THE DEEP-DOWN BASICS OF COMPUTATIONAL NEUROSCIENCE

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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

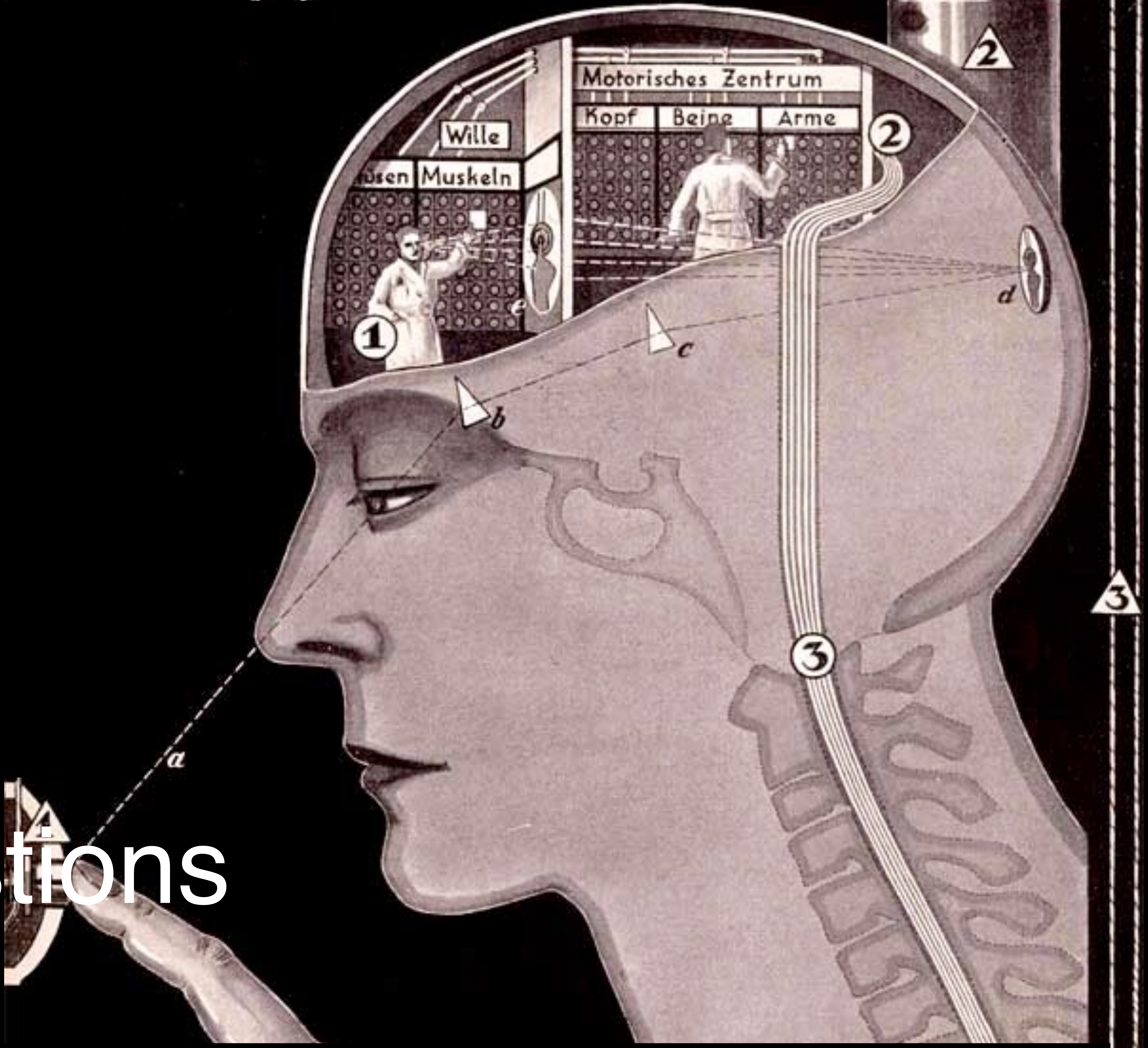
# cell types:	50
# neurons:	100,000,000,000
# synapses	100,000,000,000,000
# neuroscientists	80,000

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

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

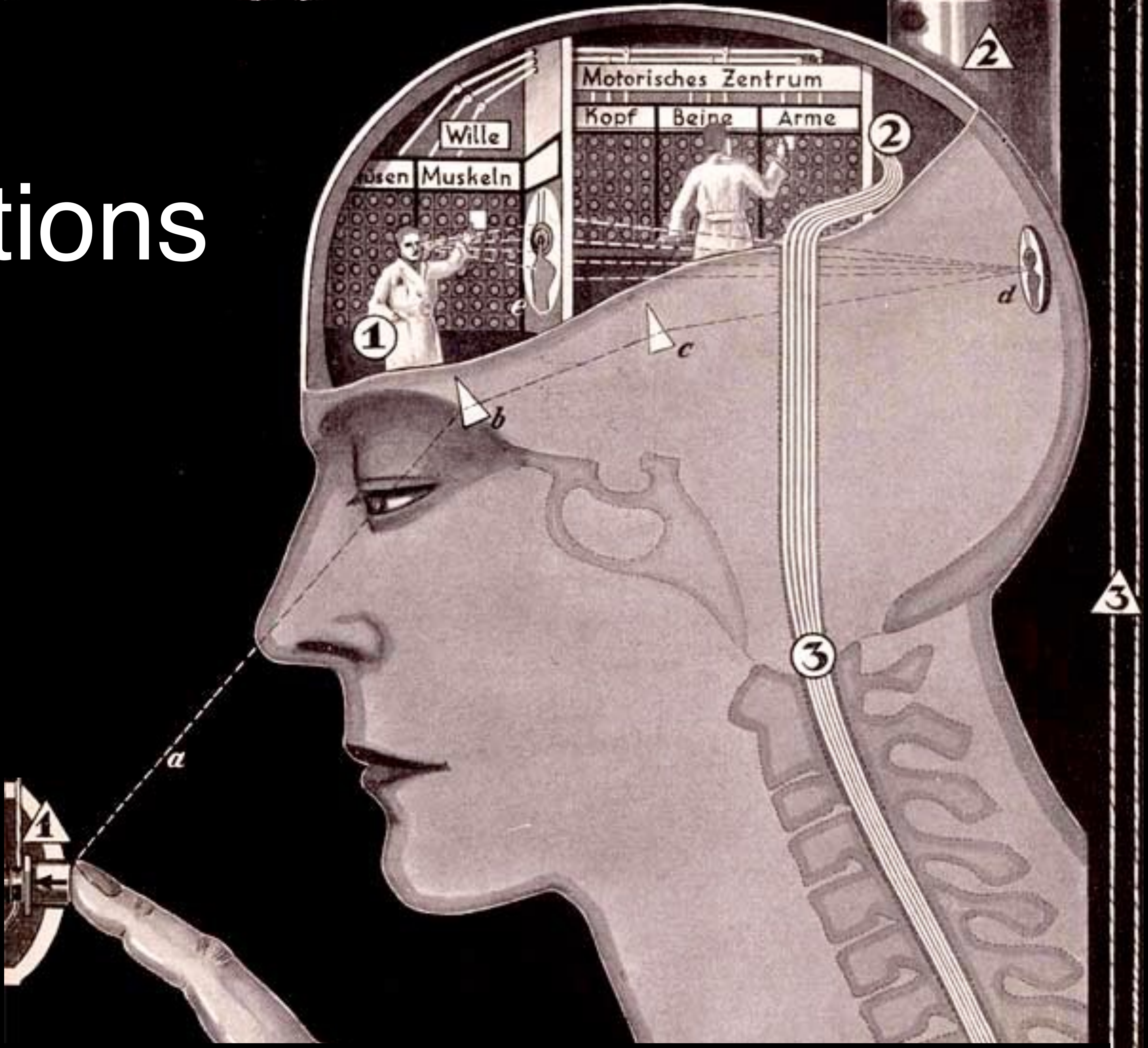
# cell types:	50
# neurons:	100,000,000,000
# synapses	100,000,000,000,000
# neuroscientists	80,000
# neurotheorists	4,000
# neuroquestions	more than 4,000!!

#neuroquestions



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

#neuroquestions



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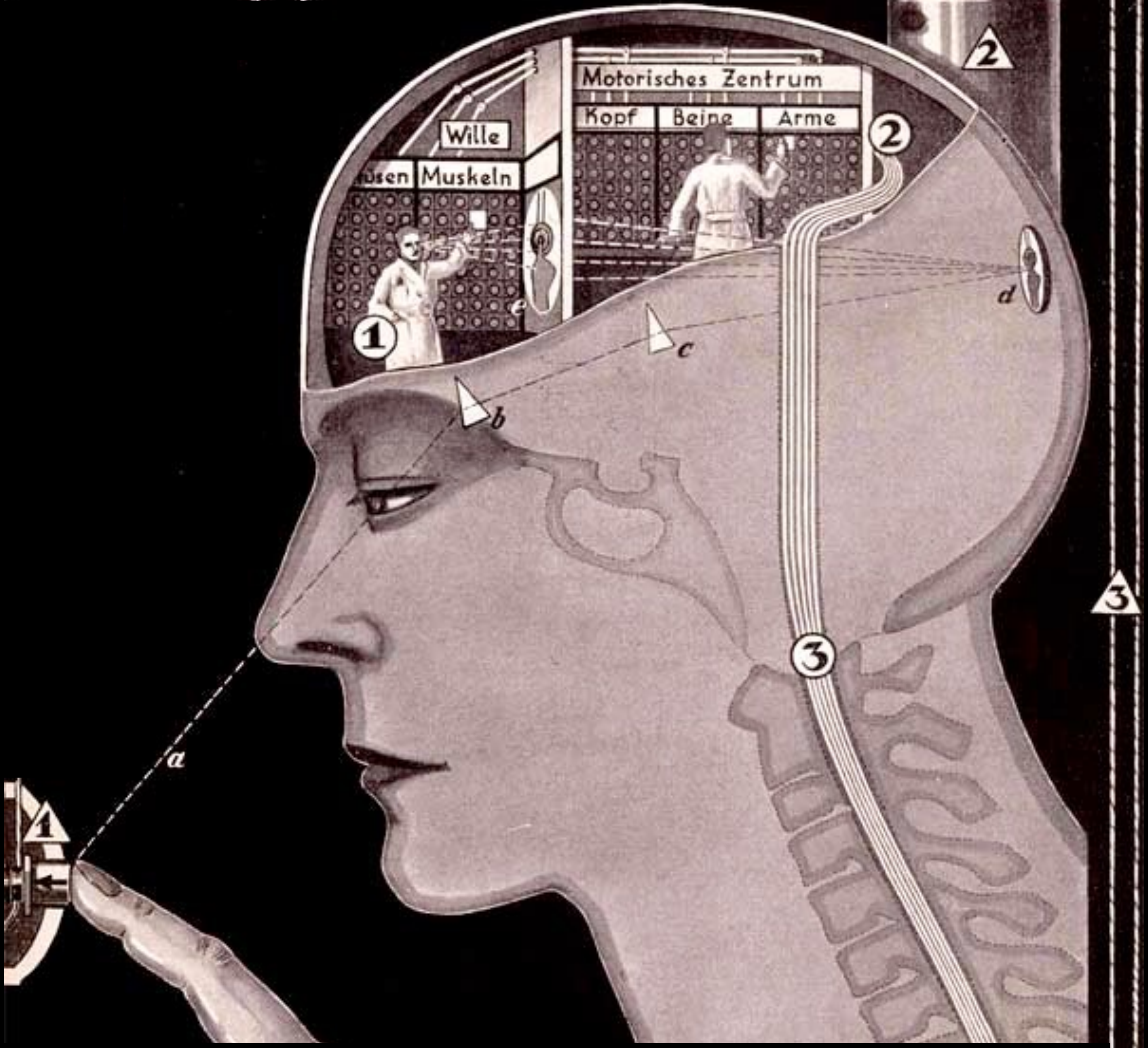
The Neural Code:

- Representation
- Transmission
- Transformation
- Interpretation

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



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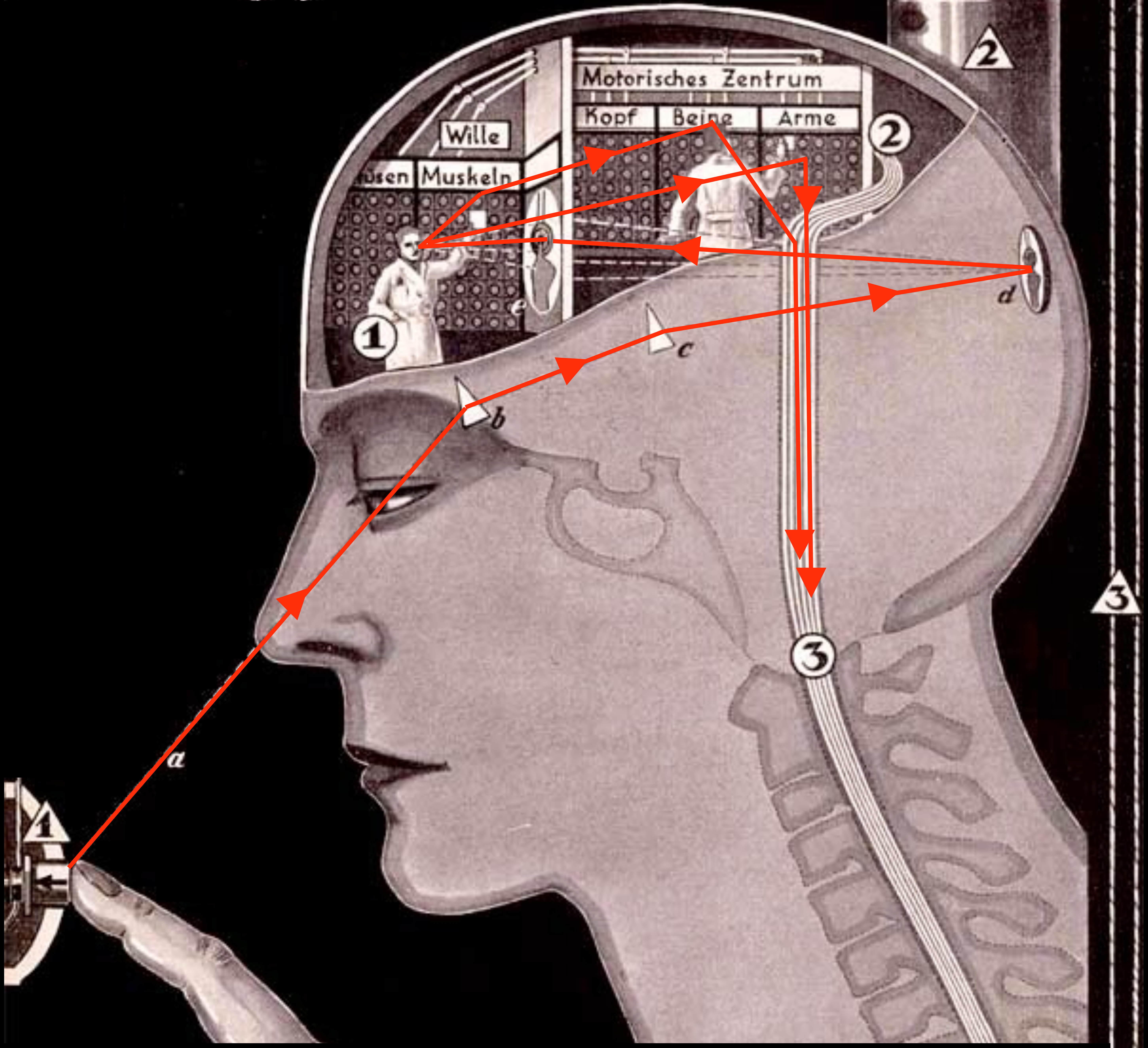

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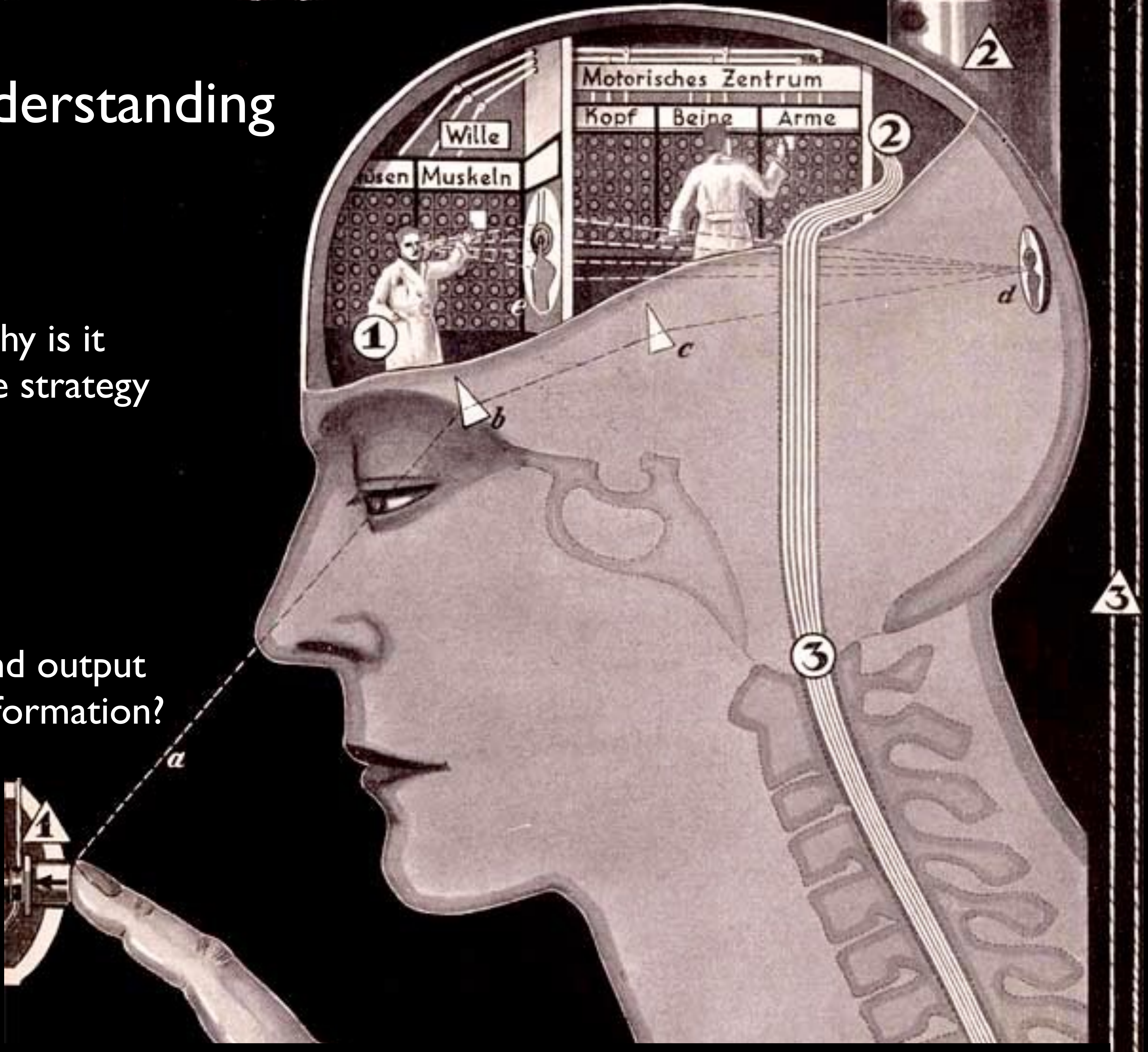
David Marr’s levels of understanding (1982)

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 level

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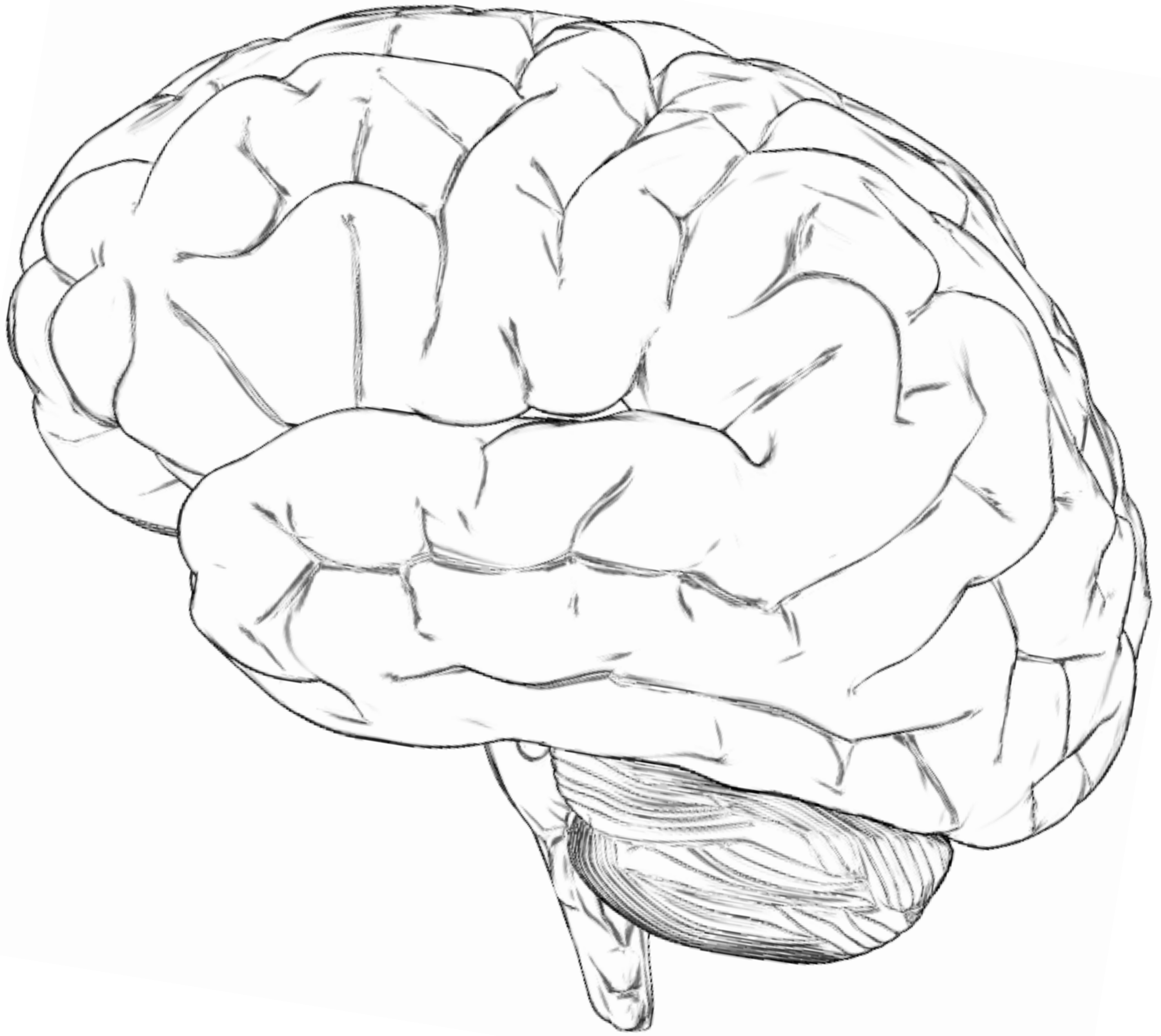
systems level

network level



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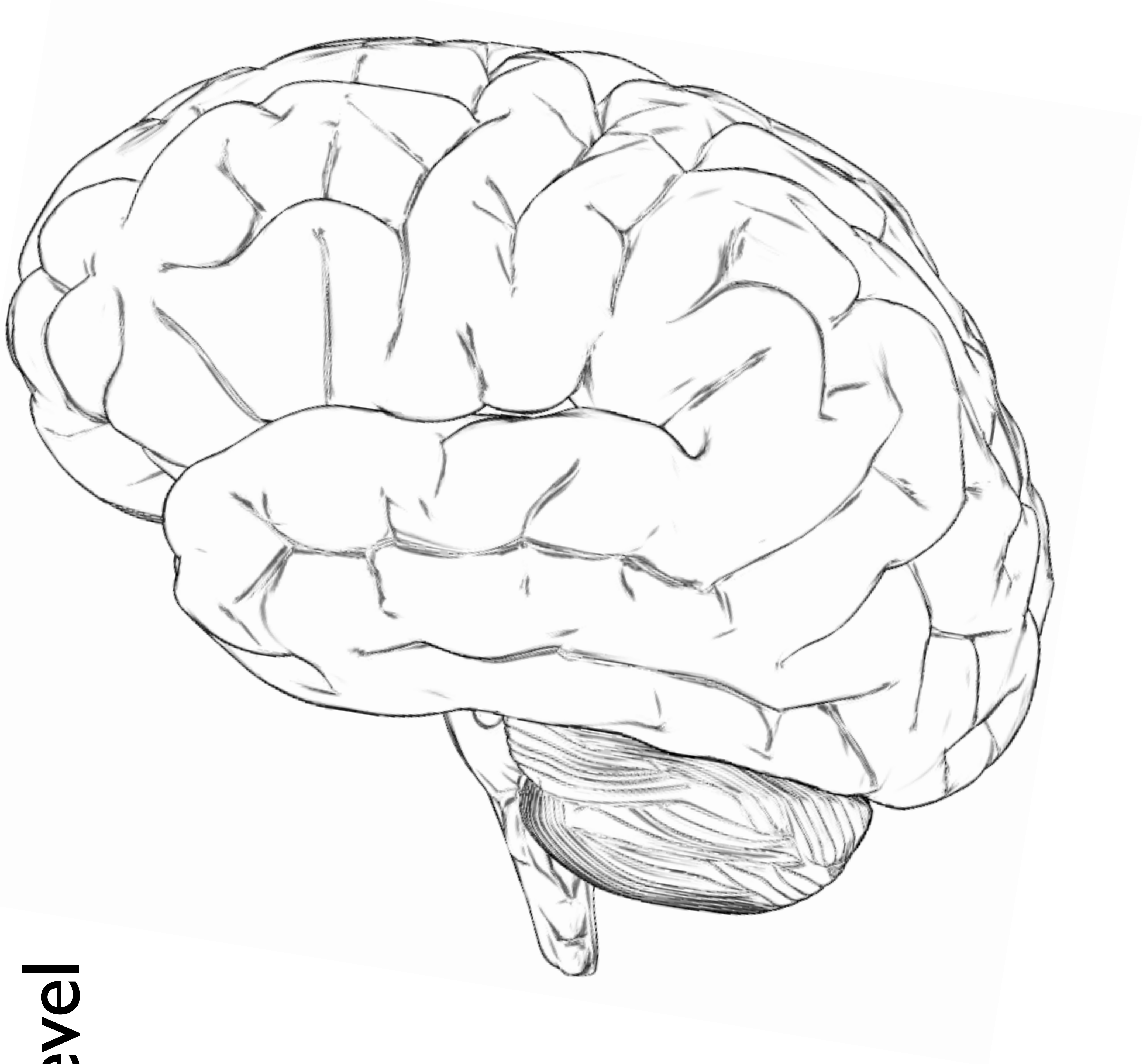
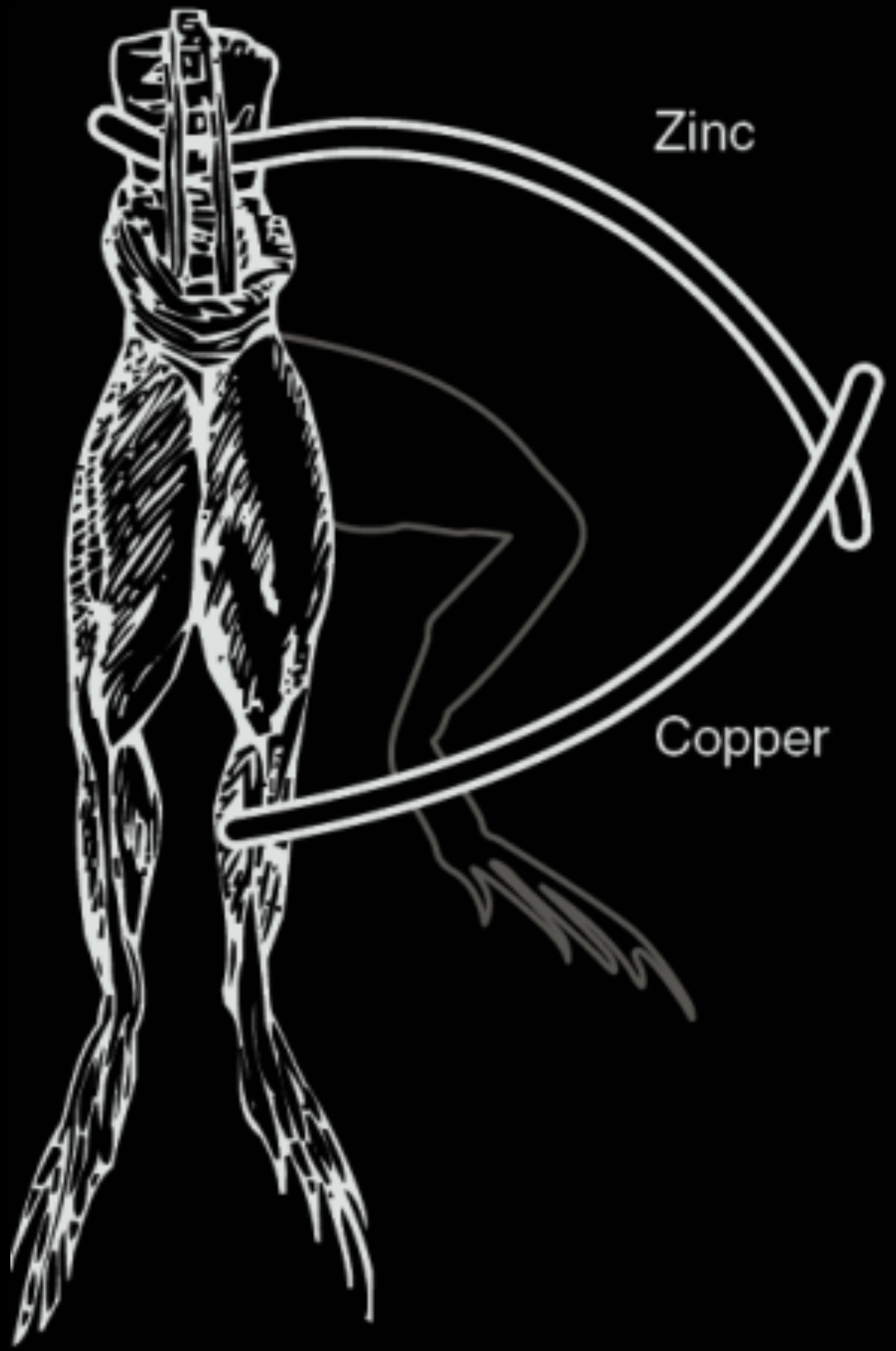
systems level

network level

single cell level



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



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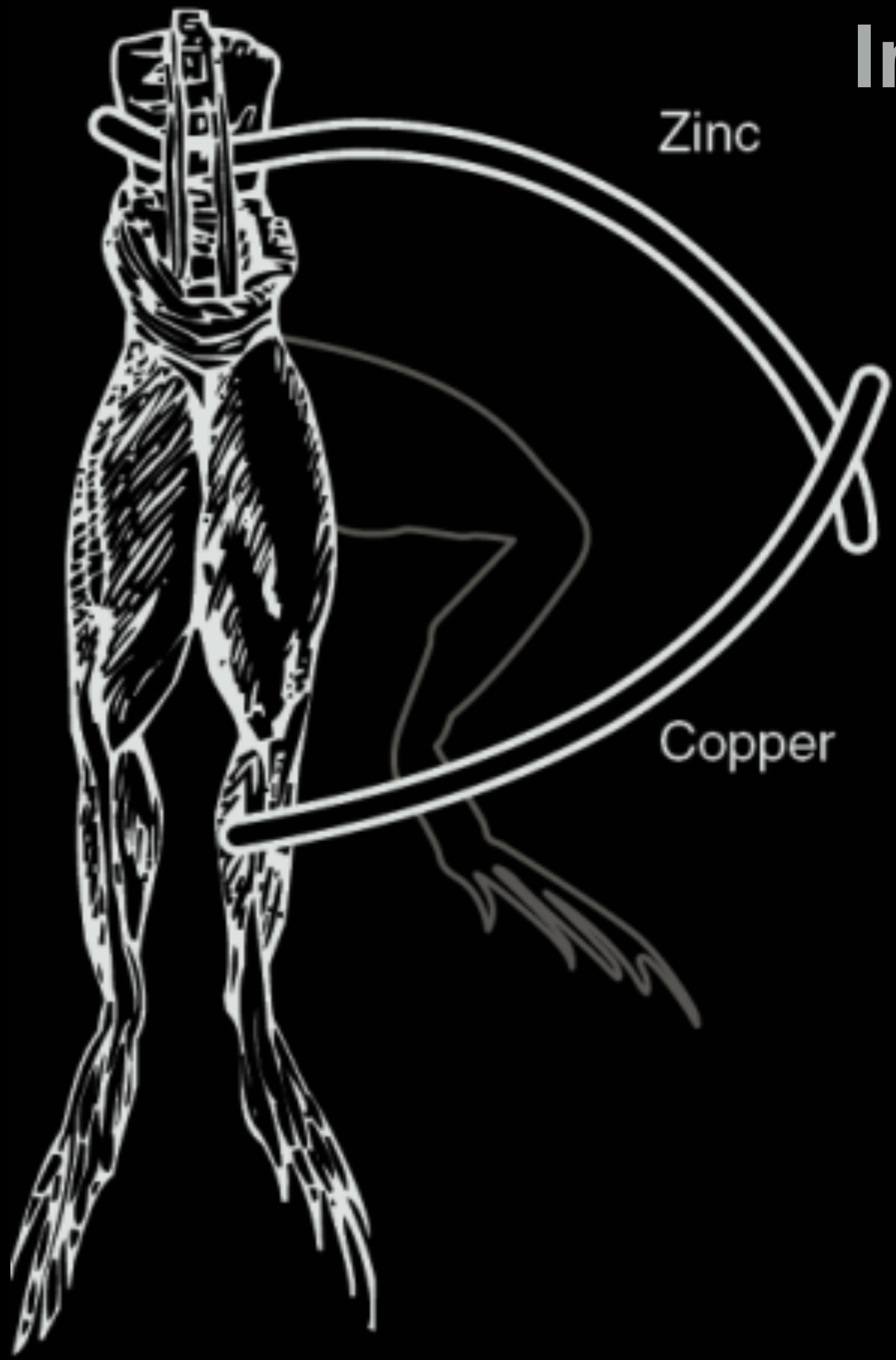

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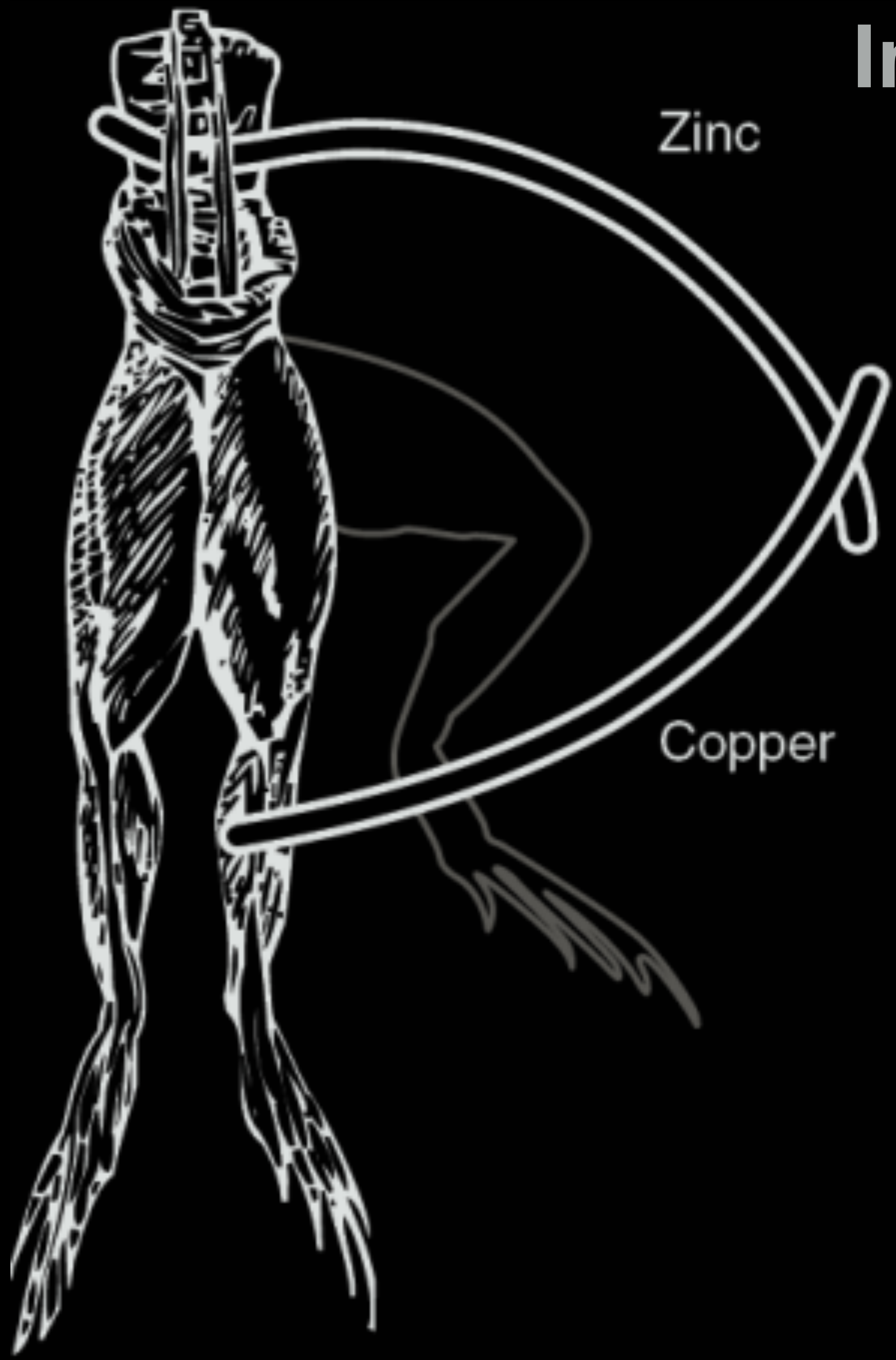

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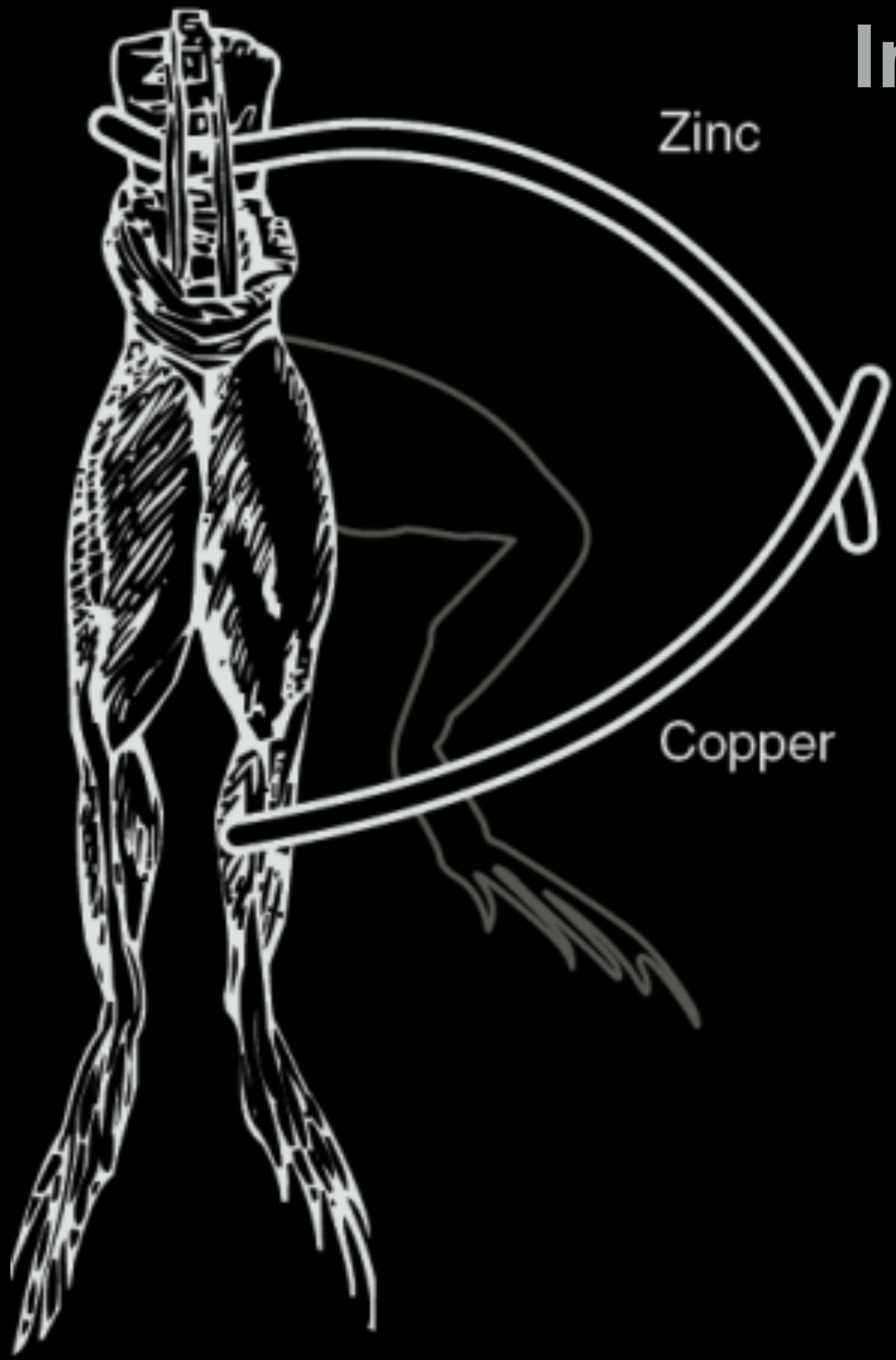


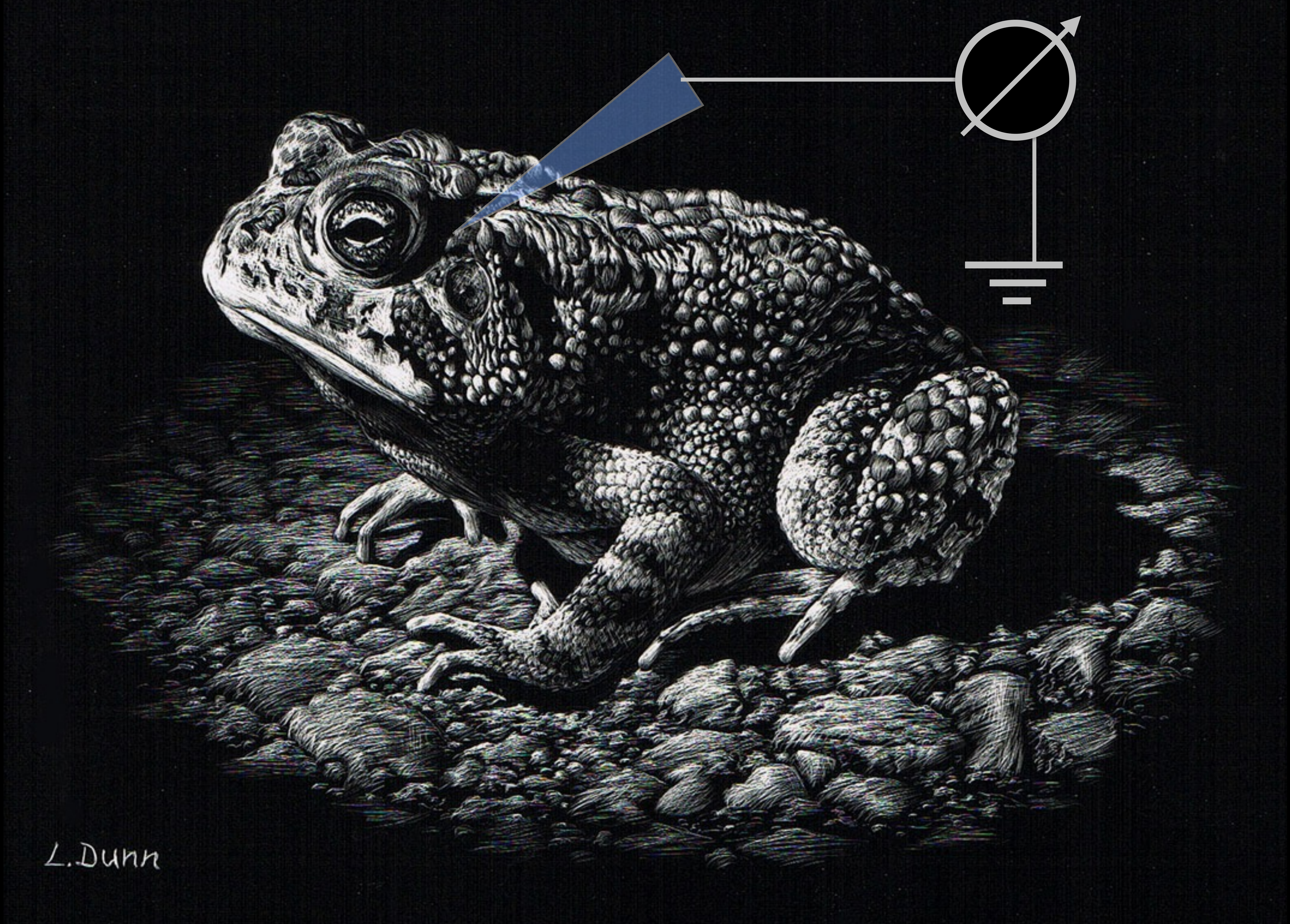
In 1836 Valentin recognises neurons.

In 1887 Golgi and Cajal start fighting about synapses.

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
(Nernst, Goldman Hodgkin Katz)

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

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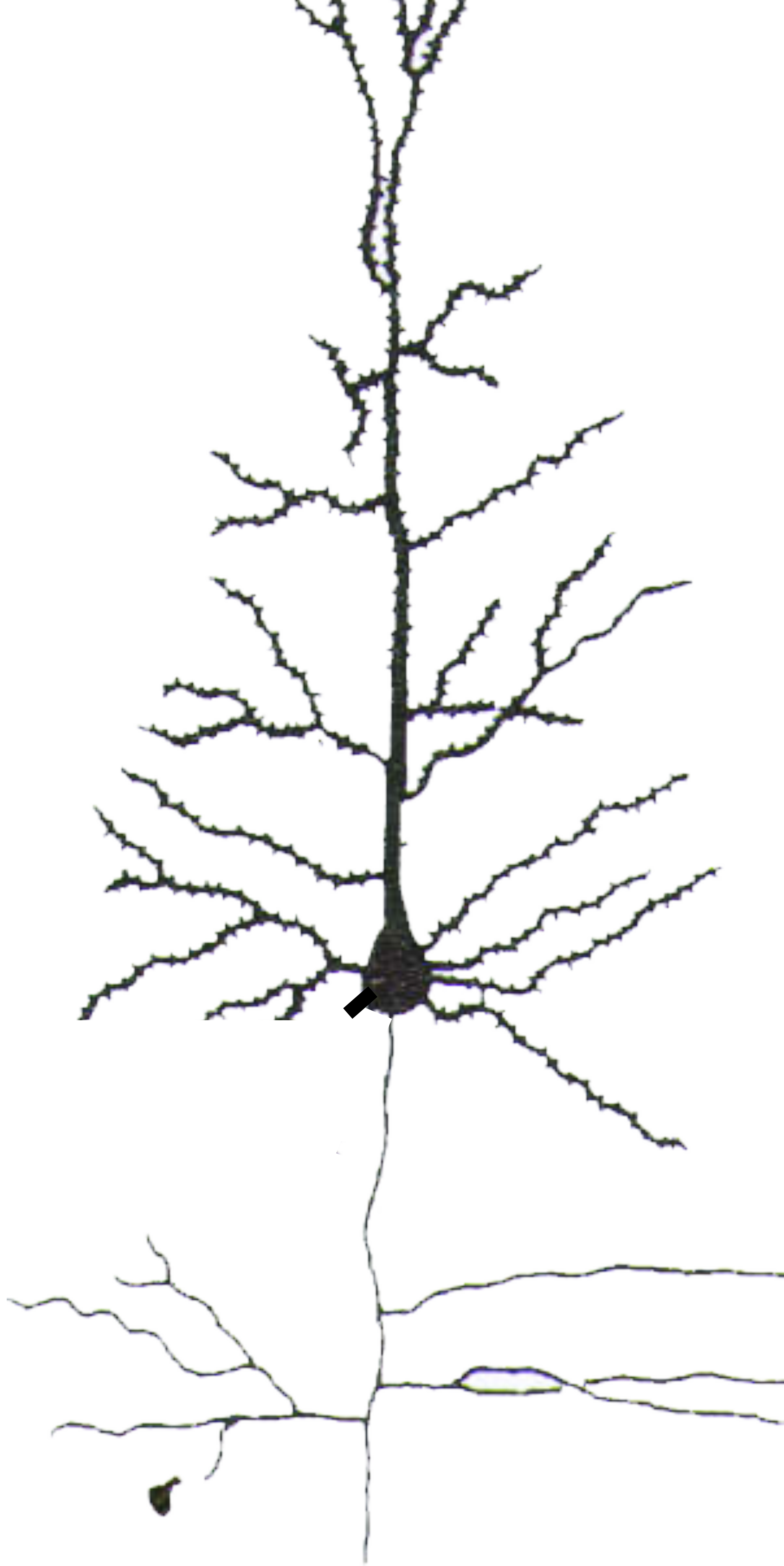
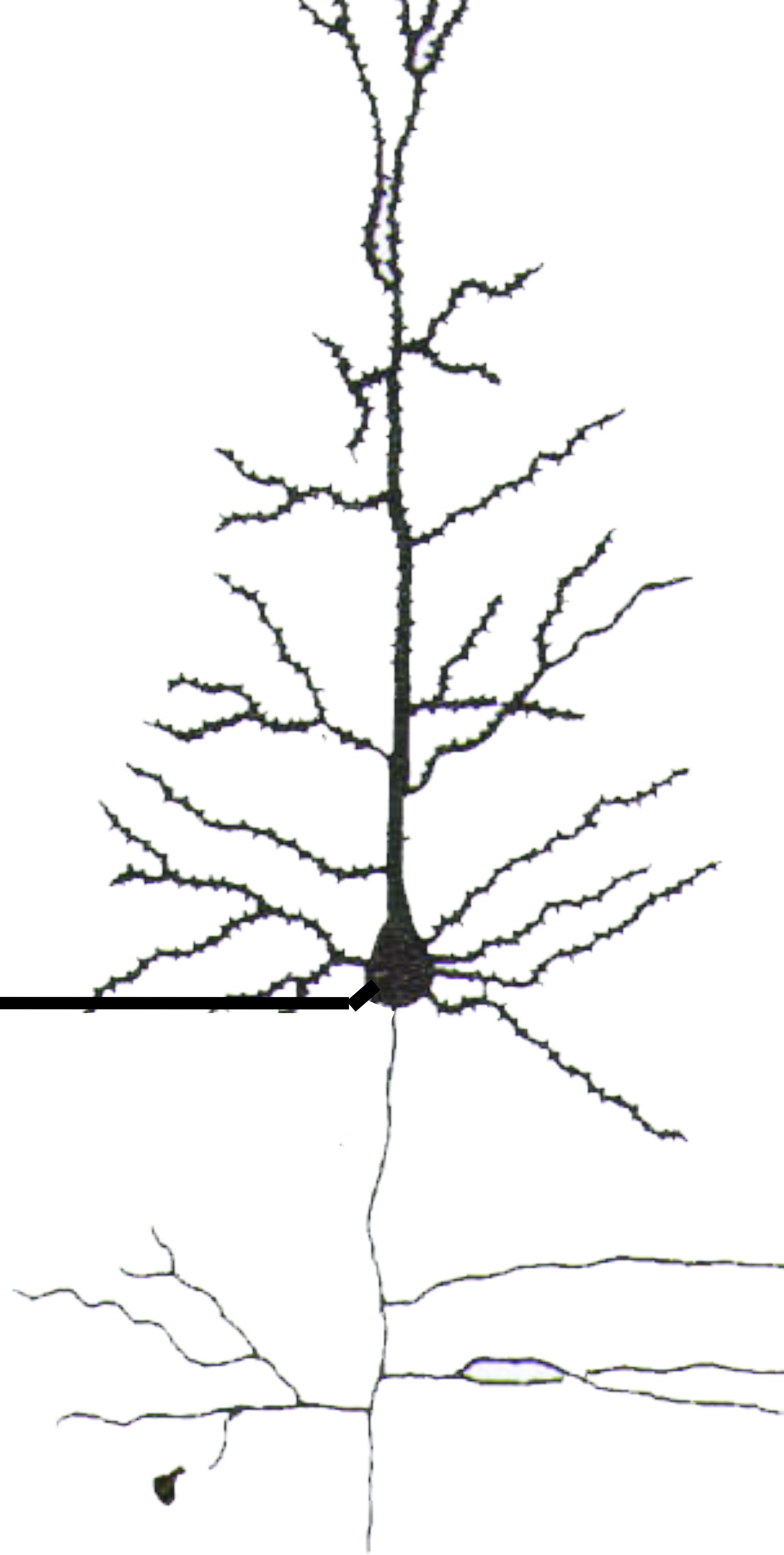


Collect

&

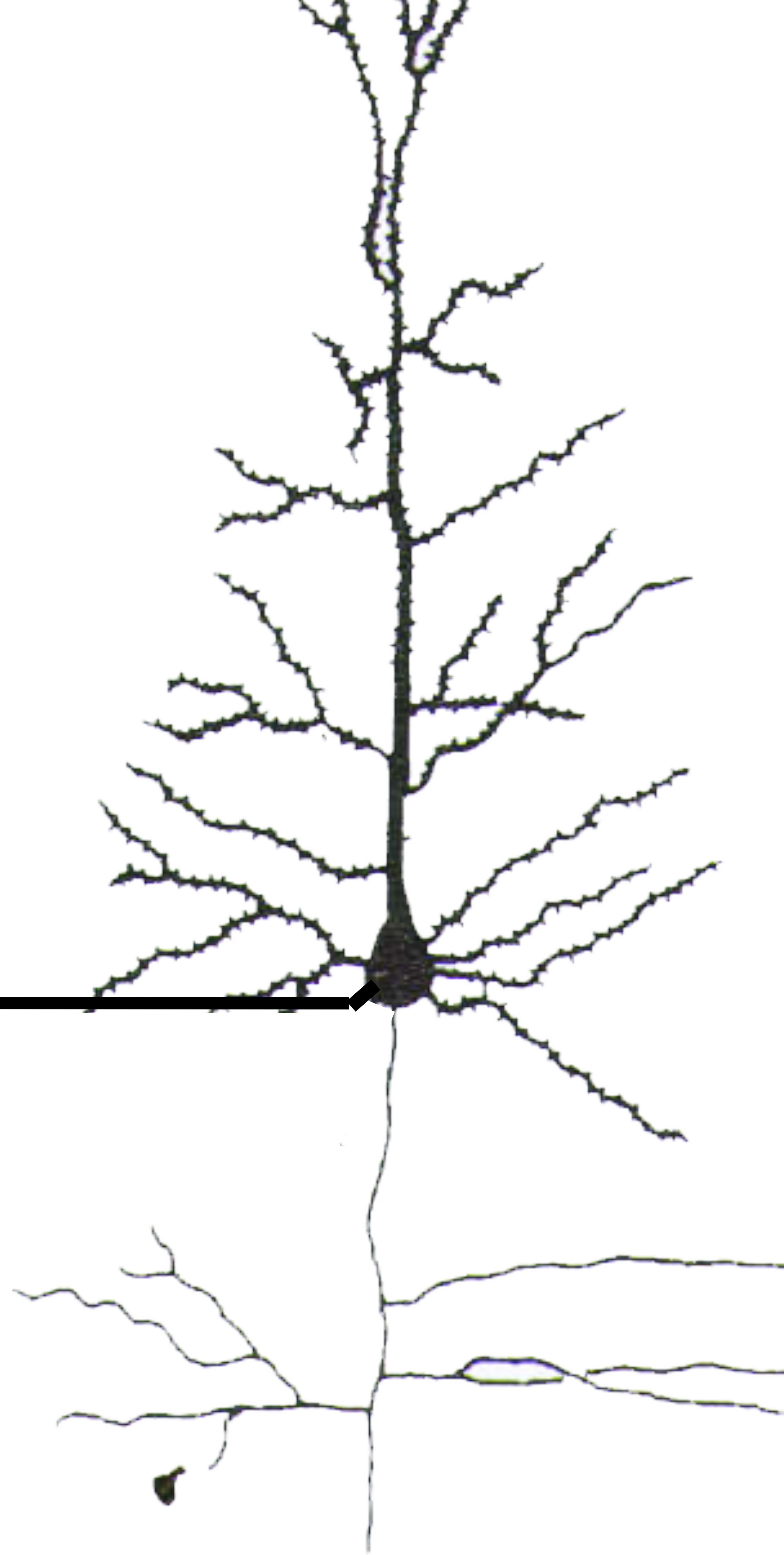
Dispense



Collect: voltage deflections (PSPs)

&

Dispense: voltage deflections (APs)



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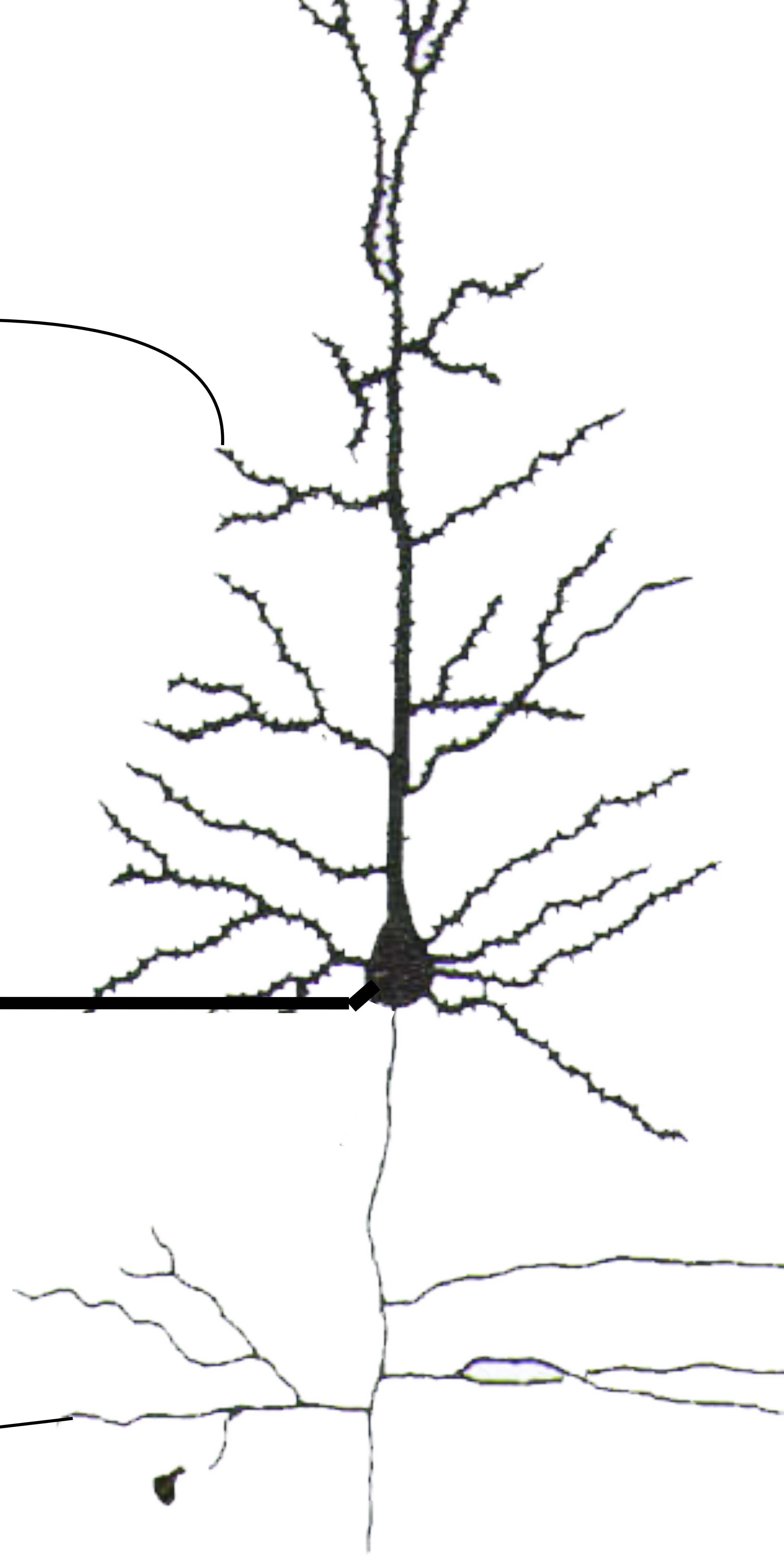

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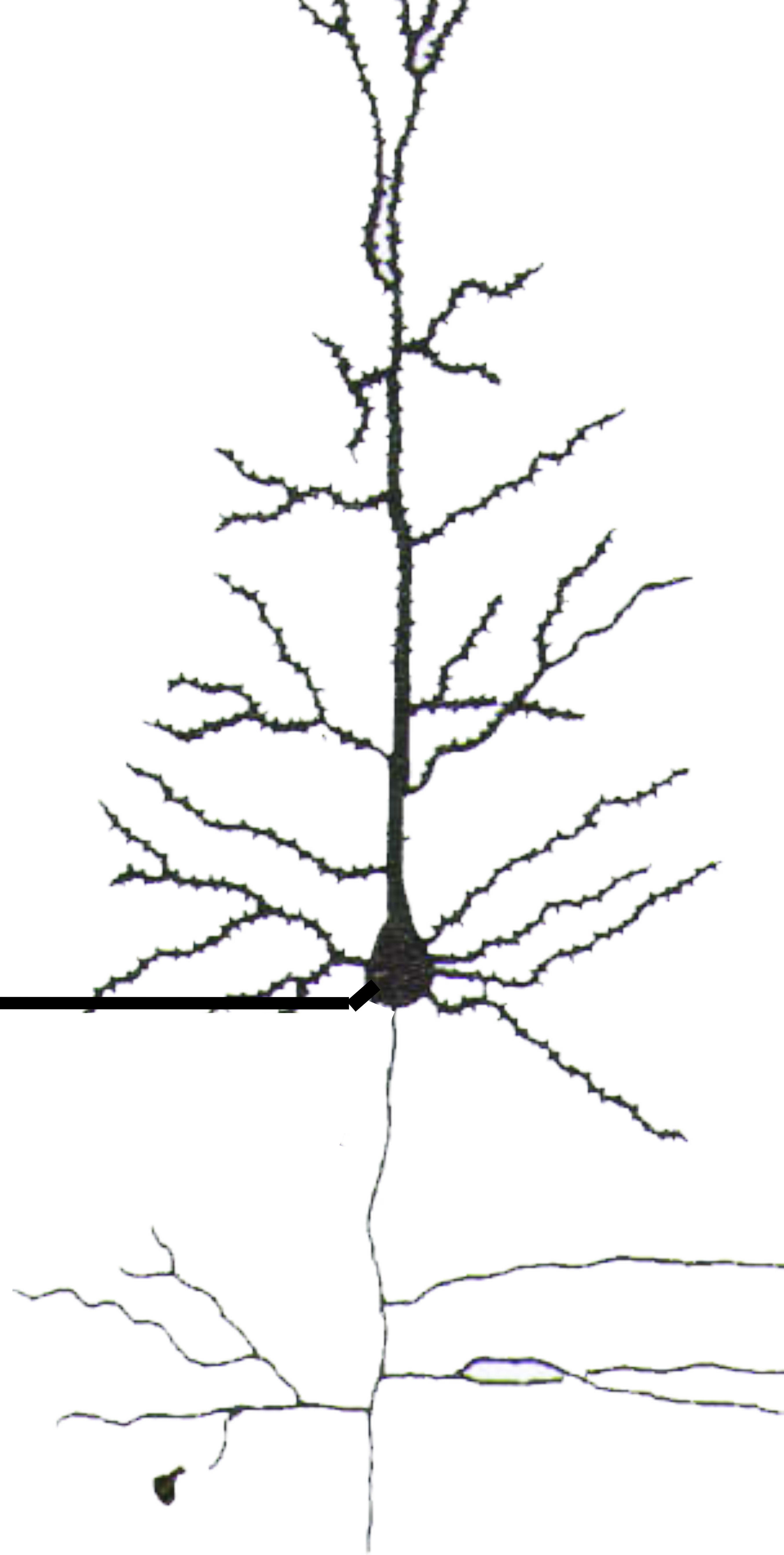
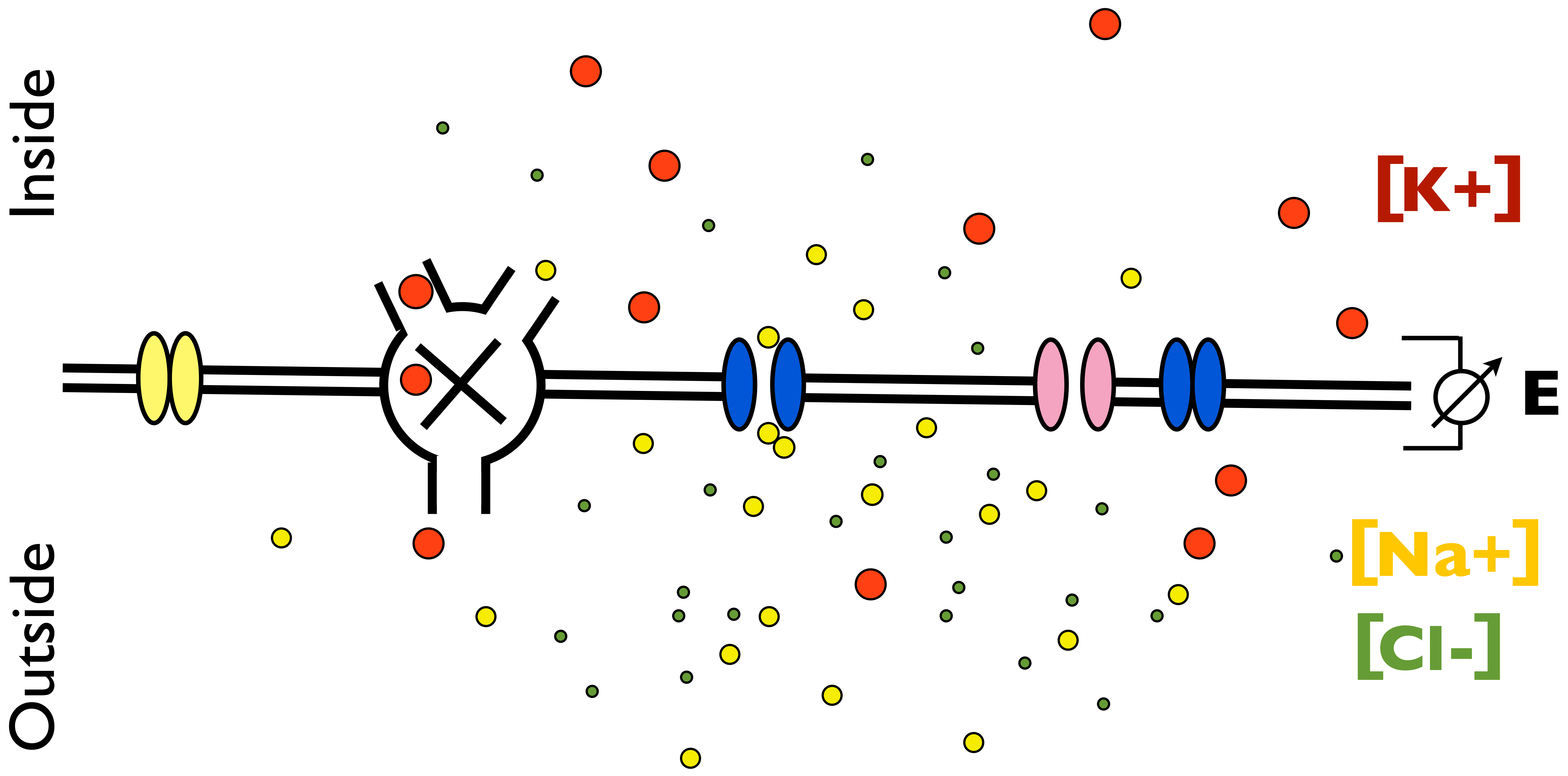
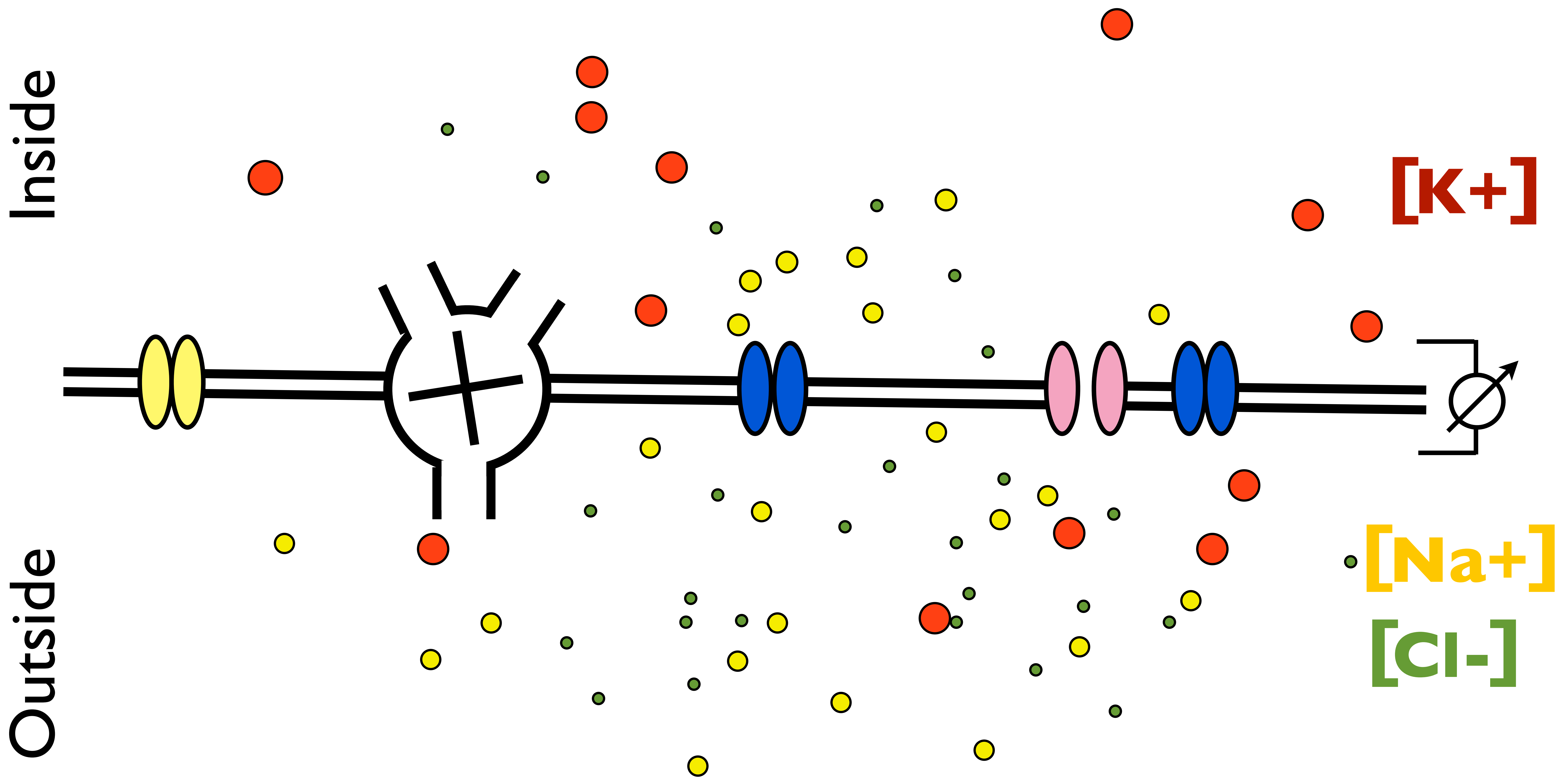


voltage

voltage

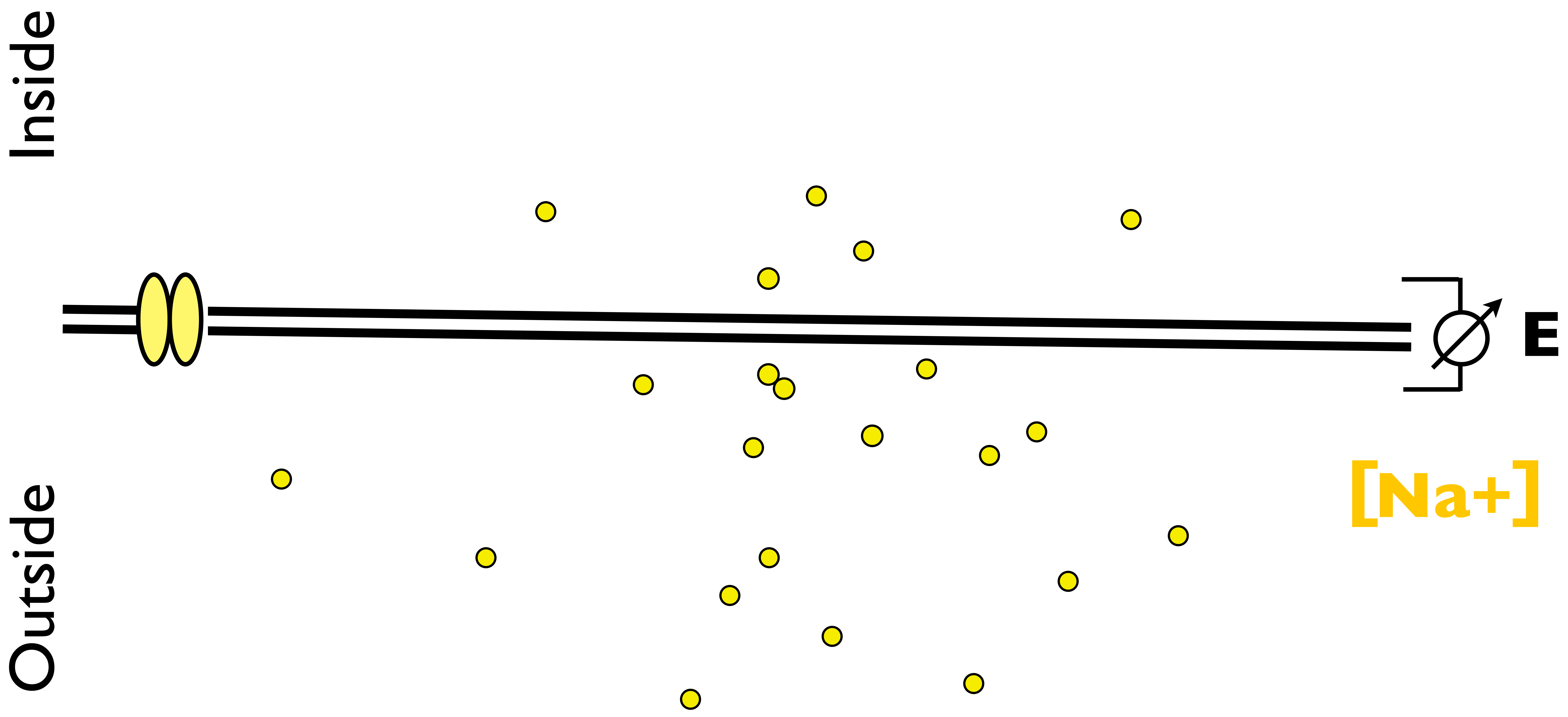

voltage


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


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

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

Nernst equation, 1887



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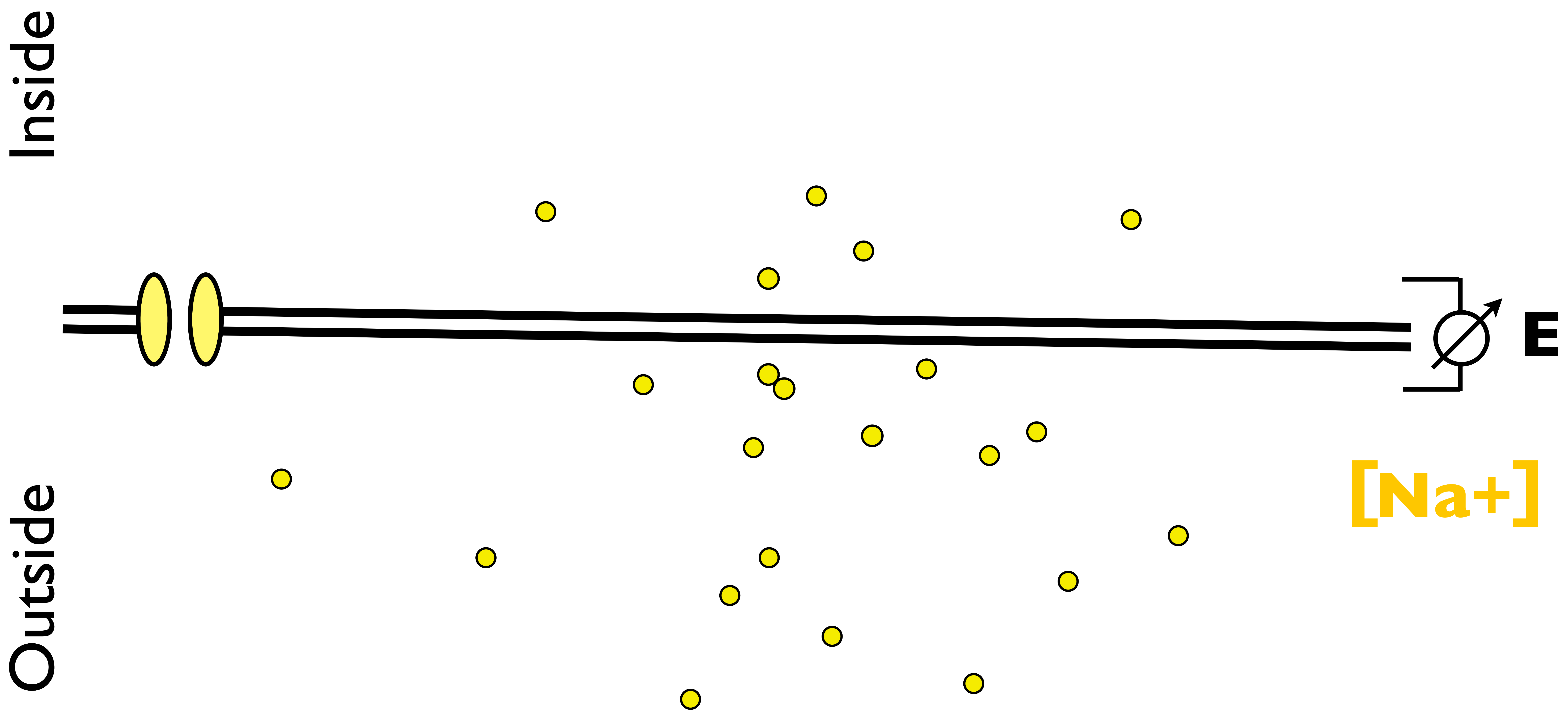
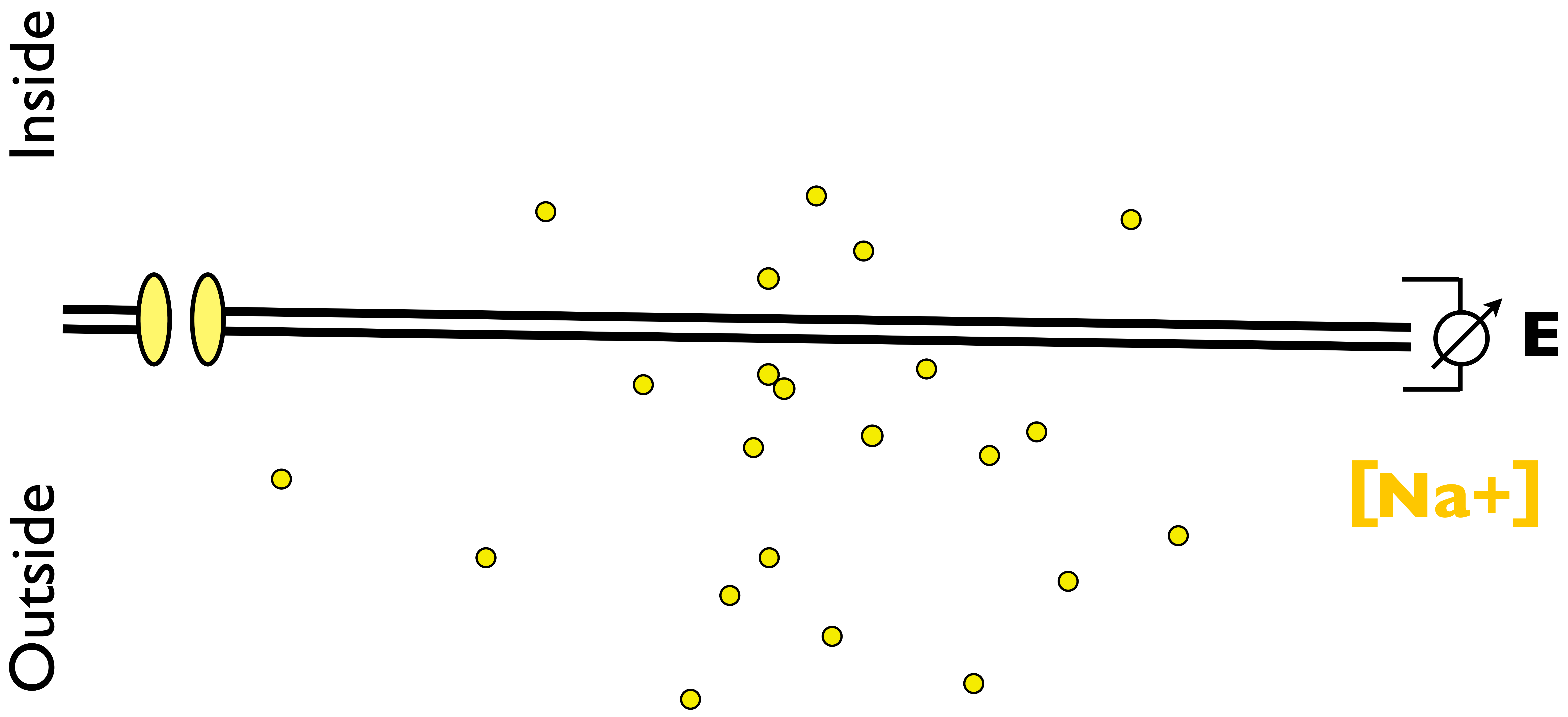
Nernst equation, 1887



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



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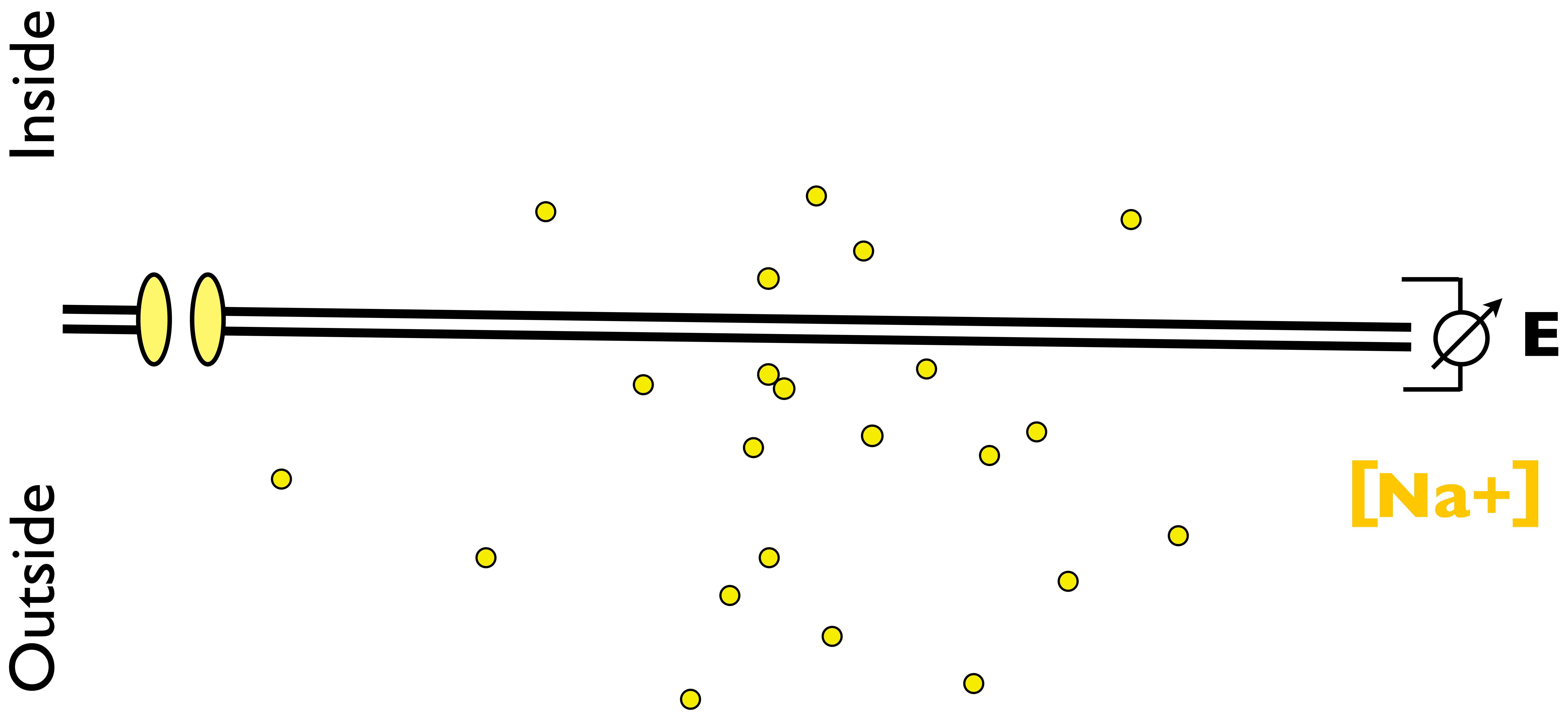
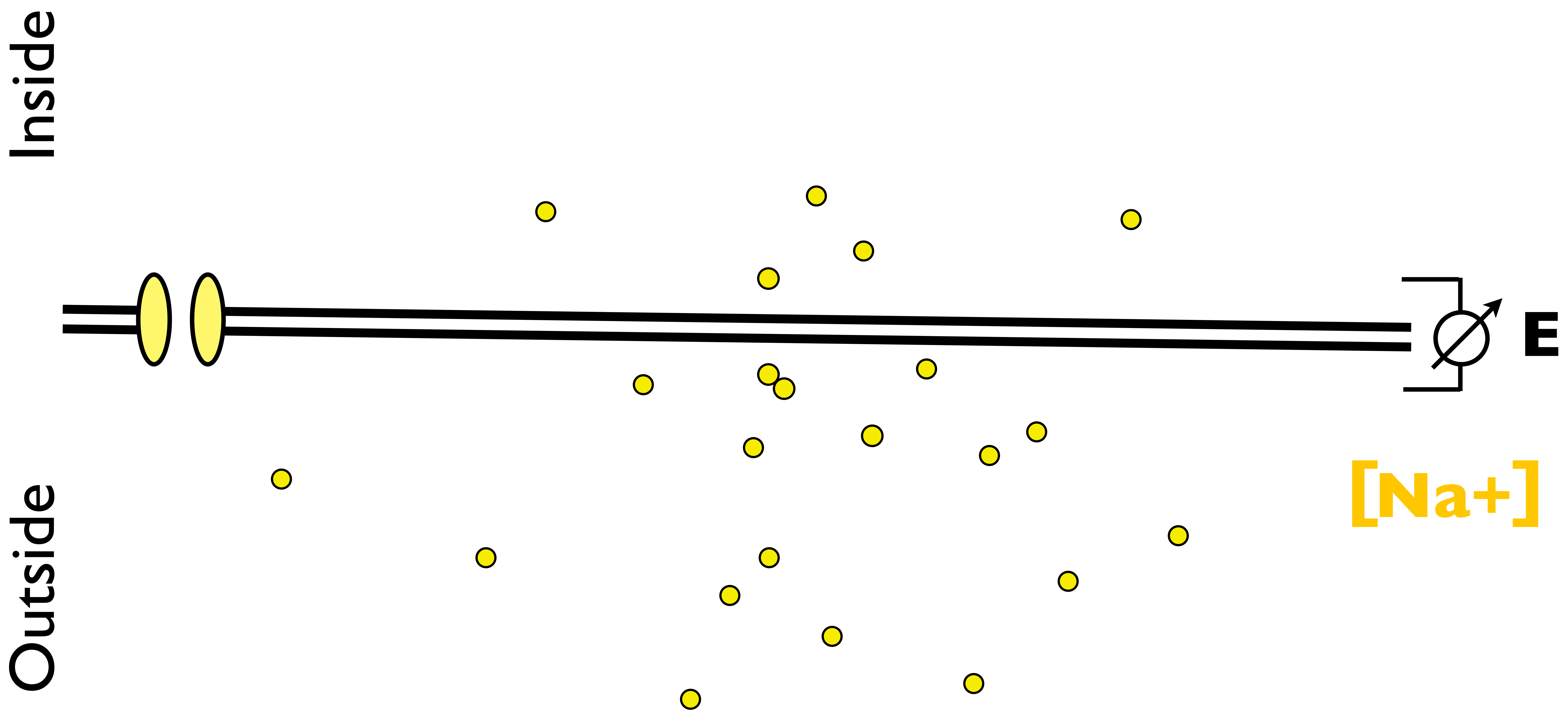
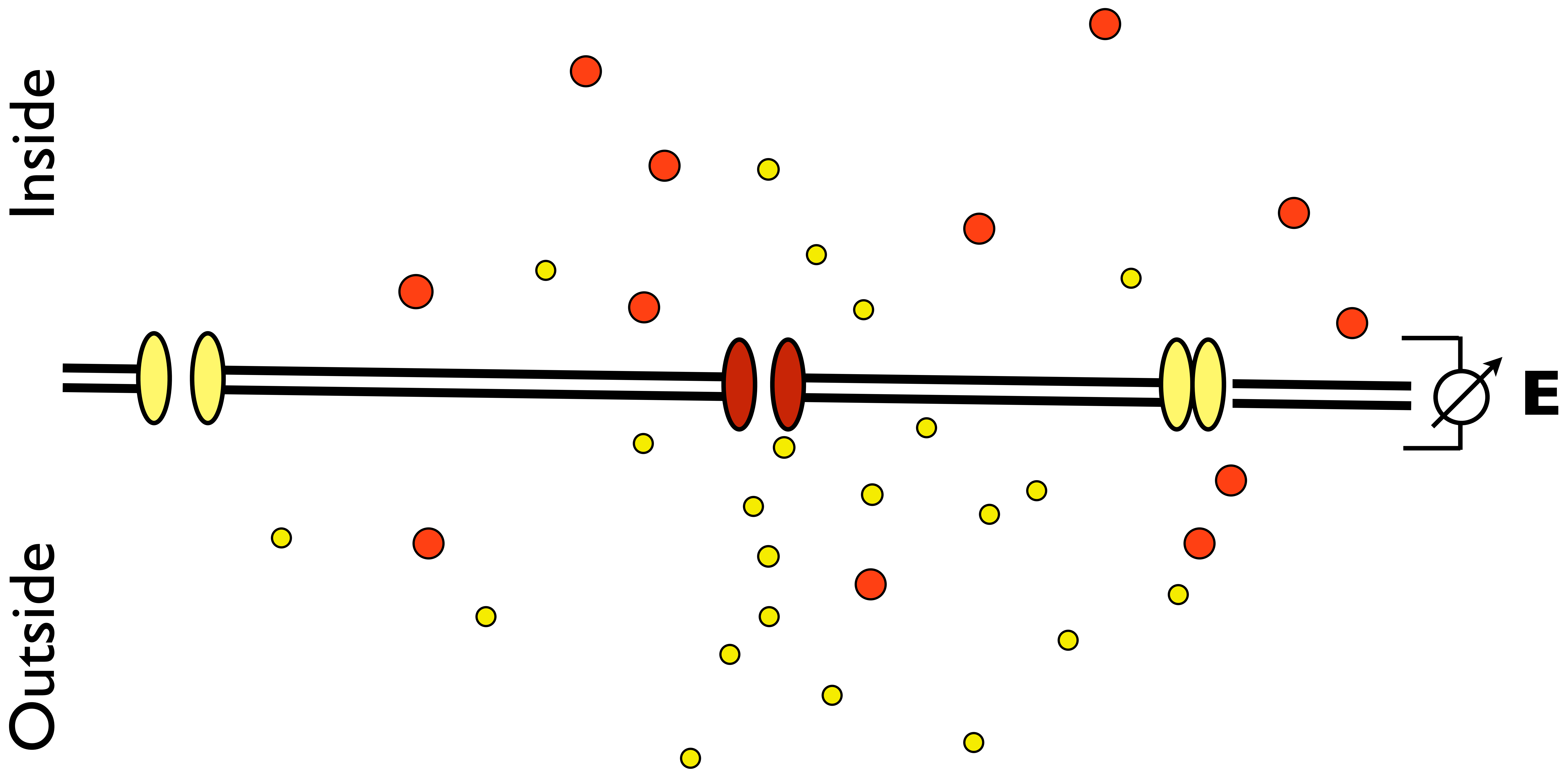


$$\mathbf{E} = C \ln\left(\frac{p[Na+]_{out}}{p[Na+]_{in}}\right)$$

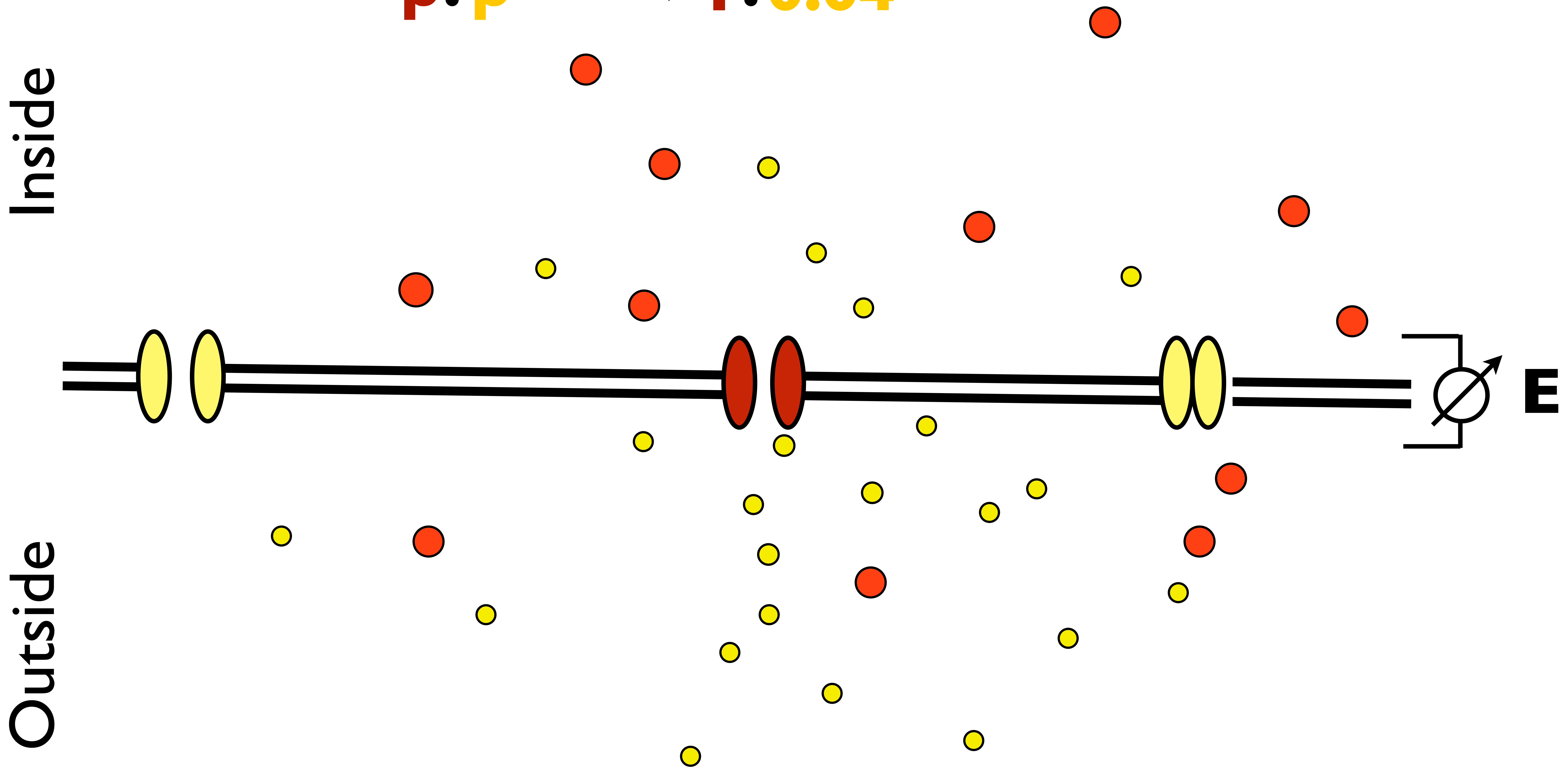


$$\mathbf{E} = C \ln\left(\frac{p[K+]_{out} + p[Na+]_{out}}{p[K+]_{in} + p[Na+]_{in}}\right)$$



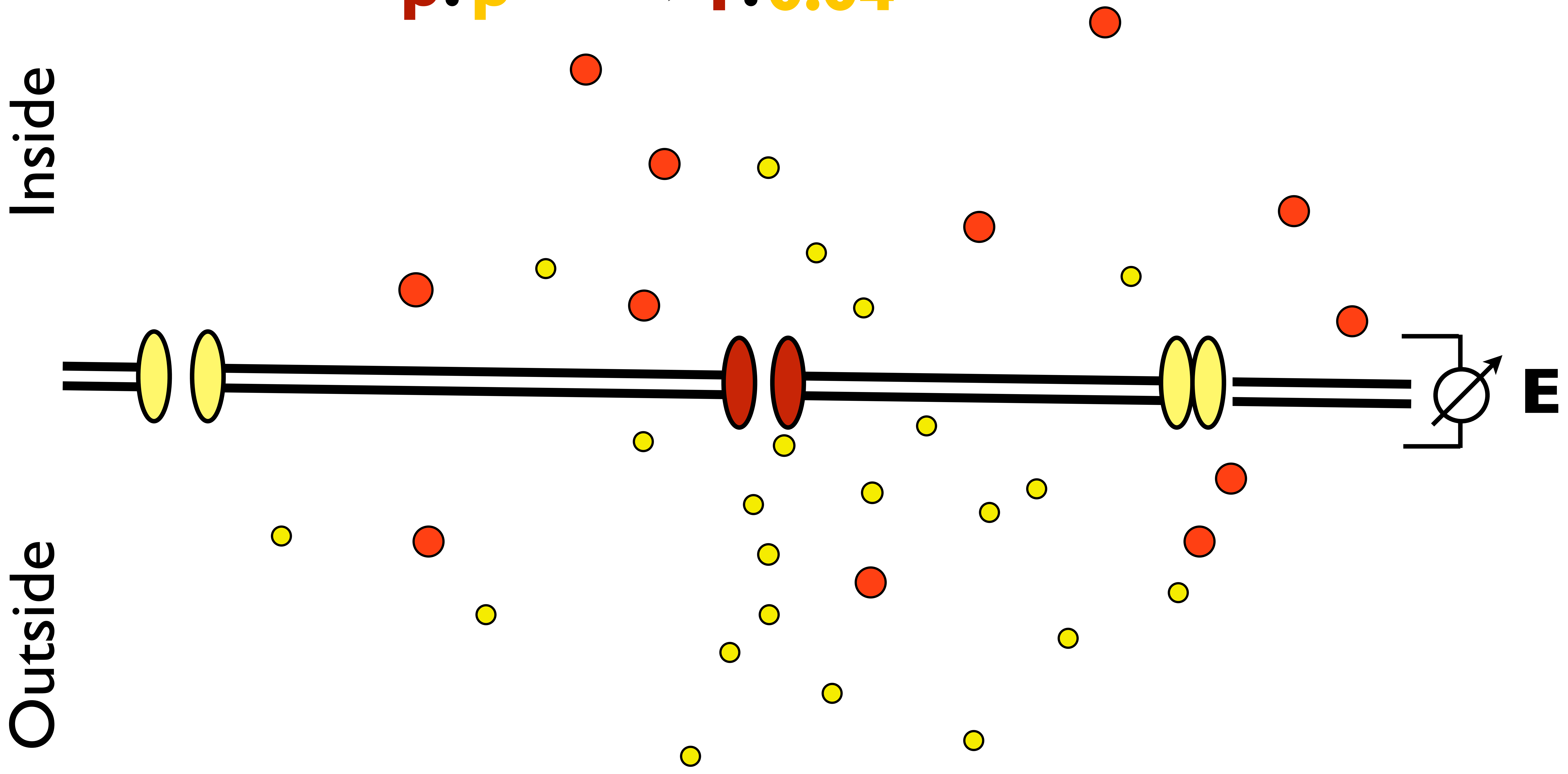
$$\mathbf{E} = C \ln\left(\frac{p[K+]_{out} + p[Na+]_{out}}{p[K+]_{in} + p[Na+]_{in}}\right)$$

$p : p \longrightarrow 1 : 0.04$



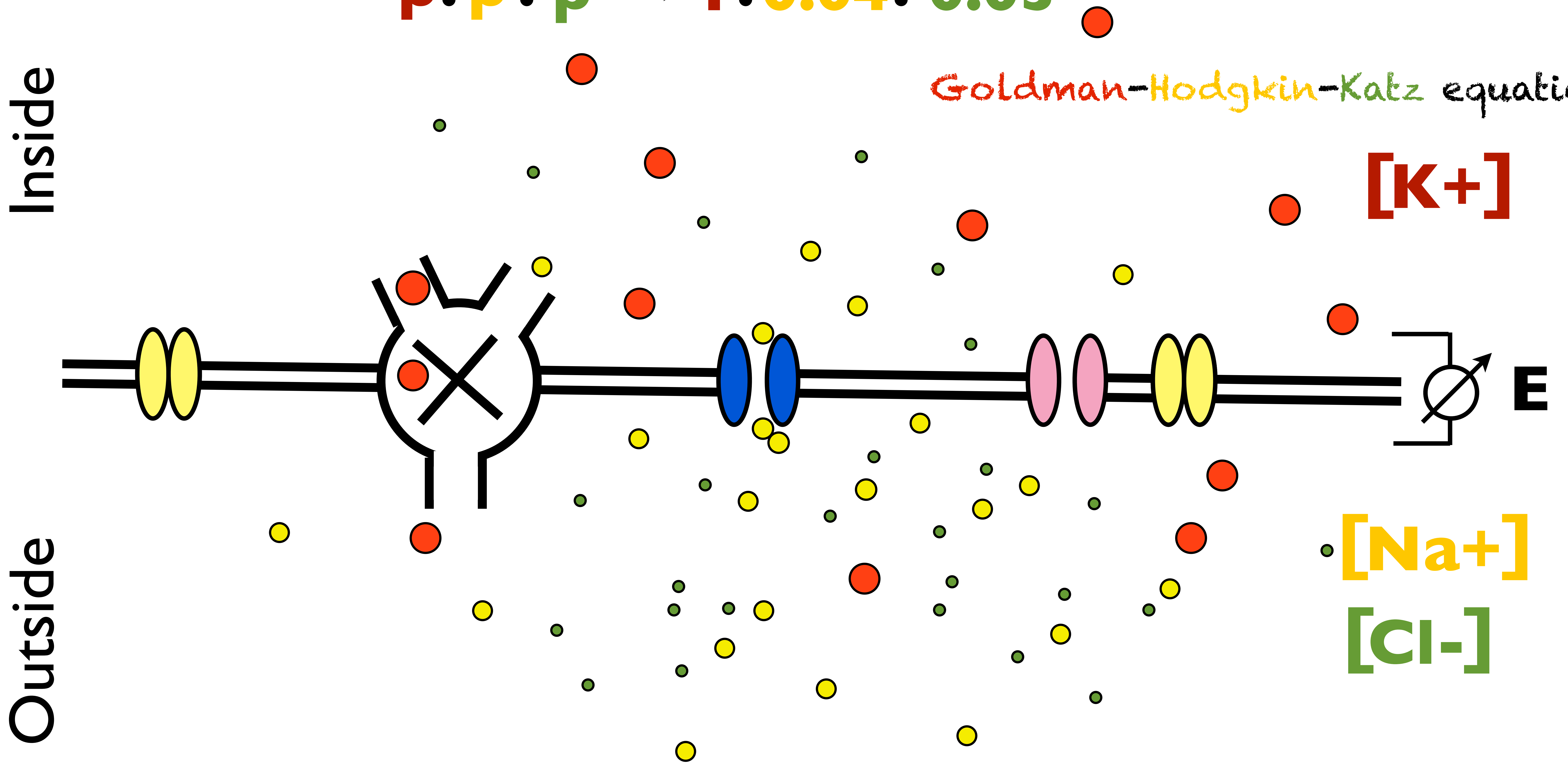
$$\mathbf{E} = C \ln\left(\frac{p[K+]_{out} + p[Na+]_{out}}{p[K+]_{in} + p[Na+]_{in}}\right) \quad -X$$

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



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

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

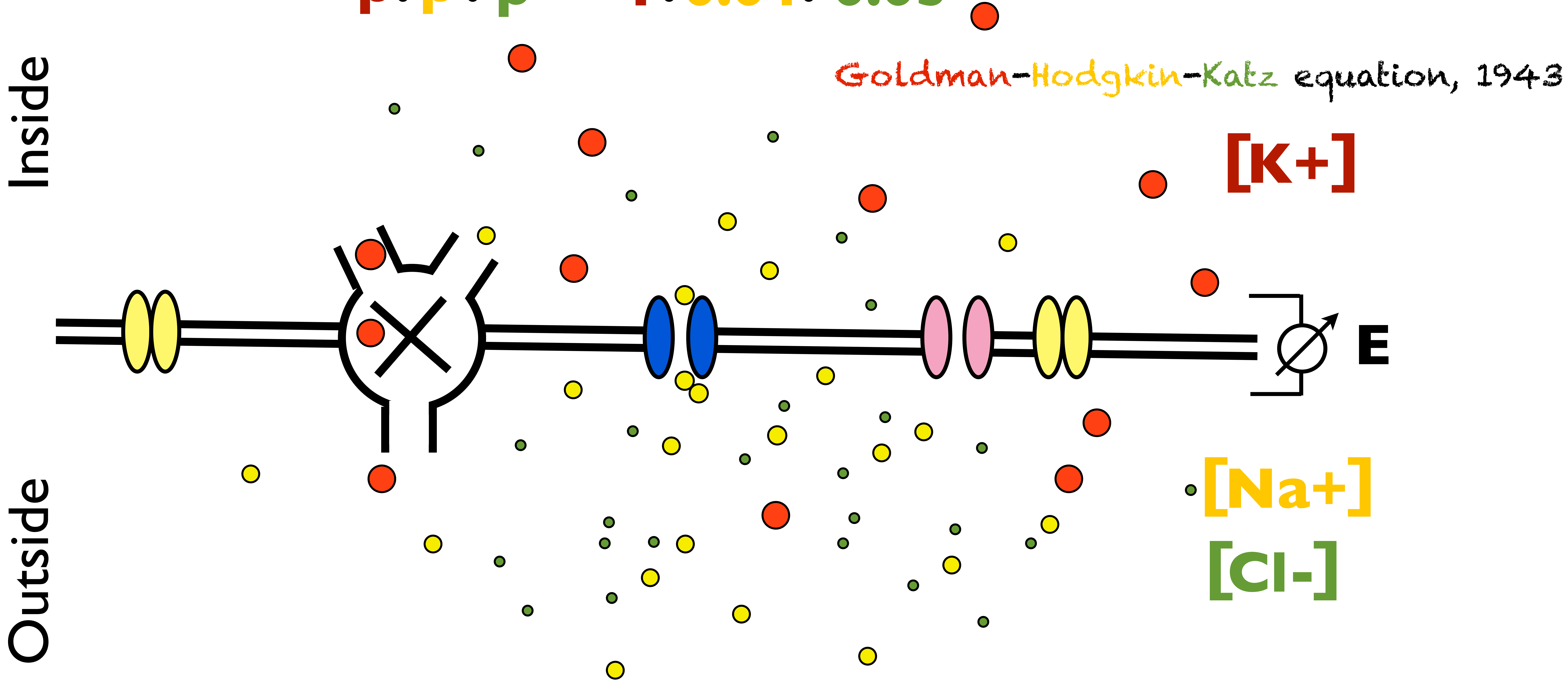


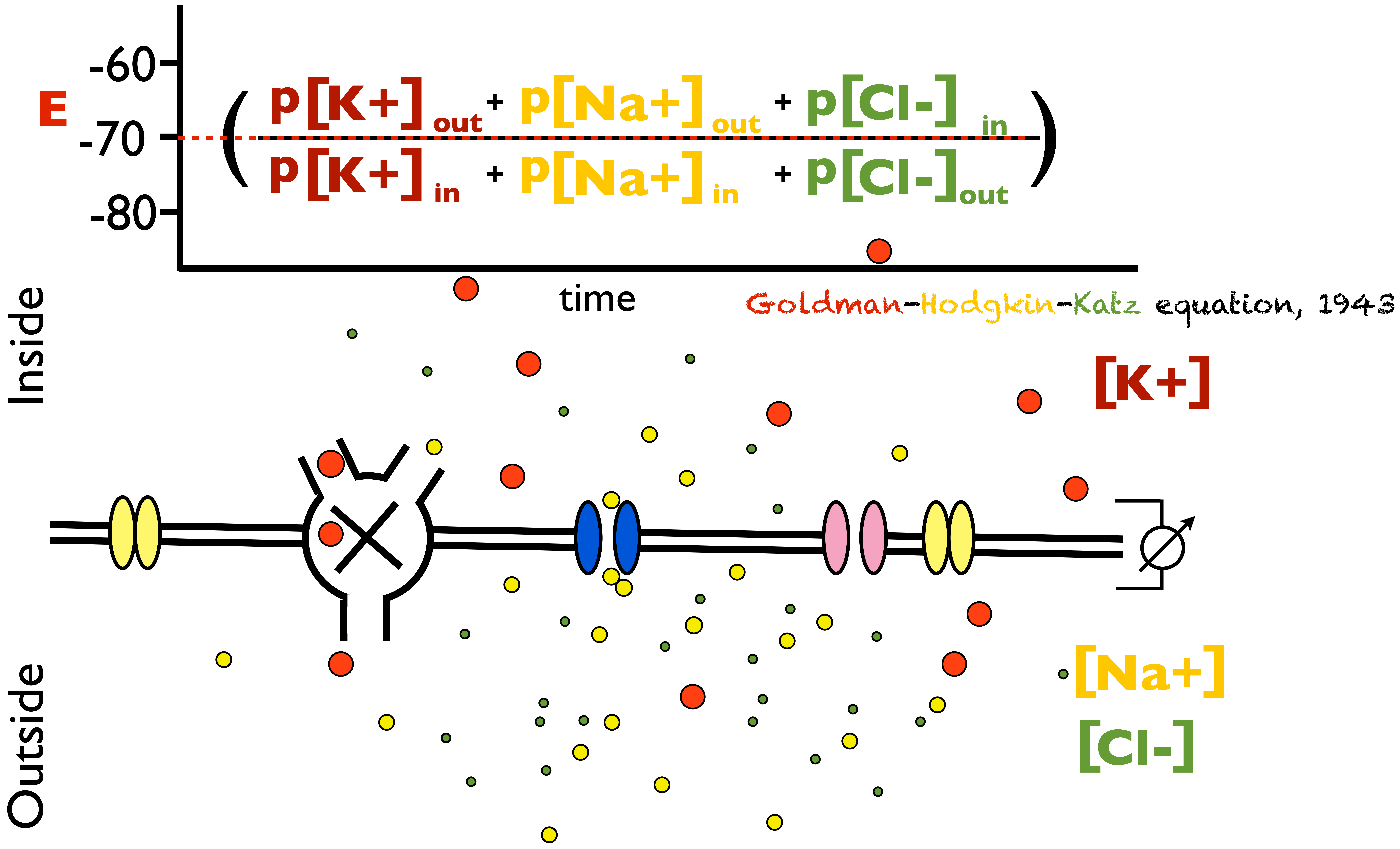
Goldman-Hodgkin-Katz equation, 1943

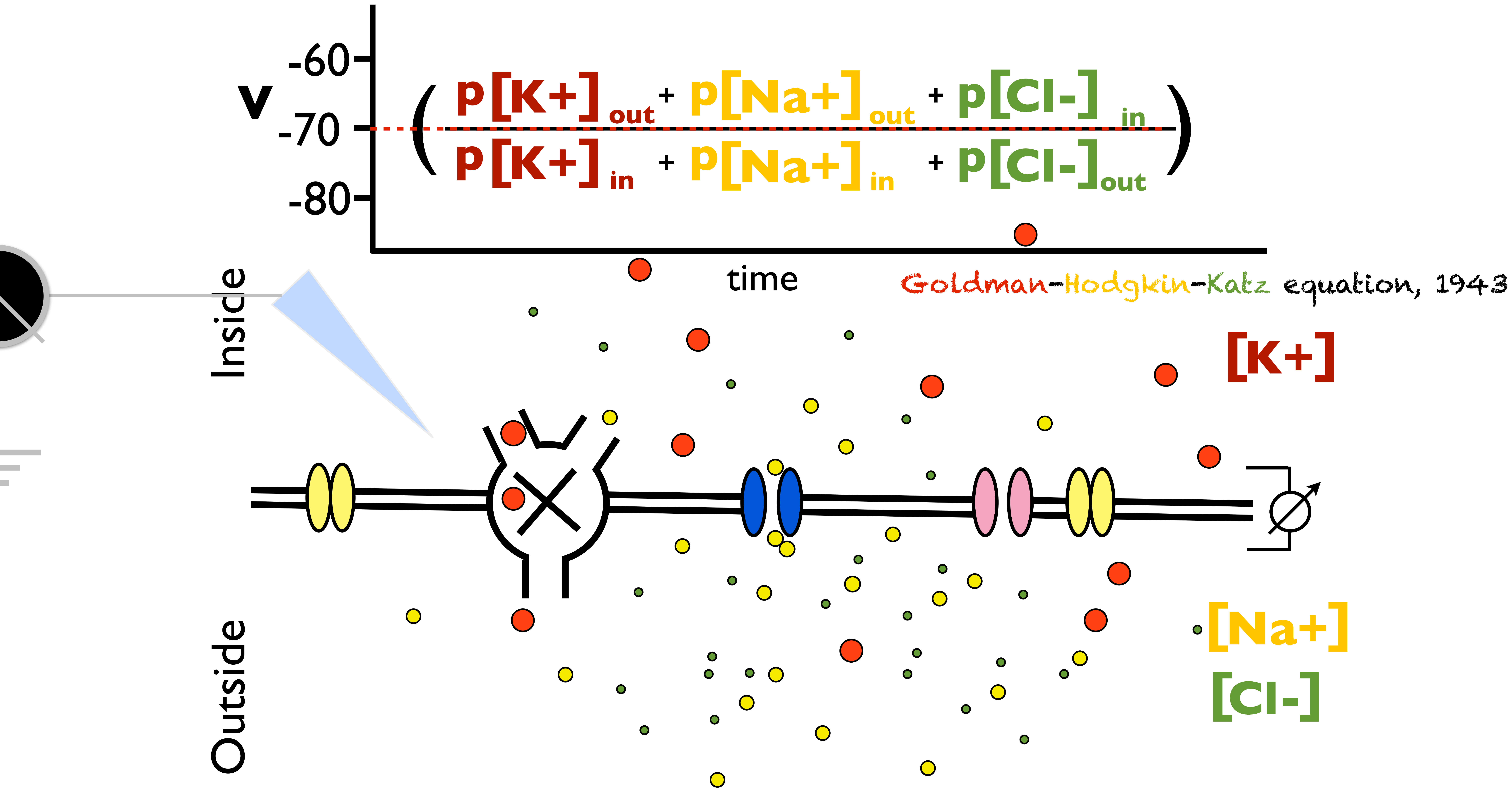
$$\mathbf{E} = C \ln\left(\frac{p[K+]_{out} + p[Na+]_{out} + p[Cl-]_{in}}{p[K+]_{in} + p[Na+]_{in} + p[Cl-]_{out}}\right) = -70\ \mathrm{mV}$$

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

Goldman-Hodgkin-Katz equation, 1943




E
-60
-70
-80
p[K+]out + p[Na+]out + p[Cl-] in
p[K+]in + p[Na+]in + p[Cl-]out
time
Goldman-Hodgkin-Katz equation, 1943
Inside
Outside
[K+]
[Na+]
[Cl-]



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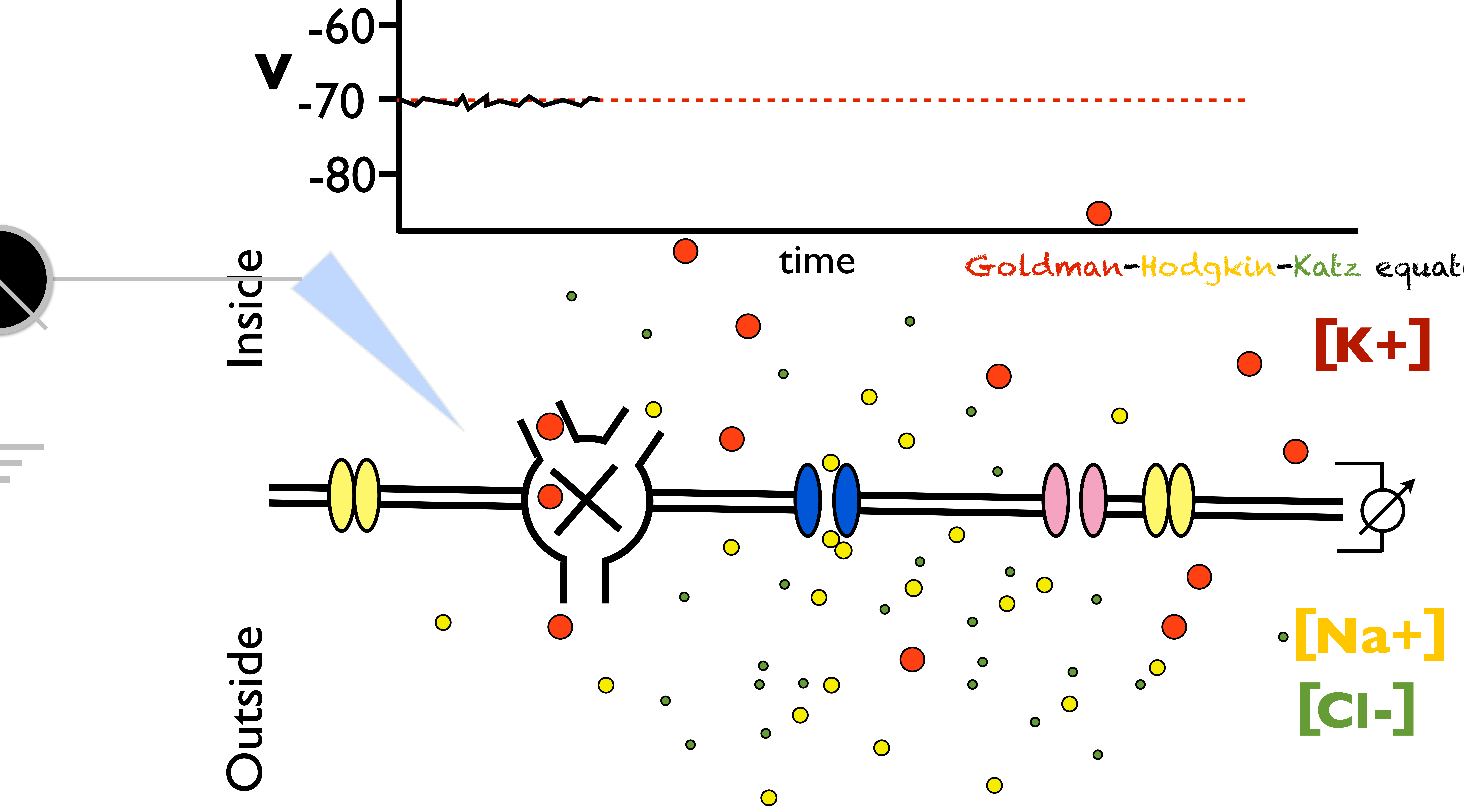
$$E = C \ln\left(\frac{P[K+]_{out} + P[Na+]_{out} + P[Cl-]_{in}}{P[K+]_{in} + P[Na+]_{in} + P[Cl-]_{out}}\right)$$



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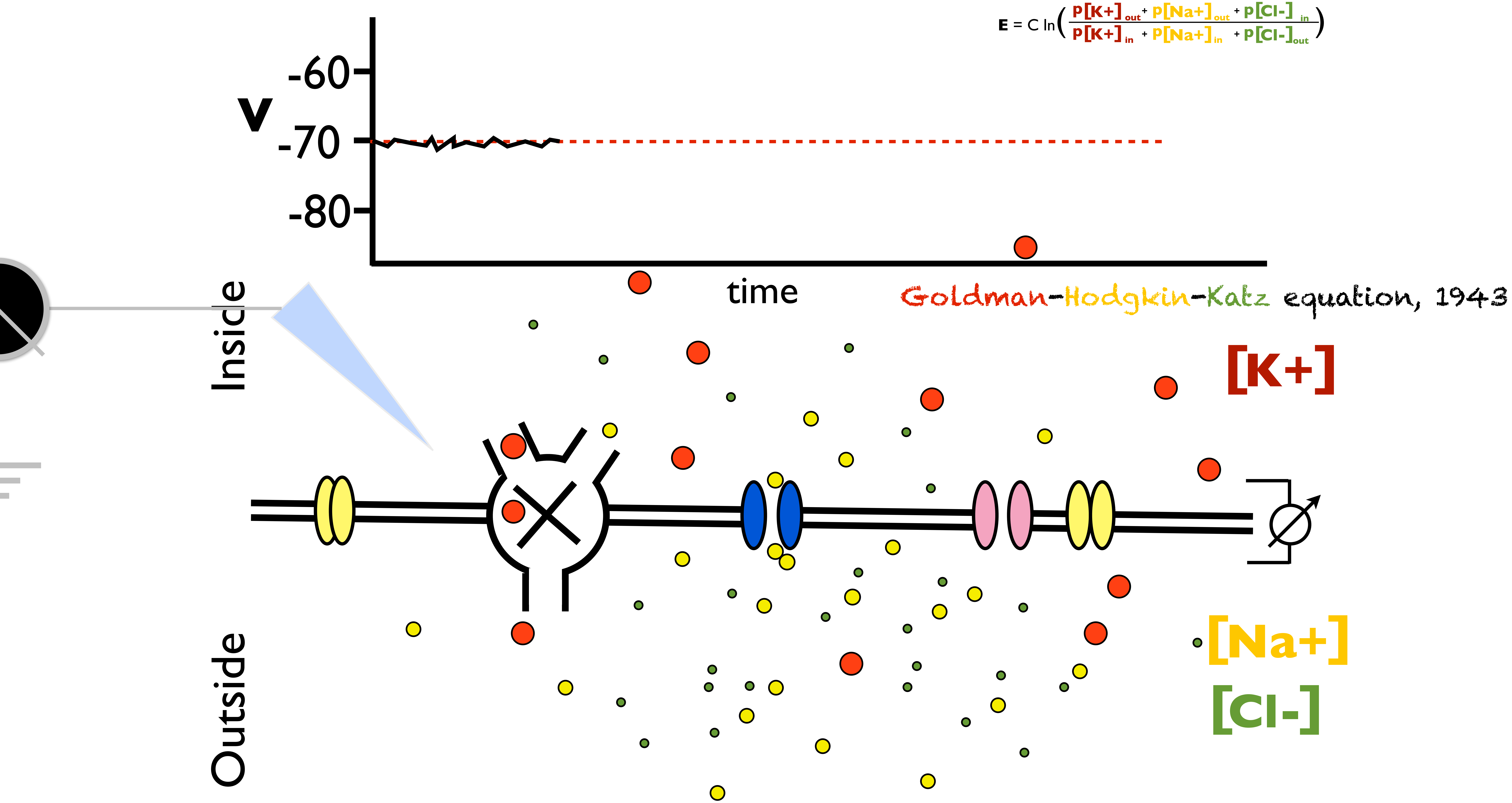

E = C ln(P[K+]out + P[Na+]out + P[Cl-]in / P[K+]in + P[Na+]in + P[Cl-]out)
V
-60
-70
-80
time
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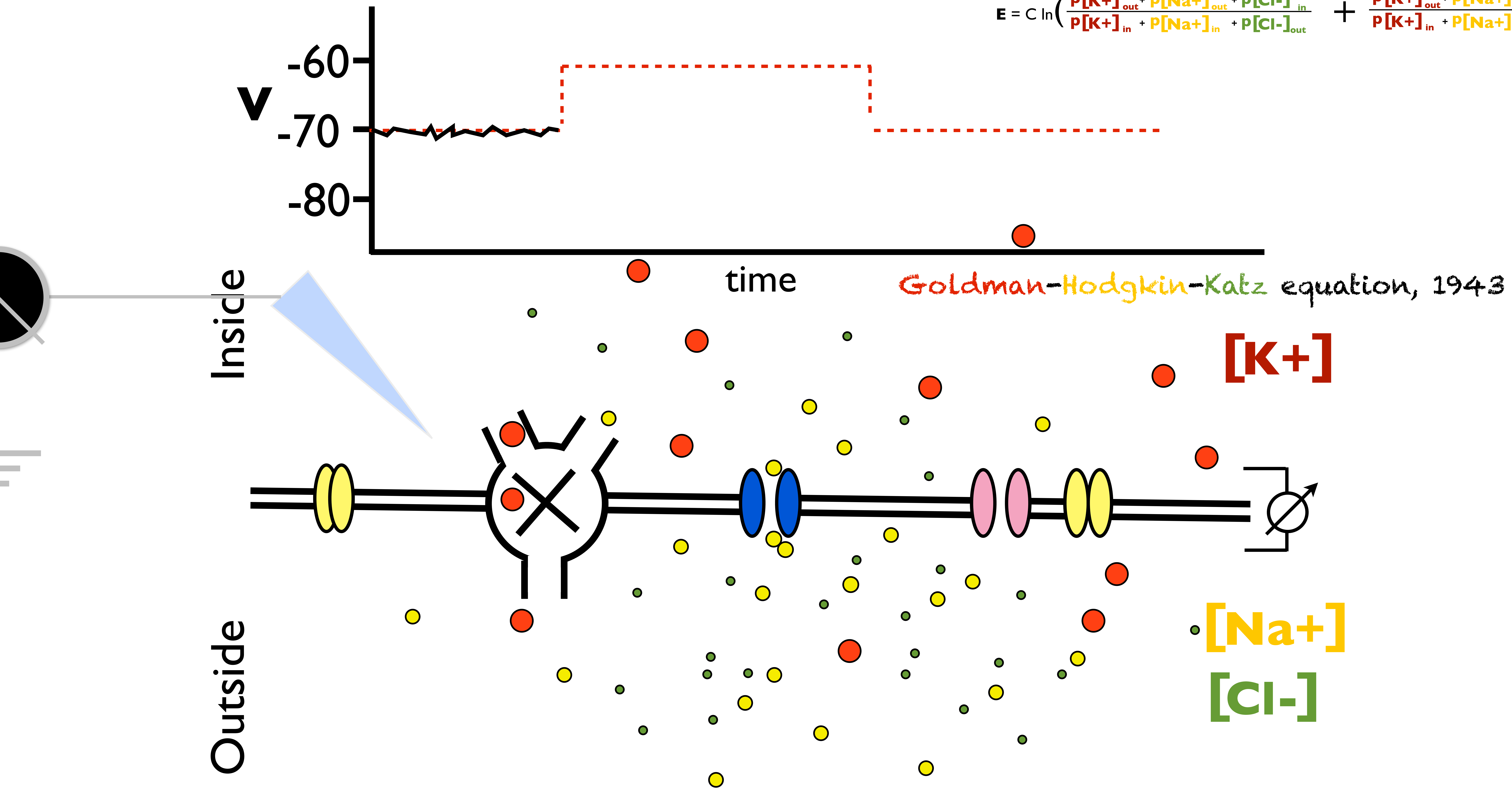
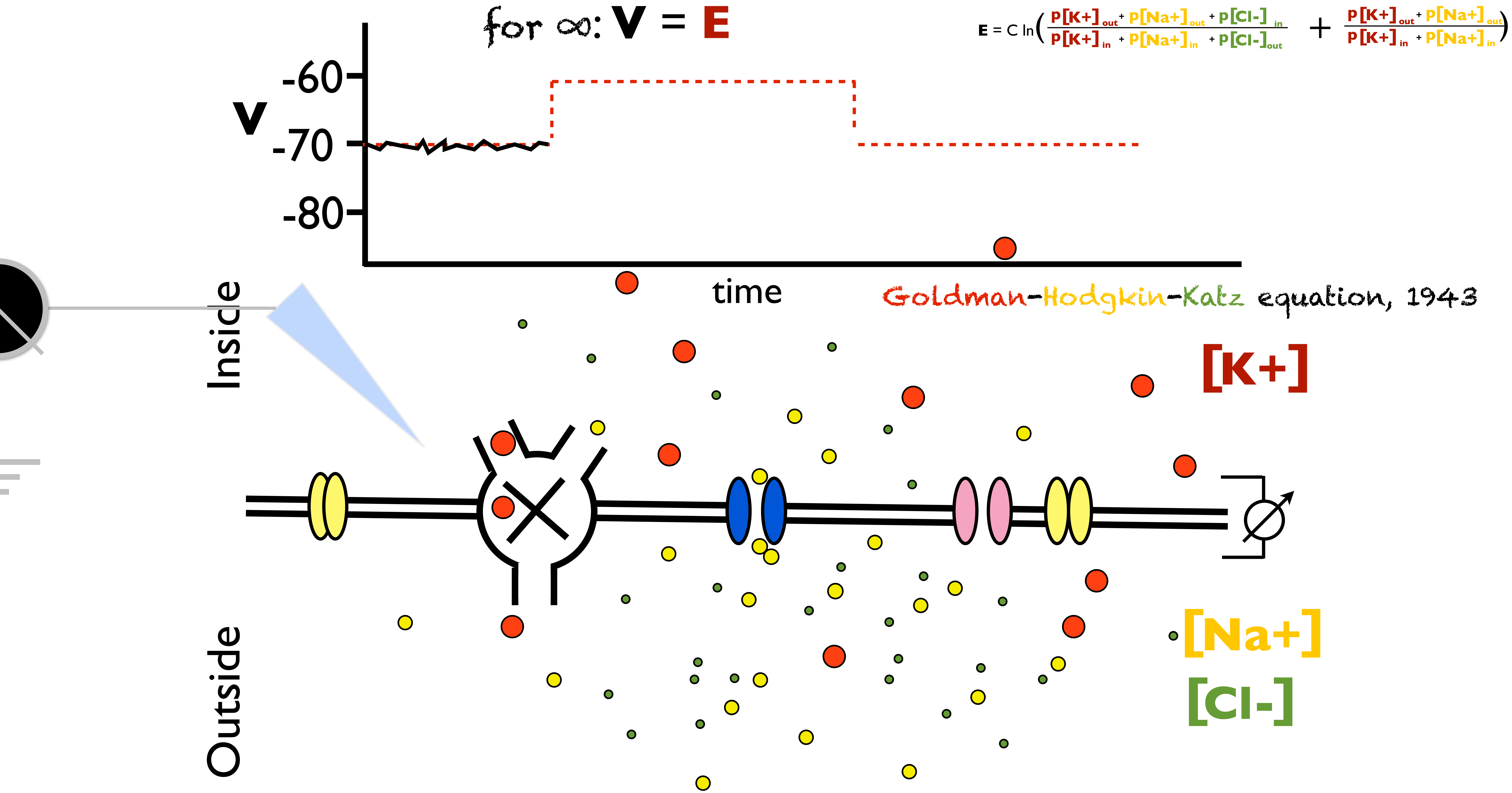
Inside
Outside
[K+]
[Na+]
[Cl-]

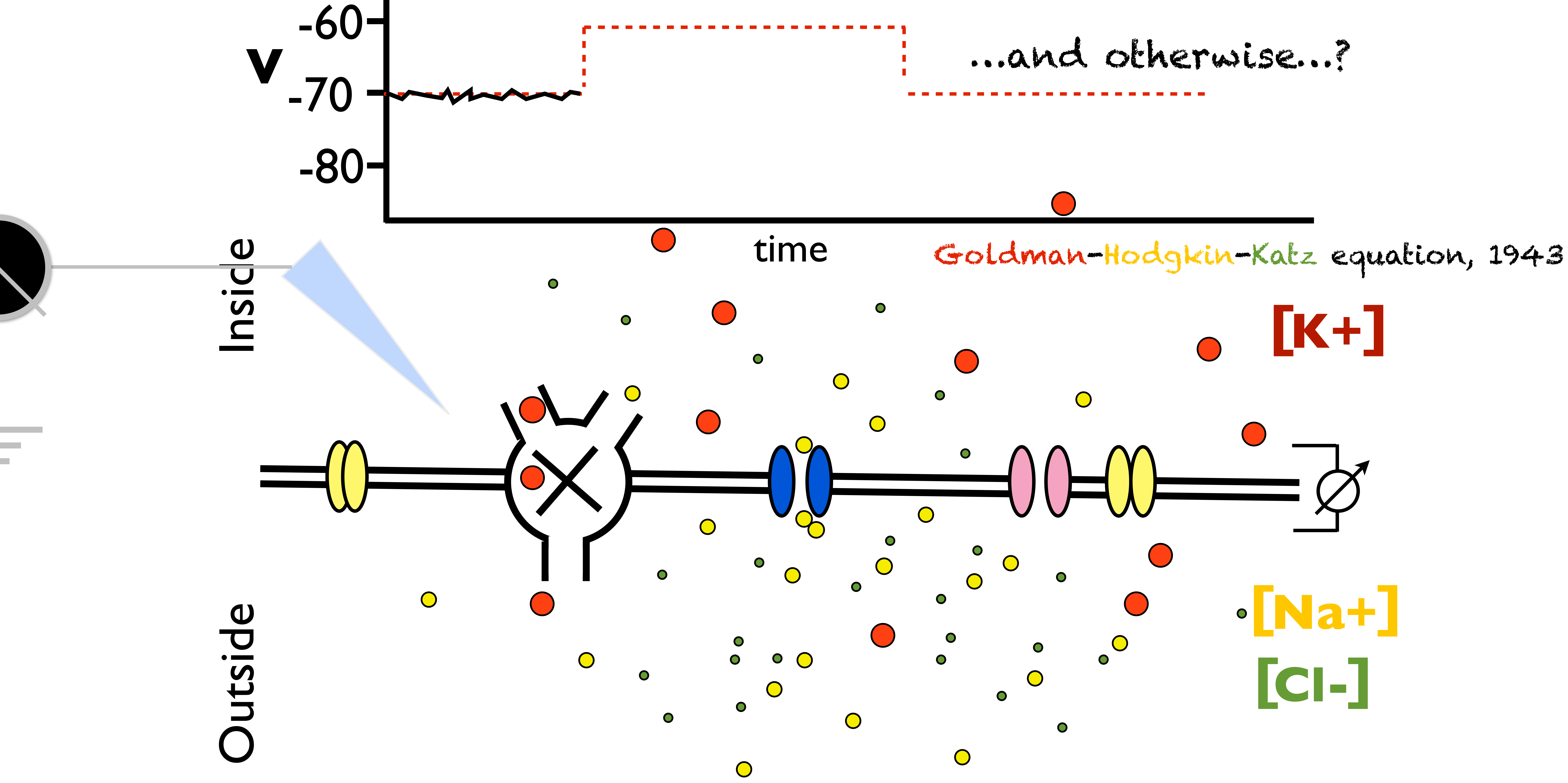
$$E = C \ln\left(\frac{p[K+]_{out} + p[Na+]_{out} + p[Cl-]_{in}}{p[K+]_{in} + p[Na+]_{in} + p[Cl-]_{out}} + \frac{p[K+]_{out} + p[Na+]_{out}}{p[K+]_{in} + p[Na+]_{in}}\right)$$




for ∞: V = E
E = C ln((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**

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



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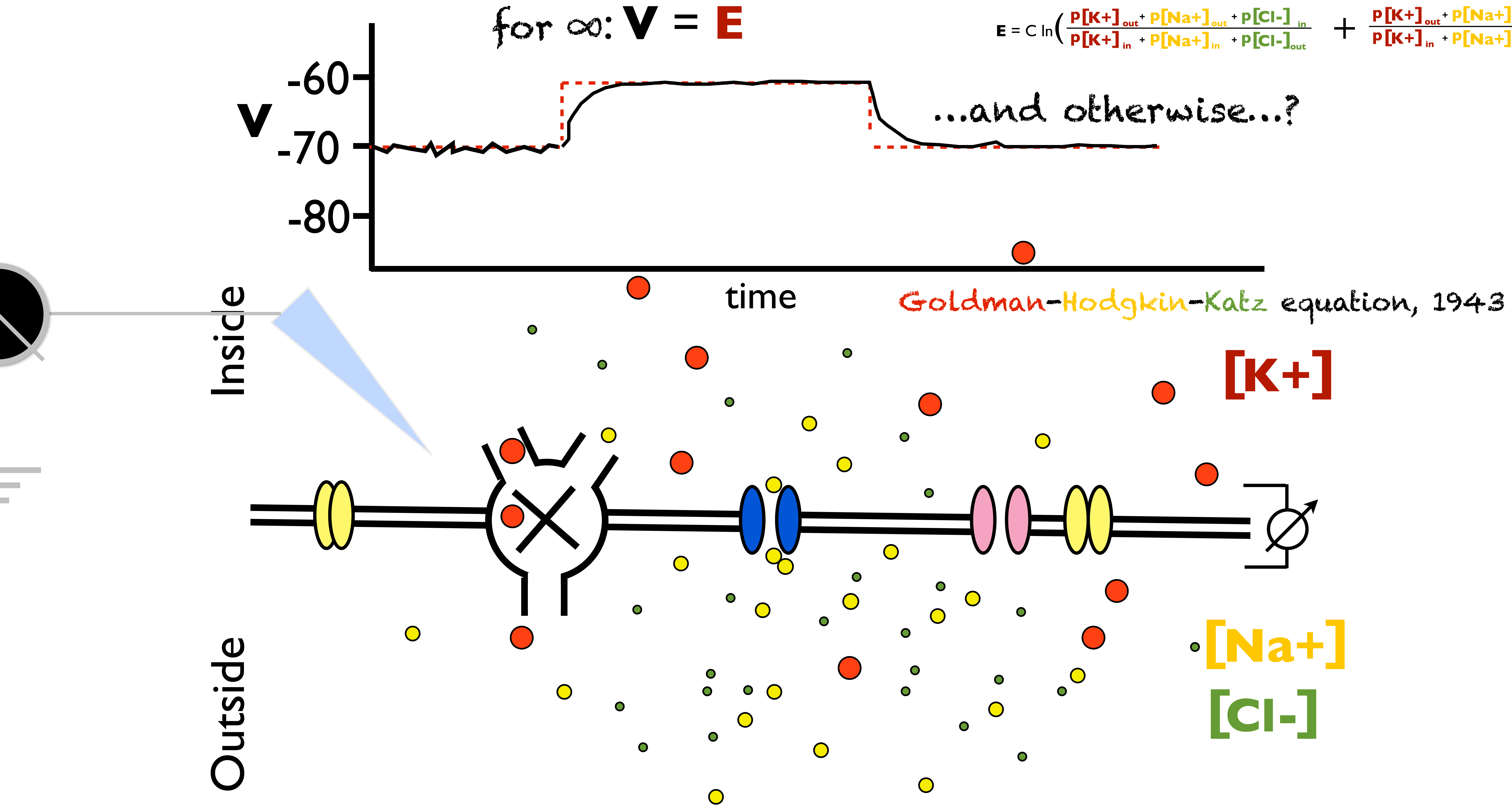
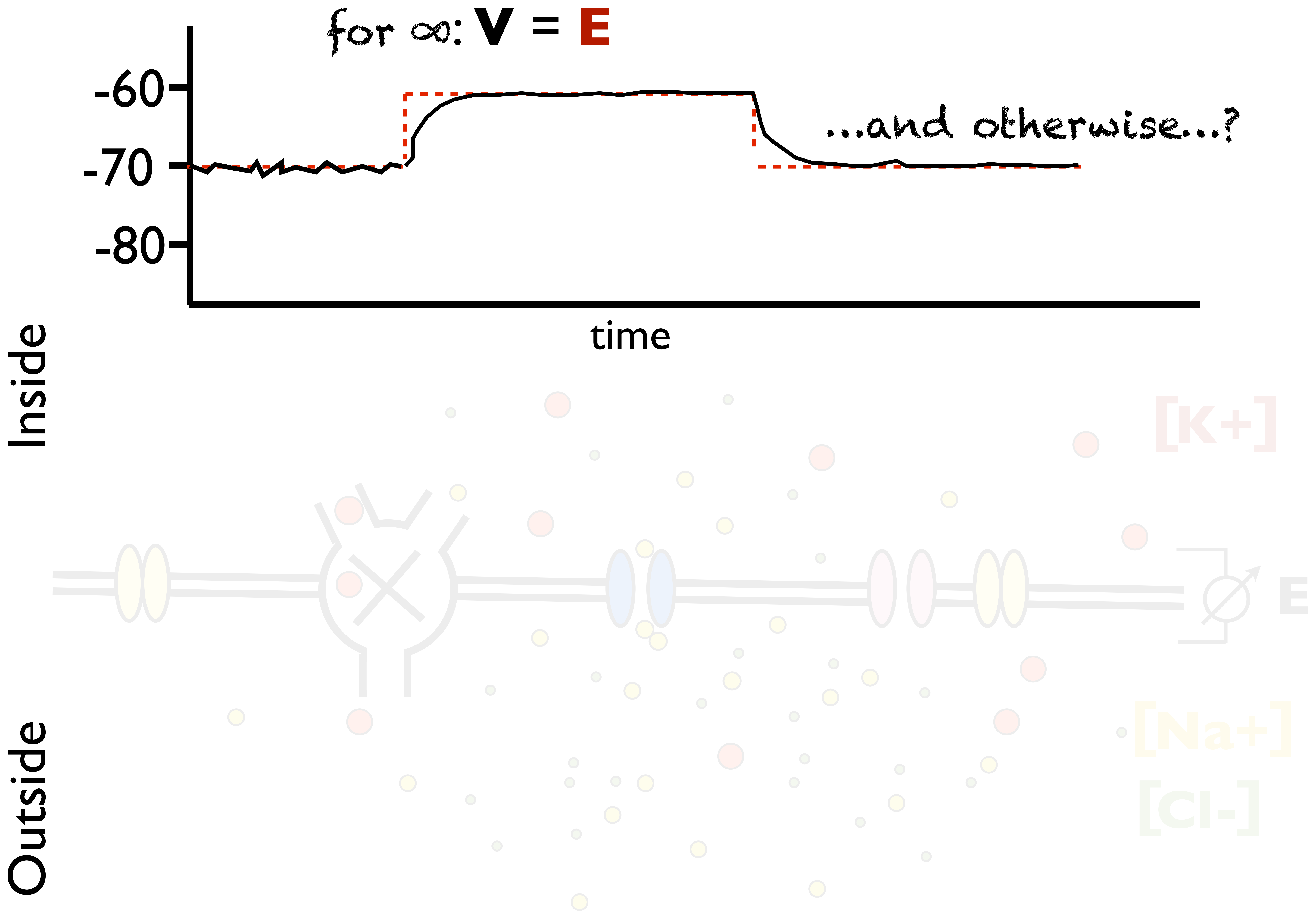
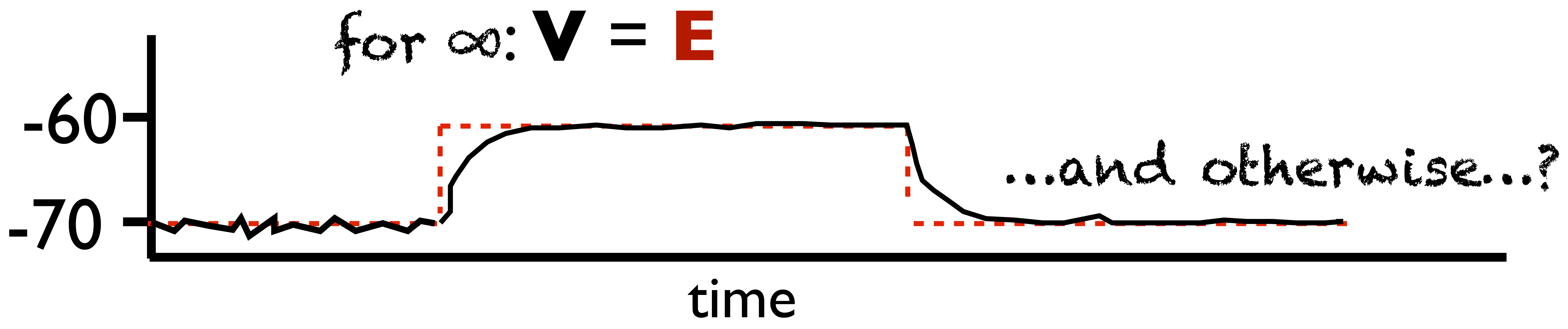




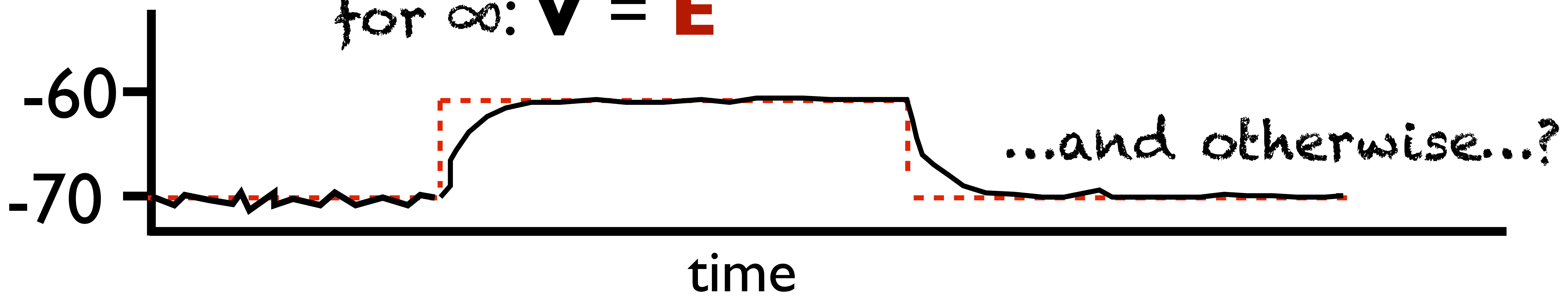
for ∞: V = E
-60
-70
-80
...and otherwise...?
time
Inside
Outside
[K+]
E
[Na+]
[Cl-]

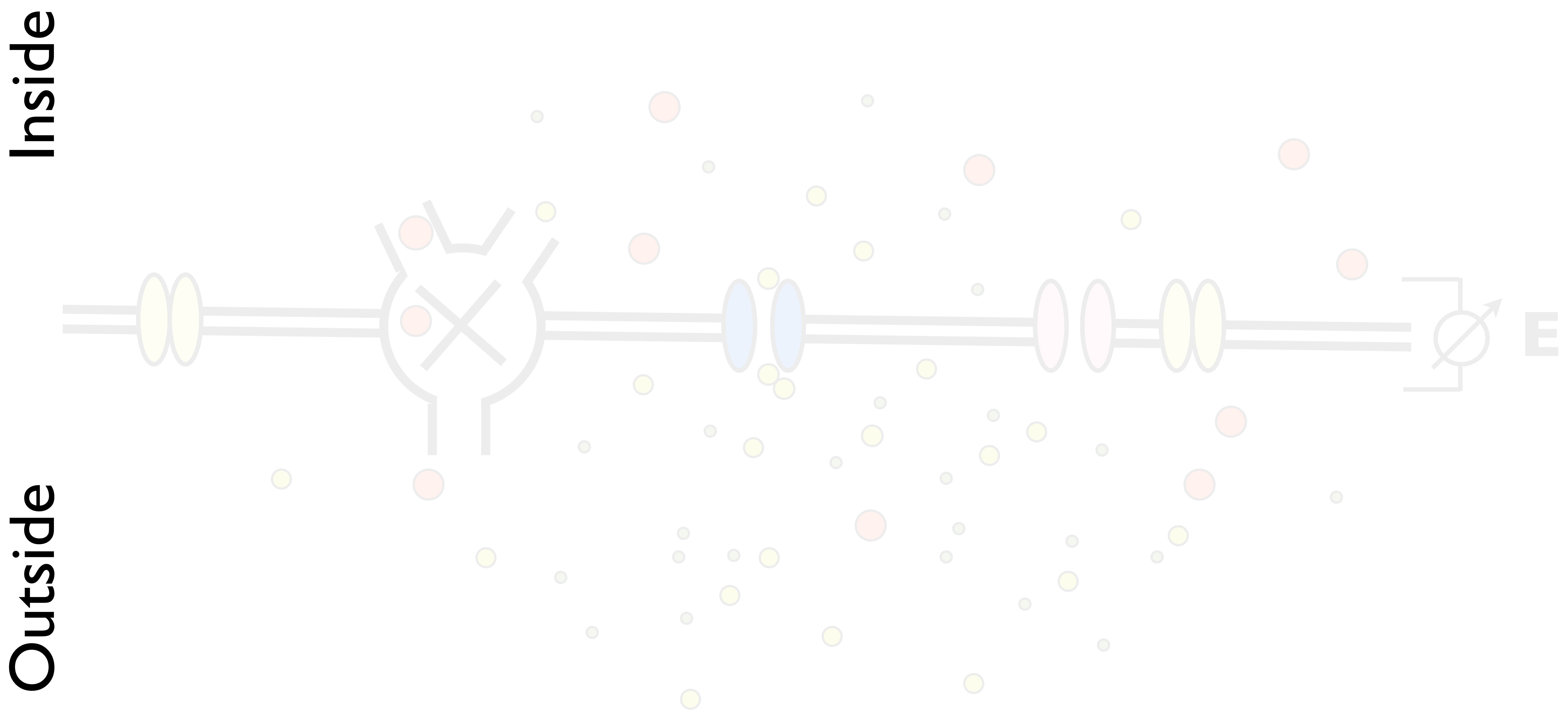


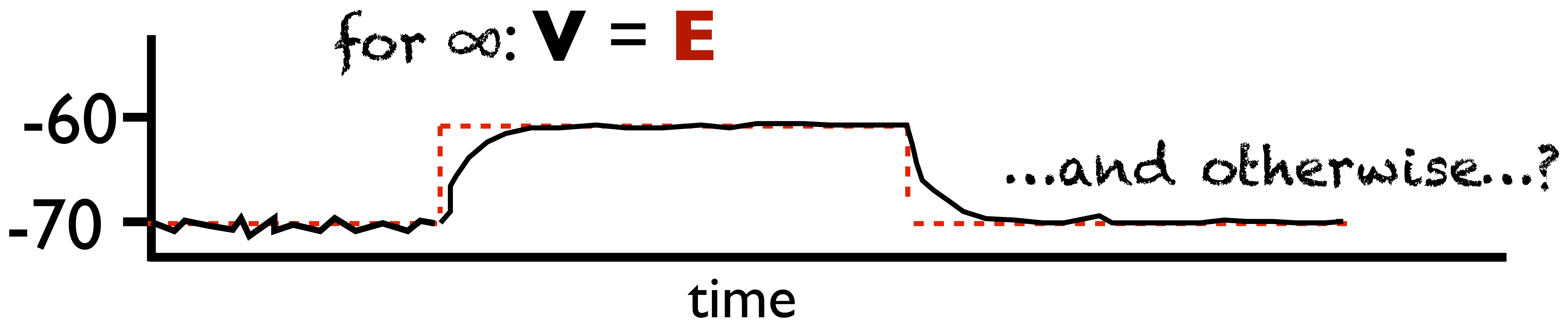
Inside

Outside

for ∞: **V** = **E**



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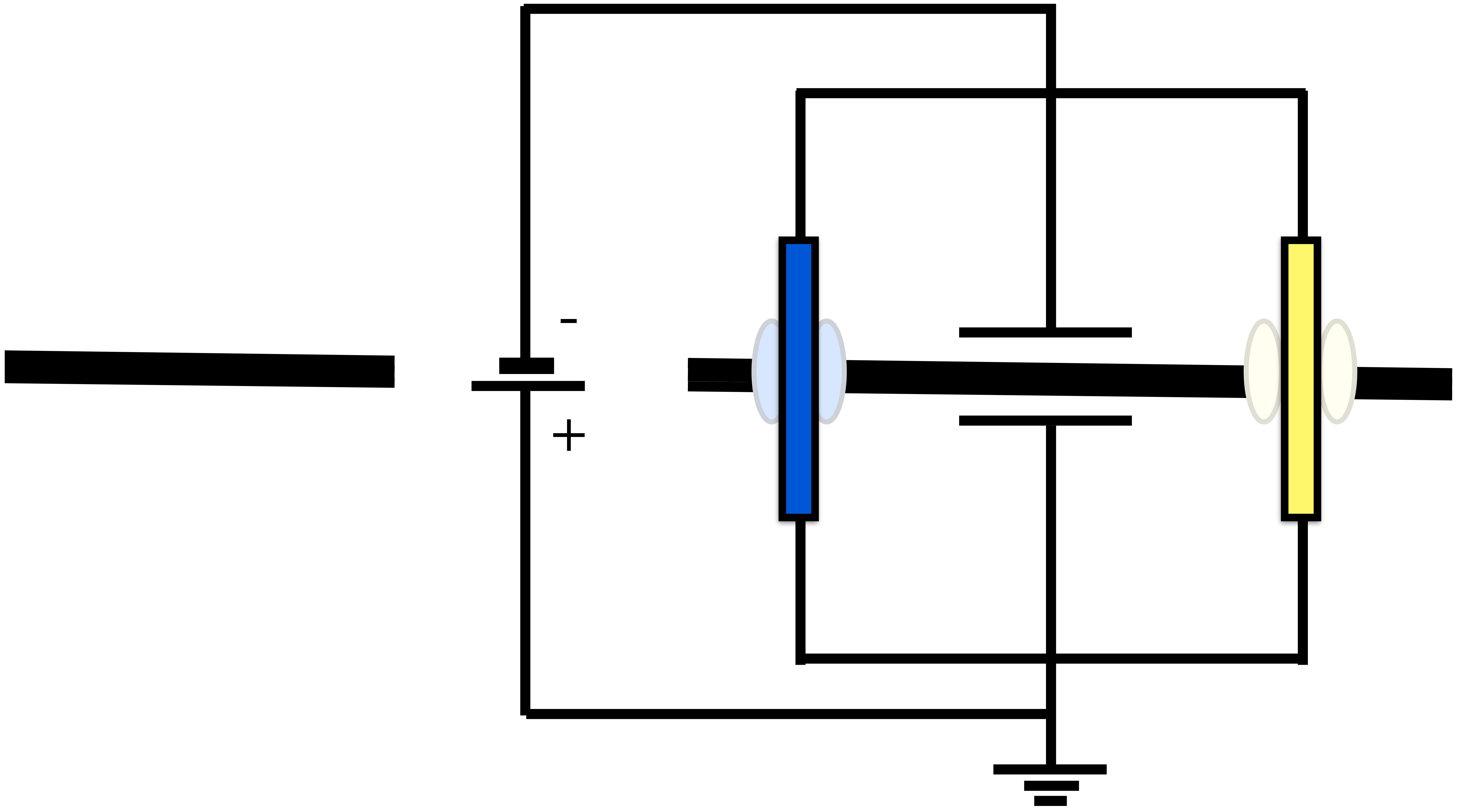
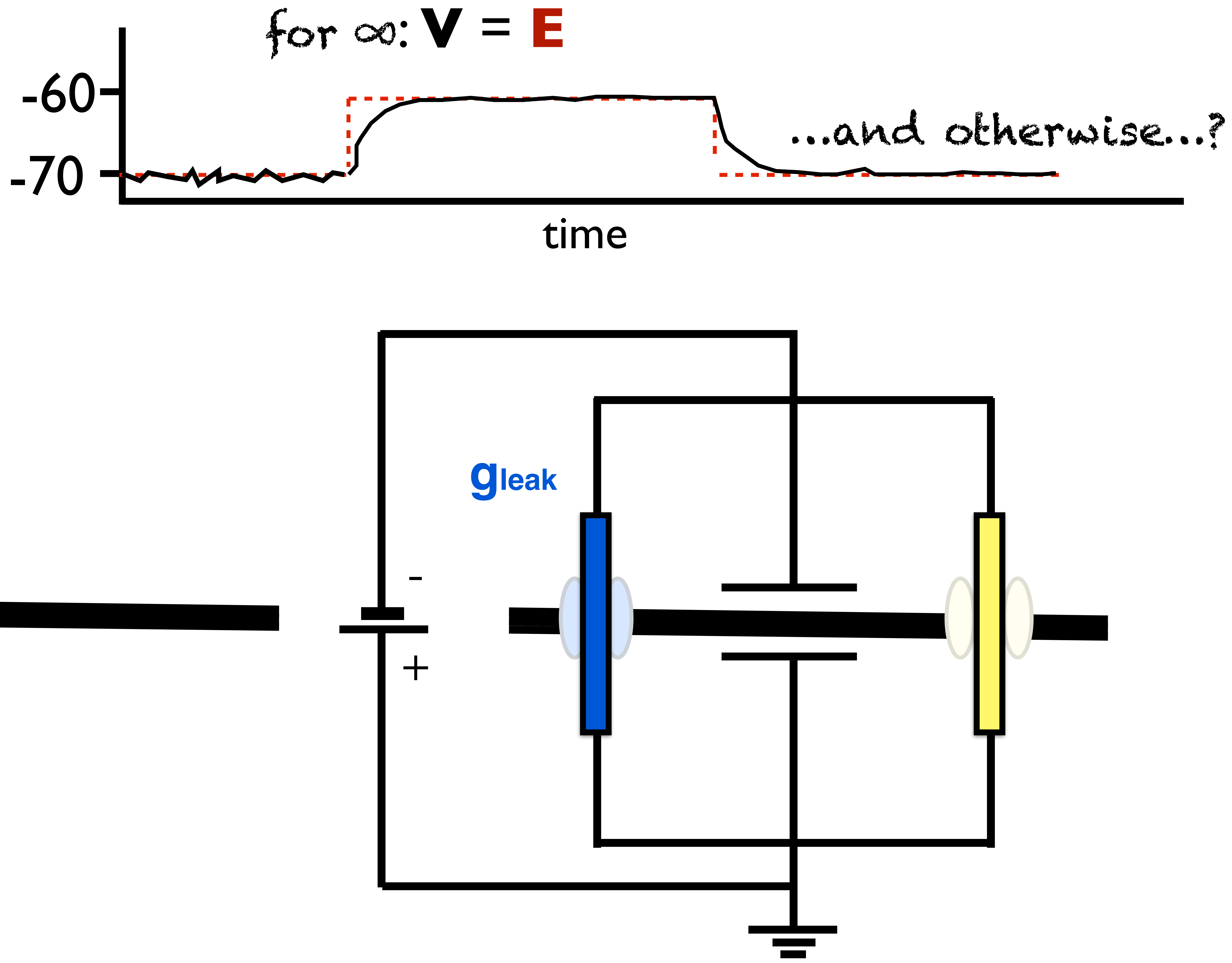

-
+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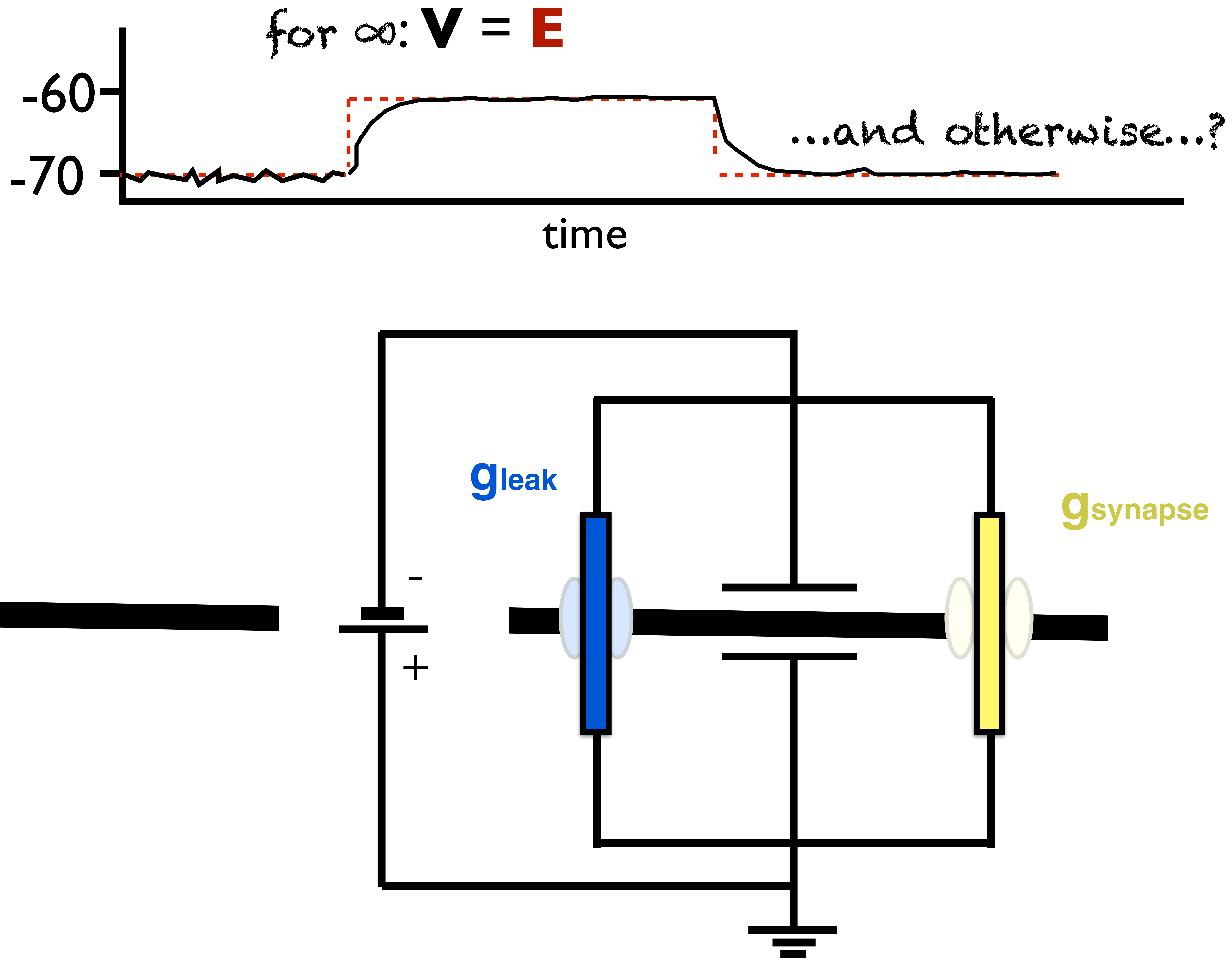
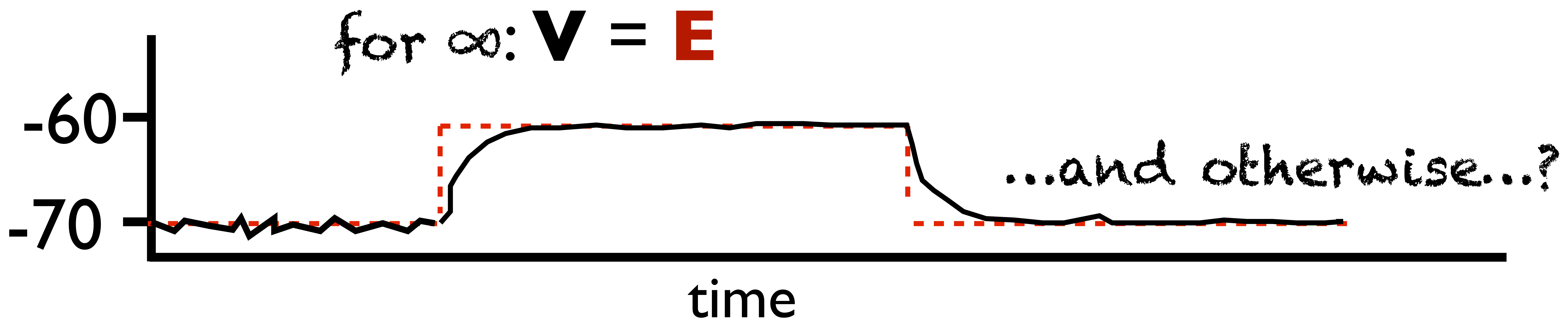
time
...and otherwise...?
gleak
-
+



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



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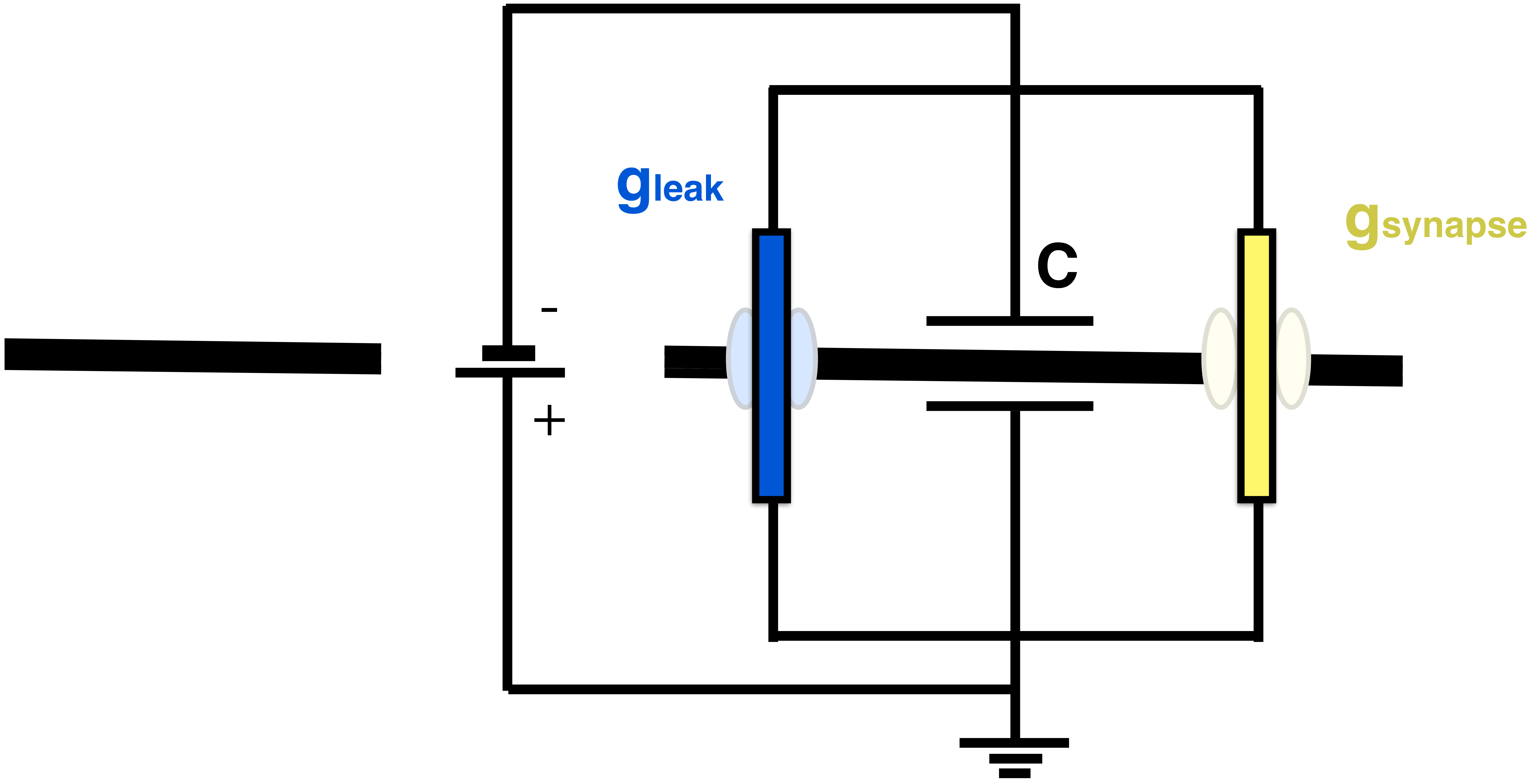
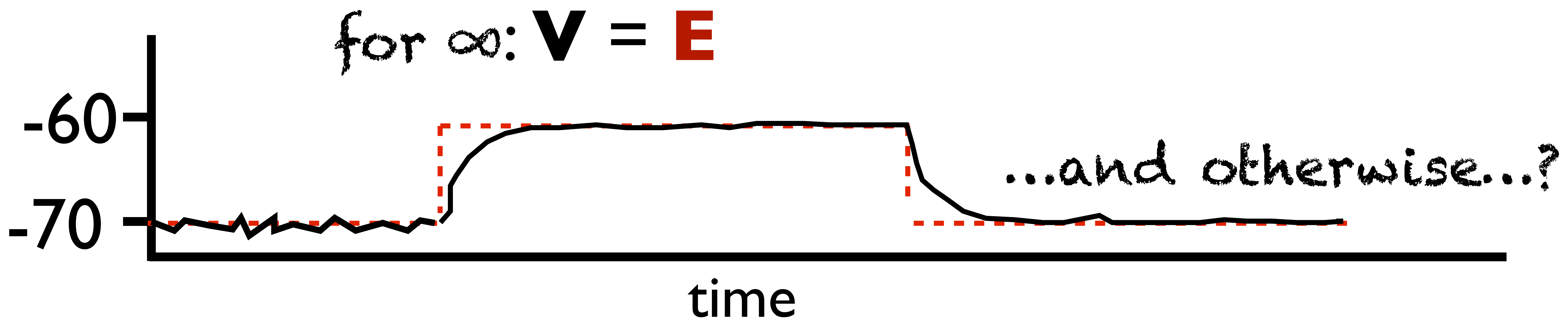


gleak
C
gsynapse
-
+


for ∞: V = E
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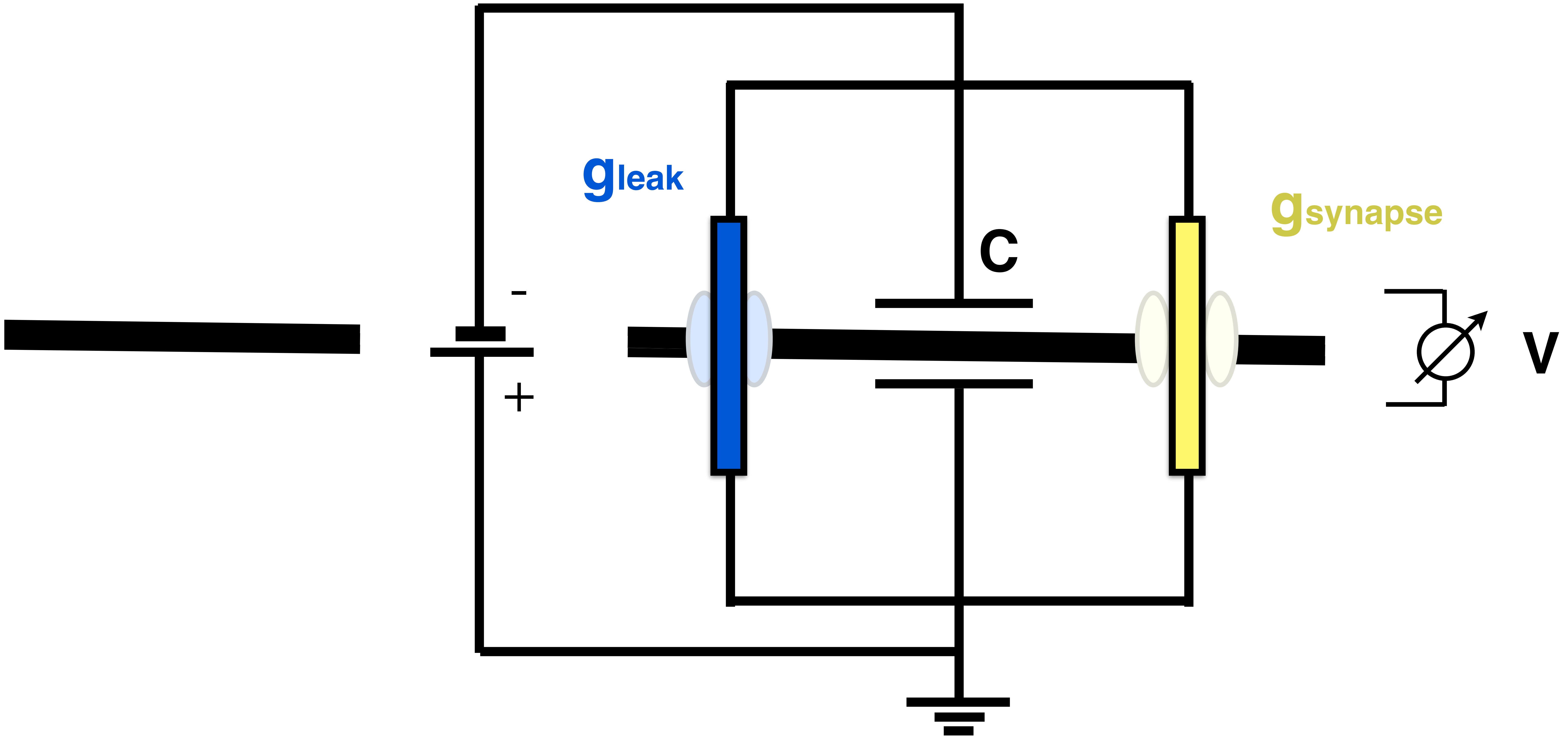
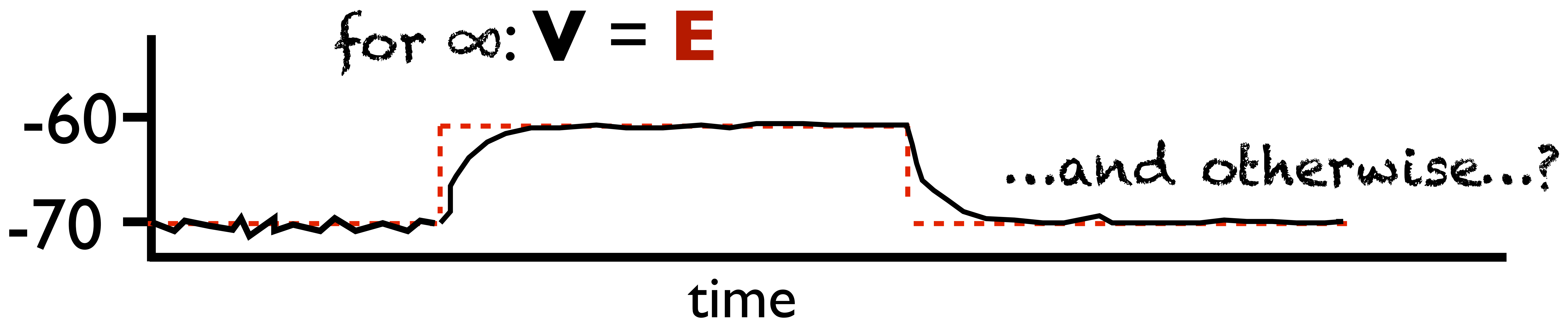

gleak
C
gsynapse
-
+
V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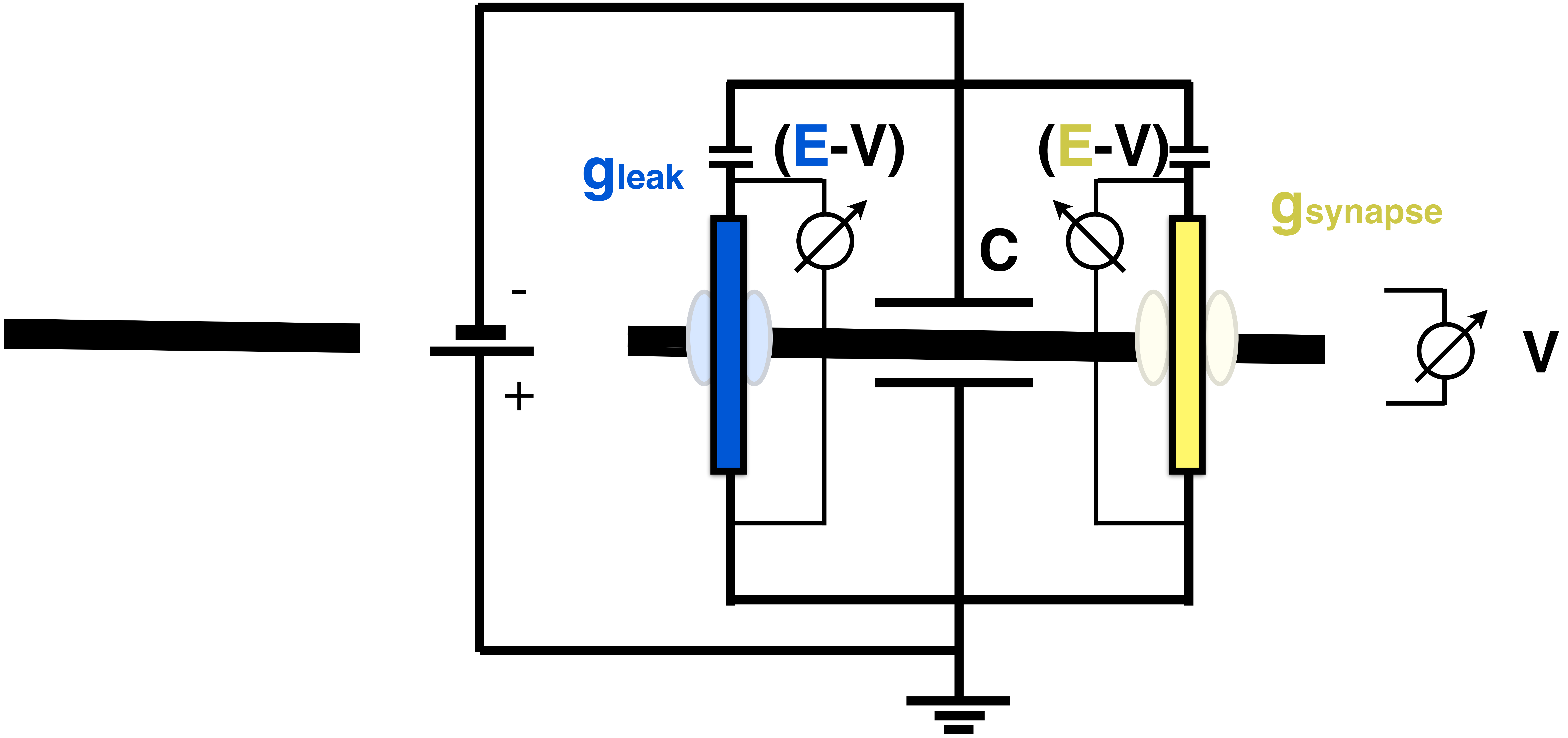
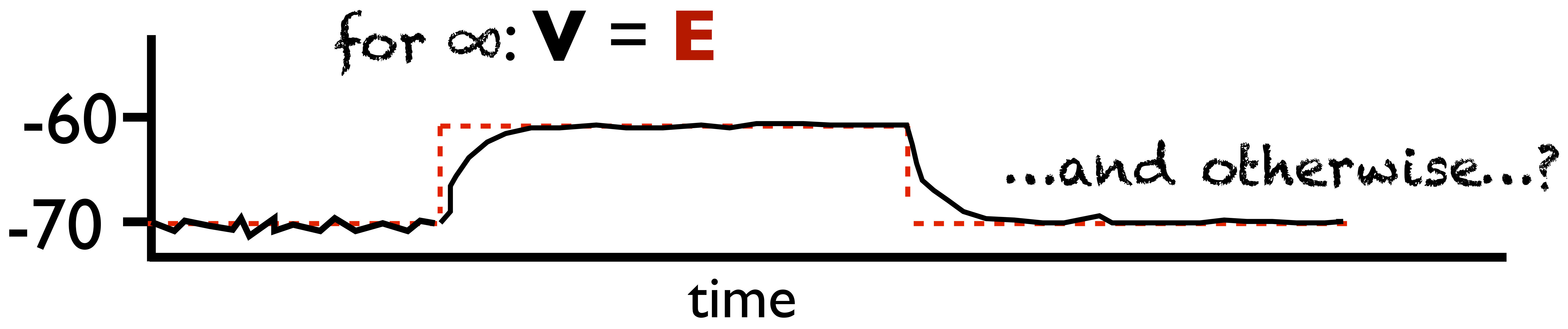

gleak
(E-V)
(E-V)
gsynapse
C
-
+
V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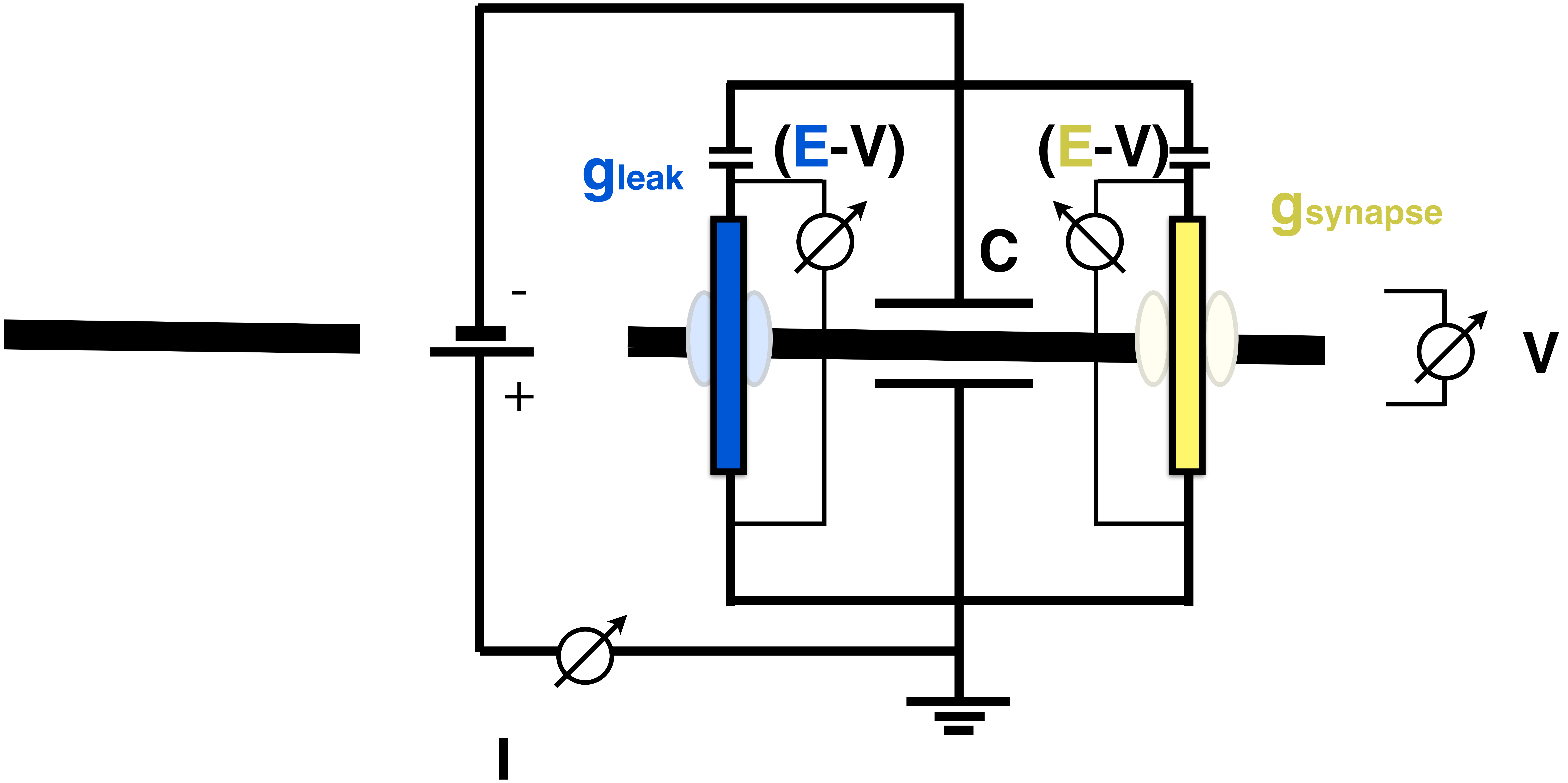
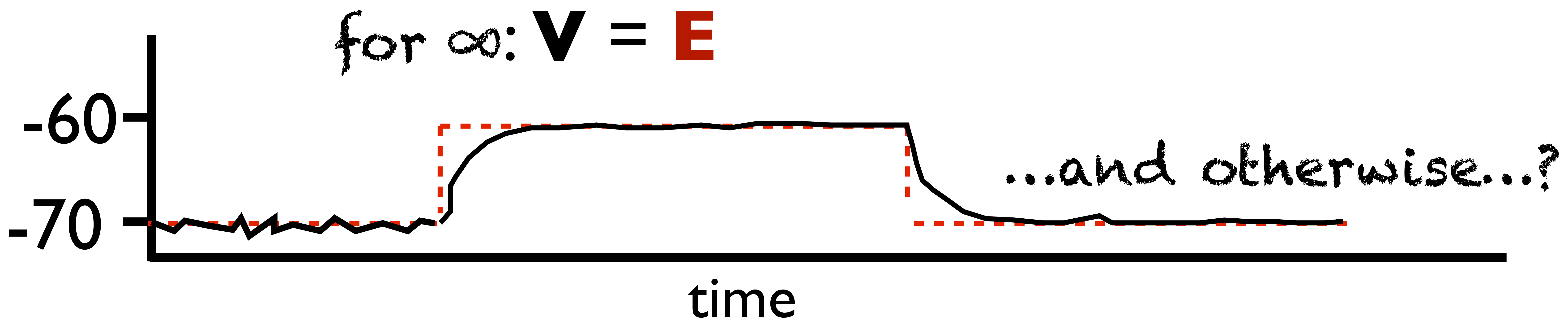
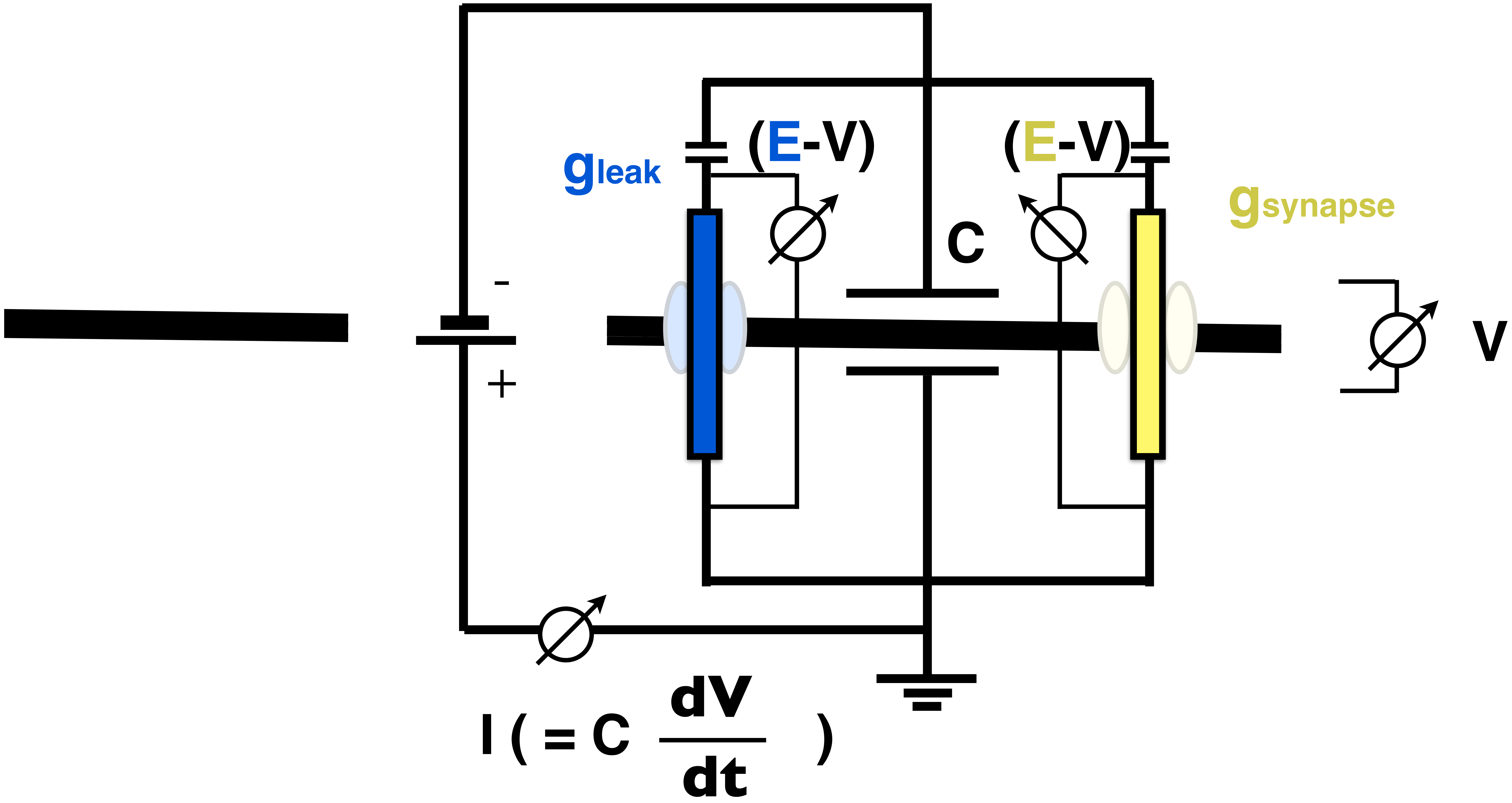

gleak
(E-V)
(E-V)
gsynapse
C
-
+
V
I

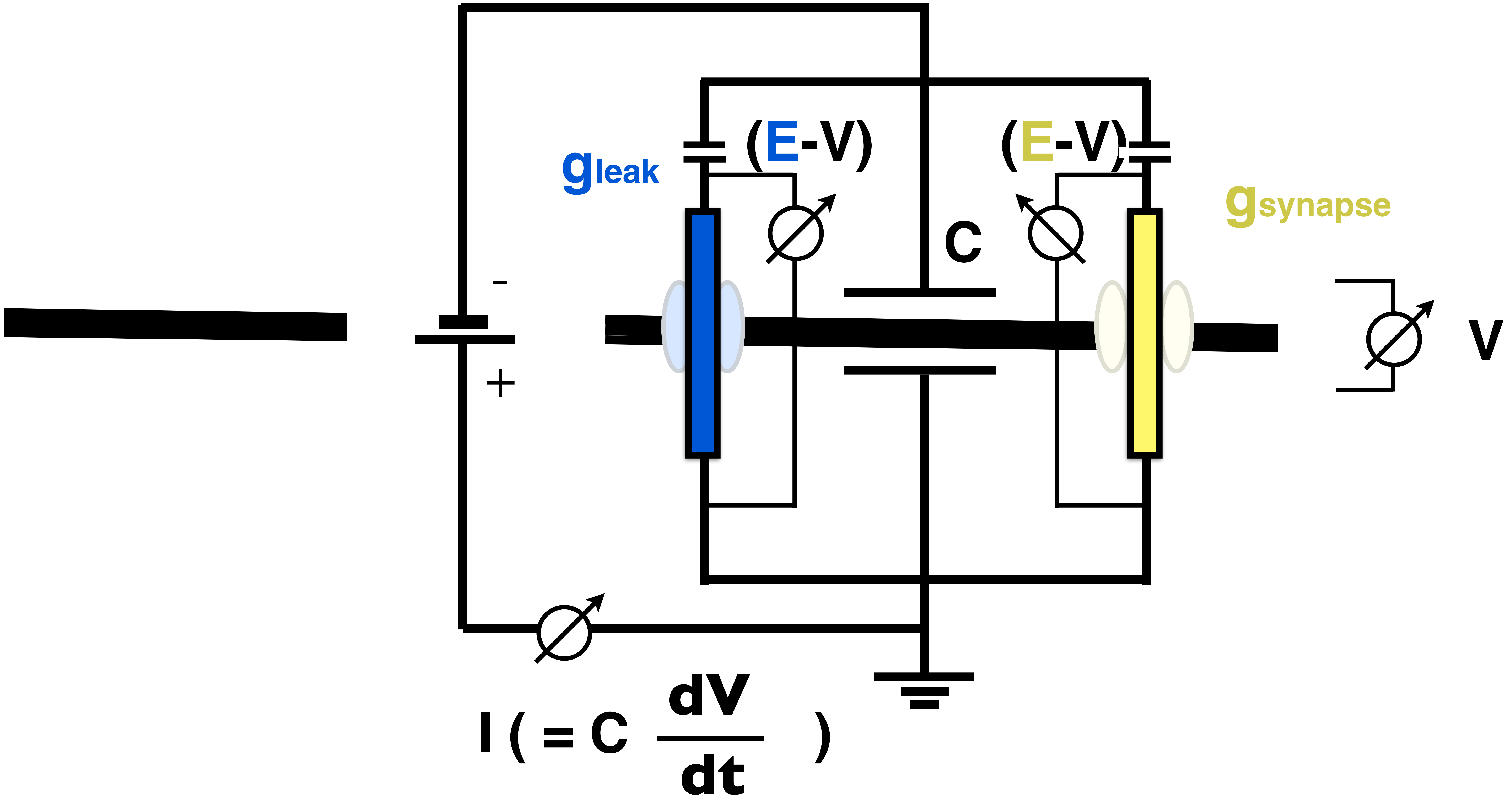


for ∞: V = E
-60
-70
...and otherwise...?
time



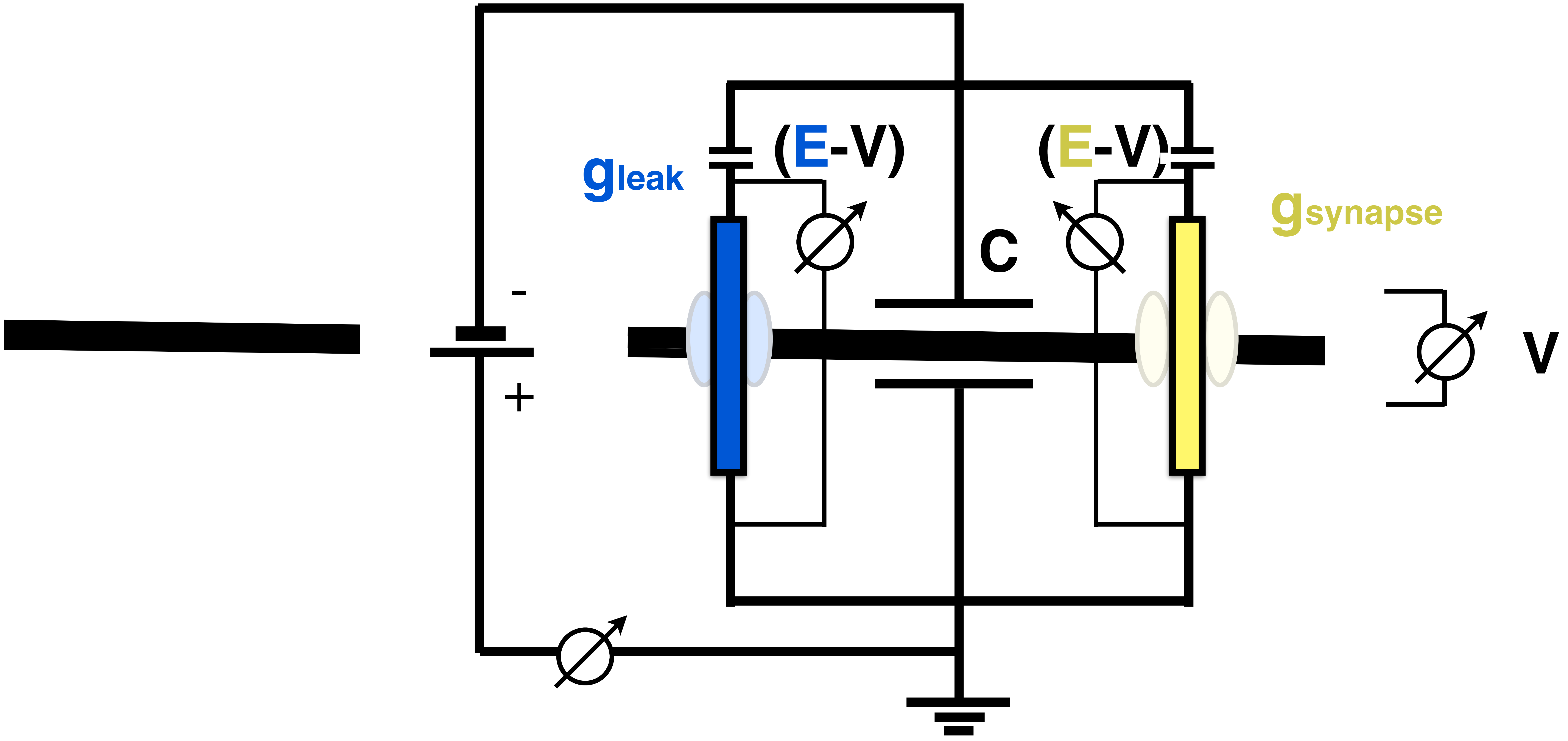
gleak
(E-V)
(E-V)
gsynapse
C
-
+
V
I (= C dV/dt)

...and otherwise...?



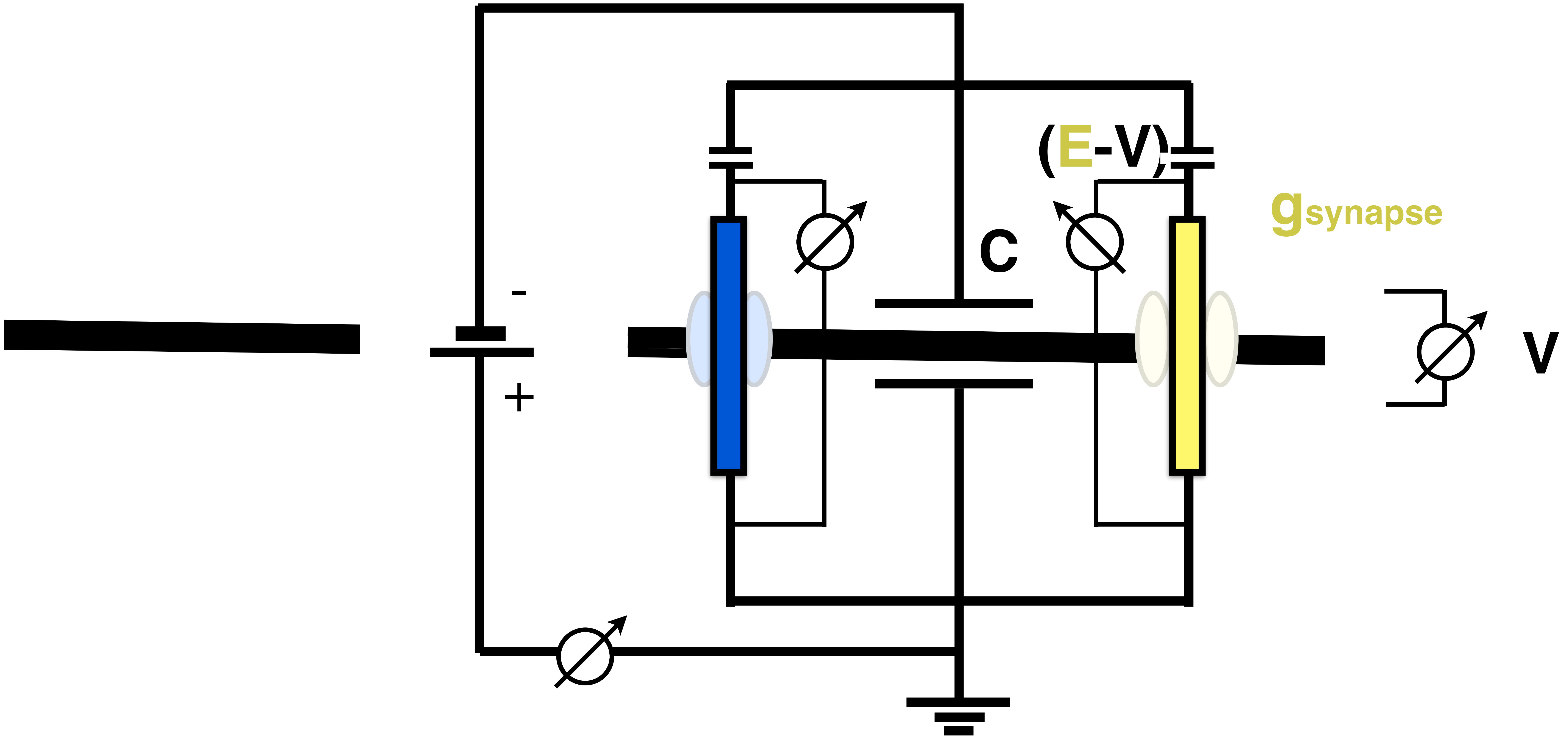
$$\frac{dV}{dt} =$$

...and otherwise...?



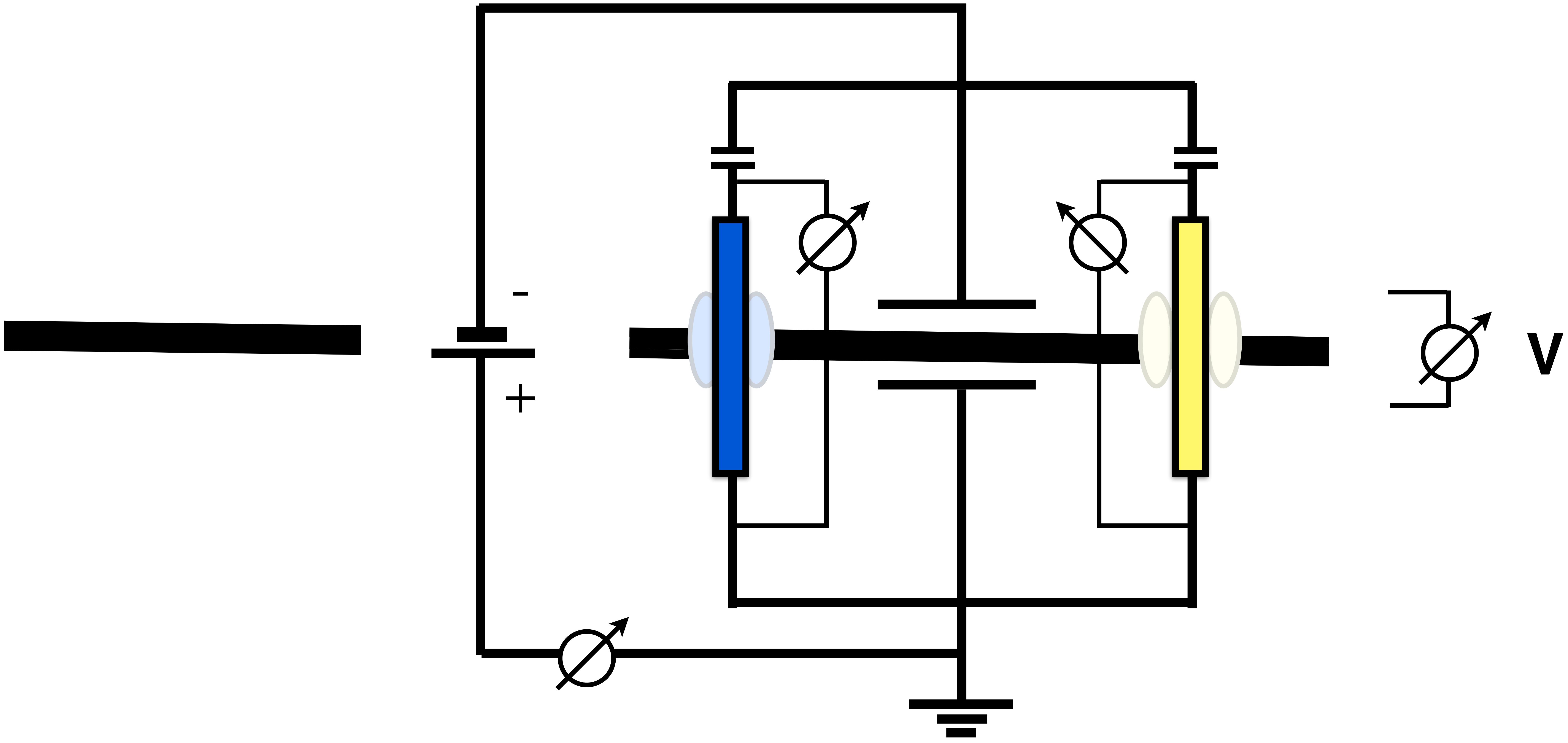
$$\frac{dV}{dt} = g_{leak}\,(E\text{-}V)$$

...and otherwise...?



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

...and otherwise...?



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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

$$\frac{C}{g_{total}} = \tau_{eff}$$

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

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

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$$\frac{C}{g_{total}} = \tau_{eff}$$

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

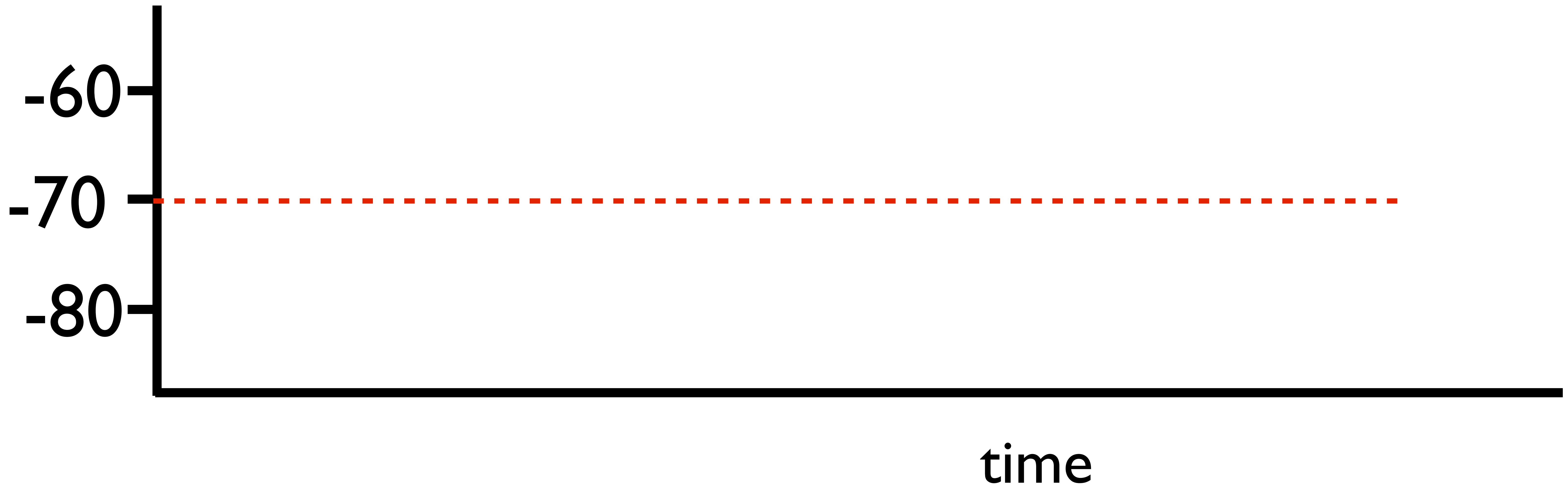
$$V(t) = E + \left(V(0) - E\right) e^{-\frac{t}{\tau}}$$

A General Solution:

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

A General Solution:

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



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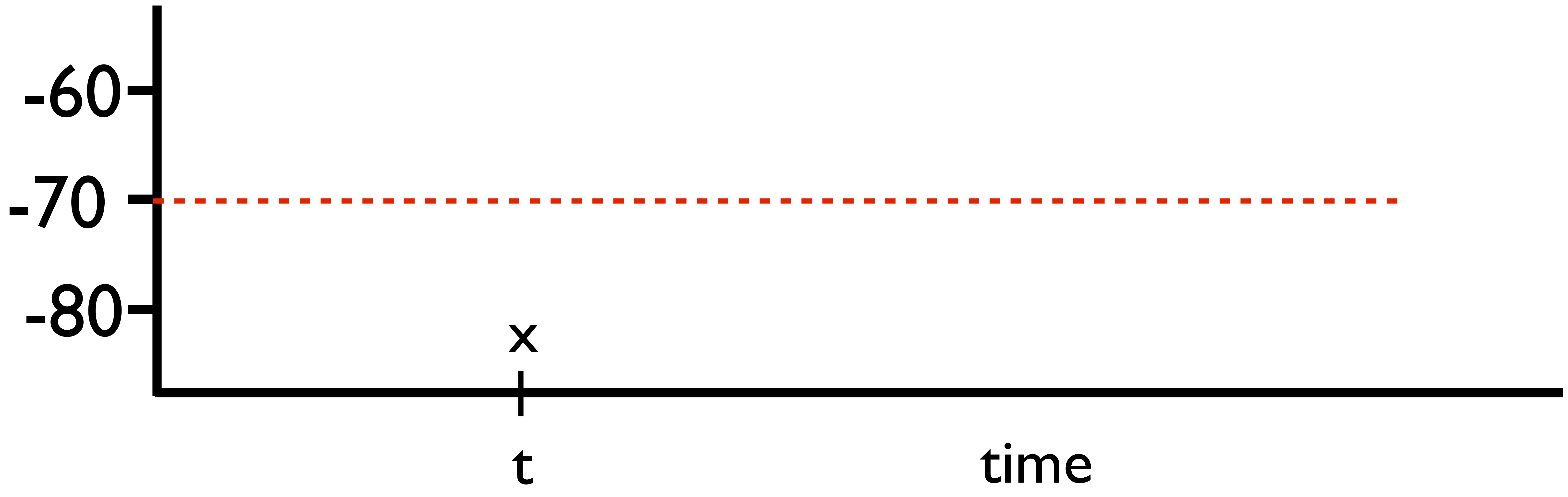

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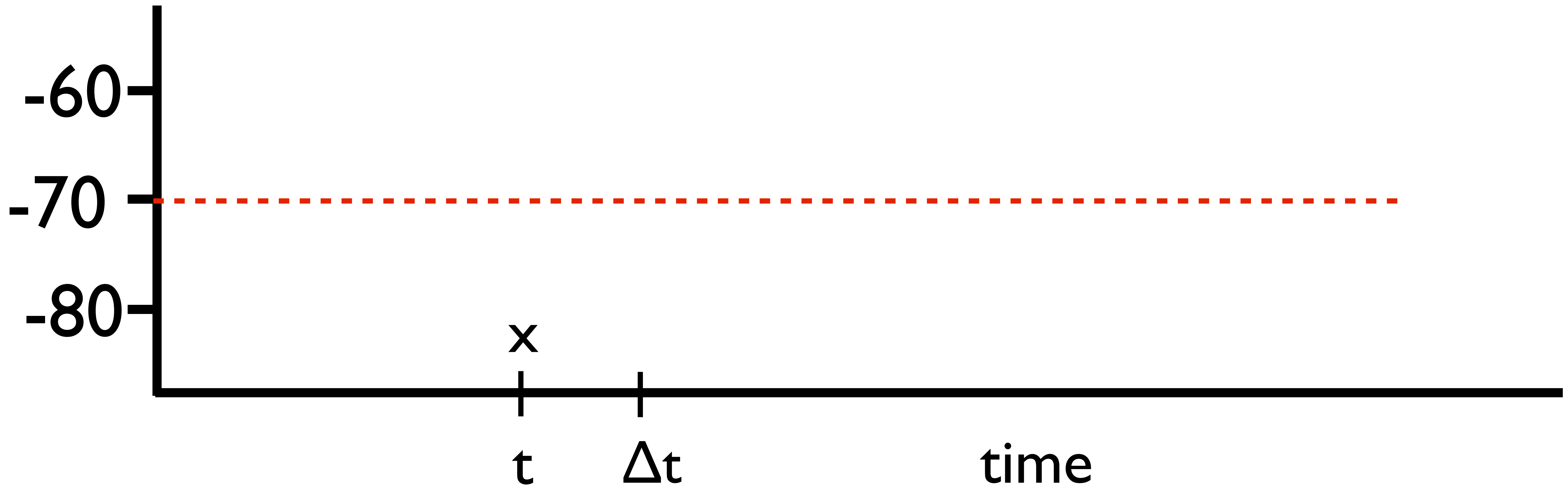

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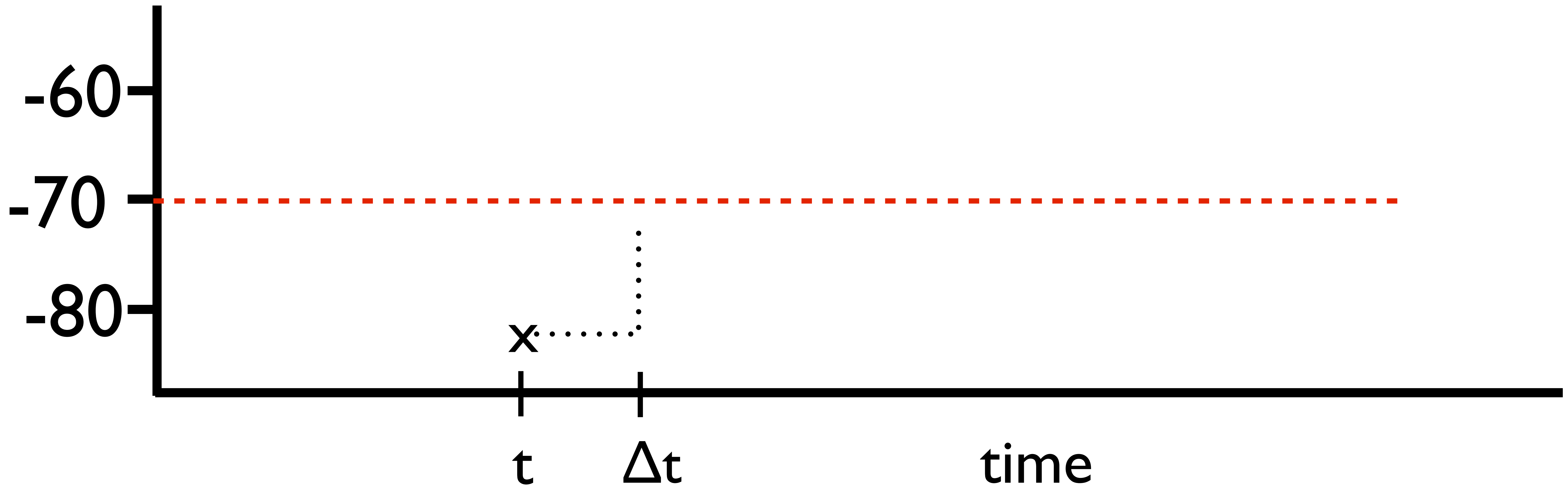

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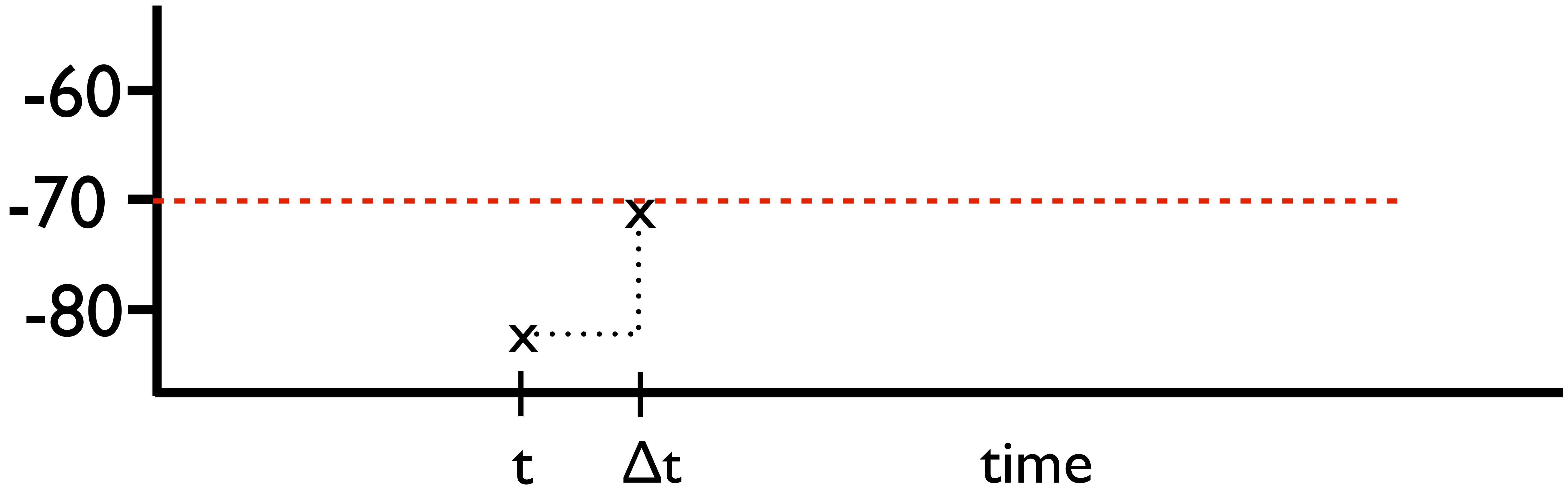

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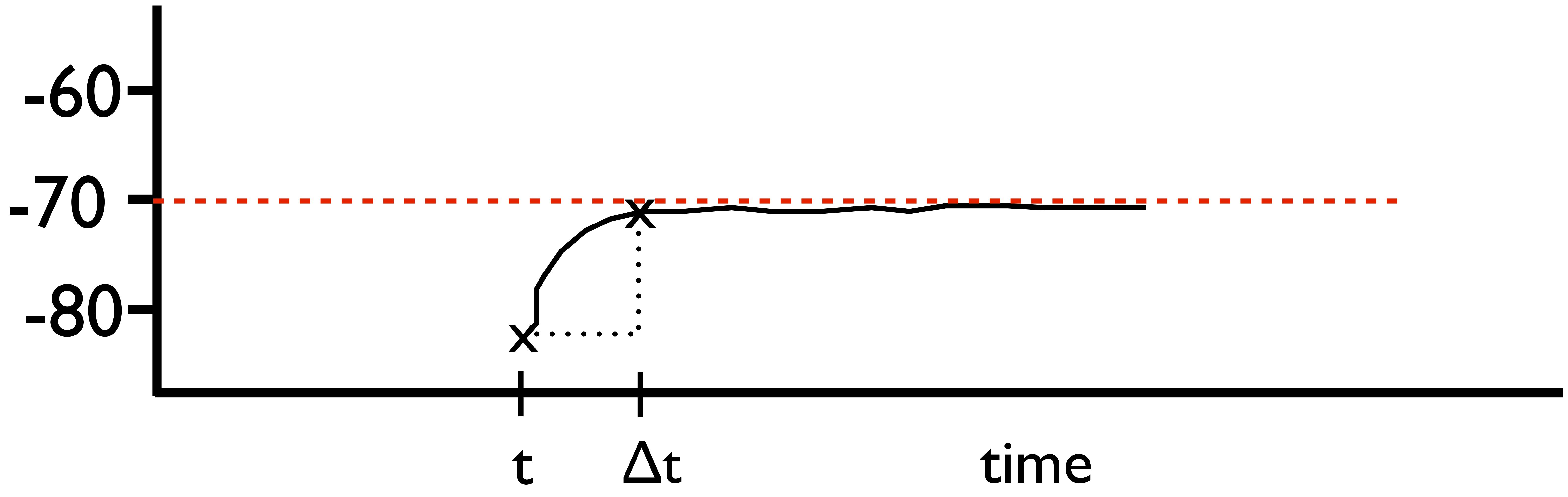
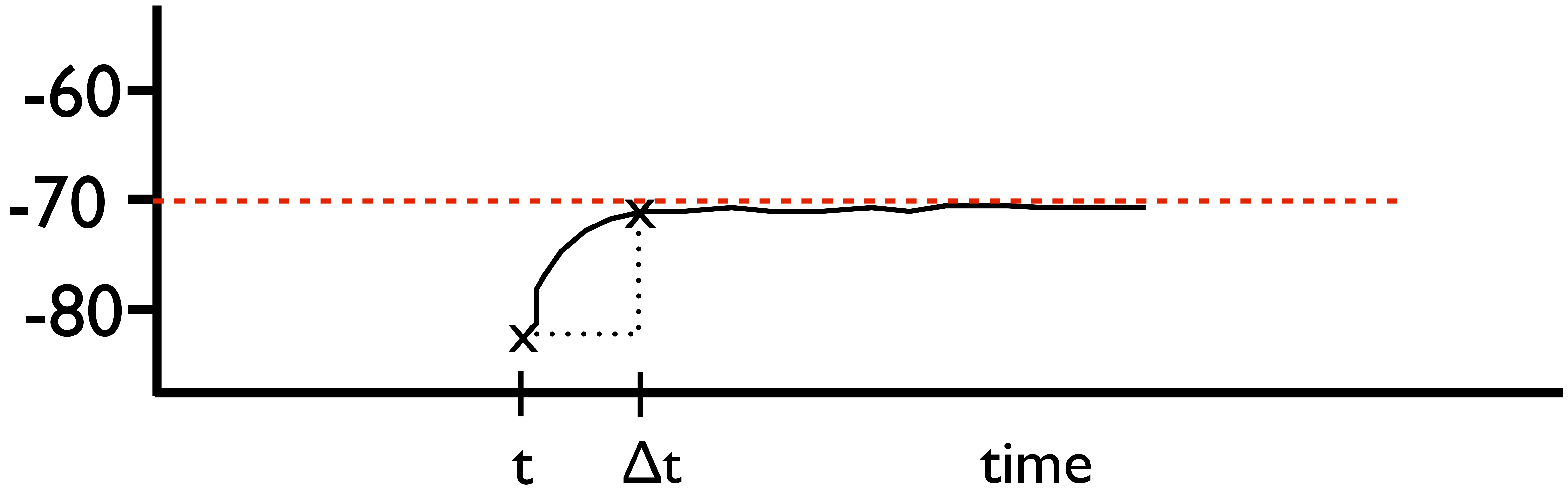


A General Solution:

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

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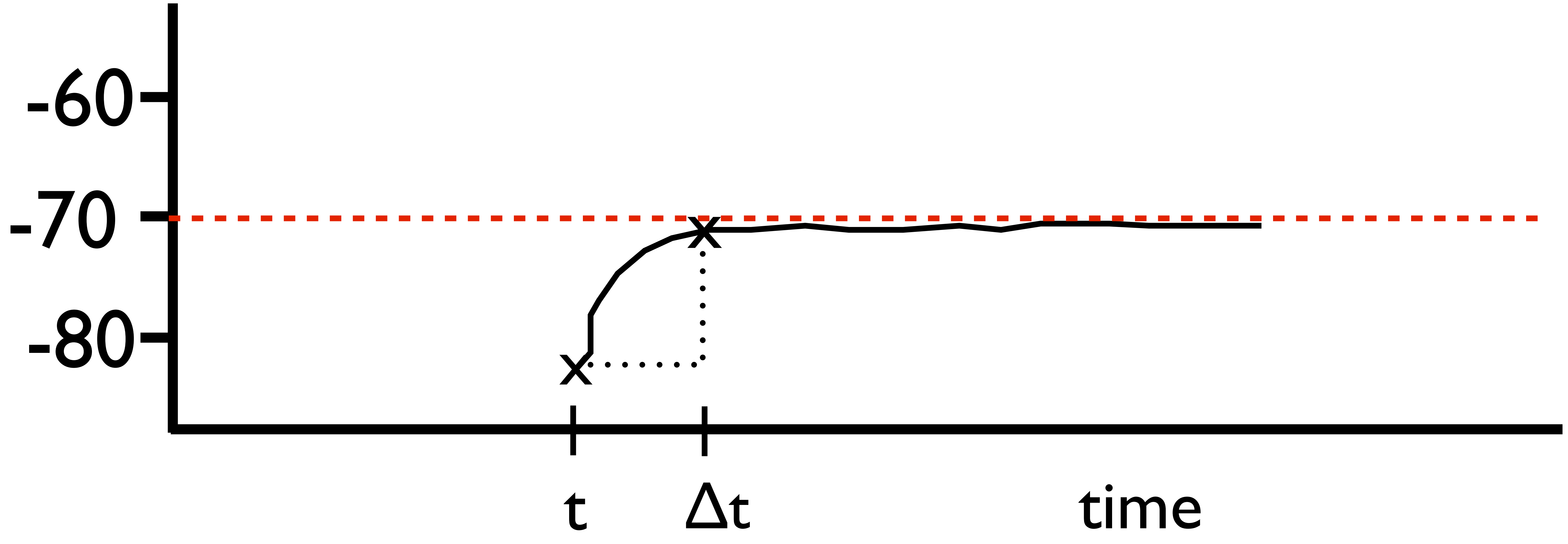

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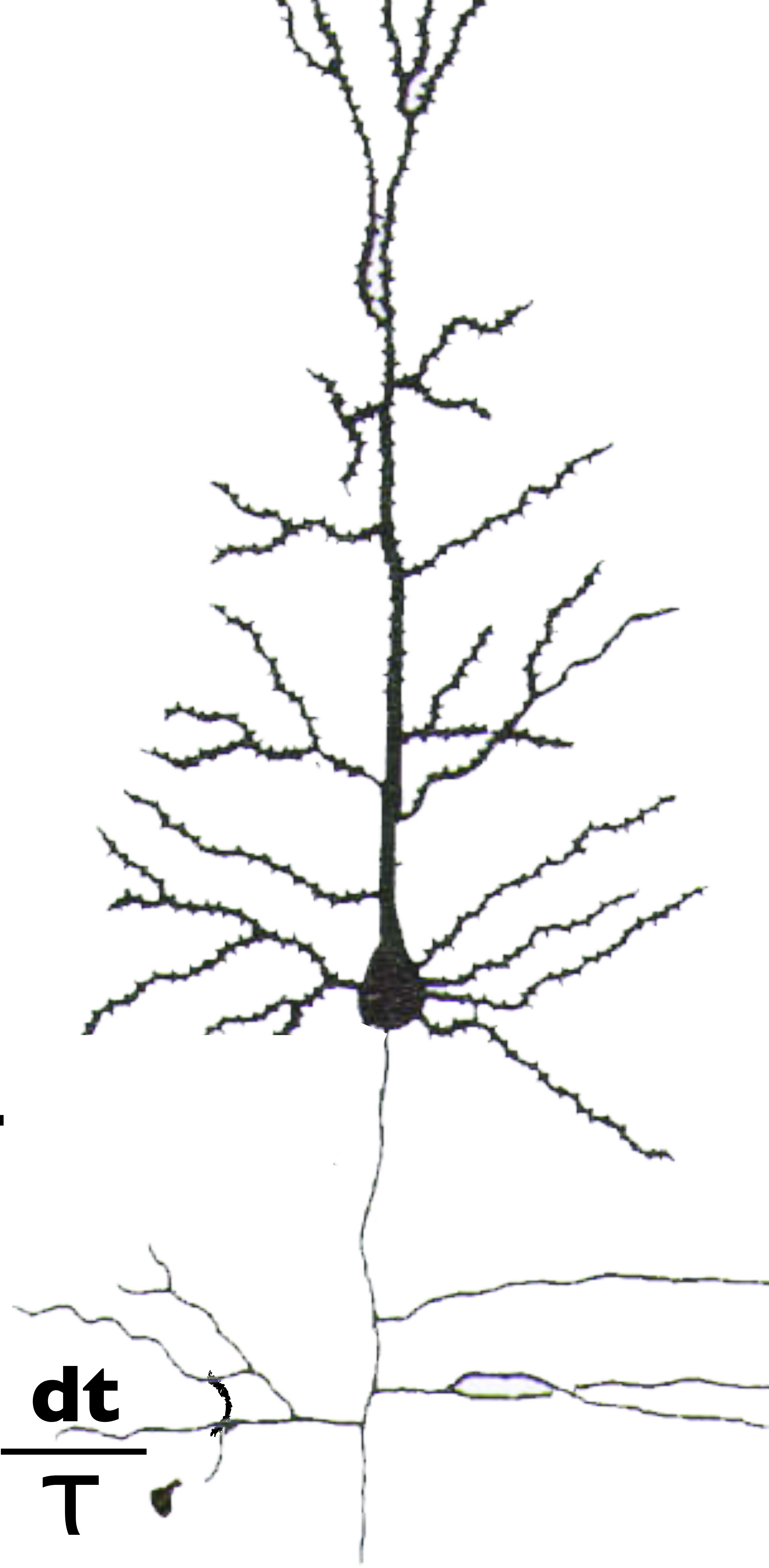

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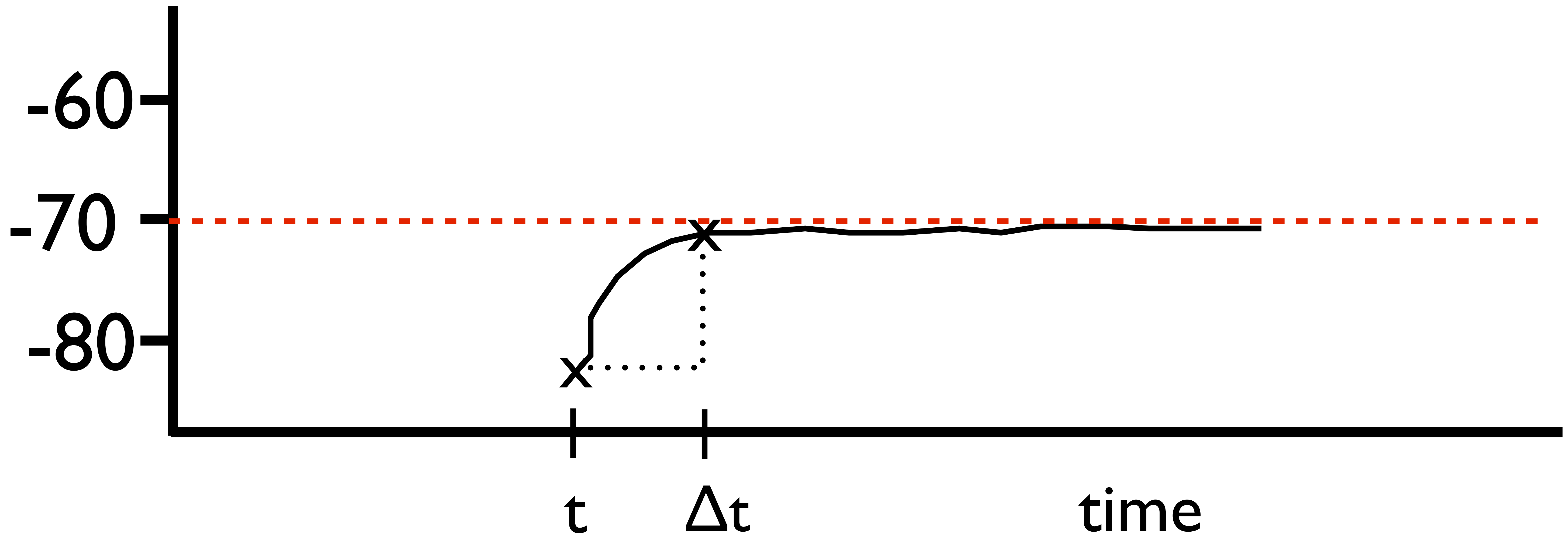

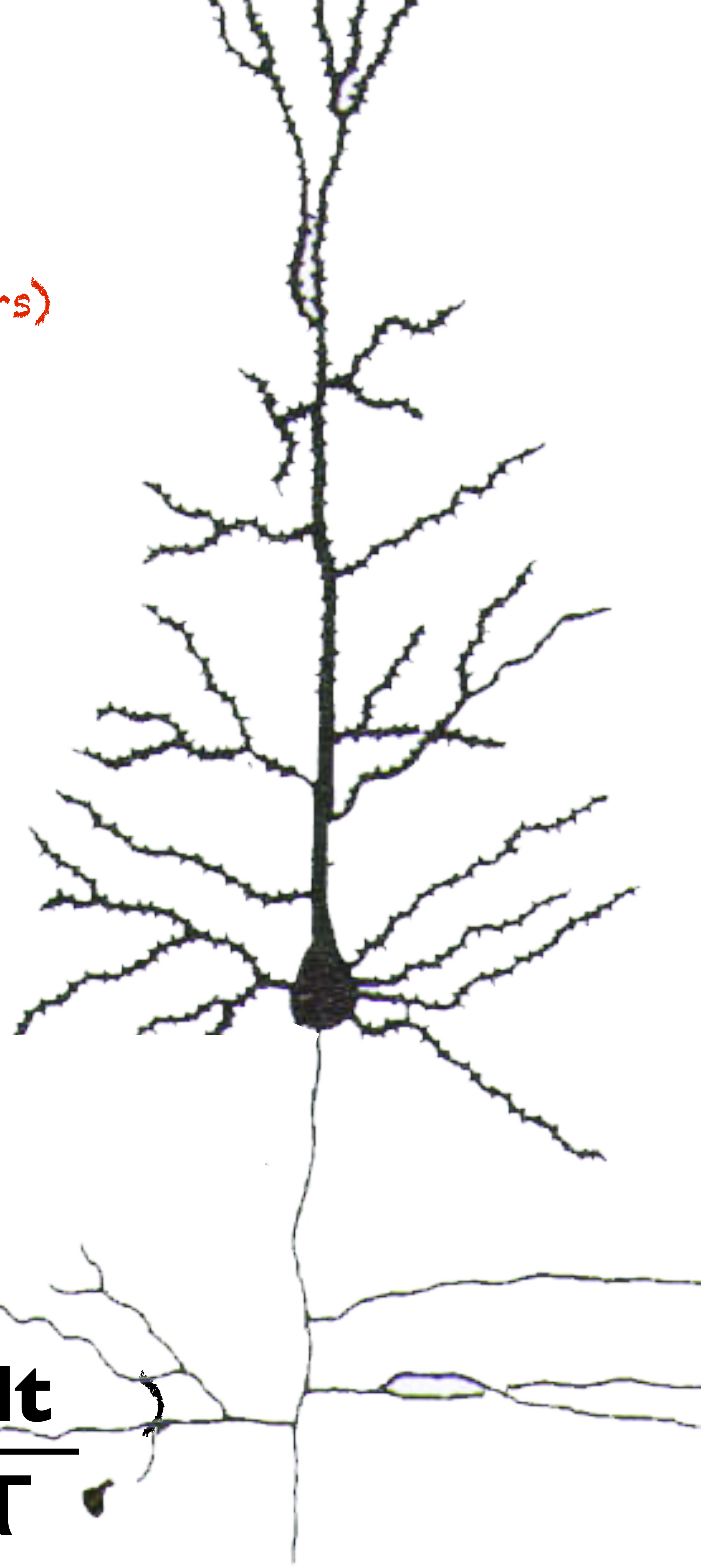

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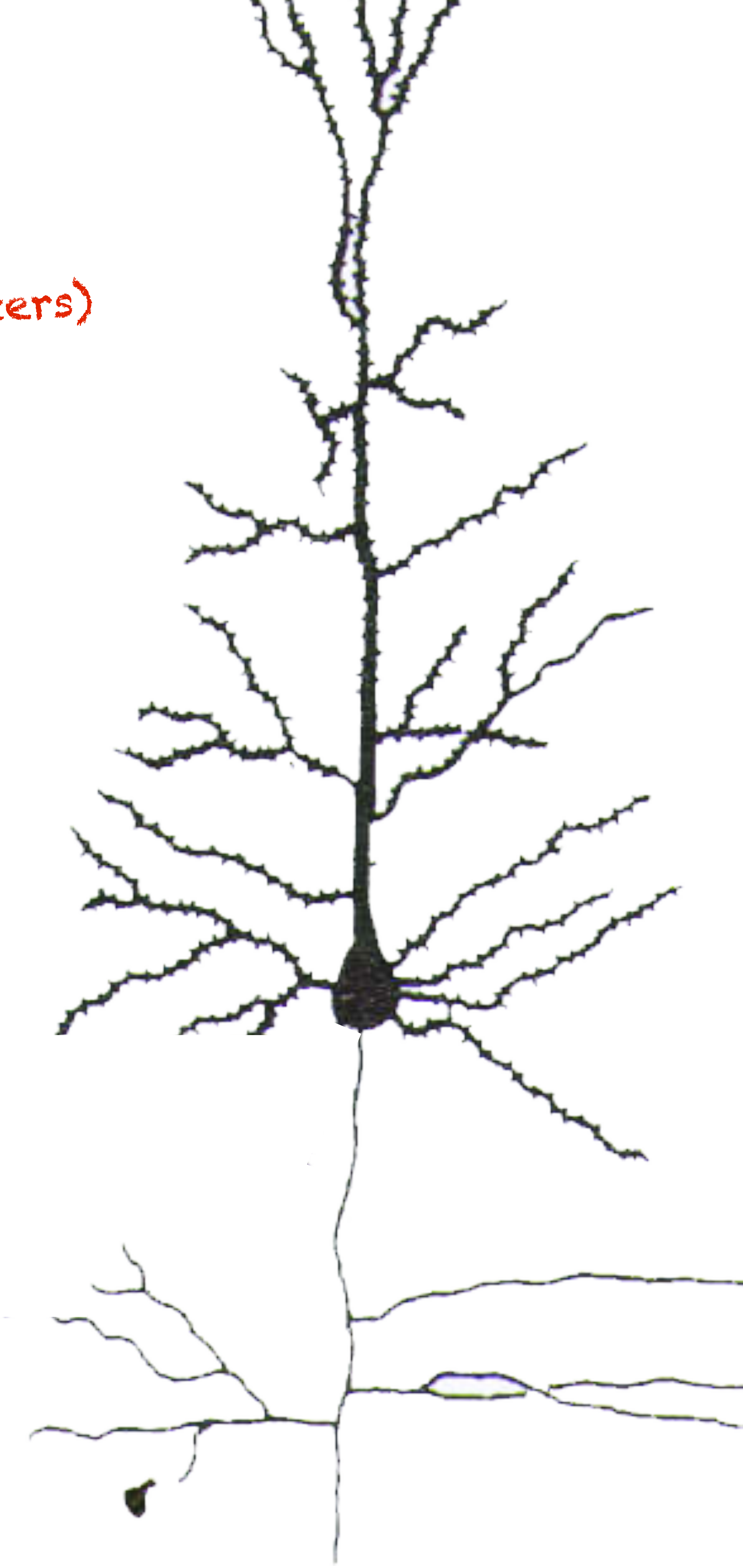

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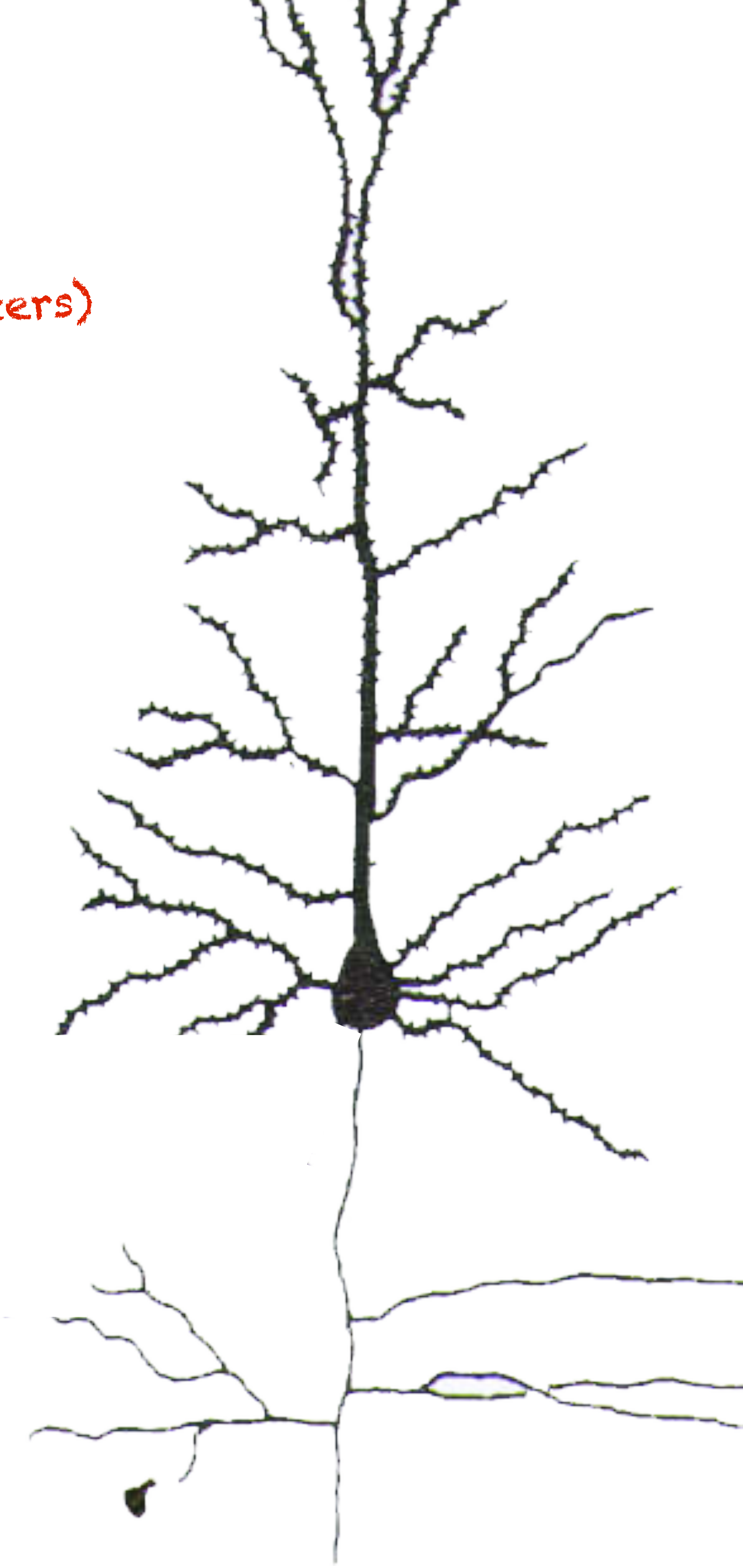
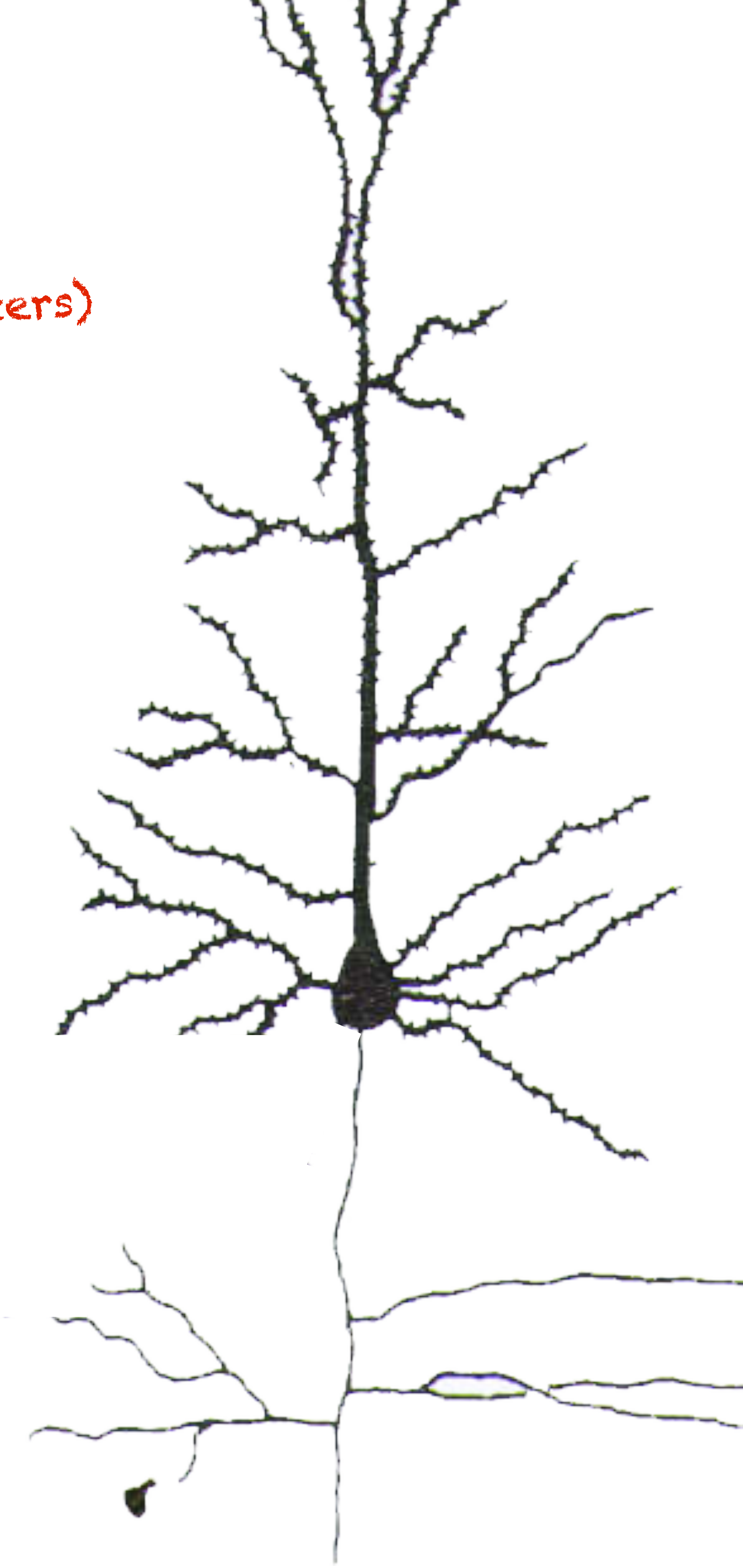


A General Solution:

(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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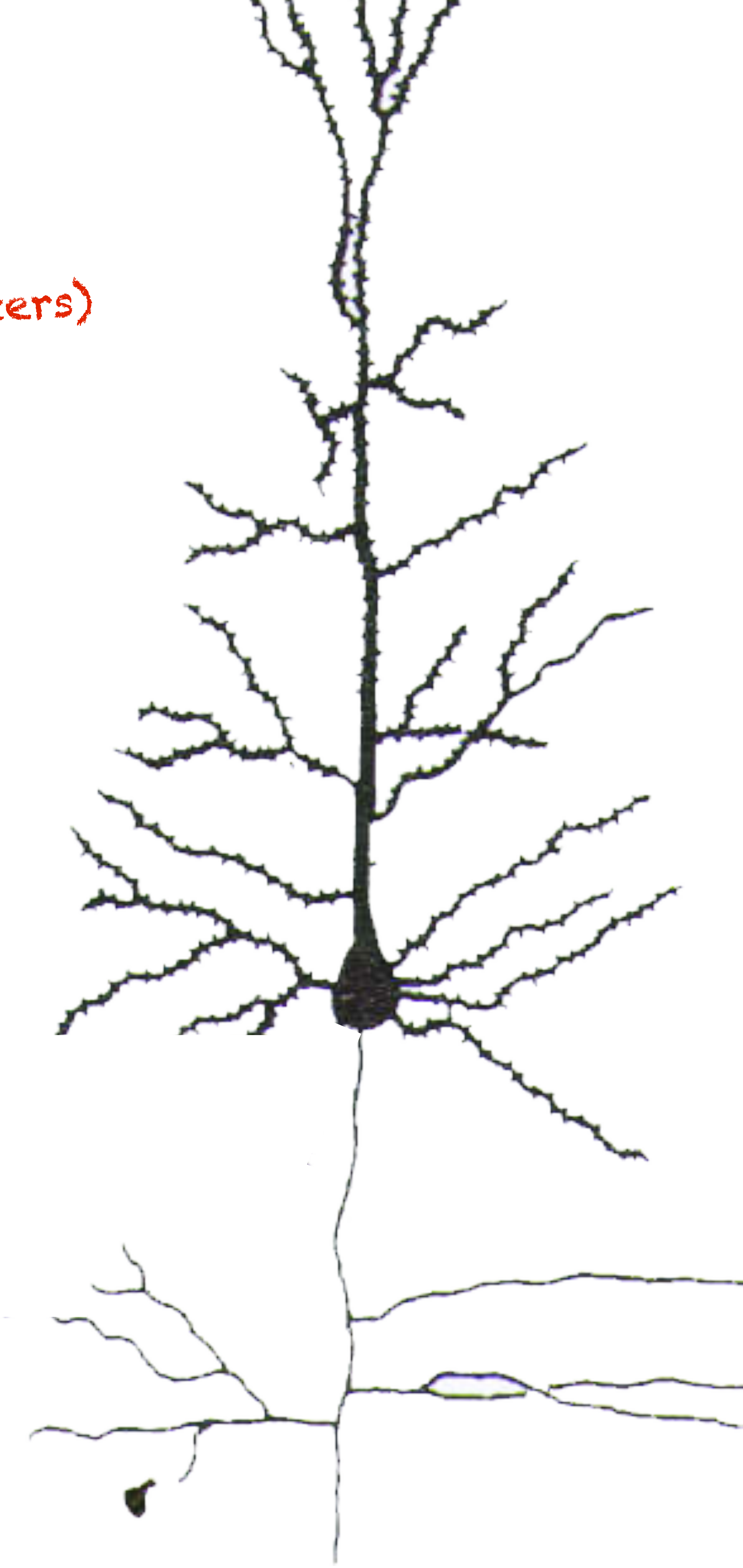

This is called a "conductance based model".

- 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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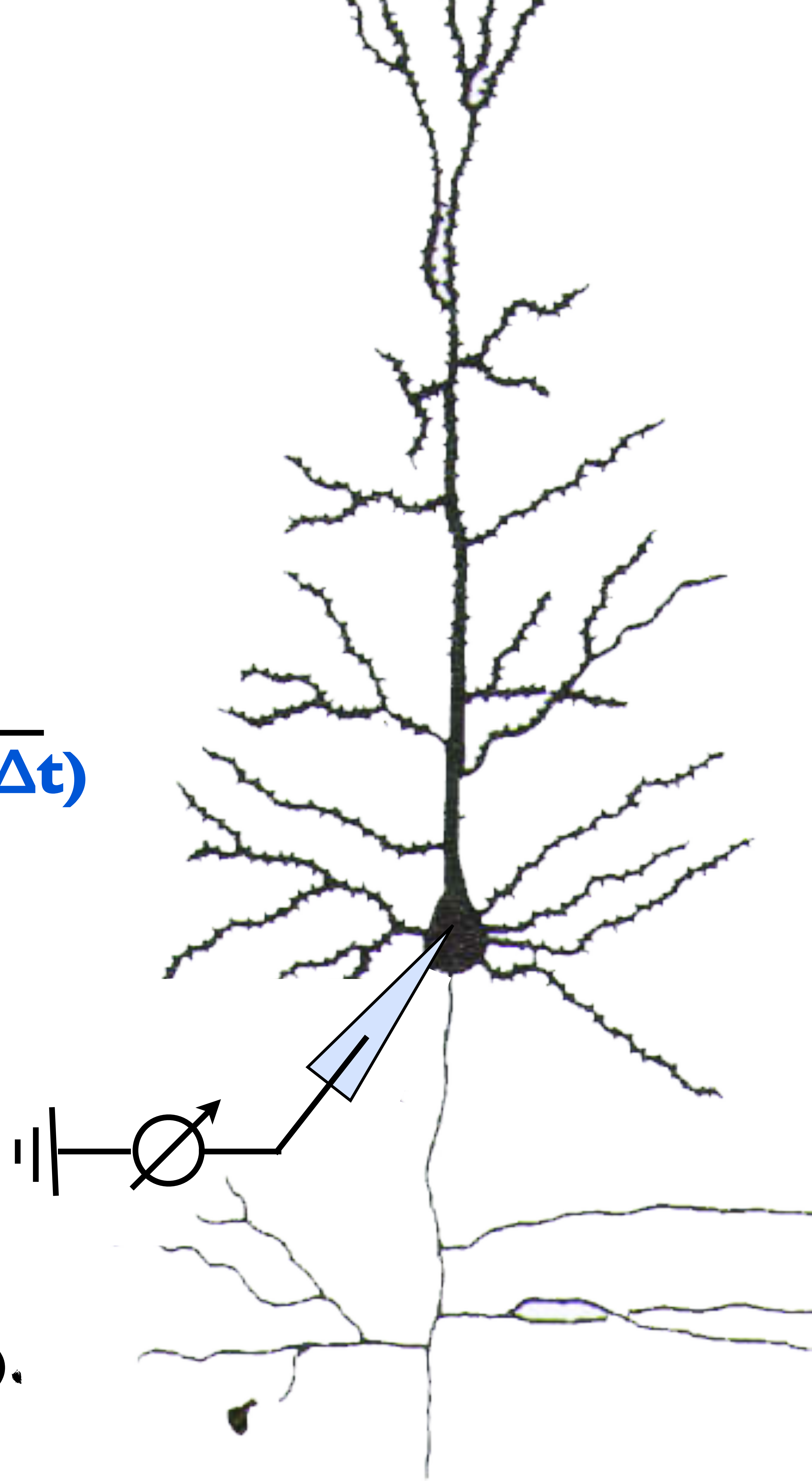
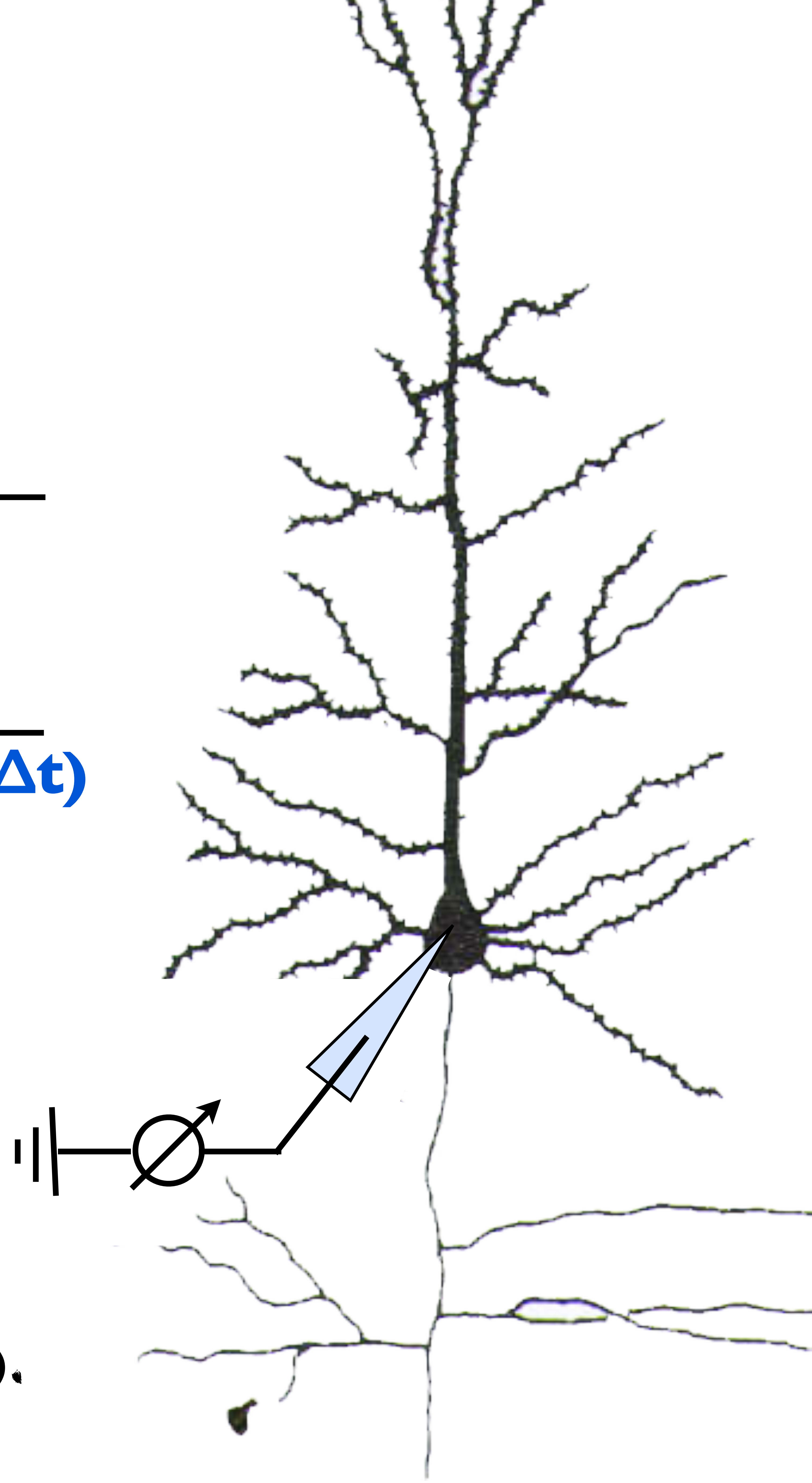


$$E(\Delta t) = \frac{g_{leak}\, E_{leak} + g_{syn}\, E_{syn}}{g_{tot}}$$

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



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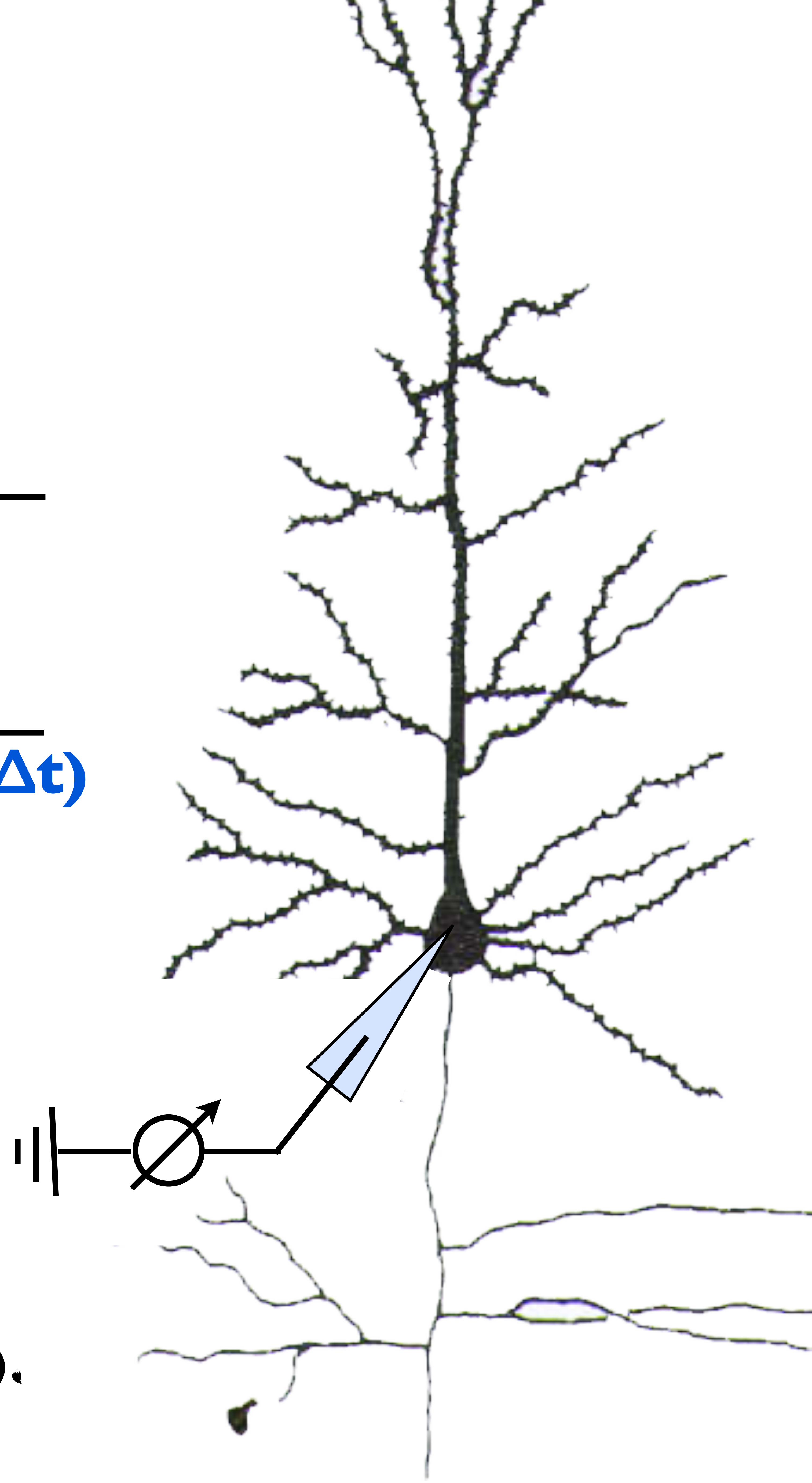
- Assumes stable **E** for the duration of Δt
- Uses computers to iteratively calculate $V(t+\Delta t)$.
- Δt must be very small (<0.1ms!)



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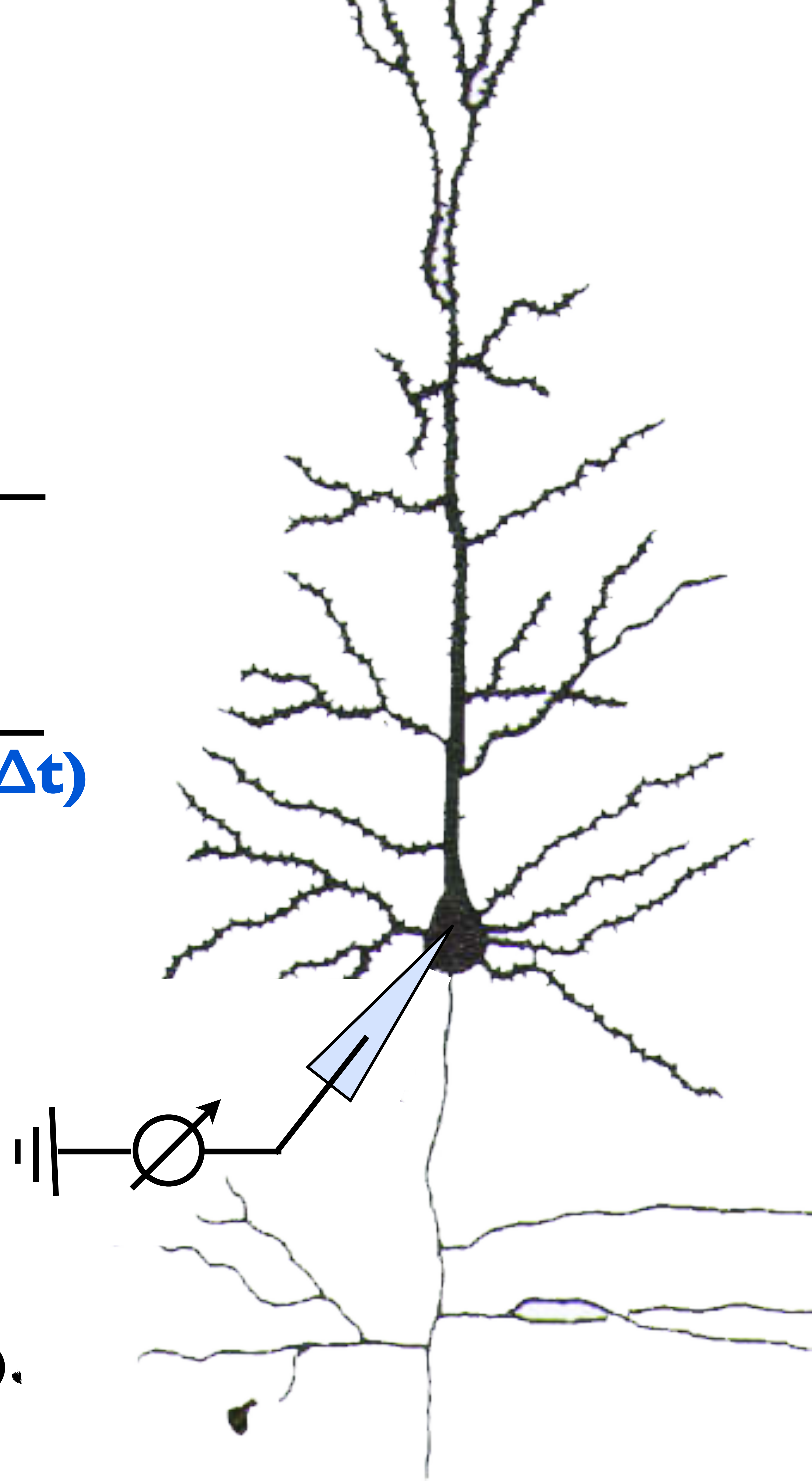

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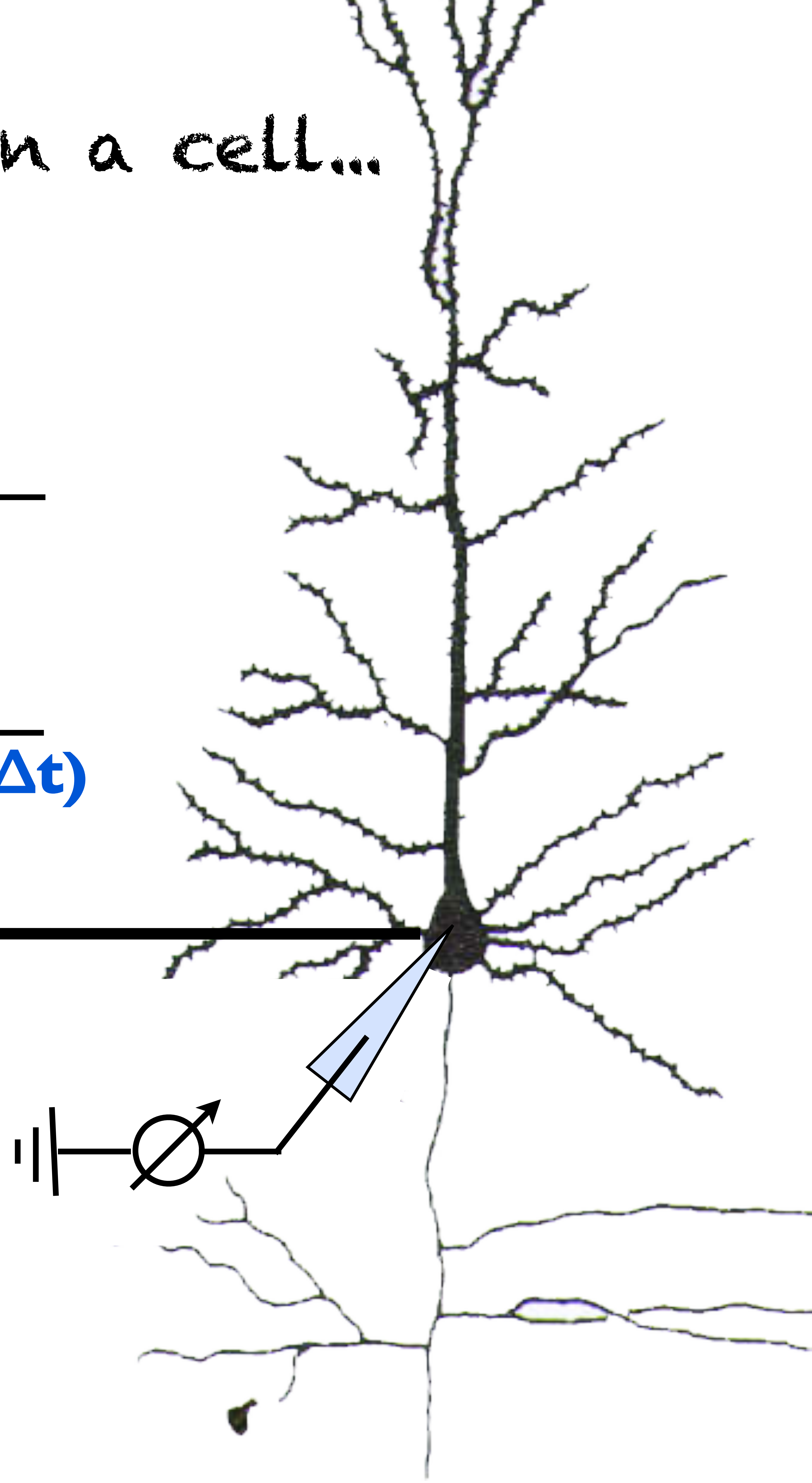

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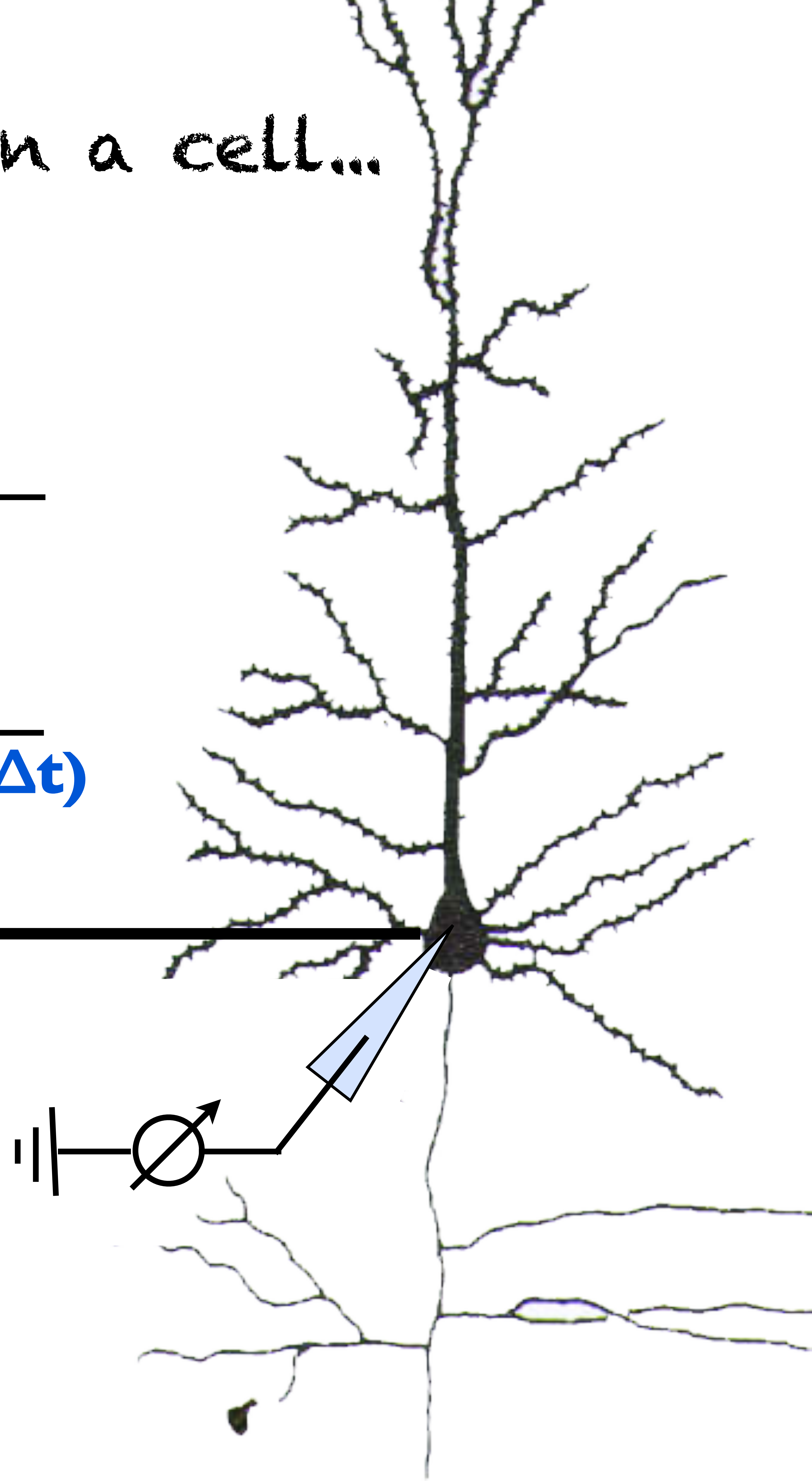
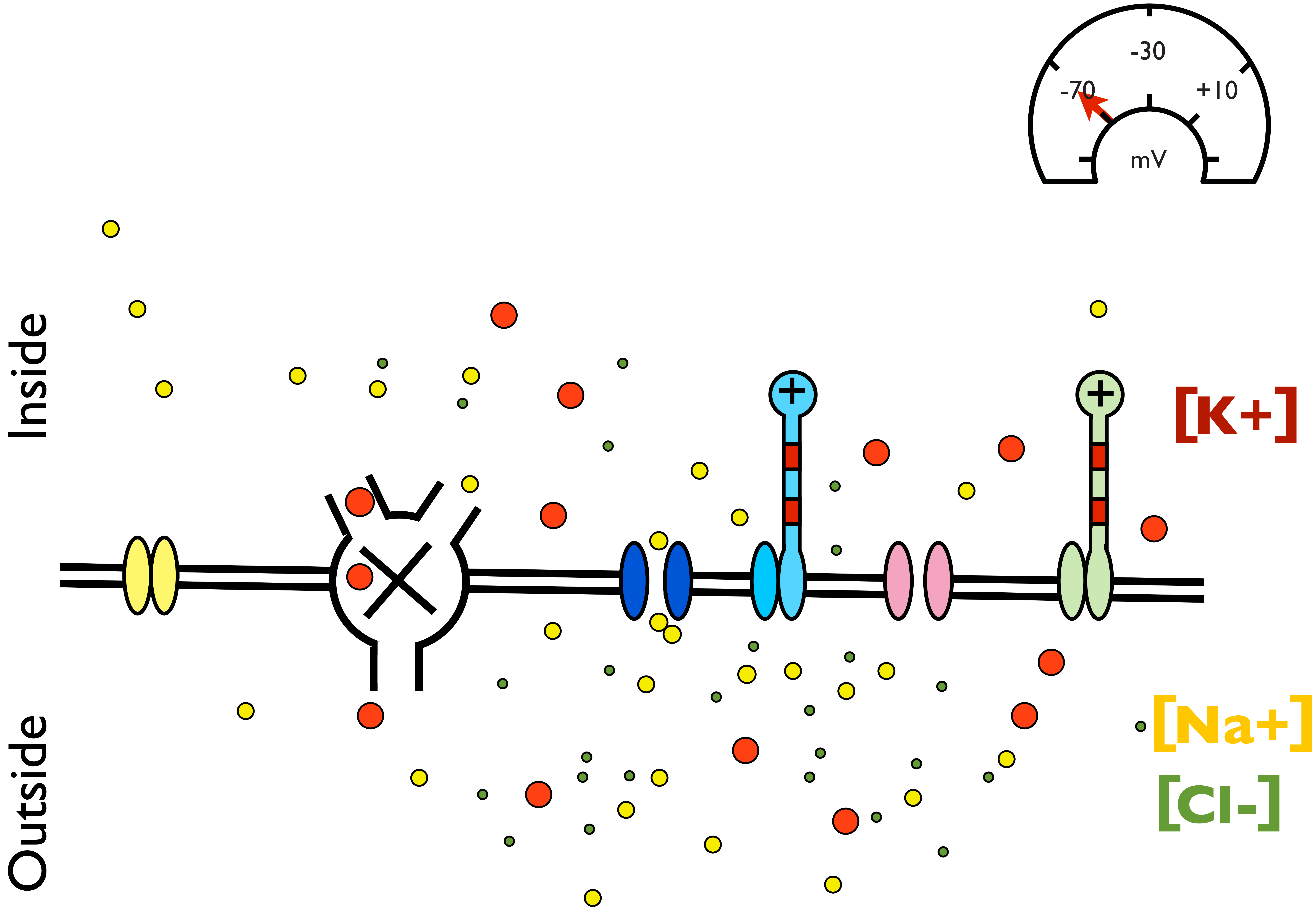
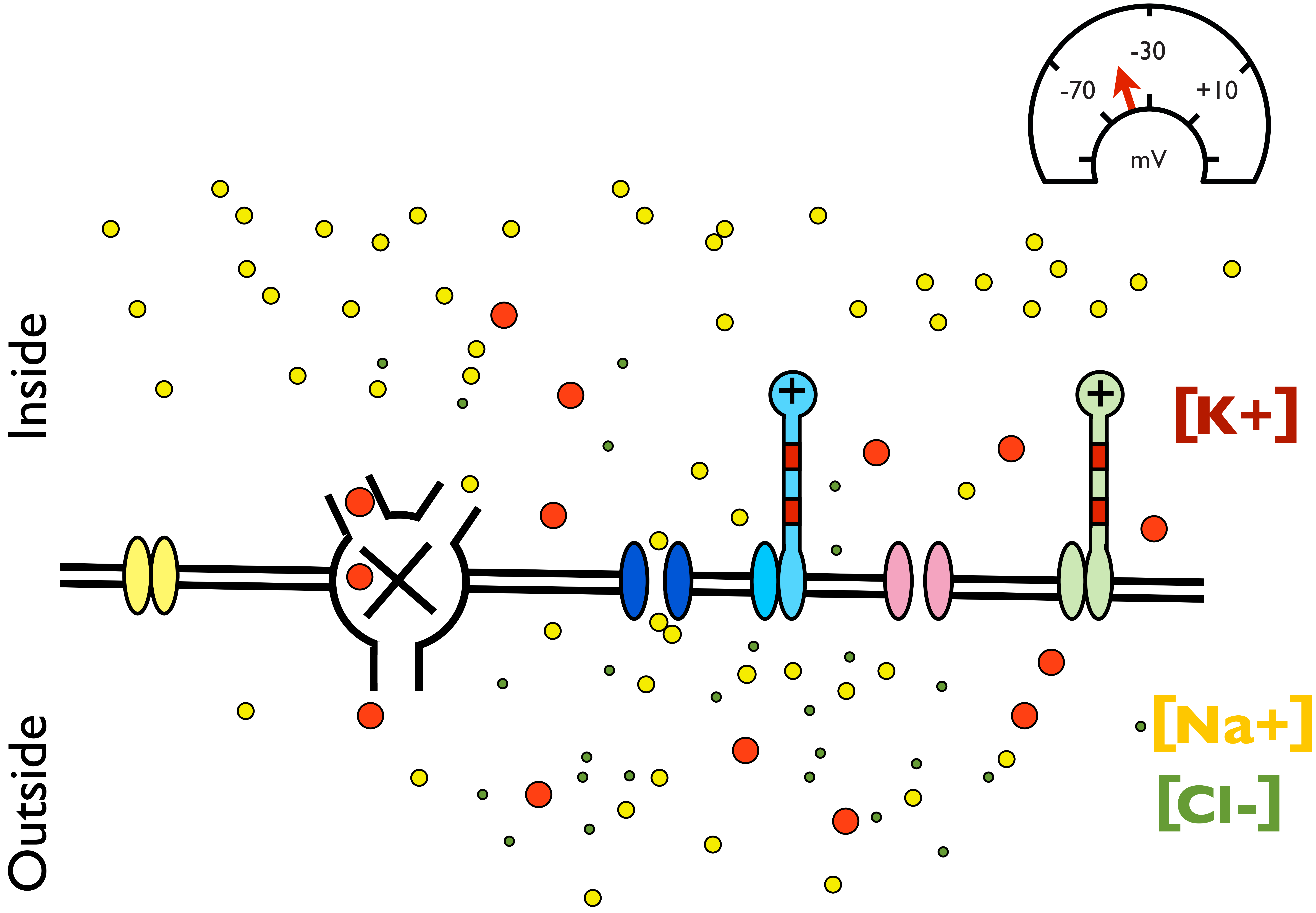


...but what about the "fire"?


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



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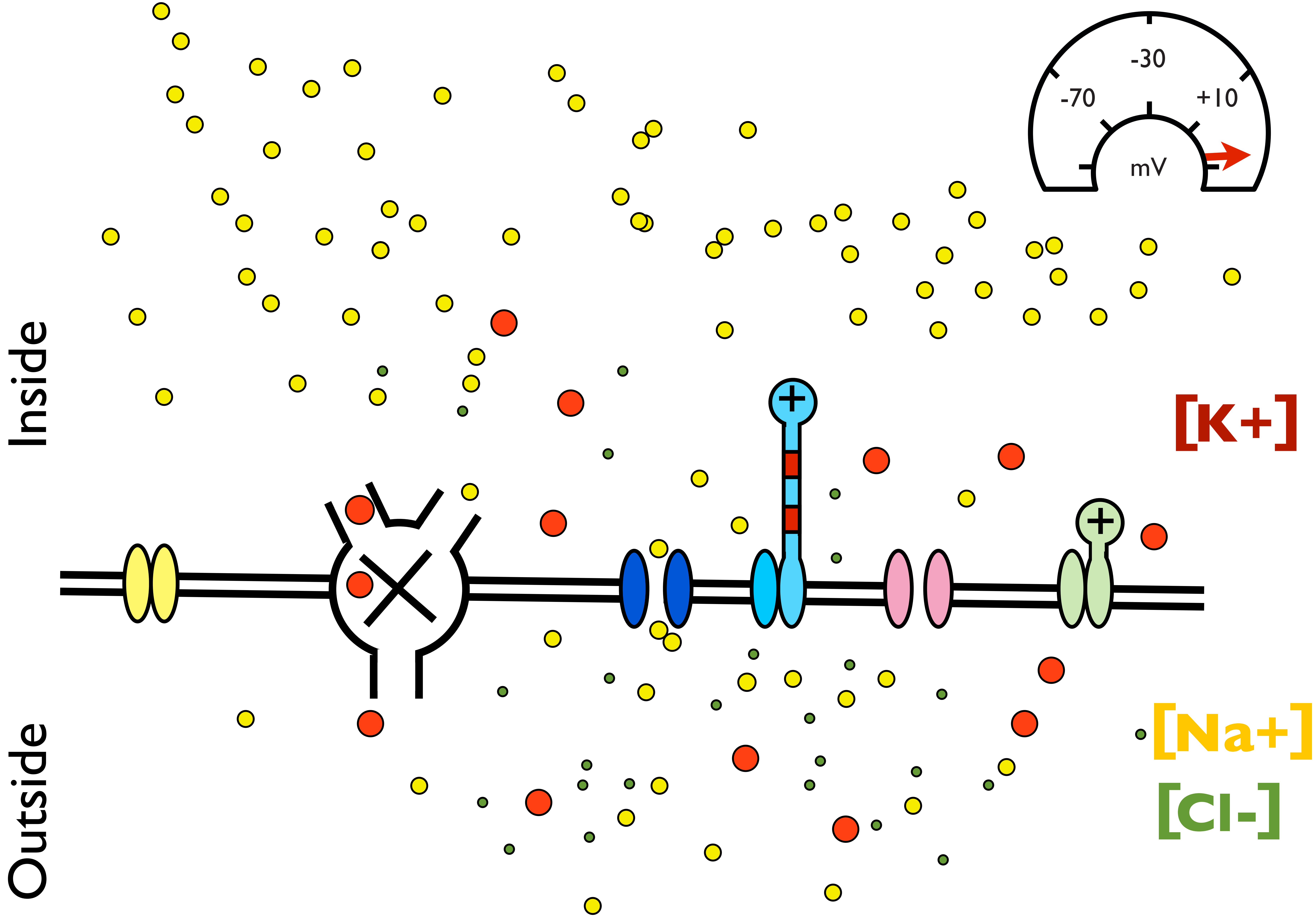

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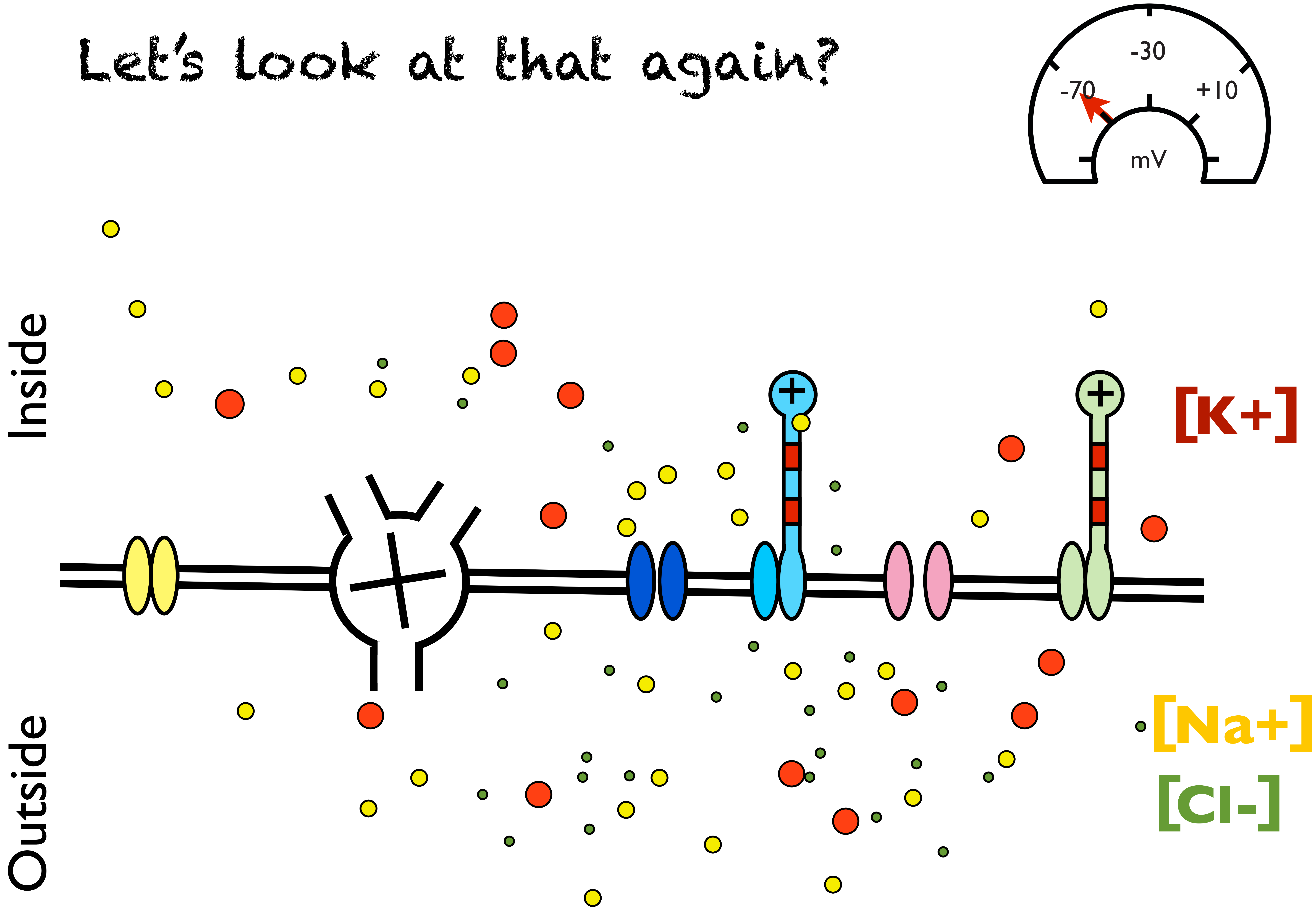
Let's look at that again?



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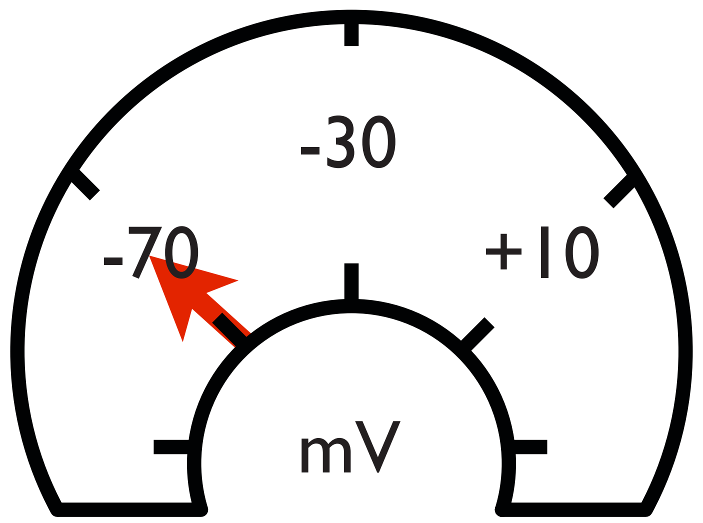

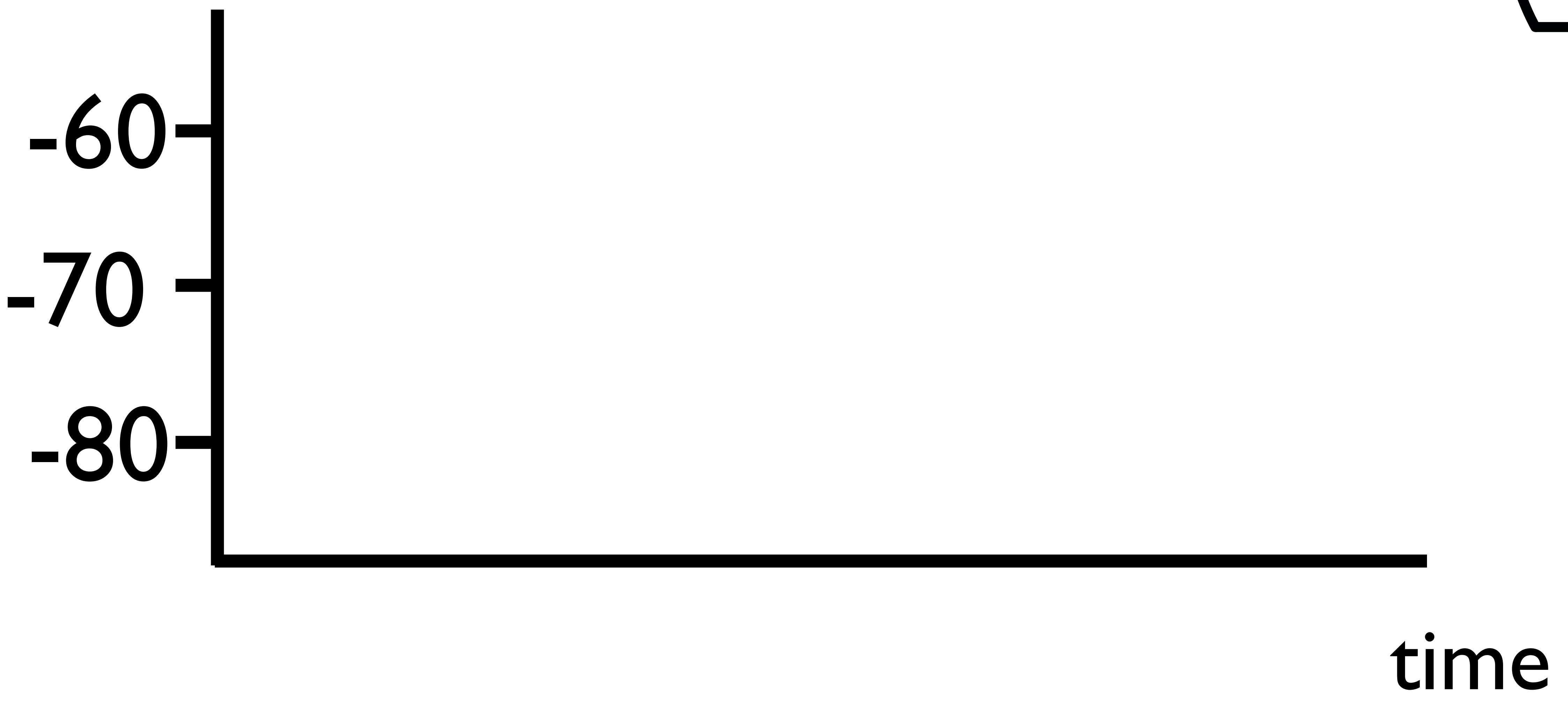

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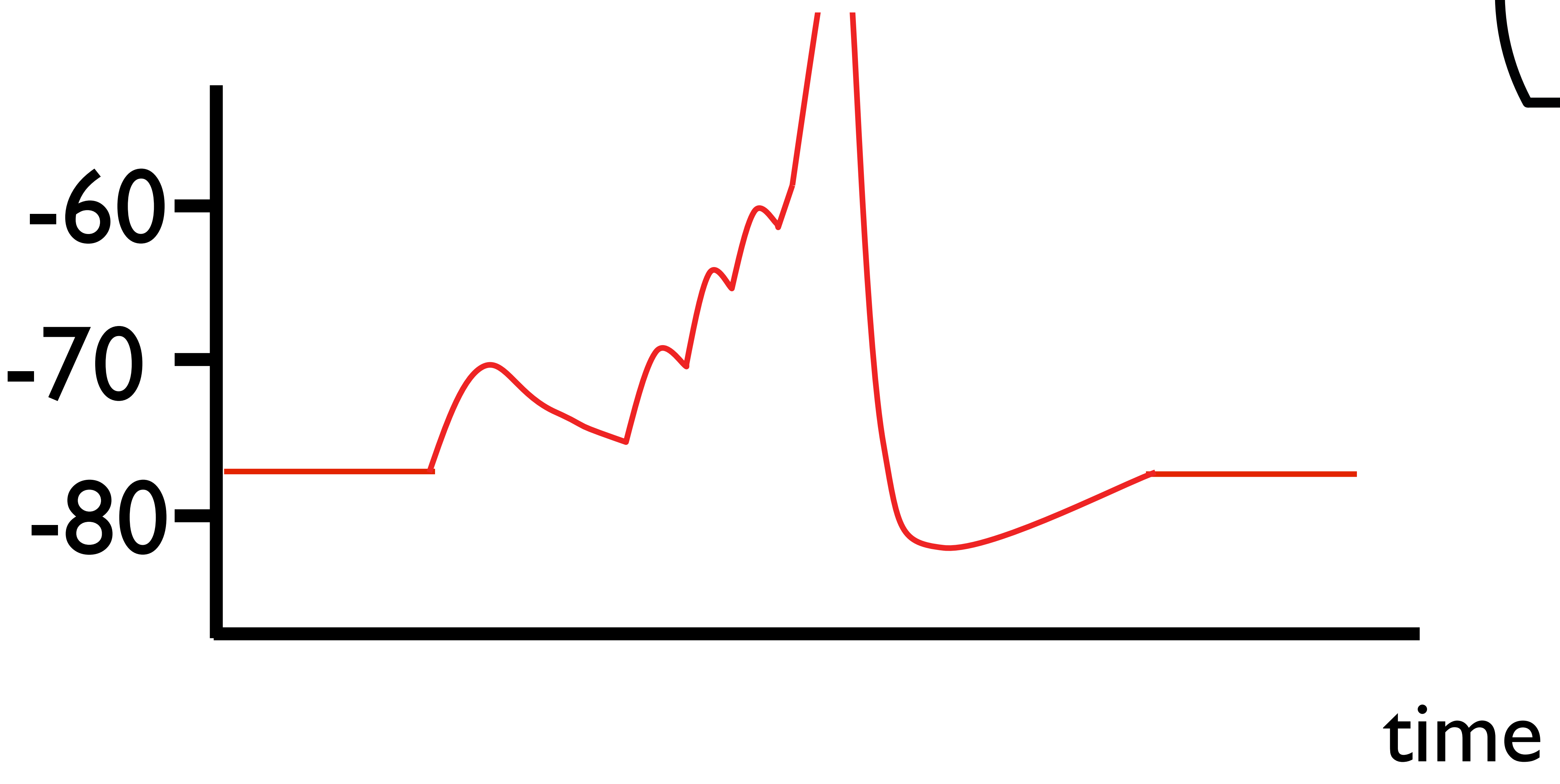

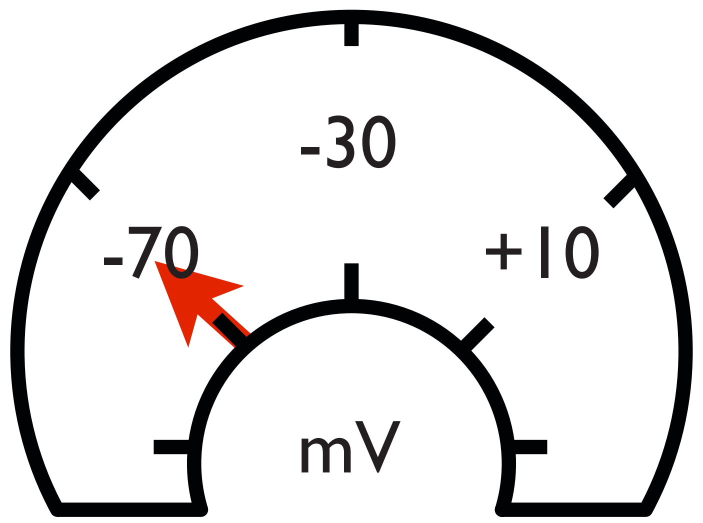

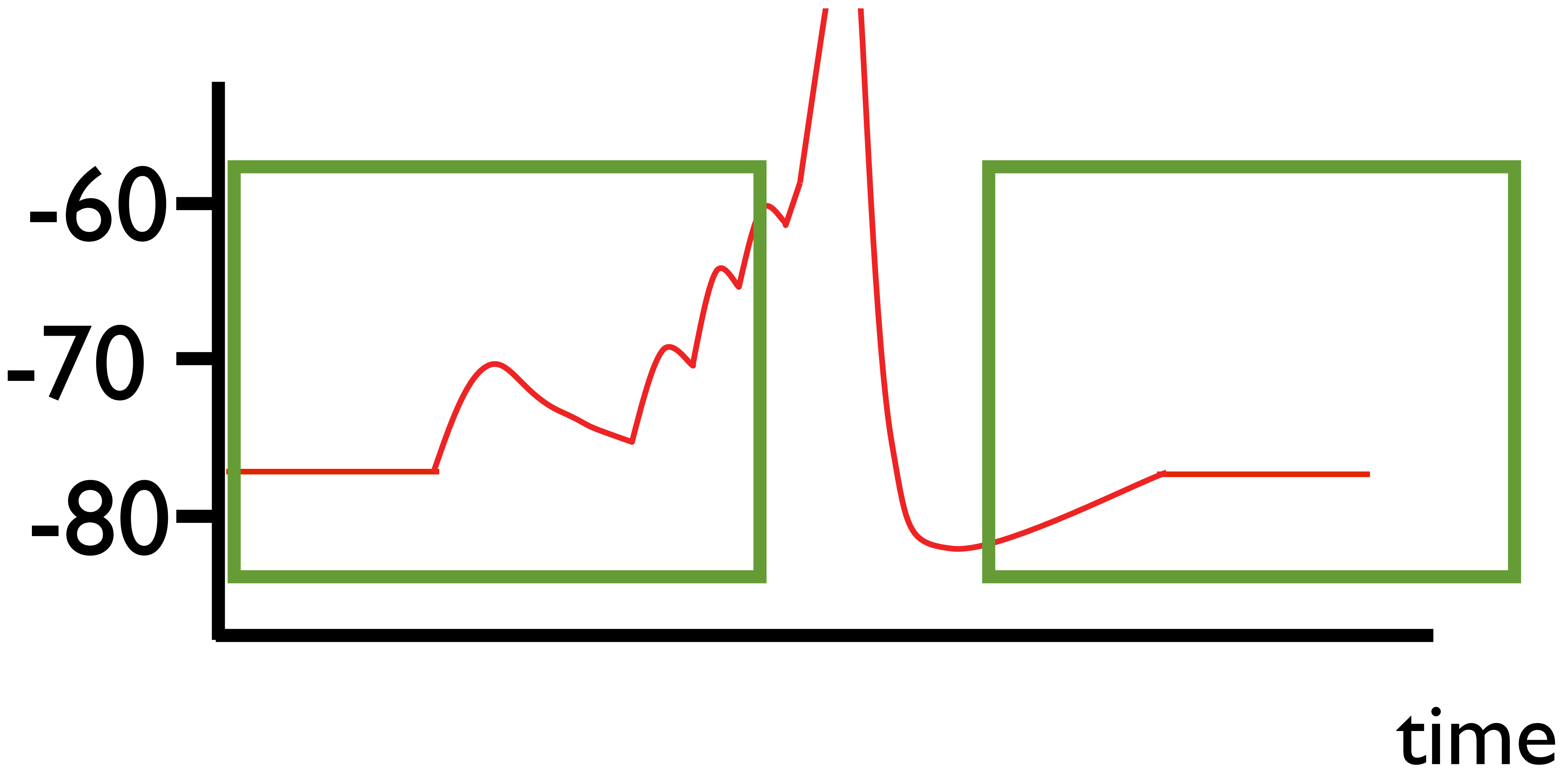

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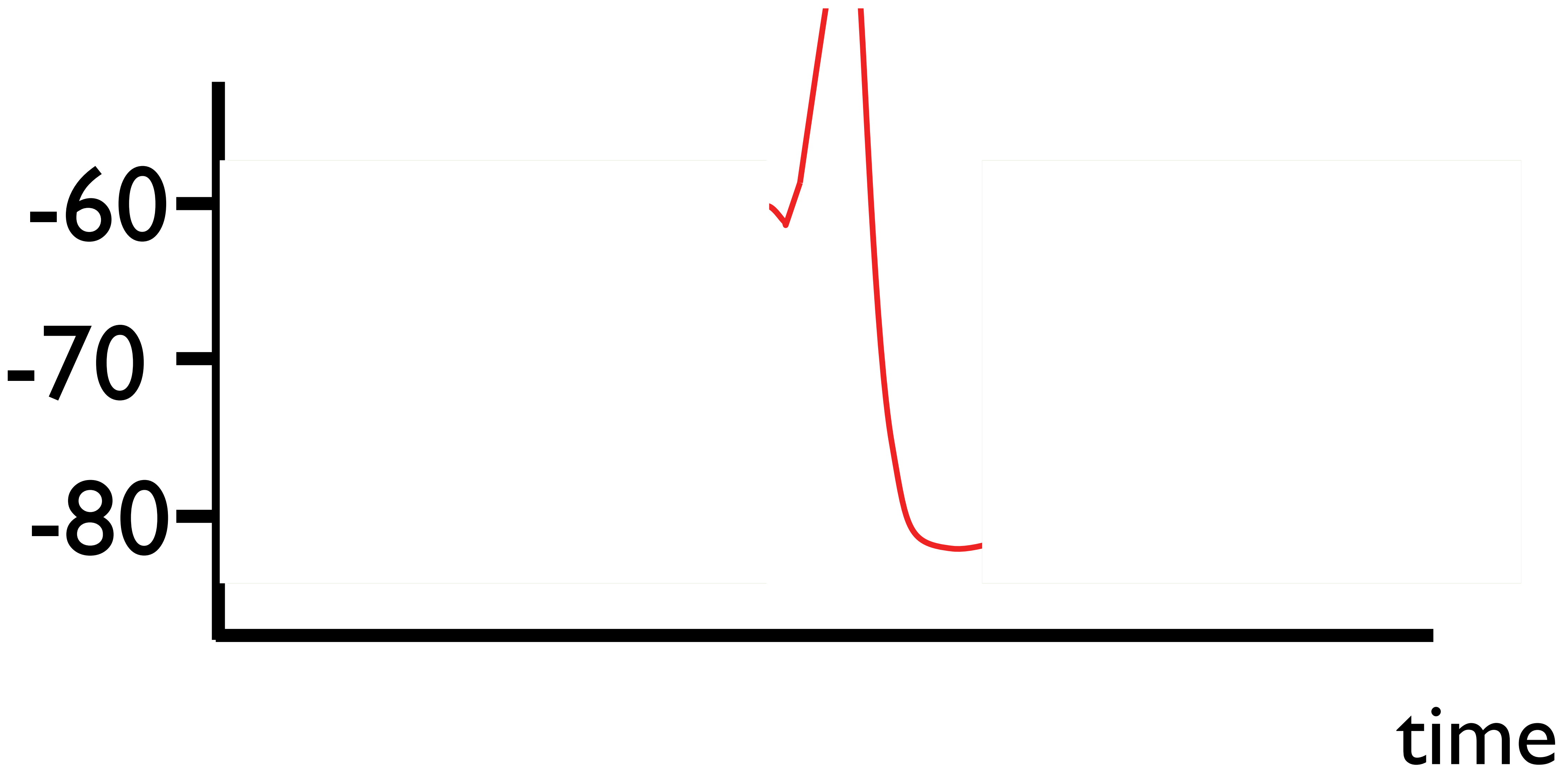

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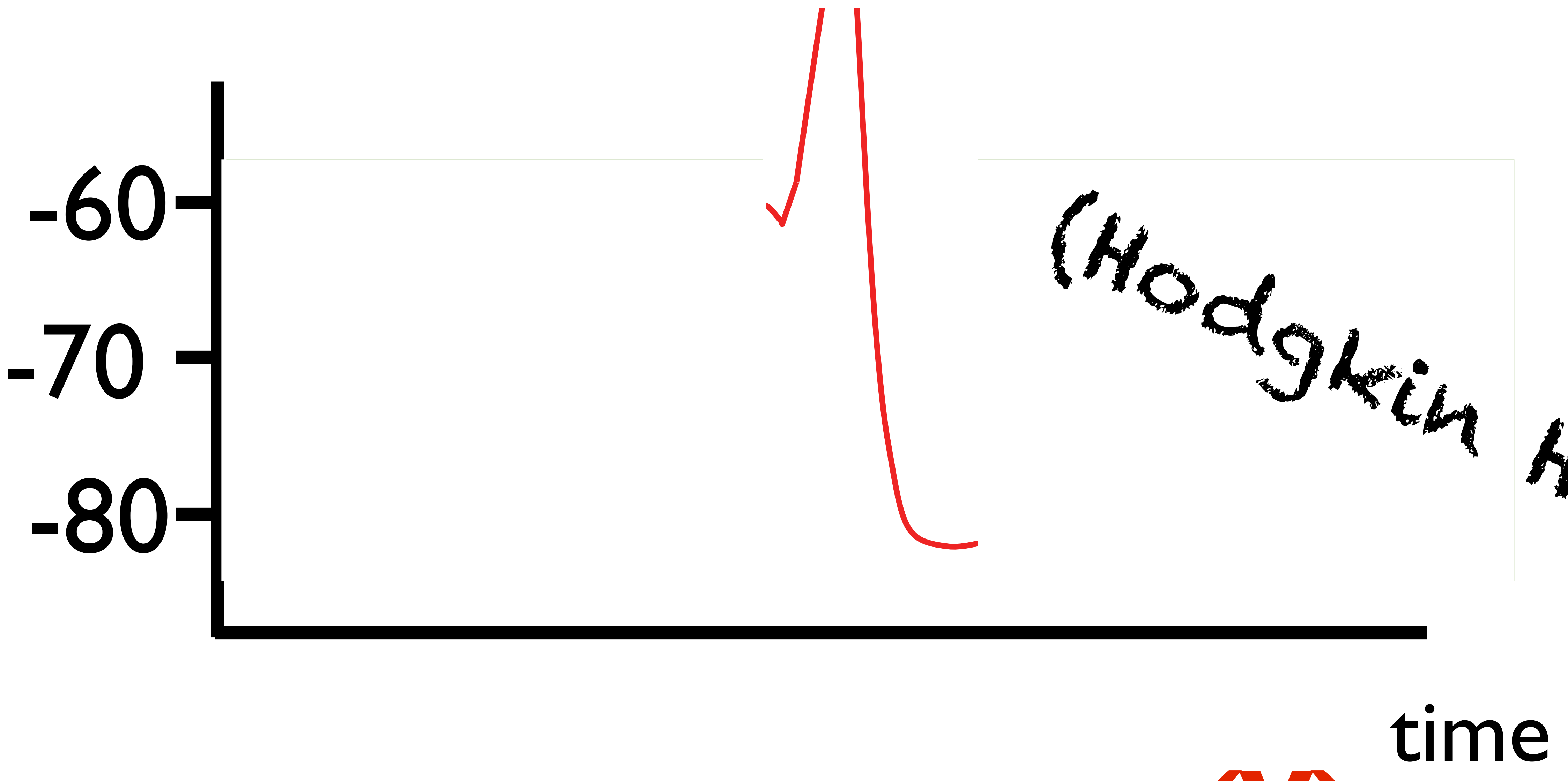

(Hodgkin Huxley style)

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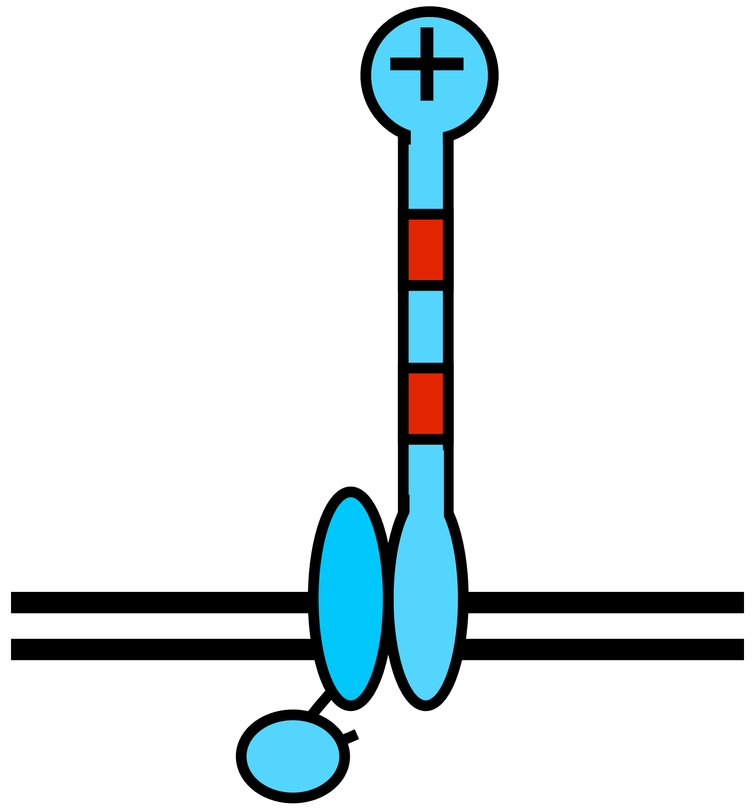

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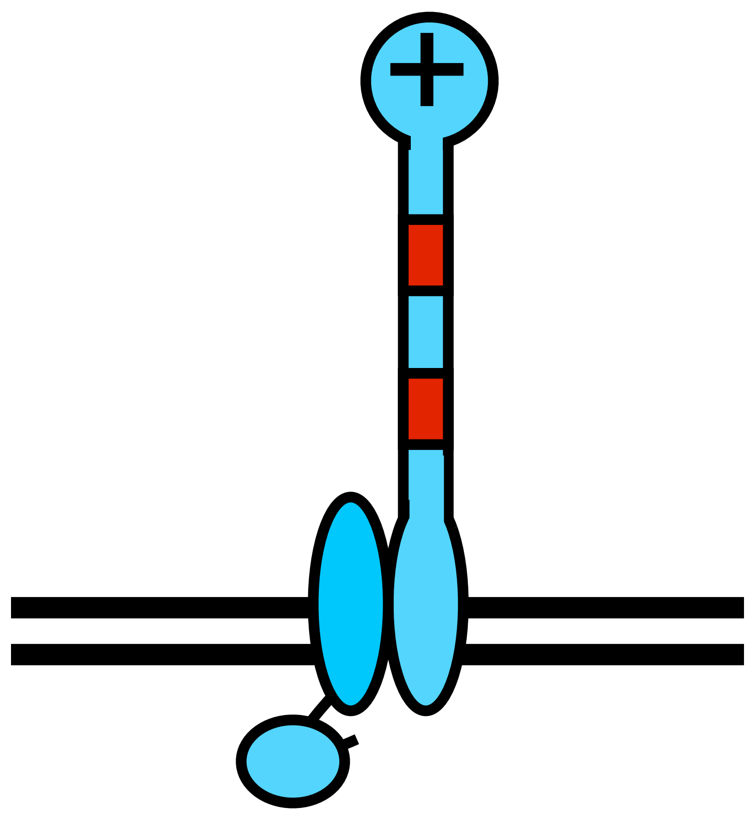

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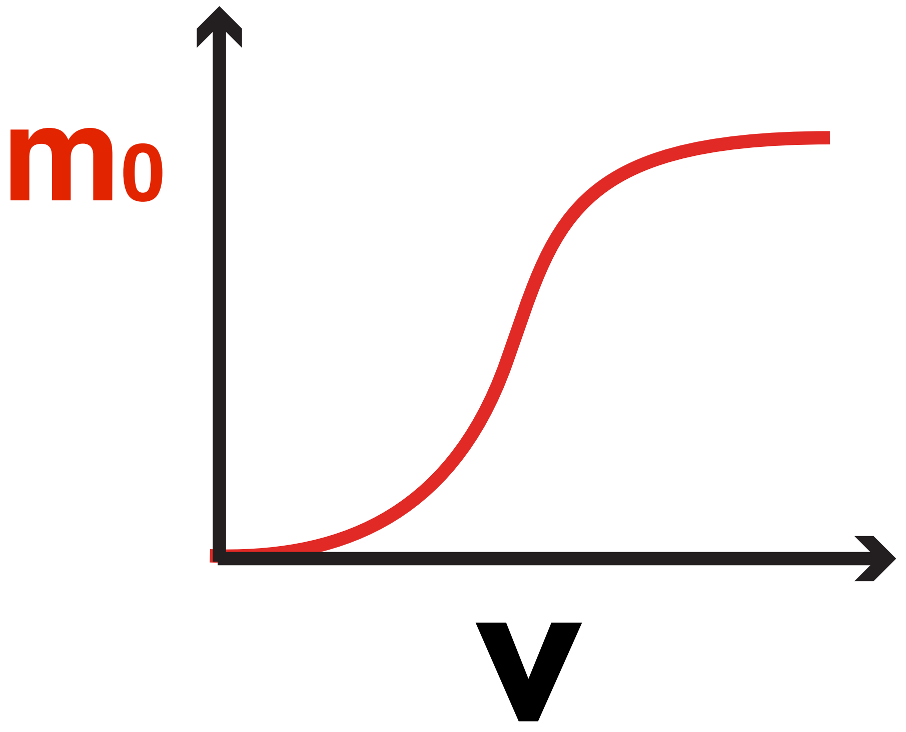

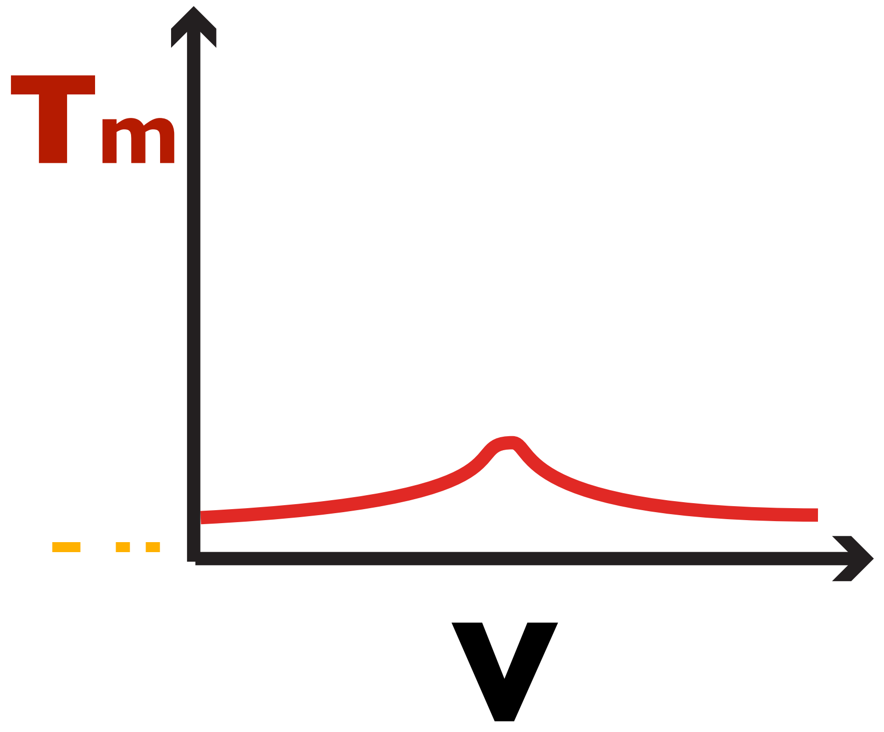

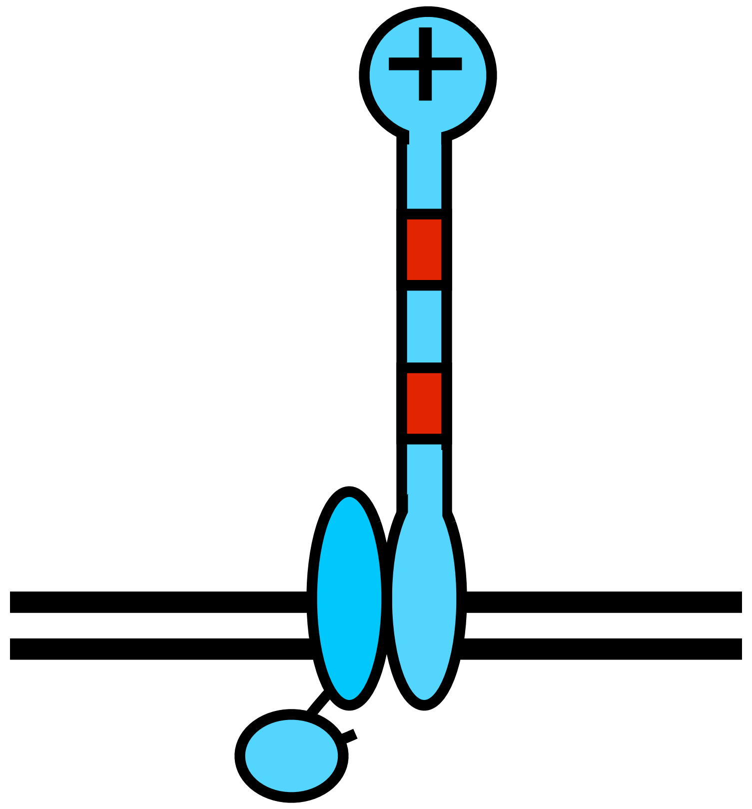

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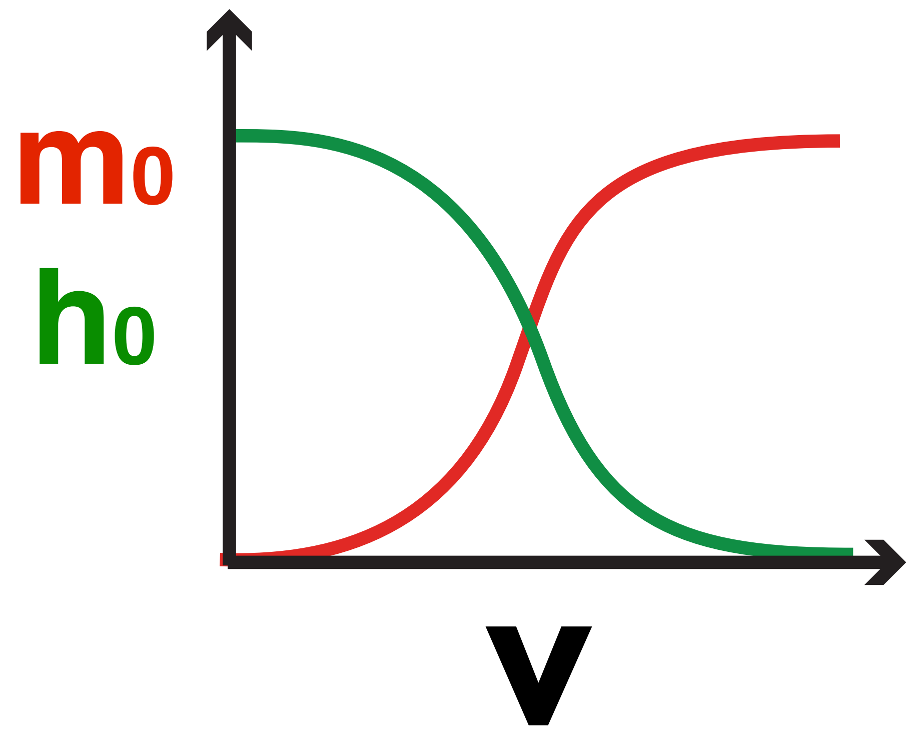

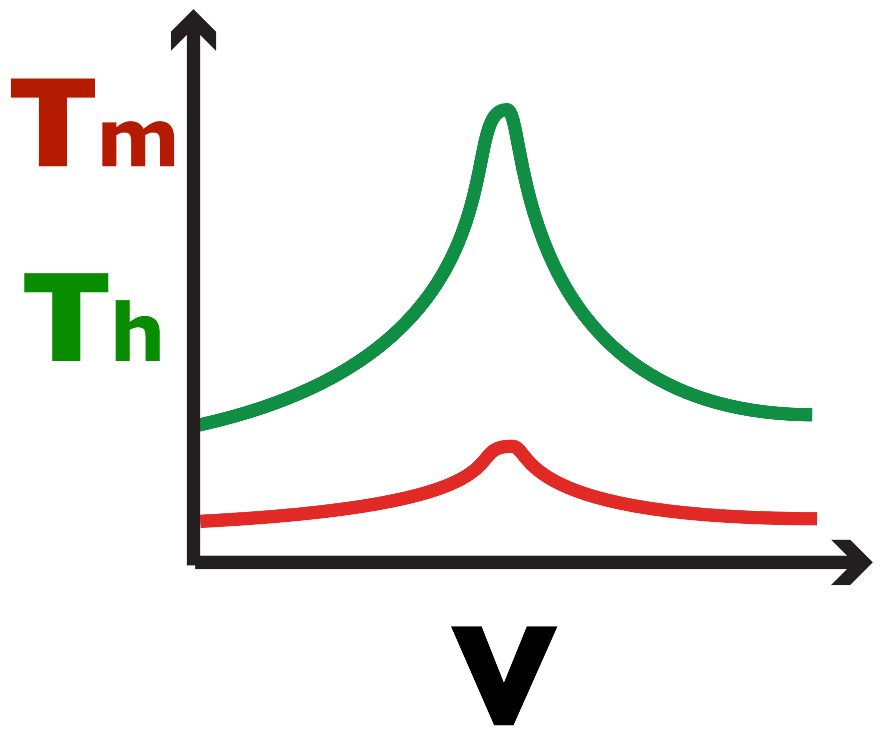

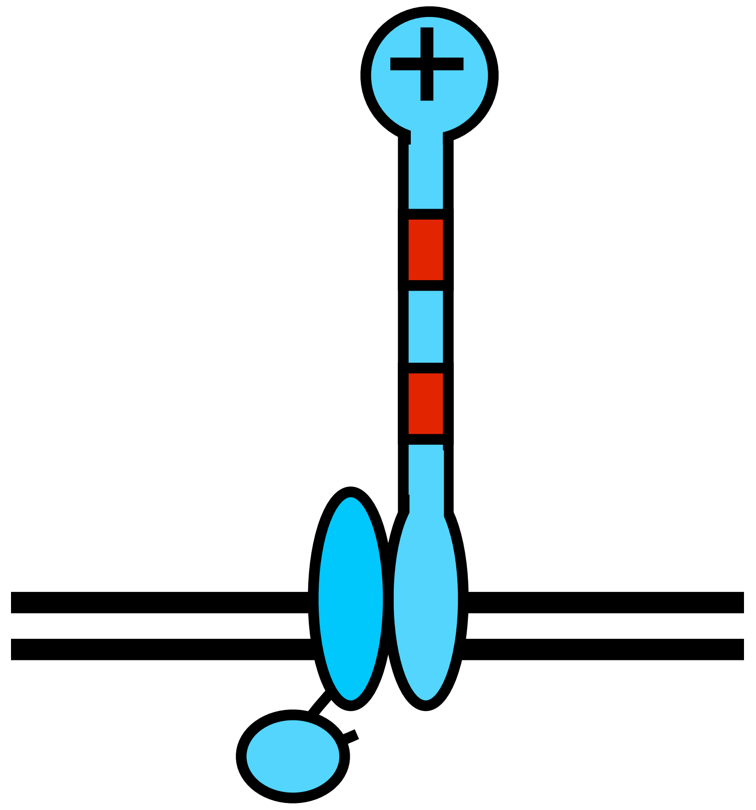

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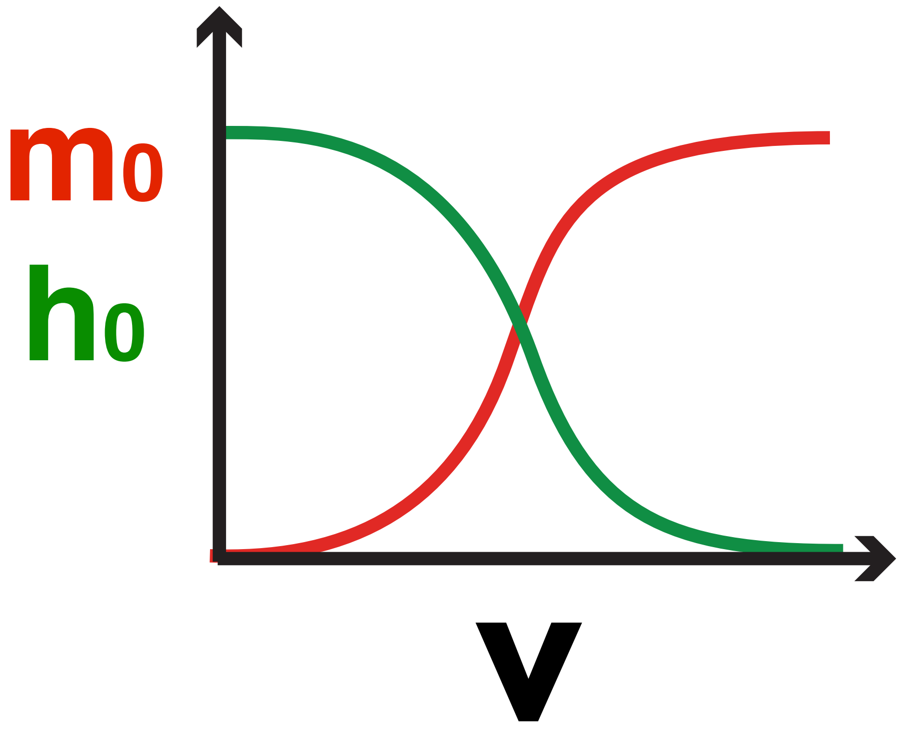

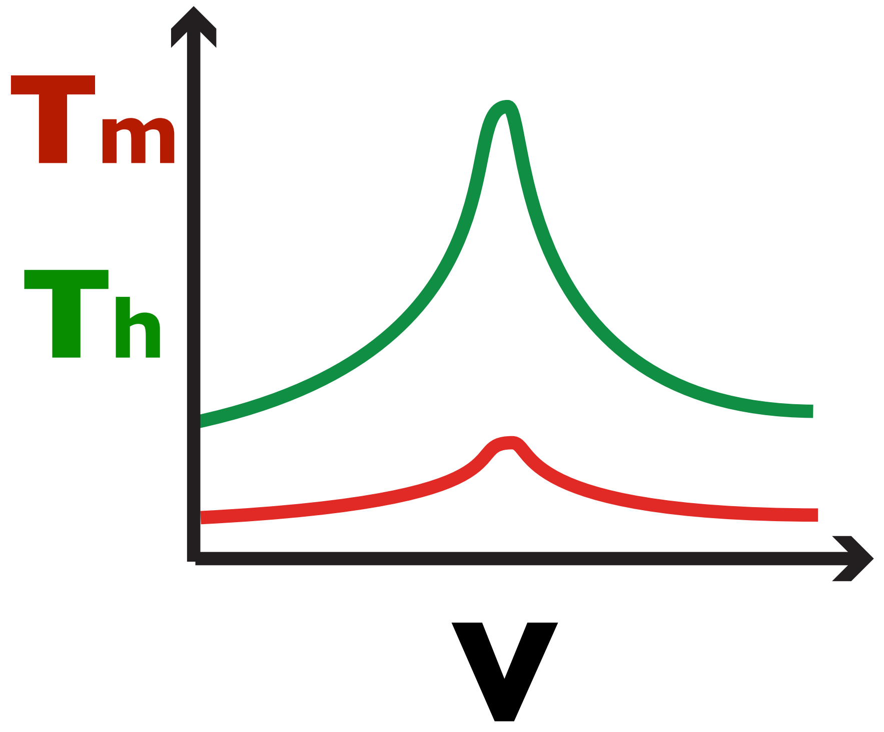

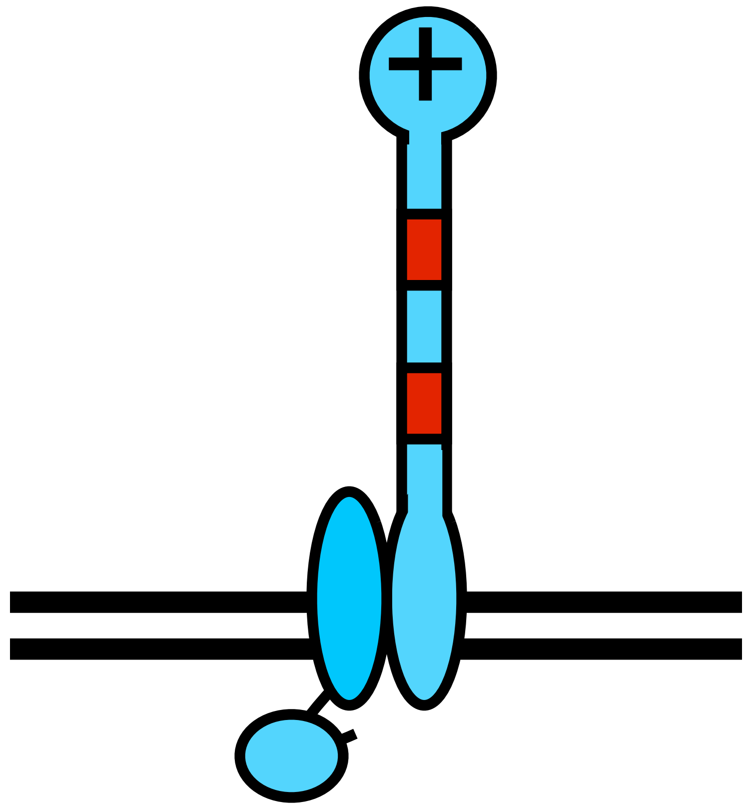

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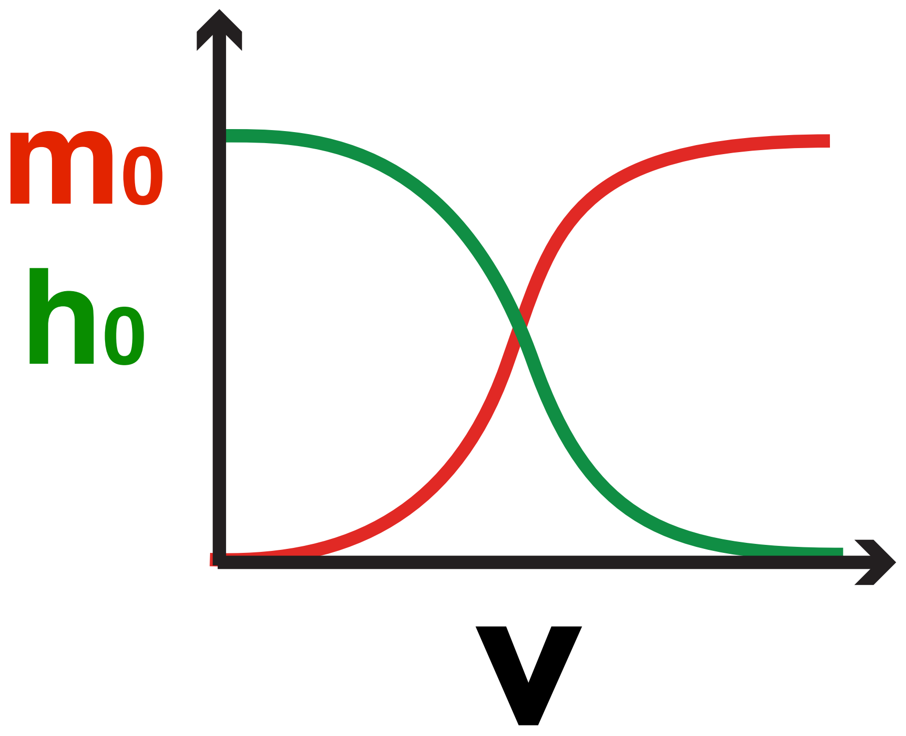

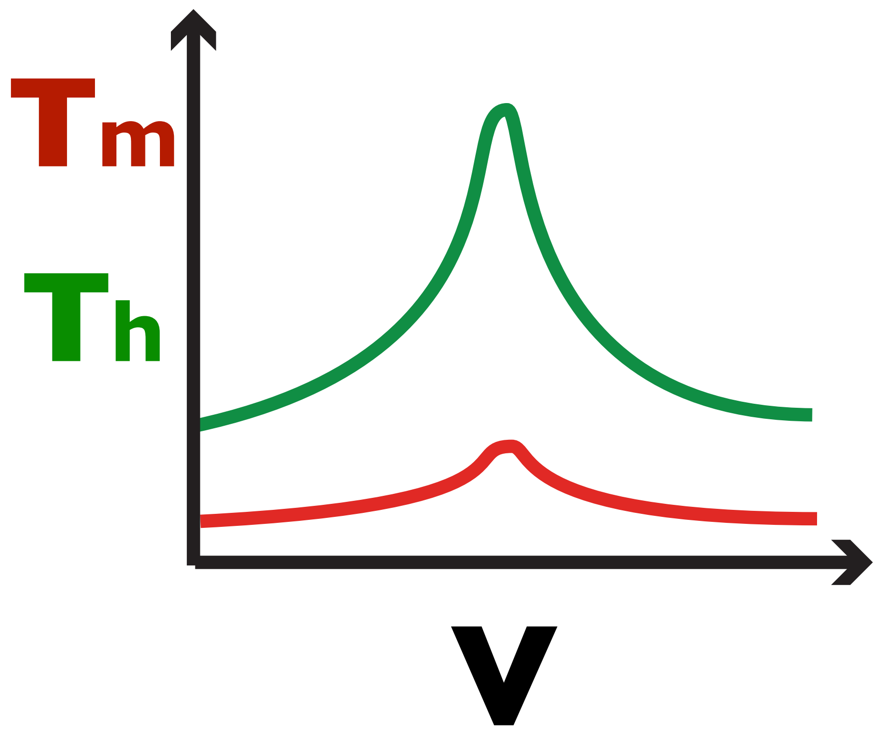

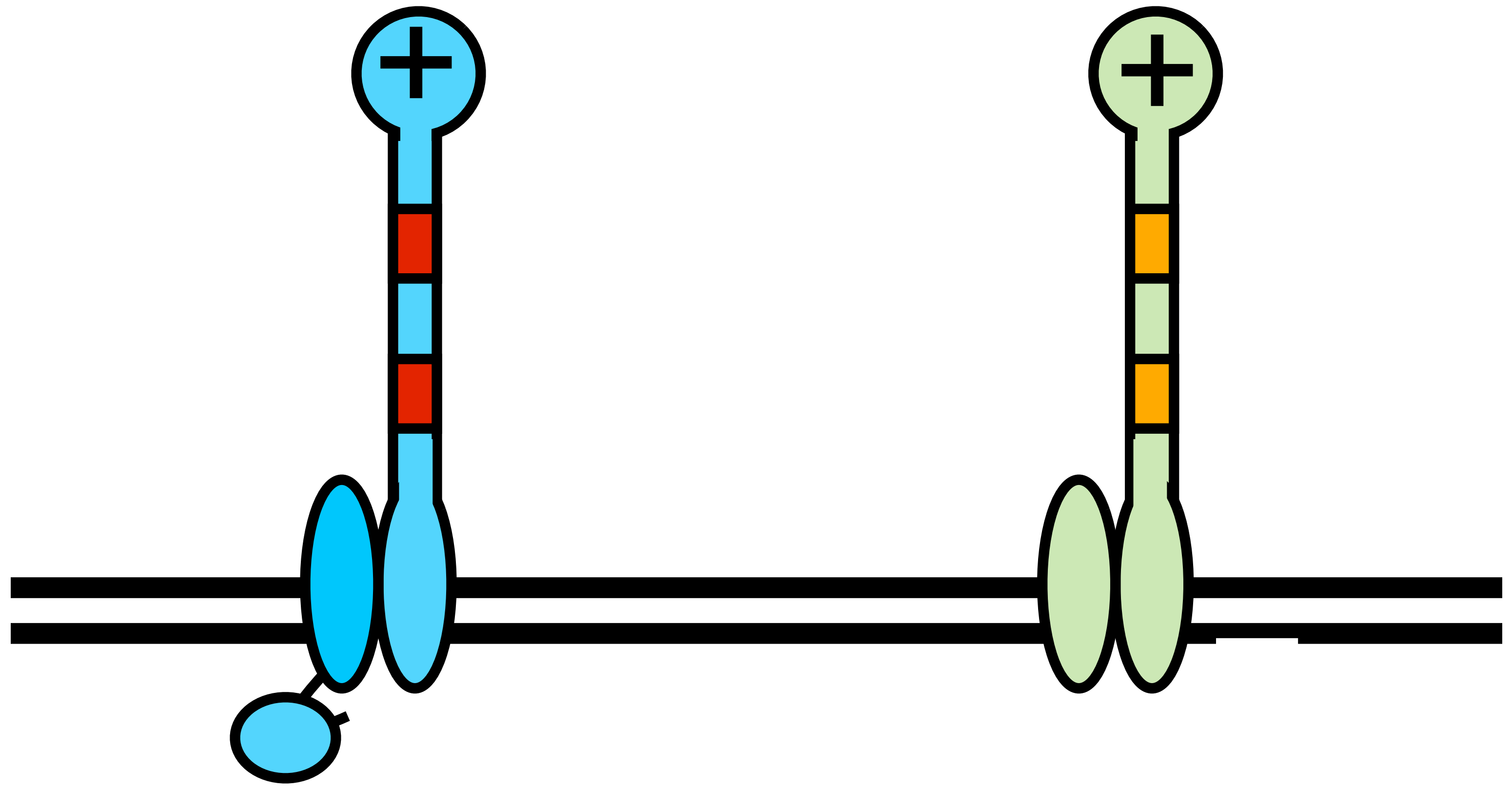

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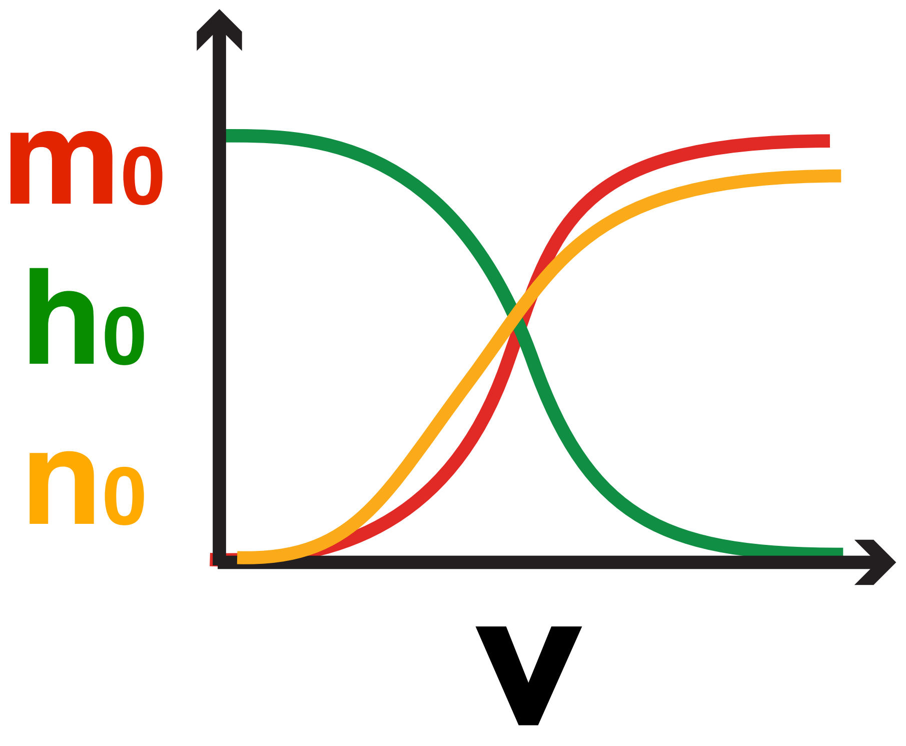

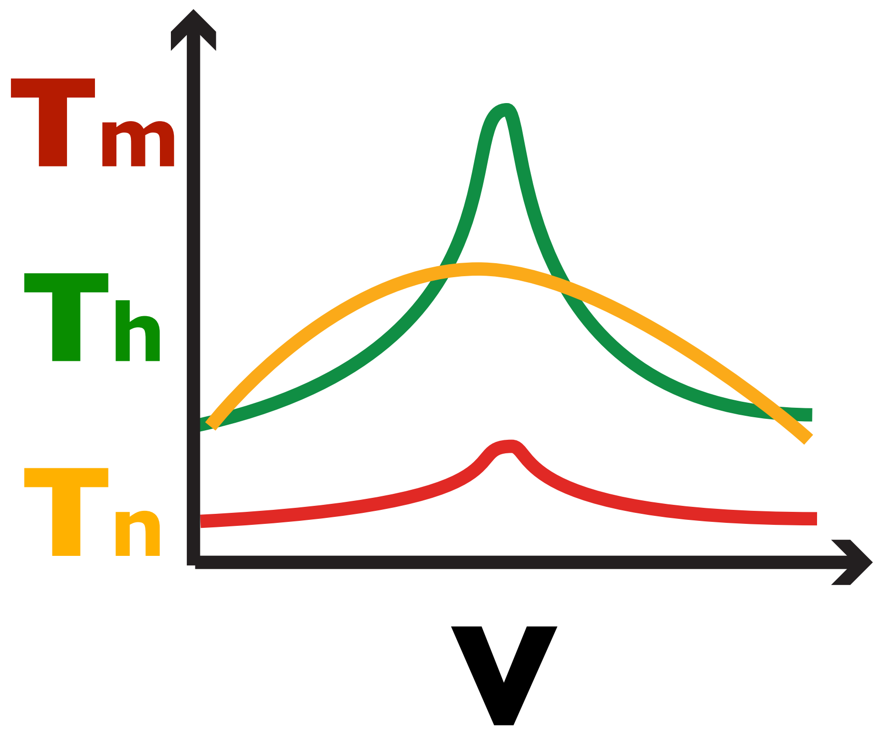

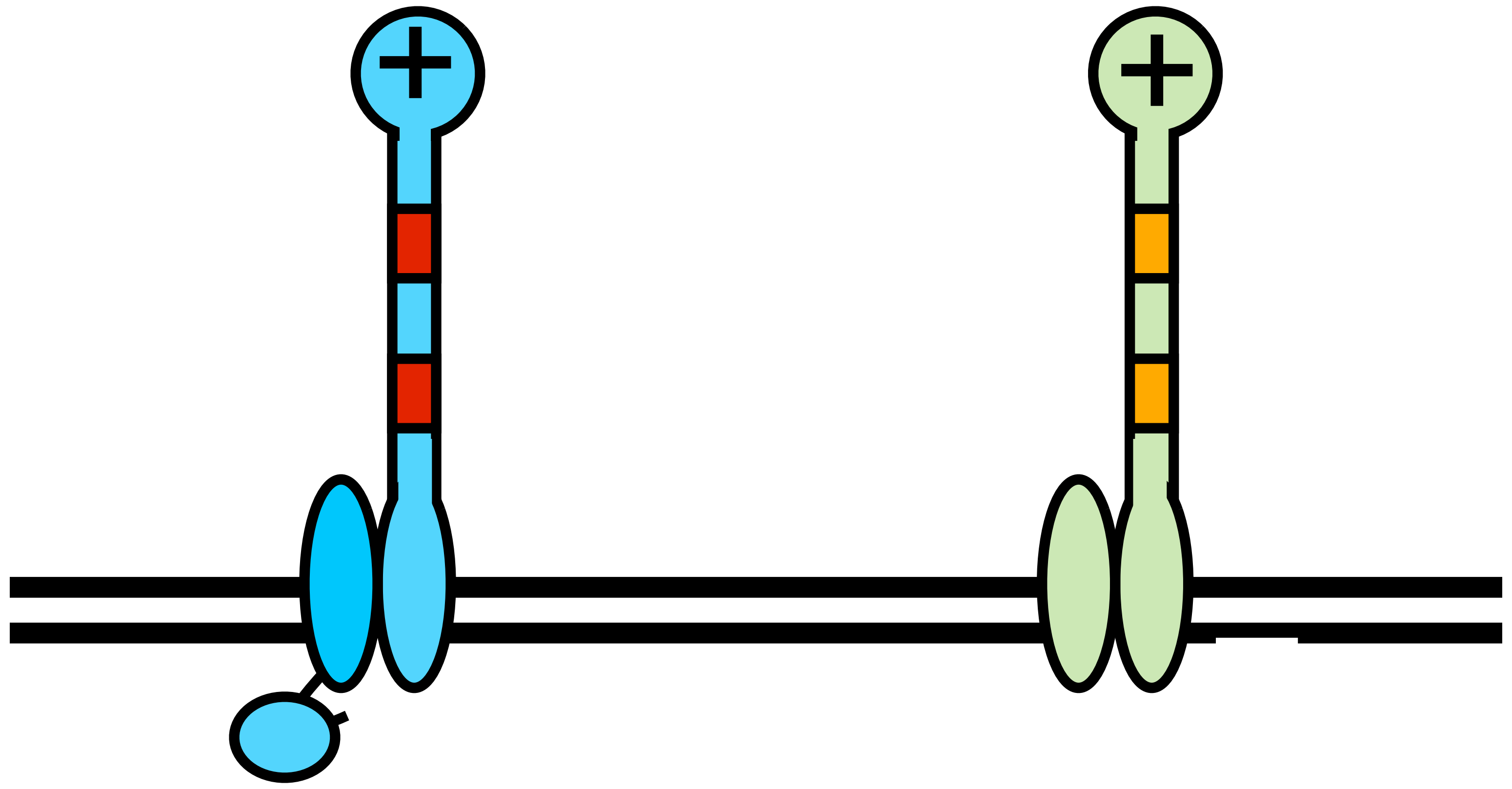

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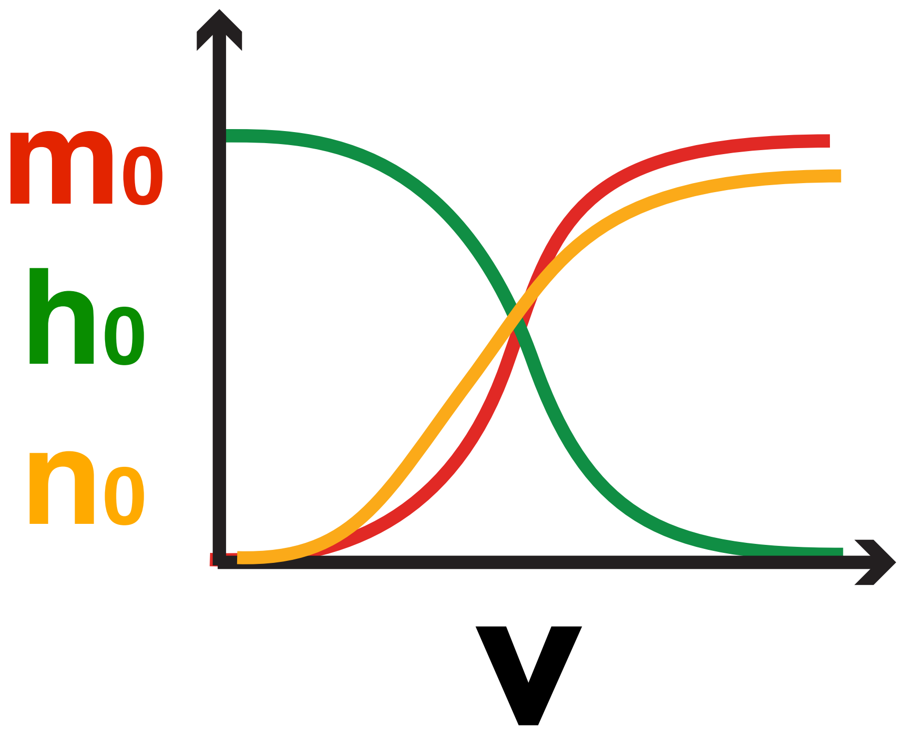
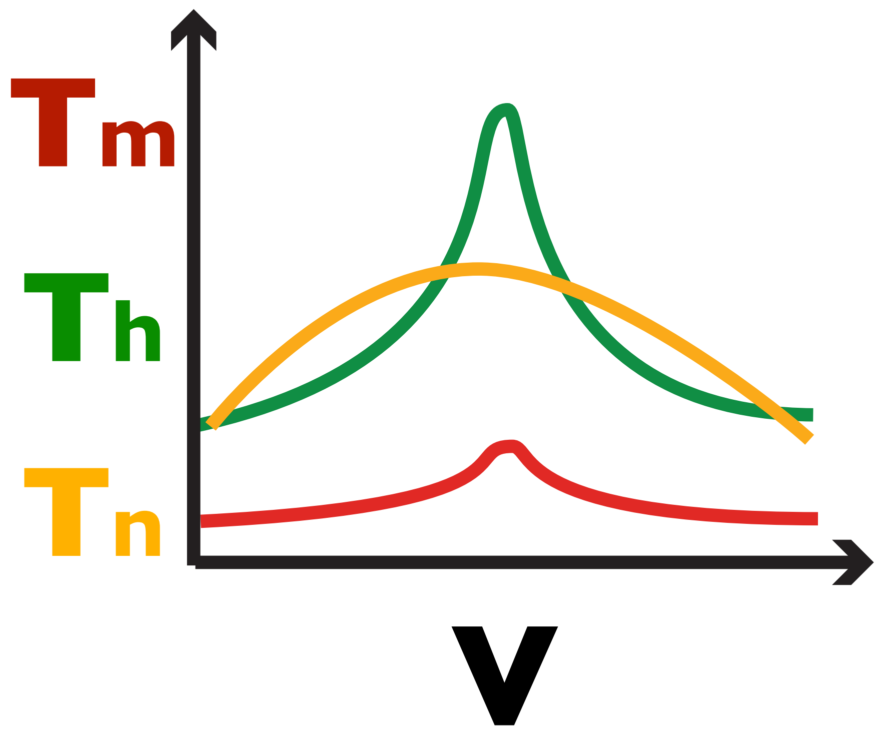
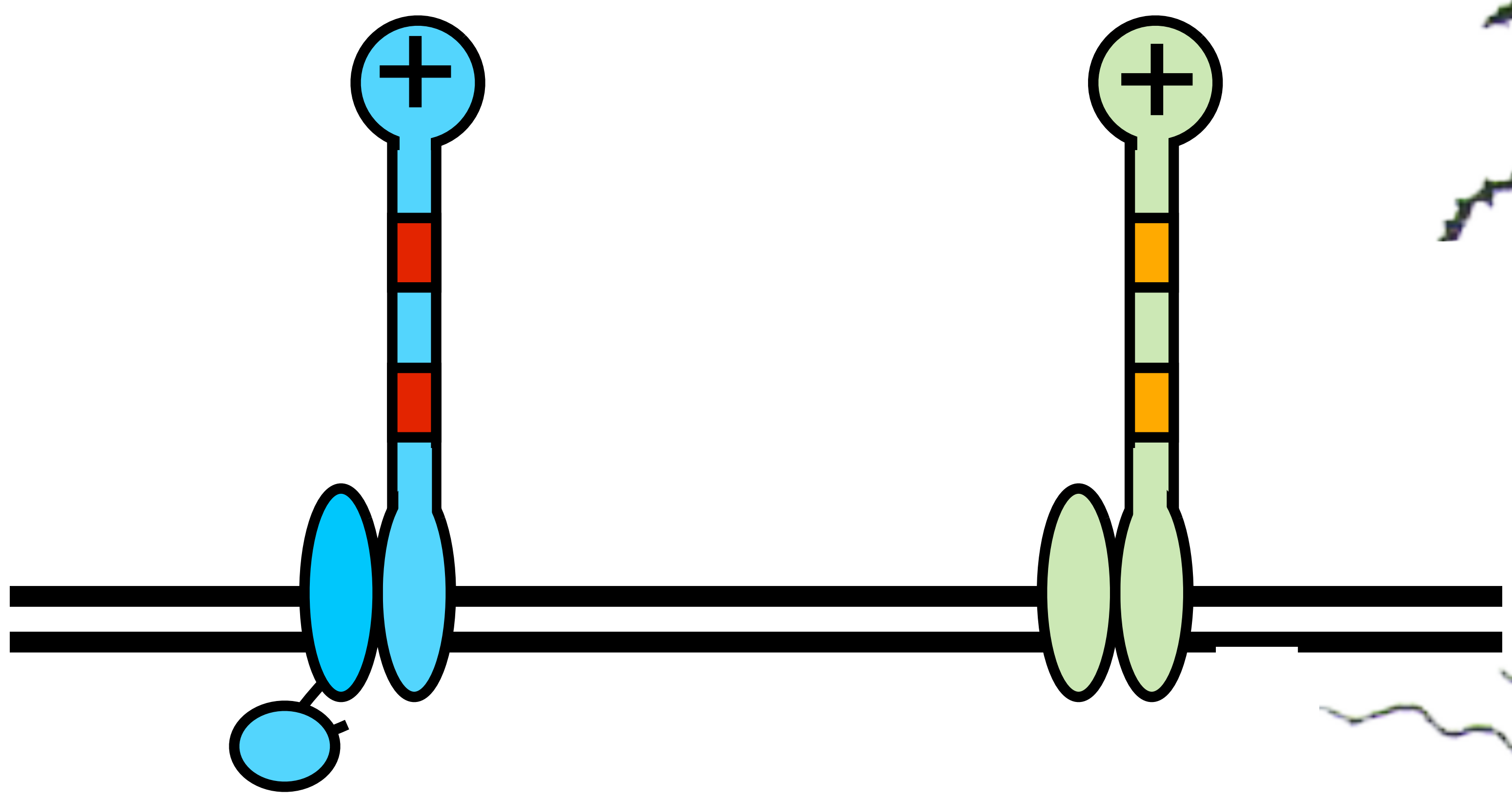
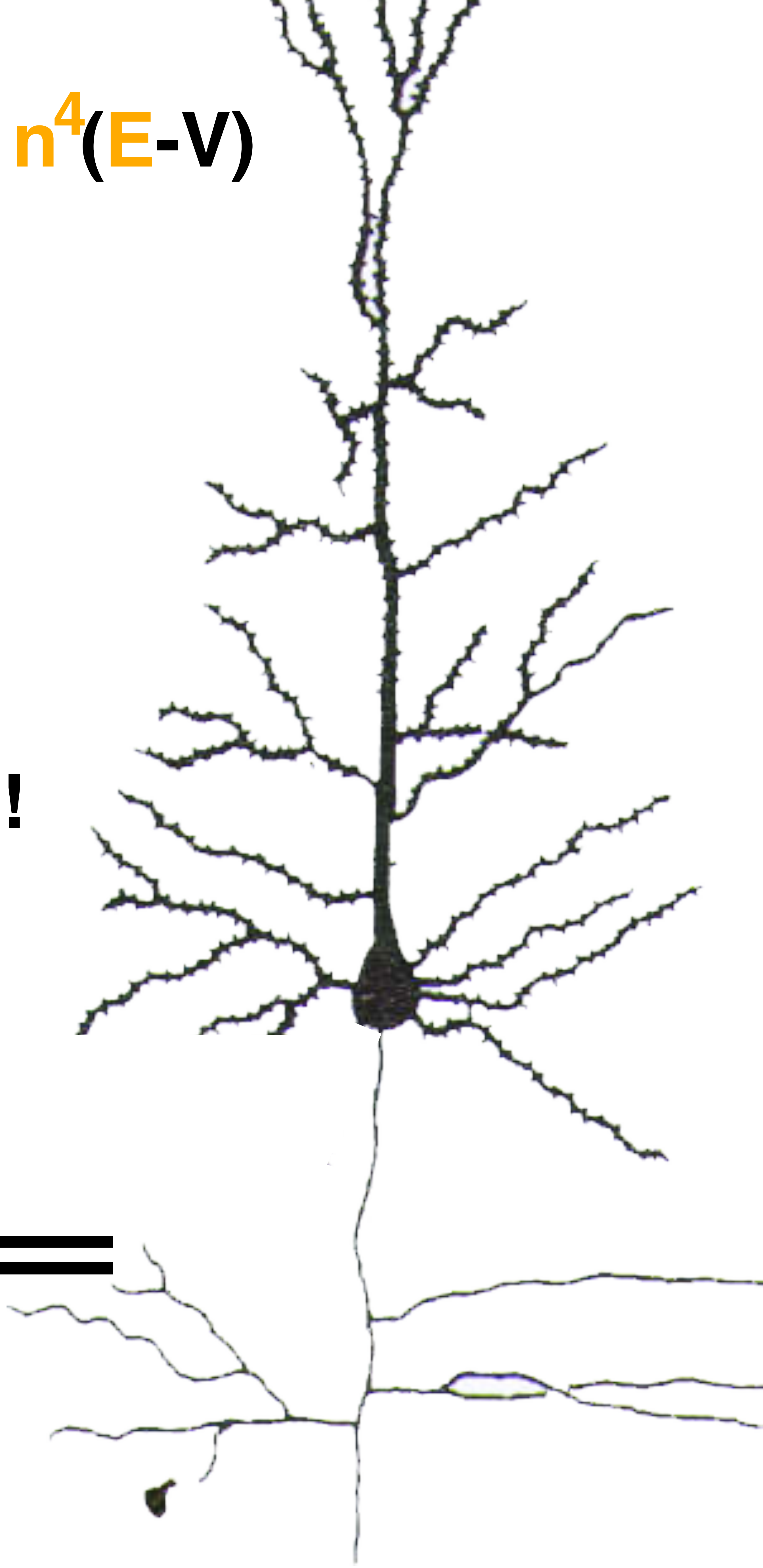




A complete description of a neuron!





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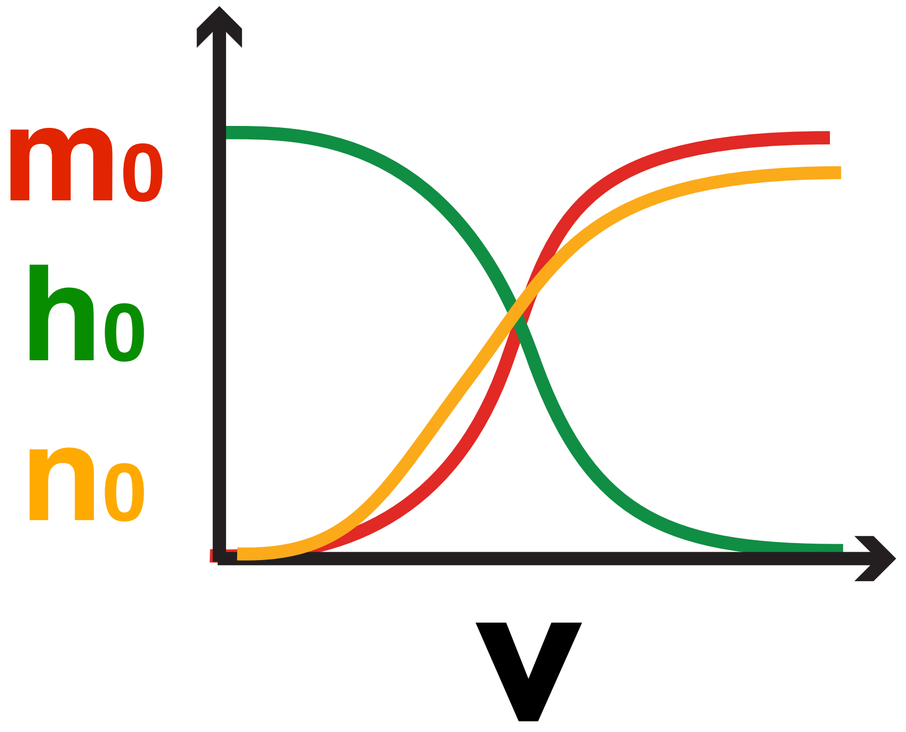

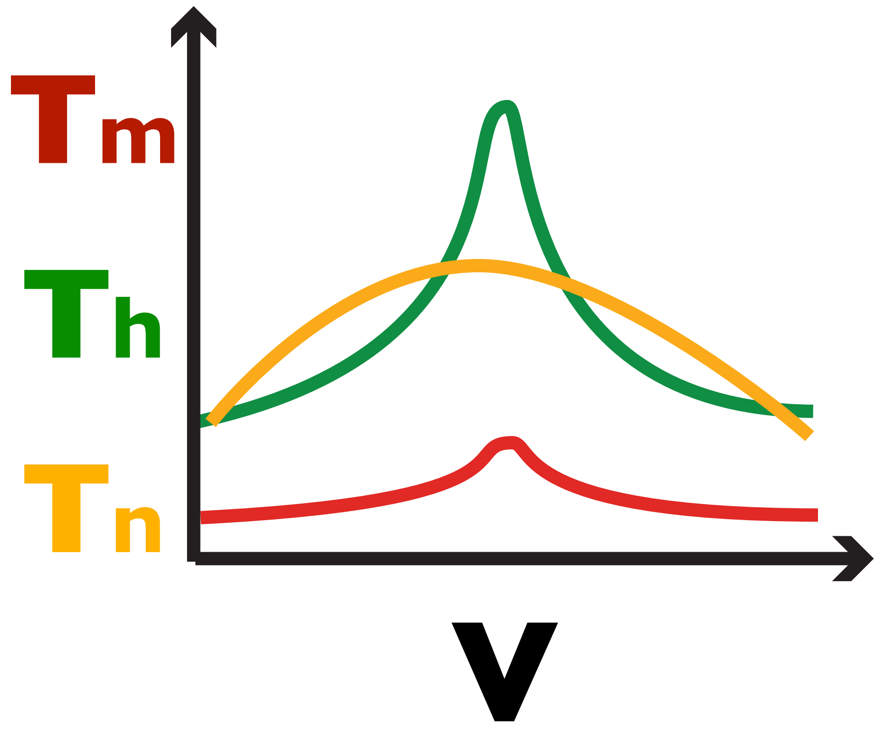

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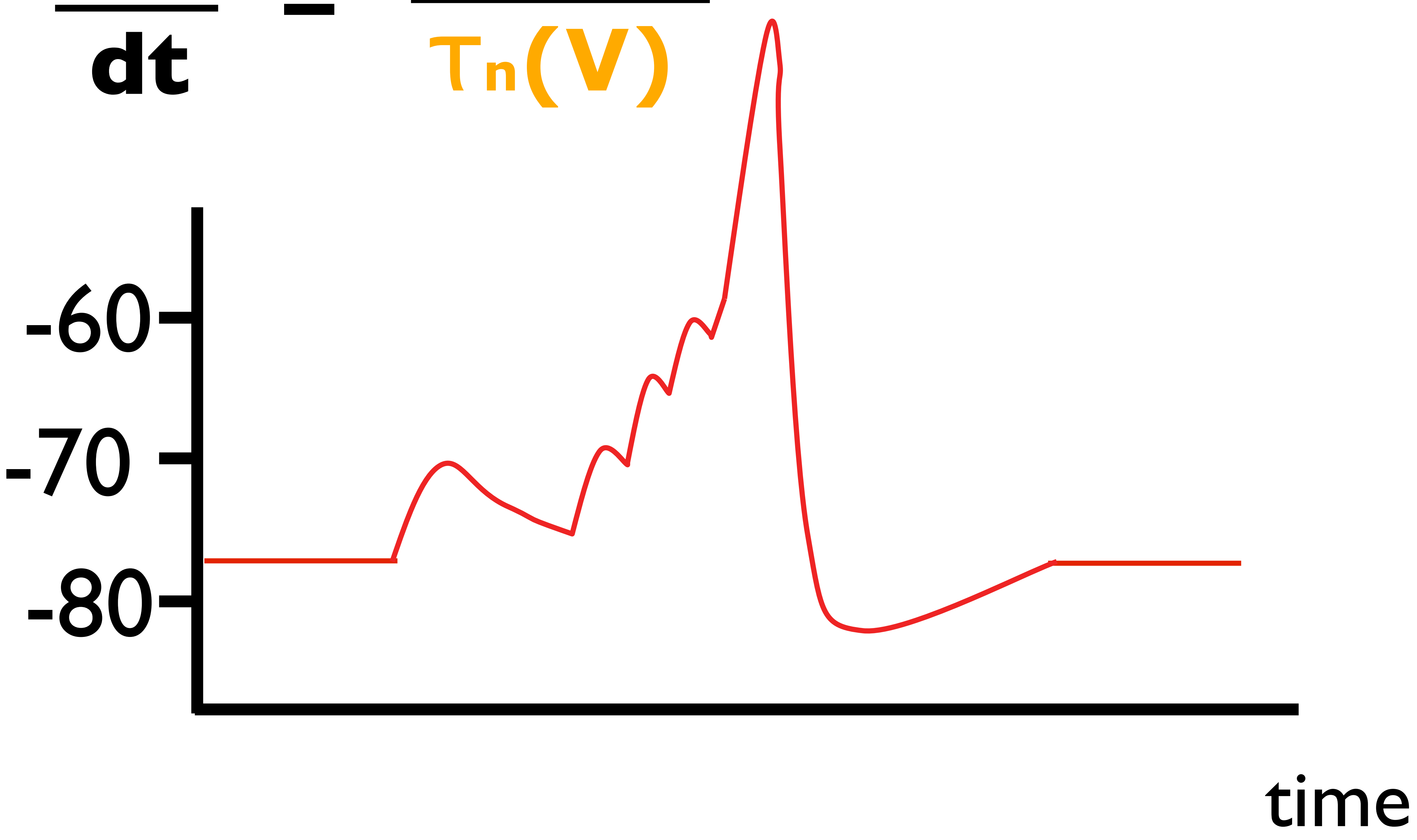
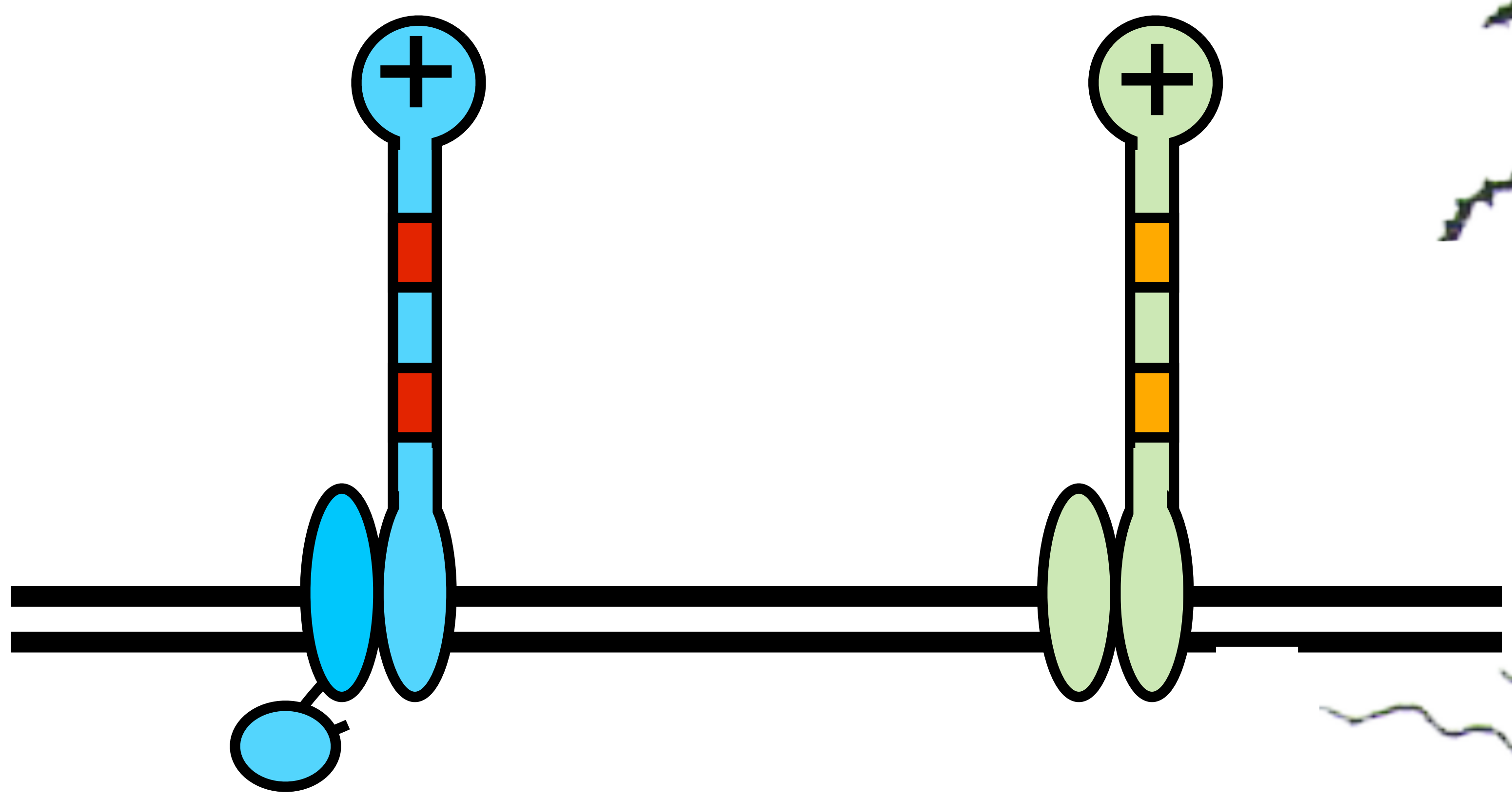
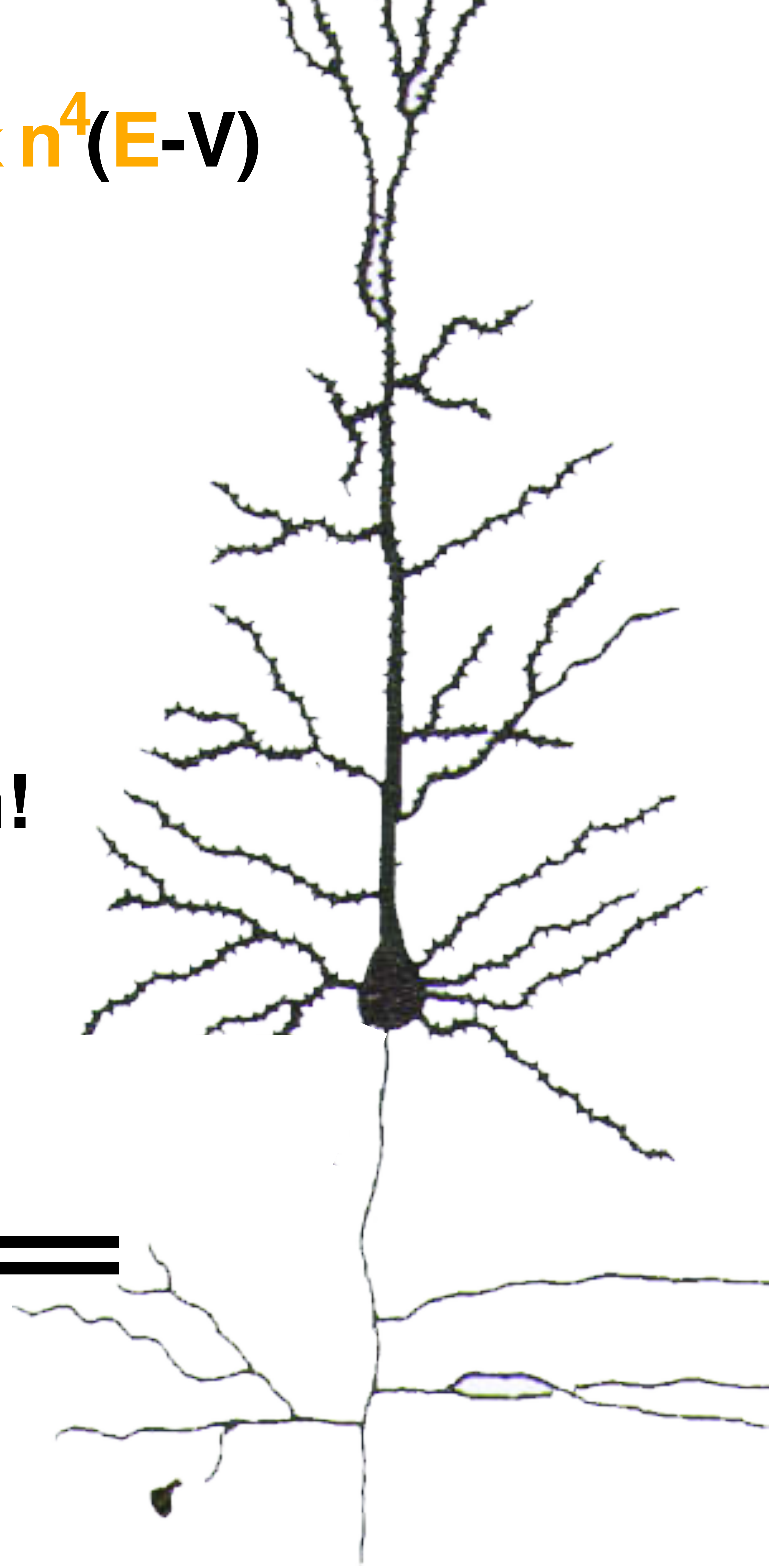
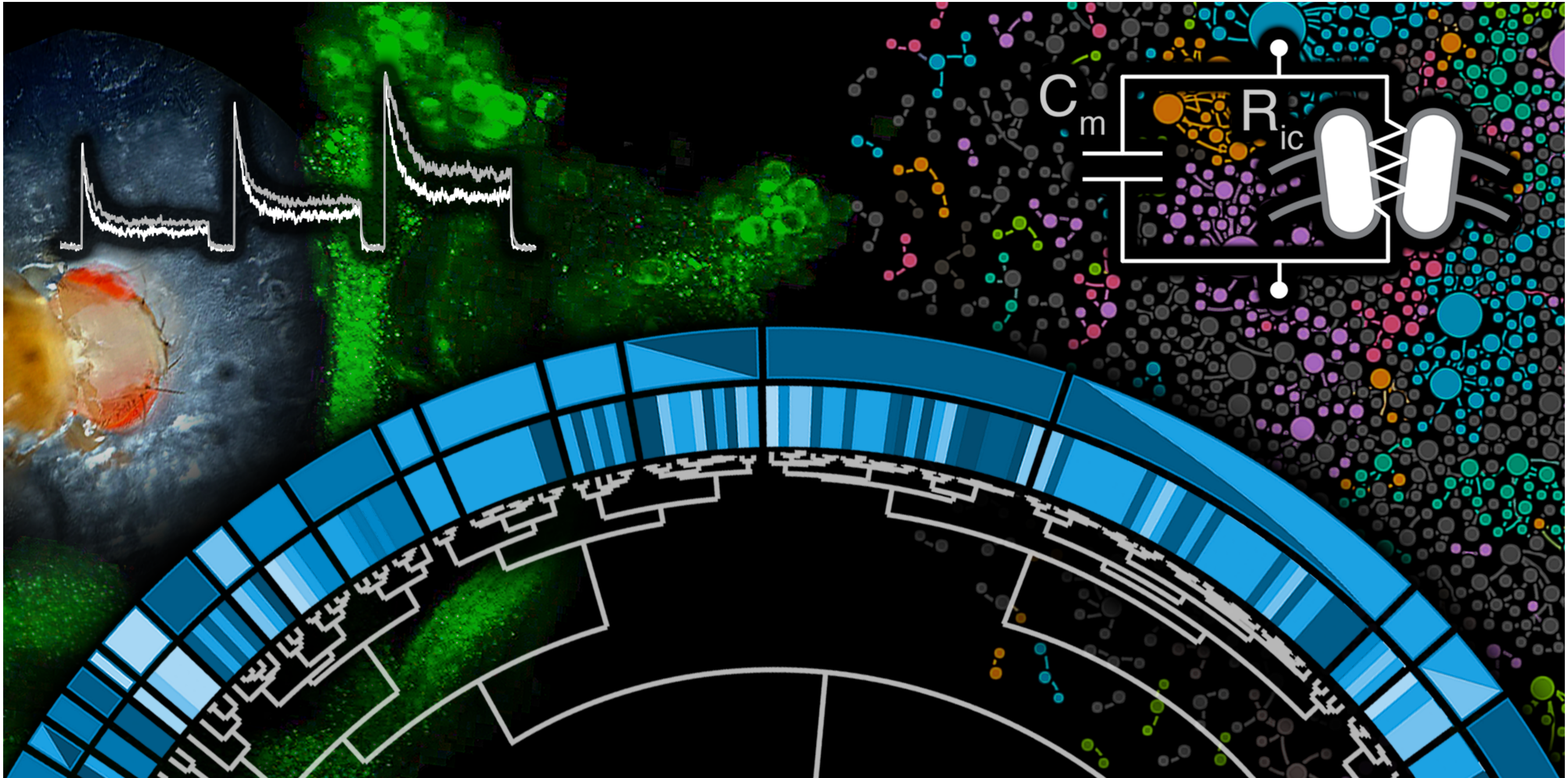






Mapping the function of neuronal ion channels in model and experiment

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



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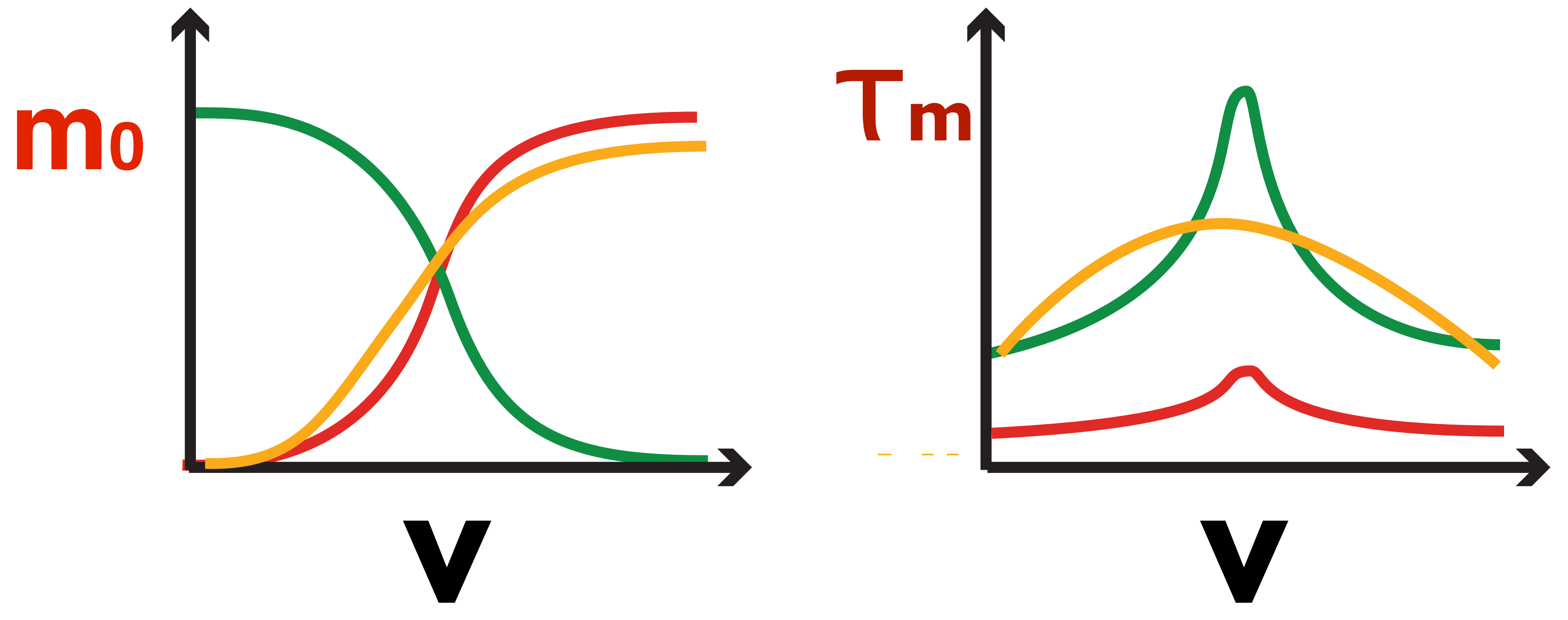

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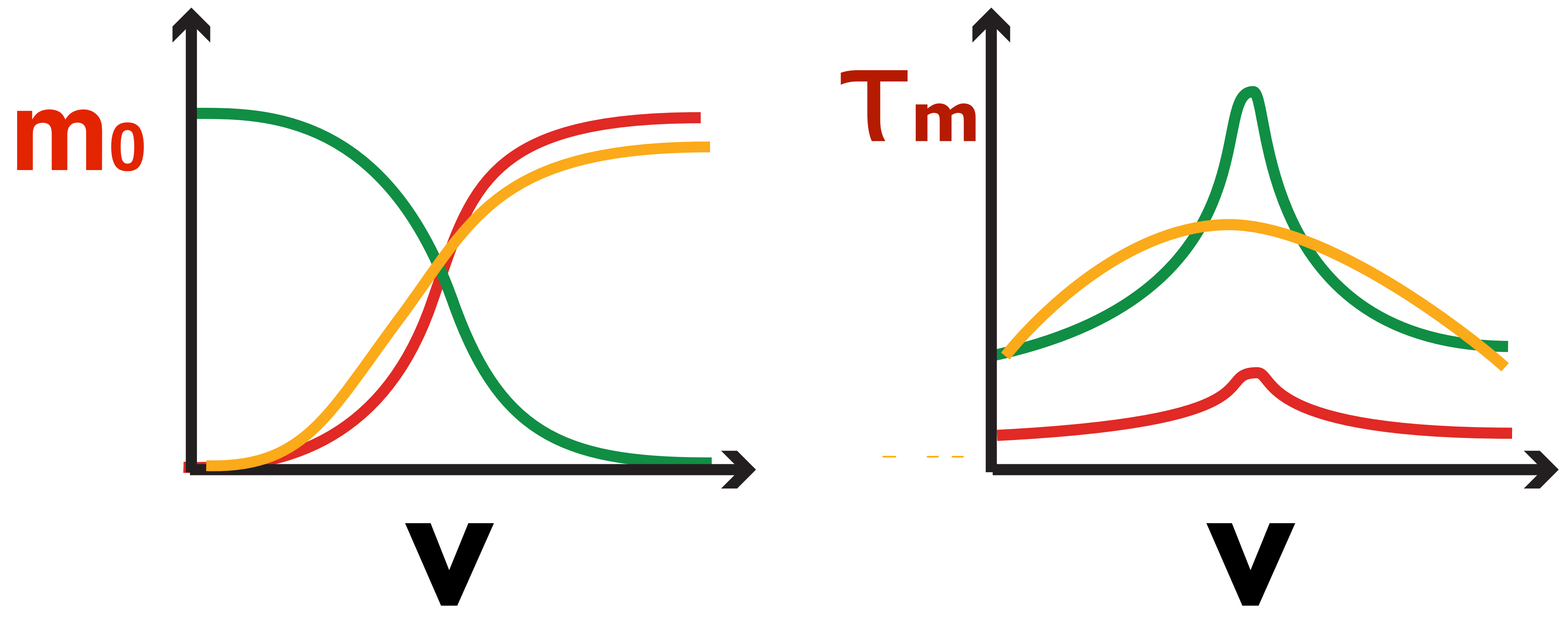

A complete description of neuron!

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

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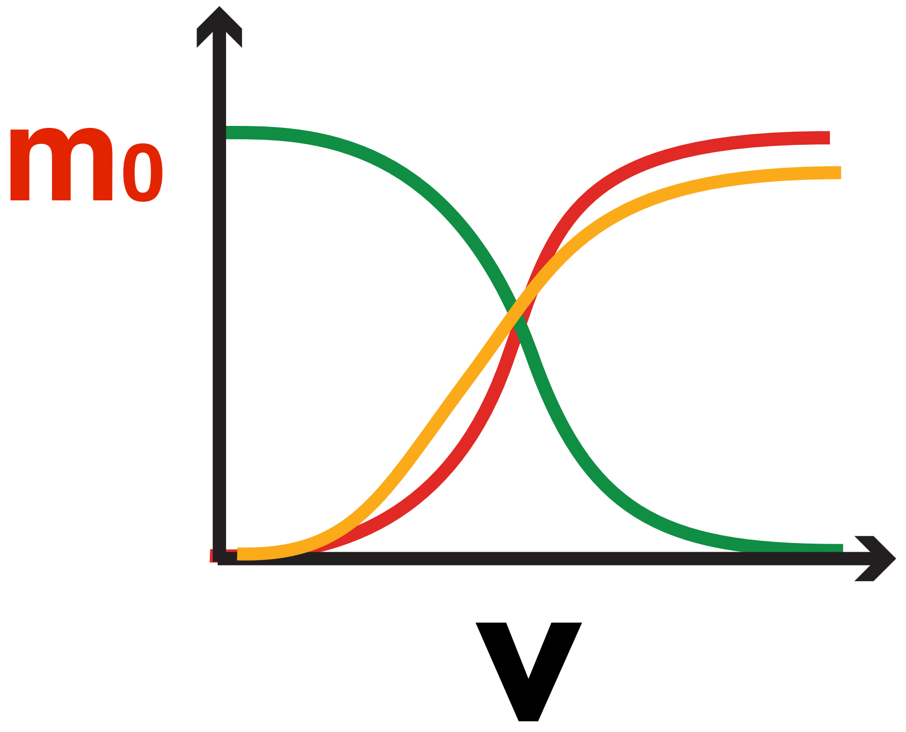

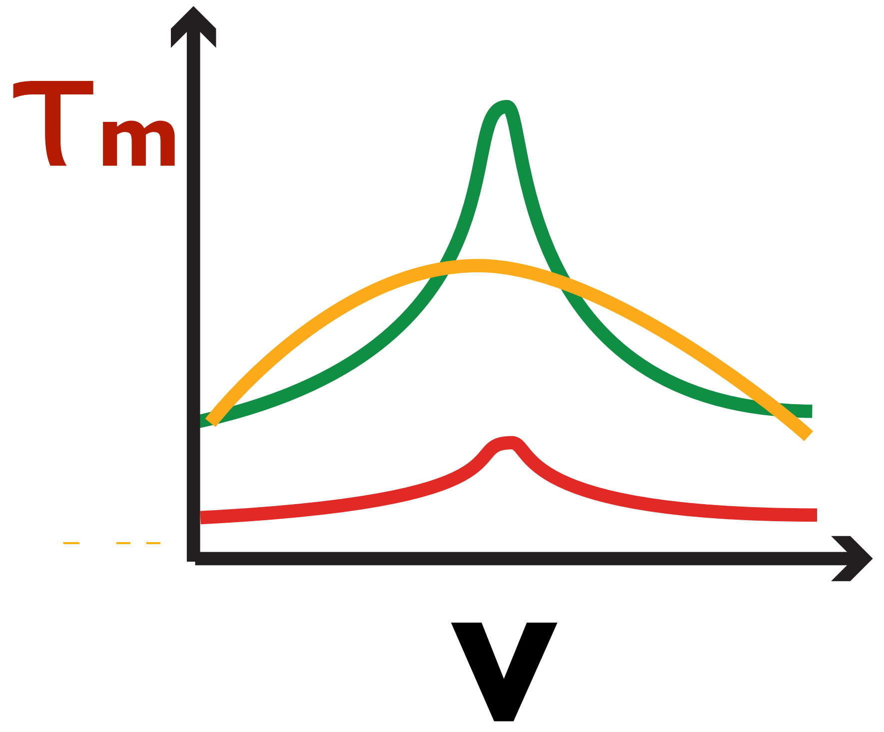

A complete description of neuron!

For easy access to any channel:

http://vogelslab.org/icgenealogy

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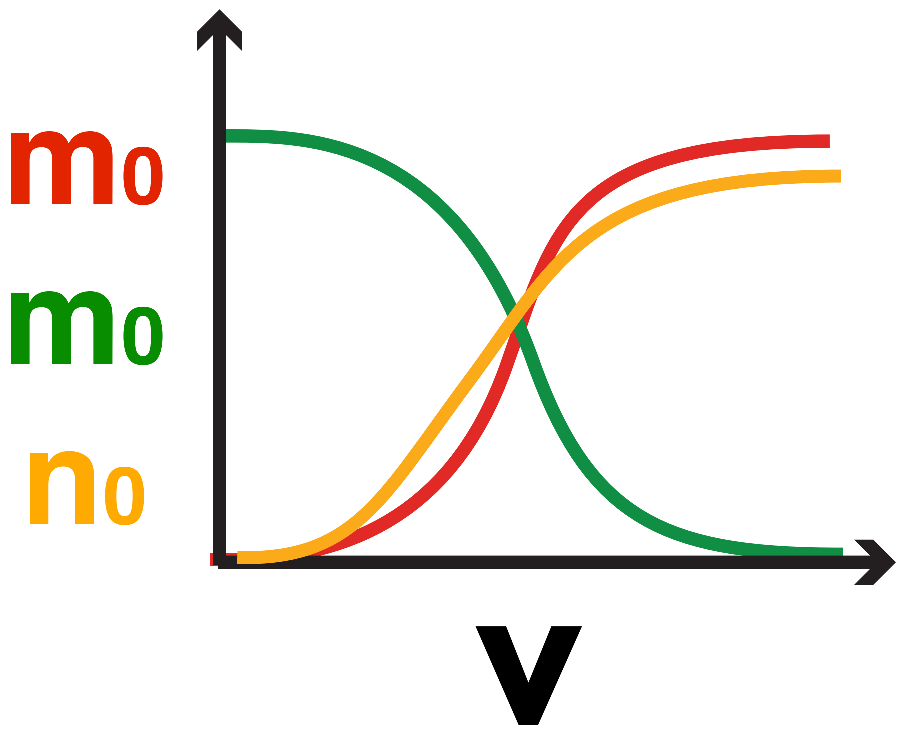

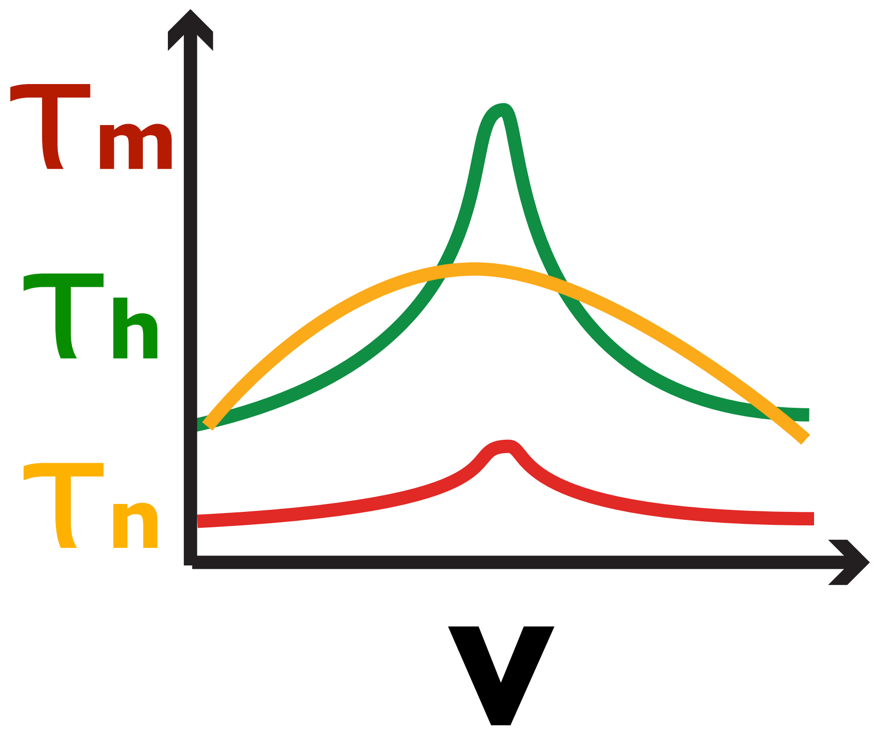

But do we understand, fully, mathematically?

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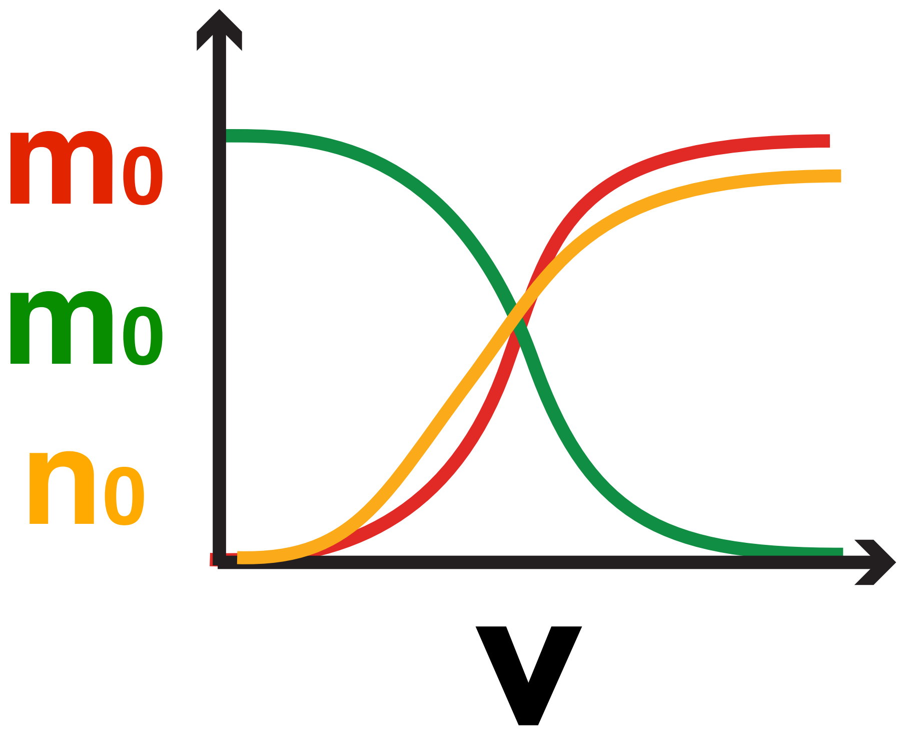

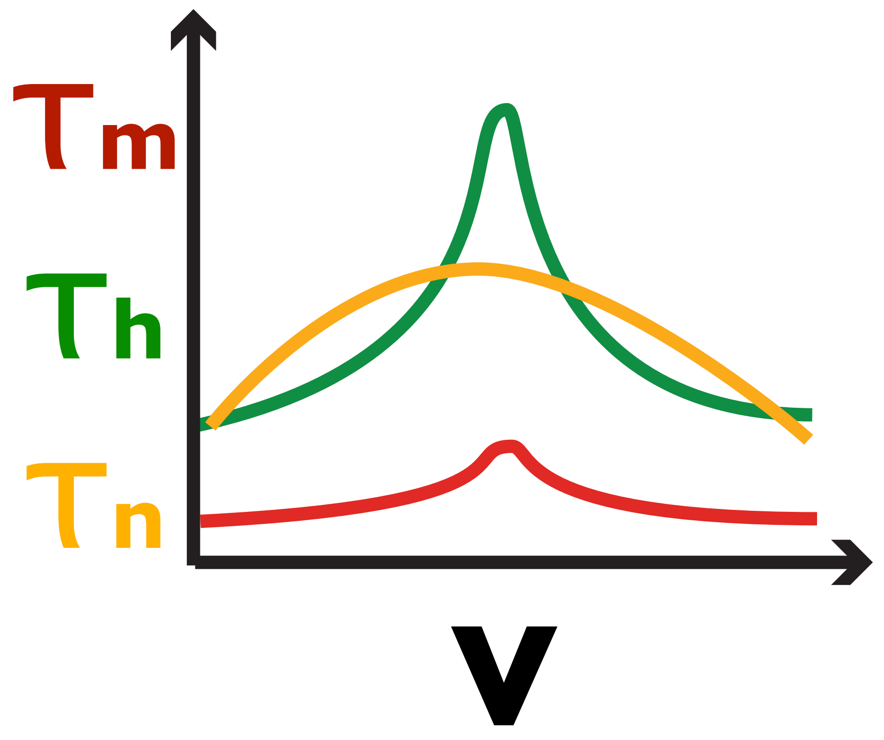

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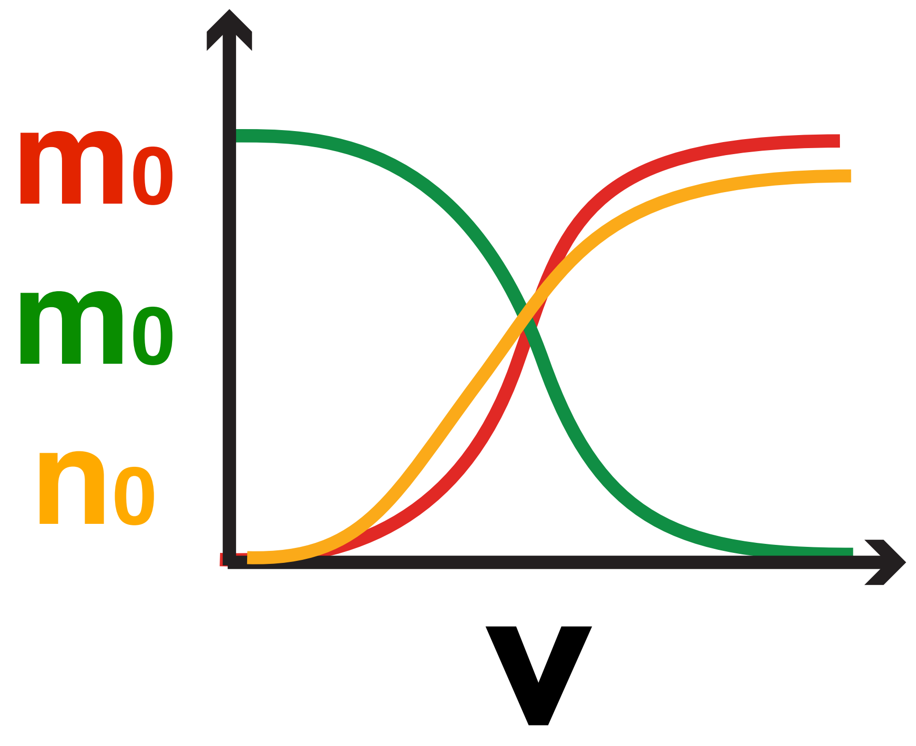

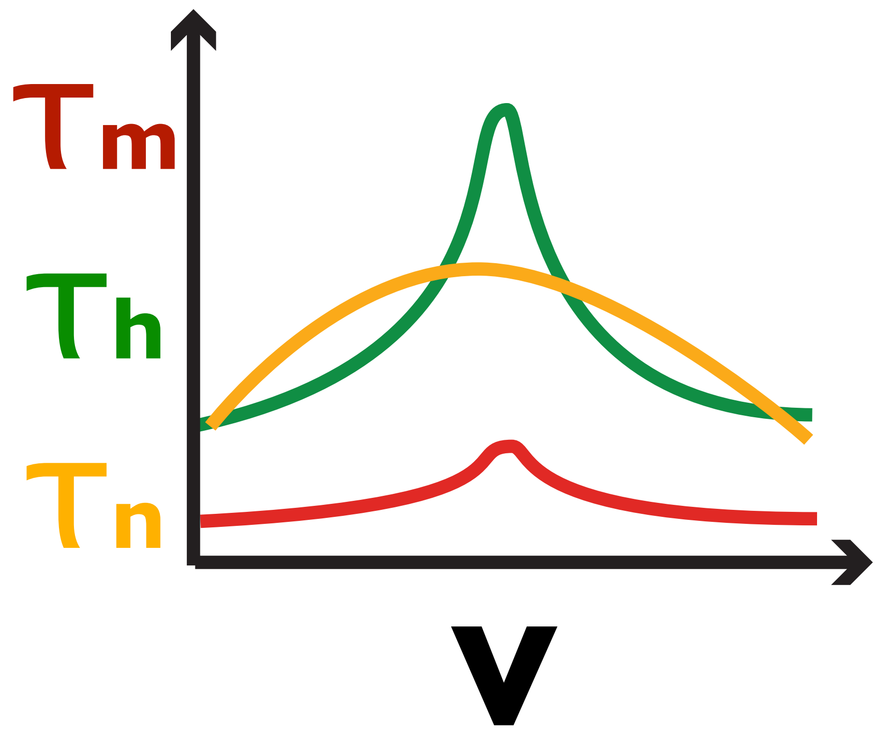

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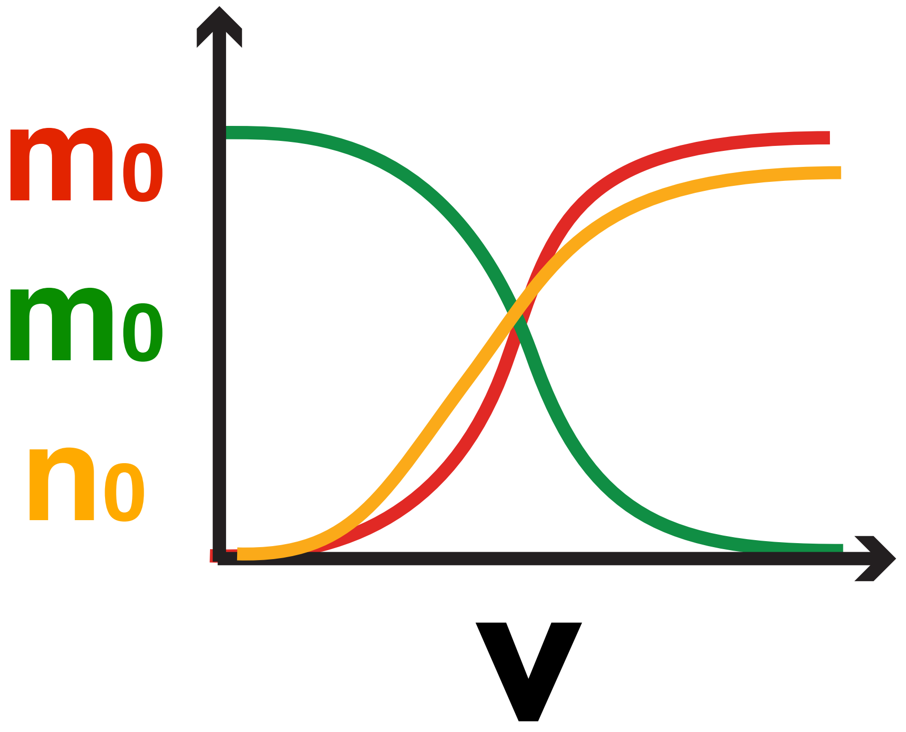

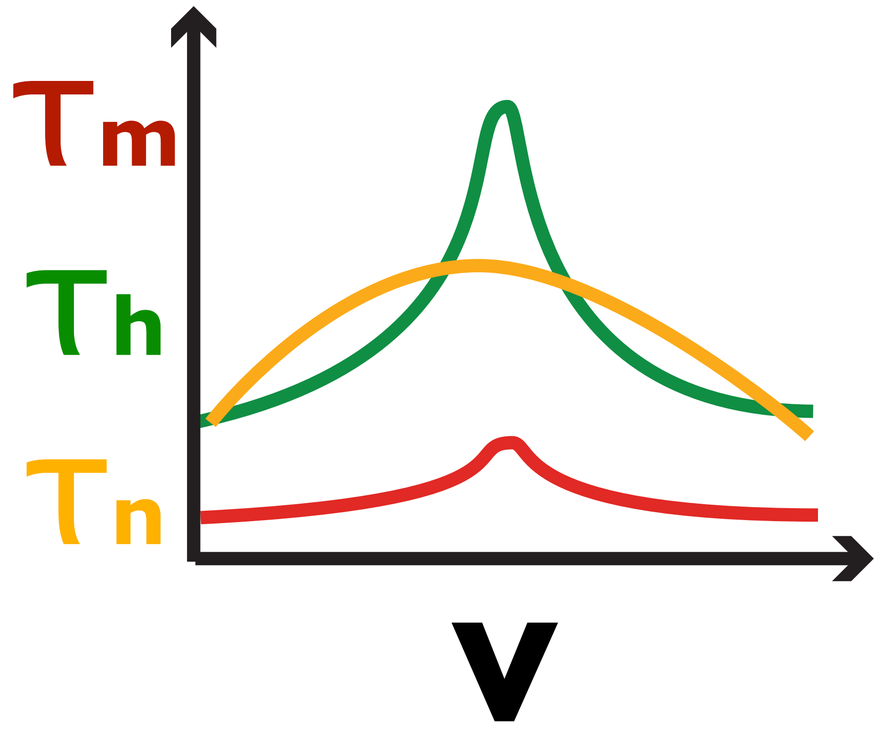

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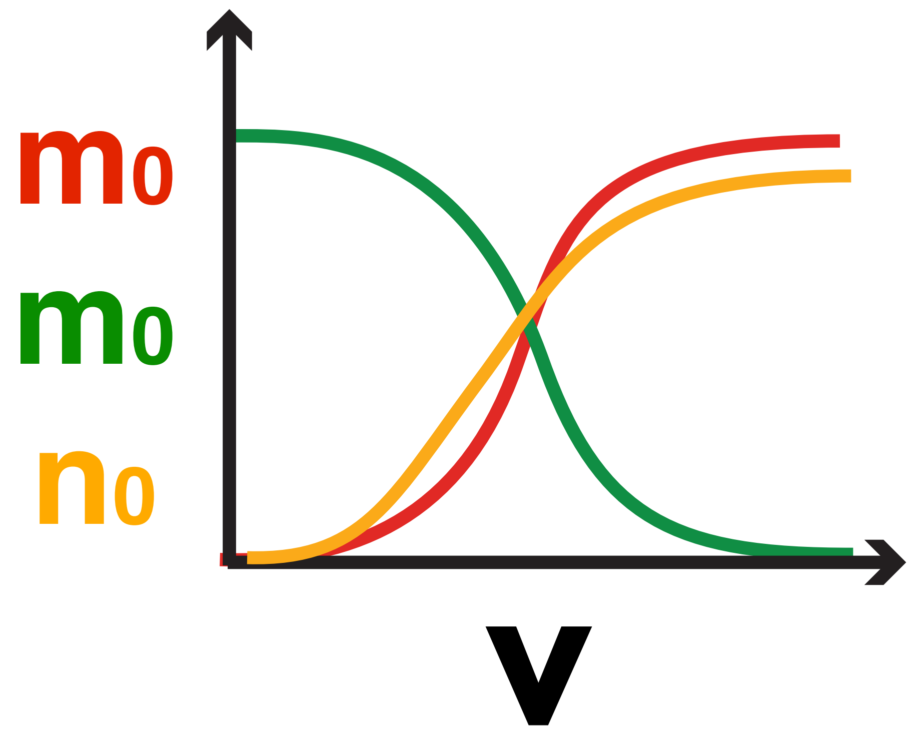

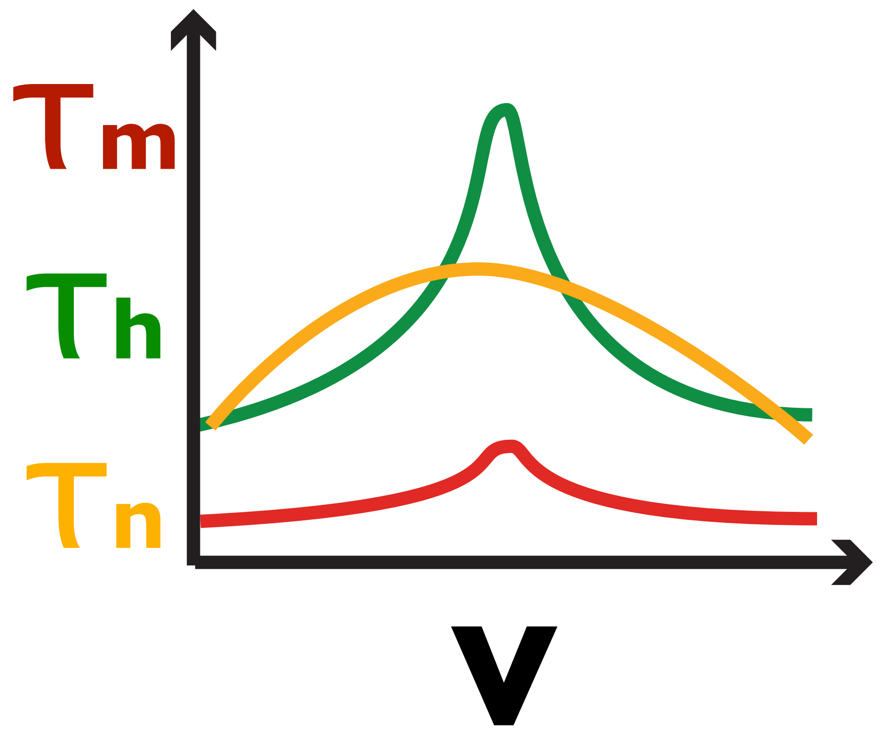

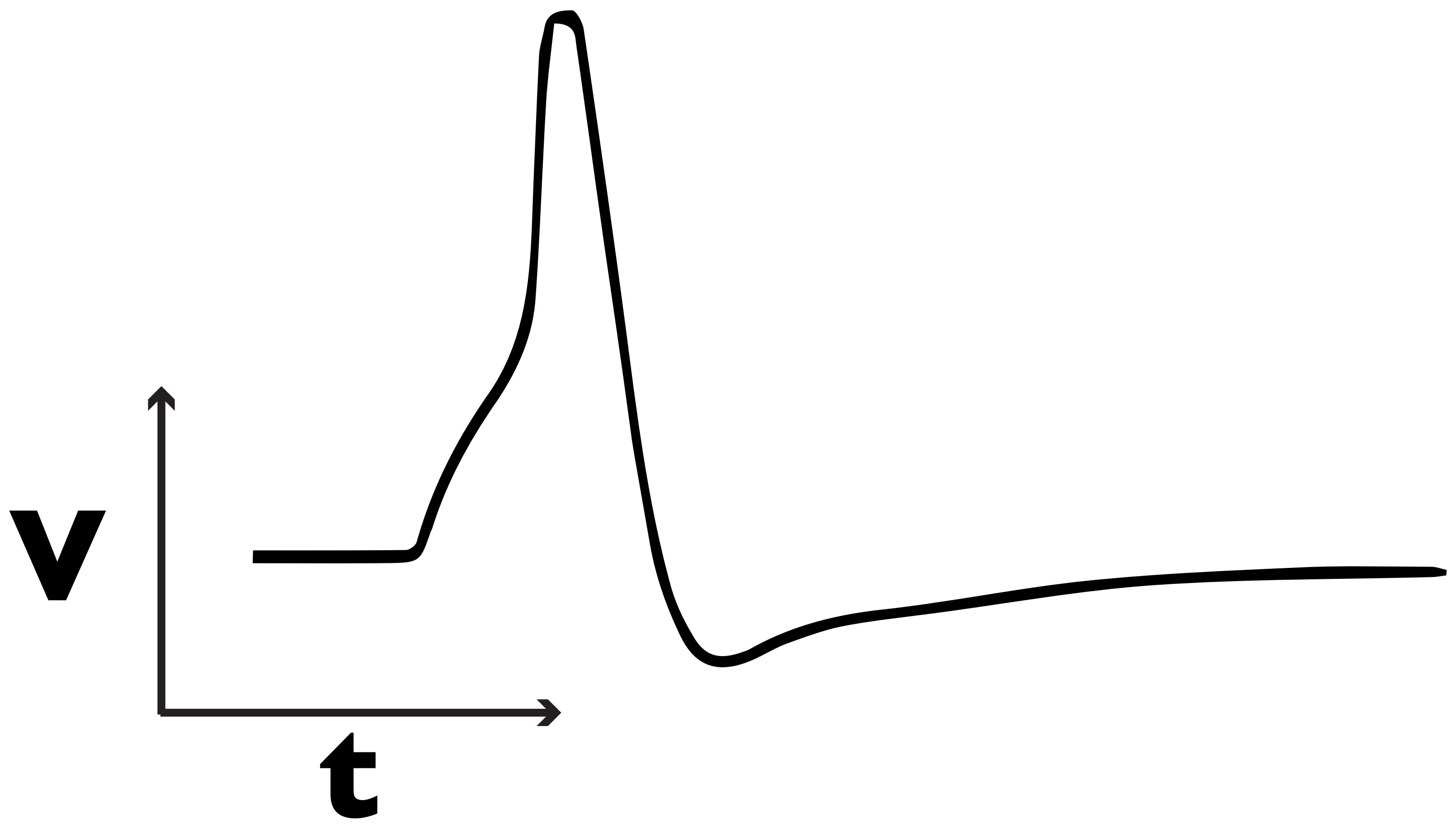

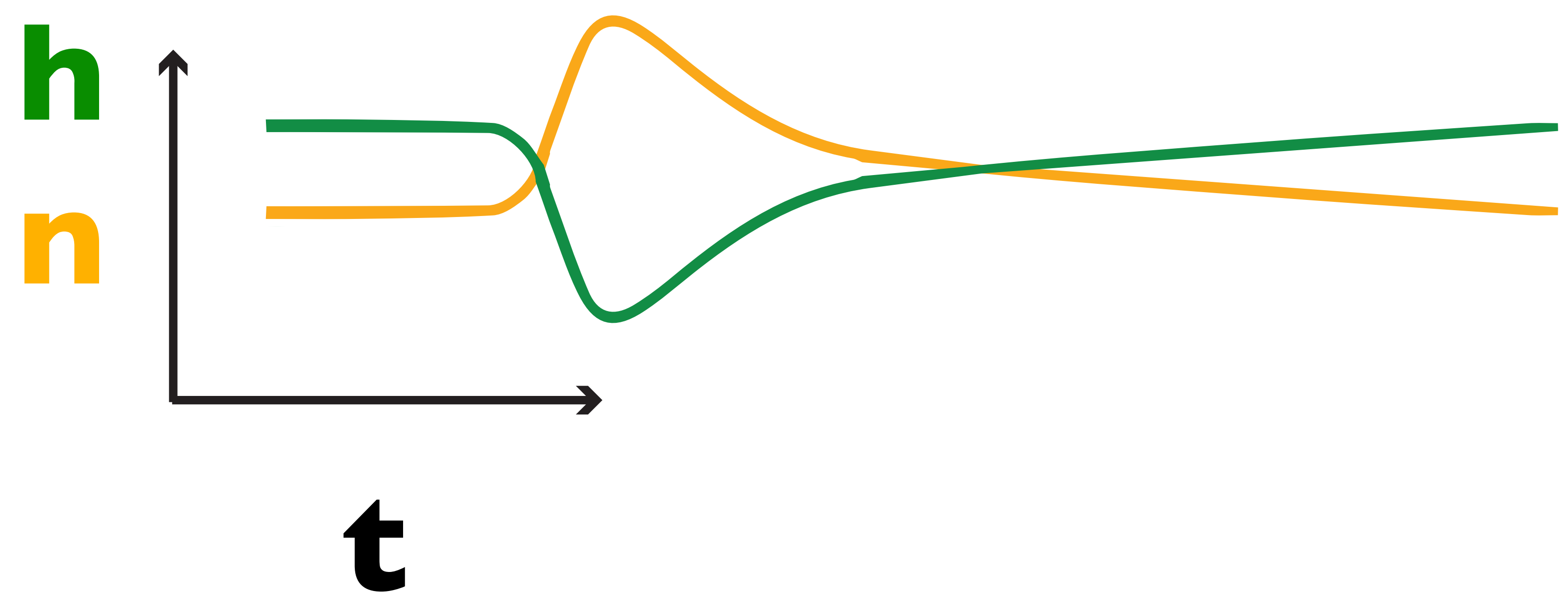

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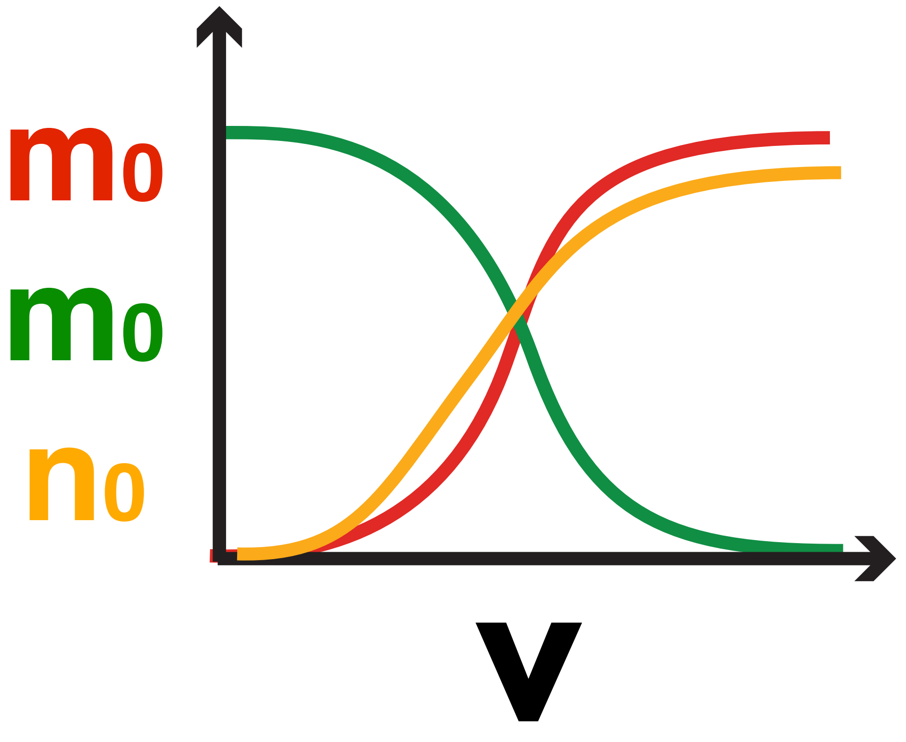

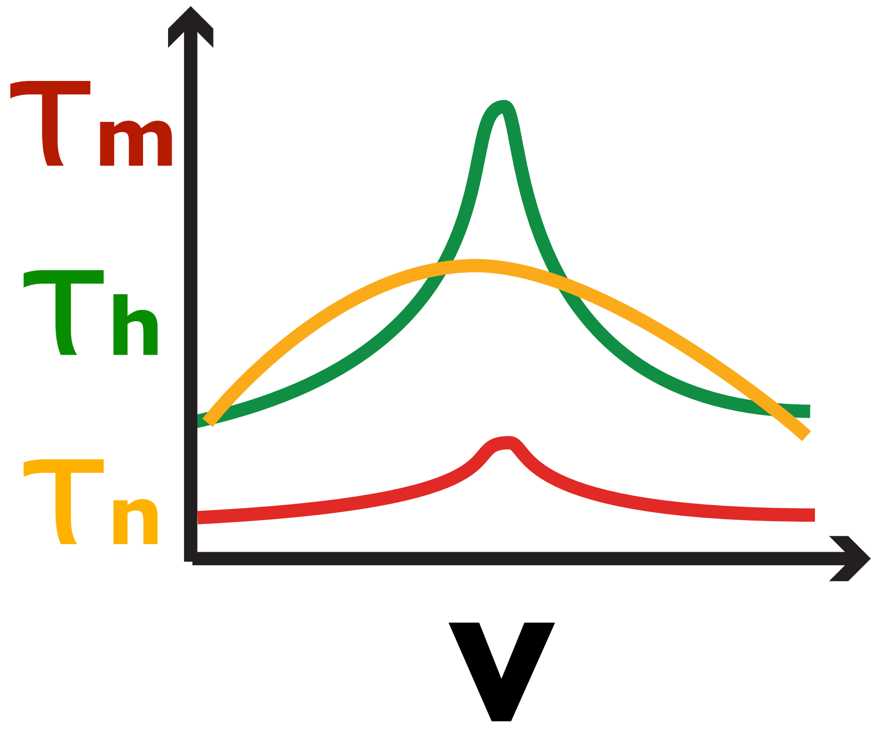

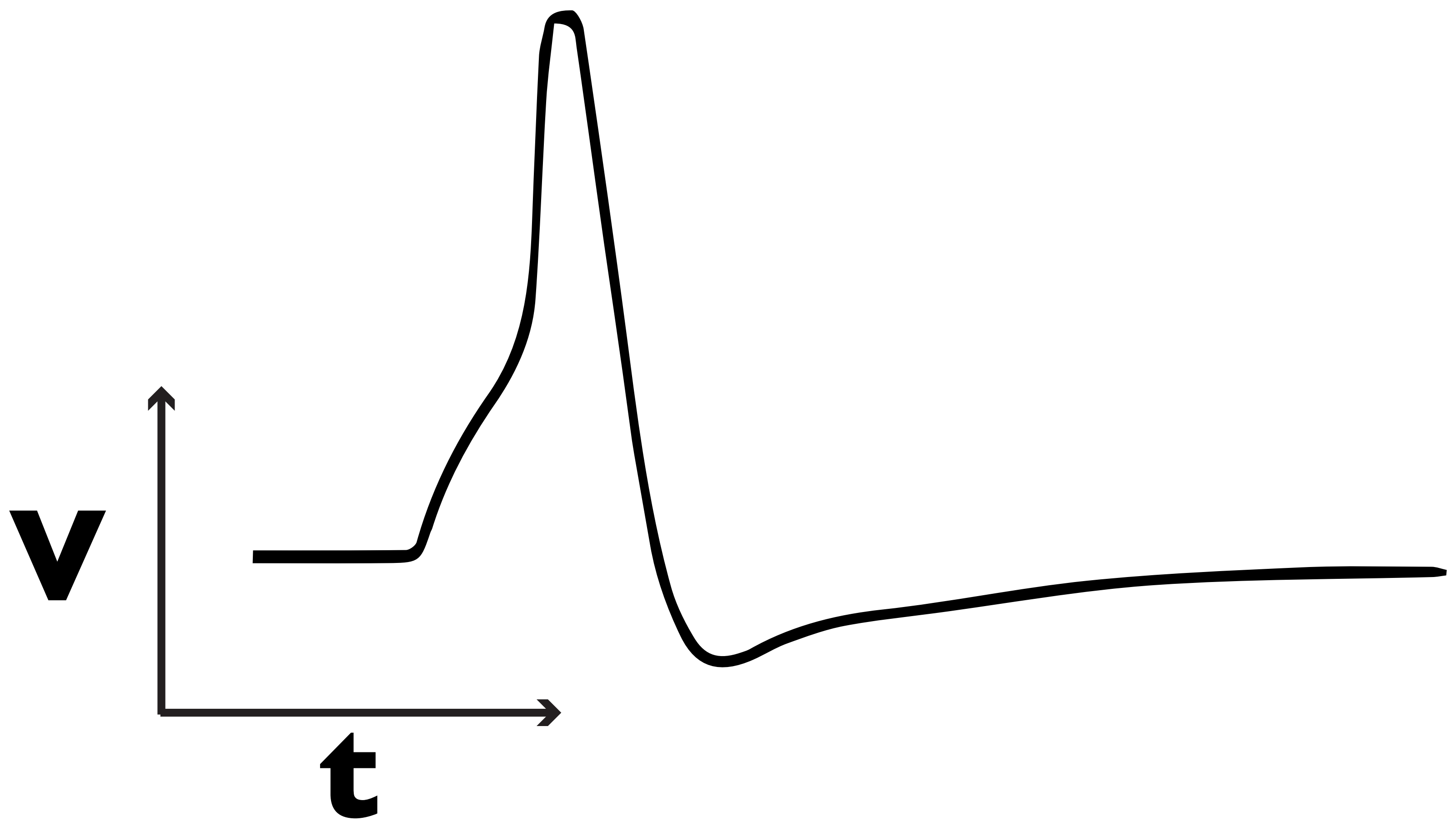

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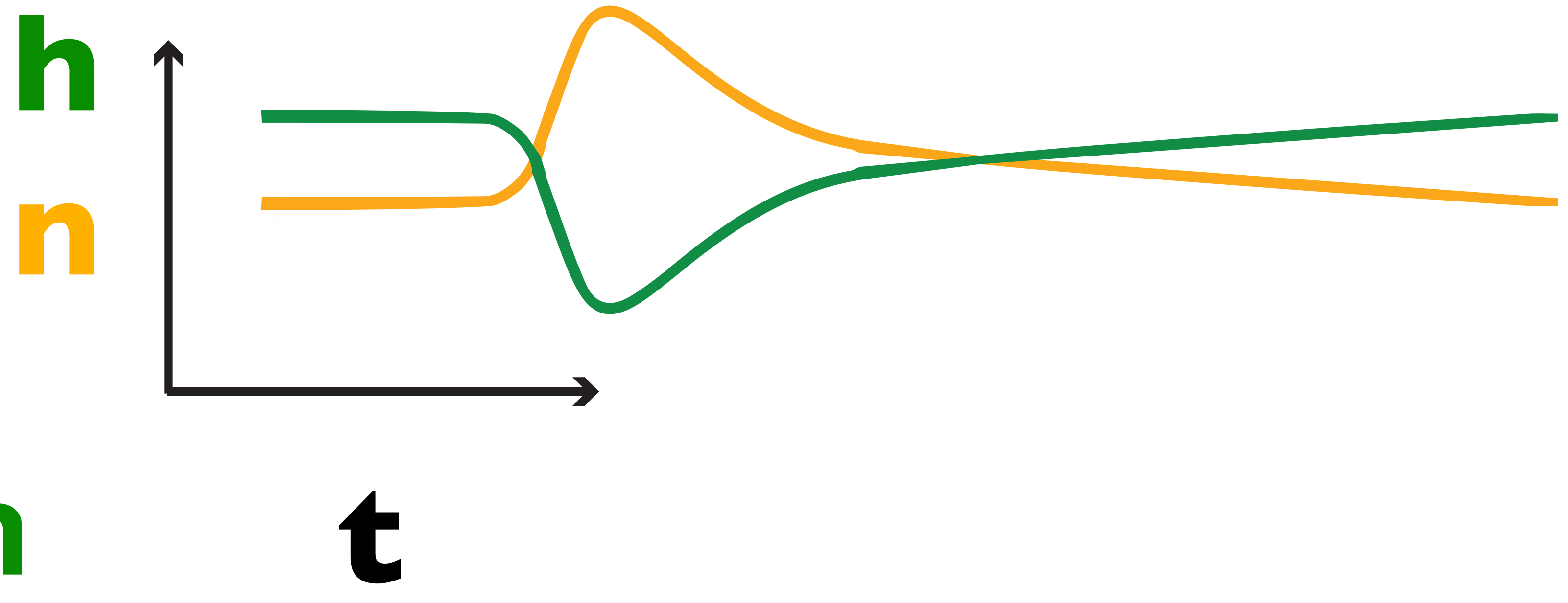

$an = 1-h$

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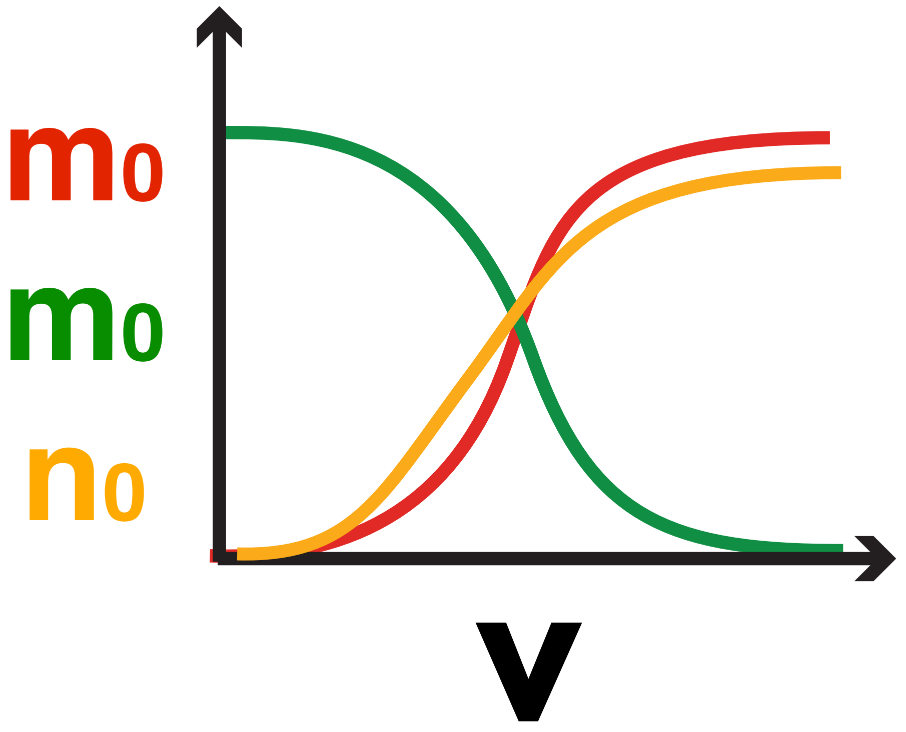

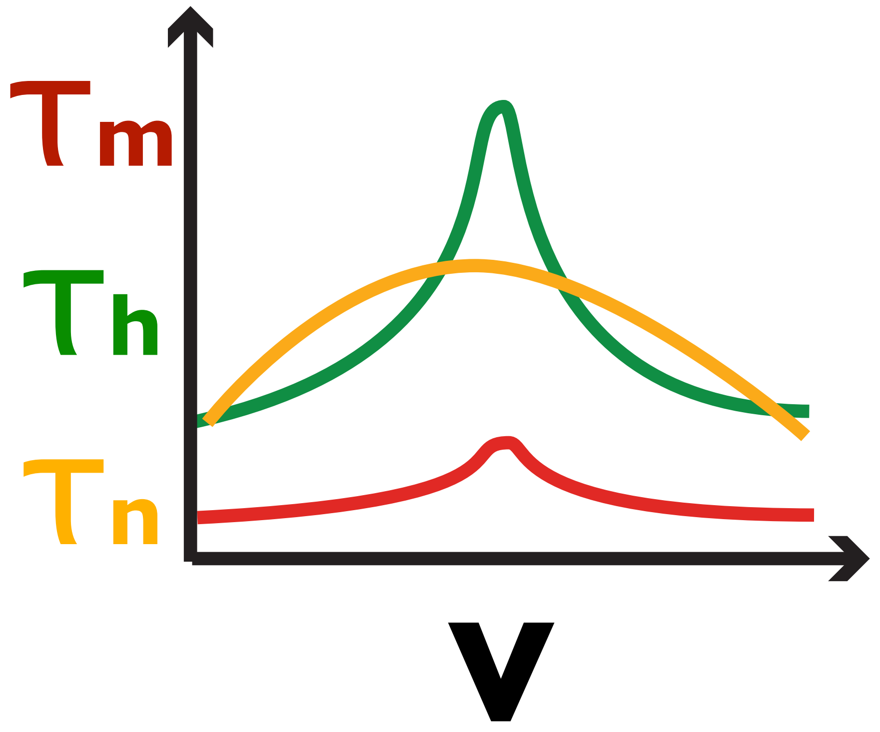

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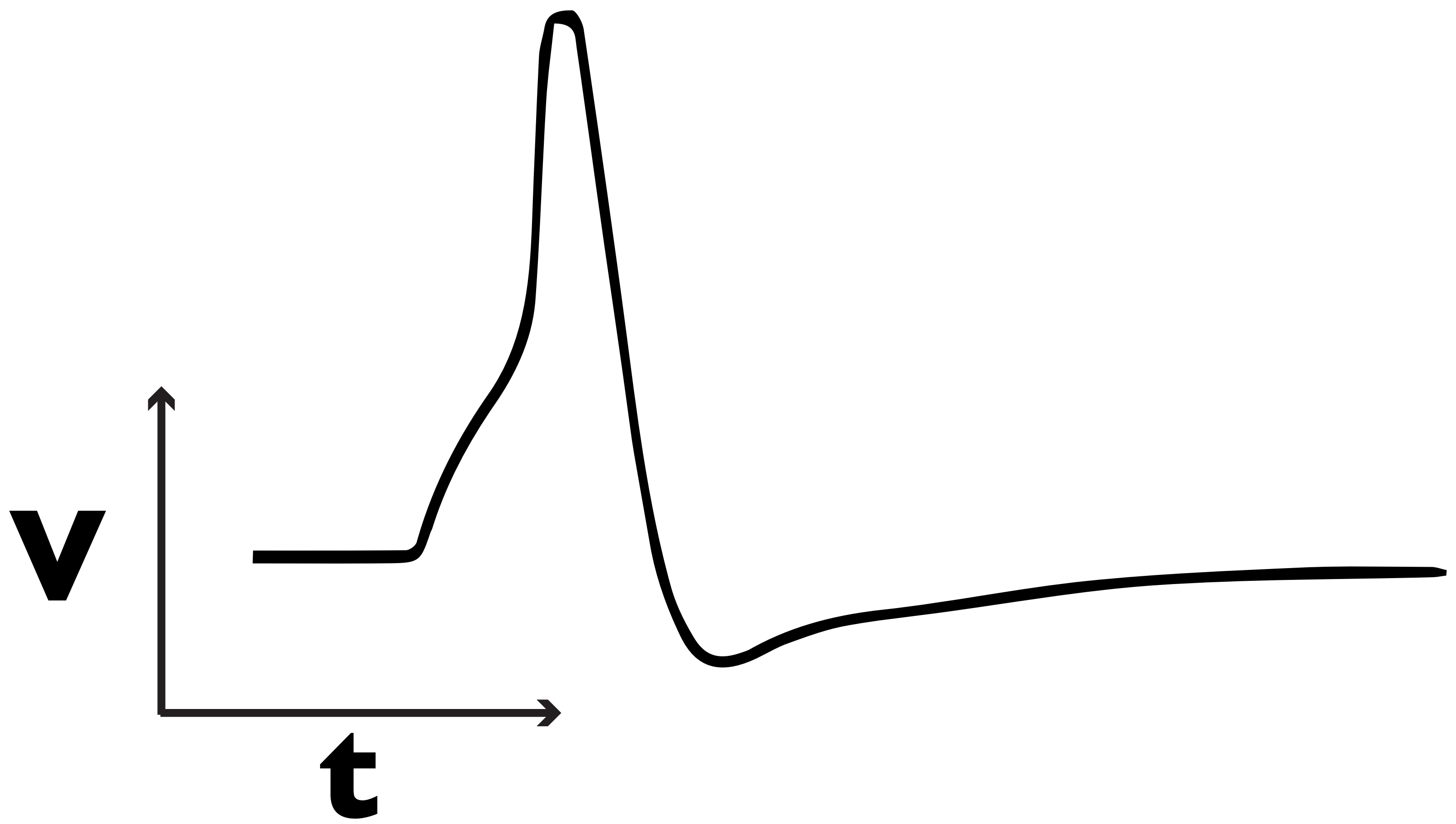

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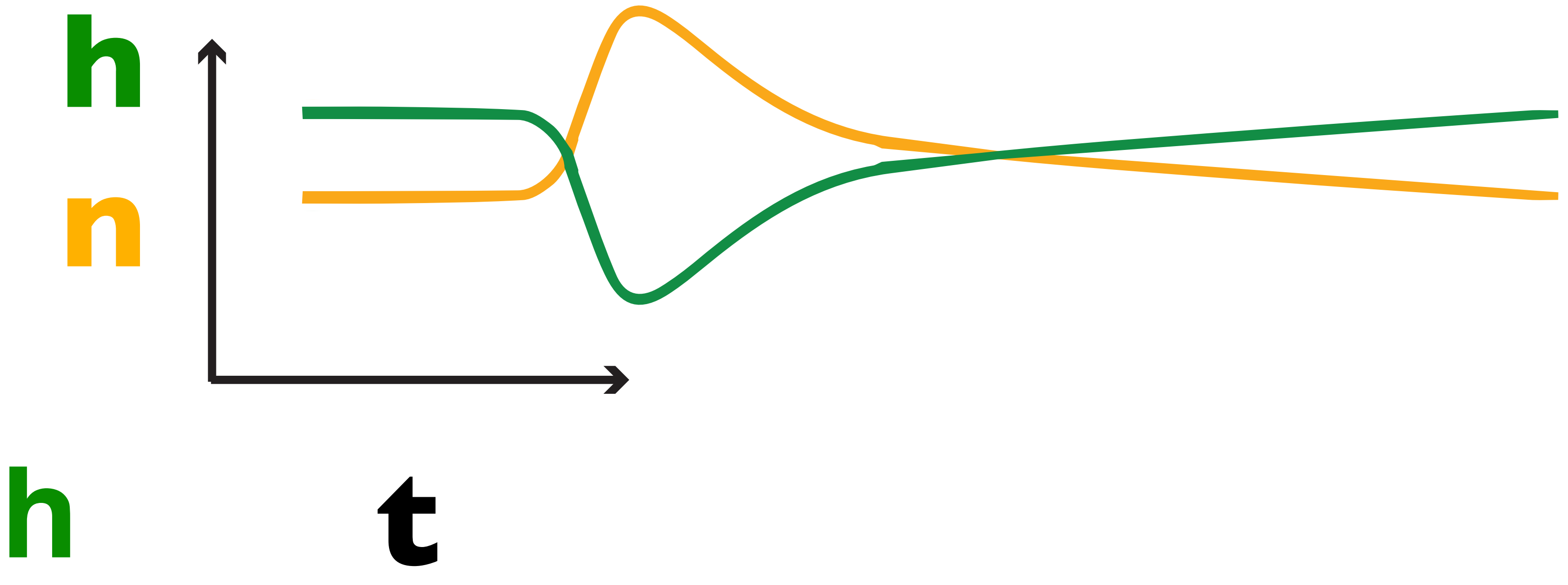

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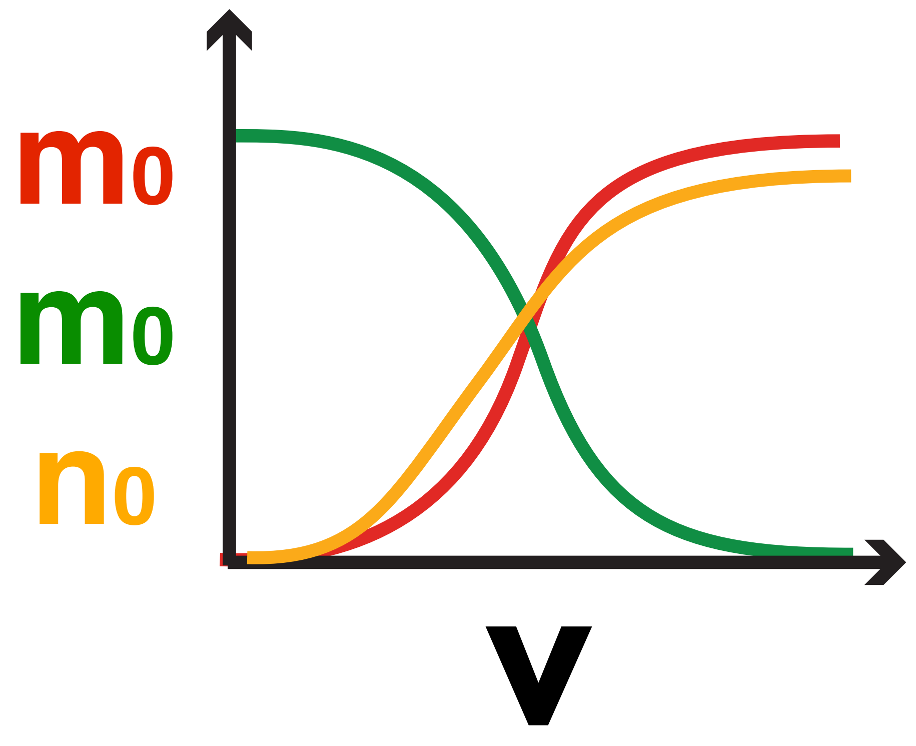

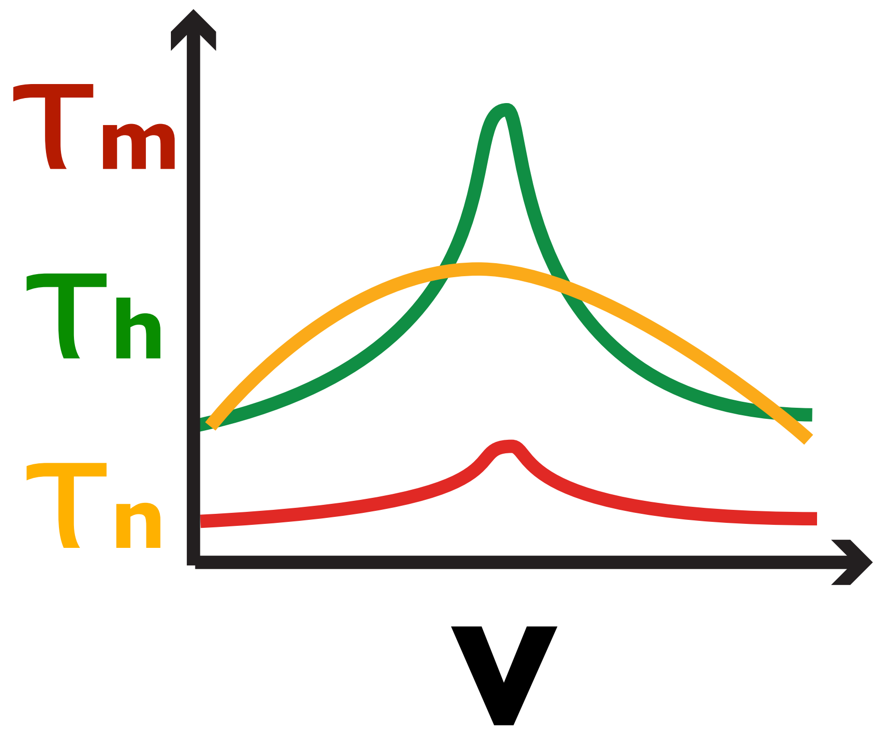

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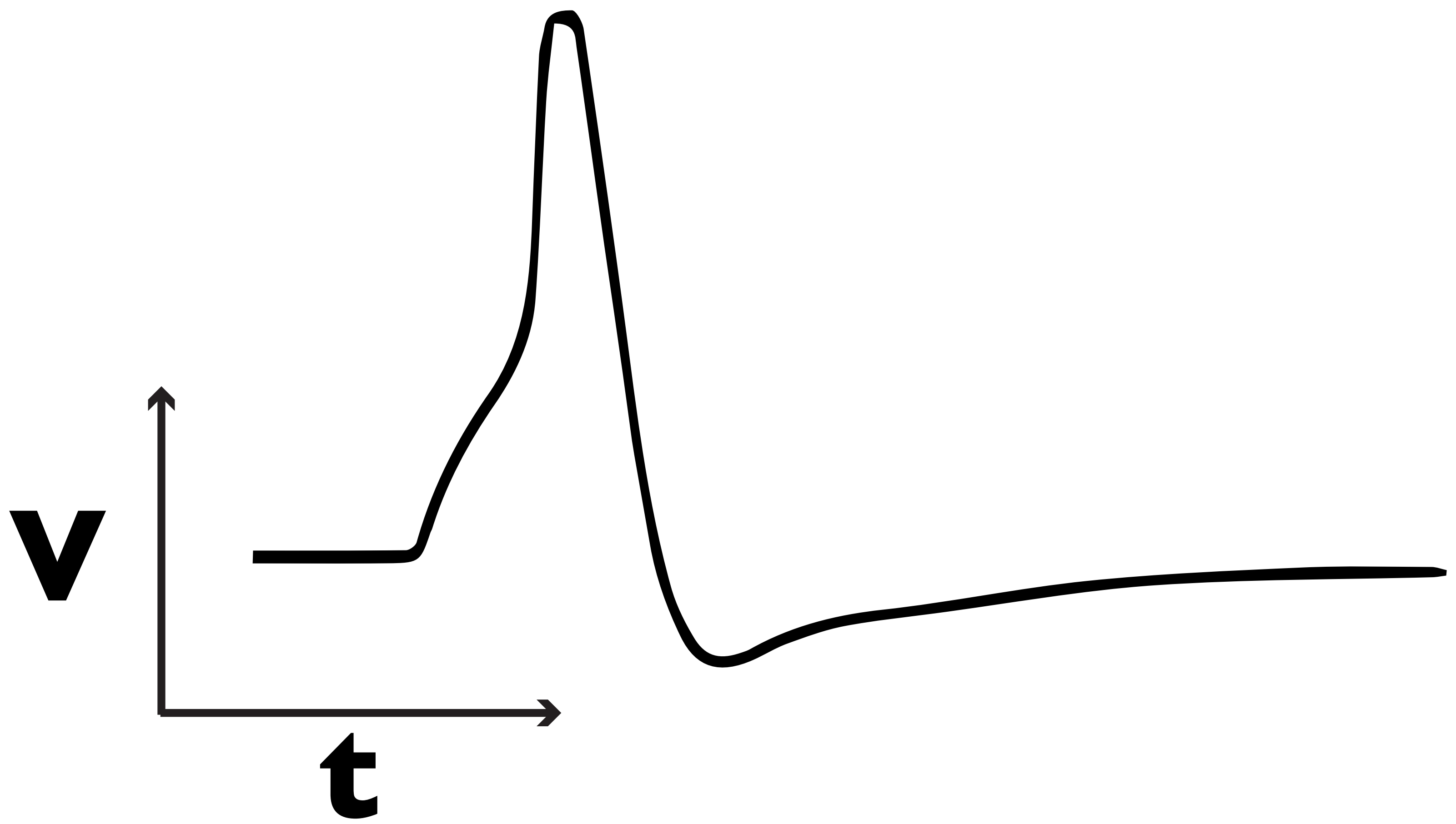

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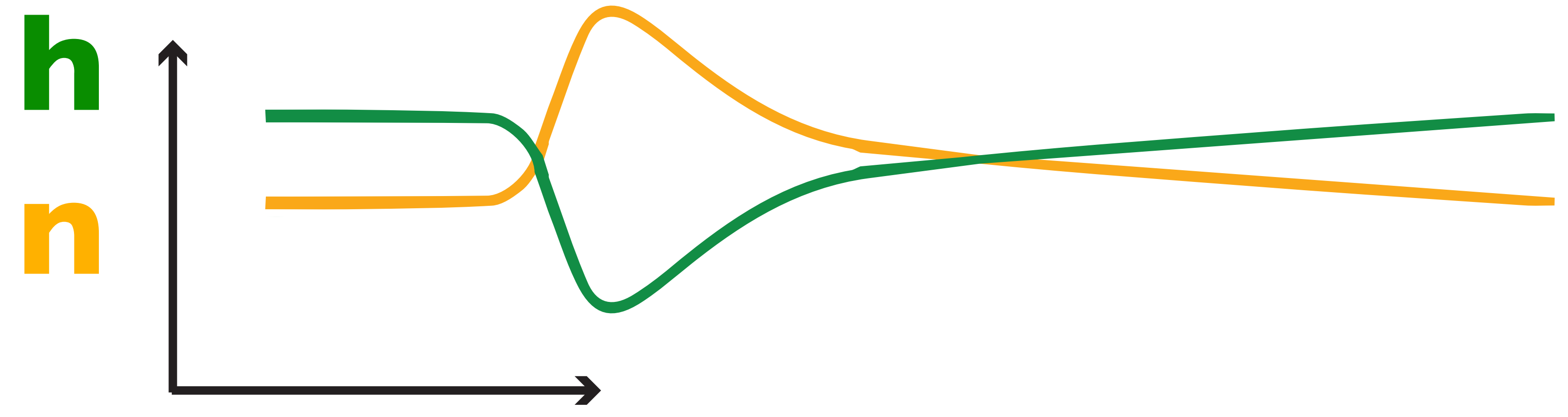

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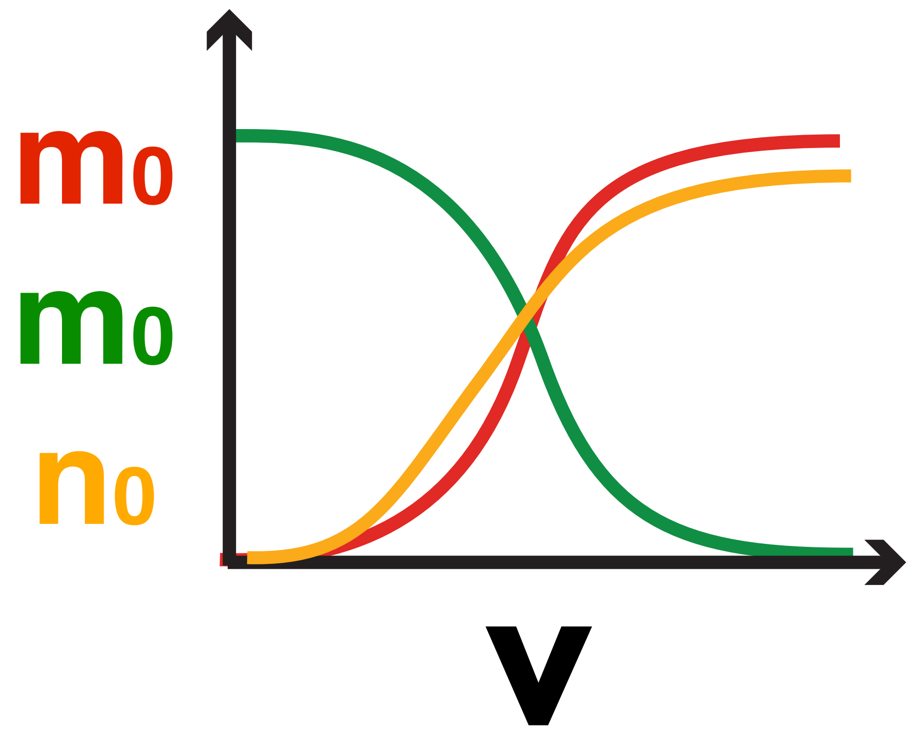

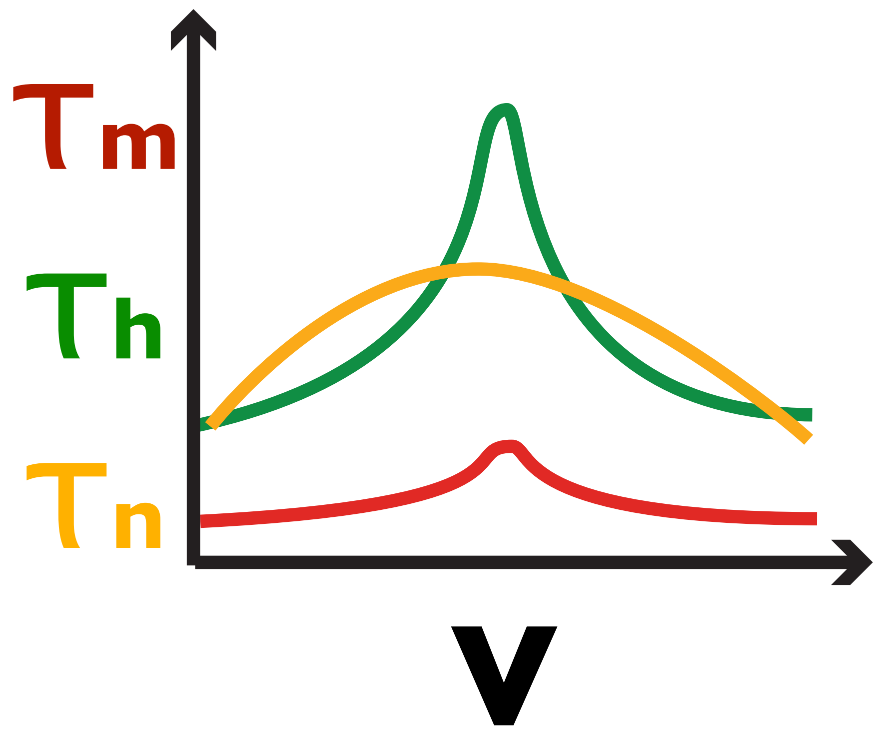

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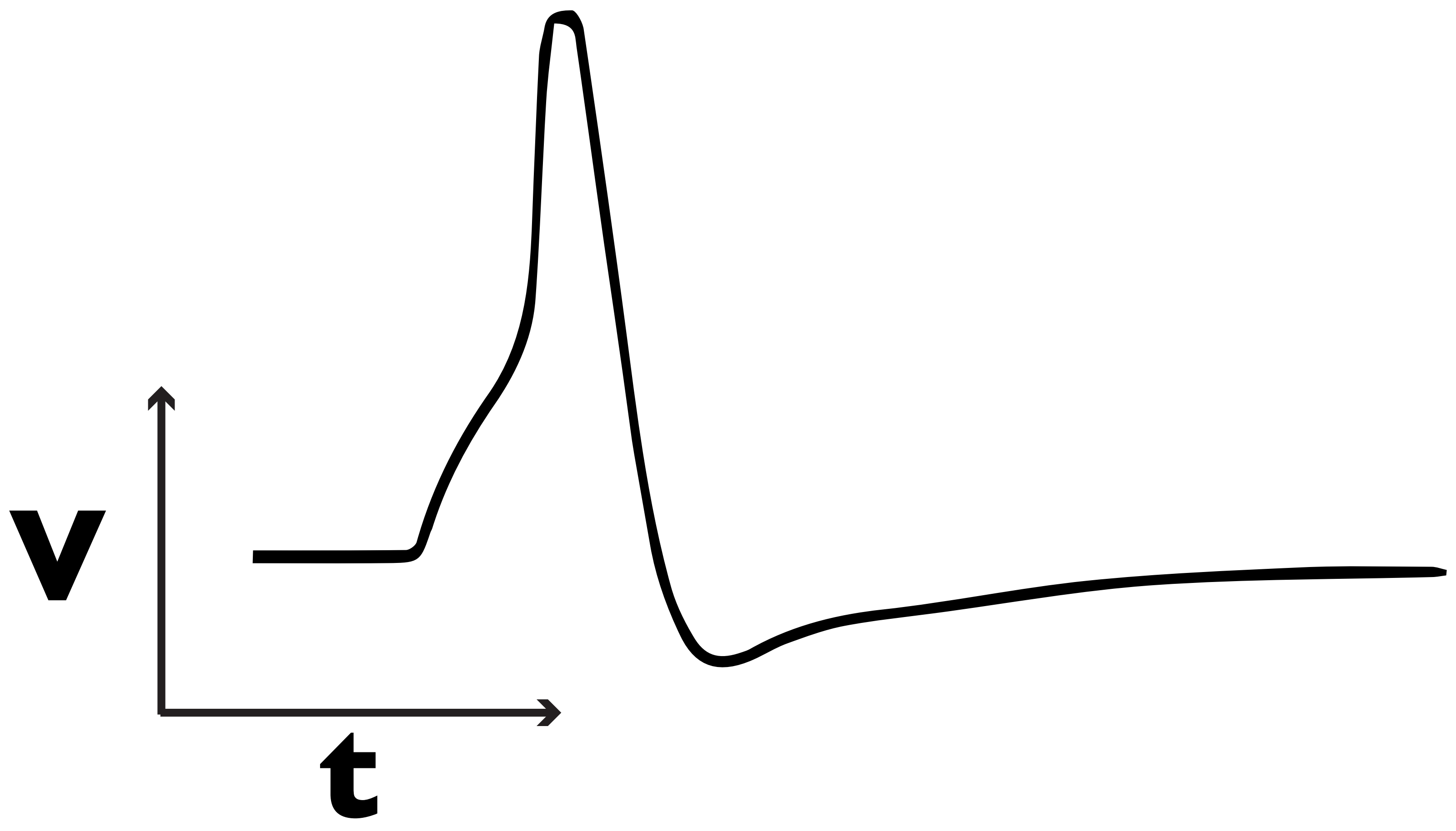

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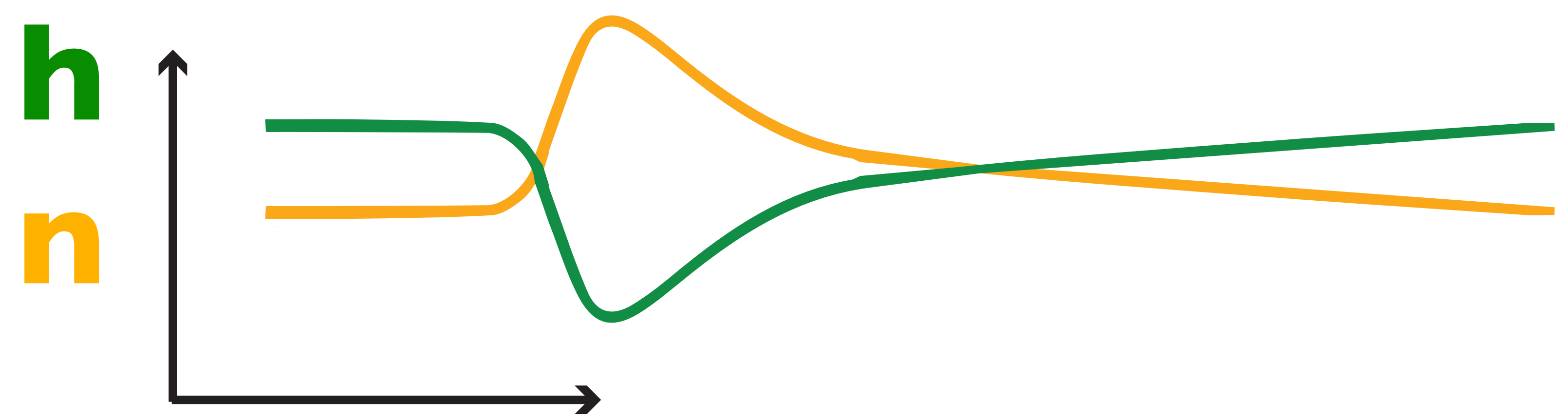

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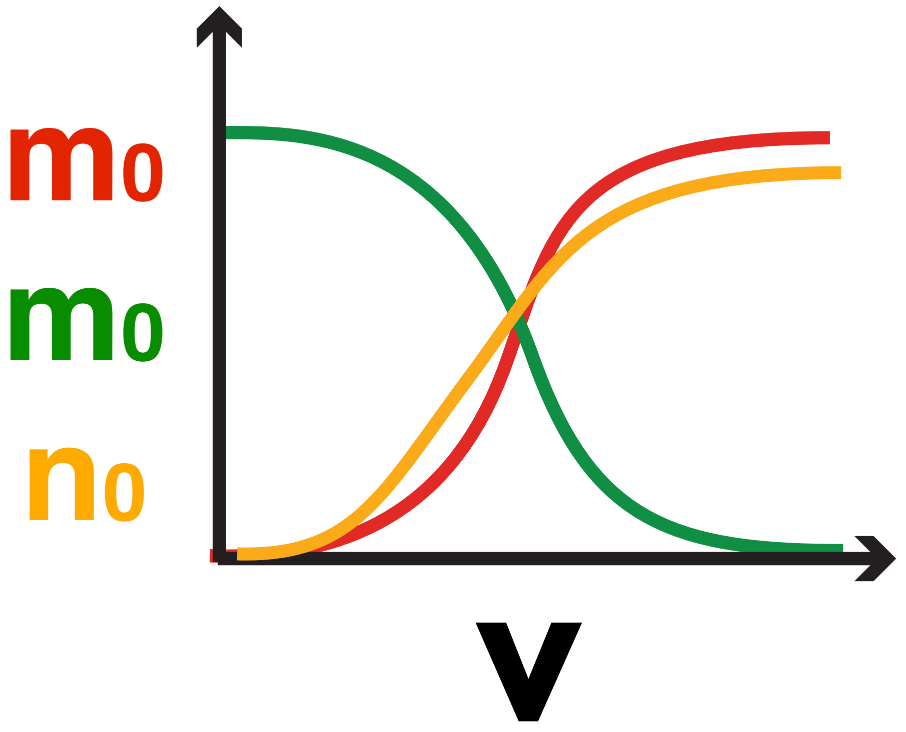

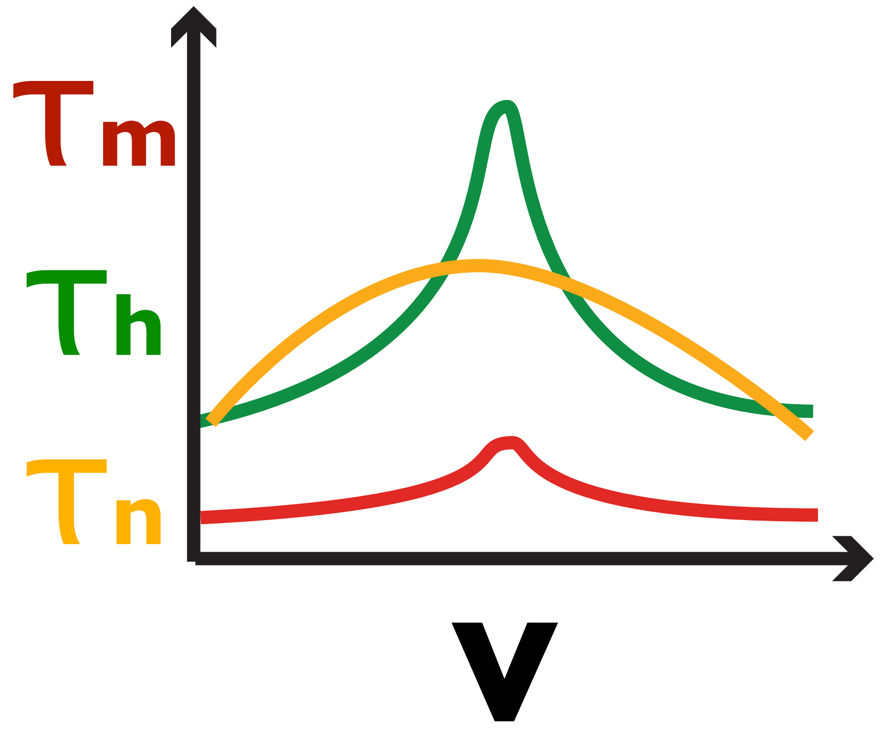

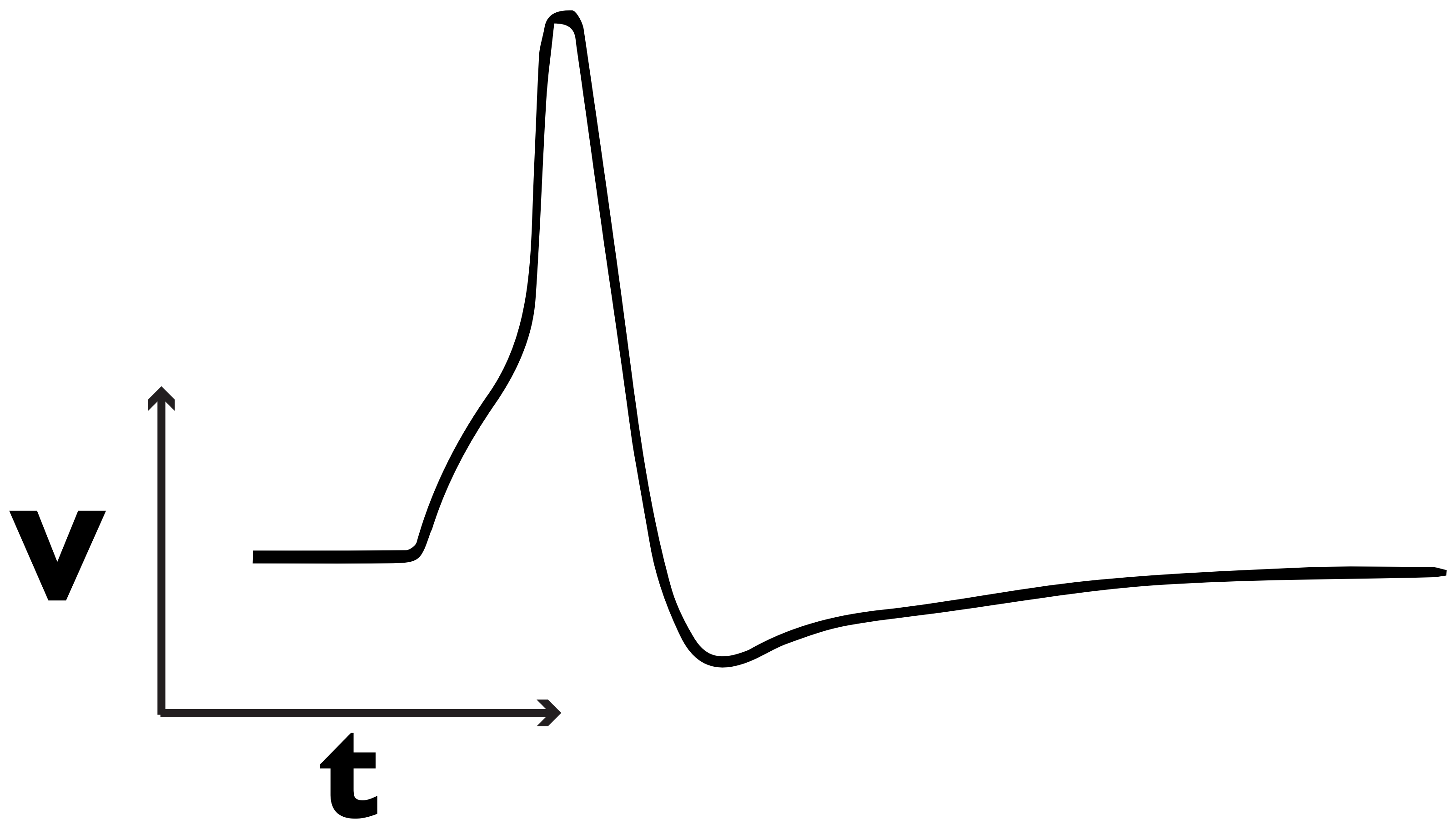

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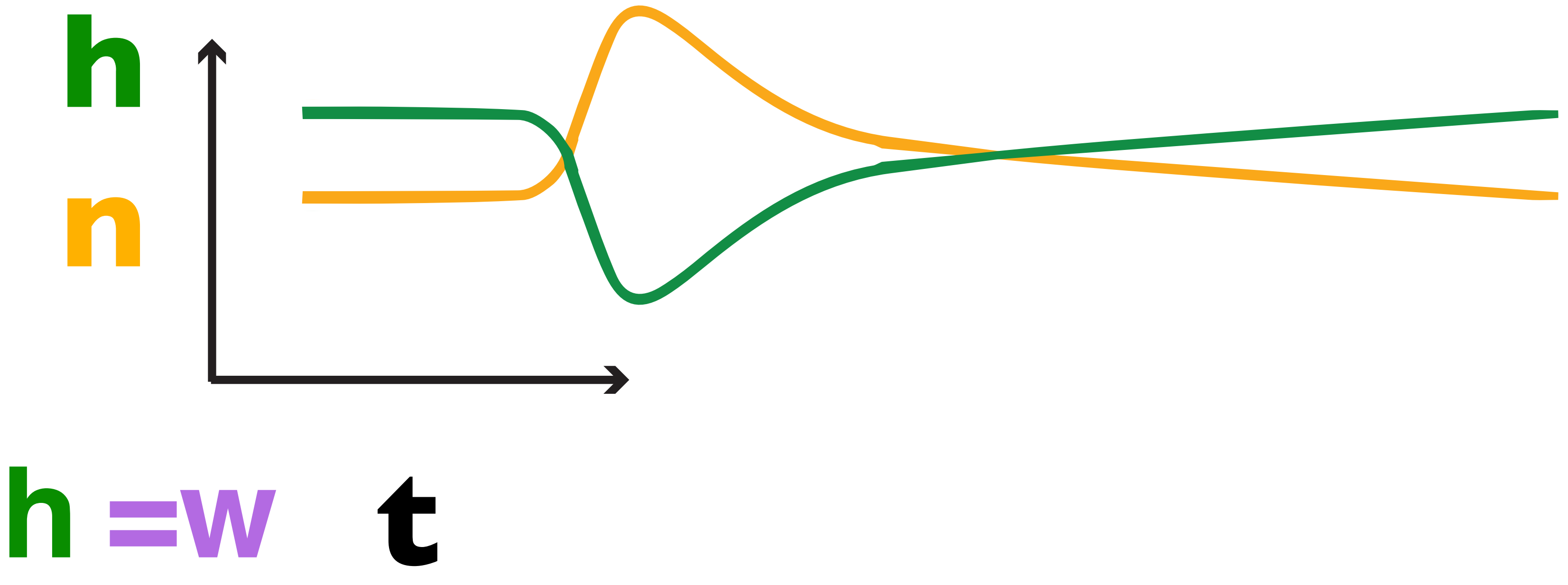

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$$\frac{dw}{dt} = \frac{w - w_0(V)}{\tau_n(V)}$$

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

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

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

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

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

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

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FitzHugh-Nagumo model

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

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

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

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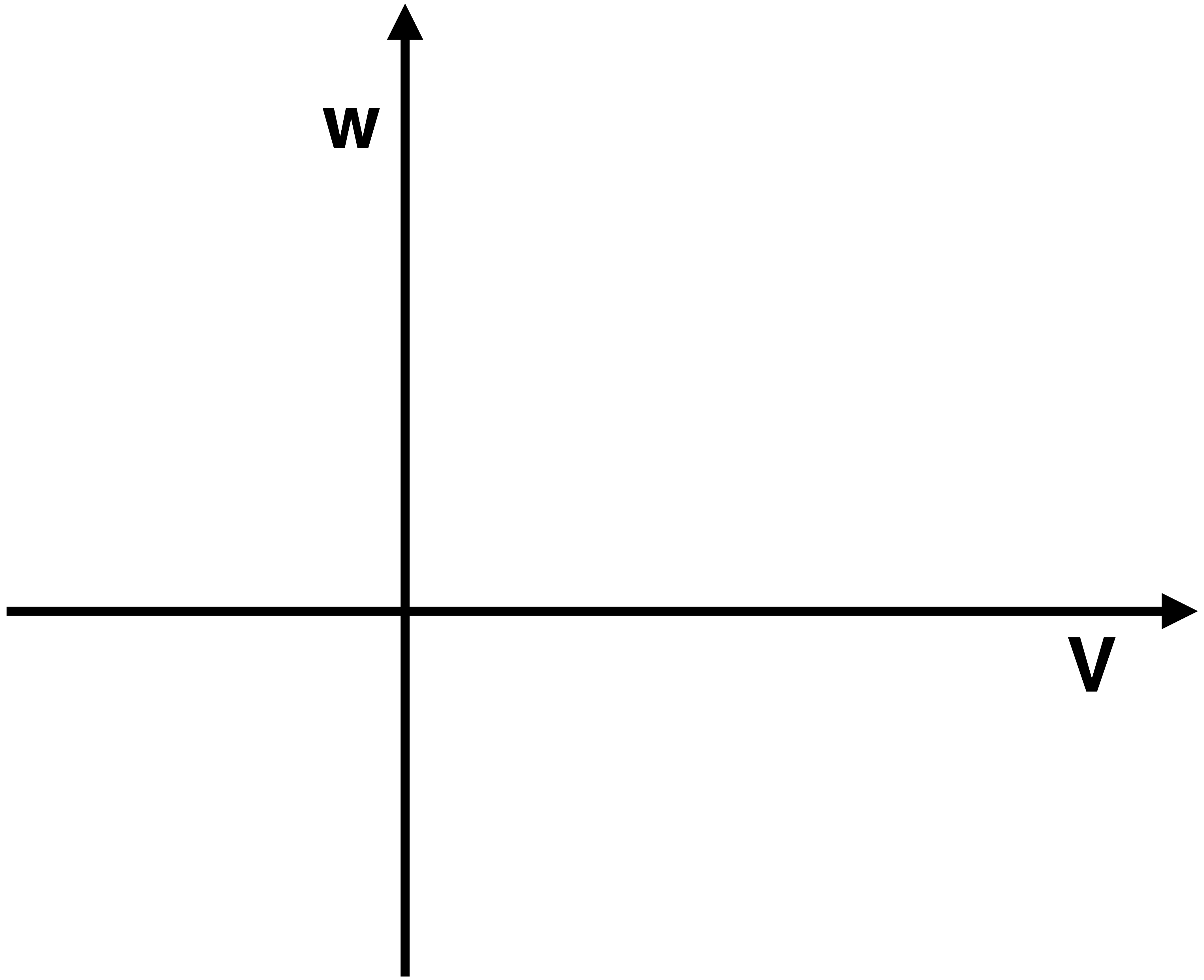

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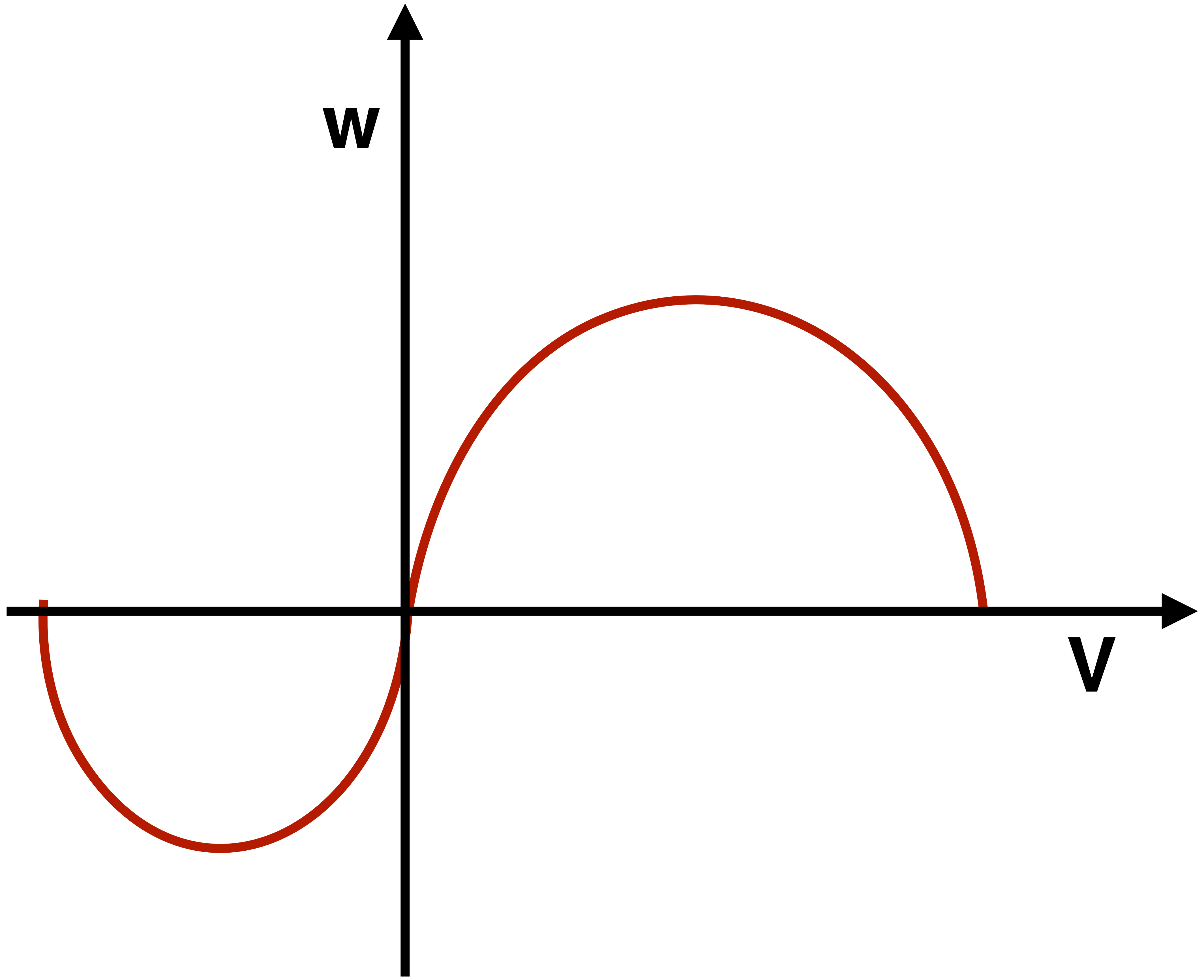

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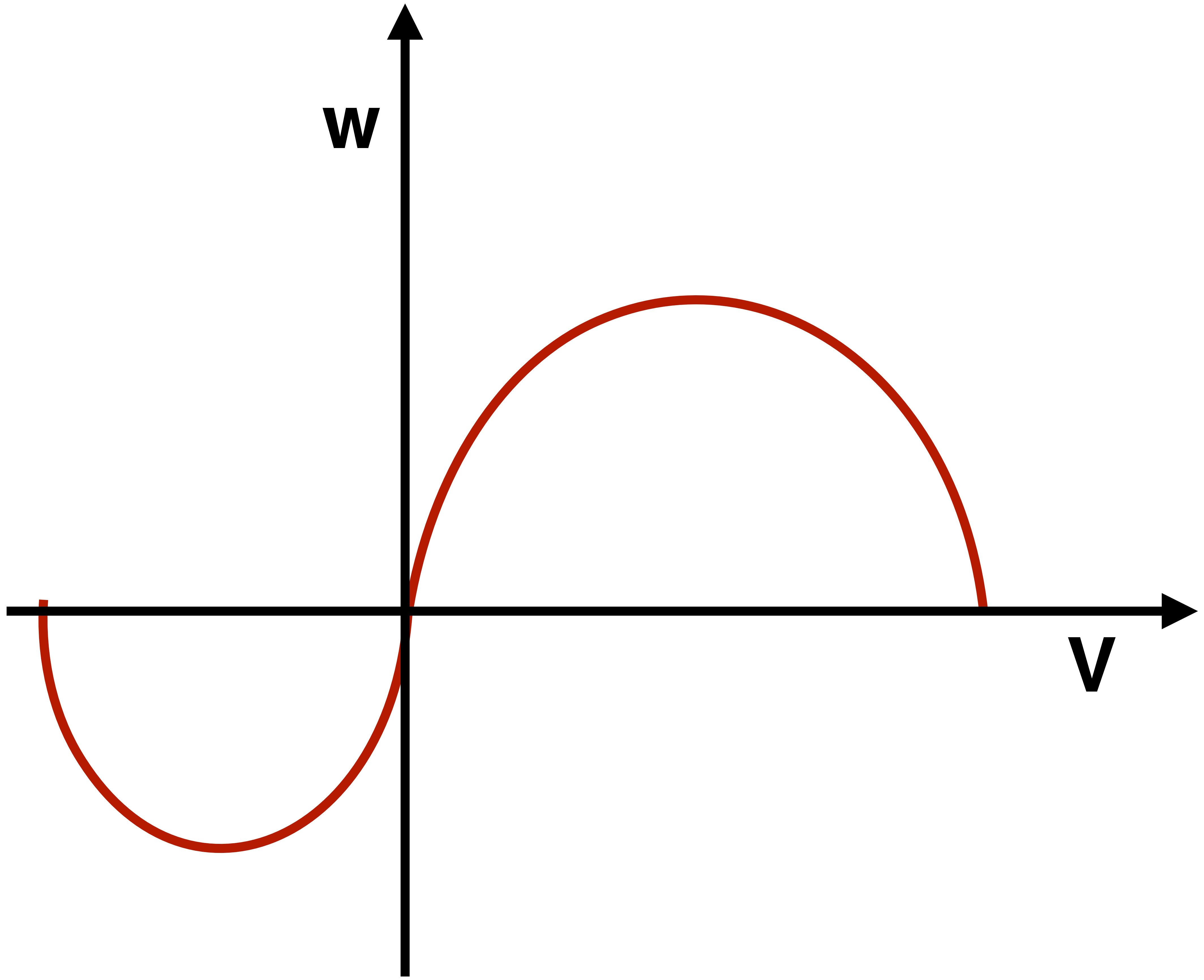

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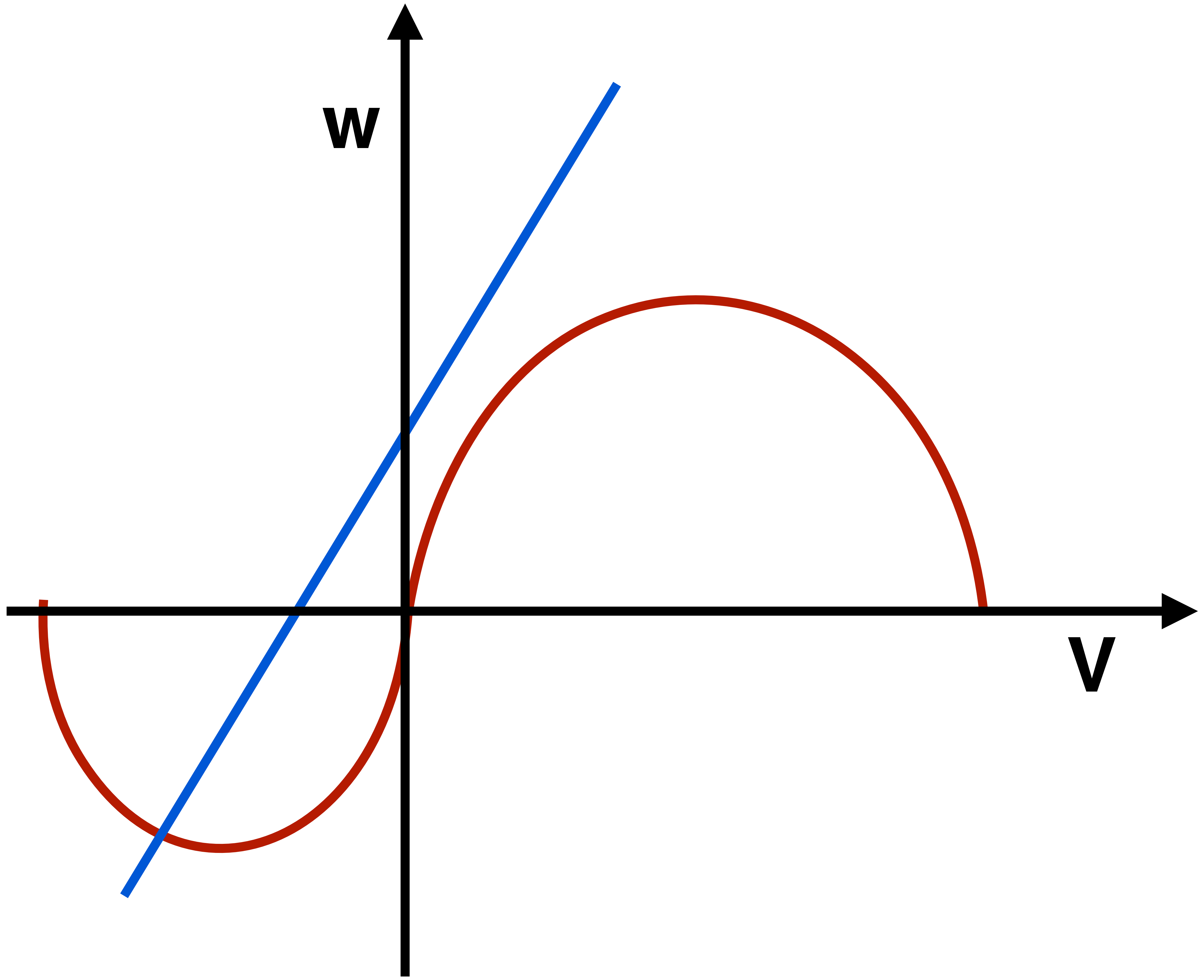

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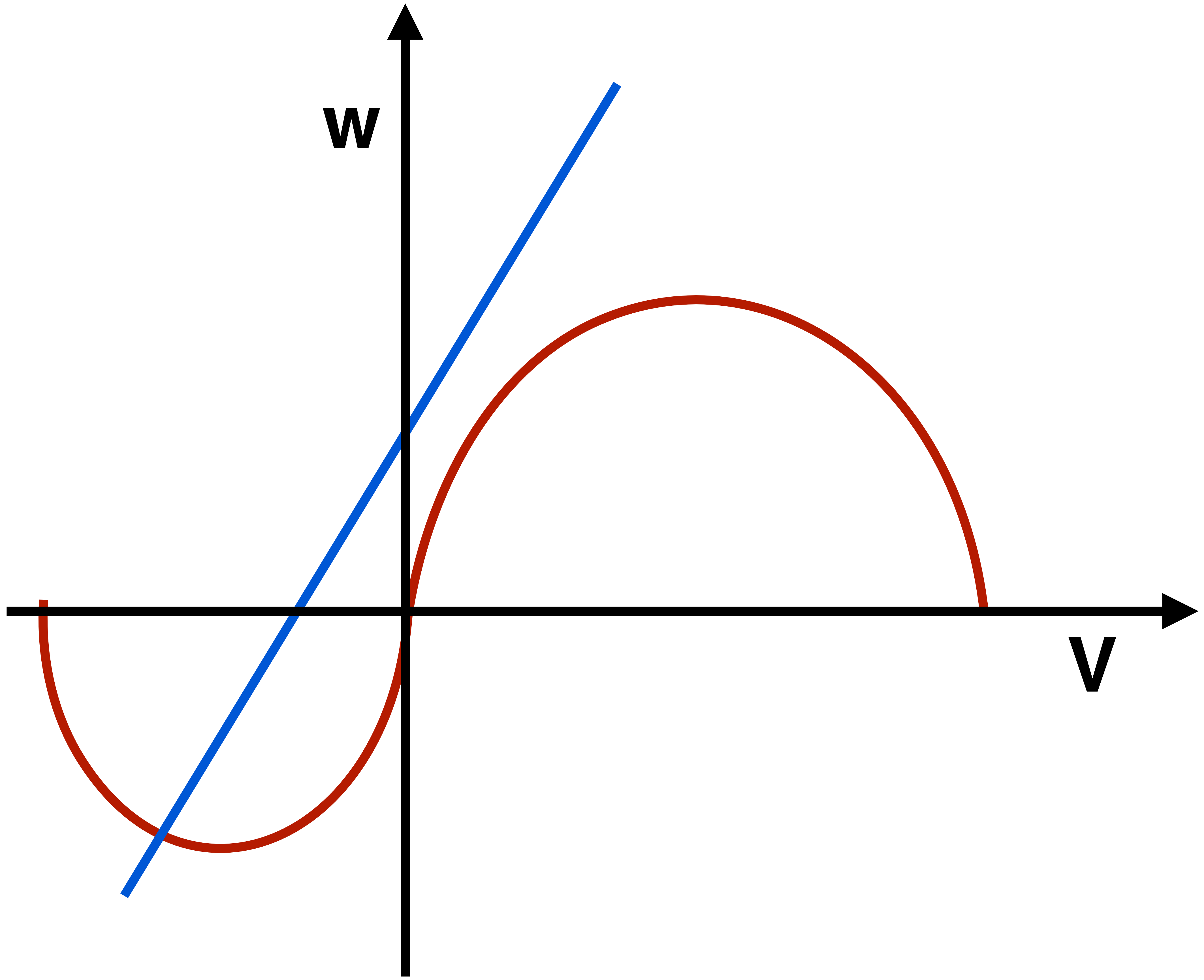

nullclines

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

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

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

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

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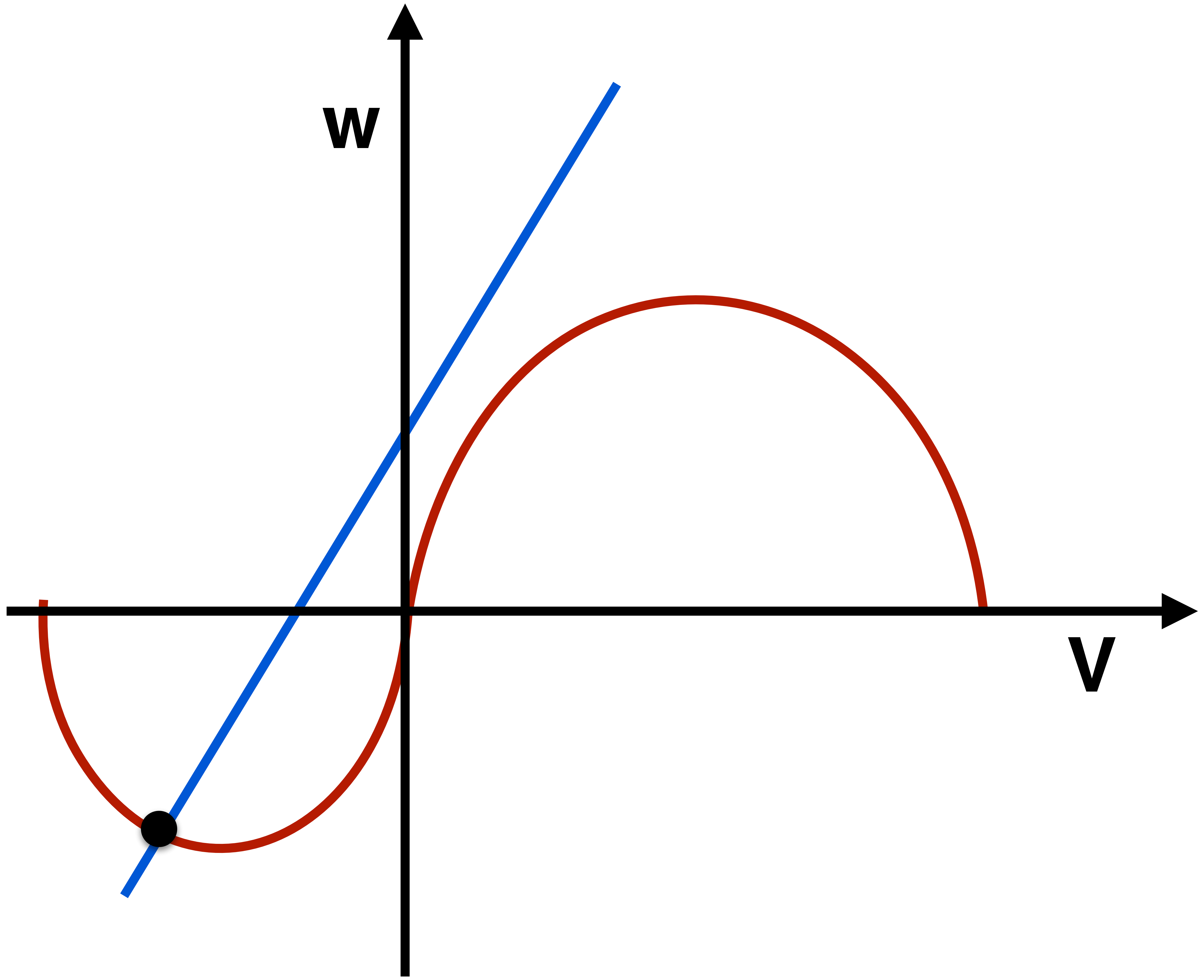

nullclines

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FitzHugh-Nagumo model

nullclines

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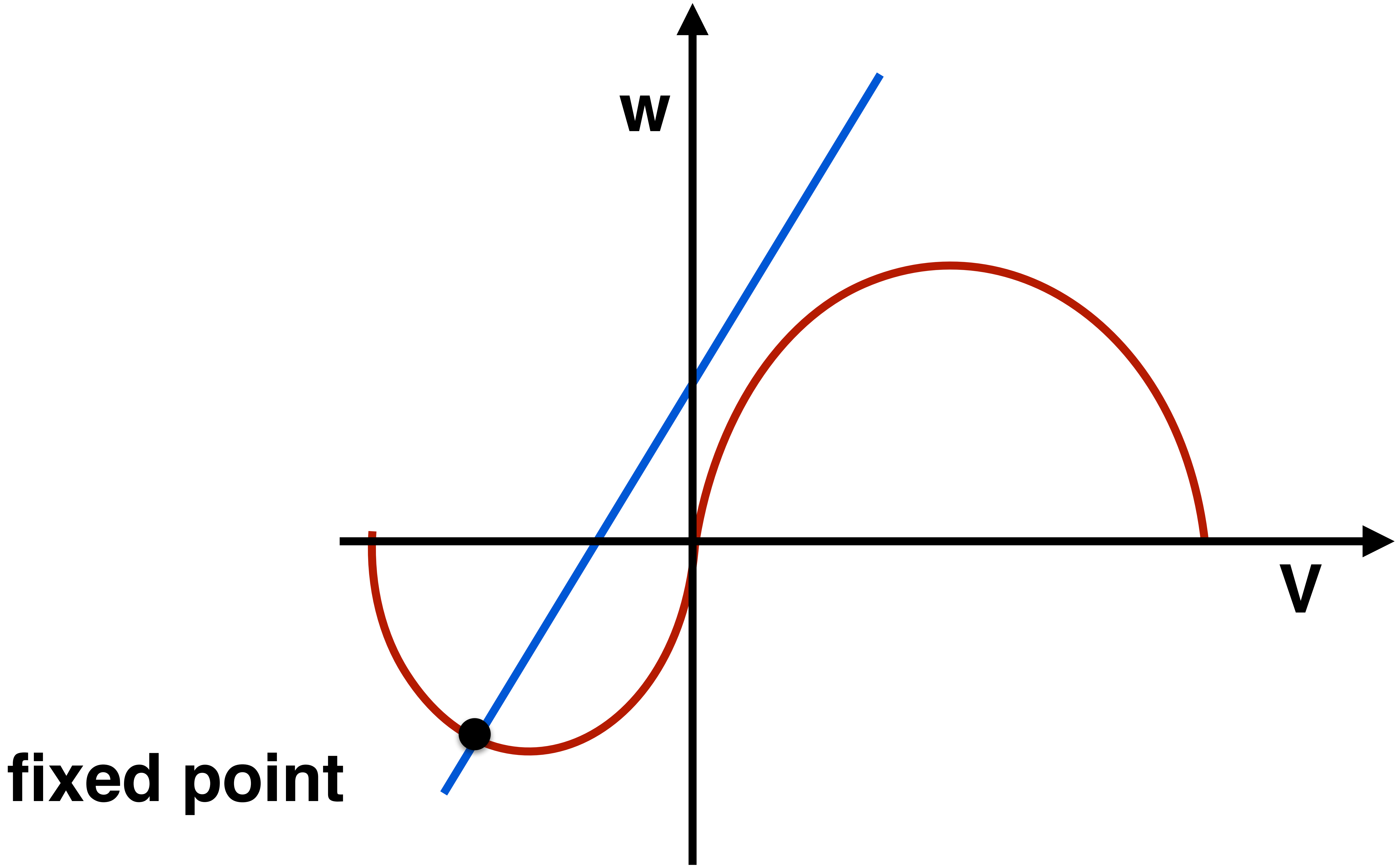

FitzHugh-Nagumo model

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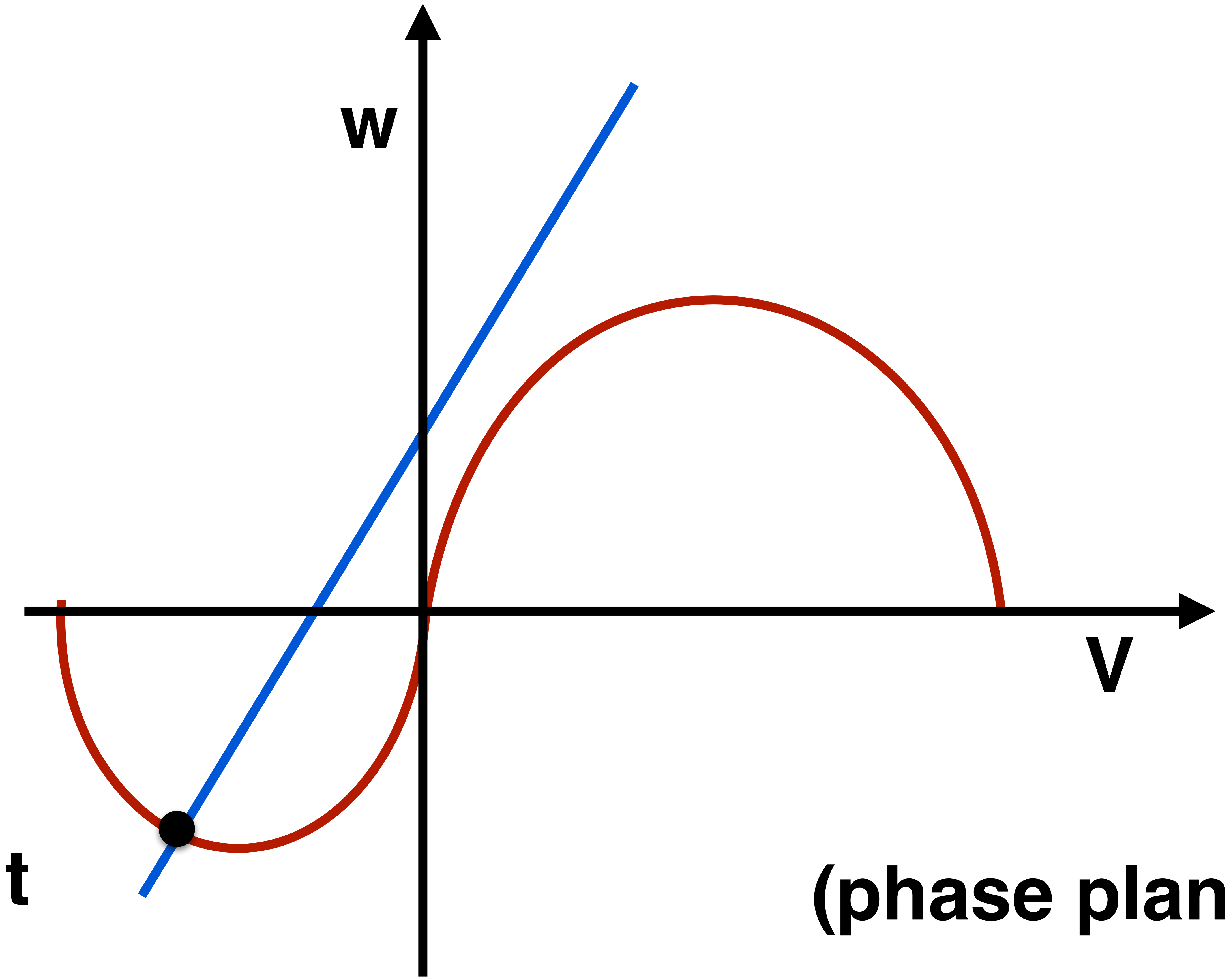


fixed point

(phase plane analysis)

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

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

FitzHugh-Nagumo model

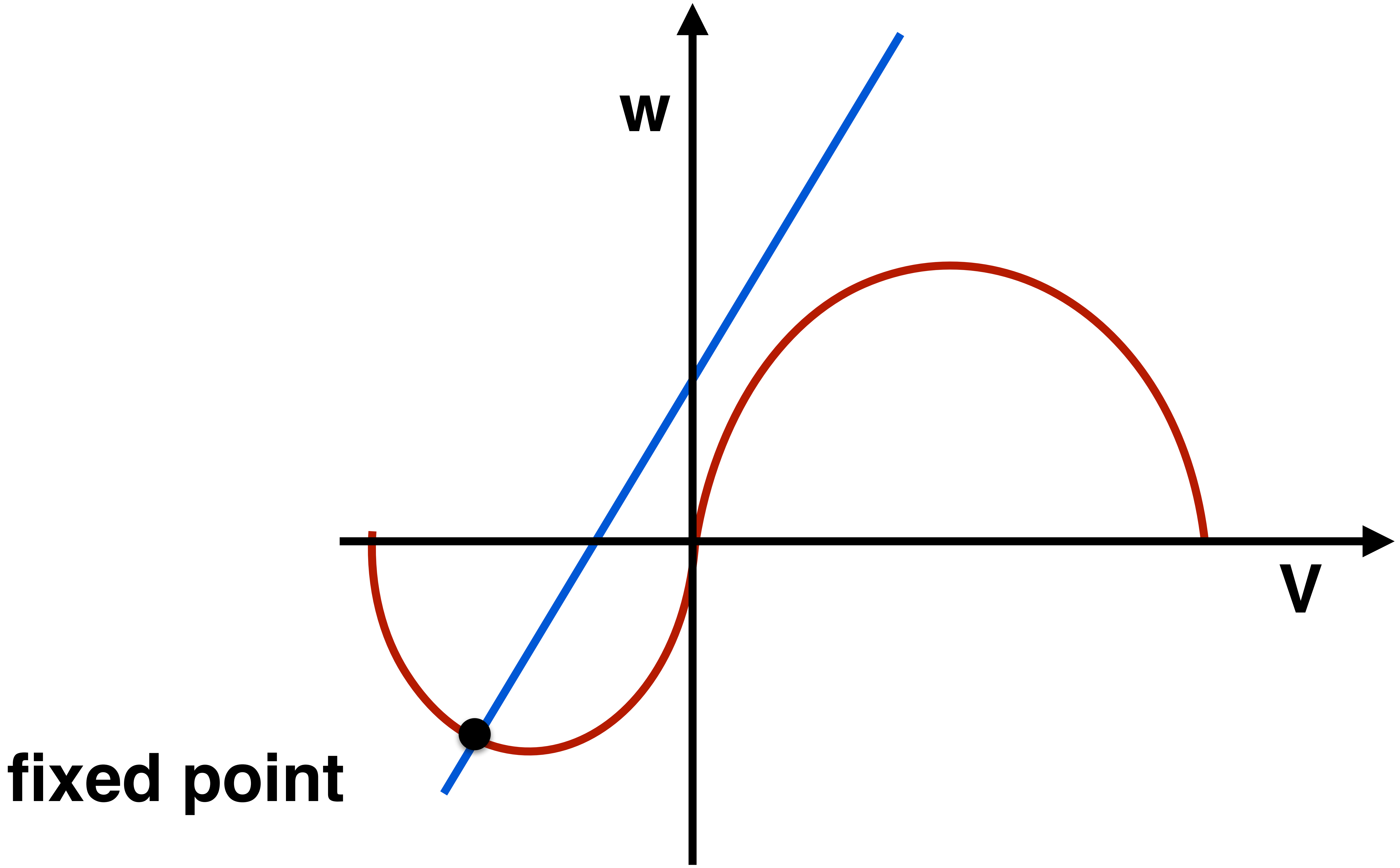
nullclines

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

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

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

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



FitzHugh-Nagumo model

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

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

nullclines

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

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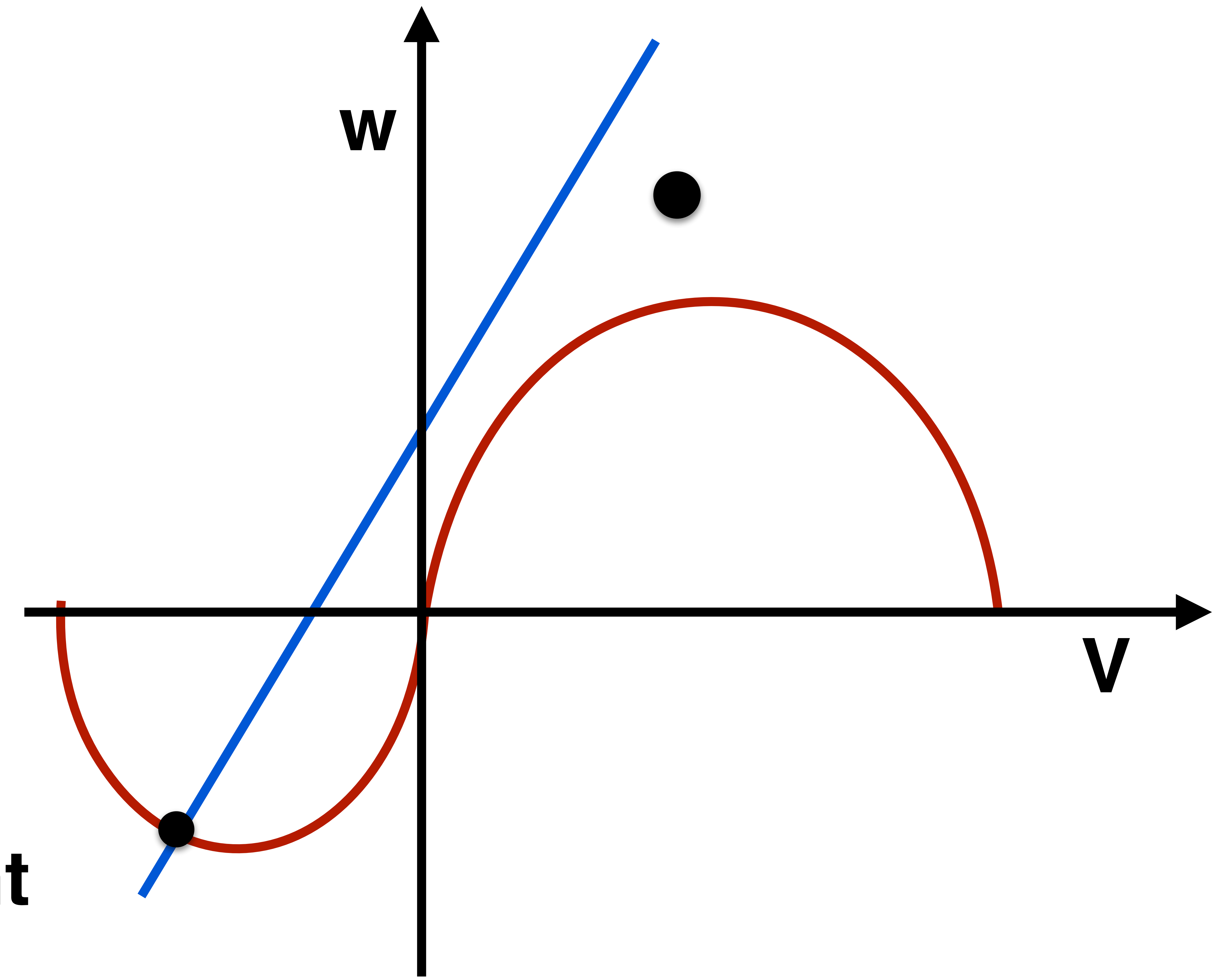

fixed point

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FitzHugh-Nagumo model

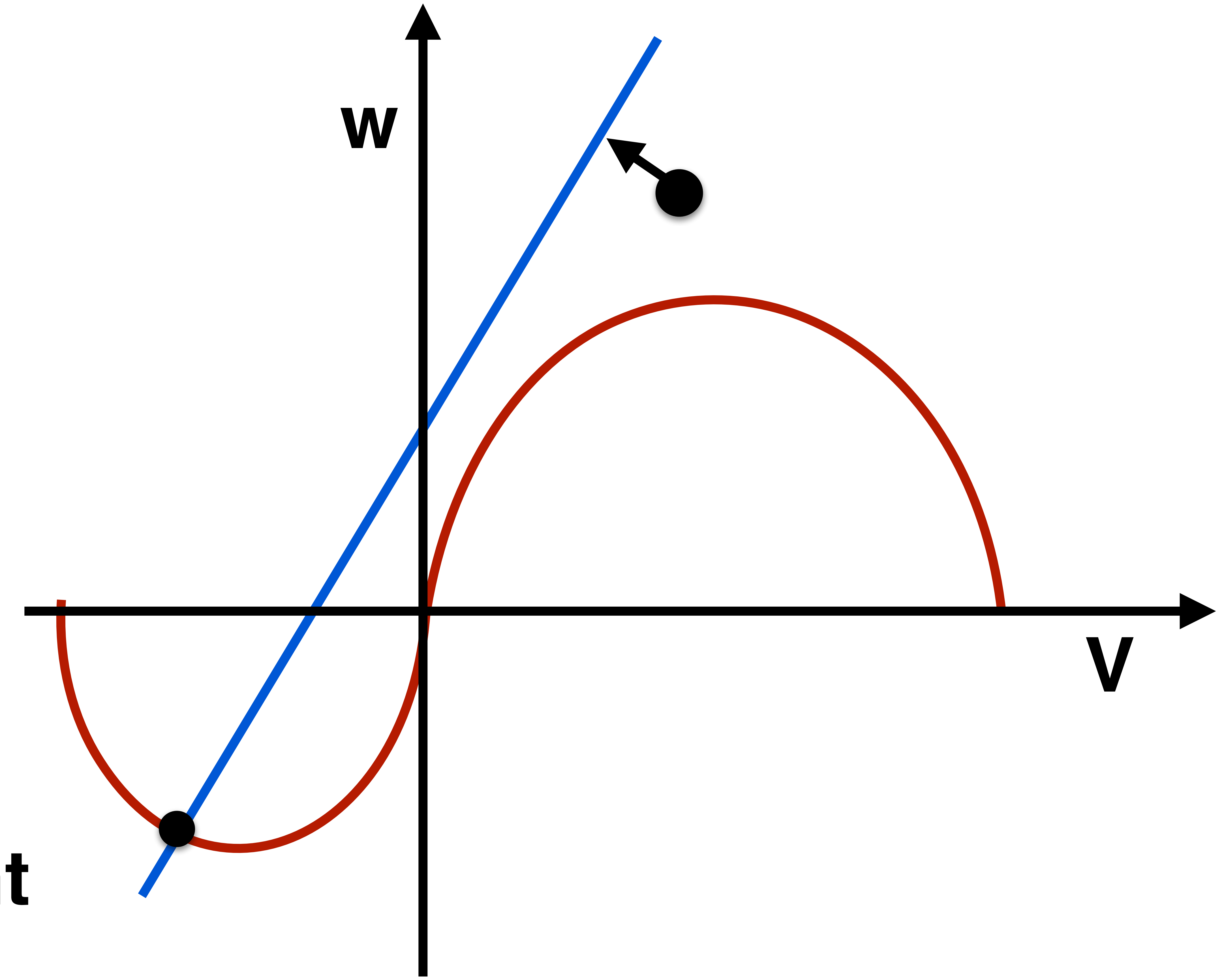
nullclines

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

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

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

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



fixed point

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

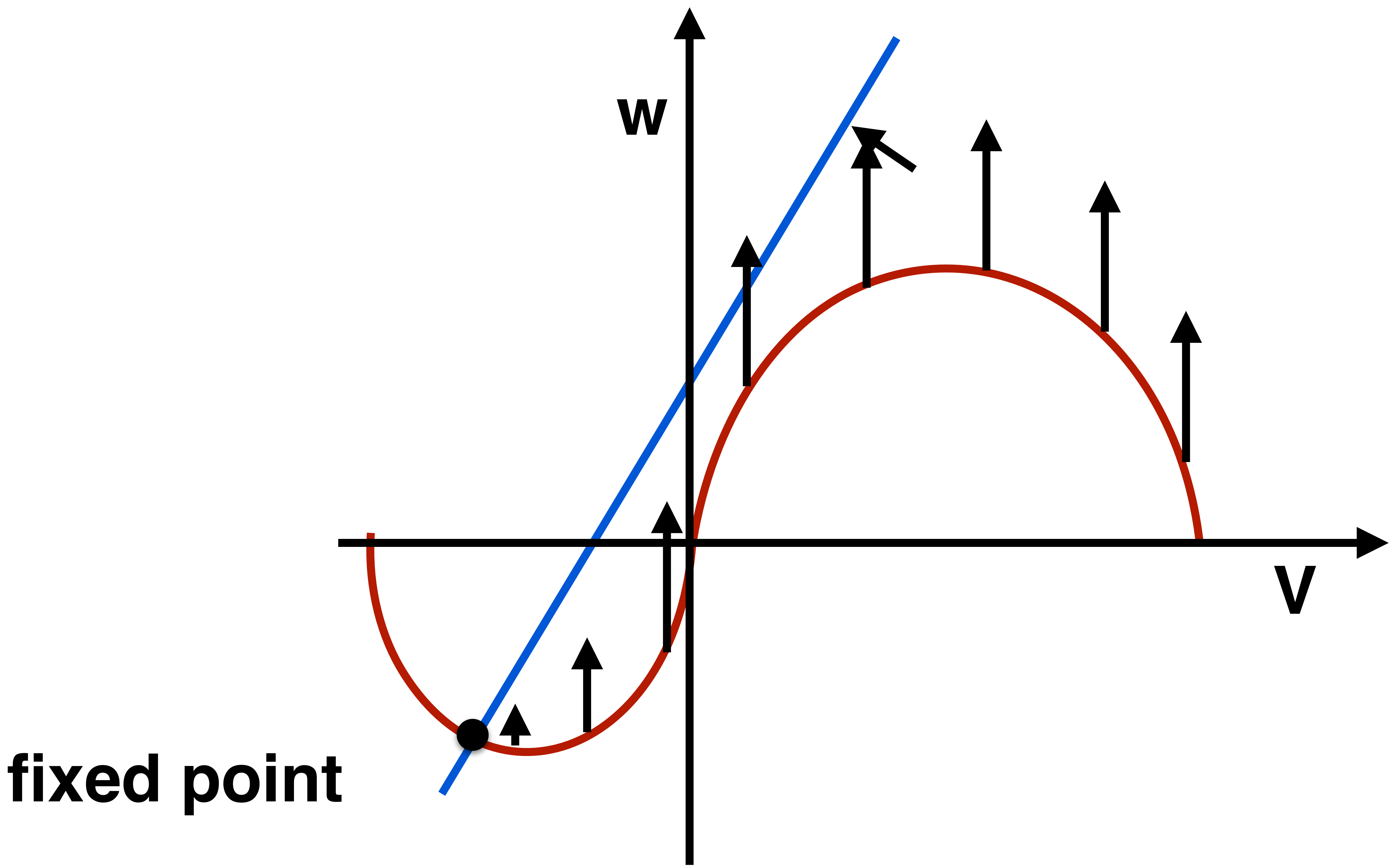
$$\frac{dw}{dt} = a + bV - w$$

FitzHugh-Nagumo model

nullclines

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

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



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FitzHugh-Nagumo model

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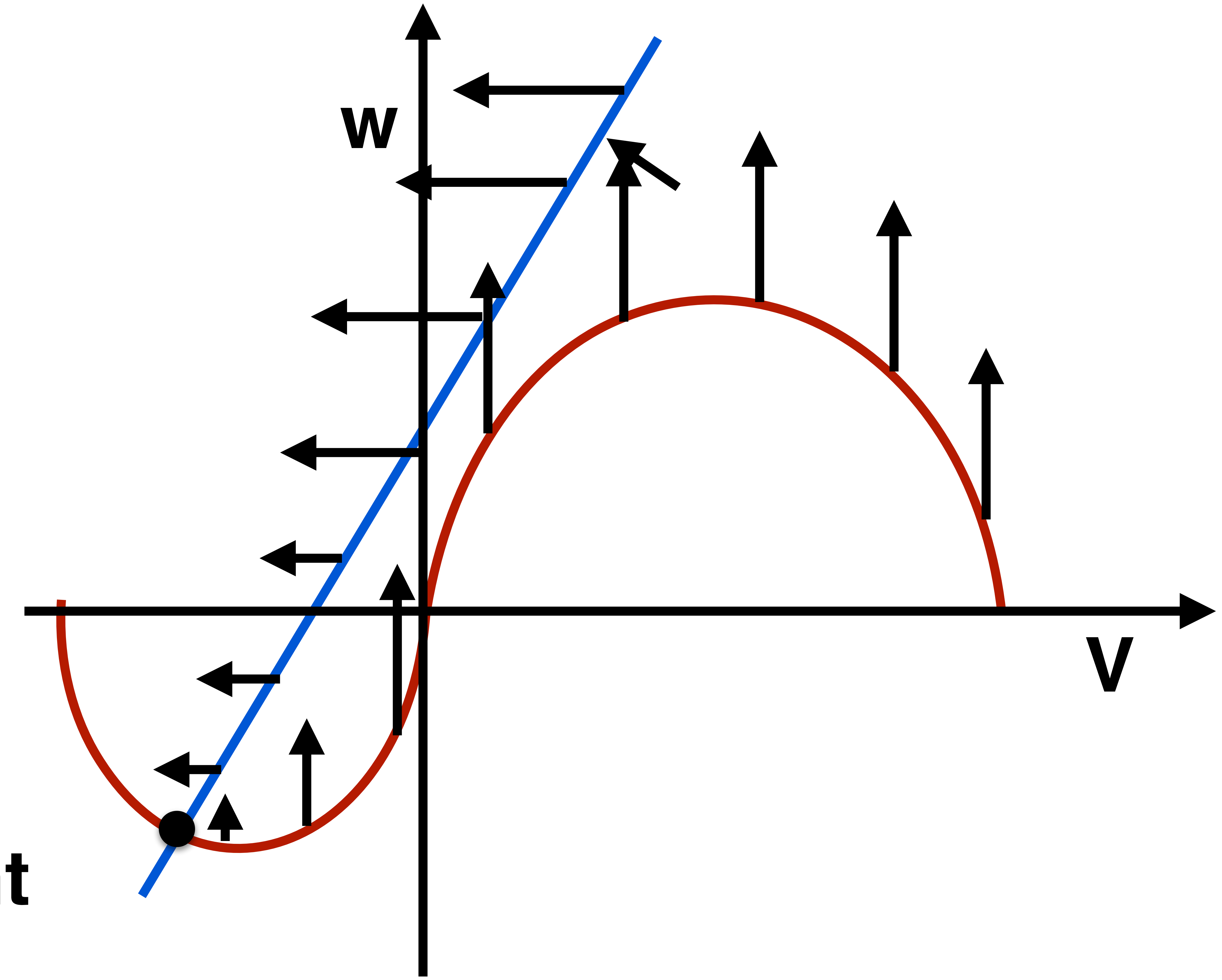

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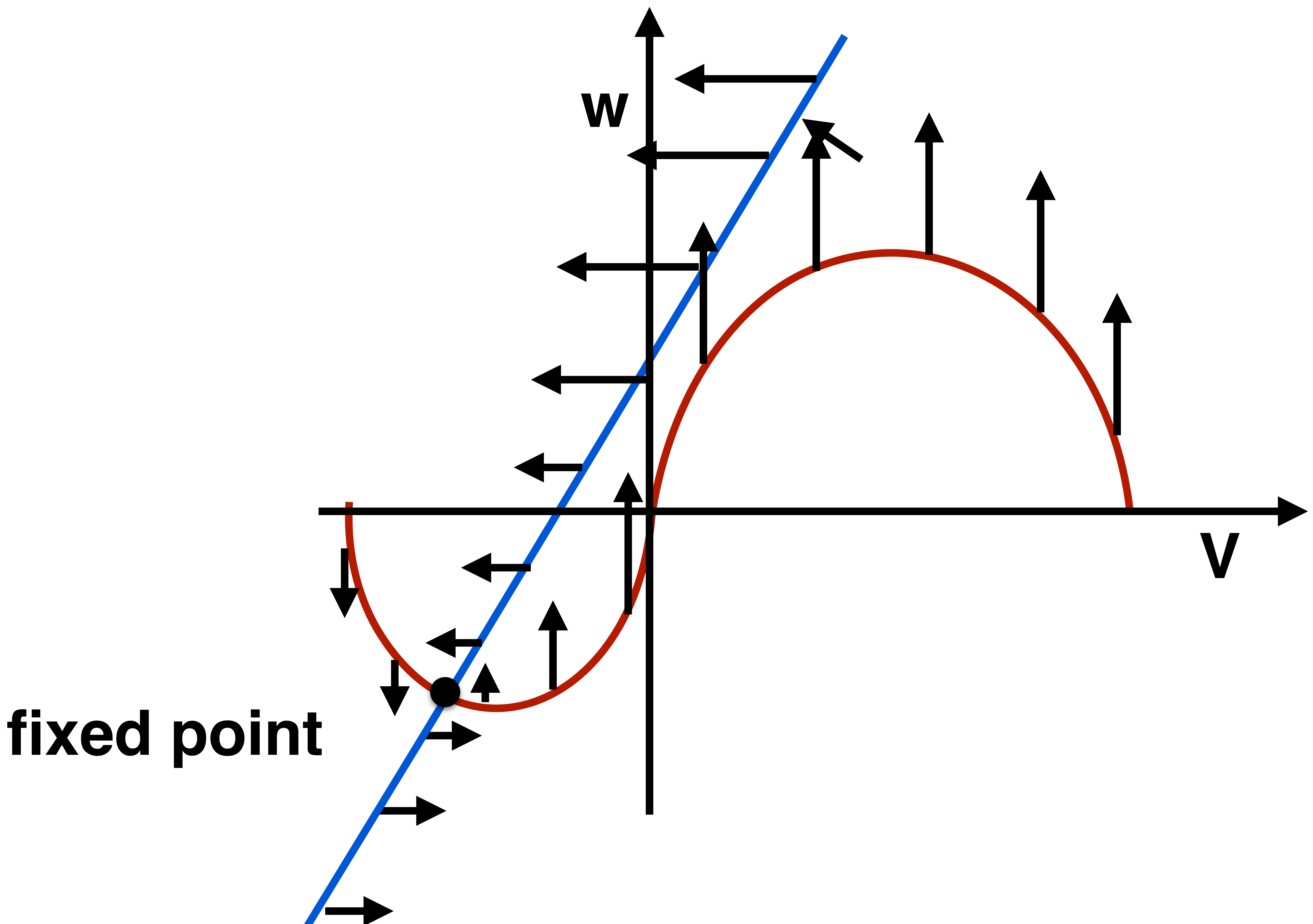

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FitzHugh-Nagumo model

nullclines

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

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

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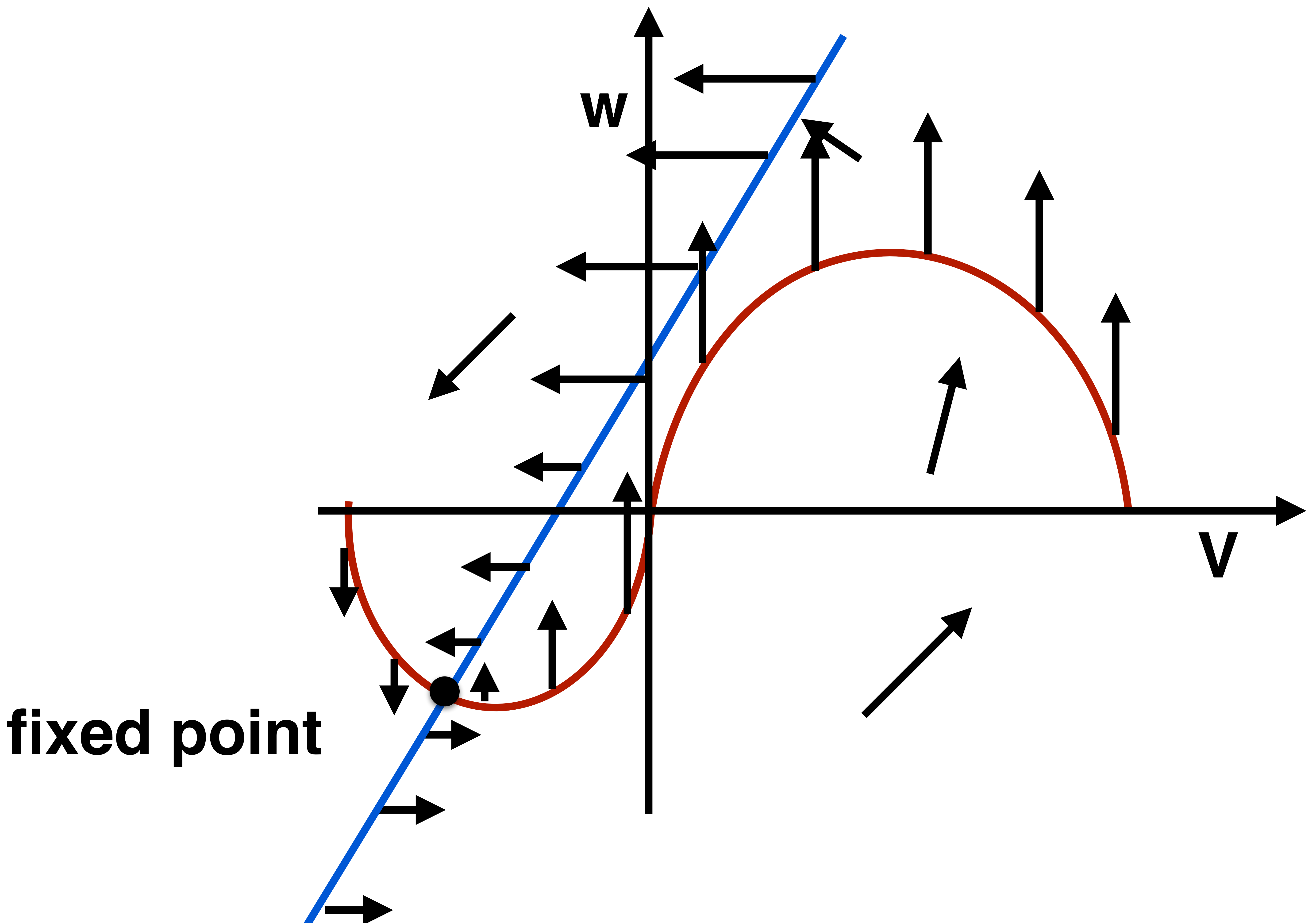

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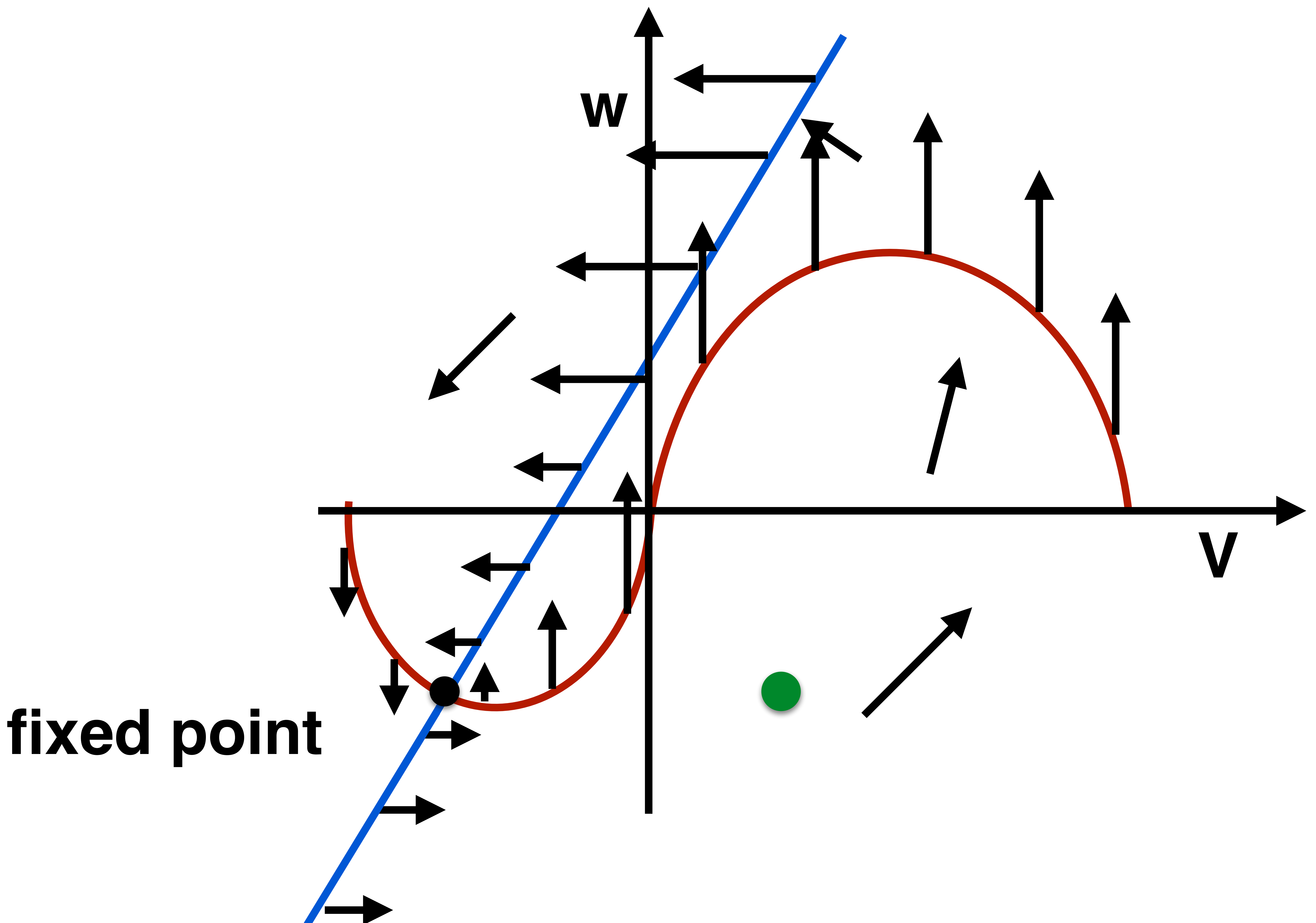

nullclines

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

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FitzHugh-Nagumo model

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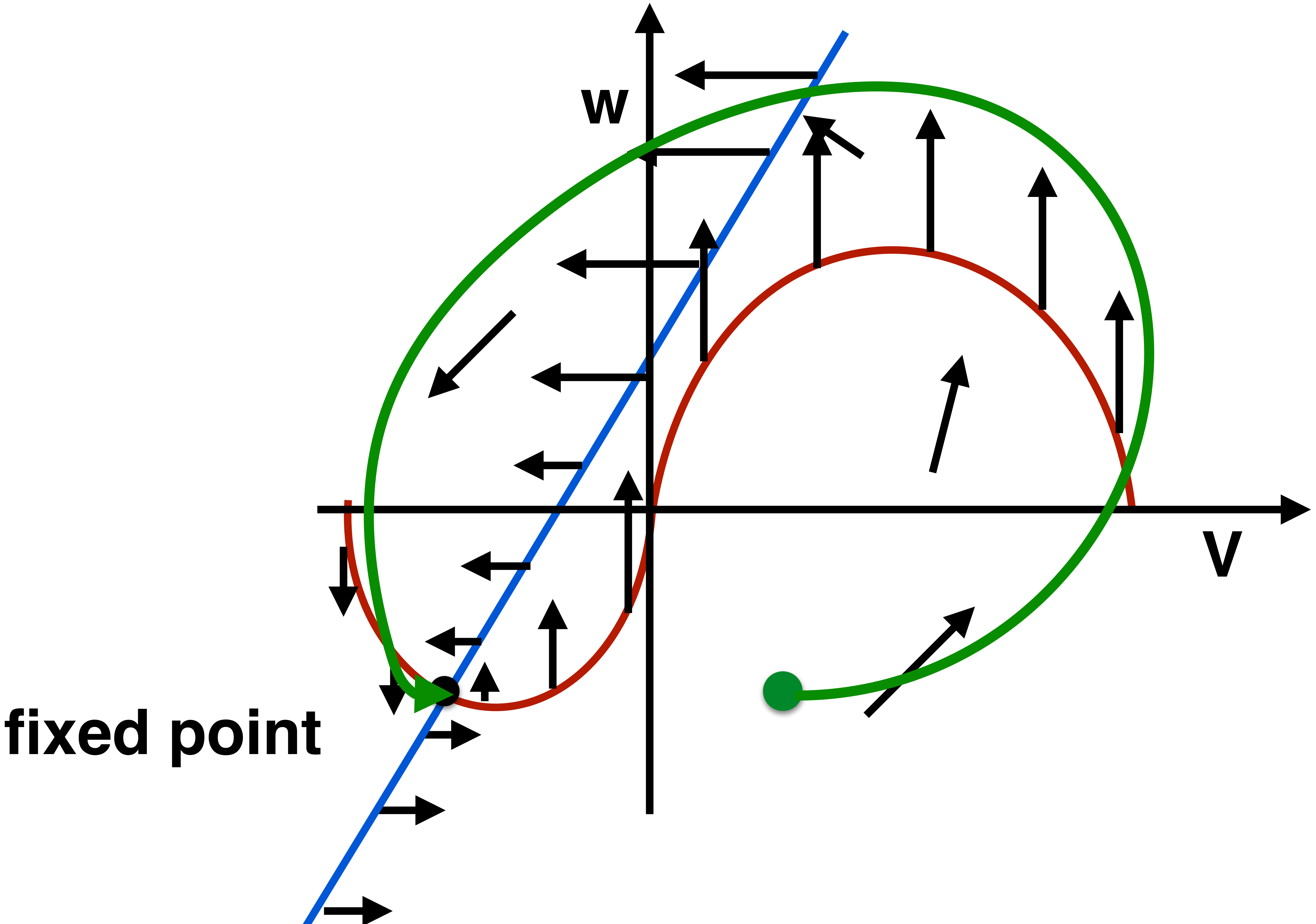

nullclines

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

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

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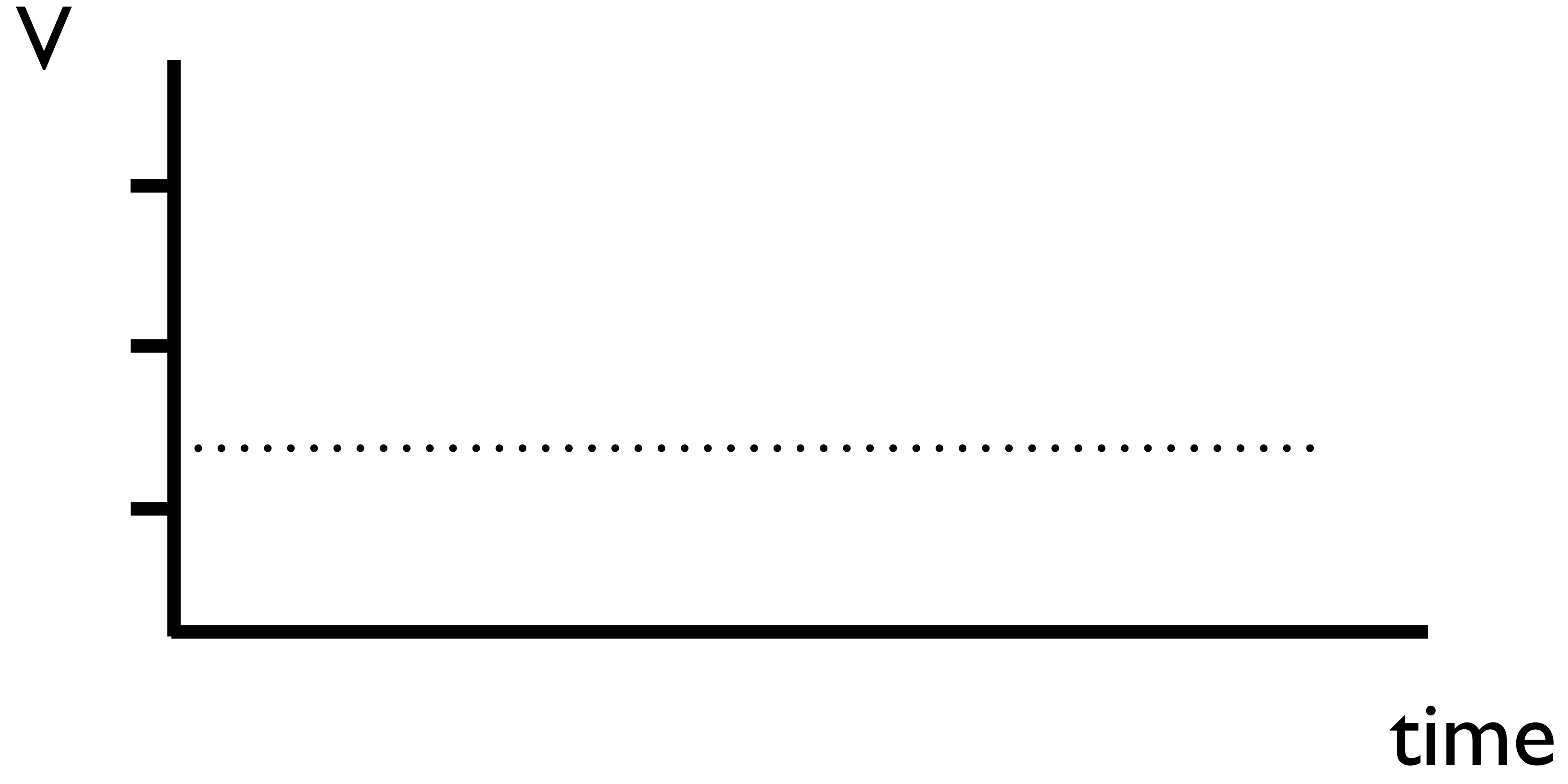

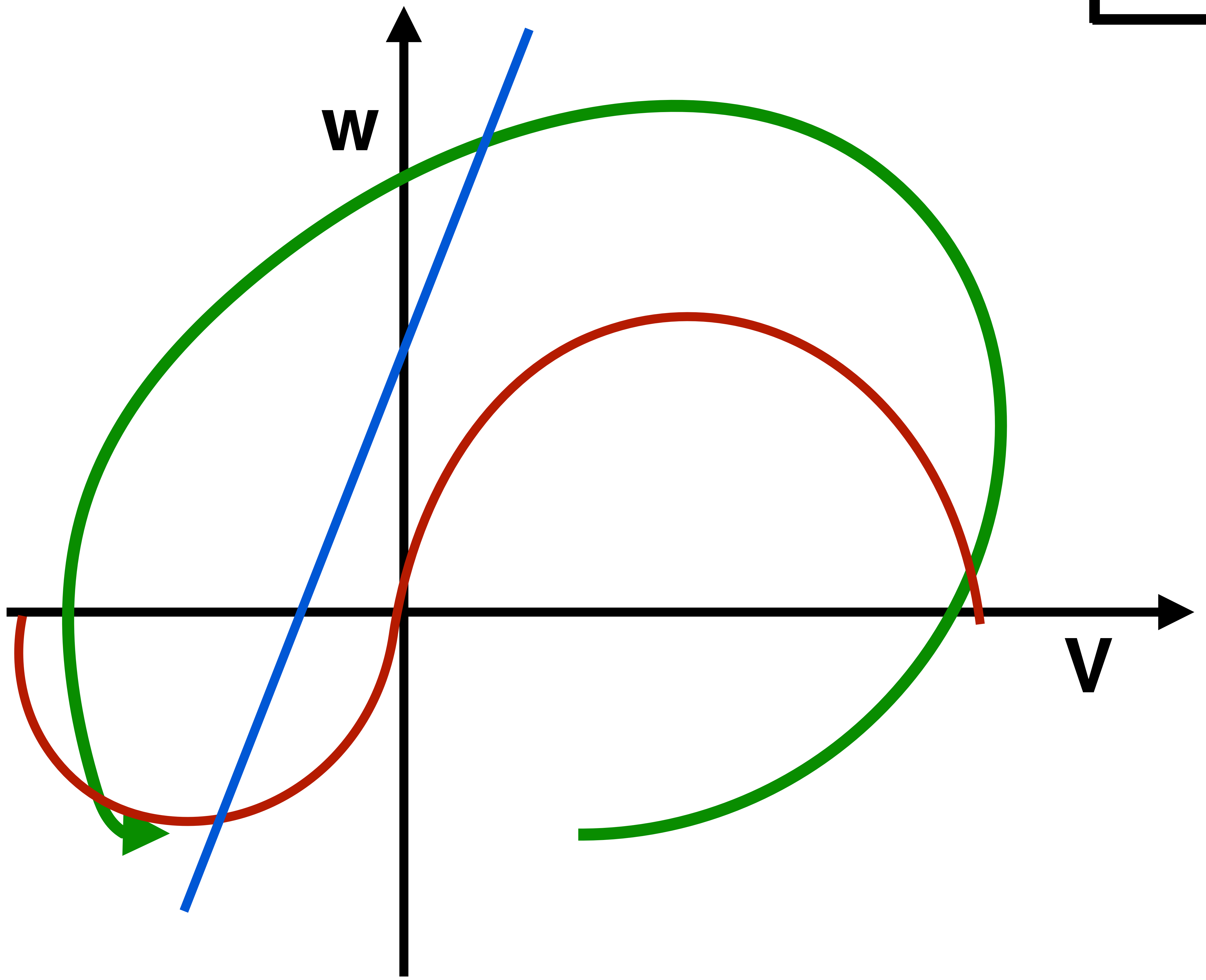

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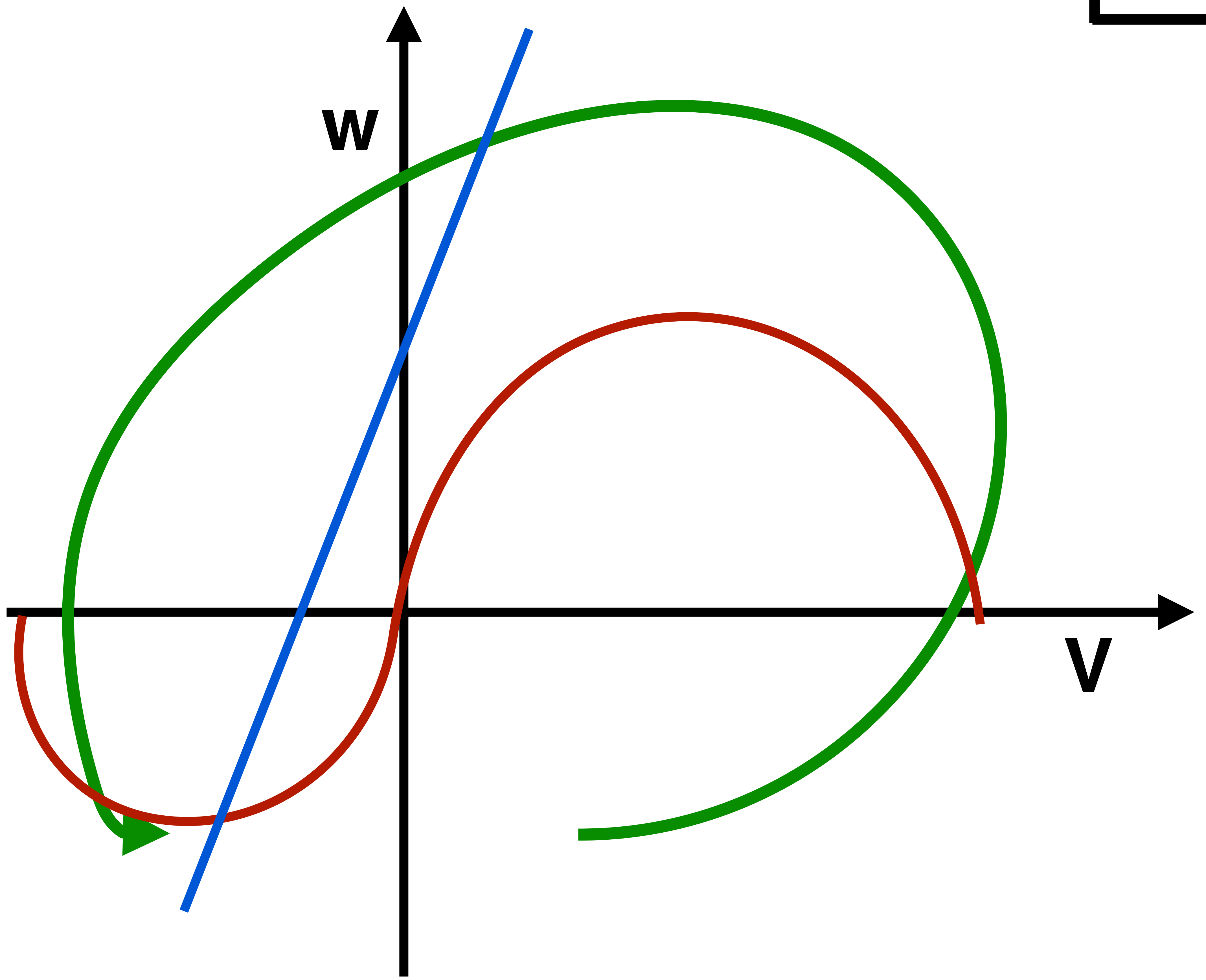

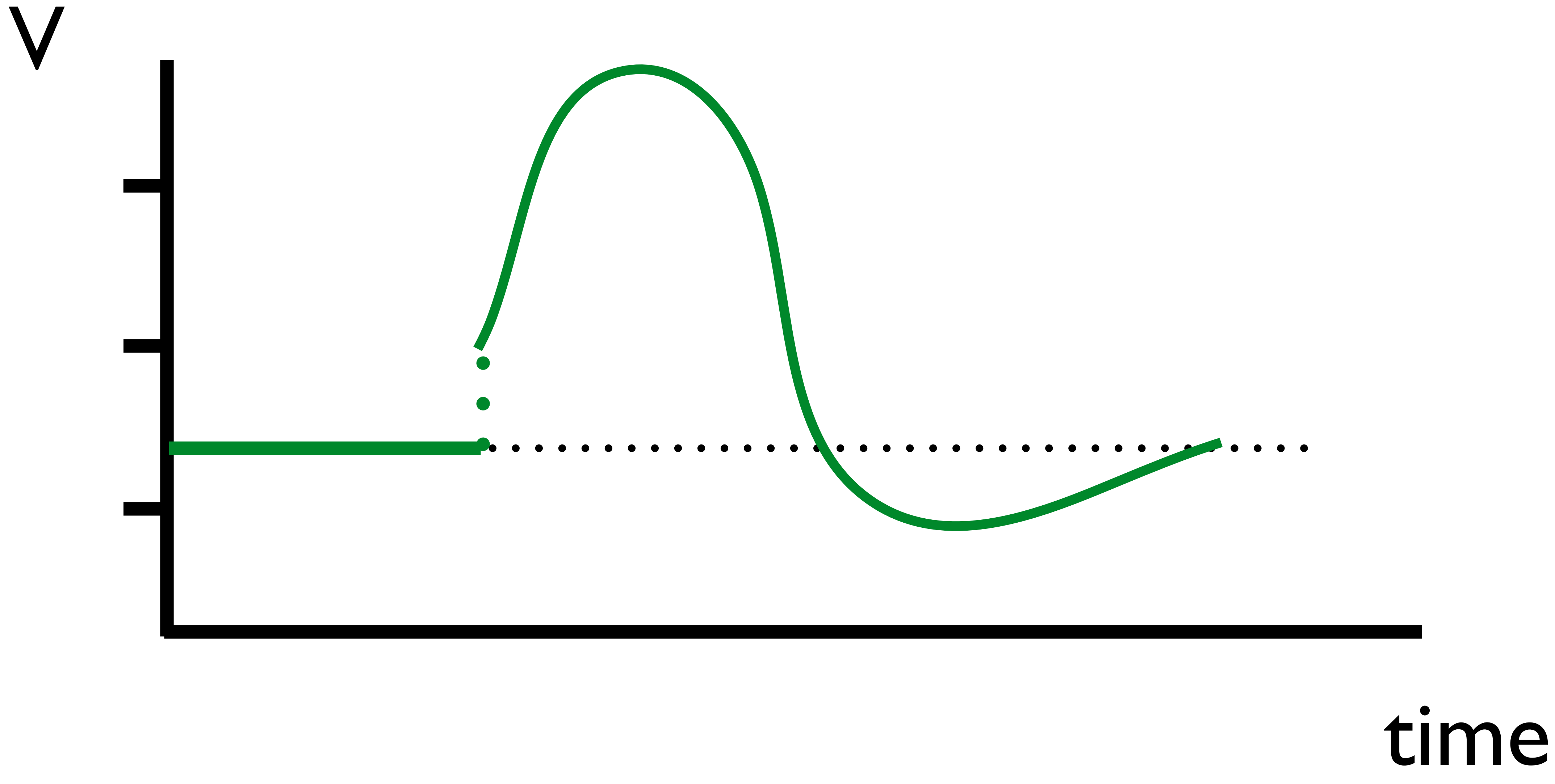

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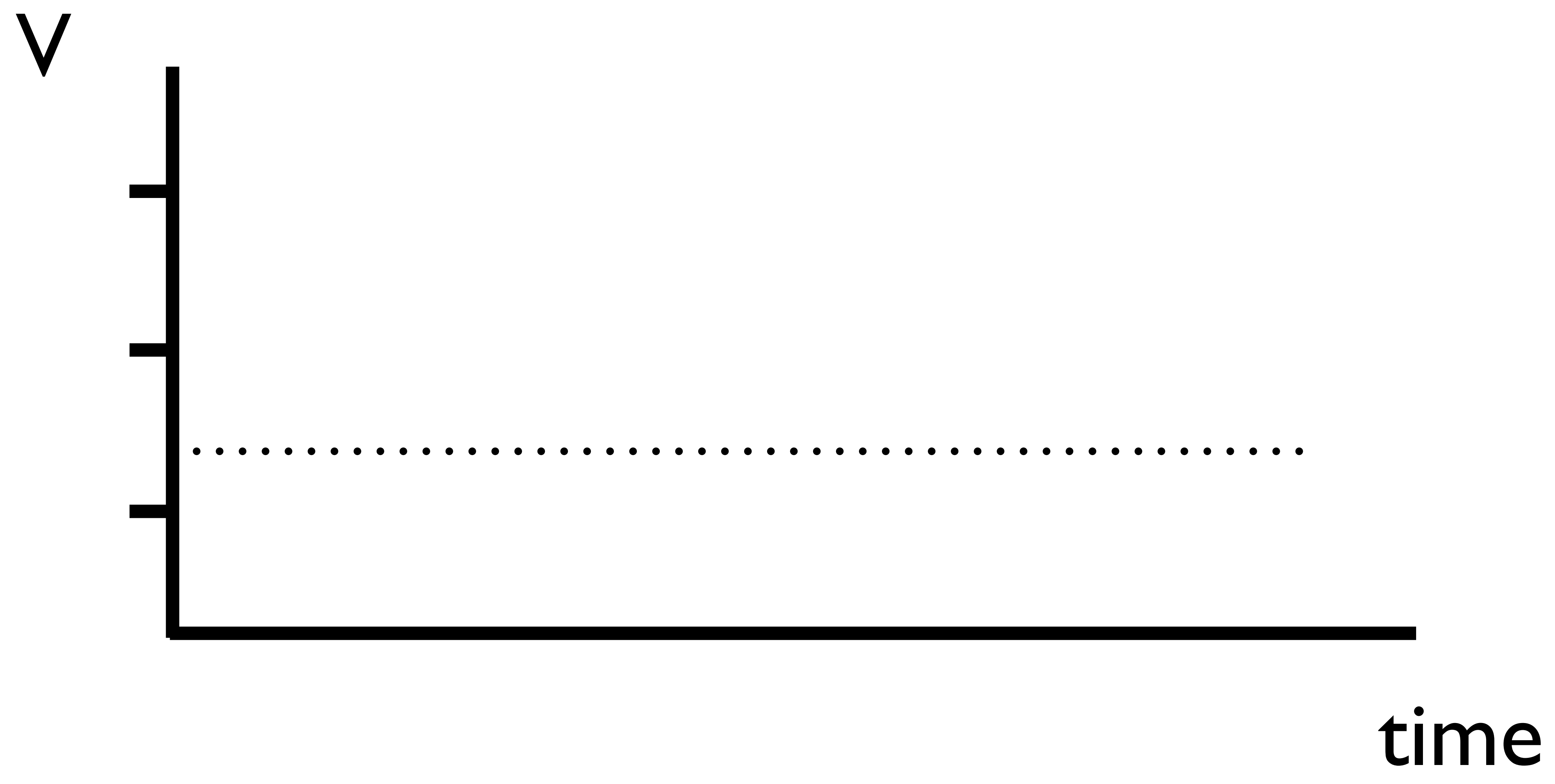
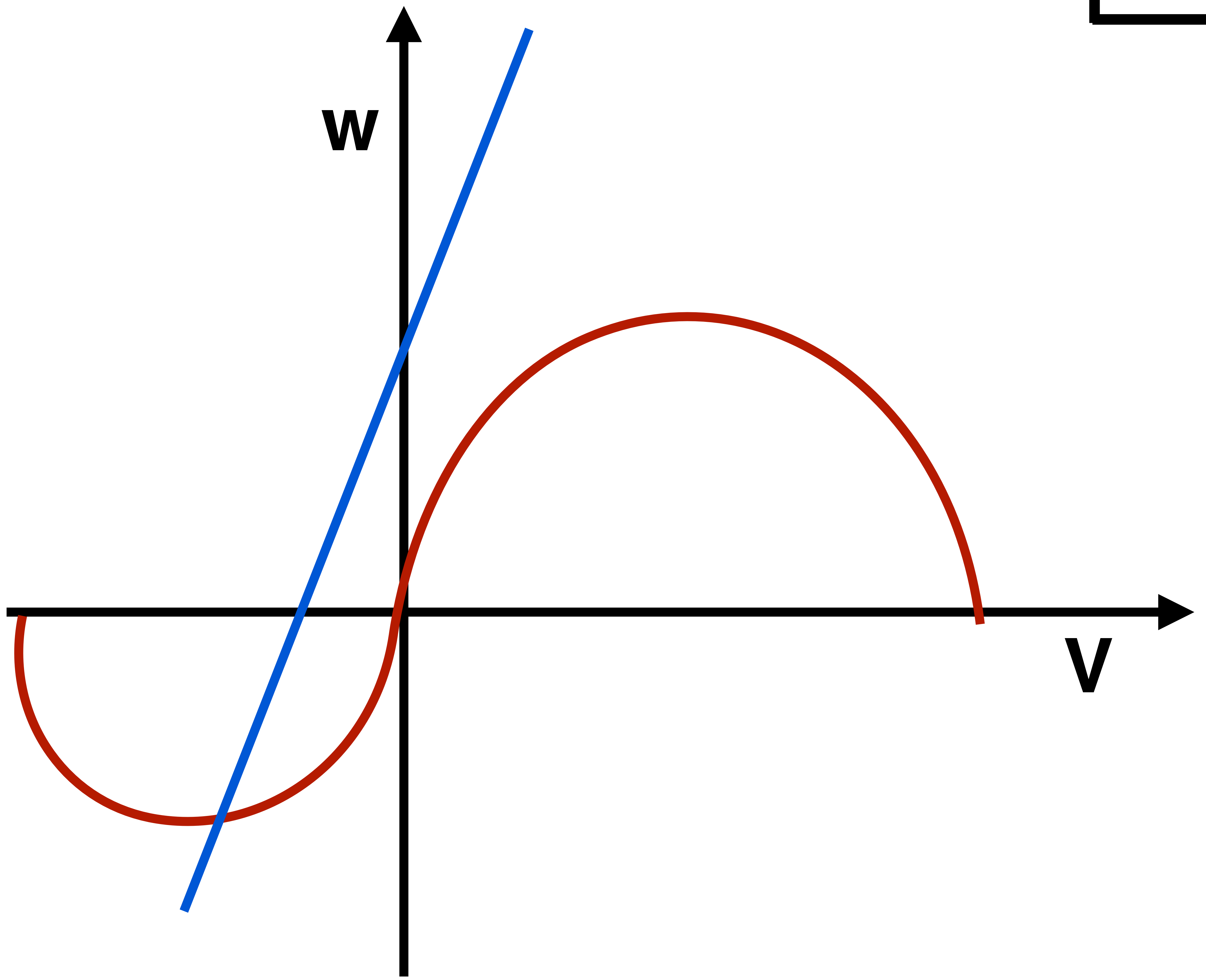
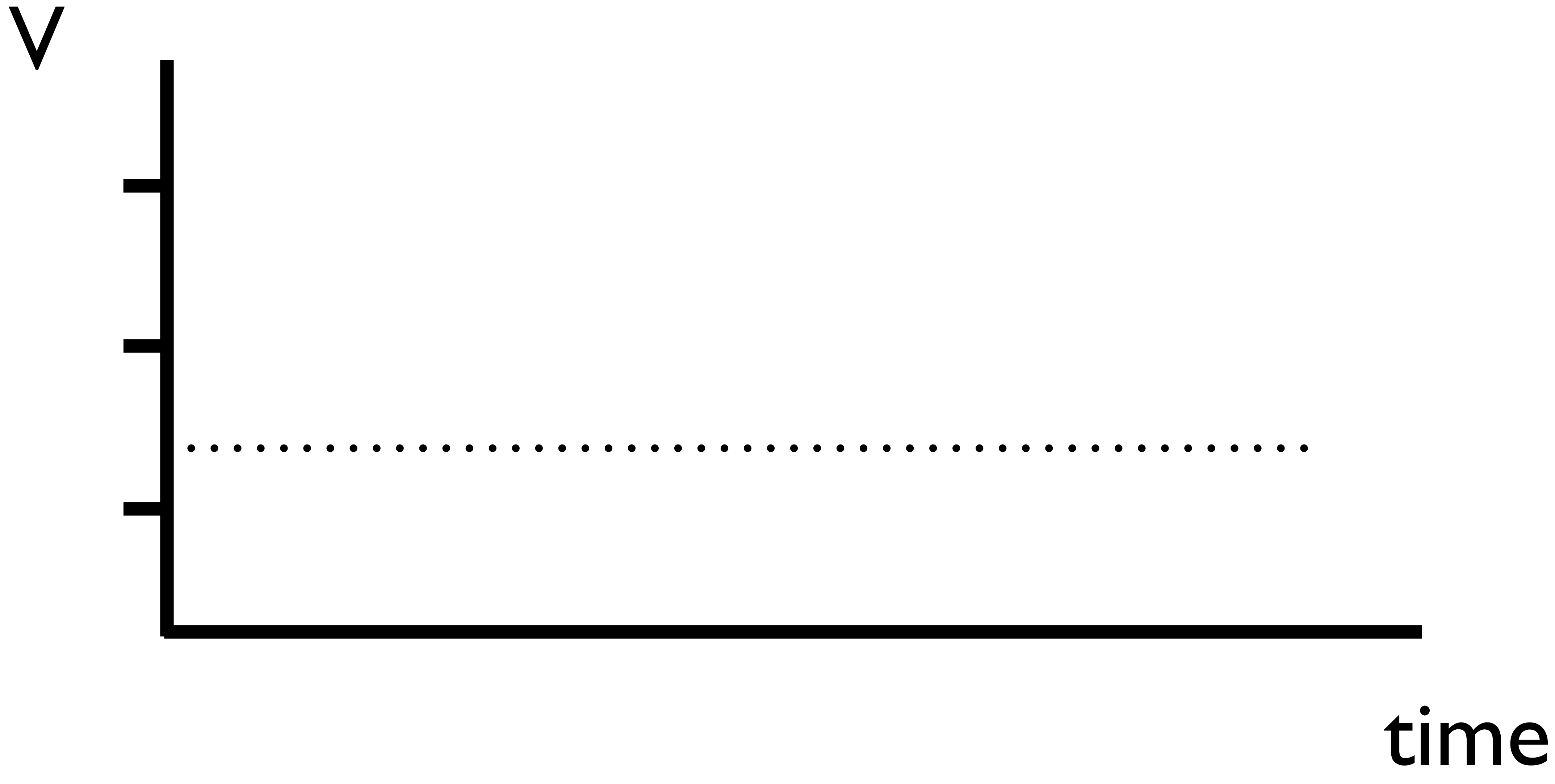
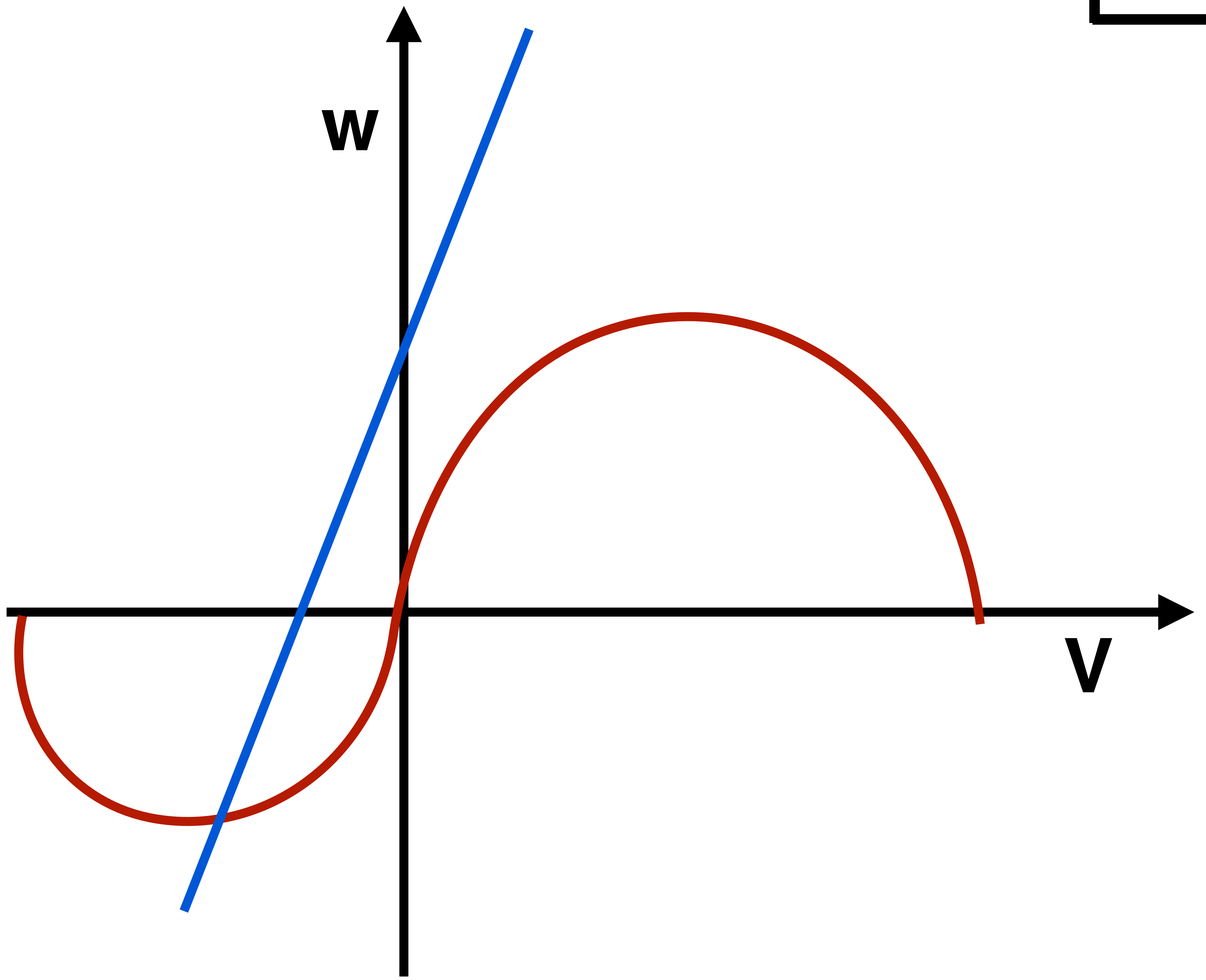




$$\frac{dV}{dt} = V - \frac{1}{3}V^3 - w + I$$

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





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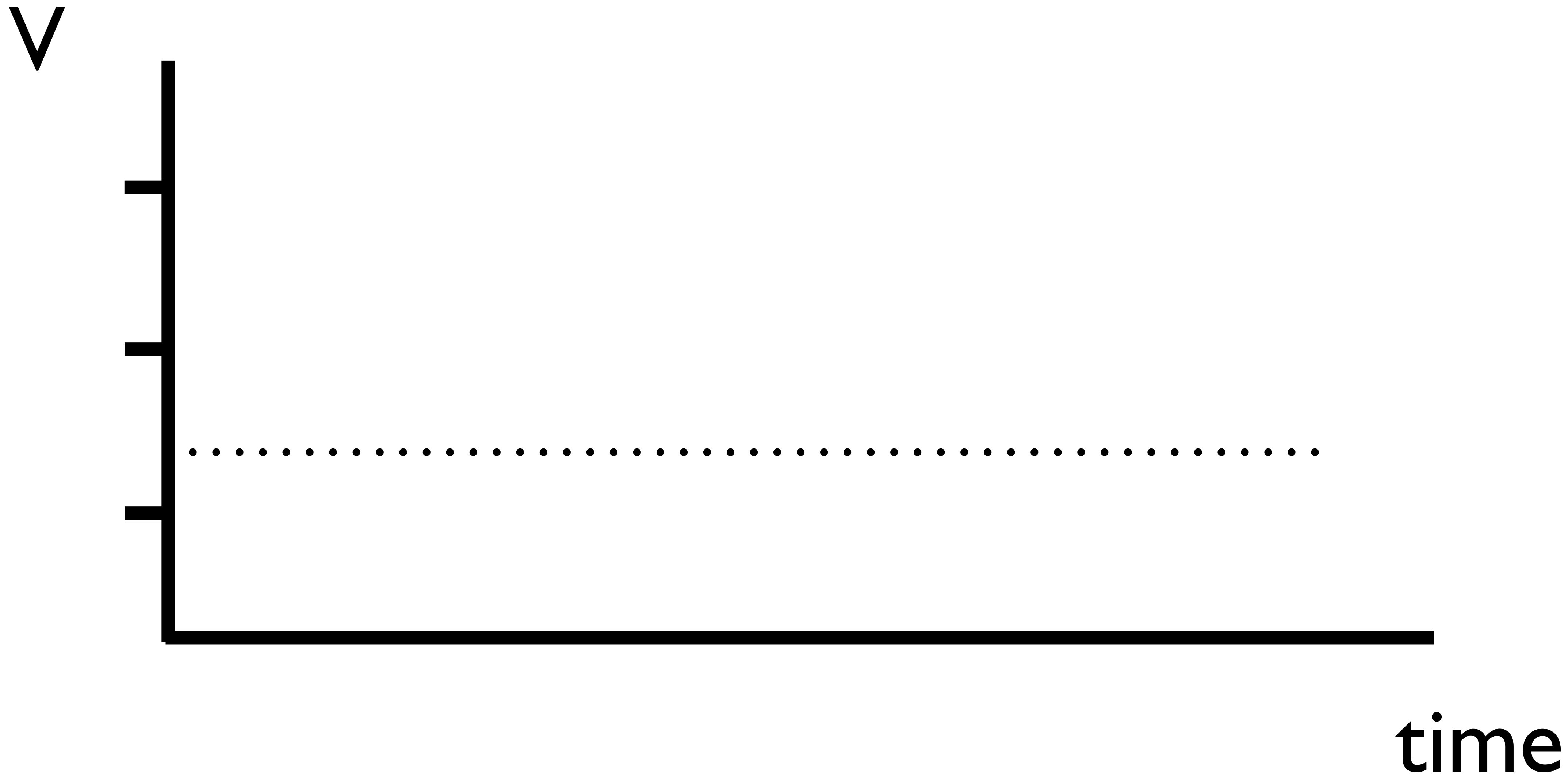

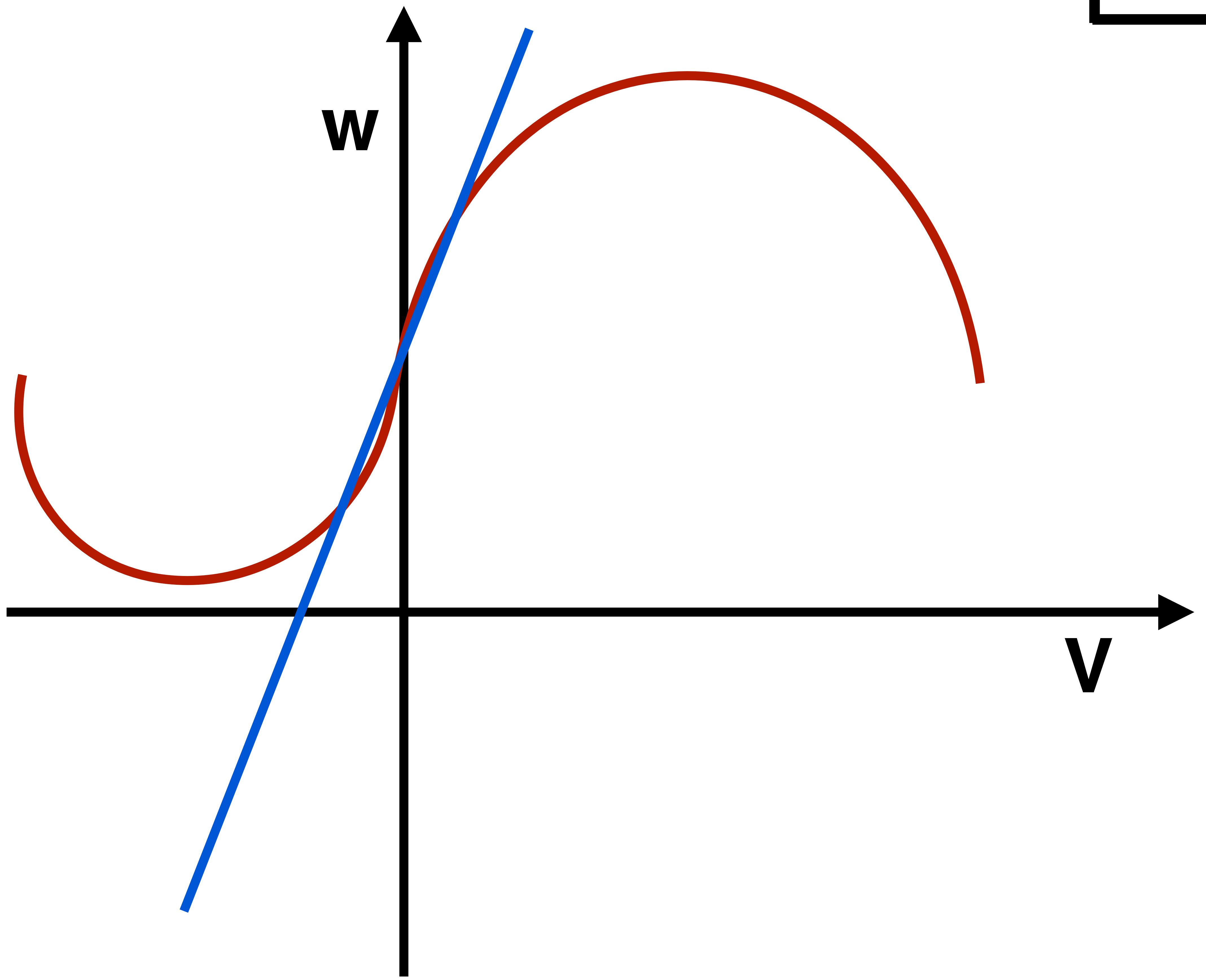

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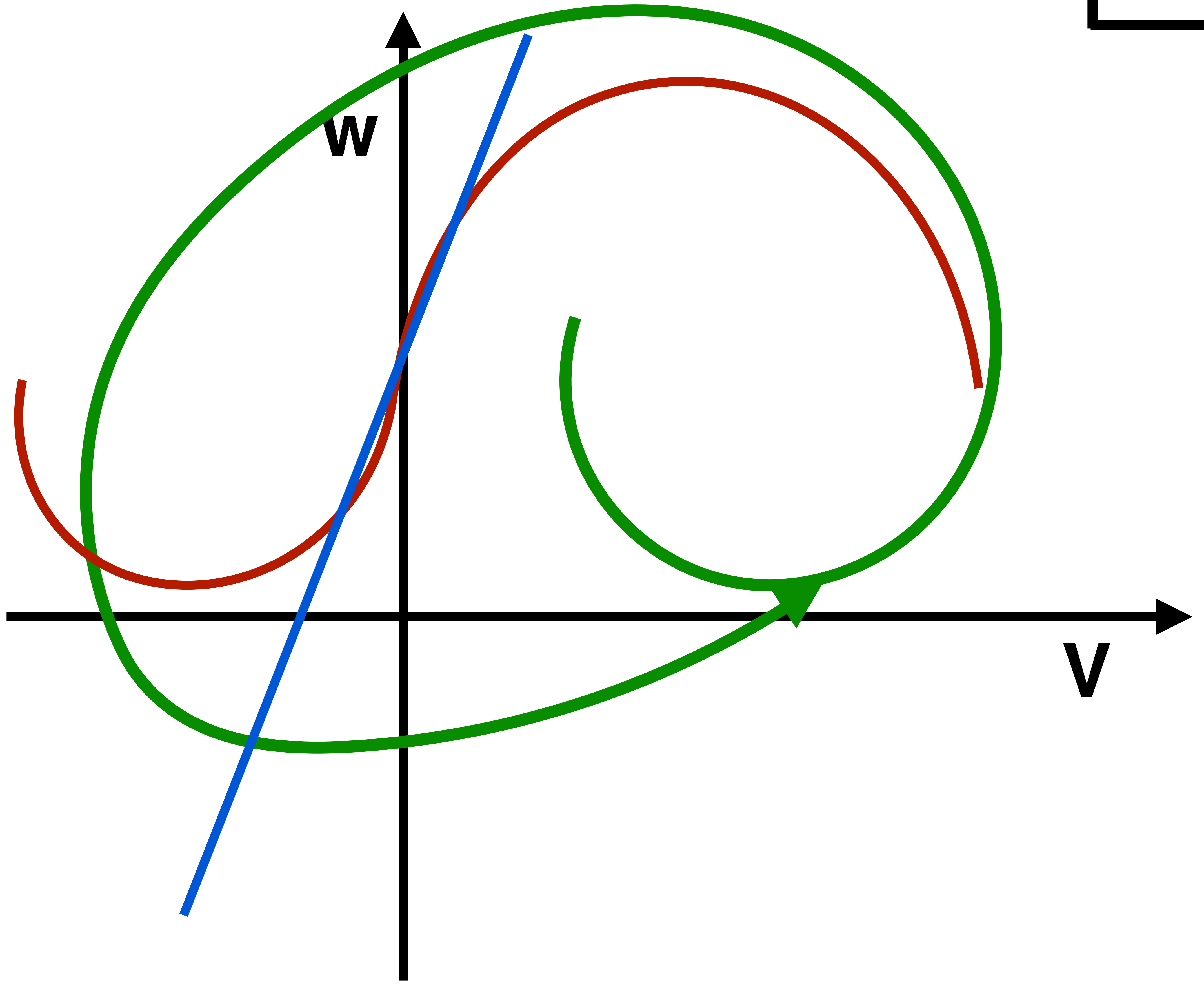
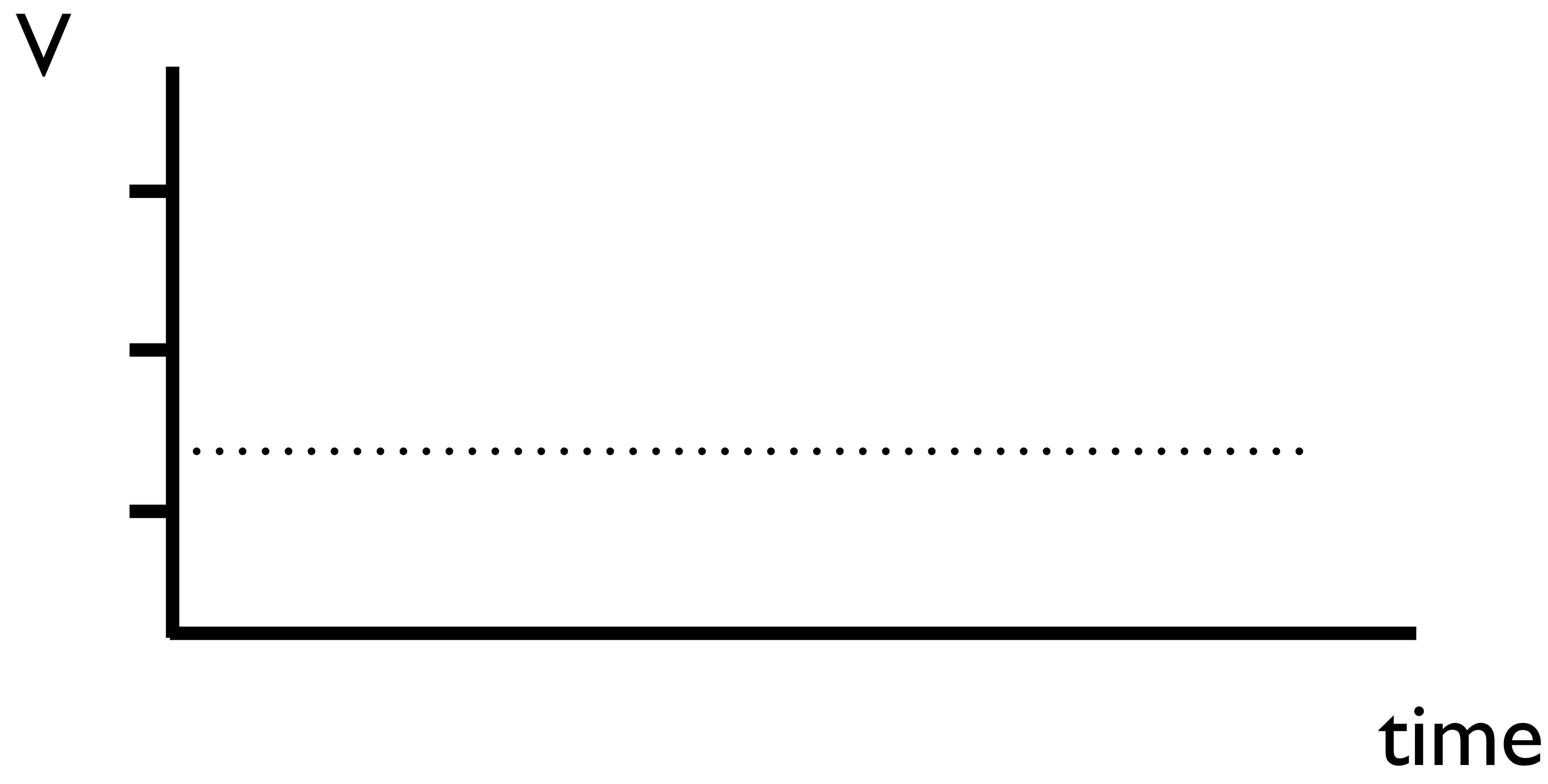
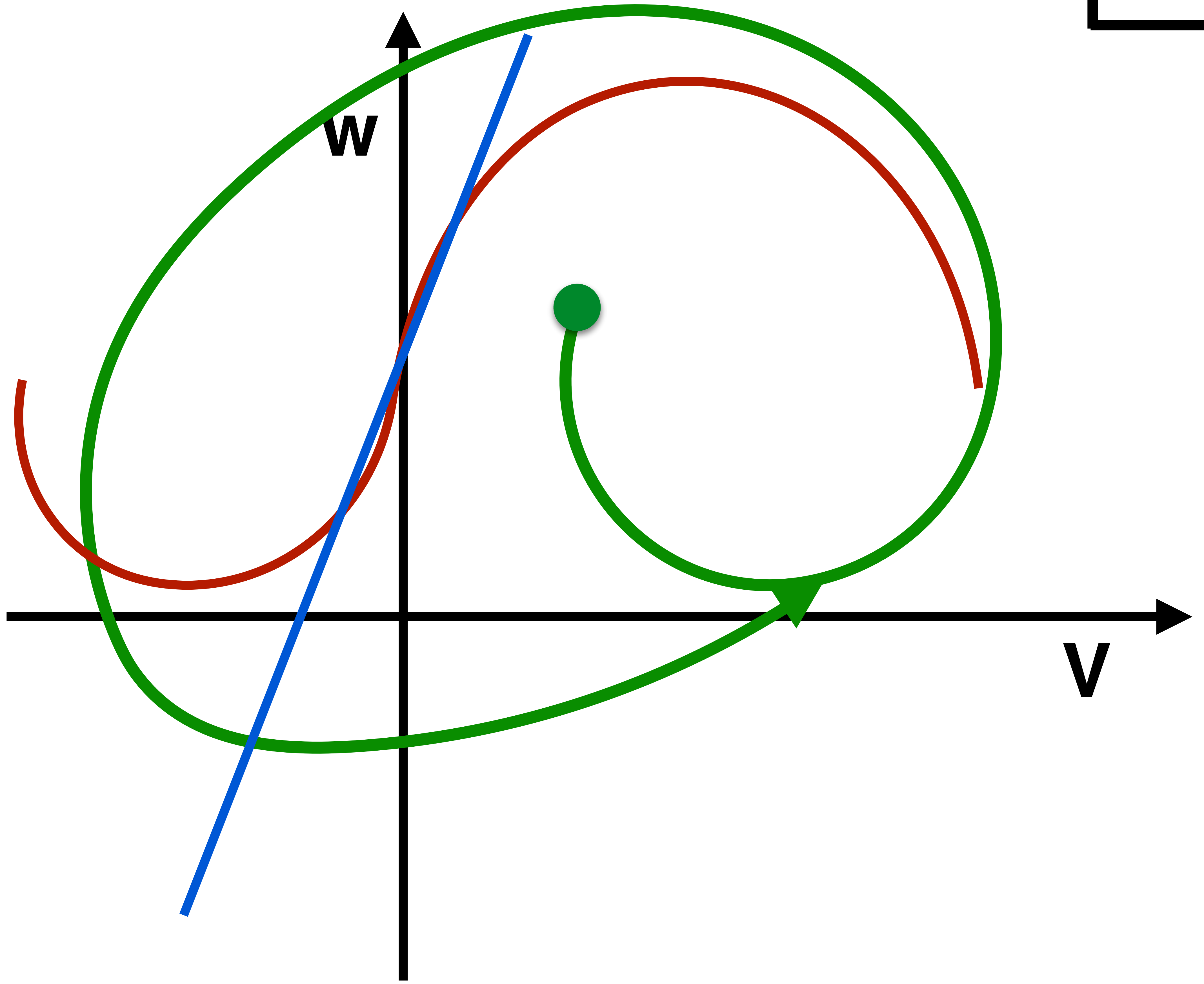


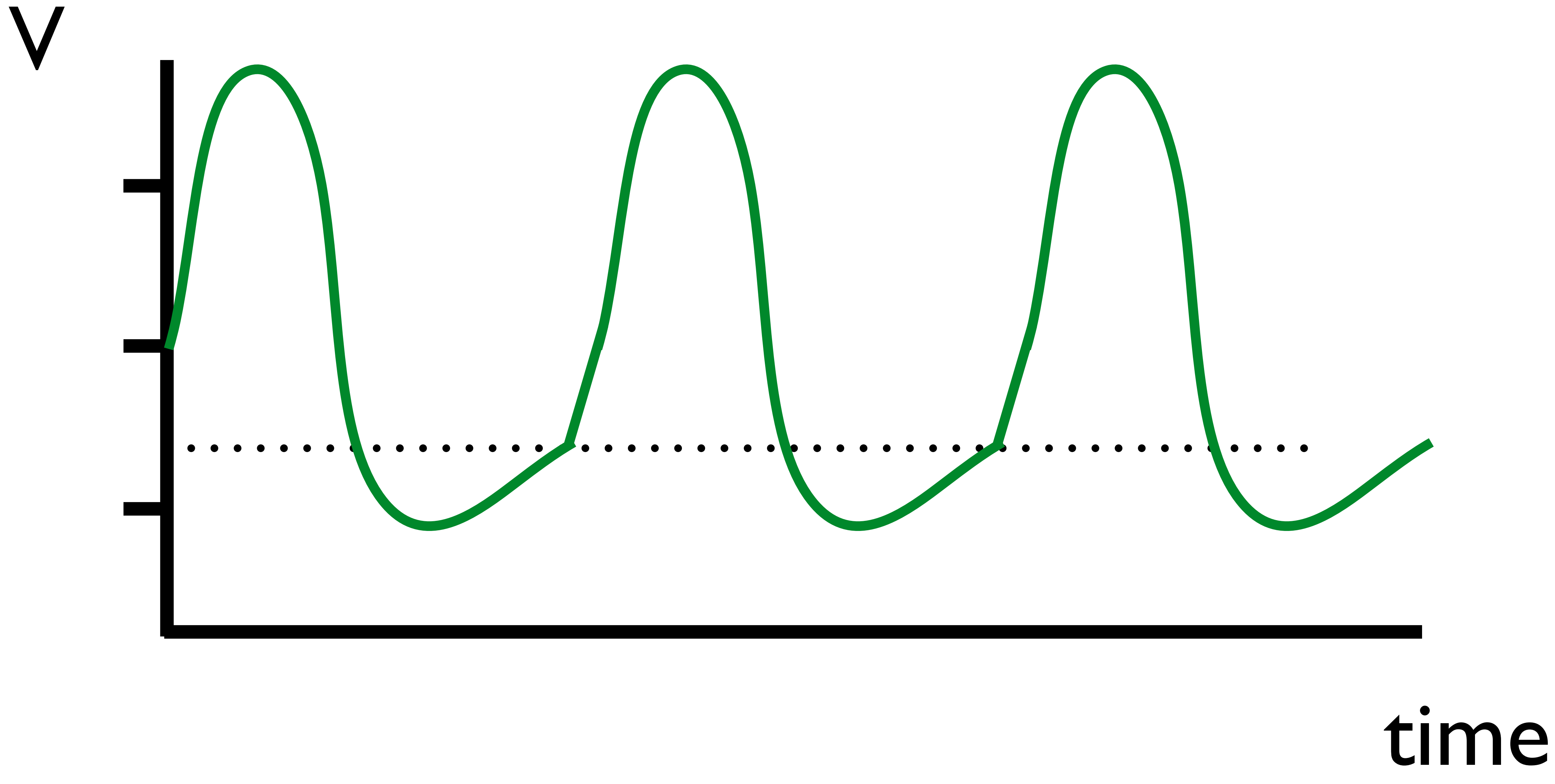


Limit Cycle

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

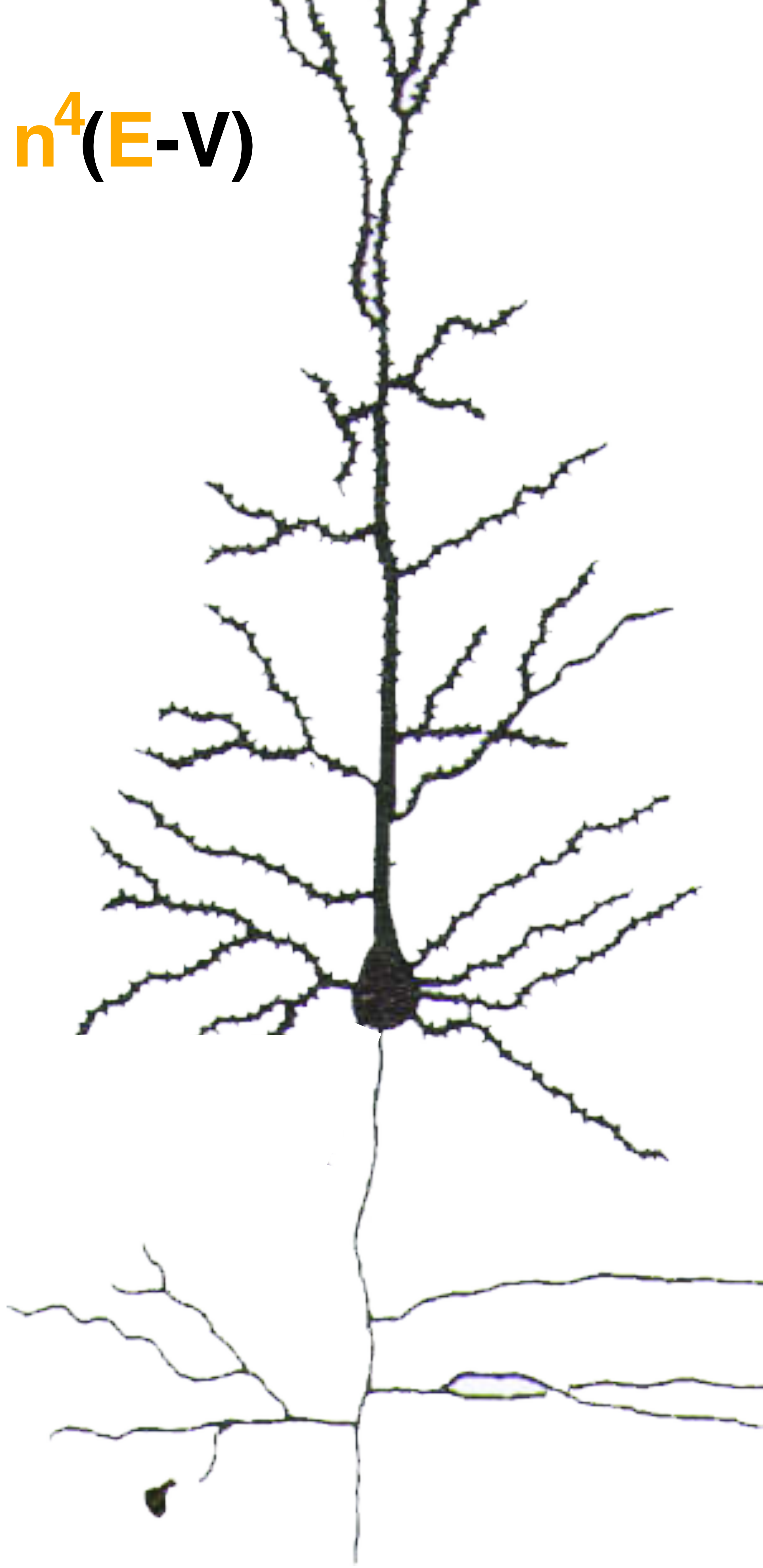
$$\frac{dw}{dt} = a + bV - w$$



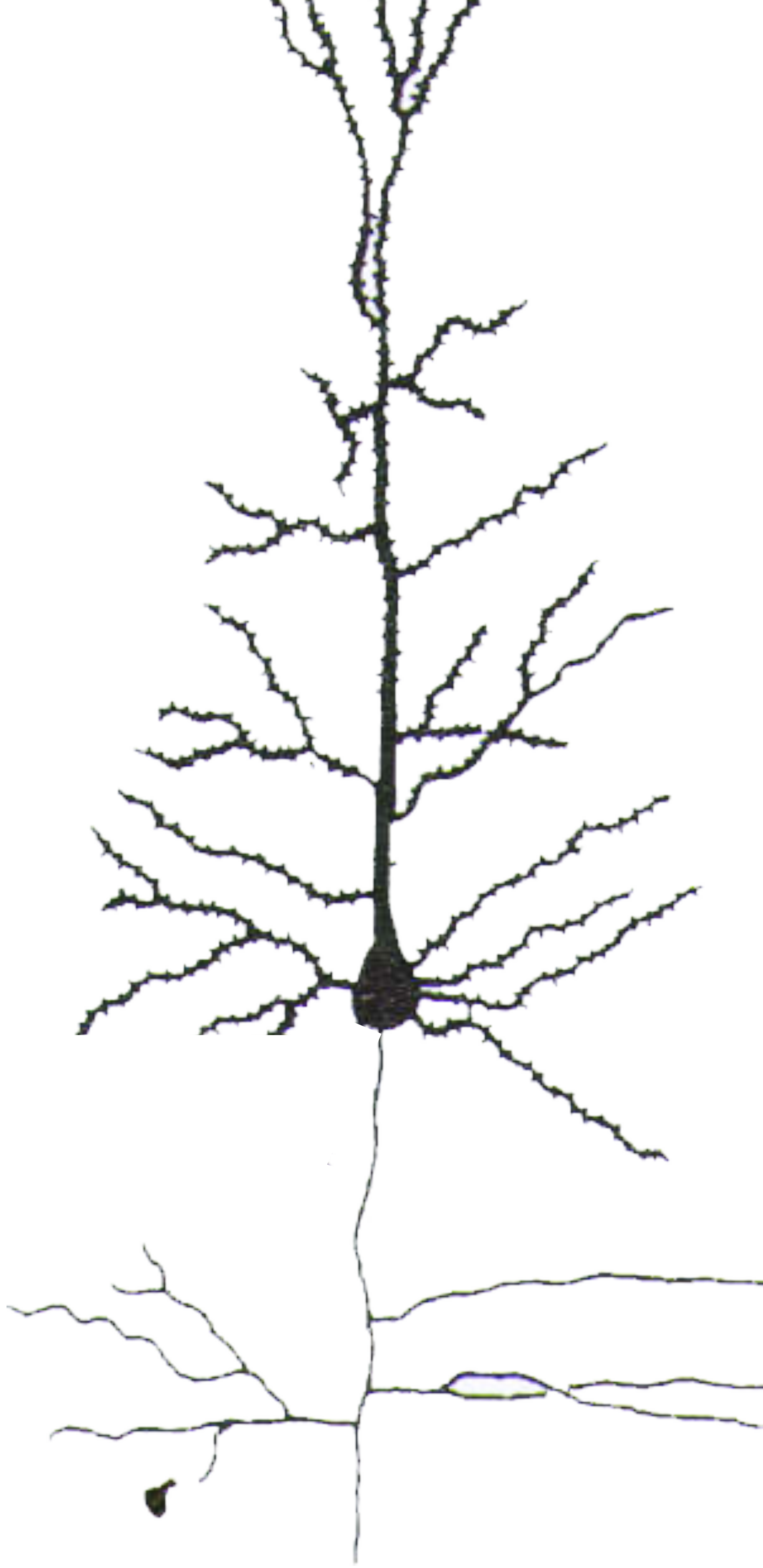


Limit Cycle

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



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



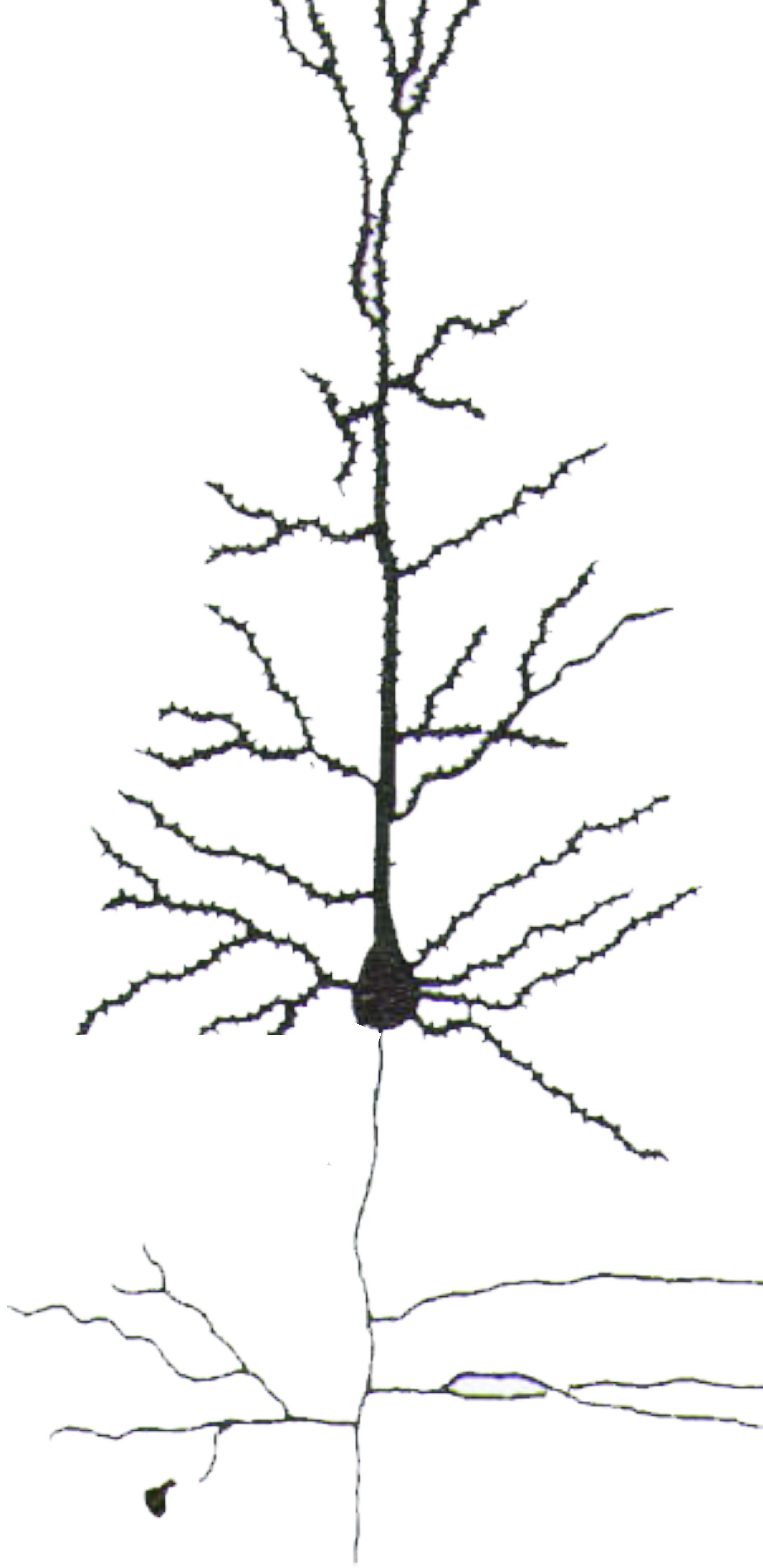
$$C \frac{dV}{dt} = g_{leak}\,(E-V) + g_{synapse}\,(E-V)$$

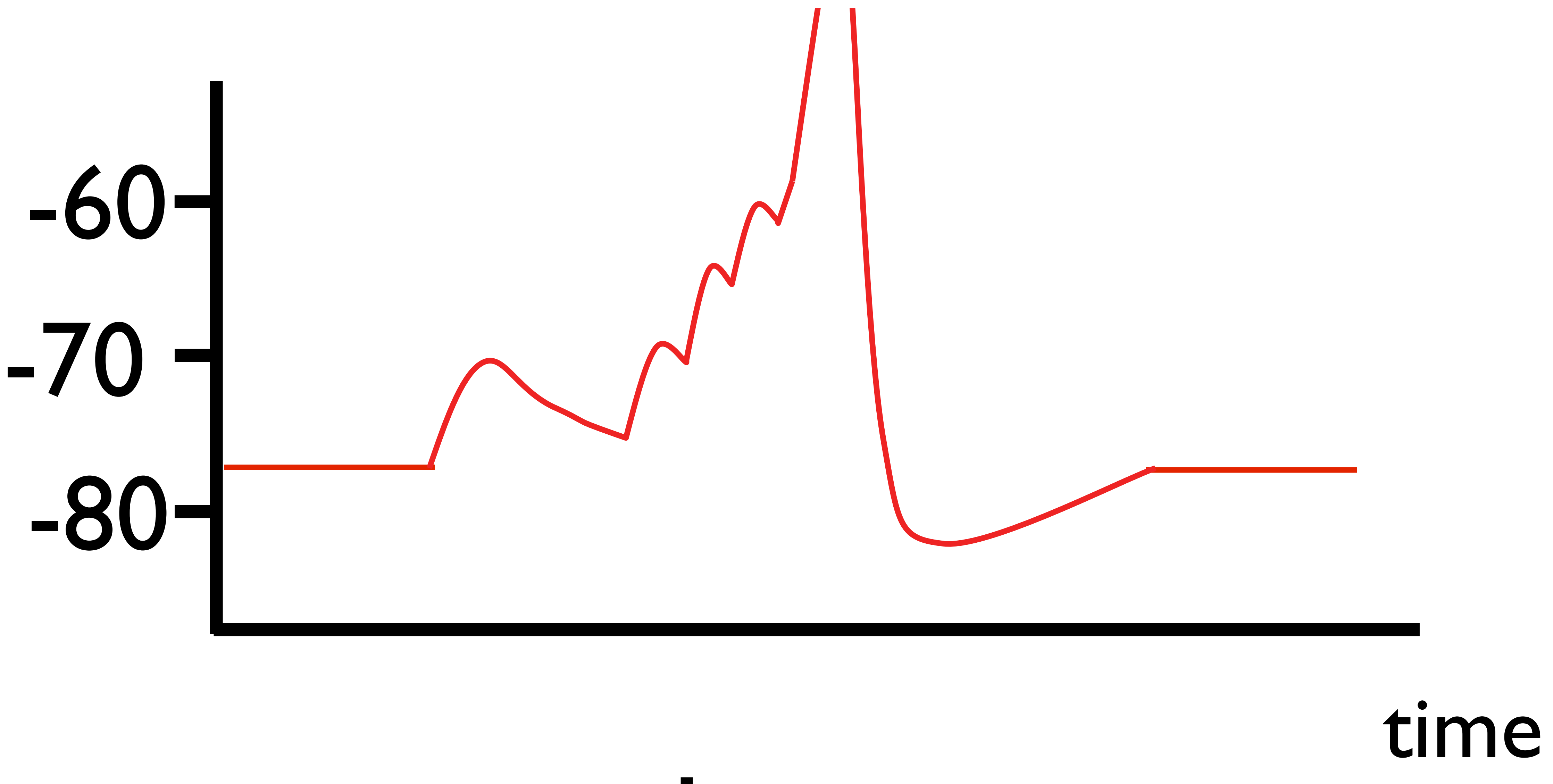
$$g_{tot} = g_{leak} + g_{syn}$$

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

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

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





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

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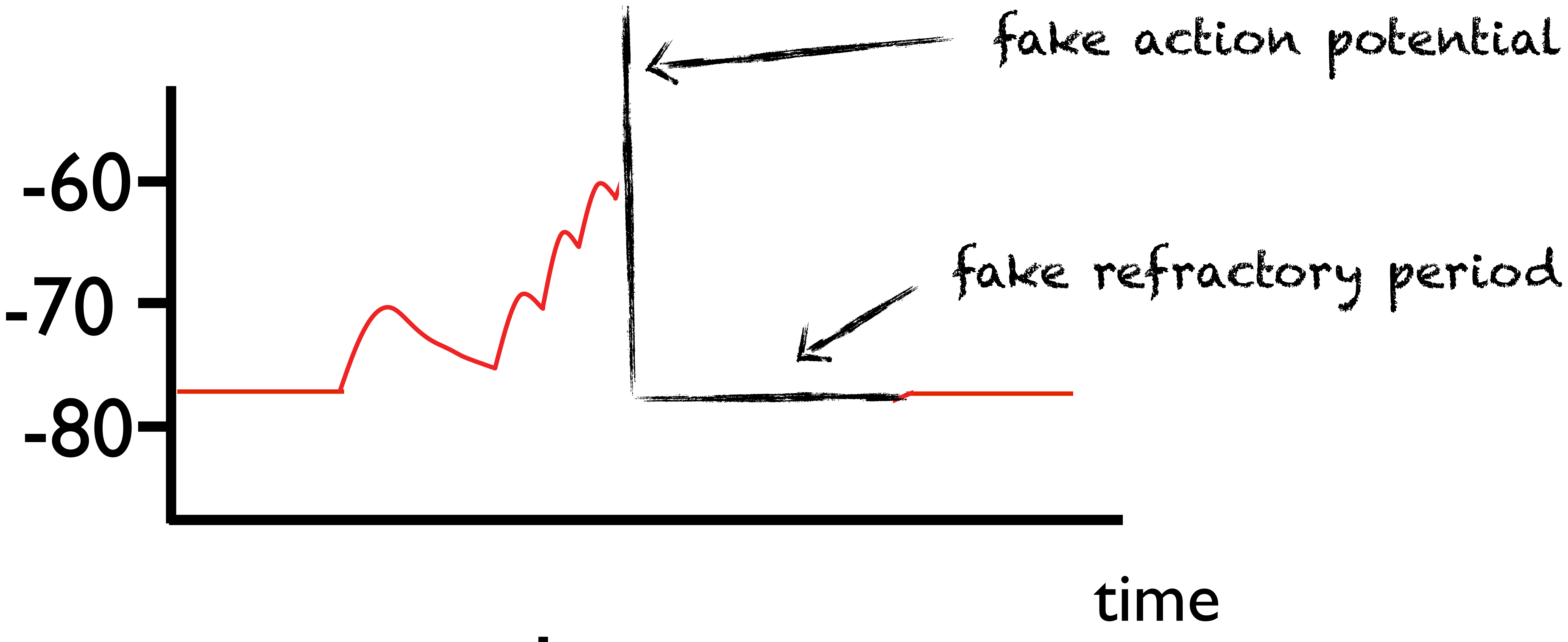

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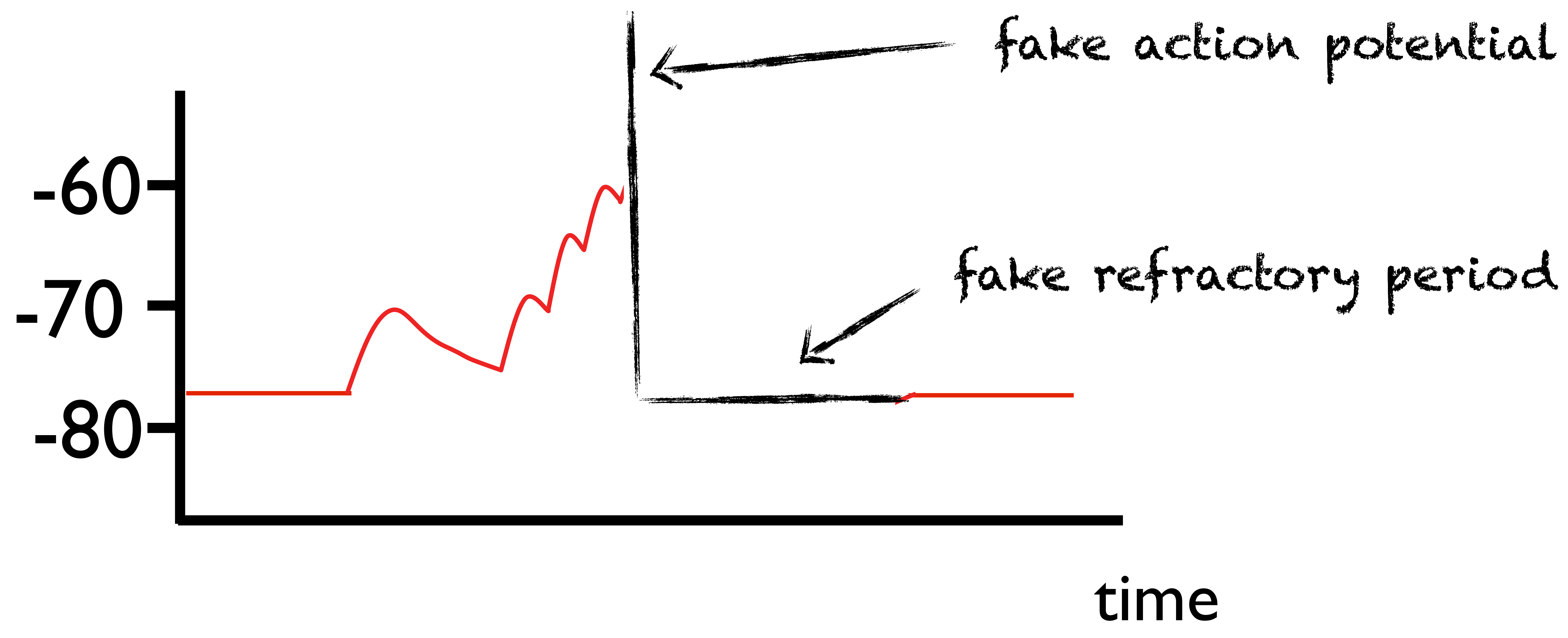
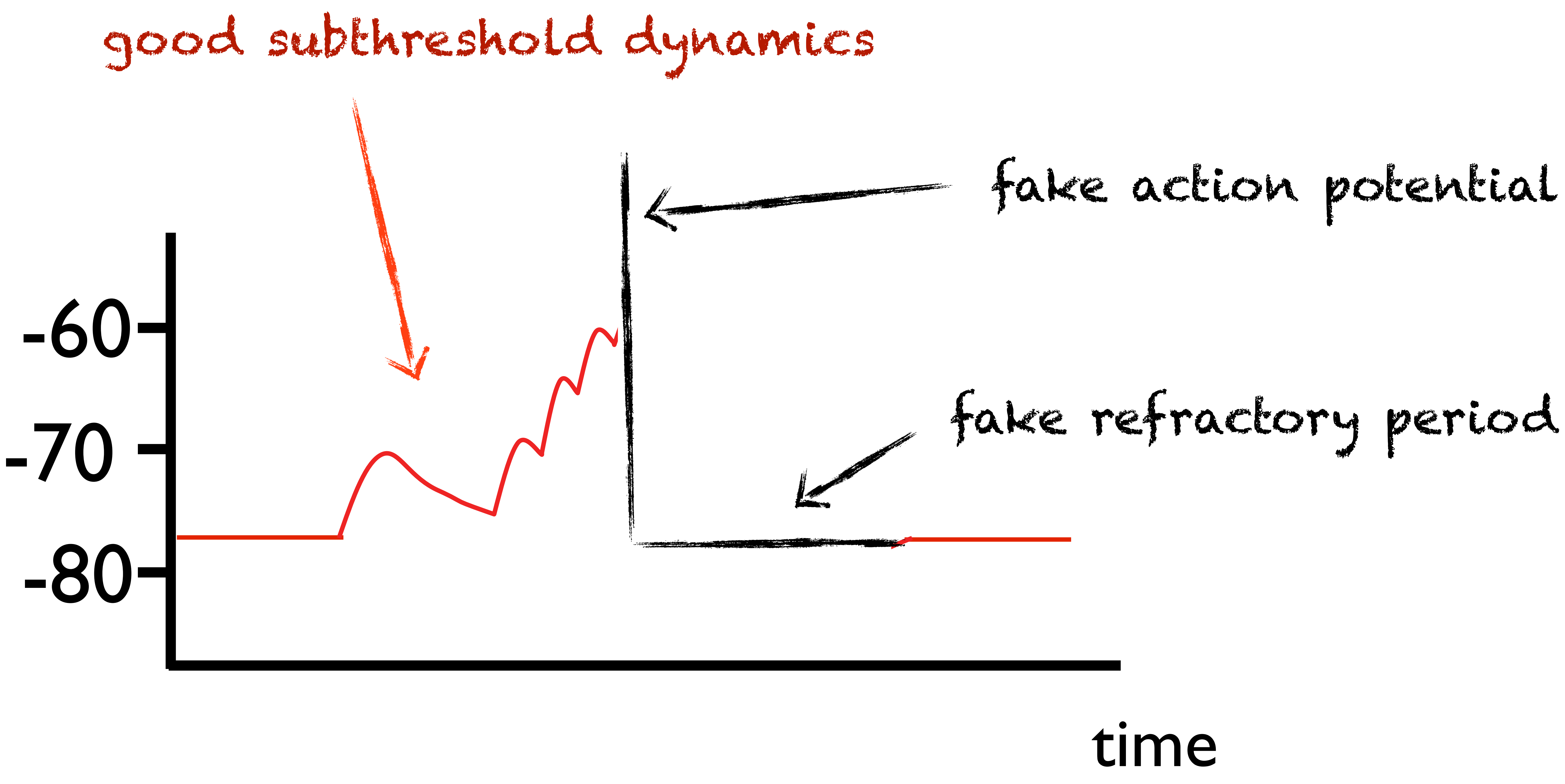
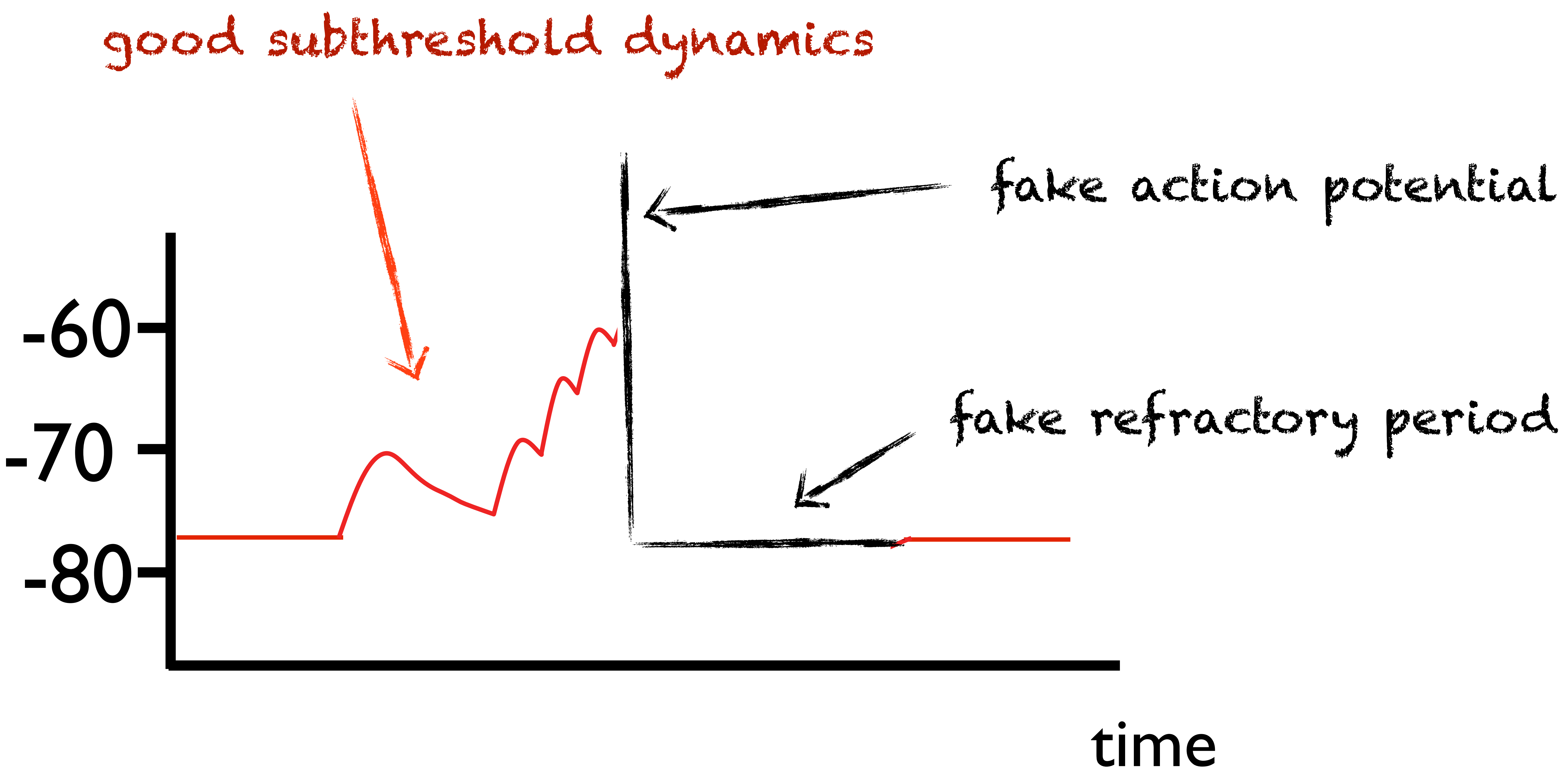


fake action potential
fake refractory period
-60
-70
-80
time

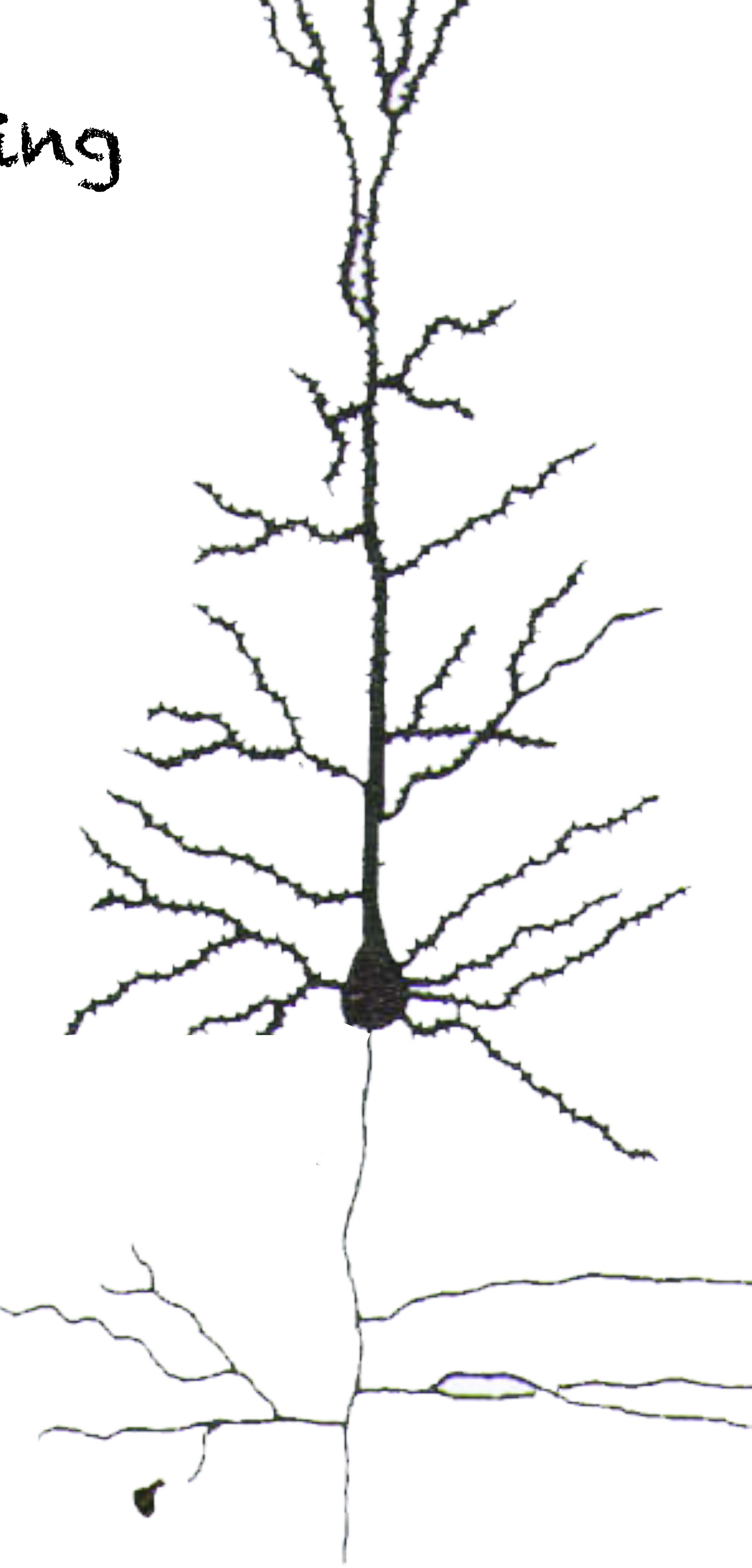

good subthreshold dynamics
fake action potential
fake refractory period
-60
-70
-80
time



Voilà,...

Integrate & fire!!

A cheap and accurate method to simulate spiking



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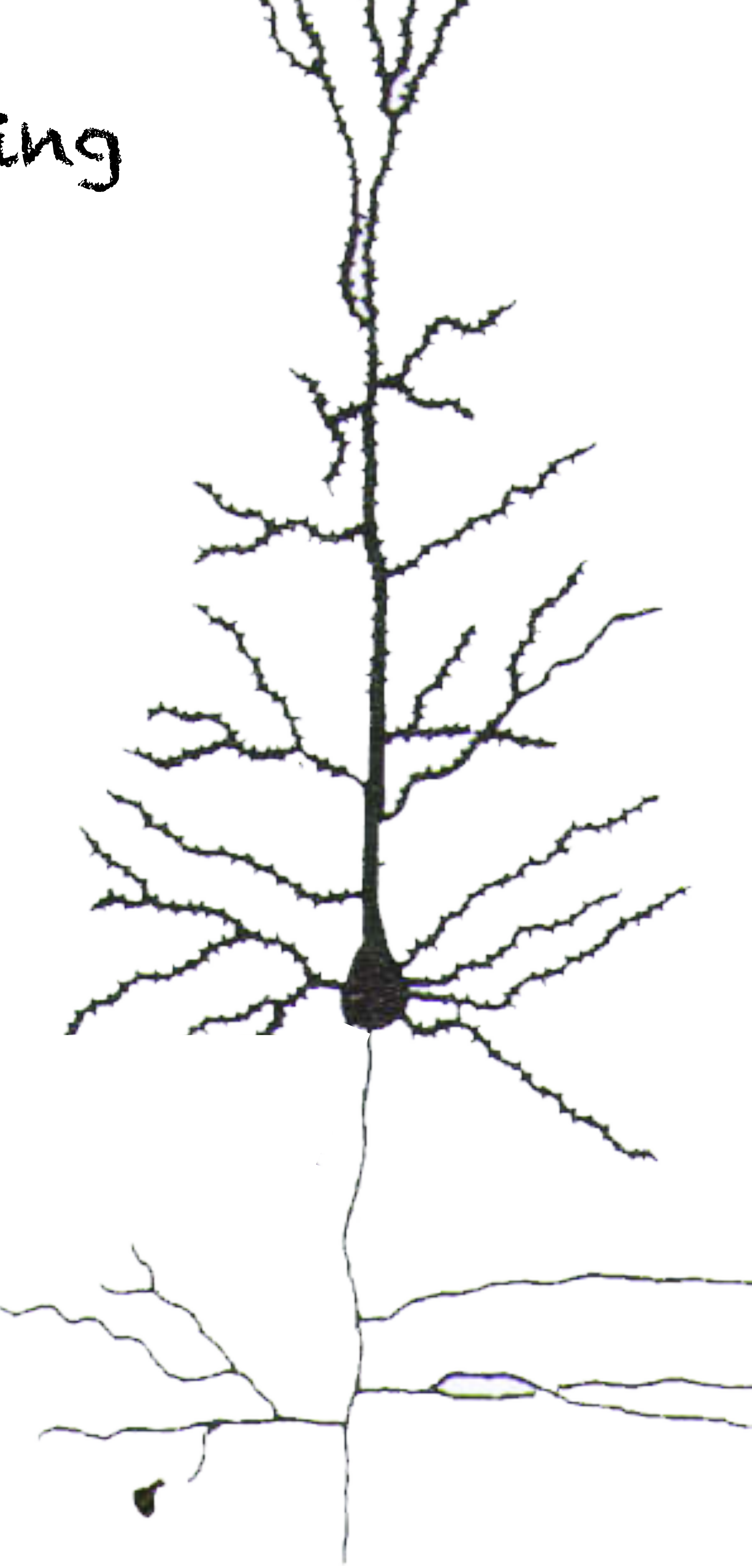
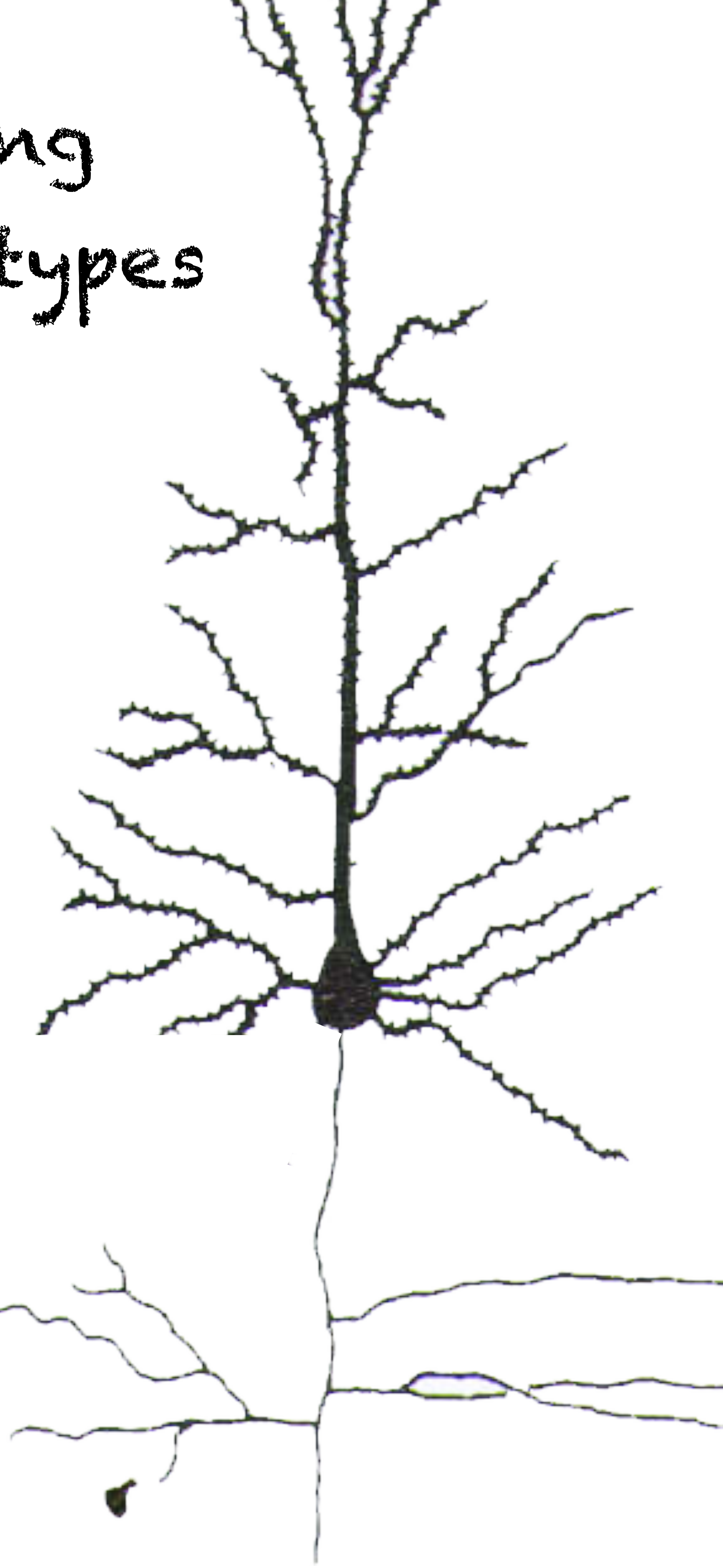


A cheap and accurate method to simulate spiking neurons that works for all neuron types



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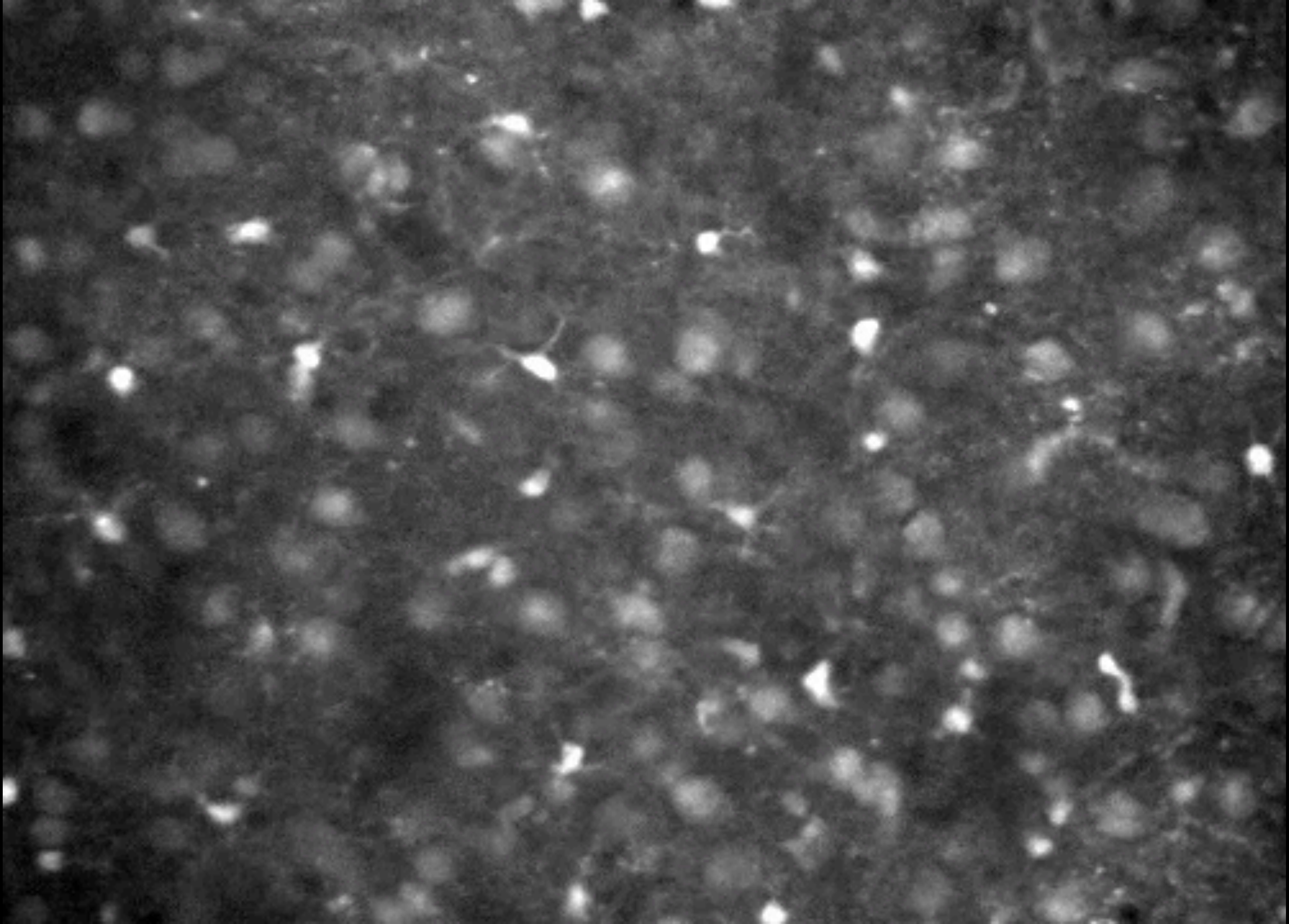
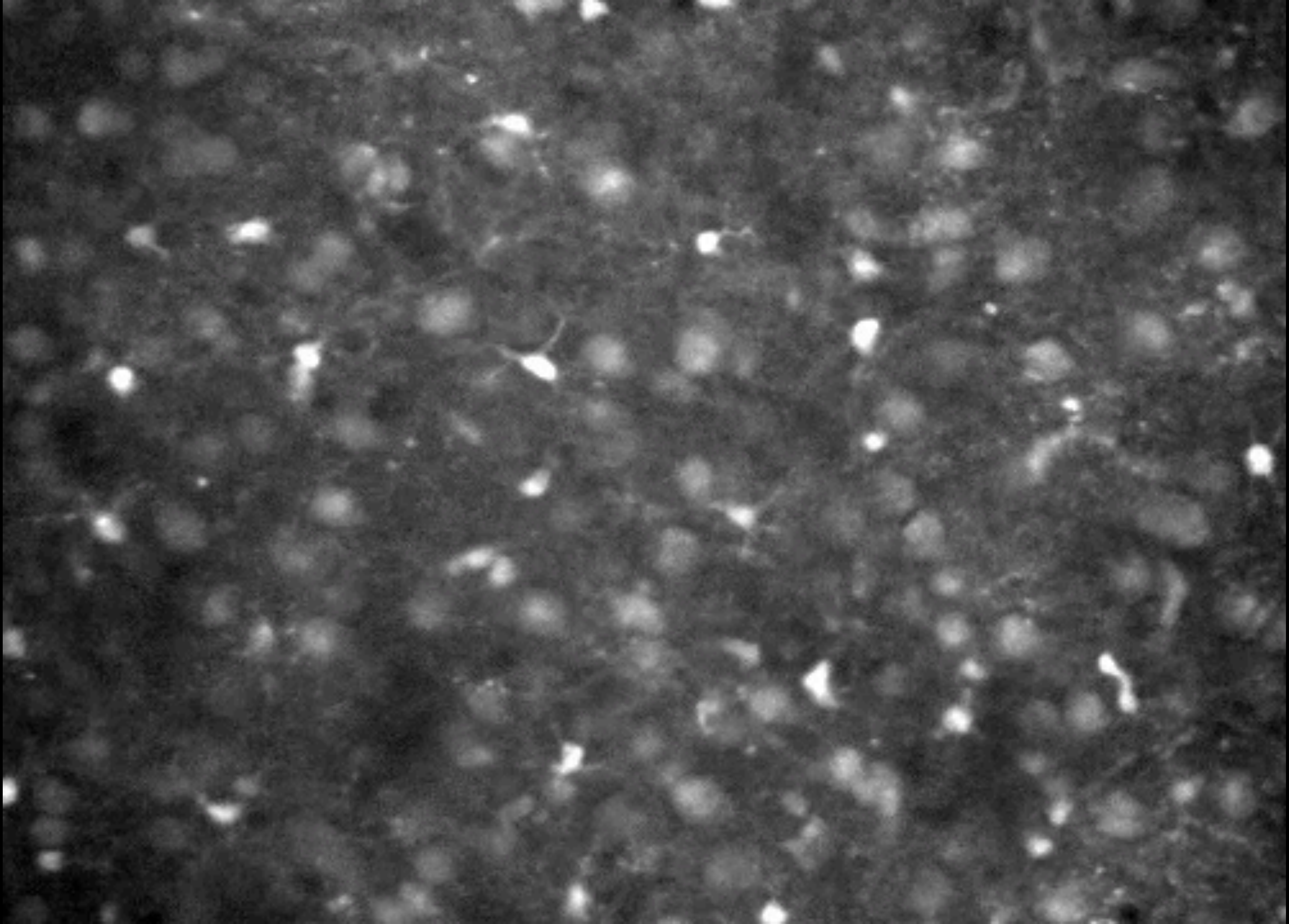
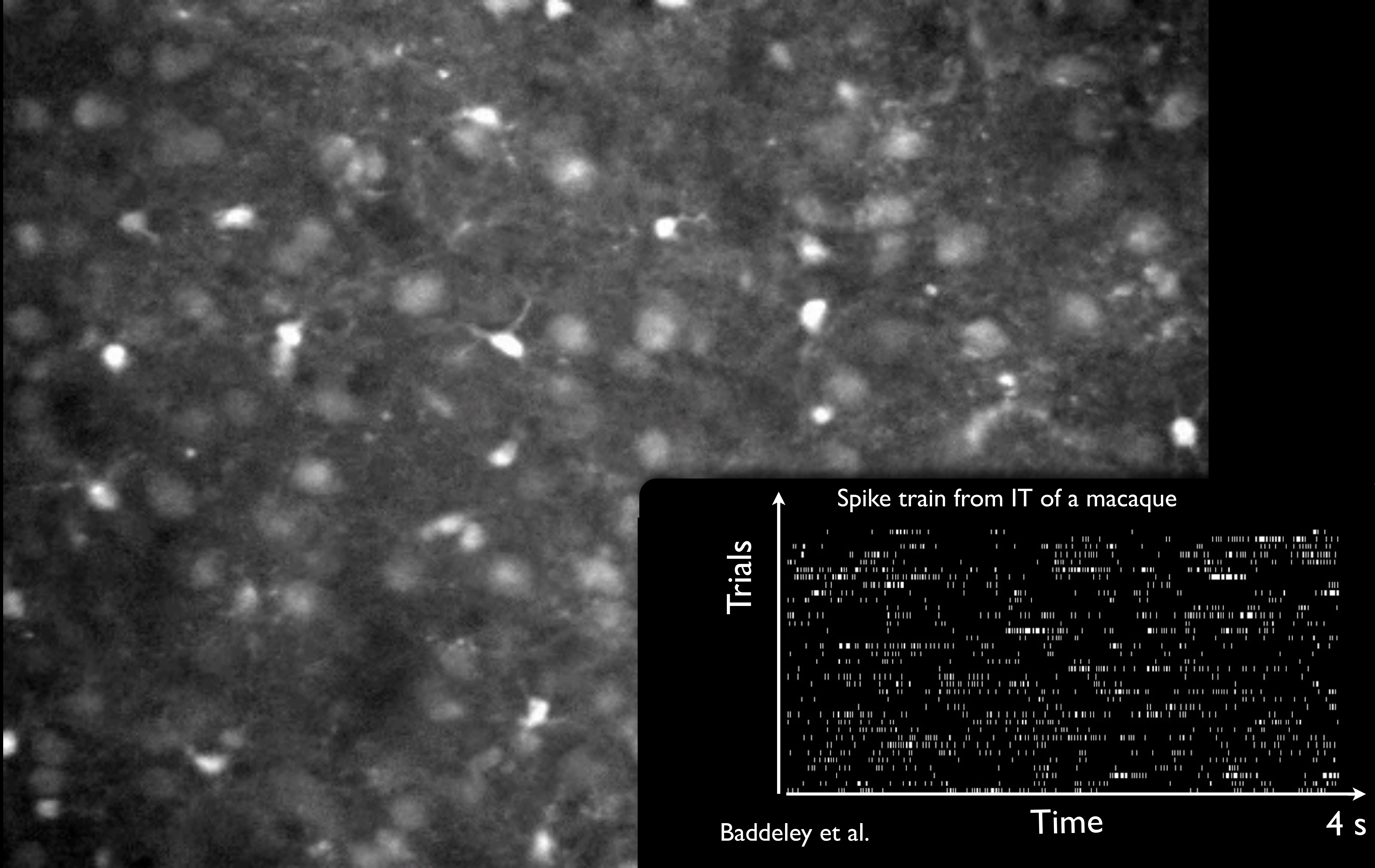
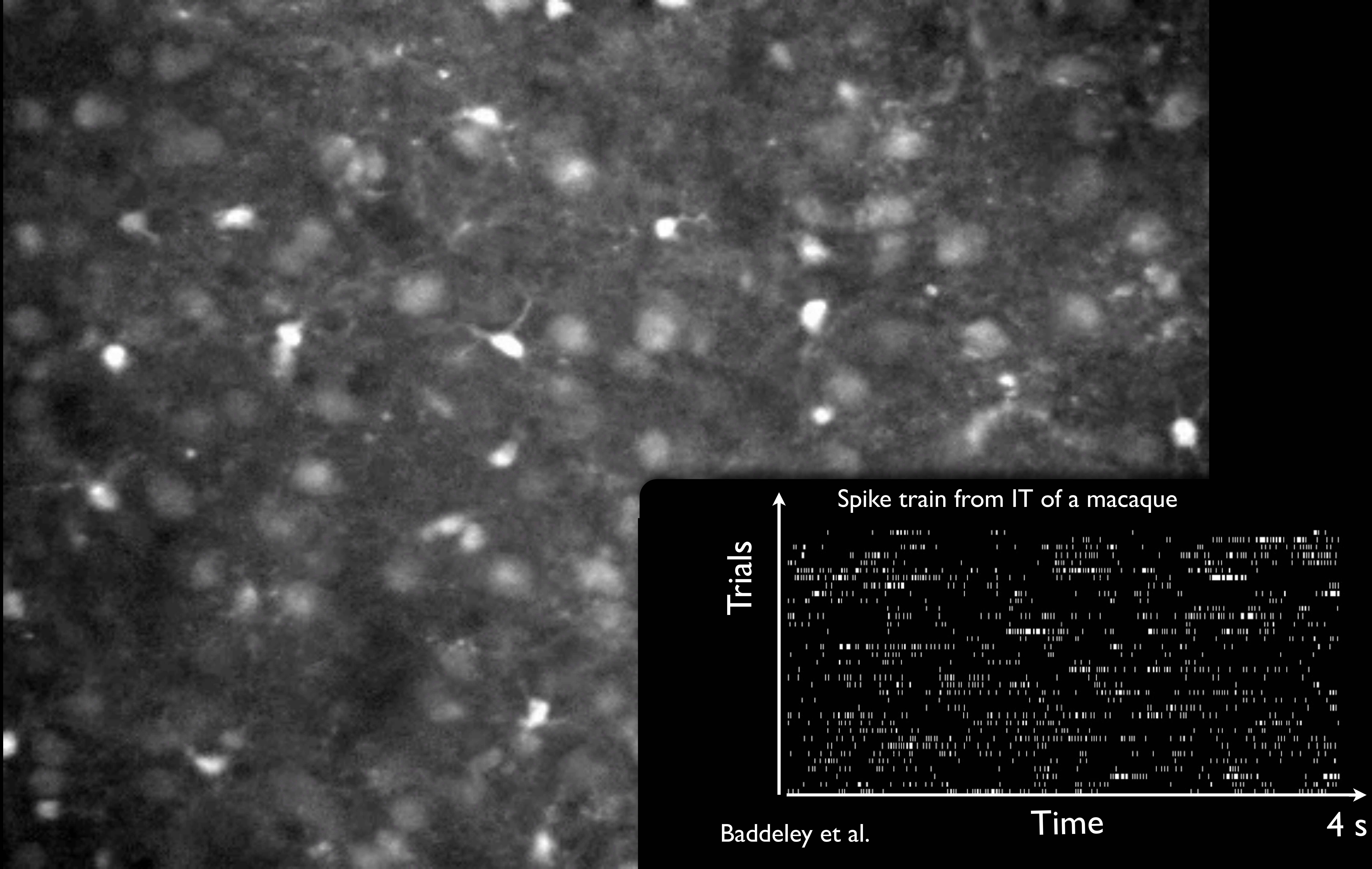
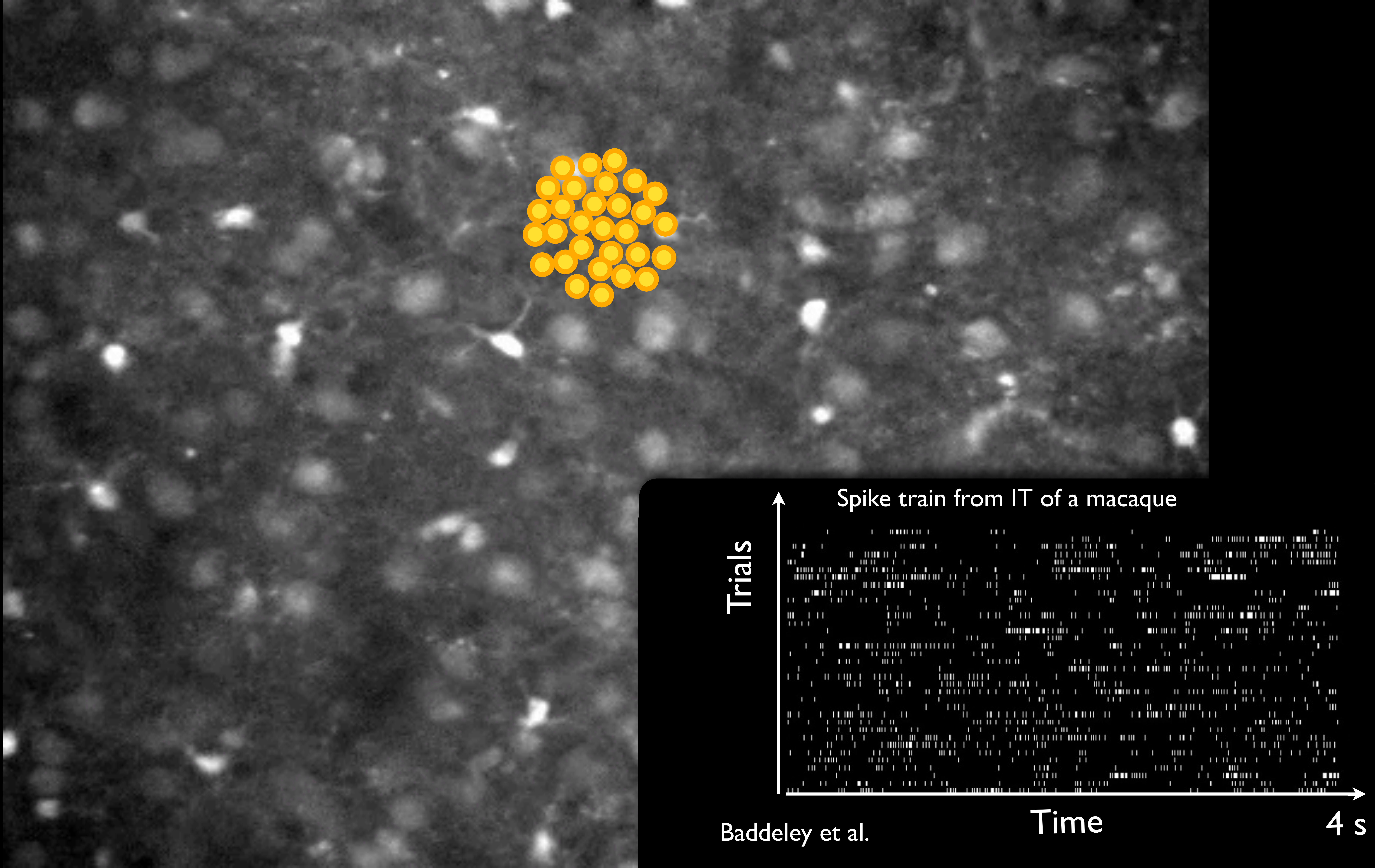





Spike train from IT of a macaque
Trials
Time
4 s
Baddeley et al.



Baddeley et al.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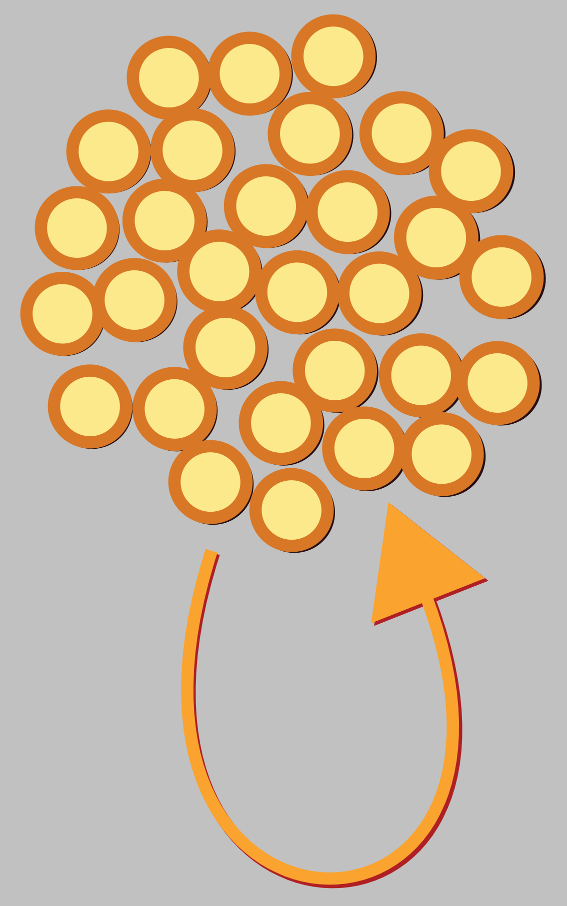

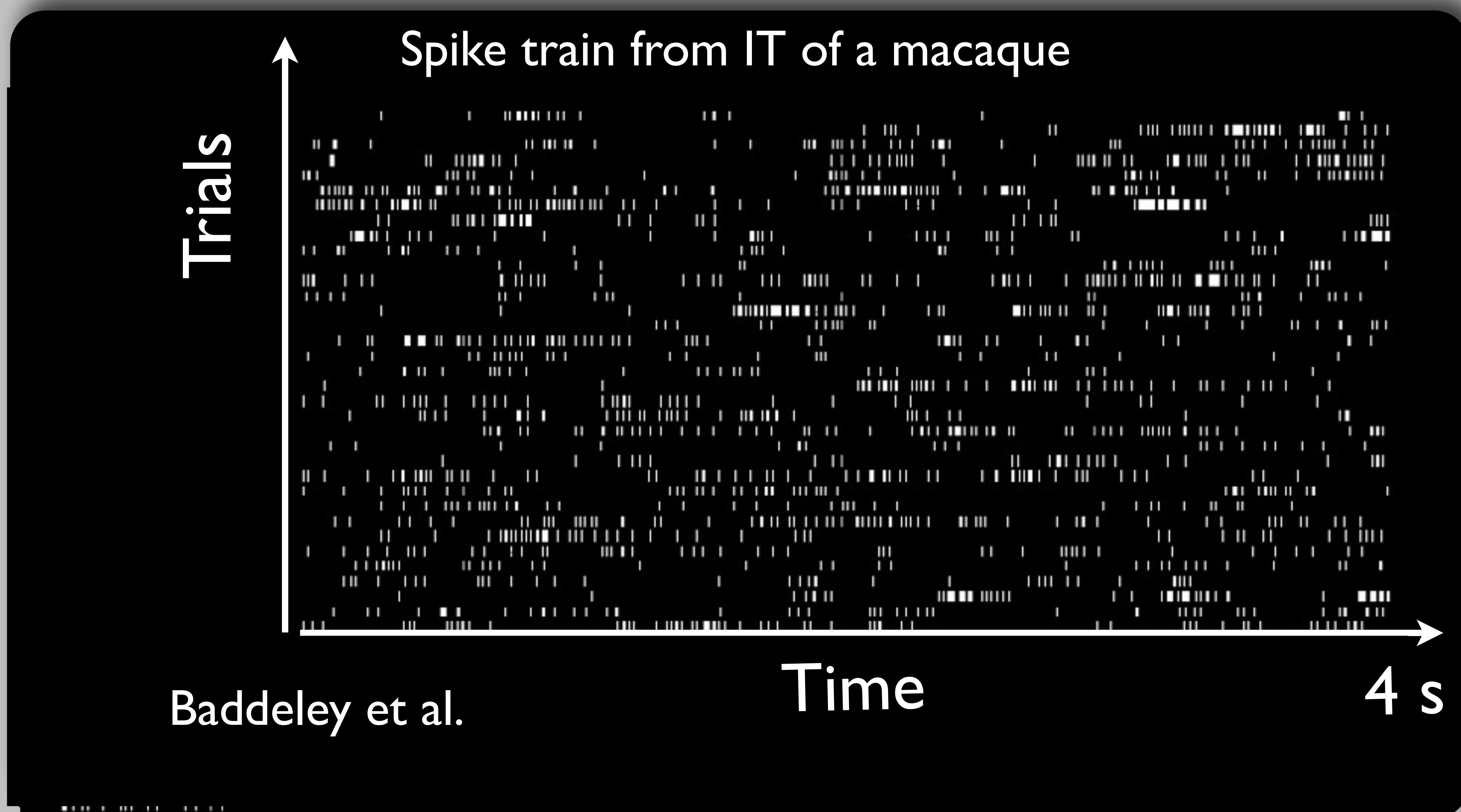
Spike train from IT of a macaque
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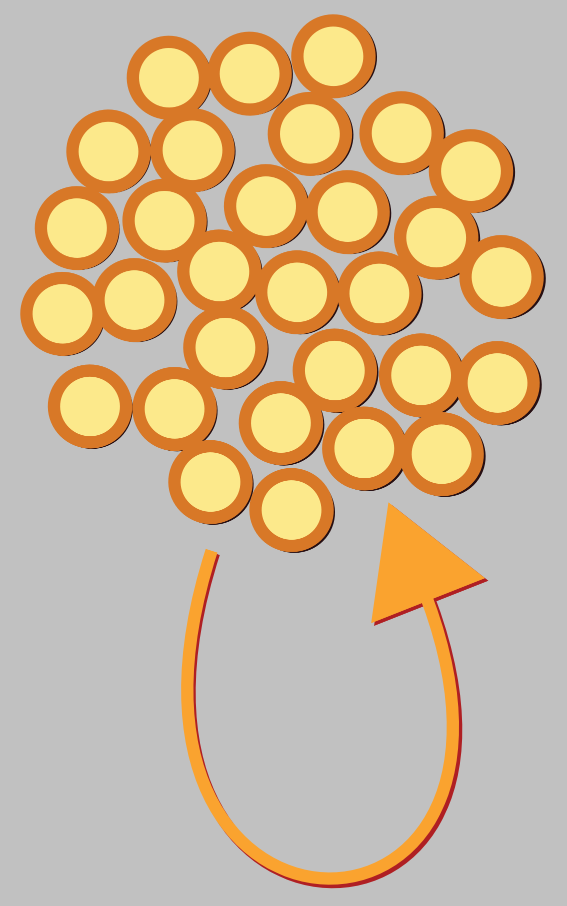
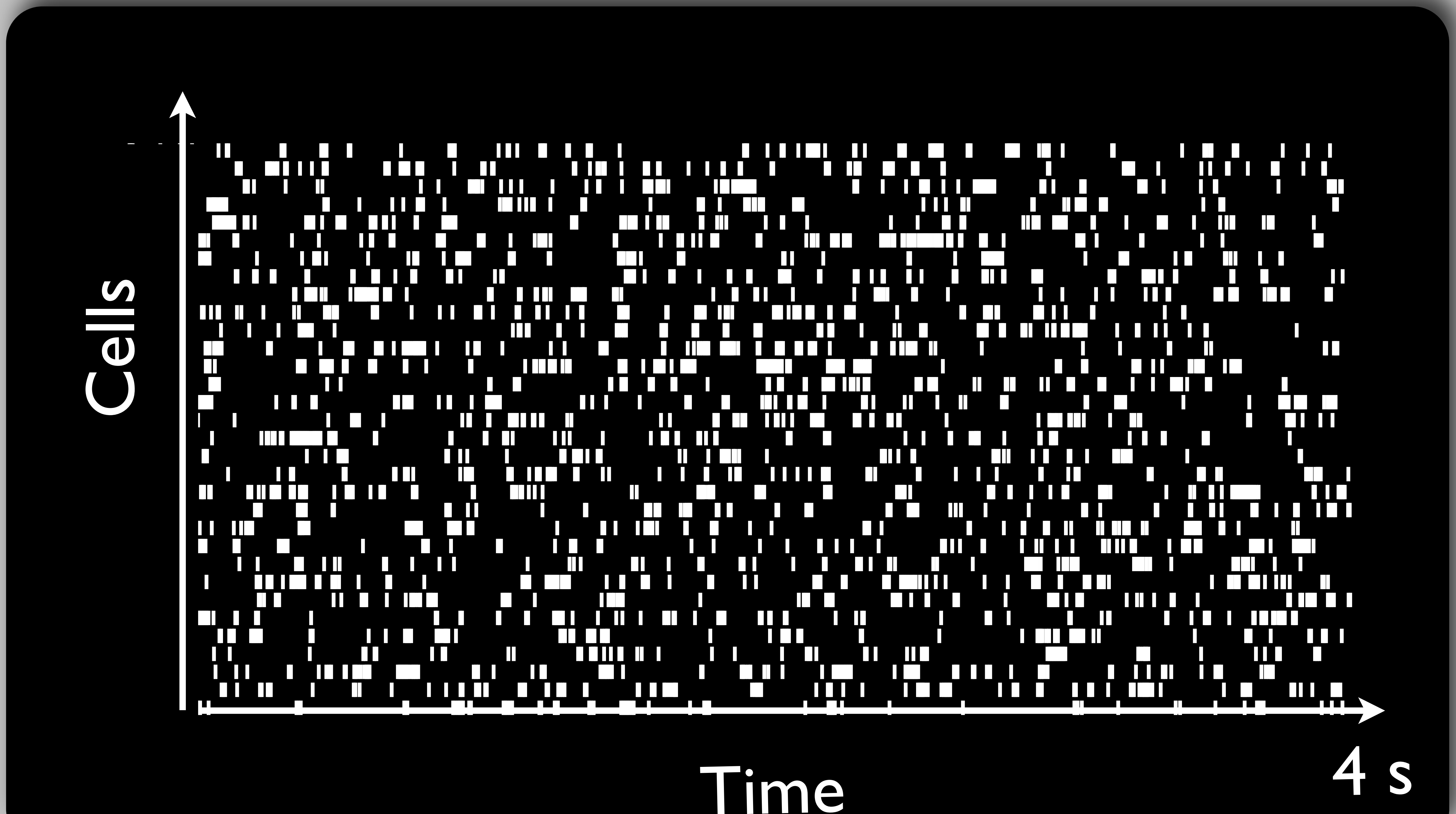
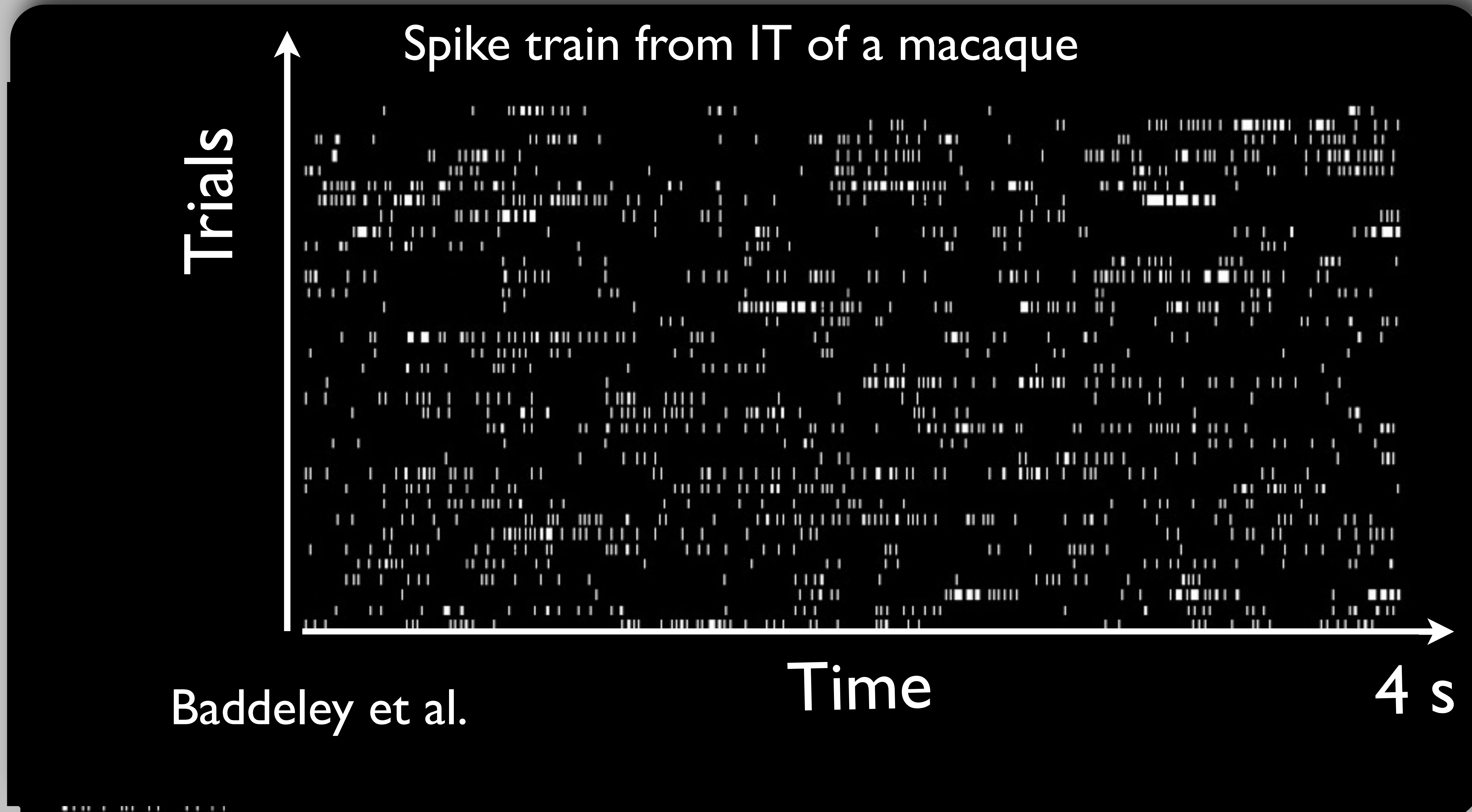
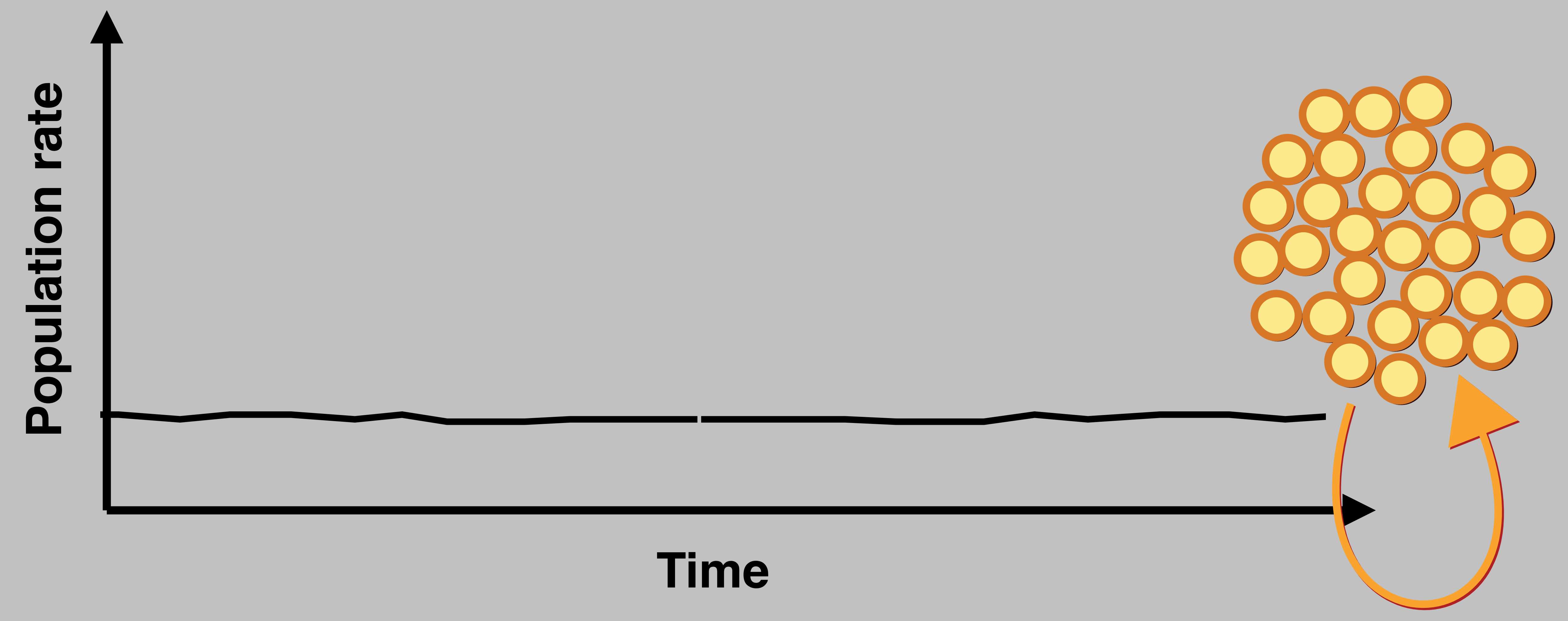
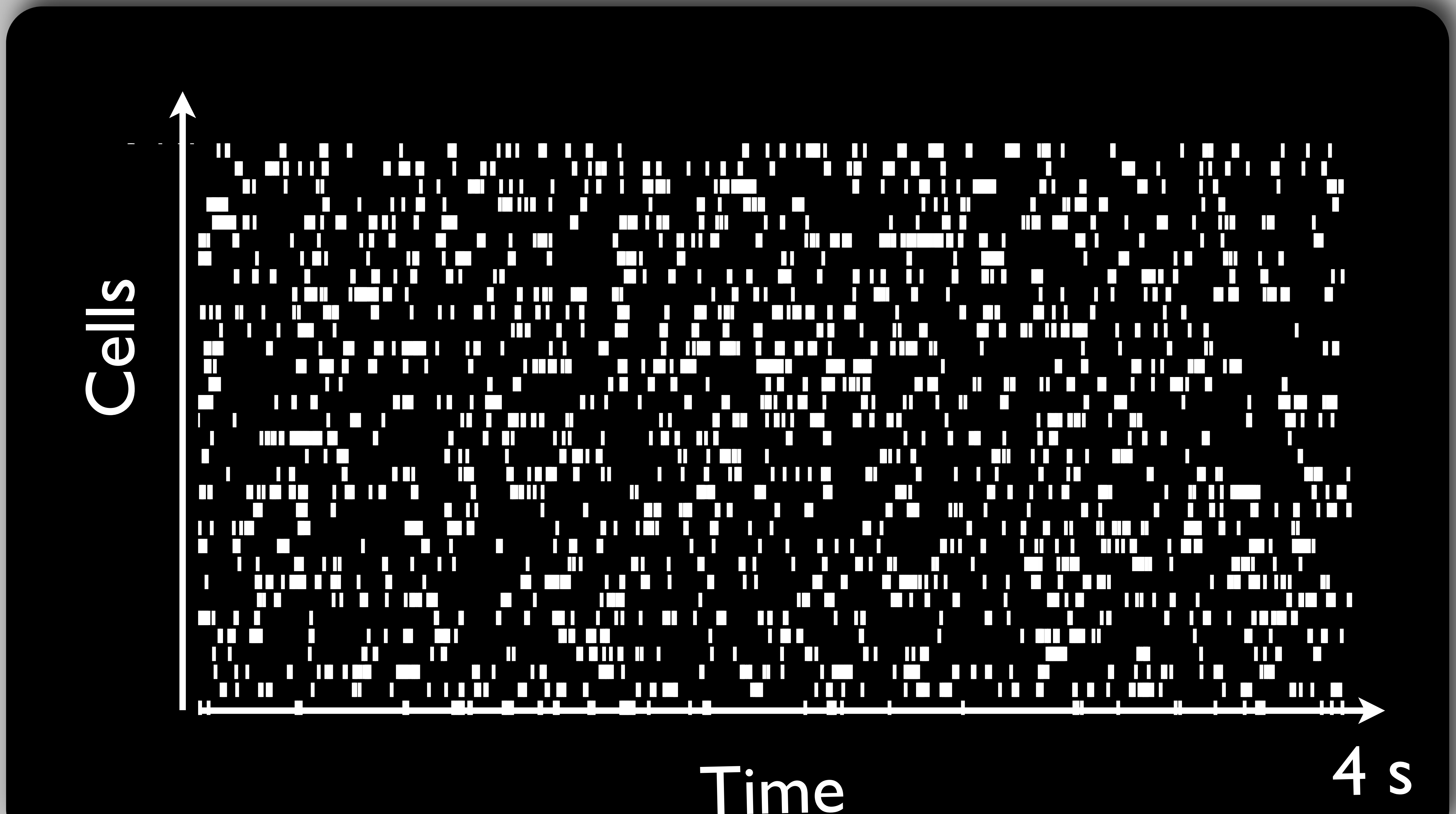
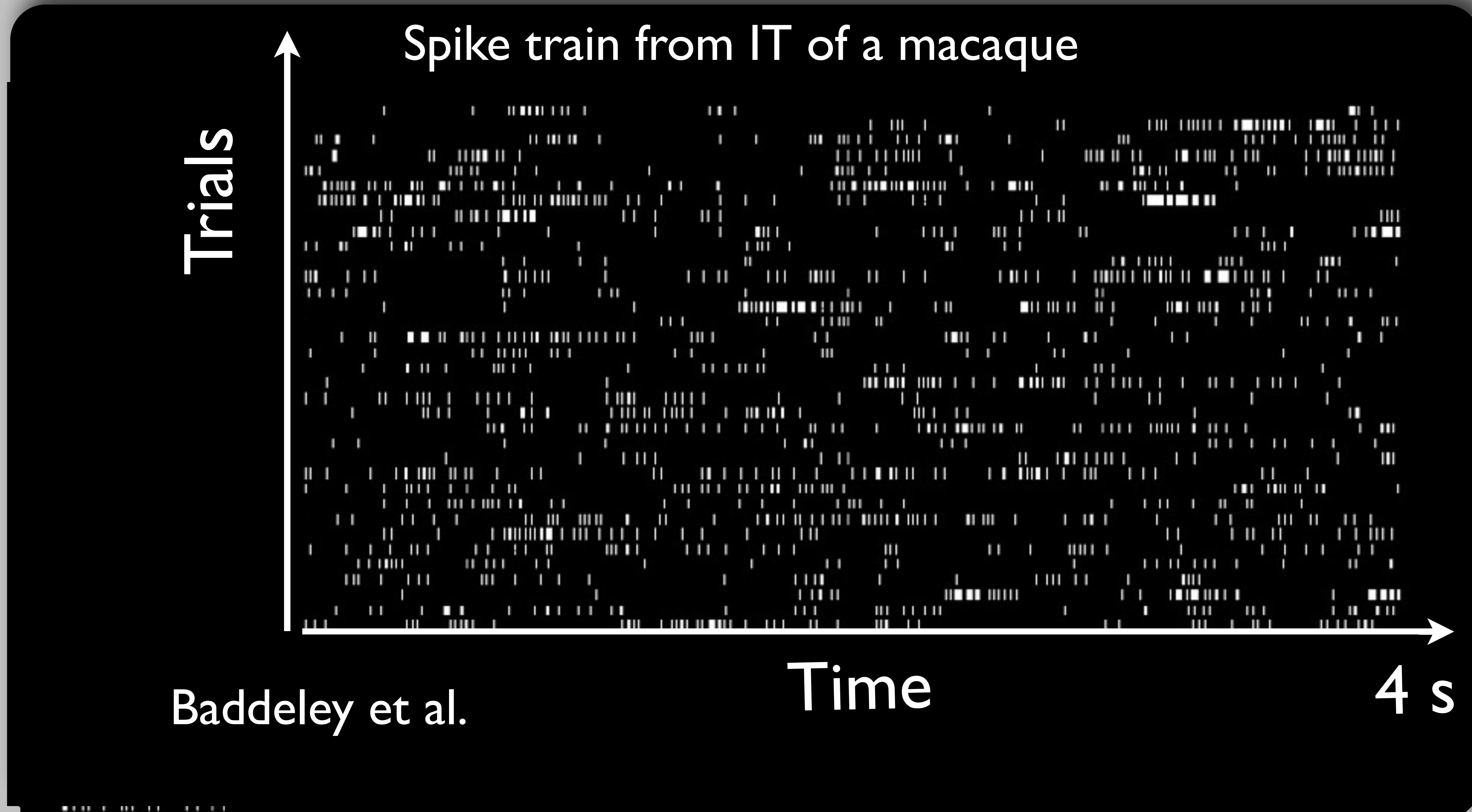



Cells
Time
4 s


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


Population rate
Time


Cells
Time
4 s


Spike train from IT of a macaque
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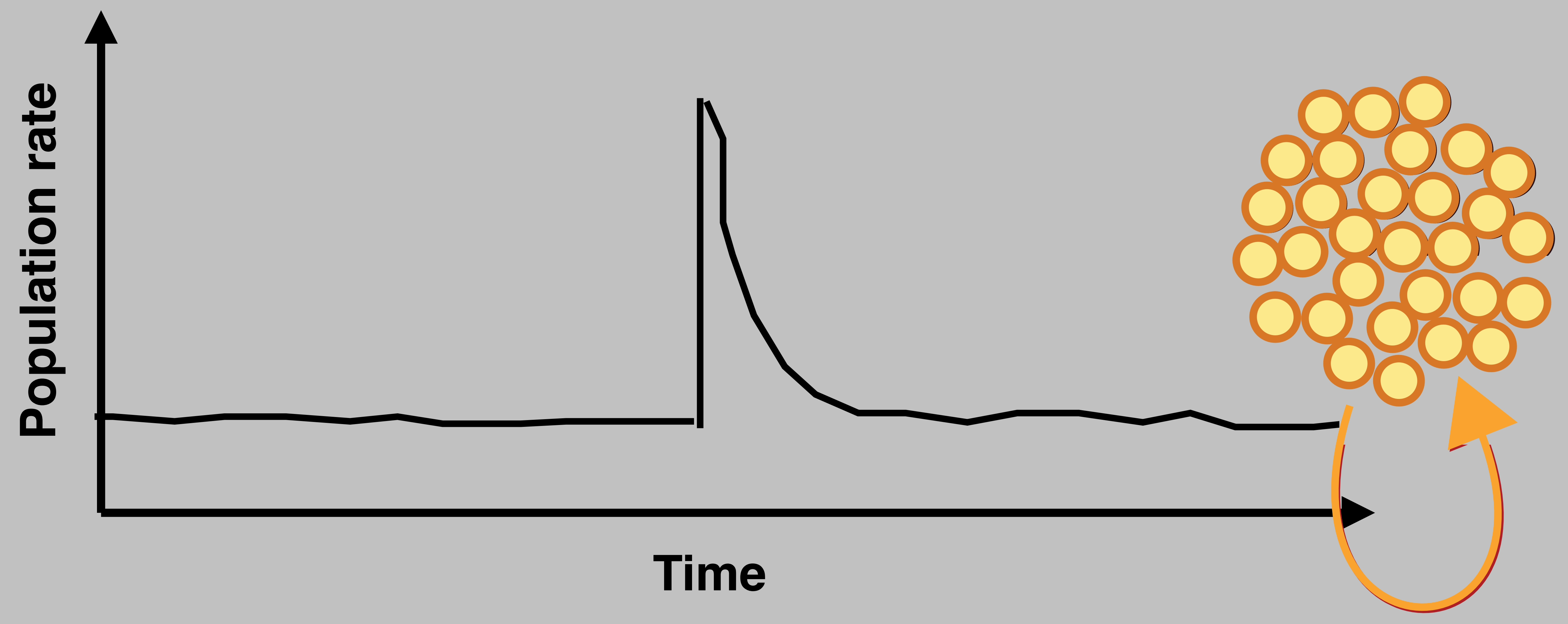
Baddeley et al.


Population rate
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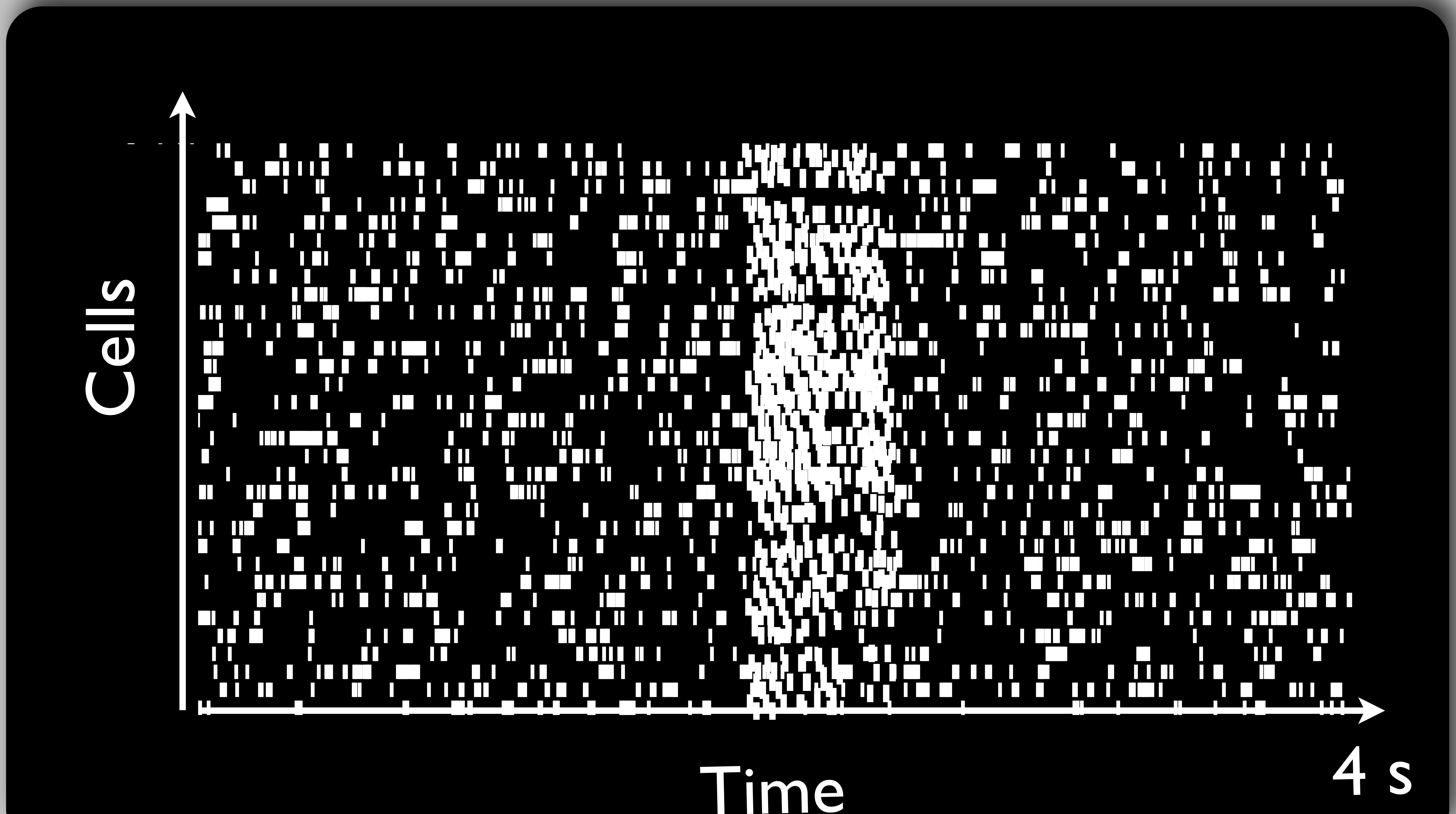
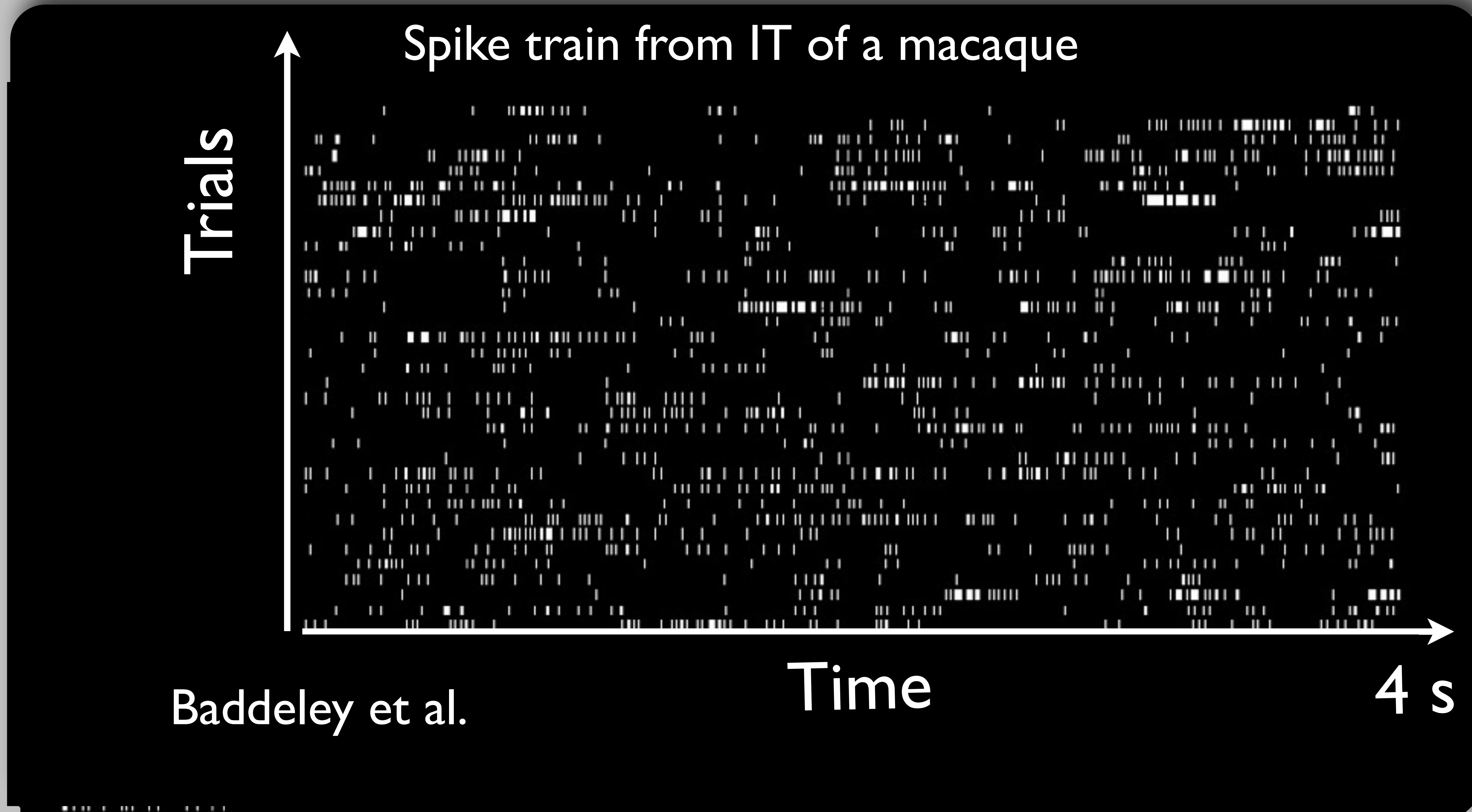

Cells
Time
4 s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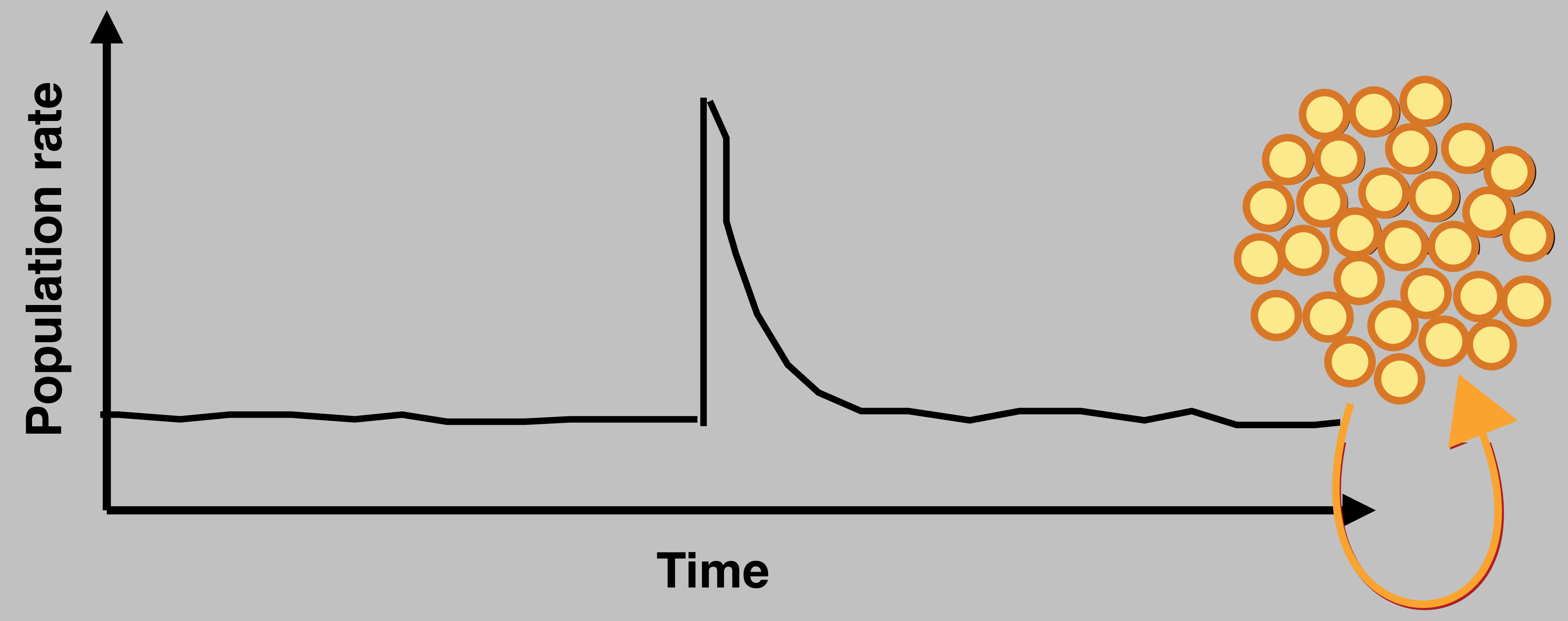
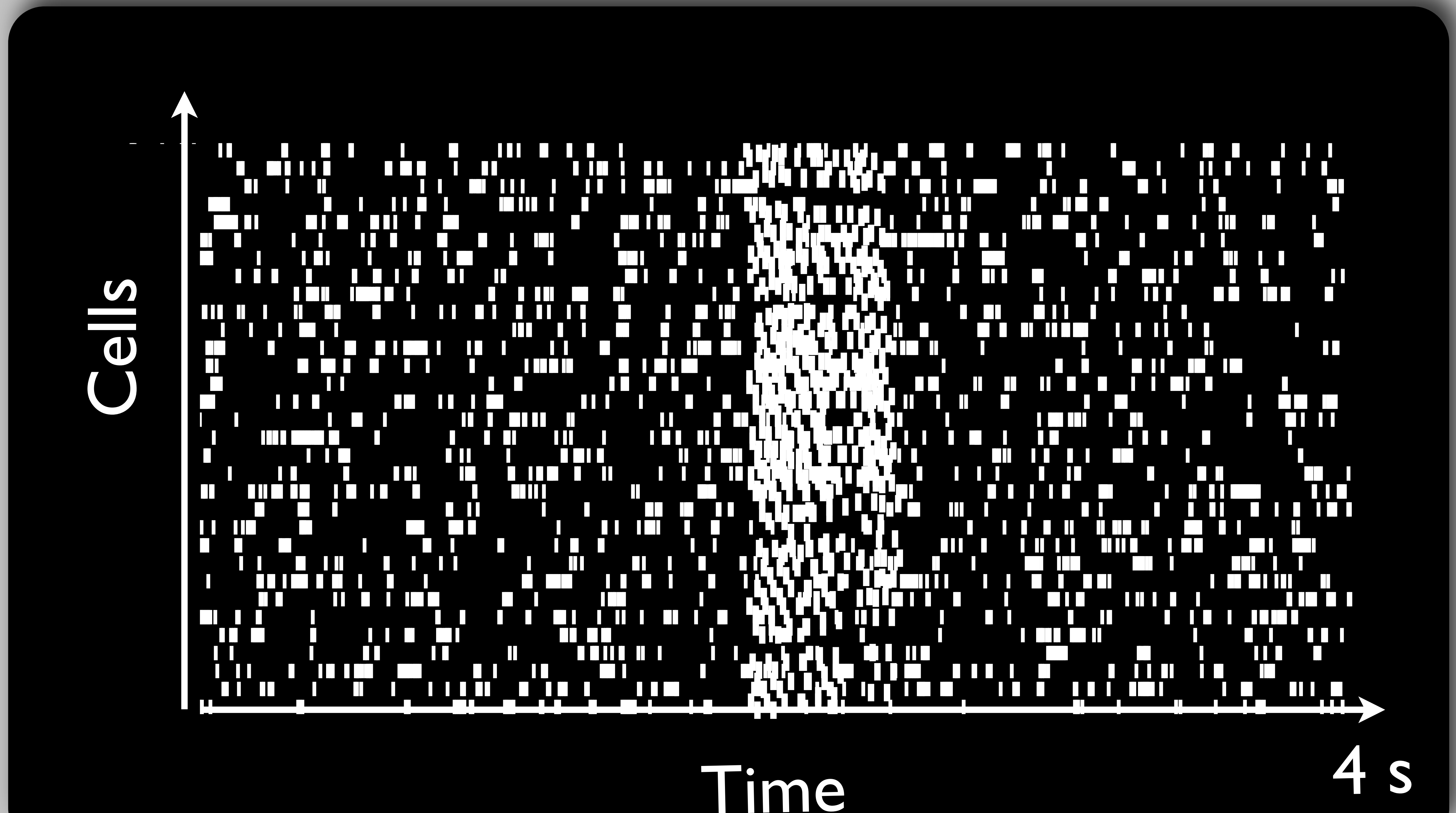
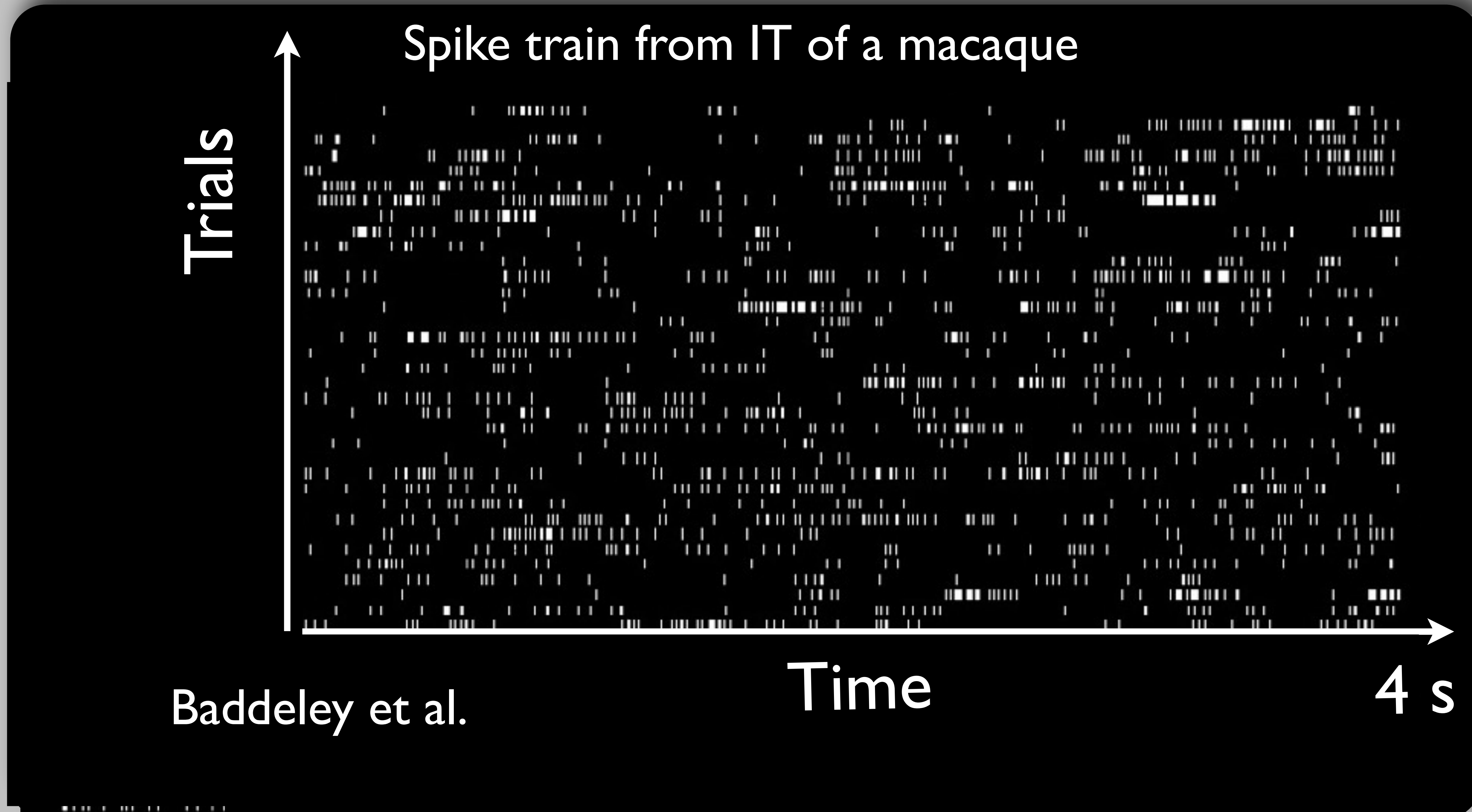
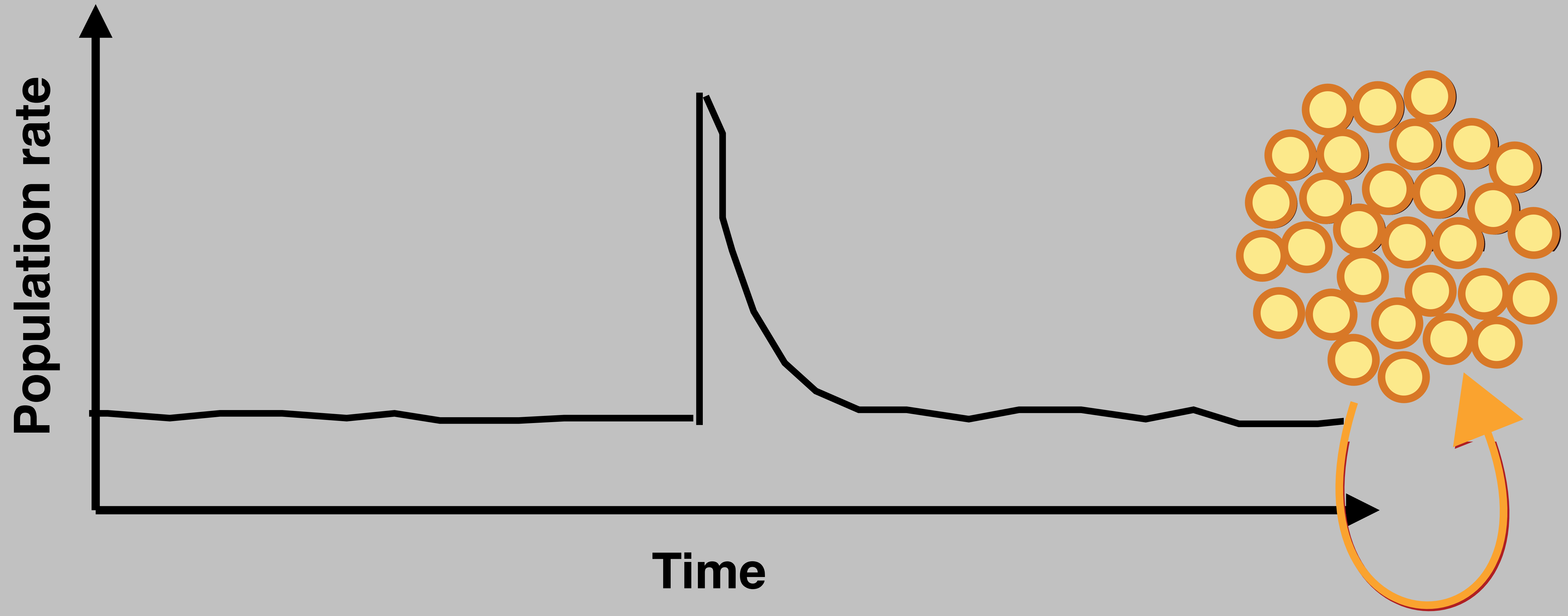


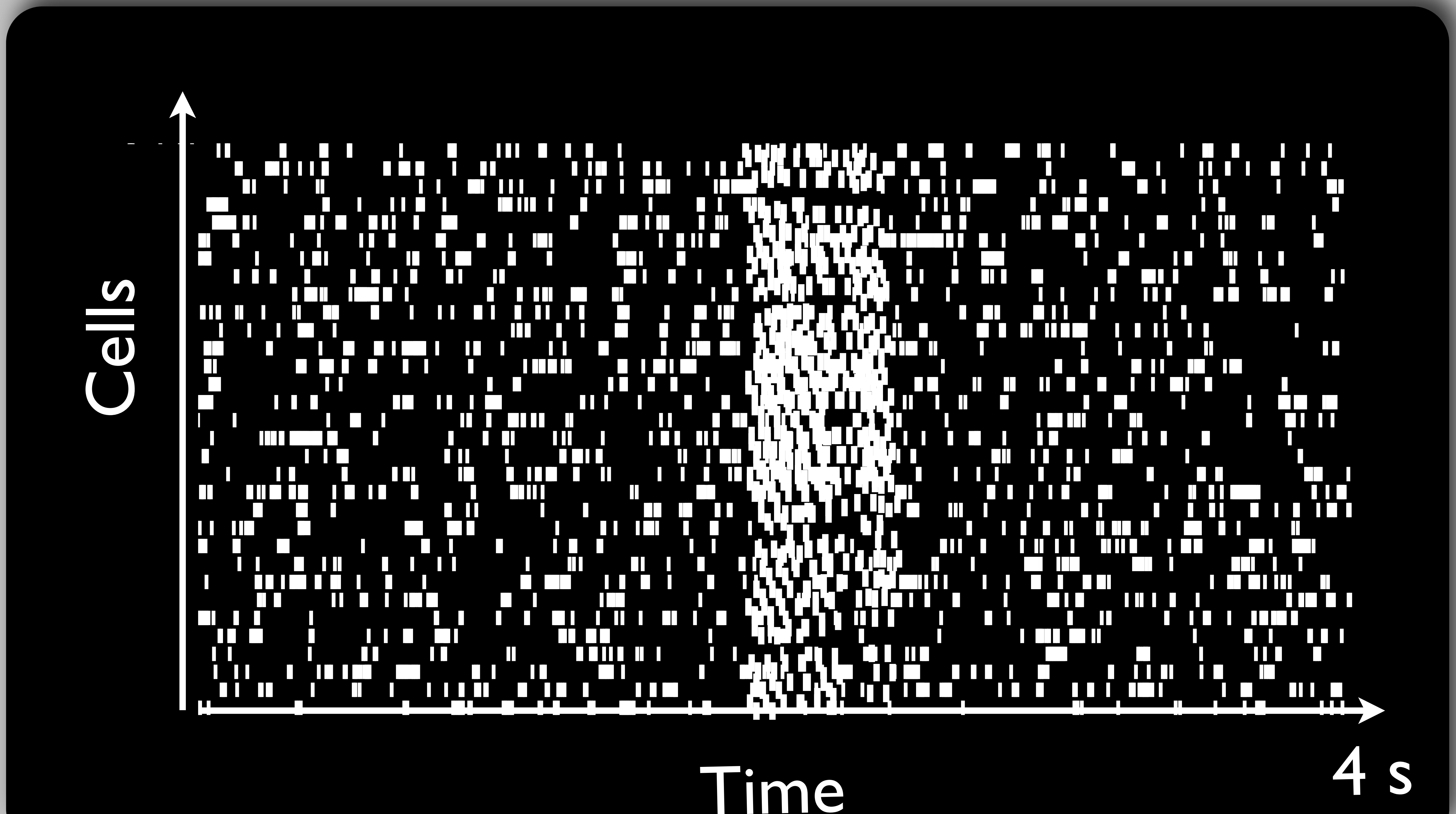
$$\tau \frac{dr}{dt} = (r_0 - r)$$

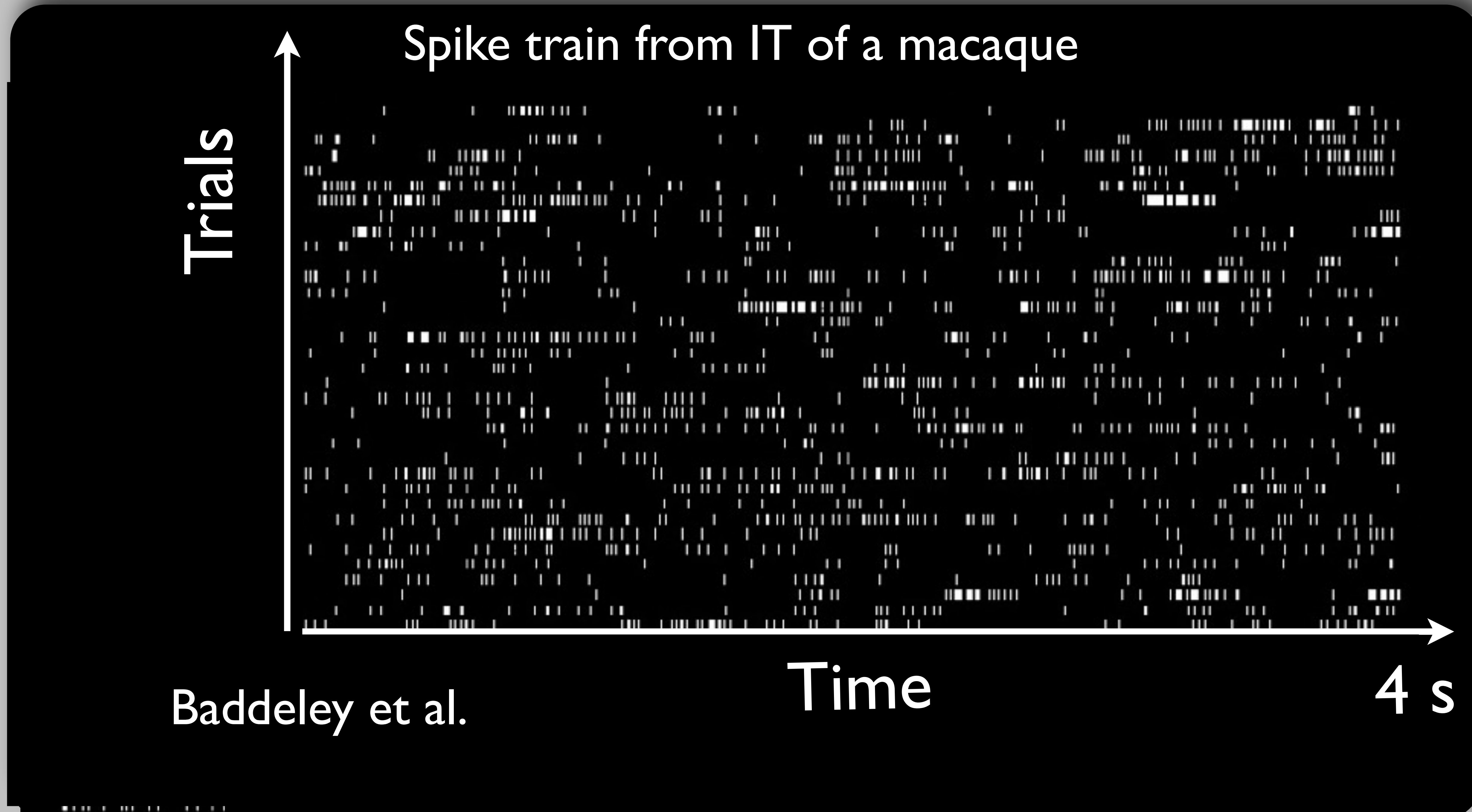


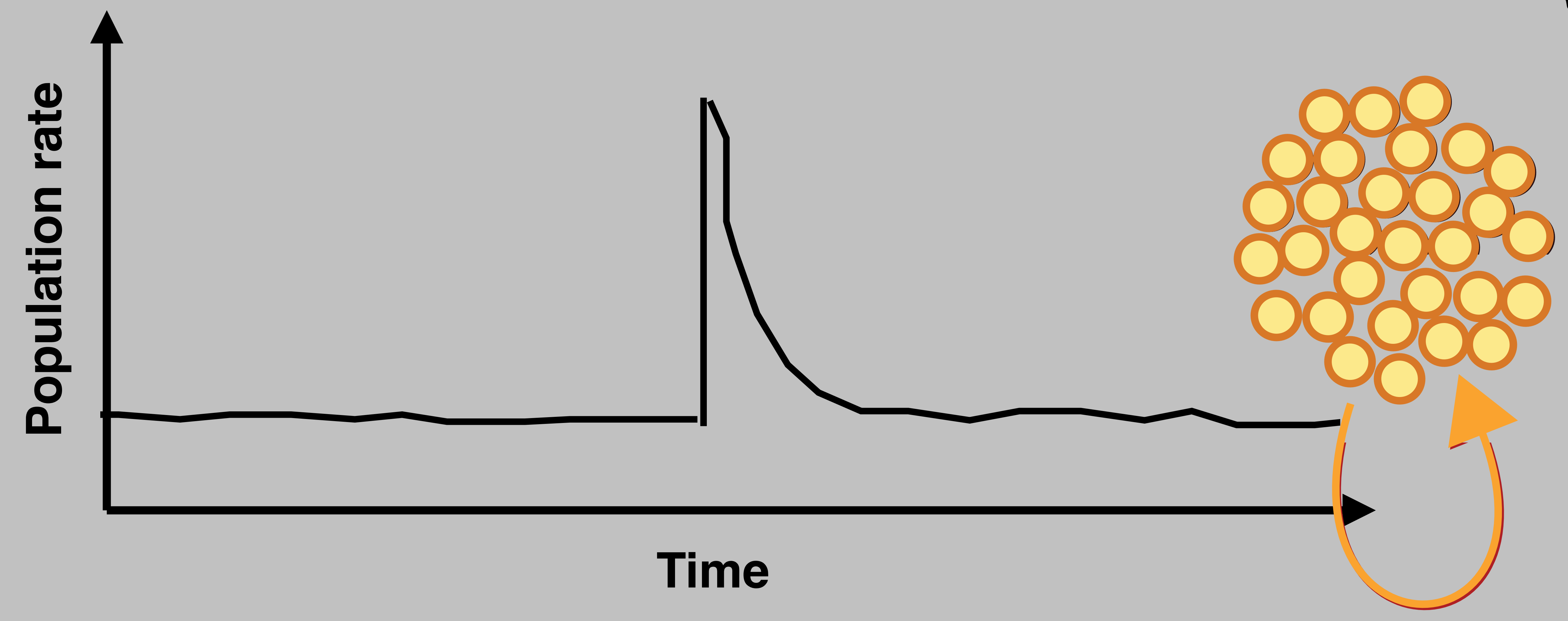




$$\tau \frac{dr}{dt} = (r_0 - r) + f(W r)$$



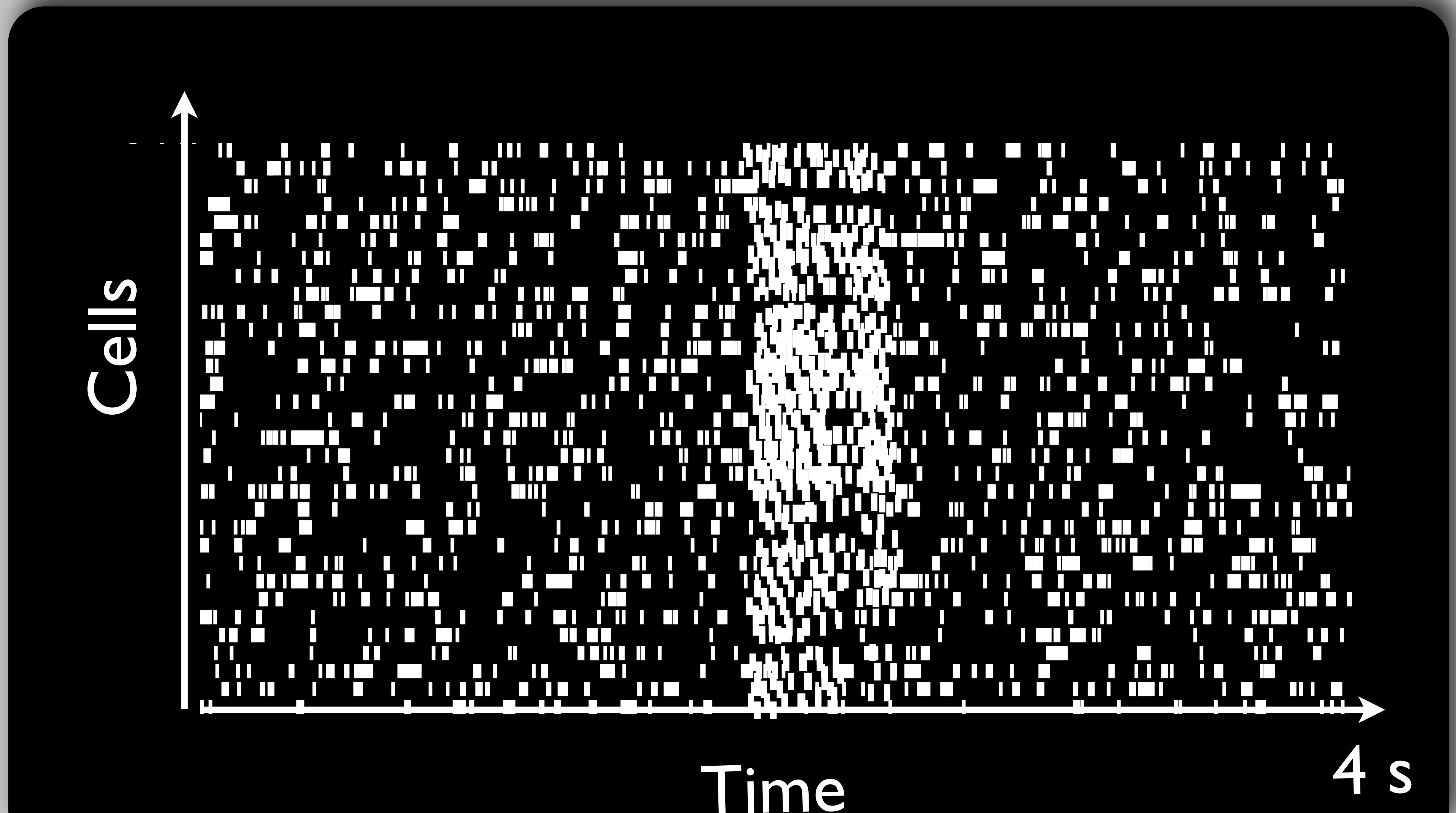


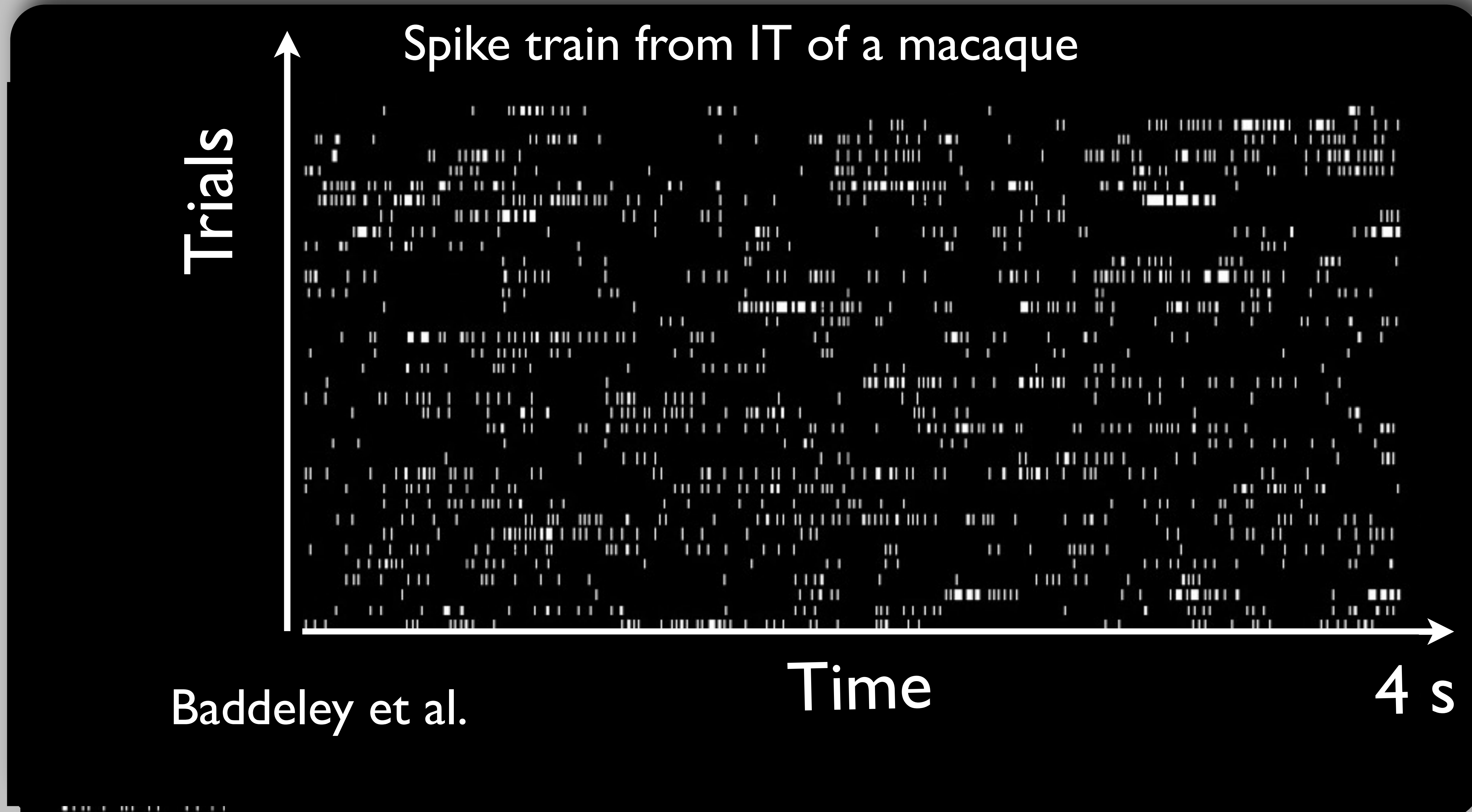


Voilà,...

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

the “rate model”!





Voilà,...

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

the "rate model"!

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