Simplified models of (recurrent) networks

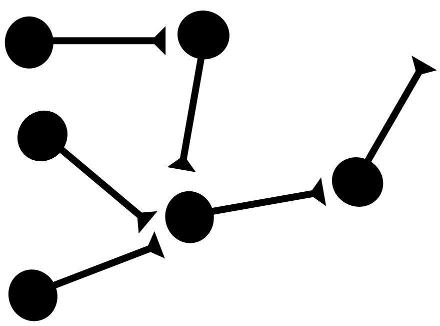
Computational Neuroscience

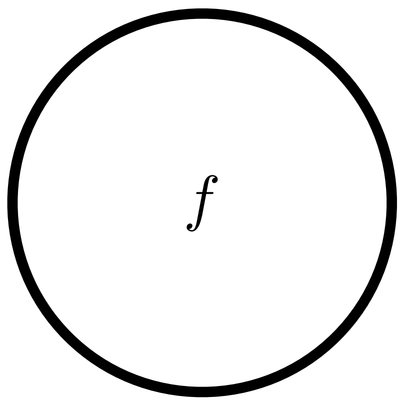
$$\frac{d}{dt} < I_{syn} > \approx -\beta < I_{syn} > + N \ c \ w \ f$$

Plan for the day

- Simplified models of networks: mean-field hypothesis
- Recurrent excitation as a mean to amplify
- Recurrent excitation as a mean to change equilibria
- Feedback inhibition as a mechanism for rate oscillations
- Intrinsic cell properties as additional contributing mechanisms for (sparse) rate oscillation

- each neuron has identical [intrinsic] parameters...
- each neuron fires independently from each other...
- each one firing asynchronously, irregularly [Poisson], ~f





$$\frac{d}{dt} \langle I_{syn} \rangle \approx -\beta \langle I_{syn} \rangle + N\ c\ w\ f$$

$$f = F(I_{syn})$$

$$\frac{d}{dt} < I_{syn} > \approx -\beta < I_{syn} > + N\ c\ w\ f$$

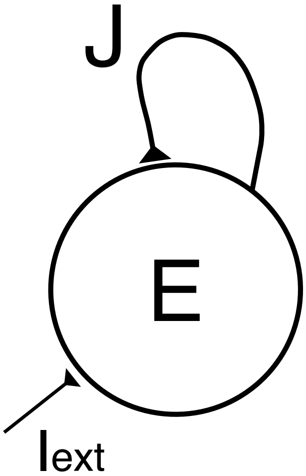
$$f = F(I_{syn})$$

$$\tau \frac{dh}{dt} = -h + J\ E$$

$$E = F(h)$$

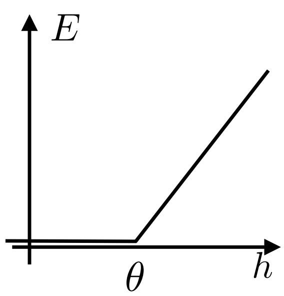
$$\boxed{\tau = \frac{1}{\beta}} \qquad \boxed{J = N\ c\ w}$$

Rate model describing a single
large population of excitatory neurons
recurrently connected



$$\tau\ \dot{h} = -h + J\ E + I_{ext}$$

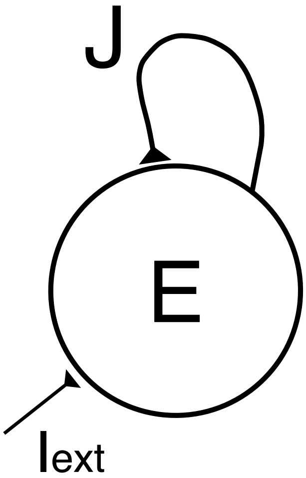
$$E = [\alpha\ (h - \theta)]_+$$



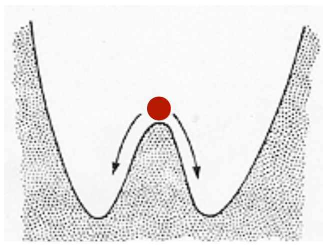
$$[x]_+ = x \qquad for \quad x > 0$$
$$[x]_+ = 0 \qquad for \quad x < 0$$

see e.g. Abbott & Dayan, 2000

What do we learn on recurrent networks using (mean-field) rate models?



- amplification of steady-state responses
- slowing down of *reaction times*
- altering of *equilibria*



"Amplification" by recurrent excitation (i.e., positive feedback)

$$h > \theta$$

$$\tau \dot{h} = -h + J \alpha (h - \theta) + I_{ext}$$

$$\tau \dot{h} = -(1 - J \alpha) h + I_{ext} - J \alpha \theta$$

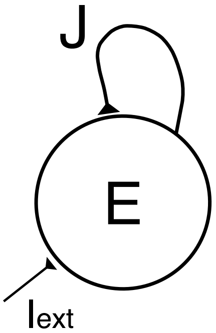
$$\dot{h} = \frac{h_\infty - h}{\tau_h}$$

$$E = [\alpha (h - \theta)]_+$$

$$h_\infty = \frac{I_{ext} - J \alpha \theta}{1 - J\alpha}$$

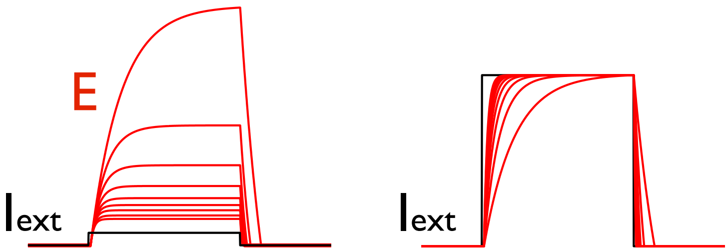
$$\tau_h = \frac{\tau}{1 - J\alpha}$$

Recurrent excitation (i.e., positive feedback)



- amplifies steady-state responses
- slows down the reaction times
- alters equilibrium points

$$\tau \dot{h} = -h + J E + I_{ext}$$



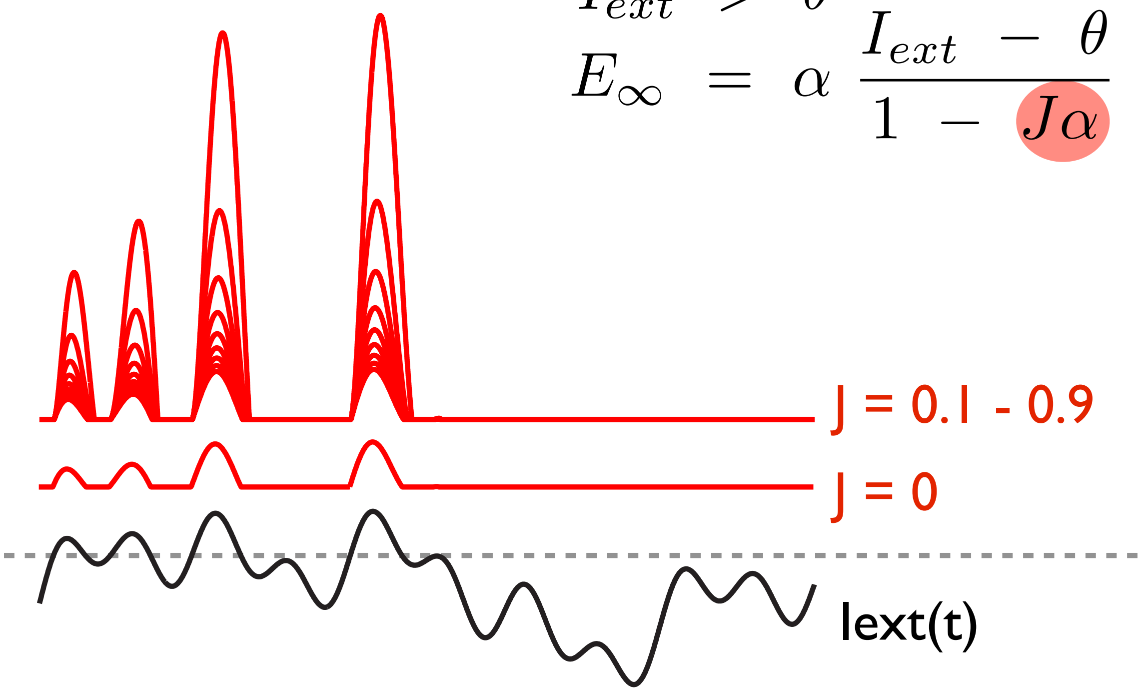
$$h_\infty = \frac{I_{ext} - J \alpha \theta}{1 - J\alpha}$$

$$\tau_h = \frac{\tau}{1 - J\alpha}$$

Amplification by recurrent excitation (i.e., positive feedback)

$$I_{ext} > \theta$$

$$E_\infty = \alpha \frac{I_{ext} - \theta}{1 - J\alpha}$$

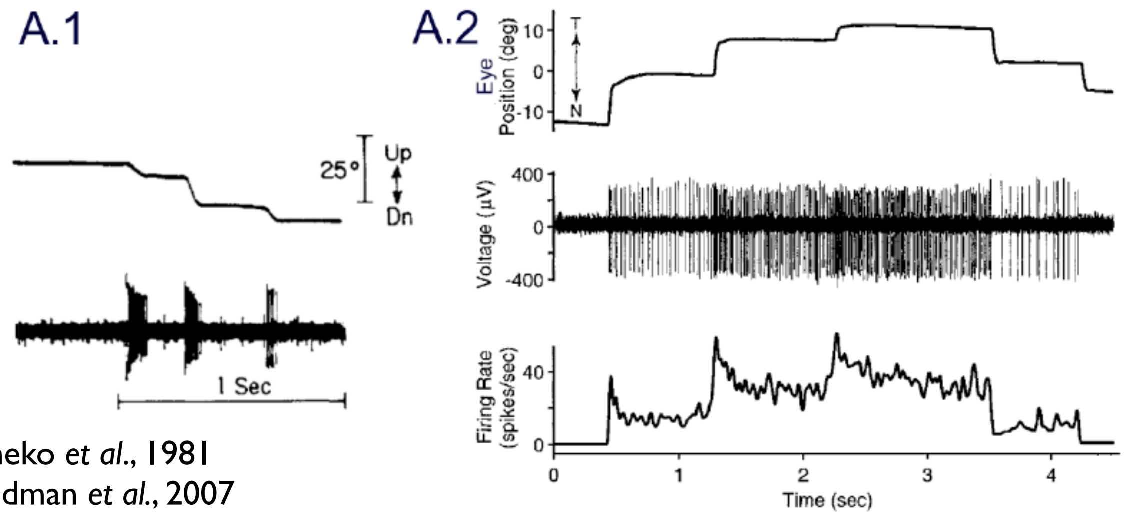


"Temporal integration"

Oculomotor system

Brainstem nuclei neurons encode (eye-velocity) motor commands for saccades as APs bursts. Neurons downstream fire tonically during fixations to maintain the eye muscles' tension and, thereby, the eye position stable.

A **neural "integrator" was hypothesised,** in order to explain how transient inputs as in A.1 result in sustained responses as in A.2. It is not yet known whether it is implemented with network mechanisms or single-cell properties (e.g. complicated extra ion-channels)...



Kaneko *et al.*, 1981
Goldman *et al.*, 2007

"Temporal integration" by recurrent excitation (i.e., finely-tuned positive feedback)

$$h > \theta$$

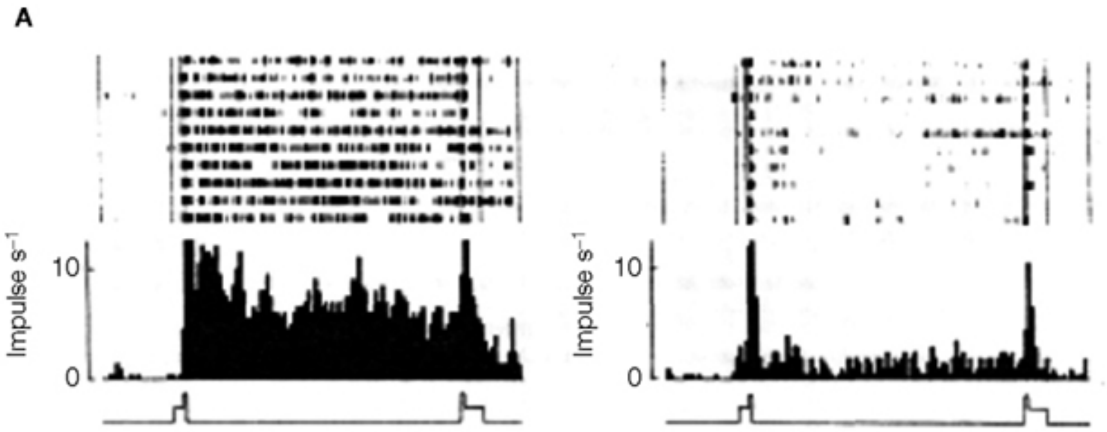
$$\tau \dot{h} = -h + J\,\alpha\,(h - \theta) + I_{ext}$$

$$\tau \dot{h} = -(1 - J\,\alpha)\,h + I_{ext} - J\,\alpha\,\theta$$

$$J = \alpha^{-1} \qquad \tau \dot{h} = I_{ext} - \theta$$

$$h(t) = h(0) + \int_0^t I_{ext}(t') - \theta\,dt'$$

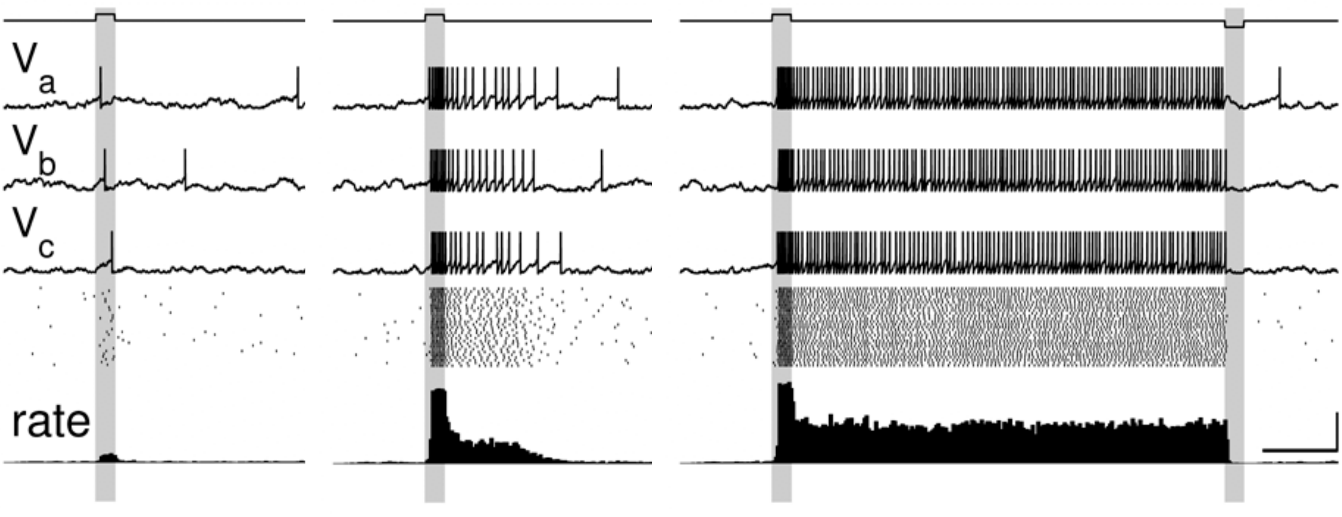
"Persistent activity" in the primate Infero-temporal cortex, during delay match-to-sample tasks

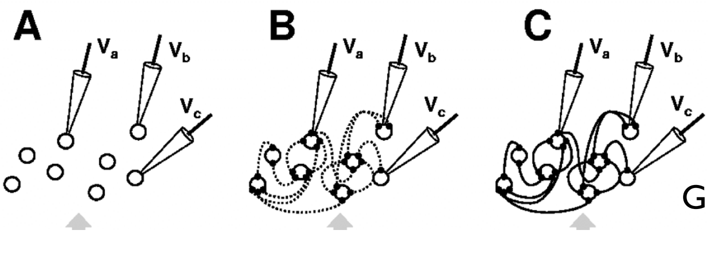


Miyashita, 1988

"Persistent activity" with a recurrent population of excitatory neurons

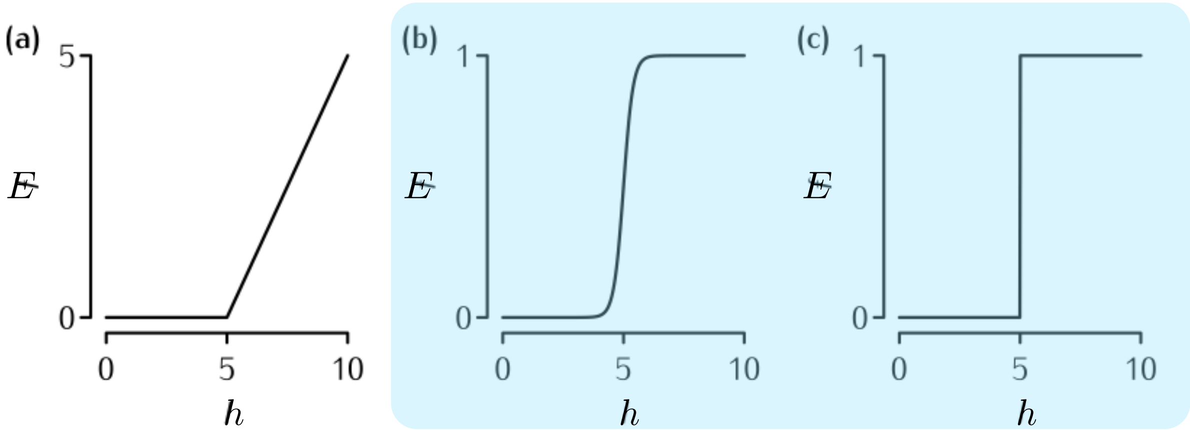
Recurrent network of Integrate-and-Fire model units





Giugliano *et al.*, 2004

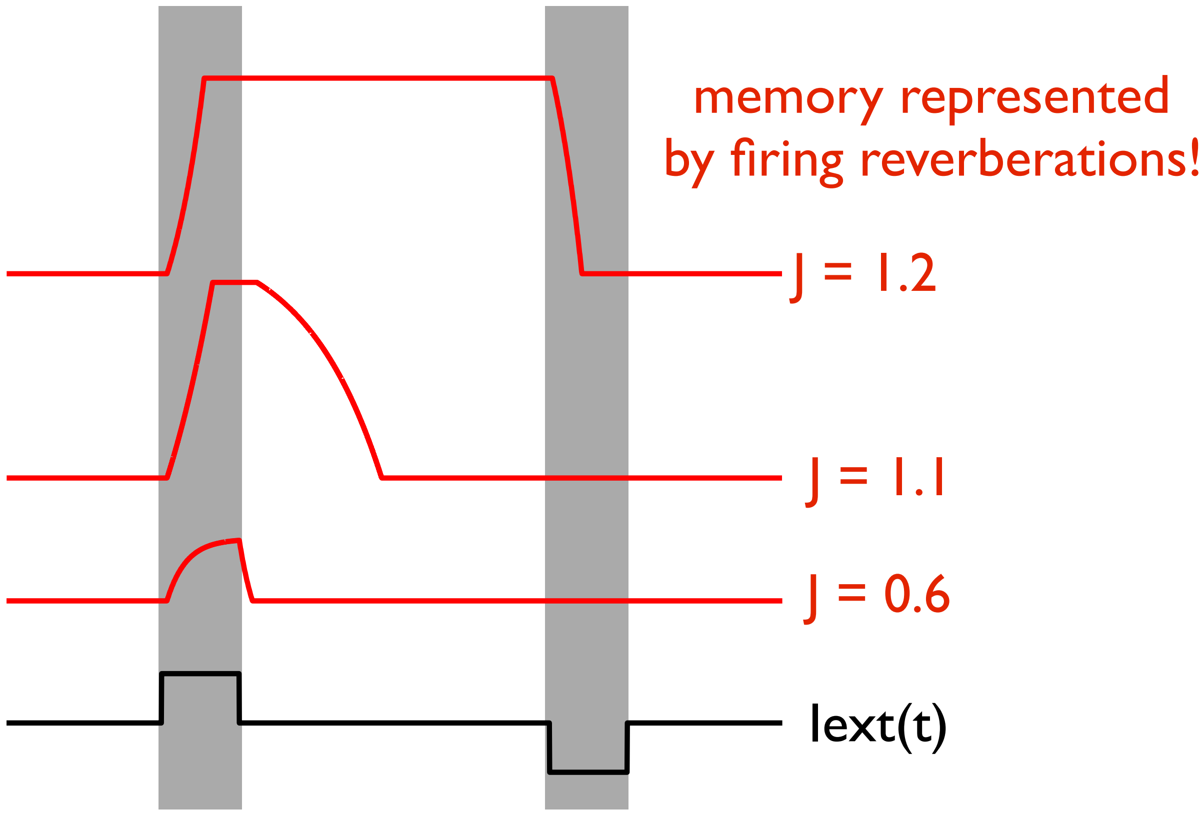
“Persistent activity” with a recurrent population of excitatory neurons



It is only possible with “saturating f-I” curve
(or with short-term depressing synapses...)

from Sterratt et al., 2011

“Persistent activity” with a recurrent population of excitatory neurons

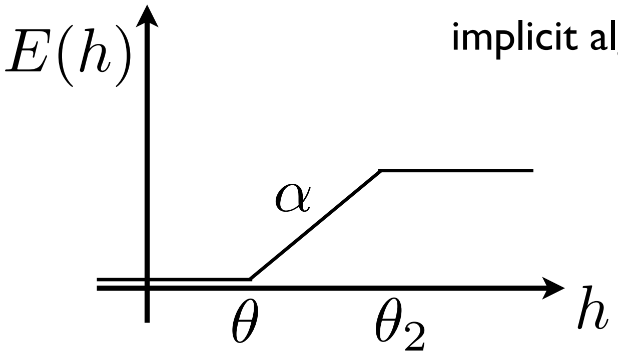


Analysis of the equilibrium points (i.e. steady-states or fixed-points)

$$\tau \, \dot{h} \; = \; -h \; + \; J \; E \; + \; I_{ext}$$

$$\dot{h}_{ss} \; = \; 0$$

$$h_{ss} \; = \; J \; E(h_{ss}) \; + \; I_{ext}$$



implicit algebraic equation: how to solve it??

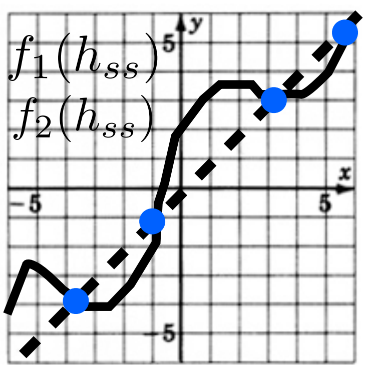
graphically

numerically with a PC

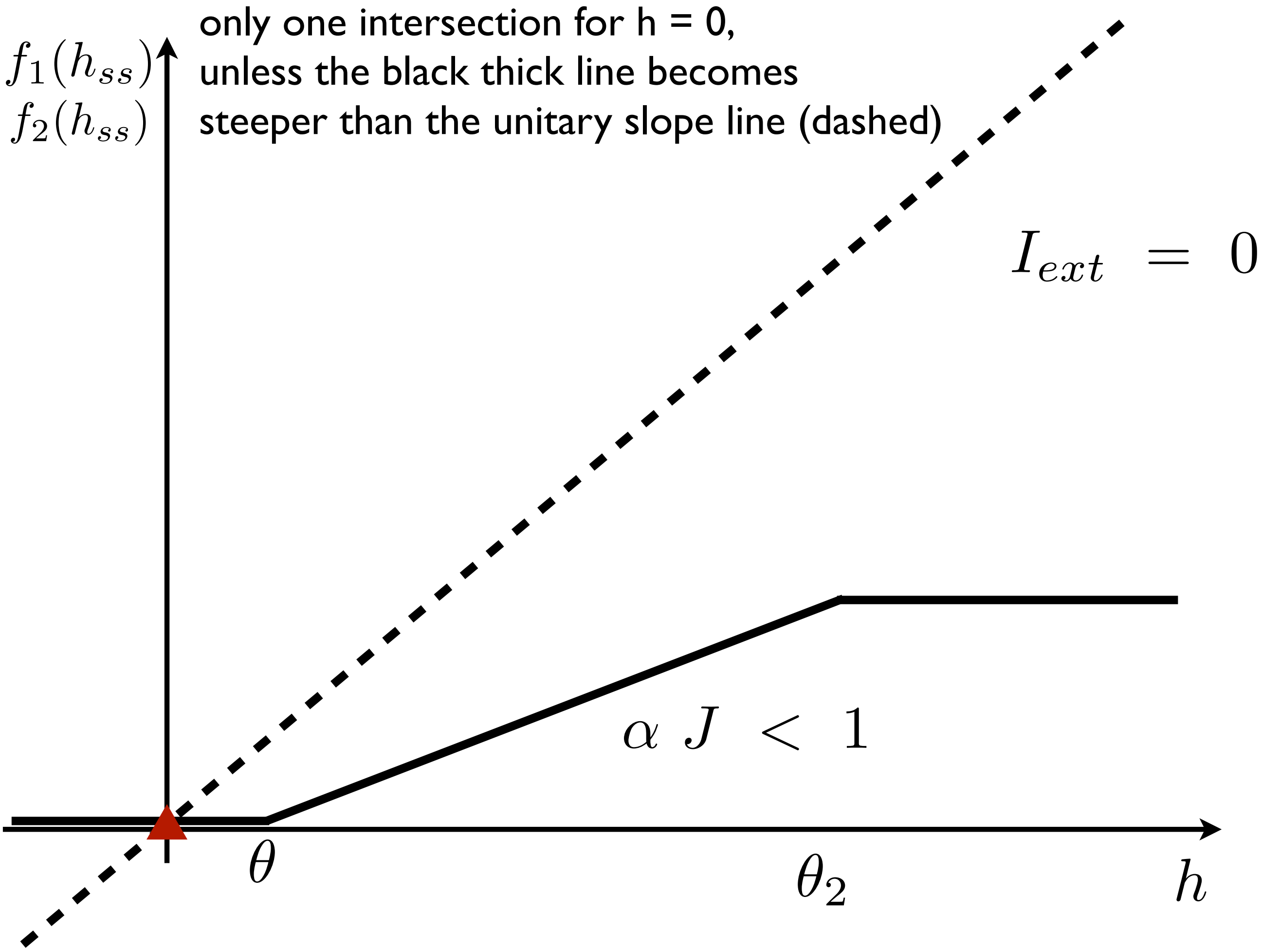
$$h_{ss} \; = \; J \; E(h_{ss}) \; + \; I_{ext}$$

this is the unitary slope line (easy to draw!!!)

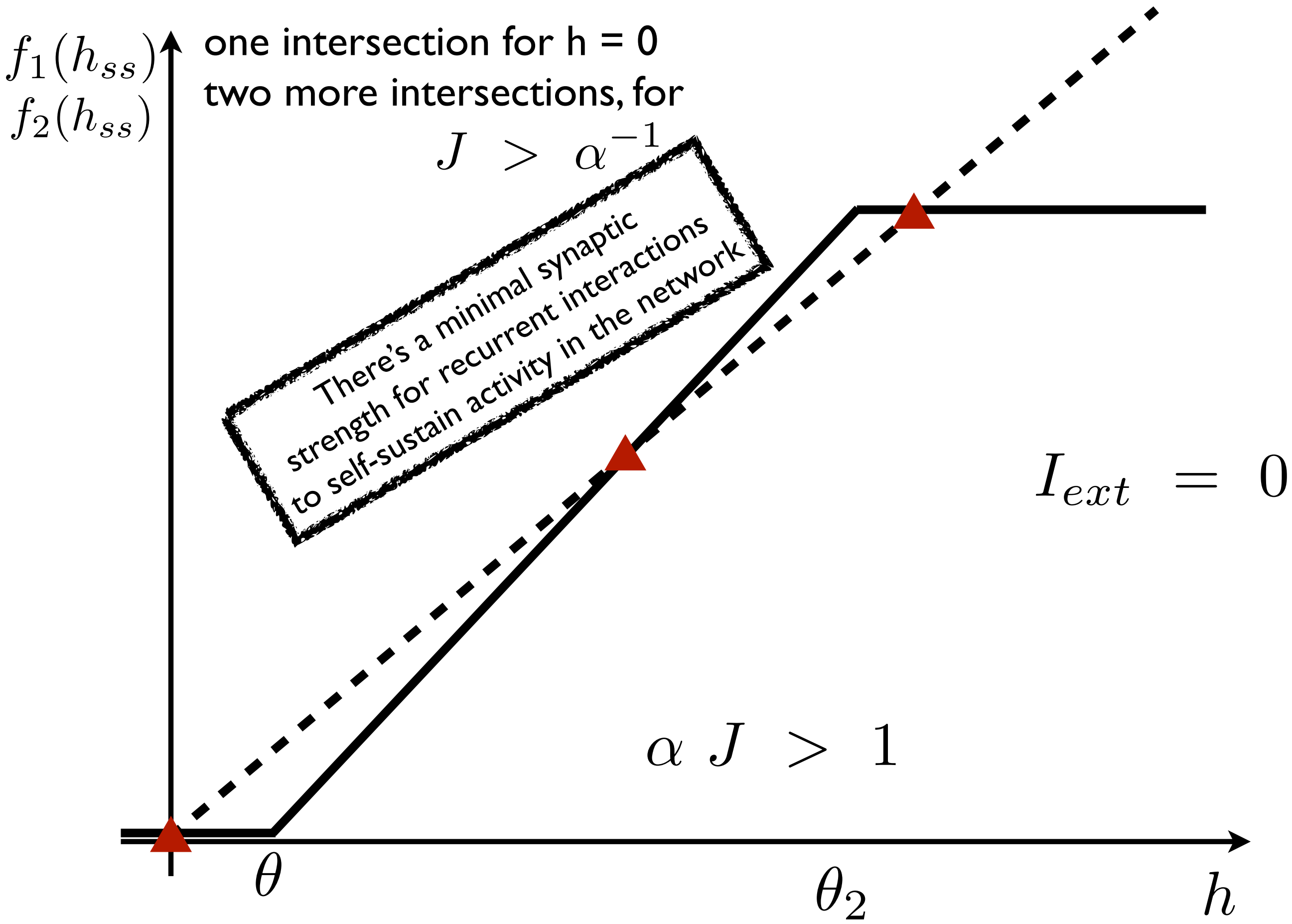
$$\begin{cases} f_1(h_{ss}) \; = \; h_{ss} \\ f_2(h_{ss}) \; = \; J \; E(h_{ss}) \; + \; I_{ext} \end{cases}$$



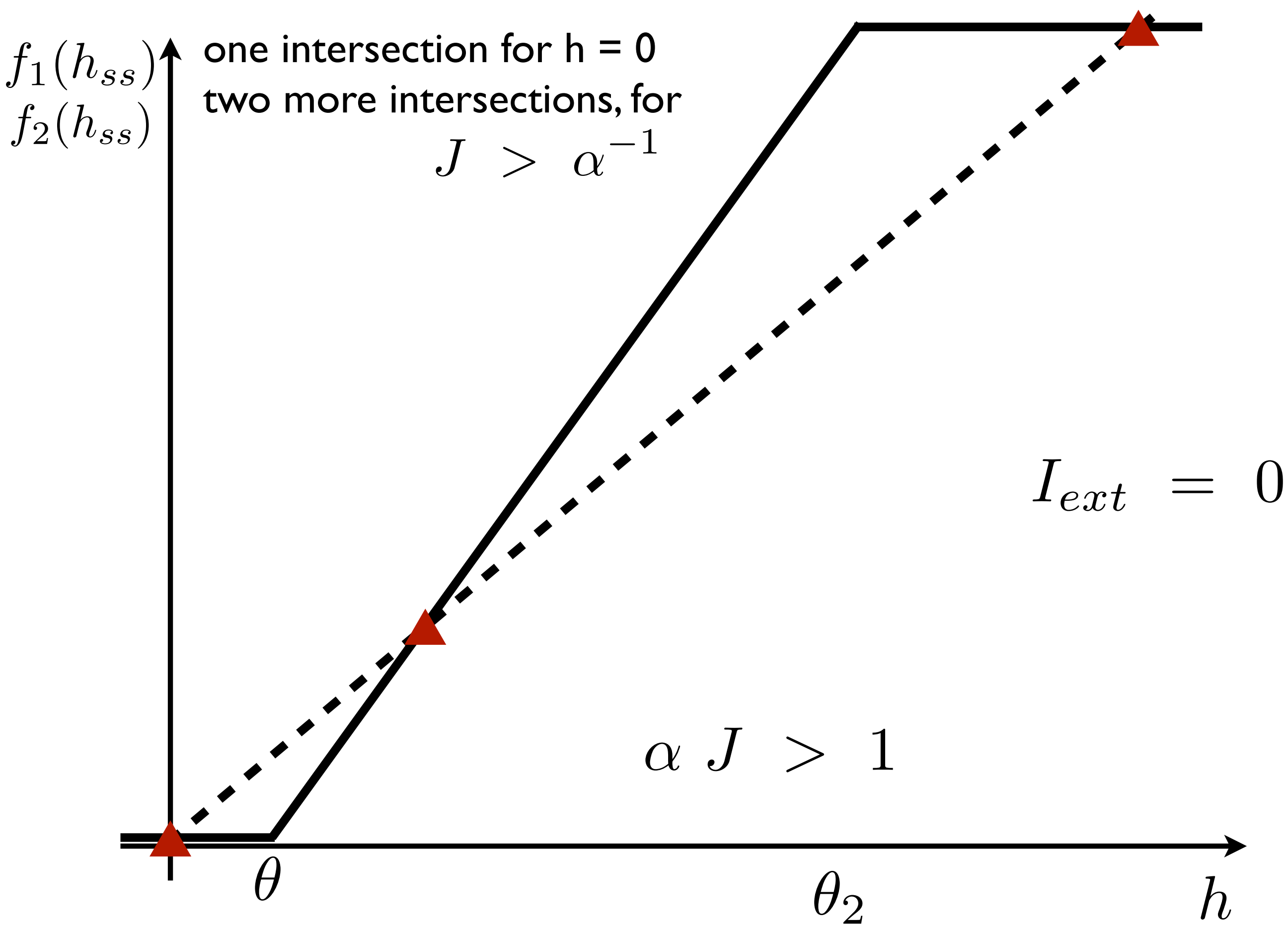
this is a piece-wise linear function (easy to draw)



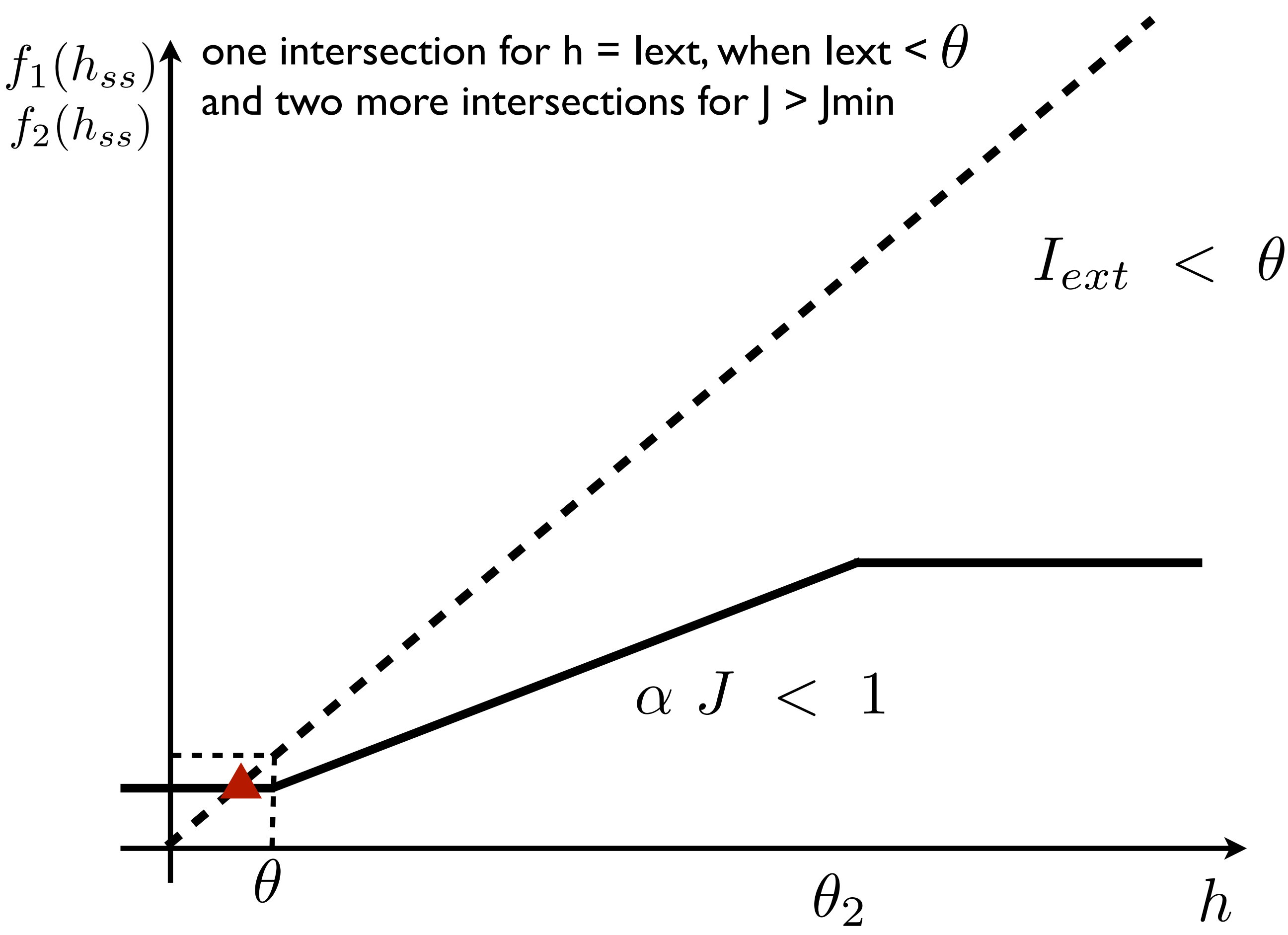
$f_1(h_{ss})$
$f_2(h_{ss})$
only one intersection for h = 0,
unless the black thick line becomes
steeper than the unitary slope line (dashed)
$I_{ext} = 0$
$\alpha J < 1$
θ
θ_2
h



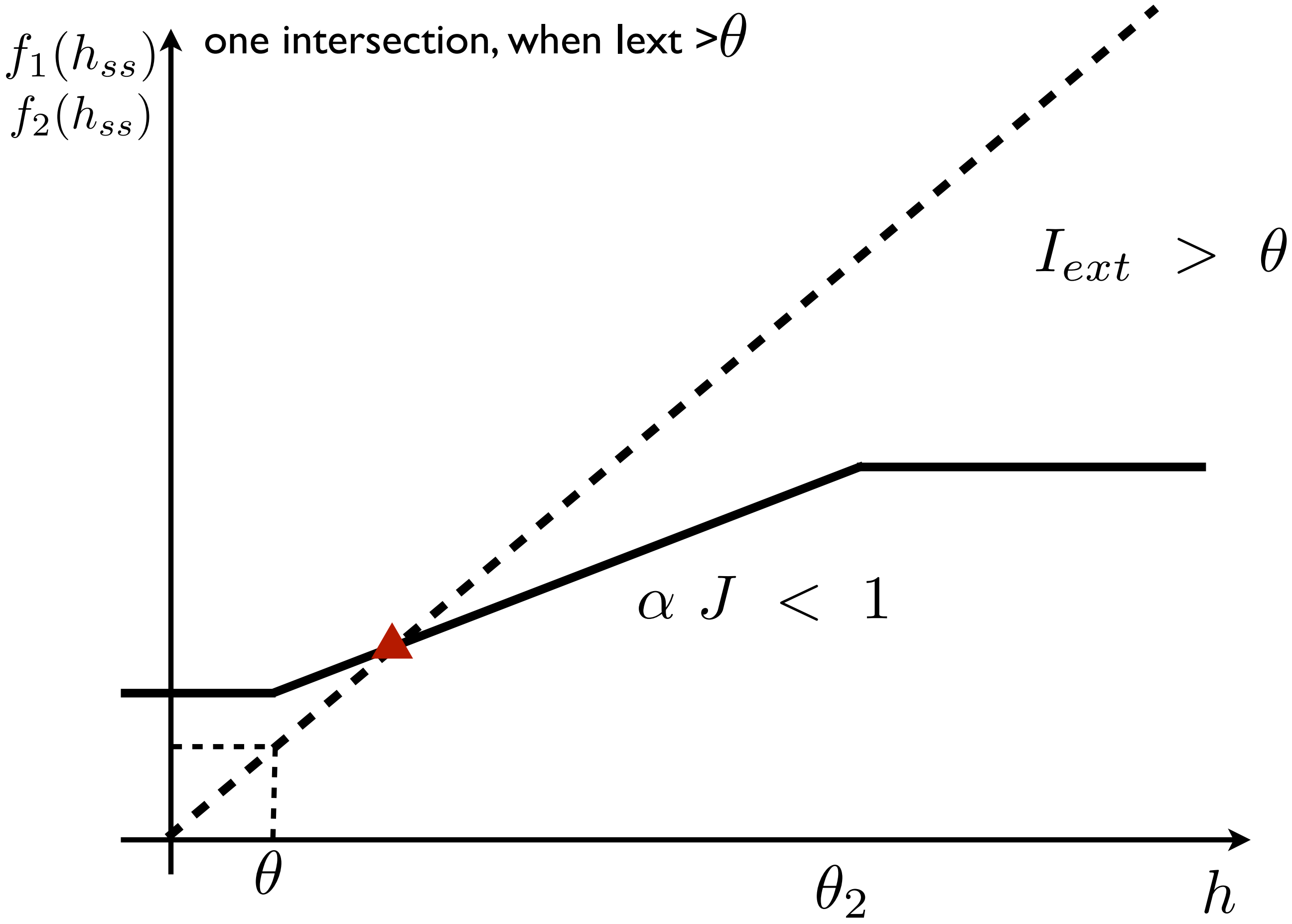
$f_1(h_{ss})$
$f_2(h_{ss})$
one intersection for h = 0
two more intersections, for
$J > \alpha^{-1}$
There's a minimal synaptic strength for recurrent interactions to self-sustain activity in the network
$I_{ext} = 0$
$\alpha J > 1$
θ
θ_2
h

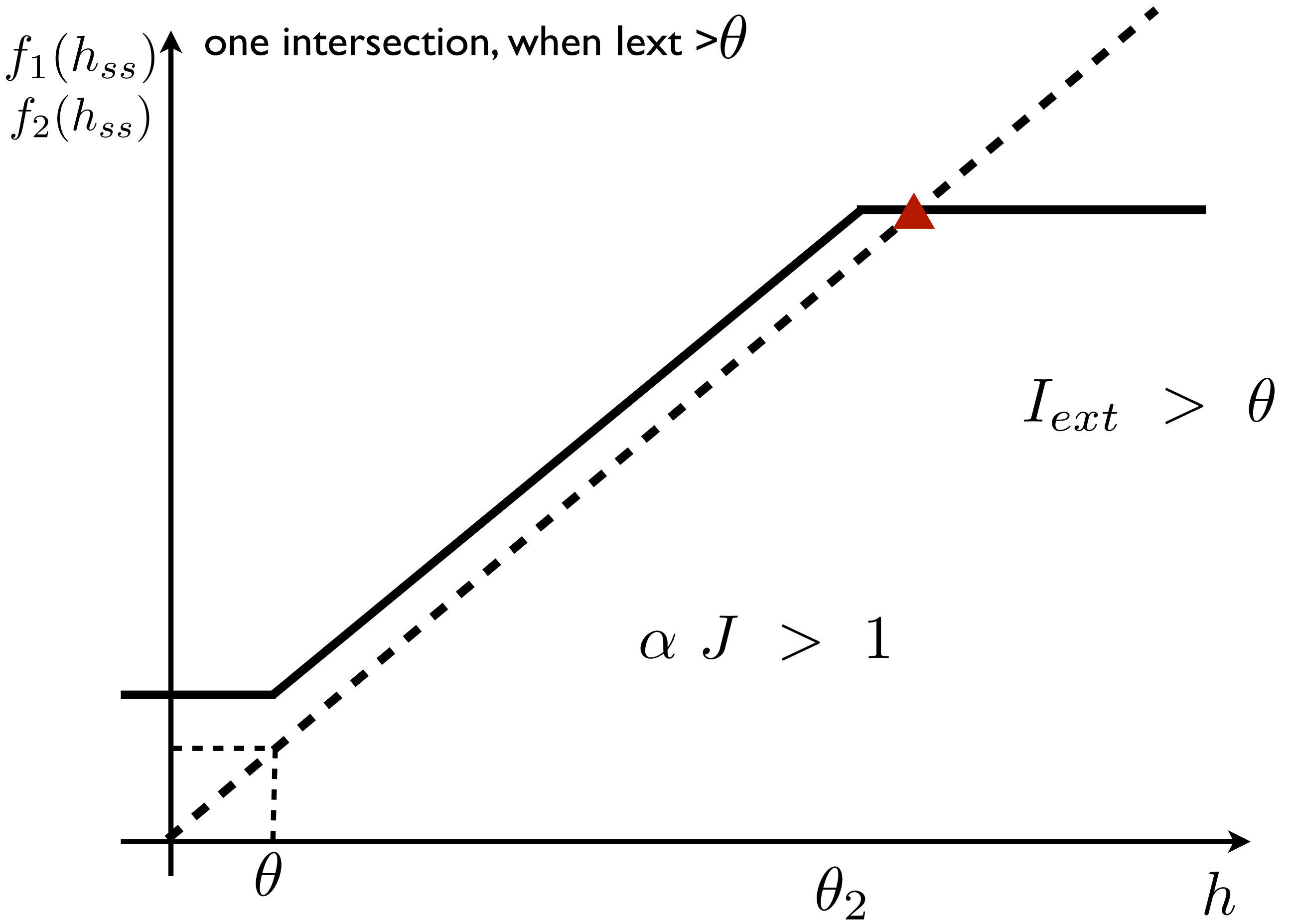


$f_1(h_{ss})$
$f_2(h_{ss})$
one intersection for h = 0
two more intersections, for
$J > \alpha^{-1}$
$I_{ext} = 0$
$\alpha J > 1$
θ
θ_2
h

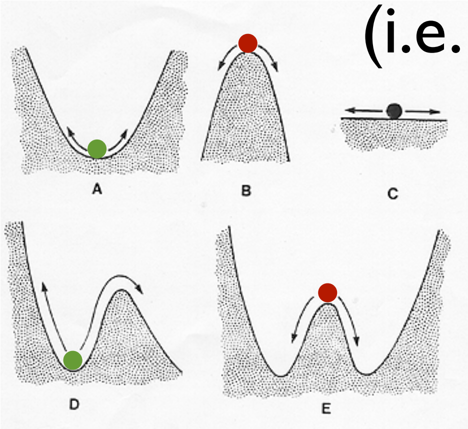


$f_1(h_{ss})$
$f_2(h_{ss})$
one intersection for h = Iext, when Iext < θ
and two more intersections for J > Jmin
$I_{ext} < \theta$
$\alpha J < 1$
θ
θ_2
h


$f_1(h_{ss})$
$f_2(h_{ss})$
one intersection, when Iext >θ
$I_{ext} > \theta$
$\alpha J < 1$
θ
θ_2
h


$f_1(h_{ss})$
$f_2(h_{ss})$
one intersection, when Iext >θ
$I_{ext} > \theta$
$\alpha J > 1$
θ
θ_2
h

Analysis of the stability of the equilibria
(i.e. stable or unstable)



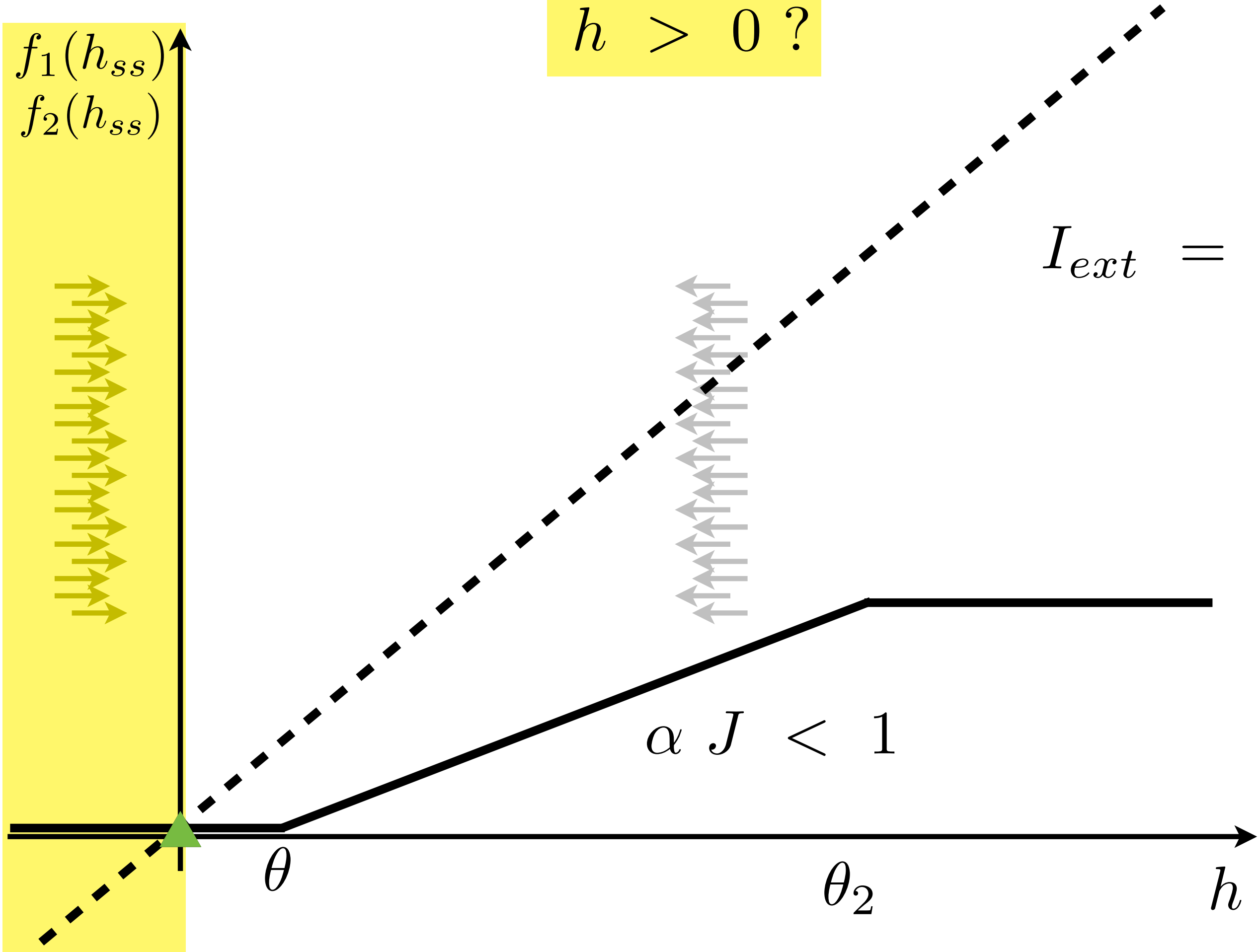
$$\tau\ \dot{h}\ =\ -h\ +\ J\ E\ +\ I_{ext}$$

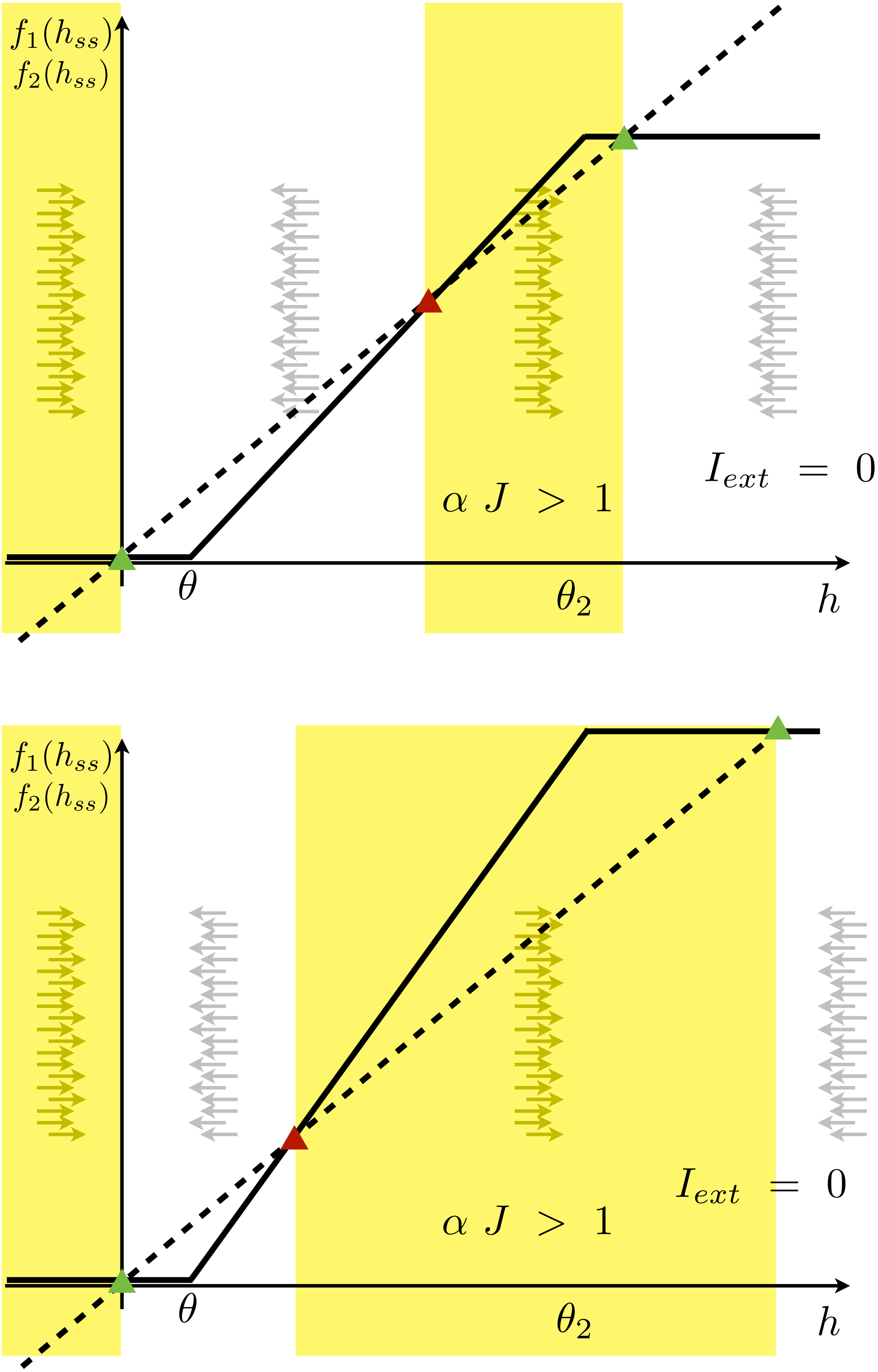
$$\dot{h}\ >\ 0\ ? \qquad\qquad h\ <\ J\ E(h_{ss})\ +\ I_{ext}$$

implicit algebraic inequality: how to solve it??

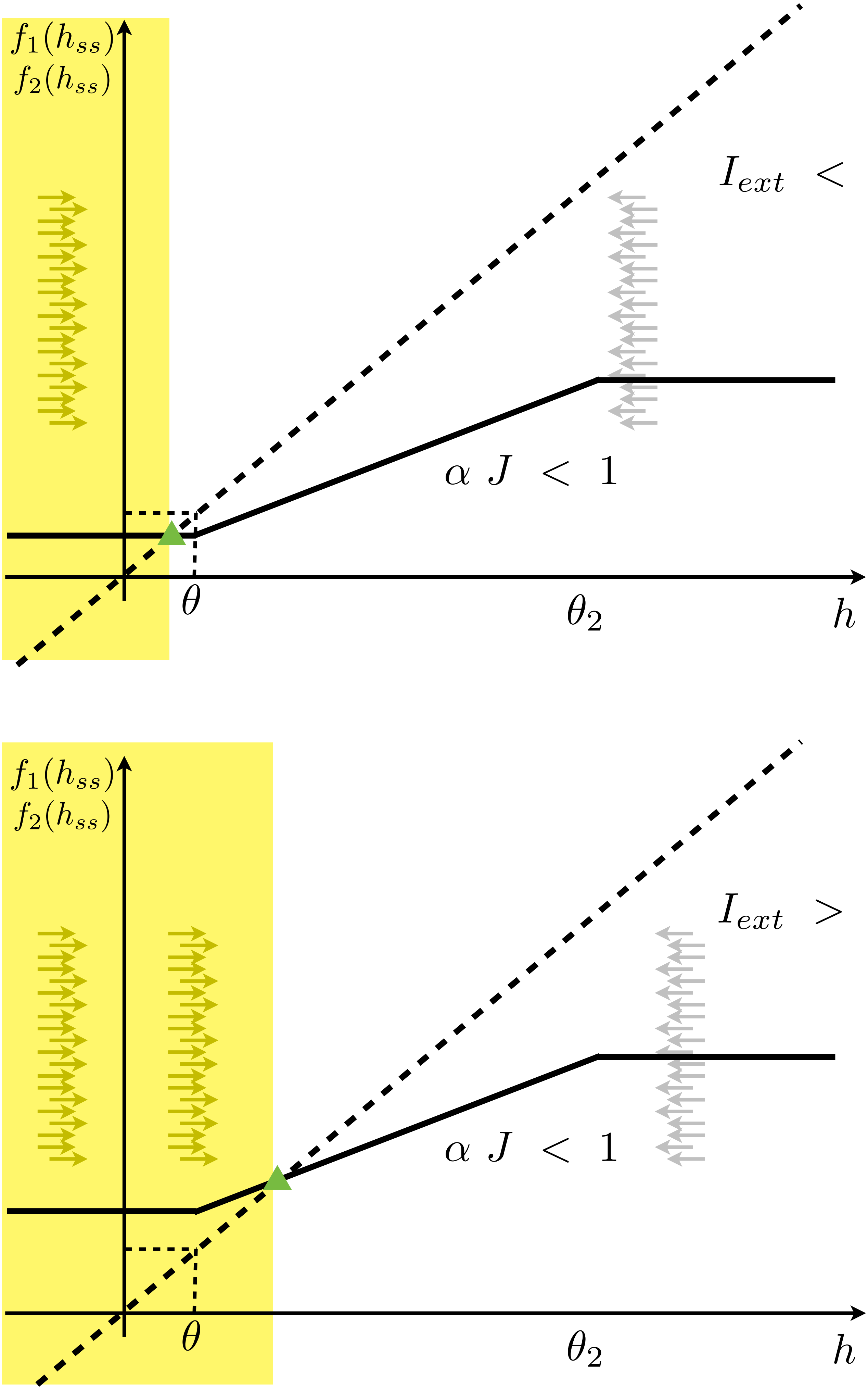
graphically

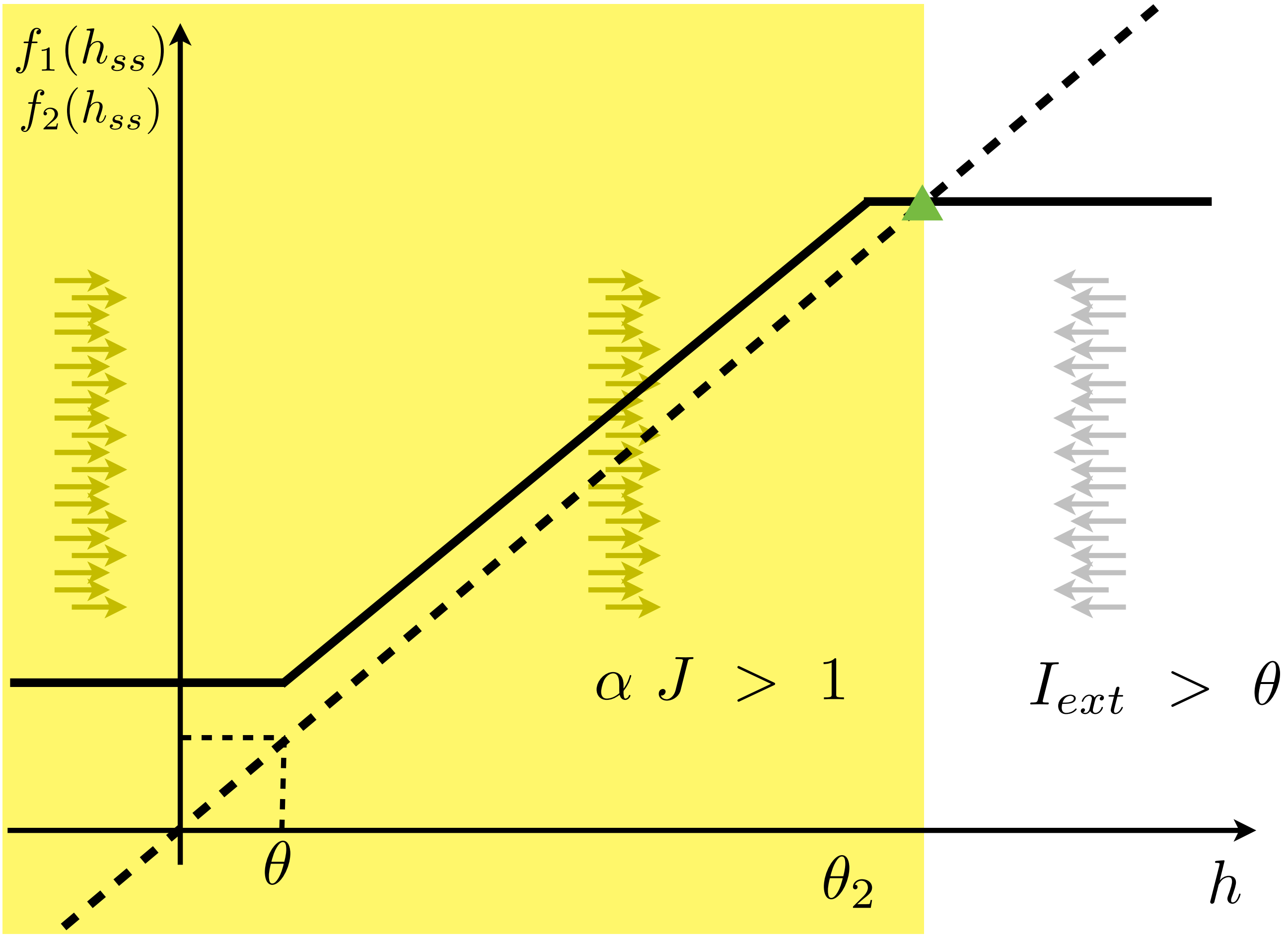
$$\dot{h}\ >\ 0\ ?$$





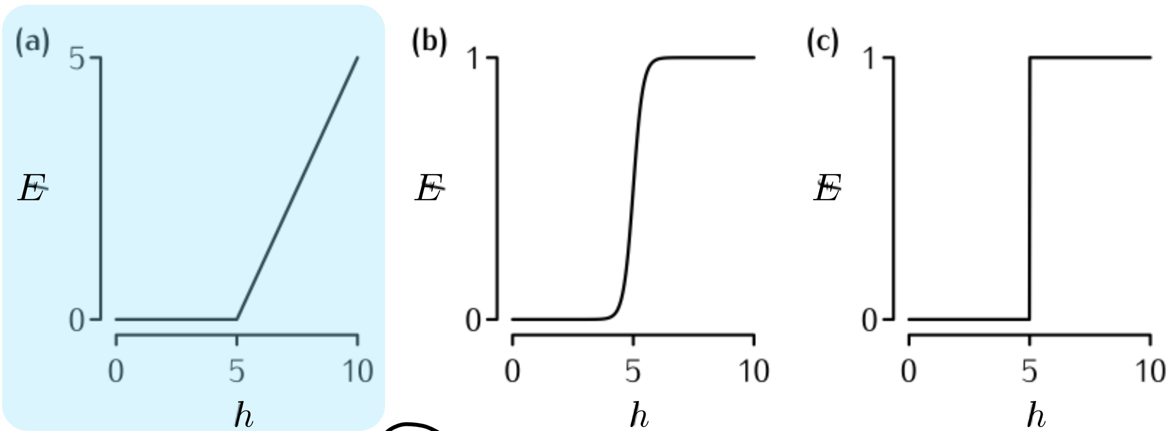
$f_1(h_{ss})$
$f_2(h_{ss})$
$I_{ext} = 0$
$\alpha\ J > 1$
θ
θ_2
h
$f_1(h_{ss})$
$f_2(h_{ss})$
$I_{ext} = 0$
$\alpha\ J > 1$
θ
θ_2
h

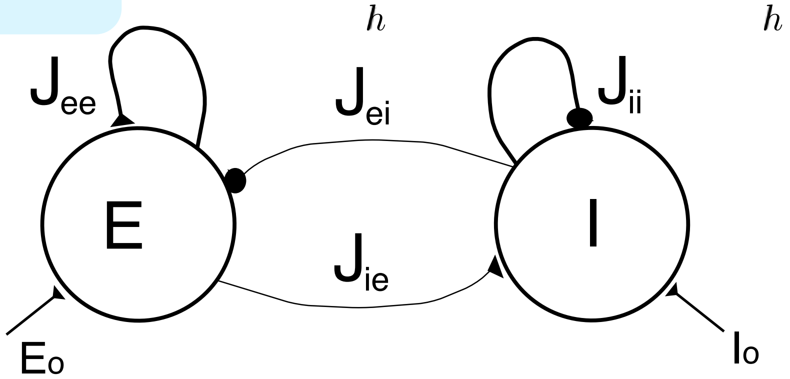

$f_1(h_{ss})$
$f_2(h_{ss})$
$I_{ext} < \theta$
$\alpha J < 1$
θ
θ_2
h
$f_1(h_{ss})$
$f_2(h_{ss})$
$I_{ext} > \theta$
$\alpha J < 1$
θ
θ_2
h



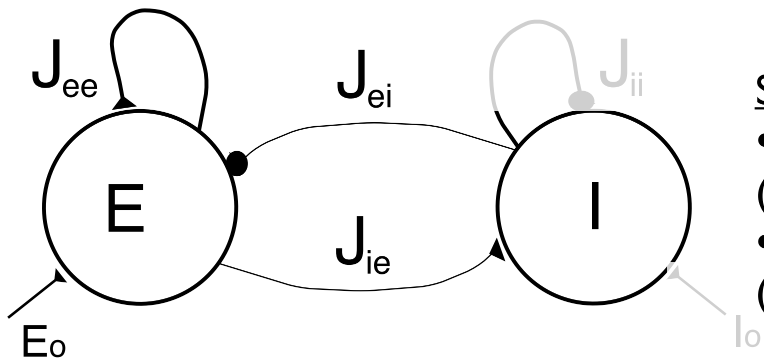
"Persistent activity" with two populations of excitatory and inhibitory neurons

No "saturating f-I" curve is necessary...





"Persistent activity" with two populations of excitatory and inhibitory neurons



Simplifying hypotheses:

- no recurrent inhibition (Jii = 0)
- no input to the inhibitory pop. (Io = 0)

$$\tau_e \, \dot{h}_e = -h_e + J_{ee} \, E - J_{ei} \, I + E_0$$

$$\tau_i \, \dot{h}_i = -h_i + J_{ie} \, E$$

$$E = [\alpha_e \, (h_e - \theta_e)]_+ \text{ and } I = [\alpha_i \, (h_i - \theta_i)]_+$$

Analysis of the equilibrium points (i.e. steady-states of fixed-points)

$$\tau_e \, \dot{h}_e = -h_e + J_{ee} \, E - J_{ei} \, I + E_0$$

$$\tau_i \, \dot{h}_i = -h_i + J_{ie} \, E$$

$$E = [\alpha_e \, (h_e - \theta_e)]_+ \text{ and } I = [\alpha_i \, (h_i - \theta_i)]_+$$

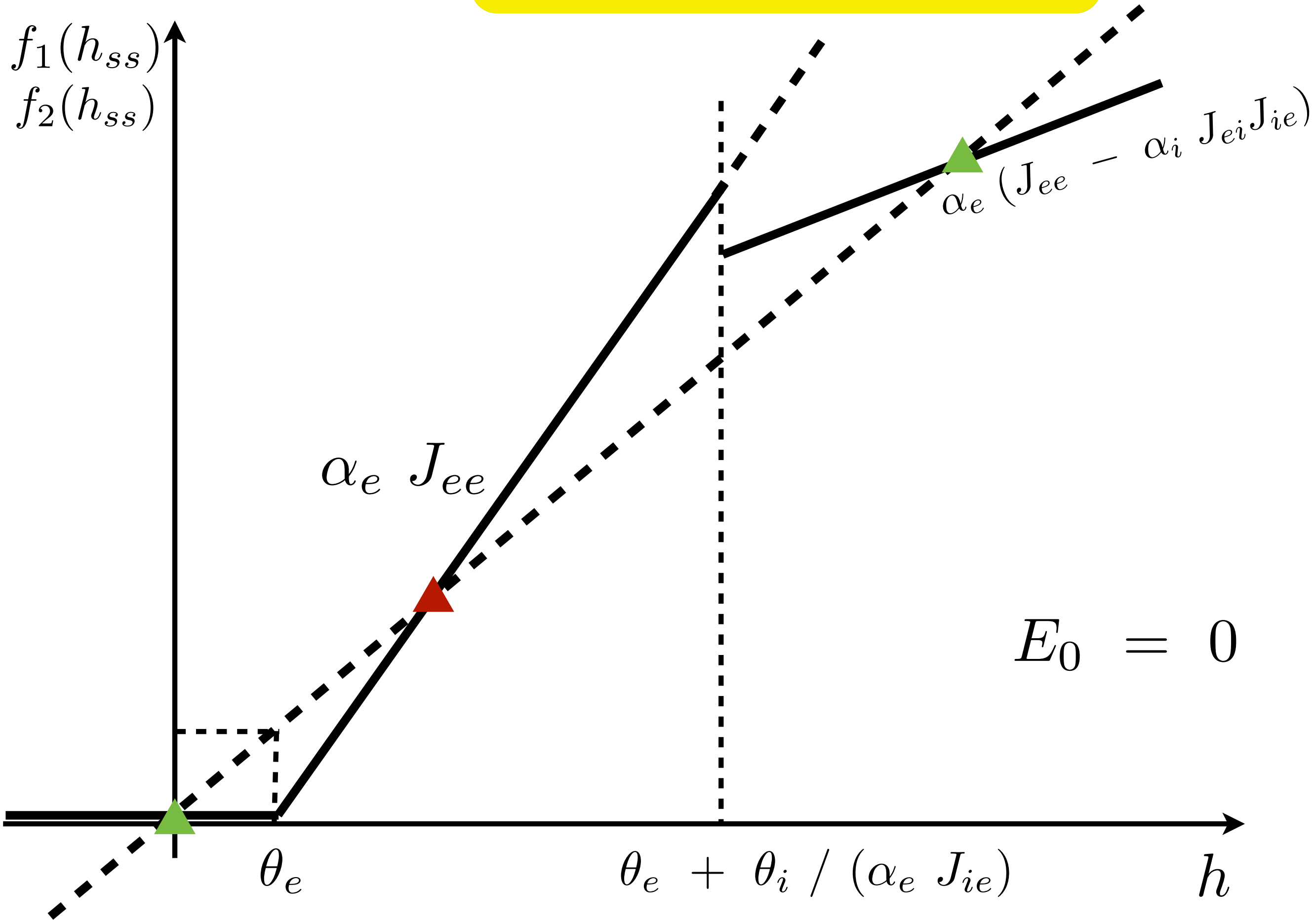
$$\dot{h}_e = \dot{h}_i = 0$$

$$h_e = J_{ee} \, E - J_{ei} \, I + E_0$$

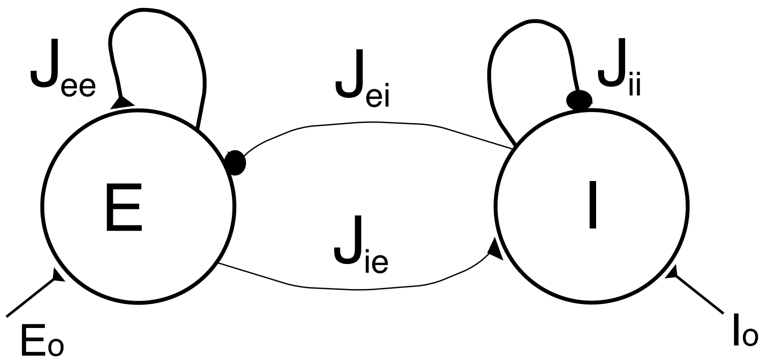
$$h_i = J_{ie} \, E$$

$$h_e = J_{ee} \, E - J_{ei} \, [\alpha_i \, (J_{ie} \, E - \theta_i)]_+ + E_0$$

$$h_e = J_{ee}\, E - J_{ei}\, [\alpha_i\, (J_{ie}\, E - \theta_i)]_+ + E_0$$



"Oscillations" with two populations of excitatory and inhibitory neurons

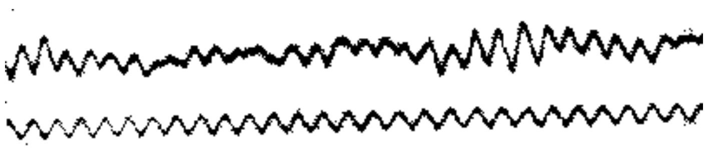


$$\tau_e\, \dot{h}_e = -h_e + J_{ee}\, E - J_{ei}\, I + E_0$$

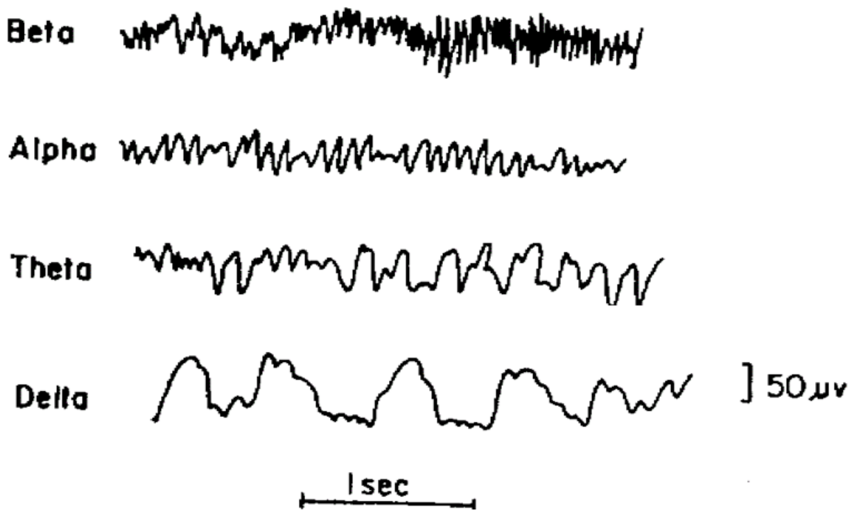
$$\tau_i\, \dot{h}_i = -h_i + J_{ie}\, E - J_{ii}\, I + I_0$$

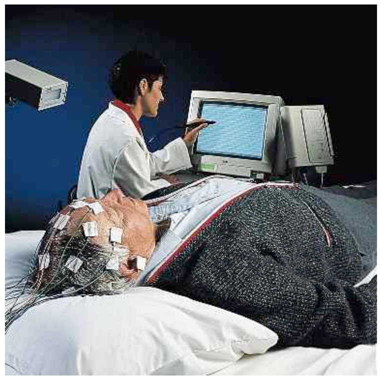
$$E = [\alpha_e\, (h_e - \theta_e)]_+ \text{ and } I = [\alpha_i\, (h_i - \theta_i)]_+$$

"Oscillations" in cortical networks revealed by EEG (electroencephalography)



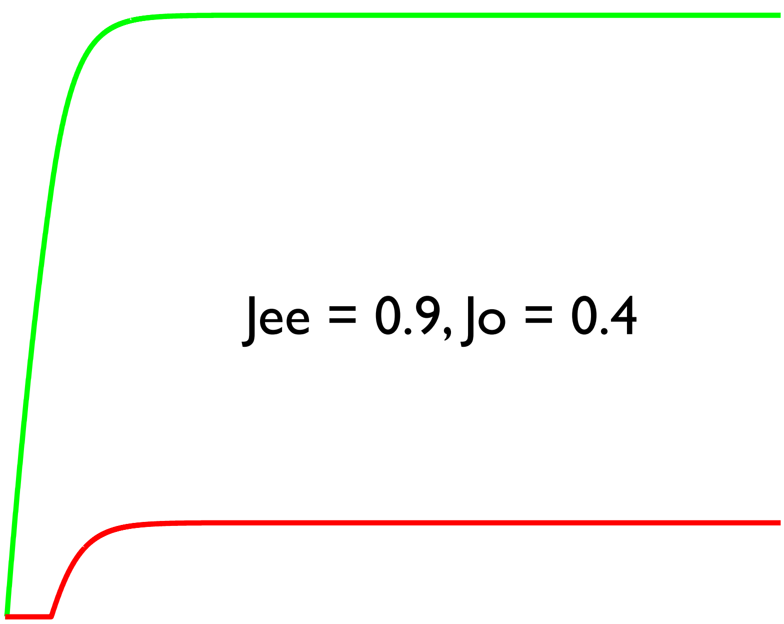
First EEG recorded by Hans Berger, circa 1928.





from Sabbatini, online

$$
\begin{aligned}
J_{ii} &= 0 \\
\tau_e &= \tau_i \\
J_{ie} &= J_{ei} = J_o \\
\alpha_e &= \alpha_i = 1 \\
\theta_e &= \theta_i
\end{aligned}
$$



“Oscillations” with two populations of excitatory and inhibitory neurons

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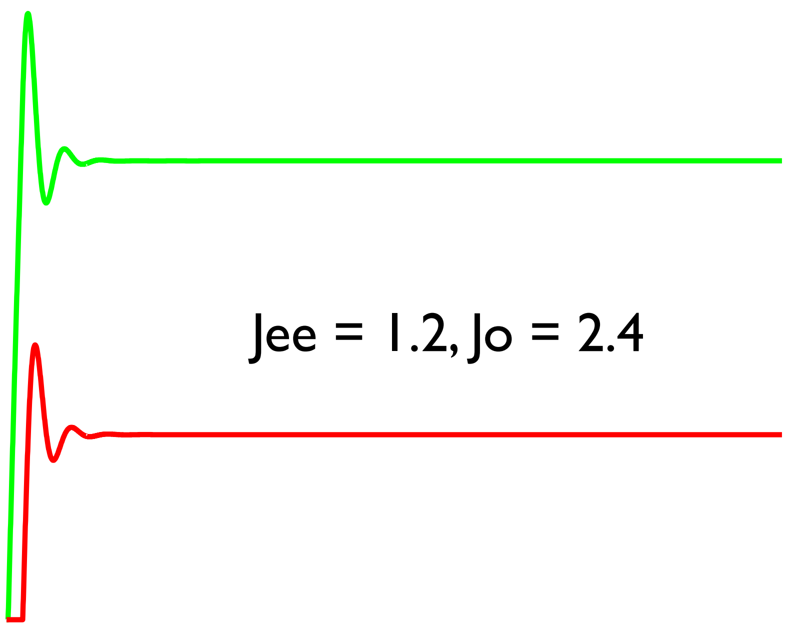

“Oscillations” with two populations of excitatory and inhibitory neurons

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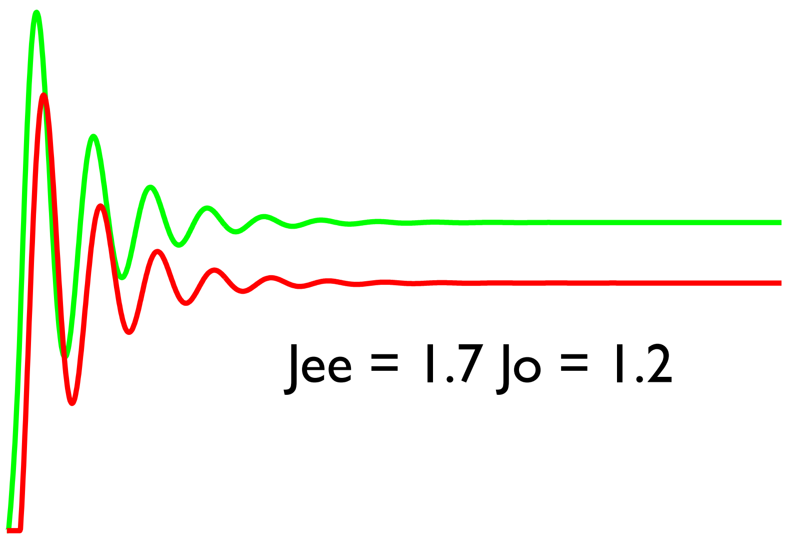

“Oscillations” with two populations of excitatory and inhibitory neurons

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\end{aligned}
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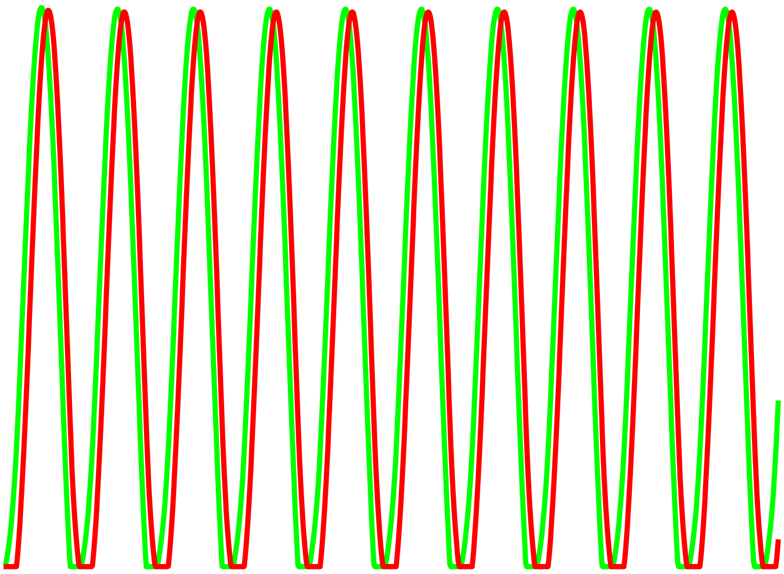
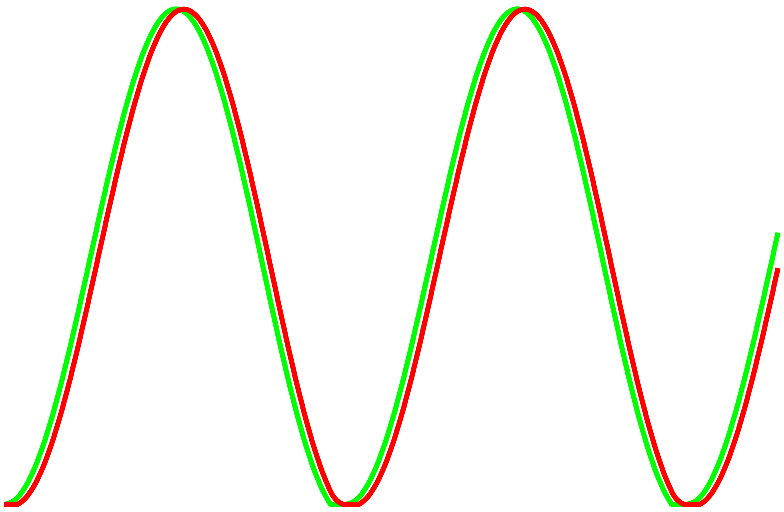


Jee = 2 Jo = 1.2

“Oscillations” with two populations of excitatory and inhibitory neurons

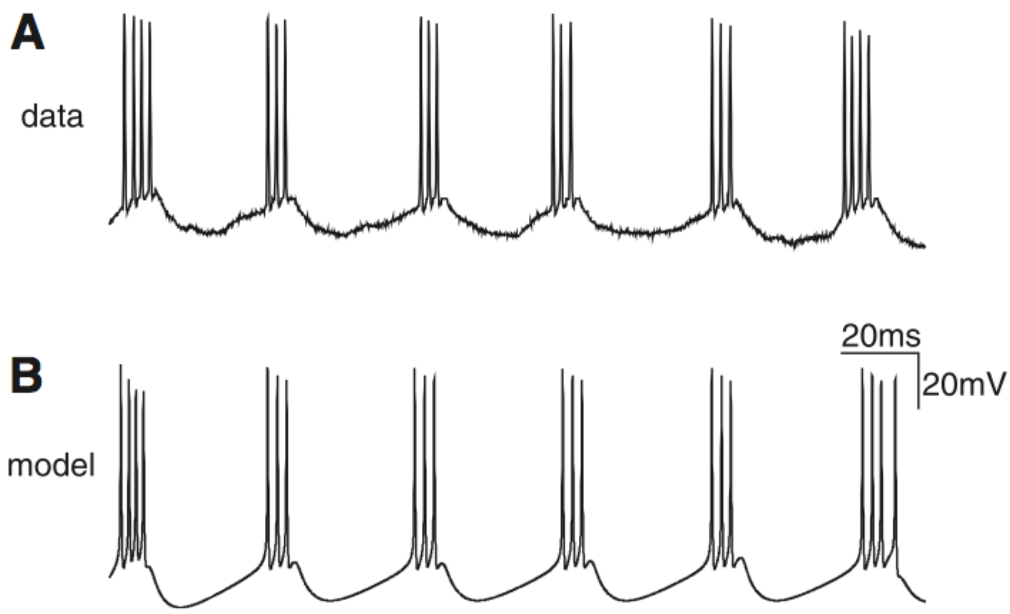
$$
\begin{aligned}
J_{ii} &= 0 \\
\tau_e &= \tau_i \\
J_{ie} &= J_{ei} = J_o \\
\alpha_e &= \alpha_i = 1 \\
\theta_e &= \theta_i
\end{aligned}
$$



Jee = 2 Jo = 1.01

“Oscillations”: single-cell or network phenomena?

Cortical "chattering" neurons



Gray and McCormick, 1996
Wang, 1999