Orientation Selectivity in Random Networks

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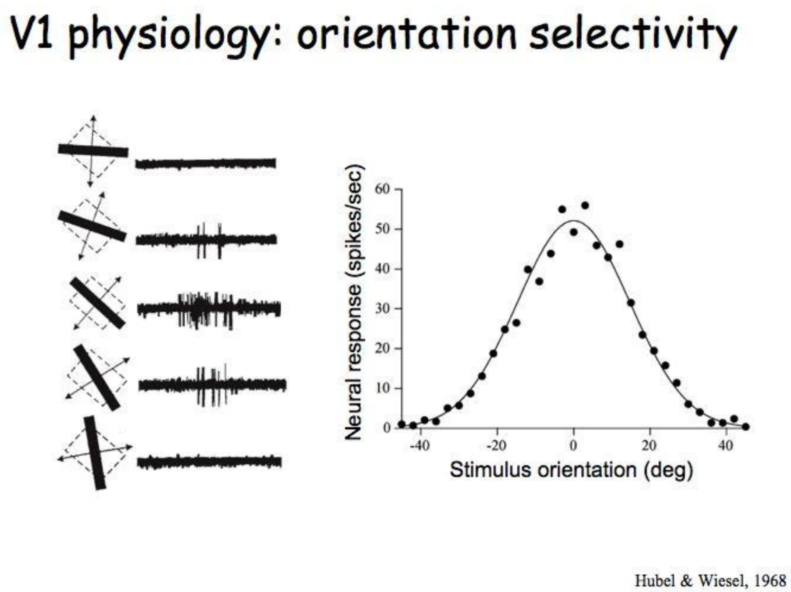
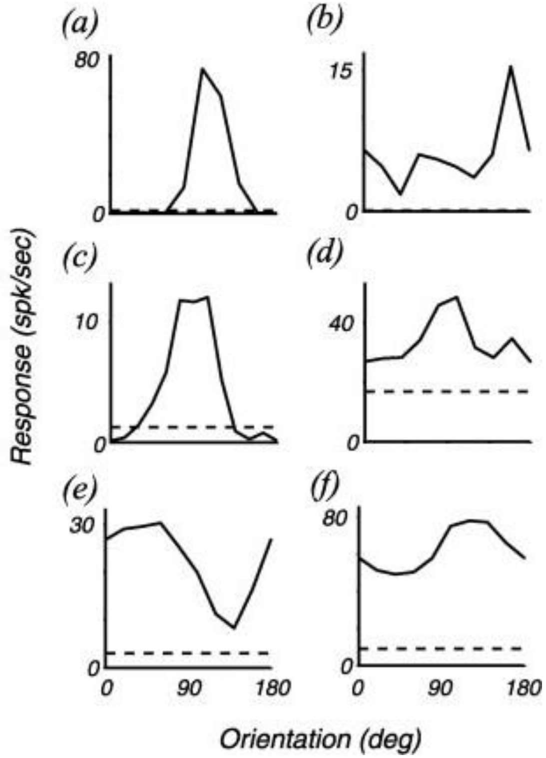
Orientation selectivity in cat, monkey V1

Cat

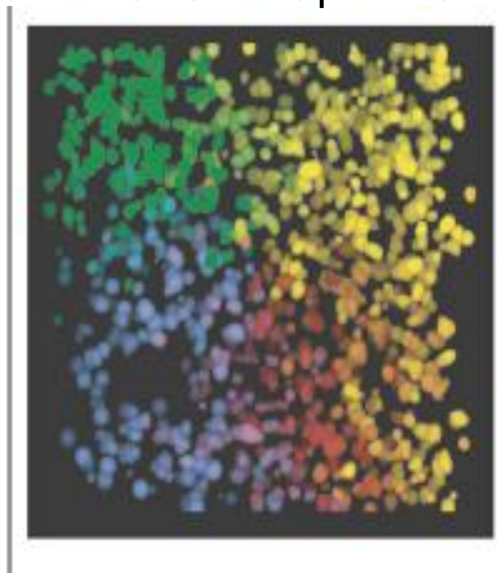


Monkey



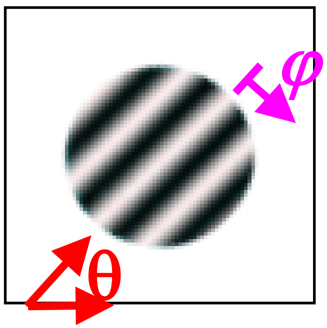
Ringach et al 2002

Orientation map in cat



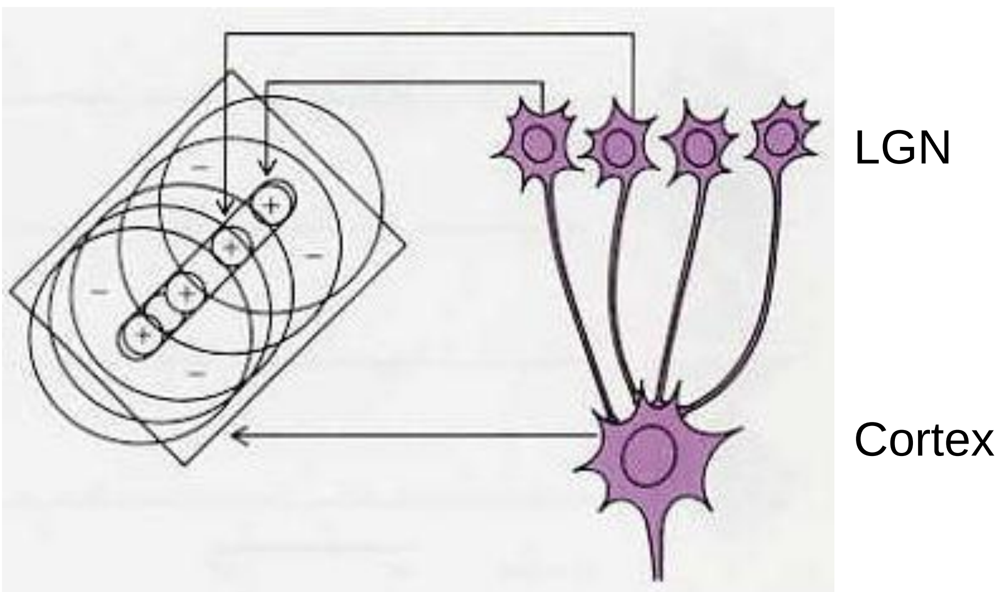
Ohki and Reid, 2007

Drifting Grating



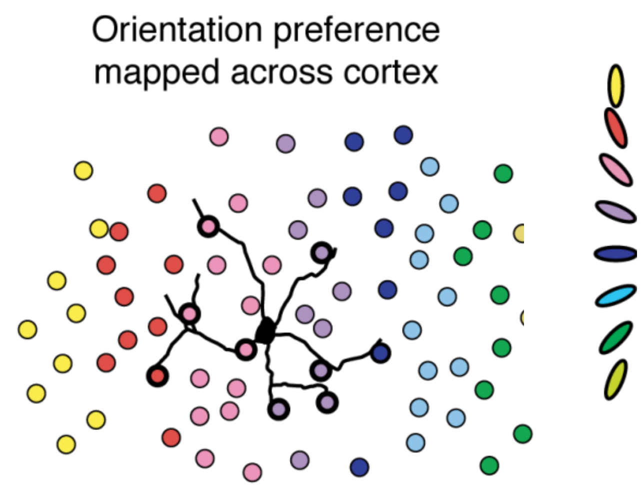
Mechanism underlying OS in cortex of cat and monkey

Thalamic projections to the cortex are **organized**



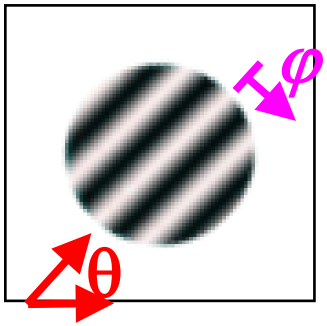
Convergence of multiple untuned LGN inputs generate orientation selective excitation of Layer 4 neurons

Recurrent connectivity in cortex is **feature specific**

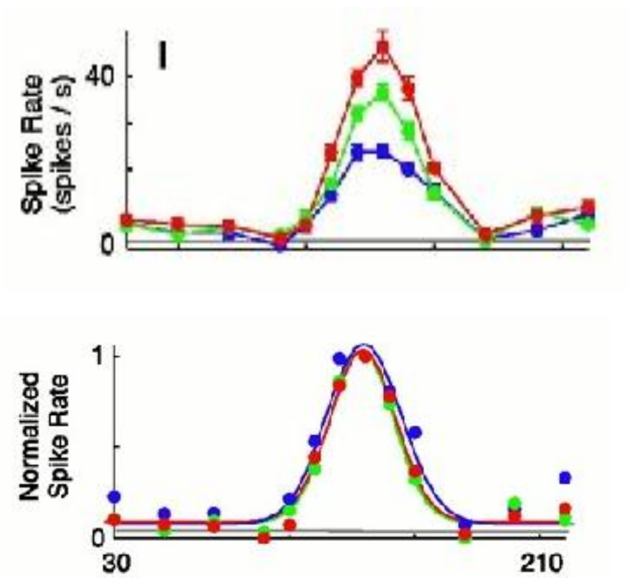


Excitatory neurons with similar preferred orientation have higher probability to interact

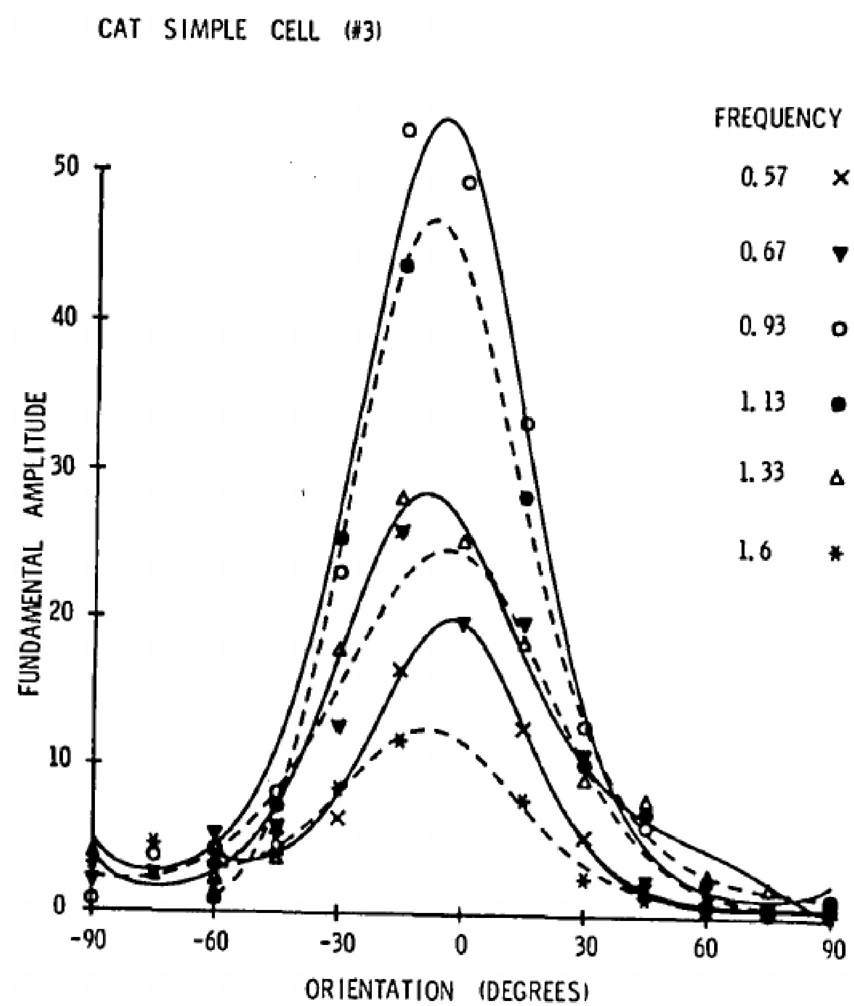
Mechanism underlying OS in cortex of cat and monkey



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



Anderson et al 2000

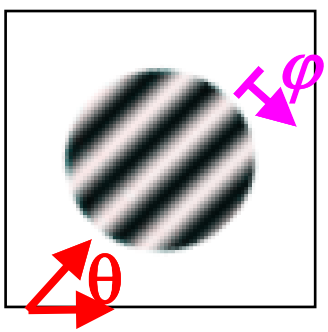


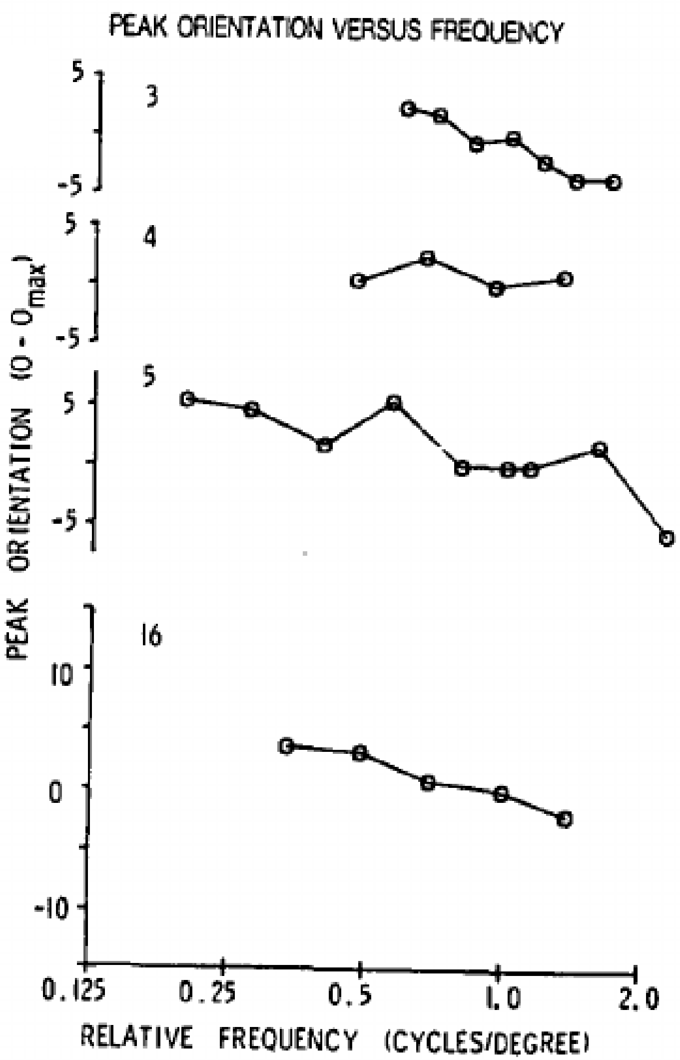
Webster and De Valois, 1985

Mechanism underlying OS in cortex of cat and monkey

Preferred orientations DO NOT depend on the stimulus spatial frequency

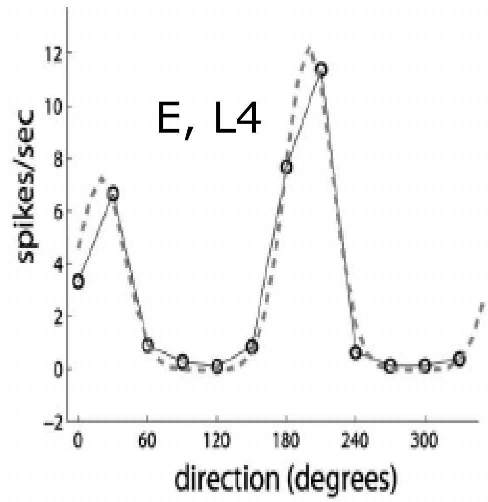
Cells in V1 are selective AND code for orientation

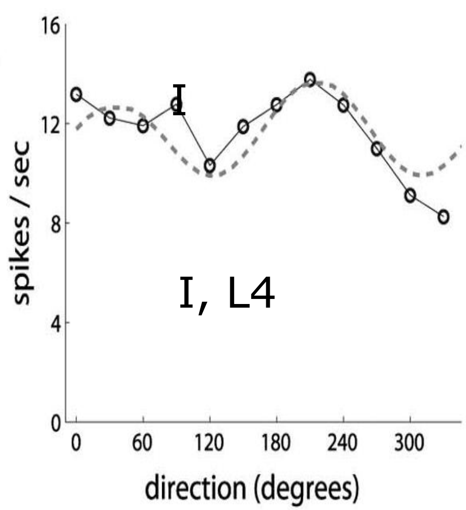




Webster and De Valois, 1985

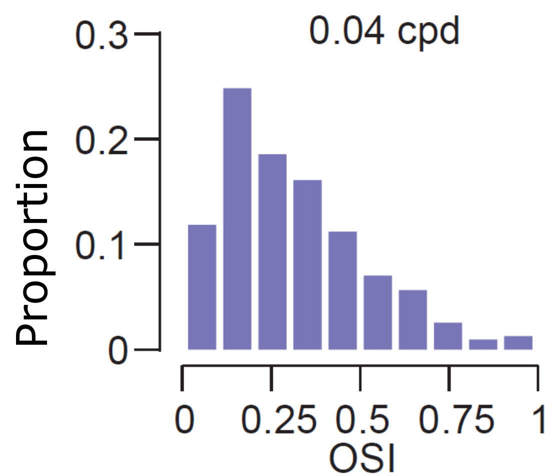
Orientation selectivity in rodent V1





Niell and Stryker, 2008

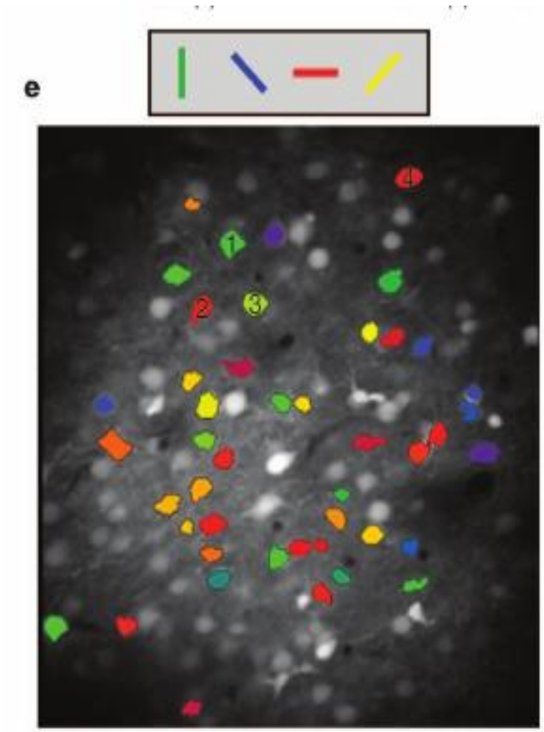
Mouse V1



Pattadkal and Priebe, unpublished

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

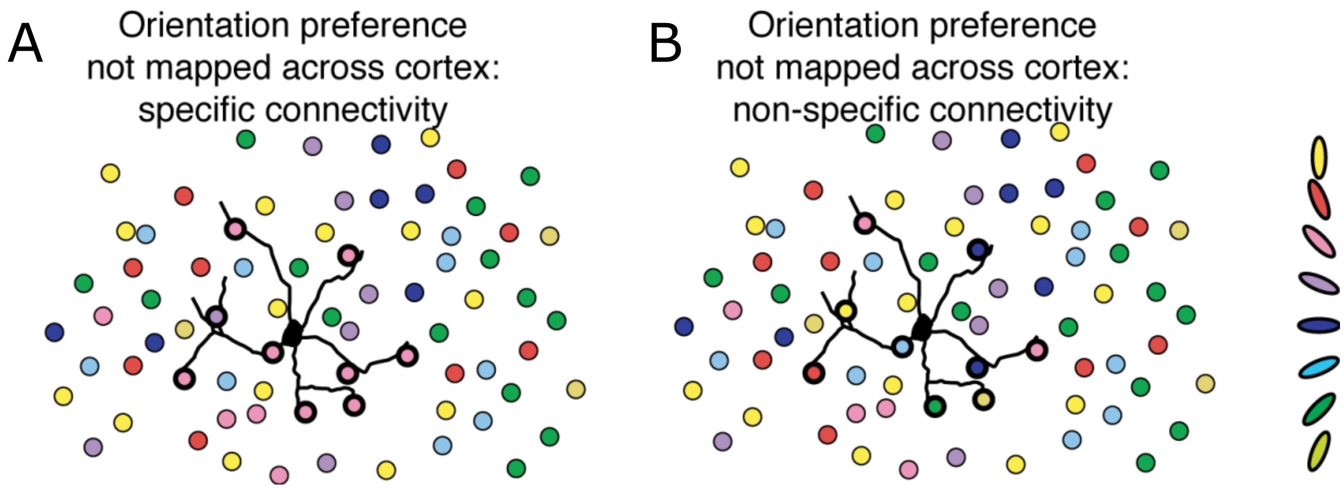
Niell and Stryker, 2008



Salt & pepper organization,
Rat V1

Ohki and Reid, 2007

Mechanism underlying orientation selectivity in rodent V1 ?

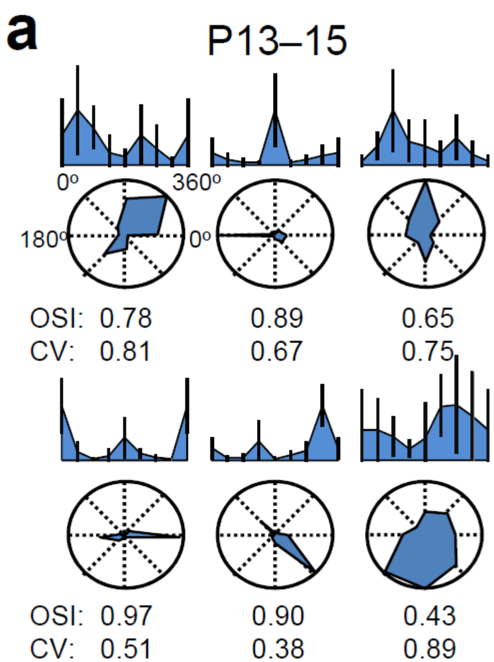


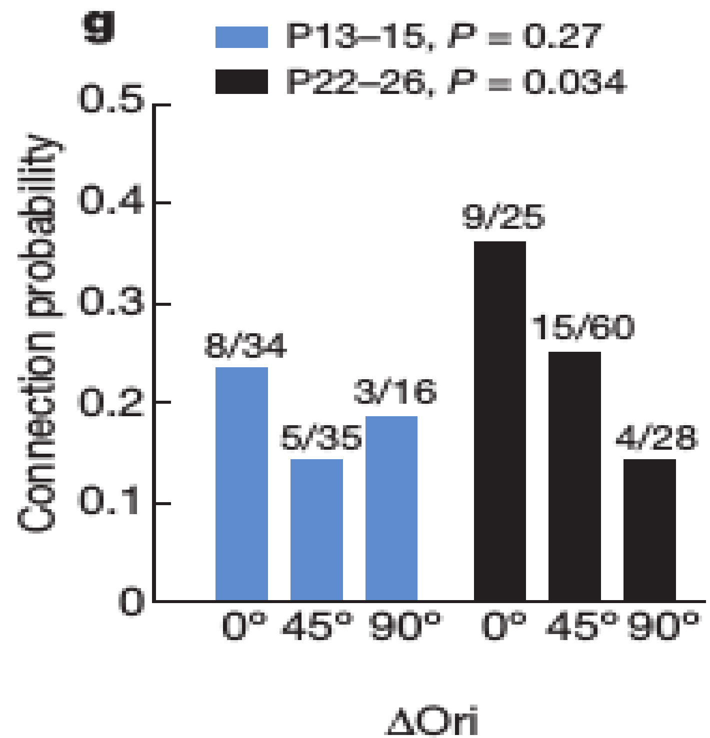
«The mixed salt-and-pepper organization of preferred orientation in rodents [...] argues for specific connectivity between neurons»

(Ohki and Reid, 2007)

Selectivity present in mouse at eye opening

Ko et al, 2013

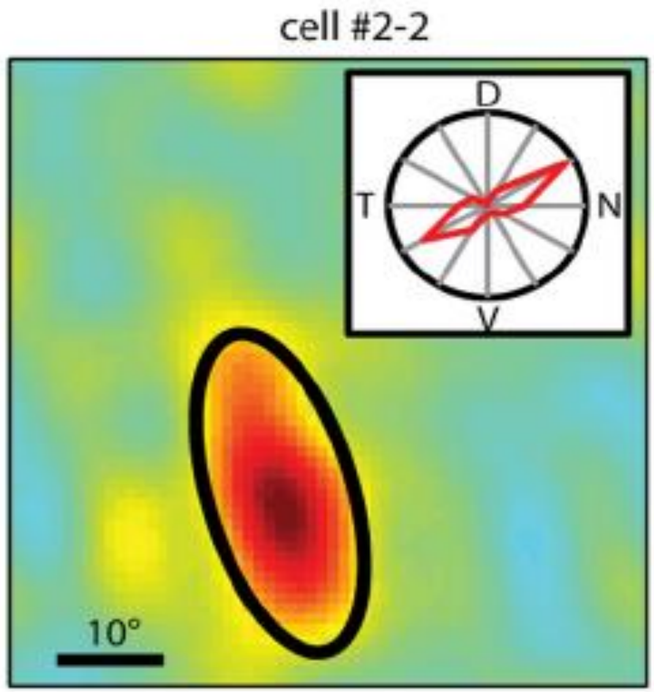


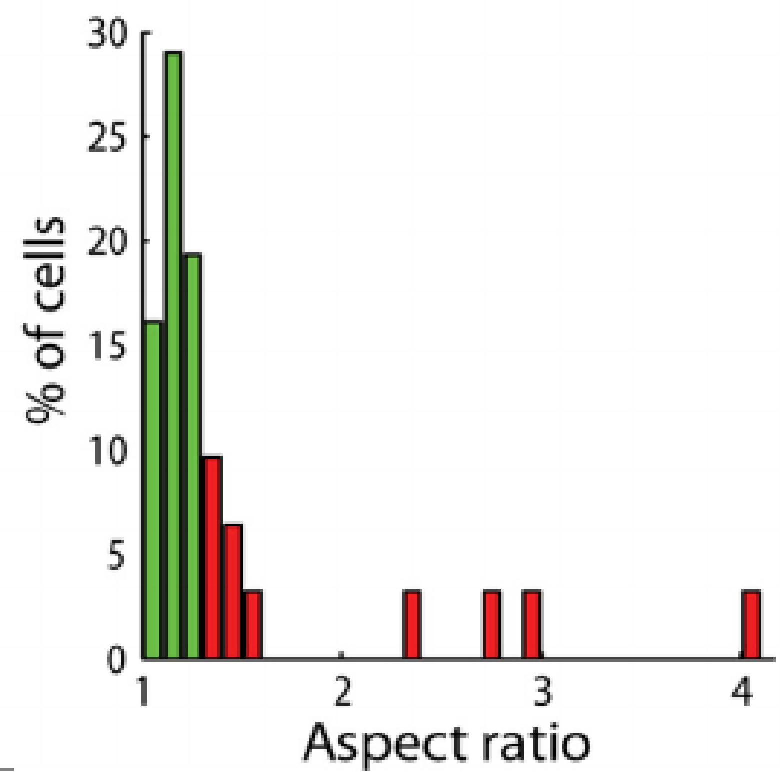


- At eye opening: Neurons are selective to orientation; EE connectivity is non specific.
- After critical period: Specificity in the EE connectivity

Elongated receptive fields in LGN (adults)

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





Zhao et al, 2013

The question

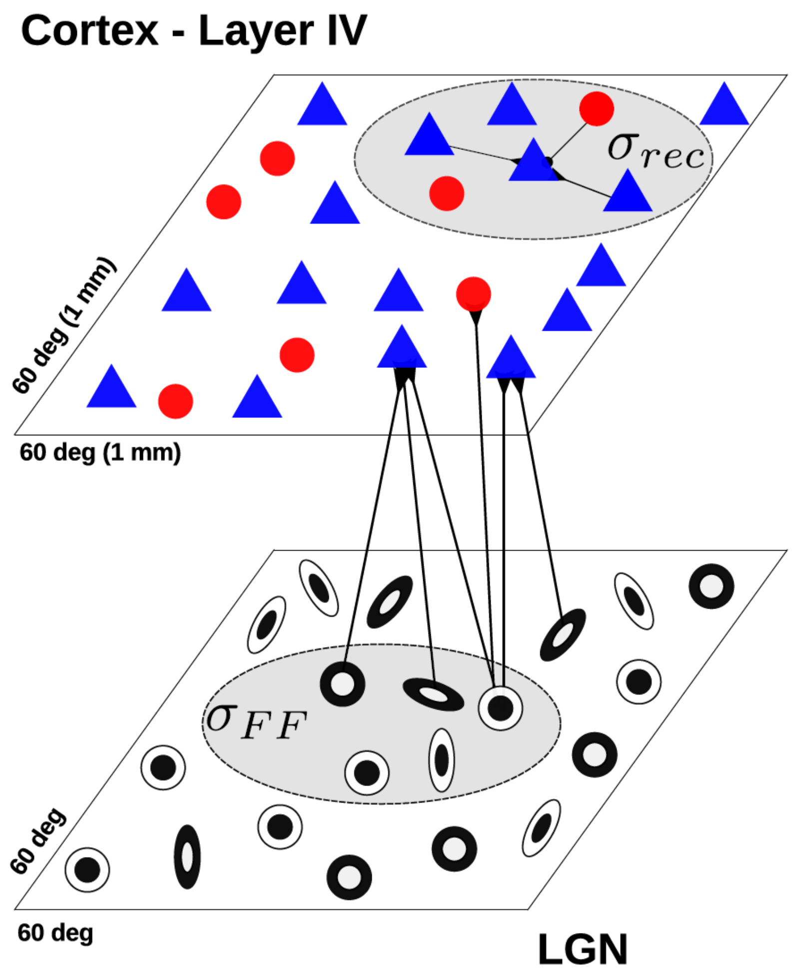
- Is random organization sufficient to account for orientation selectivity observed in the LGN – Layer 4 – Layer 2/3 ?

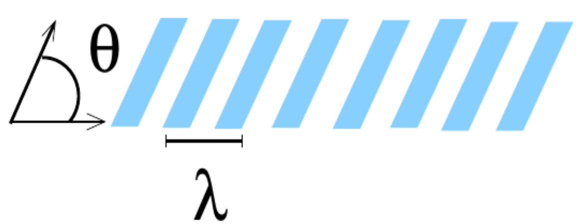
- What are the consequences of this organization from the point of view of selectivity and coding?

Outline

- Computational model LGN+V1
- Validation in terms of the properties of the thalamic input
- Selectivity properties of V1 cells

Model of LGN + Layer 4 in mouse V1



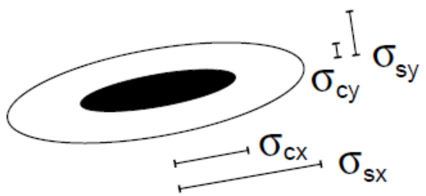


Stimulus

- L4: 2-D network of conductance-based N_E=19600, N_I=4900 neurons. 1mm^2= 60°x60° of visual field (Kalatsky & Stryker, 2003).
- Recurrent connectivity: random with footprint σ_{rec} and mean number of connections per neurons =500.

- LGN: N_L=10000 stochastically spiking Neurons connected randomly to L4 cells. Footprint σ_{FF}. Average K inputs from LGN per L4 neuron.

- LGN receptive fields:



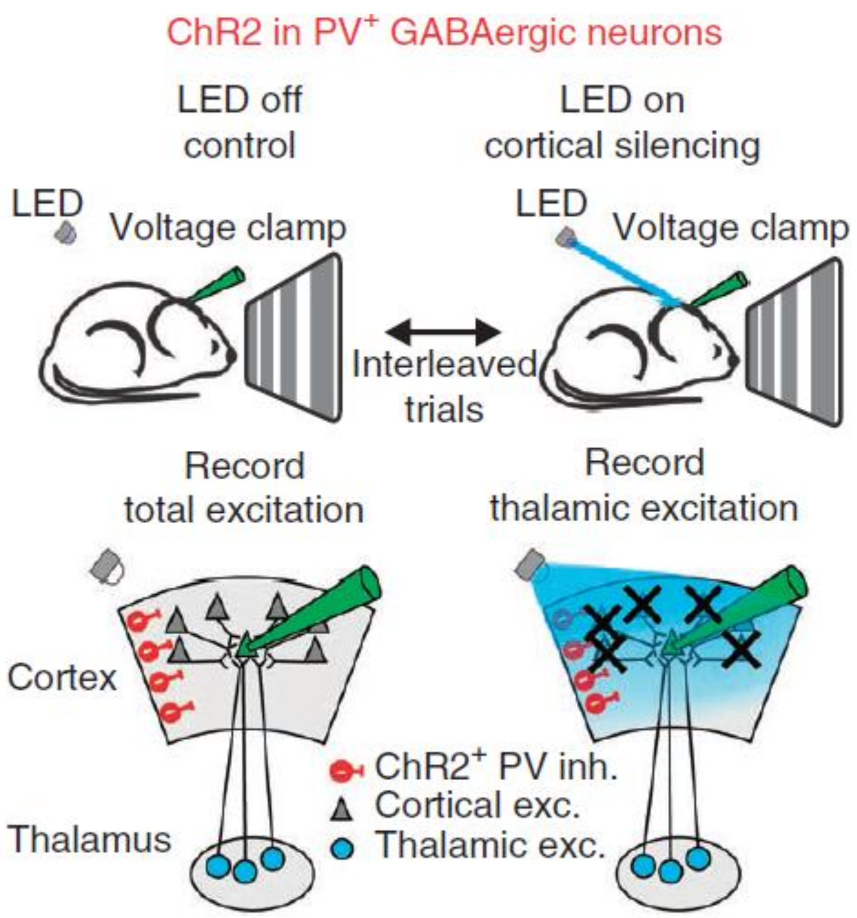
aspect ratio 1+α

Results 1

Properties of the thalamic input

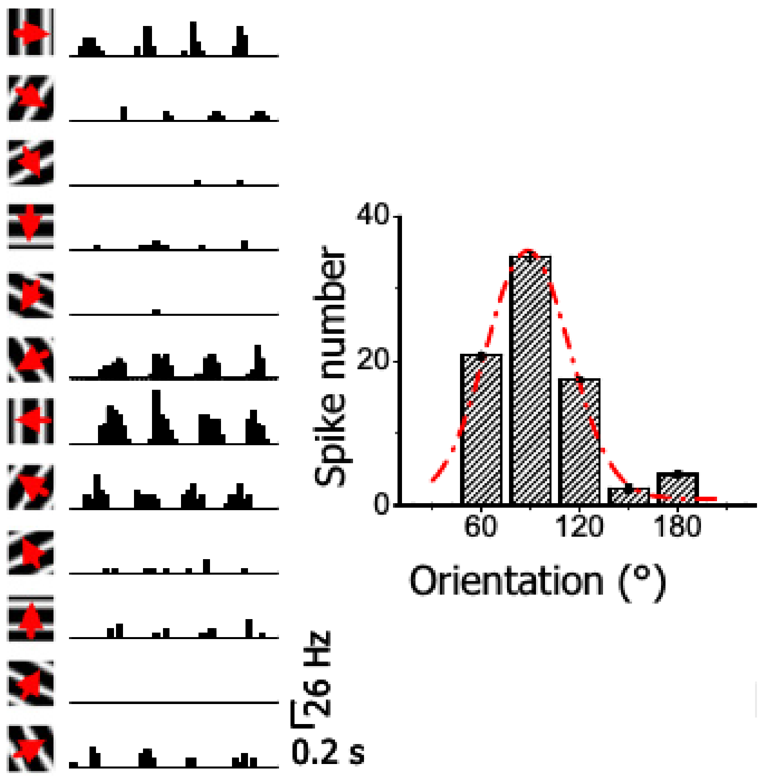
The thalamic excitation: average tuning

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



Lien & Scanziani, 2013

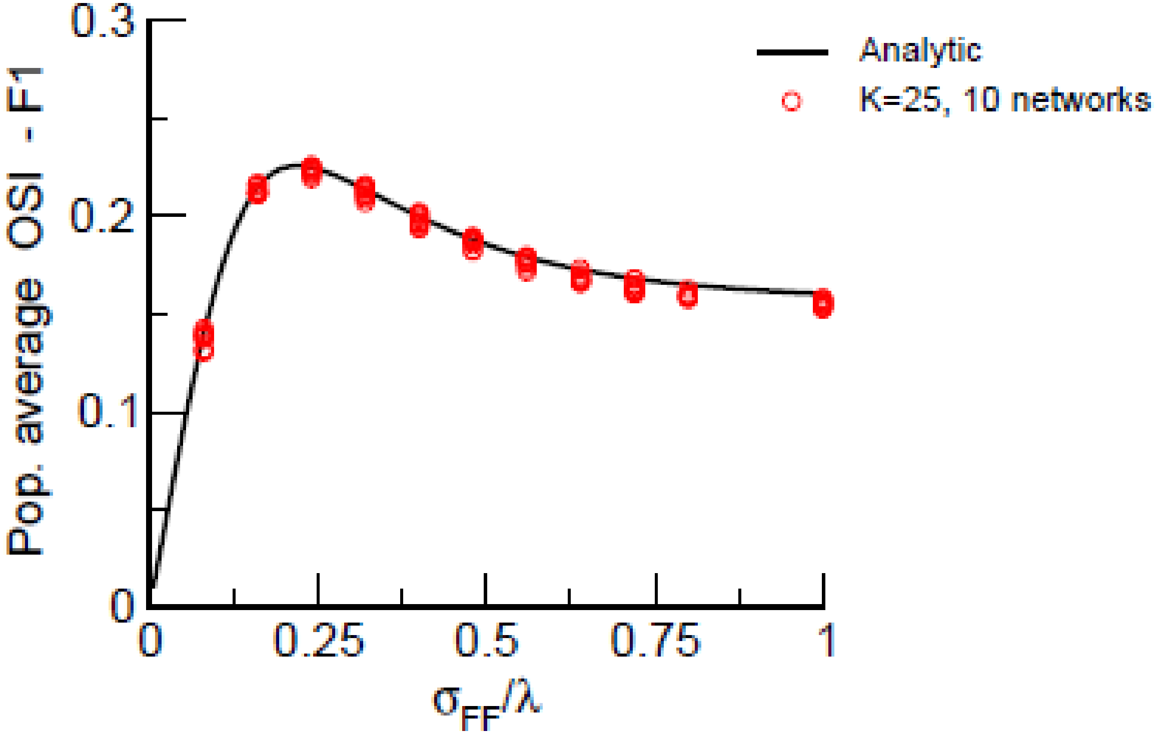
F0 vs F1



Liu et al, 2011

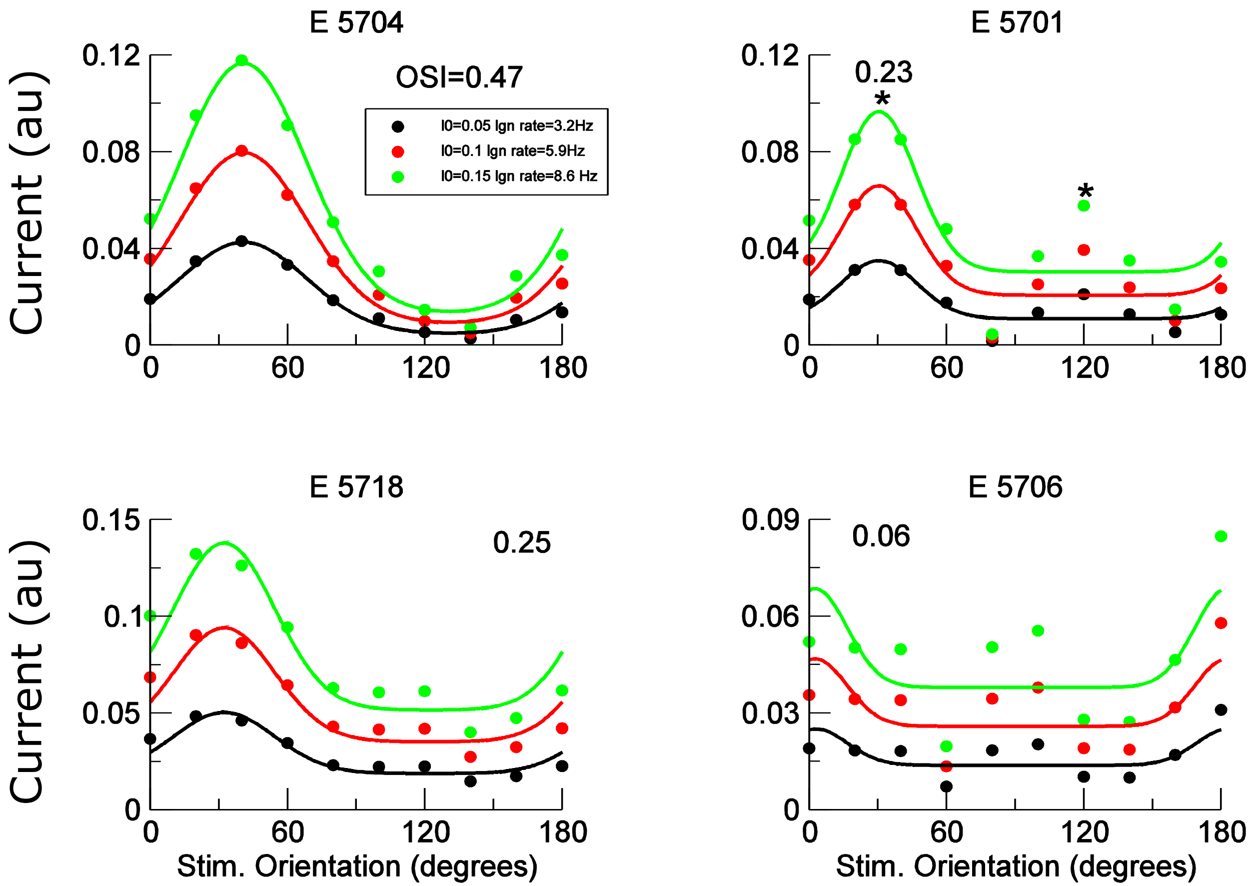
The thalamic excitation: average tuning

- 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)
- F0 component: OSI =0.
- F1 component: depends on σ_{FF}/λ and very weakly on K, the number of LGN inputs per cell, K



For $\sigma_{FF}/\lambda > 0.2$: mean OSI ~0.2

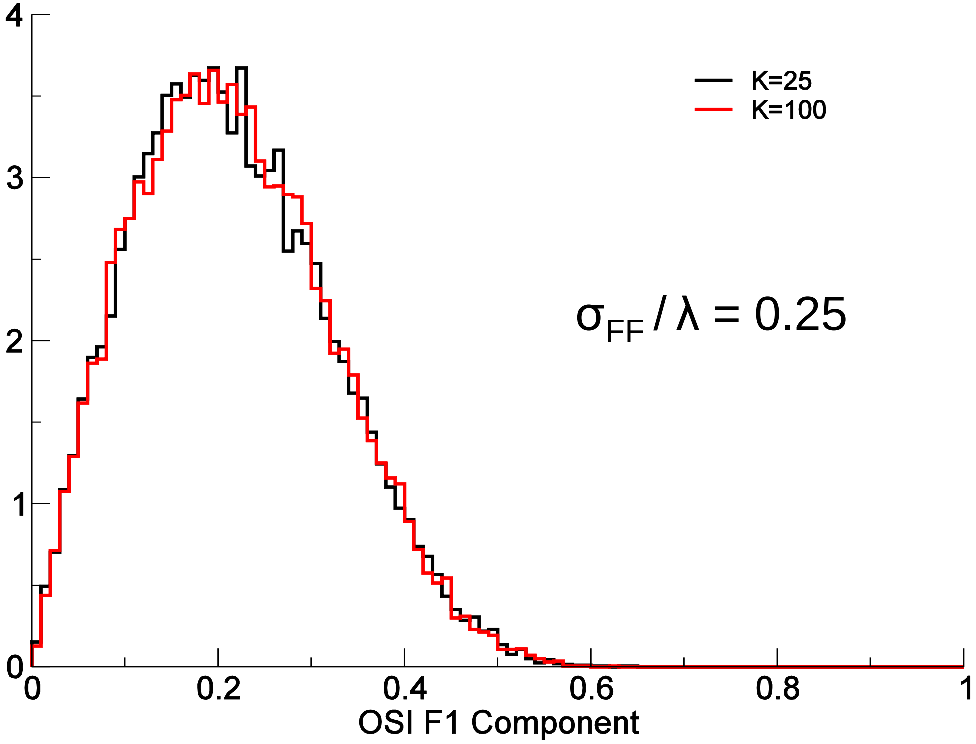
The F1 component of the thalamic excitation is tuned

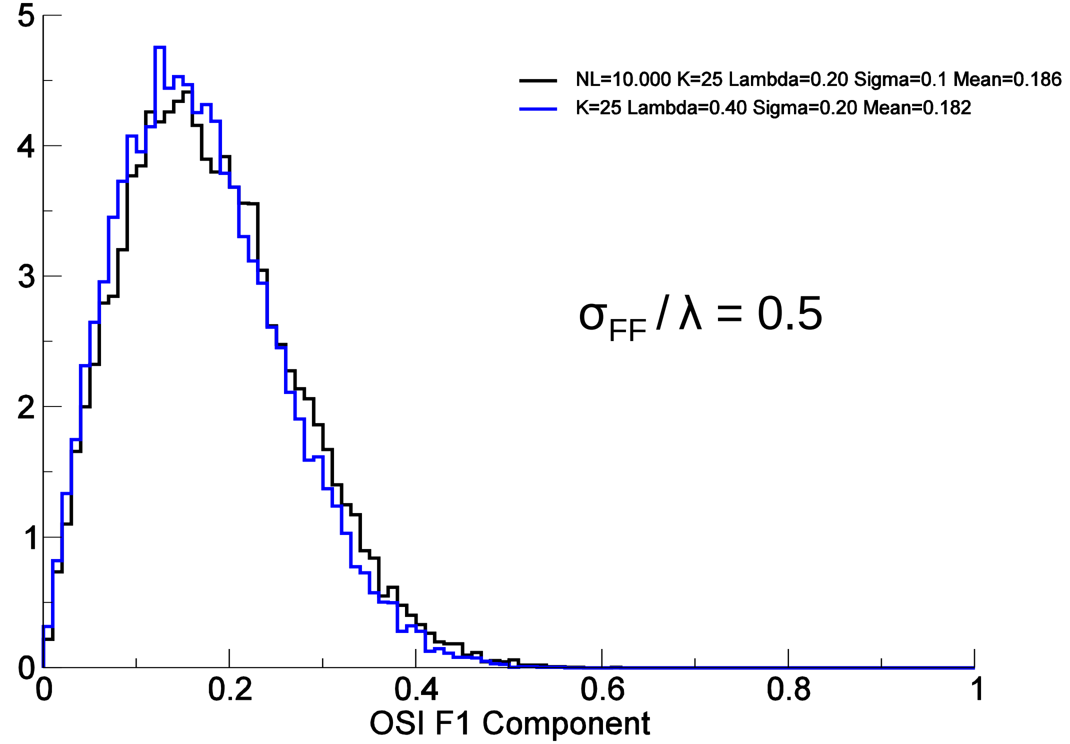


K=25

$\sigma_{FF} / \lambda = 0.25$

Distribution of the OSIs

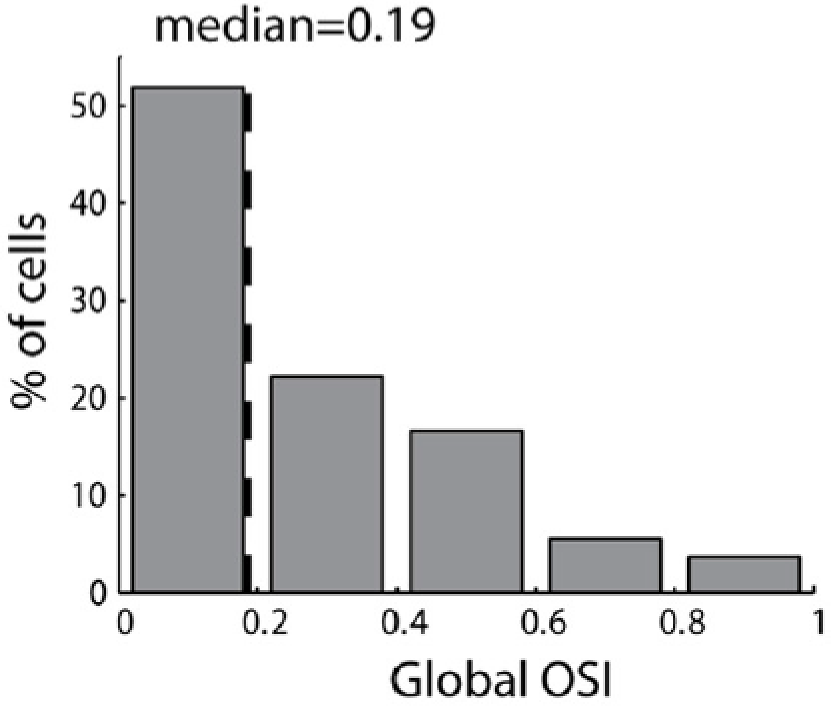


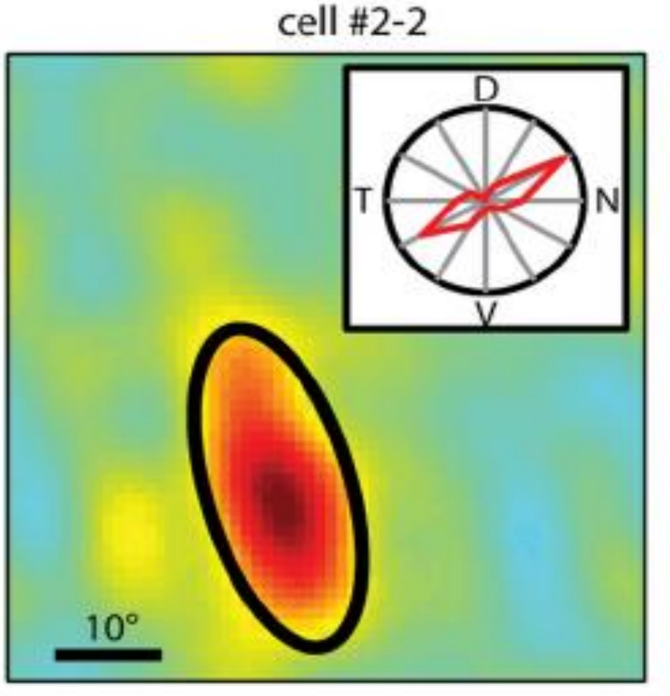


Results 2

What happens if LGN cells are orientation selective ?

Orientation tuning in mouse LGN

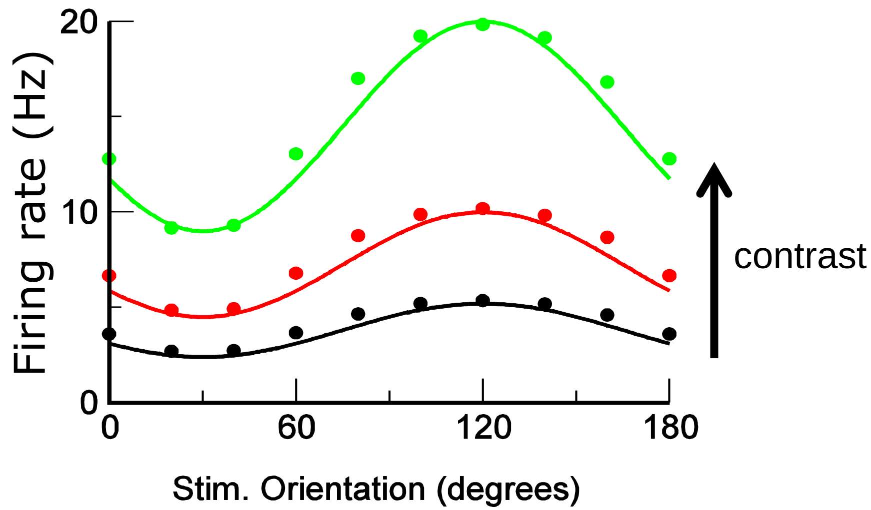


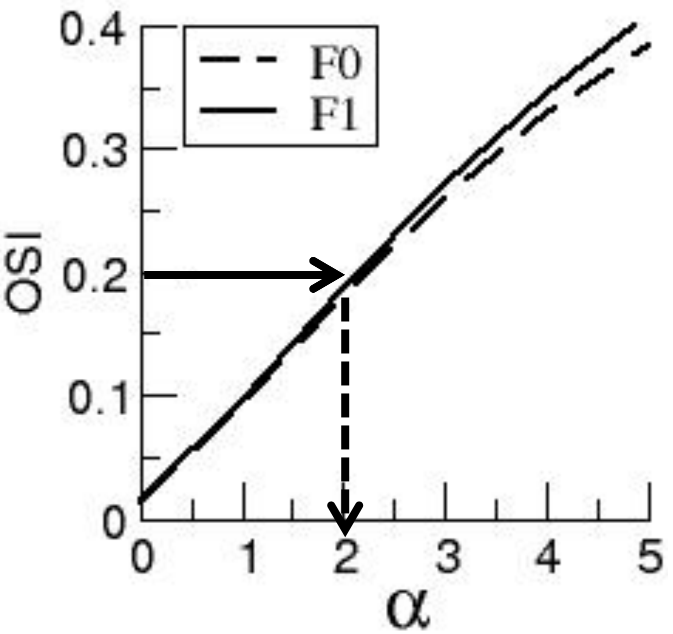


Zhao et al, 2013

Piscopo et al, 2013; Scholl et al, 2013; Zhao et al. 2013; Kondo & Ohki, 2015;
Sun et al, 2015…

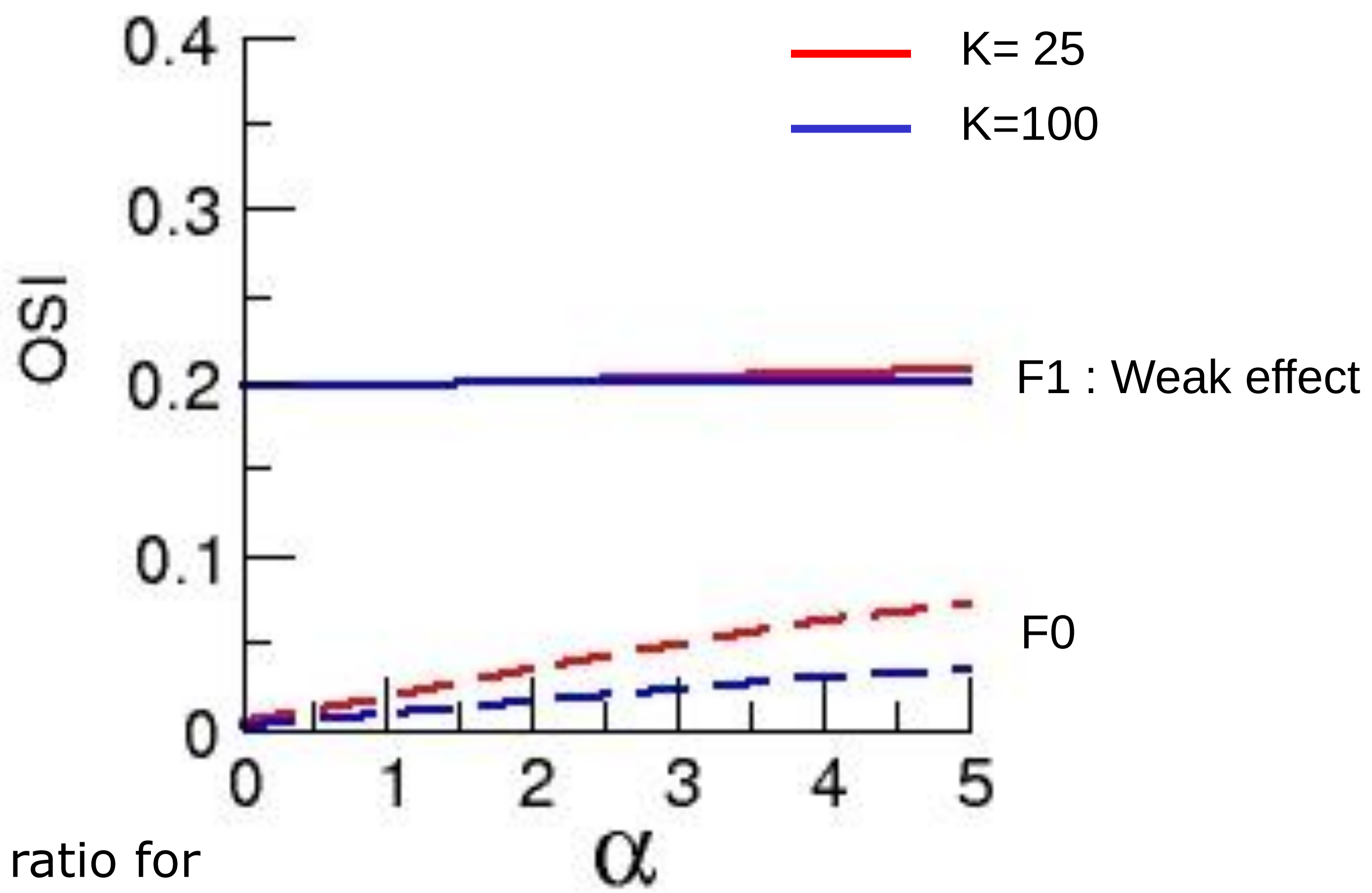
In the model LGN neurons are orientation selective





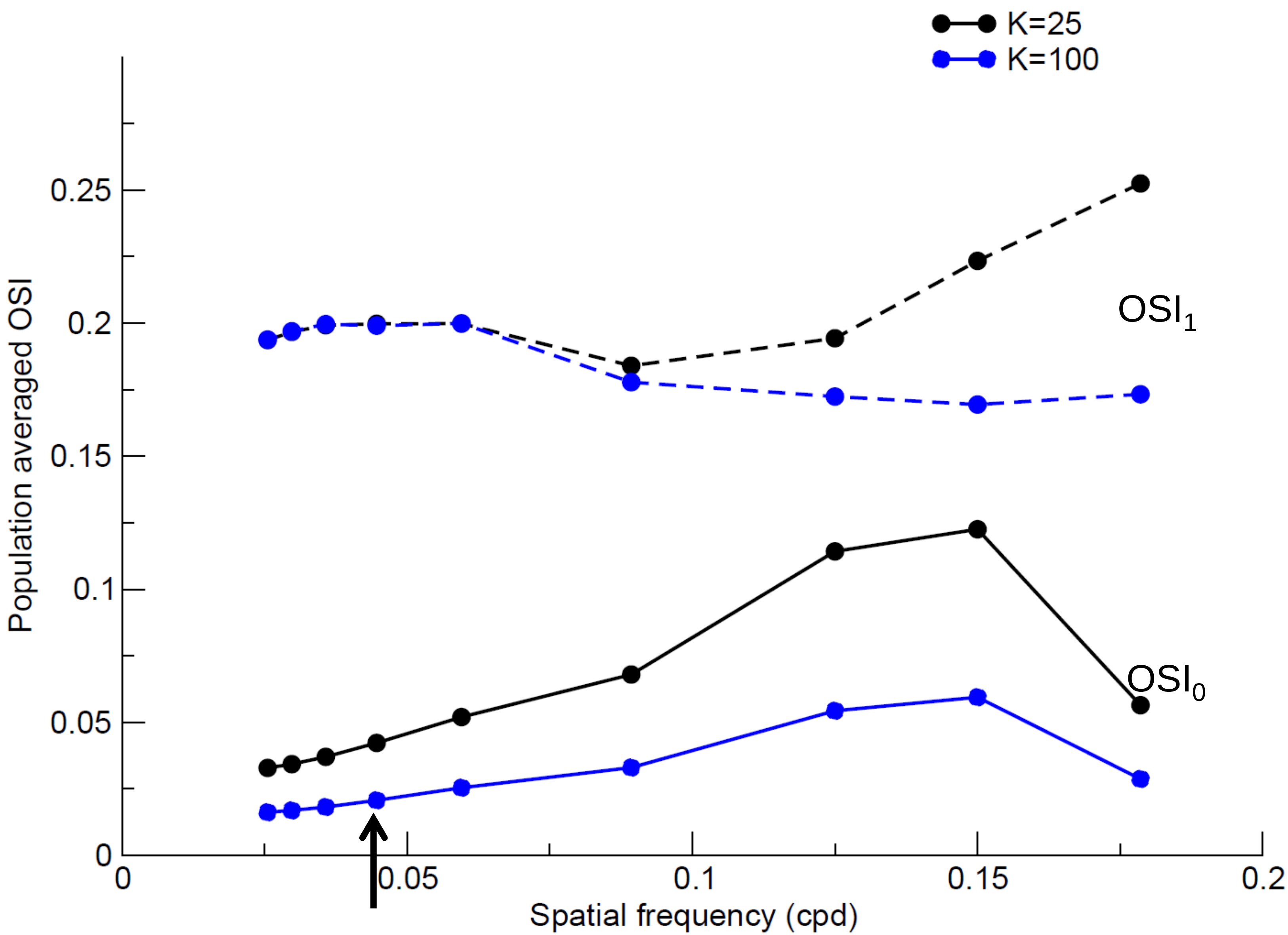
λ = 28° i.e spatial frequency=0.035 cpd

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



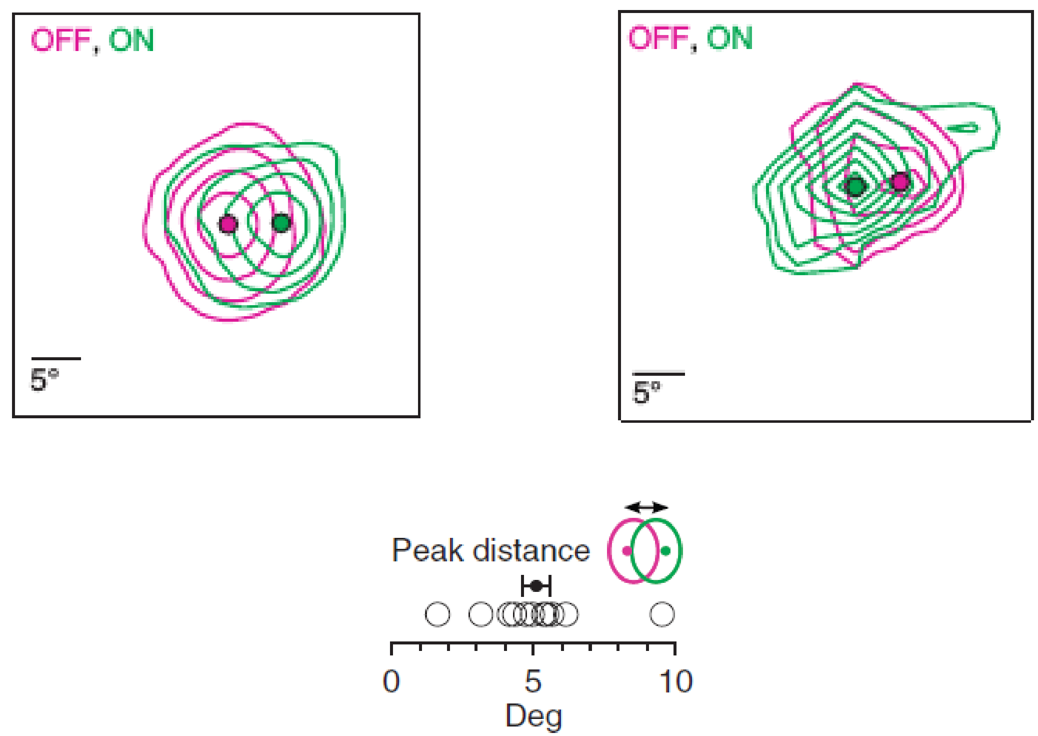
Lien & Scanziani, 2013

Thalamic excitation to mouse V1: strength and selectivity

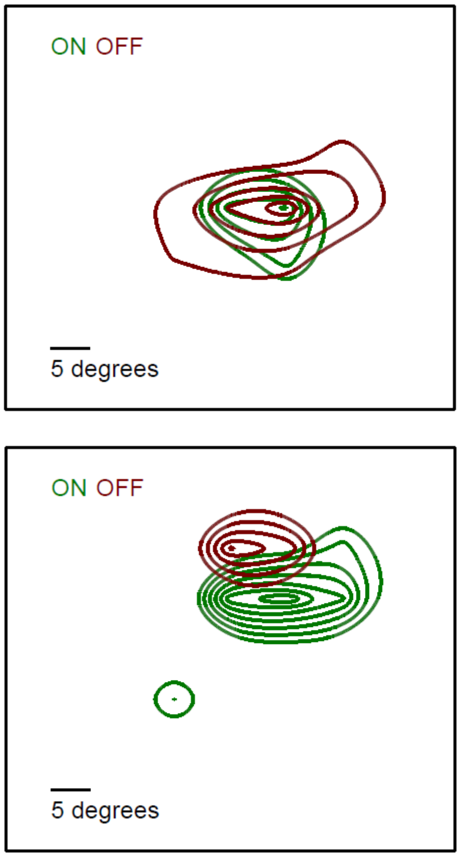
- OSI of LGN inputs: : F_0=0.03 ; F_1=0.23 (drifting gratings; spatial freq.= 0.04 cpd)
- ON/OFF subregions of LGN inputs overlap and offset (flashed stimuli)

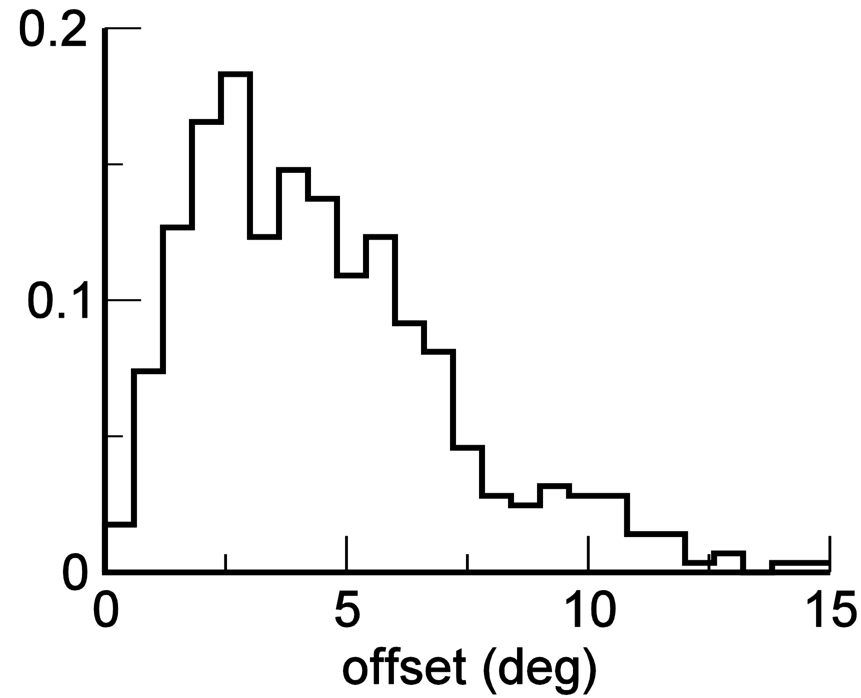
Lien & Scanziani, 2013

Adult mouse



Organisation of ON/OFF subregions of the thalamic excitation





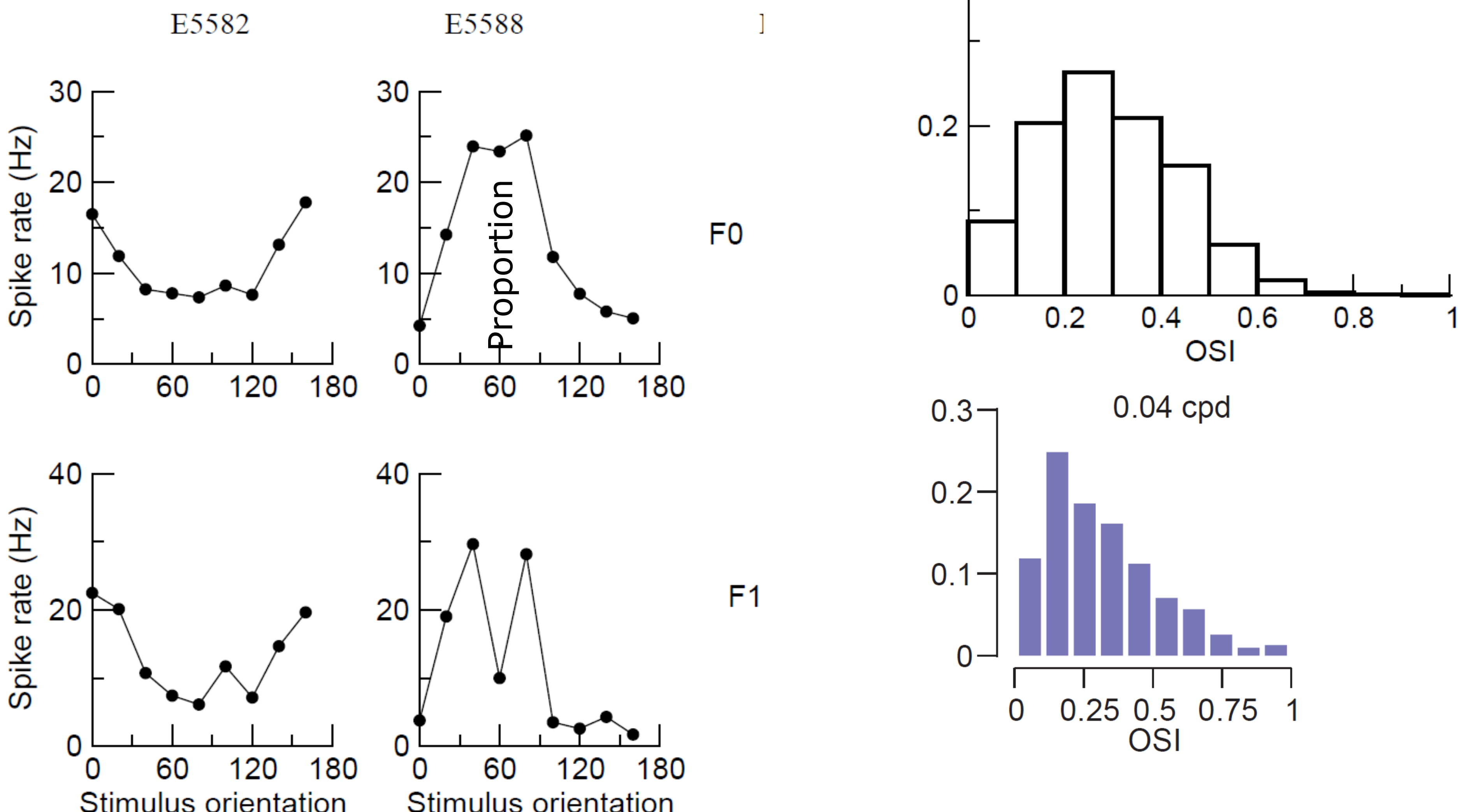
Mean offset = 5 deg

Results 3

Orientation tuning of Layer 4 neurons in the model

Layer 4 neurons are tuned to orientation

Examples of tuning curves



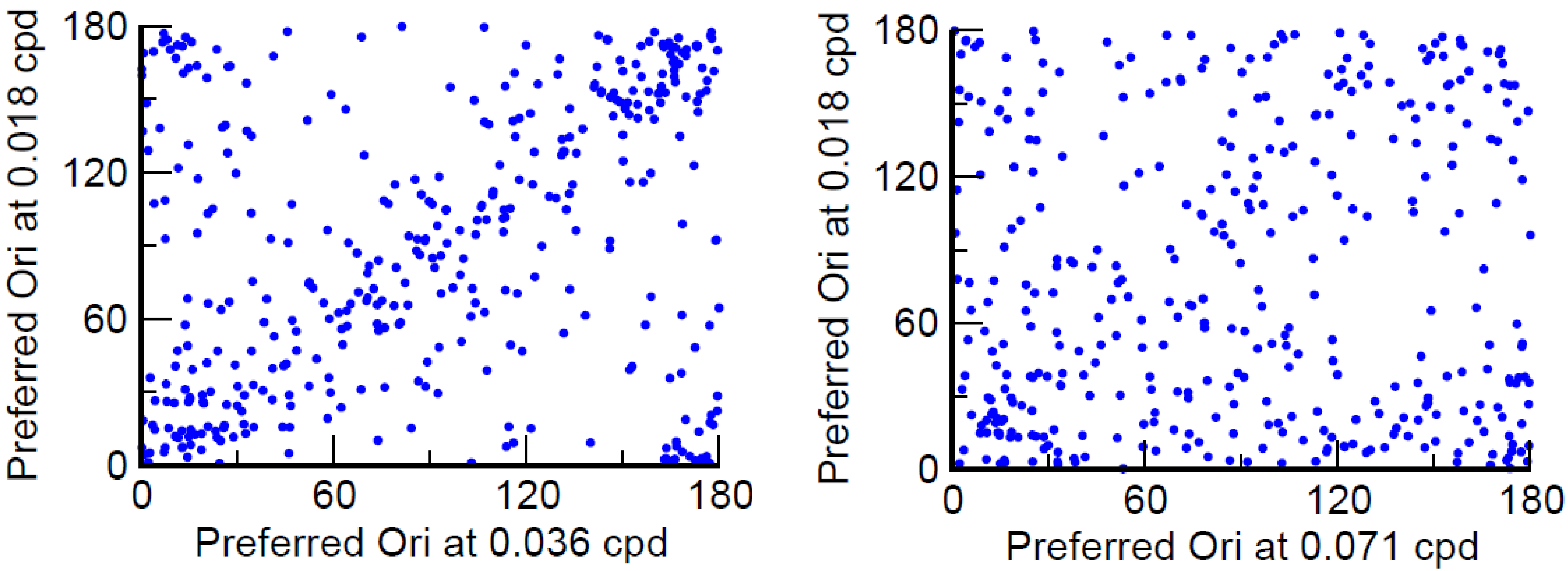
Pattadkal and Priebe, unpublished

Results 4

Do you have a prediction ?

Is the prediction verified experimentally ?

Prediction: preferred orientation depends of spatial frequency …

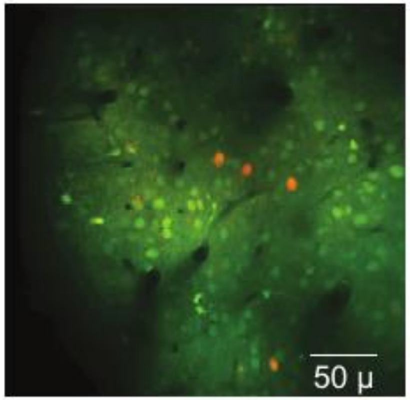


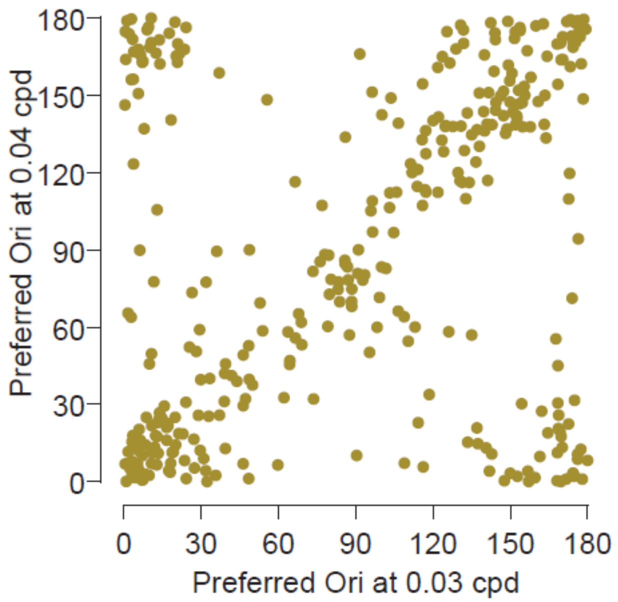
OSI>0.2
cc=0.13

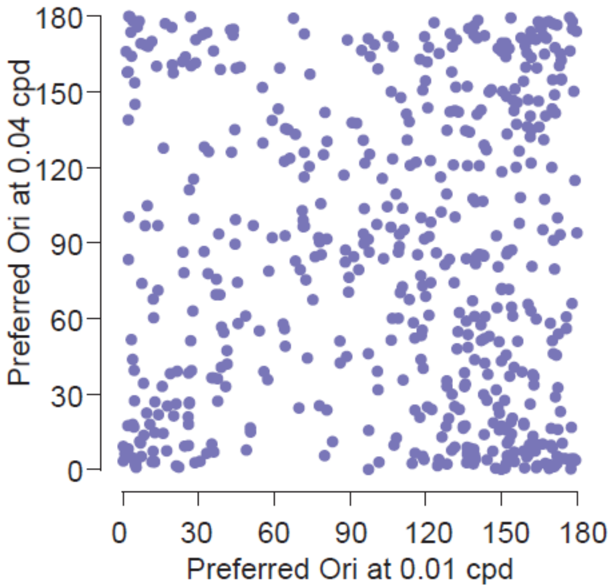
OSI>0.2
cc=0.02

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

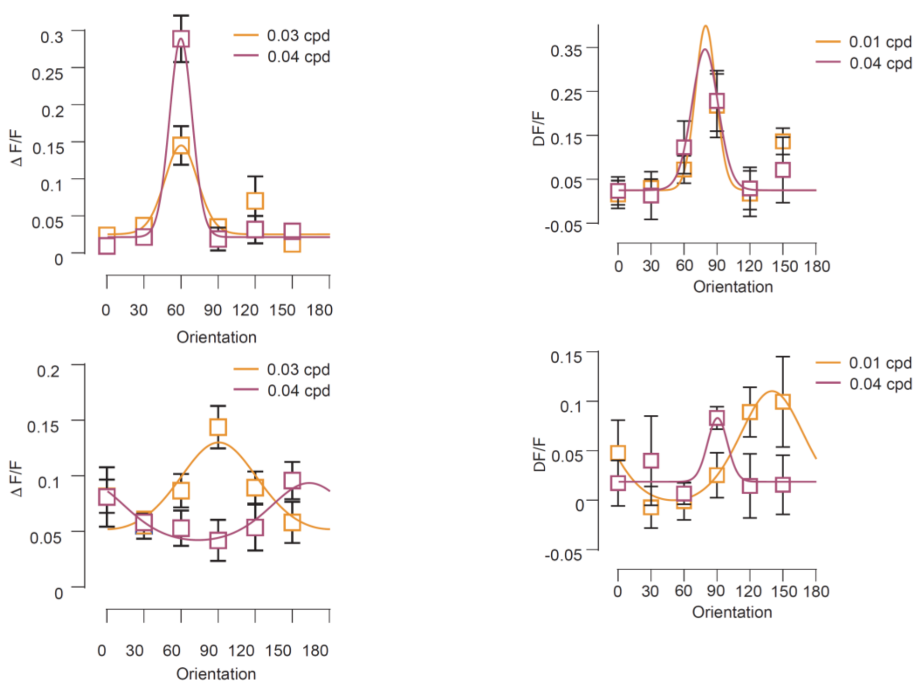
PO depends on spatial frequency



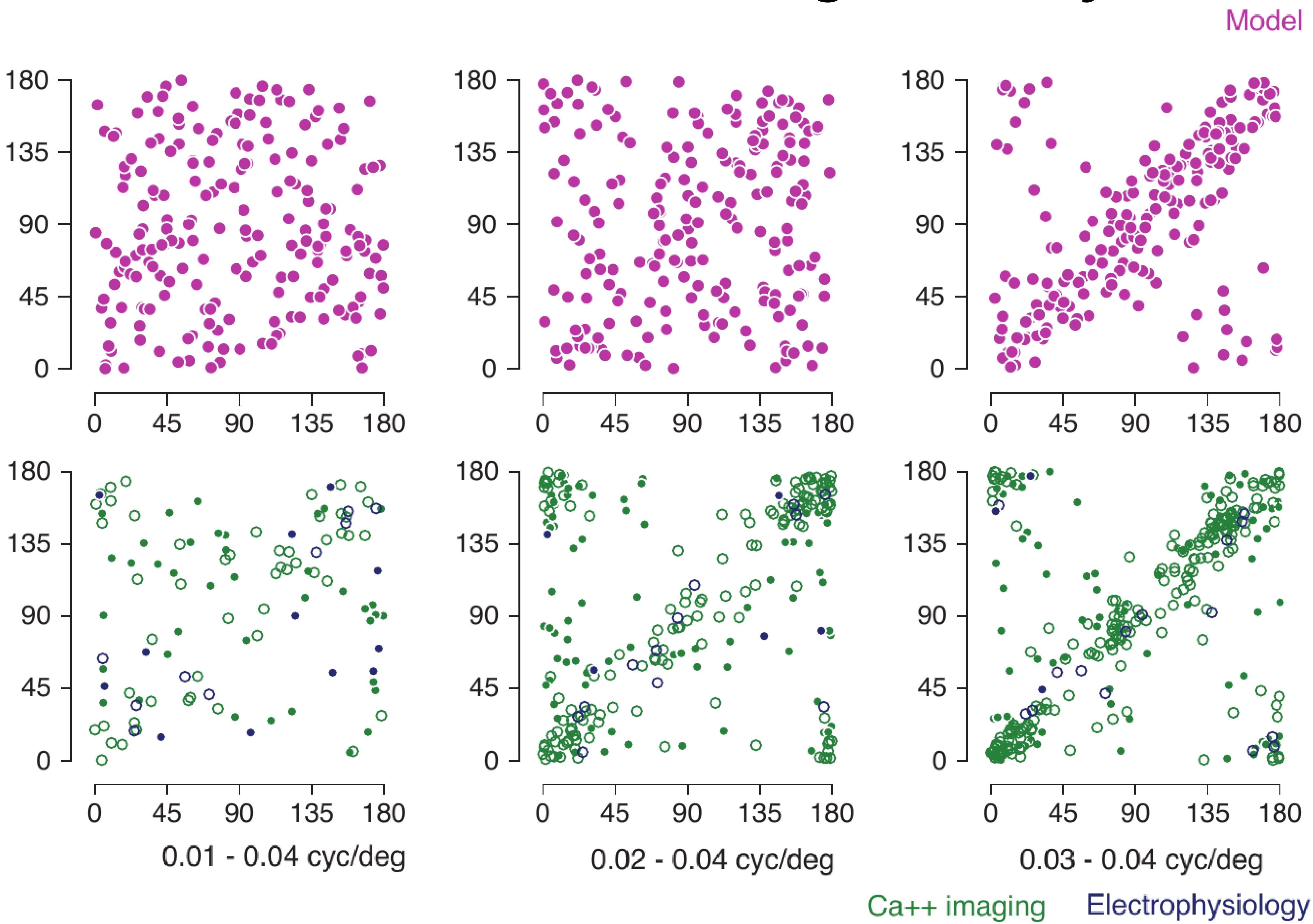




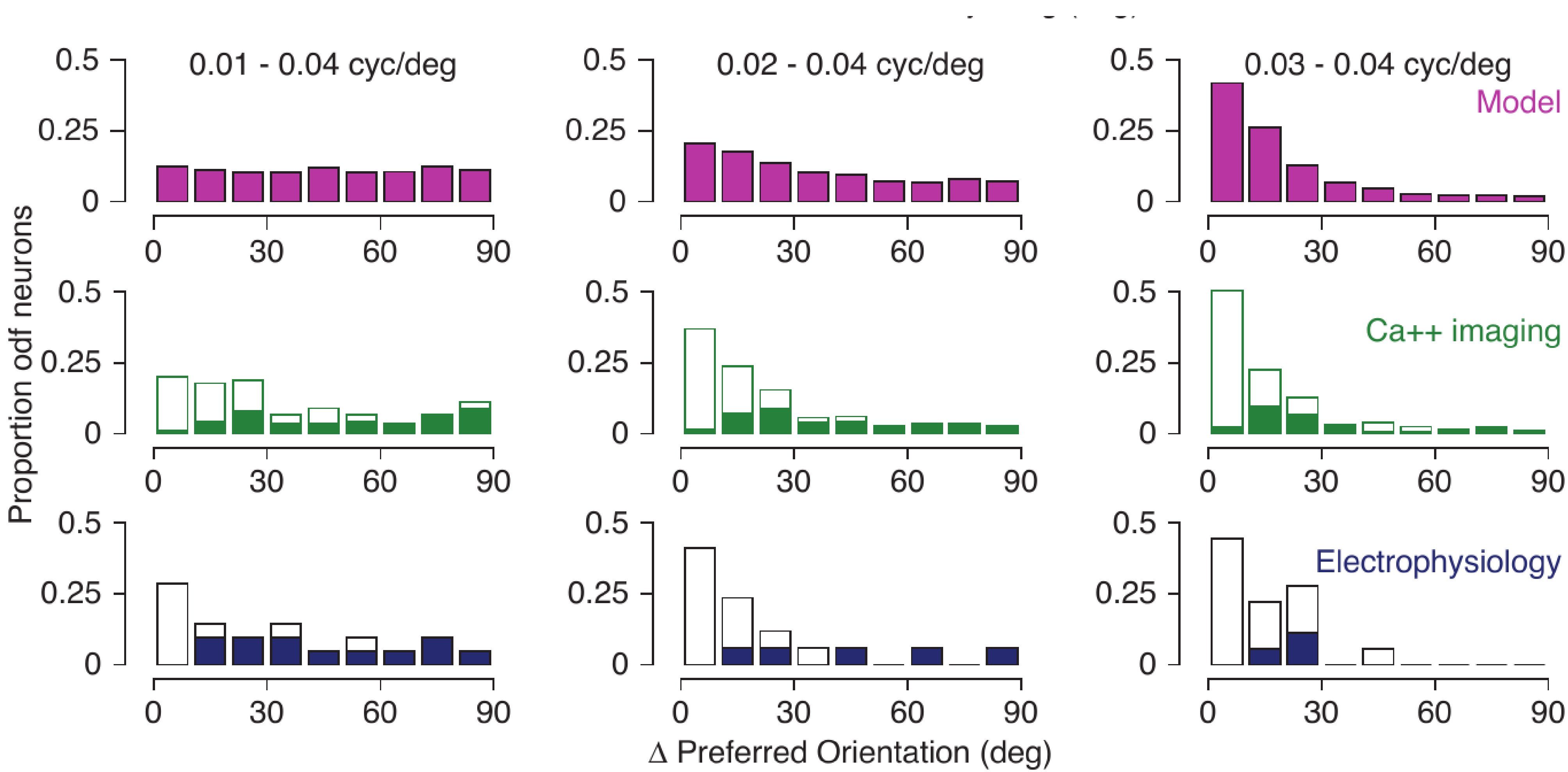
Mouse
Drifting gratings
Calcium



Correlation is lost gradually

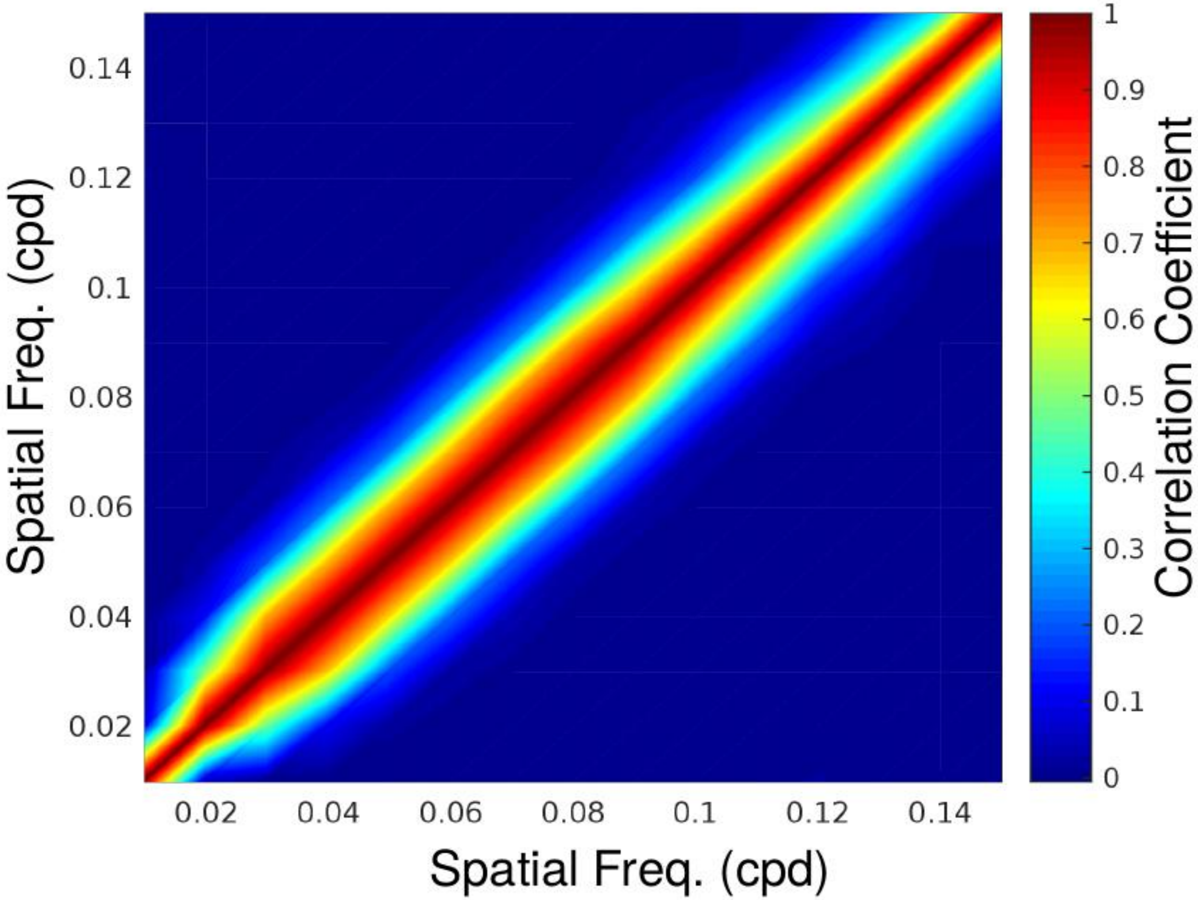


Correlation is lost gradually

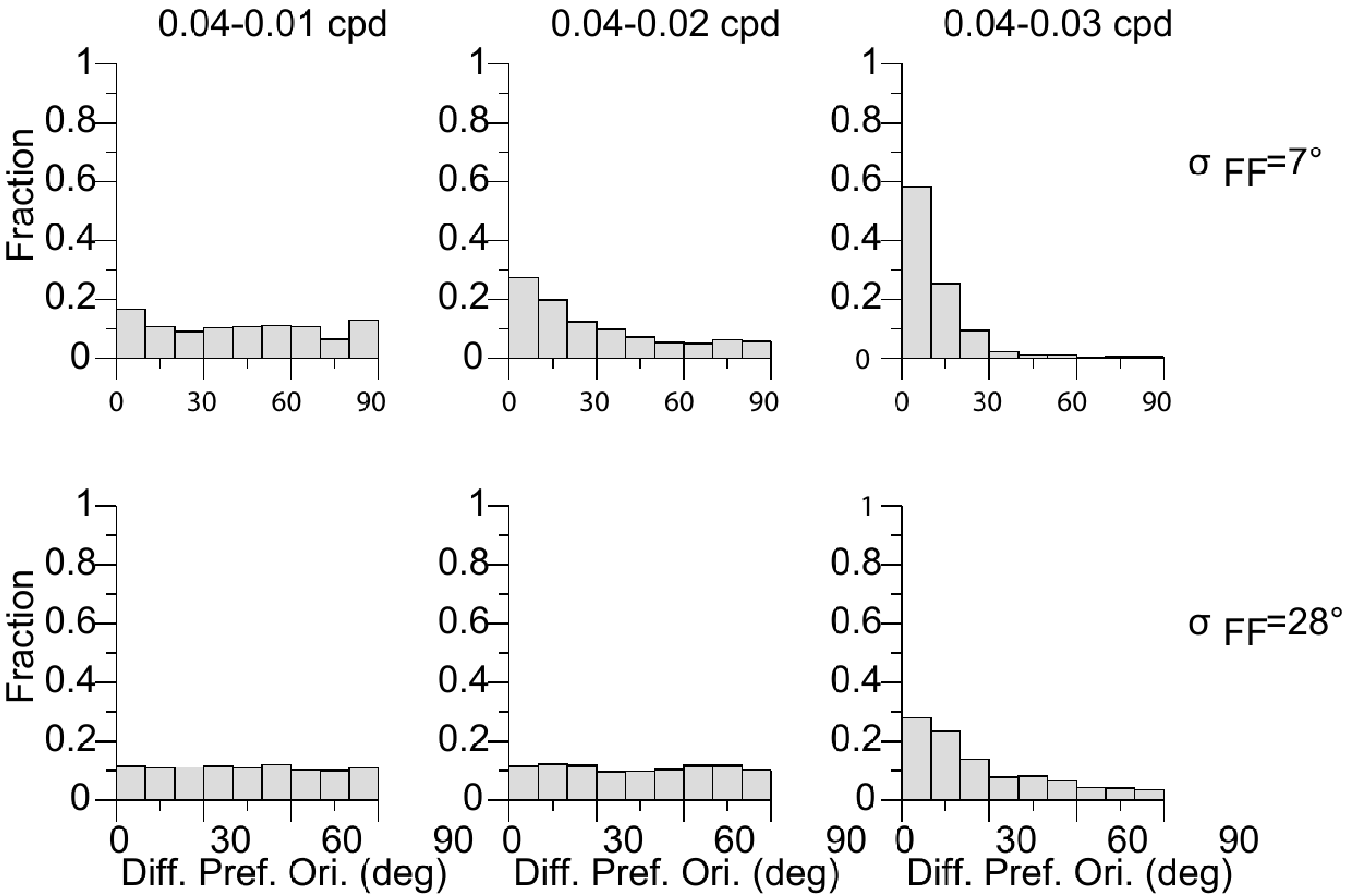


Correlation is lost gradually

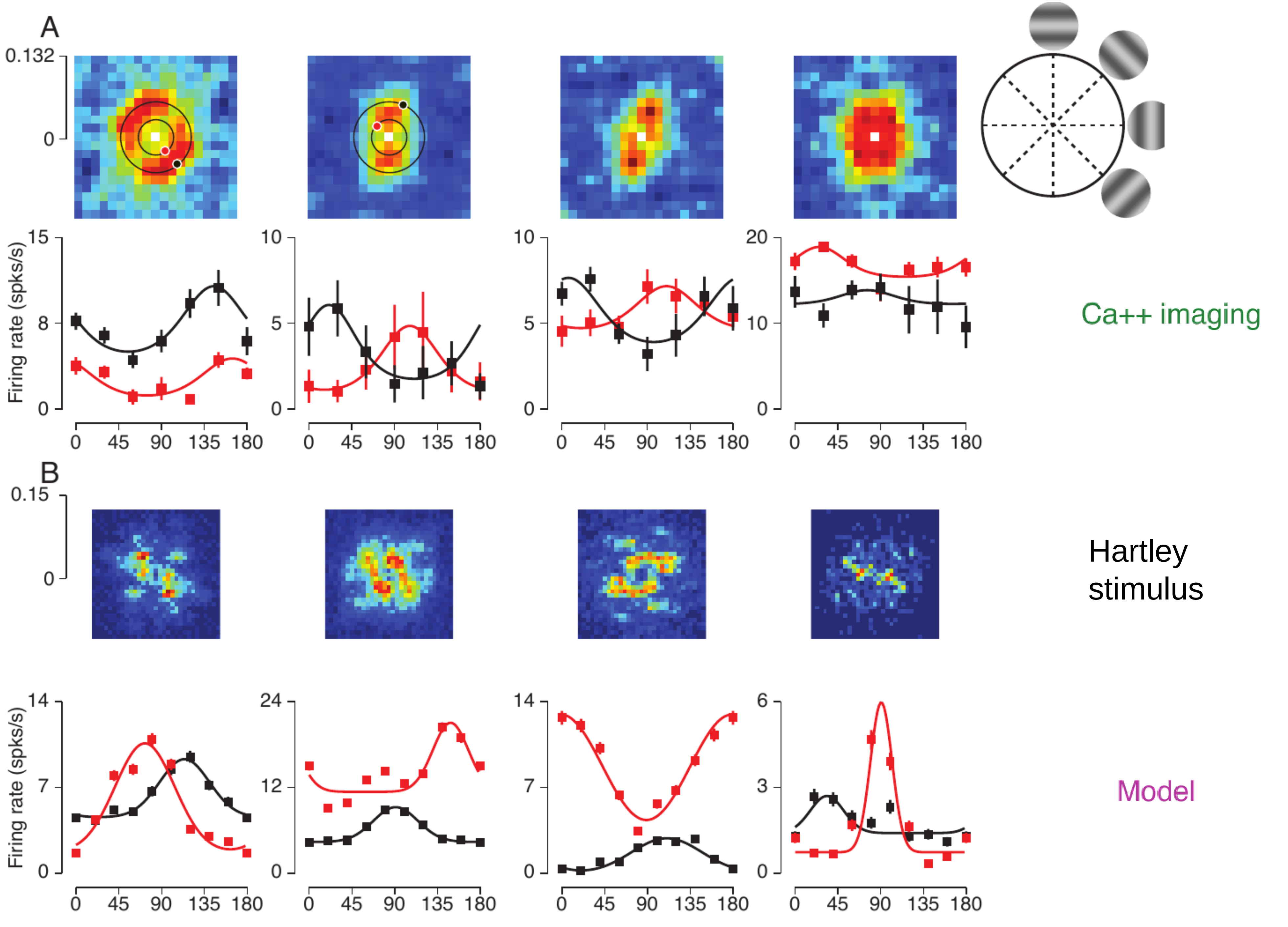
$$cc = \frac{\sum_{i,j} \sin(PO_i - PO_j)\sin(PO'_i - PO'_j)}{\sqrt{\sum_{i,j} \sin(PO_i - PO_j)^2 \sum_{i,j} \sin(PO'_i - PO'_j)^2}}$$



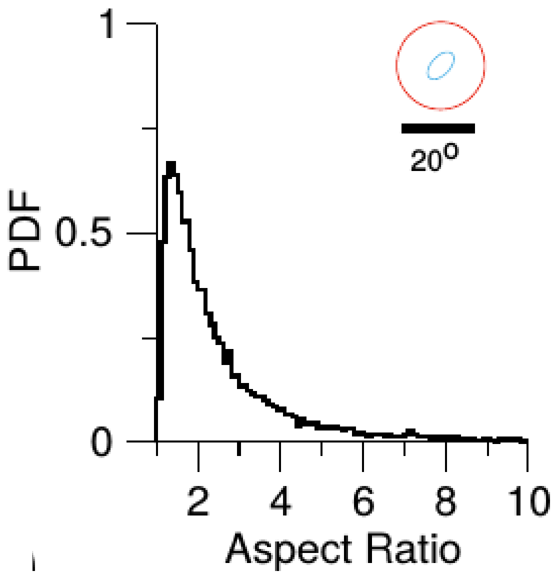
Correlation is controlled by σ_{FF}

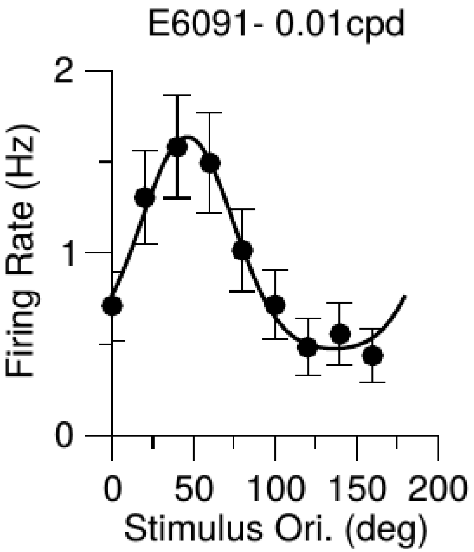


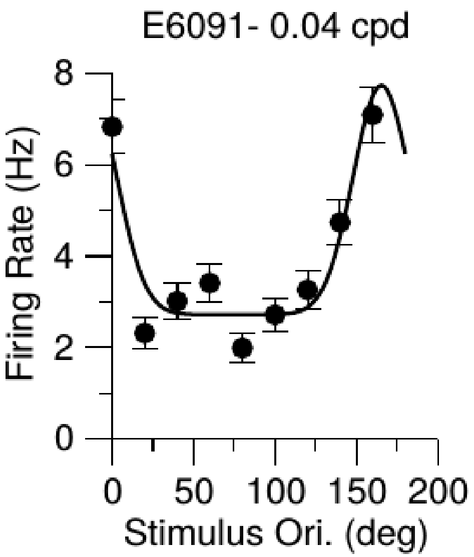
Rotation of TCs



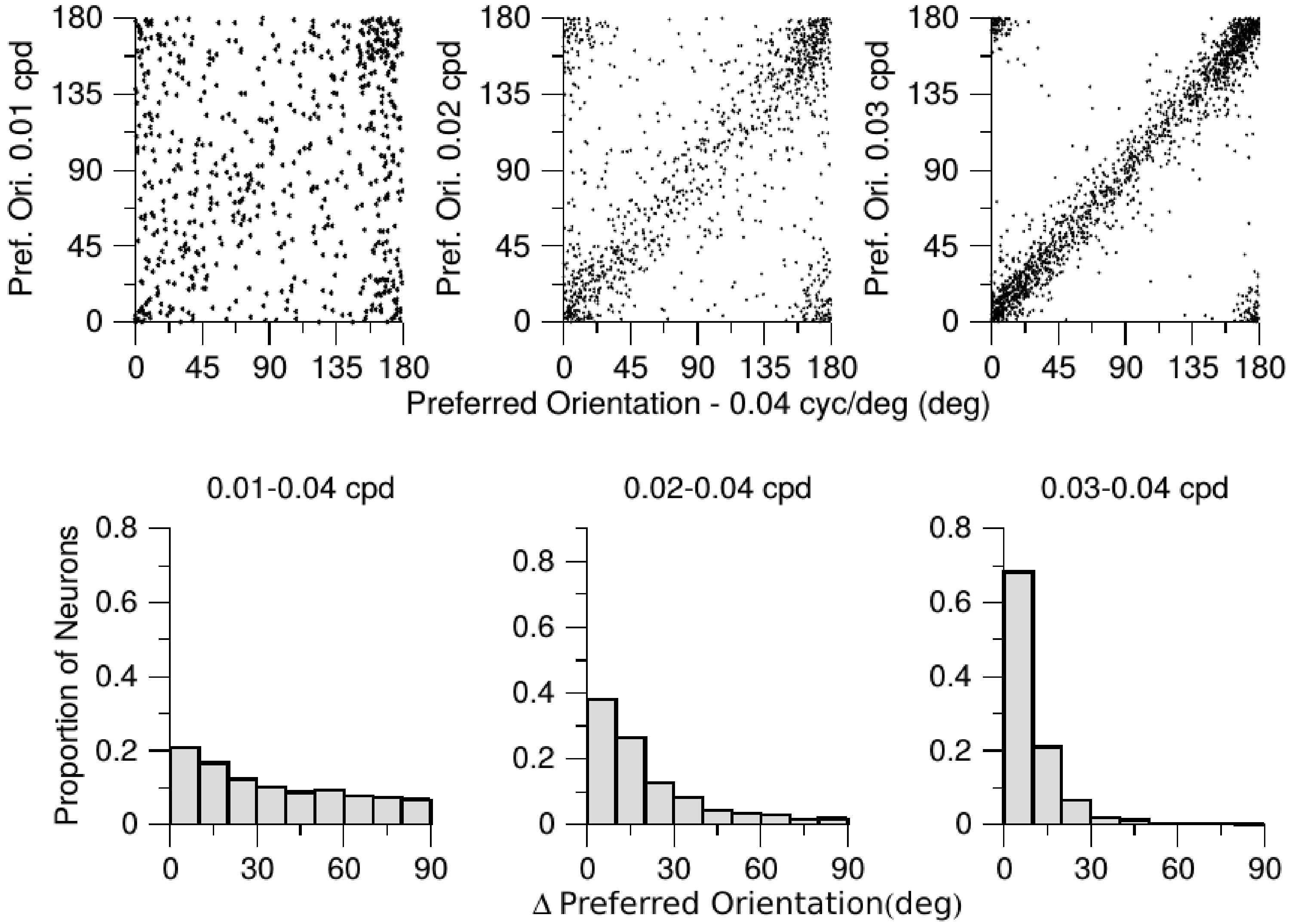
Elongated LGN RFs







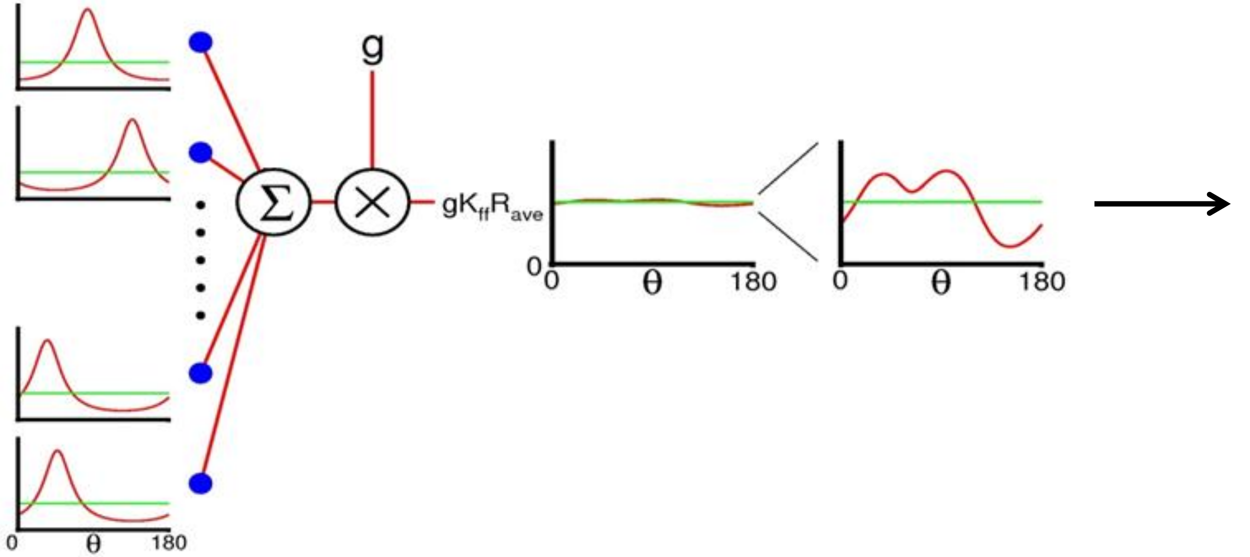
Correlation with elongated LGN RFs



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

LGN



Layer 4 neuron

- 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.

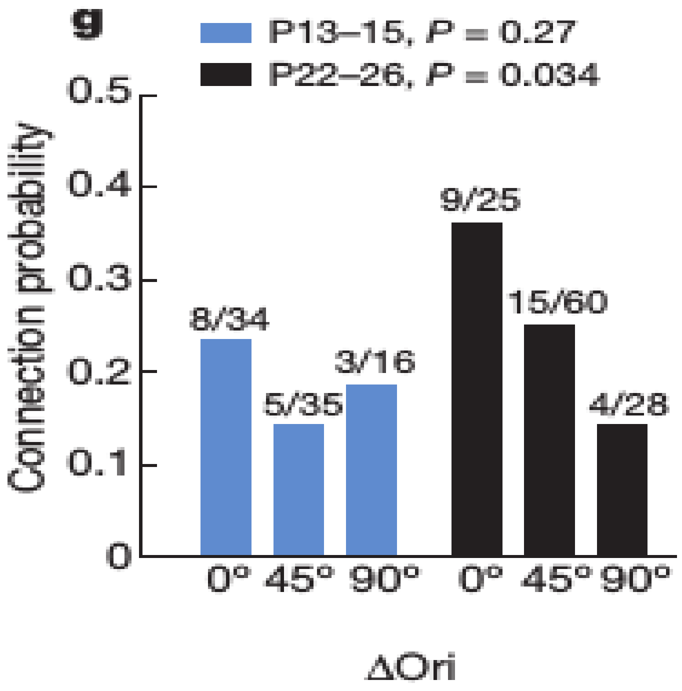
- The resulting thalamic excitation gives rise to orientation selectivity in Layer 4.

- 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”?

Acknowledgements

<u>Theory</u>

David Hansel, CNRS, Paris Descartes University

Carl van Vreeswijk, CNRS, Paris Descartes University

<u>Experiments</u>

Nicholas Priebe, University of Austin, USA

Jagruti Pattadkal, University of Austin, USA

The mechanism of OS: the intuition

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

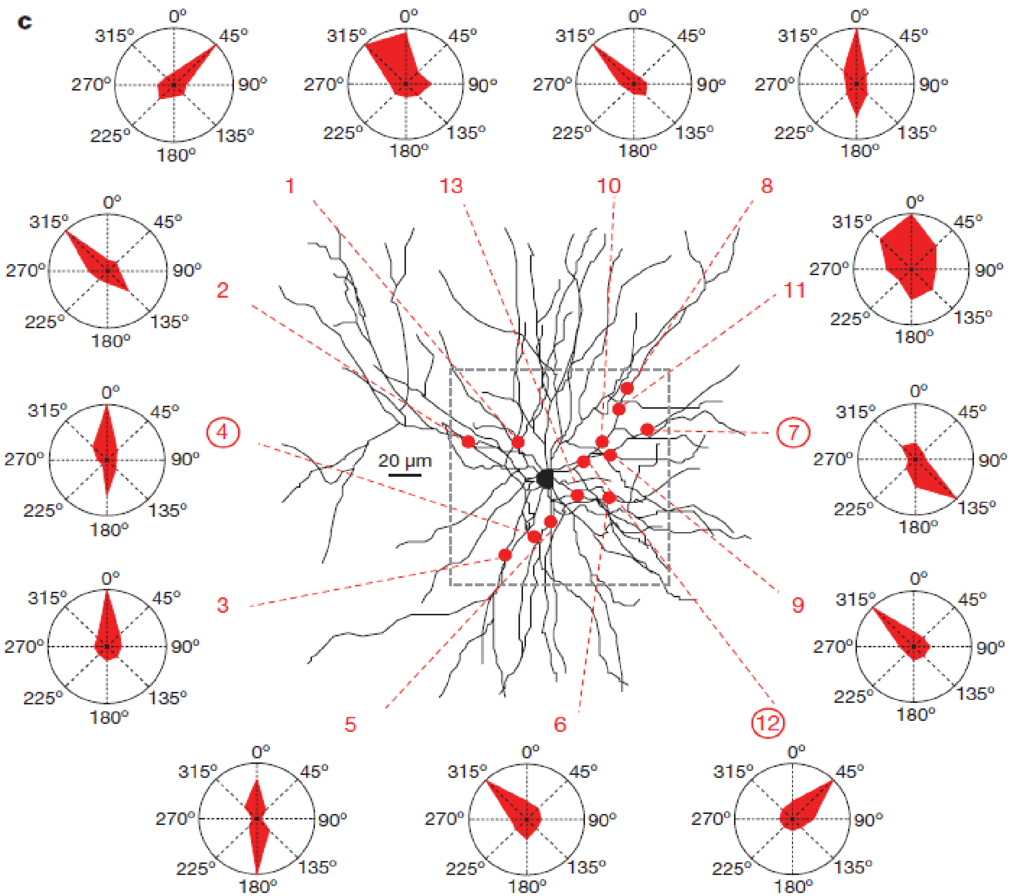
•If $g \propto T/\sqrt{K_{ff}}$, the modulation of *FF-Input* is of order *T* but its average is much larger.

•If the strength of the recurrent interactions are on the order of $T/\sqrt{K}$ the total excitatory and inhibitory recurrent inputs into an L4 neuron have an average of order $\sqrt{K}T$ 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.

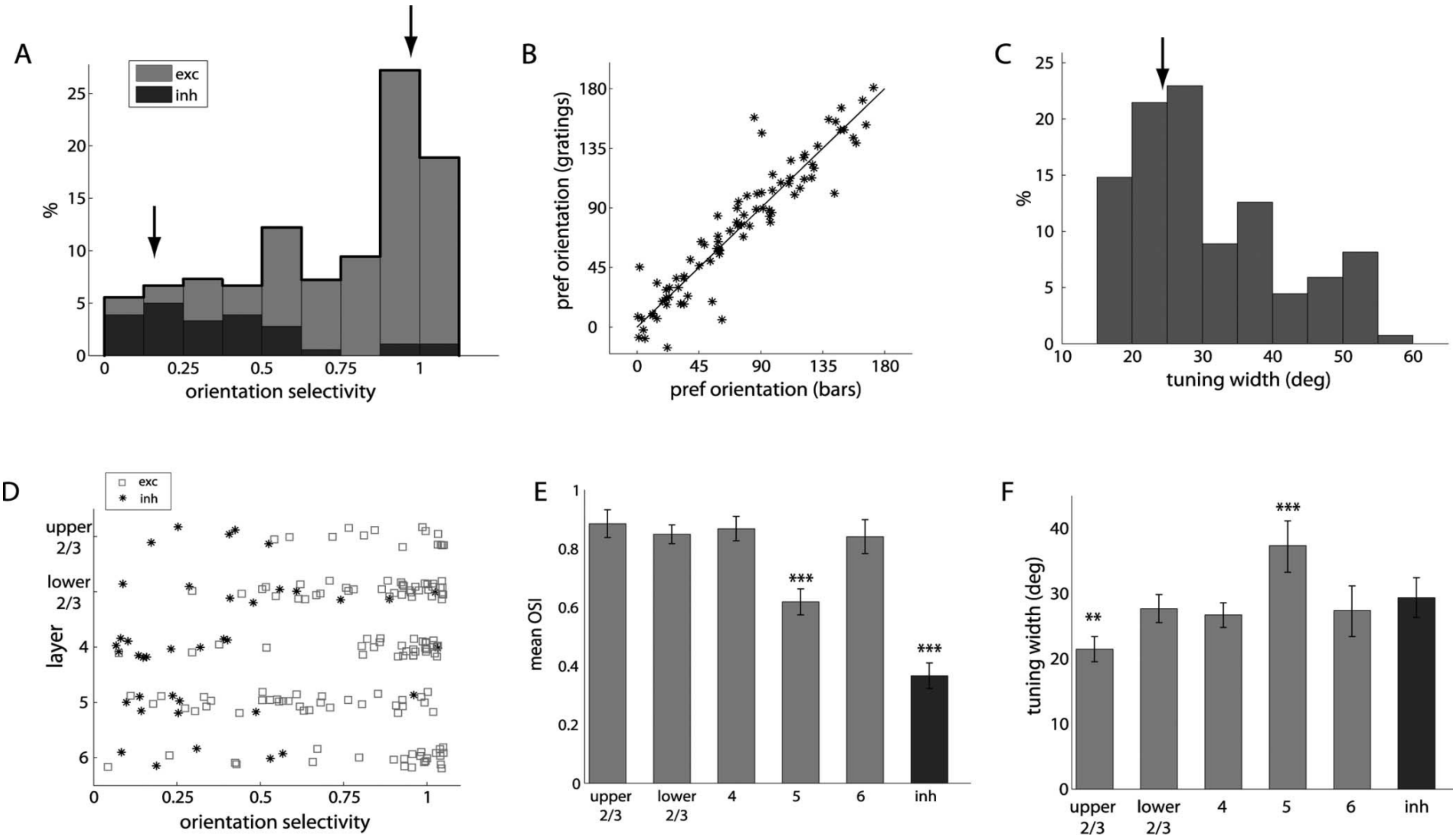
Organization of inputs to V1 cortical neurons in mouse



Jia et al., 2010

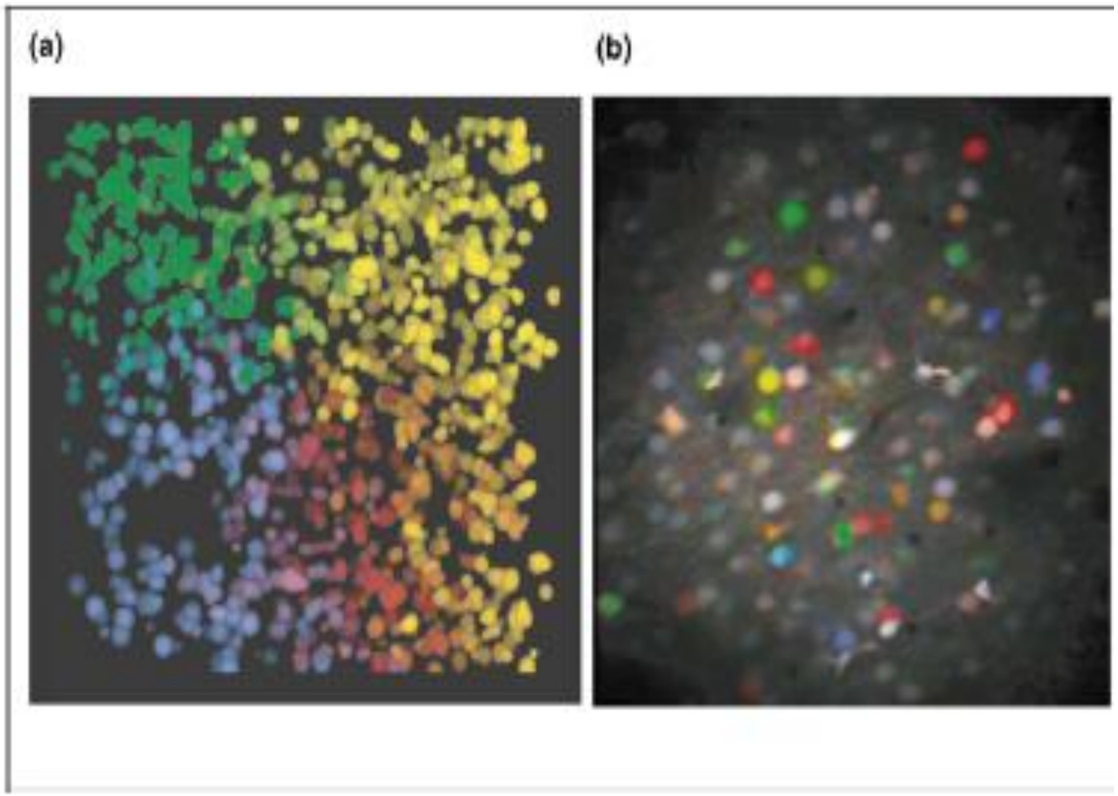
Dendritic calciul signals evoked by drifting gratings at different orientations

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.