

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

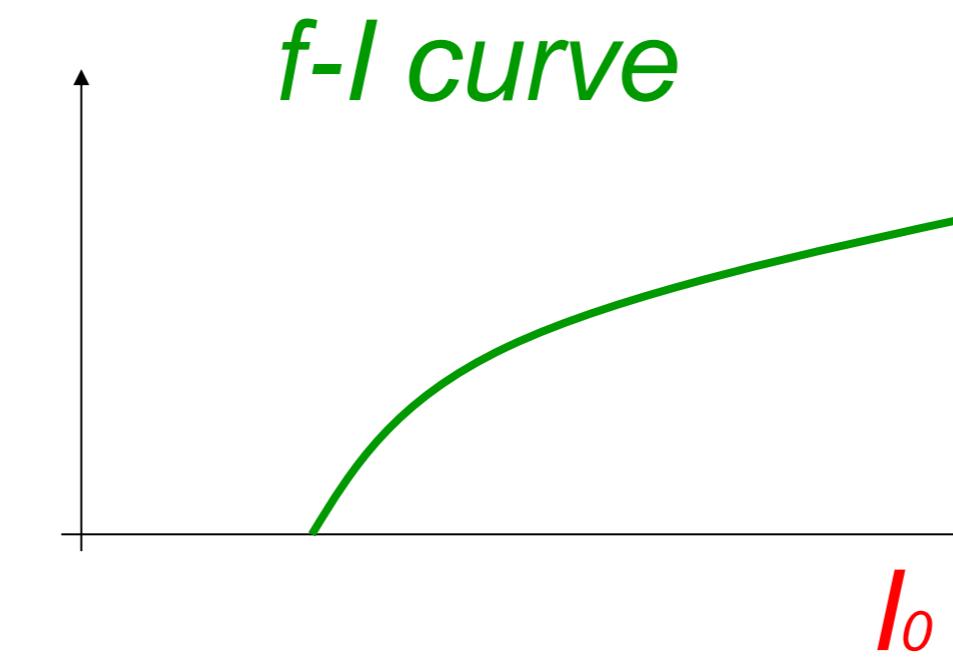
Neuronal Dynamics – 4.4. Type I and II Neuron Models

ramp input/
constant input

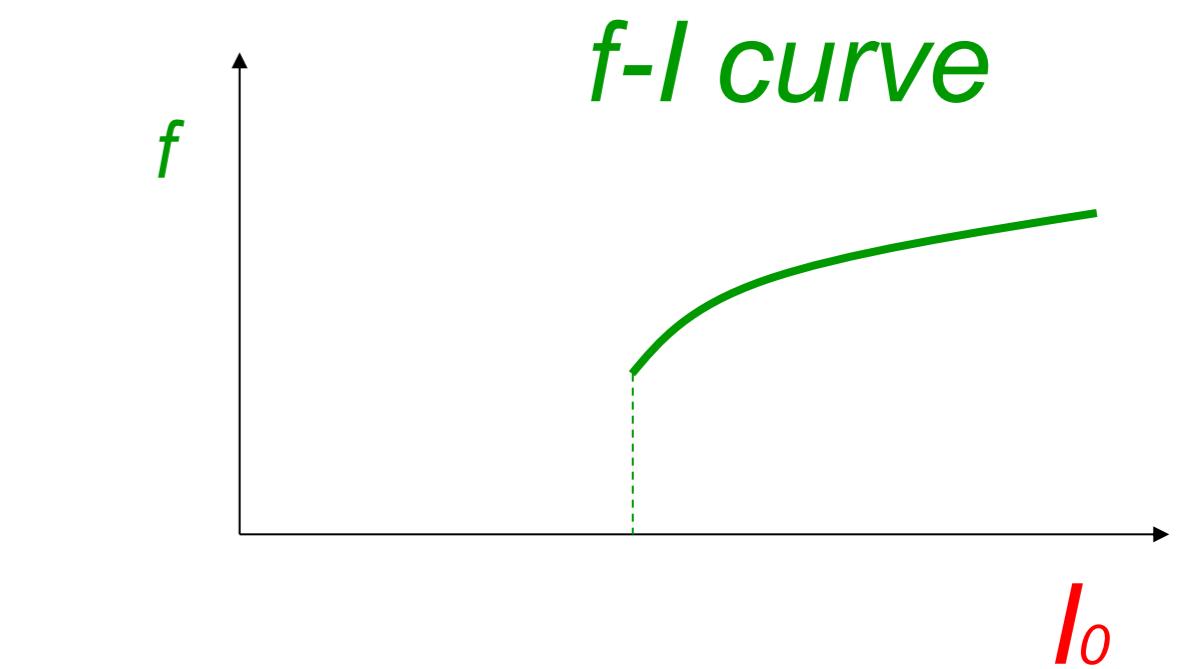


neuron

Type I and type II models



f-*I* curve



f-*I* curve

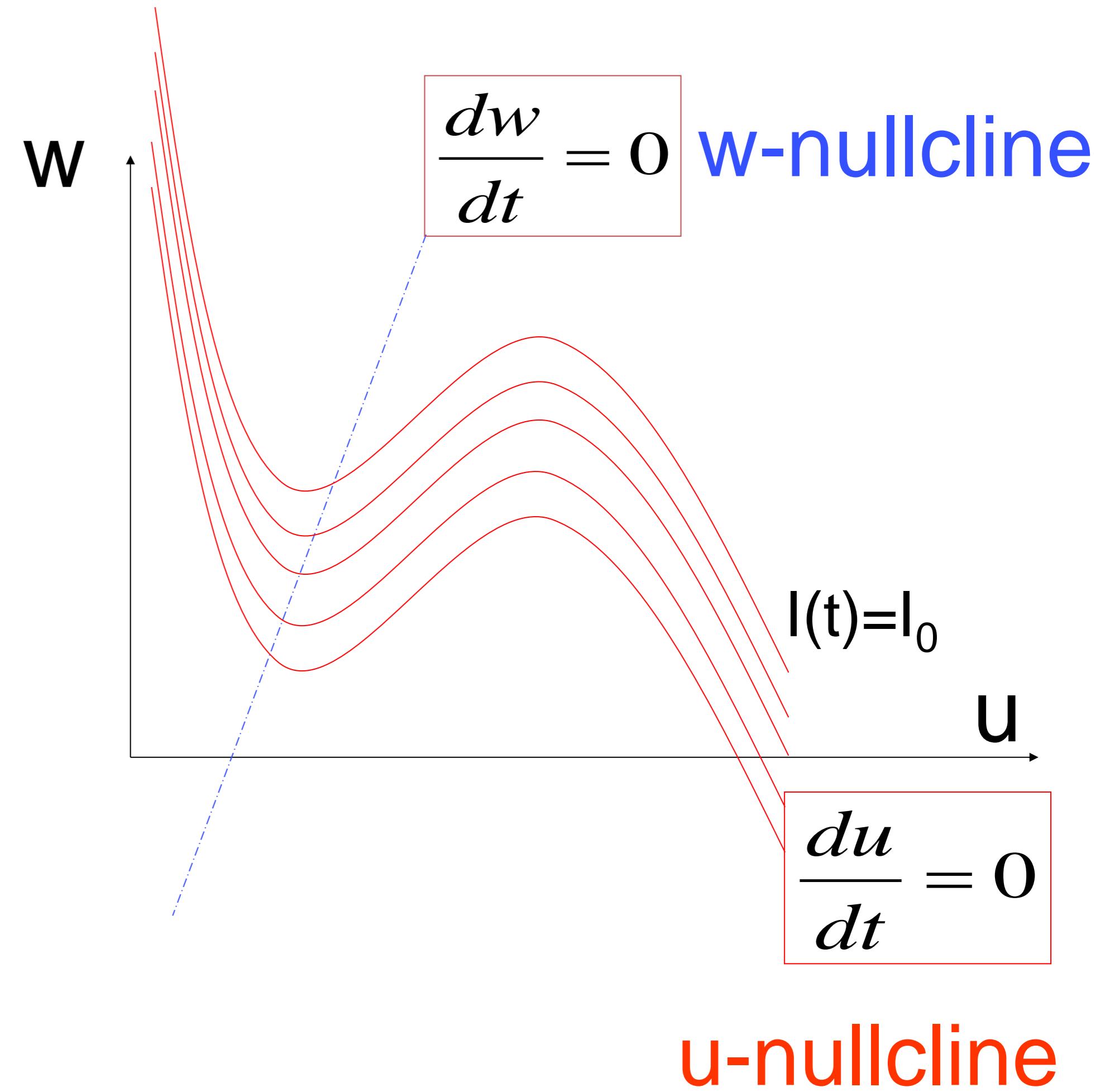
2 dimensional Neuron Models

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

stimulus

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

apply constant stimulus I_0



FitzHugh Nagumo Model – limit cycle

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

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

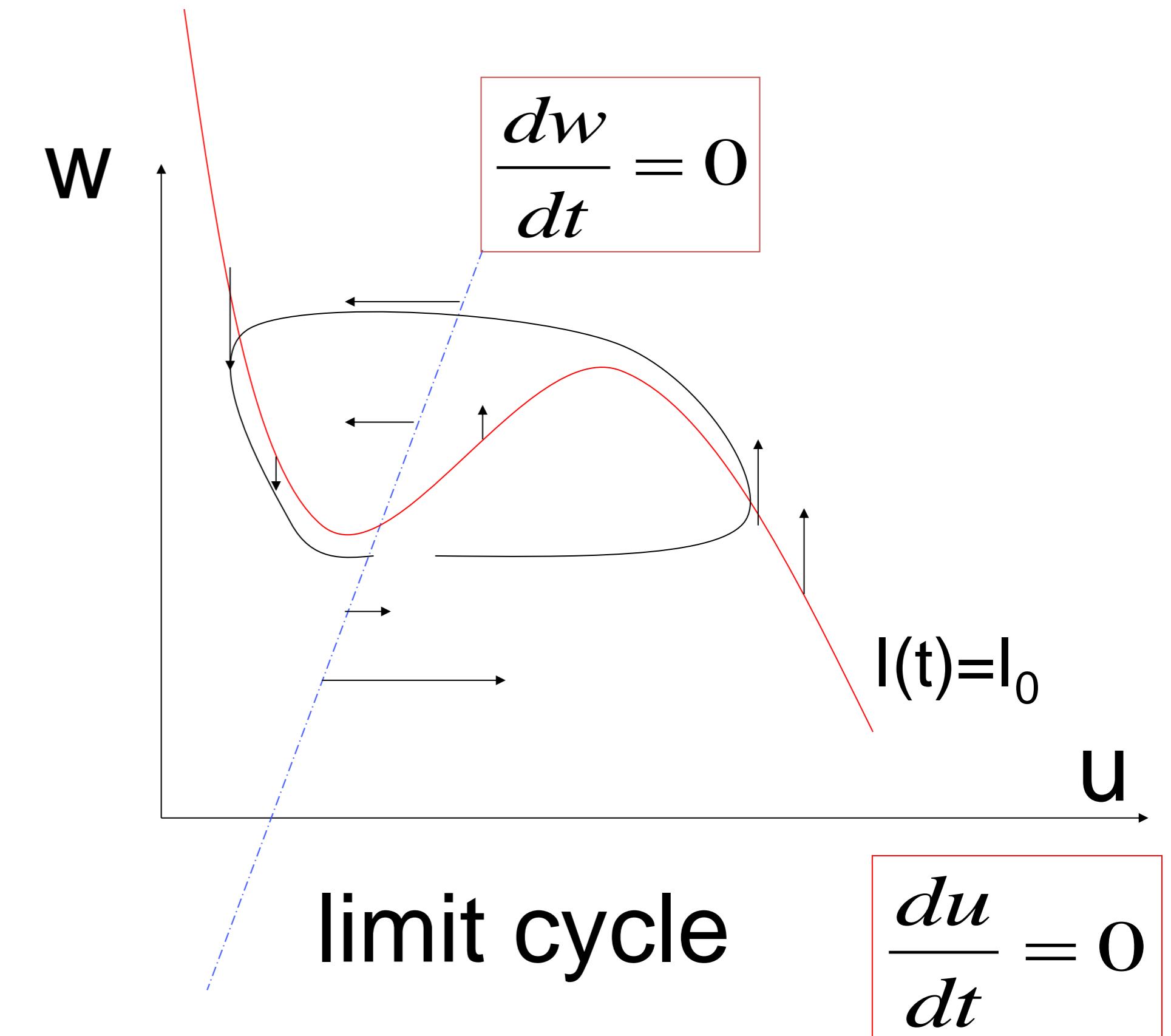
-unstable fixed point

-closed boundary

with arrows pointing inside

→ limit cycle

stimulus

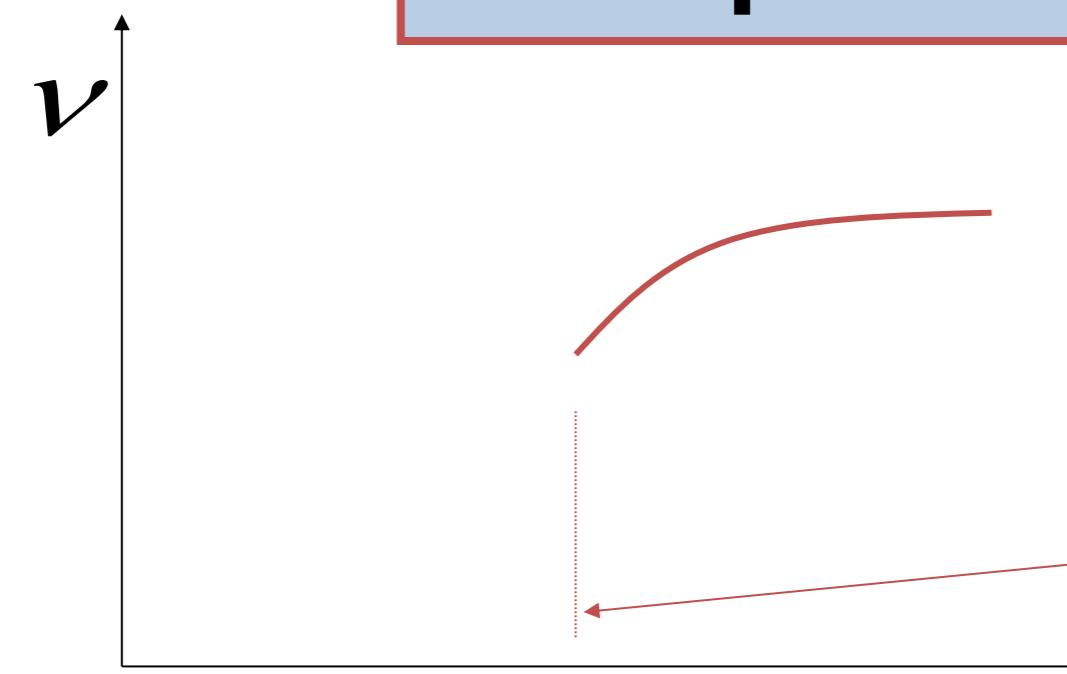


Type II Model constant input

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

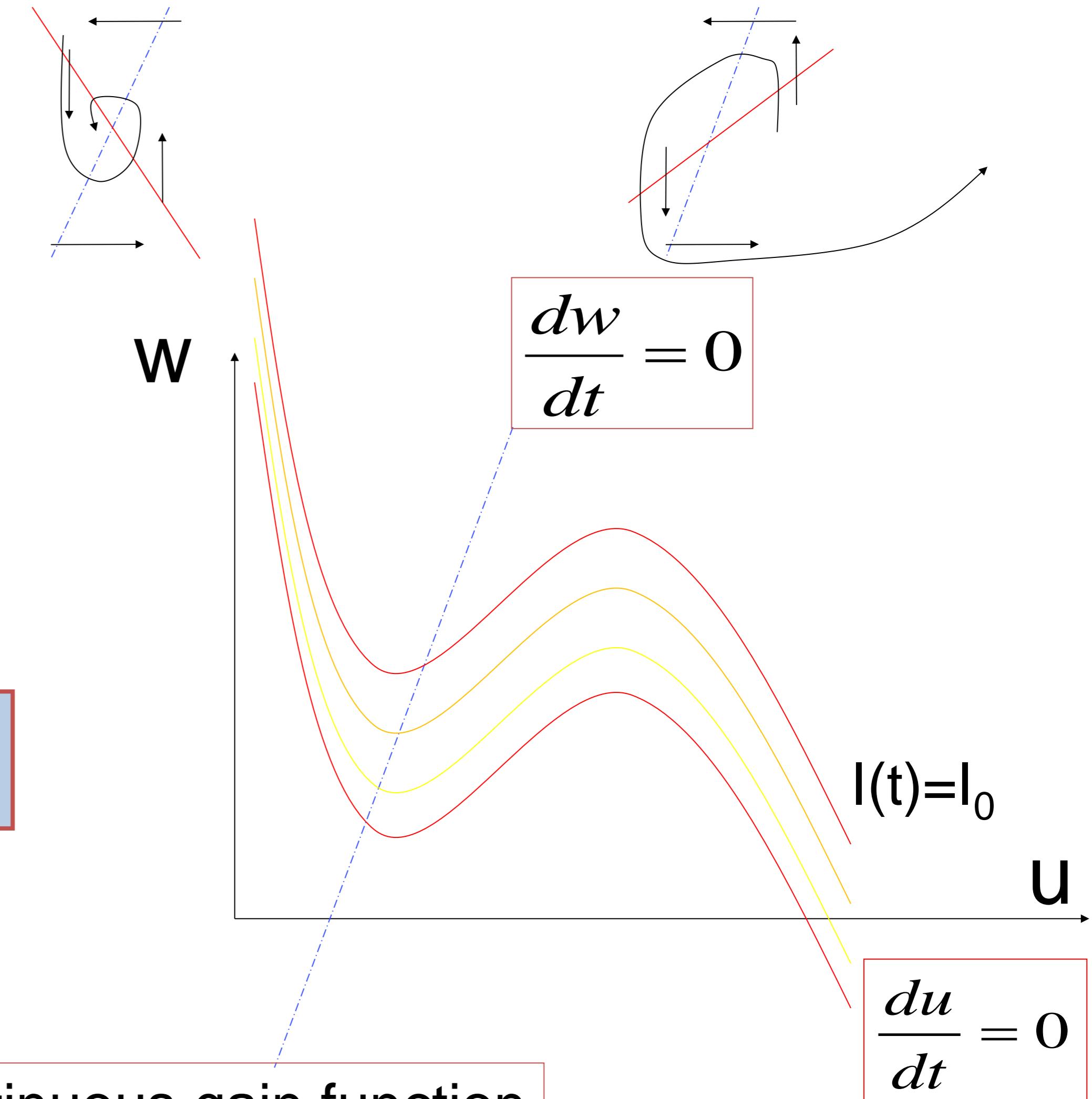
$$\tau_w \frac{dw}{dt} = G(u, w)$$

Hopf bifurcation



Discontinuous gain function

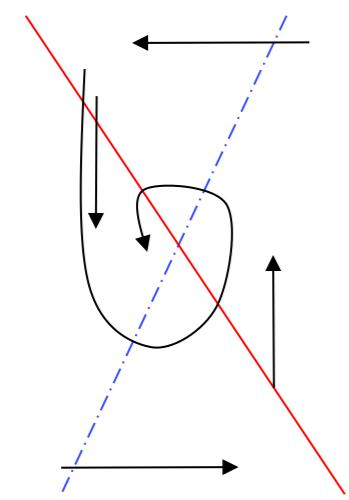
Stability lost \rightarrow oscillation with finite frequency



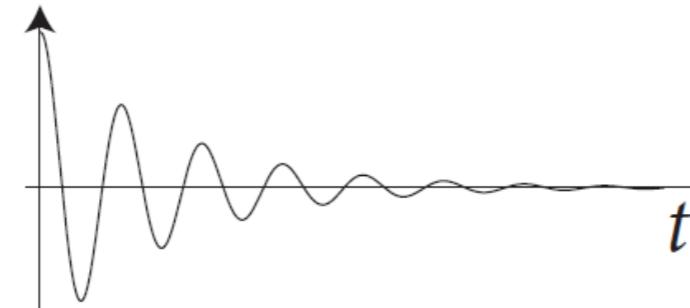
Neuronal Dynamics – 4.4. Hopf bifurcation

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

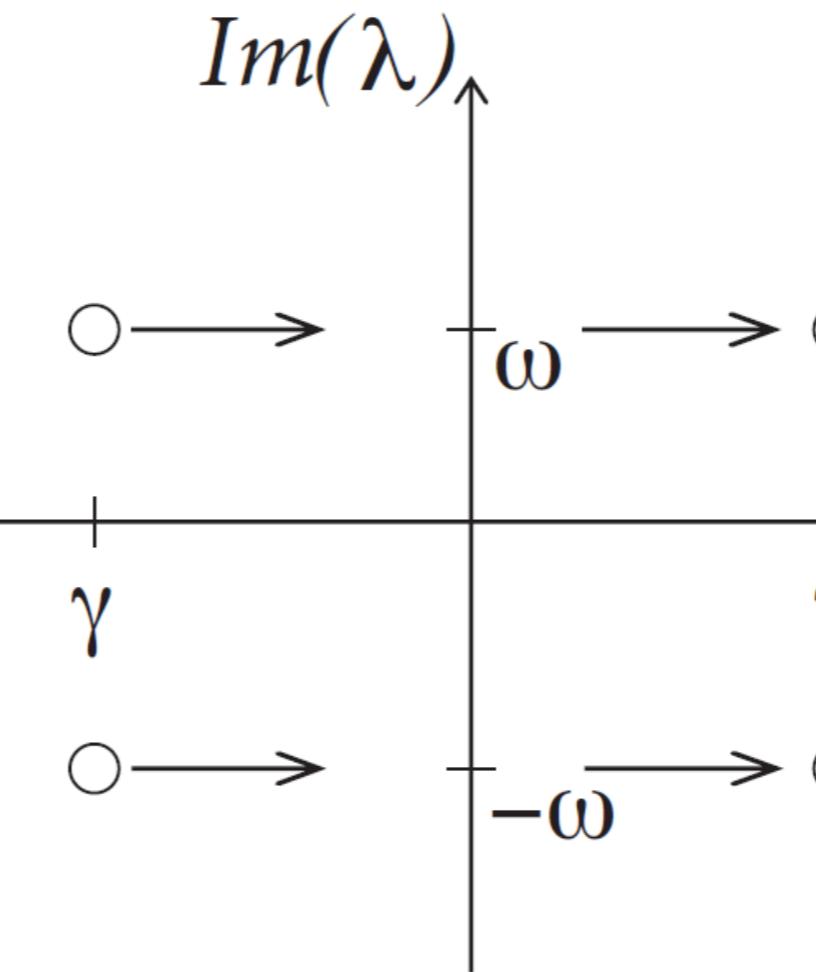
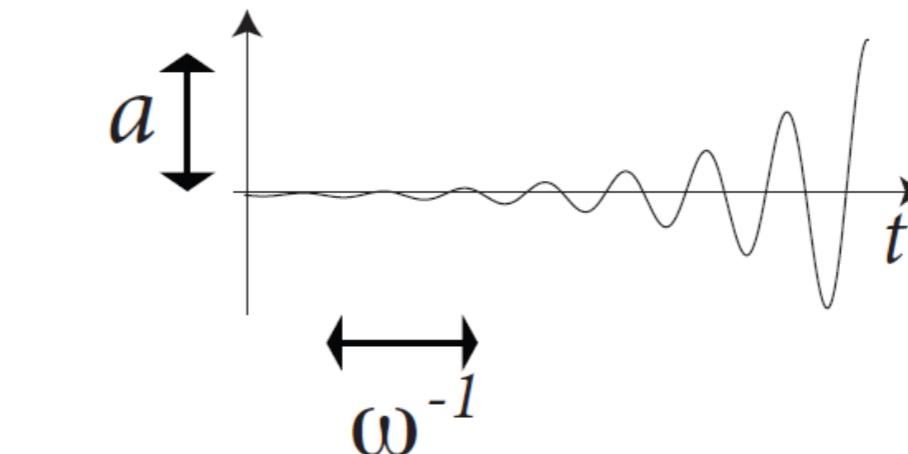
$$\gamma < 0$$



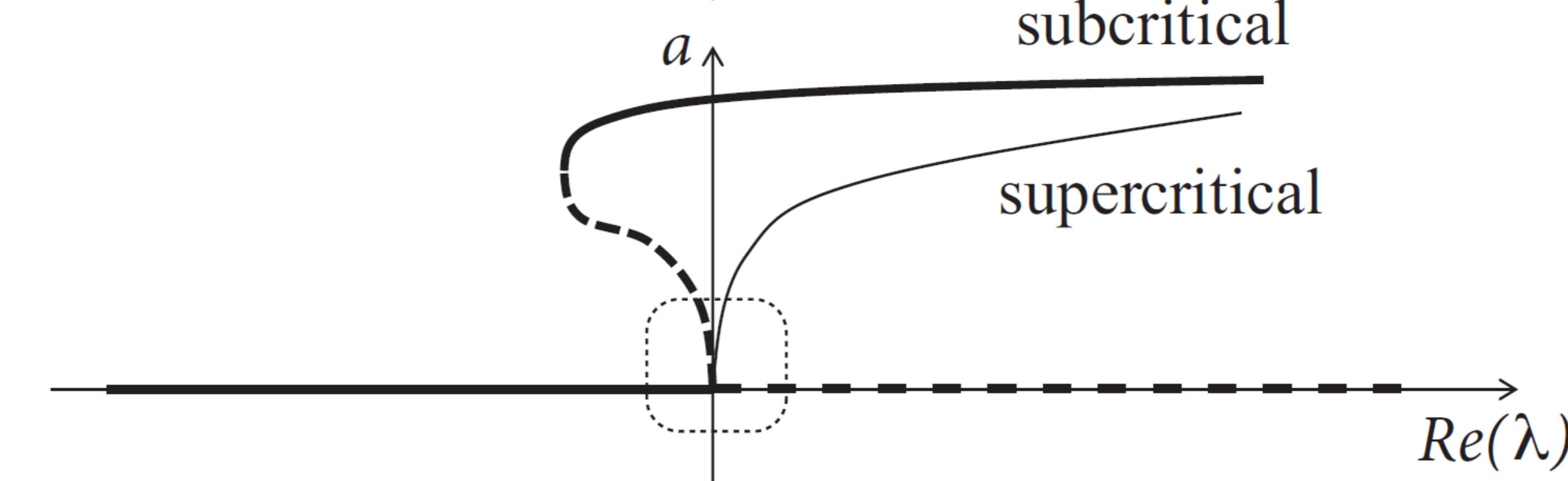
stable fixed point ($\gamma < 0$)



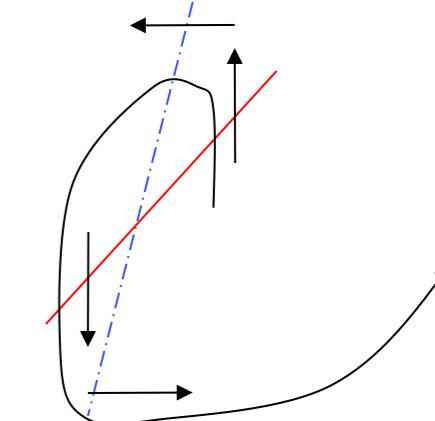
unstable fixed point ($\gamma > 0$)



subcritical
supercritical

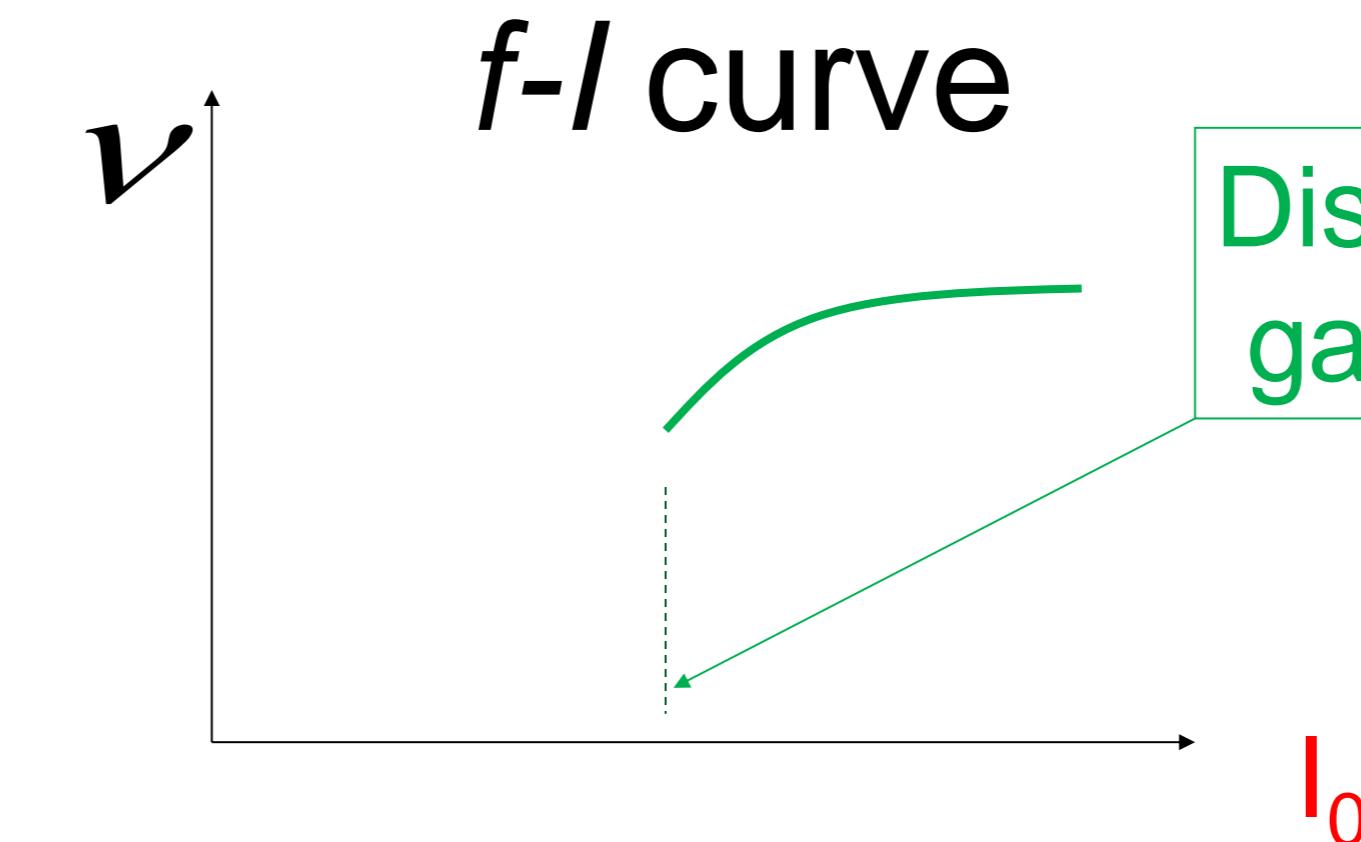
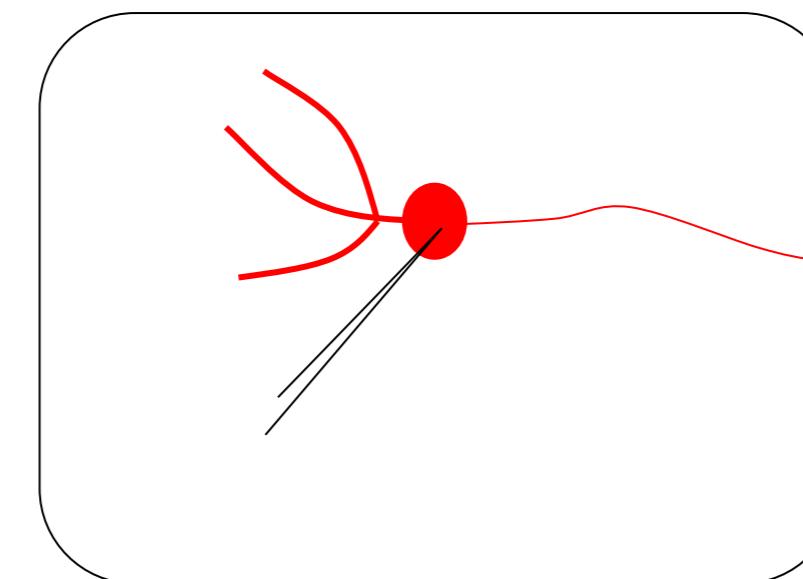


$$\gamma > 0$$

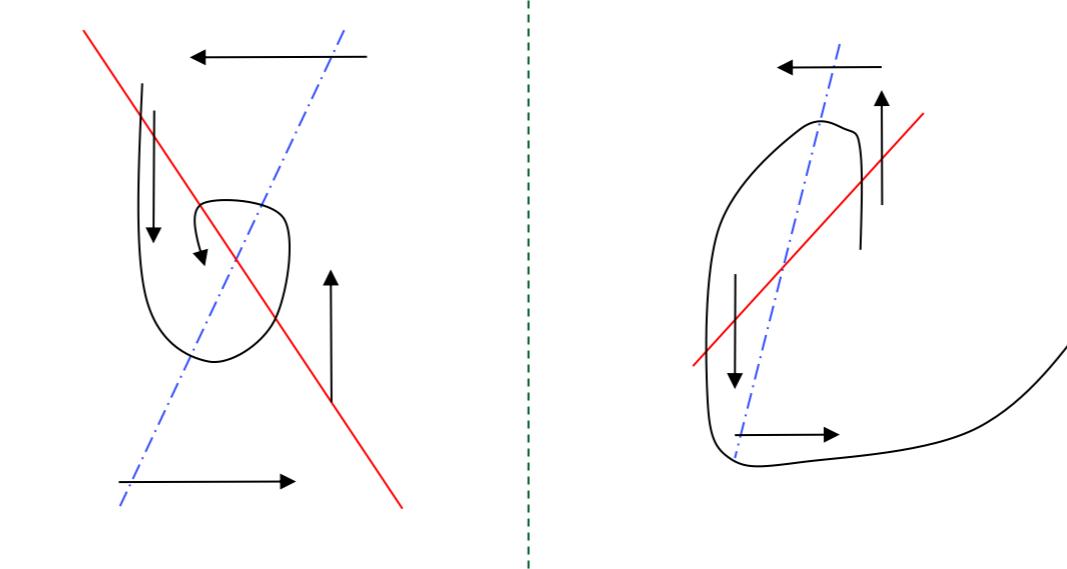


Neuronal Dynamics – 4.4. Hopf bifurcation: *f-I*-curve

ramp input/
constant input

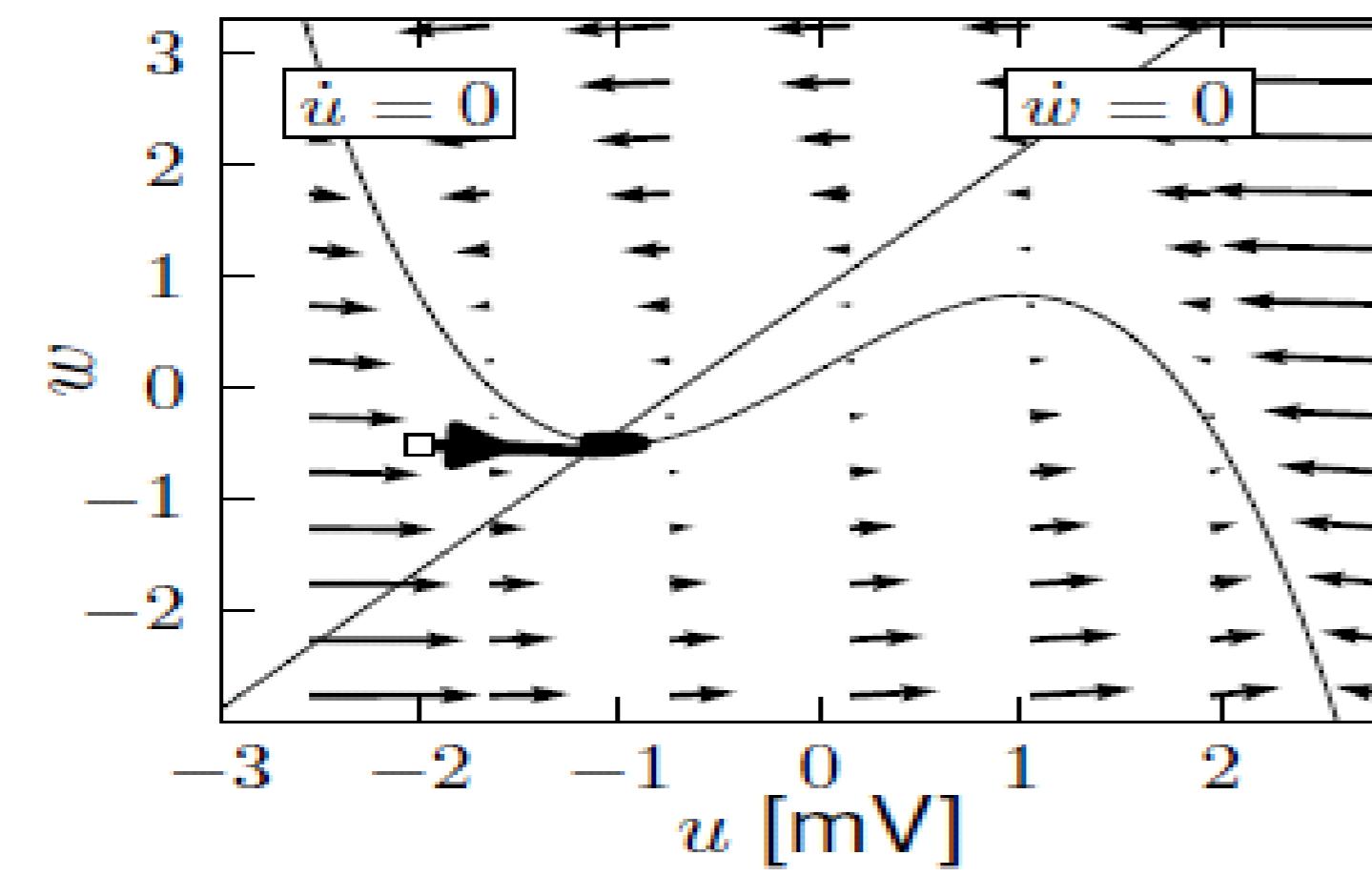
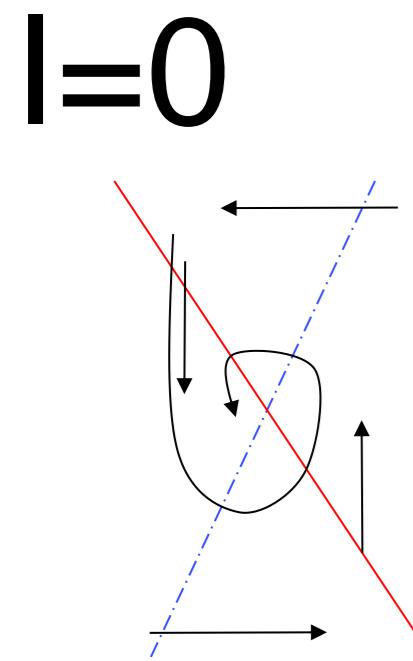


Discontinuous
gain function: Type II

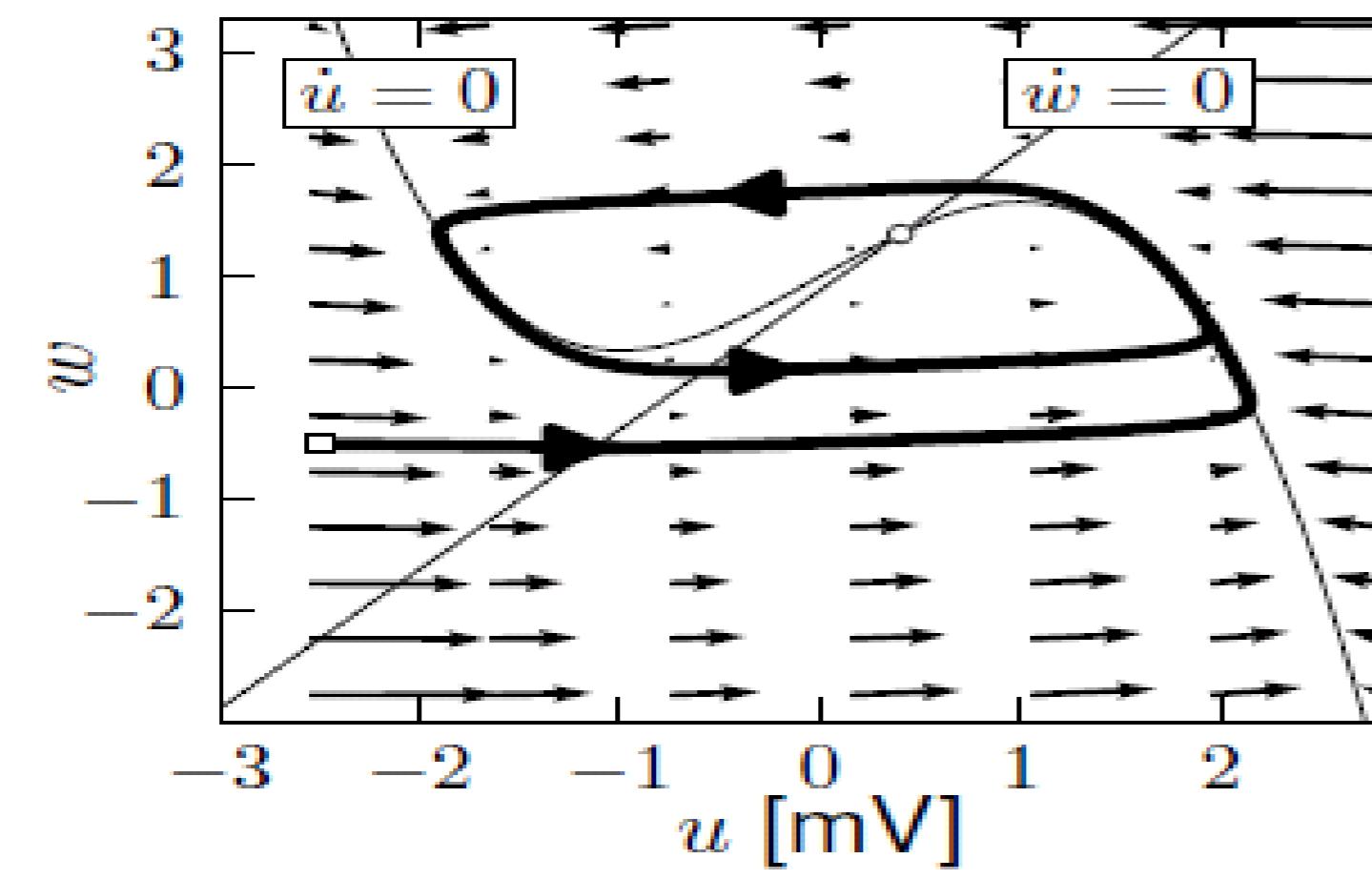
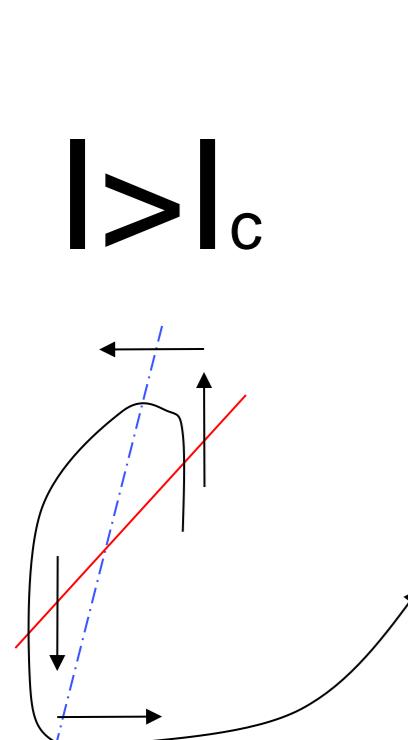
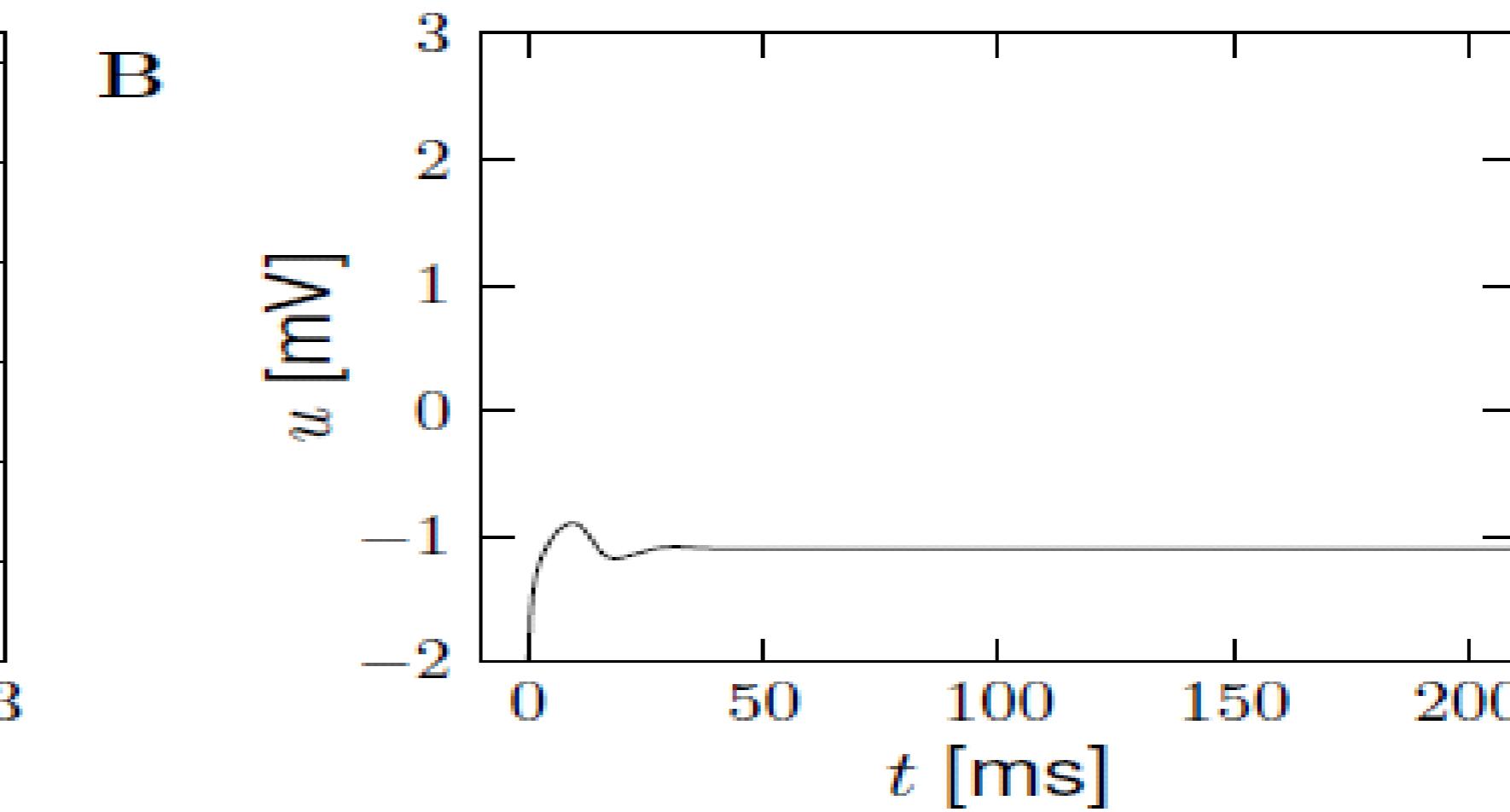


Stability lost \rightarrow oscillation with finite frequency

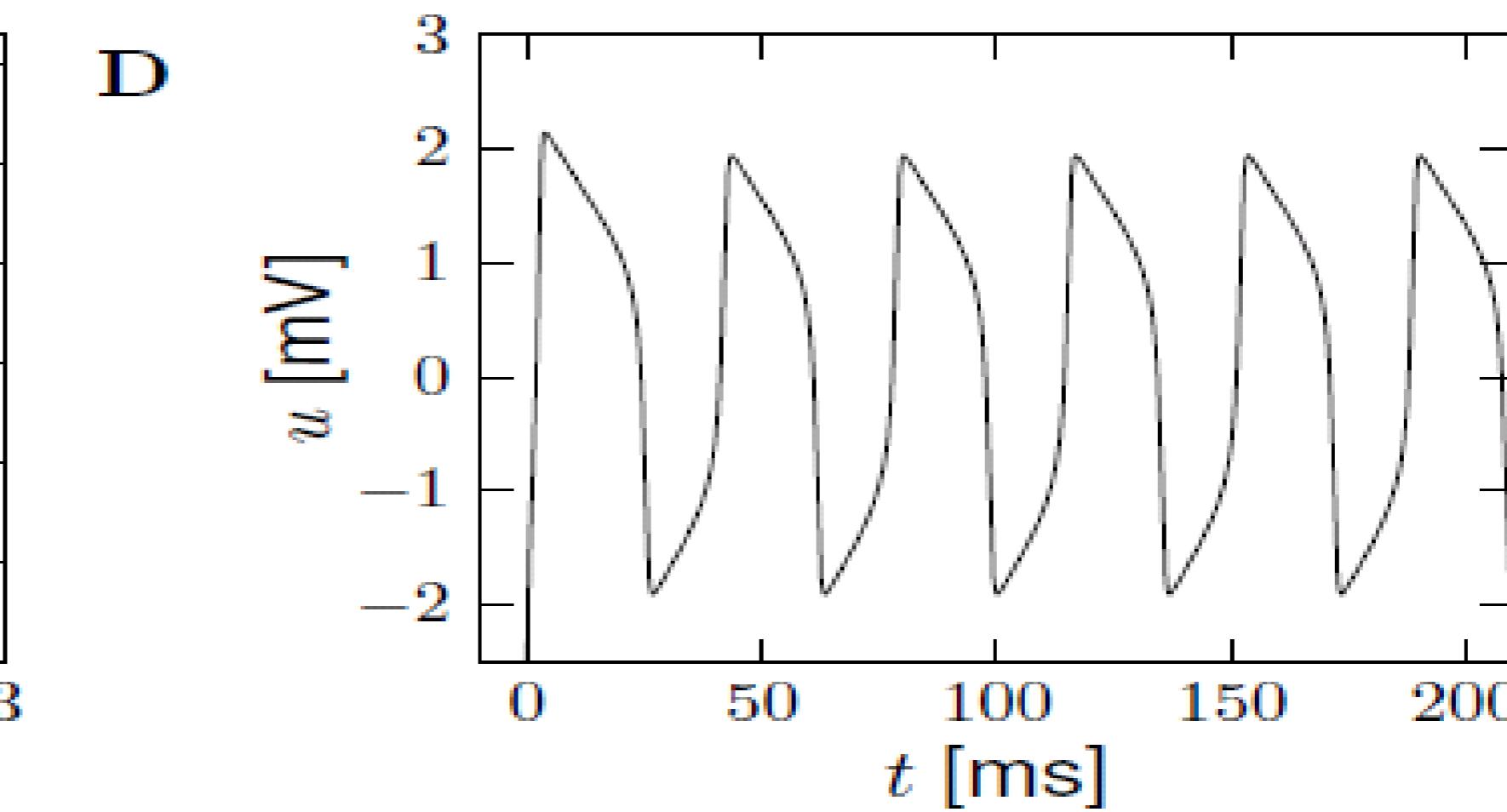
FitzHugh-Nagumo: type II Model – Hopf bifurcation



B



D



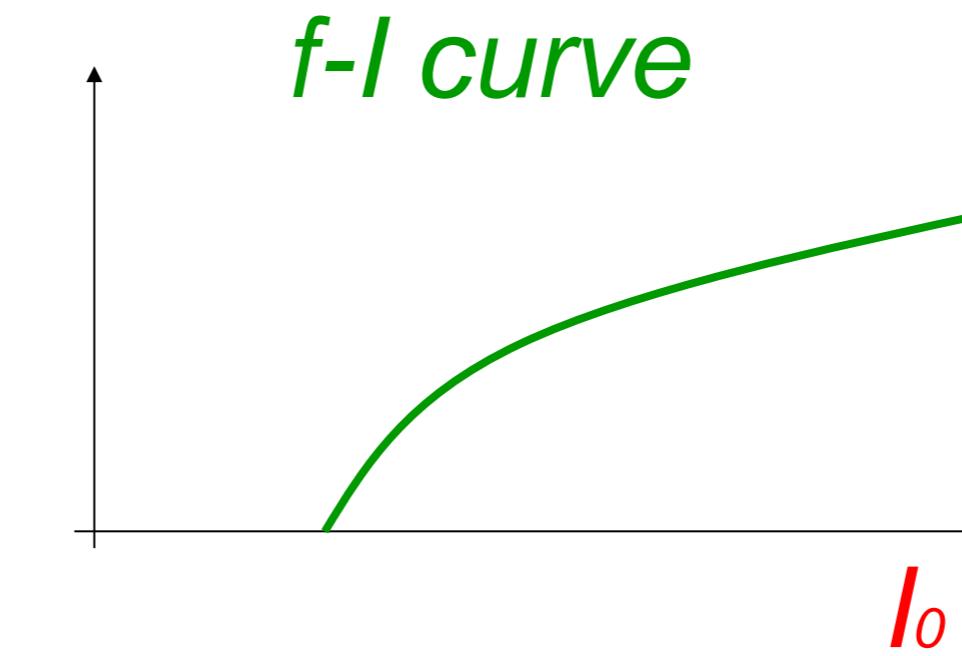
Neuronal Dynamics – 4.4. Type I and II Neuron Models

ramp input/
constant input

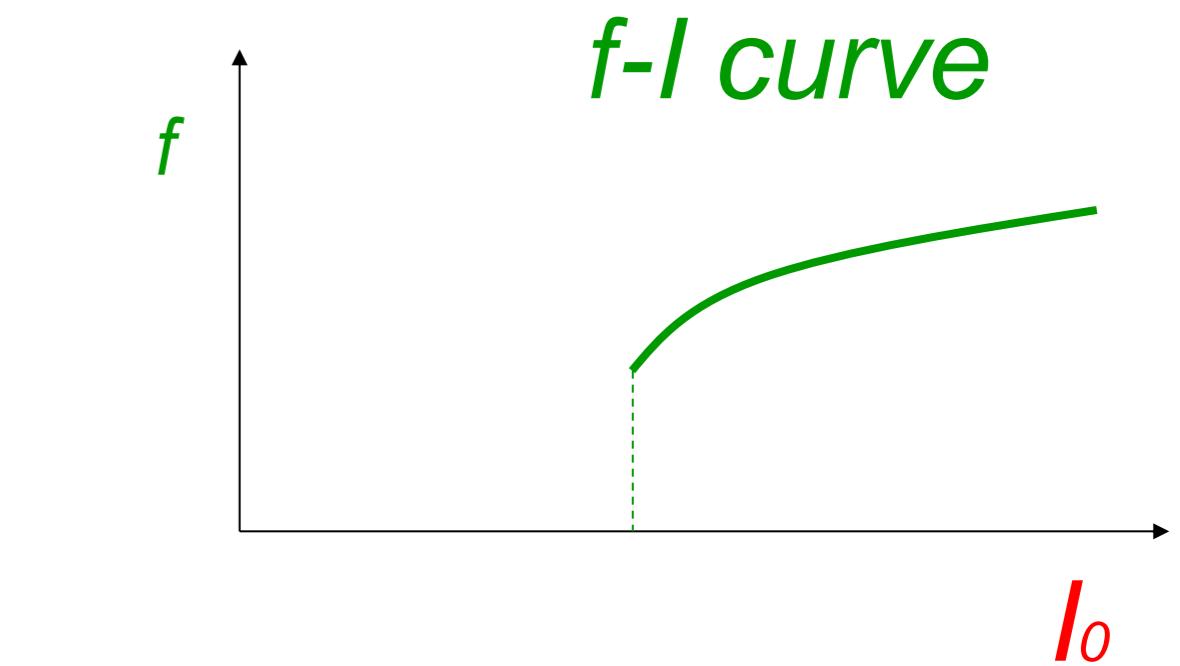


neuron

Type I and type II models



f-*I* curve



f-*I* curve

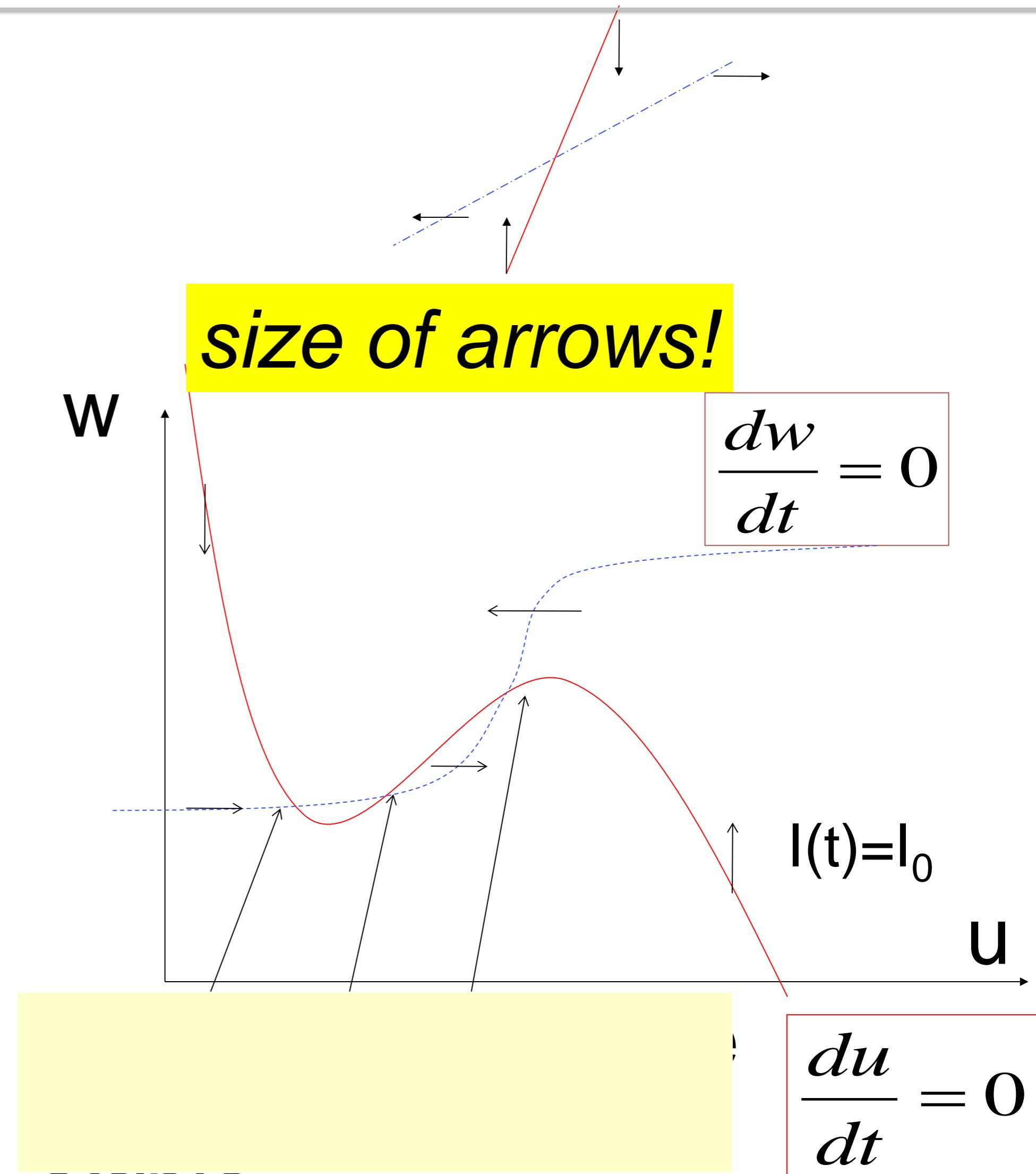
Neuronal Dynamics – 4.4. Type I and II Neuron Models

type I Model: 3 fixed points

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

apply constant stimulus I_0

Saddle-node bifurcation



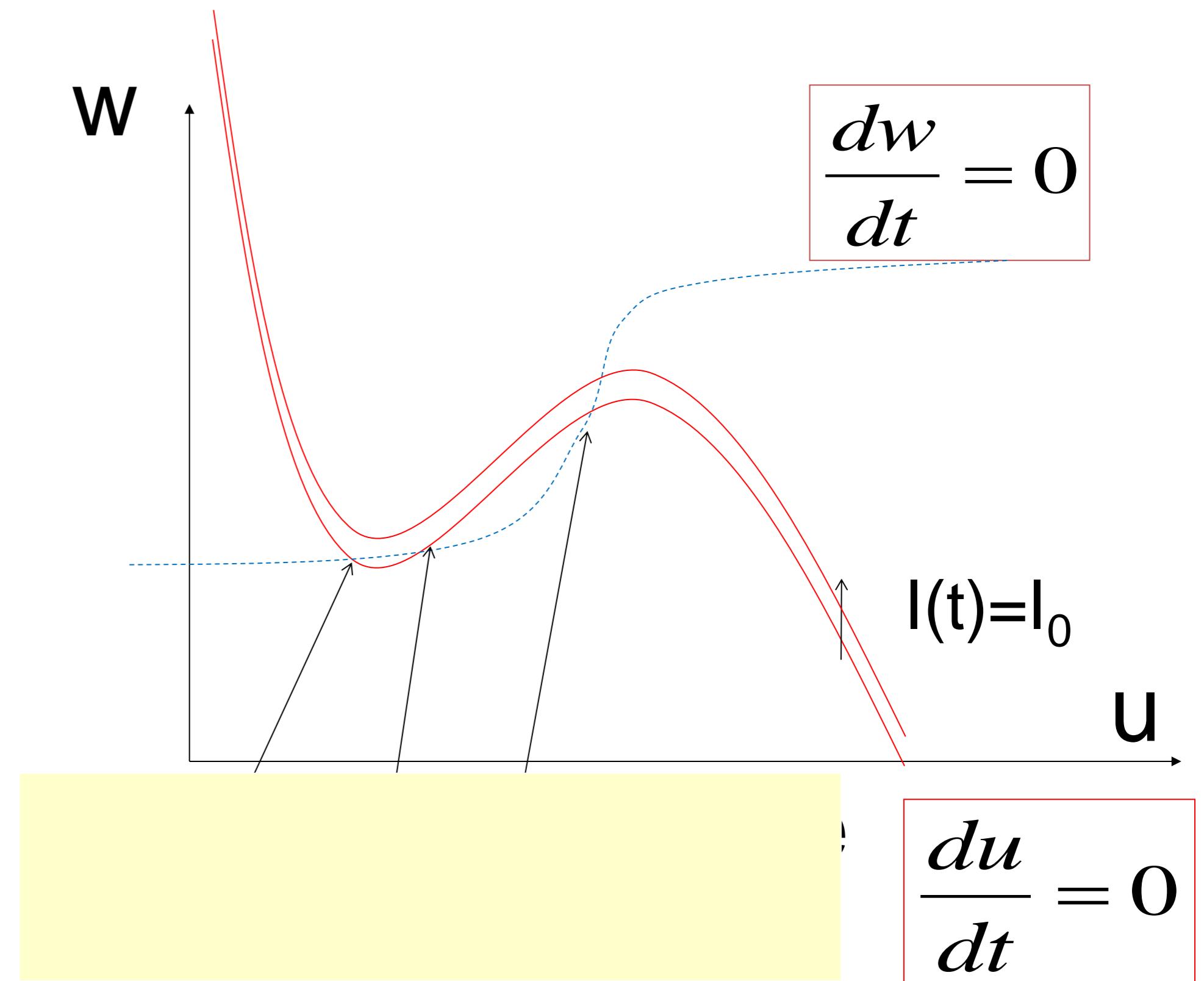
Saddle-node bifurcation

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

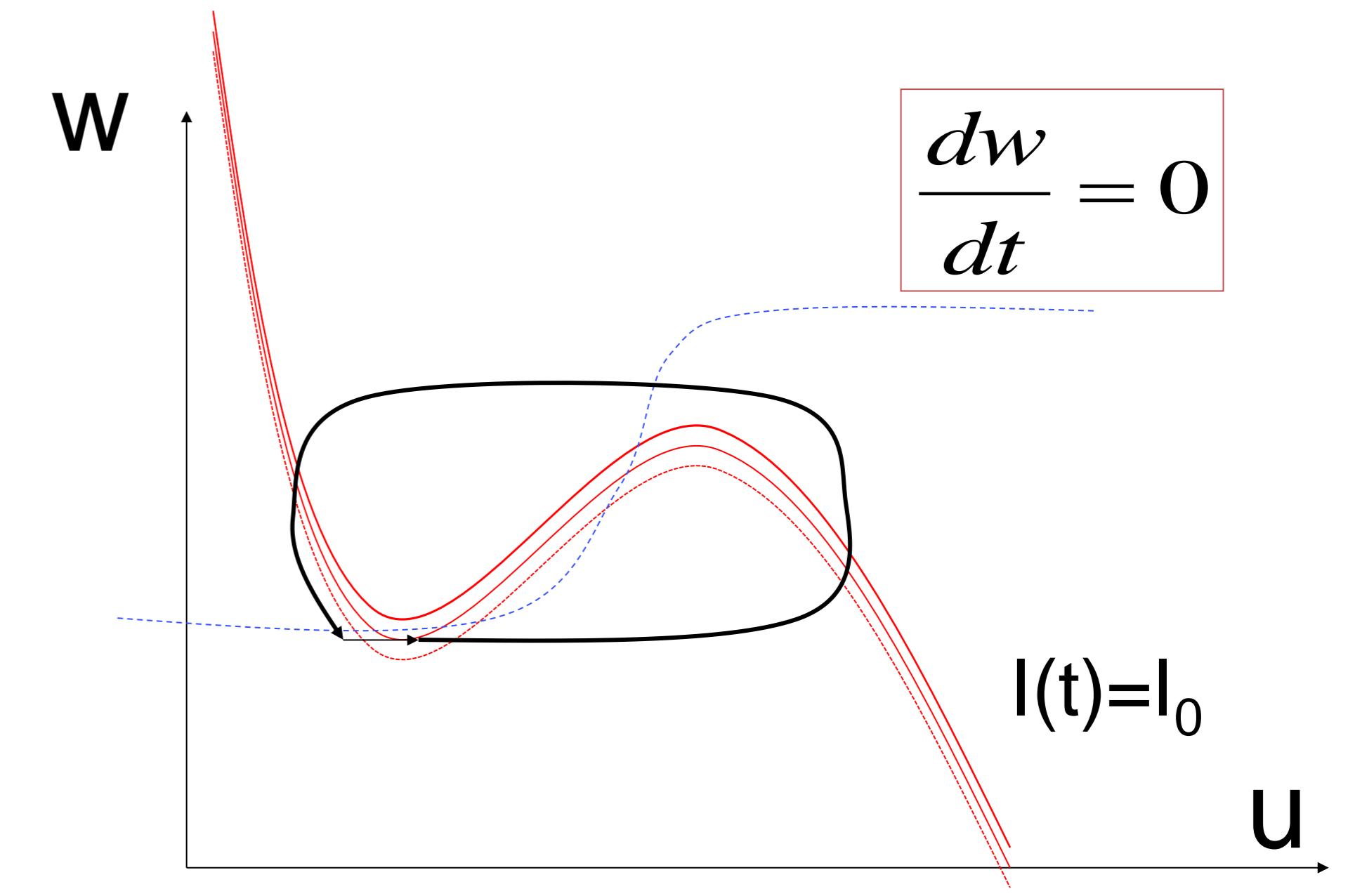
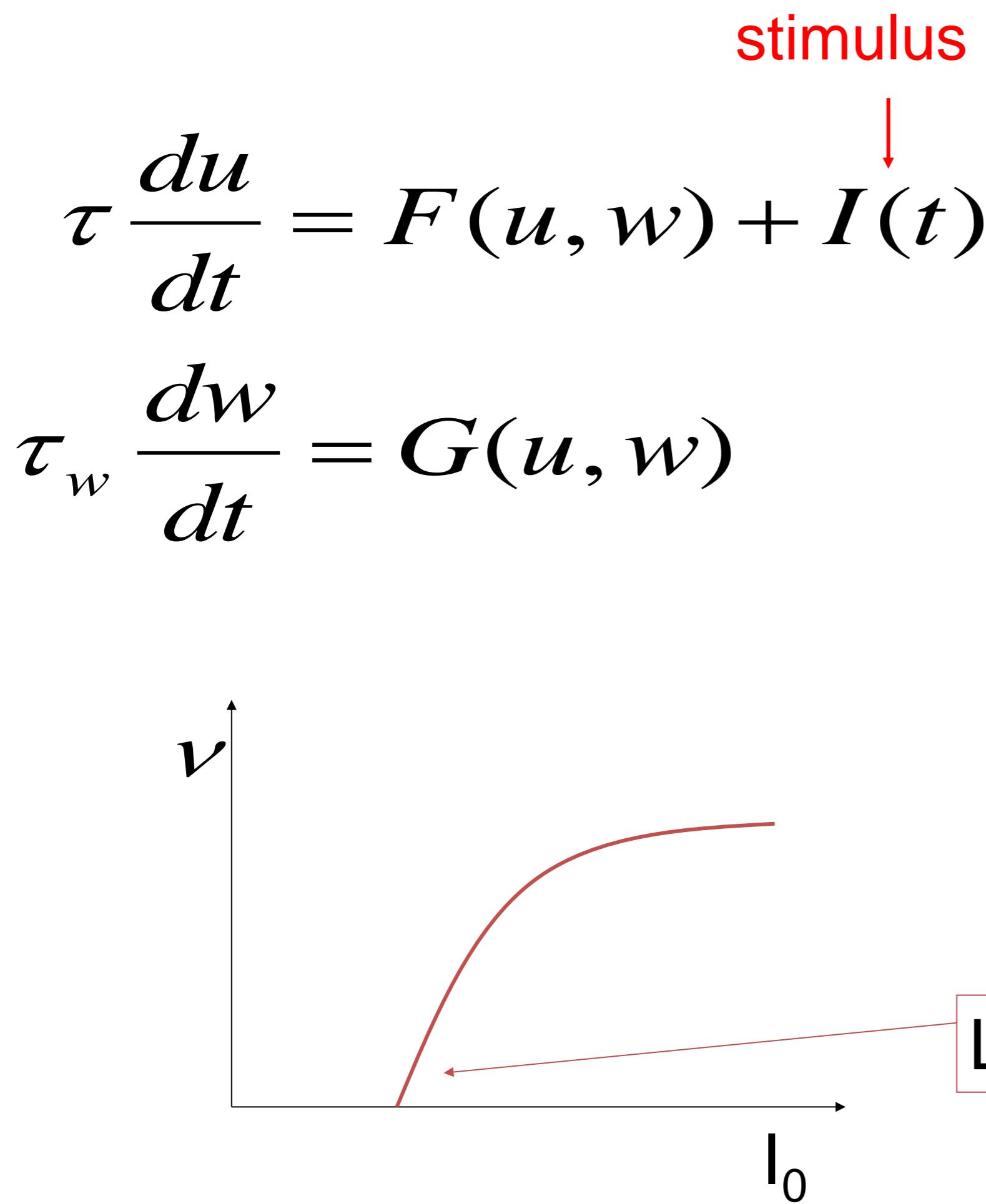
stimulus

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

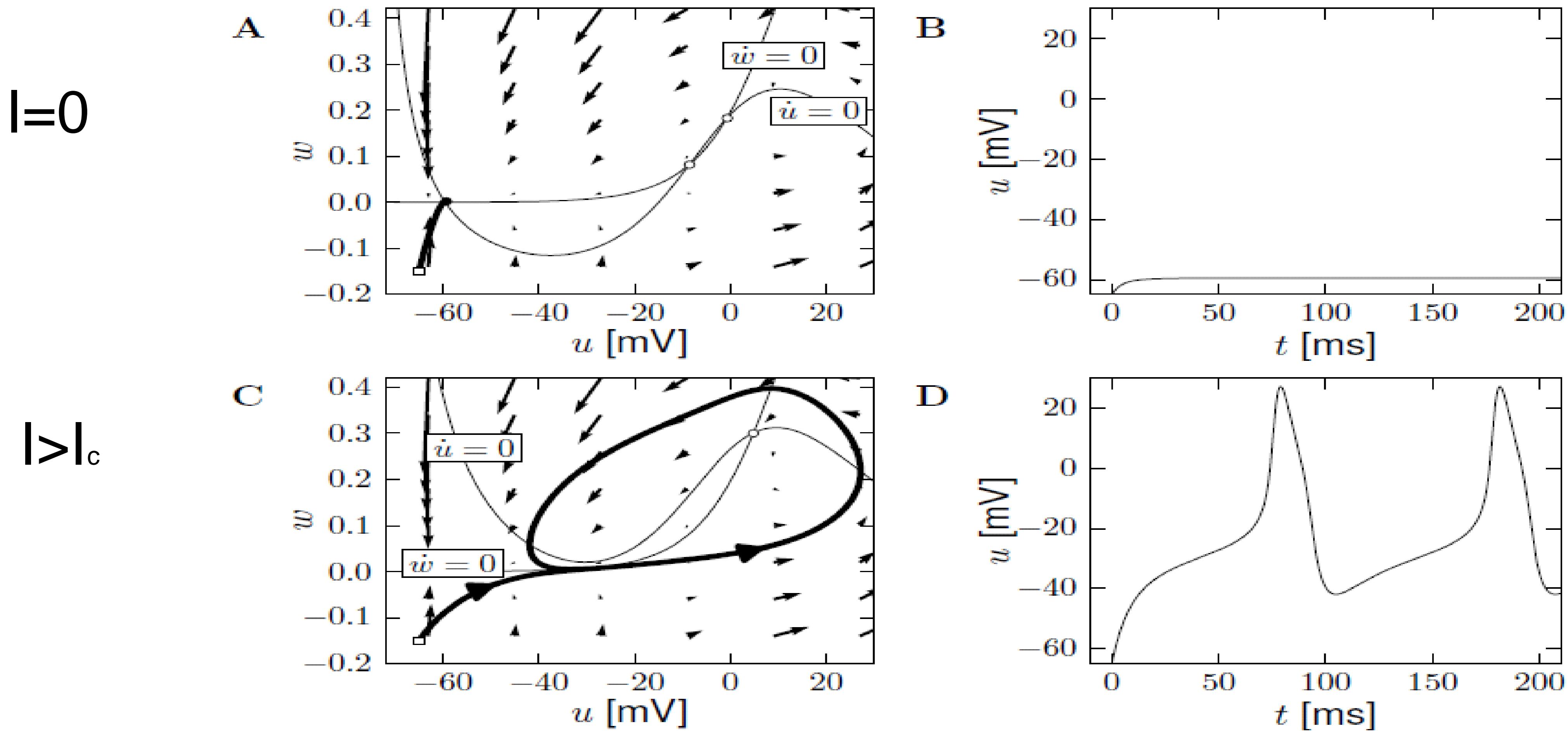
flow arrows



type I Model – constant input



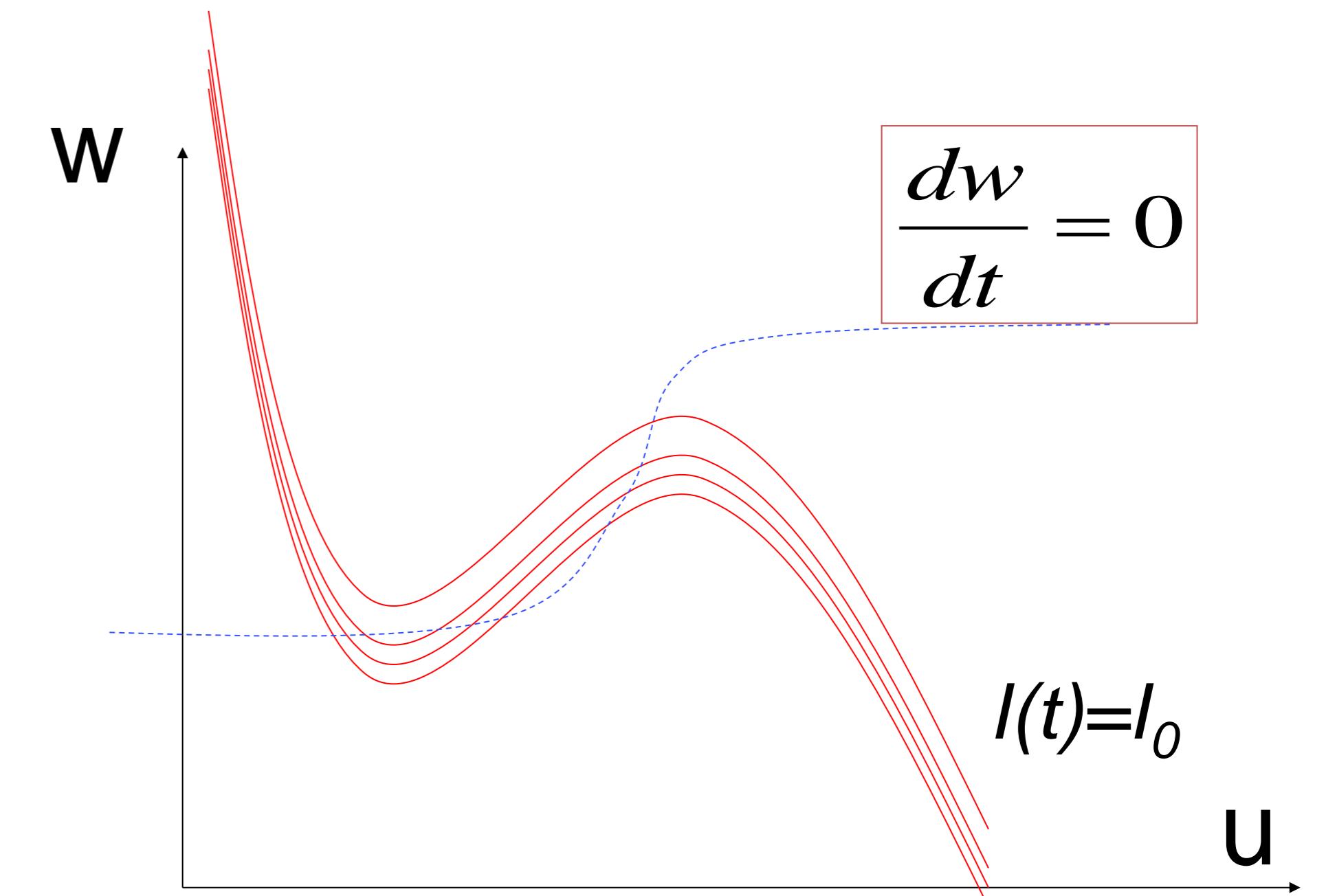
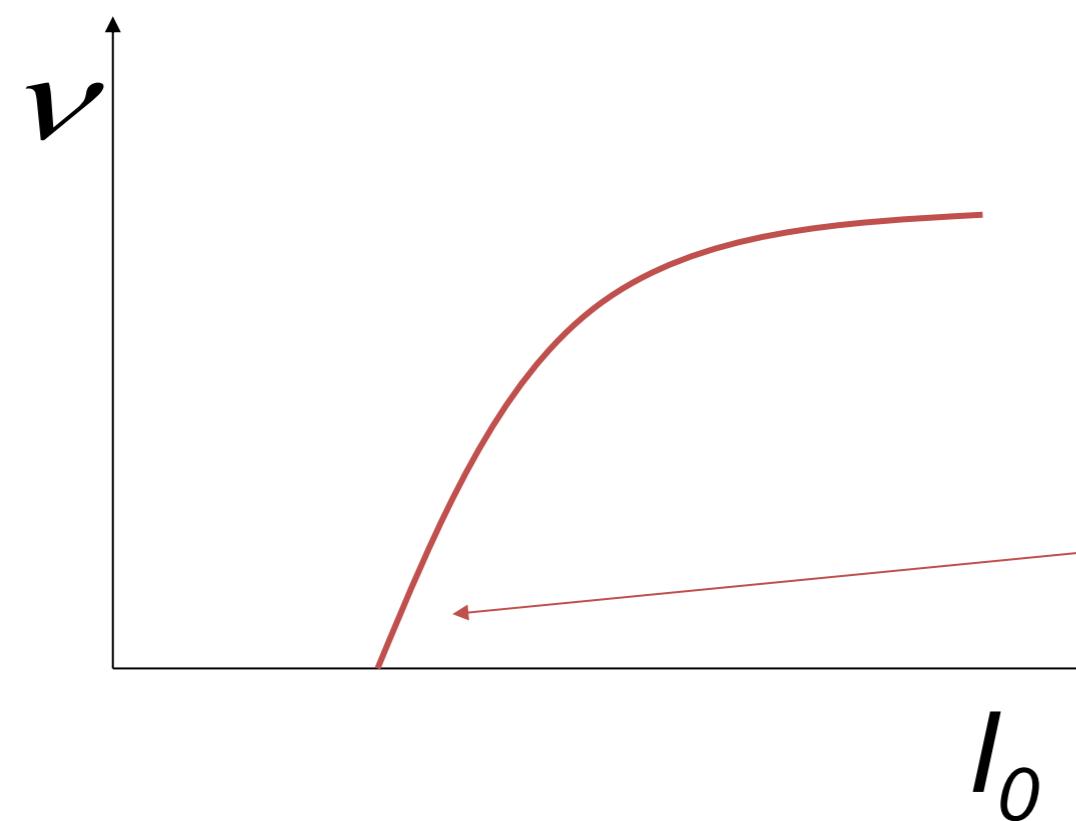
Morris-Lecar, type I Model – constant input



type I Model – constant input

stimulus

$$\tau \frac{du}{dt} = F(u, w) + I(t)$$
$$\frac{dw}{dt} = -\frac{w - w_0(u)}{\tau_{eff}(u)}$$
$$w_0(u) = 0.5[1 + \tanh(\frac{u - \theta}{d})]$$



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

Low-frequency firing

Type I and type II models

Response at firing threshold?

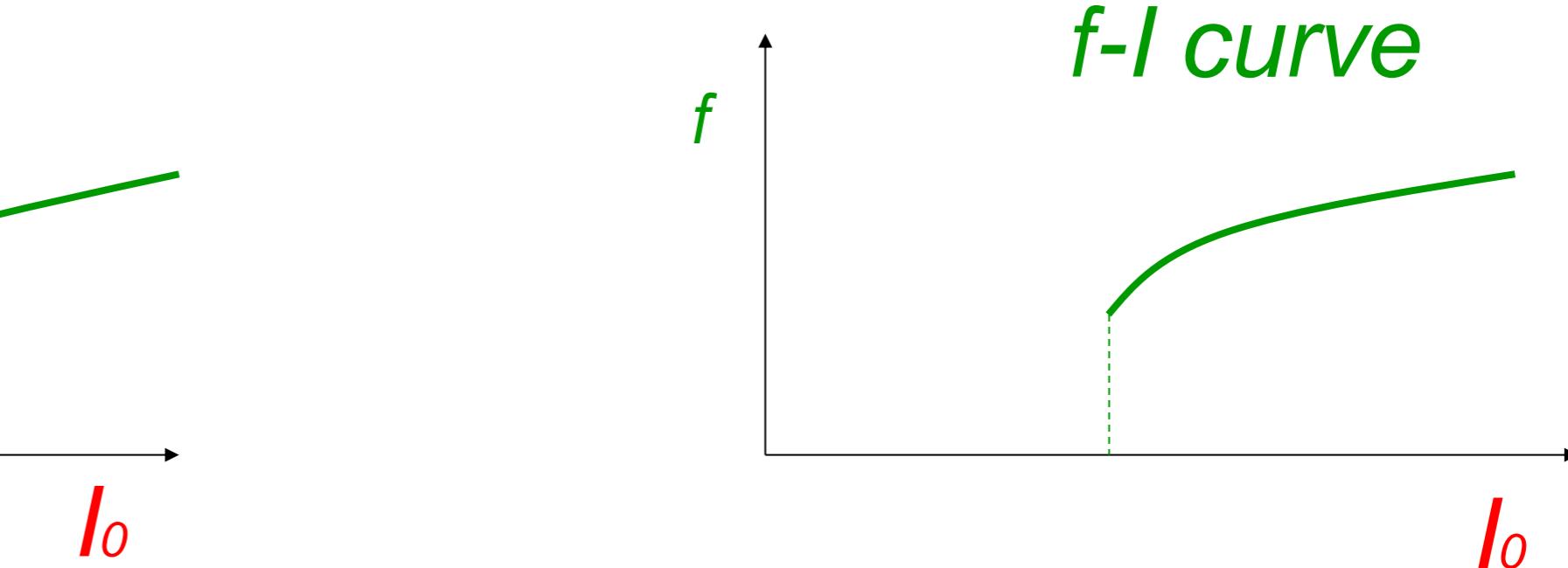
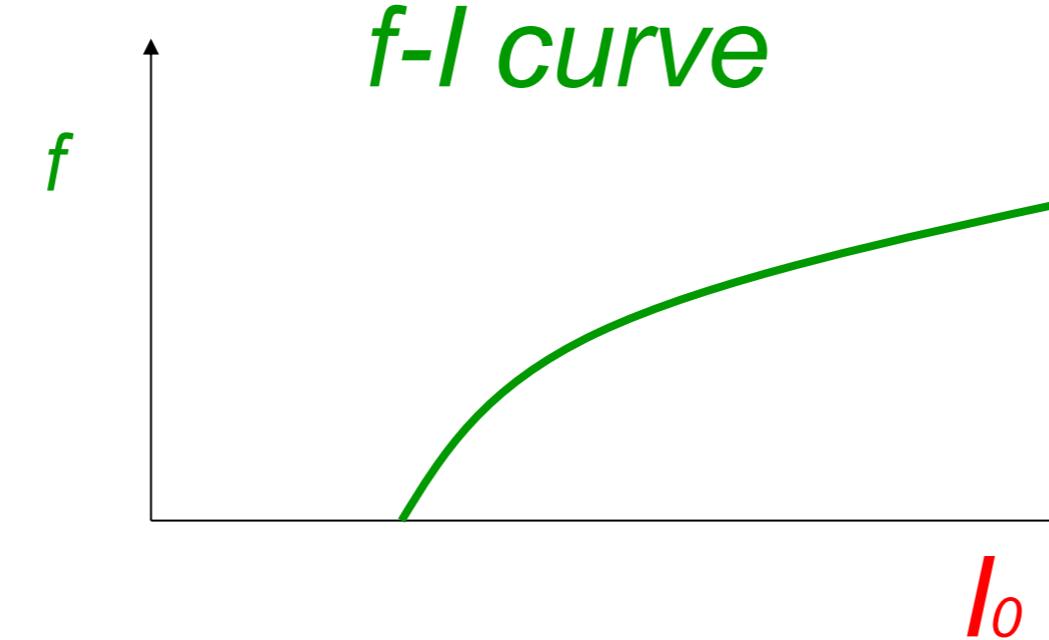
Type I

type II

Saddle-Node
Onto limit cycle

For example:
Subcritical Hopf

ramp input/
constant input



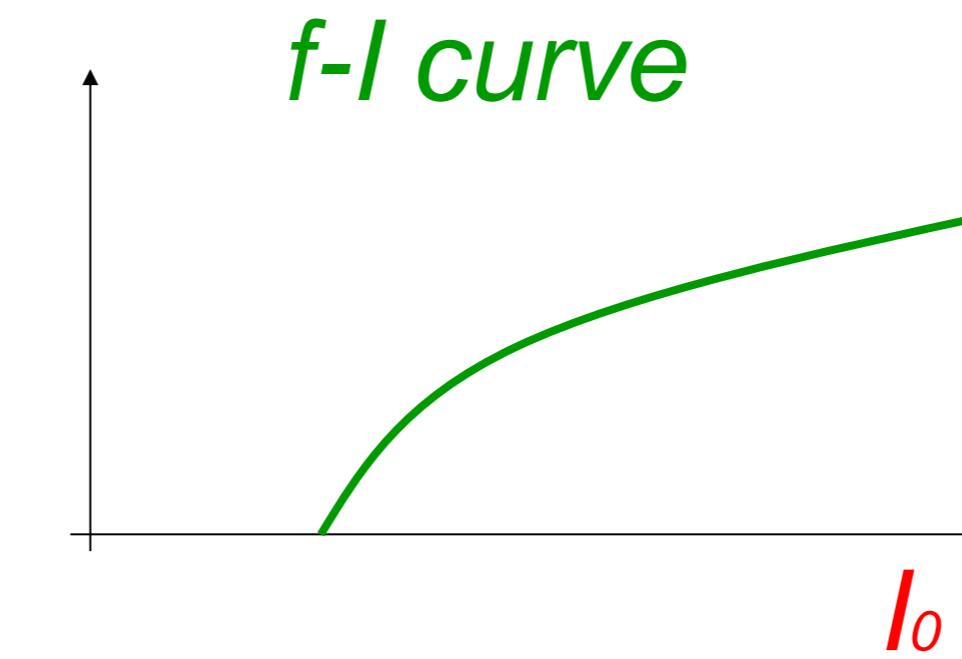
Neuronal Dynamics – 4.4. Type I and II Neuron Models

ramp input/
constant input

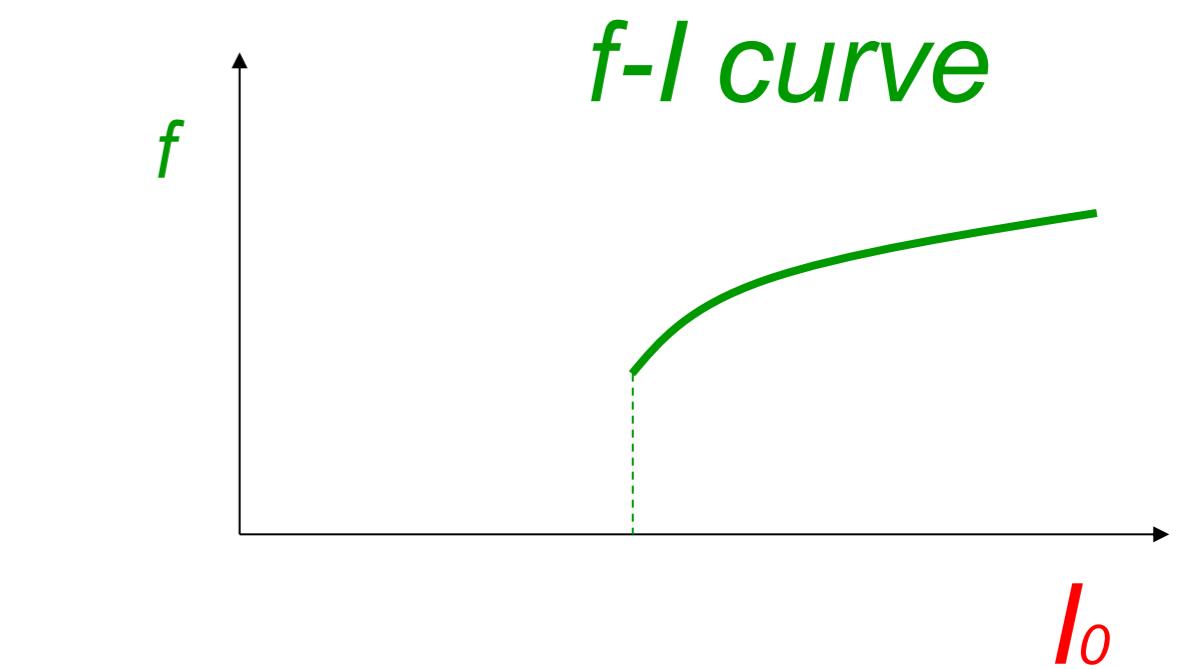


neuron

Type I and type II models



f-*I* curve



f-*I* curve

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



Neuronal Dynamics: Computational Neuroscience of Single Neurons

**Week 4 – Reducing detail:
Two-dimensional neuron models**

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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?

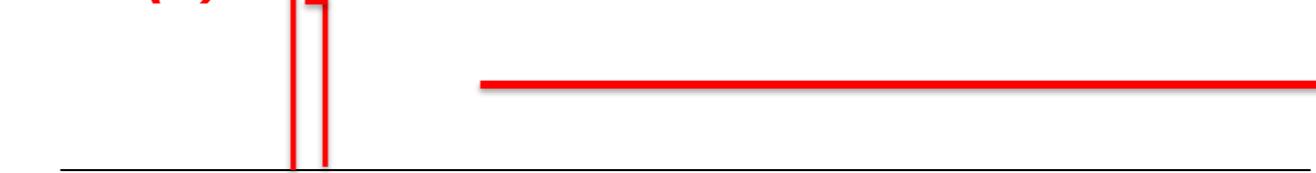
4.5. Nonlinear Integrate-and-fire

- from two to one dimension

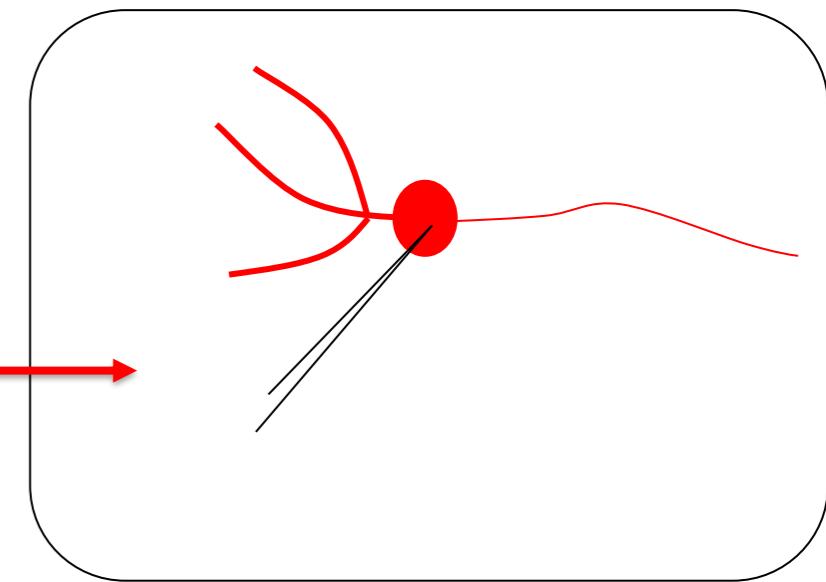
Neuronal Dynamics – 4.4b Threshold in 2dim. Neuron Models

pulse input

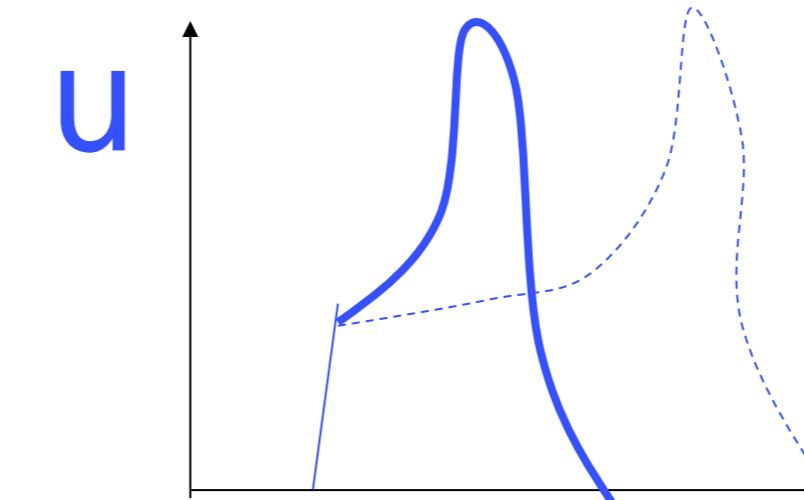
$I(t)$



neuron



Delayed spike



Reduced amplitude

Neuronal Dynamics – 4.4 Bifurcations, simplifications

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

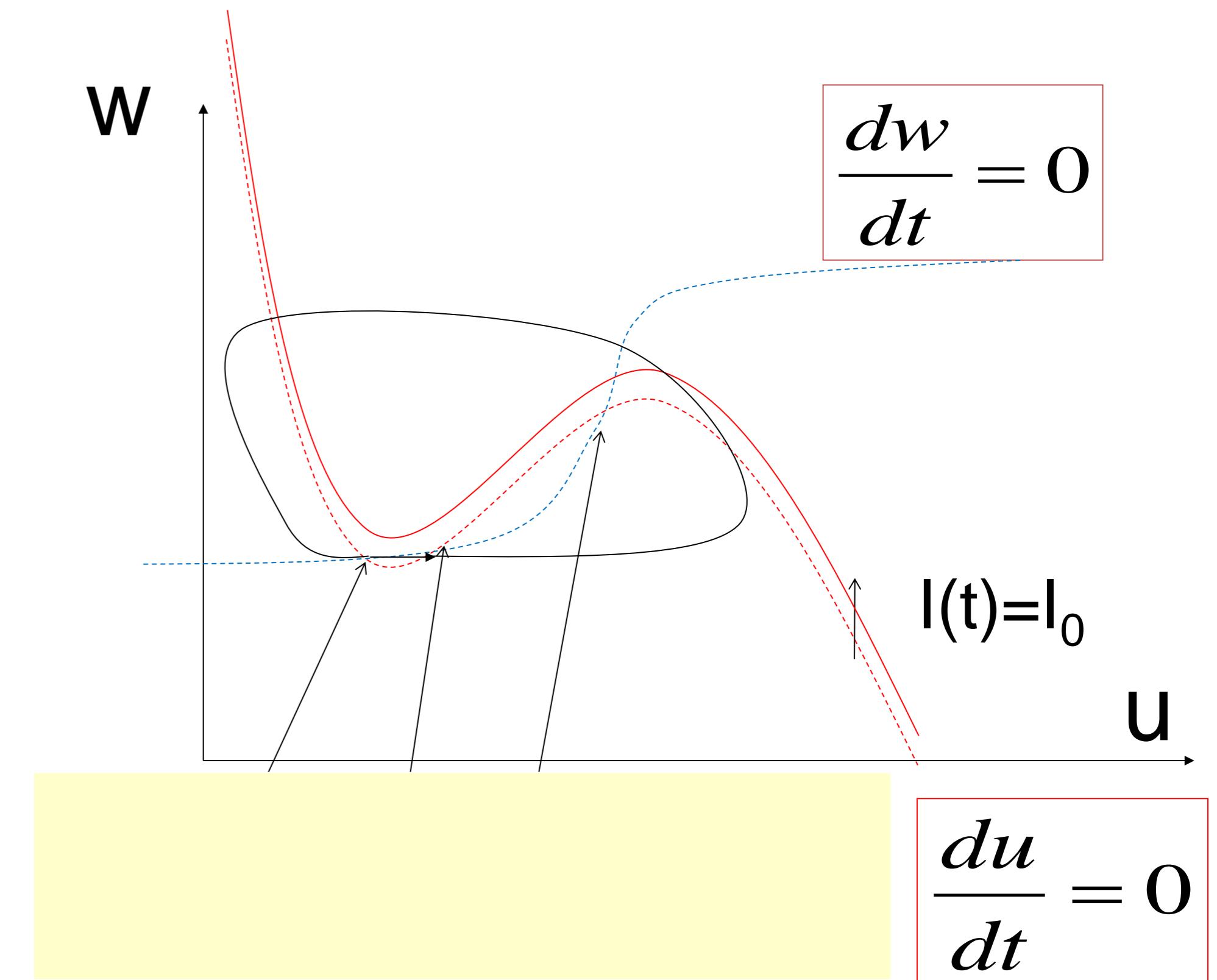
*Nancy Kopell,
Bart Ermentrout,
John Rinzel,
Eugene Izhikevich
and many others*

Saddle-node onto limit cycle bifurcation

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

stimulus

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



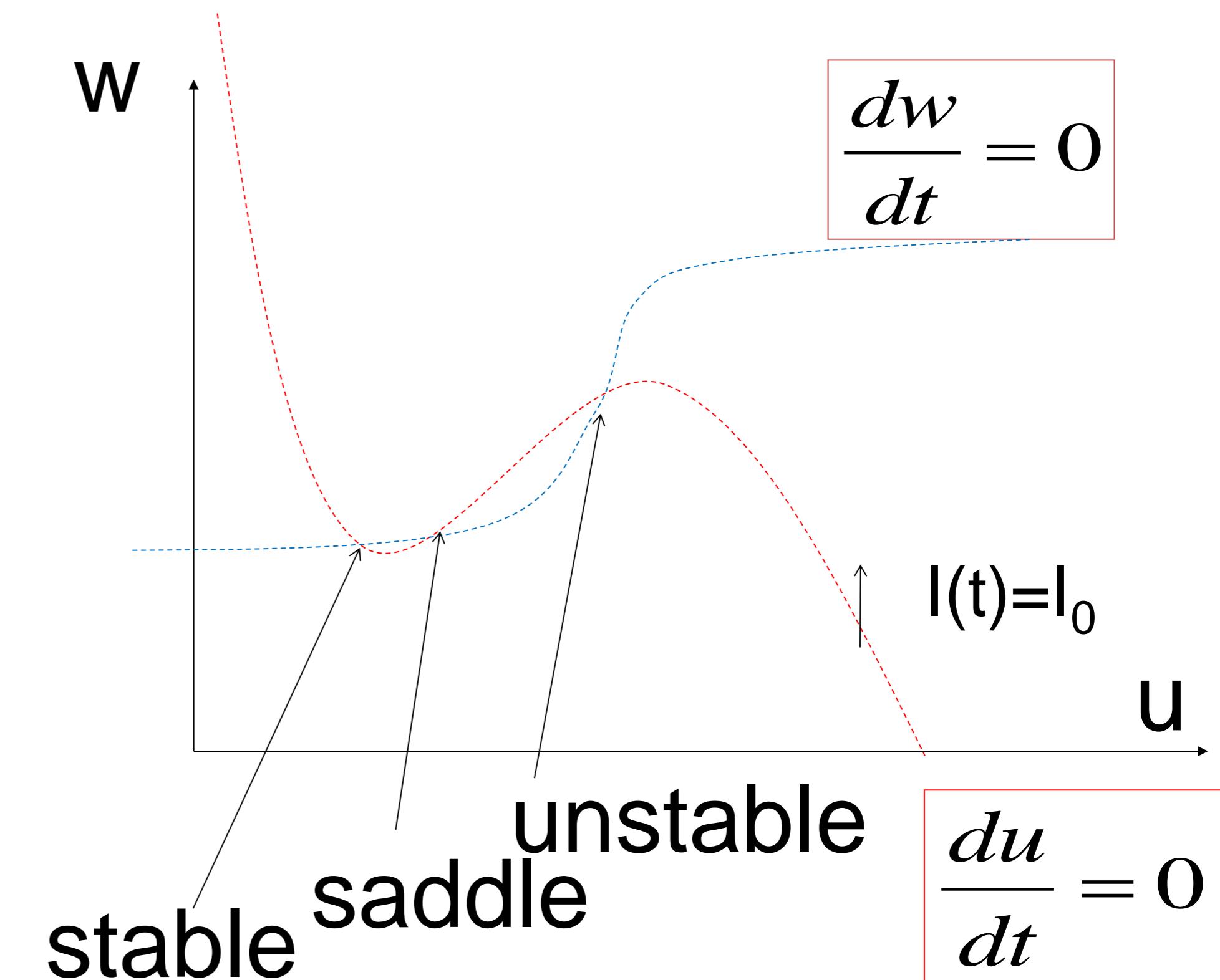
Neuronal Dynamics – 4.4b Pulse input

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

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

pulse input

$$I(t)$$



stable saddle unstable

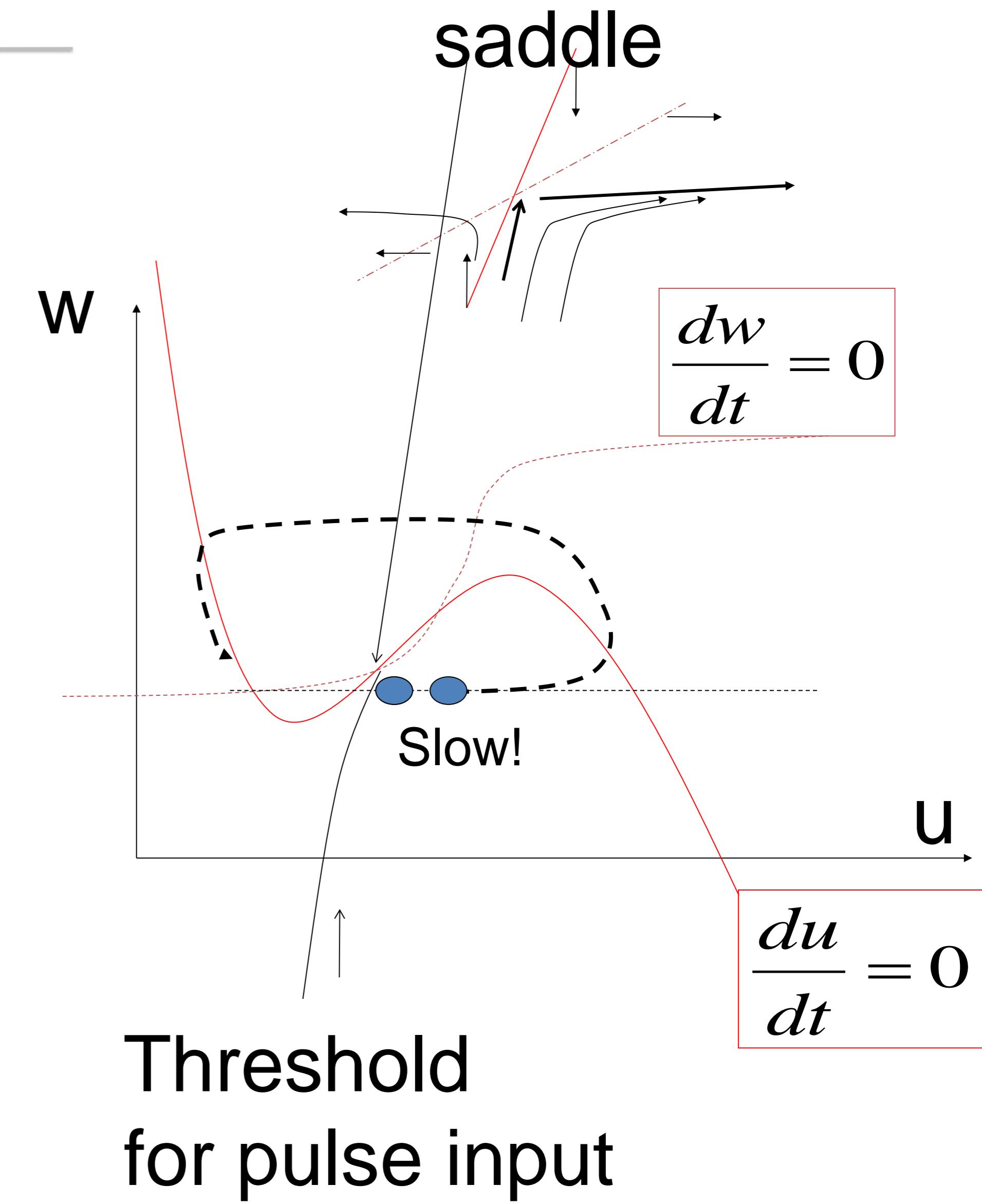
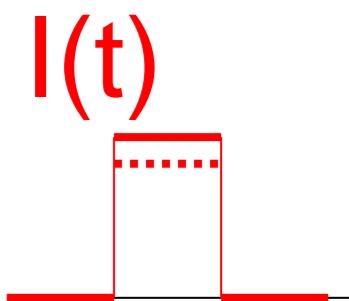
$$\frac{du}{dt} = 0$$

4.4b Type I model: Pulse input

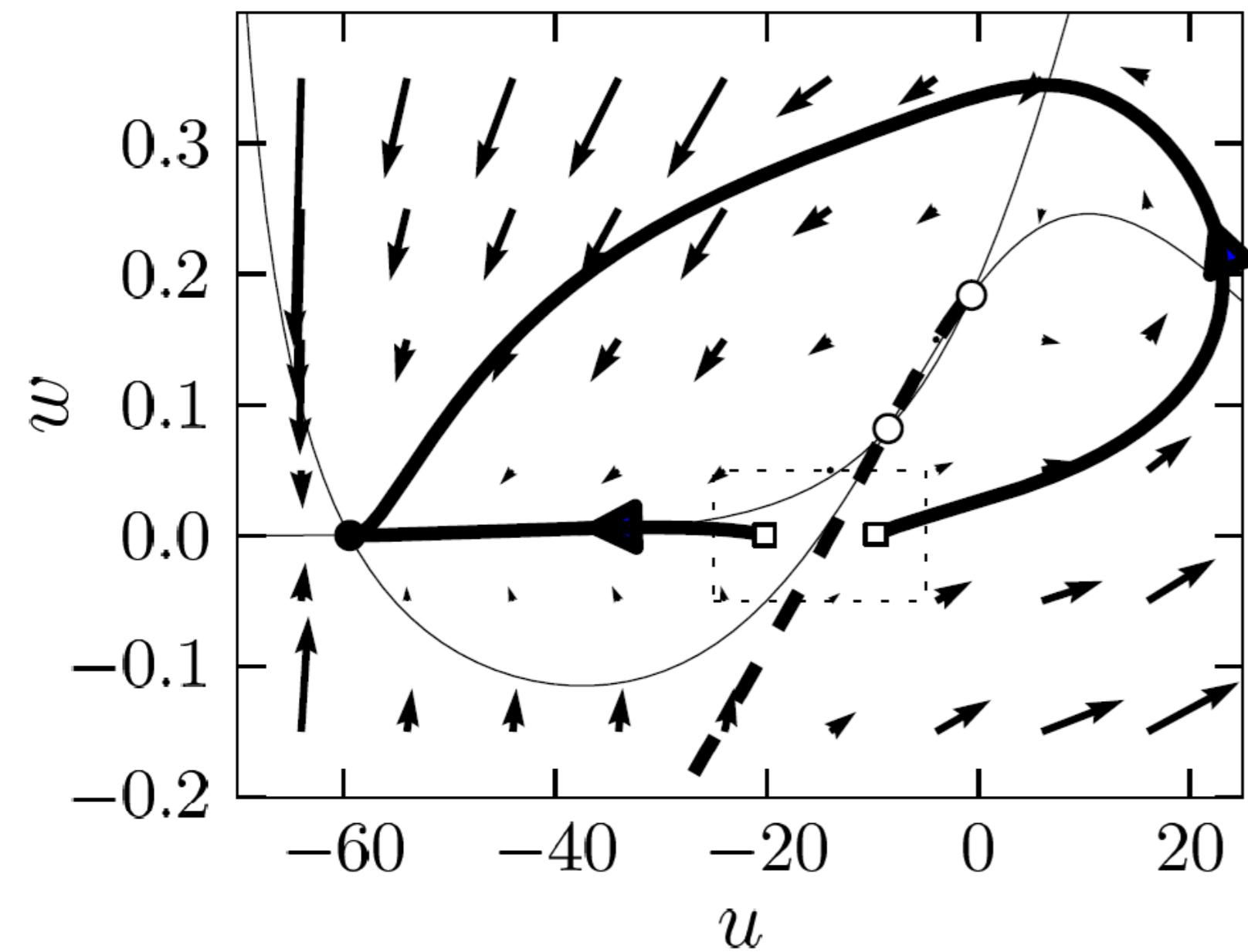
$$\tau \frac{du}{dt} = F(u, w) + RI(t)$$

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

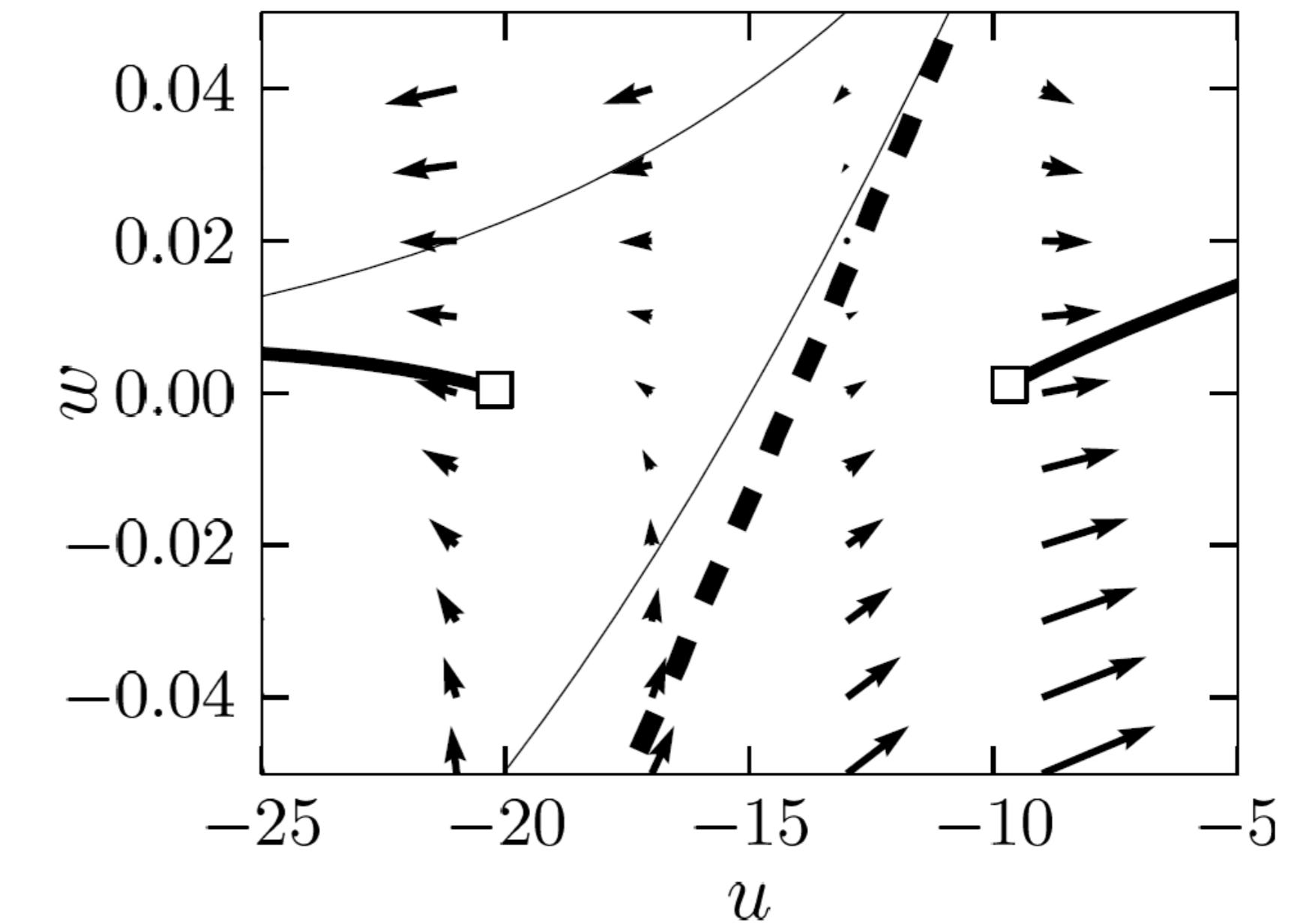
pulse input



4.4b Type I model: Threshold for Pulse input

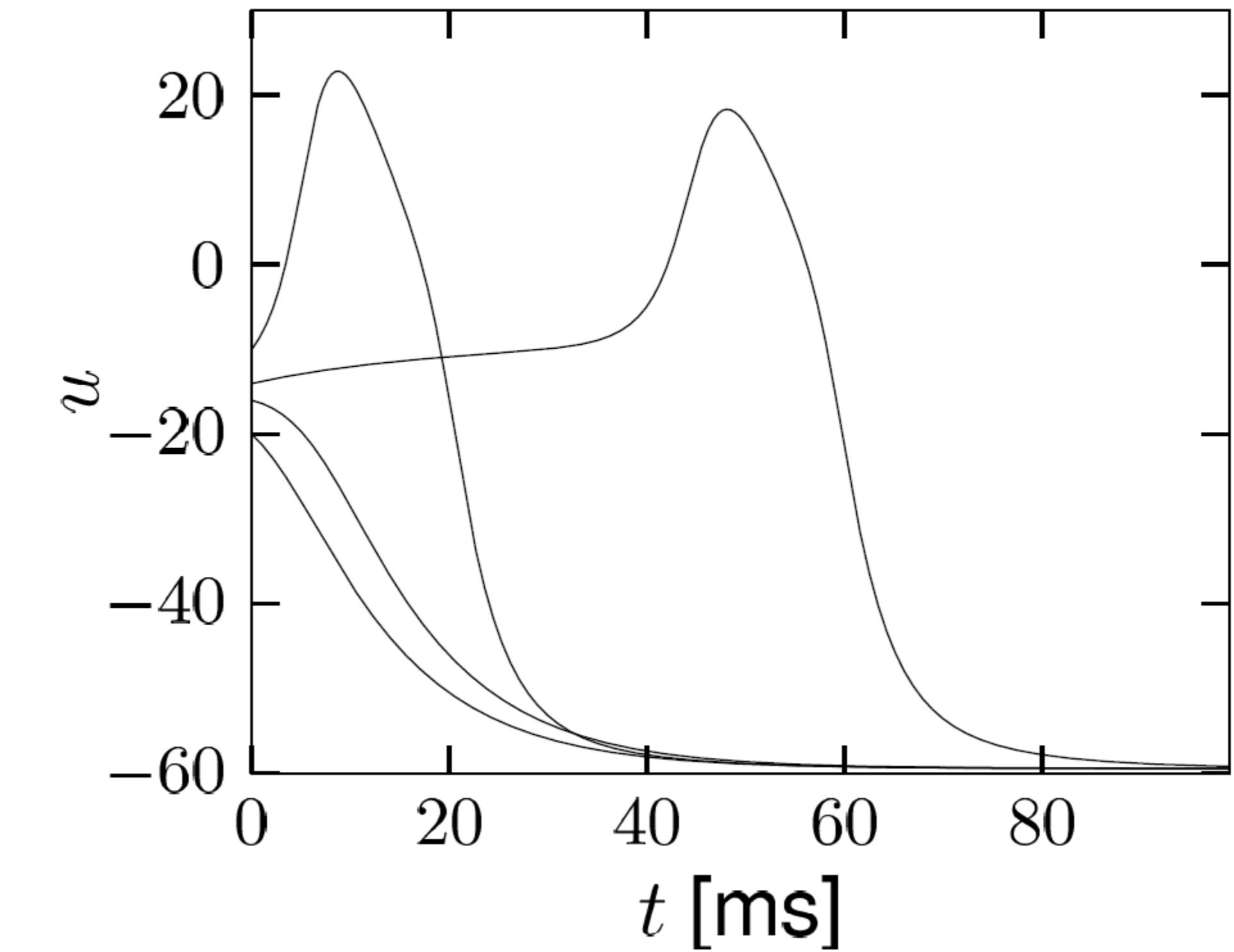
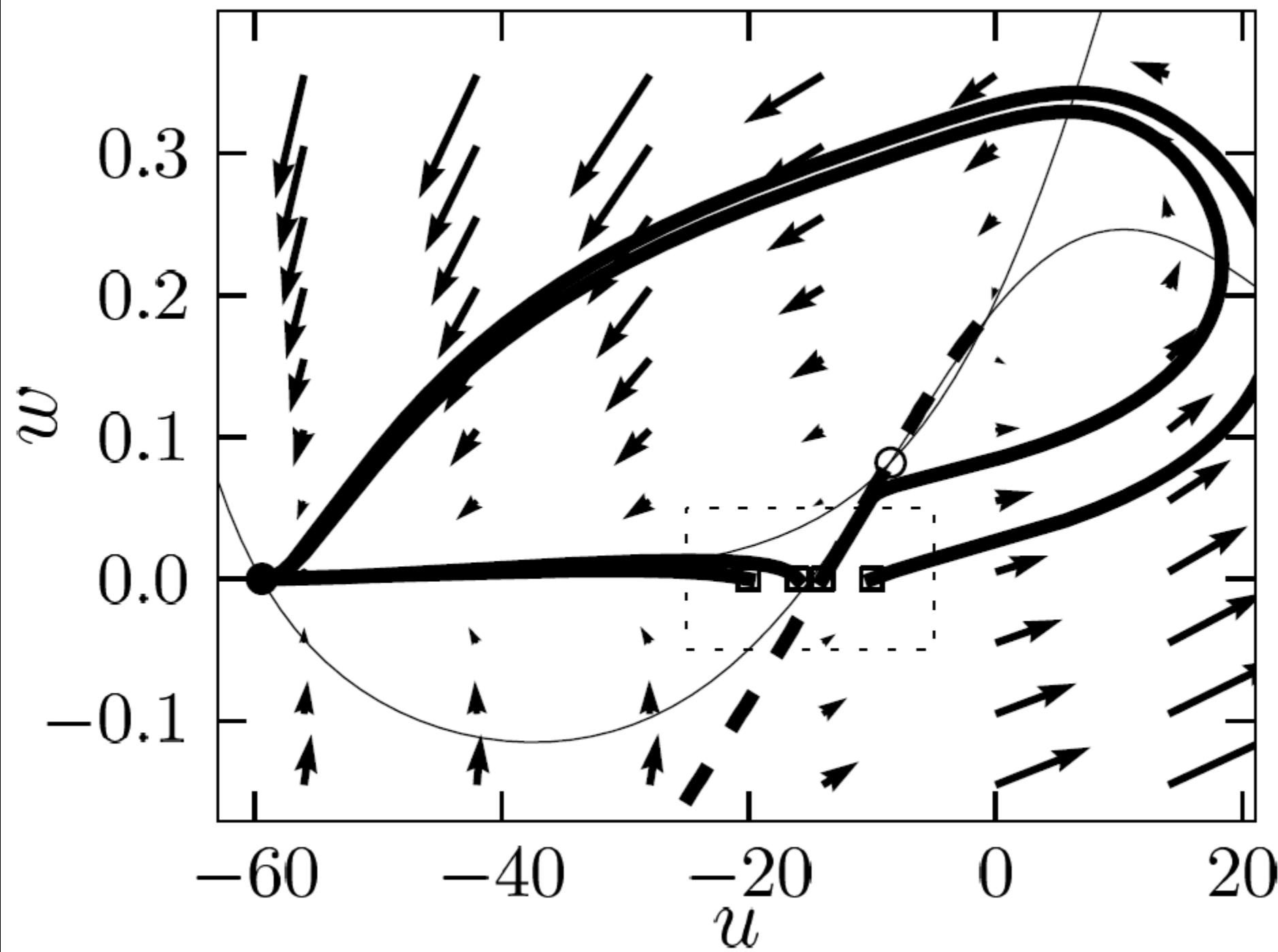


Stable manifold plays role of
'Threshold' (for pulse input)



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

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



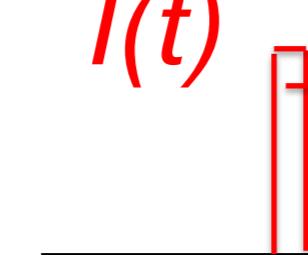
Delayed spike initiation close to
'Threshold' (for pulse input)

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

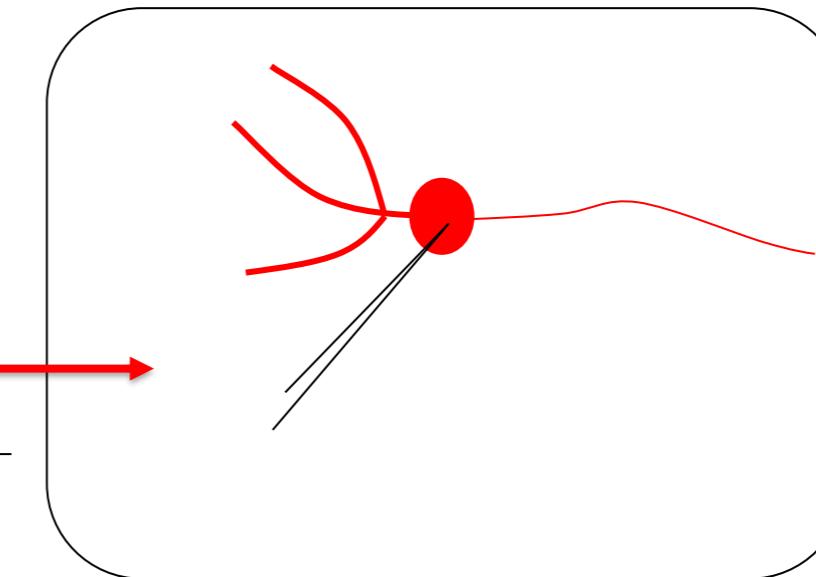
Neuronal Dynamics – 4.4b Threshold in 2dim. Neuron Models

pulse input

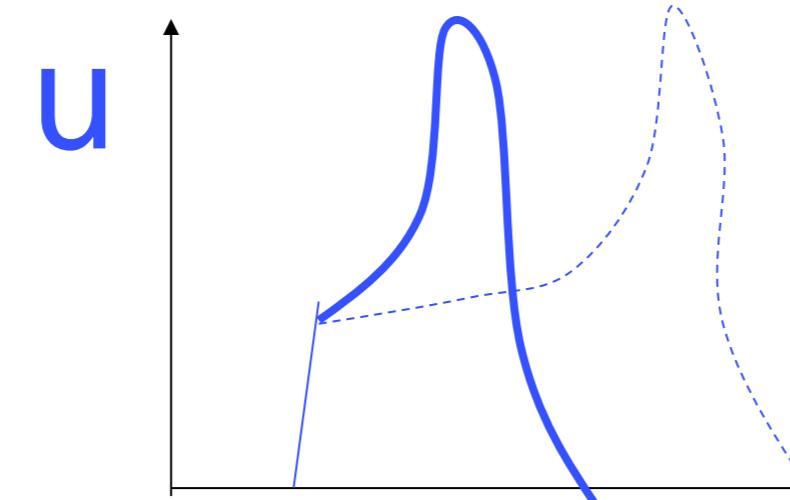
$I(t)$



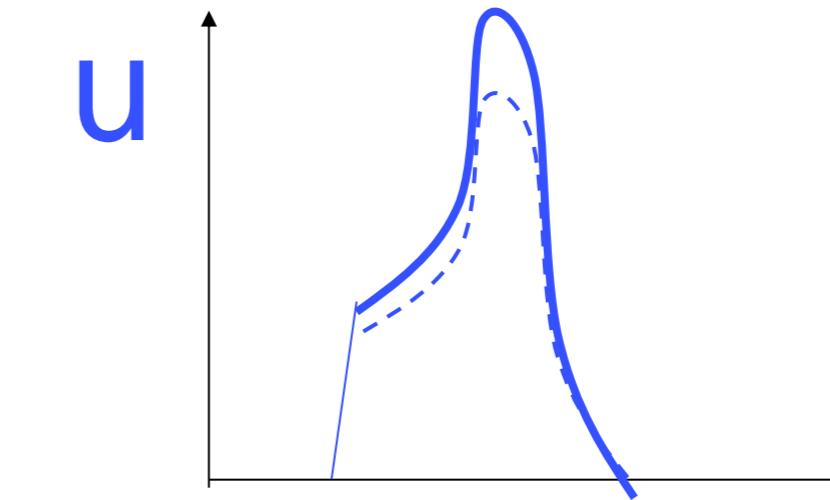
neuron



Delayed spike



Reduced amplitude



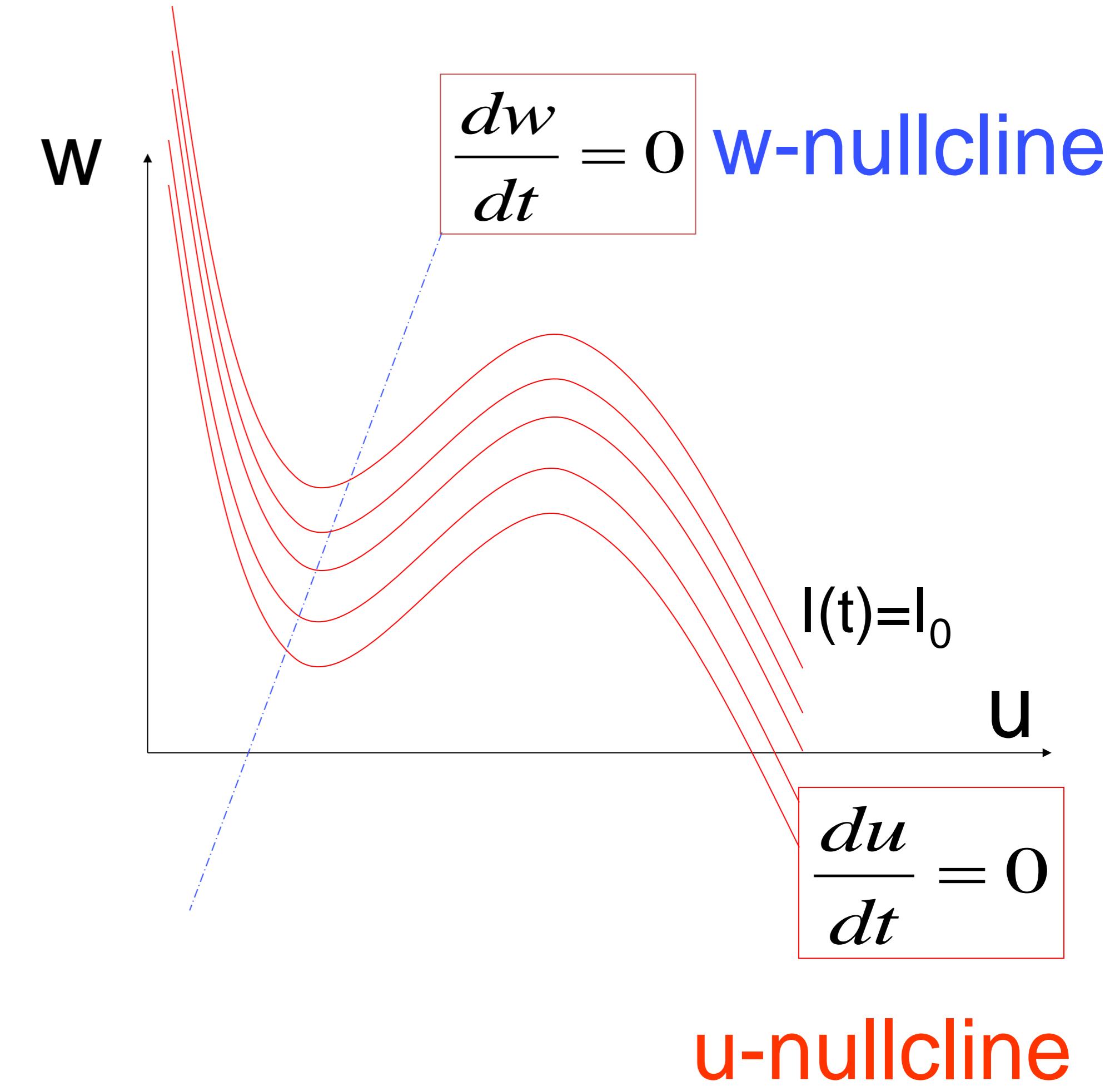
FitzHugh-Nagumo Model: Hopf bifurcation

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

stimulus

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

apply constant stimulus I_0



FitzHugh-Nagumo Model - pulse input

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

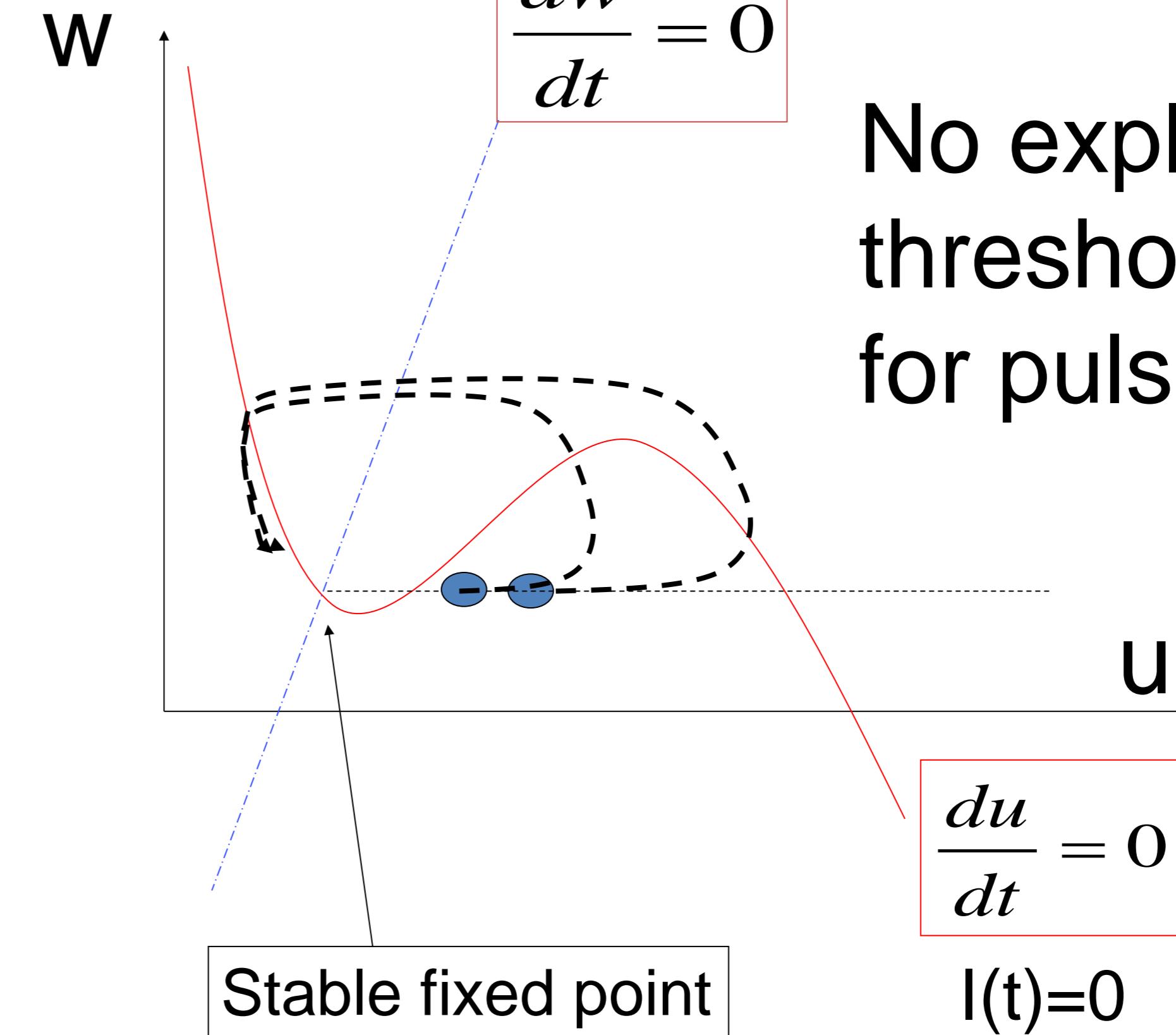
$$\tau_w \frac{dw}{dt} = G(u, w)$$

pulse input

$$I(t)$$




stimulus



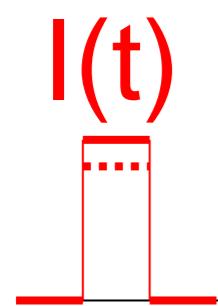
FitzHugh-Nagumo Model - pulse input threshold?

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

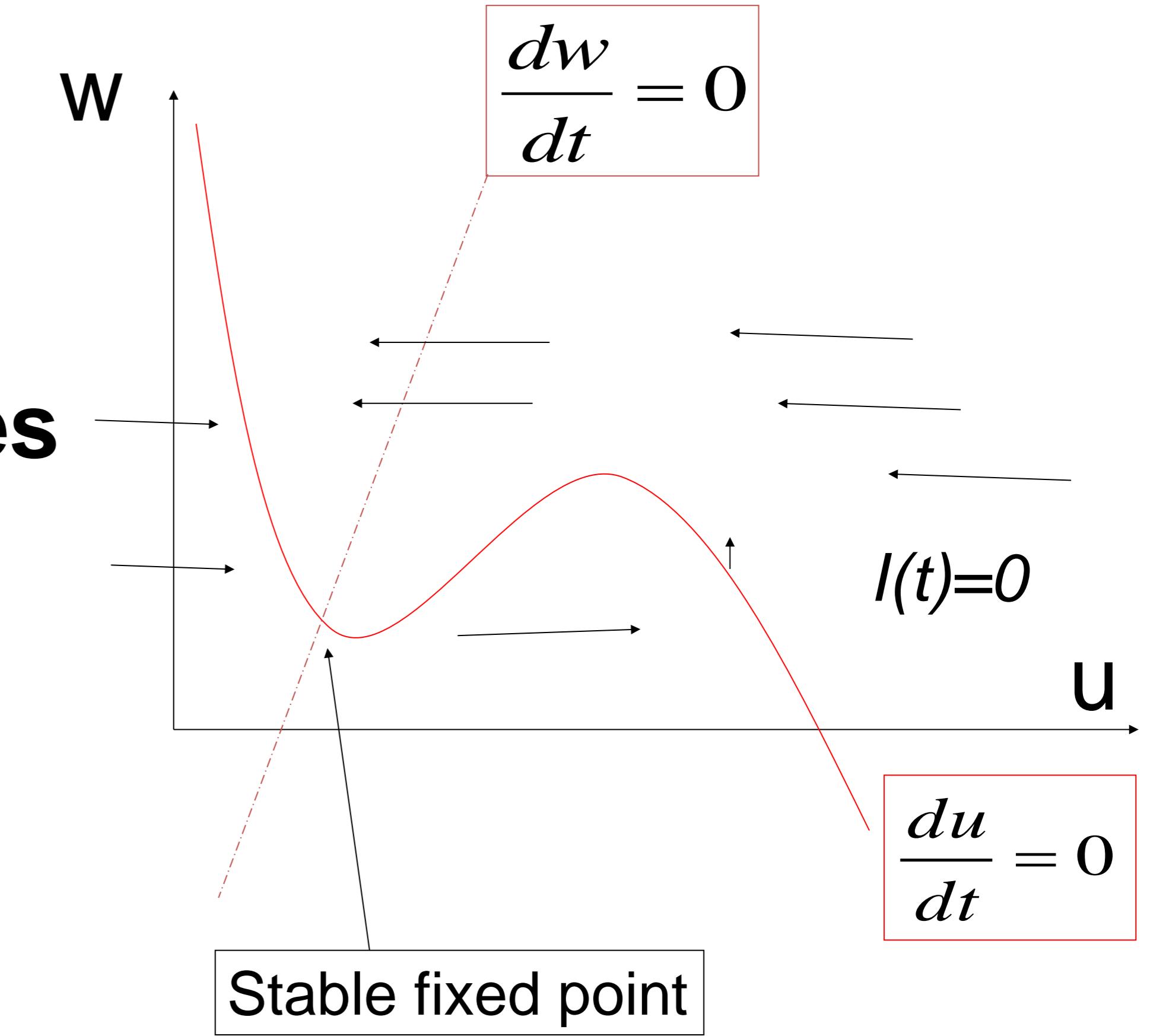
$$\tau_w \frac{dw}{dt} = G(u, w)$$

Separation of time scales

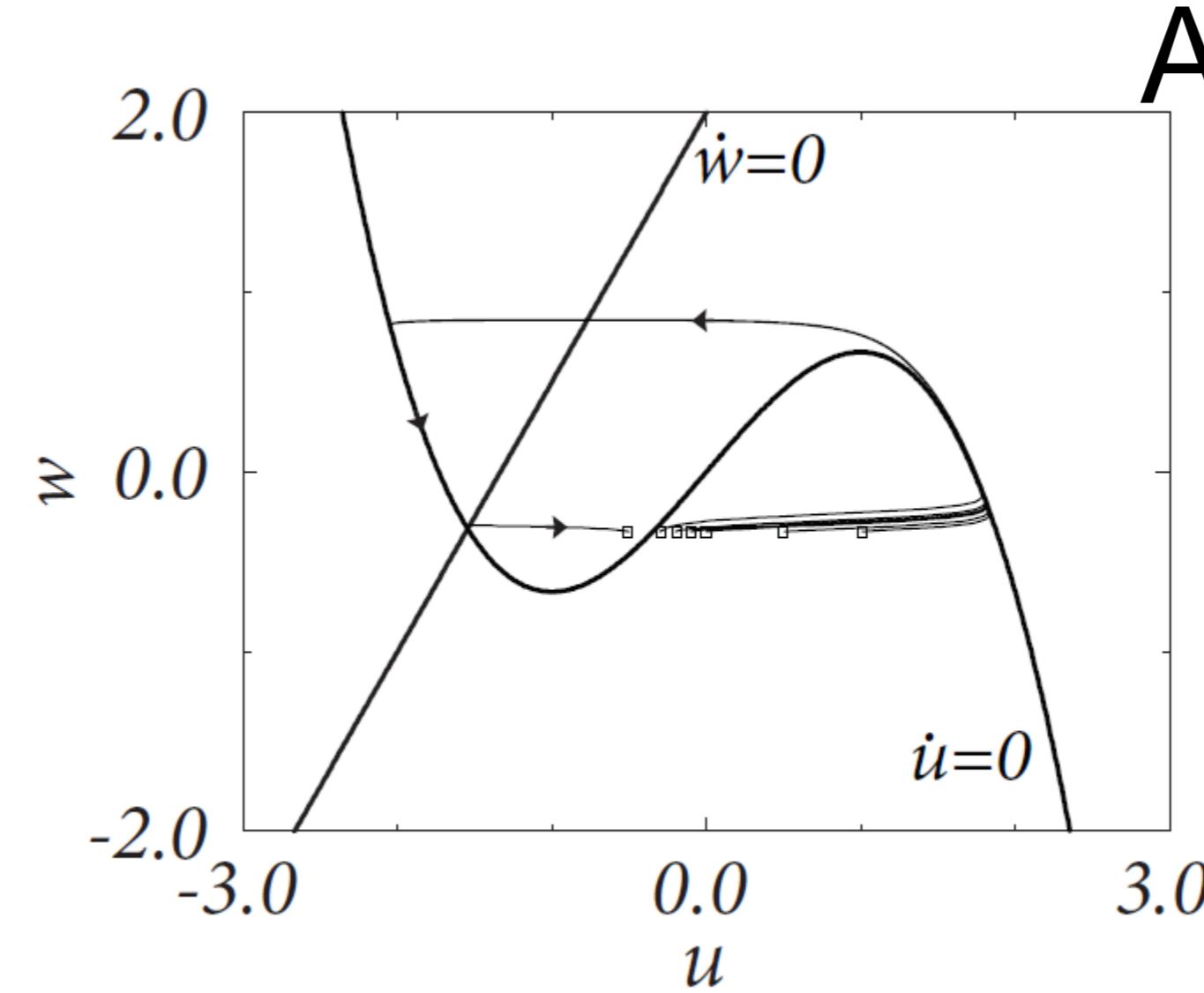
pulse input



$$\tau_w \gg \tau_u$$

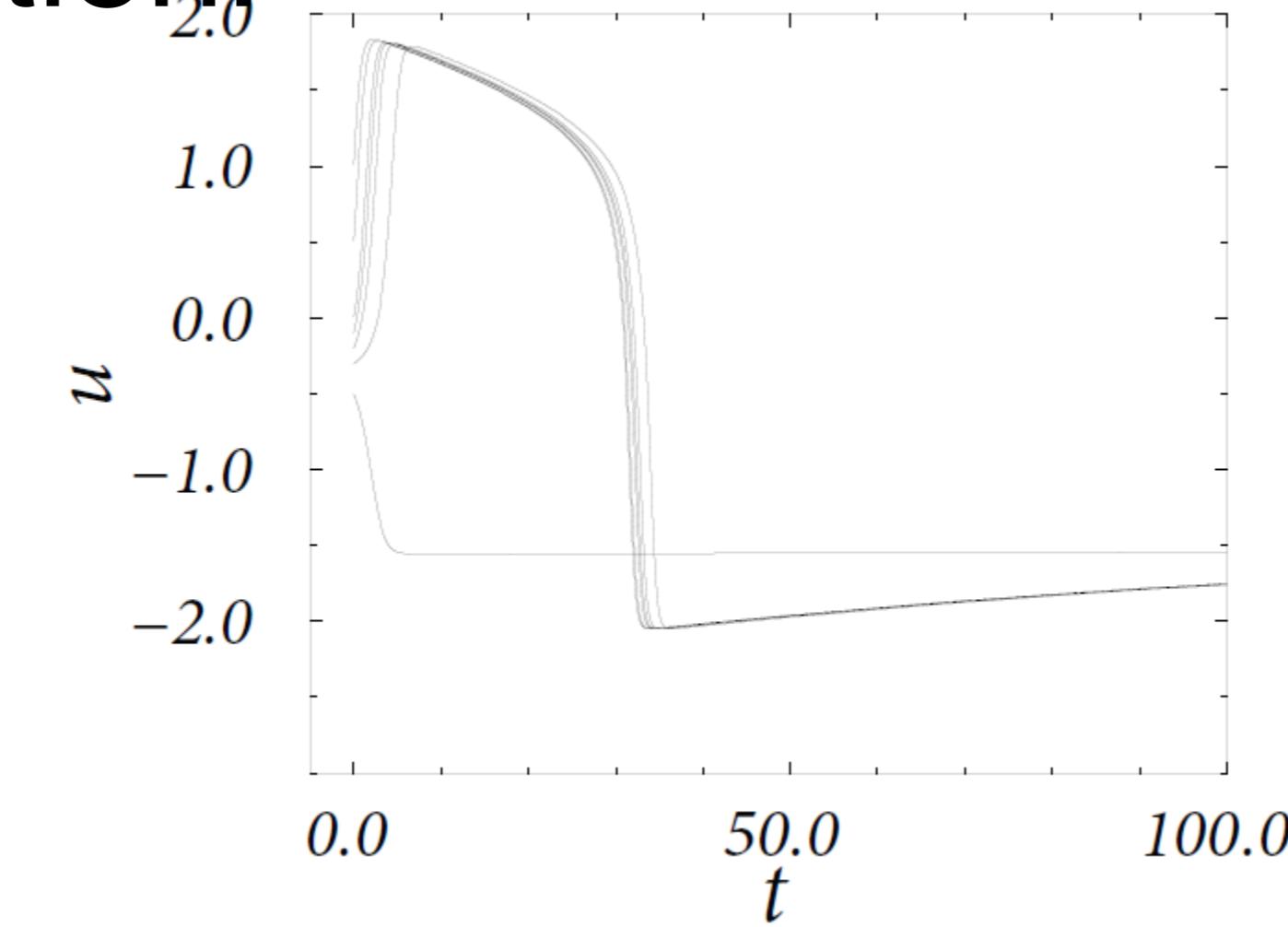


4.4b FitzHugh-Nagumo model: Threshold for Pulse input



Assumption:

$$\tau_w \gg \tau_u$$



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

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

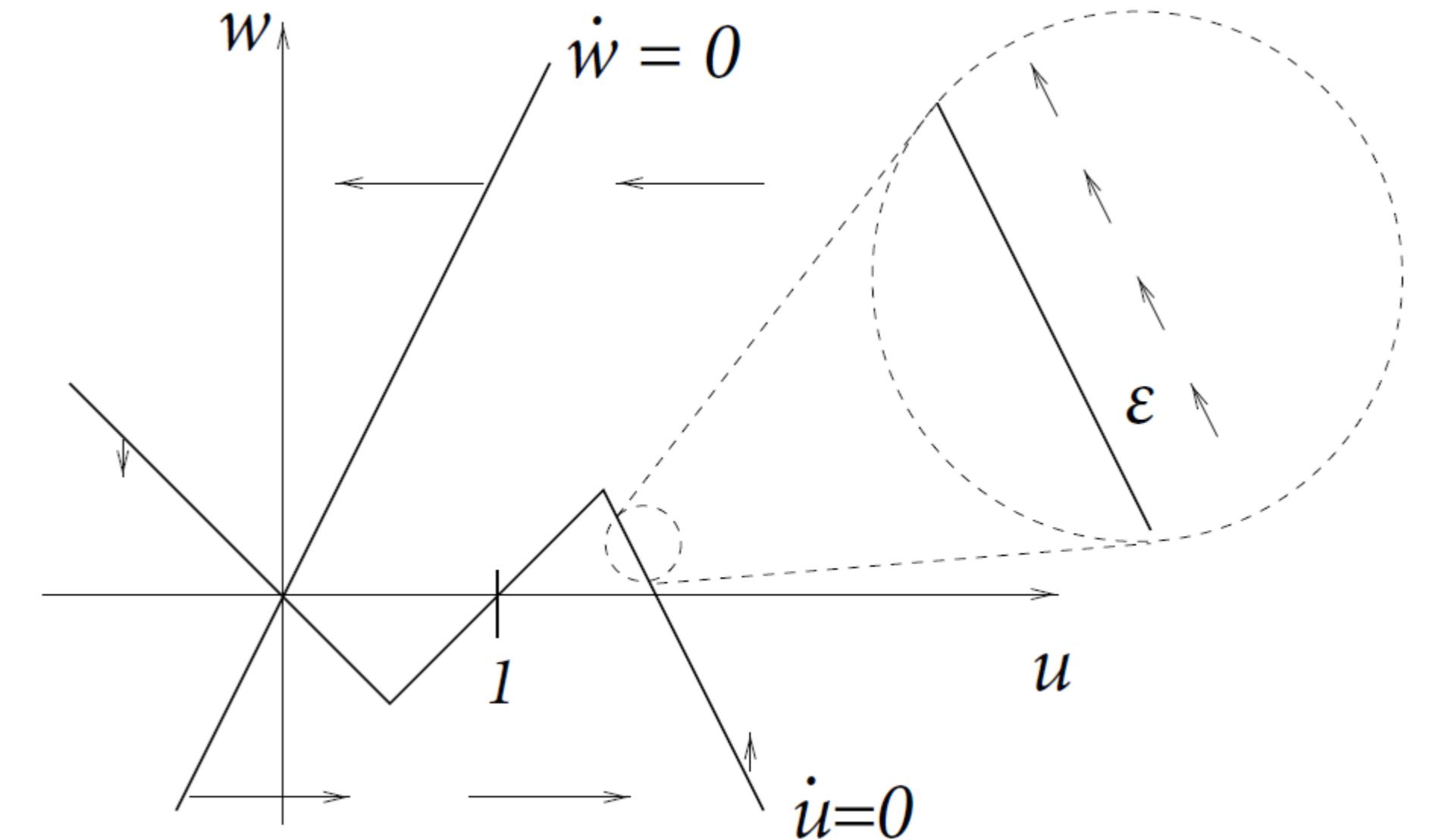
4.4b Detour: Separation fo time scales in 2dim models

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

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

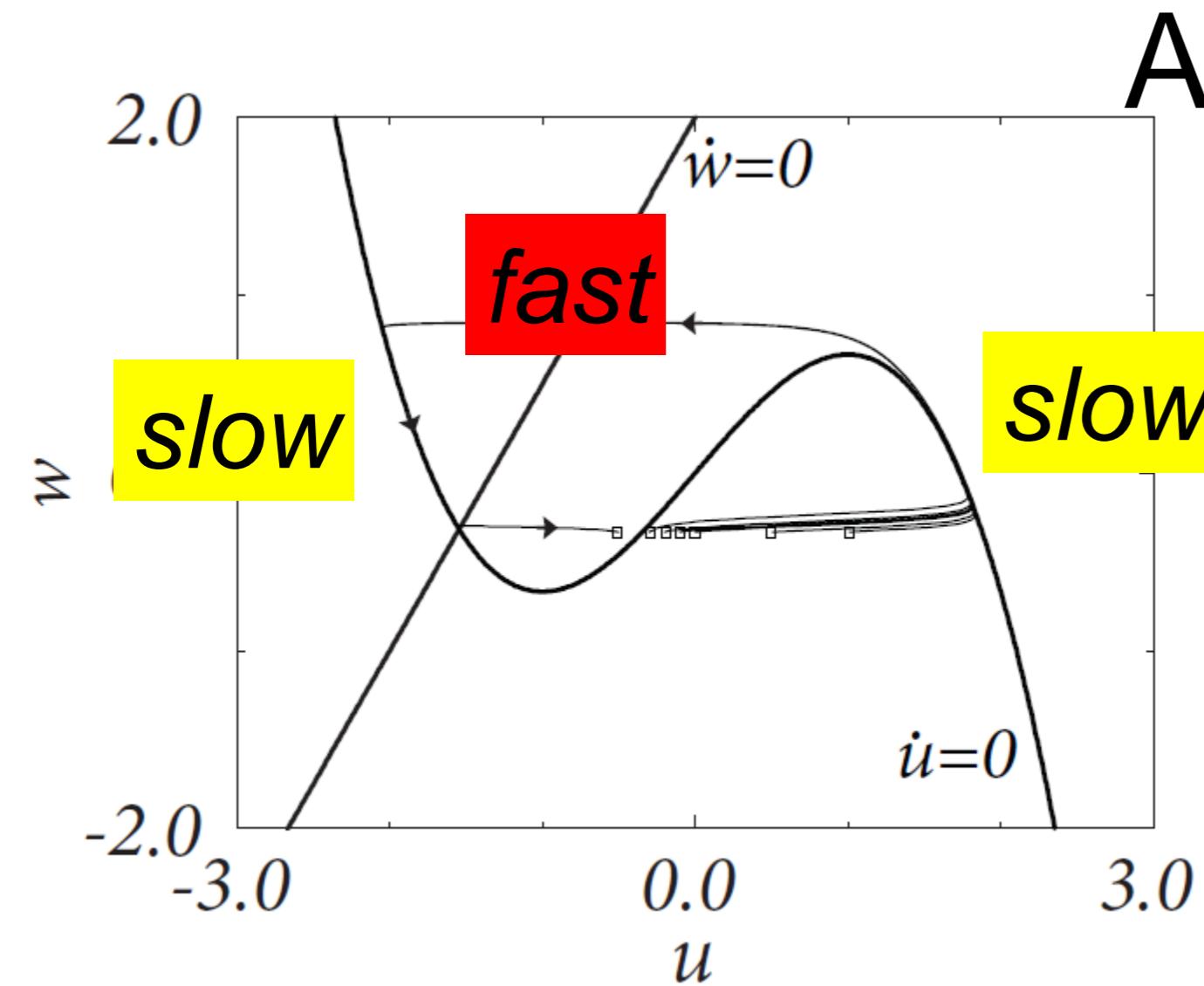
Assumption:

$$\tau_w \gg \tau_u$$



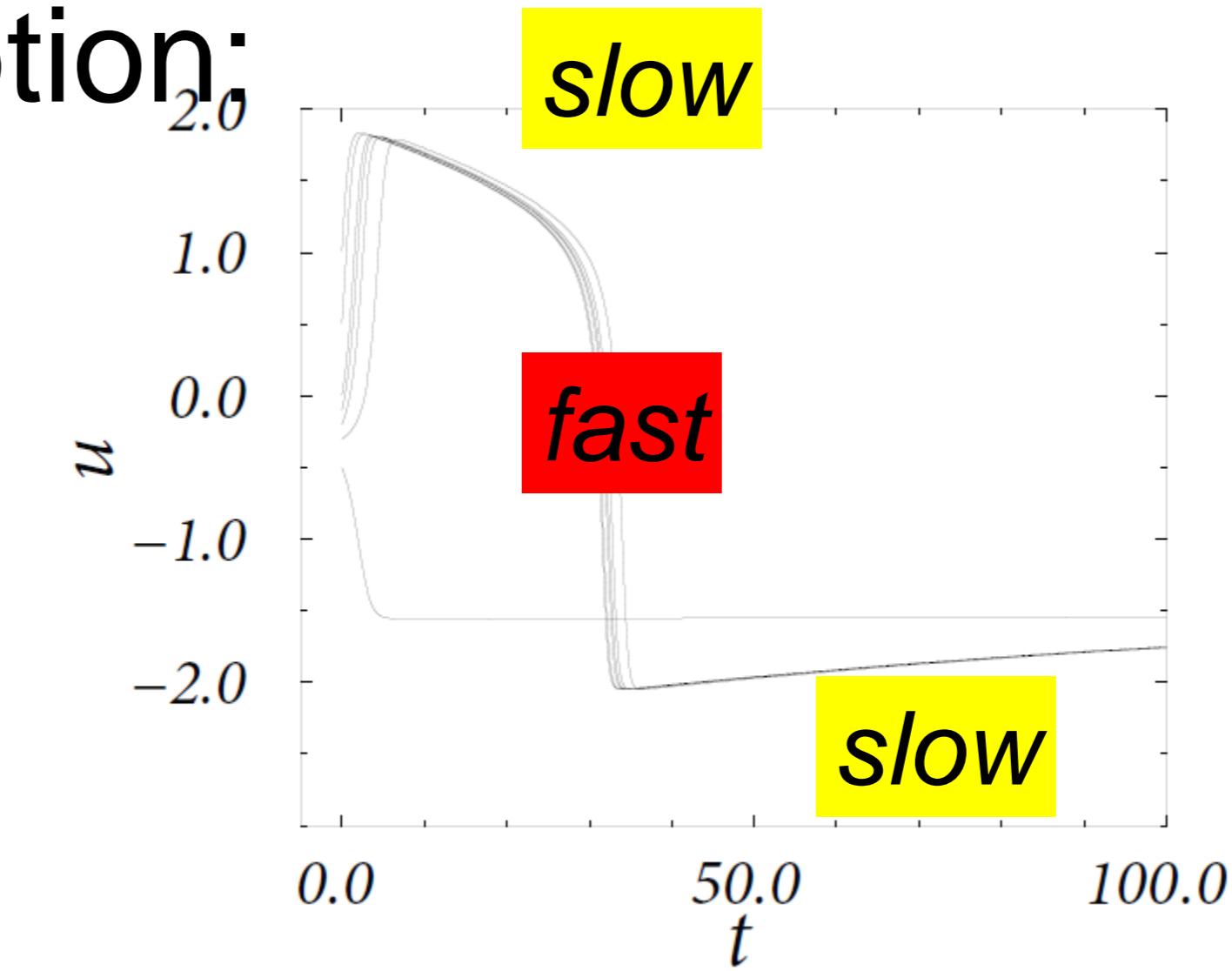
*Image: Neuronal Dynamics,
Gerstner et al.,
Cambridge Univ. Press (2014)*

4.4b FitzHugh-Nagumo model: Threshold for Pulse input



Assumption:

$$\tau_w \gg \tau_u$$



trajectory

-follows u -nullcline: slow

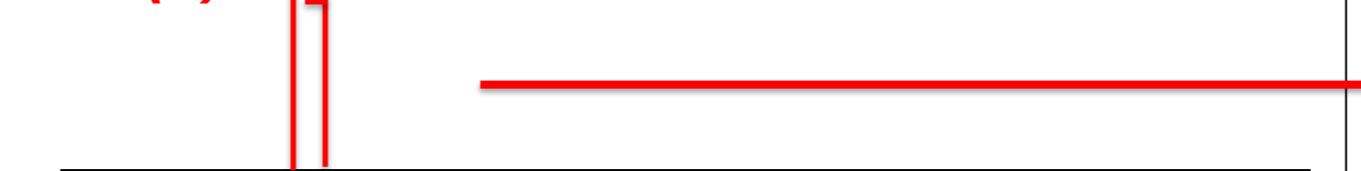
-jumps between branches: fast

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

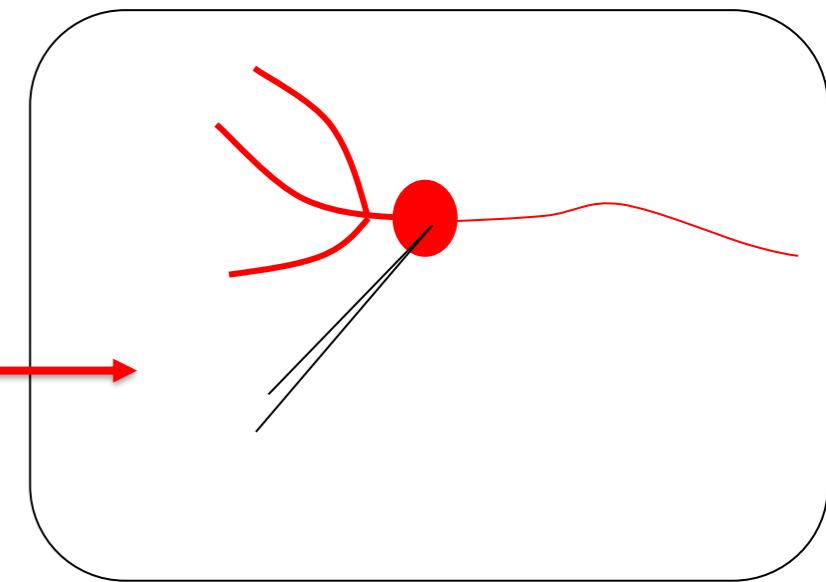
Neuronal Dynamics – 4.4b Threshold in 2dim. Neuron Models

pulse input

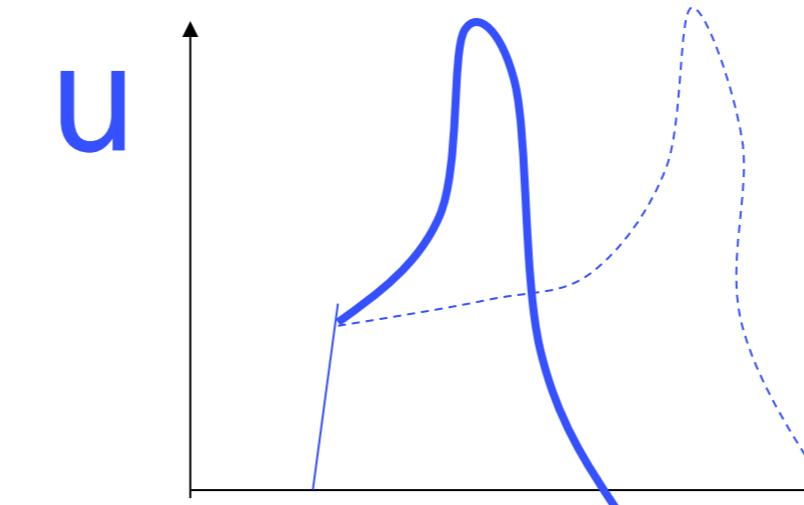
$I(t)$



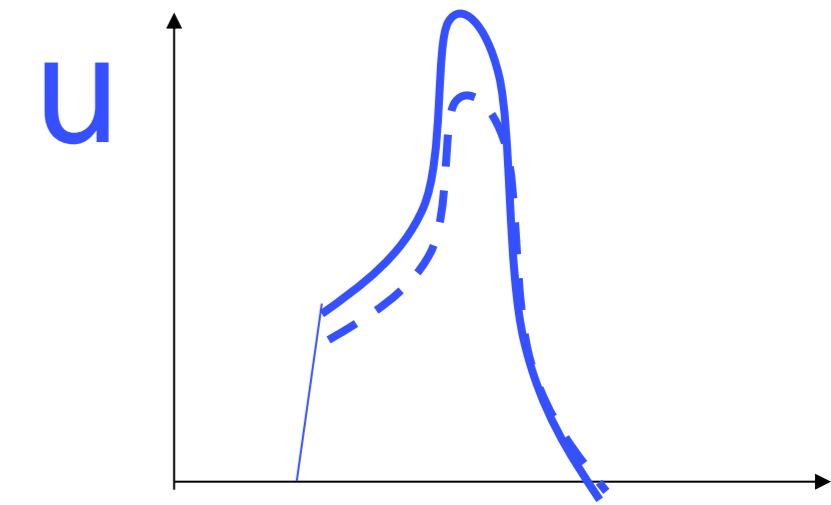
neuron



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.
- Fourcaud-Trocme, N., Hansel, D., van Vreeswijk, C., and Brunel, N. (2003). *How spike generation mechanisms determine the neuronal response to fluctuating input*. J. Neuroscience, 23:11628-11640.
- Badel, L., Lefort, S., Berger, T., Petersen, C., Gerstner, W., and Richardson, M. (2008). 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**

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EPFL, Lausanne, Switzerland

4.1 From Hodgkin-Huxley to 2D

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4.3 Analysis of a 2D Neuron Model

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- 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!

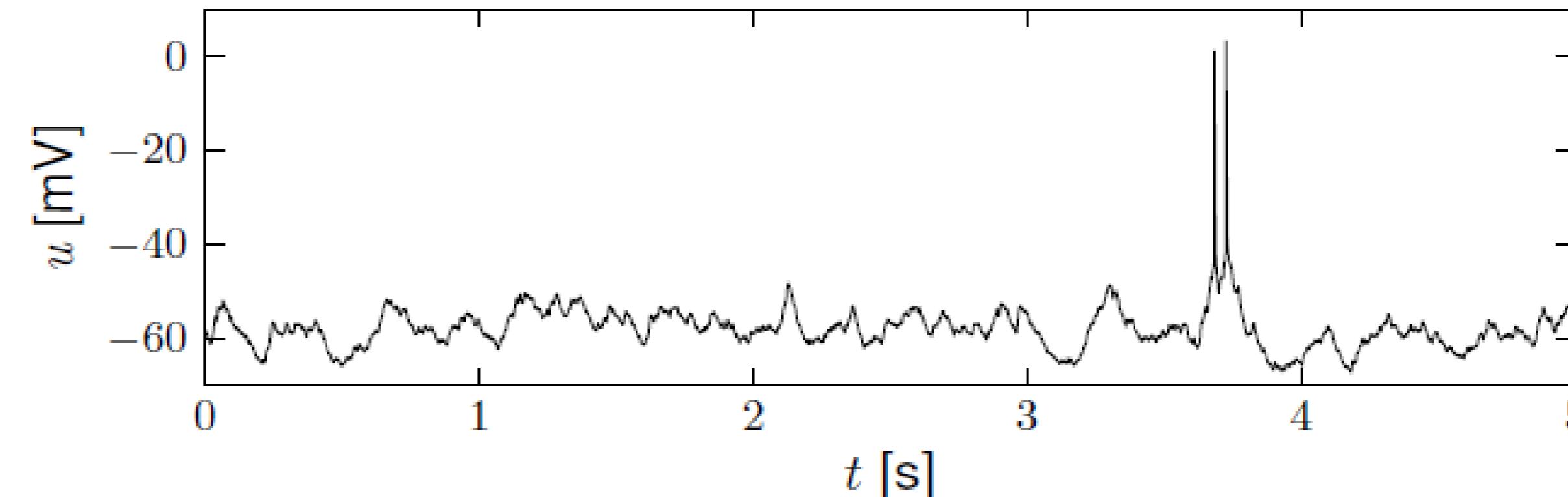
Separation of time scales

- 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

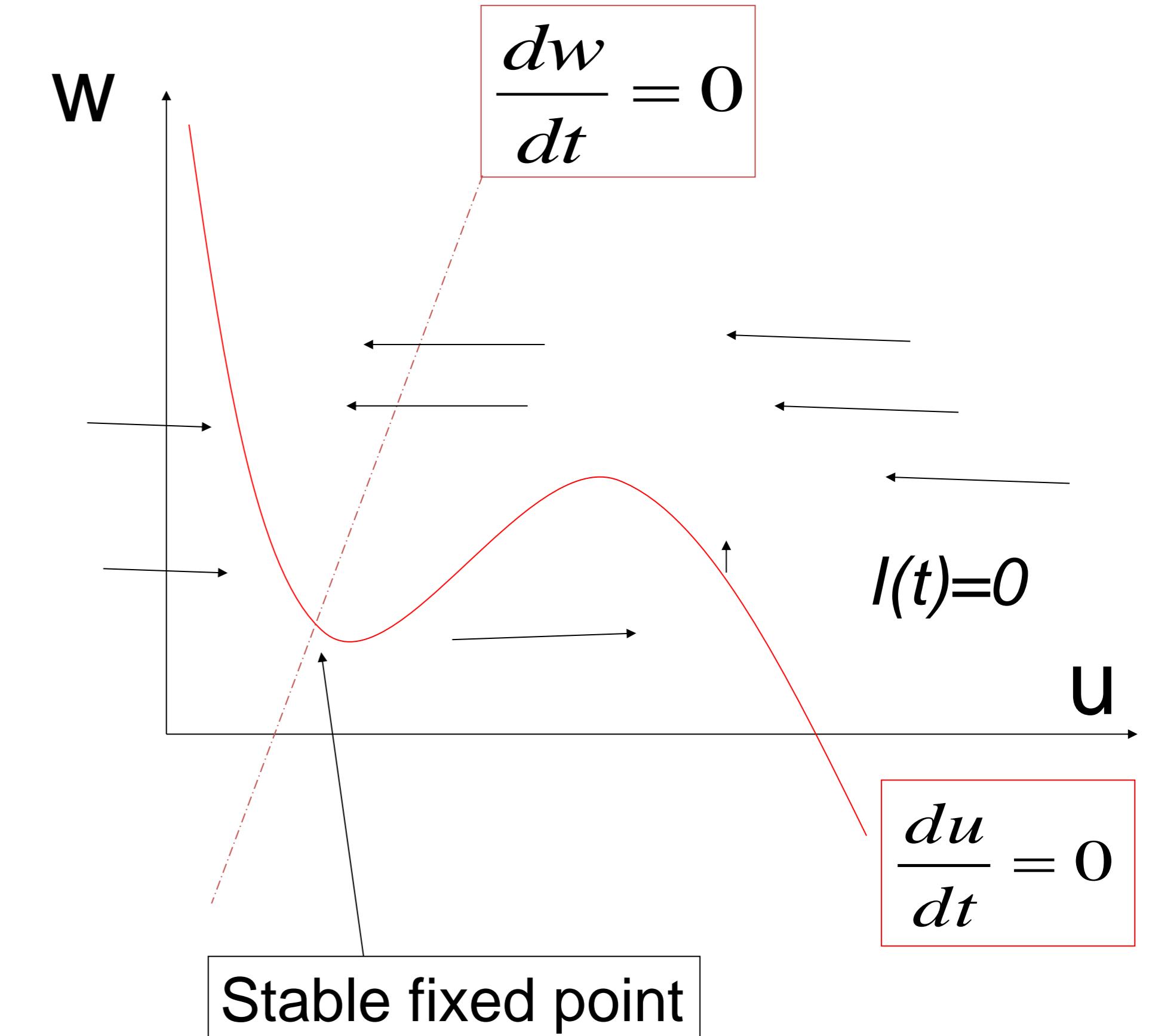
$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

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

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

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

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

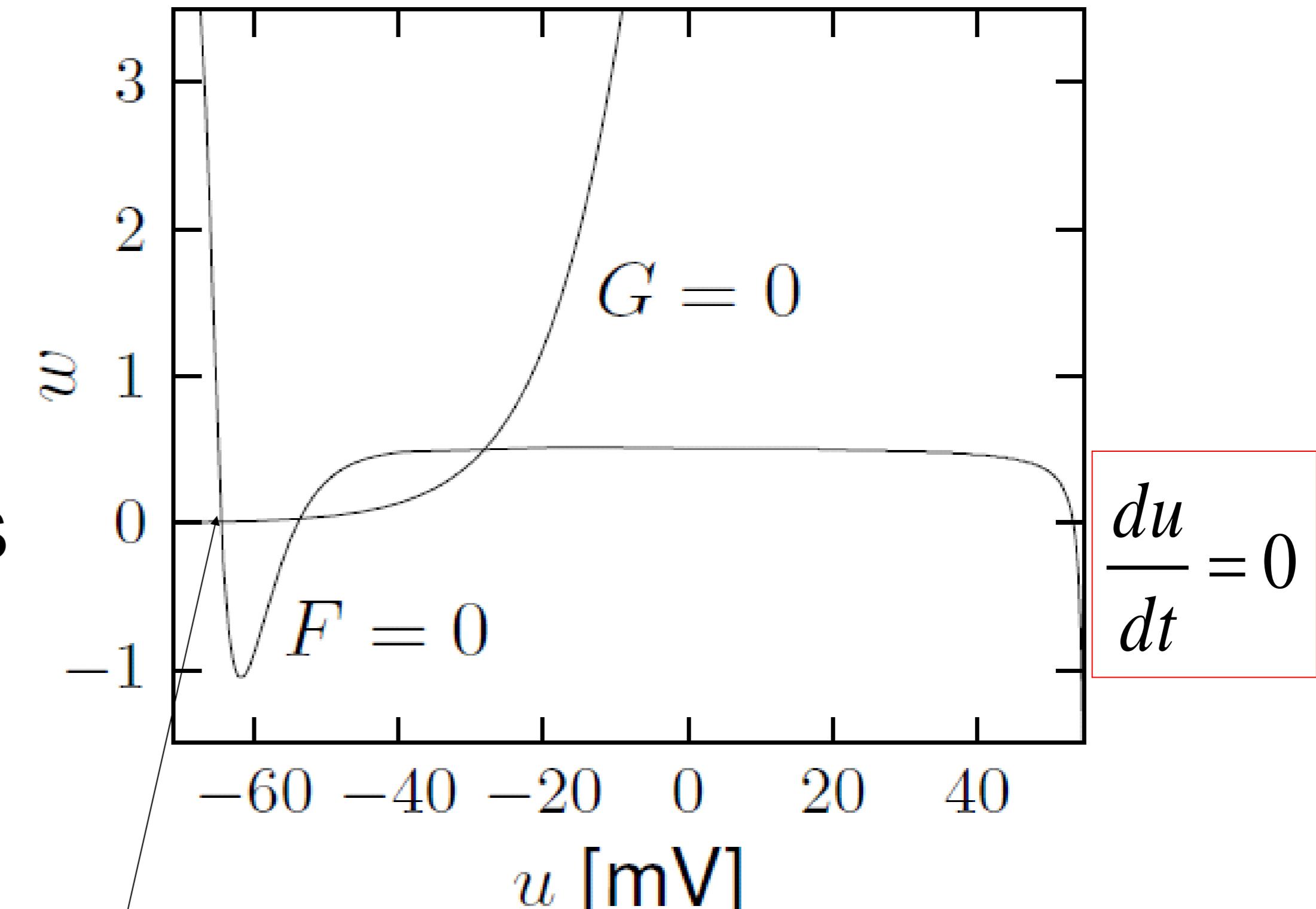
Separation of time scales

$$\tau_w \gg \tau_u$$

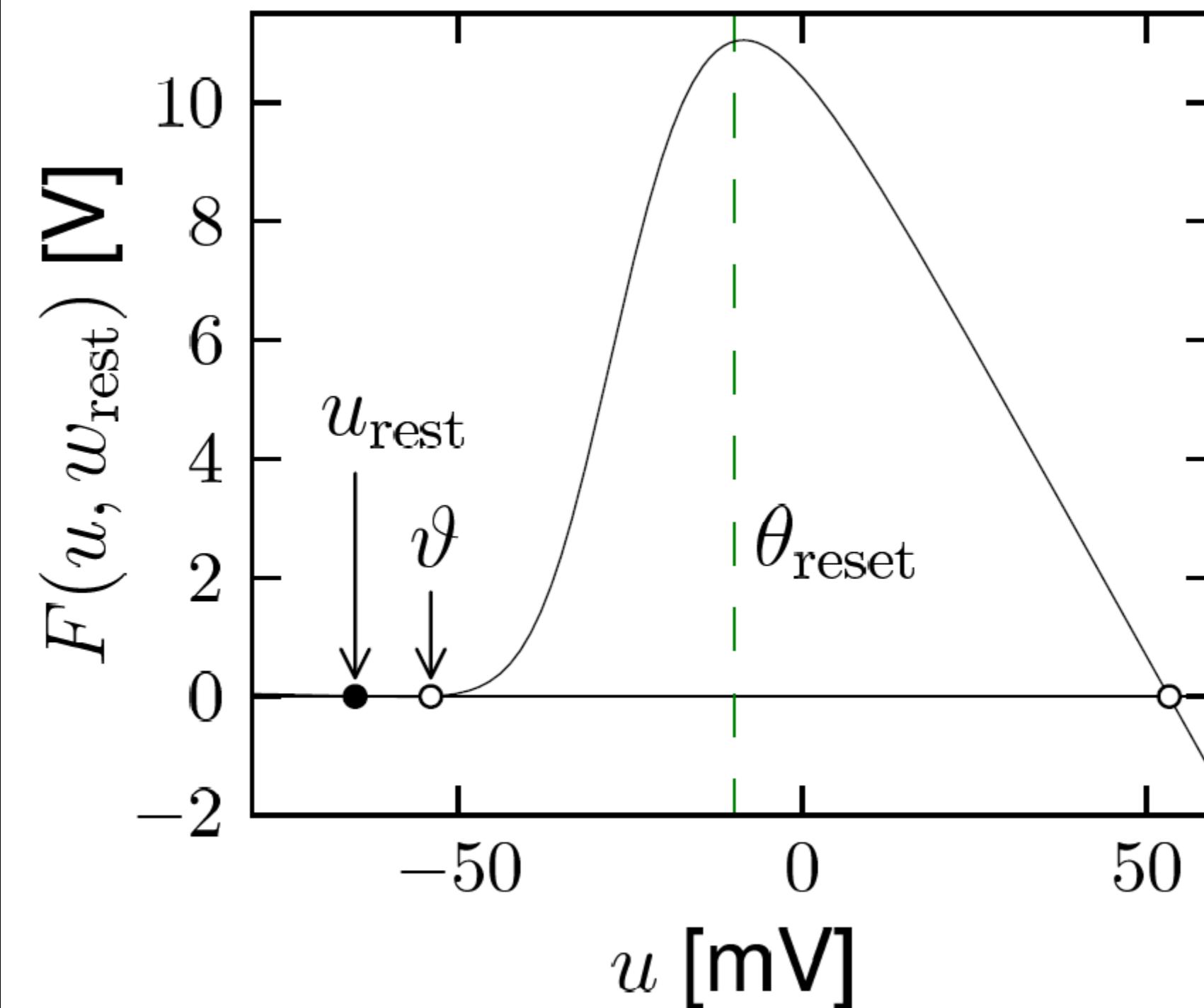
$$\tau_w \frac{dw}{dt} \approx 0 \rightarrow w \approx w_{rest}$$

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

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

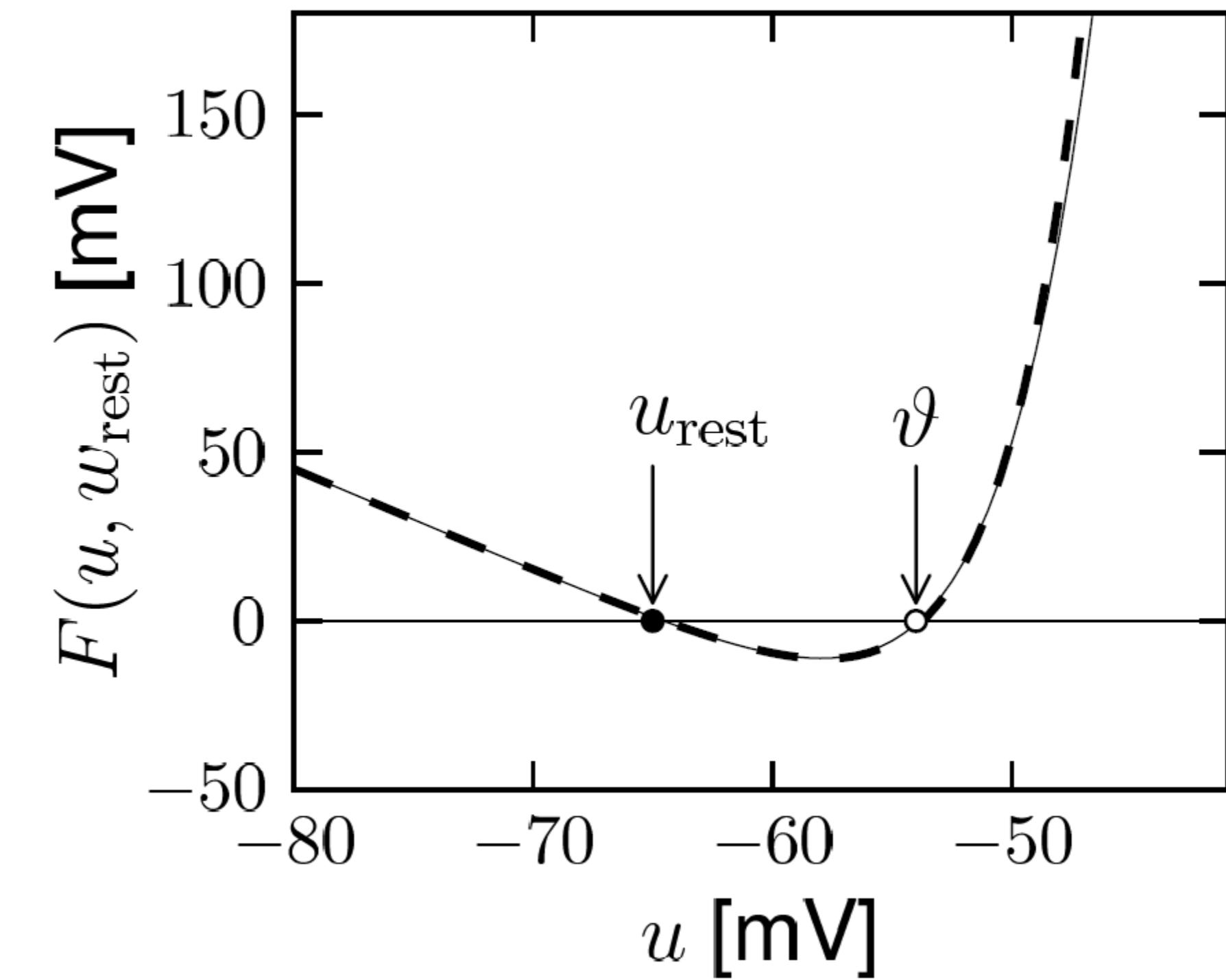


Neuronal Dynamics – 4.5. Nonlinear Integrate-and-Fire Model



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

→ Nonlinear I&F (see week 1!)

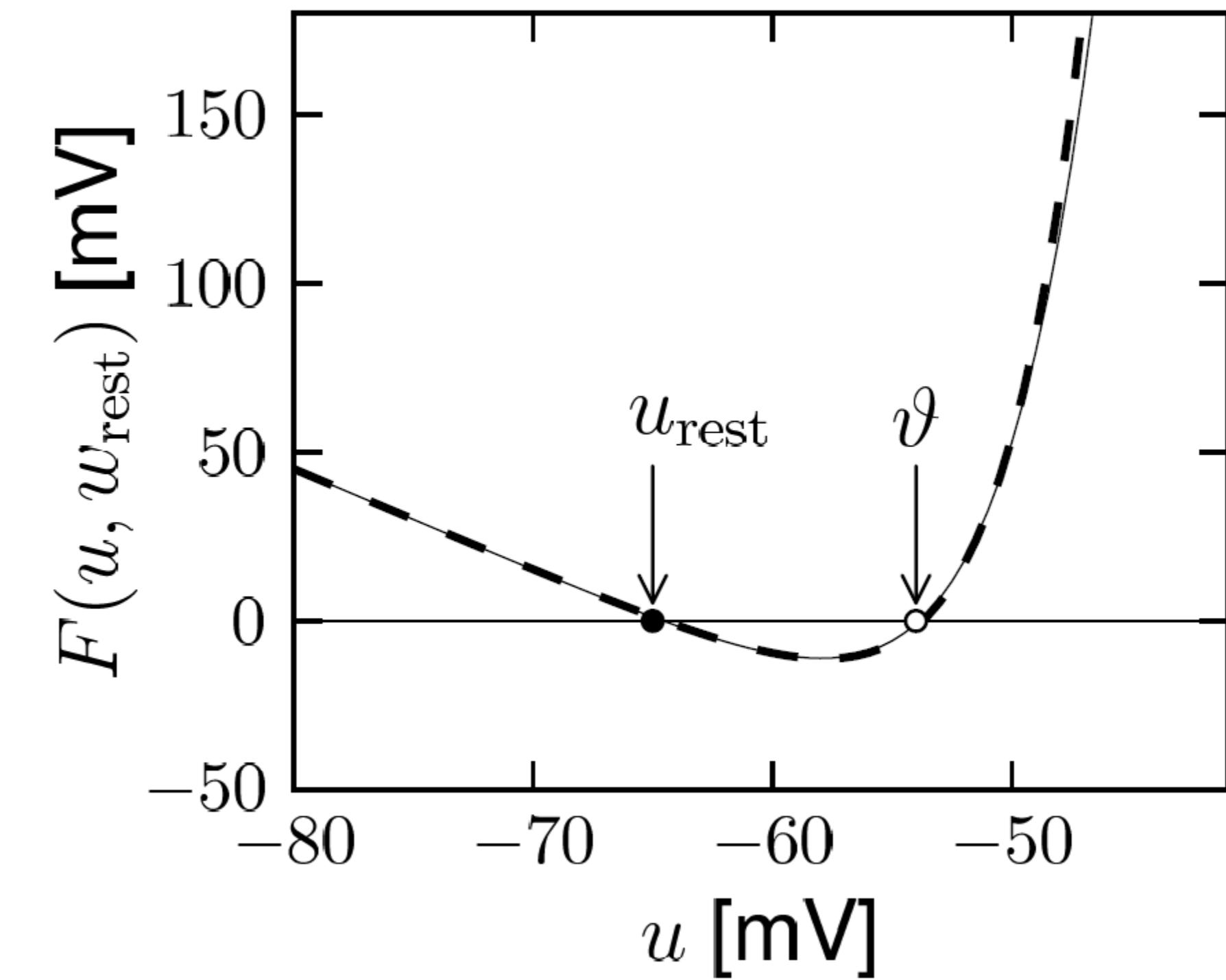


*Image: Neuronal Dynamics,
Gerstner et al.,
Cambridge Univ. Press (2014)*

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!)

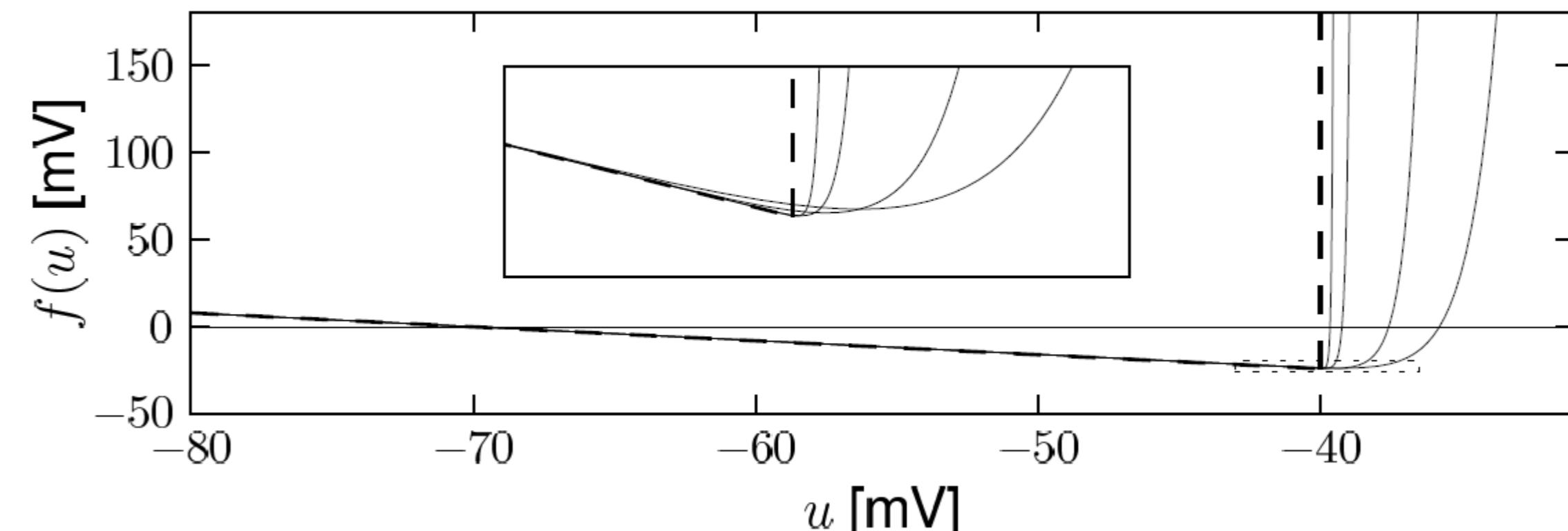
*Image: Neuronal Dynamics,
Gerstner et al.,
Cambridge Univ. Press (2014)*

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

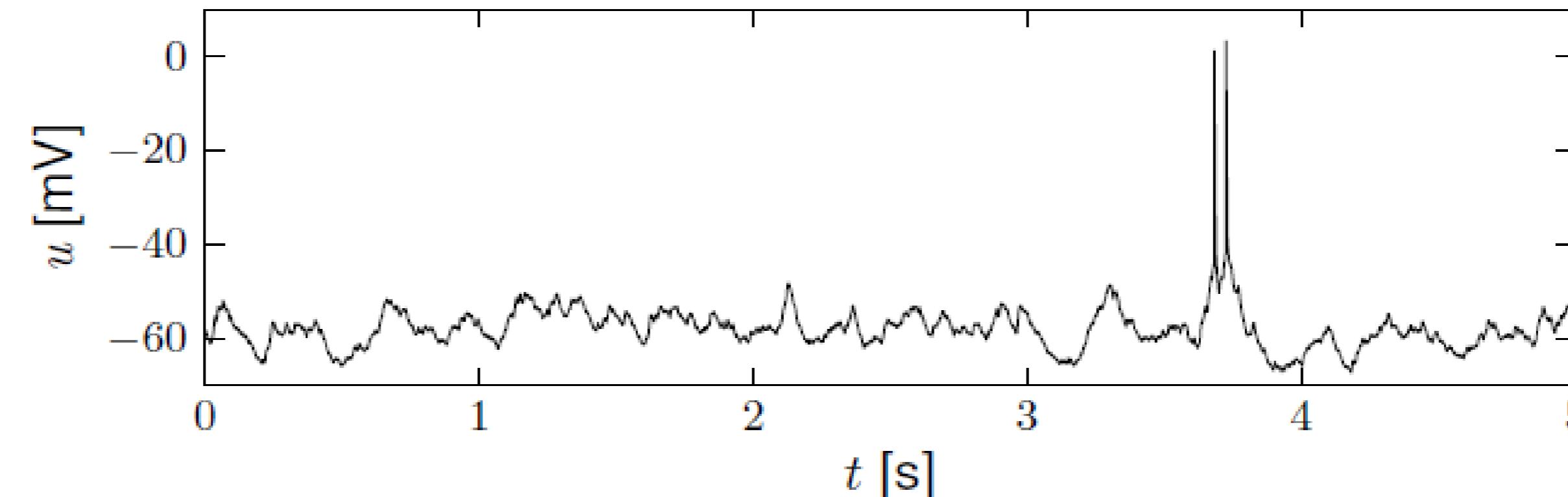


*Image: Neuronal Dynamics,
Gerstner et al.,
Cambridge Univ. Press (2014)*

Neuronal Dynamics – 4.5 sparse activity *in vivo*

Spontaneous activity *in vivo*

awake mouse, cortex, freely whisking,



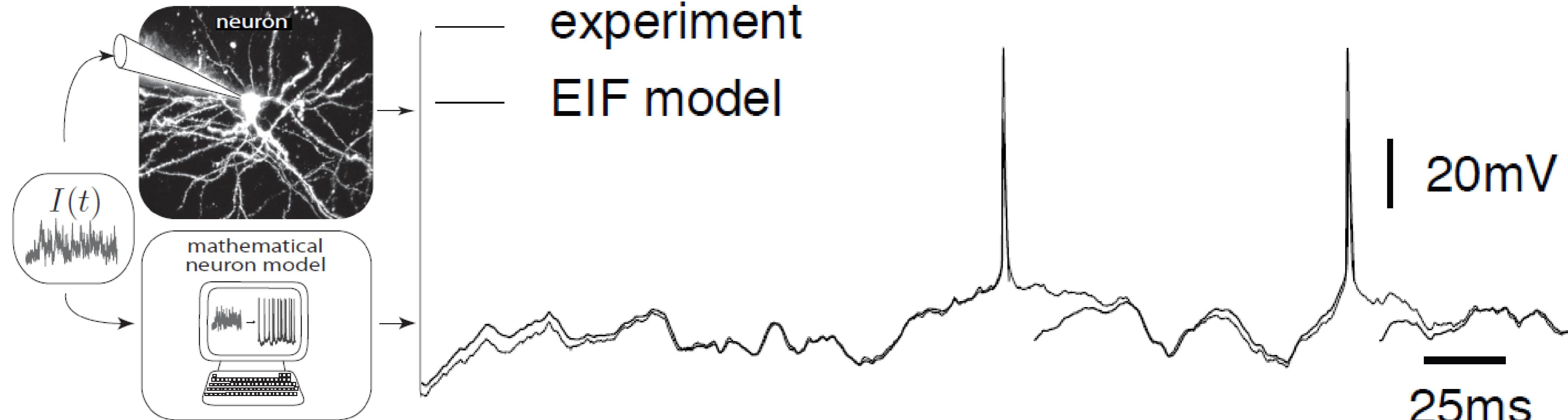
-spikes are rare events

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

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

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

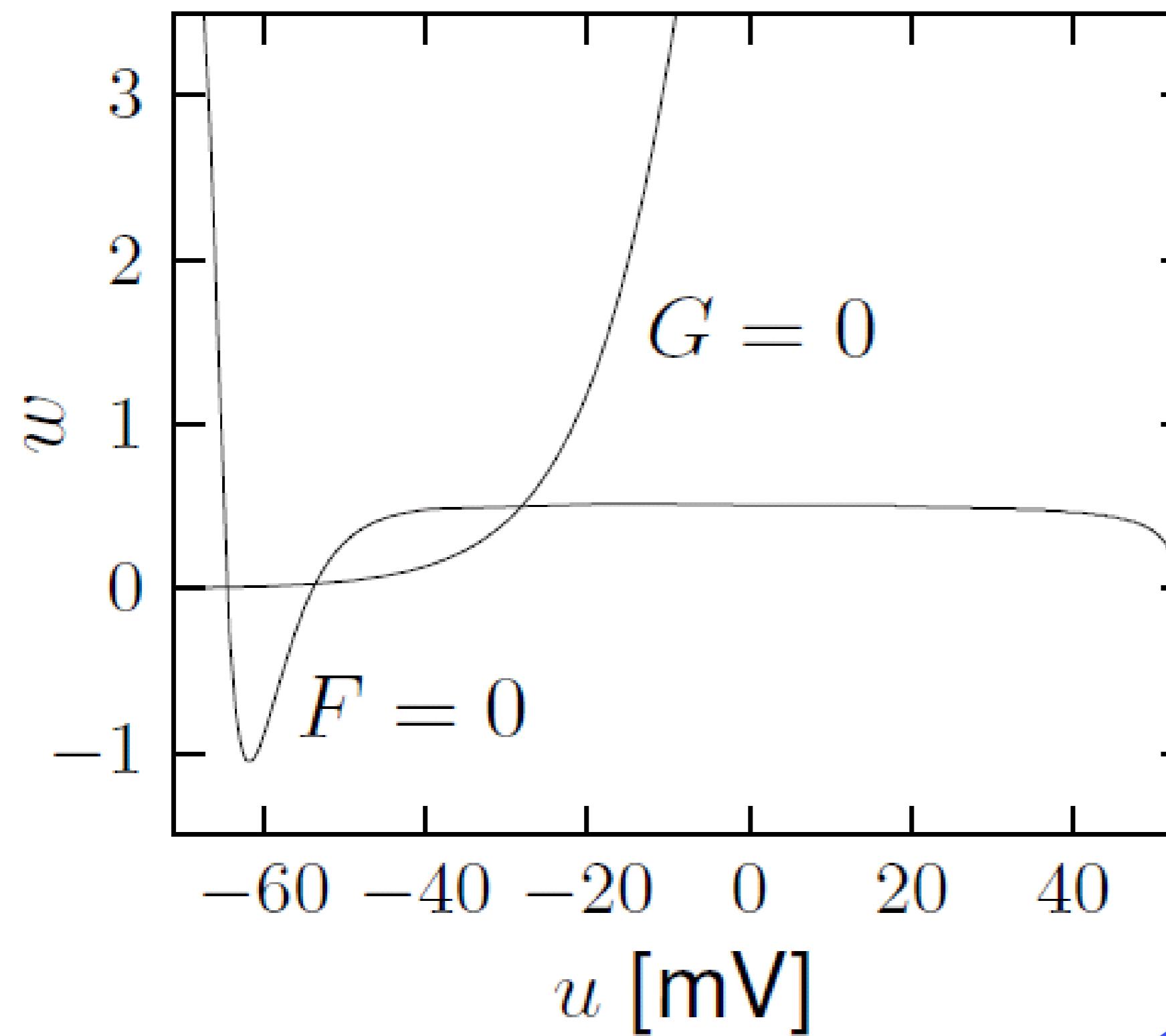
Fourcaud-Trocme et al, *J. Neurosci.* 2003

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

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

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*)

Cambridge Univ. Press, 2014

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.

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- Ermentrout, G. B. (1996). *Type I membranes, phase resetting curves, and synchrony.* Neural Computation, 8(5):979-1001.
- Fourcaud-Trocme, N., Hansel, D., van Vreeswijk, C., and Brunel, N. (2003). *How spike generation mechanisms determine the neuronal response to fluctuating input.* J. Neuroscience, 23:11628-11640.
- Badel, L., Lefort, S., Berger, T., Petersen, C., Gerstner, W., and Richardson, M. (2008). *Biological Cybernetics*, 99(4-5):361-370.
- E.M. Izhikevich, *Dynamical Systems in Neuroscience*, MIT Press (2007)

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