Biological Modeling of Neural Networks

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Week 4

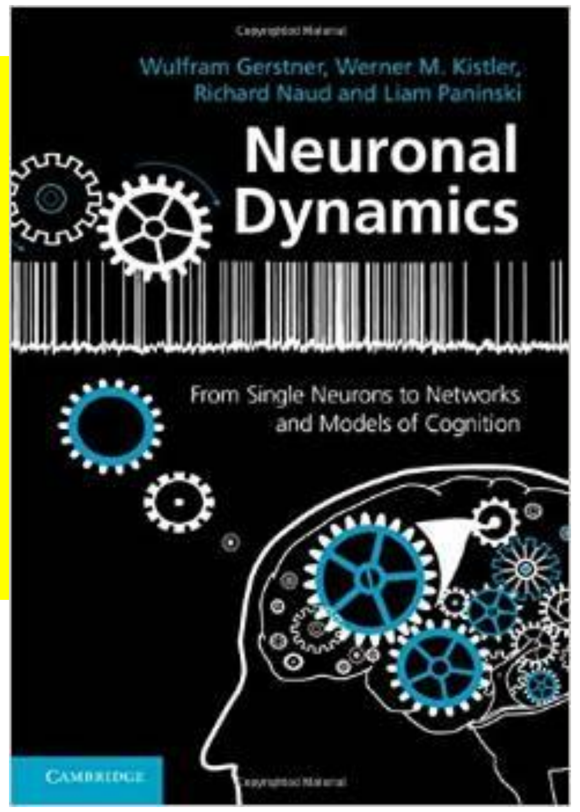
Reducing detail:

Analysis of 2D models

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading for week 4:
NEURONAL DYNAMICS
- Ch. 4.4 – 4.7



Cambridge Univ. Press

√ 3.1 **From Hodgkin-Huxley to 2D**

√ 3.2 **Phase Plane Analysis**

√ 3.3 **Analysis of a 2D Neuron Model**

4.1 Separation of time scales

4.2 Type I and II Neuron Models

- limit cycles: constant input

4.3 Pulse input

- where is the firing threshold?

4.4. Further reduction to 1 dim

- nonlinear integrate-and-fire (again)

Week 4 – Review from week 3

-**Reduction of Hodgkin-Huxley to 2 dimension**

-step 1: separation of time scales

-step 2: exploit similarities/correlations

Week 4 – Review from week 3

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

$$C\frac{du}{dt} = -g_{Na}\, m_0(u)^3(1-w)(u-E_{Na}) - g_K[\frac{w}{a}]^4(u-E_K) - g_l(u-E_l) + I(t)$$

1) dynamics of *m* are fast → $m(t) = m_0(u(t))$

2) dynamics of *h* and *n* are similar → $\underbrace{1-h(t)}_{w(t)} = \underbrace{a\,n(t)}_{w(t)}$

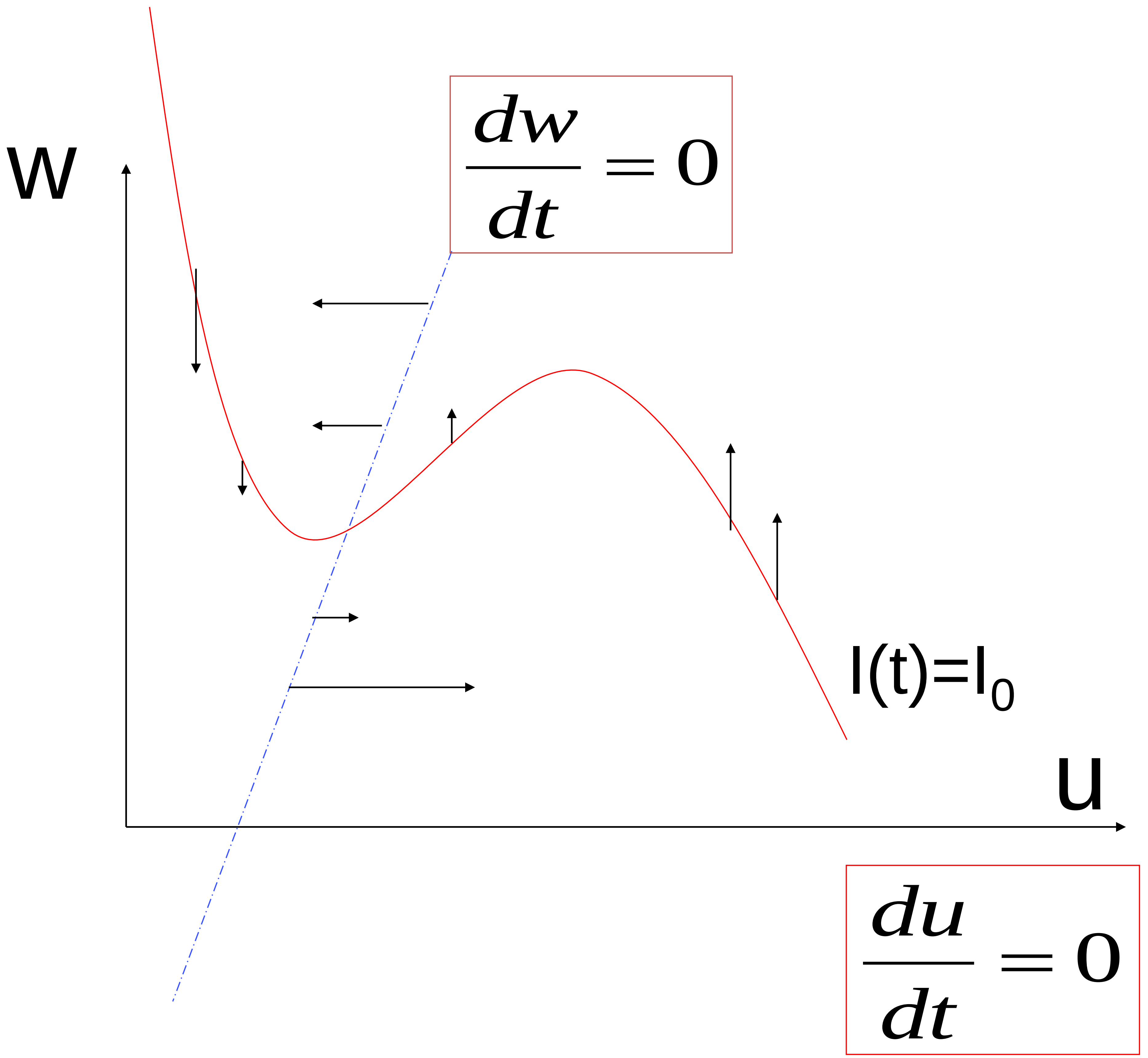
$$\frac{dh}{dt} = -\frac{h-h_0(u)}{\tau_h(u)}$$

$$\frac{dn}{dt} = -\frac{n-n_0(u)}{\tau_n(u)}$$

→

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

Week 4 – review from week 3



2-dimensional equation

stimulus

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

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

Enables graphical analysis!

-Pulse input

→ AP firing (or not)

- Constant input

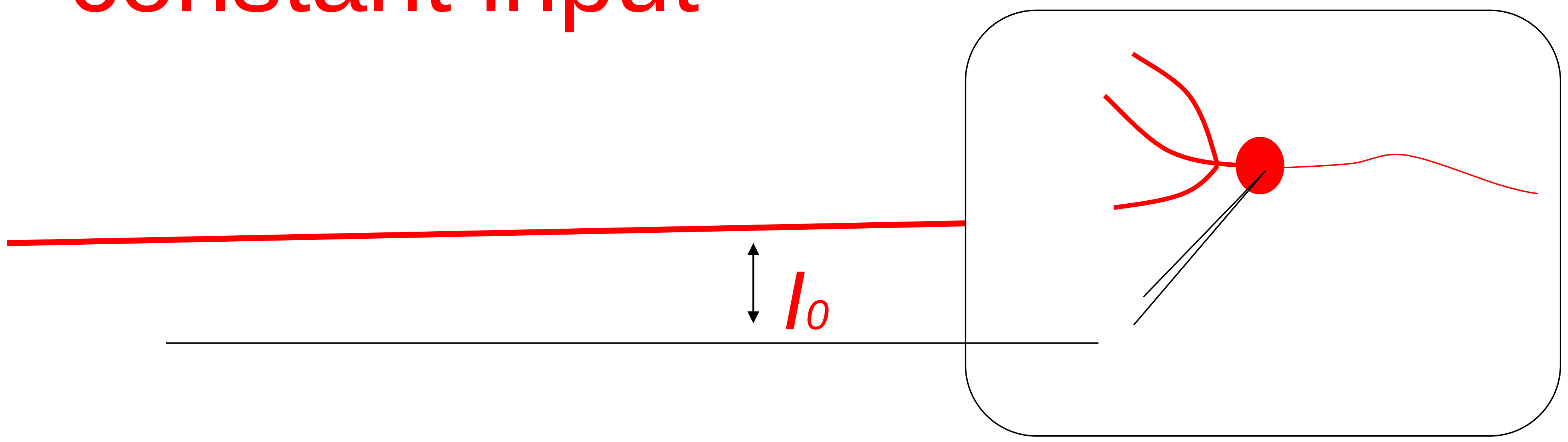
→ repetitive firing (or not)

→ limit cycle (or not)

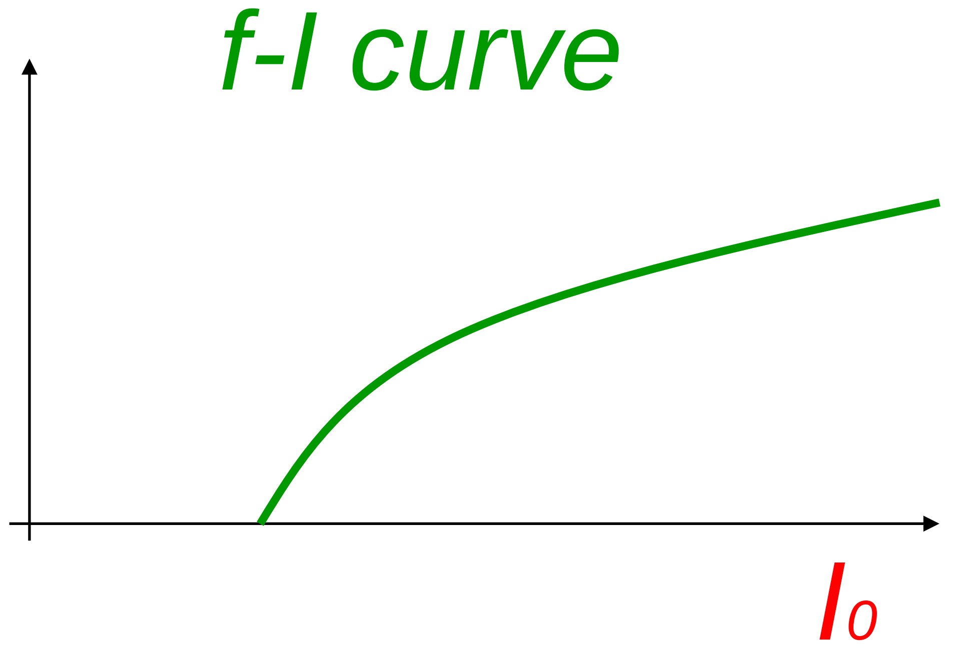
Week 4 – Reducing Detail – 2D models

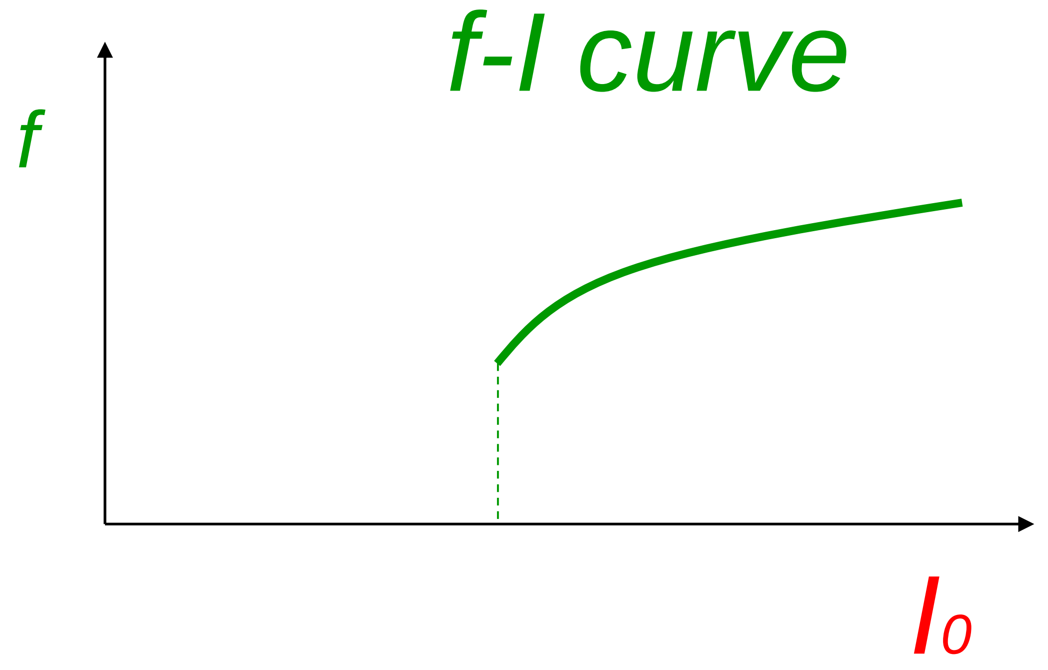
ramp input/
constant input

neuron



Type I	and	type II





4.1 Nullclines change for constant stimulus

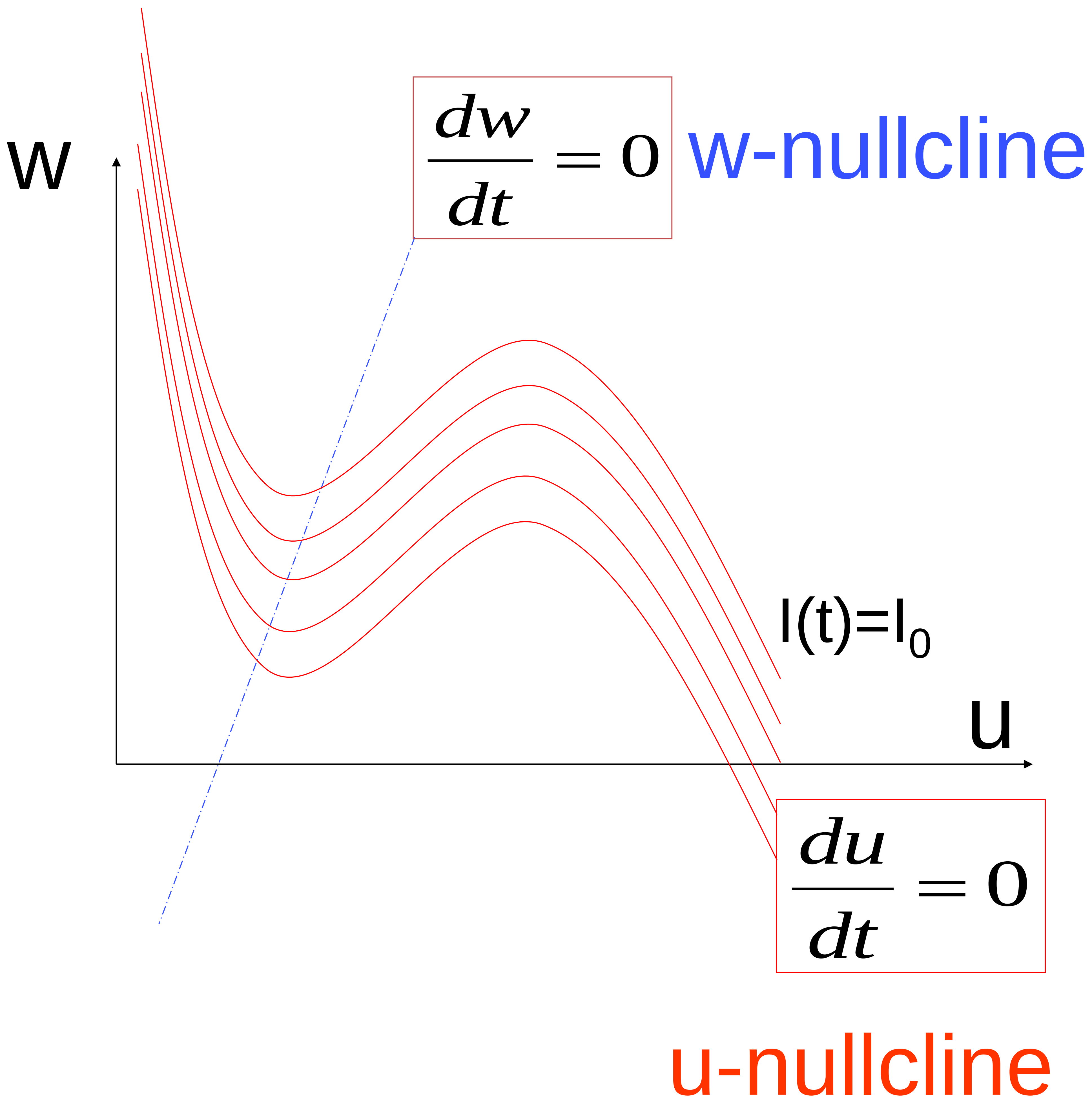
stimulus

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

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

apply constant stimulus I_0

Blackboard 1 $\varepsilon = \frac{\tau}{\tau_w}$



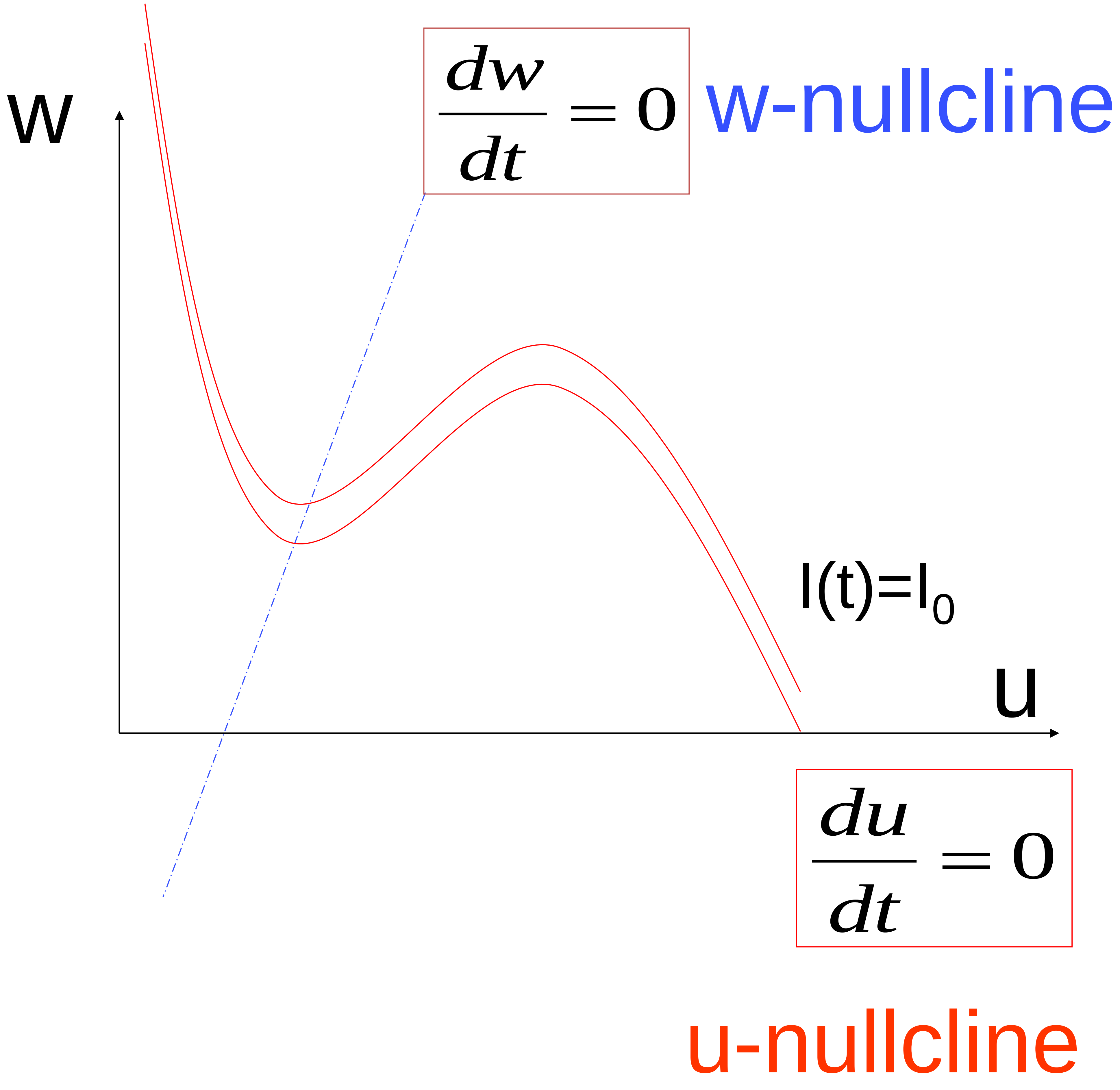
4.1 Separation of time scales

stimulus

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

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

Blackboard 1 $\varepsilon = \frac{\tau}{\tau_w}$



4.1. Separation of time scales

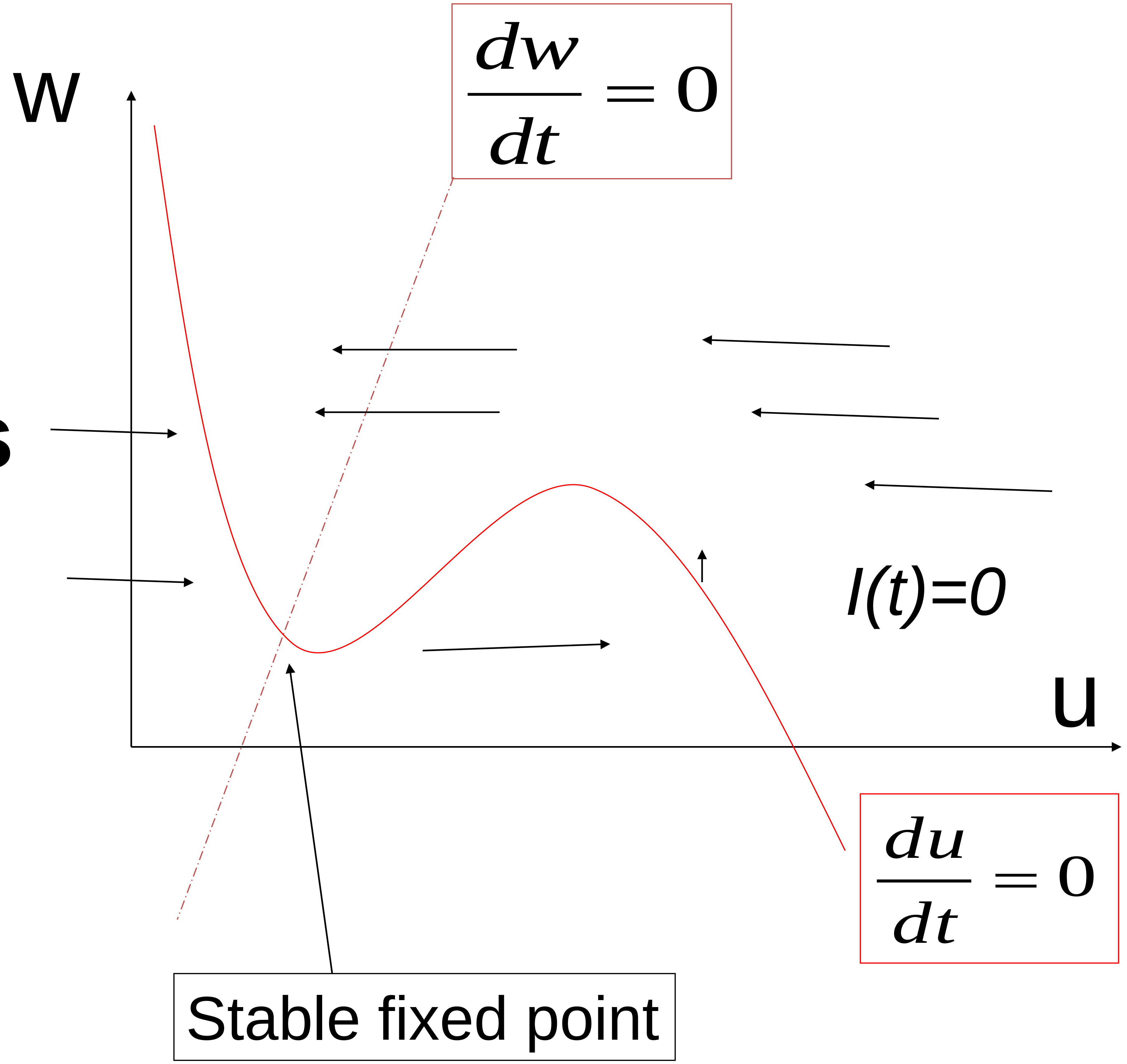
stimulus

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

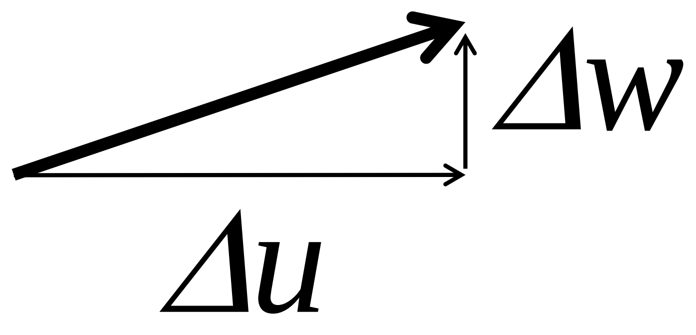
$$\tau_w \frac{dw}{dt} = G(u,w)$$

Separation of time scales

$$\tau_w >> \tau_u$$



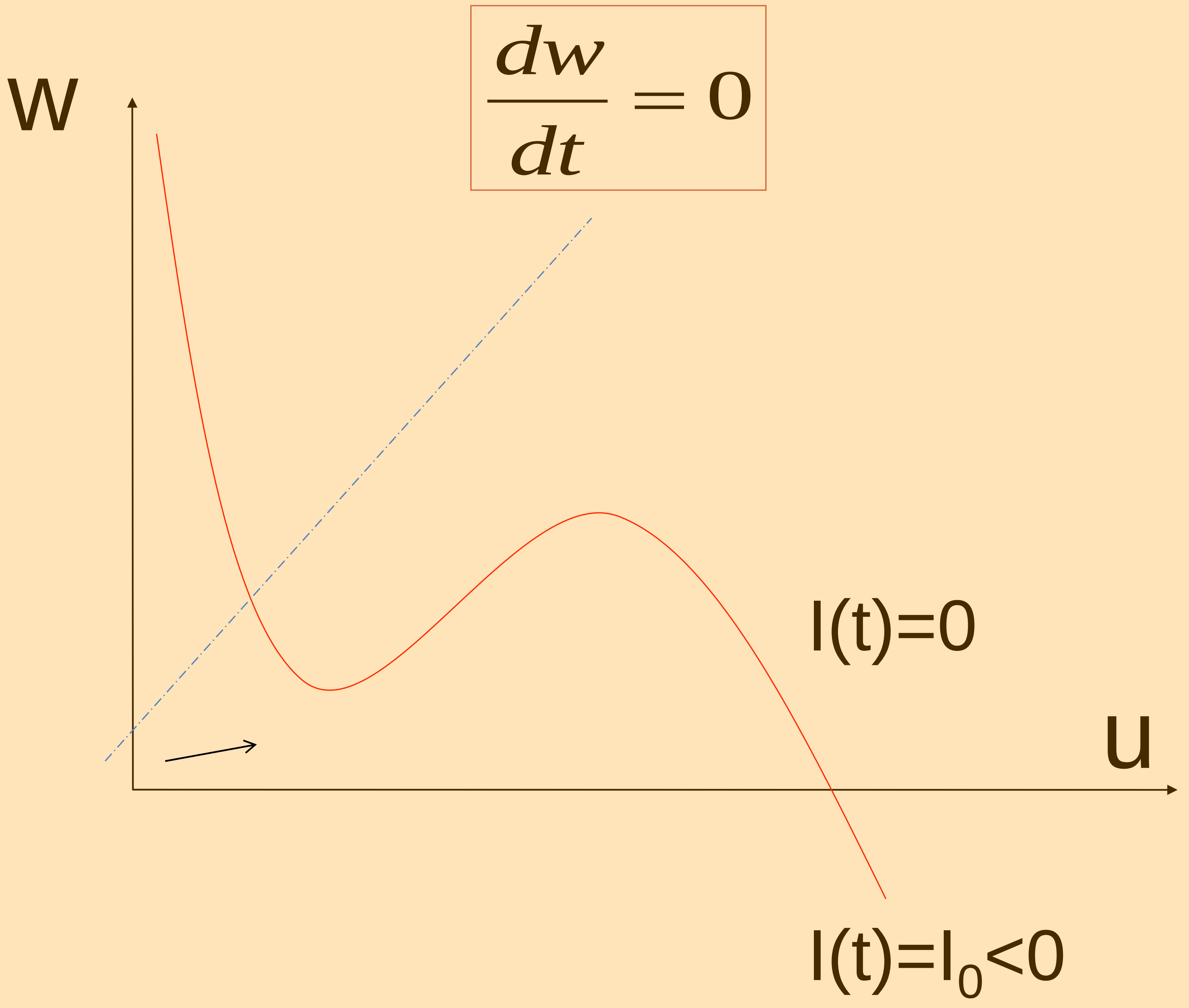
Blackboard 1



$$\tau_w >> \tau_u \longrightarrow \Delta w << \Delta u$$

Unless close to nullcline

Week 4 – **Exercise 1 preparation**



Now exercises

Exercise 1: Inhibitory rebound

Start at 9:30
Next lecture at 9:40

Consider the following two-dimensional Fitzhugh-Nagumo model:

$$\left[\begin{array}{ccc} \frac{du}{dt} & = & u\left(1-u^2\right) - w + I \equiv F(u,w) \\ \frac{dw}{dt} & = & \varepsilon\left(u - 0.5w + 1\right) \equiv \varepsilon G(u,w)\,, \end{array}\right. \quad (1)$$

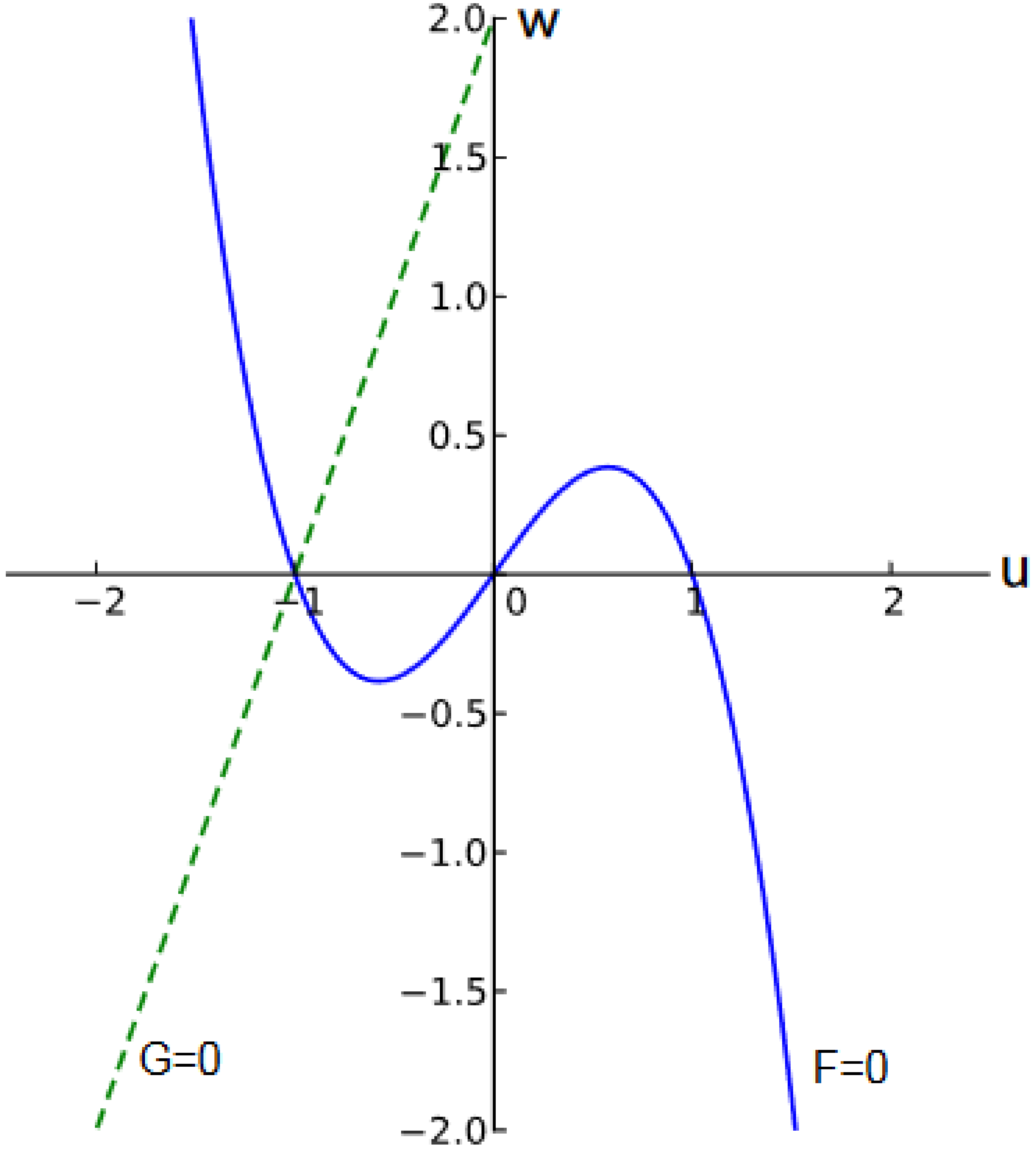
where $\varepsilon \ll 1$.

1.1 Suppose that an inhibitory current step is applied,

$$I(t) = \begin{cases} -I_0 & t \leq 0 \\ 0 & t > 0 \end{cases}$$

How does the fixed point move?

1.2 What happens after the driving current is removed? Sketch the form of the trajectories for increasing values of I_0. What happens for large I_0?



4.1. Summary: Separation of time scales

We have seen a first separation of time scales last week to remove the m-variable. Today I have introduced a second separation of time scale: the w-variable is (in reality a bit) slower than the voltage variable.
For mathematical reasons we considered the limit where w is MUCH slower than the voltage variable.
In this limit, the flow arrows are all horizontal – except in the region very close to the u-nullcline.
This condition can be exploited for two interesting stimuli:

(i) A constant stimulus strong enough to evoke a limit cycle. In this case the trajectory either jumps or follow the u-nullcline.
(ii) A pulse stimulus. In this case, the voltage either goes rapidly back to the fixed point or it takes a detour.

We look at both stimulation paradigms again throughout the lecture.

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Week 4

Reducing detail:

Analysis of 2D models

√ 3.1 **From Hodgkin-Huxley to 2D**

√ 3.2 **Phase Plane Analysis**

√ 3.3 **Analysis of a 2D Neuron Model**

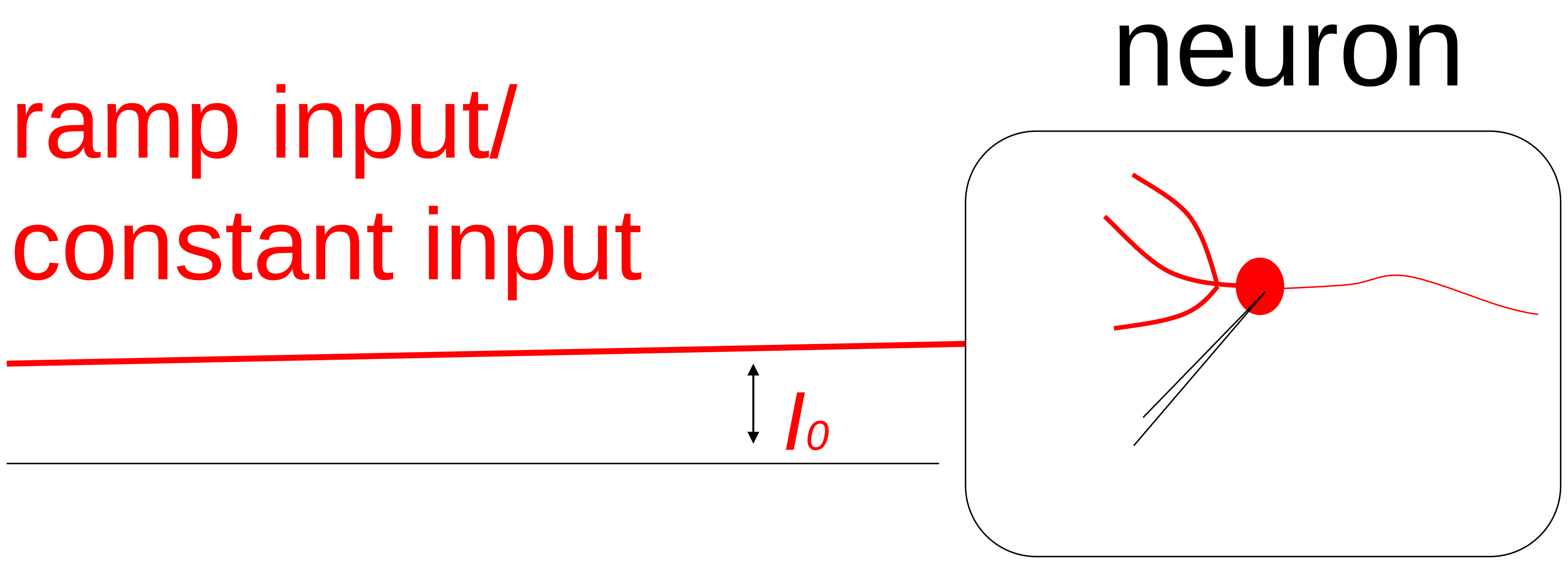
4.1 Separation of time scales

4.2 Type I and II Neuron Models
- limit cycles: constant input

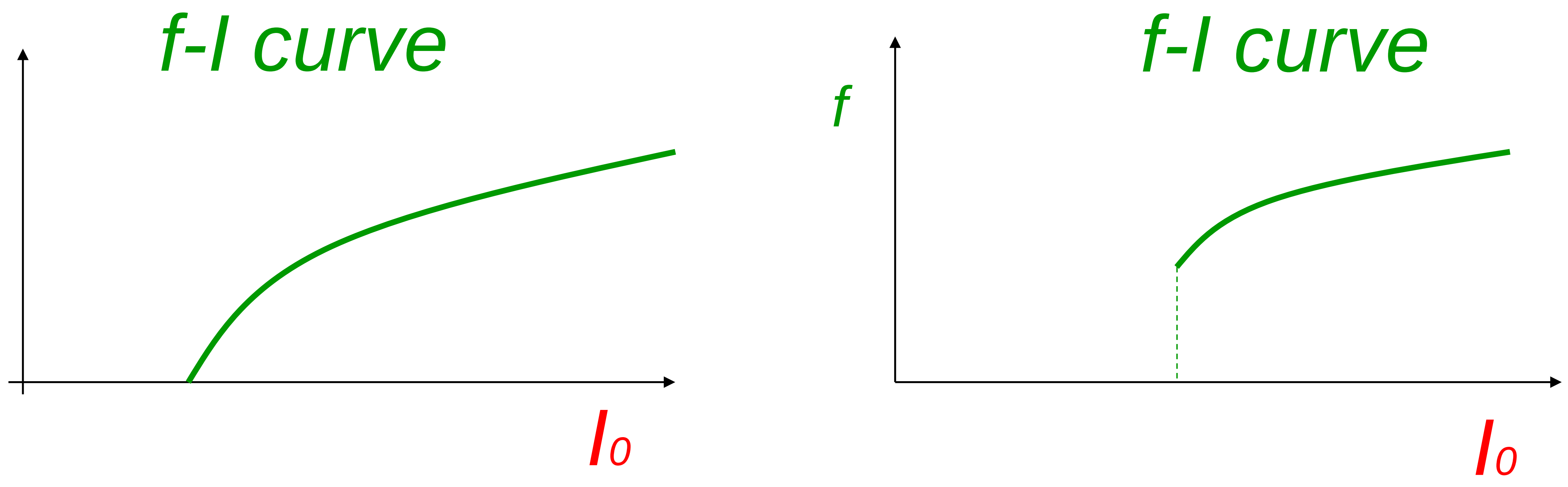
4.3 Pulse input
- where is the firing threshold?

4.4. Further reduction to 1 dim
- nonlinear integrate-and-fire (again)

Week 4 – 4.2. Type I and II Neuron Models



Type I and type II models



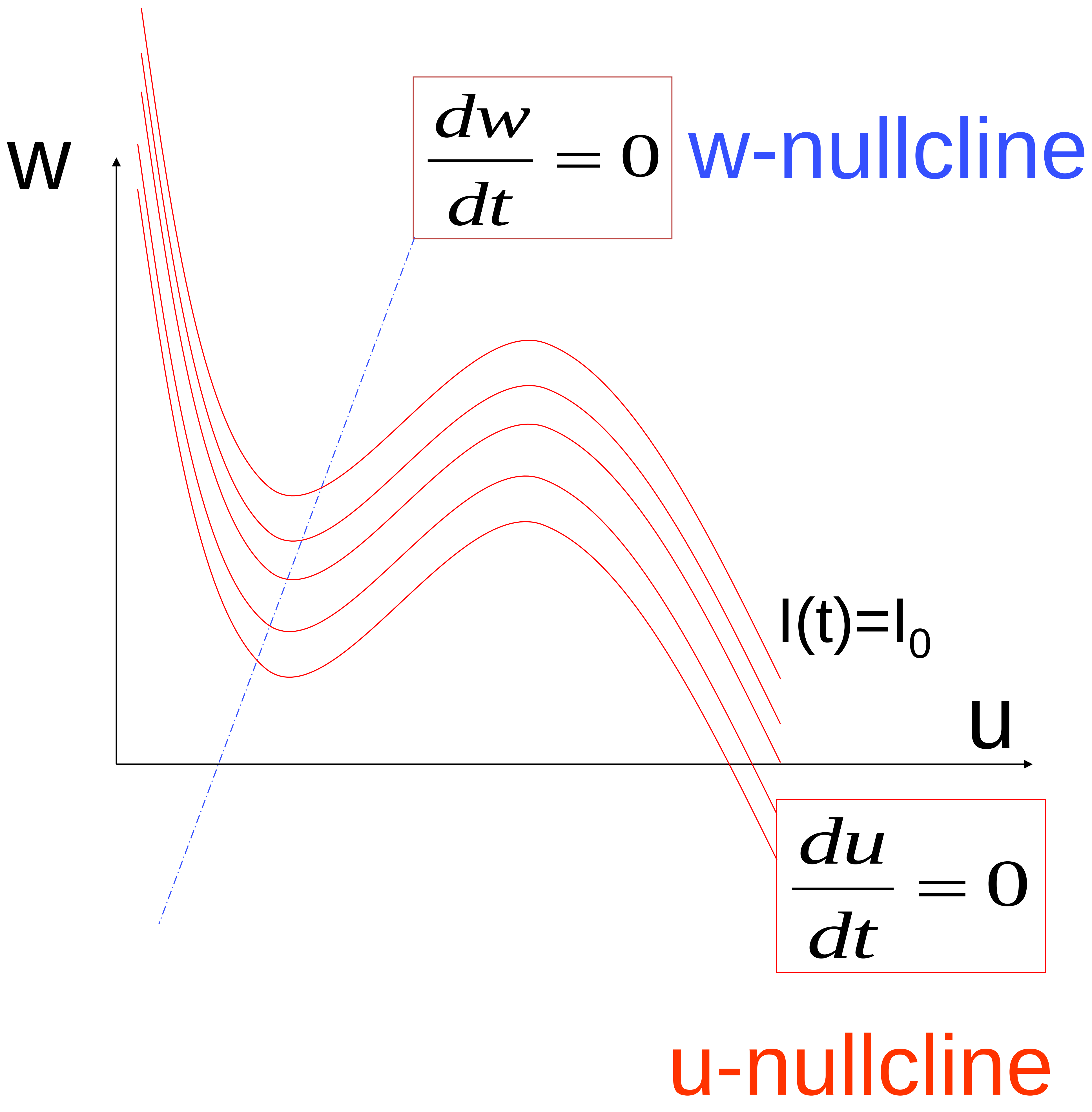
Review: Nullclines change for constant stimulus

stimulus

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

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

apply constant stimulus I_0



4.2. Limit cycle (example: FitzHugh Nagumo Model)

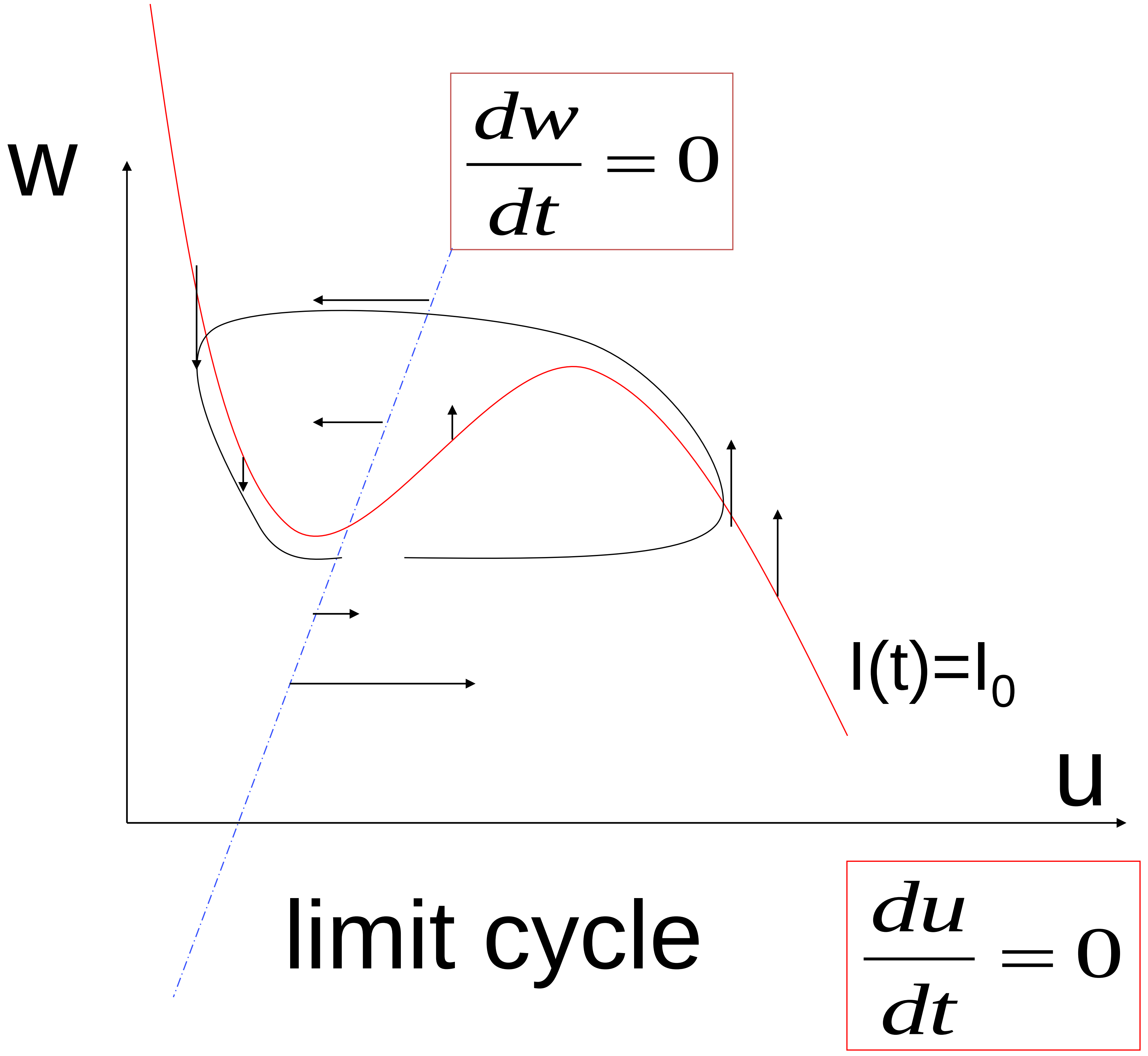
stimulus

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

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

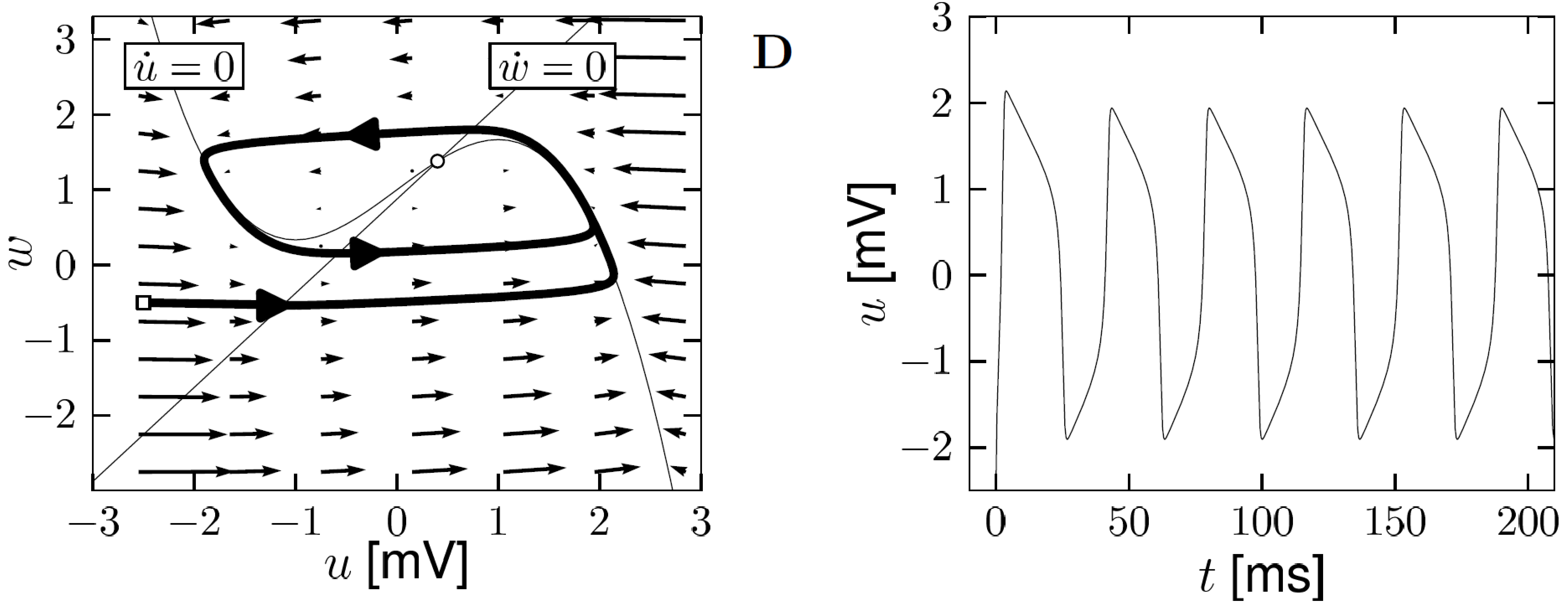
-unstable fixed point
-closed boundary
with arrows pointing inside

⟶ limit cycle



limit cycle

4.2. Limit Cycle



-unstable fixed point in 2D
-bounding box with inward flow
→ limit cycle *(Poincare Bendixson)*

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

4.2. Limit Cycle

In 2-dimensional equations,
a limit cycle must exist, if we can
find a surface

-containing one unstable fixed point
-no other fixed point
-bounding box with inward flow
→ limit cycle *(Poincare Bendixson)*

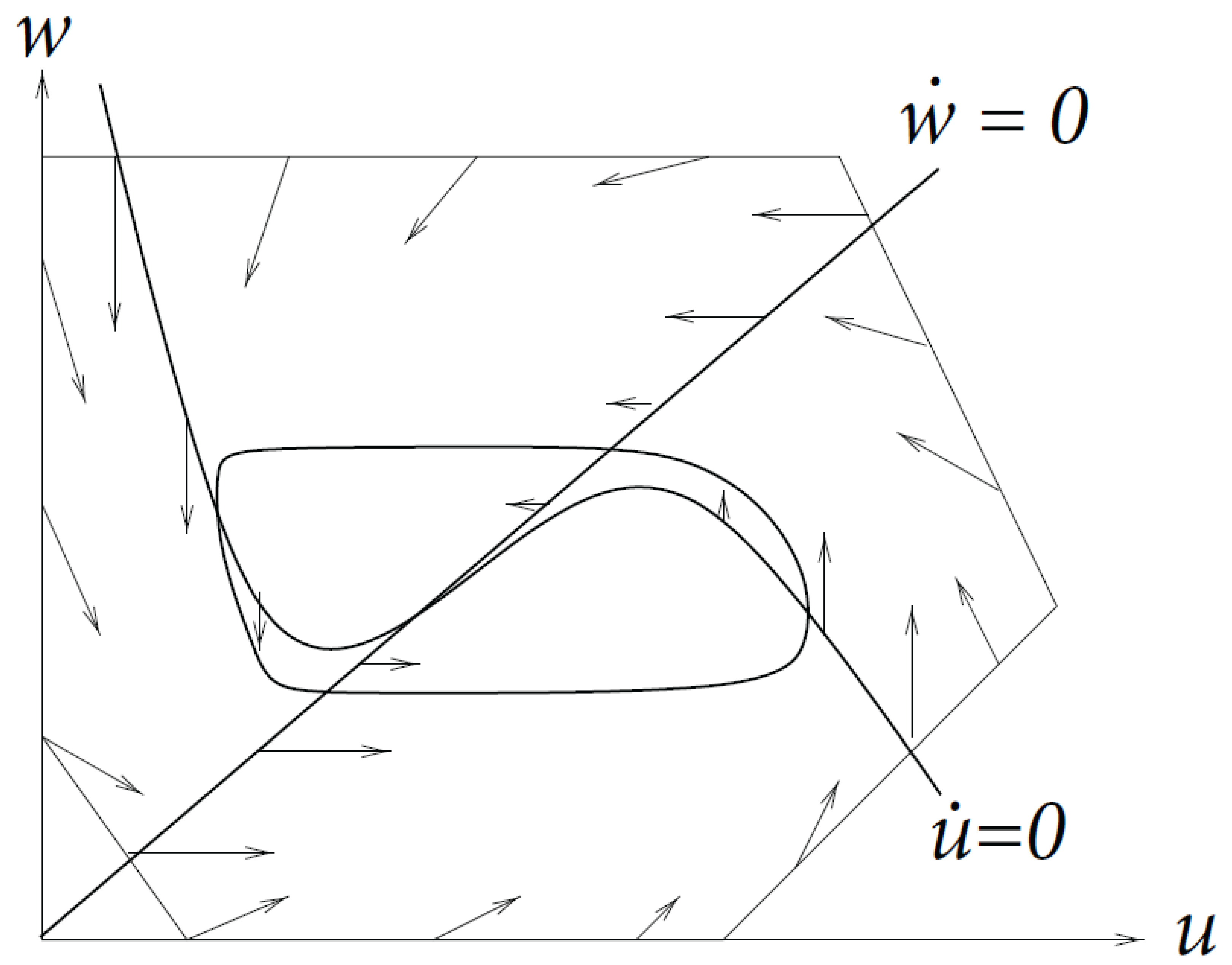


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014)

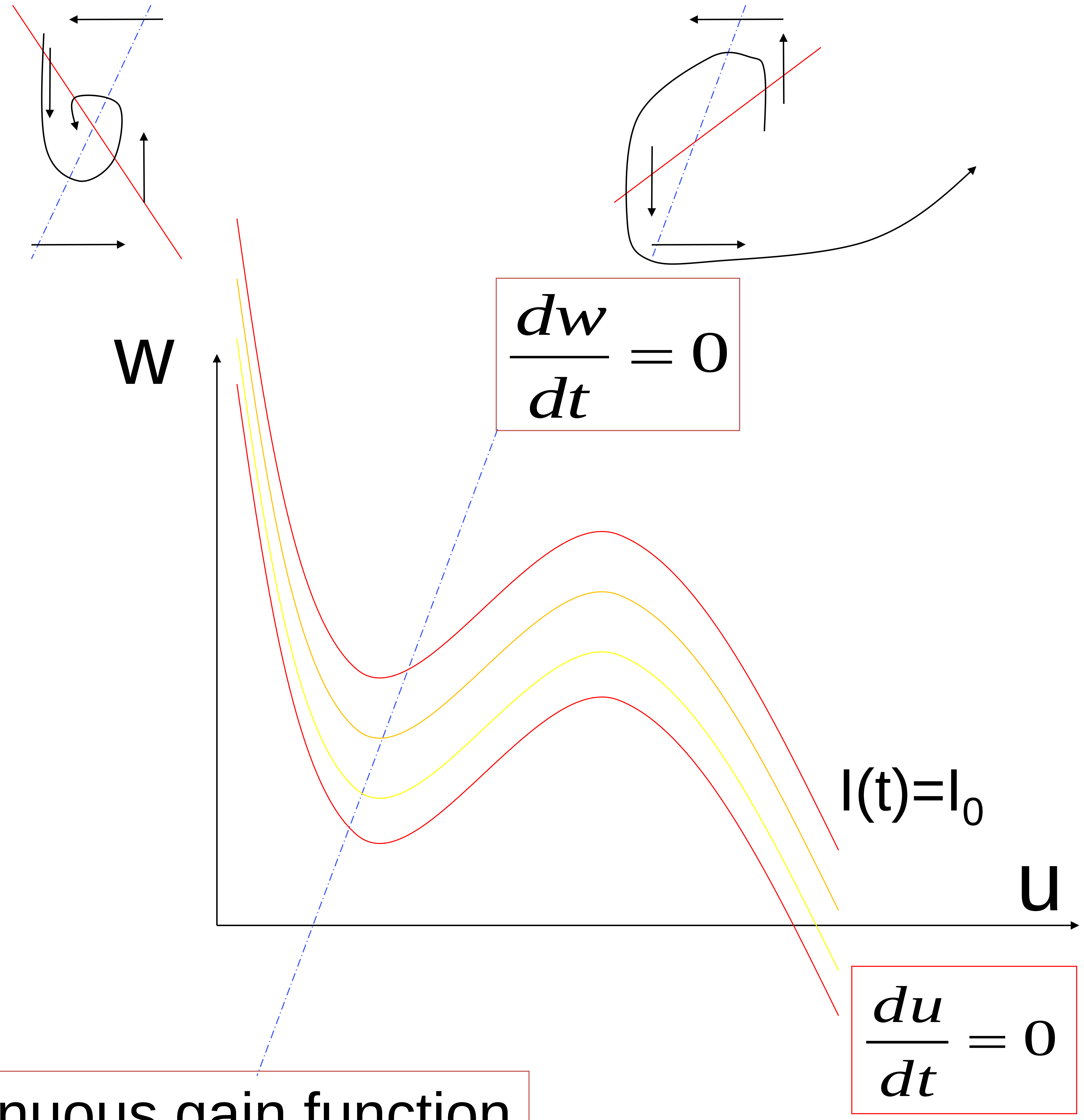
4.2 Type II Model

constant input

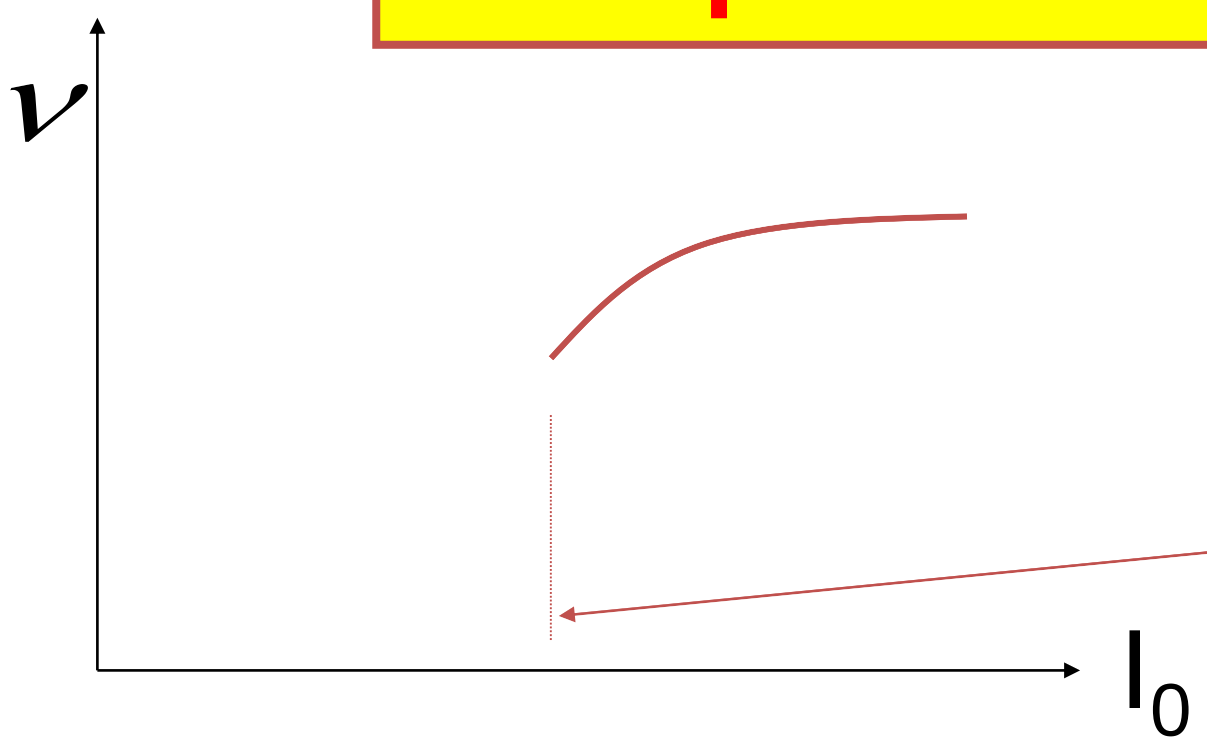
stimulus

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

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



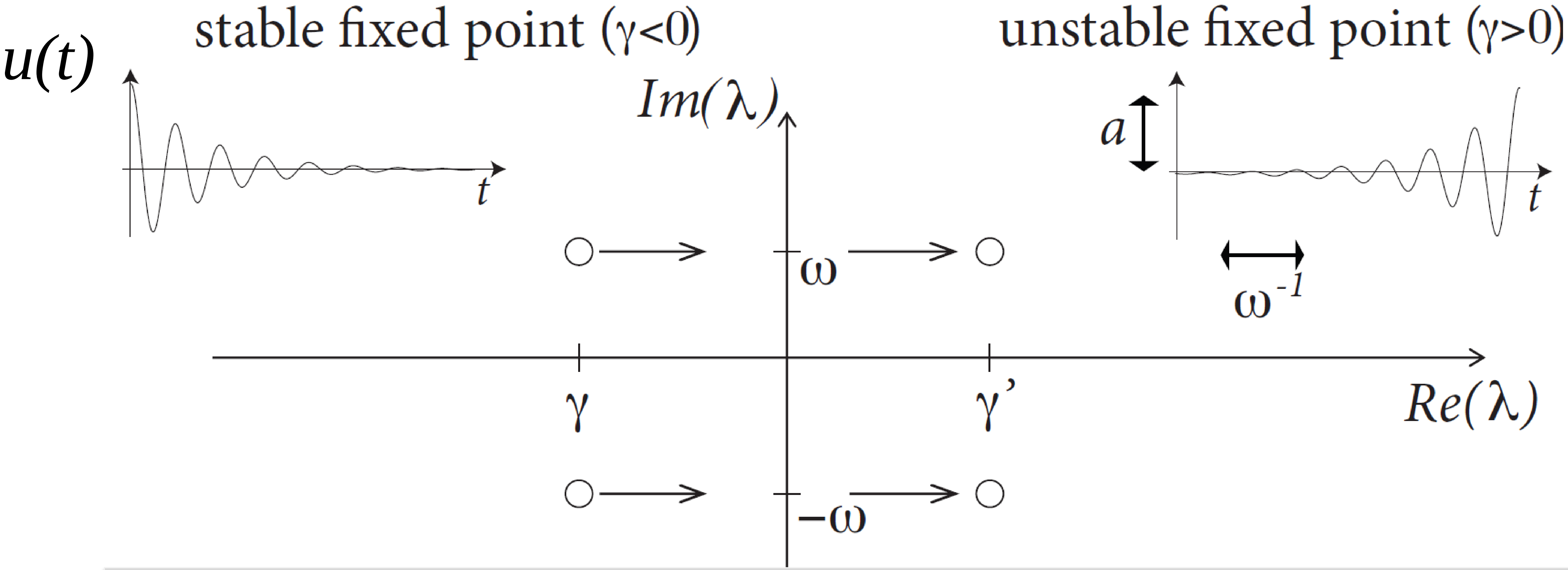
Hopf bifurcation



Discontinuous gain function

Stability lost → oscillation with finite frequency

4.1. Hopf bifurcation

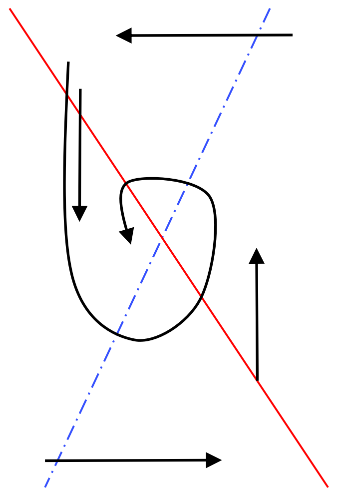


$$\lambda = \gamma + i\omega$$

$$\lambda = \gamma - i\omega$$

Blackboard 2

$$\gamma < 0$$



$$\gamma > 0$$

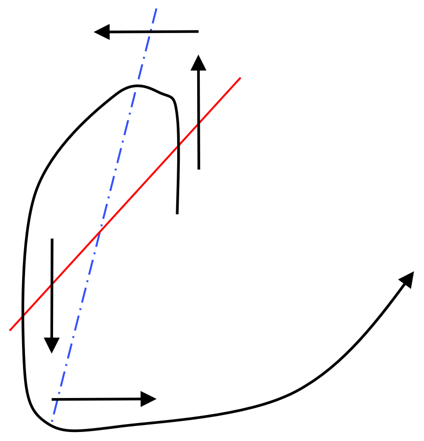
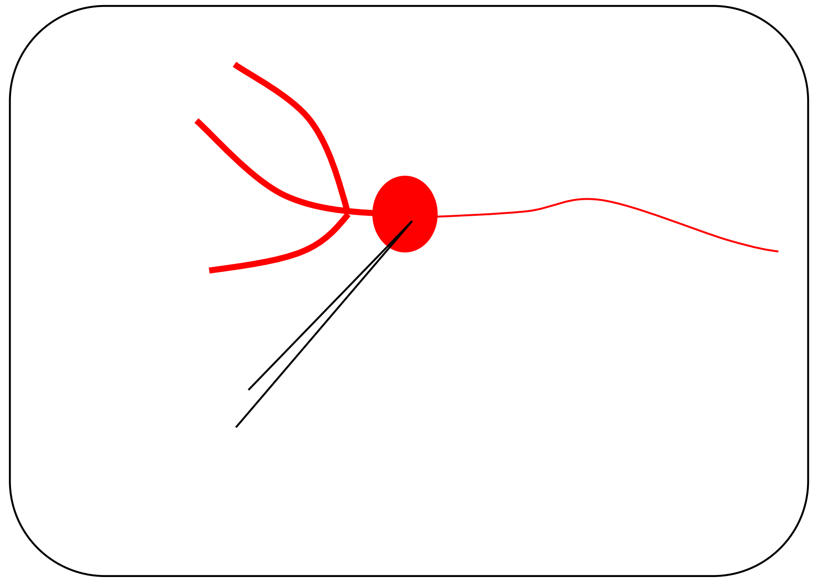
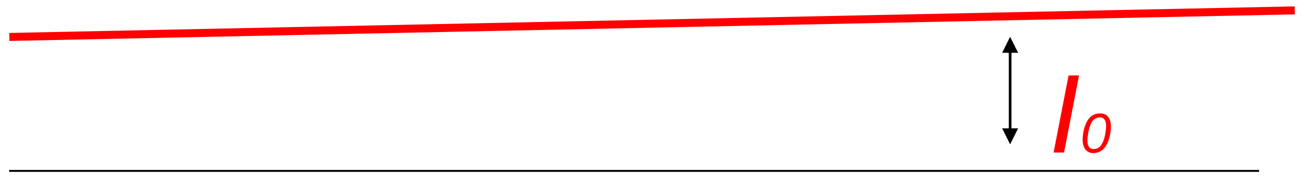


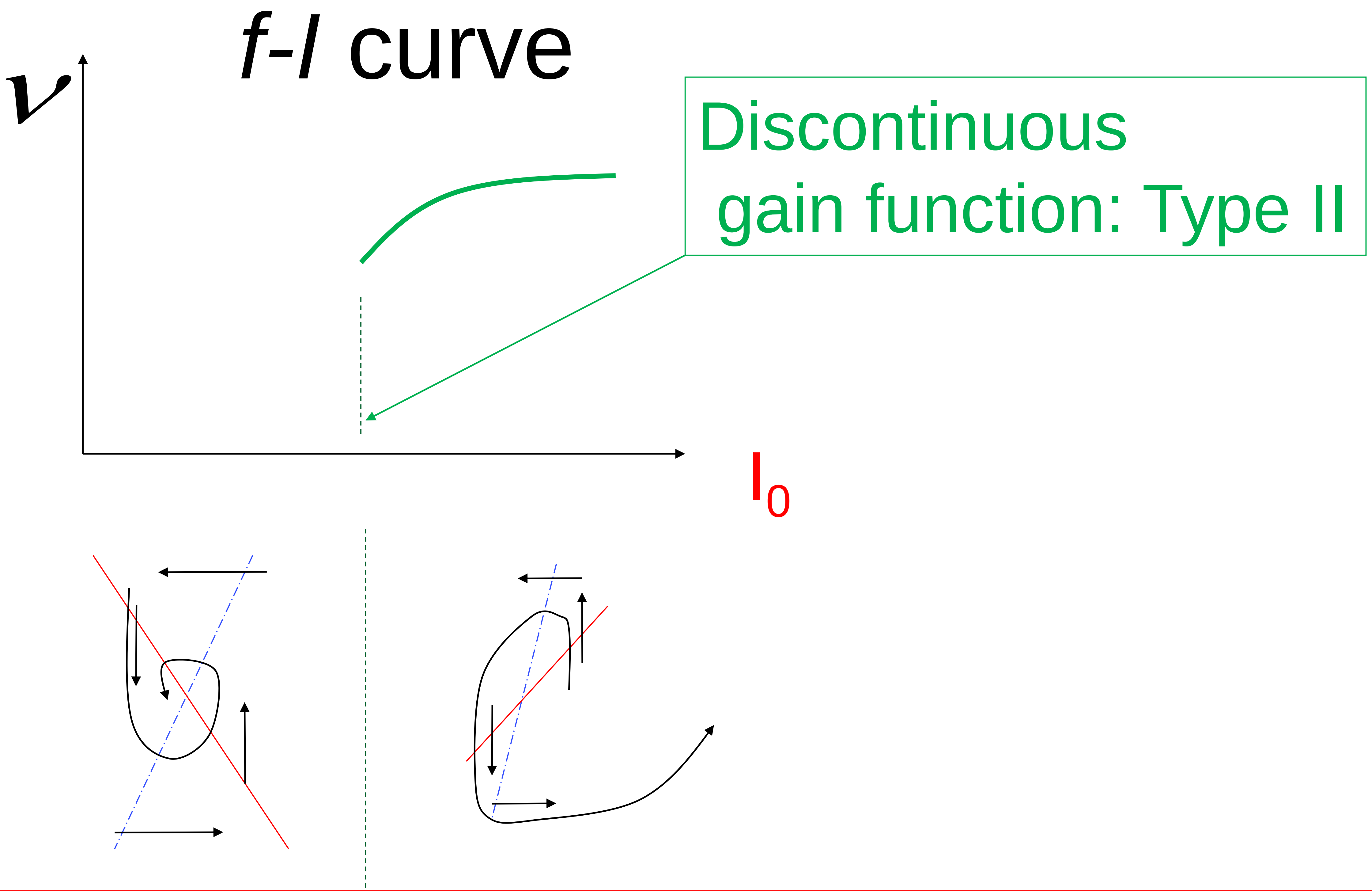
Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014)

4.2. Hopf bifurcation: *f-I* -curve



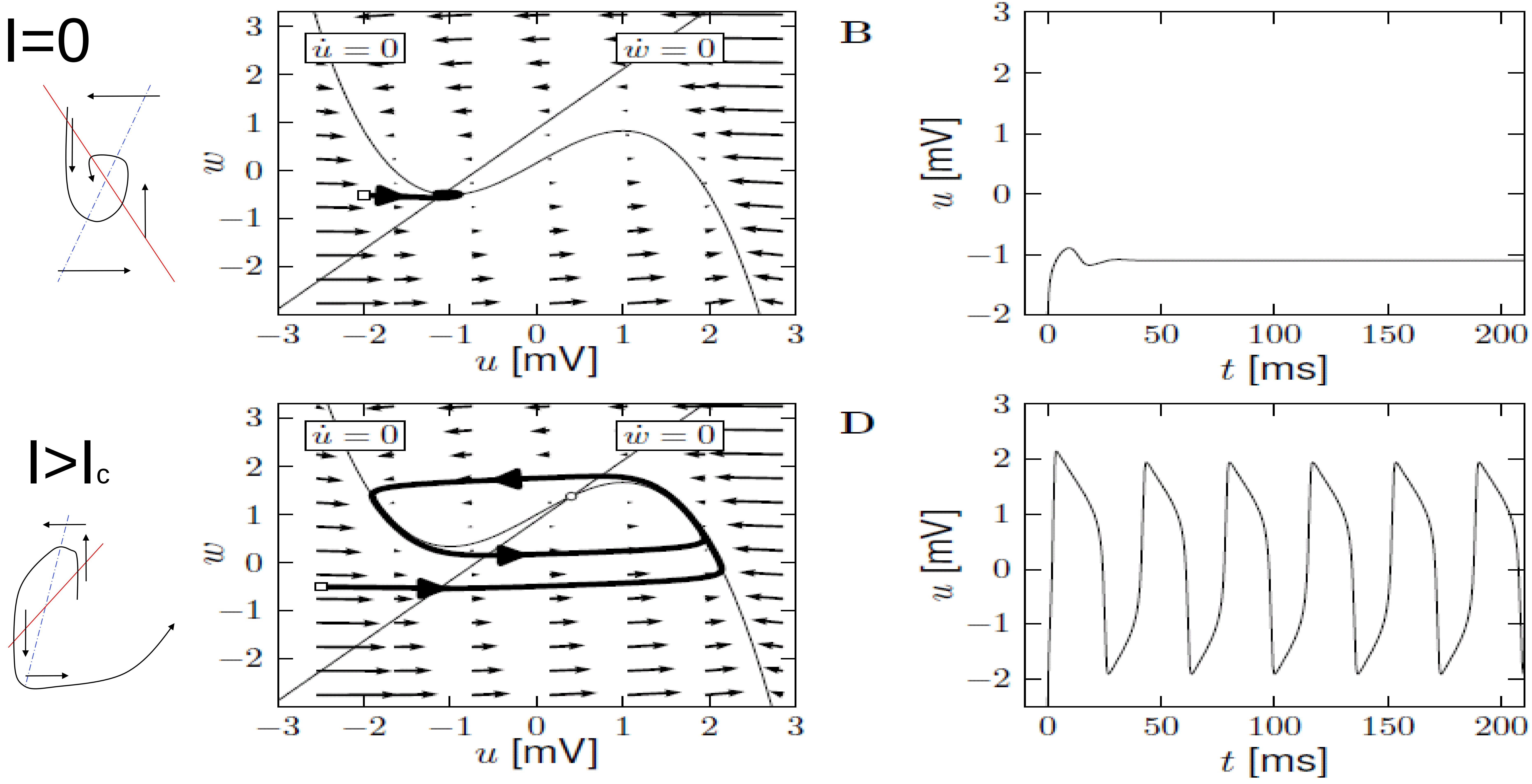
ramp input/
constant input



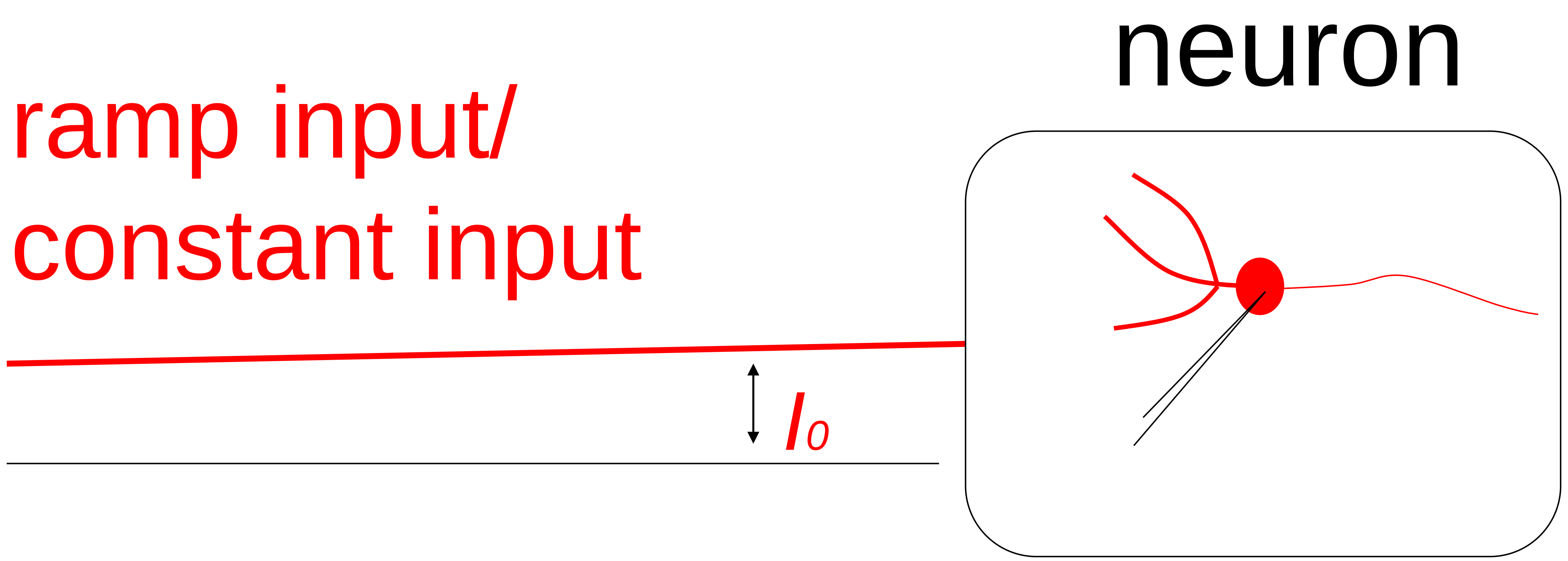


Hopf bifurcation: pair of complex Eigenvalues
Stability lost → oscillation with finite frequency
Subcritical → local oscillation is also unstable, and therefore jump (in neuron models) to a large limit cycle

4.2 Example: FitzHugh-Nagumo / Hopf bifurcation

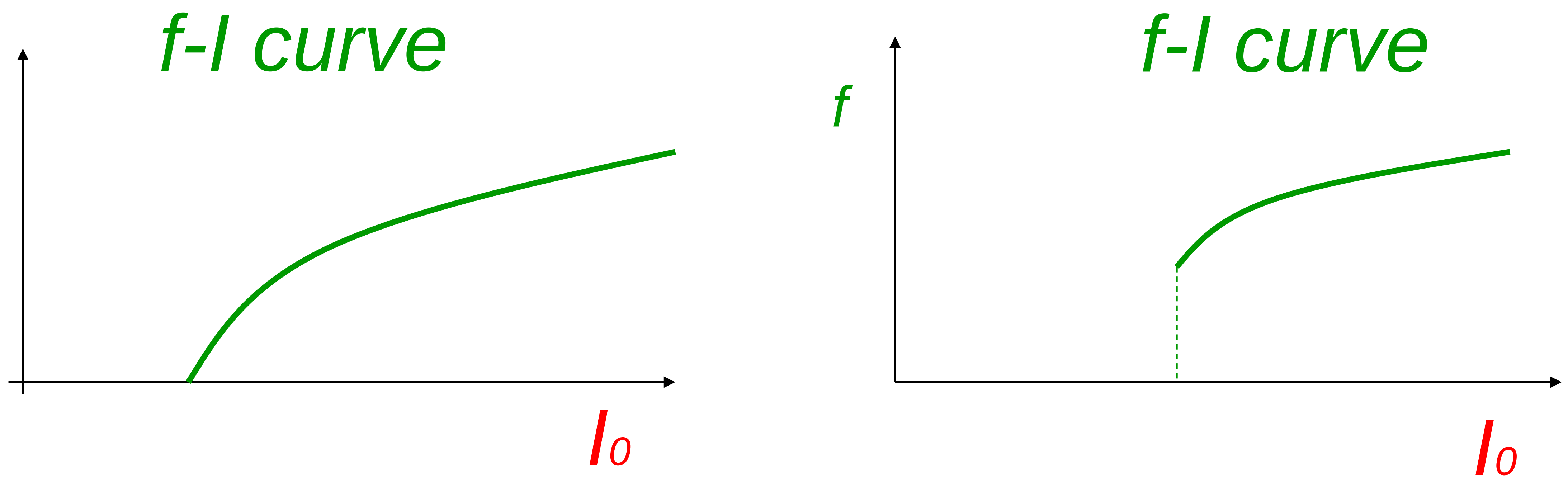


4.2. Type I and II Neuron Models



Now:
Type I model

Type I and type II models



type I Model: 3 fixed points

stimulus

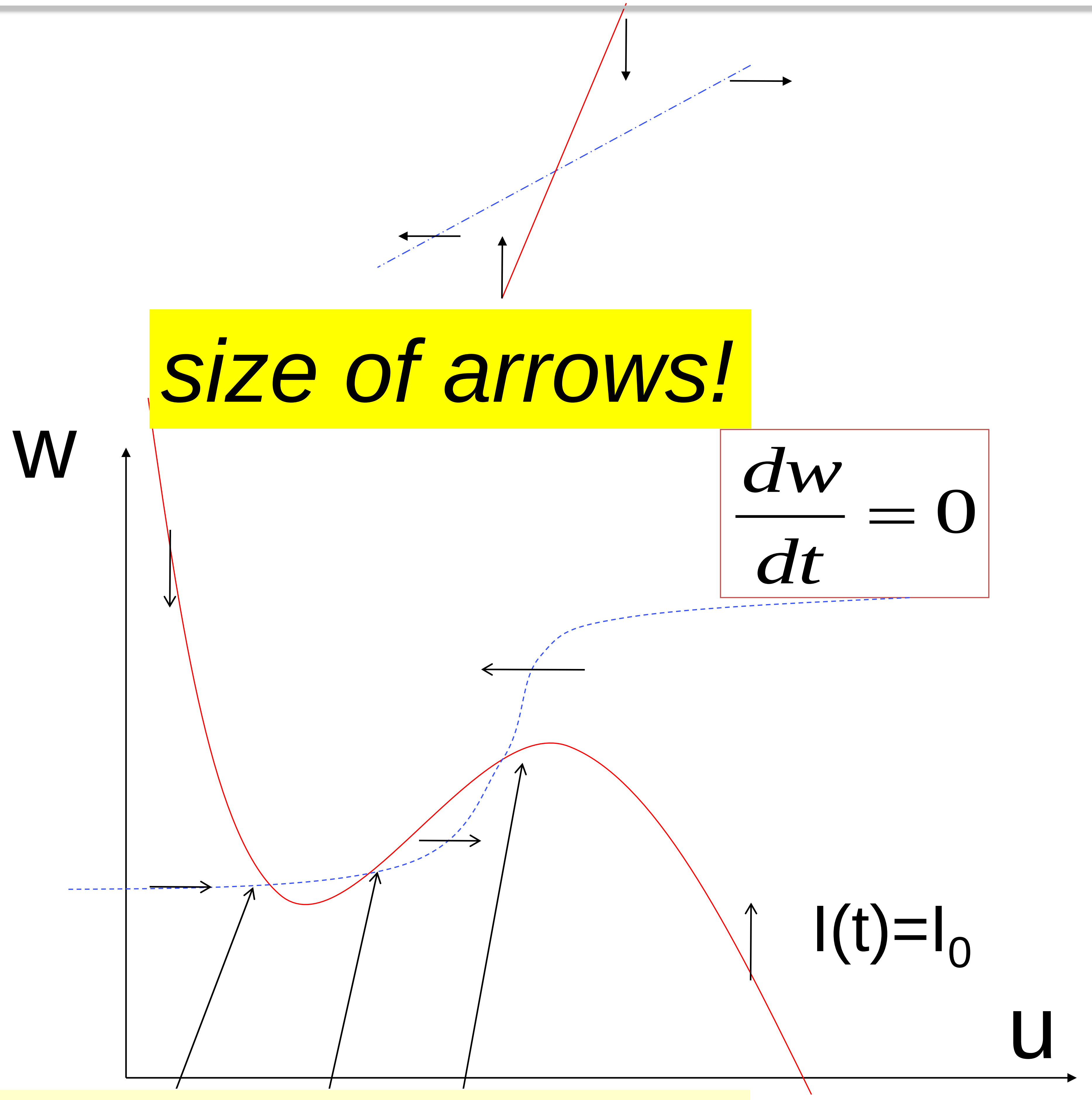
$$\tau \frac{du}{dt} = F(u,w) + I(t)$$

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

apply constant stimulus I_0

Saddle-node bifurcation

size of arrows!



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

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

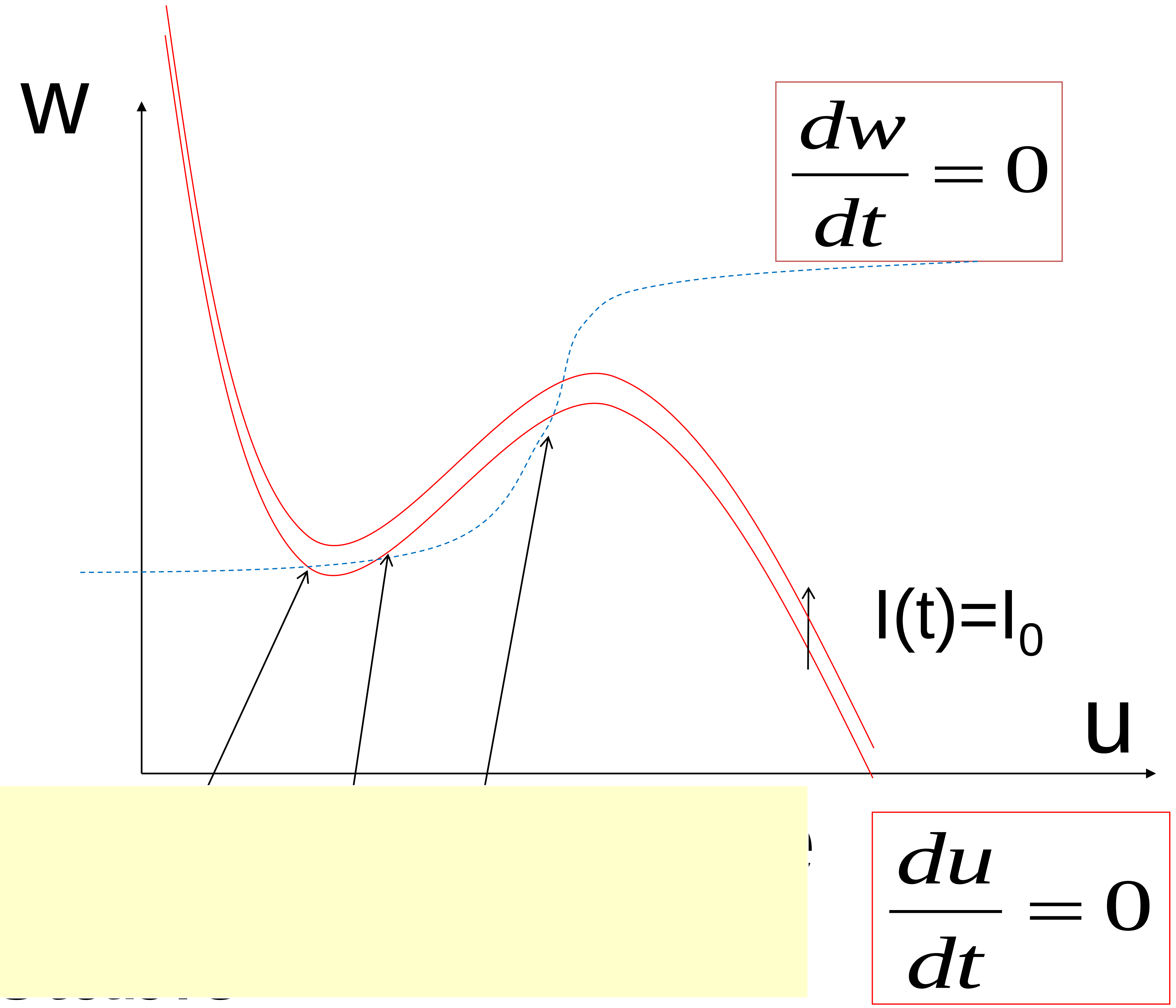
4.2. Type I Neuron Models: saddle-node bifurcation

stimulus

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

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

constant input



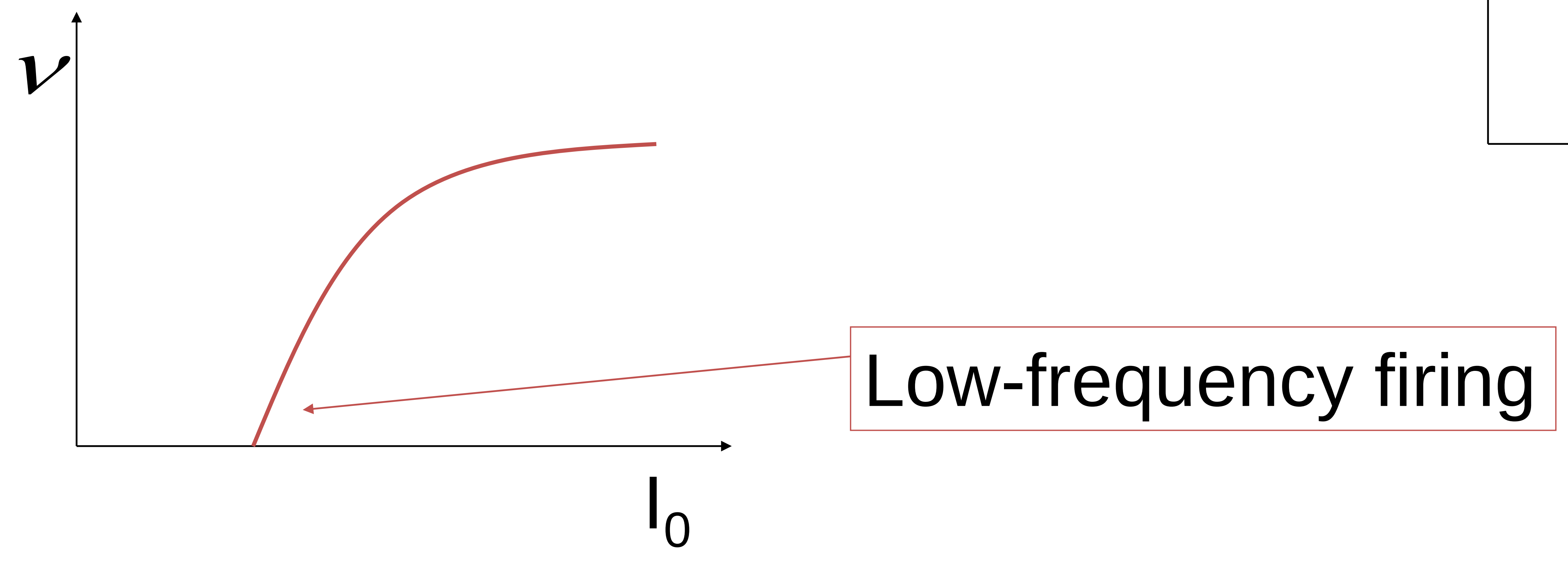
Blackboard 3:
- flow arrows,
- ghost/ruins

4.2. Type I Neuron Models: saddle-node bifurcation

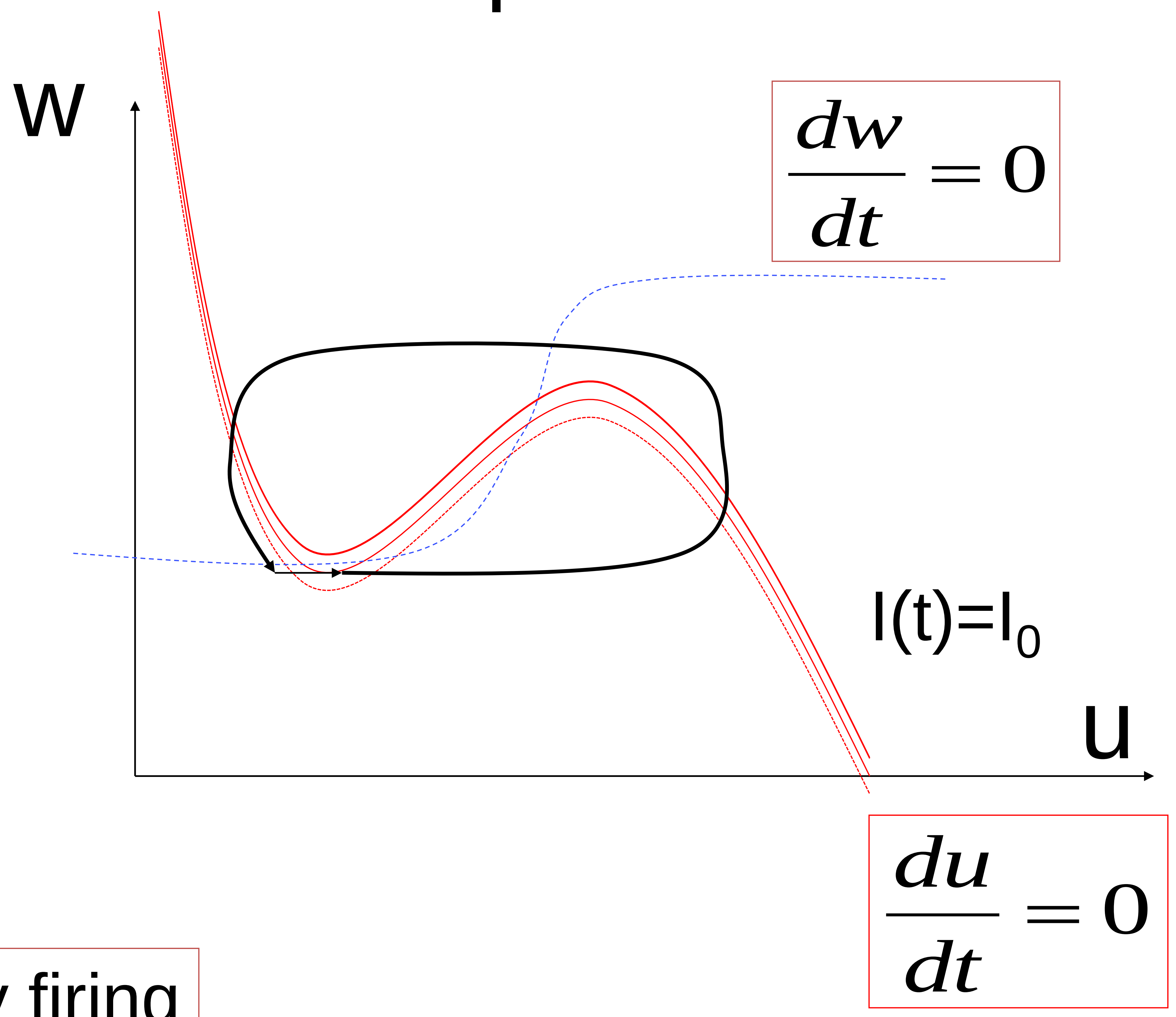
stimulus

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

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



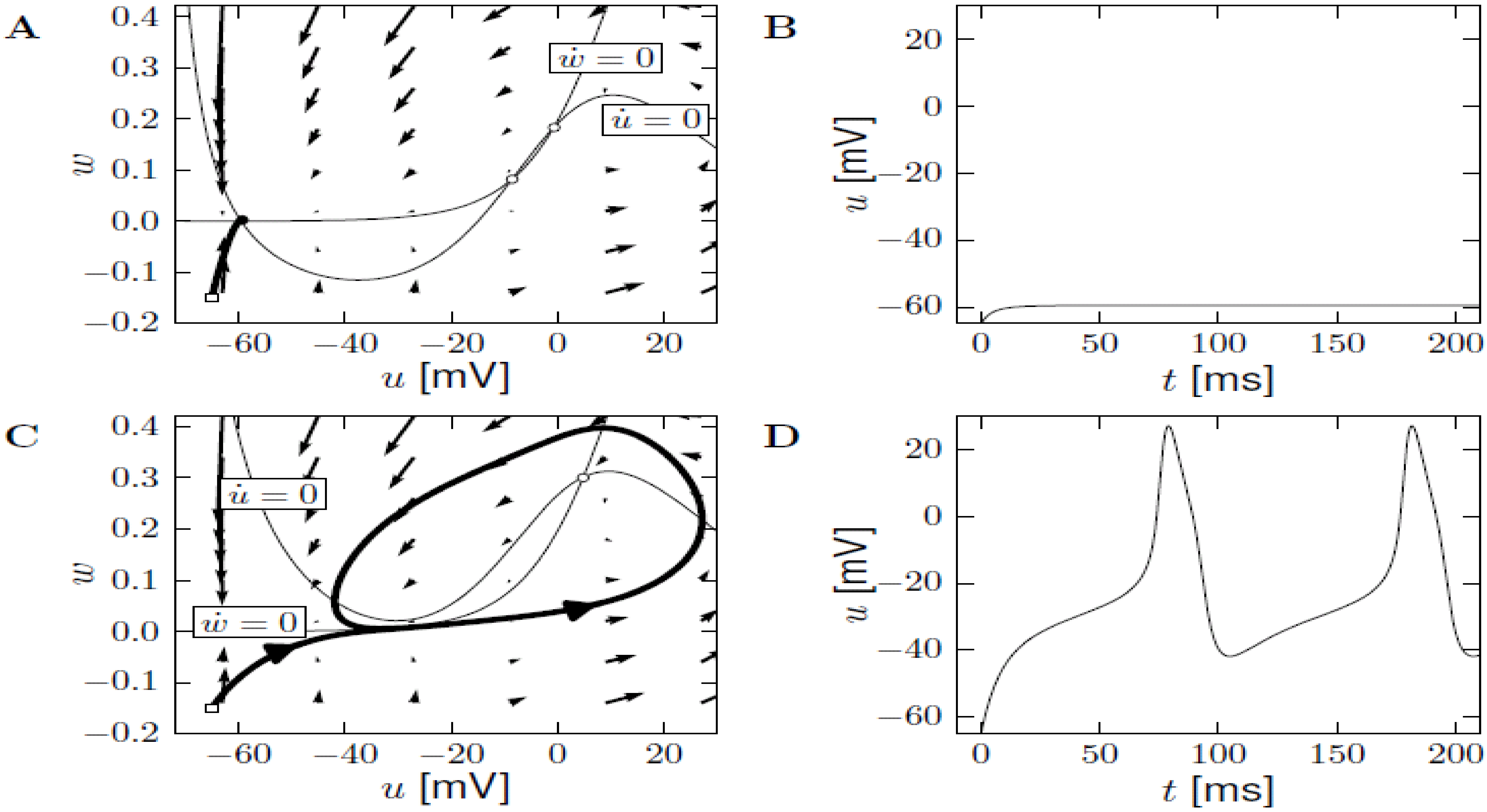
constant input



4.2. Example: Morris-Lecar as type I Model

I=0

I>I$_c$



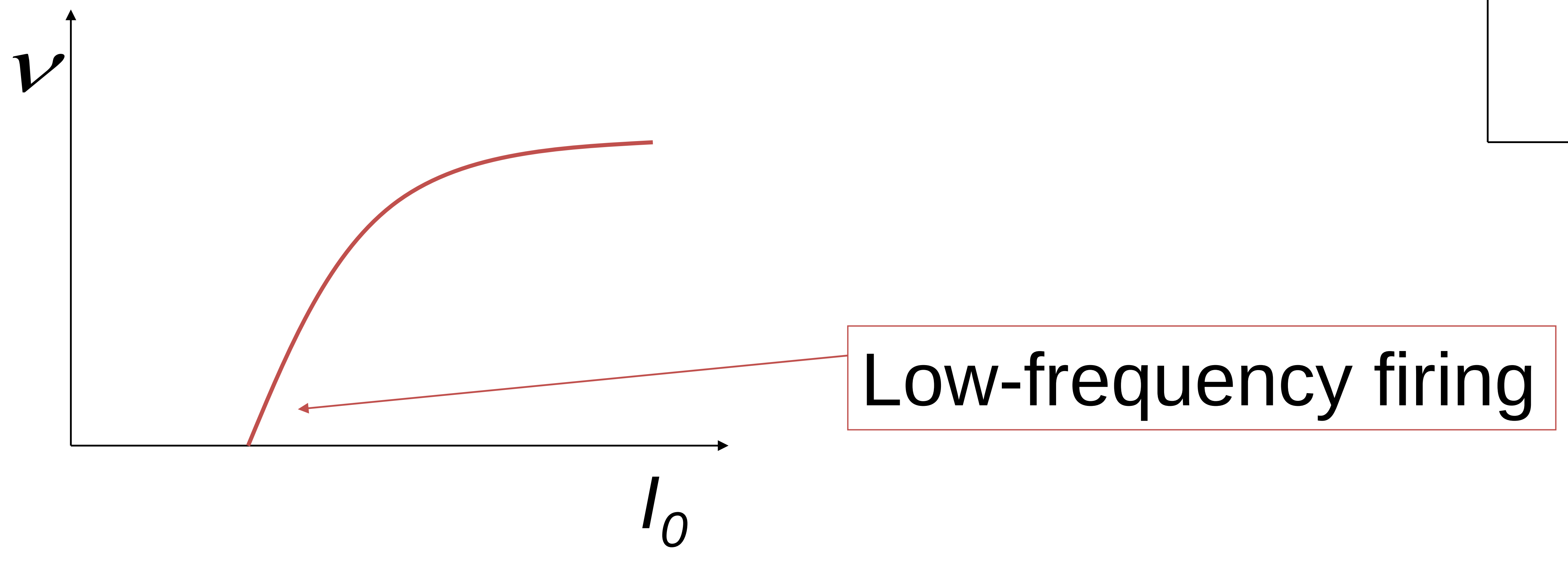
4.2. Example: Morris-Lecar as type I Model

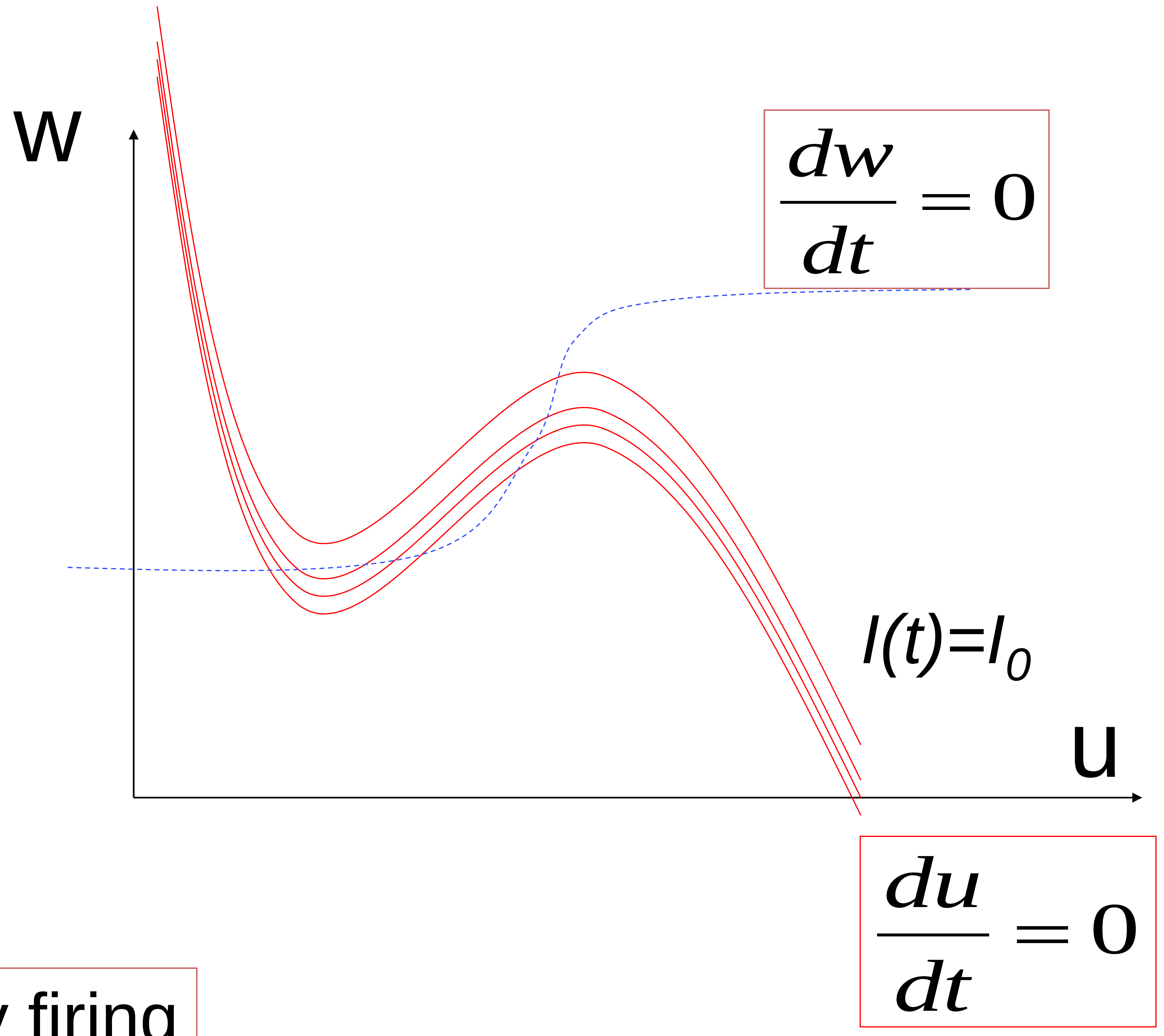
stimulus

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

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

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





4.2. Type I and II Neuron Models

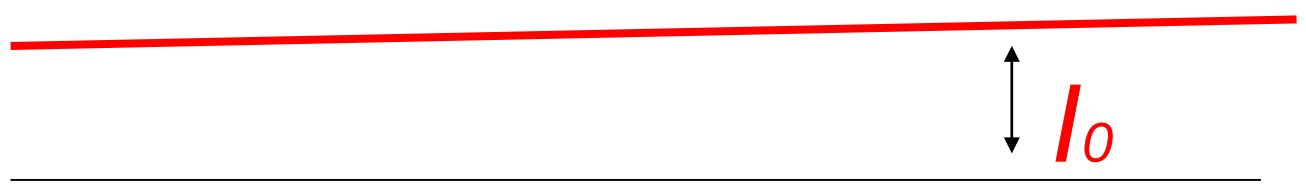
Response at firing threshold?

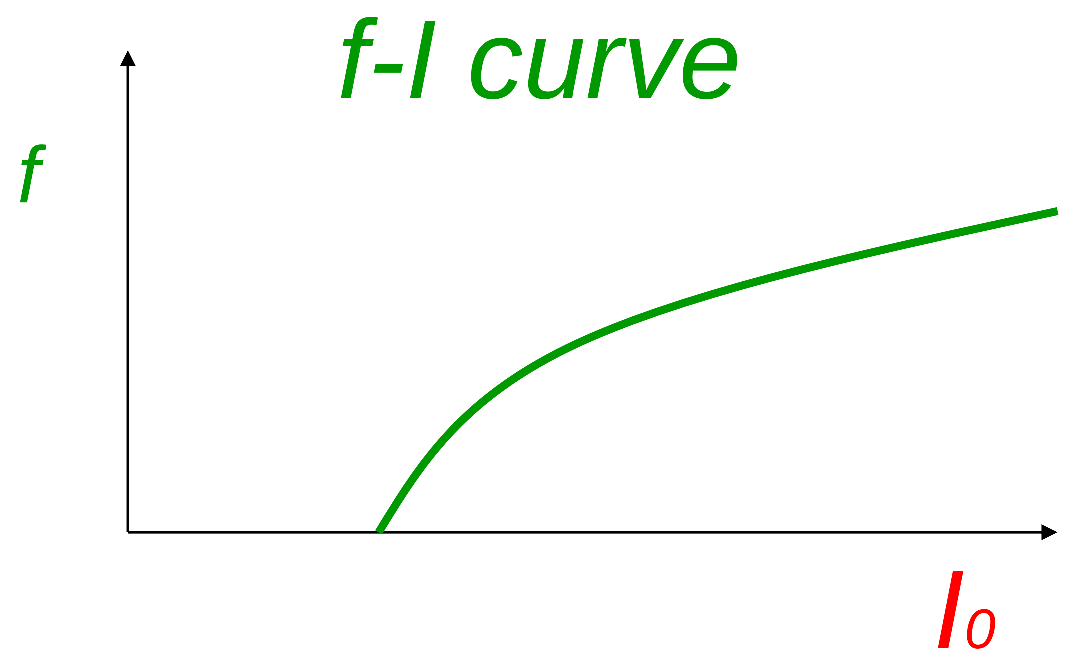
Type I	type II

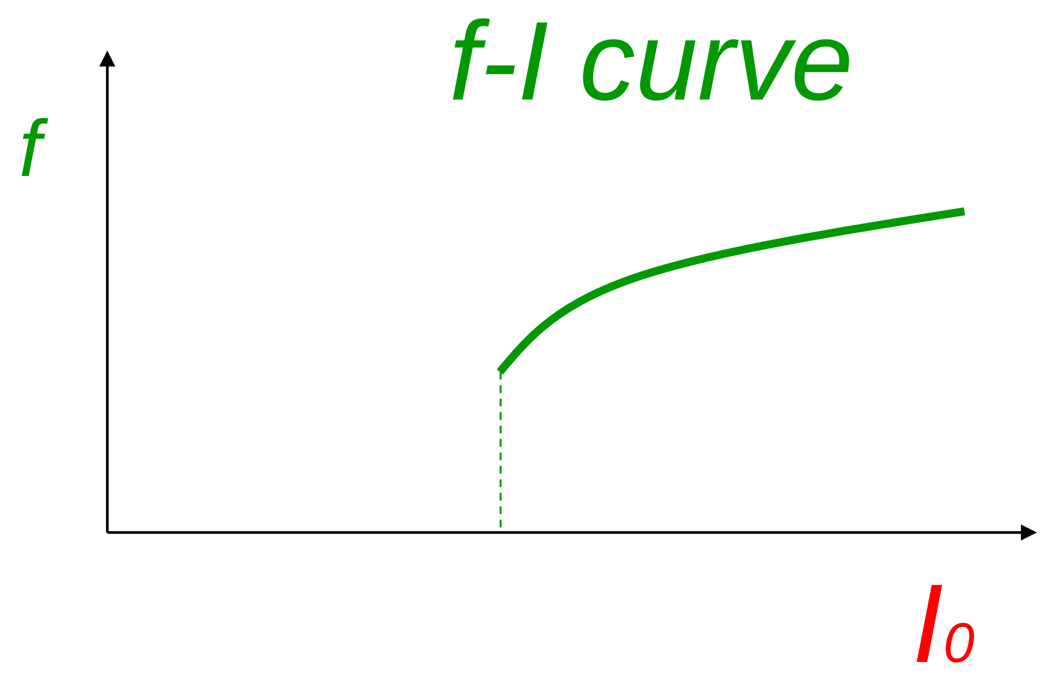
Saddle-Node
Onto limit cycle

For example:
Subcritical Hopf

ramp input/
constant input







4.2. Type I and II Neuron Models

2-dimensional equation

stimulus

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

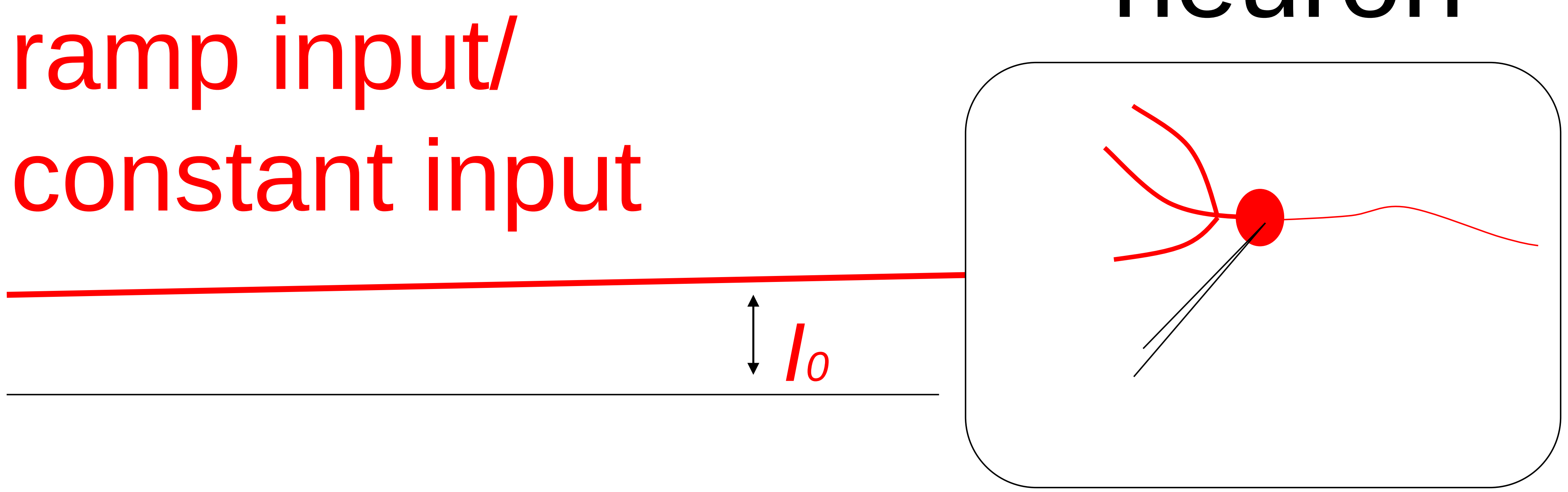
$$\tau_w \frac{dw}{dt} = G(u,w)$$

Enables graphical analysis!

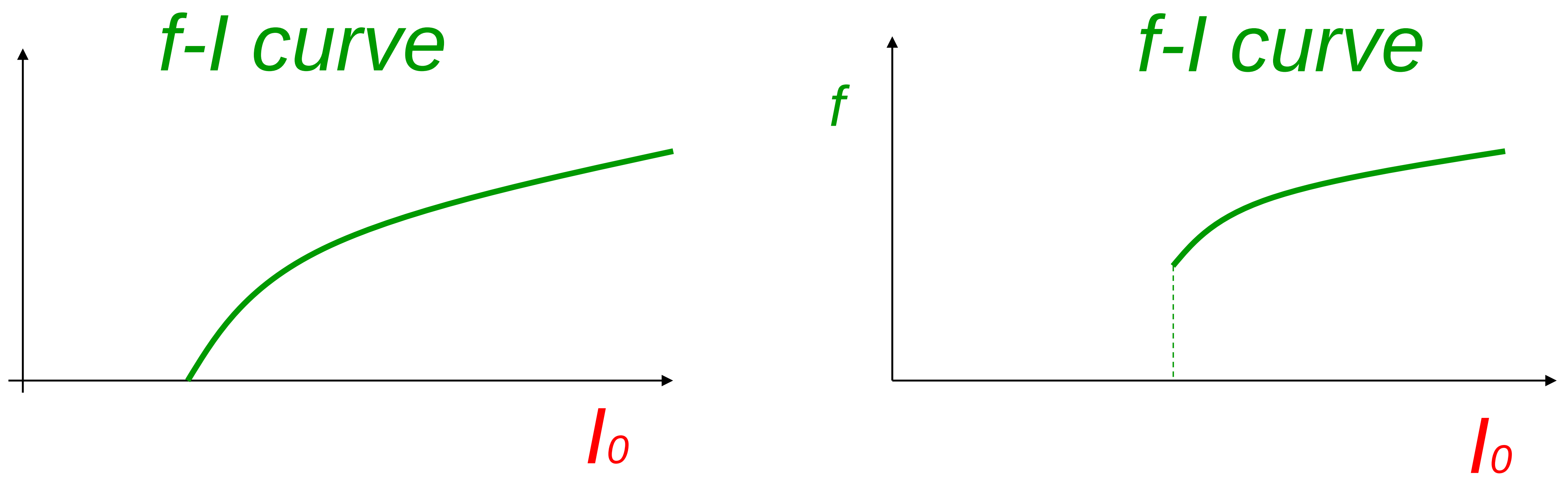
Constant input

→ repetitive firing (or not)

→ limit cycle (or not)



Type I and type II models



Neuronal Dynamics – Quiz 4.1.

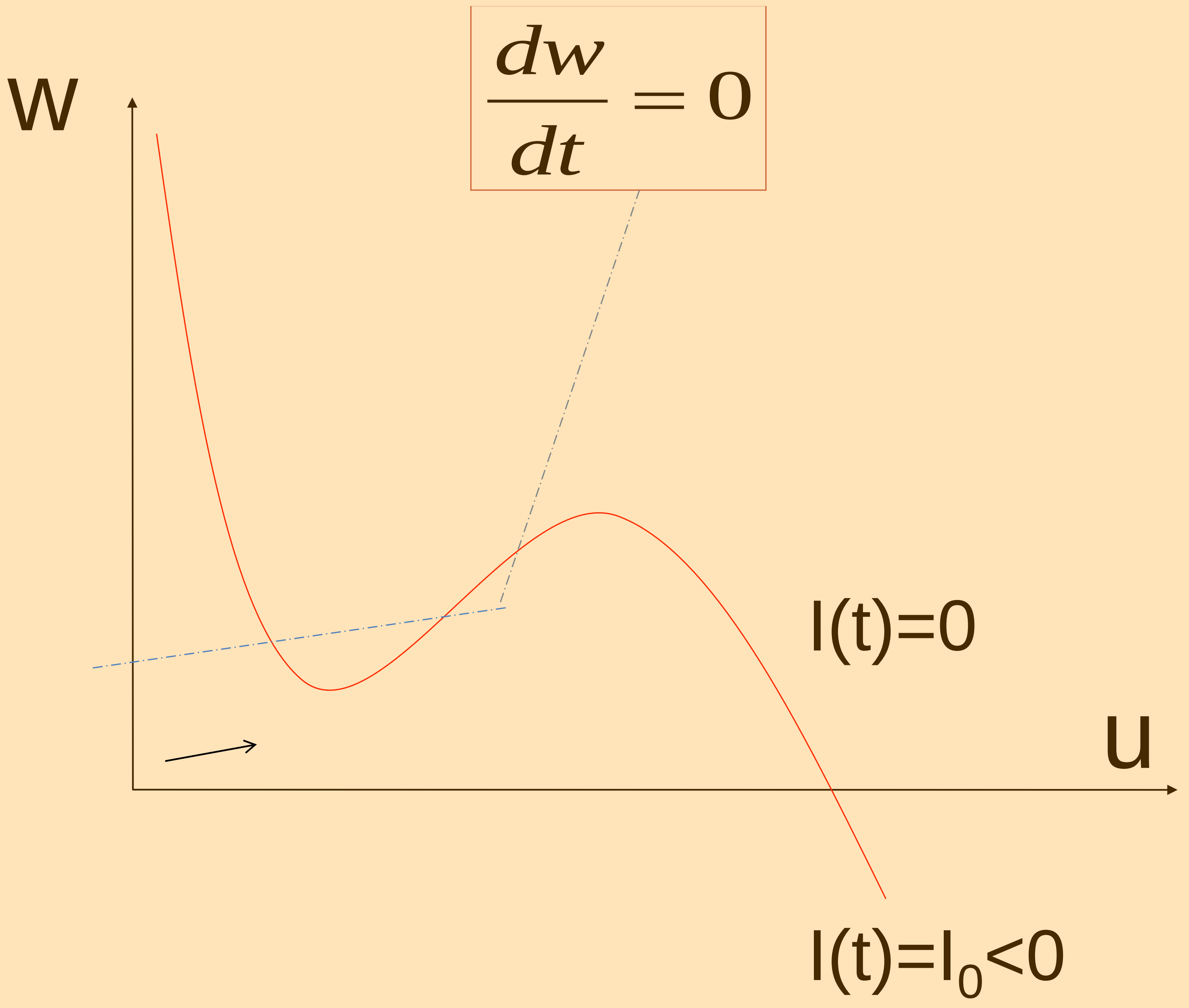
A. 2-dimensional neuron model with (supercritical) saddle-node-onto-limit cycle bifurcation

[ ] The neuron model is of type II, because there is a jump in the f-I curve
[ ] The neuron model is of type I, because the f-I curve is continuous
[ ] The neuron model is of type I, if the limit cycle passes through a regime where the flow is very slow.

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

[ ] The neuron model is of type II, because there is a jump in the f-I curve
[ ] The neuron model is of type I, because the f-I curve is continuous
[ ] starting with zero current, and slowly increasing the current, is this true?
“ in the regime below the Hopf bifurcation, the neuron is at rest or will necessarily converge to the resting state”

Week 4 - Exercise 2.1-2.5: NOW!



Now exercises

Next lecture at 11:15

Exercise 2: Phase Plane Analysis

In this exercise, we use the phase plane to study the dynamics of a two dimensional, nonlinear neuron model. The system is described by:

$$\begin{cases} \frac{d}{dt}u = F(u,w) \\ \frac{d}{dt}w = G(u,w) \end{cases} \quad (2)$$

where $F(u,w) = f(u) - w + I(t)$ and $G(u,w) = \epsilon(g(u) - w)$ with $\epsilon = 0.1$. $I(t)$ is an external current.

Figure 1 shows the u- and w-nullclines for the case $I(t) = 0$:

2.1 Given $F(u_4, 0) = 5, G(u_4, 0) = 1$, draw a few flow arrows along the two nullclines in figure 1.

2.2 Without doing any computation, can you determine the stability of the fixed point 2 (the one at (u_2, w_2))? Justify your answer.

2.3 Discuss the stability of the third fixed point (the one at (u_3, w_3)) analytically. That is, linearize the system at the fixed point 3 and discuss the evolution of a small perturbation around that point. For the numeric calculations, use $\epsilon = 0.1$ and approximate the values of $\frac{d}{du}f(u)_{|u_3}$ and $\frac{d}{du}g(u_3)_{|u_3}$ from figure 1.

2.4 Assume the neuron is at rest. Then, at t_0 we apply a pulse stimulus $I(t)$ to this system:

$$I(t) = (u_3 - u_1)\delta(t - t_0)$$

(i) Sketch the trajectory $(u(t), w(t))$ in Figure 1.

(ii) Sketch the membrane potential $u(t)$ vs. time in a new figure.

Make sure you get the two plots qualitatively correct: Clearly indicate important states, for example at $t < t_0$, at t_0, and at $t > t_0$. Furthermore, in your $u(t)$ plot, fast and slow regions should be distinguishable.

2.5 Refering to figure 1, discuss the effect of injecting pulse currents $I(t) = q\delta(t - t_0)$ of different amplitudes q into the neuron. What happens if we gradually increase q ? Does this neuron model have a threshold?

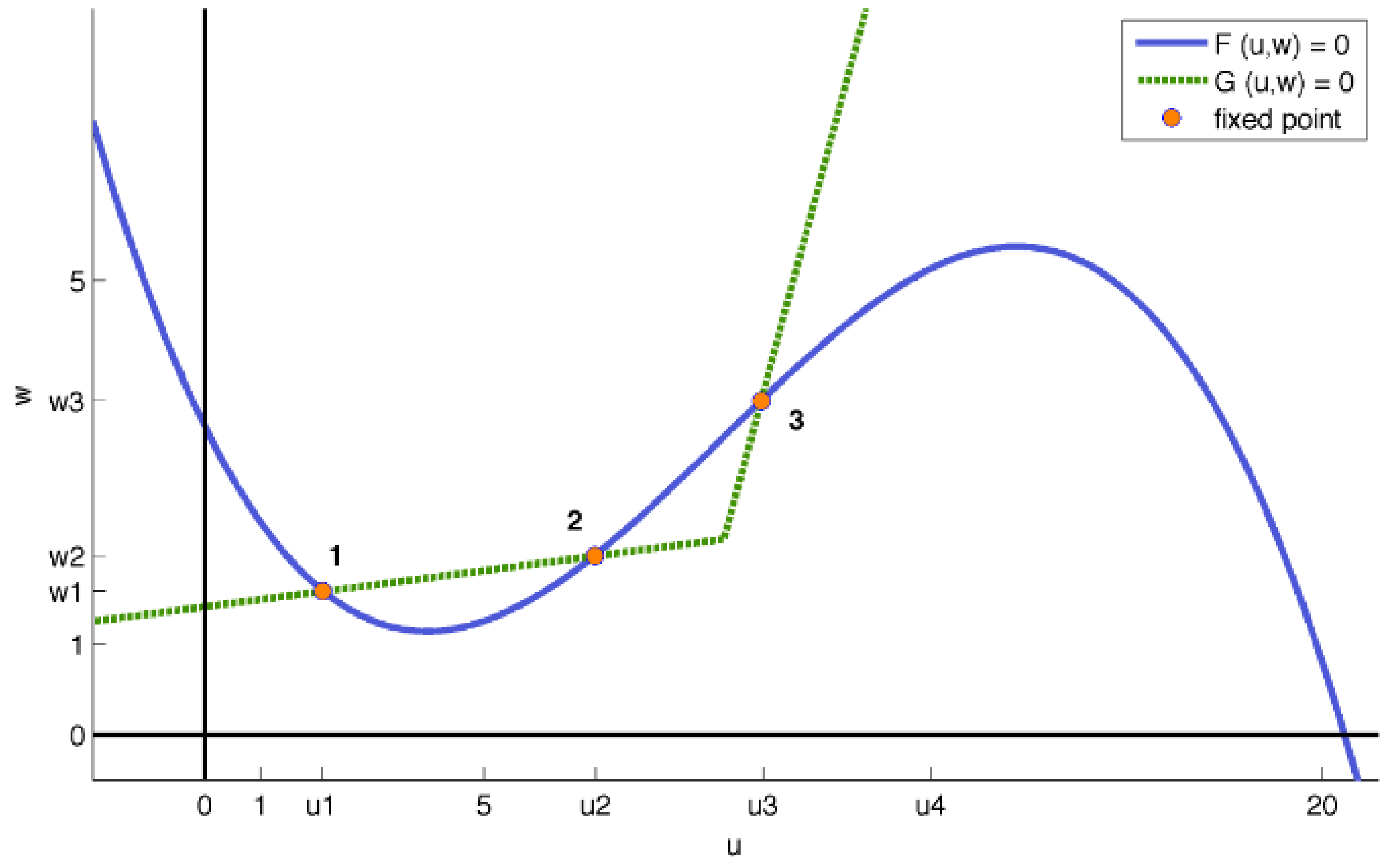


Figure 1

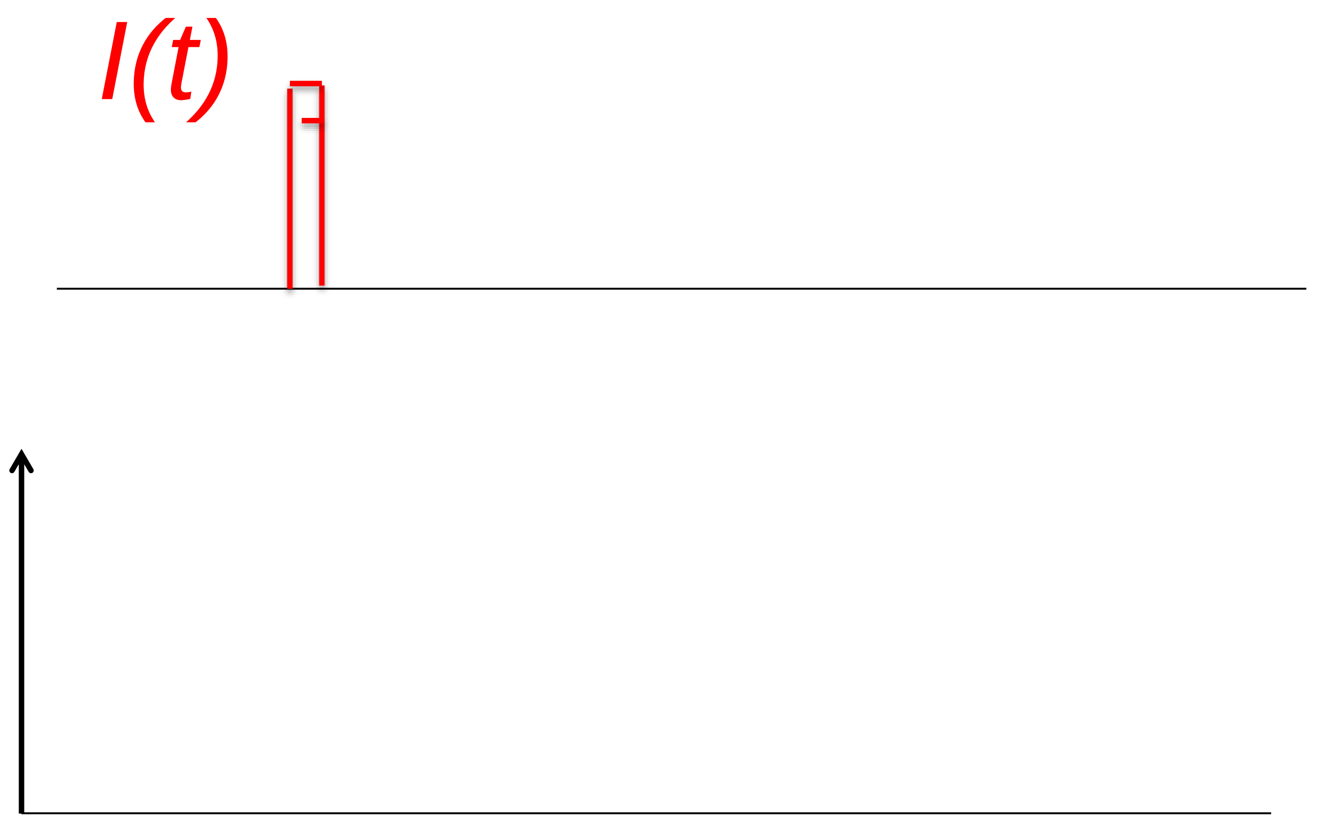
4.2. Exercise

stimulus

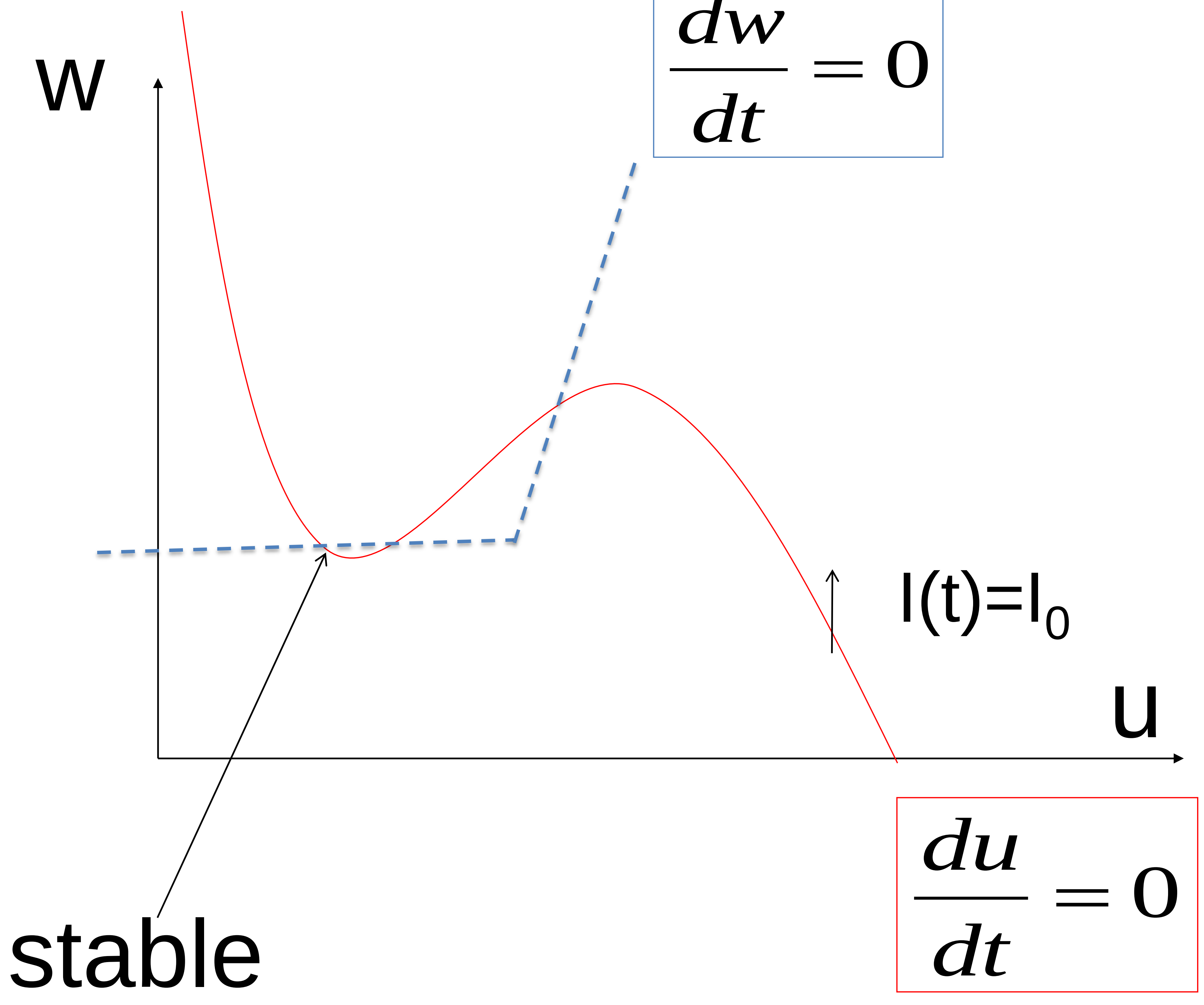
$$\tau \frac{du}{dt} = F(u,w) + RI(t)$$

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

pulse input



Blackboard 4:
Saddle, stable manifold,
Slow response



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

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

4.2 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

4.2. Summary: Limit cycles and neuron models

1) In 2 dimensions we have a powerful theorem: if we can find a bounding box around an unstable fixed such that all flow arrows point inside the box, then there must be a limit cycle.
2) We can change the stability of the fixed point(s) by a constant input.
3) The limit cycle MAY appear at the moment when the fixed point looses stability. In this case it would often be a limit cycle of small amplitude in the neighborhood of the fixed point.
4) But we can also observe bistability between the stable fixed point and a limit cycle.
5) Neuron models can be classified according to the bifurcation type that makes a limit cycle appear. Type 1 neuron models have a smooth f-I curve and are always linked to a saddle-node-onto limit cycle bifurcation.
6) Type 2 models can have various origins; an example is the subcritical Hopf-bifurcation

Biological Modeling of Neural Networks

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Week 4

Reducing detail:

Analysis of 2D models

√ 3.1 From Hodgkin-Huxley to 2D

√ 3.2 Phase Plane Analysis

√ 3.3 Analysis of a 2D Neuron Model

4.1 Separation of time scales

4.2 Type I and II Neuron Models

- limit cycles: constant input

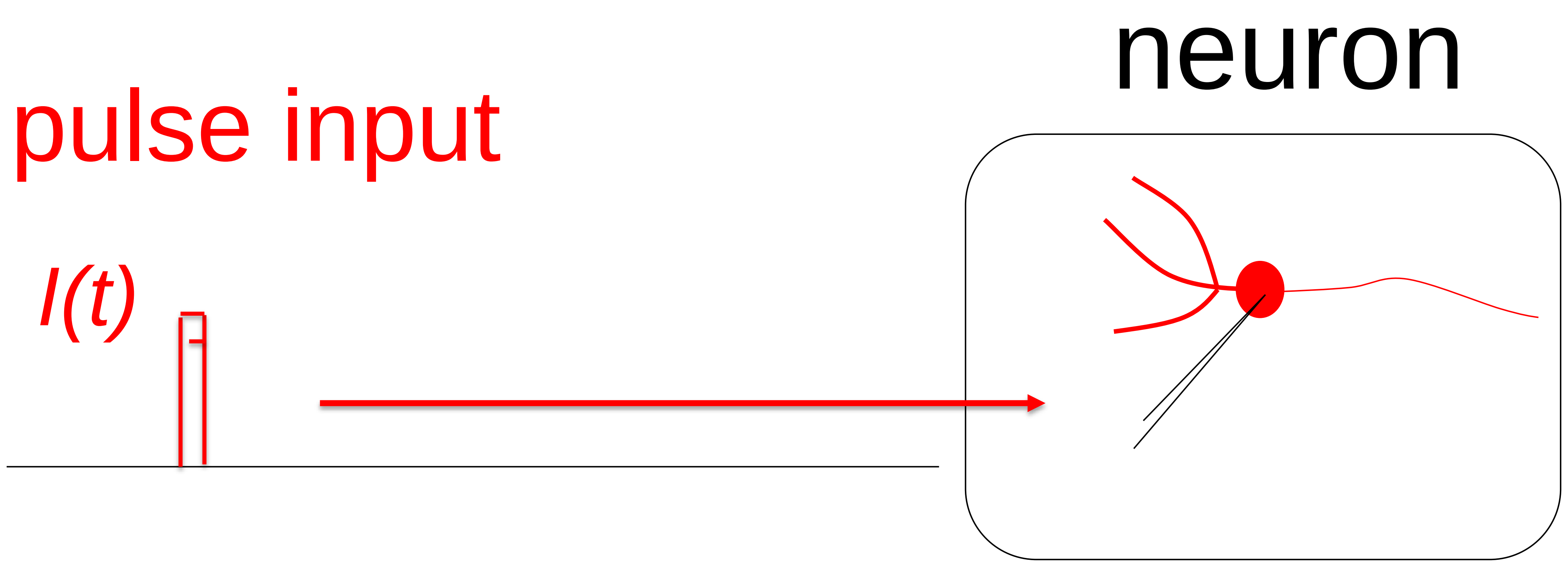
4.3 Pulse input

- where is the firing threshold?

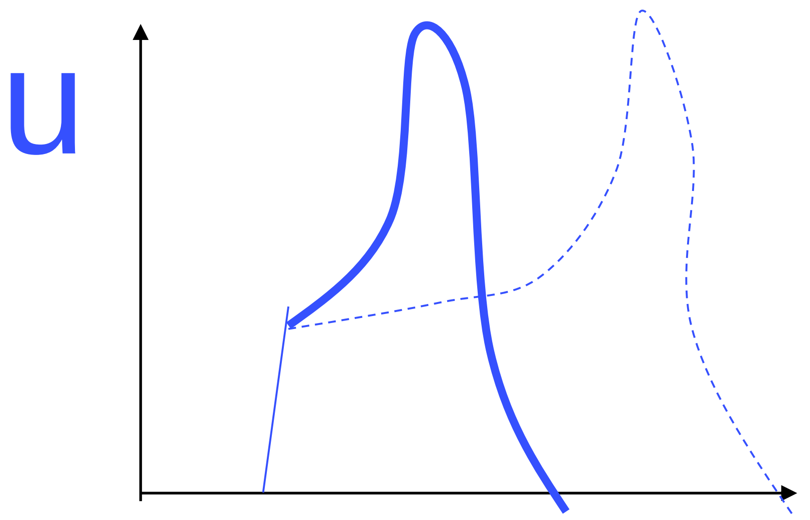
4.4. Further reduction to 1 dim

- nonlinear integrate-and-fire (again)

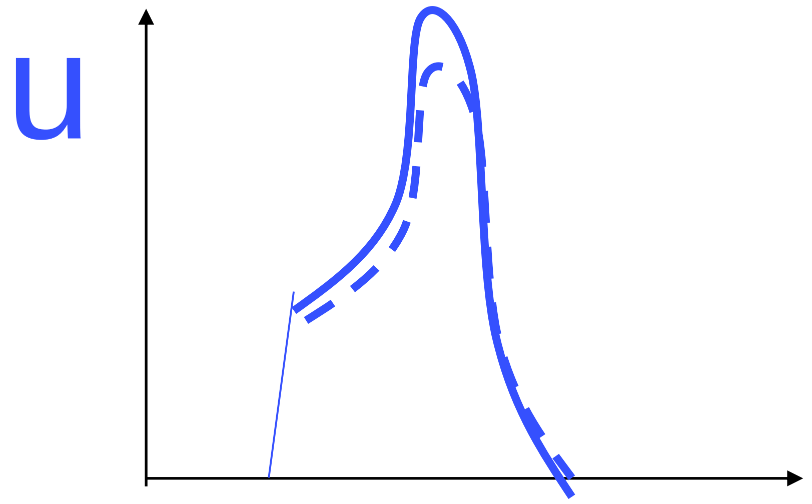
4.3. Threshold for Pulse Input in 2dim. Neuron Models



Delayed spike



Reduced amplitude

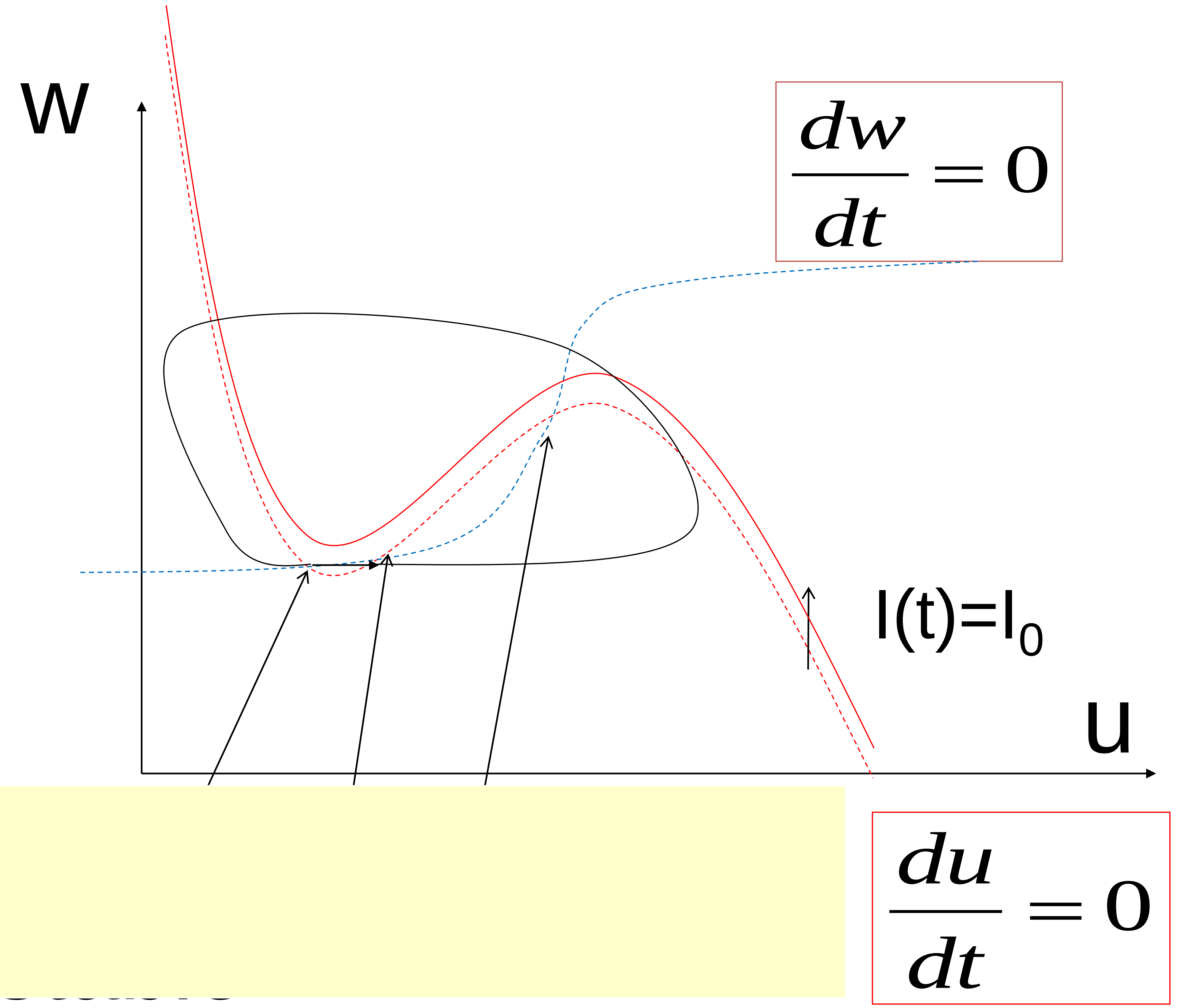


Review from 4.1: Saddle-node onto limit cycle bifurcation

stimulus

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

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



4.3 Threshold for Pulse input

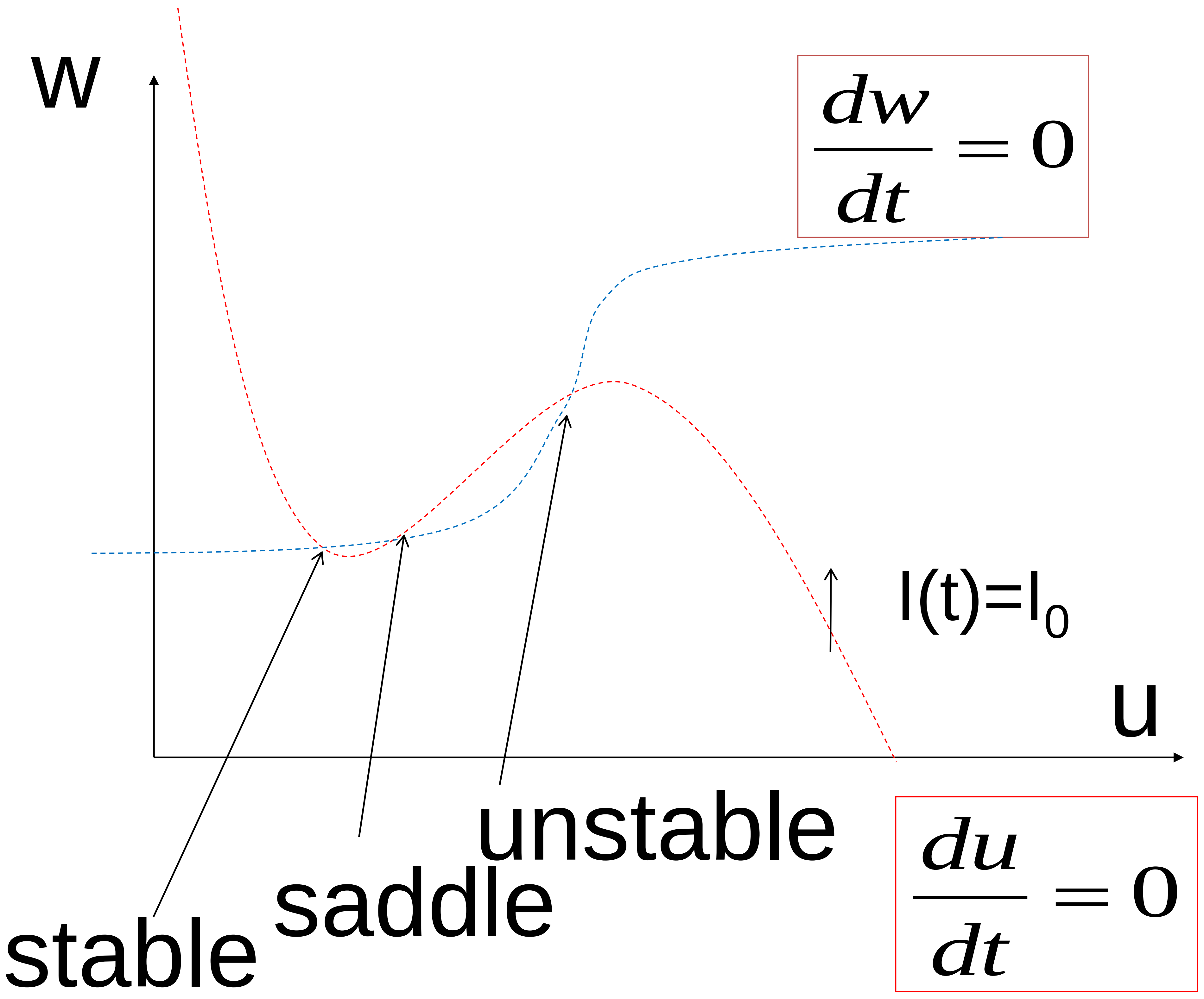
stimulus

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

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

Blackboard 4:
Saddle, stable manifold,
Slow response

pulse input



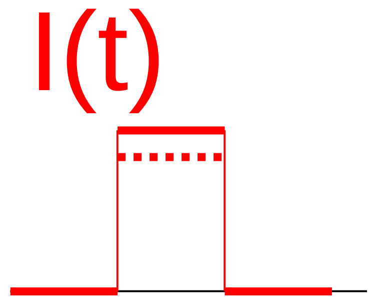
4.3 Type I model: Pulse input

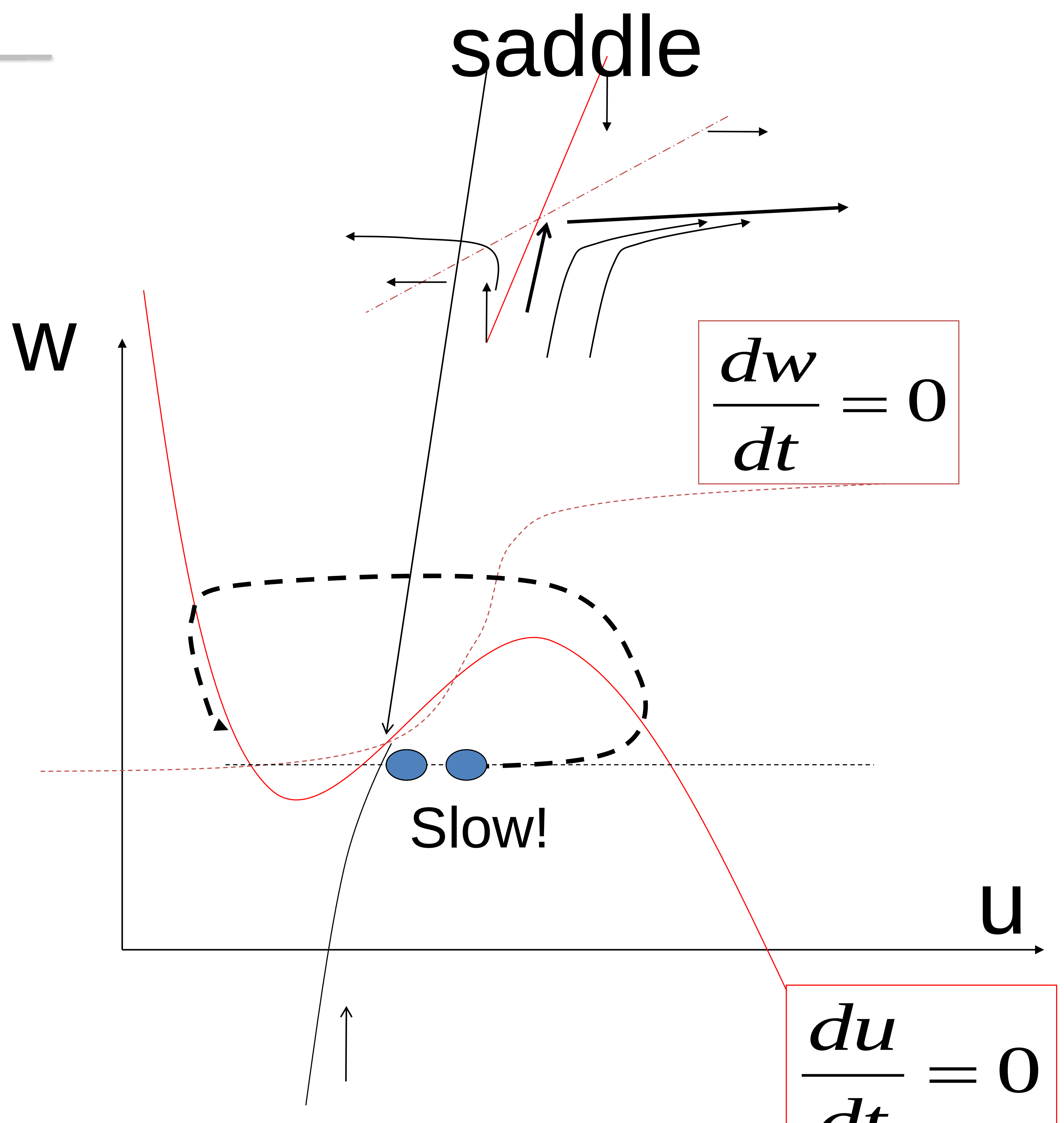
stimulus

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

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

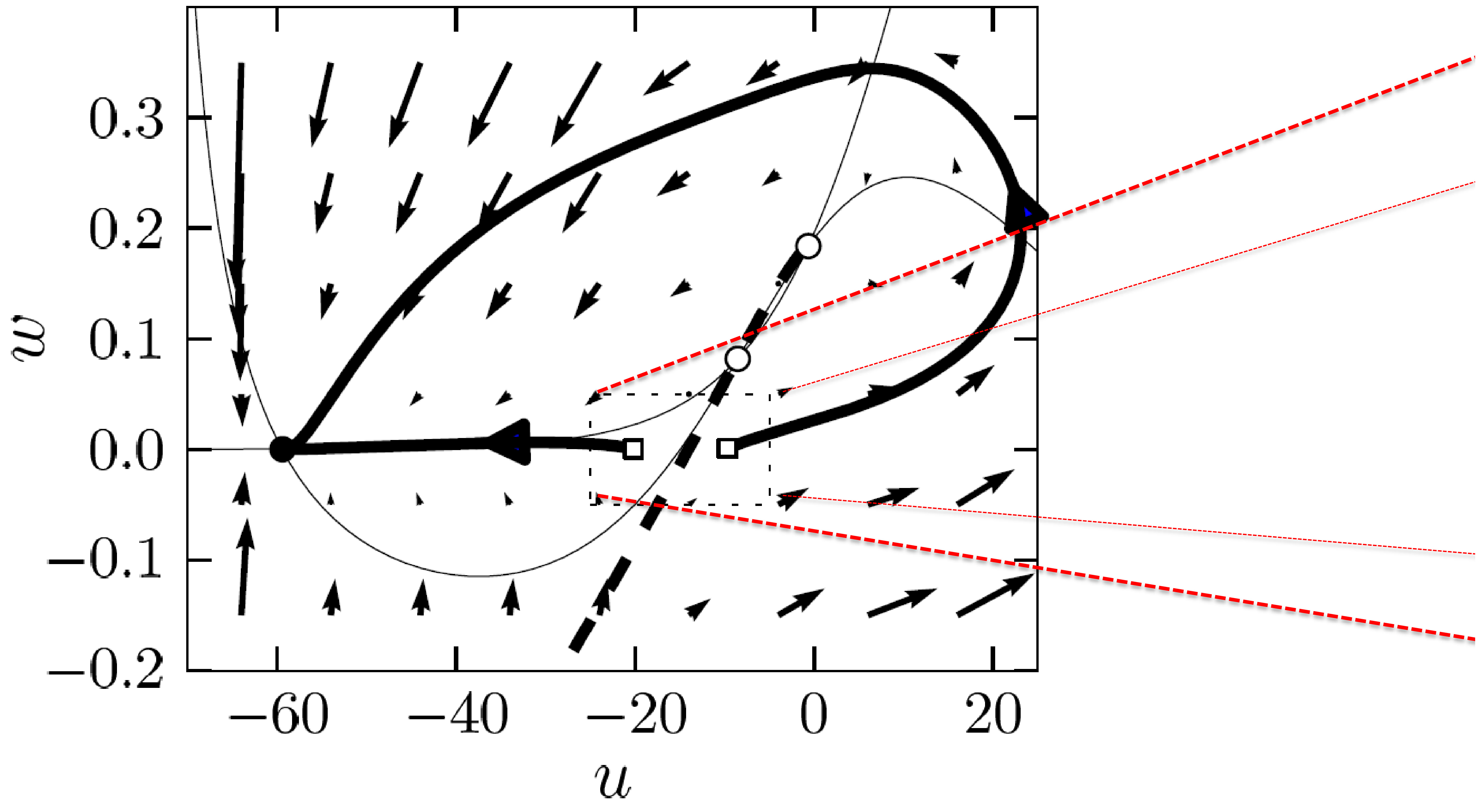
pulse input





Threshold
for pulse input

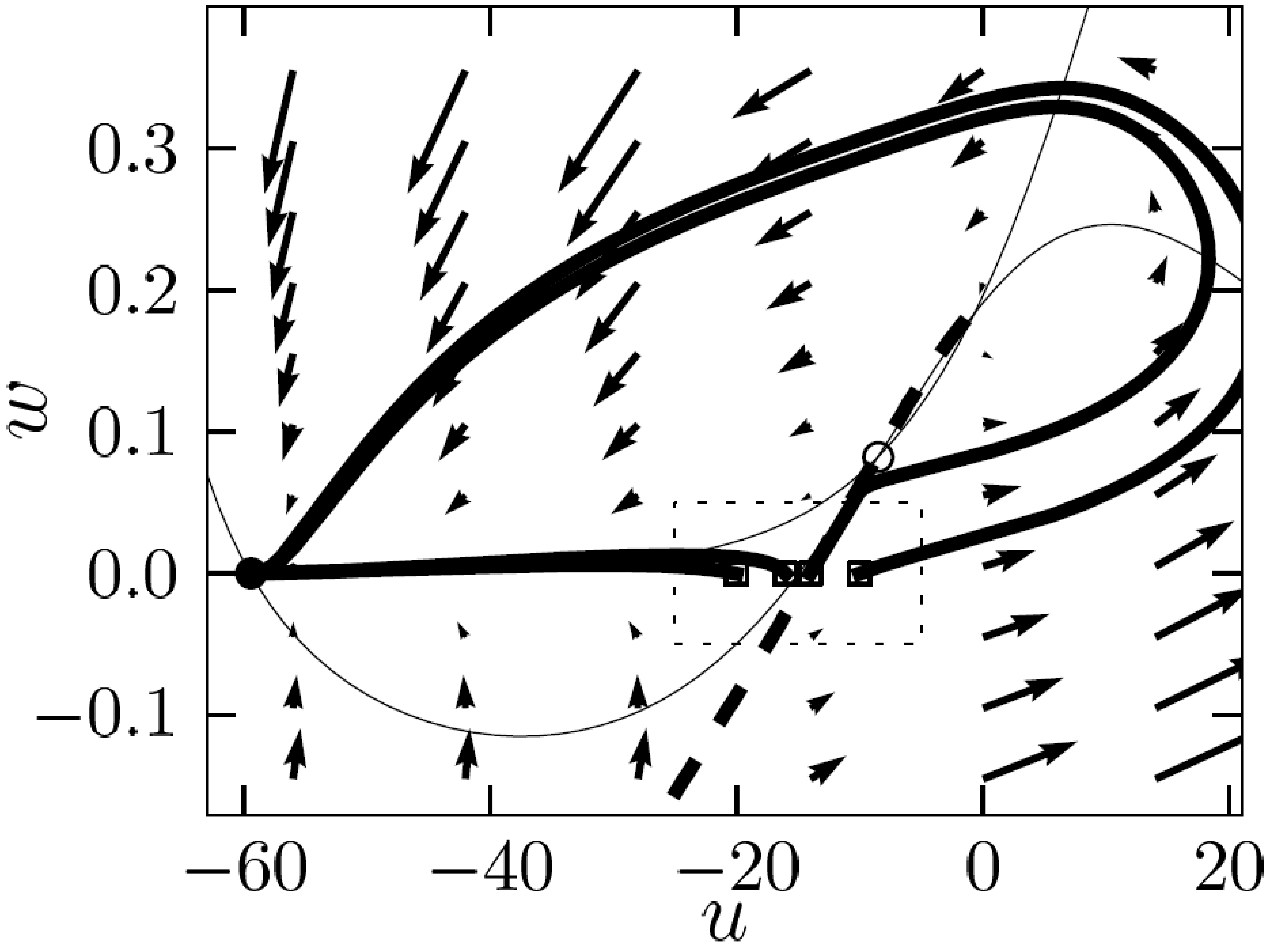
4.3 Type I model: Threshold for Pulse input

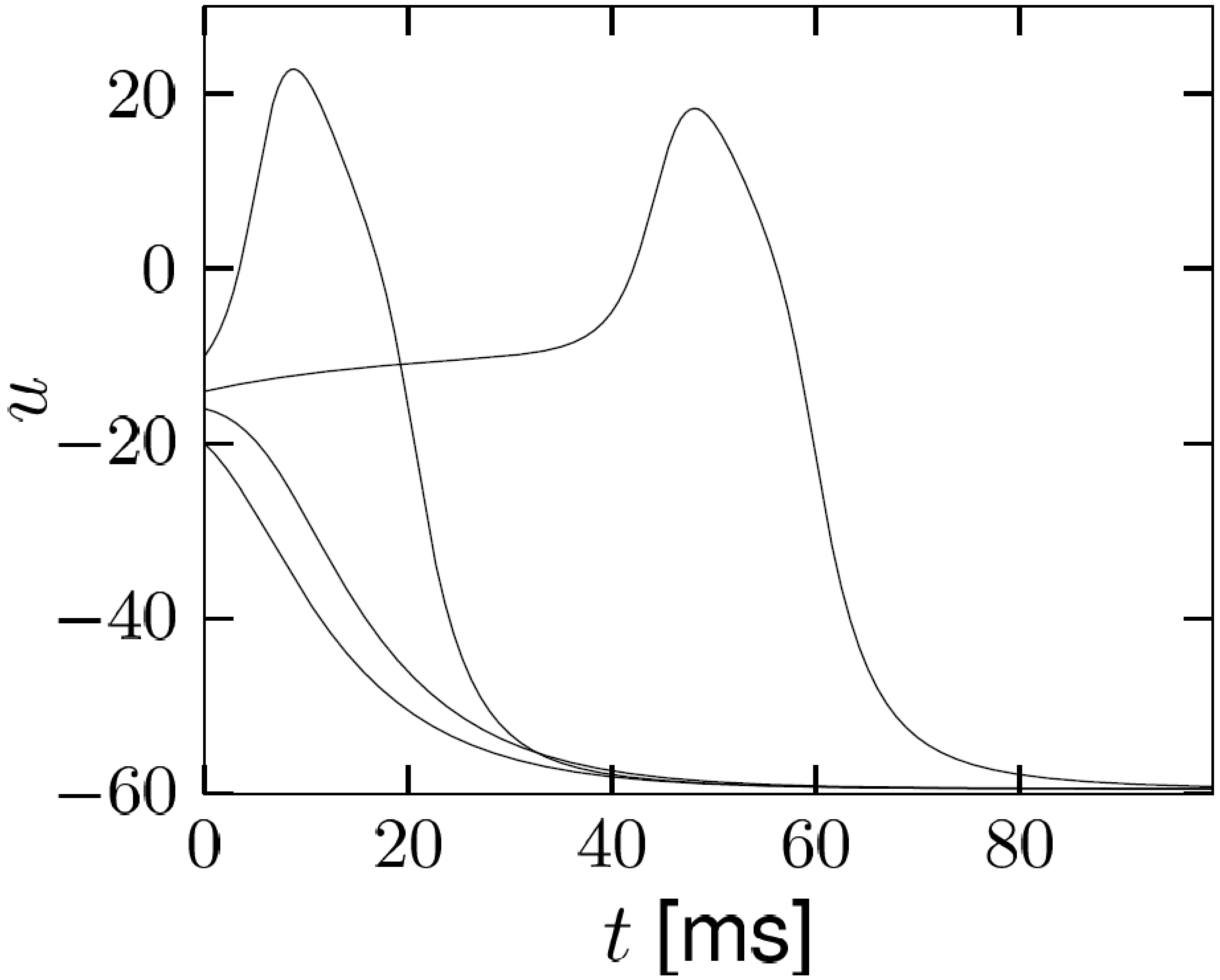


Stable manifold plays role of 'Threshold' (for pulse input)

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

4.3 Type I model: Delayed spike initation for Pulse input





Delayed spike initiation close to ‘Threshold’ (for pulse input)

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

Week 4– Quiz 4.2.

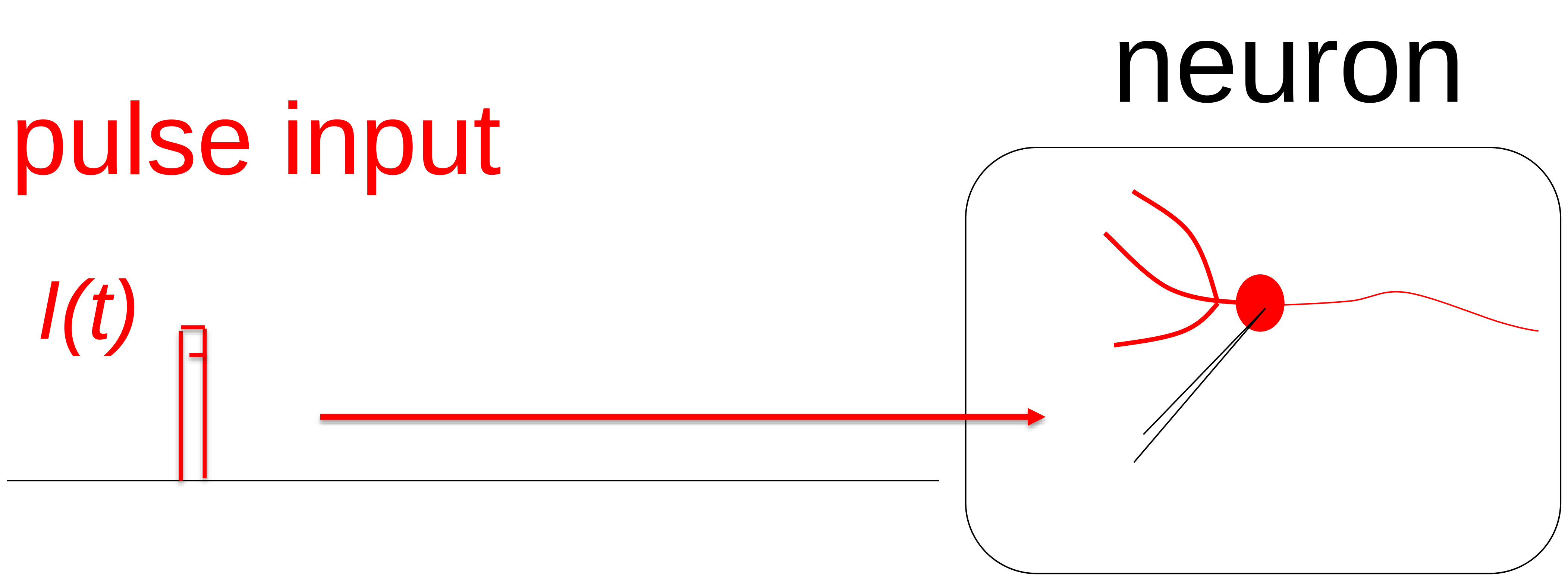
A. Threshold in a 2-dimensional neuron model with saddle-node bifurcation

[ ] The voltage threshold for repetitive firing is always the same as the voltage threshold for pulse input.

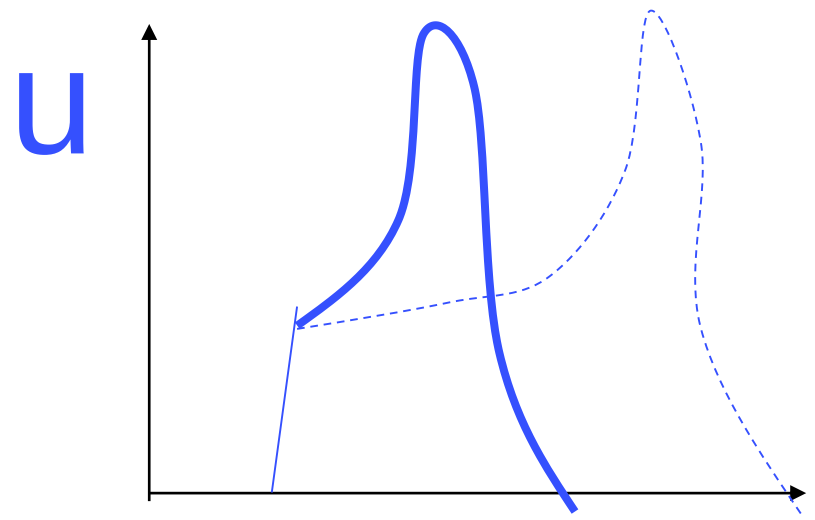
[ ] in the regime below the saddle-node bifurcation, the voltage threshold for repetitive firing is given by the stable manifold of the saddle.

[ ] in the regime below the saddle-node bifurcation, the voltage threshold for action potential firing in response to a short pulse input is given by the stable manifold of the saddle point.

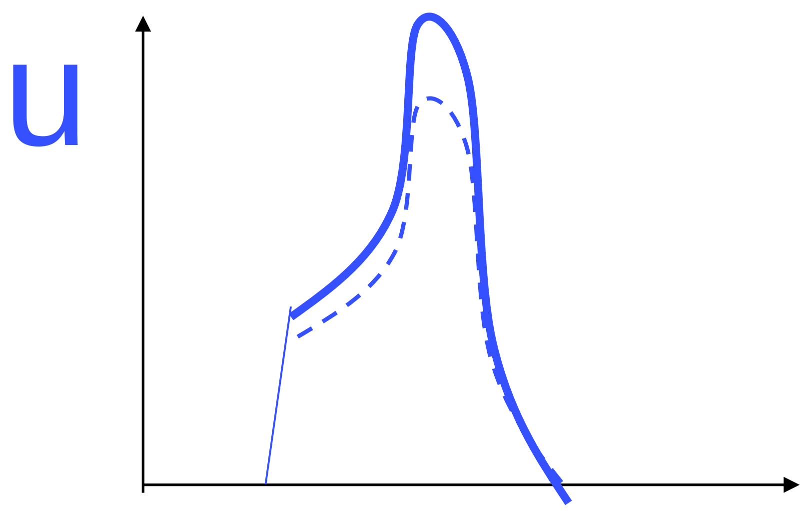
4.3 Threshold for pulse input in 2dim. Neuron Models



Delayed spike



Reduced amplitude



NOW: model with subc. Hopf

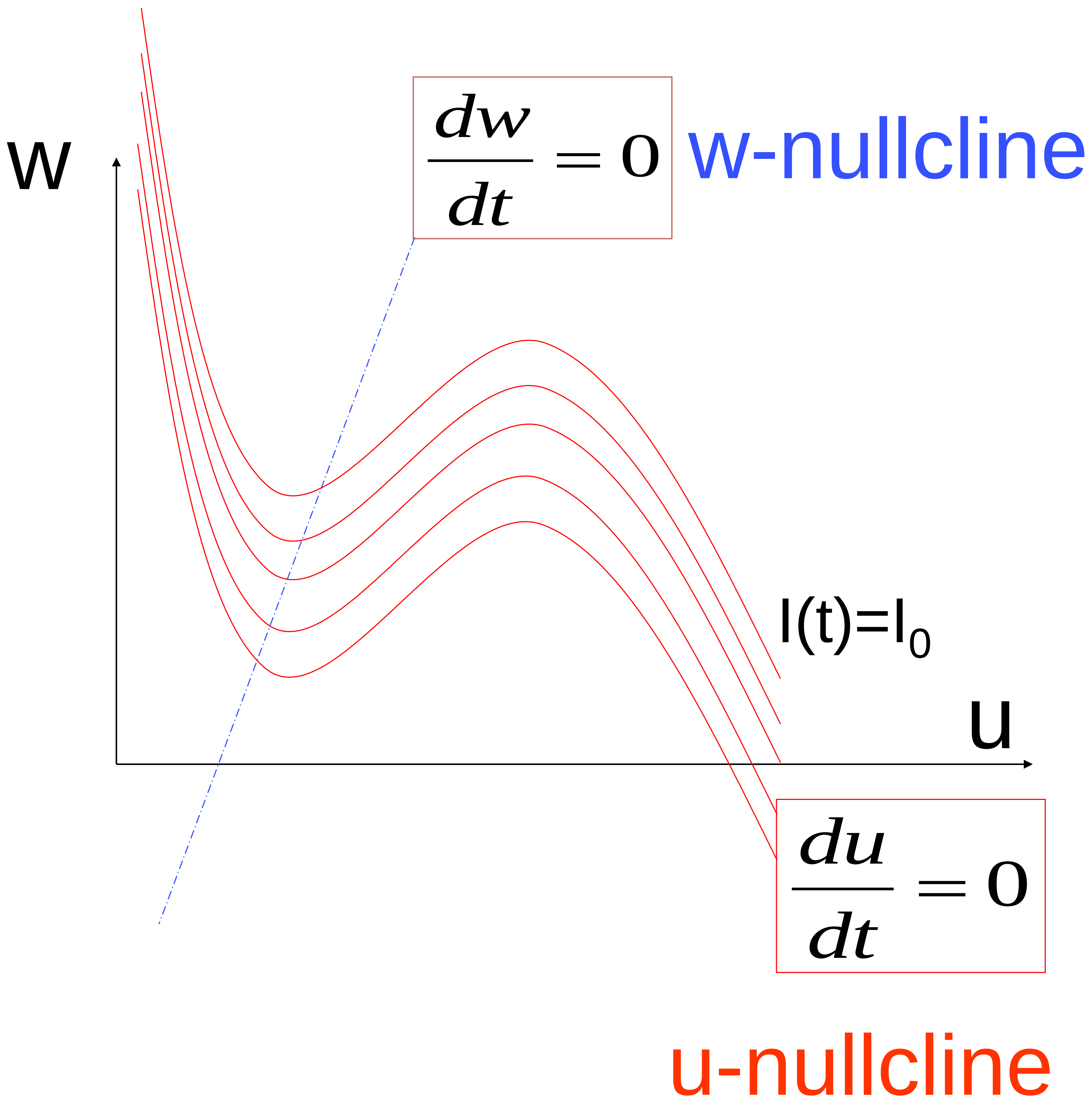
Review from 4.1: FitzHugh-Nagumo Model: Hopf bifurcation

stimulus

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

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

apply constant stimulus I_0



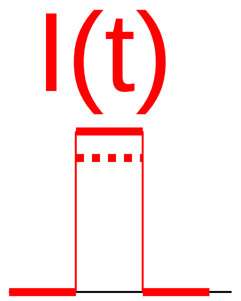
4.3 FitzHugh-Nagumo Model with pulse input

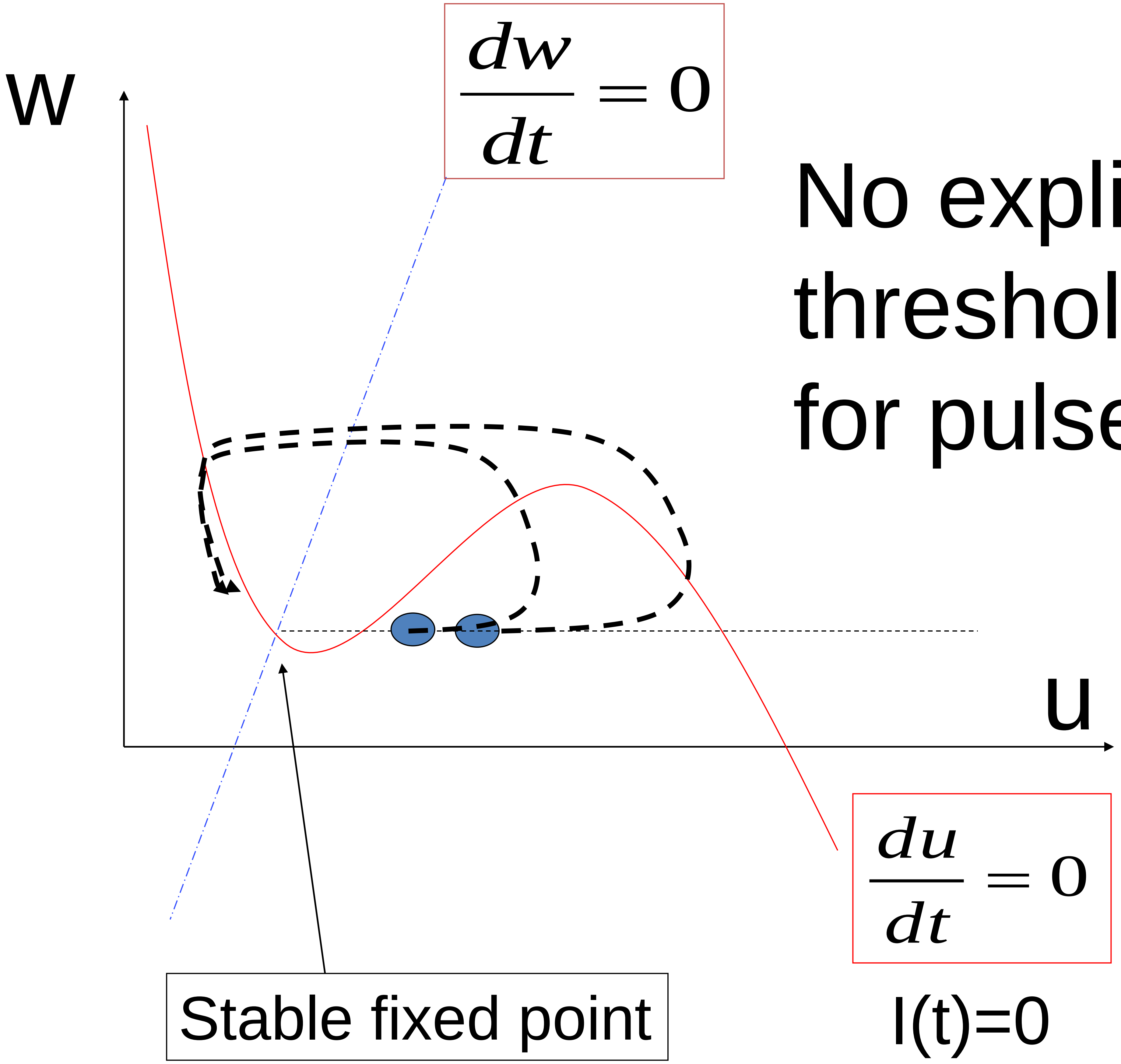
stimulus

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

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

pulse input





No explicit threshold for pulse input

Biological Modeling of Neural Networks

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Week 4

Reducing detail:

Analysis of 2D models

√ 3.1 **From Hodgkin-Huxley to 2D**

√ 3.2 **Phase Plane Analysis**

√ 3.3 **Analysis of a 2D Neuron Model**

4.1 Separation of time scales

4.2 Type I and II Neuron Models

- limit cycles: constant input

4.3 Pulse input

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

4.4. Further reduction to 1 dim

- nonlinear integrate-and-fire (again)

4.3 Separation of time scales, example FitzHugh-Nagumo Model

stimulus

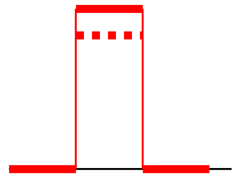
$$\tau \frac{du}{dt} = F(u,w) + RI(t)$$

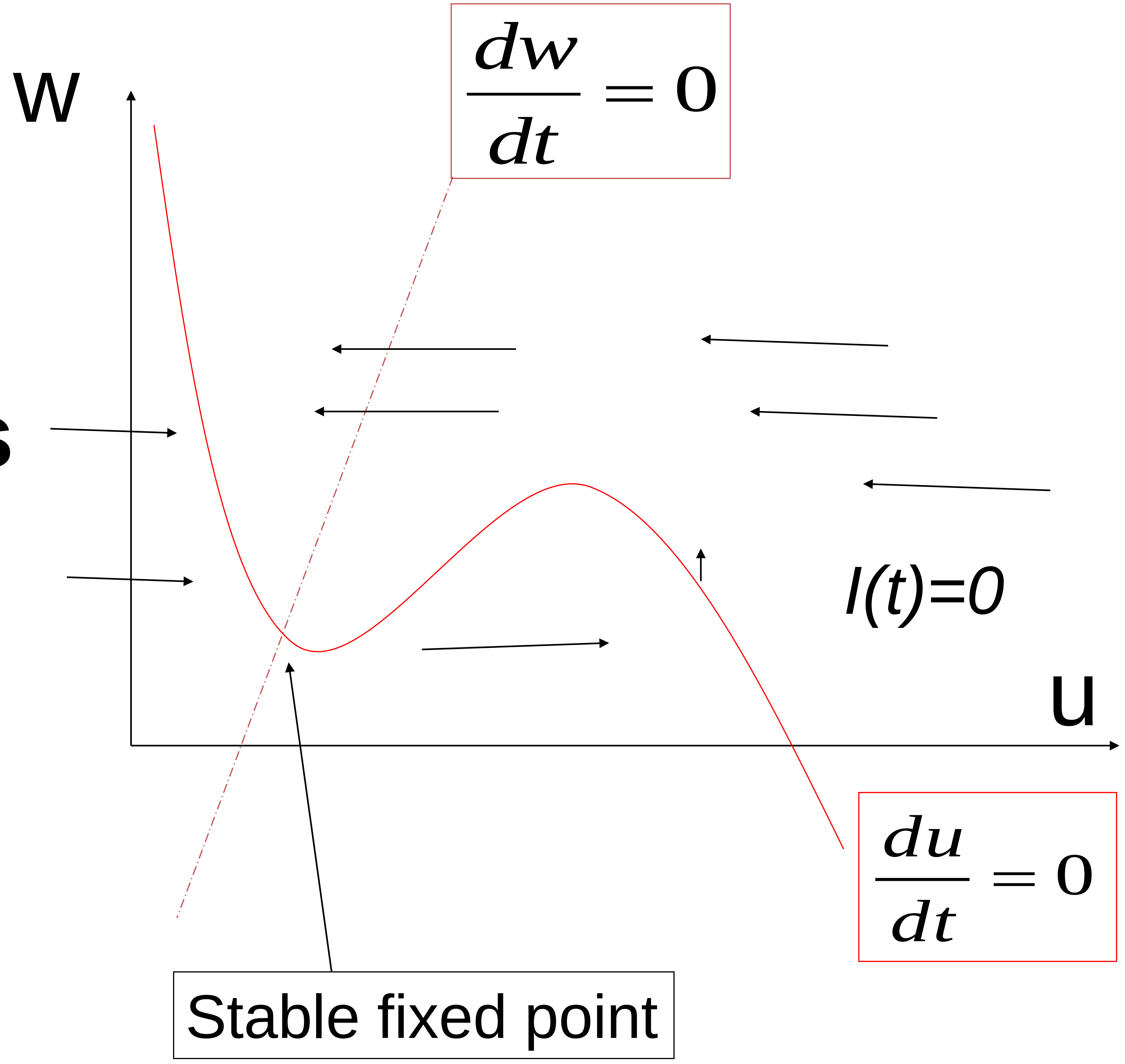
$$\tau_w \frac{dw}{dt} = G(u,w)$$

Separation of time scales

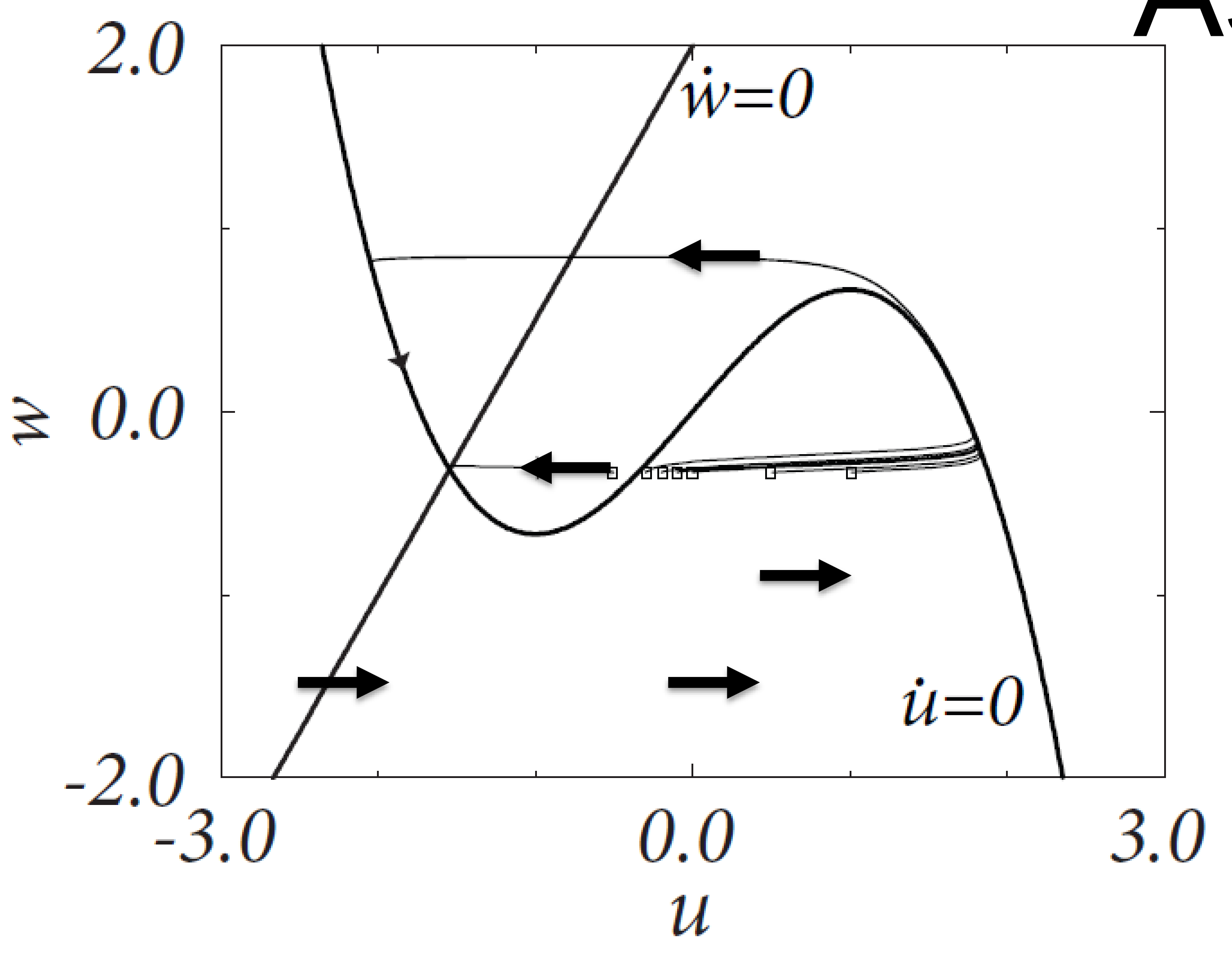
pulse input $\tau_w >> \tau_u$

I(t)



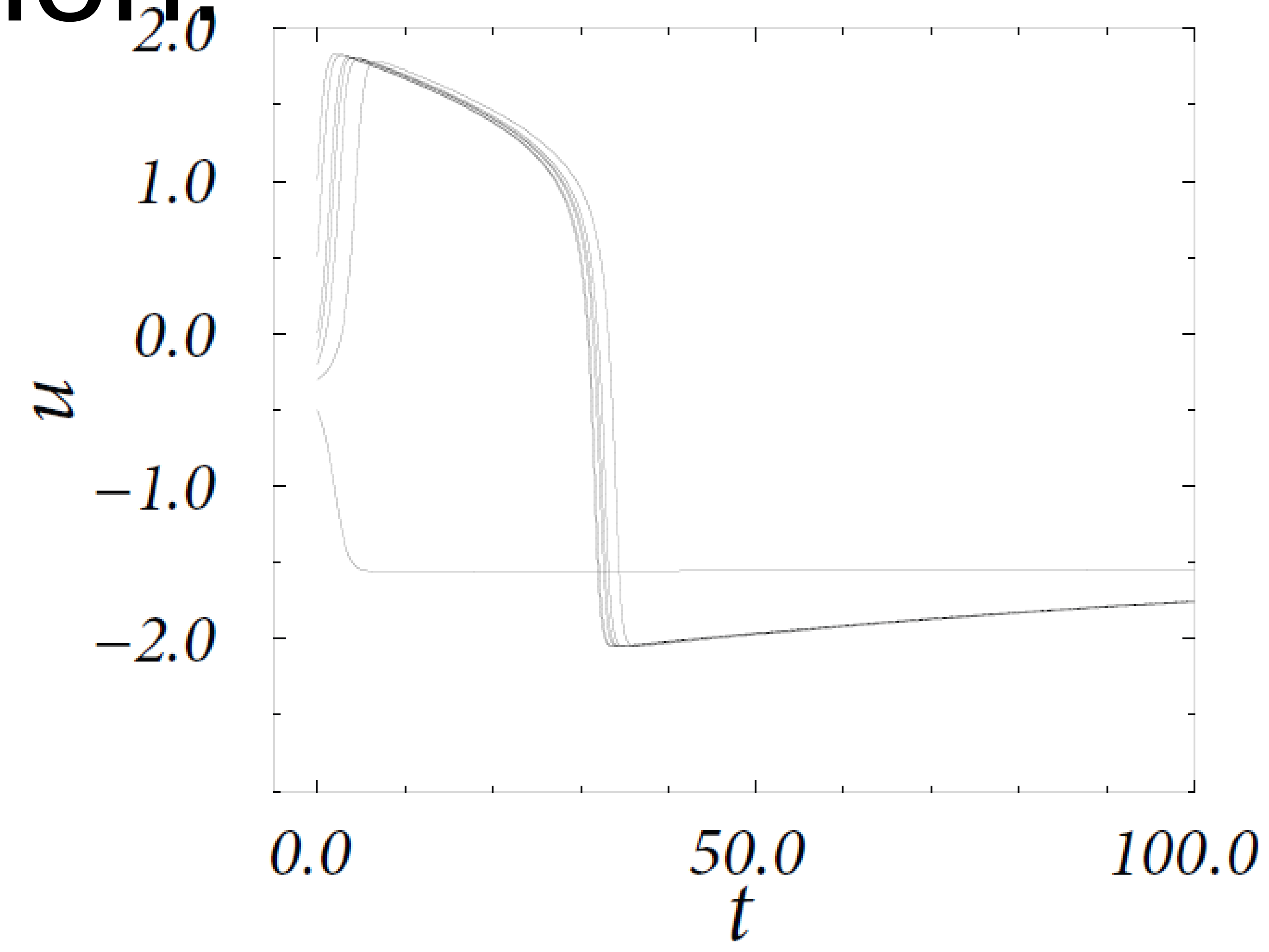


4.3 FitzHugh-Nagumo model: Threshold for Pulse input



Assumption:

$\tau_w >> \tau_u$



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

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

4.3 Detour: Separation fo time scales in 2dim models

stimulus

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

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

Assumption:

$$\tau_w >> \tau_u$$

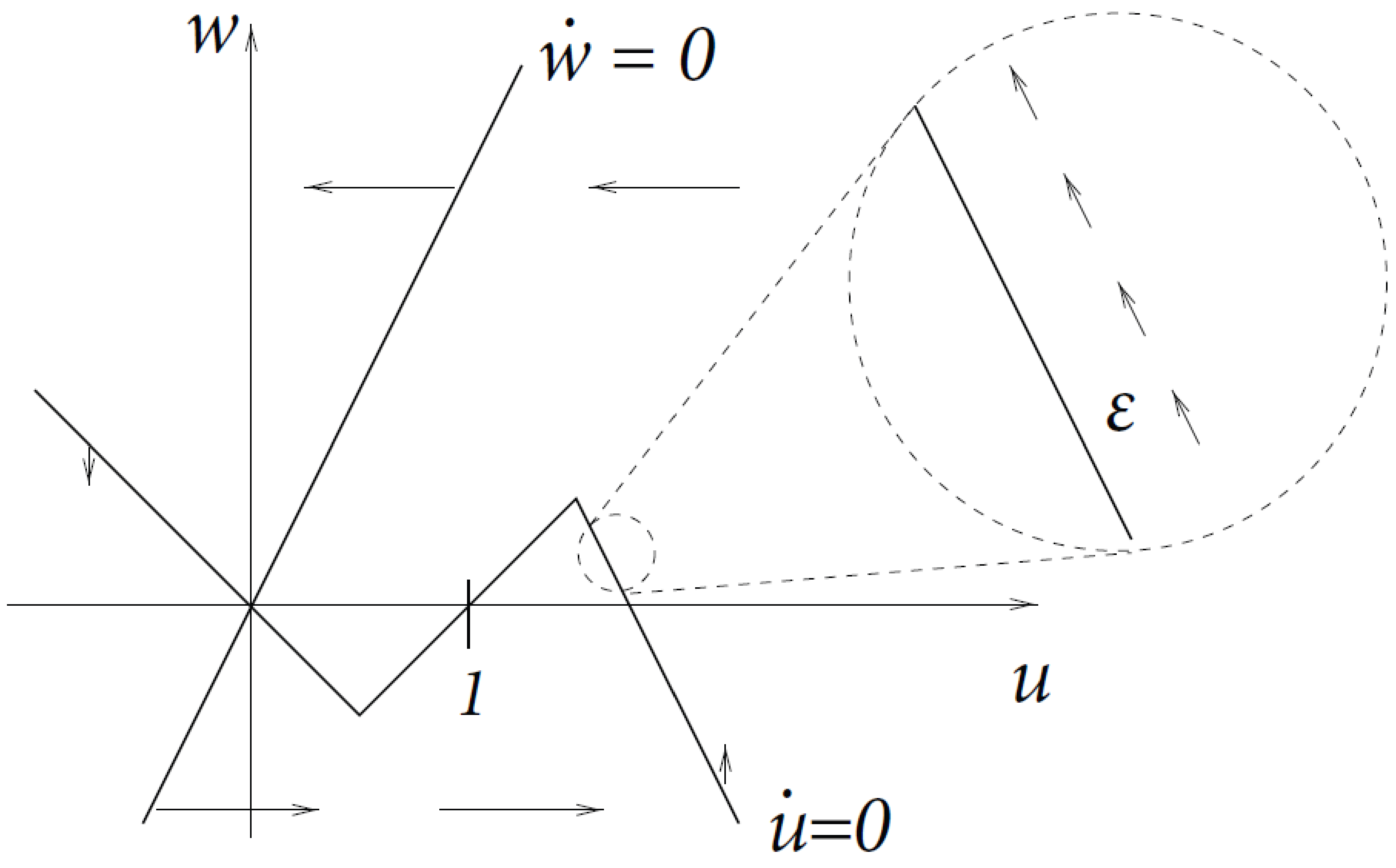
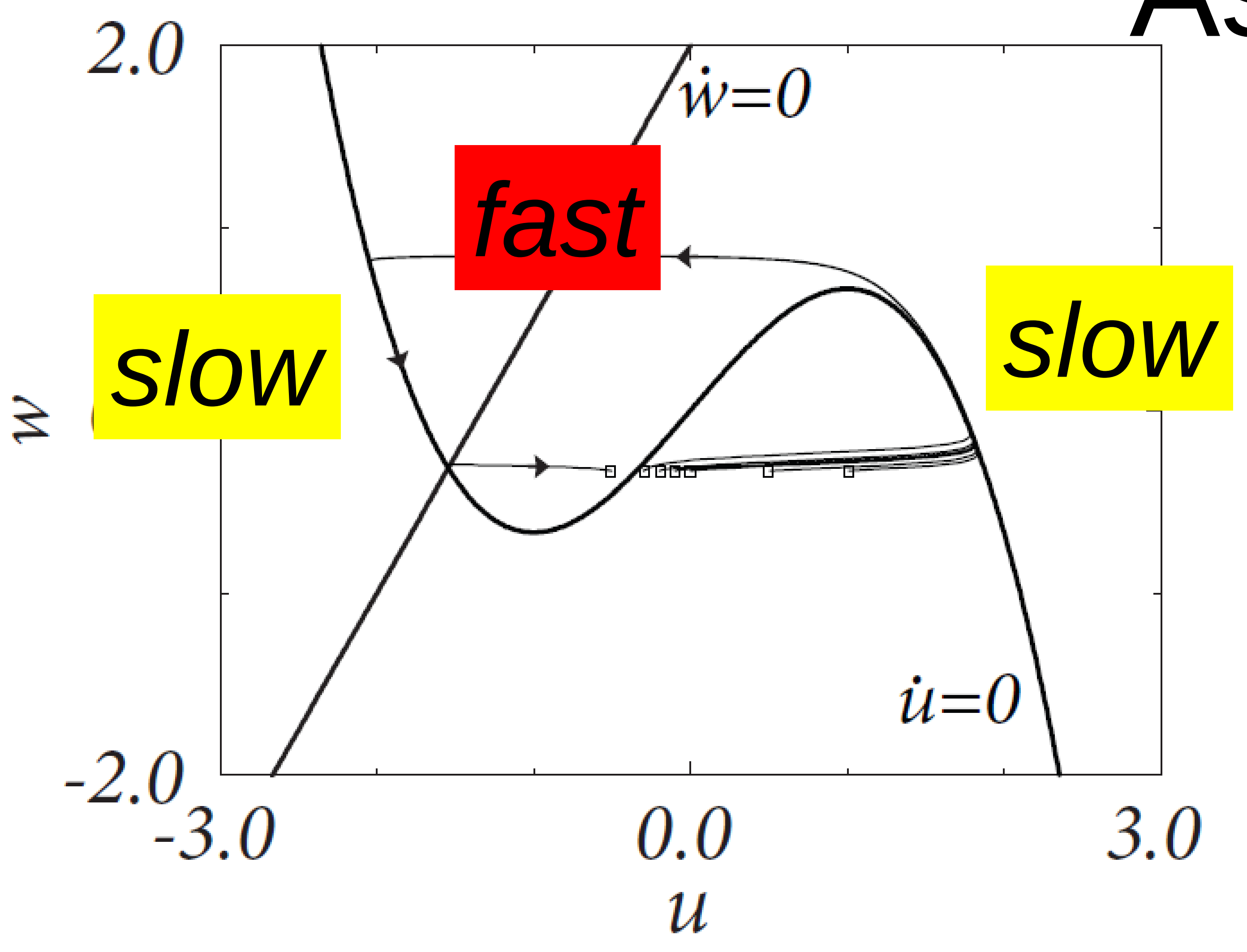


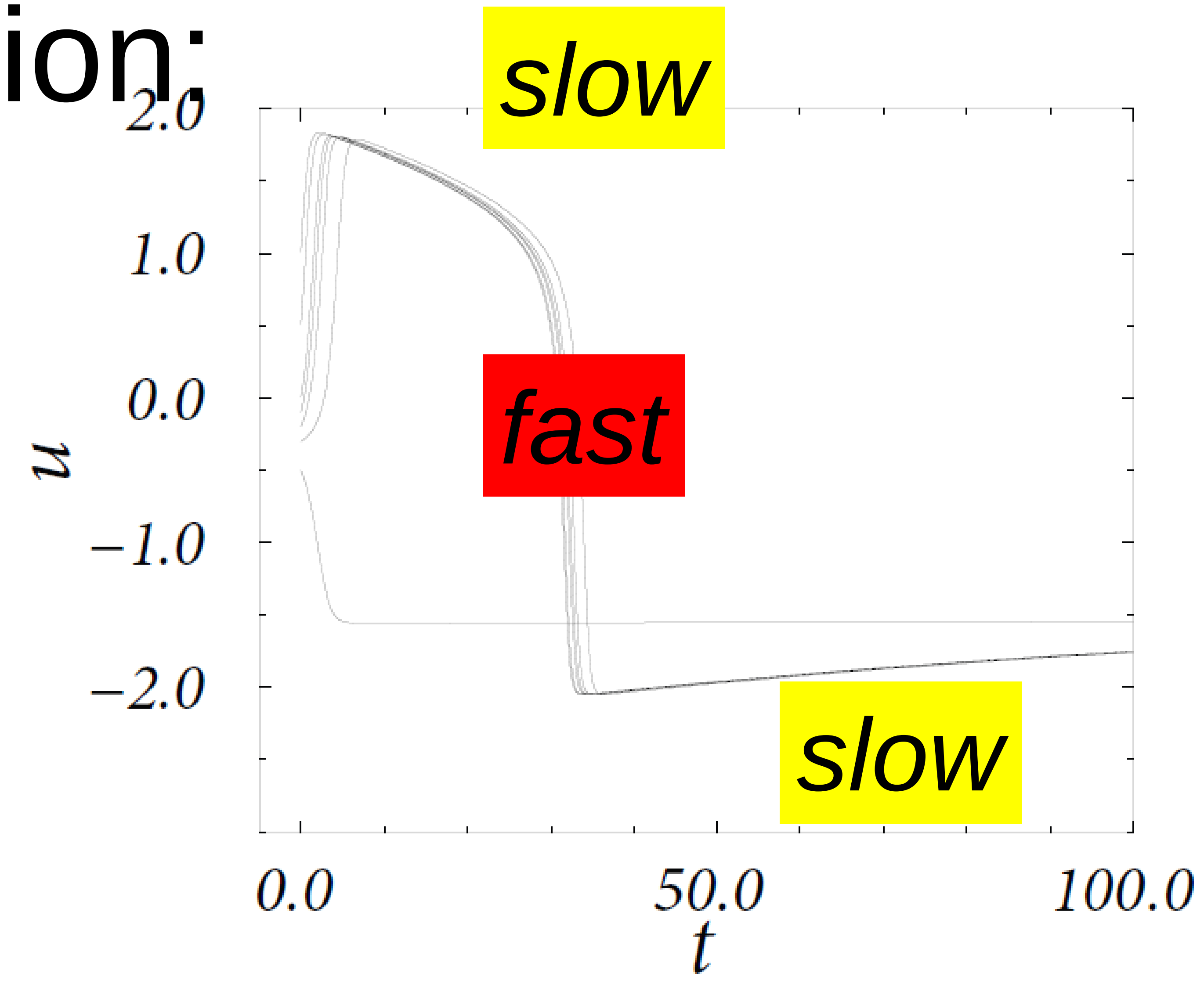
Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014)

4.3 FitzHugh-Nagumo model: Threshold for Pulse input



Assumption:

$$\tau_w >> \tau_u$$



trajectory

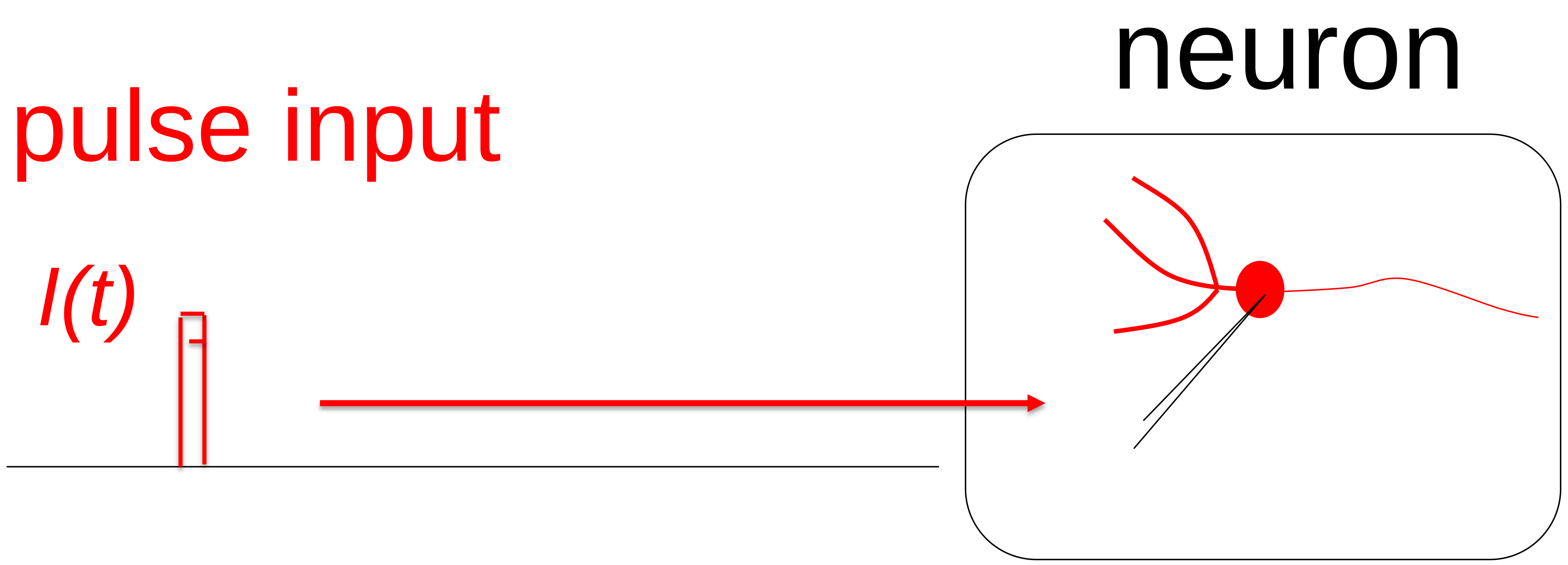
-follows u-nullcline: slow

-jumps between branches: fast

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

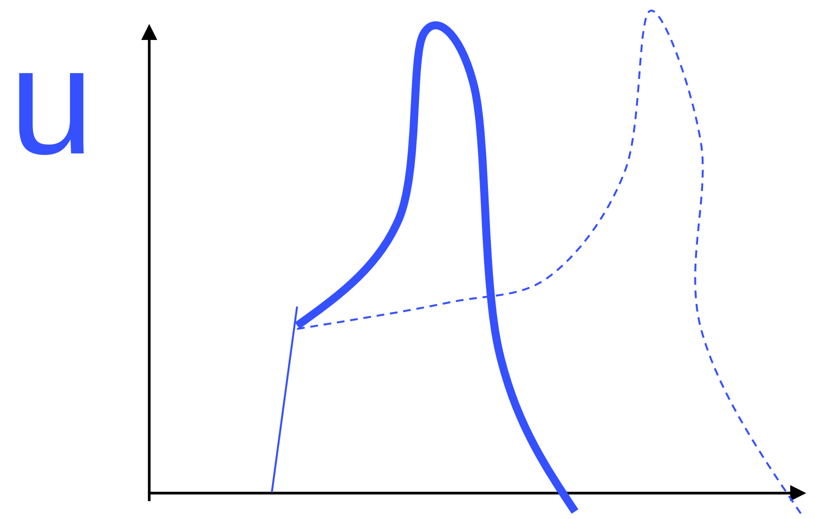
4.2 Threshold for pulse input in 2dim. Neuron Models

Biological input scenario

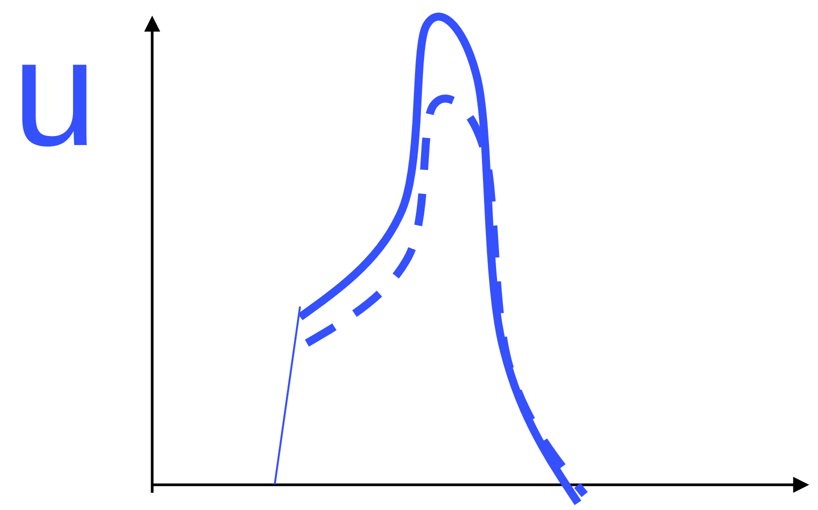


Mathematical explanation:
Graphical analysis in 2D

Delayed spike



Reduced amplitude



Week 4– Quiz 4.3.

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

[ ] in the regime below the Hopf bifurcation, the voltage threshold for action potential firing in response to a short pulse input is the middle branch of the u-nullcline.

[ ] in the regime below the bifurcation, a voltage threshold for action potential firing in response to a short pulse input exists only if $\tau_w >> \tau_u$

4.3. Summary: Pulse input and thresholds

Neuron models with Saddle-node-onto limit cycle bifurcation have

- a smooth f-I curve
- a well-defined threshold for pulse input: either and AP occurs or not.
- Transition from subthreshold to superthreshold happens via an AP with very large delay.

Neuron models with subcritical Hopf-bifurcation have

- a non-smooth f-I curve
- not a well-defined voltage: there is a small regime where AP transforms into non-AP
- However, together with a separation of time scale, the middle branch of the u-nullcline acts as a voltage threshold.

The END

The END

Biological Modeling of Neural Networks

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4.1 Separation of time scales

4.2 Type I and II Neuron Models

- limit cycles: constant input

4.3 Pulse input

- where is the firing threshold?

4.4. Further reduction to 1 dim

- nonlinear integrate-and-fire (again)

4.4. Further reduction to 1 dimension

stimulus

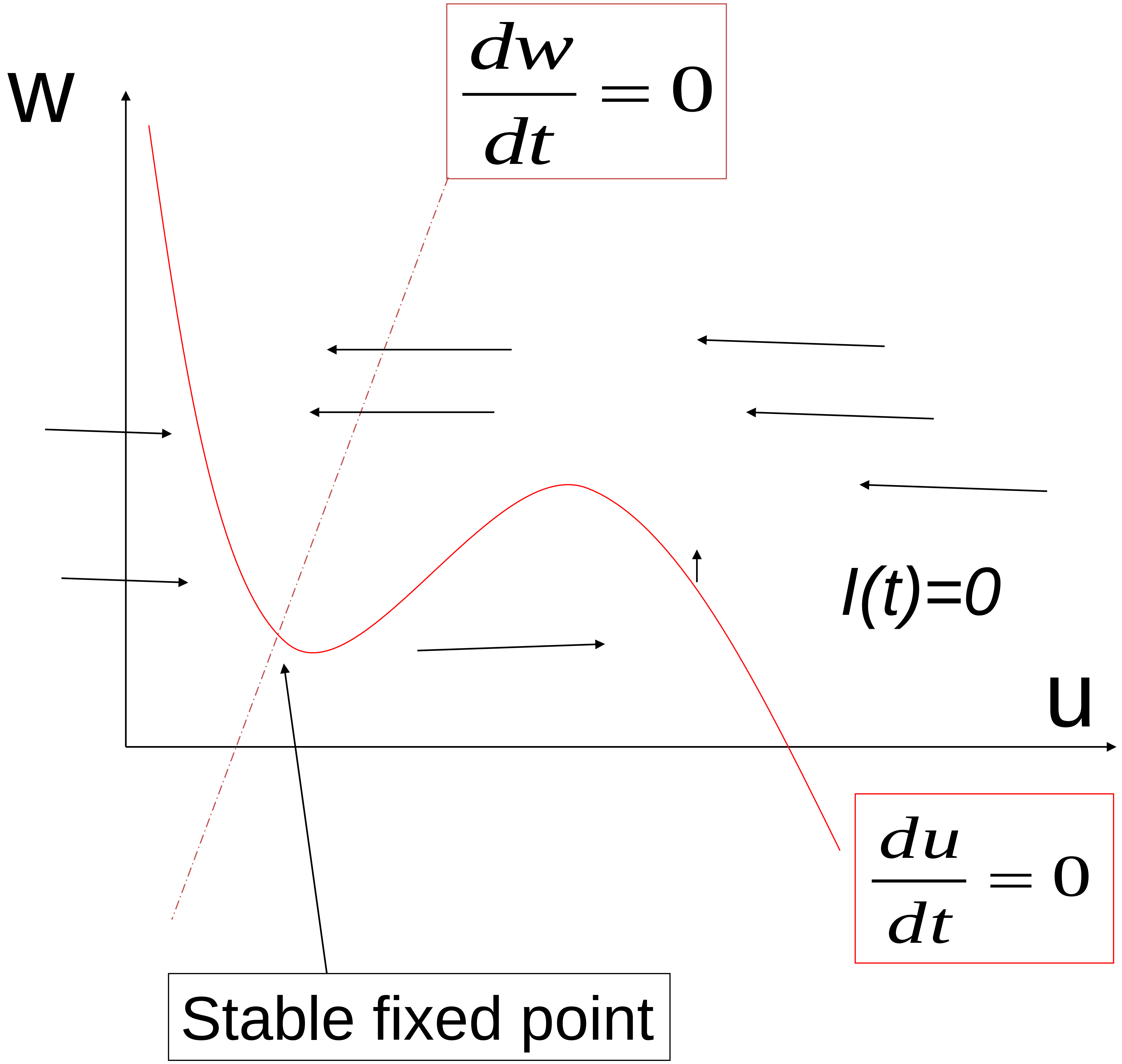
$$\tau \frac{du}{dt} = F(u,w) + I(t)$$

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

Separation of time scales

$$\tau_w >> \tau_u$$

→ Flux nearly horizontal



4.4. 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)

4.4. Further reduction to 1 dimension

Hodgkin-Huxley reduced to 2dim

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

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

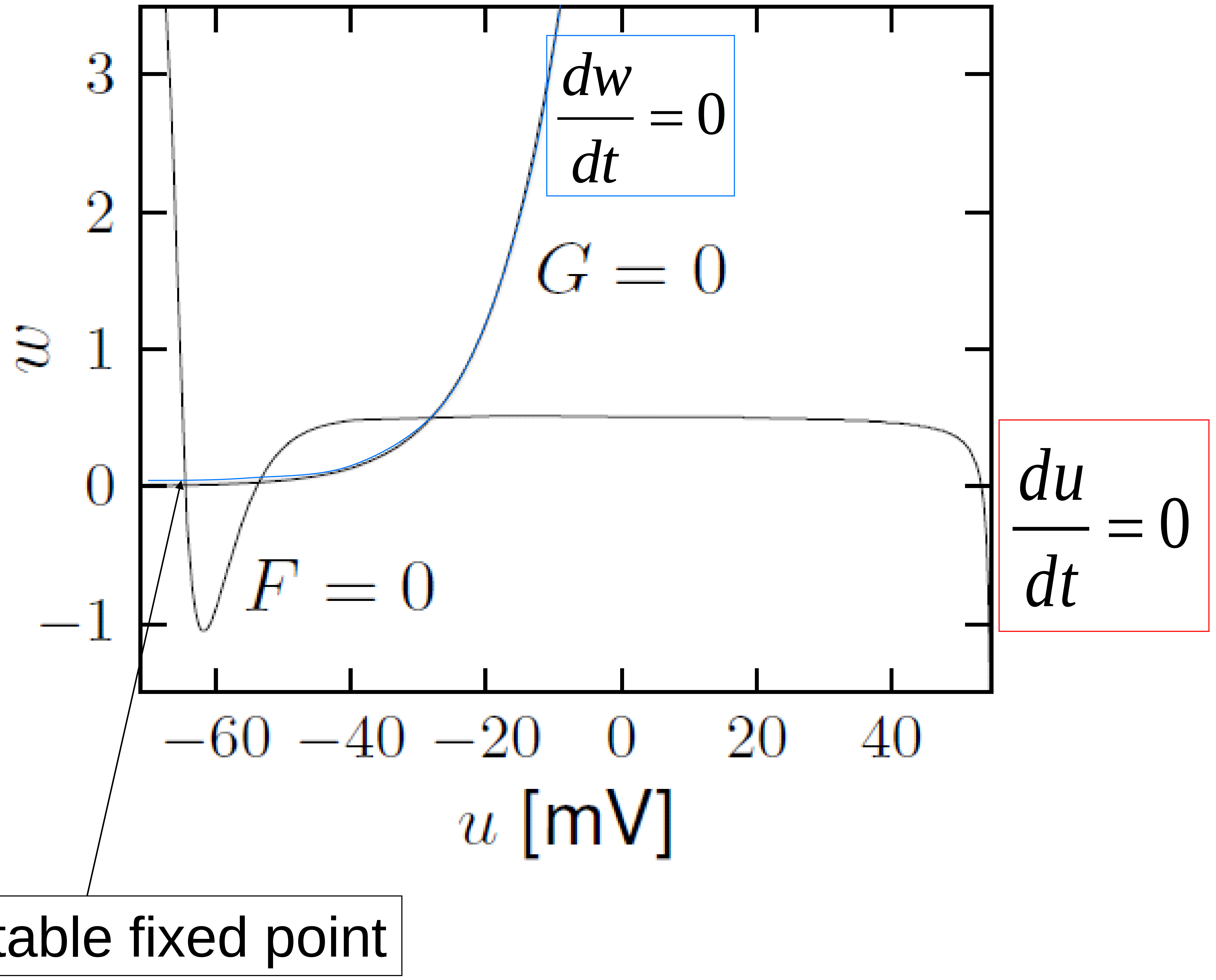
Separation of time scales

$$\tau_w >> \tau_u$$

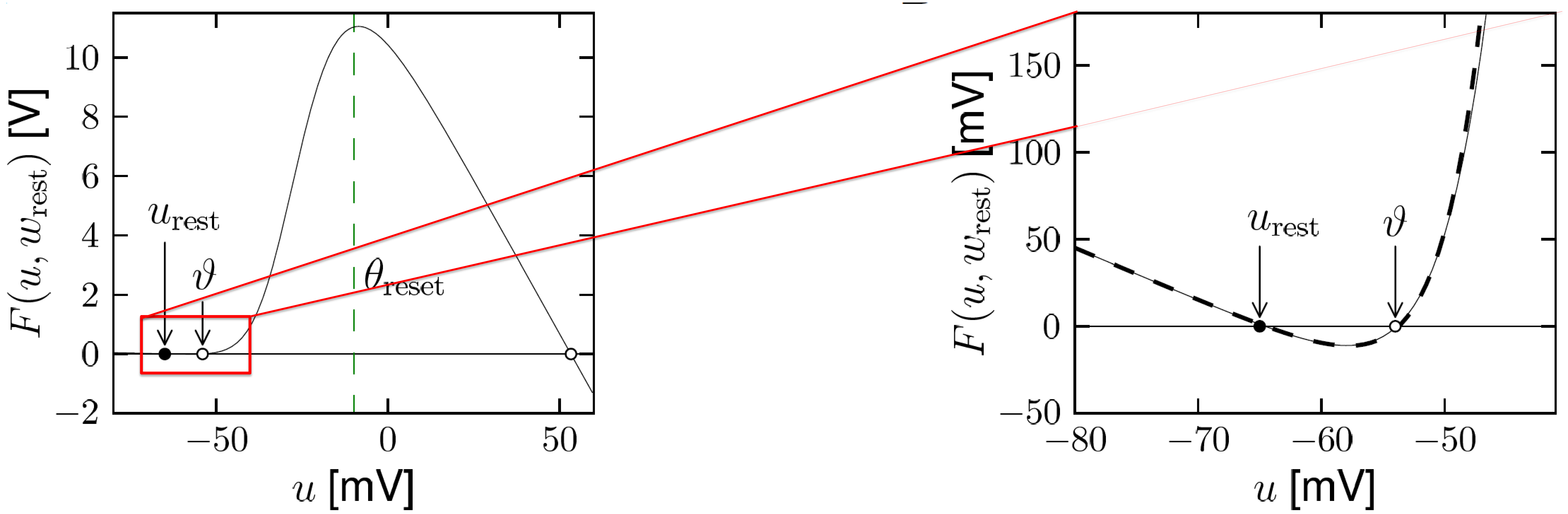
$$\tau_w \frac{dw}{dt} \approx 0 \rightarrow \; w \approx w_{rest}$$

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

← During preparation/initation of spike



4.4. Spike initiation: Nonlinear Integrate-and-Fire Model



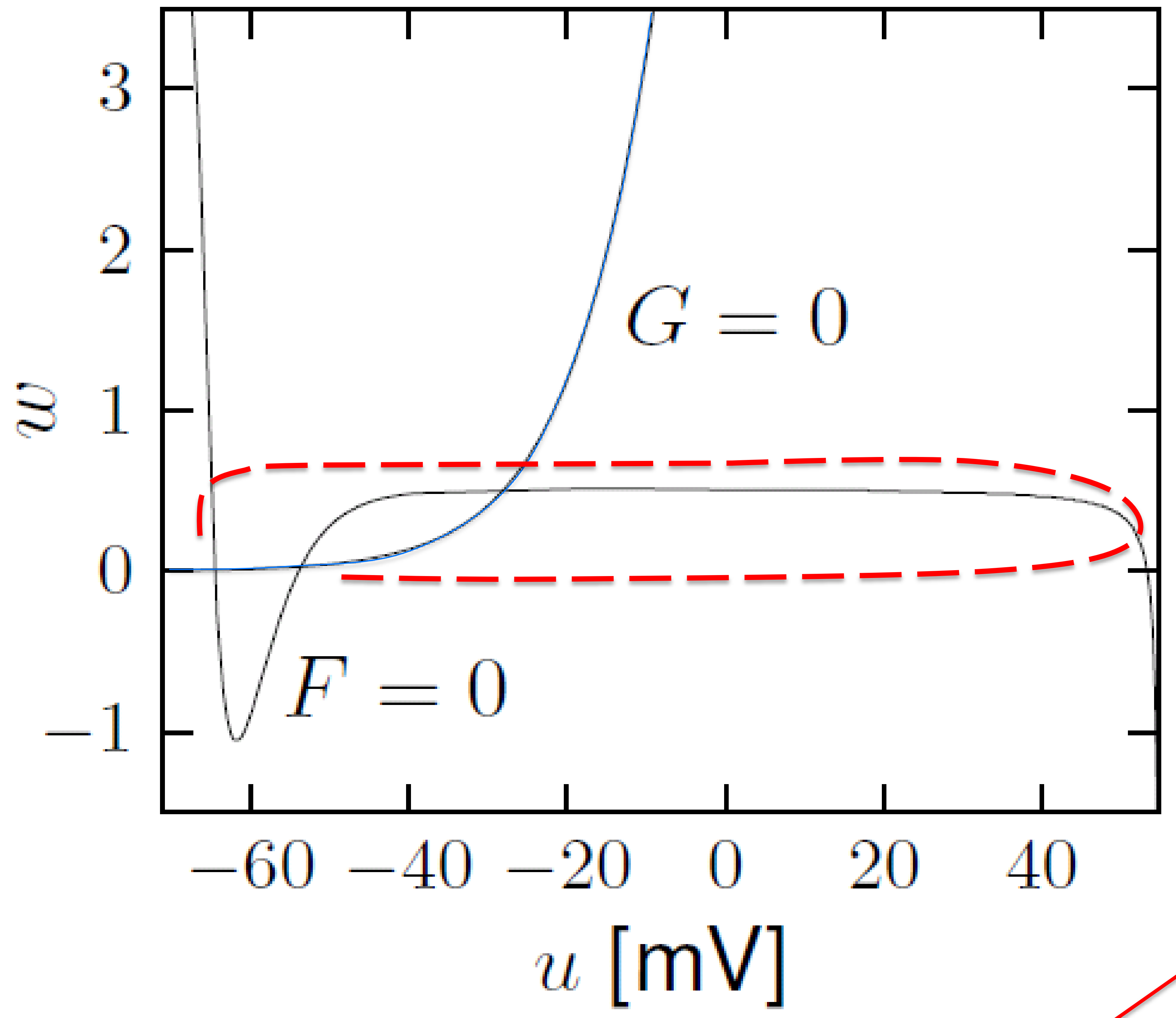
$$\tau \frac{du}{dt} = F(u, w_{rest}) + RI(t) = f(u) + RI(t)$$

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

→ Nonlinear I&F (see week 1!)

During spike initiation, the 2D models with separation of time scales can be reduced to a 1D model equivalent to nonlinear integrate-and-fire

4.4. 2D model, after spike initiation



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)

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

Integrate-and-fire: threshold+reset for AP

4.4. From 2D to Nonlinear Integrate-and-Fire Model

2-dimensional equation

2dimensional Model

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

Relevant during spike and downswing of AP →

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

Separation of time scales

-w is constant (if not firing)

Nonlinear Integrate-and-Fire Model

w-dynamics replaced by Threshold and reset in Integrate-and-ire

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

↑ Linear plus exponential

Neuronal Dynamics – Literature for week 3 and 4.1

Reading: W. Gerstner, W.M. Kistler, R. Naud and L. Paninski,
Neuronal Dynamics: from single neurons to networks and models of cognition. Chapter 4 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.

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)

4.3. Nonlinear Integrate-and-Fire Model

Exponential integrate-and-fire model (EIF)

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

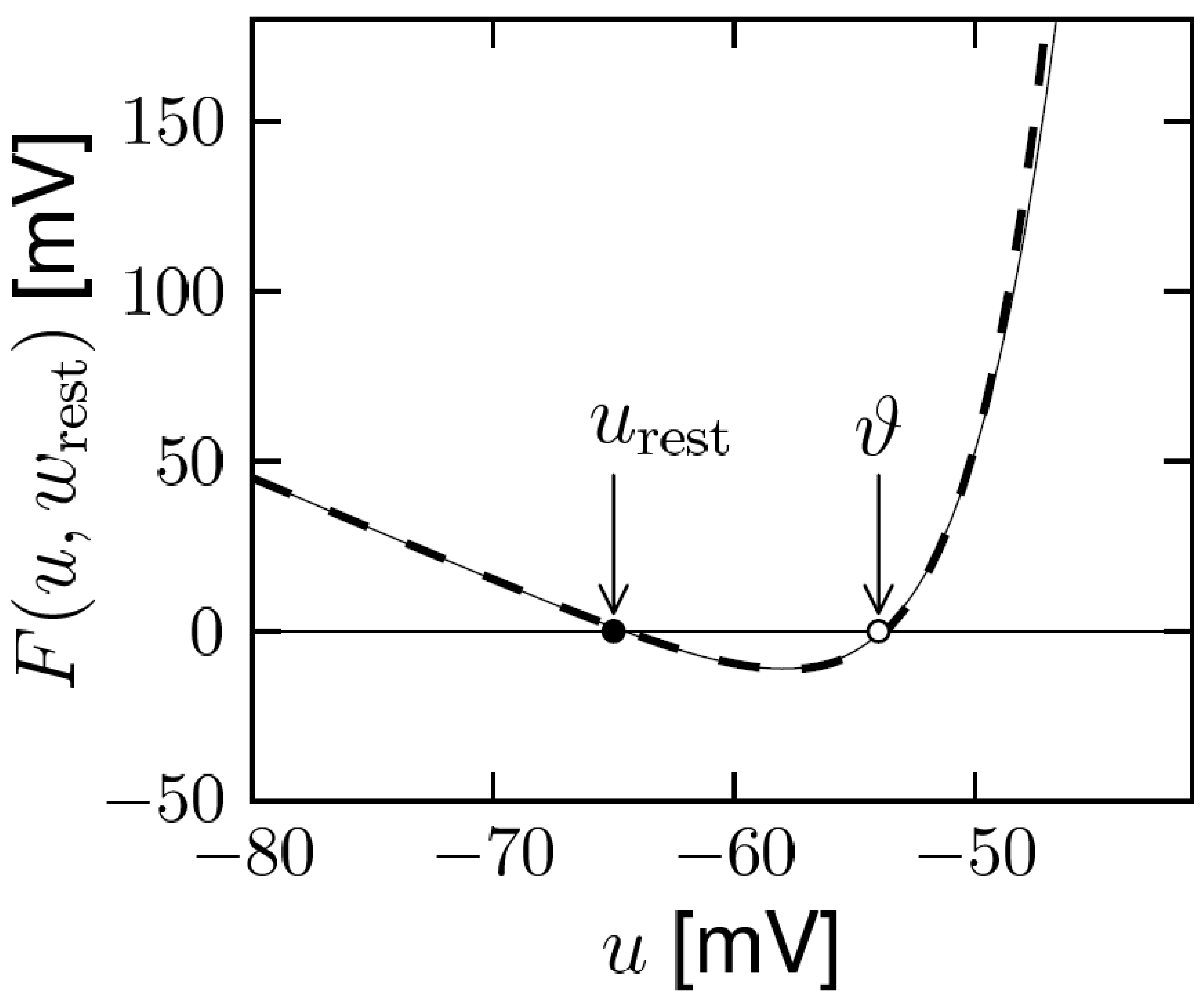


Image: Neuronal Dynamics, Gerstner et al., Cambridge Univ. Press (2014)

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

→ Nonlinear I&F (see week 1!)

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

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

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

gives expon. I&F

Neuronal Dynamics – Quiz 4.3.

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