Feedforward, Lateral and Feedback interactions in Visual Cortex

Alessandra Angelucci
Professor

MORAN EYE INSTITUTE – *University of Utah*

Supported by: NSF, NIH, RPB

ACKNOWLEDGMENTS

ANATOMY AND IMAGING:

Fred Federer, *postdoc*
Sam Merlin, *postdoc*
Jeff Yarch, *PhD student*
Kesi Sainsbury, *Technician*

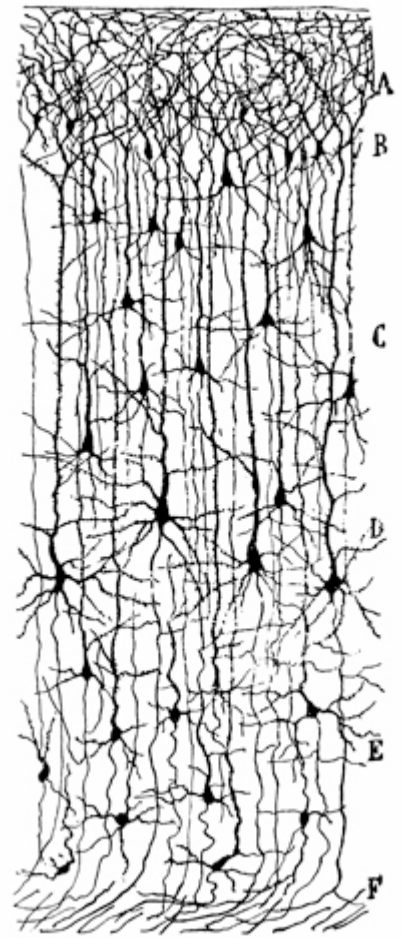
PHYSIOLOGY:

Jennifer M. Ichida, *former postdoc*
Shushruth, *former PhD student*
Maryam Bijanzadeh, *PhD student*
Lauri Nurminen, *postdoc*

MODELING:

Paul Bressloff, *collaborator, Mathematics, Univ. Utah*
Lars Schwabe, *collaborator, Computer Sci., Univ. Rostock (Germany)*

Research goal: Understand how neural circuits compute neuronal responses in the visual cortex and visual perception.



Ramon y Cajal, 1904

The six layers of the neocortex

?

Escalante River
Southern Utah

What do theories of neural computation need? Be provocative!

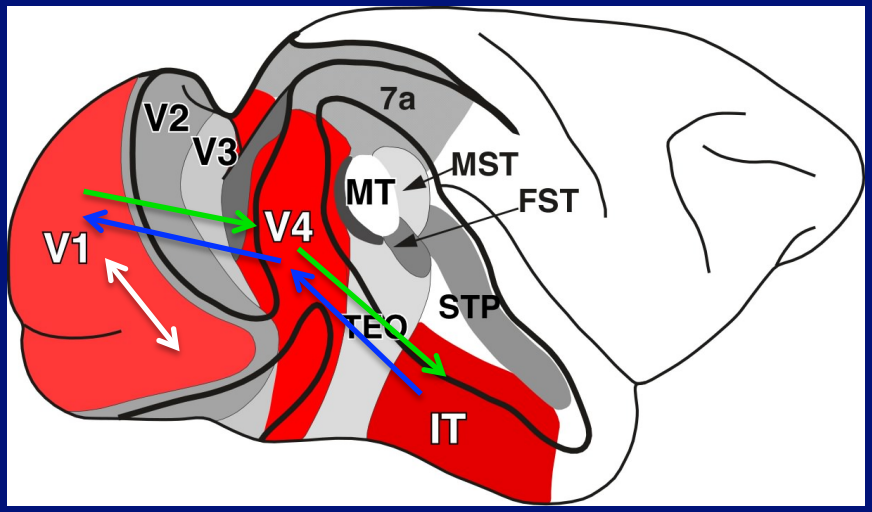
1. Need to go beyond hierarchical feedforward processing

2. We need to understand anatomy and function of feedback connections

3. I am going to challenge traditional views of feedback organization

4. I am going to emphasize that there is a lot of specificity in the connectivity, at different scales (from areal to single cell types). Theoretical models need to incorporate this specificity

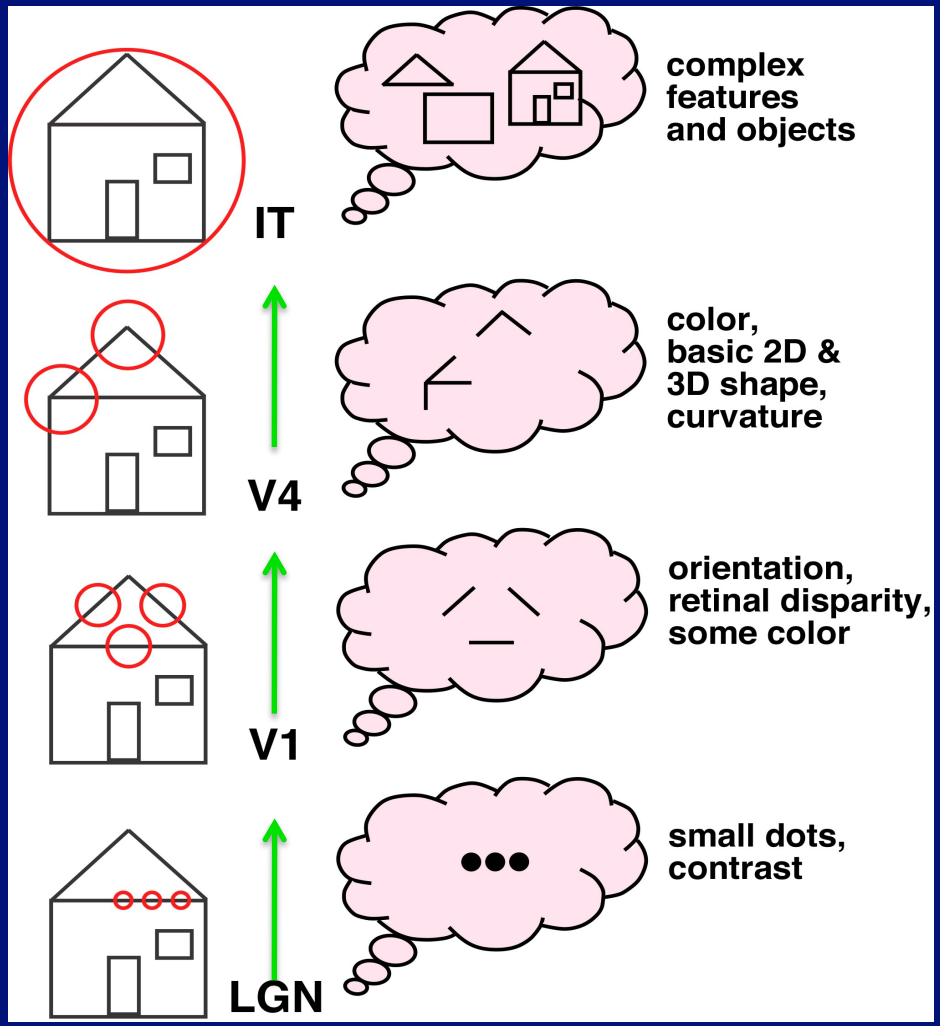
The receptive field and feedforward models of visual processing



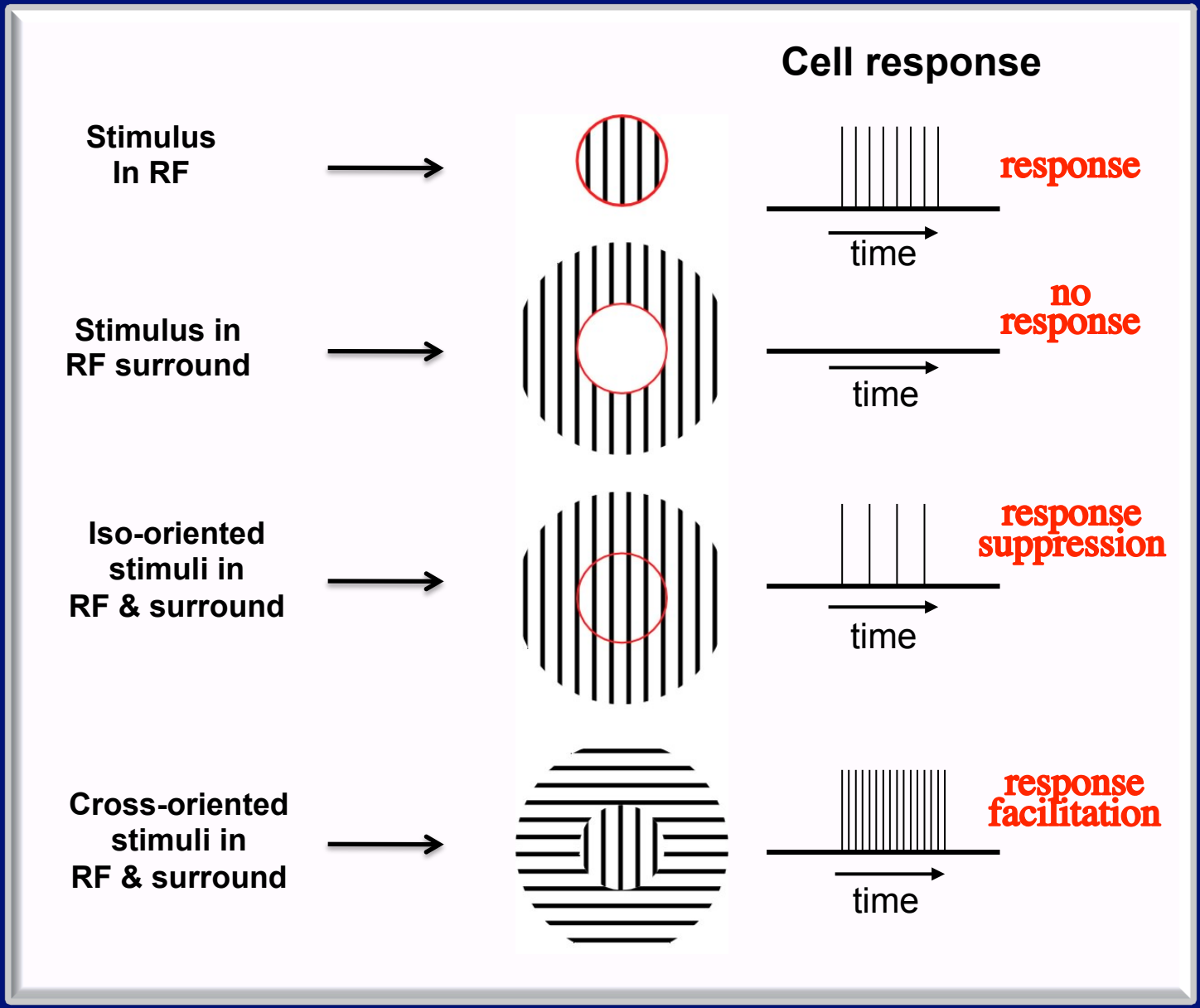
Feedforward (bottom-up)

Feedback (top-down)

Horizontal (lateral)

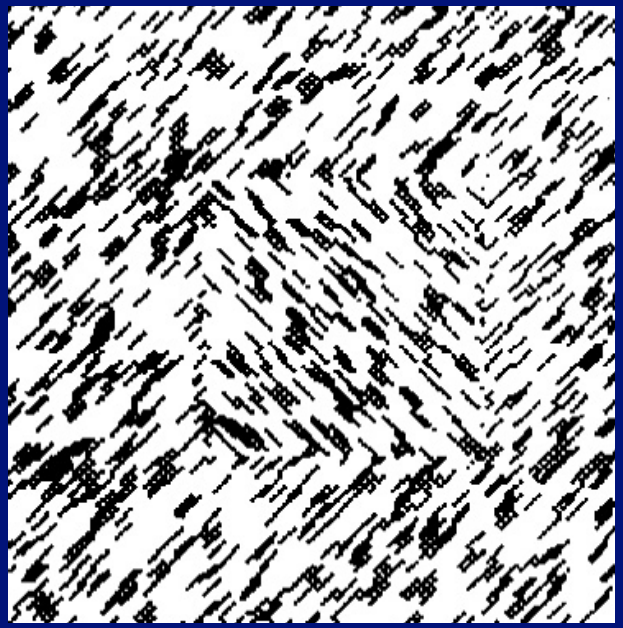


Surround Modulation



Role of surround modulation in visual perception:

Figure-ground



1. Figure-ground segregation
(Lamme 1995; Li 1999; Malik & Perona 1990)

2. Detection of salient targets for subsequent saccades
(Petrov & McKee 2006)

3. Optimal coding of visual information (contrast normalization, redundancy reduction in natural images)
(Schwartz & Simoncelli 2001; Vinje & Gallant 2000, 2002)

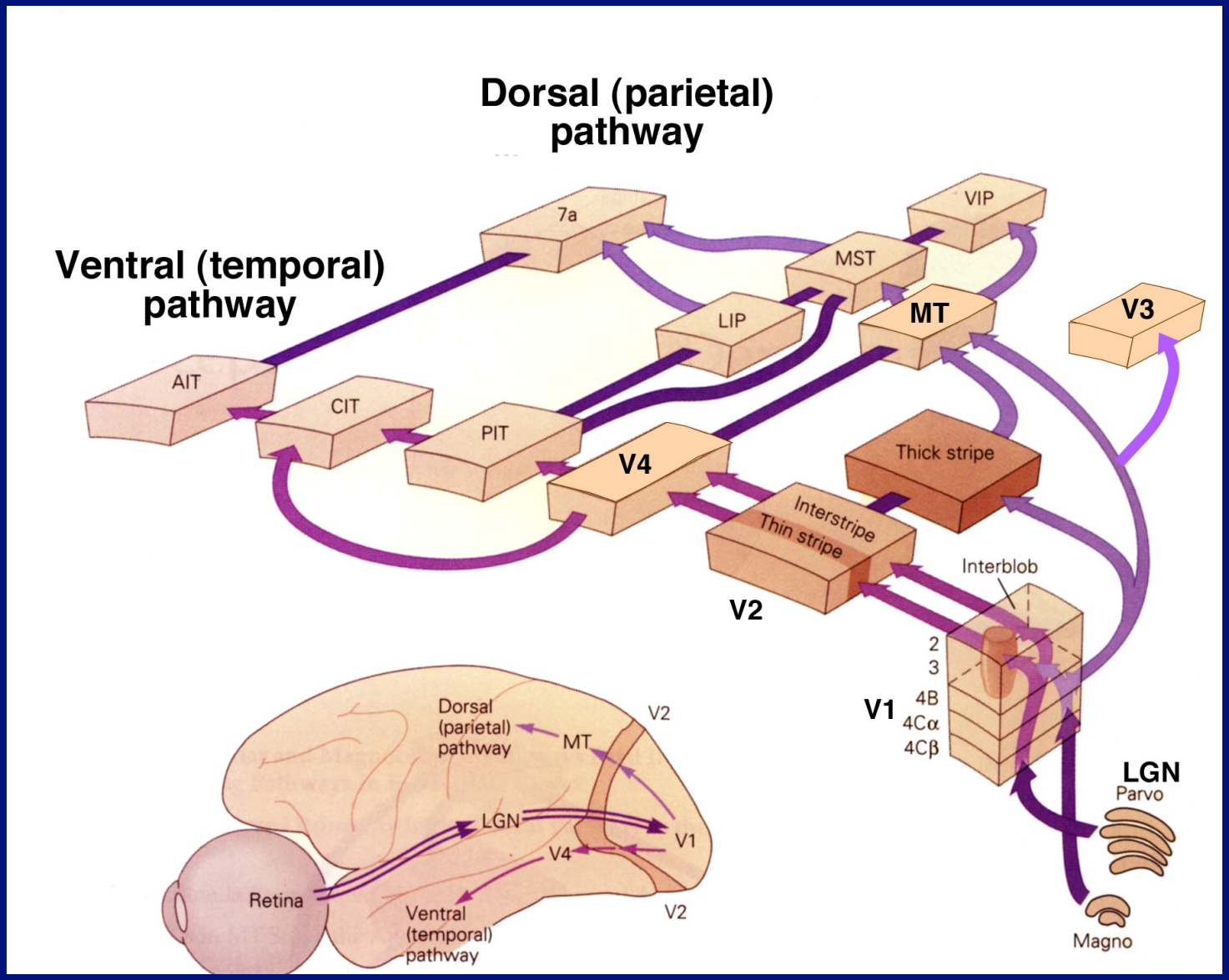
Presentation outline

1. Anatomy of FF, H, FB circuits
2. Possible functions
3. Mechanisms

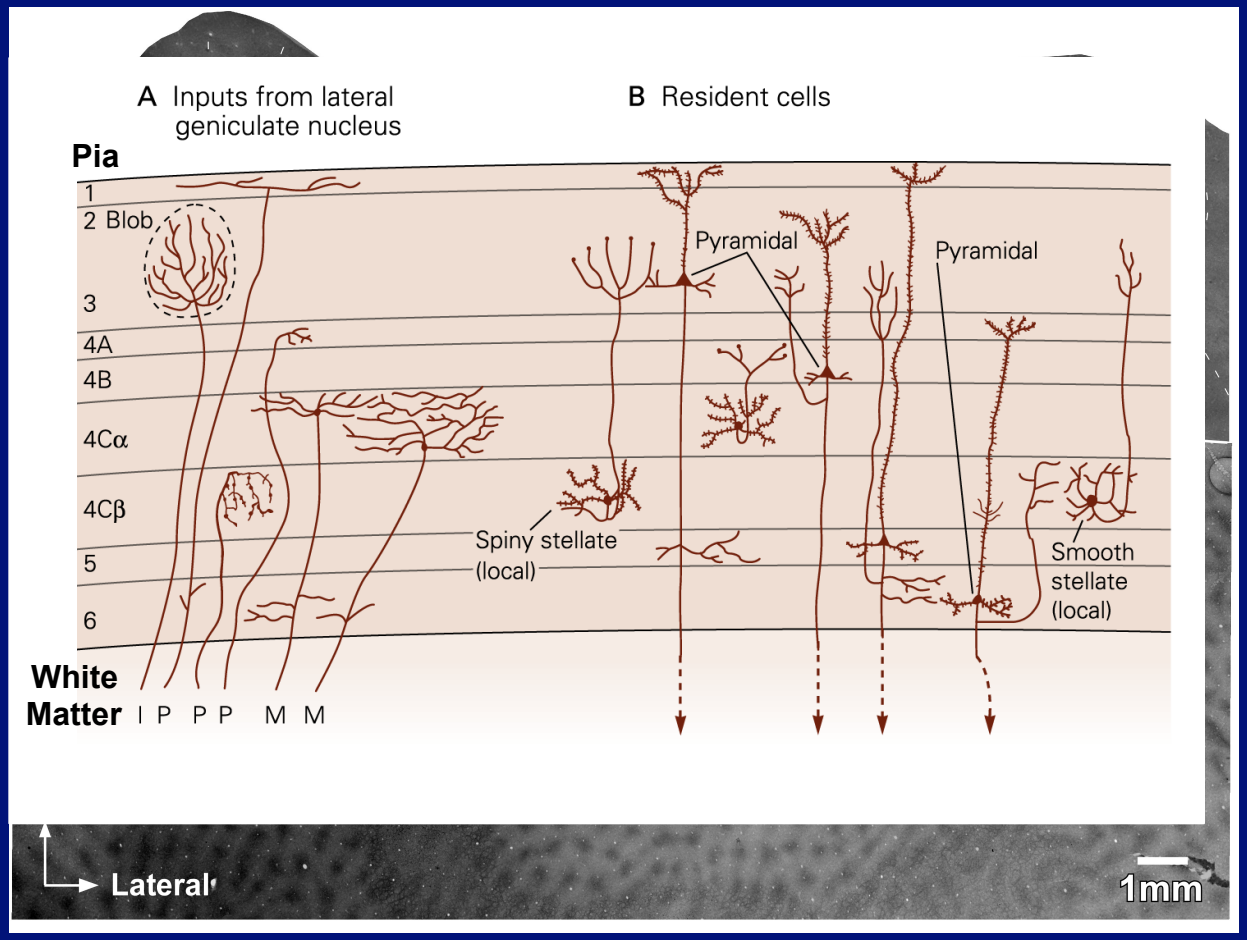
1. Anatomy of FF, H and FB

similar anatomical and functional specificity at different scales

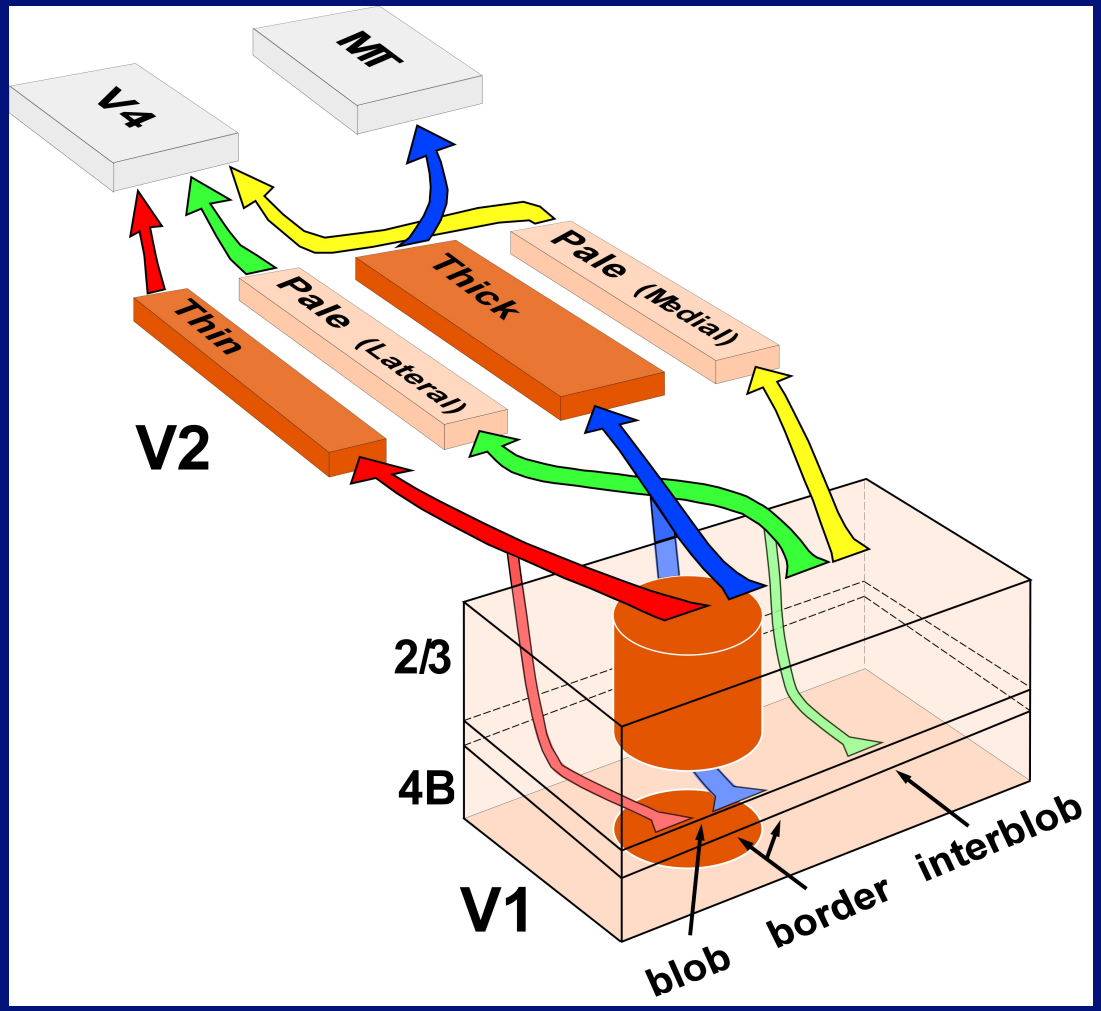
FF: Parallel processing: areal specificity



FF: Parallel processing: compartmental and laminar specificity

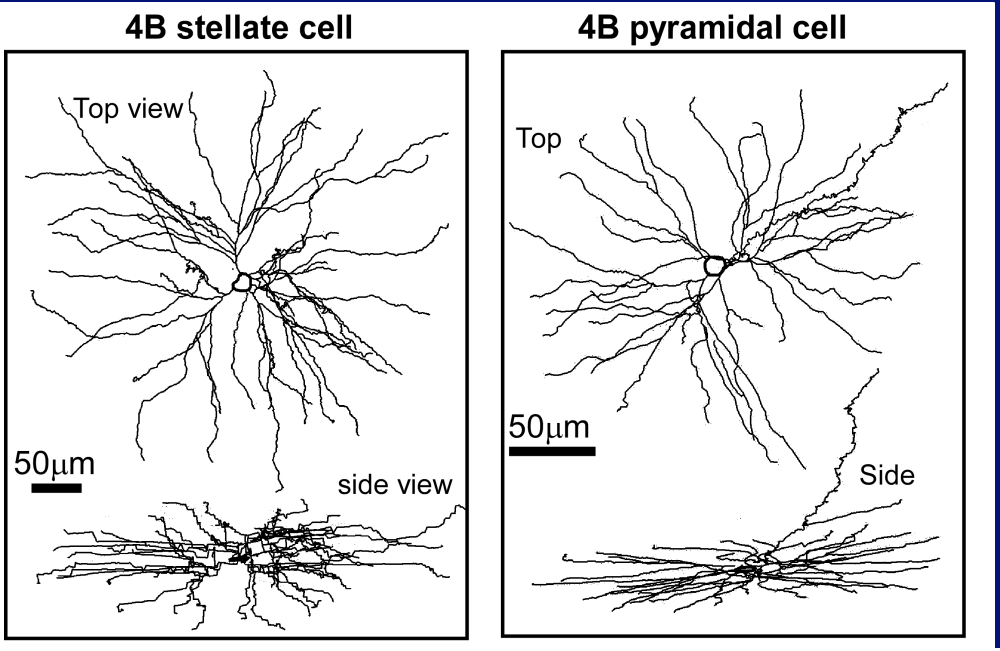


FF: Parallel processing: compartmental and laminar specificity

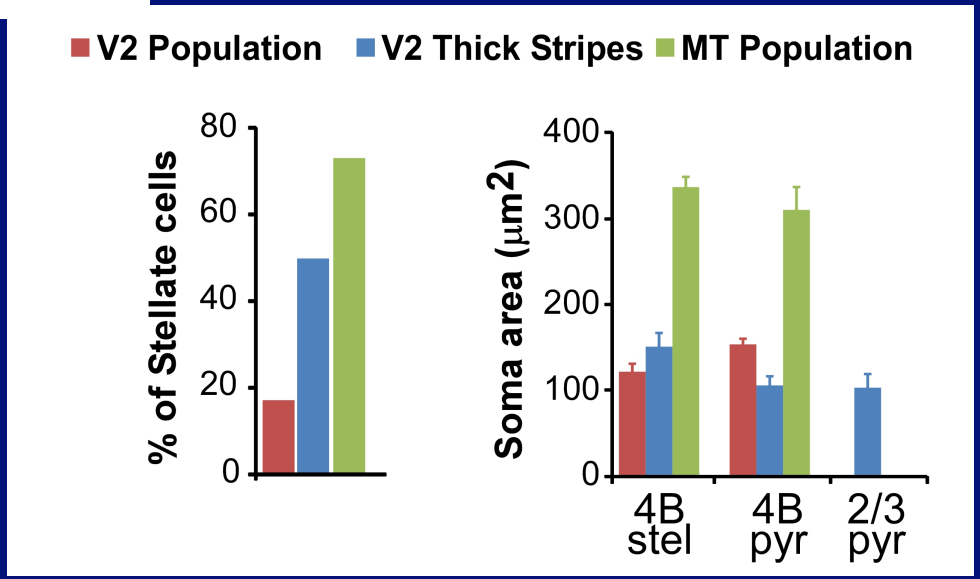


Federer et al. J Neurosci 2009 (marmoset), 2013 (macaque)

FF: Parallel processing: cell-type specificity

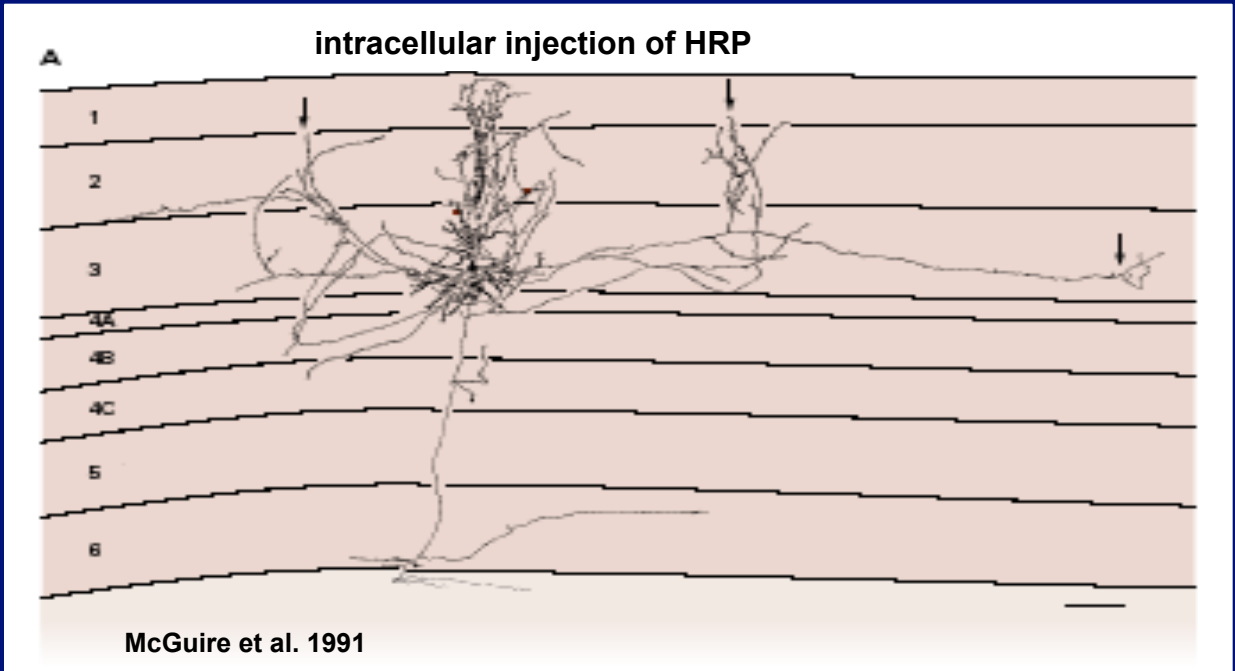


Reconstructions of V1 L4B cells labeled by injections of G-deleted rabies virus-GFP in V2 thick stripes



Yarch et al. SFN 2013
Nassi and Callaway, 2007

Horizontal (H) connections: compartmental and laminar specificity



Properties of HC in V1 Layer 2/3:

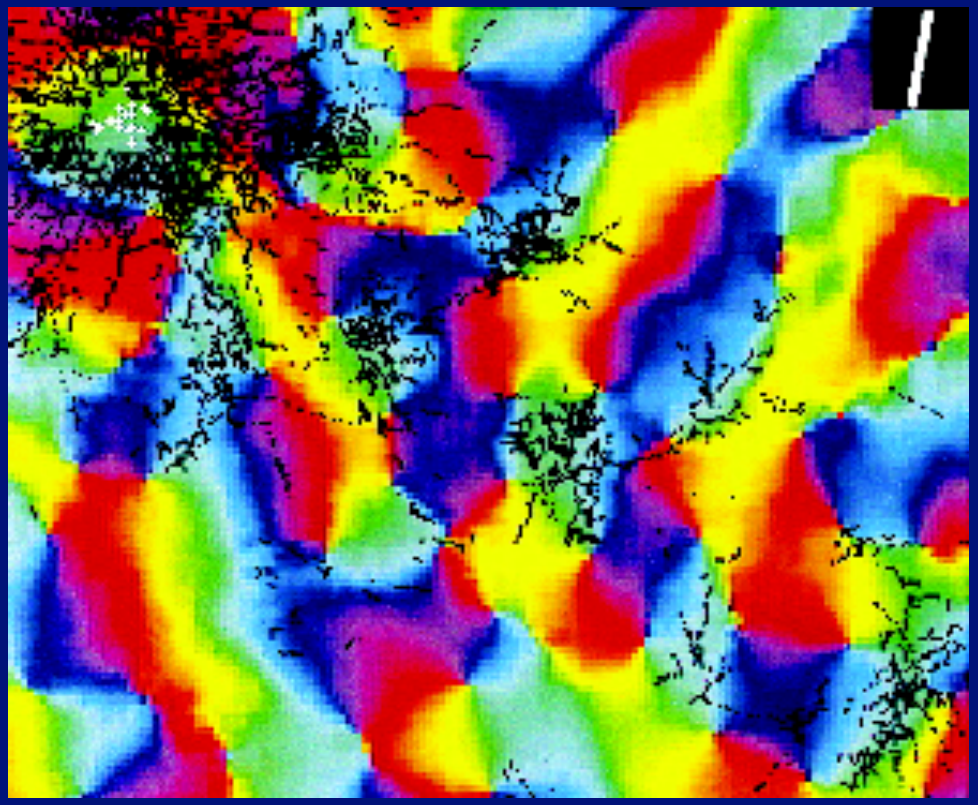
1. Long-range (6-9 mm diameter)
2. Intralaminar
3. Patchy and Reciprocal
4. Arise from pyramidal (excitatory cells) and terminate on excitatory (80%) and inhibitory (20%) neurons
5. Link neurons in same V1 CO compartments, and same ocular dominance

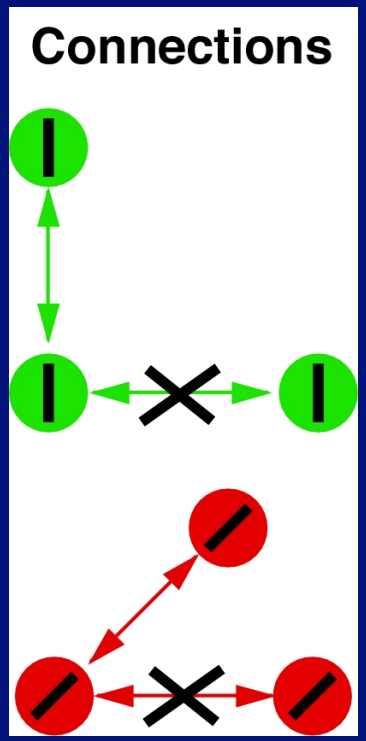
Laminar Specificity:

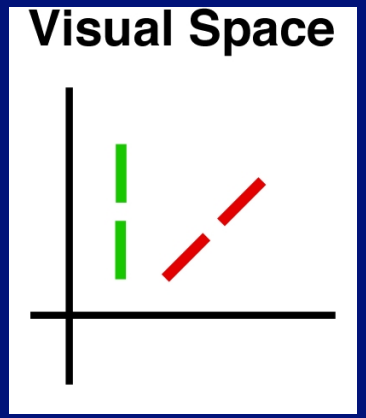
- Exist in all layers except L4C (V1) and L4 (extrastriate)
- Less patchy and more extensive in L6

V1 H connections: orientation specificity

– In layers 2/3 link V1 regions of similar orientation preference



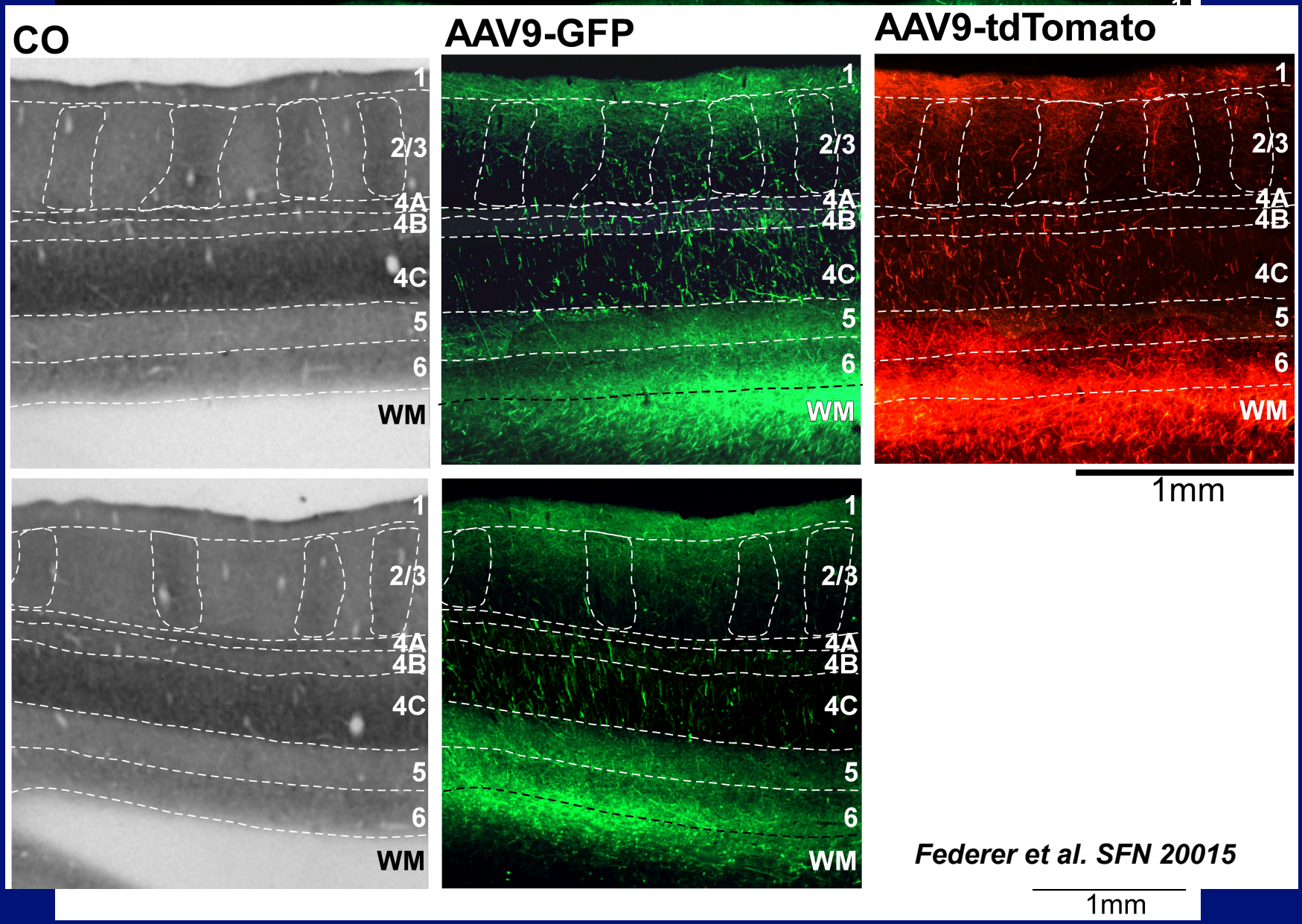




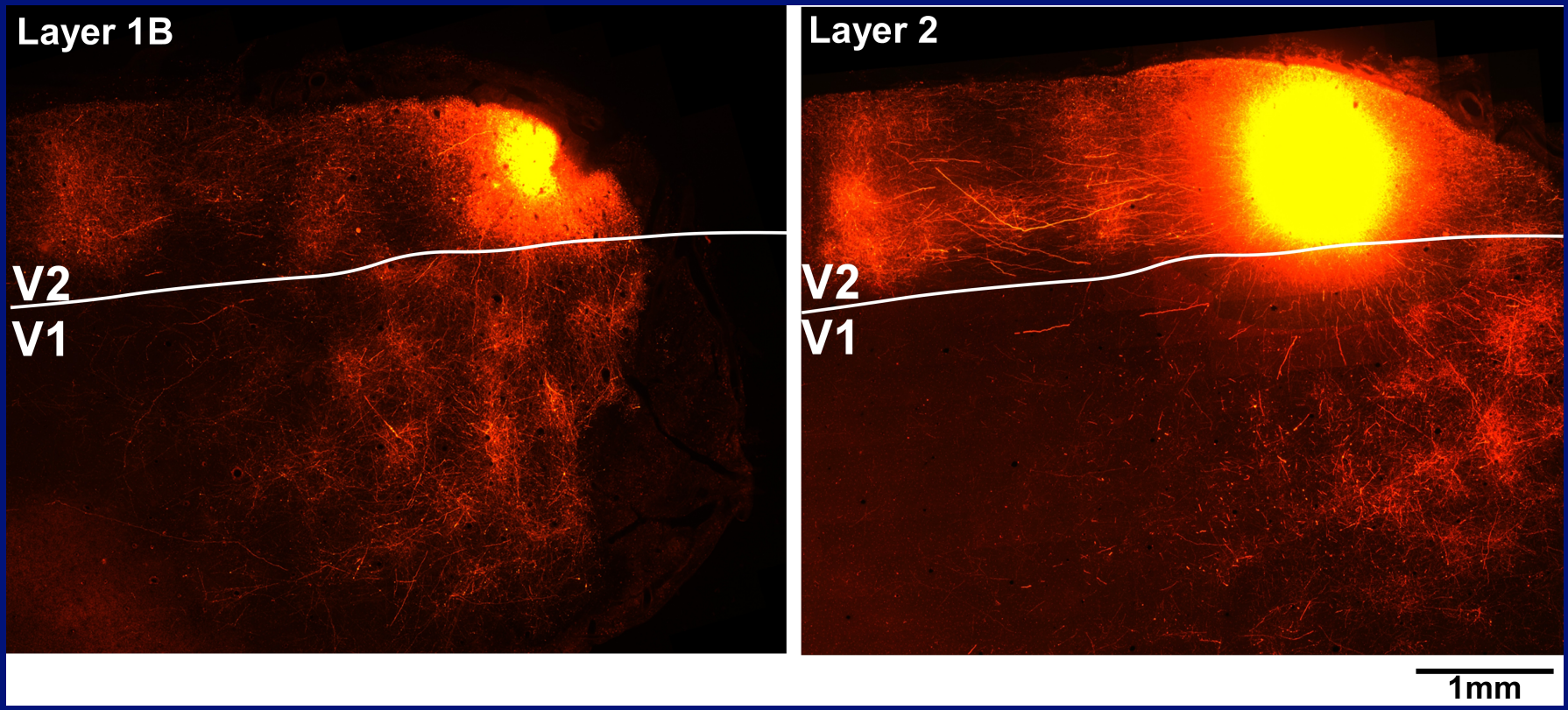
Bosking et al. (1997)

FB connections: specific or not specific?

FB connections: laminar specificity

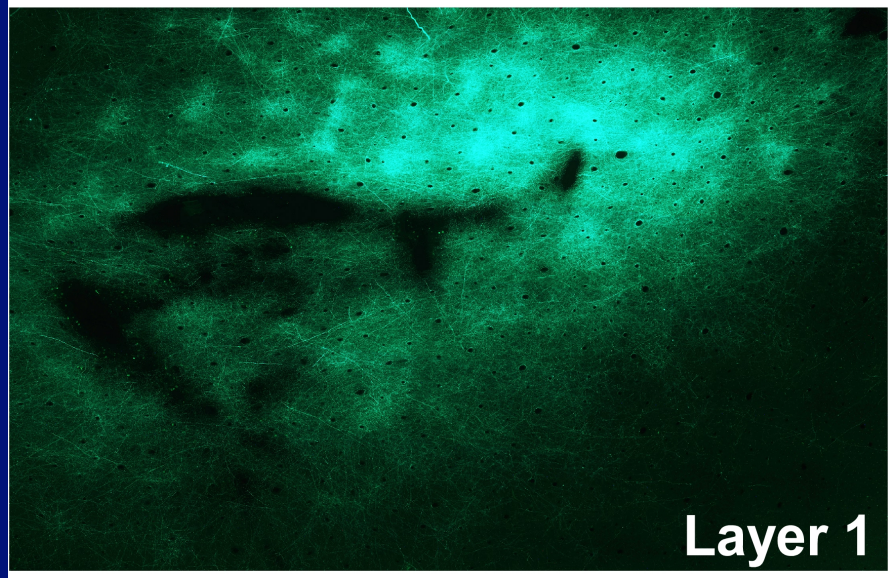


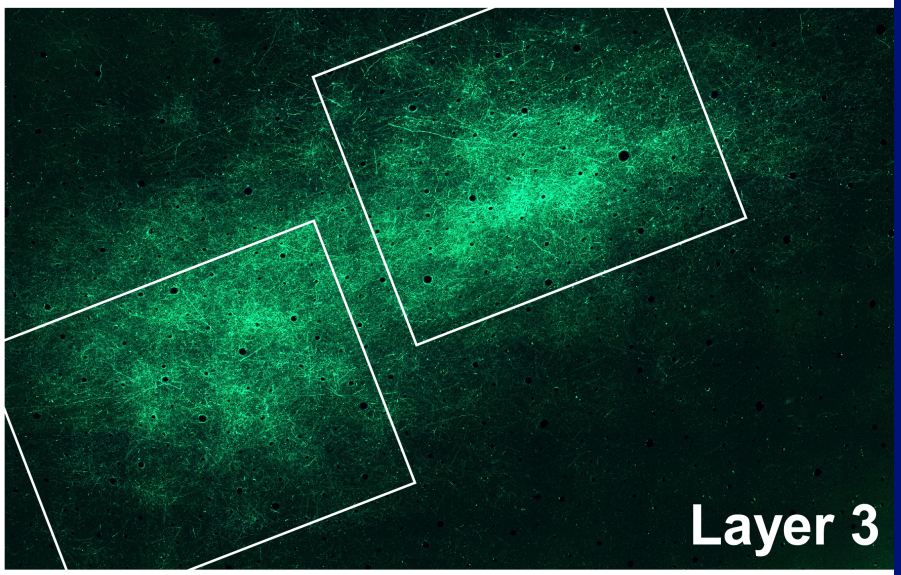
Patchy FB terminations

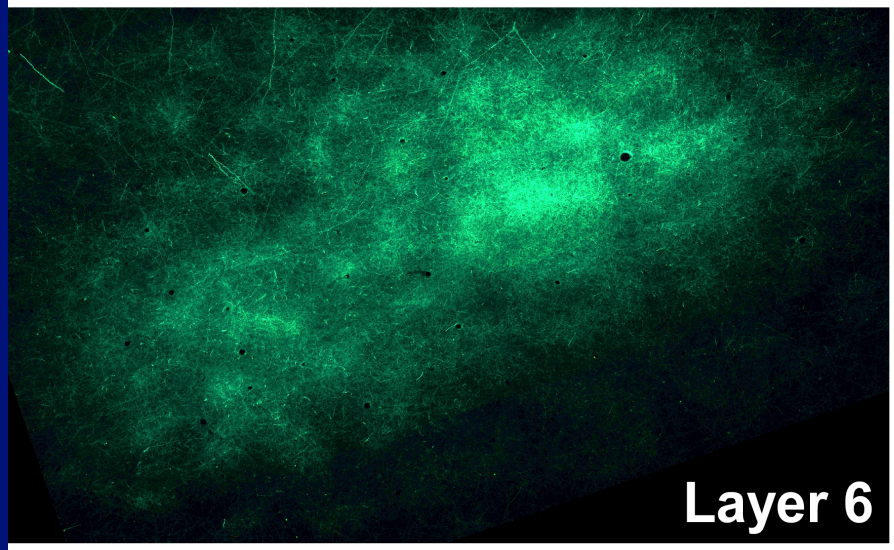


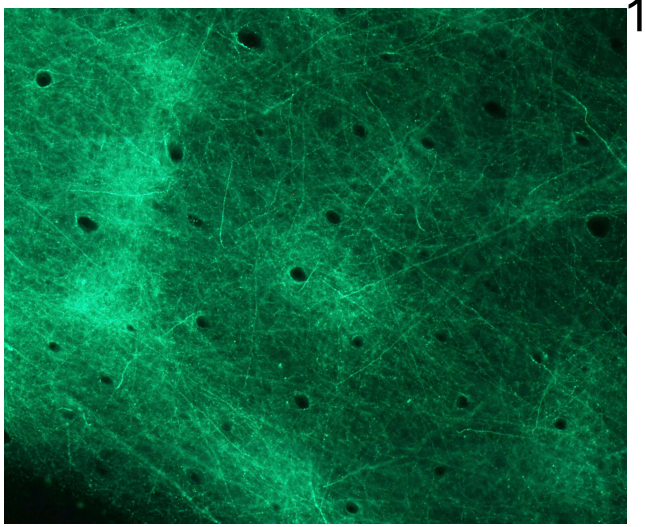
Federer et al. SFN 2015

Patchy FB terminations





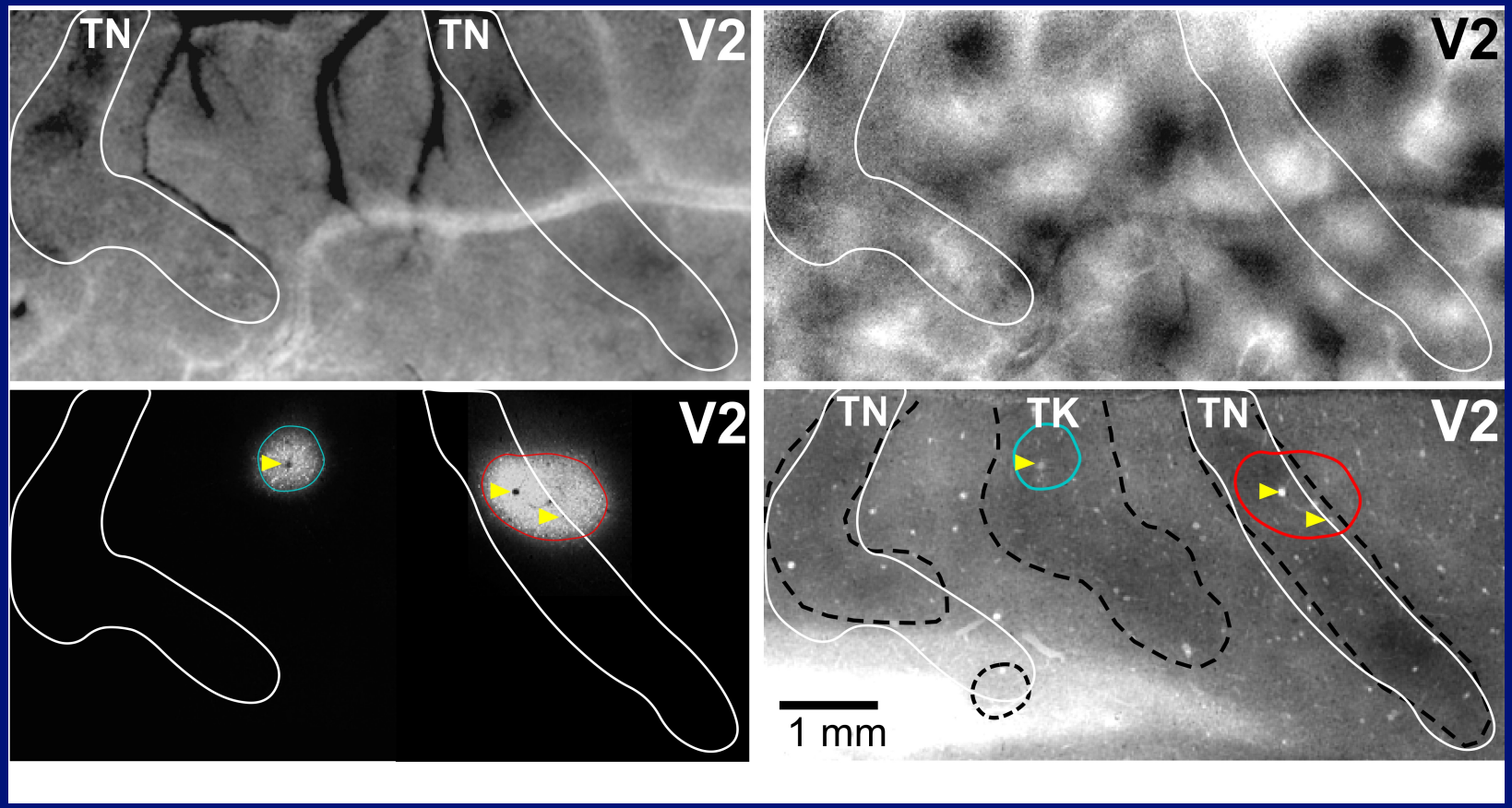




Federer et al. SFN 2005

Federer et al. SFN 2015

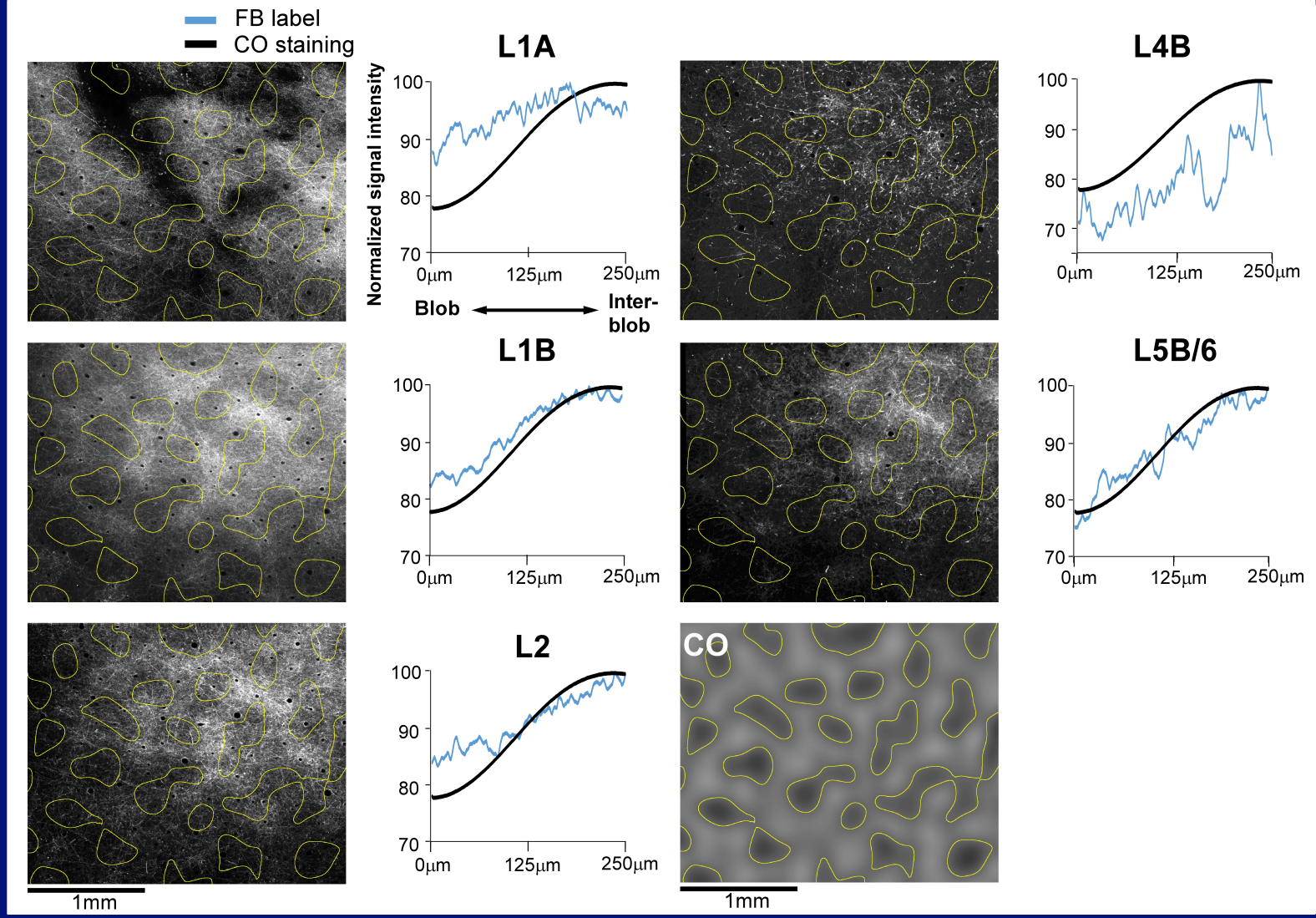
Patchy FB terminations



Federer et al. SFN 2015

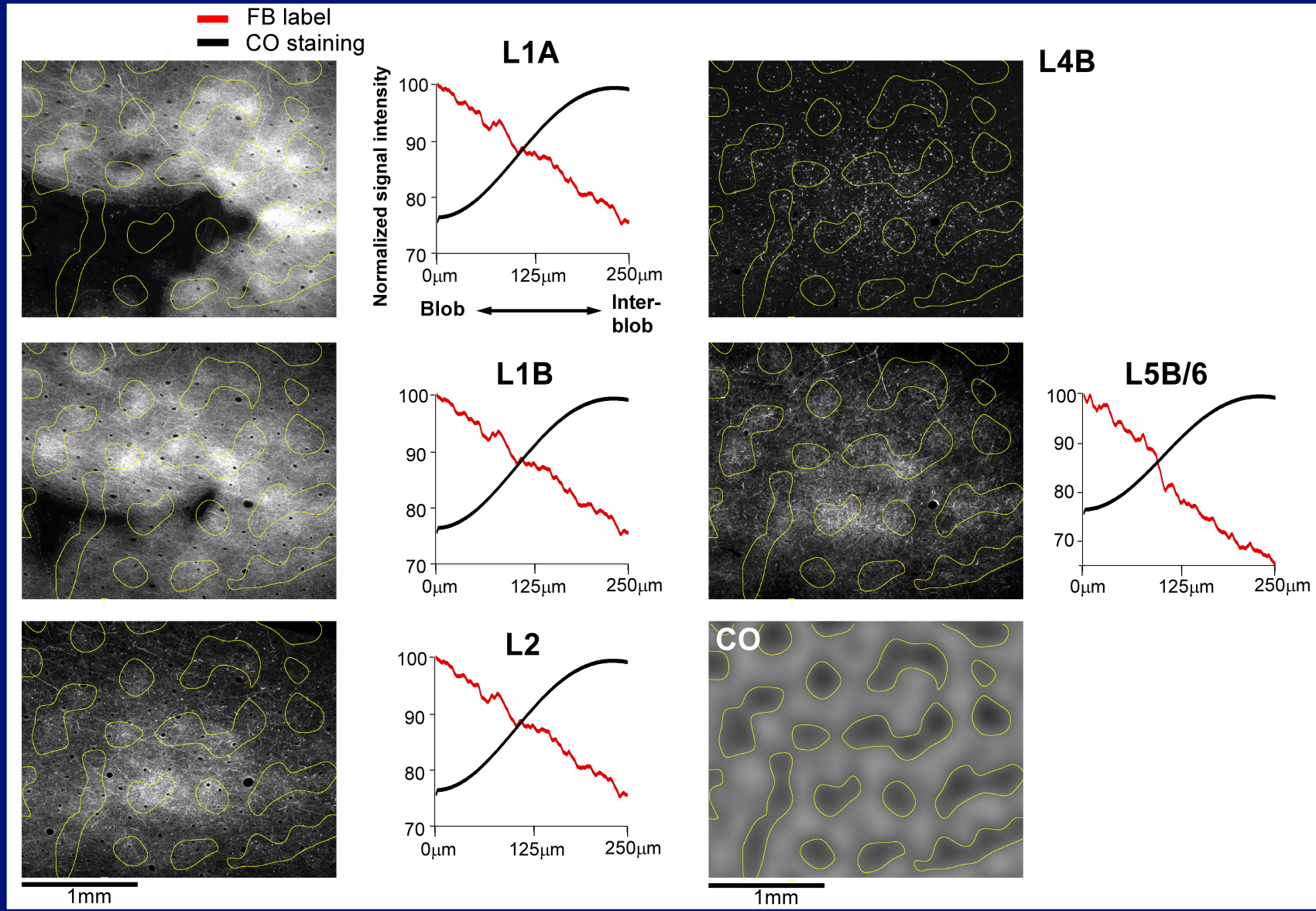
FB connections: compartmental specificity

THICK stripe injection



FB connections: compartmental specificity

THIN stripe injection



ANATOMY OF FF, H, FB: SUMMARY

FF V1-to-V2 connections:

- arise from pyramidal cells in V1 L2/3, 4B, 6
- terminate in V2 L3B-4
- are area, compartment and cell type specific
- drive target cells

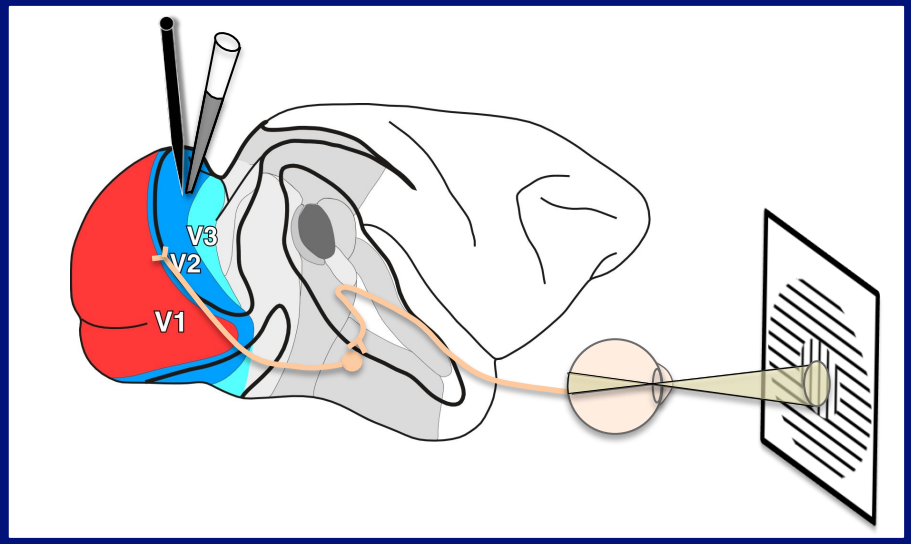
Intra-V1 H connections:

- exist in all layers except 4C and 1
- are compartment specific
- are orientation-specific (in L2/3) – collinearity axis
- modulate target cells

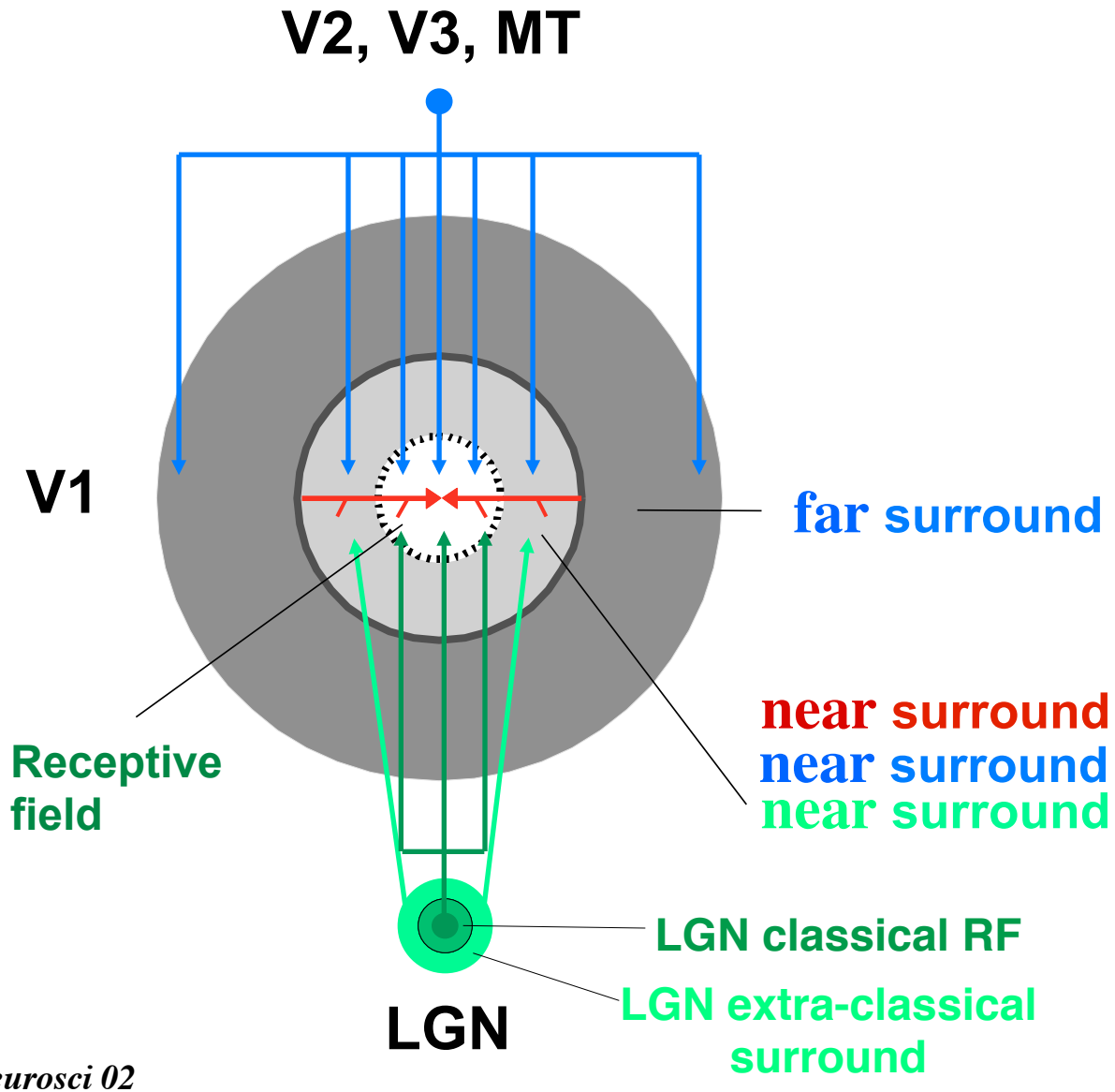
FB V2-to-V1 connections:

- arise from pyramidal cells in V2 L2/3A, 5/6
- terminate in V1 L1-2, 3A, 4B, 5B, 6B
- are area, compartment specific
- Are functionally (orientation specific) - – collinearity axis
- likely to directly contact FF-projecting cells
- modulate target cells

Visuotopic extent of FF, H and FB connections



Angelucci et al. J Neurosci 02
Angelucci & Sainsbury, J Comp Neurol 06



Angelucci et al. J Neurosci 02
Angelucci & Sainsbury, J Comp Neurol 06

2. Function of FF, H and FB

1. FF connections contribute to the RF size and tuning properties of their target cells

2. H and FB connections contribute to surround modulation at different spatial scales.

FB connections are as fast as FF connections and 10 times faster than H connections

Horizontal axons' conduction velocities= 0.1-0.3 m/s
Feedback axons' conduction velocities= 2-6 m/s

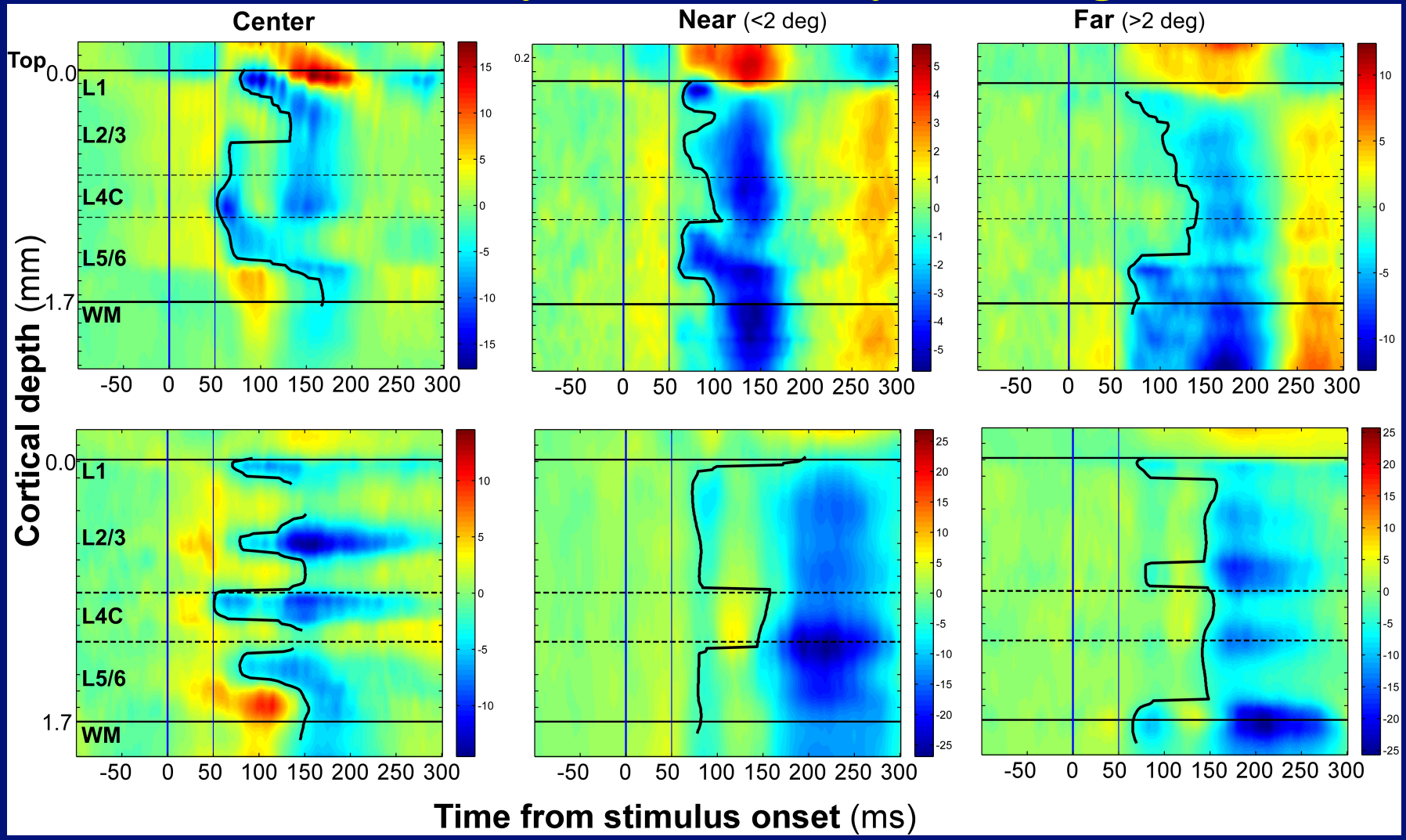
(Grinvald et al. '94; Bringuier et al. '99; Girard et al. '01; Slovin et al. '02)

Onset of far surround suppression = 9-60 ms

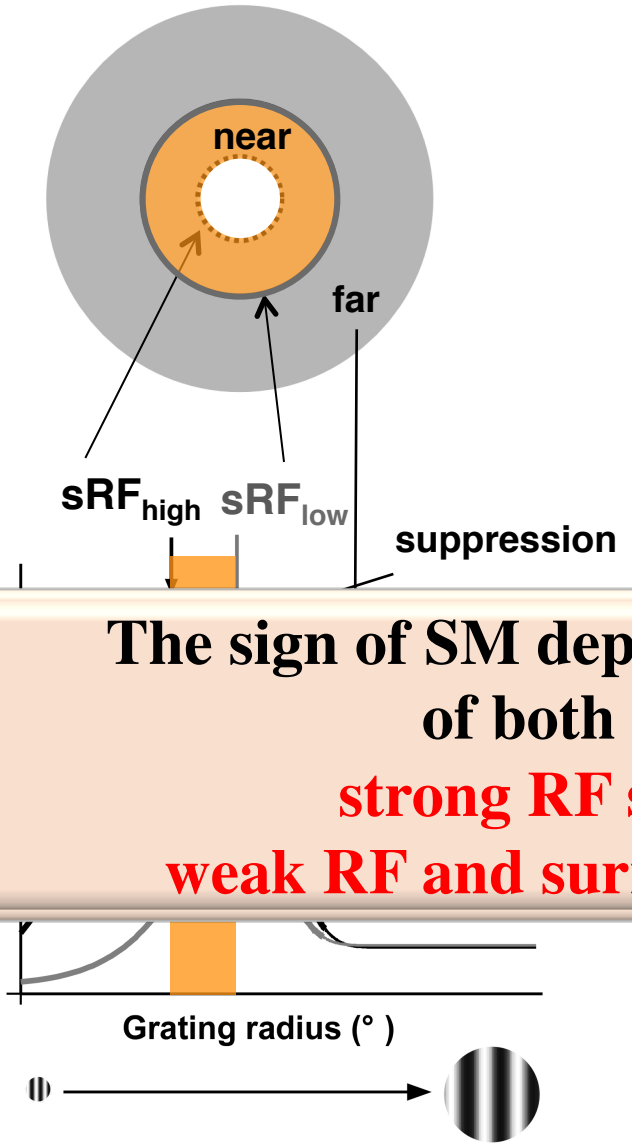
(*Knierim & Van Essen '92; Hupe' et al. '01; Bair et al. '03*)

It would take >290 ms for horizontal connections to cover a distance of 13 deg (the far surround)

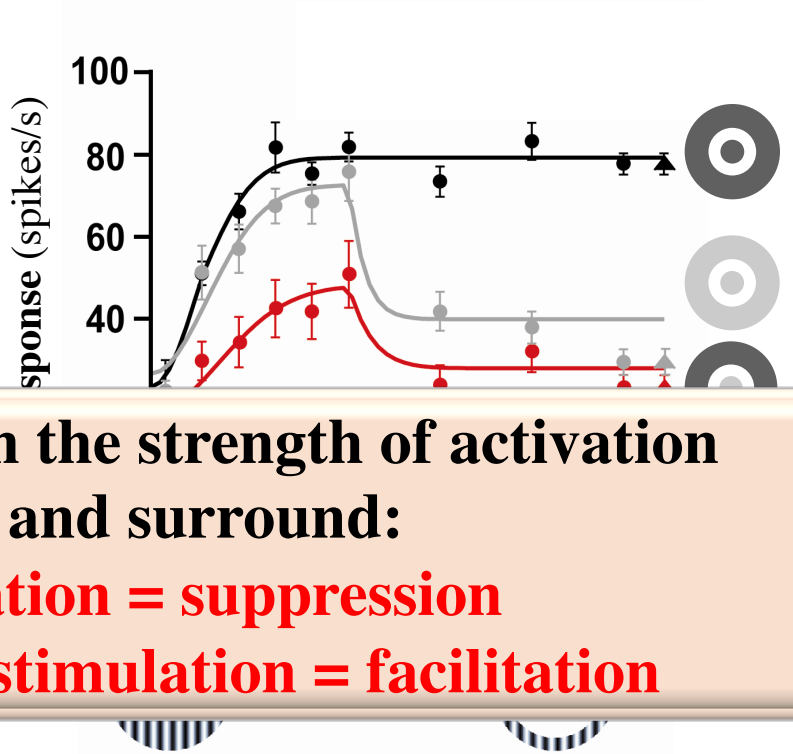
Center, near and far surround stimuli activate different V1 layers: linear array recordings



Near and far surround facilitation and suppression



Sceniak et al., 1999



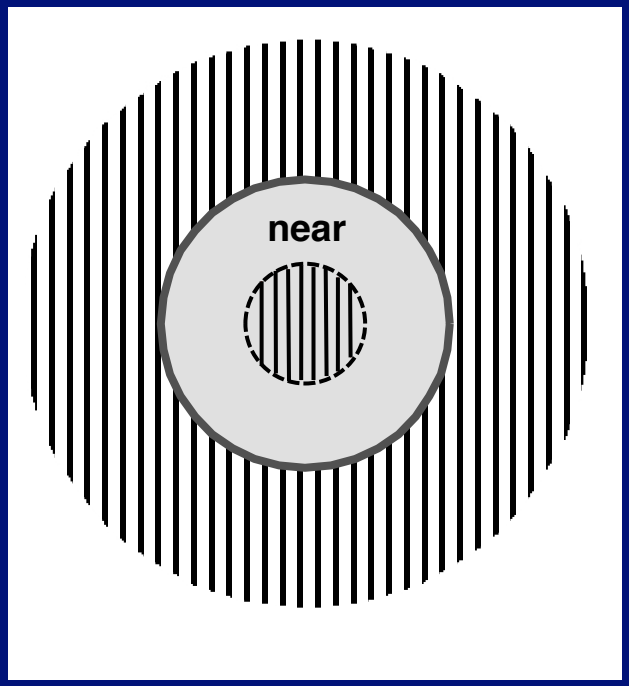
Ichida et al., J Neurophysiol. 2007
Shushruth et al., J. Neurophysiol. 2009

The sign of SM depends on the strength of activation of both the RF and surround:

strong RF stimulation = suppression

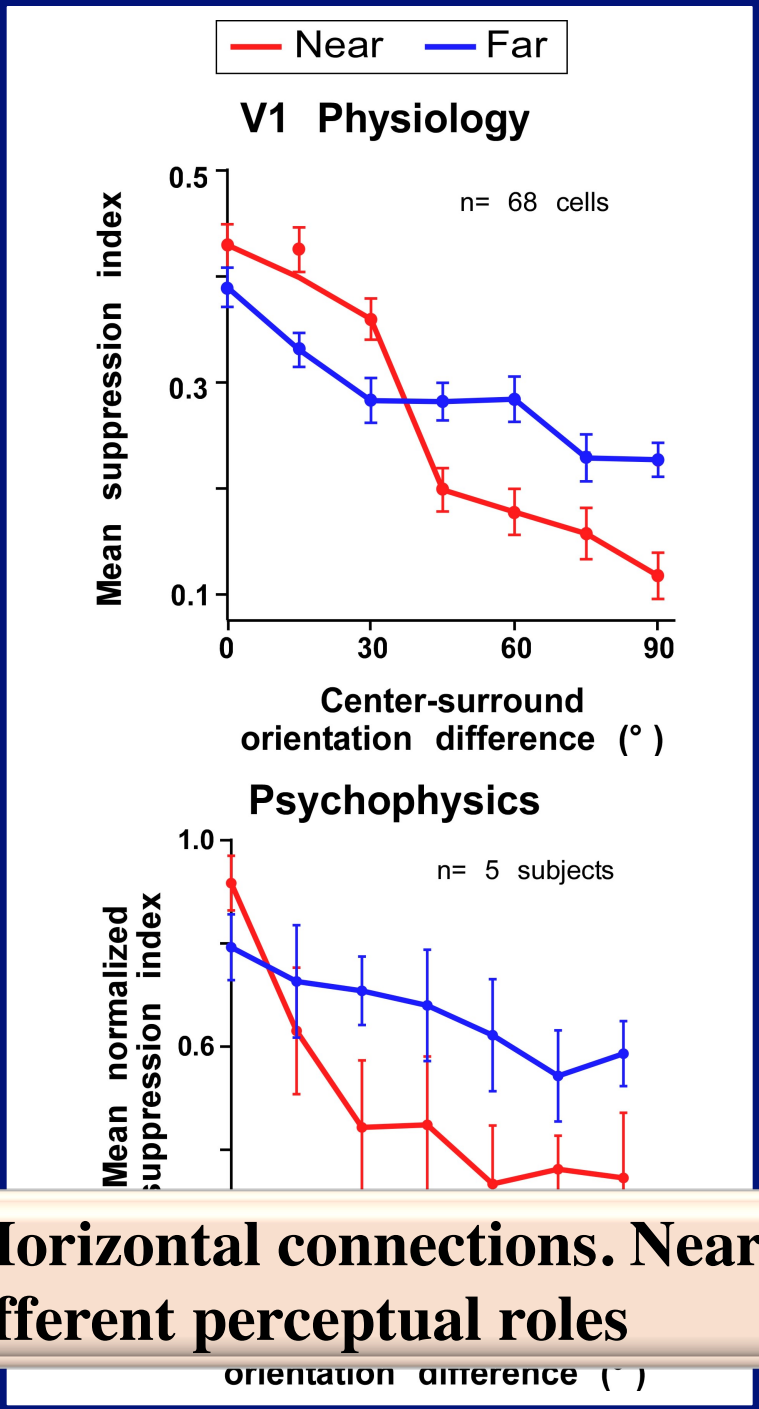
weak RF and surround stimulation = facilitation

Near and far surround suppression differ in orientation tuning



SUPPRESSION INDEX

$SI = 1-(R_{CTR+SURR} / R_{CTR})$



FB is less orientation specific than Horizontal connections. Near and far surround may have different perceptual roles

3. Mechanisms for surround modulation: a computational model

Schwabe et al., J. Neurosci. 2006
Schwabe et al. Neuroimage, 2010
Shushruth et al., J. Neurosci., 2012

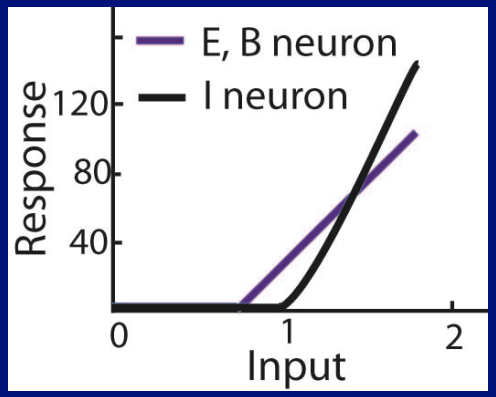
Collaborators:

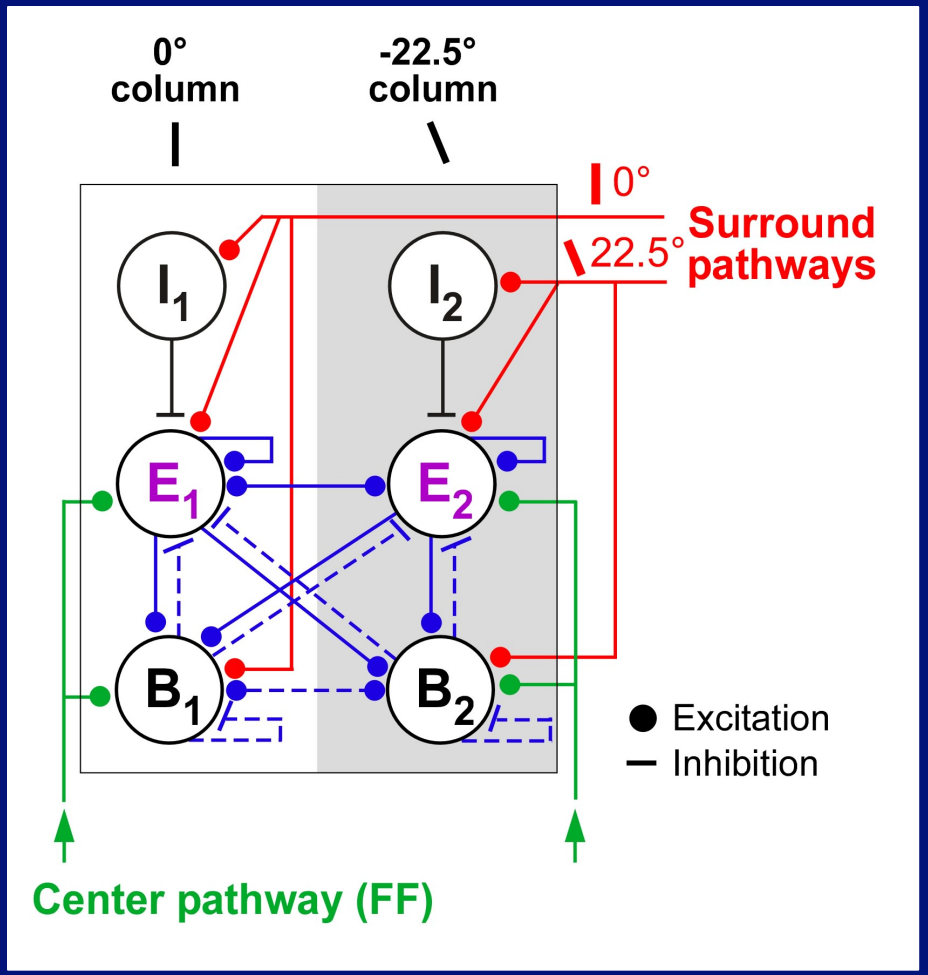
– **Paul Bressloff,** , *Mathematical Institute, Oxford University (UK)*

– **Lars Schwabe,** *Computer Science Dept., Rostock University (Germany)*

Key Properties

- High threshold and gain I neurons
- Orientation specific intra-areal horizontal and inter-areal feedback connections .
- Network is operated in a regime of strong, but balanced recurrent local connections between E and B neurons





Model predictions stem from E-I neurons response asymmetry

1) **Expansion of the RF size at low contrast (*Sceniak et al.* 1999).**

2) **Far surround facilitation for low contrast center stimuli**
(Ichida et al. J Neurophysiol. 2007)

3) **Near and far surround facilitation for sub-optimally oriented stimuli in the RF center**
(Shushruth et al, J. Neurosci. 2012)

4) **Weaker surround suppression for lower contrast center-stimuli**
(Schwabe et al., Neuroimage 2010)

SUMMARY

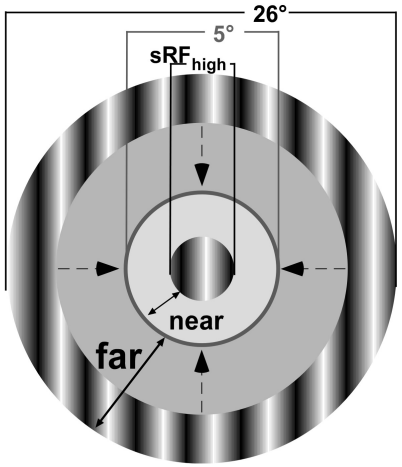
1) H and FB connections show similar functional organizations, and may have a similar impact on V1 neuron responses (both act by modulating the recurrent connections) but act at different spatial and temporal scales.

2) H connections generate orientation-tuned suppression from the near surround, FB connections more broadly tuned suppression from the far surround. Near SM may serve contour detection and far SM visual saliency

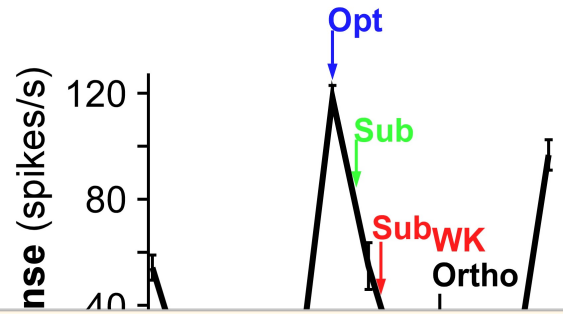
QUESTIONS FOR THEORY AND FUTURE STUDIES

1) Why have different FB systems even within a channel (L2/3A vs 6; FB to different V1 layers). And which one is involved in surround?

Orientation tuning of suppression and facilitation

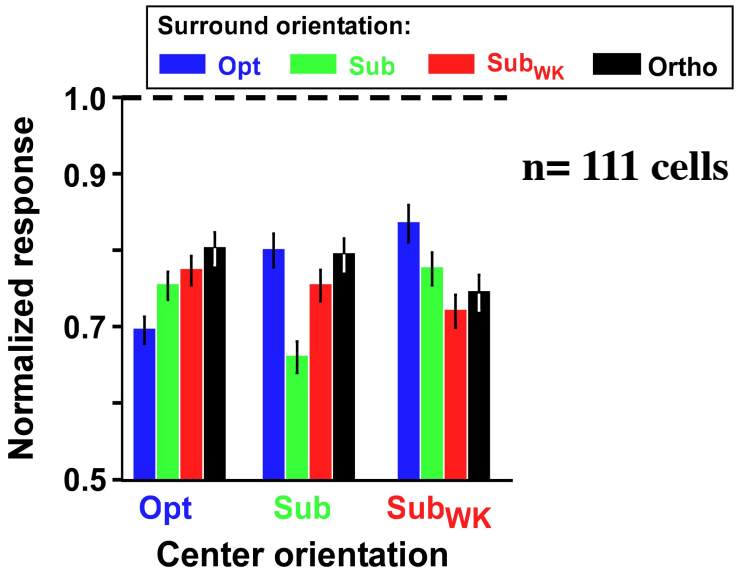


Tuning of sRF

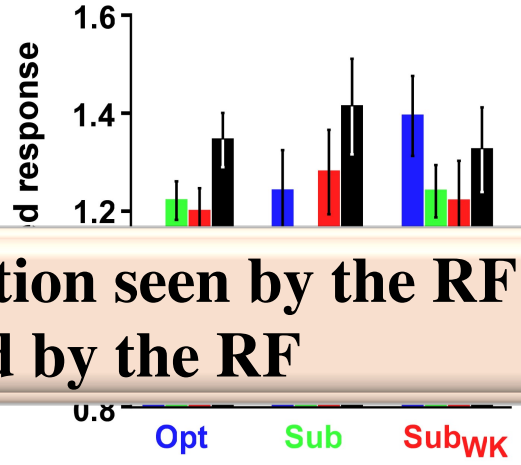


Center orientation (°)

Tuning of surround suppression



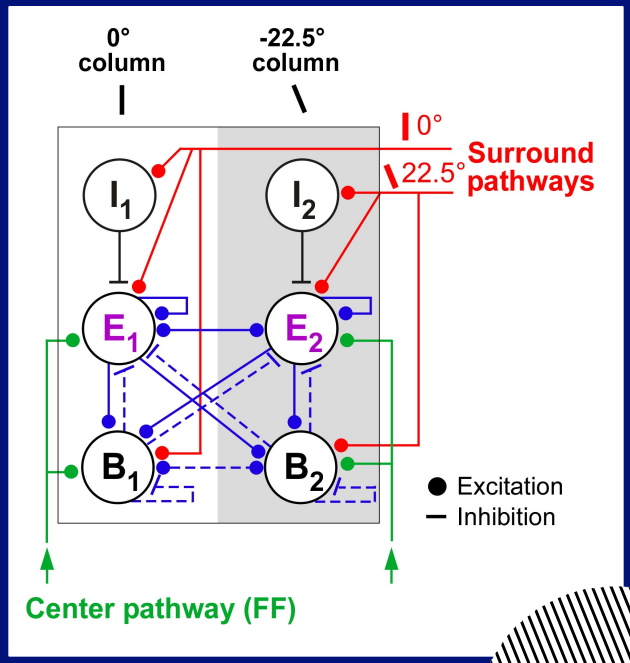
Tuning of surround facilitation



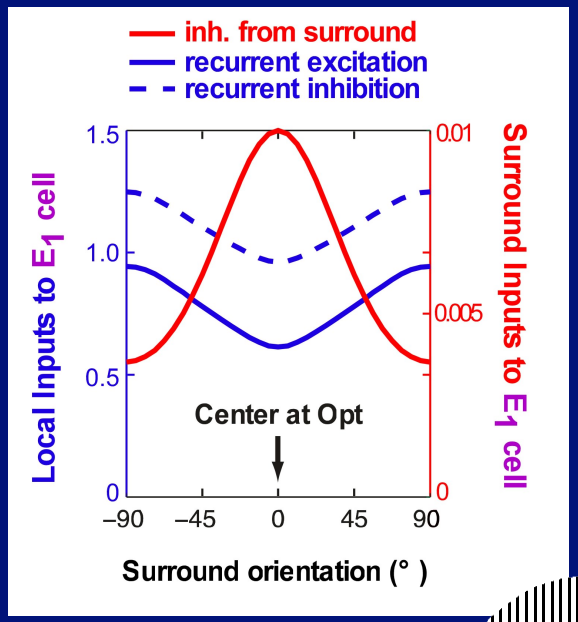
The surround is tuned to the orientation seen by the RF not the orientation preferred by the RF

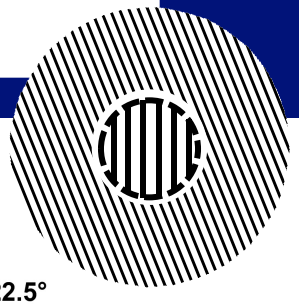
Shushruth et al., J. Neurosci. 2012

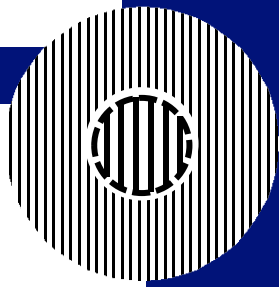
Model: stimulus-dependent orientation specificity of surround modulation



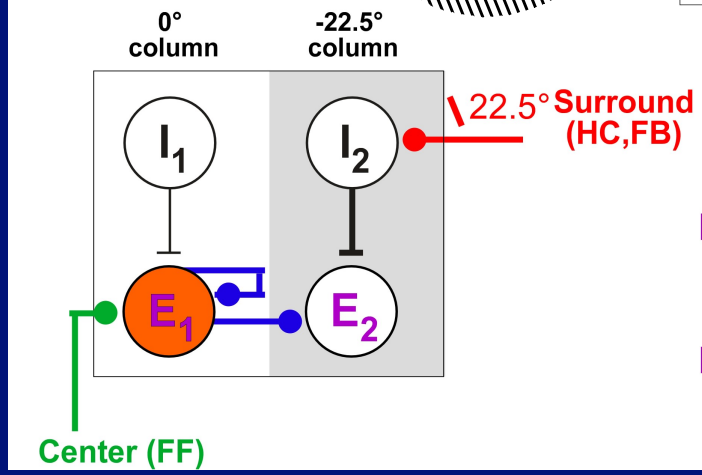
Center at optimal orientation (0°)





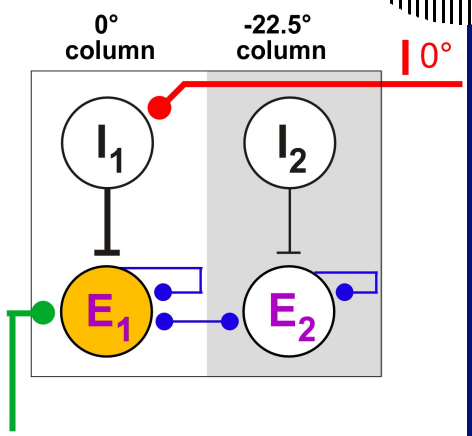


E_1 cell response
Low High

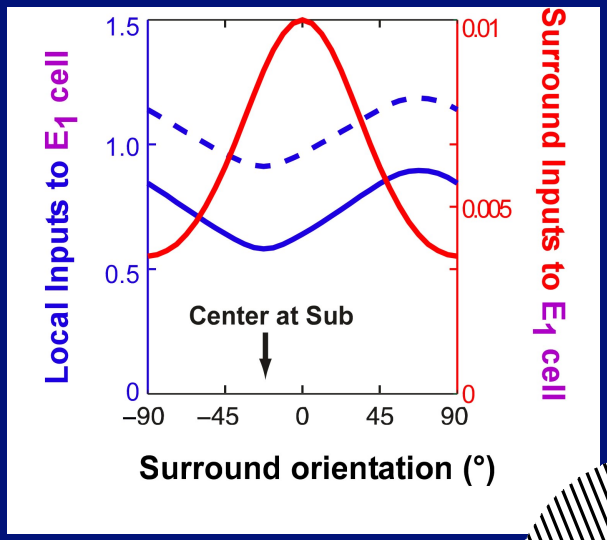


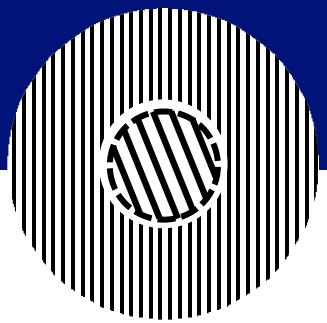
E_1 ***more*** inh. from Sur.

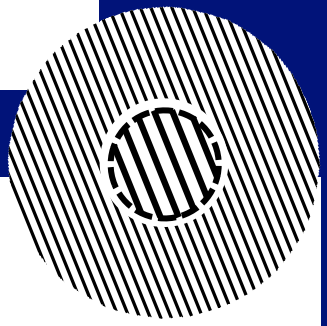
E_1 ***less*** recurrent exc.



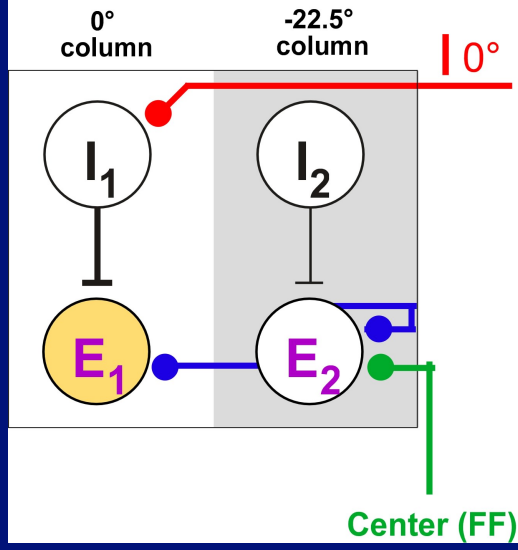
Center at sub-optimal orientation (-22.5°)







E_1 cell response
Low High



E_1 ***less*** inh. from Sur.

E_1 ***less*** recurrent exc.