

# Introduction to mesoscopic models of visual cortical structures

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M2 MVA / M2 Maths-Bio

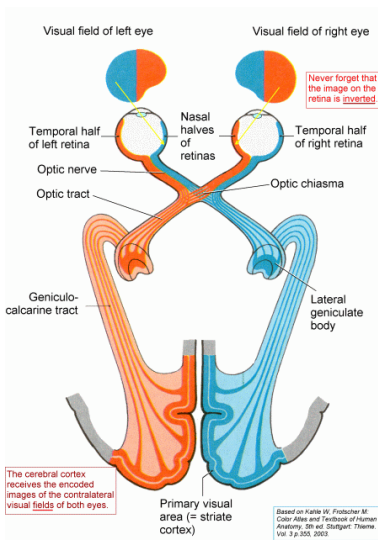
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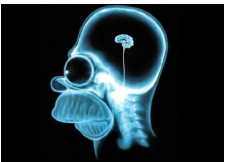
# Outline

- 1 Structure of primary visual cortex (V1)
  - Anatomy
  - Retinotopy
  - Cortical layers organization
- 2 Functional architecture of V1
- 3 Neural fields models
- 4 Applications

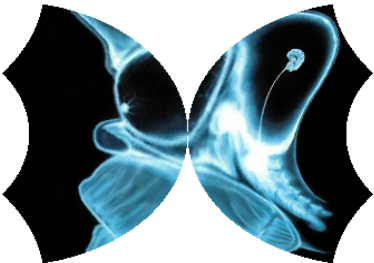
# Anatomy of the visual cortex



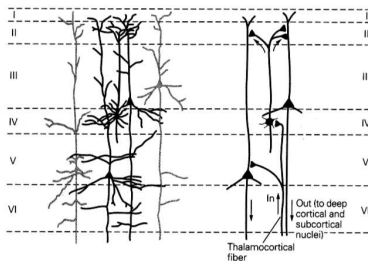
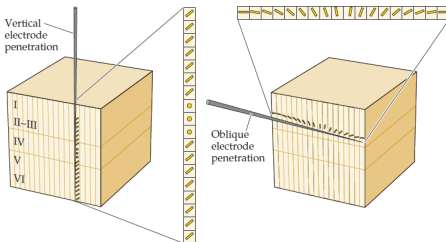
# Retinotopy



$$f(z) = \log \left( \frac{z+0.33}{z+6.66} \right)$$



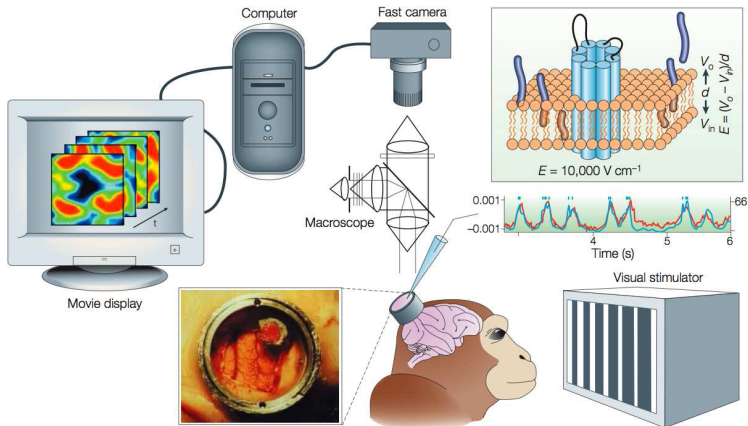
# Cortical layers organization of V1 (Purves et al)



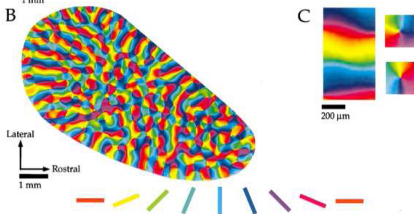
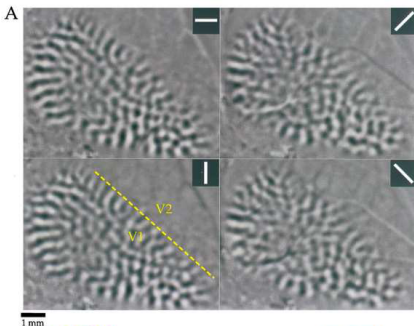
# Outline

- 1 Structure of primary visual cortex (V1)
- 2 Functional architecture of V1
  - Optical imaging
  - Hypercolumnar structure of the primary visual cortex
  - Lateral connections
  - Other cortical maps
- 3 Neural fields models
- 4 Applications

# Optical imaging: methods

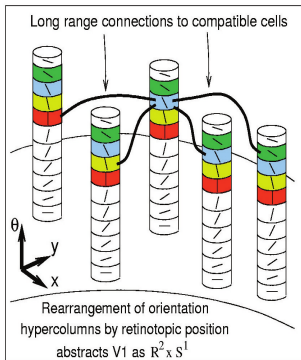
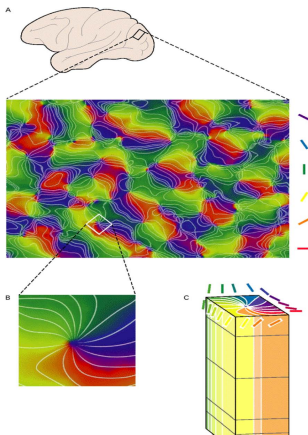


# Results for orientation (Bosking et al 97)





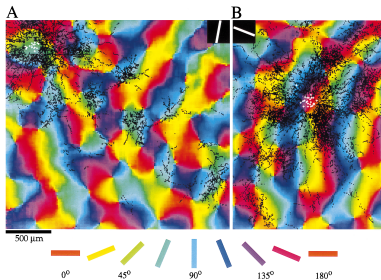
# Hypercolumns of orientation in V1



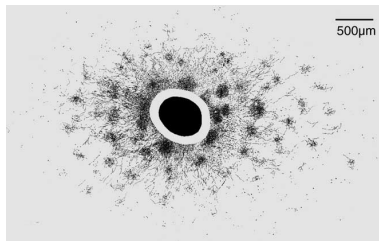
**b**

Ben Sahar and Zucker 2004.

# Intra-cortical connections in V1: anisotropy?

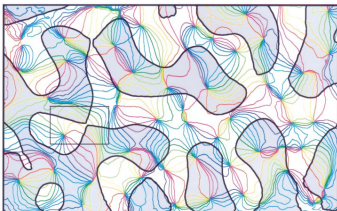


Bosking et al 97 (Tree shrew).

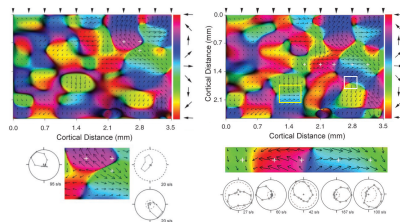


Lund et al 03 (Macaque).

# Other cortical maps: ocular dominance, direction of motion etc...



Hubener et al 97 (Cat).



Diogo et al 03 (area MT of Monkey).

# Visual cortex: summary

- The cortex is a folded sheet of width 2cm.
- It has a layered structure (6) and is retinotopically organized (the mapping between the visual field and the cortical coordinates is approximatively log-polar).
- From the LGN the information is transmitted to the visual cortex (back of the head) mostly to the area V1.
- Where does the information go after V1? Mainly: V2,V4, MT, MST... (there are 30 visual areas that are different by their architecture, connectivity or functional properties)
- V1 is spatially organized in columns that share the same preferred functional properties (orientation, ocular dominance, spatial frequency, direction of motion, color etc...)
- Existence of particular points: pinwheels (all orientations are represented).
- Local excitatory/inhibitory connections are homogeneous, whereas long-range connections (mainly excitatory neurons) are patchy, modulatory and anisotropic.

# Outline

- 1 Structure of primary visual cortex (V1)
- 2 Functional architecture of V1
- 3 Neural fields models
  - Local models
  - Continuum models
  - General framework
- 4 Applications

# Local models for $n$ interacting neural masses

- each neural population  $i$  is described by its **average membrane potential**  $V_i(t)$  or by its **average instantaneous firing rate**  $\nu_i(t)$  with  $\nu_i(t) = S_i(V_i(t))$ , where  $S_i$  is sigmoidal:

$$S_i(x) = \frac{S_{im}}{1 + e^{-\sigma_i(x - \theta_i)}}$$

$\sigma_i$  is the nonlinear gain and  $\theta_i$  is the threshold,

- a single action potential from neurons in population  $j$ , is seen as a **post-synaptic potential**  $PSP_{ij}(t - s)$  by neurons in population  $i$  ( $s$  is the time of the spike hitting the synapse and  $t$  the time after the spike)
- the number of spikes arriving between  $t$  and  $t + dt$  is  $\nu_j(t)dt$ , then the average membrane potential of population  $i$  is:

$$V_i(t) = \sum_j \int_{t_0}^t PSP_{ij}(t - s) S_j(V_j(s)) ds$$

$$\nu_i(t) = S_i \left( \sum_j \int_{t_0}^t PSP_{ij}(t - s) \nu_j(s) ds \right)$$

# The voltage-based model

- post-synaptic potential has the same shape no matter which presynaptic population caused it, this leads to

$$PSP_{ij}(t) = w_{ij}PSP_i(t)$$

$w_{ij}$  is the average strength of the post-synaptic potential and if  $w_{ij} > 0$  (resp.  $w_{ij} < 0$ ) population  $j$  excites (resp. inhibits) population  $i$

- if we assume that  $PSP_i(t) = e^{-t/\tau_i} H(t)$  or equivalently

$$\tau_i \frac{dPSP_i(t)}{dt} + PSP_i(t) = \delta(t)$$

we end up with a system of ODEs:

$$\tau_i \frac{dV_i(t)}{dt} + V_i(t) = \sum_j w_{ij} S_j(V_j(t)) + I_{ext}^i(t).$$

We rewrite in vector form:

$$\dot{\mathbf{V}}(t) = -\mathbf{L}\mathbf{V}(t) + \mathbf{W}\mathbf{S}(\mathbf{V}(t)) + \mathbf{I}_{ext}(t)$$

# The activity-based model

- the same shape of a PSP depends only on the presynaptic cell, this leads to

$$PSP_{ij}(t) = w_{ij}PSP_j(t)$$

- we also suppose that  $PSP_j(t) = e^{-t/\tau_j}H(t)$  and we end up with a system of ODEs:

$$\tau_i \frac{dA_i(t)}{dt} + A_i(t) = S_i \left( \sum_j w_{ij}A_j(t) + I_{ext}^i(t) \right).$$

We rewrite in vector form:

$$\dot{\mathbf{A}}(t) = -\mathbf{L}\mathbf{A}(t) + \mathbf{S}(\mathbf{W}\mathbf{A}(t) + \mathbf{I}_{ext}(t))$$



# Neural fields models

- idea: combine local models to form a continuum of neural fields
- $\Omega \subset \mathbb{R}^d$ ,  $d = 1, 2$  is a part of the cortex
- we note  $\mathbf{V}(\mathbf{r}, t)$  (resp.  $\mathbf{A}(\mathbf{r}, t)$ ) the state vector at point  $\mathbf{r}$  of  $\Omega$
- we introduce the  $n \times n$  matrix function  $\mathbf{W}(\mathbf{r}, \mathbf{r}', t)$

## Voltage neural fields equation

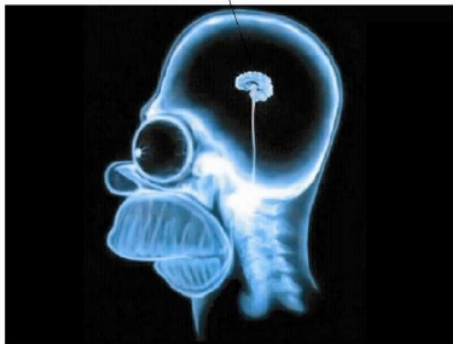
$$\frac{d\mathbf{V}(\mathbf{r}, t)}{dt} = -\mathbf{L}\mathbf{V}(\mathbf{r}, t) + \int_{\Omega} \mathbf{W}(\mathbf{r}, \mathbf{r}', t) \mathbf{S}(\mathbf{V}(\mathbf{r}', t)) d\mathbf{r}' + \mathbf{I}_{\text{ext}}(\mathbf{r}, t) \quad (1)$$

## Activity neural fields equation

$$\frac{d\mathbf{A}(\mathbf{r}, t)}{dt} = -\mathbf{L}\mathbf{A}(\mathbf{r}, t) + \mathbf{S} \left( \int_{\Omega} \mathbf{W}(\mathbf{r}, \mathbf{r}', t) \mathbf{A}(\mathbf{r}', t) d\mathbf{r}' + \mathbf{I}_{\text{ext}}(\mathbf{r}, t) \right) \quad (2)$$

# Remarks

$$\tau_s \frac{\partial a(x, t)}{\partial t} = -a(x, t) + \int W(x|y) f(a(y, t)) dy$$



# Remarks

- when  $d = 1$ , most widely studied because of its relative mathematical simplicity but of limited biological interest
- when  $d = 2$ , the more interesting from a biological point of view (the thickness is neglected), received less interest because of the computational difficulty
- unbounded domains:  $\Omega = \mathbb{R}^d$  raise some mathematical questions and unrealistic (always used)
- number of populations:  $n = 1$  or 2
- the sigmoid function can be approximated by a Heaviside function
- $\mathbf{W}(\mathbf{r}, \mathbf{r}', t)$  is often chosen symmetric and translation invariant:

$$\mathbf{W}(\mathbf{r}, \mathbf{r}', t) = \mathbf{W}(\mathbf{r} - \mathbf{r}', t)$$

- in the case  $n = d = 1$ , the connectivity function has a “Mexican-hat shape”
- features can be taken into account:  $\mathbf{V}(\mathbf{r}, \theta, t)$  in the case of orientation

# Cauchy problem

$\Omega$  is an open bounded set of  $\mathbb{R}^d$ . We define  $\mathcal{F} = L^2(\Omega, \mathbb{R}^n)$  (Hilbert space). We can rewrite equation (1) in a compact form (function  $\mathbf{V}(t)$  is thought of as a mapping  $\mathbf{V} : \mathbb{R}^+ \rightarrow \mathcal{F}$ ):

$$\begin{cases} \frac{d\mathbf{V}}{dt} &= -\mathbf{L}\mathbf{V} + \mathbf{R}(t, \mathbf{V}) & t > 0 \\ \mathbf{V}(0) &= \mathbf{V}_0 \in \mathcal{F} \end{cases} \quad (3)$$

The nonlinear operator  $\mathbf{R}$  is defined by:

$$\mathbf{R}(t, \mathbf{V}(\mathbf{r}, t)) = \int_{\Omega} \mathbf{W}(\mathbf{r}, \mathbf{r}', t) \mathbf{S}(\mathbf{V}(\mathbf{r}', t)) d\mathbf{r}' + \mathbf{I}_{\text{ext}}(\mathbf{r}, t) \quad \forall \mathbf{r} \in \Omega$$

## Theorem (Existence and uniqueness of a solution)

*If the following two hypotheses are satisfied:*

- ①  $\mathbf{W} \in \mathcal{C}(\mathbb{R}^+, L^\infty(\Omega^2, \mathbb{R}^n))$  and is uniformly bounded in time,
- ② the external input  $\mathbf{I}_{\text{ext}} \in \mathcal{C}(\mathbb{R}^+, \mathcal{F})$

*then for any function  $\mathbf{V}_0 \in \mathcal{F}$  there is a unique solution  $\mathbf{V}$  defined on  $\mathbb{R}^+$  and continuously differentiable of the initial value problem (3).*

# Elements of proof

- 1 for all  $t > 0$ ,  $\mathbf{R}(t, \cdot) : \mathcal{F} \rightarrow \mathcal{F}$  (well-posedness of the problem)
- 2  $\mathbf{R} : (t, \mathbf{V}) \rightarrow \mathbf{R}(t, \mathbf{V})$  is continuous in  $(t, \mathbf{V})$
- 3  $\|\mathbf{R}(t, \mathbf{V}_1) - \mathbf{R}(t, \mathbf{V}_2)\|_{\mathcal{F}} \leq DS_m \sup_{t \in \mathbb{R}^+} \|\mathbf{W}(t)\|_{\mathcal{F}} \|\mathbf{V}_1 - \mathbf{V}_2\|_{\mathcal{F}}$  for all  $t > 0$  and  $\mathbf{V}_1, \mathbf{V}_2 \in \mathcal{F}$ , where  $DS_m = \sup_{i=1 \dots n} \sup_{x \in \mathbb{R}} |S'_i(x)|$  (Lipschitz continuity of  $\mathbf{R}$  with respect to its second argument, uniformly with respect to the first)
- 4 application of the Cauchy Lipschitz theorem in Banach spaces

# More properties for the nonlinearity

## Lemma

If  $\mathbf{W} \in \mathcal{C}(\mathbb{R}^+, L^\infty(\Omega^2, \mathbb{R}^n))$ , then  $\mathbf{R}$  satisfies the following properties:

- ①  $\forall q \in \mathbb{N}$ ,  $\mathbf{R}(t, \cdot) \in \mathcal{C}^q(L^\infty(\Omega, \mathbb{R}^n), L^\infty(\Omega, \mathbb{R}^n))$  and  $D^q \mathbf{R}(t, \mathbf{V}_0) = \mathbf{W}(t) \mathbf{S}^{(q)}(\mathbf{V}_0)$
- ②  $\mathbf{R}(t, \cdot)$  is a compact operator for all  $t > 0$ .

- ①
  - if it exists:
 
$$D^q \mathbf{R}(t, \mathbf{V}_0)[U_1, \dots, U_q] = \mathbf{W}(t) (\mathbf{S}^{(q)}(\mathbf{V}_0)(U_1 \cdots U_q))$$
  - $D^q \mathbf{R}(t, \mathbf{V}_0)$  is well defined because  $U_1 \cdots U_q \in L^\infty(\Omega, \mathbb{R}^n)$
  -

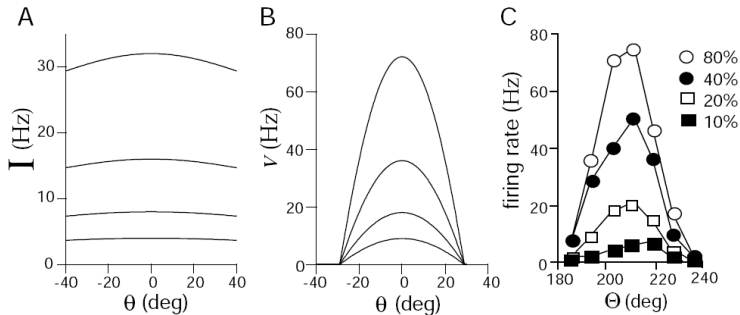
$$\begin{aligned} & \|D^q \mathbf{R}(t, \mathbf{V}_0)[U_1, \dots, U_q]\|_{L^\infty(\Omega, \mathbb{R}^n)} \\ & \leq |\Omega| \left\| \mathbf{W}(t) \mathbf{S}^{(q)}(\mathbf{V}_0) \right\|_{L^\infty(\Omega^2, \mathbb{R}^n)} \|U_1 \cdots U_q\|_{L^\infty(\Omega, \mathbb{R}^n)} \end{aligned}$$

- ② direct application of Arzelà-Ascoli theorem

# Outline

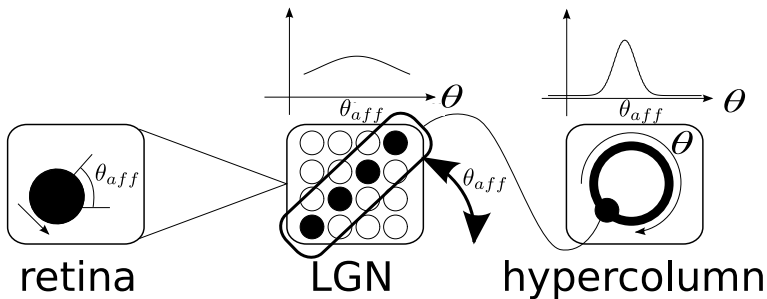
- 1 Structure of primary visual cortex (V1)
- 2 Functional architecture of V1
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- 4 Applications
  - Ring Model of orientation
  - Ermentrout-Cowan model of patterns formation
  - Geometric visual hallucinations

# Ring Model of orientation: facts





# Ring Model of orientation: mechanism



# Ring Model of orientation: equation

We consider the following equation:

$$\tau \frac{\partial V(\theta, t)}{\partial t} = -V(\theta, t) + \int_{-\pi/2}^{\pi/2} J(\theta - \theta') S(\mu V(\theta')) \frac{d\theta'}{\pi} + \epsilon I(\theta) \quad (4)$$

where  $\tau$  is a temporal synaptic constant ( $\tau = 1ms$ ),  $J(\theta - \theta')$  is a connectivity function (excitatory/inhibitory) and  $S$  is the sigmoidal function:

$$S(x) = \frac{1}{1 + \exp(-x + \kappa)},$$

$I(\theta)$  is an input coming from the LGN given by:

$$I(\theta) = 1 - \beta + \beta \cos(2(\theta - \theta_{aff}))$$

Without loss of generality we take  $\theta_{aff} = 0$ . Moreover, we take the simplest possible connectivity function:

$$J(\theta) = -1 + J_1 \cos(2\theta), \quad J_1 > 0$$

# Ermentrout-Cowan model

We consider the following equation:

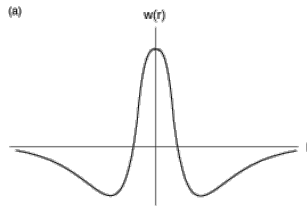
$$\tau \frac{\partial}{\partial t} a(\mathbf{r}, t) = -a(\mathbf{r}, t) + \int_{\mathbb{R}^2} w(\mathbf{r}|\mathbf{r}') S(\mu a(\mathbf{r}', t)) d\mathbf{r}' \quad (5)$$

where  $\tau$  is a temporal synaptic constant ( $\tau = 1ms$ ),  $w(\mathbf{r}|\mathbf{r}') = w(\|\mathbf{r} - \mathbf{r}'\|)$  is a connectivity function (excitatory/inhibitory) and  $S$  is the sigmoidal function:

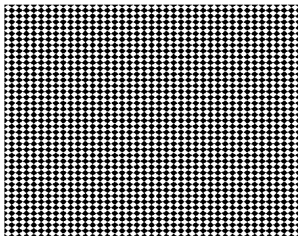
$$S(x) = \frac{1}{1 + \exp(-x + \kappa)} - \frac{1}{1 + \exp(\kappa)},$$

We choose a “Mexican-hat” connectivity function:

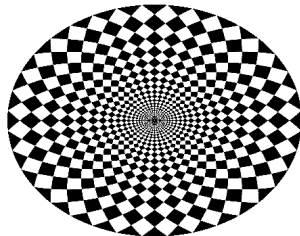
$$w(x) = \frac{A_1}{\sigma_1} e^{-\frac{x^2}{\sigma_1^2}} - \frac{A_2}{\sigma_2} e^{-\frac{x^2}{\sigma_2^2}} \quad (6)$$



# Patterns of the Ermentrout-Cowan model



V1



Visual field

# Bresslof-Cowan-Golubitsky-Thomas-Wiener model

We consider the following equation:

$$\tau \frac{\partial}{\partial t} a(\mathbf{r}, \theta, t) = -a(\mathbf{r}, \theta, t) + \int_{\mathbf{R}^2} \int_{-\pi/2}^{\pi/2} w(\mathbf{r}, \theta | \mathbf{r}', \theta') S(\mu a(\mathbf{r}', \theta', t)) d\mathbf{r}' \frac{d\theta'}{\pi} \quad (7)$$

with

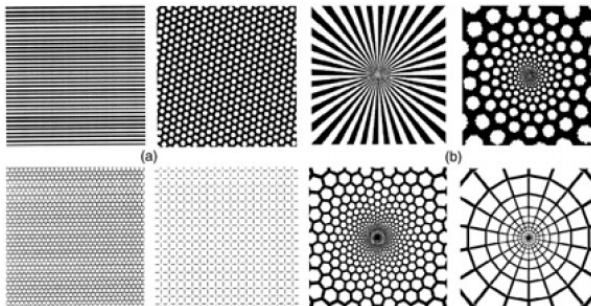
$$S(x) = \frac{1}{1 + \exp(-x + \kappa)} - \frac{1}{1 + \exp(\kappa)},$$

and

$$w(\mathbf{r}, \theta | \mathbf{r}', \theta') = J(\theta - \theta') \delta_{\mathbf{r}, \mathbf{r}'} + \beta(1 - \delta_{\mathbf{r}, \mathbf{r}'}) w_{lat}(\mathbf{r} - \mathbf{r}', \theta)$$

- for  $\beta = 0$ , we recover the Ring Model of orientation
- if  $a(\mathbf{r}, \theta, t)$  is independent of  $\theta$  we recover the Ermentrout-Cowan model
- we will try to infer some properties from the case  $\beta = 0$  to the case  $0 < \beta \ll 1$  and in the same time we will use similar method as for the Ermentrout-Cowan model

# Geometric visual hallucinations





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