Orientation Selectivity in Random Networks

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Orientation selectivity in cat, monkey V1

**Cat**

V1 physiology: orientation selectivity

Orientation map in cat

Ringach et al 2002

**Monkey**

Drifting Grating

Ohki and Reid, 2007
Convergence of multiple untuned LGN inputs generate orientation selective excitation of Layer 4 neurons.

Thalamic projections to the cortex are organized.

Recurrent connectivity in cortex is feature specific.

Excitatory neurons with similar preferred orientation have higher probability to interact.

Orientation preference mapped across cortex.
Mechanism underlying OS in cortex of cat and monkey

Preferred orientations DO NOT depend on the contrast or on stimulus spatial frequency

Anderson et al 2000

Webster and De Valois, 1985
Mechanism underlying OS in cortex of cat and monkey

Preferred orientations DO NOT depend on the stimulus spatial frequency

Cells in V1 are selective AND code for orientation

Webster and De Valois, 1985
Orientation selectivity in rodent V1

Niell and Stryker, 2008

Mouse V1

Pattadkal and Priebe, unpublished

\[ OSI = \frac{\sqrt{\sum R(\theta) \sin 2\theta}^2 + \sum R(\theta) \cos 2\theta)^2}{\sum R(\theta)} \]

Niell and Stryker, 2008

Salt & pepper organization, Rat V1

Ohki and Reid, 2007

Niell and Stryker, 2008
Mechanism underlying orientation selectivity in rodent V1?

“The mixed salt-and-pepper organization of preferred orientation in rodents [...] argues for specific connectivity between neurons”

(Ohki and Reid, 2007)
Selectivity present in mouse at eye opening

- At eye opening: Neurons are selective to orientation; EE connectivity is non-specific.

- After critical period: Specificity in the EE connectivity

Ko et al, 2013
Elongated receptive fields in LGN (adults)

Piscopo et al, 2013; Scholl et al, 2013; Zhao et al. 2013

Zhao et al, 2013
The question

• Is random organization sufficient to account for orientation selectivity observed in the LGN – Layer 4 – Layer 2/3?

• What are the consequences of this organization from the point of view of selectivity and coding?
Outline

• Computational model LGN+V1
• Validation in terms of the properties of the thalamic input
• Selectivity properties of V1 cells
• L4: 2-D network of conductance-based \( N_E = 19600, \ N_I = 4900 \) neurons. 1mm\(^2\)= 60°\(\times\)60° of visual field (Kalatsky & Stryker, 2003).
• Recurrent connectivity: random with footprint \( \sigma_{\text{rec}} \) and mean number of connections per neurons =500.

• LGN: \( N_L = 10000 \) stochastically spiking Neurons connected randomly to L4 cells. Footprint \( \sigma_{\text{FF}} \). Average K inputs from LGN per L4 neuron.

• LGN receptive fields:
Results 1

Properties of the thalamic input
The thalamic excitation: average tuning

- Thalamic input can be measured with optogenetics
- Blocking activity of pyramidal neurons

Lien & Scanziani, 2013

Liu et al, 2011
The thalamic excitation: average tuning

- Circular LGN RFs, linear regime
- OSI of $F_0$ and $F_1$ components of the LGN input to L4 can be evaluated analytically (if $K$ is large)
- $F_0$ component: OSI =0.
- $F_1$ component: depends on $\sigma_{FF}/\lambda$ and very weakly on $K$, the number of LGN inputs per cell, $K$

For $\sigma_{FF}/\lambda > 0.2$: mean OSI $\sim 0.2$
The F1 component of the thalamic excitation is tuned

\[ K = 25 \]

\[ \sigma_{FF}/\lambda = 0.25 \]
Distribution of the OSIs

\[ \sigma_{FF} / \lambda = 0.25 \]

\[ \sigma_{FF} / \lambda = 0.5 \]
Results 2

What happens if LGN cells are orientation selective?
Orientation tuning in mouse LGN

Zhao et al, 2013

Piscopo et al, 2013; Scholl et al, 2013; Zhao et al. 2013; Kondo & Ohki, 2015; Sun et al, 2015...
In the model LGN neurons are orientation selective

$\lambda = 28^\circ$ i.e spatial frequency=0.035 cpd
Selectivity of the thalamic excitation vs. receptive field elongation

Same aspect ratio for all receptive fields
Selectivity of the thalamic excitation vs. grating spatial frequency

Lien & Scanziani, 2013
Thalamic excitation to mouse V1: strength and selectivity

- OSI of LGN inputs: $F_0 = 0.03$; $F_1 = 0.23$ (drifting gratings; spatial freq. = 0.04 cpd)

- ON/OFF subregions of LGN inputs overlap and offset (flashed stimuli)

Lien & Scanziani, 2013

Adult mouse
Organisation of ON/OFF subregions of the thalamic excitation

Mean offset = 5 deg

5 degrees

Mean offset = 5 deg
Results 3

Orientation tuning of Layer 4 neurons in the model
Layer 4 neurons are tuned to orientation

Examples of tuning curves

Pattadkal and Priebe, unpublished
Results 4

Do you have a prediction?

Is the prediction verified experimentally?
Prediction: preferred orientation depends on spatial frequency ...

\[
cc = \frac{\sum_{i,j} \sin(PO_i - PO_j) \sin(PO'_i - PO'_j)}{\sqrt{\sum_{i,j} \sin(PO_i - PO_j)^2 \sum_{i,j} \sin(PO'_i - PO'_j)^2}}
\]

\text{OSI} > 0.2
\text{cc} = 0.13

\text{OSI} > 0.2
\text{cc} = 0.02
PO depends on spatial frequency

Mouse
Drifting gratings
Calcium
Correlation is lost gradually
Correlation is lost gradually
Correlation is lost gradually

\[ cc = \frac{\sum_{i,j} \sin(PO_i - PO_j) \sin(PO'_i - PO'_j)}{\sqrt{\sum_{i,j} \sin(PO_i - PO_j)^2 \sum_{i,j} \sin(PO'_i - PO'_j)^2}} \]
Correlation is controlled by $\sigma_{FF}$
Rotation of TCs

Ca++ imaging

Hartley stimulus

Model
Elongated LGN RFs

PDF

Aspect Ratio

Firing Rate (Hz)

Stimulus Ori. (deg)

E6091 - 0.01 cpd

E6091 - 0.04 cpd

20°

25°
Correlation with elongated LGN RFs
Intuition for the loss of correlation

- L 4 neuron receives inputs from LGN neurons with random Pos
- The balanced dynamics cancels most of the non tuned component of the input
- Stimuli with different spatial frequency will activate different neurons in LGN
Conclusions

• Thalamic excitation: The observed orientation tuning and receptive field properties can be accounted for with random LGN to L4 projections. No specific organization is required.

• The resulting thalamic excitation gives rise to orientation selectivity in Layer 4.

• Prediction: the preferred orientation of the cells in V1 in response to a drifting grating changes dramatically with the spatial frequency of the grating.

• Prediction is verified experimentally.
Conclusions

• It is necessary to rethink this type of results:

Ko et al, 2013. *The emergence of functional microcircuits in visual cortex*

• What is the meaning of “functional microcircuits”?
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The mechanism of OS: the intuition

• If the connection strength \( g \propto \frac{T}{K_{ff}} \text{FF-Input} \) is of order \( T \) but its modulation is smaller by a factor \( \frac{1}{\sqrt{K_{ff}}} \). Therefore its tuning is negligible for large \( K_{ff} \).

• If \( g \propto \frac{T}{\sqrt{K_{ff}}} \), the modulation of \( \text{FF-Input} \) is of order \( T \) but its average is much larger.

• If the strength of the recurrent interactions are on the order of \( \frac{T}{\sqrt{K}} \) the total excitatory and inhibitory recurrent inputs into an L4 neuron have an average of order \( \sqrt{KT} \) while their modulations is of order \( T \).

• The average recurrent inhibition cancels the average (FF + recurrent) excitatory input. Therefore the average and the modulation of the net input are both of order \( T \).

The neuronal response is orientation selective with reasonable rates.
Organization of inputs to V1 cortical neurons in mouse

Dendritic calcium signals evoked by drifting gratings at different orientations

Jia et al., 2010
Orientation selectivity in mouse V1

Niell and Stryker, 2008
Cat /Monkey vs. Rat/Mouse V1

Ohki and Reid, 2007

Single-cell resolution orientation maps from (a) a pinwheel in cat visual cortex [42] and (b) rat visual cortex [38**] obtained with in vivo two-photon calcium imaging. One side is 300 μm. Cells are colored according to their preferred orientation. In (a), ~1000 cells from nine different depths are overlaid. Cells are arranged up to the very center of the pinwheel in cat visual cortex. In (b), cells in one depth of rat visual cortex are displayed. Even neighboring cells are tuned to different orientations.