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## Mathematically modelling the retina: what for ?

Bruno Cessac

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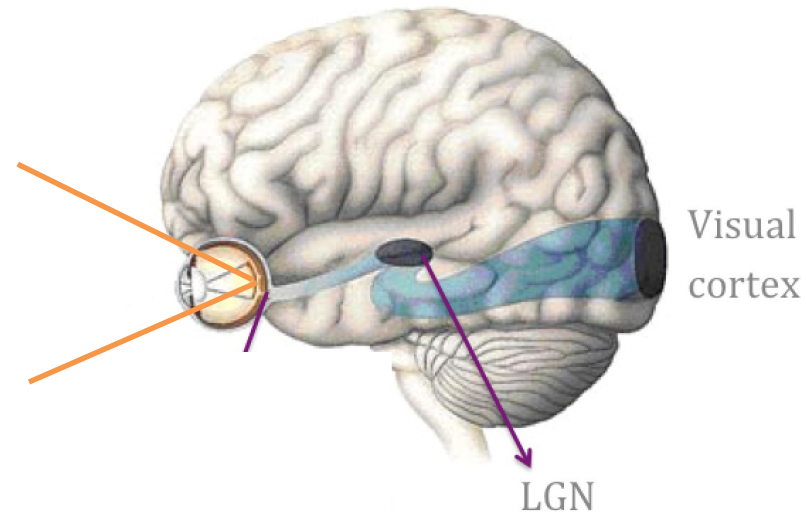
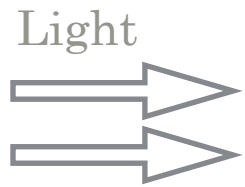
# Mathematically modelling the retina: what for ?

B. Cessac, Université Côte d'Azur, INRIA,  
Biovision team and Neuromod Institute  
Sophia Antipolis, France

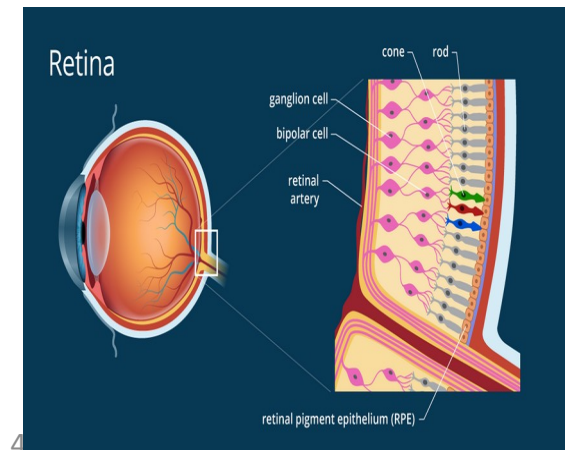
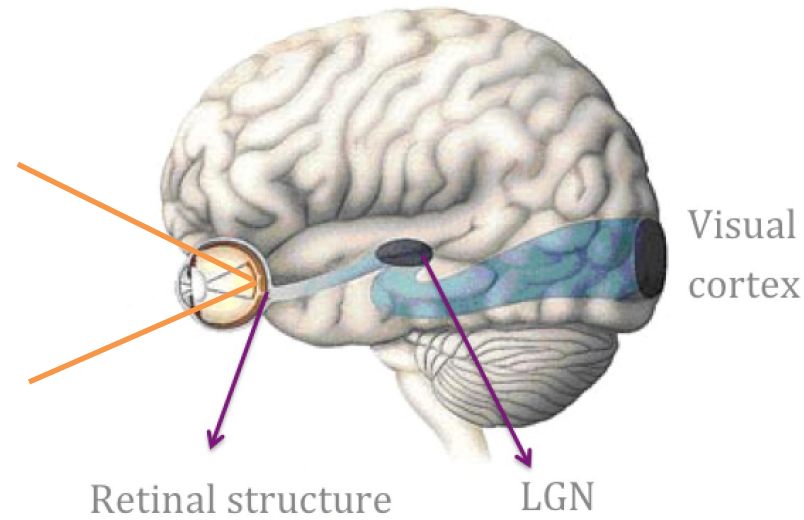
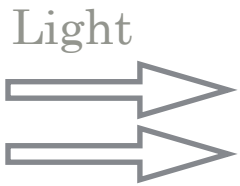


# The visual system

# The visual system

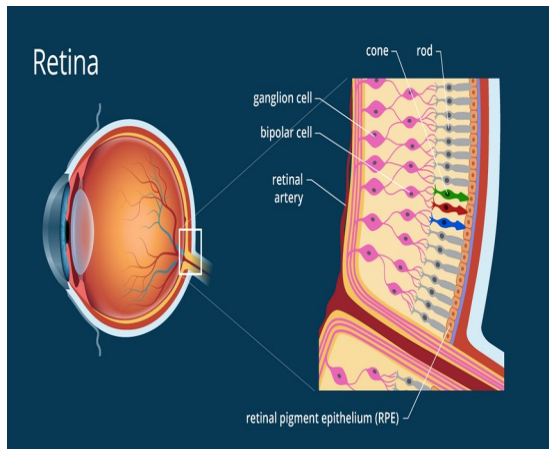
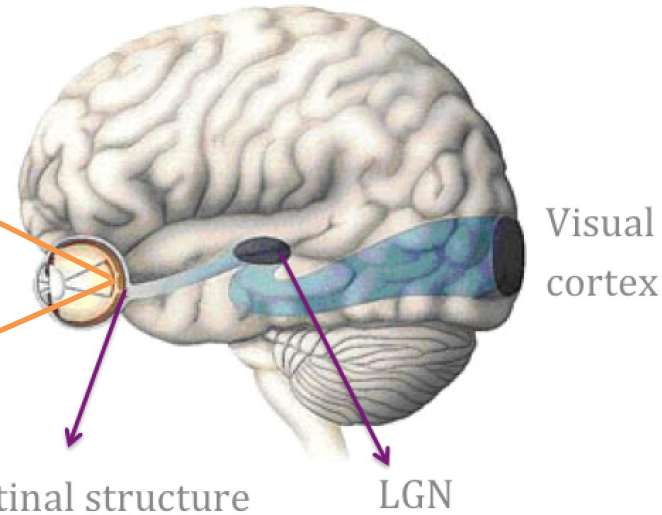
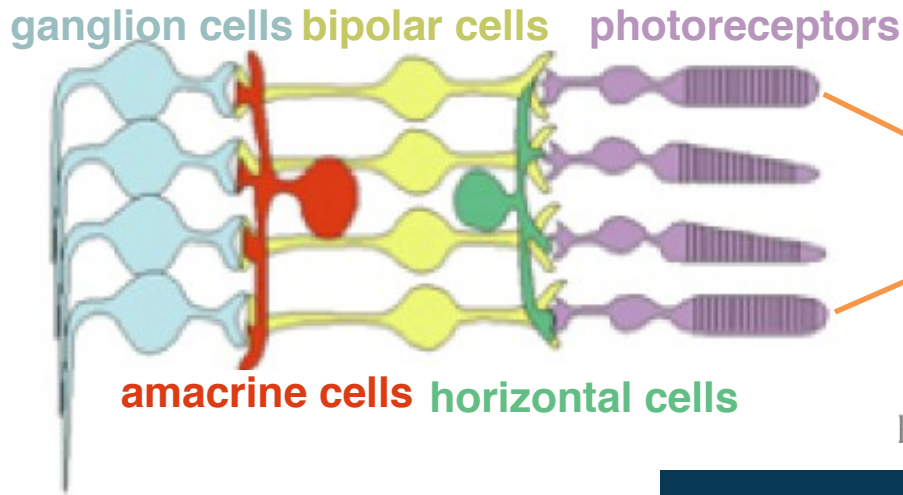


# The visual system



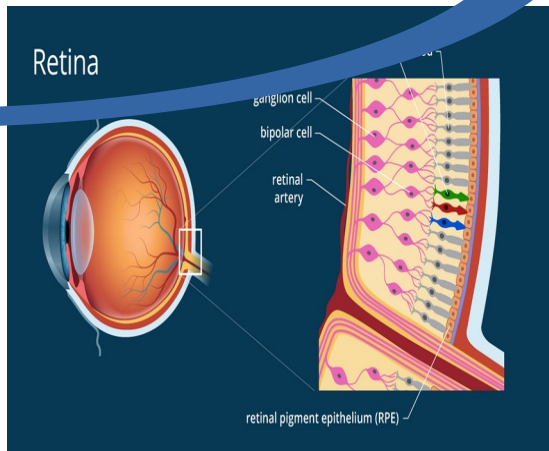
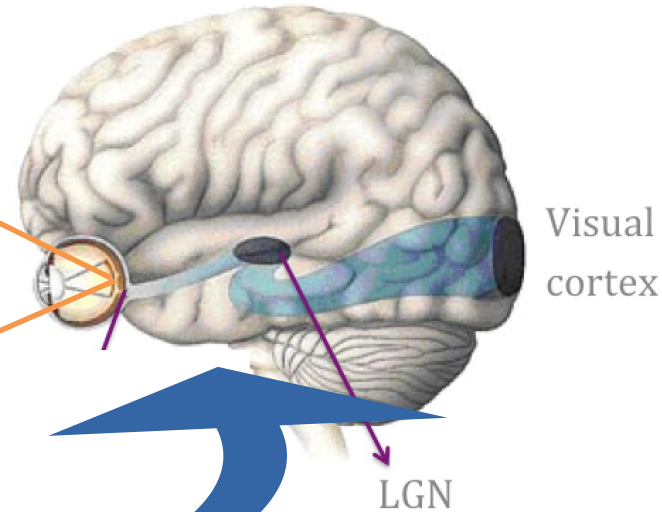
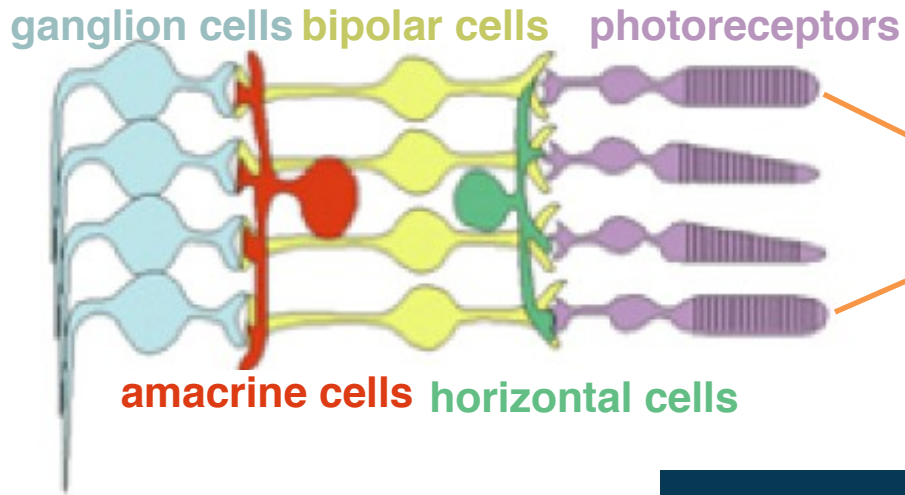
# The visual system

## Retina's layered structure



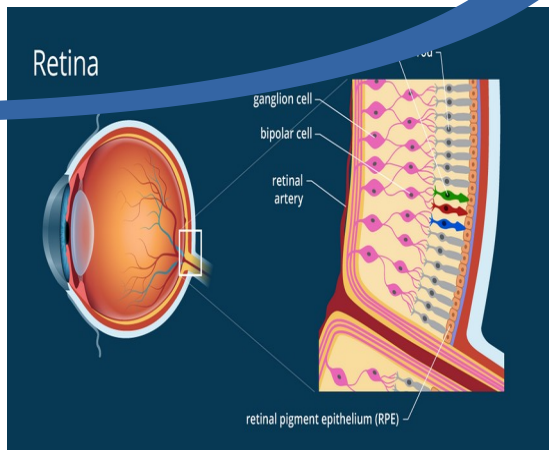
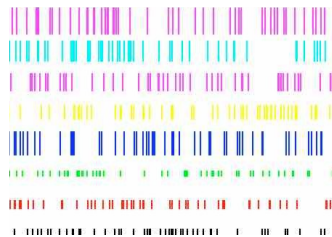
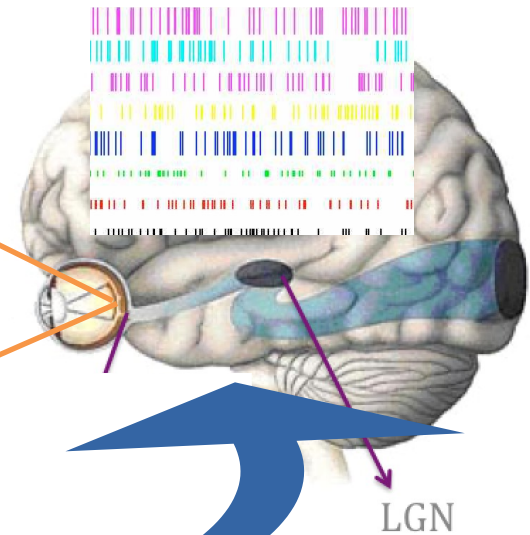
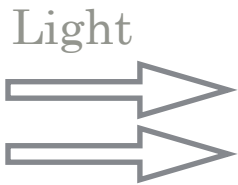
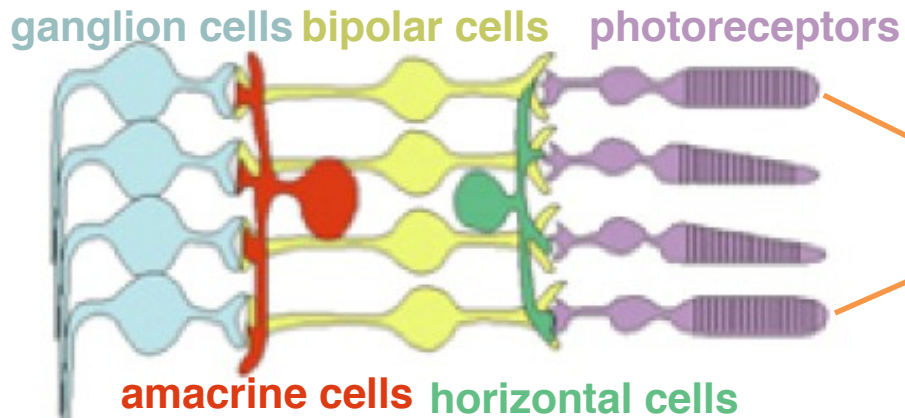
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## Retina's layered structure



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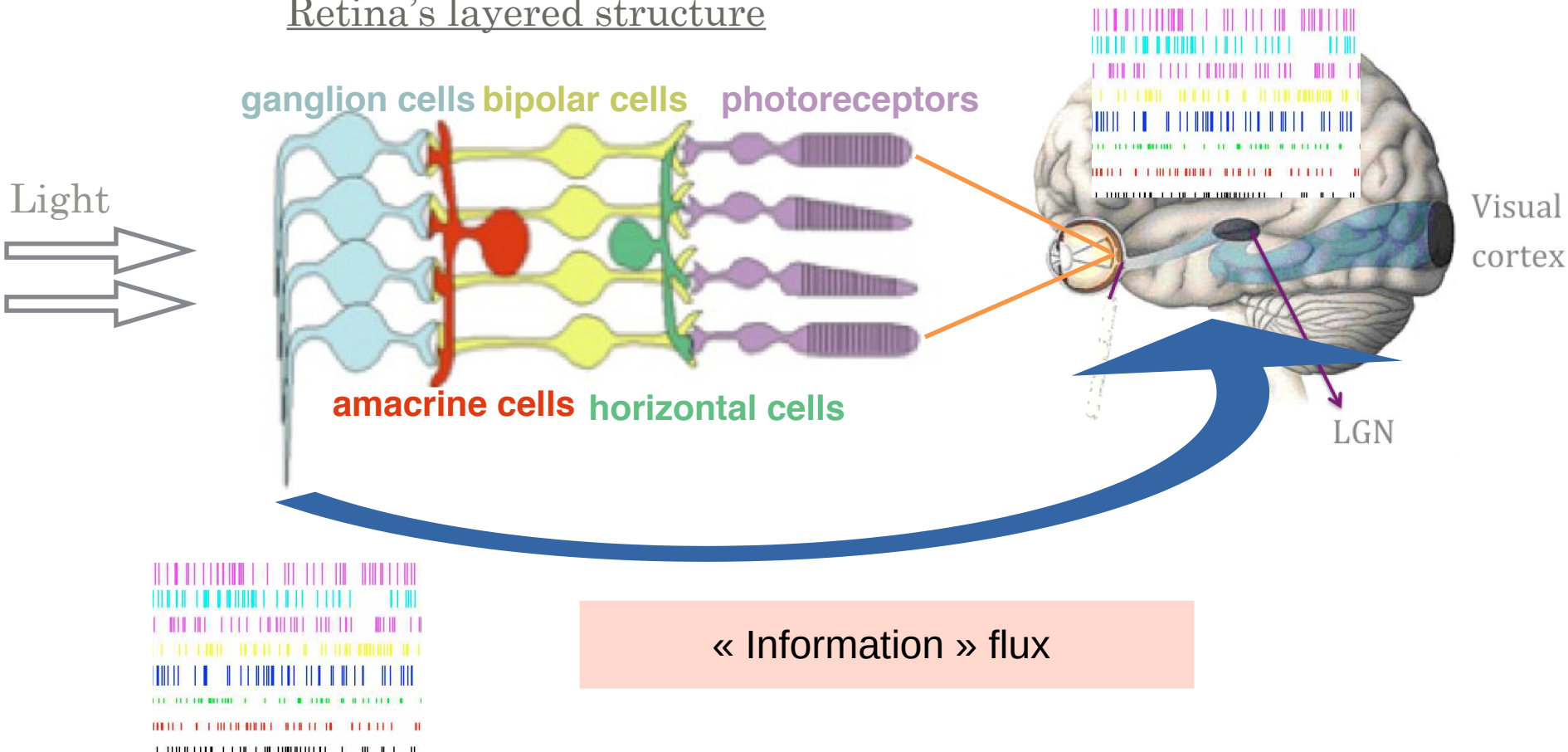
## Retina's layered structure





# The visual system

## Retina's layered structure

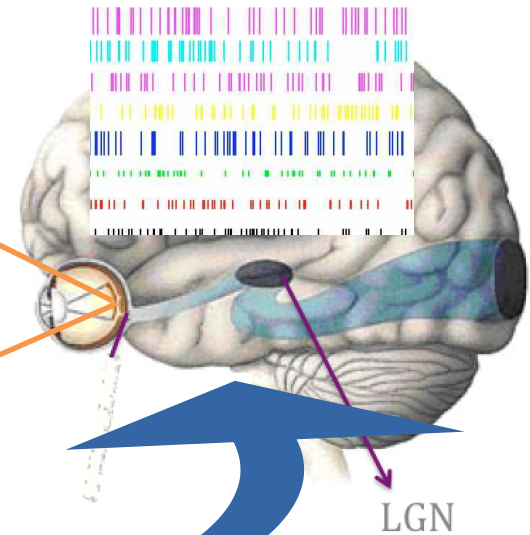
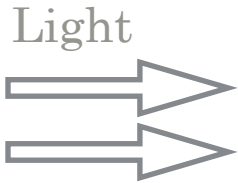
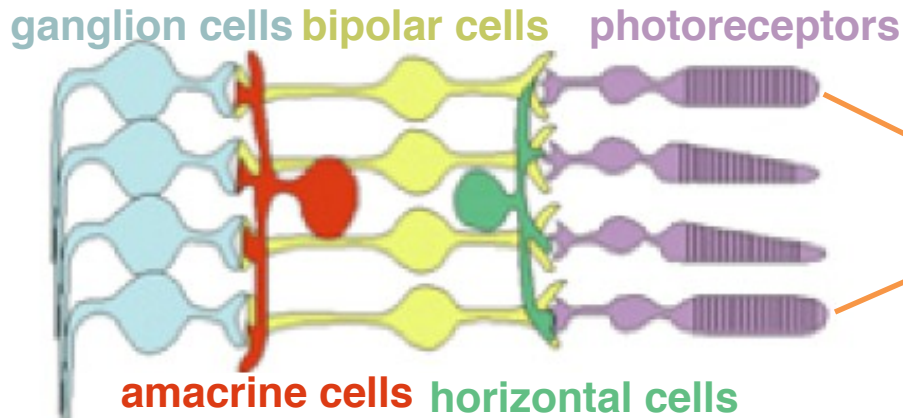


# The visual system

Encoder

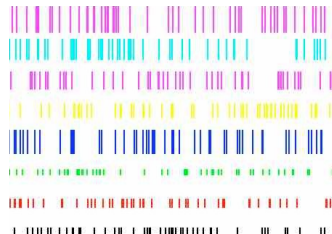
Decoder

Retina's layered structure



Visual cortex

LGN



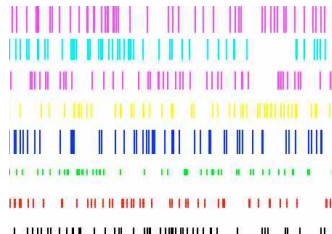
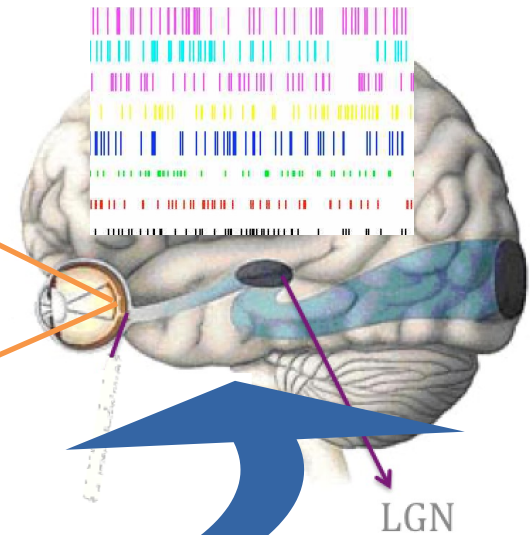
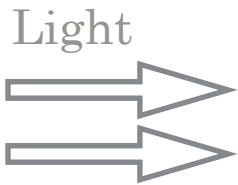
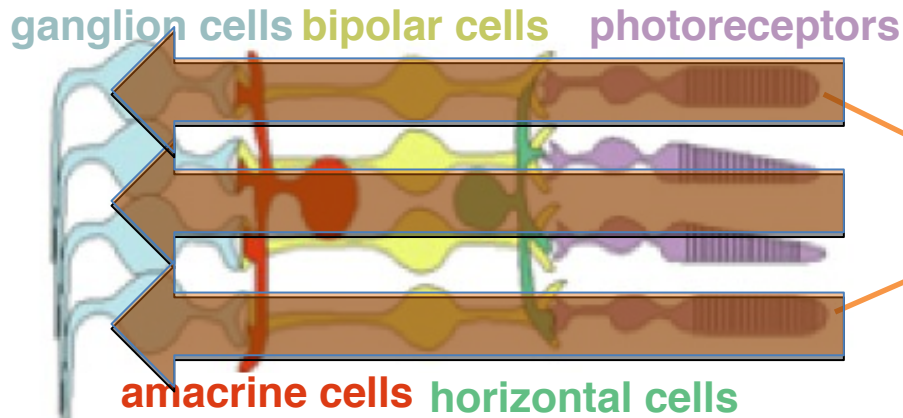
« Information » flux

# The visual system

Encoder

Decoder

Retina's layered structure



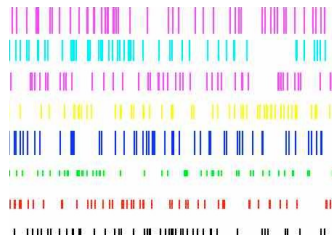
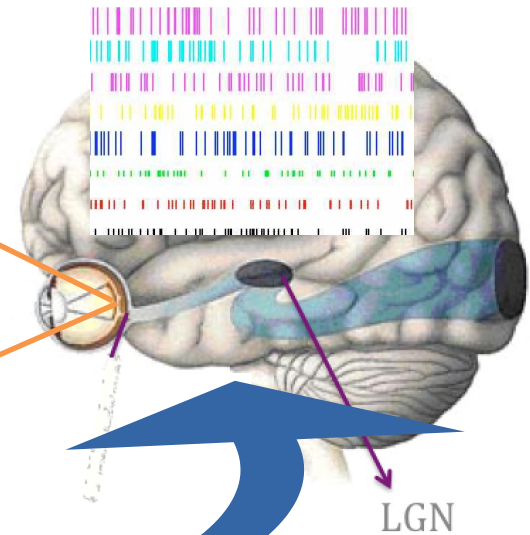
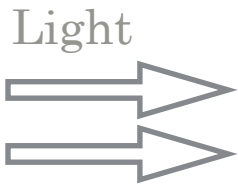
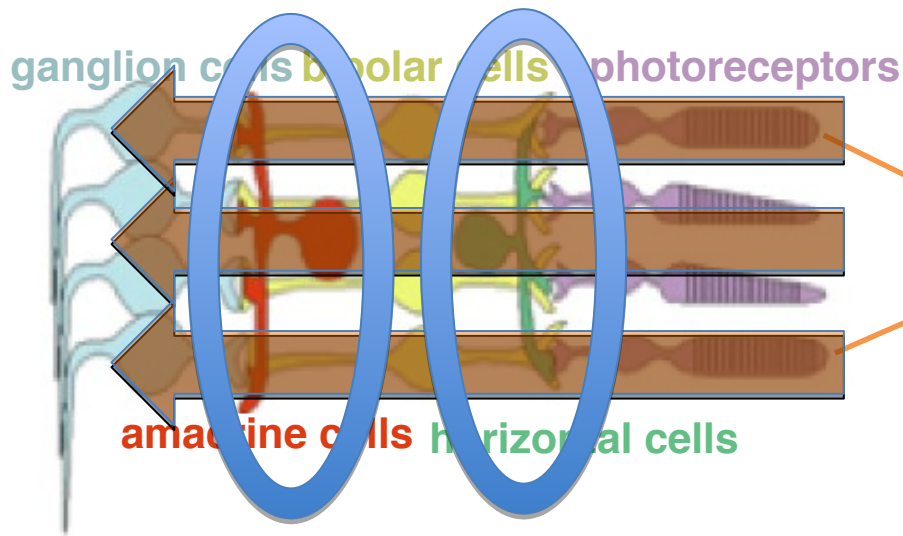
« Information » flux

# The visual system

Encoder

Decoder

Retina's layered structure

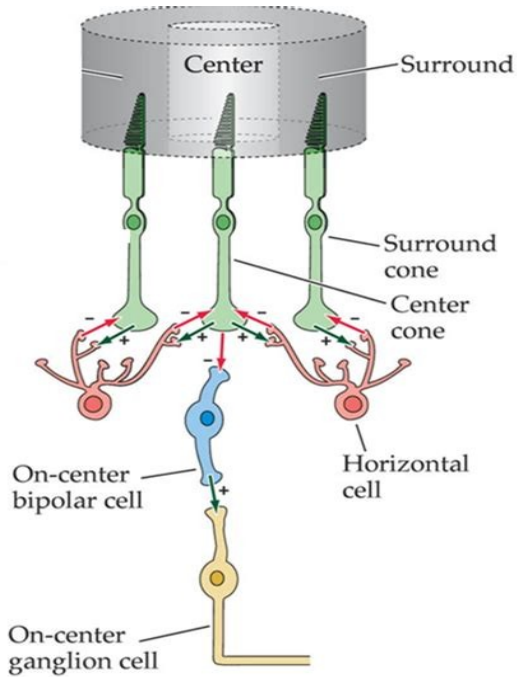


« Information » flux

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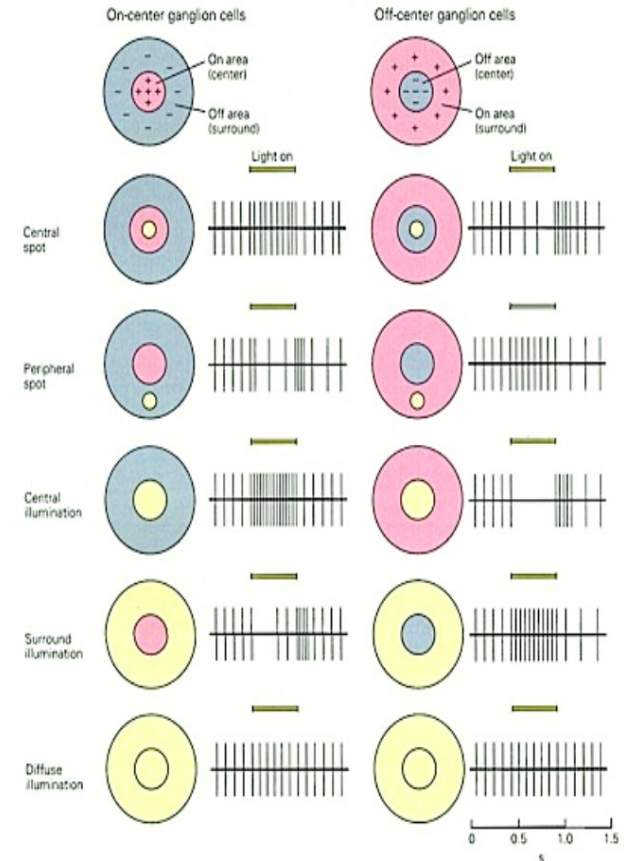
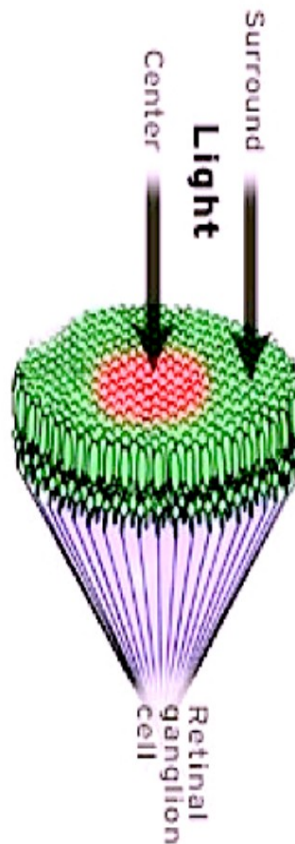
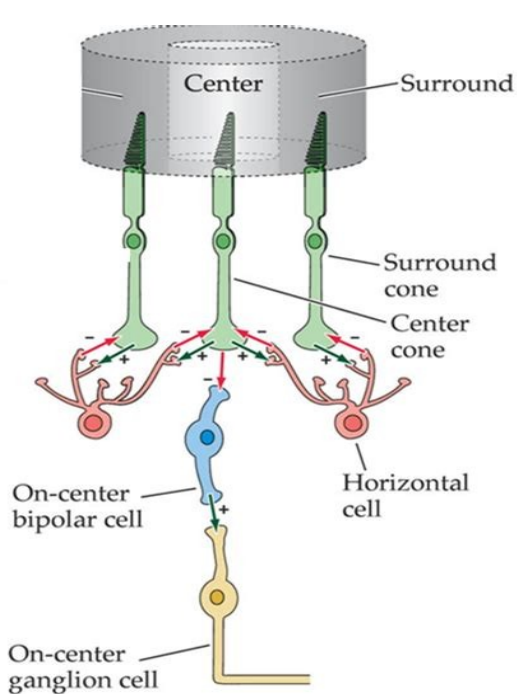
**Horizontal cells contributes to the center surround structure of receptive fields (basic « bricks » of vision)**

# The visual system



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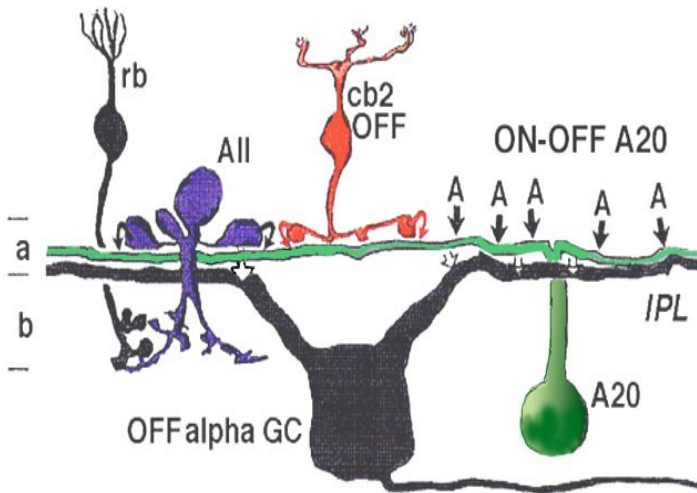
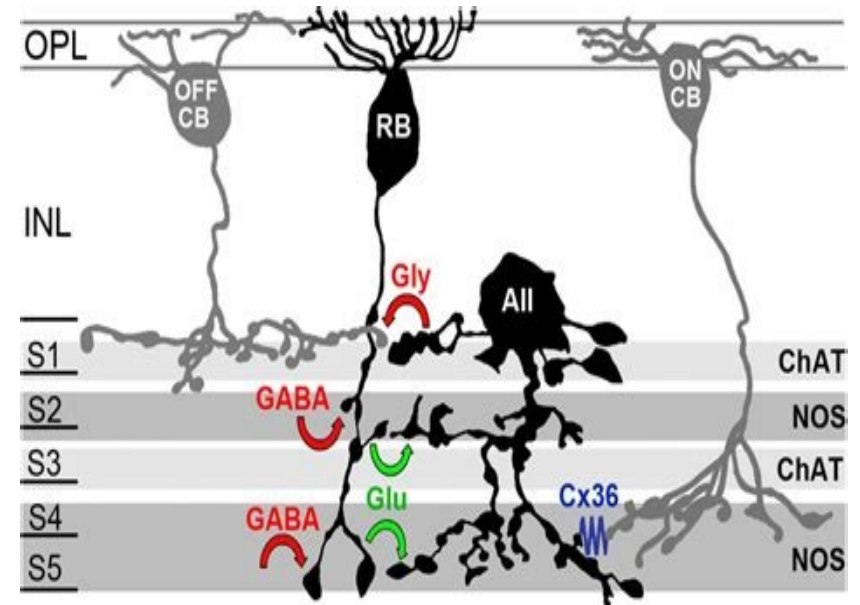


Fig. 27. Wiring diagram of the ON-OFF A20 amacrine cell (displaced).



**Amacrine cells are involved in many fundamental retina « circuits » like the rod cone pathway, or direction sensitivity but their role is still not well understood.**

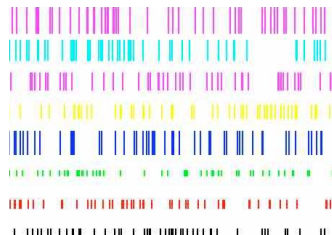
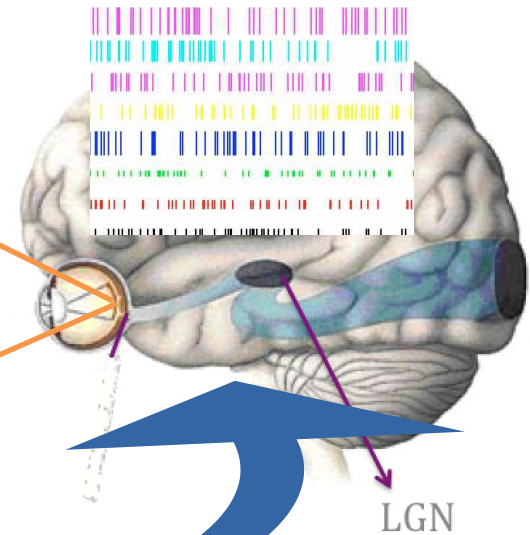
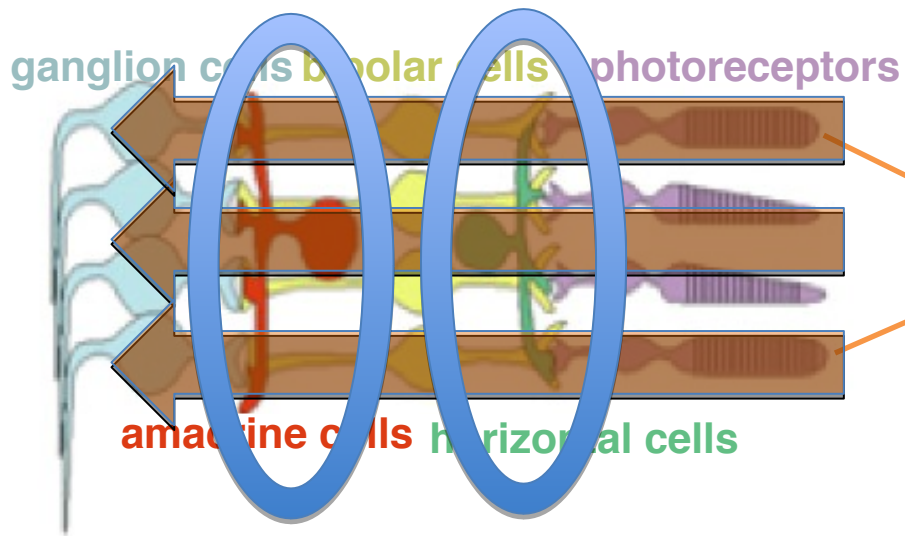


# The visual system

Encoder

Decoder

Retina's layered structure



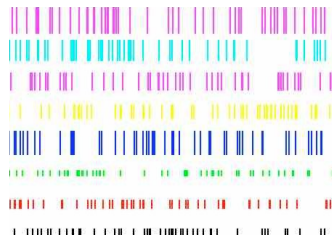
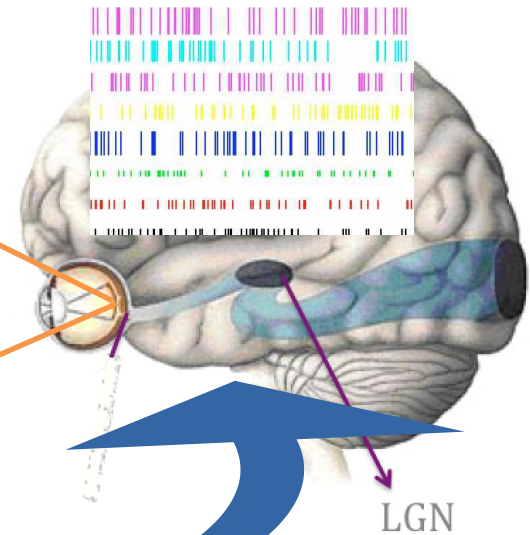
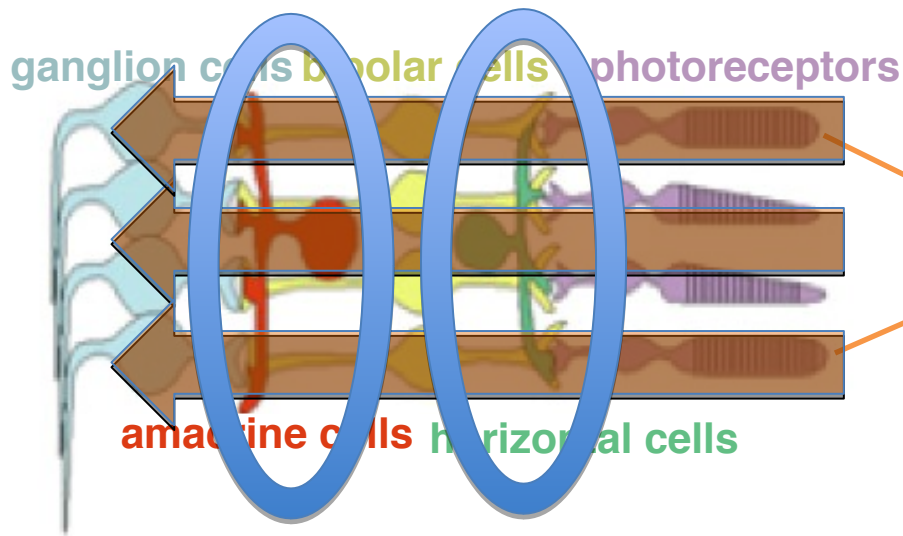
« Information » flux

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Retina's layered structure



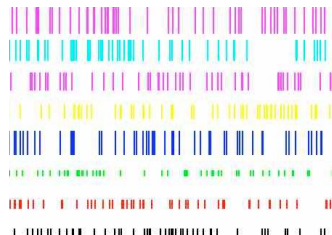
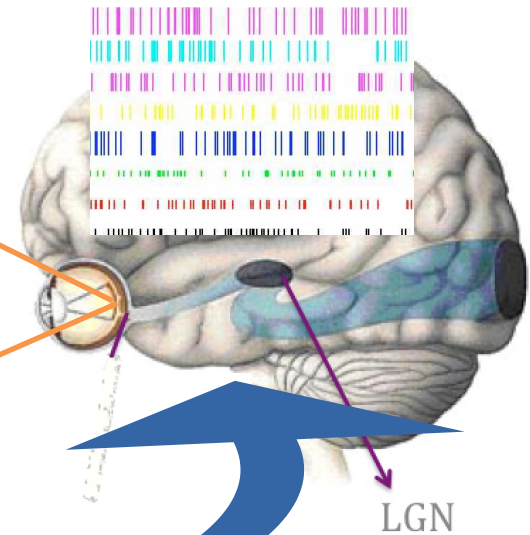
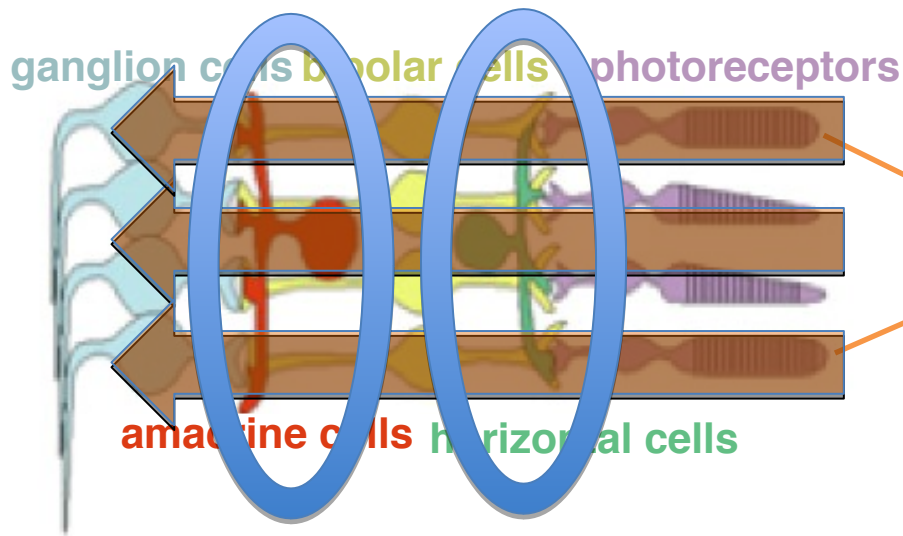
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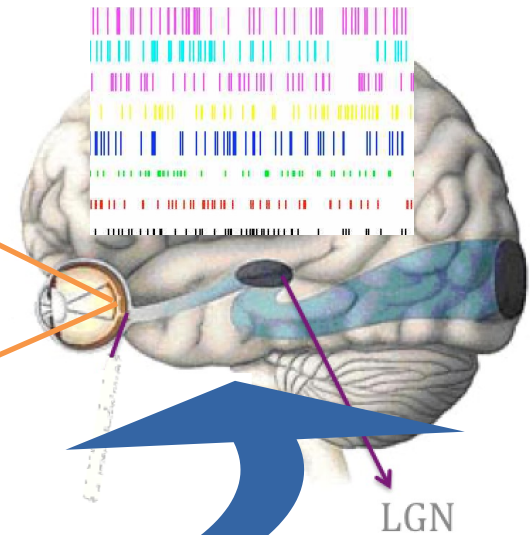
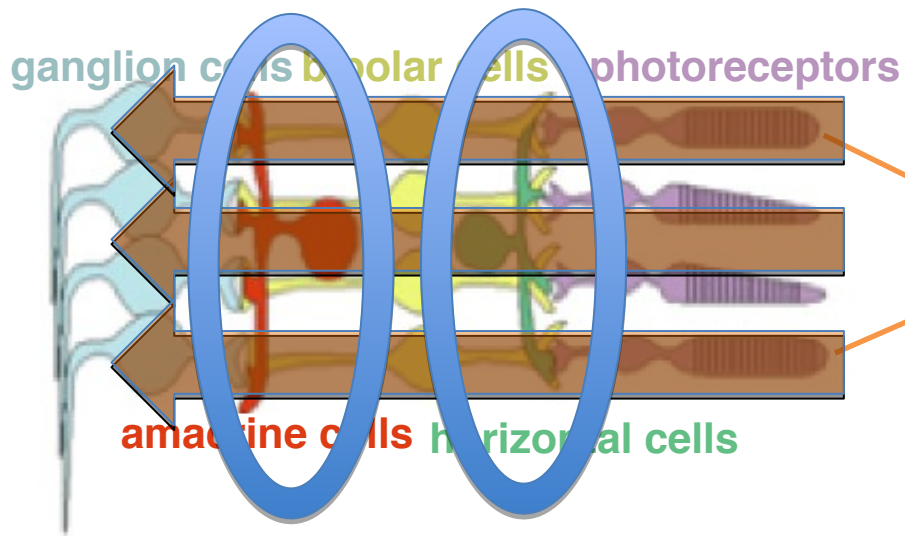
« Information » flux

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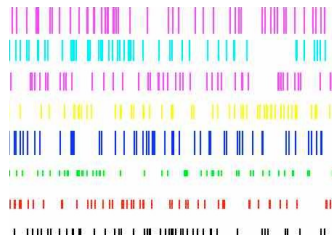
Encoder

Decoder

Retina's layered structure



« Information » flux



# The visual system

Encoder

Decoder

Retina's layered structure

.... handles motion and spatio-temporal structures.

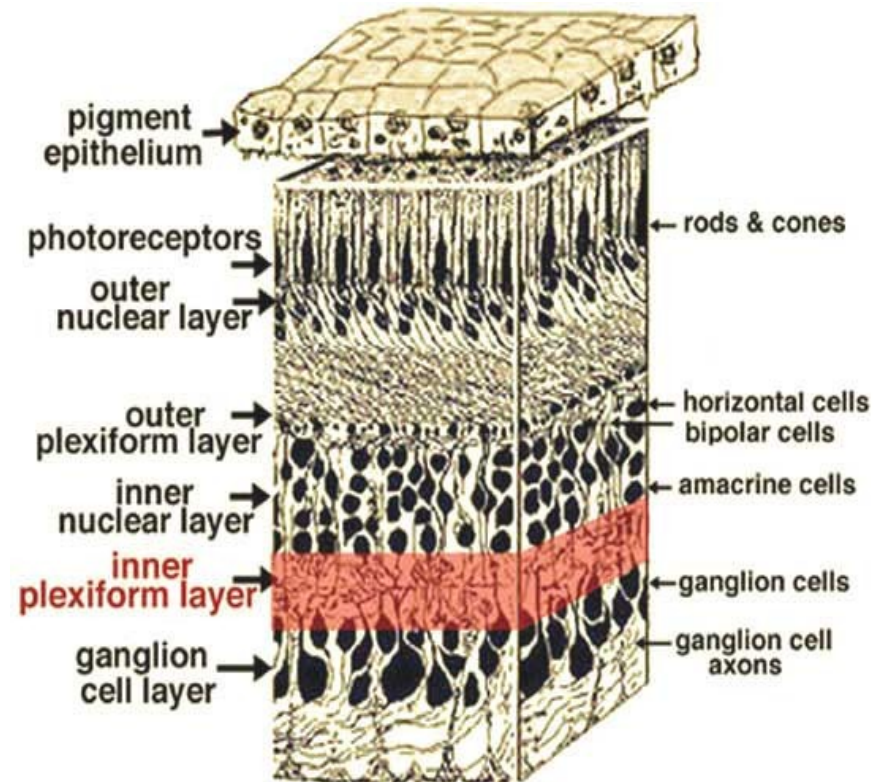
Static images do not exist.

How does the retina encode this huge information to be efficiently and rapidly decoded by the brain ?

« Information » flux

# Brief summary

- The retina is organized into a feedforward and lateral structure made of specific cell types and specific synapses.

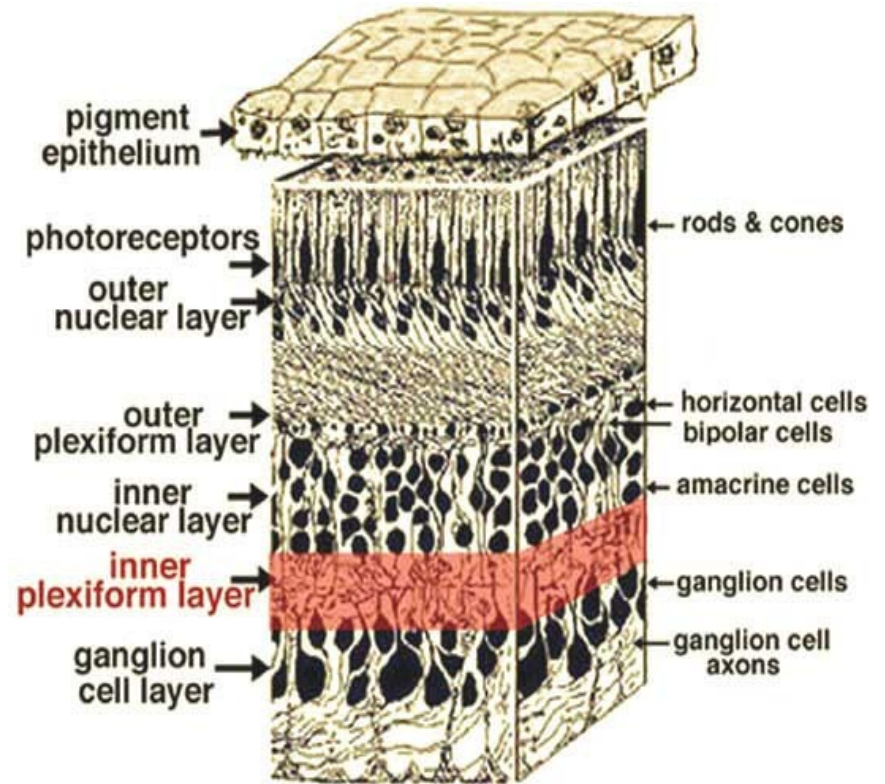


*Fig. 7. 3-D block of retina with the inner plexiform layer highlighted (red).*

From <http://webvision.org.es>

# Brief summary

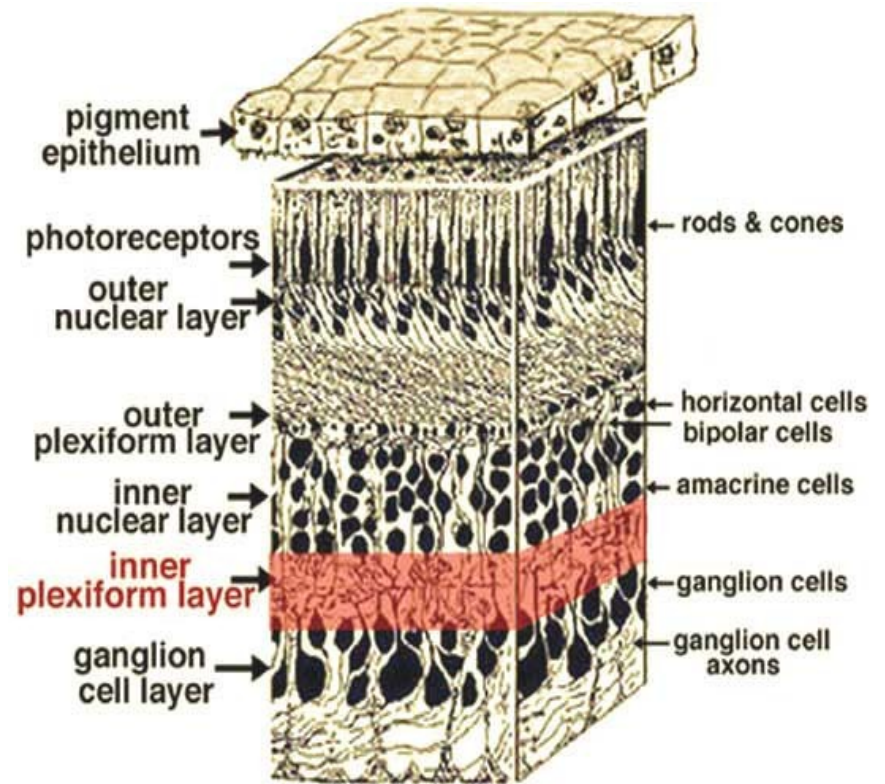
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*Fig. 7. 3-D block of retina with the inner plexiform layer highlighted (red).*

# Brief summary

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*Fig. 7. 3-D block of retina with the inner plexiform layer highlighted (red).*



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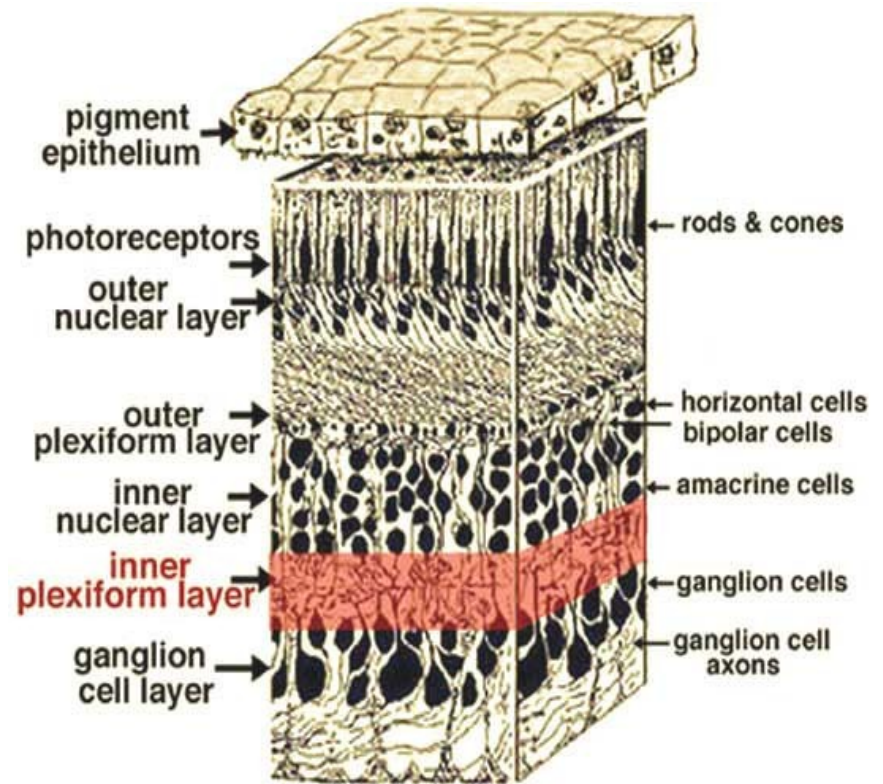
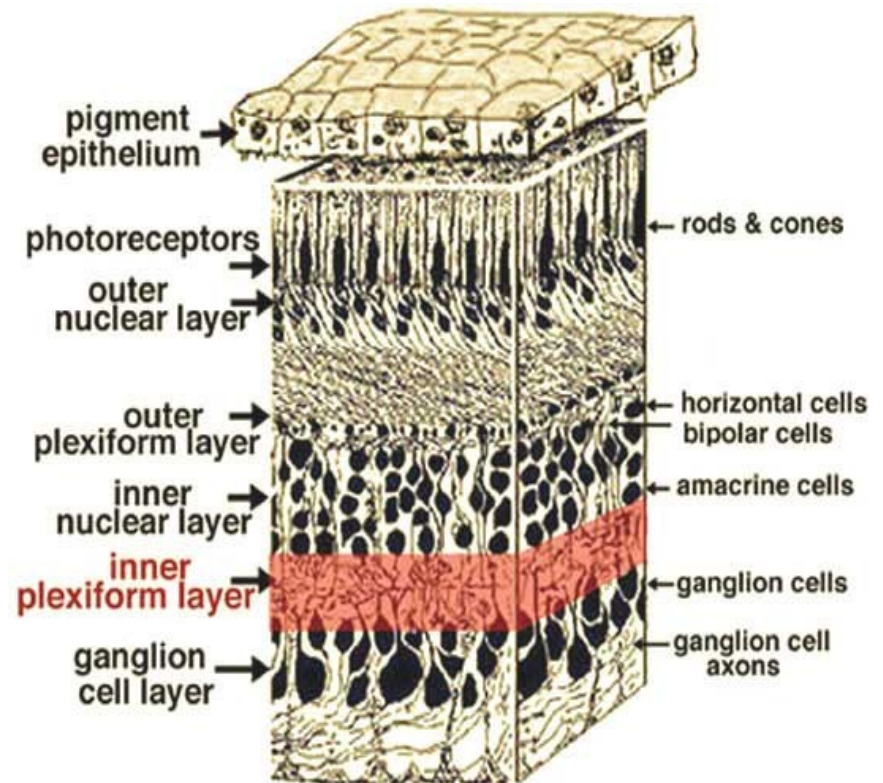


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- Local circuits, involving a few cells and synapses, process the local visual information.
- These circuits tile the whole retina, spanning the whole visual field.
- The output of each circuit is a spike train, encoding the visual information from Gcells to thalamus and visual cortex.
- These circuits are entangled (sharing cells).



*Fig. 7. 3-D block of retina with the inner plexiform layer highlighted (red).*

From <http://webvision.org.es>

# A modeller point of view

1. The retina is a ***high dimensional, non autonomous and noisy*** dynamical system, layered and structured, with ***non stationary and spatially inhomogeneous entries*** (visual scenes).

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3. The conjunction of non linearities and regular structure can produce highly complex ***spatio-temporal*** dynamics.
4. The retina is sensitive to ***changes in its physiology*** (development, pharmacology, pathologies). These changes can be addressed from the point of view of ***bifurcations theory***.

# The Biovision lab

## **Understanding the normal visual system at neuronal and perceptual levels**

- *Better understanding the early visual system*
- *Reading, moving, behaving in 3D virtual environments*
- *Analysis of visual media and user perception*

## **Understanding the impact of low vision at neuronal and perceptual levels**

- *Modeling of retinal prostheses stimulation and cortical responses*
- *Understanding eccentric vision pointing for selection and identification*
- *Understanding low vision impact on attentional and oculo-motor behaviors when reading*
- *Attentional and behavioural studies using virtual reality*

## **Diagnosis, rehabilitation, and low vision aids**

- *Exploring new solutions for diagnosis*
- *Designing rehabilitation methods in virtual reality (VR)*
- *Developing innovative vision-aid digital systems*

# Retinal waves

Random dynamical structures in the  
developing visual system

**D. Karvouniari (PhD 2014-2018)**, Biovision team, INRIA, Sophia Antipolis

L. Gil, InPhyNi, Nice-Sophia-Antipolis

O. Marre, Institut de la Vision, Paris

S. Picaud, Institut de la Vision, Paris

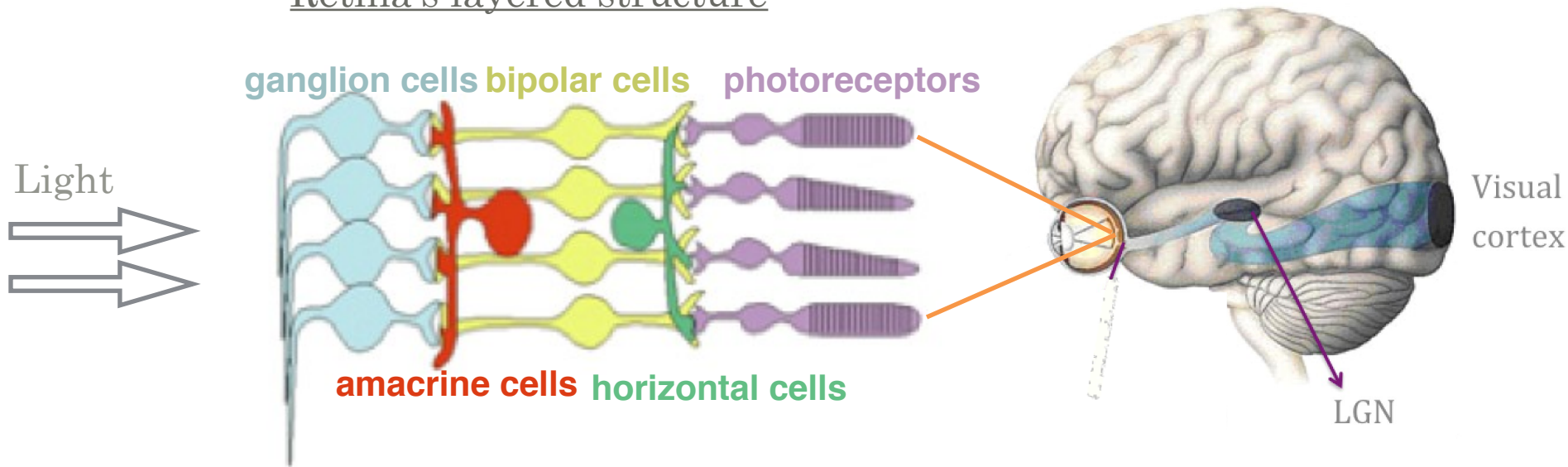
B. Cessac, Biovision team, INRIA, Sophia Antipolis

Acknowledgement: M. Hennig (U. Edinburgh), E. Sernagor (U. Newcastle).



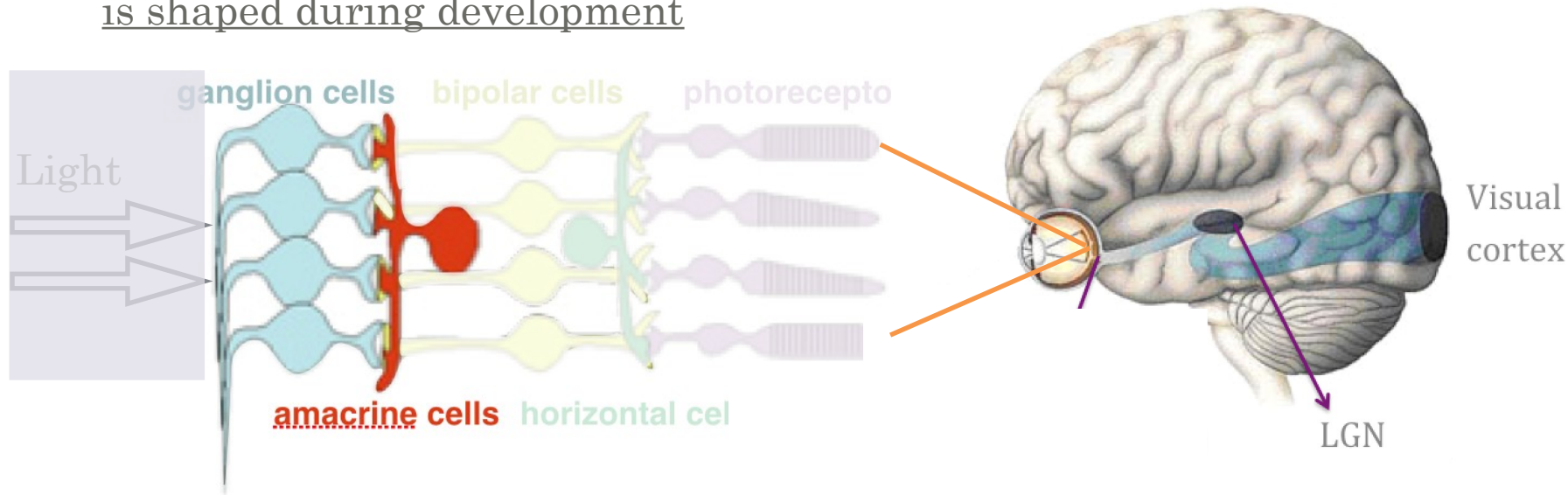
# The structure of the adult retina

## Retina's layered structure



# The structure of the retina during development

Retina's layered structure  
is shaped during development



But How?

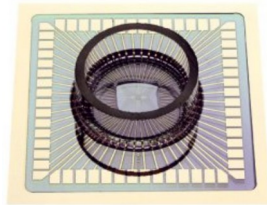
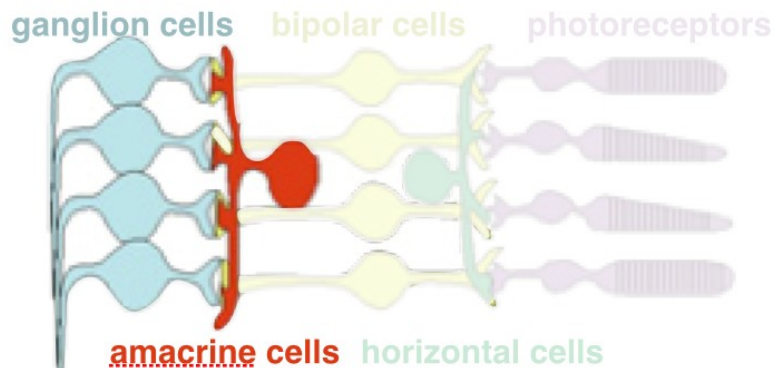


Retinal waves!

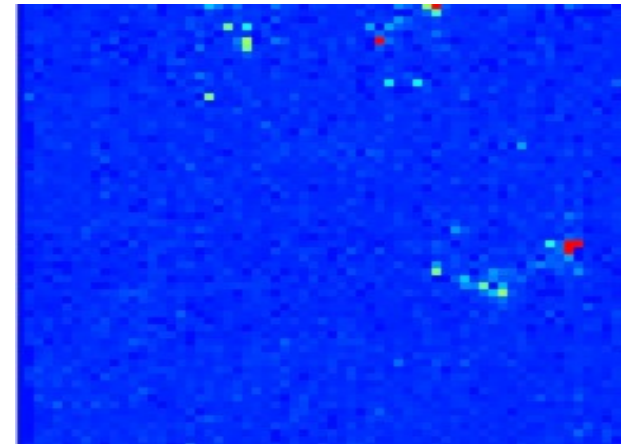
# Retinal waves

Spontaneous spatio-temporal waves during development  
Disappear short after birth when vision is functional

Recordings from the retina



**Multi-electrode array (MEA)**

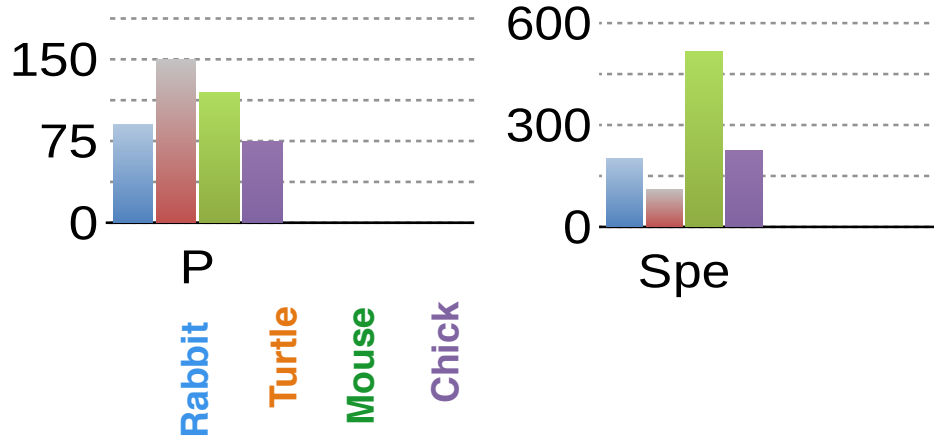


*MEA recording of the voltage from a mouse retina (courtesy E Sernagor).*

# Variability within retinal waves

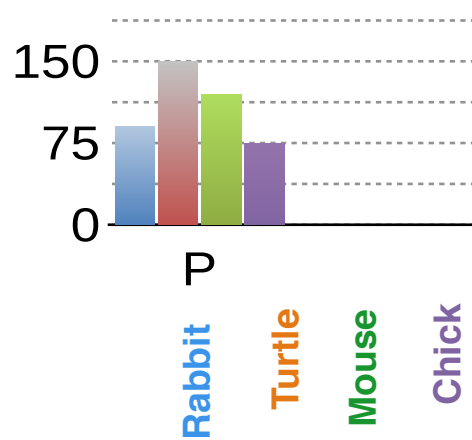
## i) Across species

Godfrey et al. 2007

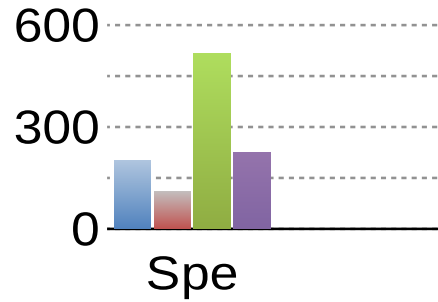


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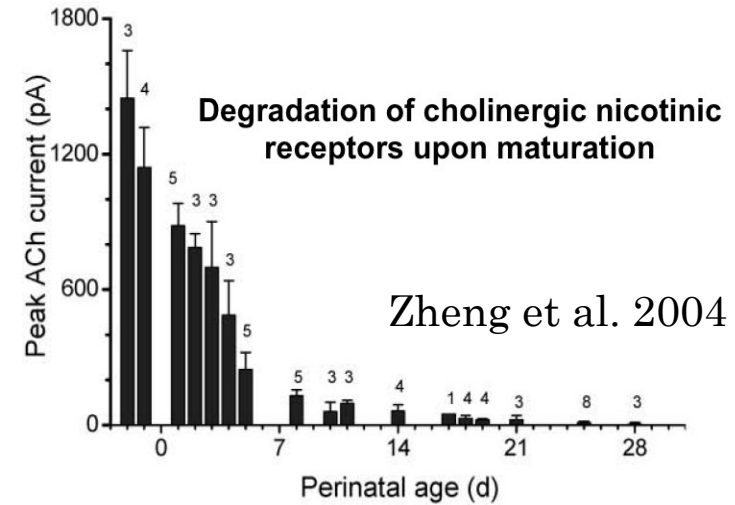
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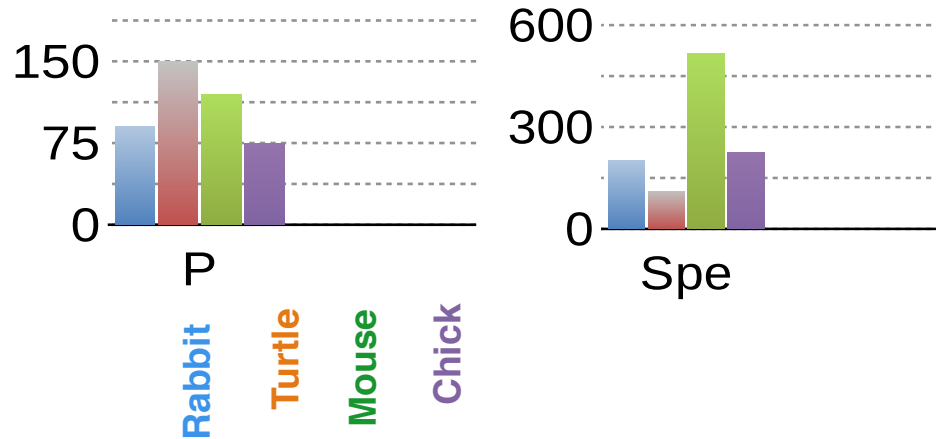
## ii) Development



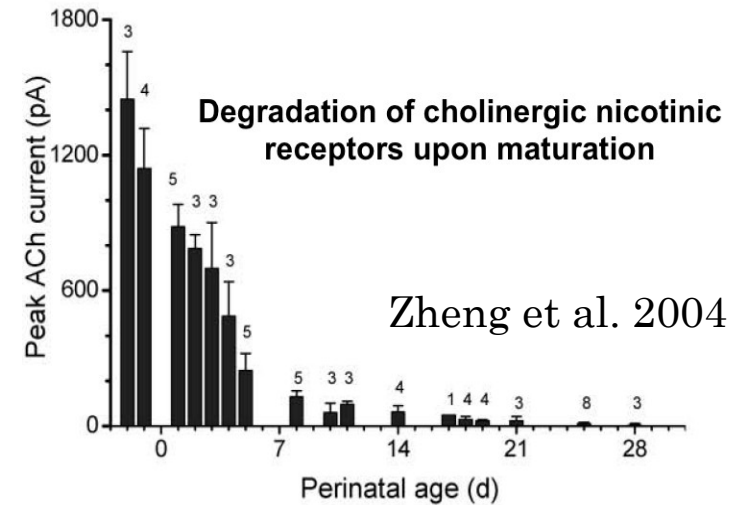
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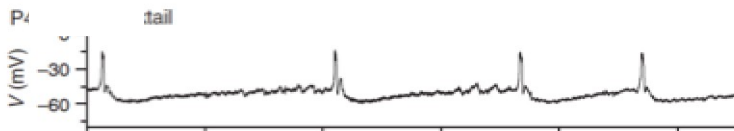


## ii) Development



## iii) Pharmacology

P4



P8

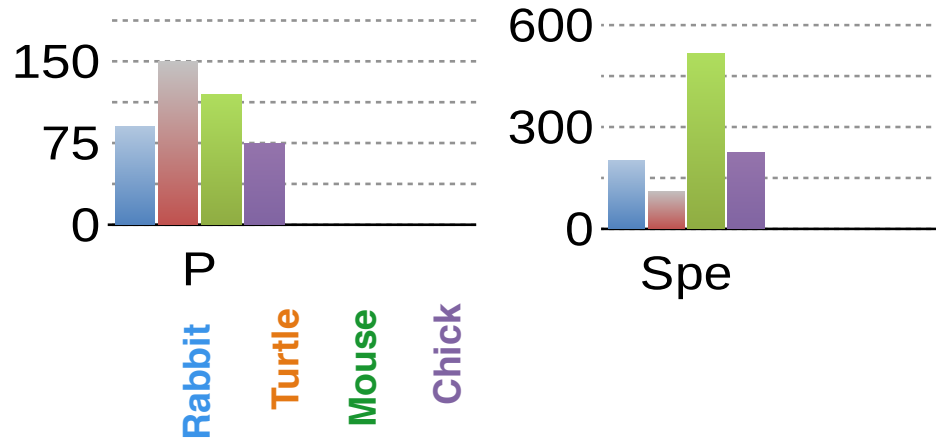


0 Time (sec) 50

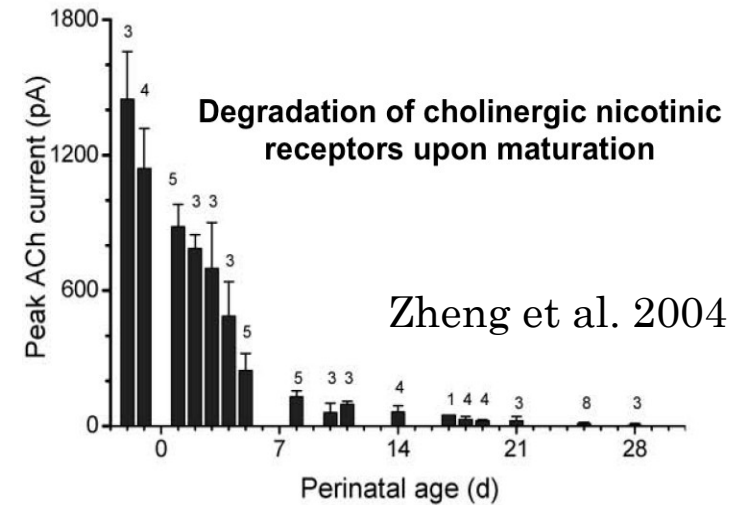
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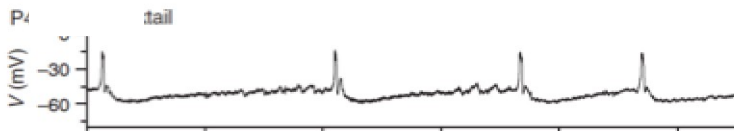


## ii) Development



## iii) Pharmacology

P4

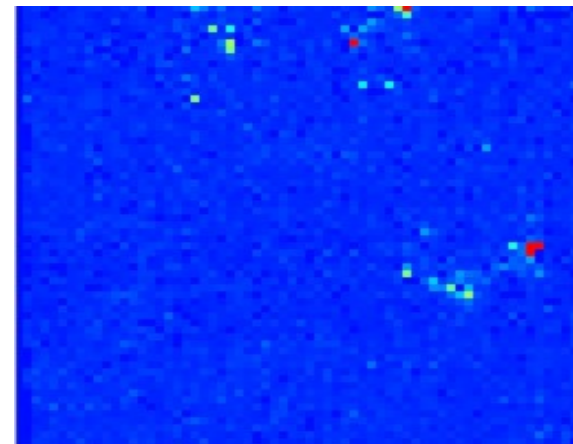


P8



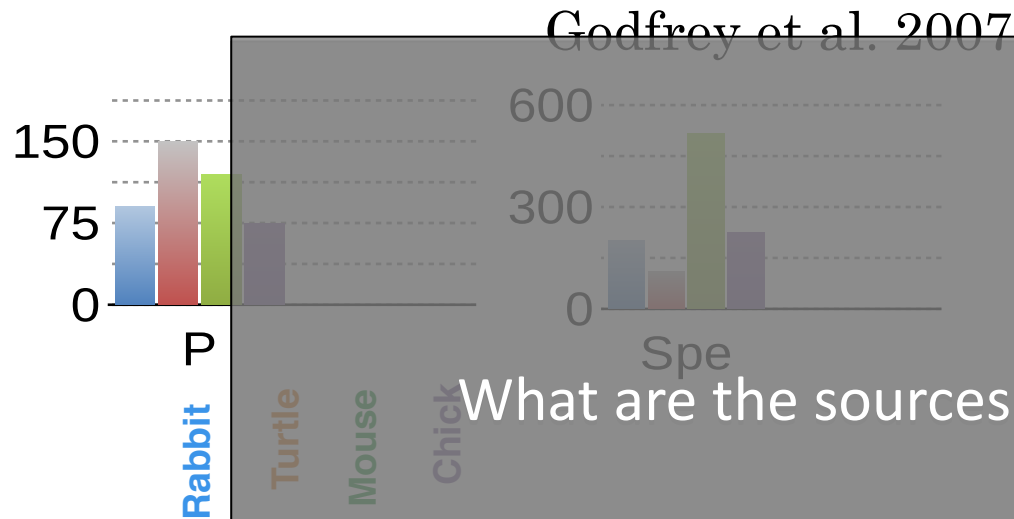
0 Time (sec) 50

## iv) Spatial Variability

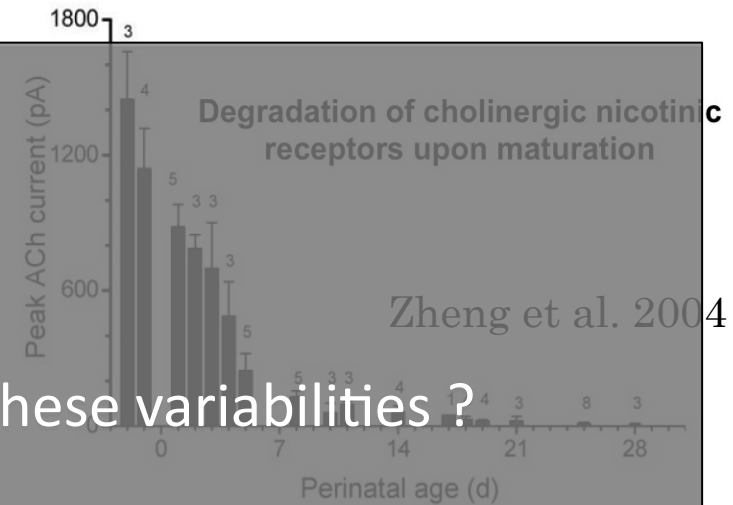


# Variability within retinal waves

## i) Across species



## ii) Development



What are the sources of these variabilities?

## iii) Pharmacology

P4



P8



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## iv) Spatial Variability

Is there a unique, global, mechanism explaining them?



# A network model for stage II retinal waves

*A biophysical model explains the spontaneous bursting behavior in the developing retina*

*Dora Matzakos-Karvouniari, Lionel Gil, Elaine Orendorff, Olivier Marre, Serge Picaud, Bruno Cessac*

*Scientific Reports, Nature Publishing Group, 2019, 9 (1), pp.1-23. [10.1038/s41598-018-38299-4](https://doi.org/10.1038/s41598-018-38299-4)*

$$\left\{ \begin{array}{l} C_m \frac{dV_i}{dt} = -g_L(V_i - V_L) - g_C M_\infty(V_i)(V_i - V_C) - g_K N_i(V_i - V_K) \\ \quad - G_{sAHP}(R_i)(V_i - V_K) - G_A(\{A_k\}_{k \in \mathcal{B}_i})(V_i - V_A) \\ \\ \tau_N \frac{dN_i}{dt} = \Lambda(V_i)(N_\infty(V_i) - N_i) \\ \\ \tau_C \frac{dC_i}{dt} = -\frac{\alpha_C}{H_X} C_i + C_0 - \delta_C g_C M_\infty(V_i)(V_i - V_C) \\ \\ \tau_S \frac{dS_i}{dt} = \alpha_S(1 - S_i)C_i^4 - S_i \\ \\ \tau_R \frac{dR_i}{dt} = \alpha_R S_i(1 - R_i) - R_i \\ \\ \frac{dA_i}{dt} = -\mu A_i + \beta_A T_A(V_i), \end{array} \right.$$

# A network model for stage II retinal waves

N neurons, 6 N equations

$$\left\{ \begin{array}{l}
 C_m \frac{dV_i}{dt} = -g_L(V_i - V_L) - g_C M_\infty(V_i)(V_i - V_C) - g_K N_i(V_i - V_K) \\
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~ 20 parameters per neuron

(But neurons are assumed identical)

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~ 20 parameters per neuron

(But neurons are assumed identical)

Time scale separation

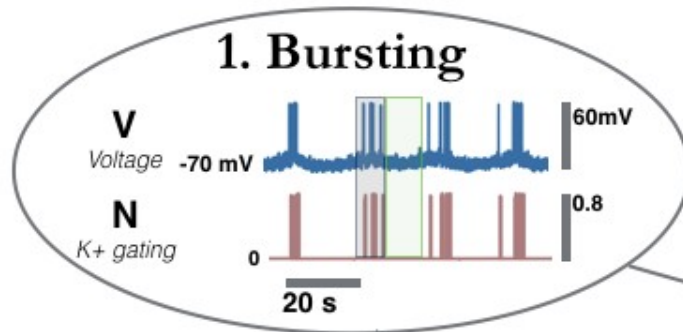
**Fast**  $V, N$ .  $\tau_L = 11$  ms,  $\tau_N = 5$  ms.

**Medium**  $C, A$ .  $\tau_C = 2$  s,  $\tau_A = 1.86$  s.

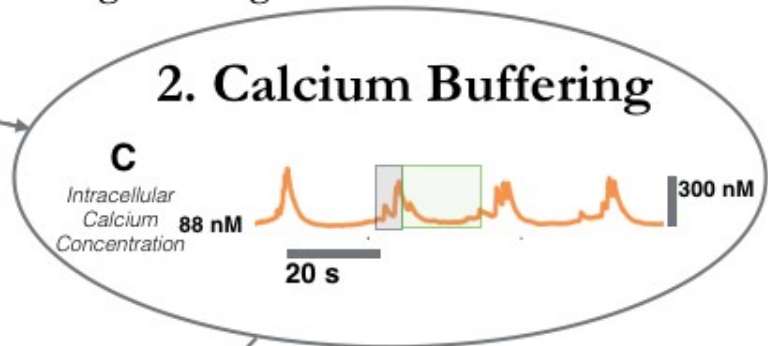
**Slow**  $S, R$ .  $\tau_R = \tau_S = 44$  s.

# Spontaneous Bursting Mechanism of SACs

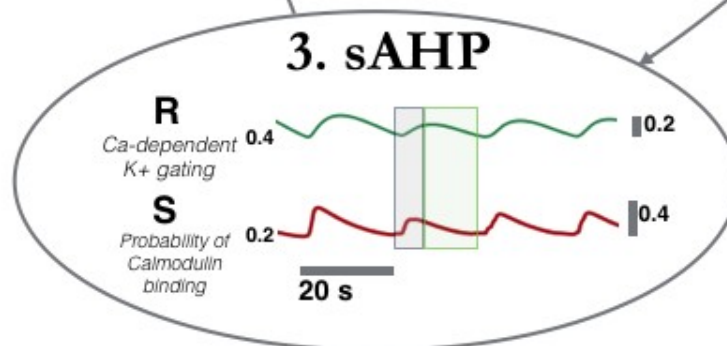
■ Bursting  
■ sAHP



Increase of Calcium load during bursting



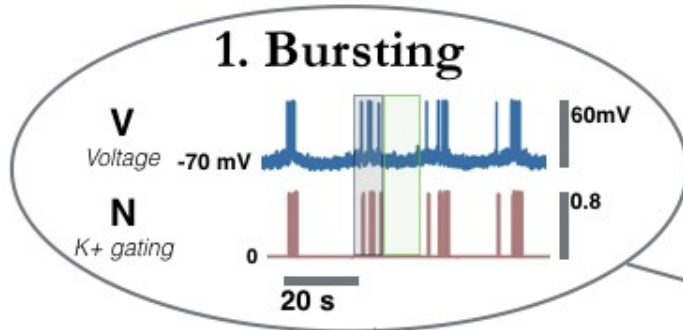
Bursting starts again when the Calcium load is low enough



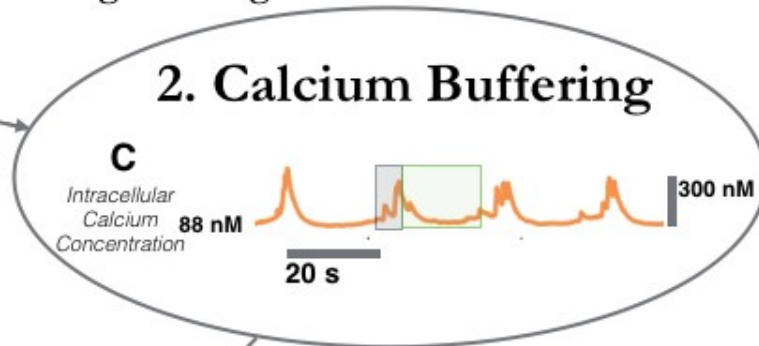
Calcium controls the sAHP phase. Voltage is low and Calcium starts offloading

# Spontaneous Bursting Mechanism of SACs

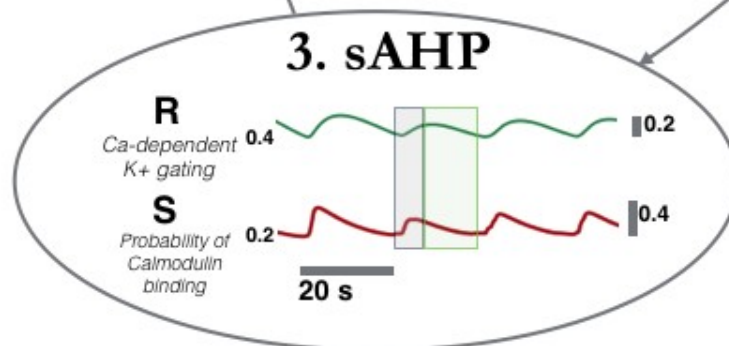
**Bursting**  
 **sAHP**



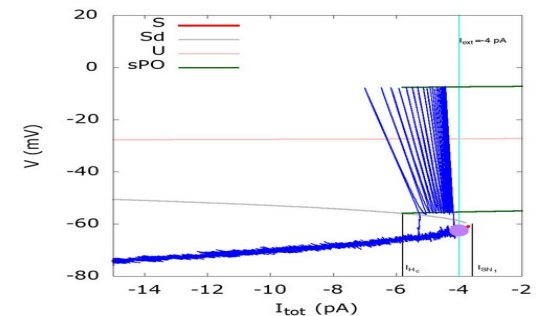
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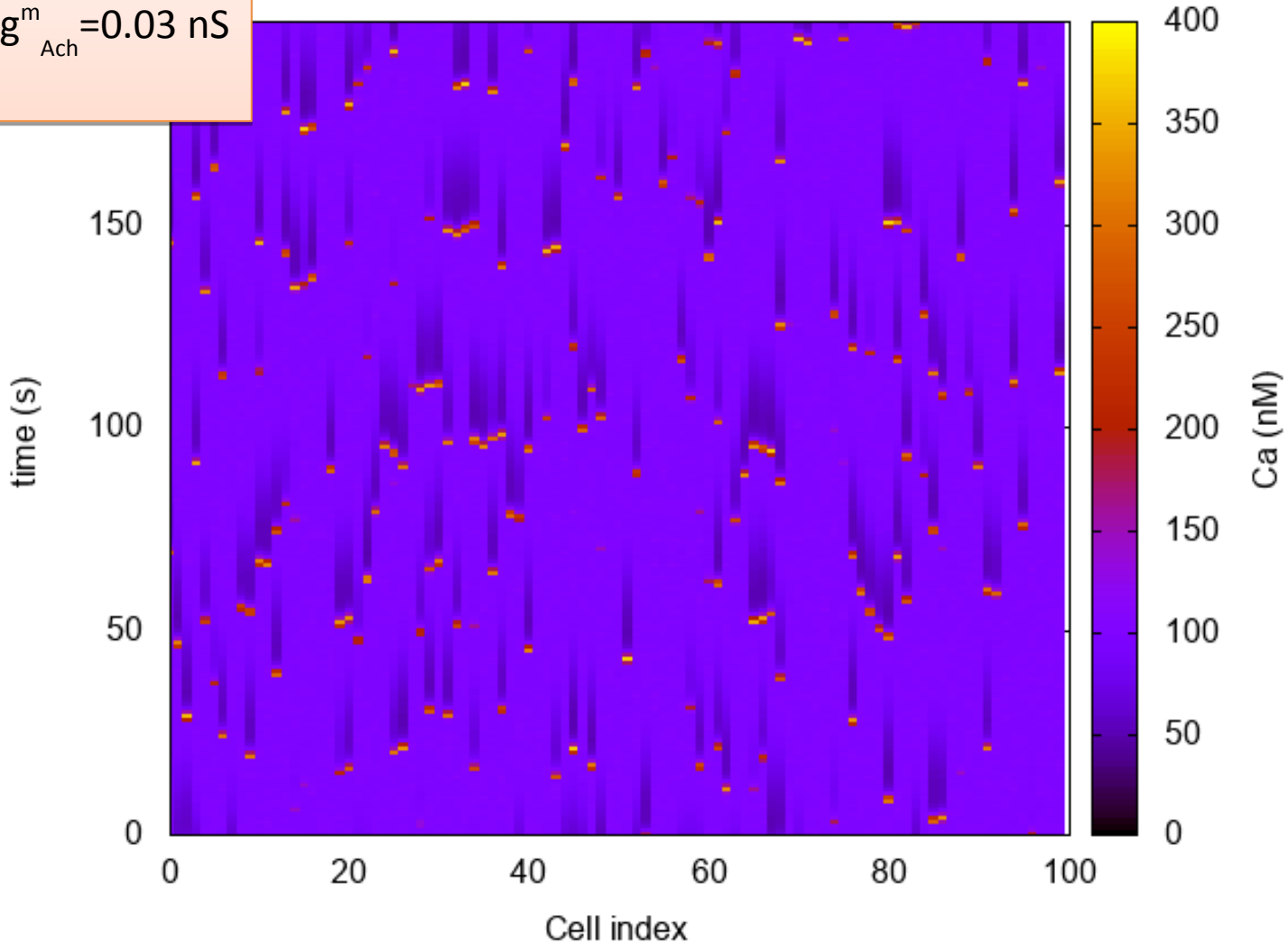


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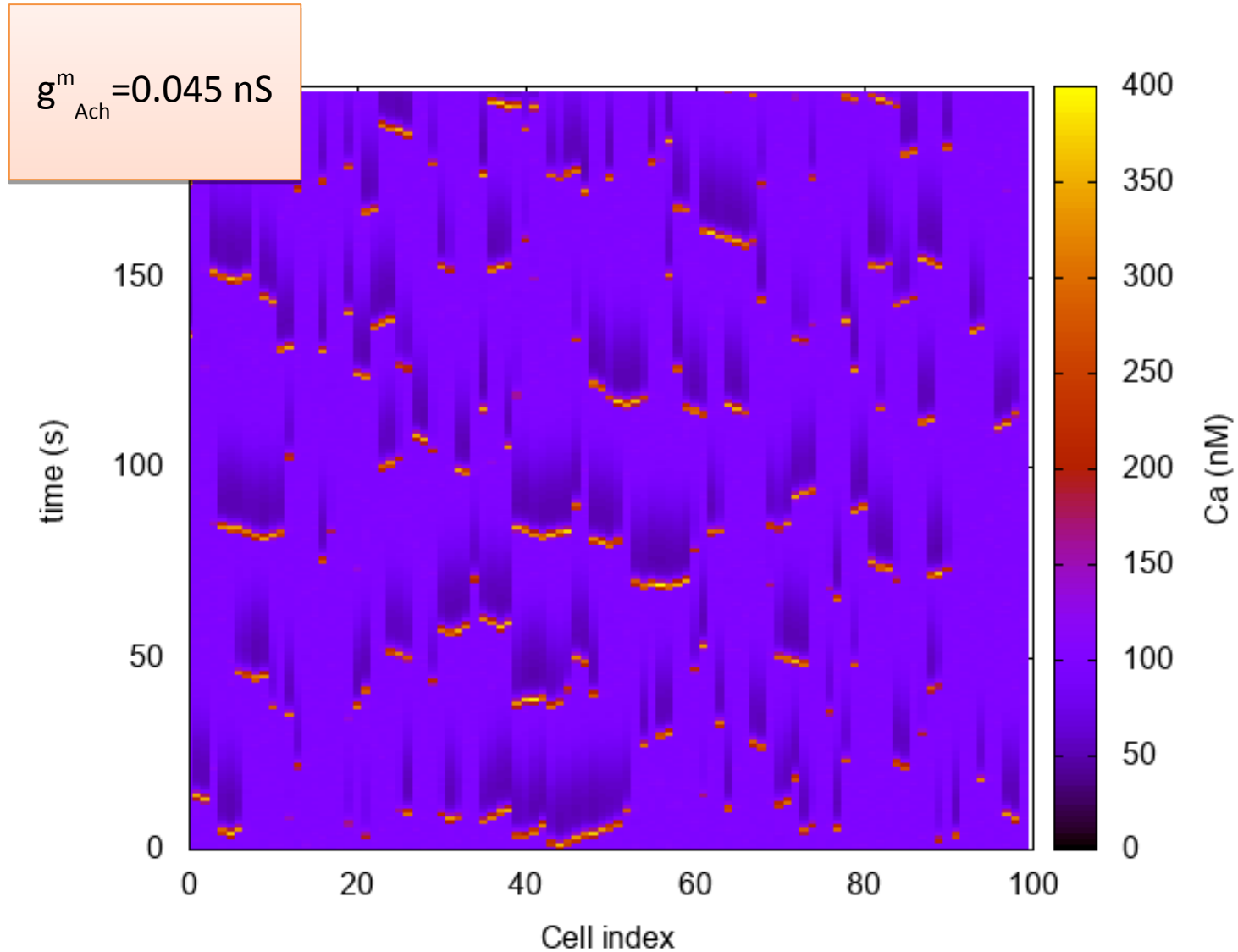


# Waves propagation

$$g_{\text{Ach}}^m = 0.03 \text{ nS}$$

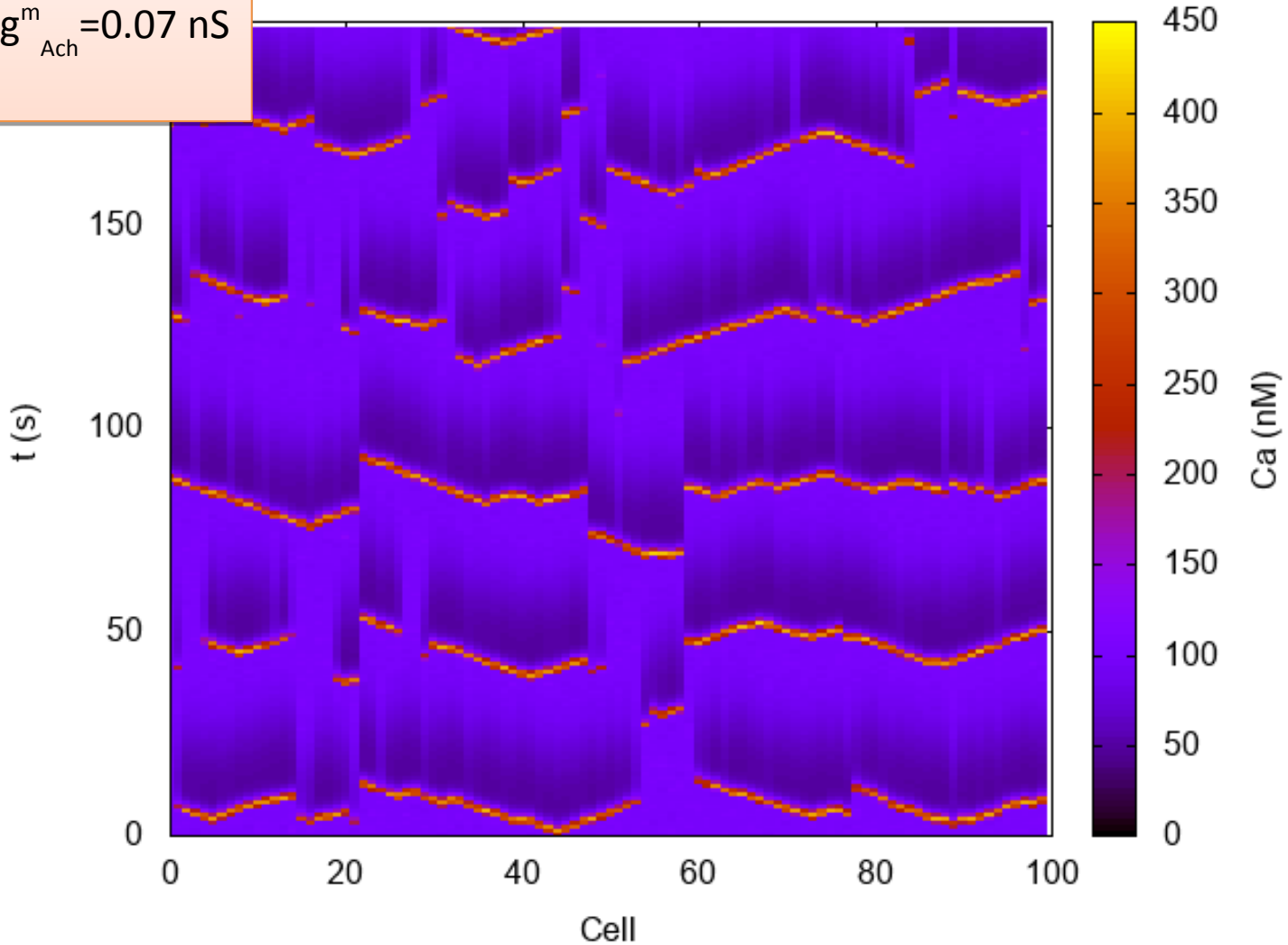


# Waves propagation



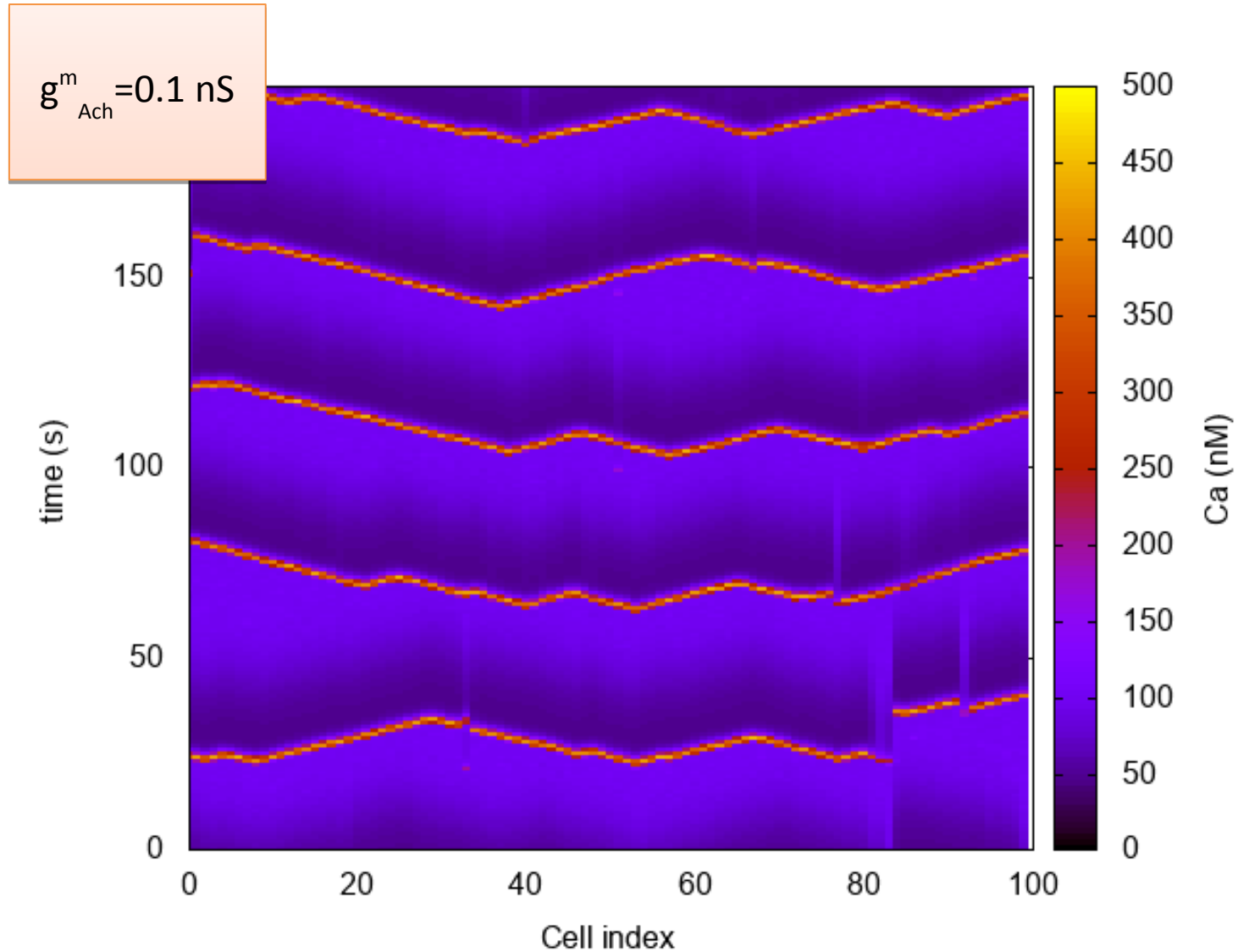
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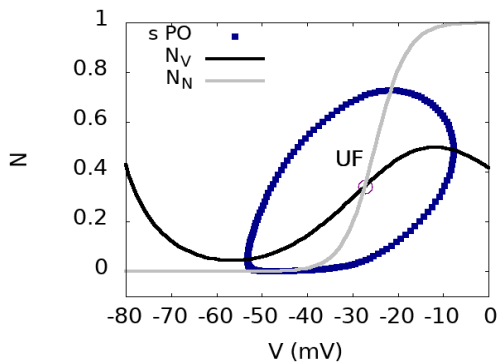
$$g_{\text{Ach}}^m = 0.07 \text{ nS}$$



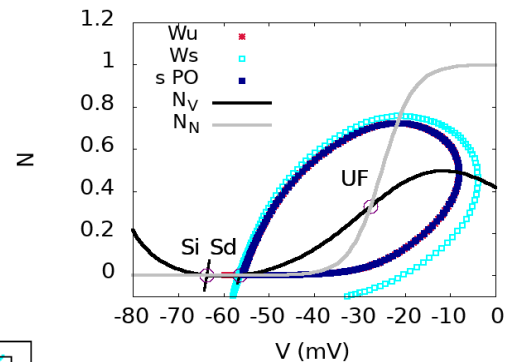


# Waves propagation

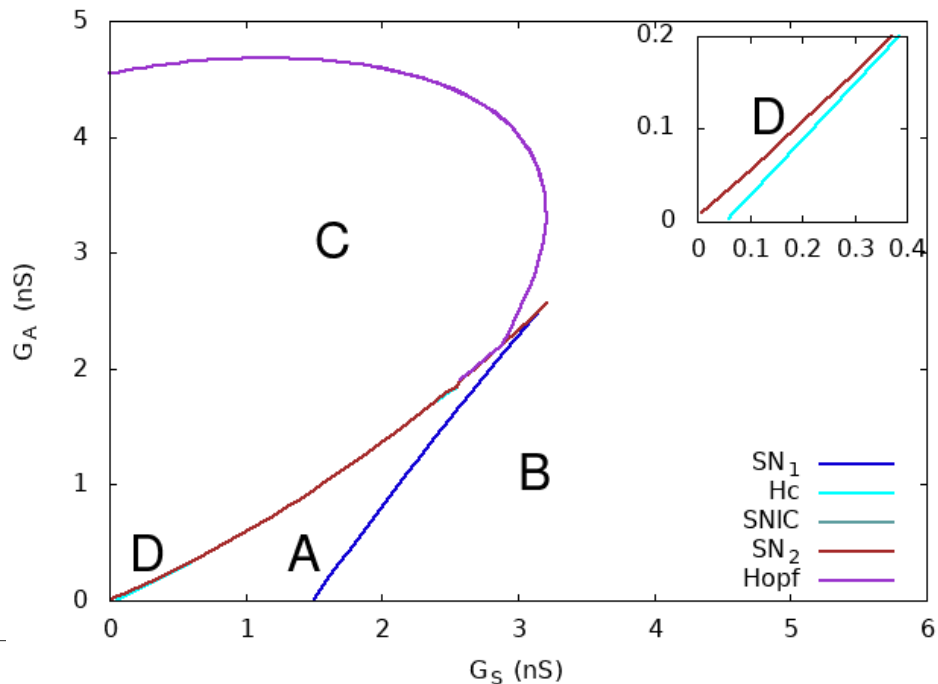




C

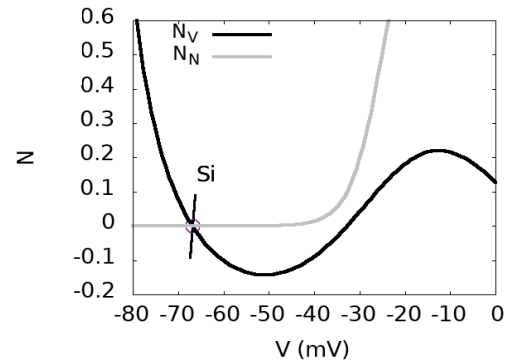
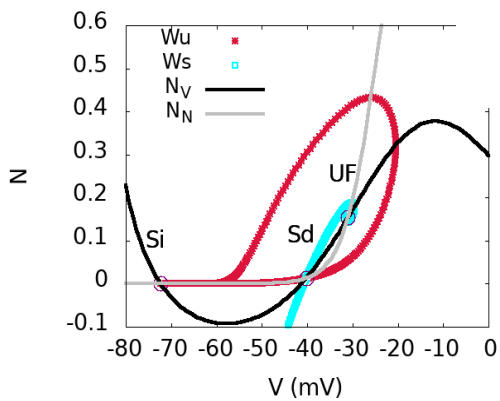


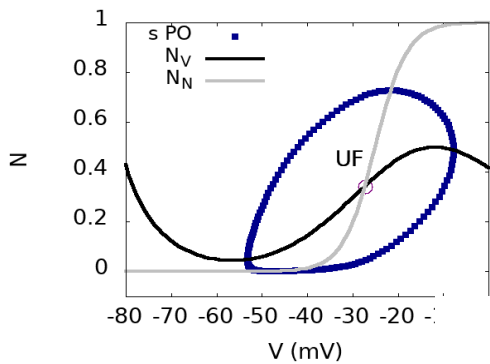
D



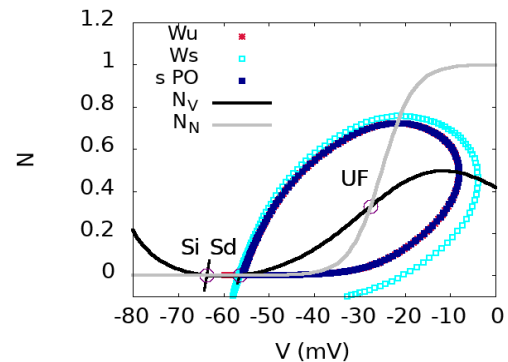
A

B

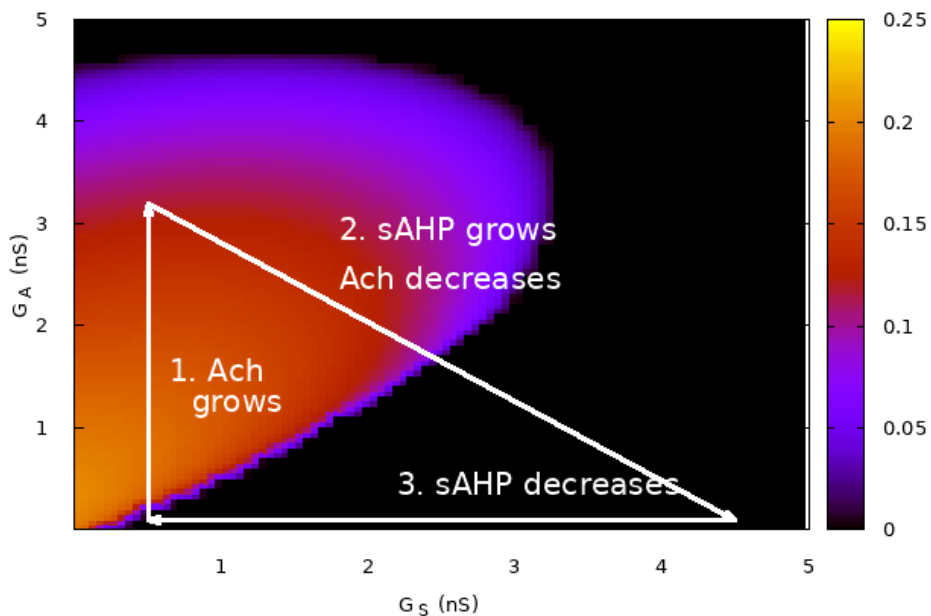




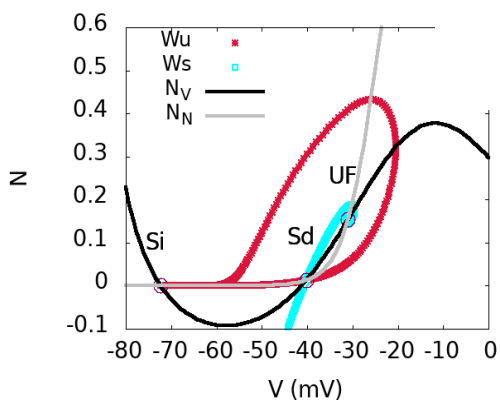
C



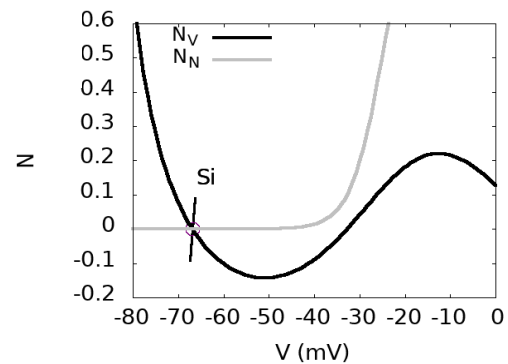
D



A



B



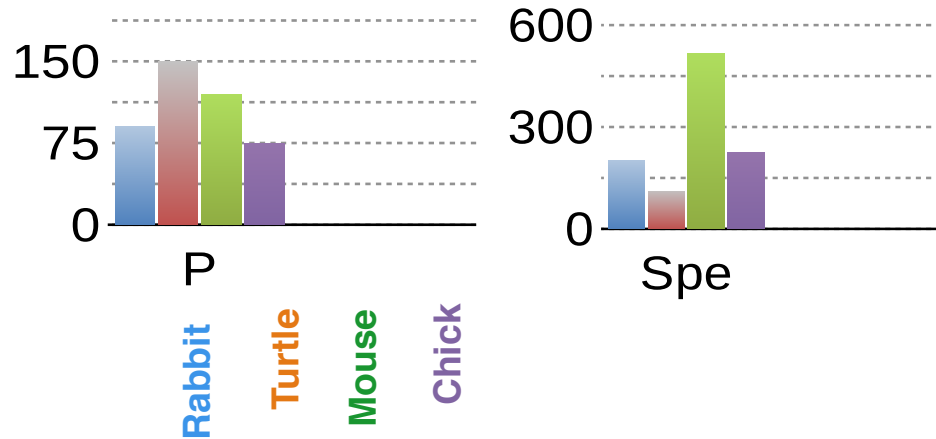
# Main mechanisms

- There is a **competition** between 2 mechanisms:
  - Refractoriness and desynchronisation (sAHP).
  - Mutual excitation and synchronisation (Acetylcholine).
- There is an intermediate regime of coupling, where **variability** is maximum.
- Therefore there is a wide repertoire of patterns
  - **Weak coupling** leads to small **localized activity**
  - **Moderate coupling** leads to **propagating patterns**
  - **Strong coupling** leads to **complete synchrony** of neurons

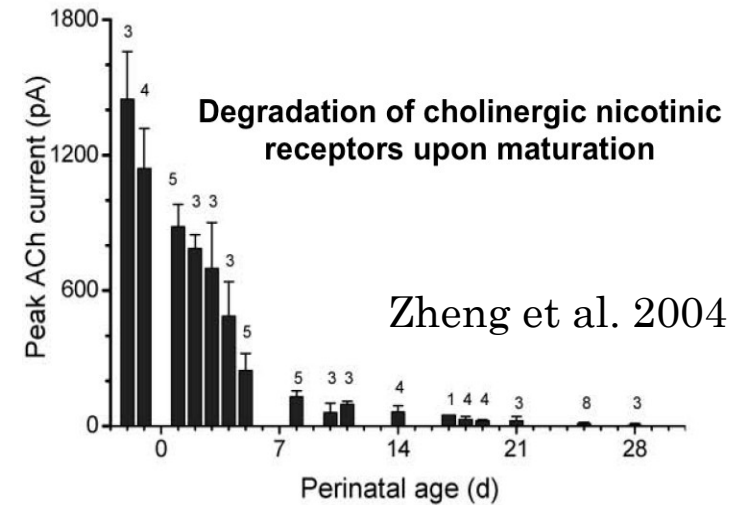
# Variability within retinal waves

## i) Across species

Godfrey et al. 2007

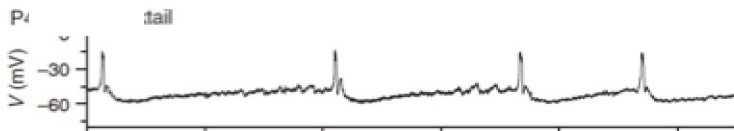


## ii) Development



## iii) Pharmacology

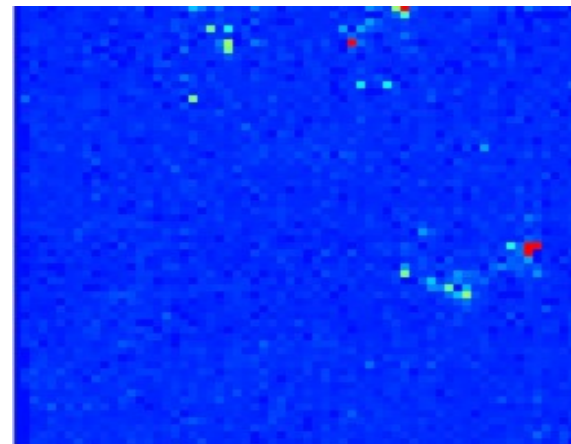
P4



P8

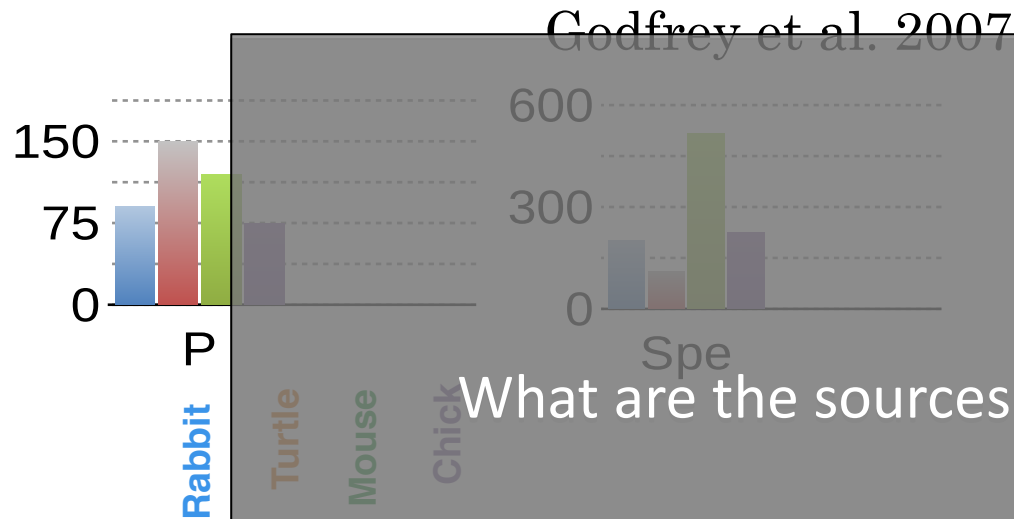


## iv) Spatial Variability

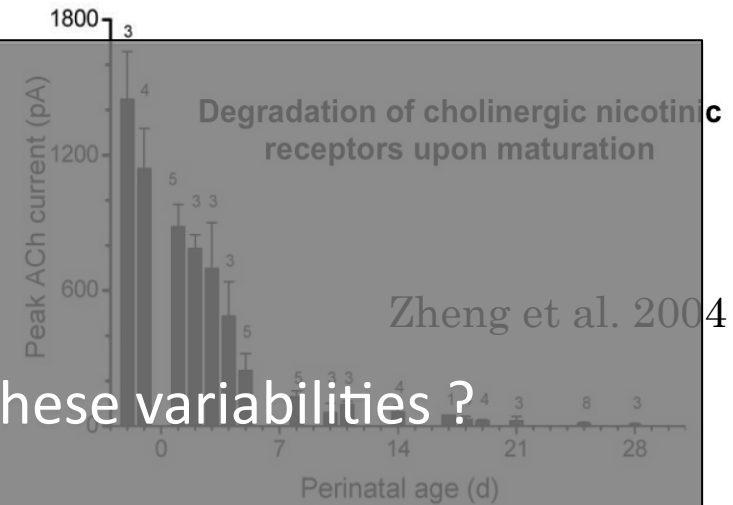


# Variability within retinal waves

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What are the sources of these variabilities?

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P4



P8



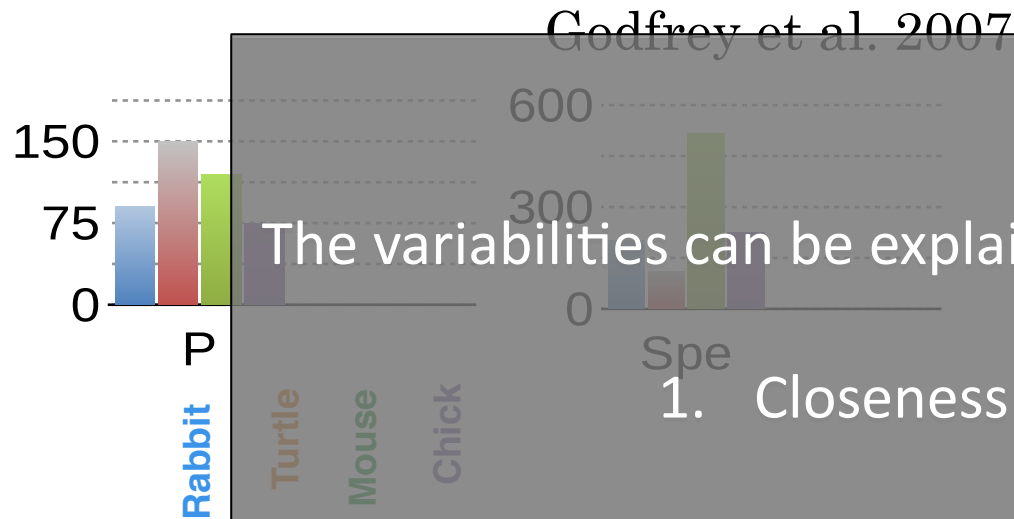
0 Time (sec) 50

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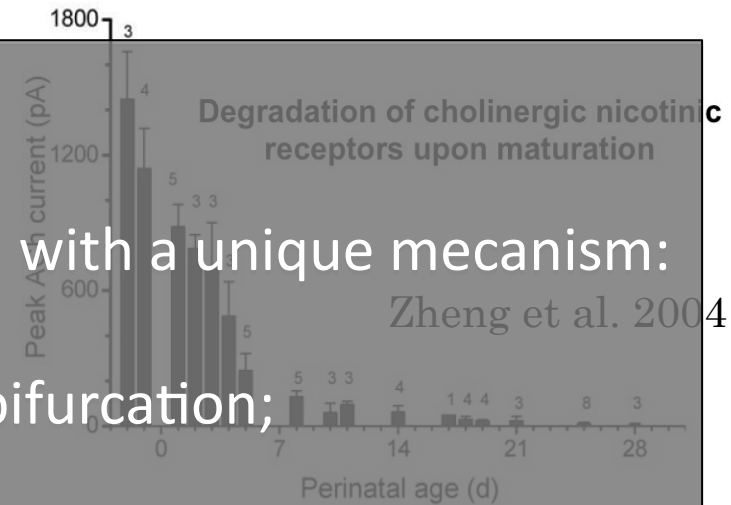
Is there a unique, global, mechanism explaining them?

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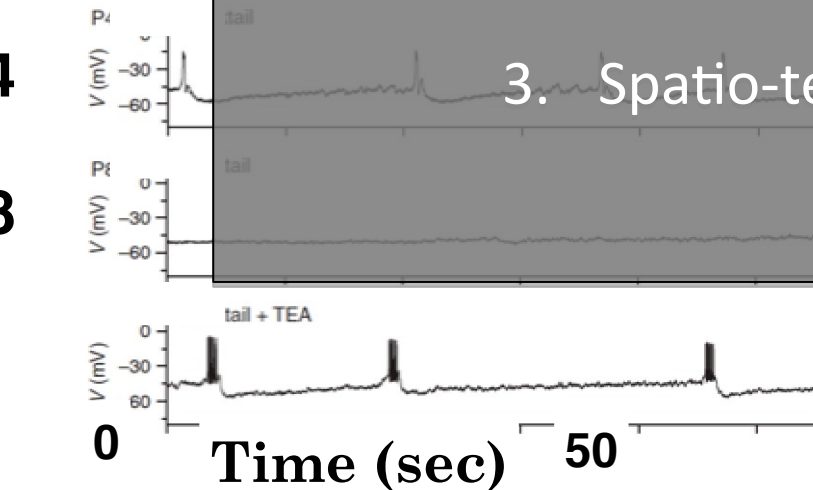


The variabilities can be explained with a unique mechanism:

1. Closeness to bifurcation;

2. Dynamic coupling via Ach.

## iii) Pharmacology



3. Spatio-temporal variability of sAHP.

## iv) Spatial Variability





# Retinal anticipation

Random connectivity and motion  
anticipation

**S. Souihel (PhD 2016-2019)**, Biovision team,  
INRIA, Sophia Antipolis

F. Chavane, INT, Marseille

A. Destexhe, UNIC, Paris

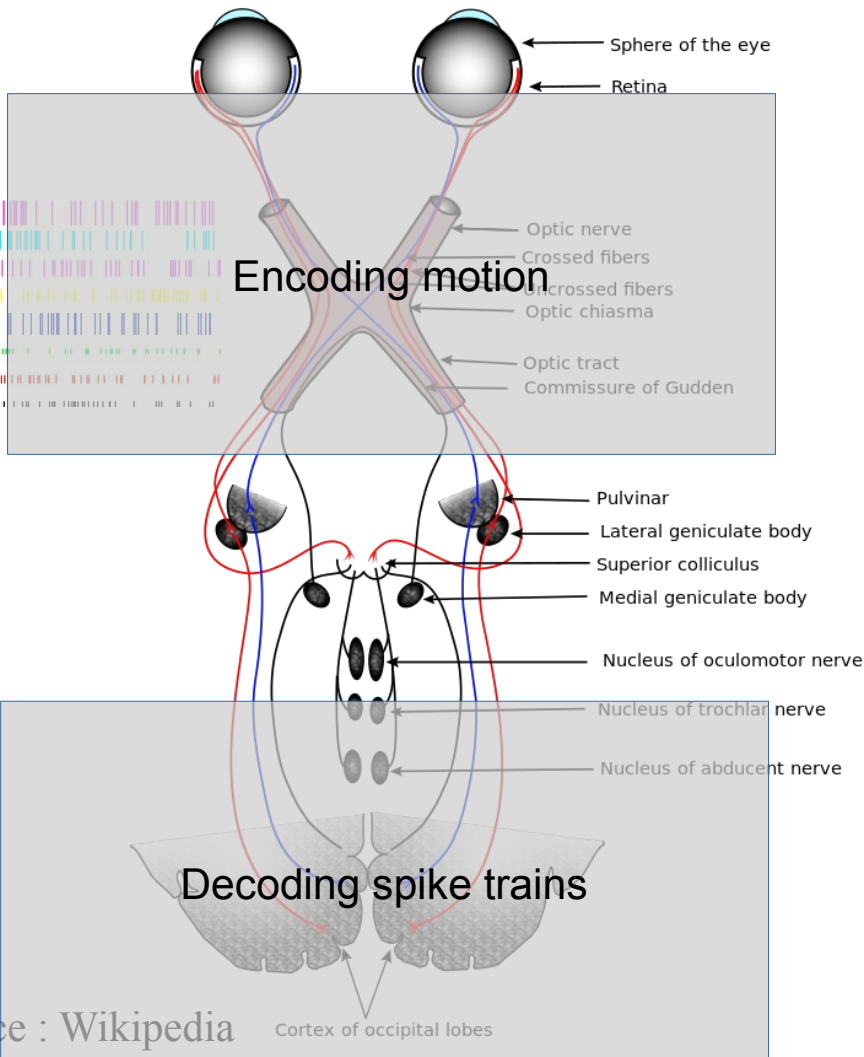
O. Marre, Institut de la Vision, Paris

B. Cessac, Biovision team, INRIA, Sophia Antipolis



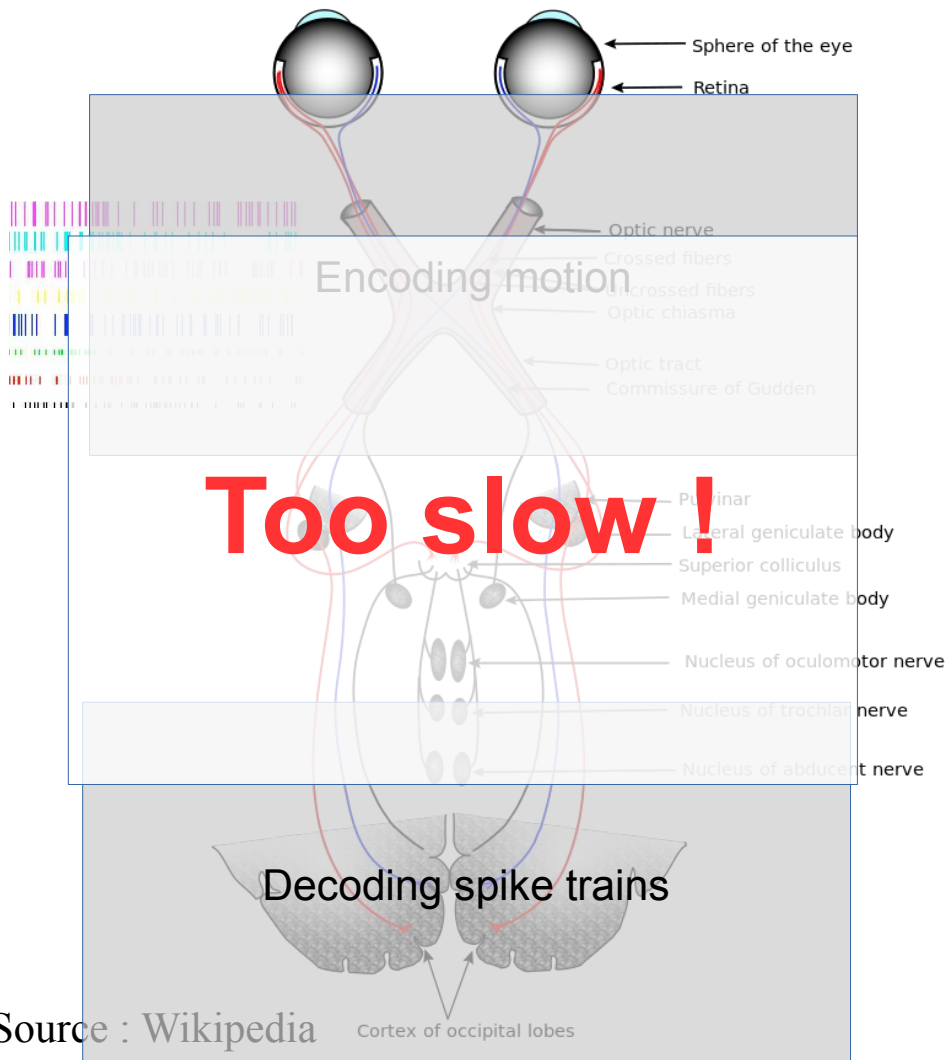
Project : ANR Trajectory.

# The visual flow



- **The retina is NOT a camera**
- High transduction rate : 1 photon can trigger a membrane voltage variation of ~1 mV
- Able to detect approaching motion
- Able to detect differential motion
- Sensitive to « surprise » in a visual scene
- Able to perform motion anticipation

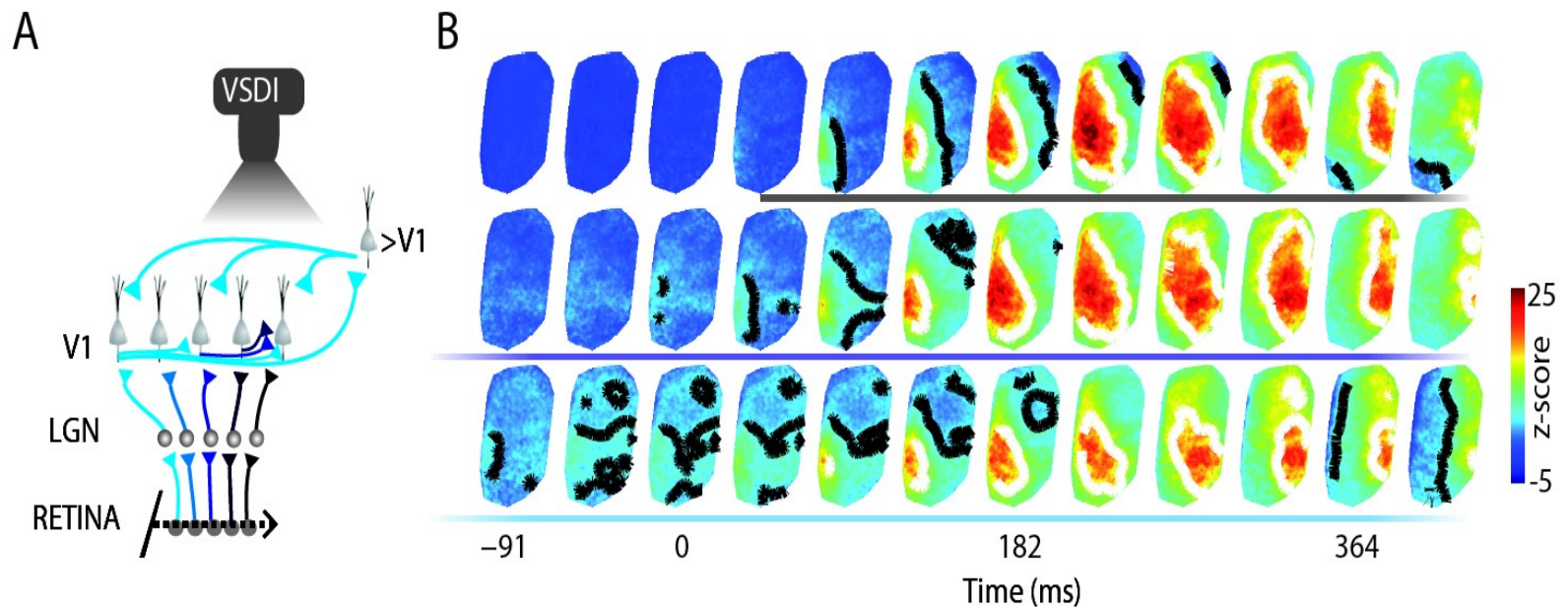
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# Visual Anticipation

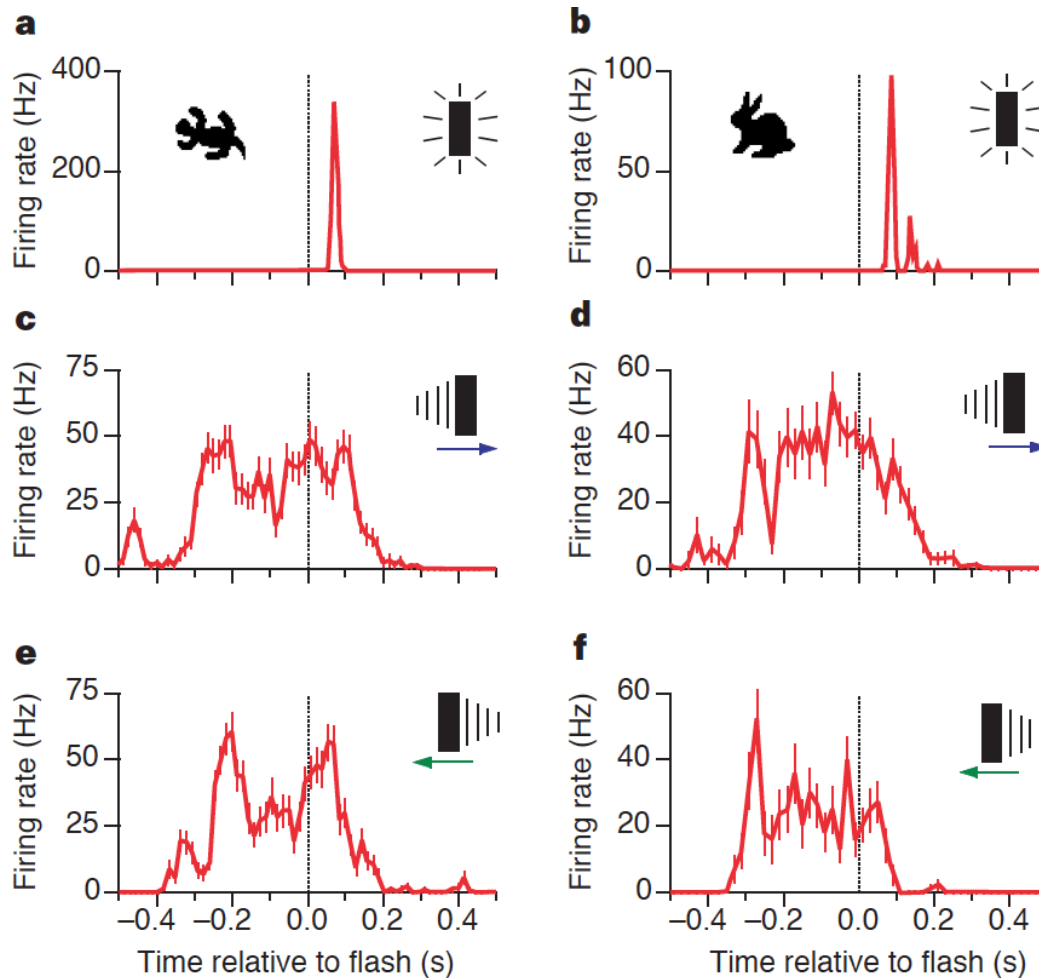
**Anticipation** is carried out by the primary visual cortex (V1) through an activation wave



Source : Benvenutti et al. 2015

# Visual Anticipation

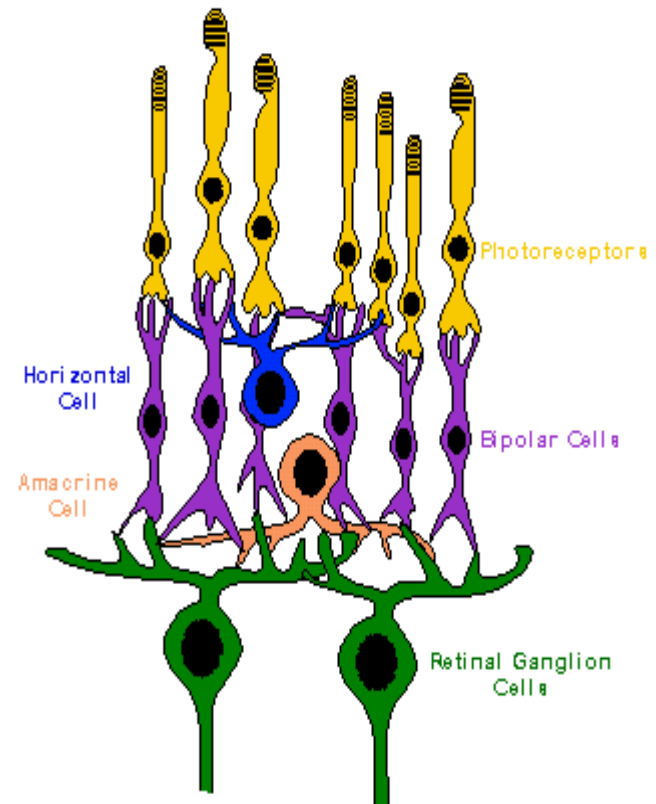
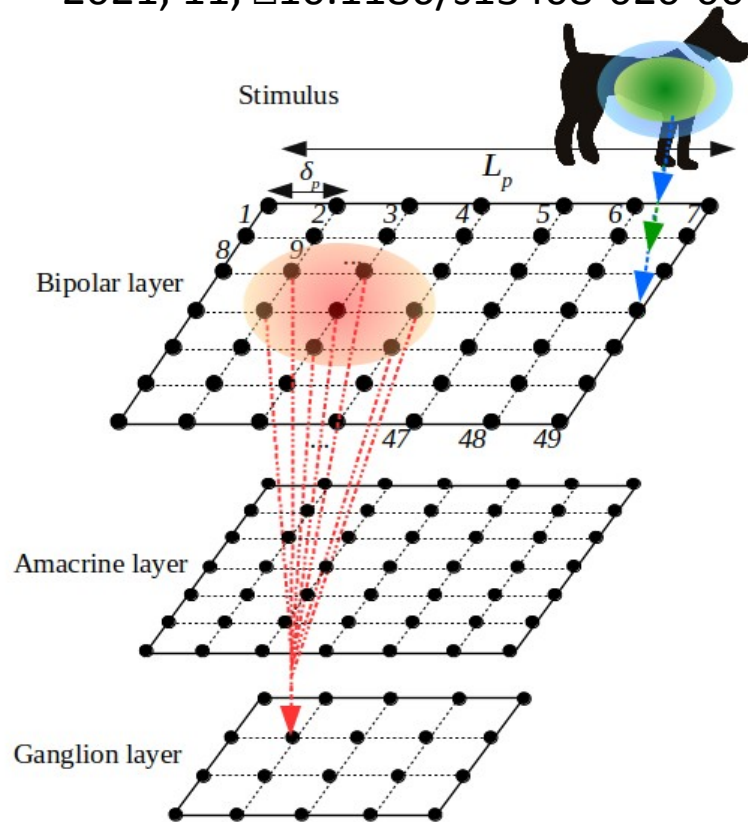
**Anticipation** also takes place in the retina



Source :  
Berry et al.  
1999

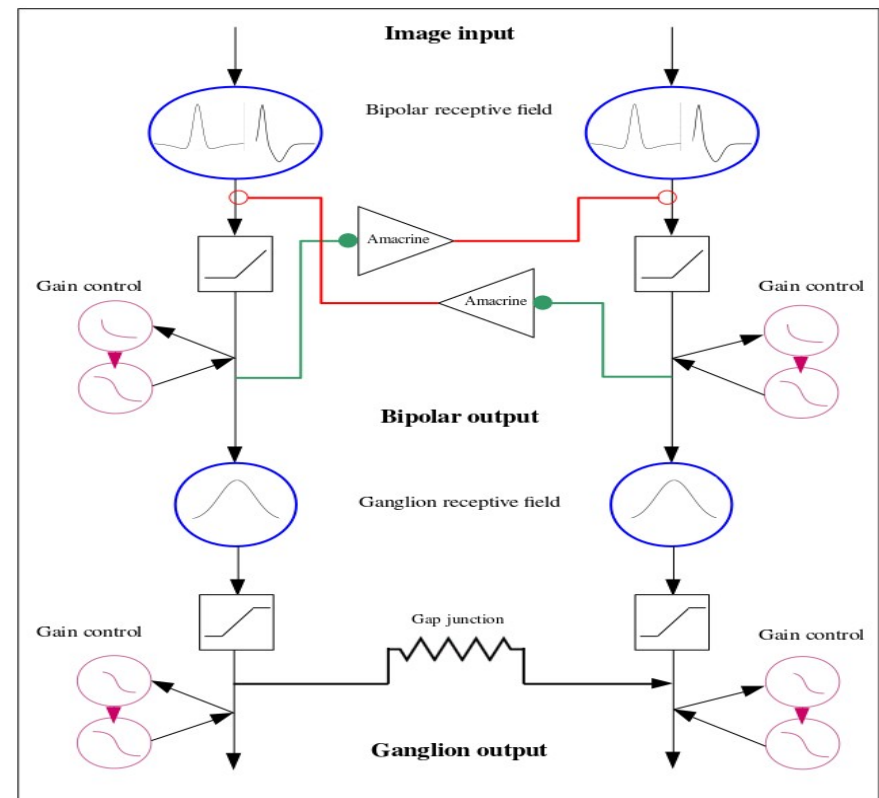
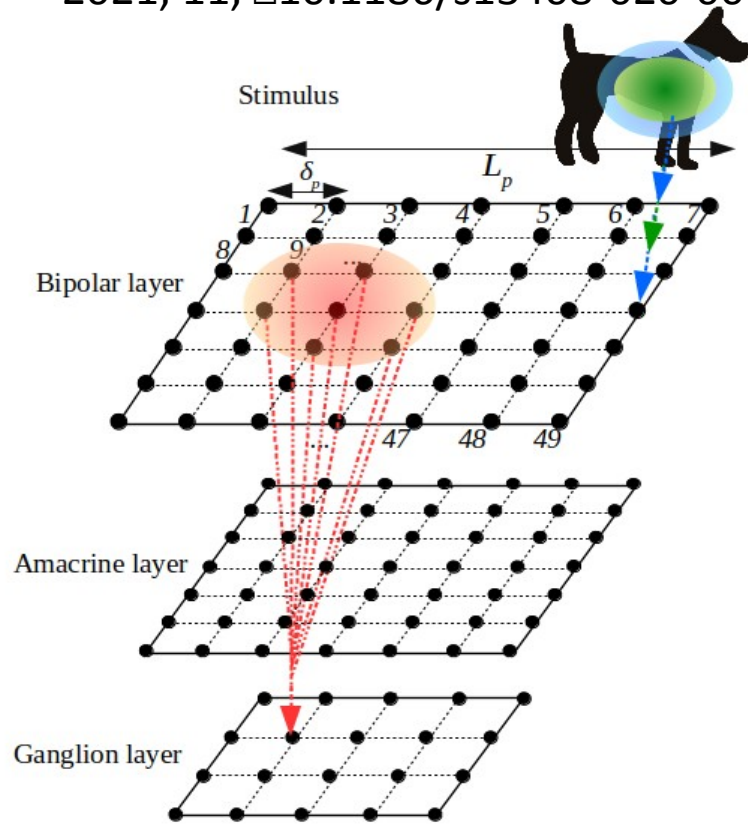
# Building a 2D retina model for motion anticipation

Souihel S., Cessac B., "On the potential role of lateral connectivity in retinal anticipation", Journal of Mathematical Neuroscience, BioMed Central, 2021, 11, [10.1186/s13408-020-00101-z](https://doi.org/10.1186/s13408-020-00101-z)



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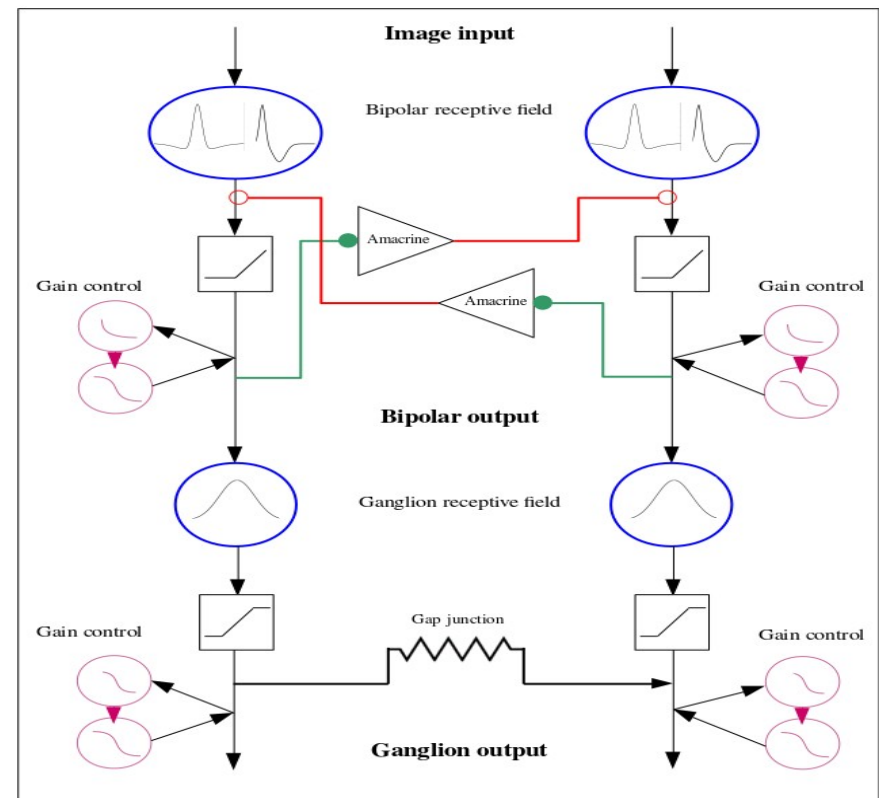
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$$\begin{cases} \frac{dV_{B_i}}{dt} = -\frac{1}{\tau_B} V_{B_i} + \sum_{j=1}^{N_A} W_{B_i}^{A_j} V_{A_j} + F_{B_i}(t), \\ \frac{dV_{A_j}}{dt} = -\frac{1}{\tau_A} V_{A_j} + \sum_{i=1}^{N_B} W_{A_j}^{B_i} R_{B_i}, \\ \frac{dA_{B_i}}{dt} = -\frac{A_{B_i}}{\tau_a} + h_B \mathcal{N}(V_{B_i}). \end{cases}$$



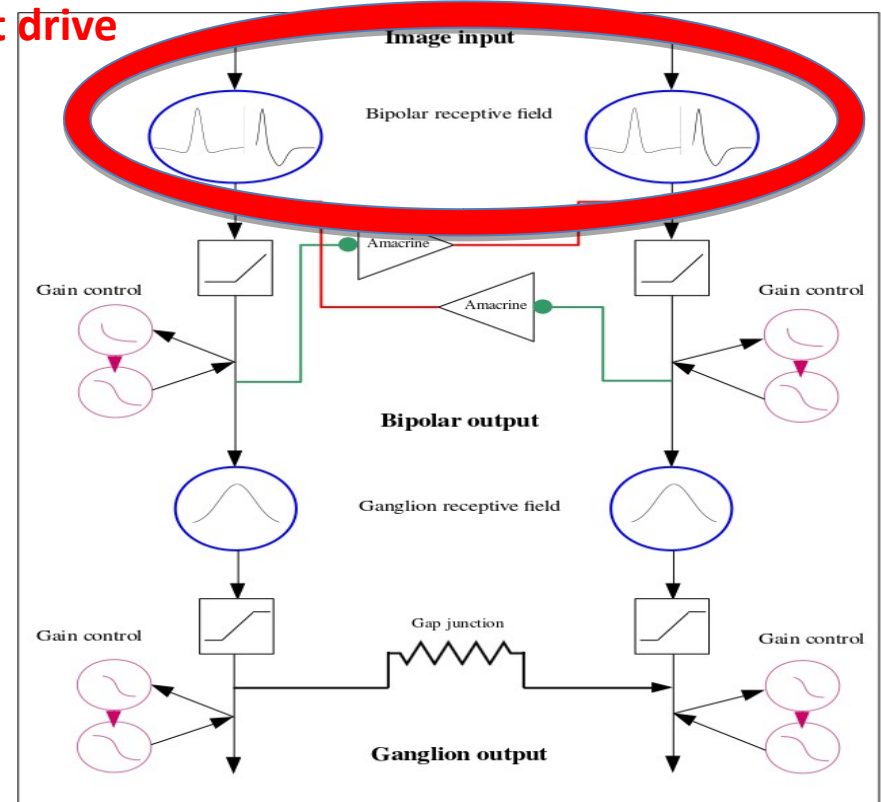


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## Stimulus dependent drive

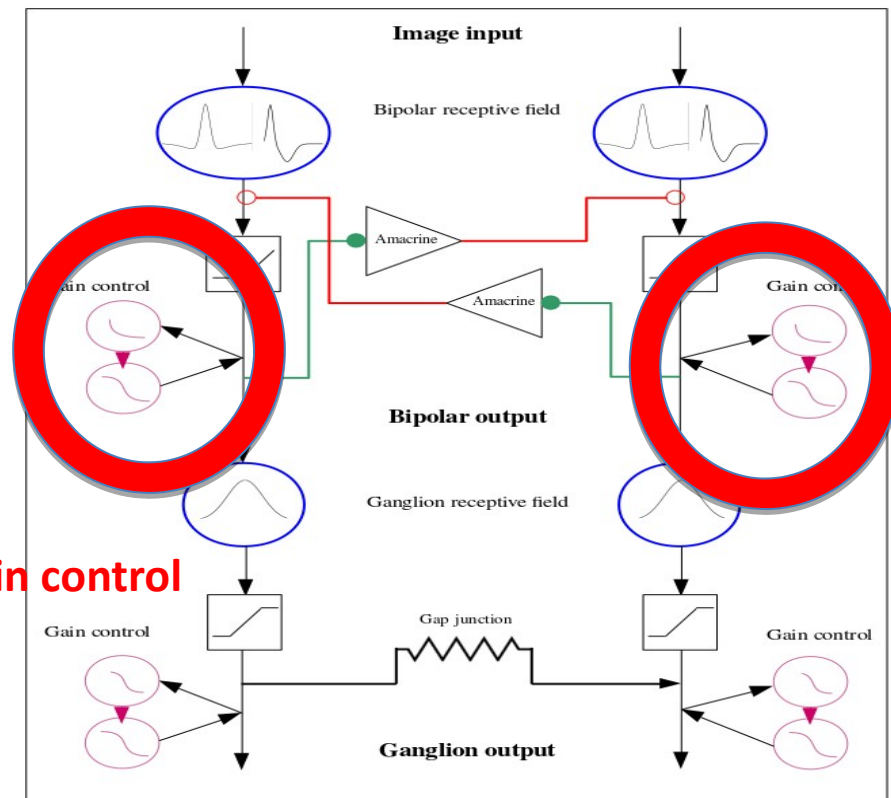
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**Non linear gain control**

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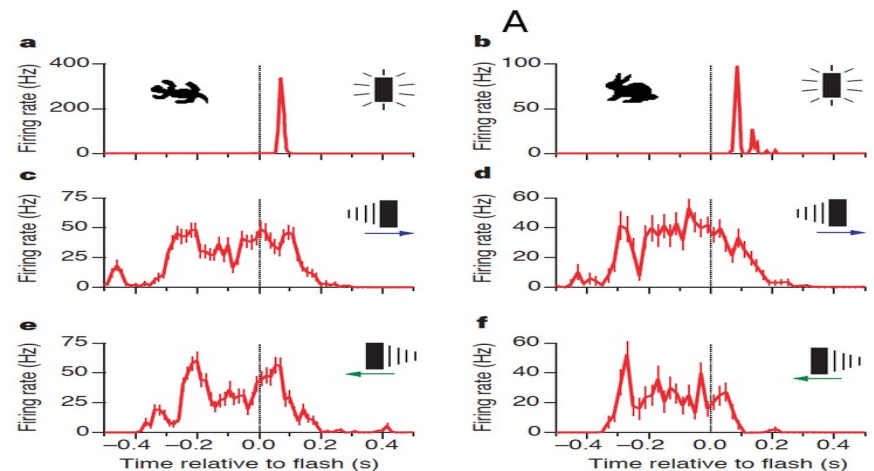
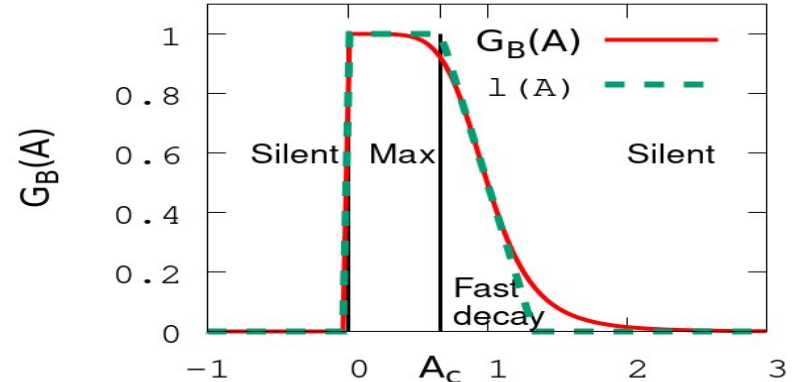
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$$\frac{dV_{A_j}}{dt} = -\frac{1}{\tau_A} V_{A_j} + \sum_{i=1}^{N_B} W_{A_j}^{B_i} R_{B_i},$$

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

**Non linear gain control**

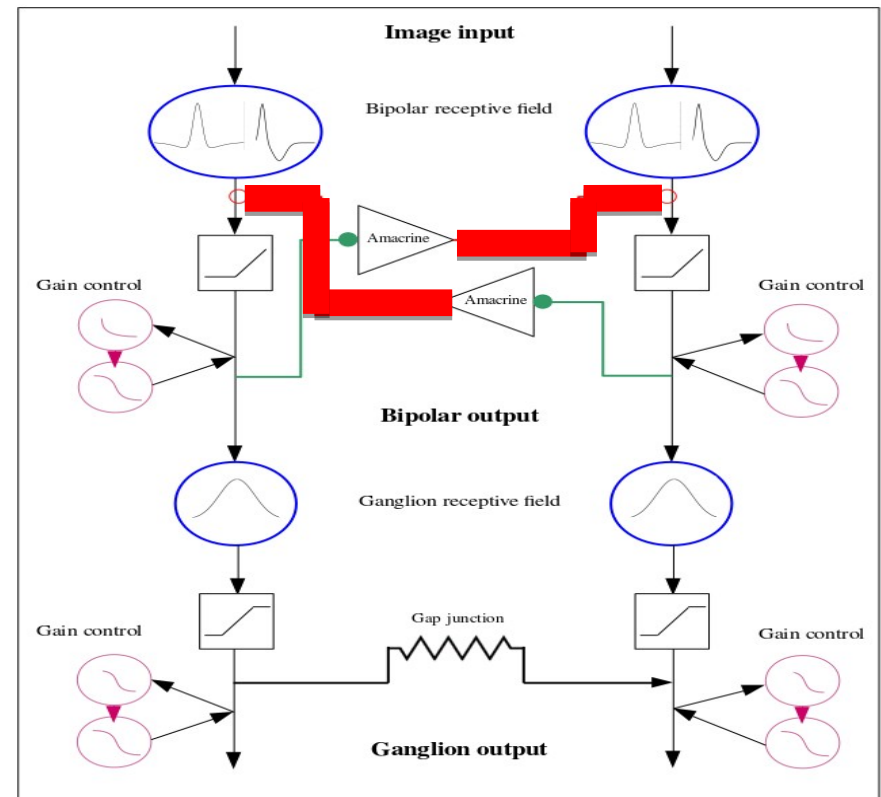


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**Inhibition**

$$\left\{ \begin{aligned} \frac{dV_{B_i}}{dt} &= -\frac{1}{\tau_B} V_{B_i} + \sum_{j=1}^N W_{B_i}^{A_j} V_{A_j} + F_{B_i}(t), \\ \frac{dV_{A_j}}{dt} &= -\frac{1}{\tau_A} V_{A_j} + \sum_{i=1}^{N_B} W_{A_j}^{B_i} R_{B_i}, \\ \frac{dA_{B_i}}{dt} &= -\frac{A_{B_i}}{\tau_a} + h_B \mathcal{N}(V_{B_i}). \end{aligned} \right.$$

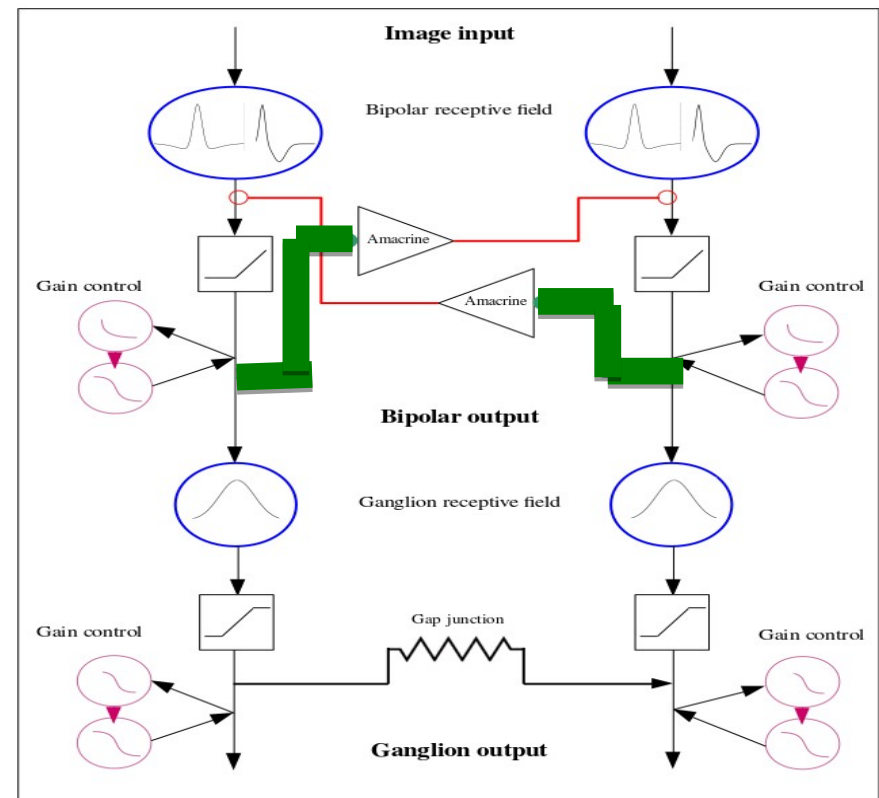


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**Excitation**



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Souihel S., Cessac B., "On the potential role of lateral connectivity in retinal anticipation", Journal of Mathematical Neuroscience, BioMed Central, 2021, 11, [10.1186/s13408-020-00101-z](https://doi.org/10.1186/s13408-020-00101-z)

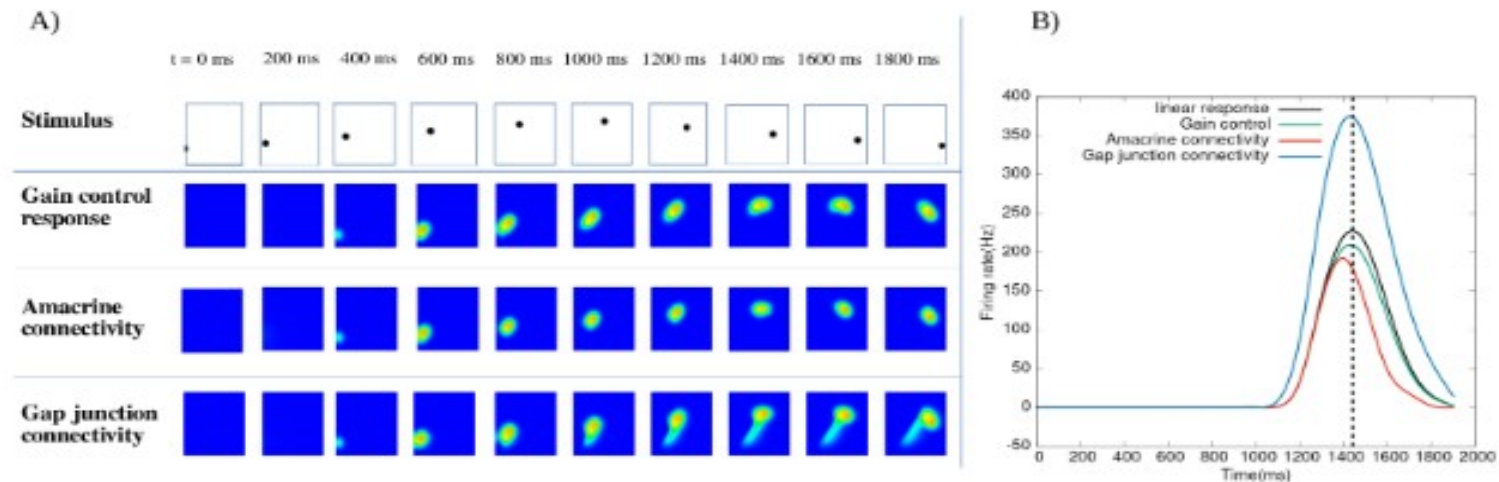


Figure 15: **Effect of anticipatory mechanisms on a parabolic trajectory.** A) Response to a dot moving along a parabolic trajectory. The first line shows the stimulus, the second line shows the GCells response with gain control, the third line presents the effect of lateral ACells connectivity with  $w = 0.3 \text{ ms}^{-1}$ , and the last line shows the effect of asymmetric gap junctions with  $v_{gap} = 9 \text{ mm/s}$ . B) Time course response of a cell responding to the dot near the trajectory turning point. Linear response corresponds to the response to the stimulus without gain control.



# Retino-cortical model of anticipation

- A retino-cortical (V1) model of anticipation (with F. Chavane, S. Chemla, A. Destexhe, S. Souihel, M. Di Volo).

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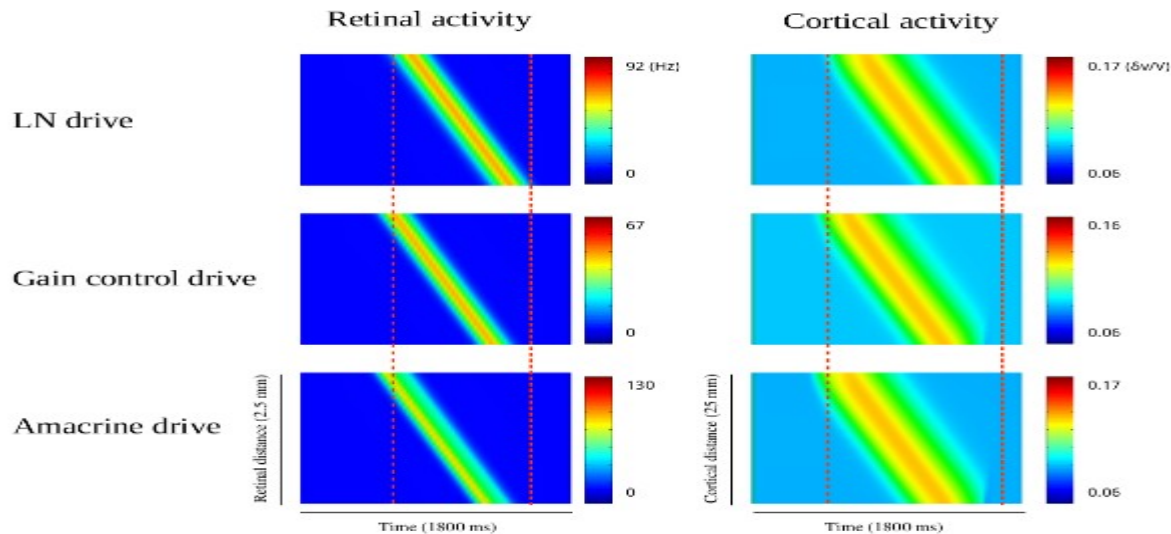


Figure 11: Comparing the spatio-temporal activity with the different drives. Left column figures display the spatio-temporal retinal activity with different anticipatory mechanisms, and the right column displays the corresponding spatio-temporal cortical activity. The red dashed lines denote the start and the end times of the LN retinal and cortical activities, as a reference base.



# Retino-cortical model of anticipation

- A retino-cortical (V1) model of anticipation (with F. Chavane, S. Chemla, A. Destexhe, S. Souihel, M. Di Volo).
- 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 ?



# A question about retinal coding

R. Cofré, CIMFAV, Facultad de Ingenieria,  
Universidad de Valparaiso, Valparaiso, Chile

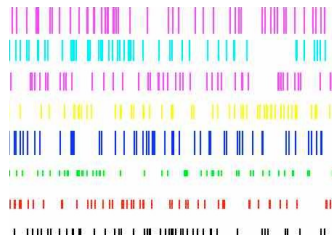
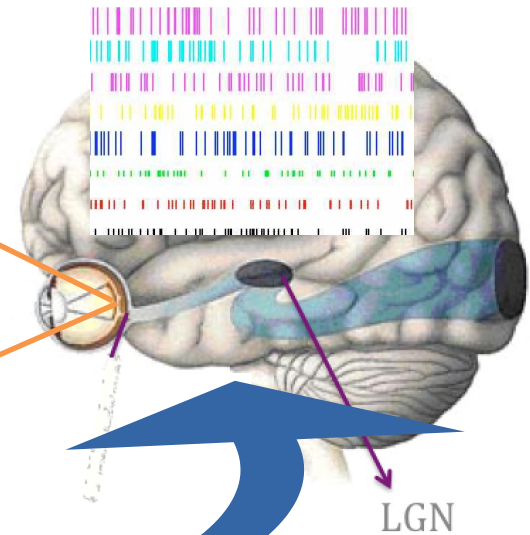
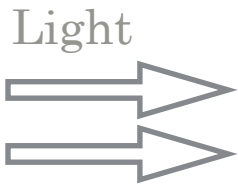
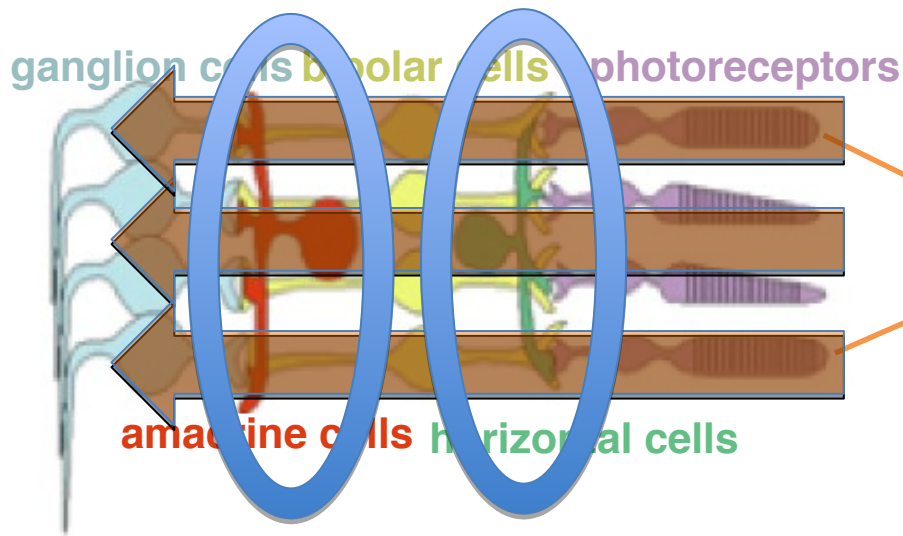
Ignacio Ampuero, Departamento de Informatica,  
Universidad Tecnica Federico Santa Maria,  
Valparaiso, Chile

# The visual system

Encoder

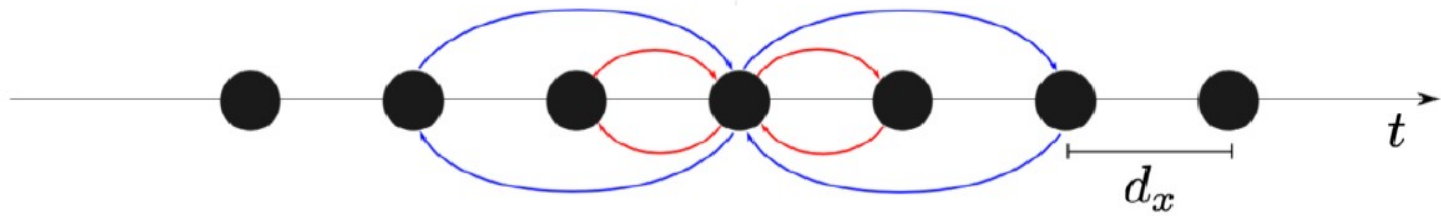
Decoder

Retina's layered structure

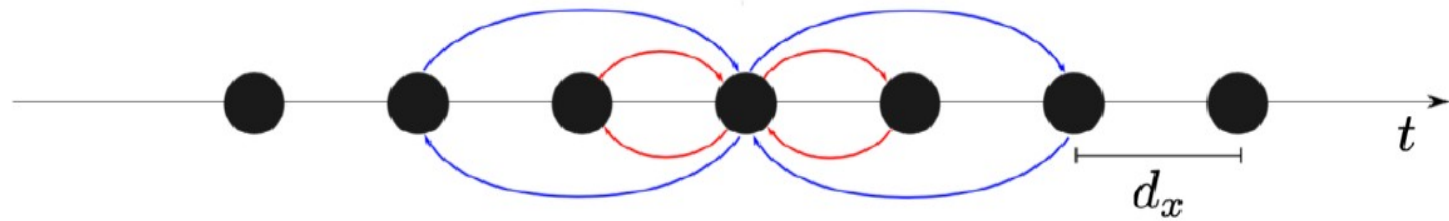


« Information » flux

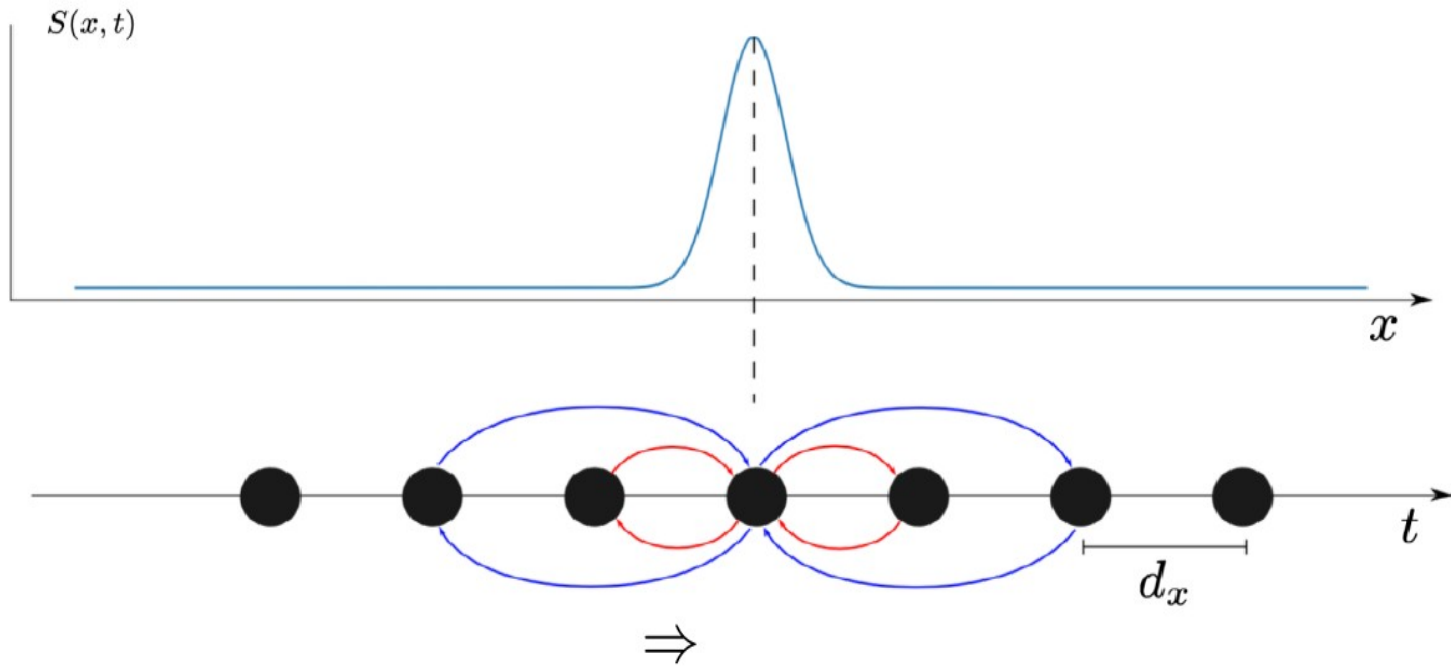
# Spontaneous spiking activity



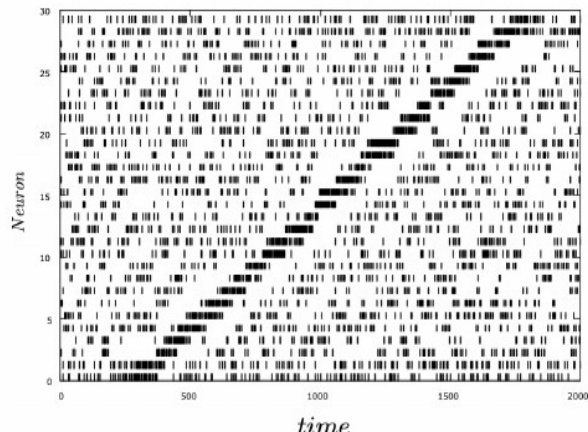
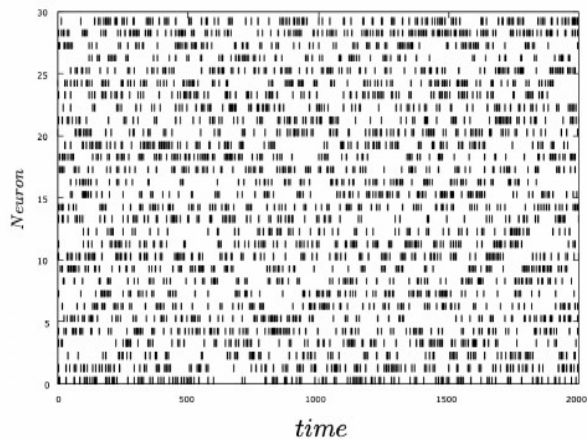
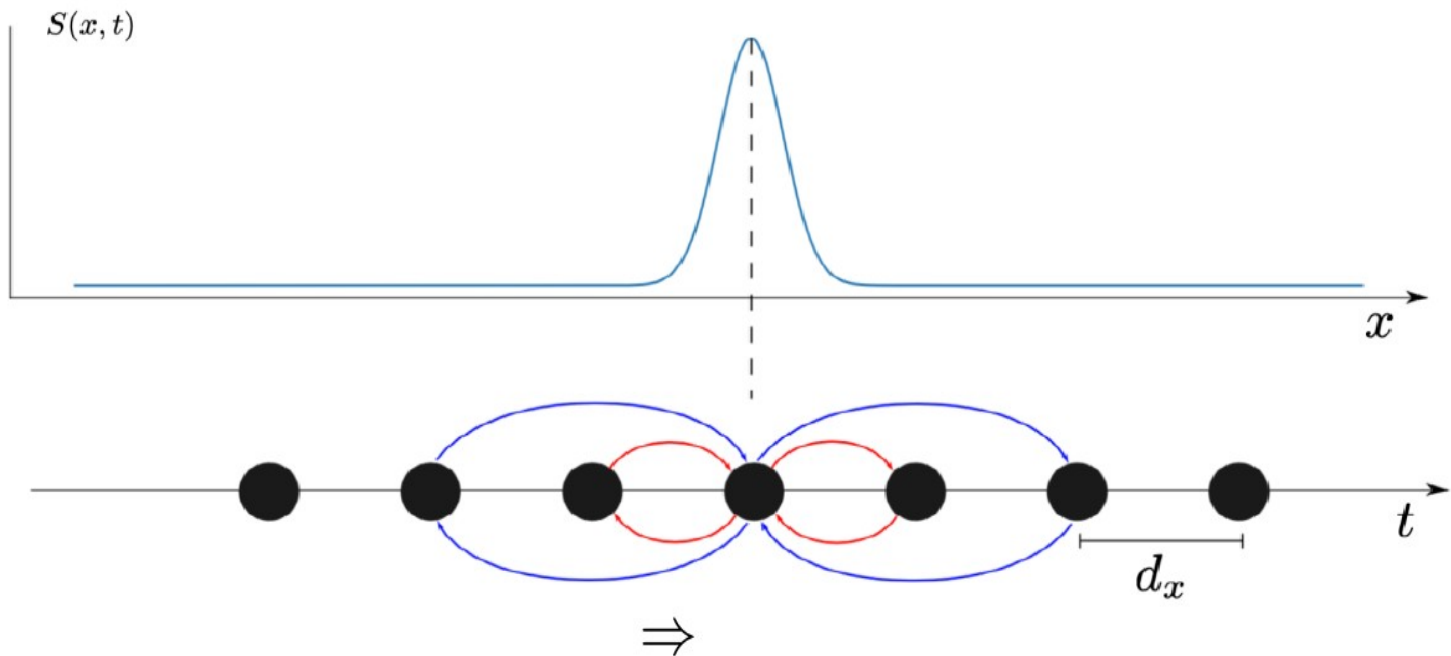
# Spontaneous spiking activity



# Spontaneous spiking activity

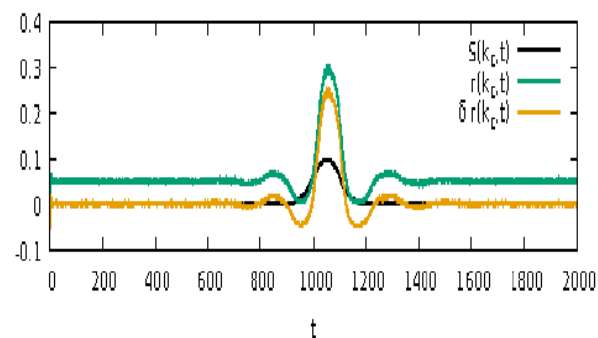
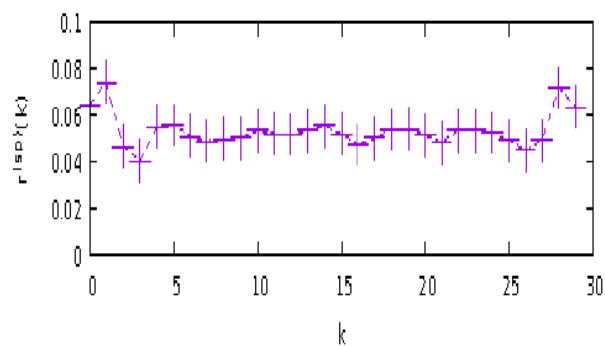
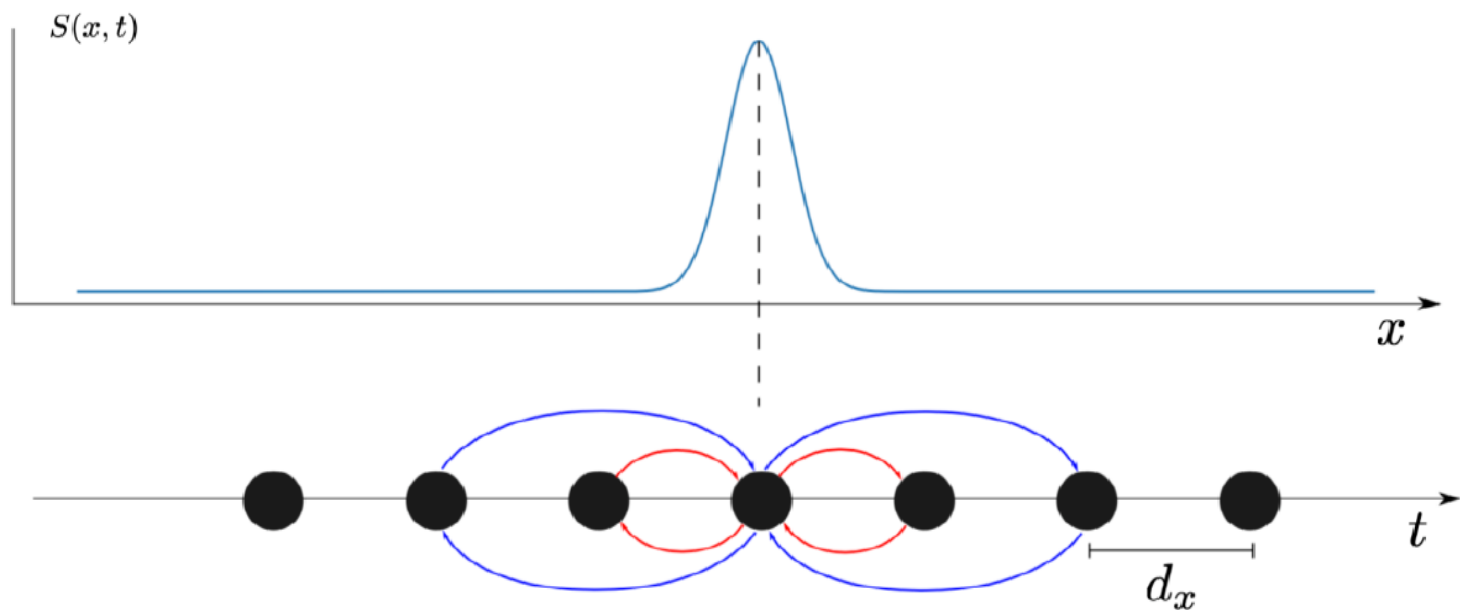


# Spontaneous spiking activity



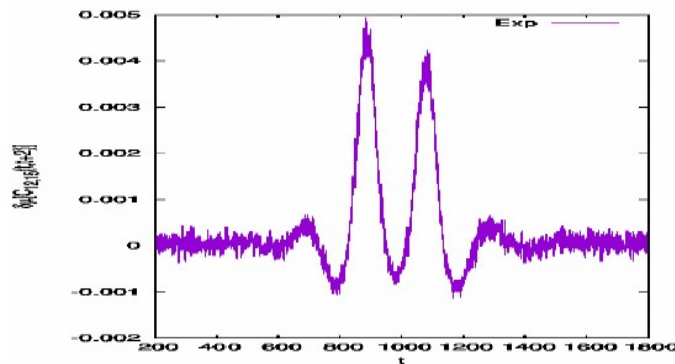
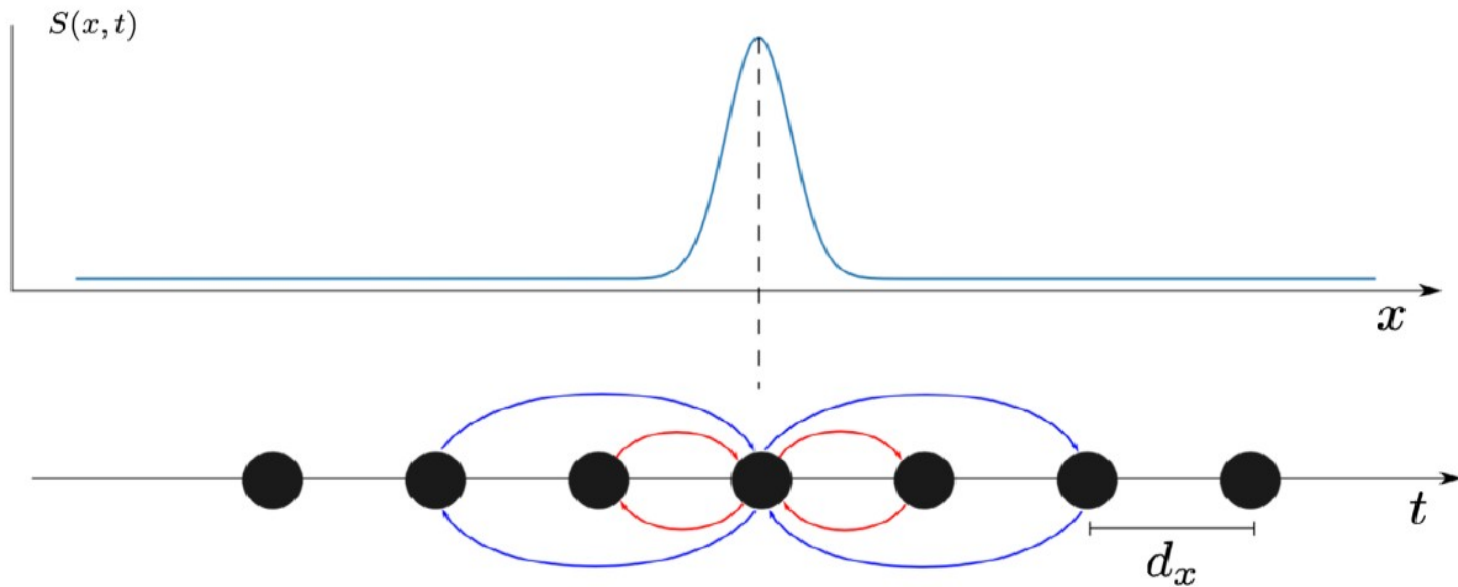


# Spontaneous spiking activity



Sample averaging (non stationary)

# Spontaneous spiking activity



Variation in the correlation  $C_{12,15}(t, t+2)$

Correlation variations are triggered by the stimulus, but they are constrained by the network dynamics.

How to compute the spatio-temporal response of a neuronal network to a time dependent stimulus ?

Can we compute the time variation of spike-observables as a function of the stimulus and spontaneous dynamics ?

B. Cessac, I. Ampuero, R. Cofre, Linear response for spiking neuronal networks with unbounded memory. Entropy, MDPI, 2021, 23 (2), pp.155.

# Response to stimuli

B. Cessac, I. Ampuero, R. Cofre, Linear response for spiking neuronal networks with unbounded memory. Entropy, MDPI, 2021, 23 (2), pp.155.

GIF model without stimulus  $\Rightarrow$  *stationary Gibbs distribution*.

*time-dependent* stimulus  $S(t) \Rightarrow$  *non stationary Gibbs distribution*.

*How is the average of an observable  $f(\omega, t)$  affected by the stimulus ?*

If  $S$  is weak enough:  $\delta\mu[f(t)] = [\kappa_f * S](t)$  , (linear response).

$$\kappa_{k,f}(t - t_1) = \frac{1}{C_k} \sum_{r=-\infty}^{n=[t]} C^{(sp)} \left[ f(t, \cdot), \frac{\mathcal{H}_k^{(1)}(r, \cdot)}{\sigma_k(r-1, \cdot)} \int_{\tau_k(r-1, \cdot)}^{r-1} S_k(t_1) \Gamma_k(t_1, r-1, \cdot) dt_1 \right]$$

# Firing rates

Computations have been done using the INRIA Pranas software, B. Cessac et al, *Frontiers in Neuroinformatics*, Vol 11, page 49, (2017).

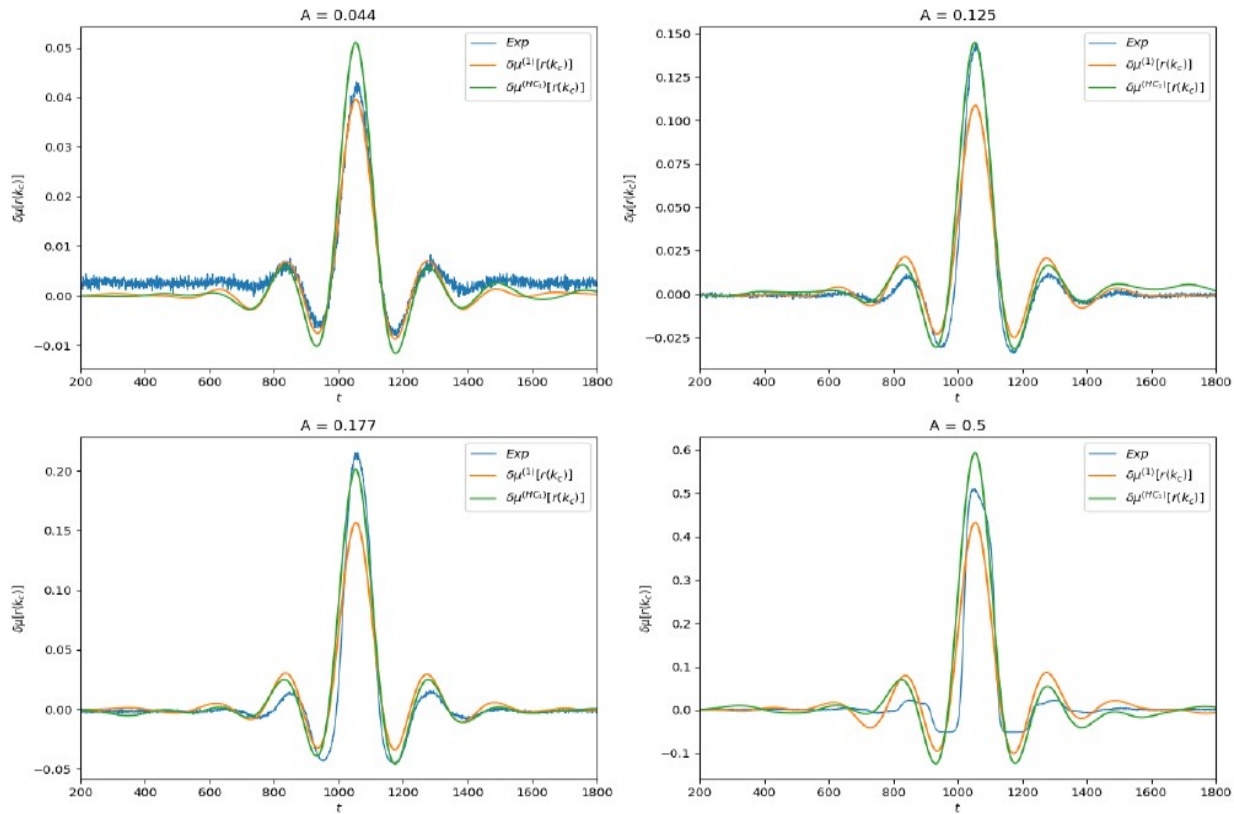


Figure: Linear response of  $f(\omega, n) = \omega_{k_c}(n)$  for different values of stimulus amplitude  $A$ .

# Higher order observable

Computations have been done using the INRIA Pranas software, B. Cessac et al, *Frontiers in Neuroinformatics*, Vol 11, page 49, (2017).

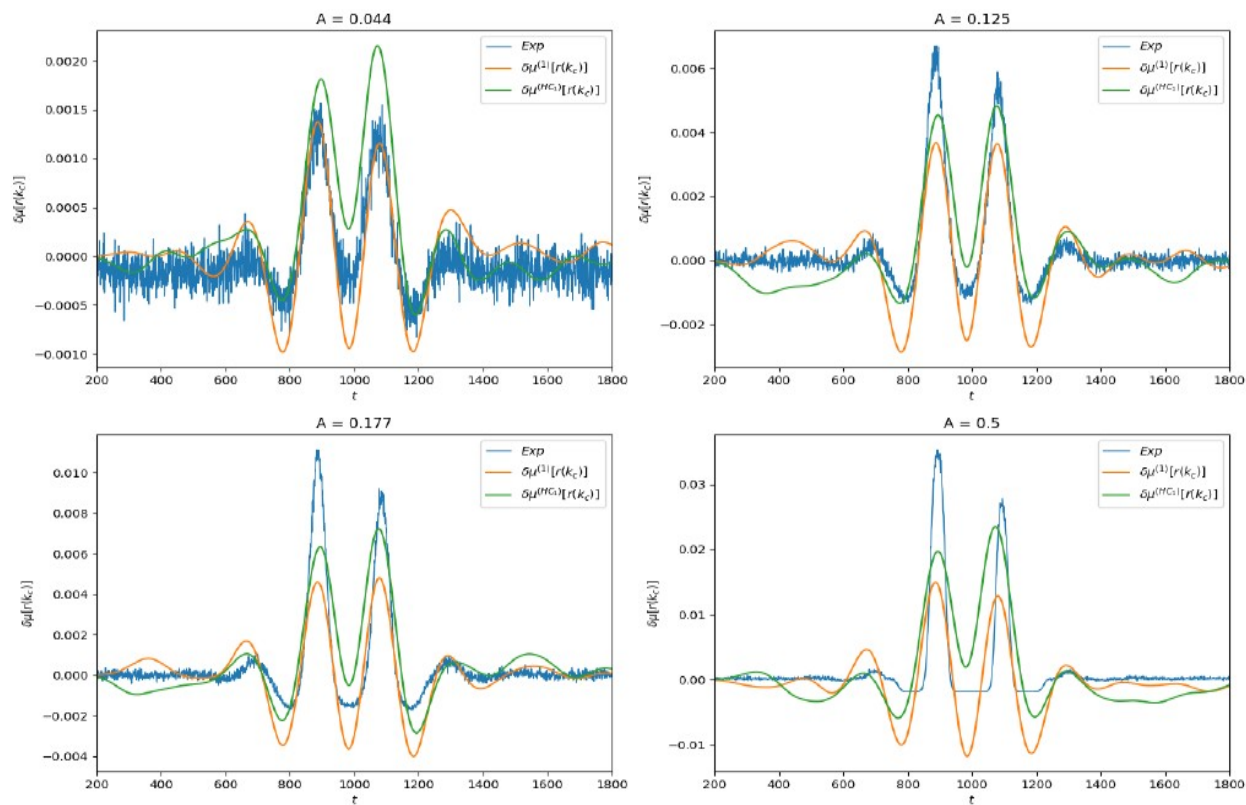


Figure: Linear response of the observable  $f(n, \omega) = \omega_{k_c - 2}(n - 3)\omega_{k_c}(n)$ .

# Conclusions

- Visual entries are neither stationary, nor spatially regular.
- The « longitudinal » pathways PhotoReceptors => Bipolar cells => Ganglion cells efficiently encode the visual information into parallel flows.
- Lateral connectivity (Horizontal and Amacrine) cells contributes to visual encoding as well. Horizontal cells contribute to the shaping of spatio-temporal receptive fields. What is the role of Amacrine cells ?
- On the basis of biophysical modelling + mathematical analysis we found that Amacrine cells may generate, from the non stationary stimulus, spatio-temporal correlations (waves) contributing to better deciphering a visual scene (anticipation).
- This is very different from the « efficient coding » paradigm where longitudinal pathways are assumed to be independent. We switch from a paradigm of « rate » decoding to « correlations » decoding.

Thanks 😊