Introduction to mesoscopic models of visual cortical structures

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Structure	of	primary	visual	cortex	(V1)

Neural fields models

Applications 0000000

Outline

1 Structure of primary visual cortex (V1)

- Anatomy
- Retinotopy
- Cortical layers organization
- 2 Functional architecture of V1
- 3 Neural fields models



Structure of primary visual cortex (V1) $\bullet \circ \circ$

Functional architecture of V1 000000

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Anatomy of the visual cortex



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Structure of primary visual cortex (V1) $\circ \bullet \circ$

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Retinotopy





Structure of primary visual cortex (V1) $\circ \circ \bullet$

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Cortical layers organization of V1 (Purves et al)



	primary		(V1)

Neural fields models

Applications

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

Functional architecture of V1 $\bullet 00000$

Neural fields models

Applications

Optical imaging: methods



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Neural fields models

Applications 0000000

Results for orientation (Bosking et al 97)



Functional architecture of V1

Neural fields models

Applications

Hypercolumns of orientation in V1



Functional architecture of V1

Neural fields models

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Hypercolumns of orientation in V1





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Ben Sahar and Zucker 2004.

Functional architecture of V1

Neural fields models

Applications

Intra-cortical connections in V1: anisotropy?



Bosking et al 97 (Tree shrew).

Functional architecture of V1

Neural fields models

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Intra-cortical connections in V1: anisotropy?



Bosking et al 97 (Tree shrew).



Lund et al 03 (Macaque).

Functional architecture of V1 $\circ \circ \circ \circ \circ \circ$

Neural fields models

Applications

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



Hubener et al 97 (Cat).

Functional architecture of V1 $\circ \circ \circ \circ \circ \circ$

Neural fields models

Applications

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



Hubener et al 97 (Cat).



Diogo et al 03 (area MT of Monkey).

Structure of primary visual cortex (V1) 000	Functional architecture of V1 ○○○○○●	Neural fields models	Applications 0000000
Visual cortex: summa	ry		

• The cortex is a folded sheet of width 2cm.

Structure of primary visual cortex (V	(1) Functional architecture of V1	Neural fields models	Applications
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Visual cortex: su	immary		

- 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).

Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields models	Applications
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- 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)

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- 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.

	primary		(V1)

Neural fields models

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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

Functional architecture of V1 000000 Neural fields models

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:

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

 σ_i is the nonlinear gain and θ_i is the threshold,

Functional architecture of V1 000000

Neural fields models

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post-synaptic potential PSP_{ij}(t - s) by neurons in population i (s is the
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Neural fields models

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 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 ν_j(t)dt, then the average membrane potential of population i is:

$$V_{i}(t) = \sum_{j} \int_{t_{0}}^{t} PSP_{ij}(t-s)S_{j}(V_{j}(s))ds$$
$$\nu_{i}(t) = S_{i}\left(\sum_{j} \int_{t_{0}}^{t} PSP_{ij}(t-s)\nu_{j}(s)ds\right)$$

Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields models	Applications
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The voltage-based me	odel		

• 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. inhibts) population i

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

$$au_i rac{dPSP_i(t)}{dt} + PSP_i(t) = \delta(t)$$

we end up with a system of ODEs:

$$au_i rac{dV_i(t)}{dt} + V_i(t) = \sum_j w_{ij}S_j(V_j(t)) + I^i_{\mathrm{ext}}(t).$$

We rewrite in vector form:

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

Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields models	Applications
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The activity-based m	odel		

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

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

Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields models	Applications
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The activity-based n	nodel		

• 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:

$$au_i rac{dA_i(t)}{dt} + A_i(t) = S_i\left(\sum_j w_{ij}A_j(t) + I^i_{ext}(t)\right).$$

We rewrite in vector form:

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Structure of primary visual cortex (V1) 000	Functional architecture of V1 000000	Neural fields models	Applications 0000000
Neural fields models			

• idea: combine local models to form a continuum of neural fields

Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields models	Applications
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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

Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields models	Applications
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Neural fields models			

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- $\Omega \subset \mathbb{R}^d$, d = 1, 2 is a part of the cortex
- we note $V(\mathbf{r}, t)$ (resp. $A(\mathbf{r}, t)$) the state vector at point \mathbf{r} of Ω

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- we note $V(\mathbf{r}, t)$ (resp. $\mathbf{A}(\mathbf{r}, t)$) the state vector at point \mathbf{r} of Ω
- we introduc the $n \times n$ matrix function $W(\mathbf{r}, \mathbf{r}', t)$

Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields models	Applications
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Voltage neural fields equation

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

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Neural fields models			

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Activity neural fields equation

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

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Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields models	Applications
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Remarks			

• when *d* = 1, most widely studied because of its relative mathematical simplicity but of limited biological interest

Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields models	Applications
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Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields models	Applications
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Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields models
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Applications 0000000

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Neural fields models

Applications 0000000

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Neural fields models

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

Structure of primary visual cortex (V1)	Functional architecture of V1

Neural fields models

Applications

Cauchy problem

 Ω 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 $\mathbf{V} : \mathbb{R}^+ \to \mathcal{F}$):

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

The nonlinear operator **R** is defined by:

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

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Neural fields models

Applications

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Theorem (Existence and uniqueness of a solution)

If the following two hypotheses are satisfied:

($\mathbf{W} \in \mathcal{C}(\mathbb{R}^+, L^{\infty}(\Omega^2, \mathbb{R}^n))$ and is uniformly bounded in time,

2 the external input $I_{ext} \in C(\mathbb{R}^+, \mathcal{F})$

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).

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Elements of proof

1 for all t > 0, $\mathbf{R}(t, \cdot) : \mathcal{F} \to \mathcal{F}$ (well-posedness of the problem)

Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields mode
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Elements of proof

- 1 for all t > 0, $\mathbf{R}(t, \cdot) : \mathcal{F} \to \mathcal{F}$ (well-posedness of the problem)
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	primary		(V1)

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- ③ $\|\mathbf{R}(t, \mathbf{V}_1) \mathbf{R}(t, \mathbf{V}_2)\|_{\mathcal{F}} \le DS_m \sup_{t \in \mathbb{R}^+} \|\mathbf{W}(t)\|_{\mathcal{F}} \|\mathbf{V}_1 \mathbf{V}_2\|_{\mathcal{F}}$ for all t > 0and $\mathbf{V}_1, \mathbf{V}_2 \in \mathcal{F}$, where $DS_m = \sup_{i=1...n} \sup_{x \in \mathbb{R}} |S'_i(x)|$ (Lipschitz continuity of **R** with respect to its second argument, uniformly with respect to the first)

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- application of the Cauchy Lipschitz theorem in Banach spaces

Functional architecture of V1 $_{\rm OOOOOO}$

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More properties for the nonlinearity

Lemma

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

Functional architecture of V1 $_{\rm OOOOOO}$

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1
$$\forall q \in \mathbb{N}, \mathbf{R}(t, \cdot) \in C^q(L^{\infty}(\Omega, \mathbb{R}^n), L^{\infty}(\Omega, \mathbb{R}^n))$$
 and $D^q \mathbf{R}(t, \mathbf{V}_0) = \mathbf{W}(t) \mathbf{S}^{(q)}(\mathbf{V}_0)$

Functional architecture of V1 $_{\rm OOOOOO}$

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$$\begin{array}{l} \textbf{9} \quad \forall q \in \mathbb{N}, \, \textbf{R}(t, \cdot) \in \mathcal{C}^{q}(L^{\infty}(\Omega, \mathbb{R}^{n}), L^{\infty}(\Omega, \mathbb{R}^{n})) \text{ and} \\ D^{q}\textbf{R}(t, \textbf{V}_{0}) = \textbf{W}(t)\textbf{S}^{(q)}(\textbf{V}_{0}) \end{array}$$

2 $\mathbf{R}(t, \cdot)$ is a compact operator for all t > 0.

• if it exists:

$$D^{q}\mathbf{R}(t, \mathbf{V}_{0})[U_{1}, \cdots, U_{q}] = \mathbf{W}(t) \left(\mathbf{S}^{(q)}(\mathbf{V}_{0})(U_{1} \cdots U_{q})\right)$$
• $D^{q}\mathbf{R}(t, \mathbf{V}_{0})$ is well defined because $U_{1} \cdots U_{q} \in L^{\infty}(\Omega, \mathbb{R}^{n})$
•
$$\|D^{q}\mathbf{R}(t, \mathbf{V}_{0})[U_{1}, \cdots, U_{q}]\|_{L^{\infty}(\Omega, \mathbb{R}^{n})}$$

$$\leq |\Omega| \left\|\mathbf{W}(t)\mathbf{S}^{(q)}(\mathbf{V}_{0})\right\|_{L^{\infty}(\Omega^{2}, \mathbb{R}^{n})} \|U_{1} \cdots U_{q}\|_{L^{\infty}(\Omega, \mathbb{R}^{n})}$$

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1

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

$$\forall q \in \mathbb{N}, \, \mathsf{R}(t, \cdot) \in \mathcal{C}^{q}(L^{\infty}(\Omega, \mathbb{R}^{n}), L^{\infty}(\Omega, \mathbb{R}^{n})) \text{ and } \\ D^{q}\mathsf{R}(t, \mathsf{V}_{0}) = \mathsf{W}(t)\mathsf{S}^{(q)}(\mathsf{V}_{0})$$

2 $\mathbf{R}(t, \cdot)$ is a compact operator for all t > 0.

• if it exists:

$$D^{q}\mathbf{R}(t, \mathbf{V}_{0})[U_{1}, \cdots, U_{q}] = \mathbf{W}(t) \left(\mathbf{S}^{(q)}(\mathbf{V}_{0})(U_{1} \cdots U_{q})\right)$$
• $D^{q}\mathbf{R}(t, \mathbf{V}_{0})$ is well defined because $U_{1} \cdots U_{q} \in L^{\infty}(\Omega, \mathbb{R}^{n})$
•
$$\|D^{q}\mathbf{R}(t, \mathbf{V}_{0})[U_{1}, \cdots, U_{q}]\|_{L^{\infty}(\Omega, \mathbb{R}^{n})}$$

$$\leq |\Omega| \left\|\mathbf{W}(t)\mathbf{S}^{(q)}(\mathbf{V}_{0})\right\|_{L^{\infty}(\Omega^{2}, \mathbb{R}^{n})} \|U_{1} \cdots U_{q}\|_{L^{\infty}(\Omega, \mathbb{R}^{n})}$$

2 direct application of Arzelà-Ascoli theorem

	primary		(V1)

Neural fields models

Applications

Outline

1 Structure of primary visual cortex (V1)

- 2 Functional architecture of V1
- 3 Neural fields models
- Applications
 - Ring Model of orientation
 - Ermentrout-Cowan model of patterns formation
 - Geometric visual hallucinations

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Ring Model of orientation: facts



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Ring Model of orientation: mechanism



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Ring Model of orientation: equation

We consider the following equation:

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

where τ is a temporal synaptic contanst ($\tau = 1ms$), $J(\theta - \theta')$ 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:

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

Structure of primary visual cortex (V1)	Functional architecture of V1	Neural fields models	Applications
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Ermentrout-Cowan model

We consider the following equation:

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

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

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

We choose a "Mexican-hat" connectivity function:



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Patterns of the Ermentrout-Cowan model





V1

Visual field

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Bresslof-Cowan-Golubitsky-Thomas-Wiener model

We consider the following equation:

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

Functional architecture of V1 $_{\rm OOOOOO}$

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Geometric visual hallucinations



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