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Anticipation in the retina and the primary visual cortex: towards an integrated retino-cortical model for motion processing

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Anticipation in the retina and the primary visual cortex : towards an integrated retino-cortical model for motion processing

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Team : Biovision



In collaboration with :

Matteo Di Volo
Alain Destexhe



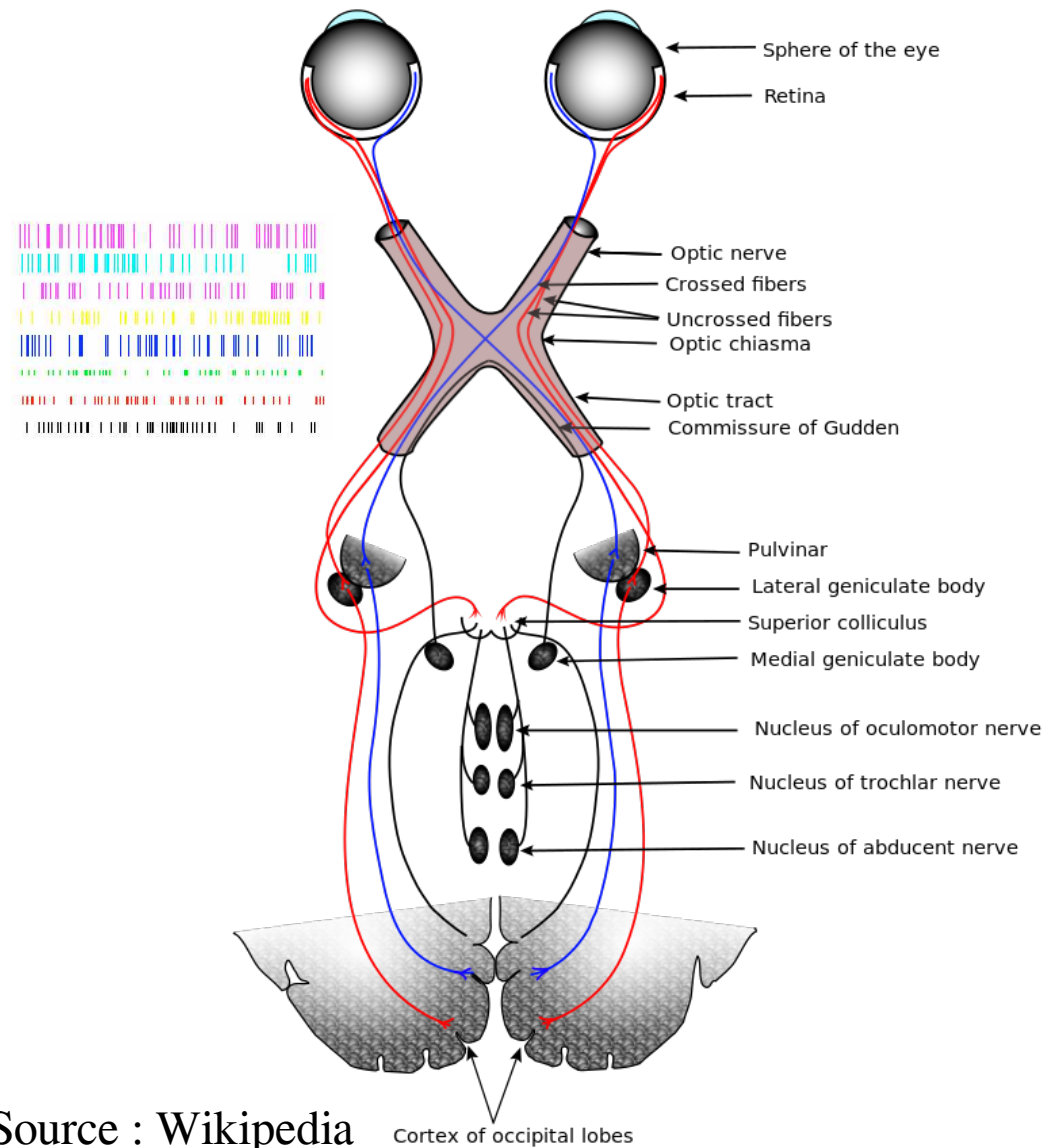
Frédéric Chavane
Sandrine Chemla



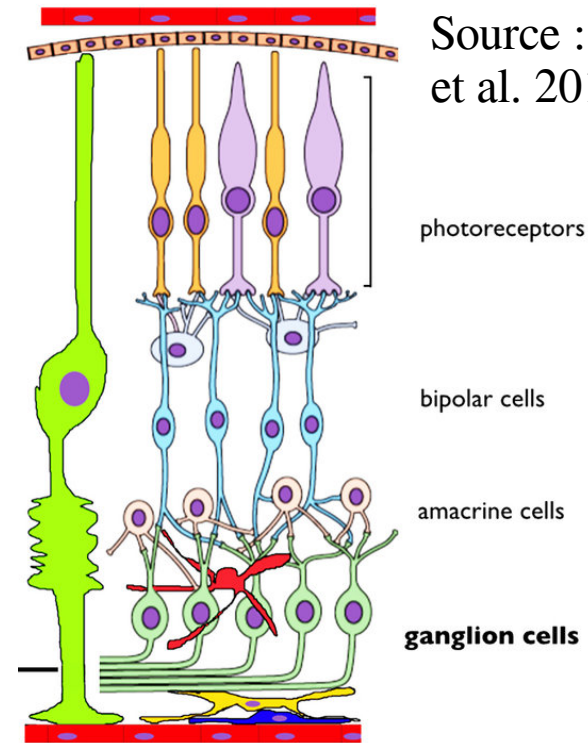
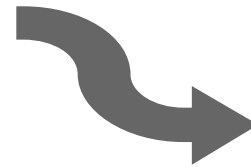
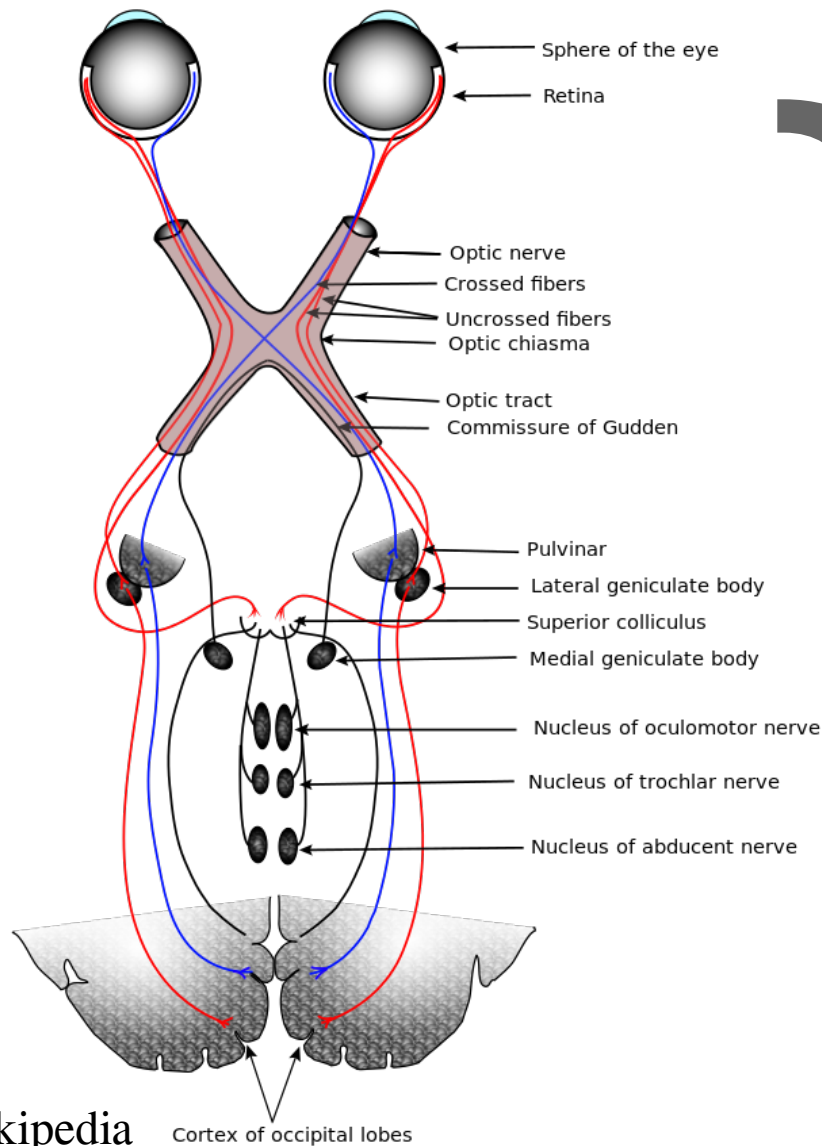
Olivier Marre



The visual flow



The visual flow



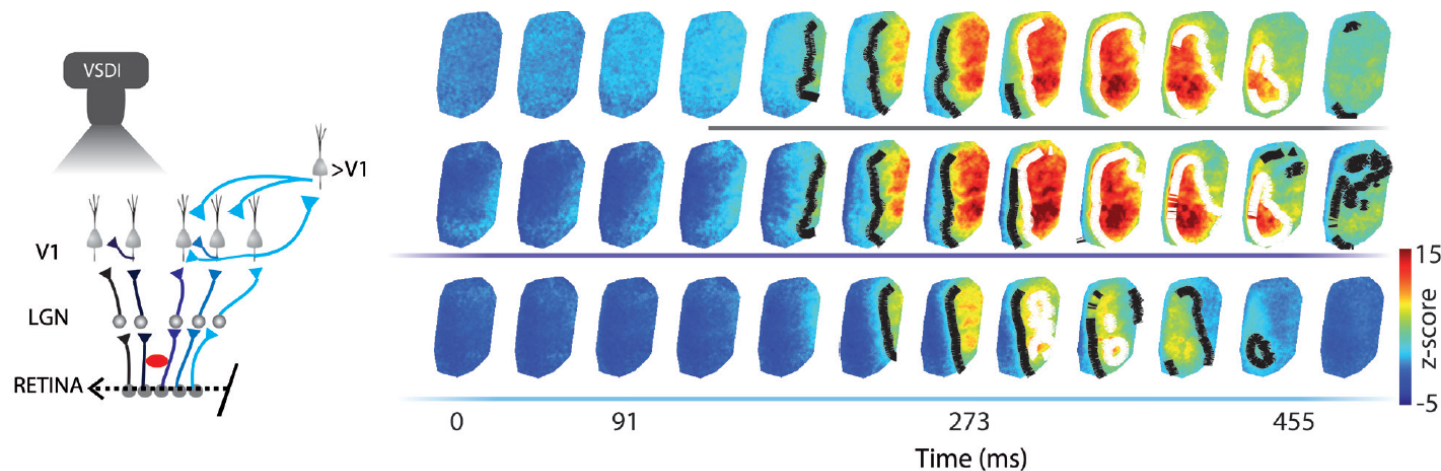
Source : Ryskamp et al. 2014



Upcoming light

Stating the problem : Visual Anticipation

Anticipation is carried out by the primary visual cortex (V1) through an activation wave



Source :
Benvenuti et
al. 2015

But the retina is not a mere transmitter, it is able to perform many computations such as :

- Orientation sensitivity
- Contrast gain control
- Sensitivity to differential motion
- and « **Motion Anticipation** »

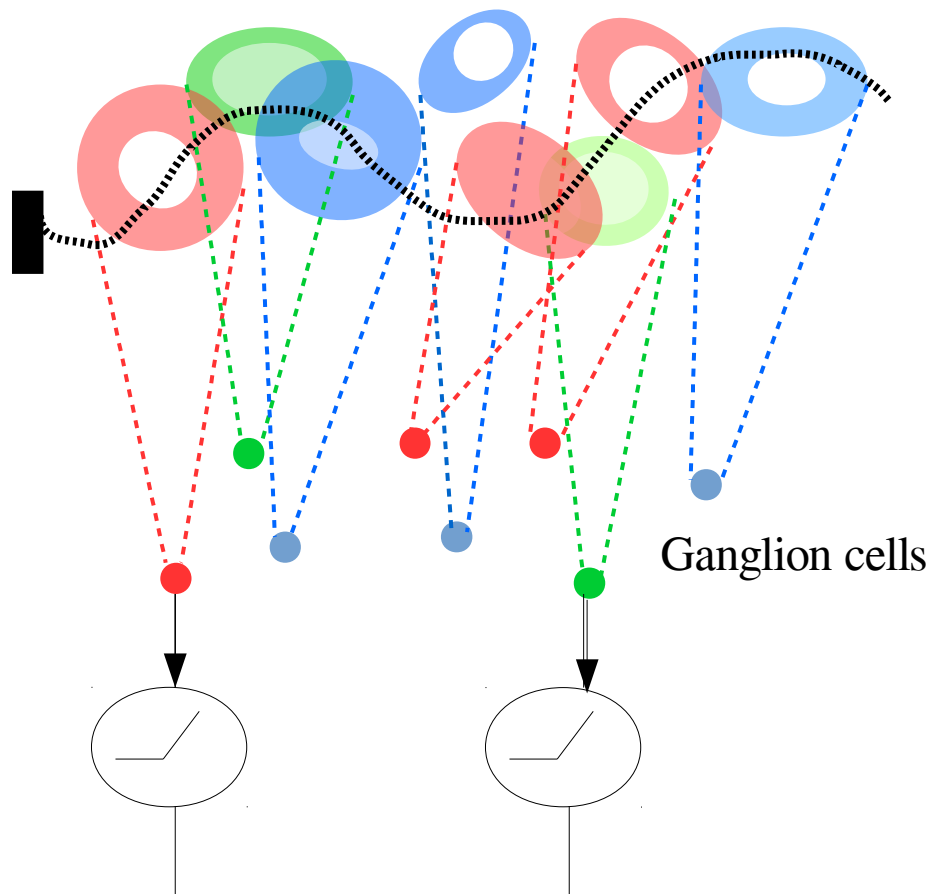
➤ **What does retinal anticipation add to the cortical one ?**

I) Anticipation in the retina

The Hubel-Wiesel view of vision

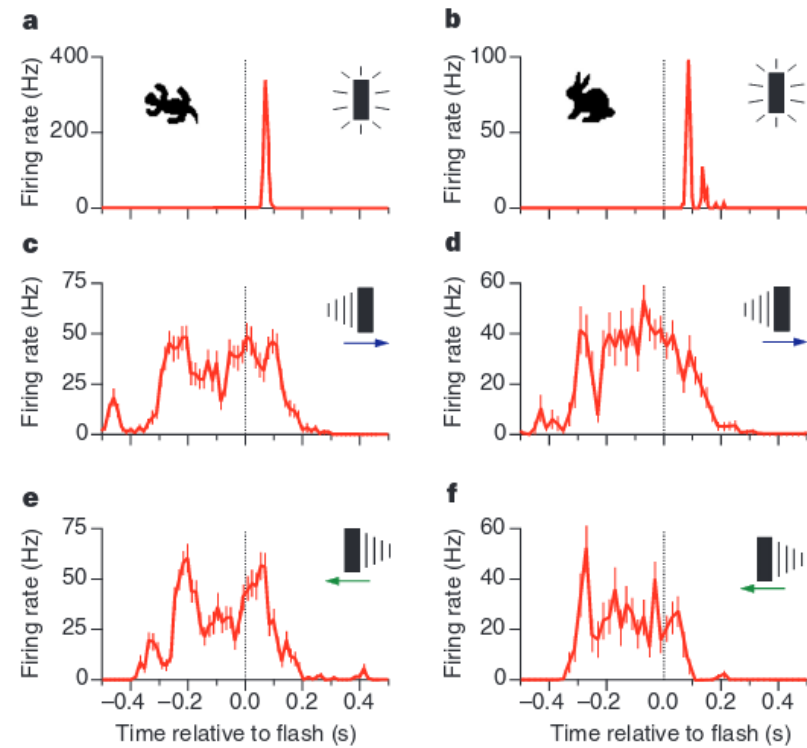
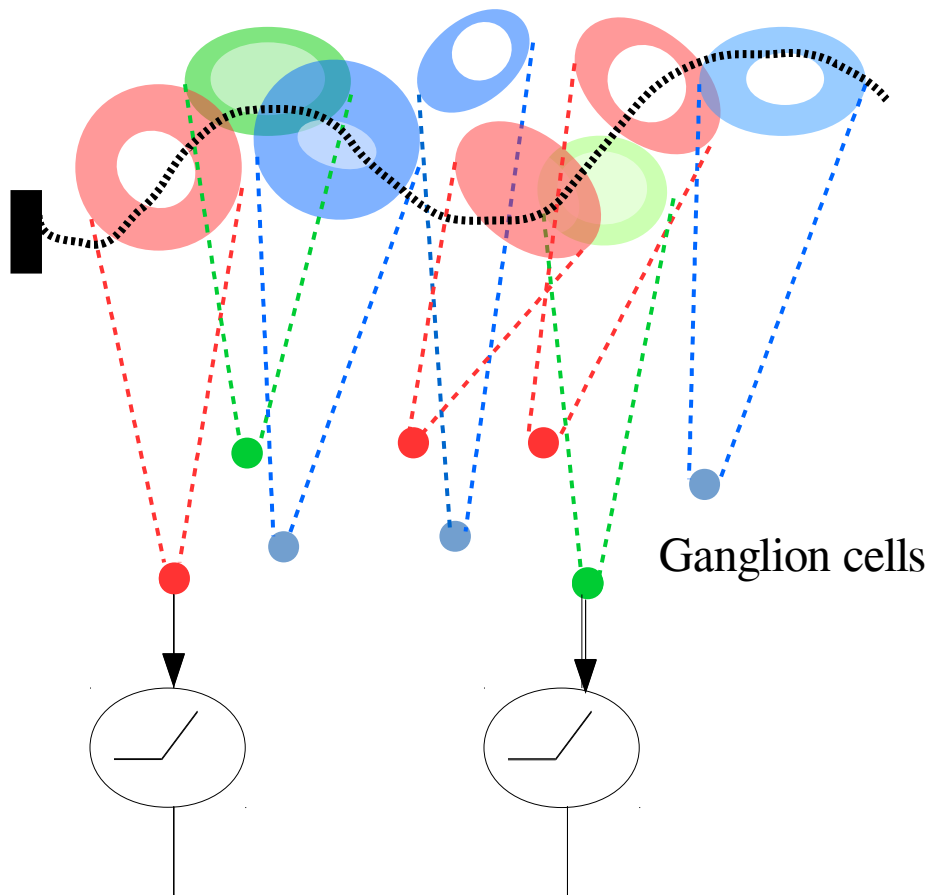
Nobel prize 1981

Ganglion cells response is the convolution of the stimulus with a spatio-temporal receptive field followed by a non linearity



The Hubel-Wiesel view of vision

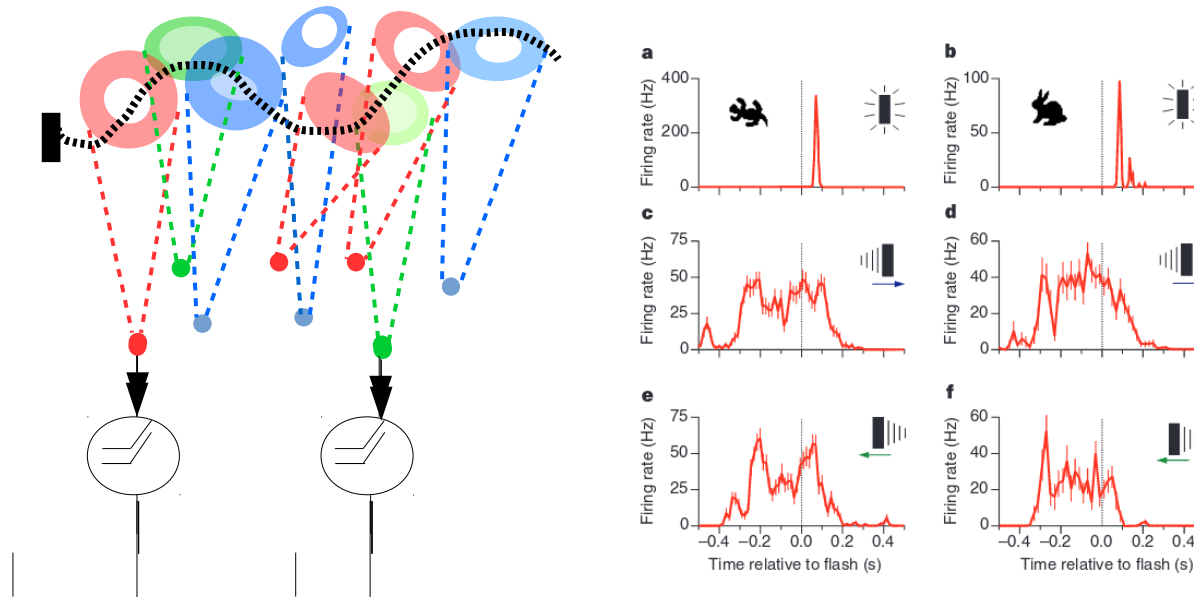
Nobel prize 1981



Source : Berry et al. 1999

The Hubel-Wiesel view of vision

Nobel prize 1981



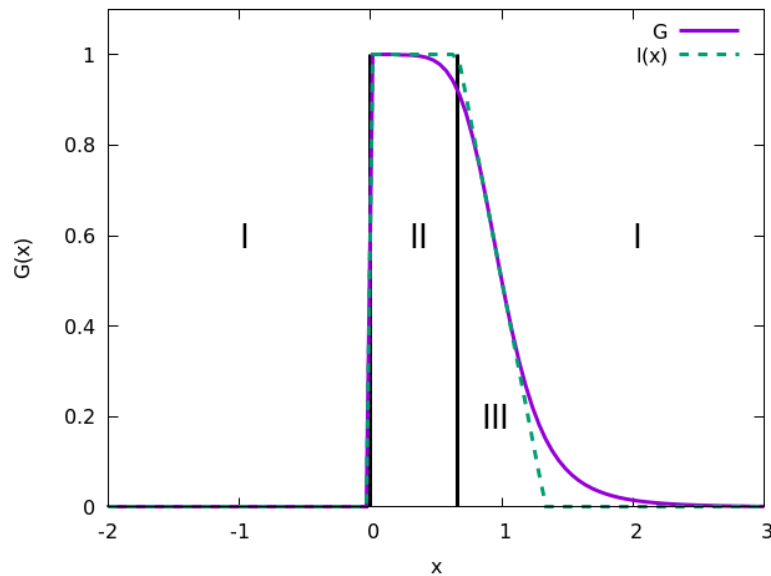
Source : Berry et al. 1999

➤ Which mechanism can account for motion anticipation in the retina ?

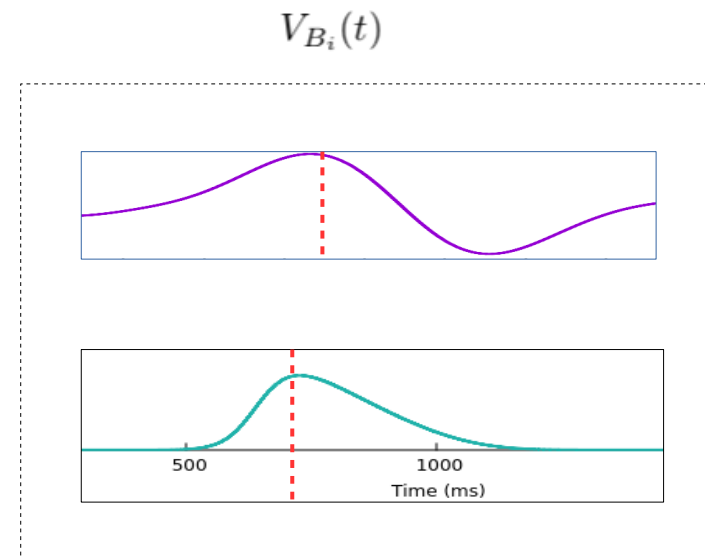
Building a 2D retina model for motion anticipation

1) Gain control

How does it work ?



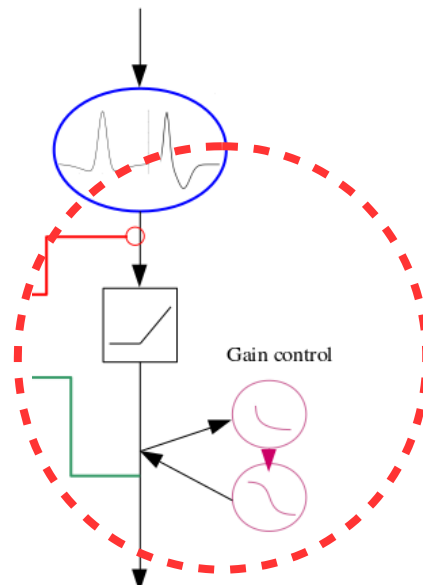
$$\mathcal{G}_B(A) = \begin{cases} 0, & \text{if } A \leq 0; \\ \frac{1}{1+A^6}, & \text{else.} \end{cases}$$



$$R_{B_i} = \mathcal{N}_B(V_{B_i}) \mathcal{G}_B(A_{B_i}).$$

Building a 2D retina model for motion anticipation

1) Gain control (Chen et al. 2013)



- Bipolar voltage :

$$V_{B_i}(t) = V_{i_{drive}}(t) + P_{B_i}(t).$$

- Non-linear function :

$$\mathcal{N}_B(V_{B_i}) = \begin{cases} 0, & \text{if } V_{B_i} \leq \theta_B; \\ V_{B_i} - \theta_B, & \text{else.} \end{cases}$$

- Activation function :

$$\frac{dA_{B_i}}{dt} = -\frac{A_{B_i}}{\tau_a} + h\mathcal{N}(V_{B_i}(t)).$$

- Gain Control function :

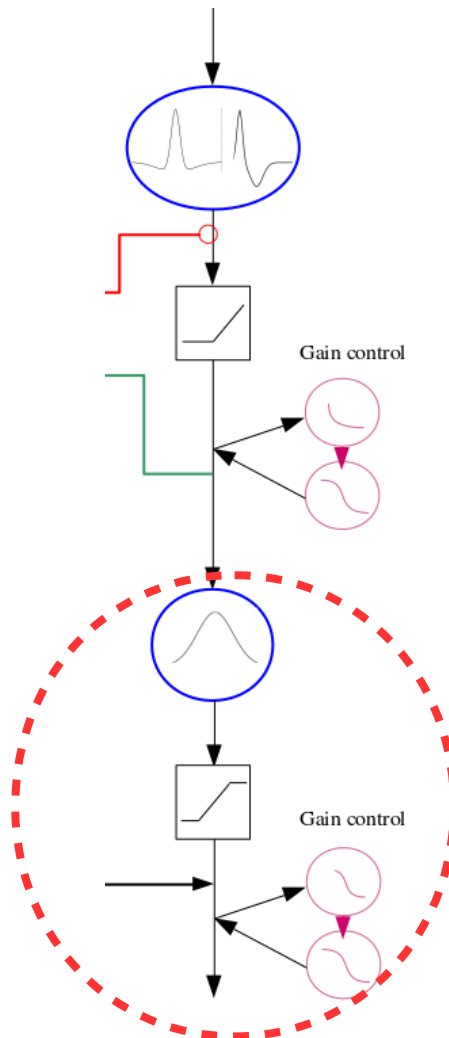
$$\mathcal{G}_B(A) = \begin{cases} 0, & \text{if } A \leq 0; \\ \frac{1}{1+A^6}, & \text{else.} \end{cases}$$

- Output :

$$R_{B_i} = \mathcal{N}_B(V_{B_i}) \mathcal{G}_B(A_{B_i}).$$

Building a 2D retina model for motion anticipation

1) Gain control (Chen et al. 2013)



- Ganglion voltage

$$V_{G_k} = \sum_i W_{G_k}^{B_i} R_{B_i}$$

- Non-linear function :

$$\mathcal{N}_{G_F}(V) = \begin{cases} 0, & \text{if } V \leq 0; \\ \alpha_{G_F}(V - \theta_{G_F}), & \text{if } \theta_{G_F} \leq V \leq N_{G_F}^{max}/\alpha_{G_F} + \theta_{G_F} \\ N_{G_F}^{max}, & \text{else.} \end{cases}$$

- Activation function :

$$\frac{dA_{G_F k_F}}{dt} = -\frac{A_{G_F k_F}}{\tau_{G_F}} + h_{G_F} \mathcal{N}_{G_F}(V_{G_F k_F})$$

- Gain Control function :

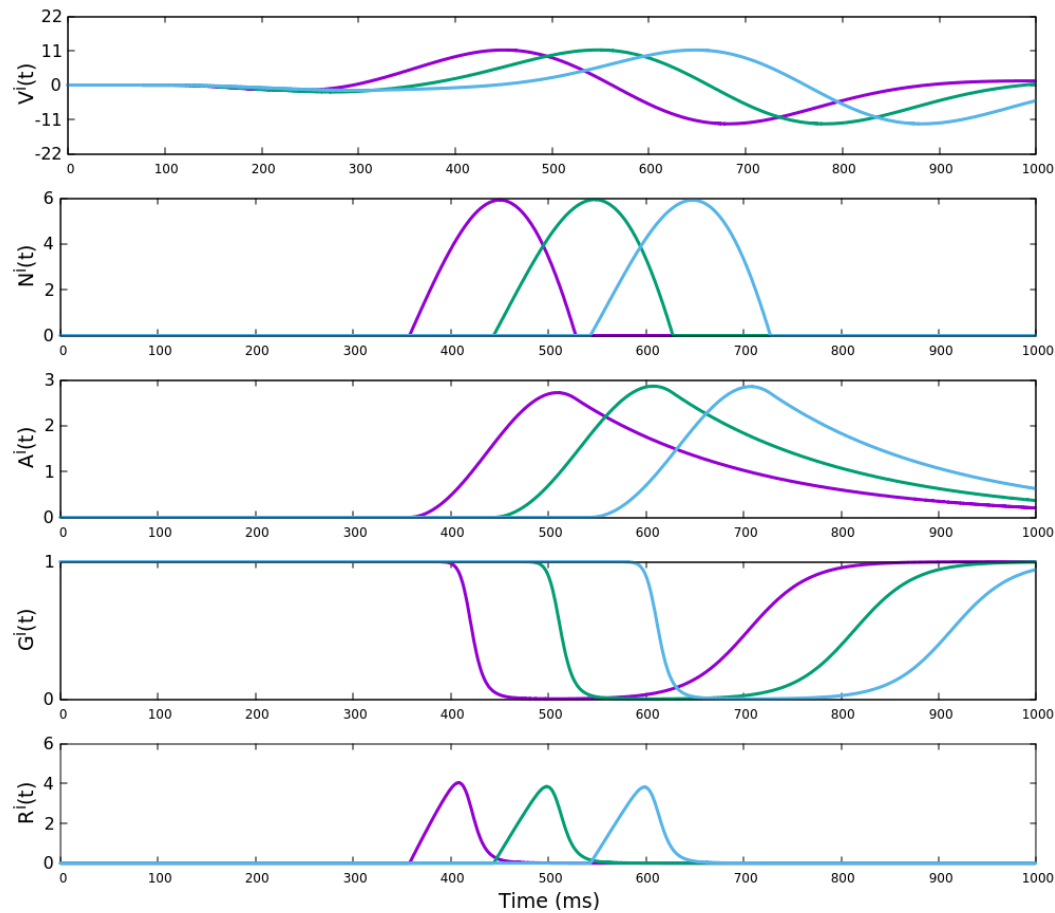
$$\mathcal{G}_{G_F}(A) = \begin{cases} 0, & \text{if } A \leq 0; \\ \frac{1}{1+A}, & \text{else.} \end{cases}$$

- Output :

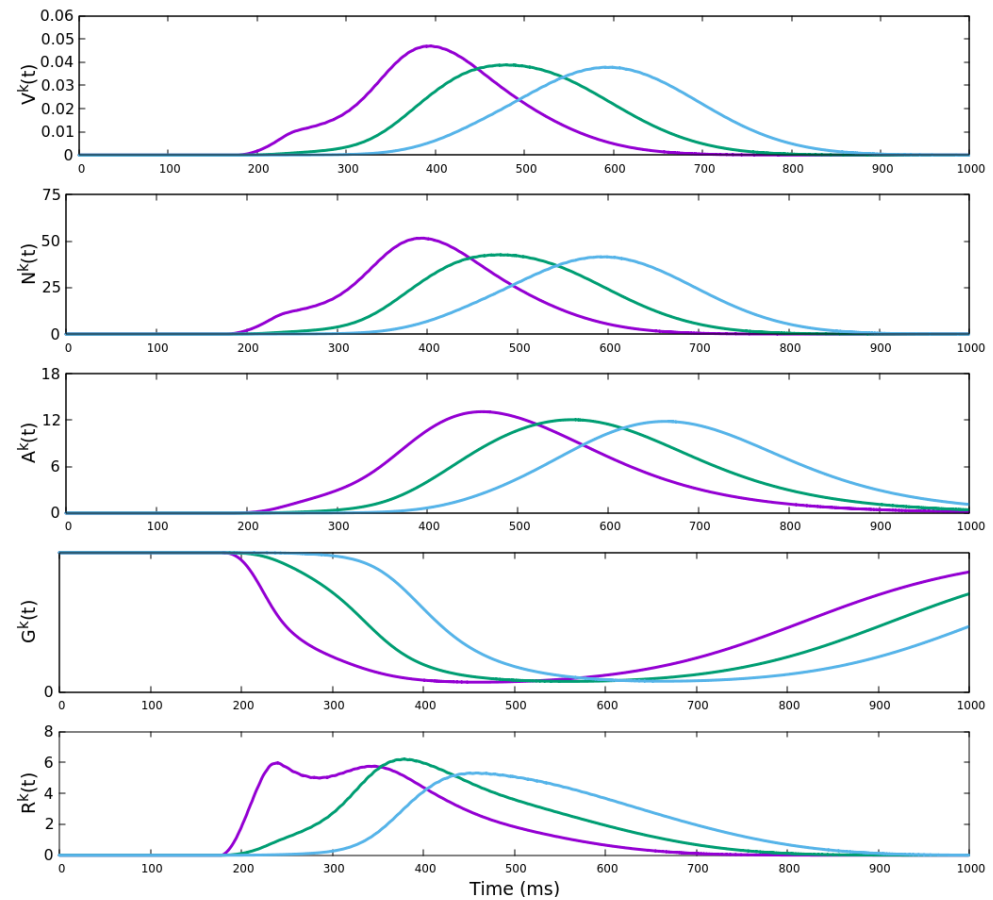
$$R_{G_F k_F}(V_{G_F k_F}, A_{G_F k_F}) = \mathcal{N}_{G_F}(V_{G_F k_F}) \mathcal{G}_{G_F}(A_{G_F k_F}).$$

1D results : smooth motion anticipation with gain control

Bipolar layer

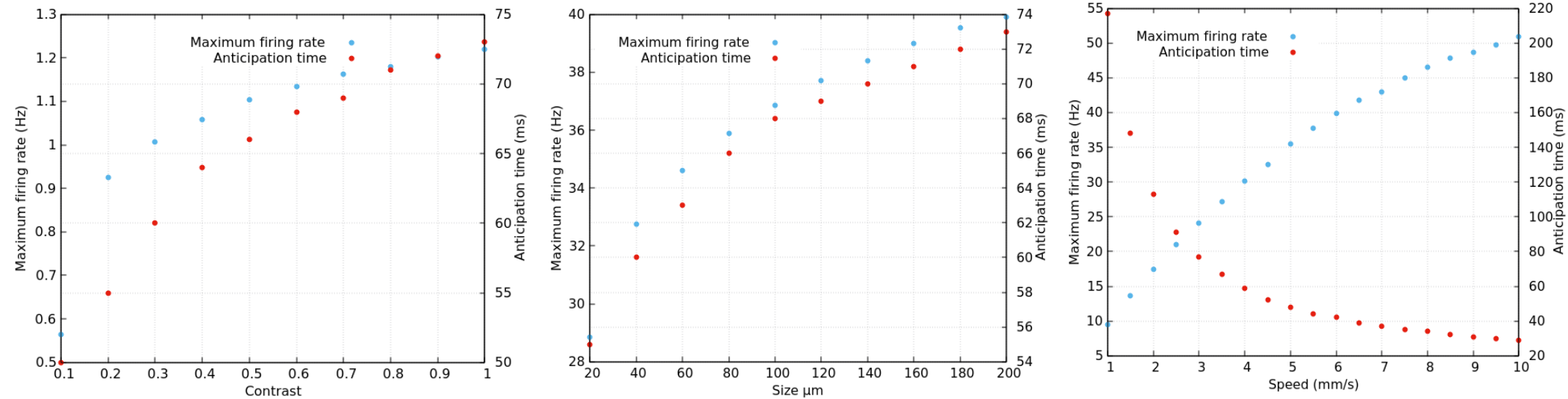


Ganglion layer



1D results : smooth motion anticipation with gain control

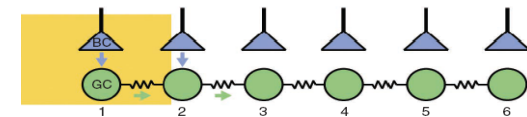
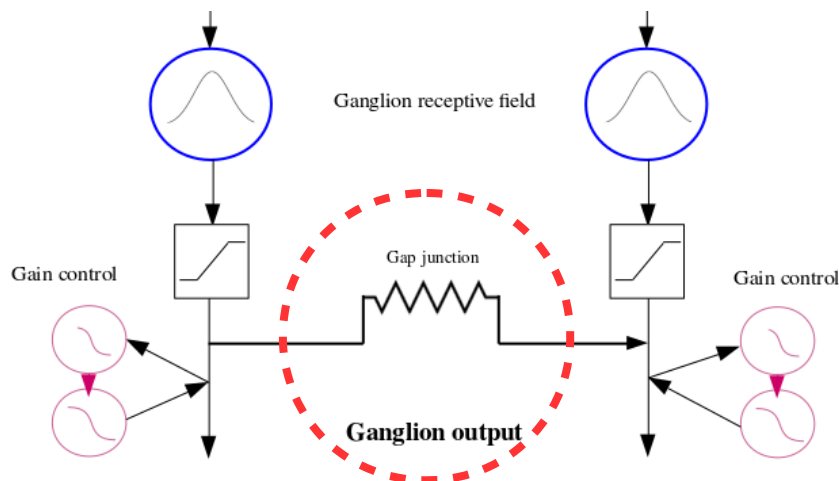
Anticipation variability with stimulus parameters



Building a 2D retina model for motion anticipation

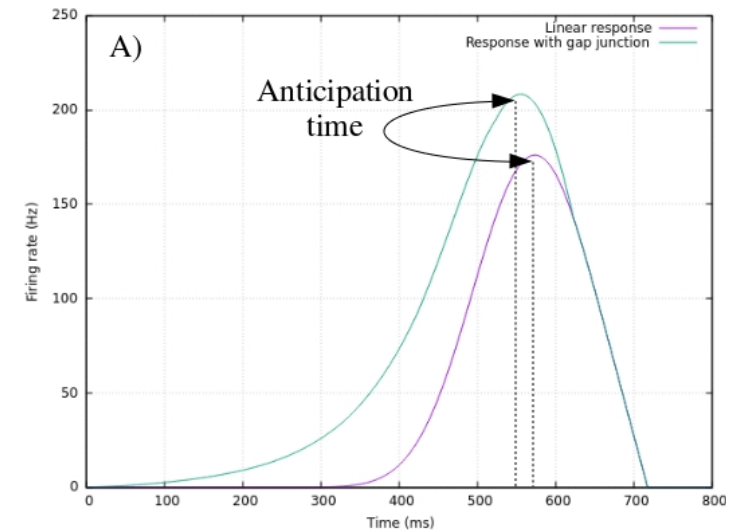
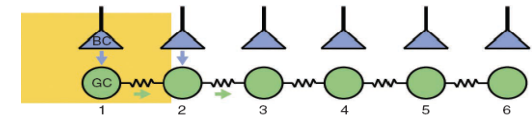
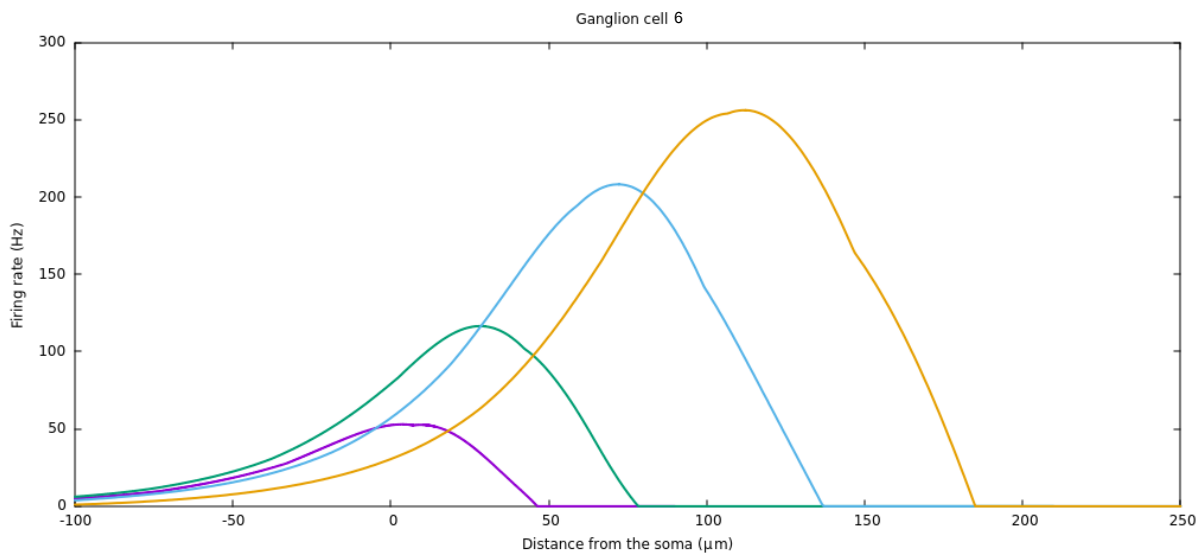
2) Gap junction connectivity

- A class of direction selective RGCs are connected through gap junctions
- Their activity comprises the activity pooled from bipolar cells and the activity coming from the downstream RGCs, in the direction of motion

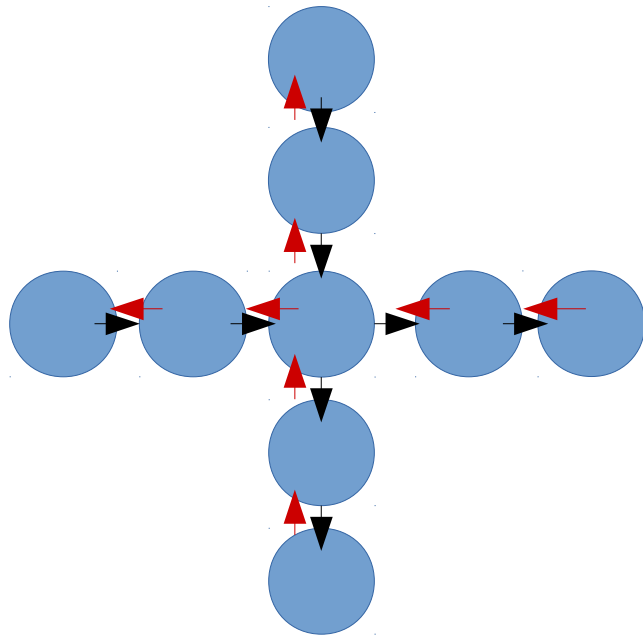


$$R_{GDkD} = V_{GDkD} + \beta R_{GDkD-1}$$

1D results : smooth motion anticipation with gap junctions

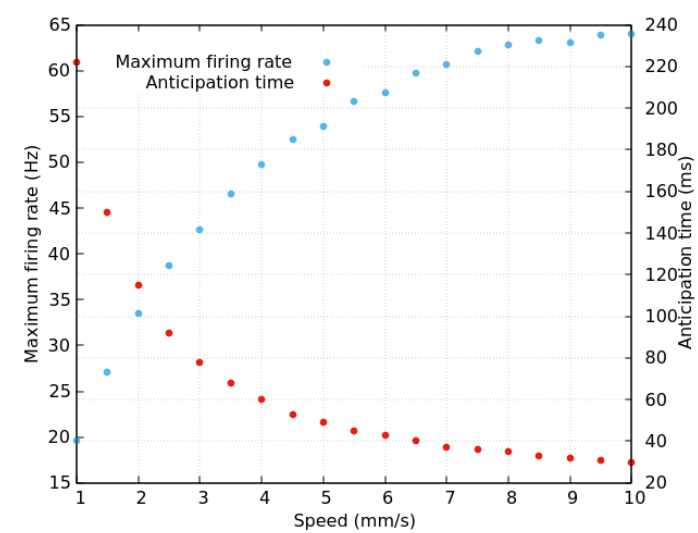
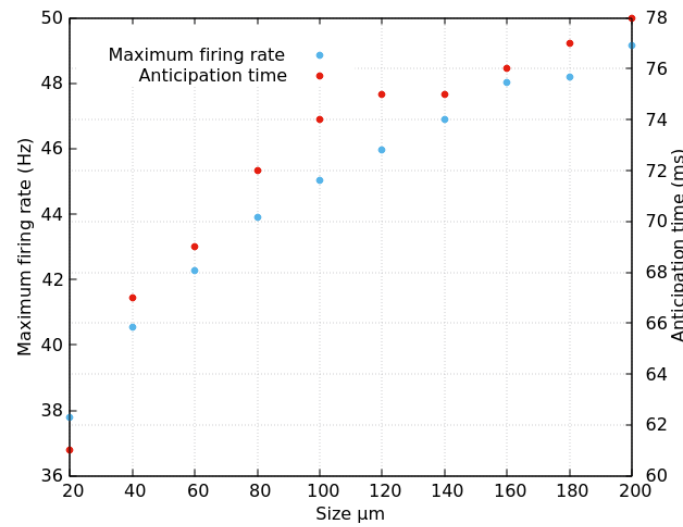
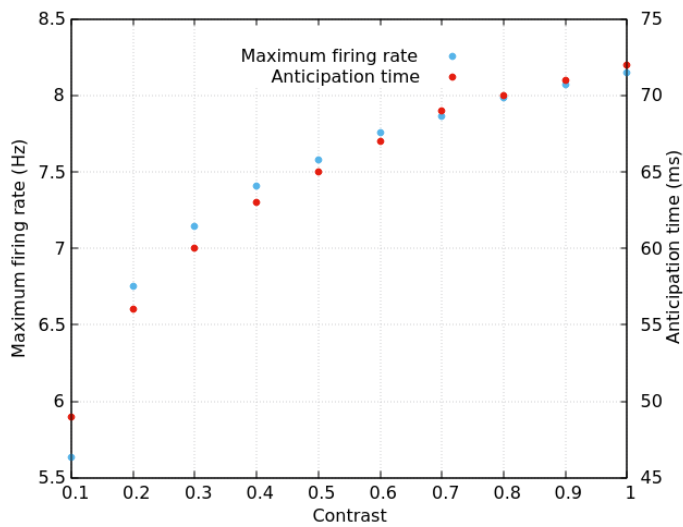


1D results : smooth motion anticipation with gap junctions



1D results : smooth motion anticipation with gap junctions

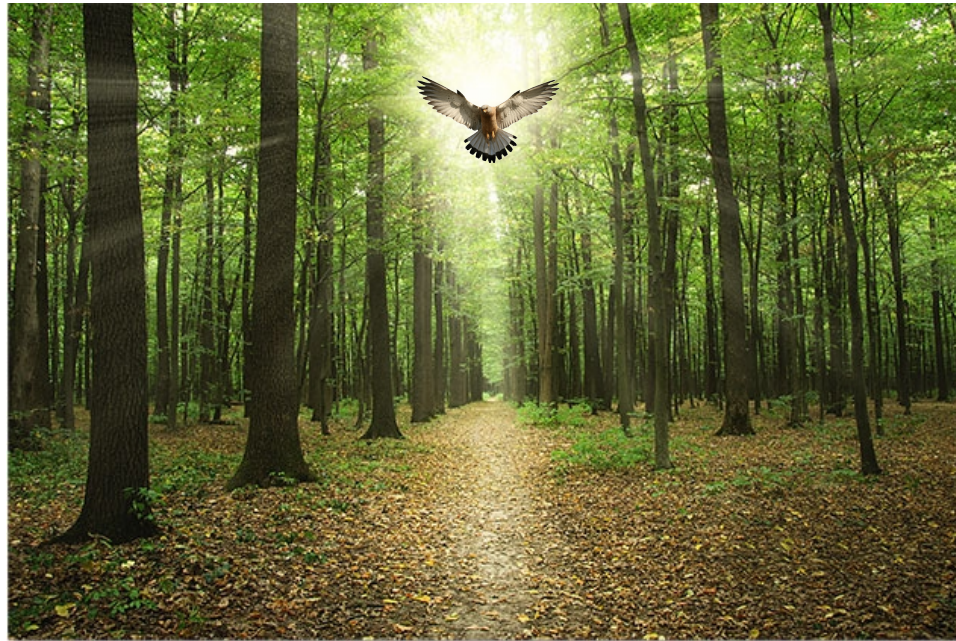
Anticipation variability with stimulus parameters



Building a 2D retina model for motion anticipation

3) Amacrine cells connectivity

- A class of RGCs are selective to differential motion



Building a 2D retina model for motion anticipation

3) Amacrine cells connectivity

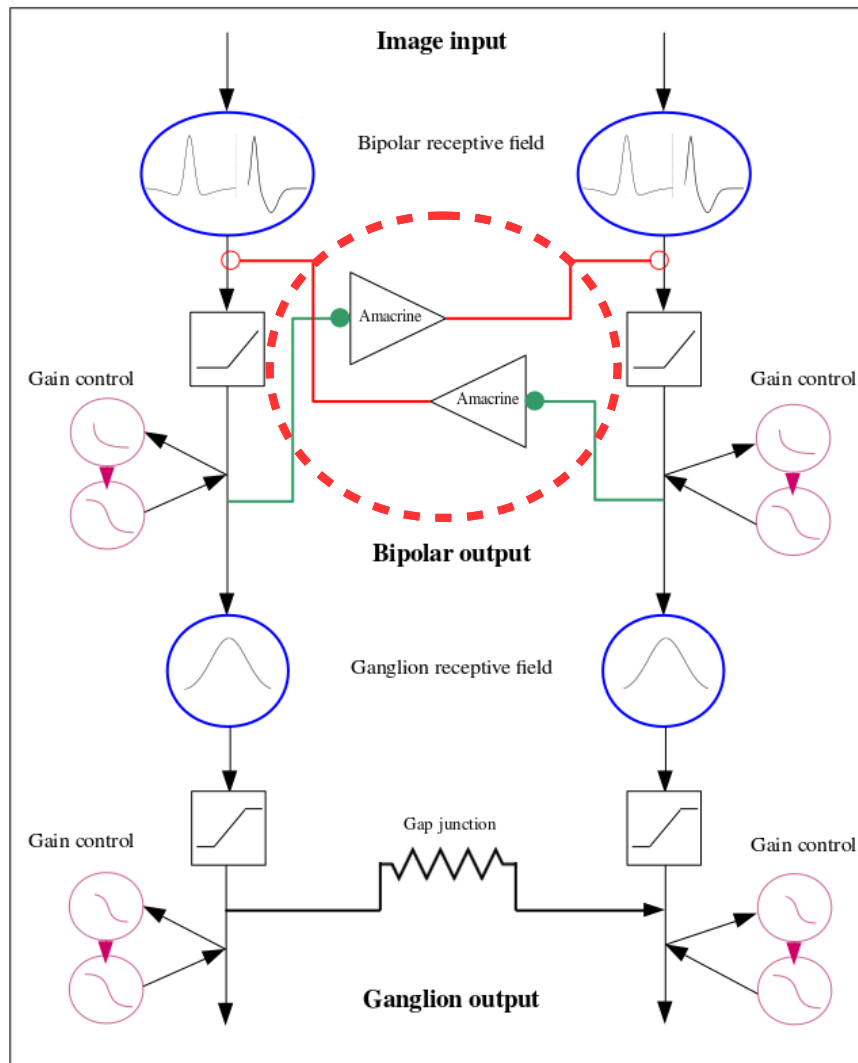
- A class of RGCs are selective to differential motion



- The circuitry involves amacrine cells connectivity upstream of ganglion cells

Connectivity pathways

2) Amacrine cells connectivity



- Bipolar voltage :

$$\frac{dV_{B_i}}{dt} = -\frac{1}{\tau_B} V_{B_i} + \sum_{j=1}^{N_A} W_{B_i}^{A_j} V_{A_j} + F_{B_i}(t).$$

- External drive :

$$F_{B_i}(t) = \left[K_i \ast \left(\frac{\mathcal{S}}{\tau_B} + \frac{d\mathcal{S}}{dt} \right) \right] (t)$$

- Amacrine voltage :

$$\frac{dV_{A_j}}{dt} = -\frac{1}{\tau_A} V_{A_j}(t) + \sum_{i=1}^{N_A} W_{A_j}^{B_i} R_{B_i}(t).$$

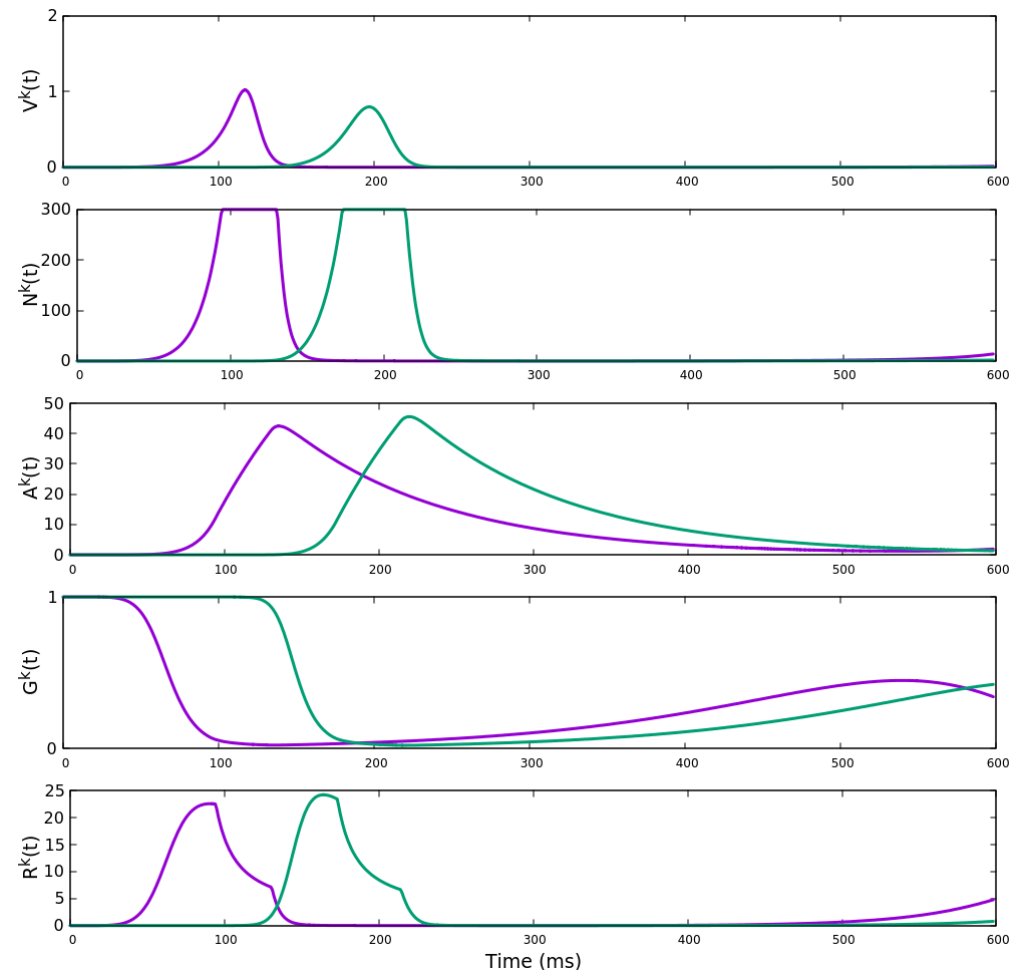
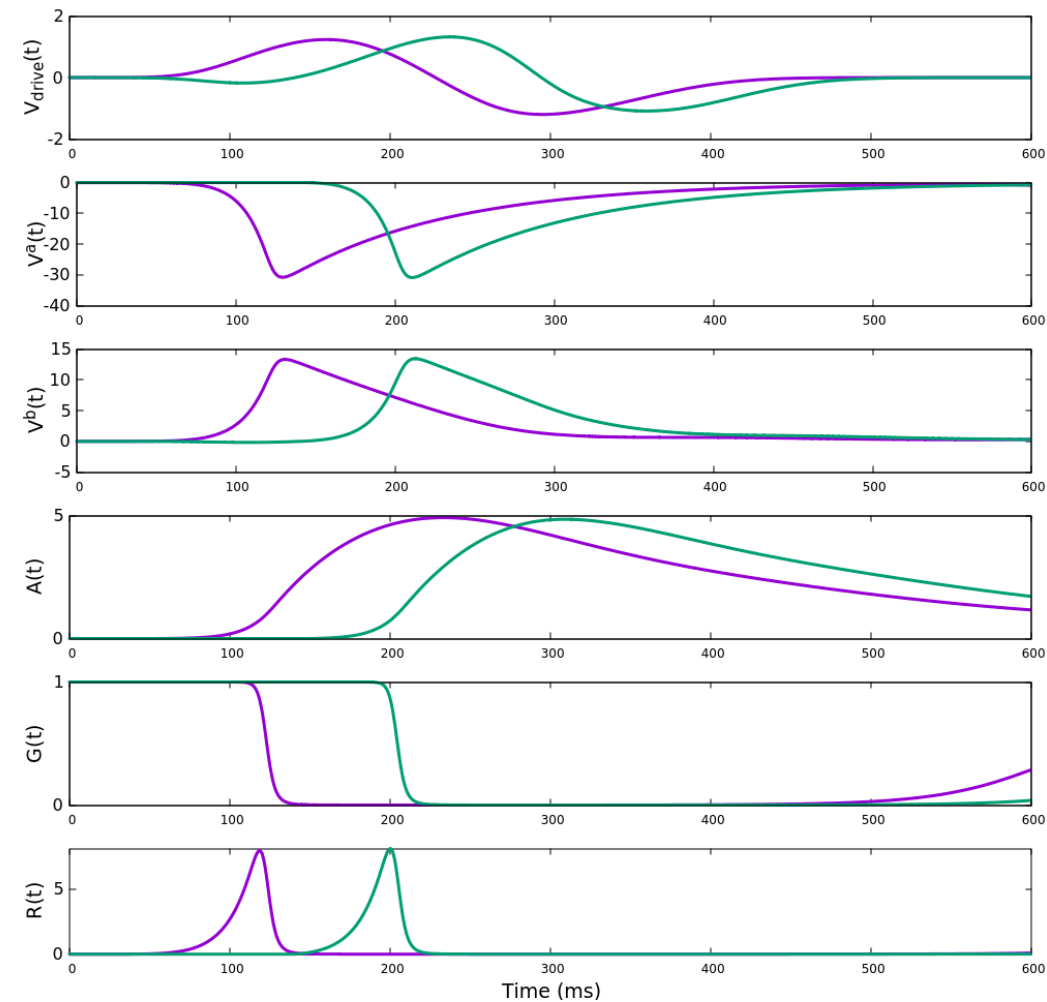
- Coupled dynamics :

$$\left\{ \begin{array}{l} \frac{dV_{B_i}}{dt} = -\frac{1}{\tau_B} V_{B_i} + \sum_{j=1}^{N_A} W_{B_i}^{A_j} V_{A_j} + F_{B_i}(t) \\ \frac{dA_{B_i}}{dt} = -\frac{A_{B_i}}{\tau_a} + h \mathcal{N}(V_{B_i}(t)), \\ \frac{dV_{A_j}}{dt} = -\frac{1}{\tau_A} V_{A_j}(t) + \sum_{i=1}^{N_A} W_{A_j}^{B_i} R_{B_i}(t). \end{array} \right. \quad 20$$

1D results : smooth motion anticipation with amacrine connectivity

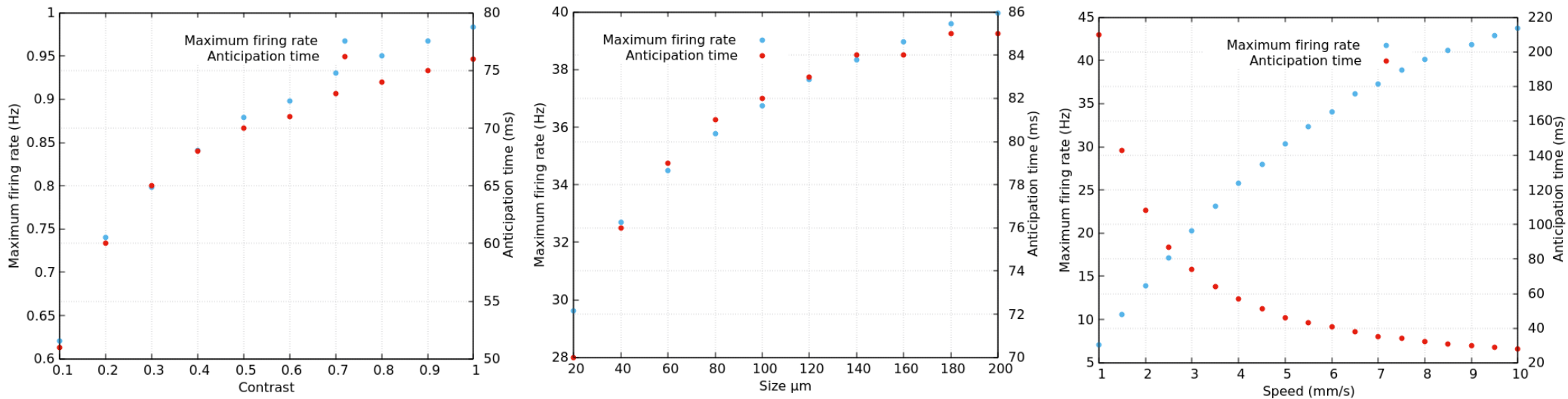
Bipolar layer

Ganglion layer

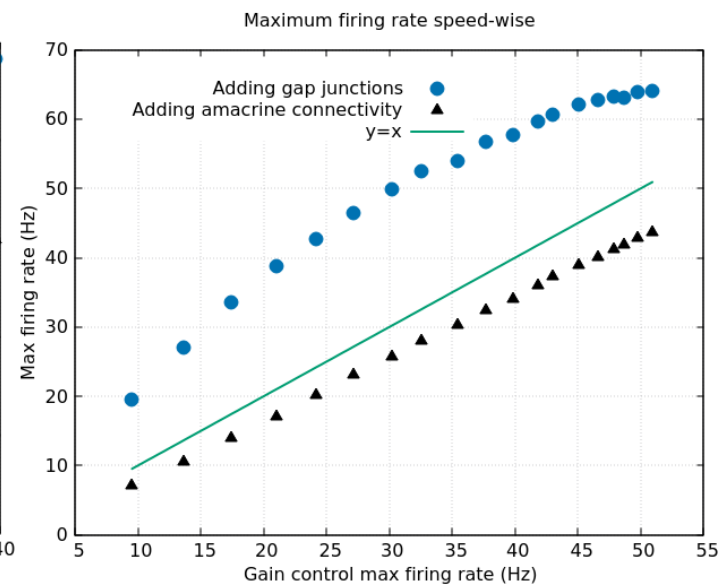
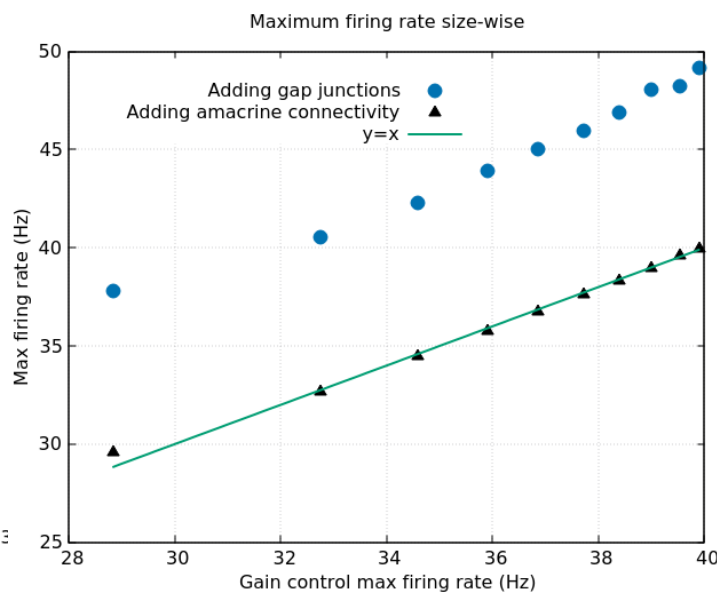
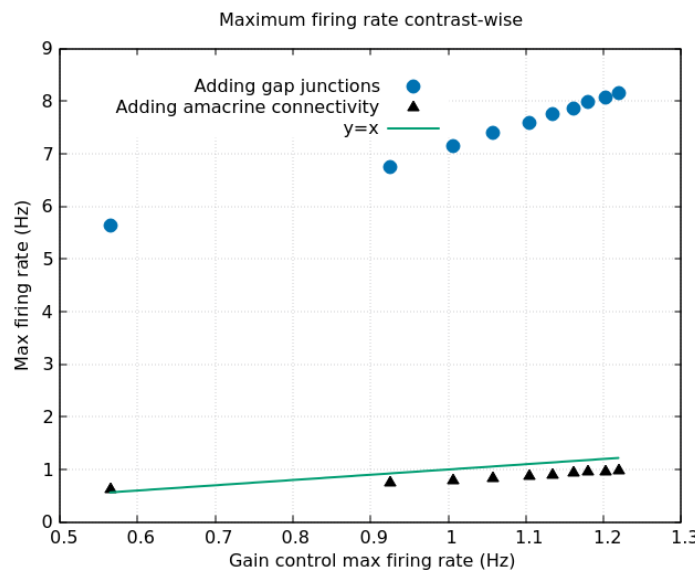
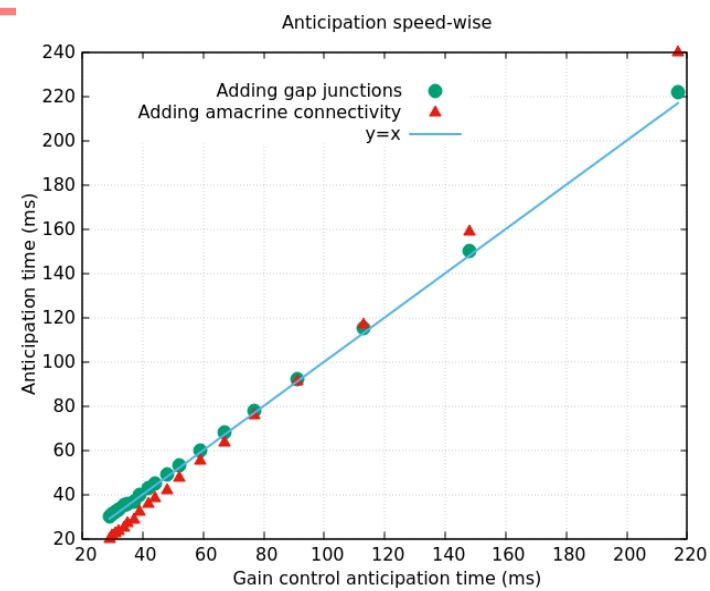
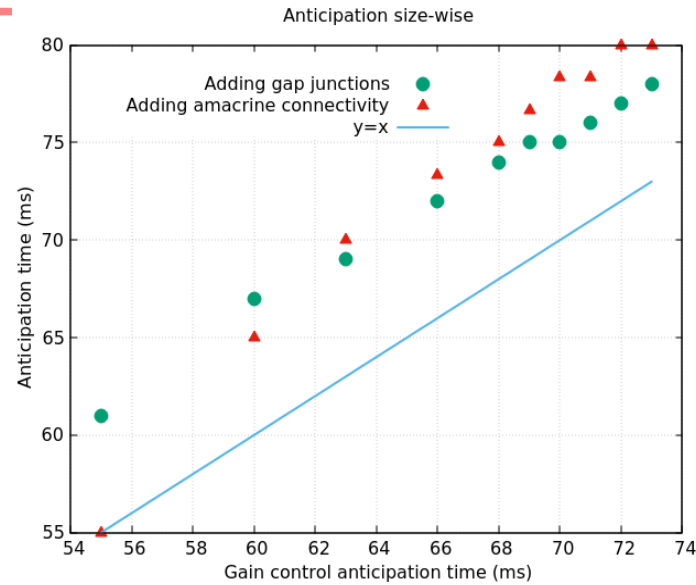
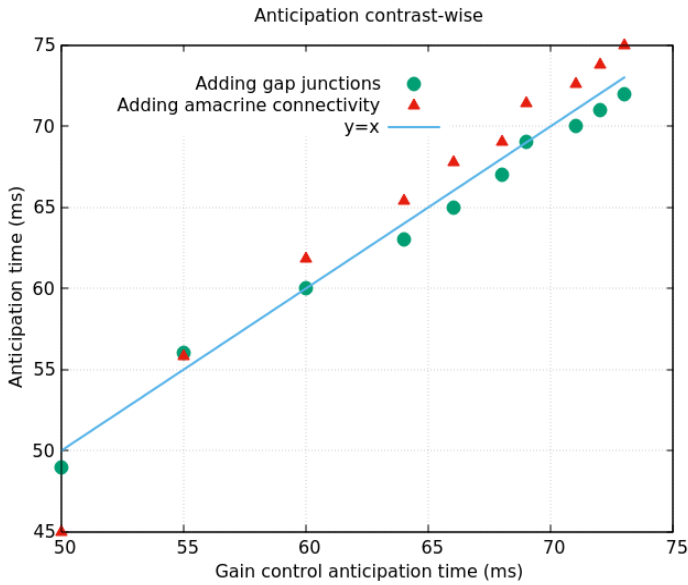


1D results : smooth motion anticipation with amacrine connectivity

Anticipation variability with stimulus parameters

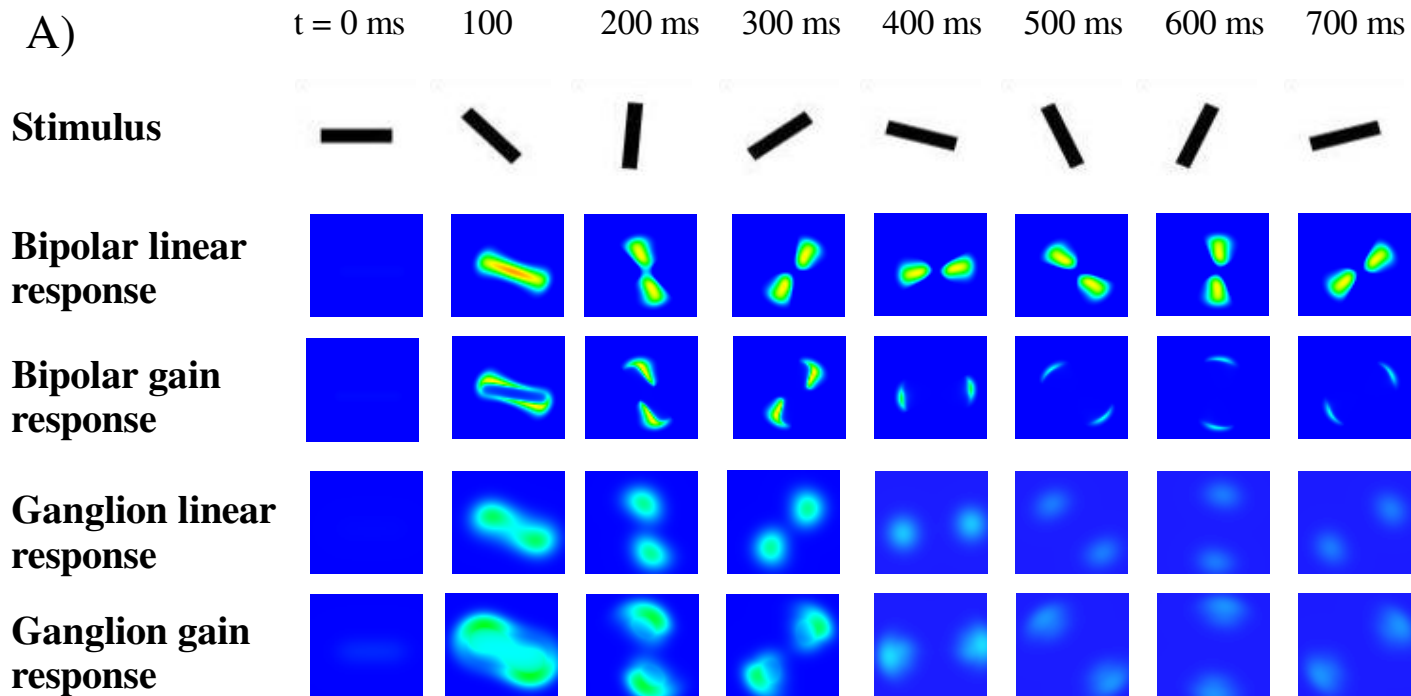


Comparing the performance of the three layers

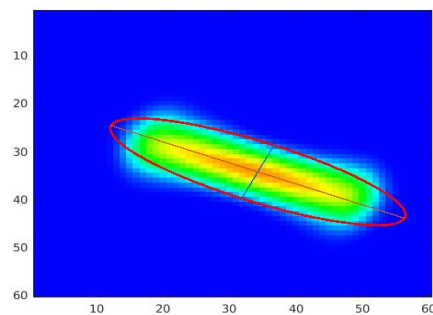


Suggesting new experiments : 2D results

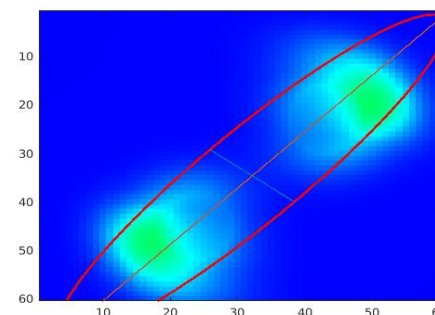
1) Angular anticipation



B)

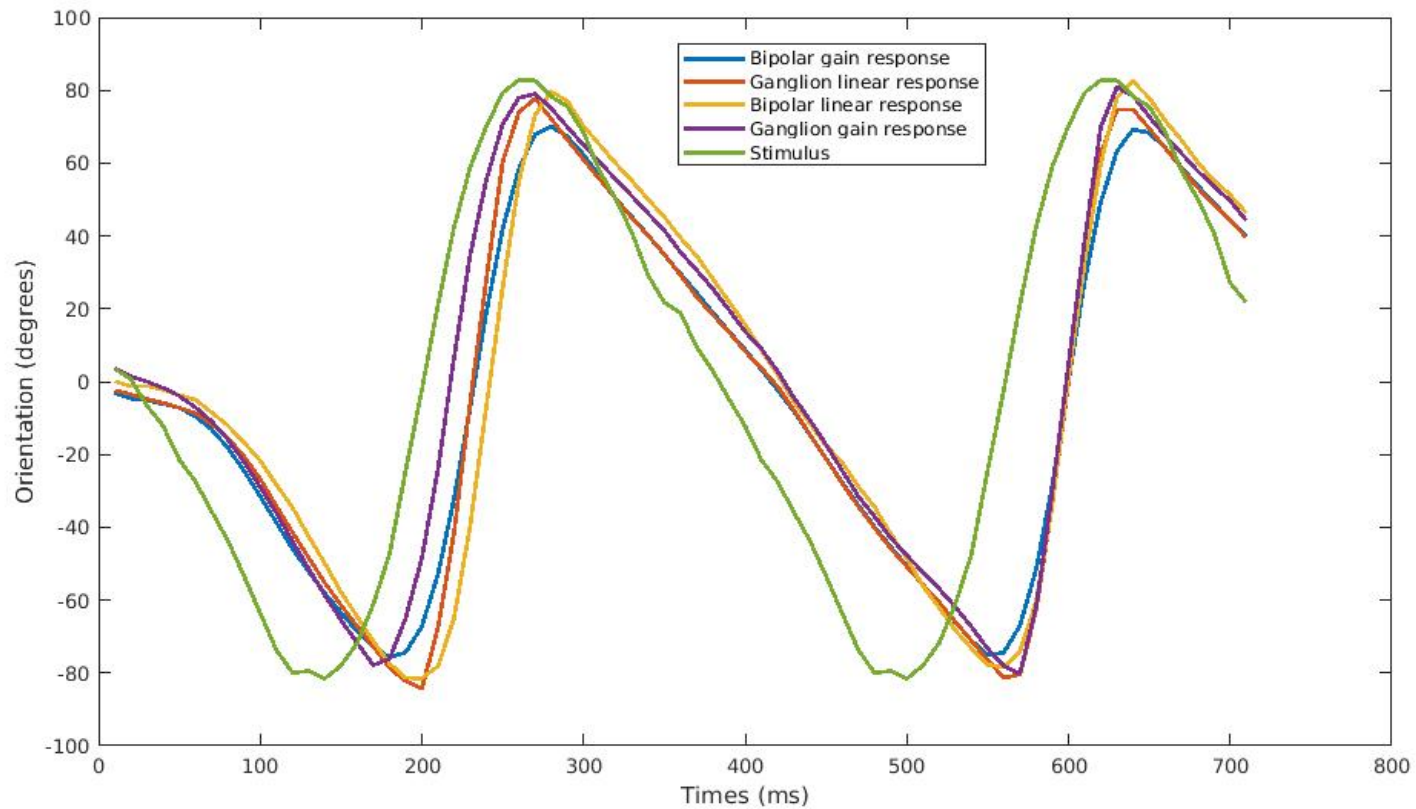


C)



Suggesting new experiments : 2D results

1) Angular anticipation



Suggesting new experiments : 2D results

2) Anticipation and shape

Stimulus



Bipolar linear
activity

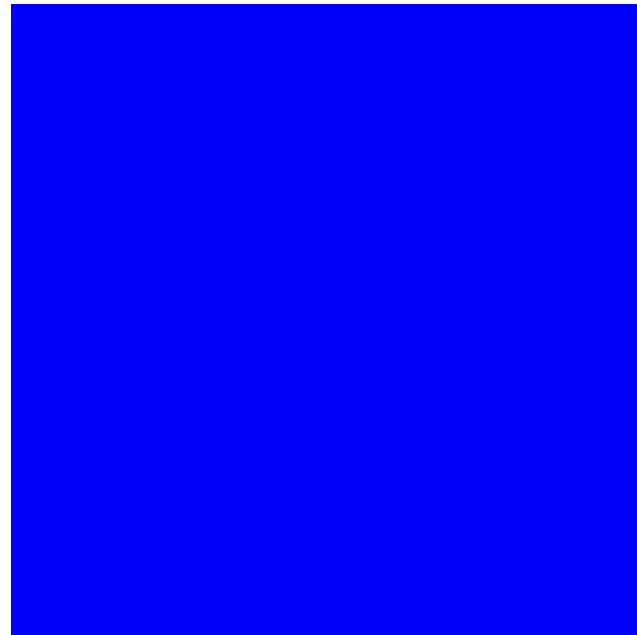


Ganglion gain
control activity



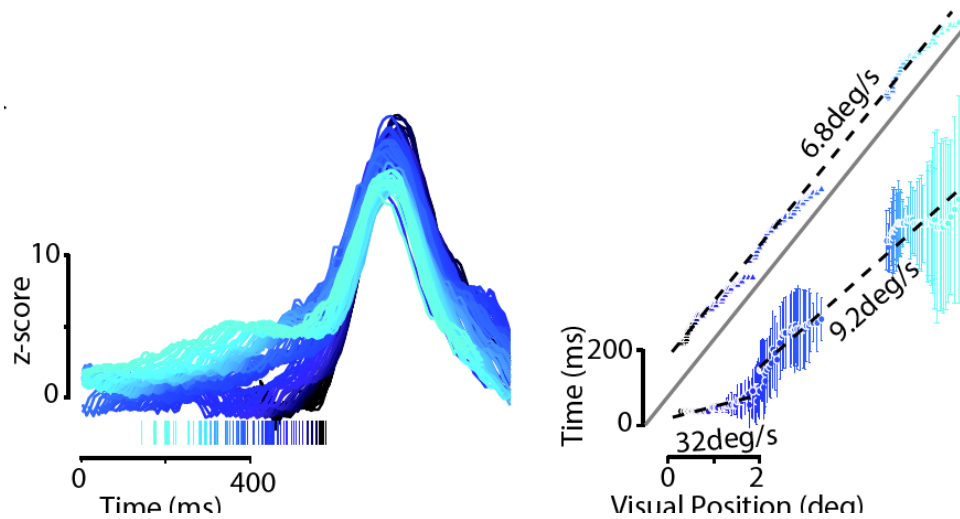
Suggesting new experiments : 2D results

2) Anticipation on a noisy background

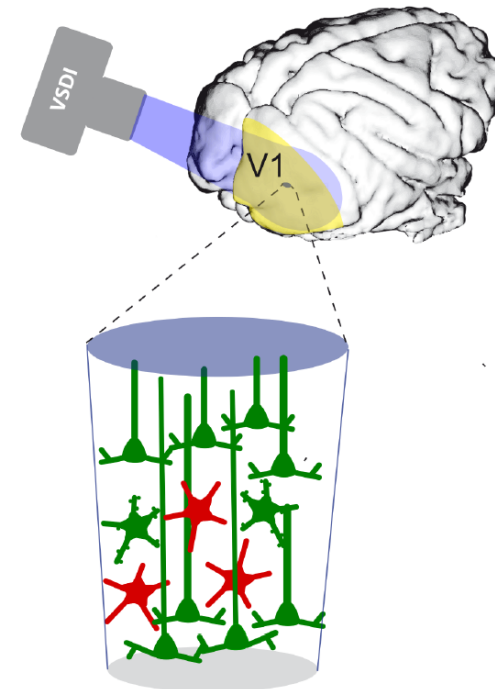


II) *Anticipation in V1*

Anticipation in V1

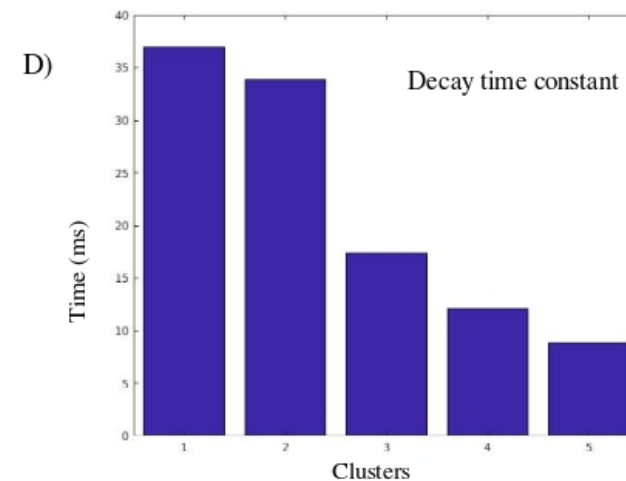
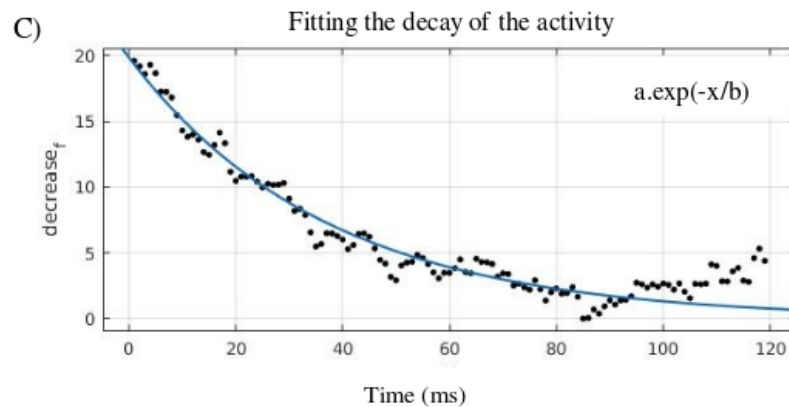
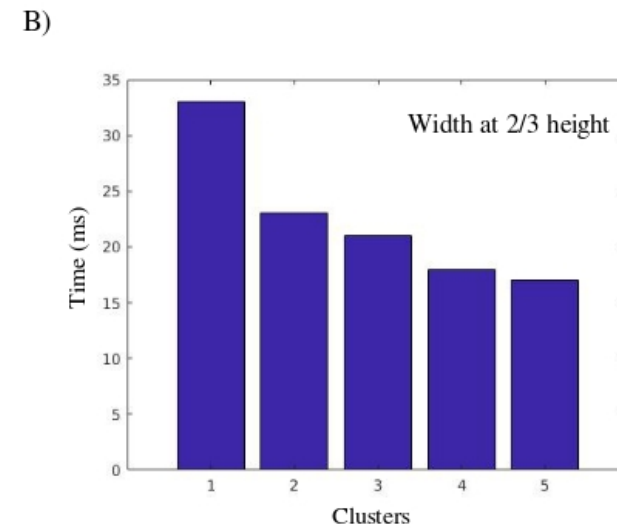
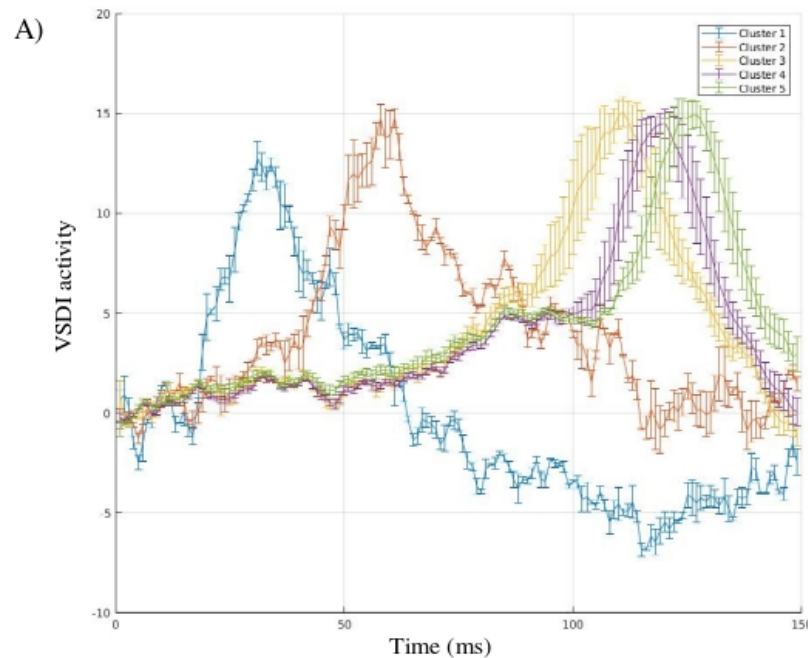


Source : Benvenuti et al. 2015



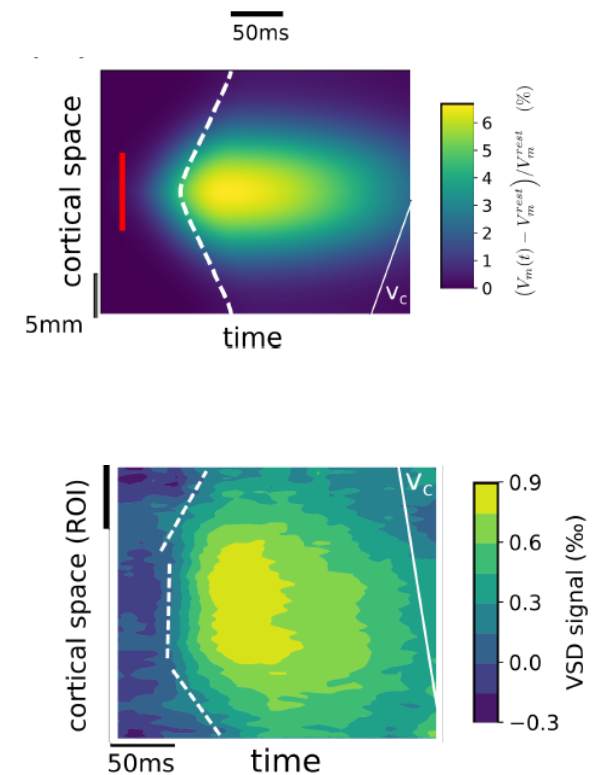
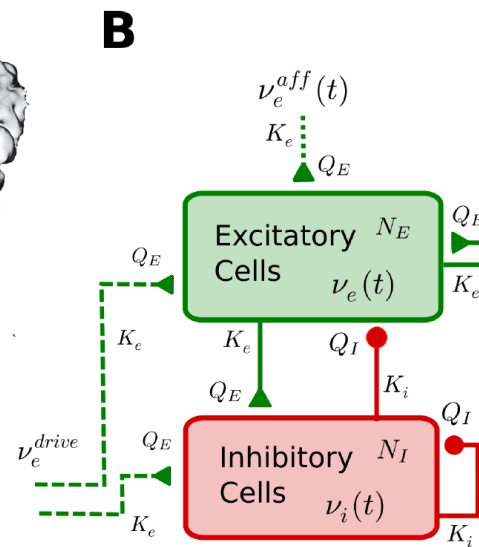
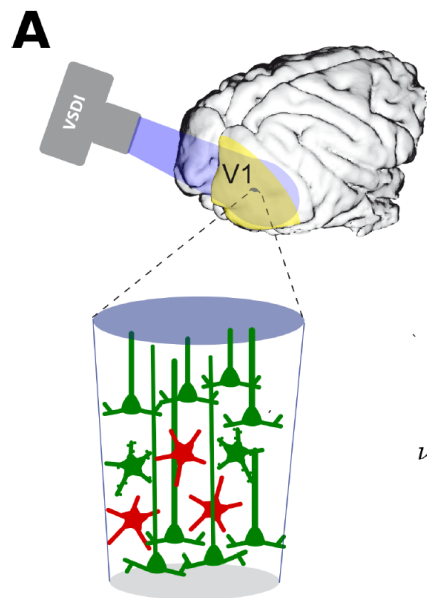
Anticipation in the cortex : VSDI data analysis

(Data courtesy of F. Chavane et S. Chemla)

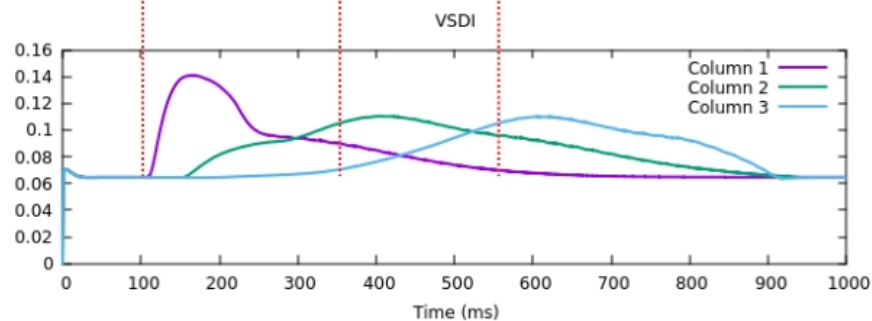
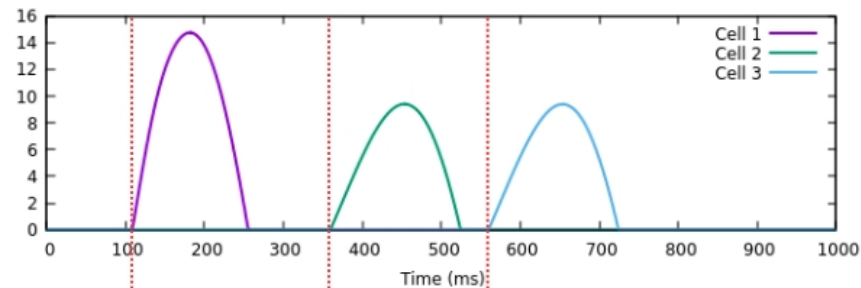
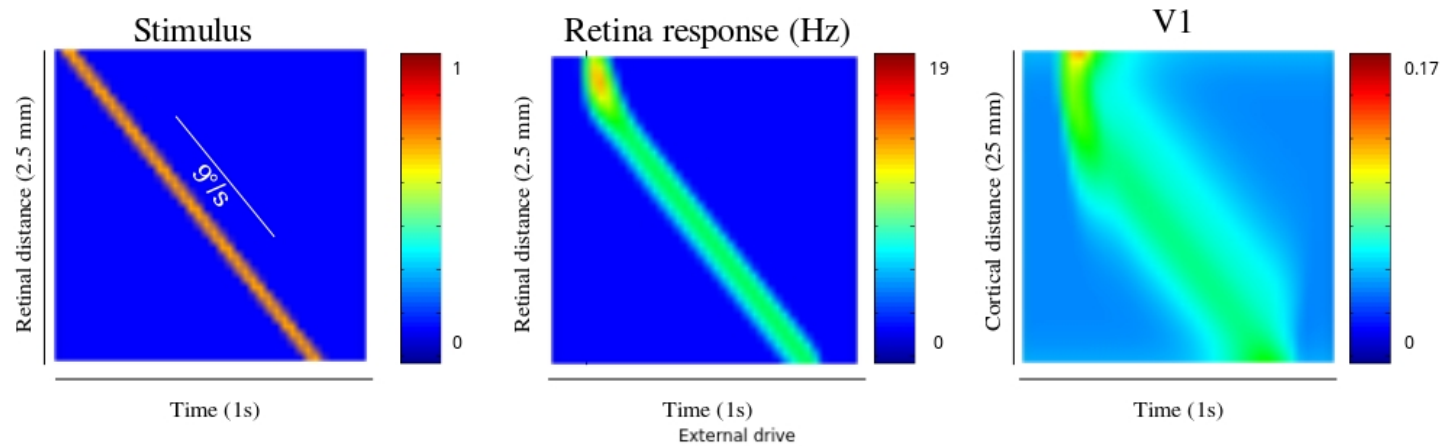


A mean field model to reproduce VSDI recordings

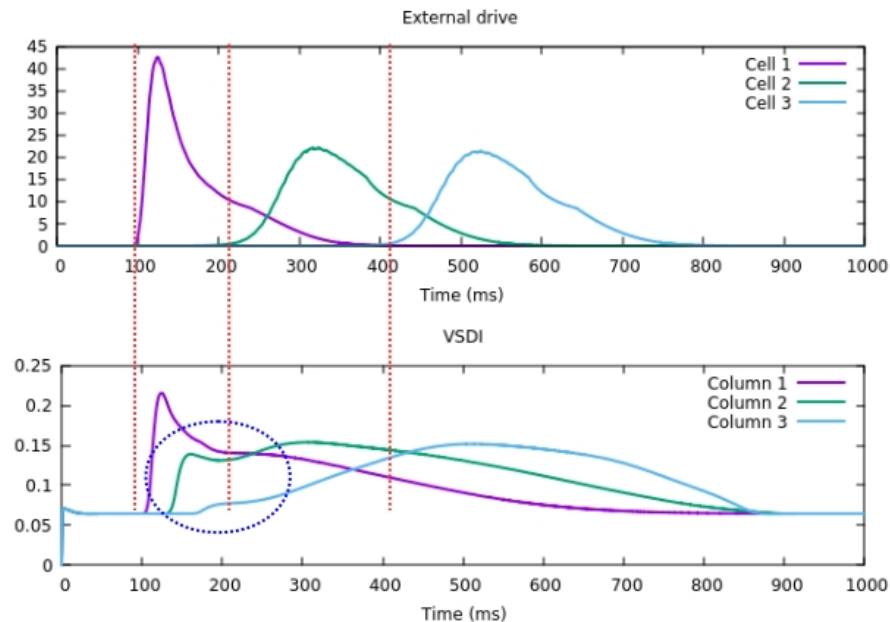
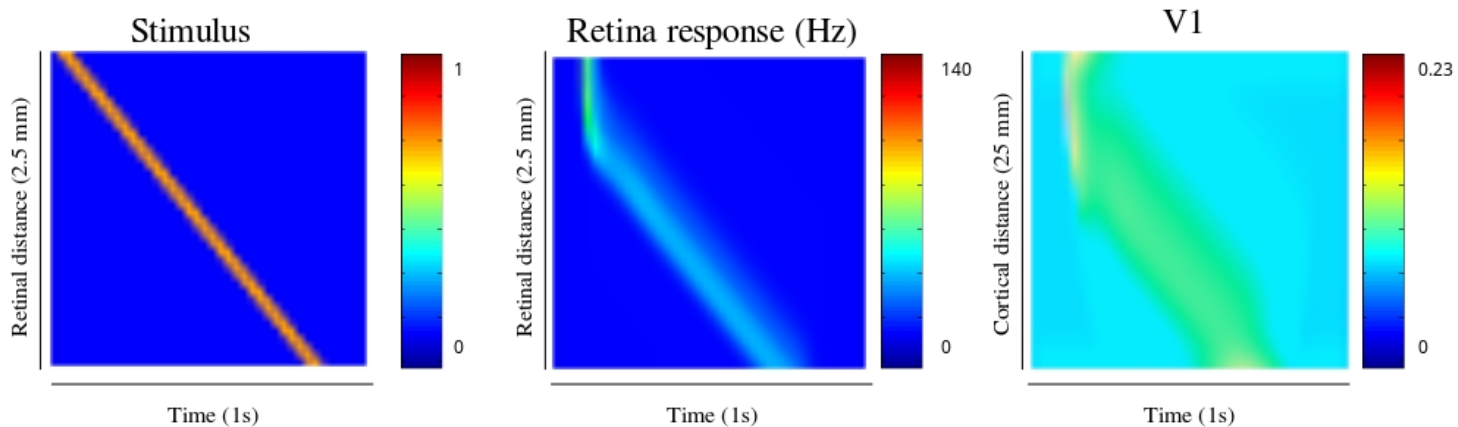
Zerlaut et al 2016
Chemla et al 2018



Response of the cortical model to a LN retina drive

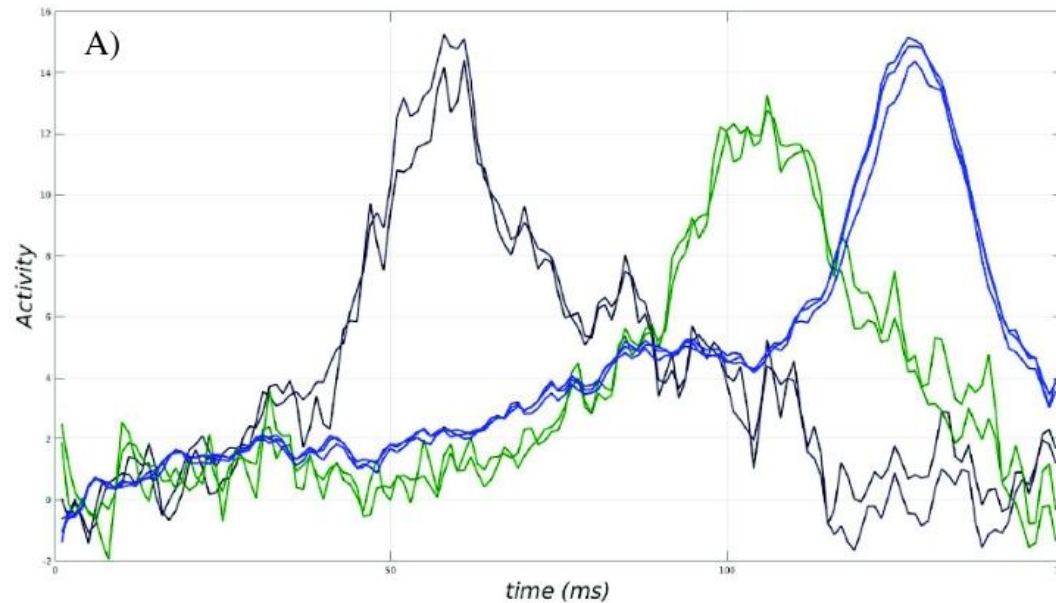


Response of the cortical model to a retina drive with gain control

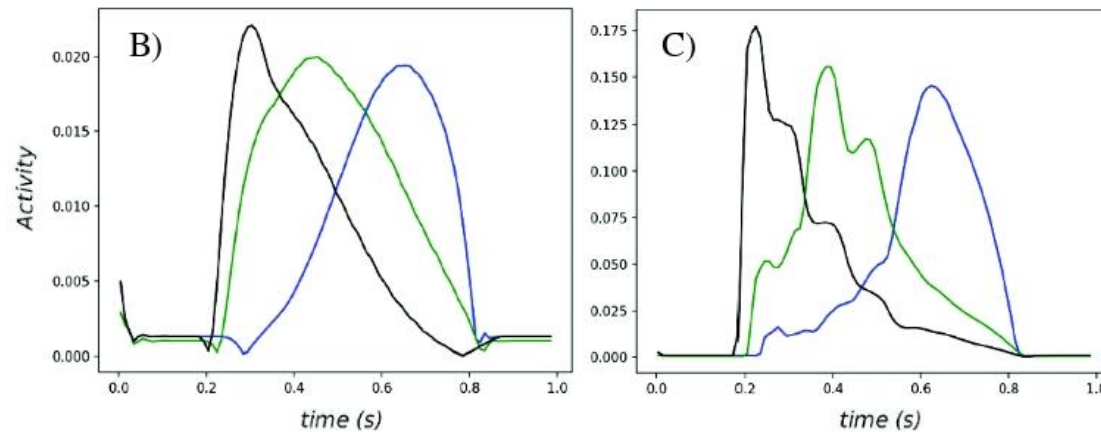


Comparing simulation results to VSDI recordings

Cortex experimental recordings



Simulation results
Response to an LN
model of the retina



Simulation results
Response to a gain
control model of the
retina

Conclusions

- We developed a 2D retina with three ganglion cell layers, implementing gain control and connectivity.
- We use the output of our model as an input to a mean field model of V1, and were able to reproduce anticipation as observed in VSDI

Questions :

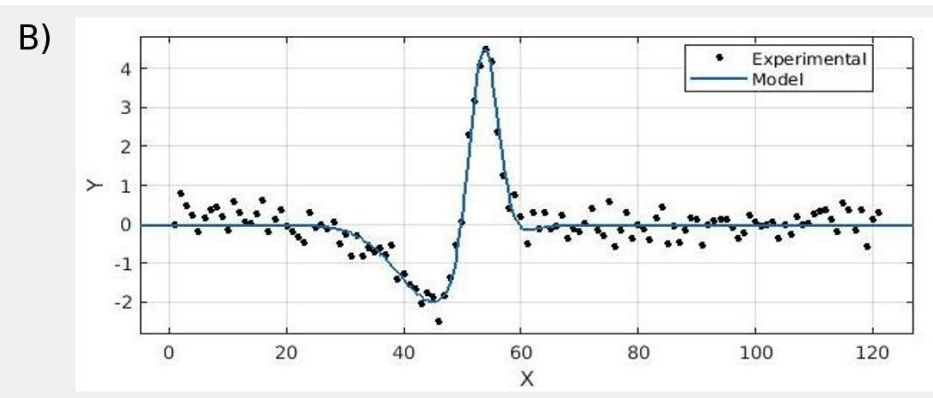
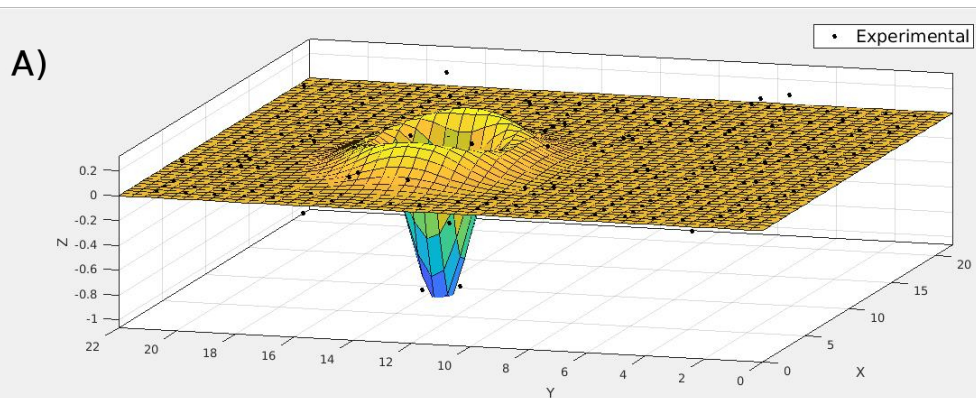
- How to improve object identification 1) exploring the model's parameters and 2) using connectivity ?
- Is our model able to anticipate more complex trajectories, with accelerations for instance ?
- How to calibrate connectivity using biology ?
- How does anticipation affect higher order correlations ?
- Would it be possible to design psycho-physical tests clearly showing the role of the retina in visual anticipation ?

Thank you for your attention !

Supplementary material

Stimulus integration

$$\left[K_i \begin{smallmatrix} S, t \\ * \end{smallmatrix} \mathcal{S} \right] (t) = \int_{-\infty}^t K_T(t-u) \left[\int_{\mathbb{R}^2} K_{i,S}(x, y) \mathcal{S}(x, y, u) dx dy \right] du \equiv V_{i,drive}(t).$$

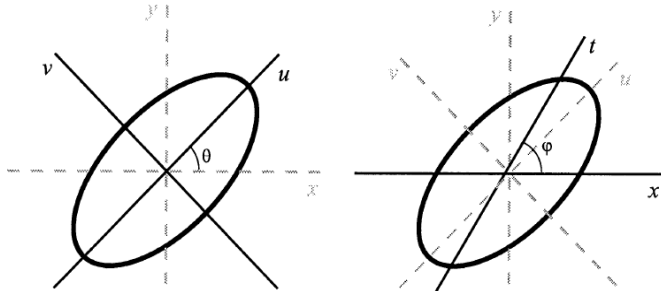


$$K_{i,S}(x, y) = \frac{A_1}{2\pi\sqrt{\det C_1}} e^{-\frac{1}{2} \bar{X}_1 \cdot C_1^{-1} \cdot X_1} - \frac{A_2}{2\pi\sqrt{\det C_2}} e^{-\frac{1}{2} \bar{X}_1 \cdot C_2^{-1} \cdot X_1},$$

$$K_T(t) = \left(\frac{K_1}{\sqrt{2\pi}\sigma_1} e^{-\frac{(t-\mu_1)^2}{2\sigma_1^2}} - \frac{K_2}{\sqrt{2\pi}\sigma_2} e^{-\frac{(t-\mu_2)^2}{2\sigma_2^2}} \right) H(t)$$

(Data courtesy of O. Marre)

Stimulus integration : anisotropy



Geusebroek et al. 2003

$$\sigma_{x'} = \frac{\sigma_x \sigma_y}{\sqrt{\sigma_x^2 \cos^2 \theta + \sigma_y^2 \sin^2 \theta}}$$

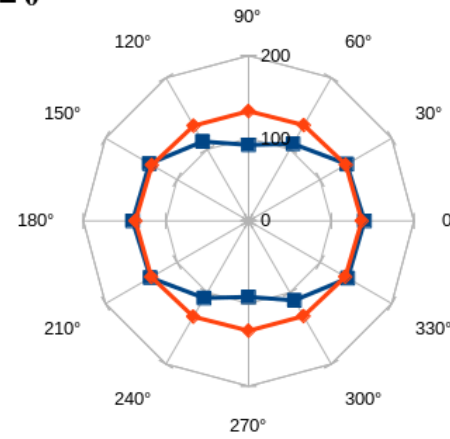
$$\sigma_\phi = \frac{\sqrt{\sigma_y^2 \cos^2 \theta + \sigma_x^2 \sin^2 \theta}}{\sin \phi}$$

$$\tan(\phi) = \frac{\sigma_y^2 \cos^2 \theta + \sigma_x^2 \sin^2 \theta}{(\sigma^2 - \sigma_y^2) \cos \theta \sin \theta}$$

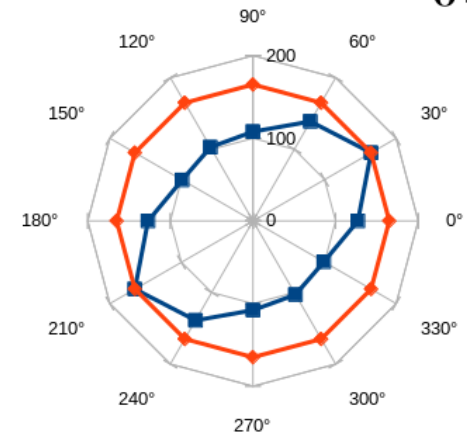
$$I = \sigma_{x'} \sqrt{\frac{\pi}{2}} \sum_{(i;j) \in [0, s_x] \times [0, s_y]} \int_{y - \frac{\delta}{\sin(\phi)}}^{(y+1) \frac{\delta}{\sin(\phi)}} C_{ij} e^{-\frac{(y' - y'_0)^2}{2\sigma_{x'}^2}}$$

$$[erf(\frac{(-\cos(\phi)y' + x + 1)\delta - x'_0}{\sqrt{2}\sigma_{x'}}) - erf(\frac{(-\cos(\phi)y' + x)\delta - x'_0}{\sqrt{2}\sigma_{x'}})] dy'$$

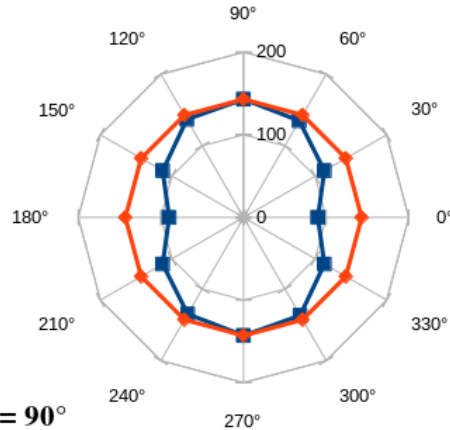
$\Theta = 0^\circ$



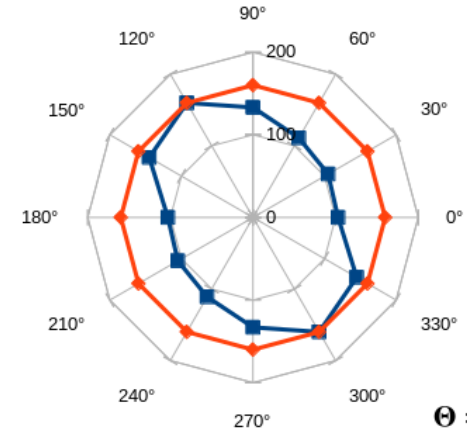
$\Theta = 30^\circ$



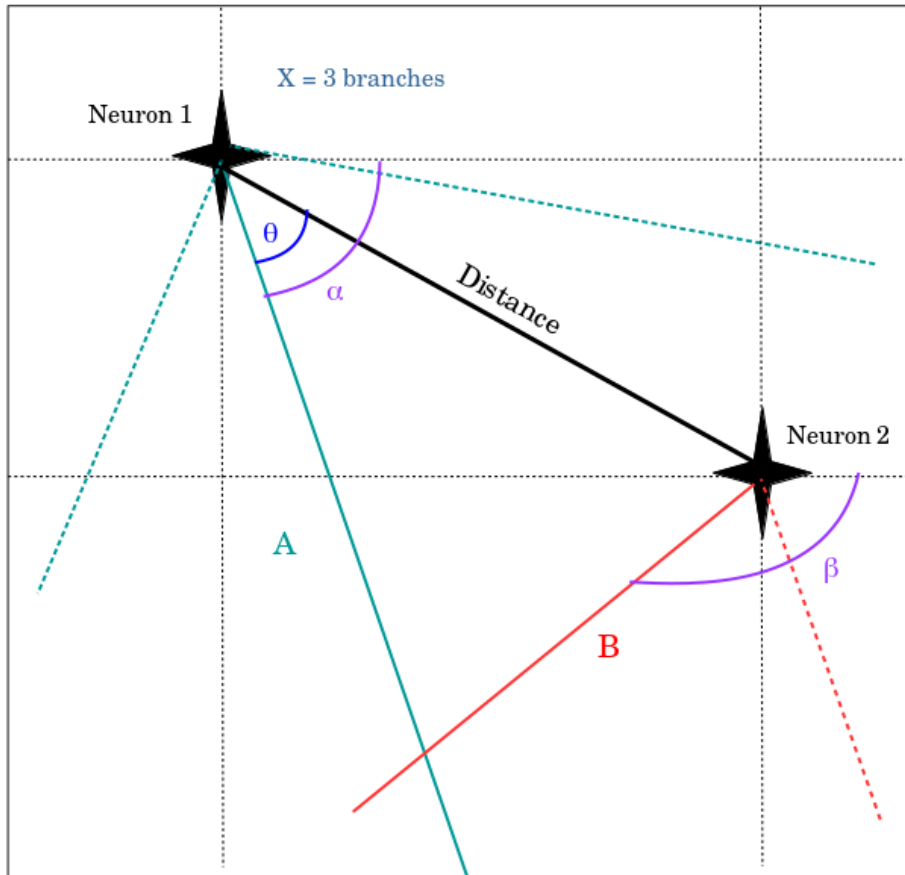
$\Theta = 90^\circ$



$\Theta = 120^\circ$



Connectivity graph



- Variables of the model :
- Number of branches N
 - Branch length X
 - Branch angle α

$$F_X(x) = \int_0^1 \frac{1}{\pi\sqrt{1-\delta^2}} \frac{x}{x+\delta} d\delta$$

$$\sin\left(\beta + \frac{\arcsin |y_j - y_i|}{\sqrt{(x_j - y_i)^2 + (y_j - x_j)^2}}\right)$$

Cortex mean field model

Zerlaut et al 2016
Chemla et al 2018

Single neuron model (The adaptive exponential integrate and fire model Brette and Gerstner, 2005)

$$\begin{cases} C_m \frac{dV}{dt} = g_L (E_L - V) + I_{syn}(V, t) + k_a e^{\frac{V - V_{thre}}{k_a}} - I_w \\ \tau_w \frac{dI_w}{dt} = -I_w + a \cdot (V - E_L) + \sum_{t_s \in \{t_{spike}\}} b \delta(t - t_s) \end{cases}$$

The conductance-based exponential synapse

$$I_{syn}(V, t) = \sum_{s \in \{e, i\}} \sum_{t_s \in \{t_s\}} Q_s (E_s - V) e^{-\frac{t-t_s}{\tau_s}} \mathcal{H}(t - t_s)$$

Semi analytical transfer function :

$$\nu_{out} = \mathcal{F}(\nu_e, \nu_i) = \frac{1}{2\tau_V} \cdot \text{Erfc}\left(\frac{V_{thre}^{eff} - \mu_V}{\sqrt{2}\sigma_V}\right) \quad \text{with} \quad V_{thre}^{eff}(\mu_V, \sigma_V, \tau_V^N) = P_0 + \sum_{x \in \{\mu_V, \sigma_V, \tau_V^N\}} P_x \cdot \left(\frac{x - x^0}{\delta x^0}\right) + P_{\mu_G} \log\left(\frac{\mu_G}{g_L}\right) \\ + \sum_{x, y \in \{\mu_V, \sigma_V, \tau_V^N\}^2} P_{xy} \cdot \left(\frac{x - x^0}{\delta x^0}\right) \left(\frac{y - y^0}{\delta y^0}\right)$$

Cortex mean field model

Zerlaut et al 2016
Chemla et al 2018

The mean, standard deviation and auto-correlation time of the excitatory and inhibitory conductance read :

$$\begin{array}{l}
 \mu_{Ge}(\nu_e, \nu_i) = \nu_e K_e \tau_e Q_e \\
 \sigma_{Ge}(\nu_e, \nu_i) = \sqrt{\frac{\nu_e K_e \tau_e}{2}} Q_e \\
 \mu_{Gi}(\nu_e, \nu_i) = \nu_i K_i \tau_i Q_i \\
 \sigma_{Gi}(\nu_e, \nu_i) = \sqrt{\frac{\nu_i K_i \tau_i}{2}} Q_i
 \end{array}
 \quad \longrightarrow \quad
 \begin{array}{l}
 \mu_G(\nu_e, \nu_i) = \mu_{Ge} + \mu_{Gi} + g_L \\
 \tau_m(\nu_e, \nu_i) = \frac{C_m}{\mu_G} \\
 \downarrow \\
 \mu_V(\nu_e, \nu_i) = \frac{\mu_{Ge} E_e + \mu_{Gi} E_i + g_L E_L}{\mu_G} \\
 \sigma_V(\nu_e, \nu_i) = \sqrt{\sum_s K_s \nu_s \frac{(U_s \cdot \tau_s)^2}{2(\tau_m^{\text{eff}} + \tau_s)}} \\
 \tau_V(\nu_e, \nu_i) = \left(\frac{\sum_s (K_s \nu_s (U_s \cdot \tau_s)^2)}{\sum_s (K_s \nu_s (U_s \cdot \tau_s)^2 / (\tau_m^{\text{eff}} + \tau_s))} \right)
 \end{array}$$

Finally, the transfer function reads :

$$\nu_{out} = \mathcal{F}(\nu_e, \nu_i) = \frac{1}{2\tau_V} \cdot \text{Erfc}\left(\frac{V_{thre}^{eff} - \mu_V}{\sqrt{2}\sigma_V}\right)$$

Cortex mean field model

Zerlaut et al 2016
Chemla et al 2018

Master equation for first and second moments local population dynamics (El Boustani and Destexhe, 2009) read :

$$\left\{ \begin{array}{l} T \frac{\partial \nu_\mu}{\partial t} = (\mathcal{F}_\mu - \nu_\mu) + \frac{1}{2} c_{\lambda\eta} \frac{\partial^2 \mathcal{F}_\mu}{\partial \nu_\lambda \partial \nu_\eta} \\ T \frac{\partial c_{\lambda\eta}}{\partial t} = A_{\lambda\eta} + (\mathcal{F}_\lambda - \nu_\lambda) (\mathcal{F}_\eta - \nu_\eta) + \\ \quad c_{\lambda\mu} \frac{\partial \mathcal{F}_\mu}{\partial \nu_\lambda} + c_{\mu\eta} \frac{\partial \mathcal{F}_\mu}{\partial \nu_\eta} - 2c_{\lambda\eta} \end{array} \right. \longrightarrow T \frac{\partial \nu_\mu}{\partial t} = \mathcal{F}_\mu - \nu_\mu$$

$$A_{\lambda\eta} = \begin{cases} \frac{\mathcal{F}_\lambda (1/T - \mathcal{F}_\lambda)}{N_\lambda} & \text{if } \lambda = \eta \\ 0 & \text{otherwise} \end{cases}$$