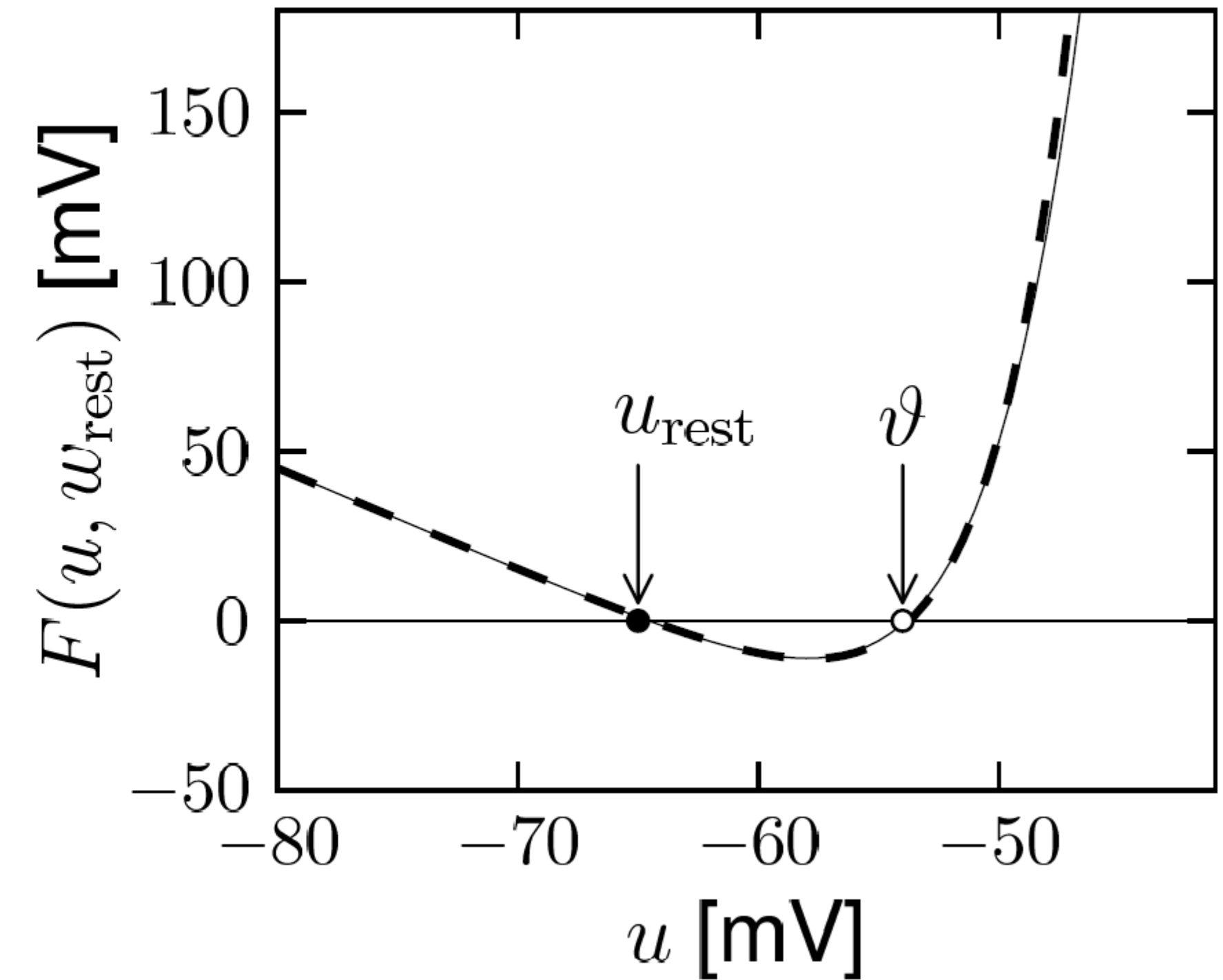
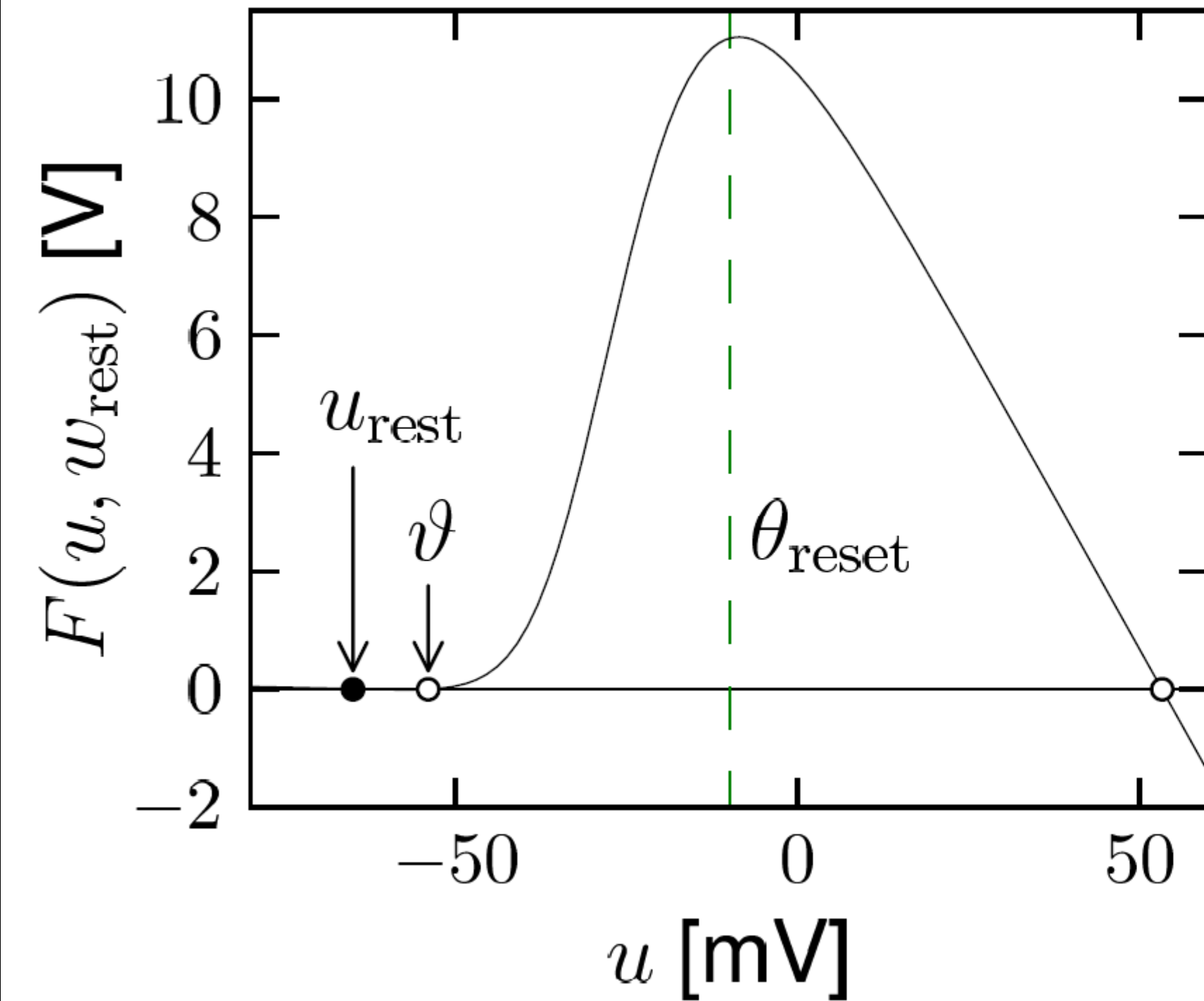
$$\tau_w \frac{dw}{dt} \approx 0 \rightarrow w \approx w_{rest}$$

$$\tau \frac{du}{dt} = F(u, w_{rest}) + RI(t)$$



Stable fixed point

Neuronal Dynamics – 4.5. Nonlinear Integrate-and-Fire Model



$$\tau \frac{du}{dt} = F(u, w_{\text{rest}}) + RI(t) = f(u) + RI(t)$$

→ Nonlinear I&F (see week 1!)

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

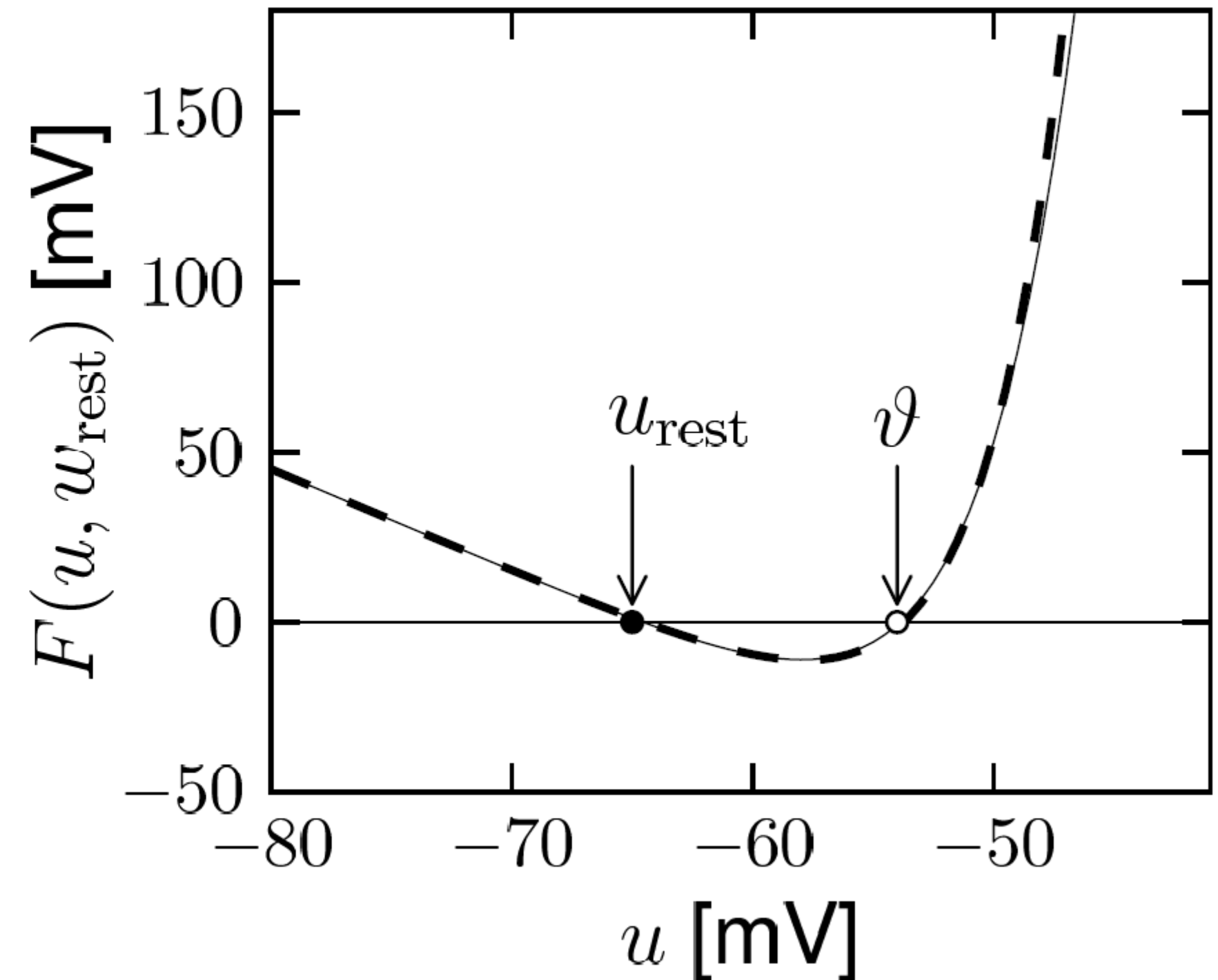
Neuronal Dynamics – 4.5. Nonlinear Integrate-and-Fire Model

Exponential integrate-and-fire model (EIF)

$$f(u) = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \vartheta}{\Delta}\right)$$

$$\tau \frac{du}{dt} = F(u, w_{rest}) + RI(t) = f(u) + RI(t)$$

→ Nonlinear I&F (see week 1!)



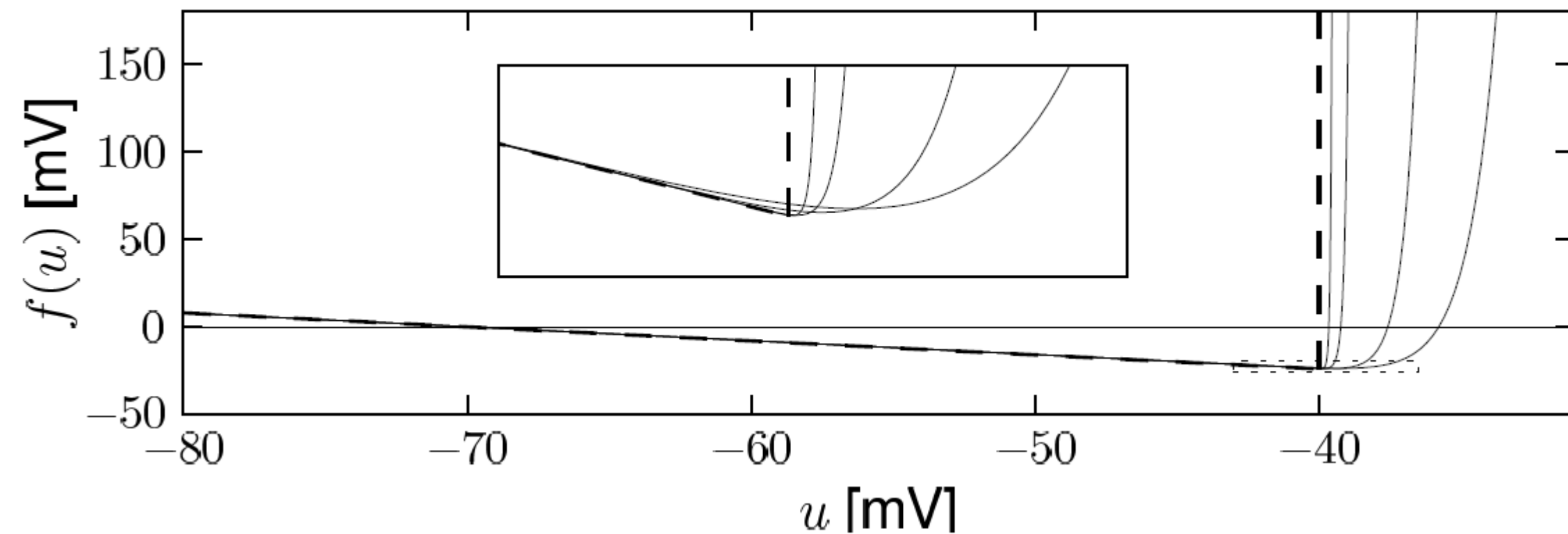
*Image: Neuronal Dynamics,
Gerstner et al.,
Cambridge Univ. Press (2014)*

Neuronal Dynamics – 4.5. Exponential Integrate-and-Fire Model

Exponential integrate-and-fire model (EIF)

$$f(u) = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \vartheta}{\Delta}\right)$$

linear

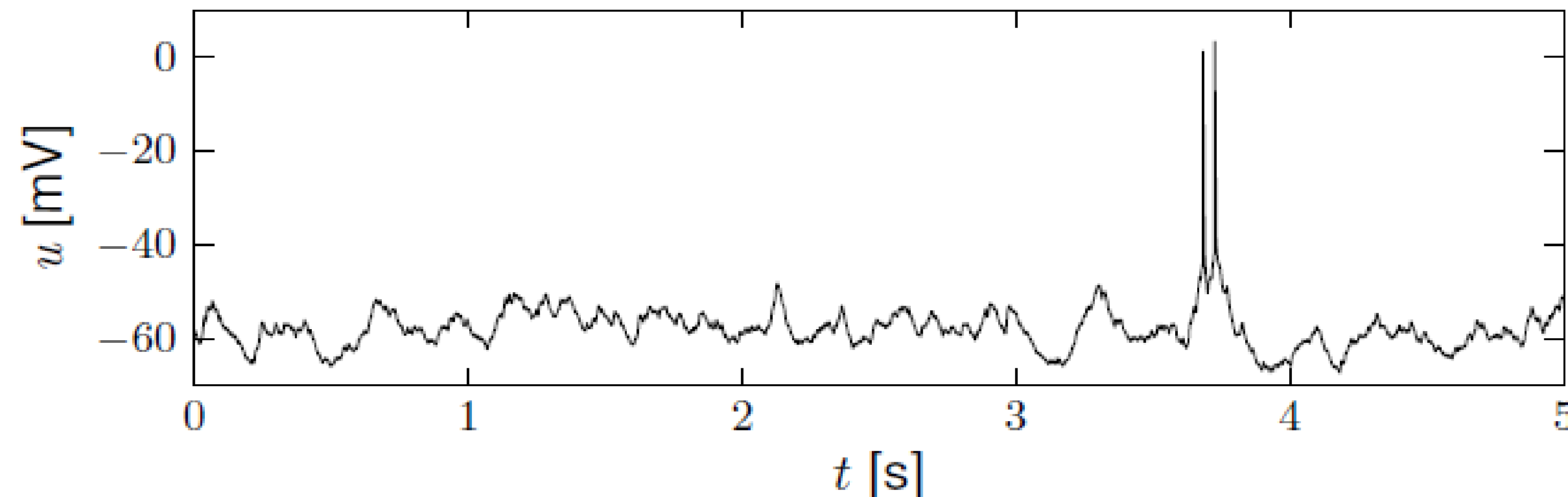


*Image: Neuronal Dynamics,
Gerstner et al.,
Cambridge Univ. Press (2014)*

Neuronal Dynamics – 4.5 sparse activity in vivo

Spontaneous activity *in vivo*

awake mouse, cortex, freely whisking,



-spikes are rare events

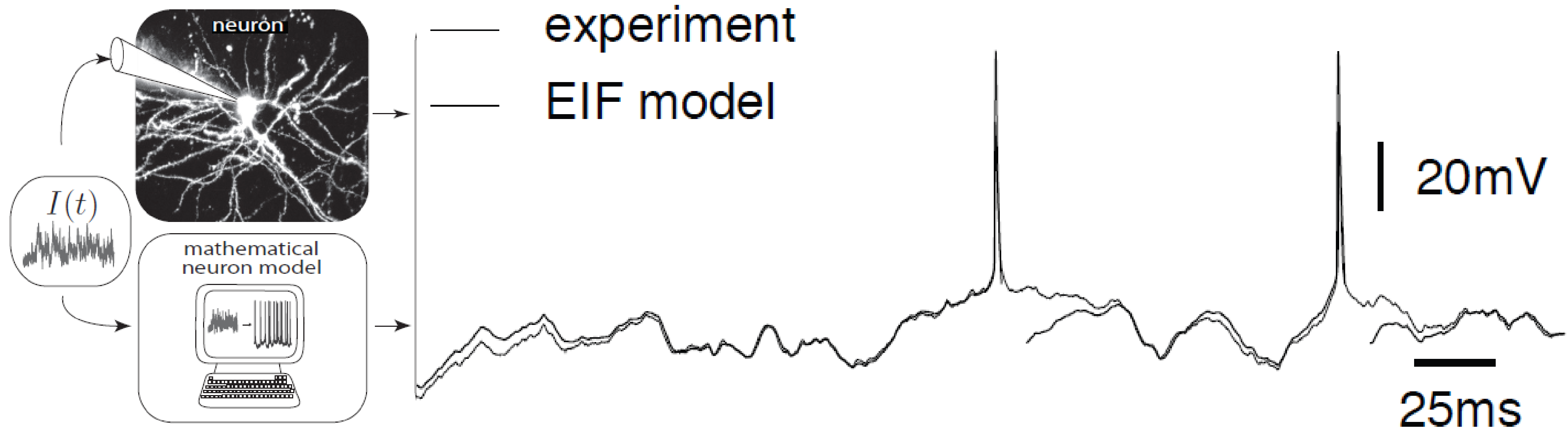
Crochet et al., 2011

-membrane potential fluctuates around 'rest'

Aims of Modeling:

- predict spike initiation times
- predict subthreshold voltage

Neuronal Dynamics – 4.5. How good are integrate-and-fire models?



Badel et al., 2008

Aims: - predict spike initiation times
- predict subthreshold voltage

*Add adaptation and
refractoriness (week 7)*

Neuronal Dynamics – 4.5. Exponential Integrate-and-Fire Model

Direct derivation from Hodgkin-Huxley

$$C \frac{du}{dt} = -g_{Na} m^3 h (u - E_{Na}) - g_K n^4 (u - E_K) - g_l (u - E_l) + I(t)$$

$$C \frac{du}{dt} = -g_{Na} [m_0(u)]^3 h_{rest} (u - E_{Na}) - g_K [n_{rest}]^4 (u - E_K) - g_l (u - E_l) + I(t)$$

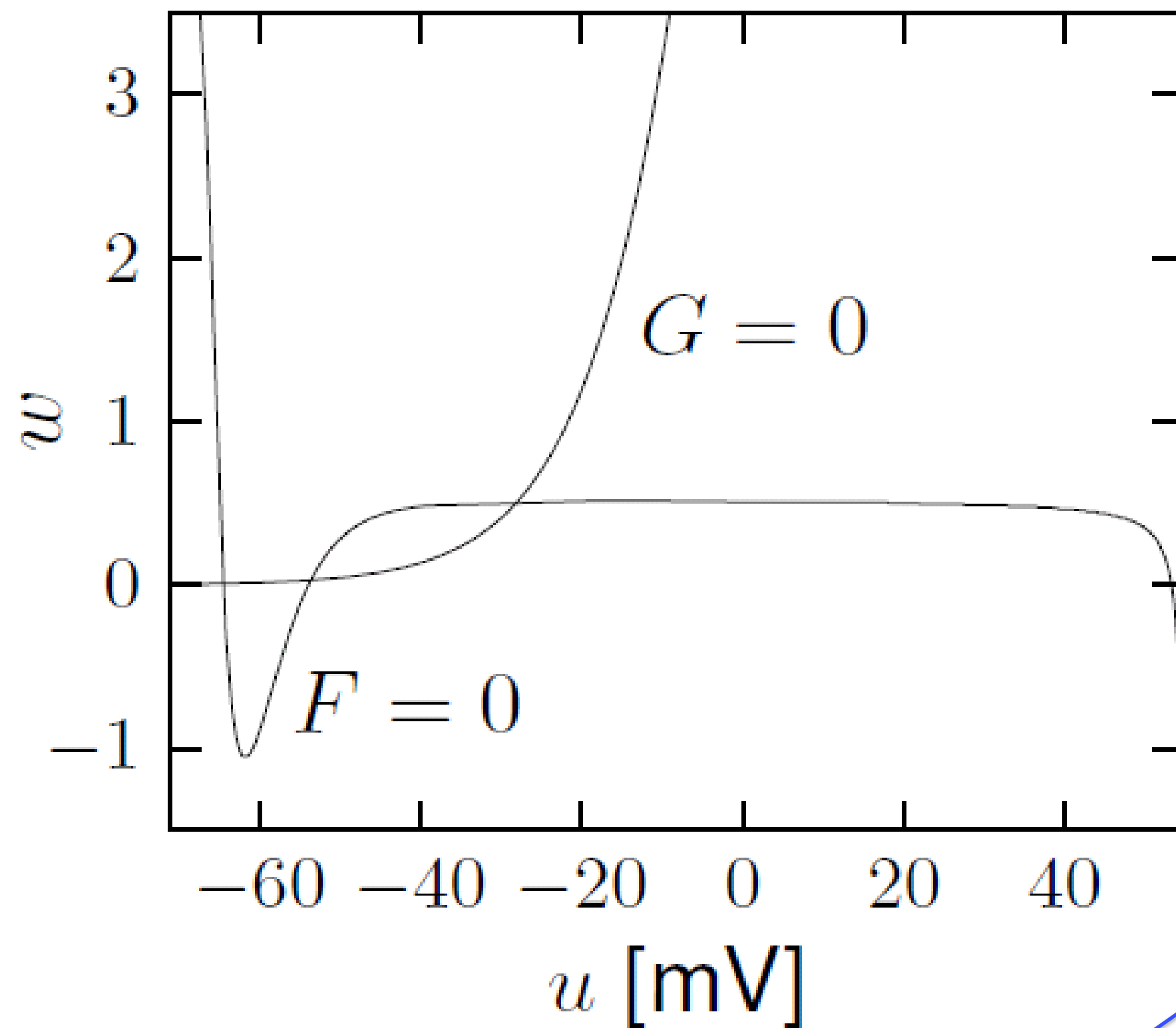
Fourcaud-Trocme et al, J. Neurosci. 2003

$$f(u) = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \vartheta}{\Delta}\right)$$

$$\tau \frac{du}{dt} = F(u, h_{rest}, n_{rest}) + RI(t) = f(u) + RI(t)$$

gives expon. I&F

Neuronal Dynamics – 4.5. Nonlinear Integrate-and-Fire Model



Relevant during spike
and downswing of AP

2-dimensional equation

$$\tau \frac{du}{dt} = F(u, w) + RI(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

Separation of time scales

-w is constant (if not firing)

$$\tau \frac{du}{dt} = f(u) + RI(t)$$

threshold+reset for firing

Neuronal Dynamics – 4.5. Nonlinear Integrate-and-Fire Model

2-dimensional equation

$$\tau \frac{du}{dt} = F(u, w) + RI(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

Separation of time scales

-w is constant (if not firing)

$$\tau \frac{du}{dt} = f(u) + RI(t)$$

Linear plus exponential

Neuronal Dynamics – Quiz 4.5.

A. Exponential integrate-and-fire model.

The model can be derived

- ☐ from a 2-dimensional model, assuming that the auxiliary variable w is constant.
- ☐ from the HH model, assuming that the gating variables h and n are constant.
- ☐ from the HH model, assuming that the gating variables m is constant.
- ☐ from the HH model, assuming that the gating variables m is instantaneous.

B. Reset.

- ☐ In a 2-dimensional model, the auxiliary variable w is necessary to implement a reset of the voltage after a spike
- ☐ In a nonlinear integrate-and-fire model, the auxiliary variable w is necessary to implement a reset of the voltage after a spike
- ☐ In a nonlinear integrate-and-fire model, a reset of the voltage after a spike is implemented algorithmically/explicitly

Neuronal Dynamics – 4.5 Literature

Reading: W. Gerstner, W.M. Kistler, R. Naud and L. Paninski,

Neuronal Dynamics: from single neurons to networks and

models of cognition. Chapter 4 (Dimension Reduction and Phase Plane analysis)

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OR J. Rinzel and G.B. Ermentrout, (1989). Analysis of neuronal excitability and oscillations.

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4.5. Summary: from HH to generalized integrate-and-fire

- The **reduction of the Hodgkin-Huxley (HH) model** from 4 to 2 dimensions generates nonlinear nullclines with several intersections.
- If we zoom in on the two left-most intersections the u-nullcline looks similar to a superposition of a linear and an exponential term
- Between (rare) spike events, the w-variable has always time to go back to resting potential. Hence during spike-initiation we can consider the w-variable as constant.
- This gives rise to the **exponential integrate-and-fire model**
- **Adaptation** means that for constant input the interspike intervals increase over time – we will add adaptation variables later
- The standard HH-model shows no (or very little) adaptation
- More complicated Hodgkin-Huxley type models would have additional variables (describing other ion channels) that cause adaptation
- In integrate-and-fire models, these additional adaptation variables can often be approximated by a linear dynamics for new variables w_k