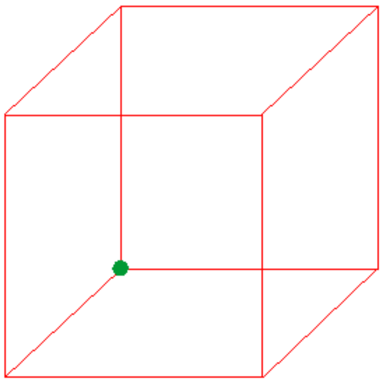
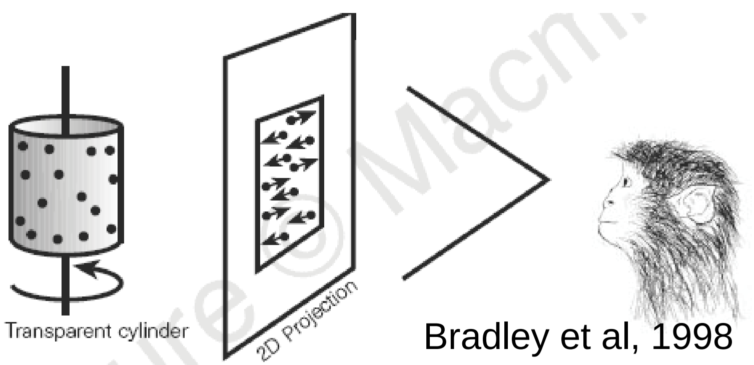
Dynamics of Perceptual Bistability

J Rinzel, NYU

What do we perceive when confronted with ambiguous sensory stimuli?



Necker Cube

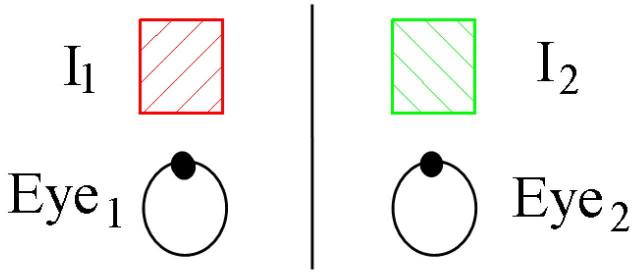


Bradley et al, 1998

w/ N Rubin, A Shpiro, R Curtu, R Moreno

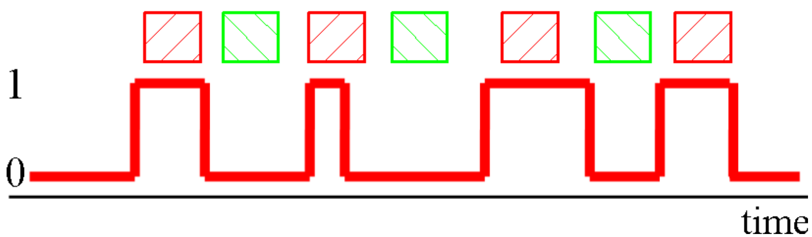
Binocular rivalry:

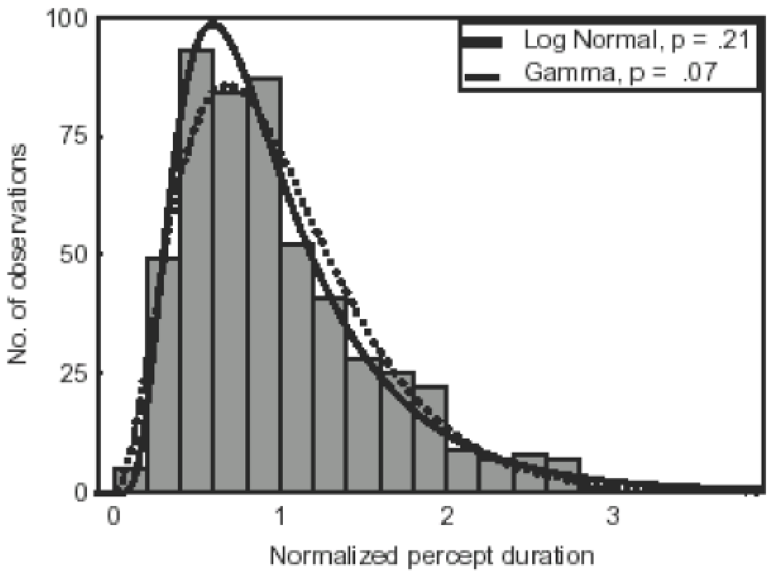
alteration of percepts when different steady images are presented to the two eyes



Mutual inhibition with slow adaptation ➔ alternating dominance and suppression

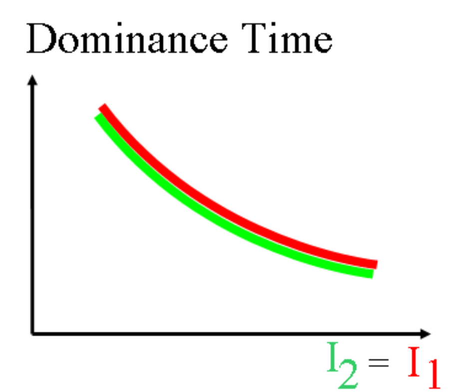
Perception and activity:





Properties:

Levelt's Proposition IV:

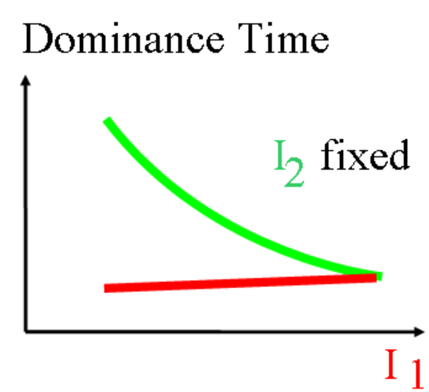


both inputs increase together

⇩

dominance time decreases

Levelt's Proposition II:



one input decreases

⇩

OTHER eye's dominance time increases

Levelt, 1968

Dynamics of Perceptual Bistability

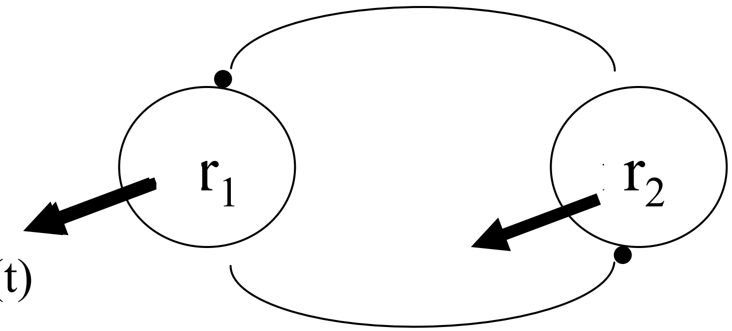
- Oscillator models – inhibition + slow negative feedback
  -- noise gives randomness to period
  -- non-monotonic T vs stimulus
  -- reconsider the experimental findings, or the models

- Attractor model (Moreno)
  – noise driven, no oscillation w/o noise
  -- double-well potential motivates neural architecture
  -- monotonic T vs stimulus
- Oscillator/attractor "regime" in the continuum
  -- stats of T distribution constrain parameters

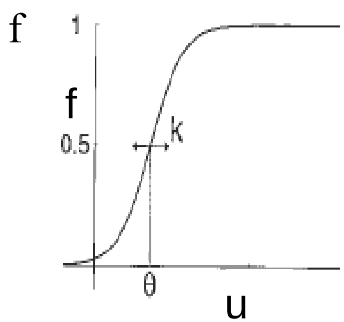
w/ N Rubin, A Shpiro, R Curtu, R Moreno

Oscillator Models for Directly Competing Populations

Two mutually inhibitory populations, corresponding to each percept.
Firing rate model: $r_1(t)$, $r_2(t)$
Slow negative feedback: adaptation or synaptic depression.



Slow adaptation, $a_1(t)$



No recurrent excitation

…half-center oscillator
… decision-making competition

$$\tau\, dr_1/dt = -r_1 + f(-\beta r_2 - g\, a_1 + I_1)$$
$$\tau_a\, da_1/dt = -a_1 + f_a(r_1)$$

$$\tau\, dr_2/dt = -r_2 + f(-\beta r_1 - \varphi\, a_2 + I_2)$$
$$\tau_a\, da_2/dt = -a_2 + f_a(r_2)$$

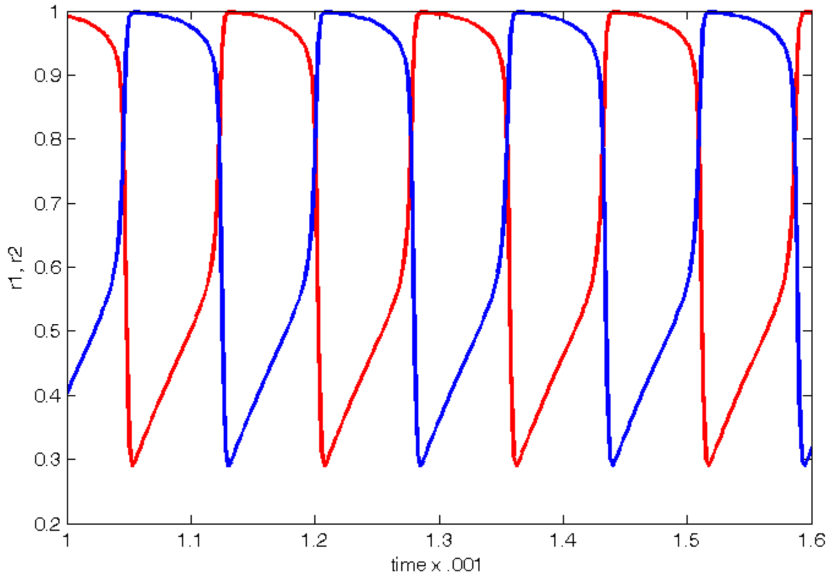
$$\tau_a >> \tau, \quad f(u)=1/(1+\exp[(\theta-u)/k])$$

w/ N Rubin, A Shpiro, R Curtu

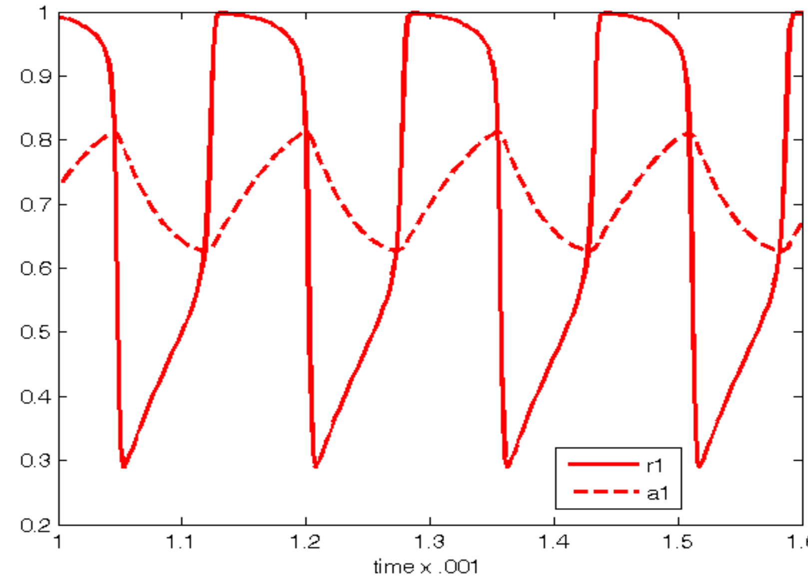
Shpiro et al, J Neurophys 2007

Wilson 2003; Laing and Chow 2003

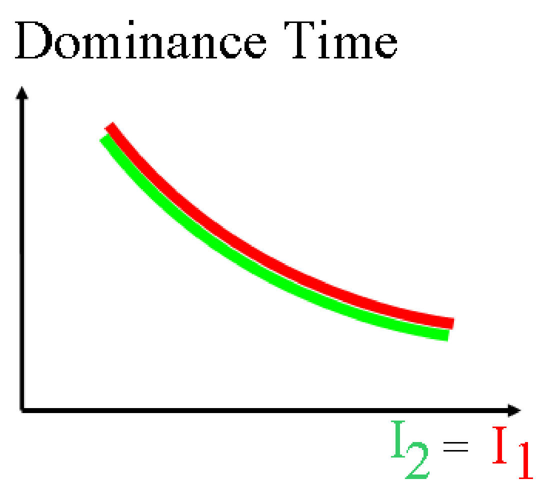
Alternating firing rates

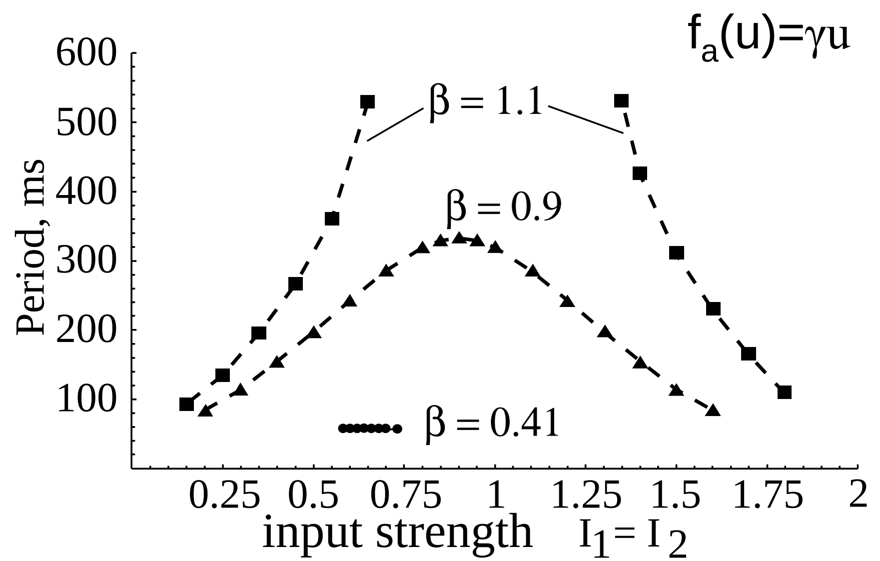


Adaptation slowly grows/decays



Levelt's Proposition IV

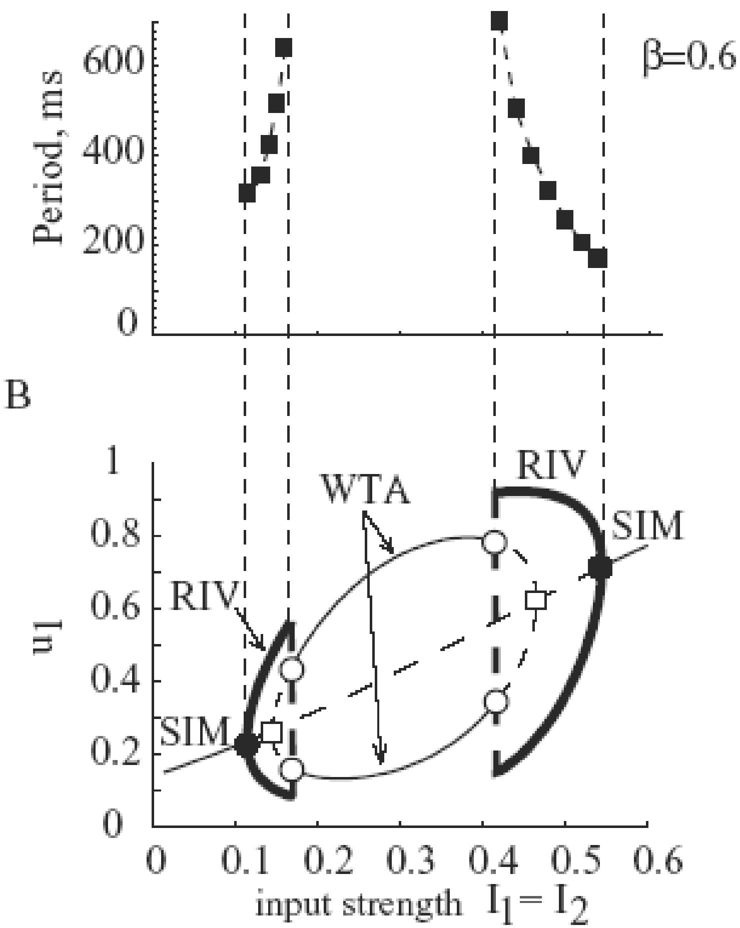




adaptation LC model

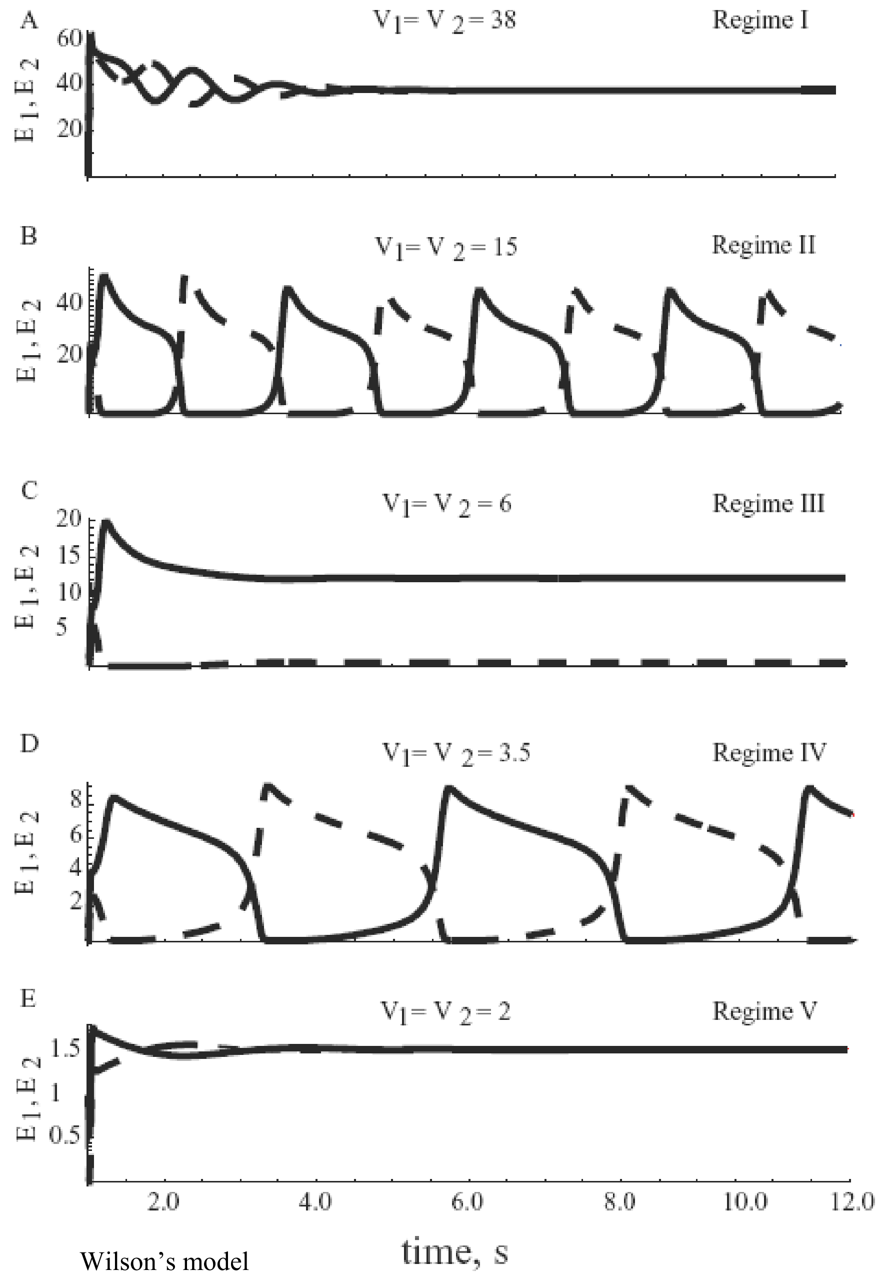
Five Regimes of Behavior, Common to Neuronal Competition Models

Shpiro et al, J Neurophys 2006



depression LC model

Increasing Stimulus

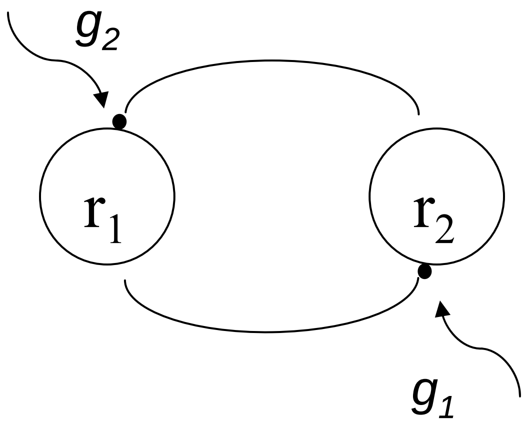


Wilson's model

Shpiro et al, J Neurophys 2007

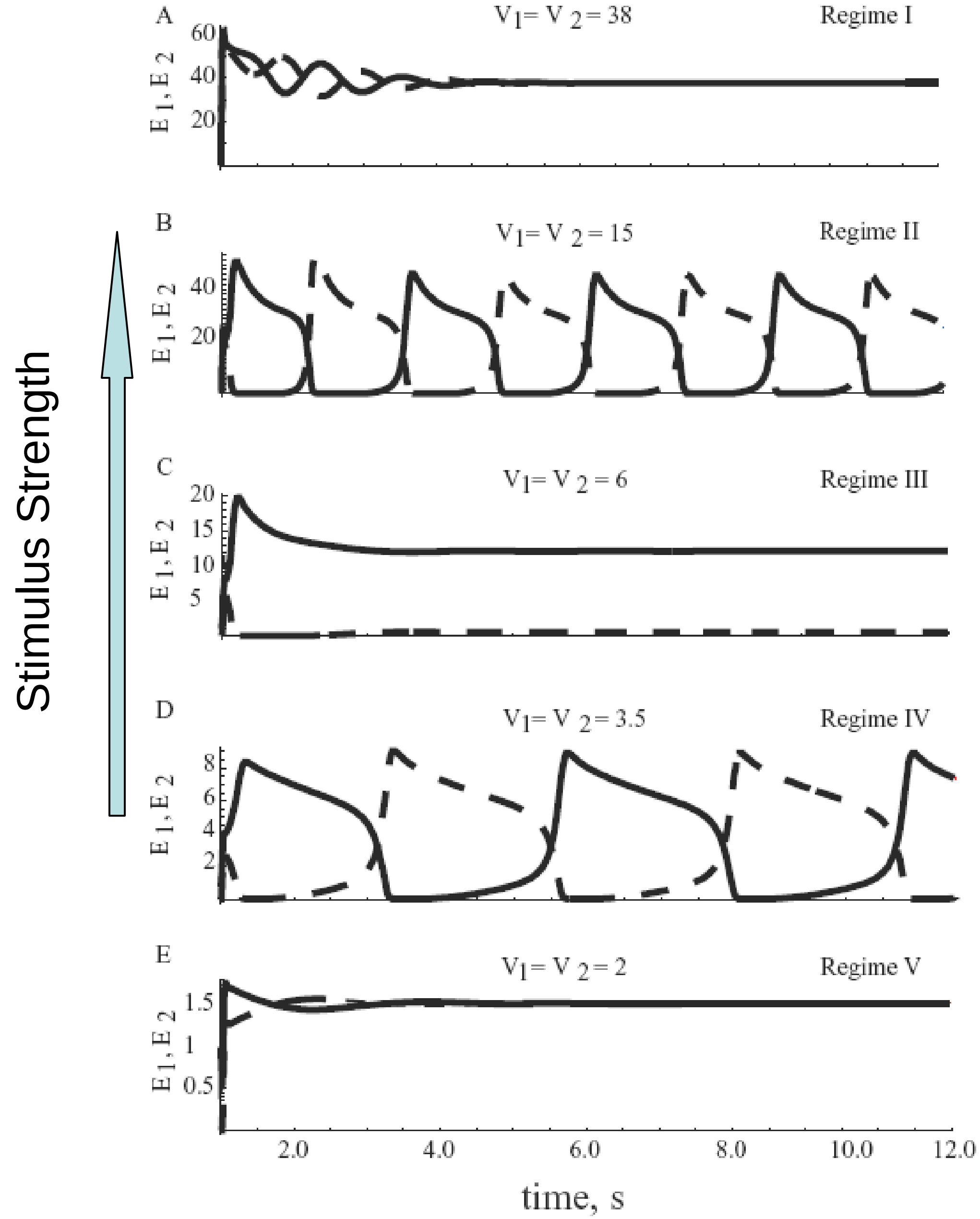
Five Regimes of Behavior, Common to Neuronal Competition Models

Model with slow synaptic depression.



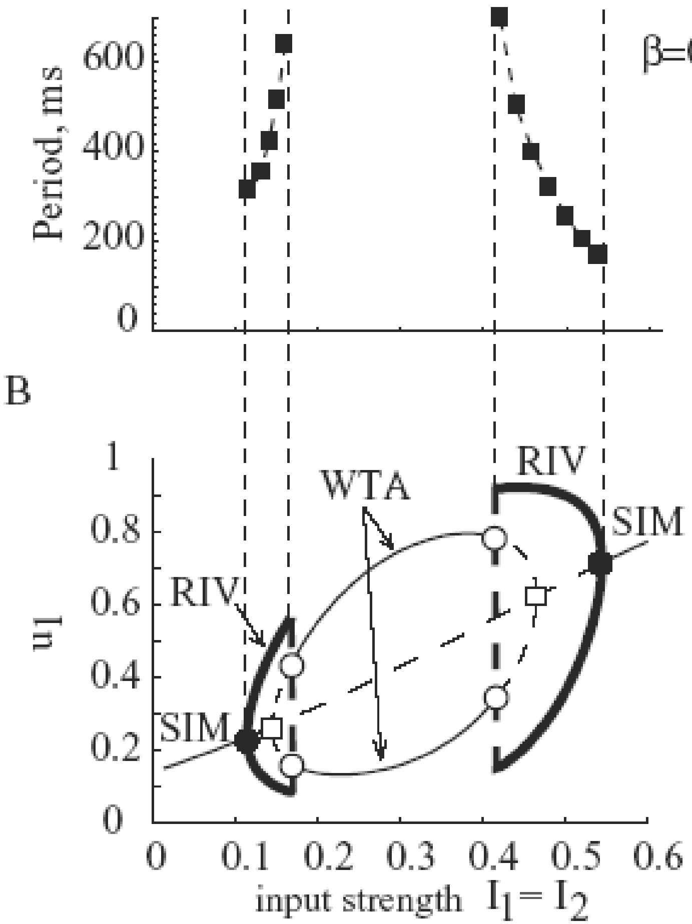
$$\dot{u}_1 = -u_1 + f(-\beta u_2 g_2 + I_1),$$
$$\tau_d \dot{g}_1 = 1 - g_1 - \gamma u_1 g_1,$$
$$\dot{u}_2 = -u_2 + f(-\beta u_1 g_1 + I_2),$$
$$\tau_d \dot{g}_2 = 1 - g_2 - \gamma u_2 g_2.$$

$\tau_d >> \tau$, $f(u)=1/(1+exp[(\theta-u)/k])$



Five Regimes of Behavior, Common to Neuronal Competition Models

Shpiro et al, J Neurophys 2006



depression LC model

Math – adaptation case:

If adaptation is slow and inhib'n is sufficient

$$\beta > \frac{1 + 1/\tau_a}{f'(\theta)}$$

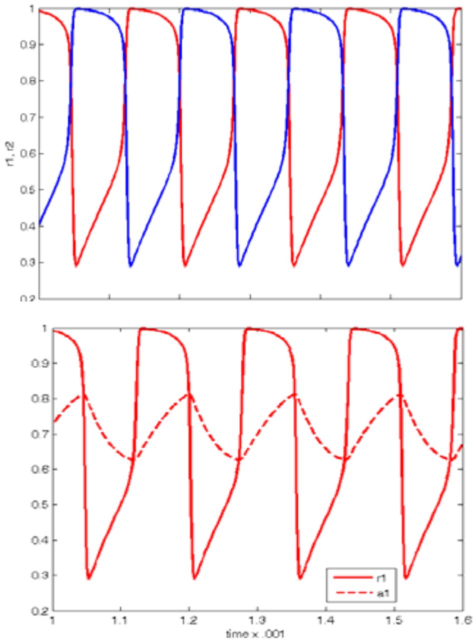
then Hopf bifur'cns (2 of them) are supercritical and to anti-phase oscill'n.

If inhibition is strong, given adaptation,

$$1/\, f'(\theta) < \beta - g < \beta/(1 + \tfrac{1}{\tau_a})$$

then also get pitchfork bifurcations.

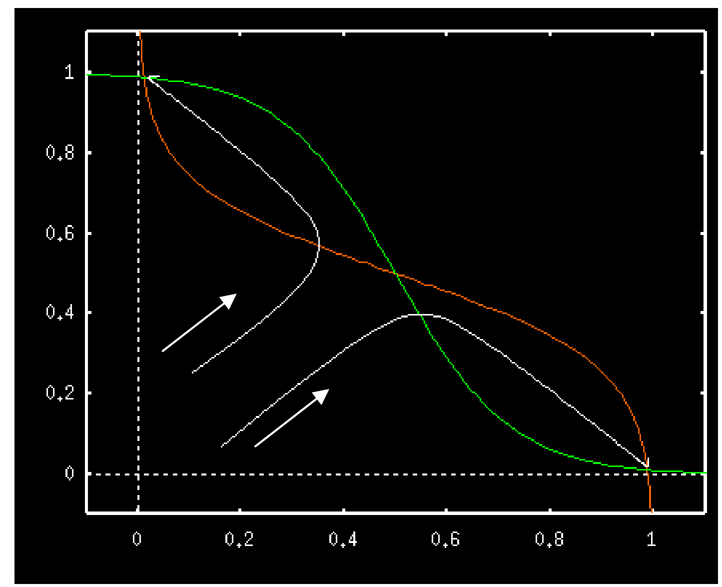
Fast/Slow Dynamics

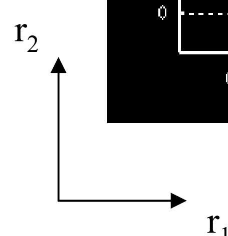


Fast-Slow dissection: r_1 , r_2 fast variables
a_1 , a_2 slow variables

Decision making

a_1, a_2 frozen



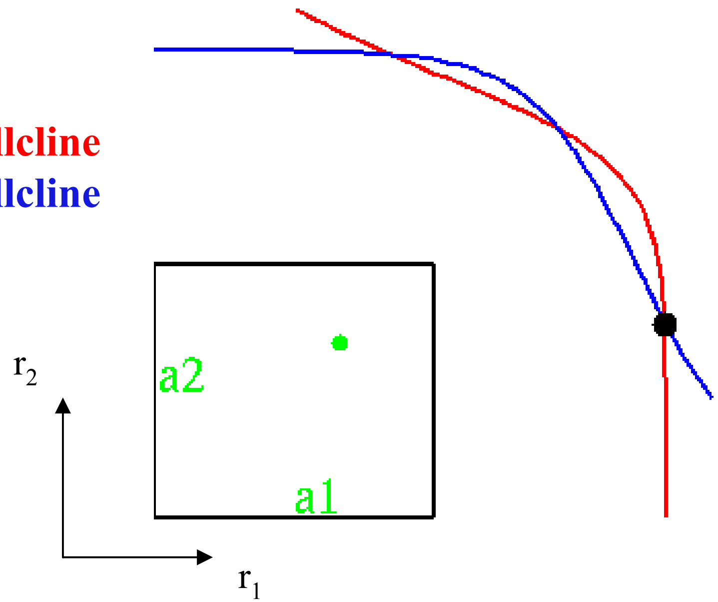


r_1- nullcline $r_1 = f(-\beta r_2 - \varphi\, a_1 + I_1)$

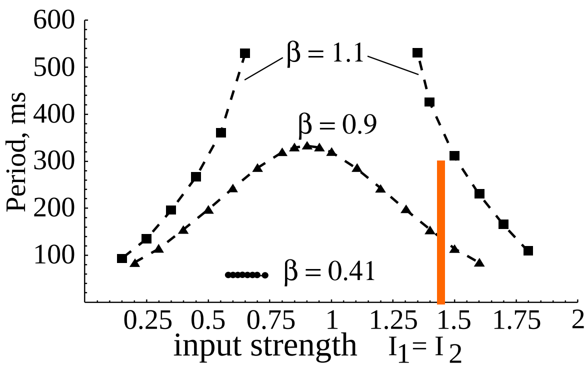
r_2- nullcline $r_2 = f(-\beta r_1 - \varphi\, a_2 + I_2)$

r_1-r_2 phase plane, slowly drifting nullclines

r_1- nullcline
r_2- nullcline



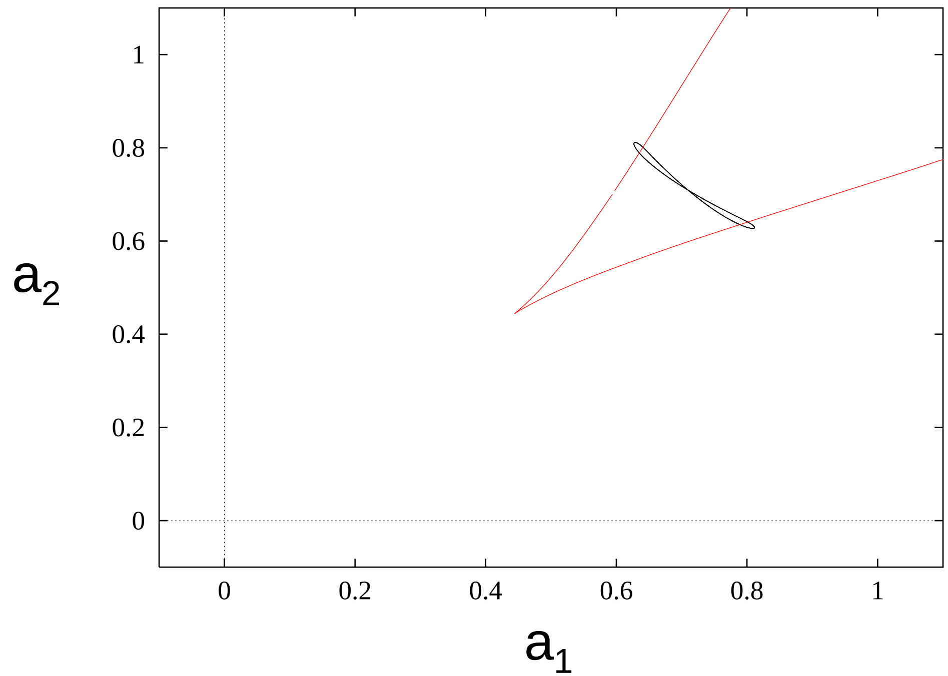
β =0.9, **I_1=I_2=1.4**



At a switch:

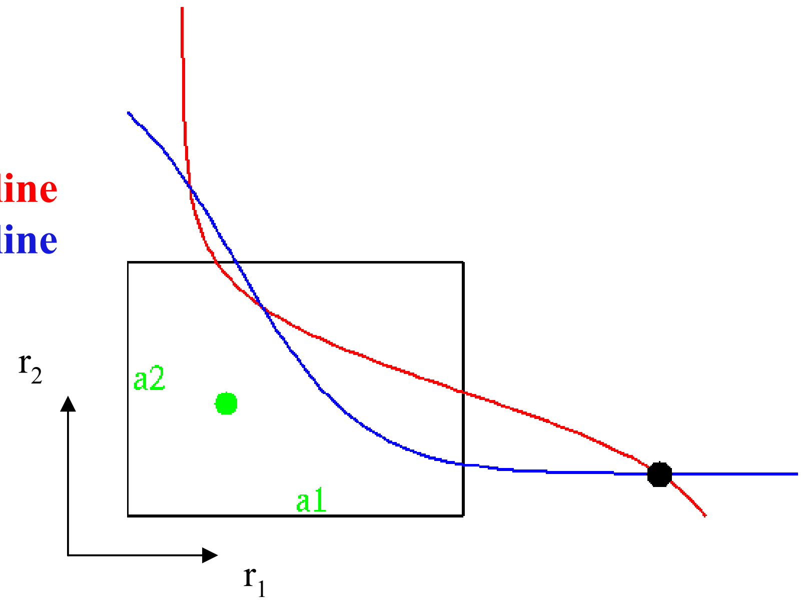
- saddle-node in fast dynamics.
- dominant r is high while system rides near "threshold"of suppressed populn's nullcline ➔ ESCAPE.

Switching occurs when a_1-a_2 traj reaches a curve of SNs (knees)

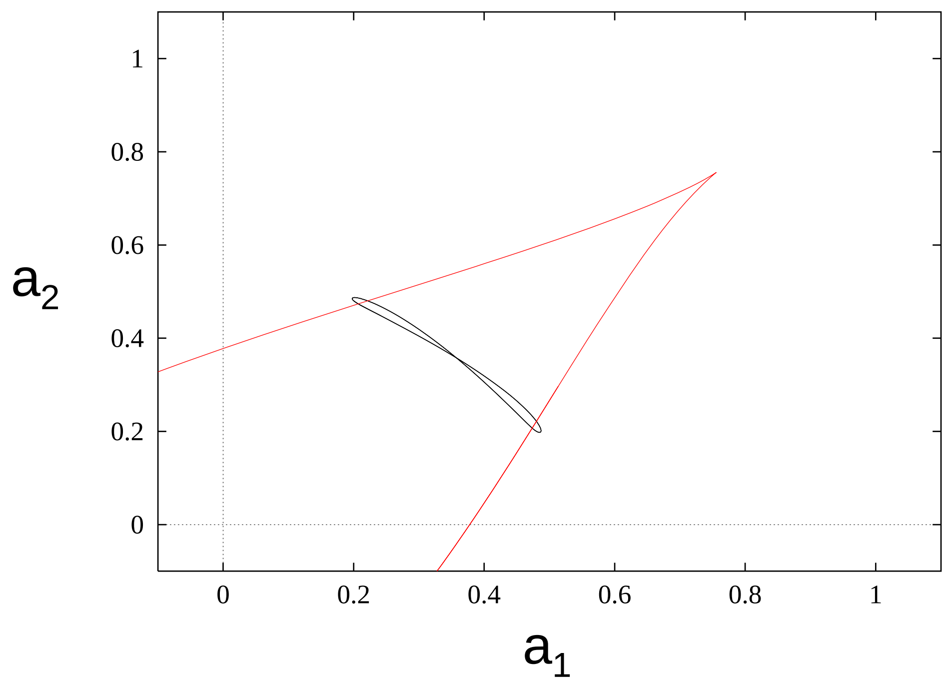


RELEASE:
At a switch: suppressed r is very low while system rides near “threshold” of dominant populn’s nullcline

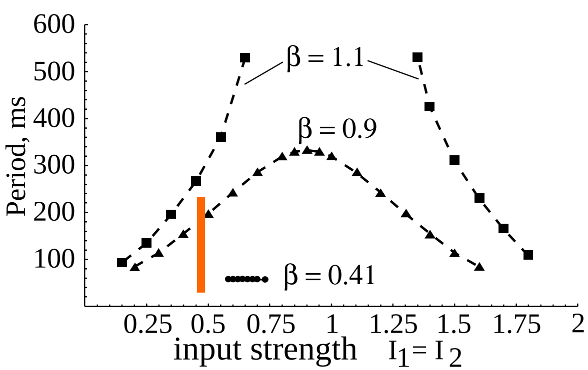
r_1- nullcline
r_2- nullcline



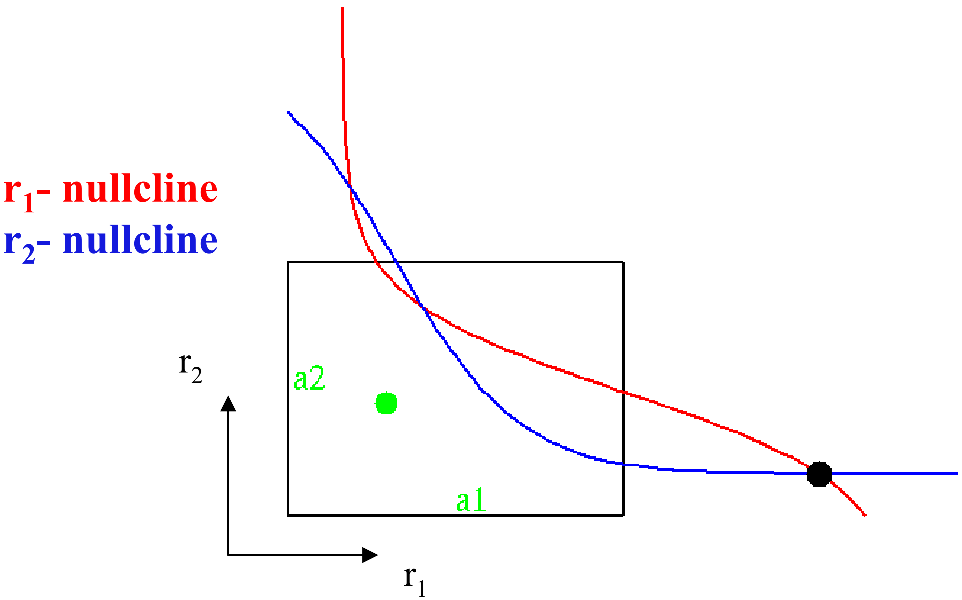
Curve of SNs (knees) for Release.



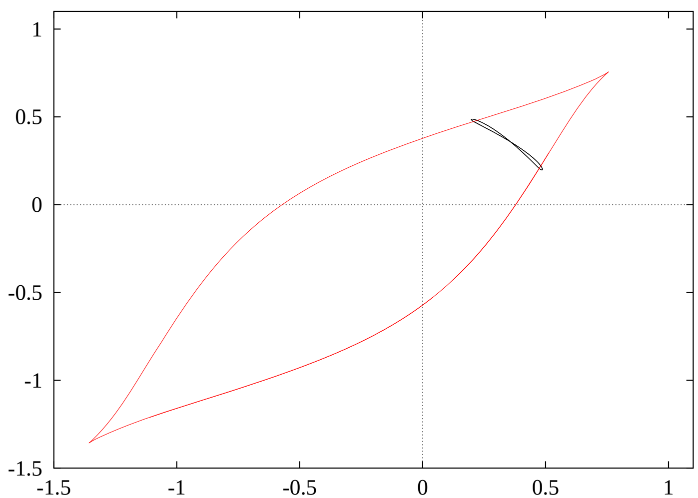
β =0.9, I_1=I_2=0.5

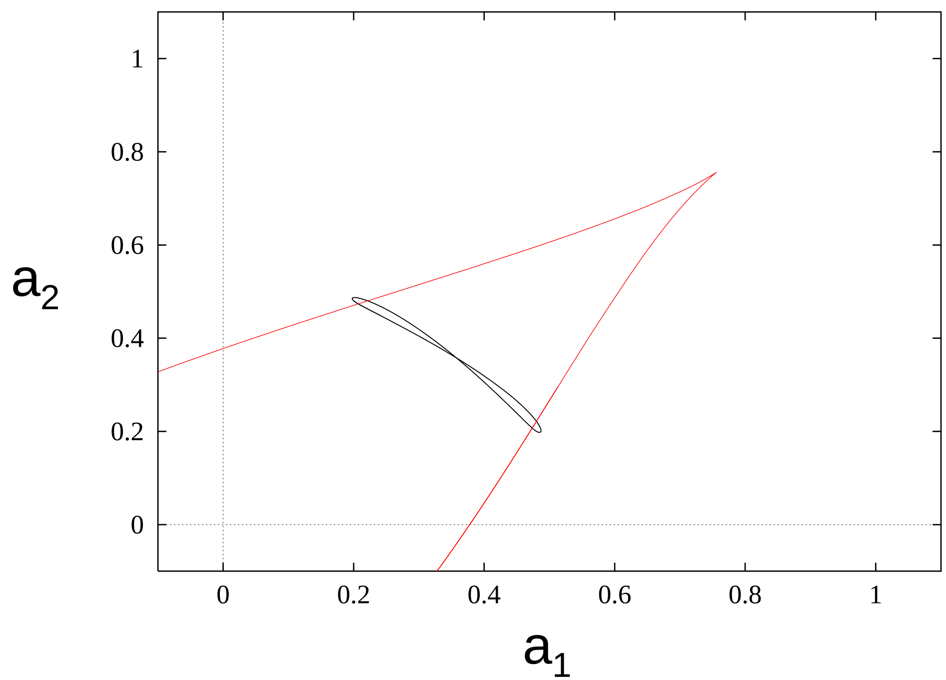


RELEASE:
At a switch: suppressed r is very low while system rides near “threshold” of dominant populn’s nullcline

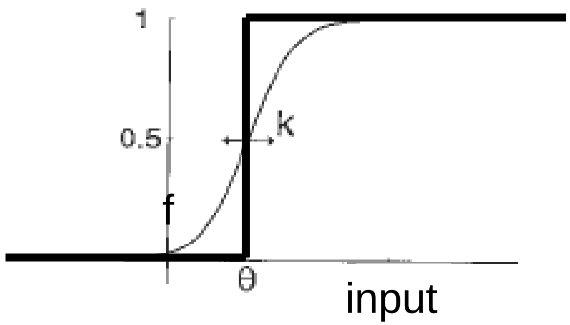


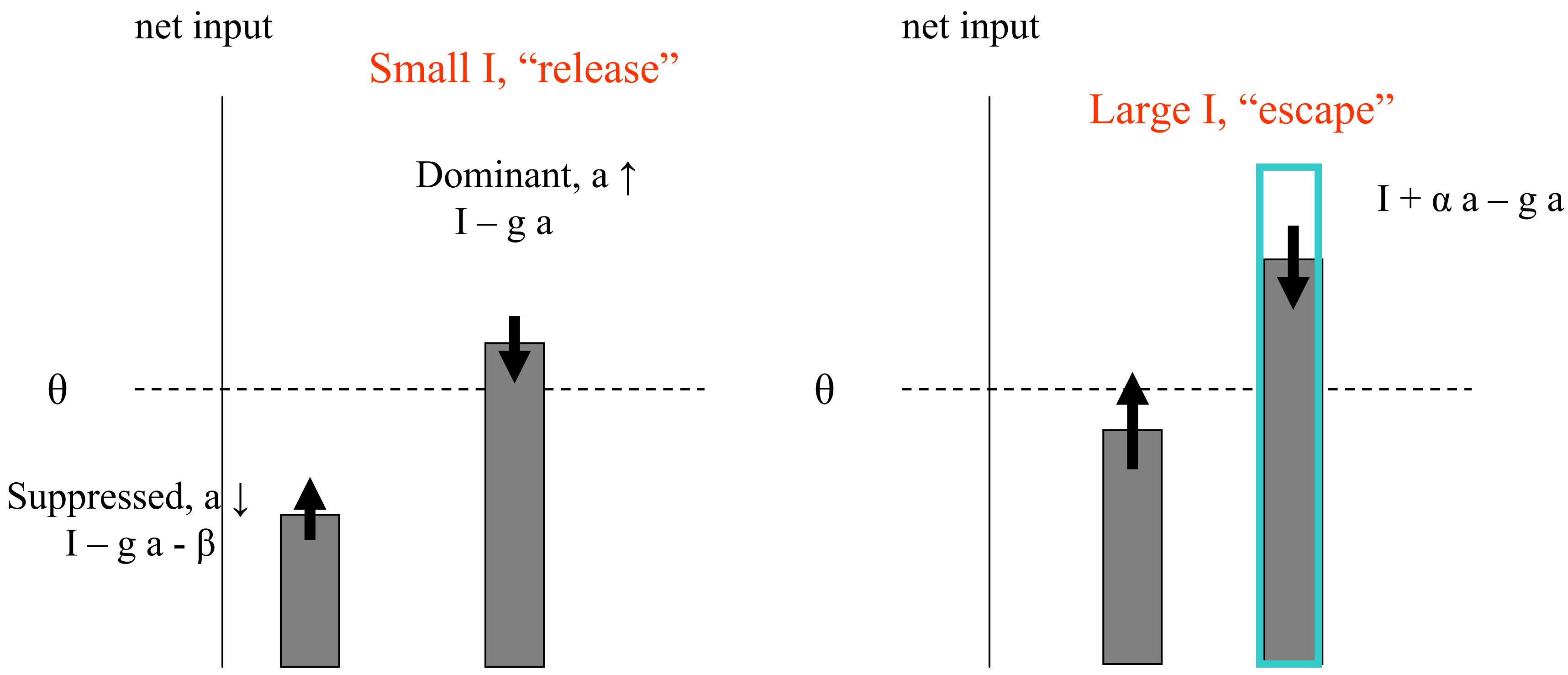
Curve of SNs (knees) for Release.





Switching due to adaptation: release or escape mechanism





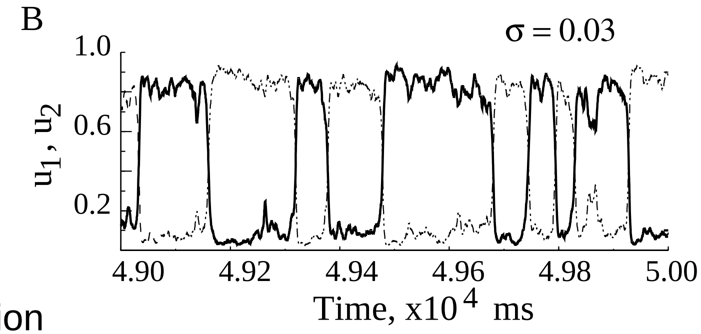
Recurrent excitation, secures “escape”

Noise leads to random dominance durations and eliminates WTA behavior.

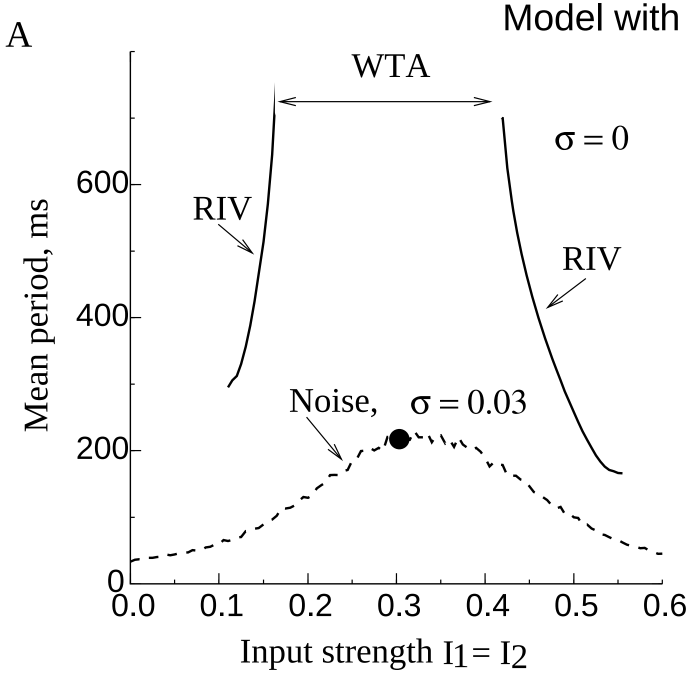
$$\dot{n}_i = -\frac{n_i}{\tau_n} + \sigma\sqrt{\frac{2}{\tau_n}}\eta(t)$$

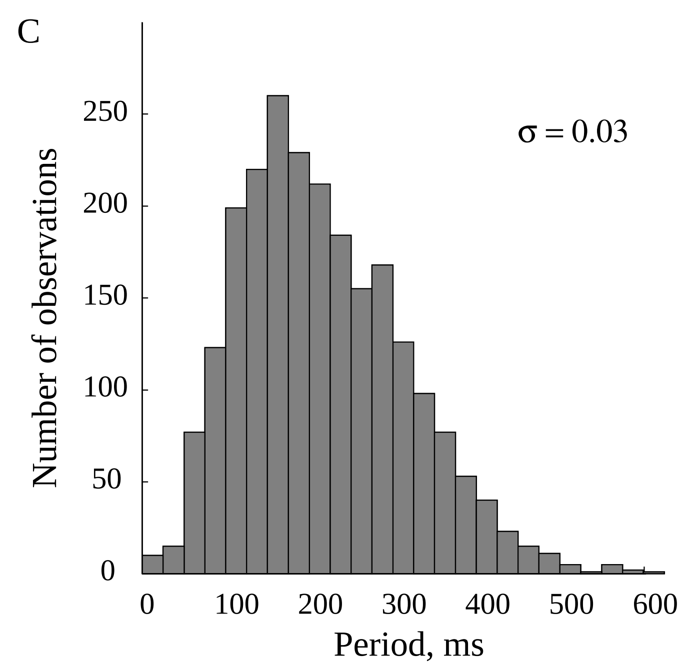
Added to stimulus $I_{1,2}$
s.d., $\sigma = 0.03$, $\tau_n = 10$

$$\tau\, dr_i/dt = -r_i + f(-\beta r_j - \varphi\, a_i + I_i + n_i)$$
$$\tau_a\, da_i/dt = -a_i + f_a(r_i)$$



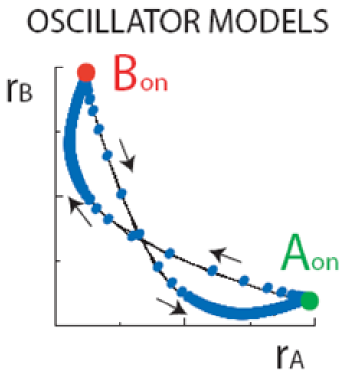
Model with synaptic depression

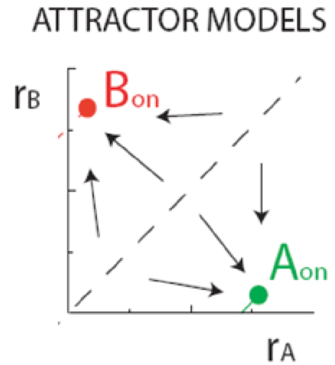




Noise-Driven Attractor Models

w/ R Moreno, N Rubin

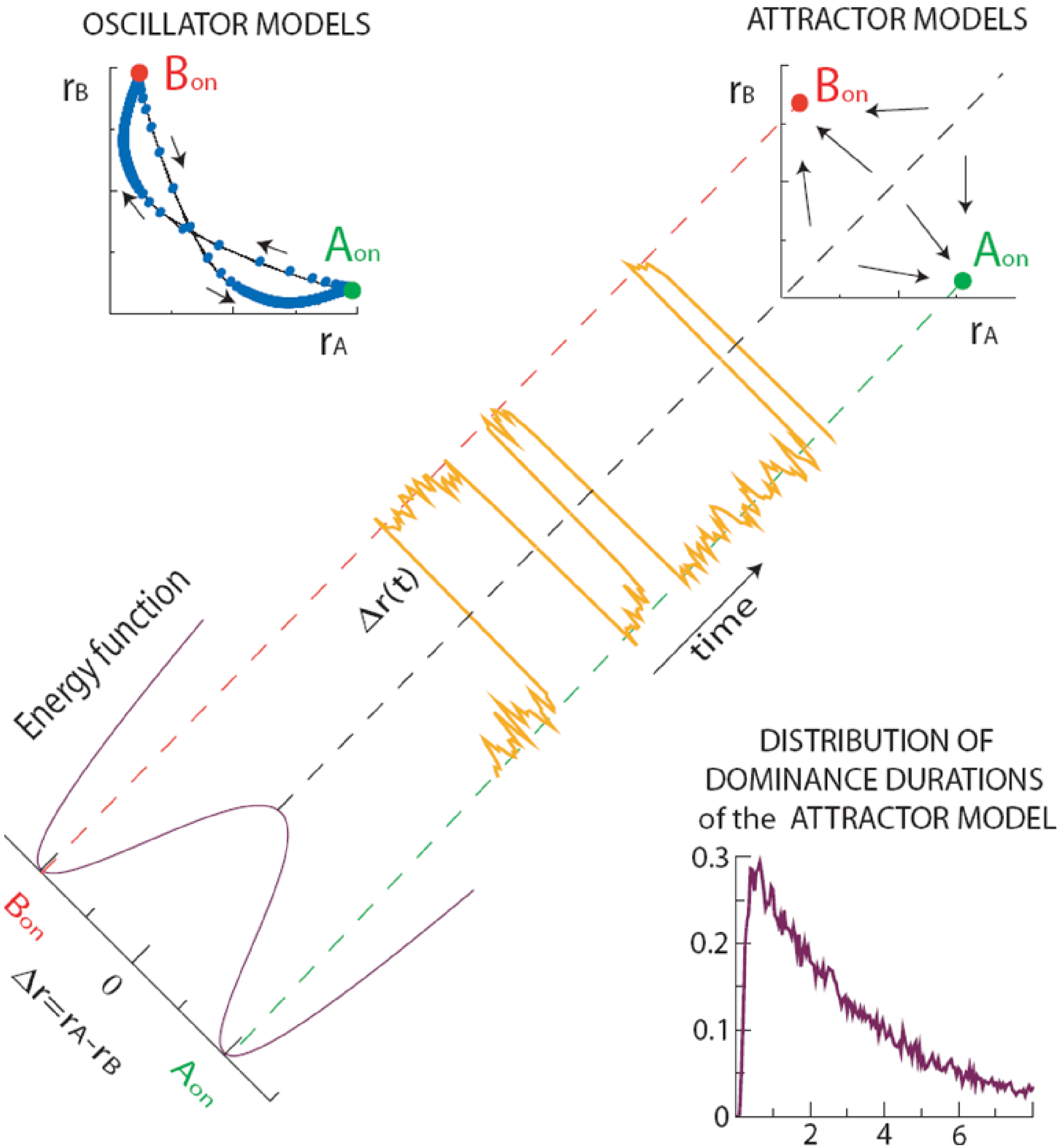




Noise-Driven Attractor Models

w/ R Moreno, N Rubin

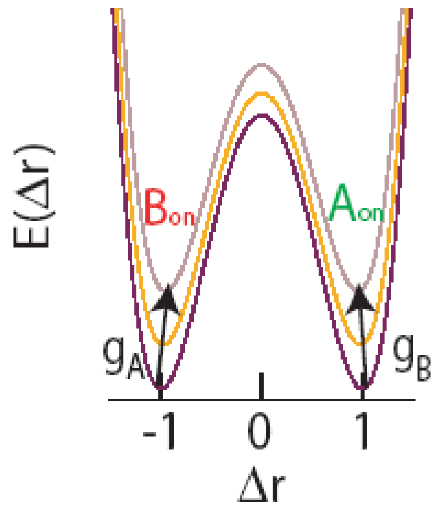
J Neurophys 2007

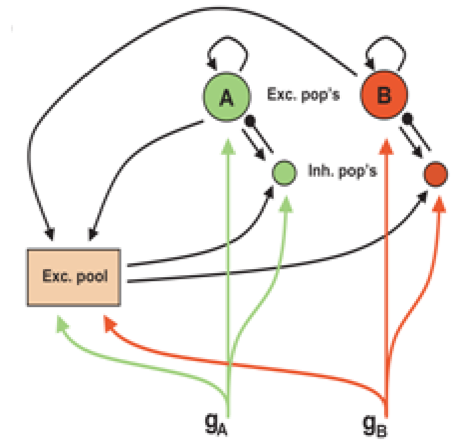


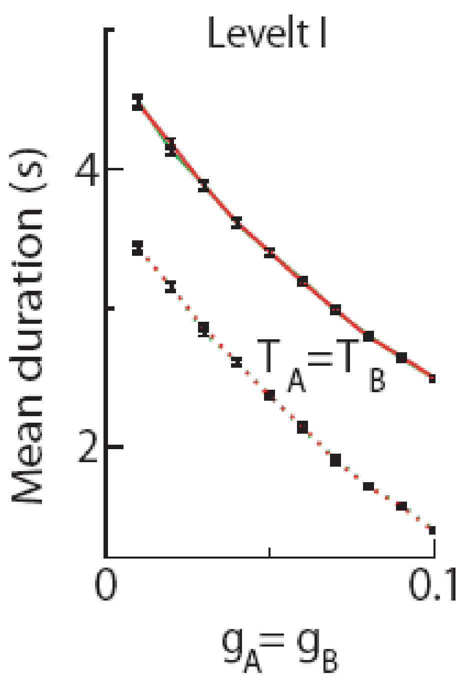
No oscillations if noise is absent.

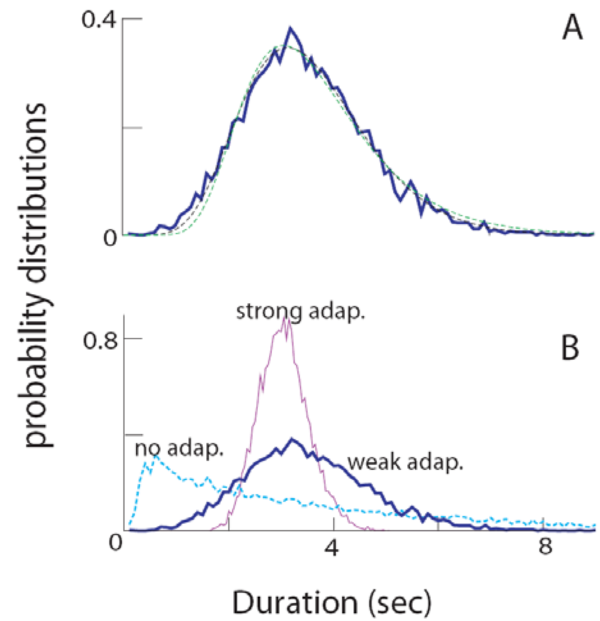
Kramers 1940

LP-IV in an attractor model

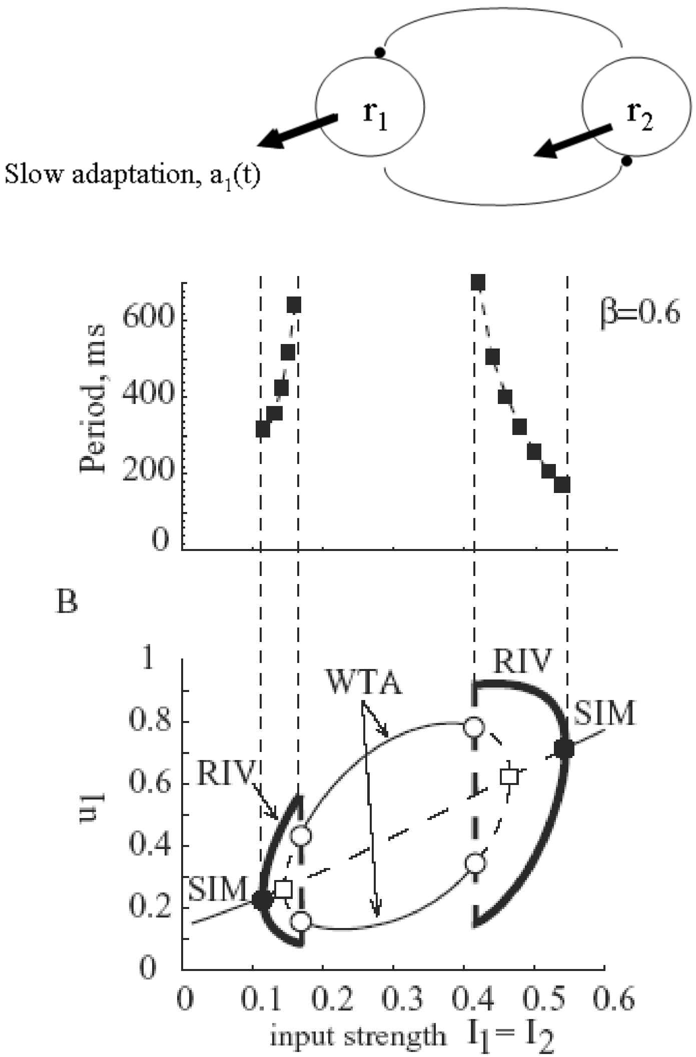




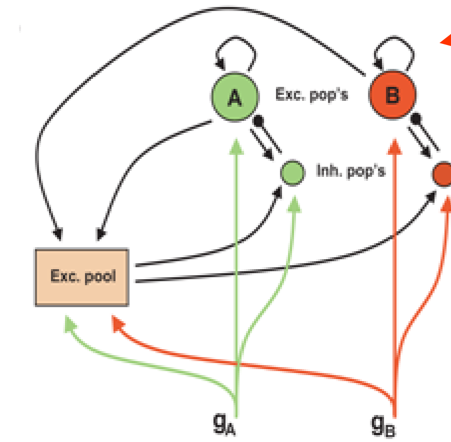


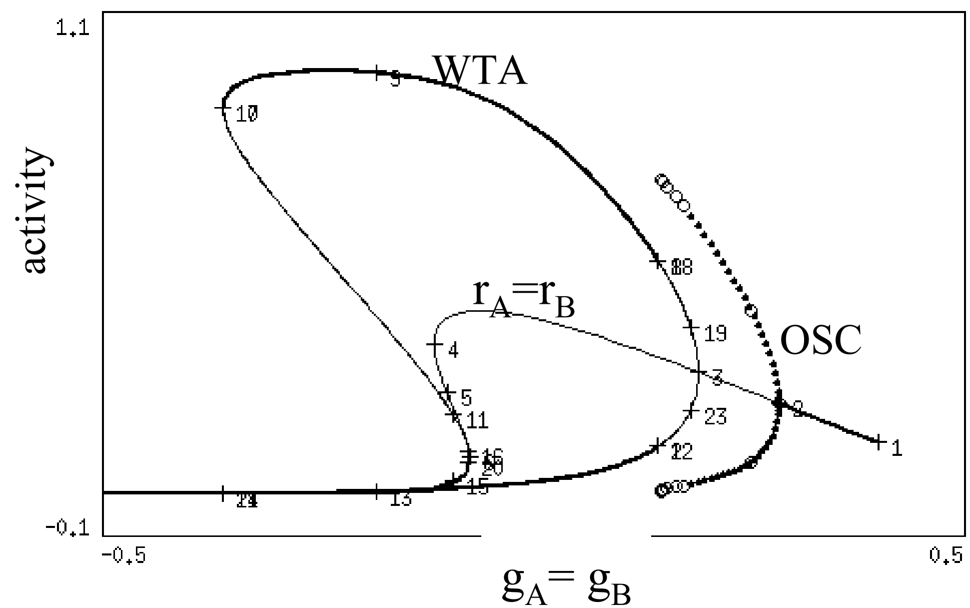


Compare dynamical skeletons: “oscillator” and attractor-based models

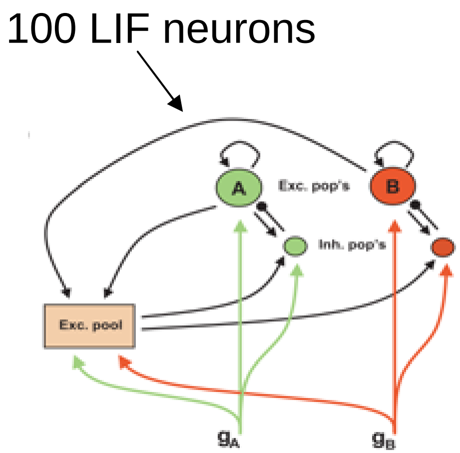


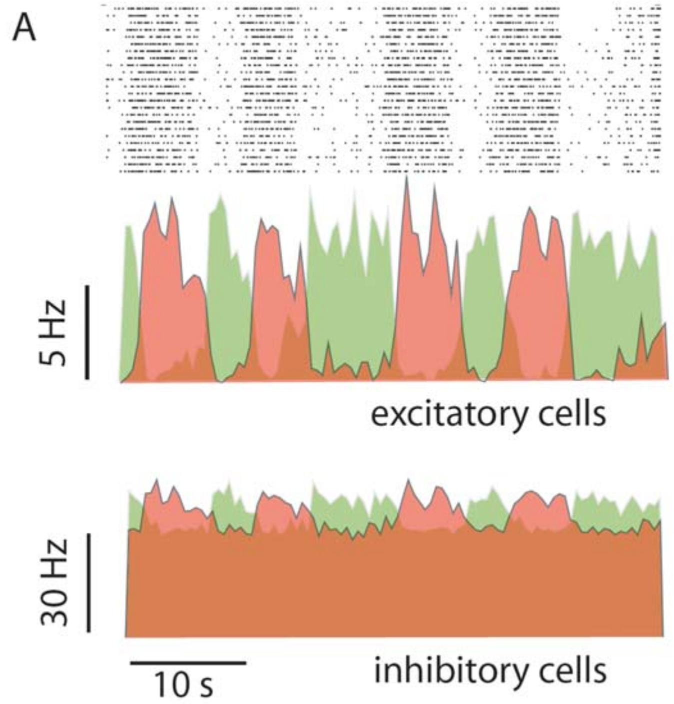
Recurrent excitation



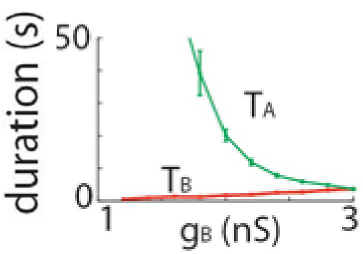


Dynamical properties of a network with spiking neurons. Simulation results.

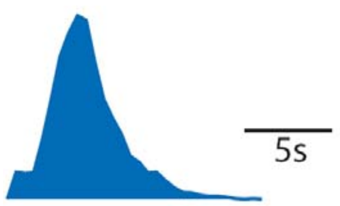




Levelt II



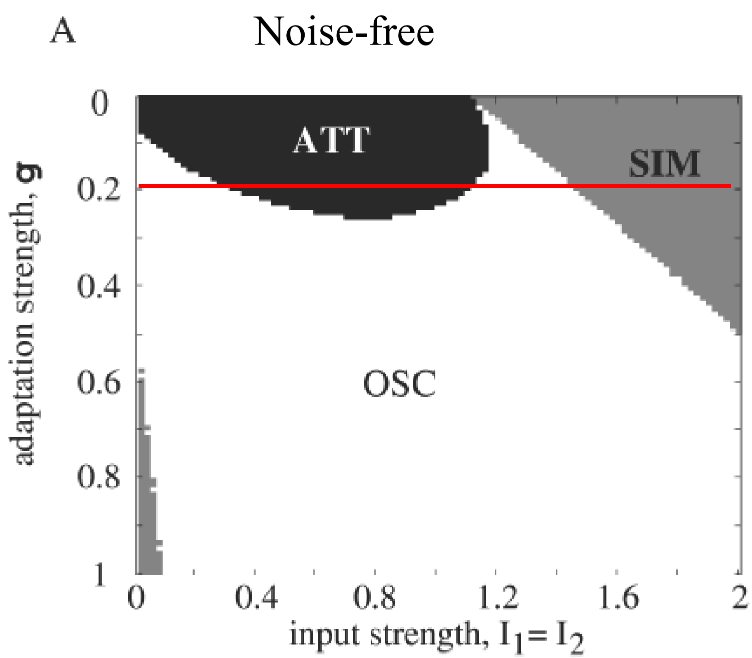
distribution



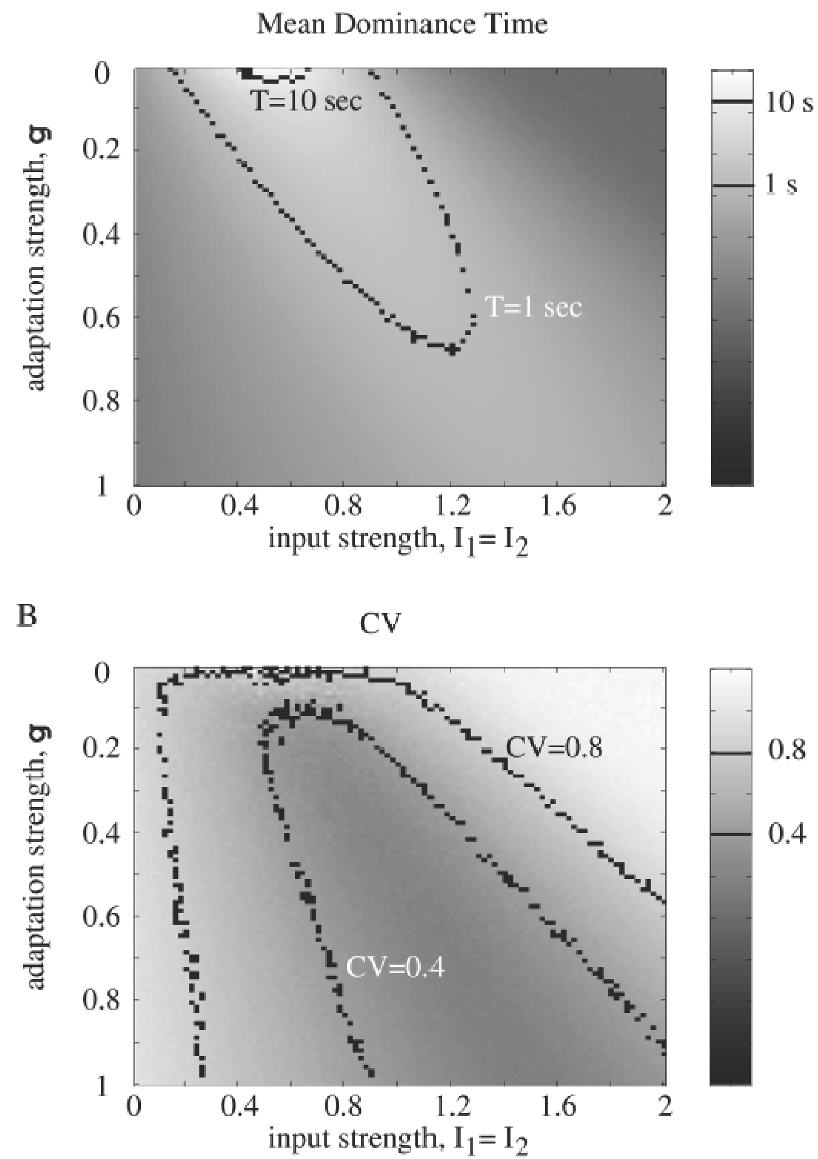
Observed variability and mean duration constrain the model.

1 sec < mean T < 10 sec

0.4 < CV < 0.6



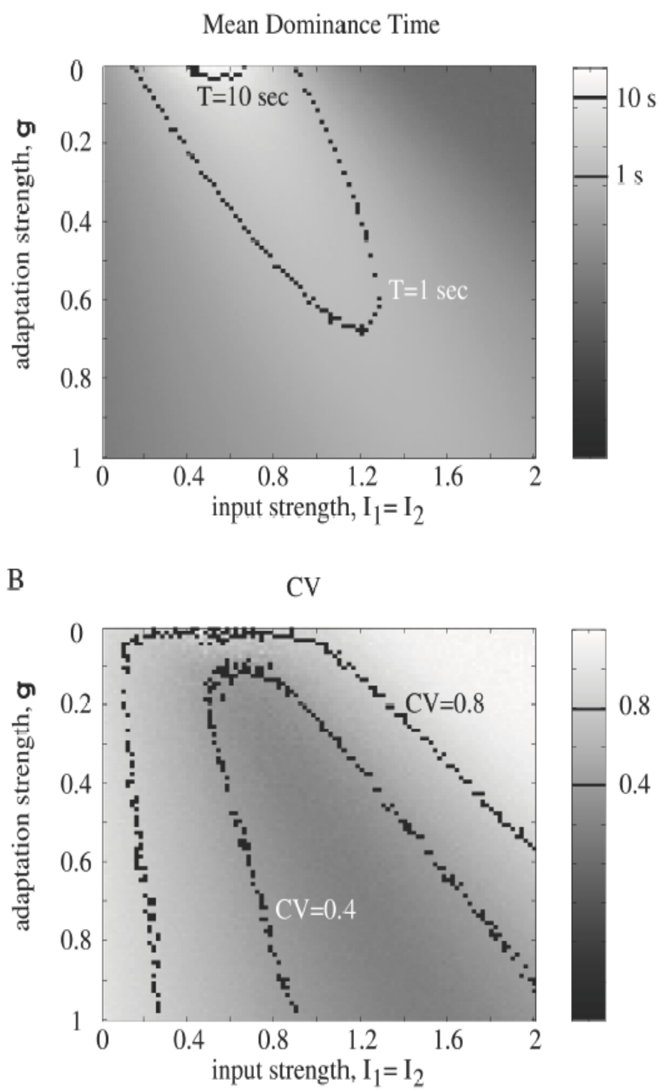
With noise

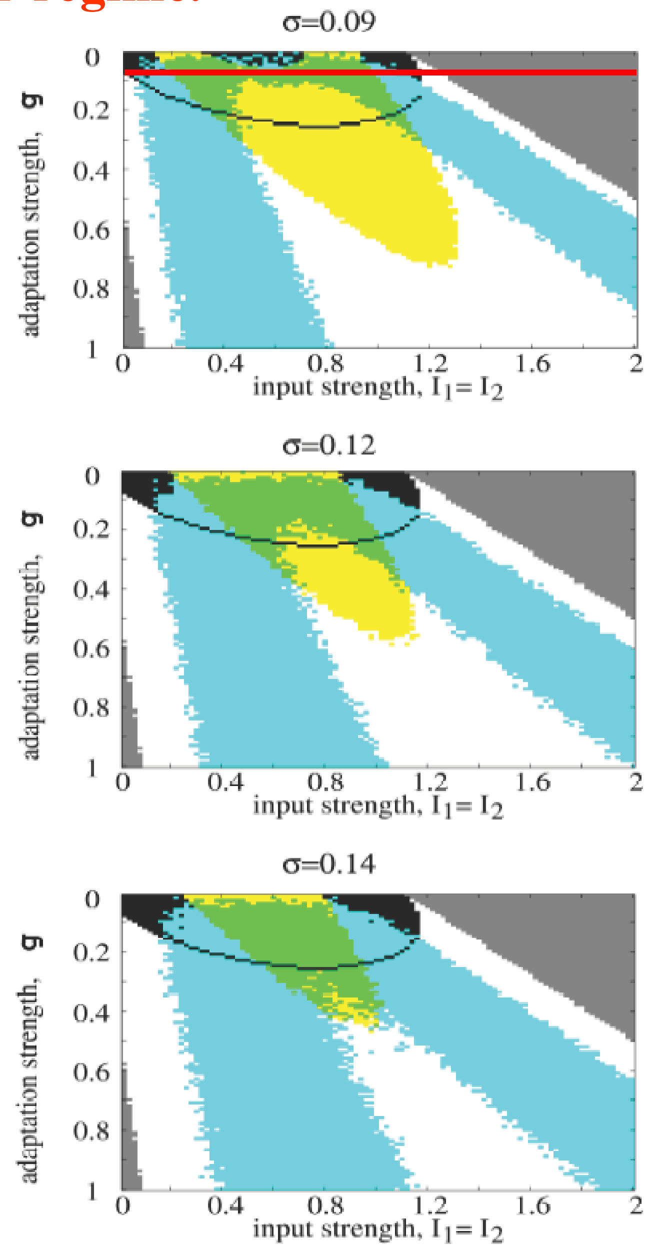


Difficult to arrange high CV and high <T> in OSC regime.

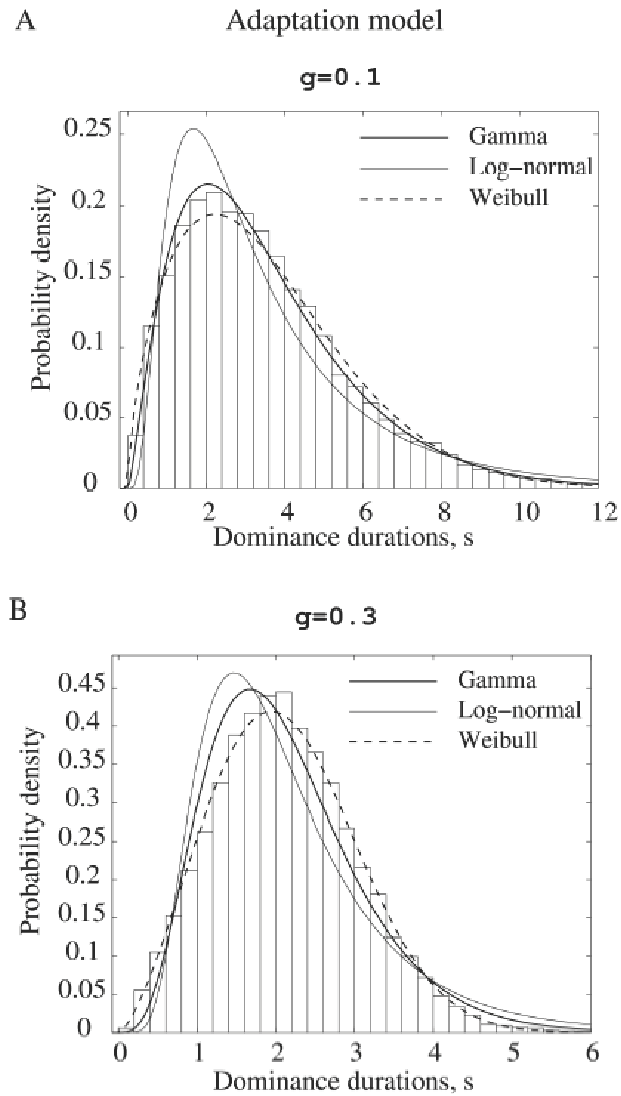
Favored: noise-driven attractor with weak adaptation – but not far from oscillator regime.

With noise





Best fit distribution depends on parameter values.



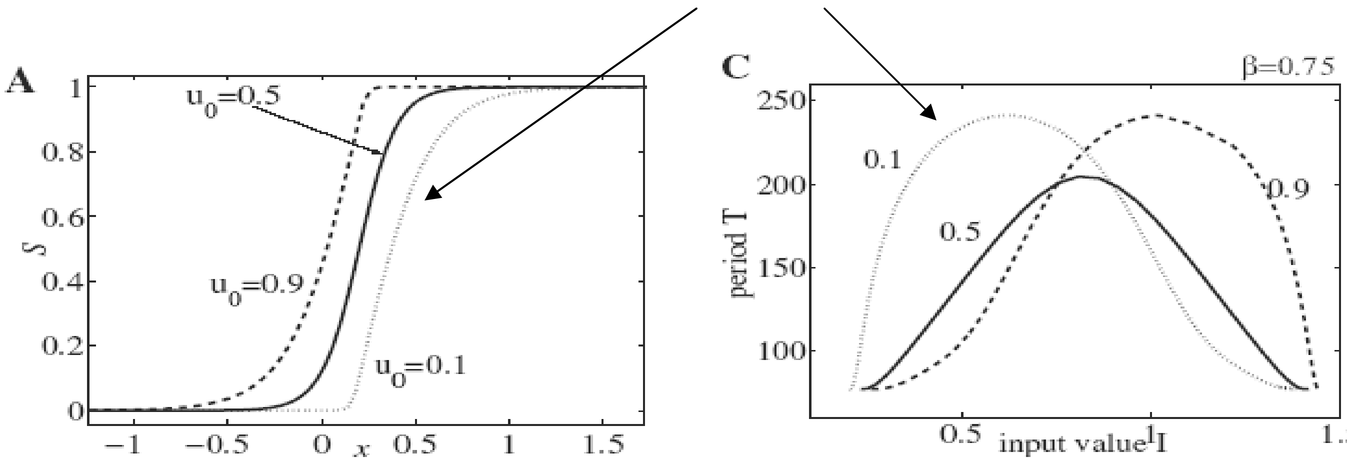
Noise dominated

Adaptation dominated

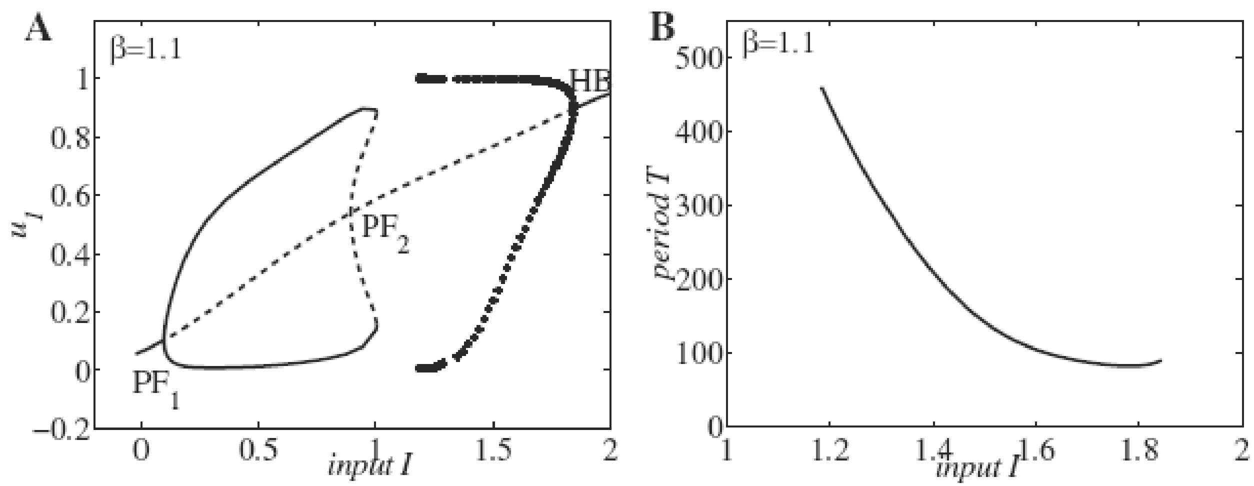
I_1 , $I_2 = 0.6$

Asymmetries may bias model toward LP-IV.

Gain fn: steep foot favors "escape", LP-IV.



Sigmoidal $a_\infty(u)$ … favors monotonic T vs I… but becomes non-monotonic w/ noise.

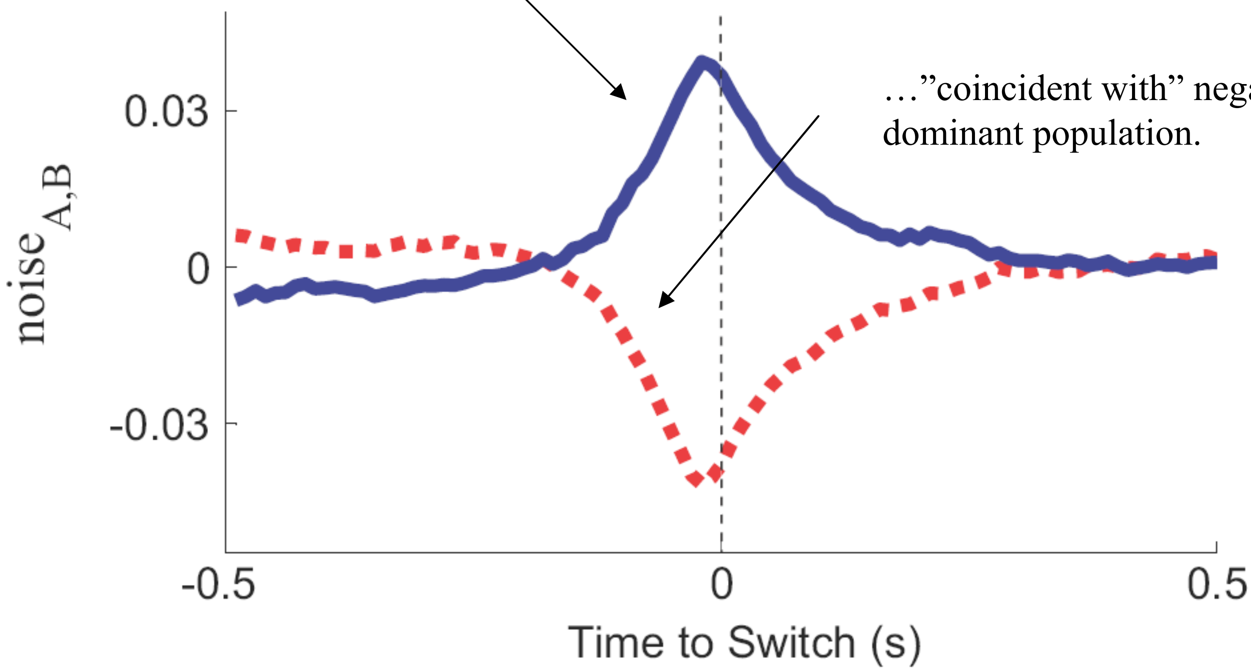


Time course of noise that causes switching.

- Reverse correlation: Switch-triggered average of noise.
- On average, positive noise to popul'n that becomes dominant and negative noise to popul'n becoming suppressed.

Positive noise, on average, induces switch from suppressed to dominant.

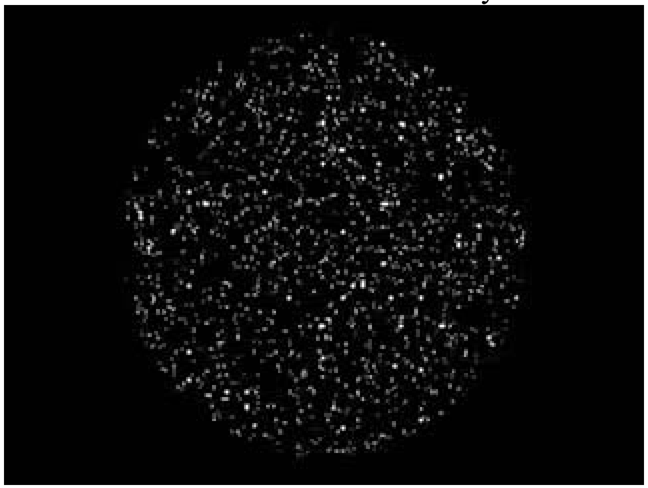
…"coincident with" negative noise to dominant population.



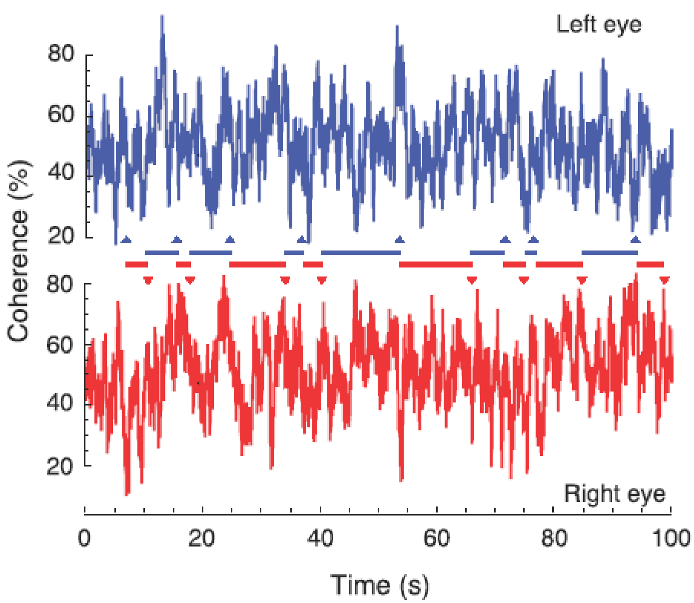
STAs for Binocular Rivalry: Experiment with moving dots

Lankheet, J Vision, 2006

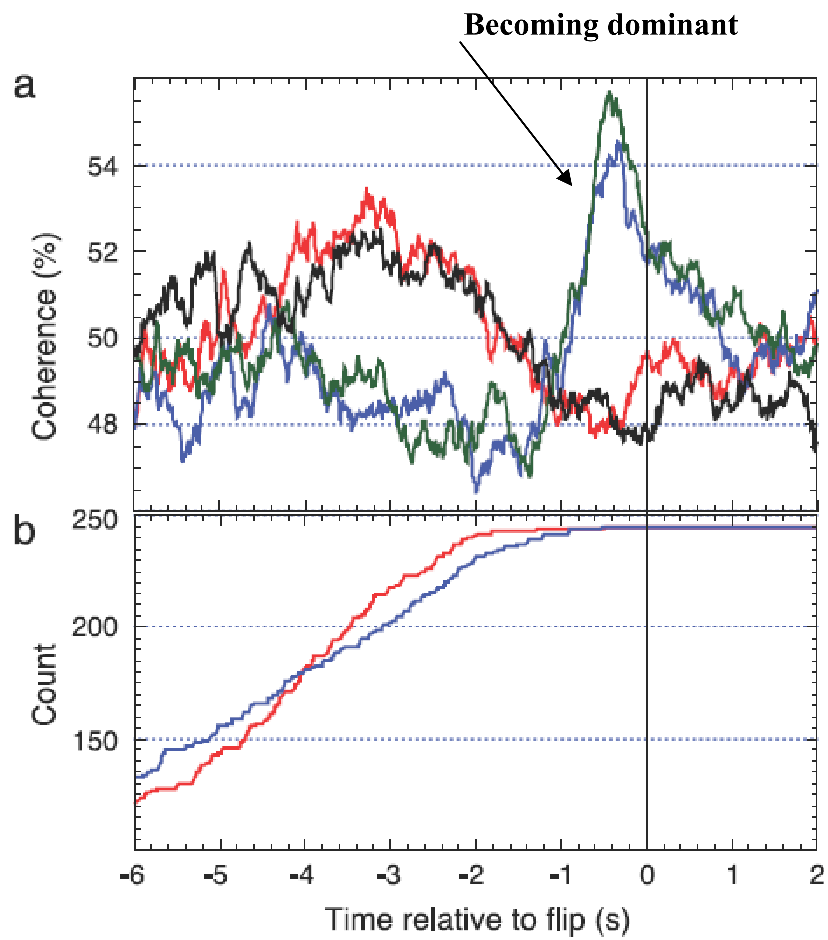
30% of dots move coherently



In Lankheet expt, coherence varies randomly – 50% on average move coherently:
NW for left eye, NE for right eye

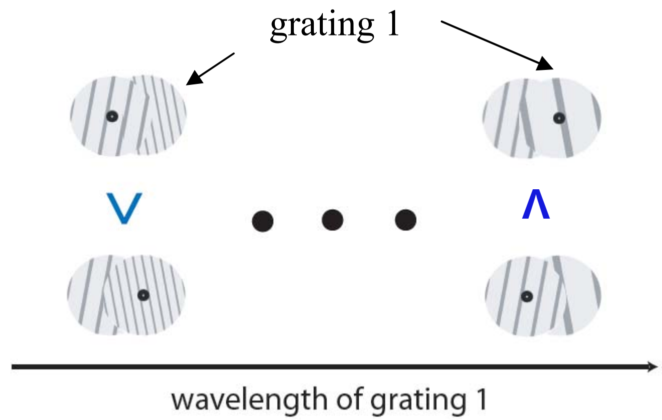


Switch triggered averages.

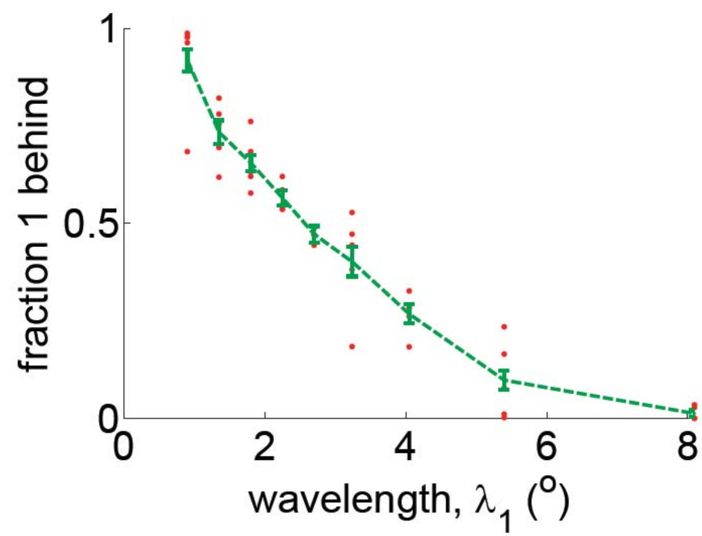


Note: this is external (sensory input) noise as opposed to internal (brain) noise.

Transparent + different freq.



Transparent + very different frequency.



Percent dominance reflects brain's estimate of probability of depth.

SUMMARY

Oscillator models:

- **predict new, non-Levelt (LP-IV), behaviors – non-monotonic dominance duration vs I_1, I_2**
- **Winner-take-all → alternation w/ noise; but non-monotonicity T vs stimulus, remains.**
- **➔ New experiments … we see only monotonic, and weakly decreasing T vs stimulus.**

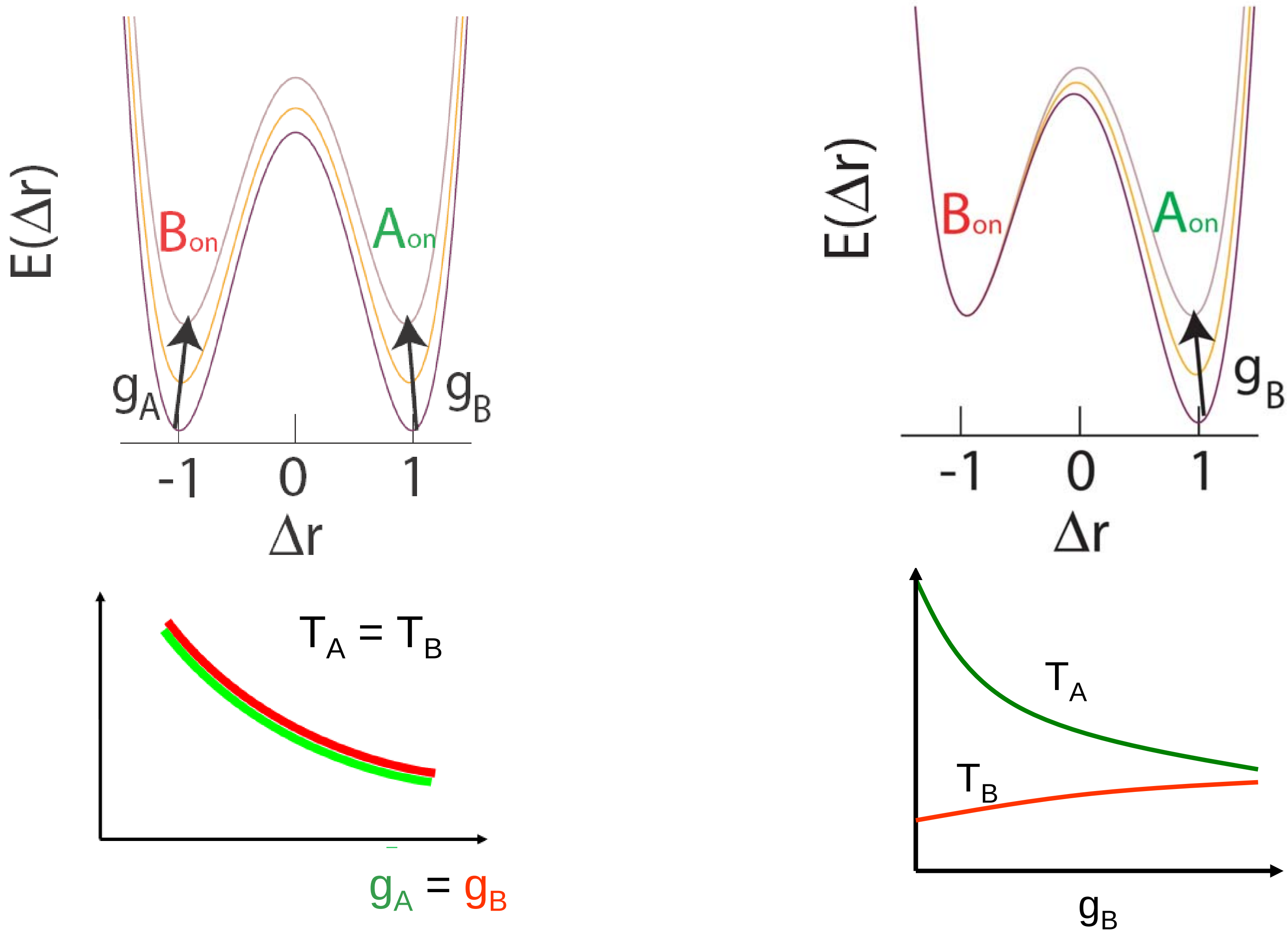
Noise-driven attractor model (Moreno):

- **Energy, rate-based and spiking network models conform to LP-IV, LP-II.**
- **Architecture:**
  -An excitatory pool receives total external and internal inputs.
  -Local inhibition and non-linear total input/local rate interaction.
- **Extendable to N-stable phenomena.**

Statistics constrains the models… noise-driven attractor but near OSC regime.

Swartz Foundation and NEI grants.

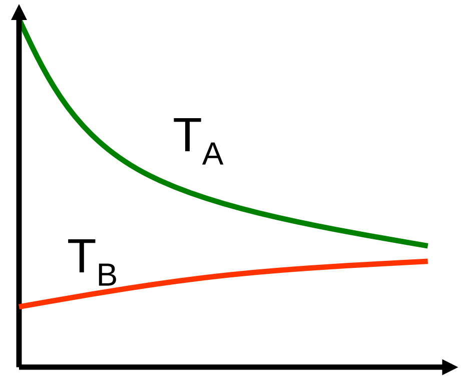
Obtaining LP-IV and LP-II in attractor models



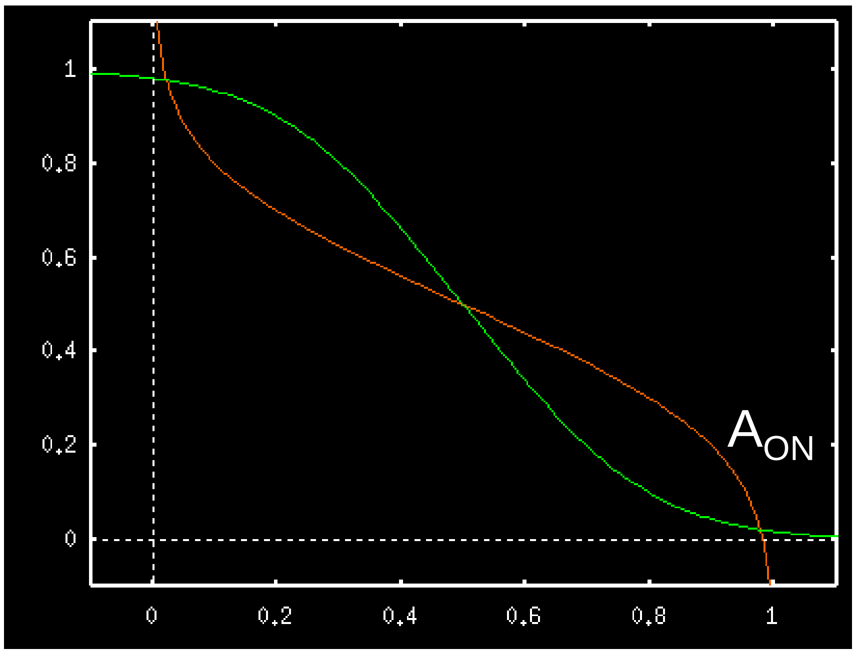
$$\tau \frac{d}{dt} r_A = -r_A + f(\alpha r_A - \beta r_B + g_A - (g_A + g_B) r_A)$$

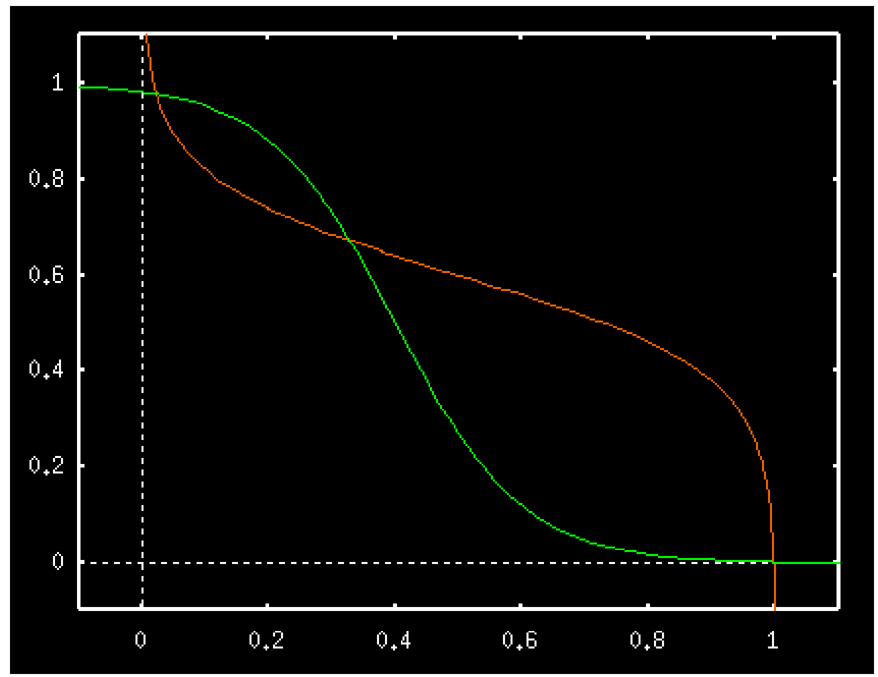
$$\tau \frac{d}{dt} r_B = -r_B + f(\alpha r_B - \beta r_A + g_B - (g_A + g_B) r_B)$$

With noise it would…



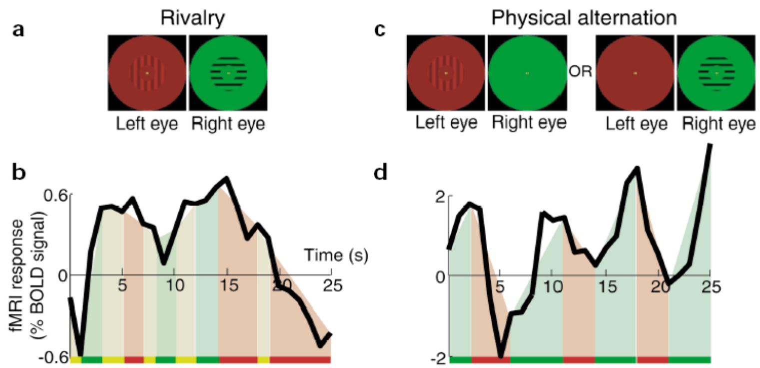
$g_A = g_B$ $\qquad$ $g_B < g_A$





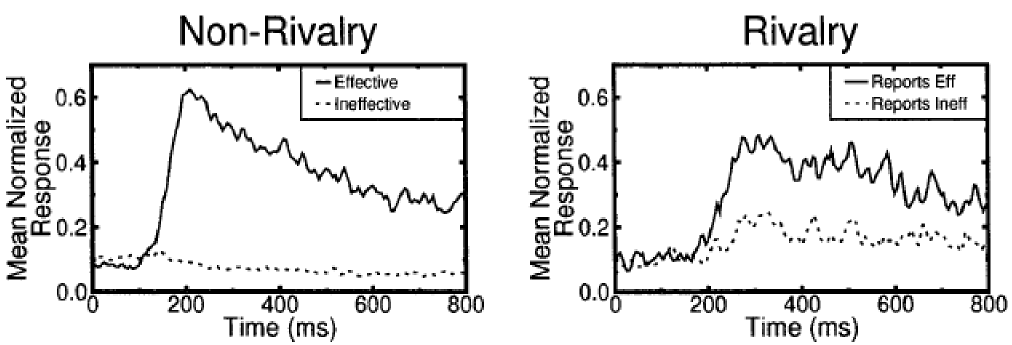
Increases residence time for A_{ON} and decrease it for B_{ON}…. analogous to LP-II.

Comparison with experimental results



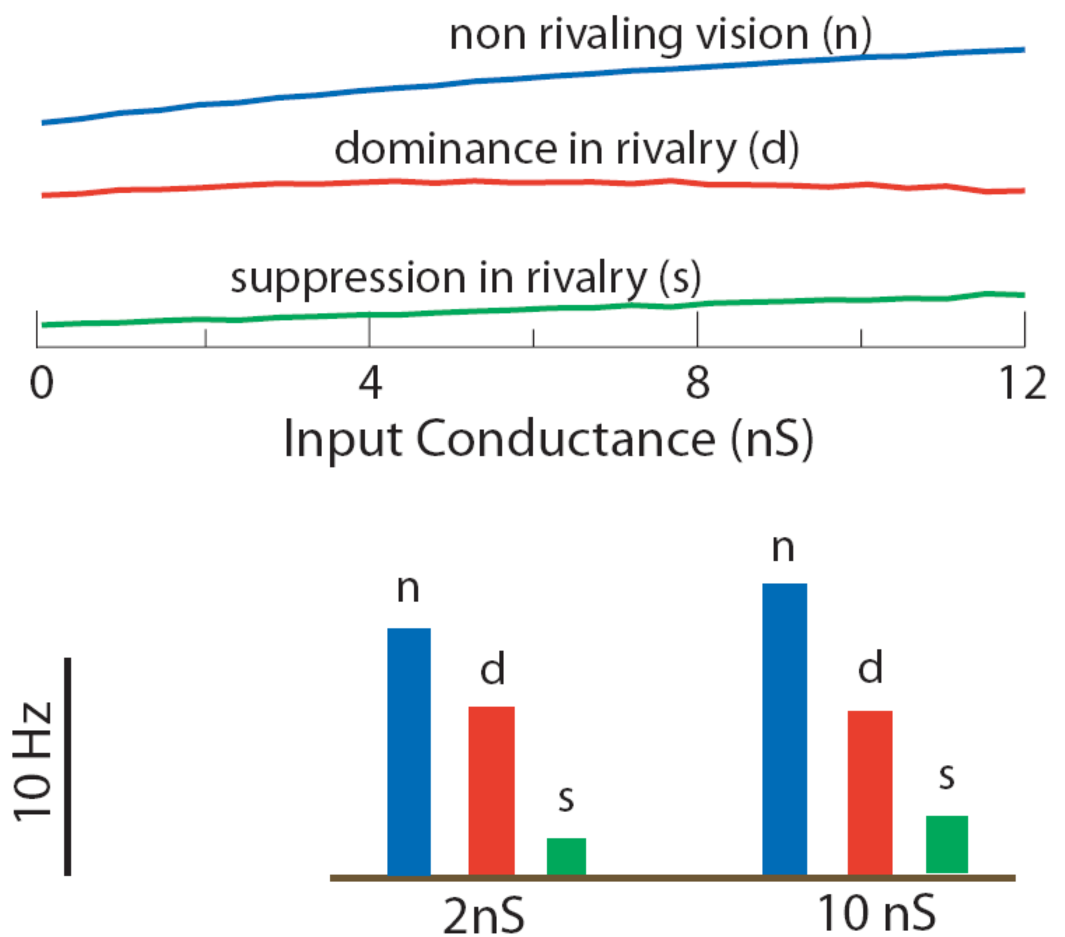
Polonsky et al, 2000
V1, V2, V3a, V4v, in humans

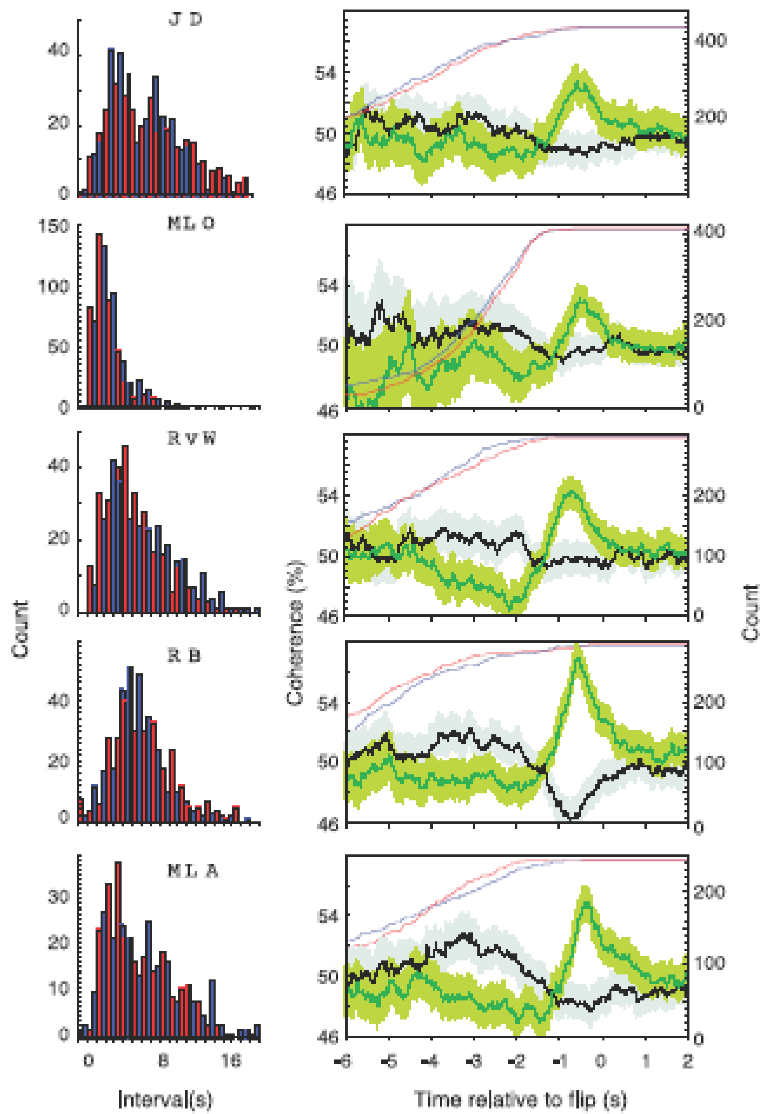
(also Lee and Blake, 2002
V1, V2, V3, V4, in humans)



Sheinberg and Logothetis, 1997
STS and IT in monkeys

Reduction of activity during rivalry compared with non-rivaling stimulation

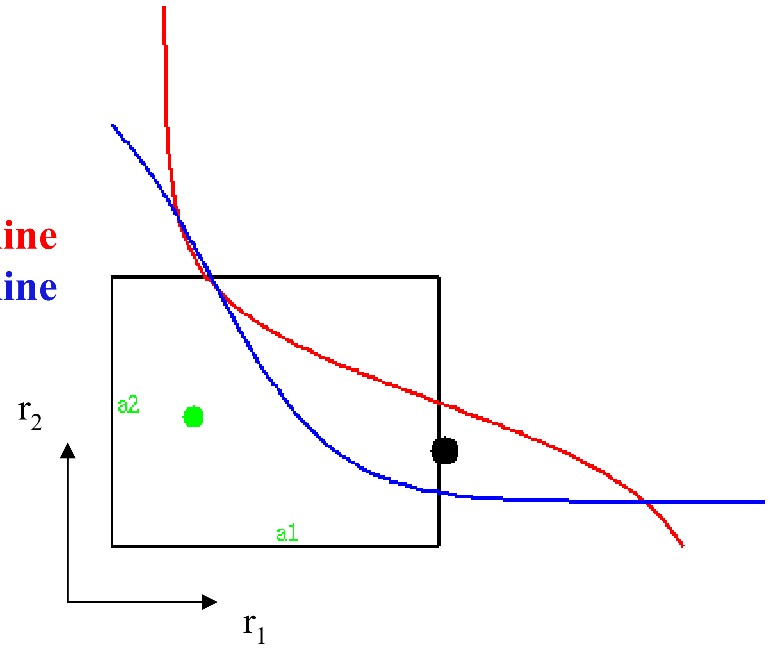




J D
ML O
R v W
R B
M L A
Count
Interval(s)
Coherence (%)
Count
Time relative to flip (s)

r_1- nullcline

r_2- nullcline

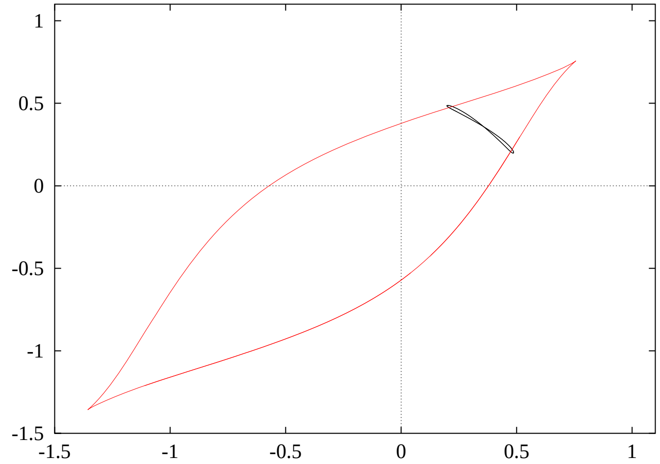


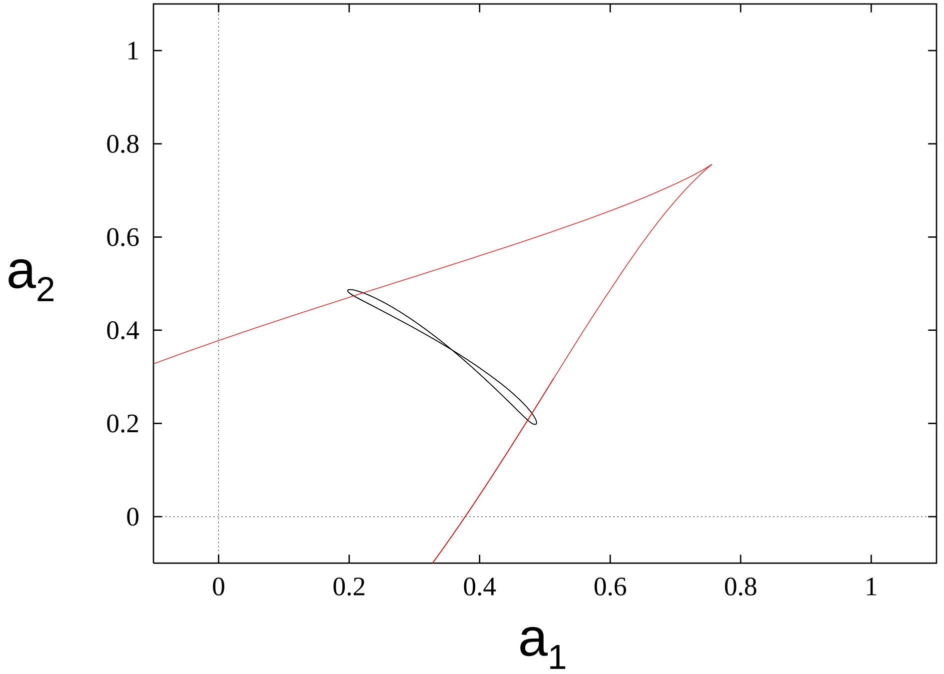
RELEASE:

At a switch: suppressed r is very low while system rides near “threshold” of dominant populn’s nullcline

$\beta = 0.9$, $I_1 = I_2 = 0.5$

Curve of SNs (knees) for Release.





Outline

Demos and basic exptl results (Levelt)
Oscillator models – noise gives randomness to period
-- inhib'n + slow neg feedback
Attractor models – noise driven
-- no oscill'n w/o noise
-- double-well potential motivates neural architecture
-- "cross-over"

To do: LP II (or not) for adaptation model
JR look at Demos
SN-curves, cusps… import to XPP w/ traj

Make Ruben model as oscillator and do AUTO
Check LP IV and LP II

Credit to Nava XXX

Curves of knees (SNs) .. From AUTO

Project onto the a1-a2 plane and show traj.

This is Escape…. Also seen by looking at moving nullclines

Show an example of Release.

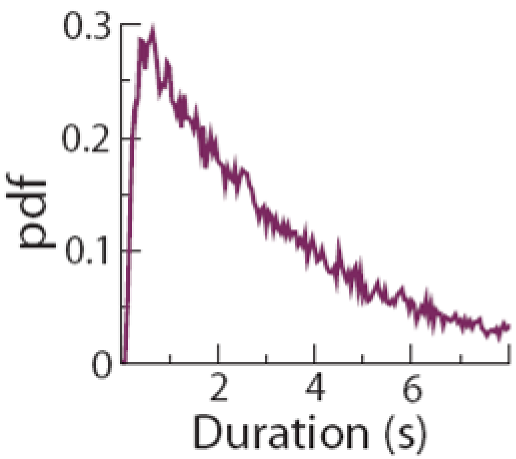
Refer to Rodica who has worked this out nicely for Heaviside. w/ Thms about some structural issues… equivalence of some models

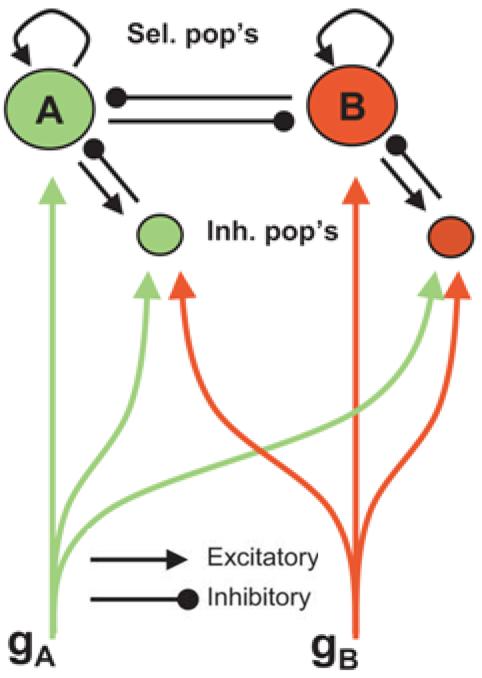
Model produces LP-II but …

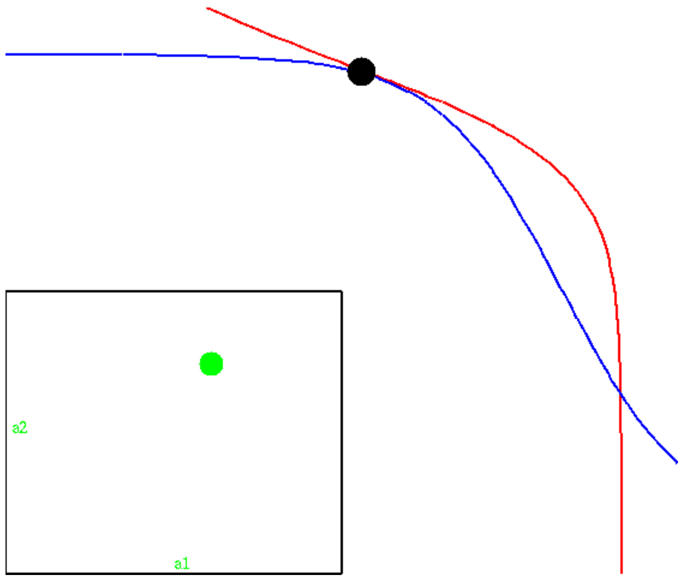
i. Direct cross-inhibition requires N^2 connections.

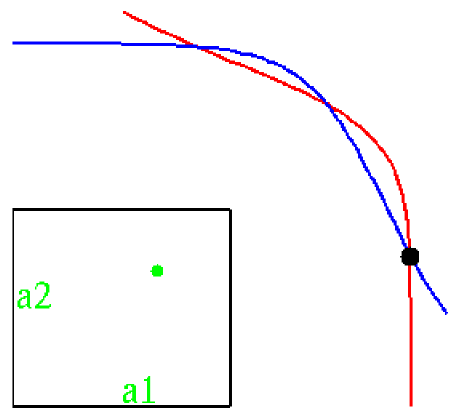
ii. Multiplicative local inhibition. How?

iii. Exponential-like distributions… role for adaptation…

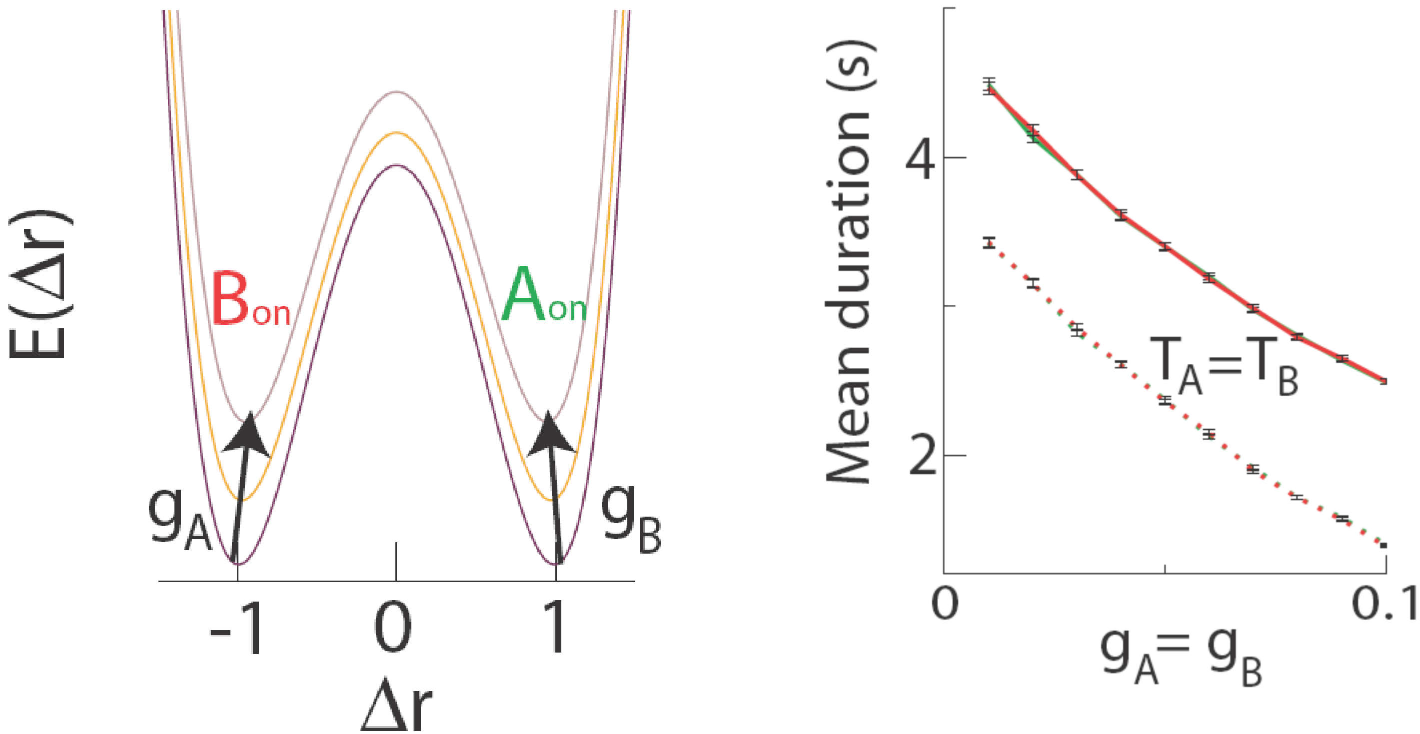




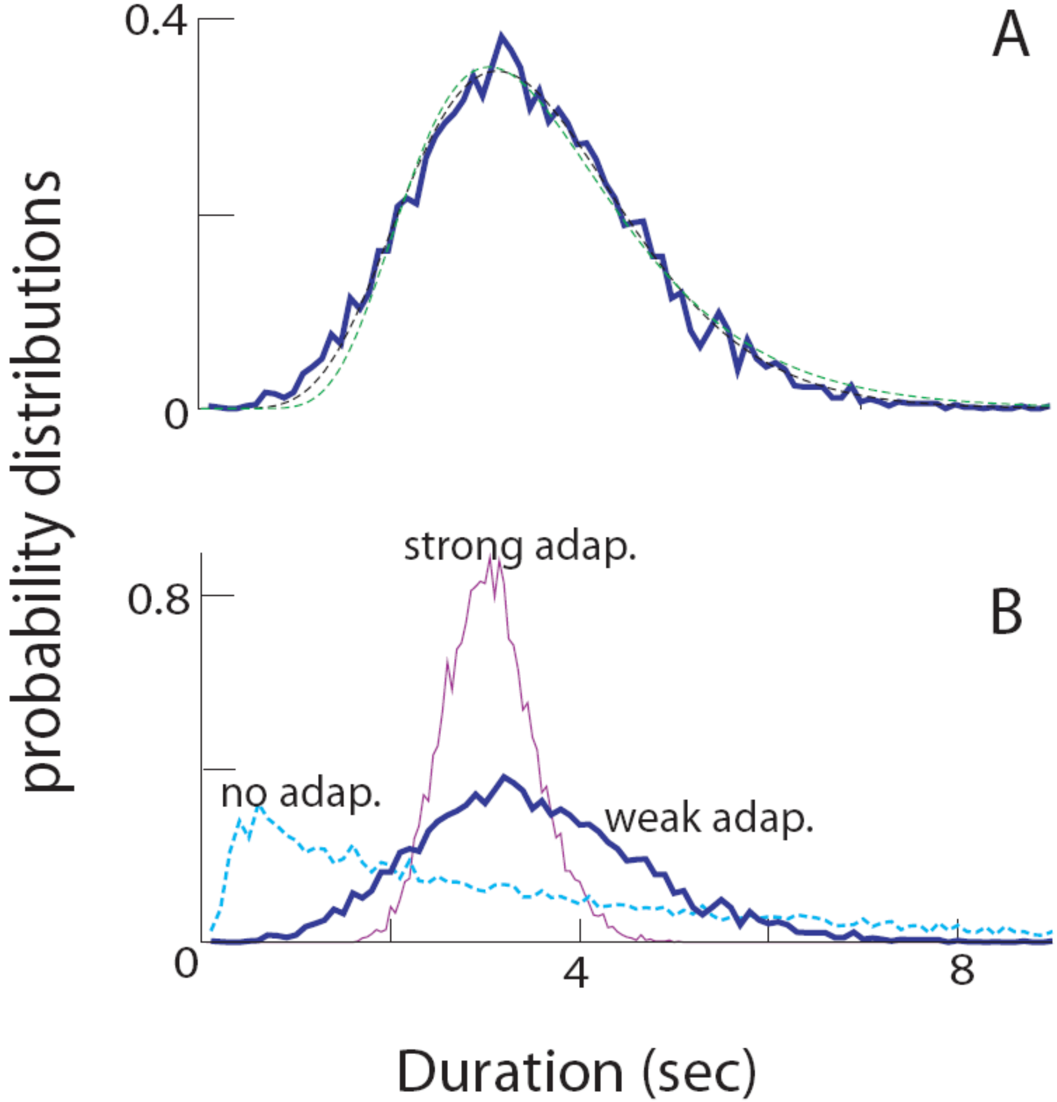

a2
a1


a2
a1

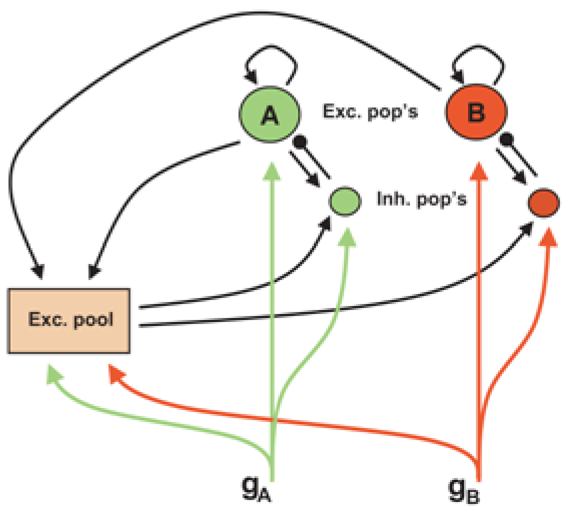
Obtaining LP-IV in attractor models

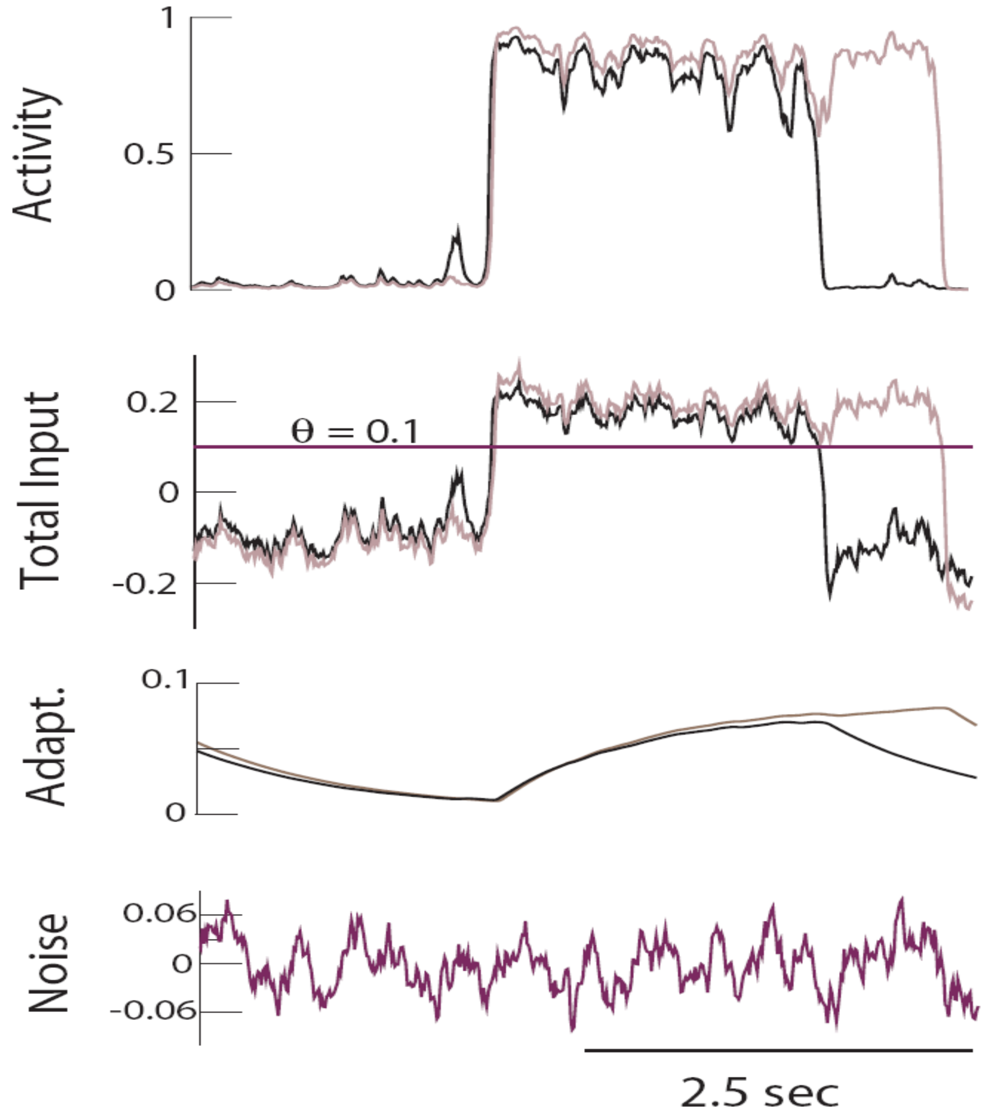


Adaptation shapes the distribution.
Weak adaptation is required.



Dynamical properties





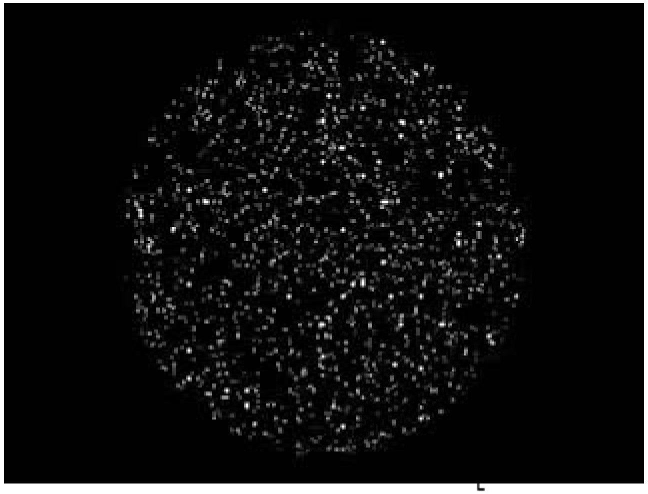
Brown: low stimulation
Black: high stimulation

Activity decreases for stronger stimulus.

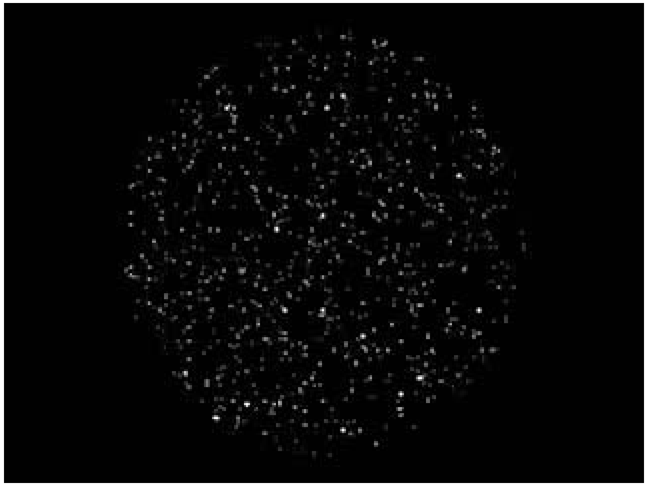
1. The two alternative forced choice task (TAFC)

Subject is shown one of two stimuli drawn at random, must respond by pushing L or R button. Simple case: visual pattern of dots, fraction $q < 1$ moving either to left (cond. 1) or right (cond. 2), $1 - q$ moving randomly; q adjusts difficulty.

30 % coherent



5 % coherent

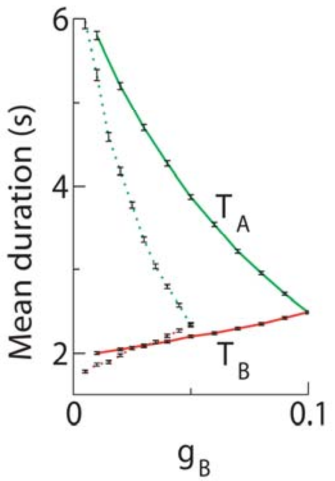


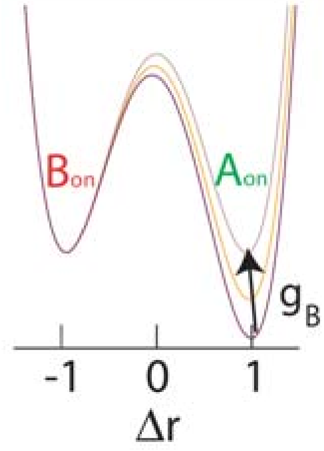
Bill Newsome

- Behavioral measures: reaction time (RT) distribution, error rate (ER).
- Neural measures: fMRI (humans), direct recordings in visual processing and motor areas (monkeys: MT, LIP, FEF).

Energy function model

Levelt II





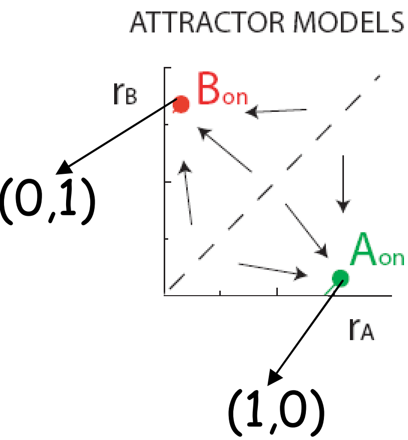
Energy function:

$$E(\Delta r) = \Delta r^4 - 2\Delta r^2 + g_A(\Delta r - 1)^2 + g_B(\Delta r + 1)^2$$

Dynamics:

$$\tau \frac{d}{dt}\Delta r = -4\Delta r(\Delta r^2 - 1) - 2g_A(\Delta r - 1) - 2g_B(\Delta r + 1) + n(t)$$

Network based-rate model



2D energy function

Dynamics:

$$\tau \dot{r}_A = -r_A + f(\alpha r_A - \beta r_B + g_A - (g_A + g_B) r_A + n_A(t))$$

Recurrent excitation

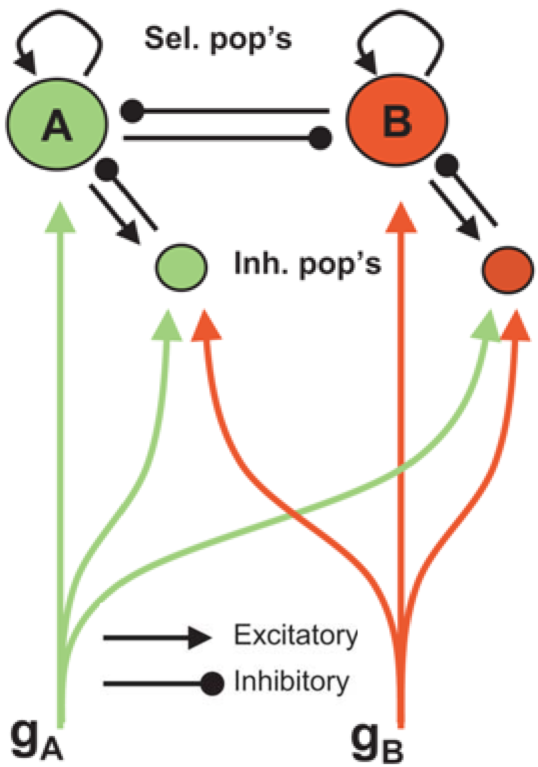
Inhibition

Input

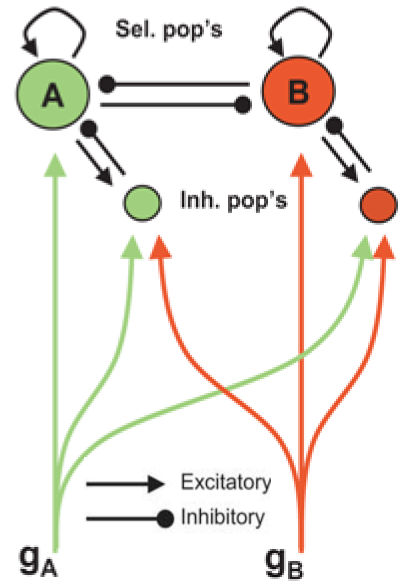
Multiplicative inhibition

Noise

Responsible for LP-II: negative input in the dominant state!



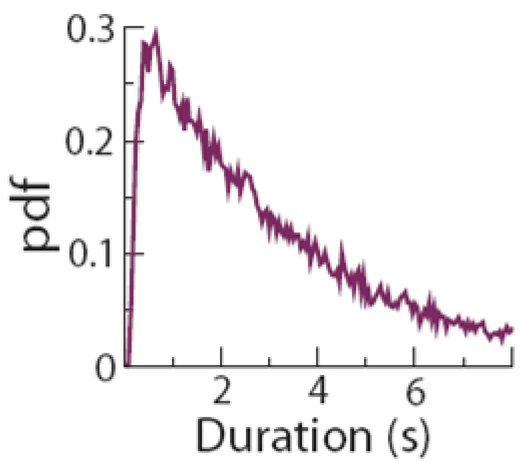
Model produces LP-II but …

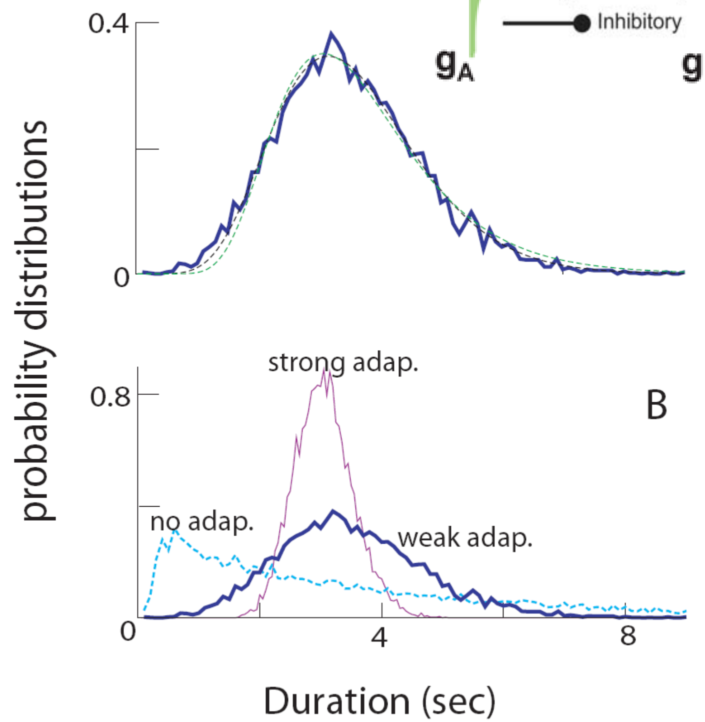


i. Direct cross-inhibition requires N^2 connections.

ii. Multiplicative local inhibition. How?

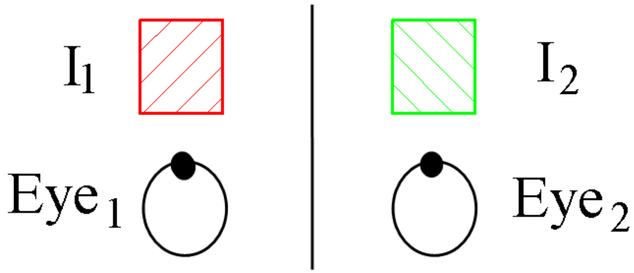
iii. Exponential-like distributions… role for adaptation…





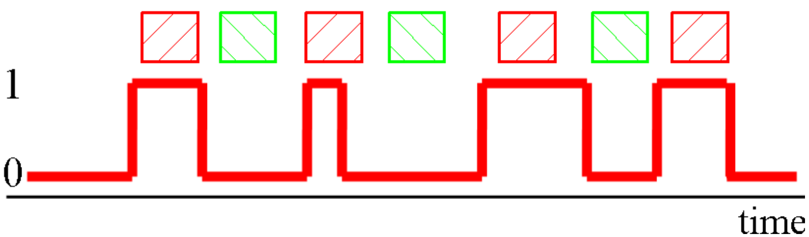
Binocular rivalry:

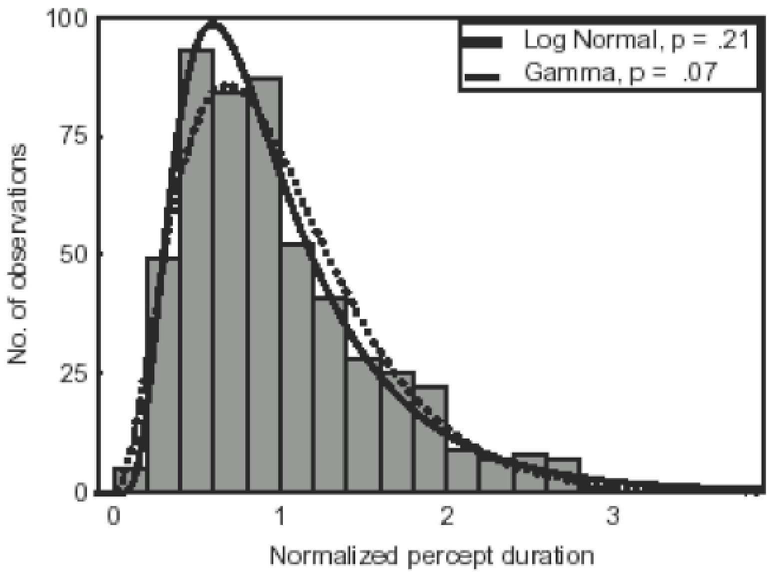
alteration of percepts when different steady images are presented to the two eyes



Mutual inhibition with slow adaptation ➔ alternating dominance and suppression

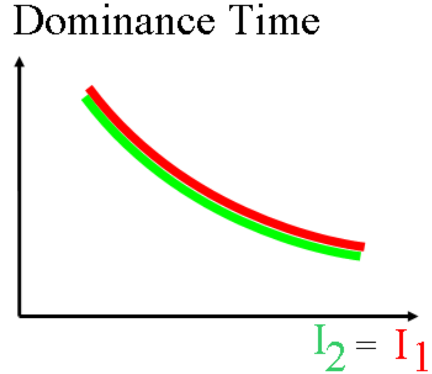
Perception and activity:





Properties:

Levelt's Proposition IV:

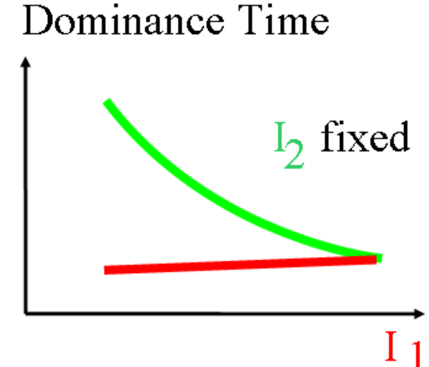


both inputs increase together

⇩

dominance time decreases

Levelt's Proposition II:

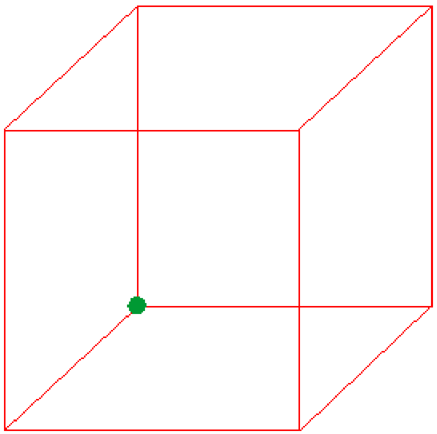


one input decreases

⇩

OTHER eye's dominance time increases

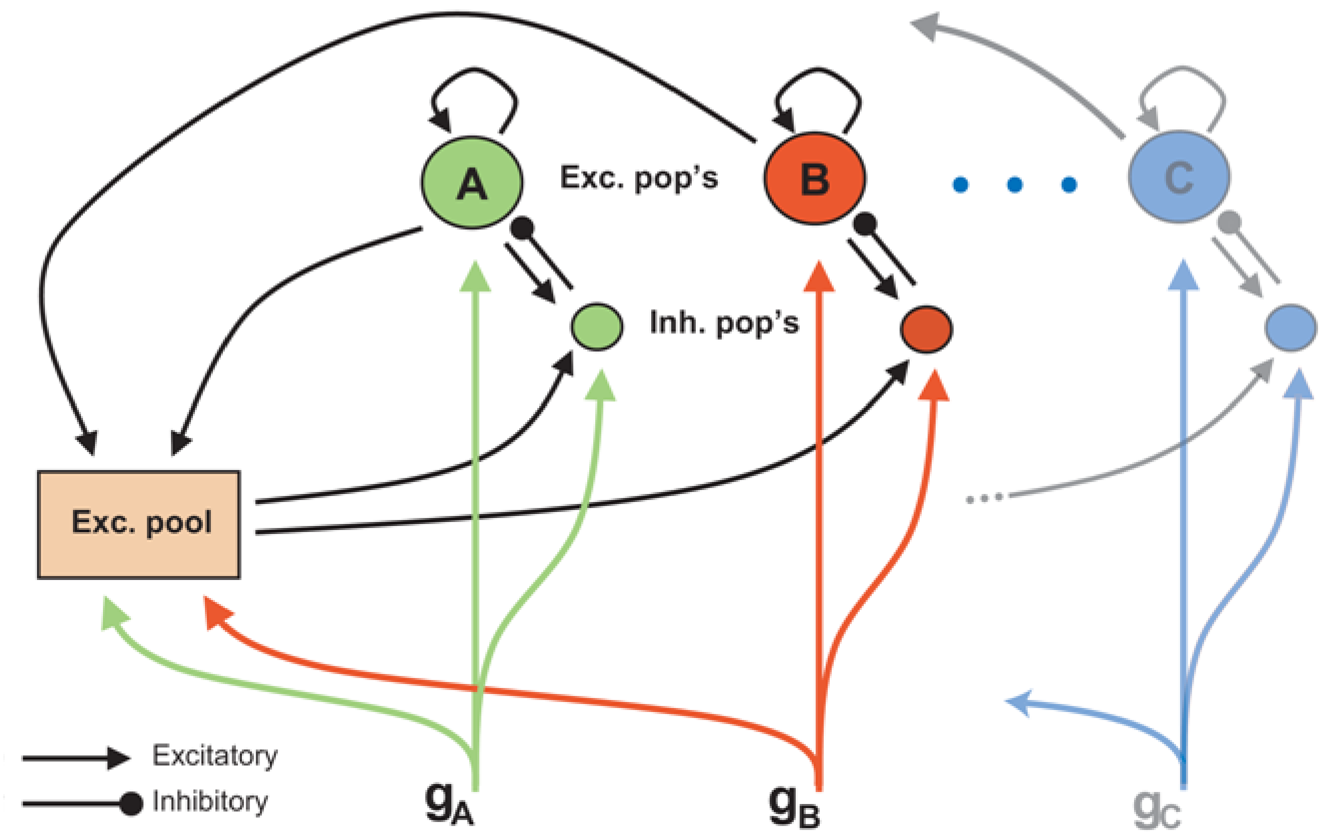
Levelt, 1968



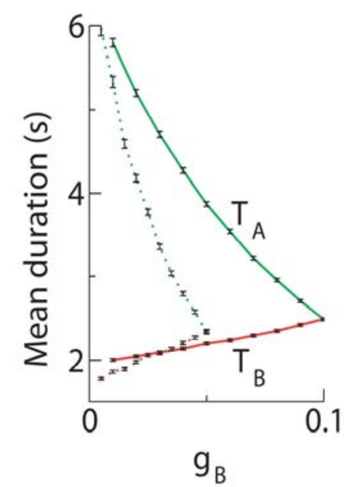
Necker Cube

Look at the green dot. Is it located in the lower left rear or in the lower left front?

Architecture with a global exc. pool.

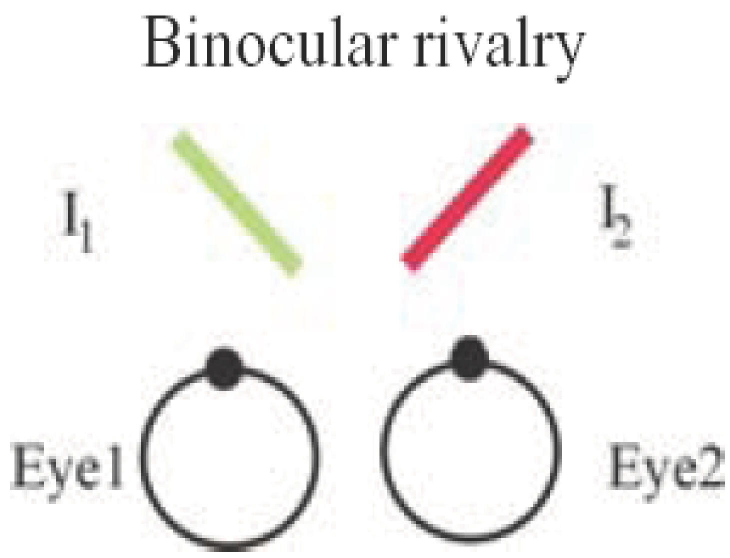


Satifies LP-IV and LP-II

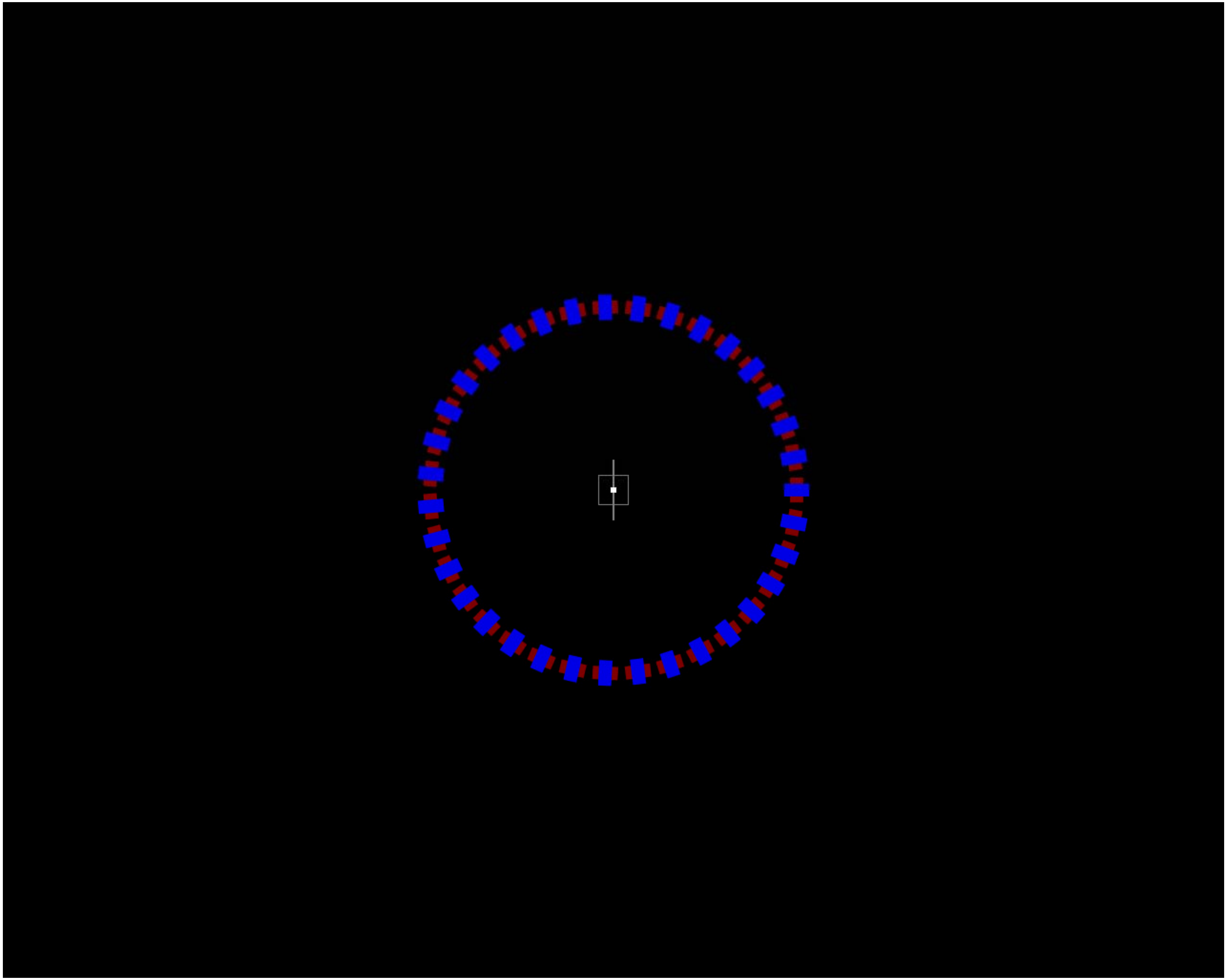


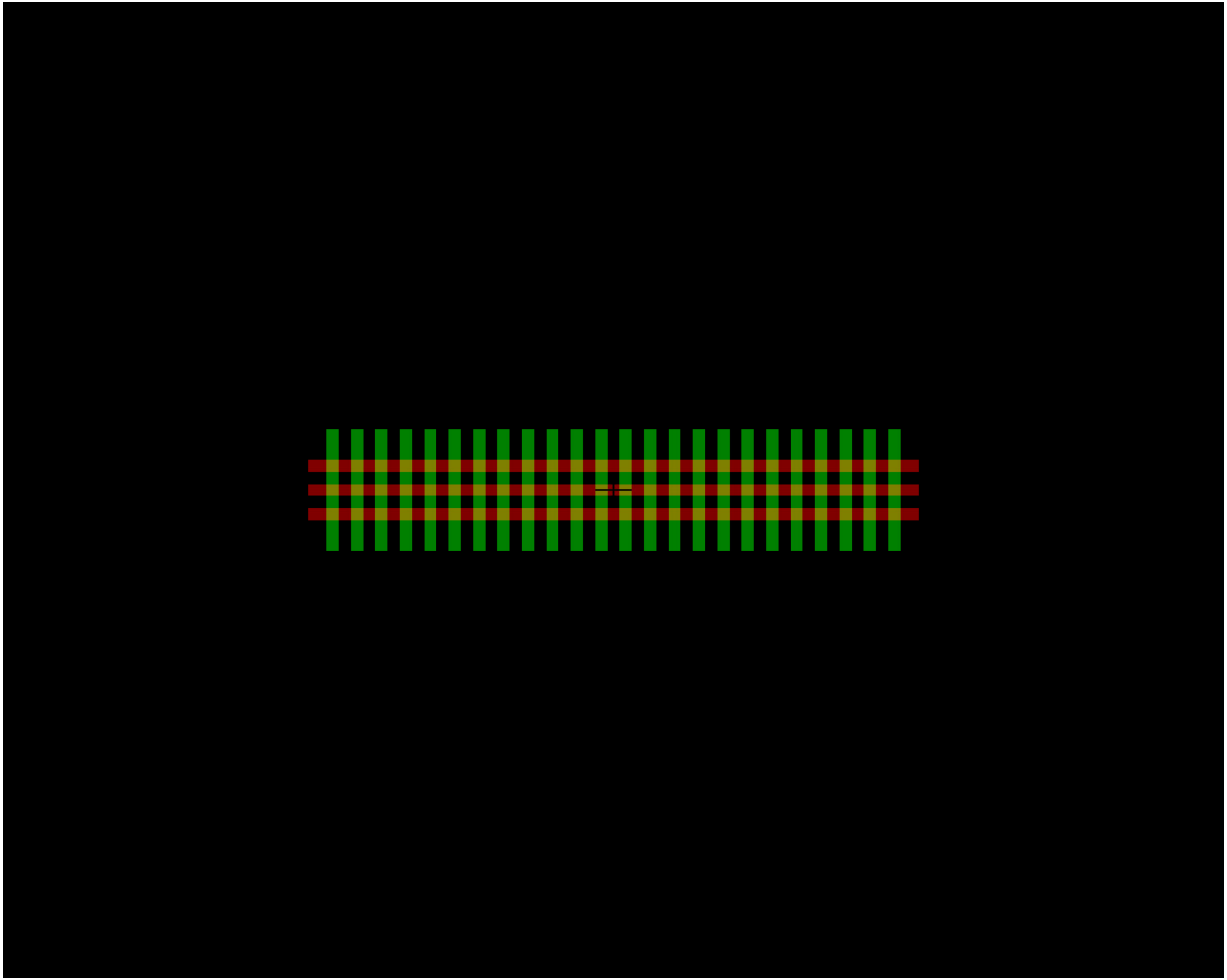
Connections scale linearly with N.

In binocular rivalry: present different images to each eye. Do we perceive an averaged image or…?



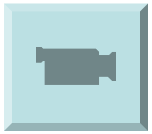
From: Tong et al. (1998)



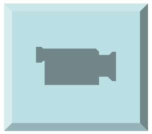


PLAID DEMO

R Moreno, N Rubin



Transparent + different freq.



Transparent + coherent.