LIF model for decision making in the LIP area

Autore:Recchioni Marco

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The brain during decision

Decision making:

- Gather the evidence from the outside world
- Elaborate those evidences
- Store the conclusions extracted from evidences in the working memory
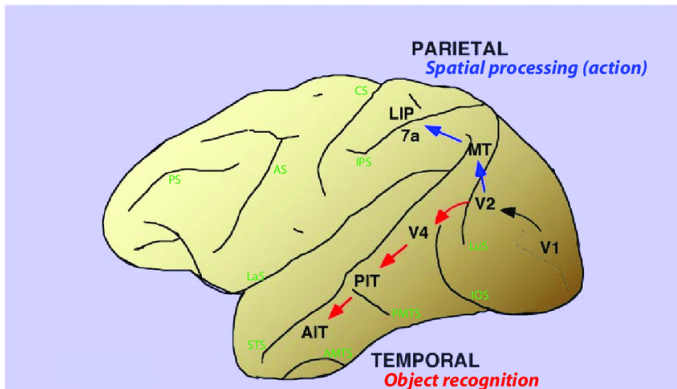- Perform a task based on the working memory

Biophysical brain activity

Studies (work of Newsome et al., 1989; Salzman, 1990; Britten et al. 1996; Shalden et al., 1996)
Neuron in the Middle Temporal area (MT) collect the data from the visual evidences
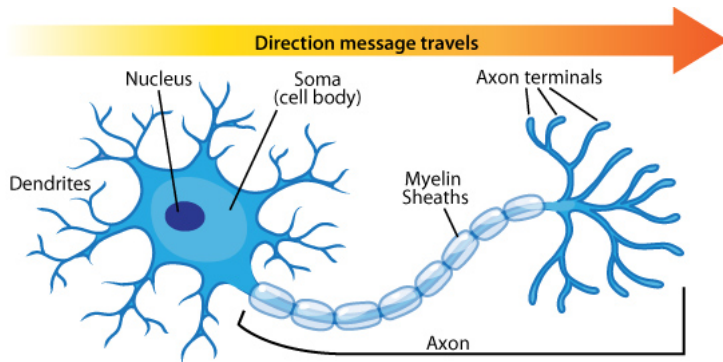Connected to the lateral intraparietal cortex (LIP area)
Mnemonic persistent activity.
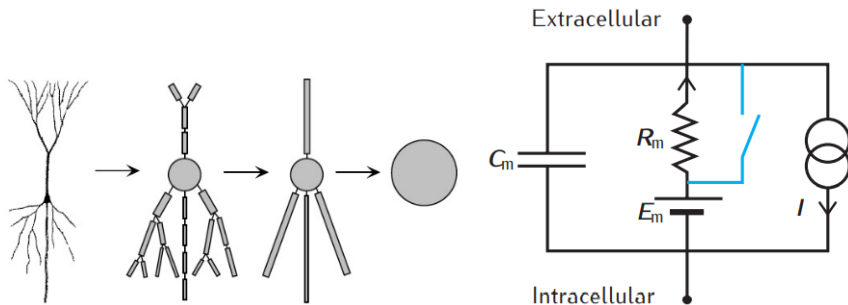
Neuron schematization

The basic feature of a neuron:

Ion channel, proteins, electro-diffusive mechanism regulate net flow of current.
Two types of neuron: pyramidal and interneurons.

Neuron simplification

Decision making $\rightarrow$ group activity

LIF model

-Integrate and fire gives us information of the activity rate of the neuron rather than the shape of the action potential

Given the circuit to schematize a neuron, the membrane potential is given by the equation:

$$C_m \frac{dV(t)}{dt} = -g_m(V(t) - V_{rest}) - I_{syn}(t) \tag{1}$$

Typical values are:

$V_{rest} = -70mV; \quad V_{thr} = -50mV; \quad V_{reset} = -55mV$

	Pyramidal	Interneuron
C_m (nF)	0.5	0.2
g_m (nS)	25	20
τ_m (ms)	20	10
τ_{rf} (ms)	2	1

The general solution for such an equation would yield:

$$V(t) = V_{rest} + \frac{R}{\tau_m} \int_0^\infty e^{-s/\tau_m} I_{syn}(t-s) ds \tag{2}$$

Biophysical model of Post-synaptic currents

Neurons pass signal through synaptic connection.
The amount of current depens on:

- it's voltage dependent
- proportional to driving force of the synaptic current i.e. the conductance
- conductance can be voltage dependent
- proportional to the number of open channel
- the regime it's working depend on a reversal potential

General equation:

$$I_{syn} = g_{syn}(V)s(t)(V(t) - V_{reversal}) \tag{3}$$

Open channels for AMPA and GABA

- The firing rate arriving at the synapse is slow compared to the dynamics of the gating channel
- Synapse always far from saturation
- Rise time of postsynaptic current almost instantaneous

The dynamics can be approximated by a first order kinetic scheme

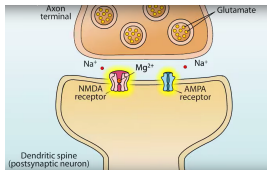$$\frac{ds}{dt} = -\frac{s}{\tau} + \sum_k \delta(t - t^k) \tag{4}$$

Typical values:
$\tau_{AMPA} = 2ms$
$\tau_{GABA} = 10ms$

Kinetics for NMDA Synapses

AMPA receptors are activated by glutamate.
NMDA activated by glutamate and regulated by glycine and D-serine $\rightarrow$ more complex dynamics

This current rise up fast as the AMPA and GABA one, but has a long time decay.
Can be described by a non-linear second order scheme. ($\tau_{decay} = 100ms; \quad \tau_{rise} = 2ms$)

$$\frac{ds(t)}{dt} = -\frac{s(t)}{\tau_{decay}} + \alpha x(t)(1 - s(t)) \tag{5}$$

$$\frac{dx}{dt} = -\frac{x(t)}{\tau_{rise}} + \sum_k \delta(t - t^k) \tag{6}$$

Final Synapse currents

$$
\begin{cases}
I_{AMPA} = g_{AMPA}V(t)\sum_{j=1}^{N_E} w_j s_j^{AMPA}(t) \\[2ex]
I_{NMDA} = \frac{1}{J(V(t))}g_{NMDA}V(t)\sum_{j=1}^{N_E} w_j s_j^{NMDA}(t); \quad J(V(t)) = 1 + [Mg+]exp(-0.062V(t))/3.57) \\[2ex]
I_{GABA} = g_{GABA}(V(t) - V_{rest})\sum_{j=1}^{N_I} s_j(t)
\end{cases}
$$

The values for the synaptic conductances are reported below:

(nS)	Pyramidal	Interneuron
g_{AMPA}^{EXT}	2.08	1.62
g_{AMPA}^{REC}	0.104	0.081
g_{NMDA}	0.327	0.258
g_{GABA}	1.25	0.973

Cortical Columns

Neurons in the brain are grouped in cortical columns. Moving perpendicularly in the column, neurons share almost same receptive fields.

In case of no stimuli presented to the LIP area:

- schematize as two assemblies of pyramidal and internerurons
- weights (w_j) are set to 1
- equal neurons with equal stimuli
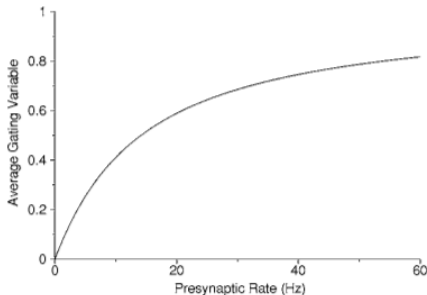- each neuron describe its group average
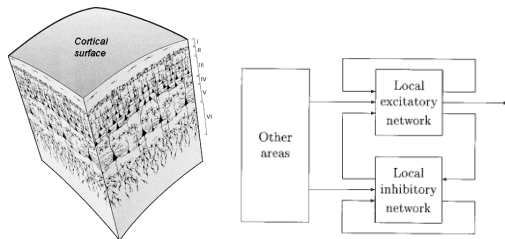
NMDA mean value

In case of a Poisson train of spike in the input it can be found (Brunel Wang 2001) an analytical form for the mean value.

- $\sum_{j=1}^{N_E} s_j^{NMDA}(t) = N_E \psi(\nu_E) + \delta S(t)_{NMDA}$

$$\begin{cases} \psi(\nu) = \frac{\nu\tau}{1+\nu\tau}(1 + \frac{1}{1+\nu}\sum_{n=1}^{\infty} \frac{(-\alpha\tau_{n,rise})^n T_n}{(n+1)!}); \quad \tau = \alpha\tau_{decay}\tau_{rise} \\ \\ T_n = \sum_{k=0}^{n}(-1)^k \binom{n}{k} \frac{\tau_{N,rise}(1+\nu\tau_{N,dec})}{\tau_{N,rise}(1+\nu\tau_{N,dec}+k\tau_{N,dec})} \end{cases}$$
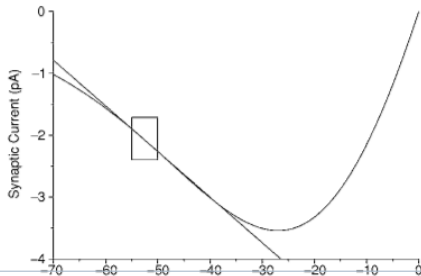
NMDA voltage Linearization

Voltage dependence for NMDA current is more complex. But, the system will spend most of the time in the box in the image. Thus the voltage dependence can be linearized:

$$\begin{cases} I = \frac{gV(t)}{J(V(T))}(N\psi(\nu) + \delta S(t)) \\ \\ \frac{V(t)}{1+\gamma exp(-\beta V(t))} \sim kV(t) + m + O((V(t) - \overline{V})^2) \quad k = (1 + \beta\overline{V}/\overline{J} - \beta\overline{V}/\overline{J}^2); \quad m = \overline{V}(\beta/\overline{J} - \beta) \end{cases}$$

$$I = g^{eff}(V(t) - V_{pol})(N\psi(\nu) + \delta S(t)) \tag{7}$$

$g^{eff} = gk; \quad V_{pol} = m/k$

Diffusion Approximation

For AMPA and GABA synapses, calling $S = \sum_{j=1}^{N} s_j$:

$$\frac{dS}{dt} = -\frac{S}{\tau} + \sum_{j=1}^{N} \sum_k \delta(t - t_k^j) \tag{8}$$

$\sum_k \delta(t - t_k^j)$ is a poisson process for which: $P(nspike, t) = \frac{(\nu t)^n}{n!} e^{-\nu t}$. For $S(t) = S'$:

$$\begin{cases} P(spike, \Delta t) = \sum_{j=1}^{N} \nu \Delta t = N\nu \Delta t \qquad S(t + \Delta t) = S' e^{-\frac{\Delta t}{\tau}} + 1 \\\\ P(NOspike, \Delta t) = 1 - N\nu \Delta t \qquad S(t + \Delta t) = S' e^{-\frac{\Delta t}{\tau}} \end{cases}$$

$$P(S, t + \Delta t | S', t) = [1 - N\nu \Delta t] \delta(S - S' e^{-\frac{\Delta t}{\tau}}) + [N\nu \Delta t] \delta(S - S' e^{-\frac{\Delta t}{\tau}} - 1) \tag{9}$$

$P(S, t + \Delta t)$ can be marginalized and eq. (4) can be integrated in the diffusion approximation:

- $1/\nu << \tau$ but $N\nu \to \infty$.
- $1 << S'$

Gaussian process

$$\tau \frac{\partial P(S,t)}{\partial t} = \frac{\partial}{\partial S}[S - N\nu\tau]P(S,t) + \frac{1}{2}[N\nu\tau]\frac{\partial^2 P(S,t)}{\partial S^2} \tag{10}$$

So in the diffusion approximation: $\sum_{j=1}^{N} \sum_k \delta(t - t_k^j)$

- The first sum over k describe a Poisson train of spikes
- The neuron is connected throught dendries trees which have huge number of connection
- Due to central limit theorem the dynamics of the gating variable follow a Gaussian distribution with mean $N\nu\tau$ and SD $\sqrt{N\nu\tau}$

So the dynamics is simplified by a mean term and a stochastic gaussian term:

$$\tau \frac{dS(t)}{dt} = -S + \tau N\nu + \sqrt{N\nu\tau}\eta(t) \tag{11}$$

$\eta(t)$ with 0 mean, $< \eta(t), \eta(t') >= \delta(t - t')$

Ornstein–Uhlenbeck process

The S variable is replaced by a mean term and a stochastic one: $S \to \overline{S} + \delta s(t)$

Assuming stationary inputs ($\overline{S} = \tau N \nu$) the equation for the noise:

$$\tau \frac{d\delta s(t)}{dt} = -\delta s(t) + \eta(t) \tag{12}$$

$$\delta s(t) = -\delta s(t')e^{-\frac{(t-t')}{\tau}} + \frac{1}{\tau}\int_{t'}^{t} e^{-\frac{t-u}{\tau}} dW_{t'} \quad ; t' < t \tag{13}$$

The moments of this process:

$$< \delta s(t) > = \delta s_0 e^{-\frac{t}{\tau}}; \quad < \delta s(t)\delta s(t') > = \frac{1}{2\tau}e^{-\frac{t-t'}{\tau}}; \quad Var(\delta s(t)) = \frac{1}{2\tau}[1 - e^{-\frac{2t}{\tau}}]$$

Since $\tau_{AMPA} < \tau_{other}$ and $g_{AMPA}^{ext} > g_{AMPA}^{rec}$ only δs_{AMPA}^{ext} is considered.

$$\delta s(t + \Delta t) = \delta s(t)e^{-\frac{\Delta t}{\tau}} + \sqrt{\frac{1}{2\tau}[1 - e^{-\frac{2\Delta t}{\tau}}]}\mathfrak{N}(0,1) \tag{14}$$

Mesoscopic description

- Approximate the noise as voltage independent
- The only fluctuating term is due to external inputs
- All currents depend linearly to the voltage
- We can rescale the term to get:

$$\tau_m^{eff}\frac{dV}{dt} = -(V(t) - V_{ss}) + \frac{\overline{V}(g_{AMPA}\sqrt{N\nu\tau})^{ext}}{g_m^{eff}}\delta s(t) \tag{15}$$

- $\tau_m^{eff} = \frac{C_m}{g_m^{eff}} = \tau_m \frac{g_m}{g_m^{eff}}$
- $g_m^{eff} = g_m + g_{AMPA}^{rec}\overline{S}_{AMPA}^{rec} + g_{AMPA}^{ext}\overline{S}_{AMPA}^{ext} + g_{GABA}\overline{S}_{GABA} + g_{NMDA}\overline{S}_{NMDA}$
- $V_{ss} = [g_m V_{rest} + g_{GABA}\overline{S}_{GABA}V_{rest} + g_{NMDA}^{eff}\overline{S}_{NMDA}V_{pol}]/g_m^{eff}$

Approximated FP equation

$$\tau_m^{eff} \frac{dV}{dt} = -(V(t) - V_{ss}) + \sigma^{eff} \delta s(t) \tag{16}$$

Time can be rescaled: $t \to t/\tau_m^{eff}$

So that:

$$< \delta s(t) \delta s(t') > = \frac{1}{\tau_m^{eff}} \frac{1}{2\overline{\tau}} e^{-\frac{t-t'}{\tau}} \tag{17}$$

with $\overline{\tau} = \frac{\tau}{\tau_m^{eff}}$

Using perturbation theory on the parameter $\overline{\tau}$ ($\overline{\tau} \to 0$ i.e $\tau << \tau_m^{eff}$) an approximated FP equation can be extracted (reference: Approximate Fokker-Planck equation with colored Gaussian noise, Cetto and Pena)) :

$$\frac{\partial P(V,t)}{\partial t} = \frac{\partial}{\partial V}[V - V_{ss}]P(V,t) + \sigma^{eff2}[1 - \overline{\tau}]^{-1} \frac{\partial^2}{\partial V^2} P(V,t) = -\frac{\partial}{\partial V} J(V,t) \tag{18}$$

Firing rate

Conditions:
$$\begin{cases} P(V_{th}, t) = 0; \\ lim_{V \to -\infty} P(V, t) = 0; \quad lim_{V \to -\infty} VP(V, t) = 0 \\ \\ S(V, t) \to S(V, t) + S^{reset}(V, t); \quad S^{reset}(V, t) = \nu(t - \tau_{ref})\Theta(V - V_{reset}) \end{cases}$$

$$P_{ss}(V) = \frac{2\nu\tau_m^{eff}}{\sigma} e^{-\frac{(V - V_{ss})^2}{\sigma^2}} \int_{\frac{V_{reset} - V_{ss}}{\sigma}}^{\frac{V_{th} - V_{ss}}{\sigma}} \Theta(x - \frac{V_{reset} - V_{ss}}{\sigma}) e^{x^2} dx \tag{19}$$

With the condition: $\int_{-\infty}^{V_{th}} P_{ss}(V, t)dV + \nu\tau_{ref} = 1$

$$\overline{V} = V_{SS} - (V_{th} - V_{reset})\nu_E\tau_m^{eff} - (V_{ss} - V_{reset})\nu_E\tau_{ref} \tag{20}$$

$$\nu_E^{post} = \phi(V_{ss}(\nu_{E,I}^{pre}), \sigma^{eff}) = [\tau_{ref} + \tau_m^{eff}\sqrt{\pi} \int_{\frac{V_{reset} - V_{ss}}{\sigma}}^{\frac{V_{th} - V_{ss}}{\sigma}} e^{x^2}(1 + erf(x))dx]^{-1} \tag{21}$$

Stability of the Firing rate

In case of stationarity the rate of the presynaptic neuron shoul be be the same as the postsynaptic one ($\nu^{pre} = \nu^{post} = \nu$). To investigate its stability a first order displacement is used:

$$\frac{ds(t)}{dt} = -\frac{s(t)}{\tau} + \nu(t) \tag{22}$$

$$\nu = \phi(s(t)) \tag{23}$$

The fixed point is thus:

- $s_{ss} = \tau\phi(s_{ss})$

Now: $s_{ss} \rightarrow s_{ss} + \delta s e^{\lambda t}$

Inserting into eq. (22):

- $\lambda = -\frac{1}{\tau} + \frac{d\phi}{ds}|_{s_{ss}}$

The final condition for stability:

$$\frac{d\phi}{d\nu}|_{\nu_{ss}} < 1 \tag{24}$$

The brain during stimuli
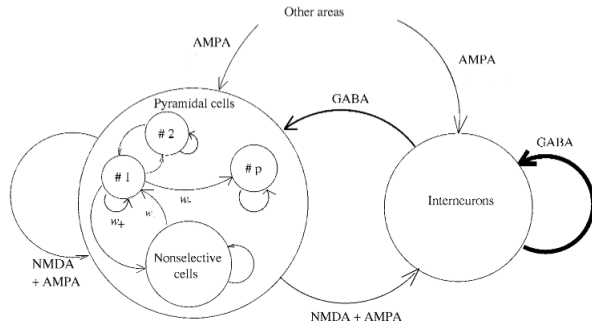
When an external stimuli selective to a particular population are added pyramidal cells subdivide:

- Neurons selective to the stimulus presented
- Neurons selective to other stimuli
- Neurons which never activate

Hebbian rule for weights

<center>fire togheter $\Rightarrow$ wire togheter</center>

p assemblies of selective neurons.

A selective stimulus for the population p activates a fraction fN_E.

$(1 - fp)N_E$ neurons which don't respond to any stimuli.

The value of w_- is set to compensate the value chosen for w_+ due the fact that spontaneous activity is unaffected by synaptic modification.

$w_- = 1 - \frac{f(w_+ - 1)}{1 - f}$

Therefore:

- $w_+ > 1$ inside the selective population responding to particular stimuli

- $w_- < 1$ from nonselective population to a selective one

- $w_j = 1$ in other case such as GABA and external stimuli

Persistent activity

The subdivision of the pyramidal neurons has the following consequences:

Activated neurons (ν_+):

- $I_{AMPA^{rec}} \sim g_{AMPA}^{rec} \overline{V_+} N_E [w_+ \nu_+ f + w_- \nu_- f(p-1) + w_- \nu_0(1-fp)]$

Non activated neurons(ν_-):

- $I_{AMPA^{rec}} \sim g_{AMPA}^{rec} \overline{V_-} N_E [w_- \nu_+ f + w_- \nu_- f(p-2) + w_+ \nu_- f + w_- \nu_0(1-fp)]$

Neurons which never activate(ν_0):

- $I_{AMPA^{rec}} \sim g_{AMPA}^{rec} \overline{V_0} N_E [w_+ \nu_0(1-fp) + w_- \nu_- f(p-1) + w_- \nu_+ f]$

The approximation for the mean field has been carried out as the same manner.

Bistability of the system
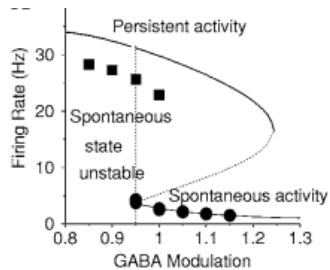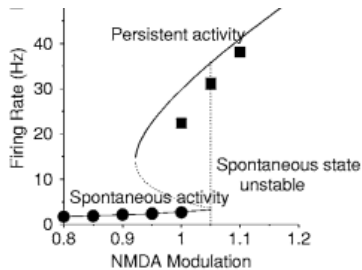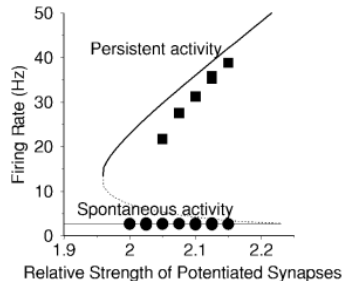
Image from: Brunel Wang et. 2001

Simulation
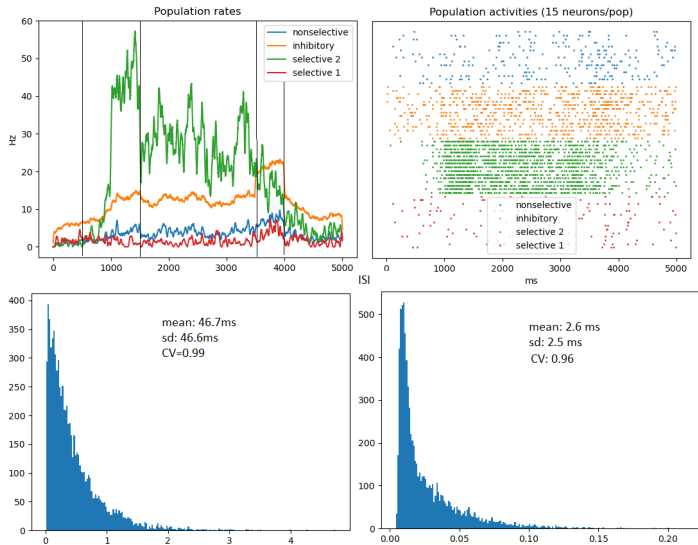
Discrimination dot task

Visual motion discrimination dot task:

privileged direction of motion ⇒ two possible decisions ⇒ winner take all competition

In the probability context (right(A), left (B)) :

- $P(A|e) = \frac{P(e|A)P(A)}{P(e)}$
- No apriori information ⇒ equal prior
- $LR = \frac{P(e|A)}{P(e|B)}$
- The brain infers based on risk/reward
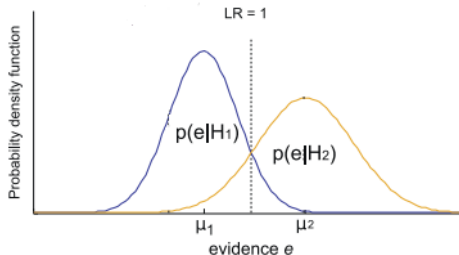
Given N independent evidences:

$$log(B_2) < log(LR) = log[\frac{P(A|e_1..e_N)}{P(B|e_1..e_N)}] = \sum_{i=1}^{N} log(\frac{P(e_i|A)}{P(e_i|B)}) < log(B_1) \quad (25)$$

Evidences as selective input

From the outside brain of our model :

- noise
- Selective stimulus to the subpopulation
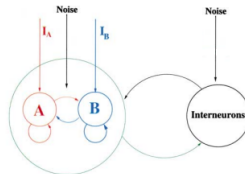
The mean rate of external stimuli for the selective population A or B change in time:

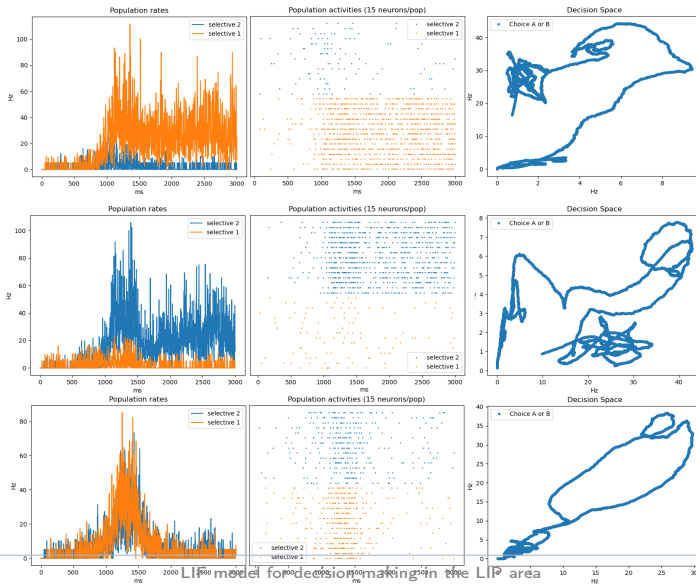$$\nu_{ext} \rightarrow \nu_{ext} + N(\mu_{A/B}, \sigma)$$
$$\mu_{A/B} = \mu_0(1 \pm c/100)$$
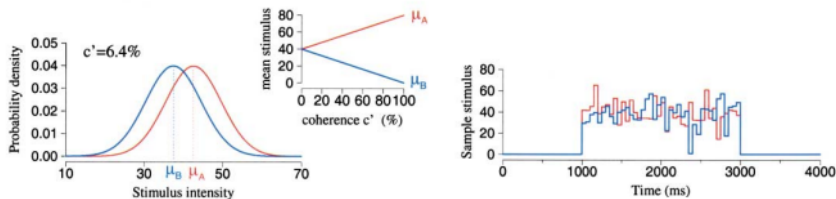
Behave for different coherence
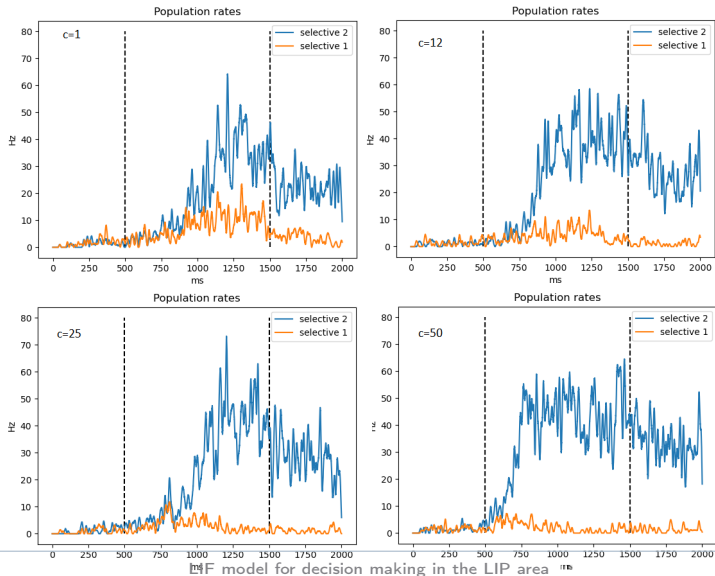
Random activity

Percentage of success

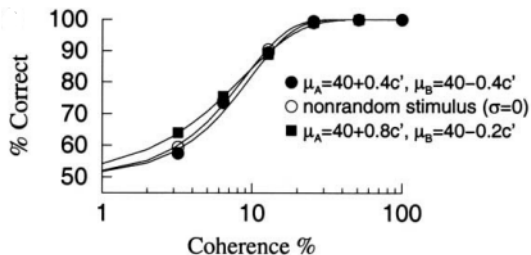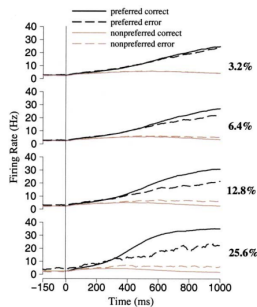-Fitted with a Weibull function: $\%correct = 1 - 0.5exp(-(c/\alpha)^{\beta})$

Image from: Wang et. 2002

Full circles: $\alpha = 9.2; \quad \beta = 1.5$
Empty circles: $\alpha = 8.9; \quad \beta = 1.5$
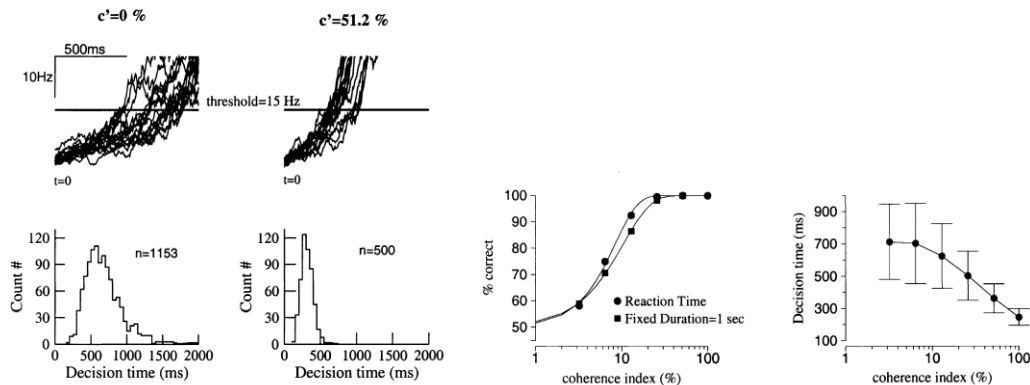Squares: $\alpha = 8.7; \quad \beta = 1.1$

Reaction time

Image from: Wang et. 2002

RT: $\alpha = 8.4$; $\beta = 1.6$
FD: $\alpha = 8.9$; $\beta = 1.5$

Time presentation of the stimulus

The stimulus has been provided for different times.
For $T_{stim} \leq 0.3$ many trial especially at low coherence didn't manage to bring the system to any of the basin of attraction of the system, restoring its resting activity. (For those kind of process a choice for A or B have been chosen at random).
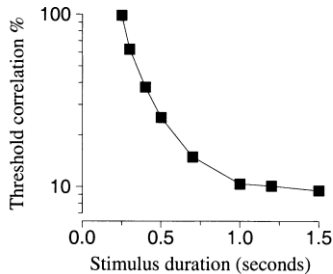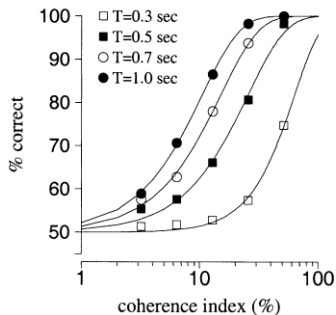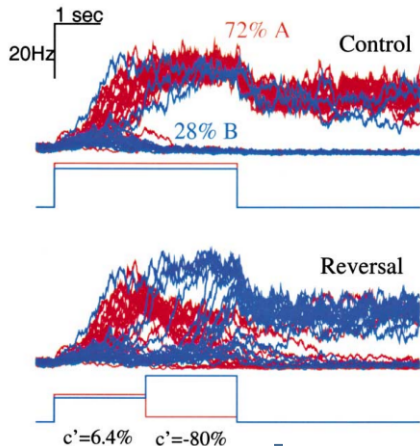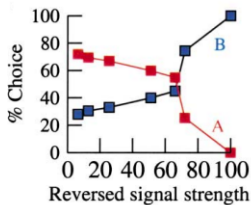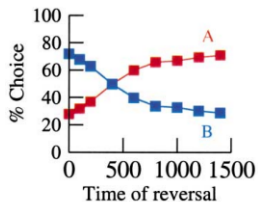

Image from: Wang et. 2002

Reversal stimulus

Integration time is essential in order to make the right decision. Can the choice be reversed?
-Reverse the coherence level at different time ($c \to -c$)
-Different strength of the reversed stimulus

Image from: Wang et. 2002

References

- Probabilistic Decision Making by Slow Reverberation in Cortical Circuits, (Wang 2002)
- Firing Frequency of Leaky Integrate-and-fire Neurons with Synaptic Current Dynamics, (Brunel Sergi 1998)
- Mean-Field Theory of Irregularly Spiking Neuronal Populations and Working Memory in Recurrent Cortical Networks, (15 chapter, Renart)
- Effects of Neuromodulation in a Cortical Network Model of Object Working Memory Dominated by Recurrent Inhibition (Brunel Wang 2001)
- Model of Global Spontaneous Activity and Local Structured Activity During Delay Periods in the Cerebral Cortex (Amit Brunel)
- Brain mechanisms for perceptual and reward-related decision-making

Grazie per l'attenzione.