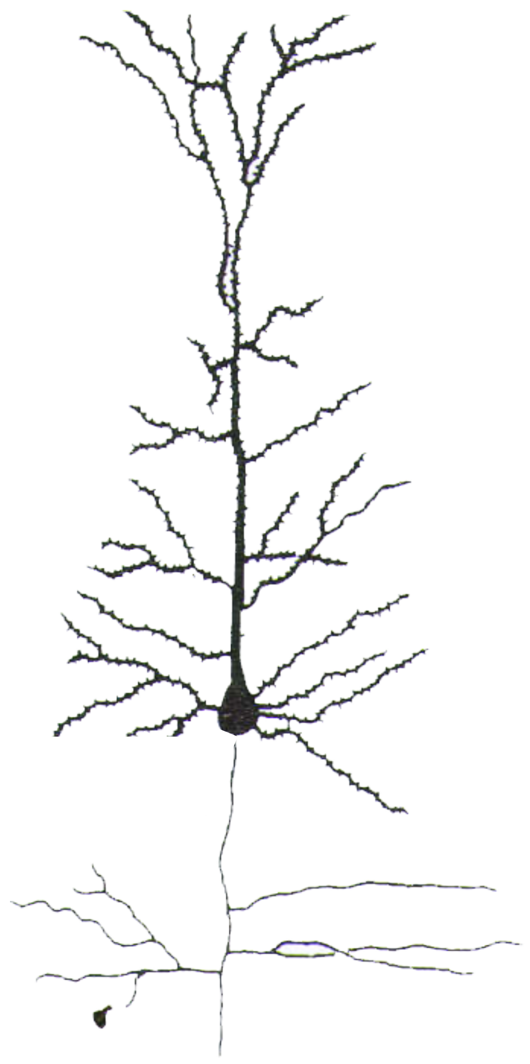

Tim Vogels

The deep down basics of (computational) neuroscience

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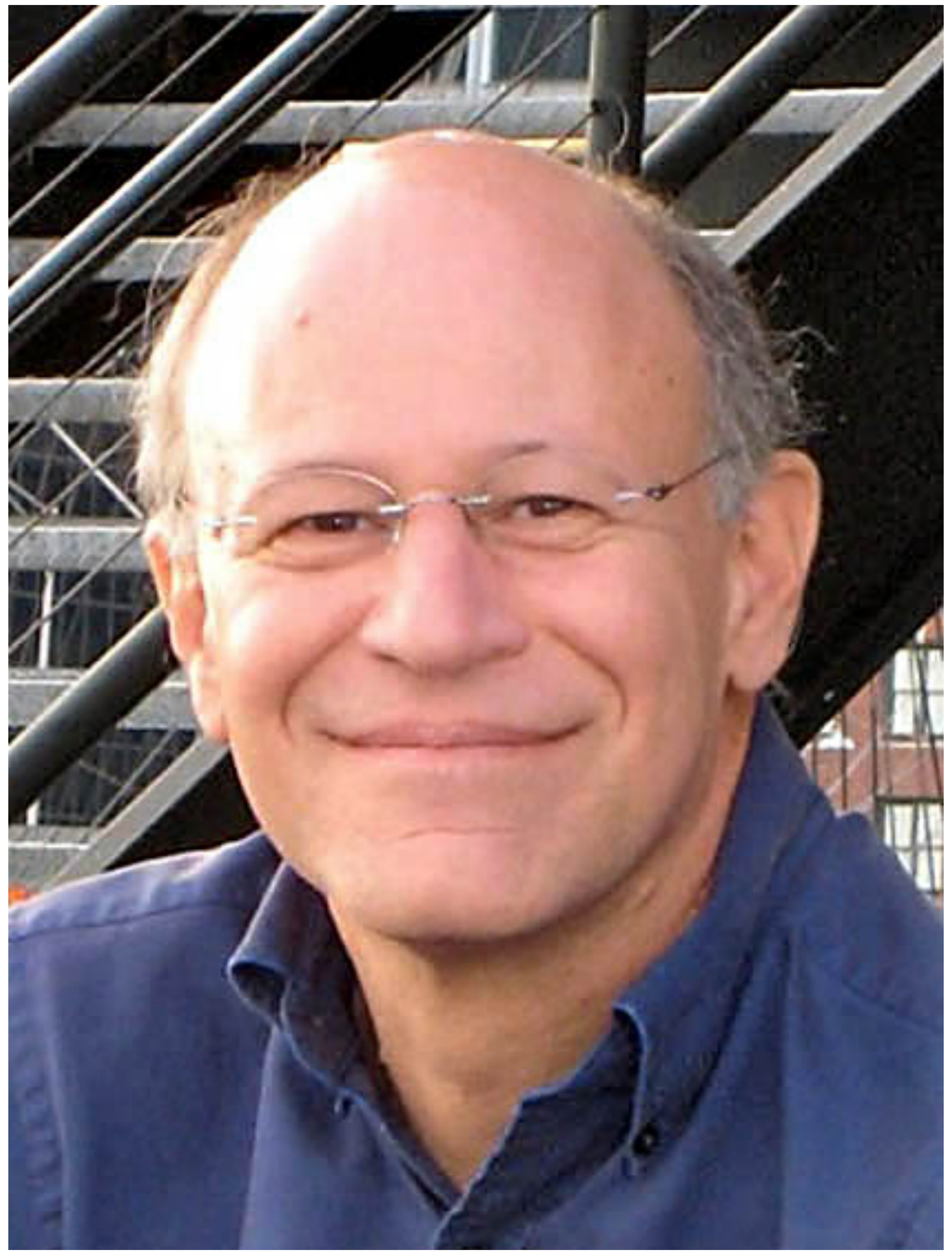

my science heros

my science heros

THE DEEP-DOWN BASICS OF COMPUTATIONAL NEUROSCIENCE

Imbizo 2022 - Your time.

Do

Learn - Network - Make friends.

Imbizo 2022 - Your time.

Do

Learn - Network - Make friends.

Sleep

Party

Talk

Ask

Shoot the shit

Make Memories

Know yourself and push yourself

Consume everything in moderation, even moderation

cell types: 50

# cell types:	50
# neurons:	100,000,000,000

# cell types:	50
# neurons:	100,000,000,000
# synapses	100,000,000,000,000

# cell types:	50
# neurons:	100,000,000,000
# synapses	100,000,000,000,000
# neuroscientists	80,000

# cell types:	50
# neurons:	100,000,000,000
# synapses	100,000,000,000,000
# neuroscientists	80,000
# neurotheorists	4,000

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# neuroquestions	

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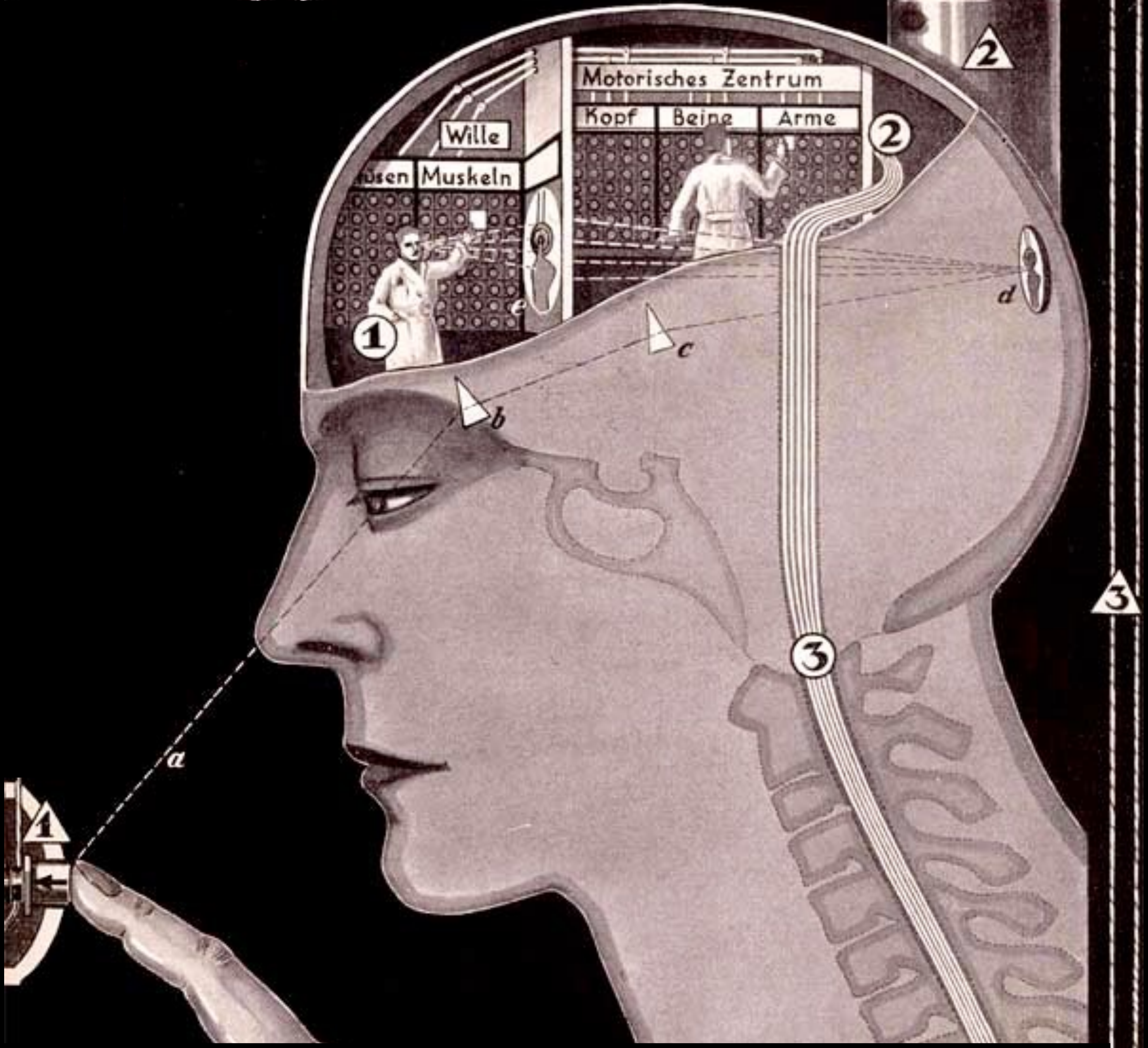
# neurotheorists	4,000
# neuroquestions	more than 4,000!!

The Neural Code:

- Representation
- Transmission
- Transformation
- Interpretation

Perkel and Bullock: Neurosciences Research Bulletin, 1968 • 6: 219-349



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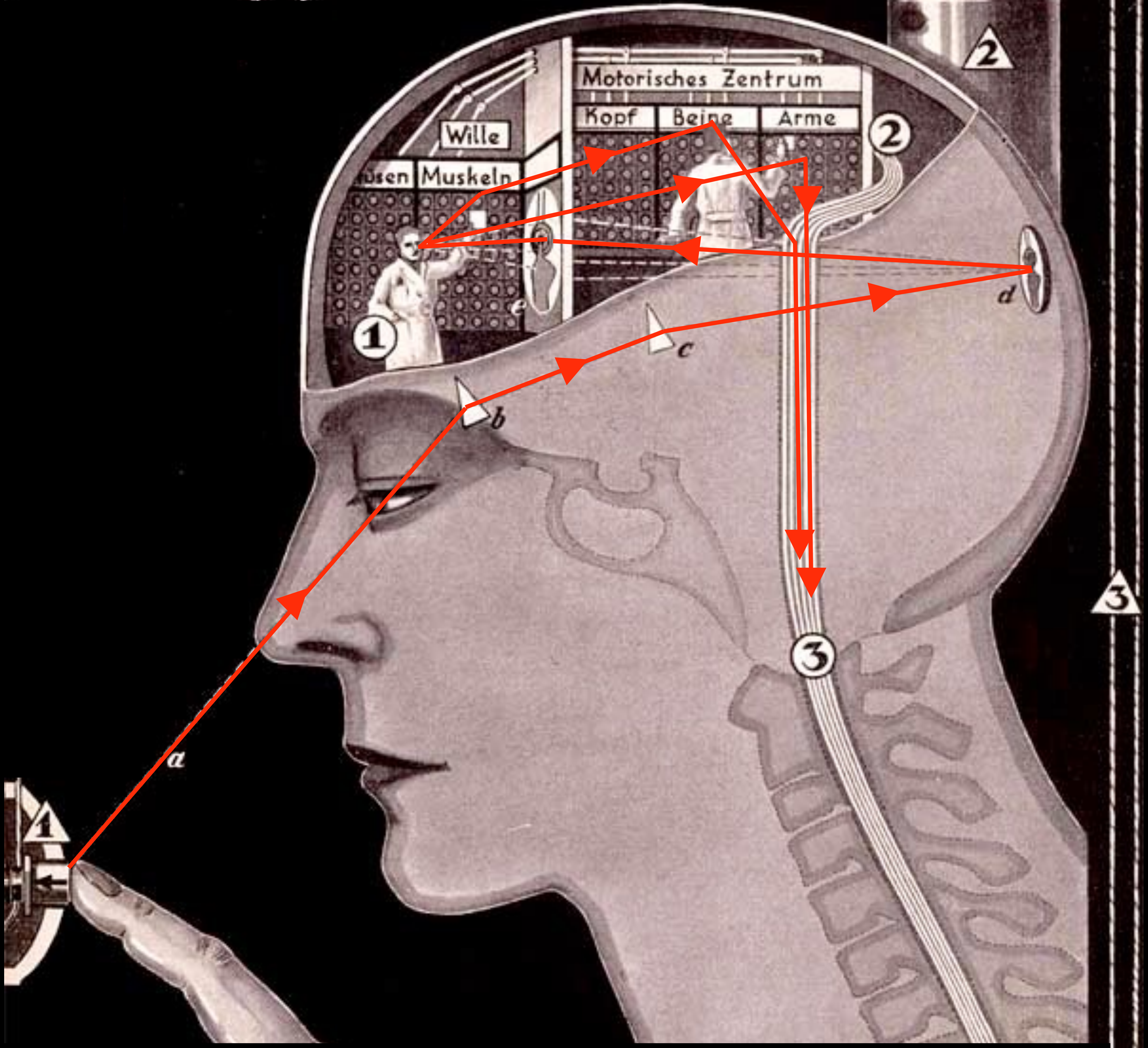

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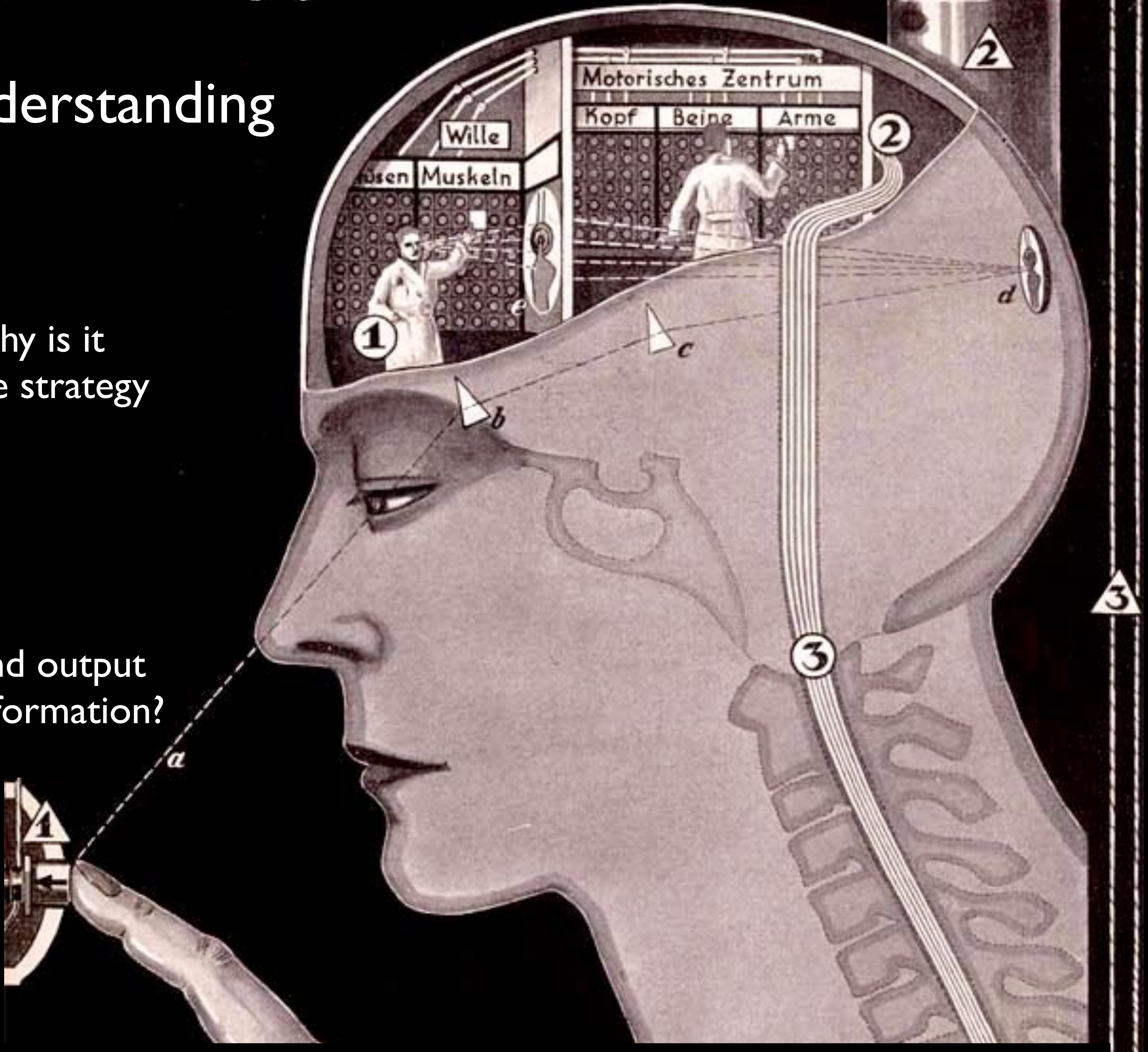
David Marr’s levels of understanding (1982)

Computational theory
What is the goal of the computation, why is it appropriate, and what is the logic of the strategy by which it can be carried out?

Representation and algorithm
How can this computational theory be implemented?
What is the representation for input and output and what is the algorithm for the transformation?

Implementation
How can the representation and algorithm be realised physically?



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Systems

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Neurons

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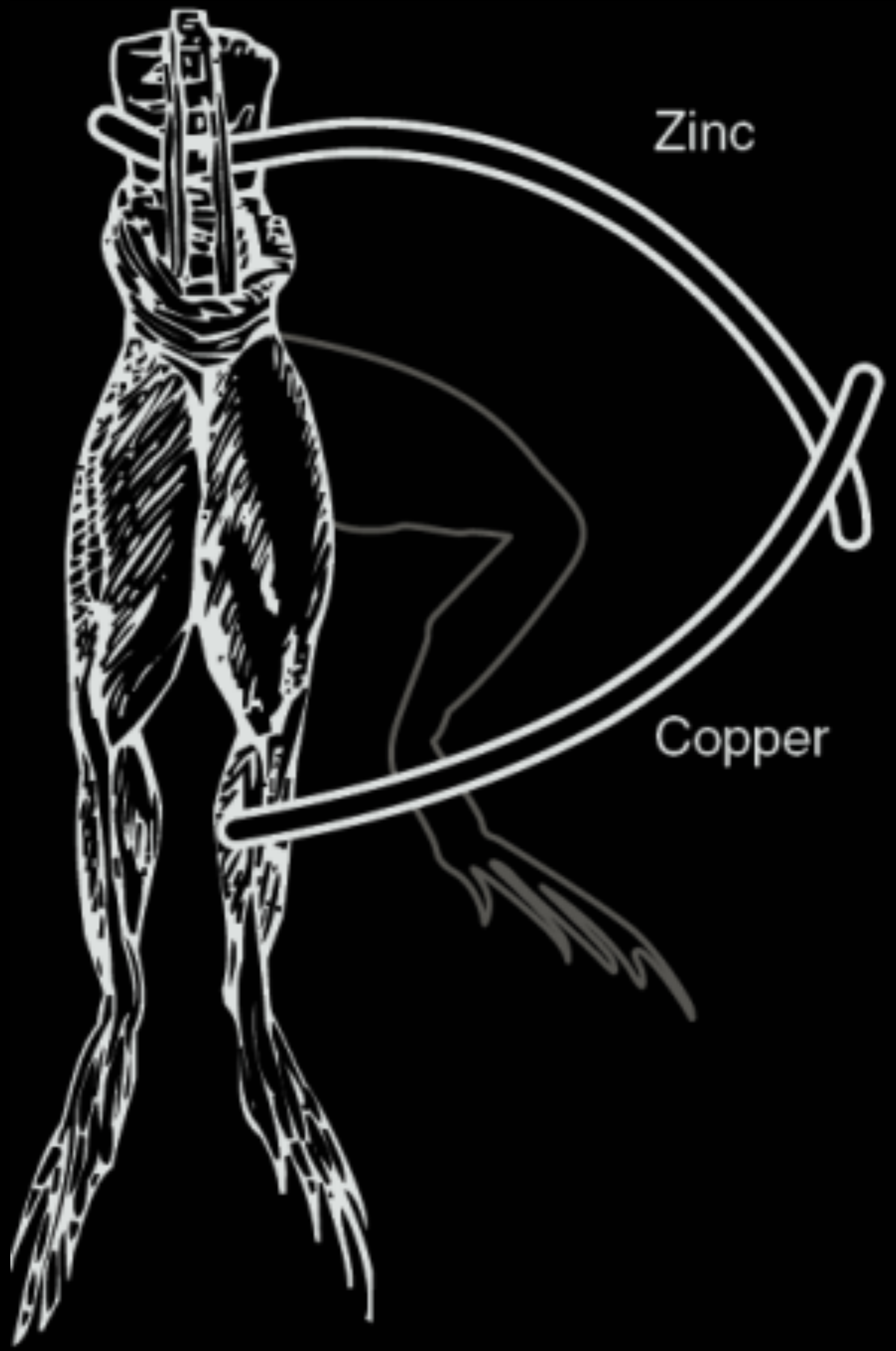
Systems

Neurons

Spikes

In 1786 Luigi Galvani discovers electricity in frog legs, starting the field of modern Neuroscience (and jumpstarting Electrodynamics)



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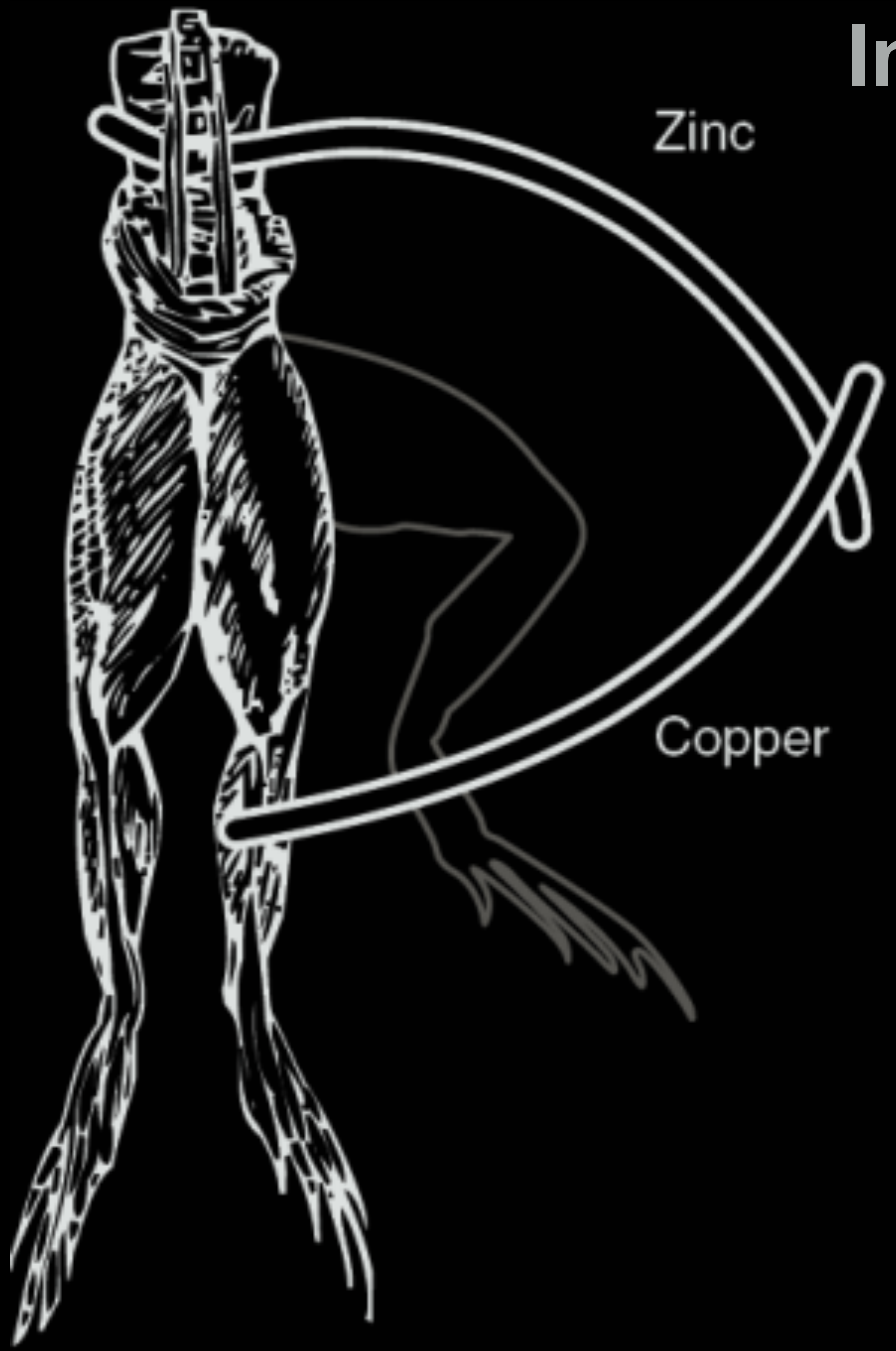

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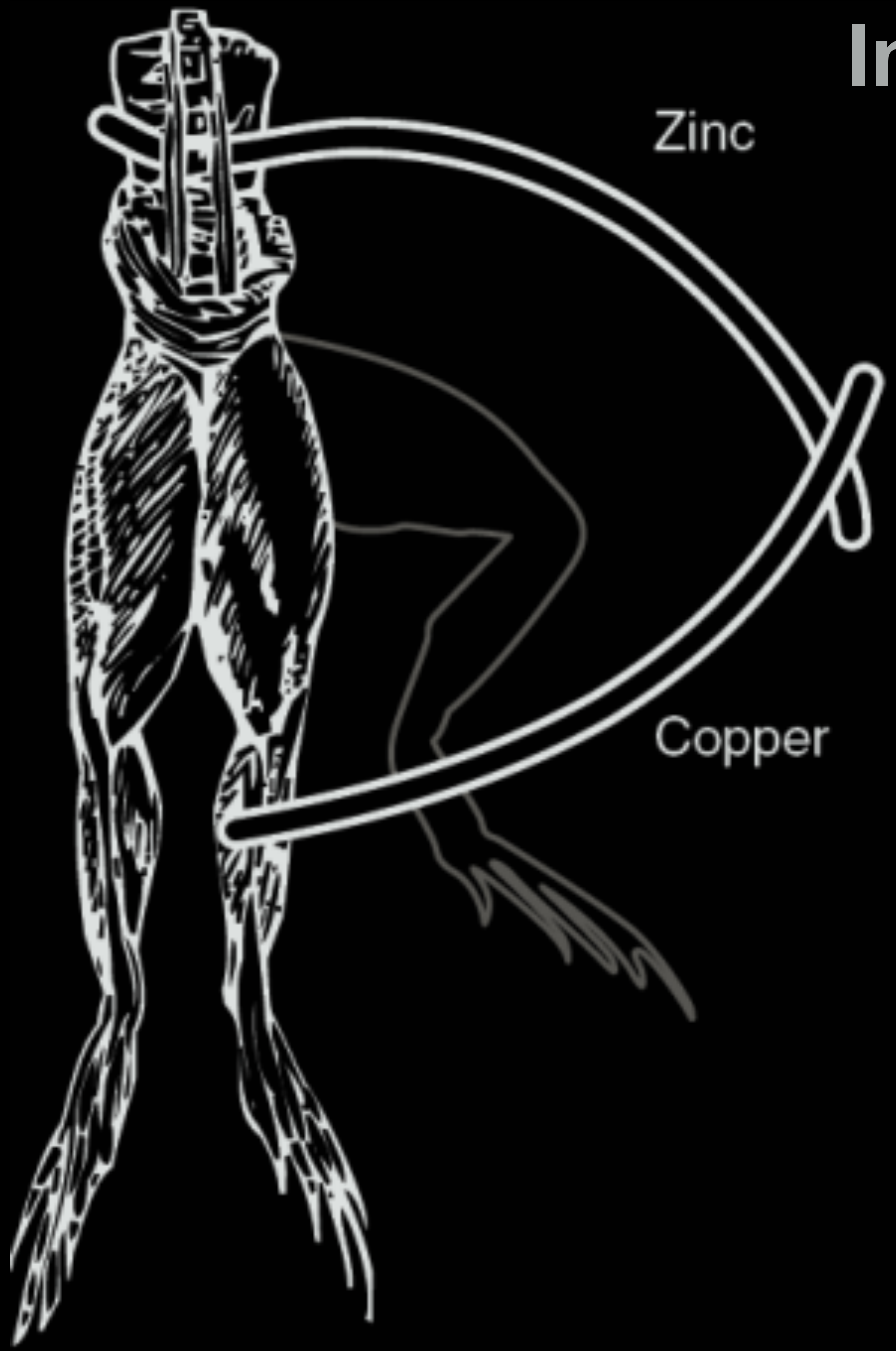

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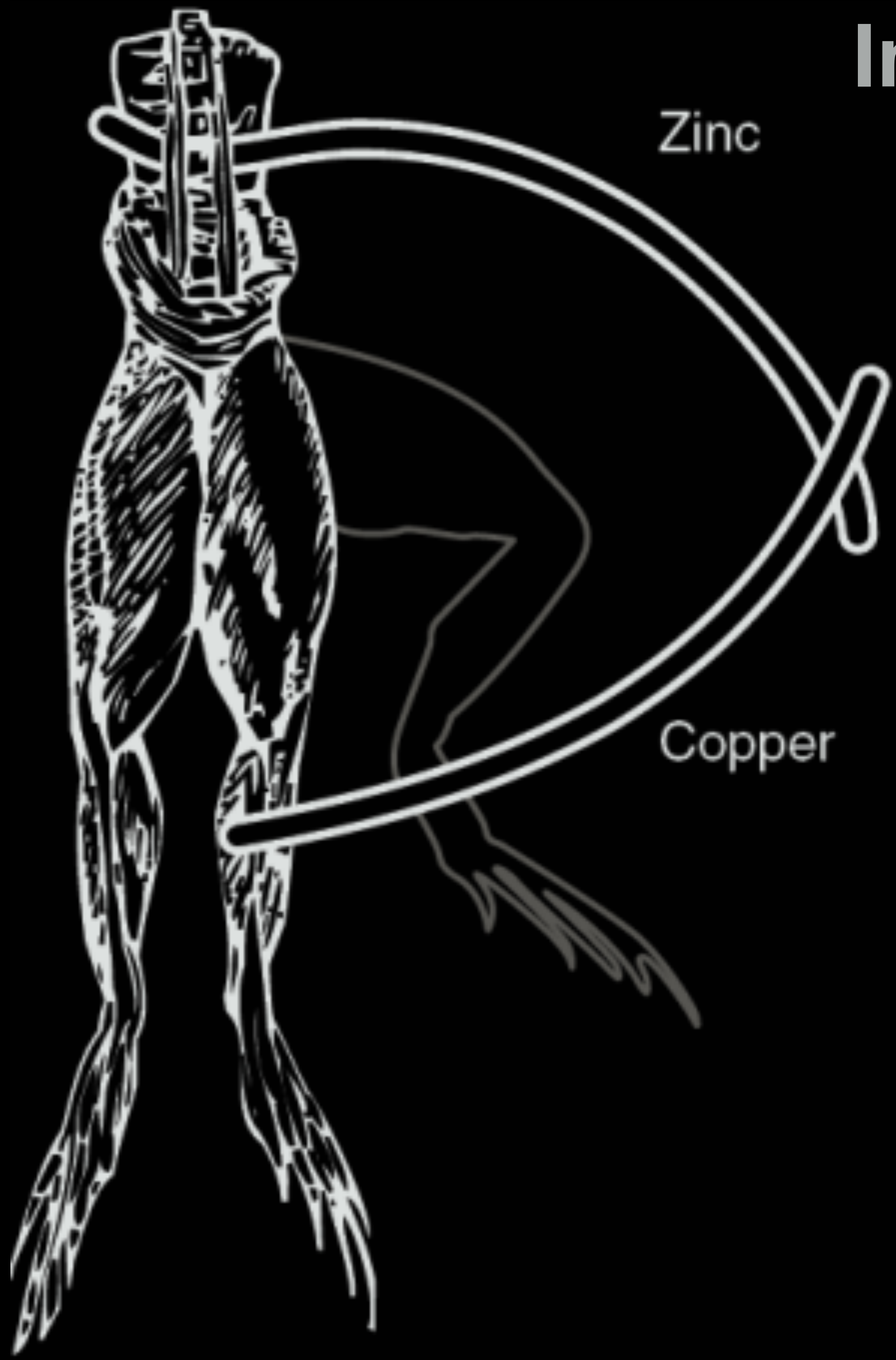

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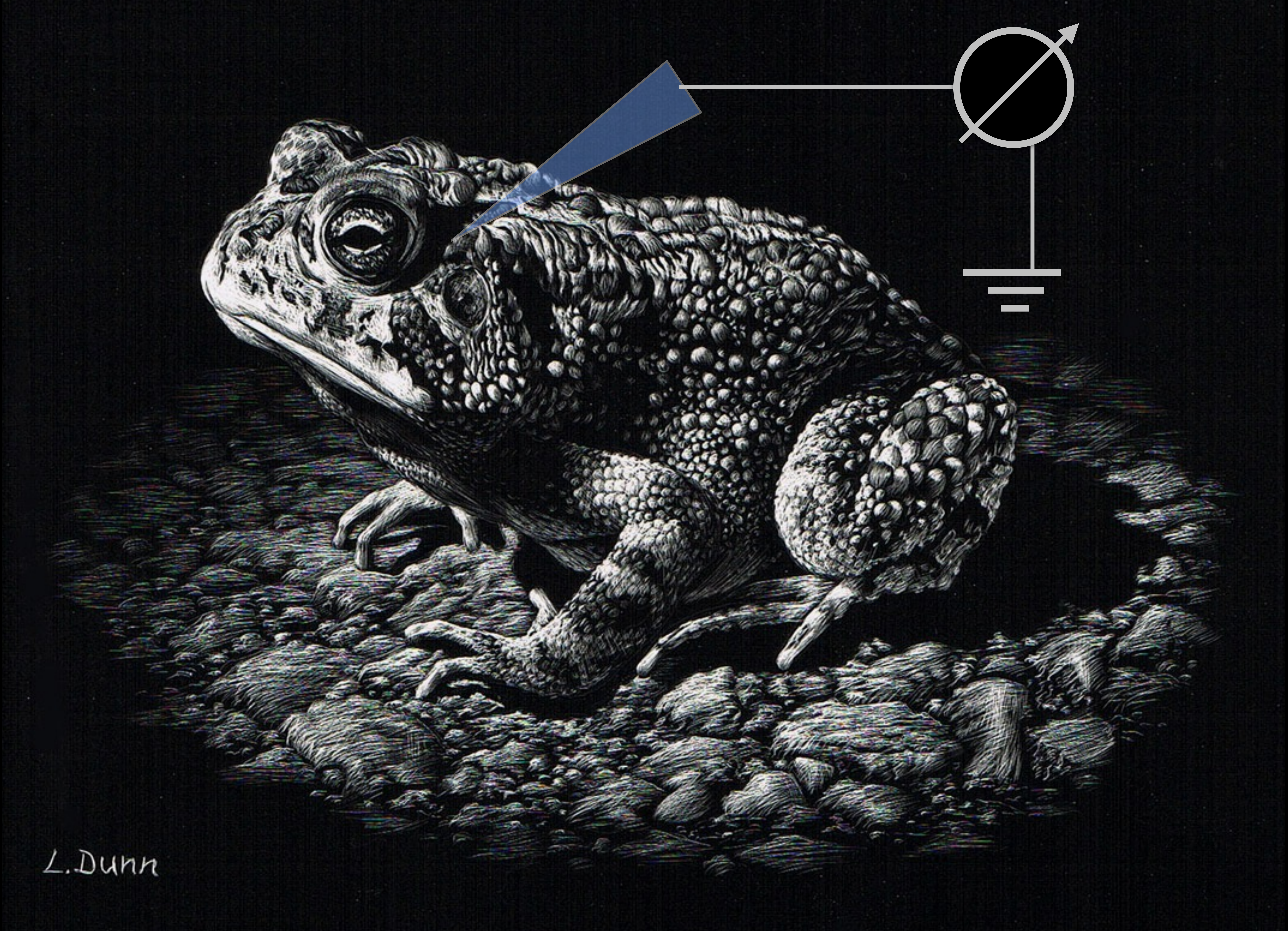
In 1907 LaPique publishes a paper that quantifies leg twitching and that becomes the mother of Integrate-and-Fire


L.Dunn

In 1926 Lord Adrian & Charles Sherrington recorded the first spikes



APs are powered by ion channels (Hodgkin Huxley,1952)

1836 - The brain runs on neurons (Gabriel Gustav Valentin)

1786, 1868, 1926 - Neurons run on action potentials
(Luigi Galvani, Julius Bernstein Lord Adrian)

1887,1943 - Neurons have a the resting state
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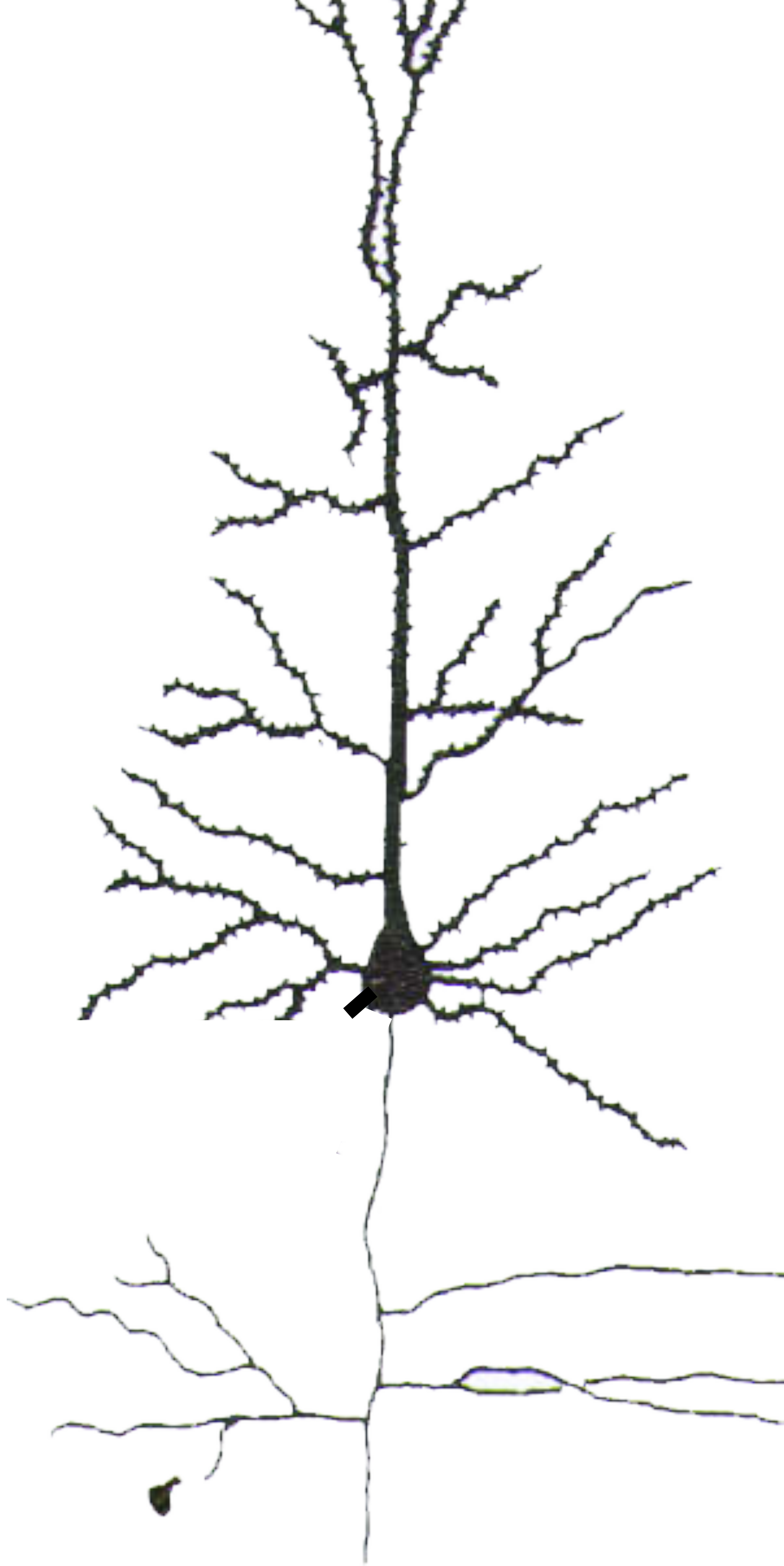
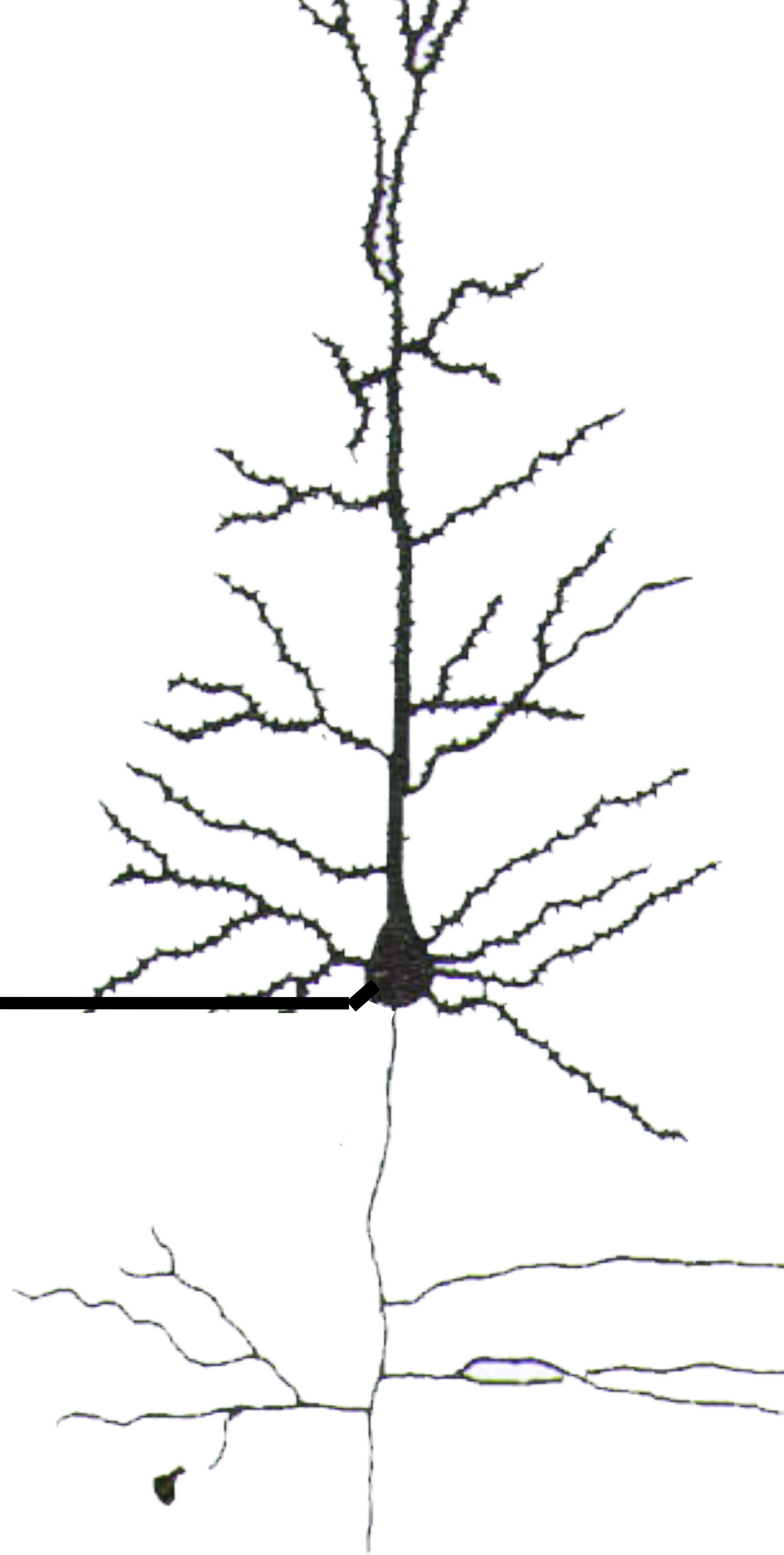


Collect

&

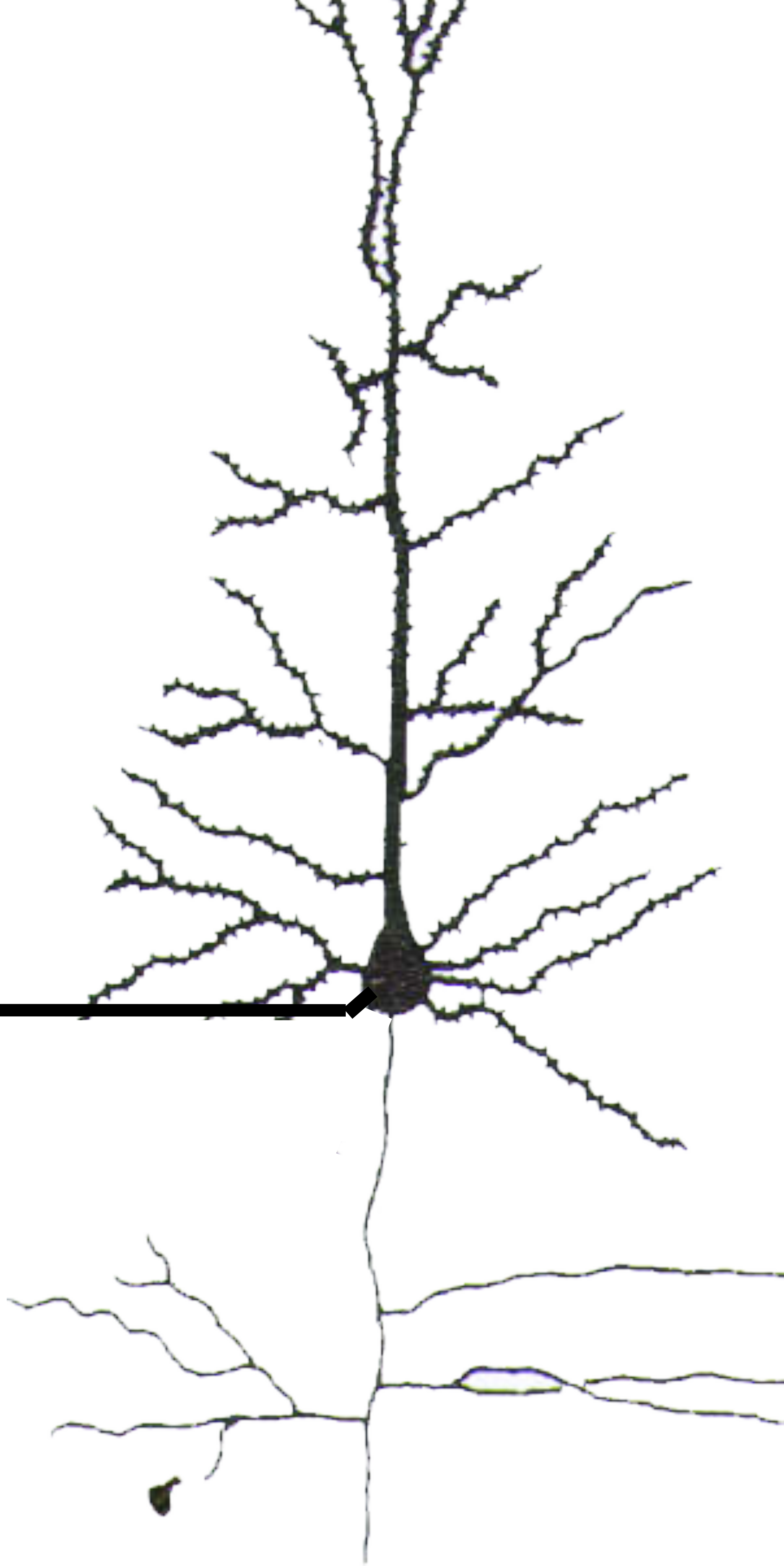
Dispense

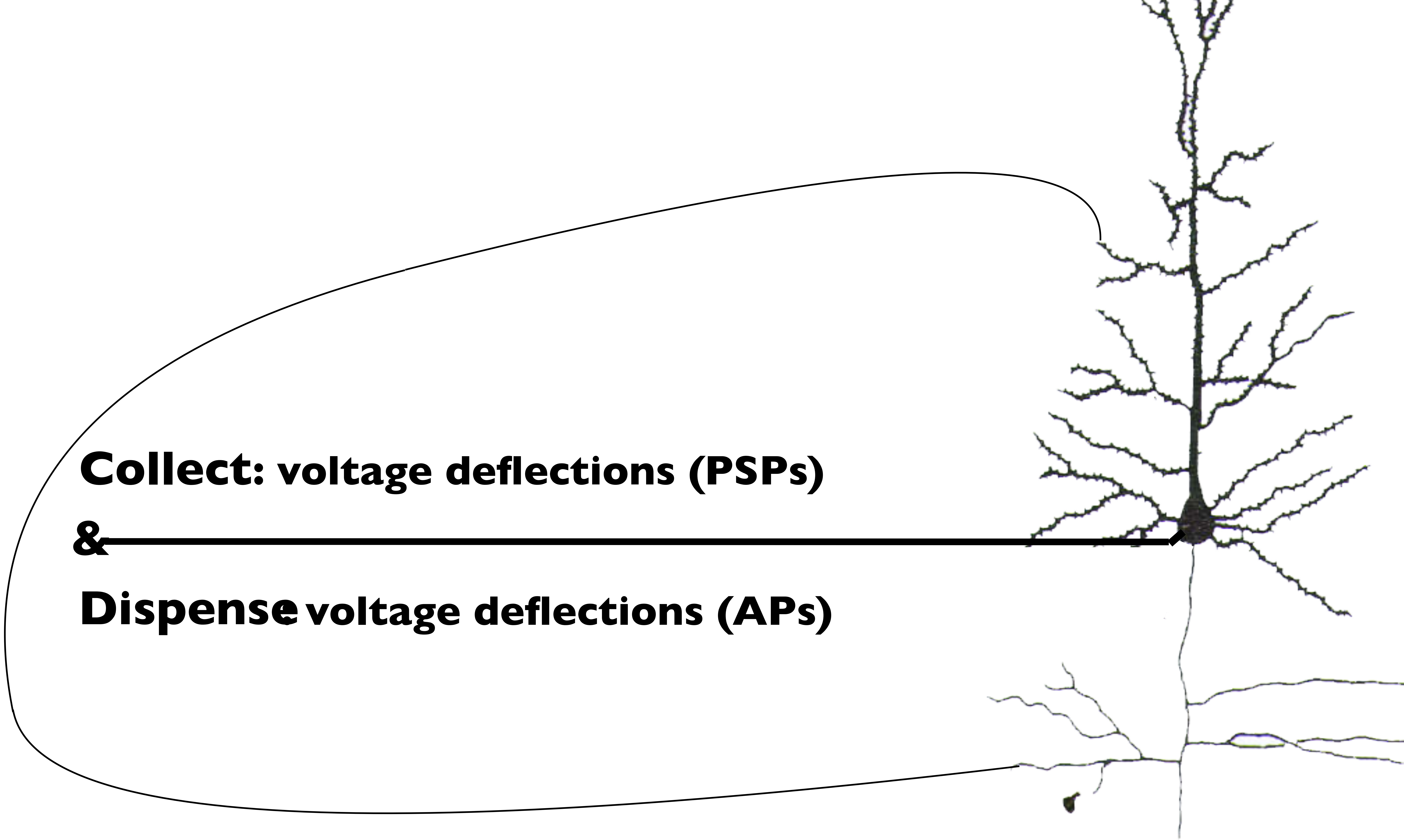


Collect: voltage deflections (PSPs)

&

Dispense: voltage deflections (APs)

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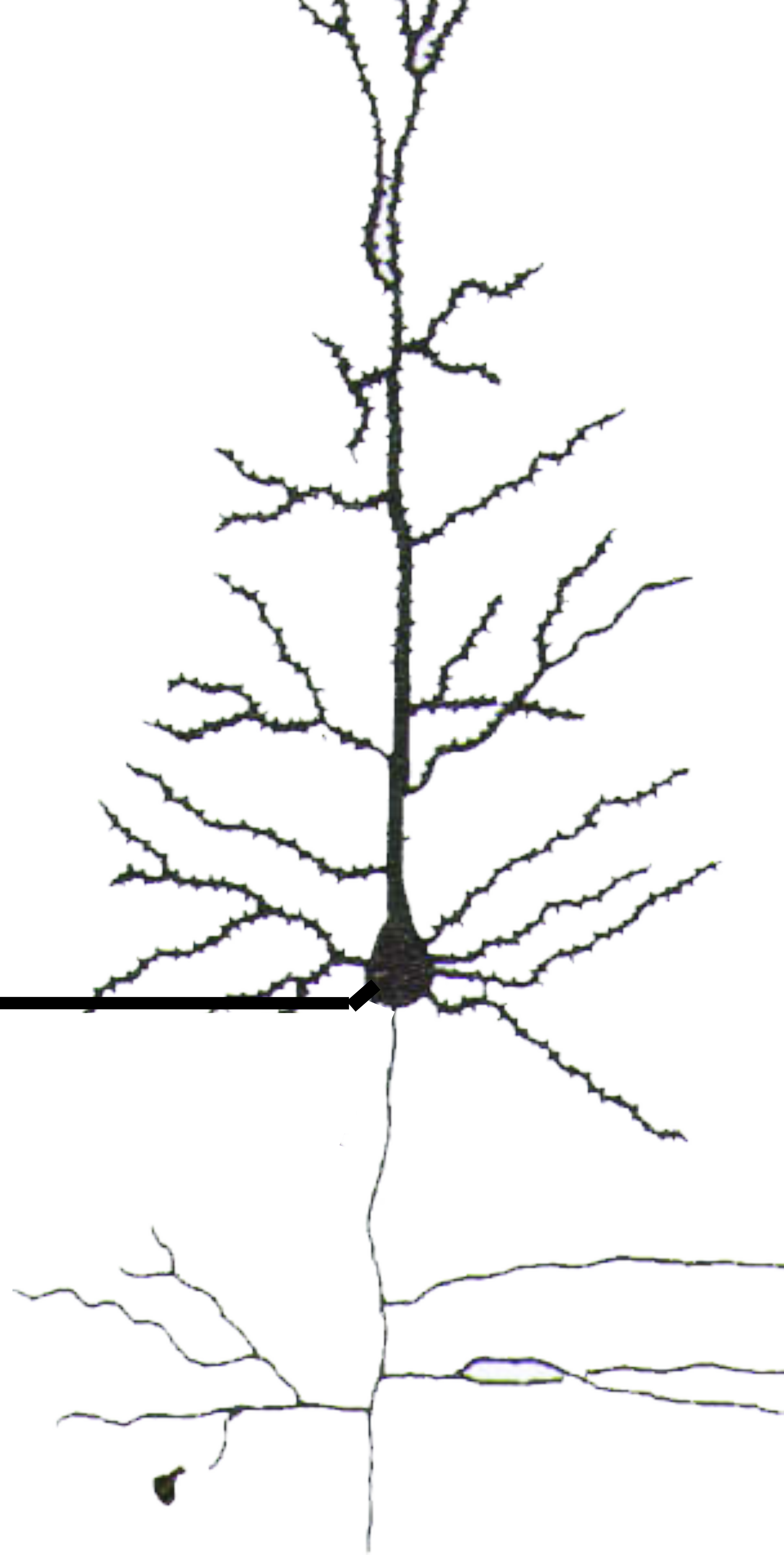
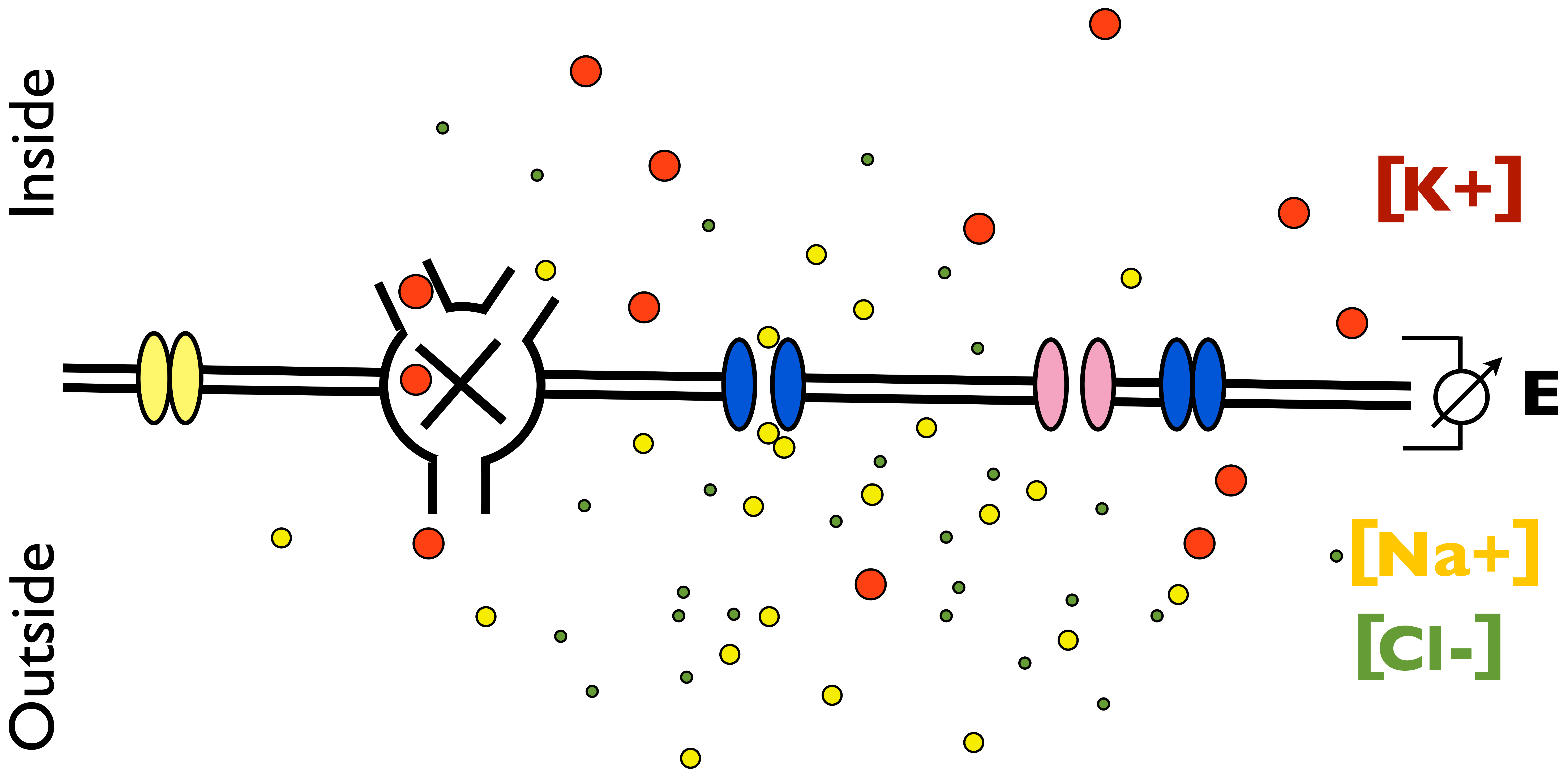


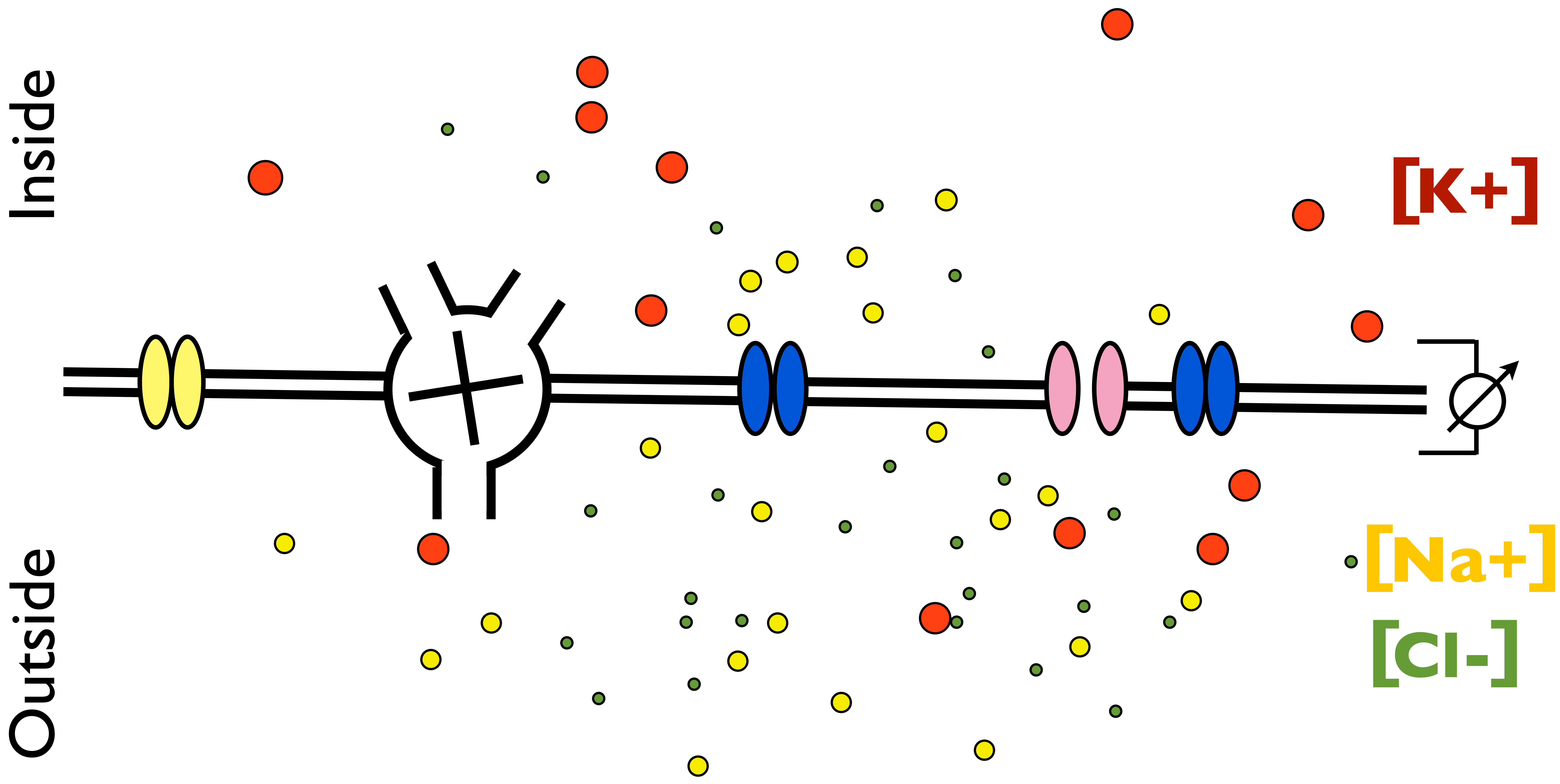
voltage

voltage


voltage

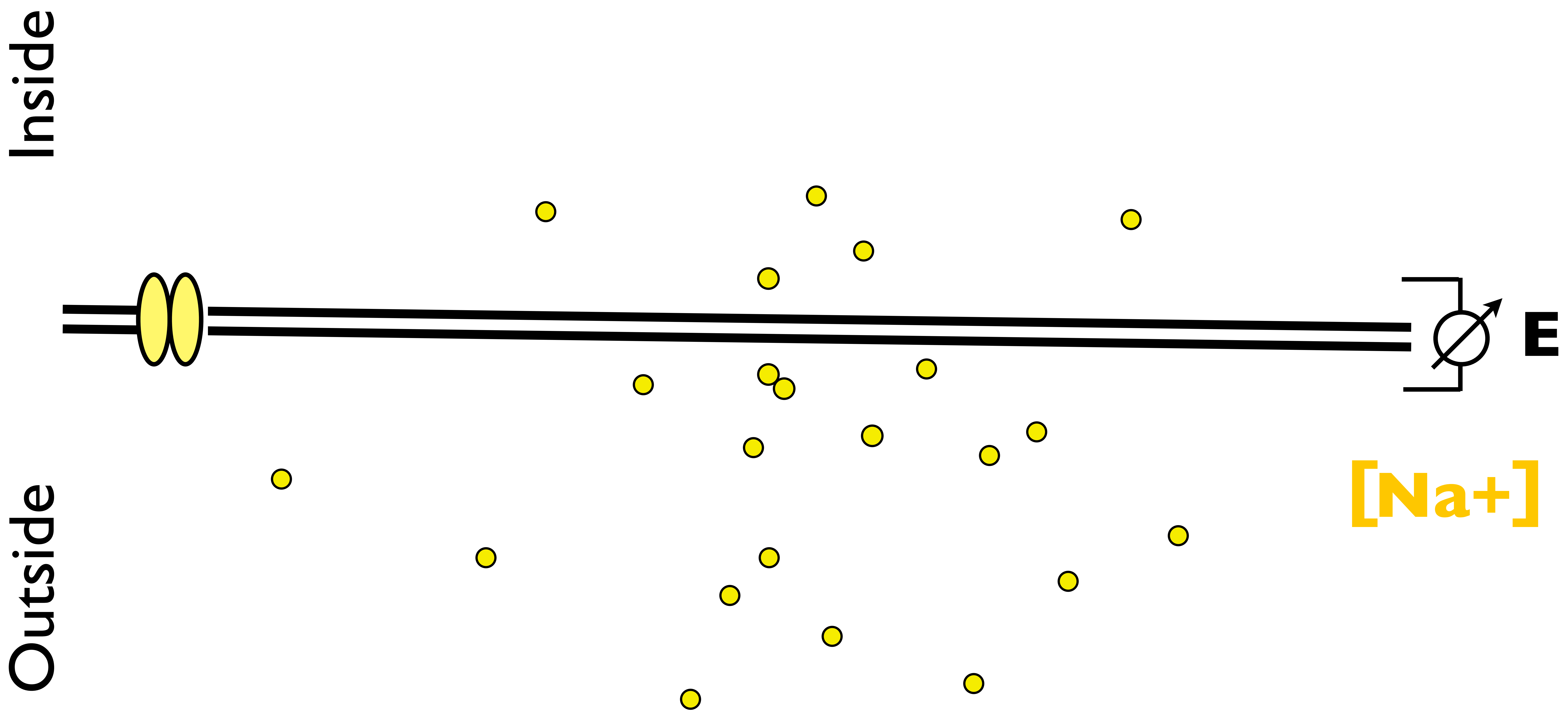


Inside
Outside
[K+]
E
[Na+]
[Cl-]


Inside
Outside
[K+]
[Na+]
[Cl-]

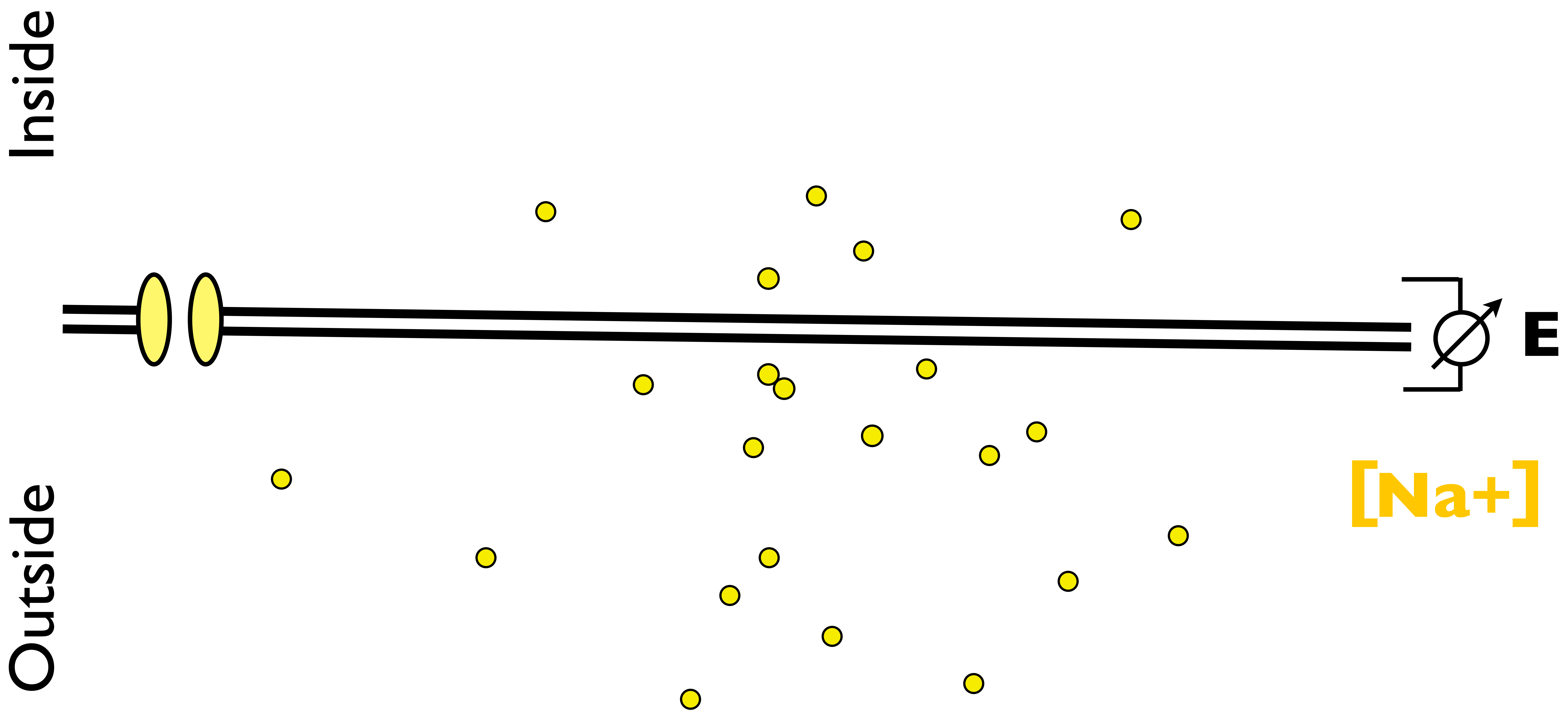
$$\mathbf{E} = K \ln\left(\frac{[Na+]_{out}}{[Na+]_{in}}\right)$$

Nernst equation, 1887

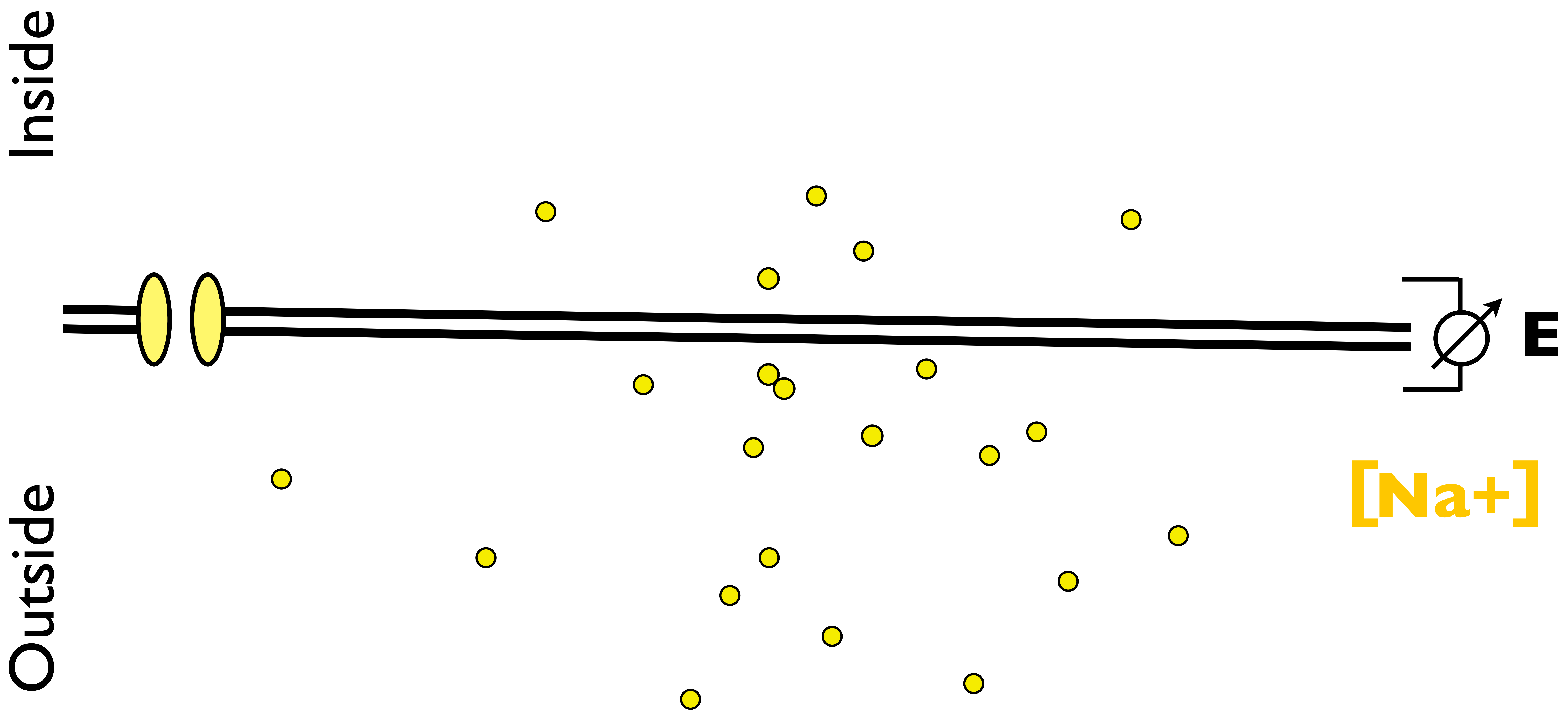


$$\mathbf{E} = K \ln\left(\frac{[Na+]_{out}}{[Na+]_{in}}\right)$$

Nernst equation, 1887



$$\mathbf{E} = C \ln\left(\frac{p[Na+]_{out}}{p[Na+]_{in}}\right)$$



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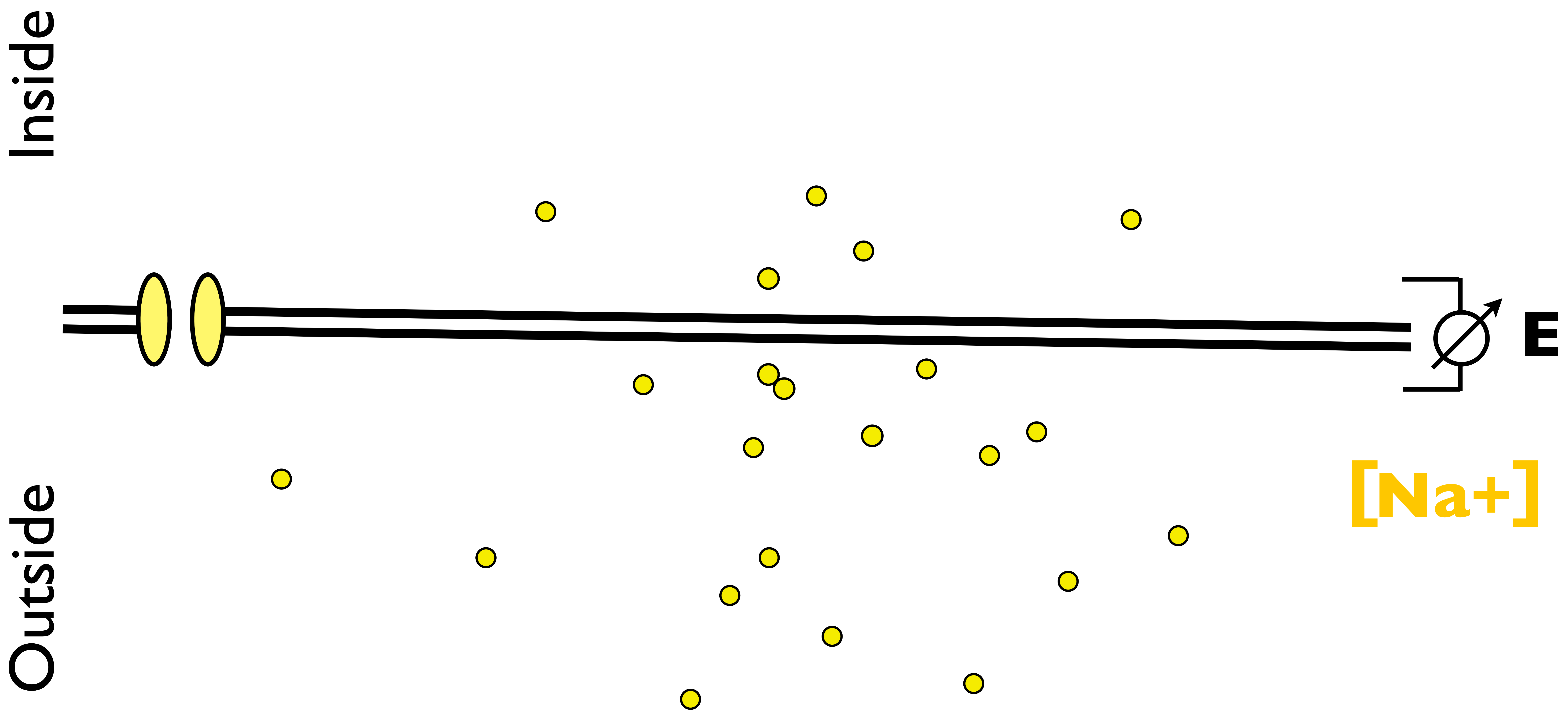
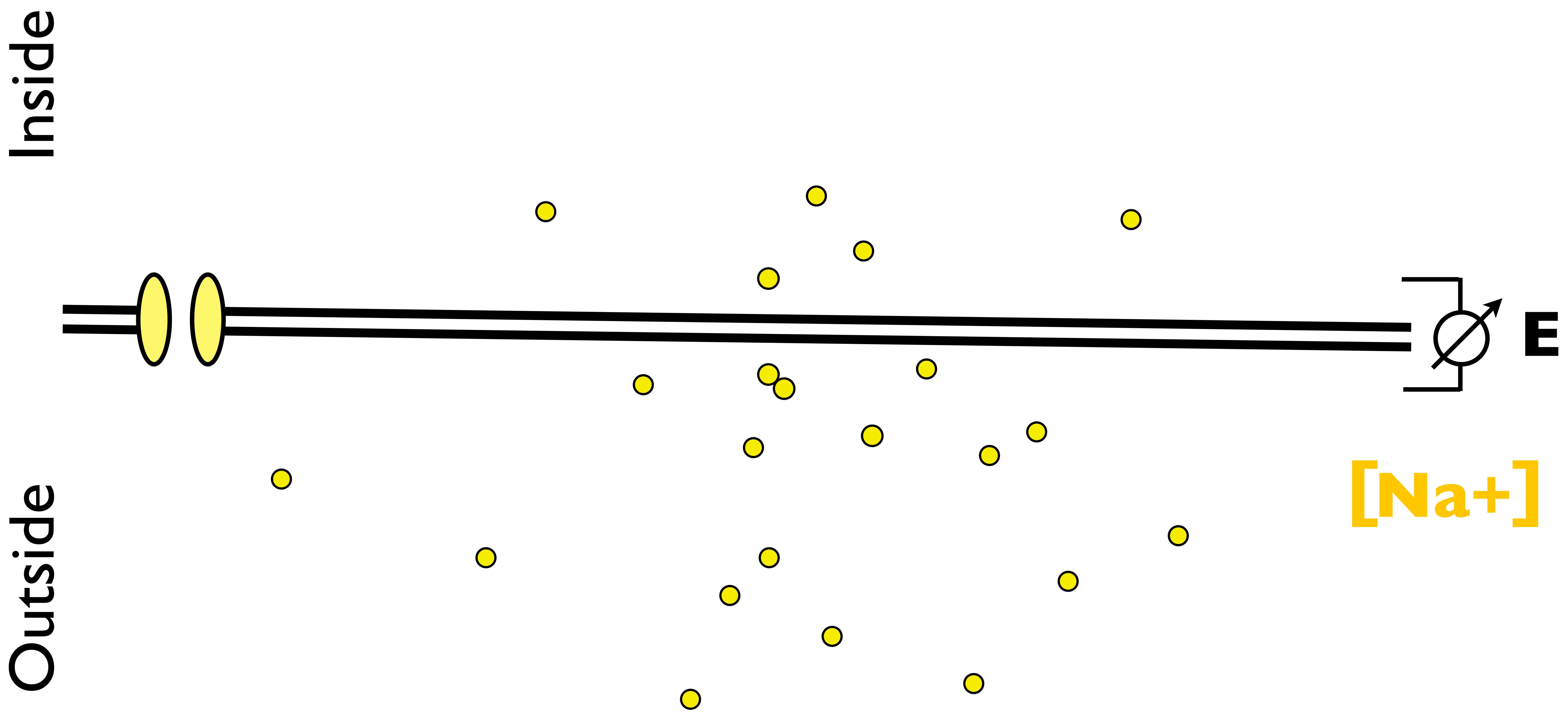
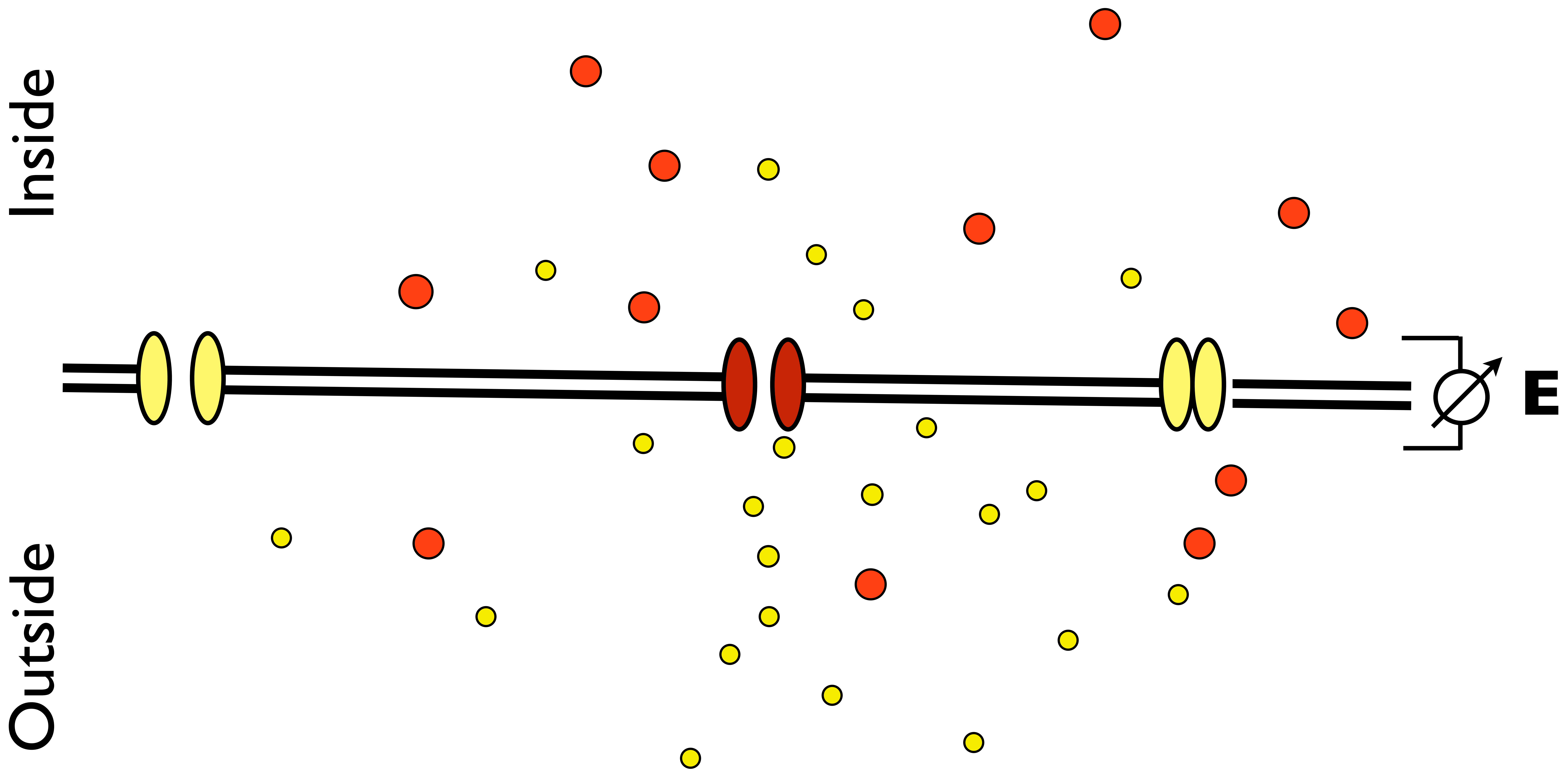


$$\mathbf{E} = C \ln\left(\frac{p[Na+]_{out}}{p[Na+]_{in}}\right)$$

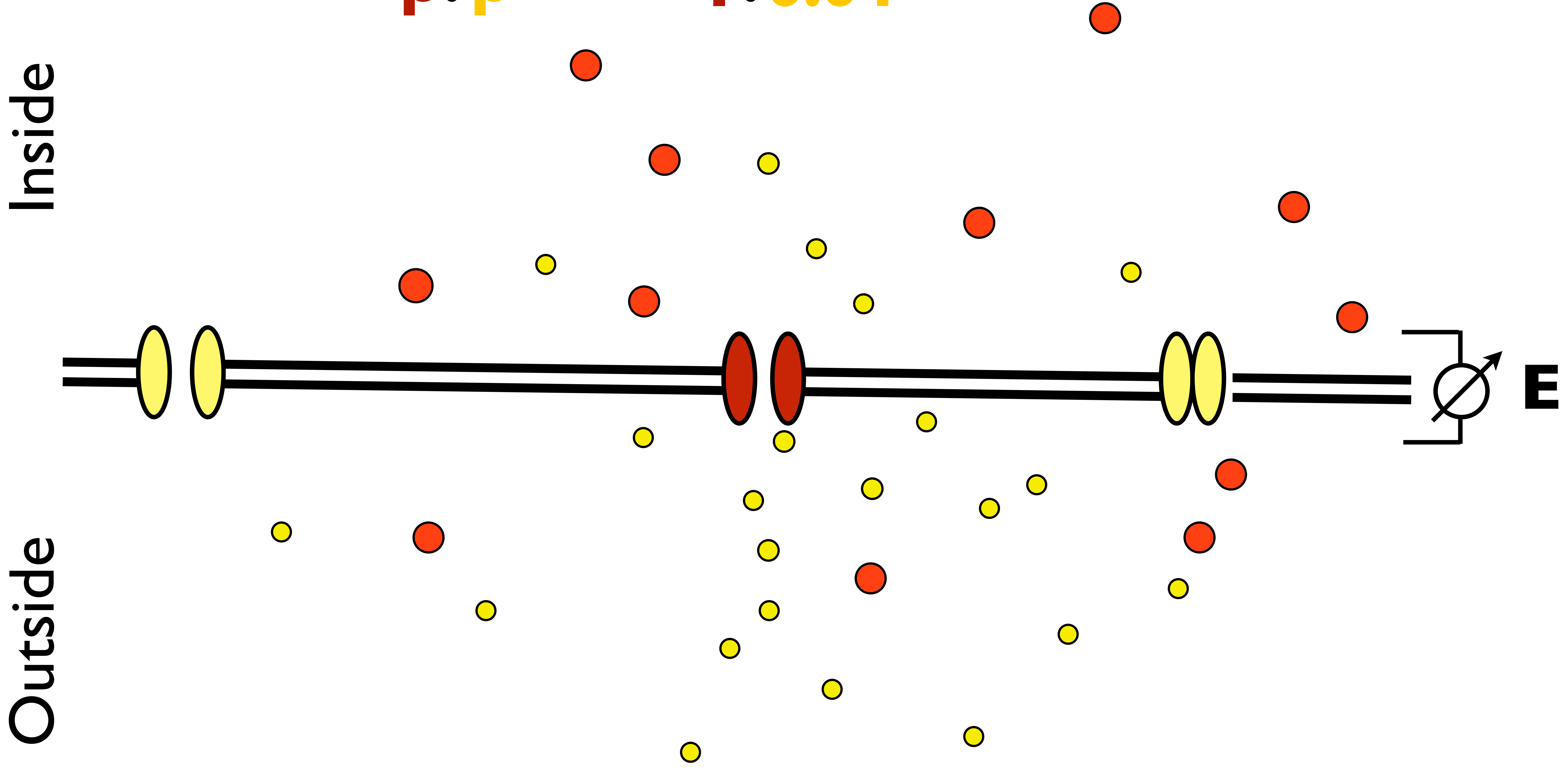


$$E = C \ln\left(\frac{p[K+]_{out} + p[Na+]_{out}}{p[K+]_{in} + p[Na+]_{in}}\right)$$



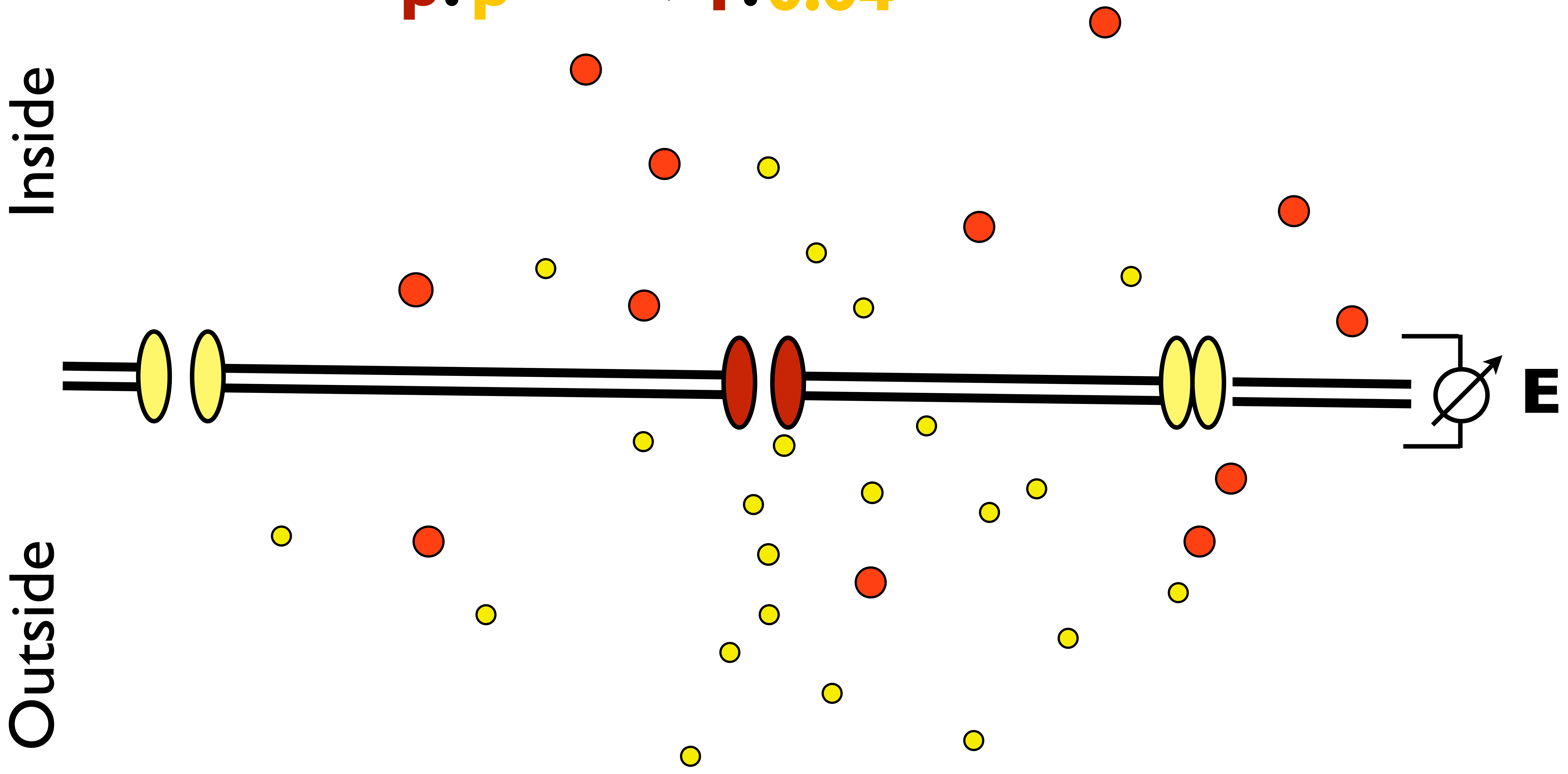
$$\mathbf{E} = C \ln\left(\frac{p[K+]_{out} + p[Na+]_{out}}{p[K+]_{in} + p[Na+]_{in}} \right)$$

$$p : p \longrightarrow 1 : 0.04$$



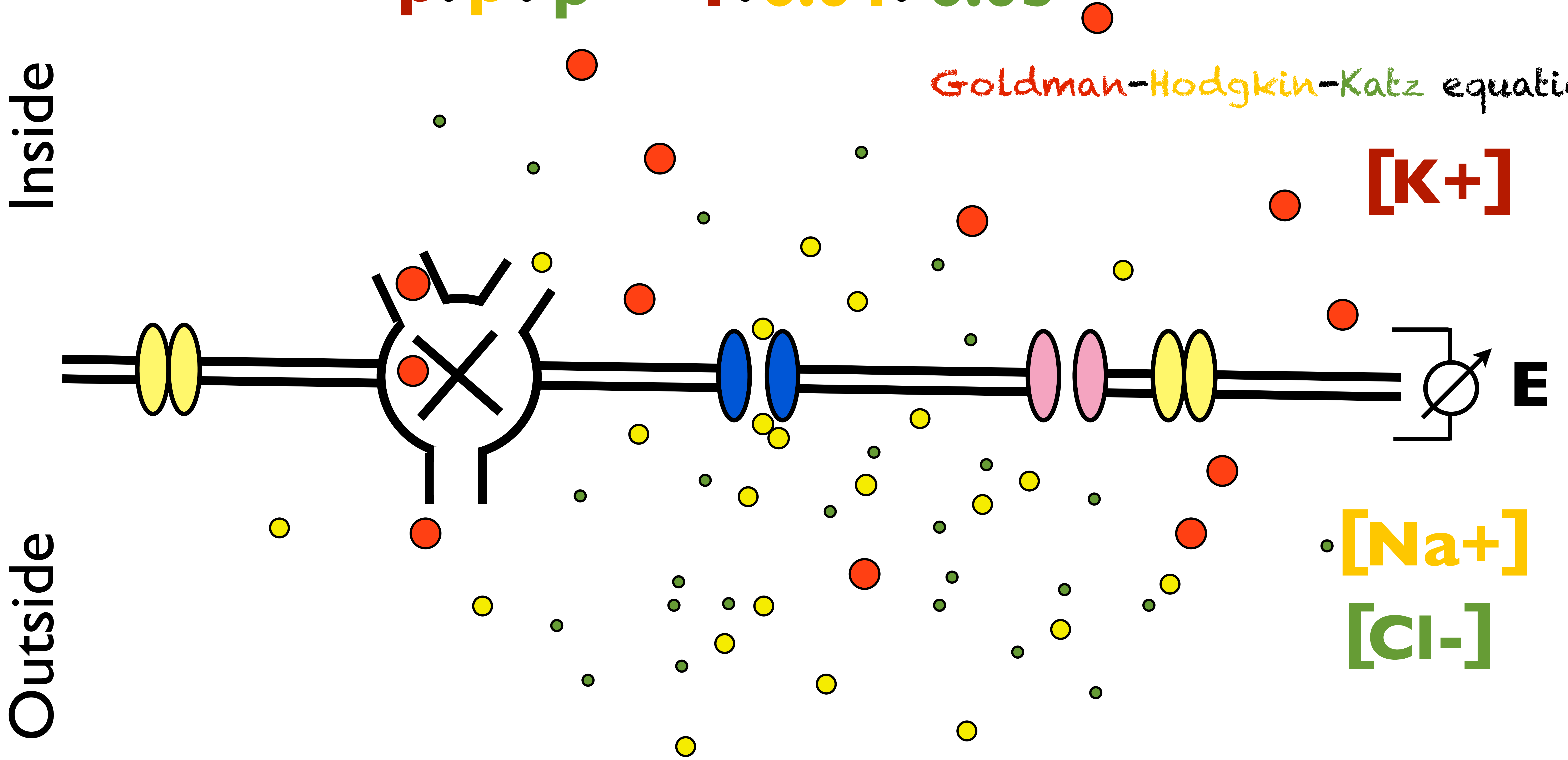
$$\mathbf{E} = C \ln\left(\frac{p[K+]_{out} + p[Na+]_{out}}{p[K+]_{in} + p[Na+]_{in}}\right) \quad -X$$

$$p : p \longrightarrow 1 : 0.04$$



$$E = C \ln\left(\frac{p[K+]_{out} + p[Na+]_{out} + p[Cl-]_{in}}{p[K+]_{in} + p[Na+]_{in} + p[Cl-]_{out}}\right)$$

$$p : p : p \longrightarrow 1 : 0.04 : 0.03$$



Goldman-Hodgkin-Katz equation, 1943

$$\mathbf{E} = C \ln\left(\frac{p[K+]_{out} + p[Na+]_{out} + p[Cl-]_{in}}{p[K+]_{in} + p[Na+]_{in} + p[Cl-]_{out}}\right) = -70\,\text{mV}$$

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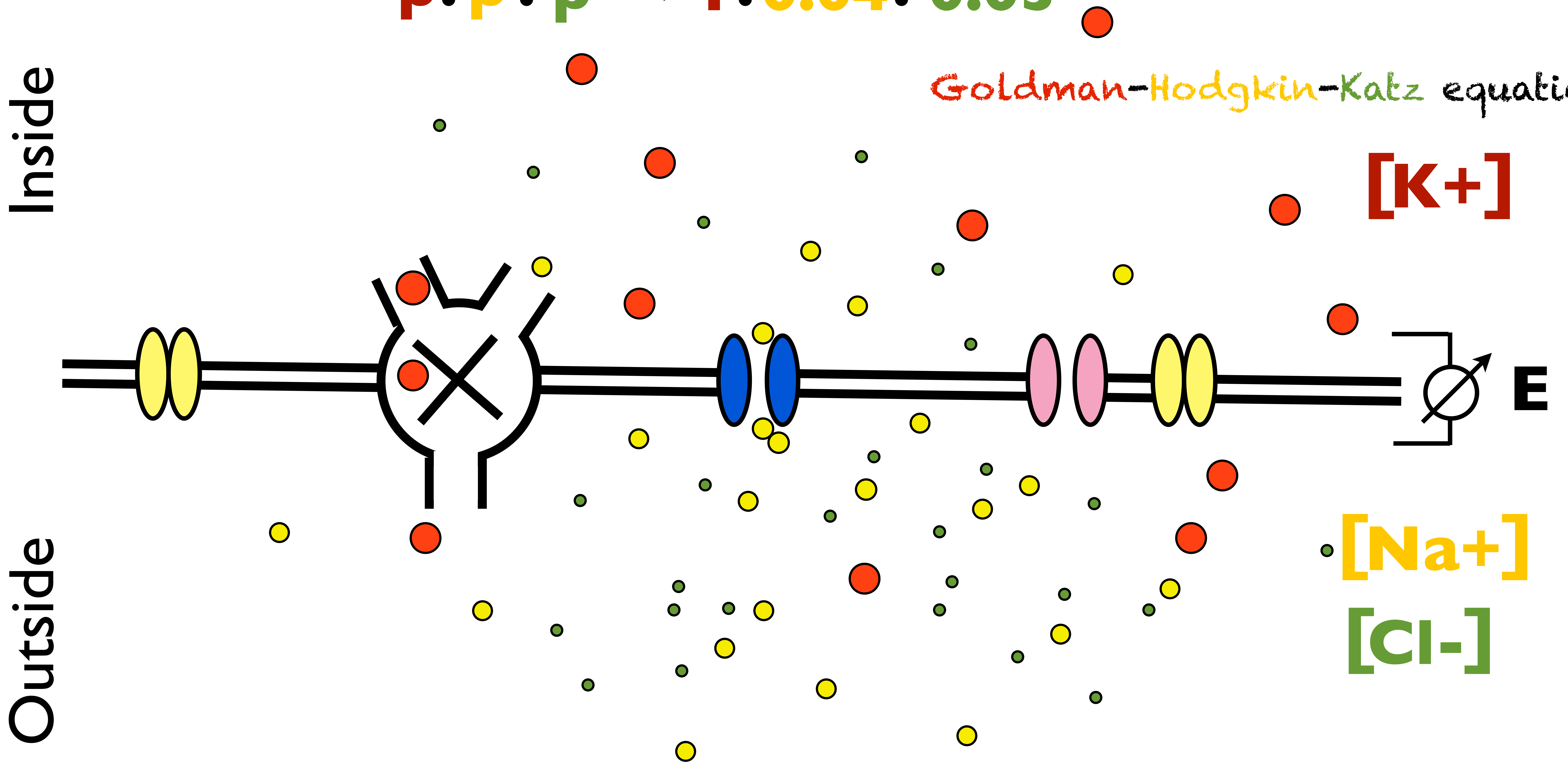
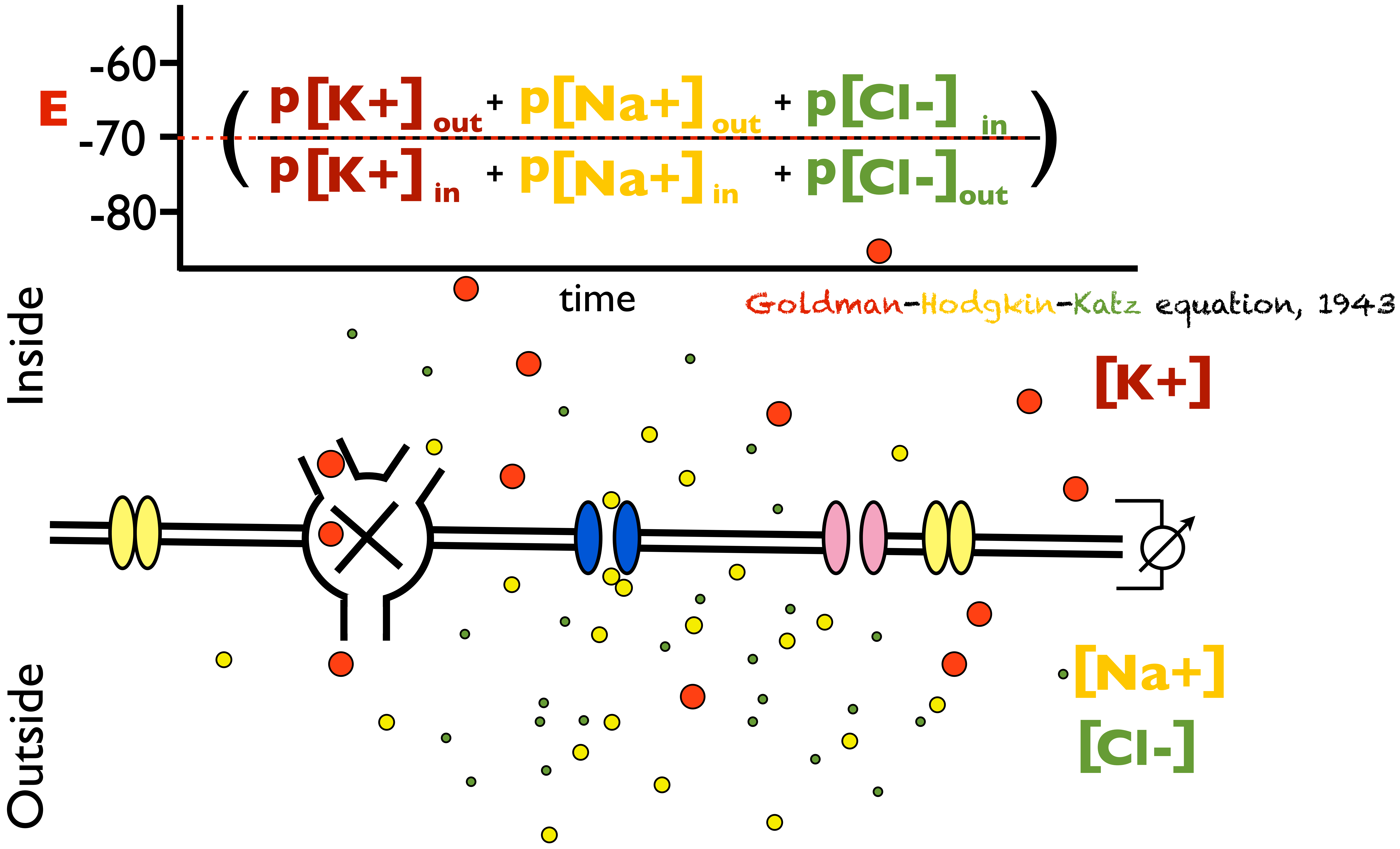
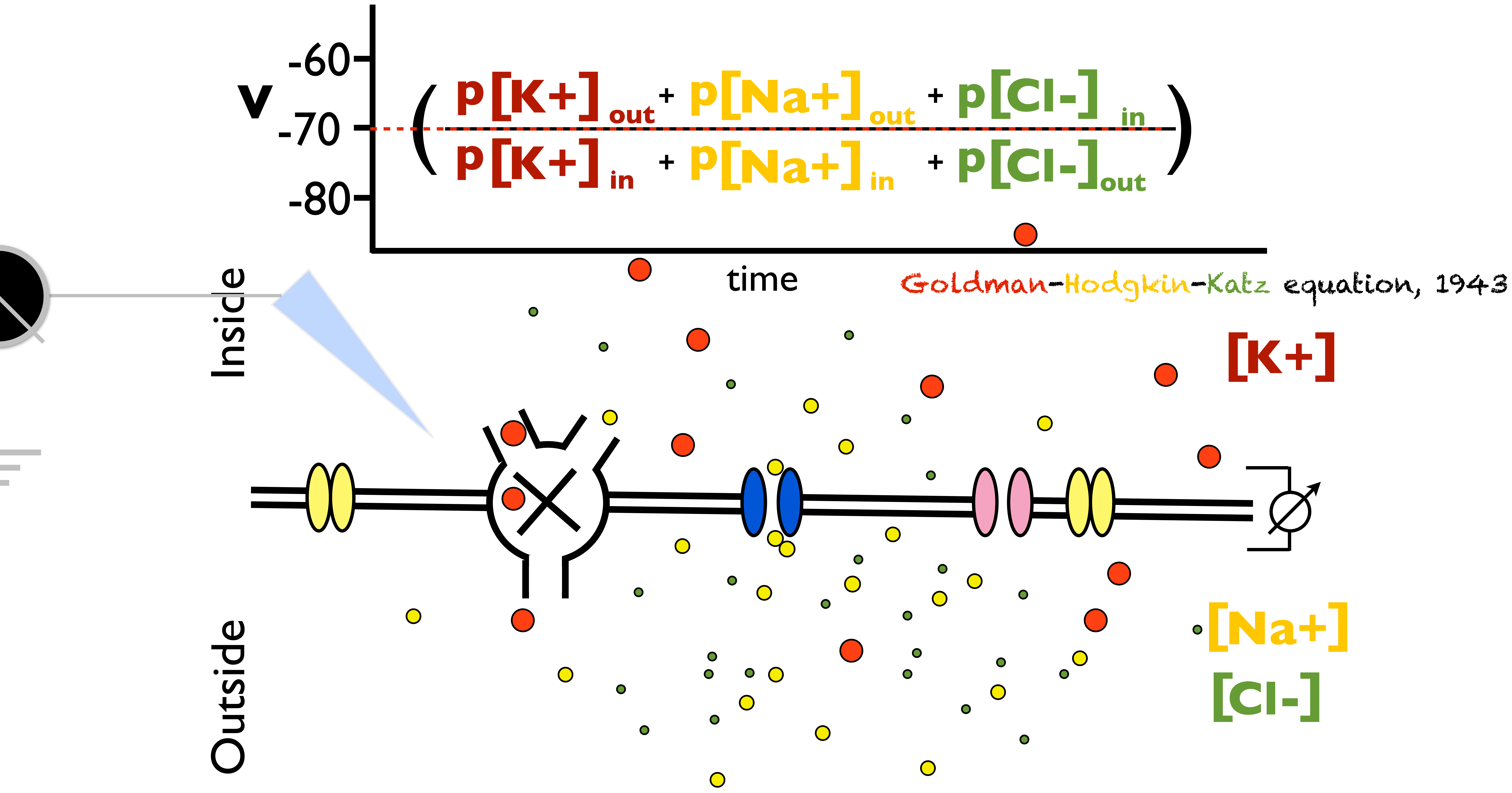




E
-60
-70
-80
$\left(\frac{p[K+]_{out} + p[Na+]_{out} + p[Cl-]_{in}}{p[K+]_{in} + p[Na+]_{in} + p[Cl-]_{out}}\right)$
time
Goldman-Hodgkin-Katz equation, 1943
Inside
Outside
[K+]
[Na+]
[Cl-]



V
-60
-70
-80
$\left(\frac{p[K+]_{out} + p[Na+]_{out} + p[Cl-]_{in}}{p[K+]_{in} + p[Na+]_{in} + p[Cl-]_{out}} \right)$
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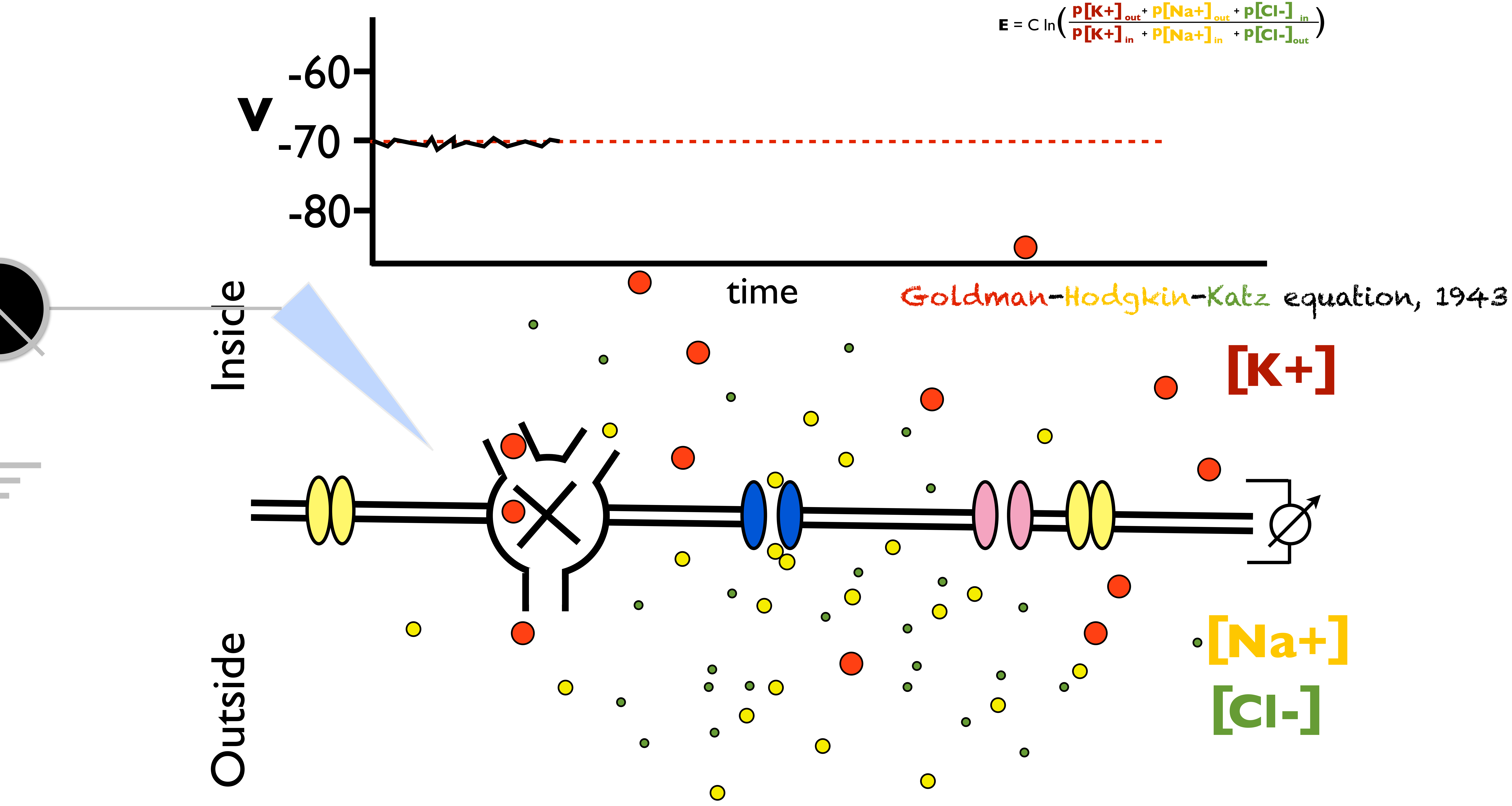

$\mathbf{E} = C \ln\left(\frac{P[K+]_{out} + P[Na+]_{out} + P[Cl-]_{in}}{P[K+]_{in} + P[Na+]_{in} + P[Cl-]_{out}}\right)$
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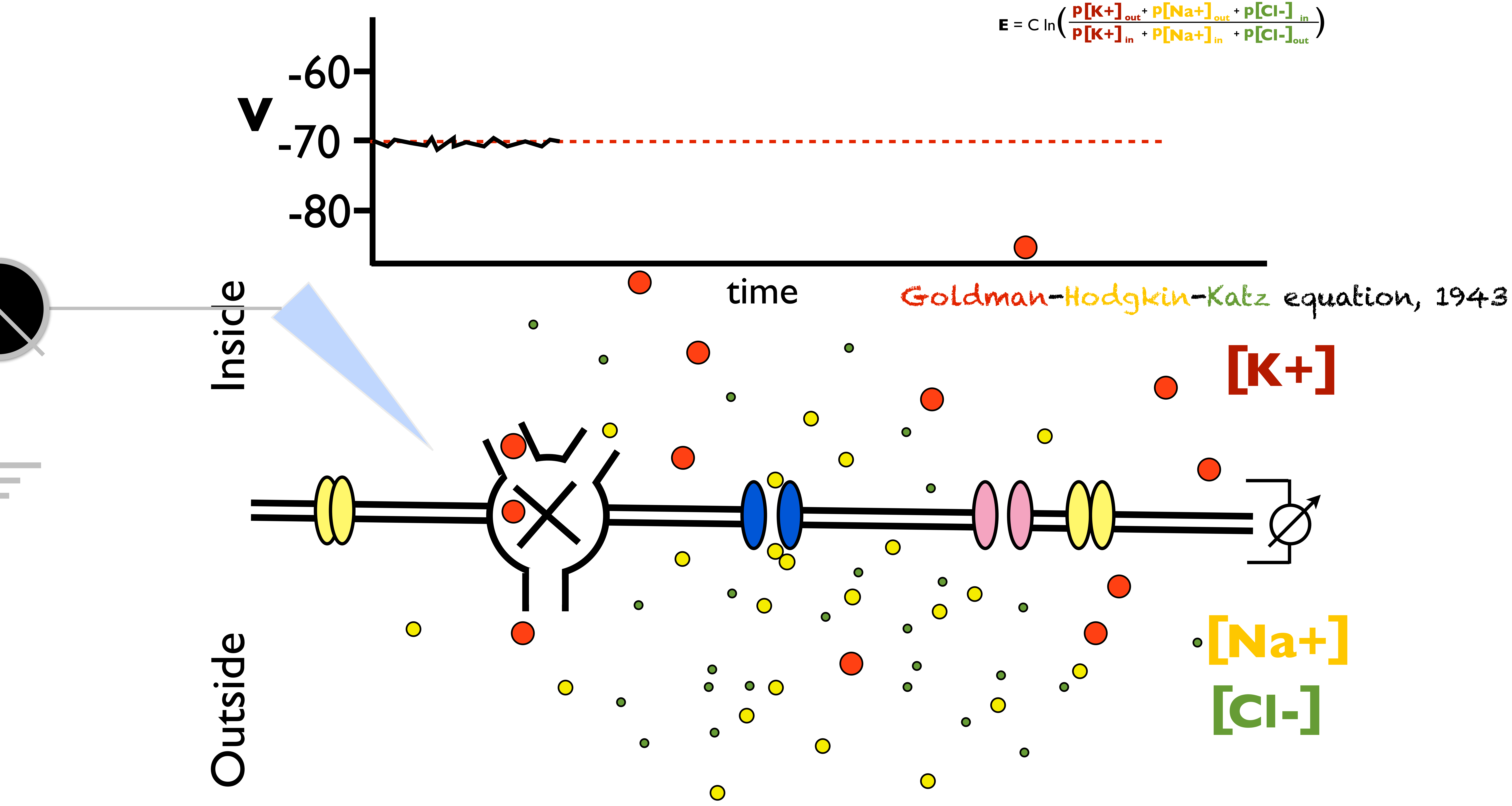

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V
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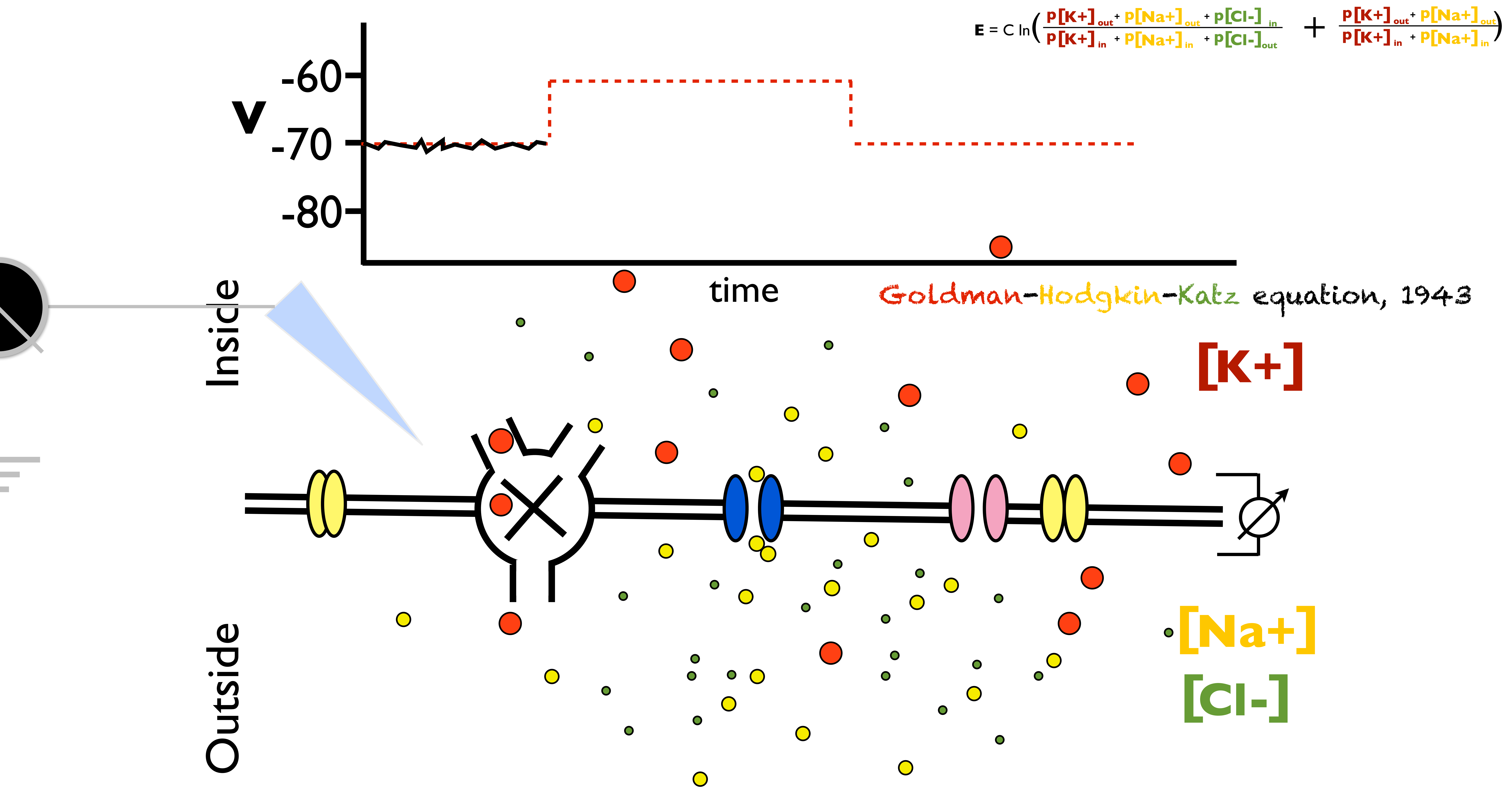
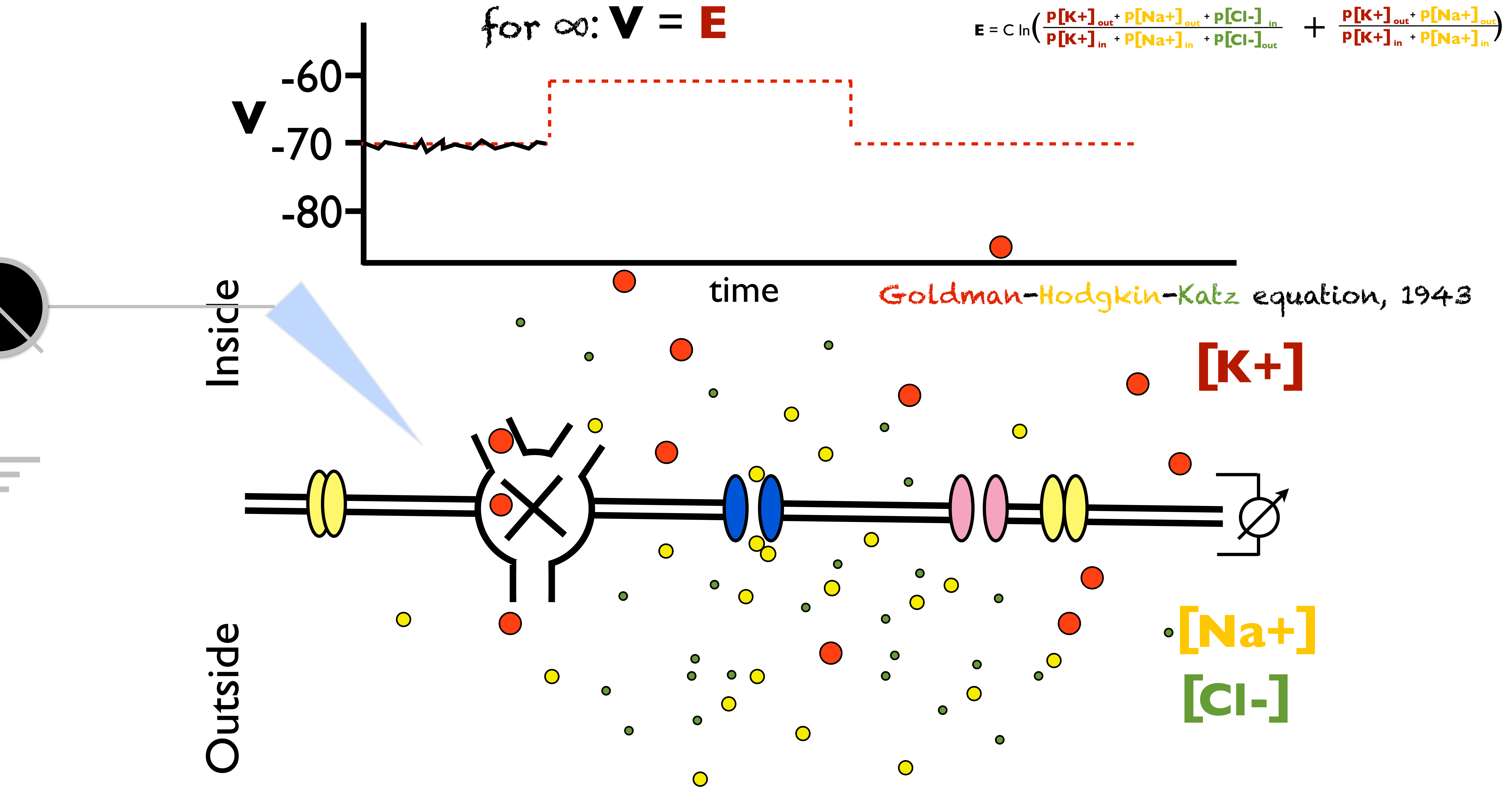


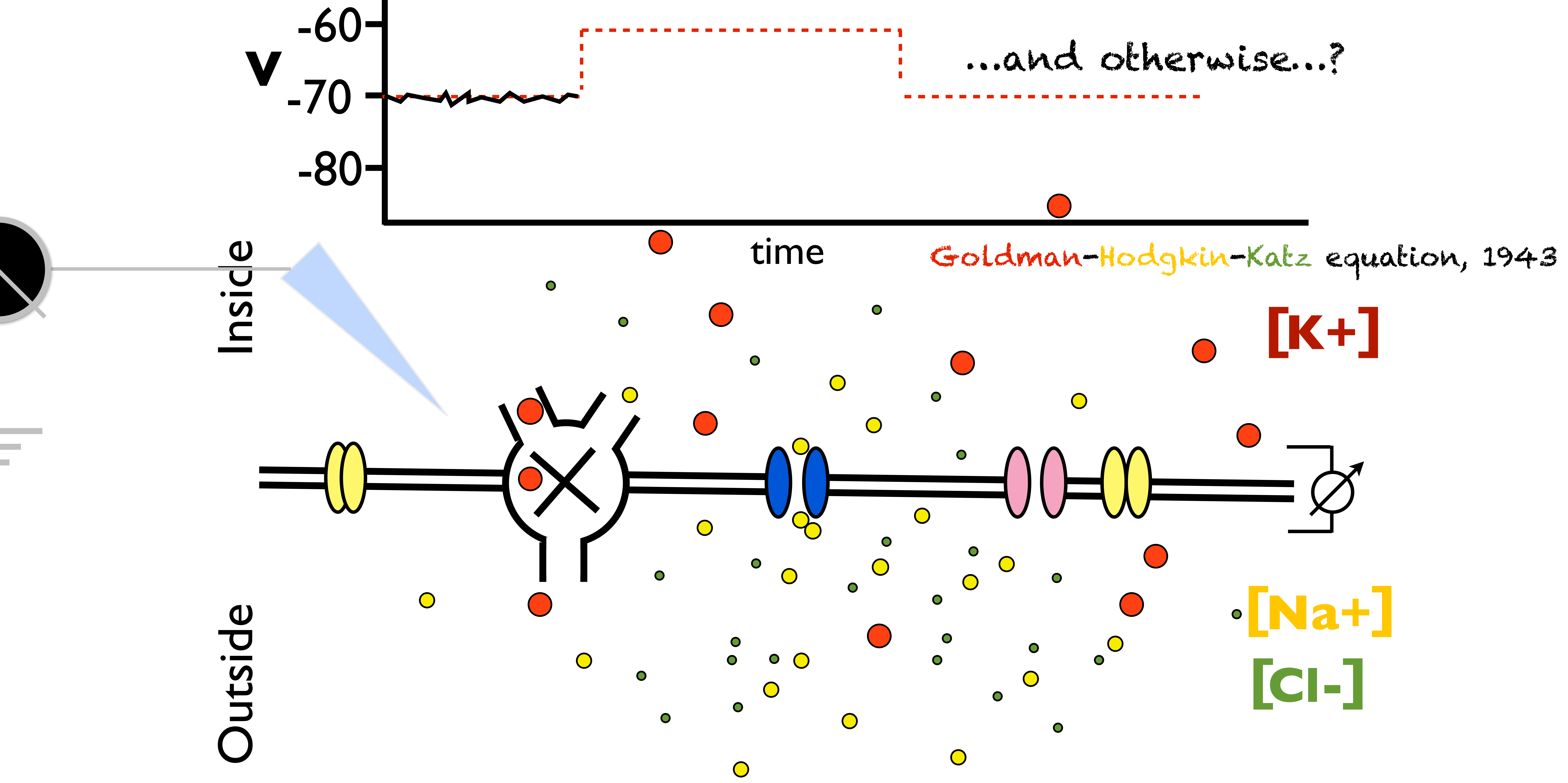
E = C ln(P[K+]out + P[Na+]out + P[Cl-]in / P[K+]in + P[Na+]in + P[Cl-]out + P[K+]out + P[Na+]out / P[K+]in + P[Na+]in)
V
-60
-70
-80
time
Goldman-Hodgkin-Katz equation, 1943
Inside
Outside
[K+]
[Na+]
[Cl-]



for ∞: V = E
$E = C \ln\left(\frac{P[K+]_{out} + P[Na+]_{out} + P[Cl-]_{in}}{P[K+]_{in} + P[Na+]_{in} + P[Cl-]_{out}} + \frac{P[K+]_{out} + P[Na+]_{out}}{P[K+]_{in} + P[Na+]_{in}}\right)$
V
-60
-70
-80
time
Goldman-Hodgkin-Katz equation, 1943
Inside
Outside
[K+]
[Na+]
[Cl-]

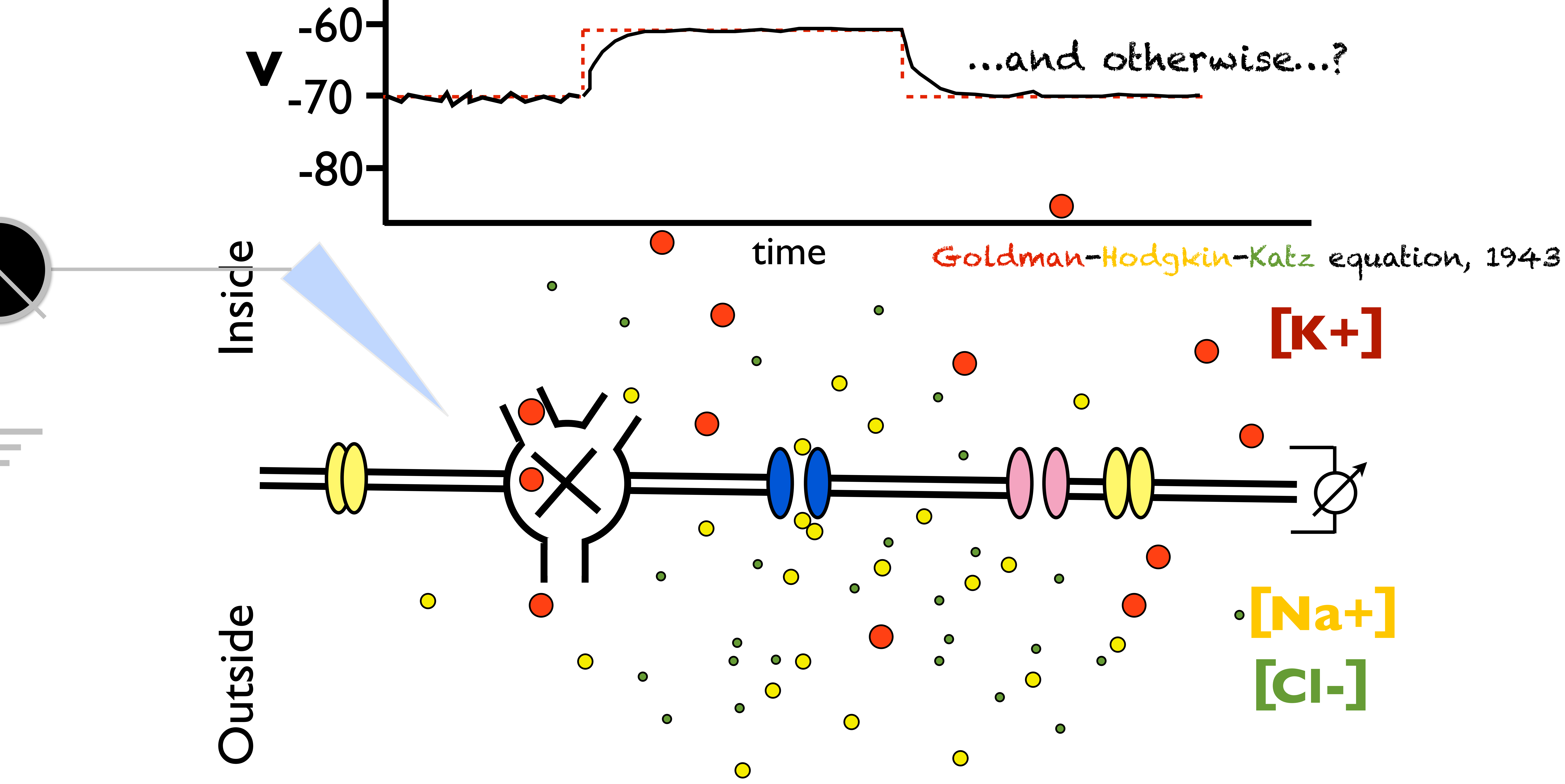
for ∞: **V = E**

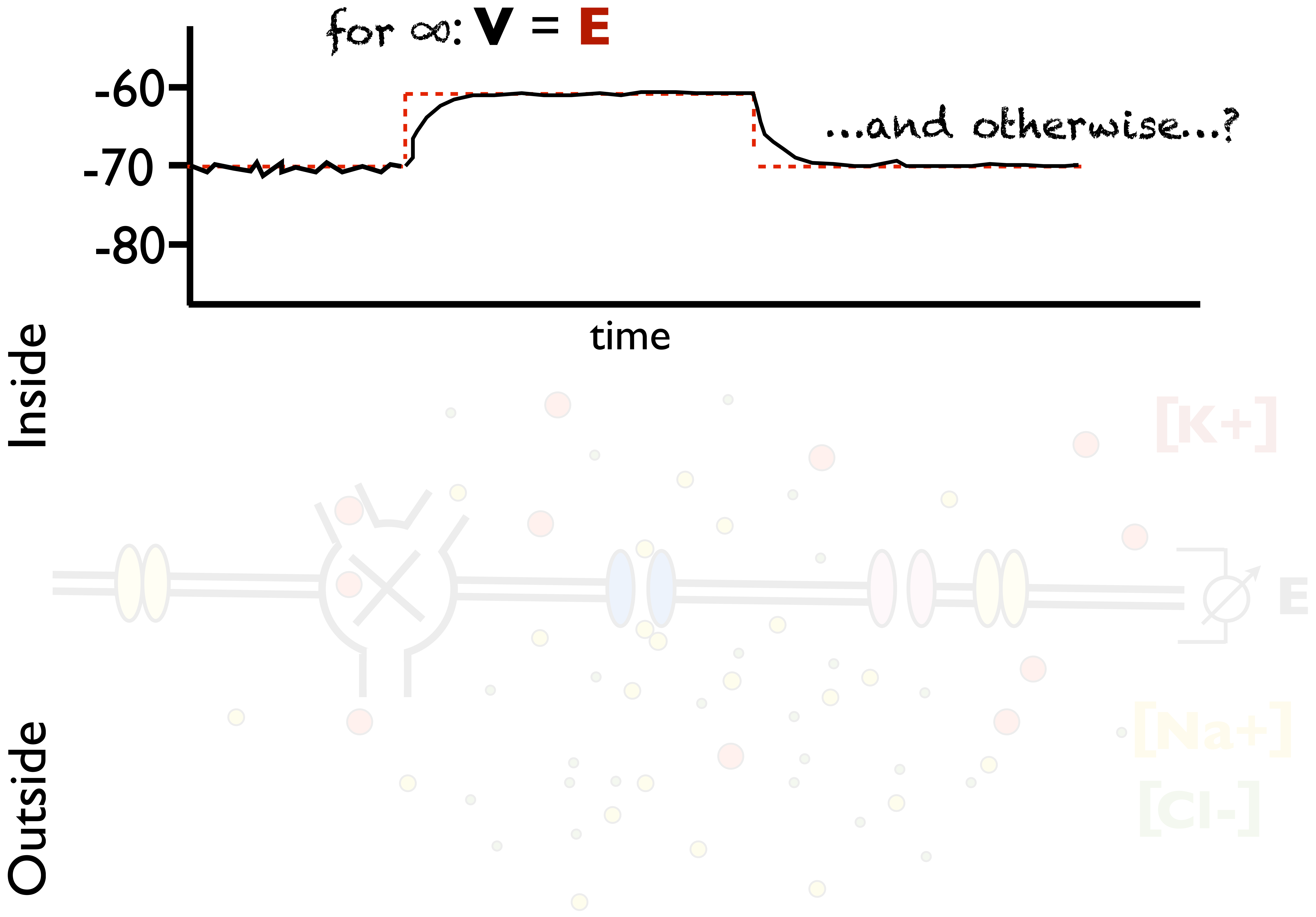
$$E = C \ln\left(\frac{P[K^+]_{out} + P[Na^+]_{out} + P[Cl^-]_{in}}{P[K^+]_{in} + P[Na^+]_{in} + P[Cl^-]_{out}} + \frac{P[K^+]_{out} + P[Na^+]_{out}}{P[K^+]_{in} + P[Na^+]_{in}} \right)$$



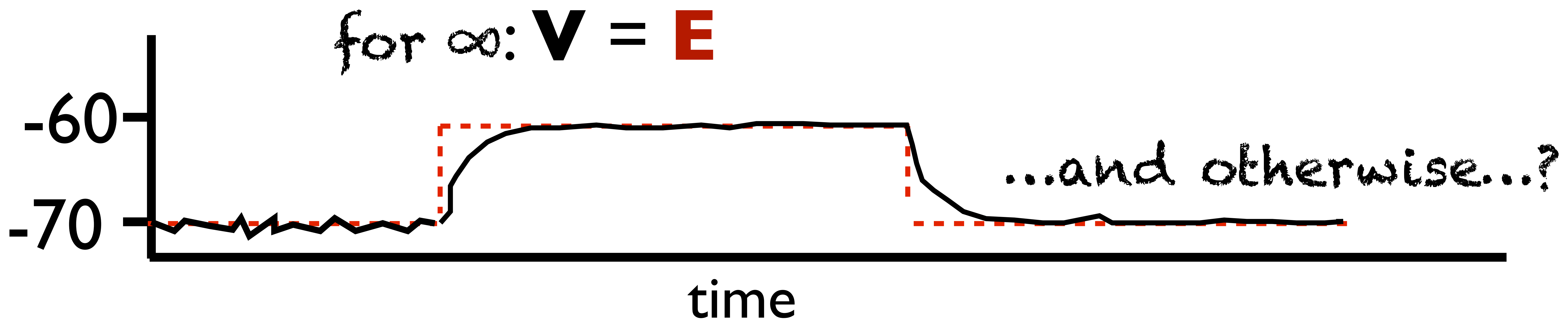
for ∞: **V** = **E**

$$E = C \ln\left(\frac{p[K+]_{out} + p[Na+]_{out} + p[Cl-]_{in}}{p[K+]_{in} + p[Na+]_{in} + p[Cl-]_{out}} + \frac{p[K+]_{out} + p[Na+]_{out}}{p[K+]_{in} + p[Na+]_{in}} \right)$$





for ∞: V = E
-60
-70
-80
...and otherwise...?
time
Inside
Outside
[K+]
E
[Na+]
[Cl-]



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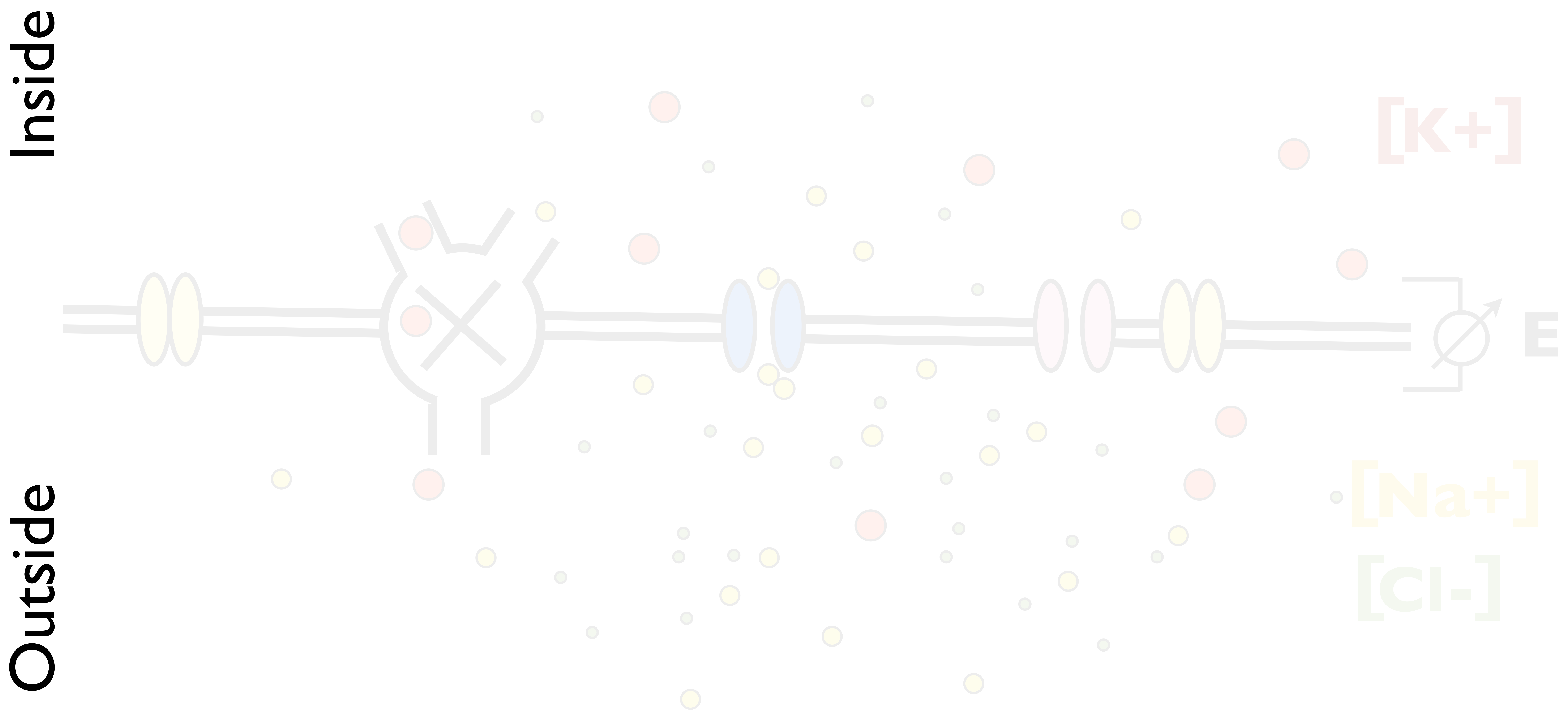
-70
...and otherwise...?
time



Inside
Outside
[K+]
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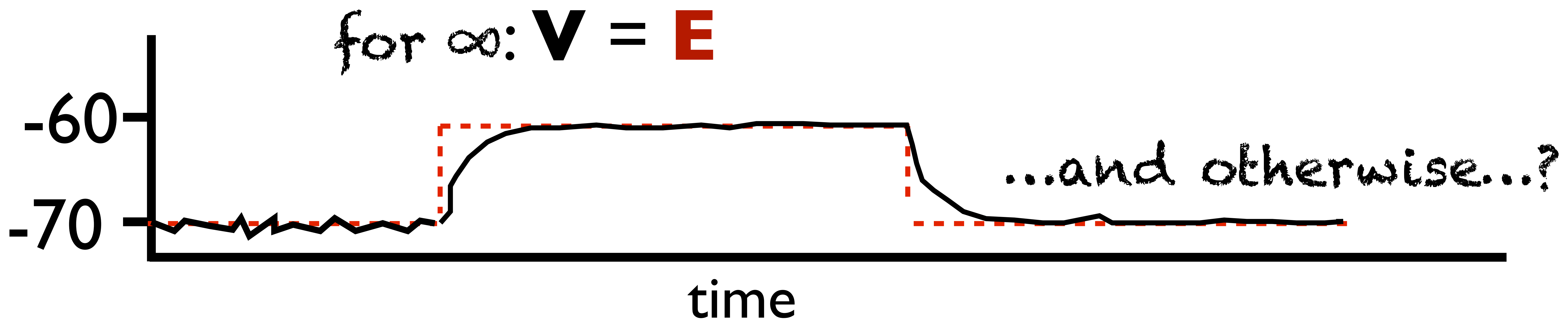
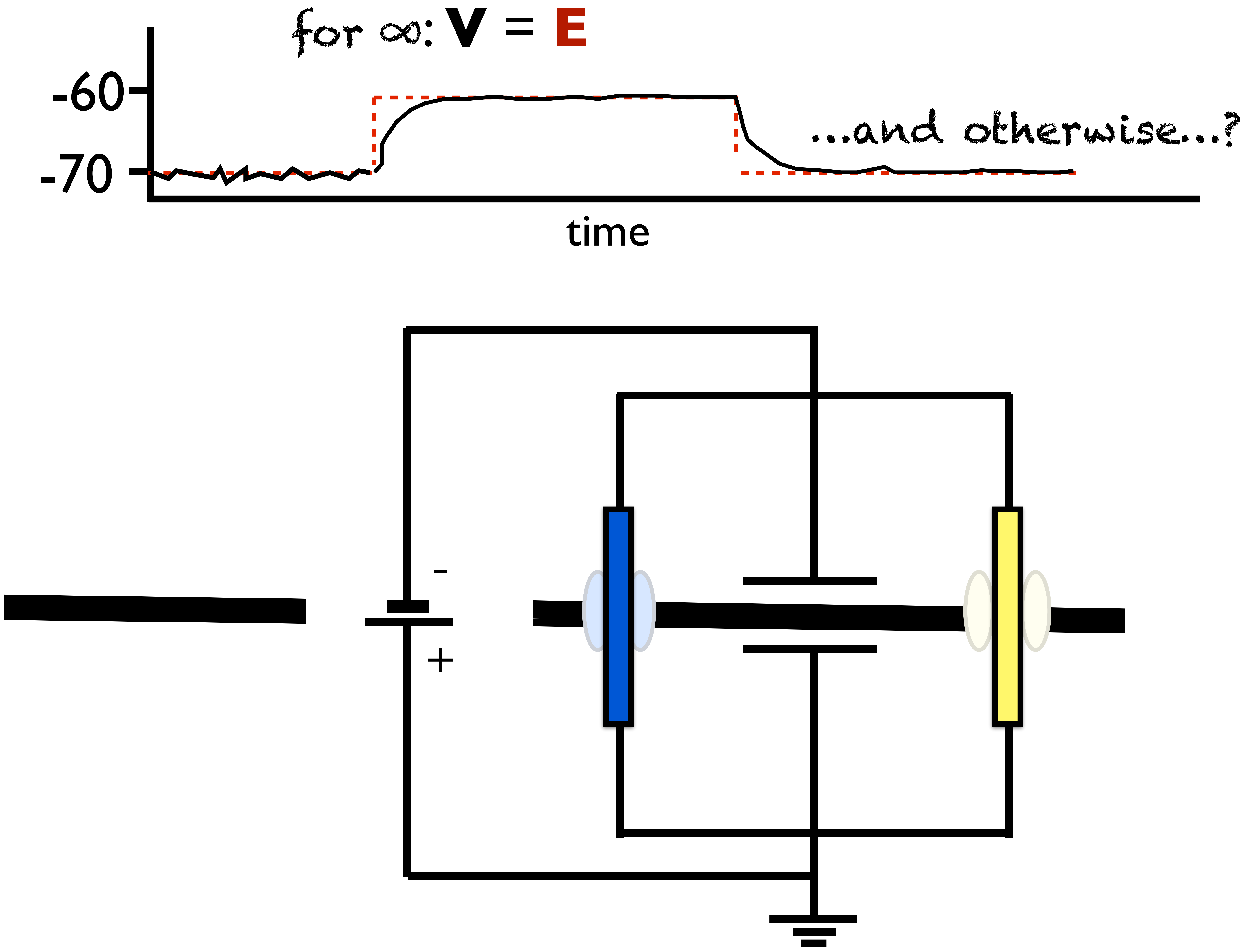
[Na+]
[Cl-]

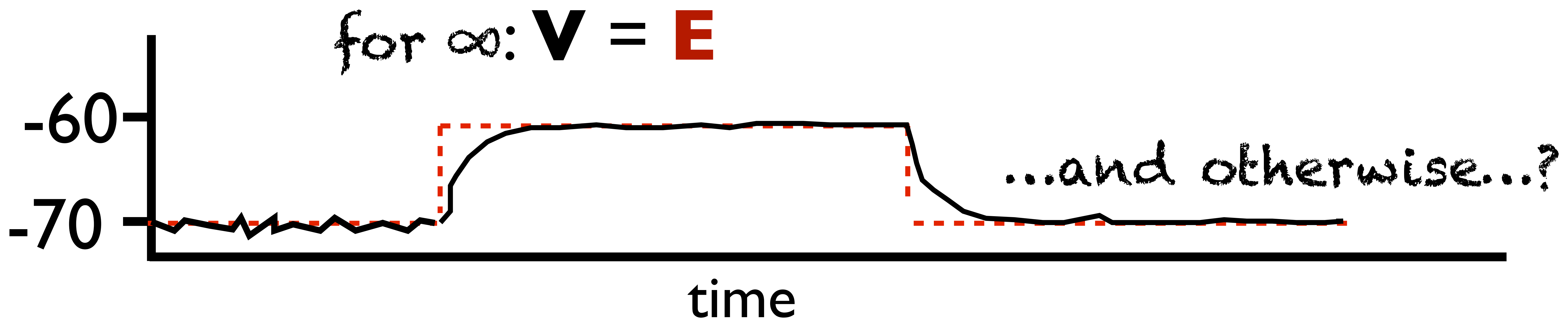


Inside

Outside



for ∞: V = E
-60
-70
...and otherwise...?
time
-
+



for ∞: V = E
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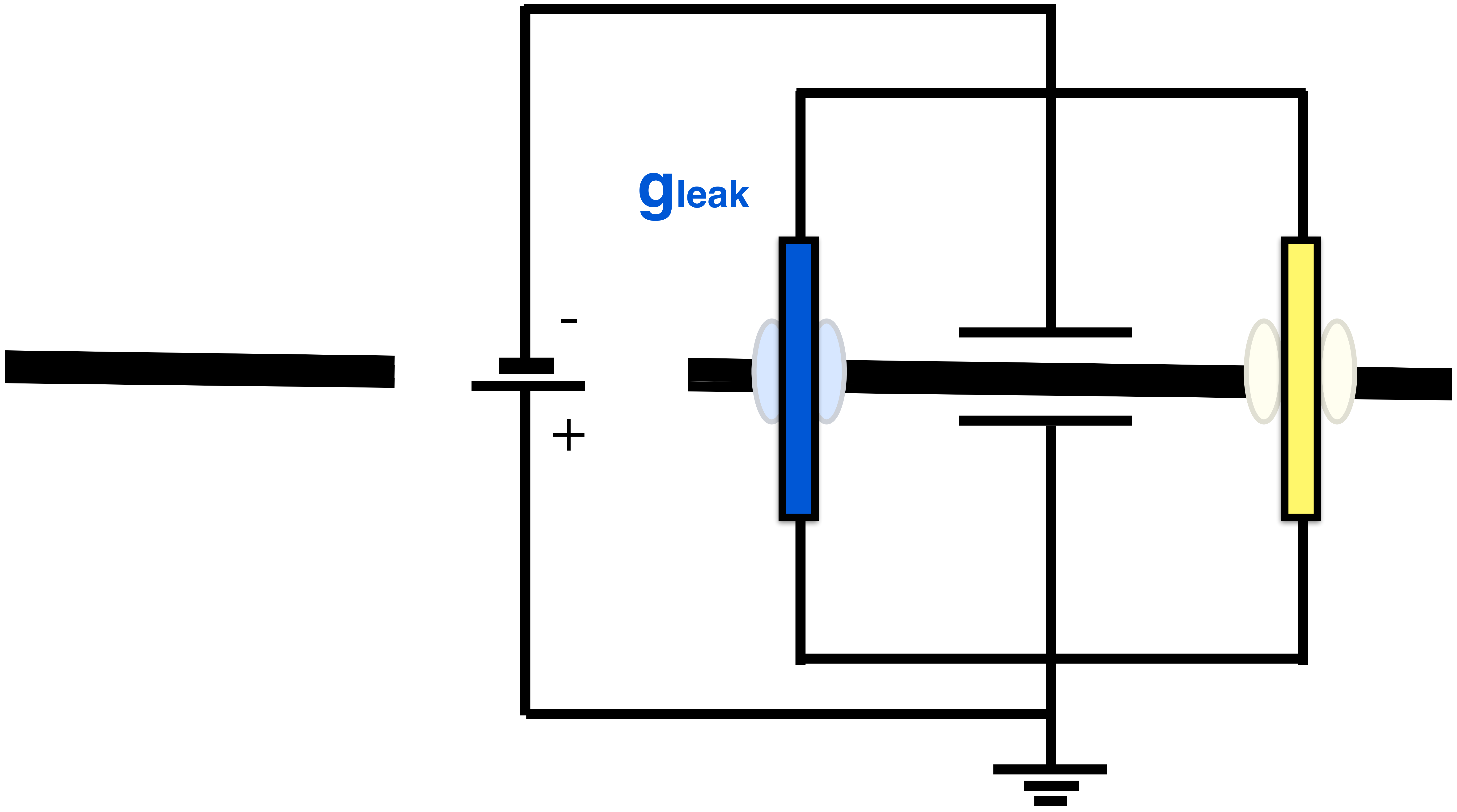
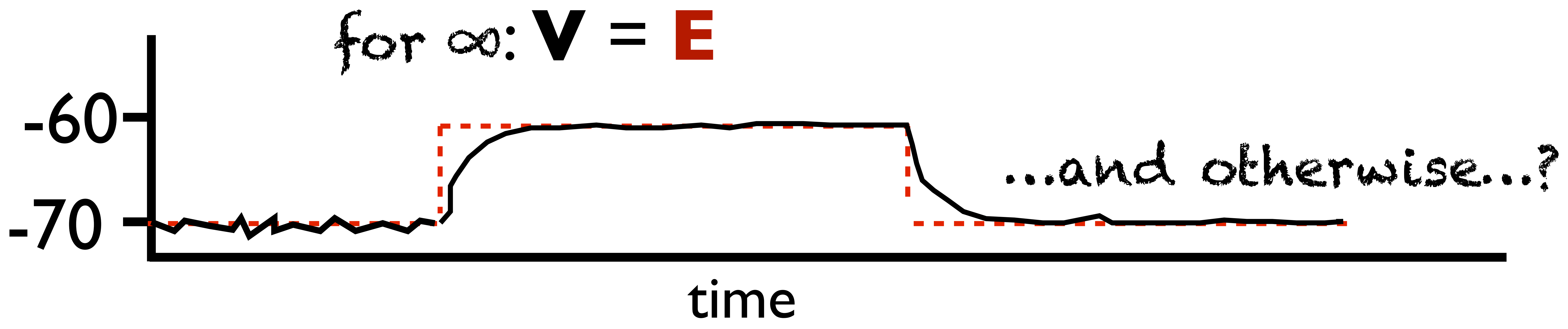
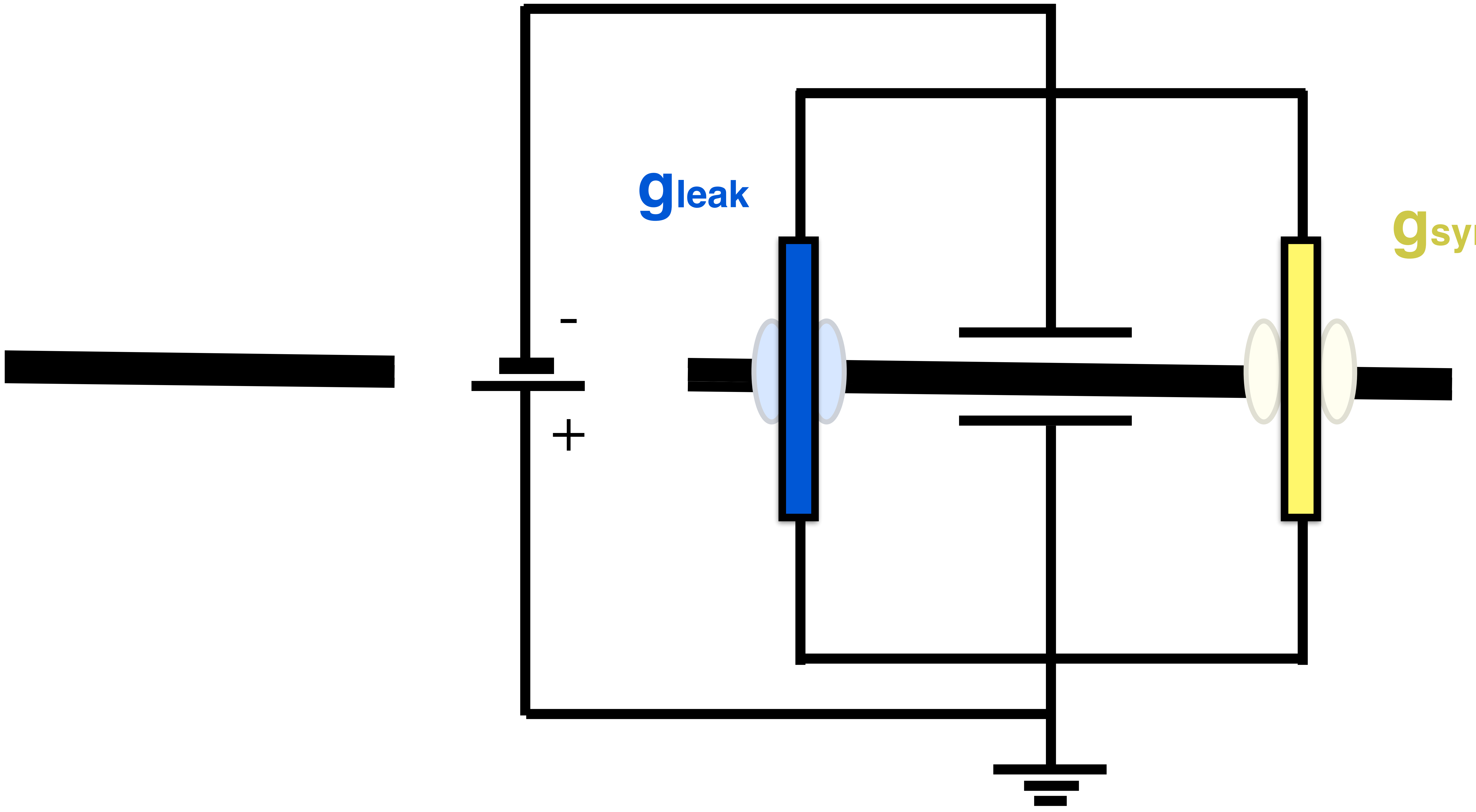
time



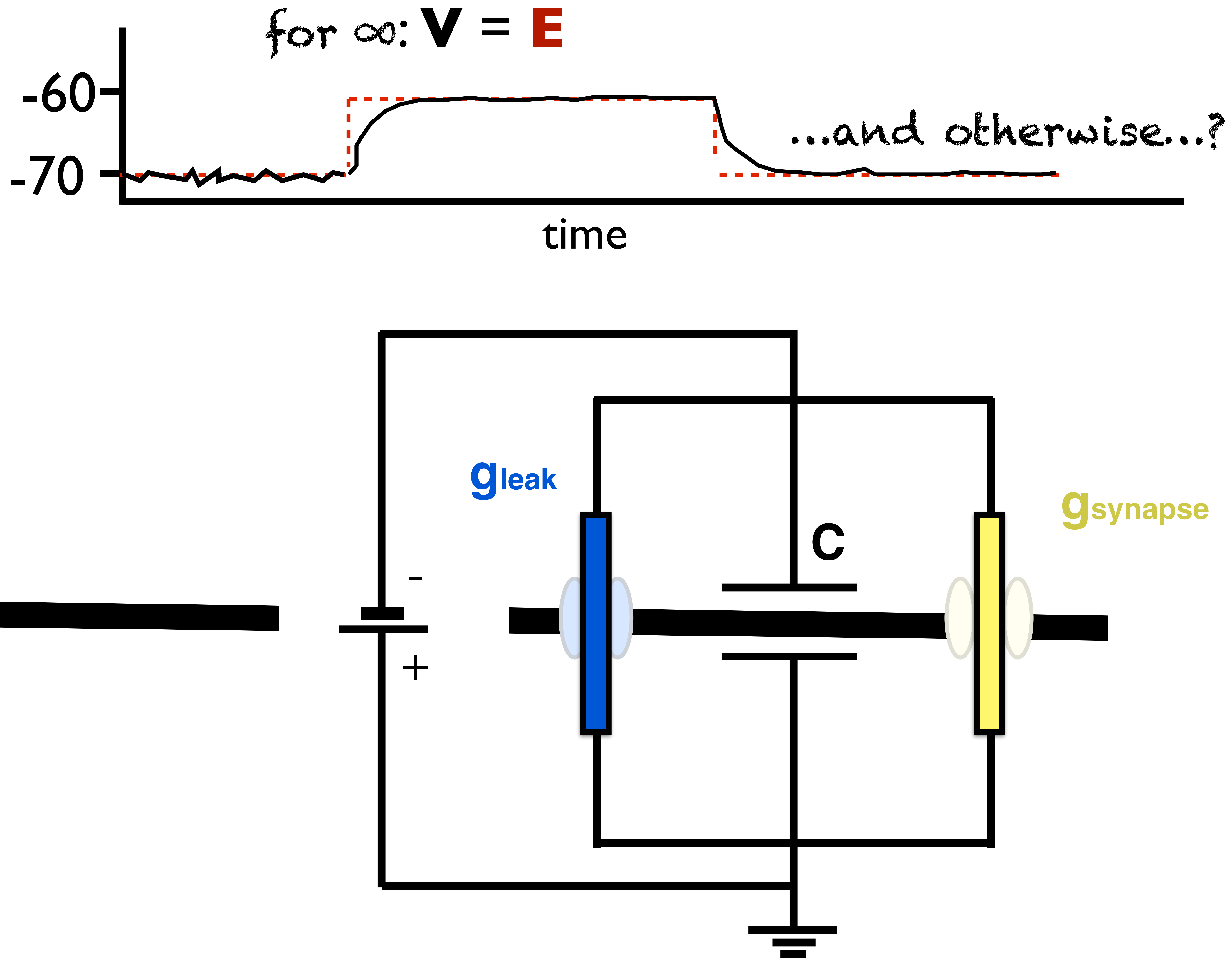
-
+
gleak



for ∞: V = E
-60
-70
...and otherwise...?
time



gleak
gsynapse
-
+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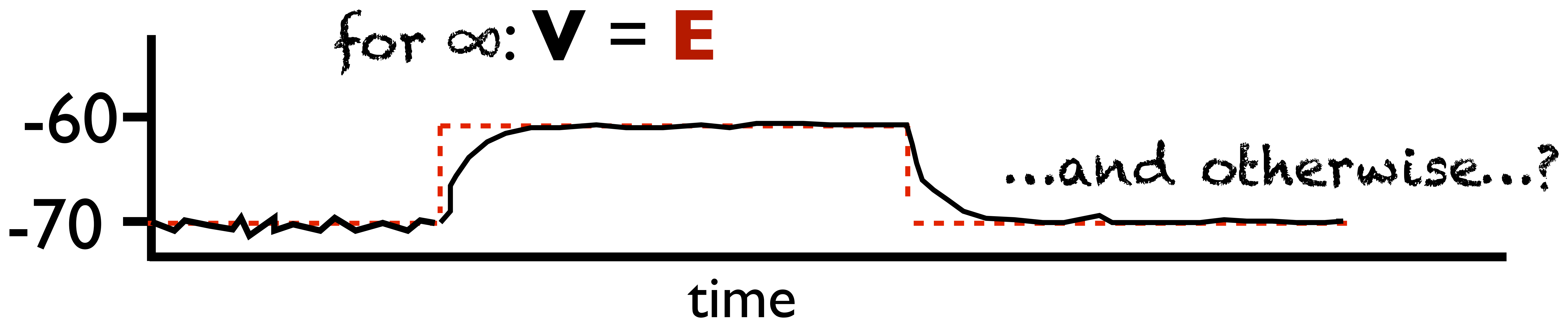
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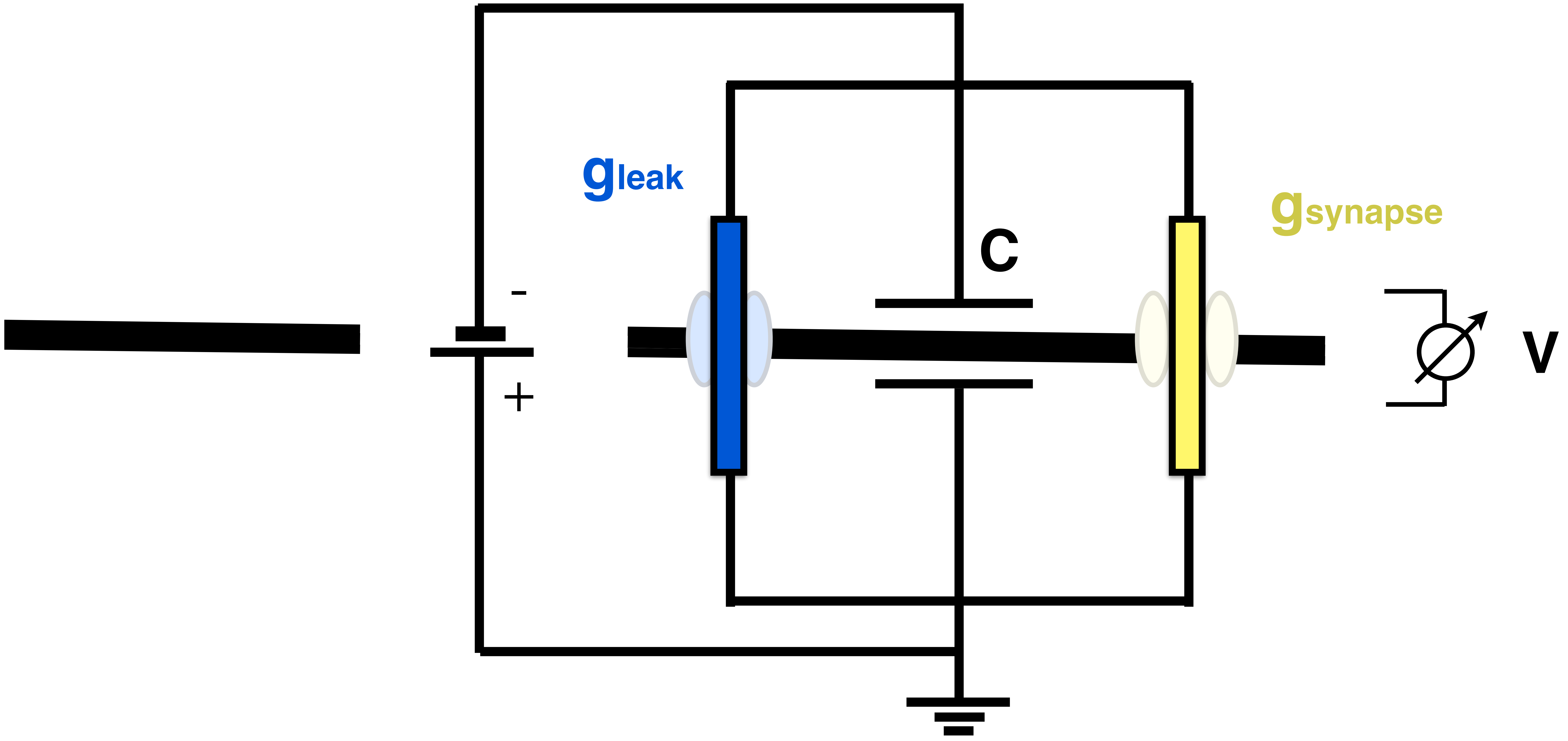
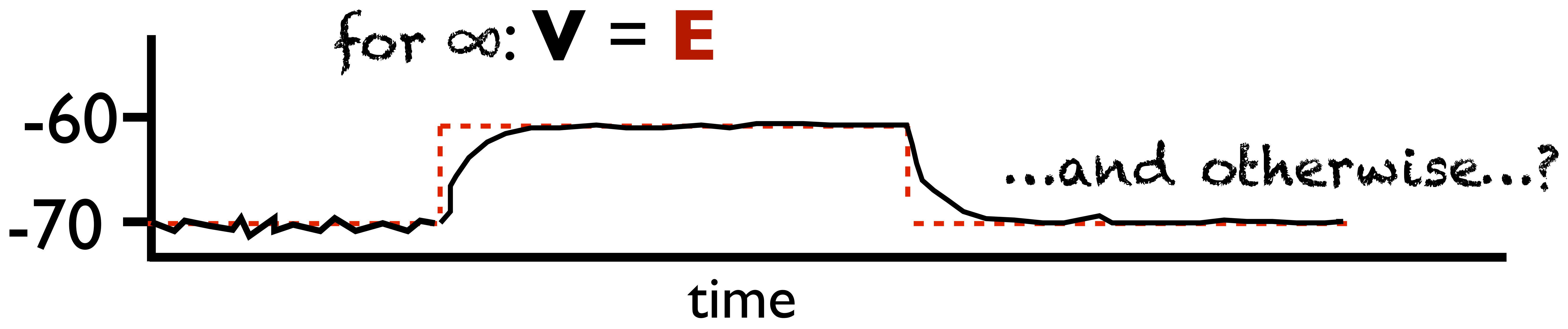

g leak
C
g synapse
-
+
V



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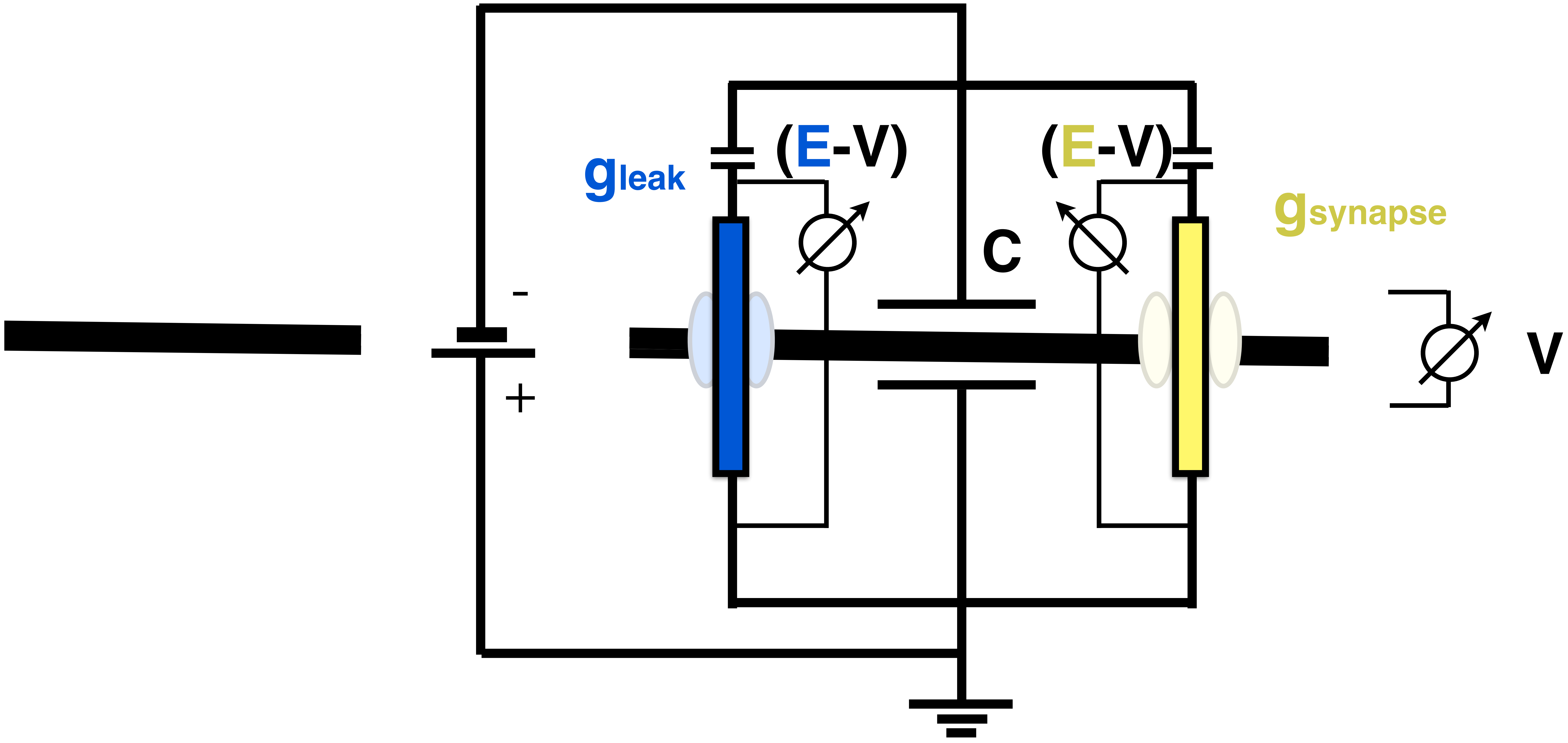
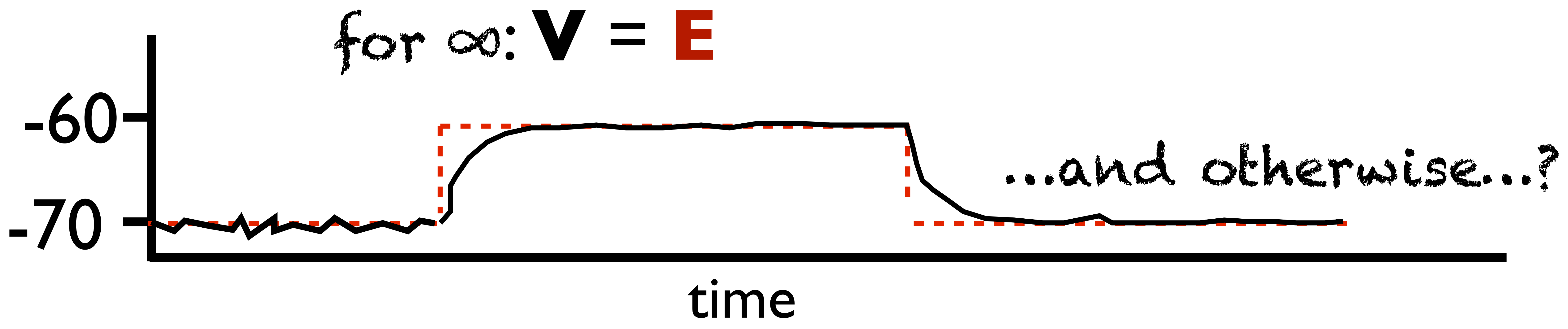


g leak
(E-V)
(E-V)
g synapse
C
-
+
V



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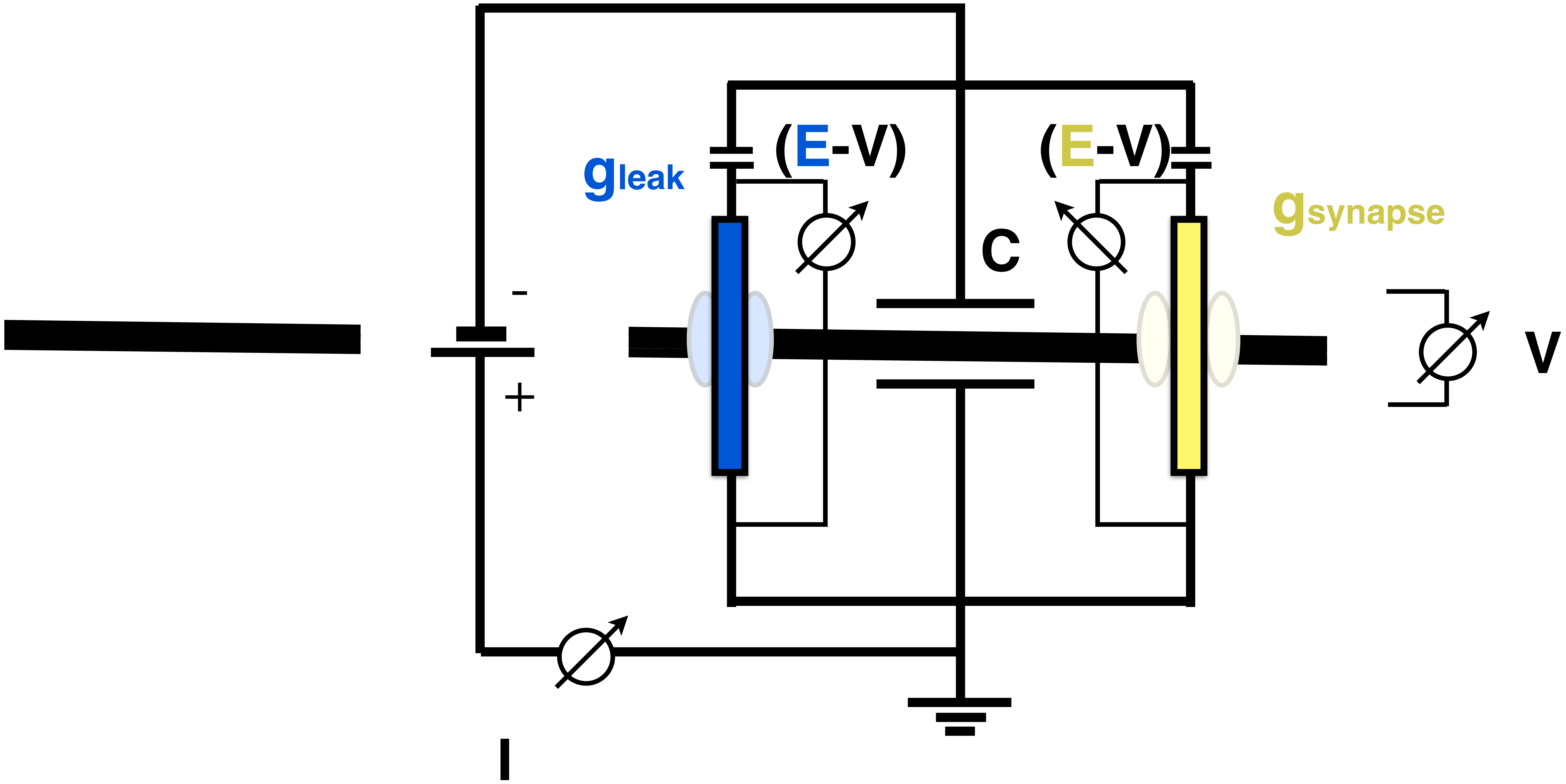
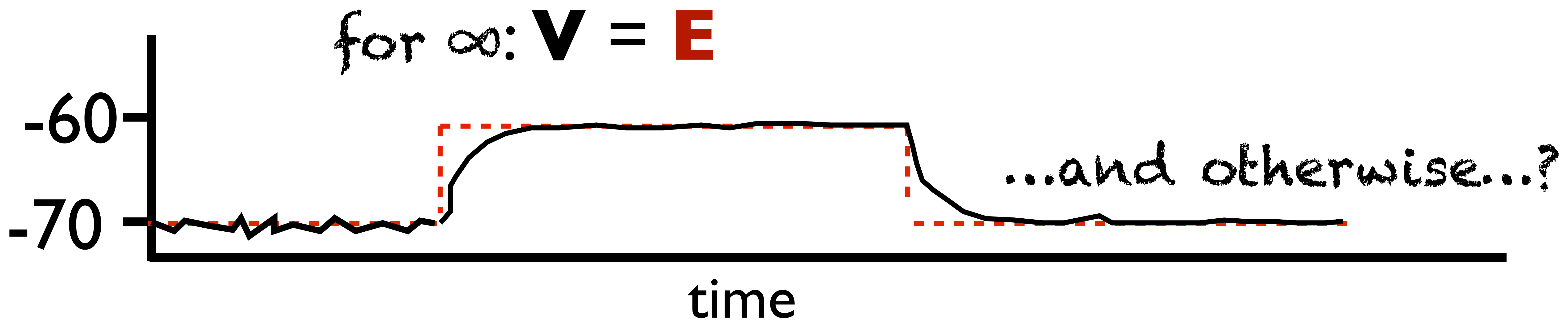
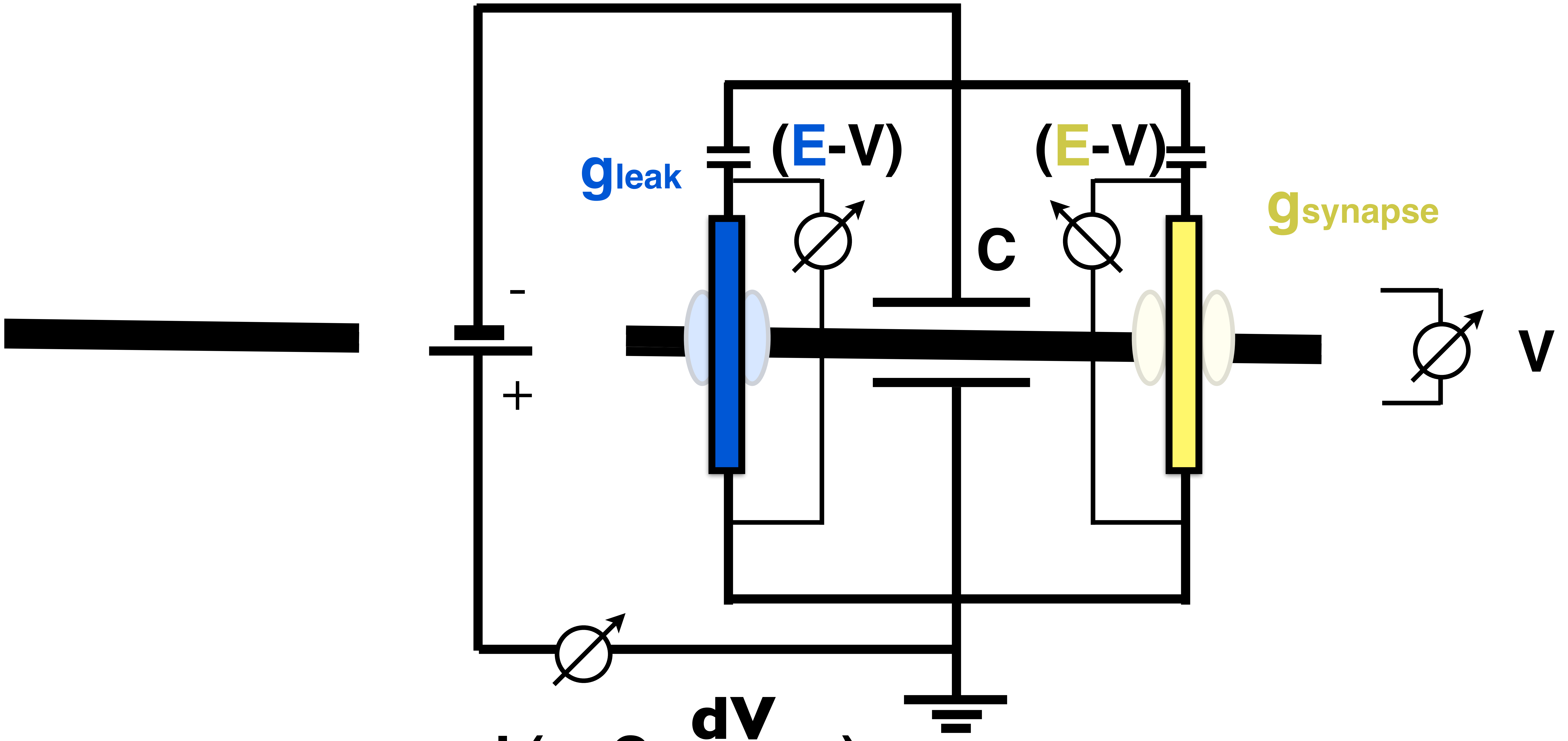


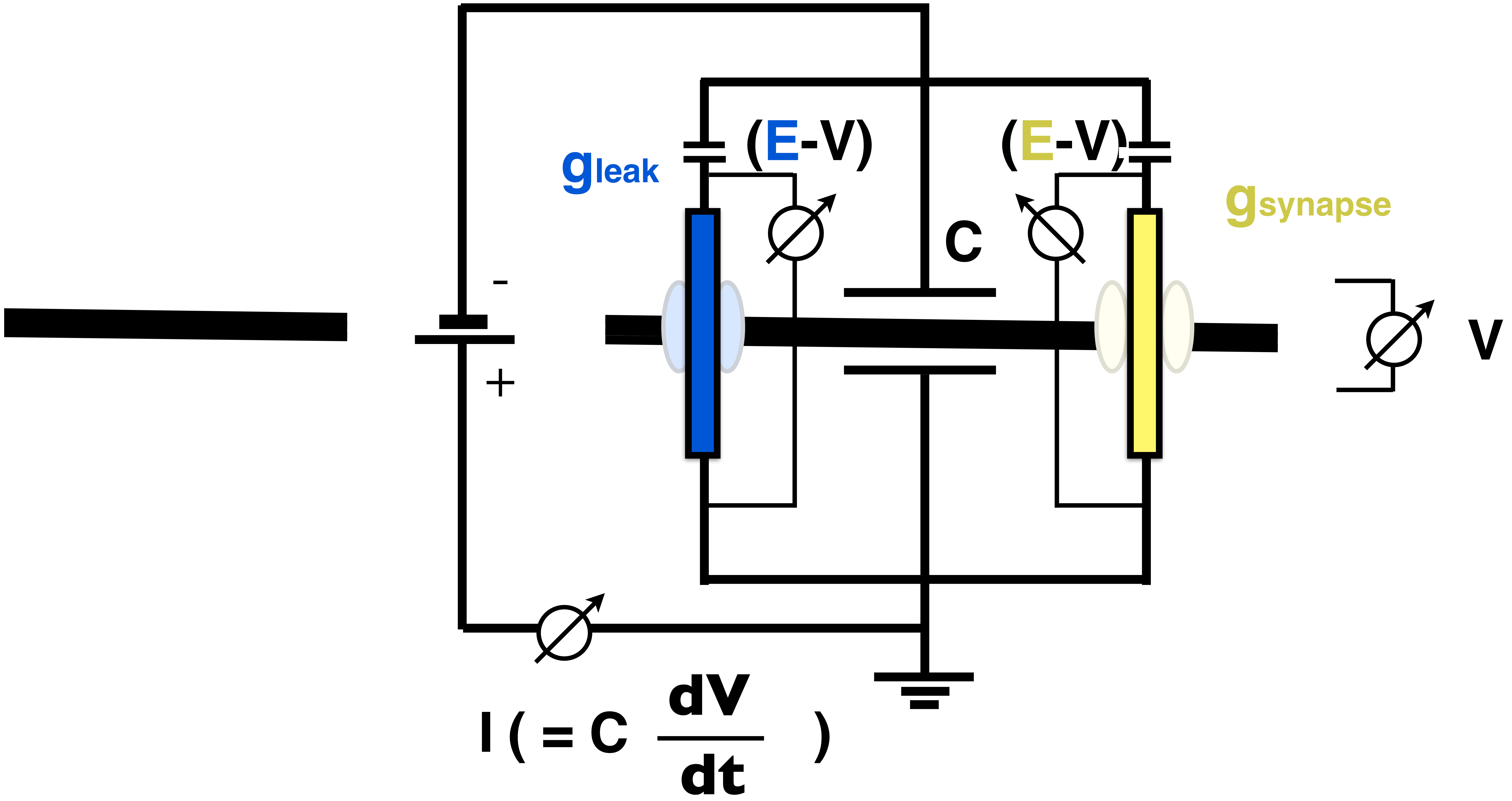
gleak
(E-V)
(E-V)
gsynapse
C
-
+
V
I





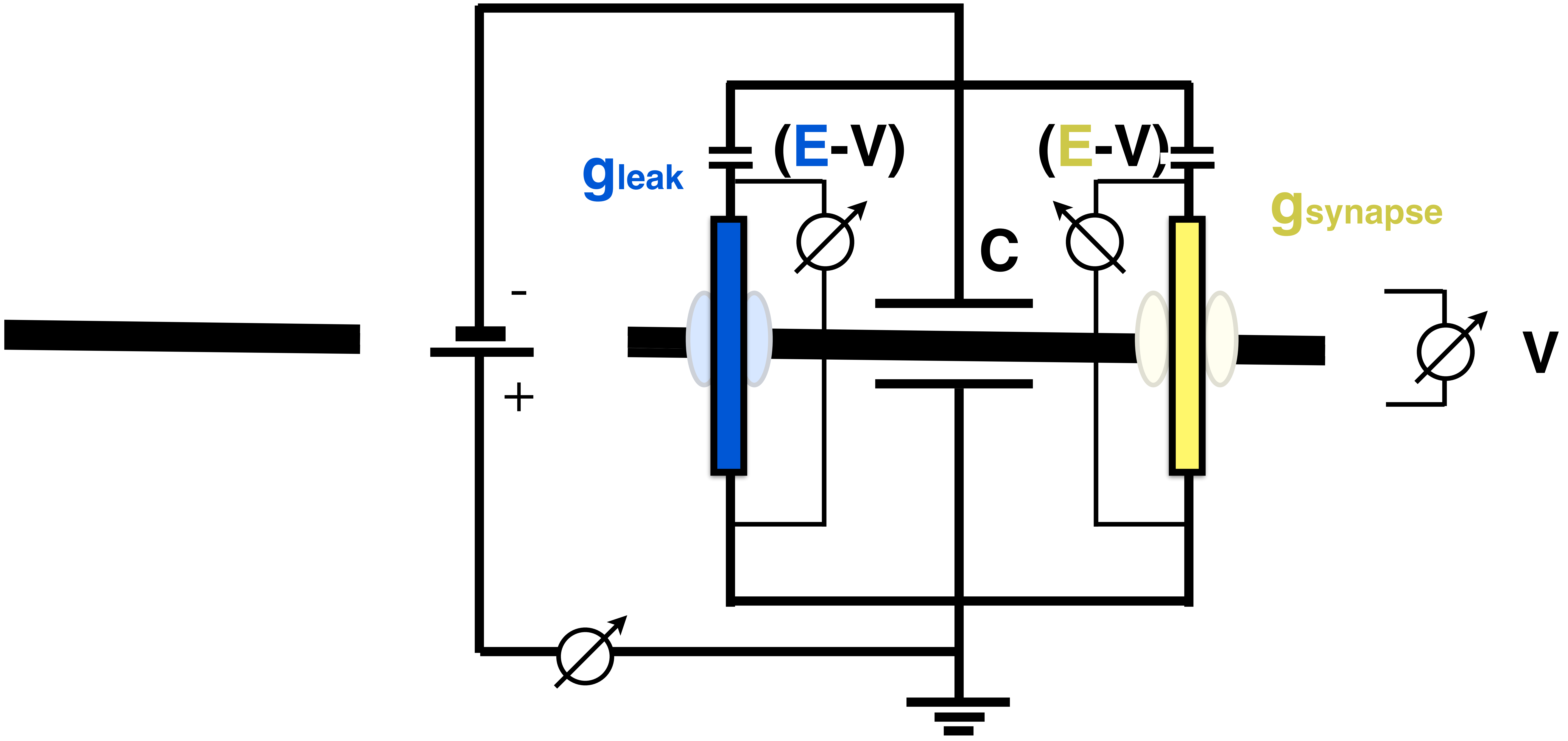
$$I \left(= C \frac{dV}{dt} \right)$$

...and otherwise...?



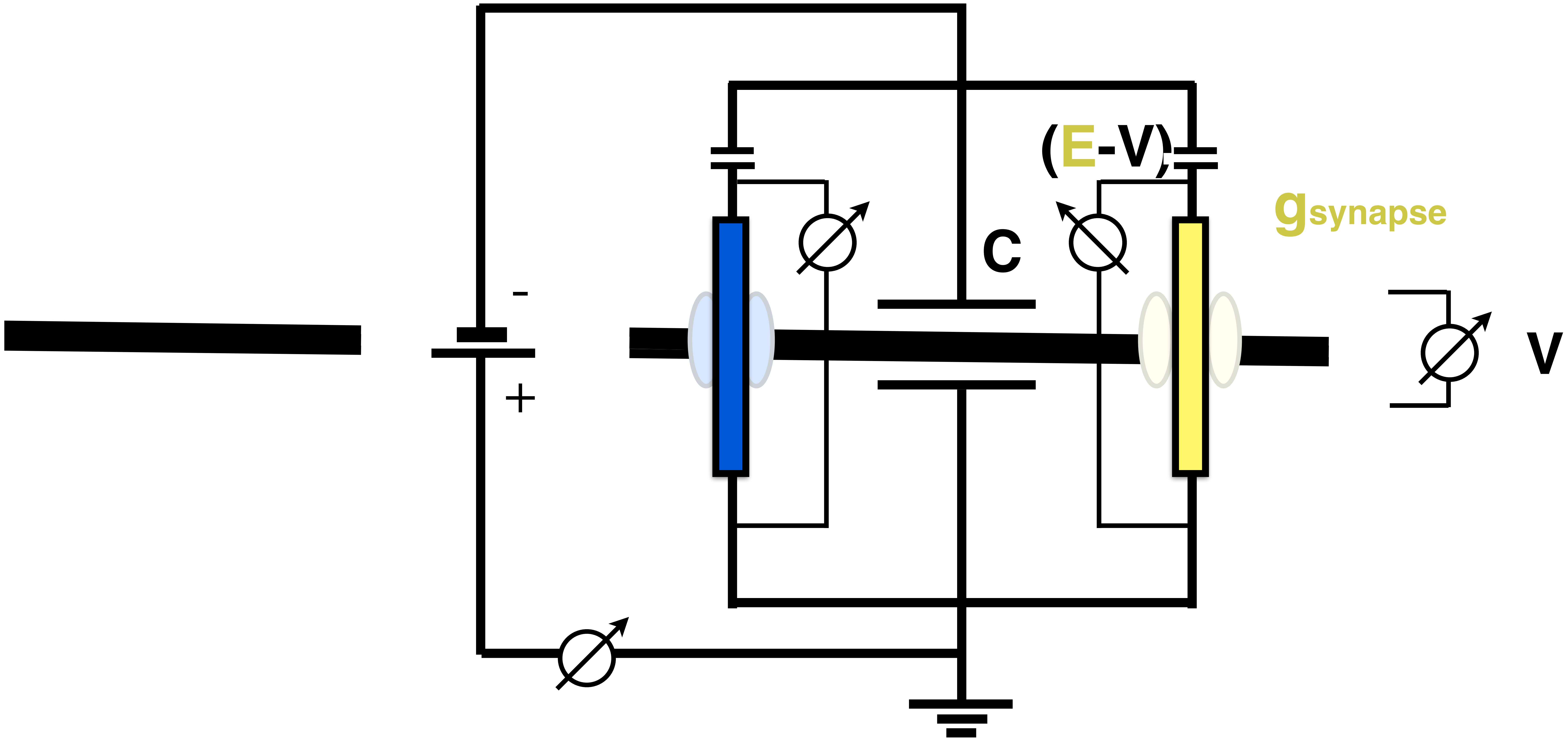
$$\frac{dV}{dt} =$$

...and otherwise...?



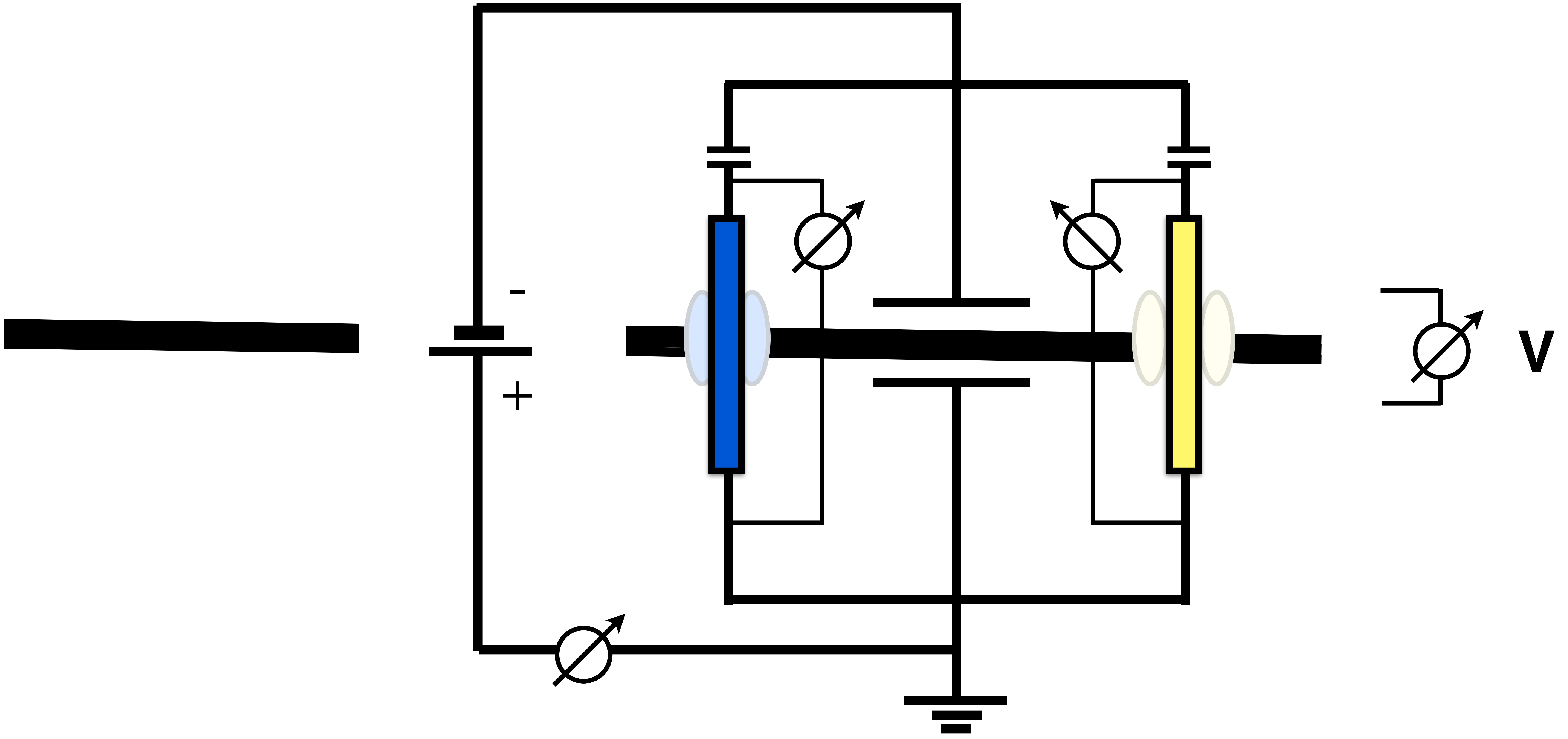
$$\frac{dV}{dt} = g_{leak}\,(E\text{-}V)$$

...and otherwise...?



$$C \frac{dV}{dt} = g_{leak} (E-V) + g_{synapse} (E-V)$$

...and otherwise...?



$$C \frac{dV}{dt} = g_{leak}(E - V) + g_{synapse}(E - V)$$

$$C \frac{dV}{dt} = g_{leak} (E-V) + g_{synapse} (E-V)$$

$$C \frac{dV}{dt} = gE \quad gV + gE \quad gV$$

$$C \frac{dV}{dt} = g_{leak}(E-V) + g_{synapse}(E-V)$$

$$C \frac{dV}{dt} = gE - gV + gE - gV$$

$$C \frac{dV}{dt} = gE - gV + gE - gV$$

$$\frac{C}{g}\frac{dV}{dt} = \frac{gE}{g} - \frac{gV}{g} + \frac{gE}{g} - \frac{gV}{g}$$

$$\frac{C}{g}\frac{dV}{dt} = \frac{gE}{g} - \frac{gV}{g} + \frac{gE}{g} - \frac{gV}{g}$$

$$\tau \frac{dV}{dt} = \frac{gE}{g} - \frac{gV}{g} + \frac{gE}{g} - \frac{gV}{g}$$

$$\tau \frac{dV}{dt} = E - V + \frac{gE}{g} - \frac{gV}{g}$$

$$\tau \frac{dV}{dt} = E - V + \frac{g}{g} E - \frac{g}{g} V$$

$$\tau \frac{dV}{dt} = E + \frac{g}{g}E - V - \frac{g}{g}V$$

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$$\tau \frac{dV}{dt} = E + \frac{g}{g} E - V - \frac{g}{g} V$$

$$- \left(1 + \frac{g}{g}\right)$$

$$- \quad V - \frac{g}{g}$$

$$\tau \frac{dV}{dt} = E + \frac{g}{g} E - \left(1 + \frac{g}{g}\right) V$$

$$\tau \frac{dV}{dt} = E + \frac{g}{g} E - \left(1 + \frac{g}{g}\right) V$$

$$\frac{g}{g} = g \ (\text{with } g_{leak} = 1)$$

$$\tau \frac{dV}{dt} = E + \frac{g}{g}E - \left(1 + \frac{g}{g}\right)V$$

$$\frac{g}{g} = g \text{ (with } g_{leak} = 1)$$

$$\tau \frac{dV}{dt} = E + g\,E - (1 + g)V$$

$$\frac{g}{g} = g \text{ (with } g_{leak} = 1)$$

$$\tau \frac{dV}{dt} = E + g\,E - (1 + g)V$$

$$\frac{g}{g} = g \text{ (with } g_{leak} = 1\text{)}$$

$$\frac{\tau}{(1+g)}\frac{dV}{dt} = \frac{E + g E}{(1+g)} - V$$

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$$\frac{\tau}{(1+g)} = \tau_{eff}$$

$$\tau_{eff} \frac{dV}{dt} = \frac{E + gE}{(1+g)} - V$$

$$\frac{g}{g} = g \text{ (with } g_{leak} = 1\text{)}$$

$$\frac{\tau}{(1+g)} = \tau_{eff}$$

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$$\tau_{eff} \frac{dV}{dt} = E_{eff} - V$$

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$$\frac{C}{g(1+g)} = \frac{\tau}{(1+g)} = \tau_{eff}$$

$$\frac{E + g\,E}{(1+g)} = E_{eff}$$

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$$\frac{g}{g} = g \text{ (with } g_{leak} = 1)$$

$$\frac{C}{\left(g + g\,\frac{g}{g}\right)} = \frac{C}{g(1+g)} = \frac{\tau}{(1+g)} = \tau_{eff}$$

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$$\frac{E + \frac{g}{g} E}{(1 + \frac{g}{g})} = E_{eff}$$

$$\frac{g}{g} = g \ (\text{with } g_{leak} = 1)$$

$$\frac{C}{g_{total}} = \frac{C}{(g + g)} = \frac{C}{\left(g + g\,\frac{g}{g}\right)} = \frac{C}{g(1 + g)} = \frac{\tau}{(1 + g)} = \tau_{eff}$$

$$\tau_{eff}\frac{dV}{dt} = E_{eff} - V$$

$$\frac{E + g\,E}{(1 + g)} = E_{eff}$$

$$\frac{E + \frac{g}{g}E}{\left(1 + \frac{g}{g}\right)} = E_{eff}$$

$$\frac{gE + gE}{g_{total}} = E_{eff}$$

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Neurons have a the resting state (Nernst, Goldman Hodgkin Katz) and we can calculate how it changes.

$$\tau \frac{dV}{dt} = (E-V)$$

$$\frac{dV}{(E-V)} = \frac{dt}{\tau}$$

$$\int_{V(0)}^{V(t)} \frac{dV}{(E-V)} = \int_{0}^{t} \frac{dt}{\tau}$$

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$$\int_{V(0)}^{V(t)} \frac{dV}{(E-V)} = \frac{t}{\tau}$$

$$-\ln(E-V)\Big|_{V(0)}^{V(t)} = \frac{t}{\tau}$$

$$-\ln (E - V) \Big|_{V(0)}^{V(t)} = \frac{t}{\tau}$$

$$-\ln\left(E - V(0)\right) + \ln\left(E - V(t)\right) = \frac{t}{\tau}$$

$$-\ln\left(E-V(0)\right)+\ln\left(E-V(t)\right) = \frac{t}{\tau}$$

$$-\ln\left(\frac{E-V(t)}{E-V(0)}\right) = \frac{t}{\tau}$$

$$-\ln\left(\frac{E-V(t)}{E-V(0)}\right) = \frac{t}{\tau}$$

$$\ln\left(\frac{E-V(t)}{E-V(0)}\right) = -\frac{t}{\tau}$$

$$e^{\left(\ln\left(\frac{E-V(t)}{E-V(0)}\right)\right)} = e^{\left(-\frac{t}{\tau}\right)}$$

$$\frac{E - V(t)}{E - V(0)} = e^{\left(-\frac{t}{\tau}\right)}$$

$$E - V(t) = \left(E - V(0)\right) e^{-\frac{t}{\tau}}$$

$$E - V(t) = \left(E - V(0)\right) e^{-\frac{t}{\tau}}$$

$$-E + E - V(t) = -E + \left(E - V(0)\right) e^{-\frac{t}{\tau}}$$

$$-V(t) = -E + \left(E - V(0)\right) e^{-\frac{t}{\tau}}$$

$$V(t) = E + \left(V(0) - E\right) e^{-\frac{t}{\tau}}$$

A General Solution:

$$V(t+\Delta t) = E + \left(V(t) - E\right) e^{-\frac{\Delta t}{\tau}}$$

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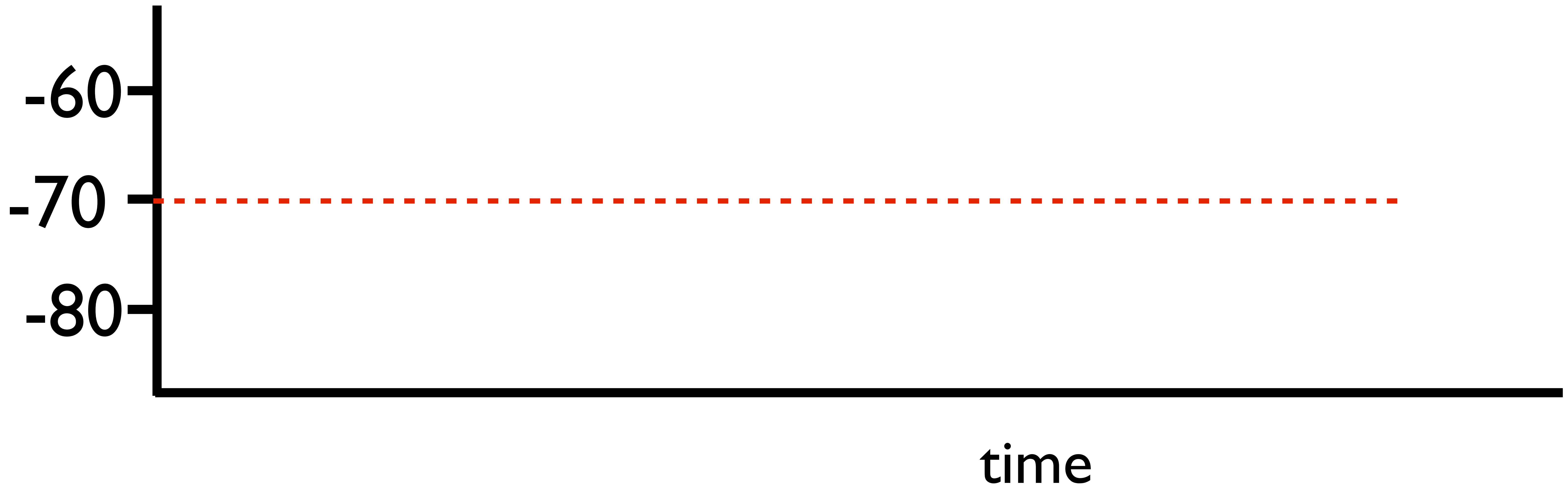
$$V_{(t+\Delta t)} = E + \left(V(t) - E\right) e^{-\frac{\Delta t}{\tau}}$$



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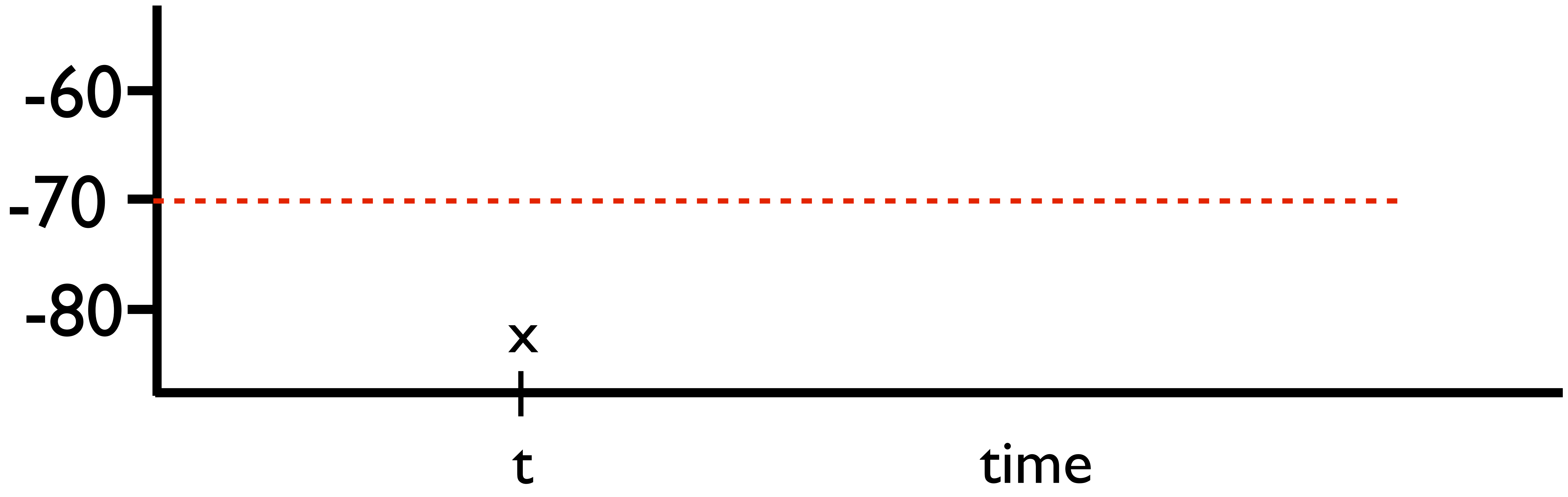

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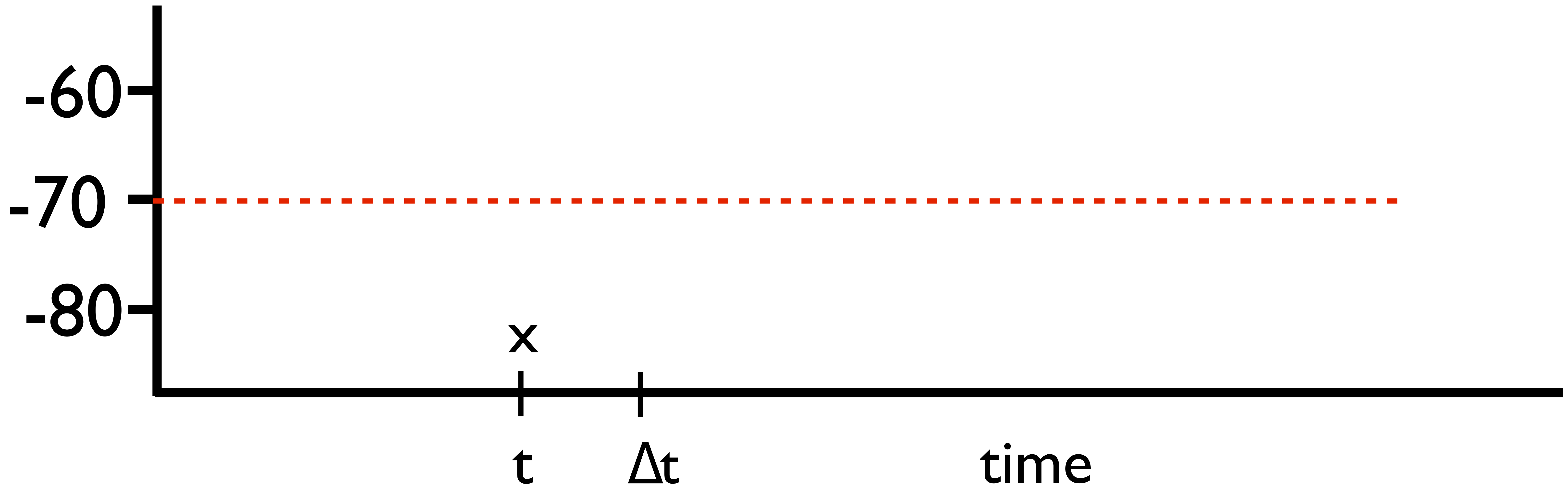

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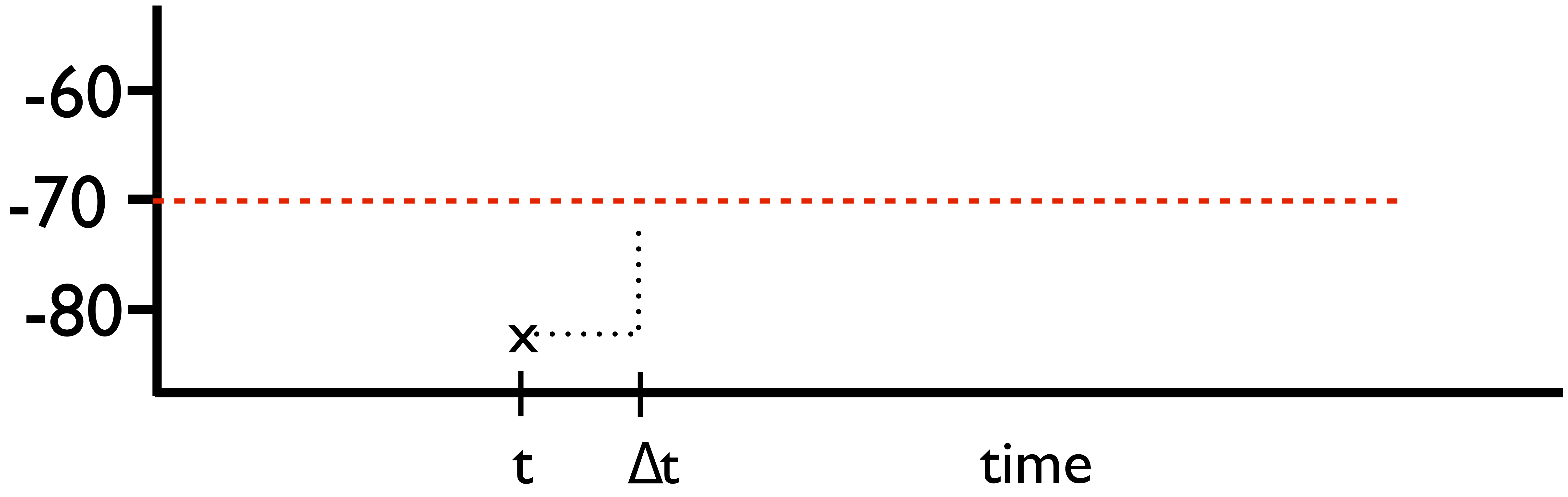

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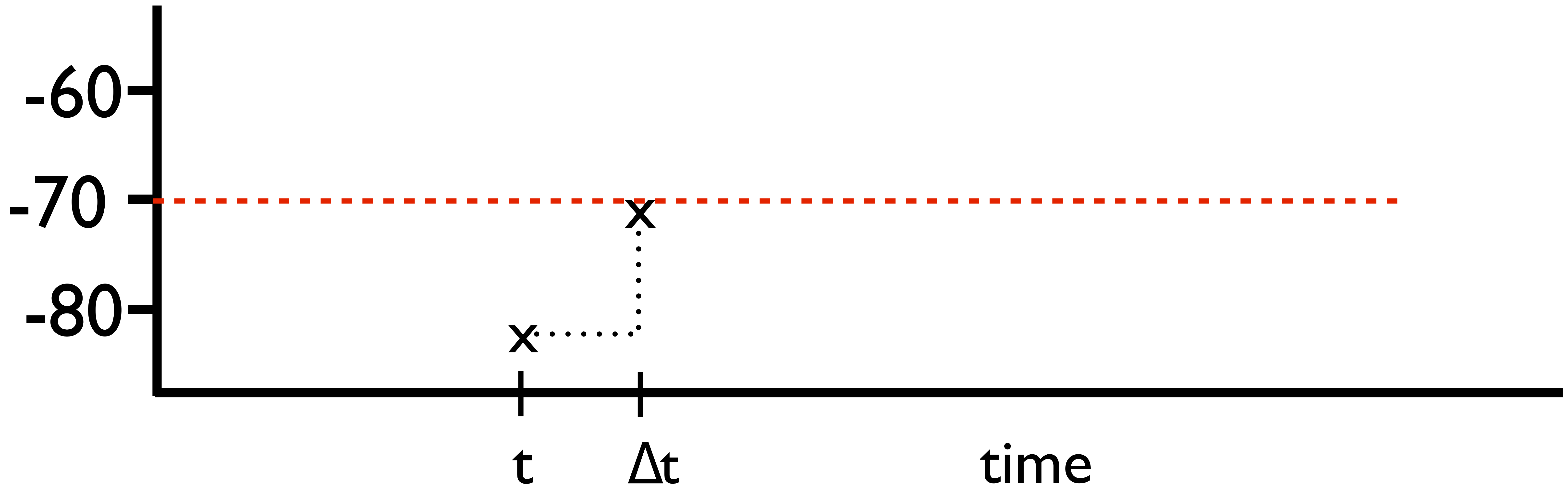

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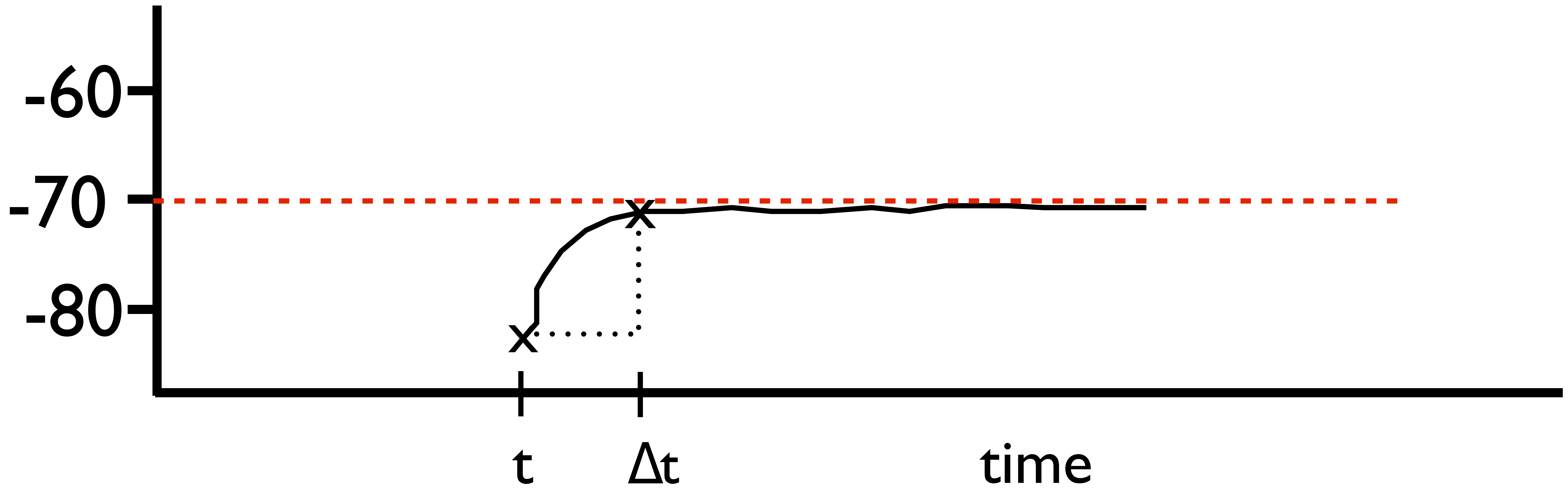
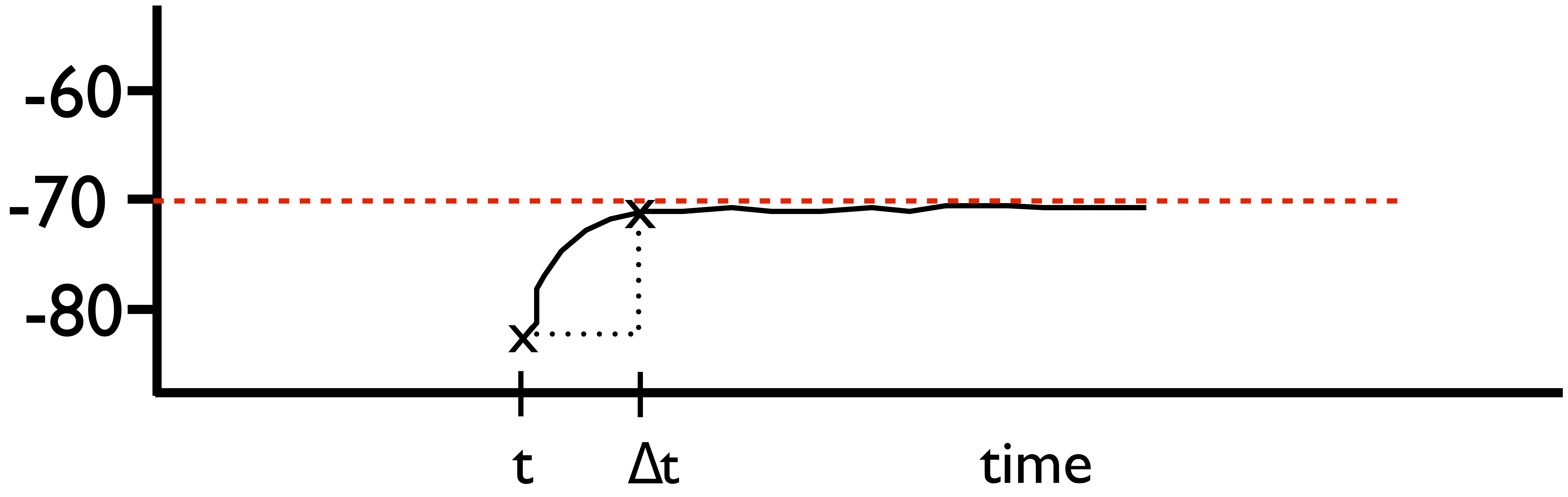


A General Solution:

(for time-independent E)

$$V(t+\Delta t) = E + \left(V(t) - E\right) e^{-\frac{\Delta t}{\tau}}$$



(because this step does not work for E(t): $\displaystyle\int_{V(0)}^{V(t)} \frac{dV}{(E-V)} = \int_{0}^{t} \frac{dt}{\tau}$)

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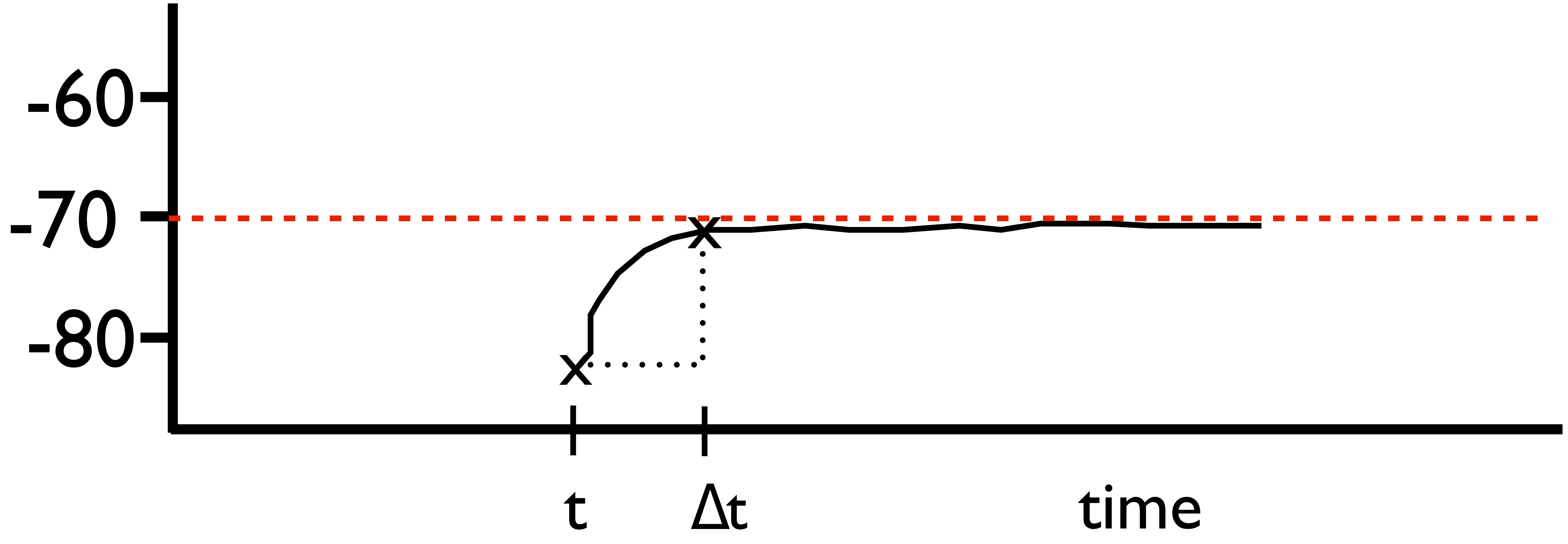

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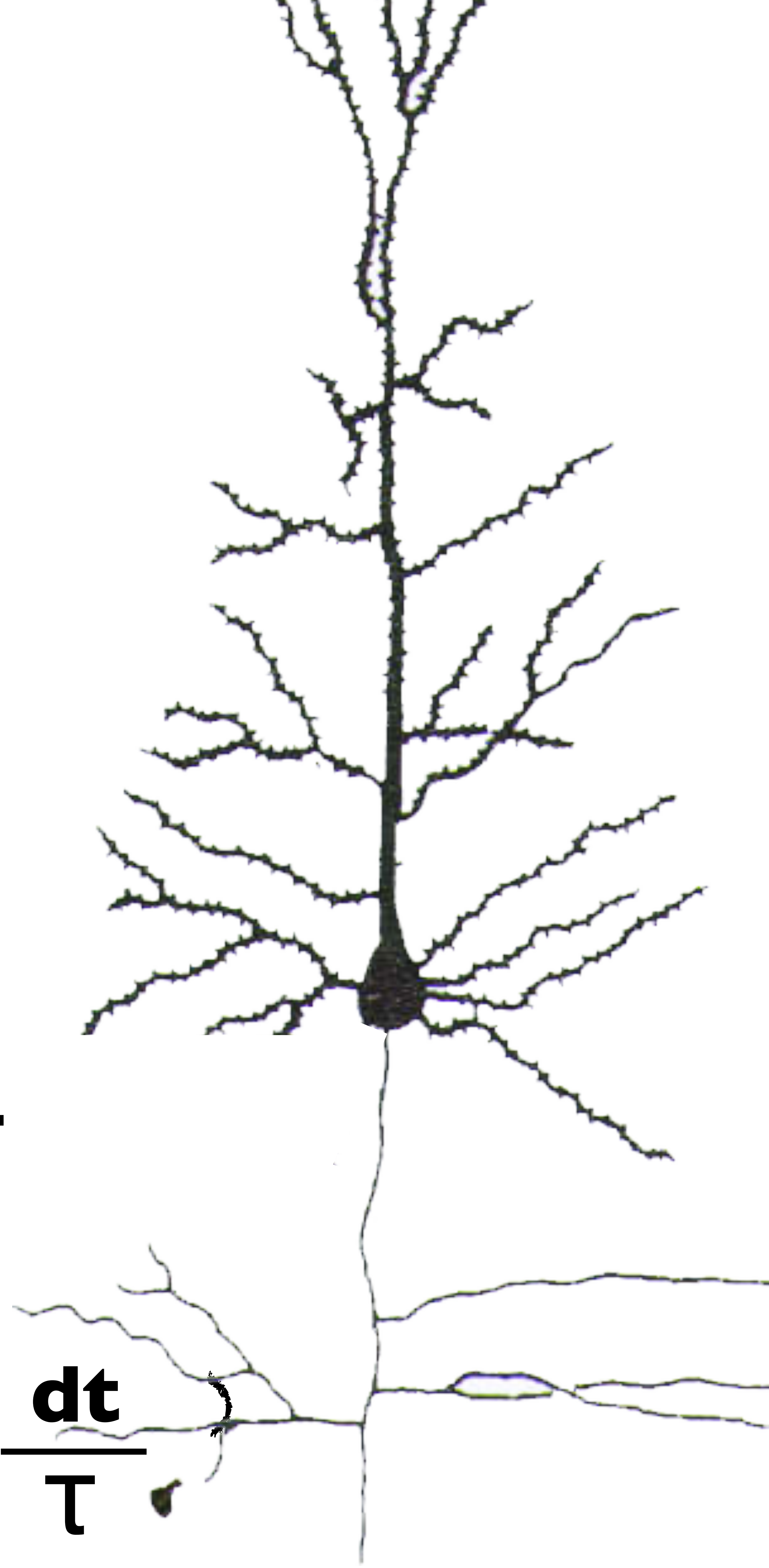

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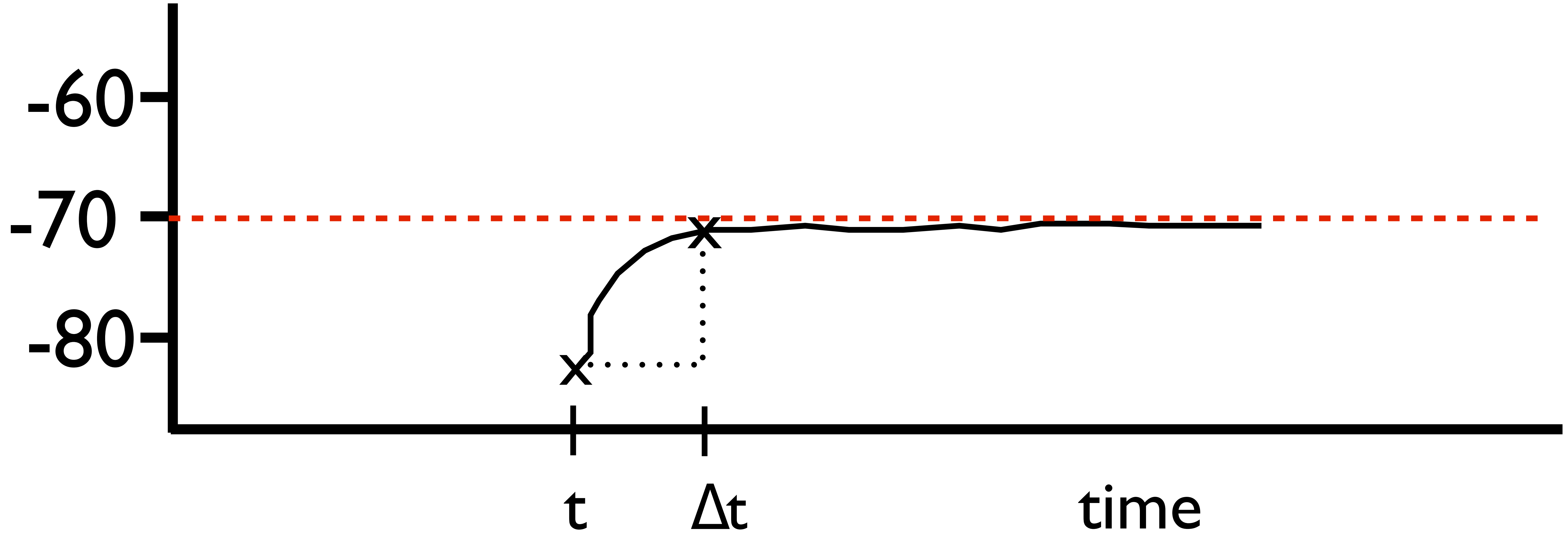

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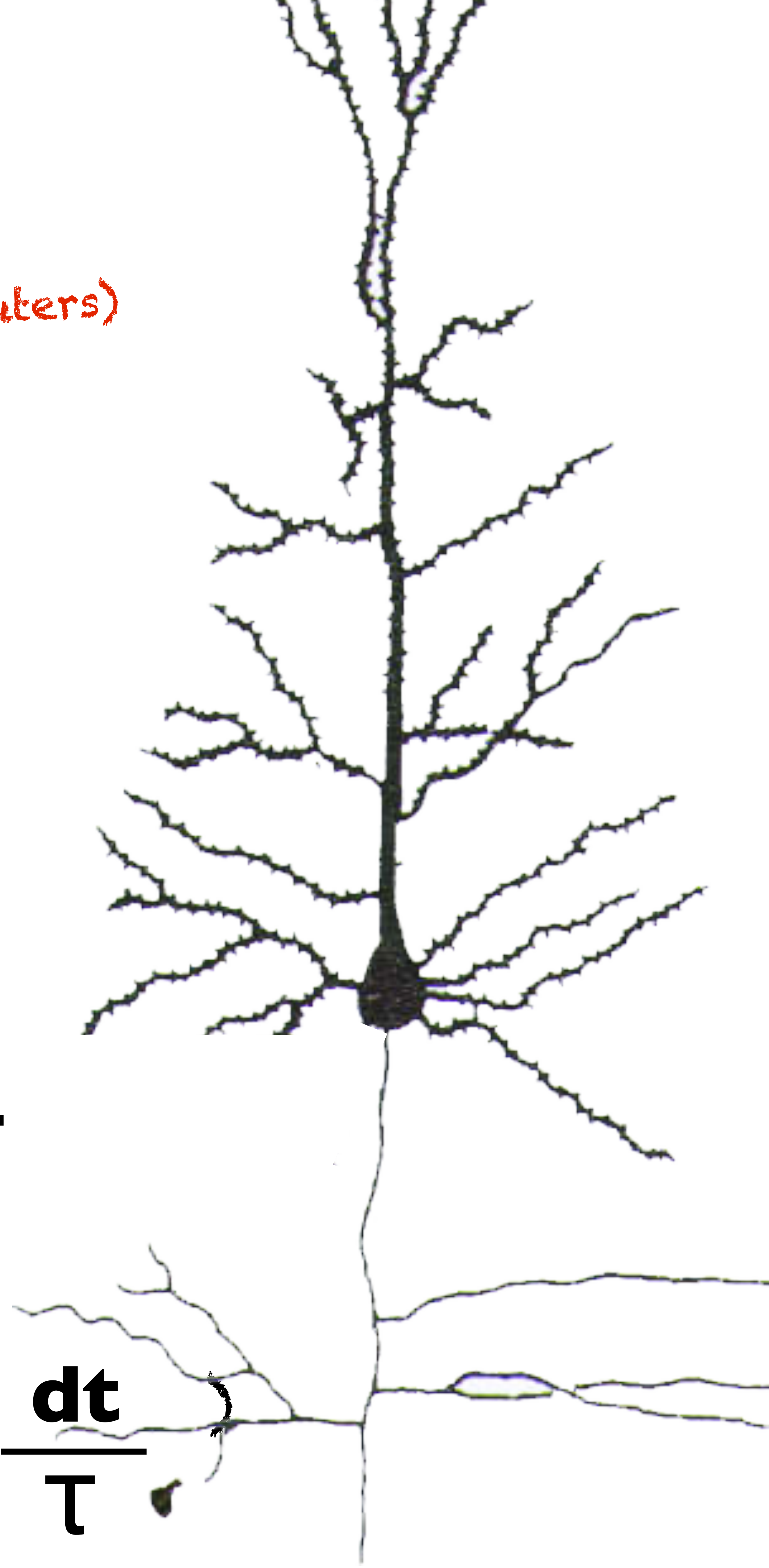

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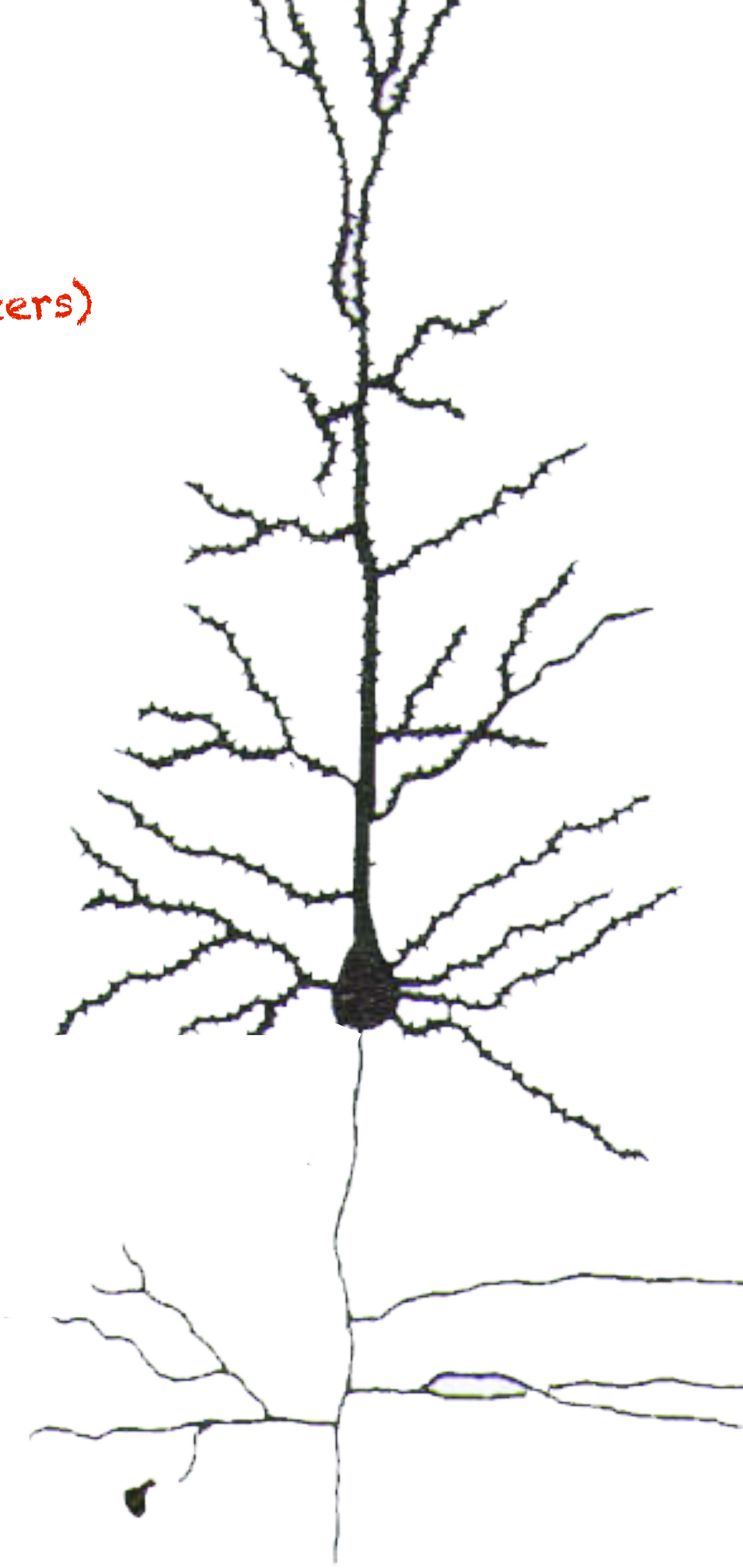

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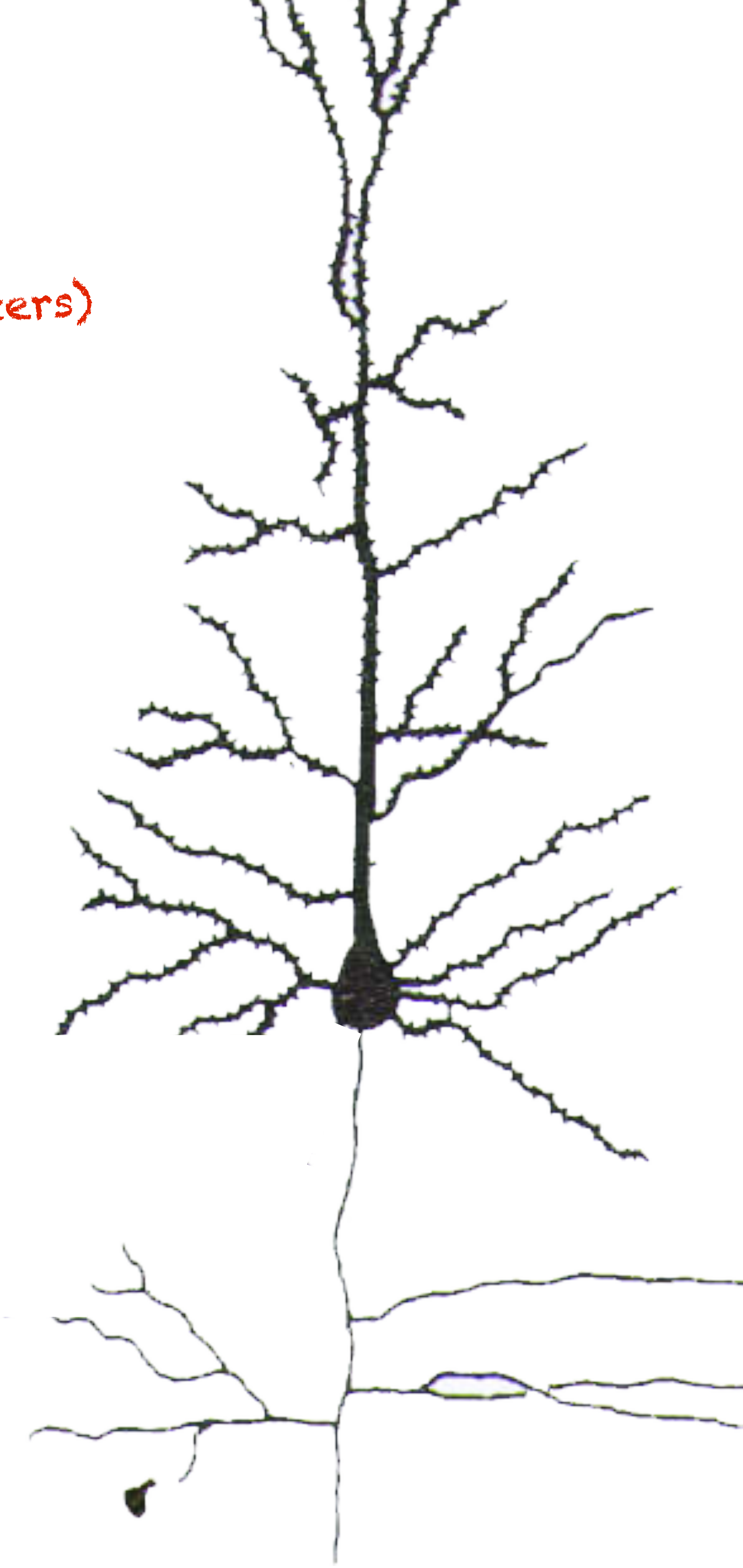
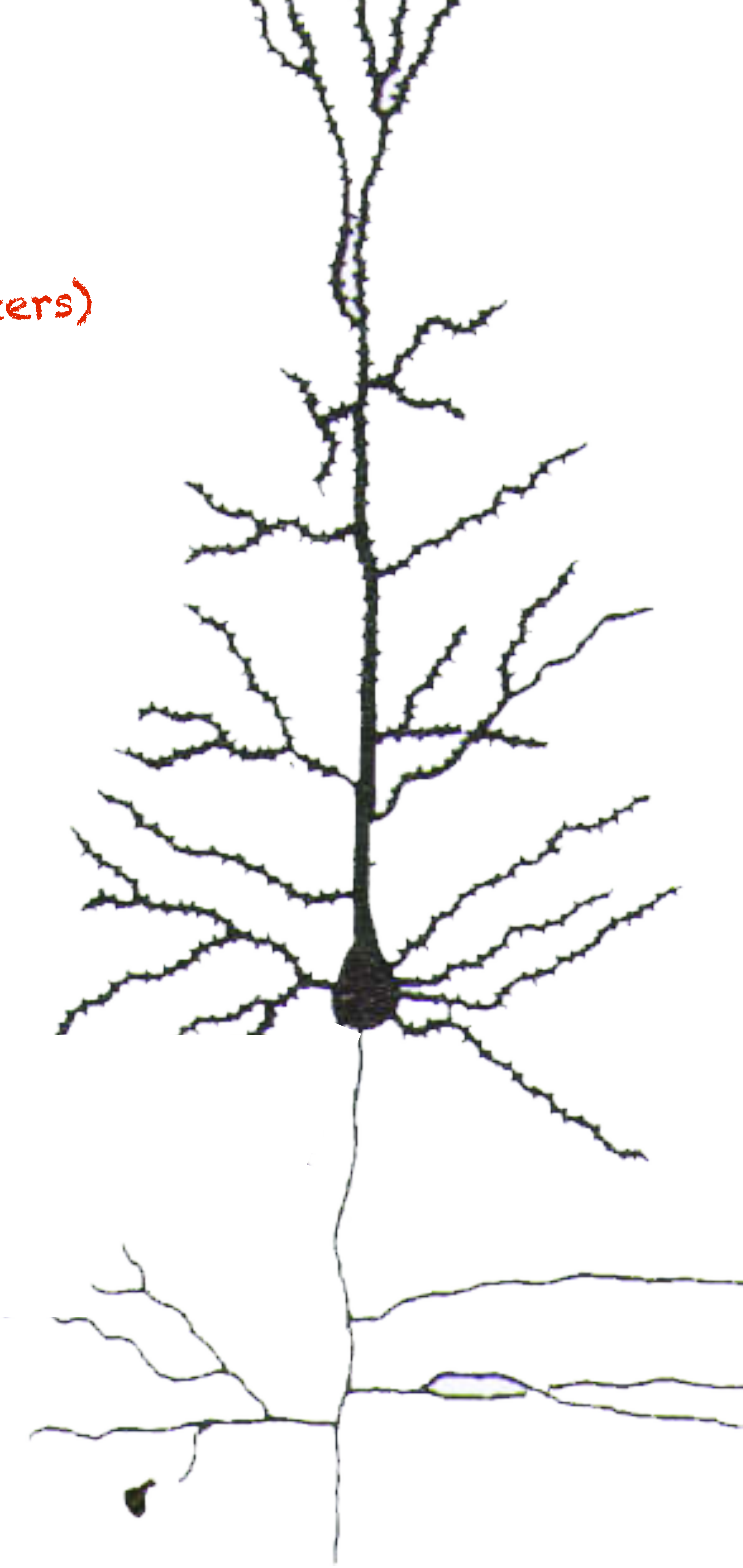


A General Solution:

(for time-independent E)
(lucky us, we have computers)

$$V(t+\Delta t) = E(\Delta t) + \left(V(t) - E(\Delta t)\right) e^{-\frac{\Delta t}{\tau(\Delta t)}}$$



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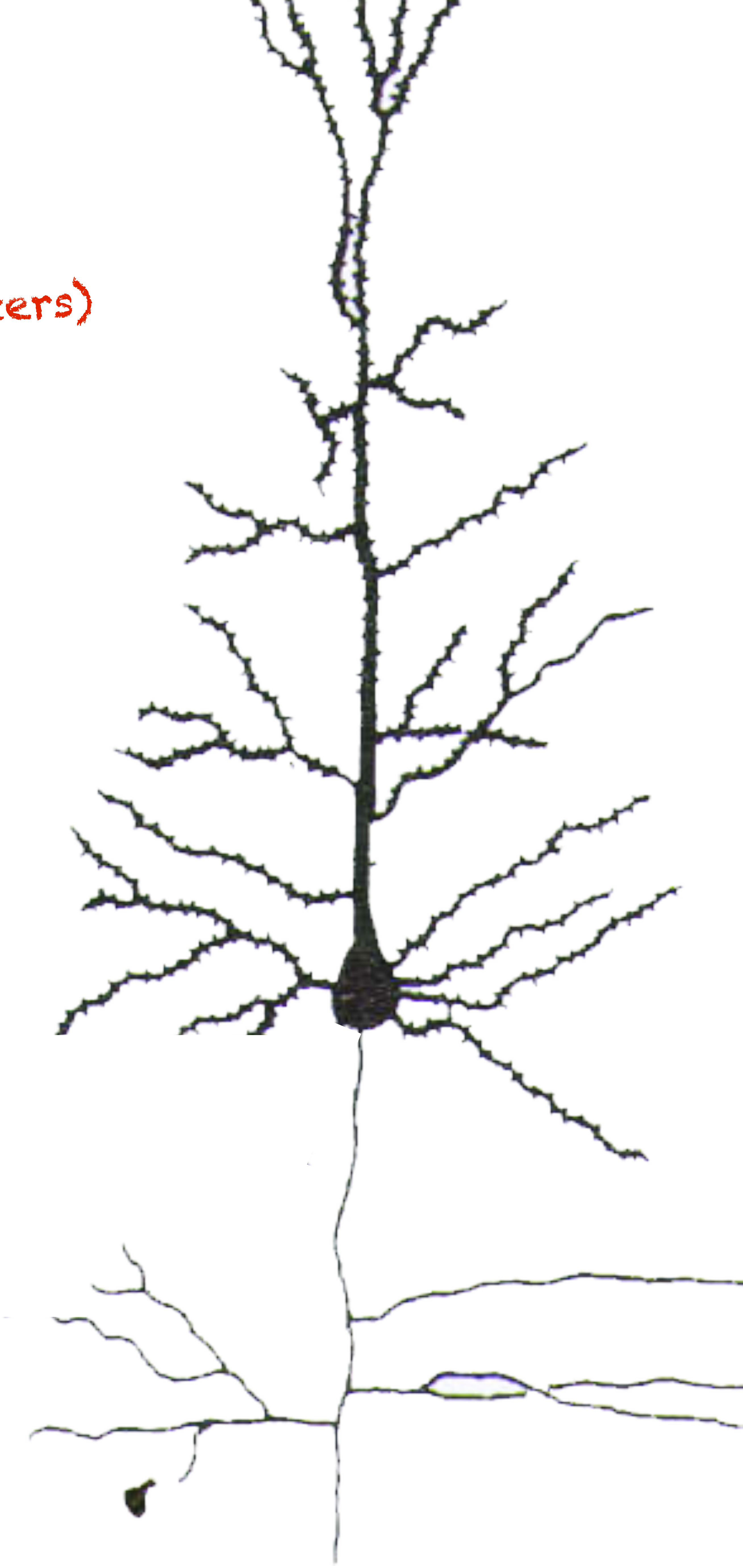

This is called a "conductance based model".

- Assumes stable E for the duration of Δt
- Uses computers to iteratively calculate $V(t+\Delta t)$.
- Δt must be very small (<0.1ms!)

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Solution:
Momentarily change the "permeability" of the membrane for specific currents.

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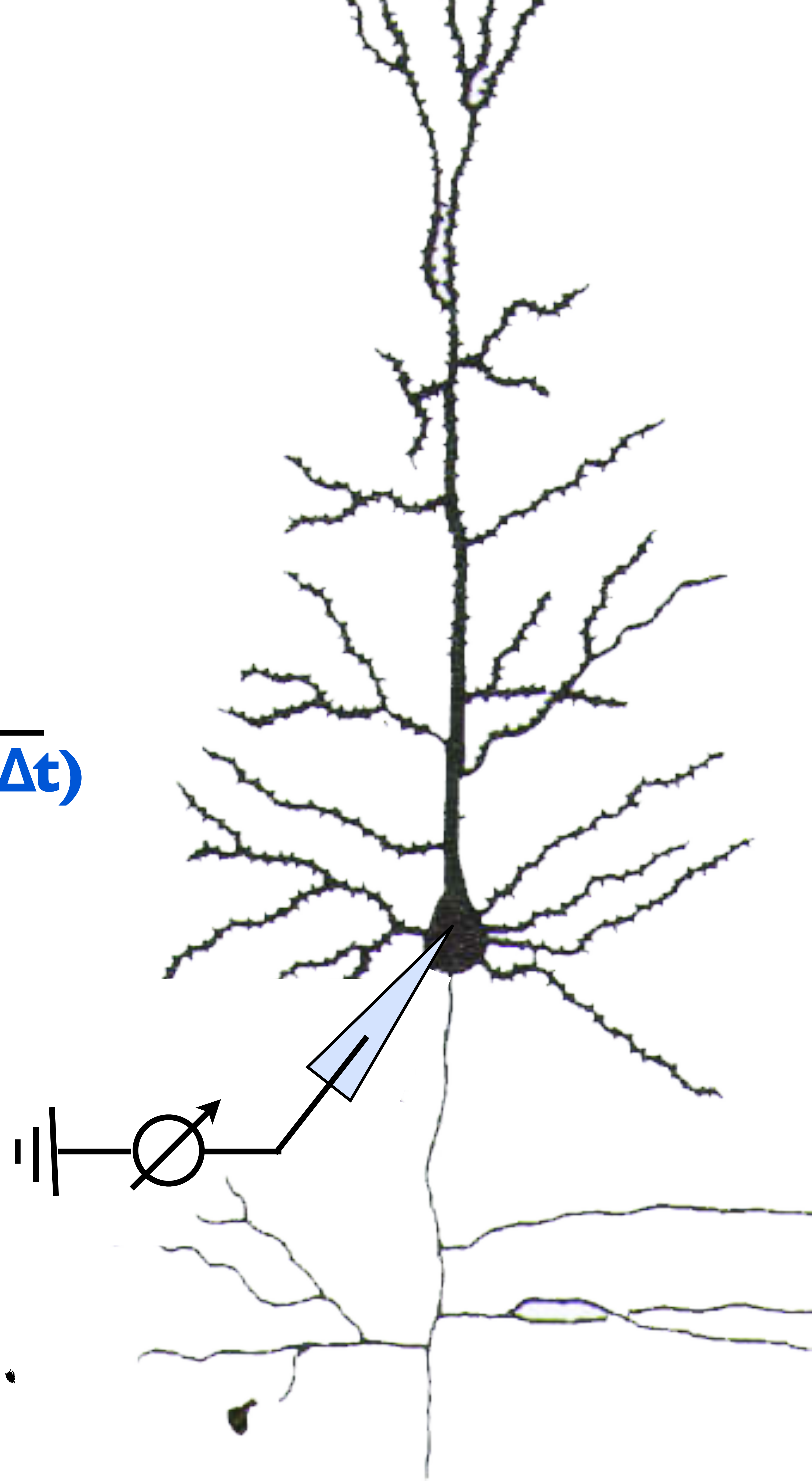

$$E(\Delta t) = \frac{g_{leak}\,E_{leak} + g_{syn}\,E_{syn}}{g_{tot}}$$

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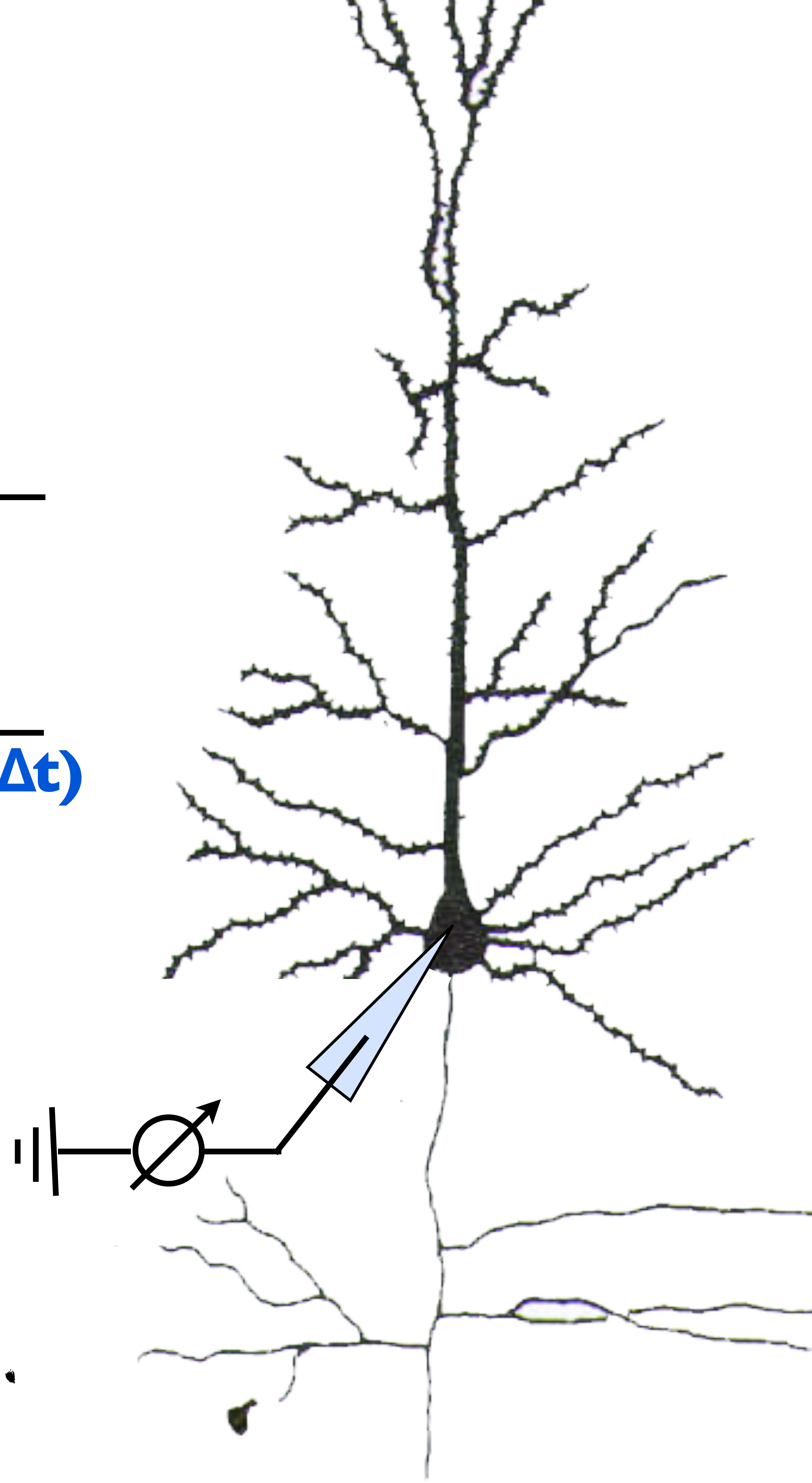

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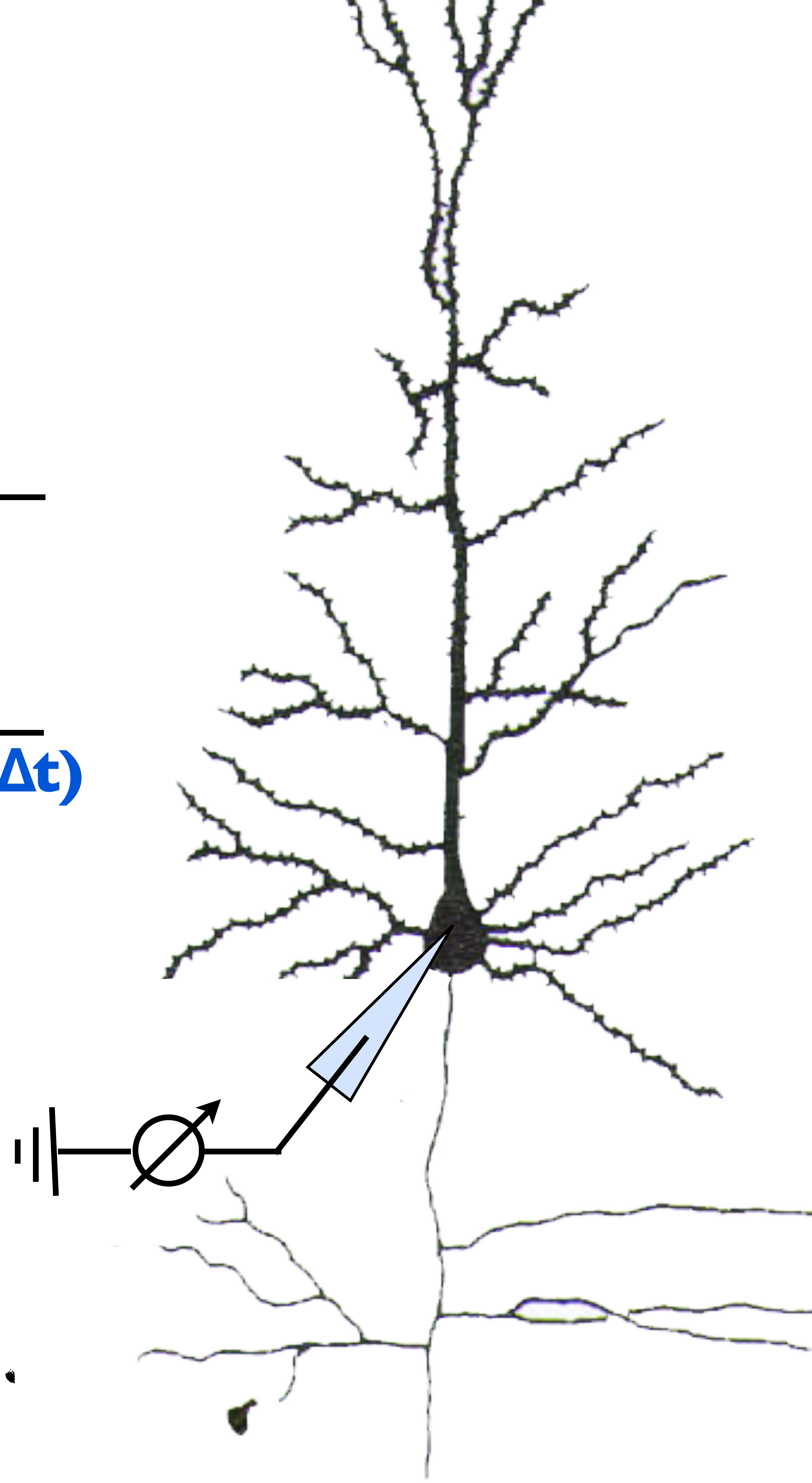
- Uses computers to iteratively calculate $V(t+\Delta t)$.
- Δt must be very small (<0.1ms!)



$$g_{tot} = g_{leak} + g_{syn}$$

$$E(\Delta t) = \frac{g_{leak}\,E_{leak} + g_{syn}\,E_{syn}}{g_{tot}}$$

$$\tau(\Delta t) = \frac{C}{g_{tot}}$$

$$V(t+\Delta t) = E(\Delta t) + \left(V(t) - E(\Delta t)\right) e^{-\frac{\Delta t}{\tau(\Delta t)}}$$

Solution:
Momentarily change the "permeability" of the membrane for specific currents.

This is called a "conductance based model".

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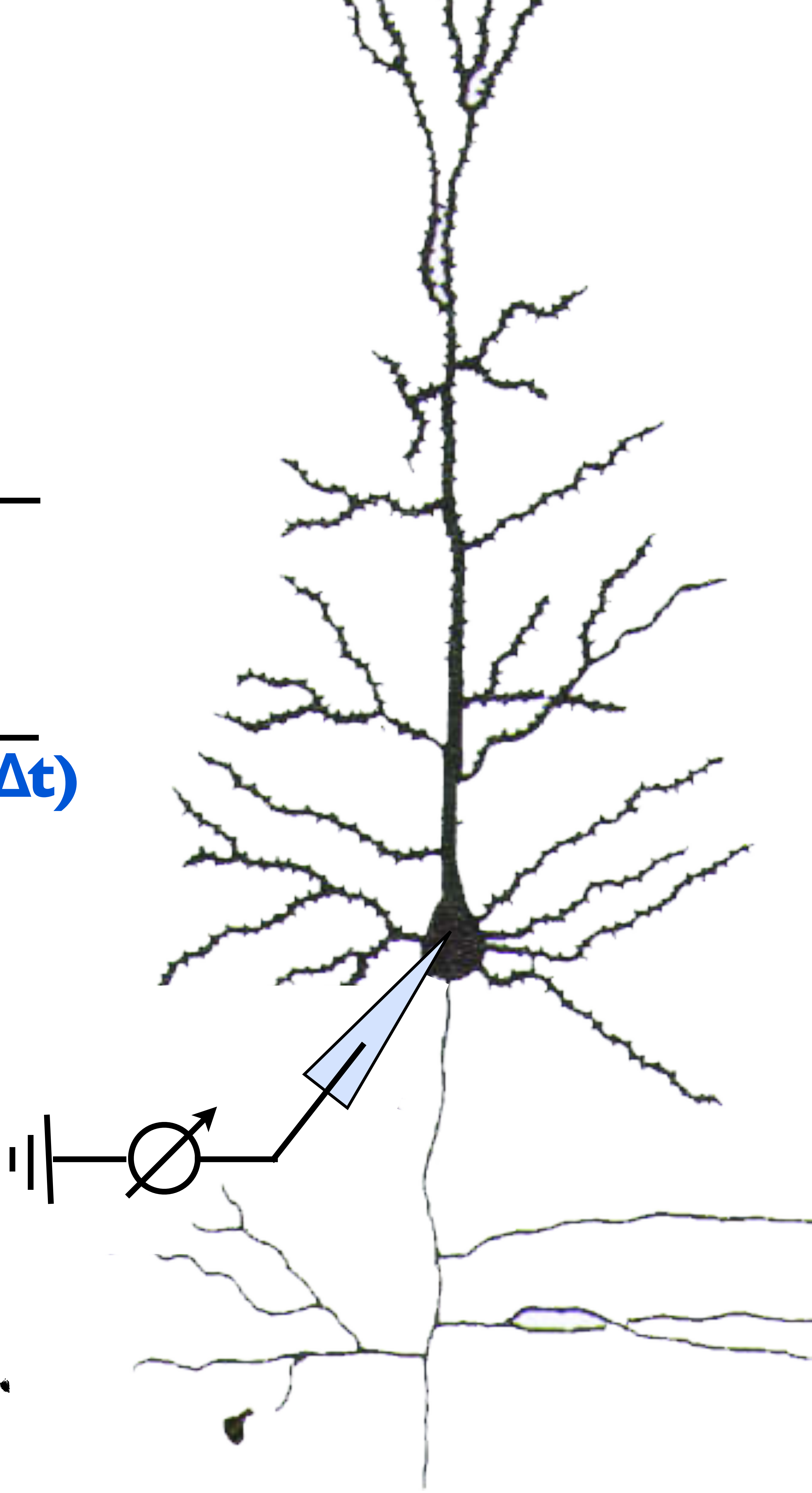

This describes the input integration in a cell...

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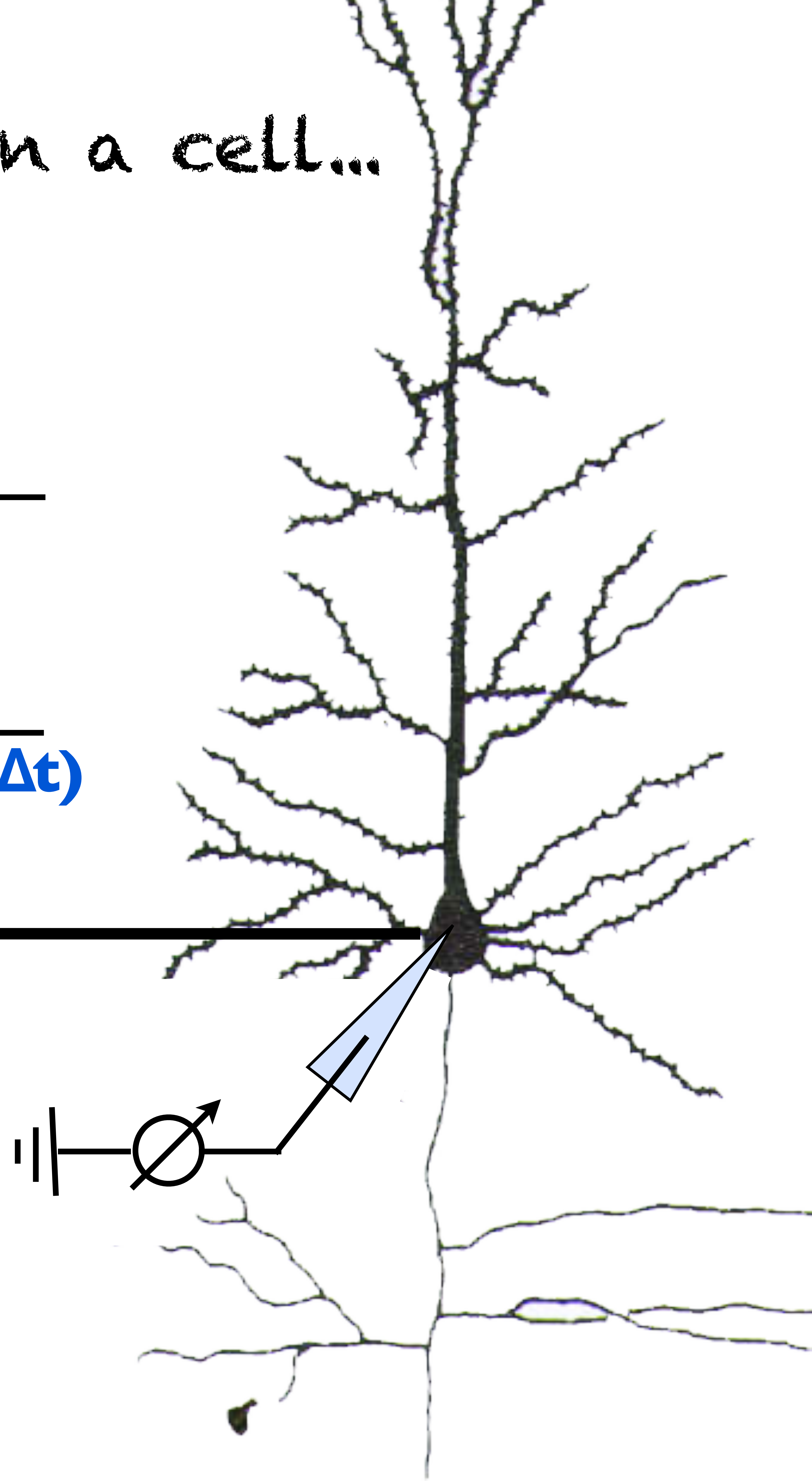

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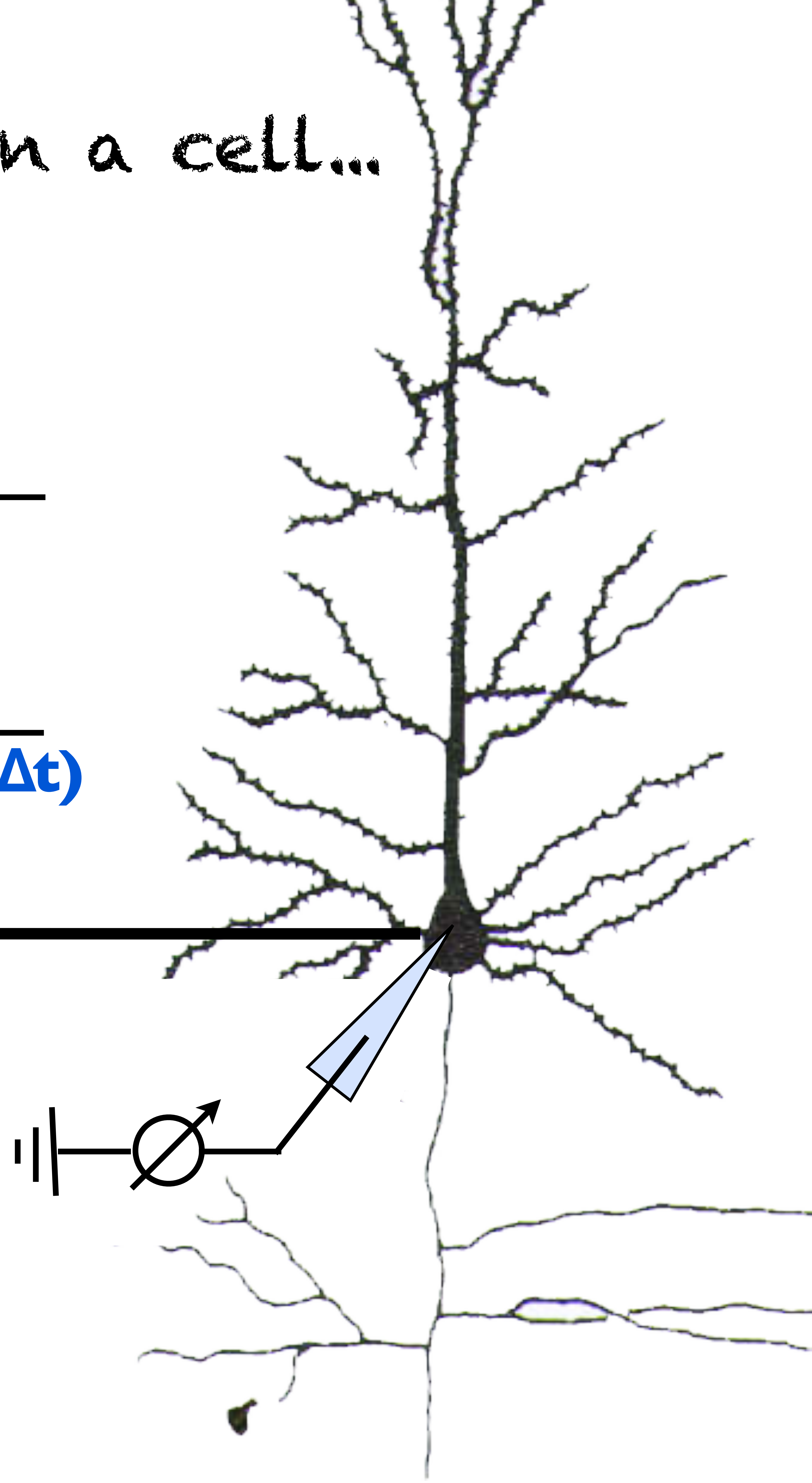
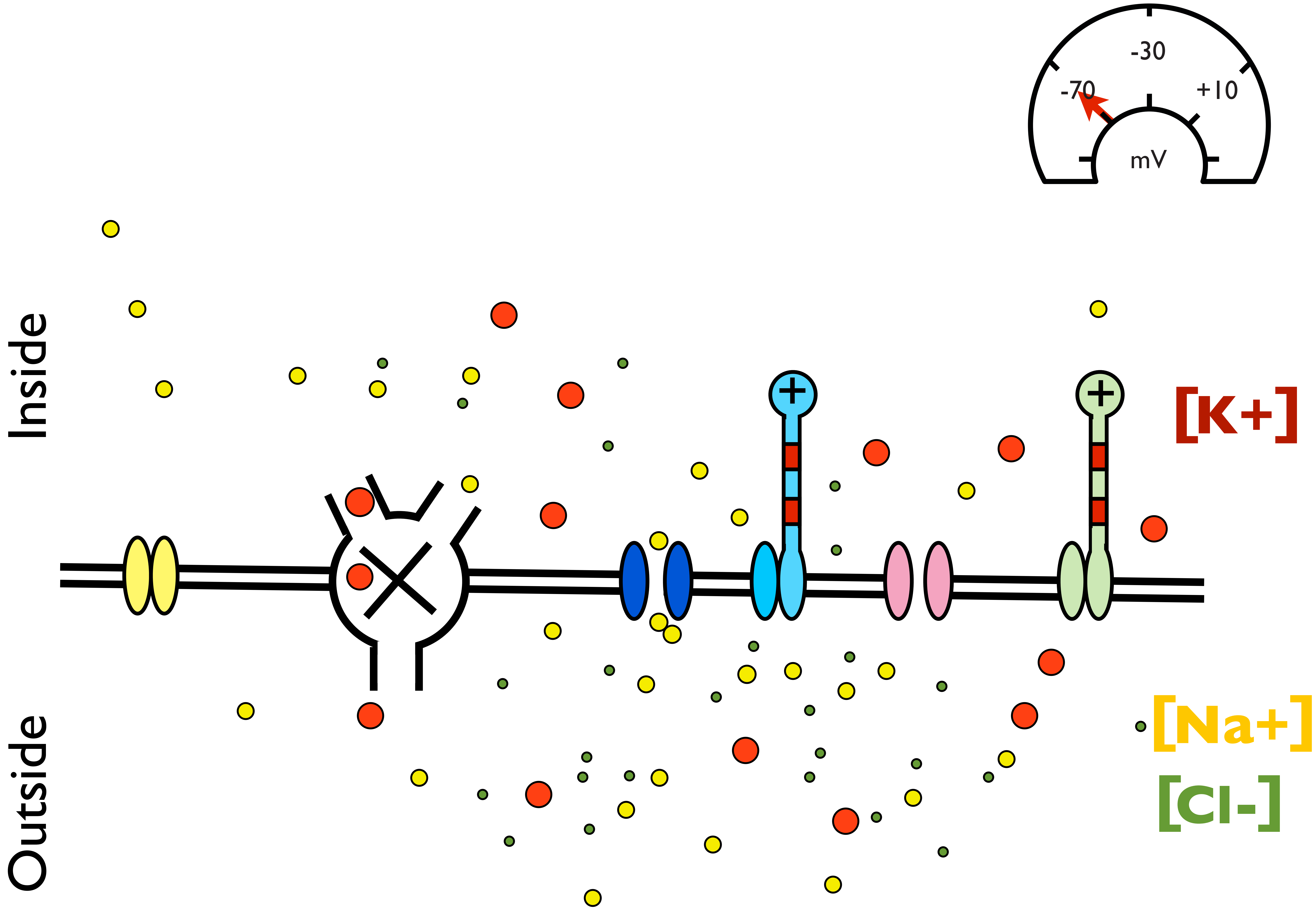
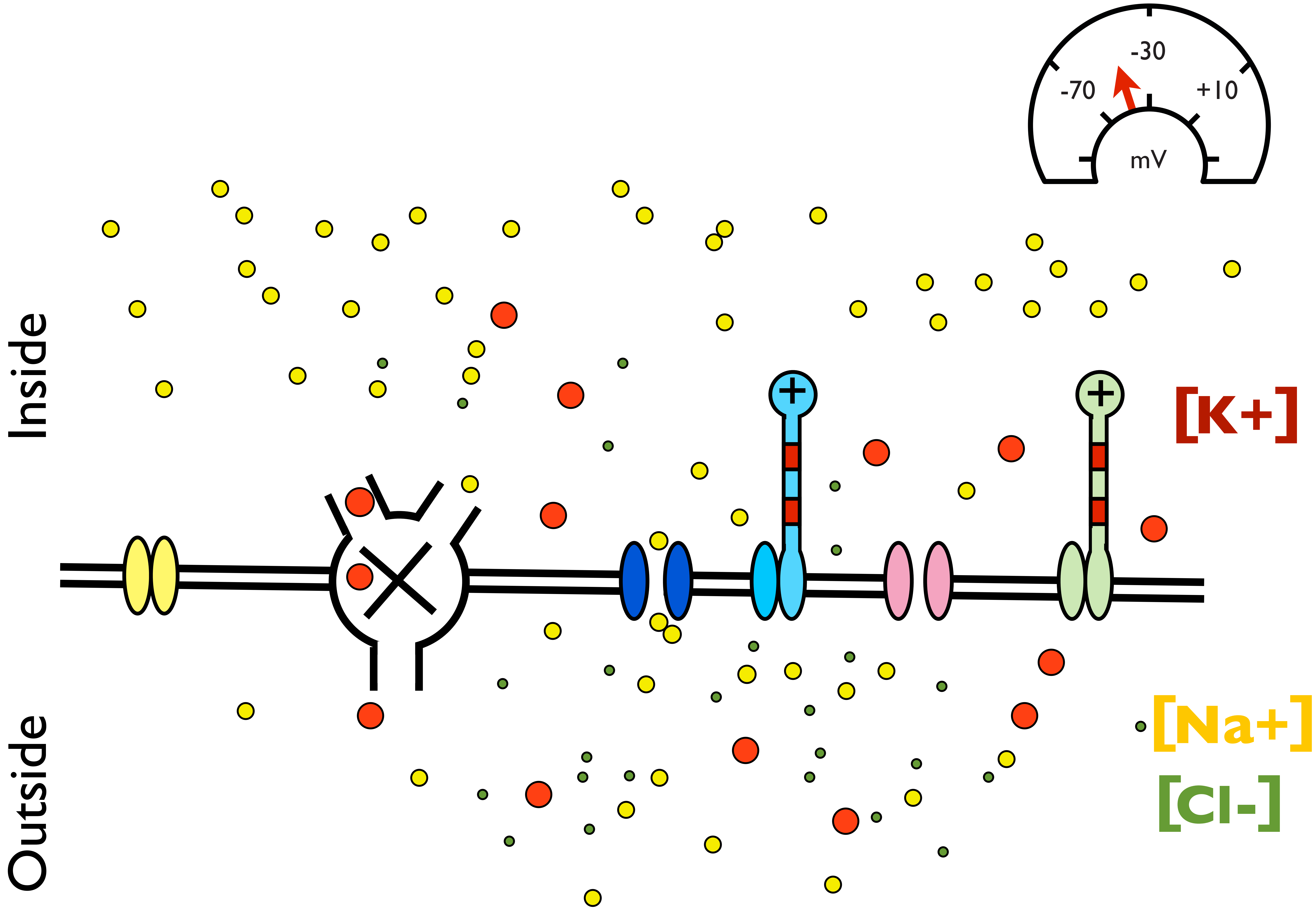


...but what about the "fire"?


-30
-70
+10
mV
Inside
Outside
[K+]
[Na+]
[Cl-]


-30
-70
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mV
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Outside
[K+]
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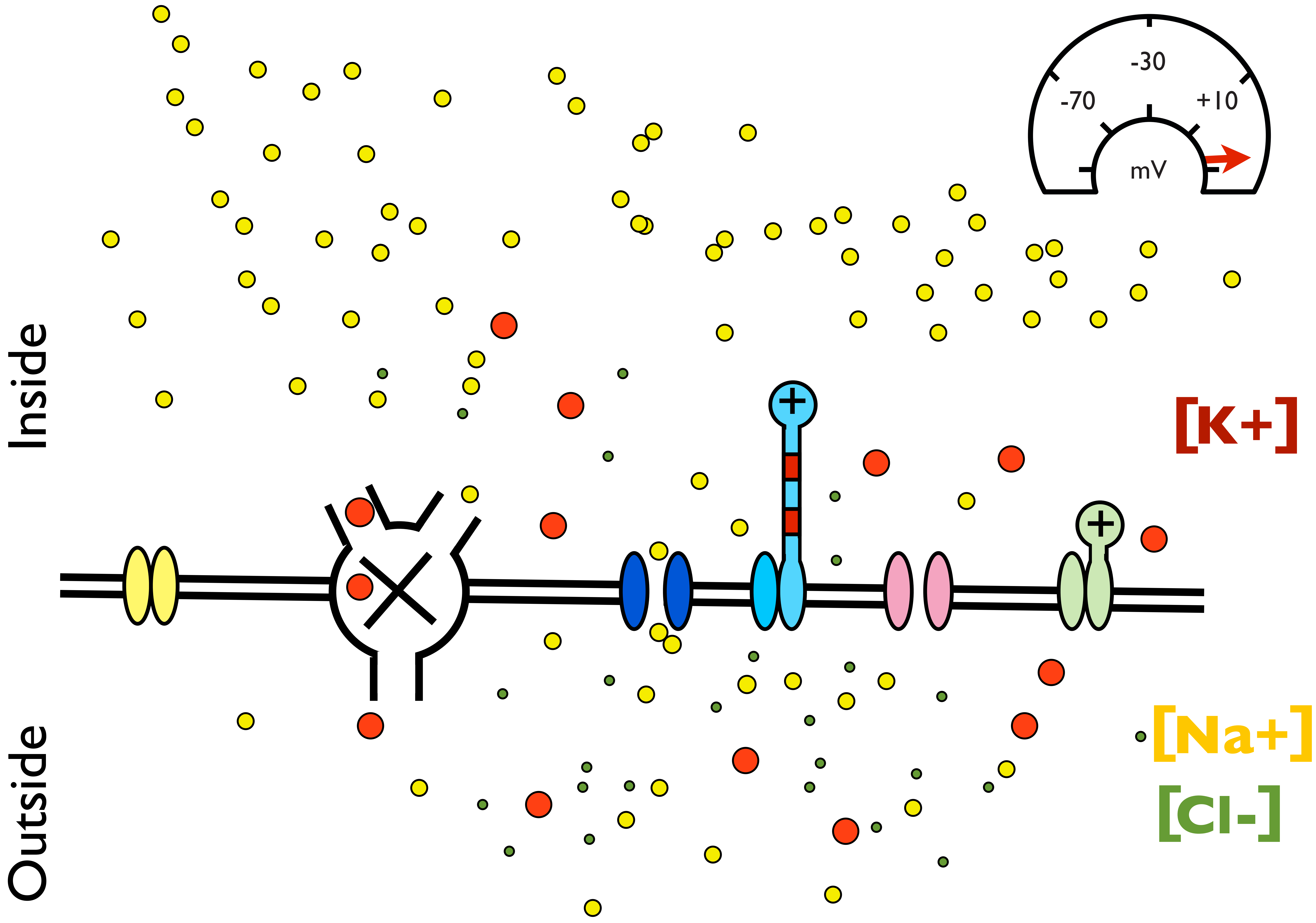
[Cl-]



Inside
Outside
-30
-70
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mV
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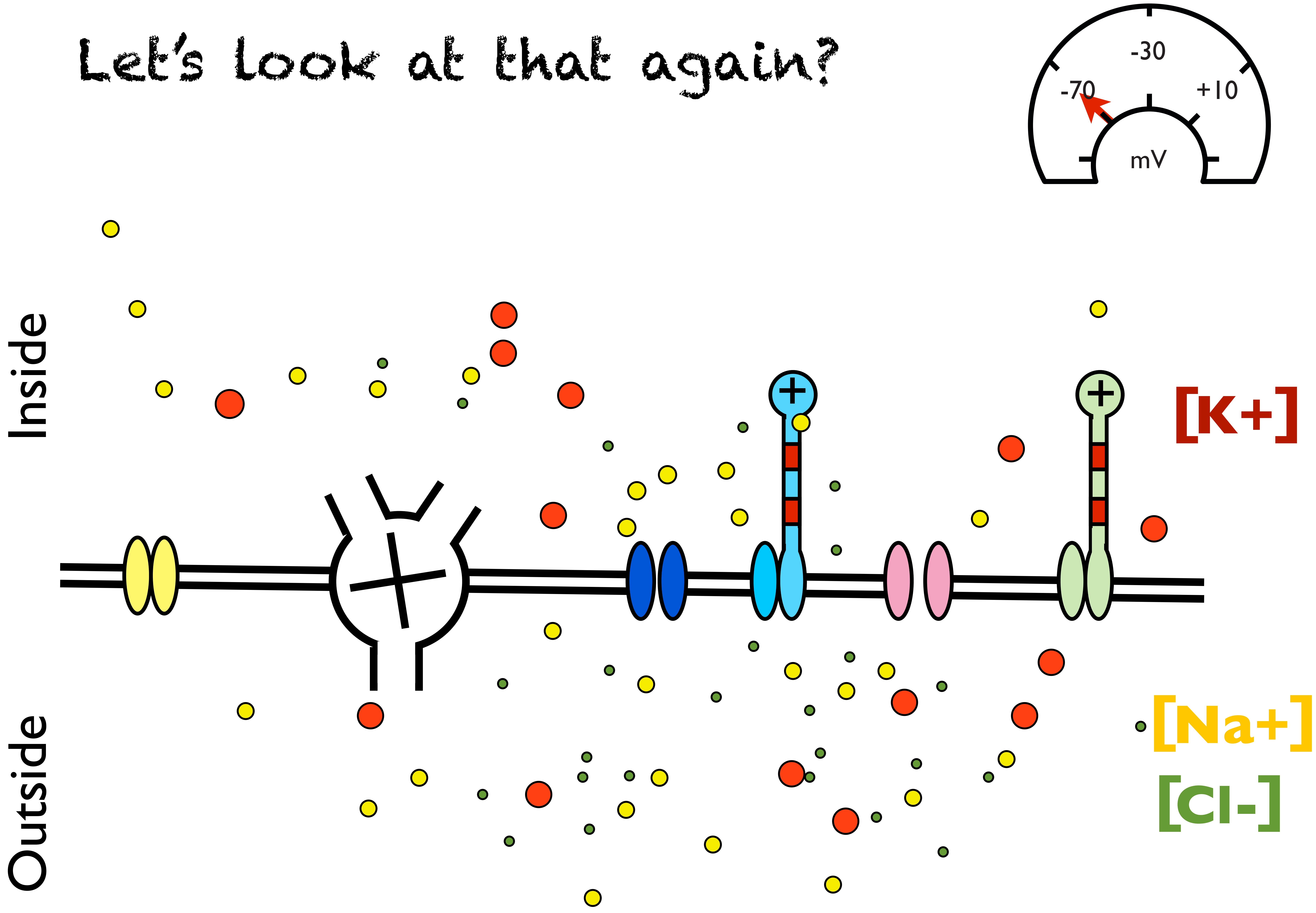
Let's look at that again?



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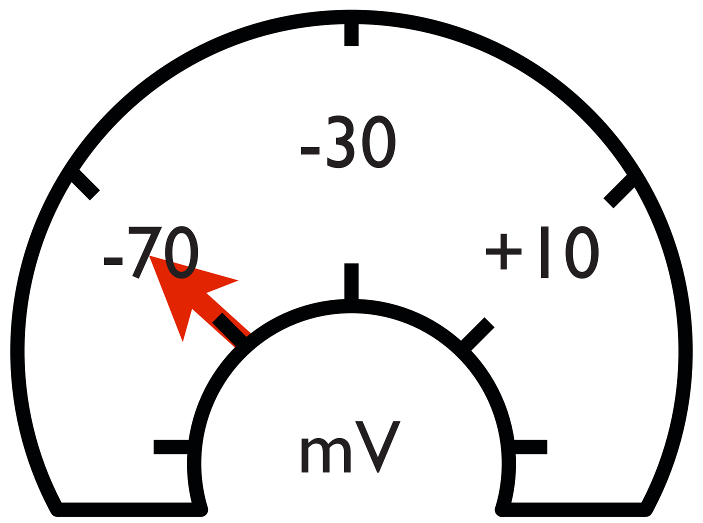

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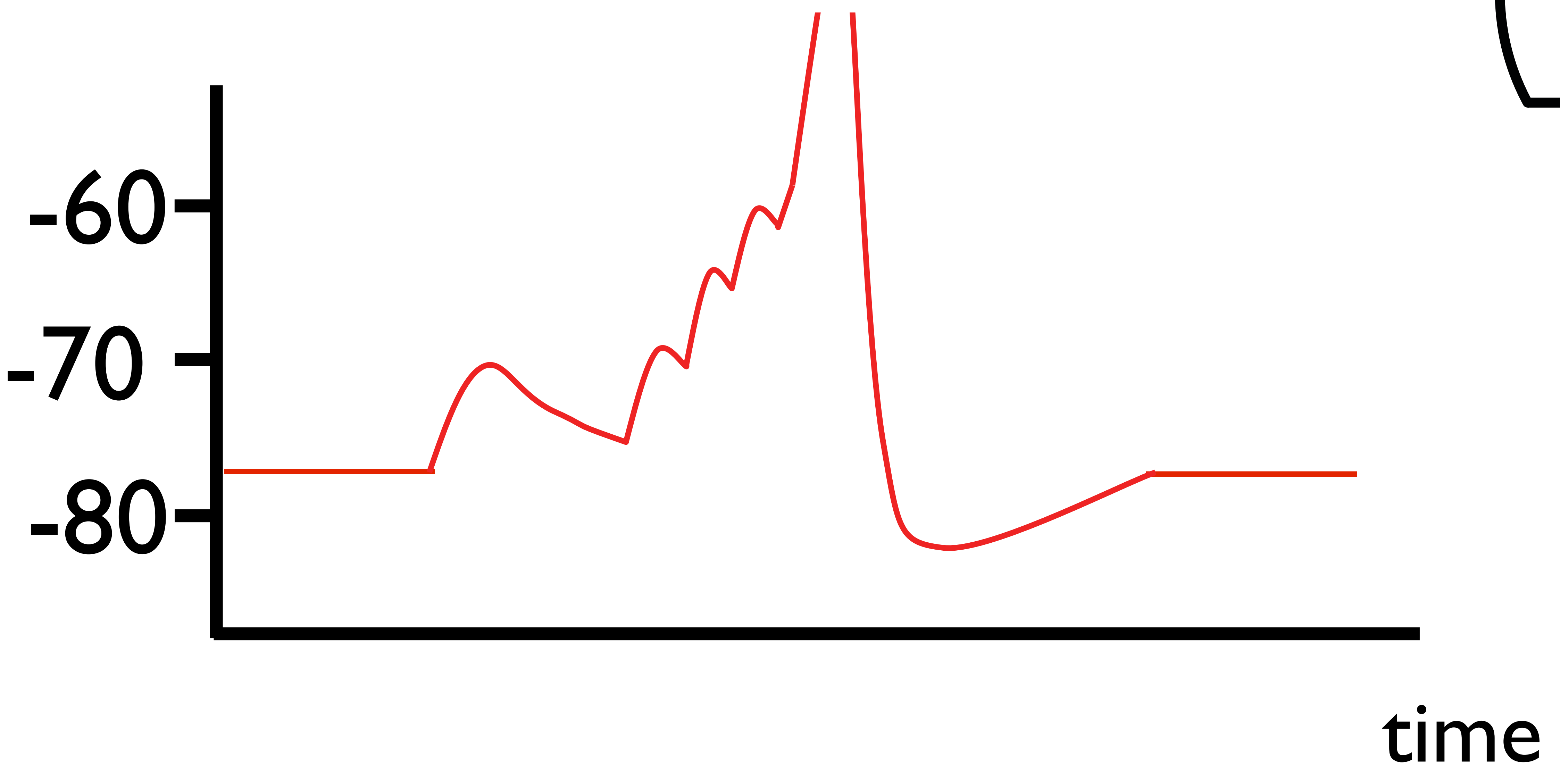

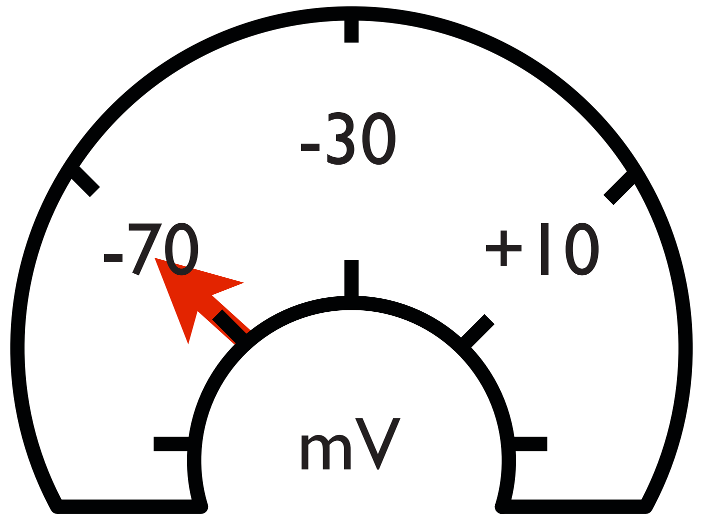

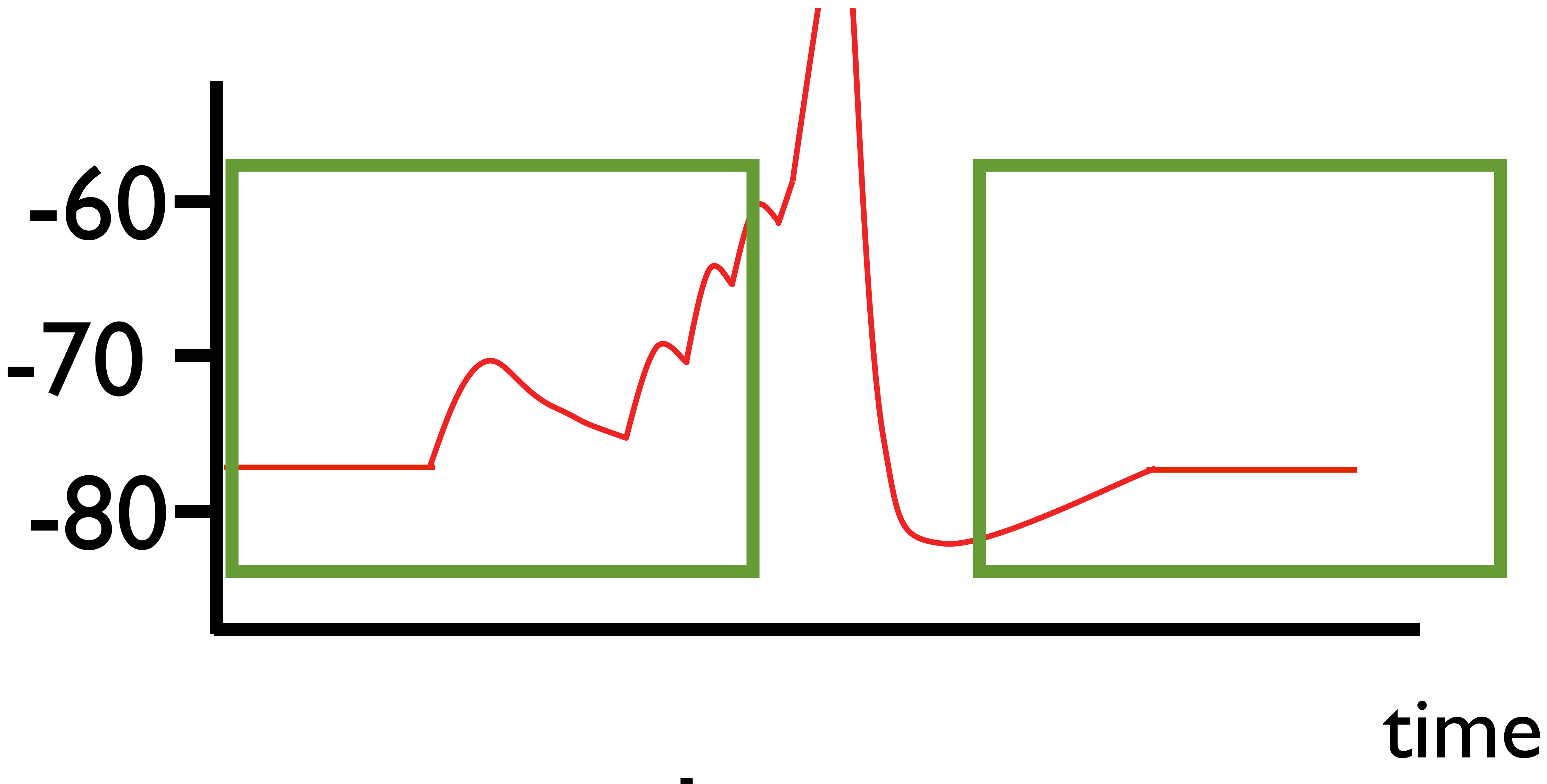

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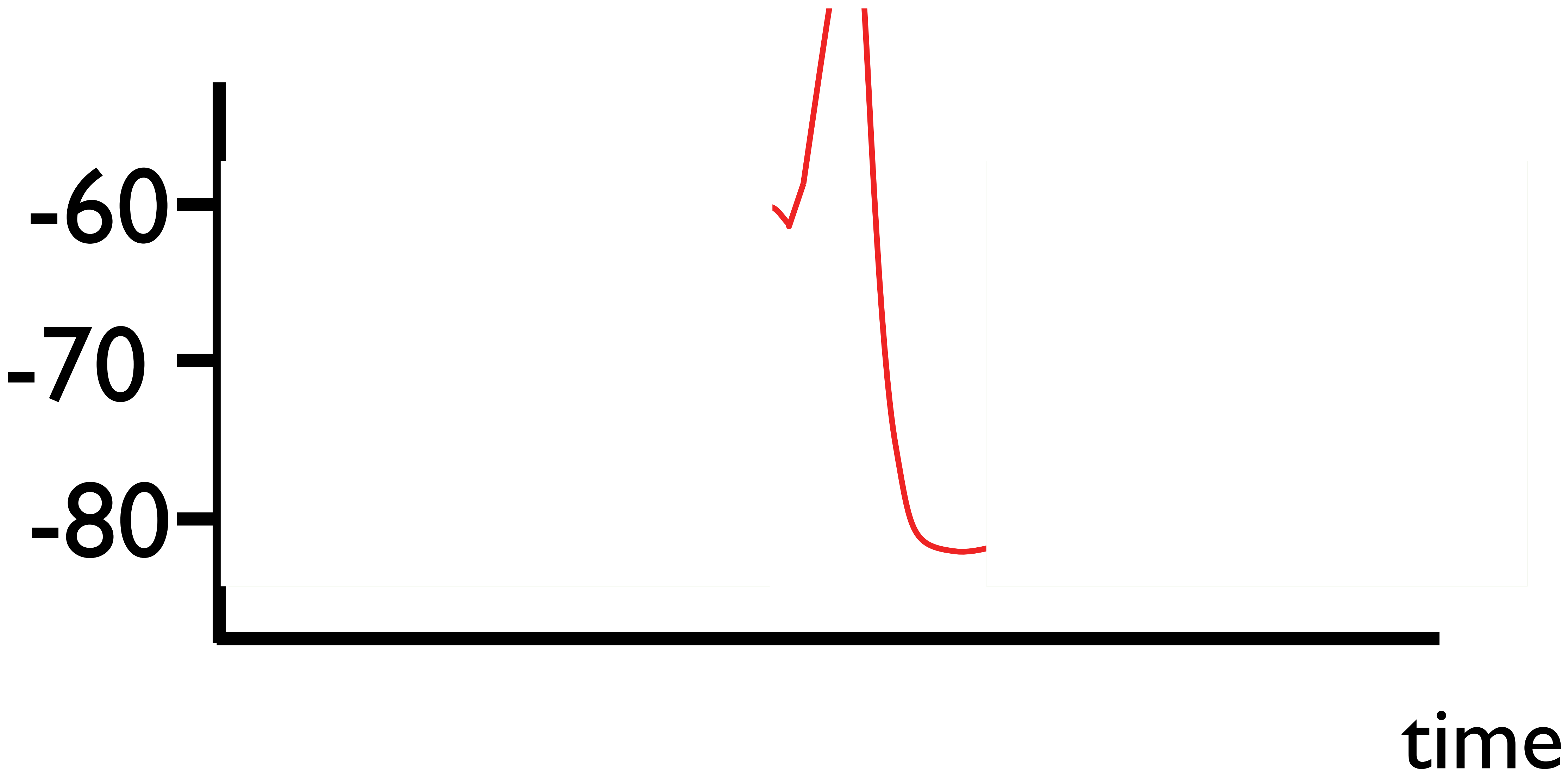

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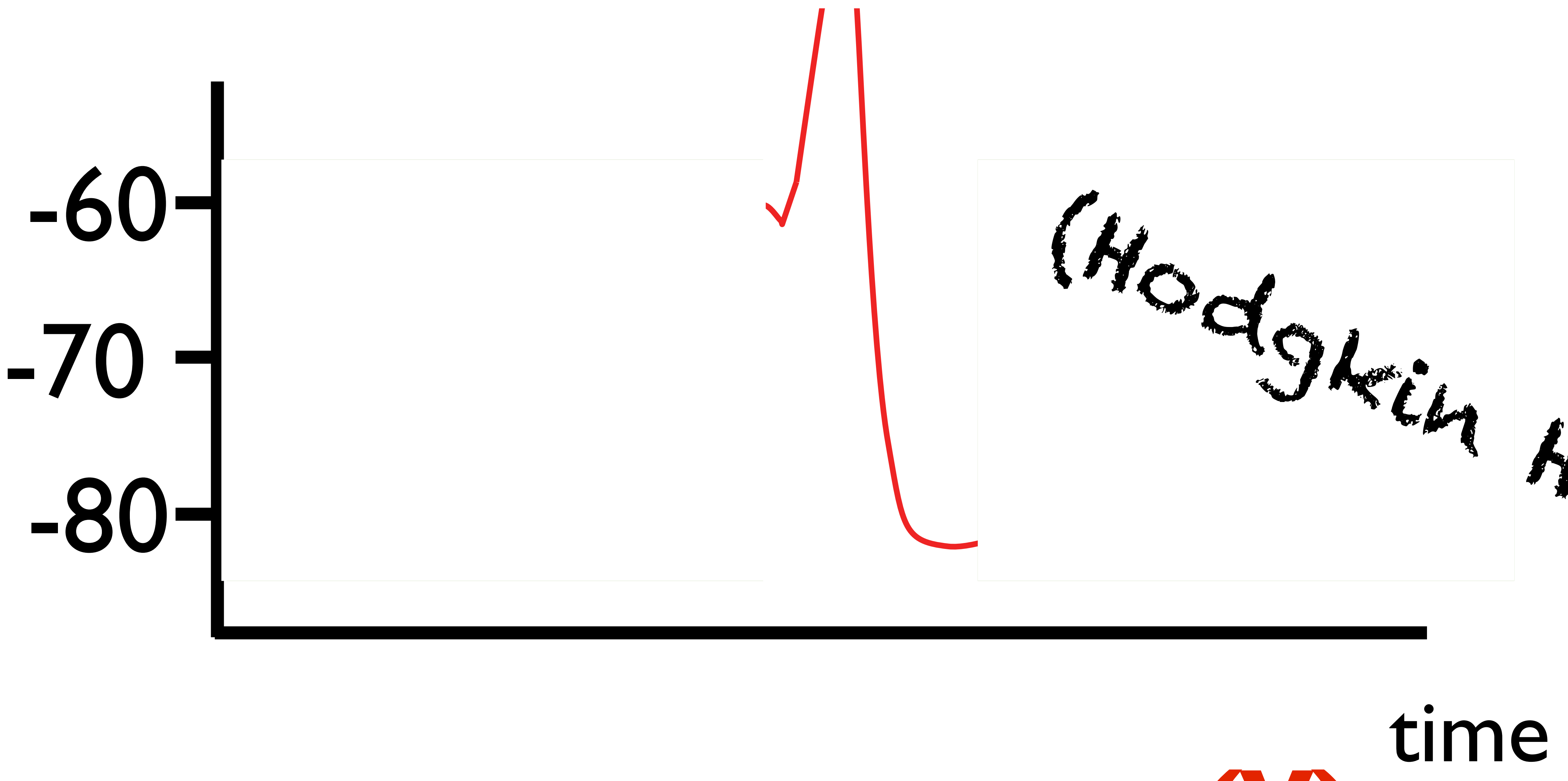

(Hodgkin Huxley style)

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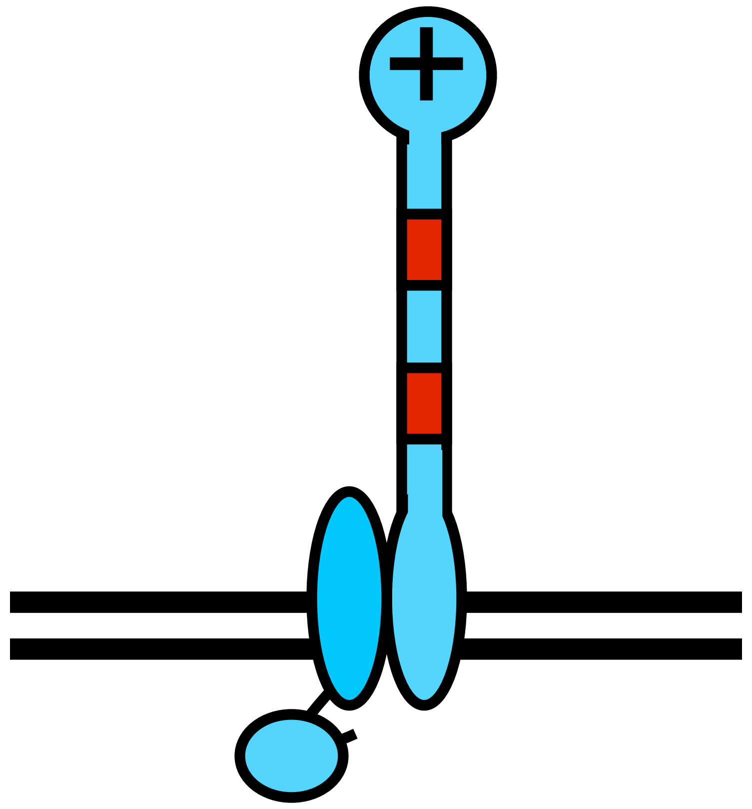

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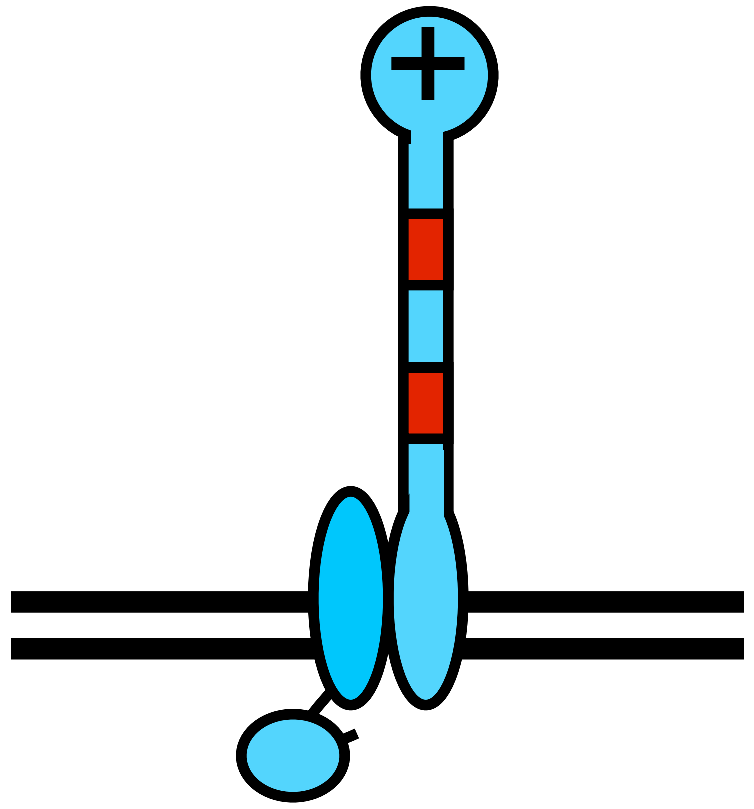

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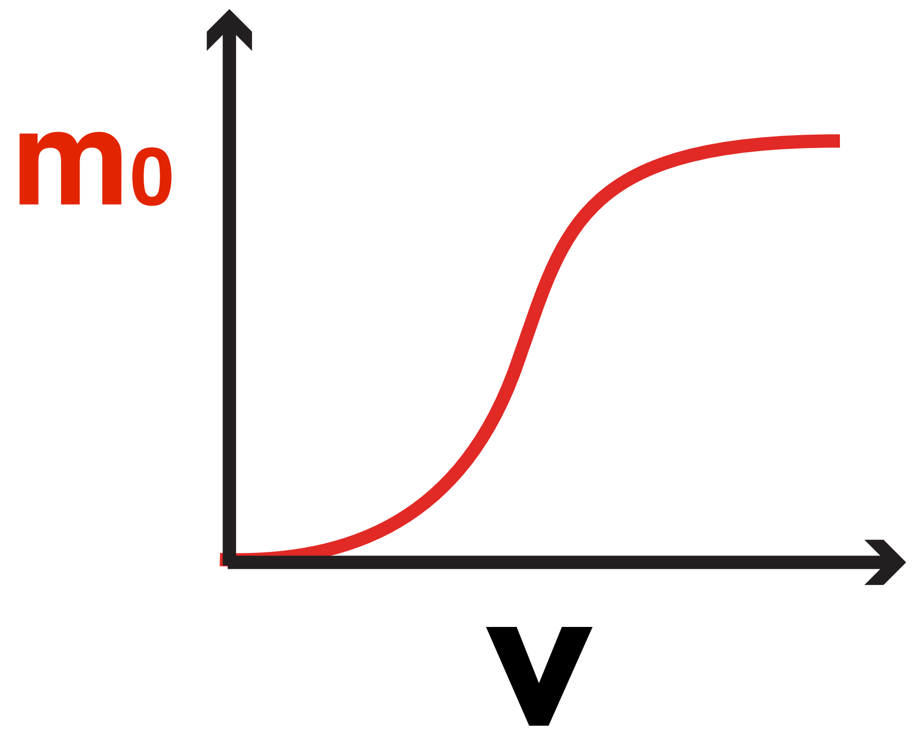

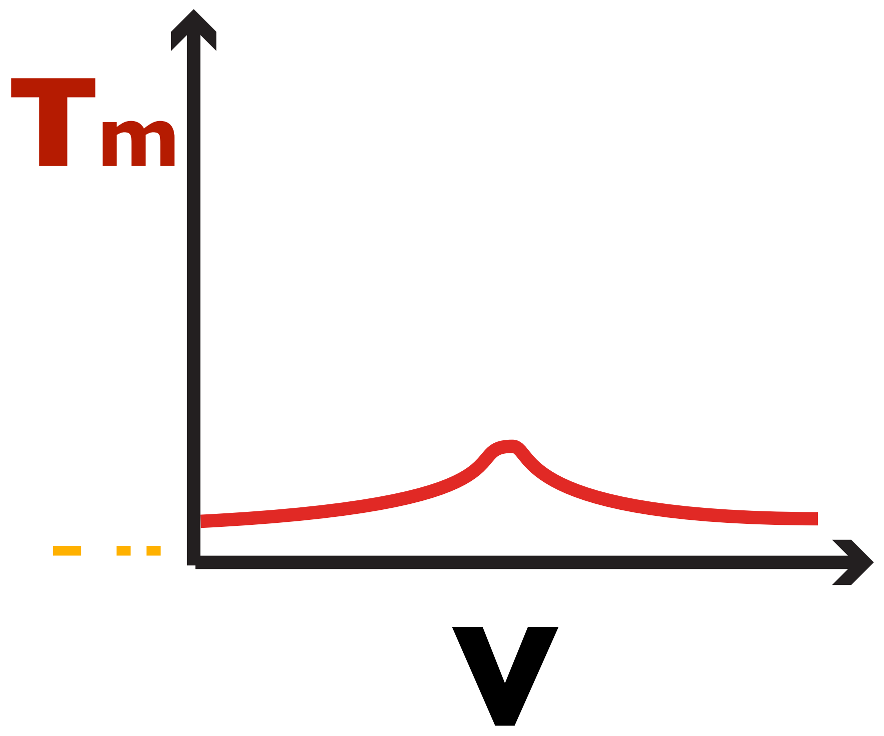

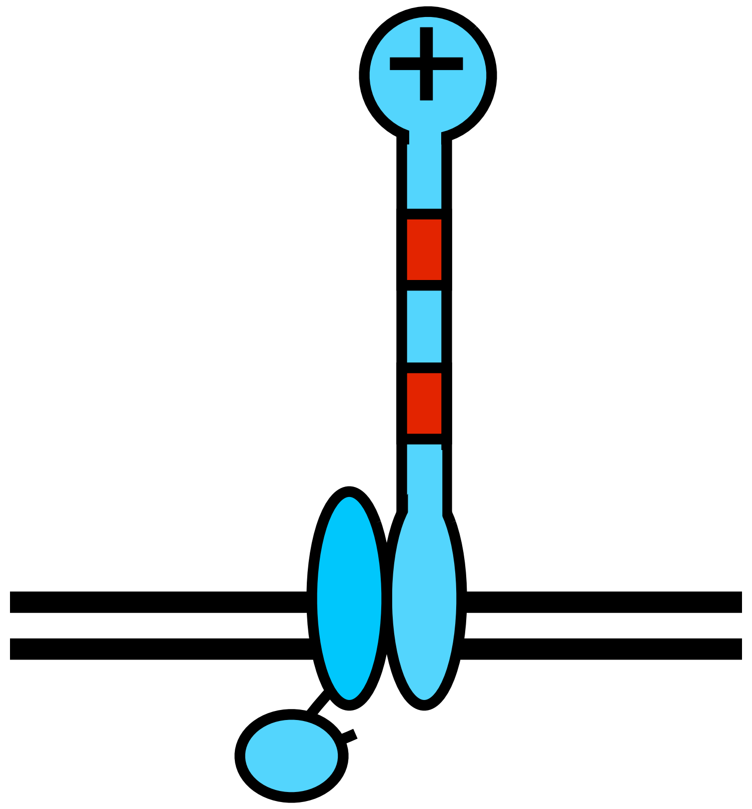

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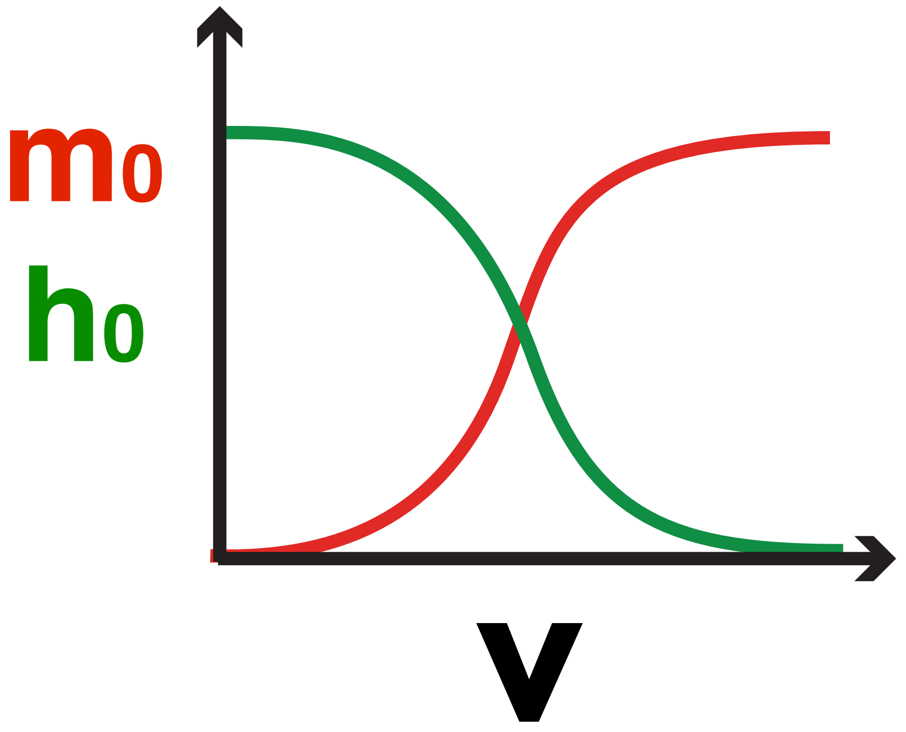

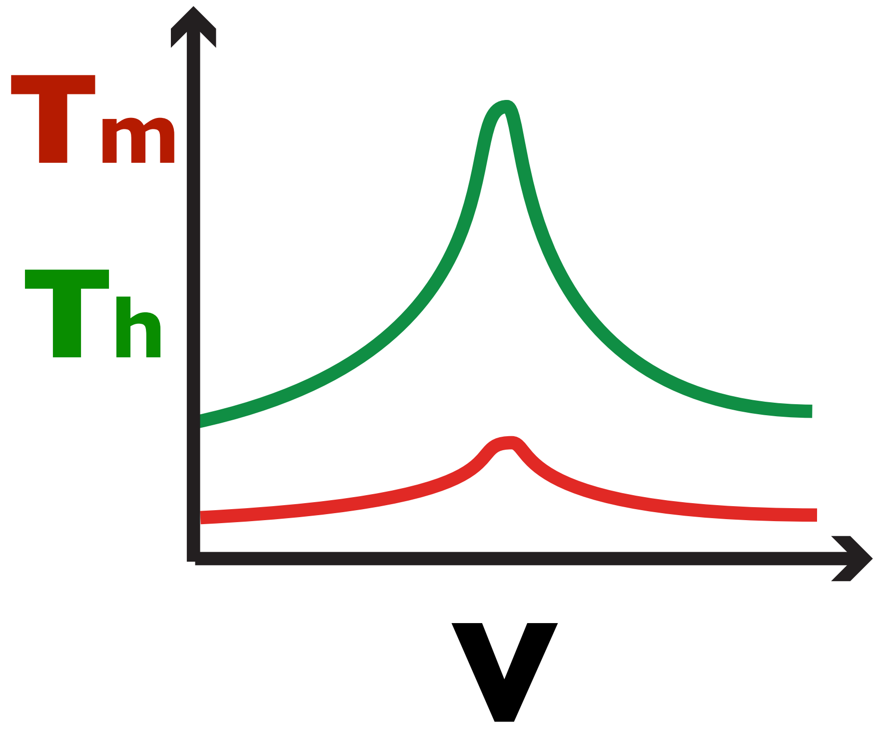

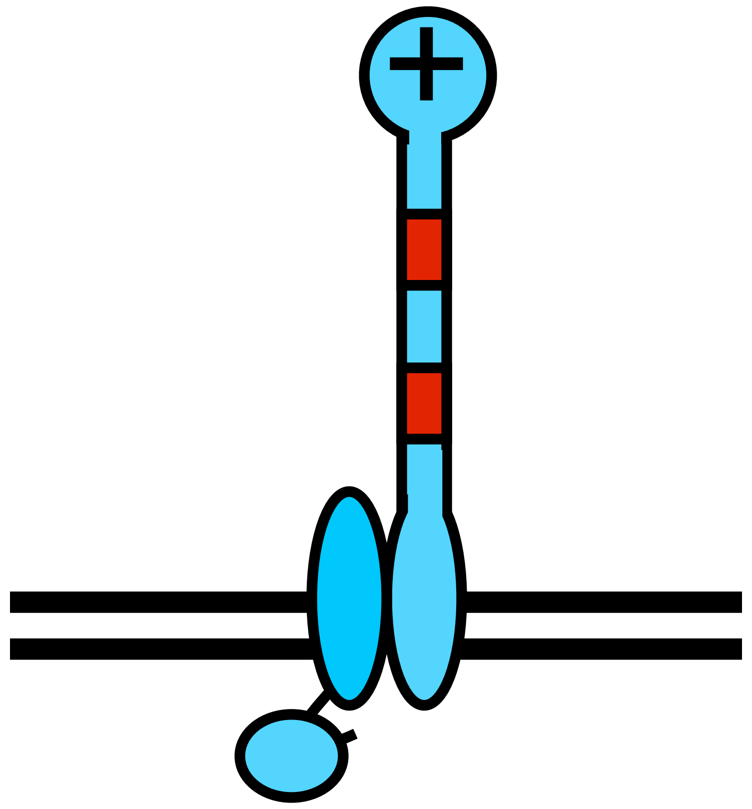

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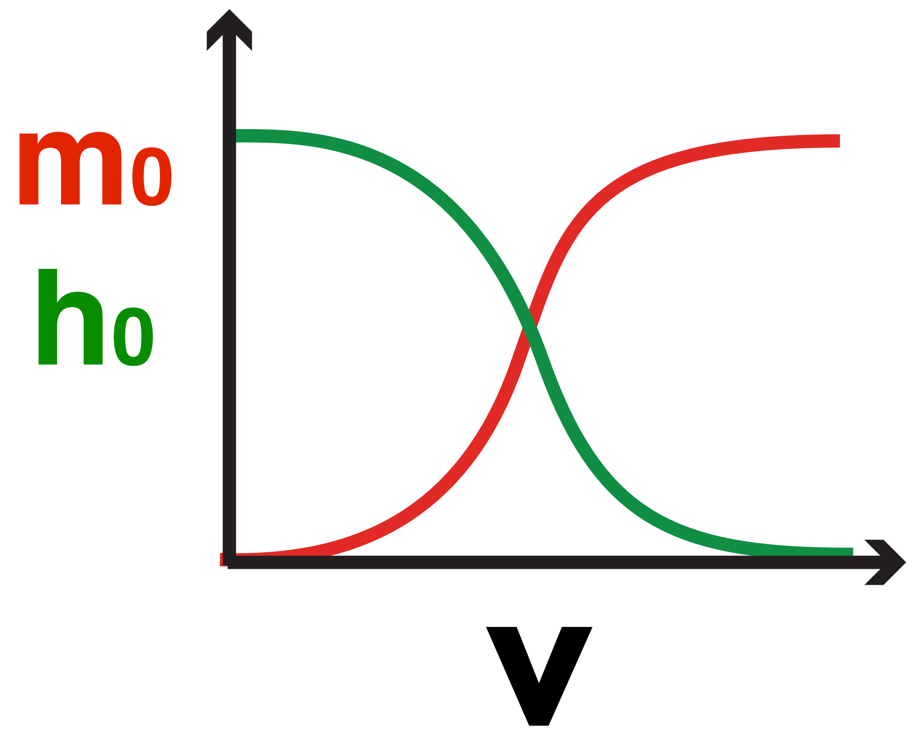

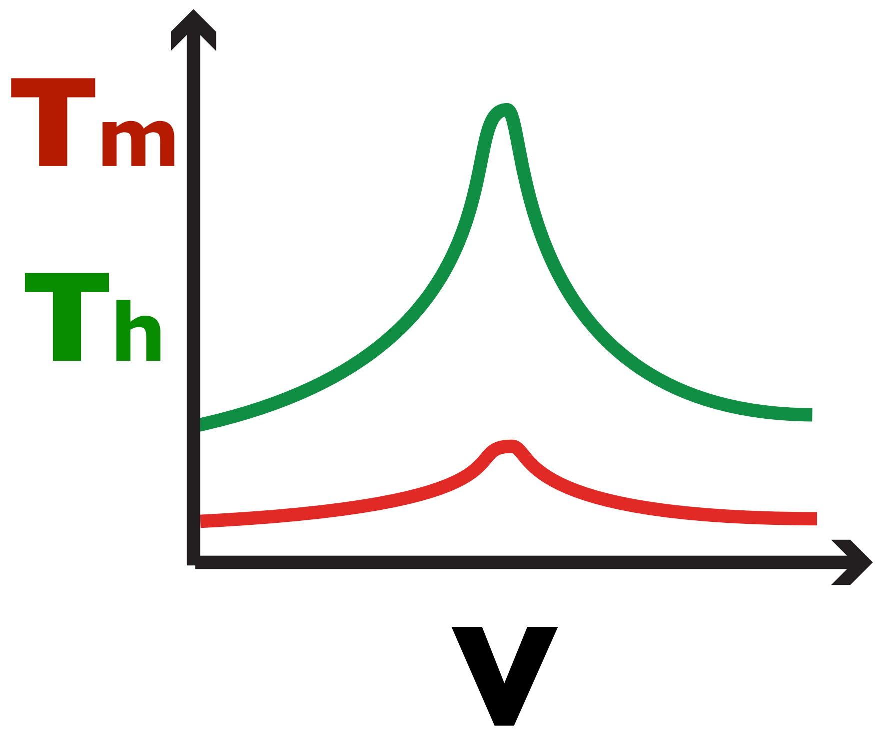

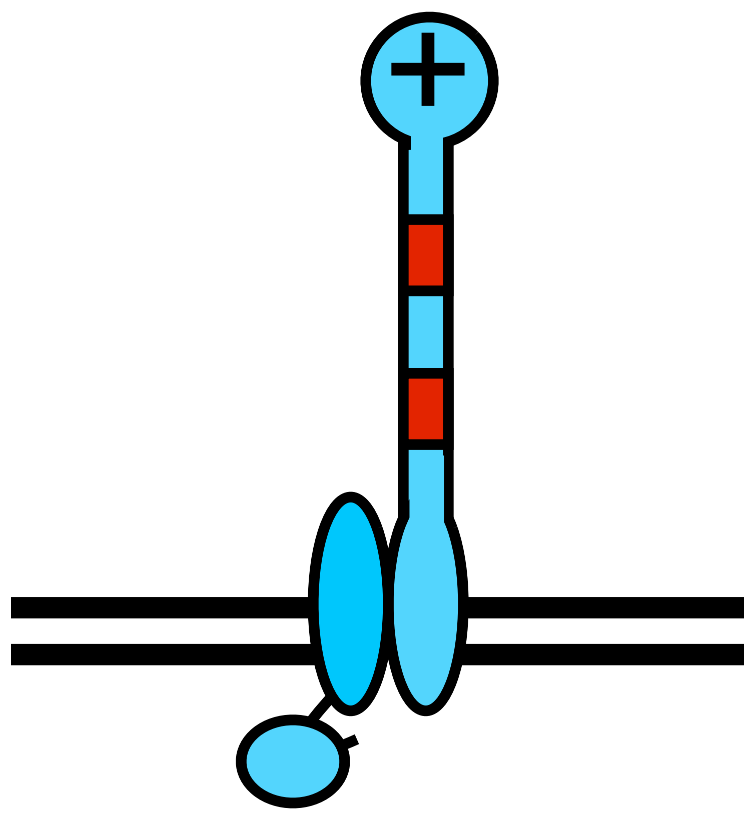

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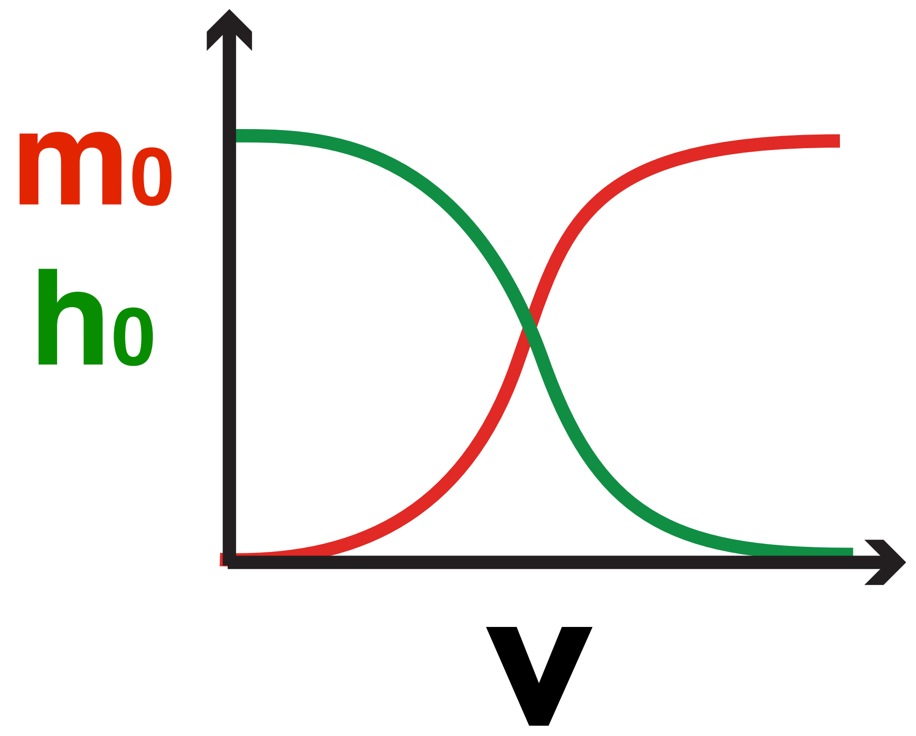

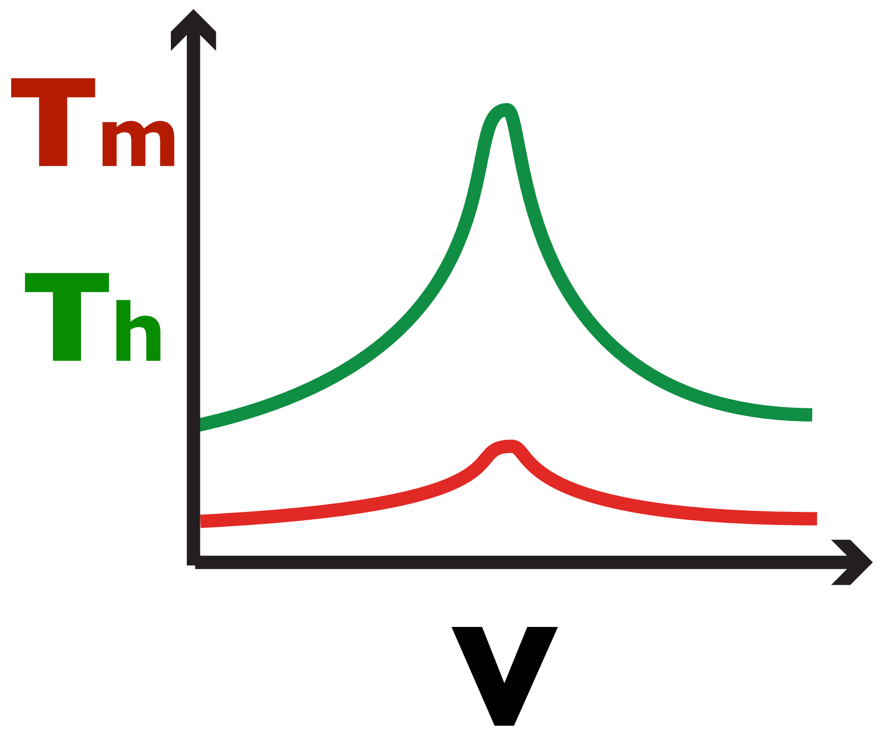

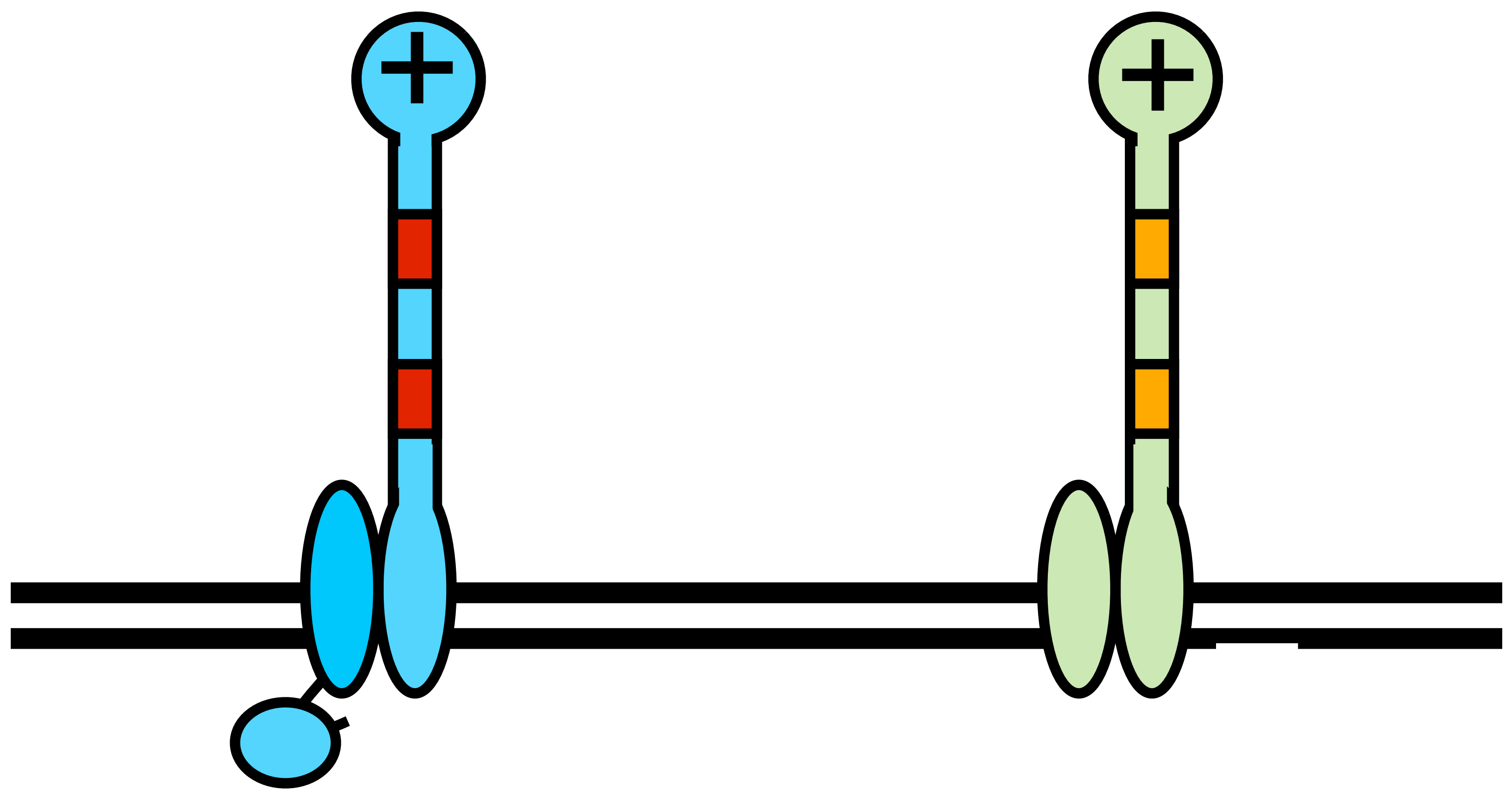

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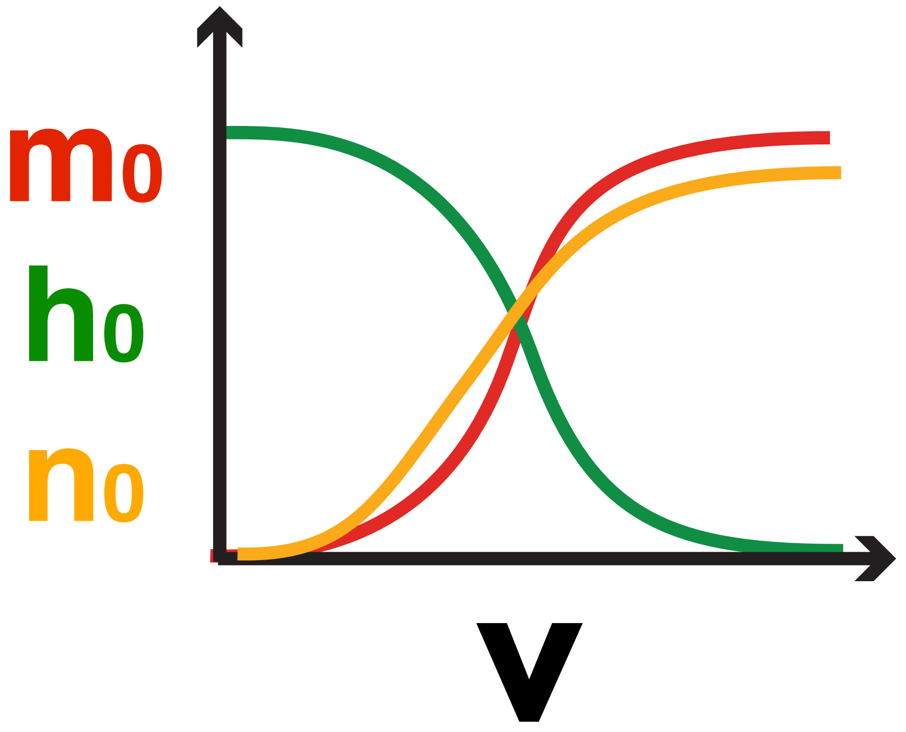

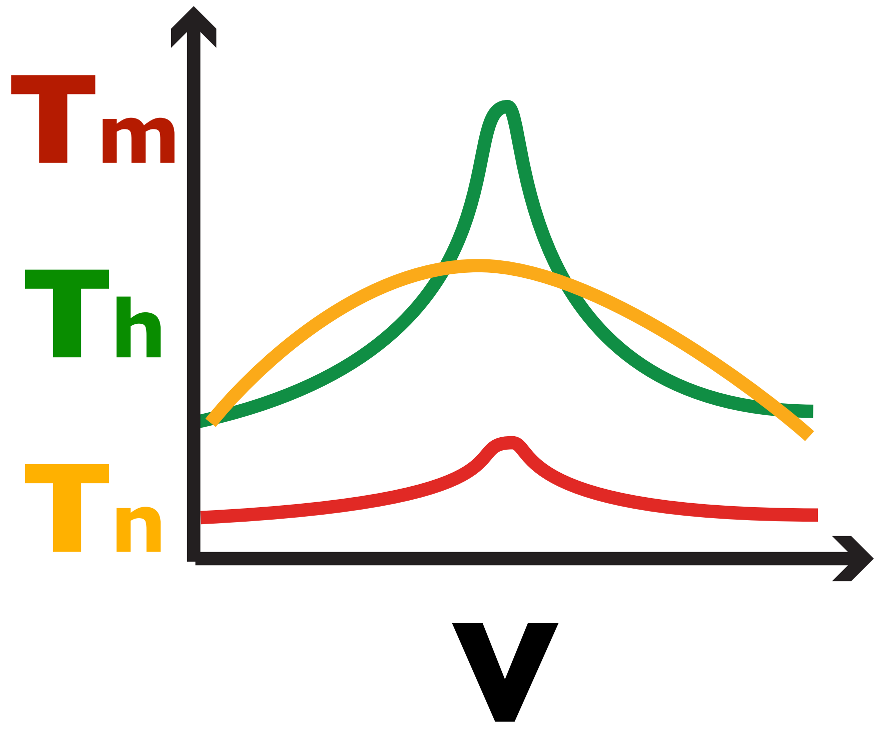

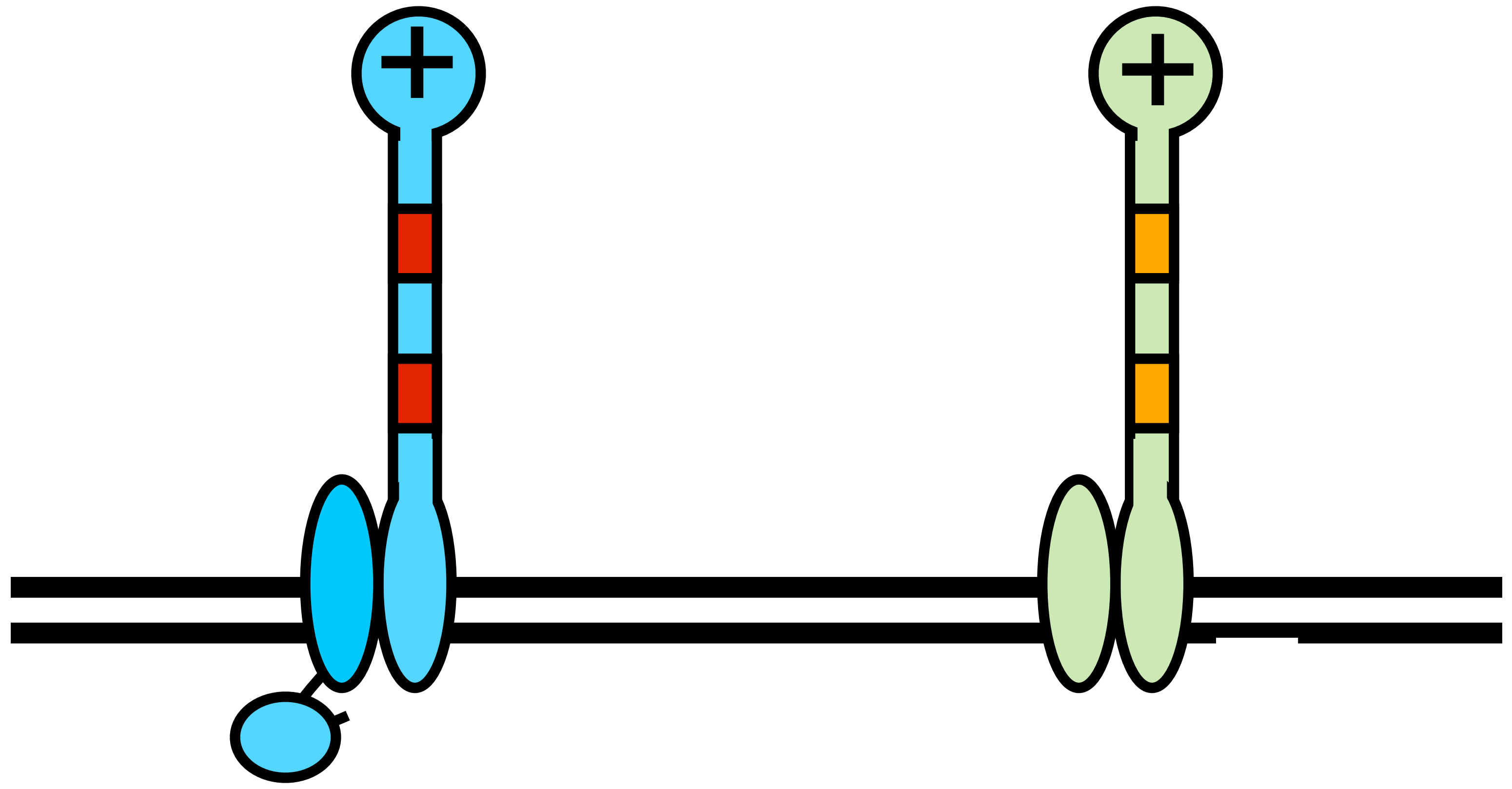

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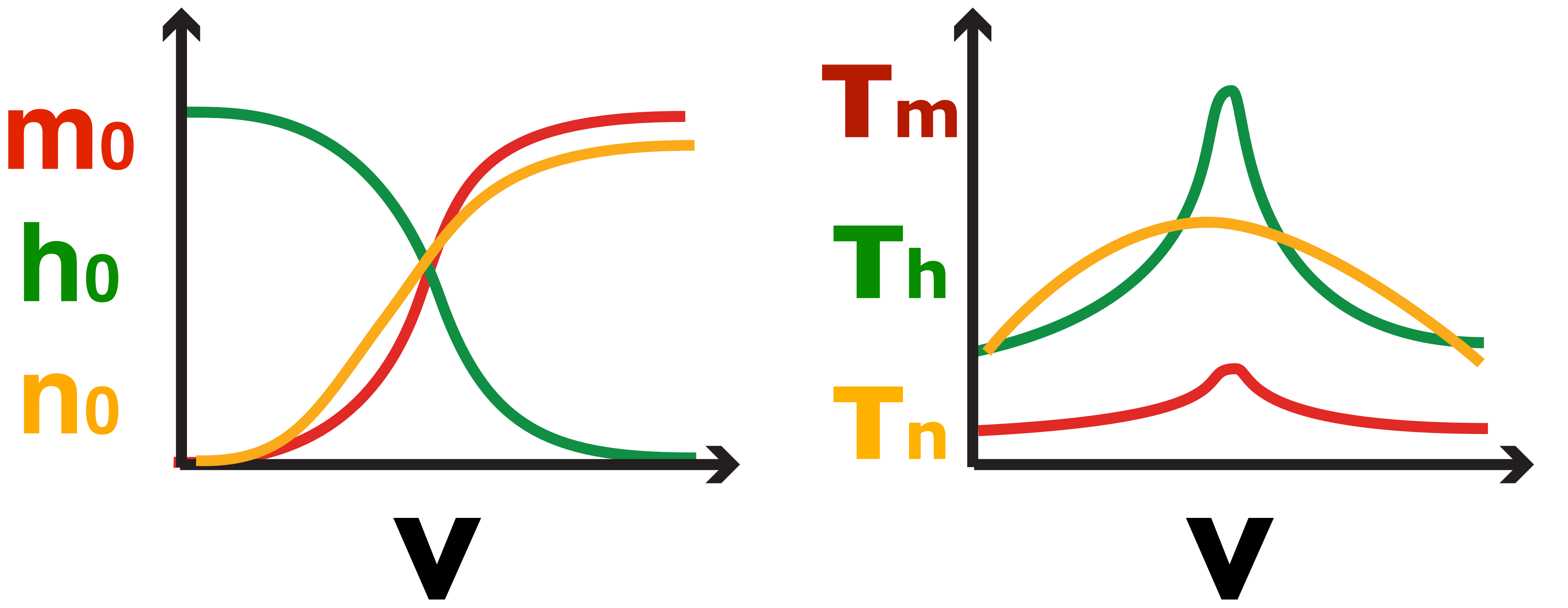
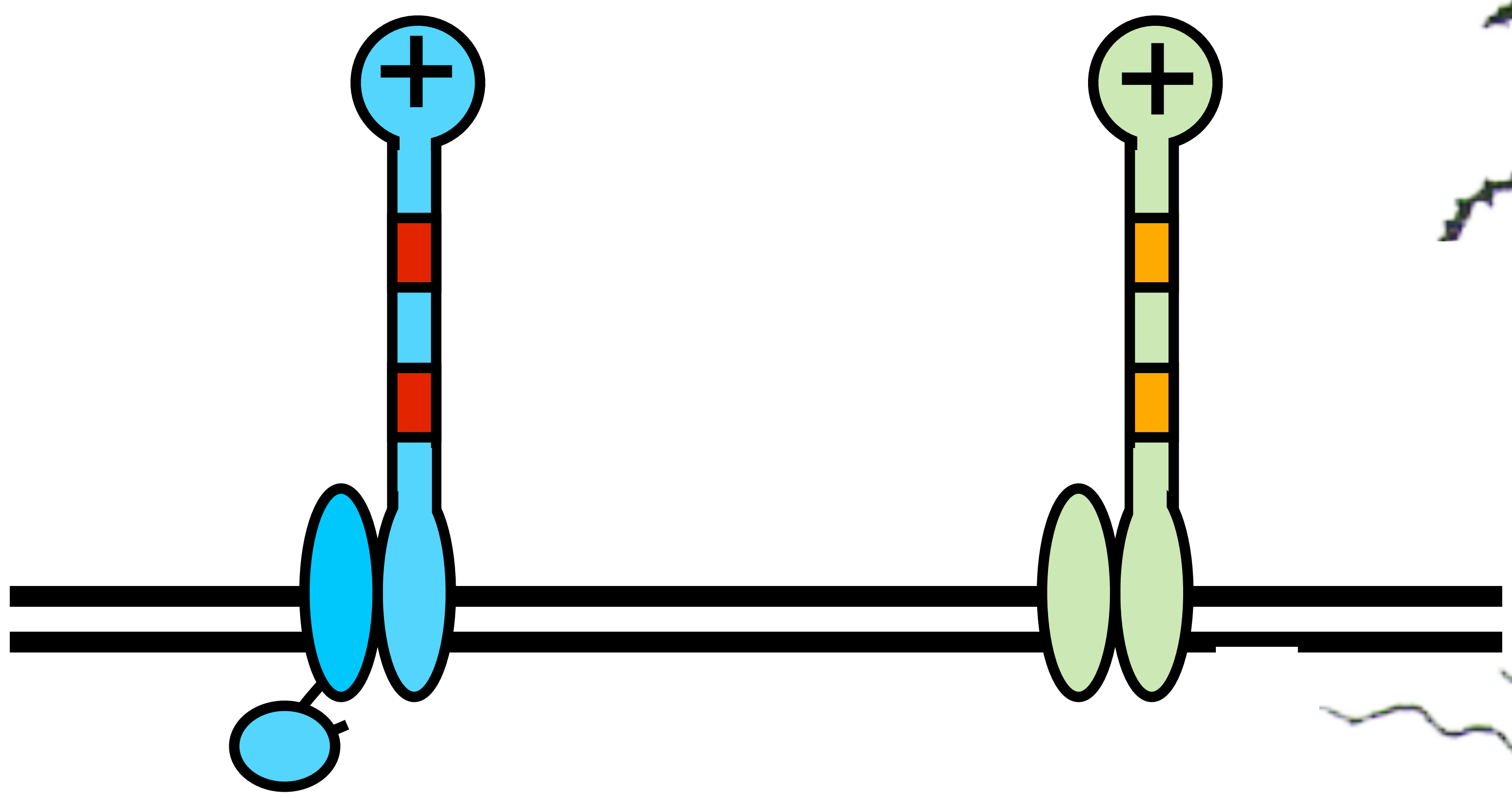
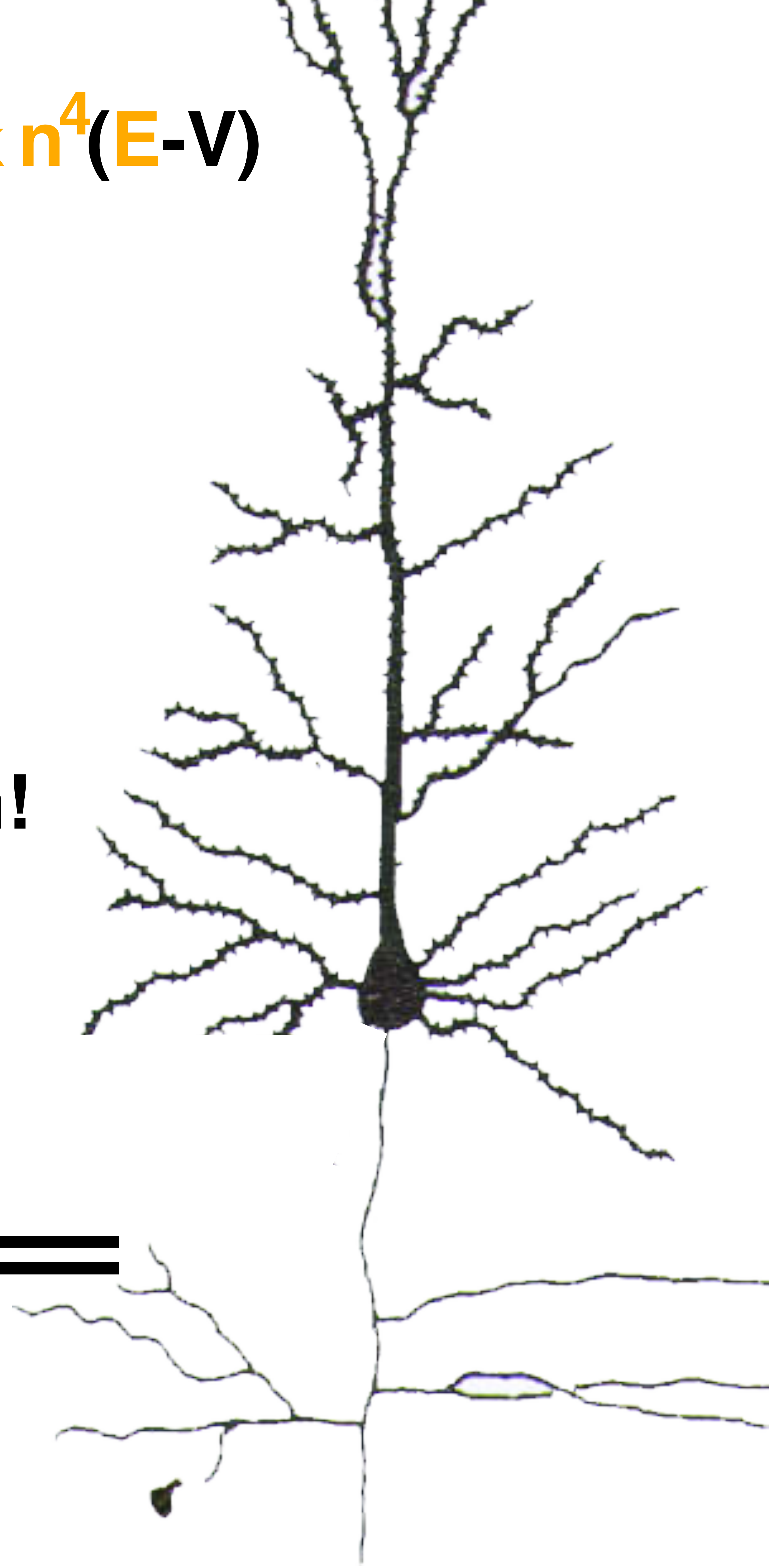


A complete description of a neuron!





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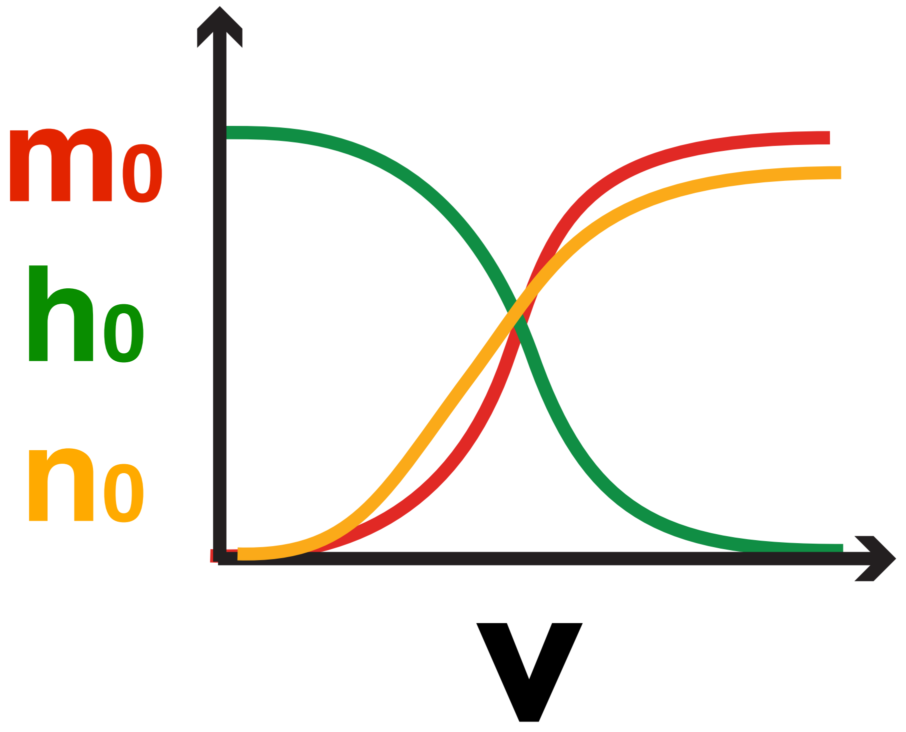

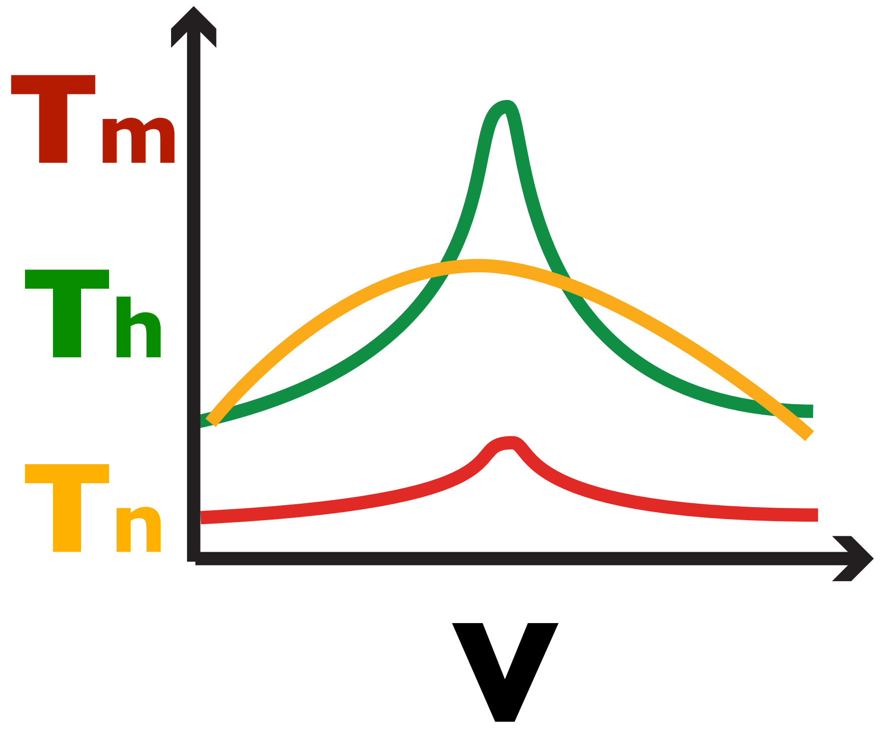

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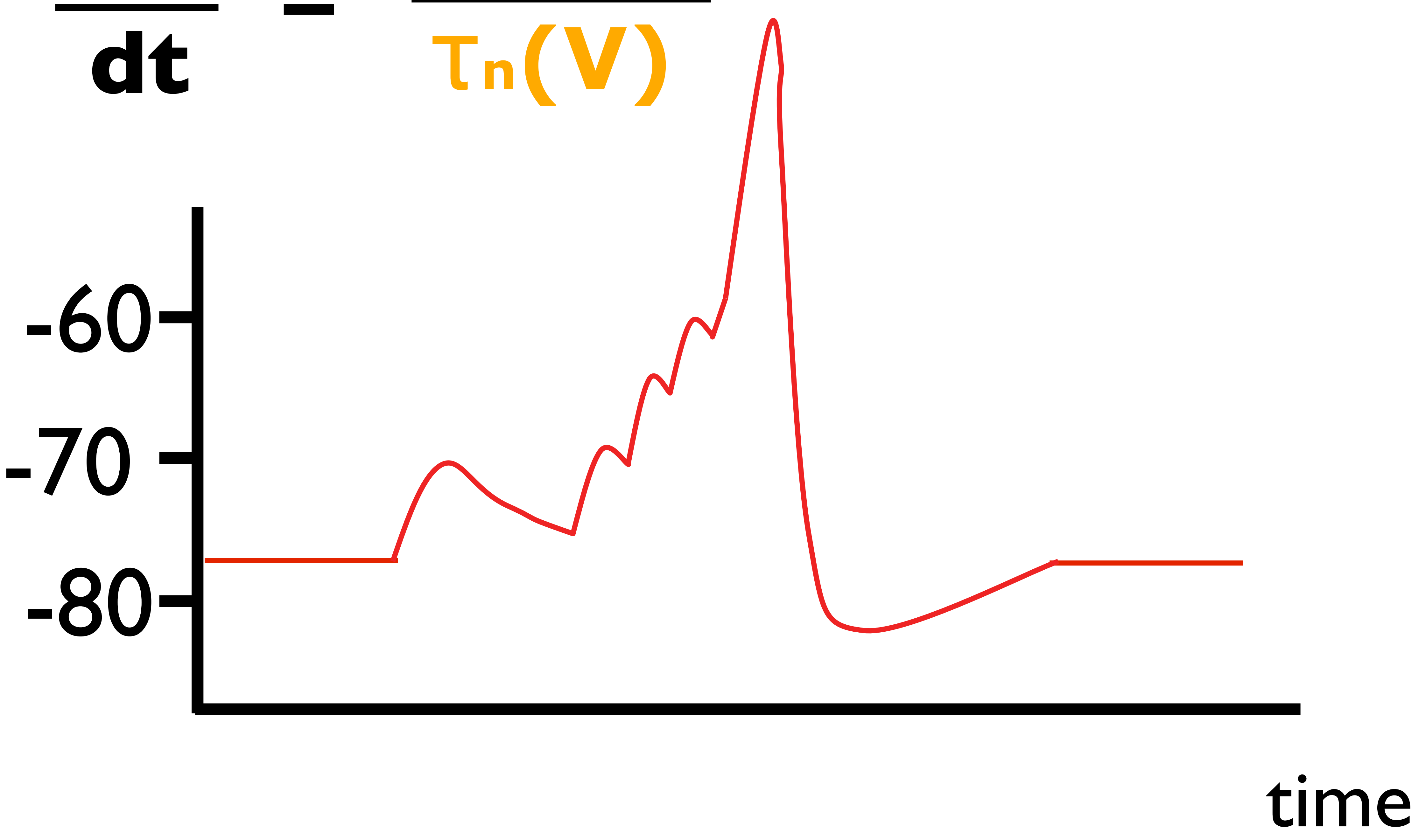
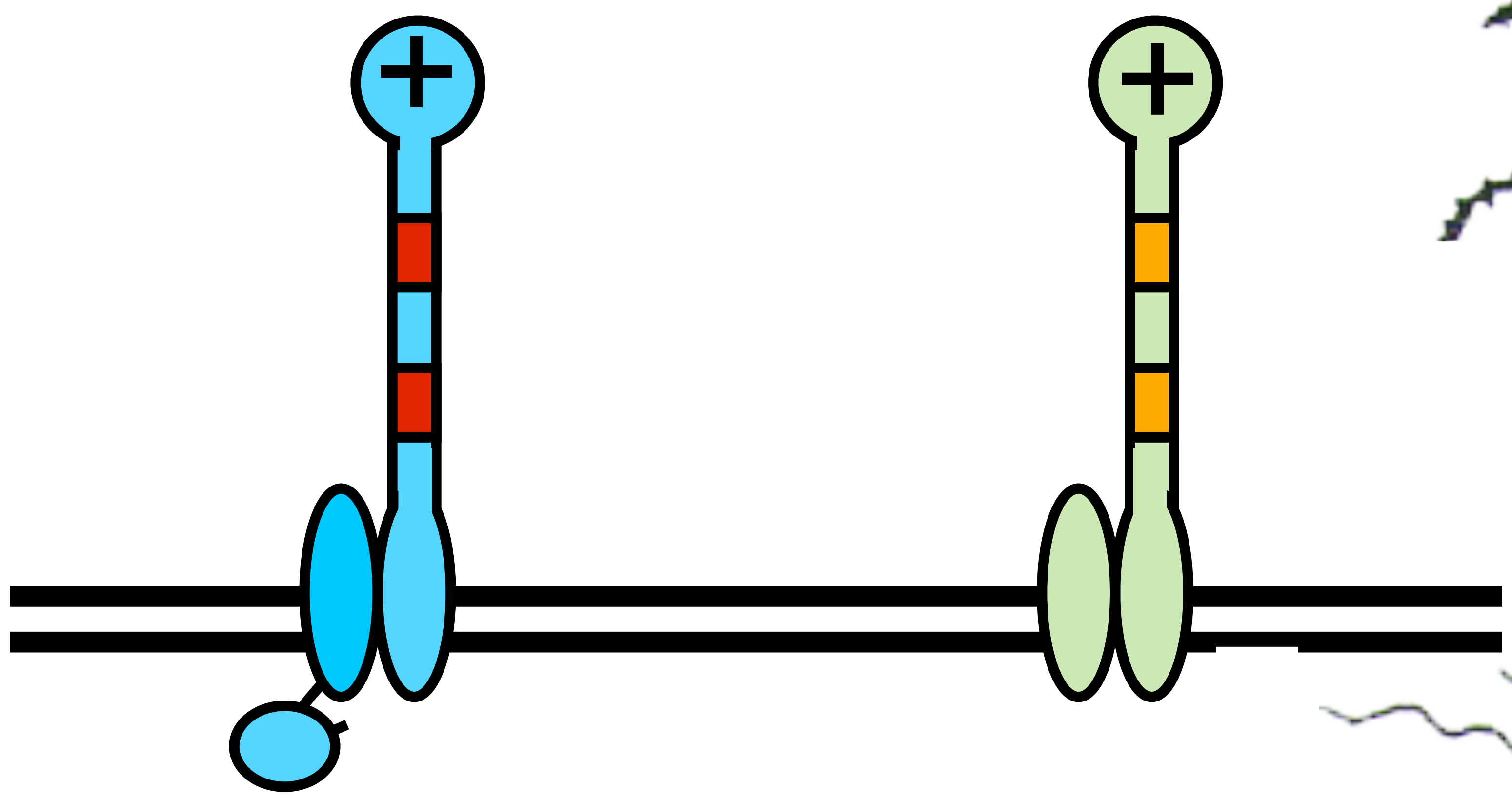
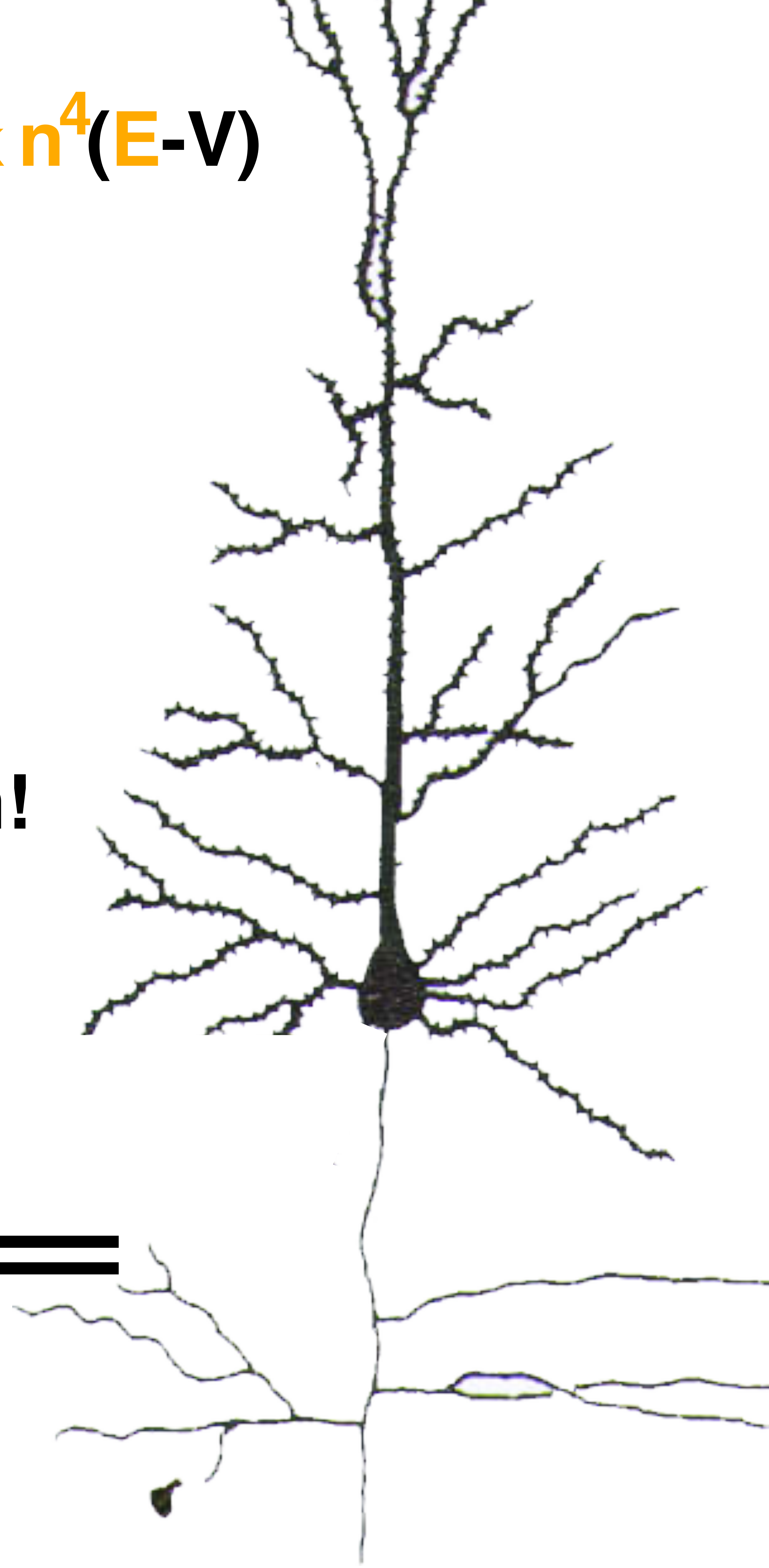
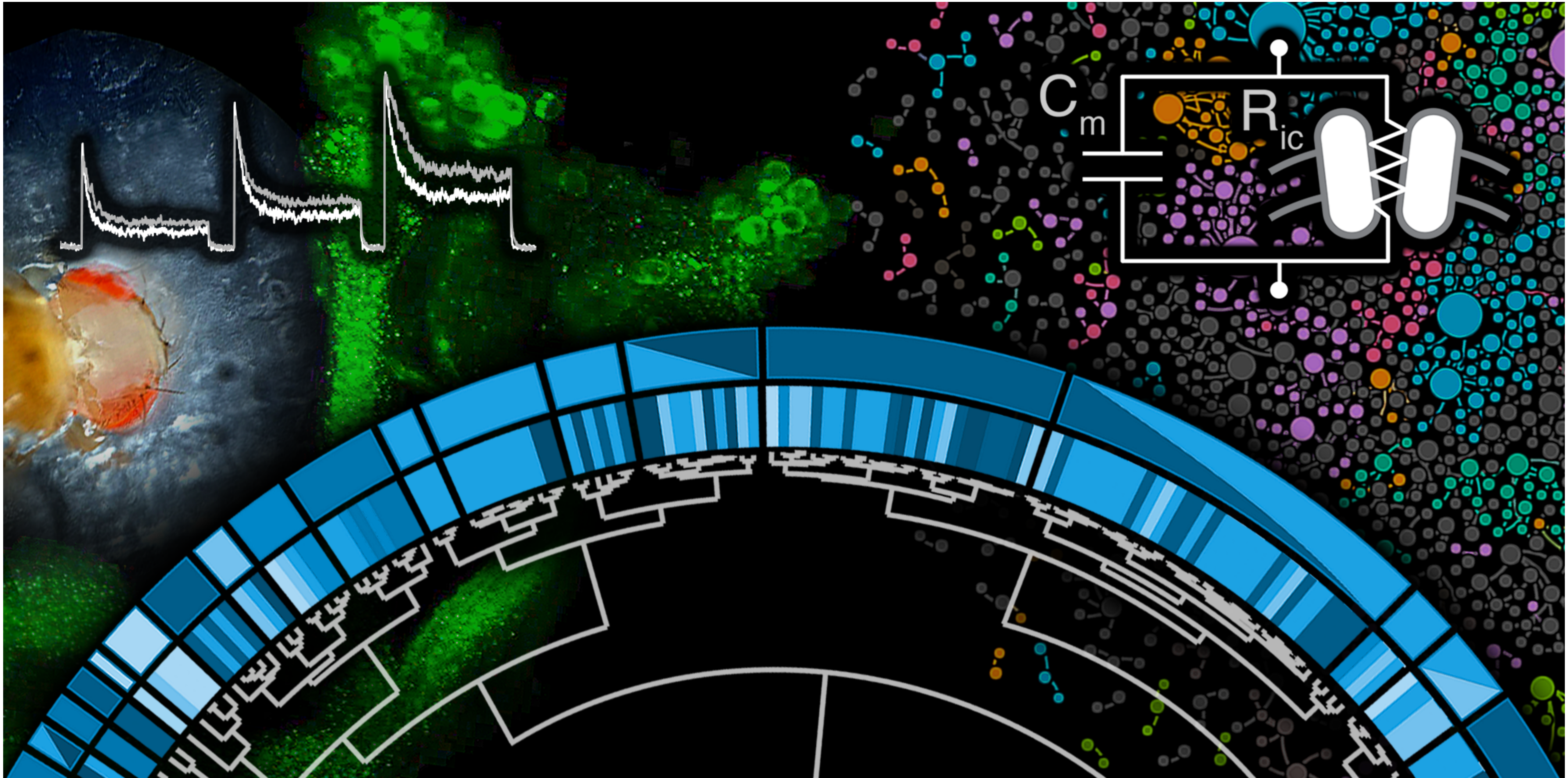






Mapping the function of neuronal ion channels in model and experiment

William F Podlaski, Alexander Seeholzer, Lukas N Groschner, Gero Miesenböck, Rajnish Ranjan, Tim P Vogels



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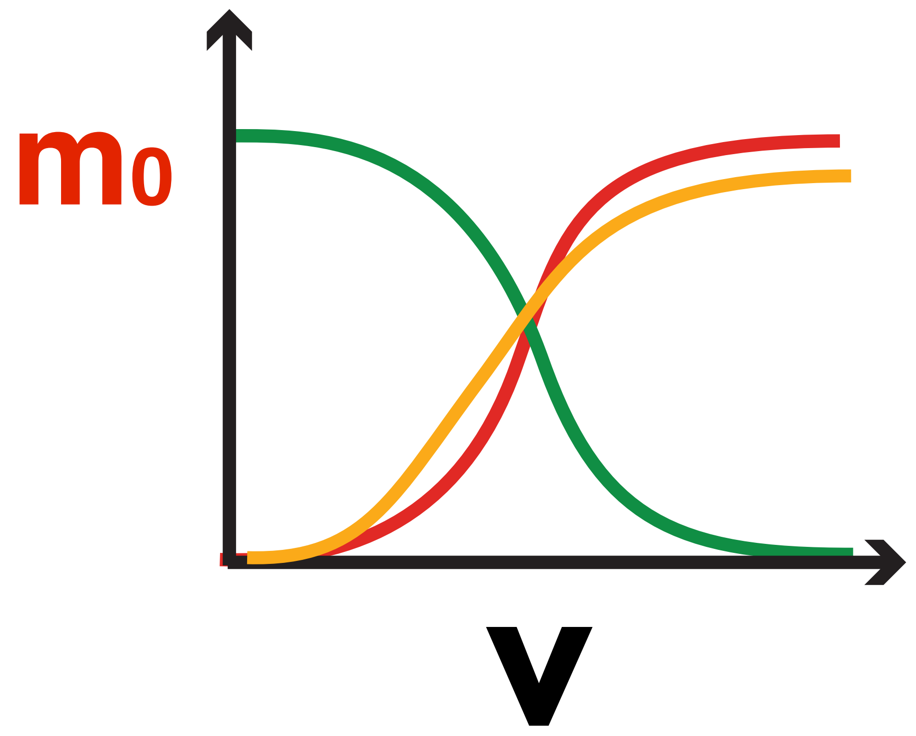

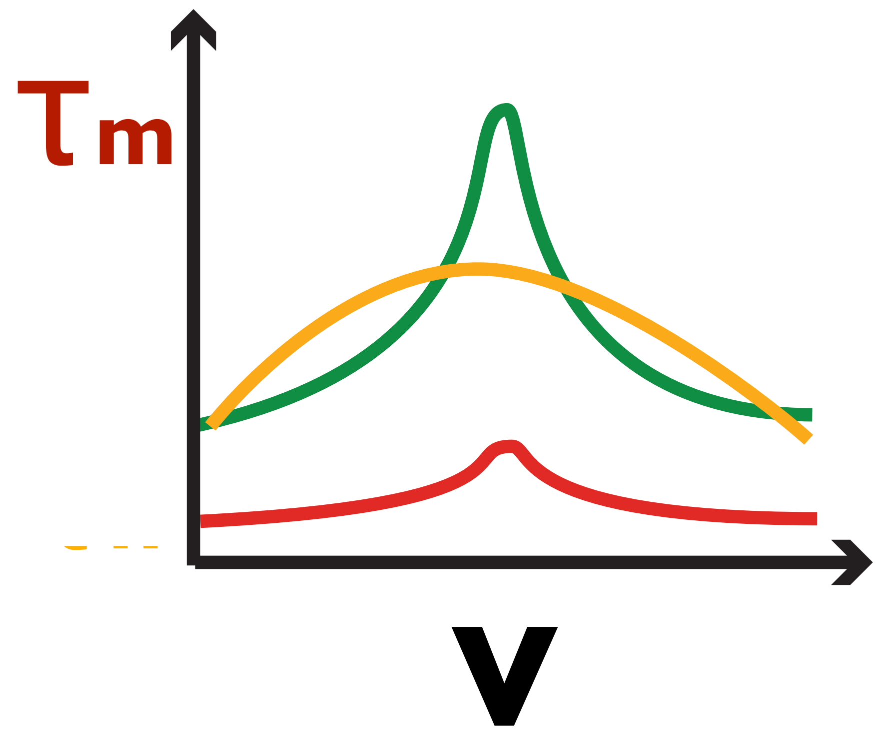

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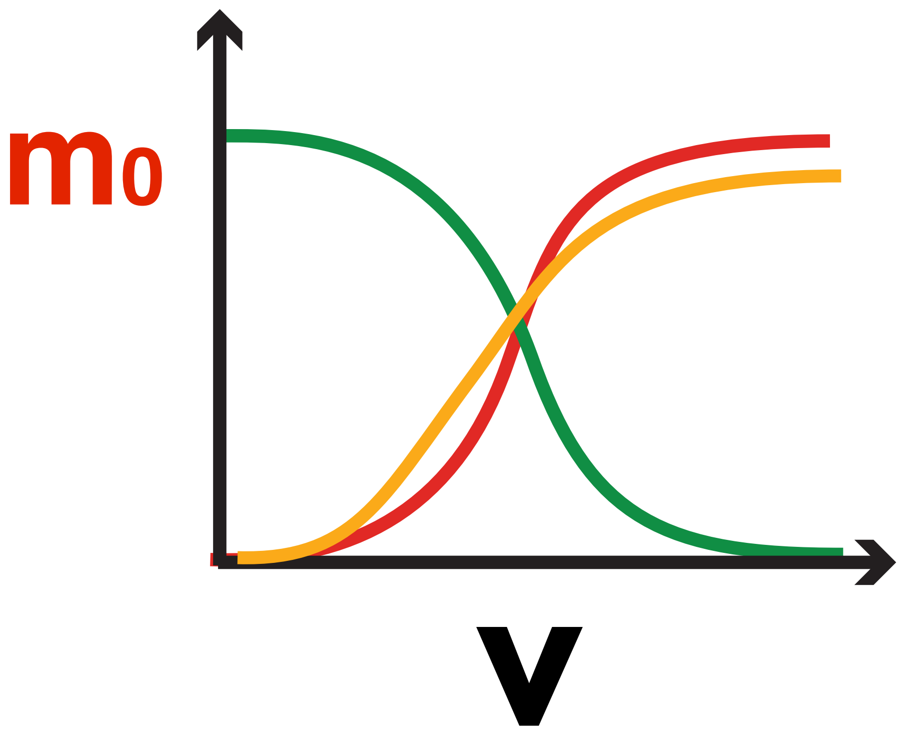

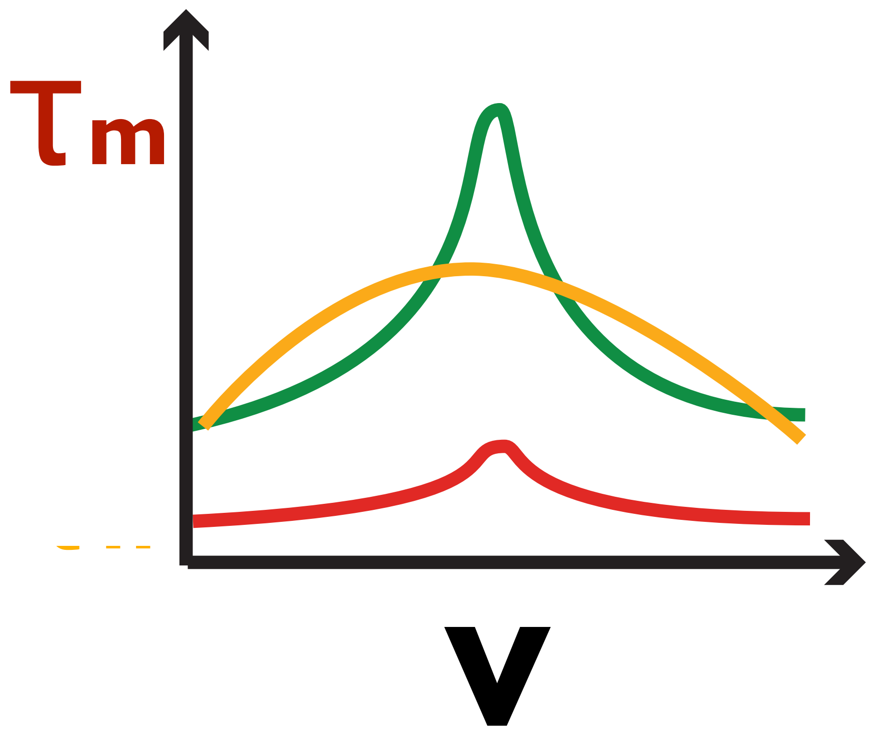

A complete description of neuron!

Action potentials
Threshold behaviour
Refractory behaviour
Test our knowledge of what is going on…

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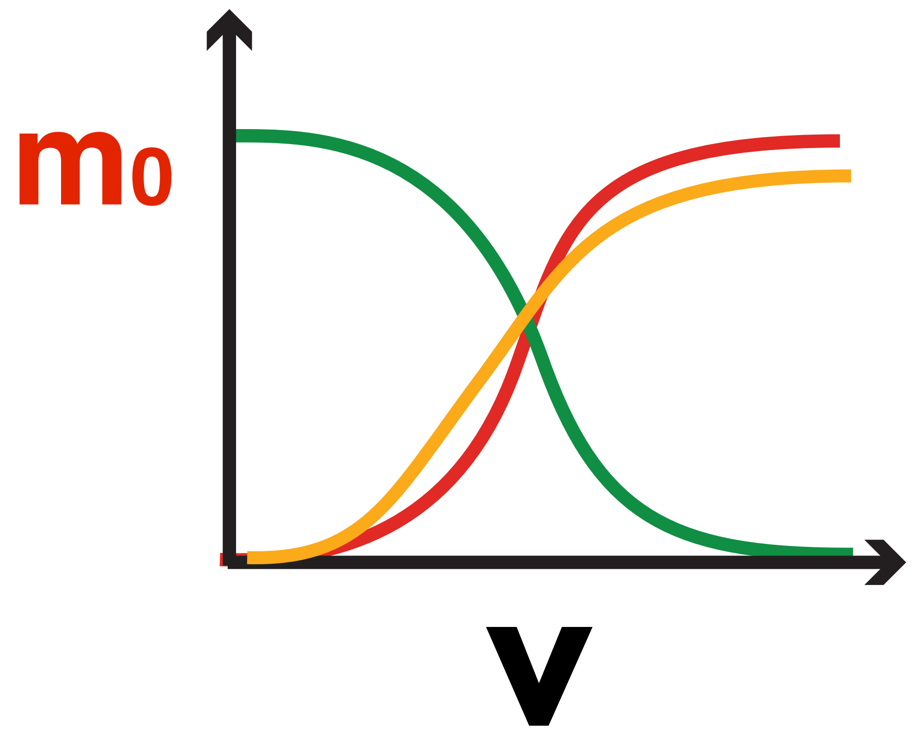

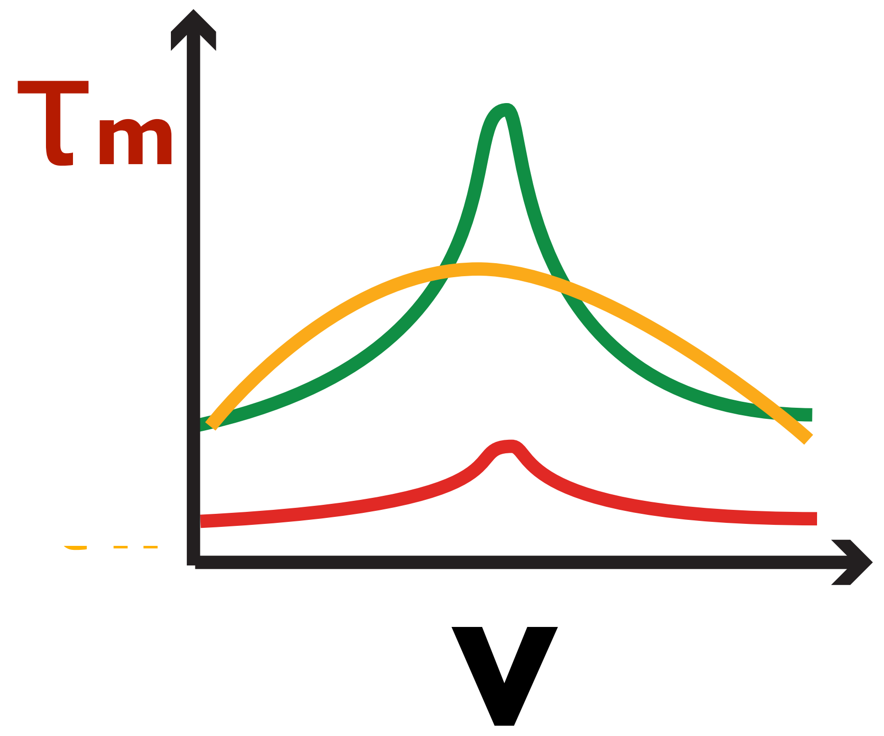

A complete description of neuron!

For easy access to any channel:

http://vogelslab.org/icgenealogy

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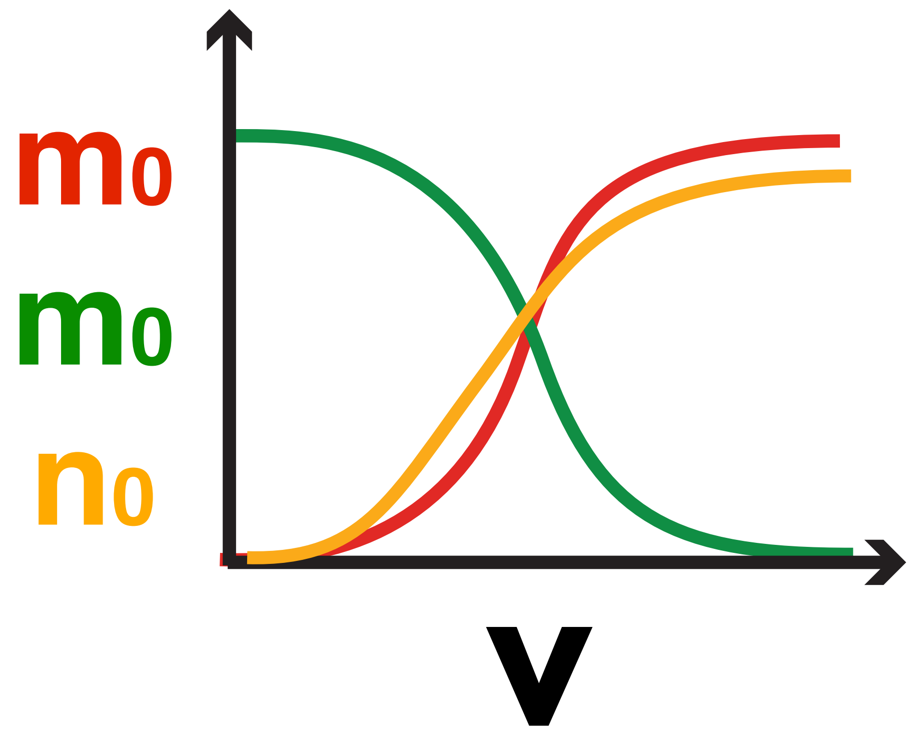

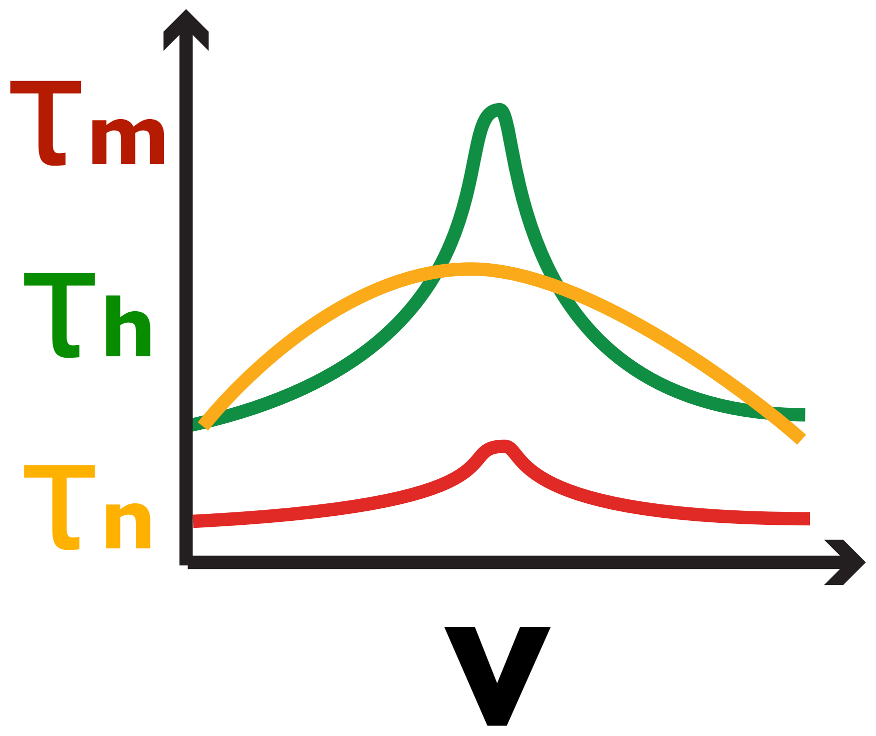

But do we understand, fully, mathematically?

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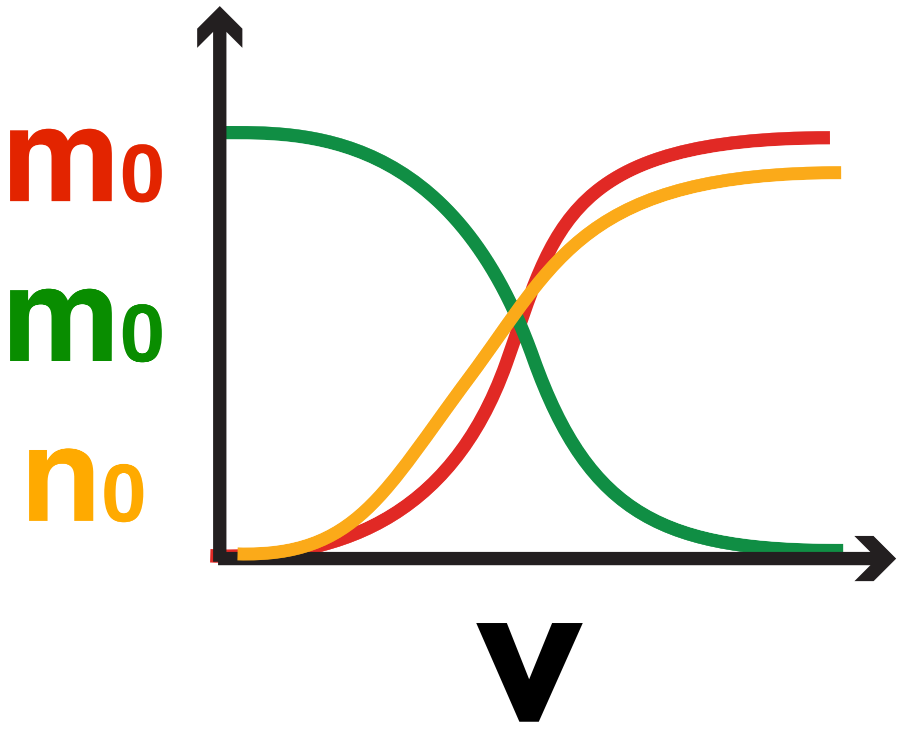

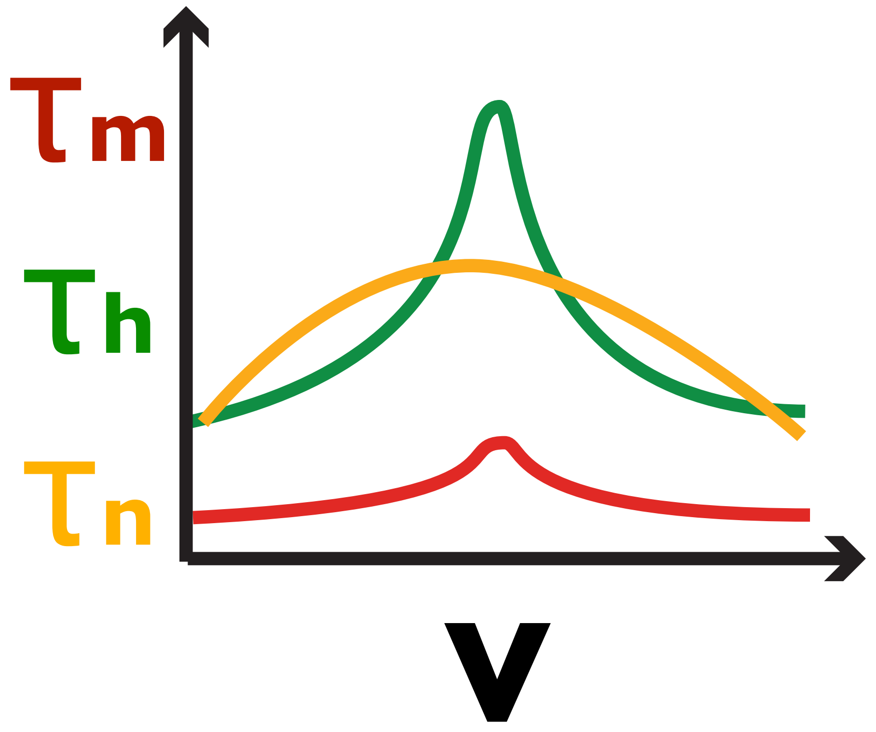

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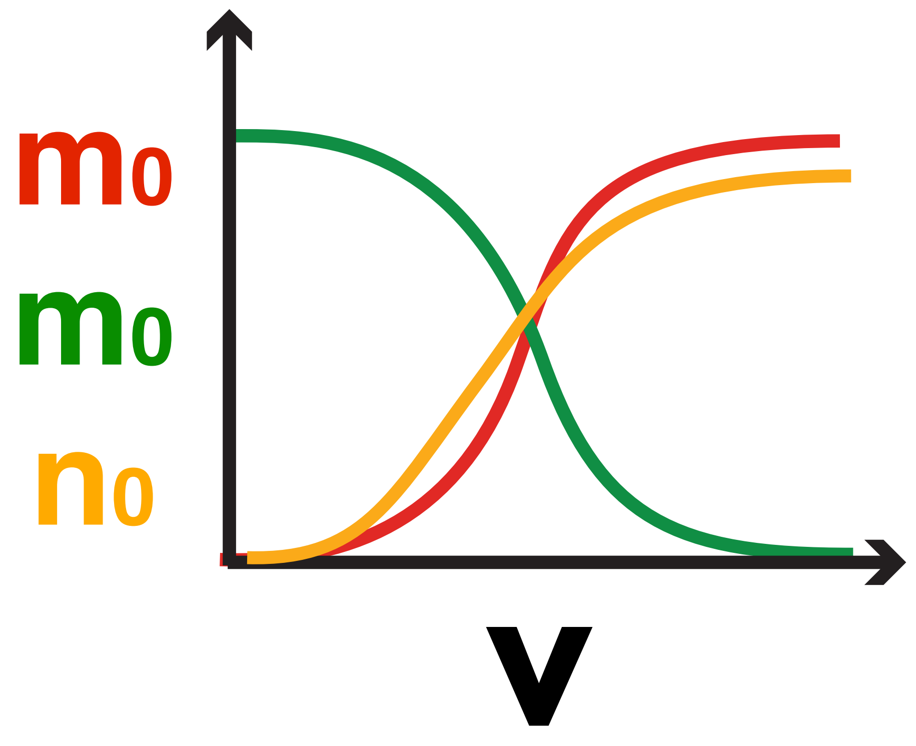

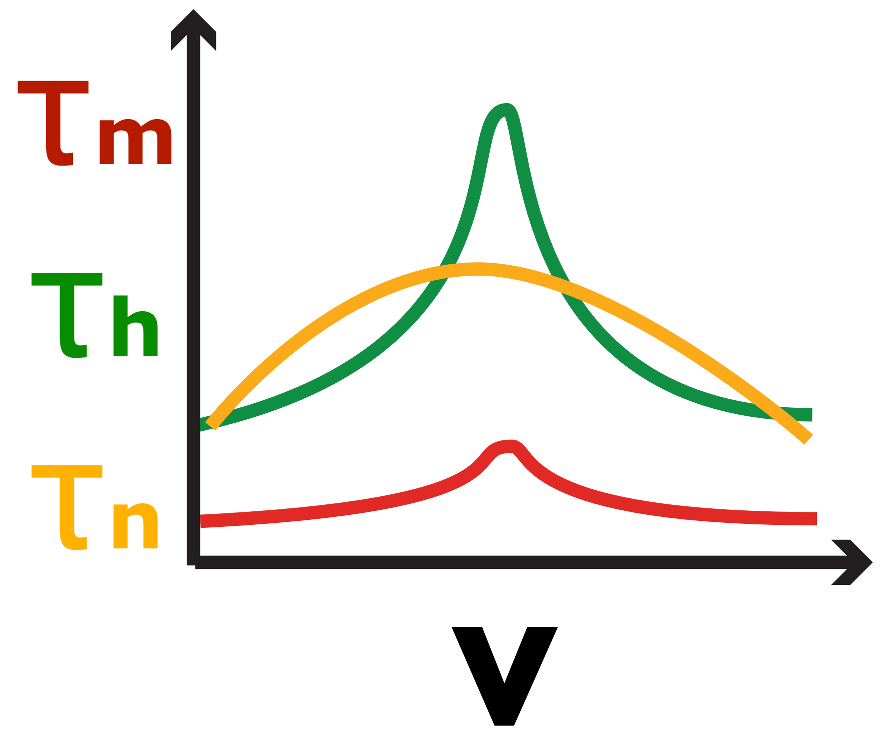

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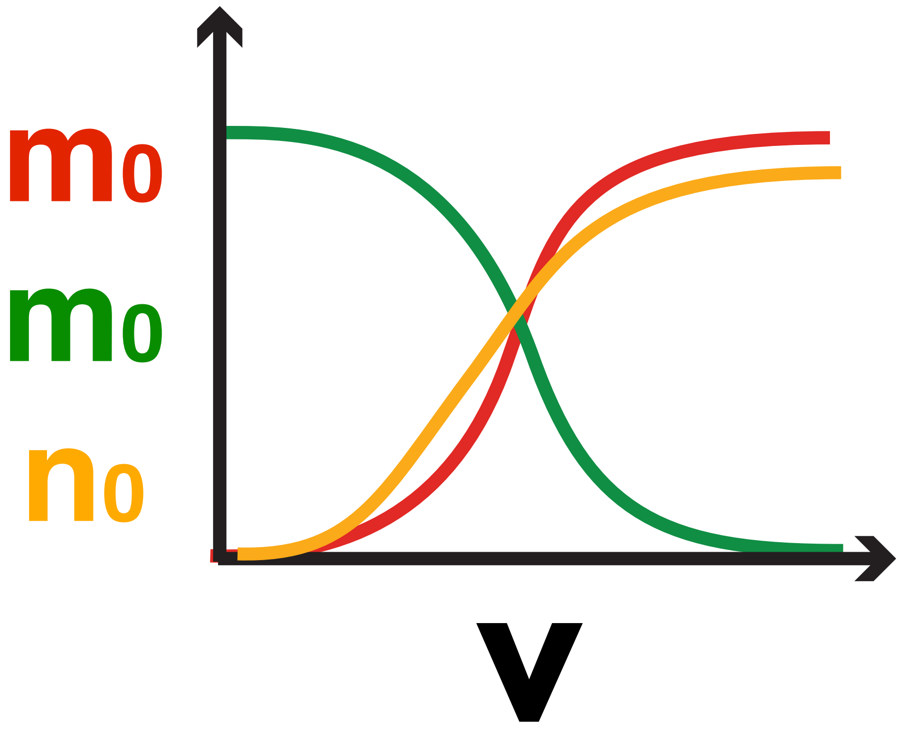

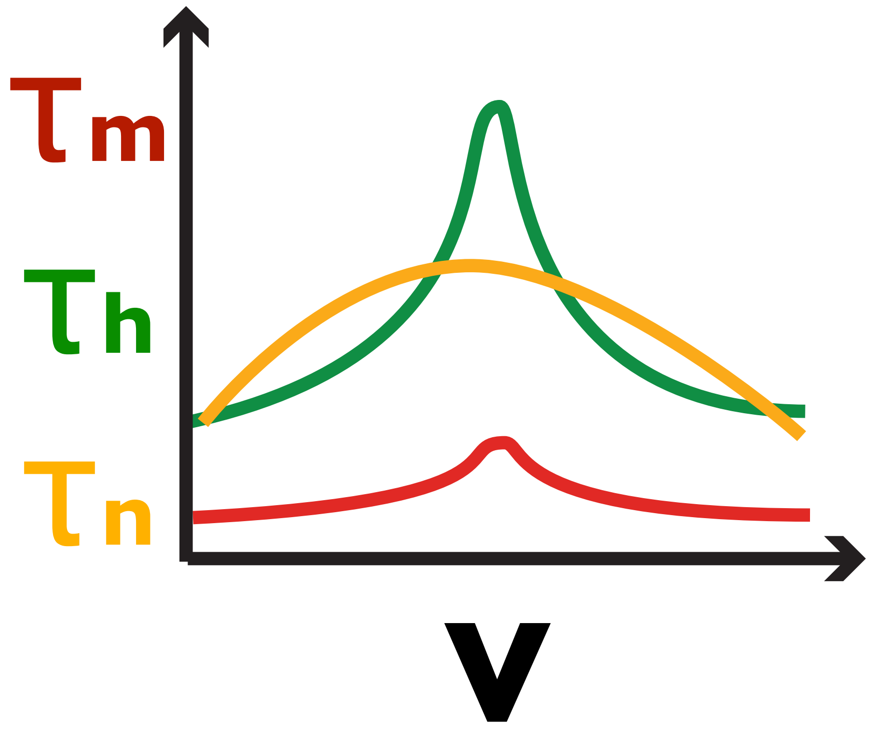

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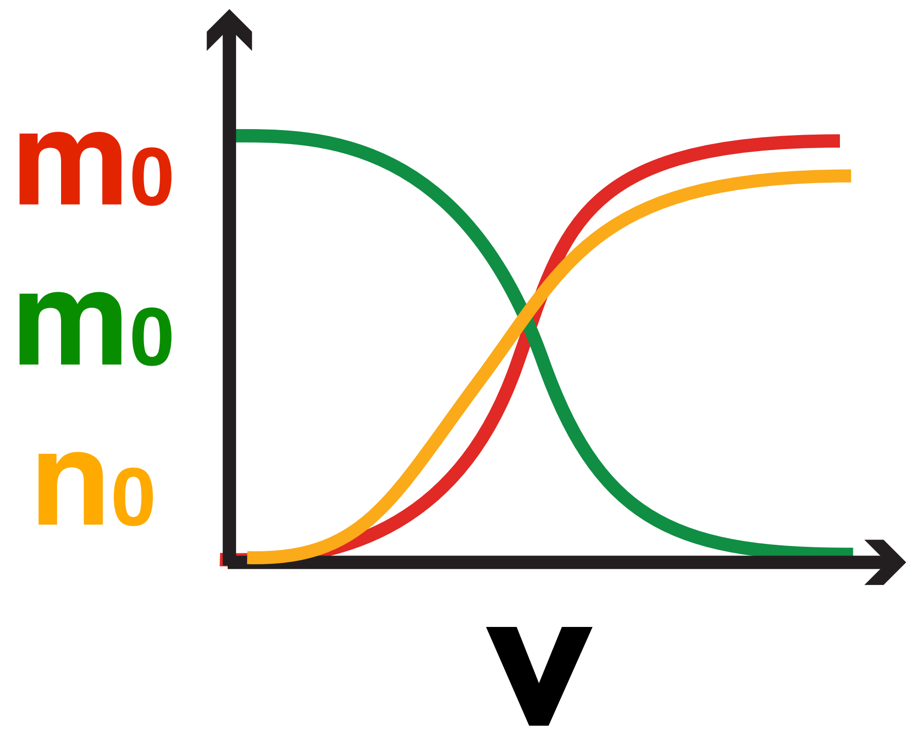

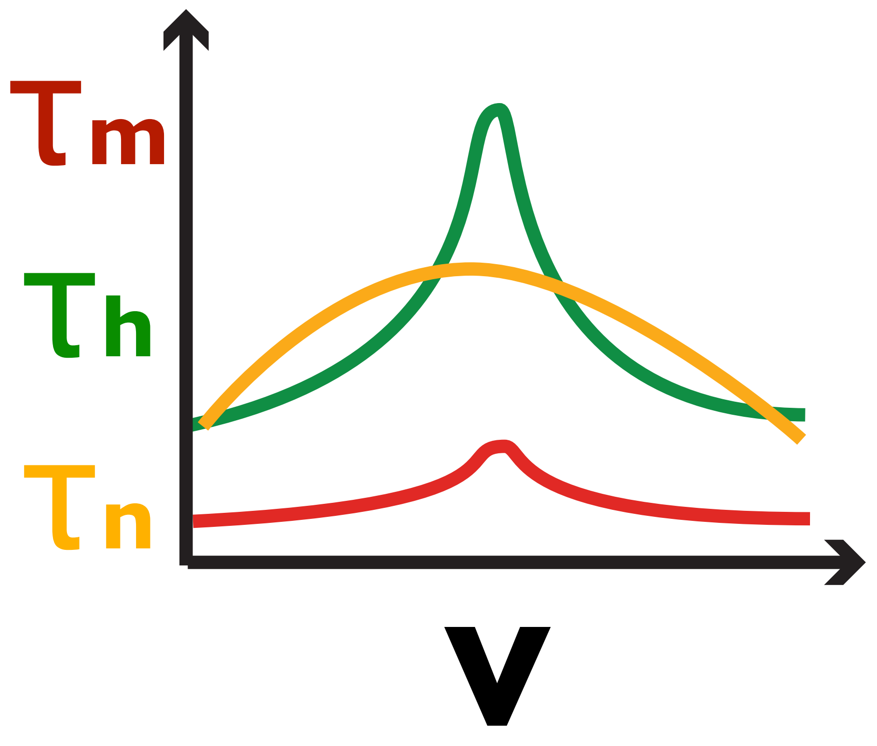

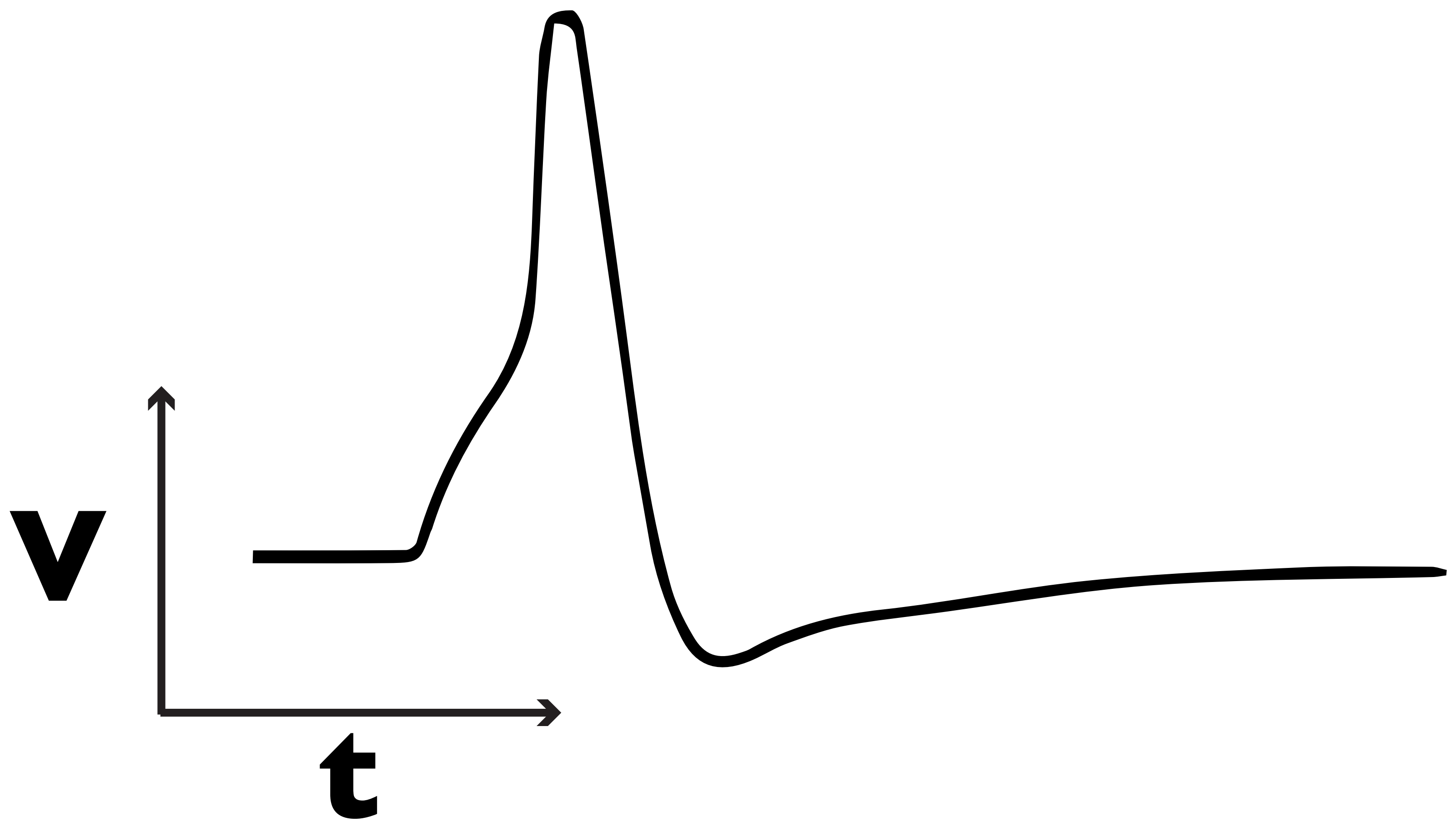

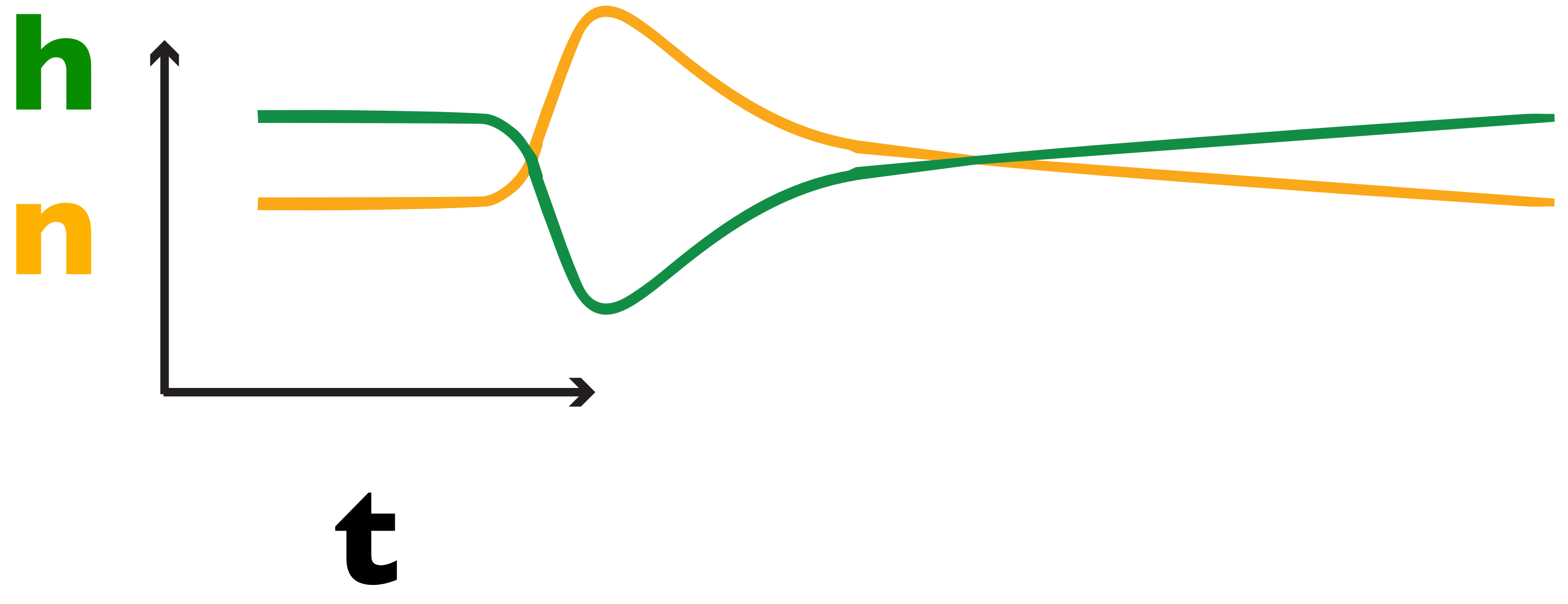

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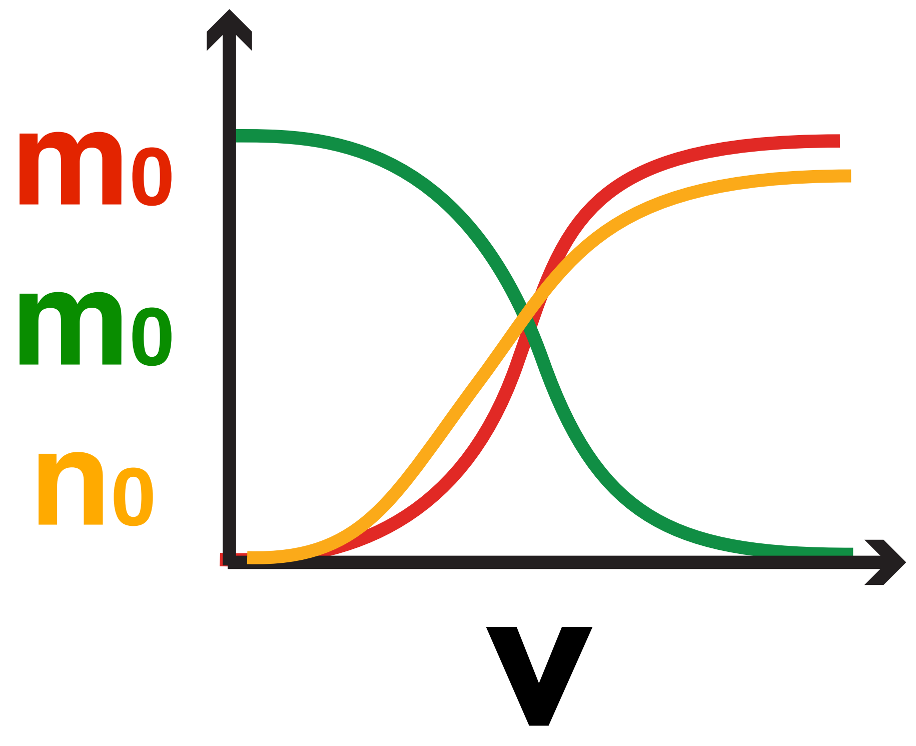

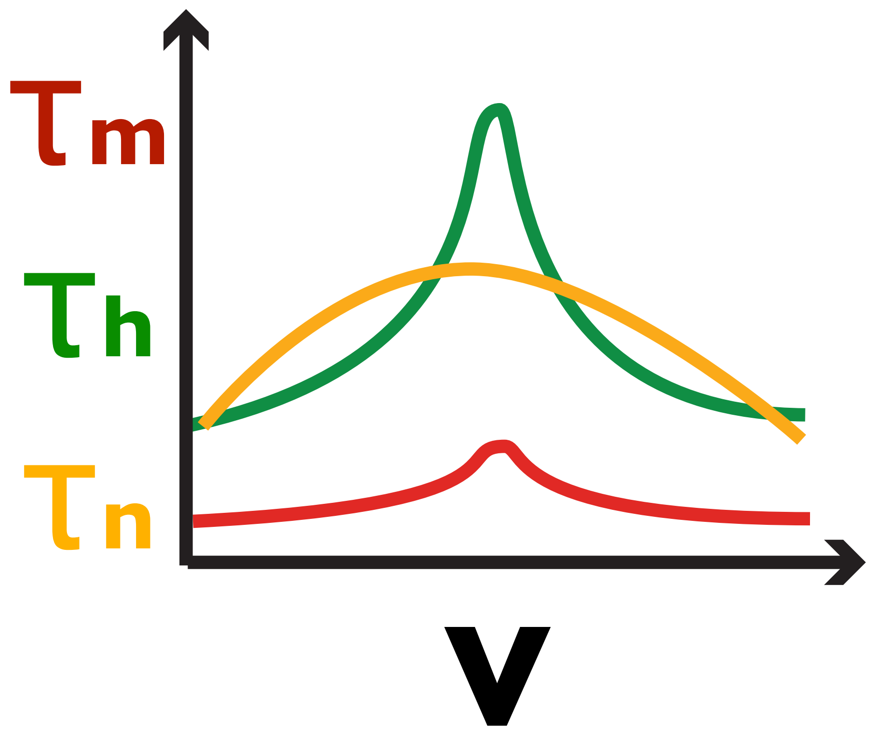

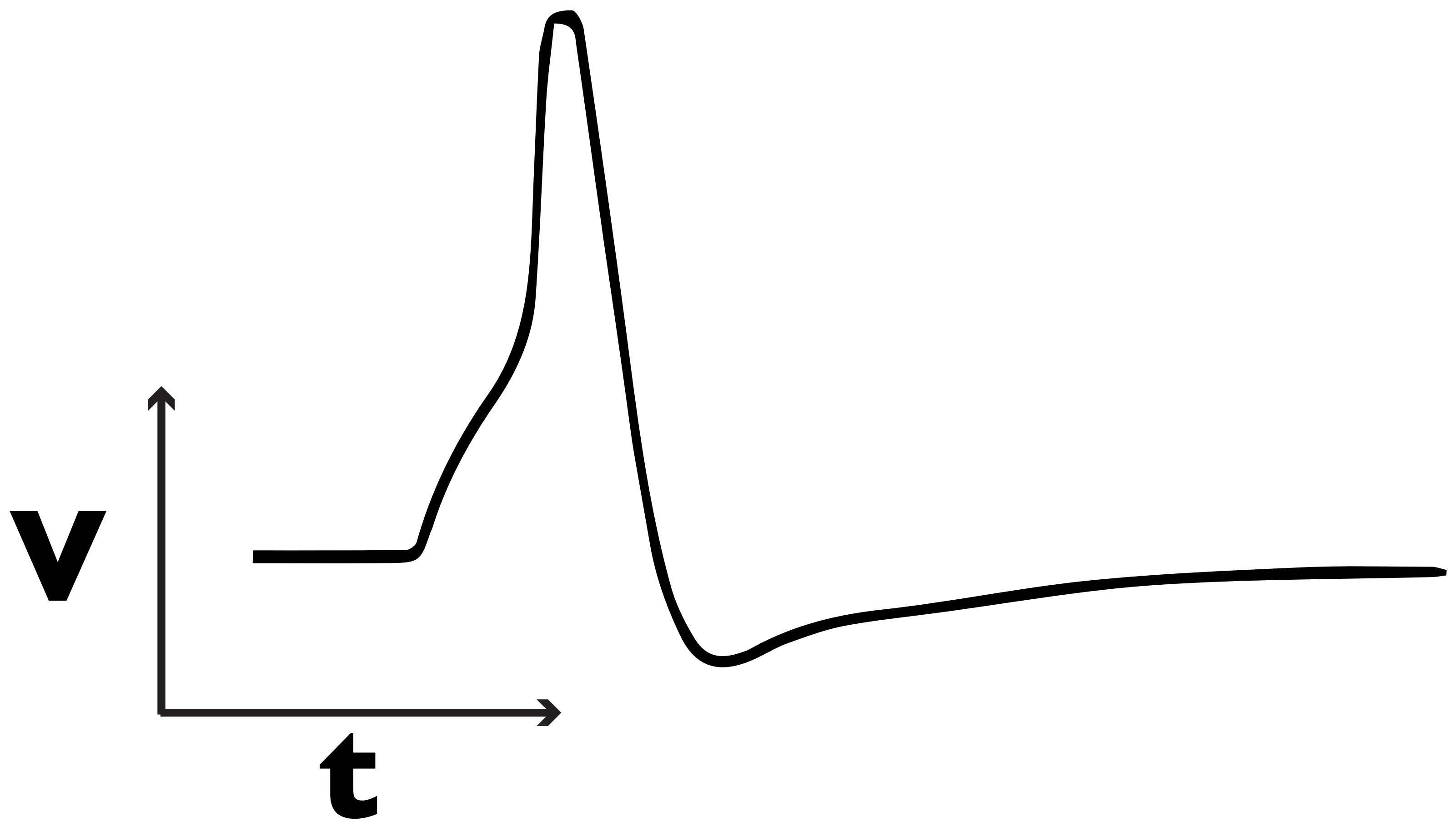

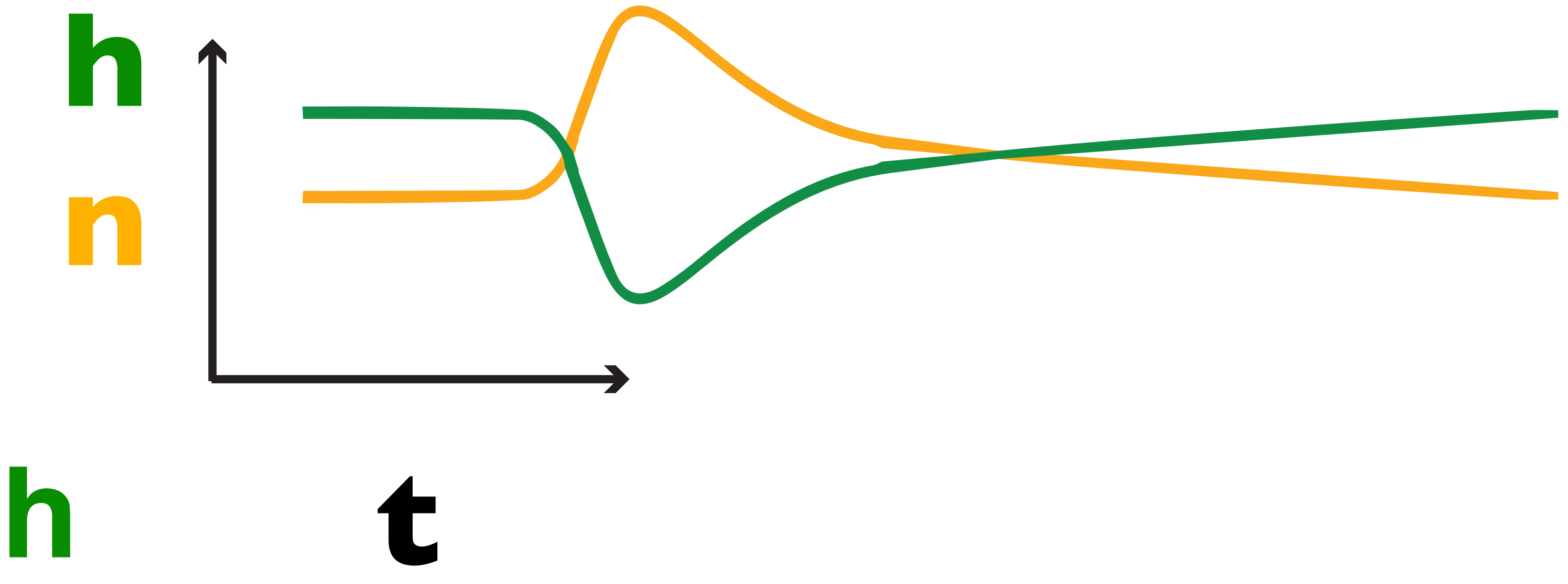

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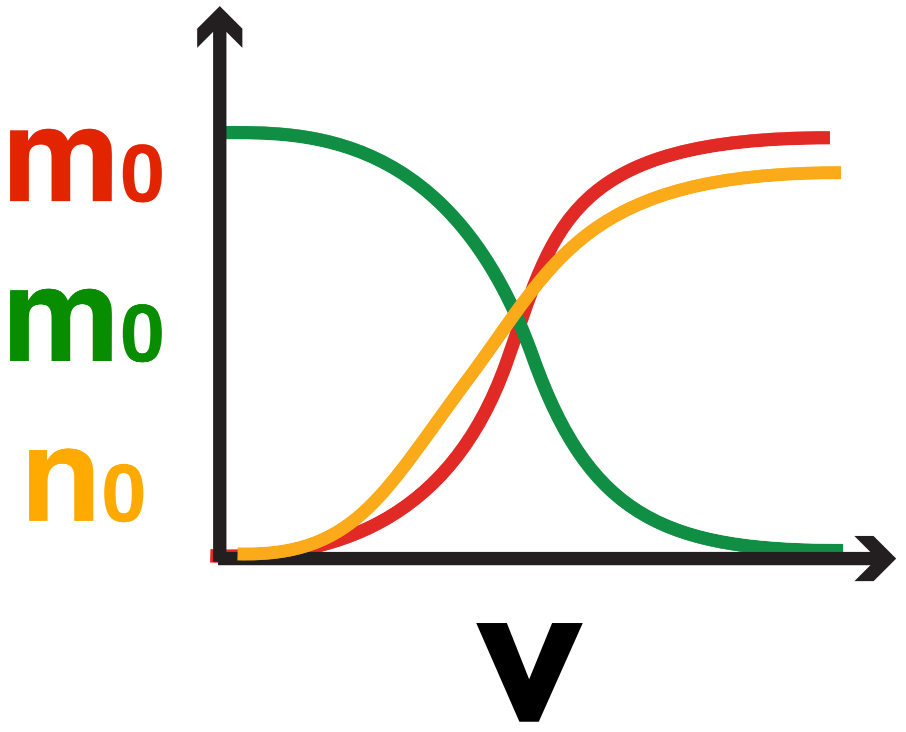

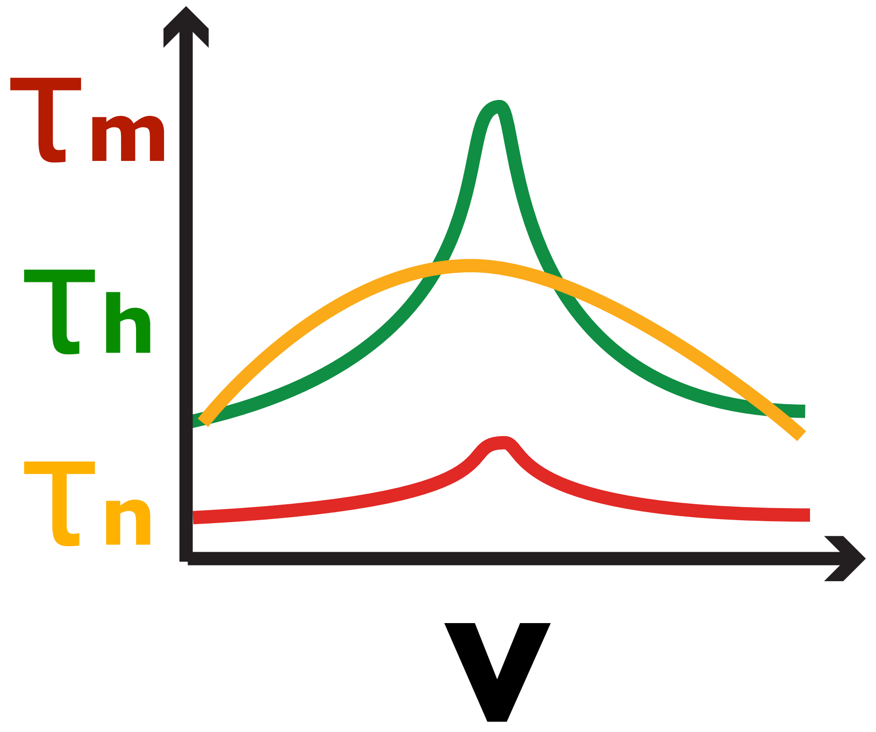

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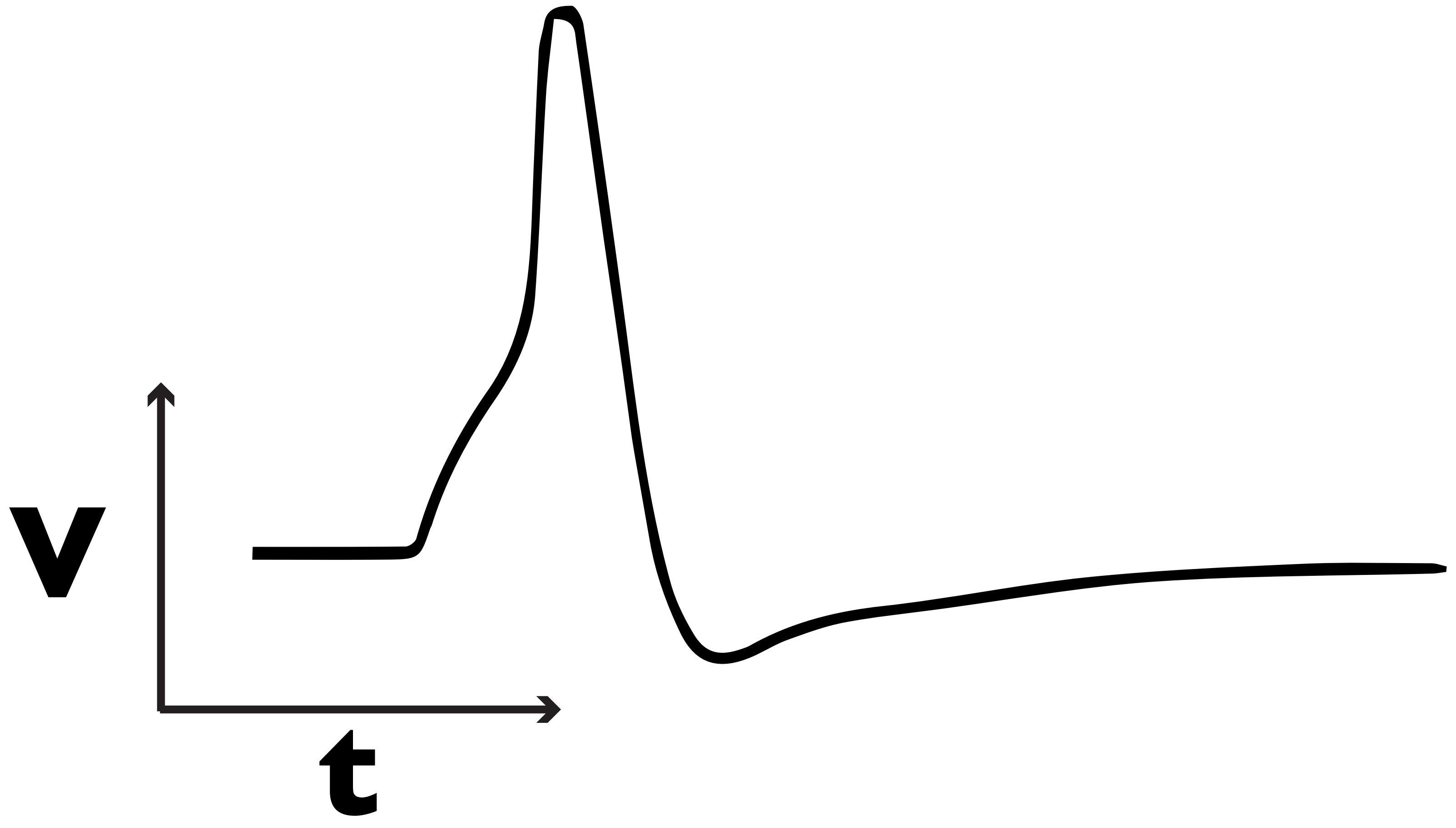

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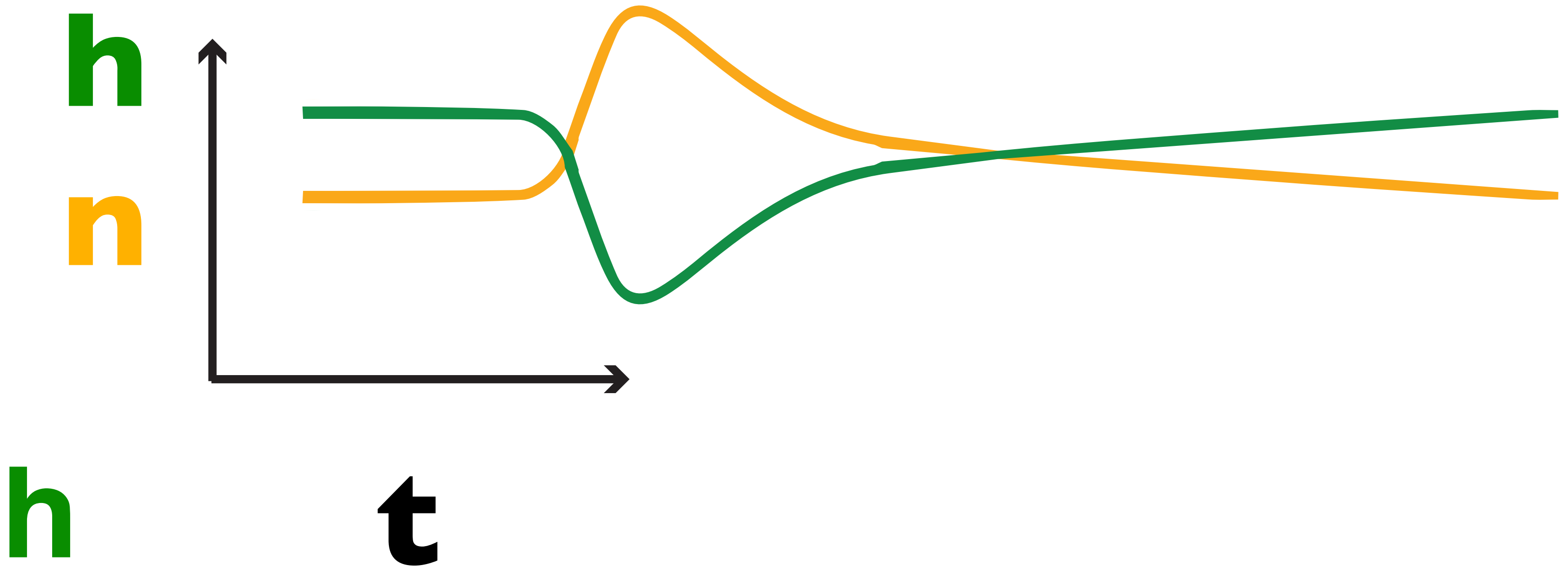

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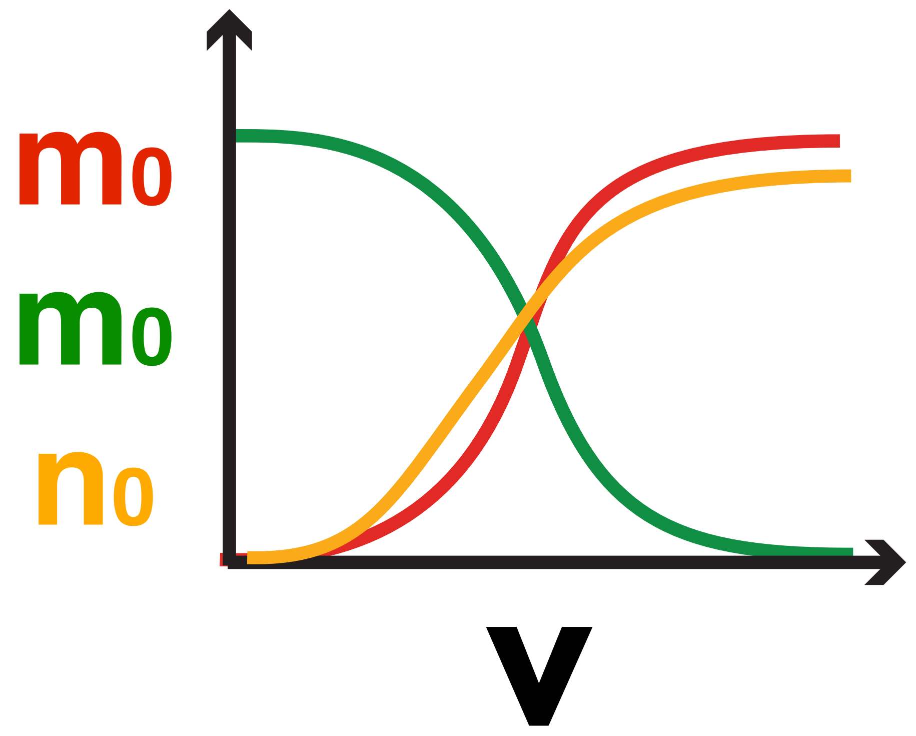

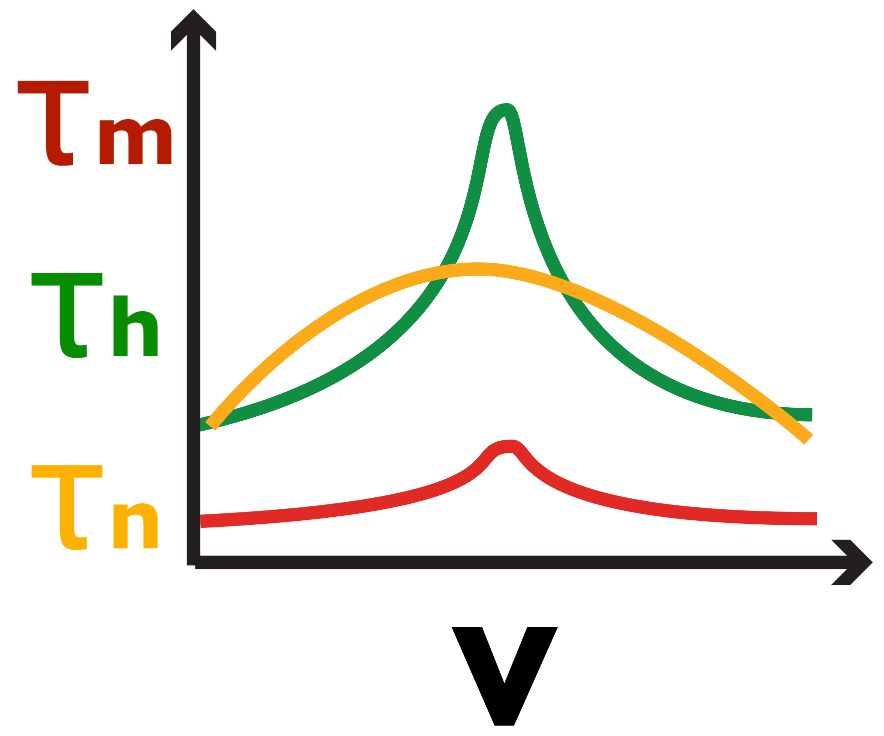

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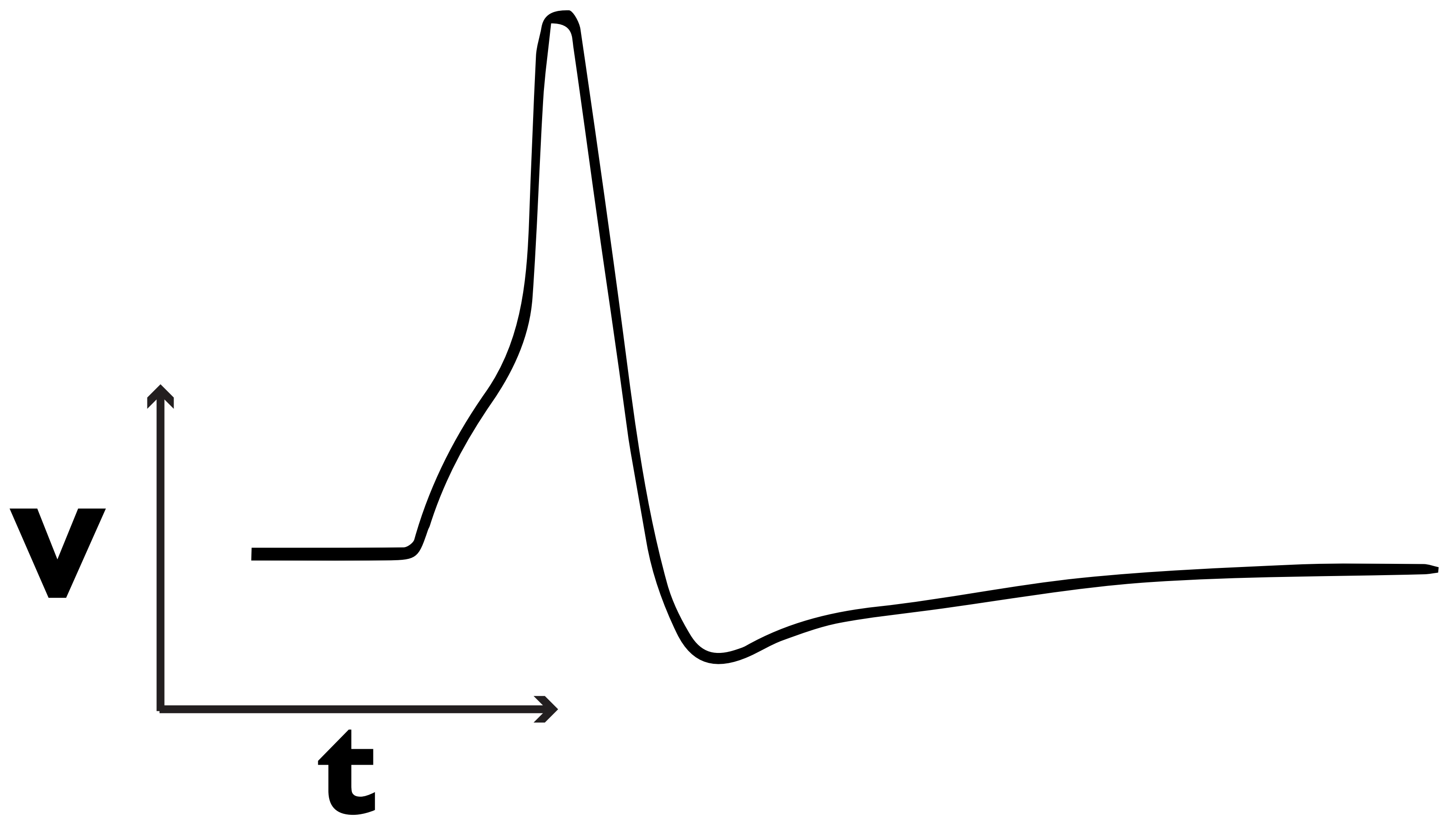

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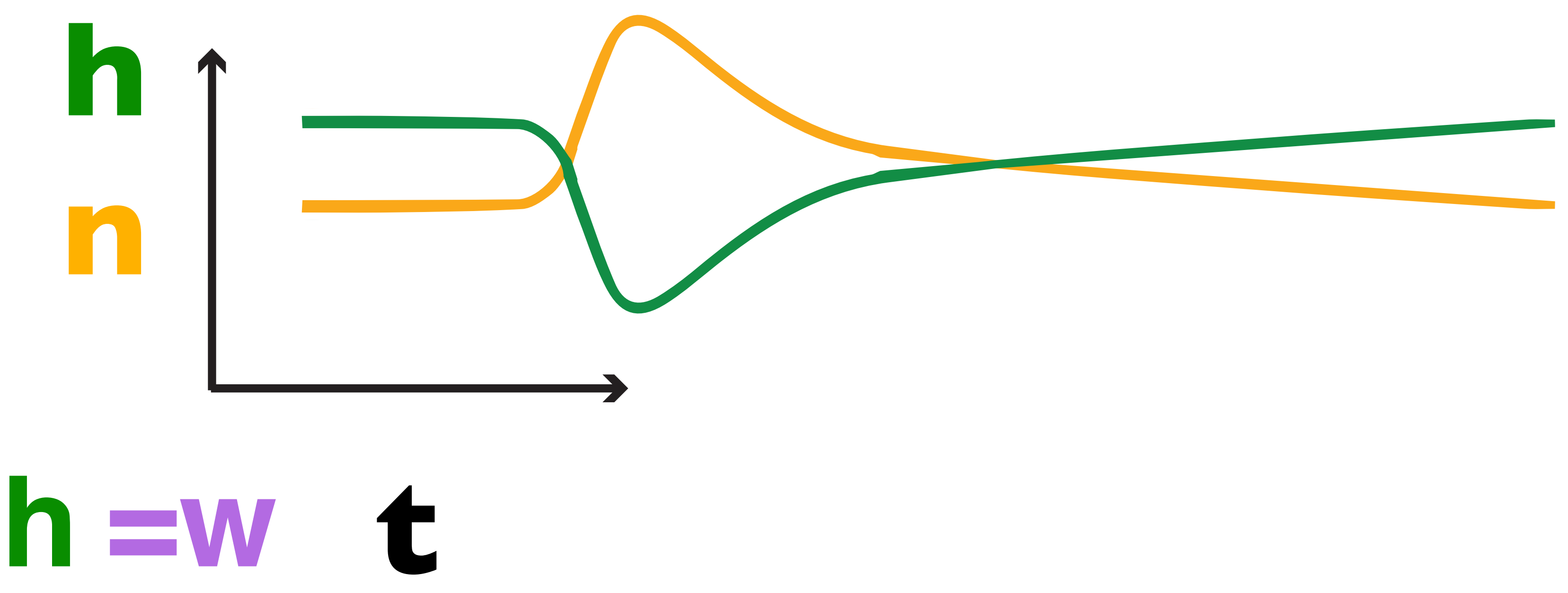

$an = 1-h = w$

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$$C\,\frac{dV}{dt} = g_{leak}\,(E-V) + g_{synapse}\,(E-V) + g_{Na}\,m_0^3\,h(E-V) + g_K \left(\frac{w}{a}\right)^4 (E-V)$$

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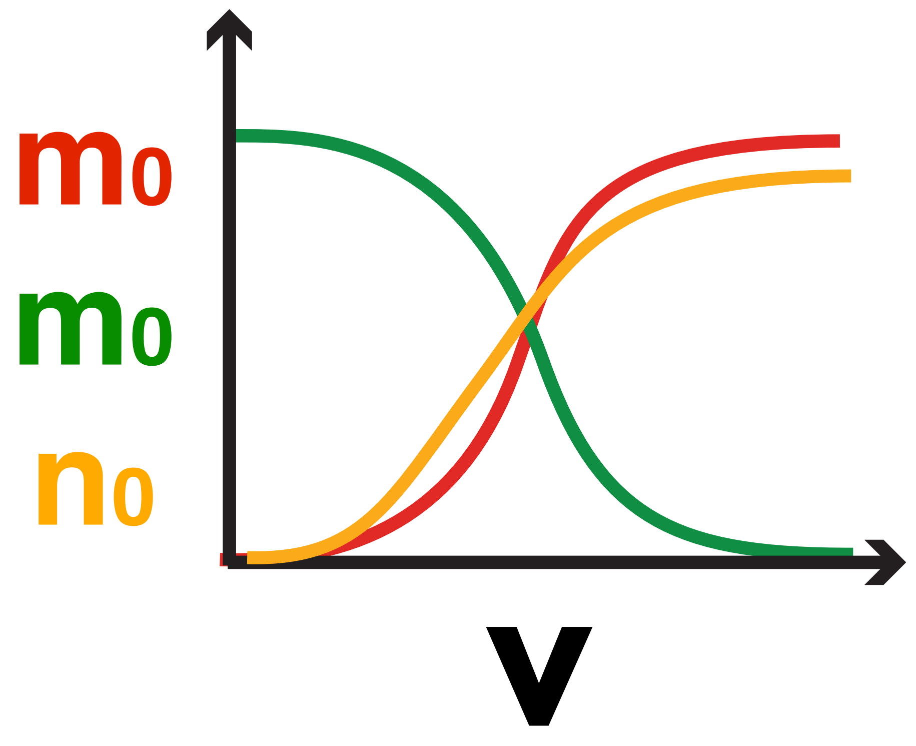

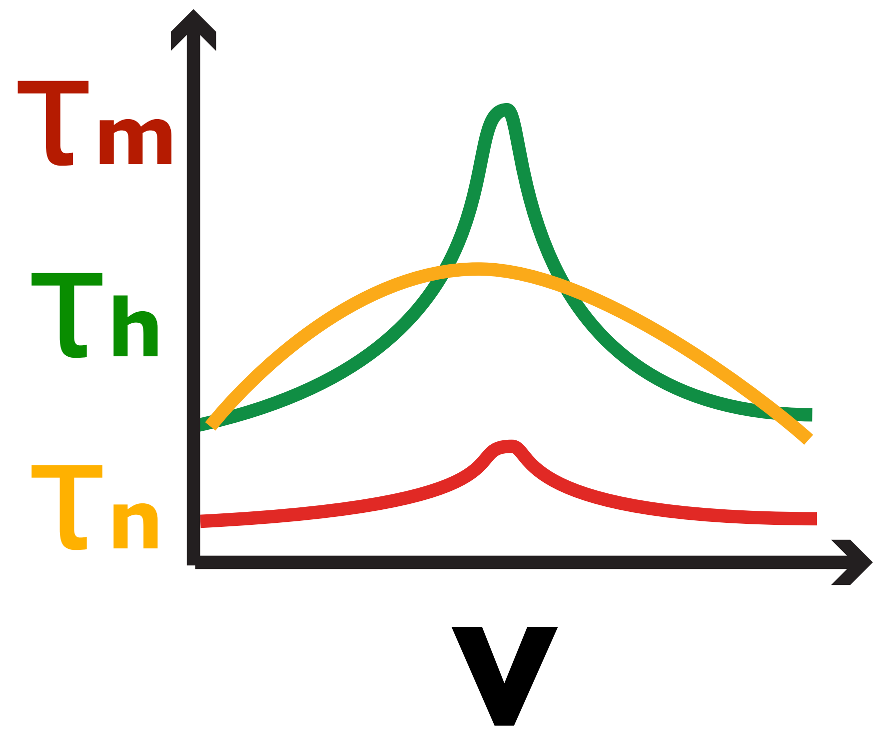

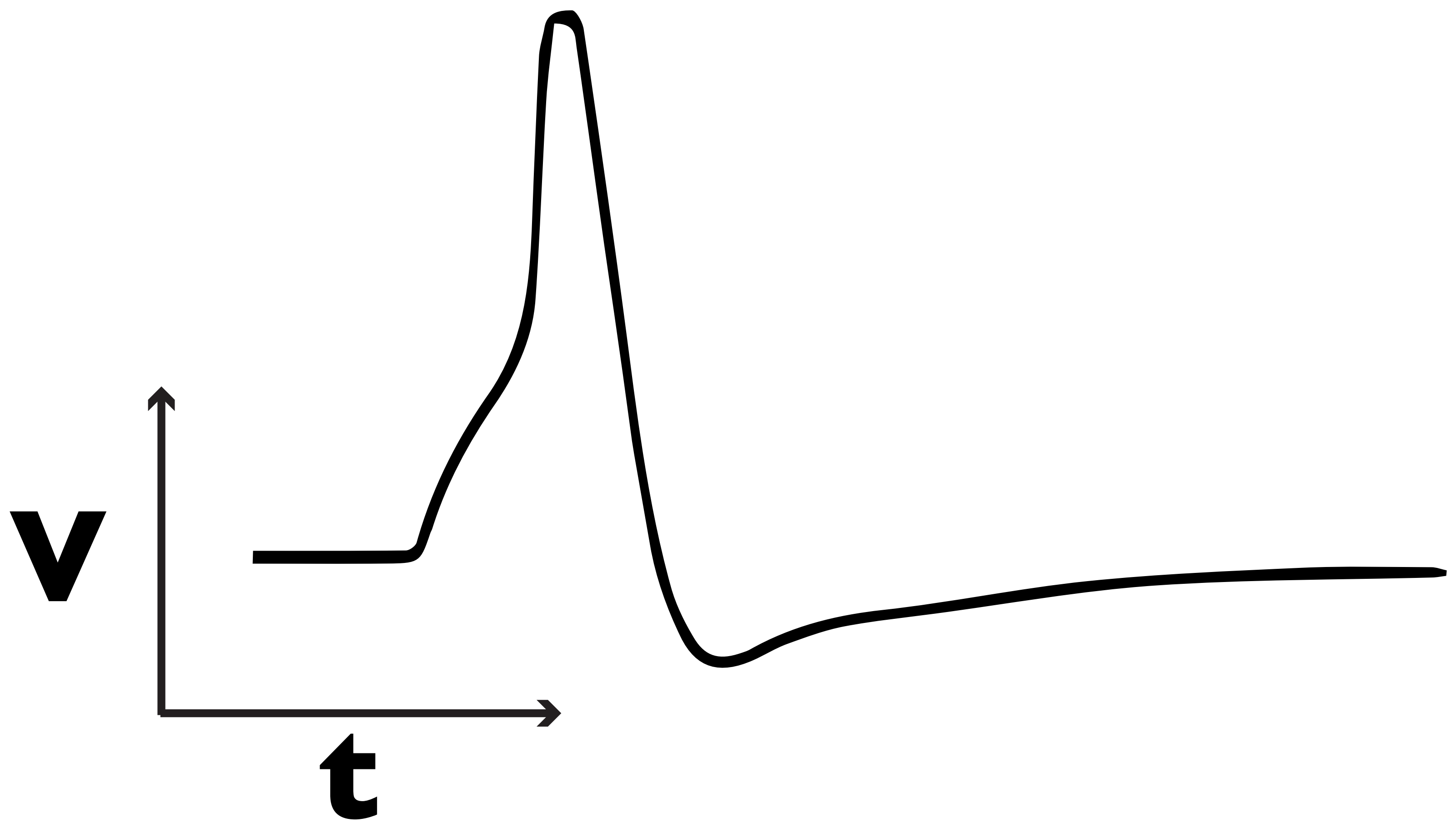

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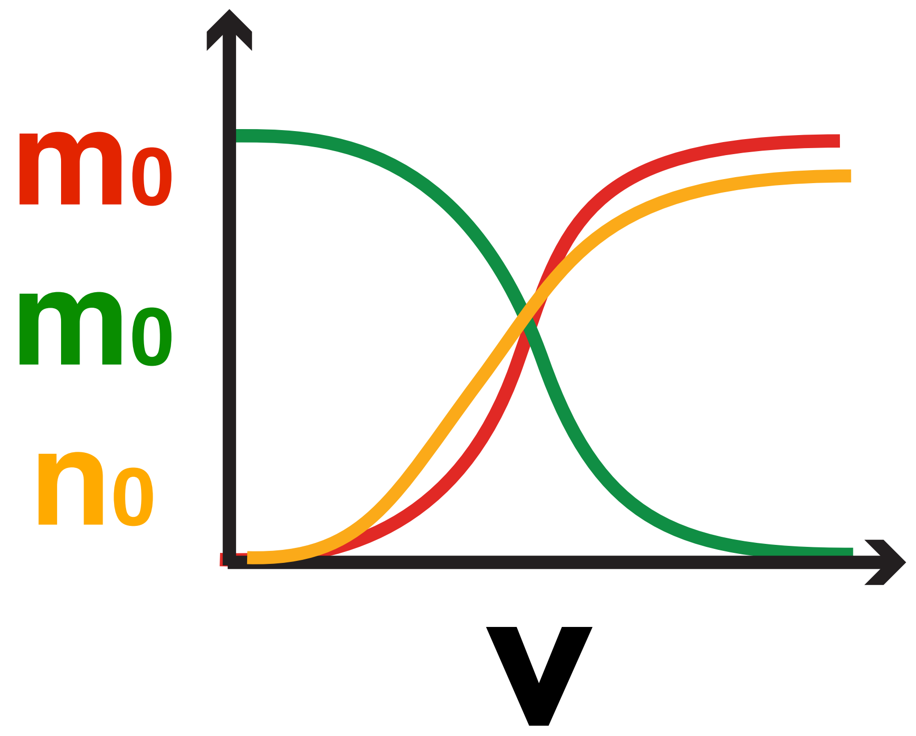

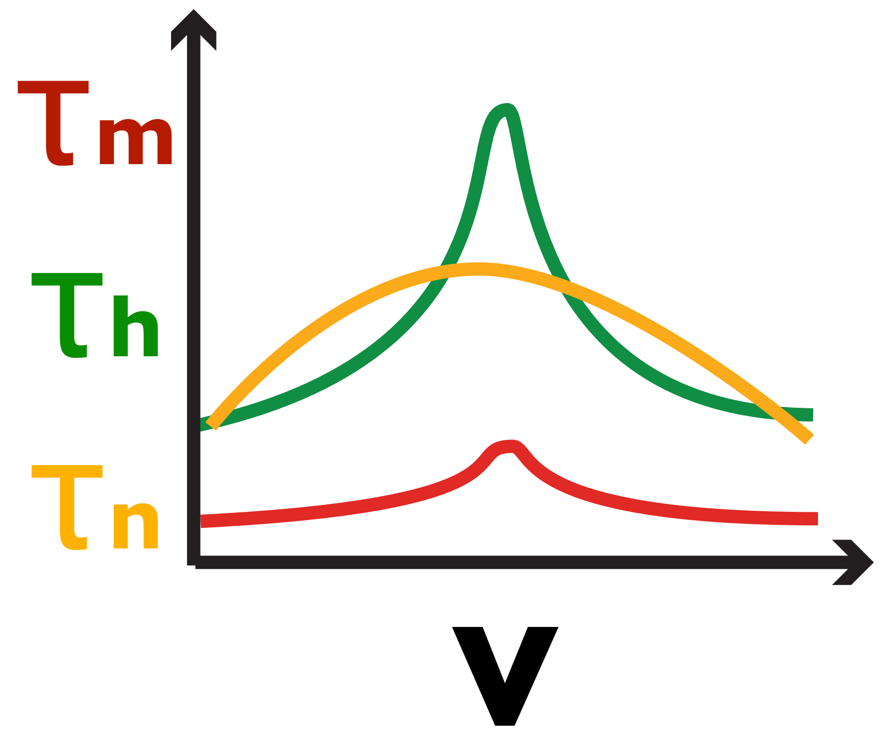

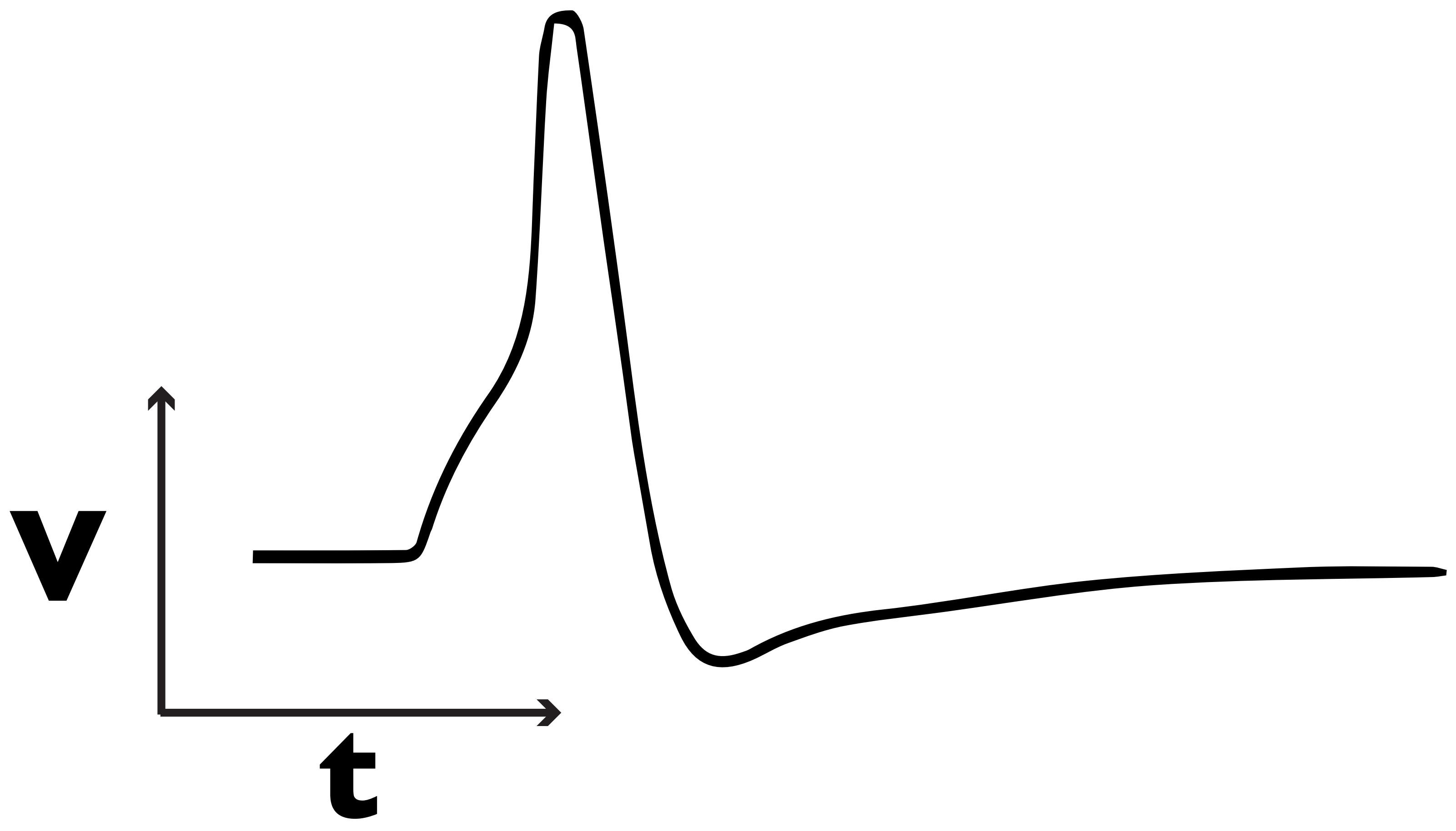

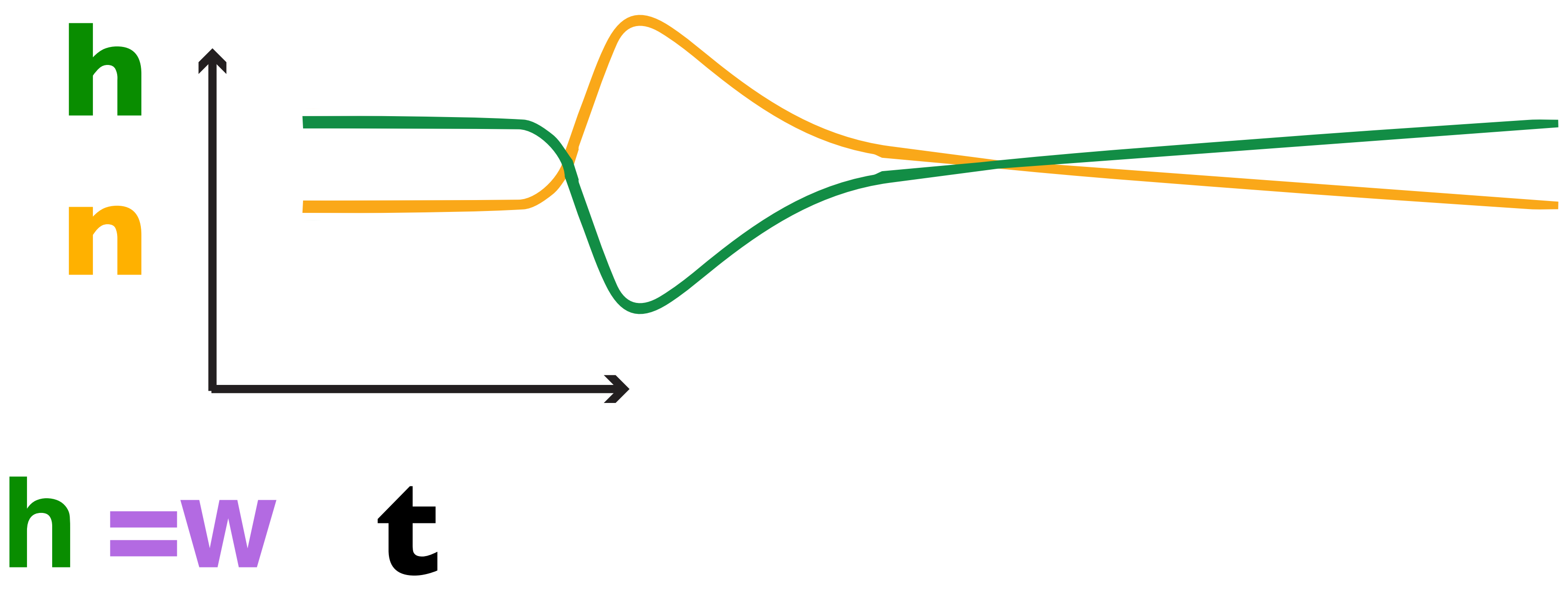

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$$\tau \frac{dV}{dt} = F(V(t), w(t))$$

$$\frac{dw}{dt} = \frac{w - w_0(V)}{\tau_n(V)}$$

$$\tau_n \frac{dw}{dt} = G(w(t), V(t))$$

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$$\tau \frac{dV}{dt} = F(V(t), w(t)) = V - \frac{1}{3} V^3 - w$$

$$\tau_n \frac{dw}{dt} = G(w(t), V(t)) = a + bV - w$$

FitzHugh-Nagumo model

$$\tau \frac{dV}{dt} = F\,(V(t), w(t)) = V - \frac{1}{3} V^3 - w$$

$$\tau_n \frac{dw}{dt} = G\,(w(t), V(t)) = a + bV - w$$

FitzHugh-Nagumo model

$$\frac{dV}{dt} = V - \frac{1}{3} V^3 - w$$

$$\frac{dw}{dt} = a + bV - w$$

FitzHugh-Nagumo model

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FitzHugh-Nagumo model

$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w$$

$$\frac{dw}{dt} = a + bV - w$$

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

FitzHugh-Nagumo model

$$\frac{dV}{dt} = V - \frac{1}{3} V^3 - w$$

$$\frac{dw}{dt} = a + bV - w$$

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

$$\Leftrightarrow V - \frac{1}{3} V^3 = w$$

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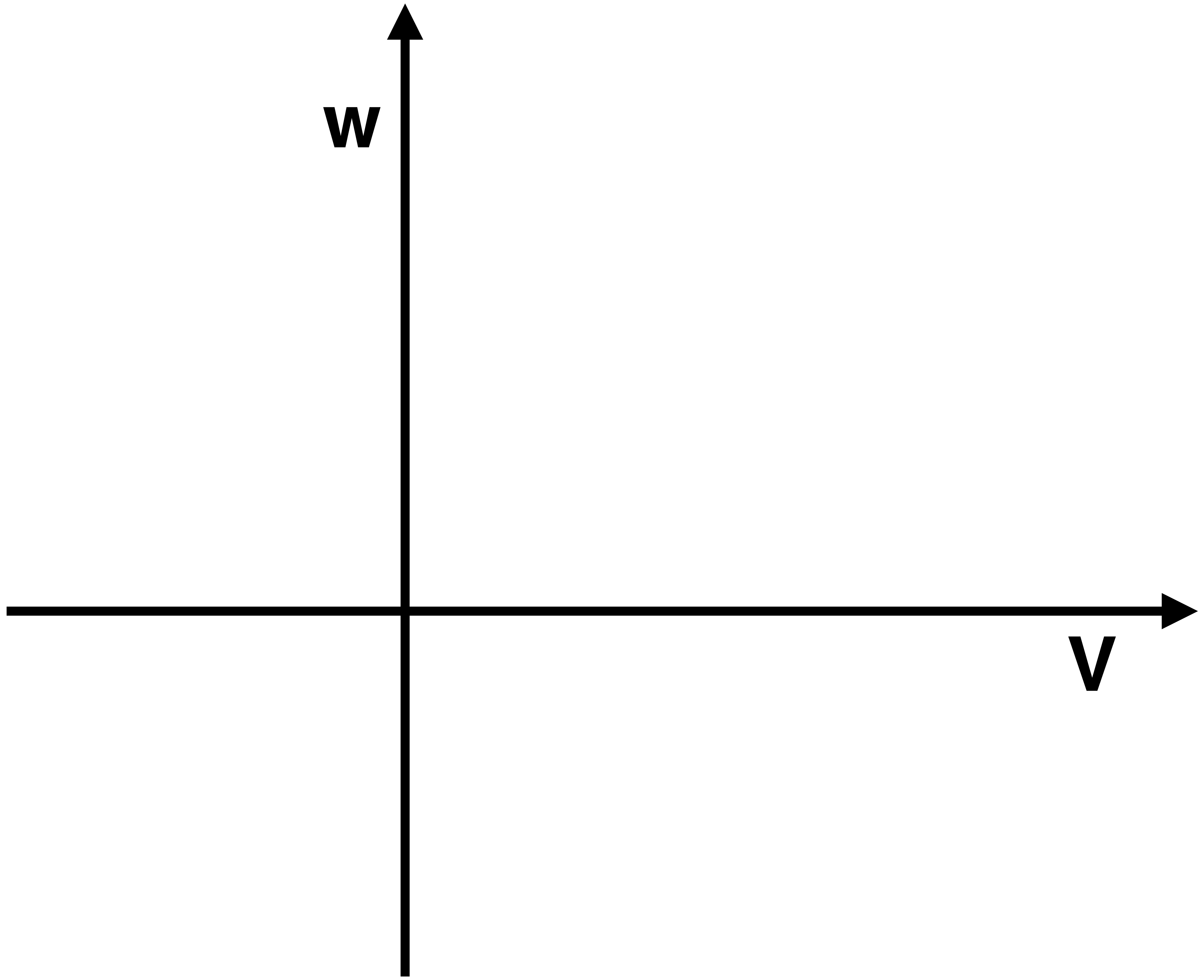

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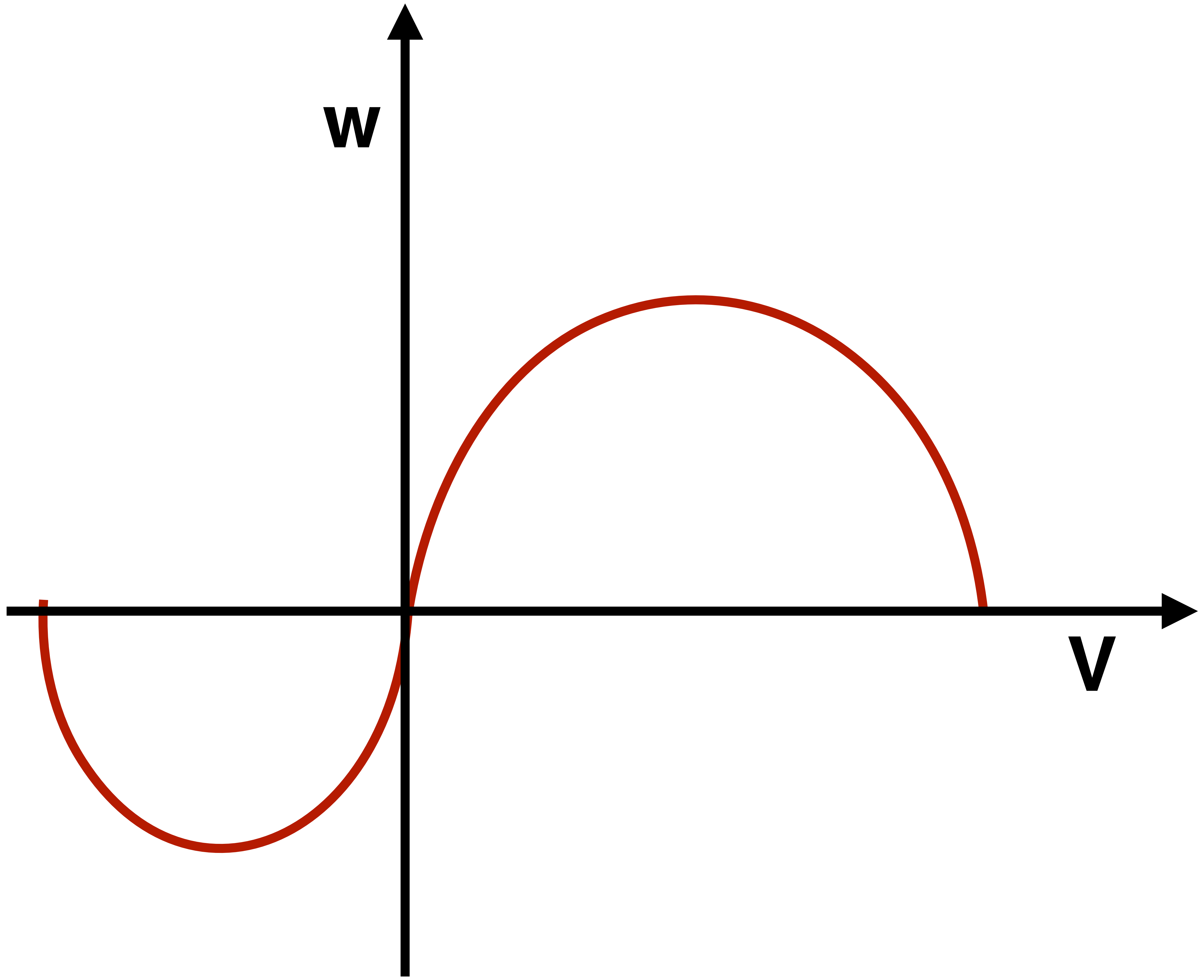

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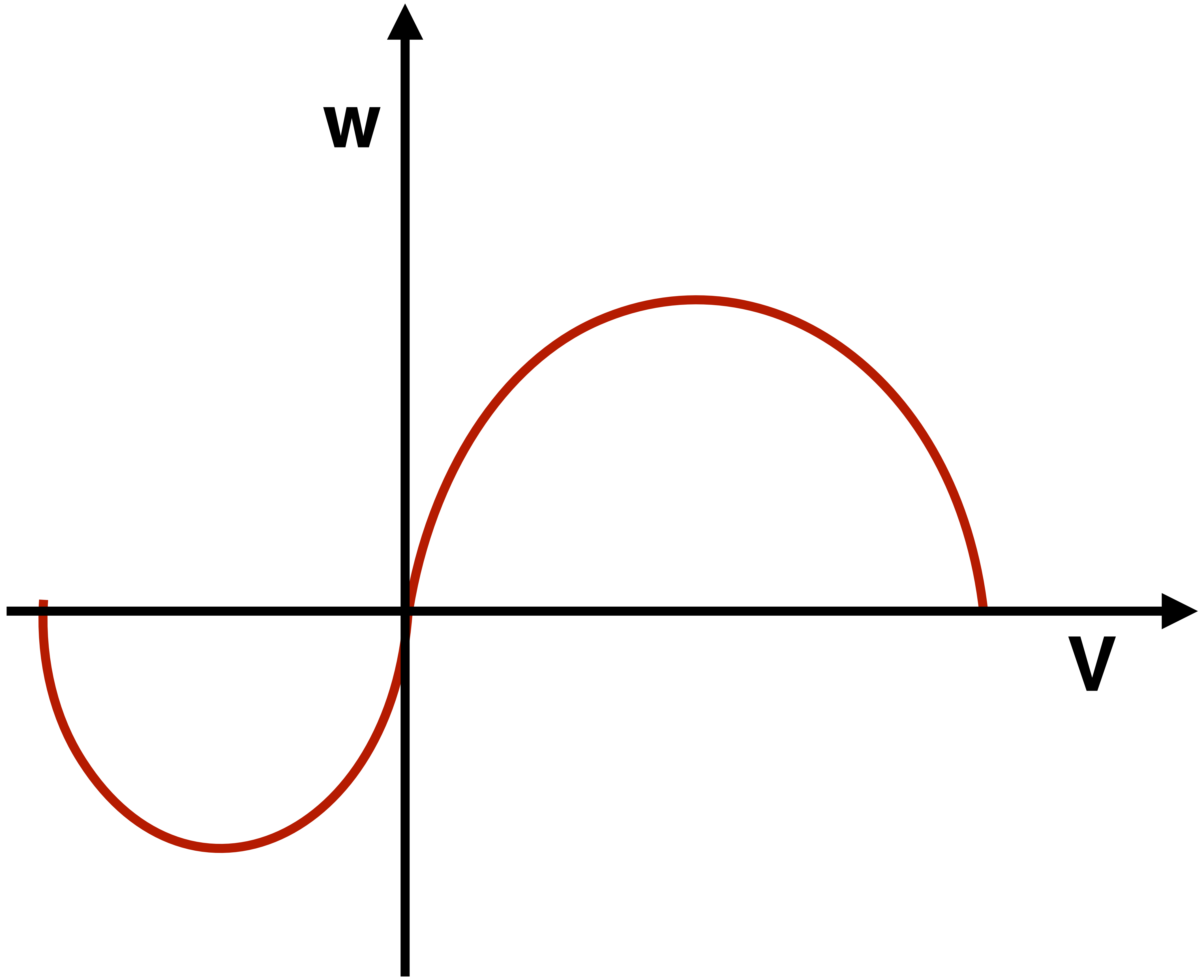

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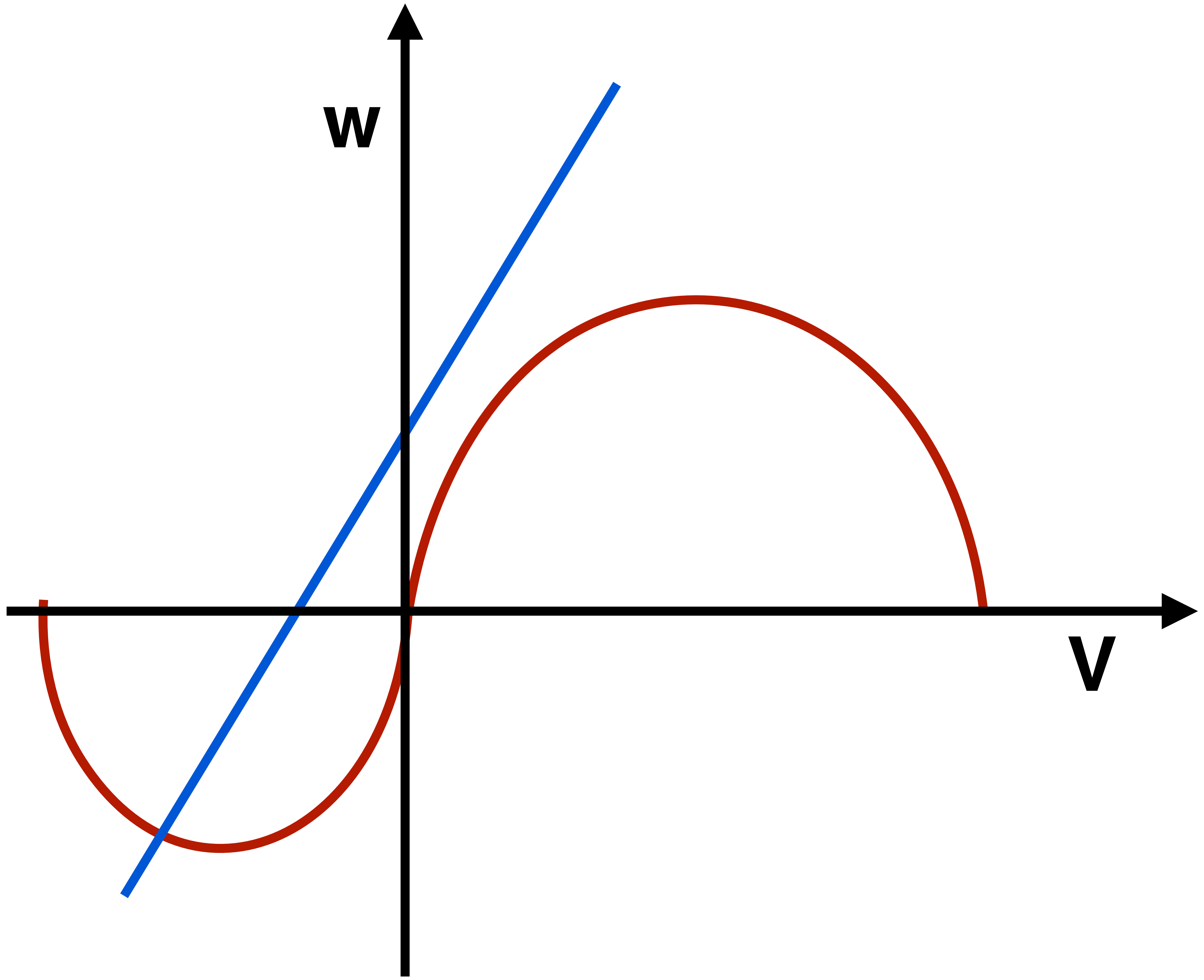

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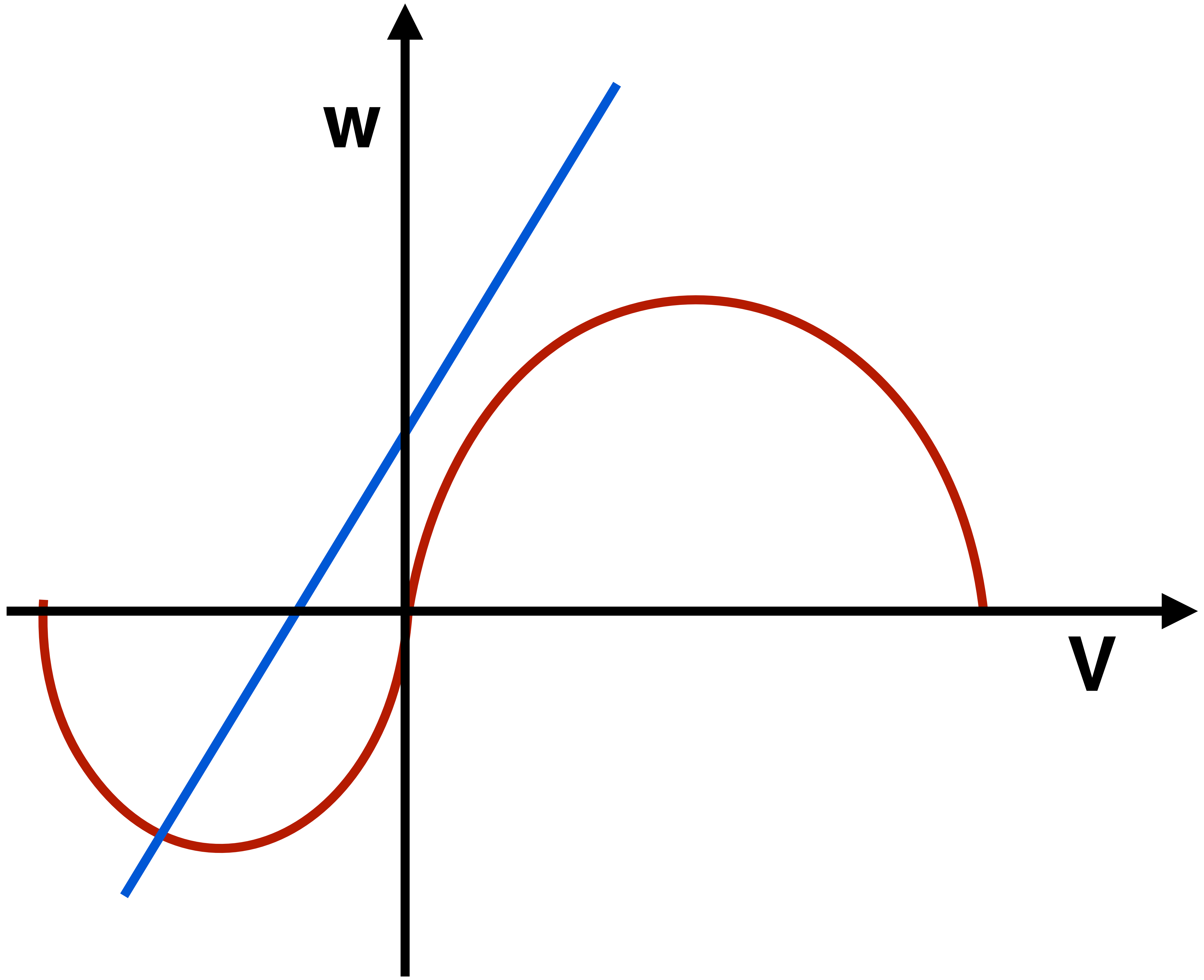


nullclines

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

$$\Leftrightarrow V - \frac{1}{3}V^3 = w$$

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

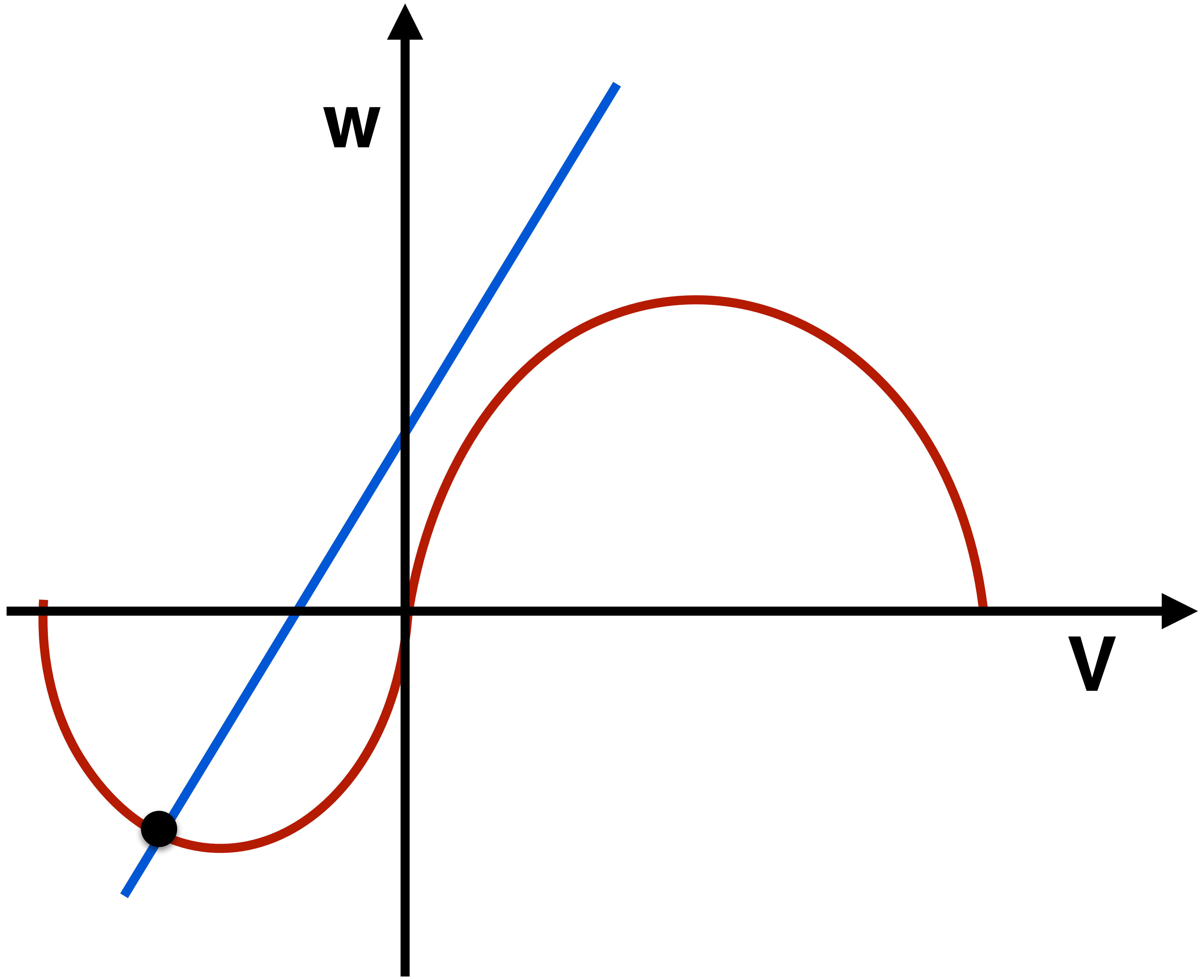
$$\Leftrightarrow a + bV = w$$

$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w$$

$$\frac{dw}{dt} = a + bV - w$$

FitzHugh-Nagumo model

nullclines



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

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FitzHugh-Nagumo model

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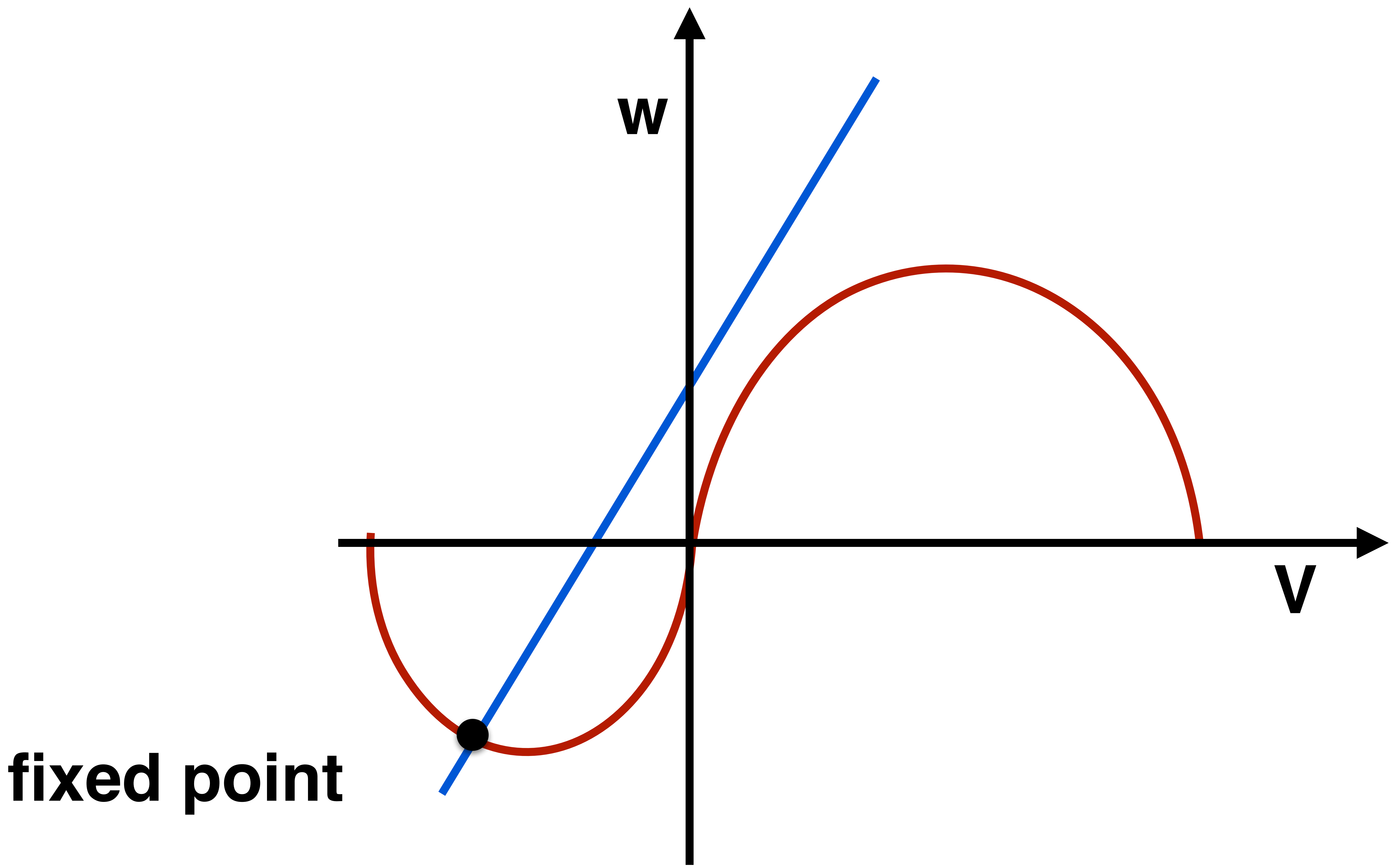

$$\frac{dw}{dt} = 0$$

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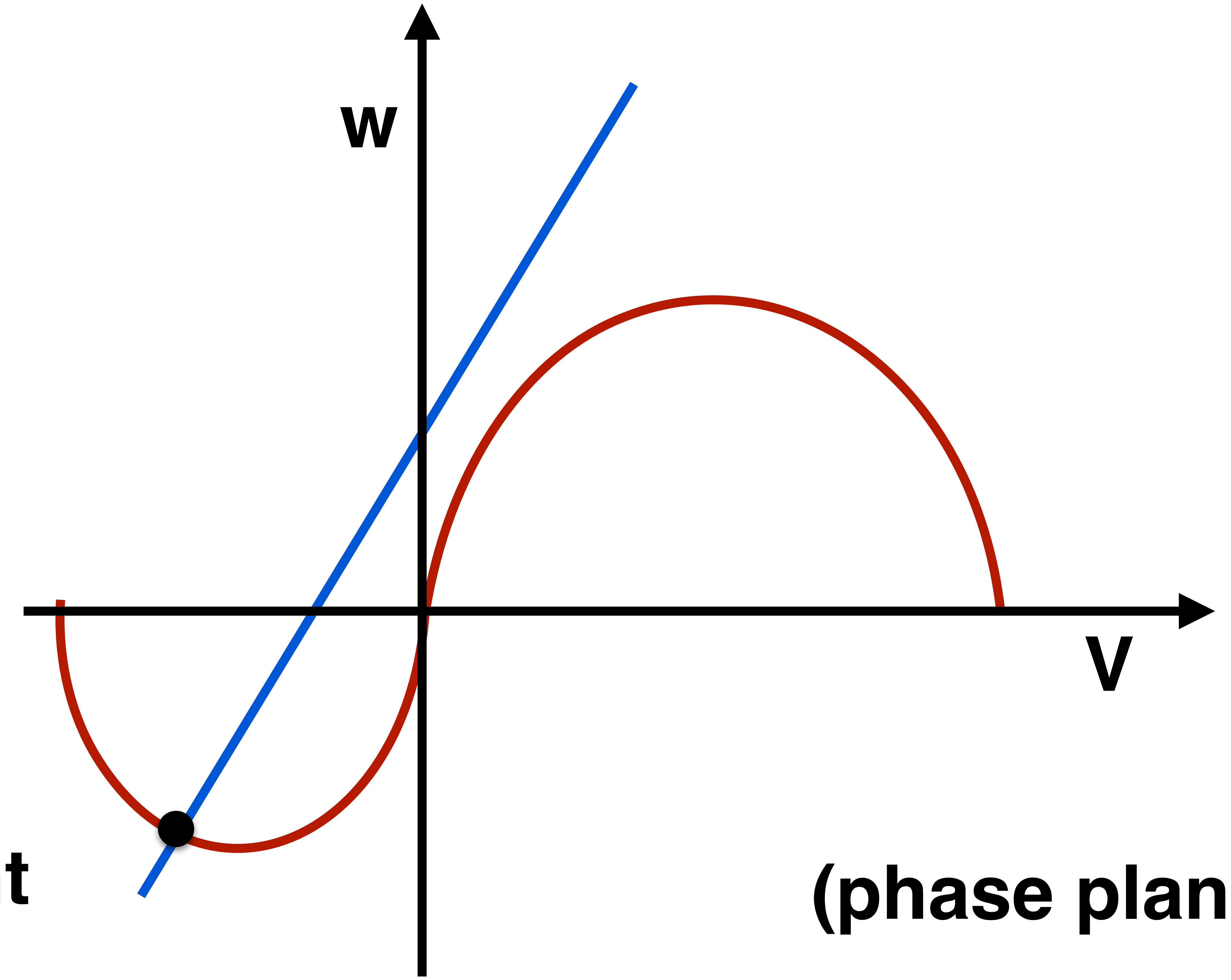


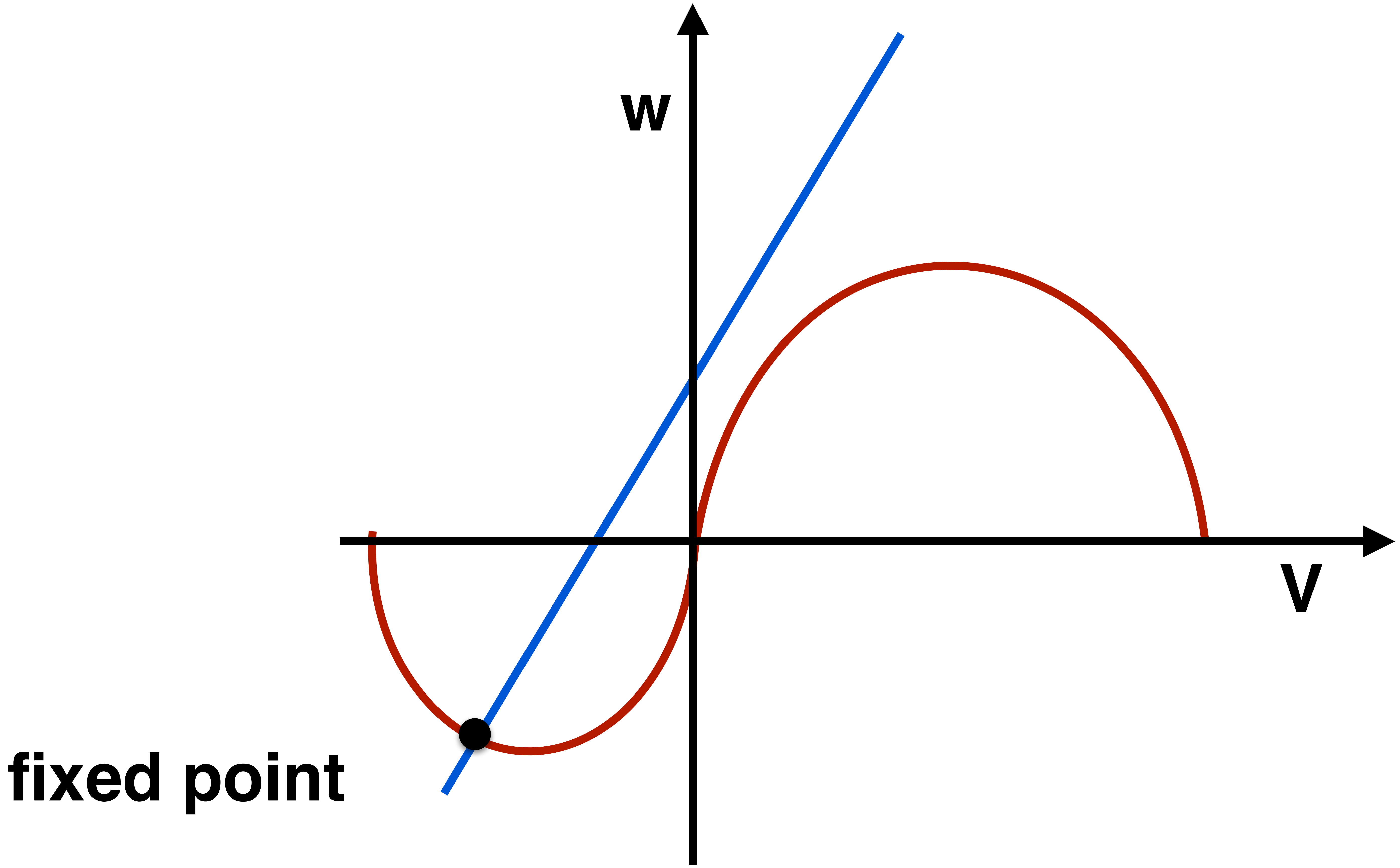
fixed point

(phase plane analysis)

$$\frac{dV}{dt} = V - \frac{1}{3} V^3 - w$$

FitzHugh-Nagumo model

$$\frac{dw}{dt} = a + bV - w$$



nullclines

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

$$\Longleftrightarrow \quad V - \frac{1}{3} V^3 = w$$

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

$$\Longleftrightarrow \quad a + bV = w$$

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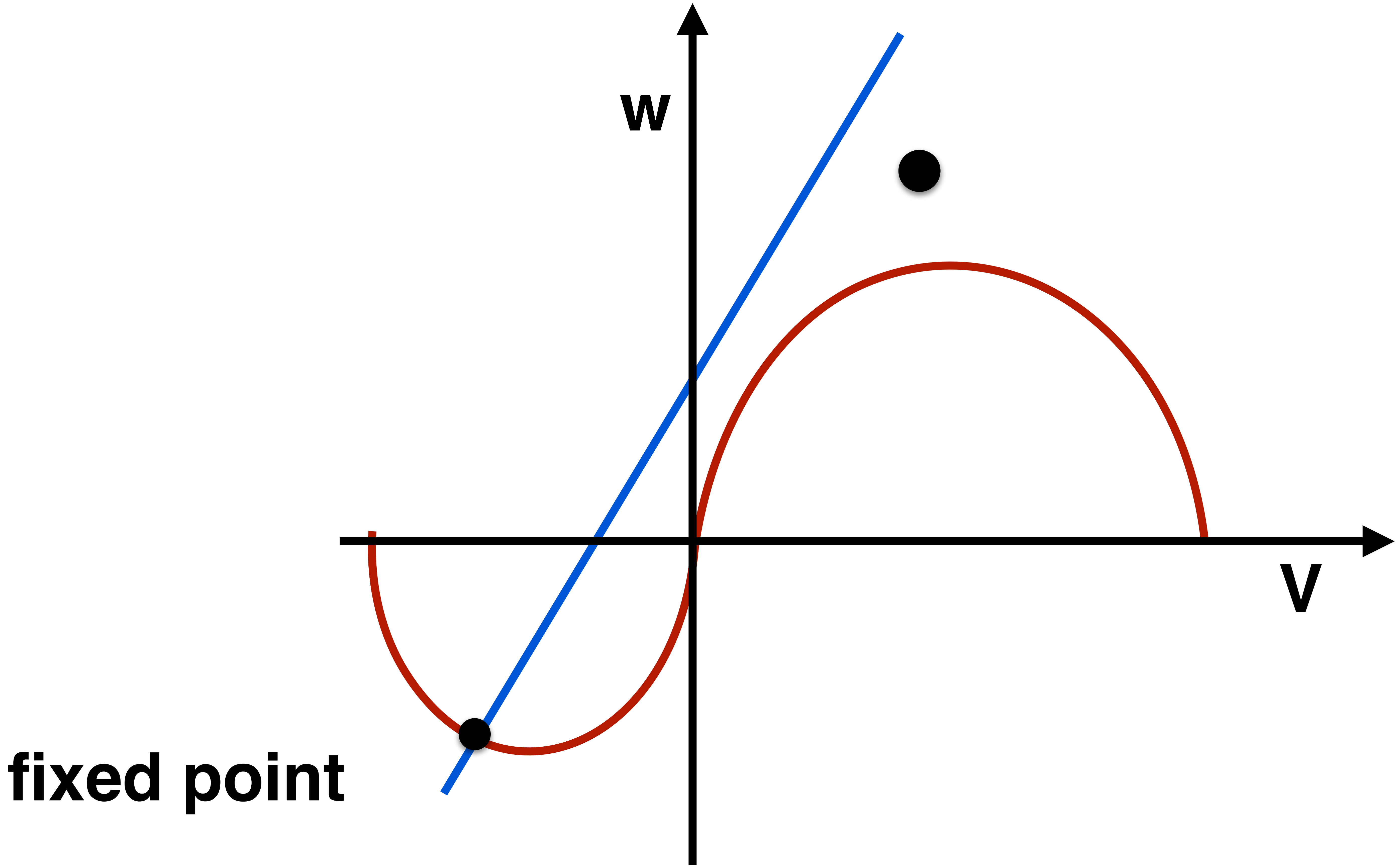

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FitzHugh-Nagumo model

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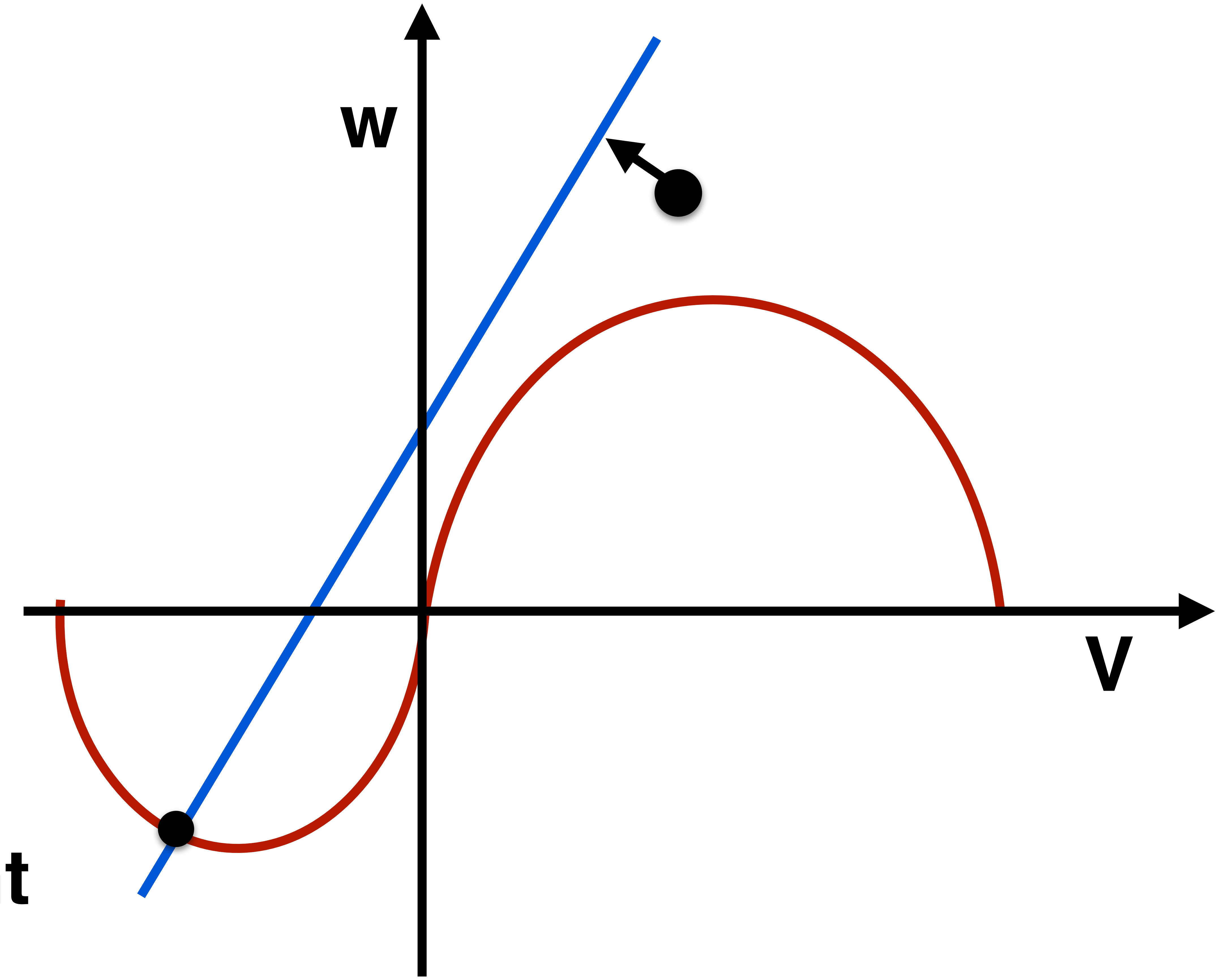


fixed point

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

$$\Leftrightarrow V - \frac{1}{3}V^3 = w$$

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

$$\Leftrightarrow a + bV = w$$

FitzHugh-Nagumo model

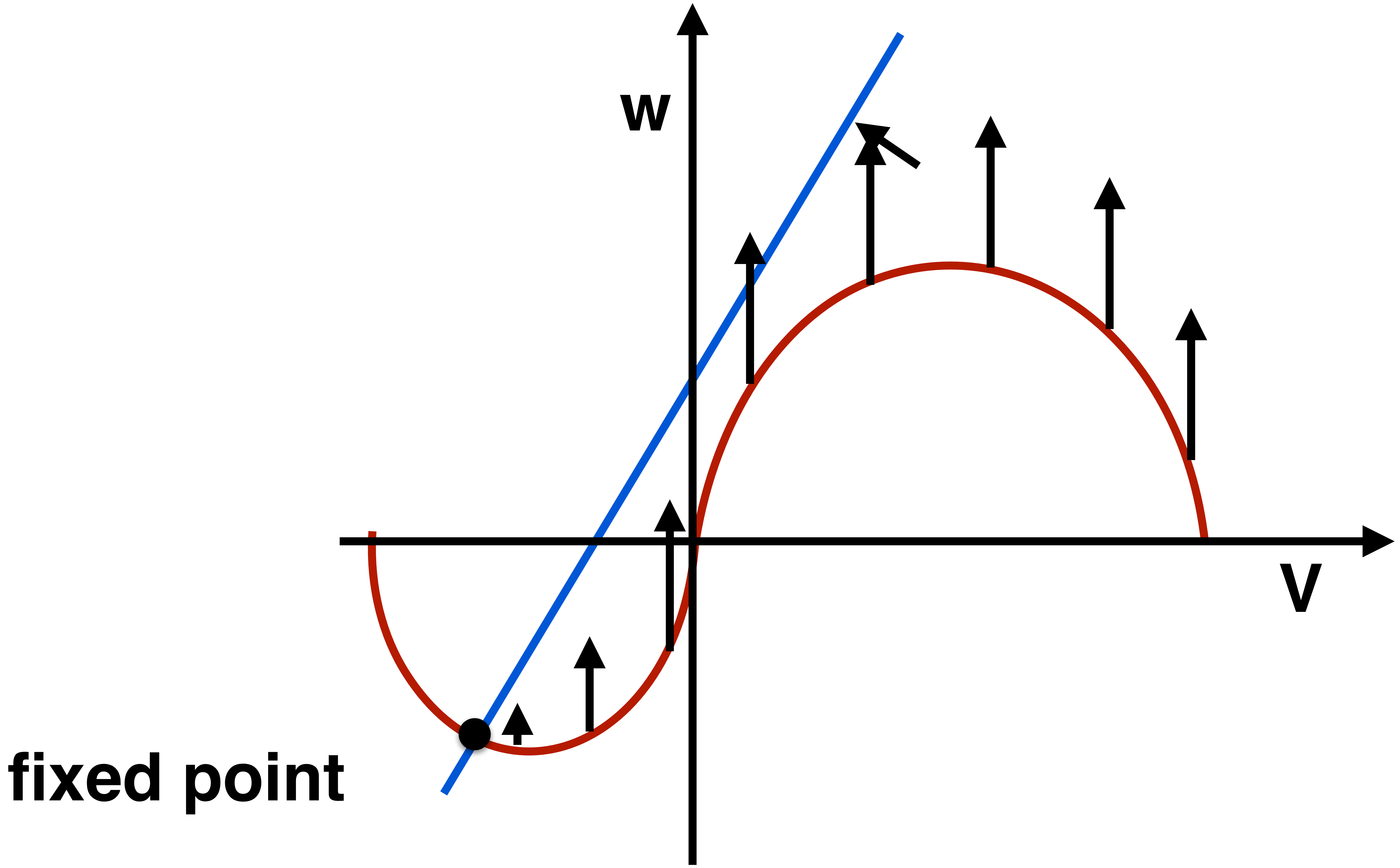
$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w$$

$$\frac{dw}{dt} = a + bV - w$$

nullclines

$$\frac{dV}{dt} = 0 \iff V - \frac{1}{3}V^3 = w$$

$$\frac{dw}{dt} = 0 \iff a + bV = w$$



FitzHugh-Nagumo model

$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w$$

$$\frac{dw}{dt} = a + bV - w$$

nullclines

$$\frac{dV}{dt} = 0 \iff V - \frac{1}{3}V^3 = w$$

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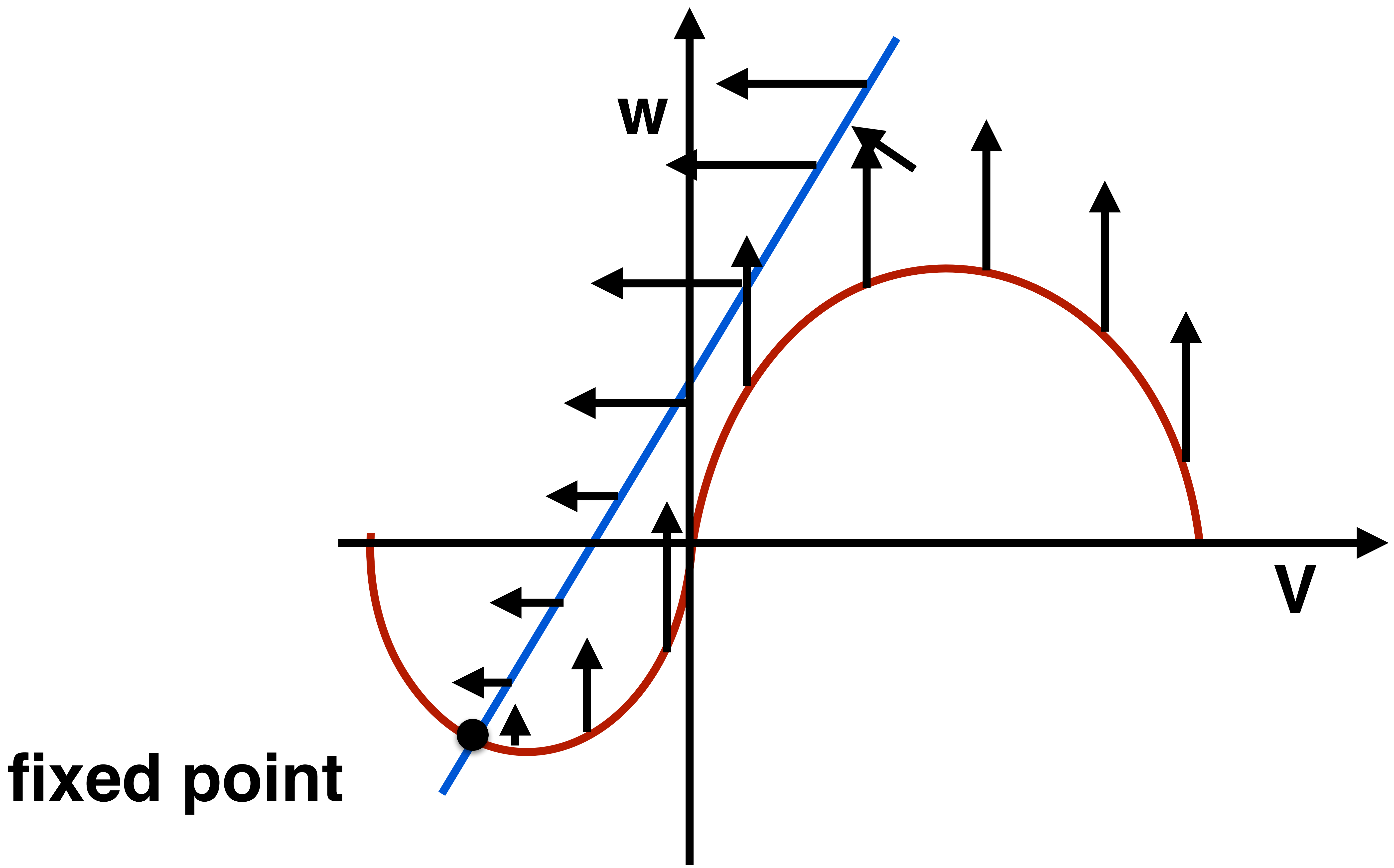

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FitzHugh-Nagumo model

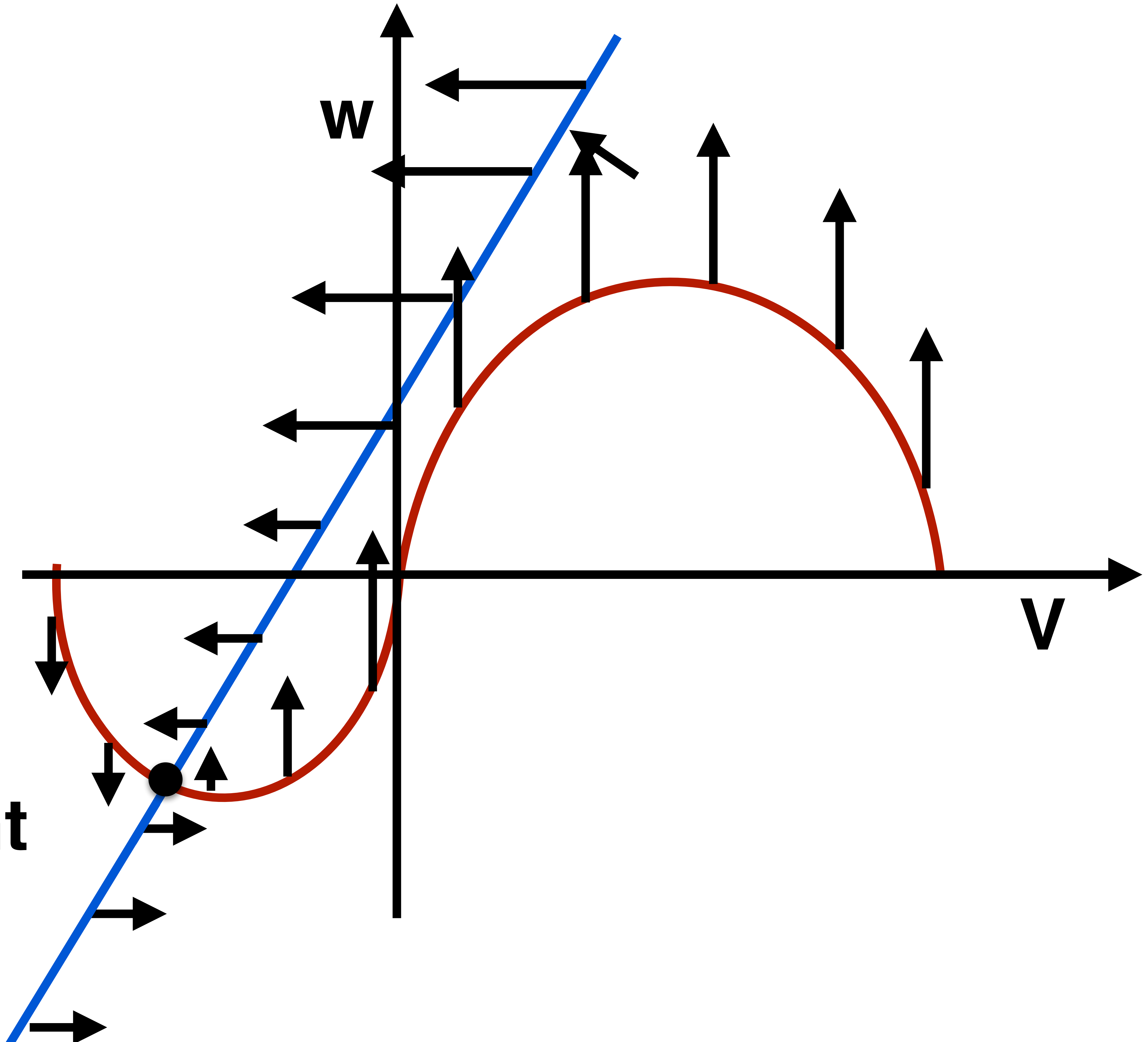
nullclines

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

$$<=> \quad V - \frac{1}{3}V^3 = w$$

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

$$<=> \quad a + bV = w$$



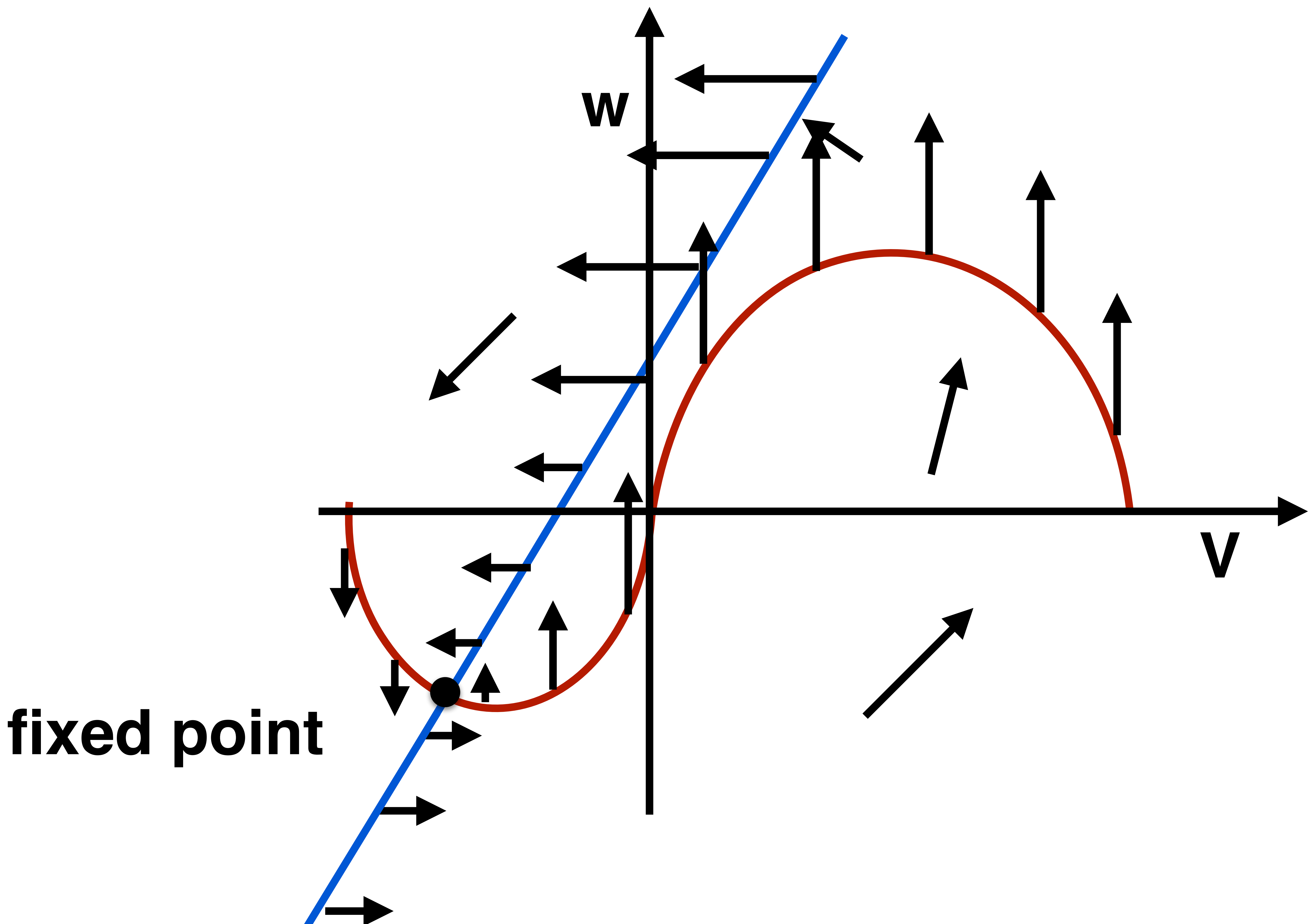
fixed point

$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w$$

FitzHugh-Nagumo model

$$\frac{dw}{dt} = a + bV - w$$

nullclines



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

$$\Leftrightarrow \quad V - \frac{1}{3}V^3 = w$$

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

$$\Leftrightarrow \quad a + bV = w$$

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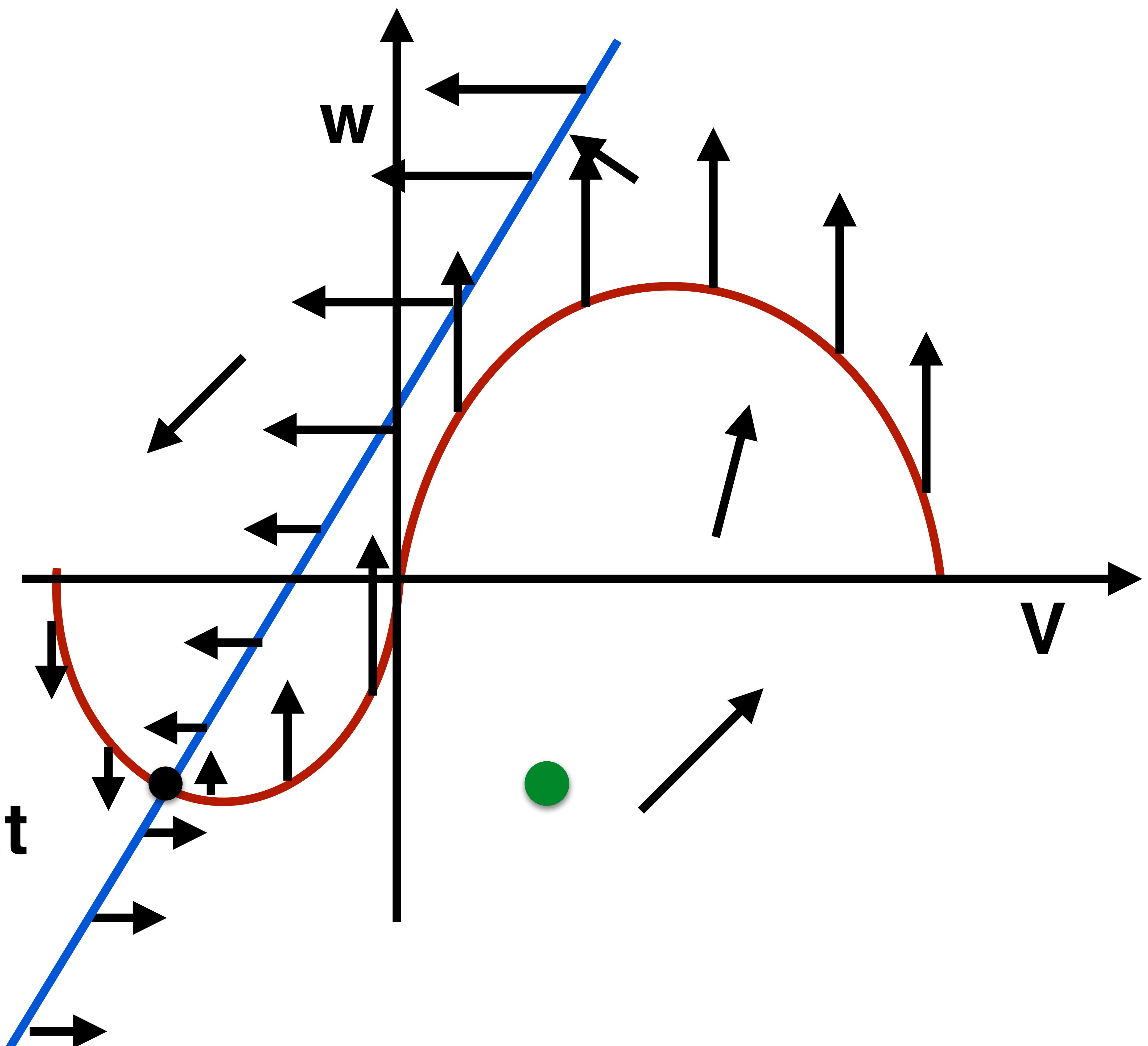

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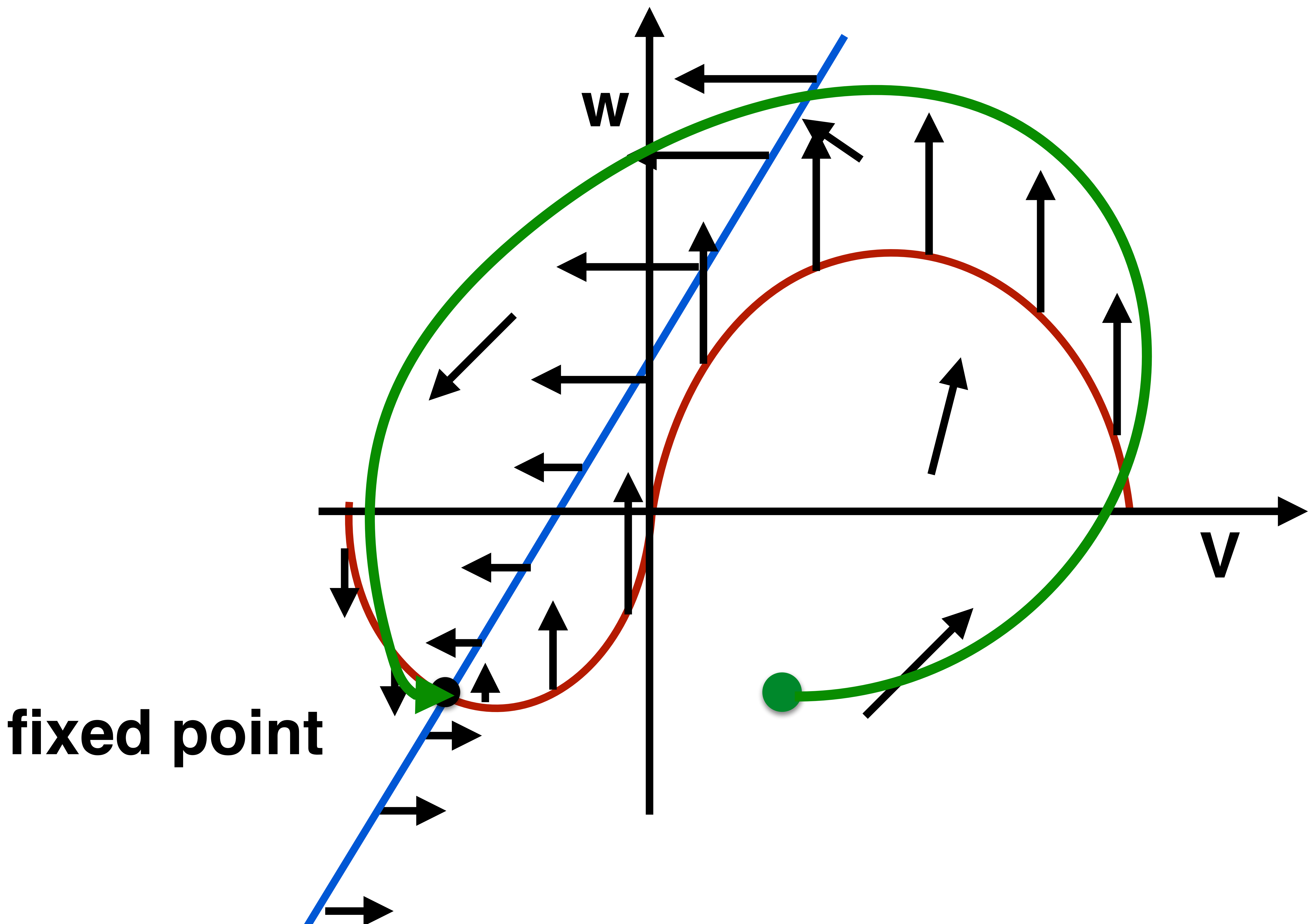

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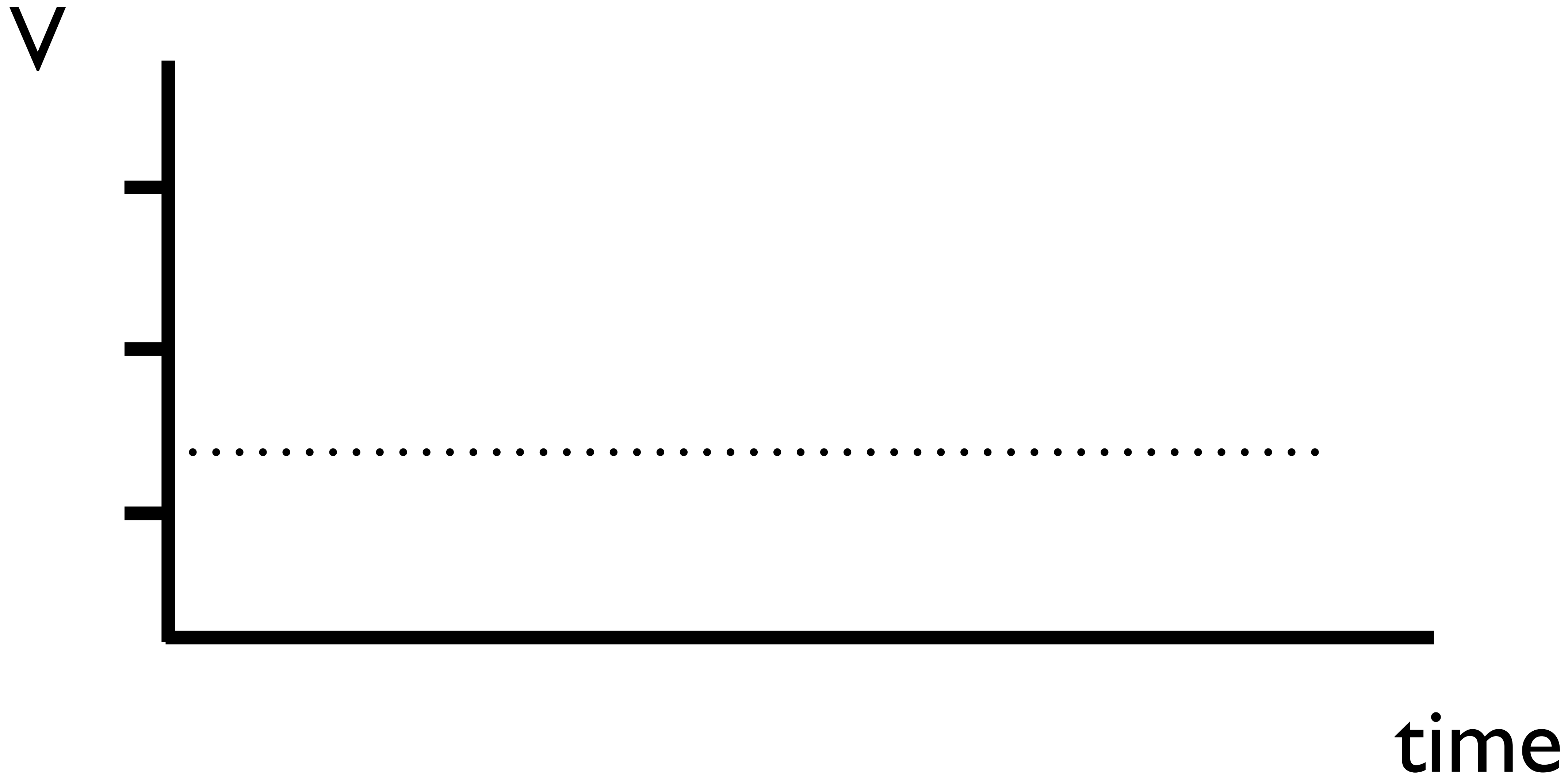

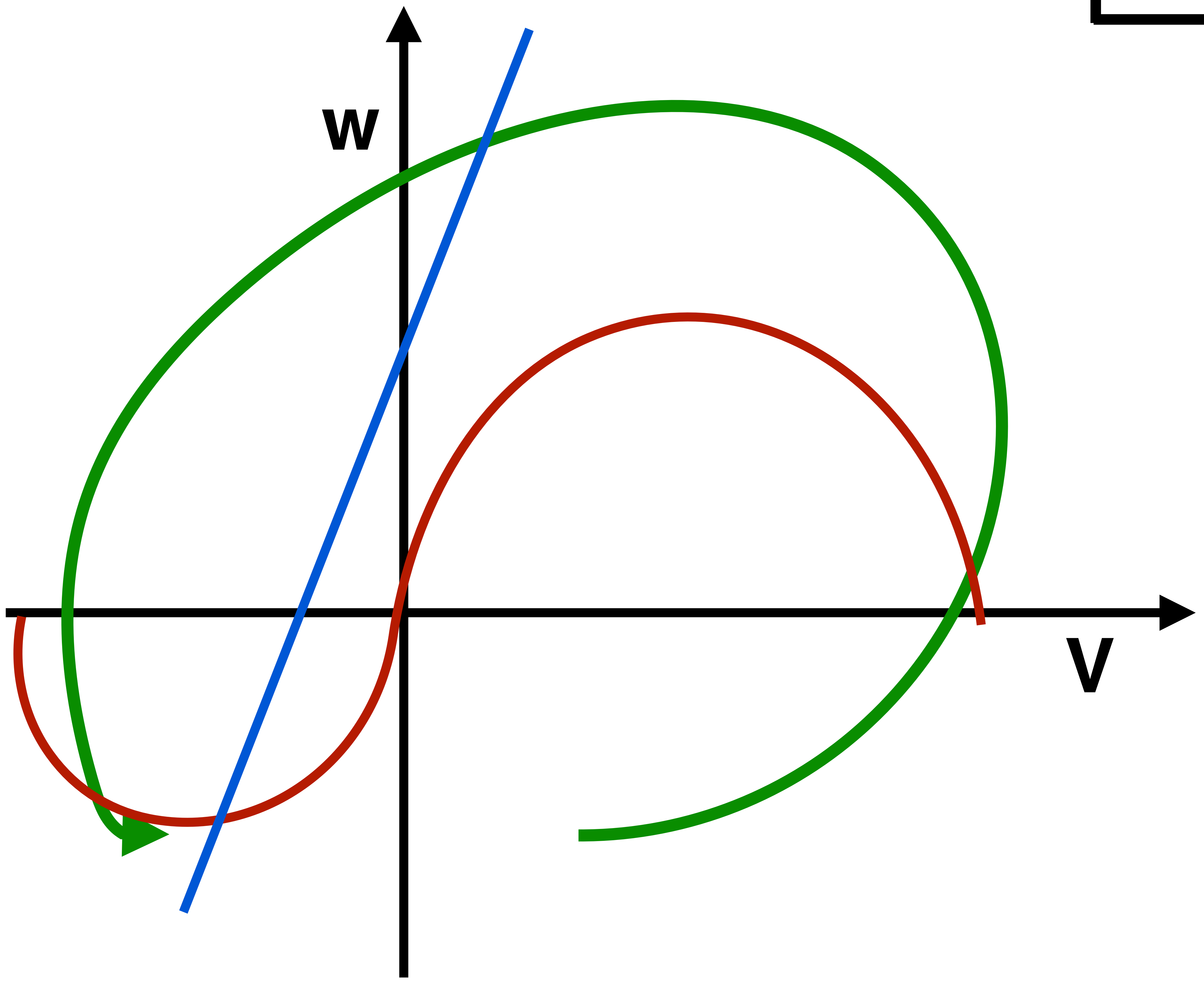

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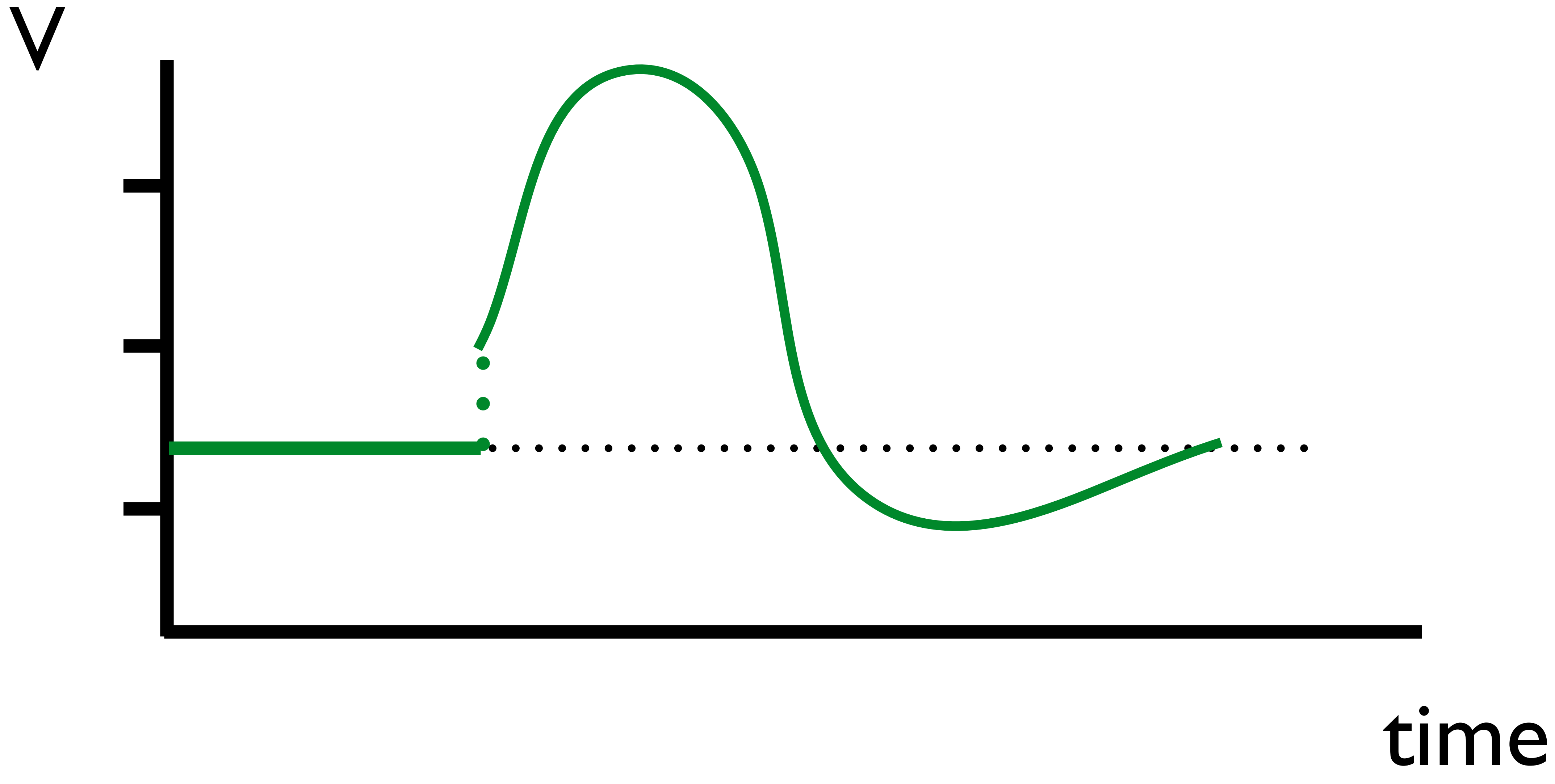

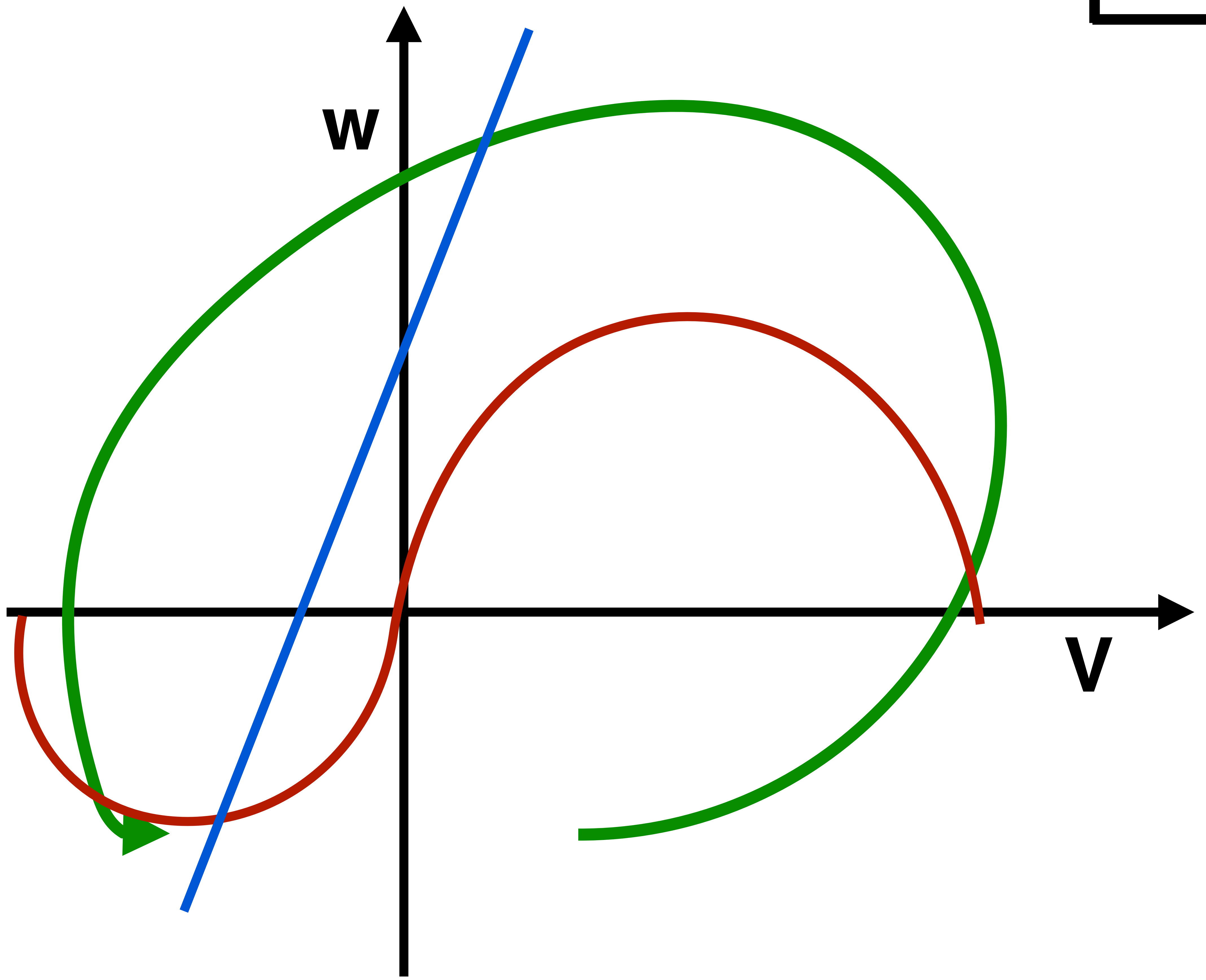

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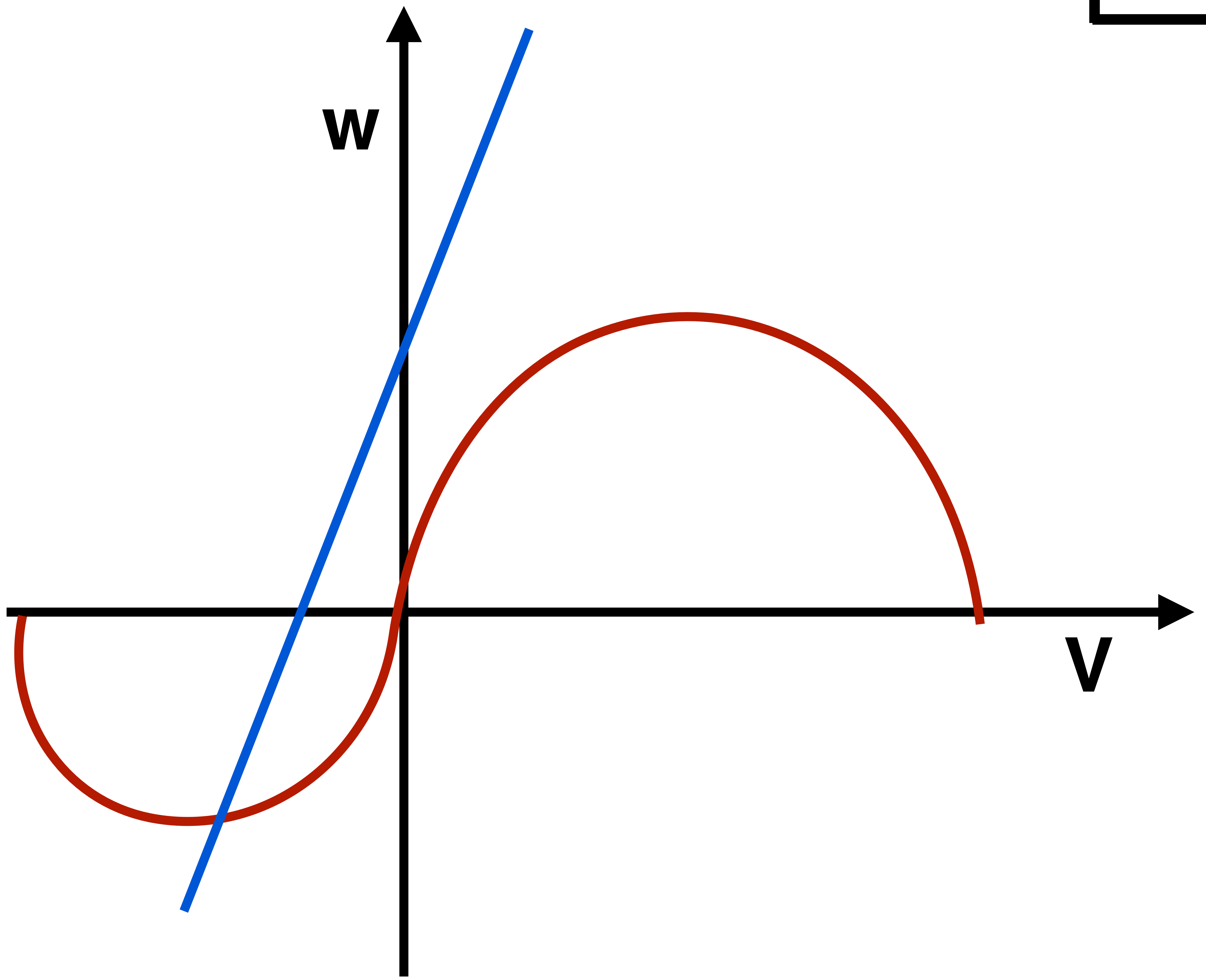
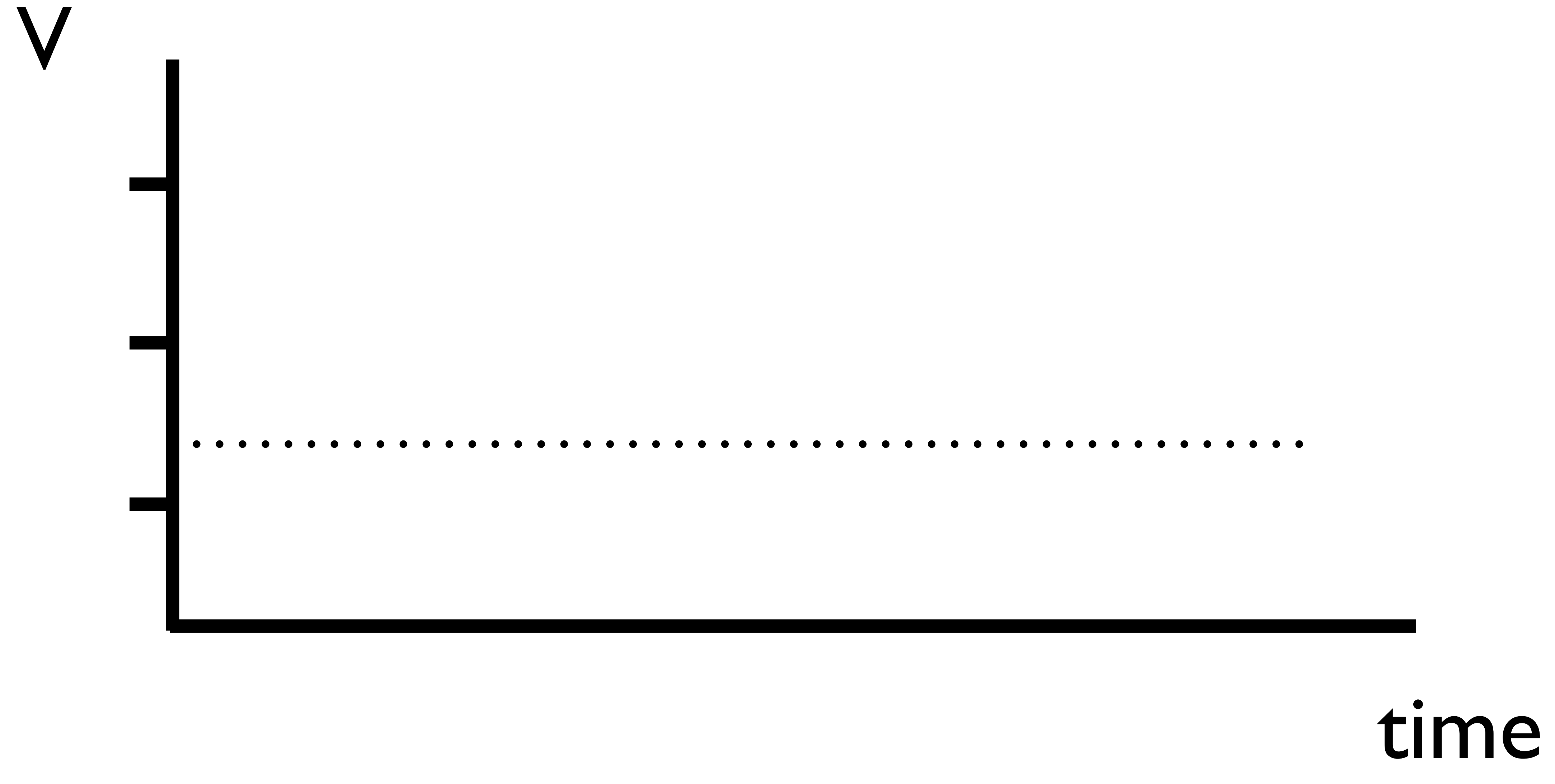
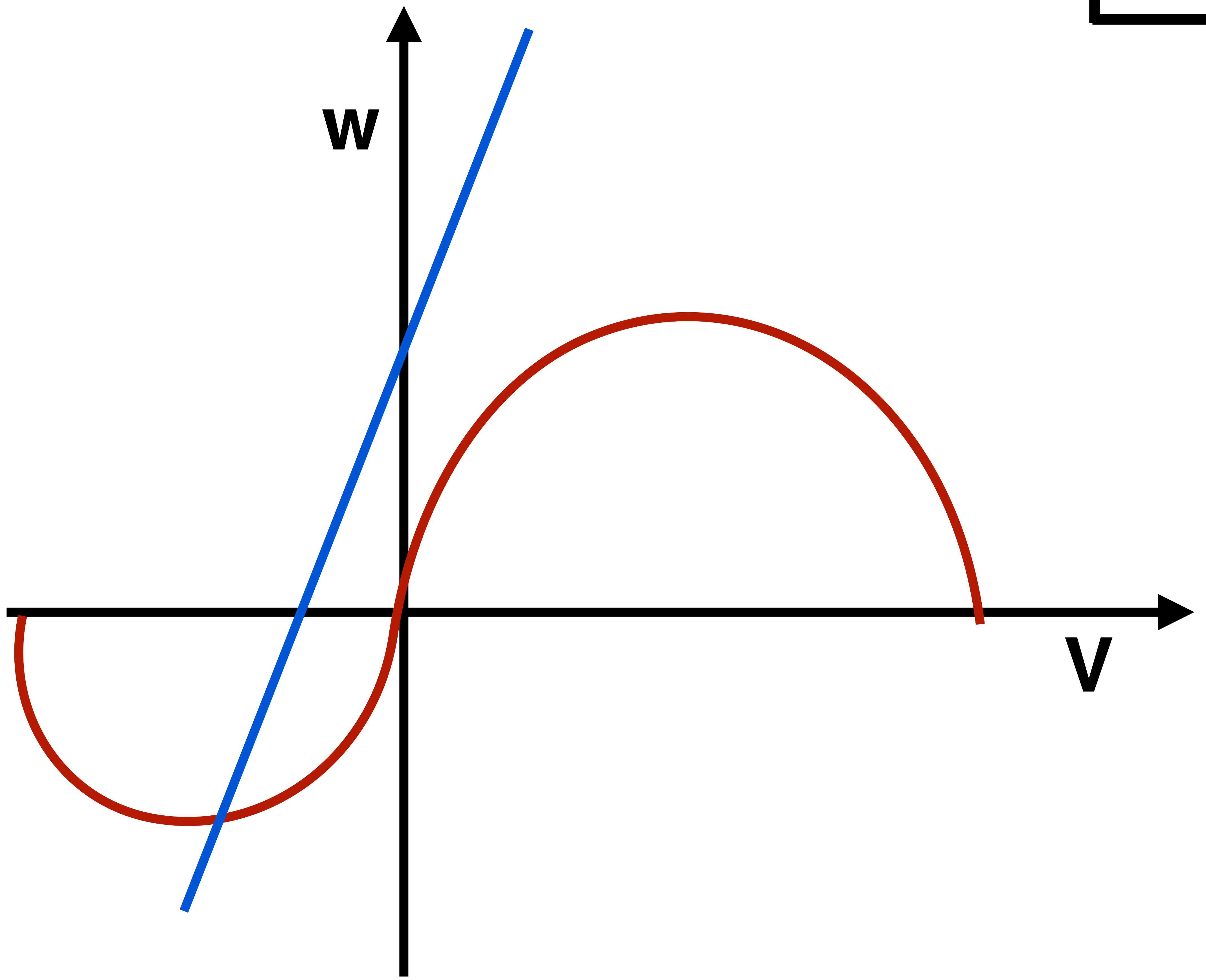


$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w + I$$

$$\frac{dw}{dt} = a + bV - w$$





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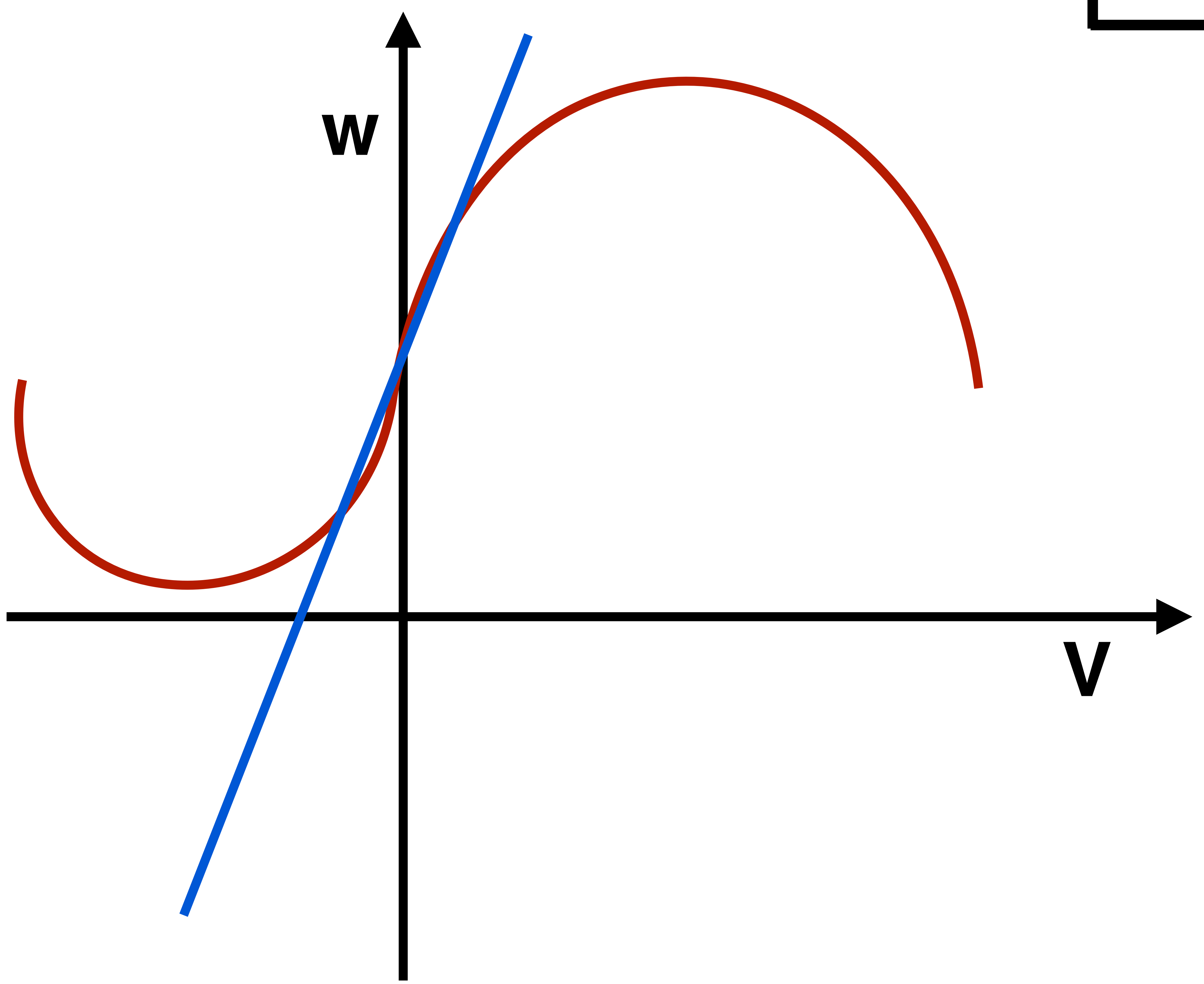

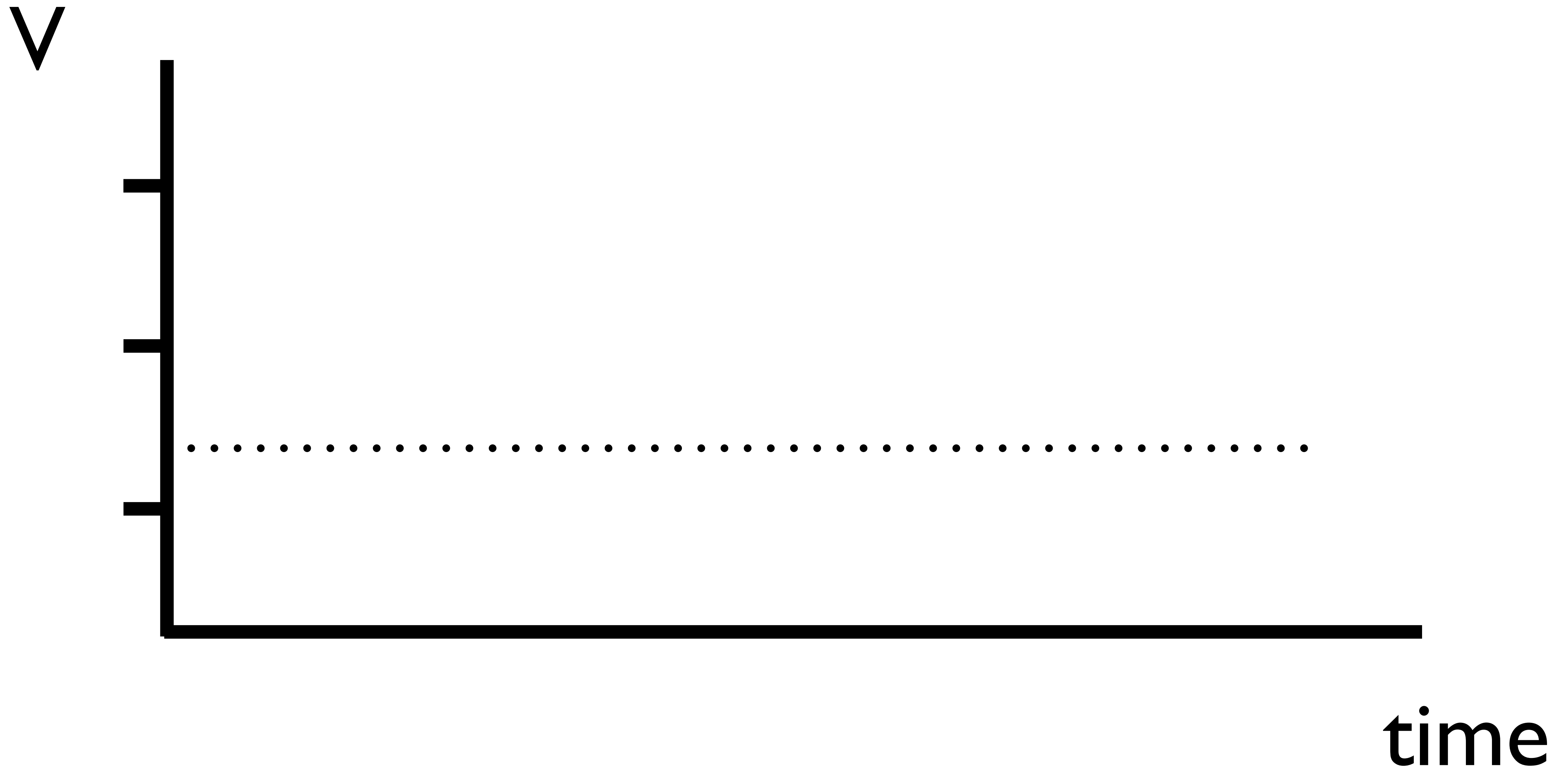

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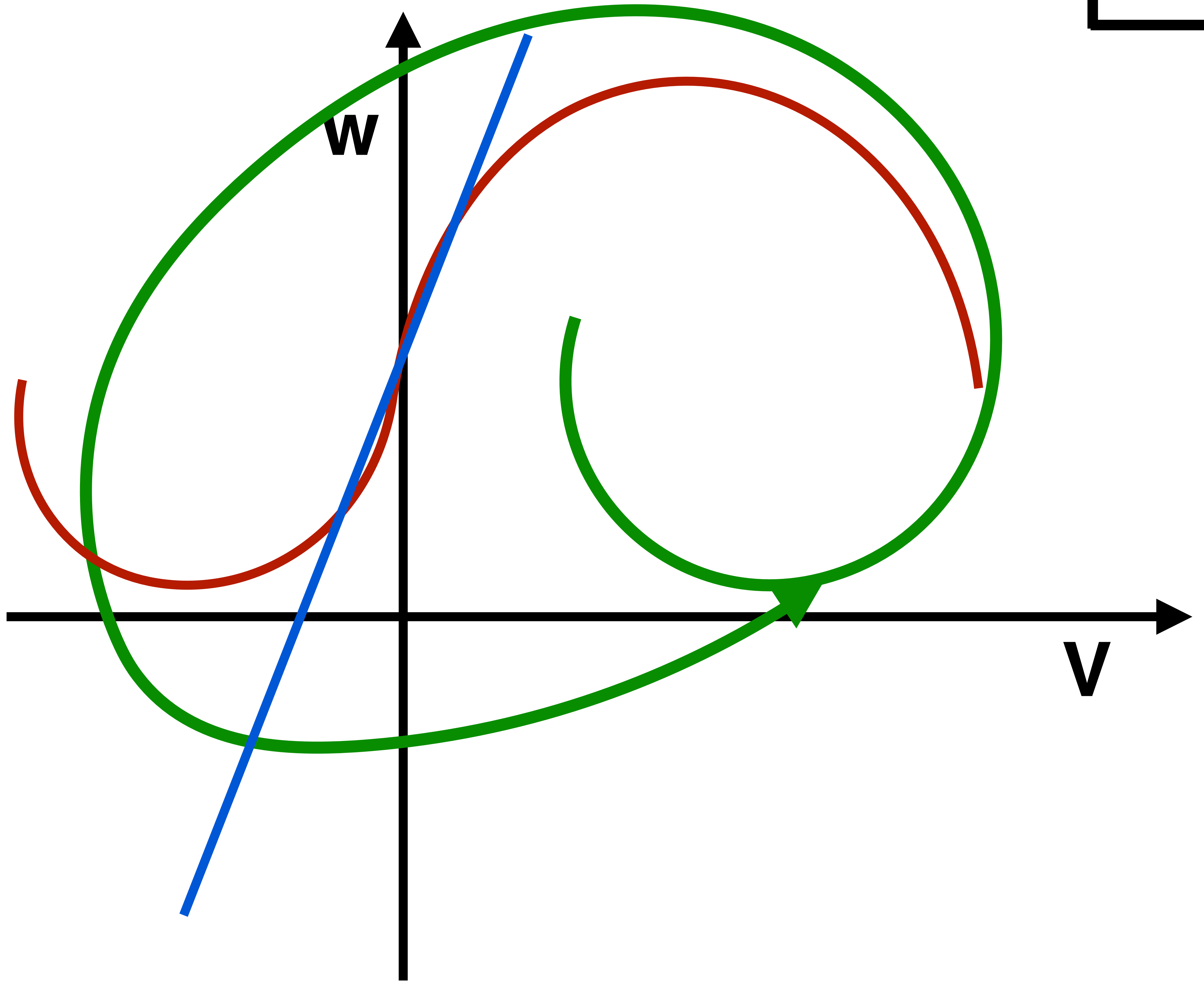
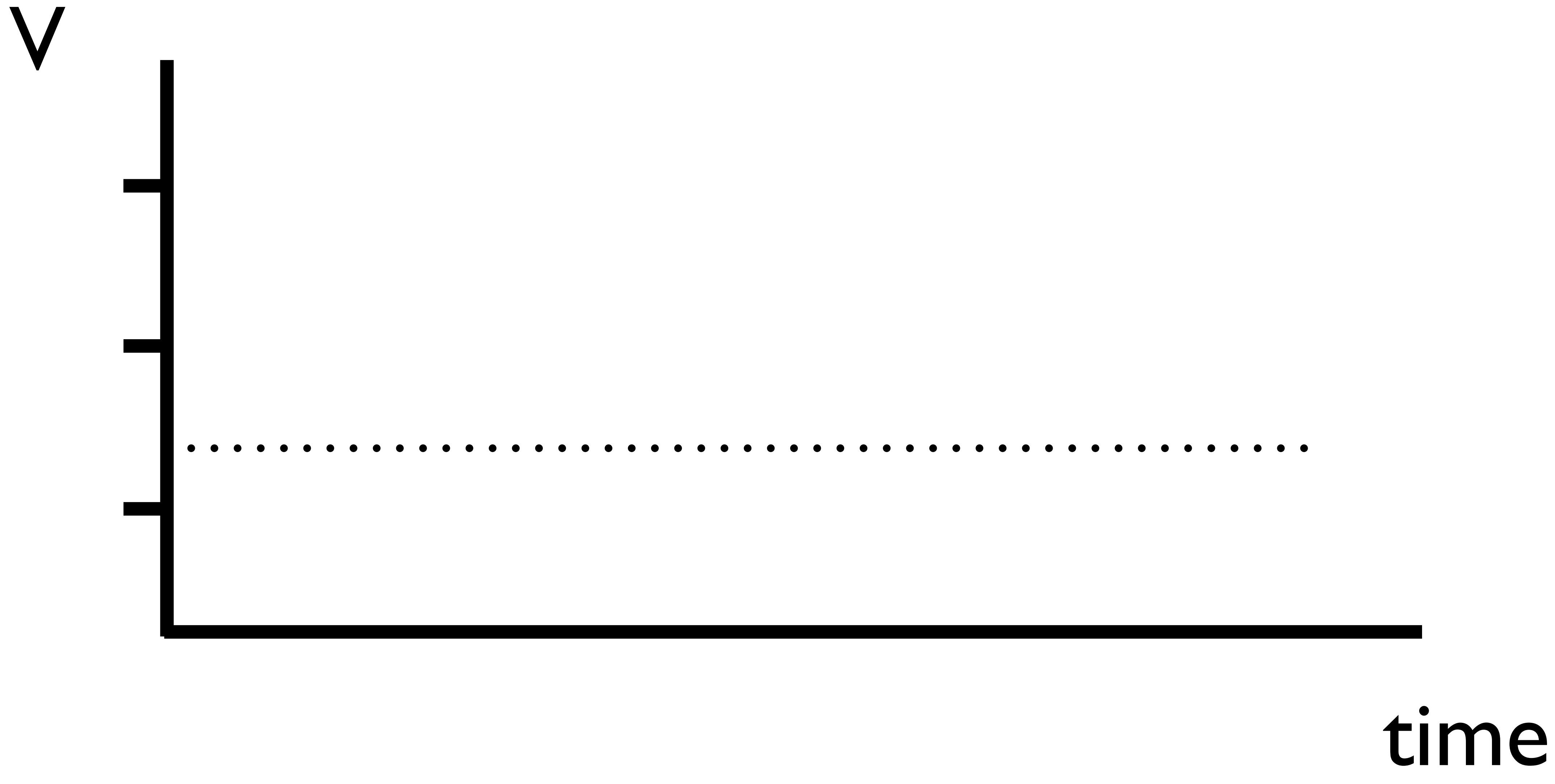
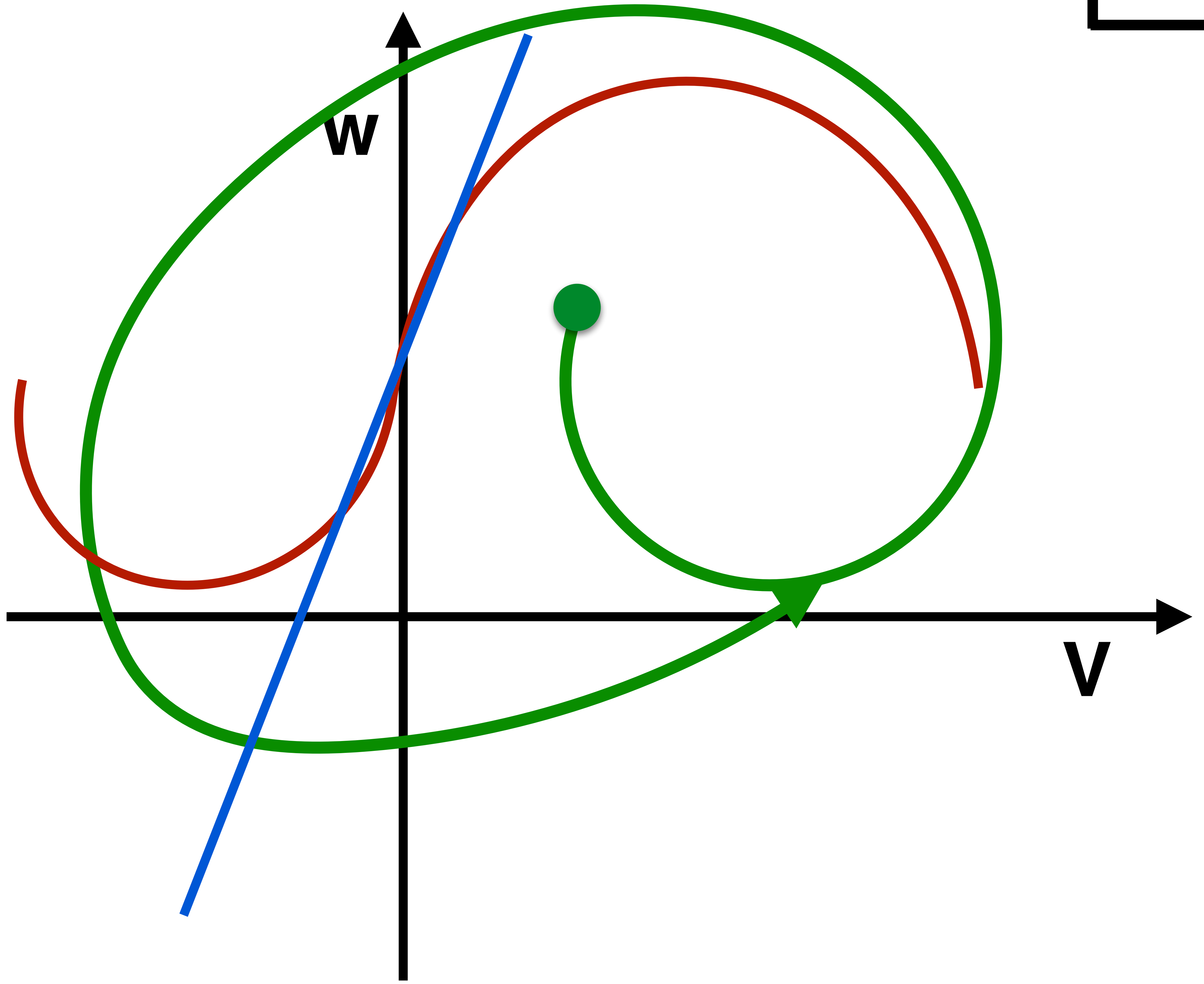


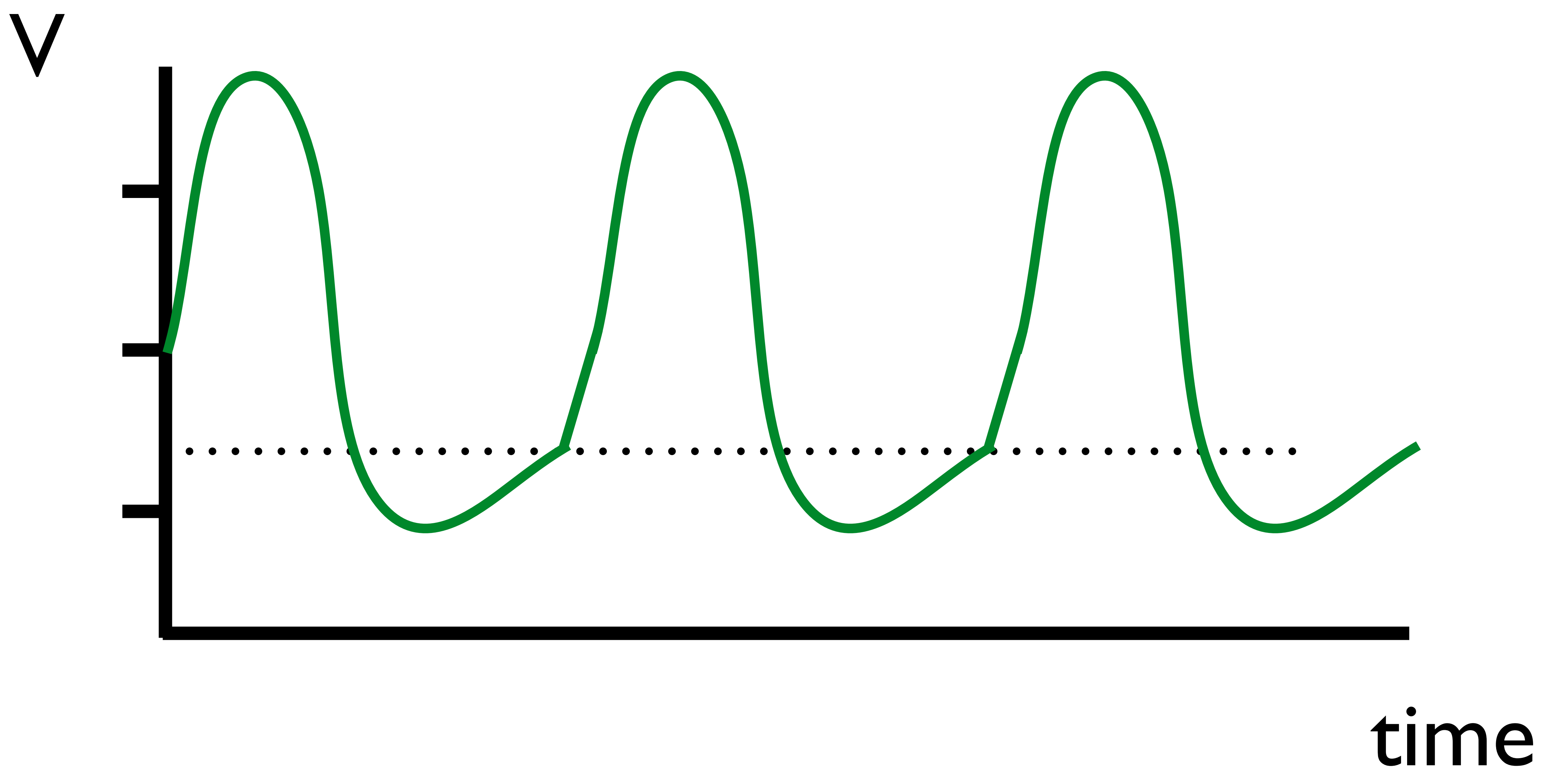


Limit Cycle

$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w + I$$

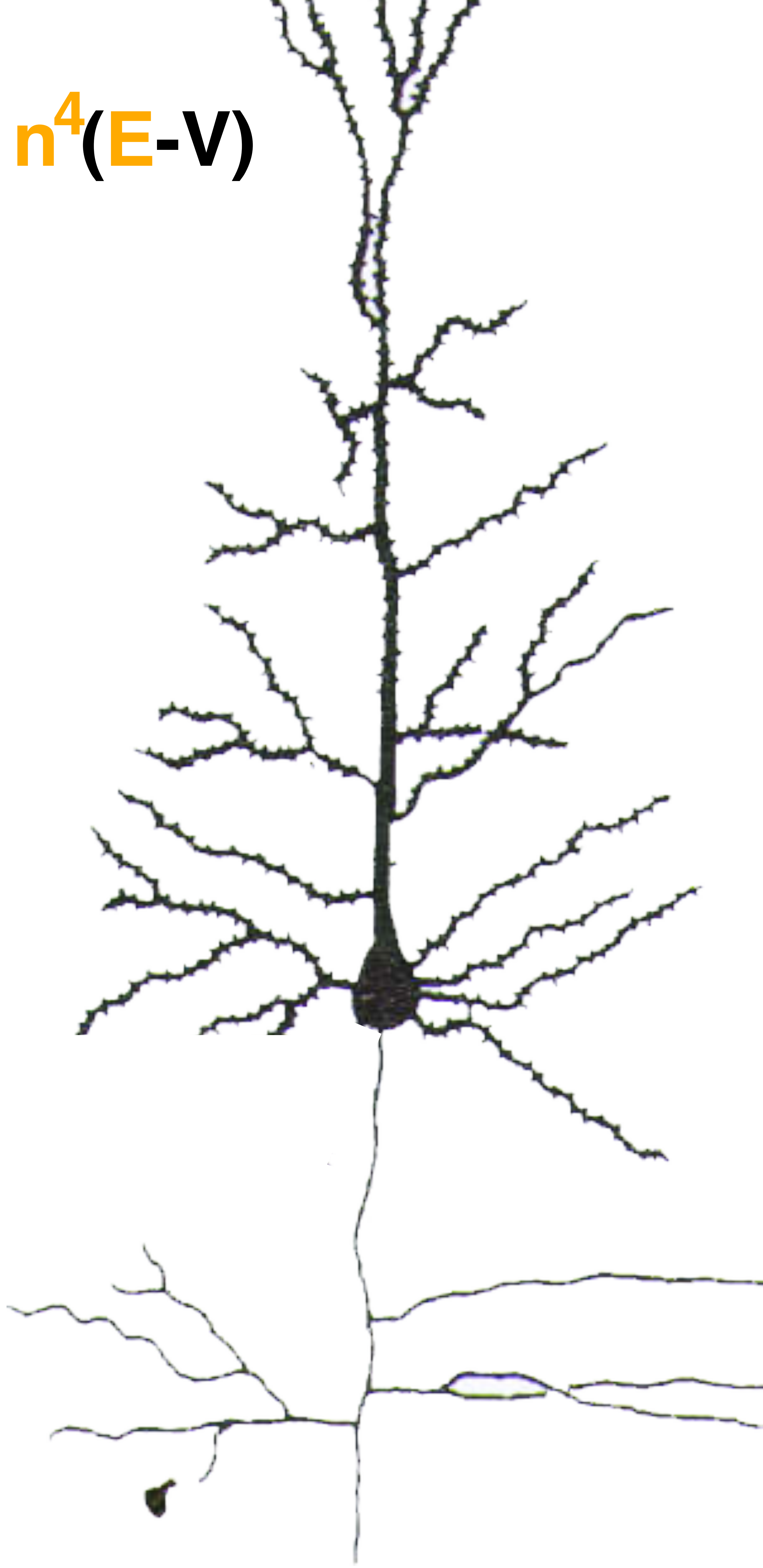
$$\frac{dw}{dt} = a + bV - w$$



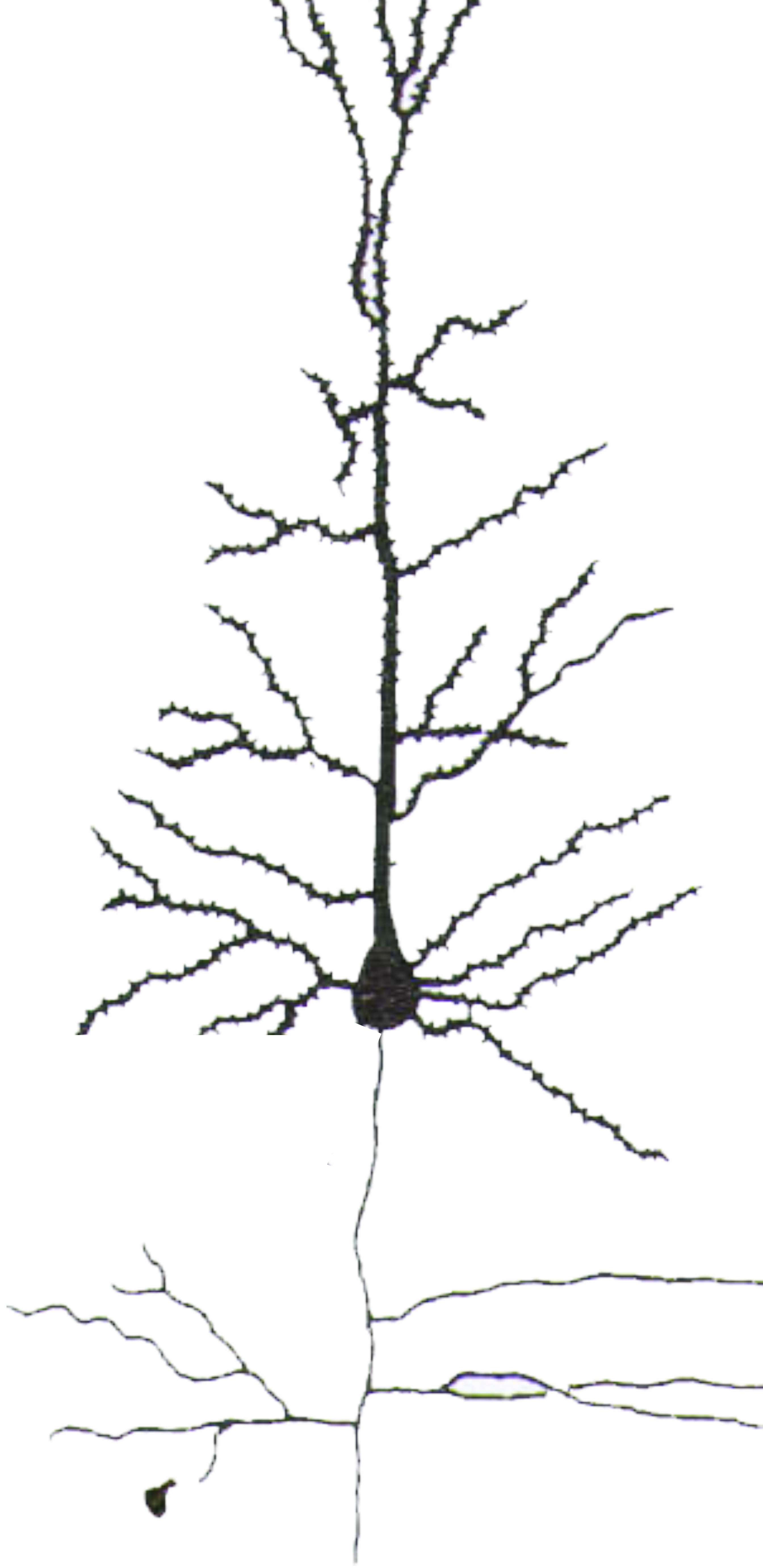


Limit Cycle

$$C \frac{dV}{dt} = g_{leak}(E-V) + g_{synapse}(E-V) + g_{Na} m^3 h(E-V) + g_K n^4 (E-V)$$



$$C \frac{dV}{dt} = g_{leak}(E-V) + g_{synapse}(E-V)$$



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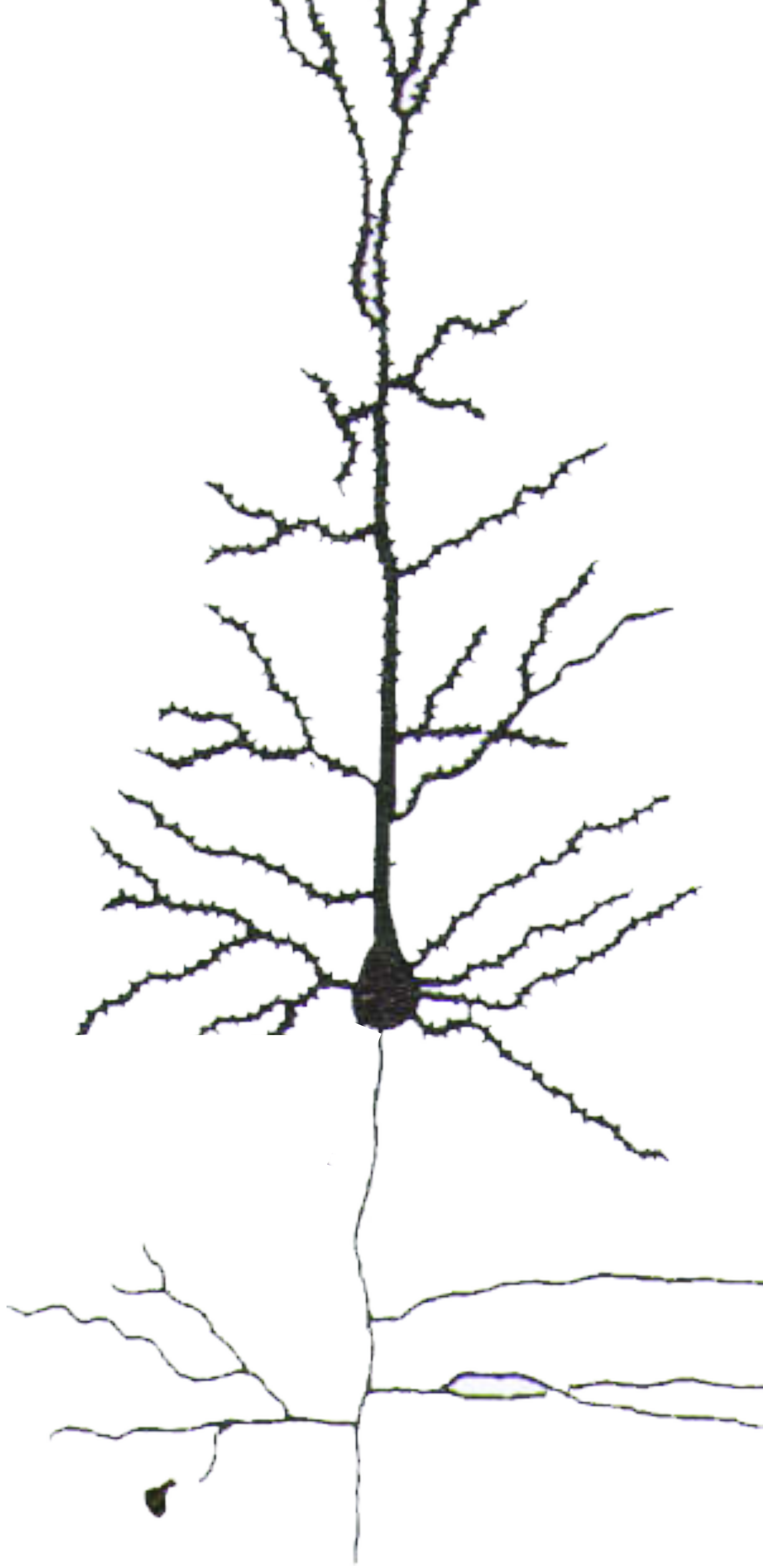
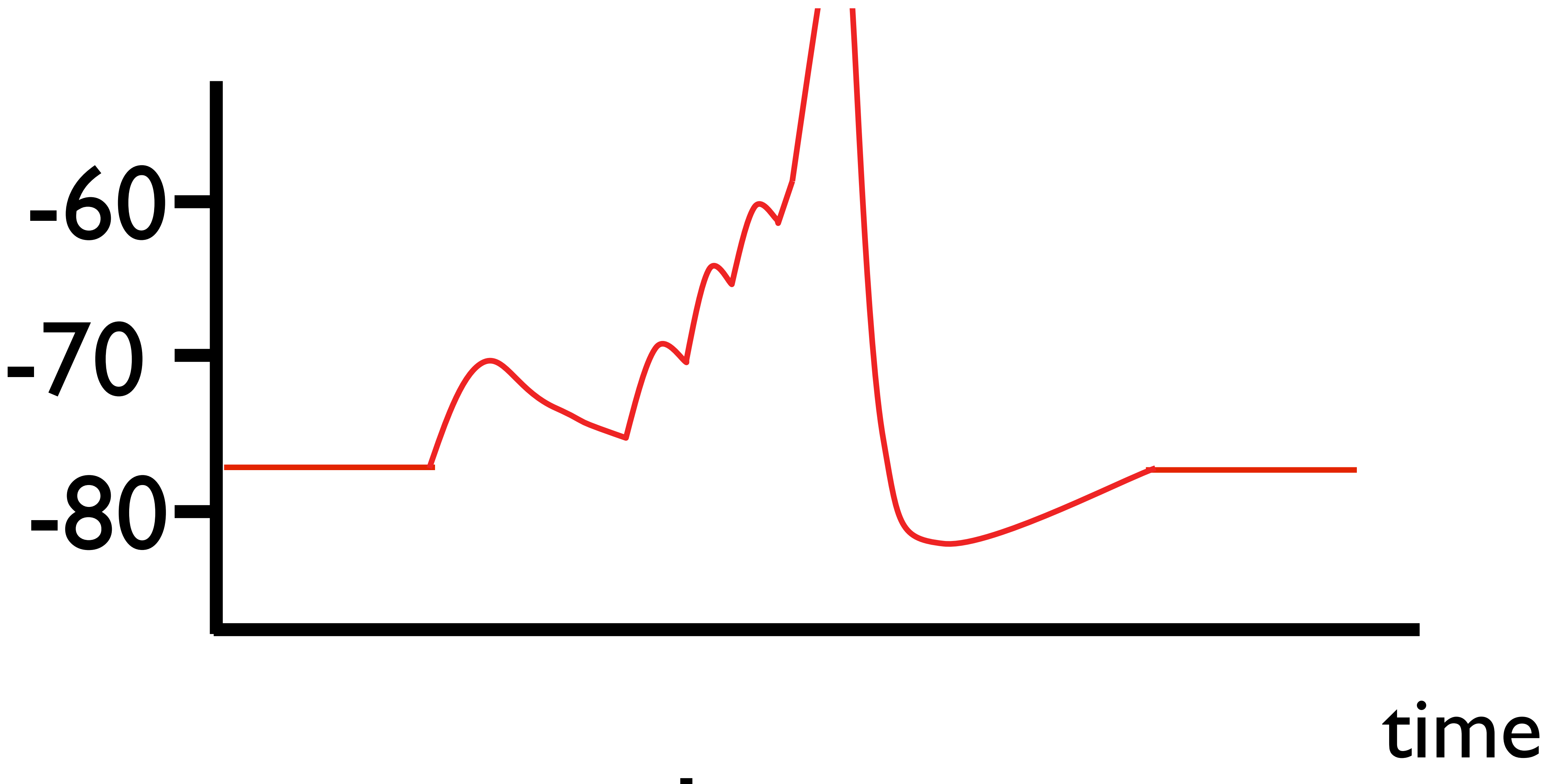


$$g_{tot} = g_{leak} + g_{syn}$$

$$E(\Delta t) = \frac{g_{leak} E_{leak} + g_{syn} E_{syn}}{g_{tot}}$$

$$\tau(\Delta t) = \frac{C}{g_{tot}}$$

$$V(t+\Delta t) = E(\Delta t) + \left(V(t) - E(\Delta t)\right) e^{-\frac{\Delta t}{\tau(\Delta t)}}$$



$$g_{tot} = g_{leak} + g_{syn}$$

$$E(\Delta t) = \frac{g_{leak}\, E_{leak} + g_{syn}\, E_{syn}}{g_{tot}}$$

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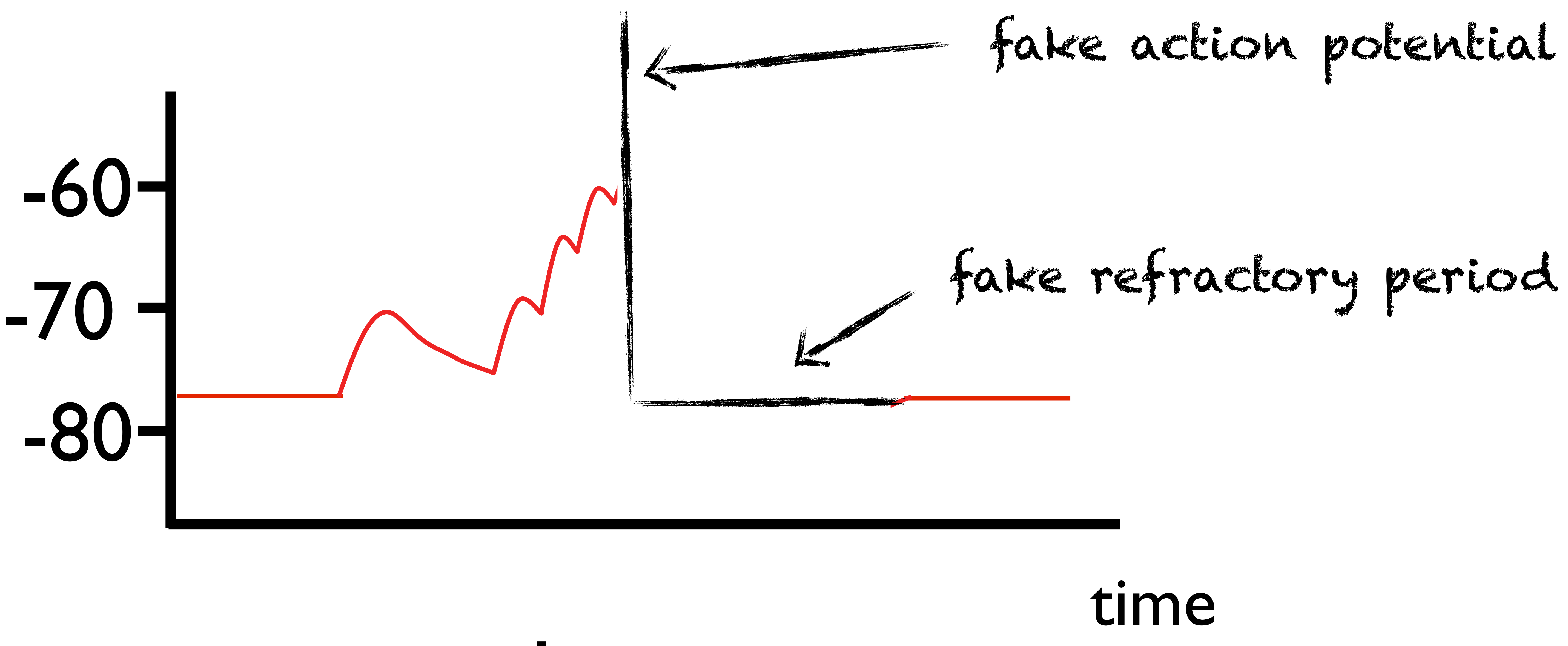

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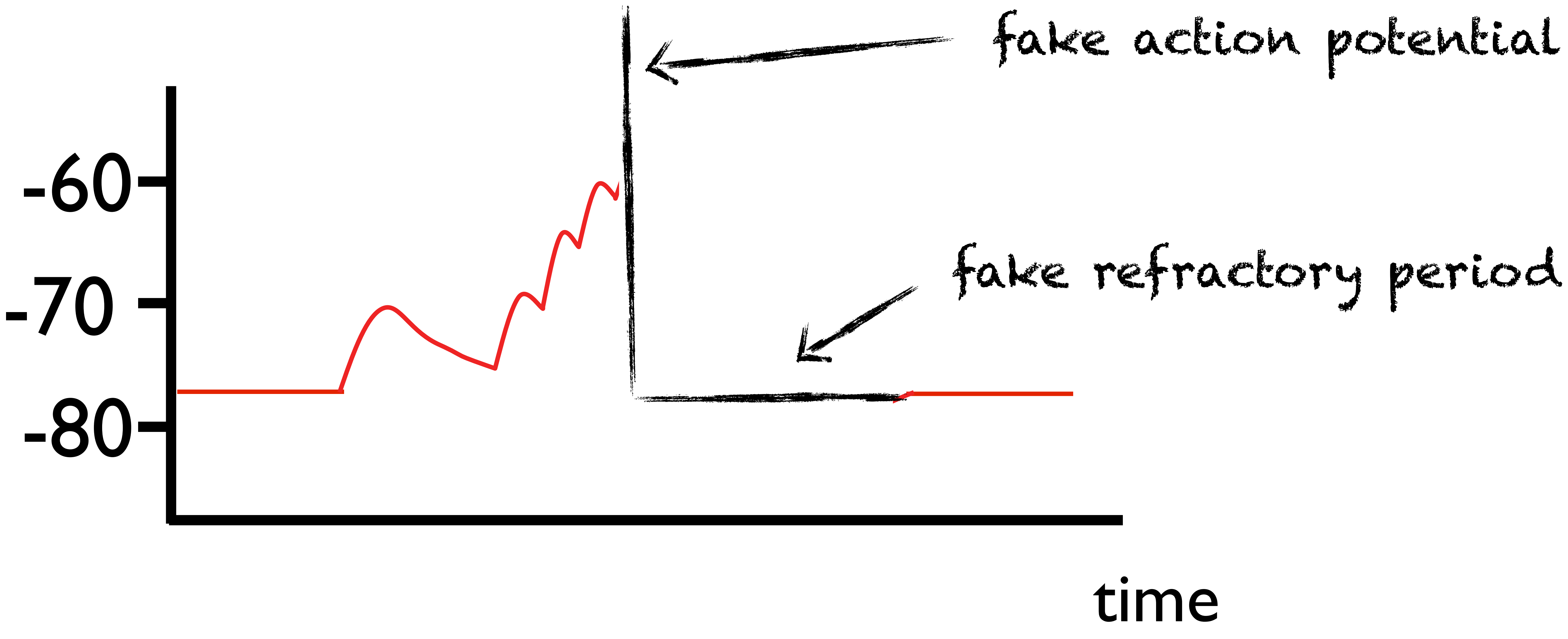
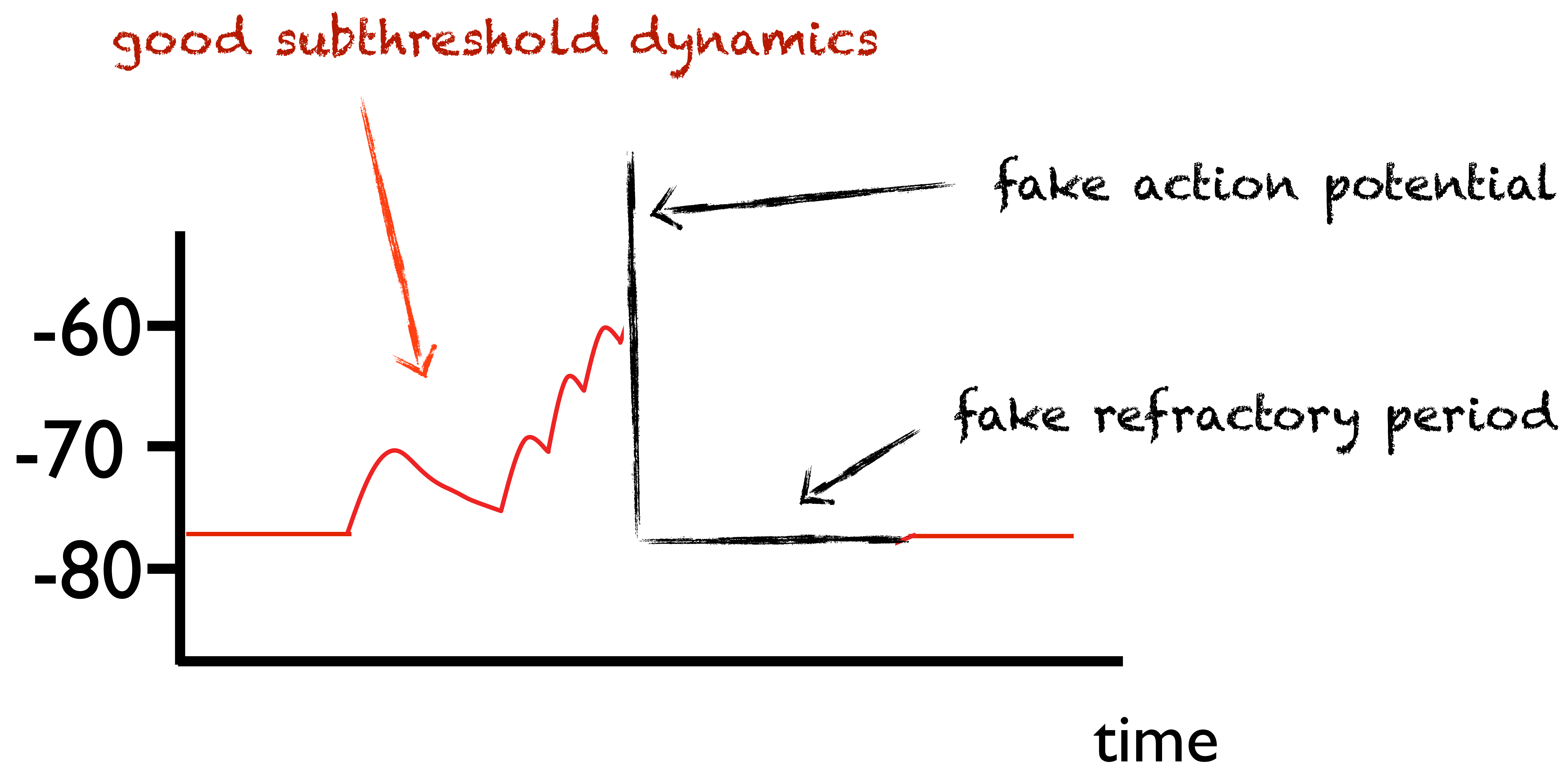
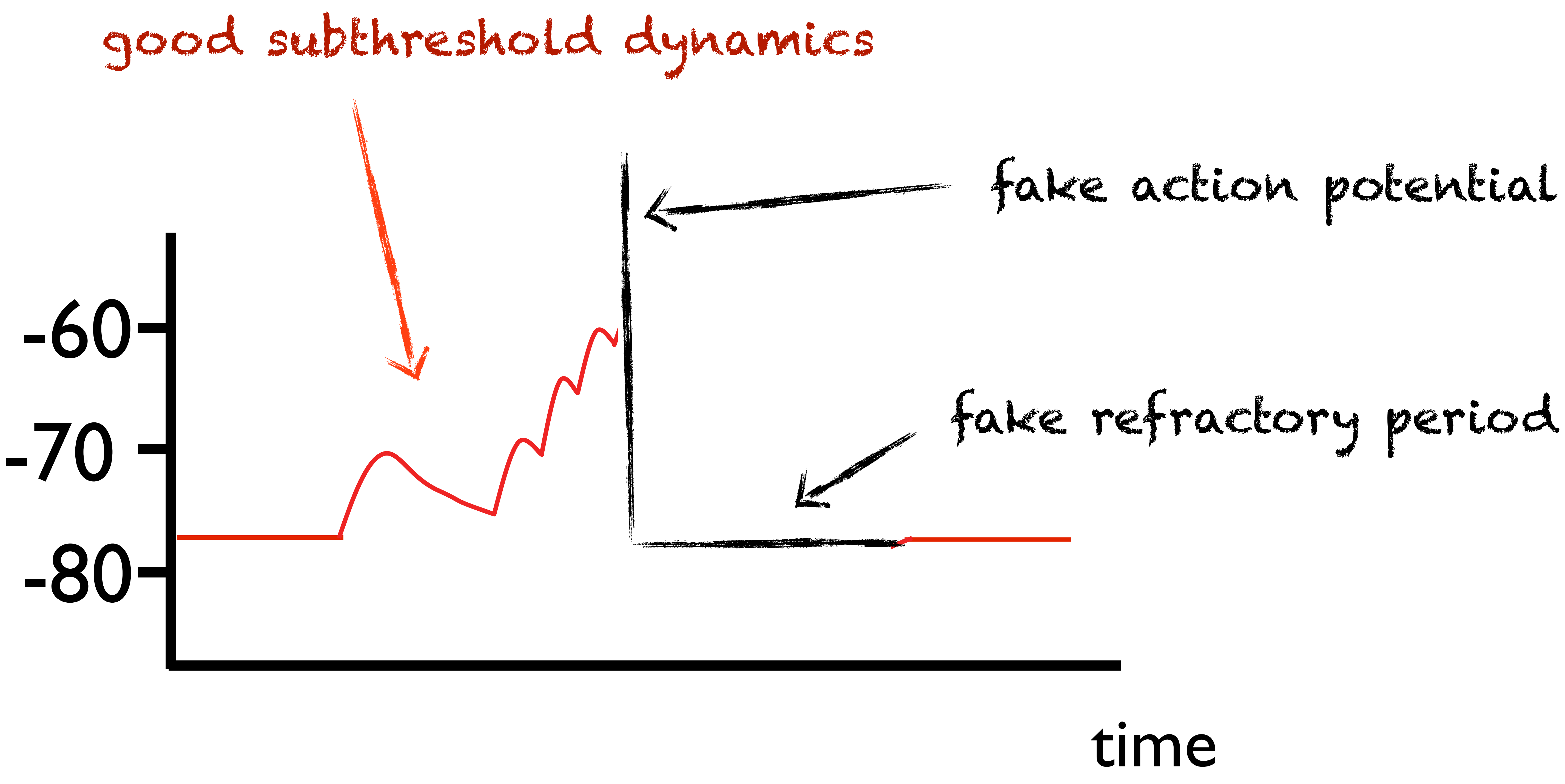

fake action potential
fake refractory period
-60
-70
-80
time


good subthreshold dynamics
fake action potential
fake refractory period
-60
-70
-80
time



Voilà,...

Integrate & fire!!

Lecture 2

1836 - The brain runs on neurons (Gabriel Gustav Valentin)

1786, 1868, 1926 - Neurons run on action potentials
(Luigi Galvani, Julius Bernstein Lord Adrian)

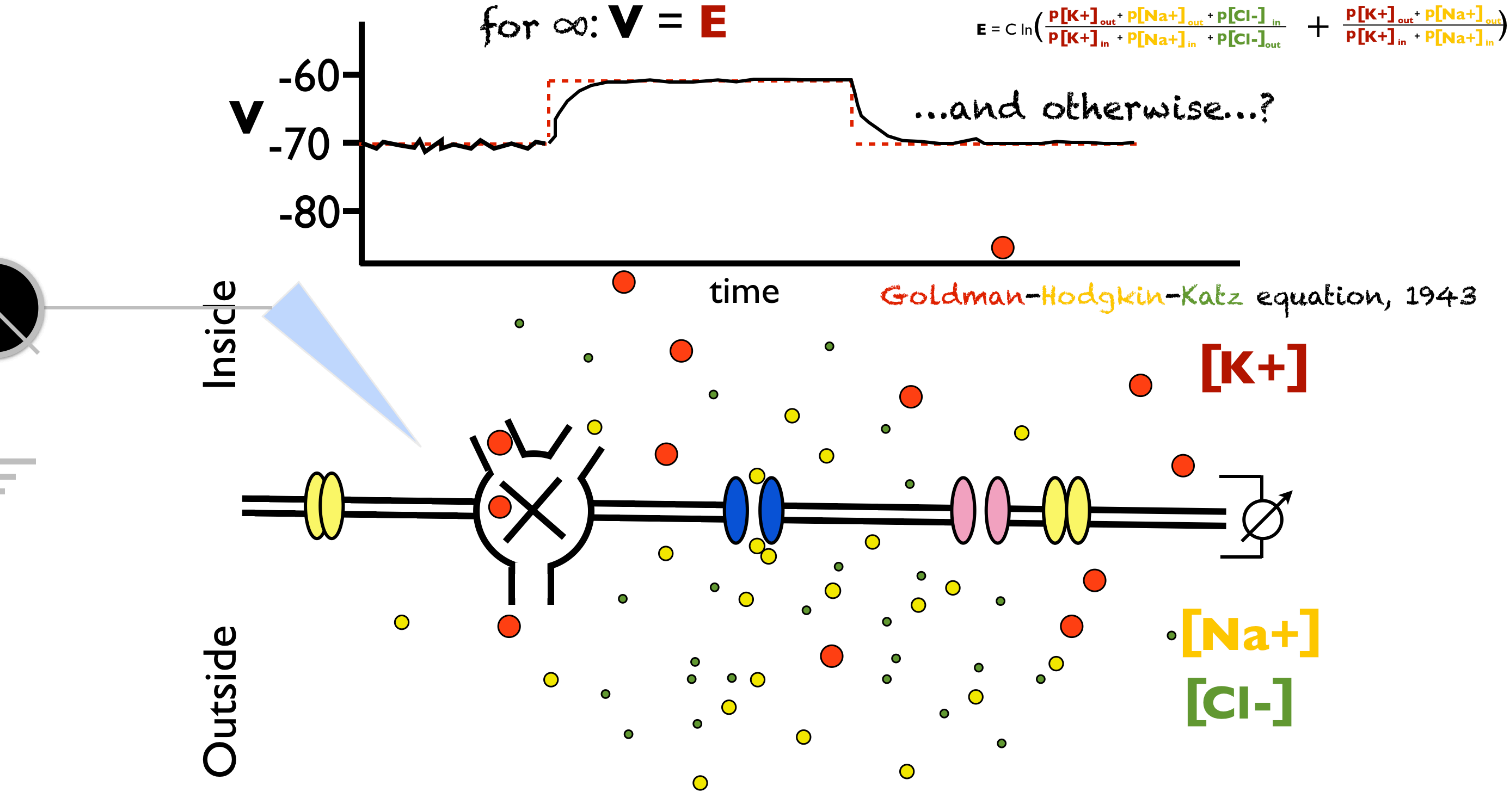
1887,1943 - Neurons have a the resting state
(Nernst, Goldman Hodgkin Katz)

In 1926 Lord Adrian & Charles Sherrington recorded the first spikes

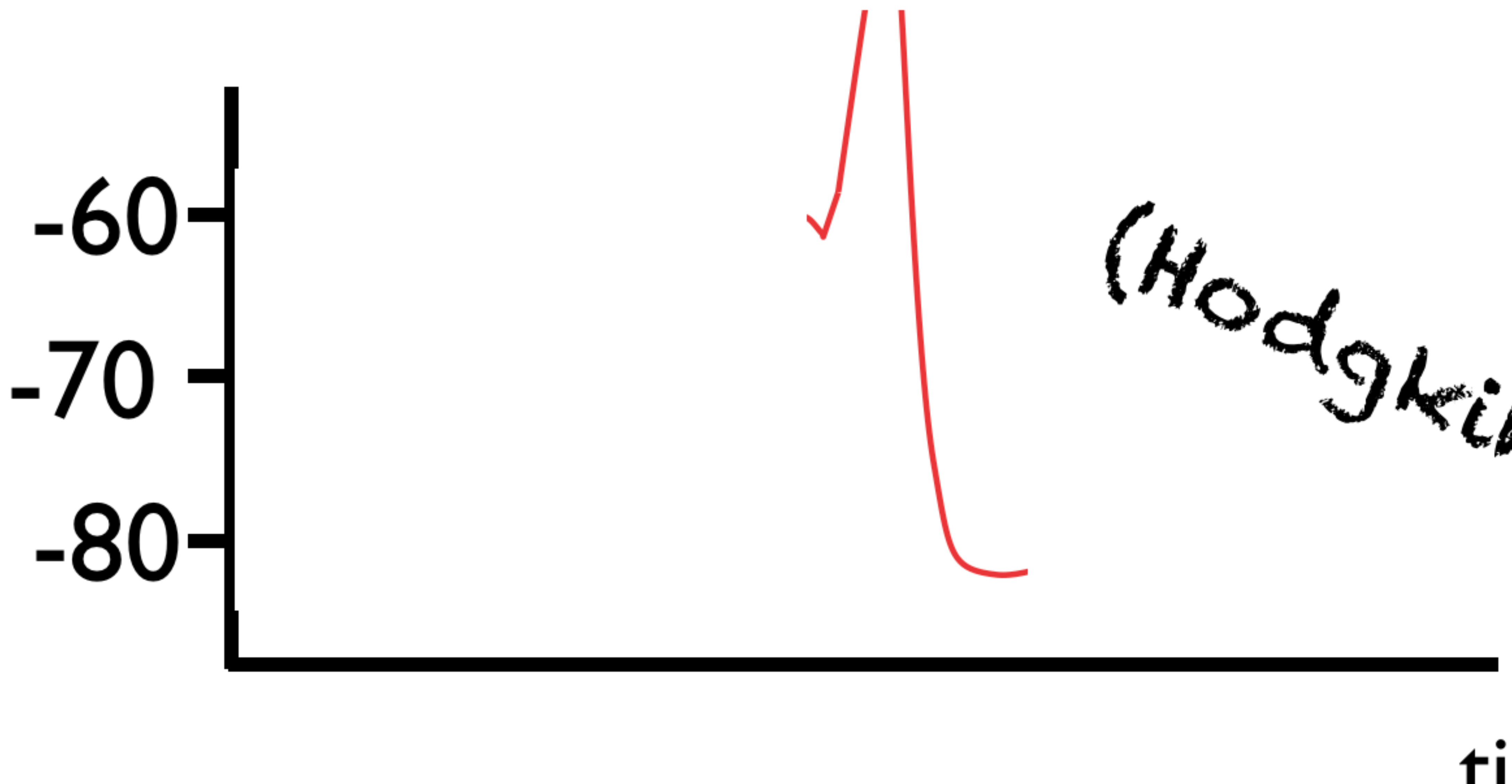
1952 APs are powered by ion channels (Hodgkin Huxley,1952)

We understand the neuron —> We understand NOTHING.
Neuroscience explodes

FitzHugh–Nagumo simplify the beast
we find it’s not enough and go (back) to I&F (1907 LaPique)
wait for computers to become powerful enough


for ∞: V = E
$E = C \ln\left(\frac{p[K+]_{out} + p[Na+]_{out} + p[Cl-]_{in}}{p[K+]_{in} + p[Na+]_{in} + p[Cl-]_{out}} + \frac{p[K+]_{out} + p[Na+]_{out}}{p[K+]_{in} + p[Na+]_{in}}\right)$
V
-60
-70
-80
time
...and otherwise...?
Goldman-Hodgkin-Katz equation, 1943
Inside
Outside
[K+]
[Na+]
[Cl-]

This is the "fire" part!



(Hodgkin Huxley style)

$$g_{tot} = g_{leak} + g_{syn} + g_{Na}(V) + g_K(V)$$

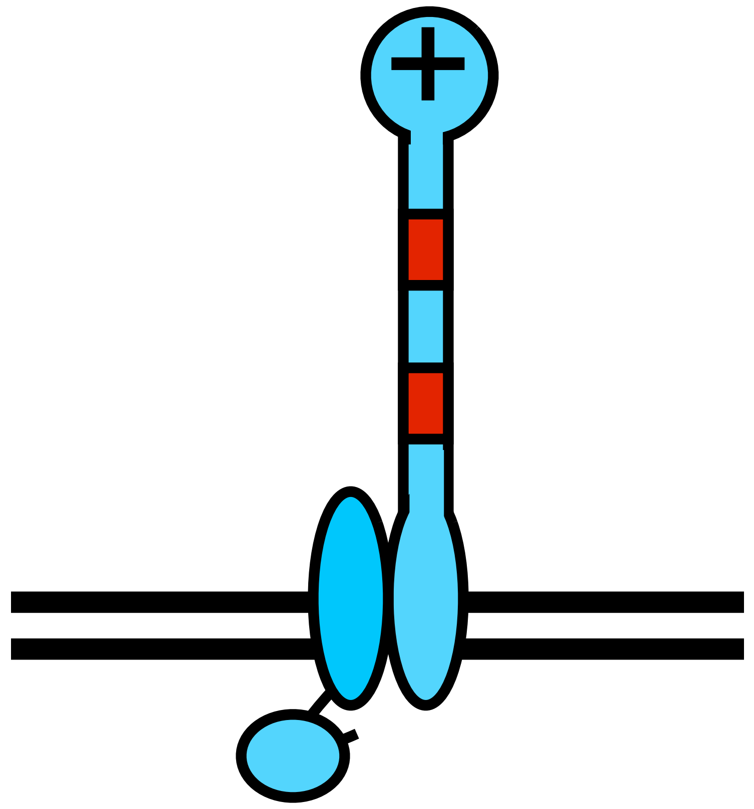
$$E(\Delta t) = \frac{g_{leak}\,E_{leak} + g_{syn}\,E_{syn} + g_{Na}(V)\,E_{Na} + g_K(V)\,E_K}{g_{tot}}$$

$$\tau(\Delta t) = \frac{C}{g_{tot}}$$

$$V(t+\Delta t) = E(\Delta t) + \left(V(t) - E(\Delta t)\right) e^{-\frac{\Delta t}{\tau(\Delta t)}}$$

$$C \frac{dV}{dt} = g_{leak}(E-V) + g_{synapse}(E-V)$$

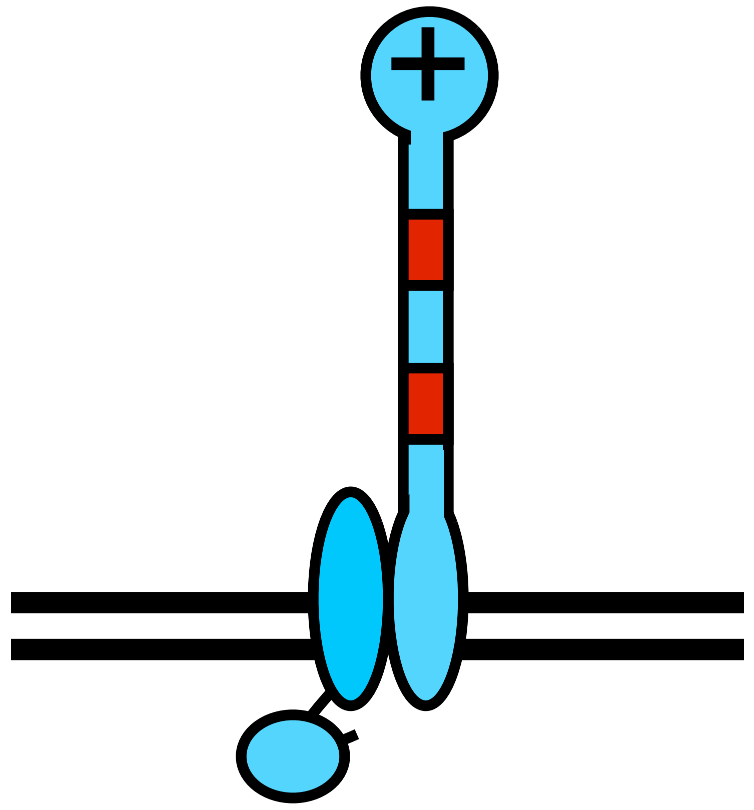
$$C \frac{dV}{dt} = g_{leak}(E-V) + g_{synapse}(E-V)$$



$$C \frac{dV}{dt} = g_{leak}(E-V) + g_{synapse}(E-V) + g_{Na}\, m^3 h (E-V)$$

$$\frac{dm}{dt} = \frac{m - m_0(V)}{\tau_m(V)}$$

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



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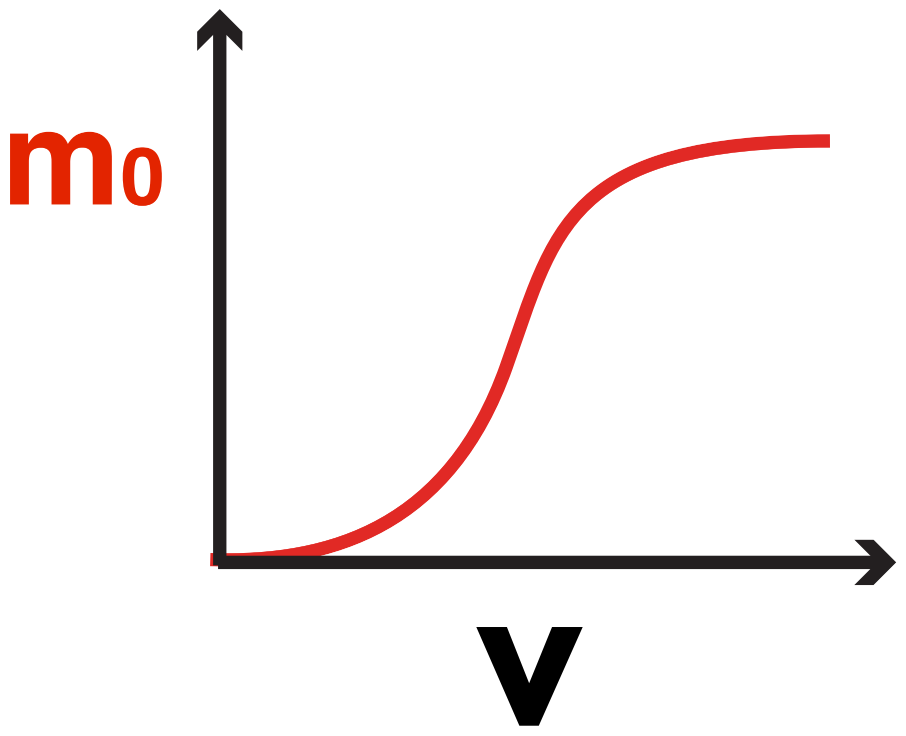

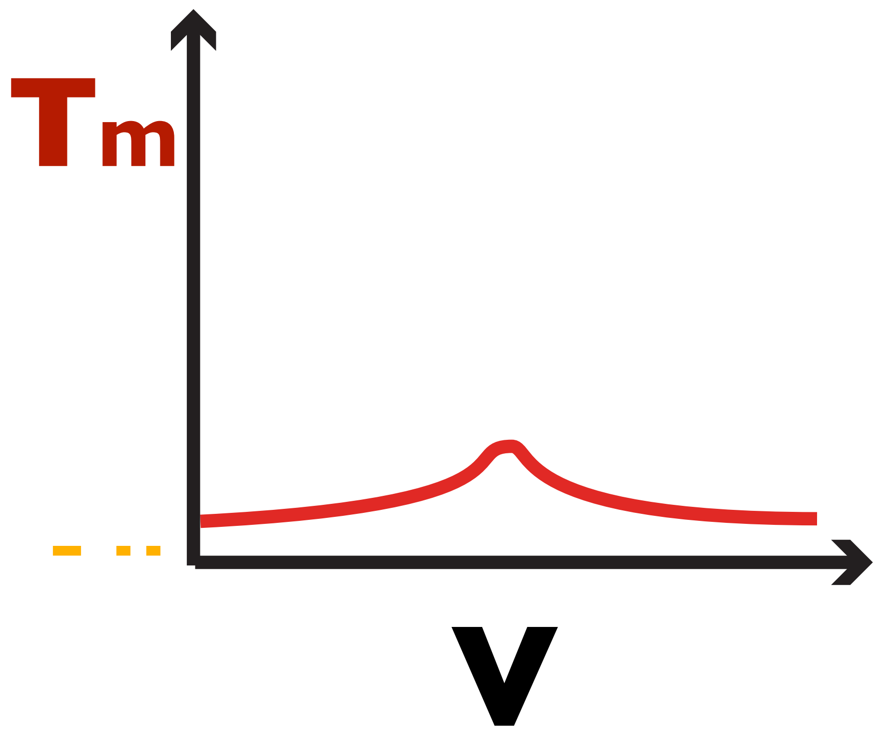

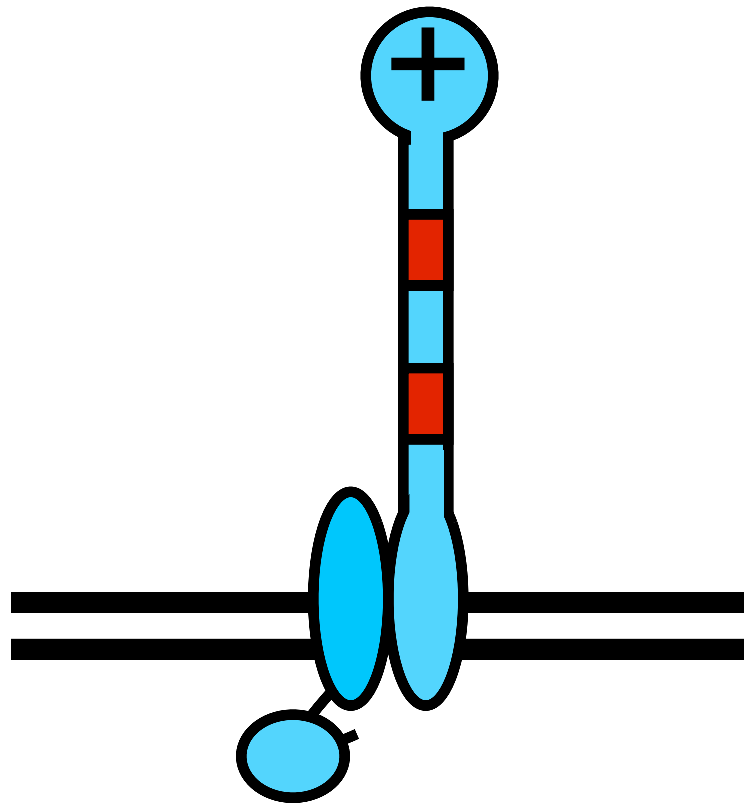

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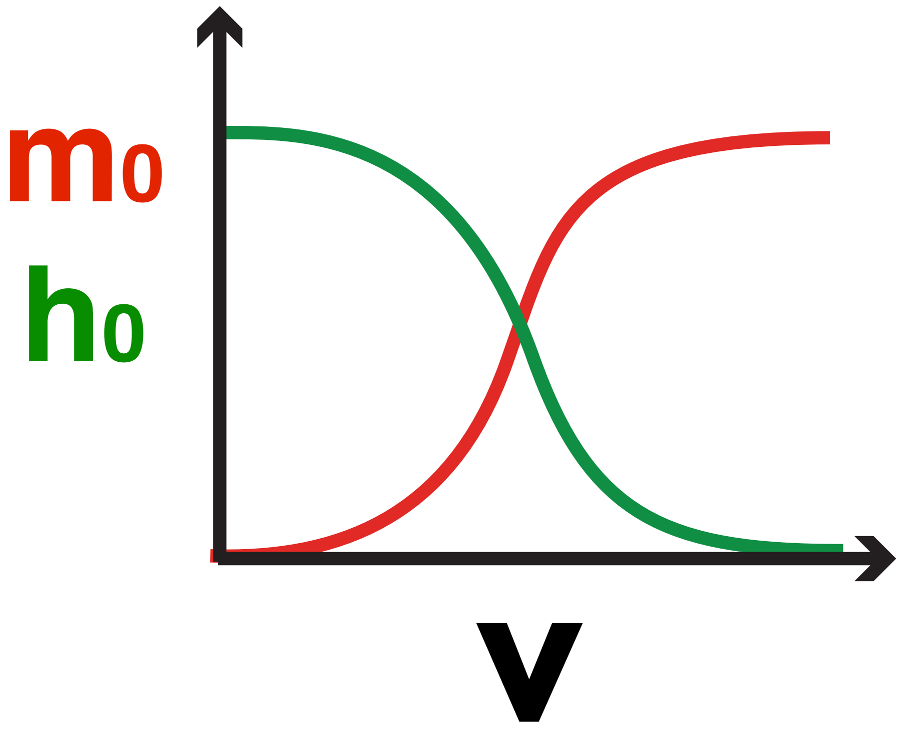

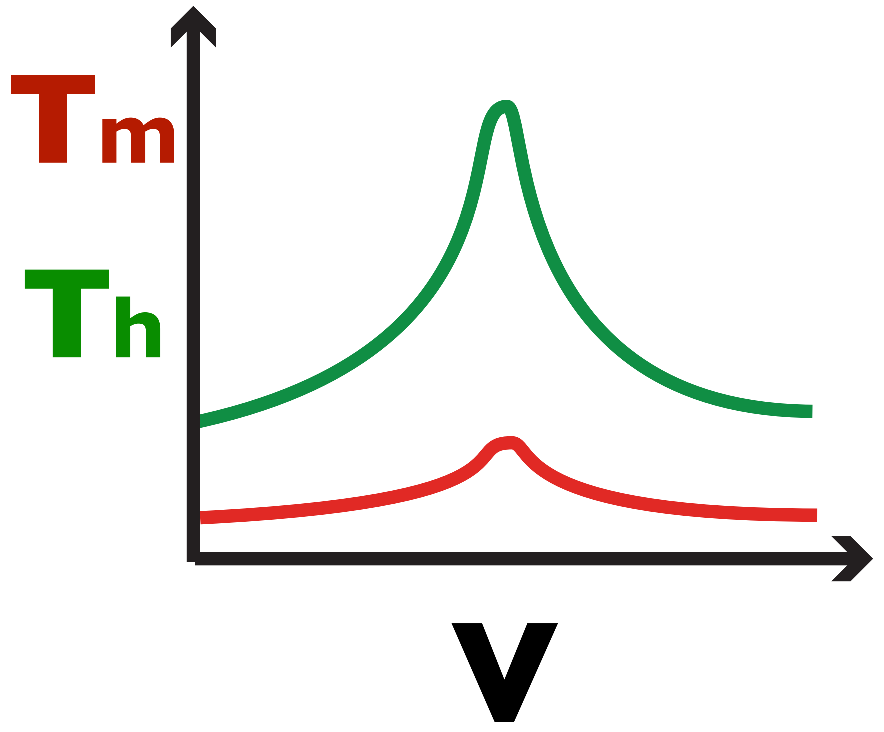

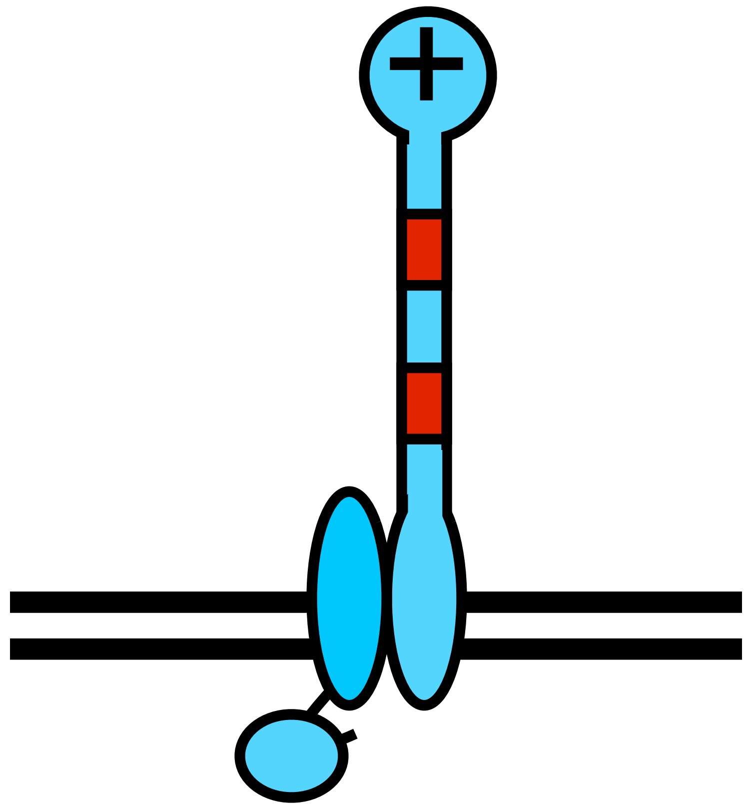

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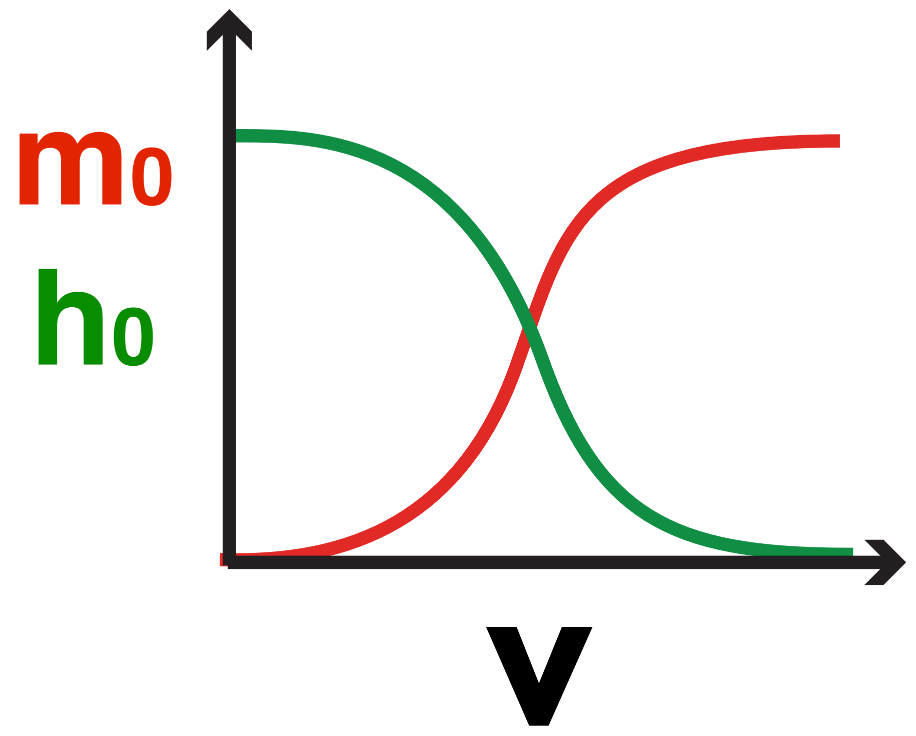

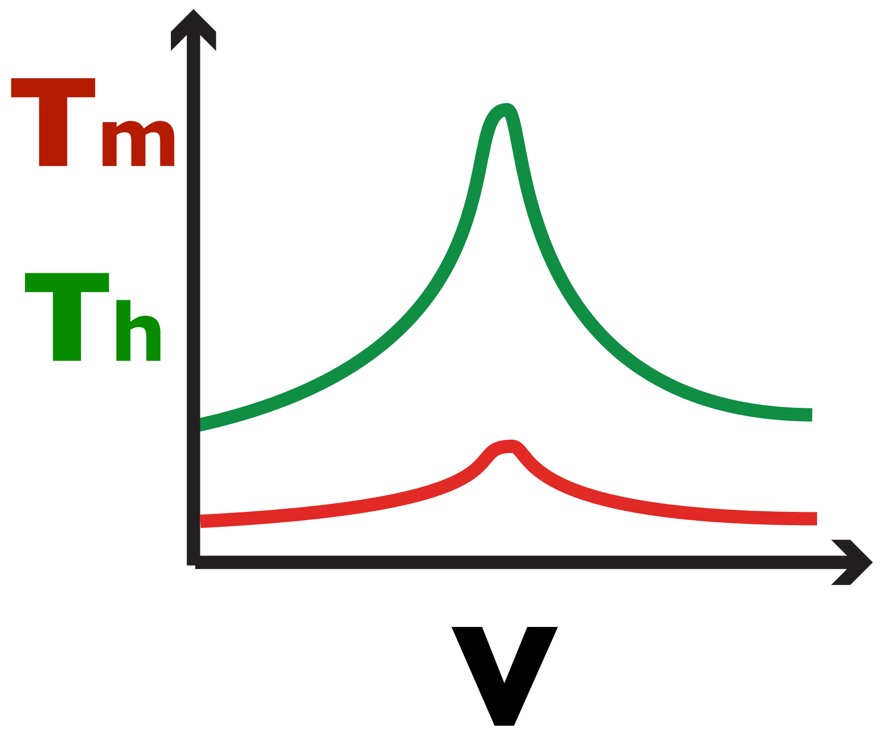

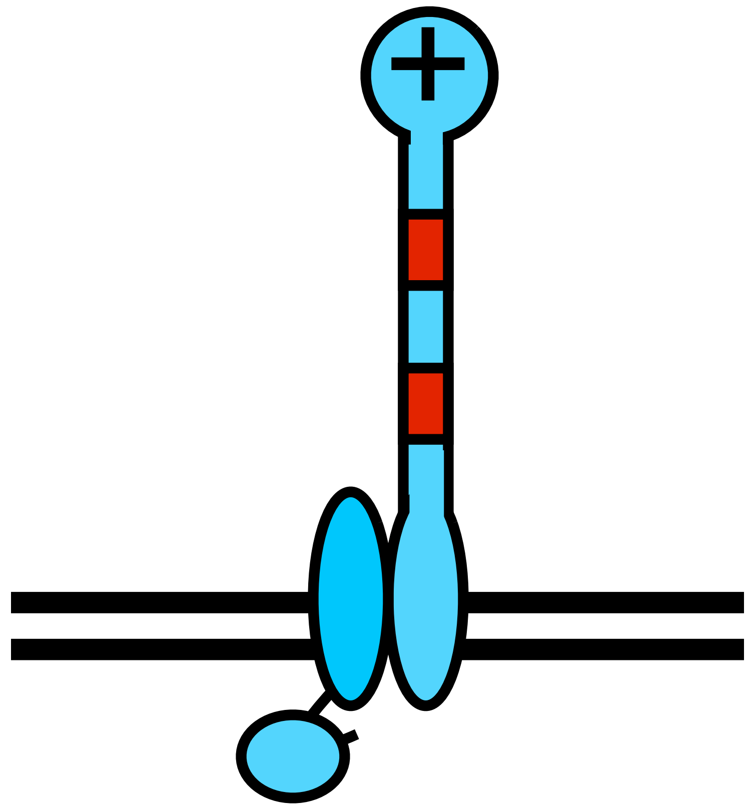

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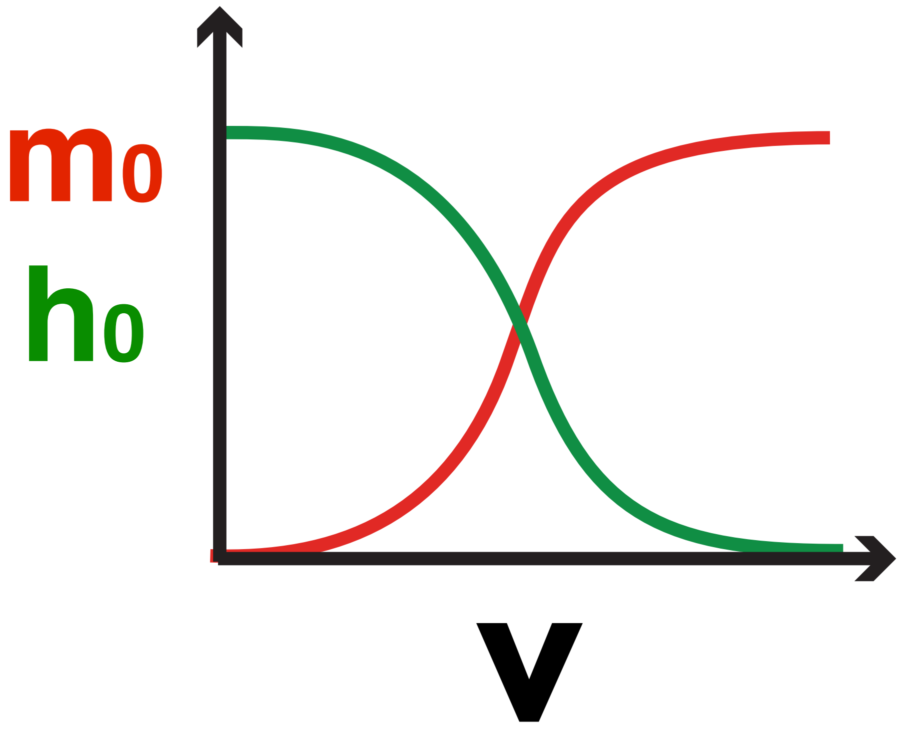

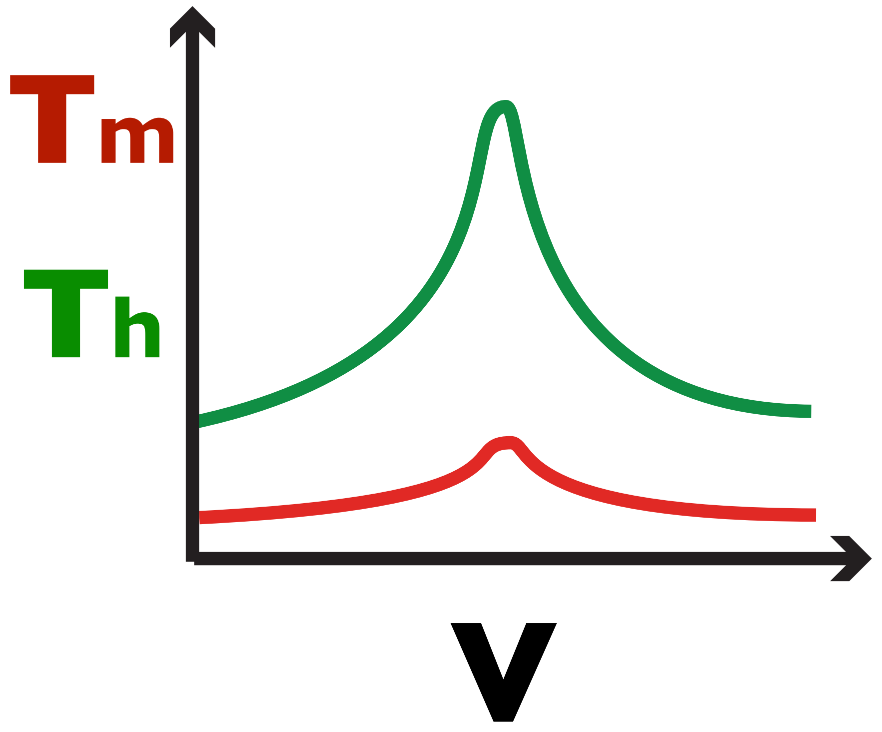

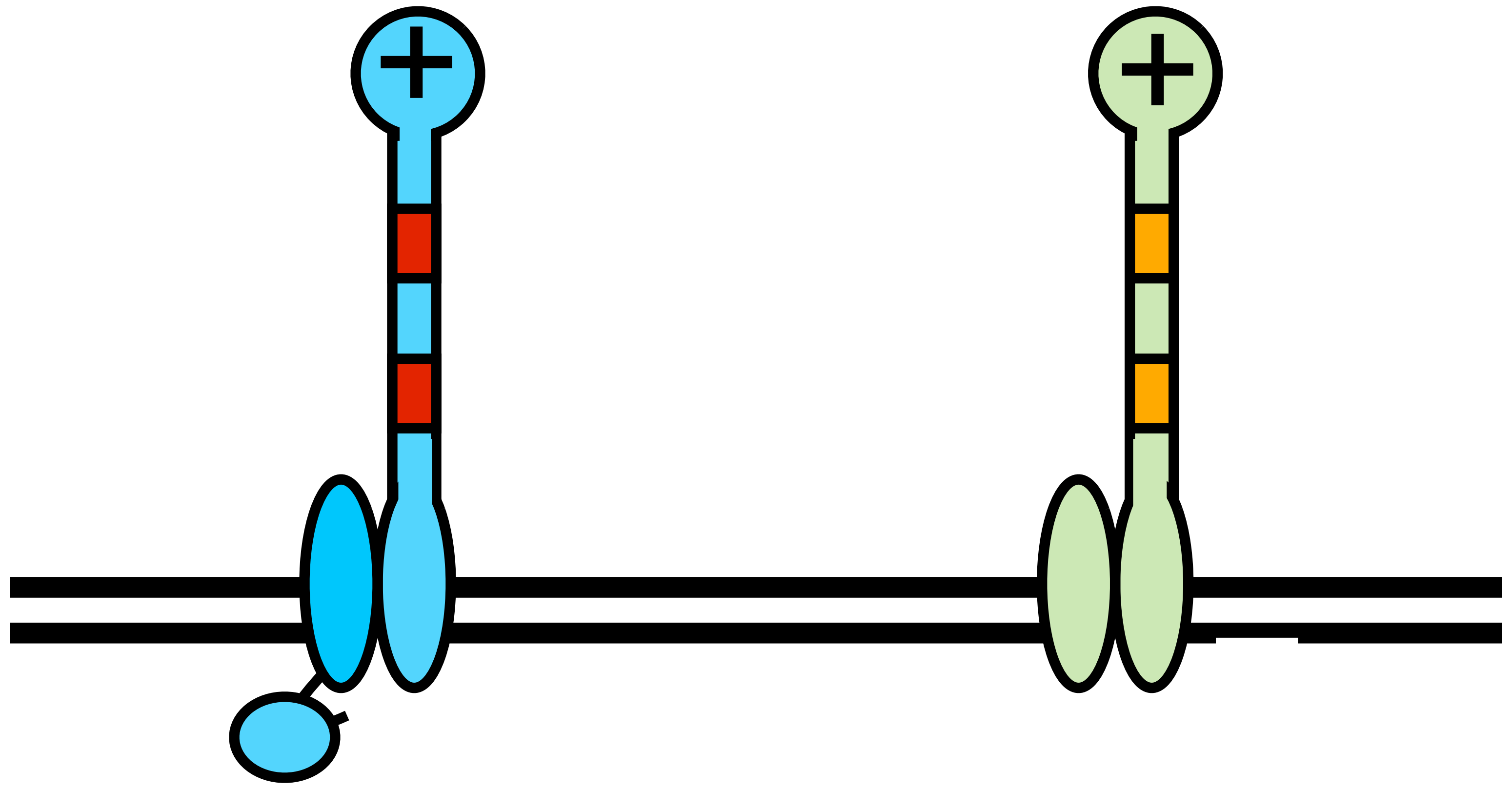

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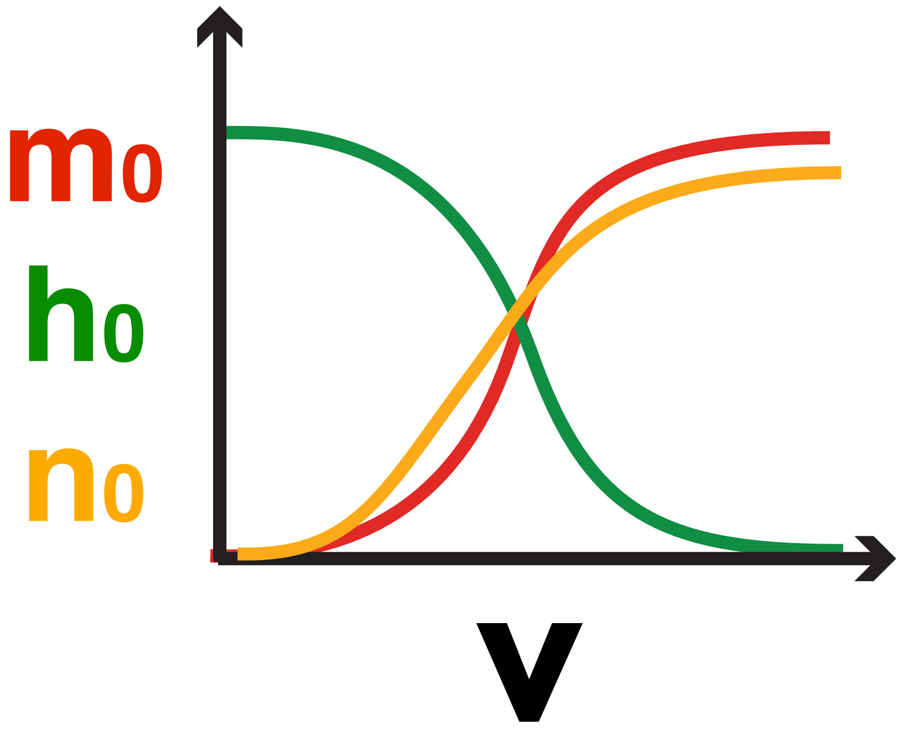

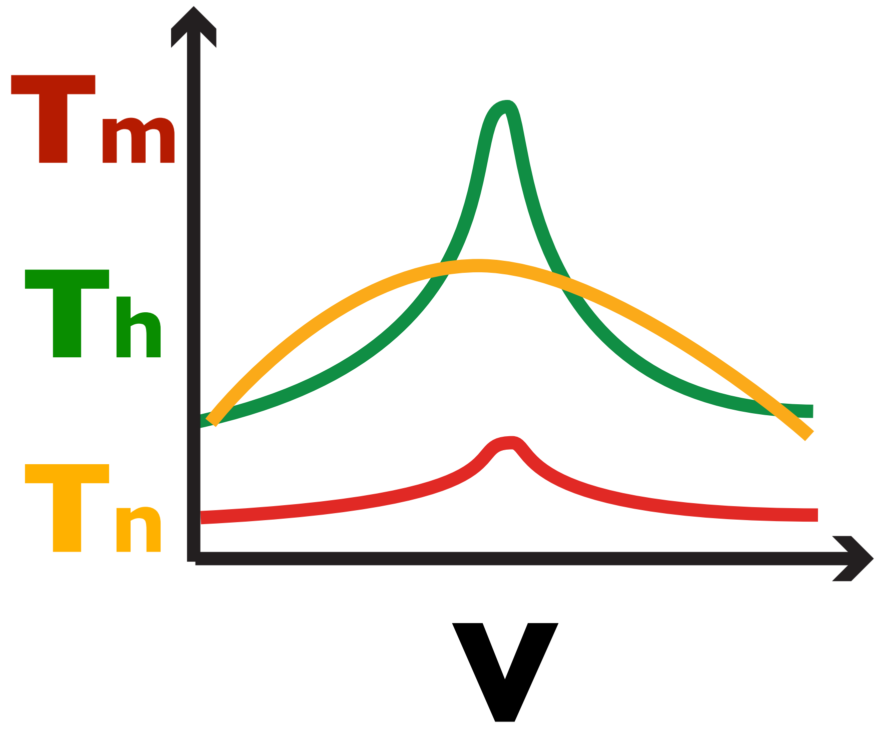

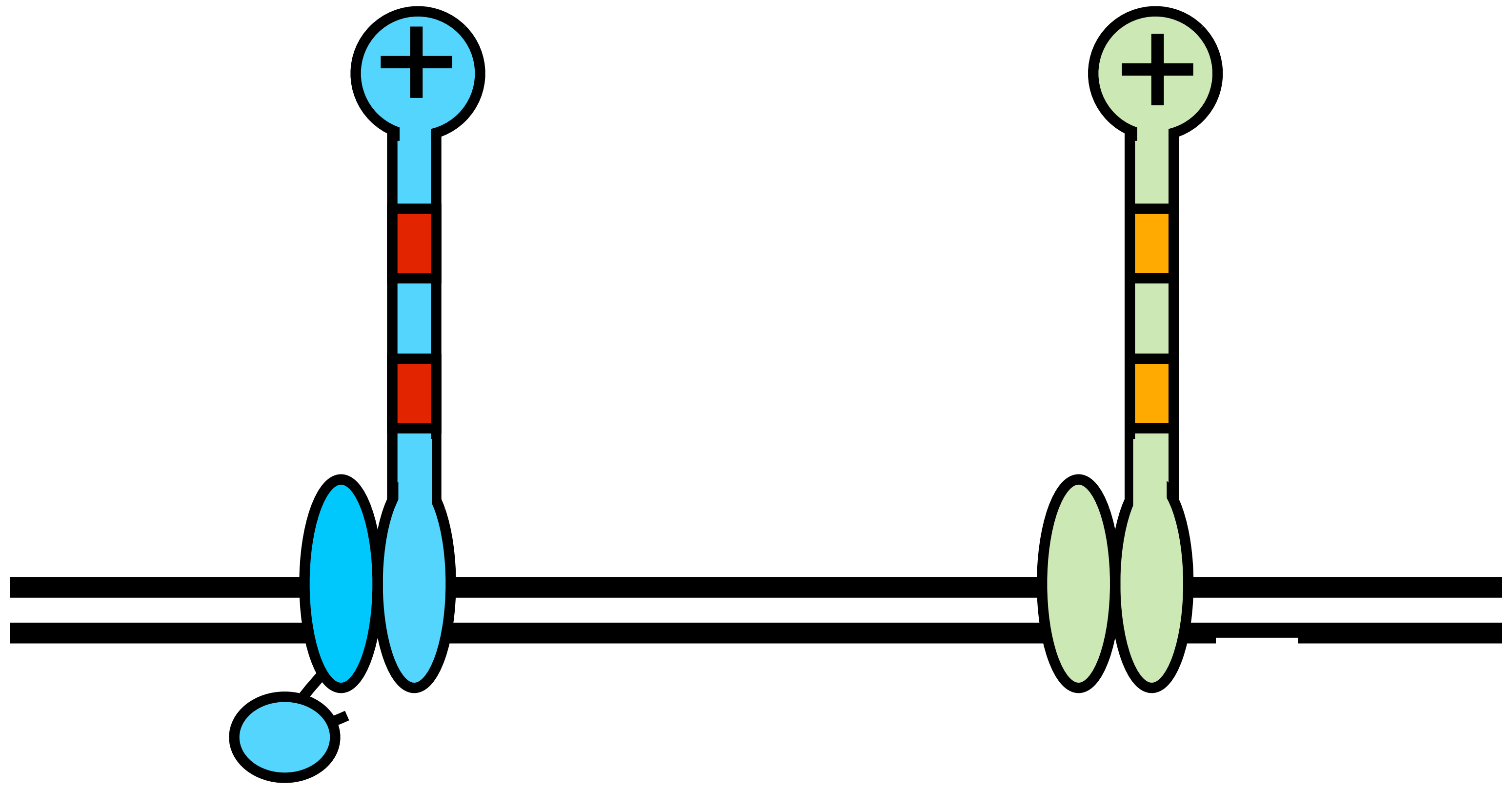

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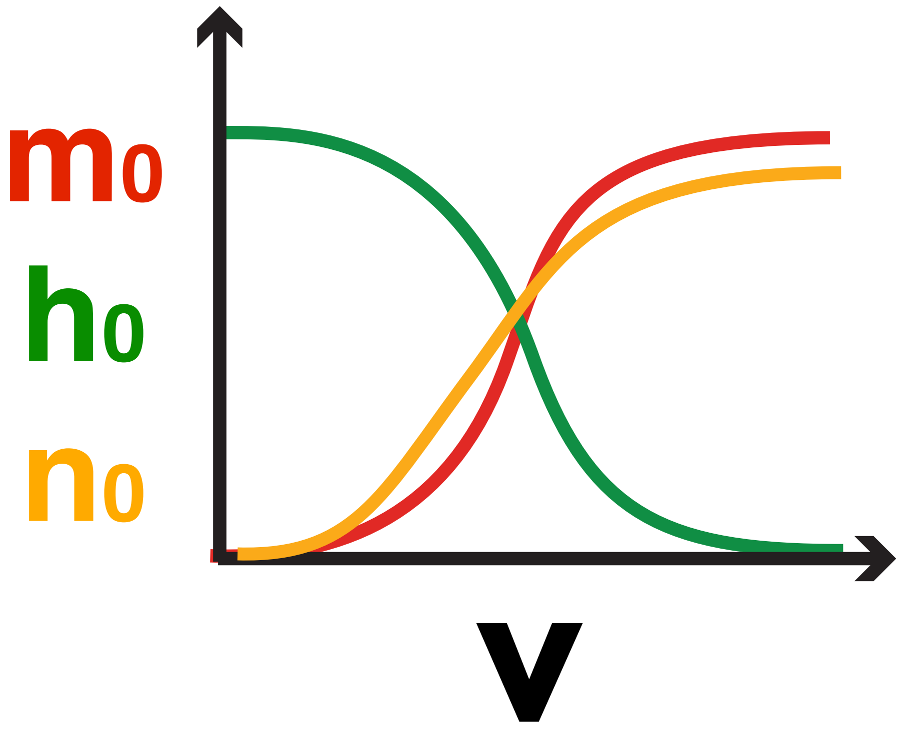
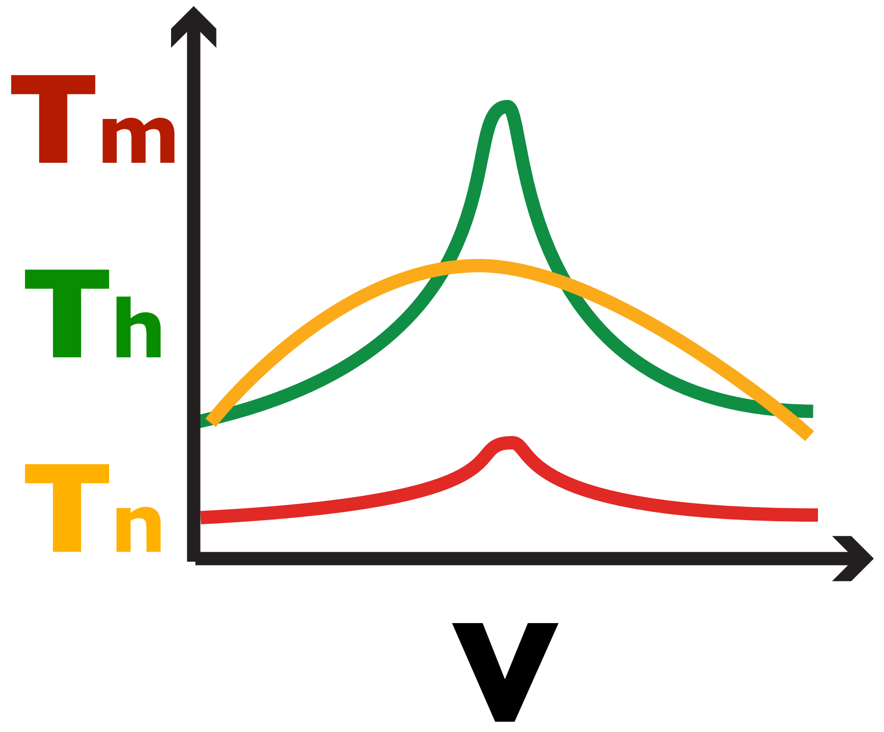
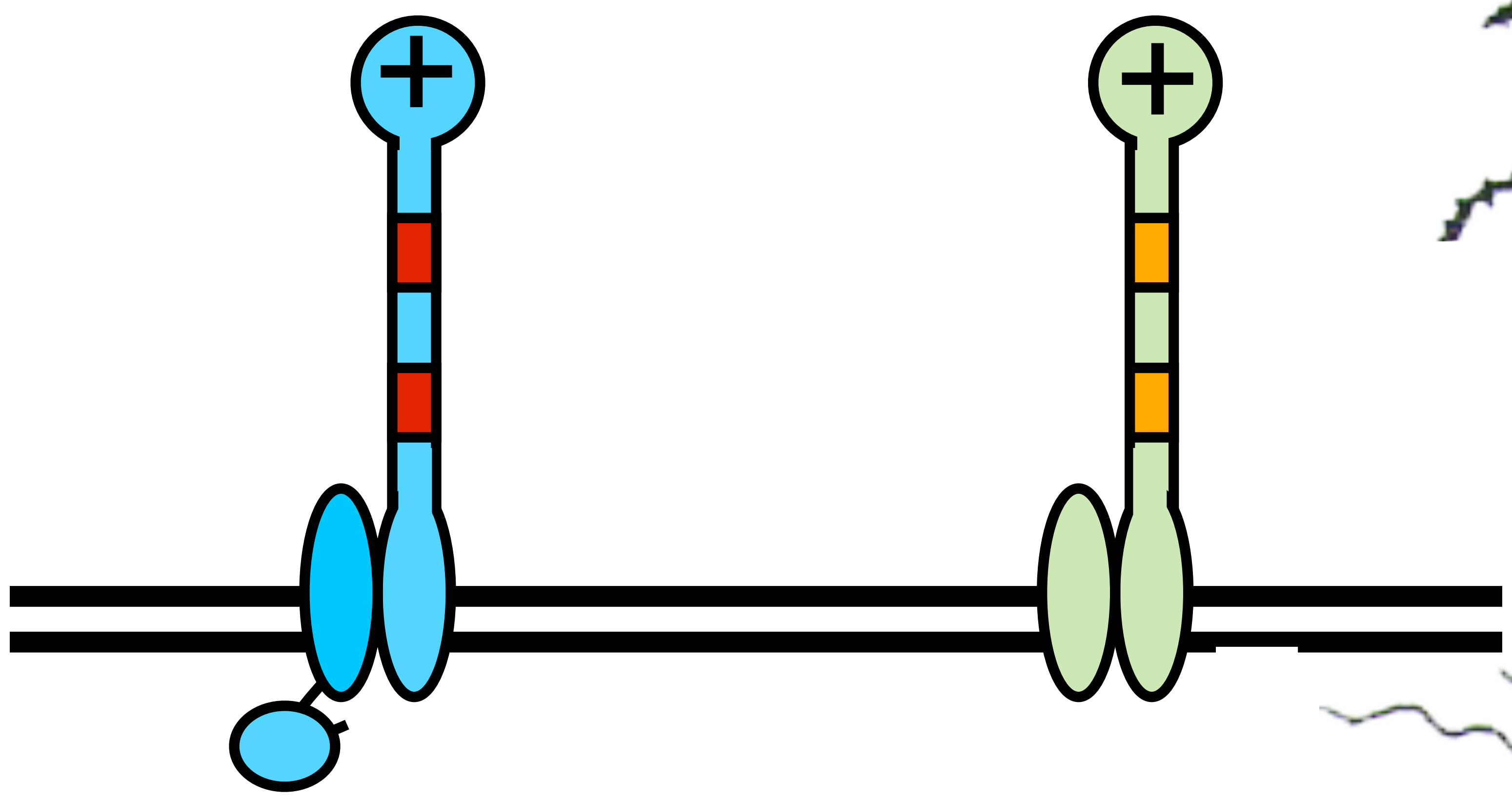
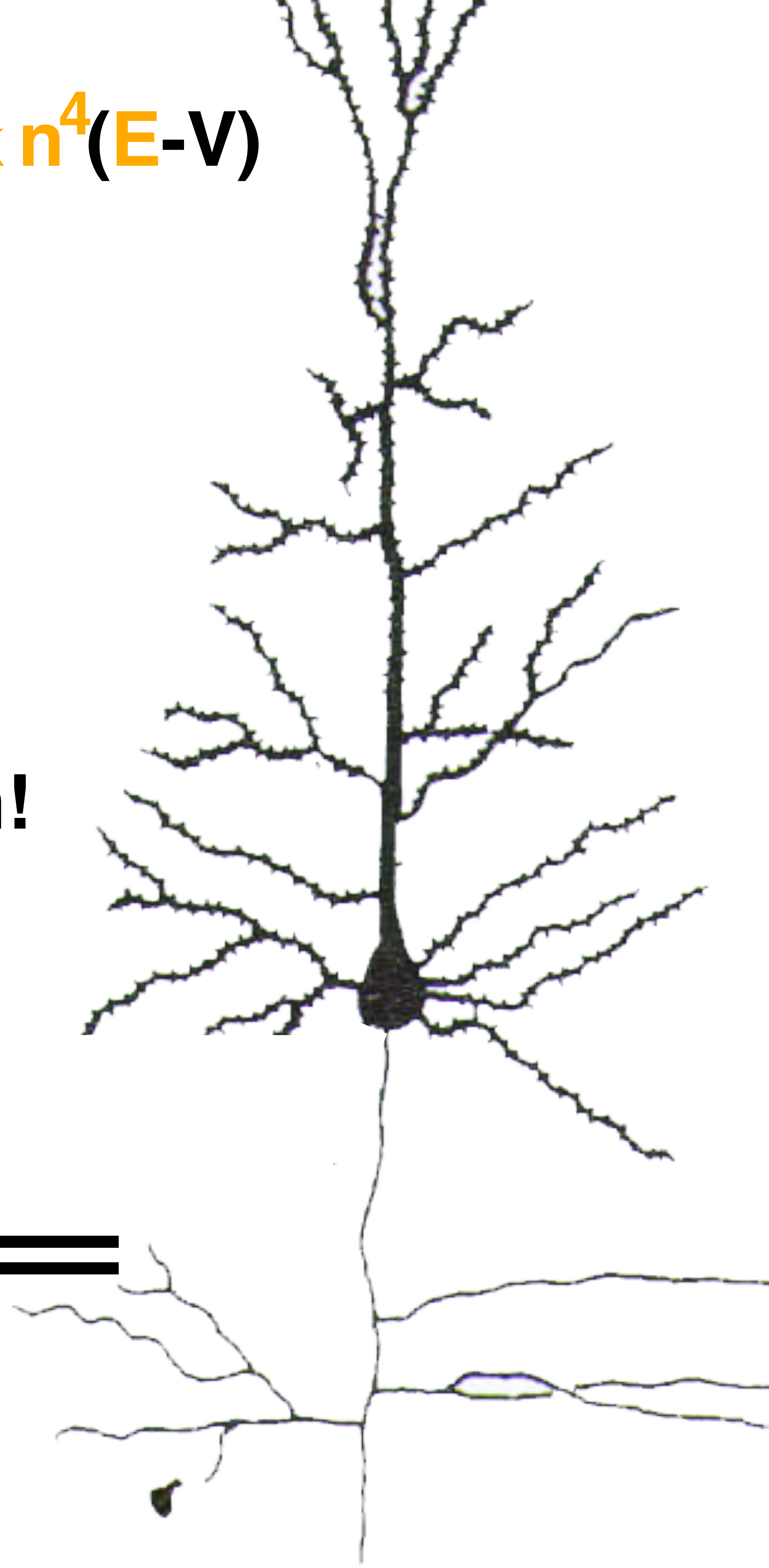




A complete description of a neuron!





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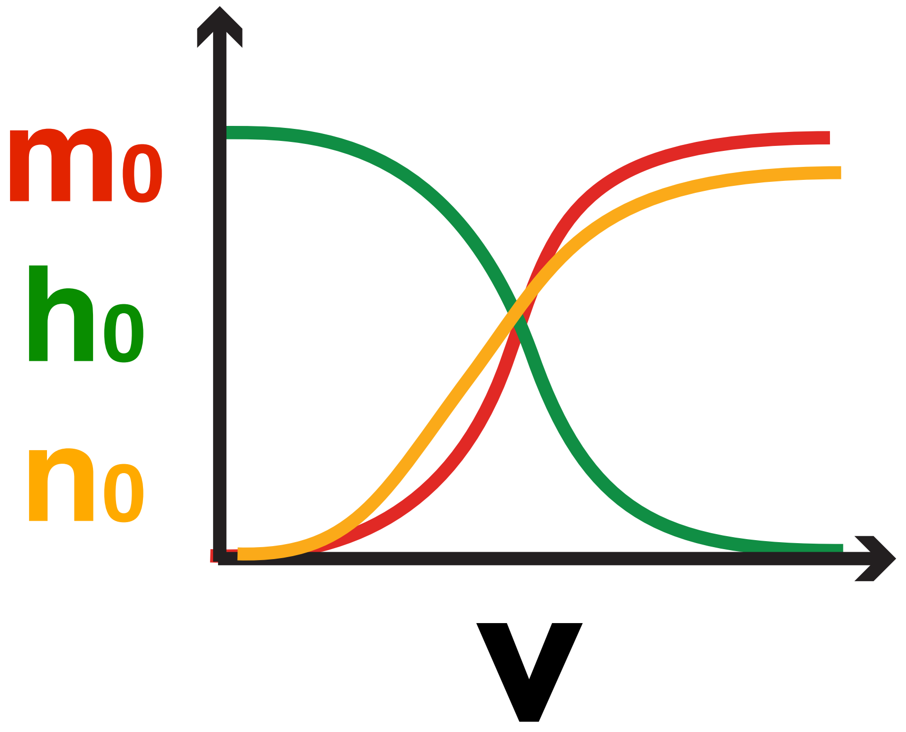
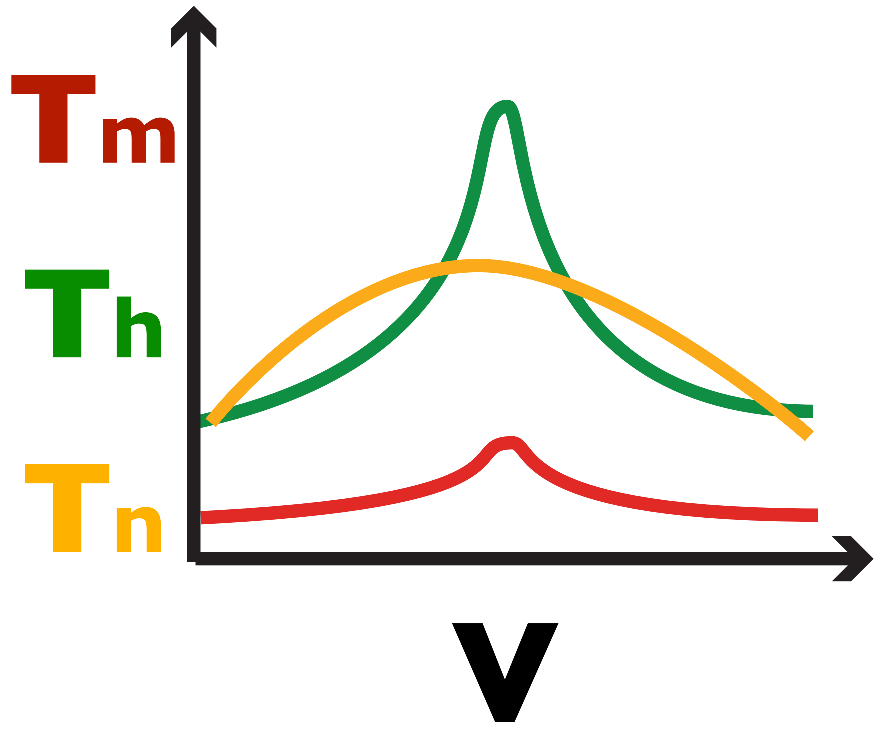
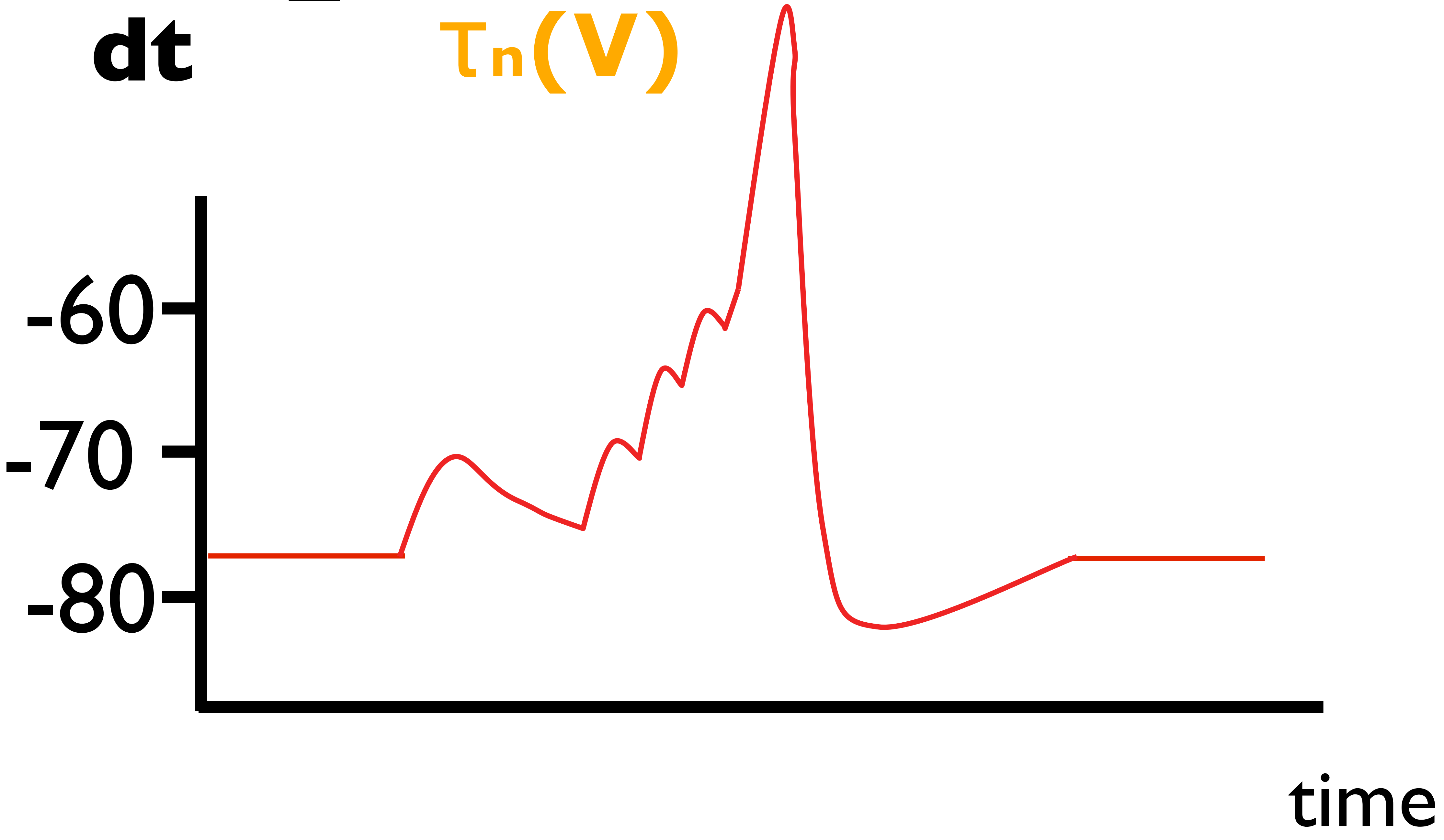
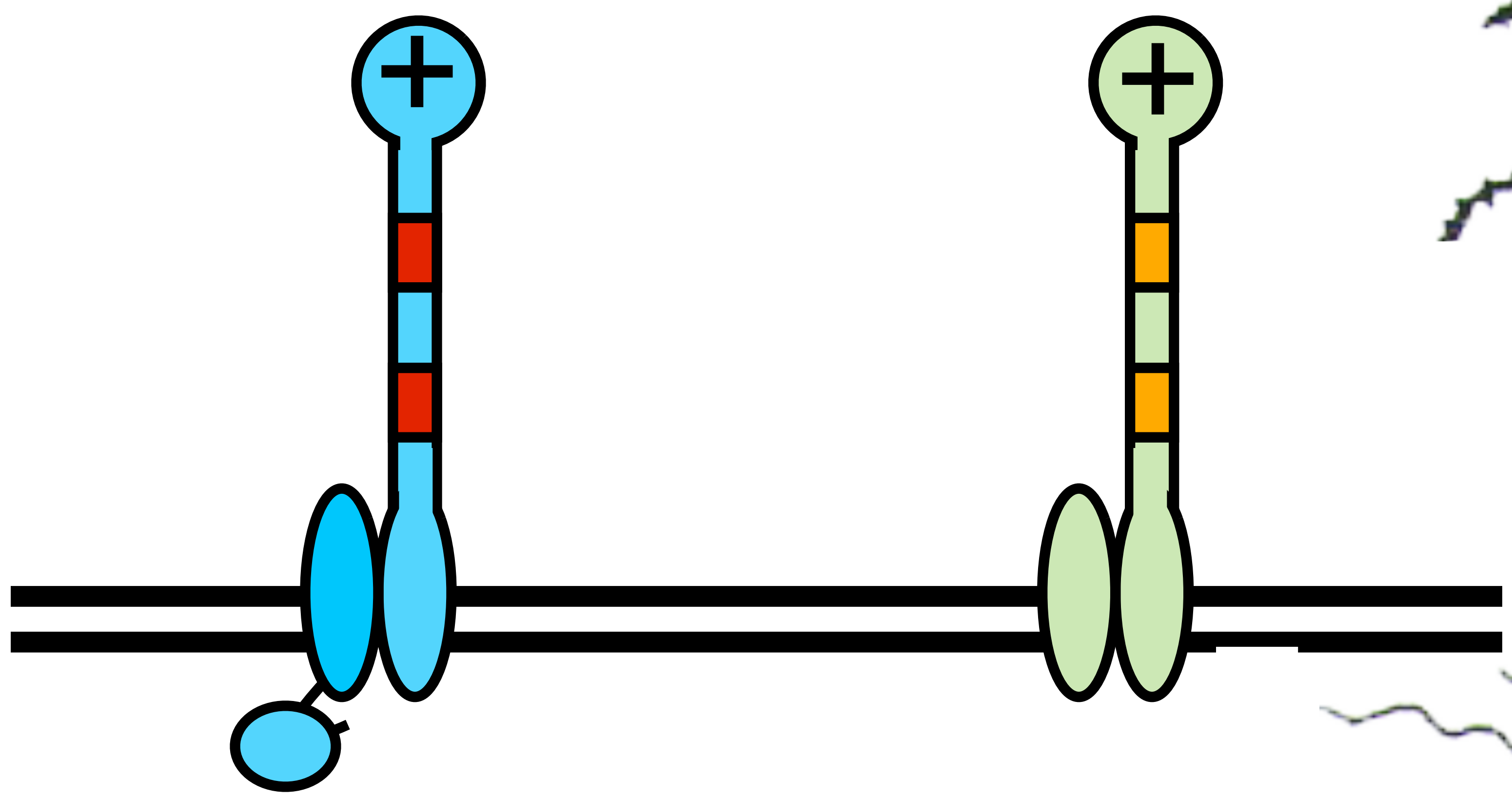
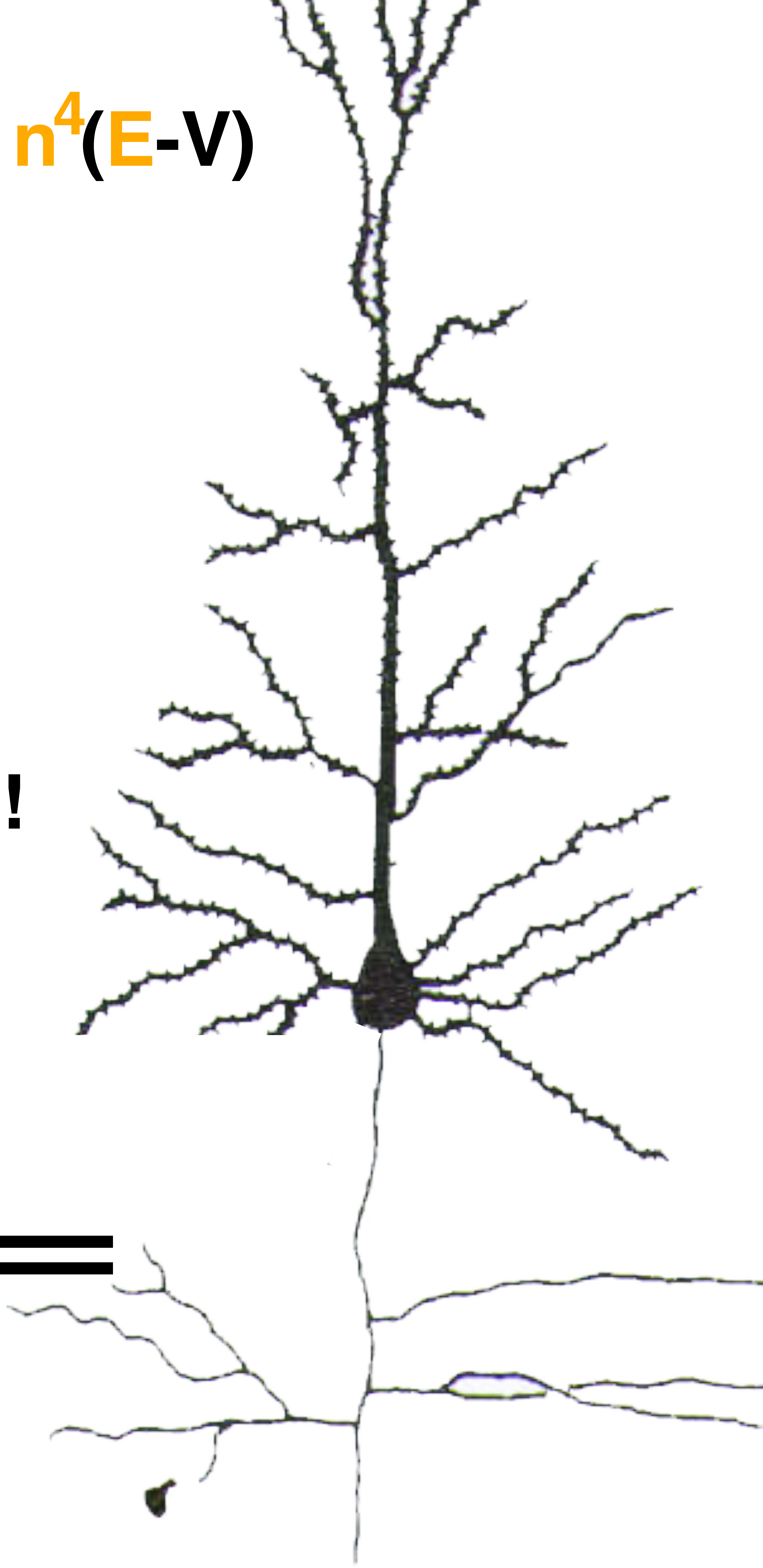




A complete description of a neuron!







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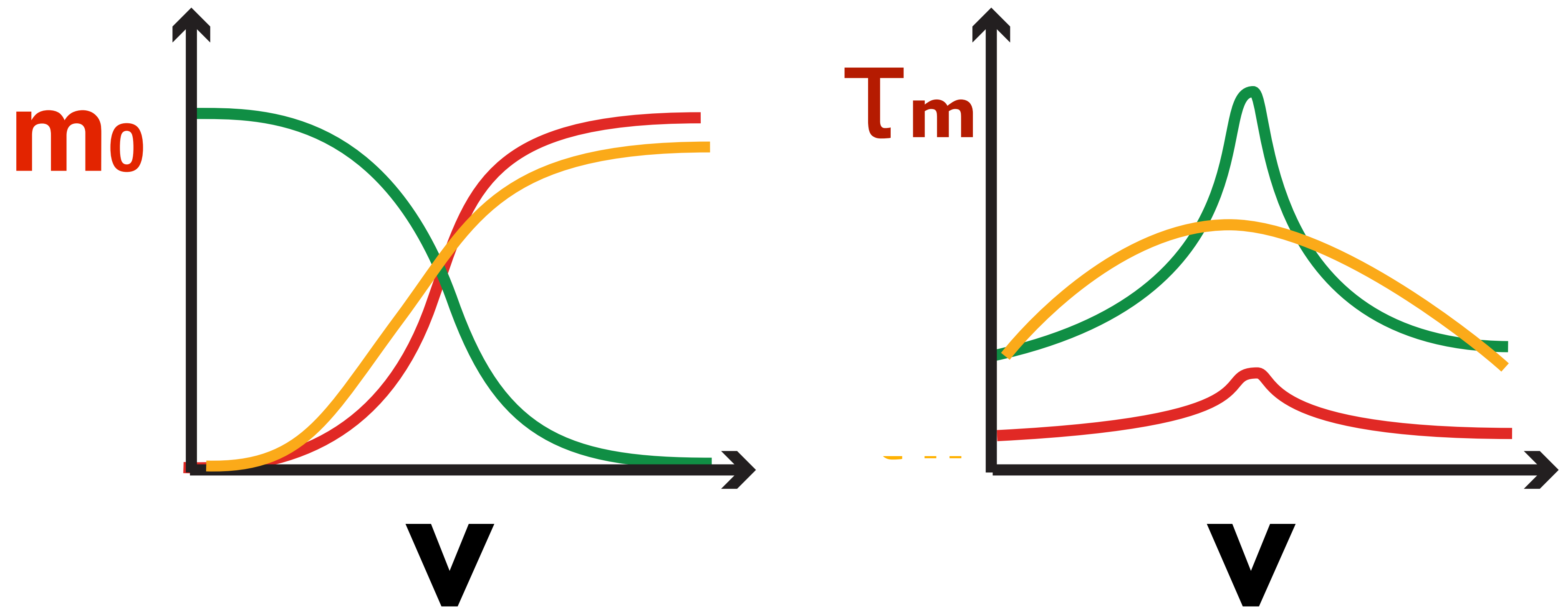

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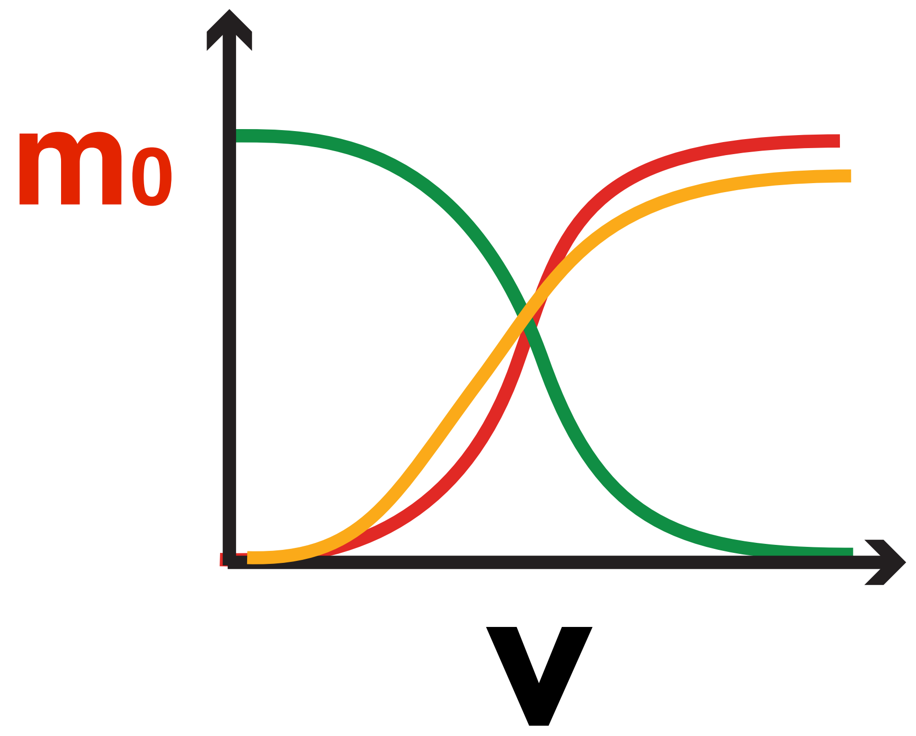

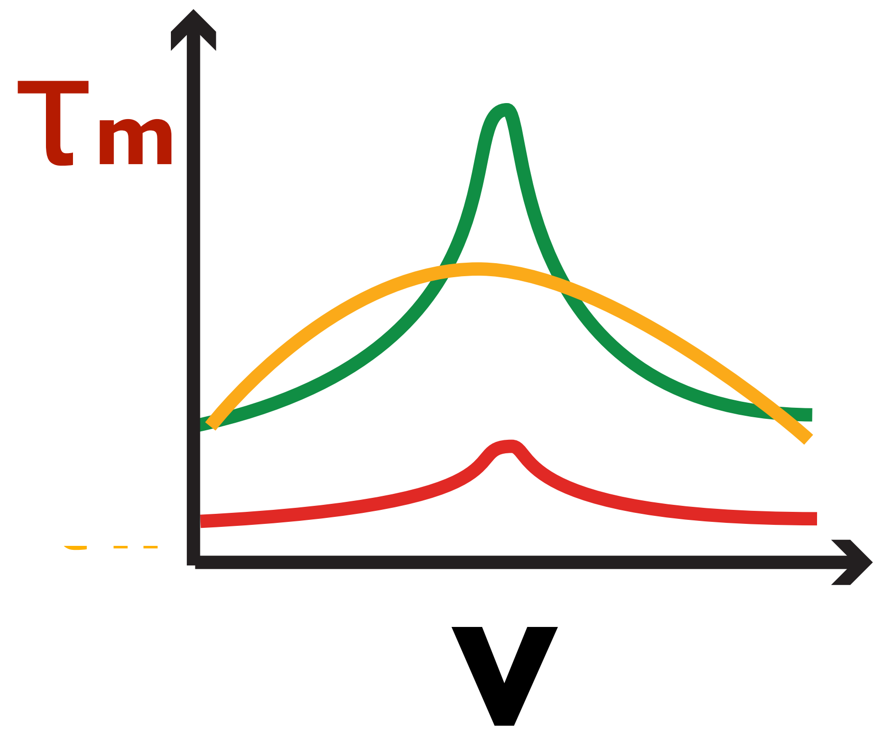

A complete description of neuron!

Action potentials
Threshold behaviour
Refractory behaviour
Test our knowledge of what is going on…

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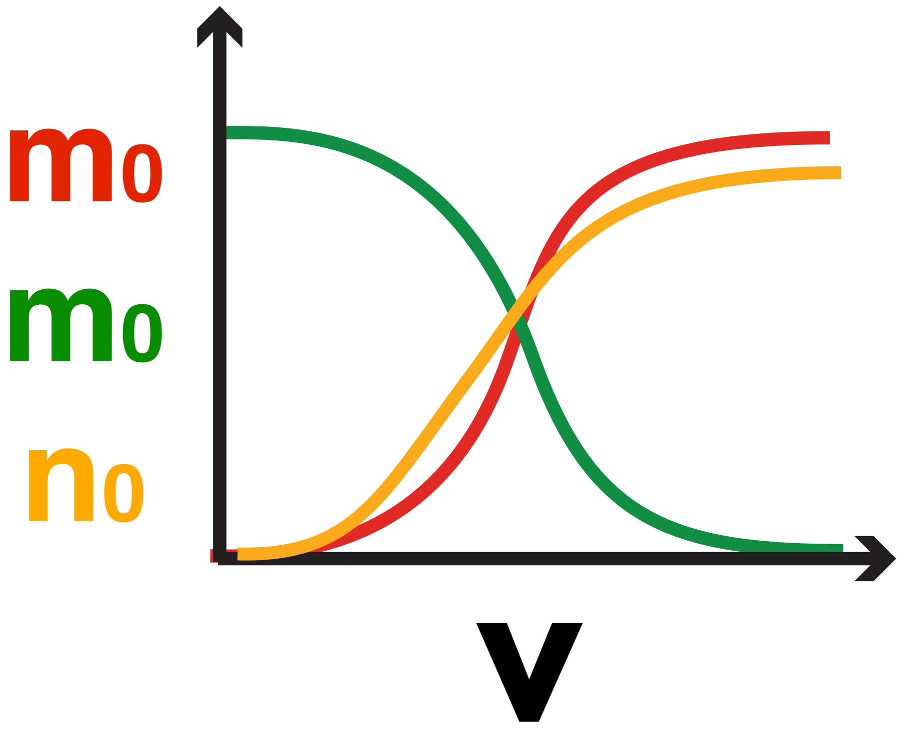

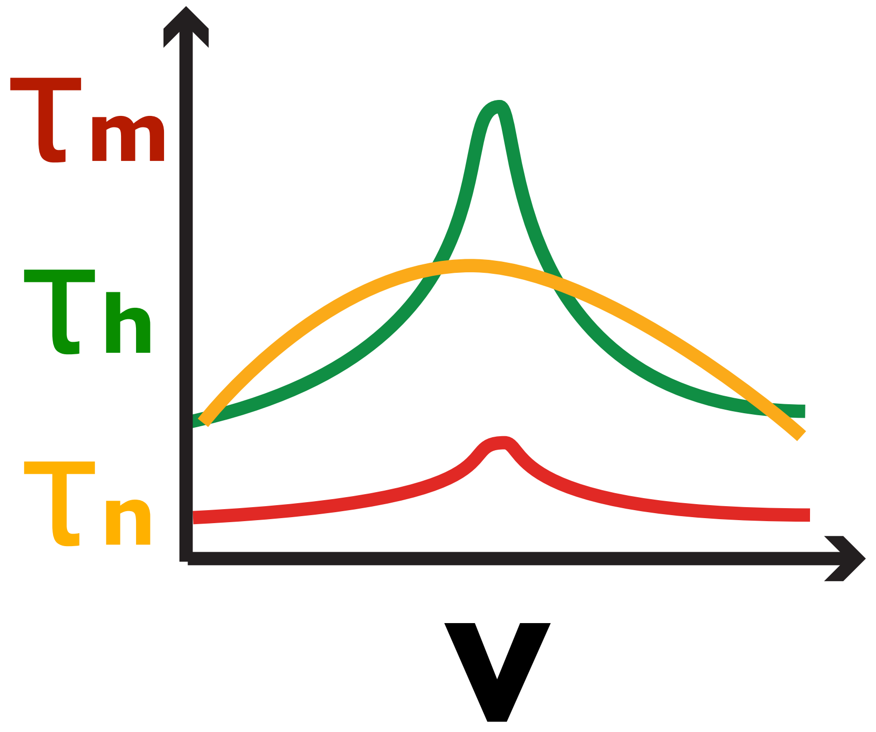

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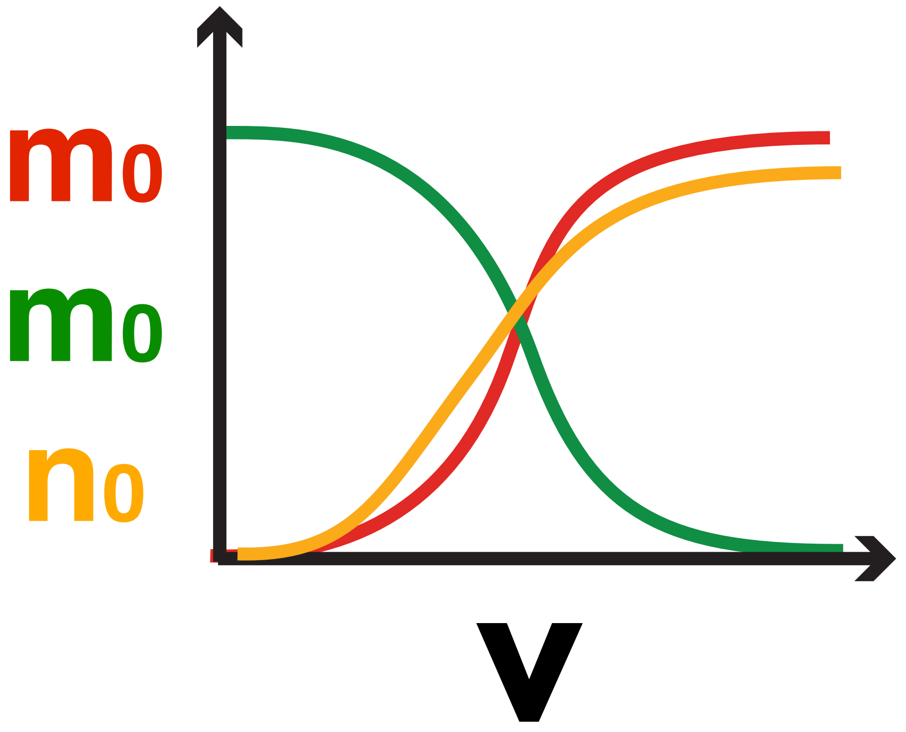

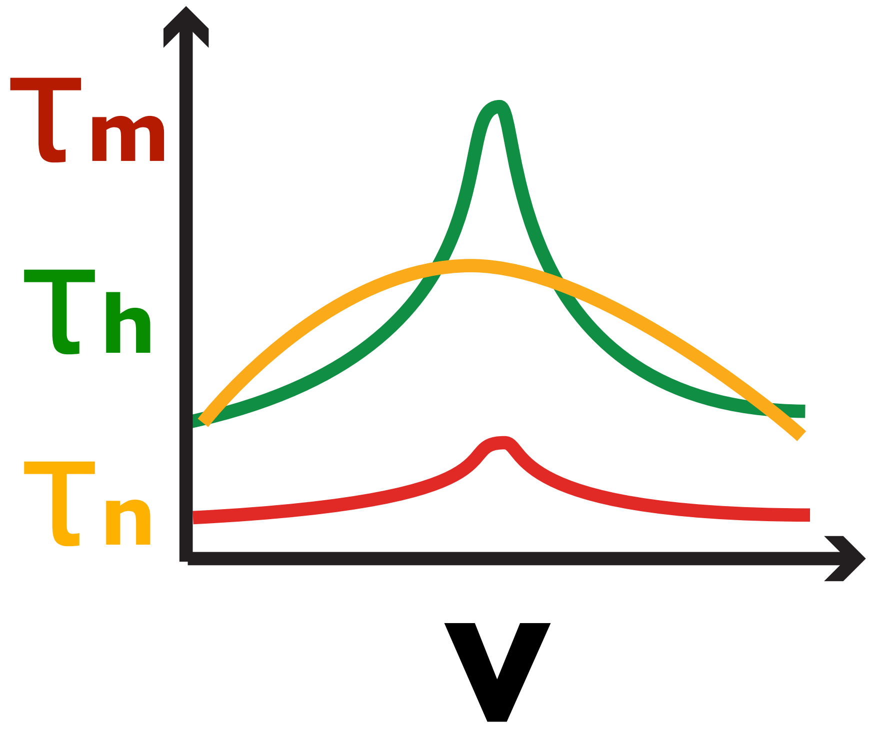

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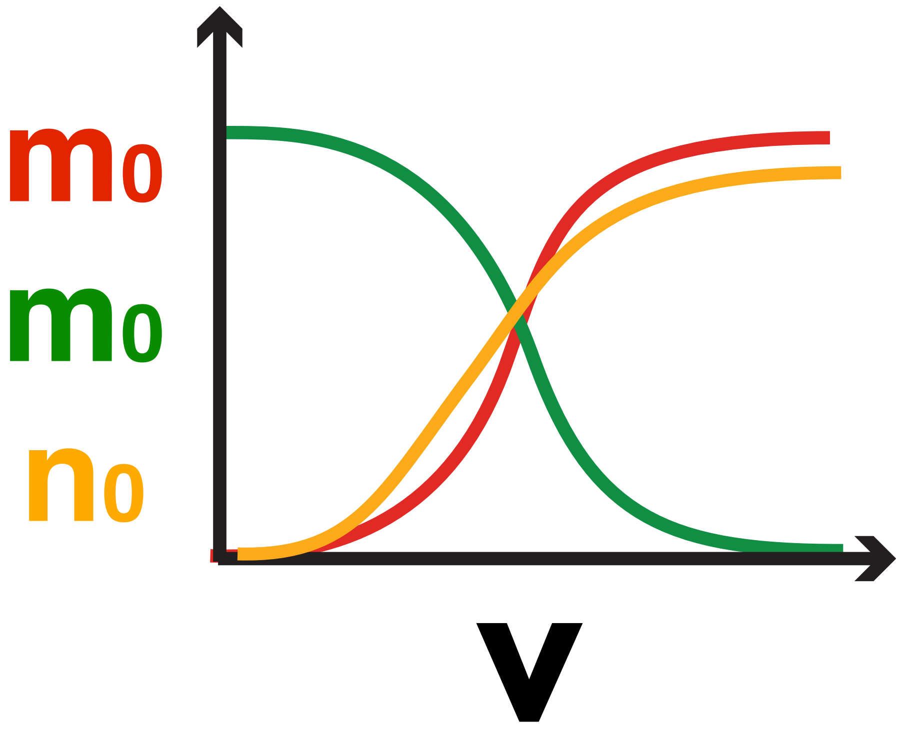

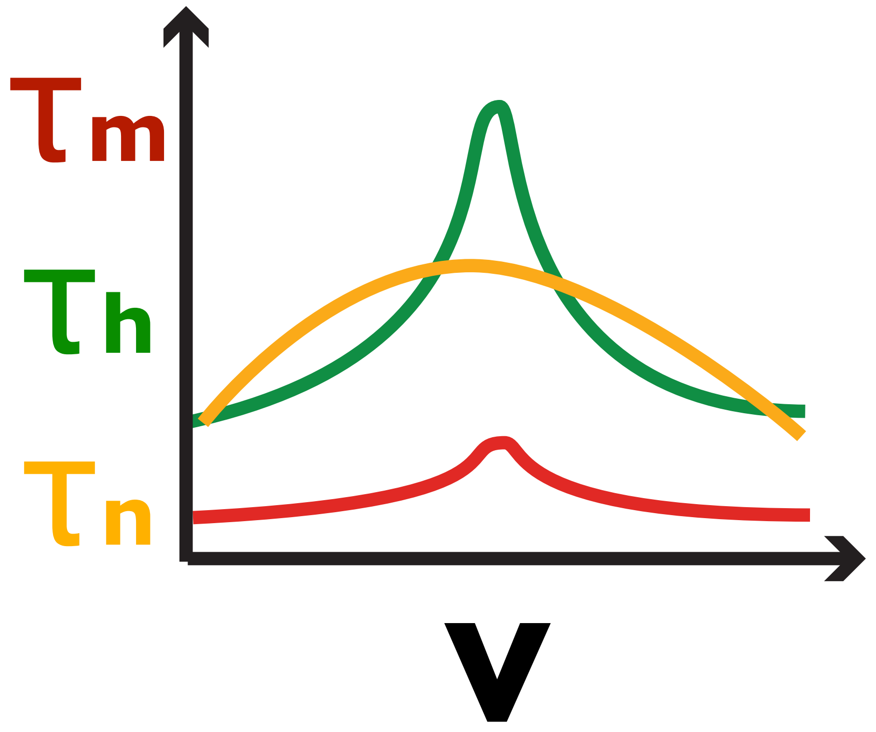

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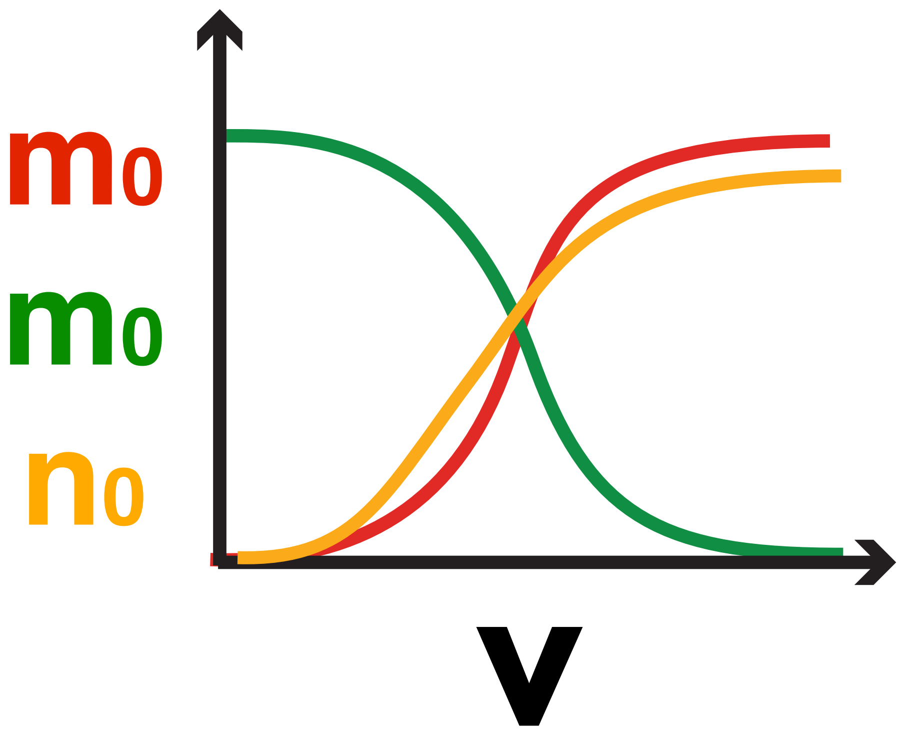

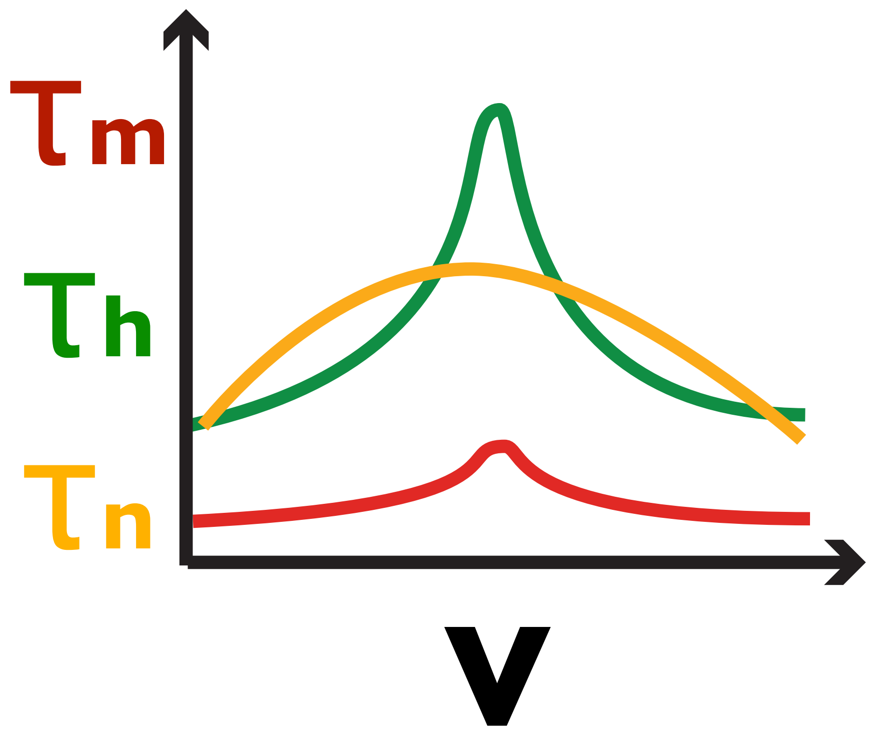

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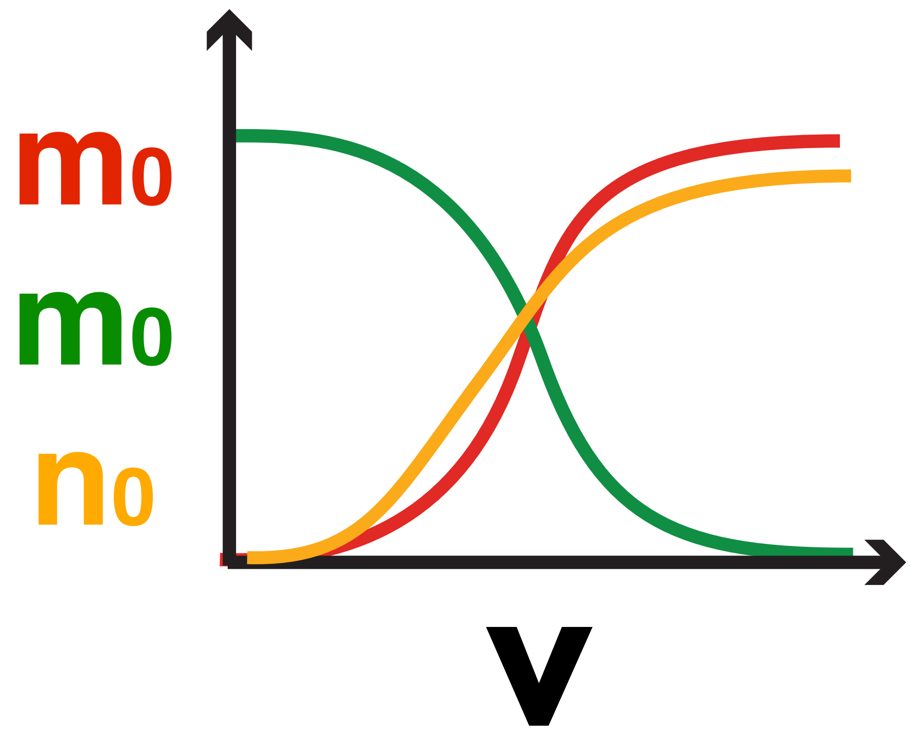

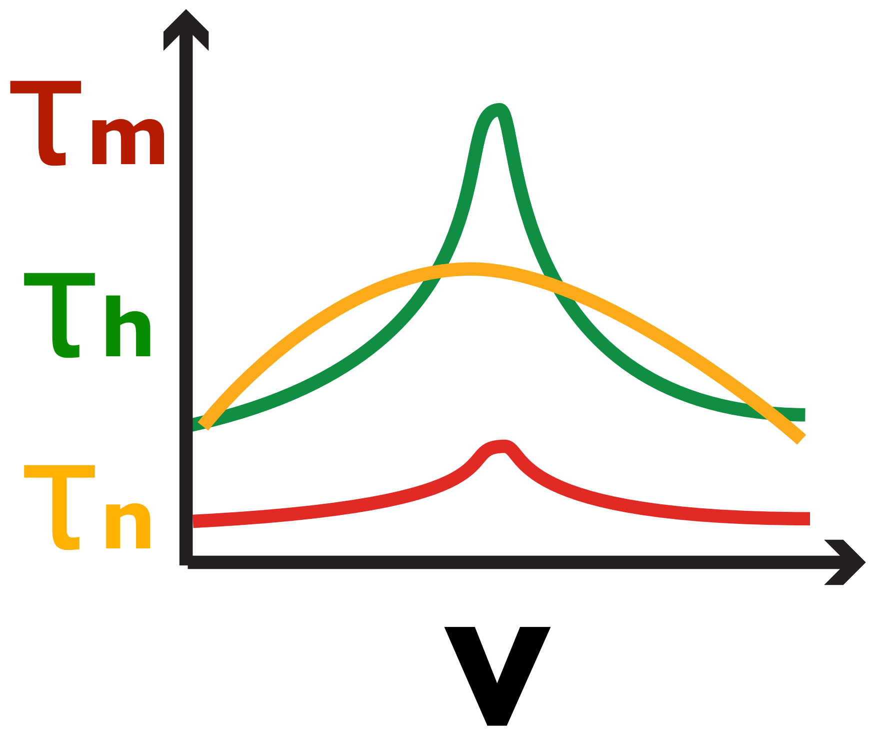

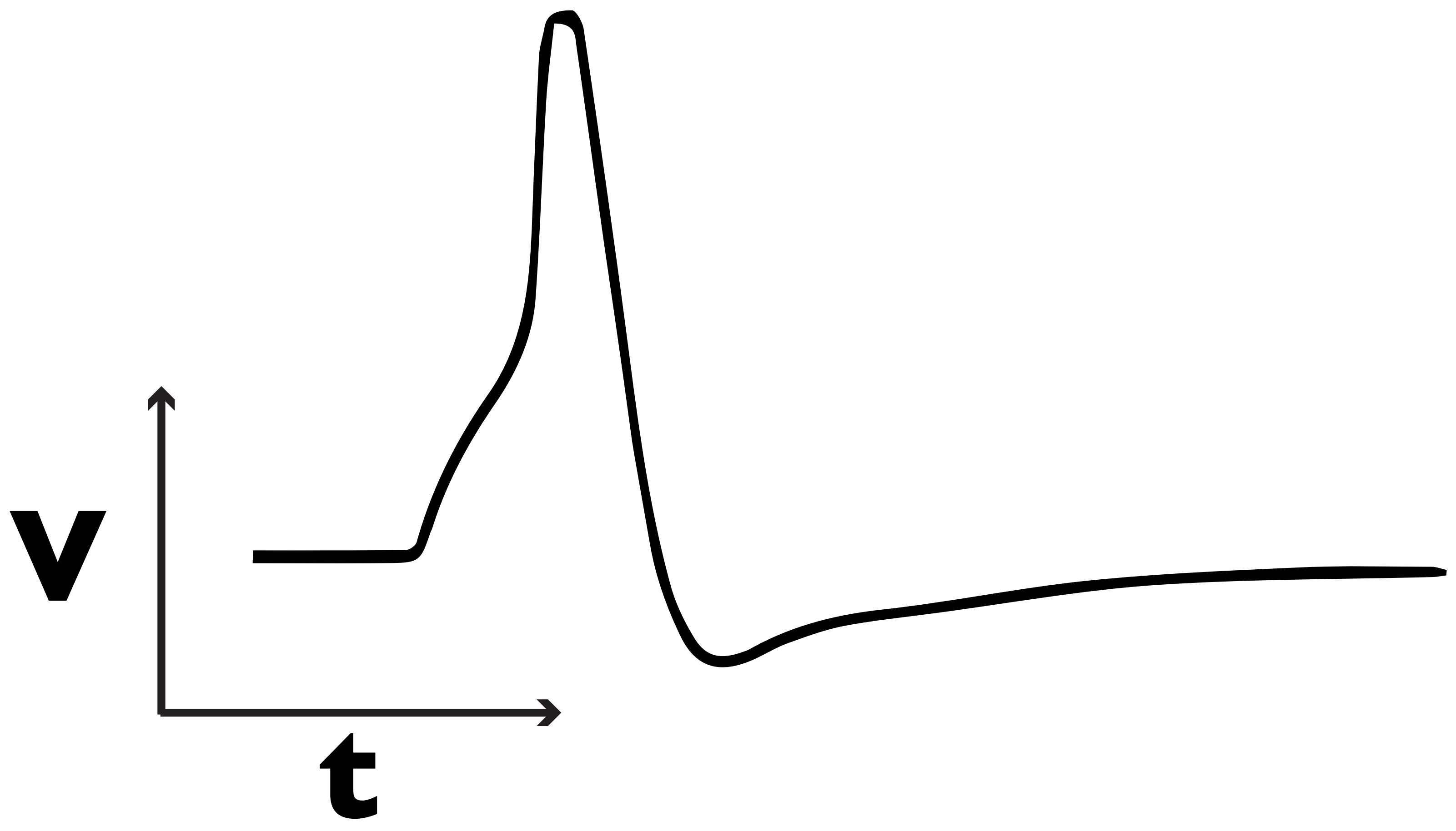

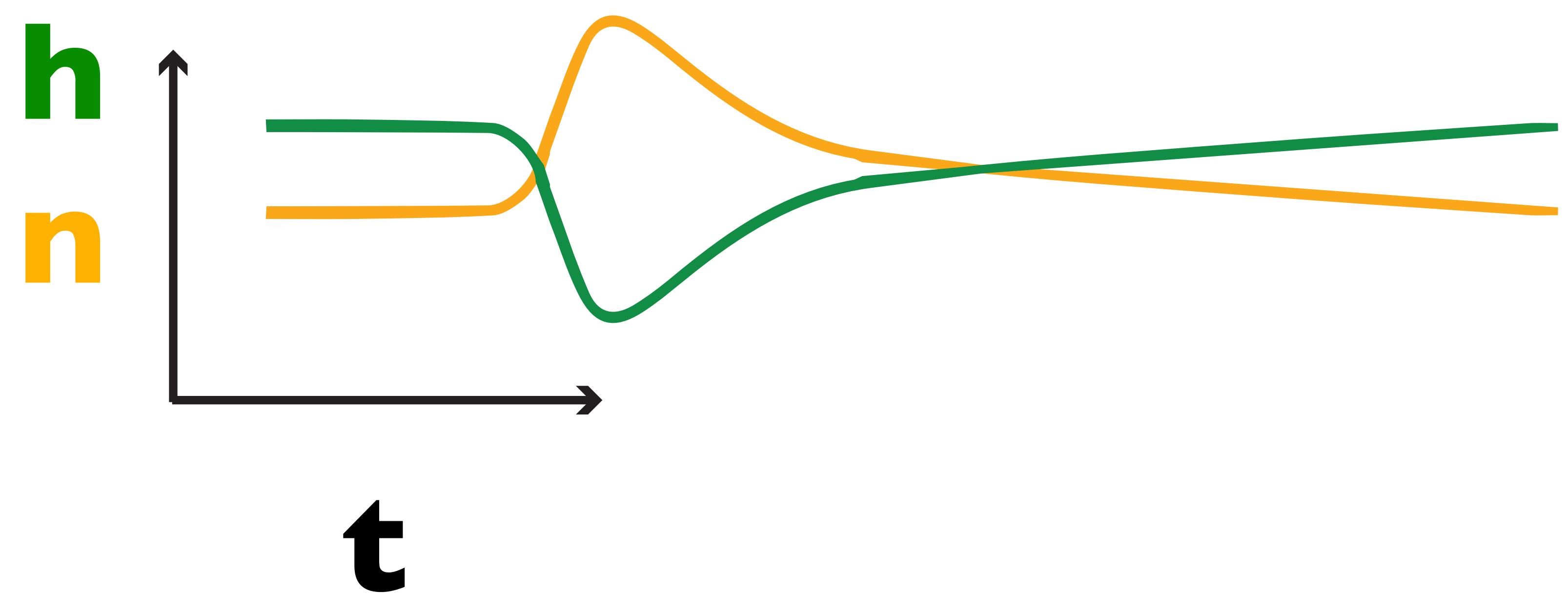

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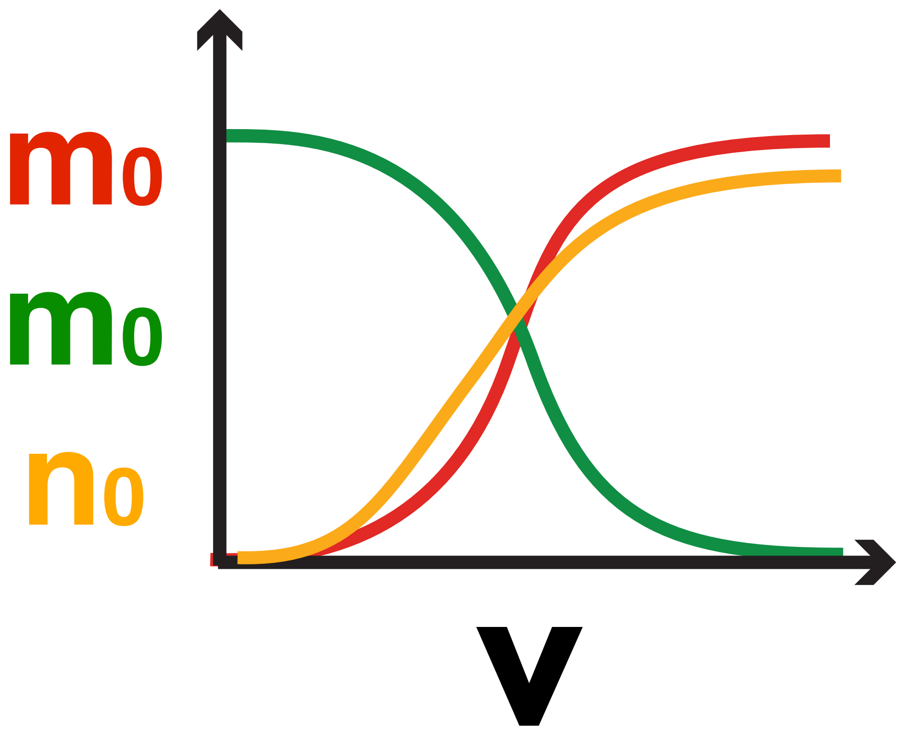

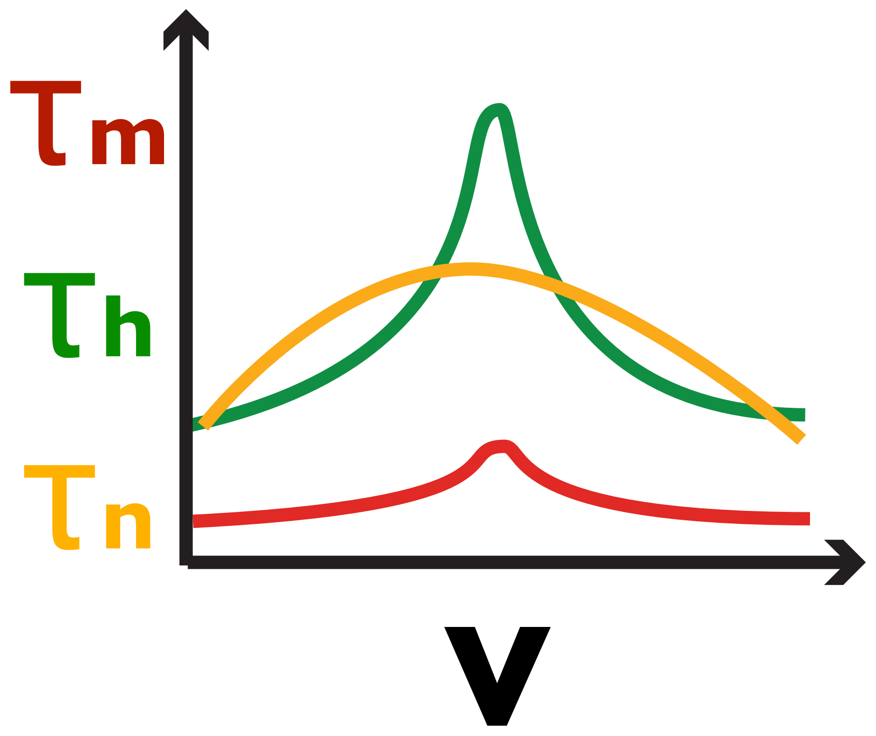

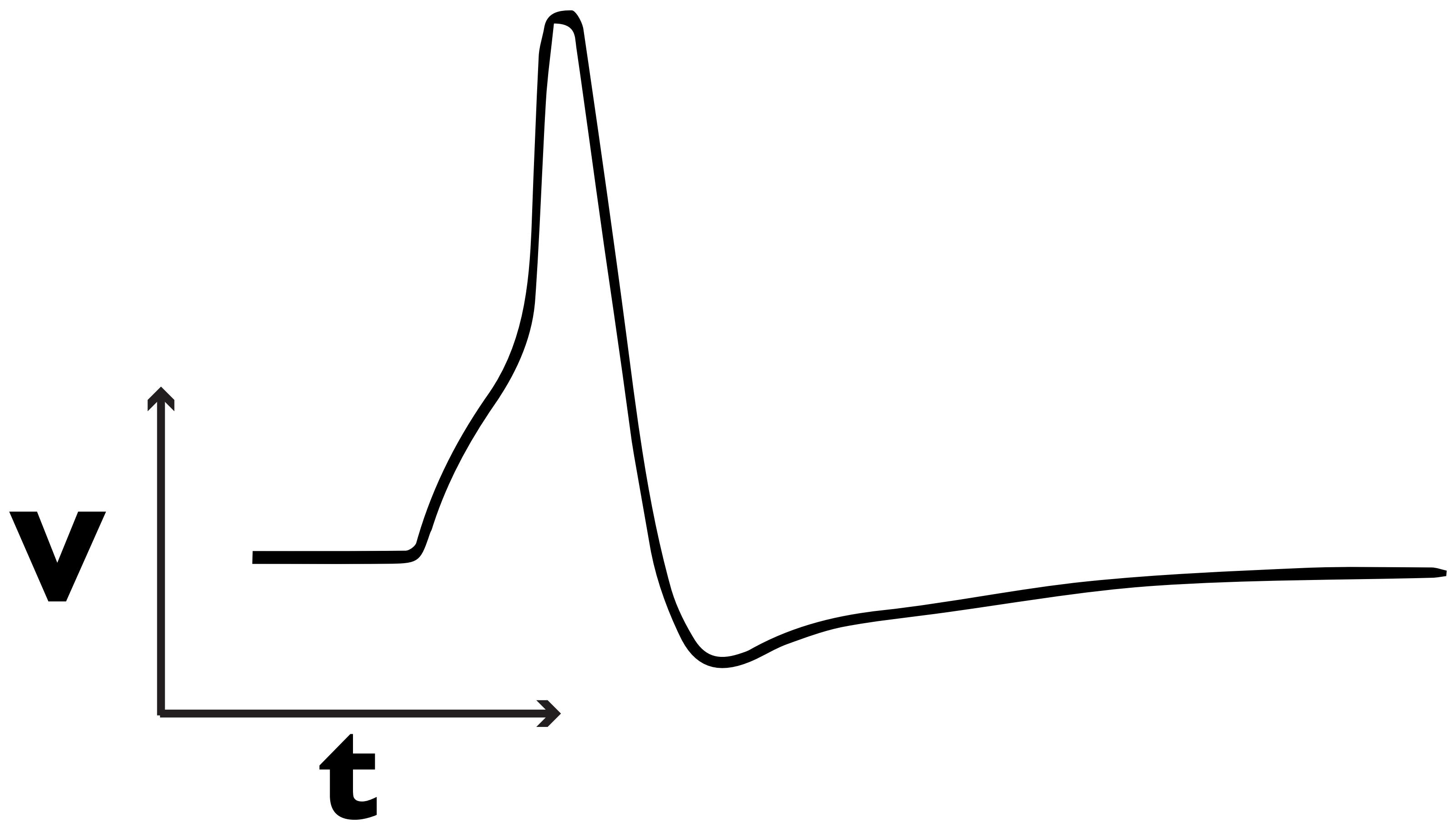

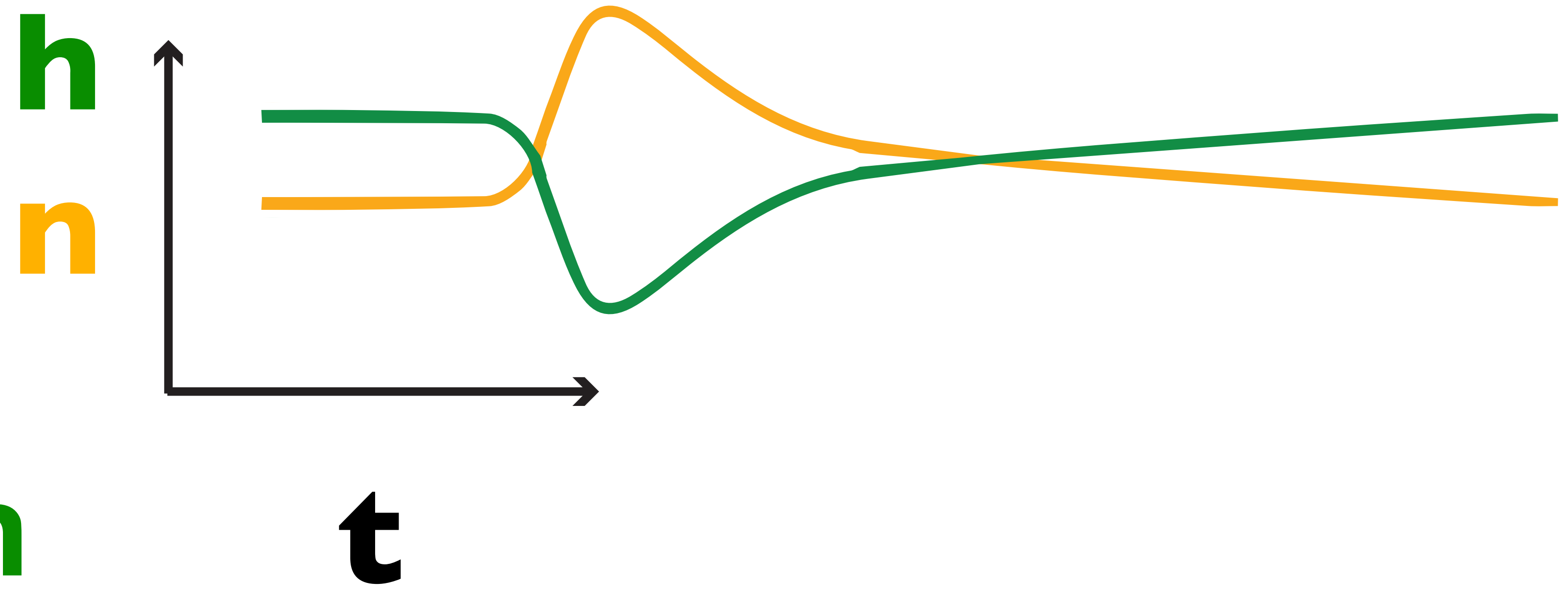

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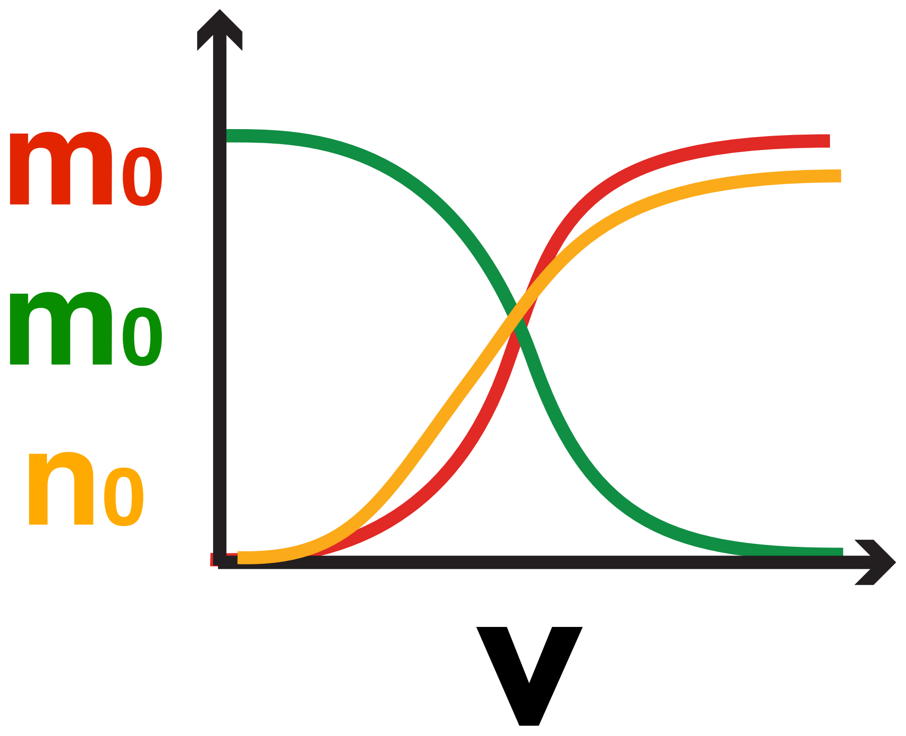

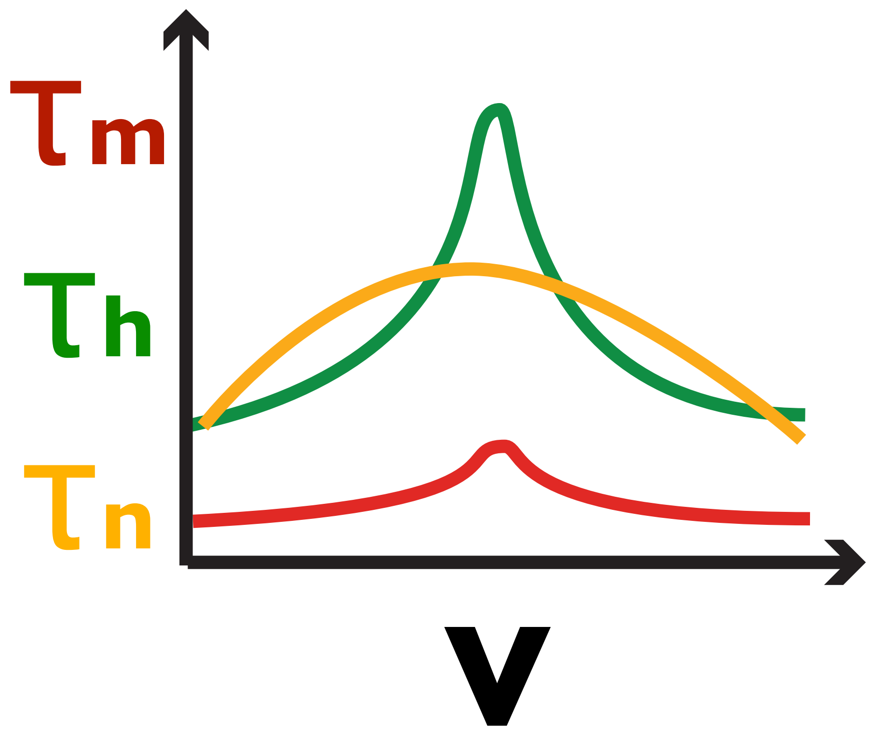

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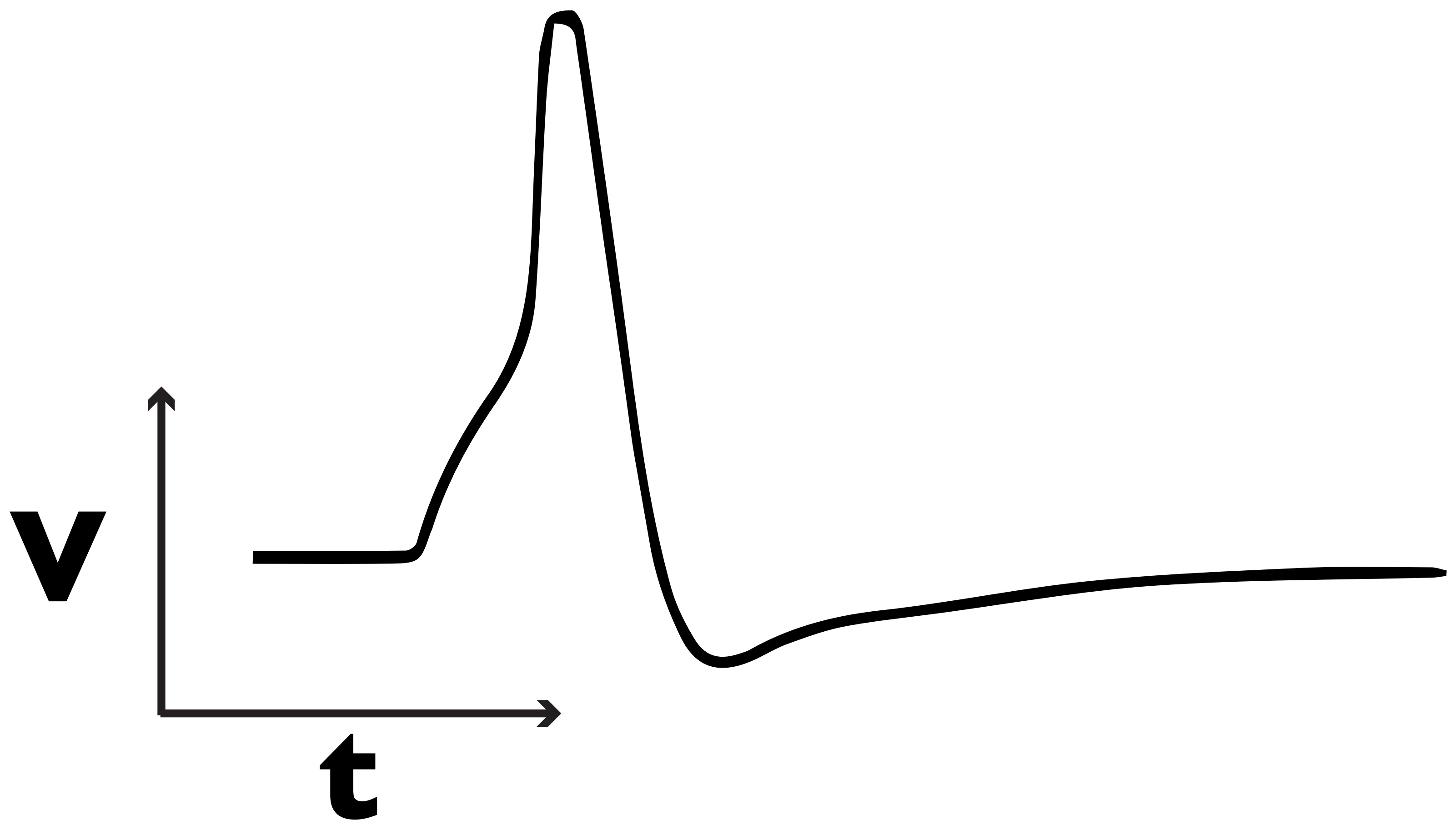

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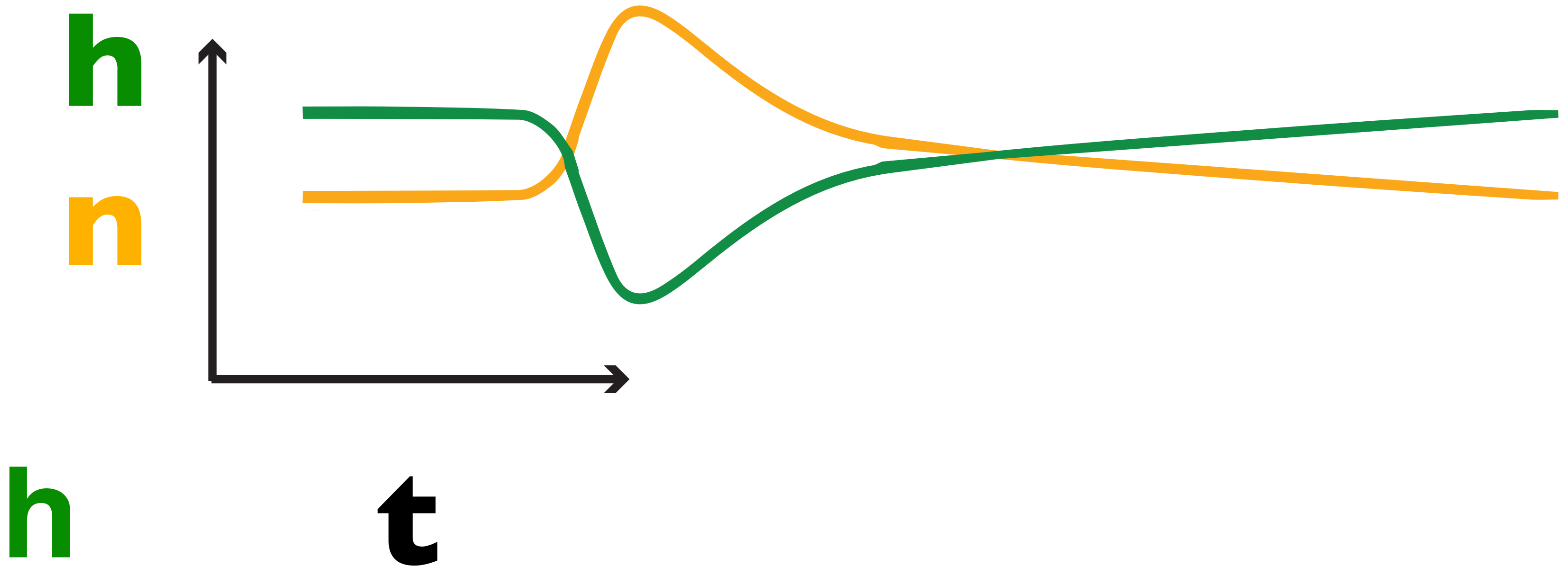

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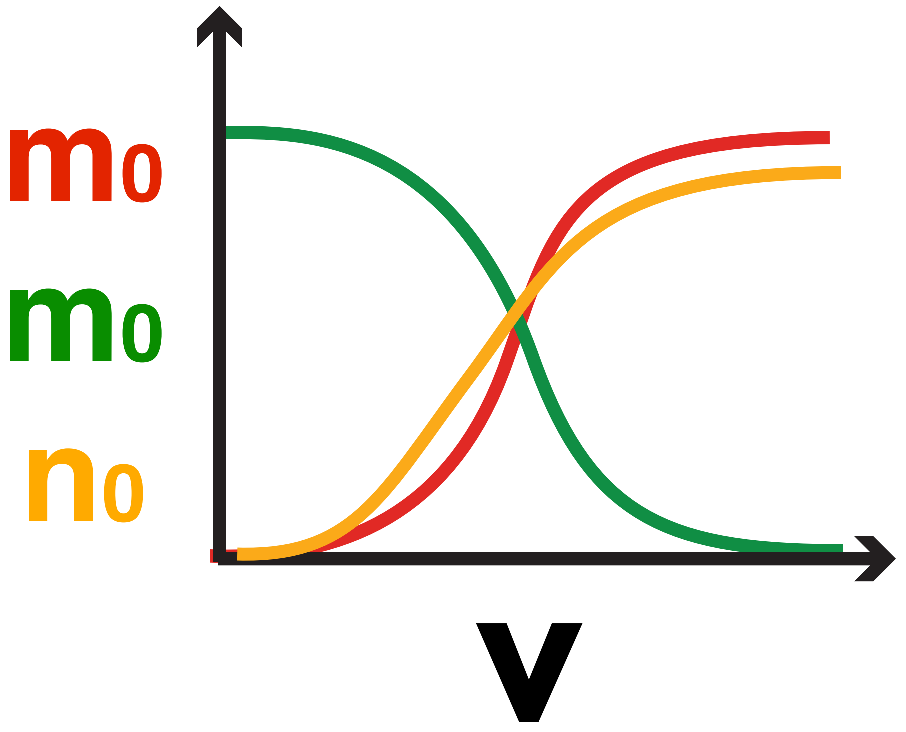

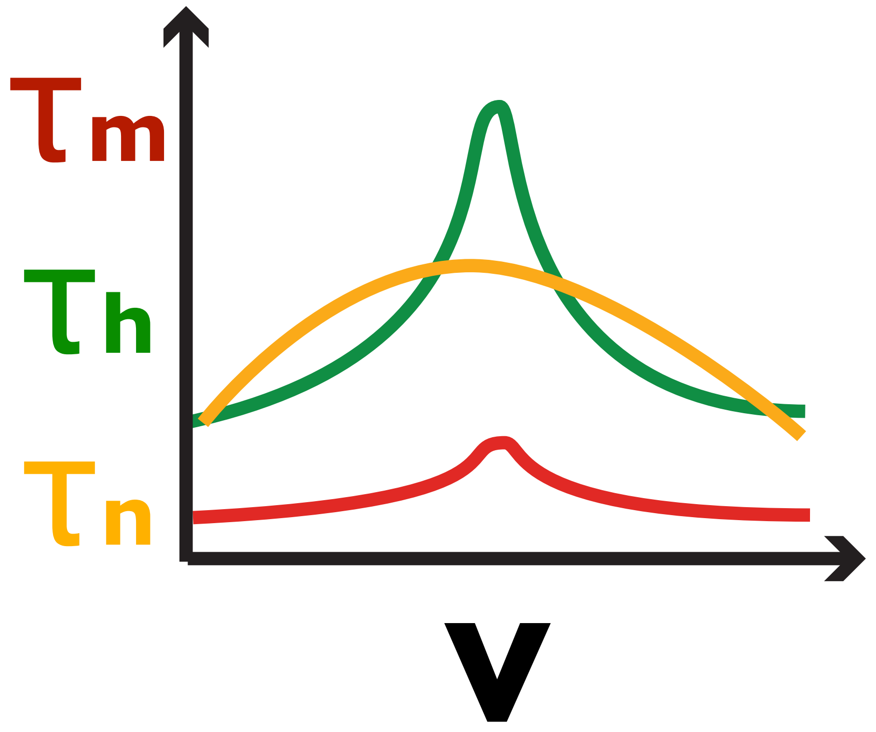

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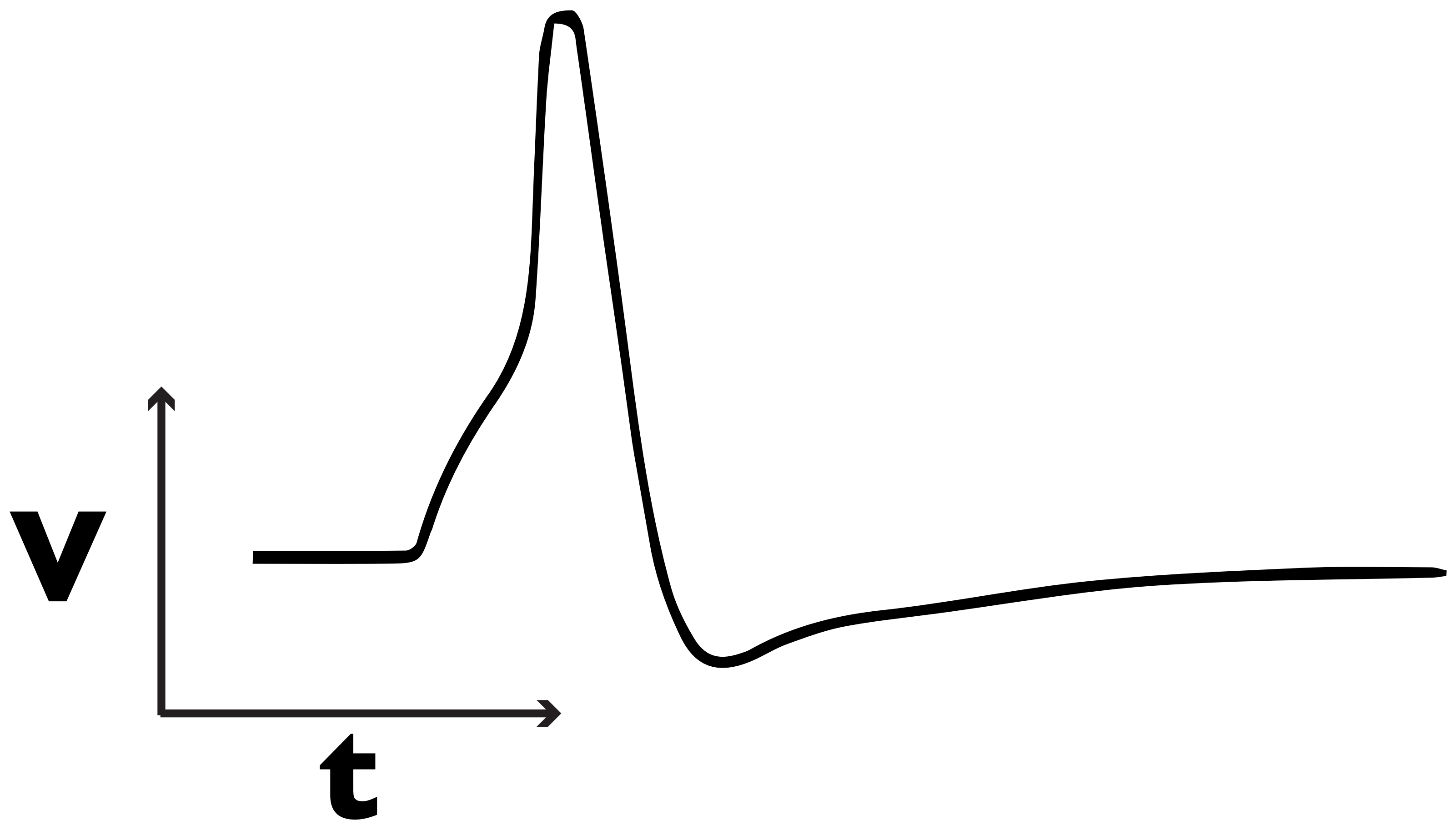

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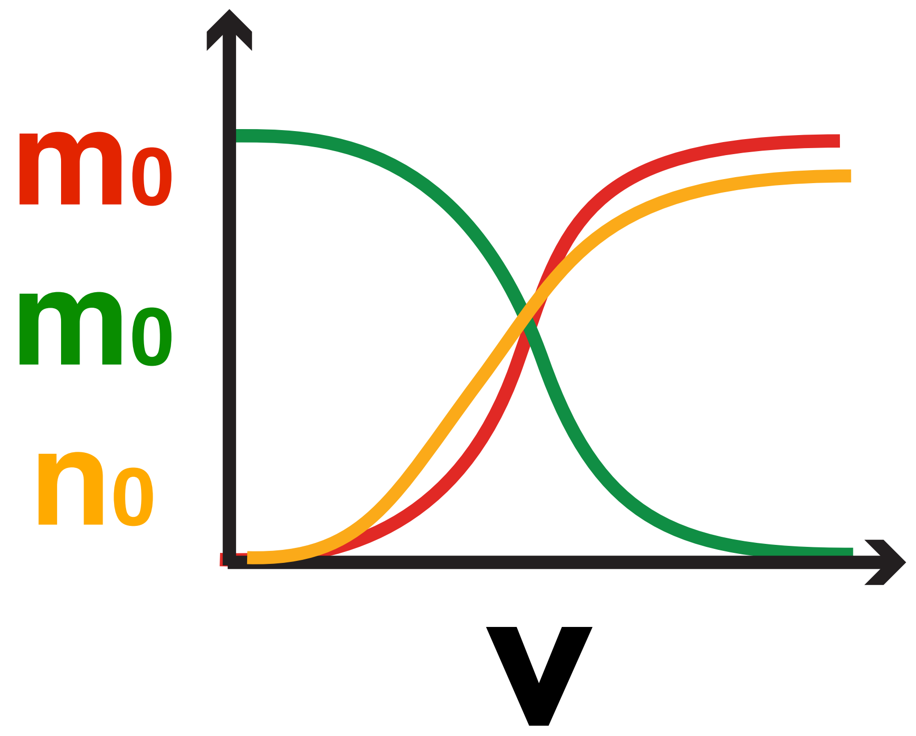

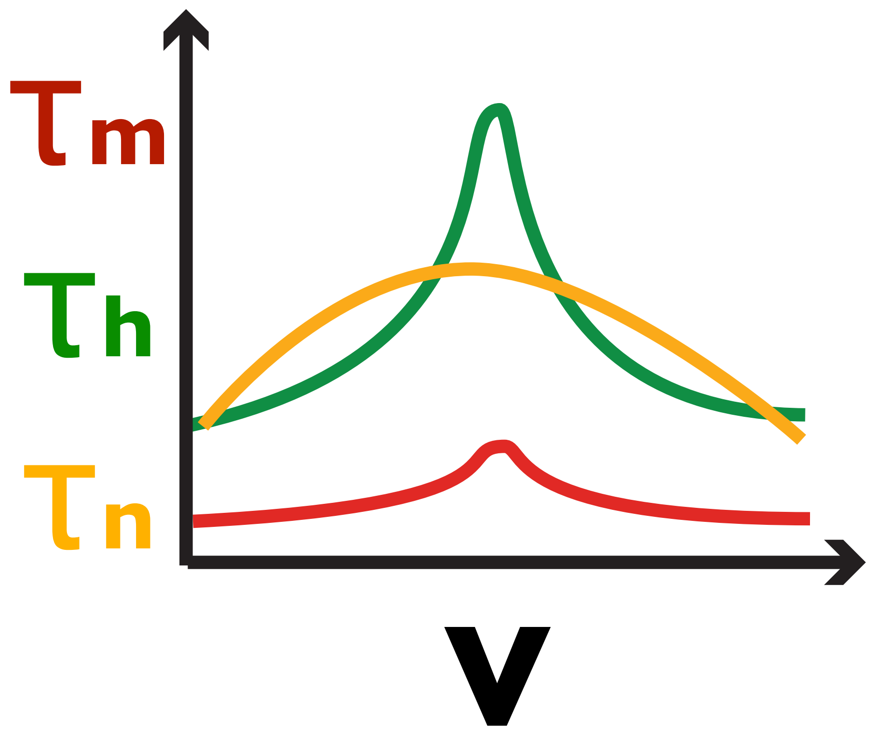

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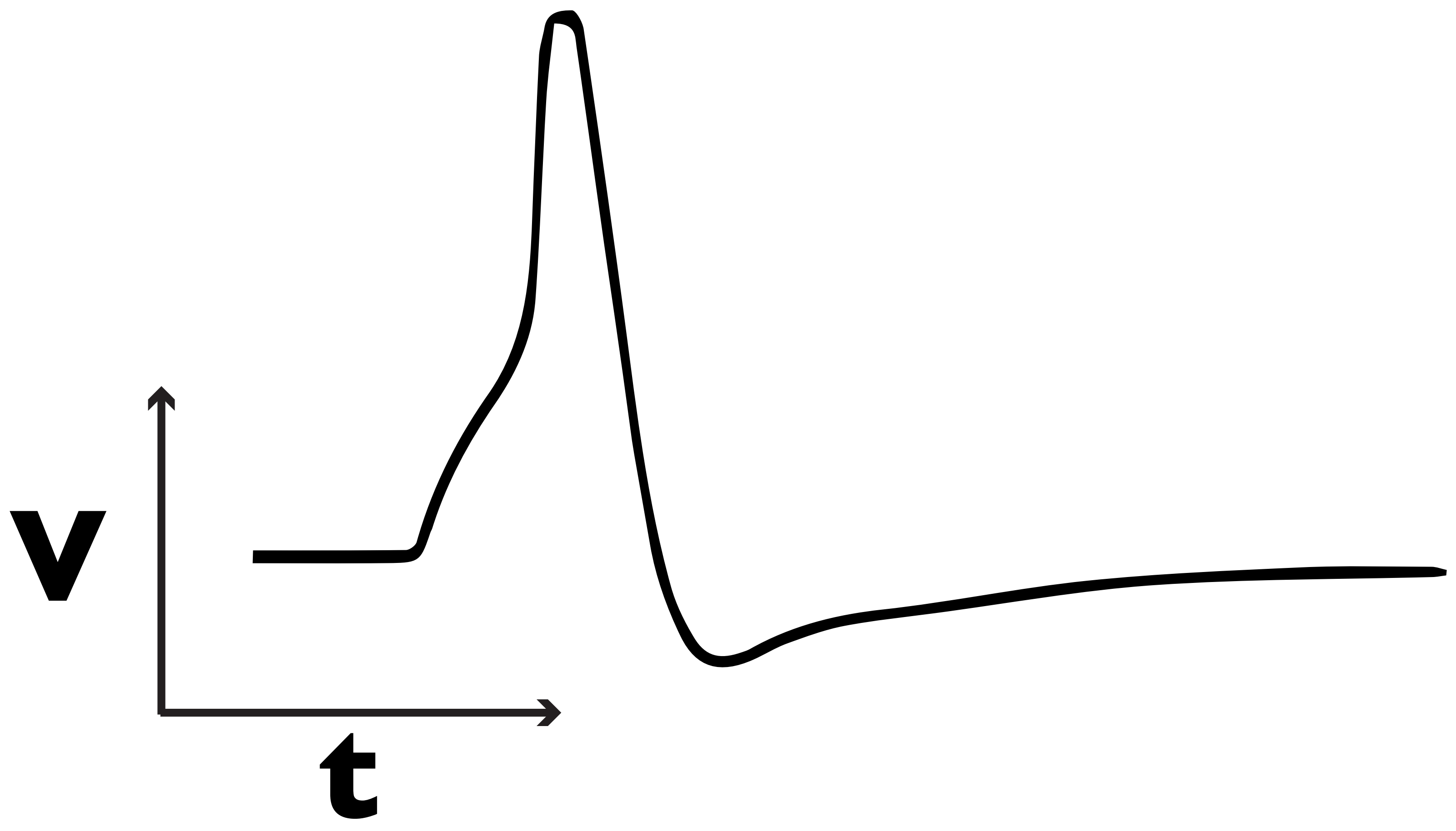

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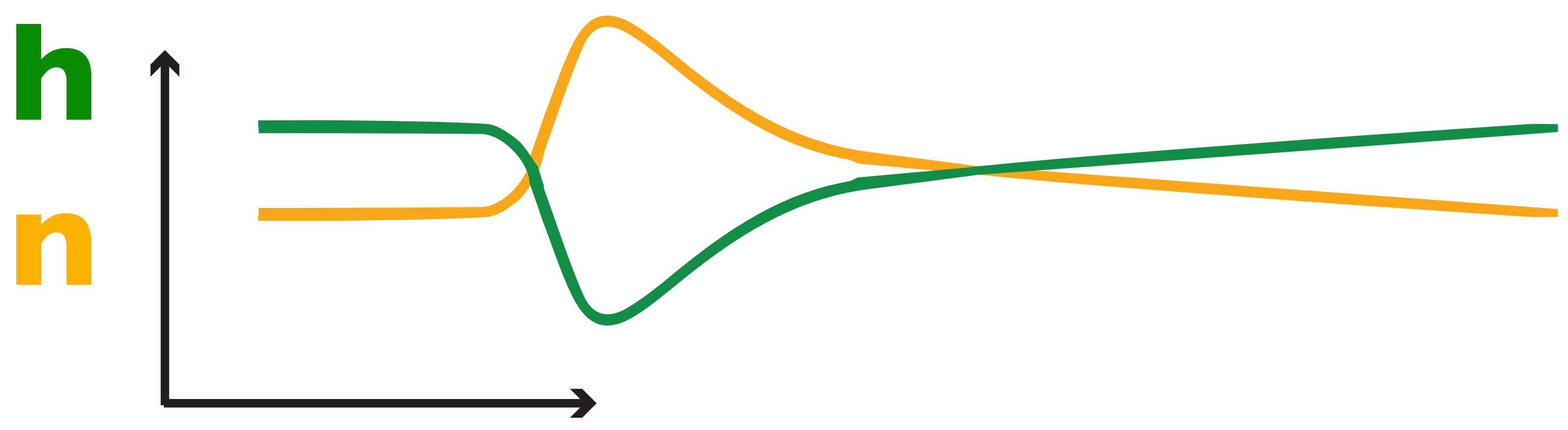

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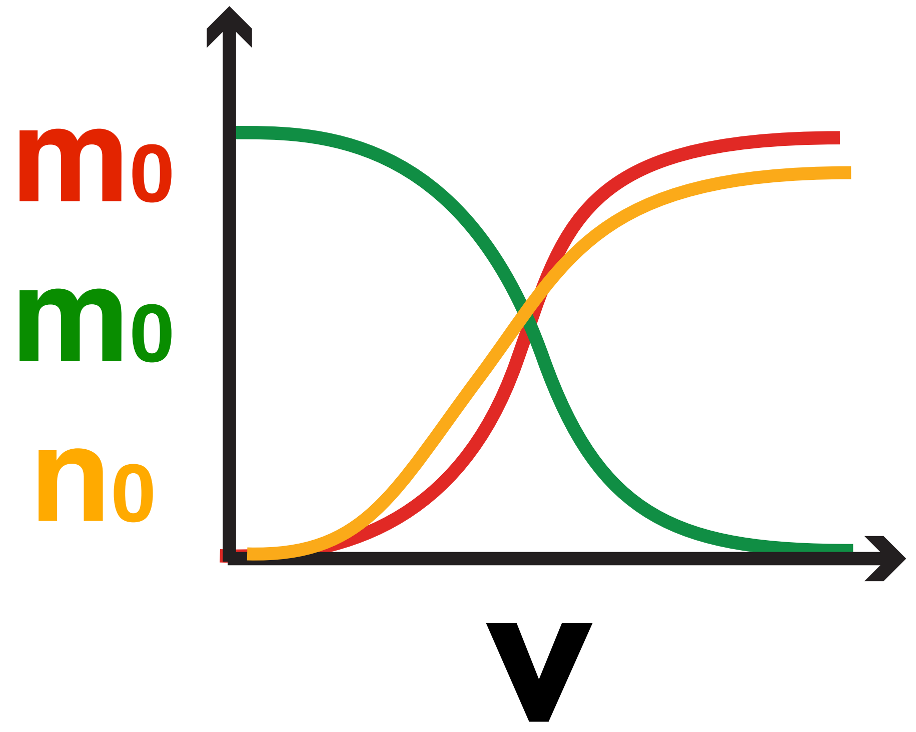

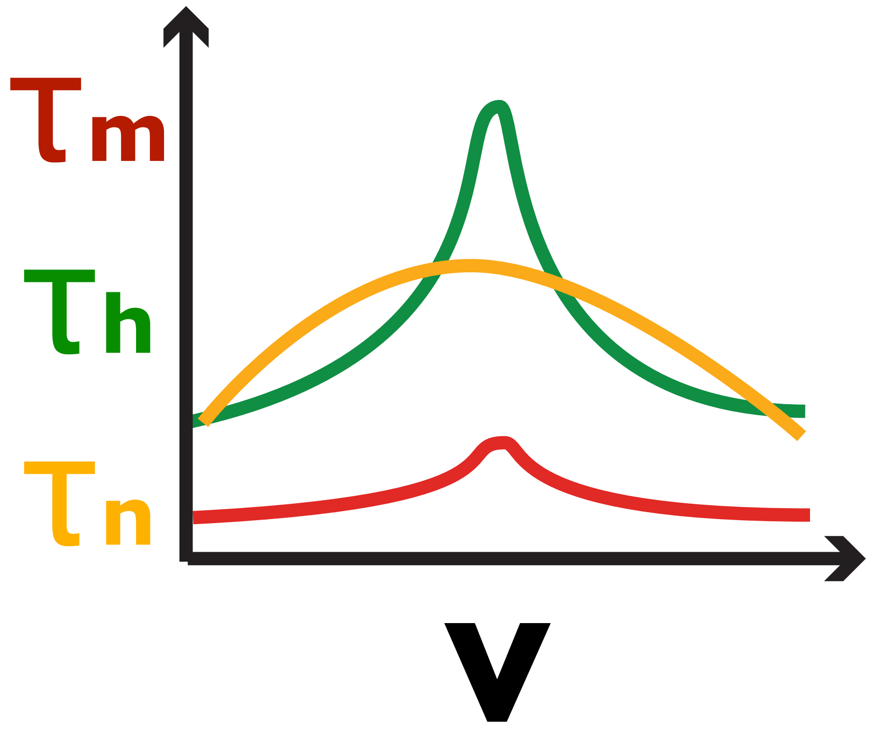

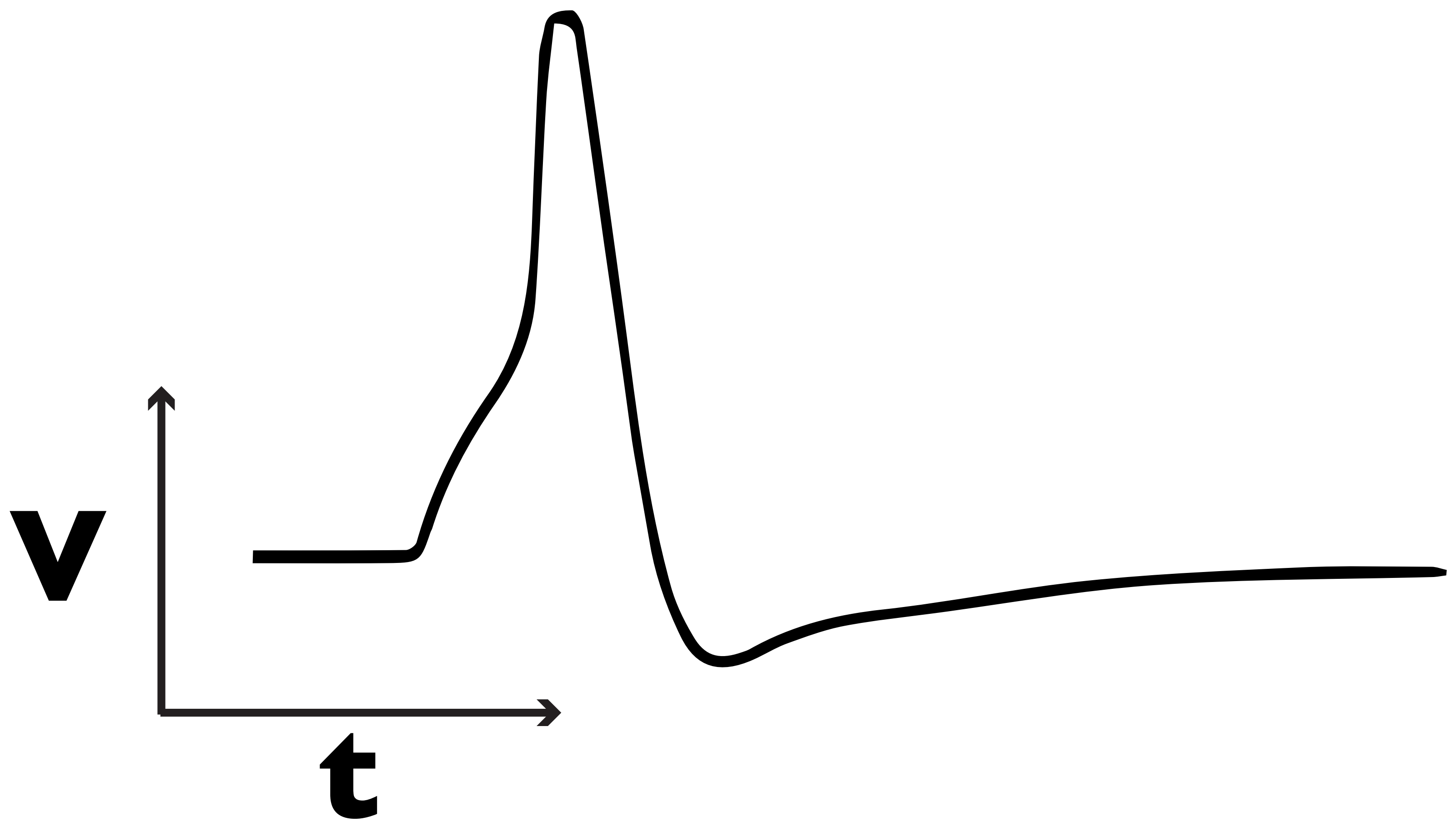

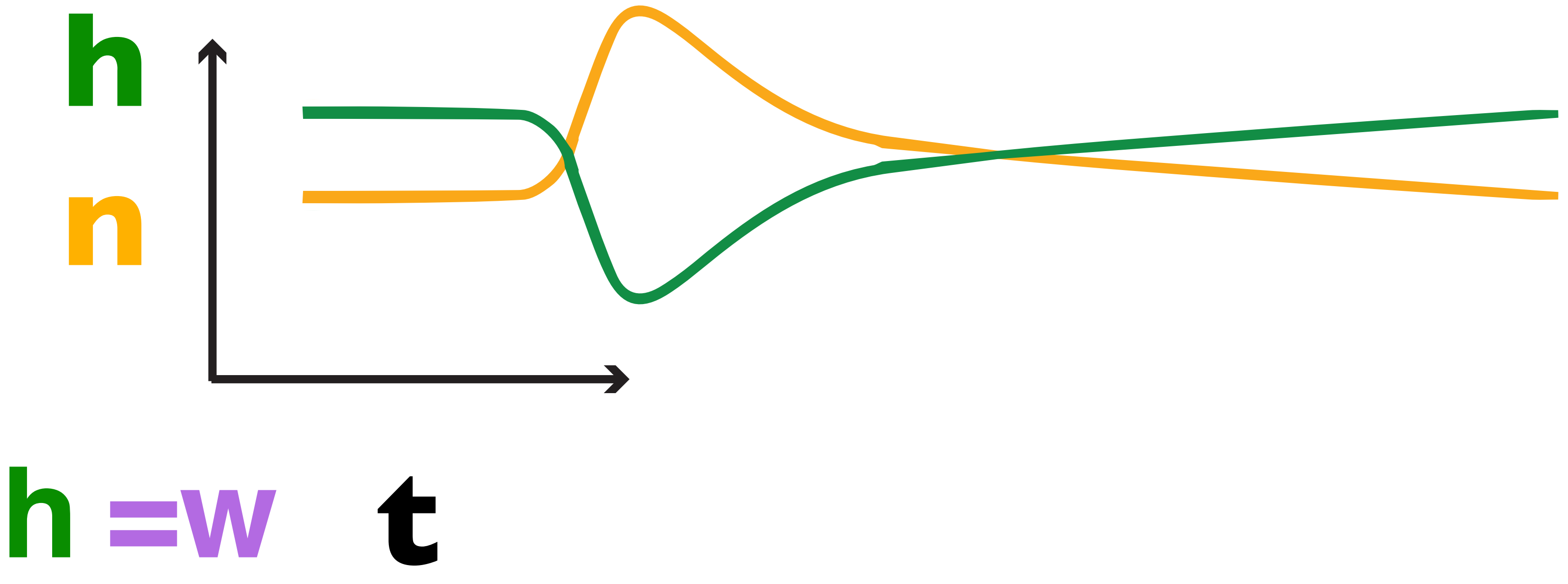

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FitzHugh-Nagumo model

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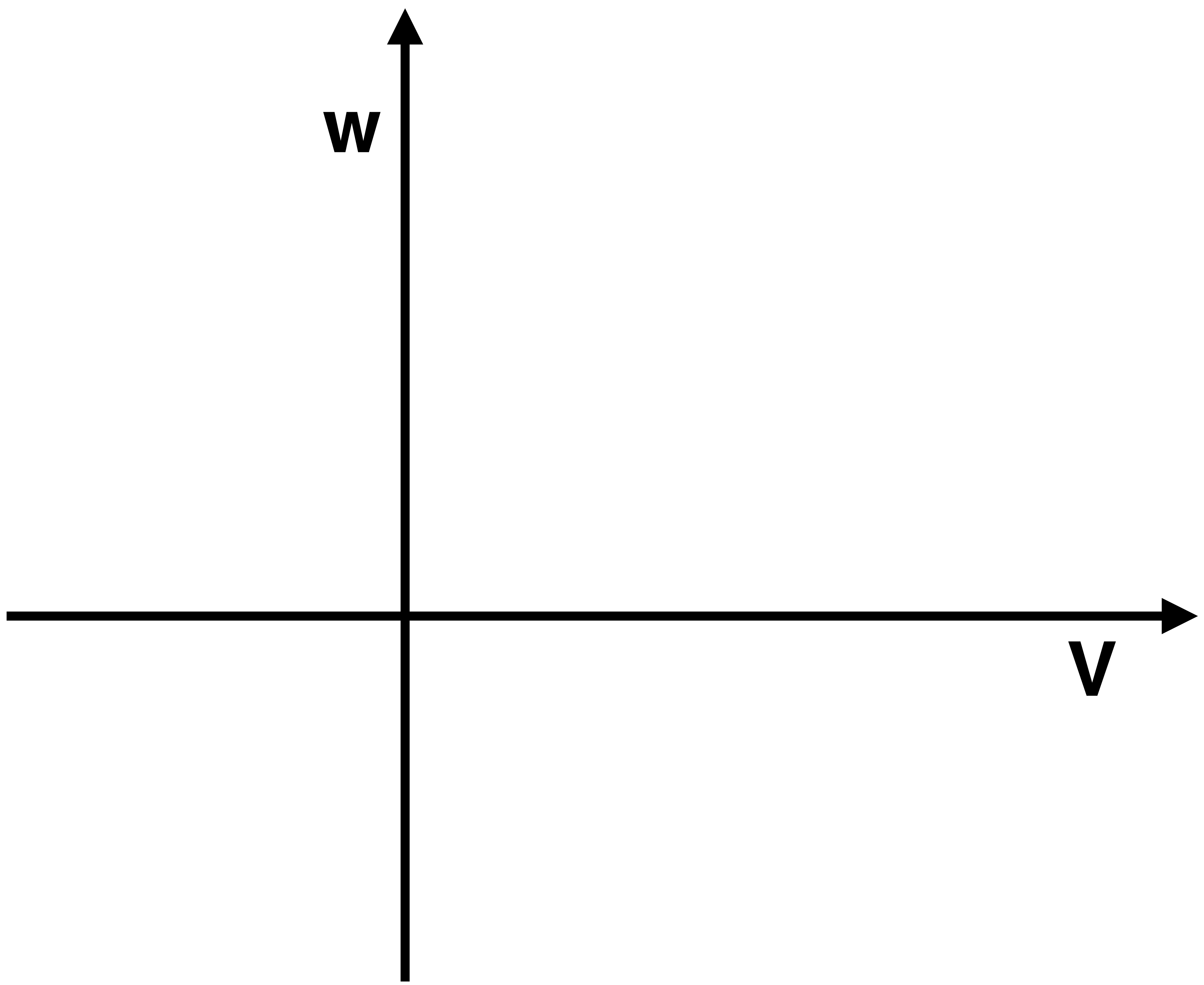

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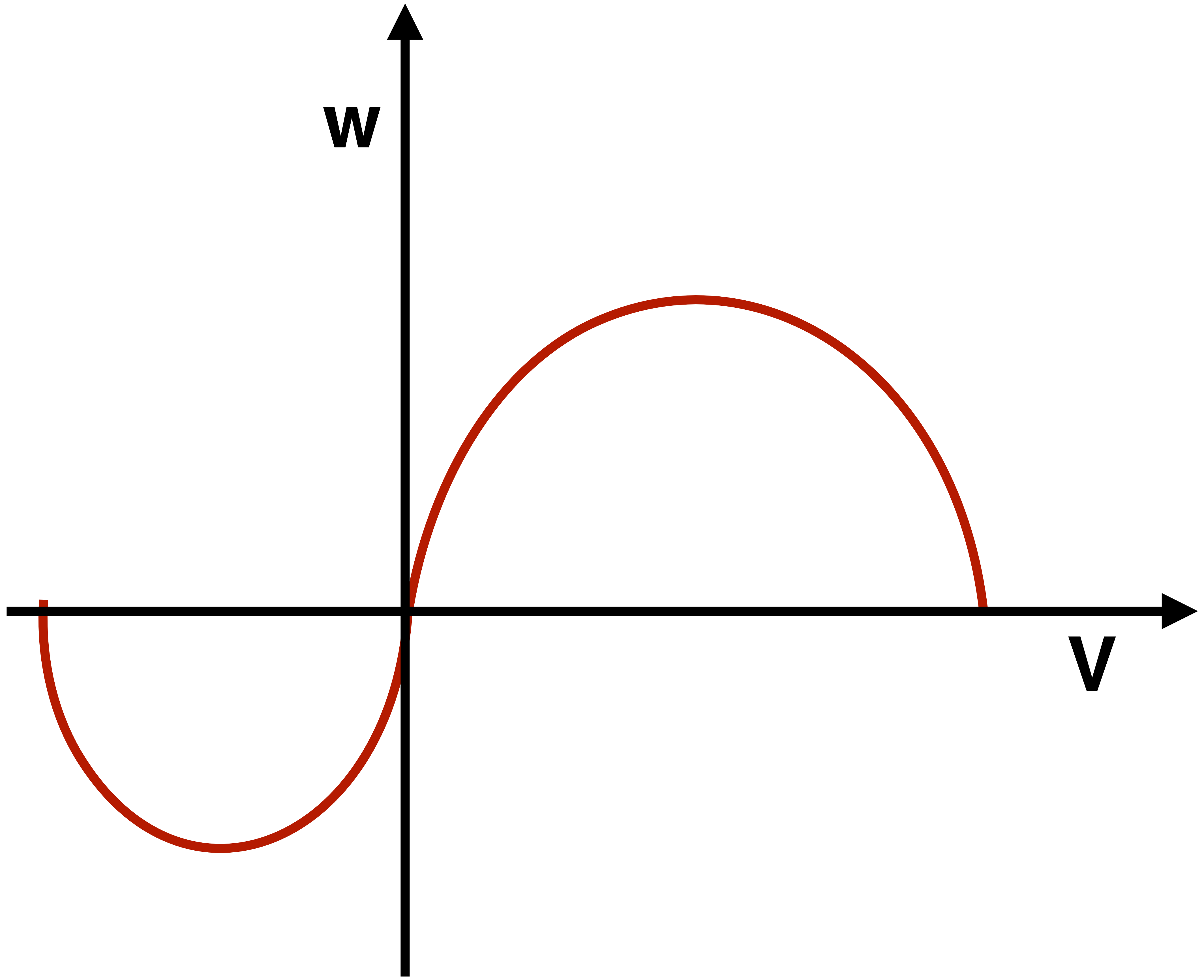

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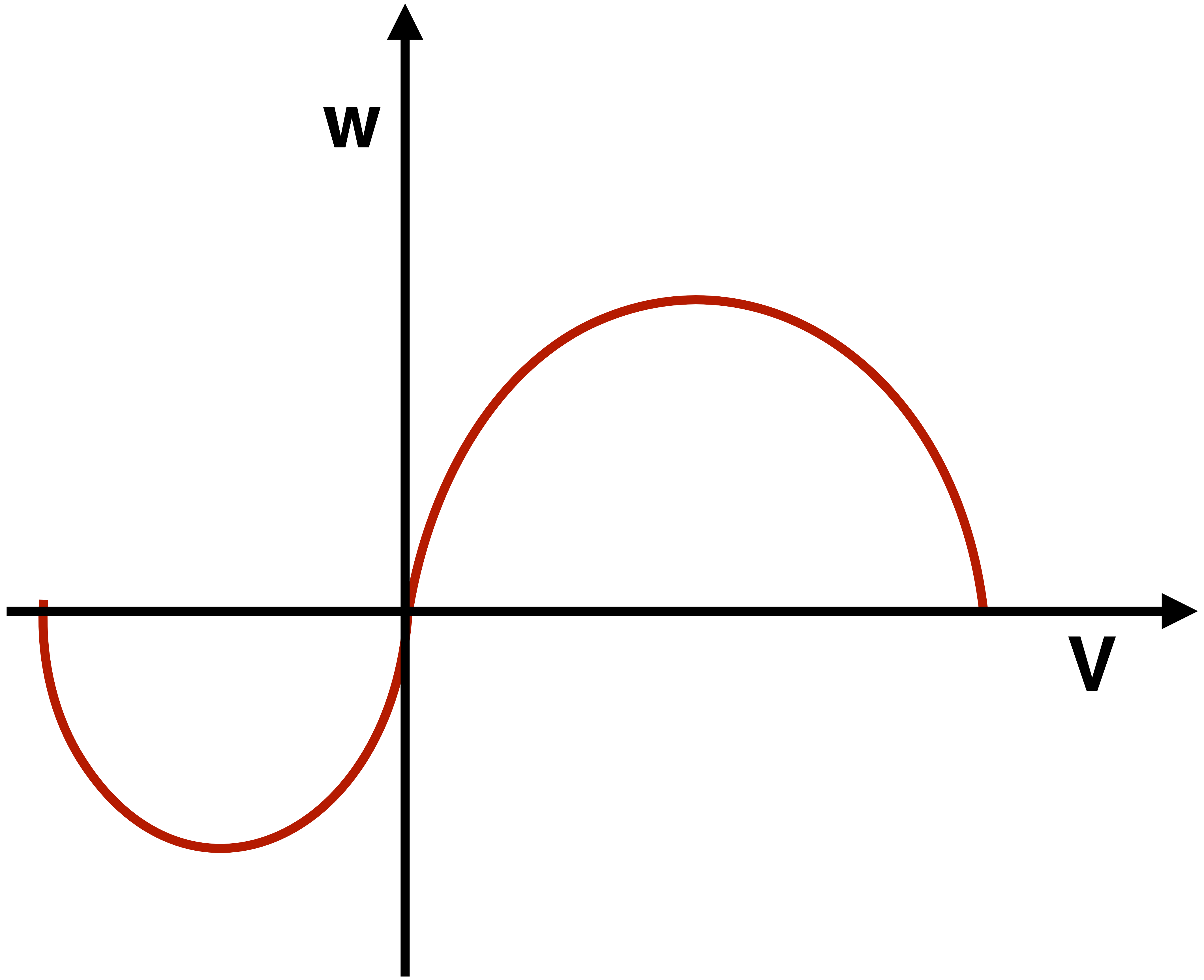

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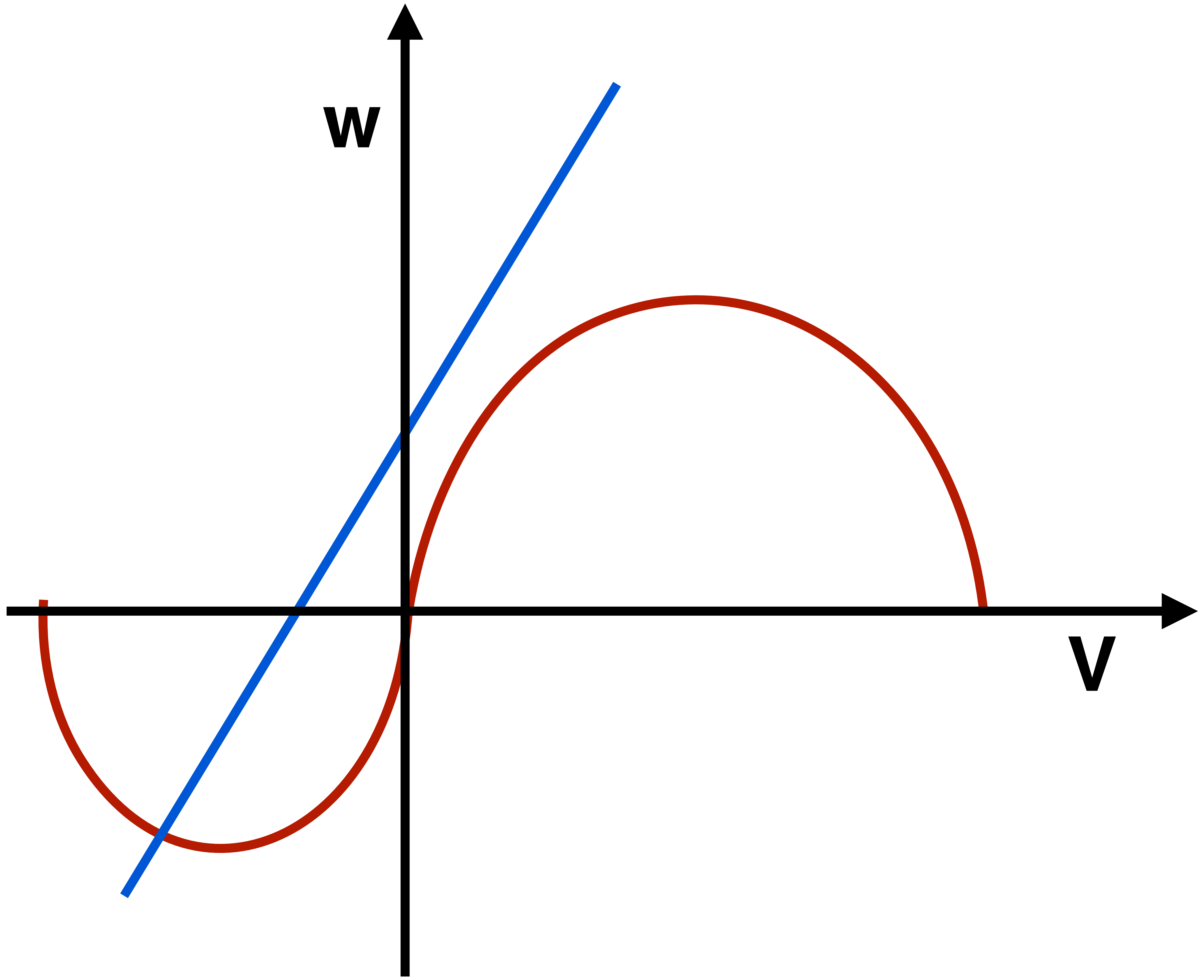

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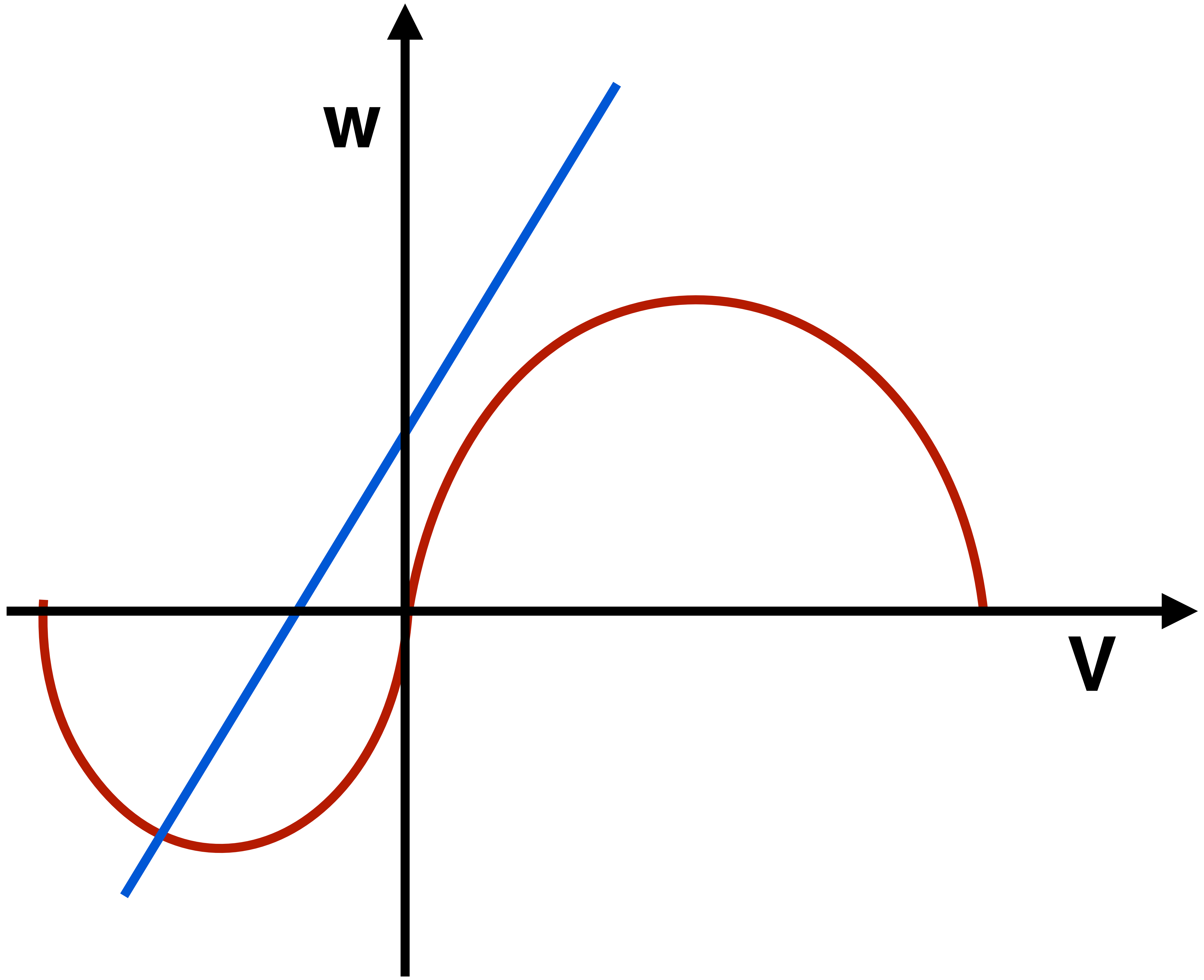
nullclines



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

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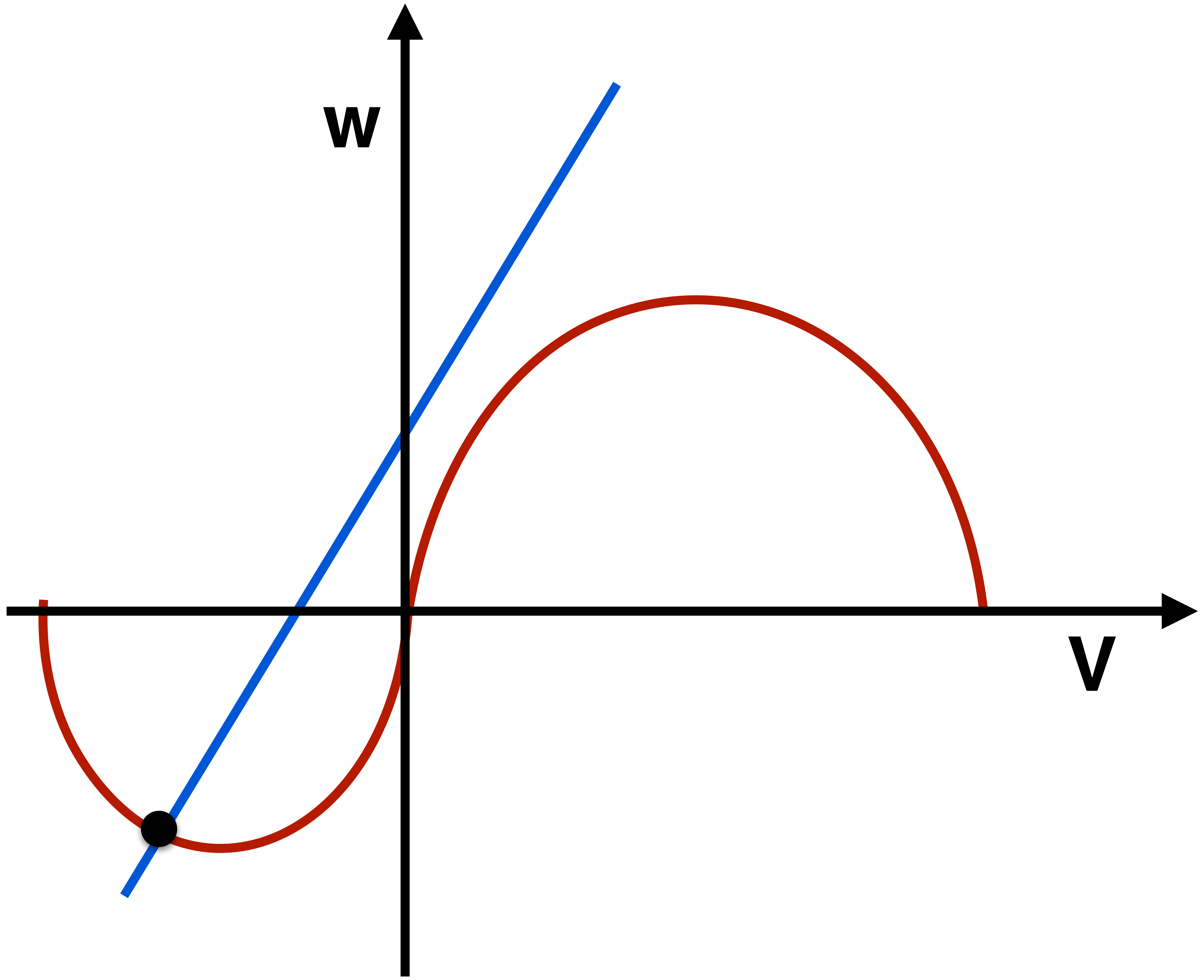


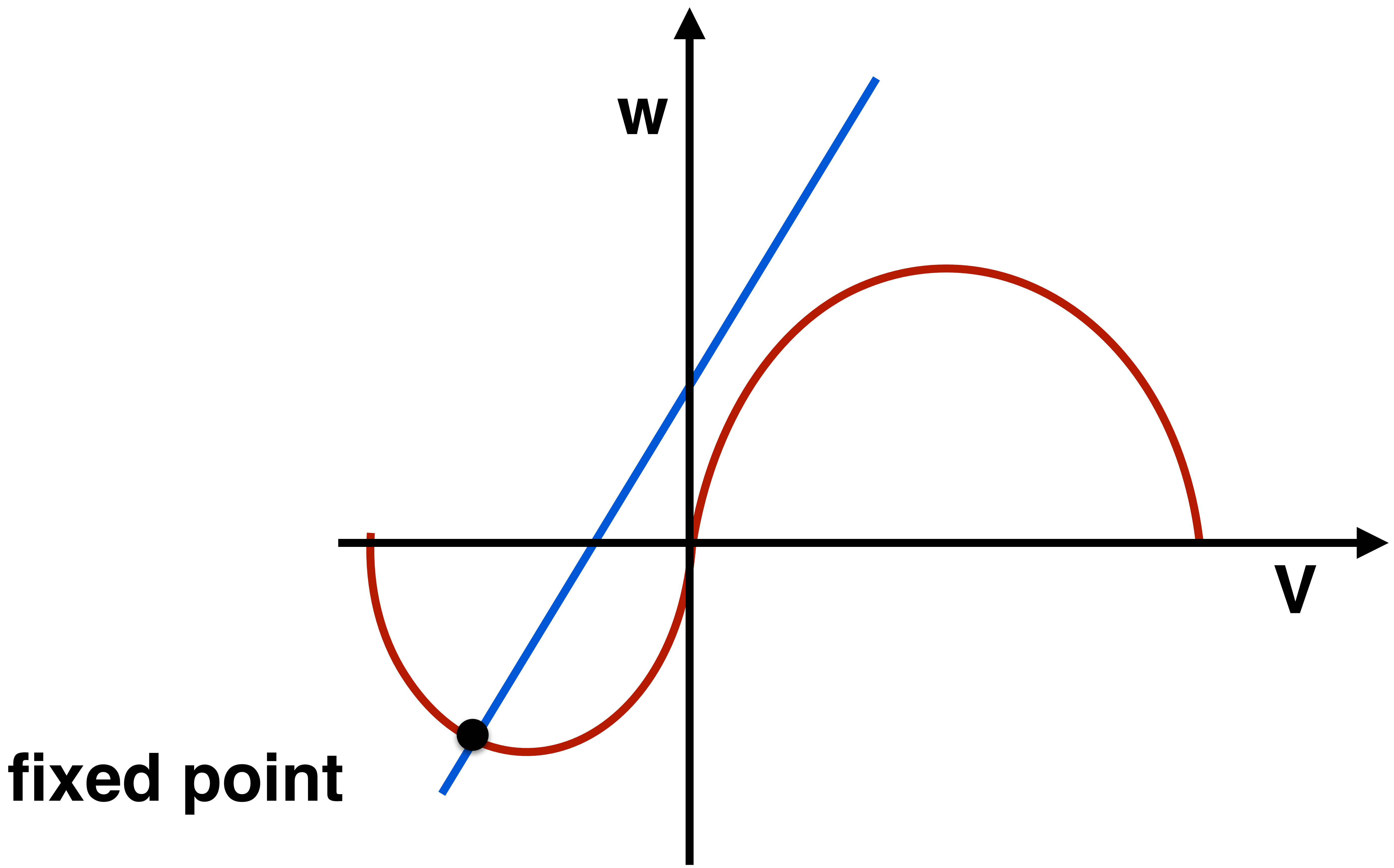
$$\frac{dw}{dt} = 0$$

$$\Leftrightarrow \quad a + bV = w$$

FitzHugh-Nagumo model

$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w$$

$$\frac{dw}{dt} = a + bV - w$$



nullclines

$$\frac{dV}{dt} = 0 \iff V - \frac{1}{3}V^3 = w$$

$$\frac{dw}{dt} = 0 \iff a + bV = w$$

FitzHugh-Nagumo model

$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w$$

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nullclines

$$\frac{dV}{dt} = 0 \iff V - \frac{1}{3}V^3 = w$$

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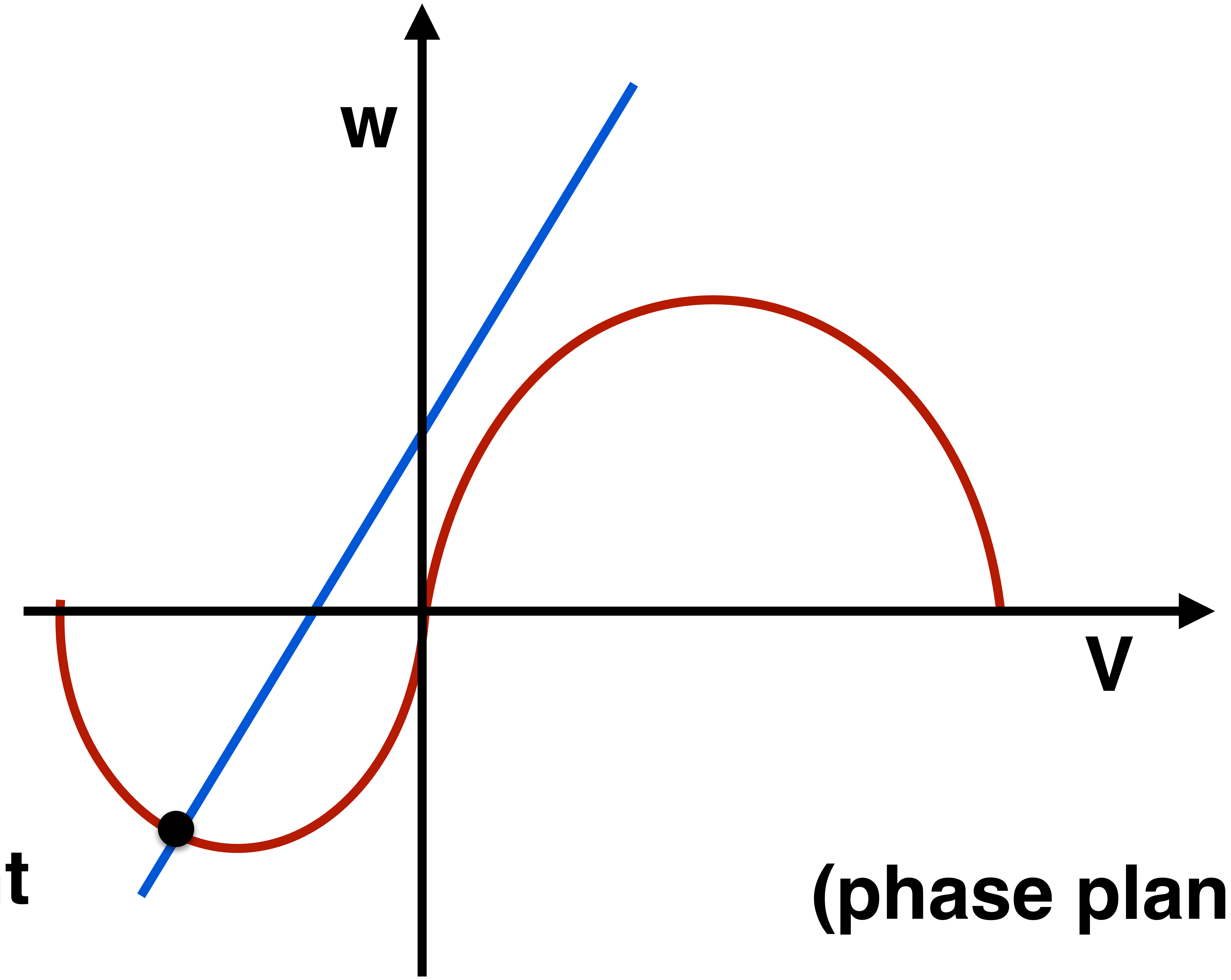


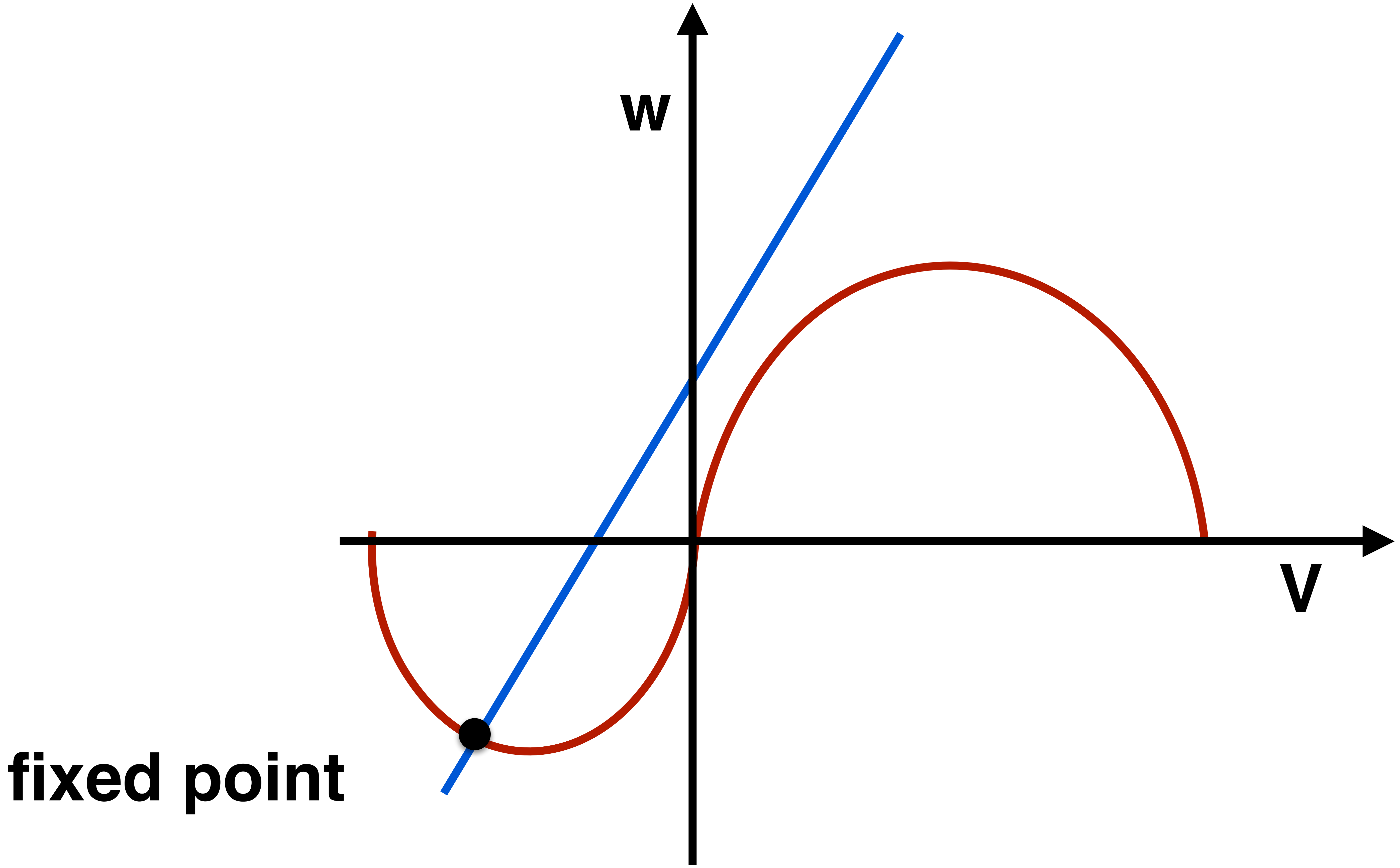
fixed point

(phase plane analysis)

FitzHugh-Nagumo model

$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w$$

$$\frac{dw}{dt} = a + bV - w$$



nullclines

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

$$\Longleftrightarrow \quad V - \frac{1}{3}V^3 = w$$

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

$$\Longleftrightarrow \quad a + bV = w$$

FitzHugh-Nagumo model

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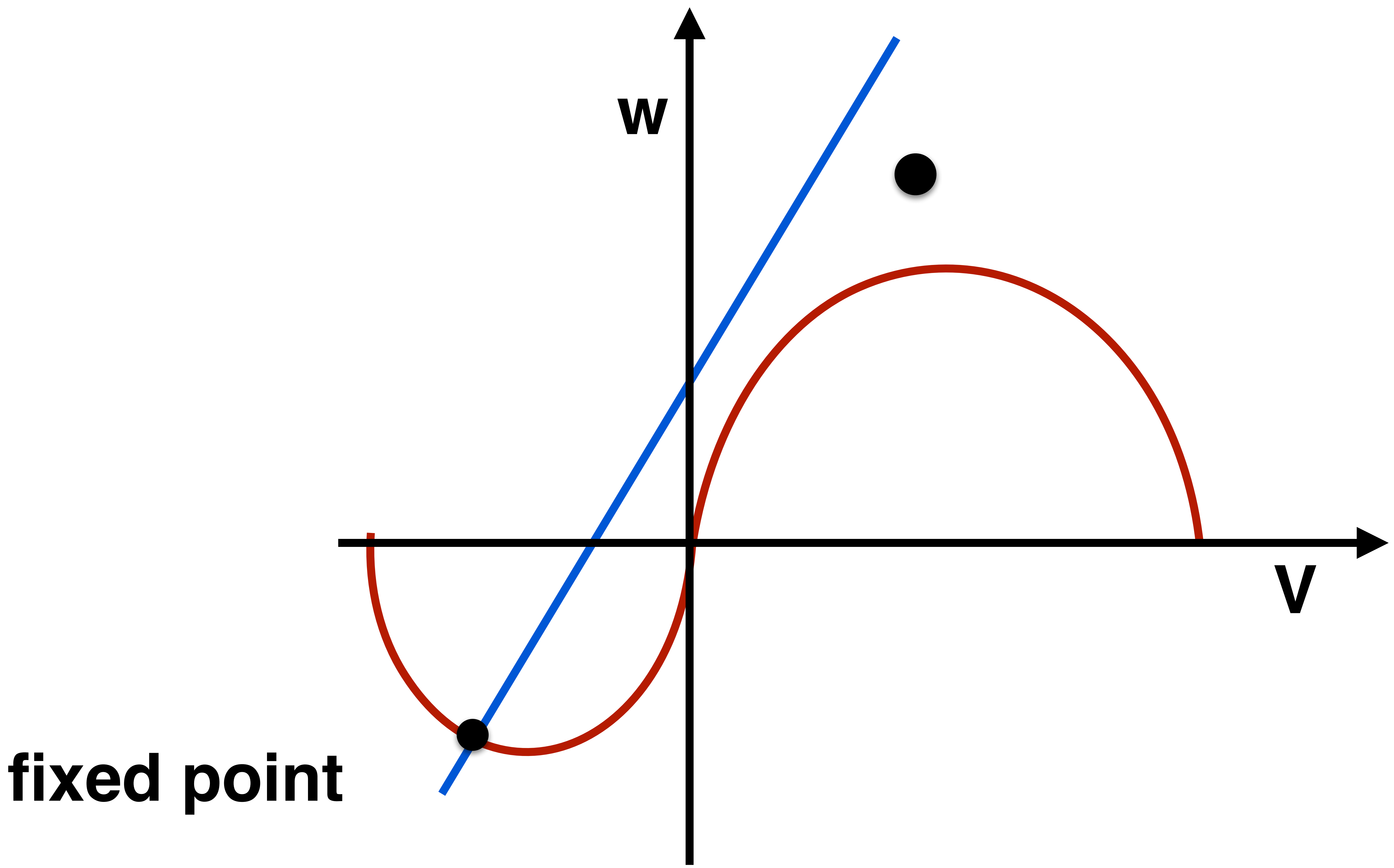

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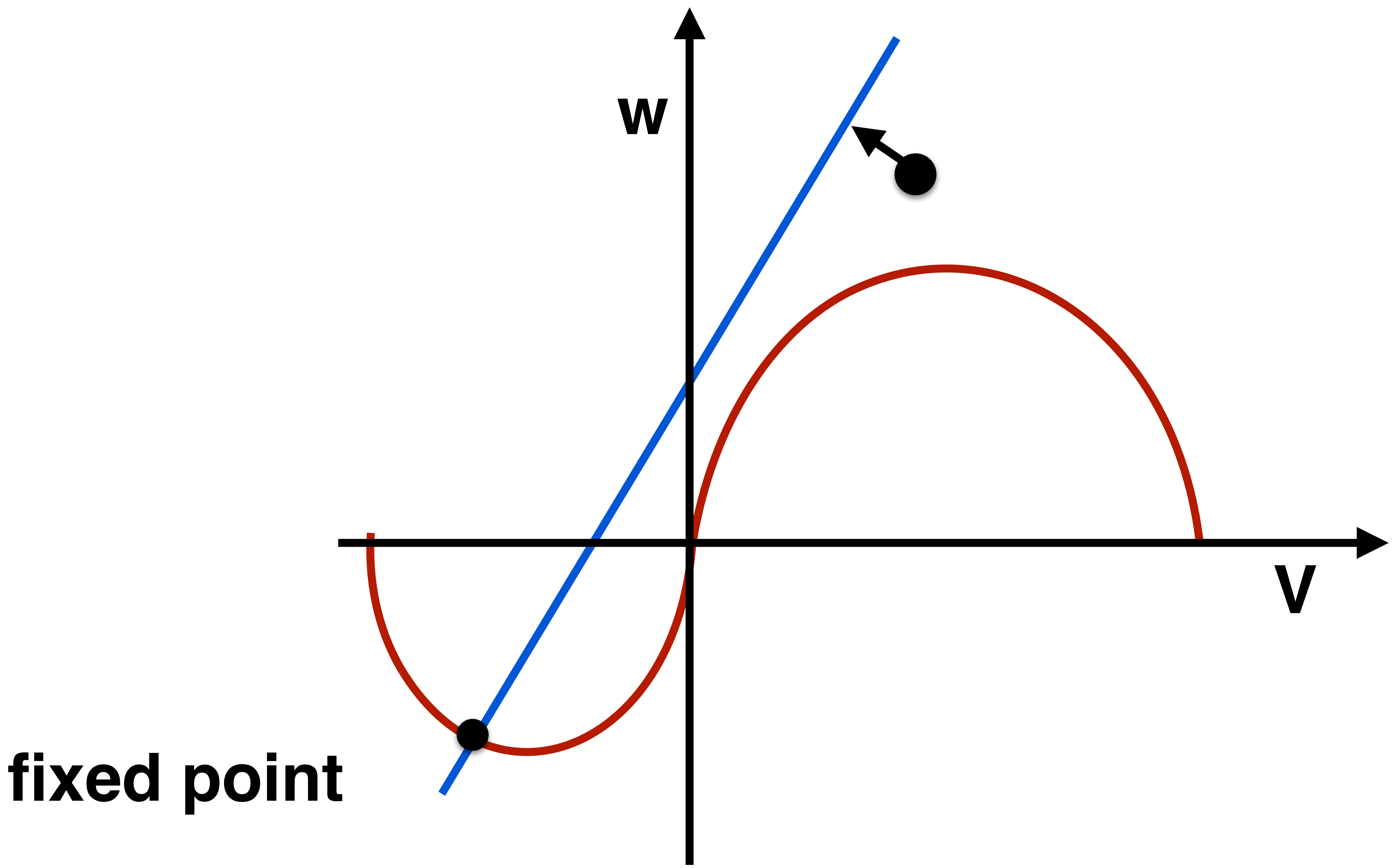

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FitzHugh-Nagumo model

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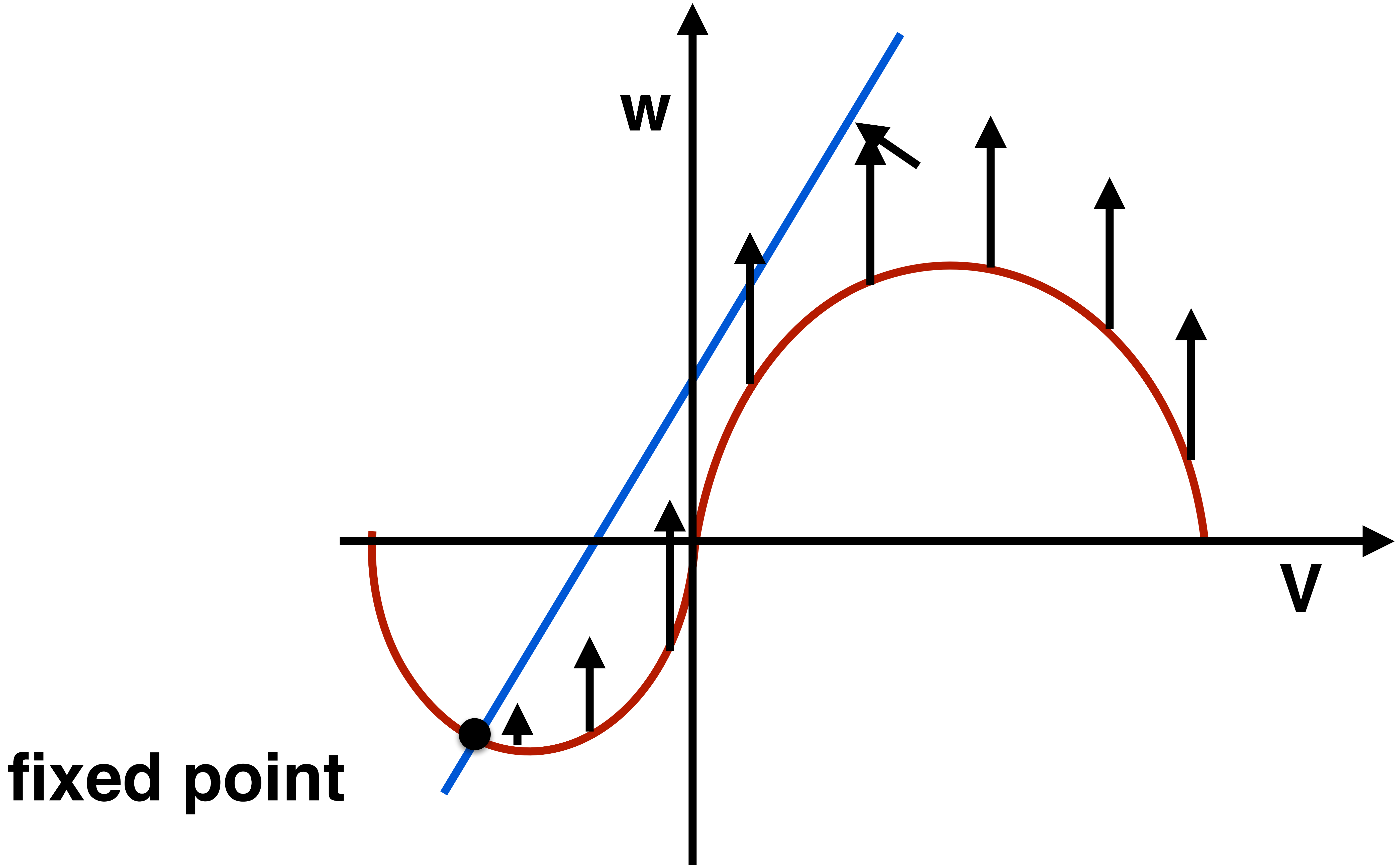

FitzHugh-Nagumo model

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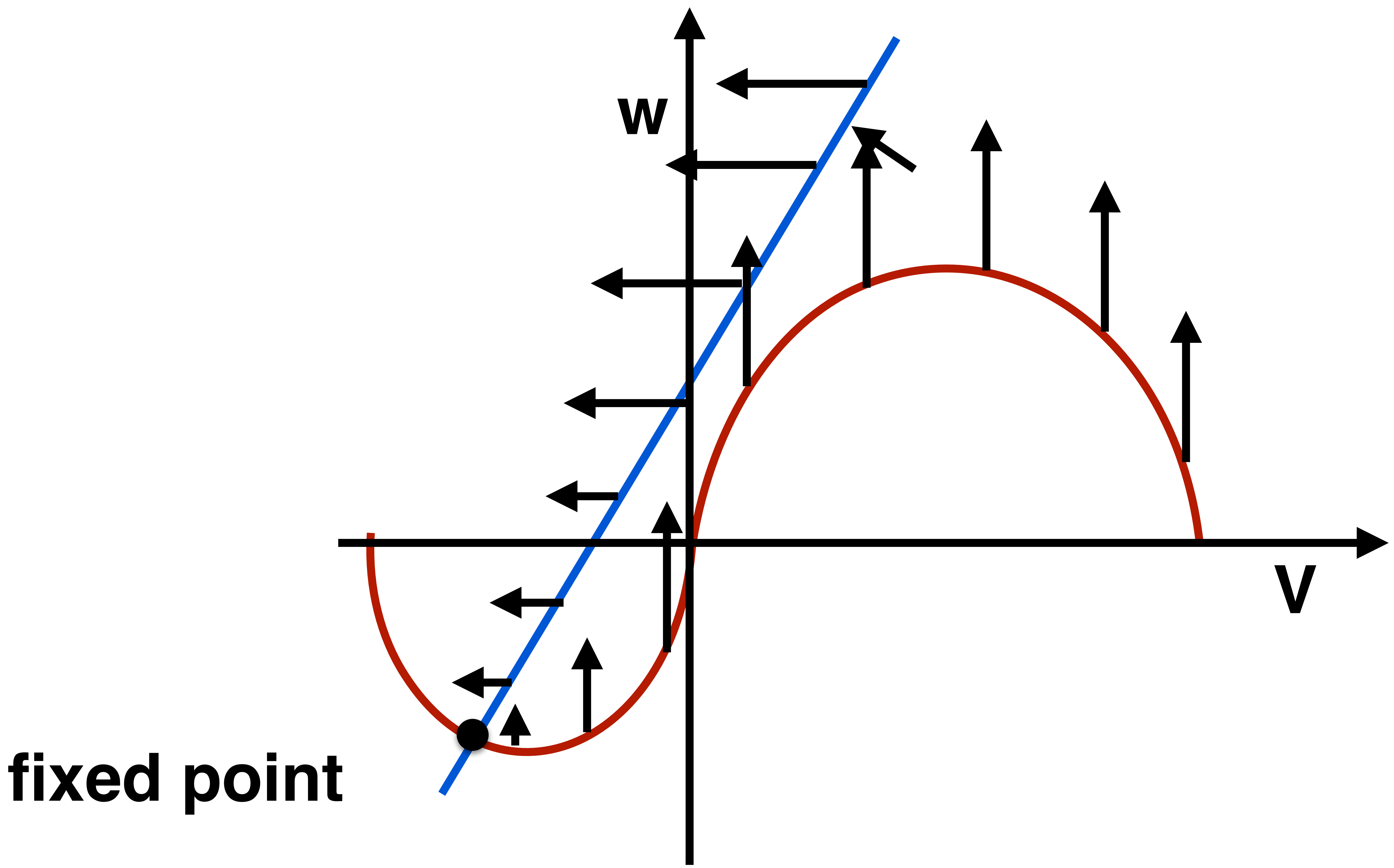

nullclines

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

$$<=> V - \frac{1}{3}V^3 = w$$

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

$$<=> a + bV = w$$

$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w$$

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FitzHugh-Nagumo model

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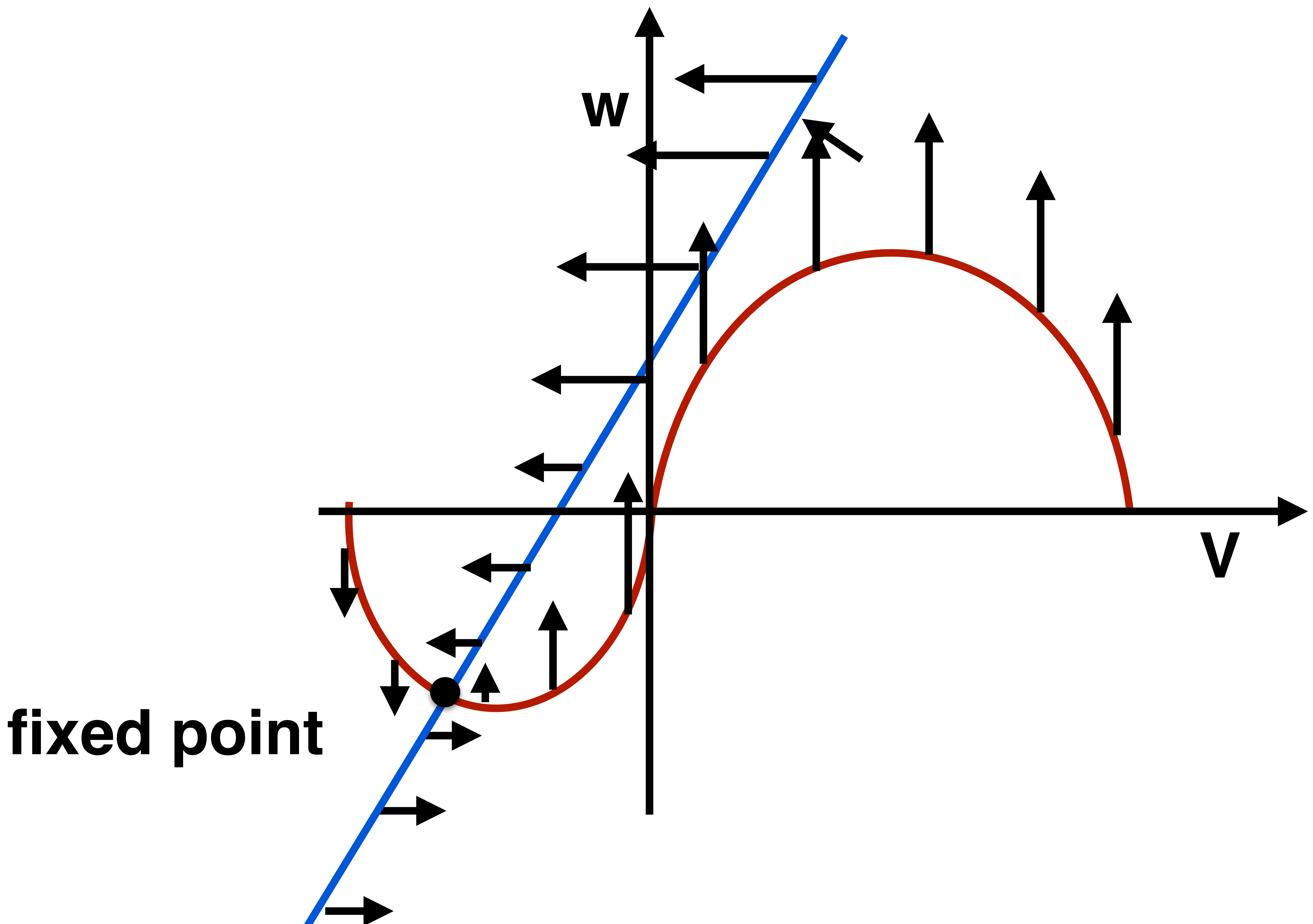

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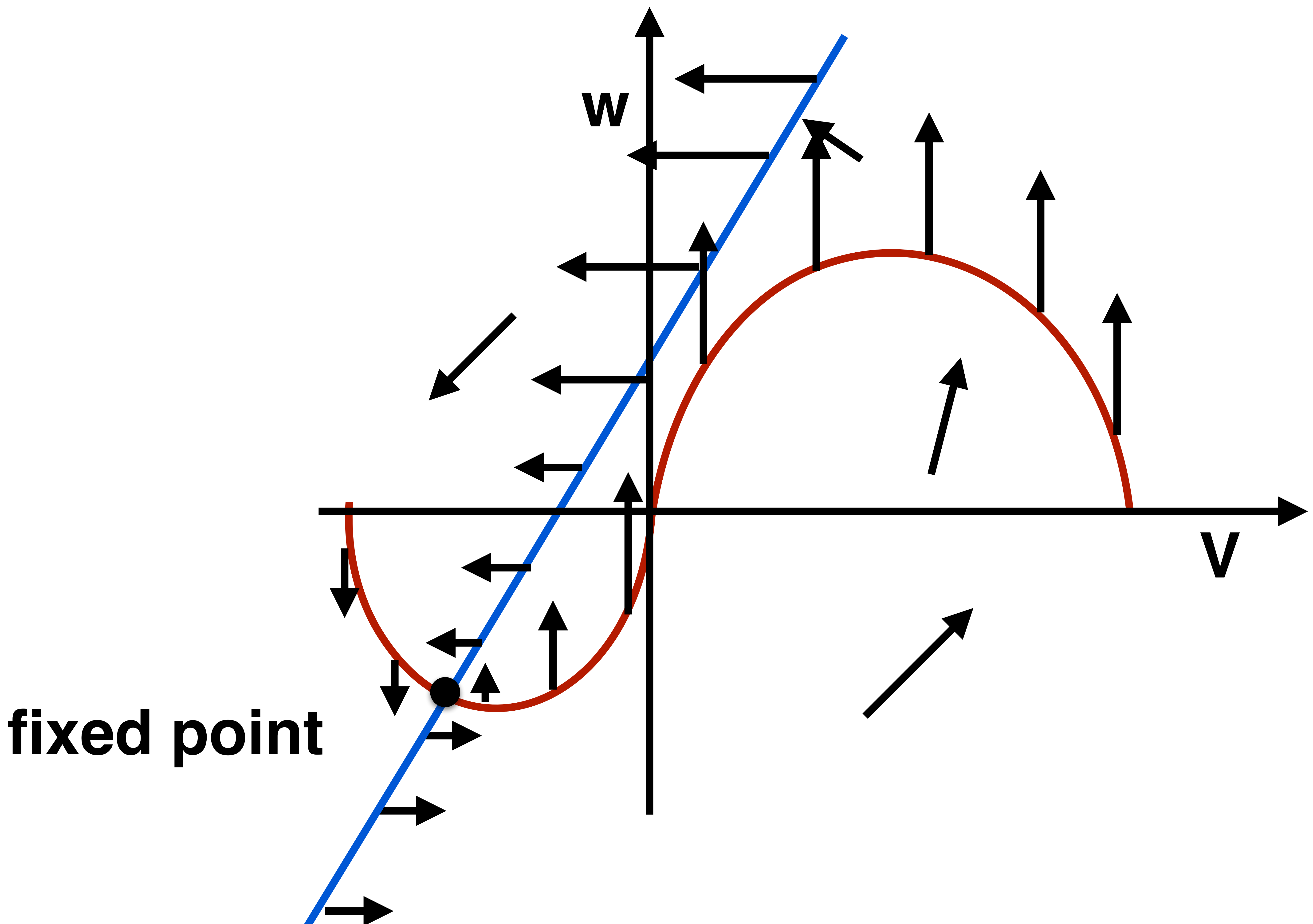

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FitzHugh-Nagumo model

nullclines

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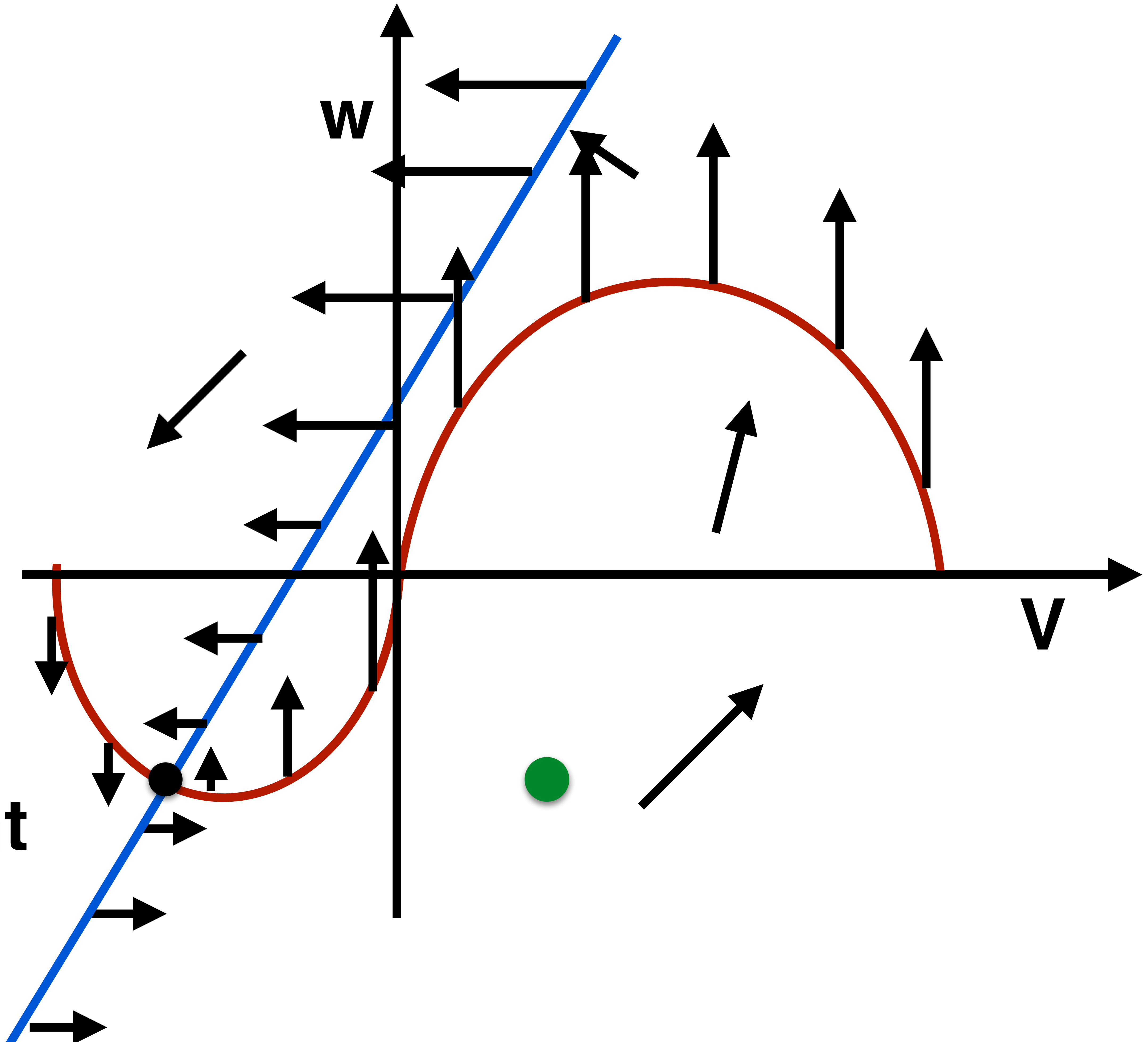


fixed point

FitzHugh-Nagumo model

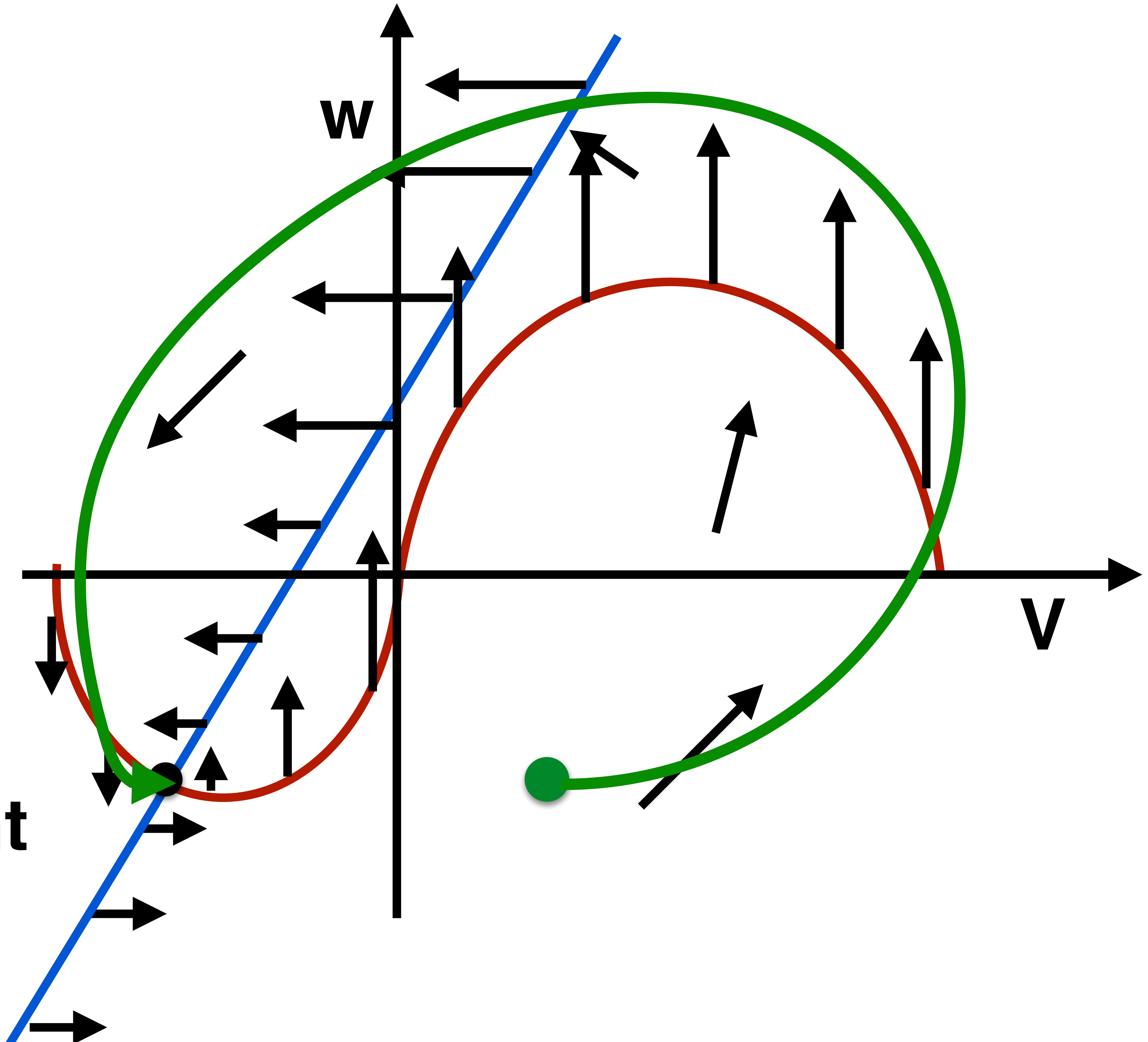
$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w$$

$$\frac{dw}{dt} = a + bV - w$$

nullclines

$$\frac{dV}{dt} = 0 \iff V - \frac{1}{3}V^3 = w$$

$$\frac{dw}{dt} = 0 \iff a + bV = w$$



fixed point

$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w$$

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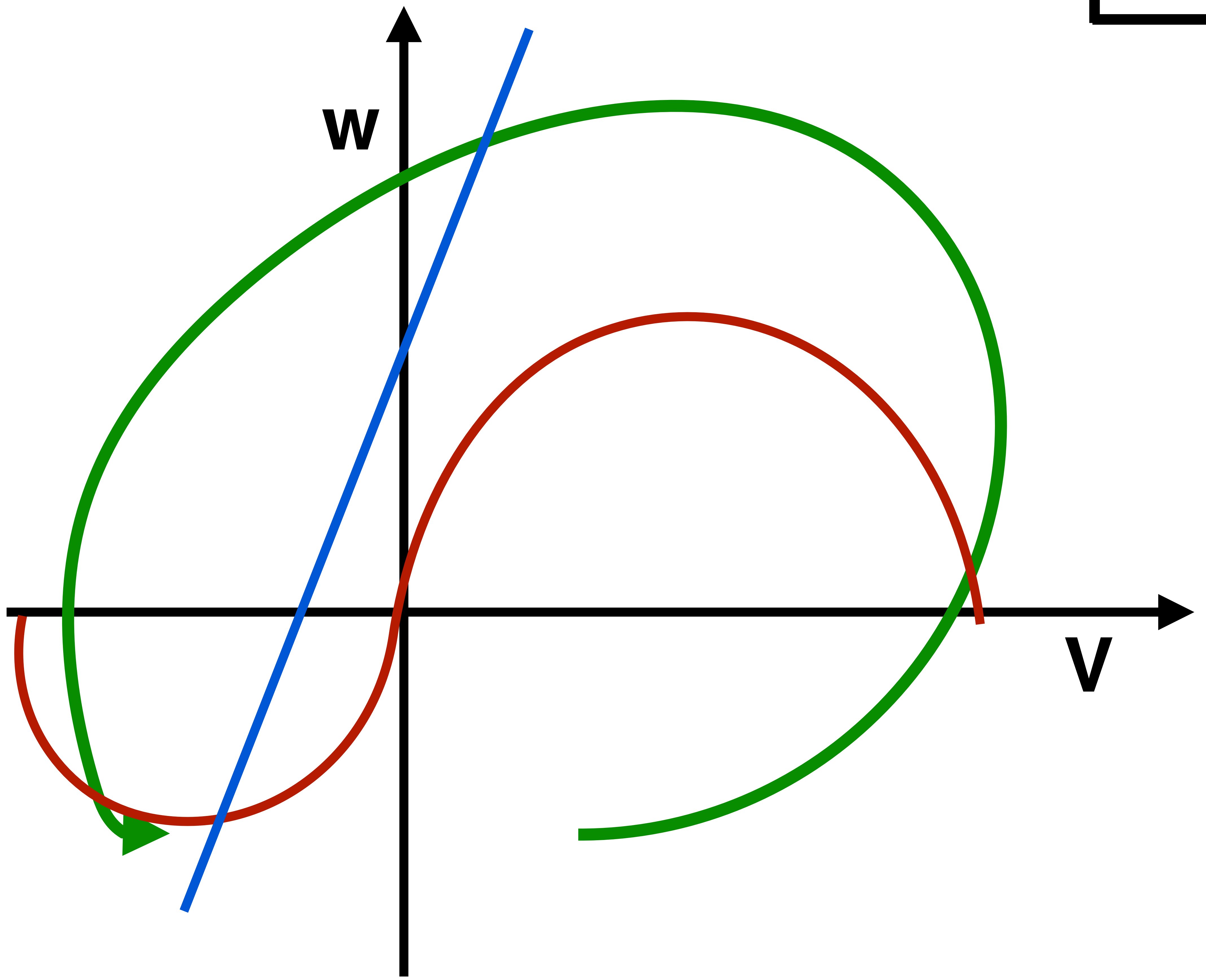

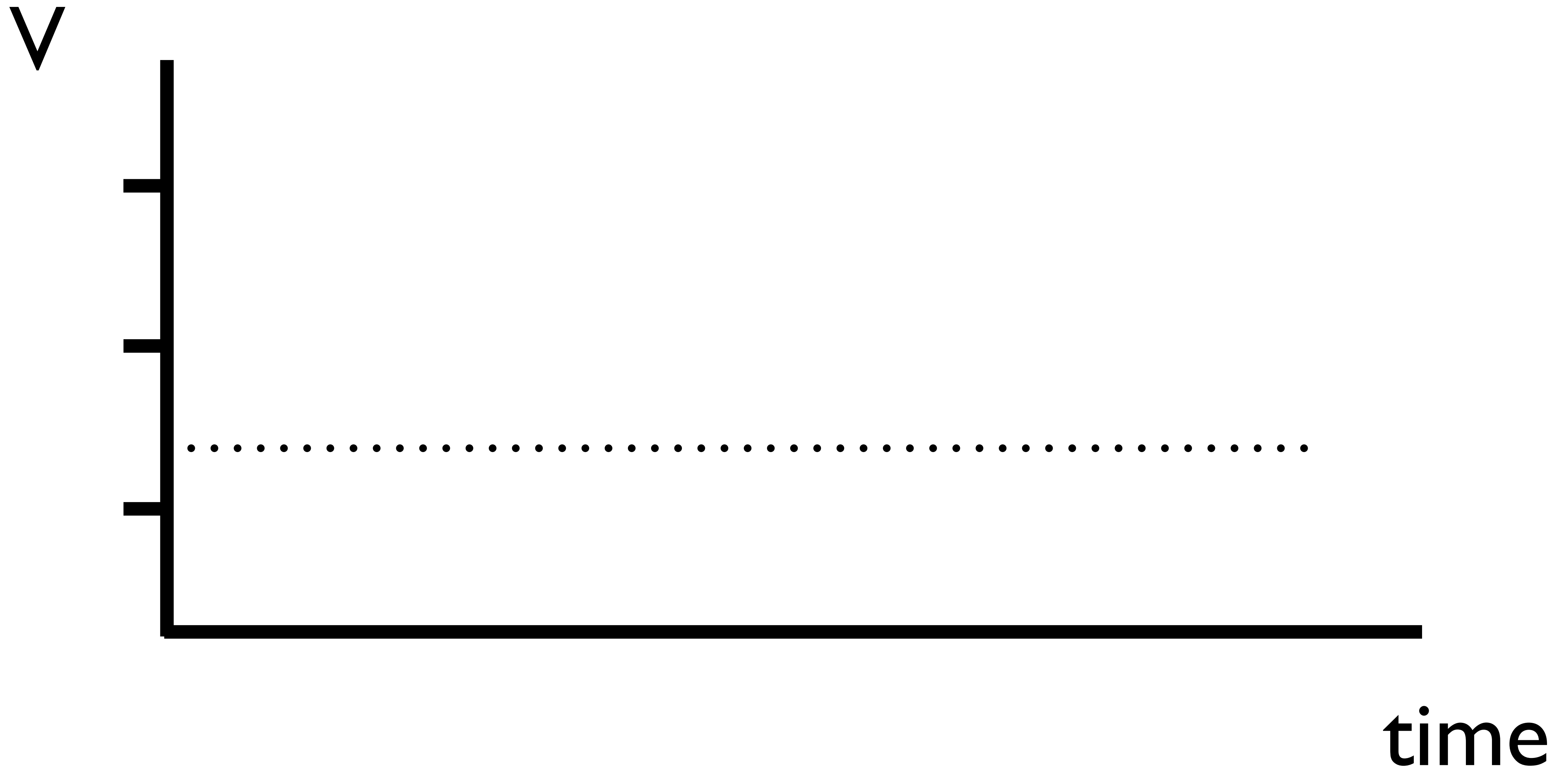

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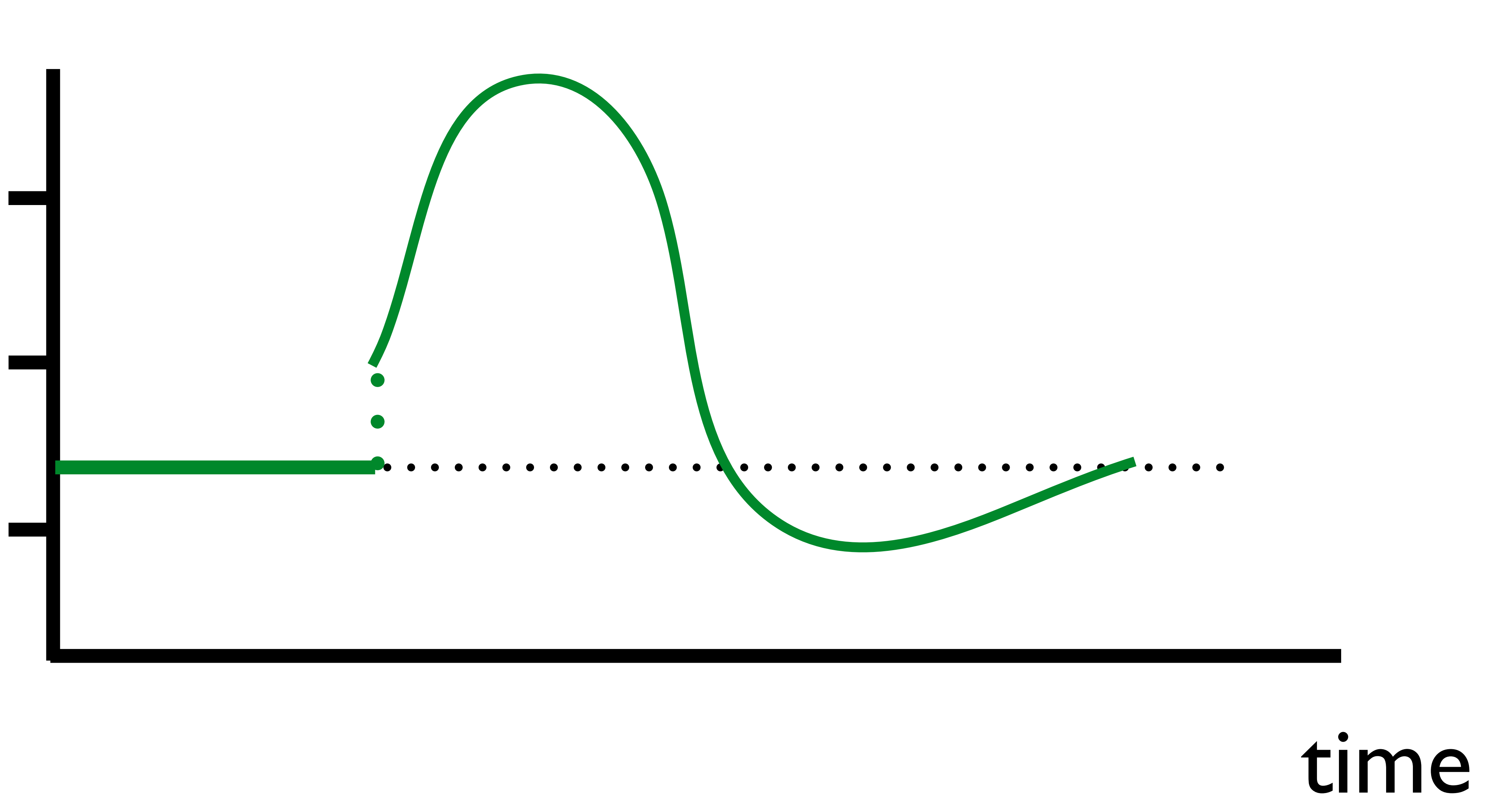

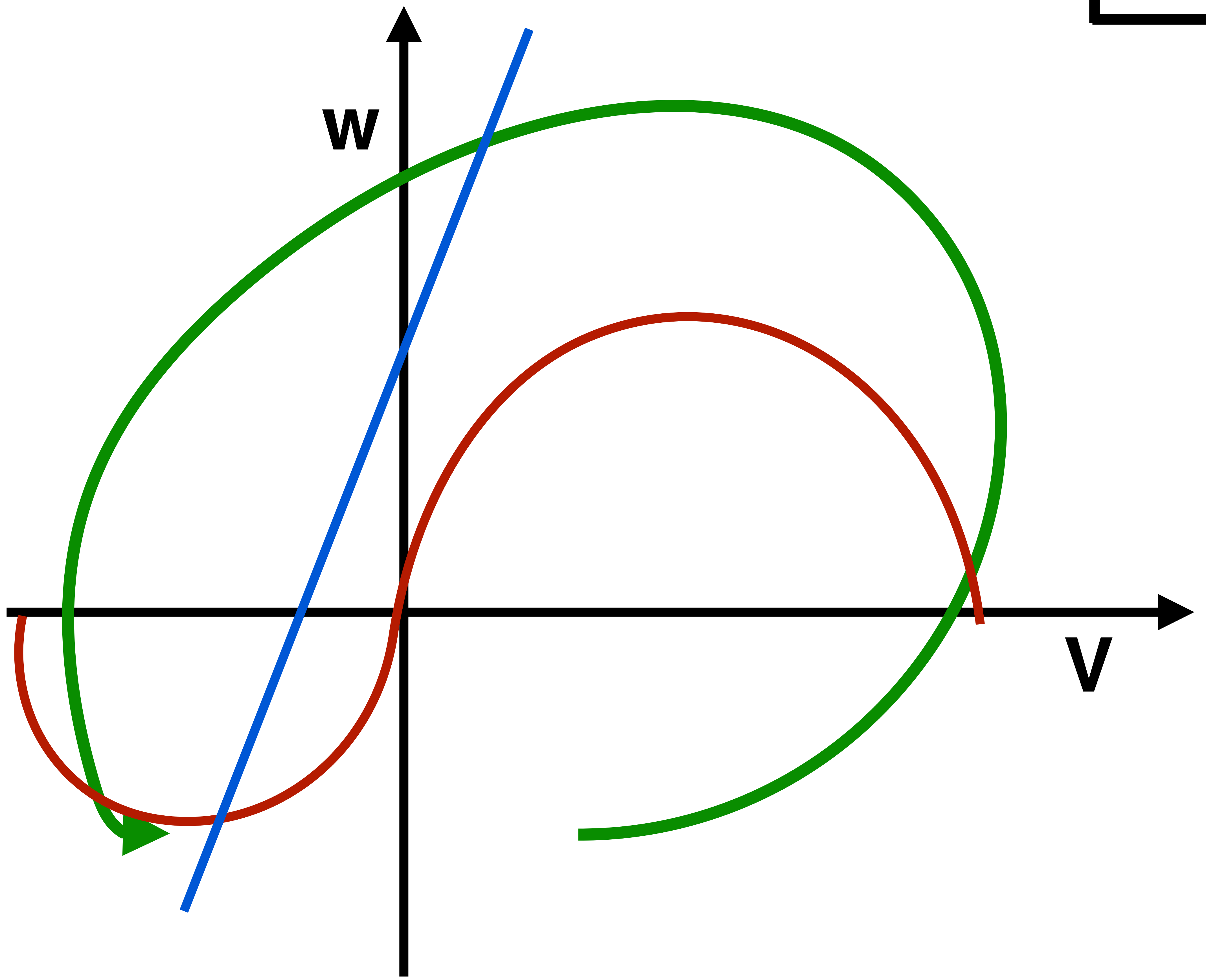

$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w$$

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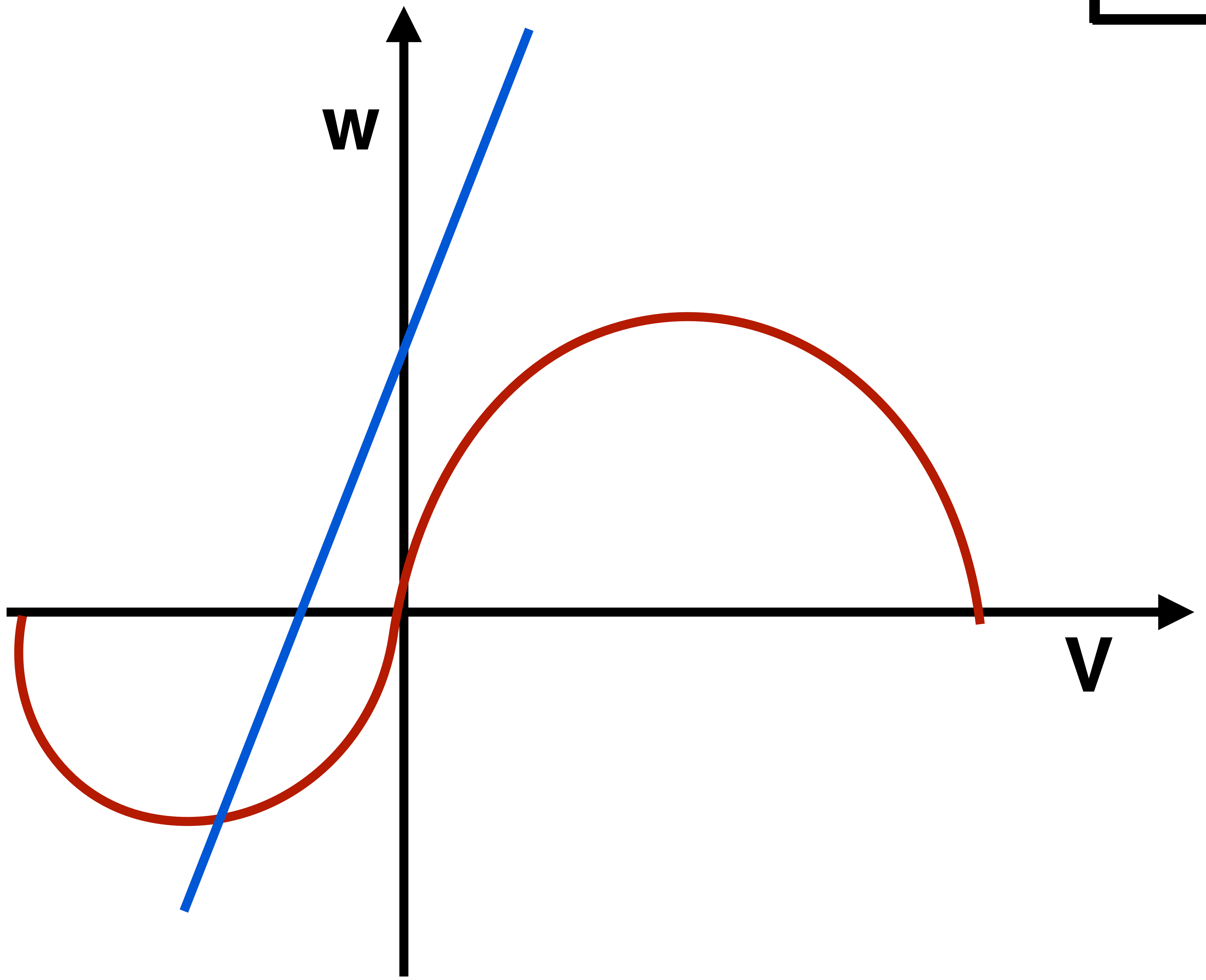
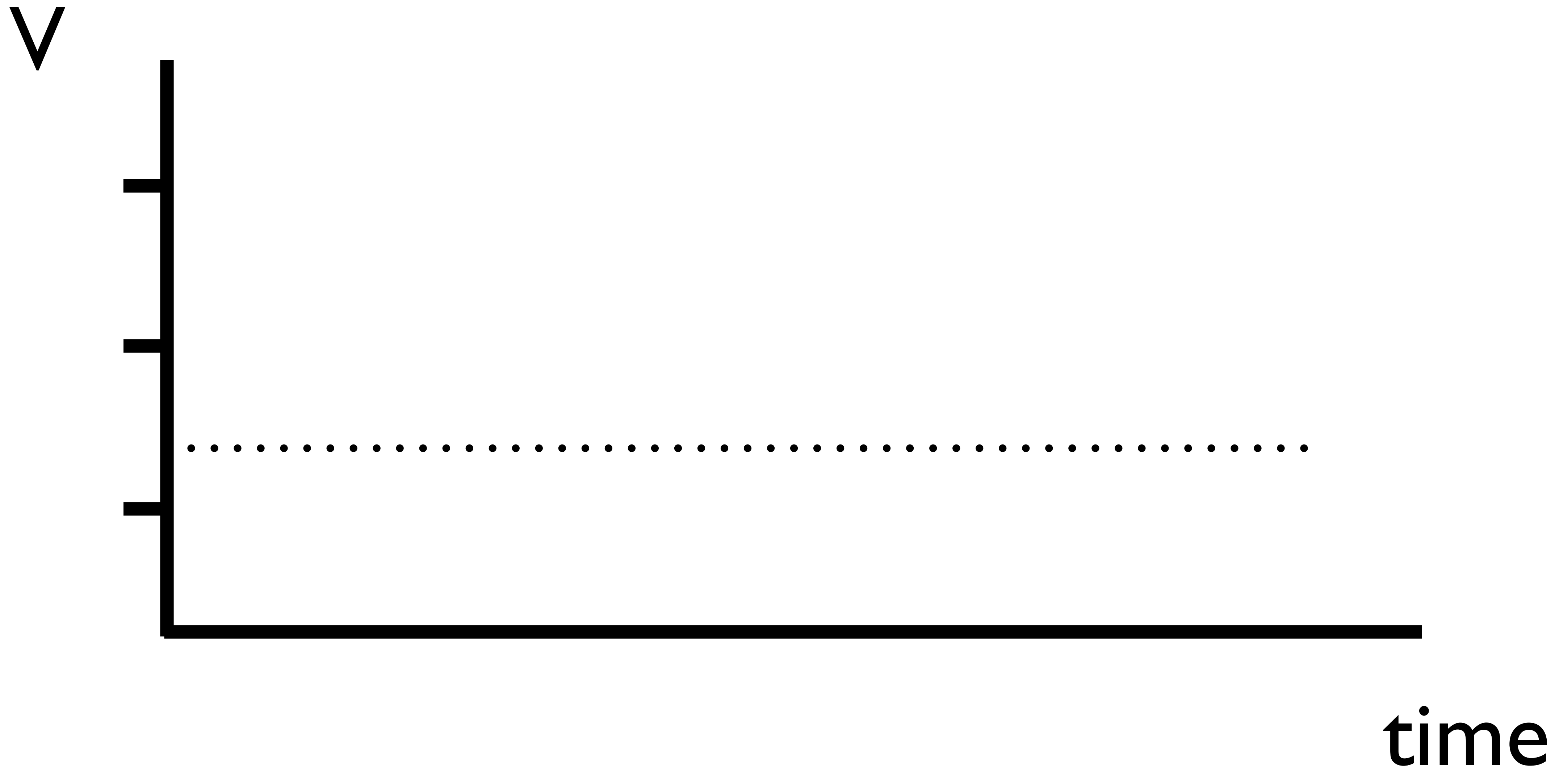
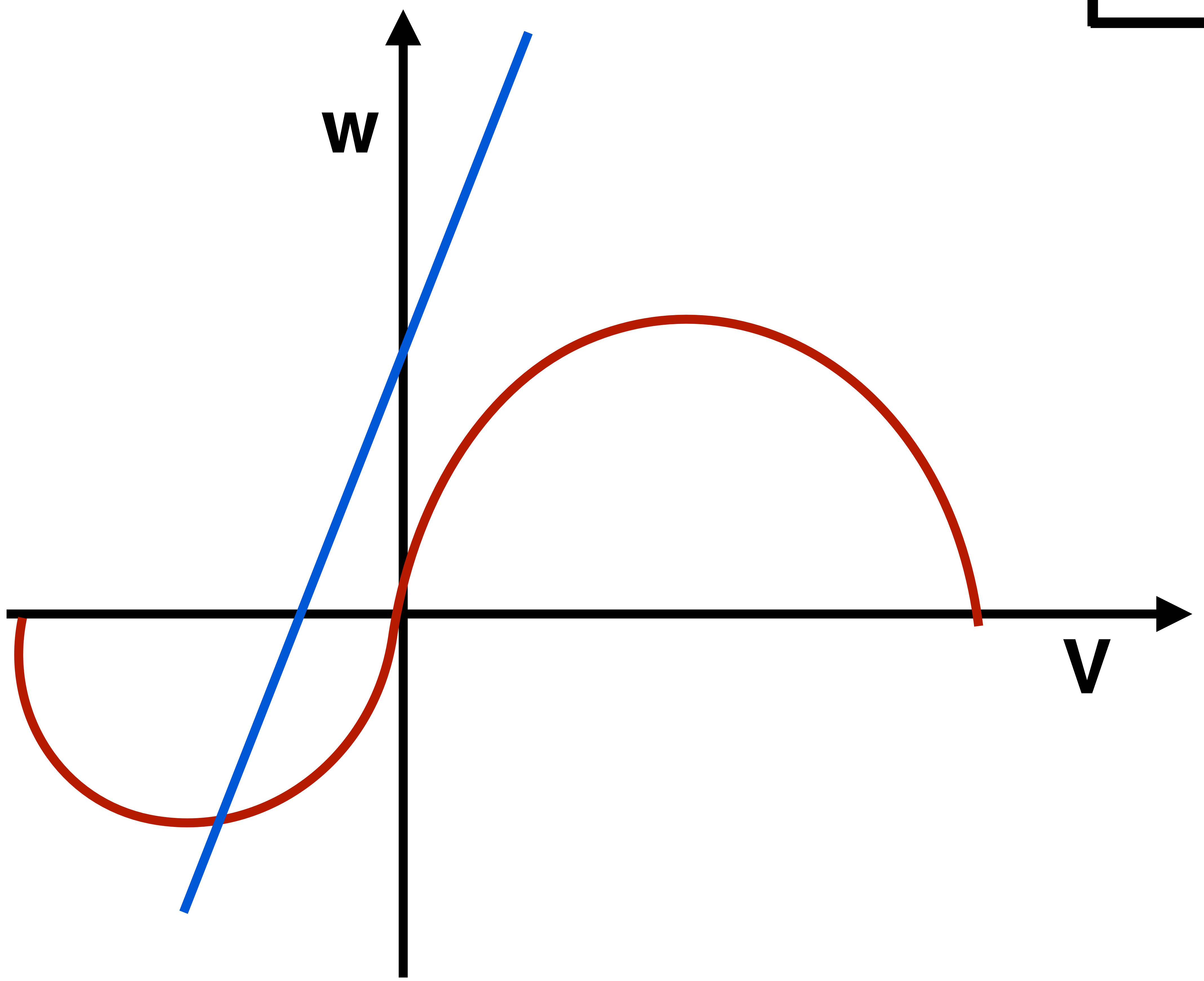
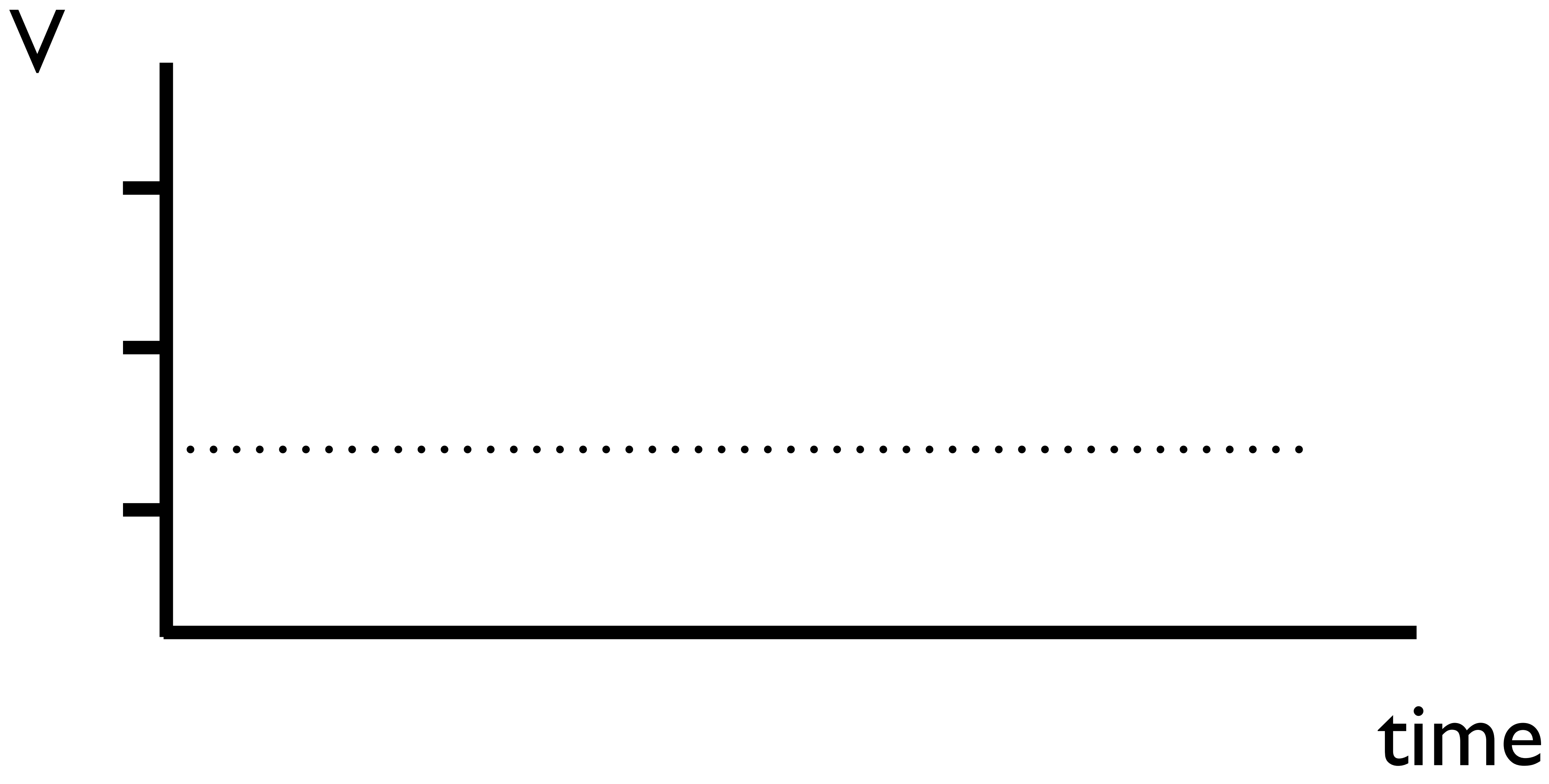




$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w + I$$

$$\frac{dw}{dt} = a + bV - w$$





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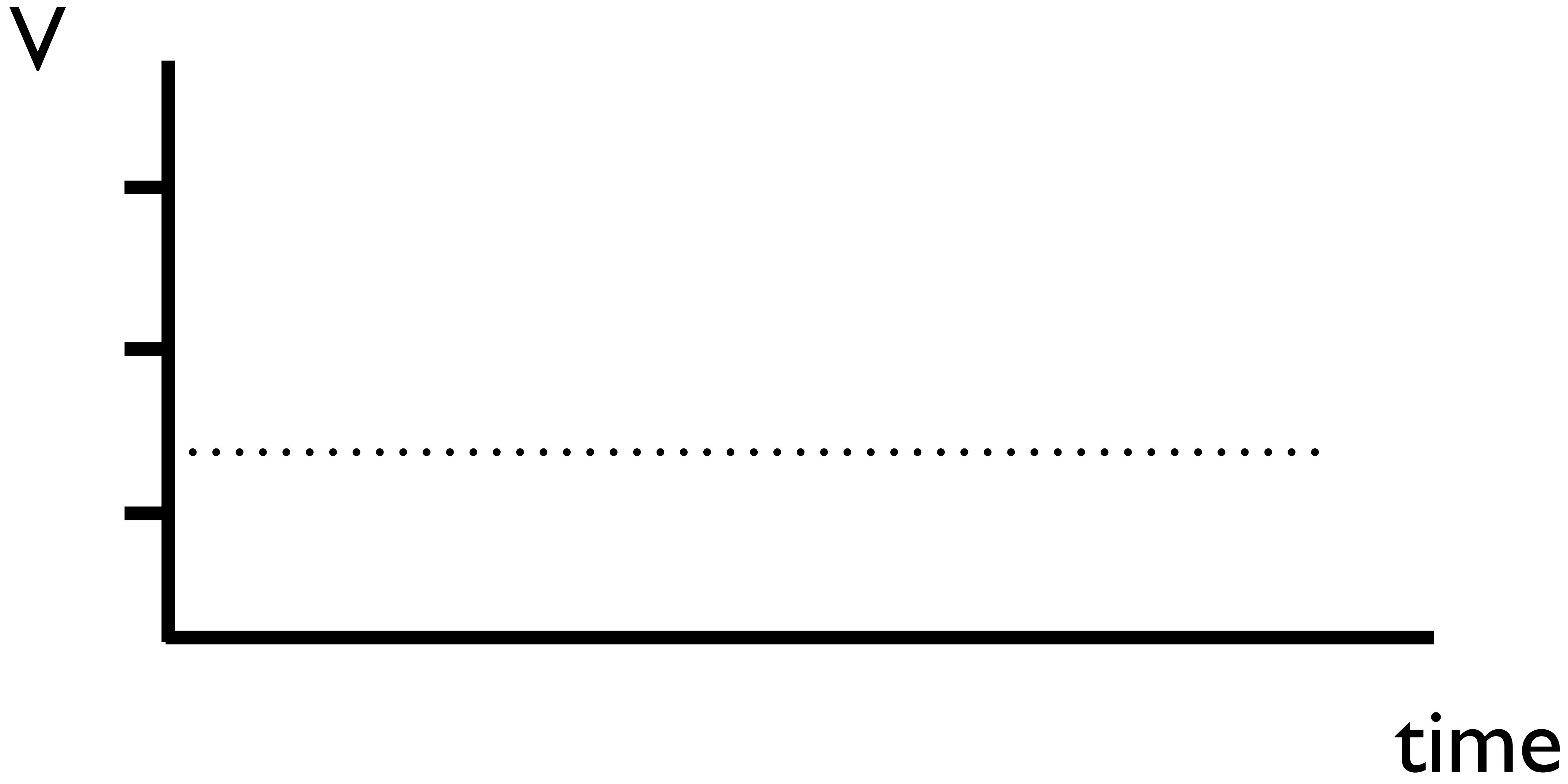

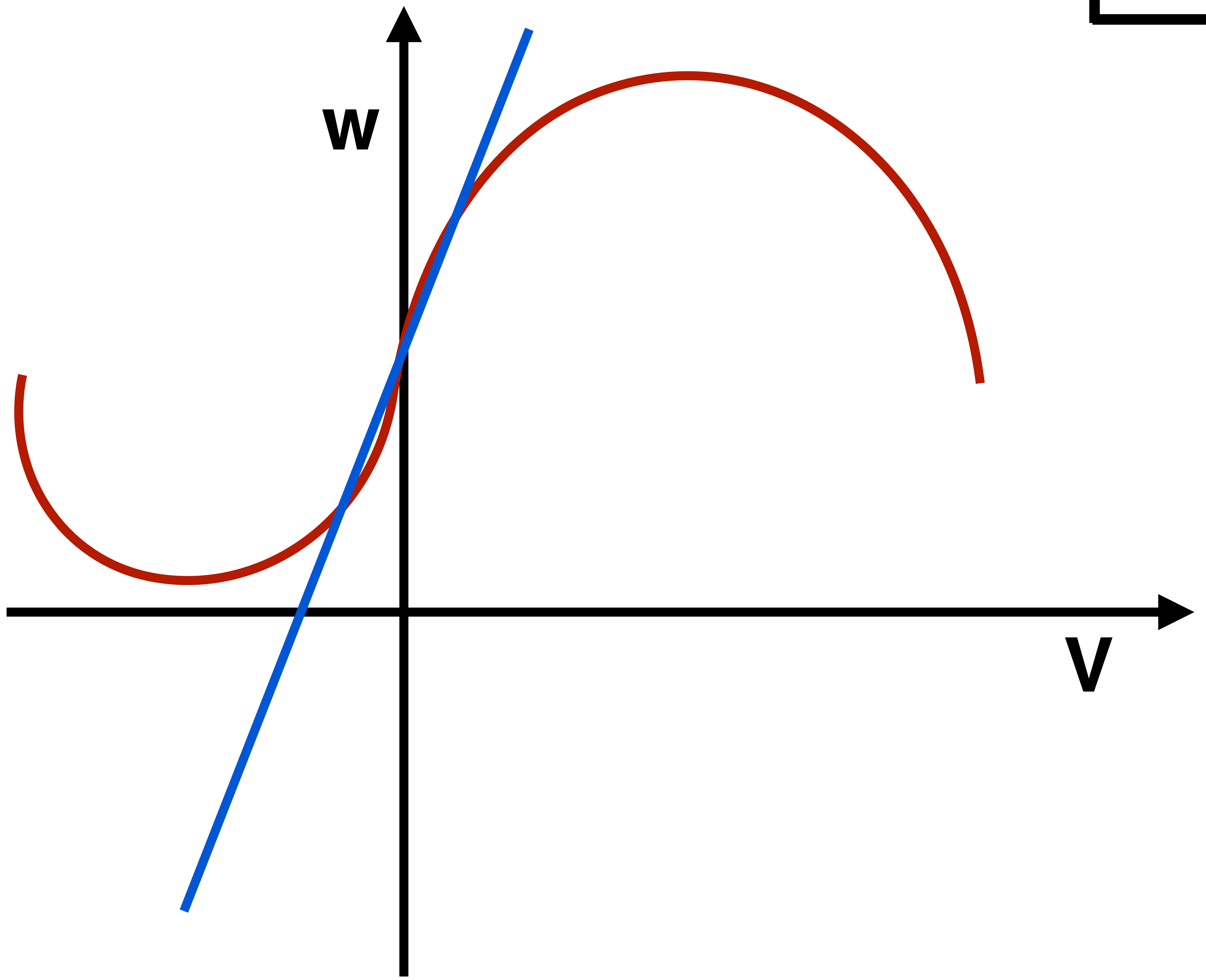

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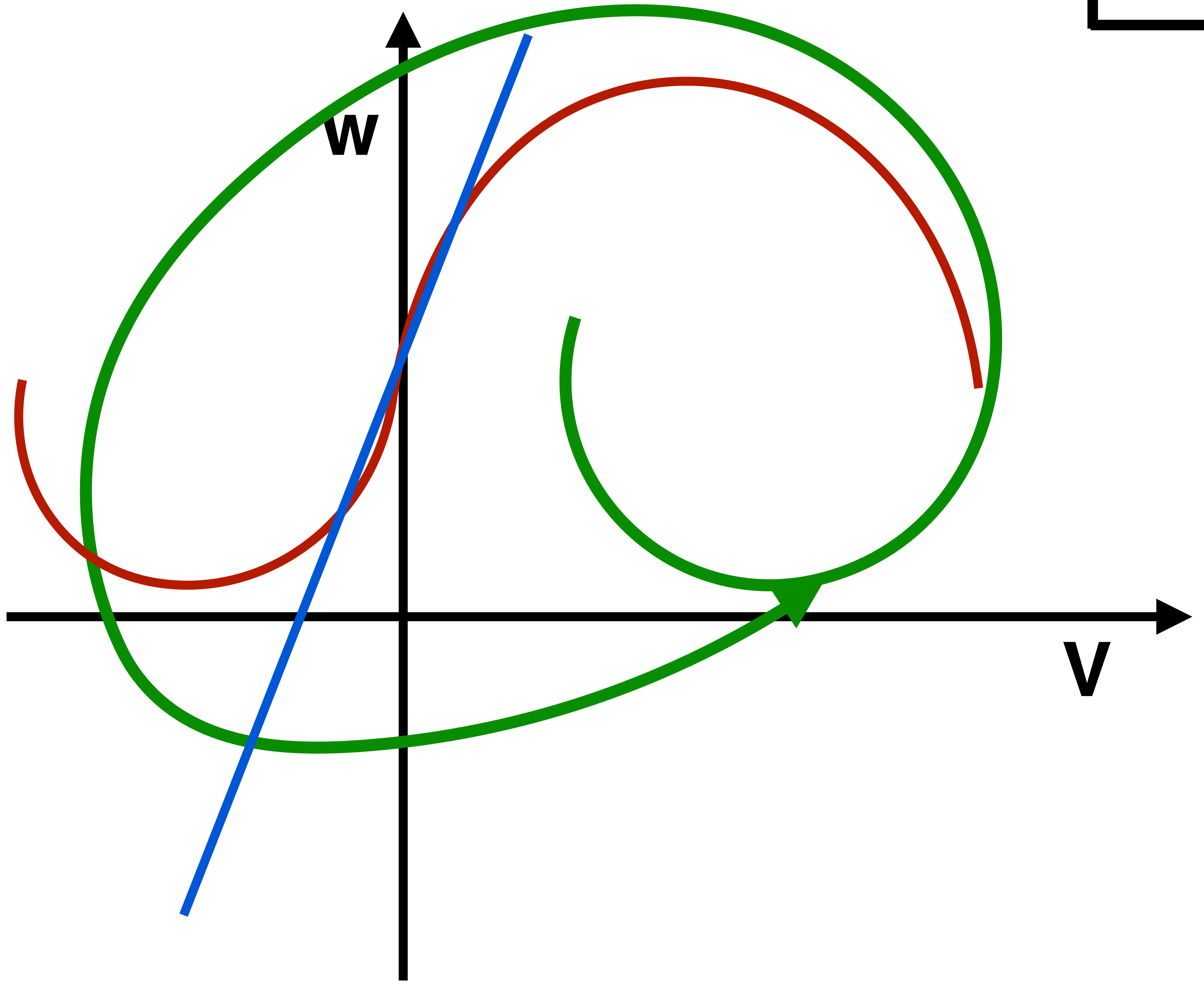
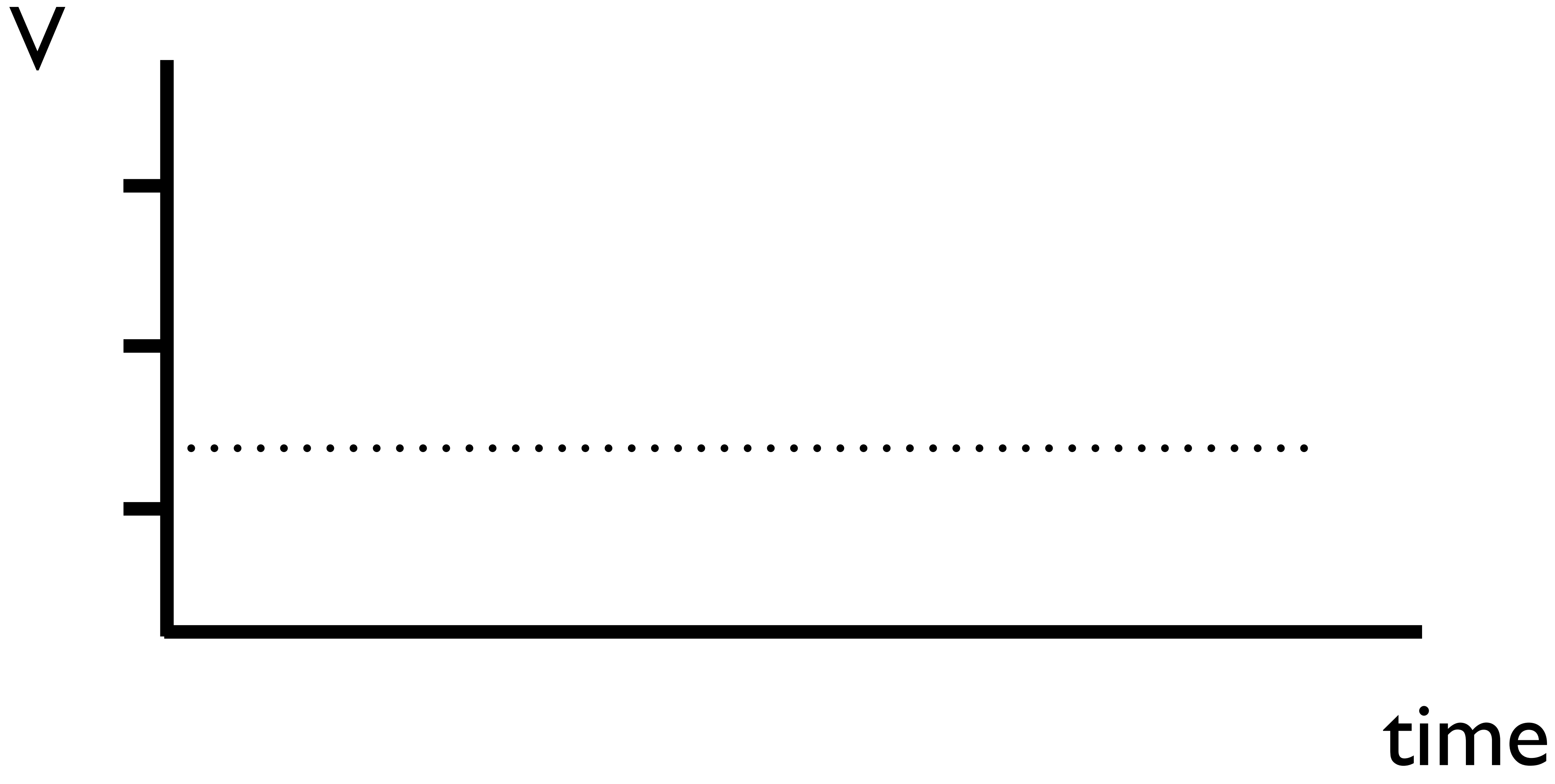
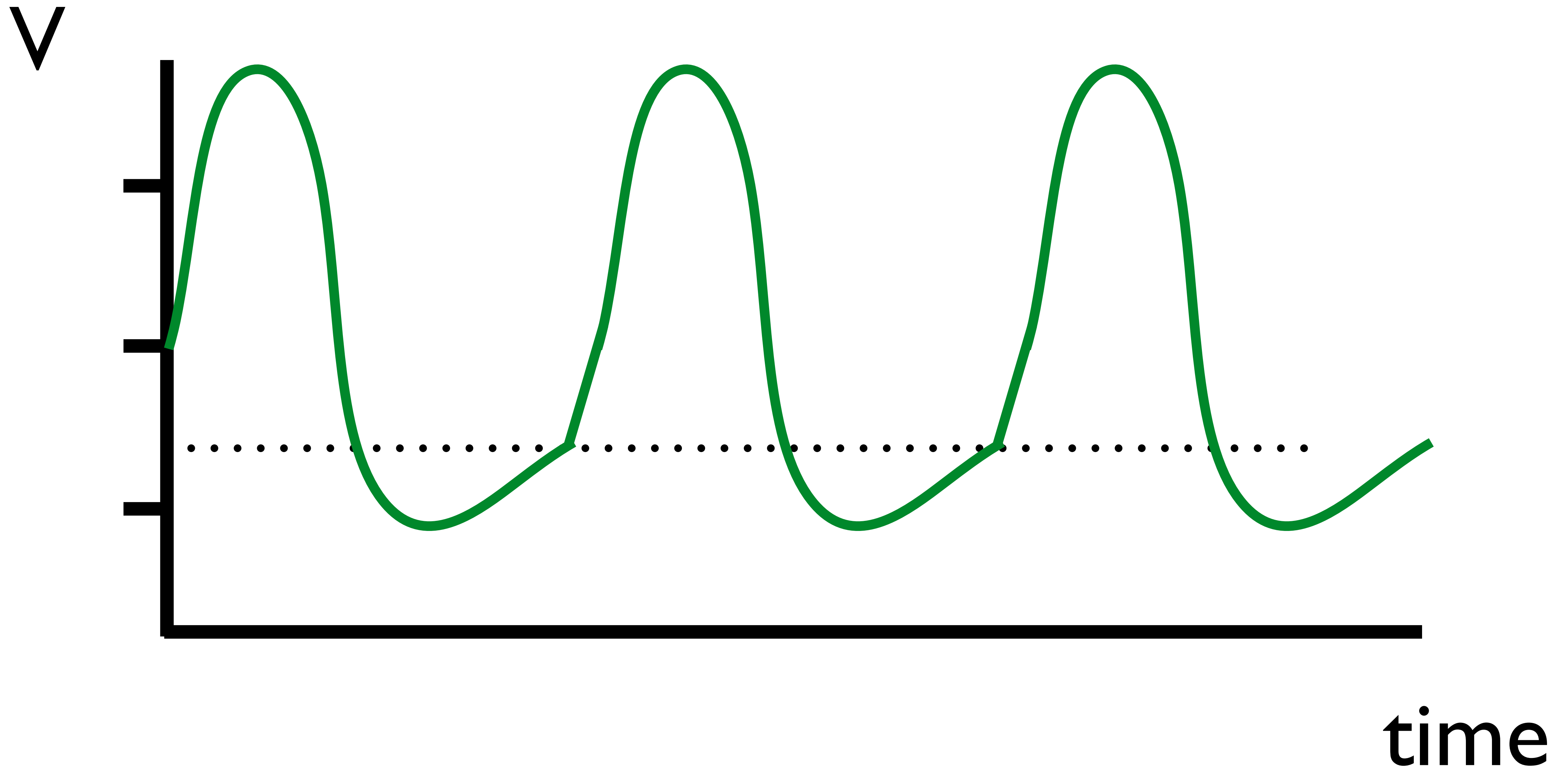


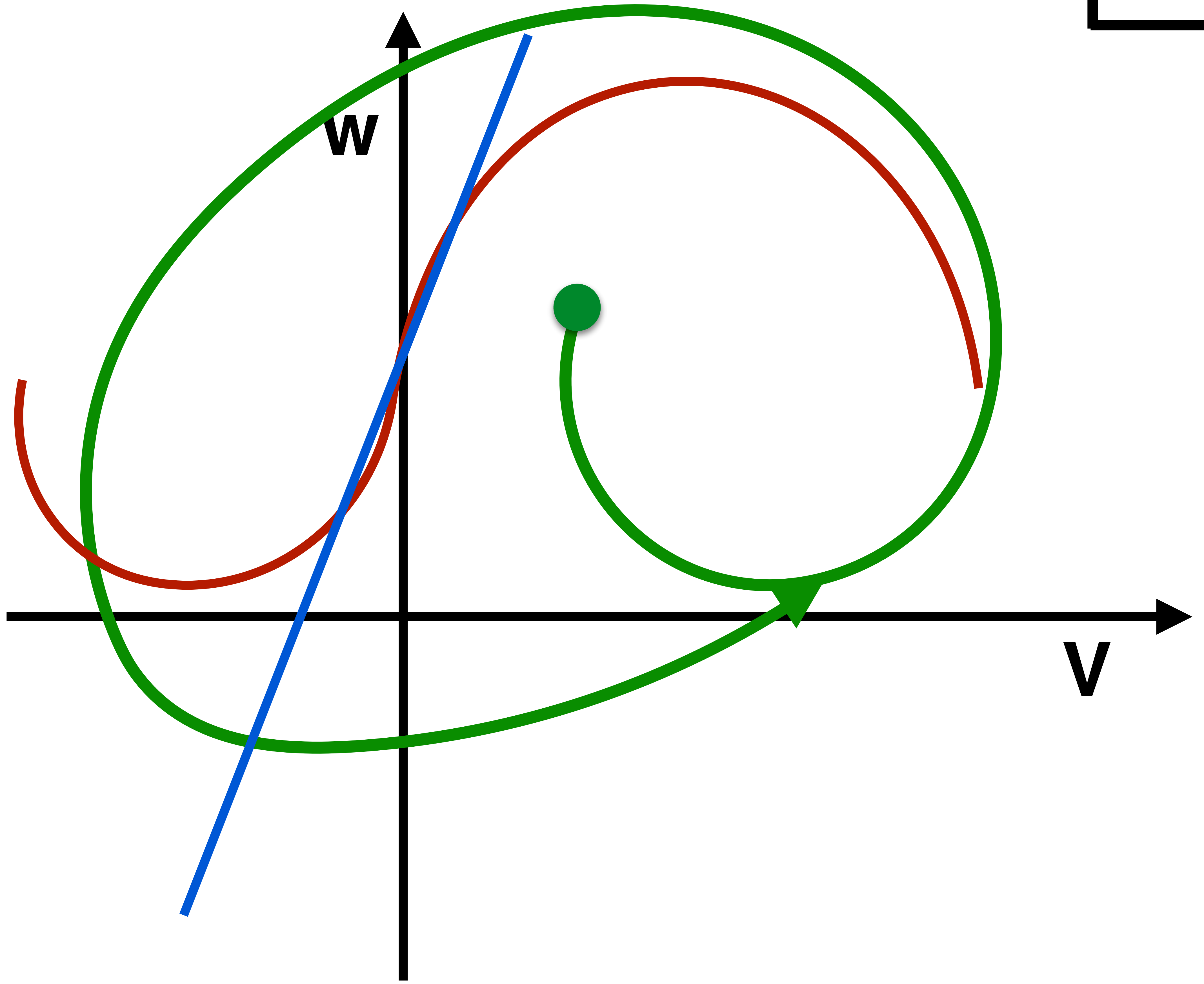


Limit Cycle

$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w + I$$

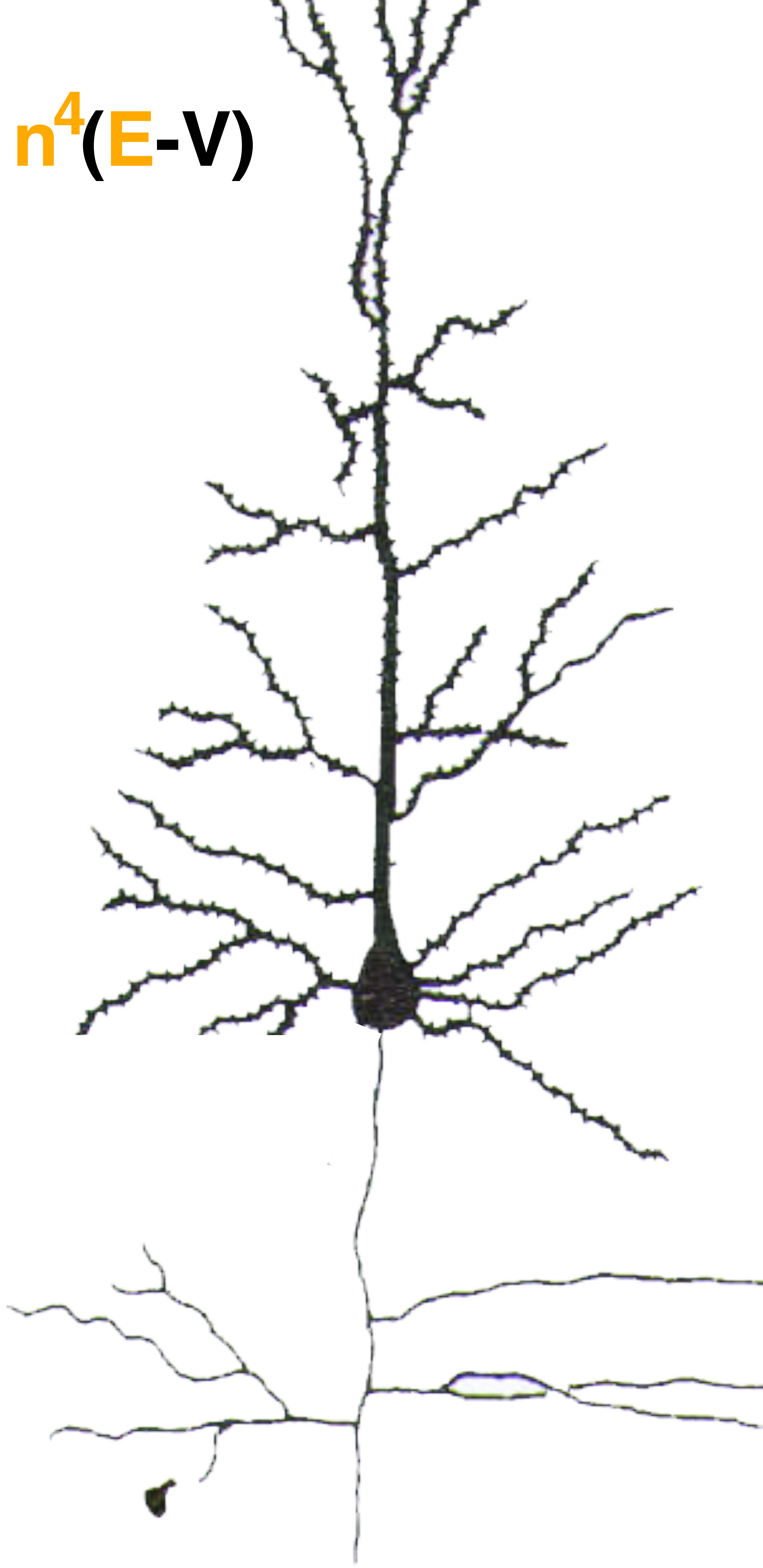
$$\frac{dw}{dt} = a + bV - w$$



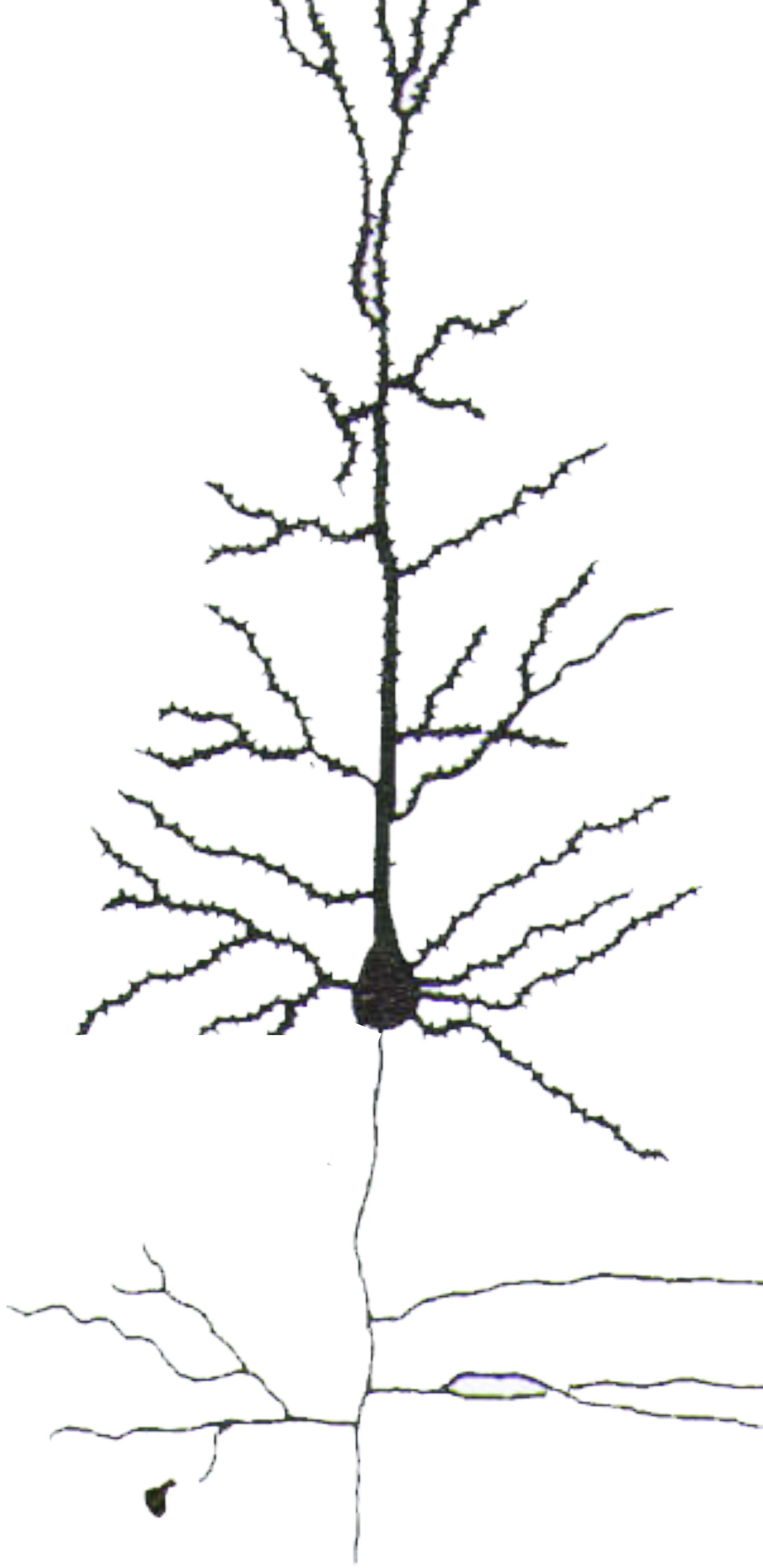


Limit Cycle

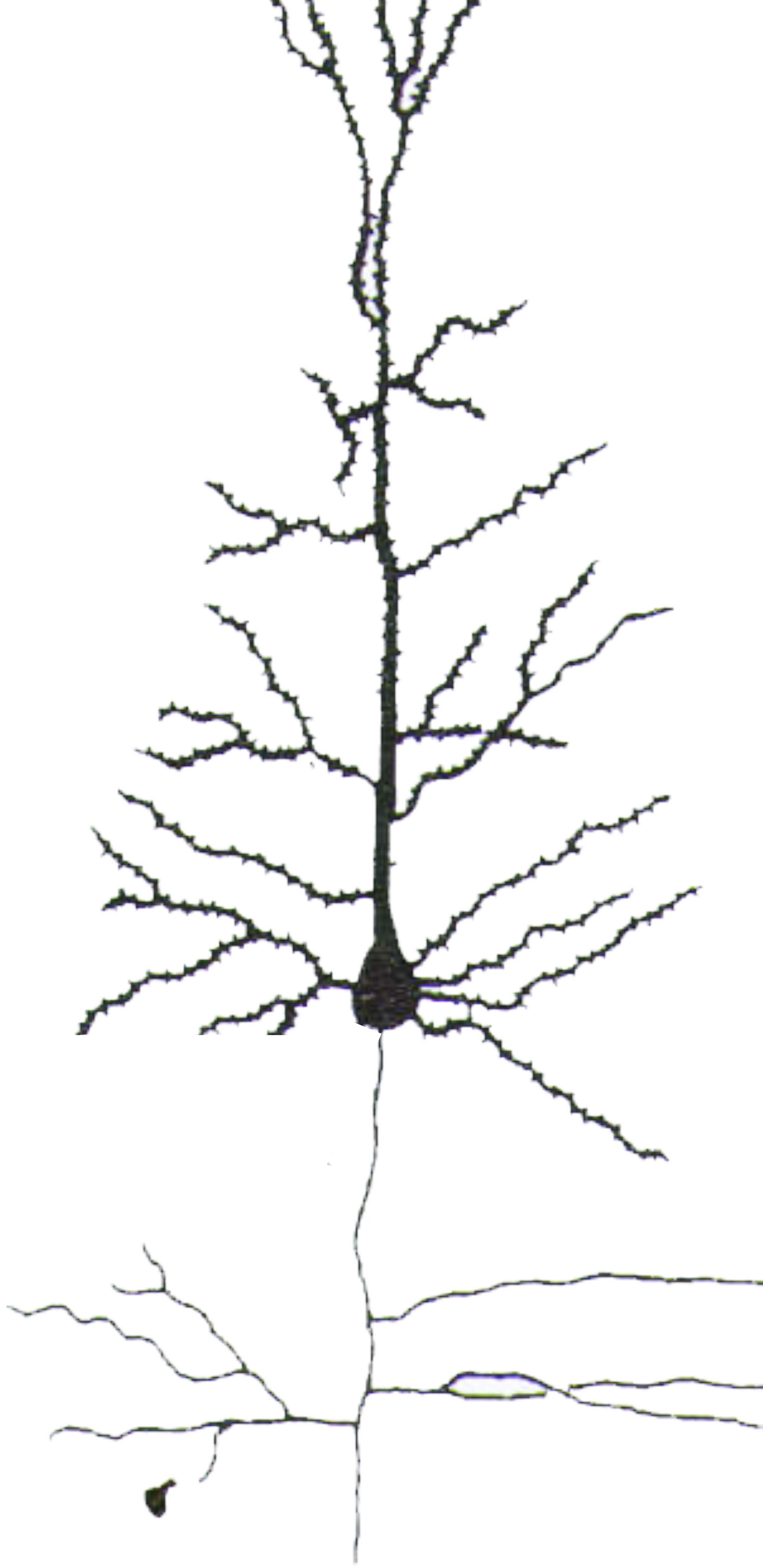
$$C \frac{dV}{dt} = g_{leak}(E-V) + g_{synapse}(E-V) + g_{Na}\, m^3 h (E-V) + g_K\, n^4 (E-V)$$



$$C \frac{dV}{dt} = g_{leak} (E-V) + g_{synapse} (E-V)$$



$$C \frac{dV}{dt} = g_{leak}\,(E\text{-}V) + g_{synapse}\,(E\text{-}V)$$

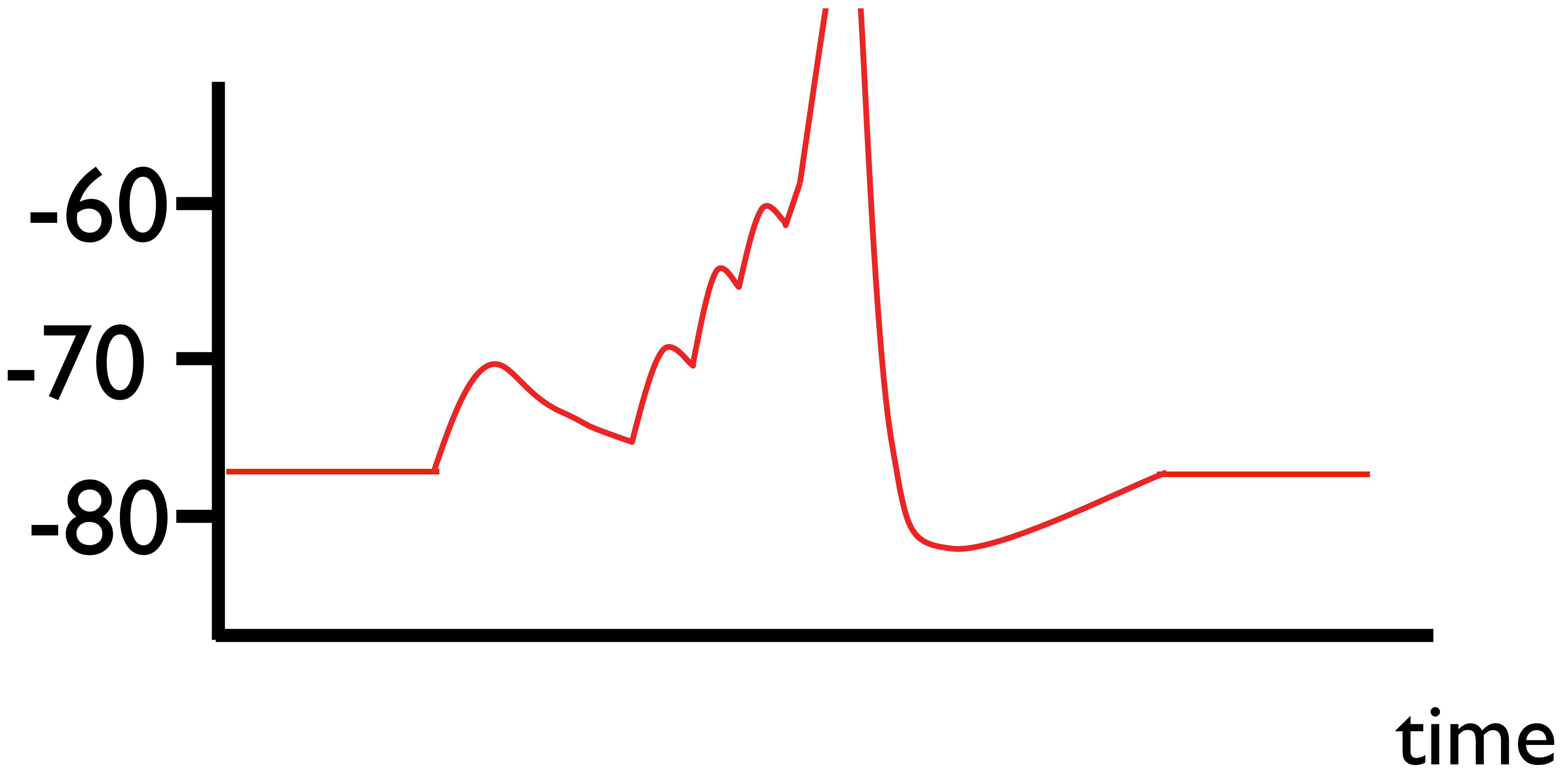


$$g_{tot} = g_{leak} + g_{syn}$$

$$E\,(\Delta t) = \frac{g_{leak}\,E_{leak} + g_{syn}\,E_{syn}}{g_{tot}}$$

$$\tau\,(\Delta t) = \frac{C}{g_{tot}}$$

$$V\,(t+\Delta t) = E\,(\Delta t) + \left(V(t) - E\,(\Delta t)\right) e^{-\frac{\Delta t}{\tau\,(\Delta t)}}$$



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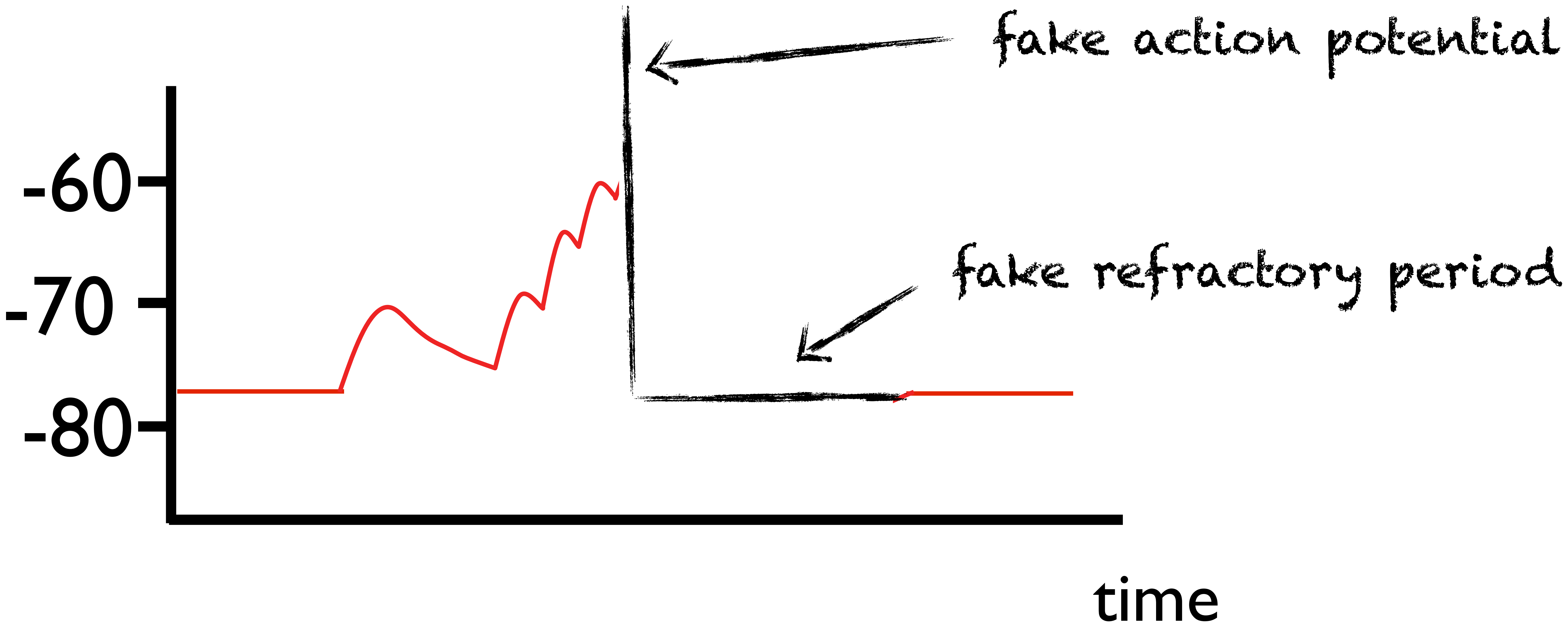

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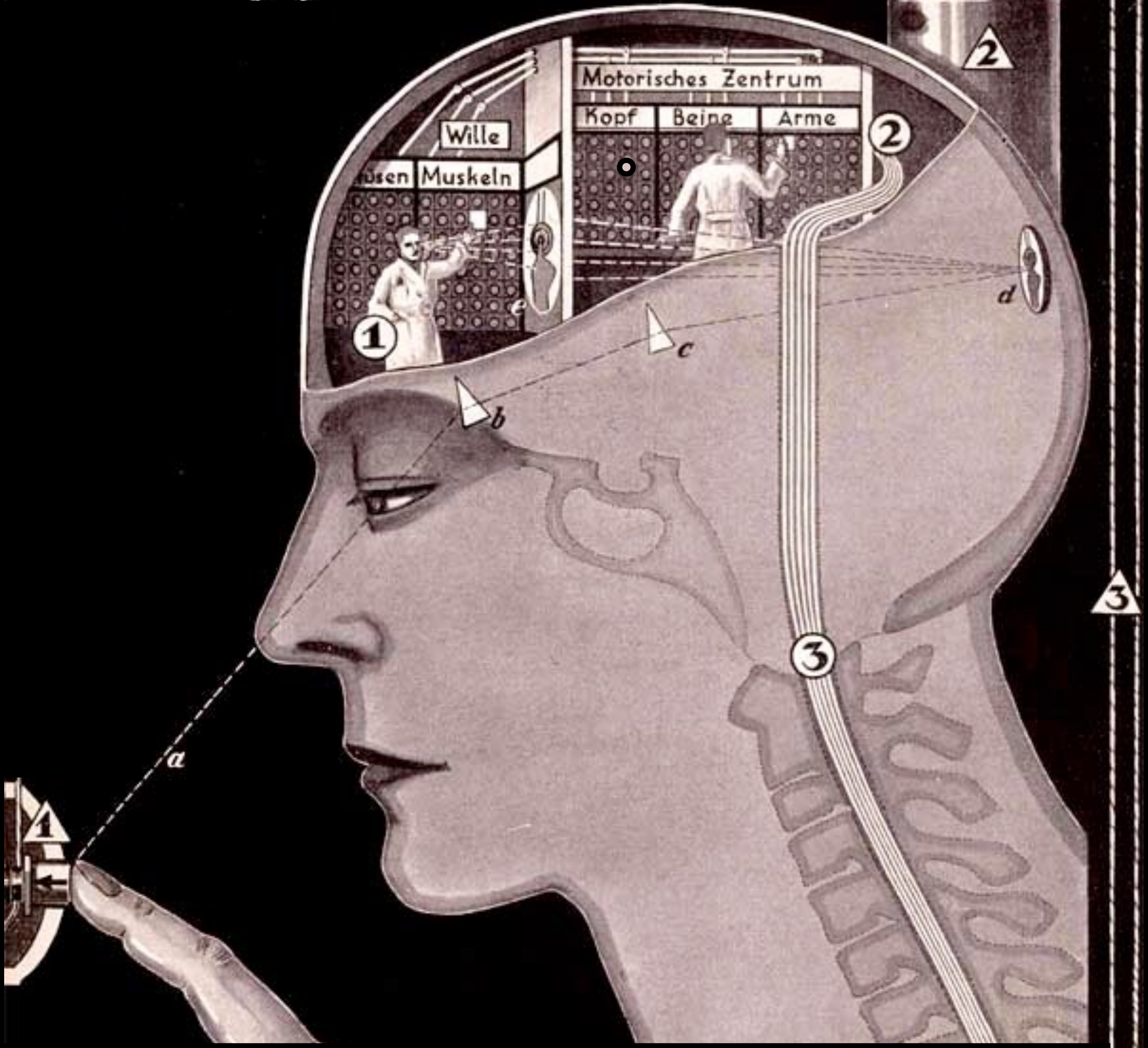
Tim Vogels,
Chaitanya Chintaluri
and
Basile Confavreux
in:

Neurotheory & Computational Neuroscience



Fritz Kahn: Das Leben des Menschen; eine volkstümliche Anatomie, Biologie, Physiologie und Entwicklungsgeschichte des Menschen. Vol. 2, Stuttgart, 1926

$$V_{(t+\Delta t)} = E_{(\Delta t)} + \left(V_{(t)} - E_{(\Delta t)} \right) e^{-\frac{\Delta t}{\tau(\Delta t)}}$$

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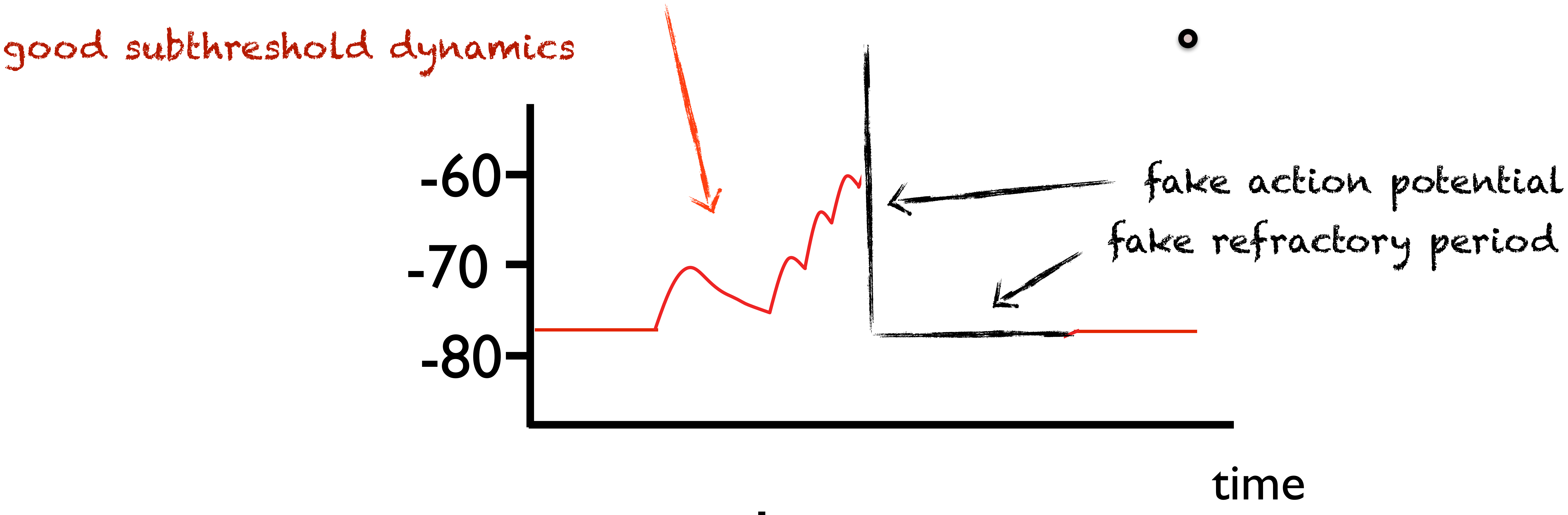

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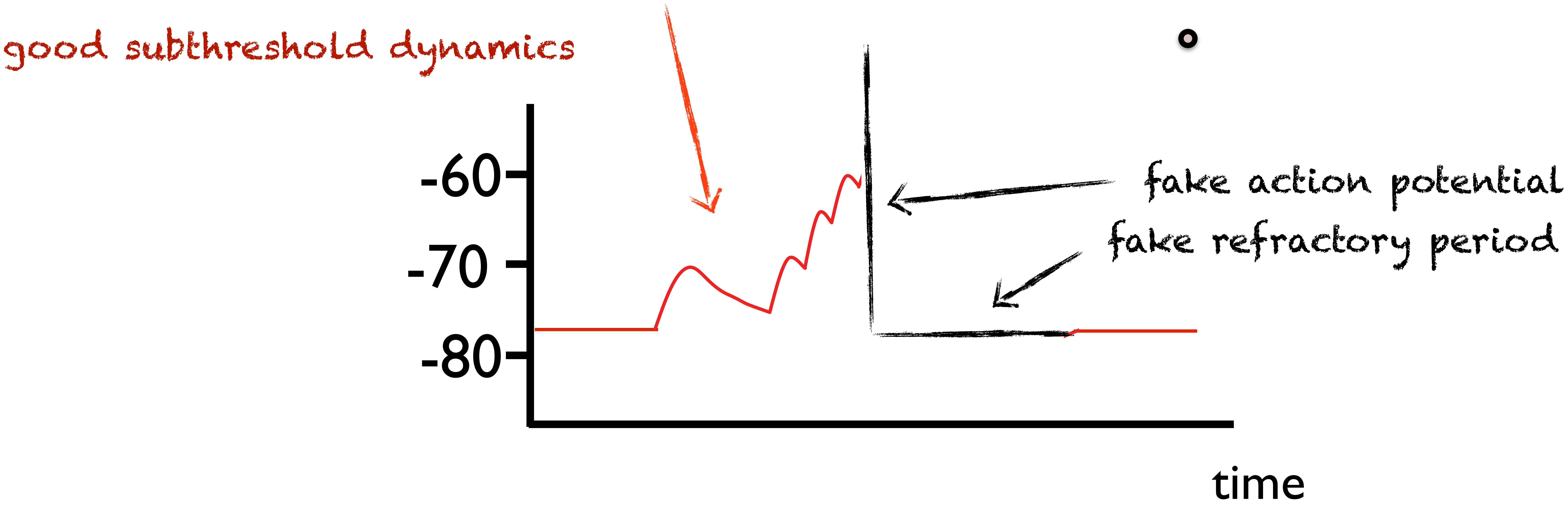
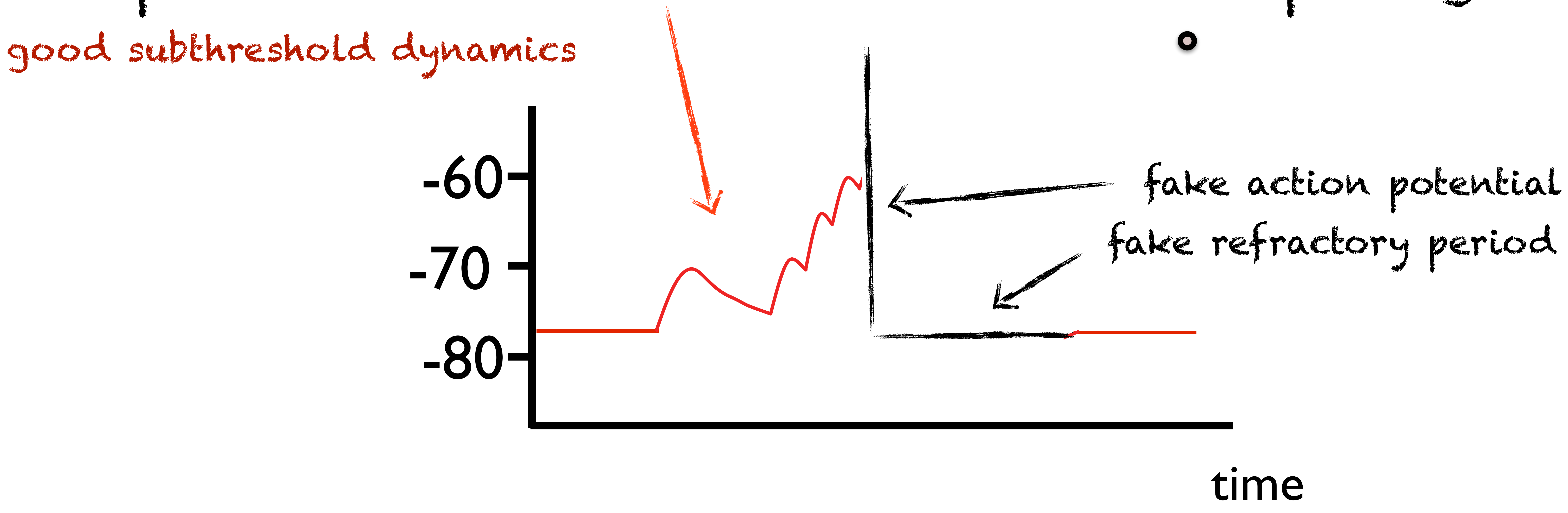


Voilà,...

Integrate & fire!!

A cheap and accurate method to simulate spiking



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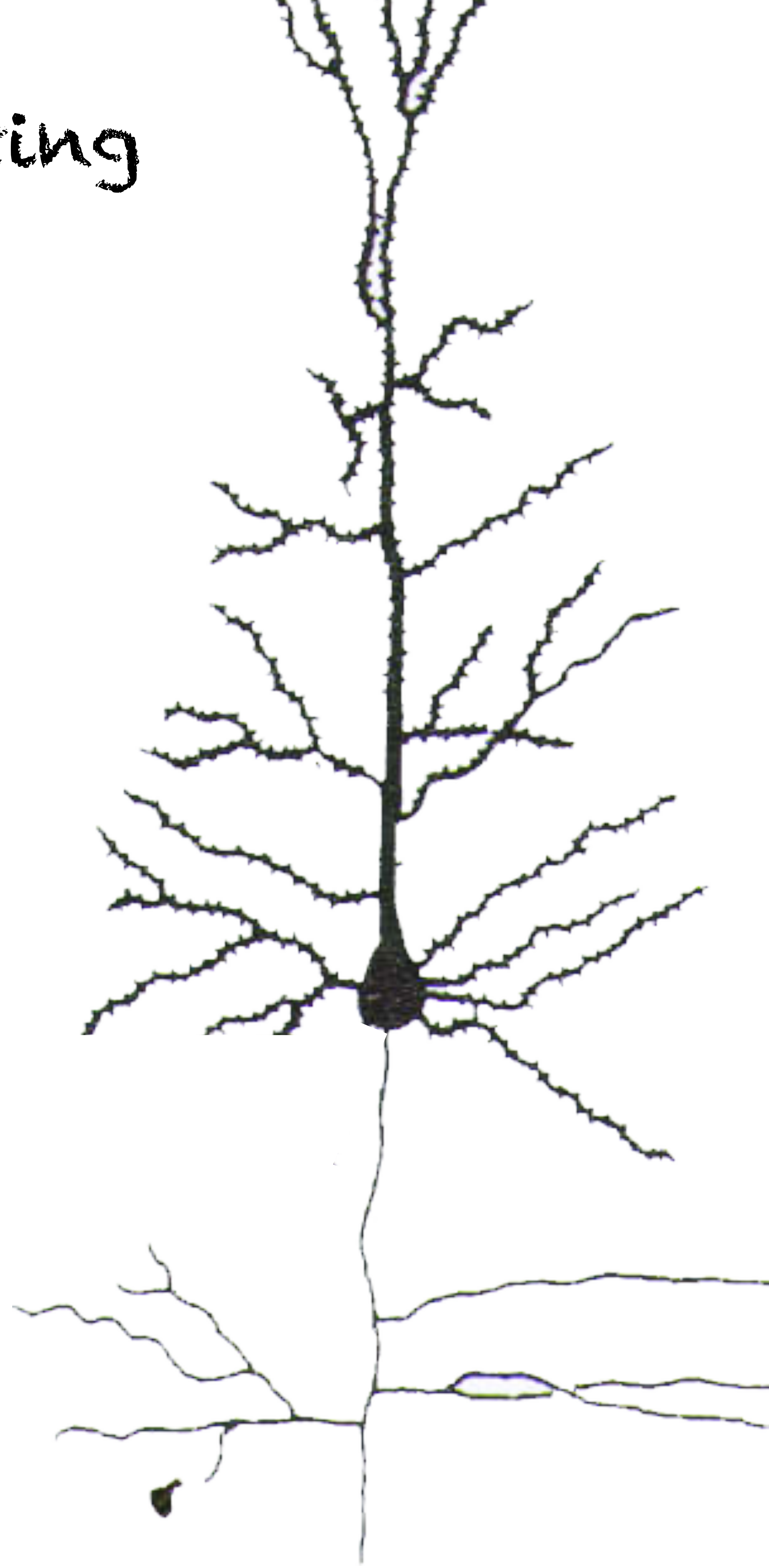
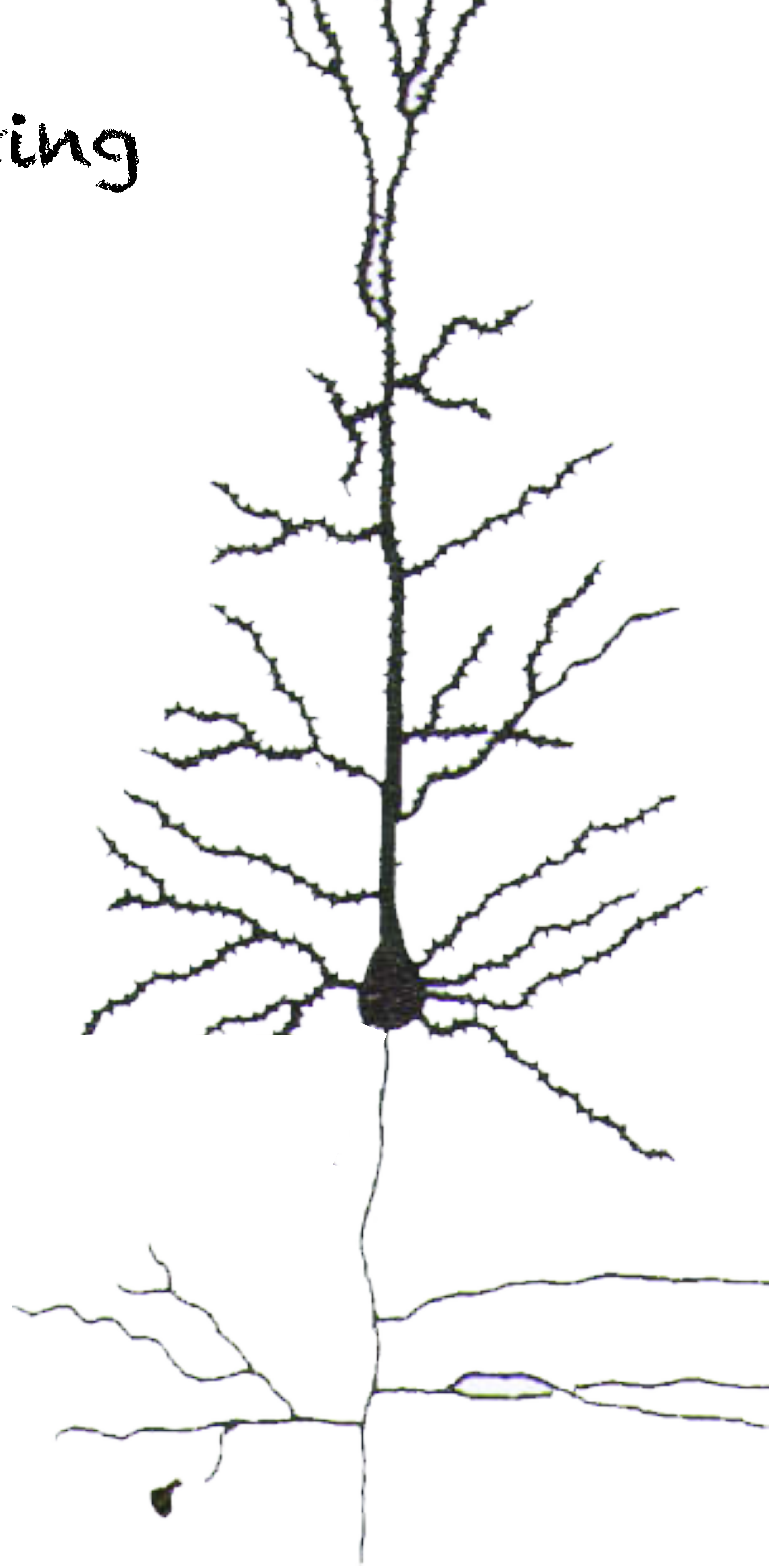
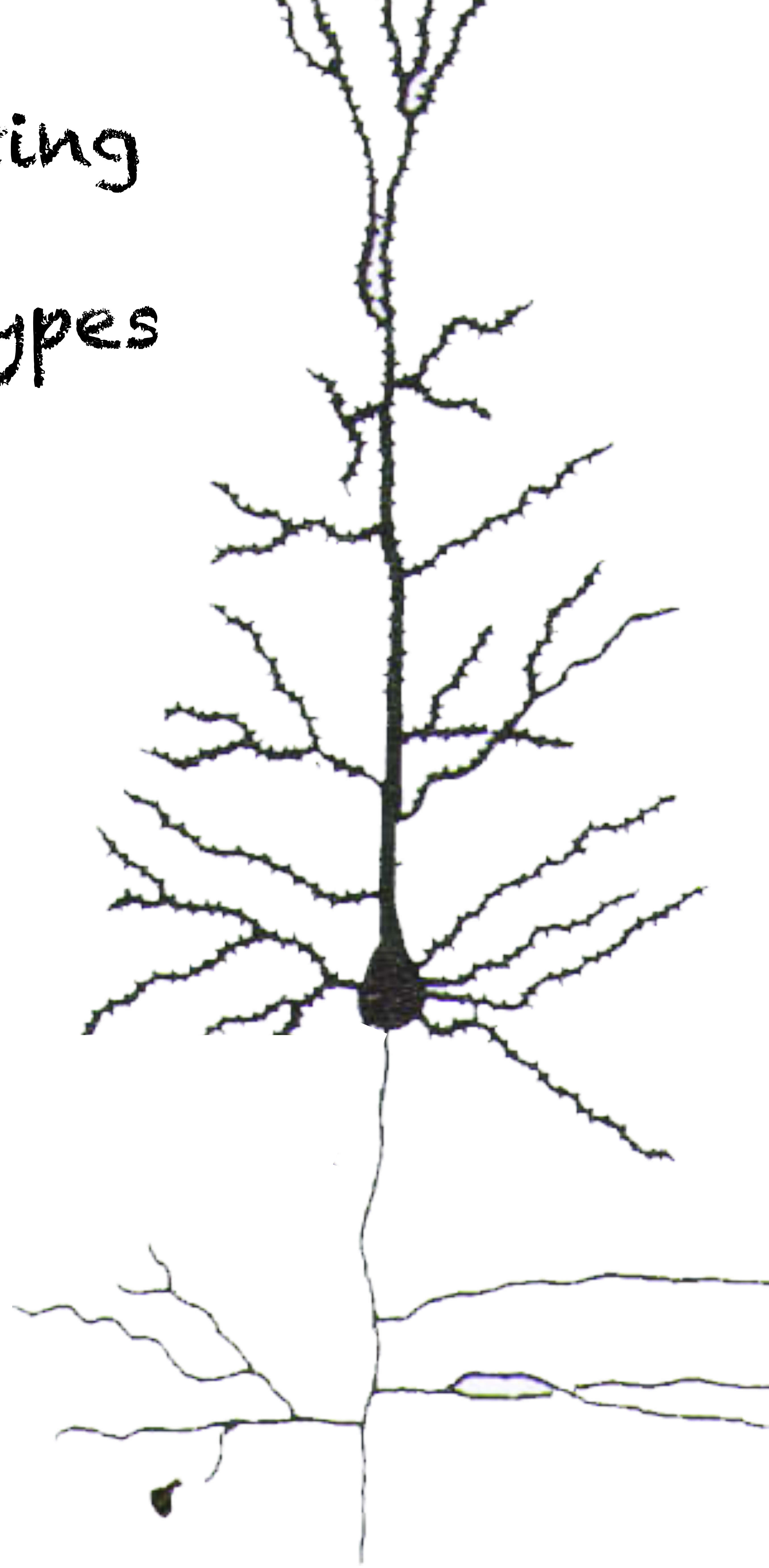
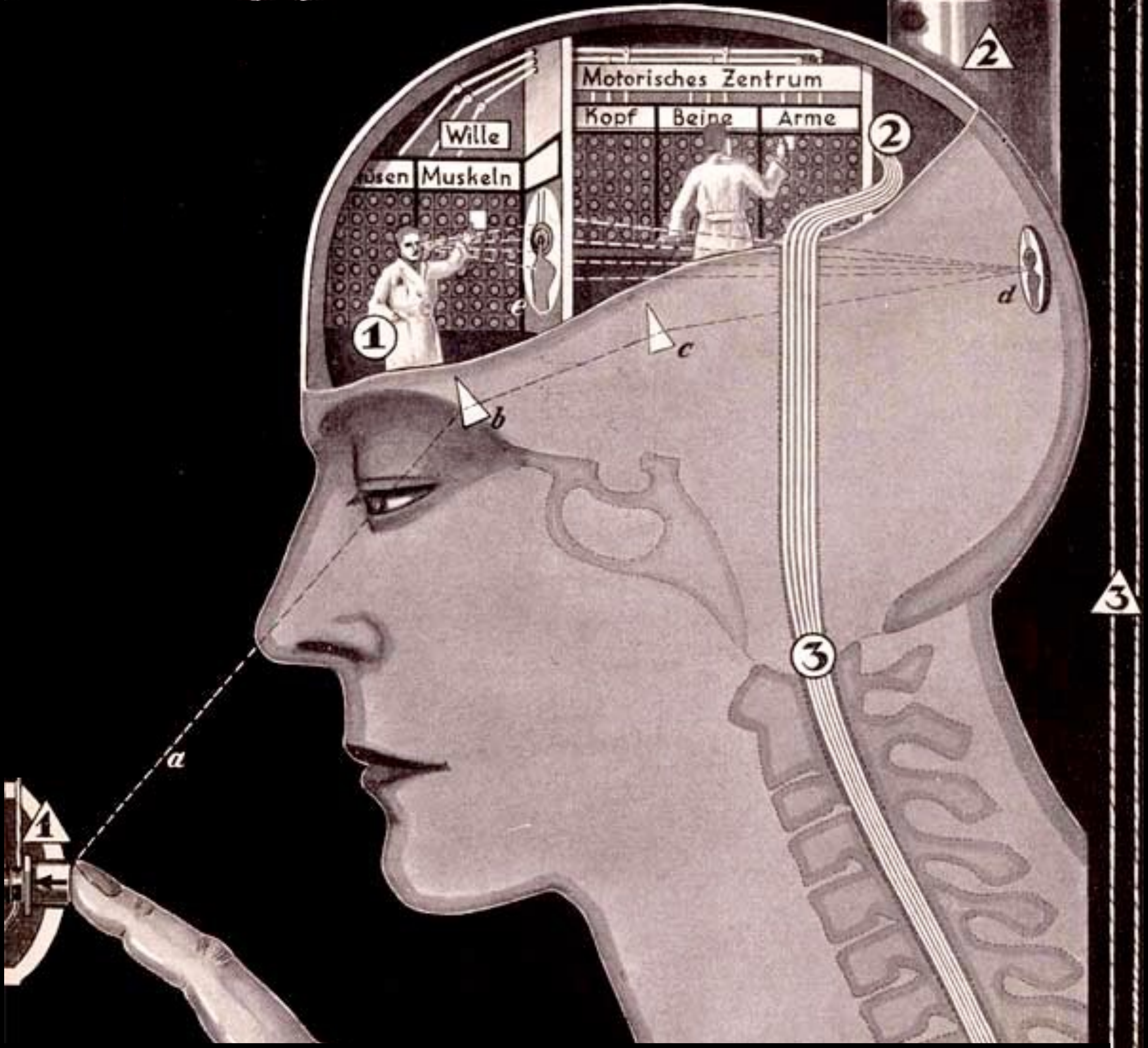


A cheap and accurate method to simulate spiking



A cheap and accurate method to simulate spiking neurons that works for all neuron types





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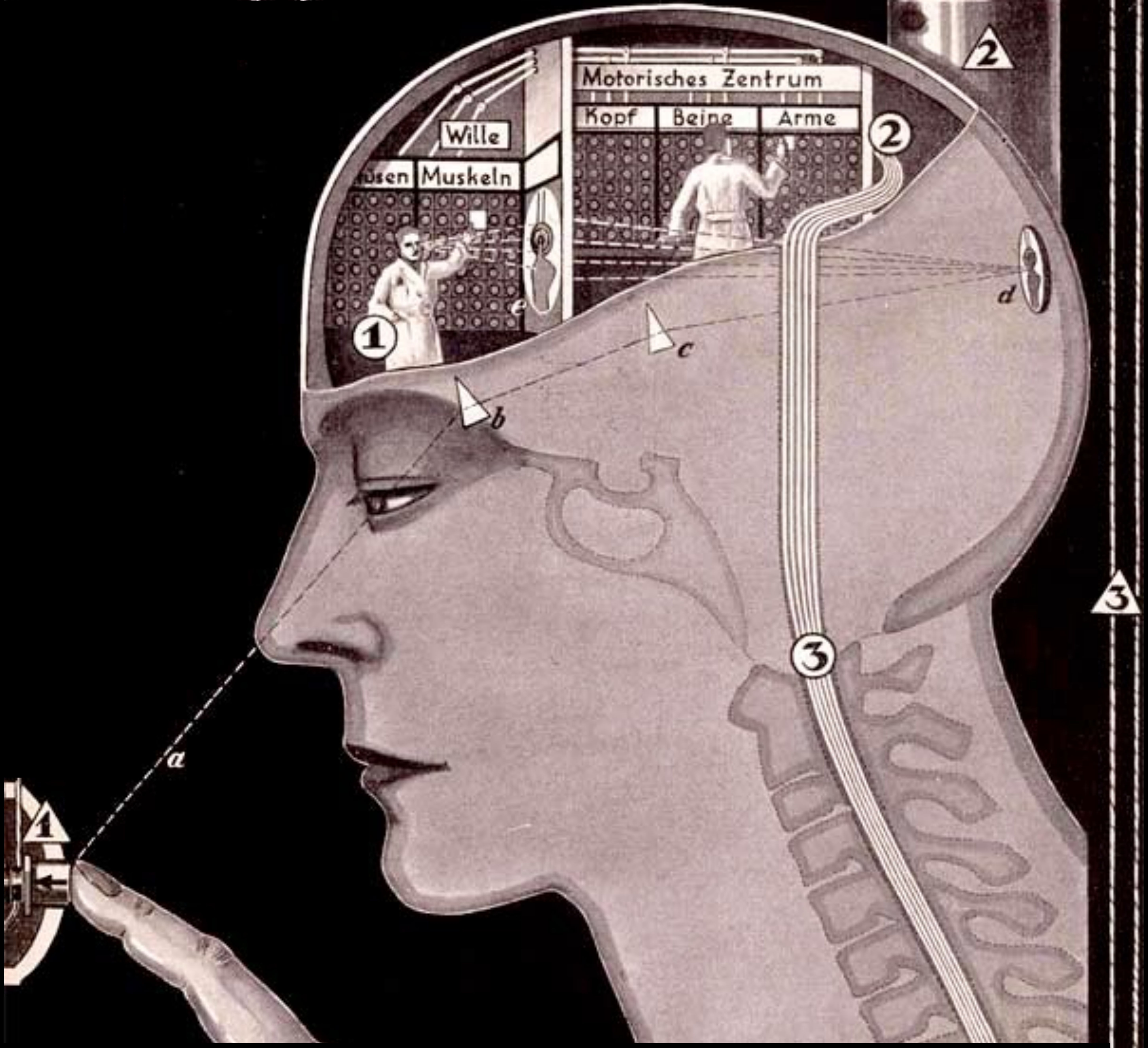
The Neural Code:

- Representation
- Transmission
- Transformation
- Interpretation

Perkel and Bullock: Neurosciences Research Bulletin, 1968 • 6: 219-349



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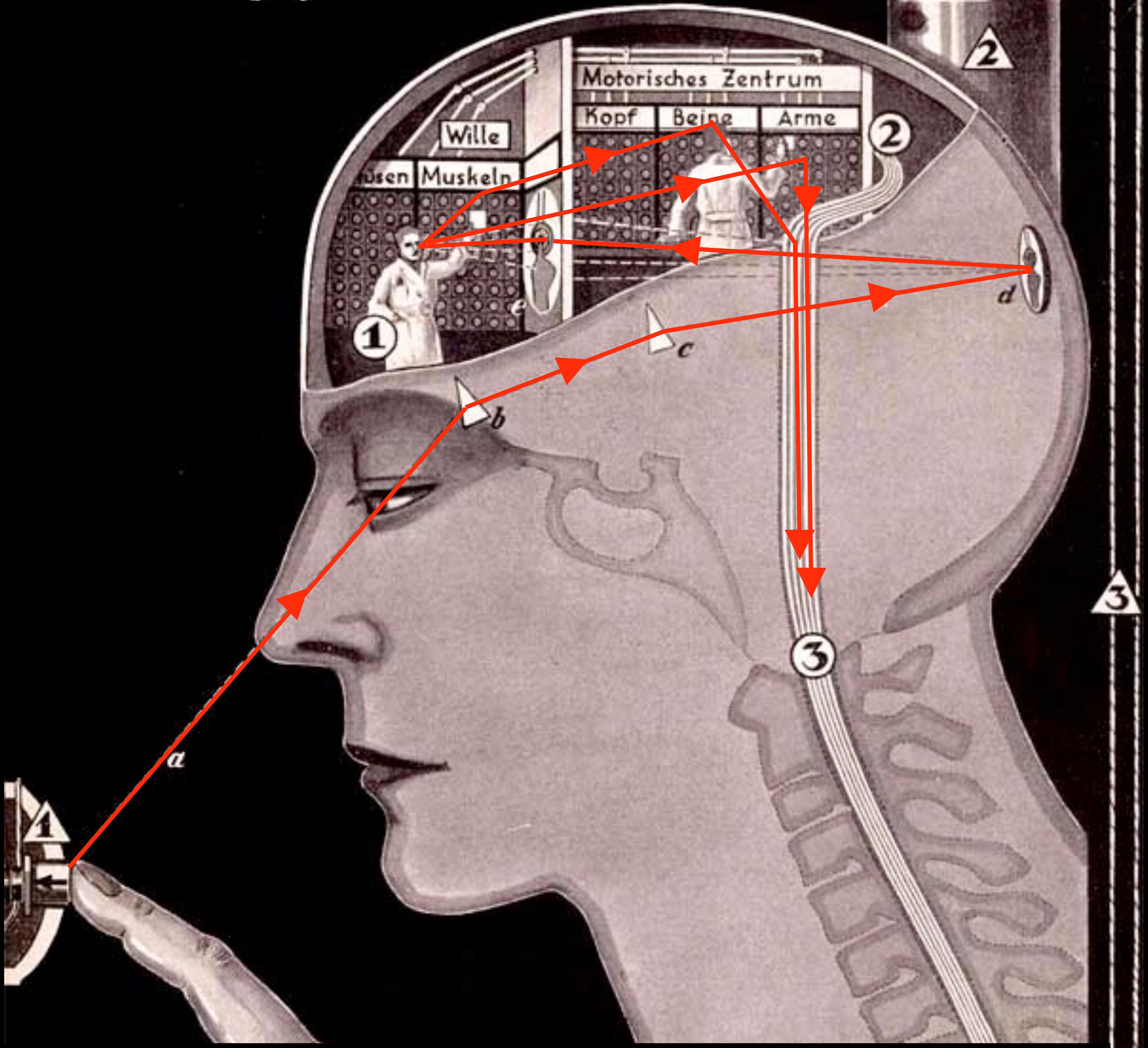

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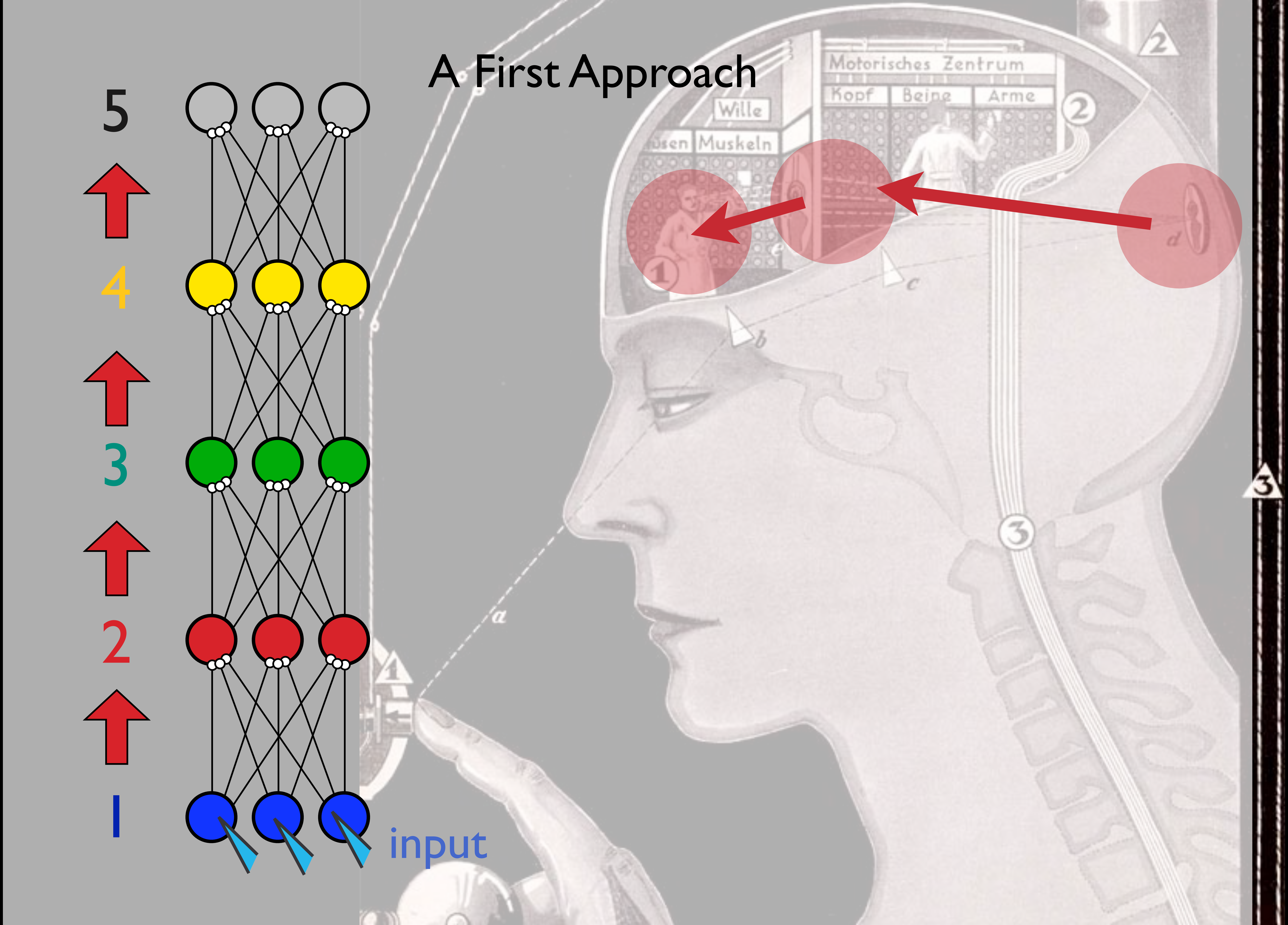
A First Approach



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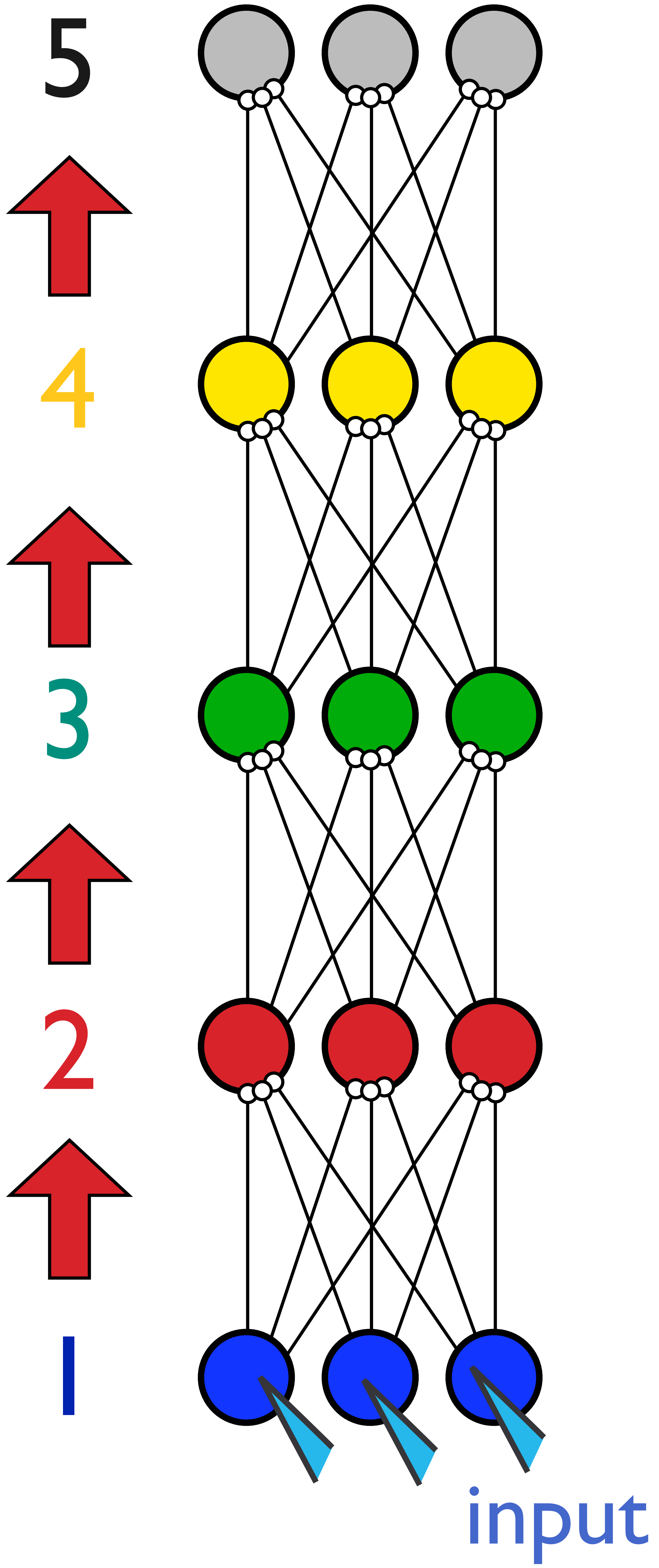
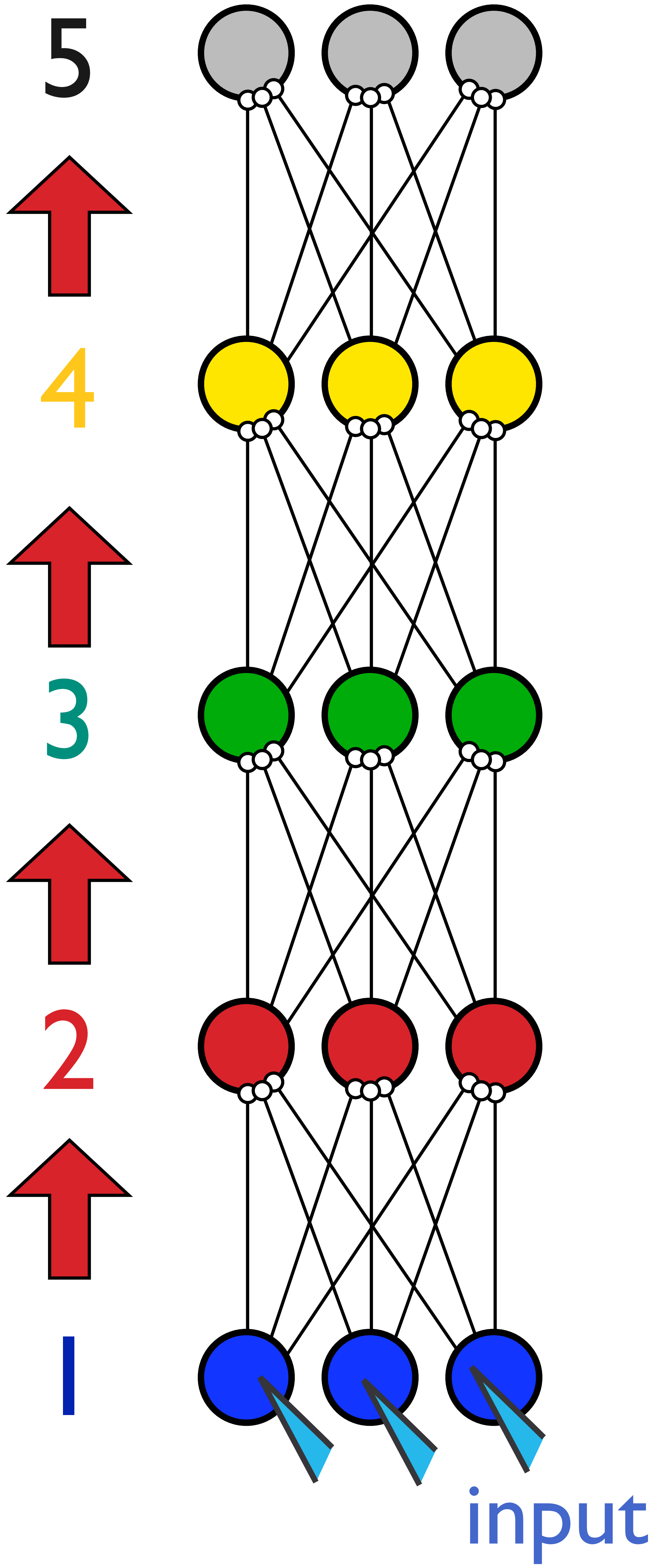
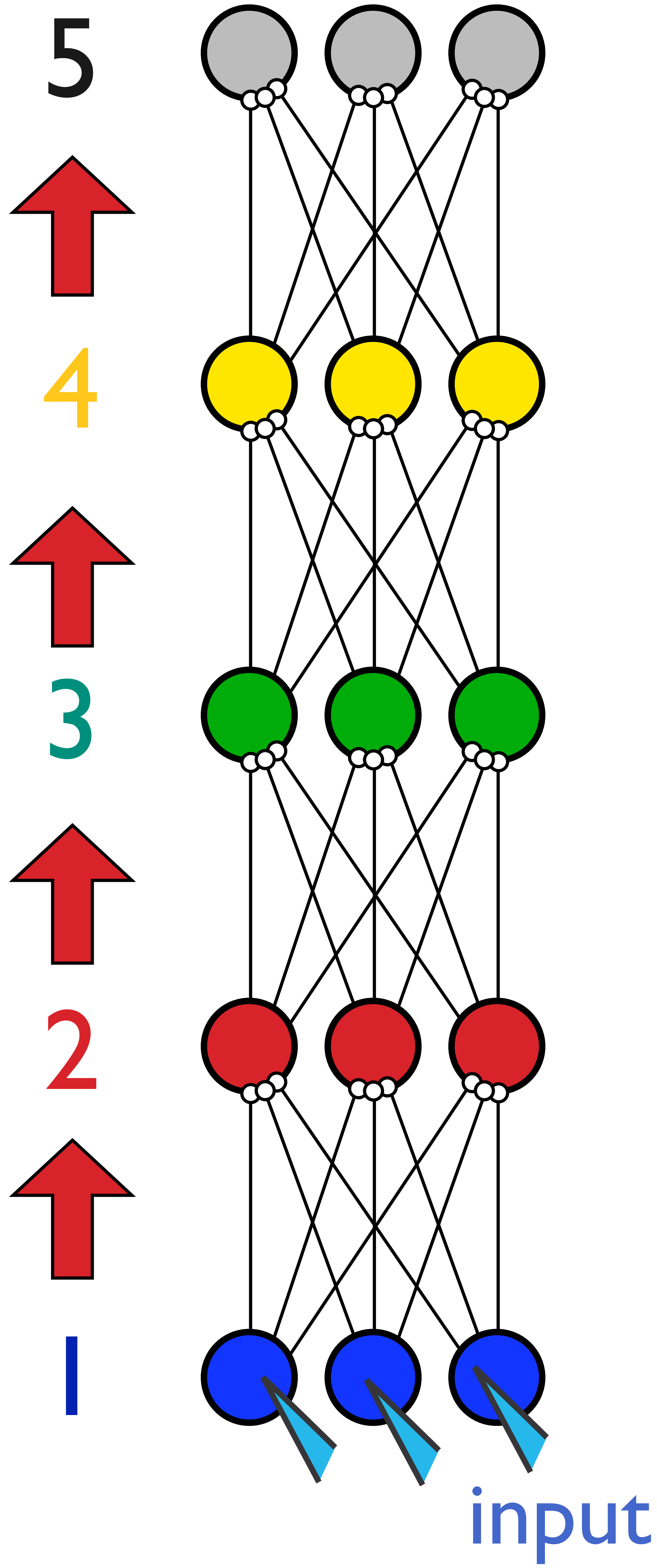


A First Approach



$$V(t) = E_{dt} + \left(V(t-1) - E_{dt}\right) e^{-\frac{dt}{\tau_{dt}}}$$

A First Approach



$$\tau_{dt} = \frac{C}{g_{tot}}$$

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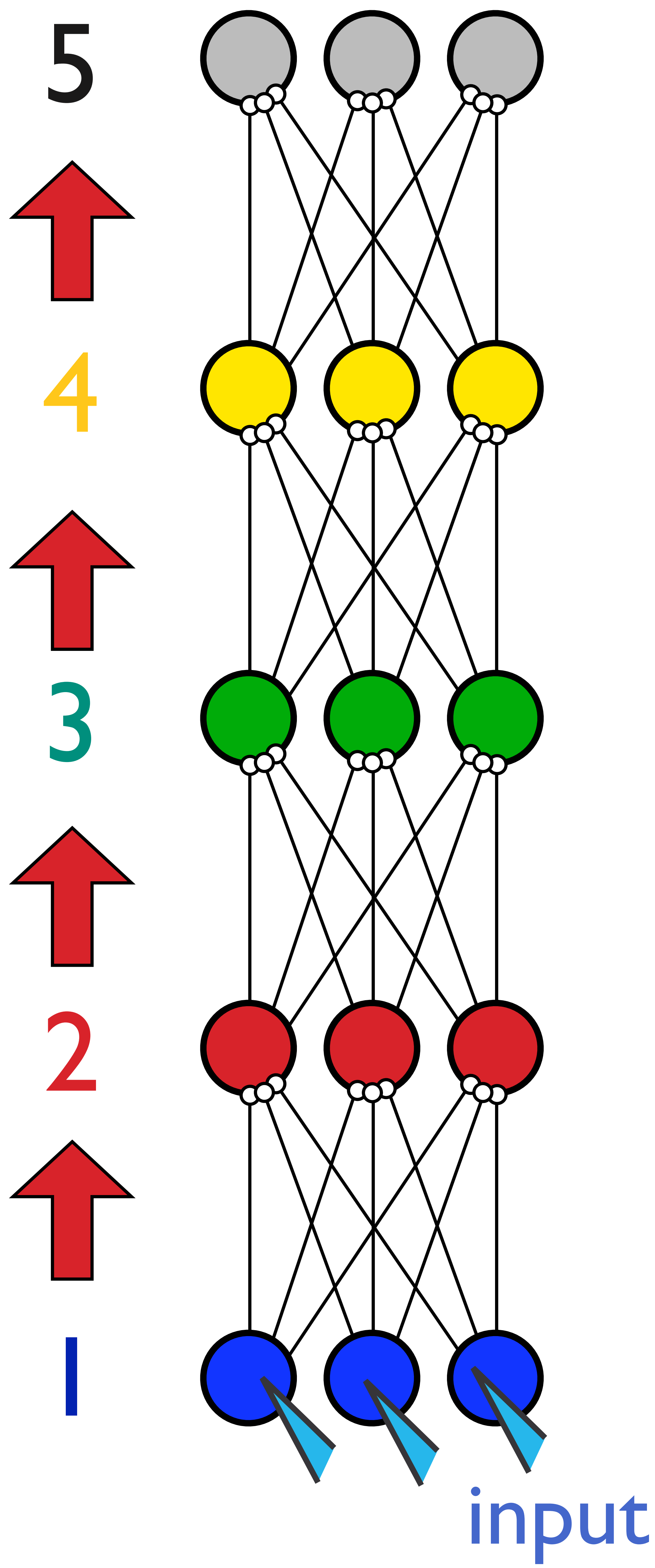
A First Approach

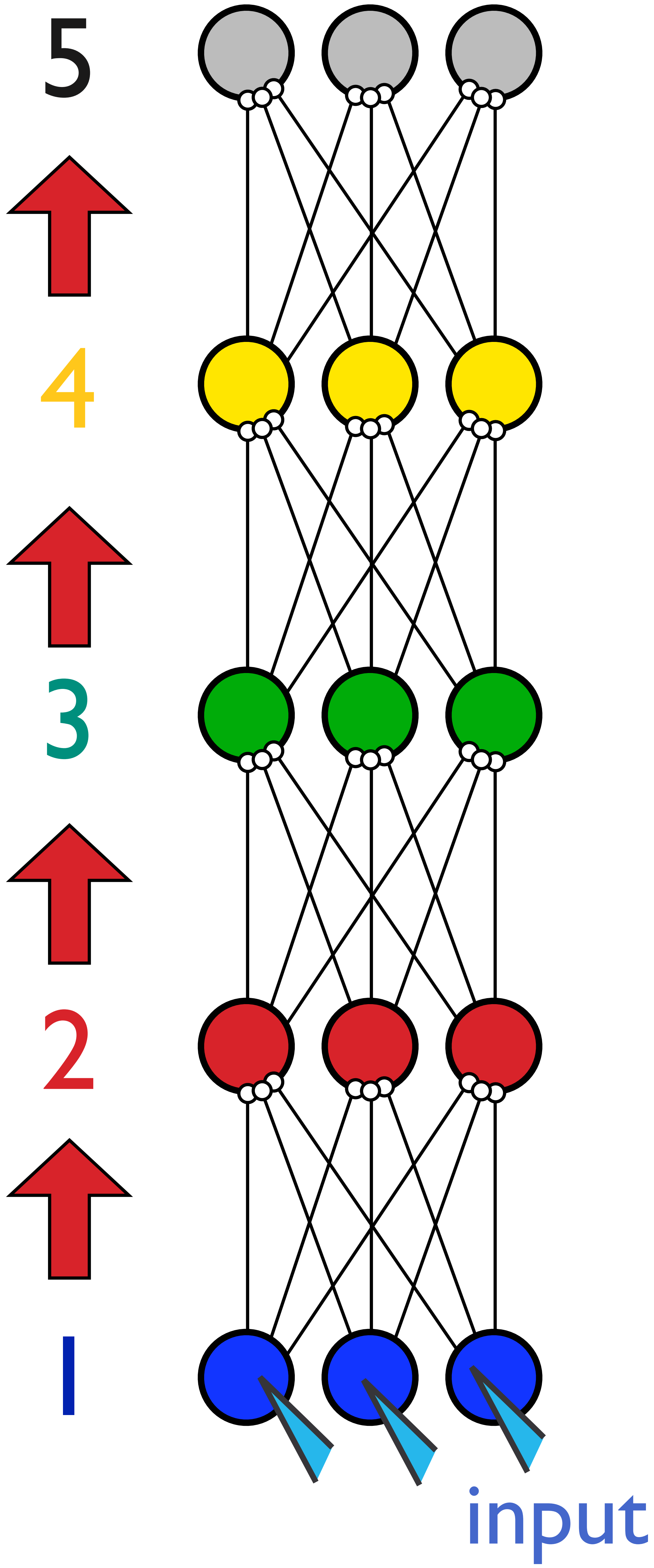


$$E_{dt} = \frac{g_{leak}\,E_{leak} + g_{syn}(t)\,E_{syn}}{g_{tot}}$$

$$\tau_{dt} = \frac{C}{g_{tot}}$$

$$V(t) = E_{dt} + \left(V(t-1) - E_{dt}\right) e^{-\frac{dt}{\tau_{dt}}}$$

A First Approach



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$$E_{dt} = \frac{g_{leak}\,E_{leak} + g_{syn}(t)\,E_{syn}}{g_{tot}}$$

$$\tau_{dt} = \frac{C}{g_{tot}}$$

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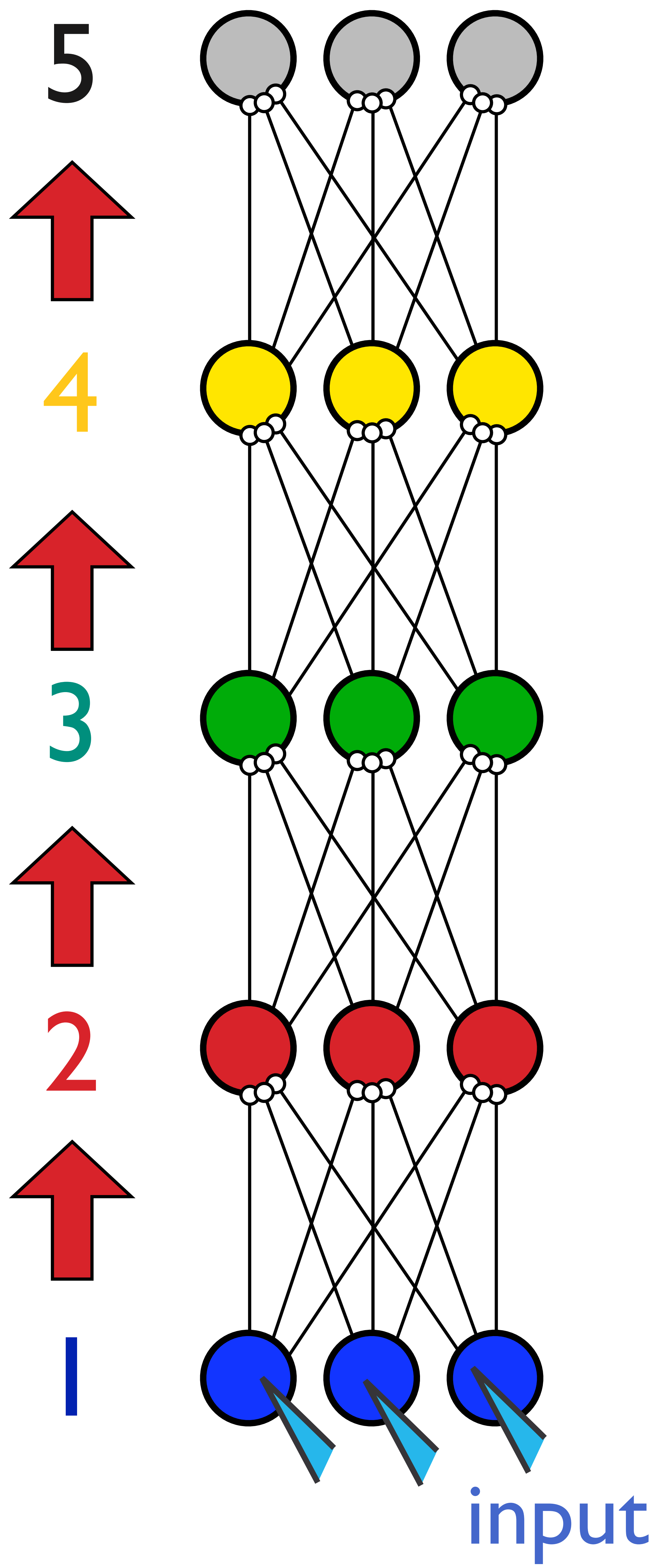
A First Approach



$$g_{tot} = g_{leak} + g_{syn}(t)$$

$$E_{dt} = \frac{g_{leak}\,E_{leak} + g_{syn}(t)\,E_{syn}}{g_{tot}}$$

$$\tau_{dt} = \frac{C}{g_{tot}}$$

$$V(t) = E_{dt} + \left(V(t-1) - E_{dt}\right) e^{-\frac{dt}{\tau_{dt}}}$$

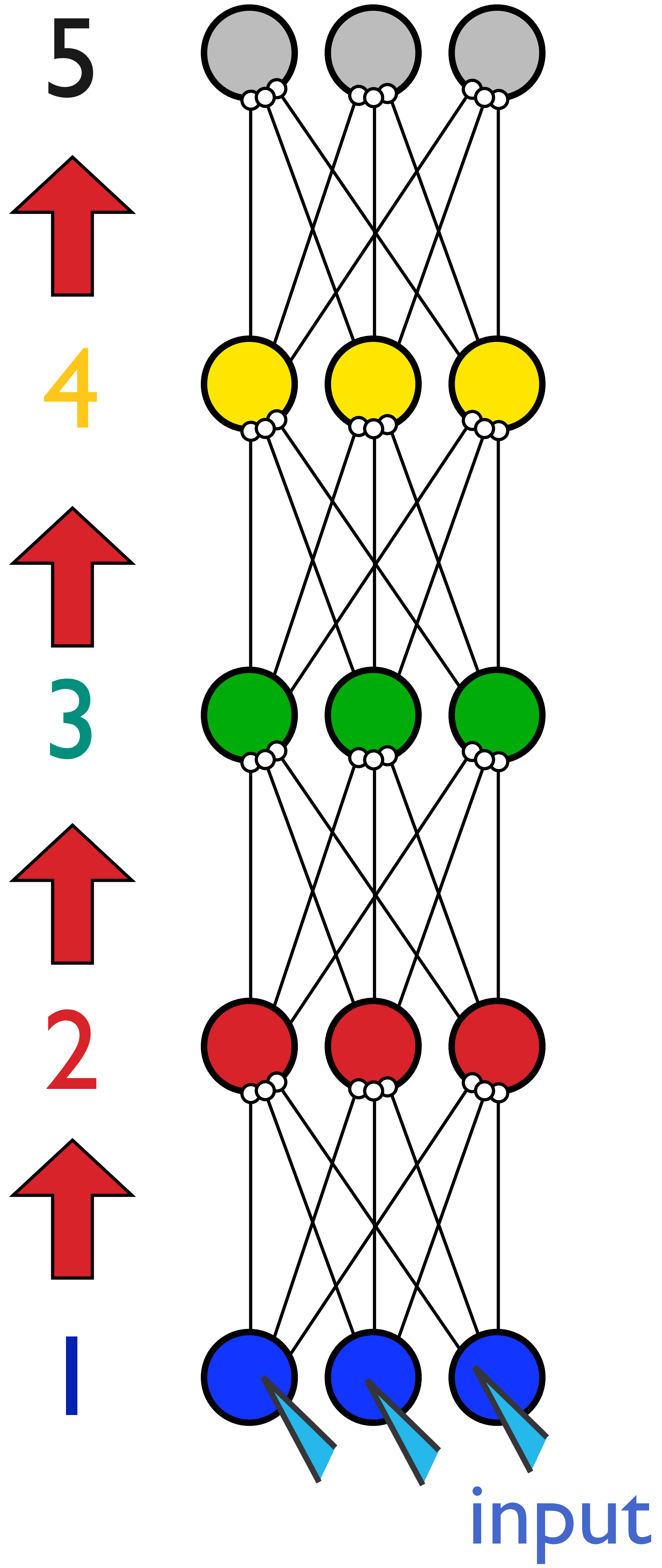
if $(V(t) > \Theta)$

$V(t-1) = 20;$

$V(t) = Vrest$

end

A First Approach



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if $(V(t) > \Theta)$

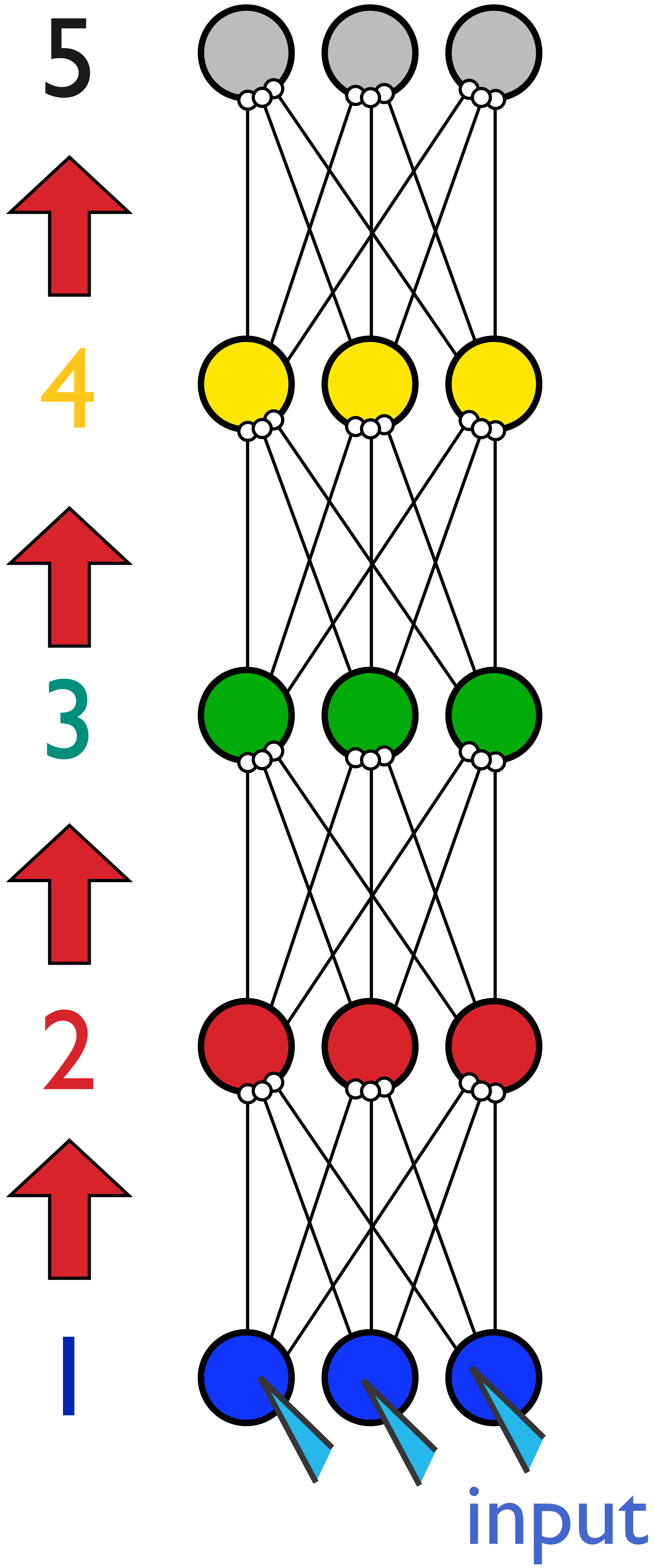
$V(t-1) = 20;$

$V(t) = Vrest$

$$g_{syn}(t_j) = g_{syn}(t) + g$$

end

A First Approach



$$g_{syn}(t,i) = g_{syn}(t-1\ )\, e^{-\frac{dt}{\tau_{syn}}}$$

$$g_{tot} = g_{leak} + g_{syn}(t\ )$$

$$E_{dt} = \frac{g_{leak}\, E_{leak} + g_{syn}\,(t\ )\, E_{syn}}{g_{tot}}$$

$$\tau_{dt} = \frac{C}{g_{tot}}$$

$$V\ (t) = E_{dt} + \left(V\ (t-1) - E_{dt}\right) e^{-\frac{dt}{\tau_{dt}}}$$

if $(V(t) > \Theta)$

$V(t-1) = 20;$

$V(t) = Vrest$

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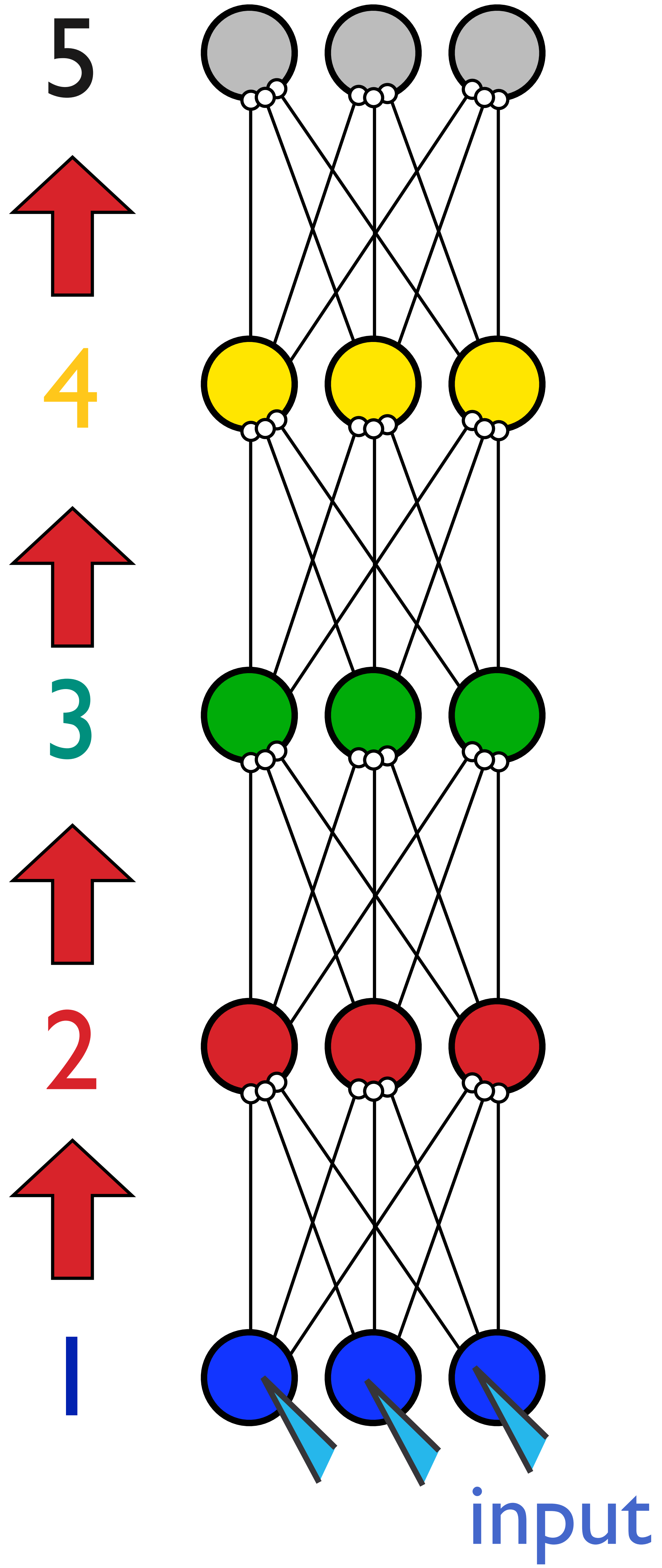
end

A First Approach



$$g_{syn}(t,i) = g_{syn}(t-1,i)\, e^{-\frac{dt}{\tau_{syn}}}$$

$$g_{tot} = g_{leak} + g_{syn}(t,i)$$

$$E_{dt} = \frac{g_{leak}\, E_{leak} + g_{syn}(t,i)\, E_{syn}}{g_{tot}}$$

$$\tau_{dt} = \frac{C}{g_{tot}}$$

$$V(t) = E_{dt} + \left(V(t-1) - E_{dt}\right) e^{-\frac{dt}{\tau_{dt}}}$$

if $(V(t) > \Theta)$

 $V(t-1) = 20;$

 $V(t) = Vrest$

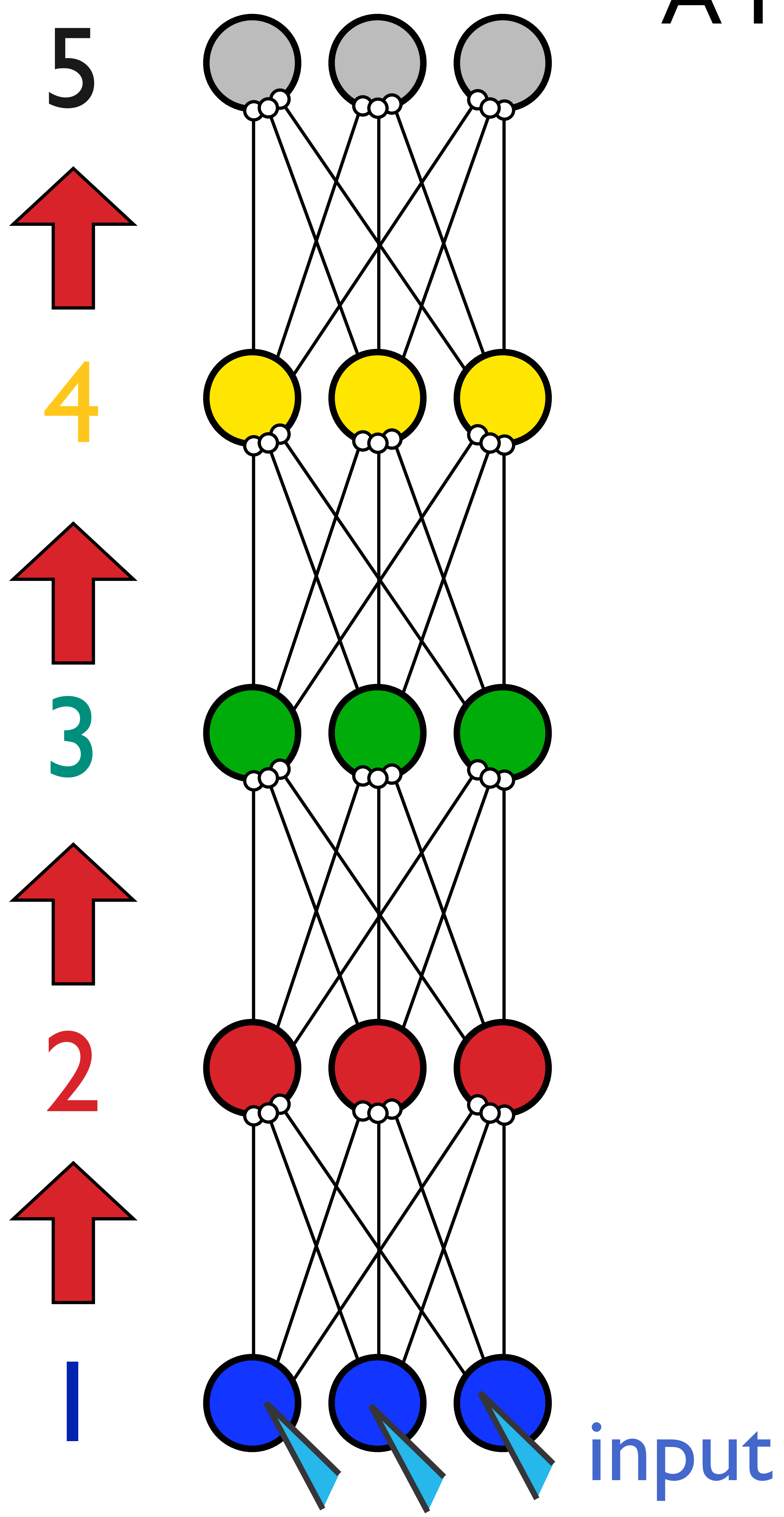
 for j=1:N

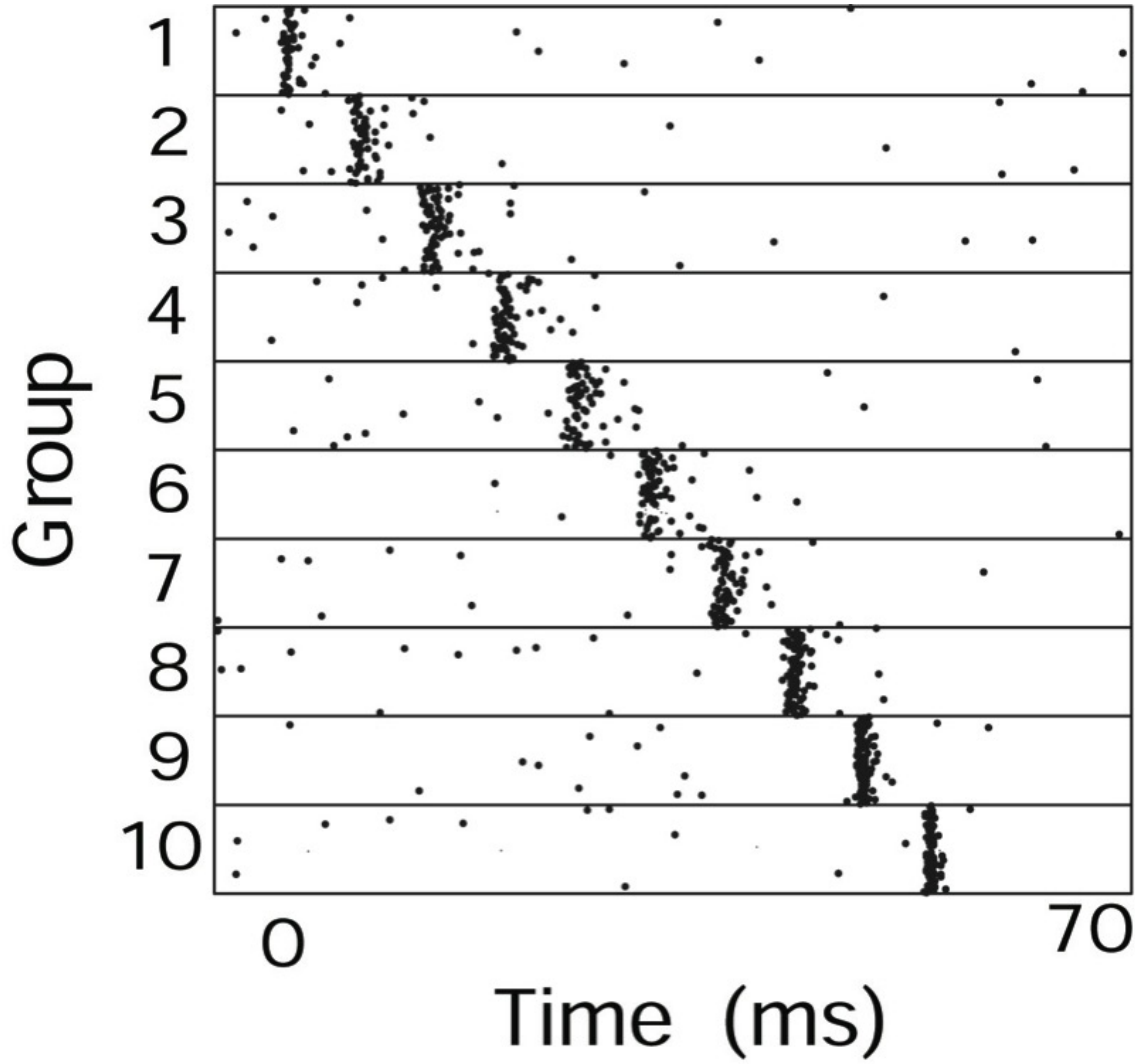
 $g_{syn}(t,j) = g_{syn}(t,j) + g * \mathbf{W}(i,j)$

 end

end

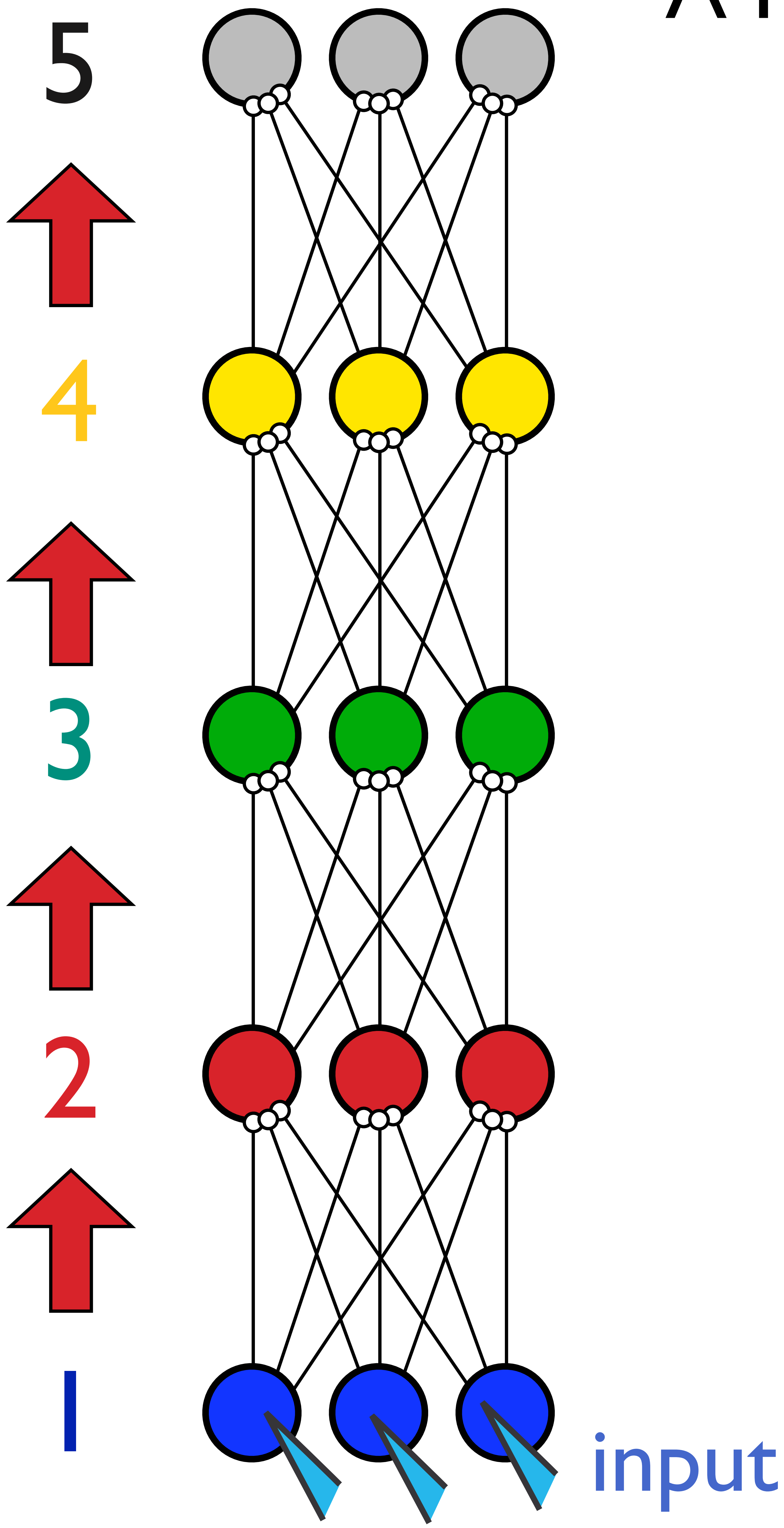
A First Approach

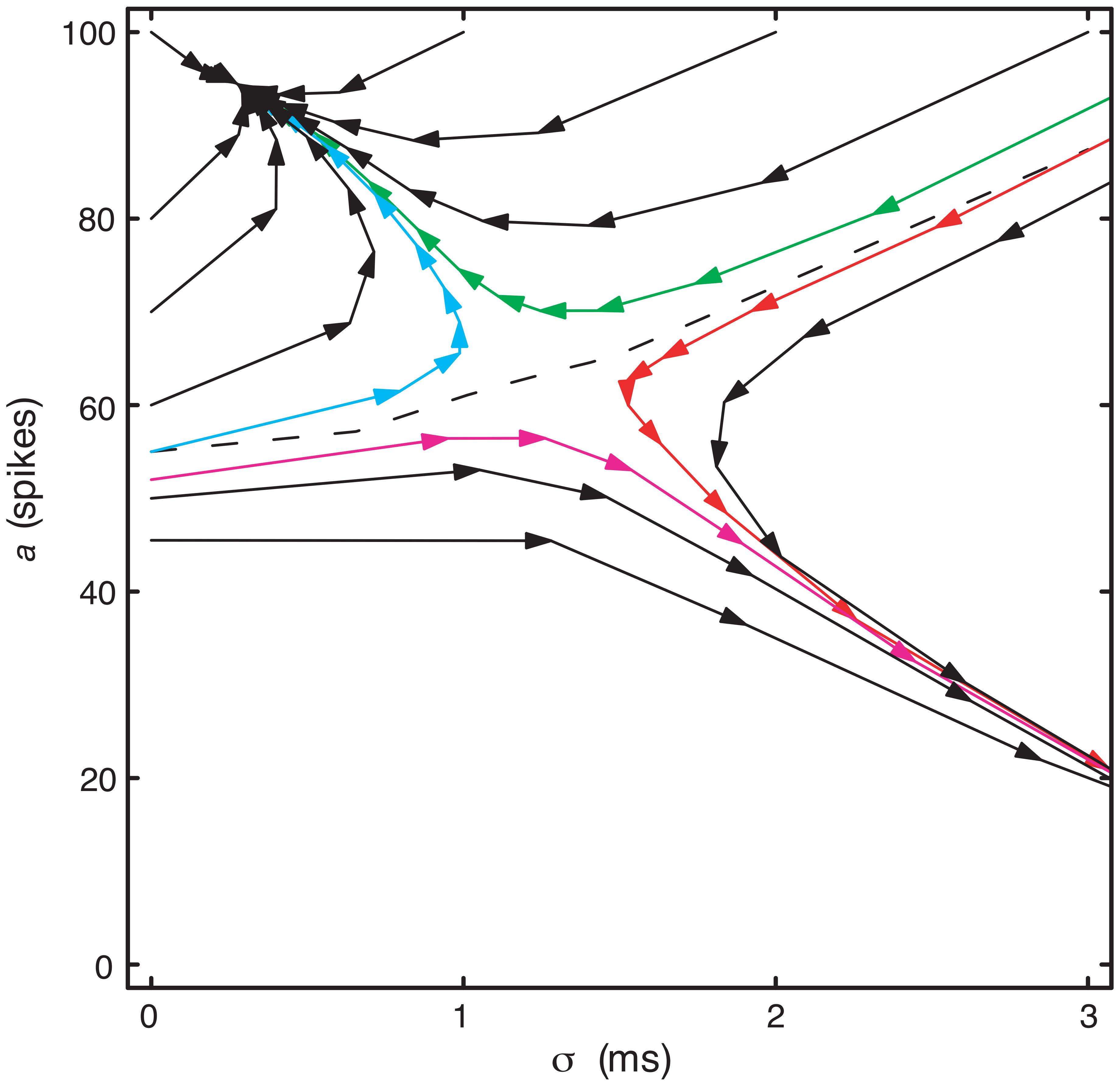




Diesmann et al. , Nature '99

A First Approach





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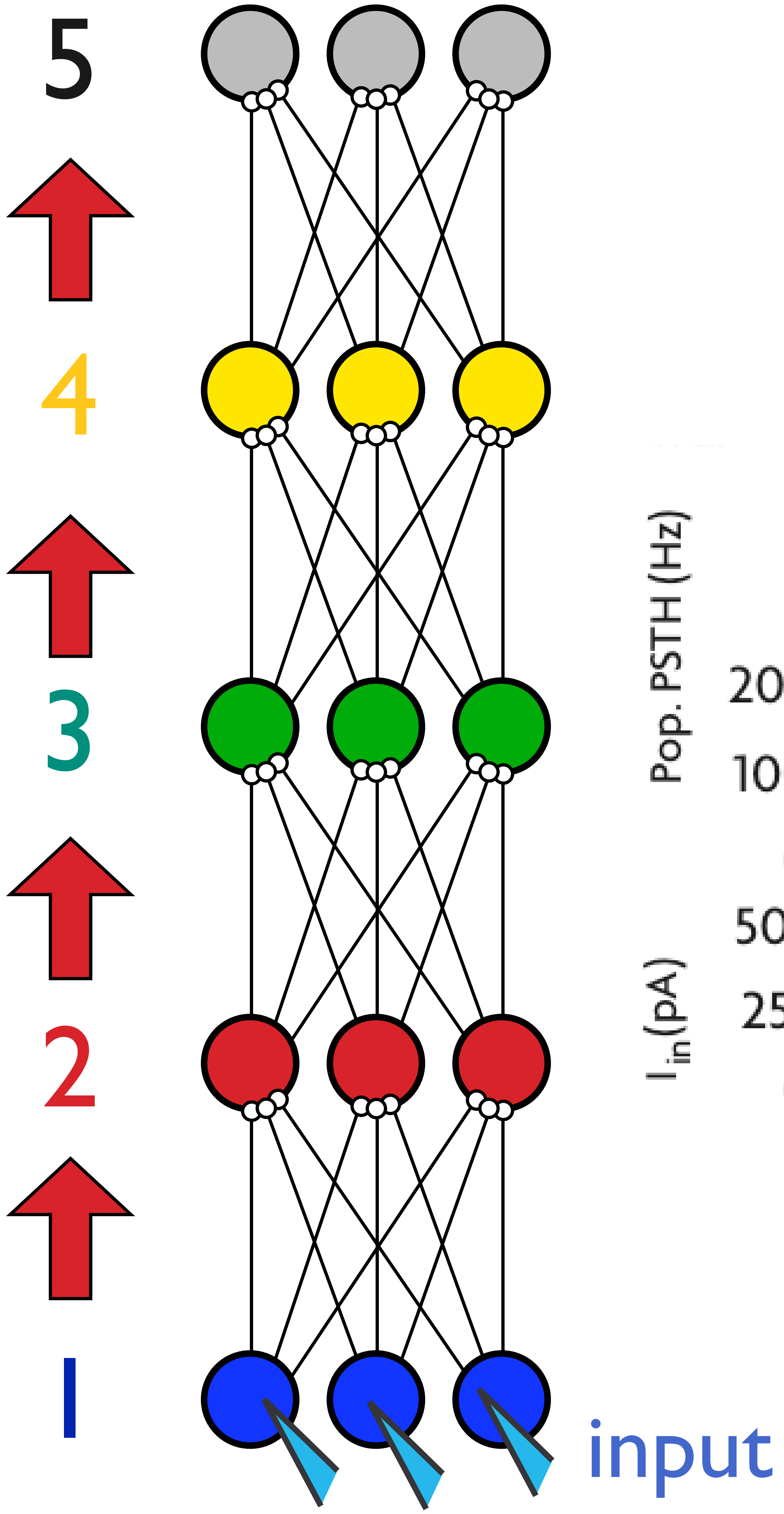
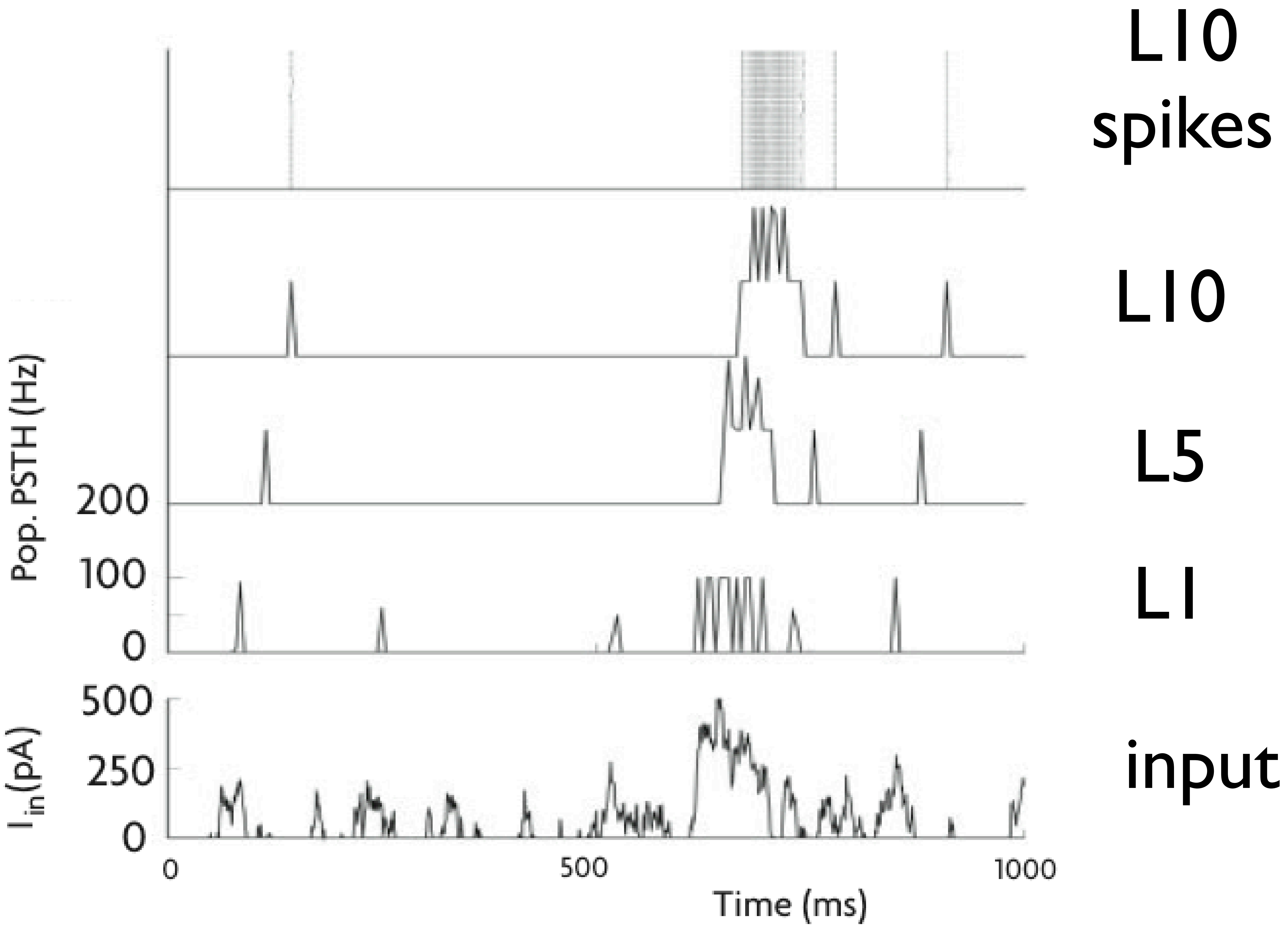
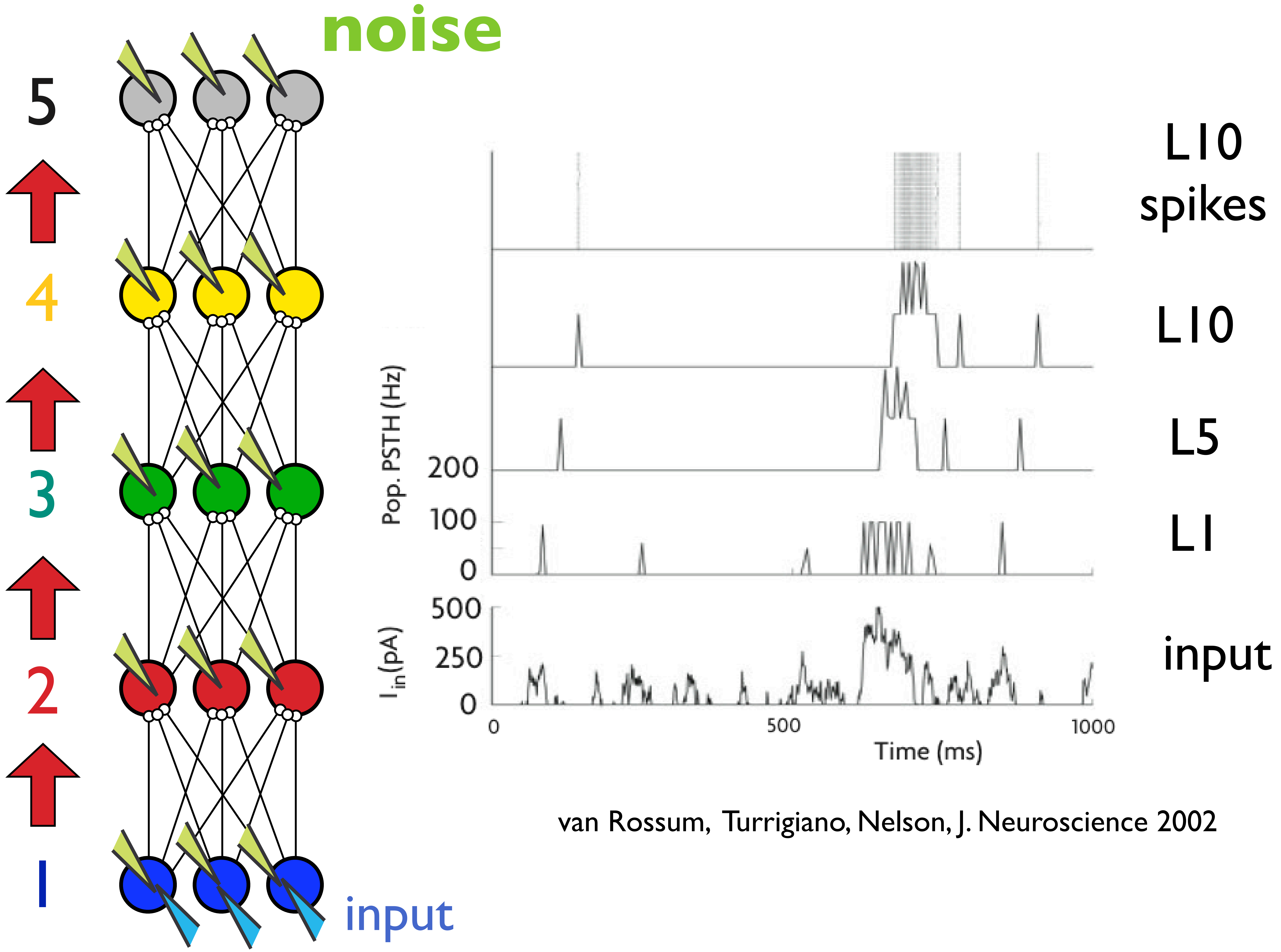
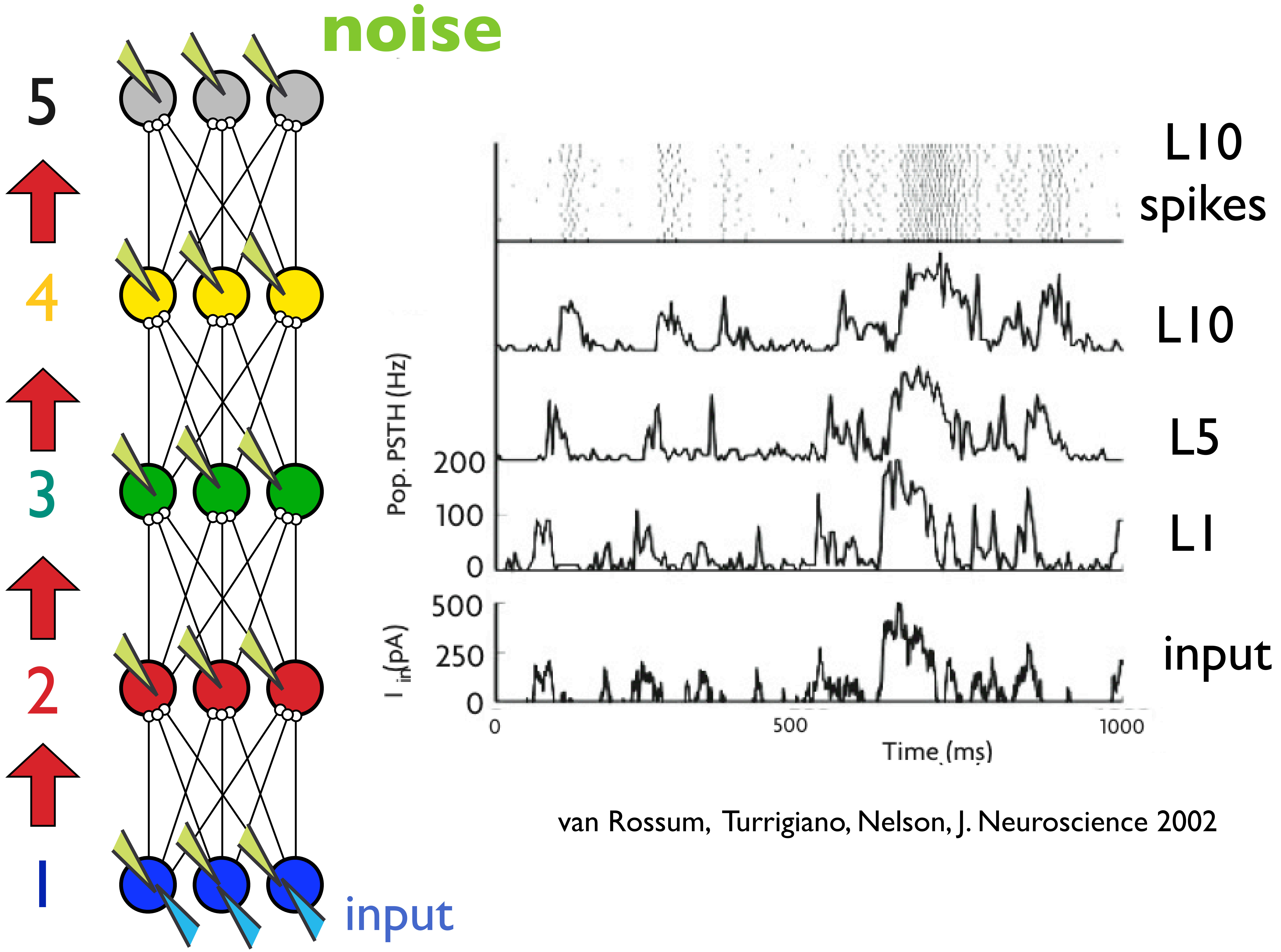




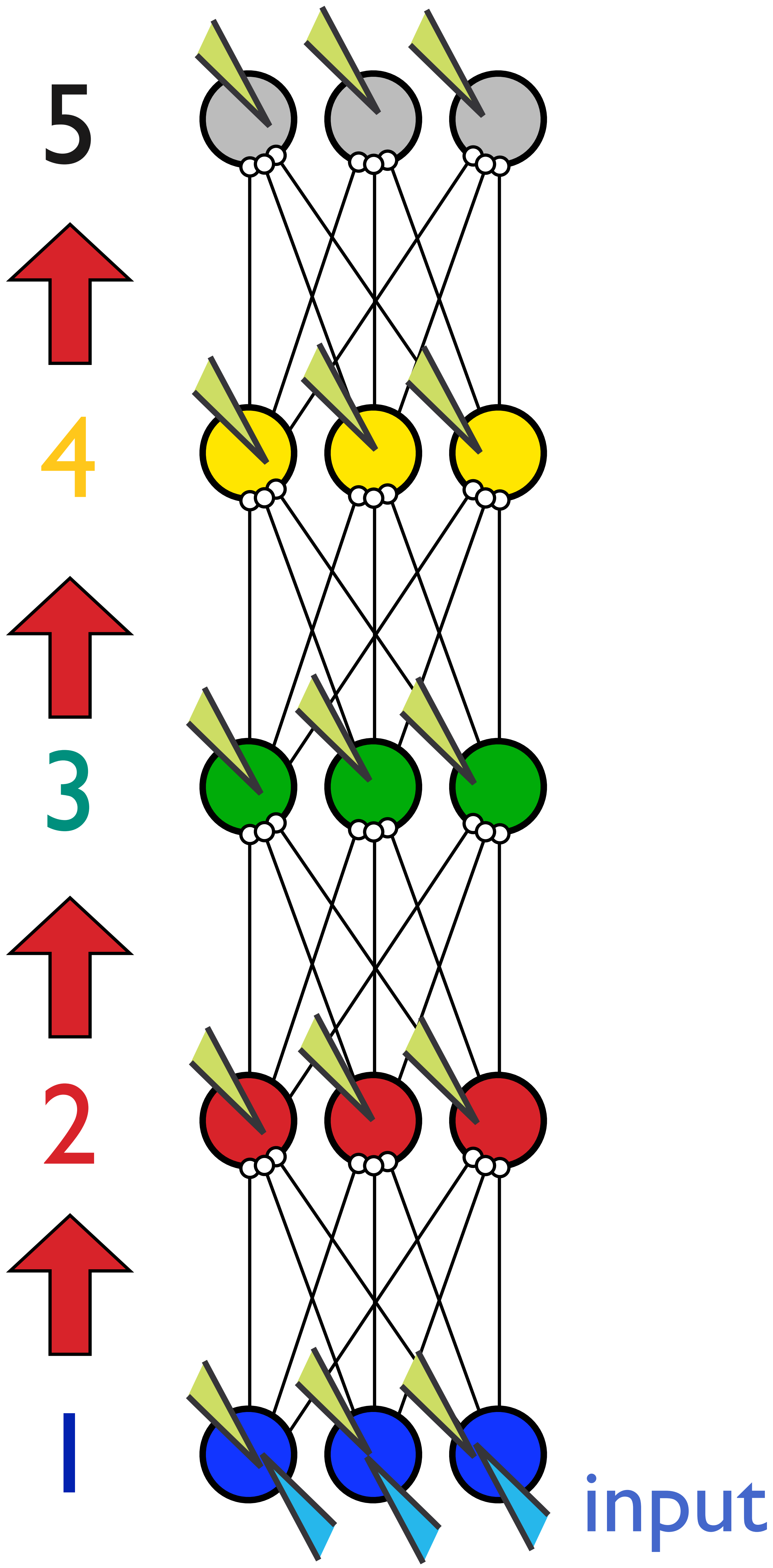
van Rossum, Turrigiano, Nelson, J. Neuroscience 2002

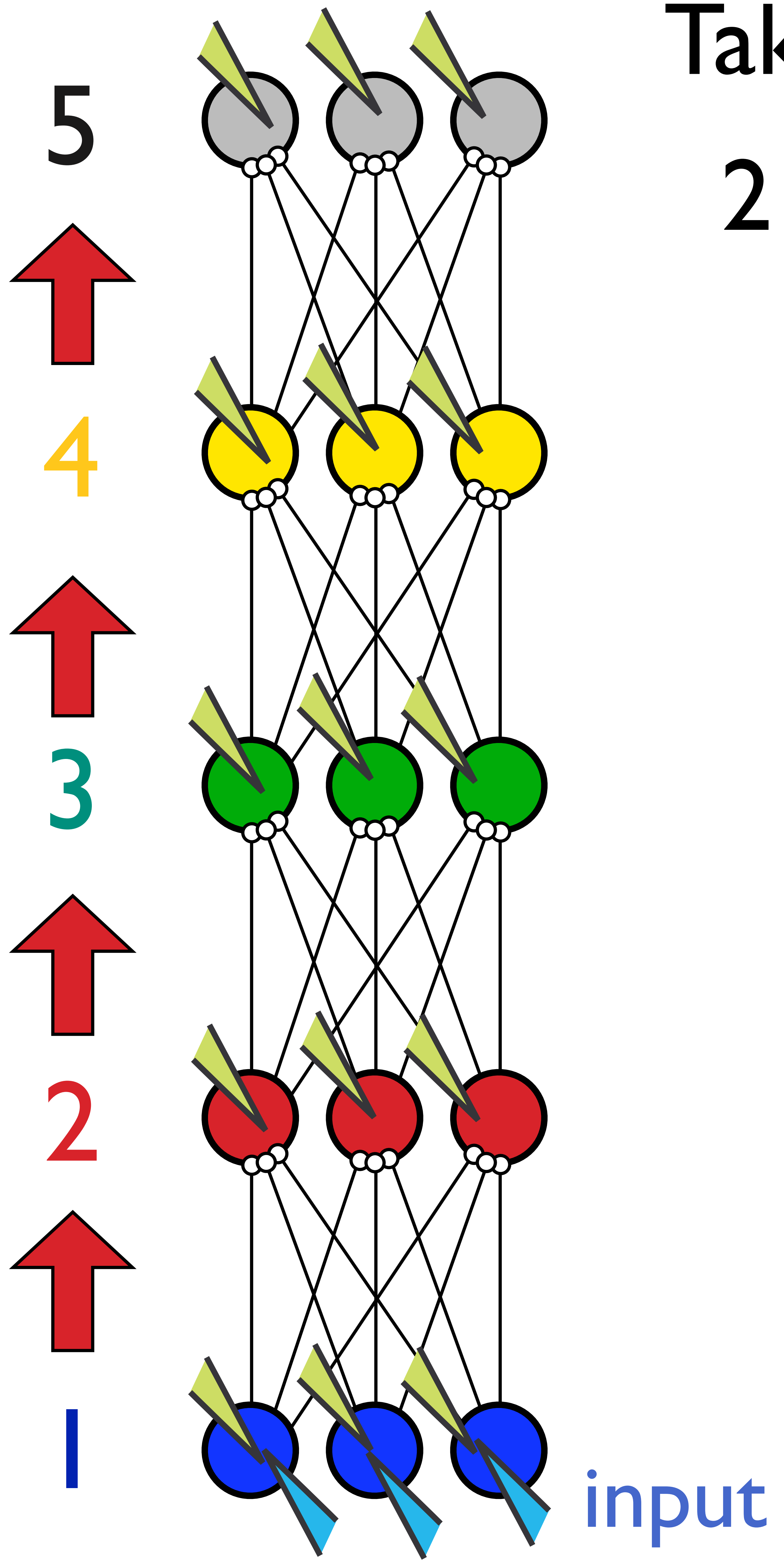


van Rossum, Turrigiano, Nelson, J. Neuroscience 2002



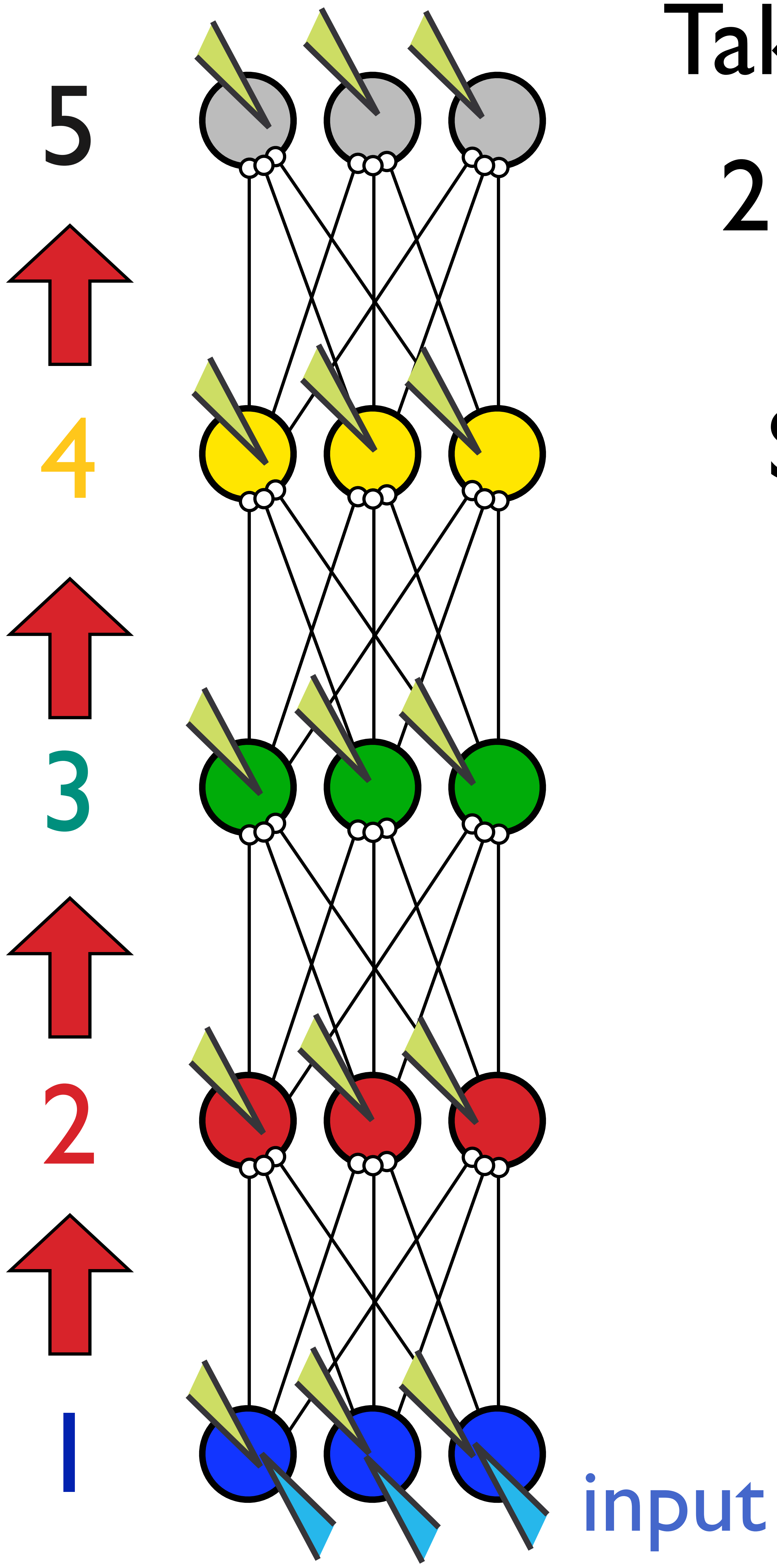
van Rossum, Turrigiano, Nelson, J. Neuroscience 2002


5
4
3
2
1
input



Take Home:

2 Extremes of Signal Propagation:



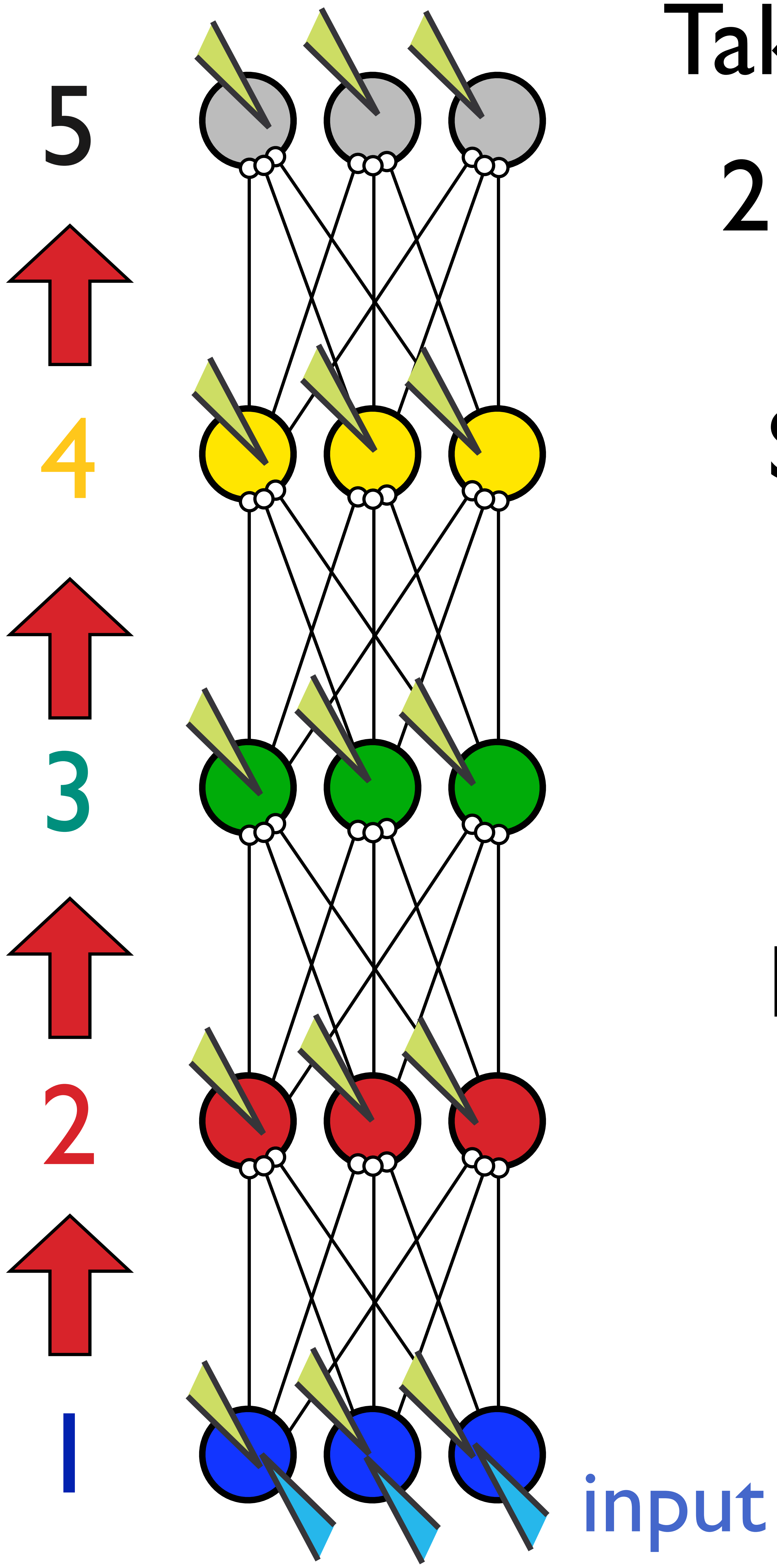
Take Home:

2 Extremes of Signal Propagation:

Synfire Propagation

Temporally precise.

Everything is encoded
in spike times



Take Home:

2 Extremes of Signal Propagation:

Synfire Propagation

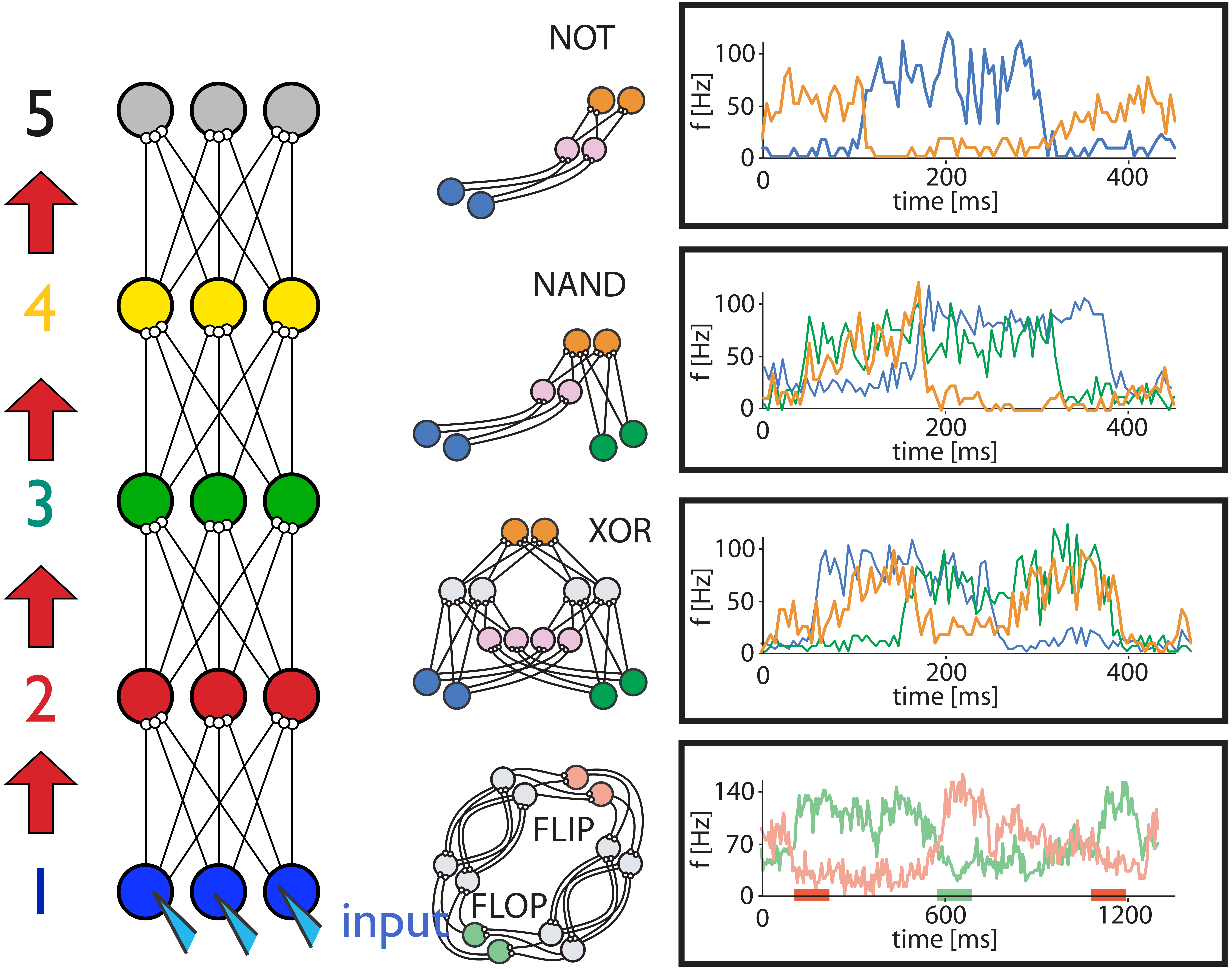
Temporally precise.

Everything is encoded
in spike times

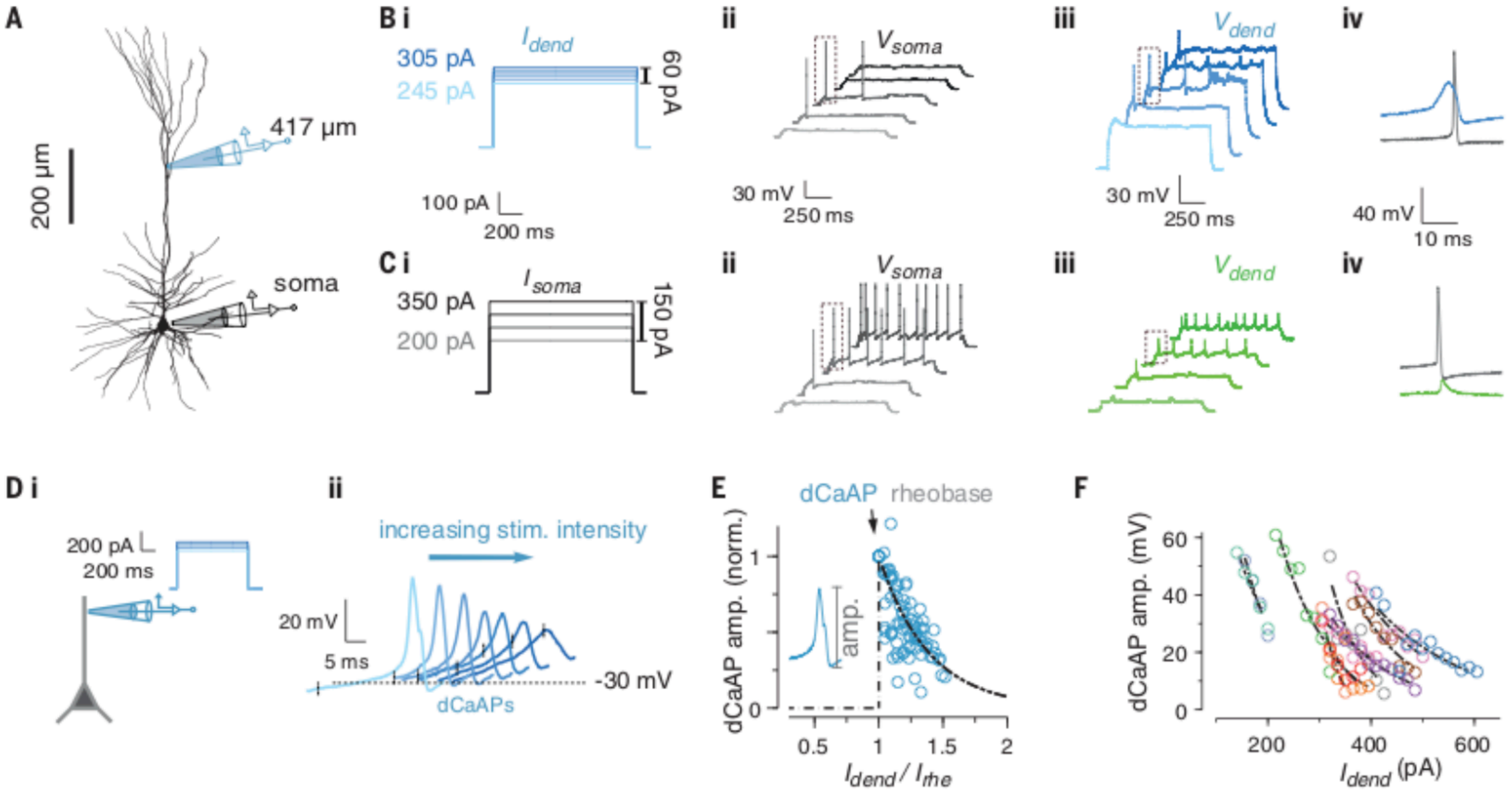
Rate Mode Propagation

Acurate Representation
of Analog Signals.

Temporally sluggish.



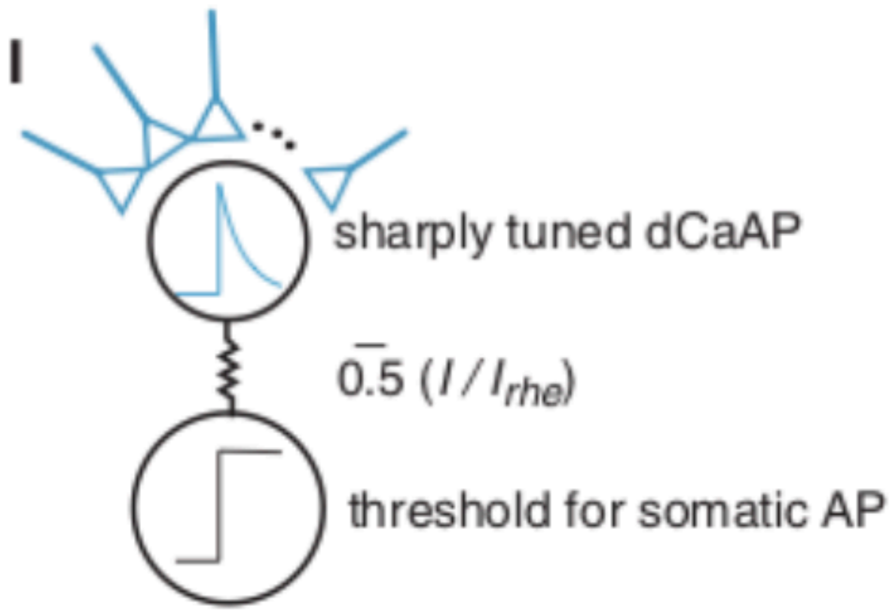
5
4
3
2
1
input
NOT
NAND
XOR
FLIP
FLOP
f [Hz]
time [ms]
0
50
100
200
400
70
140
600
1200

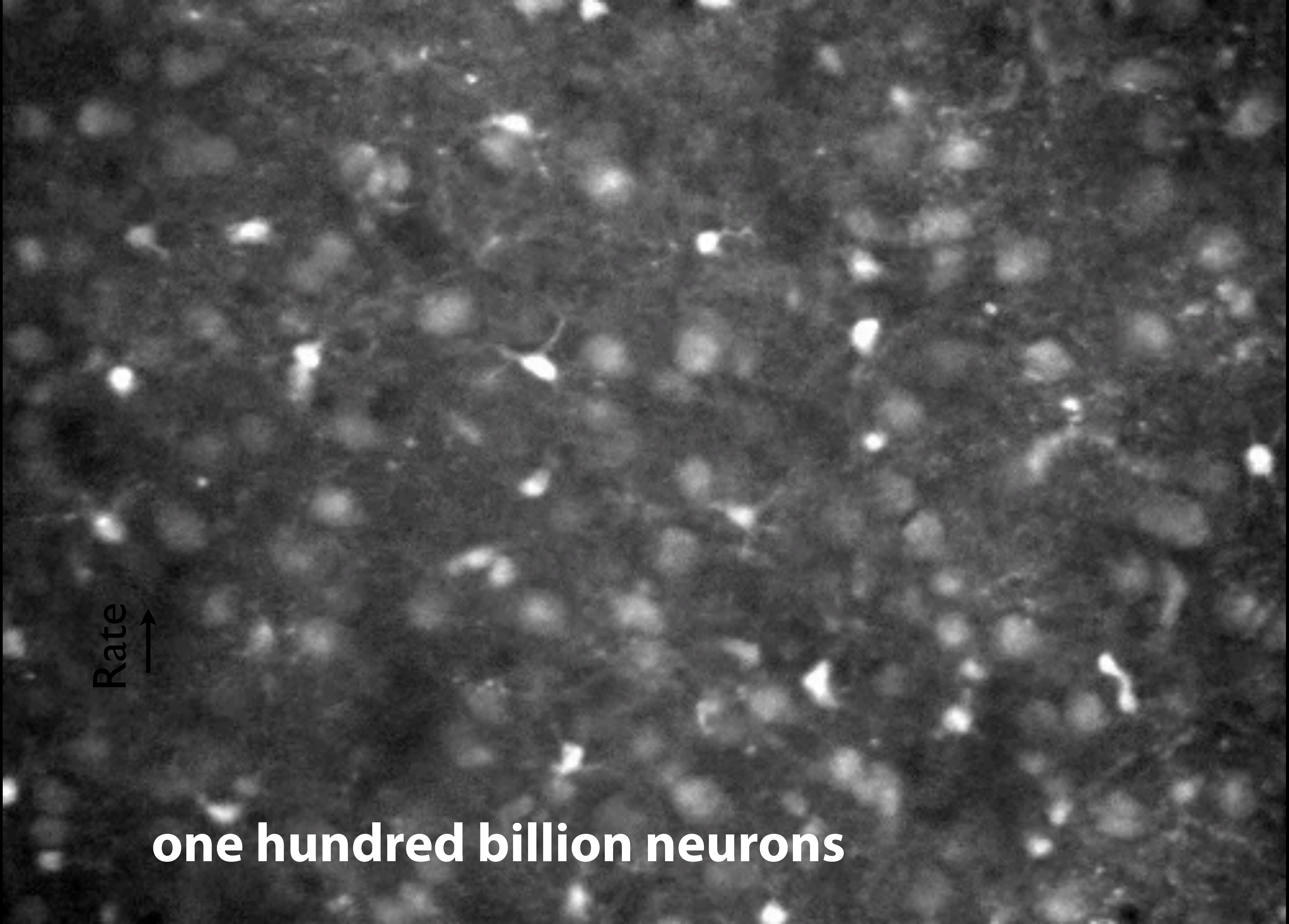


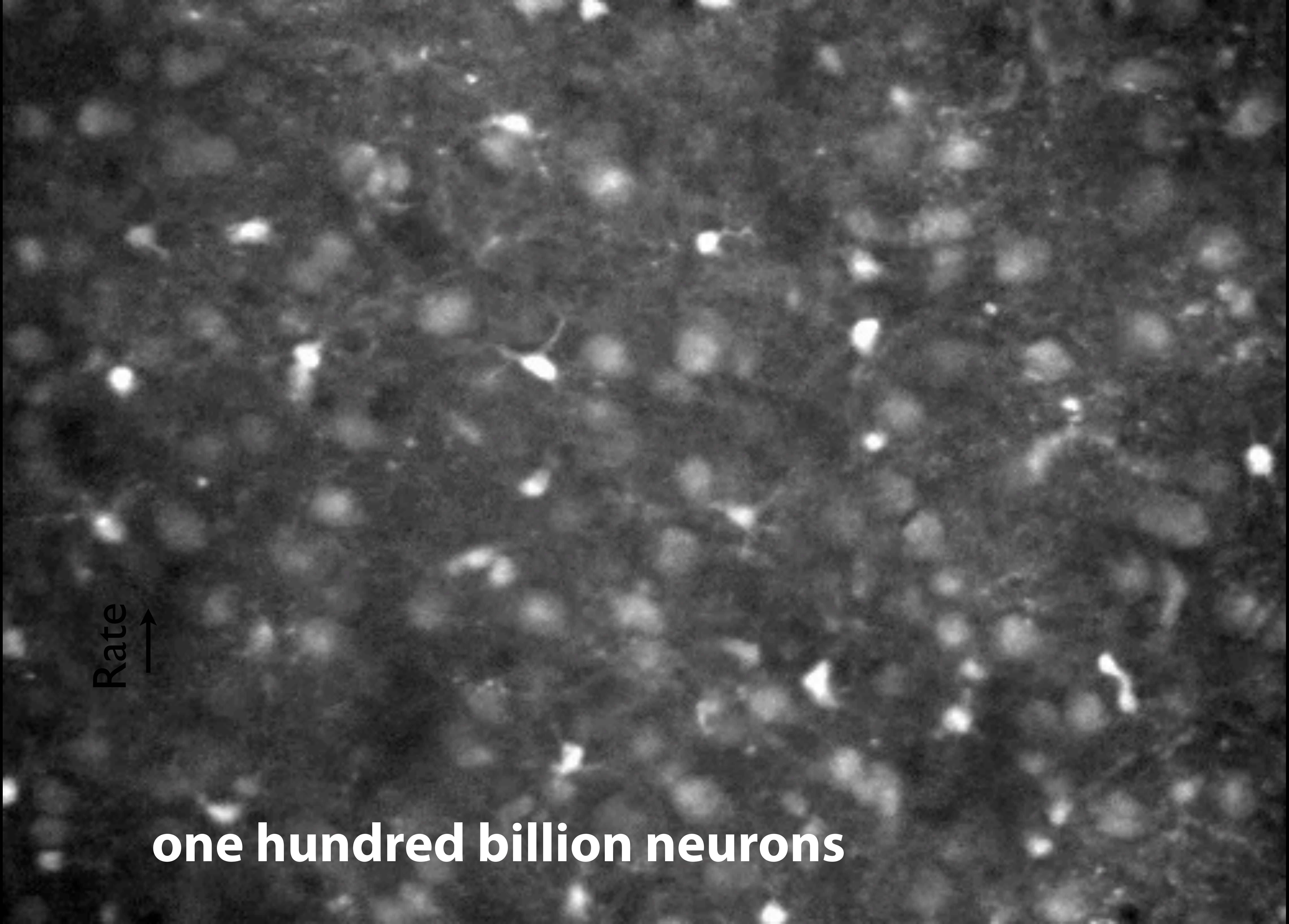
NEUROSCIENCE

Dendritic action potentials and computation in human layer 2/3 cortical neurons

Albert Gidon[1], Timothy Adam Zolnik[1], Pawel Fidzinski[2,3], Felix Bolduan[4], Athanasia Papoutsi[5], Panayiota Poirazi[5], Martin Holtkamp[2], Imre Vida[3,4], Matthew Evan Larkum[1,3]*




Rate
one hundred billion neurons


Rate
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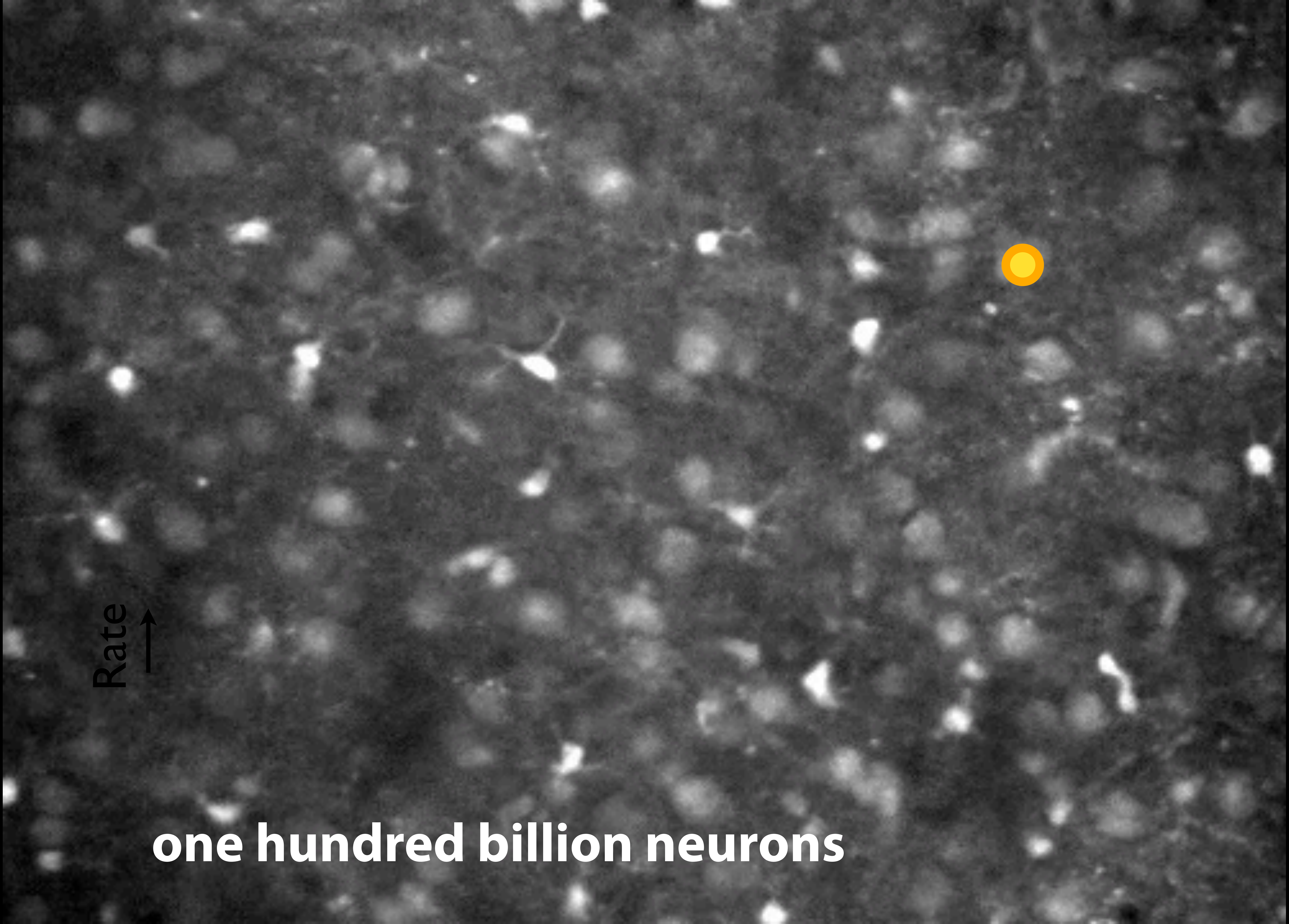
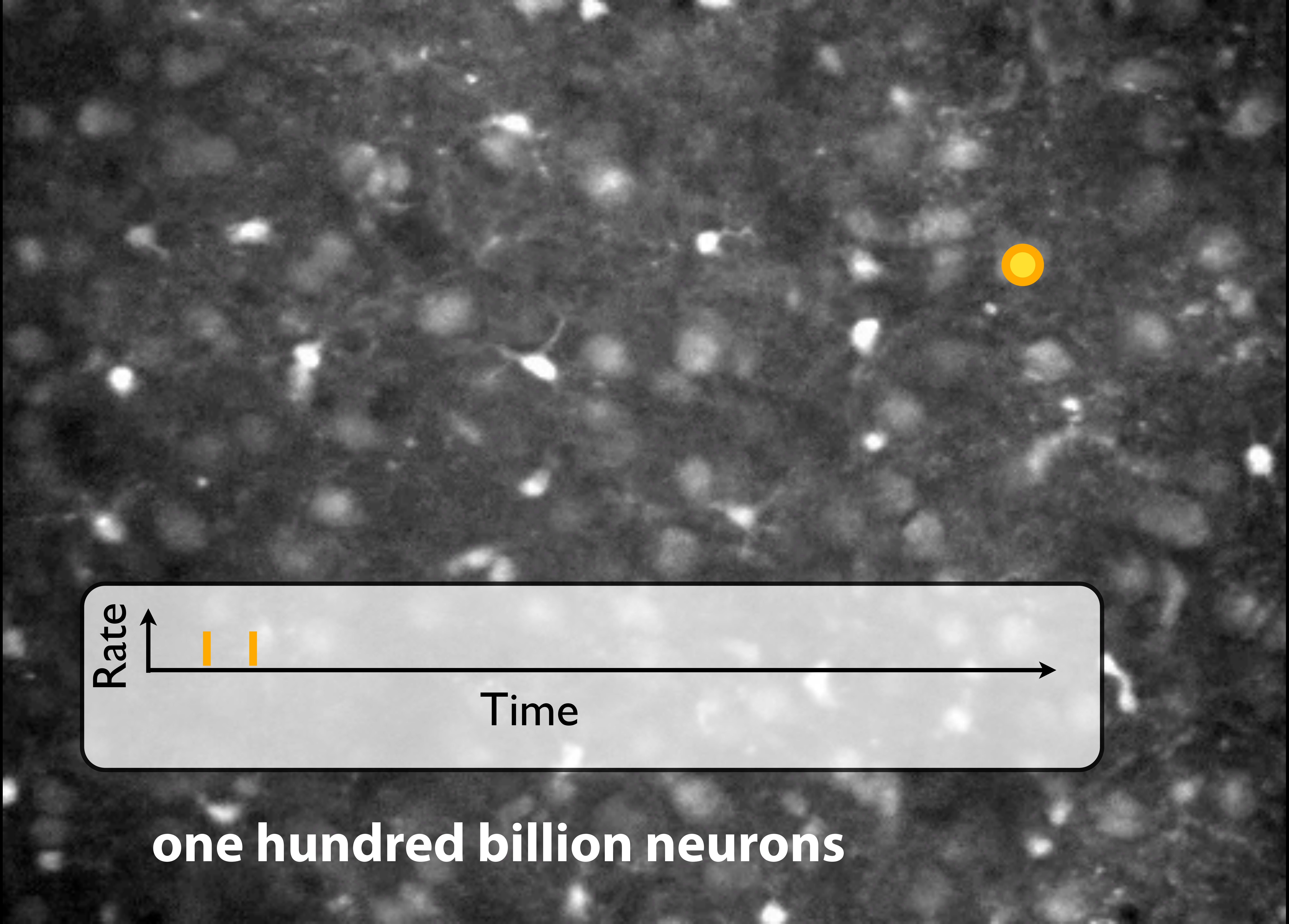
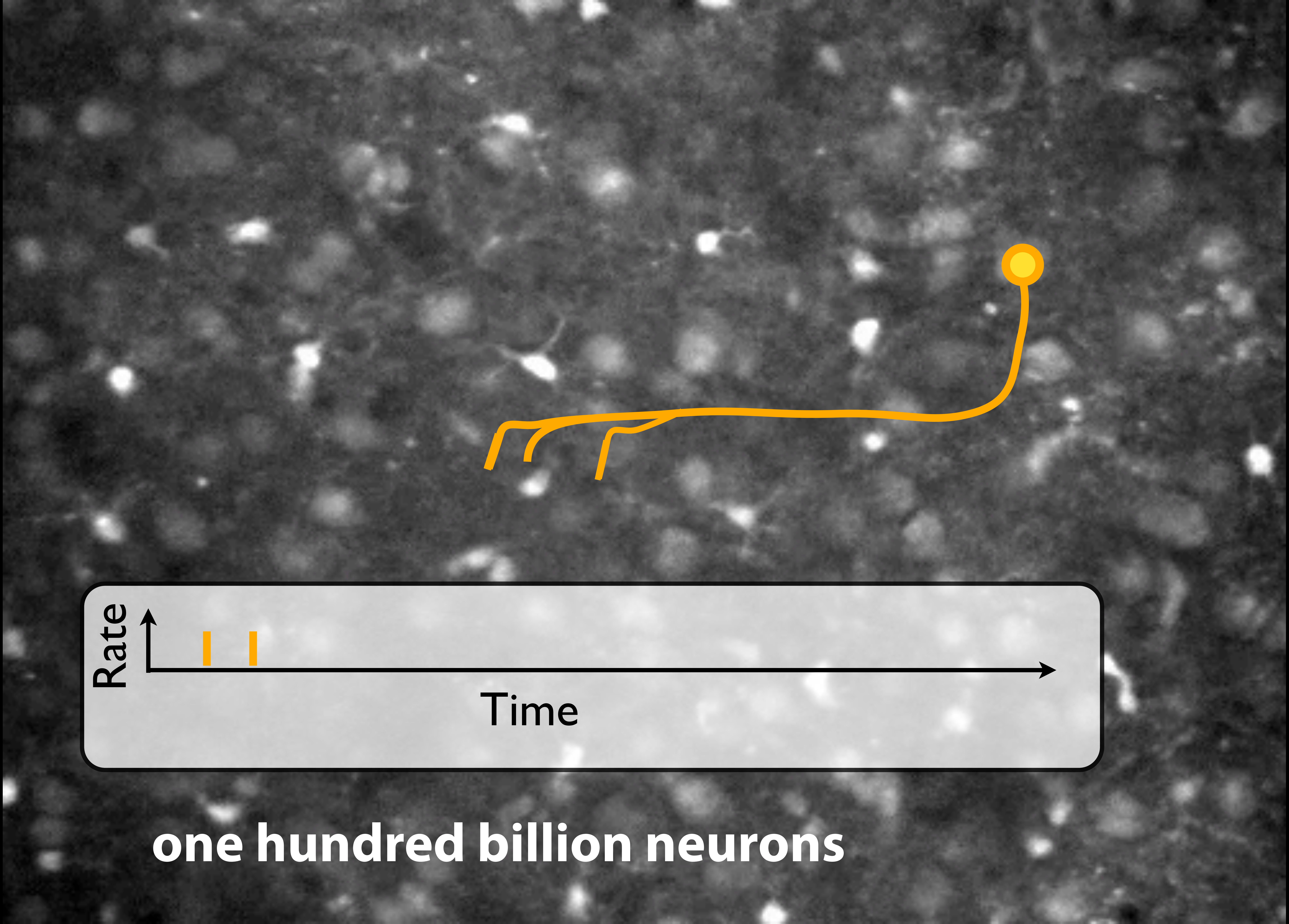
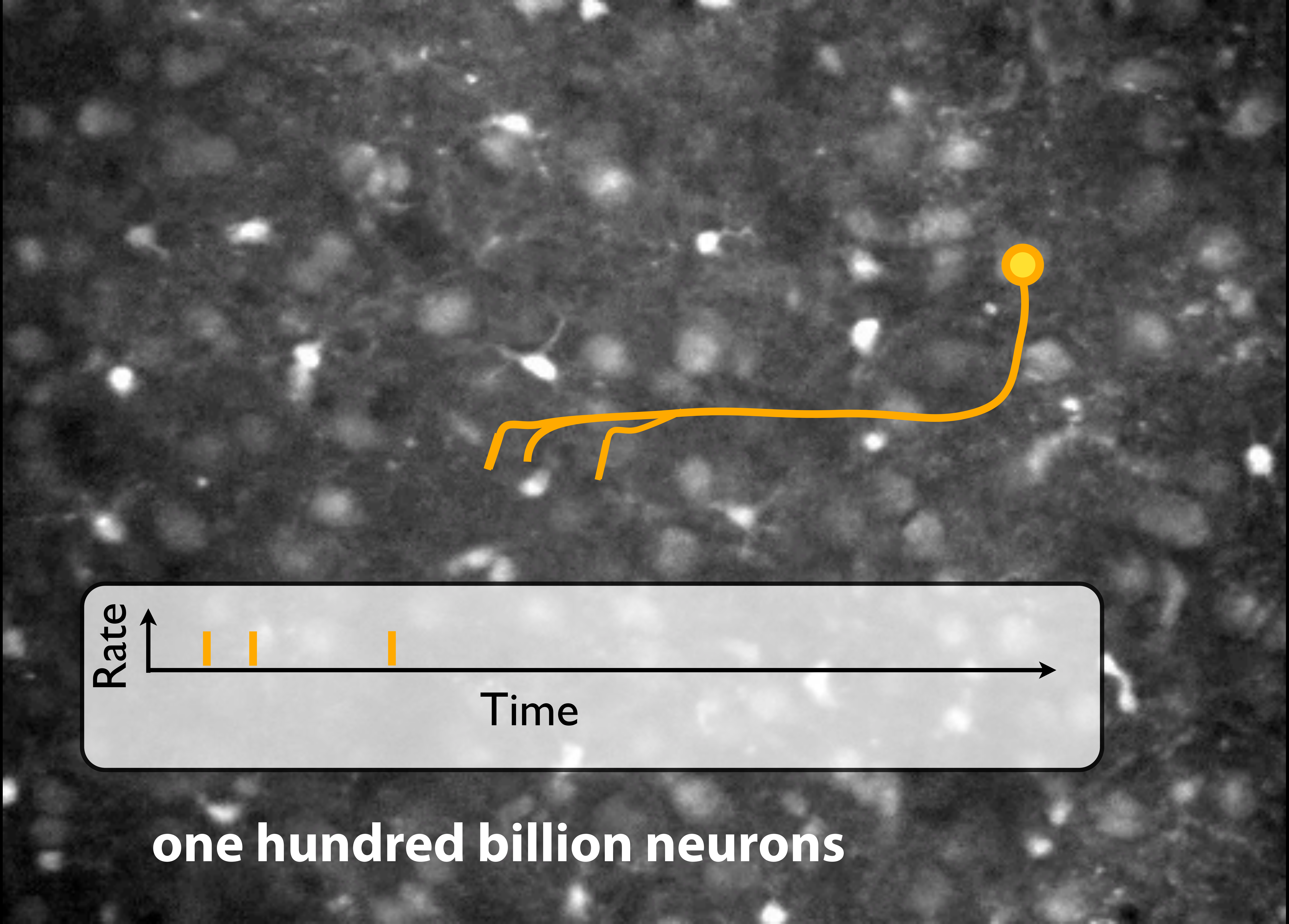
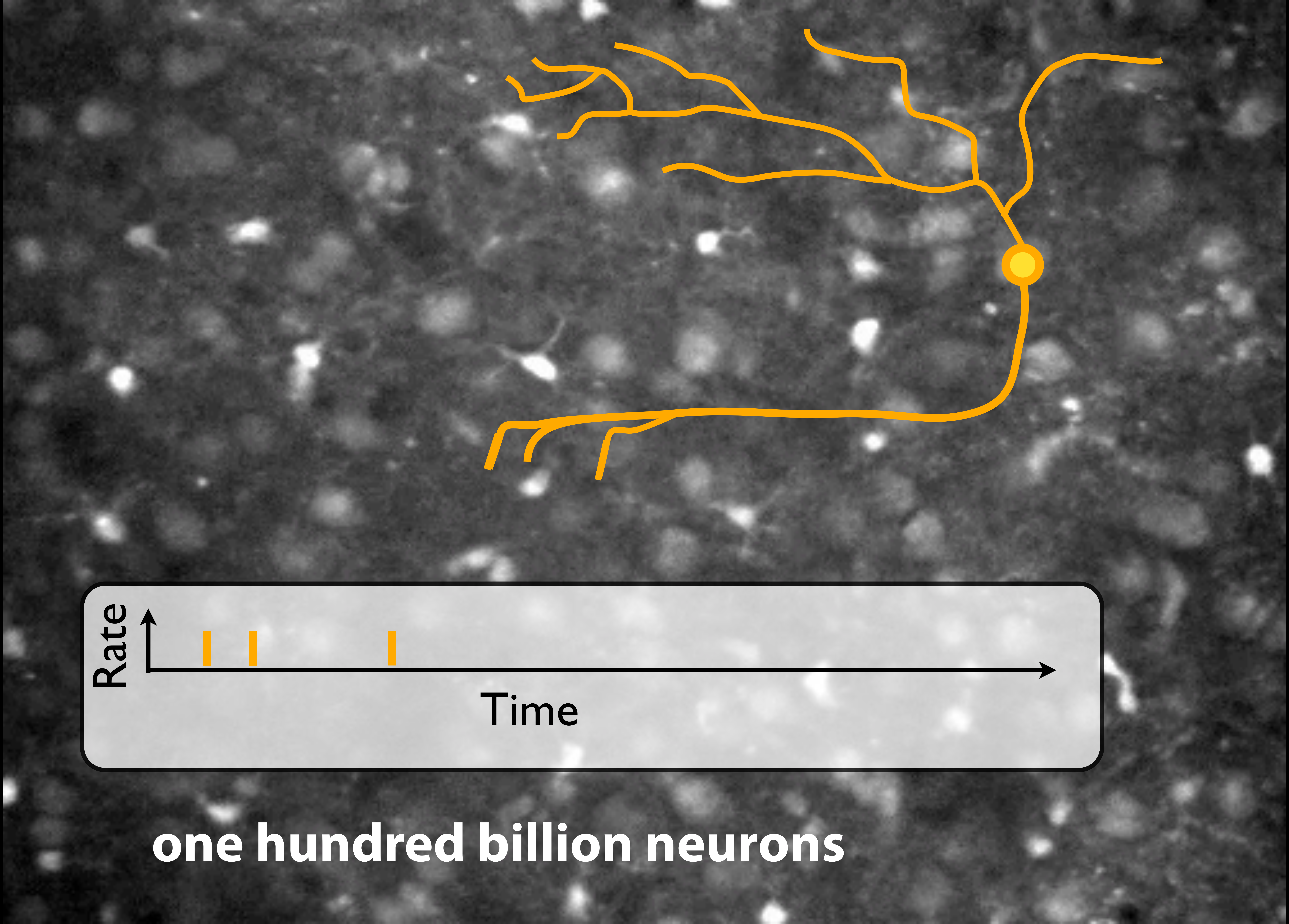

Rate
one hundred billion neurons

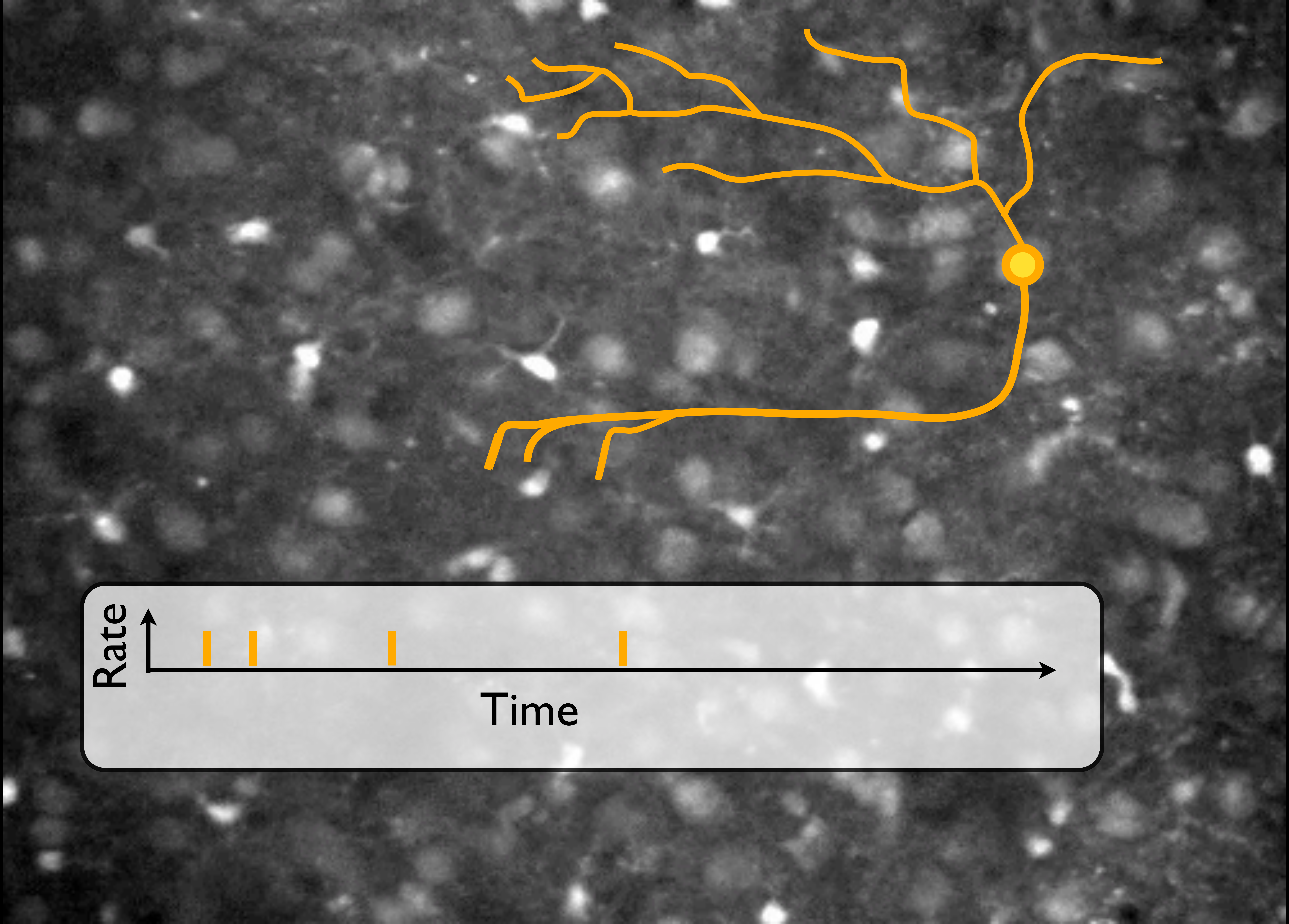

Rate
Time
one hundred billion neurons

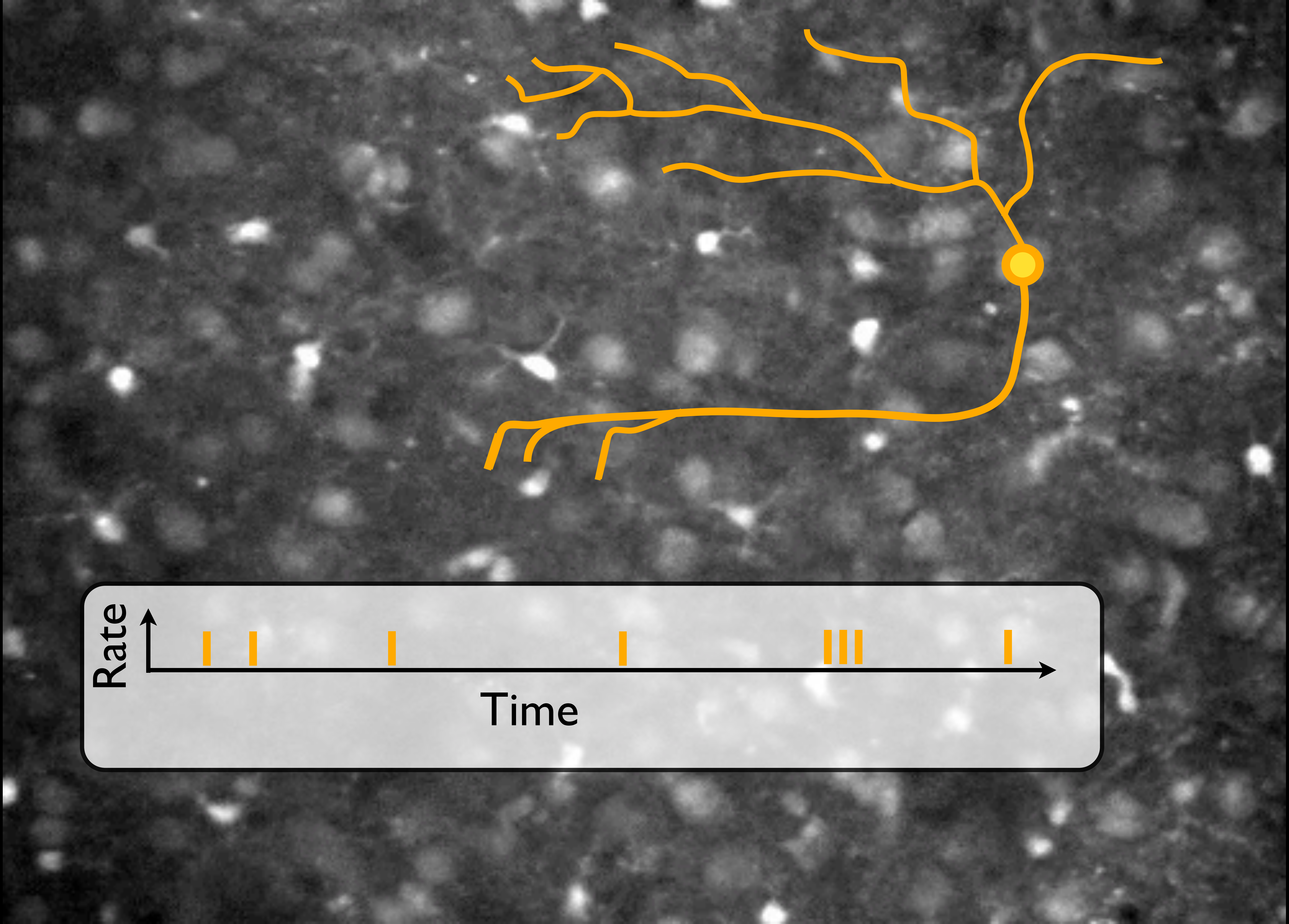

Rate
Time
one hundred billion neurons


Rate
Time
one hundred billion neurons

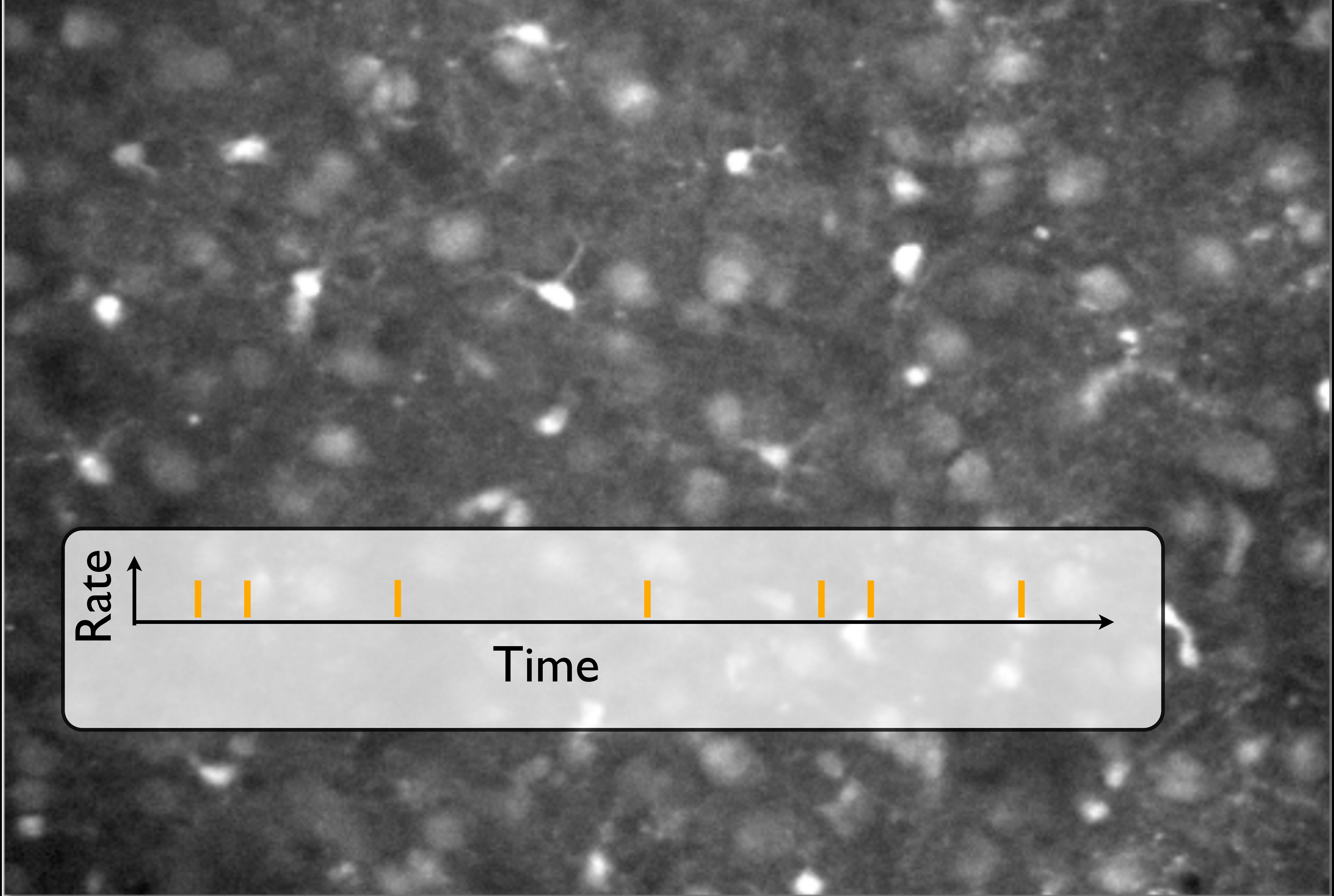


Rate
Time
one hundred billion neurons


Rate
Time


Rate
Time

Characterizing a neuron w/o much information



Characterizing a neuron w/o much information

The “CV”,
i.e. the coefficient of variation of the interspike interval

Characterizing a neuron w/o much information

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$$CV(ISI) = \frac{\sigma\ (ISI)}{\text{ø}\ (ISI)}$$

Characterizing a neuron w/o much information

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Characterizing a neuron w/o much information

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$$CV(ISI) = \frac{\sigma\ (ISI)}{\o\ (ISI)} \quad =$$

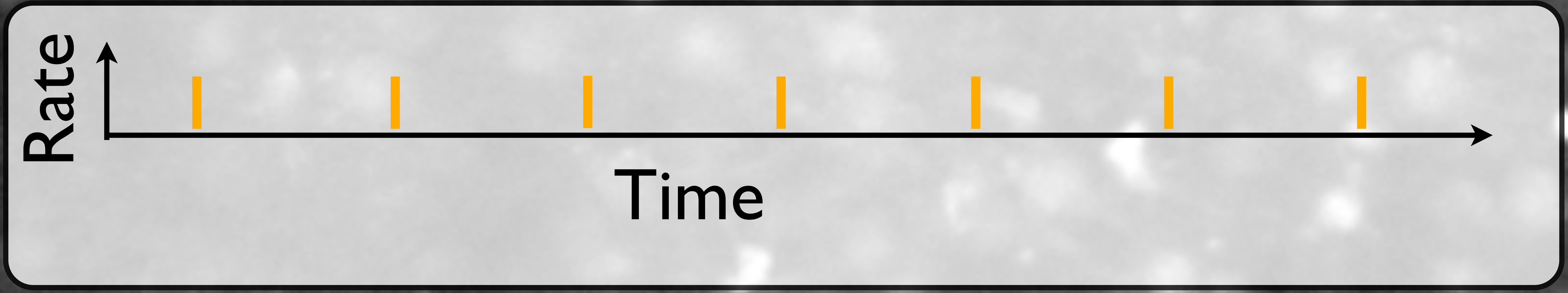
provides an intuition for the regularity of the spike train

Characterizing a neuron w/o much information

The "CV",
i.e. the coefficient of variation of the interspike interval

$$CV(ISI) = \frac{\sigma\ (ISI)}{\varnothing\ (ISI)} = \frac{1\,ms}{5\ ms}$$

provides an intuition for the regularity of the spike train

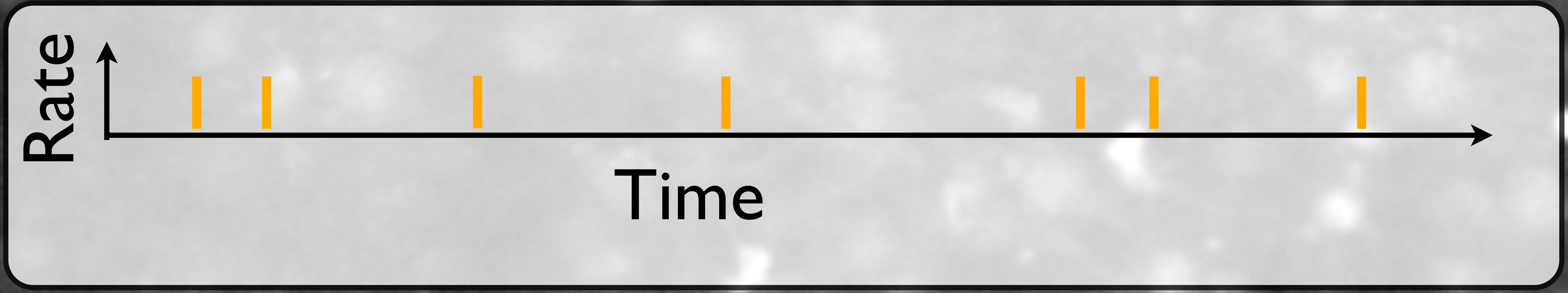


Characterizing a neuron w/o much information

The "CV",
i.e. the coefficient of variation of the interspike interval

$$CV(ISI) = \frac{\sigma\ (ISI)}{\text{ø}\ (ISI)} = \frac{5\ \text{ms}}{5\ \text{ms}}$$

provides an intuition for the regularity of the spike train

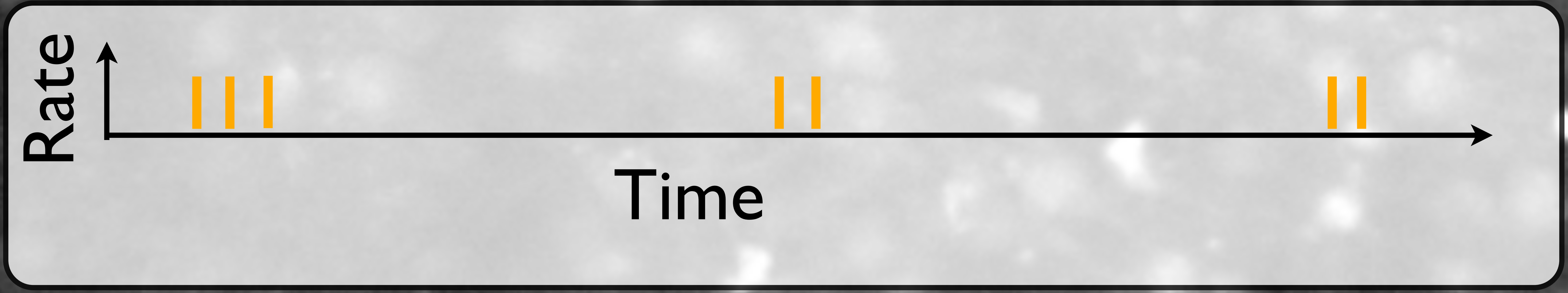


Characterizing a neuron w/o much information

The "CV",
i.e. the coefficient of variation of the interspike interval

$$CV(ISI) = \frac{\sigma\ (ISI)}{\text{ø}\ (ISI)} = \frac{15\ \text{ms}}{5\ \text{ms}}$$

provides an intuition for the regularity of the spike train



Characterizing a neuron w/o much information

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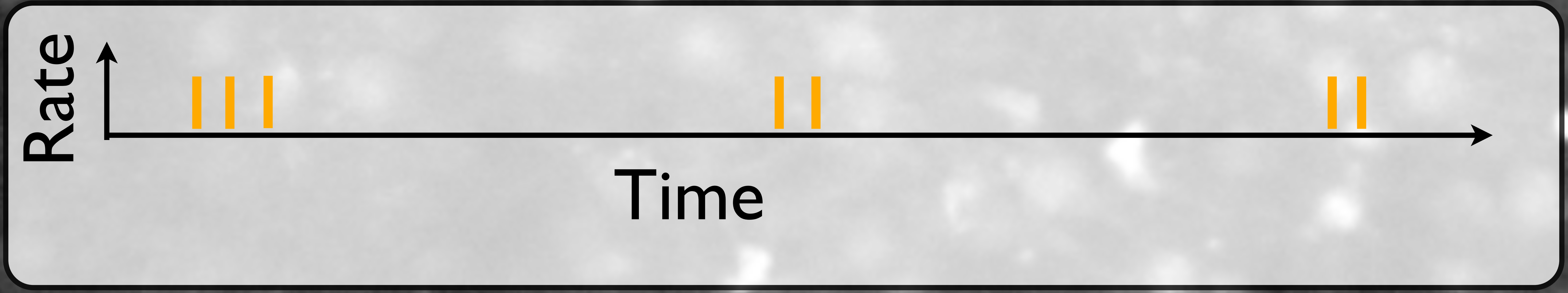

0 is regular, 1 is irregular, >1 is bursty

Characterizing a neuron w/o much information

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i.e. the coefficient of variation of the interspike interval

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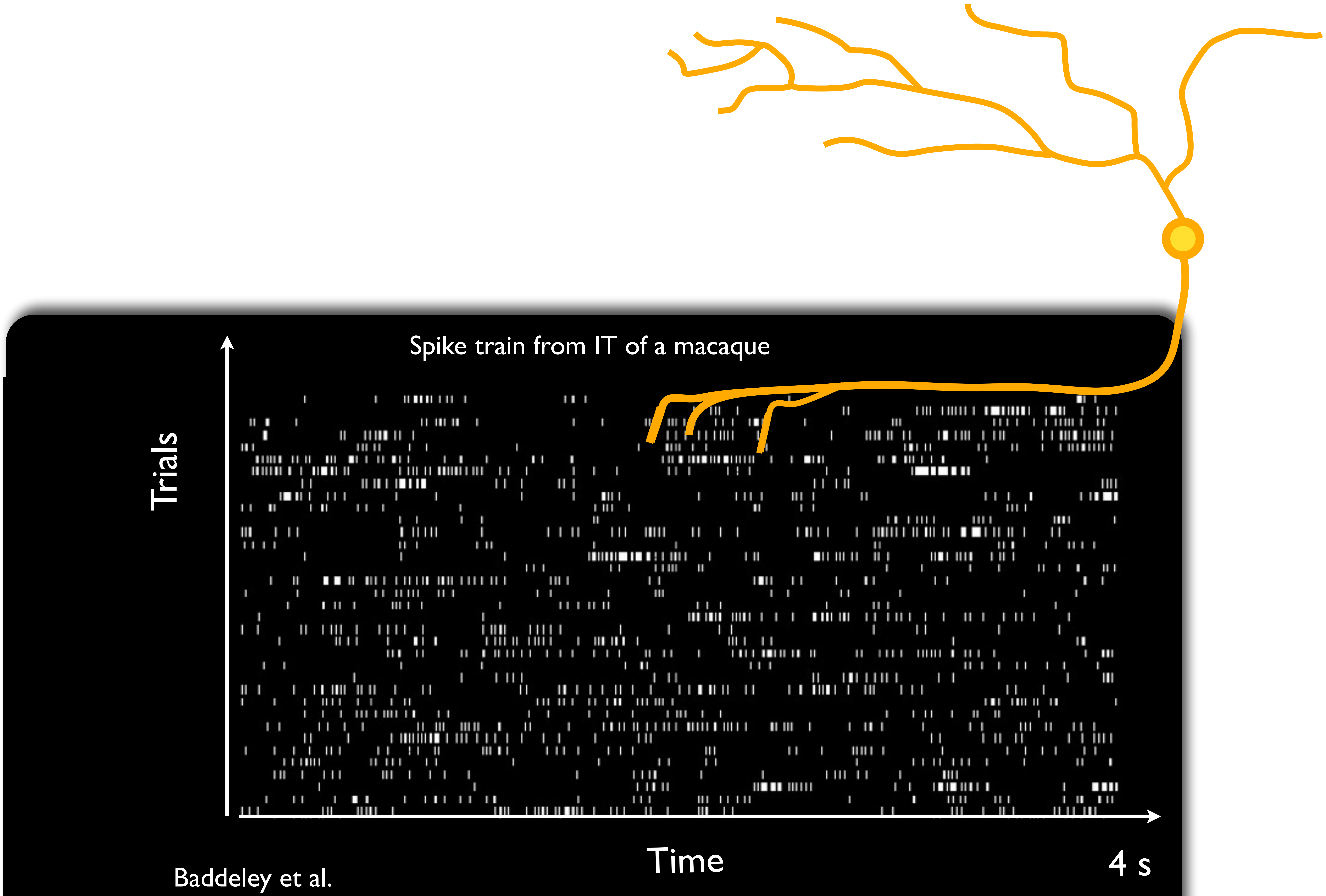
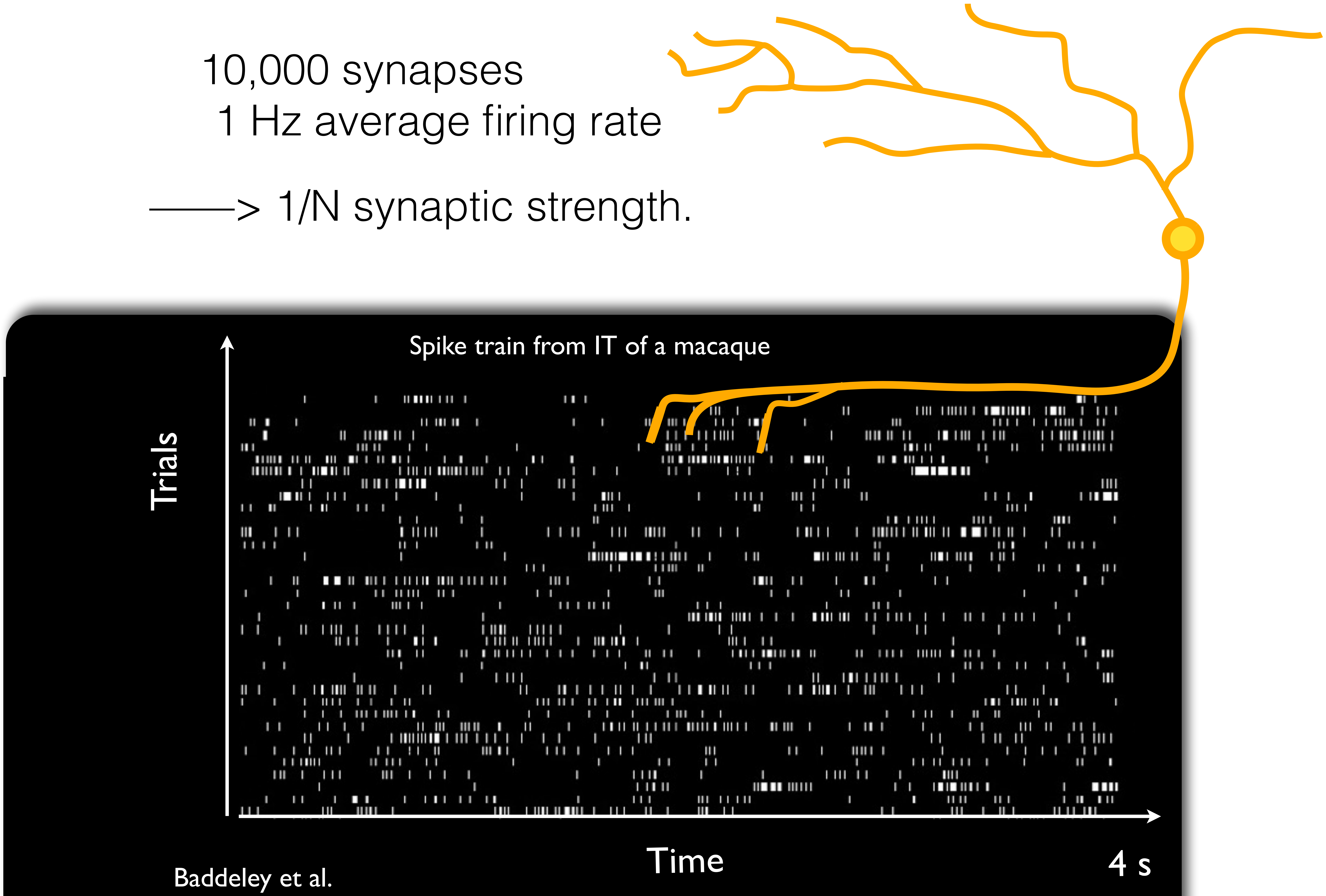


Spike train from IT of a macaque
Trials
Time
4 s
Baddeley et al.

10,000 synapses
1 Hz average firing rate

——> 1/N synaptic strength.



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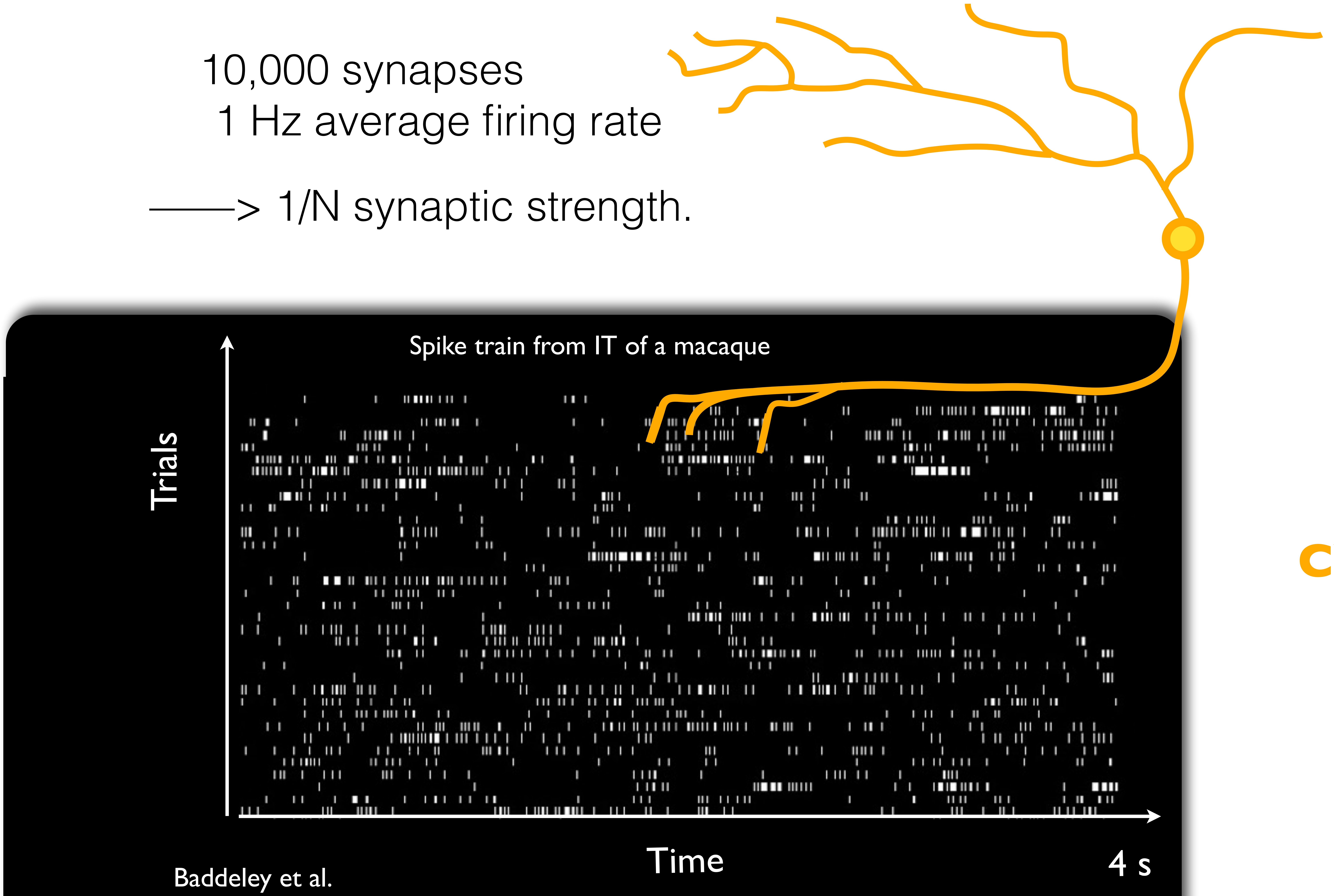
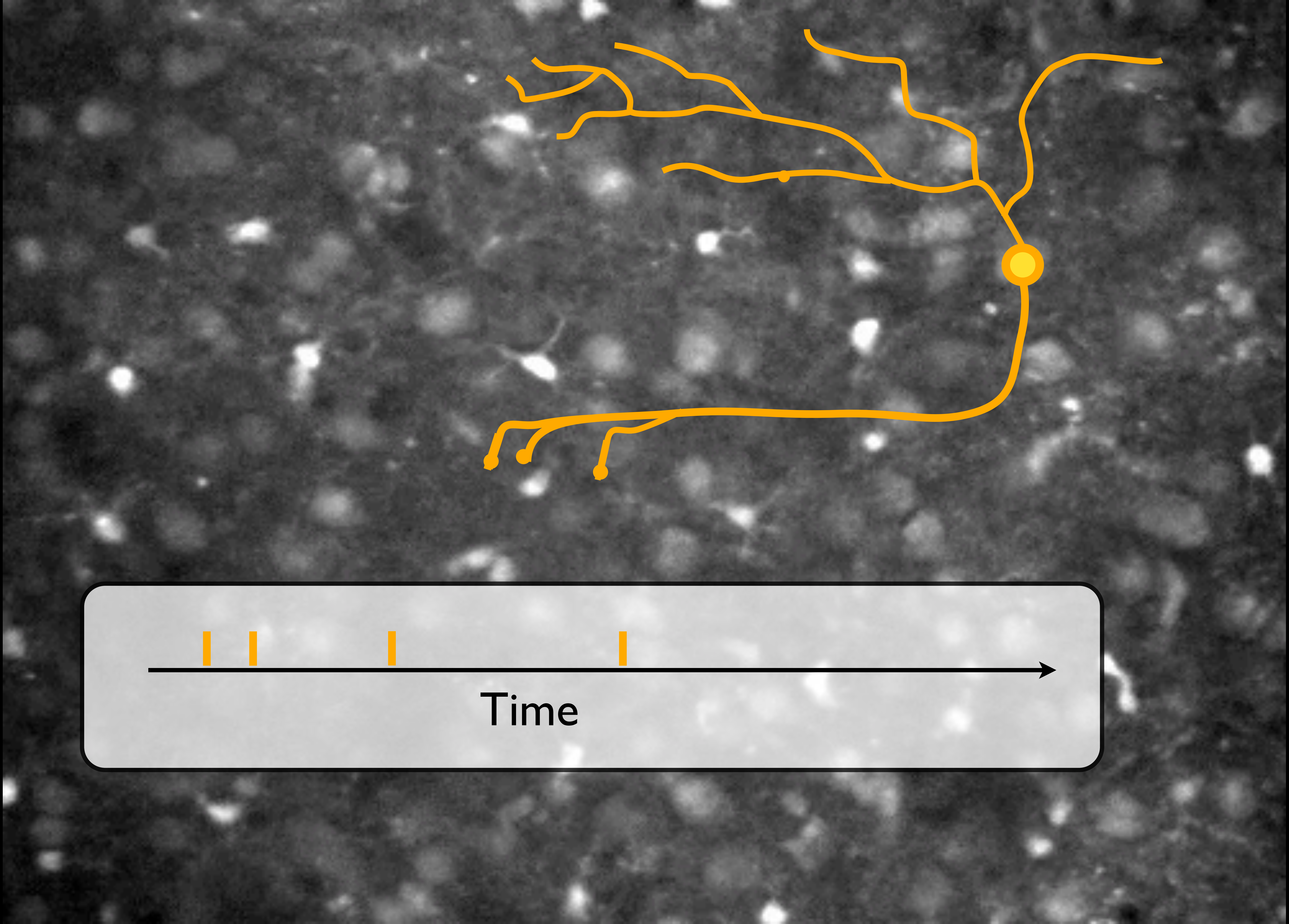
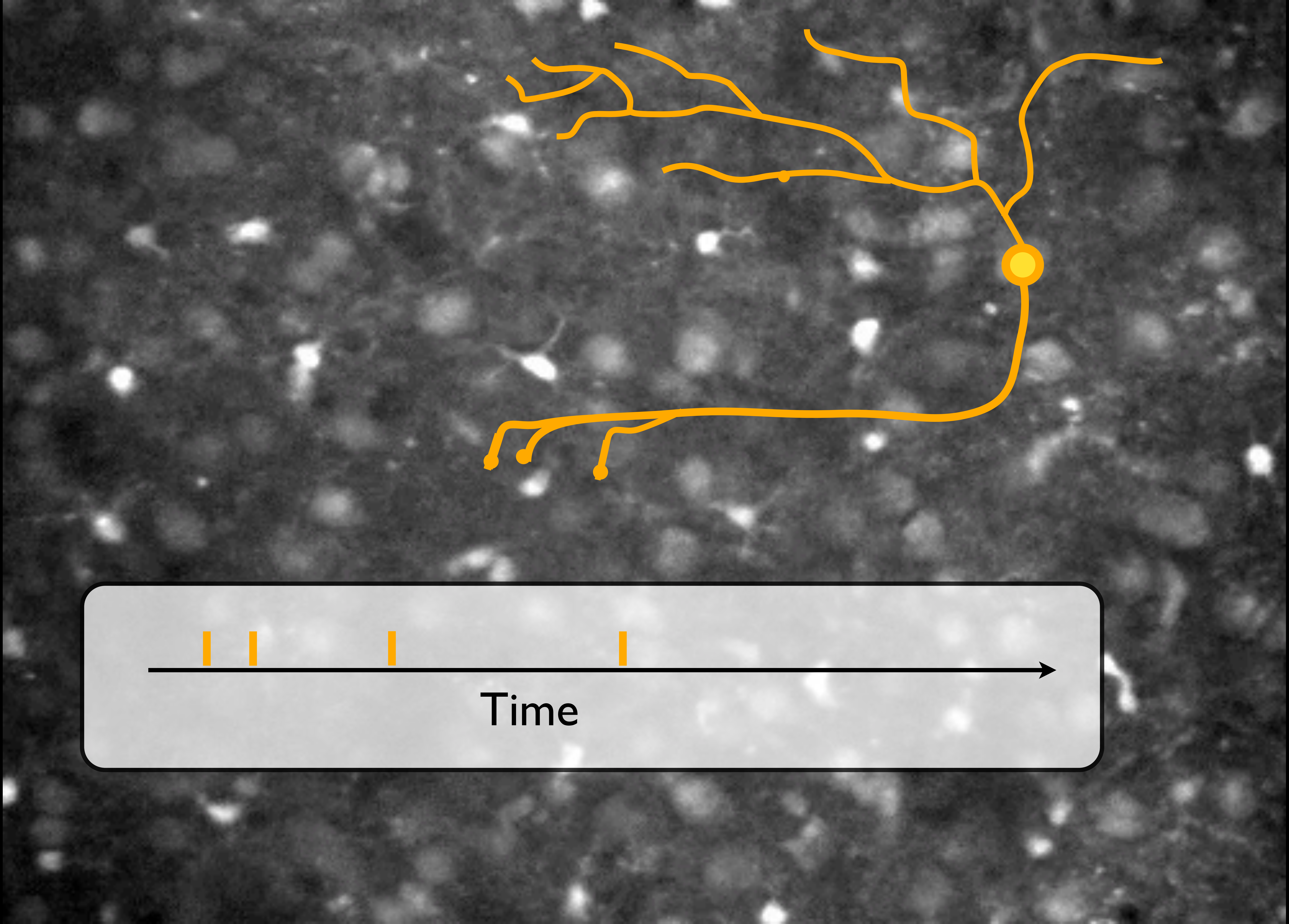
1 Hz average firing rate

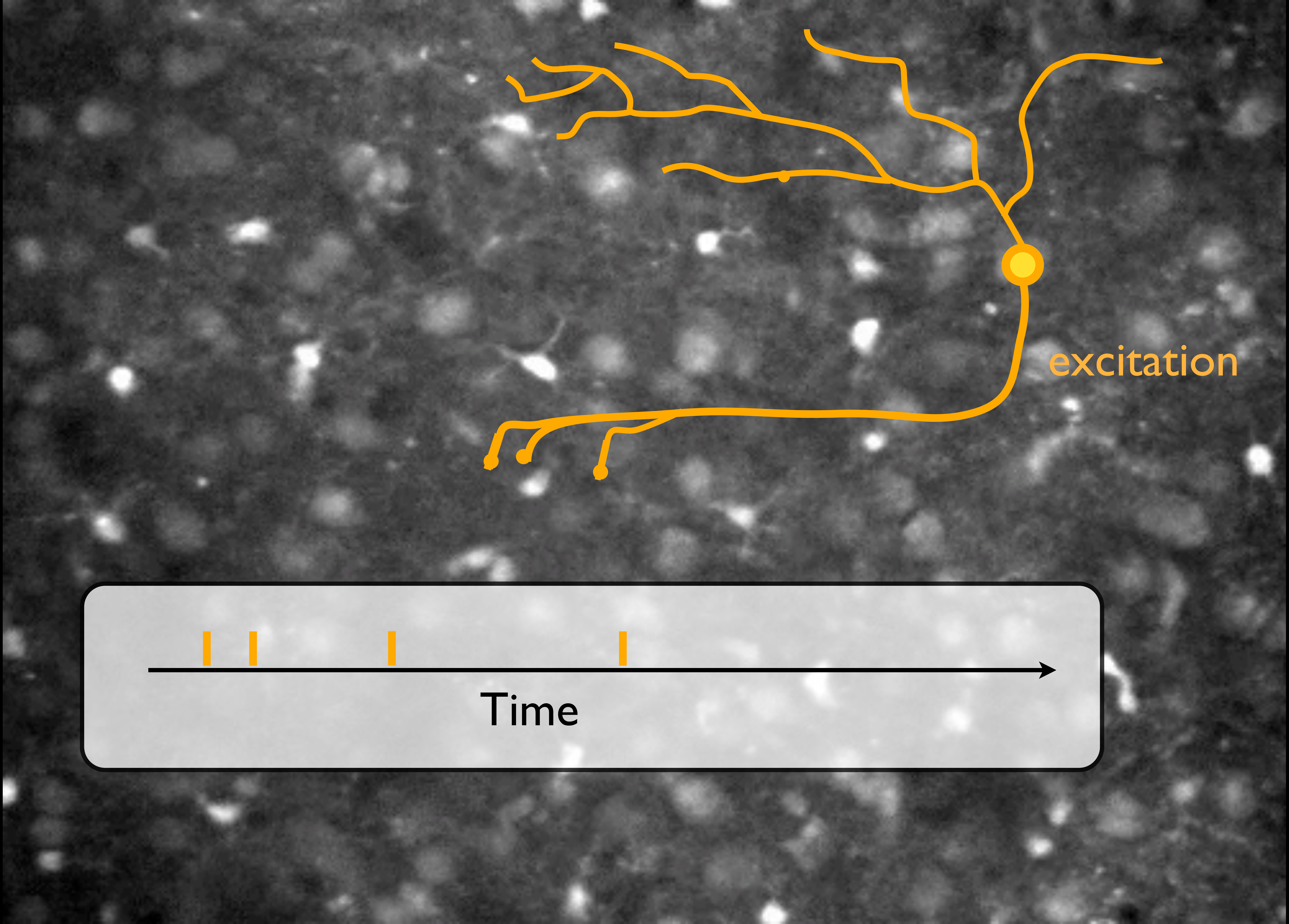
——> 1/N synaptic strength.

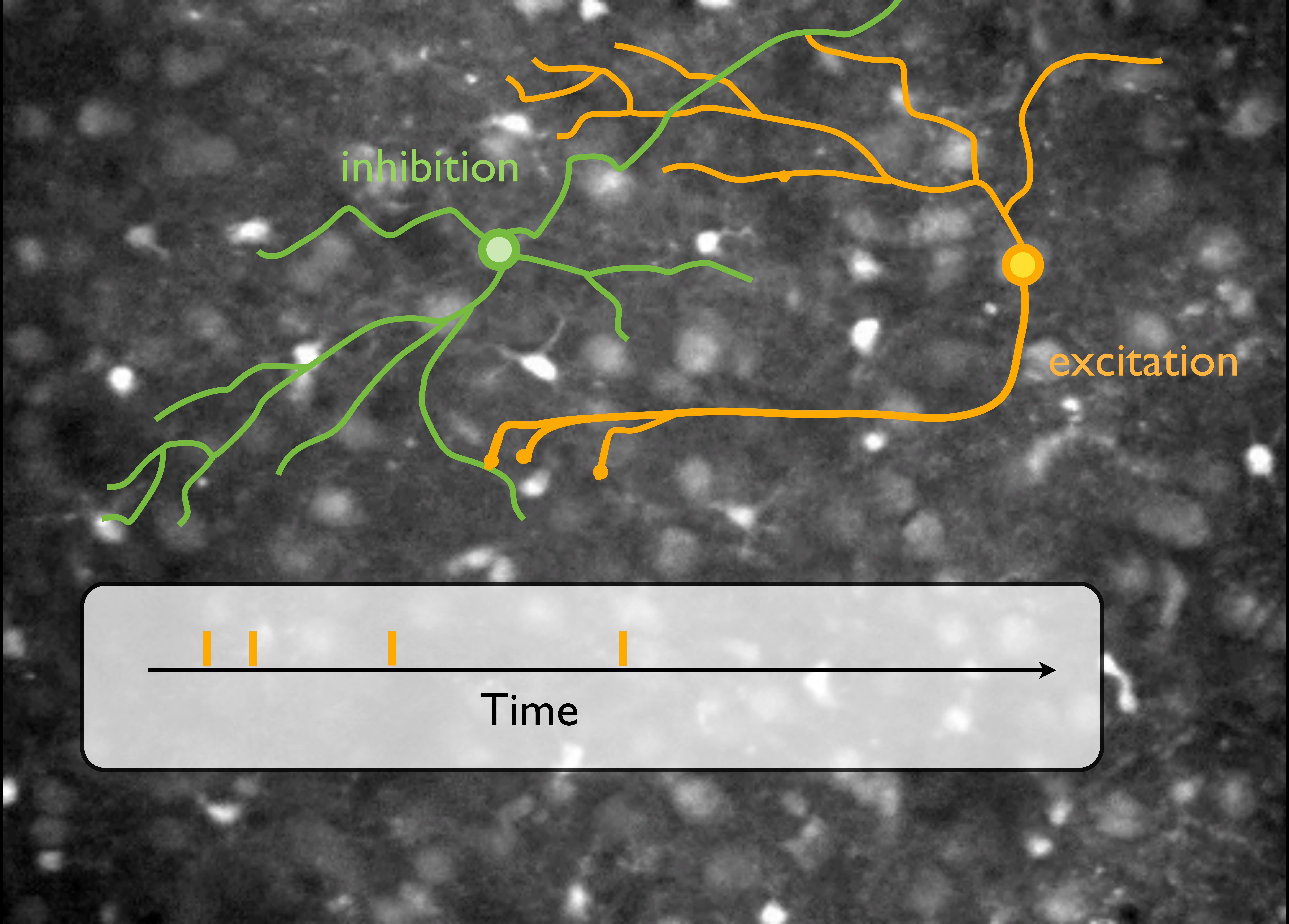


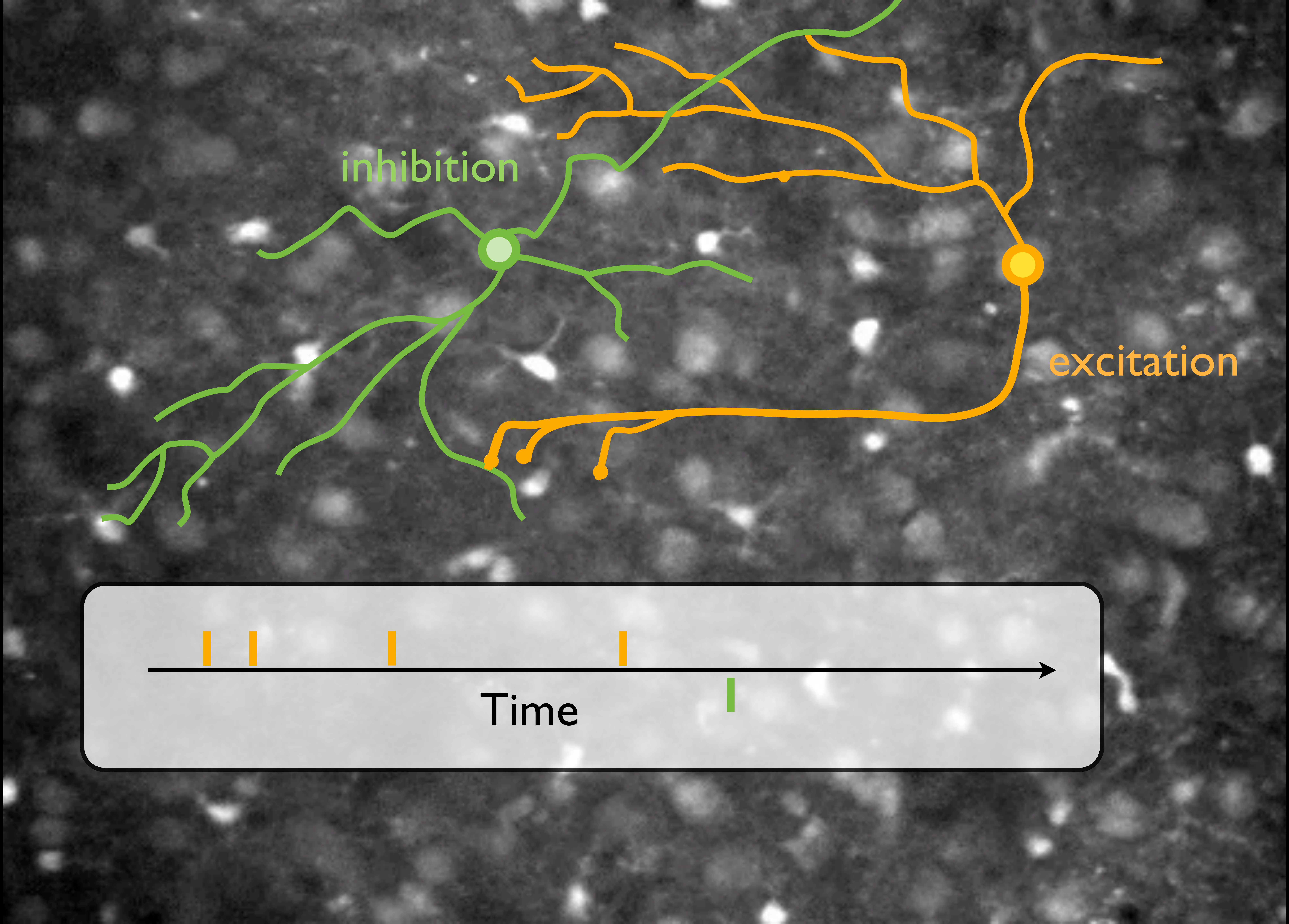
CV~=1!

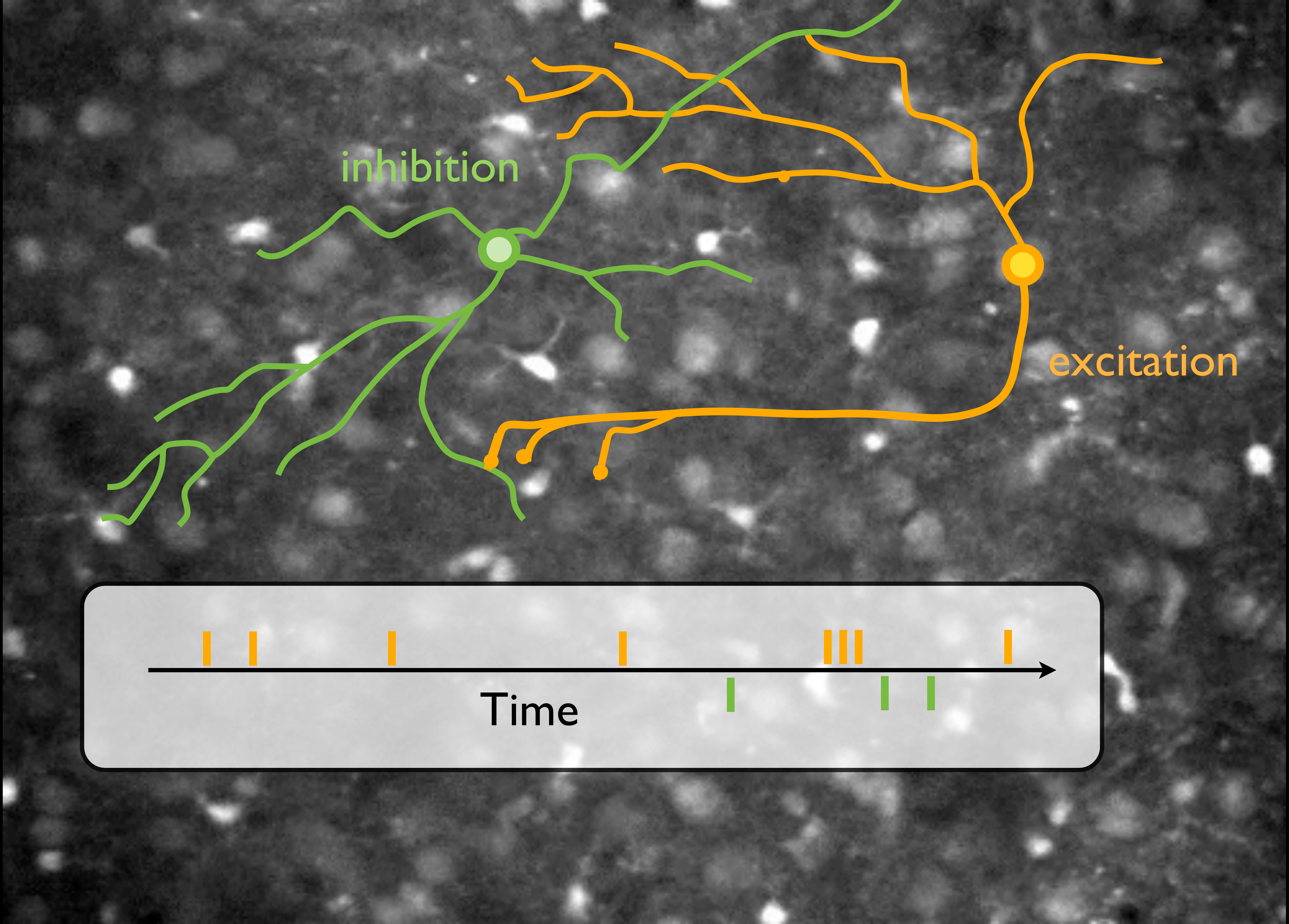

Time

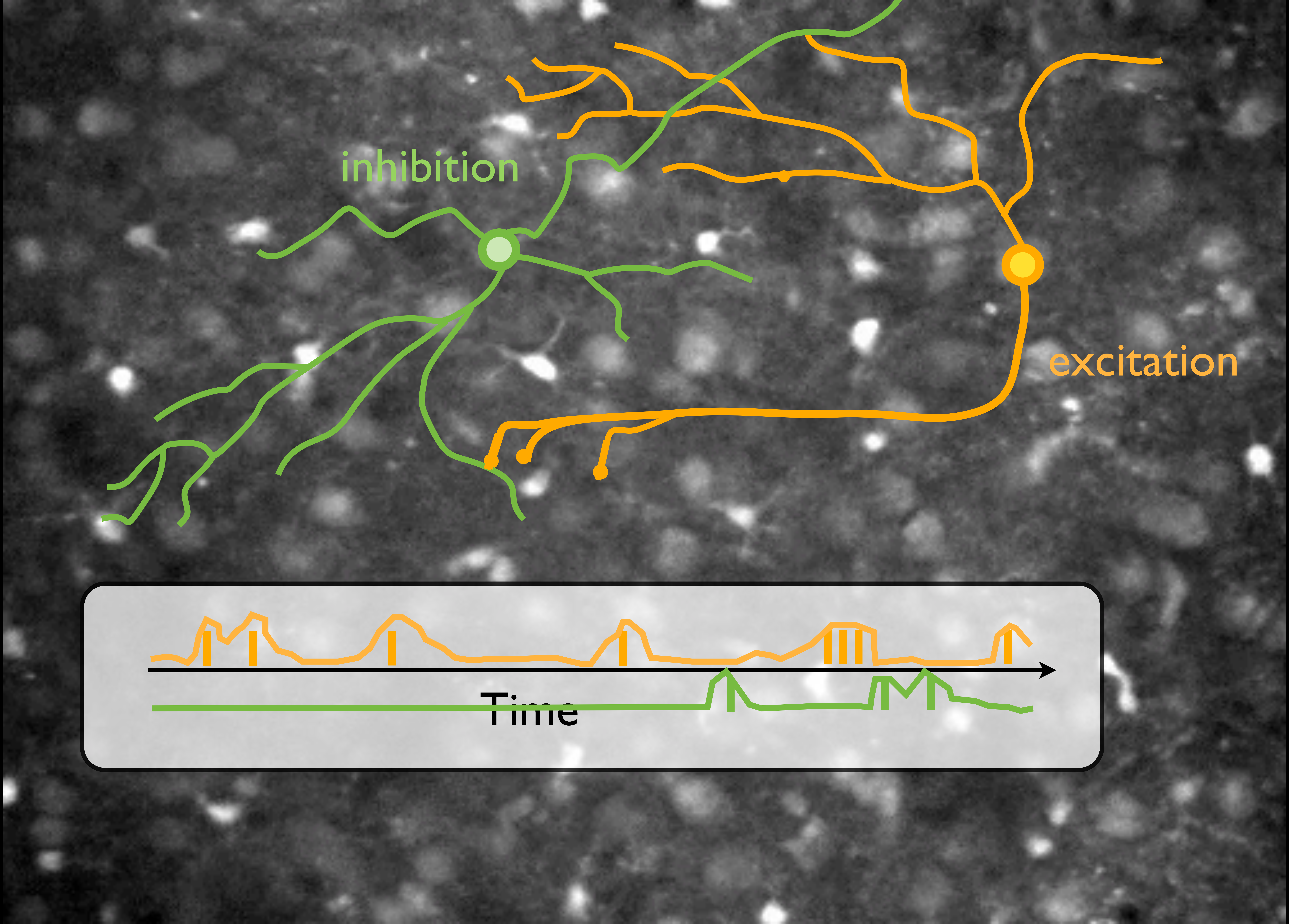

Time

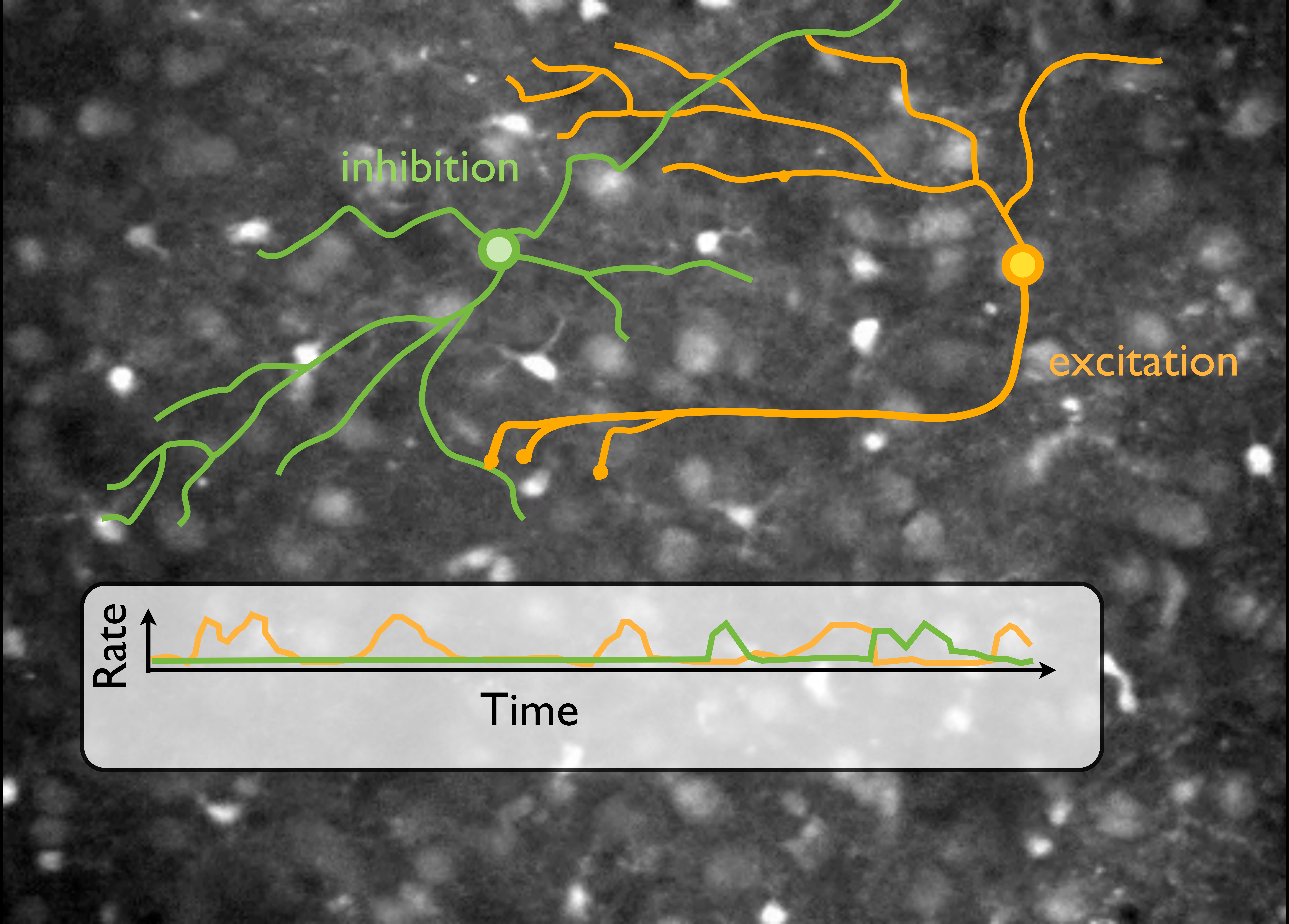

excitation
Time


inhibition
excitation
Time

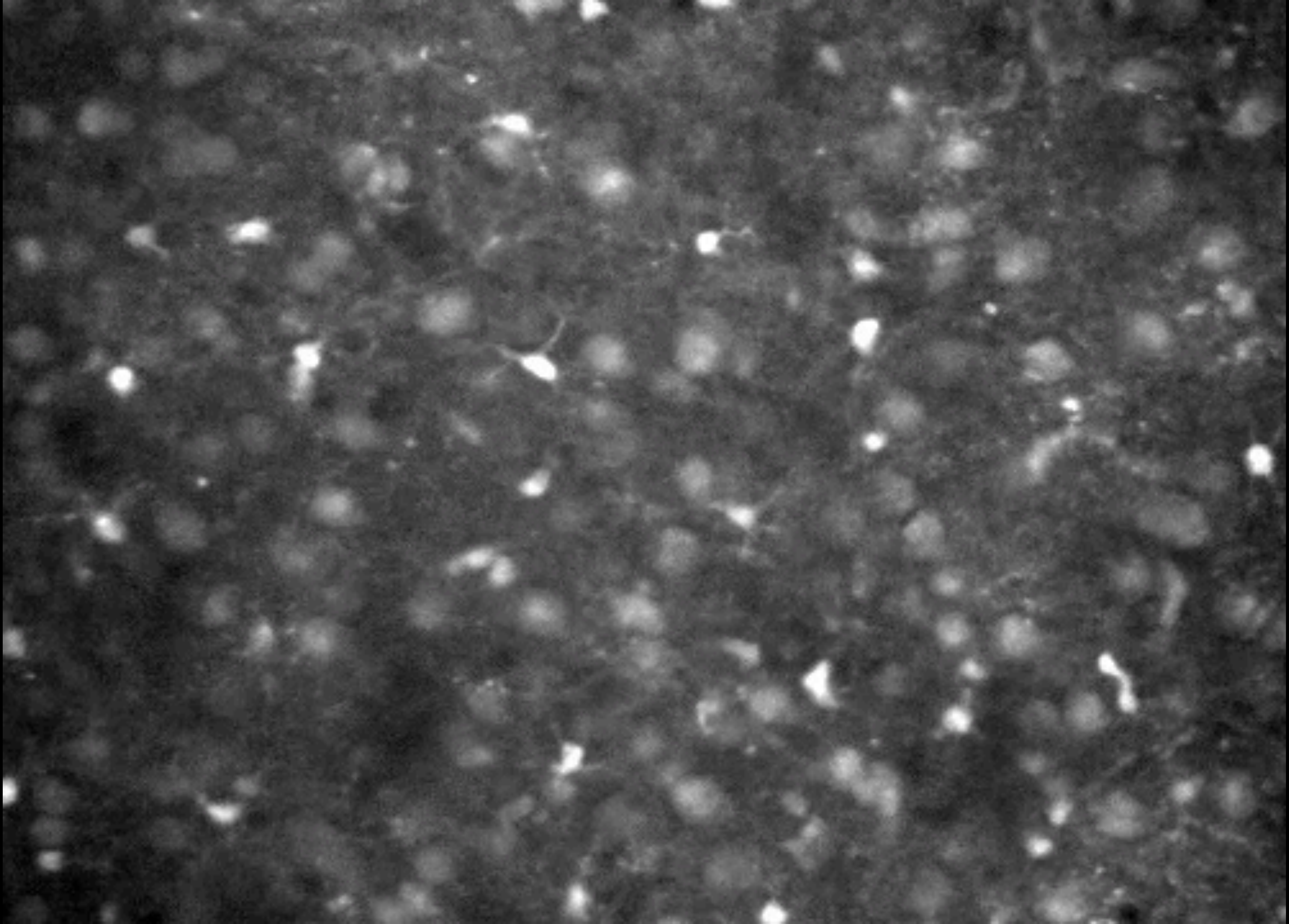

inhibition
excitation
Time

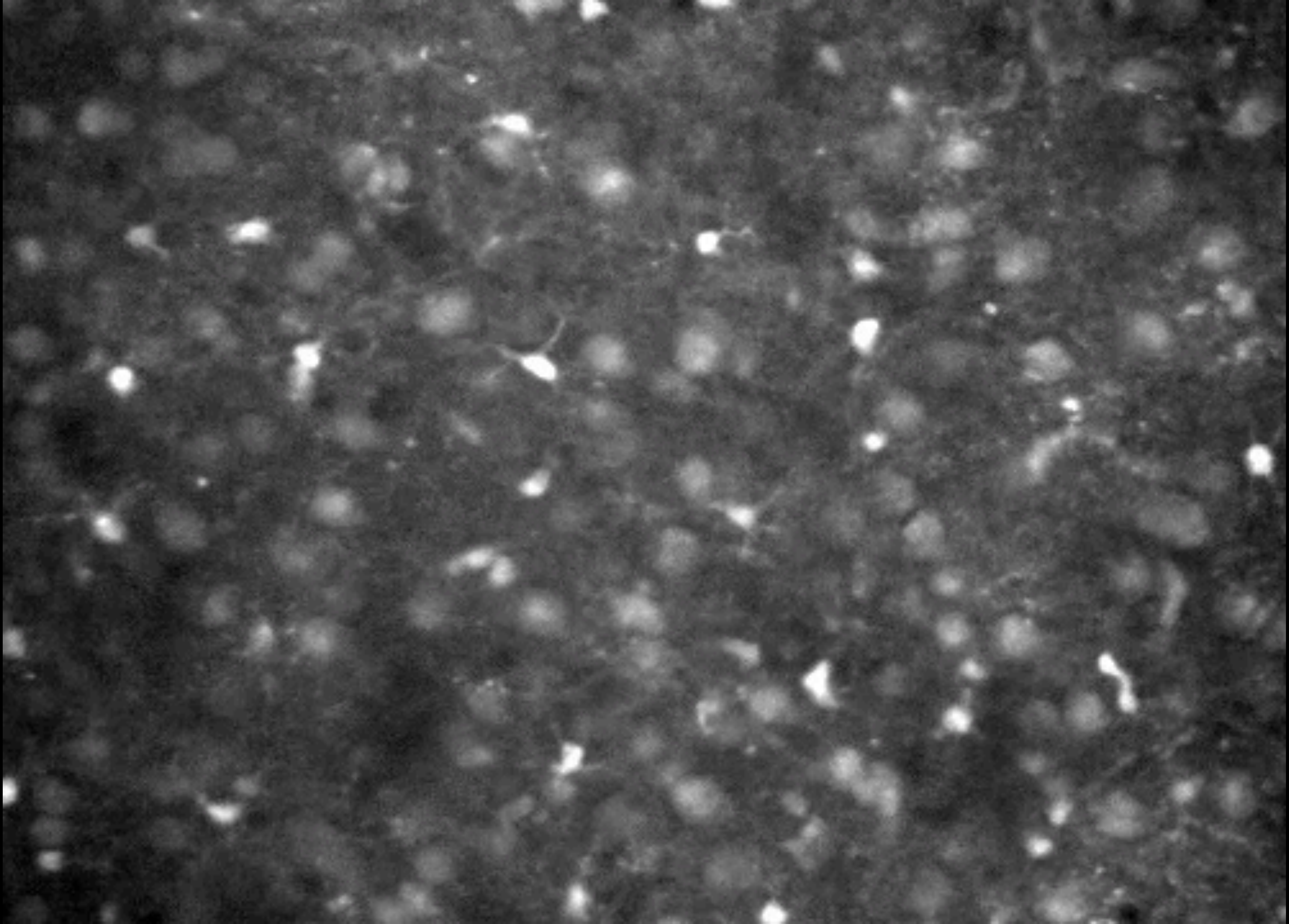

inhibition
excitation
Time

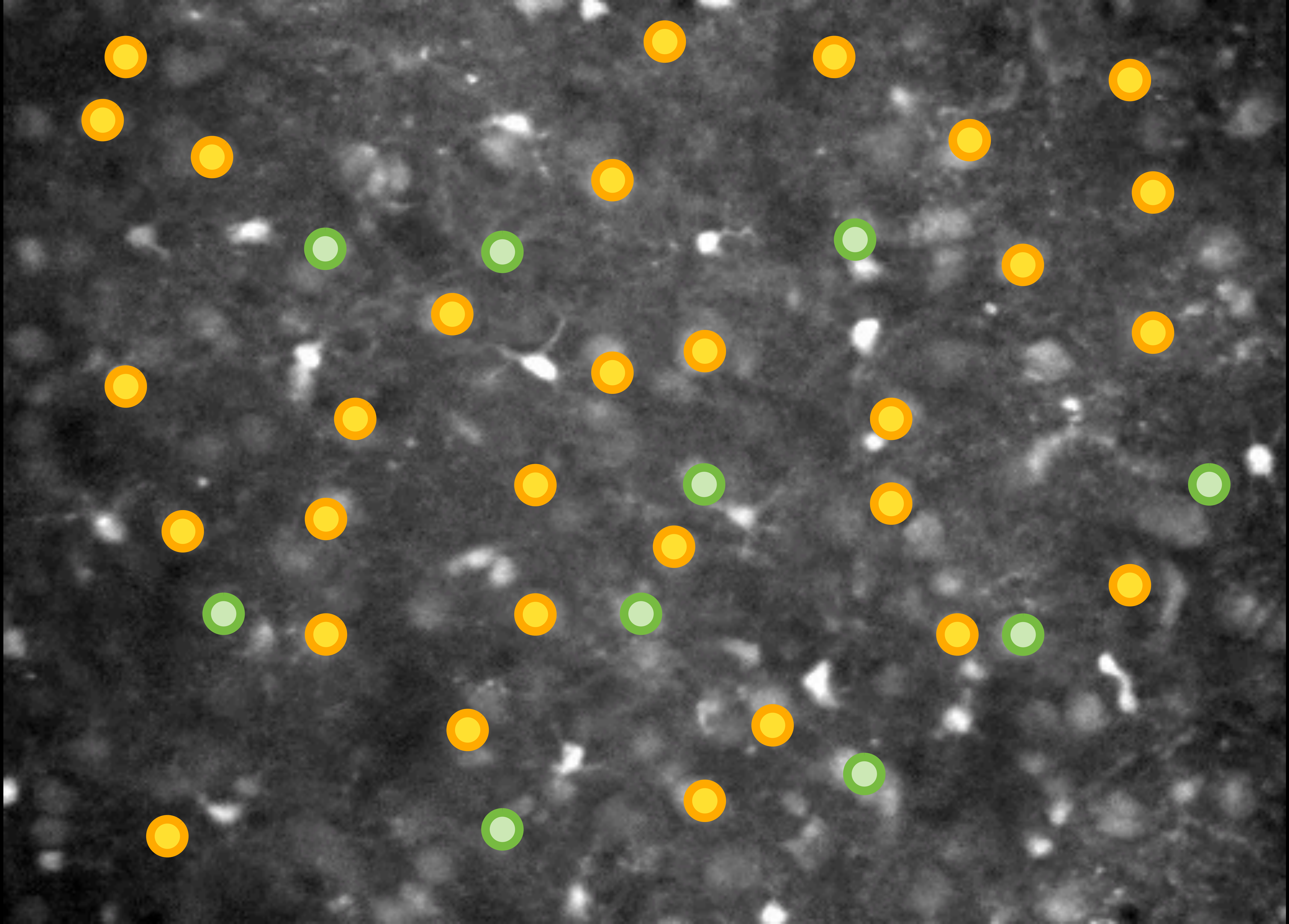

inhibition
excitation
Time

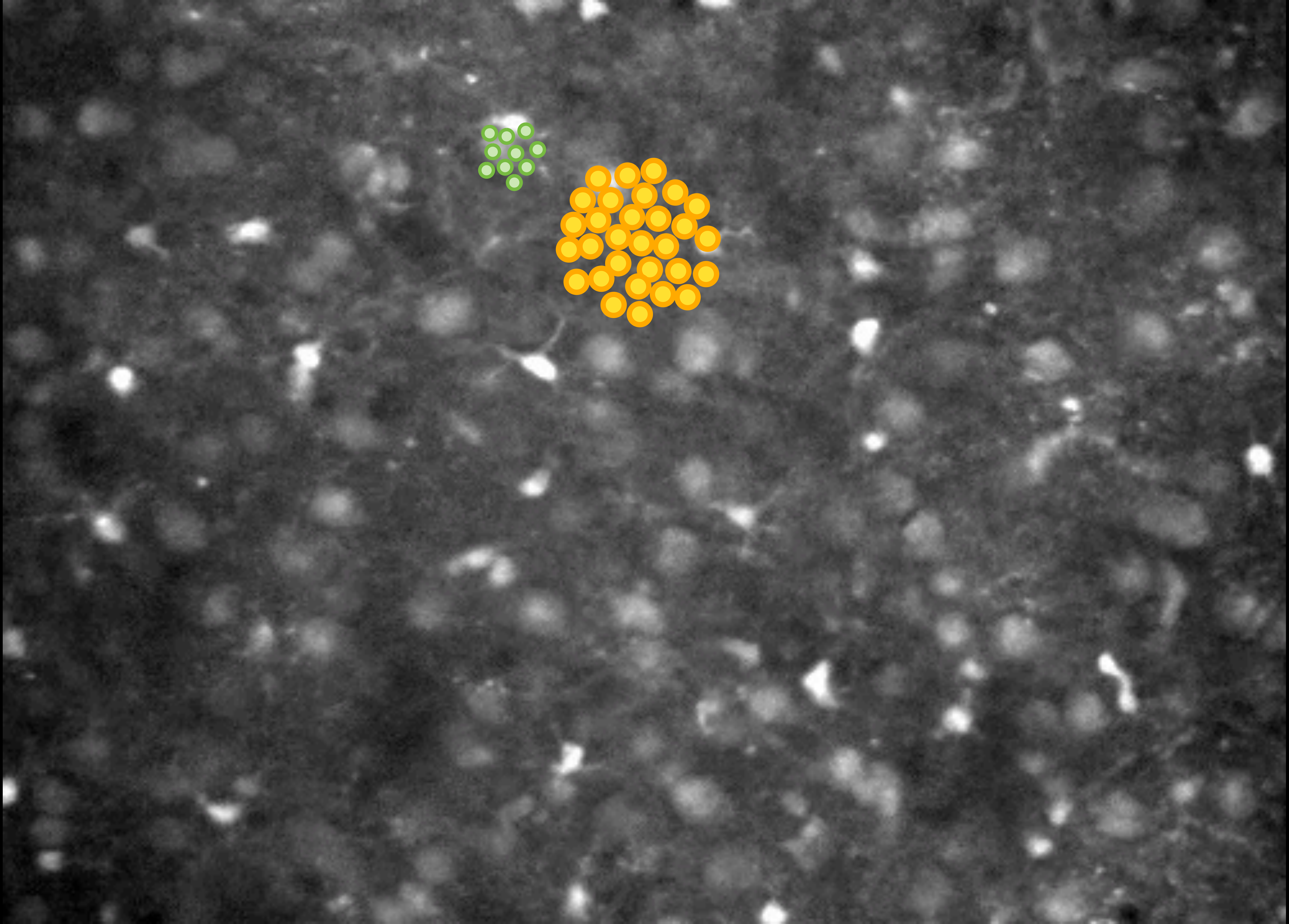


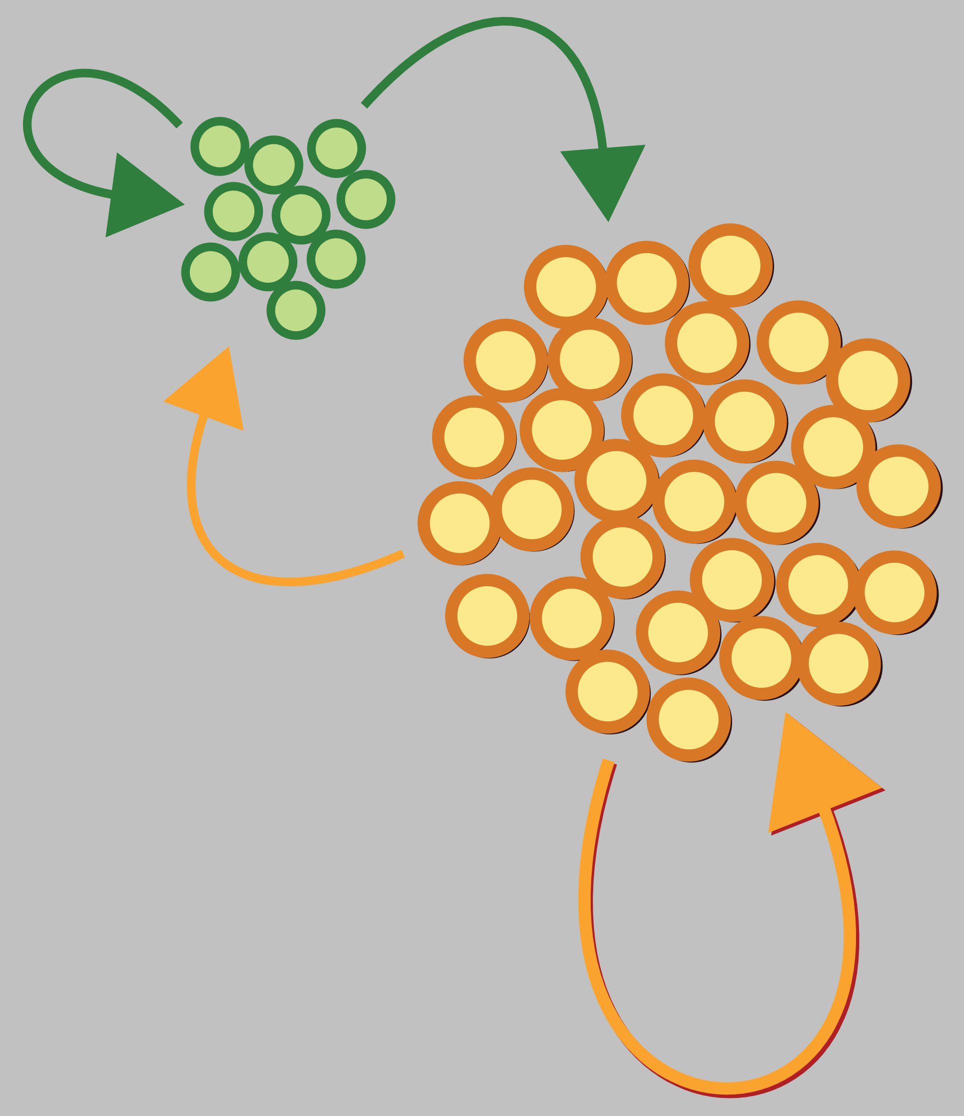
inhibition
excitation
Rate
Time



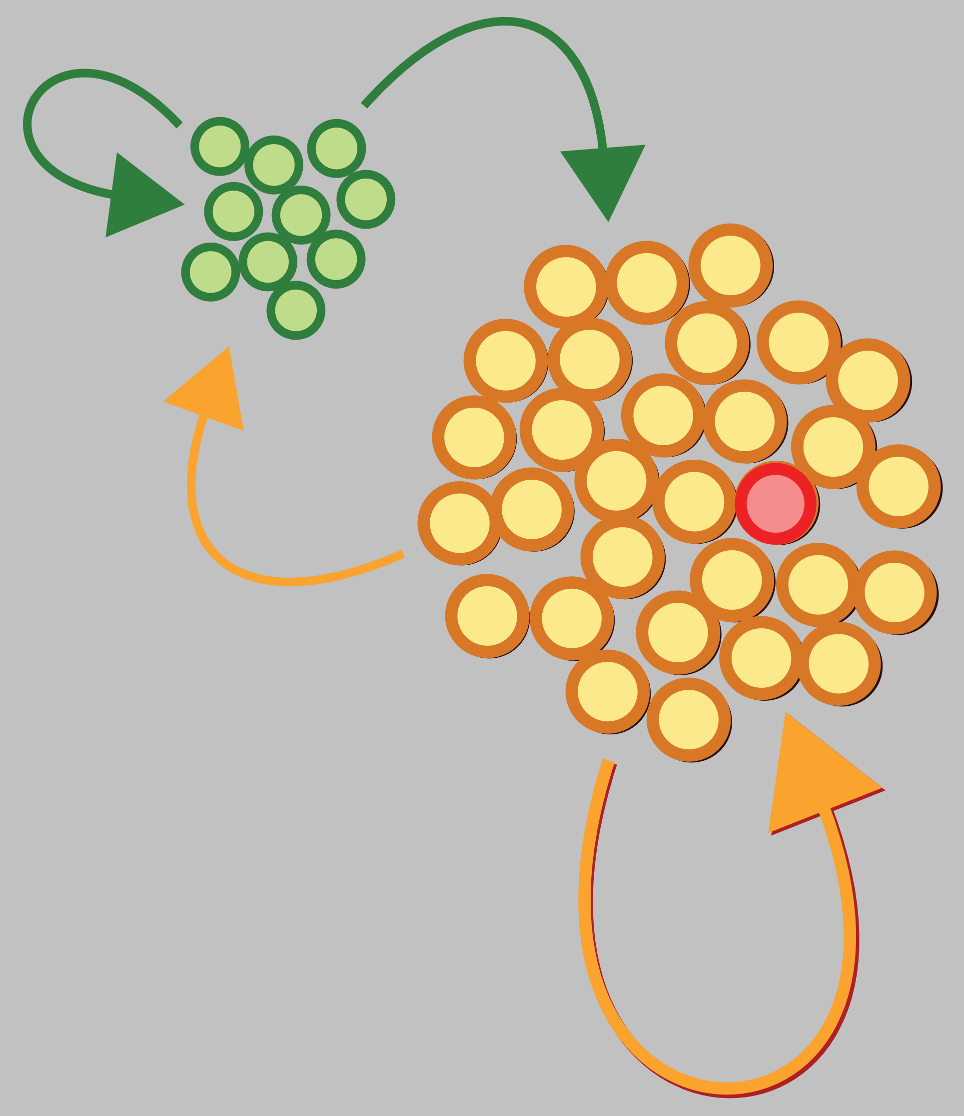








Softky & Koch, JNeuro 1993
van Vreeswijk & Sompolinsky, Science, 1996



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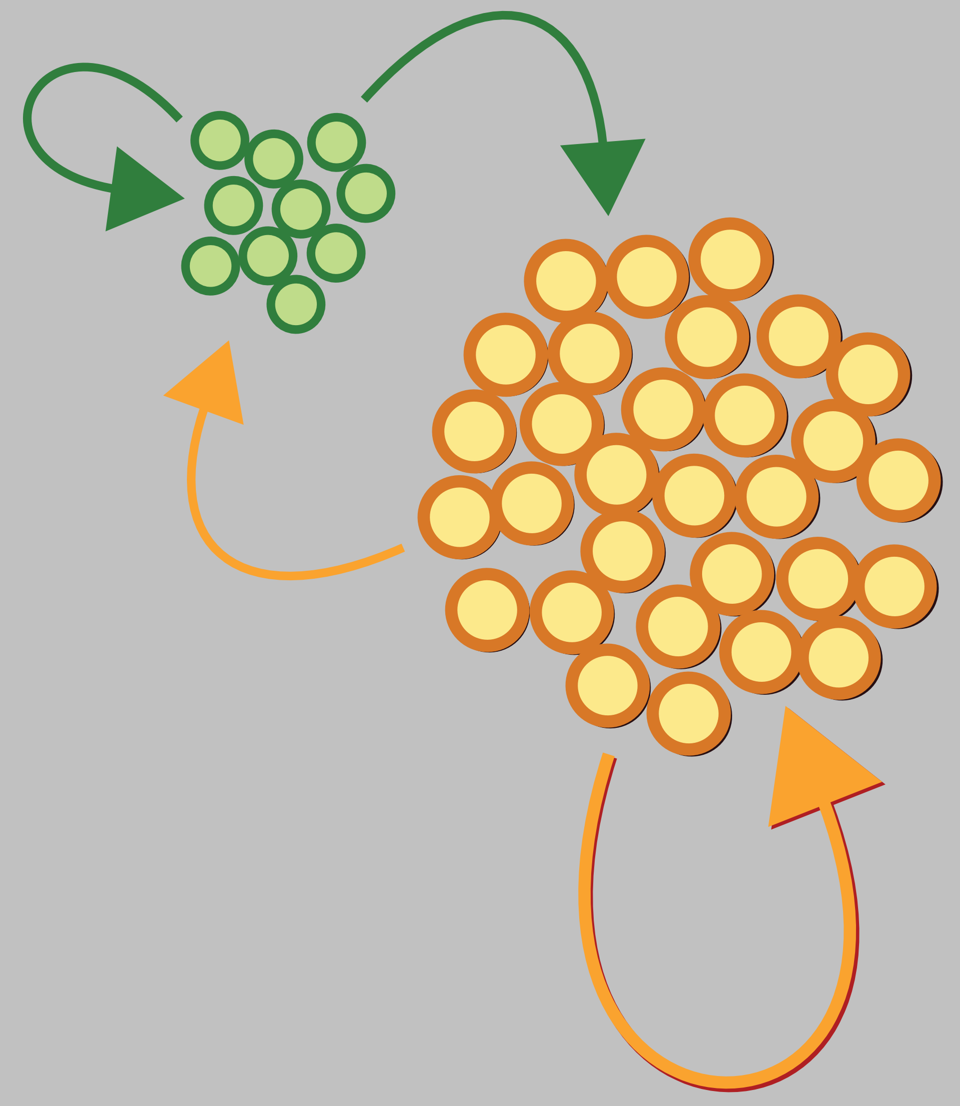
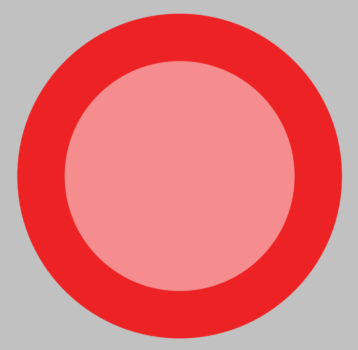
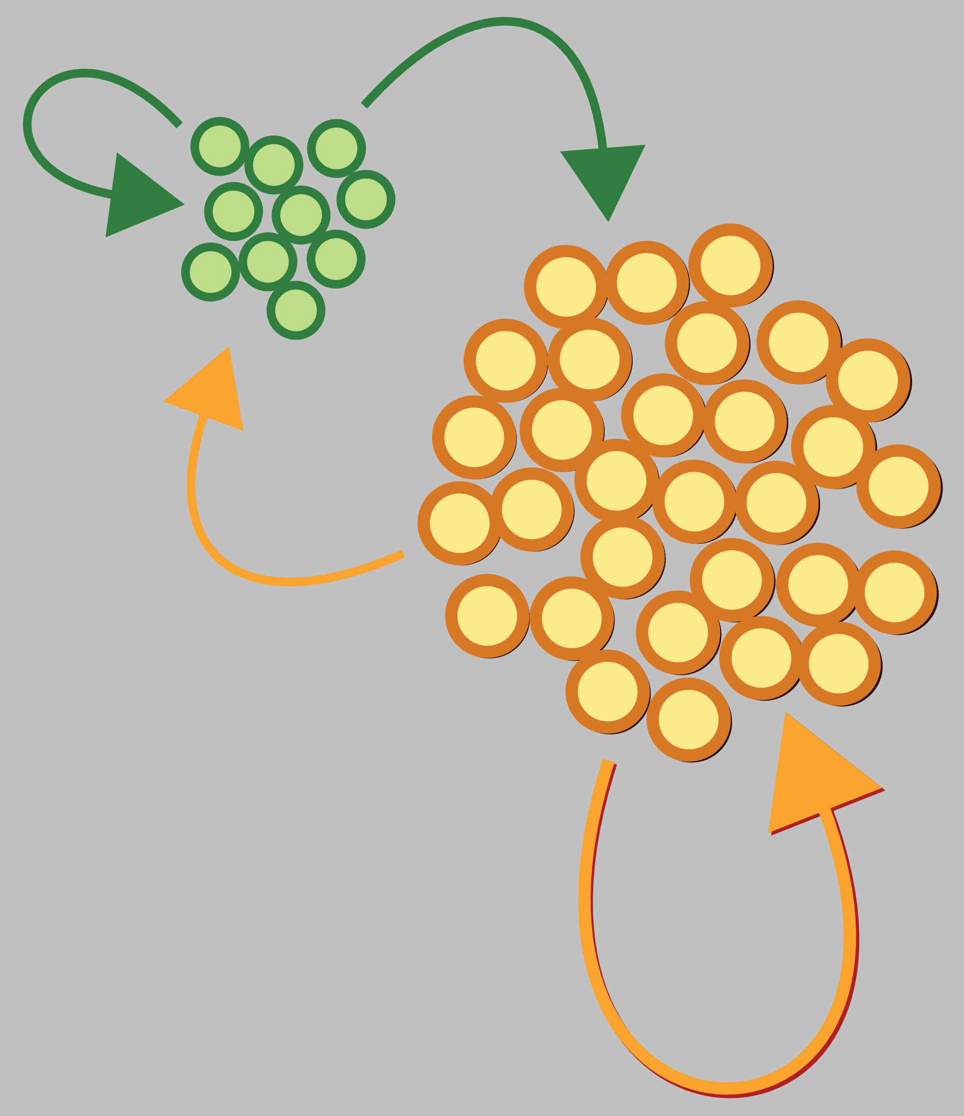


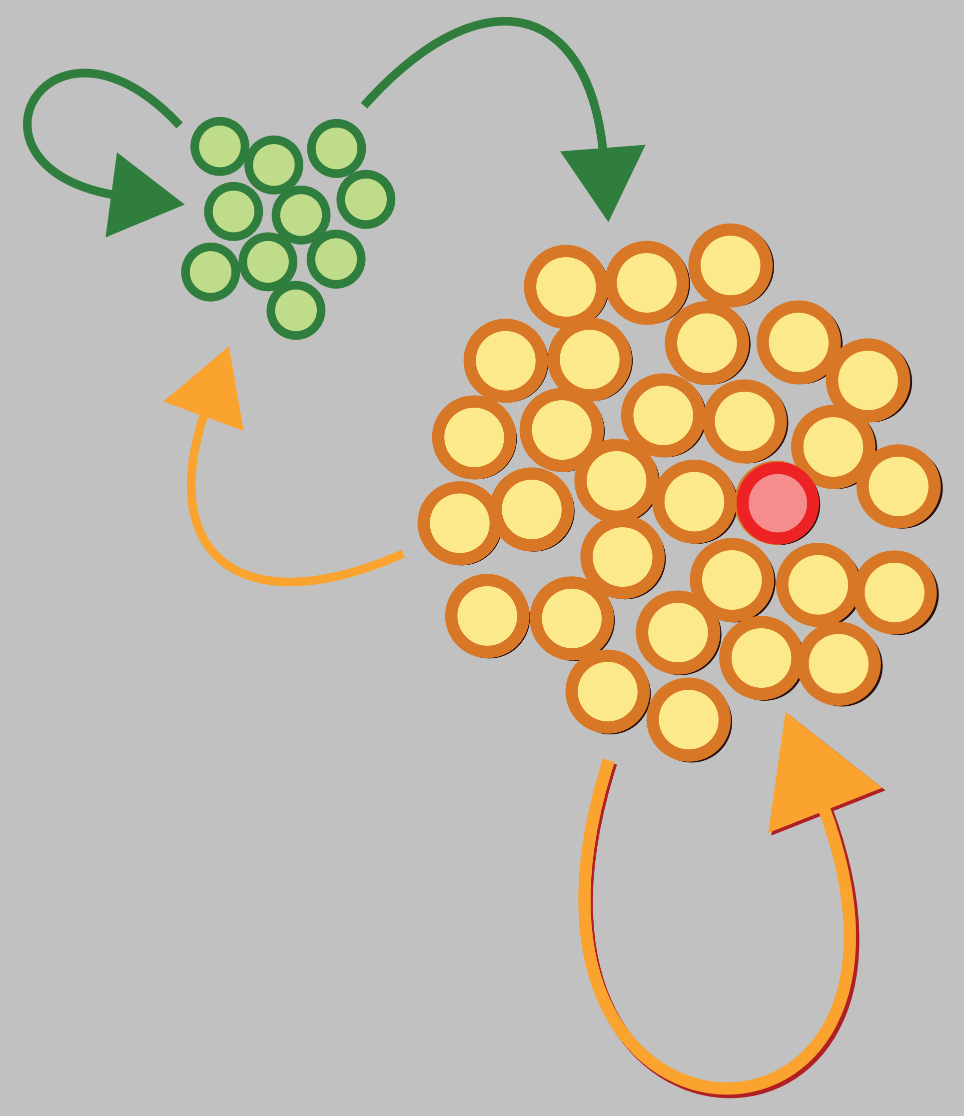


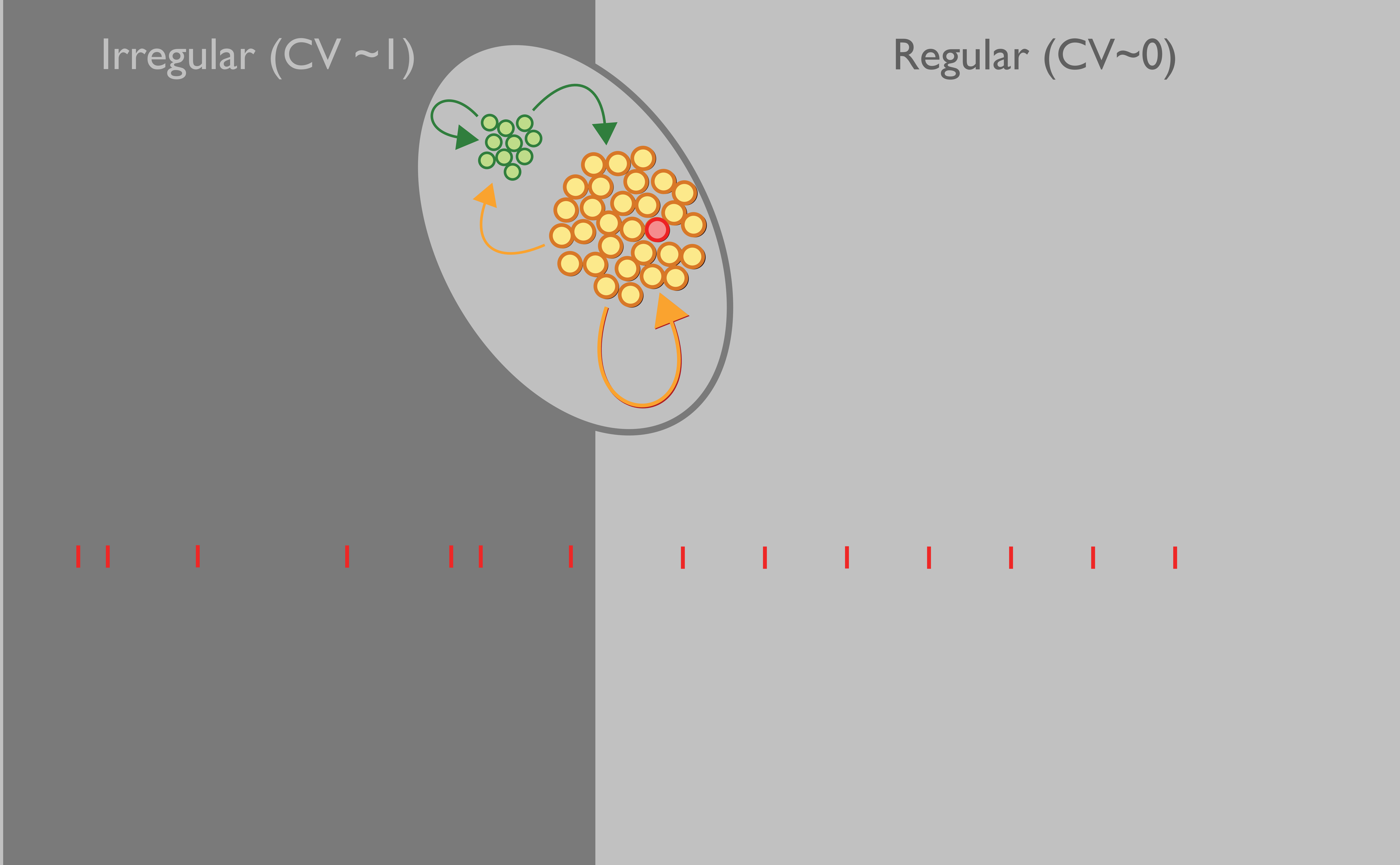
Softky & Koch, JNeuro 1993
van Vreeswijk & Sompolinsky, Science, 1996

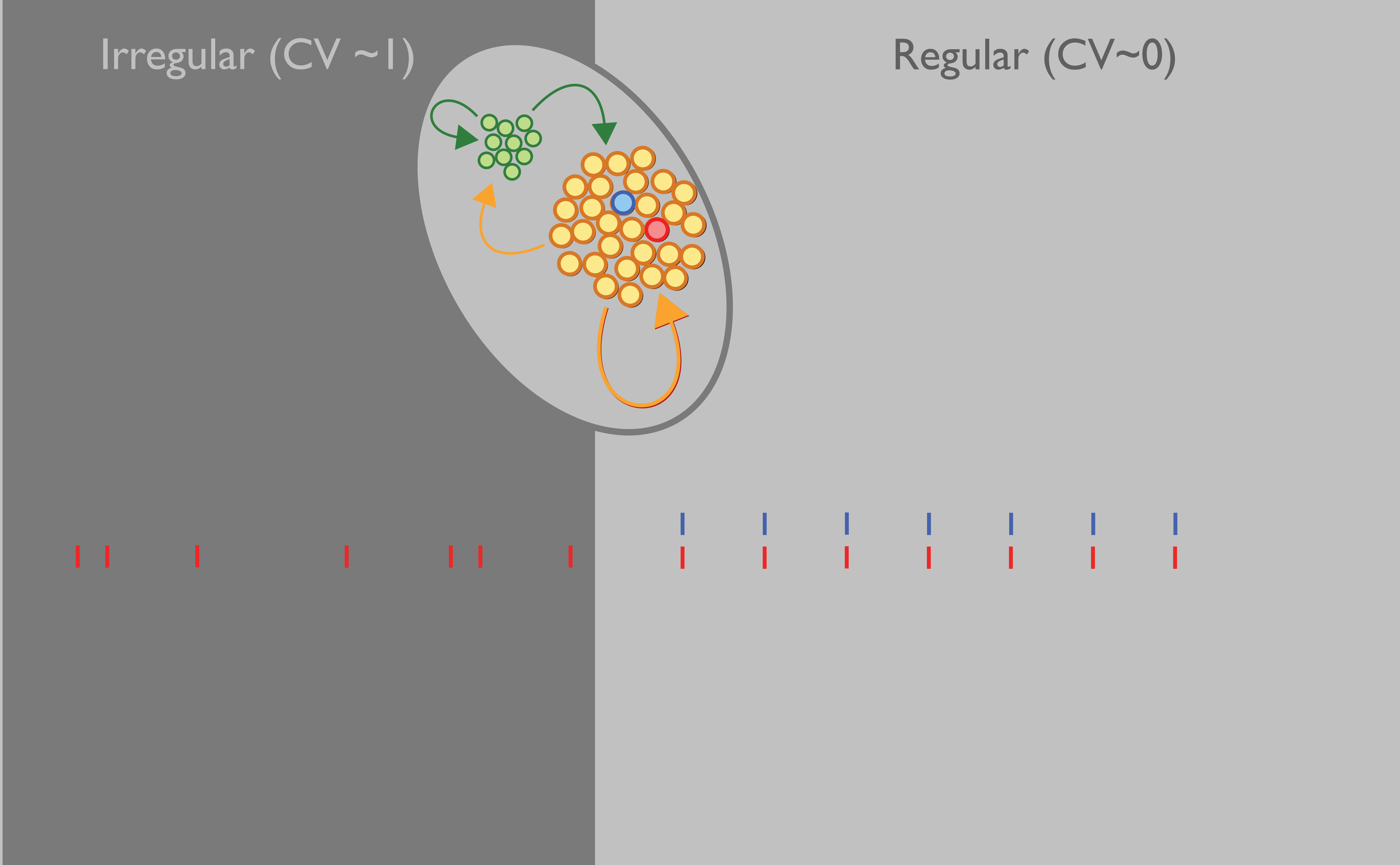
Irregular (CV ~ 1)

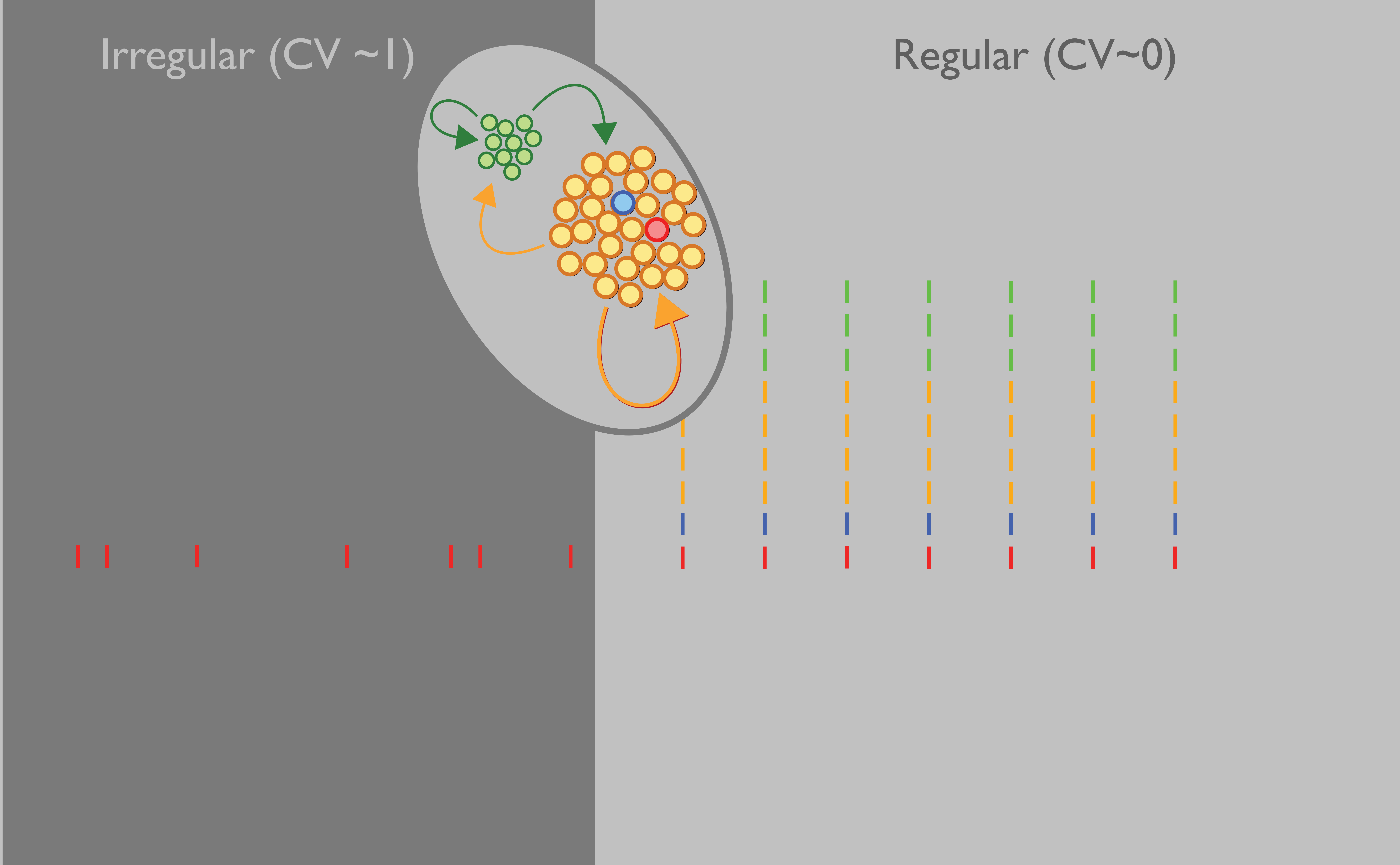


Irregular (CV ~1)

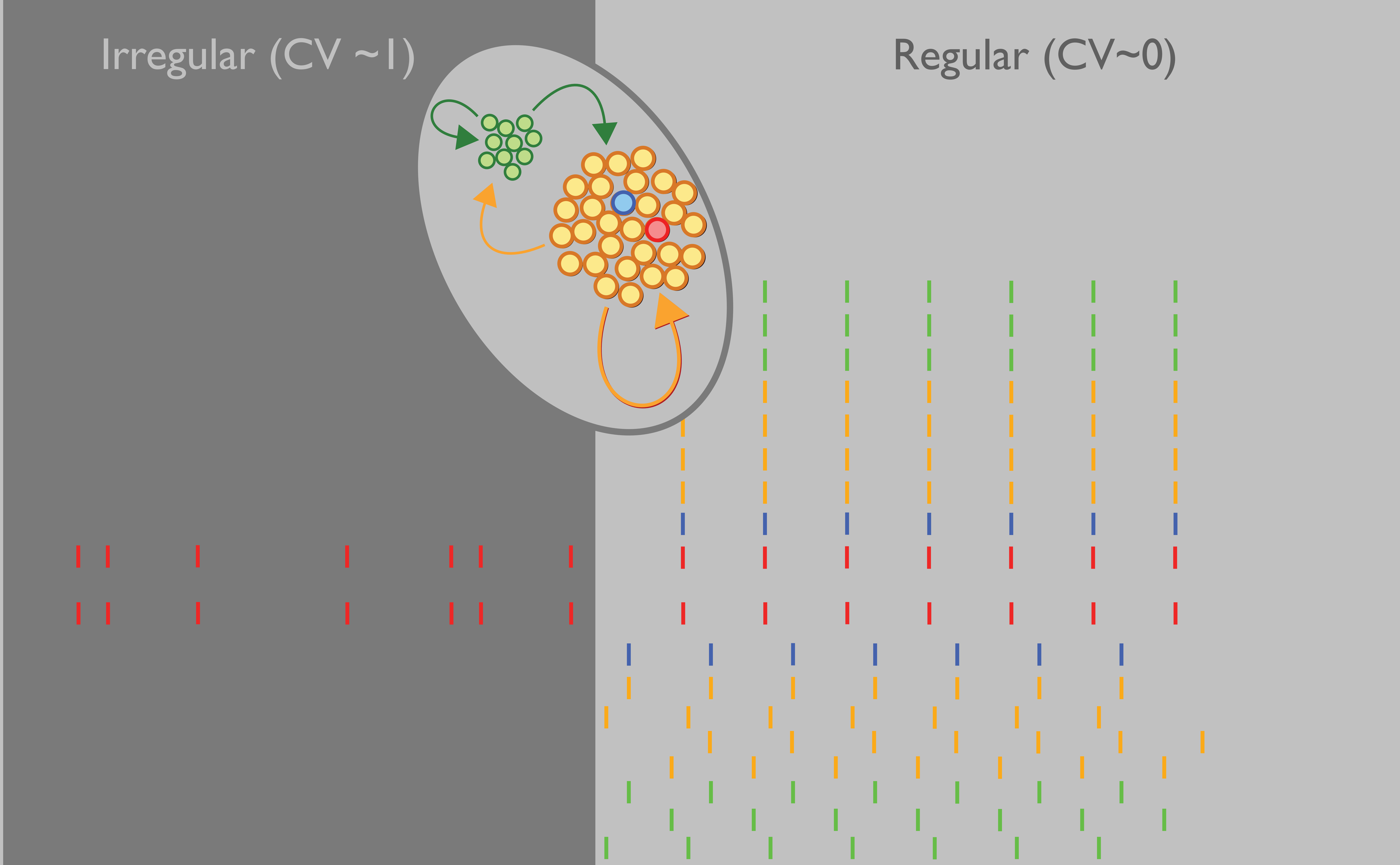



Irregular (CV ~1)
Regular (CV~0)

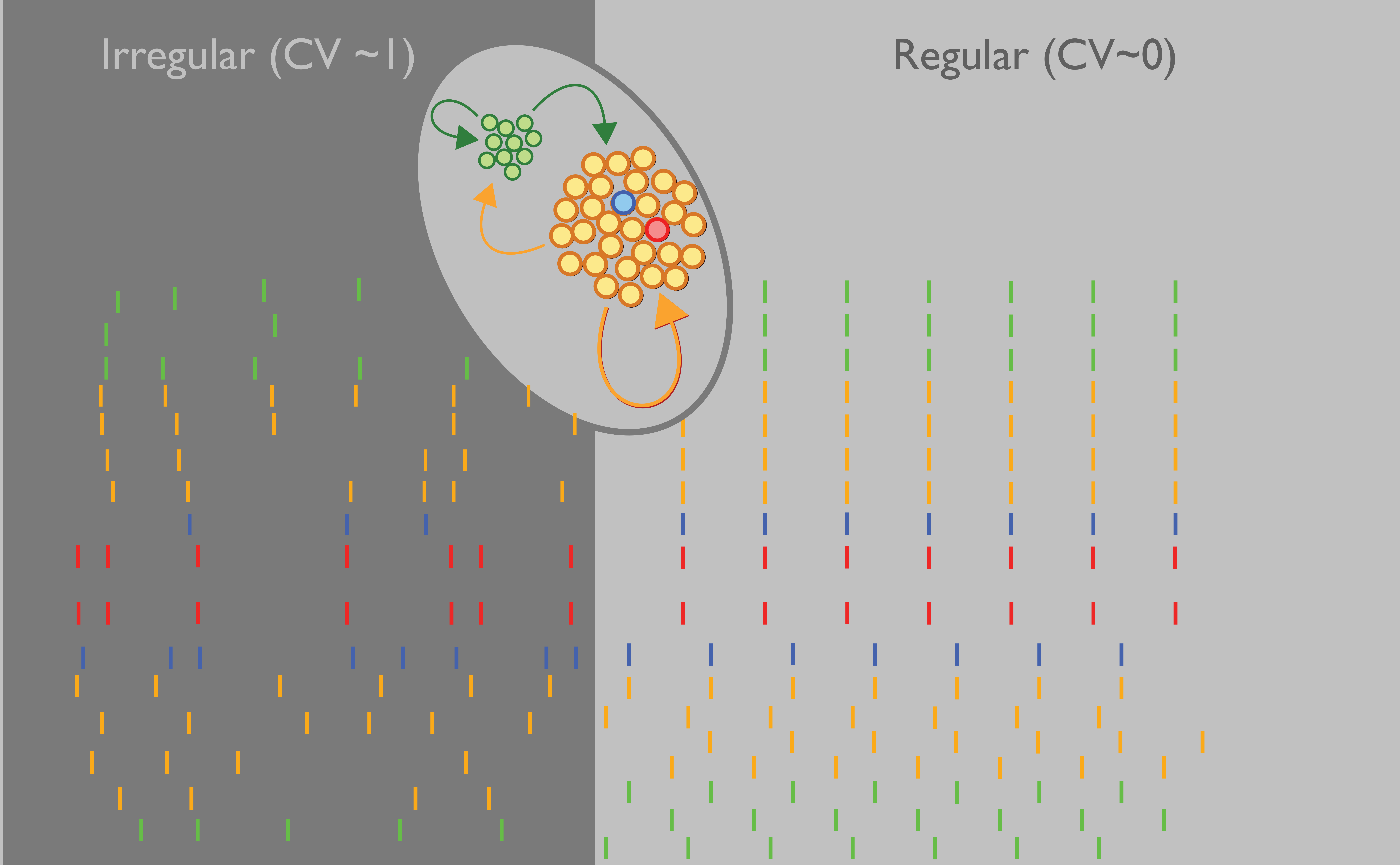

Irregular (CV ~1)
Regular (CV~0)

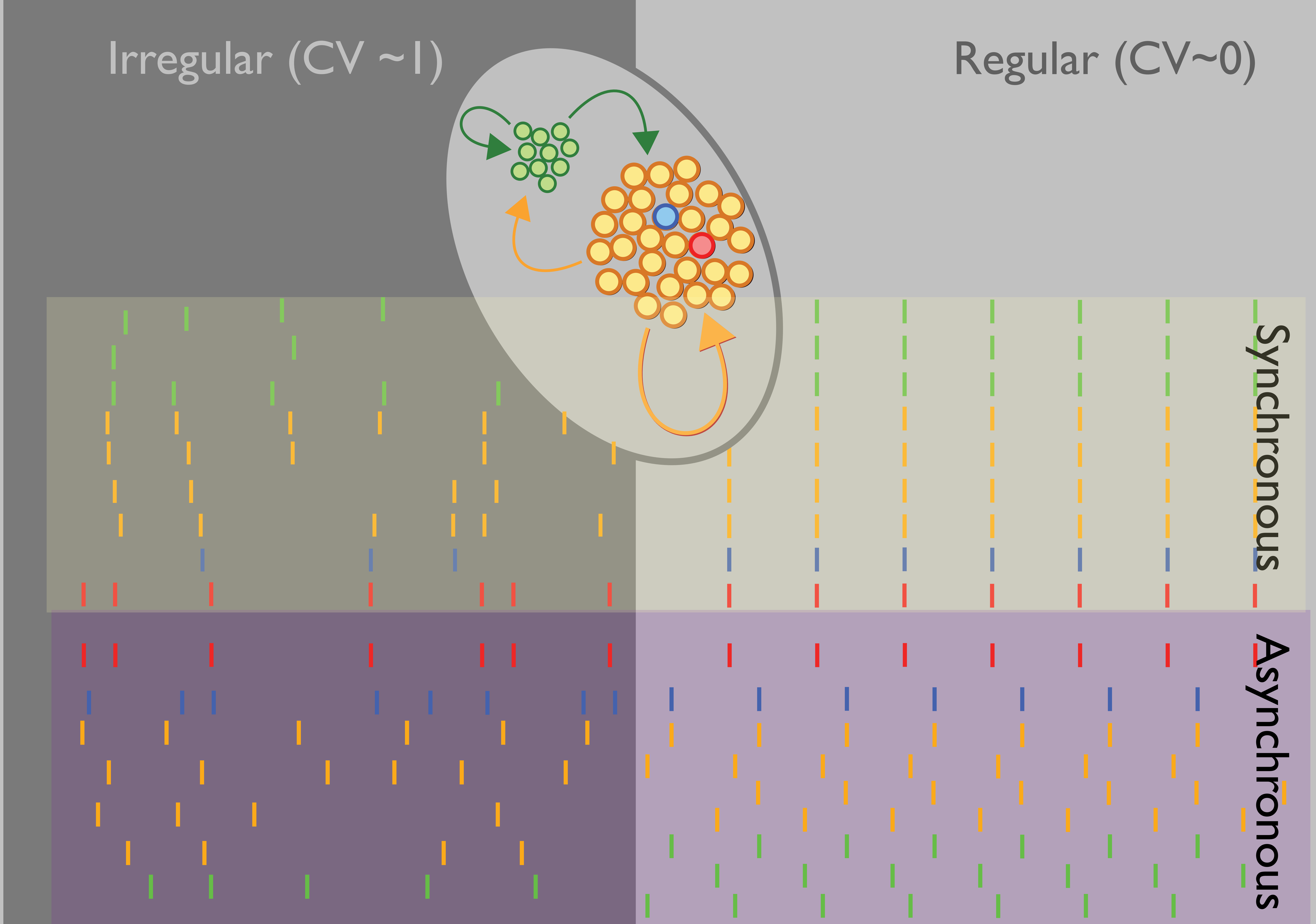


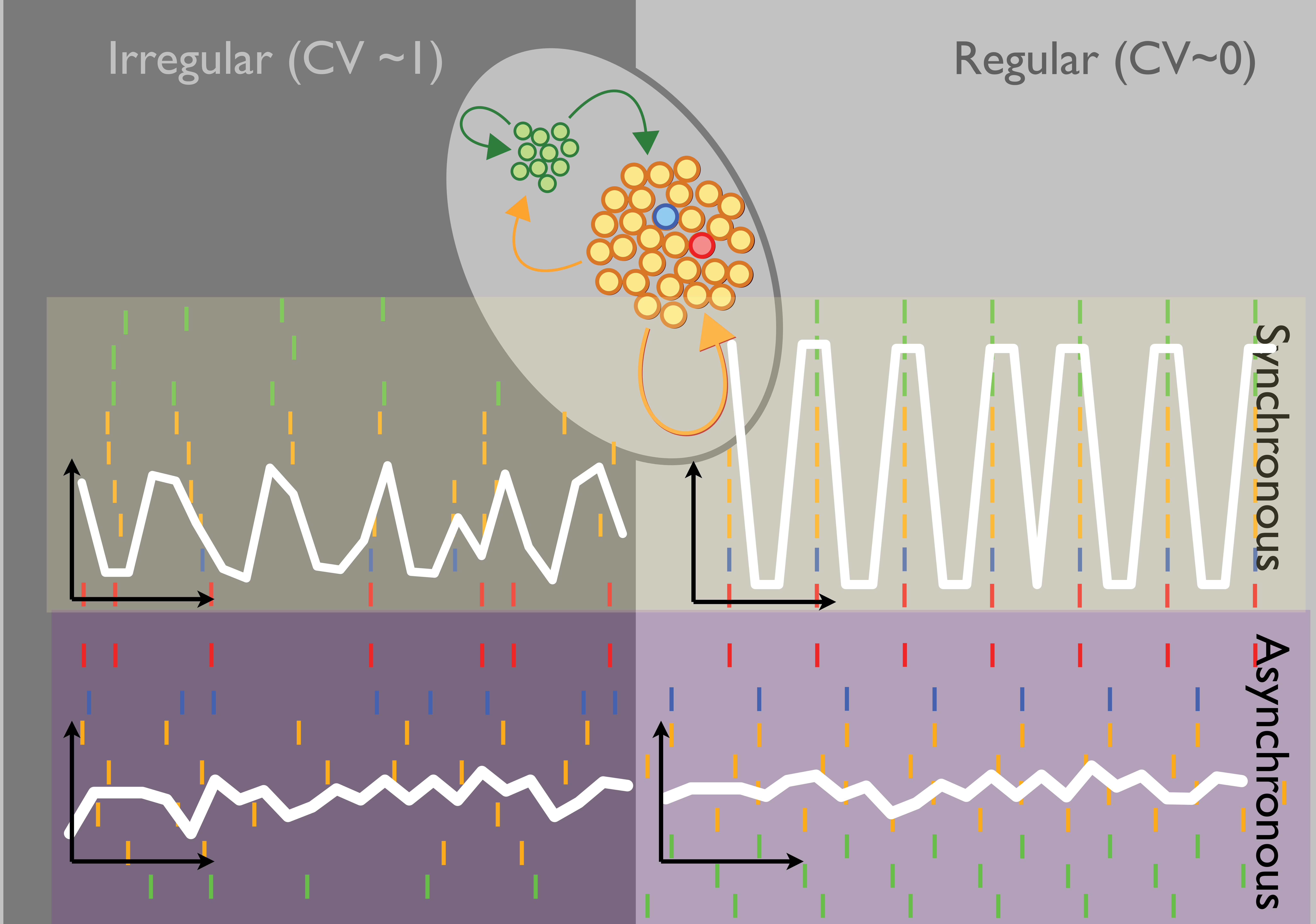
Irregular (CV ~1)
Regular (CV~0)

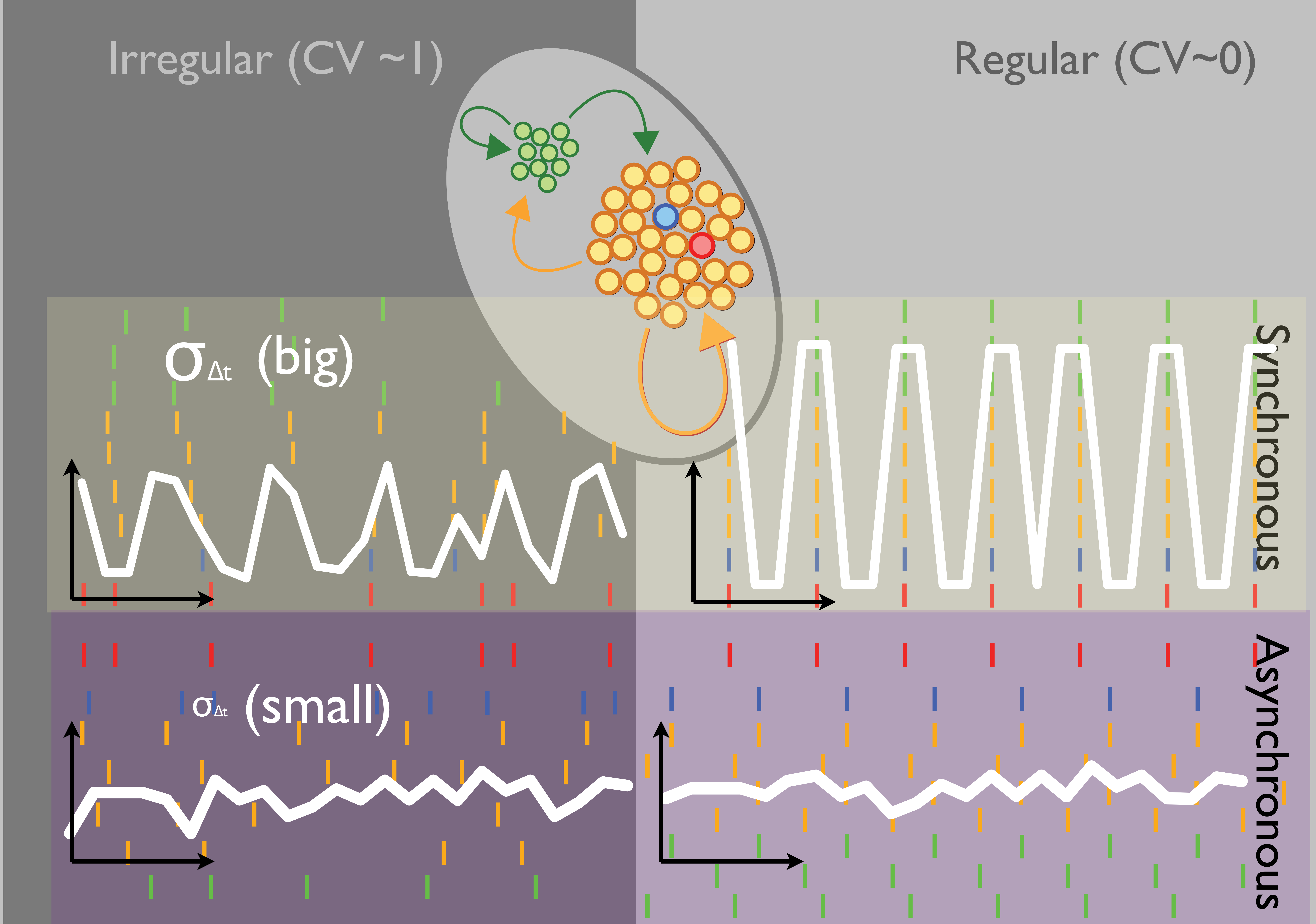


Irregular (CV ~1)
Regular (CV~0)

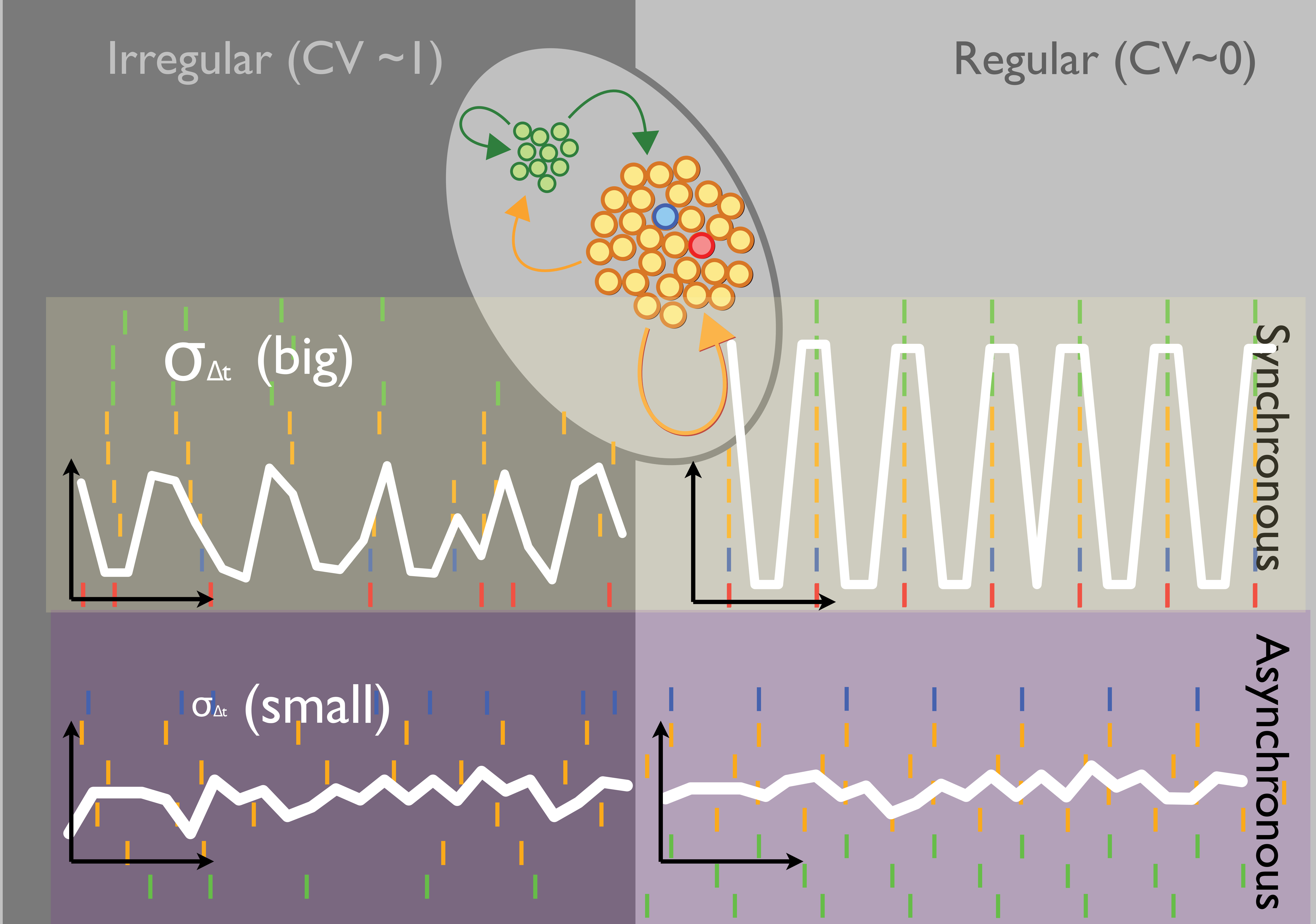

Irregular (CV ~1)
Regular (CV~0)


Irregular (CV ~1)
Regular (CV~0)
Synchronous
Asynchronous

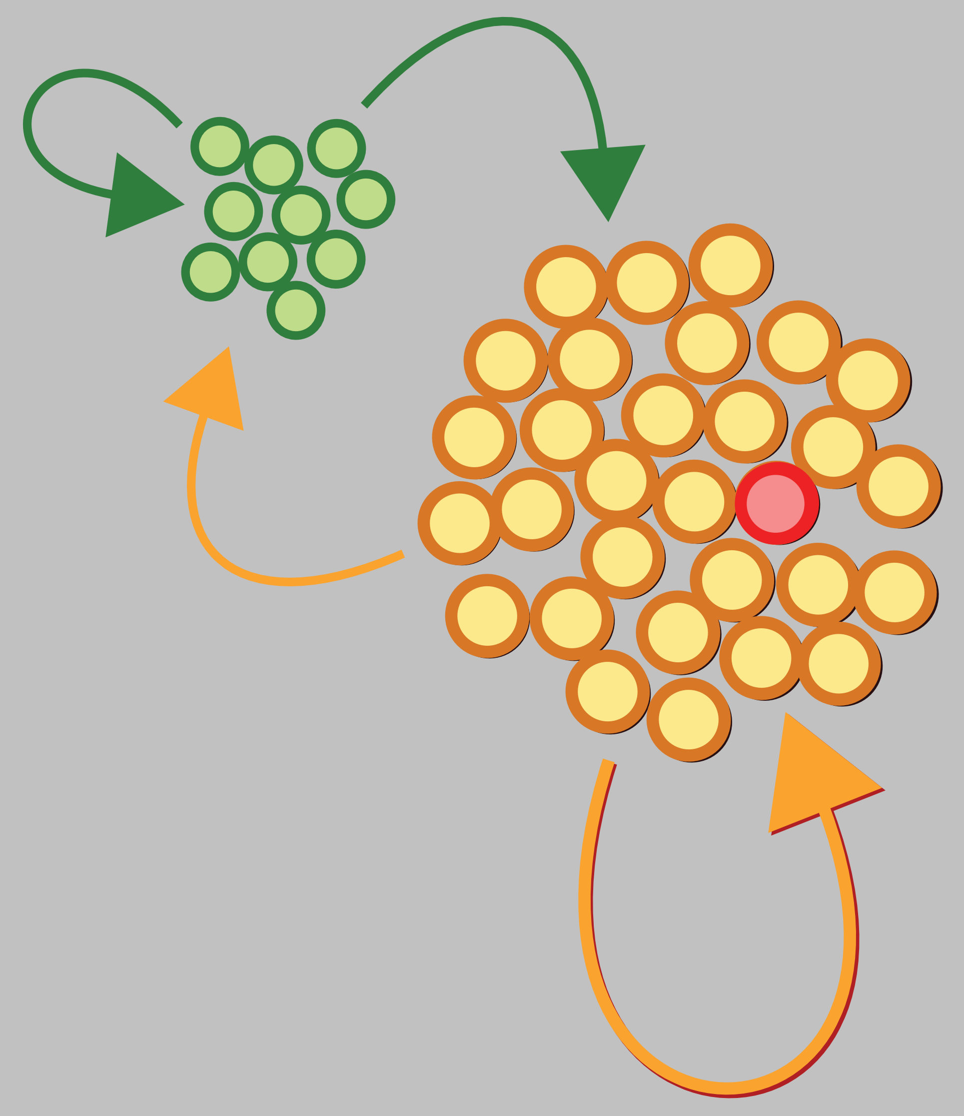

Irregular (CV ~1)
Regular (CV~0)
Synchronous
Asynchronous

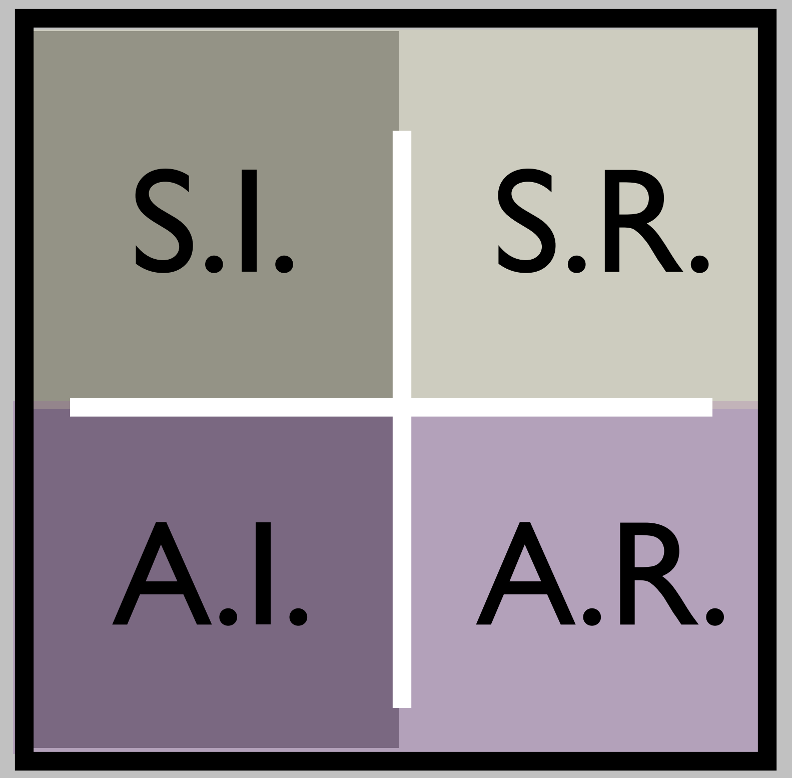


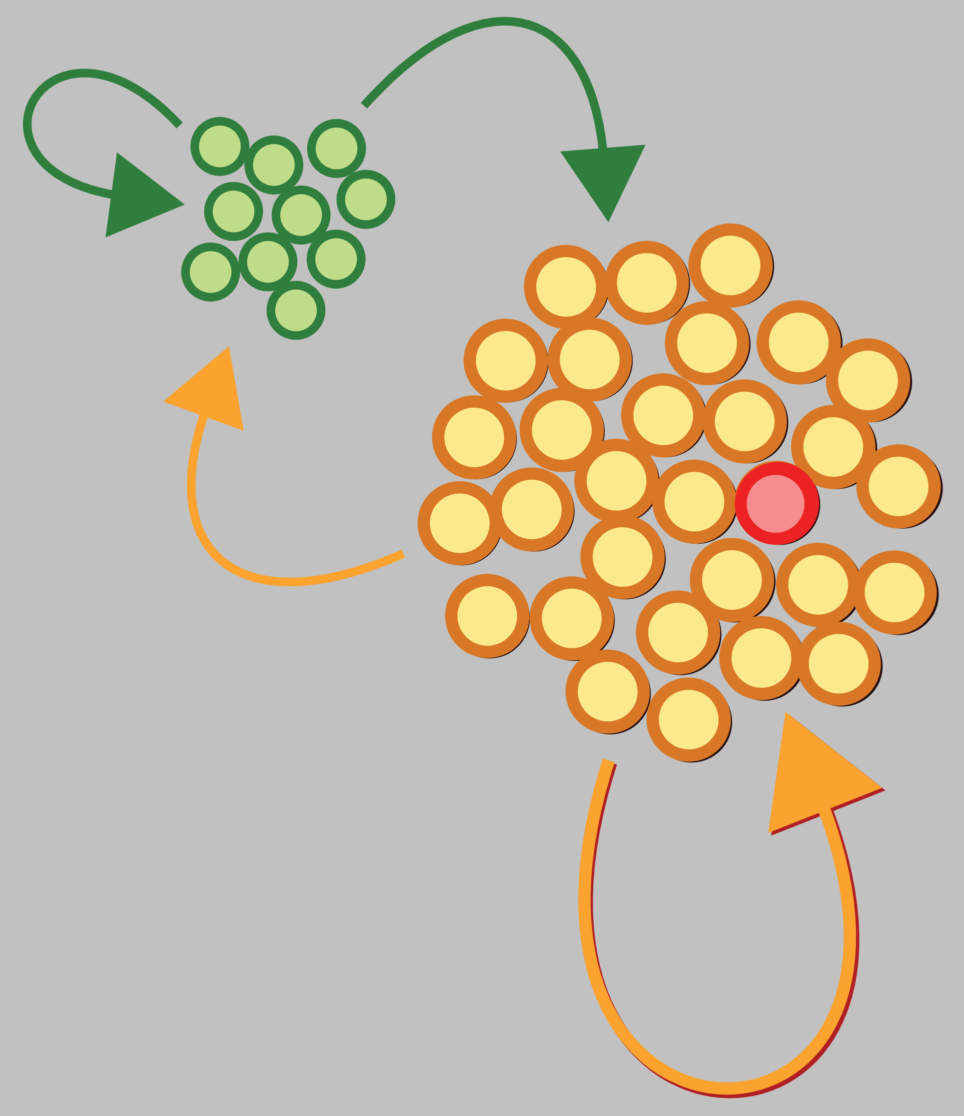
Irregular (CV ~1)
Regular (CV~0)
σΔt (big)
σΔt (small)
Synchronous
Asynchronous

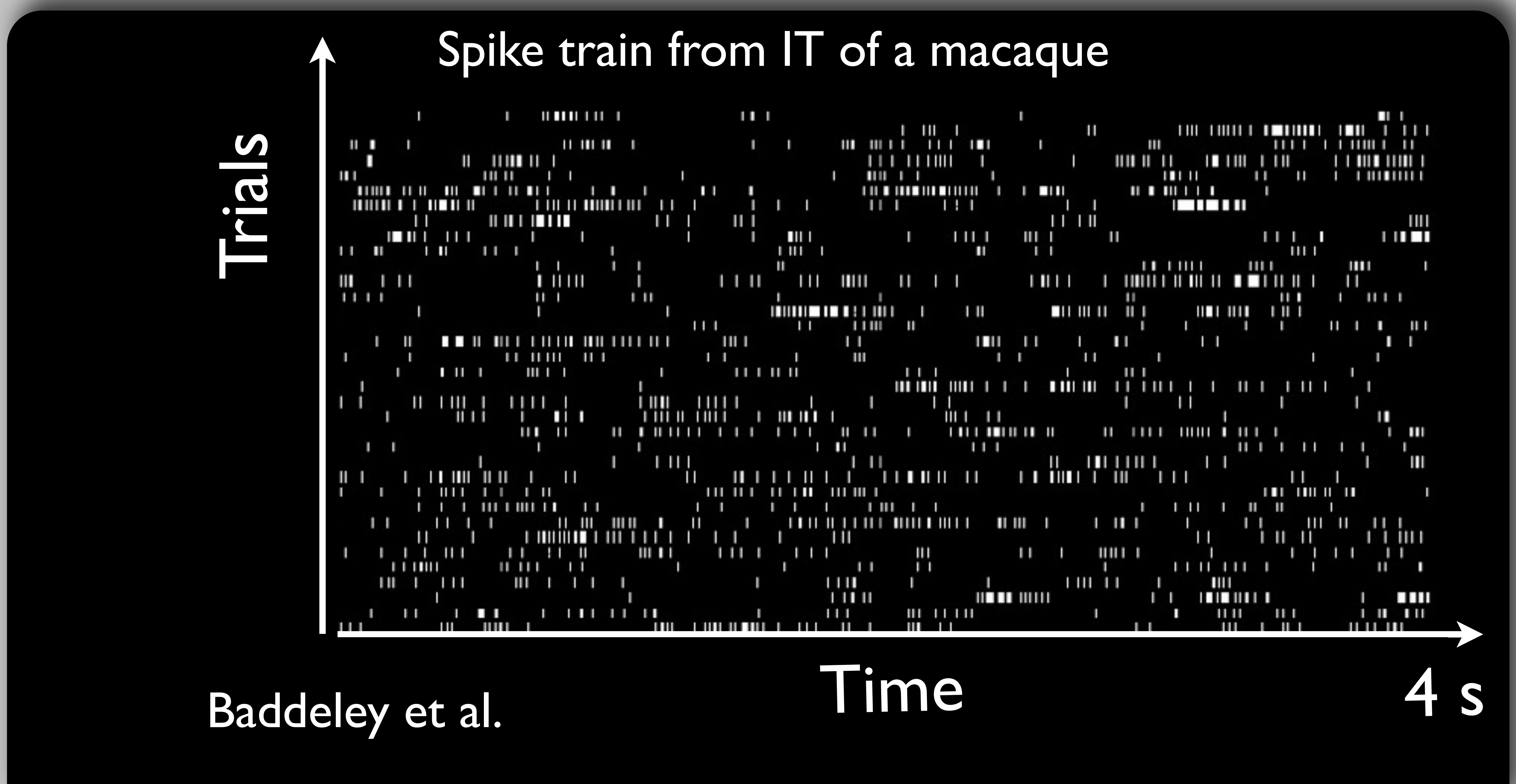


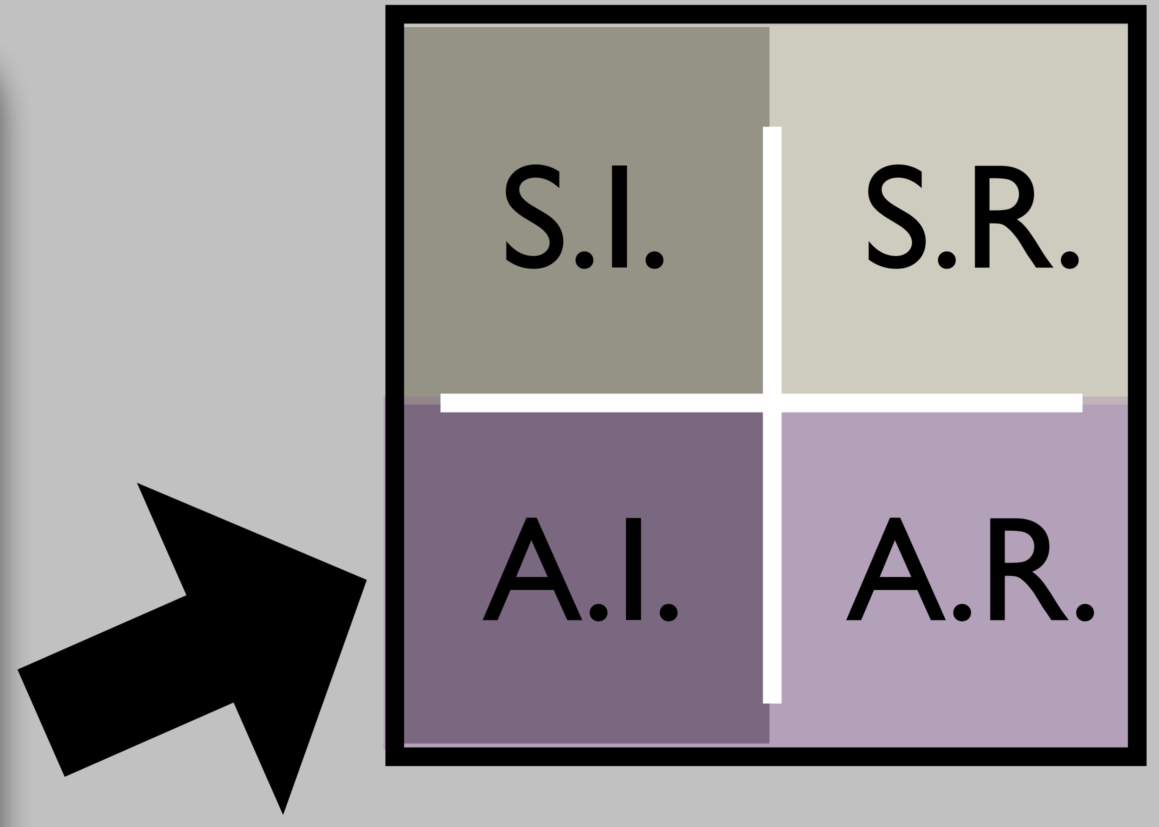
Irregular (CV ~1)
Regular (CV~0)
$\sigma_{\Delta t}$ (big)
Synchronous
$\sigma_{\Delta t}$ (small)
Asynchronous

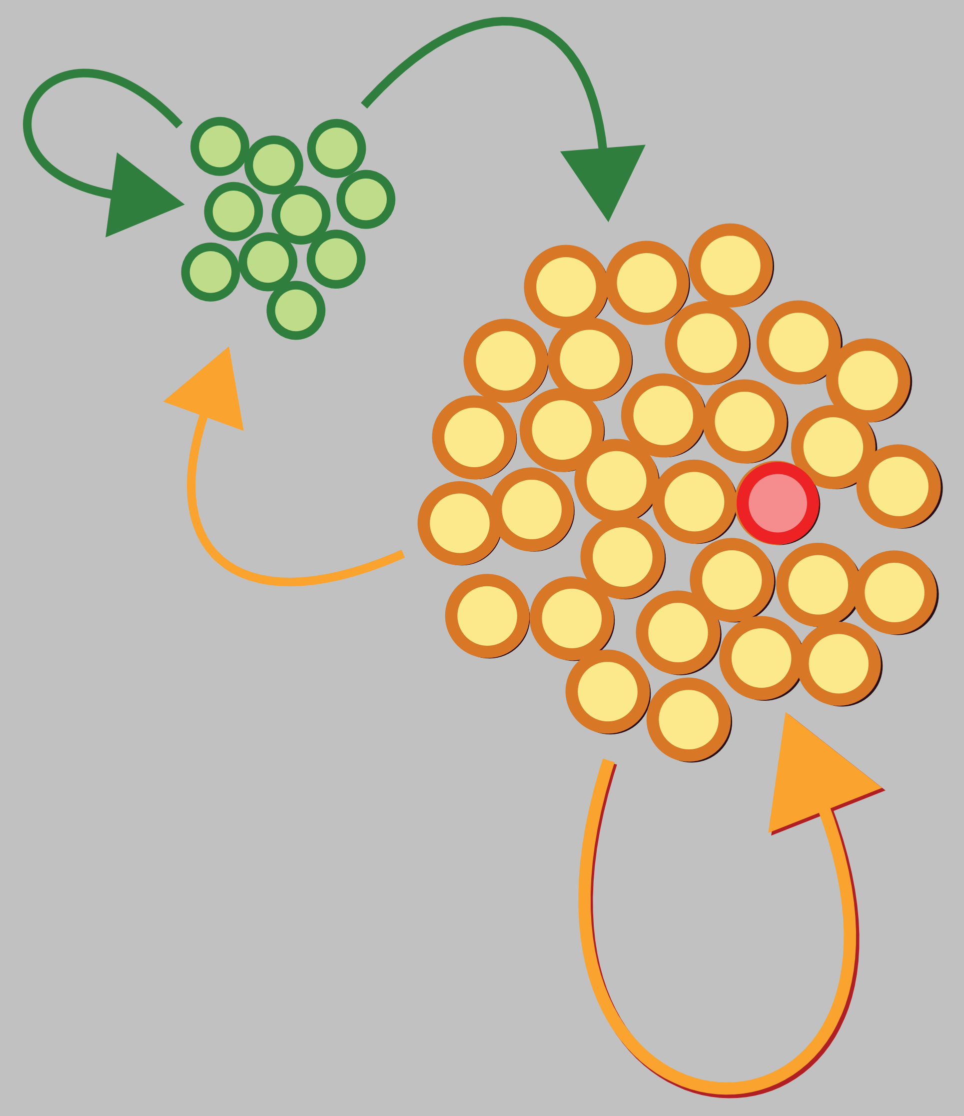


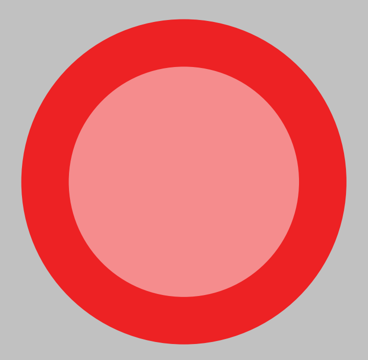

S.I.
S.R.
A.I.
A.R.

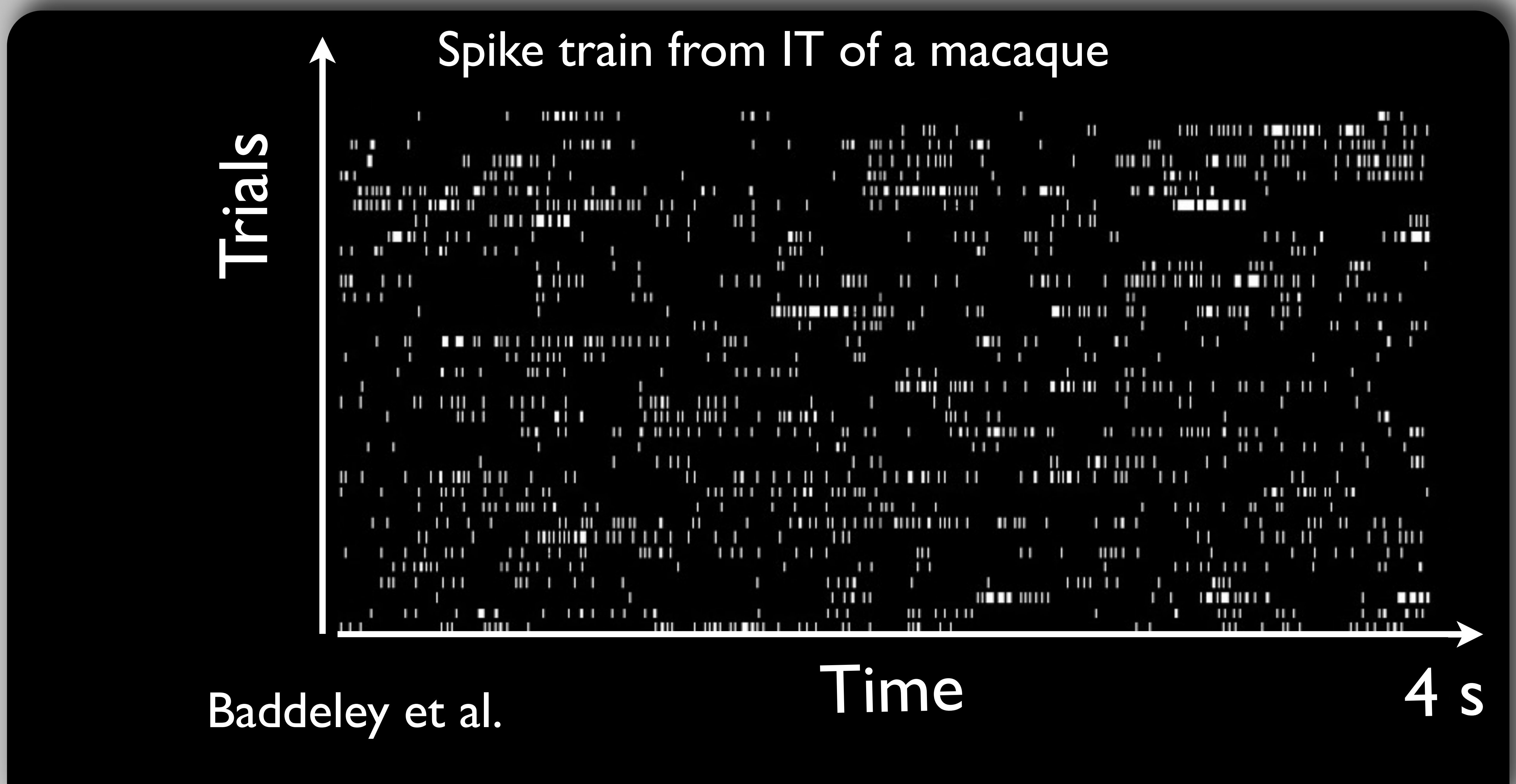



Spike train from IT of a macaque
Trials
Time
4 s
Baddeley et al.


S.I.
S.R.
A.I.
A.R.







Spike train from IT of a macaque
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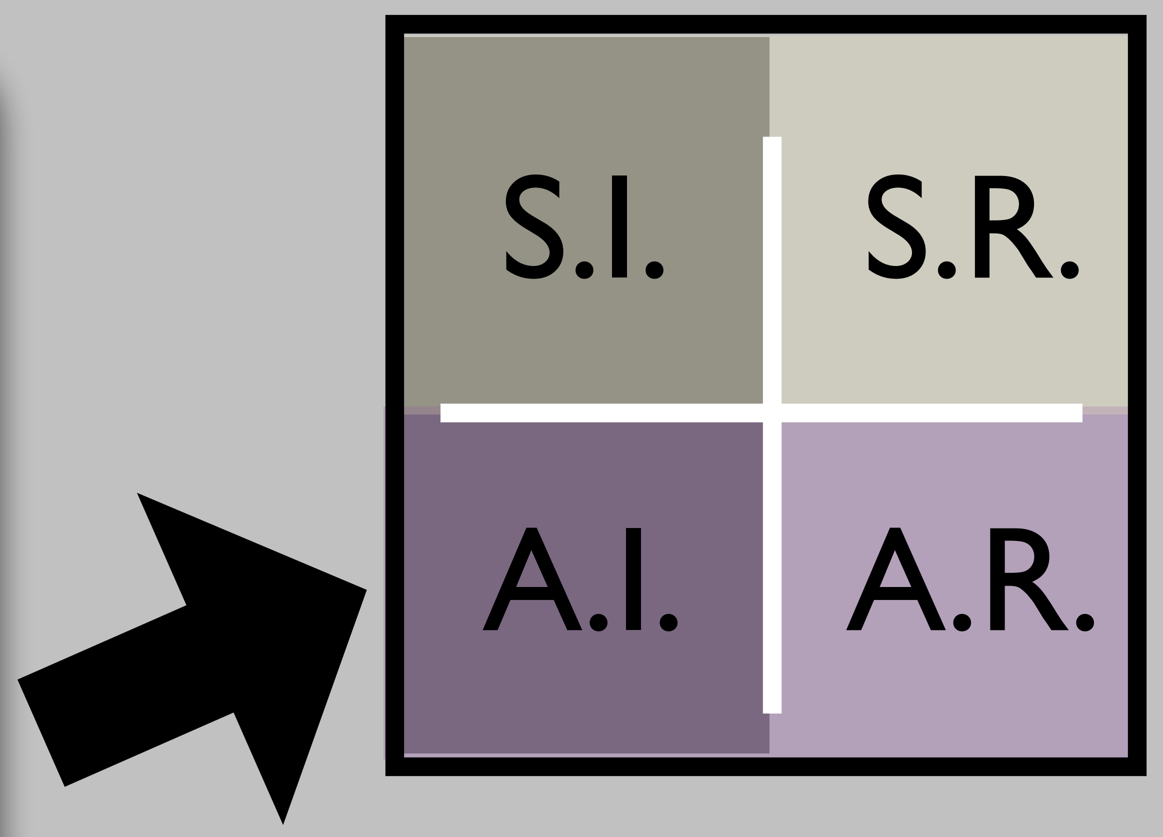
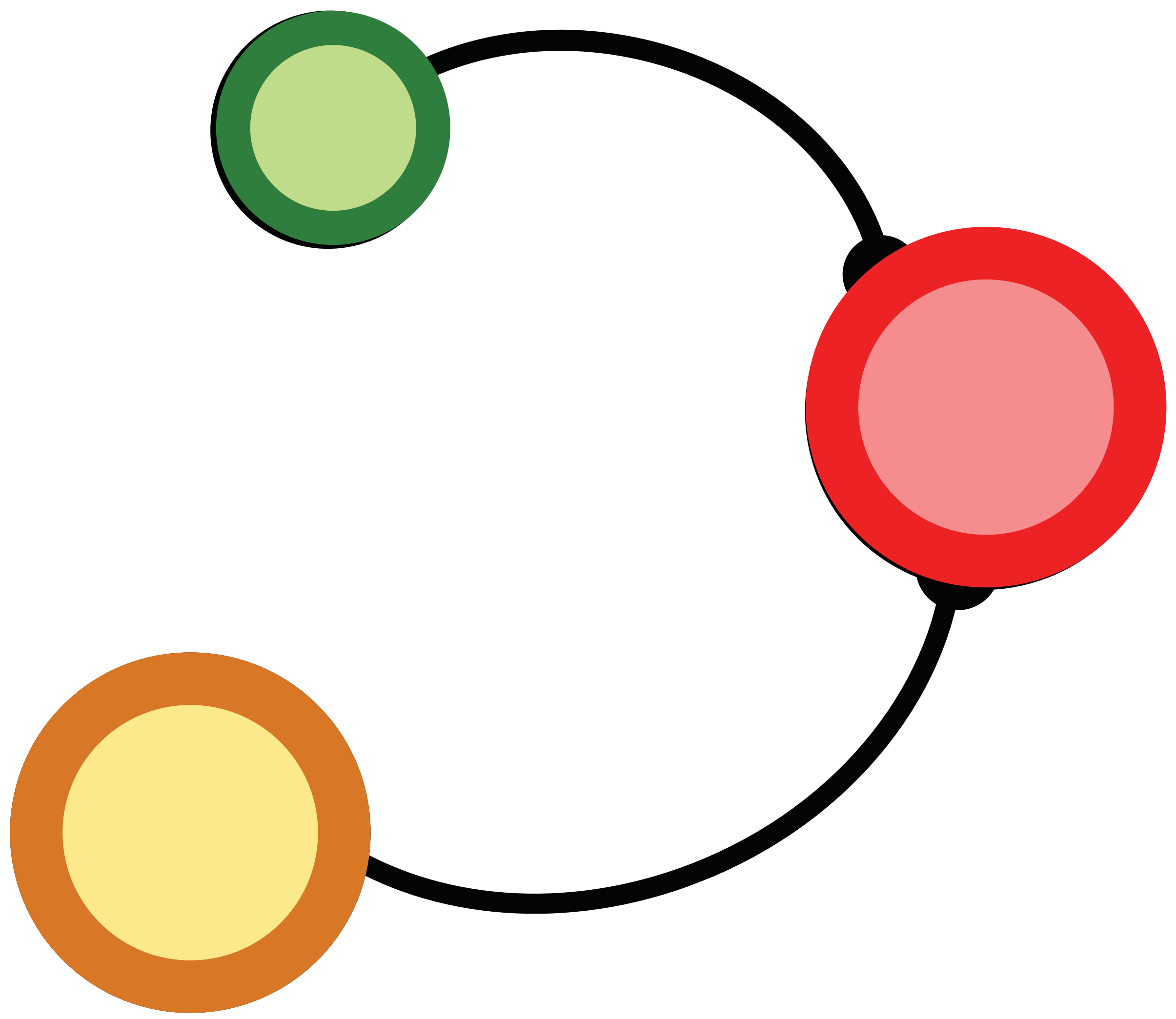
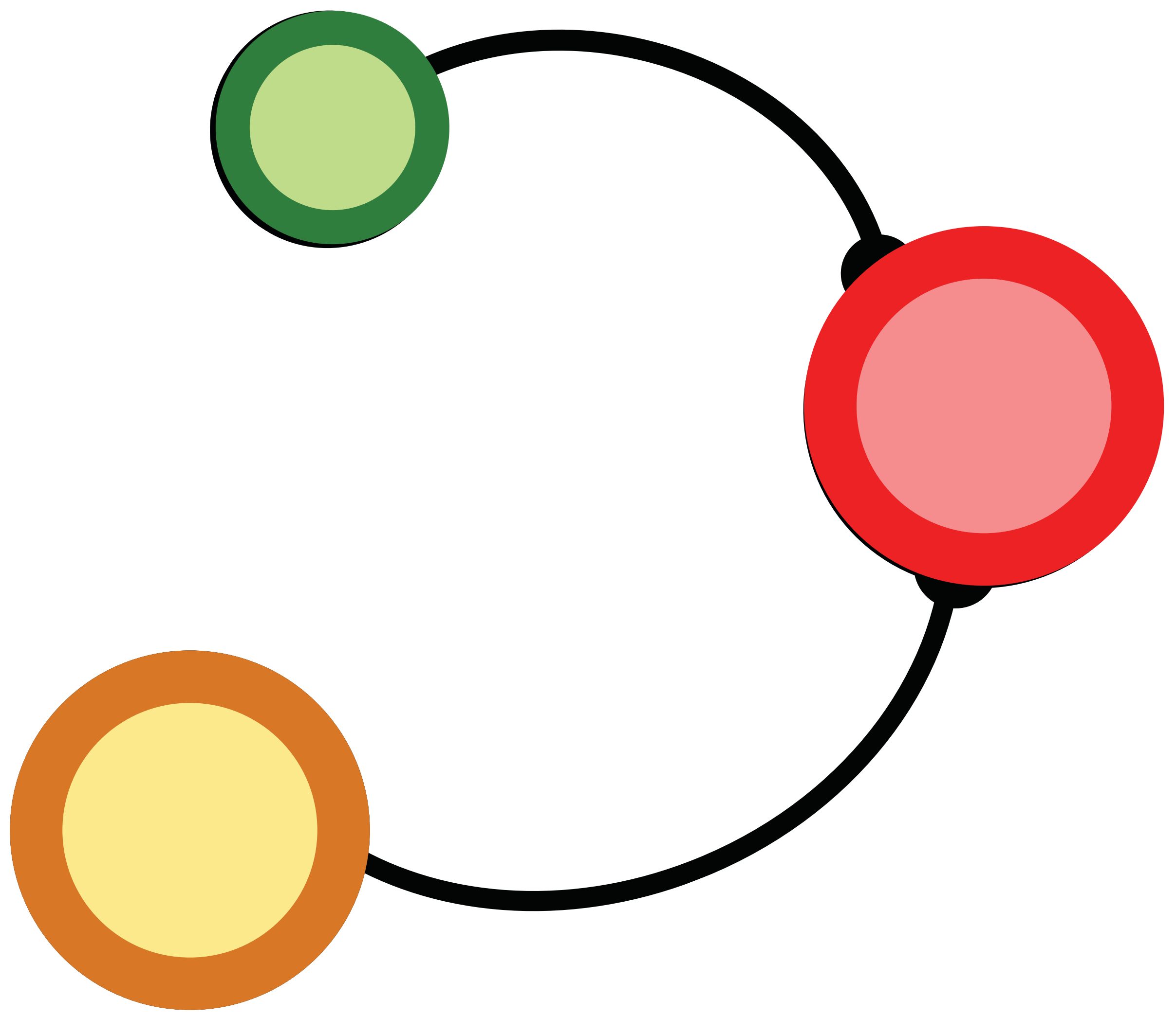
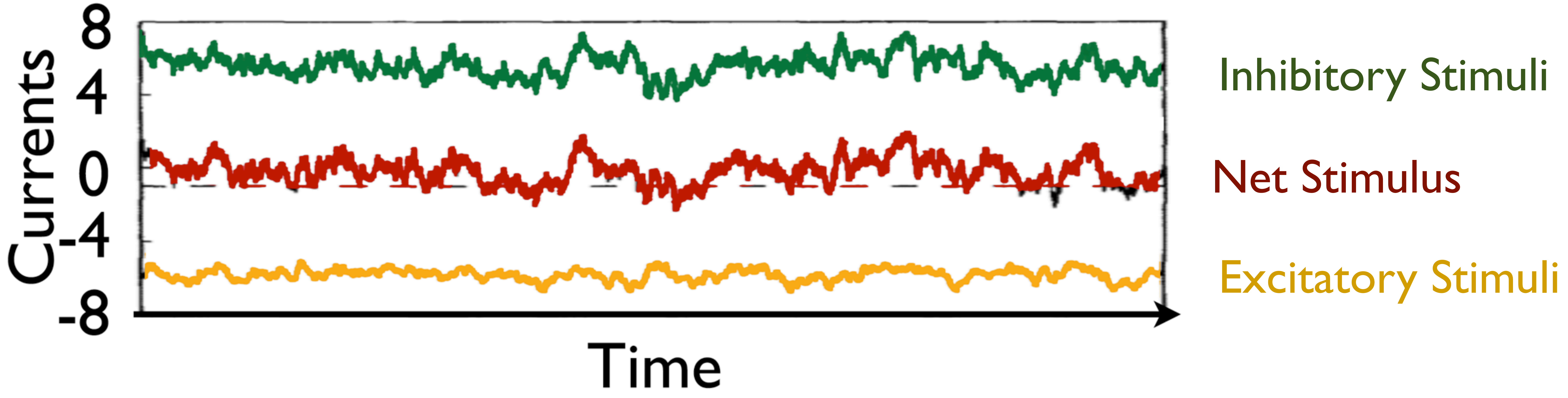


S.I.
S.R.
A.I.
A.R.

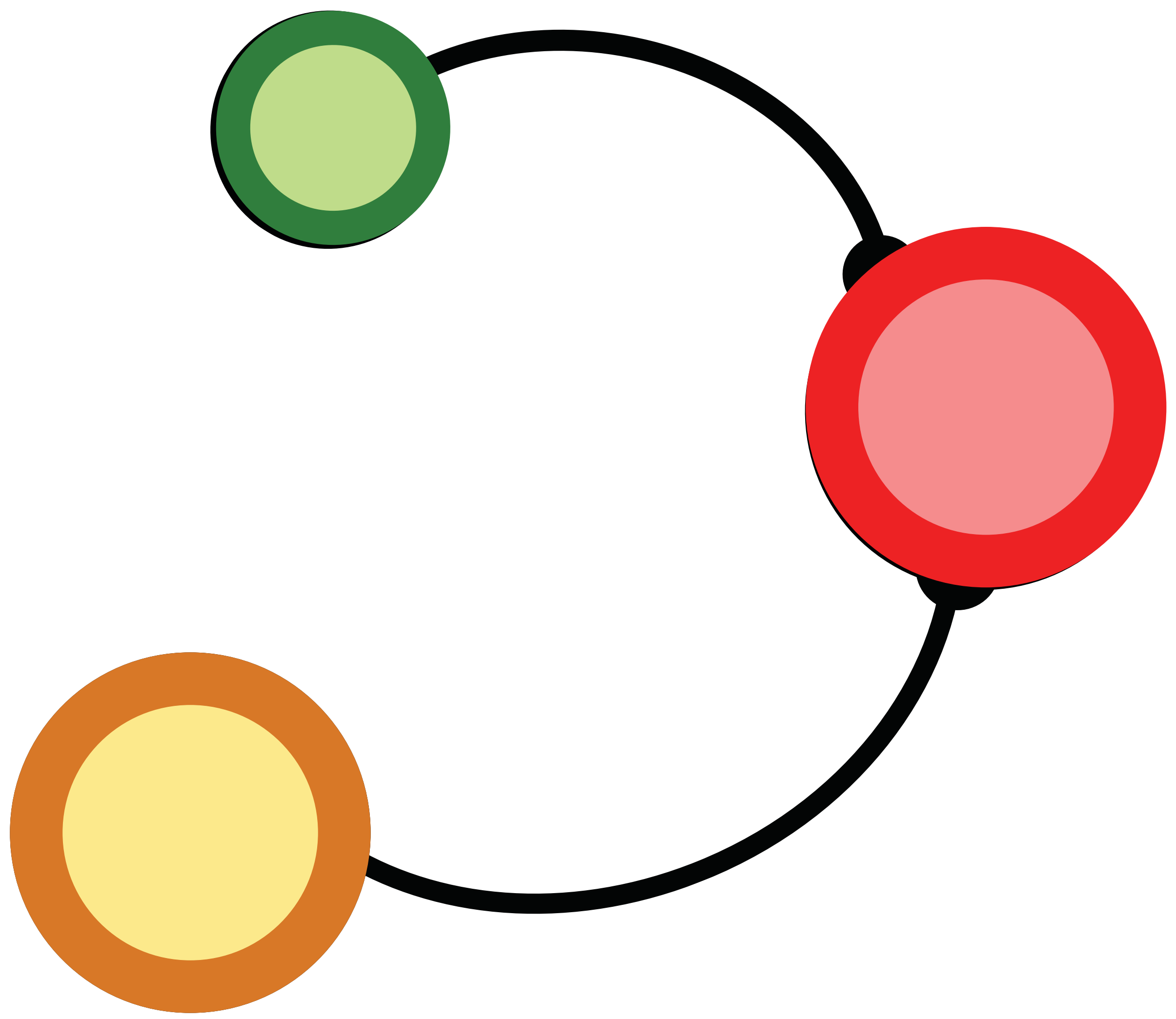


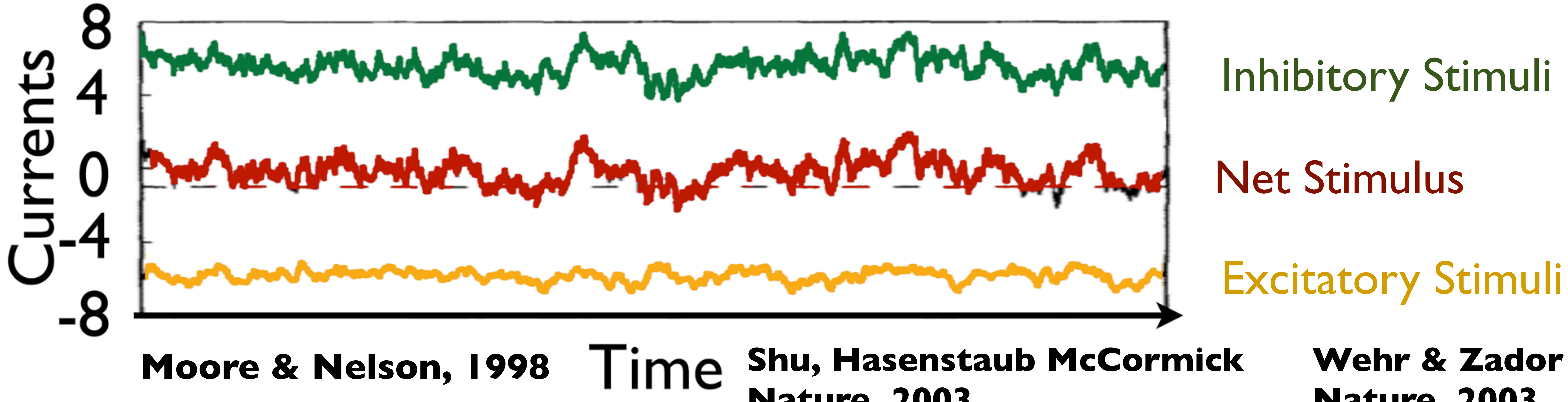
van Vreeswijk & Sompolinsky, Science, 1996





van Vreeswijk & Sompolinsky, Science, 1996



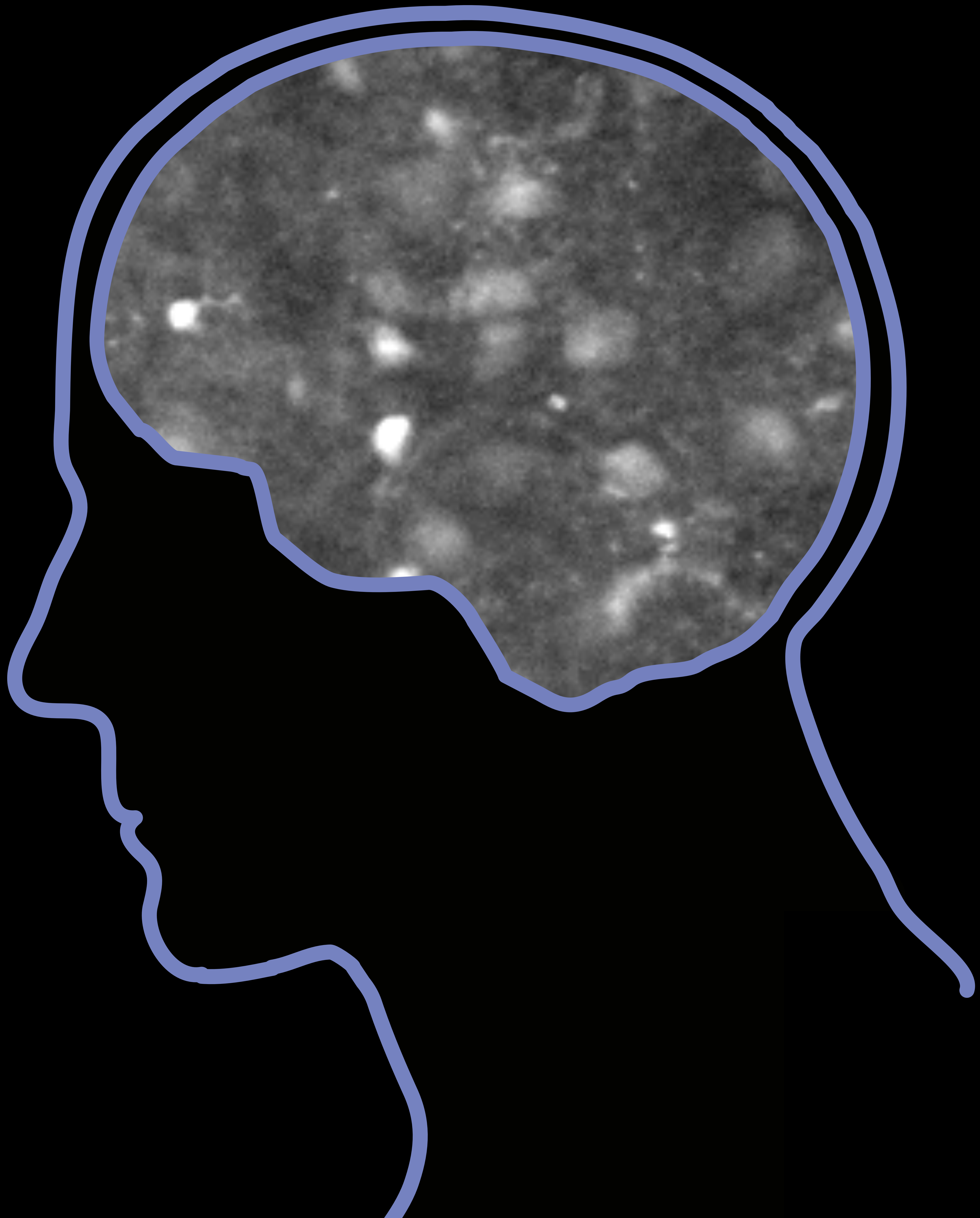


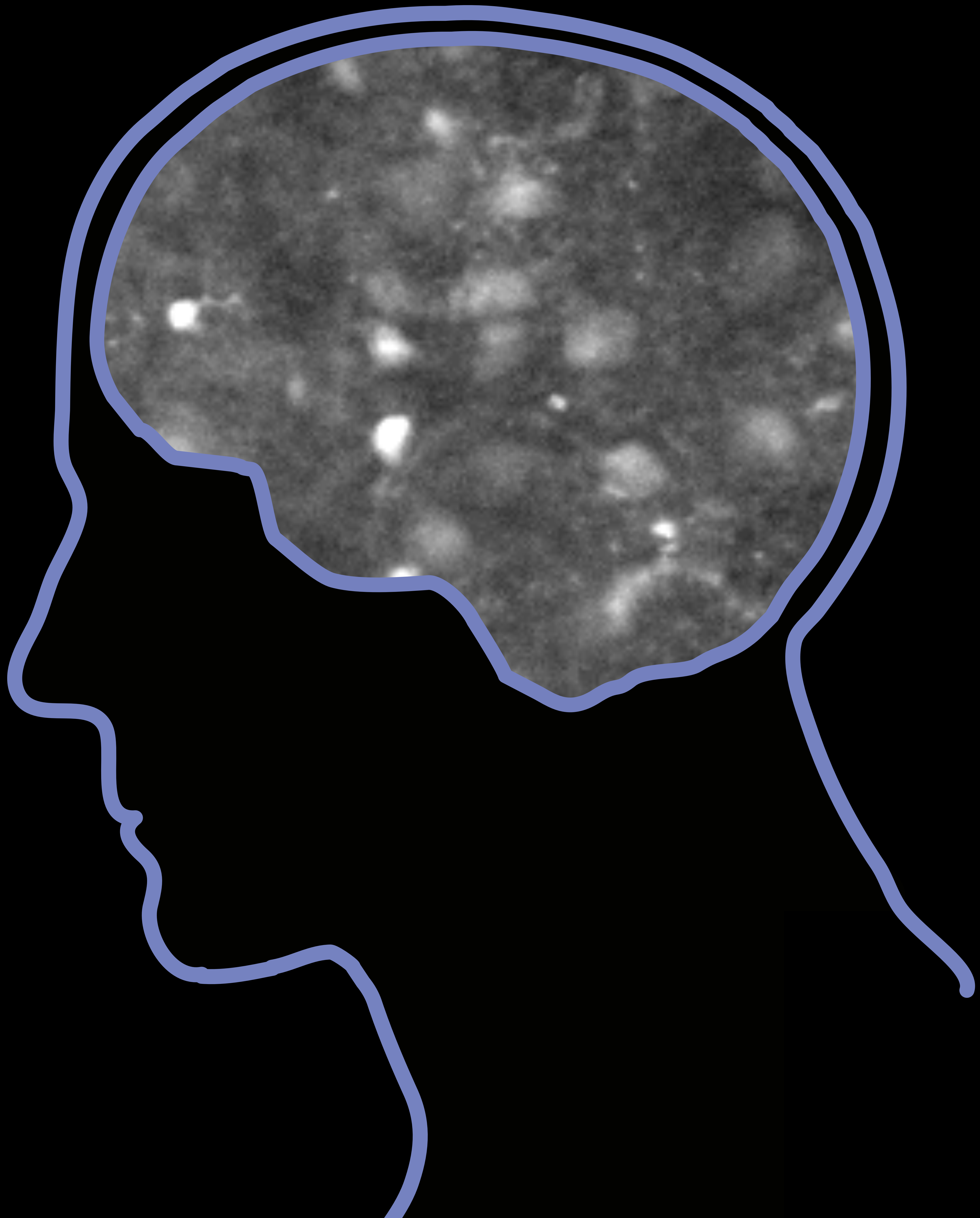
Moore & Nelson, 1998

Shu, Hasenstaub McCormick
Nature, 2003

Wehr & Zador
Nature, 2003

van Vreeswijk & Sompolinsky, Science, 1996





Voilà,...

$$\tau \frac{dr}{dt} = (r_0 - r) + f(W r)$$

the "rate model"!

next:
- the W
- excitation & inhibition
- dynamics & balance
- signal propagation