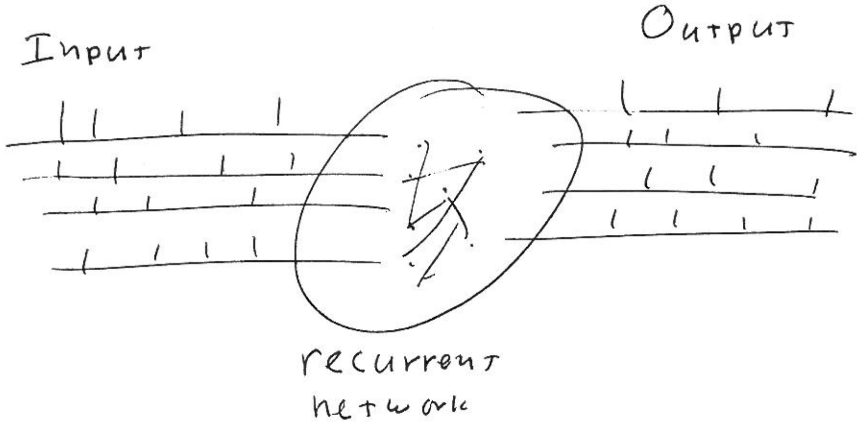
11/30/04

The standard problem:



goal: if you knew the wiring, could you predict the behavior of the network?

reason for this goal: find a mapping from desired behavior to wiring.

- ~~ff~~ vs. recurrent connections

Output = f (input; network parameters)

Want to compute $P(\text{Output} \mid \text{Input})$.

Holy grail #12

$$C_m \frac{dV_i}{dt} = -\bar{g}_L (V_i - \mathcal{E}_L) - \bar{g}_{Na} m^3 h (V_i - \mathcal{E}_{Na}) - \bar{g}_K n^4 (V_i - \mathcal{E}_K) - \sum_j \bar{g}_{ij} X_{ij} (V_j - \mathcal{E}_{ij})$$

$$\tau \frac{dx_{ij}}{dt} = \alpha_{ij} (1 - x_{ij}) \sum_l \delta (t - t_j^l) - \beta_{ij} x_{ij}$$

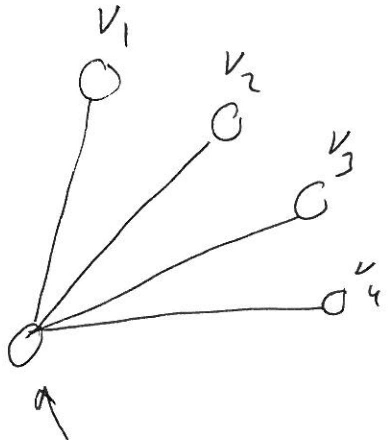
$$\dot{m} =$$

$$\vdots$$

Way too hard – wait until next decade

Equations we really solve:

$$V_i = \phi(V_1, V_2, \ldots V_N)$$



$V_5 = \phi(V_1, V_2, V_3, V_4)$

N nonlinea equations

~~Still hard.~~

~~Want to finish~~

~~1) equilibri~~

- note that we are massively simplifying everything we have learned.
- pretty good approximation if neurons are firing asynchronously
- goal is to find
  a) equilibrium
  b) Stability.

$$\tau \frac{dV_i}{dt} = \phi(V_1, V_2, .. V_N) - V_i$$

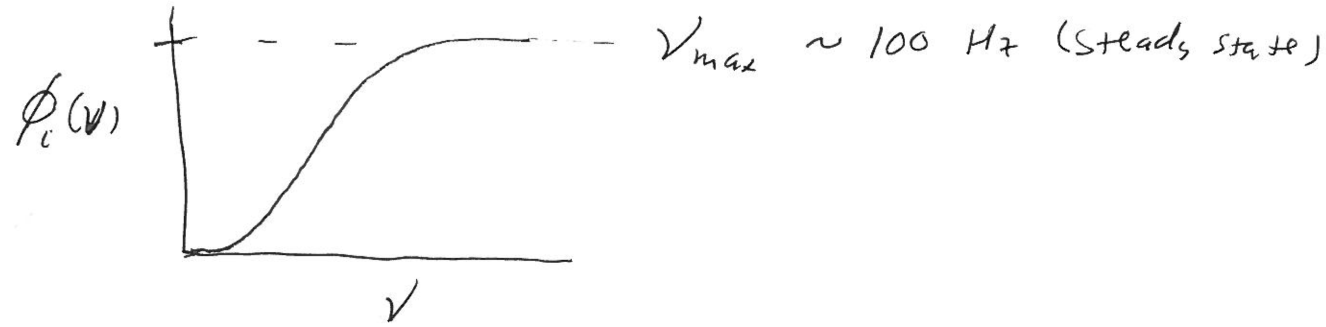
(note that were not even attemting to look at dynamics!)

3

Typical eqns:

$$\frac{d\nu_i}{dt} = \phi_i\left(\sum_j W_{ij}\nu_j\right) - \nu_i$$

positive if neuron j is excitatory
negative " " " " inhibitory



- ϕ is fairly stereotypical
- goal is to find equilibrium in terms of w
  ~~w~~
- can decree some of the neurons to be input neurons, e.g.

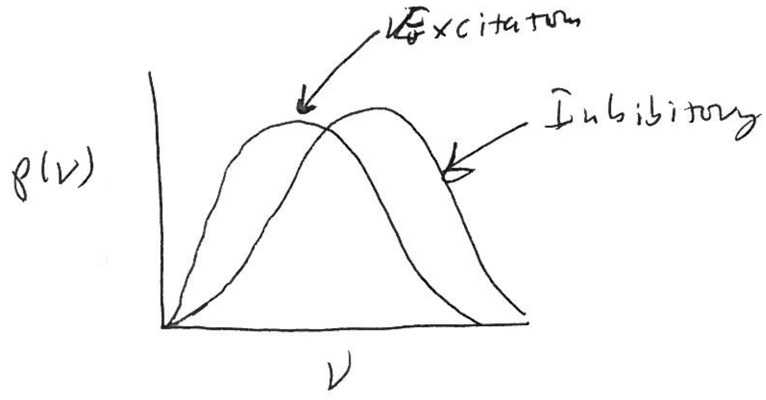
$$\frac{d\nu_i}{dt} = \phi_i\left(\sum_{j=1}^{N} W_{ij}\nu_j + \sum_{j=N+1}^{N+M} W_{ij}\nu_j\right), \quad i=1,\dots,N$$

- ~~No 3-4-7-6 equations!!~~

- mention divisive nonlinearity
as an alternative,
- + dendrites

Key point

- $10^{3-4-5-6}$ equations.
- don't want to know the firing rate of every neuron. Instead, ask about things like distributions

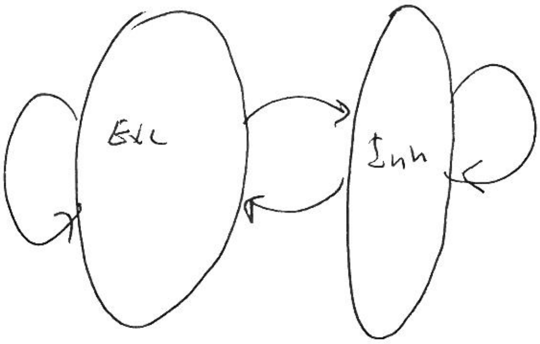


- or maybe find order parameters - parameters that tell us everything we need to know about the distribution (we'll see examples of that later).

like $\nu_E + \nu_I$ = average exc. + inh. firing rates

Wilson - Cowan equations - ~~randomly conn~~

randomly connected



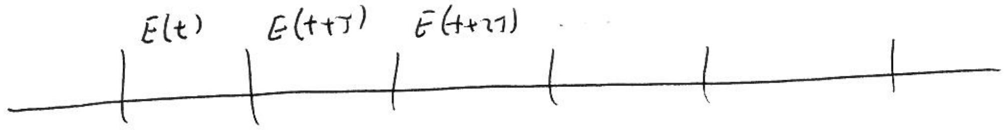
Drop derivation.
Instead, write
$\sum_i \hat{w}_i \nu_i \rightarrow N\hat{w}\bar{\nu} + \sqrt{N}\ldots \xi_i$
$= K\hat{w}\bar{\nu} + \sqrt{K}\ldots \xi_i$

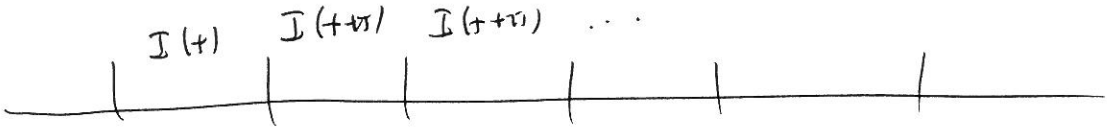
+ drop ξ_i.
then: nullclines
Then: connect scaling; contact w/ stability analysis

~~then~~ then: simple model (hybrid)

Then: E-I
Then: say something about temporal dynamics.

discretize time





$E(t)$ = fraction of excitation cells that fire in time bin t

$I(t)$ = fraction of inhibition " " " " " " "

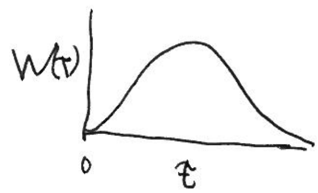
goal: find $E(t+\tau)$, $I(t+\tau)$ in terms of $E(t)$, $I(t)$.

$$E(t+T) = \left[1 - \int_{t-r}^{t} dt'\, E(t')\right] S_E \left[\int_{-\infty}^{t} dt'\, W_{EE}(t-t')\, E(t') - \int_{-\infty}^{t} dt'\, W_{EI}(t-t')\, I(t')\right]$$

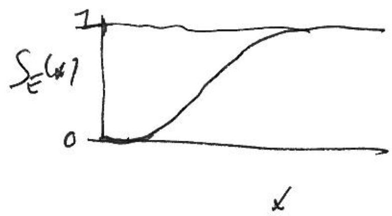
absolute refractory perion r

effect of EPSP, ~~post-synaptic~~ IPSP

synaptic drive; assumed to be the same for all cells



neurons have a range of thresholds



$$\int_{-\infty}^{t} dt'\, W_{EE}(t-t')\, E(t') \simeq \tilde{W}_{EE}\, \bar{E}(t)$$

$$\vdots$$

$$\int_{t-r}^{t} dt'\, E(t') \simeq r\, \bar{E}(t)$$

$$E(t+T) = \left[1 - r\bar{E}(t)\right] S_E \left[\tilde{W}_{EE}\, \bar{E}(t) - \tilde{W}_{EI}\, \bar{I}(t)\right]$$

$$I(t+T) = \left[1 - r\bar{I}(t)\right. S_I \left[\tilde{W}_{IE}\, E(t) - \tilde{W}_{II}\, \bar{I}(t)\right]$$

$$E(t+T) \to \bar{E}(t+T) \simeq \bar{E}(t) + T\frac{d\bar{E}}{dt}$$

$$I(t+T) \to \bar{I}(t) + T\frac{d\bar{I}}{dt}$$

$$\Rightarrow \quad T\frac{d\bar{E}}{dt} = (1-r\bar{E})\, S_E\left(\tilde{W}_{EE}\bar{E} - \tilde{W}_{EI}\bar{I}\right) - \bar{E}$$

$$T\frac{d\bar{I}}{dt} = (1-r\bar{I})\, S_I\left(\tilde{W}_{IE}\bar{E} - \tilde{W}_{II}\bar{I}\right) - \bar{I}$$

---

convert to firing rate:

$$\nu_E = \frac{\text{avg. \# of spikes in interval } T}{T}$$

$$= \frac{\frac{1}{N}[N\bar{E}]}{T}$$

$$= \frac{\bar{E}}{T}$$

$$\Rightarrow \quad \bar{E} = T\nu_E$$

$$\bar{I} = T\nu_I$$

Let ~~E~~ $T\tilde{W}_{EE} = W_{EE}$

$$\tau \frac{d}{dt}(\tau \nu_E) = (1 - r\tau\nu_E)\, S_E\left(W_{EE}\nu_E - W_{EI}\nu_I\right) - \tau\nu_E$$

$$\tau \frac{d}{dt}(\tau \nu_I) = (1 - r\tau\nu_I)\, S_I\left(W_{IE}\nu_E - W_{II}\nu_I\right) - \tau\nu_I$$

- ignore refractory period
- defn $\phi_E = \frac{S_E}{\tau}$

  $\phi_I = \frac{S_I}{\tau}$

$$\tau \frac{d\nu_E}{dt} = \phi_E\left(W_{EE}\nu_E - W_{EI}\nu_I\right) - \nu_E$$

$$\tau \frac{d\nu_I}{dt} = \phi_I\left(W_{IE}\nu_E - W_{II}\nu_I\right) - \nu_I$$

Compare to: $\cancel{\tau \frac{d\nu_i^E}{dt} = \phi_i\left(\sum_j W_{ij}^{EE}\nu_j^E - \sum_j W_{ij}^{EI} \nu_j^I\right) -}$

$$\tau \frac{d\nu_{Ei}}{dt} = \phi_{Ei}\left(\sum_j W_{EE,ij}\nu_{Ej} - W_{EI,ij}\nu_{Ij}\right) - \nu_{Ei}$$

$$\tau \frac{d\nu_{Ii}}{dt} = \phi_{Ii}\left(\sum_j W_{IE,ij}\nu_{Ej} - W_{II,ij}\nu_{Ij}\right) - \nu_{Ij}$$

- looks like we took the average inside the gain function
- we'll make this more rigorous later.

Equilibria: $\frac{dV_E}{dt} = \frac{dV_I}{dt} = 0$

E-nullcline

I-nullcline

Consider

$\frac{dV_E}{dt} = \phi_E(V_E, V_I) - V_E$ at fixed V_I

$\frac{dV_I}{dt} = \phi_I(V_E, V_I)$ at fixed V_E

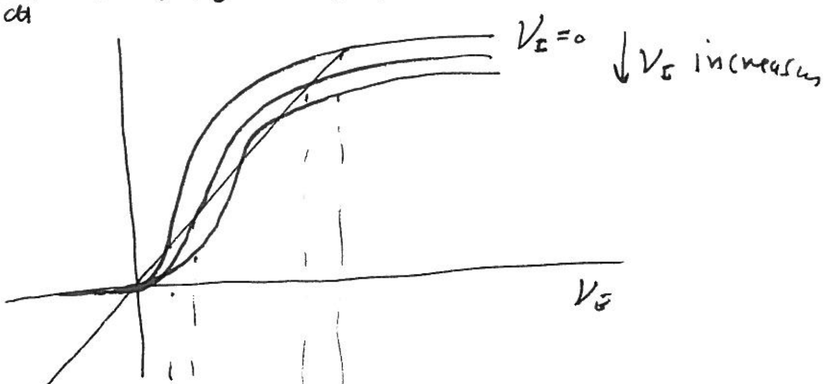
Do linear analysis!

Standard picture: all cells sit ~ K mV below threshold

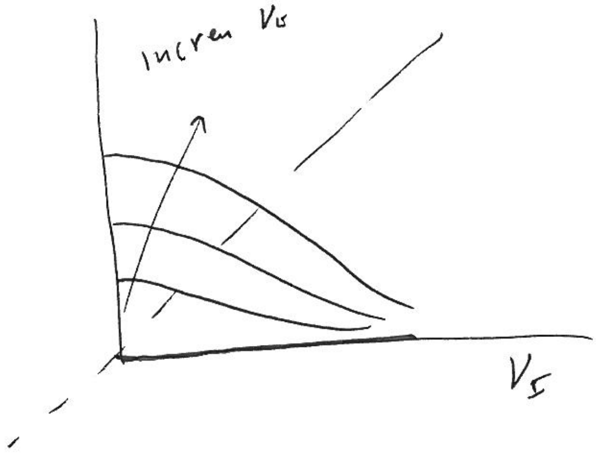
- no spontaneous activity.

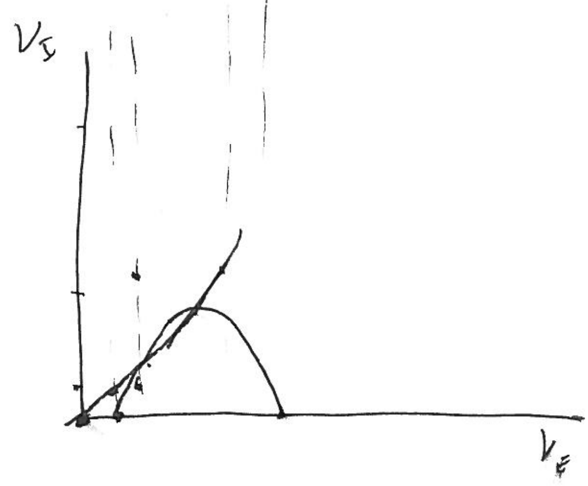
Intuitive picture first

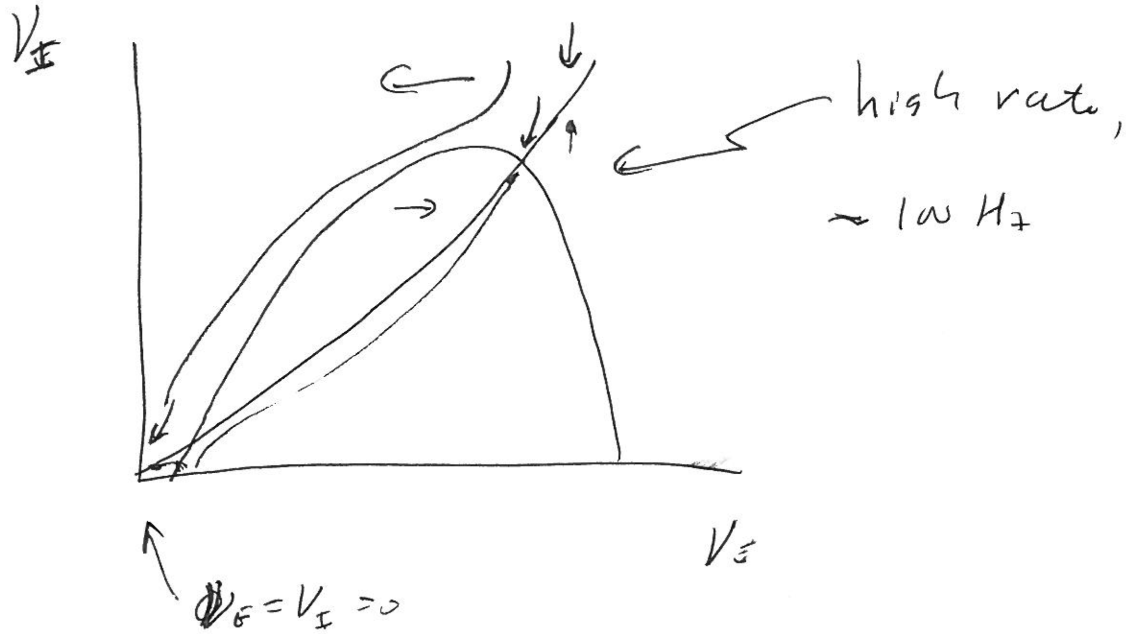
$\frac{dV_E}{dt} = 0 \Rightarrow V_E = \phi_E(W_{EE}V_E - W_{EI}V_I)$



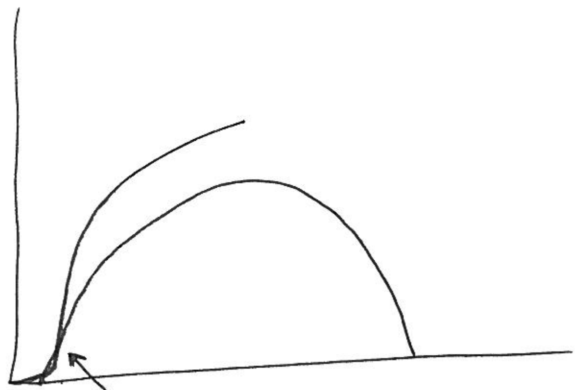
$\frac{dV_I}{dt} = 0 \Rightarrow V_I = \phi_I(W_{IE}V_E - W_{II}V_I)$







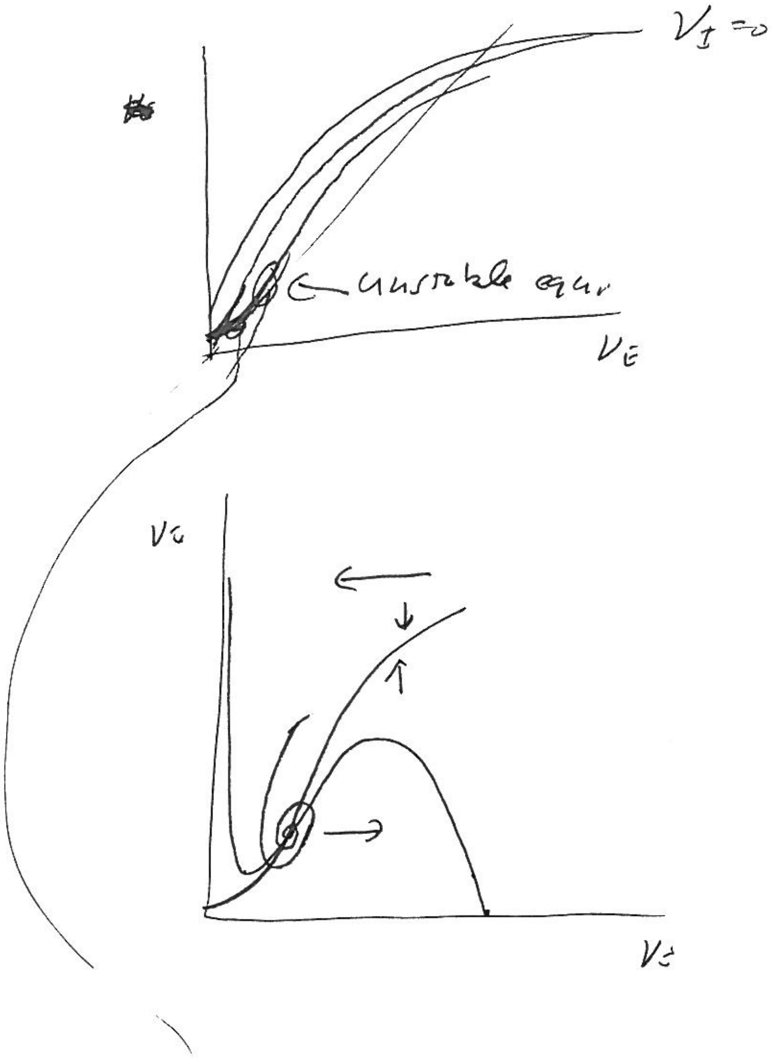
not consistent w/ experiments!



fix, but not very robust
to small perturbations

- sort of a mystery for a long time!

Solution: Endogenous activity



- Dynamically stabilized !!!
- Robust
- Almost for sure where the brain operates, but no direct evidence.

Linear analysis

$$T\dot{V}_E = \phi_E(V_E, V_I) - V_E$$

$$T\dot{V}_I = \phi_I(V_E, V_I) - V_I$$

$$V_E = V_{E0} + \partial V_E \qquad \phi_E(V_{E0}, V_{I0}) = V_{E0}$$

$$V_I = V_{I0} + \partial V_I \qquad \phi_I(V_{E0}, V_{I0}) = V_{I0}$$

$$T\partial\dot{V}_E = \phi_E(V_{E0}, V_{I0}) - V_{E0} + \phi_{E,E}\,\partial V_E + \phi_{E,I}\,\partial V_I - \partial V_E$$

$$T\partial\dot{V}_I = \phi_I(V_{E0}, V_{I0}) - V_{I0} + \phi_{I,E}\,\partial V_E + \phi_{I,I}\,\partial V_I - \partial V_I$$

$$T\frac{d}{dt}\begin{pmatrix}\partial V_E \\ \partial V_I\end{pmatrix} = \begin{bmatrix}\phi_{E,E}-1 & -|\phi_{E,I}| \\ \phi_{I,E} & -|\phi_{I,I}|-1\end{bmatrix}\begin{array}{c}\partial V_E \\ \partial V_I\end{array}$$

$$\cancel{\lambda = \phi_{EE} - |\phi_{I,E}| - 2 \pm \sqrt{\quad}}$$

$$\lambda = \frac{T \pm \sqrt{T^2 - 4D}}{2}$$

$\lambda < 0$: $\quad T < 0 \quad D > 0$

typically, large (high connection): 5000 conn, $r \uparrow 1\,\mathrm{Hz}$, $\Rightarrow$ 5000 more spks/s.
$\Rightarrow$ need I - I connections !!

$$T = \phi_{E,E} - |\phi_{I,I}| - 2$$

$$\cancel{D = \left(\phi_{E,E} - |\phi_{I,I}| - 2\right)^2 + \phi_{E,I}\,|\phi_{I,E}| > 0}$$

$$D = -\left(\phi_{E,E} - 1\right)\left(|\phi_{I,I}| + 1\right) + \phi_{E,I}\,|\phi_{I,E}|$$

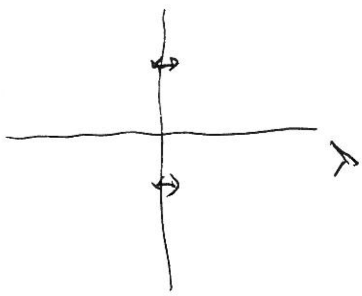
$|\phi_{I,I}|$ big

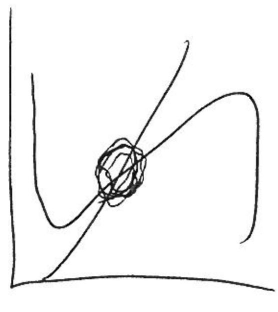
$\phi_{E,I}\,|\phi_{I,E}|$ big

$D > 0 \Leftrightarrow$

Typical mode of instability   Hopf $\Rightarrow$ oscillation

In general, oscillation ubiquitous





WC is totally ad-hoc!!!

A different approach — underlies modern Theory of neural networks.

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

$$\langle \delta W_{ij} \rangle = 0$$

$$W_{ij} = \frac{1}{N} W + \frac{1}{\sqrt{N}} \delta W_{ij}$$

$$\langle \delta W_{ij}\, \delta W_{ik} \rangle = \langle \delta W_{ji}\, \delta W_{ki} \rangle = \delta_{jk}\, \sigma_w^2$$

random matrix!!

$$\sum_j W_{ij} V_j = \sum_j \left(\frac{1}{N} W + \frac{1}{\sqrt{N}} \delta W_{ij}\right) V_j$$

$$= W \bar{V} + \frac{1}{\sqrt{N}} \sum_j \delta W_{ij} V_j$$

$$\boxed{V_i = \phi\left(W \bar{V} + \frac{1}{\sqrt{N}} \sum_j \delta W_{ij} V_j\right)}$$

$\boxed{\text{Major assumption}}$

$$\sum_j dW_{ij} \nu_j = \text{G.R.V.}$$

$$\langle \quad \rangle = \frac{1}{N} \sum_{ij} dW_{ij} \nu_j = 0$$

$$\langle (\ )^2 \rangle = \frac{1}{N} \sum_i \left(\sum_j dW_{ij} \nu_j \right)$$

$$= \frac{1}{N} \sum_i \sum_{jj'} dW_{ij} dW_{ij'} \nu_j \nu_{j'}$$

$$= \frac{N}{N} \sum_{jj'} \nu_j \nu_{j'} \left[\frac{1}{N} \sum_i dW_{ij} dW_{ij'} \right]$$

$$= \sum_{jj'} \nu_j \nu_{j'} \delta_{jj'} \cancel{\quad} \sigma_w^2$$

$$= \cancel{\quad} \sum_j \nu_j^2 \, \sigma_w^2$$

$$\left\langle \frac{1}{\sqrt{N}} \sum_j dW_{ij} \right\rangle = \frac{\sigma_w^2 \cancel{\quad}}{N} \sum_j \nu_j^2 = \overset{\sigma_w^2}{\cancel{\quad}} \langle \nu^2 \rangle \equiv \cancel{\quad} \sigma^2$$

Critical step:

$$\langle \nu \rangle = \frac{1}{N} \sum_i \phi\left(\bar{\nu} + \frac{1}{\sqrt{N}} \sum_j dw_{ij} \nu_j\right)$$

$$= \int d\xi \, \frac{e^{-\frac{1}{2}\xi^2}}{\sqrt{2\pi}} \, \phi\left(\bar{\nu} + \sigma_w \sqrt{\overline{\nu^2}}\, \xi\right)$$

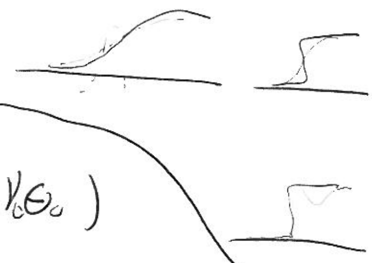
$$\langle \nu^2 \rangle = \frac{1}{N} \sum_i \phi^2\left(\bar{\nu} + \frac{1}{\sqrt{N}} \sum_j dw_{ij} \nu_j\right)$$

$$= \int d\phi \, \frac{e^{-\frac{1}{2}\xi^2}}{\sqrt{2\pi}} \, \phi^2\left(\bar{\nu} + \sigma_w \sqrt{\overline{\nu^2}}\, \xi\right)$$

Example

← Don't do this. Instead, point out that main effect is smooth

$\nu = \int Dg\, \phi(\nu + \Sigma(\nu) g)$



$$\phi(\nu) = \nu_0\, \Theta(\nu - \nu_0\theta_0)$$

$$\langle\nu\rangle = \nu_0 \int_{-\infty}^{\infty} dg\, \frac{e^{-g^2/2}}{\sqrt{2\pi}}\, \Theta\left(\bar{\nu} + \sigma_w\sqrt{\overline{\nu^2}}\, g - \nu_0\theta_0\right)$$

$$\langle\nu^2\rangle = \nu_0^2 \quad ''$$

$$= \nu_0\langle\nu\rangle$$

$$\frac{\langle\nu\rangle}{\nu_0} \equiv x \qquad \langle\nu^2\rangle = \nu_0\langle\nu\rangle = \nu_0^2 x$$

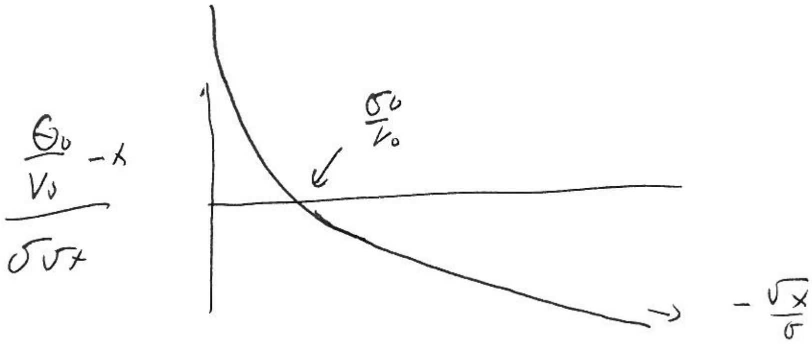
$$x = \int_{-\infty}^{\infty} dg\, \frac{e^{-g^2/2}}{\sqrt{2\pi}}\, \Theta\left(\nu_0[x + \sqrt{x}\,\sigma_w g] - \nu_0\theta_0\right) = \Theta(x + \sqrt{x}\,\sigma_w g - \theta_0)$$

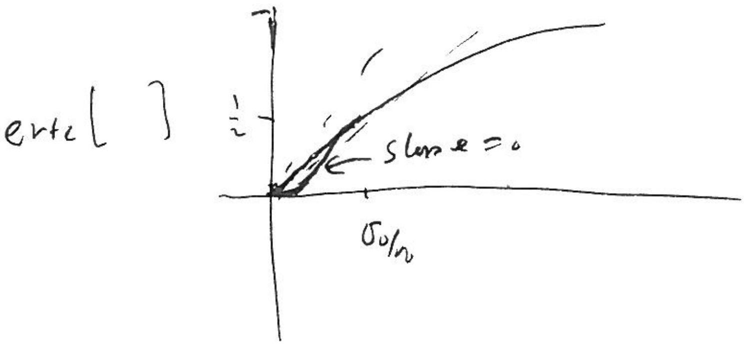
$$= \int_{\frac{\theta_0 - x}{\sigma\sqrt{x}}}^{\infty} dg\, \frac{e^{-g^2/2}}{\sqrt{2\pi}} \propto \operatorname{erfc}\left[\frac{\theta_0 - x}{\sigma_w\sqrt{x}}\right]$$

↑

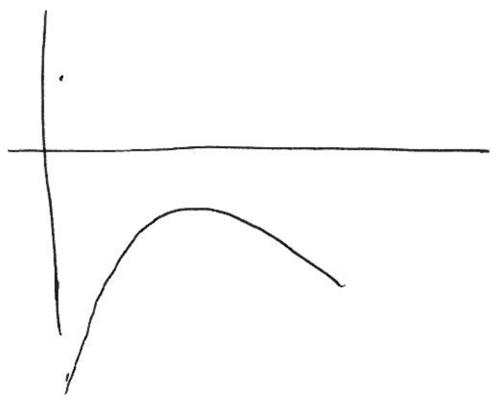
erfc

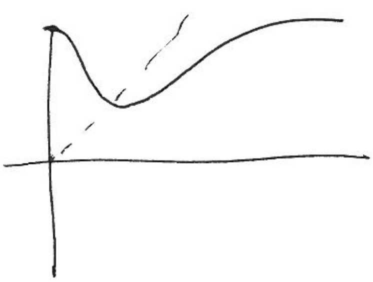
$\Theta_0 > 0$





$\Theta_0 < 0$





3 intersecion ?

$$\nu_{Ei} = \phi_E\left(\sum_j W^{EE}_{ij}\,\nu_{Ej} - W^{EI}_{ij}\,\nu_{Ij}\right)$$

$$\nu_{Ii} = \phi_I\left(\sum_j W^{IE}_{ij}\,\nu_{Ej} - W^{II}_{ij}\,\nu_{Ij}\right)$$

$$W_{ij} = \frac{W}{\sqrt{N}} + \frac{\delta W_{ij}}{\sqrt{N}}$$

$$\Rightarrow \sum_j W_{ij}\,\nu_j = \sqrt{N}\,W\,\bar{\nu} + \sigma_W \sqrt{\overline{\nu^2}}\;\xi_i$$

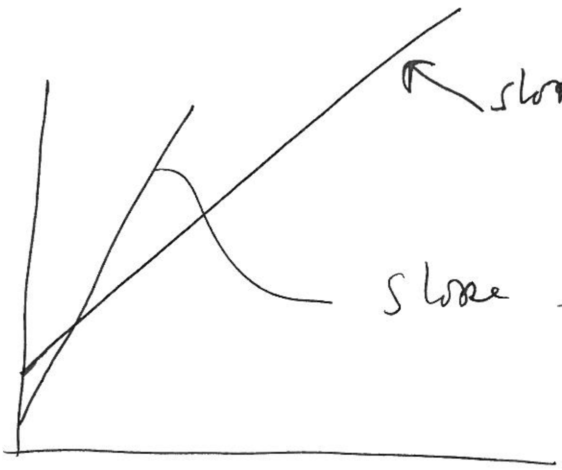
$$\nu_{Ei} = \phi_E\left(\sqrt{N}\left(W^{EE}\bar{\nu}_E - W^{EI}\bar{\nu}_I\right) + \sigma_W^{EE}\sqrt{\overline{\nu_E^2}}\;\xi_i^{EE} + \sigma_W^{EI}\sqrt{\overline{\nu_I^2}}\;\xi_i^{EI}\right)$$

$$\nu_{Ii} = \phi_I\left(\sqrt{N}\left(W^{IE}\bar{\nu}_E - W^{II}\bar{\nu}_I\right) + \quad \cdots \quad\right)$$

$$\phi(\nu) = \phi(\nu + \sqrt{N}\,\theta_E)$$

$$\Rightarrow \quad W^{EE}\bar{\nu}_E - W^{EI}\bar{\nu}_I + \theta_E \cong 0$$

$$W^{IE}\bar{\nu}_E - W^{II}\bar{\nu}_I + \theta_I \cong 0$$



slope $\frac{w^{EE}}{w^{EI}}$ (exc.)

slope $\frac{w^{IE}}{w^{II}}$ (inh)

$$\frac{w^{IE}}{w^{II}} > \frac{w^{EE}}{w^{EI}} \Rightarrow w^{EI} w^{IE} > w^{EE} w^{II}$$

(extreme version of previous analysis)

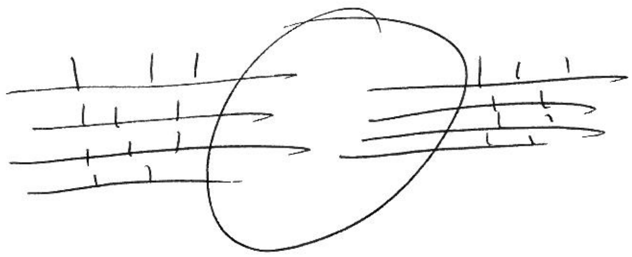
Van Vreeswijk + Sompolinsky

Science '96

Neural Comp. '98

— Key papers

Summary

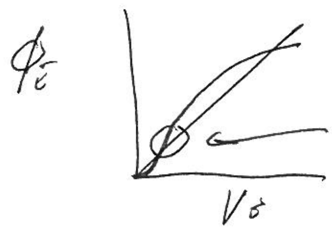


Want to solve this problem

- considered very simpler models

$$\dot{V}_i = \phi_i \Big(\sum_j W_{ij} V_j \Big) - V_i$$

- considered randomly connected network
- background is within



operating point

Dynamically stabilized