Contrast-dependent center-surround interactions & "normalizing" nonlinearities in visual cortex: A simple unified circuit model

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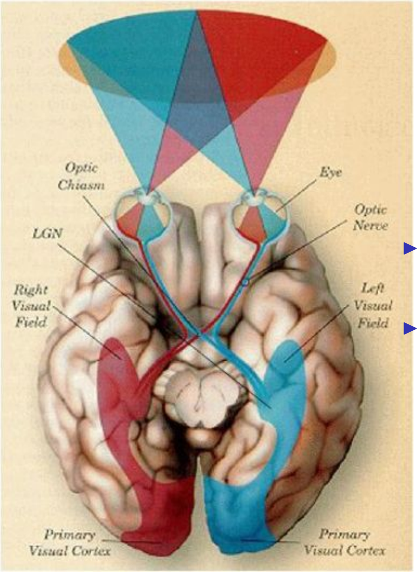
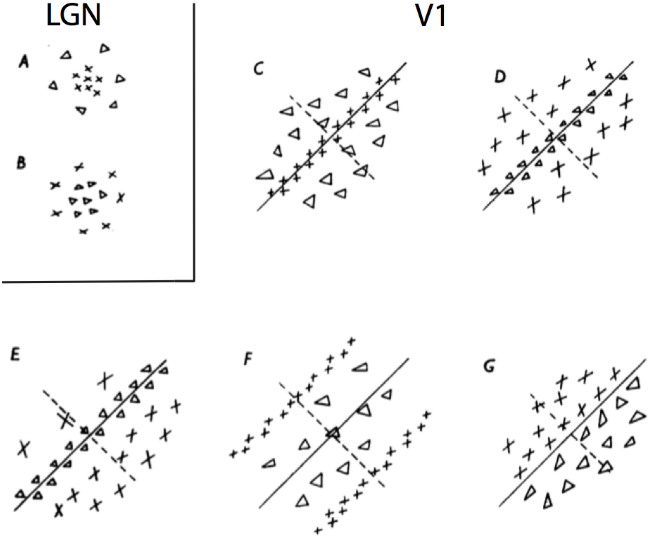
Primary visual cortex (V1)



- The first area of cortex to receive visual information (from LGN)
- Neurons respond selectively to oriented visual stimuli

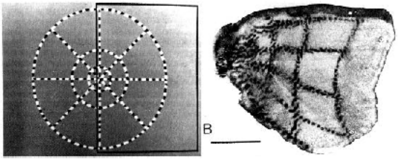
LGN and V1 Receptive Fields

LGN RFs are circularly symmetric; V1 RFs are orientation-tuned



Hubel and Wiesel, 1962

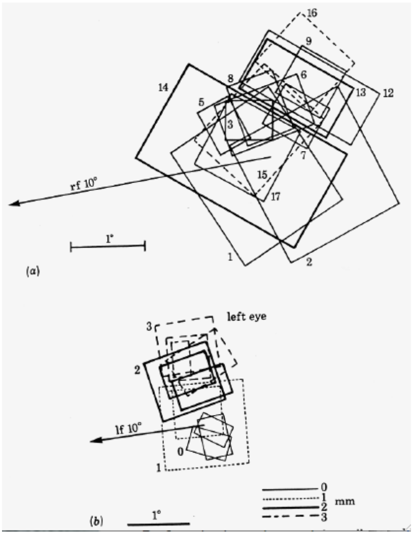
V1 has a retinotopic map



Tootell et al., 1988; scalebar= 1cm

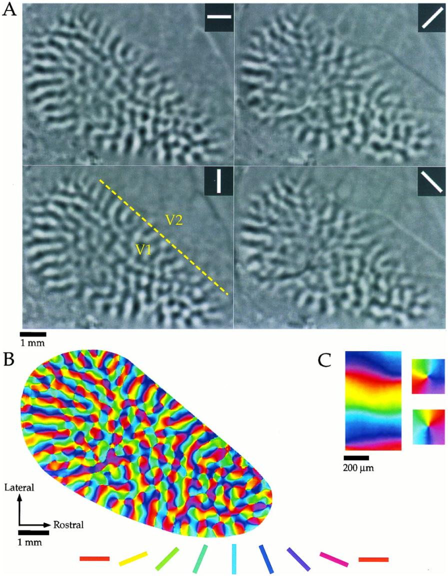
Right:

- TOP: RFs recorded in vertical penetration ($\perp$ to surface). Positions stay $\sim$constant.
- BOTTOM: RFs recorded in horizontal penetration ($\parallel$ to surface). 1mm movement $\Rightarrow$ RFs $\sim \frac{1}{2}$-overlapping.



Hubel and Wiesel, 1977

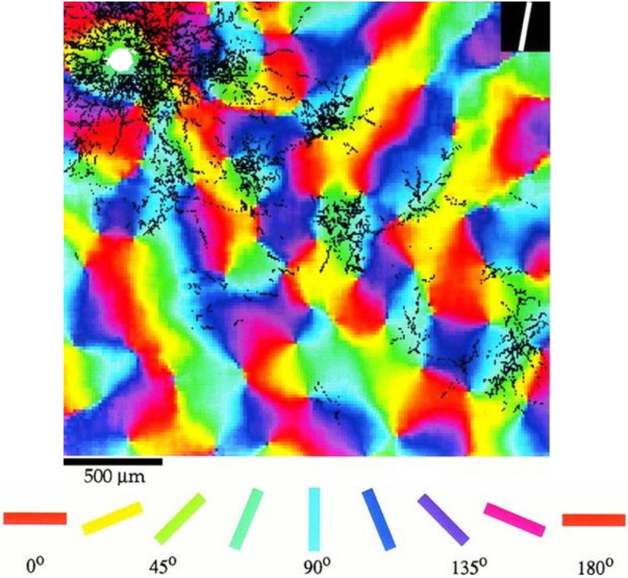
V1 has a map of orientation preference



Bosking et al 1997

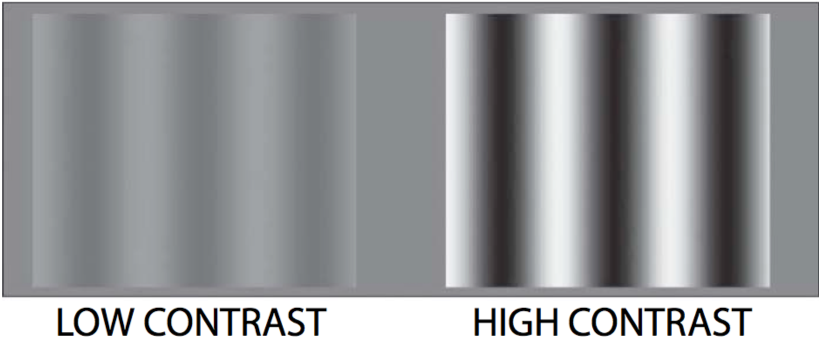
- Preferred orientation is $\sim$constant from top to bottom of cortex at a given point
- Preferred orientation varies periodically with movement across the V1 surface
- Period $\sim$1 mm: all orientations represented within a 1 mm^2 "functional unit"

Long-range V1 connections are orientation-tuned



Bosking et al 1997

Stimulus Contrast



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- Similarly on motor side: we experience high-level motor plans/intentions ("grasp my pen") invariant to, yet dependent on, detailed implementation.

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- How are objects knit together?
  - Long-range (contextual) interactions within one cortical area
  - Hierarchical feedforward/feedback between areas: larger invariant structures emerge gradually (small steps per area; *e.g.* V2, but not V1, responds to illusory contours)

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  - Context, attention appear to modulate **gain** of response

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- Largely ignore laminar structure; imagine we are modeling interactions within layers 2/3
- Only consider "excitatory" and "inhibitory" neurons, without further divisions into subtypes

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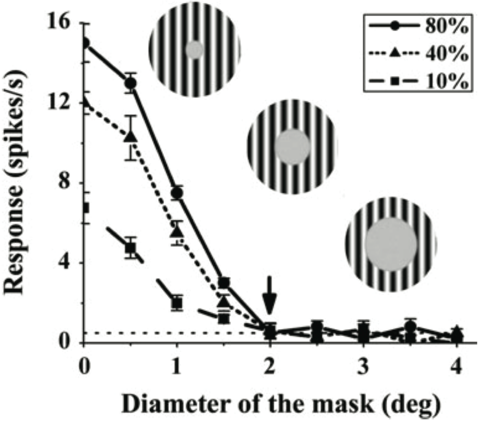
- Instead, all of this can arise from simple, generic network dynamics, in which the entire network – both E and I cells – undergo the suppression, or loss of amplification;
- An expansive input-output cellular nonlinearity (which can be identical for E and I cells) automatically leads to the two regimes: a low-contrast "facilitative" regime and a high contrast "suppressive" regime

Surround Suppression

Classical Receptive Field (CRF or "center"): region in which appropriate visual stimuli elicit spikes:
Extra-Classical Receptive Field (ECRF or "surround"): region surrounding CRF; visual stimuli do not elicit spikes:



Song & Li, 2008

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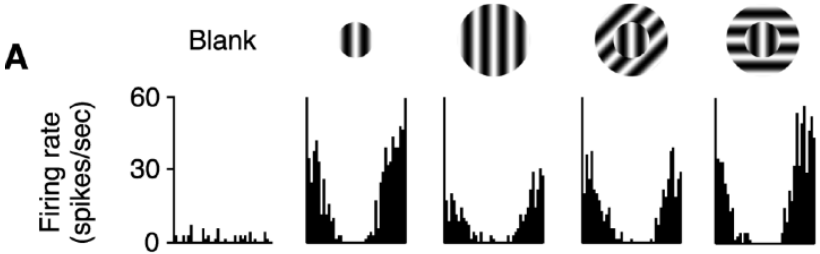

Ozeki, Finn, Schaffer, Miller and Ferster (2009)
Stimulus: 2 degree center, 20 degree surround, drifting grating

- Surround stimuli suppress responses to CRF stimuli
- Suppression is tuned for surround orientation, relative to center
- Found in $\sim 1/2$ of V1 cells in layers 2-4

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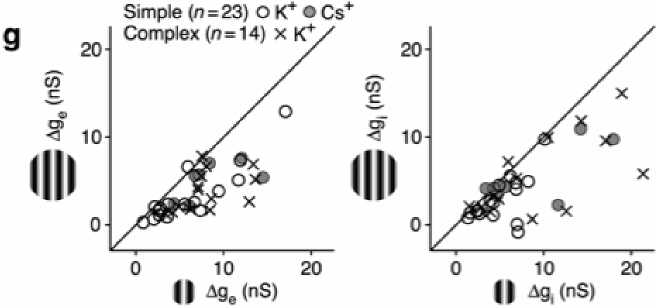
- This evokes excitatory, orientation-tuned input into local region via long-range connections
- To cause suppression, this input must preferentially drive inhibitory cells (so these inhibitory cells would *not* be surround suppressed)
- Expectation: cells should receive increased inhibition when they undergo suppression

During Suppression, Both the Inhibition and Excitation That Cells Receive *Decrease*



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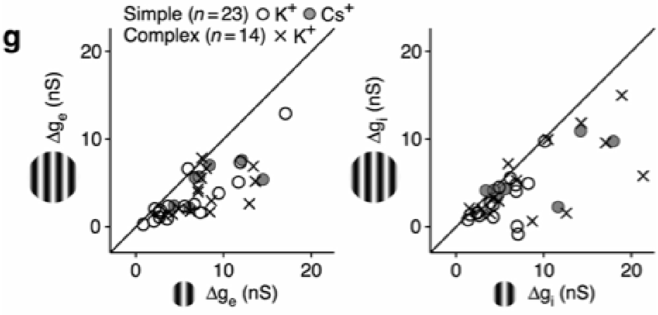

Ozeki, Finn, Schaffer, Miller and Ferster (2009)

- Interpretation: During suppression, both excitatory and inhibitory cells are suppressed (lower their firing rates)
- Has been confirmed directly (Song and Li, 2008)

Q: How Can Addition of External Excitation Onto Inhibitory Cells Cause Both Excitatory and Inhibitory Firing Rates to Decrease?

A: This will happen iff

- Excitatory recurrence alone is strong enough to be unstable
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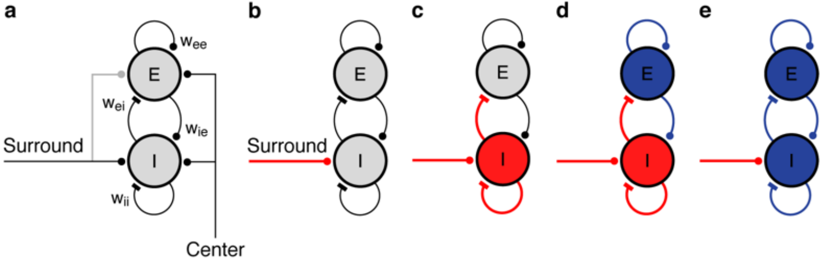

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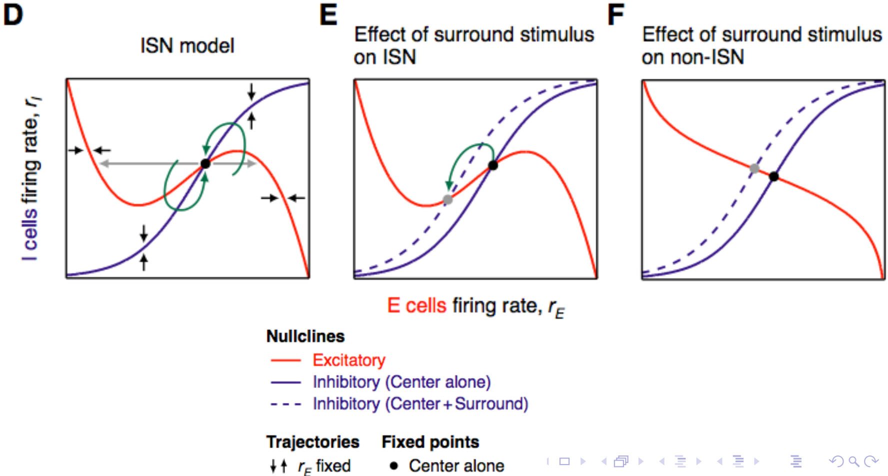
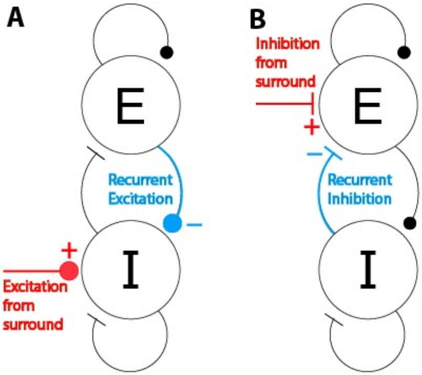


The circuit must be an ISN regardless of the nature of suppressive inputs



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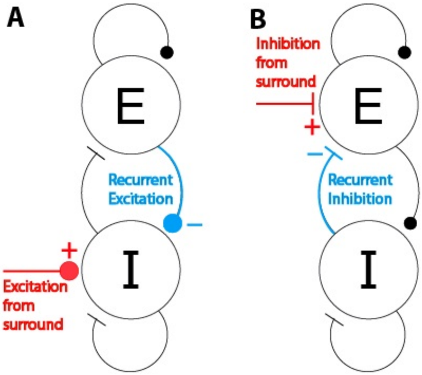

Common principle:

If E unstable

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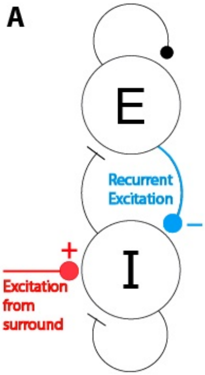

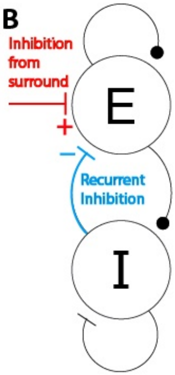

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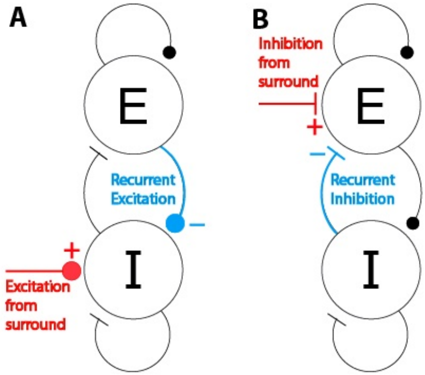

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If E stable:

- In new steady state, E must receive *more* inhibition and/or *less* external excitation (can rule out the latter scenarios)

Predictions of the ISN Model

1. Should see a transient increase in inhibition at the onset of the surround, before the steady-state decrease of inhibition

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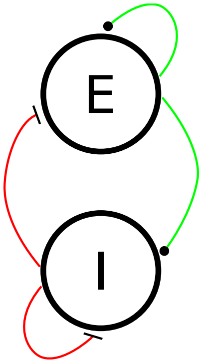
Both verified (Ozeki et al. 2009)

Surround Suppression and the ISN Model: Conclusion

- Surround suppression is not inhibition – it is de-amplification:
  - Responses are normally amplified by recurrent excitation in balanced network (“balanced amplification”)
  - Surround stimulus adds bias toward inhibition $\Rightarrow$ turns down gain for both E and I responses

Balanced Amplification



Because of separation of excitatory and inhibitory neurons, synaptic connectivity matrices are *non-normal*: $\mathbf{W}\mathbf{W}^T \neq \mathbf{W}^T\mathbf{W}$.

$$\mathbf{r} = \begin{pmatrix} \mathbf{r}_E \\ \mathbf{r}_I \end{pmatrix} \qquad \mathbf{W} = \begin{pmatrix} \mathbf{W}_{EE} & -\mathbf{W}_{EI} \\ \mathbf{W}_{IE} & -\mathbf{W}_{II} \end{pmatrix}$$

$$\mathbf{W}_{XY} \geq 0$$

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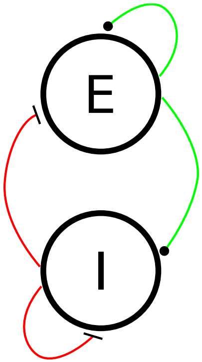

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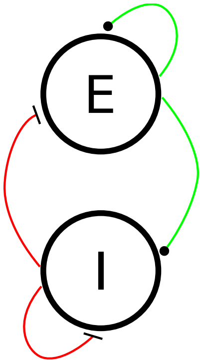

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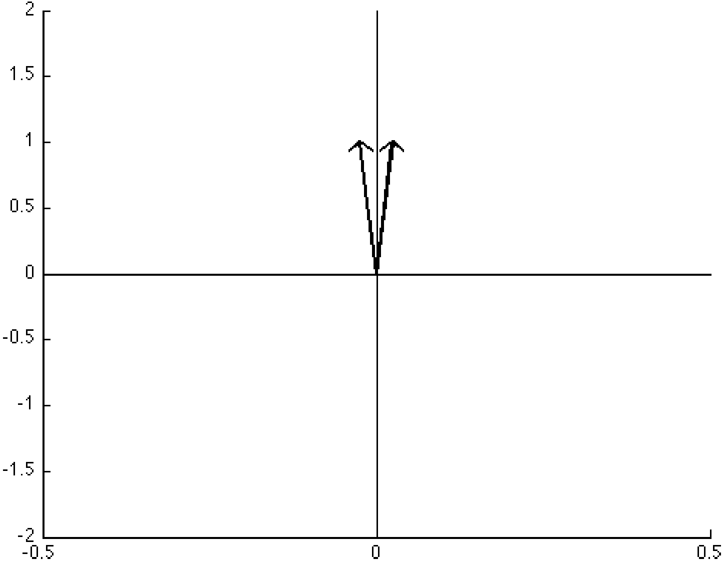
Non-normal $\Longleftrightarrow$ Eigenvectors are not orthogonal

$\Rightarrow$ can have large amplification – large transient responses to small perturbations – not predicted by eigenvalues: well known in fluid mechanics (see book by Trefethen and Embree, 2005)

Intuition for Non-Normal Transient Responses



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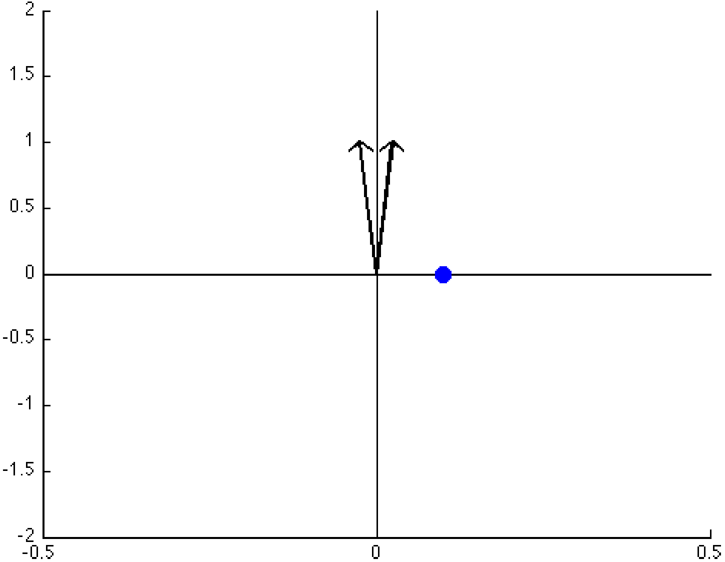

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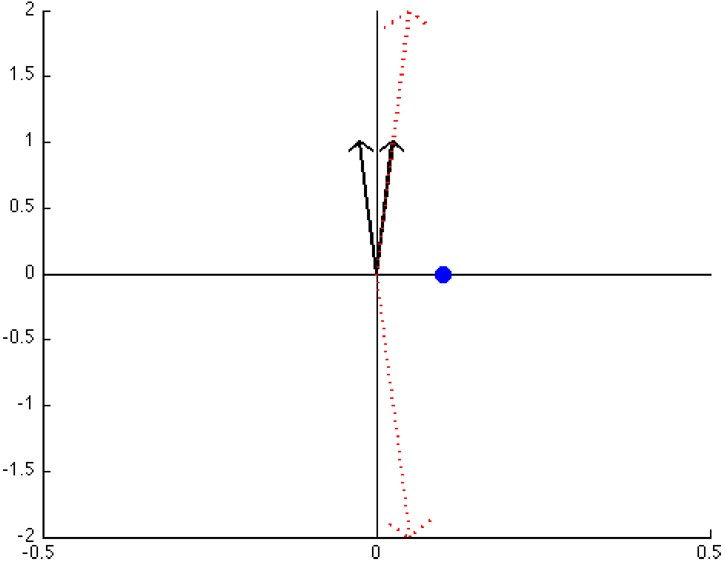

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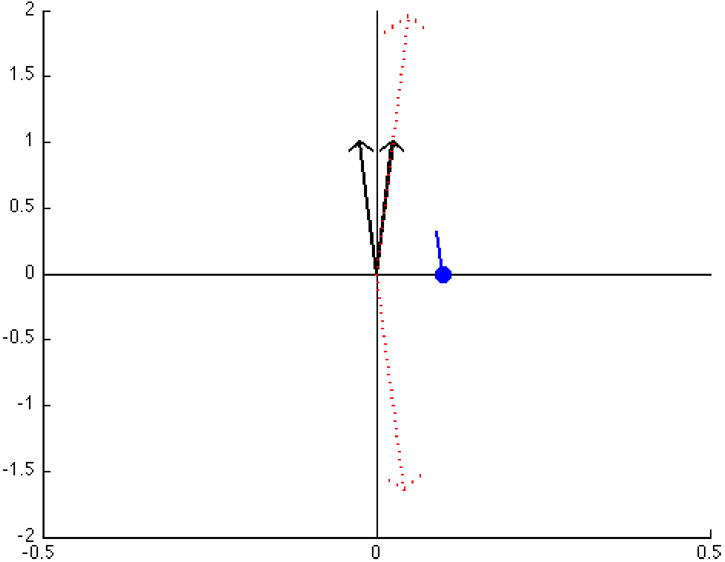

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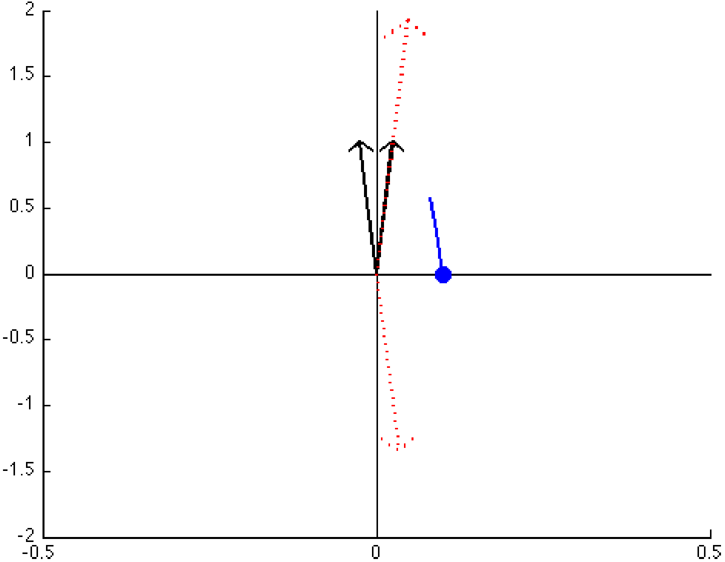

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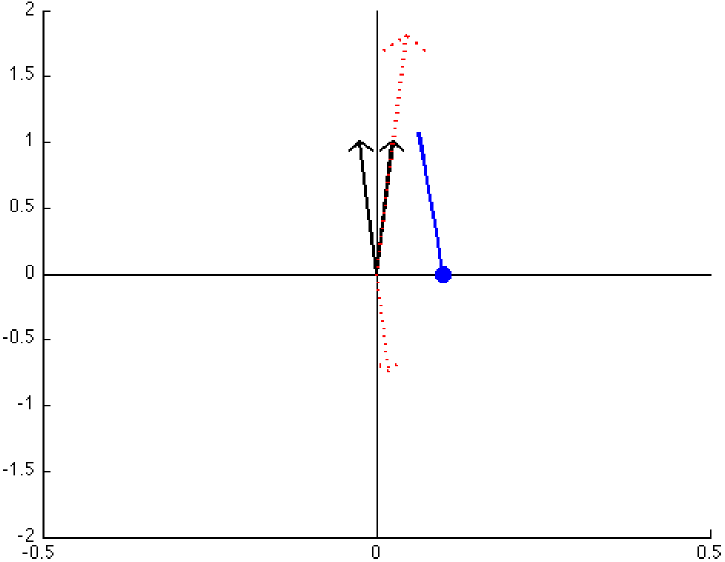

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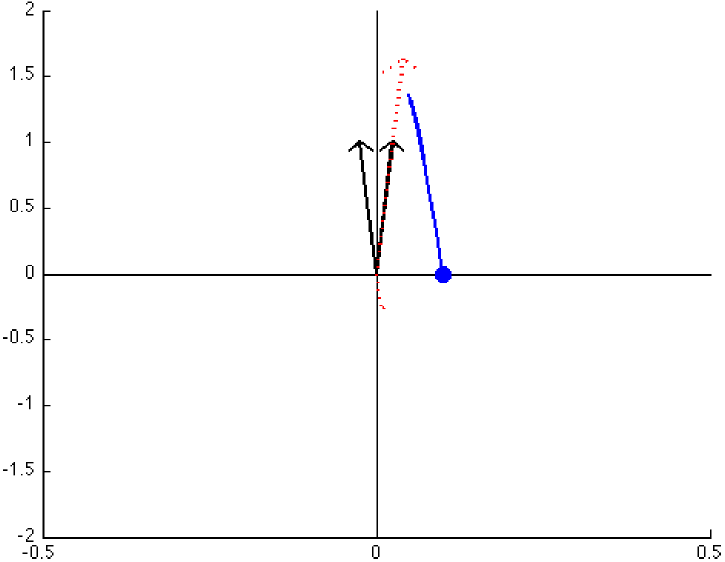

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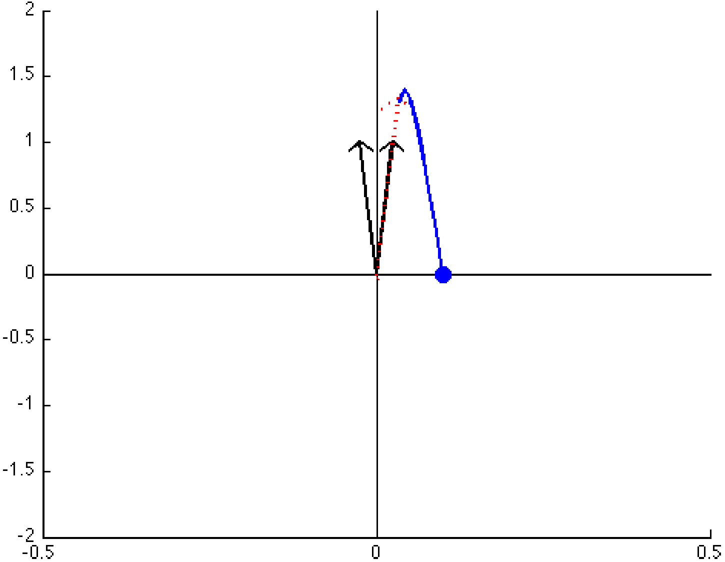

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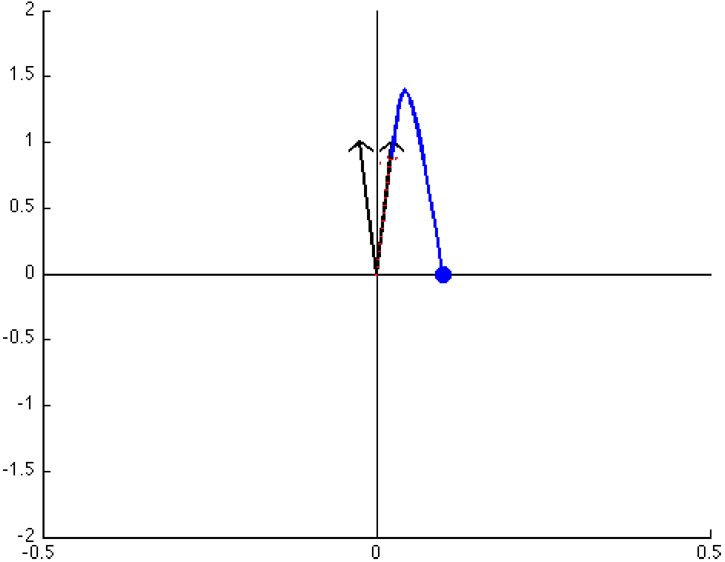

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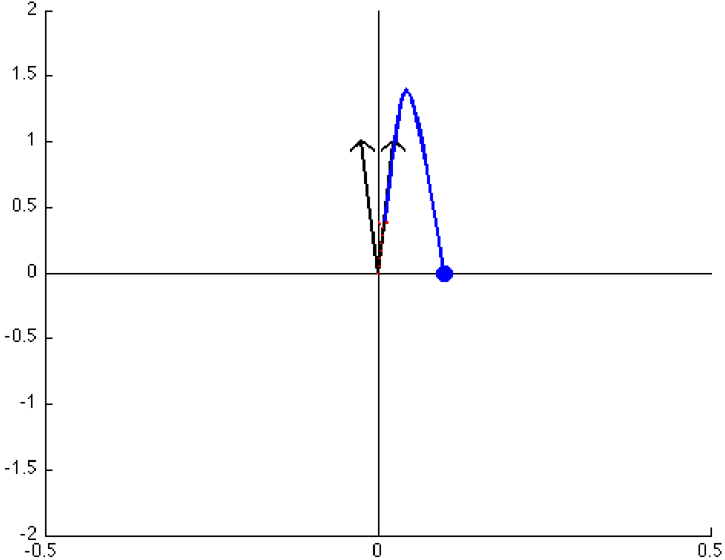

Balanced amplification: Effective Feedforward Connections

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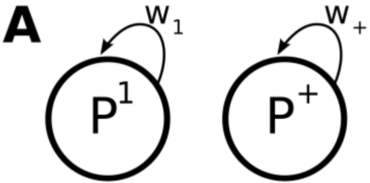
  - Network activity is growing and then shrinking, but in eigenvector basis it appears to be monotonically shrinking
- Best simplification with a unitary (non-distorting) transformation: Schur decomposition:
  - Eigenvalues on diagonal
  - Upper diagonal nonzero = "Feedforward weights"; lower diagonal zero.

Balanced Amplification vs. Eigenvector Picture

Eigenvector picture:



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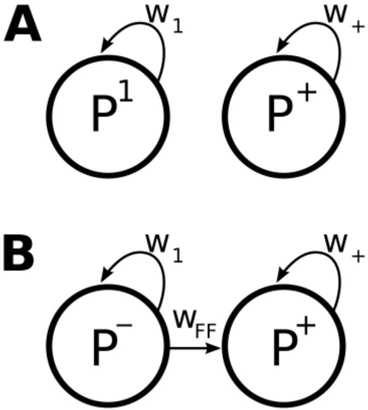
Eigenvector picture:

Schur picture:

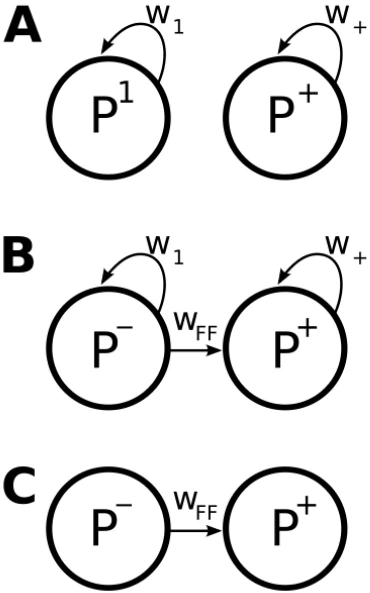


Balanced Amplification vs. Eigenvector Picture

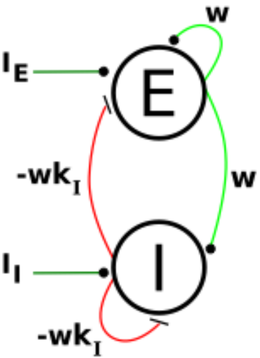
Eigenvector picture:

Schur picture:

Schur picture with small eigenvalues ("balanced"):



Surround suppression as loss of balanced amplification



$$\mathbf{r} = \begin{pmatrix} r_E \\ r_I \end{pmatrix} \quad \mathbf{W} = \begin{pmatrix} w & -k_I w \\ w & -k_I w \end{pmatrix}$$

Linear dynamics in terms of r_E and r_I:

$$\tau \frac{dr_E}{dt} = -r_E + wr_E - k_I w r_I$$
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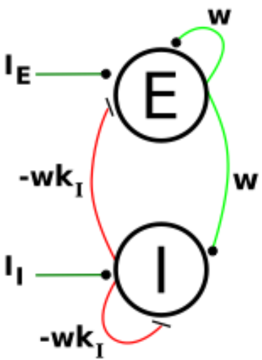

$$w_{\mathrm{FF}} \equiv w(k_I + 1)$$
$$w_+ \equiv w(k_I - 1)$$

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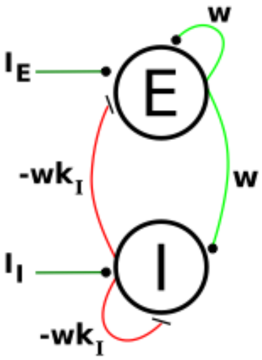
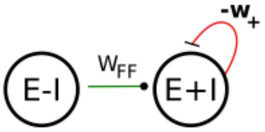
Change variables to the sum and difference, $r_\pm = r_e \pm r_i$:

$$\tau \frac{dr_+}{dt} = -r_+ - w_+ r_+ + w_{\mathrm{FF}} r_-$$
$$\tau \frac{dr_-}{dt} = -r_-$$

Surround suppression as loss of balanced amplification



$$w_{\rm FF} \equiv w(k_I + 1)$$
$$w_+ \equiv w(k_I - 1)$$



$$\mathbf{r} = \begin{pmatrix} r_E \\ r_I \end{pmatrix} \quad \mathbf{W} = \begin{pmatrix} w & -k_I w \\ w & -k_I w \end{pmatrix}$$

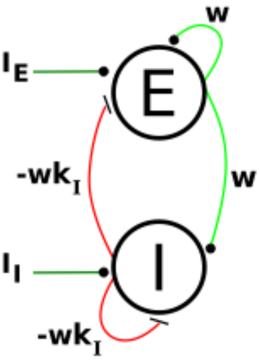
Linear dynamics in terms of r_E and r_I:

$$\tau \frac{dr_E}{dt} = -r_E + wr_E - k_I wr_I$$
$$\tau \frac{dr_I}{dt} = -r_I + wr_E - k_I wr_I$$

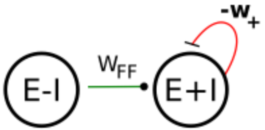
Change variables to the sum and difference, $r_\pm = r_e \pm r_i$:

$$\tau \frac{dr_+}{dt} = -r_+ - w_+ r_+ + w_{\rm FF} r_-$$
$$\tau \frac{dr_-}{dt} = -r_-$$

Surround suppression as loss of balanced amplification



$$w_{\mathrm{FF}} \equiv w(k_I + 1)$$
$$w_+ \equiv w(k_I - 1)$$



$$\mathbf{r} = \begin{pmatrix} r_E \\ r_I \end{pmatrix} \quad \mathbf{W} = \begin{pmatrix} w & -k_I w \\ w & -k_I w \end{pmatrix}$$

Linear dynamics in terms of r_E and r_I:

$$\tau \frac{dr_E}{dt} = -r_E + wr_E - k_I w r_I$$
$$\tau \frac{dr_I}{dt} = -r_I + wr_E - k_I w r_I$$

Change variables to the sum and difference, $r_\pm = r_e \pm r_i$:

$$\tau \frac{dr_+}{dt} = -r_+ - w_+ r_+ + w_{\mathrm{FF}} r_-$$
$$\tau \frac{dr_-}{dt} = -r_-$$

Small E/I imbalances drive large balanced responses (*e.g.*, surround suppression)