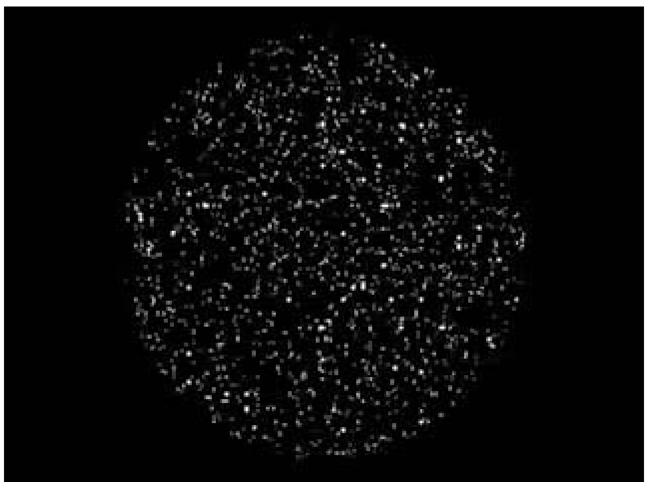
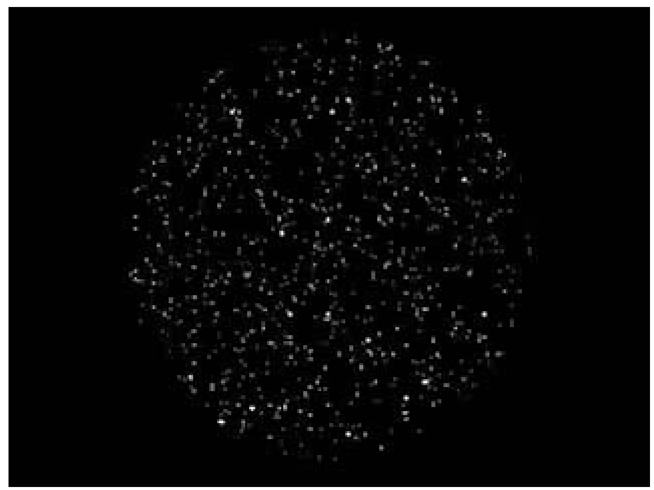
1. The two alternative forced choice task (TAFC)

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

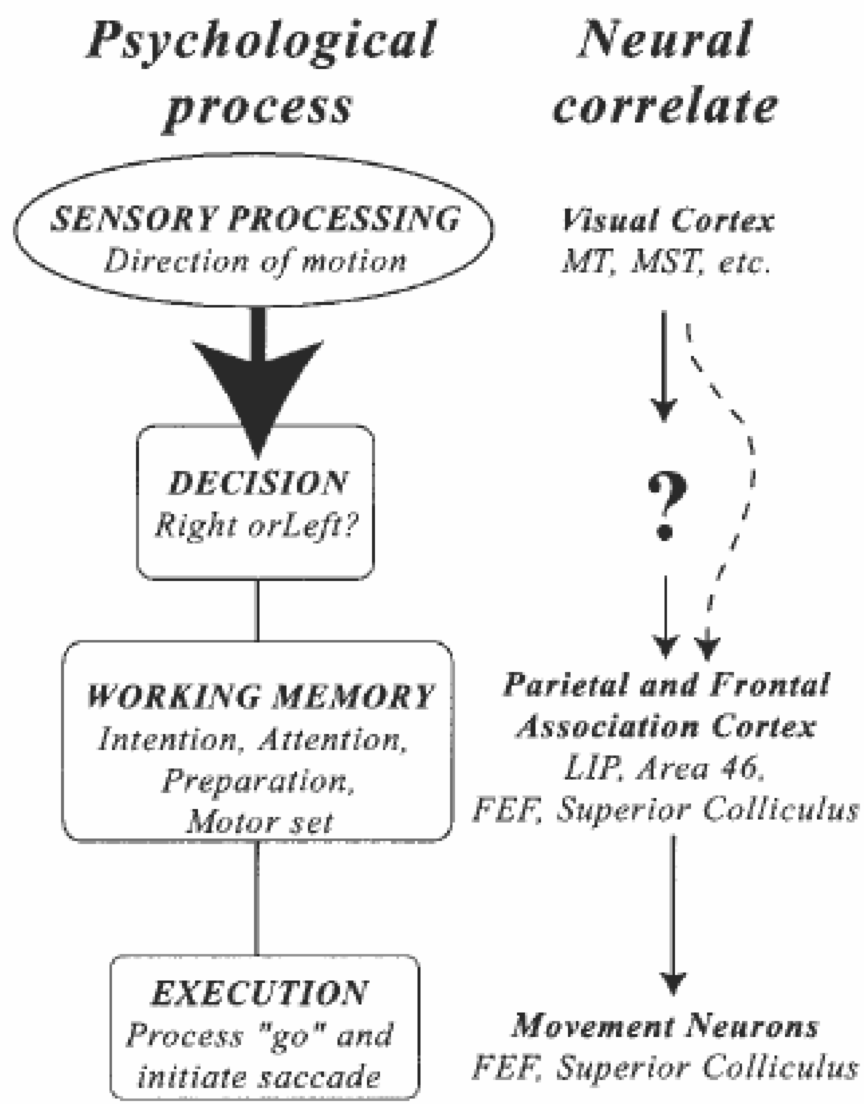


5 % coherent



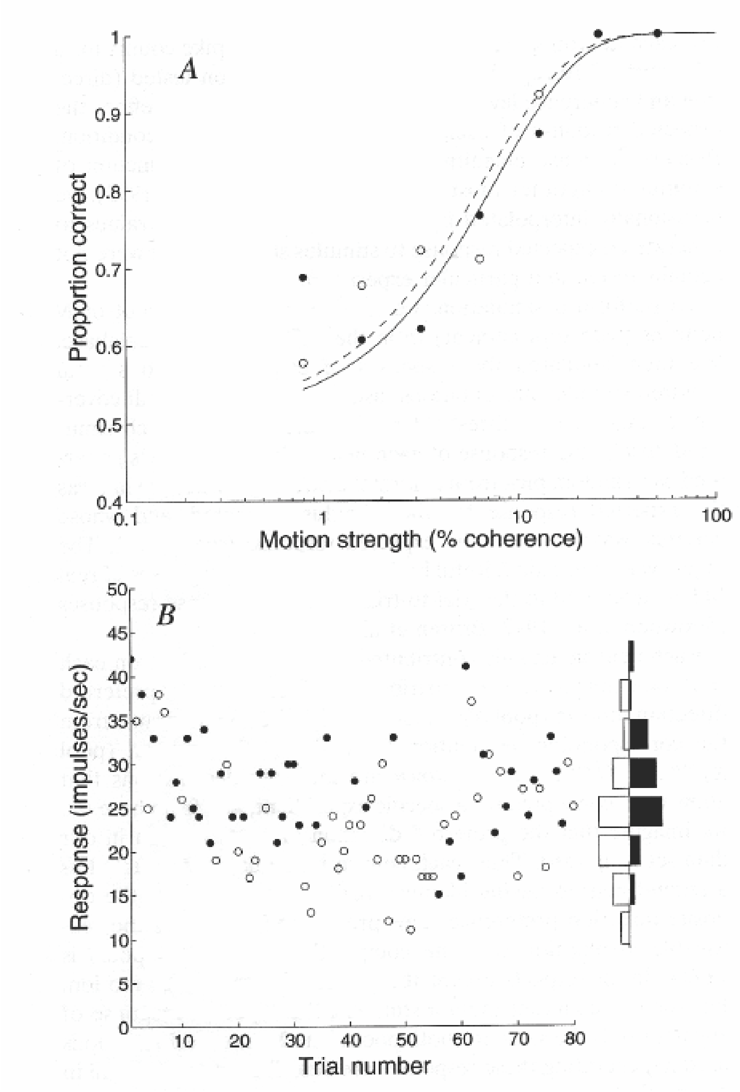
Bill Newsome

- 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).



Shadlen & Newsome, 2001

Newsome Dot Task



Open & dashed: Behavioral
Filled & solid: Neuron

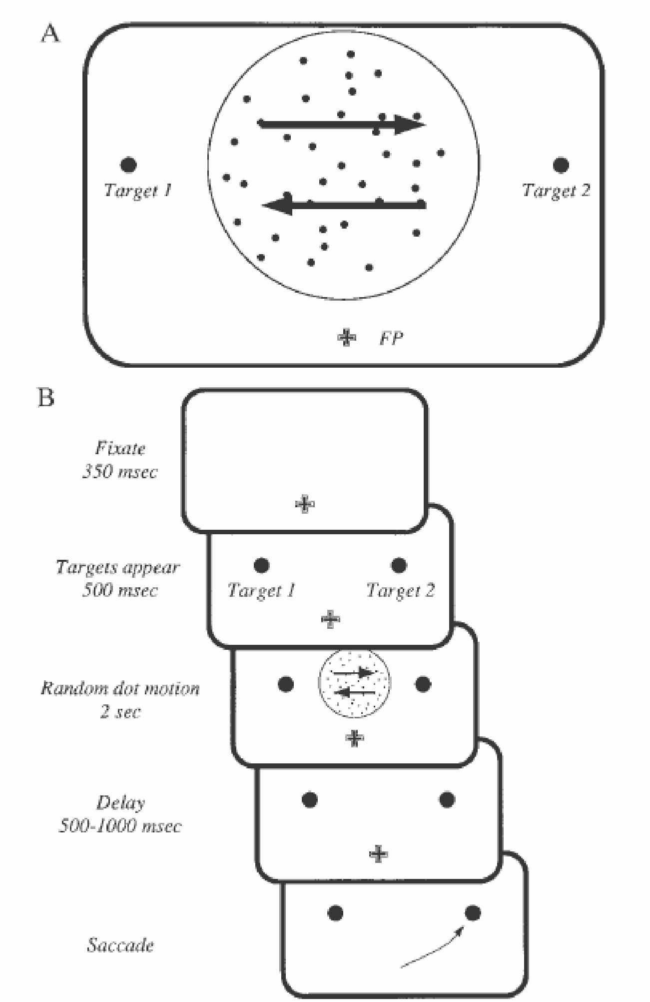
Fit w/ Weibull distribution

Filled –Target 1 chosen; Open -Target 2 chosen.

Zero coherence case: but the neuron predicted the monkey's choice w/ 68% accuracy… "choice probability"… reflected monkey's behavioral choice, not sensory input.

Shadlen MN, Britten KH, Newsome WT, Movshon JA A computational analysis of the relationship between neuronal and behavioral responses to visual motion. J Neurosci. 1996 Feb 15;16(4):1486-510.

Decision: accumulating evidence over time… for making the decision.



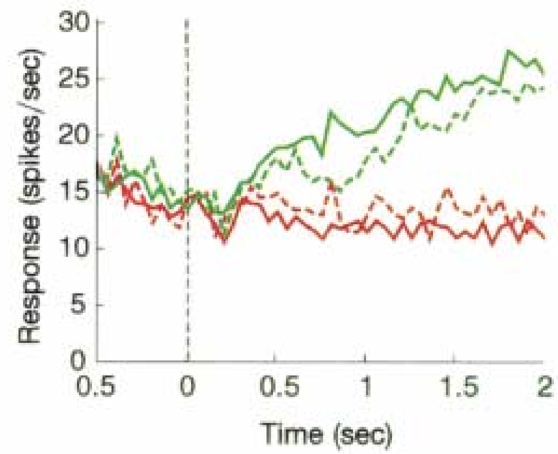
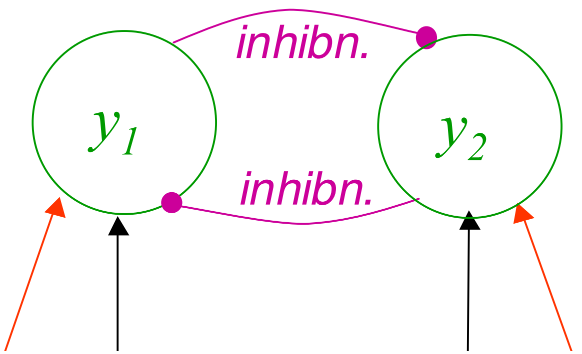


FIG. 4. A histogram comparing the average responses of a population of 47 neurons for correct choices (solid lines) and erroneous choices (dashed lines). The monkey's decision is indicated by the color (green for T1 choices, red for T2). The motion stimulus was 6.4% coherence toward or away from the movement field. Average responses were computed in 60-msec bins and plotted relative to stimulus onset (time 0). See text for details.

LIP neurons… identify salient targets
and guide the eye movement

Shadlen & Newsome, 1996, 2001

Firing rates (y_1, y_2) of competing neural pops...



$$\frac{dy_1}{dt} = -y_1 + f\left(-\beta y_2 + I_1 \quad + \eta(t)\right)$$
$$\frac{dy_2}{dt} = -y_2 + f\left(-\beta y_1 + I_2 \quad + \eta(t)\right)$$

Linearize:

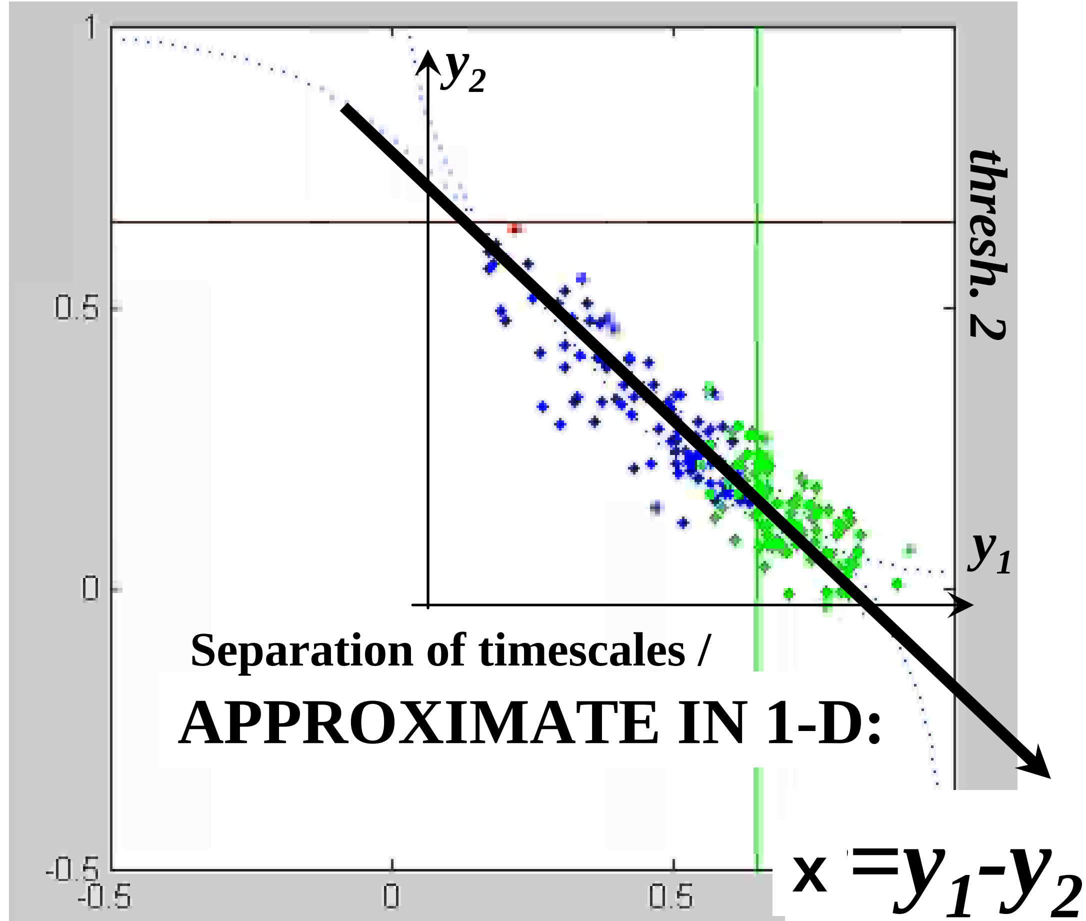
$$\frac{dy_1}{dt} = -y_1 + g * (-y_2 + I_1 \quad) + \eta_1)$$
$$\frac{dy_2}{dt} = -y_2 + g * (-y_1 + I_2 \quad) + \eta_2)$$

Subtract:

$$\frac{d\,\mathrm{x}}{dt} = -\,\mathbf{x} + g\,(\mathrm{x} + I_1 - I_2) + g\eta(t) \qquad (1)$$

TUNE GAIN to $g = 1$, define drift $A = I_1 - I_2$

$$\frac{d\,\mathrm{x}}{dt} = A + \eta(t) \qquad (2)$$

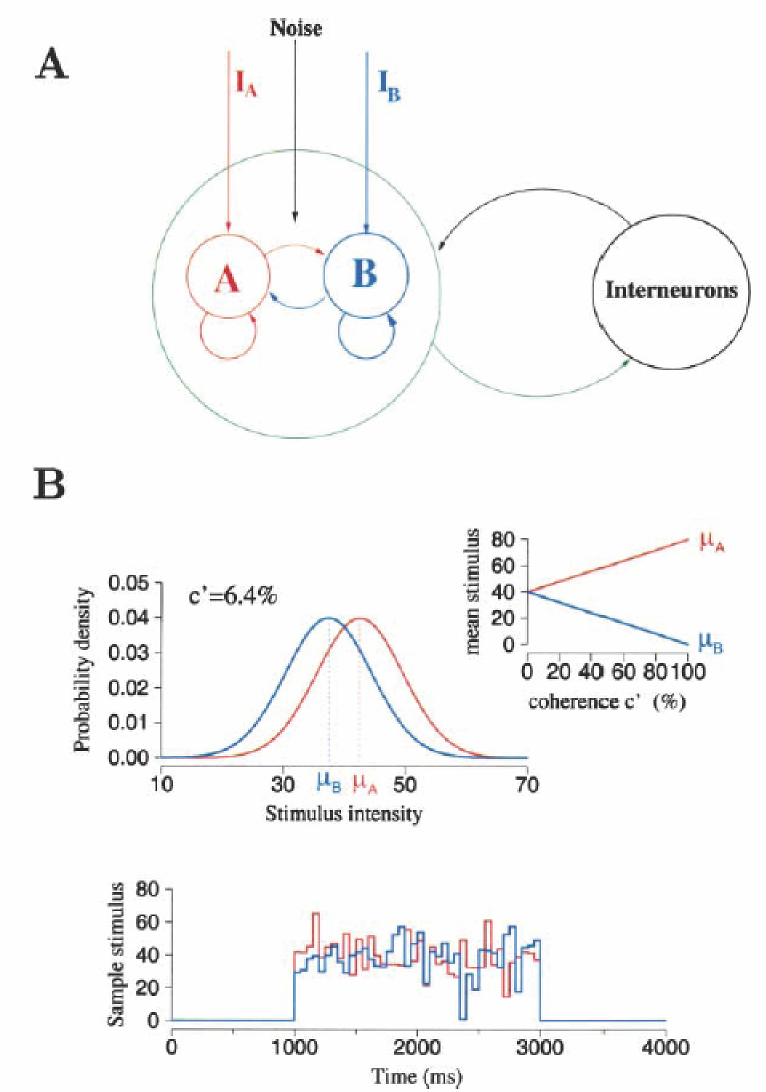


recover SPRT, optimal decision strategy

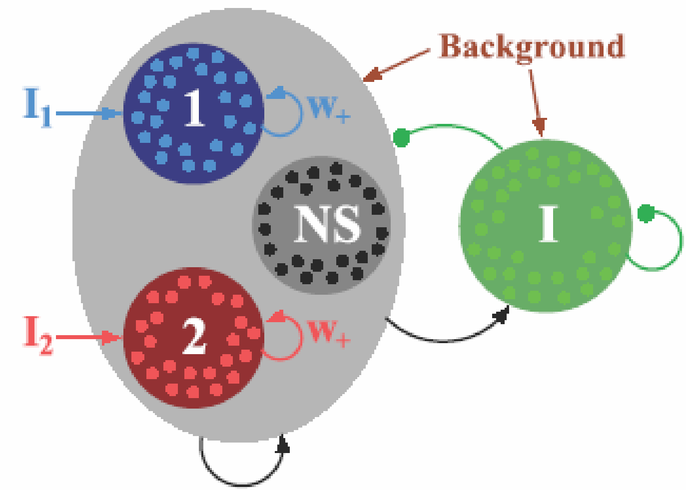
Neuron, Vol. 36, 955–968, December 5, 2002, Copyright ©2002 by Cell Press

Probabilistic Decision Making by Slow Reverberation in Cortical Circuits

Xiao-Jing Wang



Spiking neuronal network model



$N_E = 1600$
$N_I = 400$

7200
variables

Features:

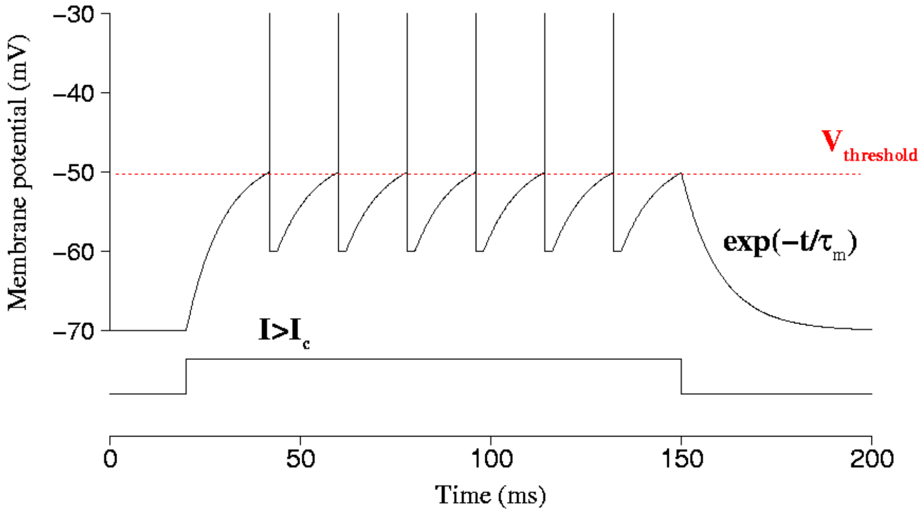
- motion-selective populns
- slow reverberation and integration
  - – NMDA syns
- WTA competition – feedback inhib'n
- random responses

- within group connections, w_+ , are stronger
- input $I_{A,B}$ is from MT = noisy.

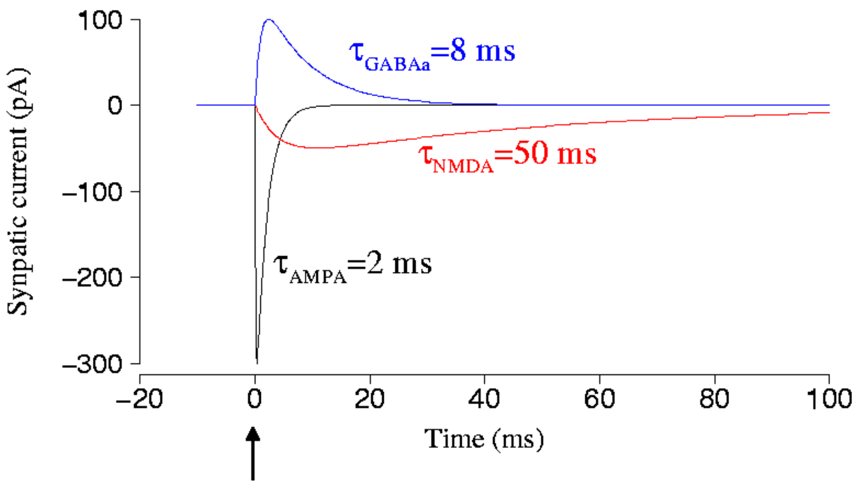
Elements of cell-based network model.

Wang 2002, Wong&Wang 2006

Point neurons, LIF.



Synapses, conductance based.



Voltage-clamp: V_m = constant (say at -60 mV)

Delayed discrimination expt.

Populn 1 Populn 2

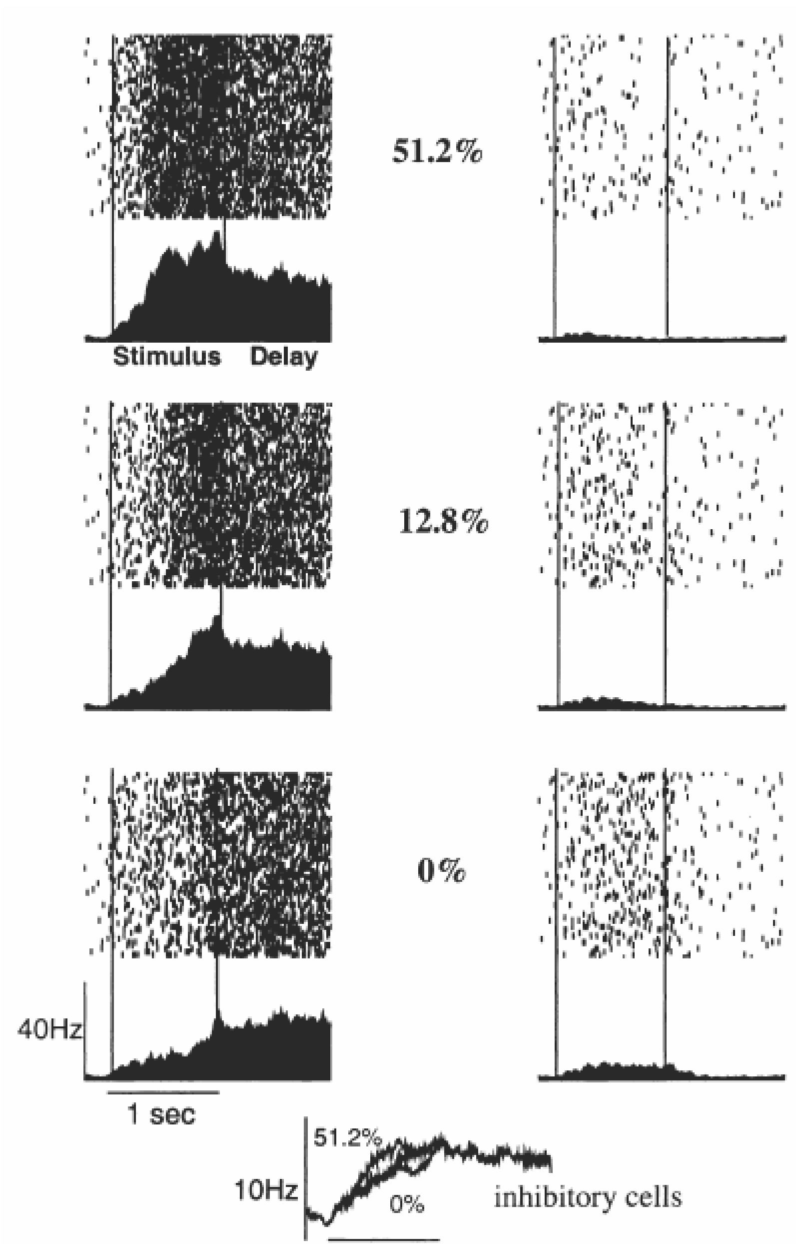


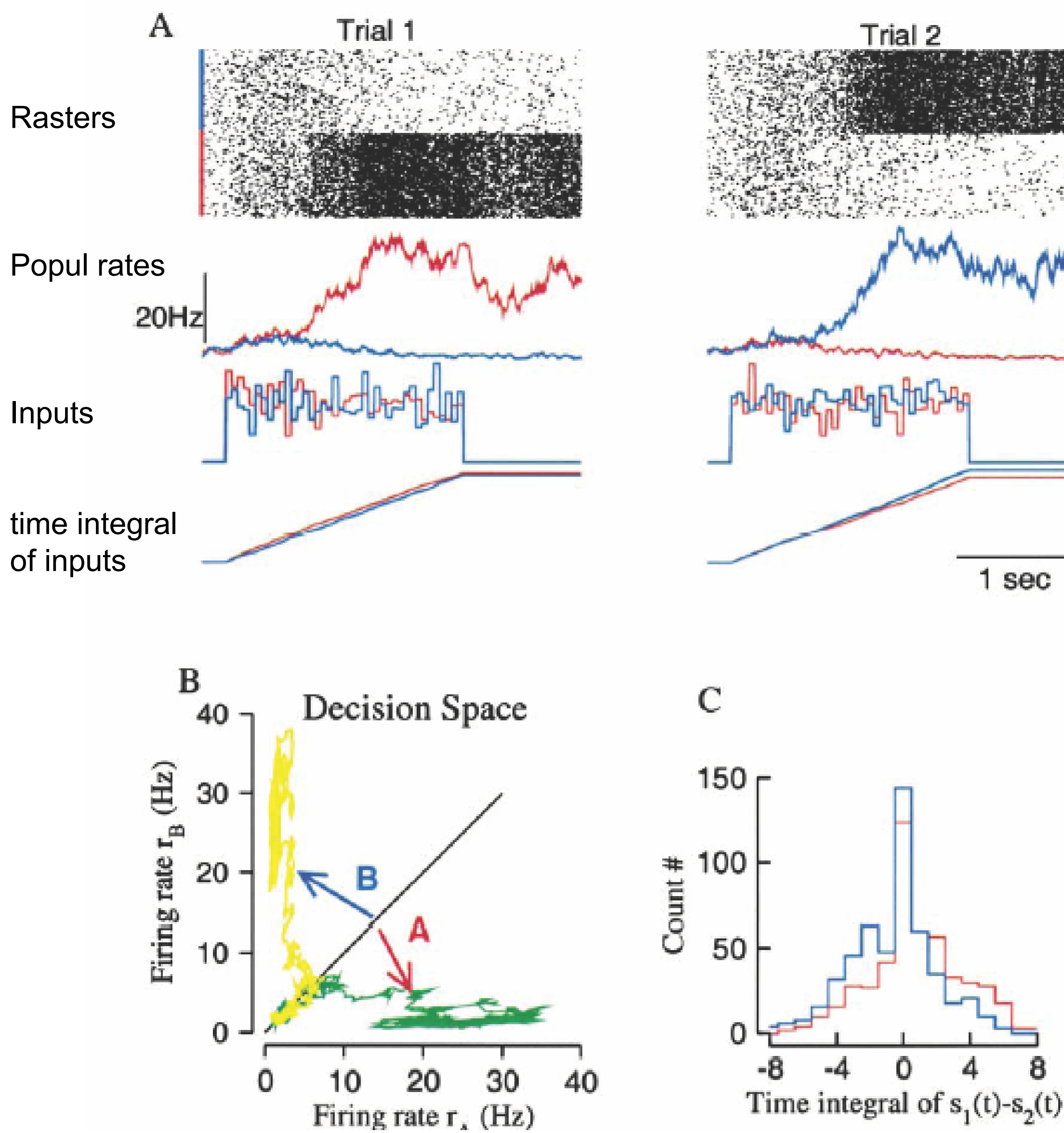
Figure 2. Model Reproduces Salient Characteristics of Decision-Correlated Neural Activity in LIP

Left, neurons in group A; right, neurons in group B. Three trials are displayed with the signal's coherence $c' = 0\%$ (bottom), 12.8% (middle), and 51.2% (top). In all three cases, the attractor A wins the competition and therefore the network's choice is said to be A (correct decision for $c' > 0\%$). Similar to the neural data from LIP, there is a slow time course of activity in group A, with the ramping slope increasing with the signal strength. Moreover, even when the coherence is zero, the firing patterns of the two neural groups diverge dramatically over time during the stimulation, leading to a categorical (binary) decision formed by the network. The inhibitory population, which does not receive direct stimulation but is recruited by pyramidal cells, also shows ramping activity (bottom), and the winner-take-all competition results from this feedback inhibition. Finally, the persistent activity in group A during the mnemonic delay period, with a level independent of the stimulus strength, stores the short-term memory of the decision choice ($\sigma = 4$ Hz).

3 trials, stim durn=1 sec, increasing c';
In each case populn #1
wins competition ➔ correct choice if c'>0.

- slow ramping in E and I populns
- ramp speed increases w/ c'
- low spont activity, 2 Hz
- short-term memory, stores info for dec'n, after stim is off
- For c'=0, there's still choice made… TAFC… model has LIP making a decision based on MT input.

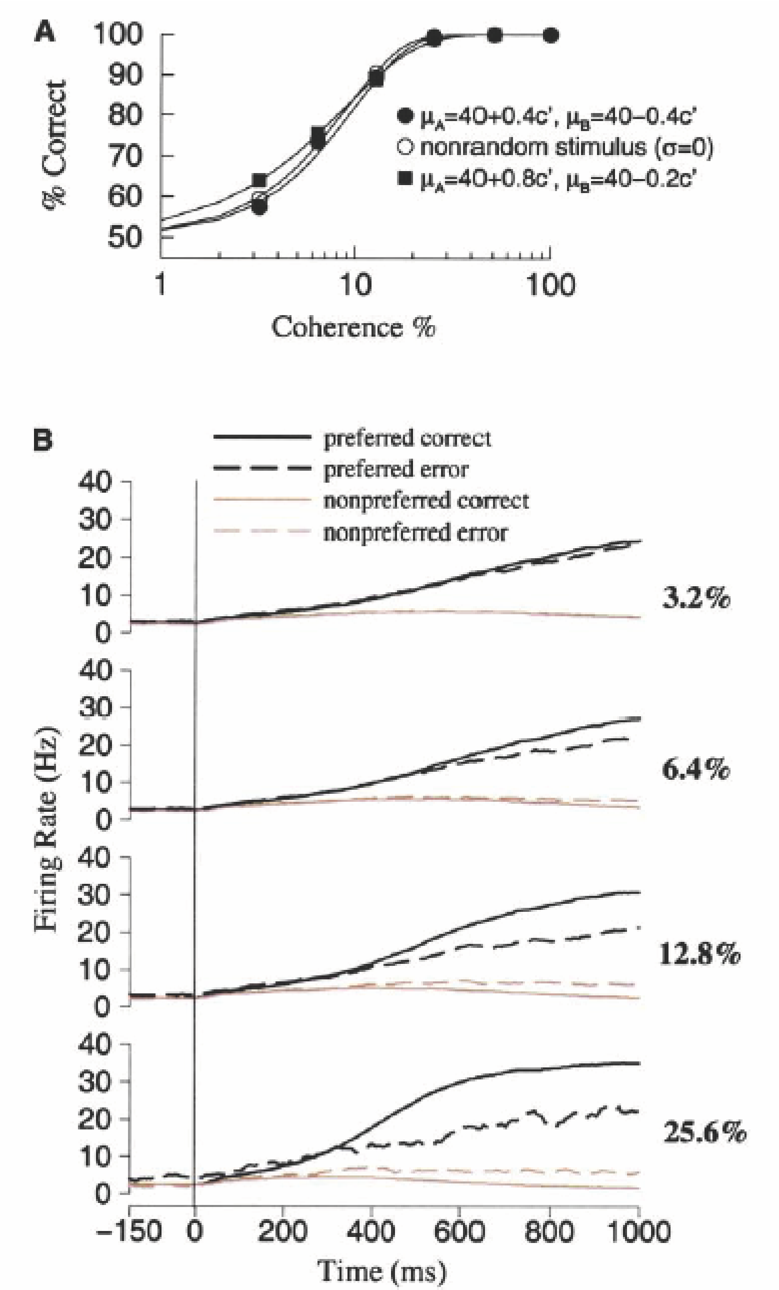
Decision dynamics for c'=0



- time integral of input correlates with decision
- populn rates increase together, then split
- in decision space, move along 1:1 then migrate toward one of the attractors
- in C: histogram over many trials of integral of $s_1(t)$-$s_2(t)$. Blue if pop 2 (B) is winner or red if popul 1 (A) is winner. BUT lots of overlap ➔ in large # of trials A wins even if integral is < 0.

- From C – suggests that external noise is not major source of stochasticity… still get 50:50 and same behavior if set σ=0; noise from background (2400 Hz) dominates… internal brain noise not from stimulus dominates… weak diff'ce in mean μ_1- μ_2 affects the bias.

  (JR: but note, no correlations assumed in inputs.)



Performance … over c’

- neurometiric fns comparable to psychometric fns of trained monkeys
- fit by Weibull dist’n:

$$\% \text{ correct} = 1-0.5*\exp[-(c'/\alpha)^{\beta}]$$

α =c’ @ 82% correct and β=slope.

model gives α=9.2% β=1.5 (expt: 6%, 1.7 from Roitman&Shadlen 2002, 15%, 1.1 from Shadlen&Newsome, 2001)

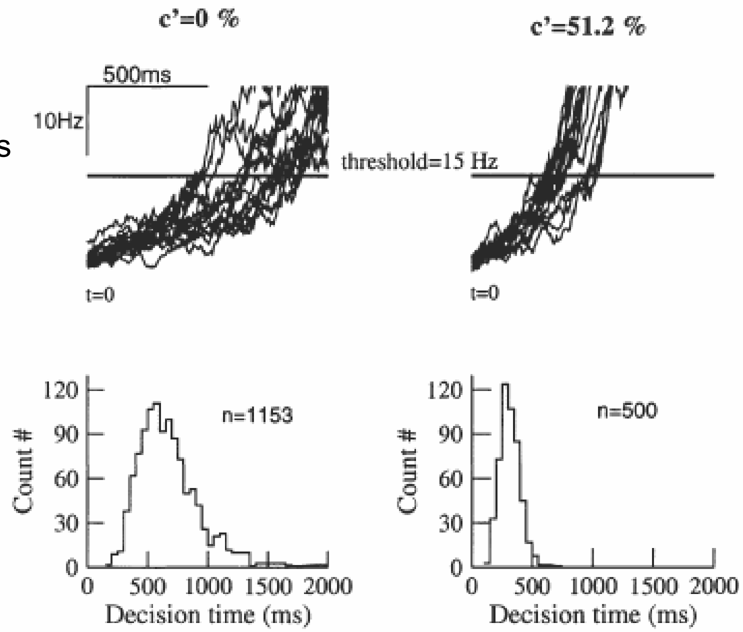
Time courses:

- diverge faster for greater c’
- small c’: chosen popul has similar response whether correct or error trial
- larger c’: response to preferred is smaller on error trial than correct (even though it wins its getting less input than on correct trial) – and slower…

Reaction time task

A

Populn rates different trials

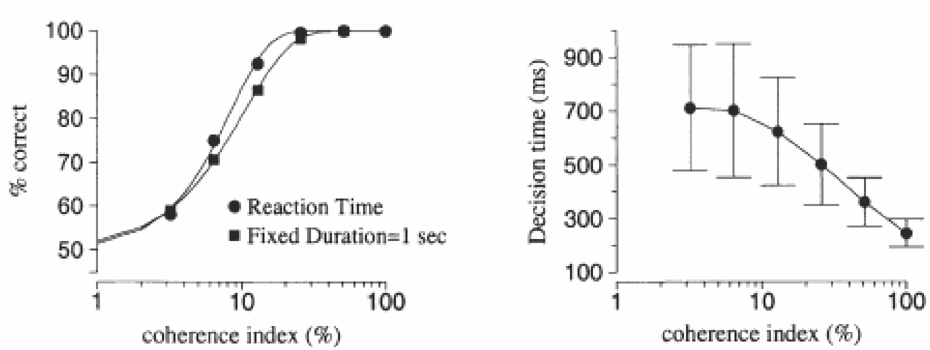


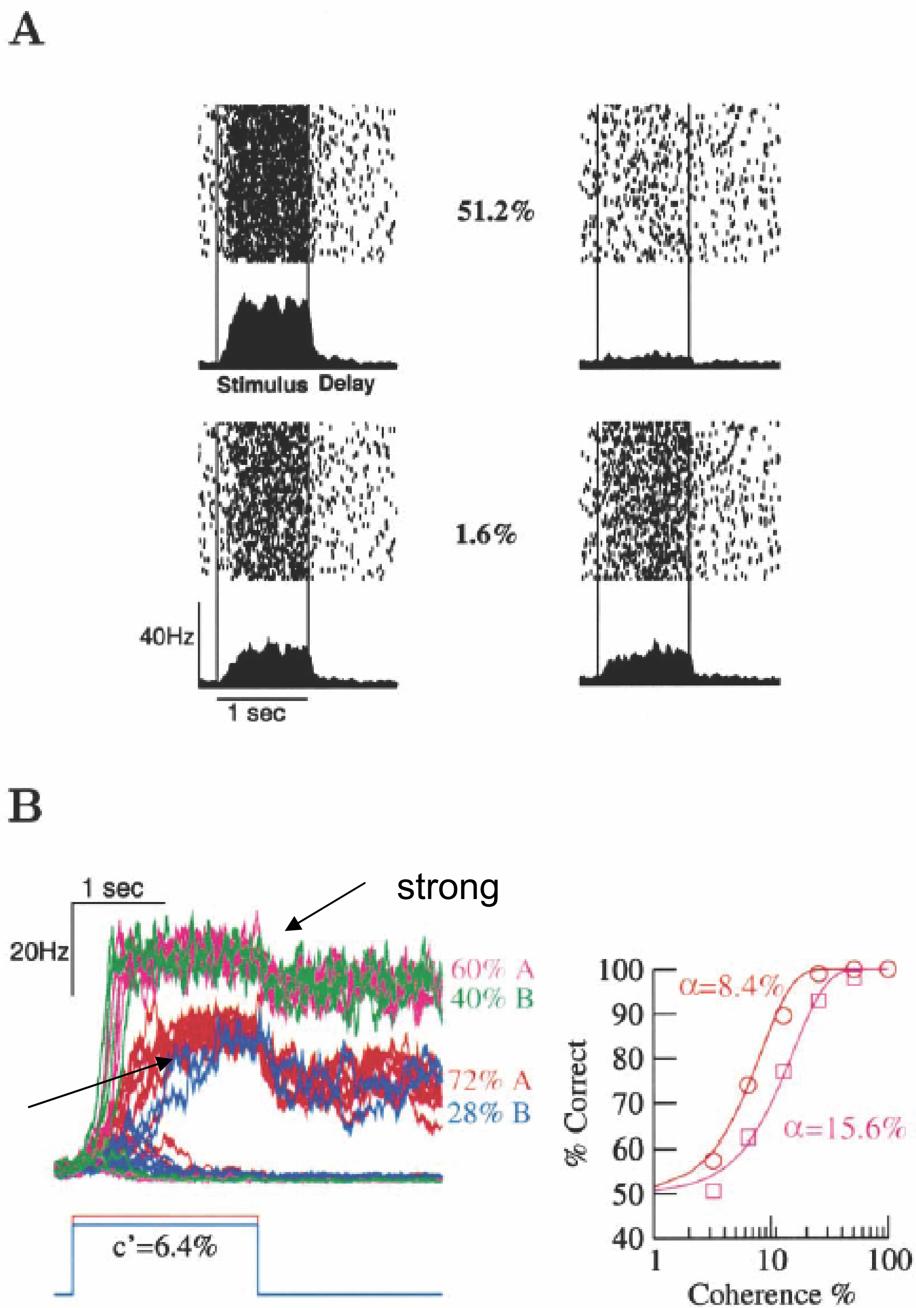
2 sec durn… but "decision" is made if a populn rate reaches threshold, set at 15 Hz.

• c' larger ➔ shorter decision time
• more variable DT for smaller c' (2 histograms and plot, lower right)

• in B, neurometric fn – shows better perf'ce from reaction time in some range of c'… (α_{RT}=8.4% vs 10.4% for 1sec) … system takes more than 1 sec to decide in some trials; comparable to expts
• <DT> drops linearly w/ log(c') over certain range.
• std dev drops w/ <DT> … scalar?

B





Reduced recurrence W_+=1.4 not 1.7

Too strong w_+=1.8 is not good.

Dec'n Making in model requires adequate NMDA strength and slow recurrent connections.

- Control case: w_+=1.7
- reduced w_+ means weaker ramping, loss of memory storage and reduced ability for categorical decision (c'=1.6%, popul'n rates are similar)

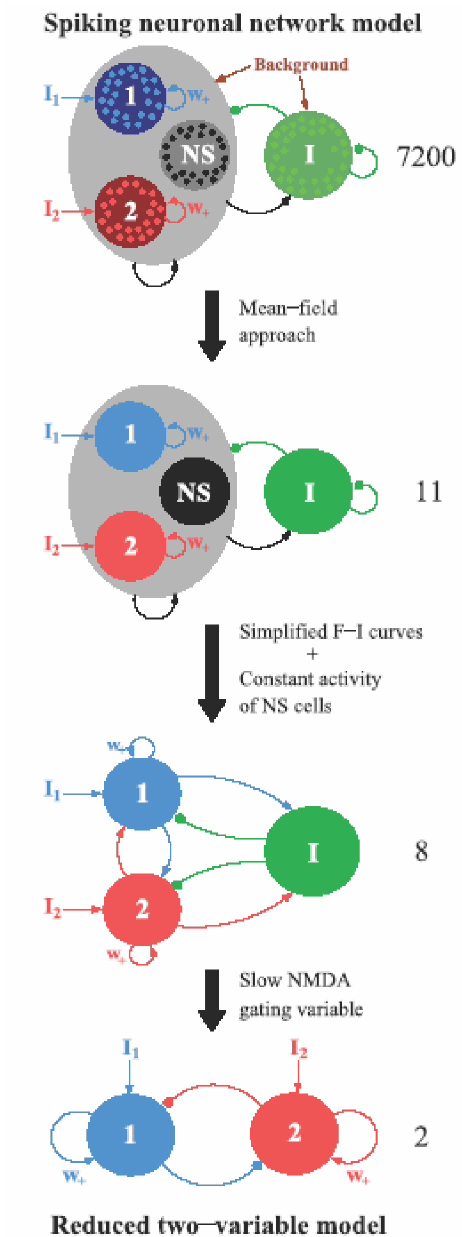
- in B, increased w_+=1.8 leads to faster ramping but less performance in RT…

Left: perf'ce 72% → 60%

Right: perf'ce vs c'…α=8,4% → α=15.6%

Reduced model for DM and RT task.

Wong & Wang, 2006



$$\tau_r \frac{dr_i}{dt} = -r_i + \phi(I_{\text{syn},i}) \qquad i = 1,2,3$$

$$\tau_r \frac{dr_I}{dt} = -r_I + \phi(I_{\text{syn},I})$$

$$\frac{dS_{\text{AMPA},i}}{dt} = -\frac{S_{\text{AMPA},i}}{\tau_{\text{AMPA}}} + r_i \qquad i = 1,2,3$$

$$\frac{dS_{\text{NMDA},i}}{dt} = -\frac{S_{\text{NMDA},i}}{\tau_{\text{NMDA}}} + (1 - S_{\text{NMDA},i})F(\psi(r_i)) \qquad i = 1,2,3$$

$$\frac{dS_{\text{GABA}}}{dt} = -\frac{S_{\text{GABA}}}{\tau_{\text{GABA}}} + r_I,$$

$\Phi(I_{syn})$ is "smooth-foot" threshold linear; $F(\psi)$ monotonic, saturating – Hill fn

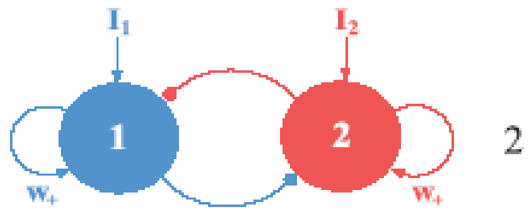
All time constants are fast except for NMDA:

τ_r, τ_{AMPA} = 2 ms, τ_{GABA} = 5 ms τ_{NMDA} = 100 ms

+ empirical observation: firing rate NS ≈ const

➔Rapid equilibrium for all var's except $S_{NMDA,i}$, i=1,2. (call them $S_{1,2}$)

Treat $S_{1,2}$ as param's in other eqns and get their steady states as fns of $S_{1,2}$ … then substitute into ode's for $S_{1,2}$



Reduced two–variable model

for the NMDA synaptic drive varibles: S_1, S_2

$$\frac{dS_1}{dt} = -\frac{S_1}{\tau_S} + (1 - S_1)\gamma r_1$$

$$\frac{dS_2}{dt} = -\frac{S_2}{\tau_S} + (1 - S_2)\gamma r_2,$$

$$r_1 = \phi(I_{\mathrm{syn},1})$$

$$r_2 = \phi(I_{\mathrm{syn},2})$$

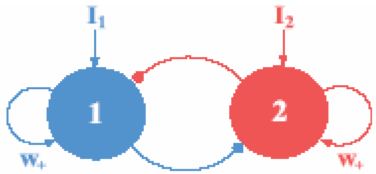
$$I_{\mathrm{syn},1} = J_{N,11}S_1 - J_{N,12}S_2 + J_{A,11}r_1 - J_{A,12}r_2 + I_0 + I_1 + I_{\mathrm{noise},1}$$

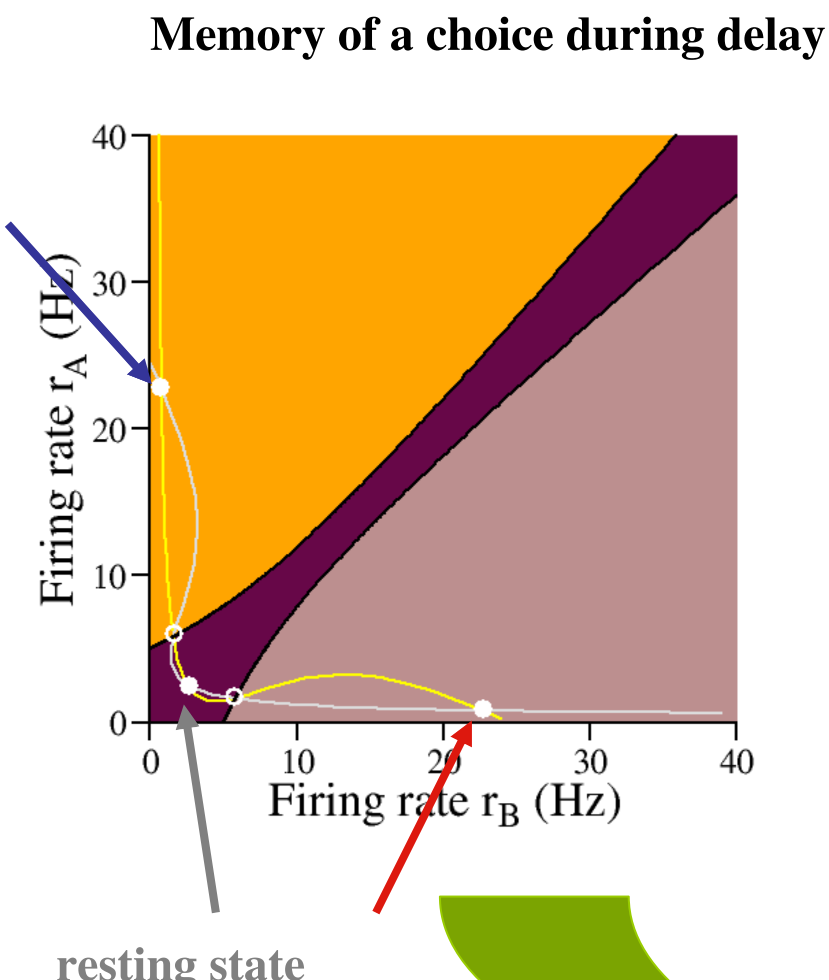
$$I_{\mathrm{syn},2} = J_{N,22}S_2 - J_{N,21}S_1 + J_{A,22}r_2 - J_{A,21}r_1 + I_0 + I_2 + I_{\mathrm{noise},2}$$

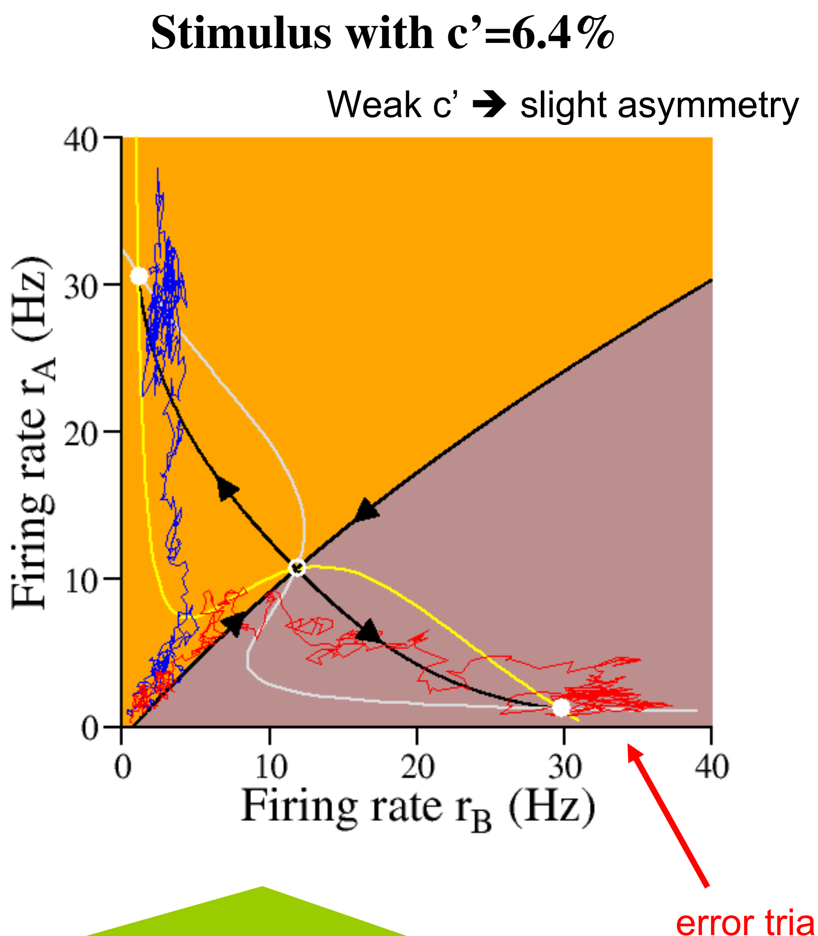
$$\tau_{\mathrm{AMPA}}\frac{dI_{\mathrm{noise}}(t)}{dt} = -I_{\mathrm{noise}}(t) + \eta(t)\sqrt{\tau_{\mathrm{AMPA}}\sigma^2_{\mathrm{noise}}},$$

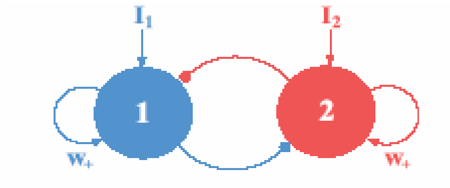
Analyze w/ phase plane methods…

Decision phase plane



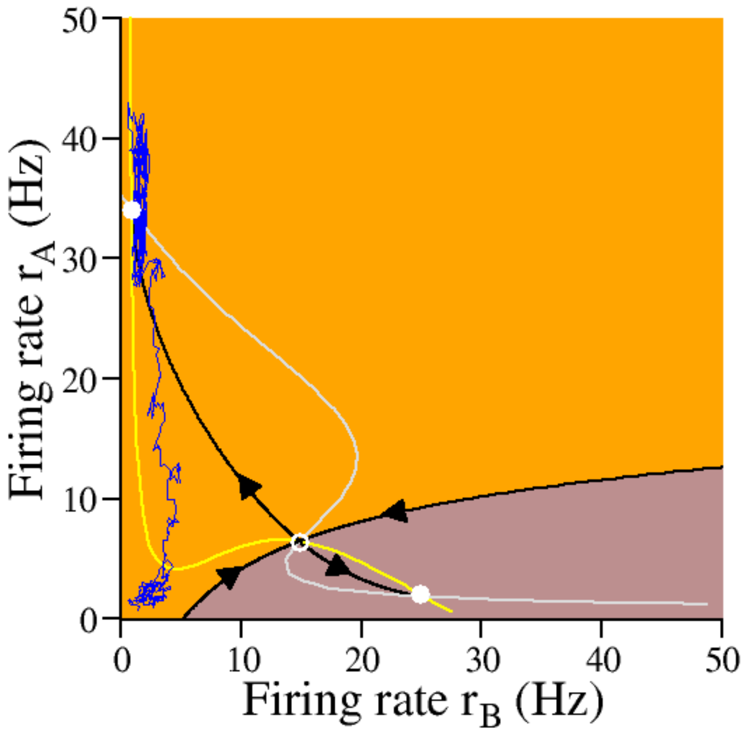




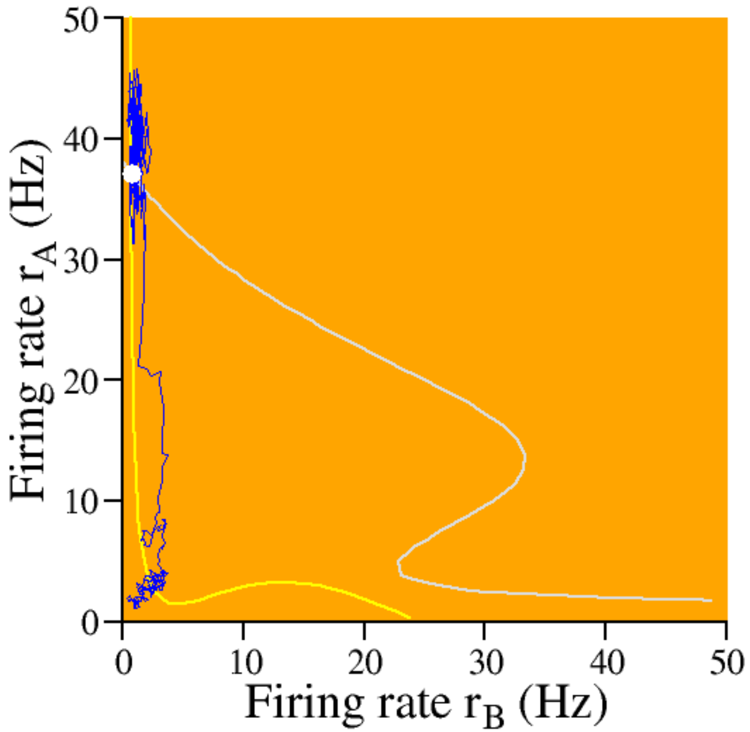


Biased competition, c' > 0

c'=51.2%



c'=75%



Reaction time task…

behaves similar to experimental results and cell-based network

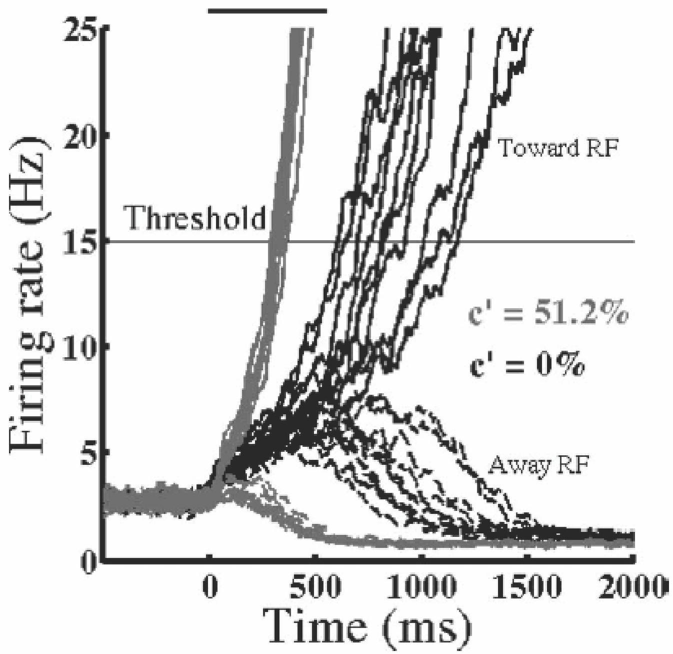


Figure 2. Time course with two different motion strengths. Motion coherence of 0% (black traces) and 51.2% (light gray traces) each with 10 sample trials. Firing rates that ramp upward (bold traces) are for saccades made toward the RF of the neuron, whereas downward (dashed traces) are for saccades away from RF. Ramping is steeper for higher coherence level. The prescribed threshold is fixed at 15 Hz. Once the firing rate crosses the threshold, a decision is made, and the decision time is the time it takes from stimulus onset (0 ms) until the threshold is crossed. The reaction time is defined as the decision time plus a nondecision latency of 100 ms. The bold horizontal line at the top of the figure denotes the duration, at zero coherence, where the firing rates toward and away from RF are indistinguishable.

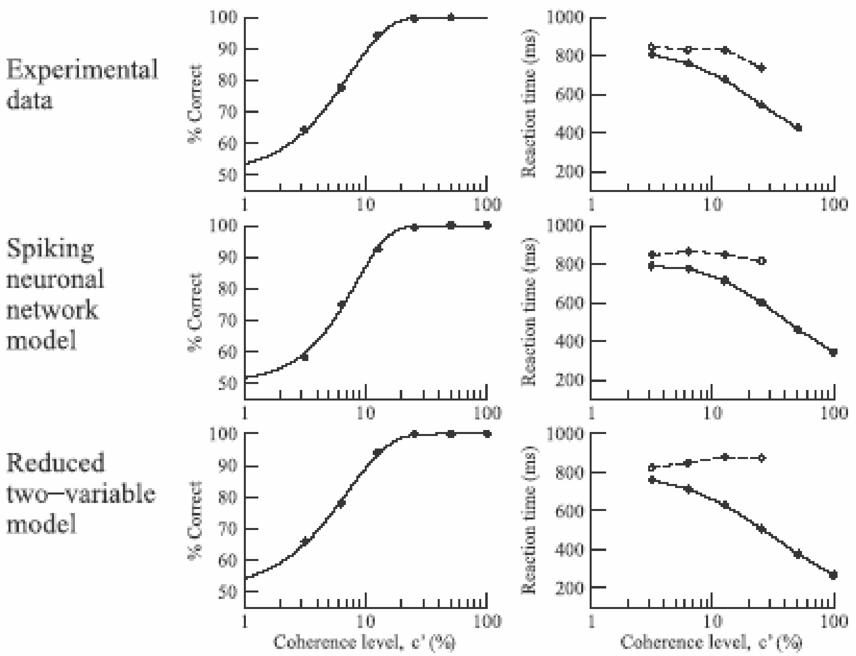


Figure 3. Performance and reaction time of models and the experiment of Roitman and Shadlen (2002). First column, Psychometric data from experiment and the models (data are fit with a Weibull function). Second column, Reaction time from experiment and the models. Open circles joined by dashed lines, Mean reaction of error trials; filled circles, correct trials. σ_{noise} = 0.008 nA. Experimental data are adapted from Mazurek et al. (2003).

How get slow integ'n ramp if $\tau_{\text{NMDA}} \approx 100$ ms ?

Recurrent excitation prolongs integration time

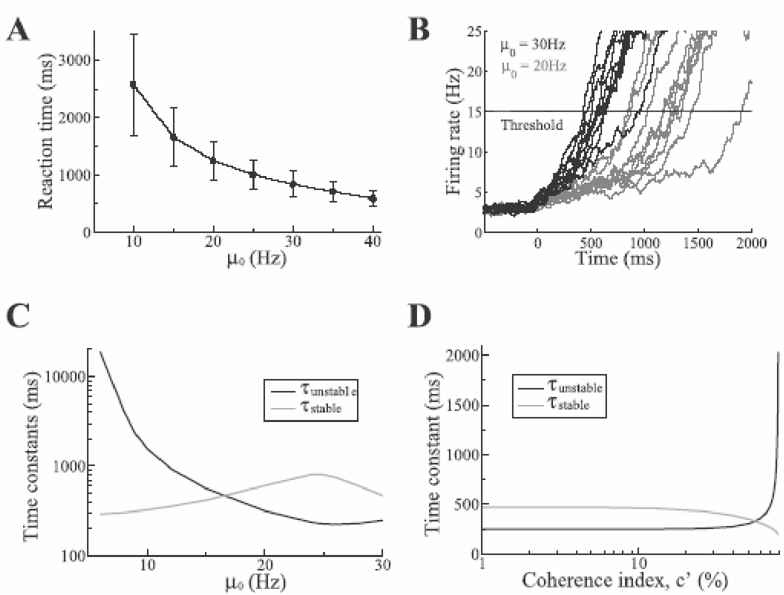


Figure 6. Decision time and local dynamics in the vicinity of a saddle point. Zero coherence level from *A* to *C*. *A*, Longer reaction time for smaller stimulus strength μ_0. Error bars indicate SD. *B*, Typical time courses: ramping is faster for larger stimulus strength, μ_0. *C*, Time constants of saddle-like unstable steady state with different μ_0. For $\mu_0 > 17$ Hz, τ_{stable} is larger than τ_{unstable}, whereas the opposite is true for $\mu_0 < 17$ Hz. *D*, Time constants of the unstable saddle as function of coherence level c' (μ_0 fixed at 30 Hz). The unstable time constant is essentially constant up to $c' \sim 70\%$. The sudden increase in τ_{unstable} happens just before the bifurcation point at which the saddle coalesces with the less favored attractor and disappears (see Fig. 5).

$$\frac{dr}{dt} = \frac{-r + w_{rec}\, r}{\tau_{syn}} + I$$

$$\tau_{network} = \frac{\tau_{syn}}{1 - w_{rec}}$$

f τ_{network}=1 sec and τ_{NMDA}=100ms, 1-w_{rec}=0.1

f τ_{network}=1 sec and τ_{AMPA}=5ms, 1-w_{rec}=0.005

If w_{rec}=1 (fine-tuning!) then $\tau_{\text{network}} = \infty$

$\rightarrow$ Perfect integrator

Effect of stimulus strength

If stimulus is too strong or too weak, lose ability for discrimination.

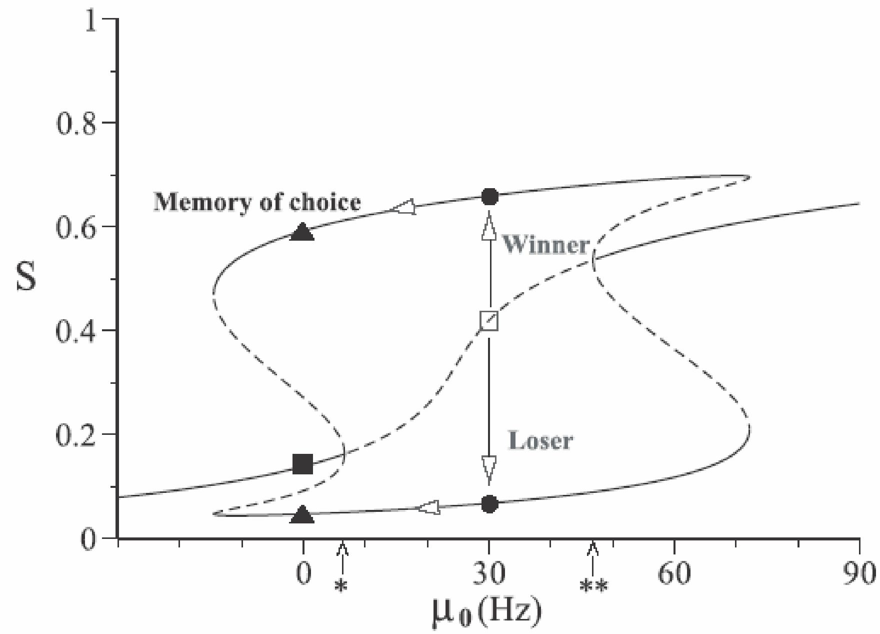


Figure 10. Bifurcation diagram of a selective population with stimulus strength μ_0 as parameter ($c' = 0\%$). Bold lines, Stable steady states; dashed lines, saddle steady states. Spontaneous state before stimulus presentation is denoted by the filled square. With a $\mu_0 = 30$ Hz stimulus, the spontaneous stable state loses stability, and a saddle steady state appears (open square). The state either goes toward the upper or lower stable state (filled circles). The population wins the competition if the upper branch is chosen, and loses otherwise. When stimulus is removed, hysteresis of the upper stable branch allows the activity to persist (memory storage of a decision choice). Arrow with an asterisk, Point where spontaneous state loses stability. Arrow with double asterisks, Saddle point turns into an attractor.

Adequate recurrent NMDA needed for delayed DM

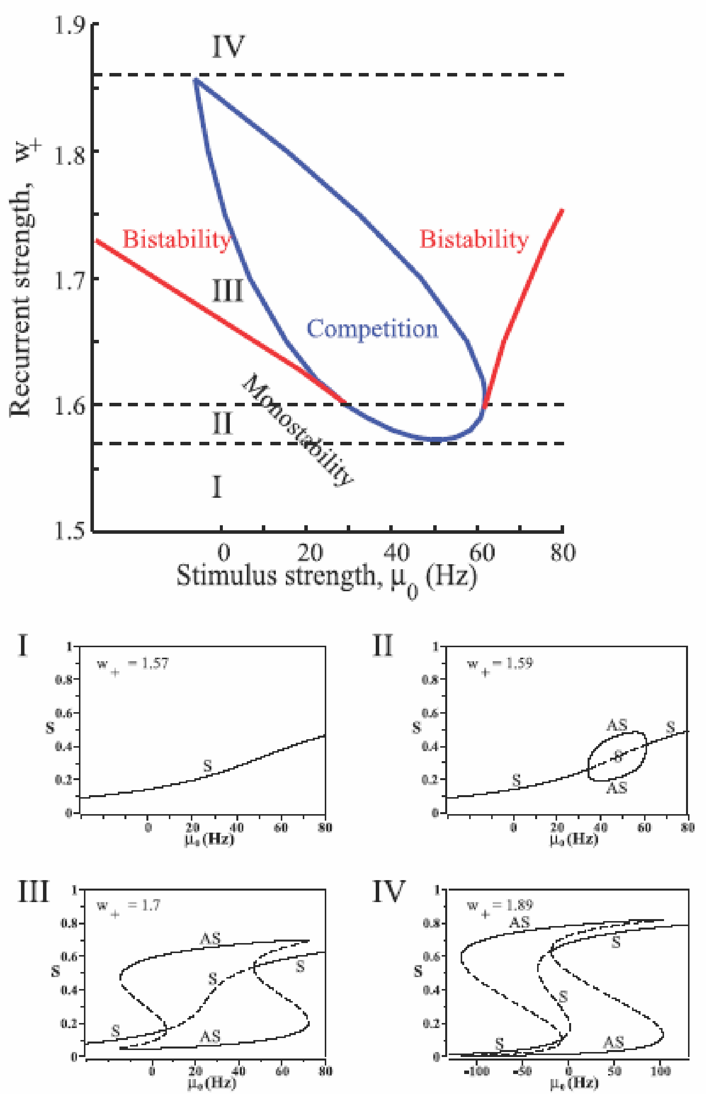
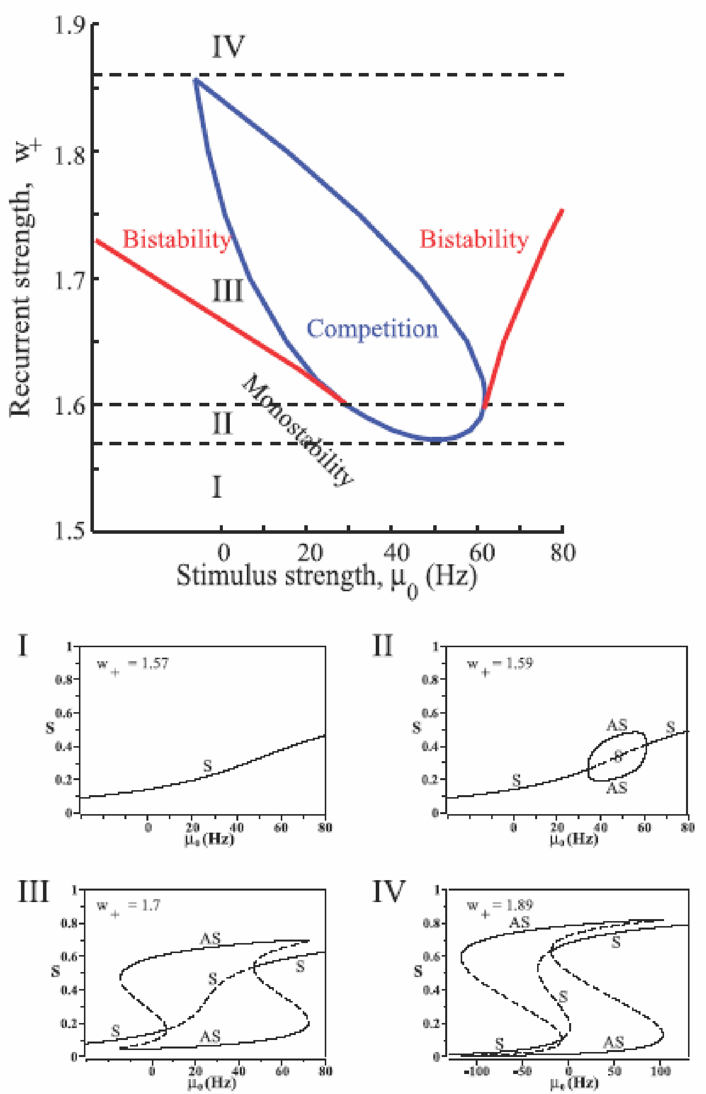


Figure 12. Distinct modes of operation in the two parameter space with zero coherence. In general, there are three types of regions. Bistable (red) region, A symmetric and two asymmetric attractors coexist; blue competition region, one saddle with two asymmetric competing attractors; monostable region, only one attractor. Depending on the strength of recurrent excitation w_+, the network responds to a stimulus (of suitable intensity μ_0) in four different ways, shown as regimes I, II, III, IV in insets. Regime I and II do not support working memory (of decision). Regime I, No decision making nor memory. Regime II, The network can produce a binary decision during stimulation but cannot store it in working memory. Regime III, The network is capable of both decision-making computation and working memory (our standard parameter set). Regime IV, For any μ_0, there is always a stable symmetric stable state. Dark and dashed branches denote loci of stable and unstable steady states, respectively. A and AS are labels for branches with symmetric and asymmetric steady states, respectively.

Adequate recurrent NMDA needed for delayed DM



Larger AMPA/NMDA shortens RT but compromises performance

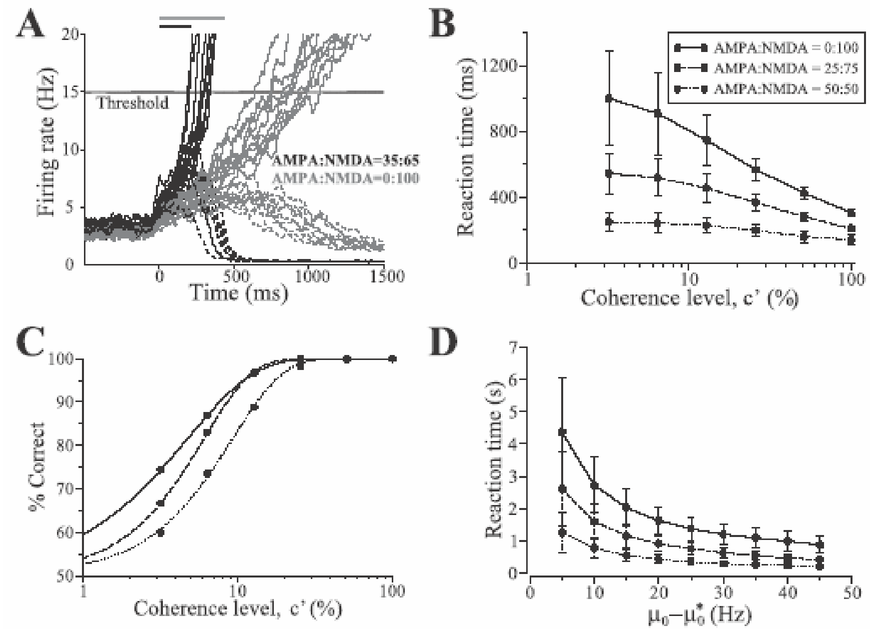


Figure 7. Dependence of decision-making behavior on the AMPA:NMDA ratio at recurrent synapses. ***A***, Typical time courses: faster ramping neural activity at larger AMPA:NMDA ratios. Top black (gray) horizontal bar denotes the duration where the firing rates are not distinguishable [i.e., the trajectory lies along the stable manifold of the saddle point, when AMPA:NMDA is 35:65 (0:100)]. ***B***, Reaction time is shorter with a higher AMPA:NMDA ratio. ***C***, The performance, however, becomes less accurate. Accuracy data are fitted by a Weibull function. ***D***, For $c' = 0\%$, a higher AMPA:NMDA ratio decreases the reaction time for the entire range of stimulus strengths μ_0. *x*-axis, Difference between μ_0 and μ_0^*, which is the bifurcation point at which the saddle steady state appears and whose value depends on the AMPA:NMDA ratio. ***C*** and ***D*** have the same symbolic notations as in ***B***. Error bars indicate SD.

Features/Issues of Slow Reverberating Attractor Networks – XJ Wang

• Competition via inhibition.

• Slow buildup w/ NMDA.   w/ τ_{NMDA} = 100 ms, slow integration time (sec) is a dynamic phenomena … look at reduced model.

• Model gives behavioral perf'ce and RTs like expts.

• Need to have memory storage, after stim is off … not in the usual stim-dependent attractor.

• Cell-based network… or reduced 2-var mean-field

• Drift-Diffusion model or "Integrate-and-decide":
  - • decision is made when a threshold is reached… not able to hold a memory for delay task
  - • to get long integ'n time need fine tuning