Introduction to Network models, continued

Comparing biological recurrent networks and the simplfied model version where neurons can be both excitatory and inhibitory to their targets.

(Reference reading for this lecture: Zhaoping Li and Peter Dayan (1999) Computational differences between asymmetrical and symmetrical networks Published in *Network: Computation in Neural Systems* 10 (1) 59-77, 1999. Available at `http://www.gatsby.ucl.ac.uk/~zhaoping/dynamics.html`)

Are interneurons simply biological hardware constraints?

If we ignore oscillations, can we model cortical networks by a simplified version: delete the interneurons, each principal neuron can arbitrarily excite or inhibit another neuron?

The simplified network model:

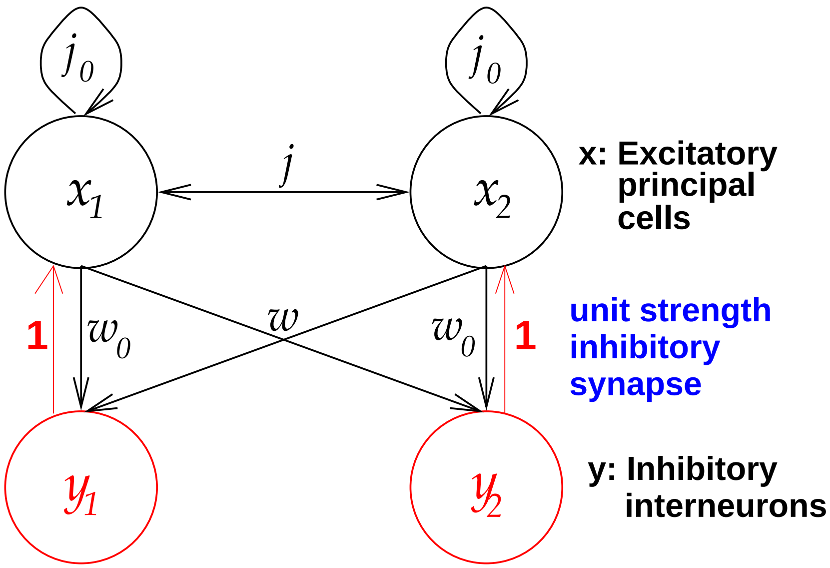
$\dot{x}_i = -x_i + \sum_j T_{ij} g(x_j) + I_i$

T_{ij} connection strength that can be positive or negative.

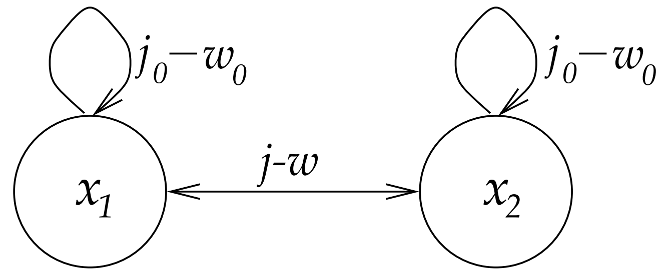
Example: Hopfield network, when $T_{ij} = T_{ji}$. This kind of symmetry may be quite suitable for visual cortical networks where there is reflection symmetry in connections.

Relating and differentiating E-I and S networks:

Asymmetric system: E-I



Symmetric system : S



Focusing on symmetric J and W

$$
\begin{aligned}
\dot{x} &= -x + Jg(x) - h(y) + I \\
\tau_y \dot{y} &= -y + Wg(x)
\end{aligned}
$$

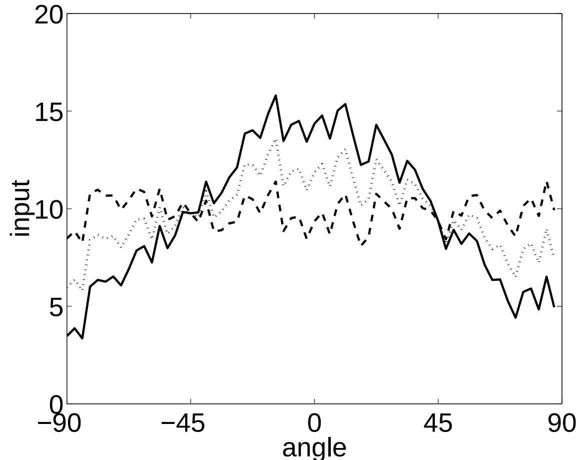
$$\dot{x} = -x + (J - W)g(x) + I$$

- when $h(y) = y$, EI and S have the same *fixed* points.
- when also $\tau_y = 0$, EI and S are *identical.*
- Many modellers use S systems to approximate the cortical networks.

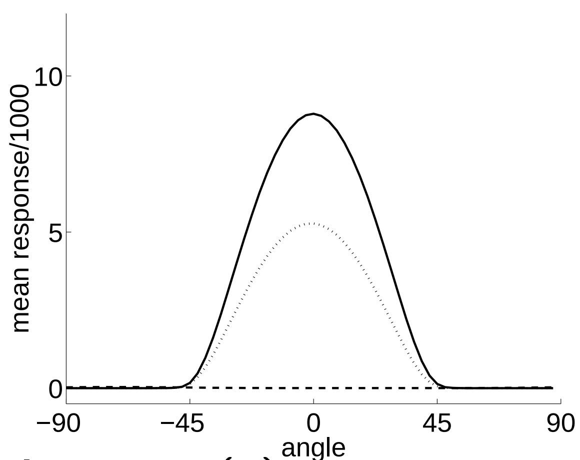
Consider the computation of Selective amplification to oriented visual inputs.

Consider an hypercolumn in the primary visual cortex, it contains many cells tuned to different orientations spanning 180^o. Each cell has an optimal orientation, and an orientation tuning width.

Orientation inputs may be noisy, output can clean it up, amplifying signals and ignoring noises.



Input I



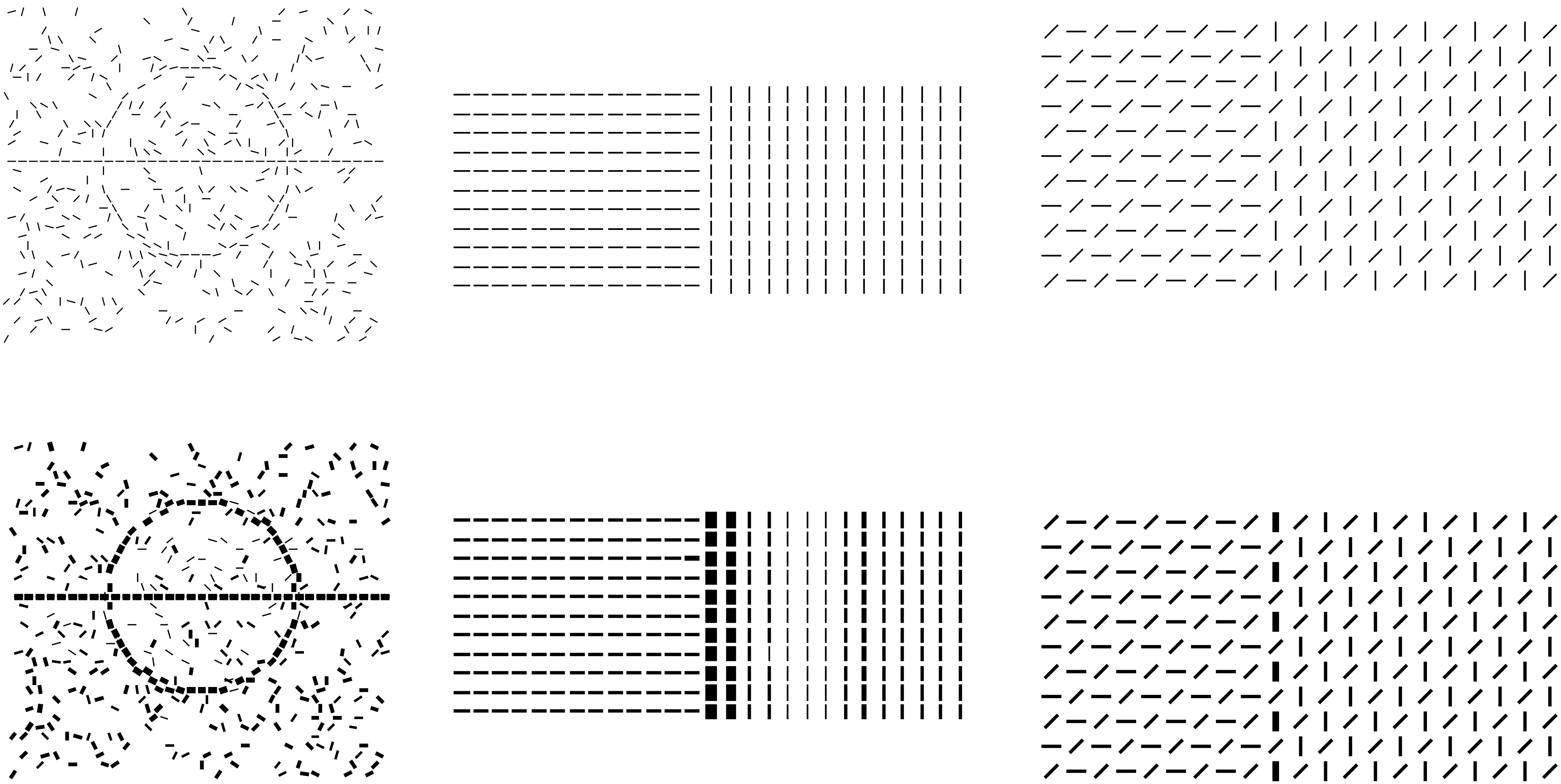
Output $g(x)$

A recurrent network of interacting orientation tuned neurons, may be used to achieve this. Would S-network work?

Consider An Important Visual Task —

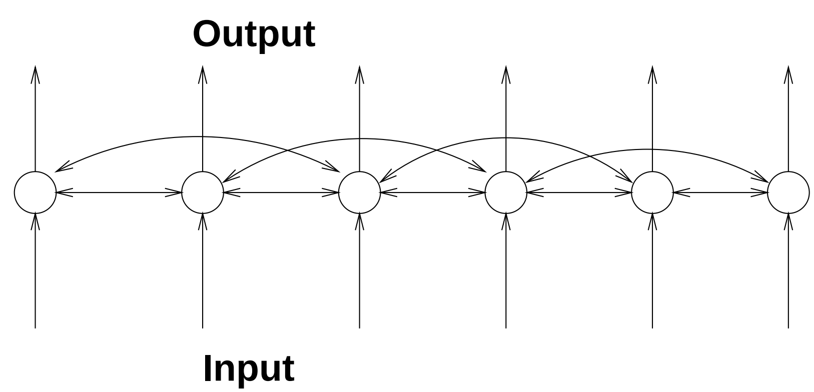
to Build a Saliency Map

selectively amplify some visual inputs



Both the orientation and saliency problem have the reflection symmetry in the system. If one uses a simplified S-system to model a recurrent network. It is like a Hopfield net:

$\dot{x}_i = -x_i + \sum_j T_{ij} g(x_j) + I_i$, where $T_{ij} = T_{ij} = J_{ij} - W_{ij}$.



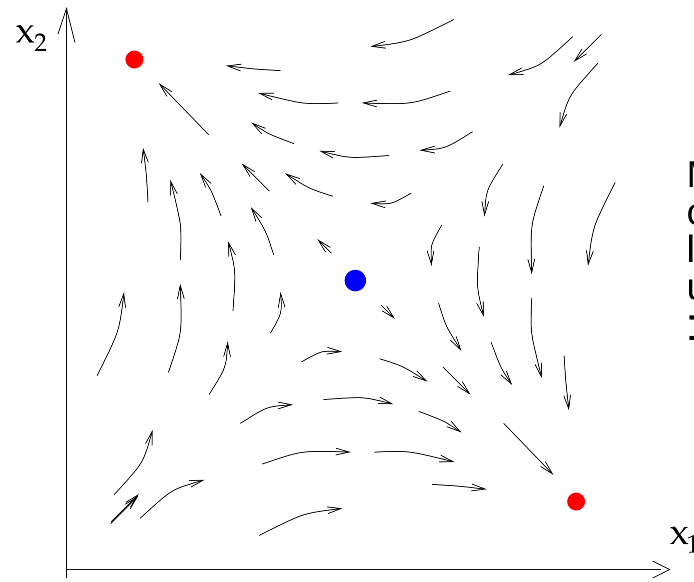
A Hopfield net is such that the dynamics always converge to fixed points, which is a local minimum of an energy function:

$$E(X) = -\frac{1}{2}\sum_{ij} T_{ij} g(x_i) g(x_j) - \sum_i I_i g(x_i) + \sum_i \int_{-\infty}^{g(x_i)} g^{-1}(s) ds$$

E is bounded and always decreases with time in dynamics (Prove this).

Input $I \rightarrow$ initial location X

Output: final location X



Motion flow or energy landscape under input **I ~ (1,1)**

Markov Random Fields is an example of such recurrent network interactions. Used to clean up noise in images, etc.

Can we used a Hopfield net like model to build an orientation system for selective amplification?

Consider x_i, I_i for an orientation θ_i, $i = 1, 2, ..., N$ (Ben-Yishai *et al:*)*

$$\dot{x}_i = -x_i + \sum_j (\mathbf{J}_{ij} - \mathbf{W}_{ij}) g(x_j) + I_i$$

$$\mathbf{J}_{ij} = \frac{1}{N}(A + B\cos(2(\theta_i - \theta_j))) \qquad \mathbf{W}_{ij} = \frac{C}{N} \qquad I_i = a + b\cos(2\theta_i)$$

$$\Rightarrow \quad \bar{x}_i = \lambda + \mu\cos(2\theta_i) \qquad g(\bar{x}_i) = \mu\,[\cos(2\theta_i) - \cos(2\theta_c)]_+$$

Findings:

Strong amplification to signals always have the consequence of hallucinating oriented inputs even under noise inputs — termed marginal states by Ben-Yishai *et al:*. To avoid hallucination means a relative gain of a factor only 2-3 to input signal and input noise.

*Ben-Yishai, R, Bar-Or, RL & Sompolinsky, H (1995). Theory of orientation tuning in visual cortex. *Proceedings of the National Academy of Science* **92**:3844-3848.

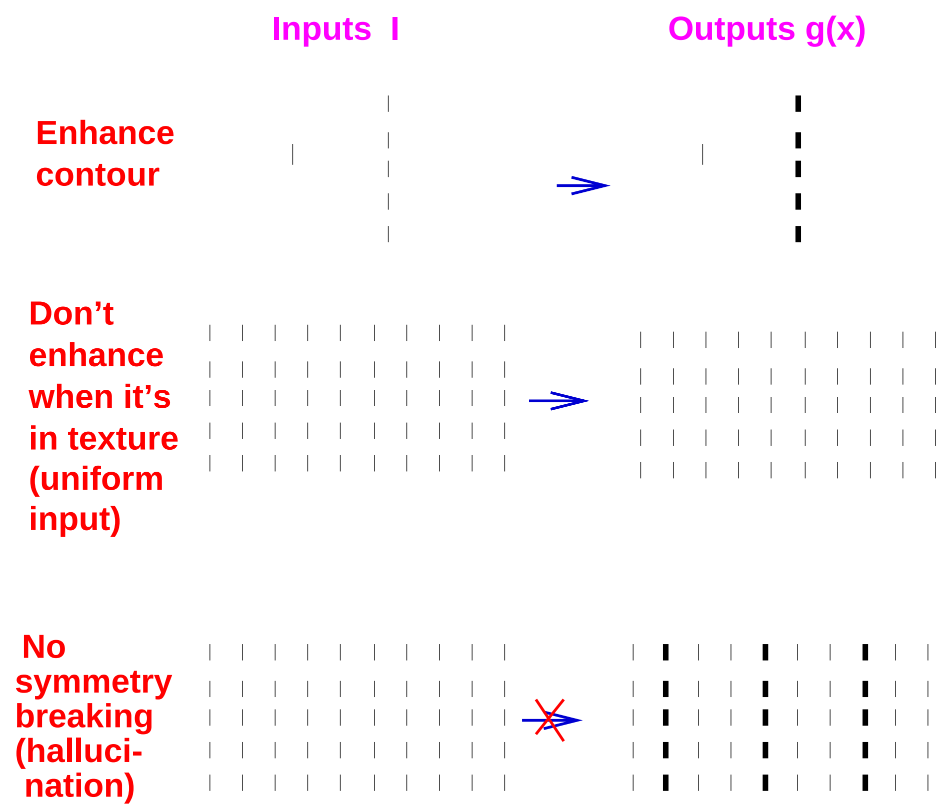
Can we use such a (simplified) recurrent network for our saliency computation?

Some $I^b \rightarrow$ strong outputs $g(x^b)$

Other $I^a \rightarrow$ weaker outputs $g(x^a)$

Example:

Visual input analysis.



Impossible to reach a satisfactory performance

— cf. Braun et al, and relaxation labeling techniques in computer vision

While S system can not carry out the selective amplification of orientation or Saliency computation, E-I System can. Why?

Same fixed pts $\bar{\mathbf{x}}$,

EI system

$$\begin{aligned}\dot{x} &= -x + Jg(x) - y + I\\ \dot{y} &= -y + Wg(x)\end{aligned}$$

S system

$$\dot{x} = -x + (J - W)g(x) + I$$

Different dynamics/stability around fixed pts

EI system

$$\begin{pmatrix}\dot{x}\\ \dot{y}\end{pmatrix} = \begin{pmatrix}-1 + JD_g, & -1\\ WD_g, & -1\end{pmatrix}\begin{pmatrix}x\\ y\end{pmatrix}$$

S system

$$\dot{x} = [-1 + (J - W)D_g]x$$

— after shifting origin of the coordinates: $x - \bar{x} \to x$, $y - \bar{y} \to y$,

$([D_g]_{ij} = \delta_{ij} g'(\bar{x}_i))$

Dynamics around fixed pts

EI system

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} -1 + JD_g, & -1 \\ WD_g, & -1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

S system

$$\dot{x} = [-1 + (J - W)D_g]x$$

Dynamic trajectory: $x(t) = \sum_k \mathbf{x}_k(0) e^{\gamma_k t}$,

If JD_g and WD_g commute with eigenvalues $\lambda_k^{\mathbf{J}}$ and $\lambda_k^{\mathbf{W}}$,

EI system

$$\gamma_k^{EI} = -1 + \frac{1}{2}\lambda_k^{\mathbf{J}} \pm (\frac{1}{4}(\lambda_k^{\mathbf{J}})^2 - \lambda_k^{\mathbf{W}})^{1/2}$$

S system

$$\gamma_k^{S} = -1 + \lambda_k^{\mathbf{J}} - \lambda_k^{\mathbf{W}}$$

$$\gamma_k^{EI} \neq \gamma_k^{S}.$$

Stability — EI is less stable than S at fixed points.

$$\gamma_k^{EI} = -1 + \tfrac{1}{2}\lambda_k^{\mathbf{J}} \pm (\tfrac{1}{4}(\lambda_k^{\mathbf{J}})^2 - \lambda_k^{\mathbf{W}})^{1/2} \qquad \gamma_k^{S} = -1 + \lambda_k^{\mathbf{J}} - \lambda_k^{\mathbf{W}}$$

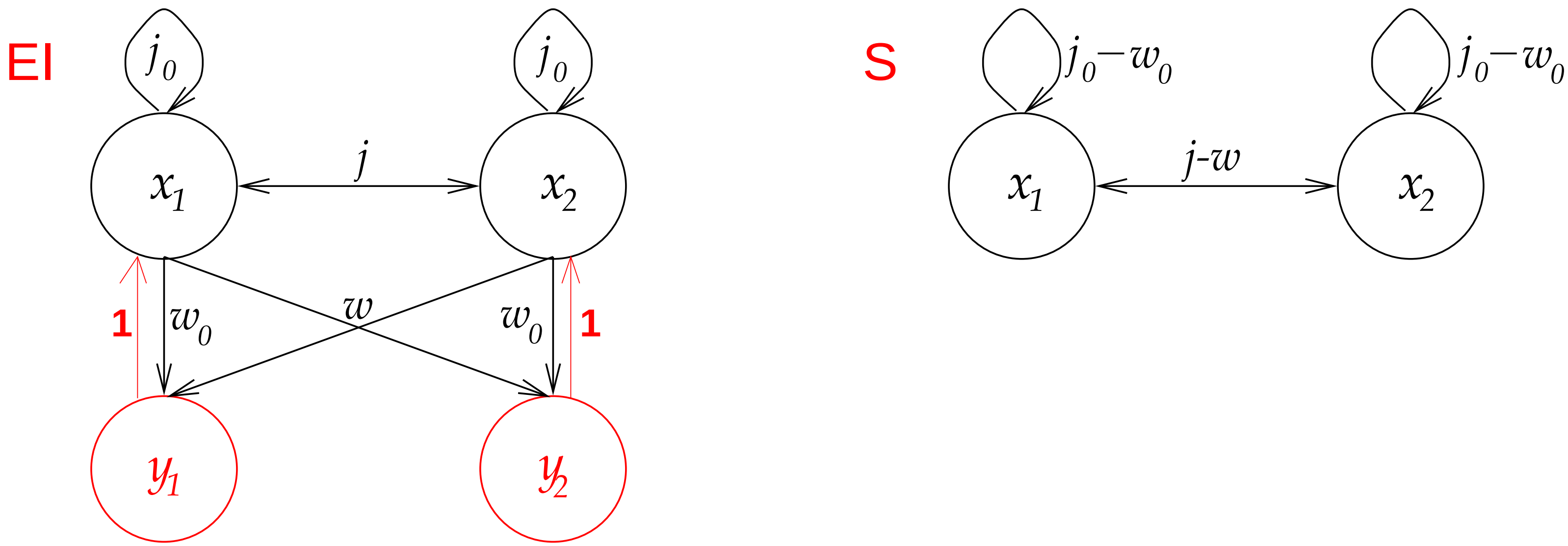
Proof for if $\lambda_k^{\mathbf{J}}$ and $\lambda_k^{\mathbf{W}}$ are *real*:

- if S mode is *unstable* $\gamma_k^S = -1 - \lambda_k^{\mathbf{W}} + \lambda_k^{\mathbf{J}} > 0$ so is the EI mode $\gamma_k^{EI} > 0$:
  $(\lambda_k^{\mathbf{J}})^2/4 - \lambda_k^{\mathbf{W}} > (\lambda_k^{\mathbf{J}})^2/4 - \lambda_k^{\mathbf{J}} + 1 = (\lambda_k^{\mathbf{J}}/2 - 1)^2$
- if the EI mode is *oscillatory* $4\lambda_k^{\mathbf{W}} > (\lambda_k^{\mathbf{J}})^2$, then S is stable even if EI isn't:

$$\gamma_k^S = -1 + \lambda_k^{\mathbf{J}} - \lambda_k^{\mathbf{W}} < -1 + \lambda_k^{\mathbf{J}} - (\lambda_k^{\mathbf{J}})^2/4 = -(1 - \lambda_k^{\mathbf{J}}/2)^2 \leq 0\ .$$

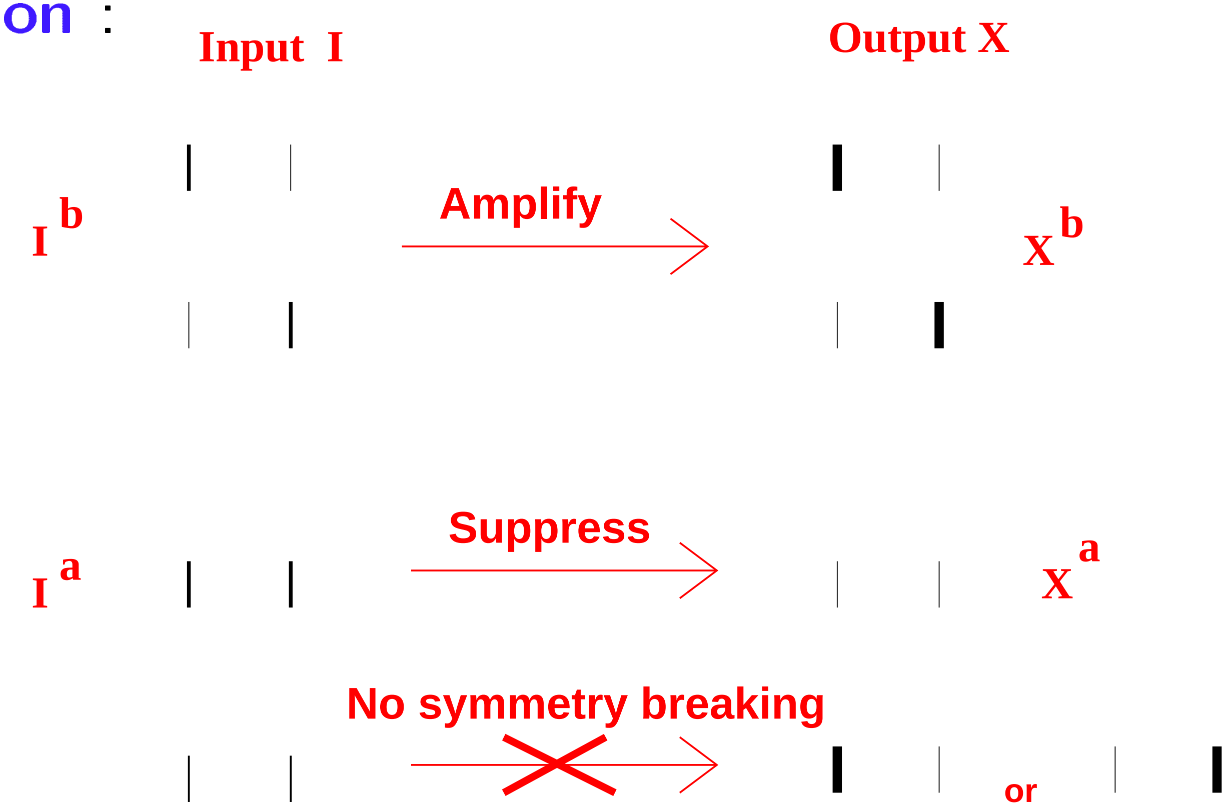
In general, singular perturbation analysis shows that sufficiently large τ_y will destabilise a stable S.

The Two Point System — a toy system

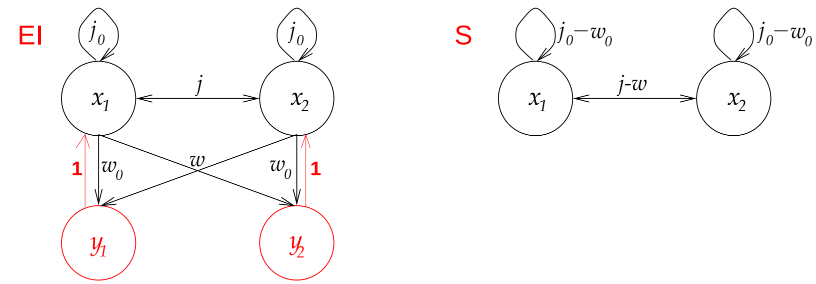


$$\mathbf{J} = \begin{pmatrix} j_0 & j \\ j & j_0 \end{pmatrix} \qquad \mathbf{W} = \begin{pmatrix} w_0 & w \\ w & w_0 \end{pmatrix}$$

The orientation or saliency problem simplified — selective amplification :



performance quantified by selectivity ratio $R = \frac{d\bar{x}_1^b/dI}{d\bar{x}_1^a/dI} = \frac{\text{gain}_b}{\text{gain}_a}$



For symmetric input $I^a = I(1,1)$,

$$\begin{pmatrix} j_0 & j \\ j & j_0 \end{pmatrix}, \begin{pmatrix} w_0 & w \\ w & w_0 \end{pmatrix} \rightarrow j_0 + j, w_0 + w$$

$$d\bar{x}_1^a/dI = \frac{1}{1+((w_o+w)-(j_o+j))}.$$

For asymmetric input $I^b = I(1,0)$,

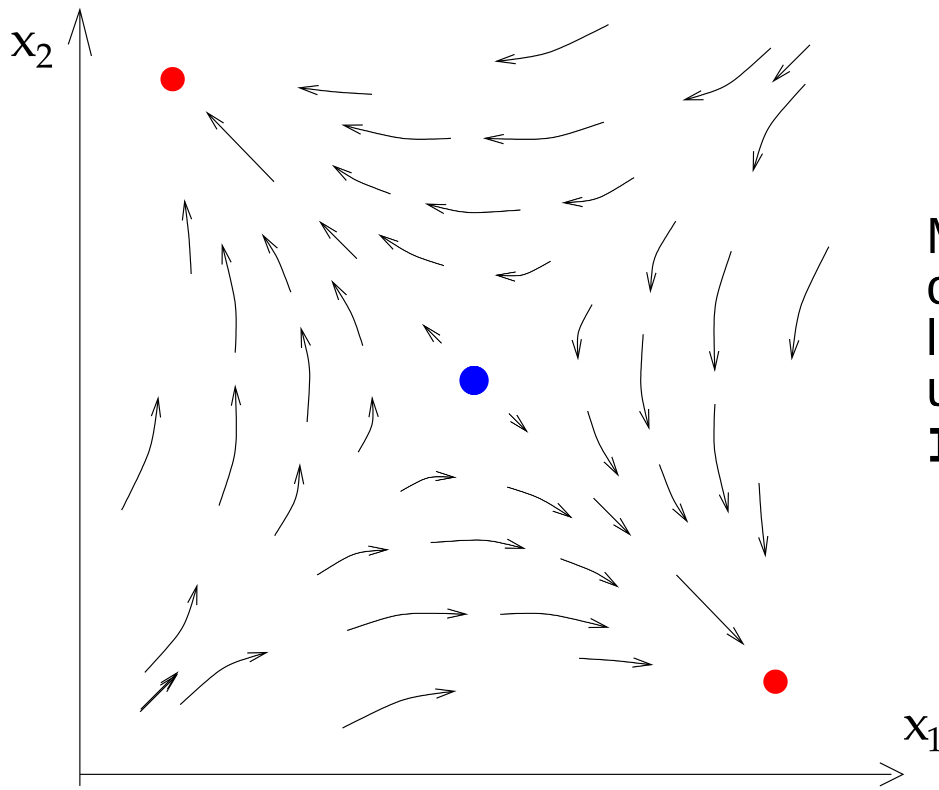
$$\begin{pmatrix} j_0 & j \\ j & j_0 \end{pmatrix}, \begin{pmatrix} w_0 & w \\ w & w_0 \end{pmatrix} \rightarrow j_0, w_0, \qquad d\bar{x}_1^b/dI = \frac{1}{1+(w_o-j_o)}.$$

selectivity ratio

$$R = \frac{d\bar{x}_1^b/dI}{d\bar{x}_1^a/dI} = \frac{1 + (w_o - j_o) + (w - j)}{1 + (w_o - j_o)}.$$

Large R requires large mutual inhibition $w - j$

$\mathbf{S}$ system



Motion flow or energy landscape under input **I ~ (1,1)**

Dynamics has an energy function, shaped by neural connections $\mathbf{J} - \mathbf{W}$ and input $\mathbf{I}$. Too much amplification for input $I_1^b \neq I_2^b$ leads to unstable fixed point $x_1^a = x_2^a$ under input $I^a = (1, 1)$:

spontaneous pattern formation in response to $x_1 \neq x_2$.

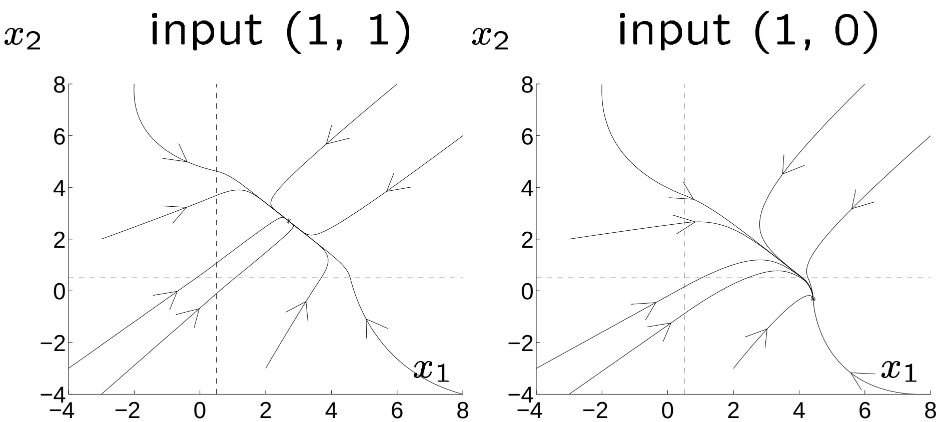
To avoid this, decrease mutual inhibition $w - j$. Analytically:

$$\text{Amplification ratio} \quad R^S = \frac{d\bar{x}_1^b/dI}{d\bar{x}_1^a/dI} < 2$$

S system — motion trajectory (energy landscape).

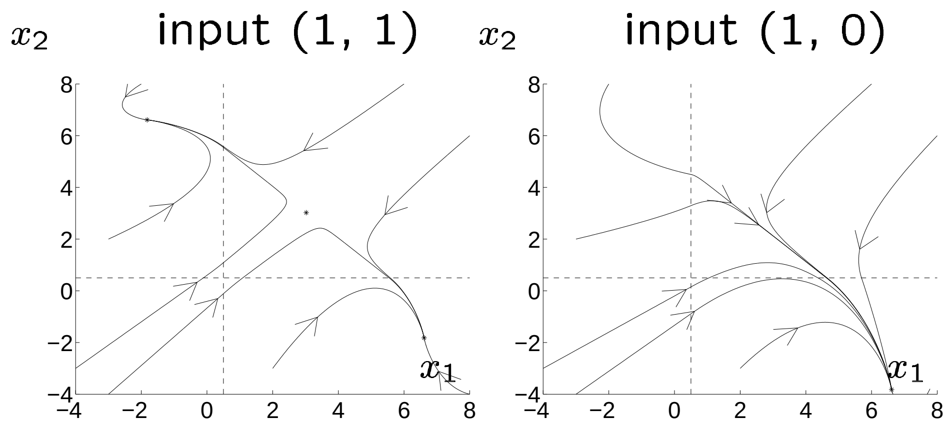
The symmetry preserving network

A particular setting of j, j_0, w, w_0



The symmetry breaking network

Another setting of j, j_0, w, w_0



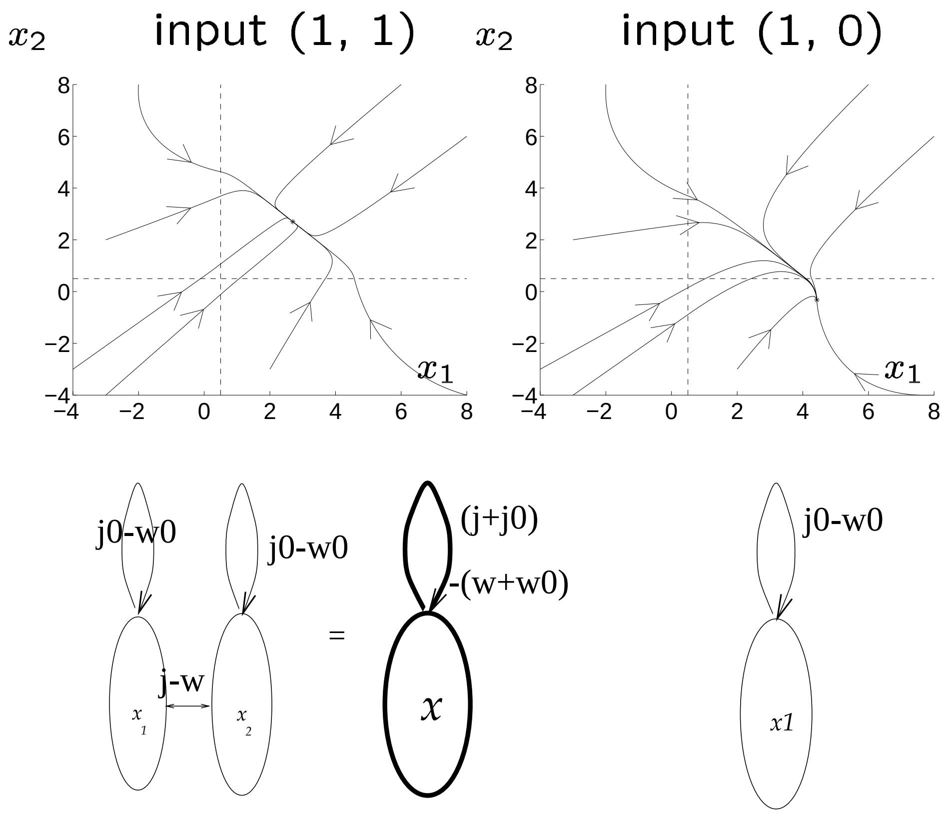
Small mutual inhibition $w - j$
One fixed pt given input
All fixed pts stable
No symmetry breaking
Small amplification R

large $w - j$
3 fixed pts under input (1,1)
Fixed pt $x_1 = x_2$ unstable
symmetry breaking
R meaningless

S system — intuition for the 2 point system

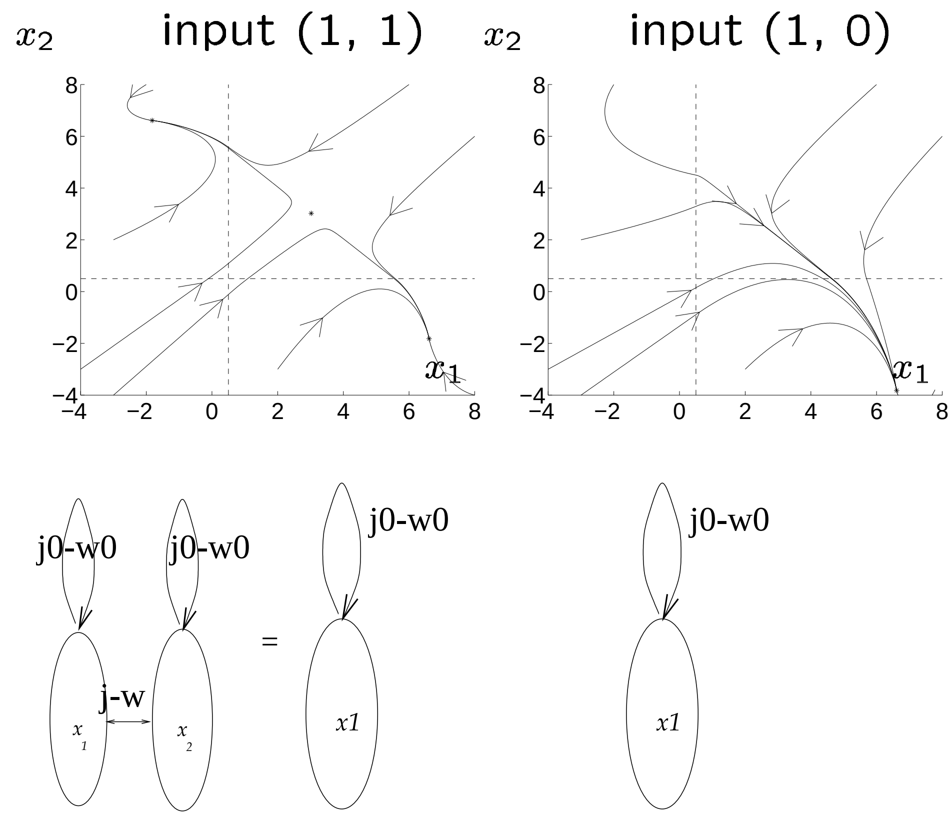
The symmetry preserving network

A particular setting of j, j_0, w, w_0

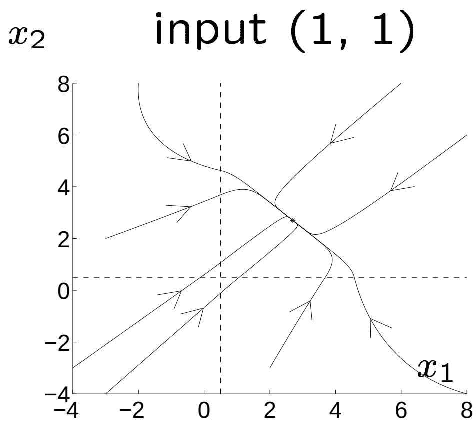


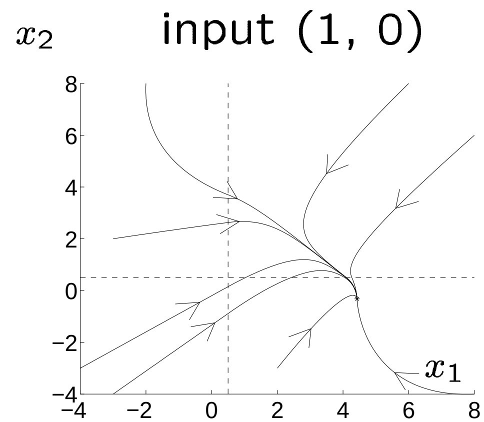
The symmetry breaking network

Another setting of j, j_0, w, w_0



In detail, to preserve symmetry:





To be stable :

$$\gamma^S_{\pm} = -(1 + (w_o \pm w) - (j_o \pm j)) < 0.$$

To be stable :

$$\gamma^S = -(1 + w_o - j_o) < 0$$

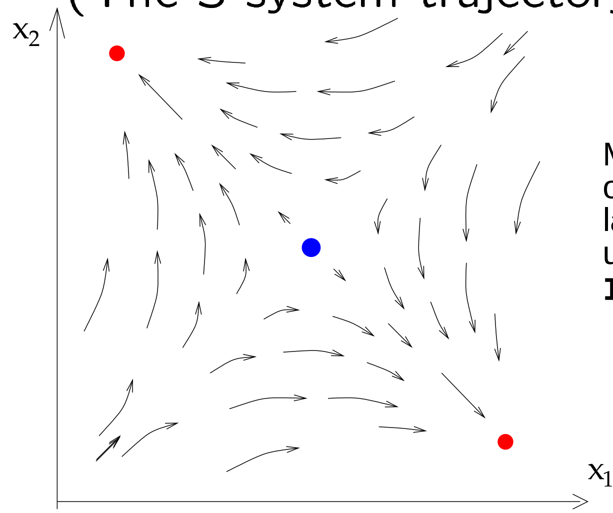
$\gamma^S_+ < 0$: against fluctuations in (1,1) direction,

$\gamma^S_- < 0$: against spontaneous symmetry breaking.

Stability in all situations leads to a limit in

$$\text{Amplification ratio} \quad R^S = \frac{d\bar{x}^b_1/dI}{d\bar{x}^a_1/dI} = \frac{1 + (w_o - j_o) + (w - j)}{1 + (w_o - j_o)} < 2$$

EI system



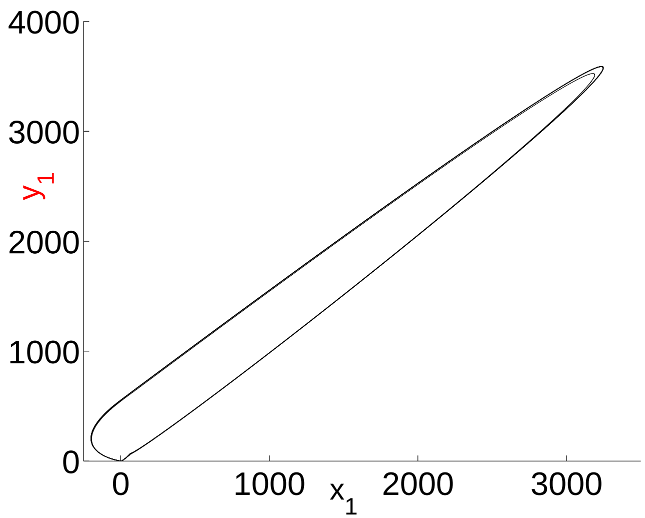
- In region when S breaks symmetry, there are 3 fixed points, $(x_1, x_2) \propto (1,0), (0,1), (1,1)$ under input $I = (1,1)$.

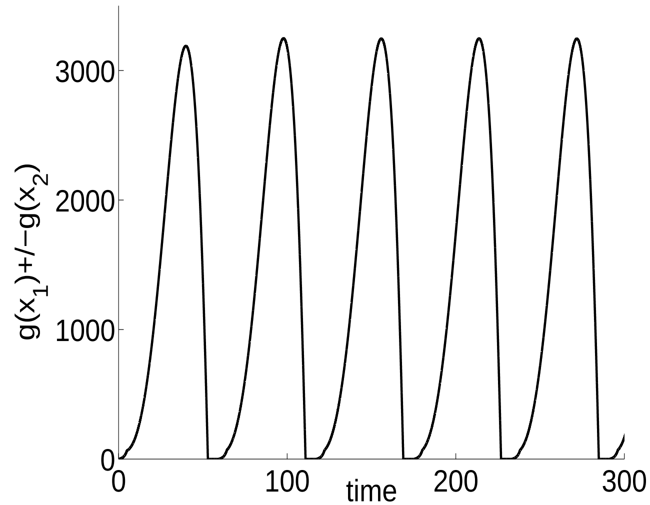
- While S system breaks symmetry from unstable $(1,1)$ to stable $\bar{x}_1 \neq \bar{x}_2$, EI can have all 3 fixed points unstable and oscillatory, motion trajectory can't approach $x_1 \neq x_2$, oscillates on trajectory $x_1 \approx x_2$ around fixed point $\bar{x}_1 = \bar{x}_2$ under input $(1,1)$ without breaking symmetry.

Then large stable selective amplification for $\mathbf{I}^b$: $R^{EI} = 97$ (example) or even larger.

Motion trajectory in EI system

Response to $\mathbf{I}^b = I(1,0)$

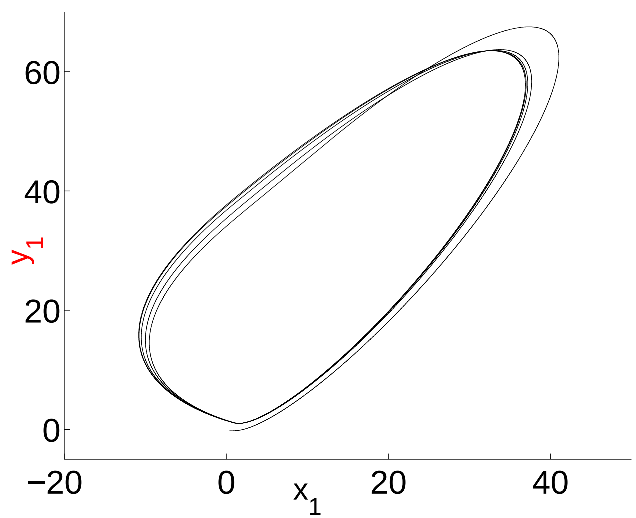


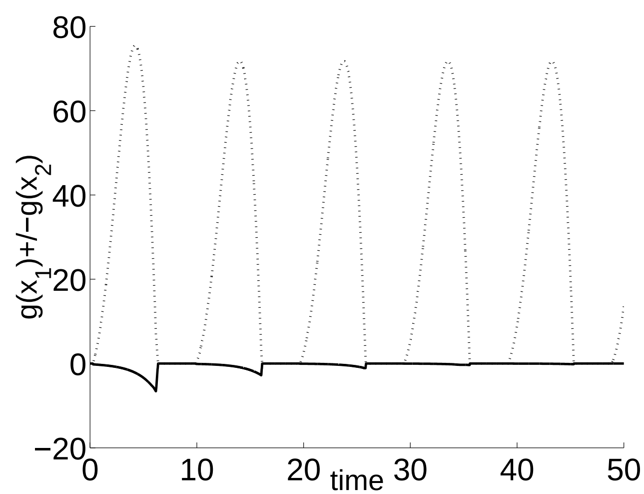


$g(x_1) - g(x_2)$ solid curve

$g(x_1) + g(x_2)$ dotted curve

Response to $\mathbf{I}^a = I(1,1)$



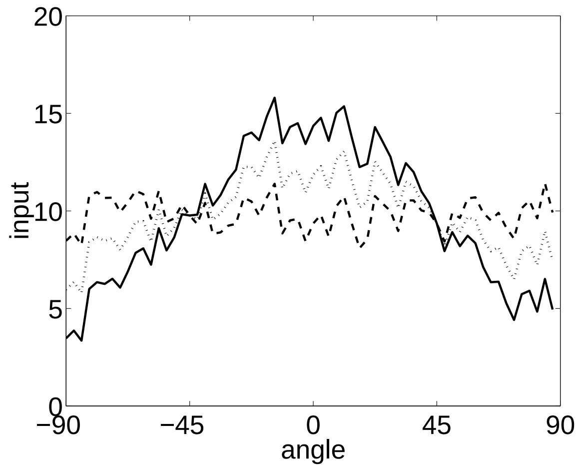


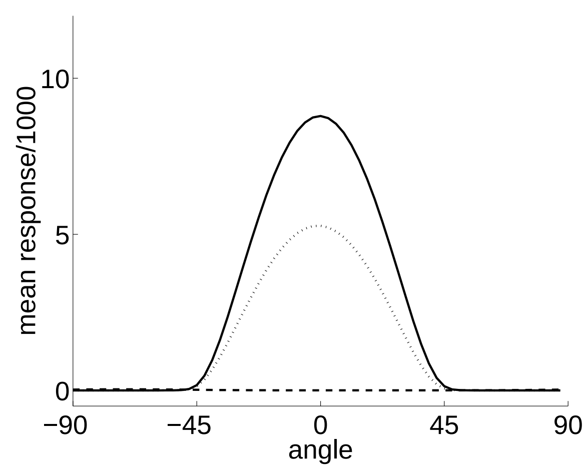
x_1 vs. y_1

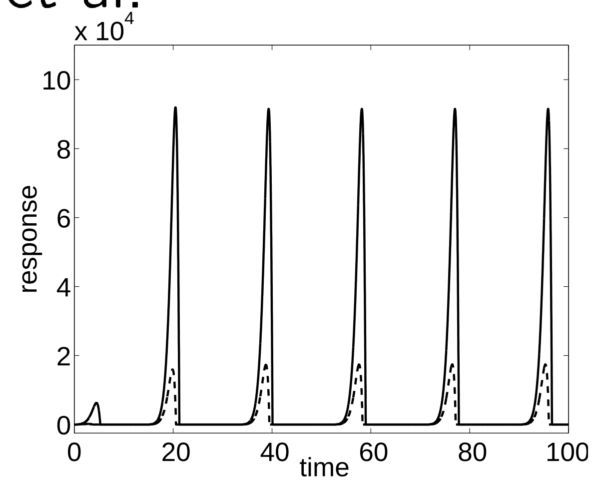
$g(x_1) \pm g(x_2)$ vs. time

$\color{red}{\text{EI}}$ Orientation System– choose $A = 6.5; B = 8.5; C = 14.5$:

An array of cells x_i, y_i for preferred orientation θ_i, and inputs I_i, with recurrent interactions like that of Ben-Yishai et al.







Input I Output $g(x)$ $g(x)$ vs. time.

Selective amplification ratio $\rightarrow$ 1000.

Analysis — rough equivalence between the orientation and two-point EI systems.

critical behavior is for the untuned or uniform mode – where non-linearities are irrelevant. Use Fourier analysis and define:

$$\lambda(f) = Re\{-1 + \tilde{J}(f)/2 + i\sqrt{\tilde{W}(f) - \tilde{J}^2(f)/4}\}$$

and f^* such that

$$\lambda(f^*) = \max_{f>0} \lambda(f)$$

Then an approximately equivalent two-point system is:

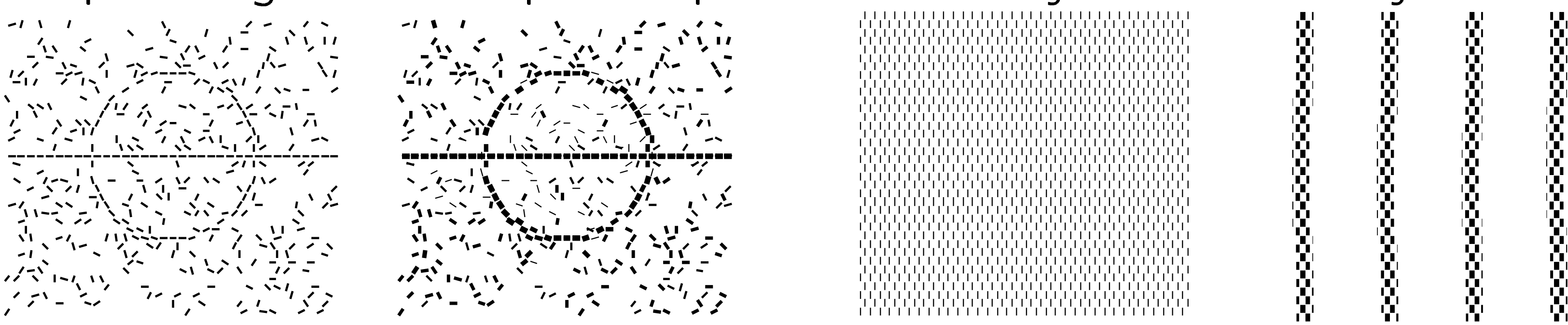
$$\begin{aligned} j_o + j &= \tilde{J}(0) & \qquad w_o + w &= \tilde{W}(0) \\ j_o - j &= \tilde{J}(f^*) & \qquad w_o - w &= \tilde{W}(f^*) \end{aligned}$$

although the amplification factor is quantitatively different

Contour-region system*

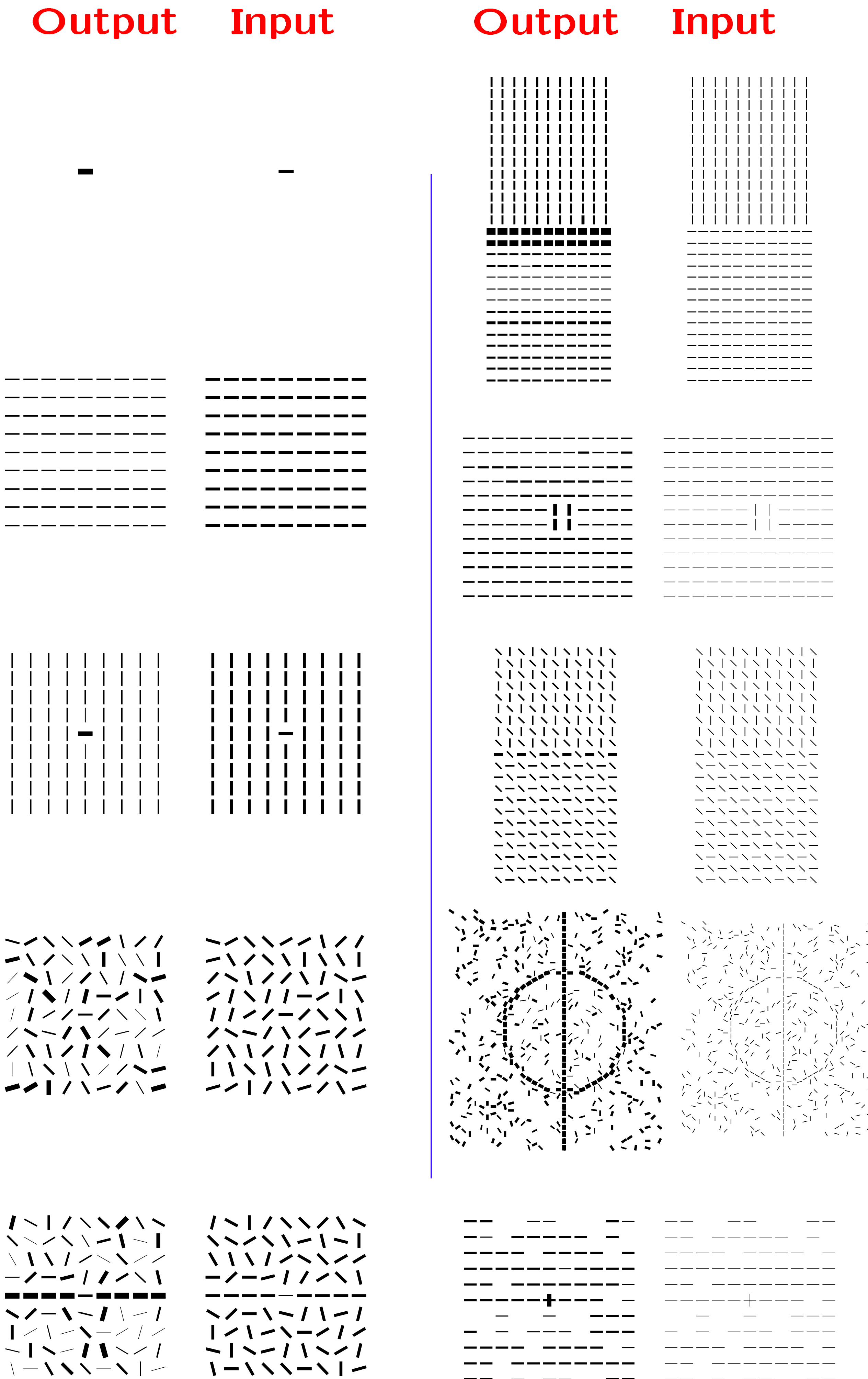
A: Contour enhancement — Input image, Output Response

B: Responses to homogeneous inputs — EI system, S system



- Want to enhance contours but suppress uniform (homogeneous) textures without symmetry breaking.
- S system hallucinates but EI does not, for high enough amplification to contour but suppression to texture regions.
- oscillations in EI responses to homogeneous and inhomogeneous inputs
- Analogy to the two-point system:
  Contour input — Input (1,0). Region input — Input (1,1).

*See Zhaoping Li (1999) Visual segmentation by contextual influences via intracortical interactions in primary visual cortex In *Network: Computation in Neural Systems* Volumn 10, Number 2, May 1999. Page 187-212, on my webpage



Model Performance consistent with biology

Summary

- Biological EI system reaches computations denied to conventional S systems.
- symmetric networks are condemned by their energy functions to fixed points, often with unstable positive feedback
- excitatory-inhibitory networks can take advantage of sub/super-threshold limit cycles to control global behavior
- neurobiologically significant cases.
- **Computation by non-conventional dynamics — biologically inspired.**