✓1. low firing rates — fall out of the nullcline picture

✓2. broad distribution of firing rates — correct scaling of weights

3. irregular activity

✓4. oscillations — nullclines

✓5. exc. activity leads inhibitory activity — nullclines

✓6. up-down states — nullclines + spike-frequency adaptation

✓7. bumps — nullclines + noise

✓8. state switching

network can transition between all behaviors!

constant ✓
oscillations
up-down
bumps

} different quantitative settings of params

$$\nu_i = \phi\Big(\frac{1}{\sqrt{n}}\sum_{j=1}^{n} \underbrace{W_{ij}}_{\text{iid } p(w)} \nu_j\Big)$$

$$\boxed{\text{main approach: treat } \sum_j W_{ij}\nu_j \text{ as a Gaussian random variable w.r.t. index } i}$$

$$\xi_i = \frac{1}{\sqrt{n}}\sum_j (\bar{w} + \delta W_{ij})\nu_j = \frac{n}{\sqrt{n}}\bar{\nu} + \underbrace{\frac{1}{\sqrt{n}}\sum_j \delta W_{ij}\nu_j}$$

$$\mathrm{Var}\Big(\frac{1}{\sqrt{n}}\sum_j \delta W_{ij}\nu_j\Big) = \frac{1}{n}\sum_i \Big(\frac{1}{\sqrt{n}}\sum_j \delta W_{ij}\nu_j\Big)^2$$

$$= \frac{1}{n}\sum_{jj'} \nu_j \nu_{j'} \underbrace{\frac{1}{n}\sum_i \delta W_{ij}\delta W_{ij'}}_{\simeq\, \delta_{jj'}\sigma_w^2}$$

$$E[\xi_i] = \sqrt{n}\,\bar{\nu}\bar{w}$$

$$\mathrm{Var}[\xi_i] = \sigma_w^2 \langle \nu^2\rangle$$

$$= \sigma_w^2 \frac{1}{n}\sum_j \nu_j^2 = \sigma_w^2\langle \nu^2\rangle$$

$$\nu_i = \phi\big(\sqrt{n}\,\bar{w}\bar{\nu} + \sigma_w\sqrt{\langle\nu^2\rangle}\, \underbrace{z_i}_{N(0,1)}\big)$$

$$\nu_i = \phi\left(\sqrt{n}\,\bar{w}\,\bar{\nu} + \boxed{\sigma_w \sqrt{\langle \nu^2 \rangle}}\, z_i\right)$$

$$\langle \nu^\ell \rangle = \frac{1}{n} \sum_i \phi^\ell(\dots) \longrightarrow \int dz\, \frac{e^{-z^2/2}}{\sqrt{2\pi}}\, \phi^\ell\left(\sqrt{n}\,\bar{w} + \sigma_w \sqrt{\langle \nu^2 \rangle}\, z\right)$$

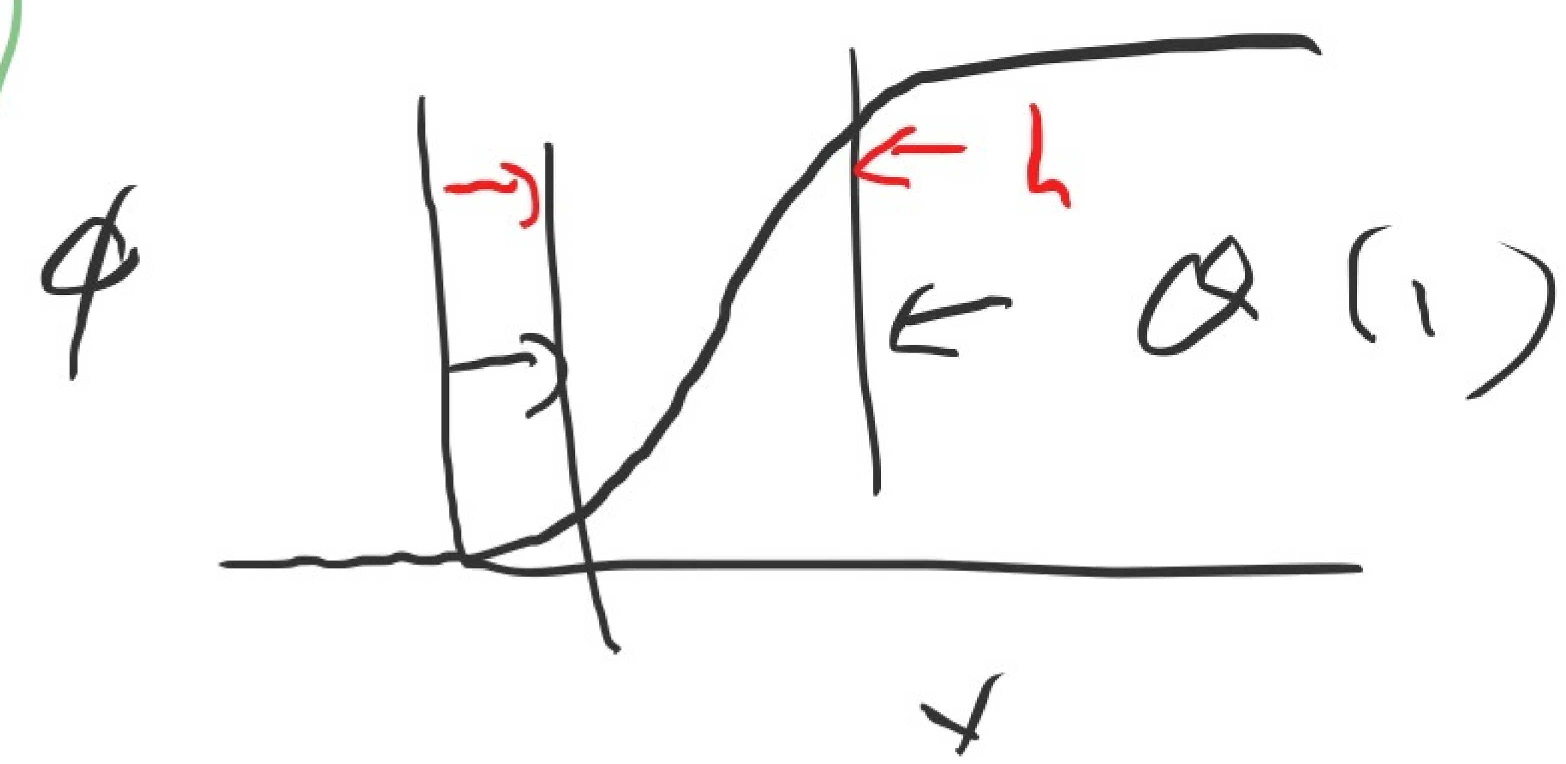
$$p(z) \longrightarrow p(\nu)$$

$$p(\nu) = \int dz\, \frac{e^{-z^2/2}}{\sqrt{2\pi}}\, \delta\left(\nu - \phi\left(\sqrt{n}\,\bar{w}\,\bar{\nu} + \sigma_w \sqrt{\langle \nu^2 \rangle}\, z\right)\right)$$

$w \sim \frac{1}{\sqrt{n}}$

$\Uparrow$

what's the range of firing rates?



$$\Rightarrow \sigma_w \sqrt{\langle \nu^2 \rangle} \sim O(1)$$

very small compared to h : actual weight $\sim \frac{1}{n}$, $\bar{w} \sim \frac{1}{\sqrt{n}}$

$\nu = 0$ or ν_{max} $\longleftarrow$ very large compared to h $\Big\{$ actual weight $\sim O(1)$, $\bar{w} \sim \sqrt{n}$

$$\tau_E \frac{d\nu_E}{dt} = \phi_E\left(\sqrt{n}\,(W_{EE}\nu_E - W_{EI}\nu_I + h_E), \langle \nu_E^2\rangle, \langle \nu_I^2\rangle\right) - \nu_E$$

$$\tau_I \frac{d\nu_I}{dt} = \phi_I\left(\sqrt{n}\,(W_{IE}\nu_E - W_{II}\nu_I + h_I), \langle \nu_E^2\rangle, \langle \nu_I^2\rangle\right) - \nu_I$$

n should be k = average number of connections per neuron

$$\left\langle \frac{1}{\sqrt{k}} \sum_{j=1}^{n} W_{ij}\nu_j \right\rangle$$

$$= \sqrt{k}\,\bar{W}\,\bar{\nu}$$

average of nonzero weights only

approximation:

$\langle \nu^2 \rangle$ just smooth out the gain functions

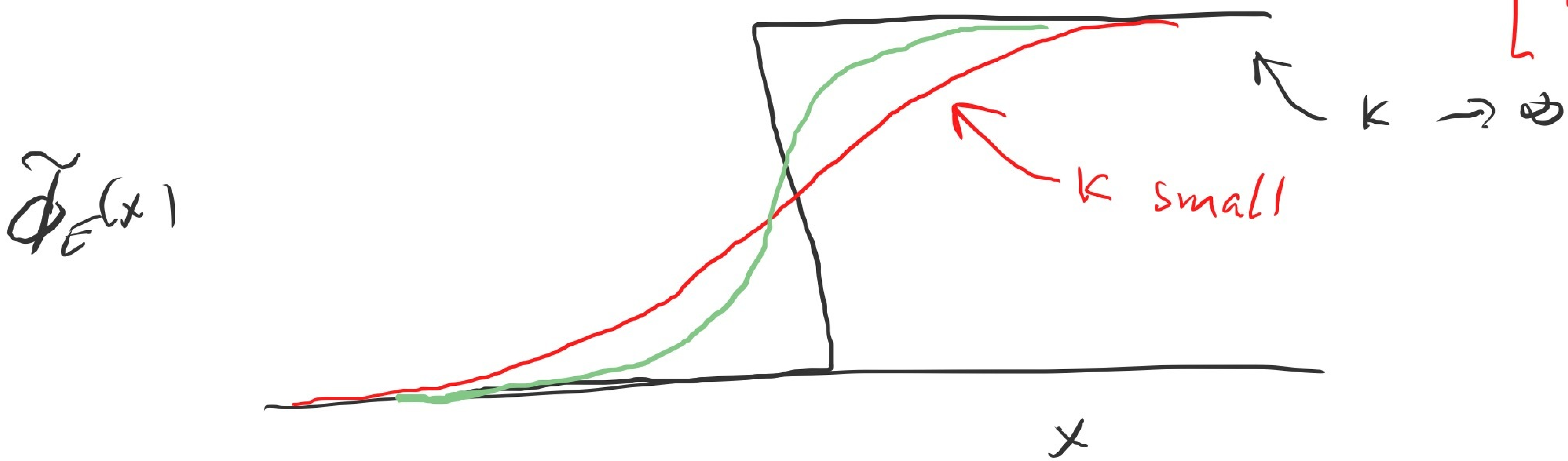
- ignore them

$$\tau_E \frac{dV_E}{dt} = \tilde{\Phi}_E \left(W_{EE} V_E - W_{EI} V_I + h_E \right) - V_E$$

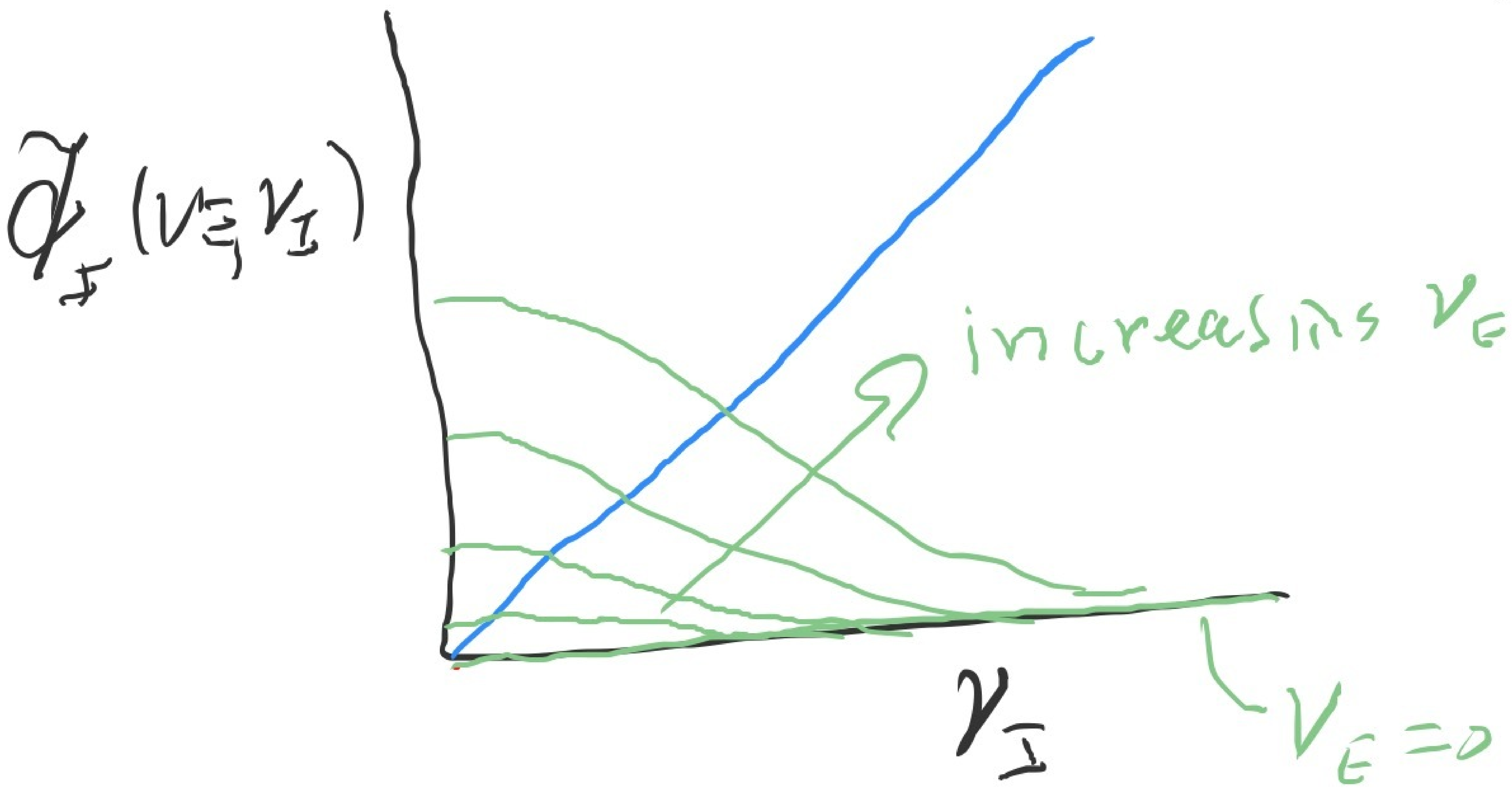
$$\tau_I \frac{dV_I}{dt} = \tilde{\Phi}_I \left(W_{IE} V_E - W_{II} V_I + h_I \right) - V_I$$

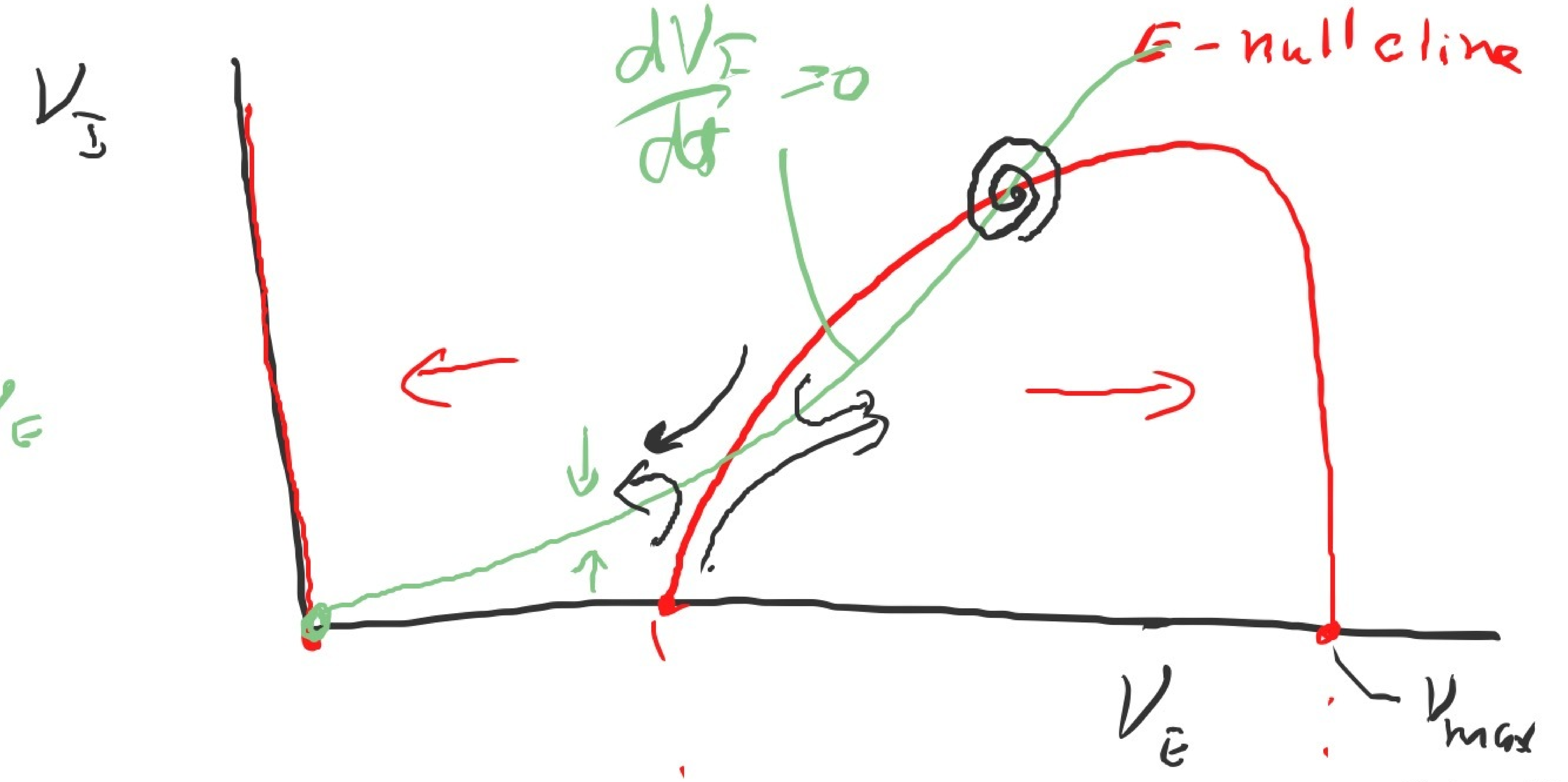
2-4 distinct inhibitory cell types

- shape of $\tilde{\Phi}_E$ & $\tilde{\Phi}_I$ depend on k



nullclines!!





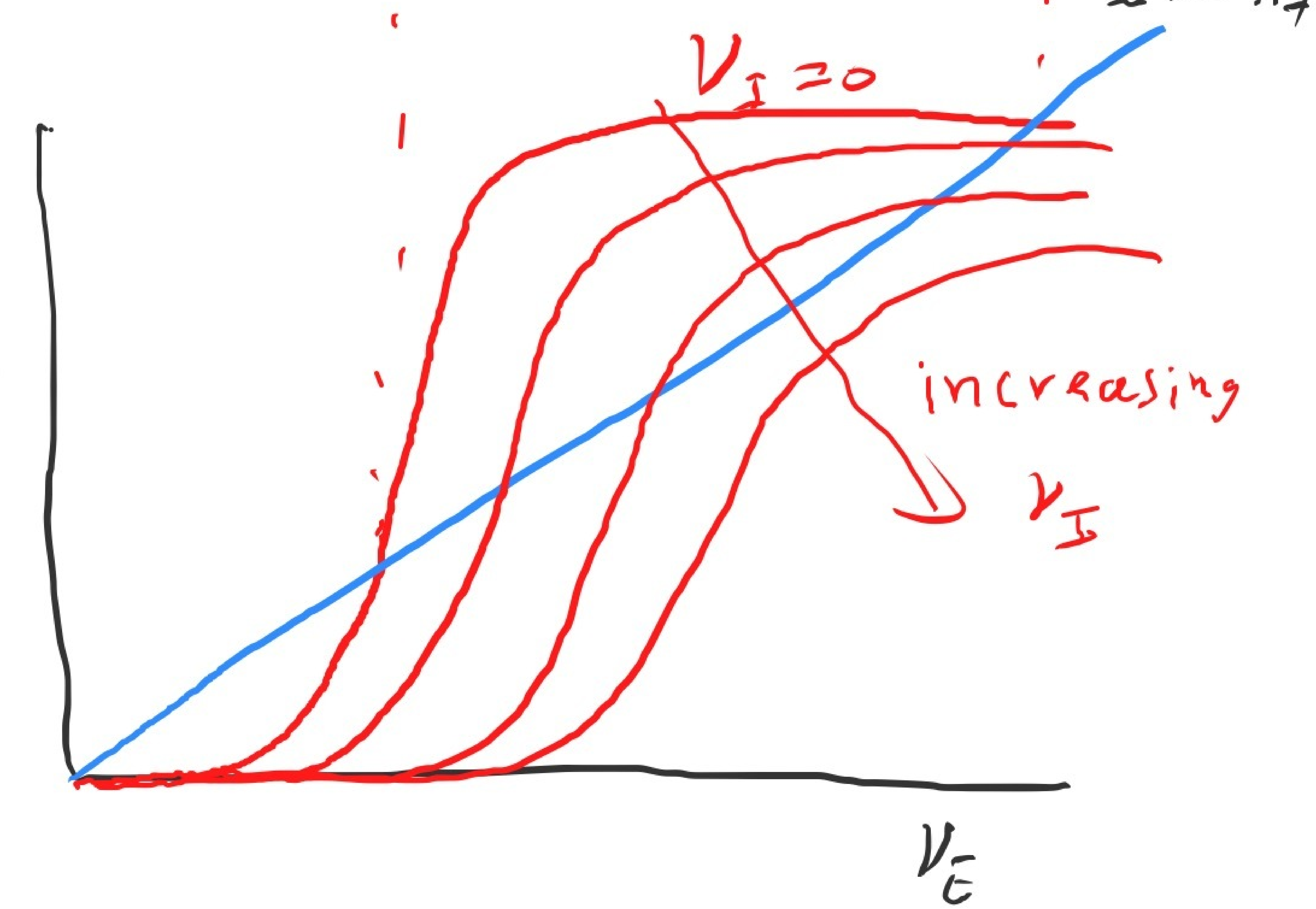
classic view:
neurons don't fire without input

wrong

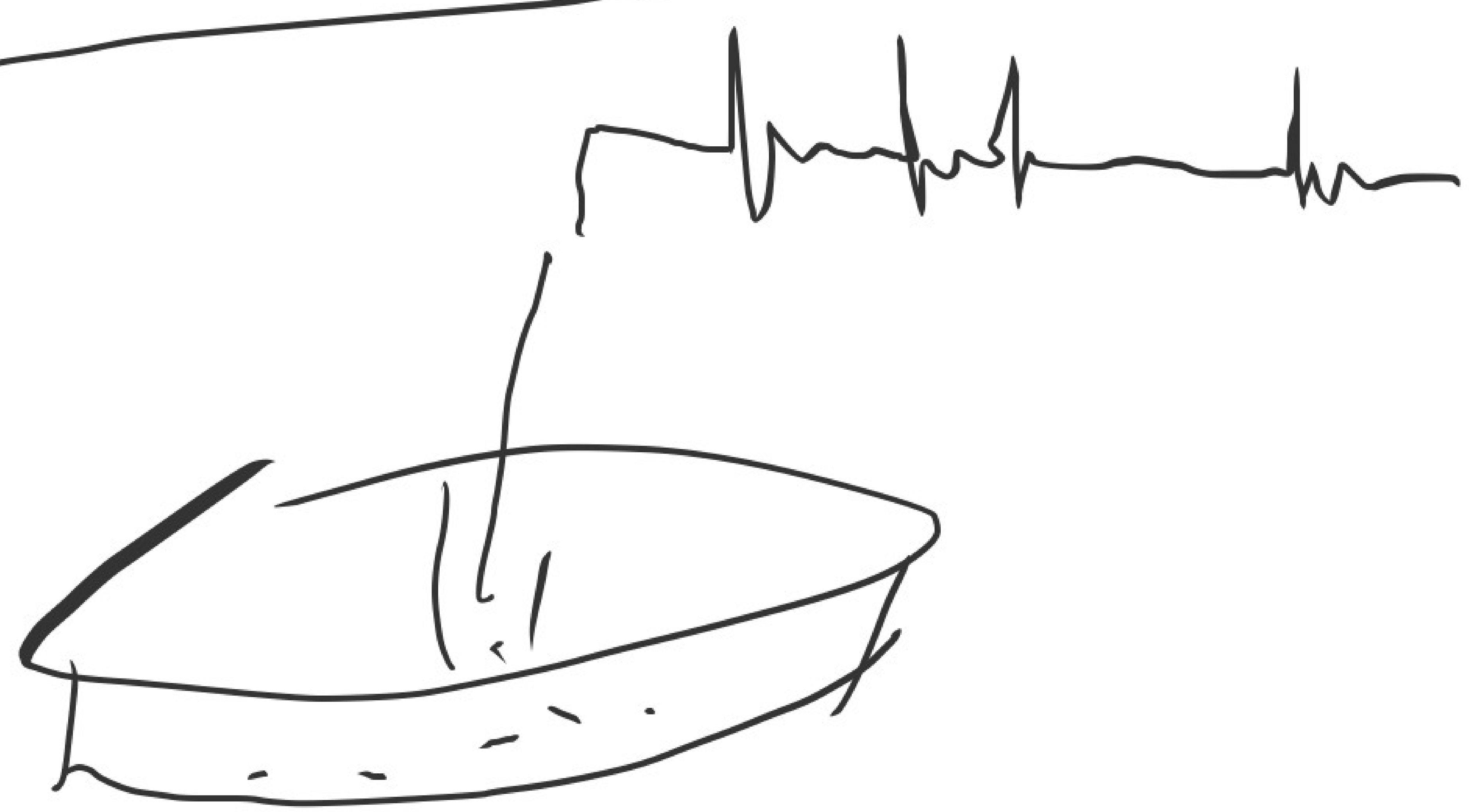
w/o input, neurons fire

$\tilde{\phi}_E(\nu_E, \nu_I)$

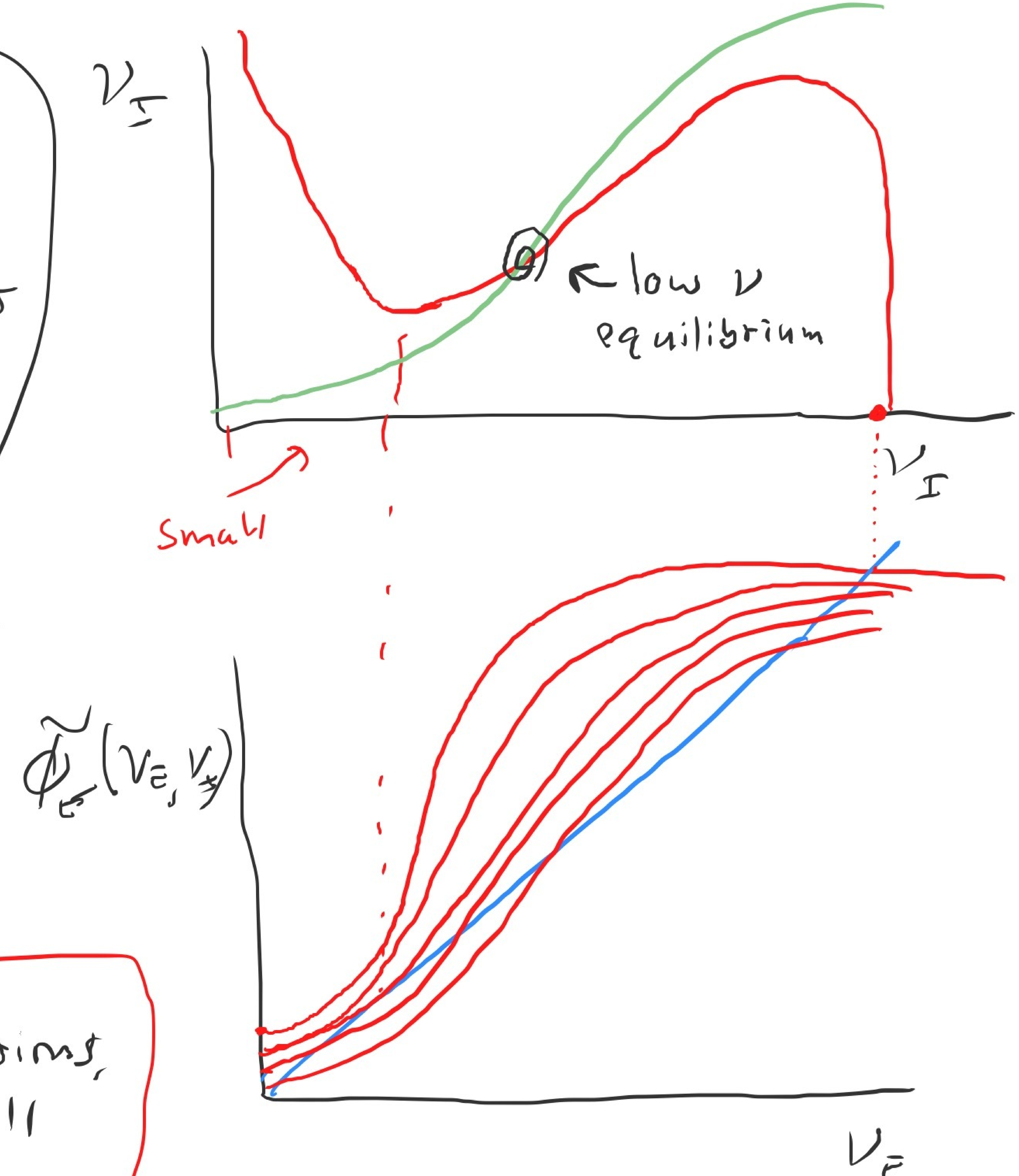
$\nu_E = \tilde{\phi}_E(\nu_E, \nu_I)$

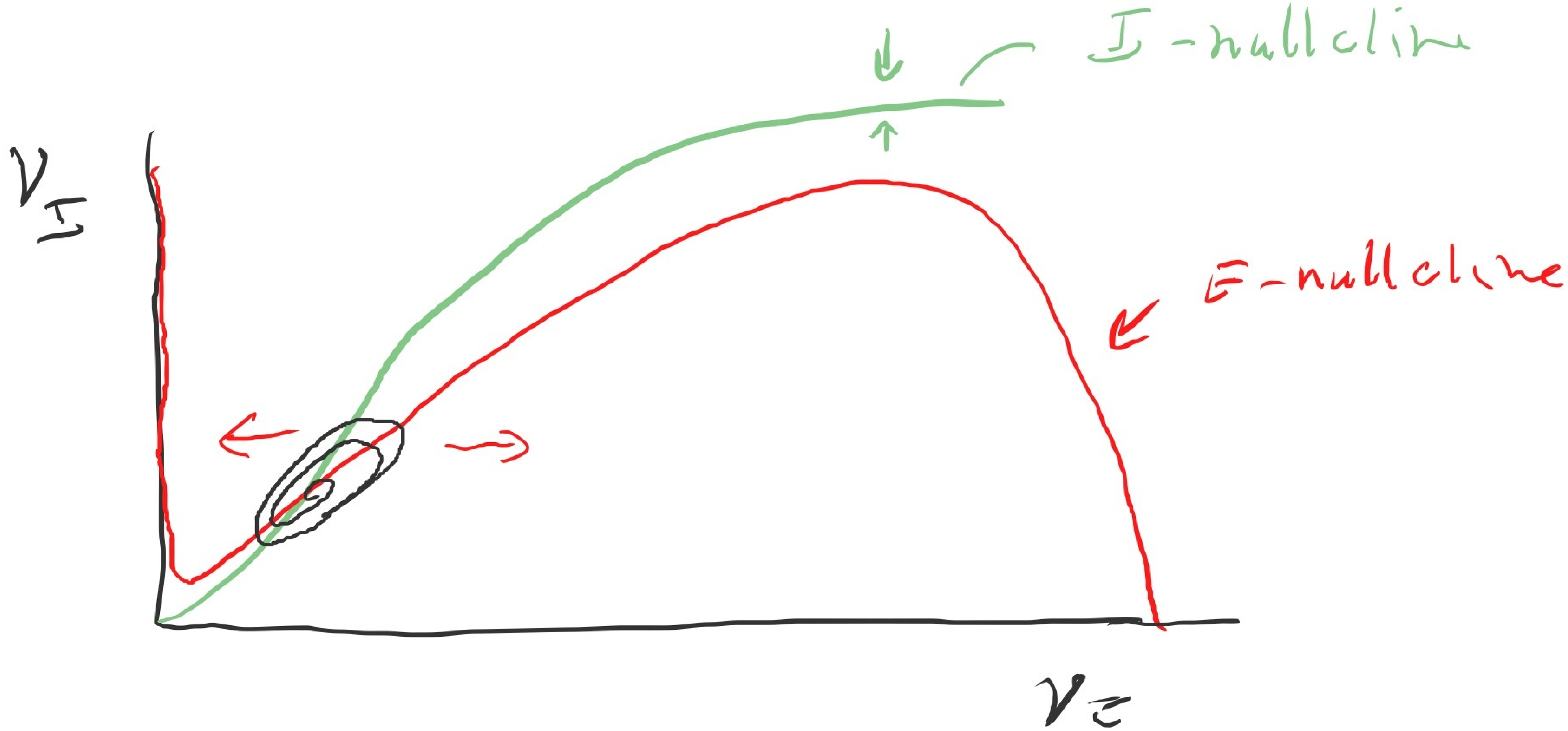


to get low firing rates, some $\begin{cases}\text{neurons} \\ \text{exc.}\end{cases}$ have to fire without input



$\Rightarrow$ block all connections, some neurons will be active

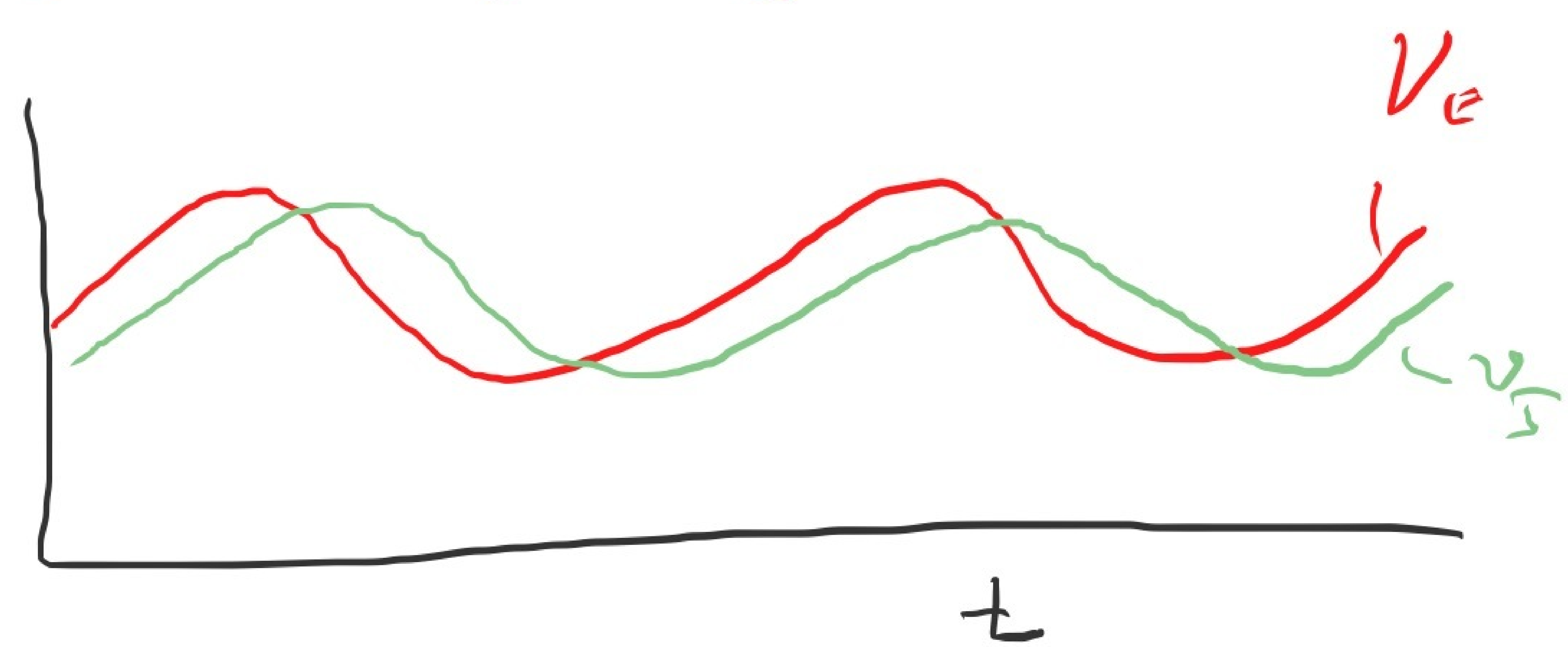




$$\tau \frac{d}{dt} \nu_E = \tilde{\phi}_E \left(w_{EE} \nu_E - w_{EI} \nu_I + h_E \right) - \nu_E$$

$$\tau \frac{d}{dt} \nu_I = \tilde{\phi}_I \left(w_{IE} \nu_E - w_{II} \nu_I + h_I \right) - \nu_I$$

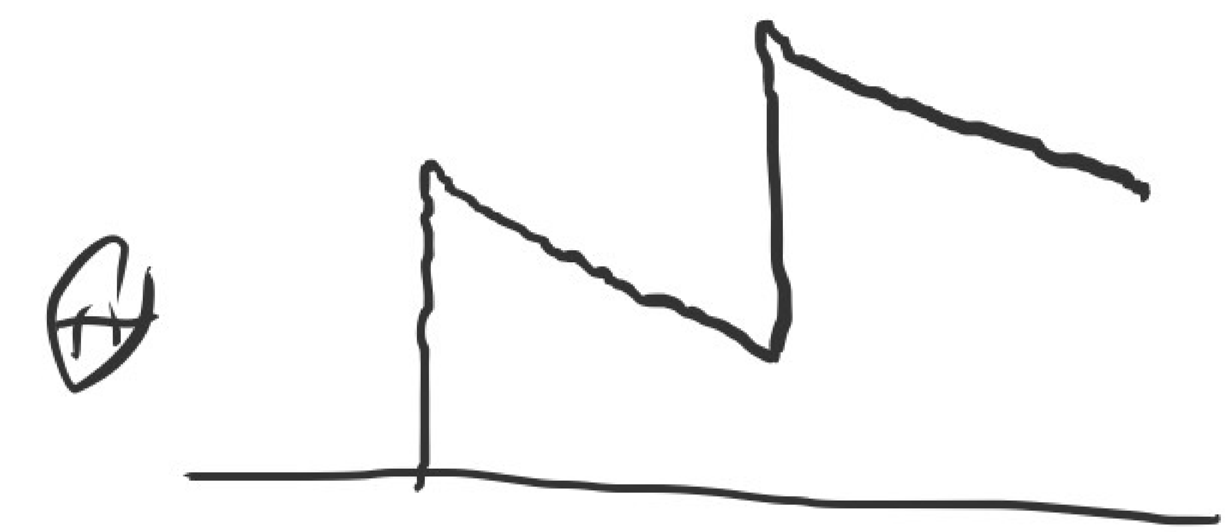
- this picture supports oscillations



neurons exhibit spike-frequency adaptation

every time a neuron spikes, threshold for spiking goes up. Ca^{++}-activated K-channel

$$\dot{\Theta} = -\frac{\Theta}{\tau} + g\sum_i \delta(t - t_i)$$

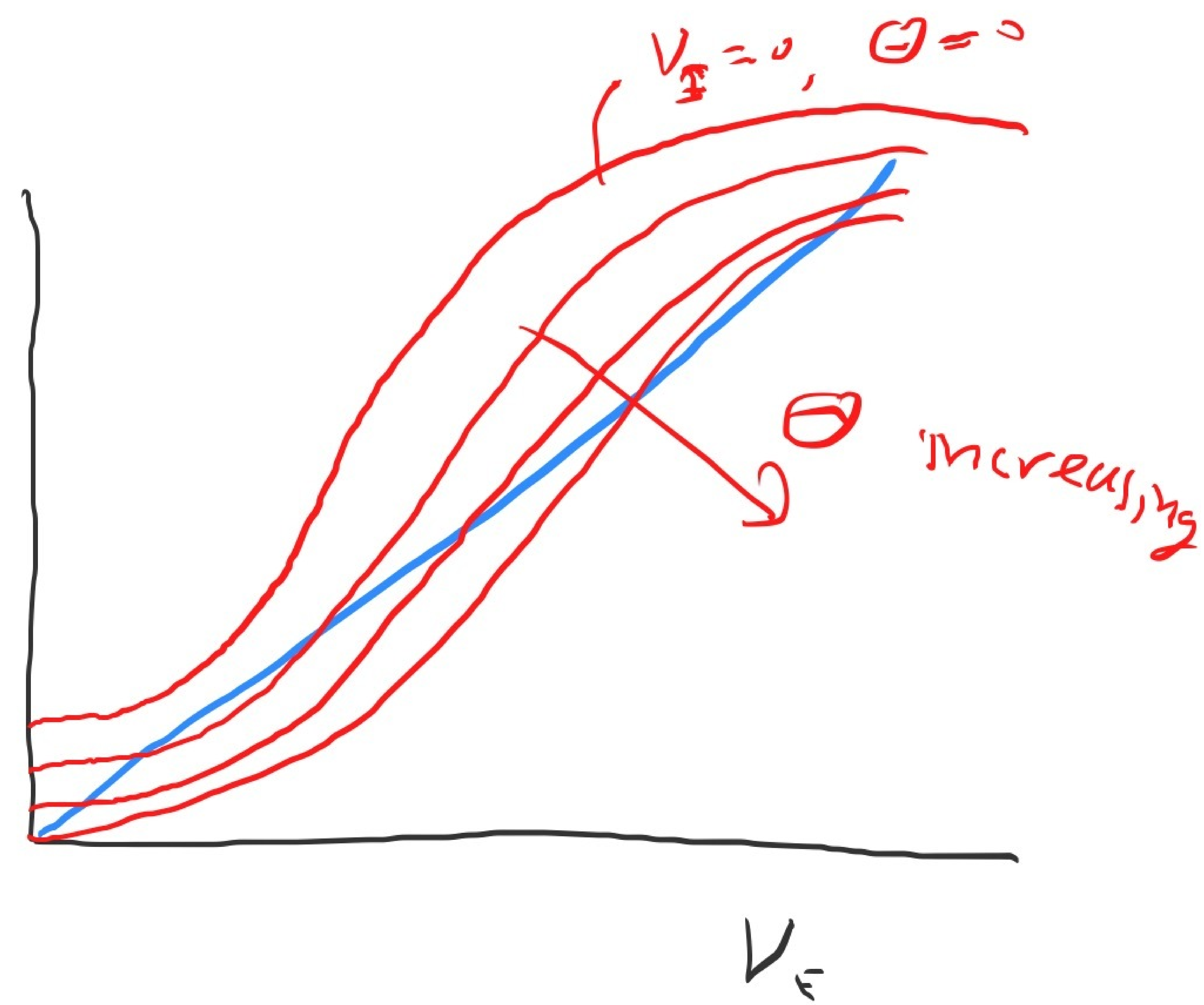


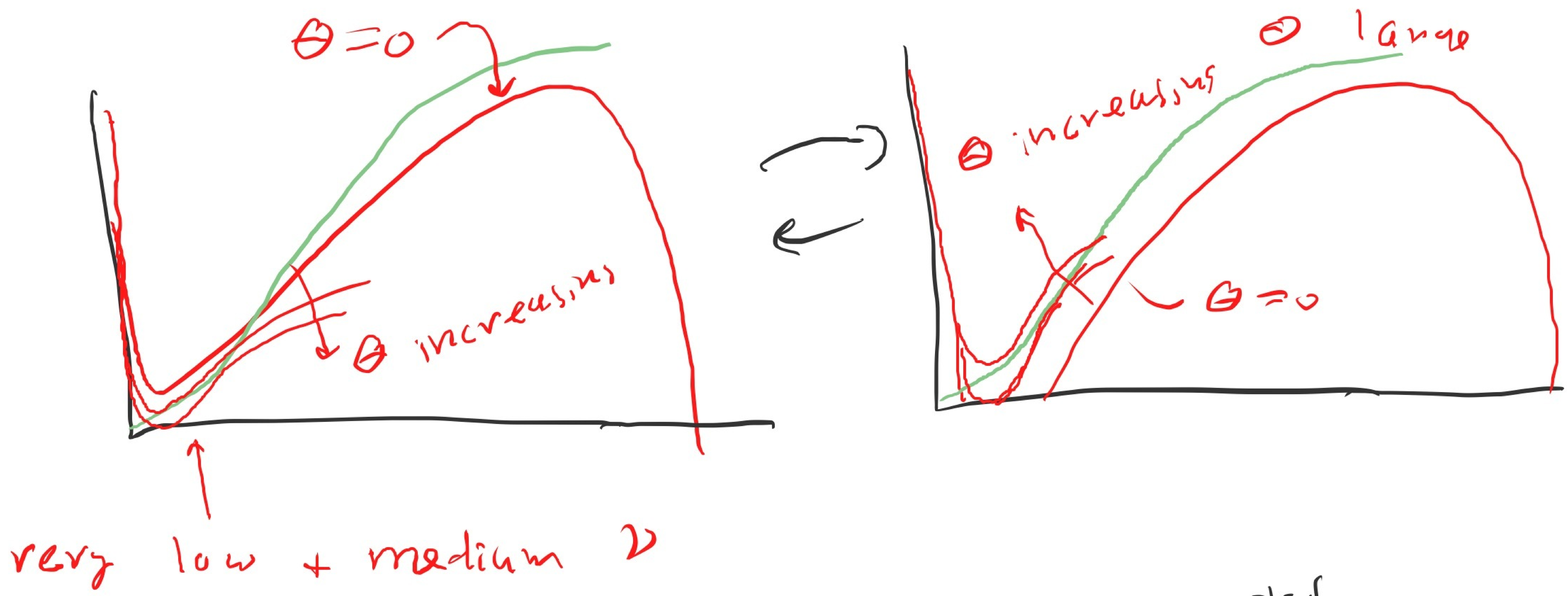
300 ms

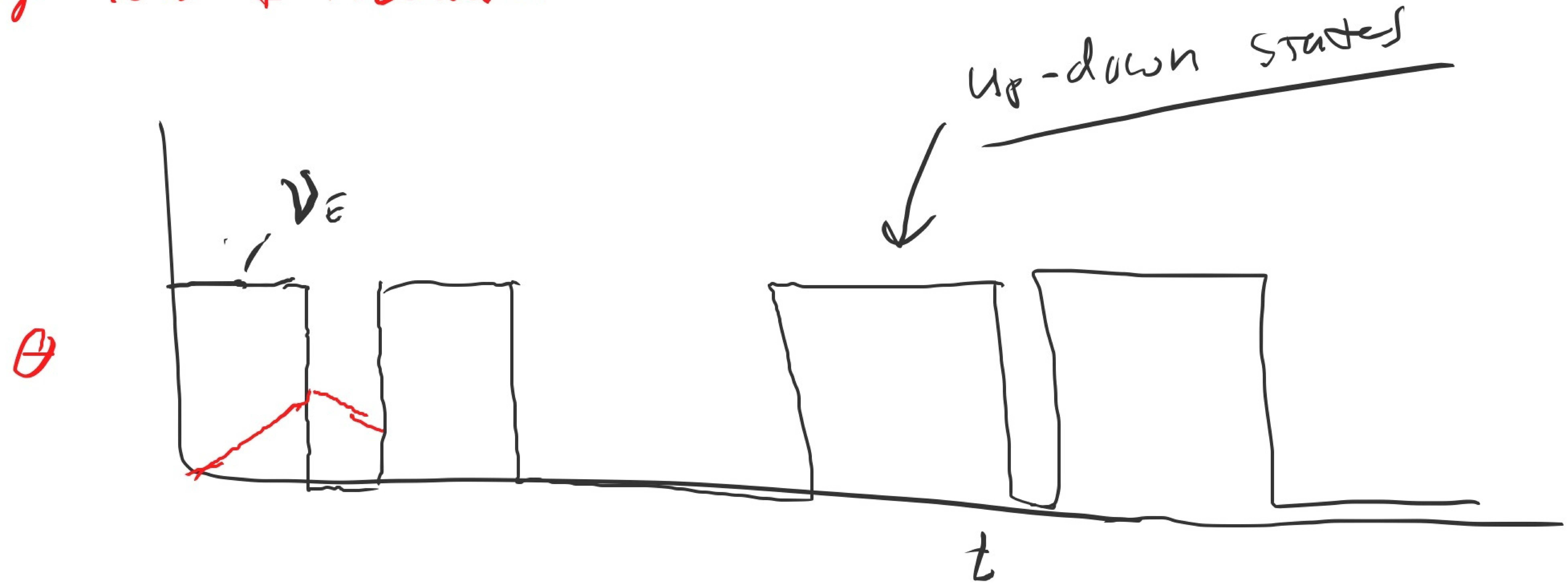
threshold for a spike

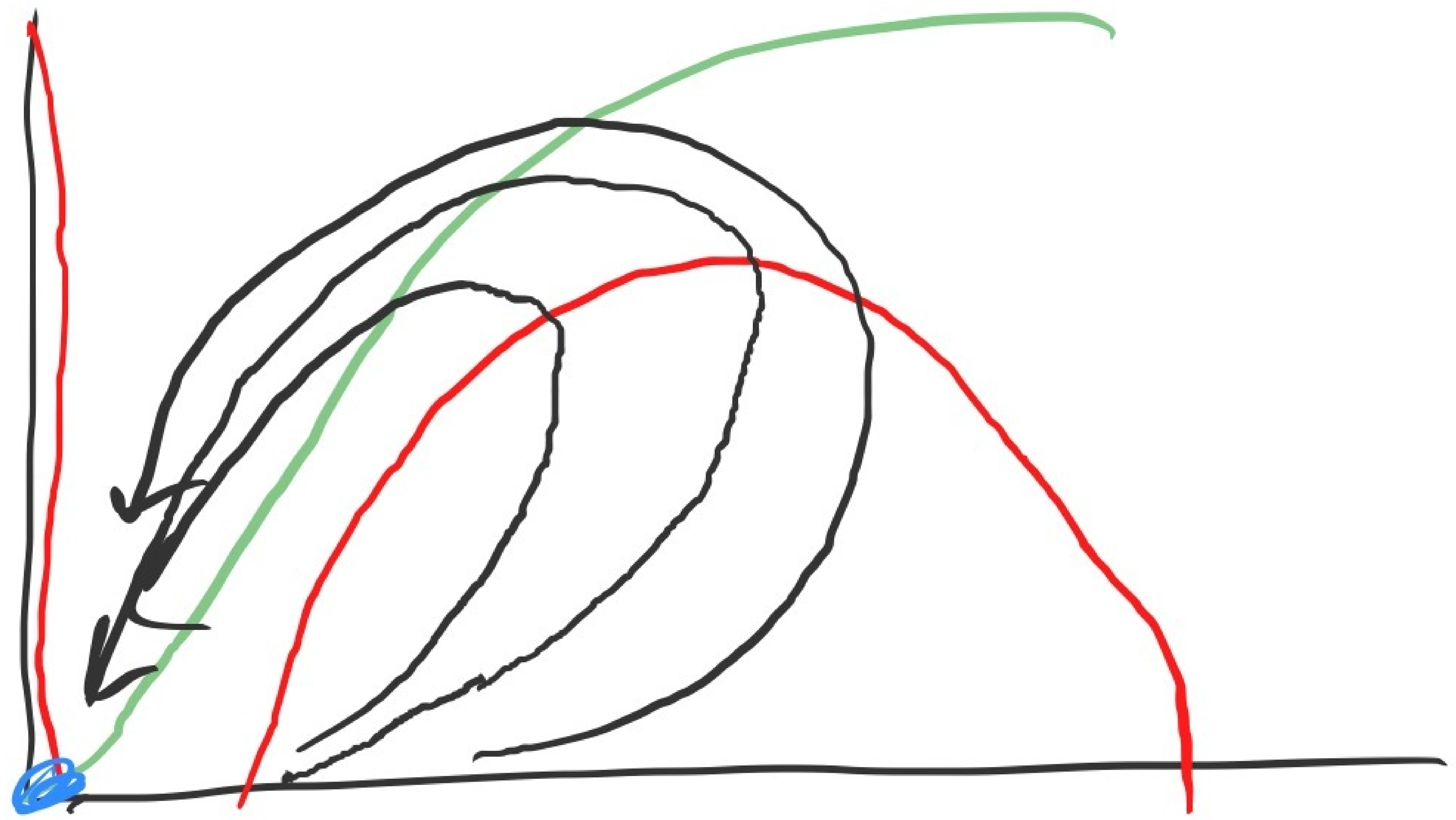
$\tilde{\Phi}_E(v_E, v_I)$

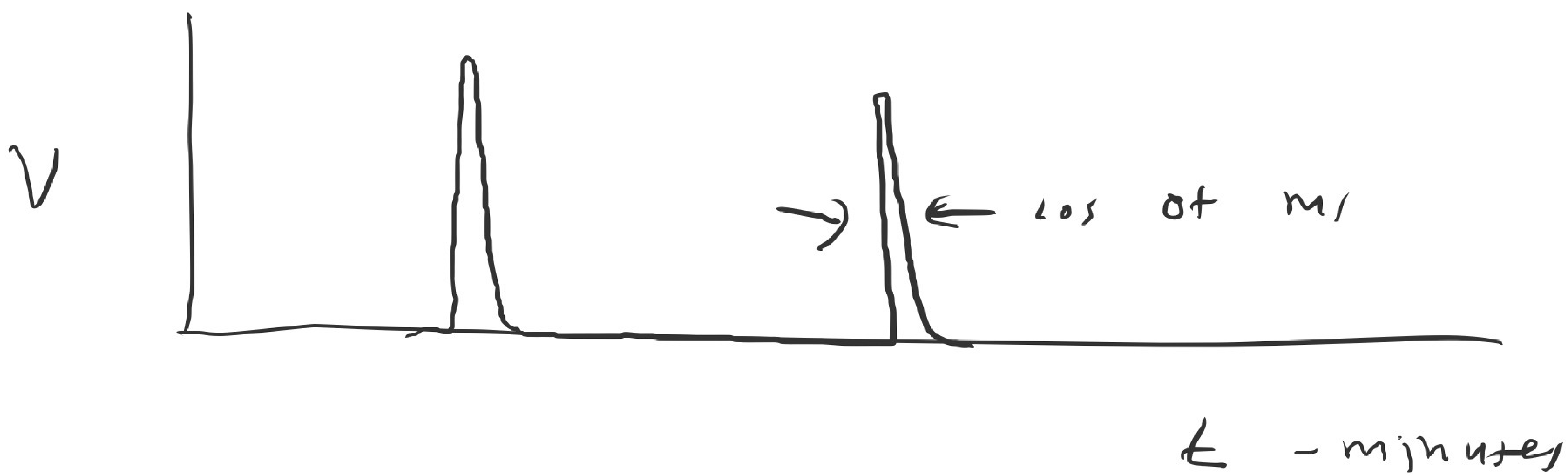
$$\tilde{\Phi}_E\left(w_{EE}v_E - w_{EI}v_I + h_E - \Theta\right)$$




θ = 0
θ increasing
θ large
θ increasing
θ = 0
very low + medium ν


up-down states
ν_E
θ
t




V
10s of ms
t - minutes

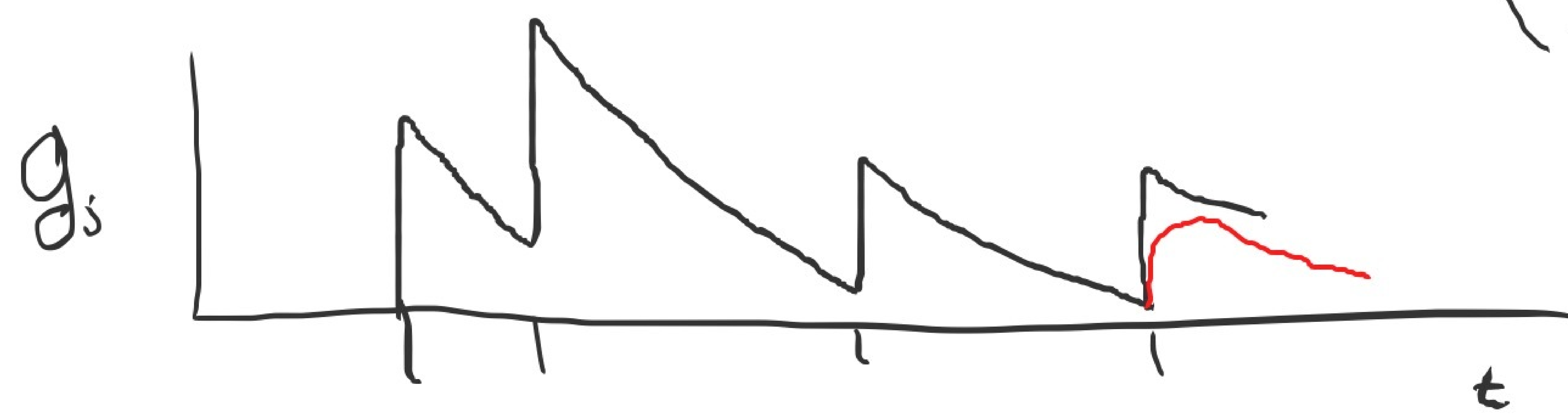
$$V_i = \phi\left(\sum_j W_{ij} V_j\right)$$

Temporal statistics determine firing pattern of neurons

$$\frac{dV_i}{dt} = (\text{single neuron dynamics}) - \boxed{\sum_j A_{ij} (V_i - \Sigma_j)\, g_j(t)}$$

voltage

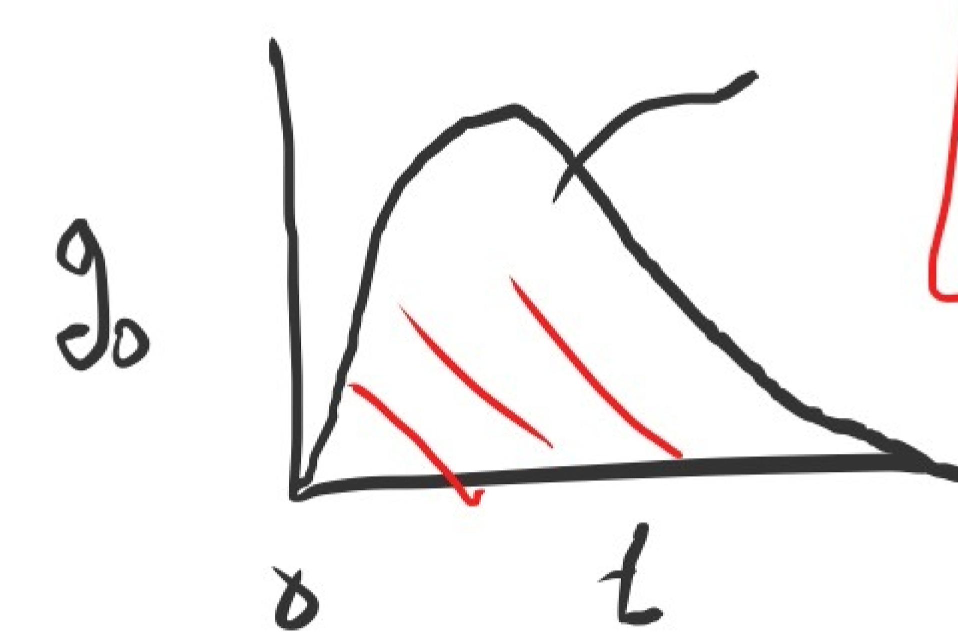
weight



spike times on neuron j

$$g_j(t) = \sum_k g_0(t - t_j^k)$$

time of k^{th} spike on neuron j



$$\boxed{\int_0^\infty dt \; g_0(t) = 1}$$

$$g_0(t<0) = 0$$

$$h_i = -\sum_j \underbrace{A_{ij}(V_i - E_j)}_{\substack{\text{constant} \\ -\tilde{A}_{ij}}} g_j(t)$$

$$\bar{g}_j = \lim_{T\to\infty} \frac{1}{T}\int_0^T \sum_k g_0(t - t_j^k) = \lim_{T\to\infty} \frac{1}{T} \cdot N_j(T) = \nu_j$$

$$h_i(t) = \sum_j \tilde{A}_{ij}\left[\bar{g}_j + g_j(t) - \bar{g}_j\right]$$

$$= \underline{\underline{\sum_j \tilde{A}_{ij} \nu_j}} + \sum_j \tilde{A}_{ij}\, \delta g_j(t)$$

↑ past lectures

$$\mathrm{cov}\left(\sum_j \tilde{A}_{ij}\, \delta g_j(t)\right) = \frac{1}{n}\sum_i \sum_j \tilde{A}_{ij} \left\langle \delta g_j(t) \sum_{j'} \tilde{A}_{ij'}\, \delta g_{j'}(t')\right\rangle$$

$$\equiv C(t - t') = \sum_j \left\langle \delta g_j(t)\, \delta g_{j'}(t')\right\rangle \frac{1}{n}\sum_i \tilde{A}_{ij} \tilde{A}_{ij'}$$

assume $\propto \delta_{jj'}$ (uncorrelated)

$$C(t-t') \cong \sum_j \langle \delta g_j(t)\, \delta g_j(t') \rangle_{\text{time}} \; \tilde{A}_{ij}^2$$

independent

$$\cong n \langle \tilde{A}_{ij}^2 \rangle \; \underbrace{\frac{1}{n} \sum_j \langle \delta g_j(t)\, \delta g_j(t') \rangle}_{C_g(t-t')}$$

ind. of j

$$\mathrm{cov}[h_i(t)\, h_{i'}(t')]$$

uncorrelated assumption

$$\rightarrow \quad n \langle \tilde{A}^2 \rangle \, C_g(t-t') \, \delta_{ii'} \qquad \text{(homework)}$$

$$\tau \frac{dV_i}{dt} = (\text{single neuron}) - n\langle A^2\rangle z(t)$$

independent of n

$$\langle z(t)\, z(t')\rangle = C_g(t-t')$$

$A \sim \frac{1}{\sqrt{n}}$

static case: only $\langle v\rangle$, $\langle v^2\rangle$ were important

dynamic case: need to solve self-consistently for $C_g(t-t')$

to get irregular activity, need $w \sim \frac{1}{\sqrt{n}}$

→ spread in firing rates

$$\tau \frac{dv_e}{dt} = \phi_e\left(\sqrt{k_i}\left(W_{ee}v_e - W_{ei}v_i + h_e\right), \langle s_i^2\rangle, \langle s_j^2\rangle\right) - v_e$$

small

how big is k_i effectively

const.

is scaled by the average

$$\tau \frac{dv_i}{dt} = (\quad) - \sum_j A_{ij}(v_i - \varepsilon_j)\, g_j(t)$$

reversal potential

single spike produces a voltage change of about 0.5 mV

$$g_j(t) \to \delta(t - t_{spike})$$

$$\Delta v_{PSP} = -\frac{1}{\tau} A_{ij}(v_i - \varepsilon_j)$$

$$\Rightarrow A_{ij}(v_i - \varepsilon_j) = -\tau \Delta v_{PSP_{ij}}$$

$$\tau \frac{dv_i}{dt} = (\ ) + \sum_j V_{PSP_{ij}} \tau g_j(t)$$

$$\langle g\rangle \cdot k_i$$

$$\left\langle \sum_j V_{PSP_{ij}} \tau g\right\rangle = \boxed{k \bar{V}_{PSP} \tau \bar{\nu}}$$

average drive

$$= \bar{h}_i = K \, \overline{v_{PSP}} \, \tau \, \bar{\nu}$$

K: 1000, v_{PSP}: 0.5 mV, τ: 10 ms, $\bar{\nu}$ (Hz)

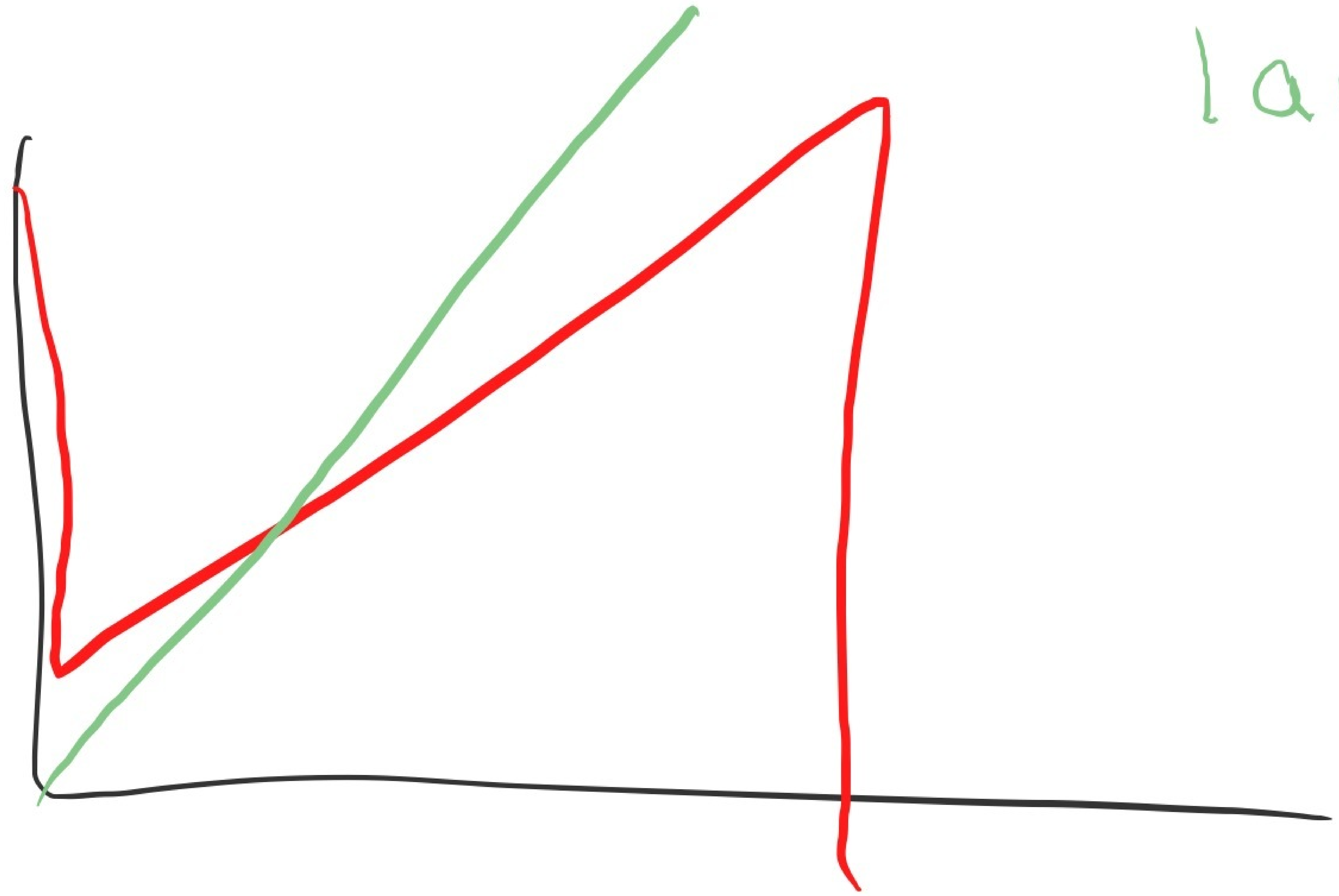
$$\tau \bar{\nu} = \frac{\bar{\nu}\,(\text{Hz})}{100}$$

$$= 5 \, \bar{\nu}\,(\text{Hz}) \text{ mV}$$

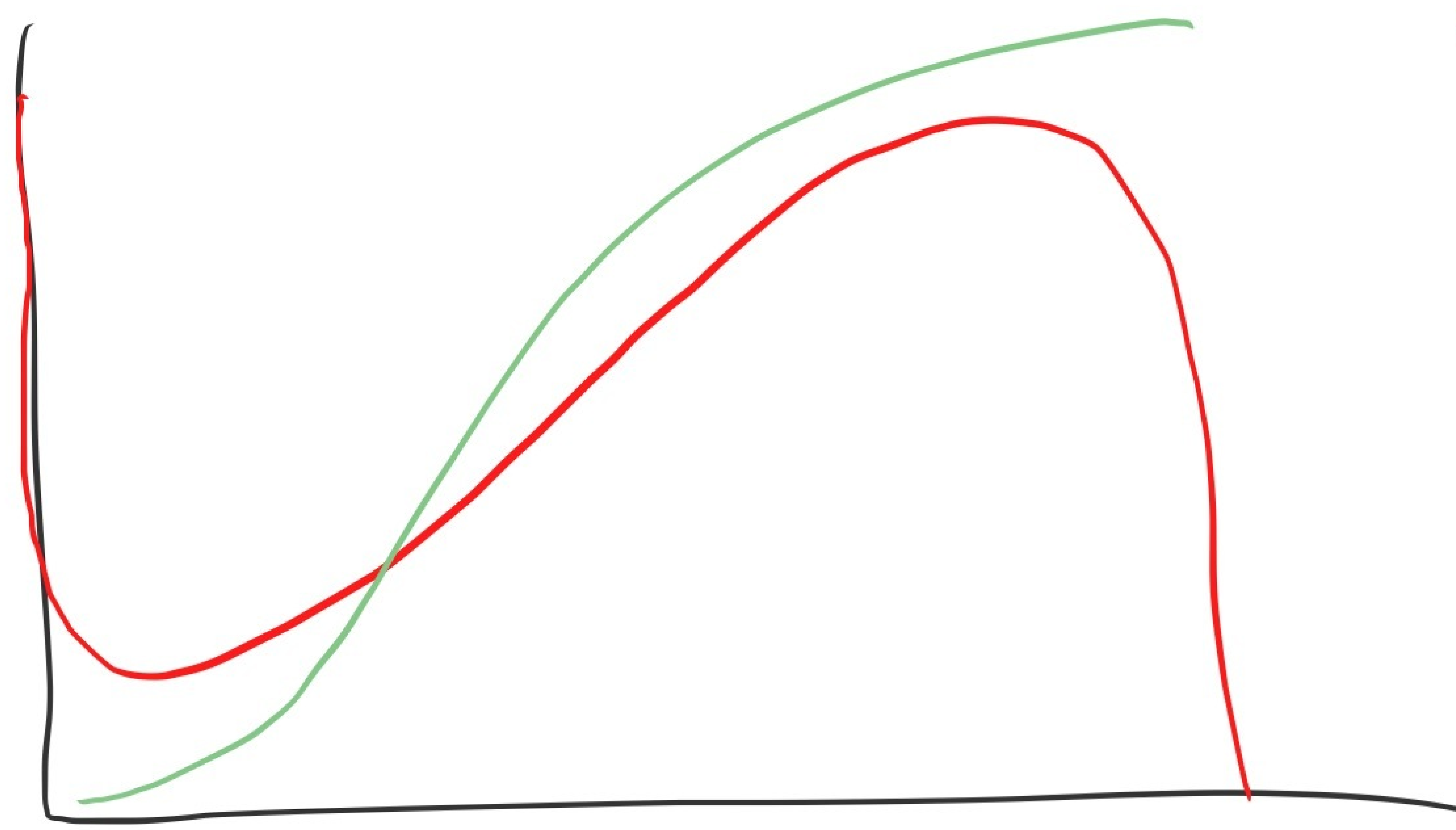
effective K

15 mV

low firing rates, K effectively small



large k



effective k
not so large

$$\tau \frac{dV_i}{dt} = (\qquad)_i + \sum_j \underbrace{V_{PSP_{ij}}}_{\left(\frac{1}{\sqrt{K}} w_{ij}\right) \sim \frac{1}{20} mV} \tau \left[V_j + \delta g_j(t) \right]$$

- it's a miracle this simple model provides a good description of bulk dynamics

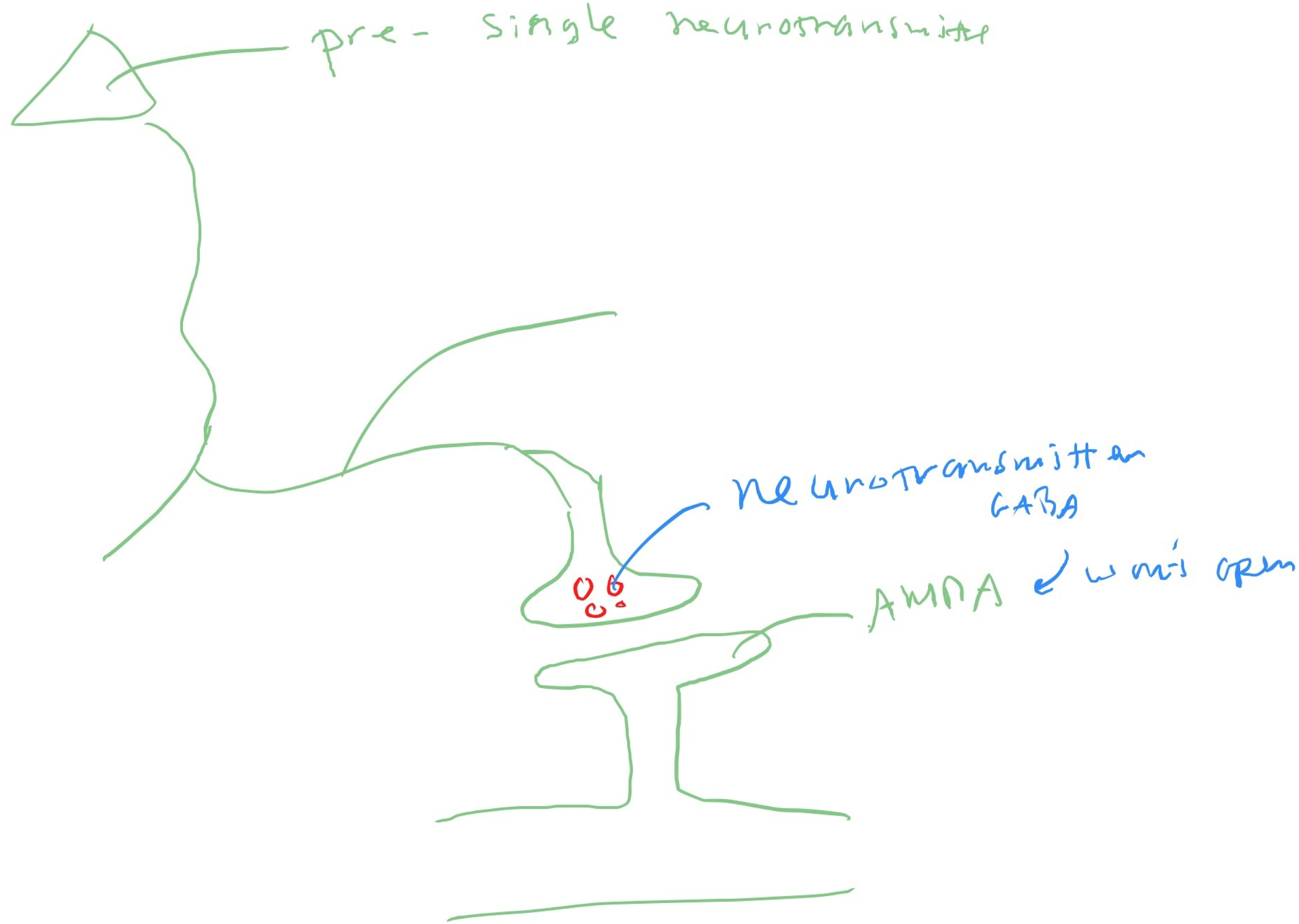
throw away terms $O\left(\frac{1}{\sqrt{K}}\right)$

or not (?)

(homework)

- random connectivity
+ math
+ independence assumption

large K


pre- single neurotransmitter
neurotransmitter
GABA
AMPA
won't open

$$\nu_{Ei} = \phi_E\left(\sqrt{K}\,\underbrace{(\bar{w}_{EE}\nu_E - \bar{w}_{EI}\nu_I)}_{\text{mean}} + \sigma_E \underbrace{z_i}_{\mathcal{N}(0,1)}\right)$$

var

$$\sigma_E^2 = \underbrace{\mathrm{Var}[w_{EE}]\langle \nu_E^2\rangle + \mathrm{Var}[w_{EI}]\langle \nu_I^2\rangle}_{\text{not too big or too small}}$$

$$\frac{1}{\sqrt{K}} w_{ij}$$

def. of weights

assume

$\mathrm{Var}[w] \sim \bar{w}^2$

$$\nu_i = \frac{1}{\sqrt{K}} \sum_j w_{ij} \nu_j$$

$w_{ij} = \bar{w}$

$$\hookrightarrow \frac{1}{\sqrt{K}} \bar{w} \sum_j \nu_j = \sqrt{K}\,\bar{w}\,\bar{\nu}$$, no i-dependence