Neurobiology HMS 130/230
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Visual Object Recognition

Primary Visual Cortex

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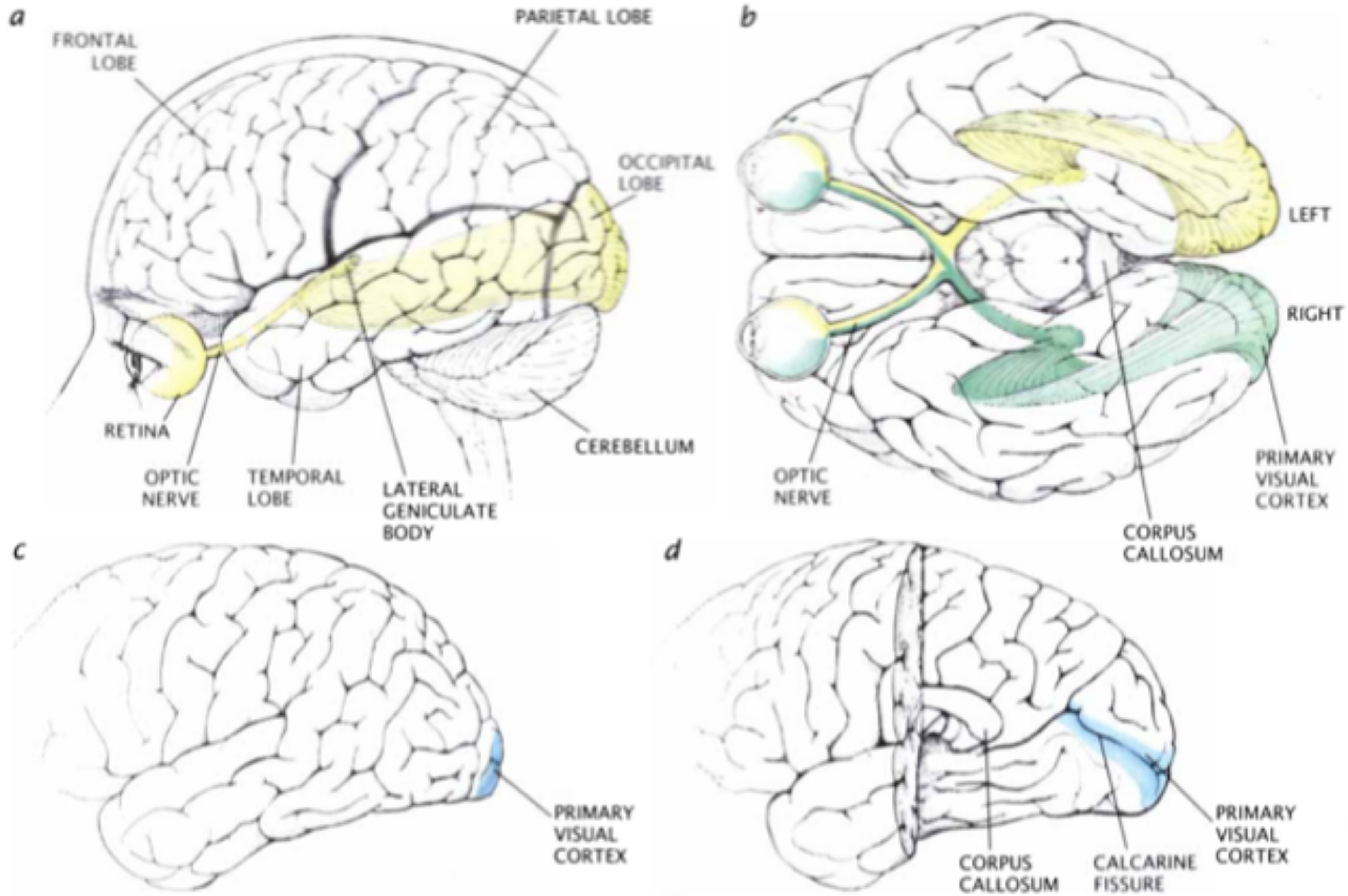
Outline

- **Visual system**
- **Anatomy and physiology**
- **Functional organization**
- **Receptive field models**
- **Neural populations**
- **Neural correlates of behavior**
- **The Unknown**

Computation:

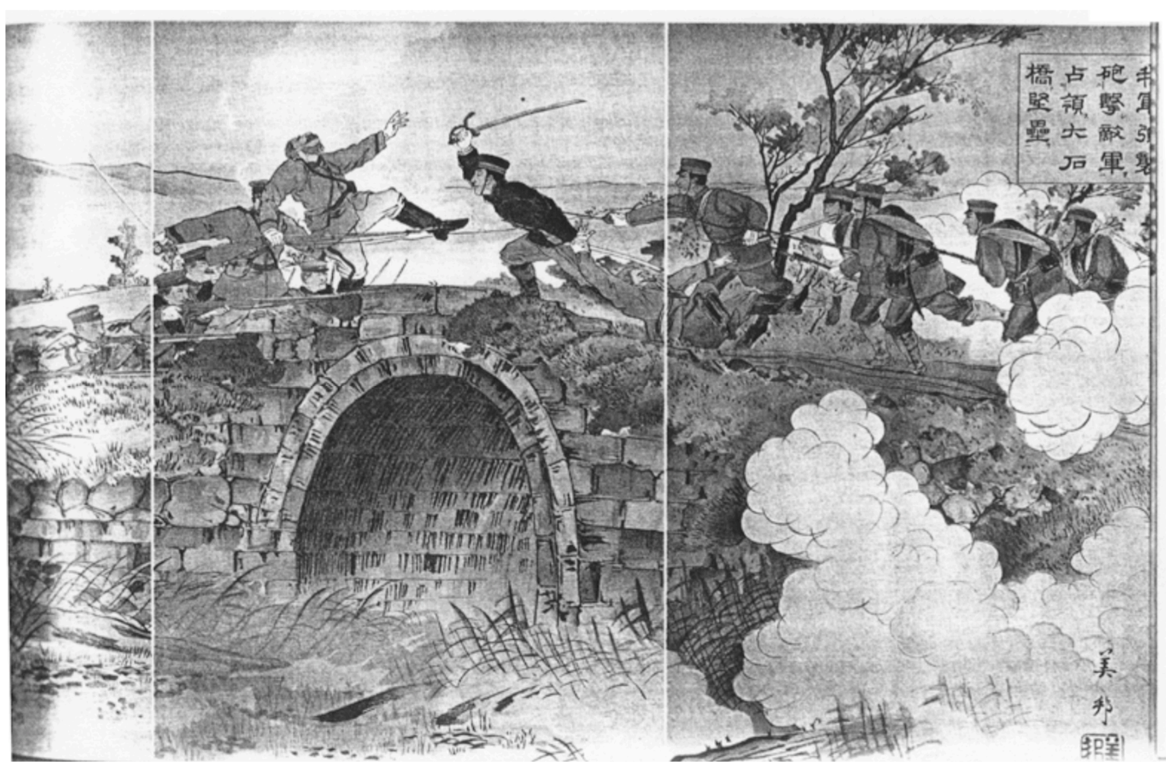
How does the brain make us *see*?

From the retina to the cortex



Glickstein, *Sci. Am.* 1988

Studies of wounded soldiers revealed topographic visual deficits



Russo-Japanese War of 1904–5

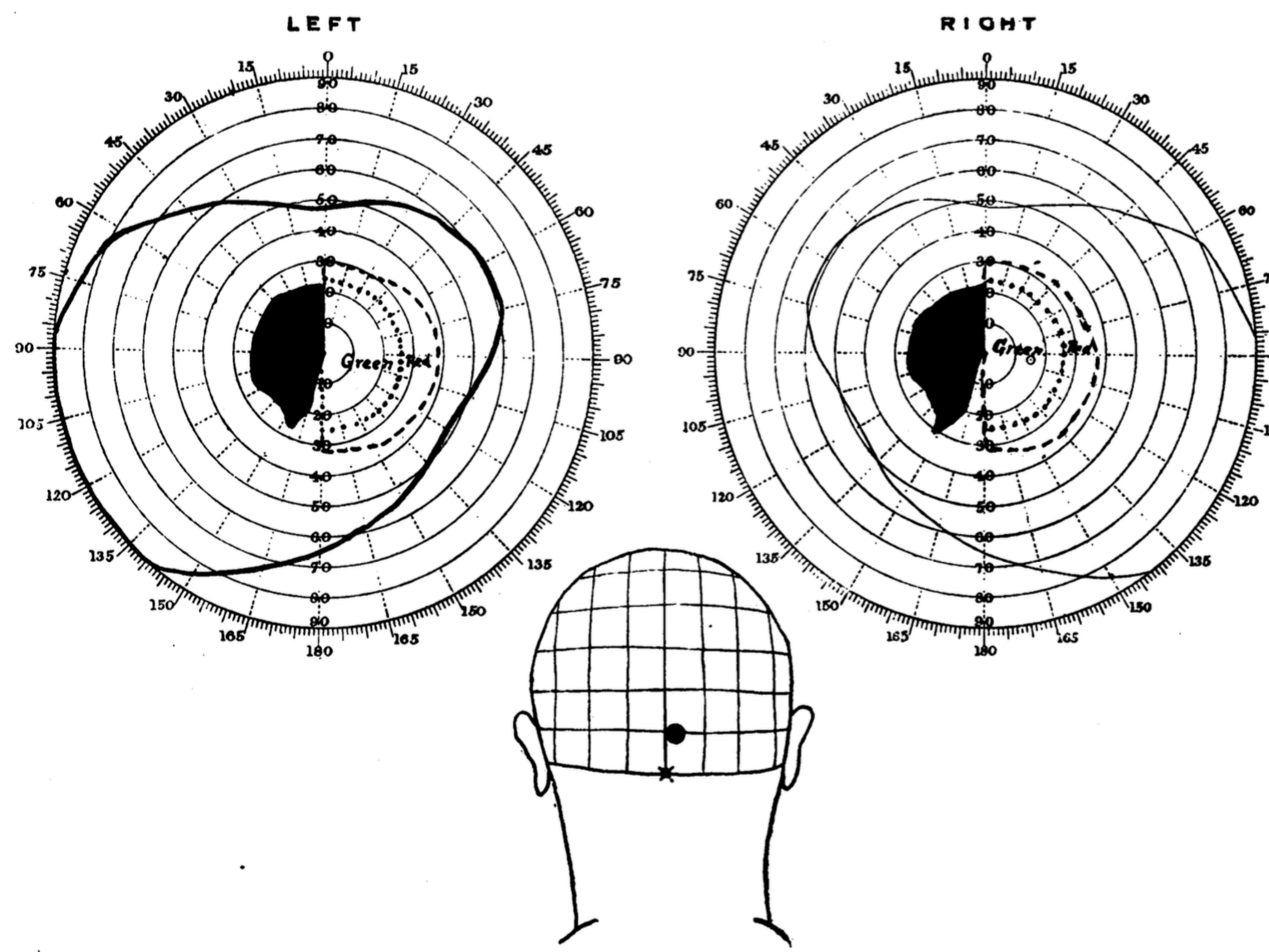


FIG. 1.

Holmes, *Br. J. Ophthalmol.* 1918

Acuity is much higher near the fovea

Fixate here

x

TRY READING THIS [44]

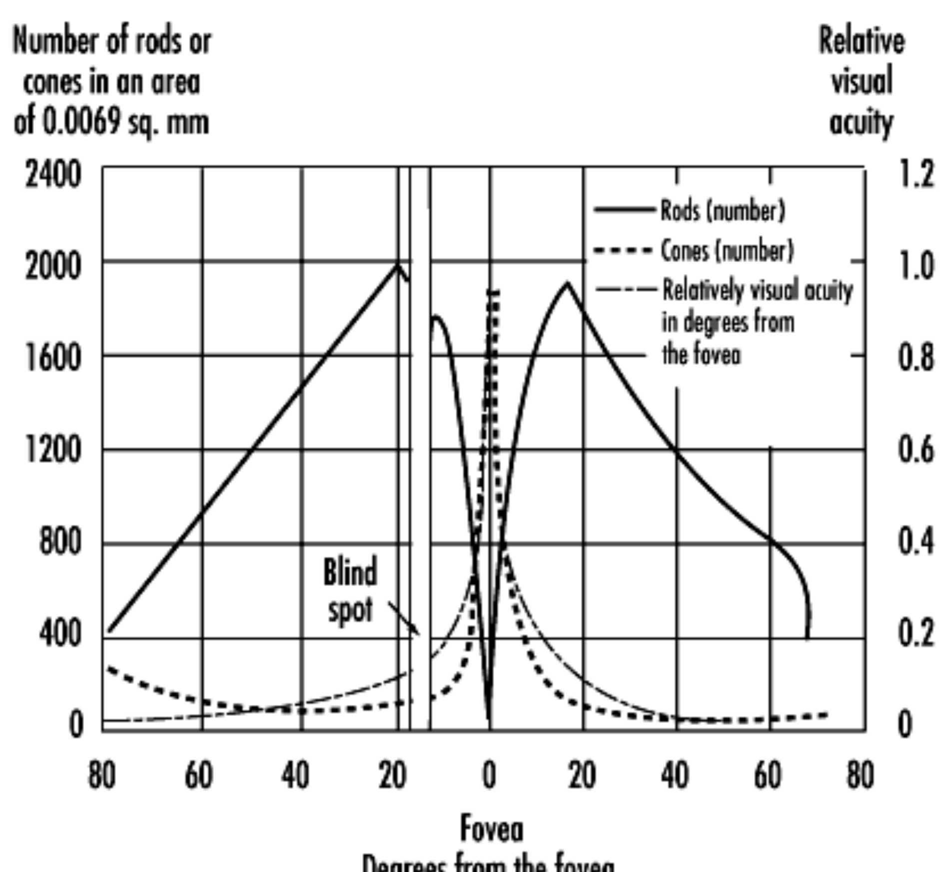
Retinal photoreceptor density [36]

Cortical magnification factor [28]

Why is it that we do not see things upside down? [20]

Or the split between the two hemifields? [12]

And do not forget about the importance of crowding! [8]



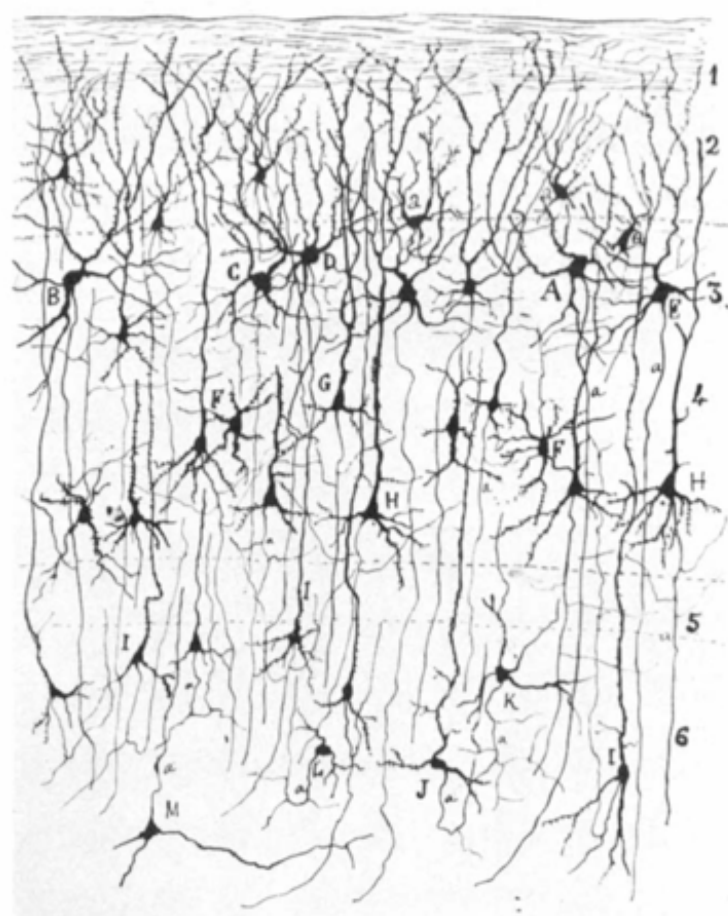
Vision is **deceptively unlike** camera photography

Brown, *Vision and Visual Perception* (eds: Graham et al.) 1965

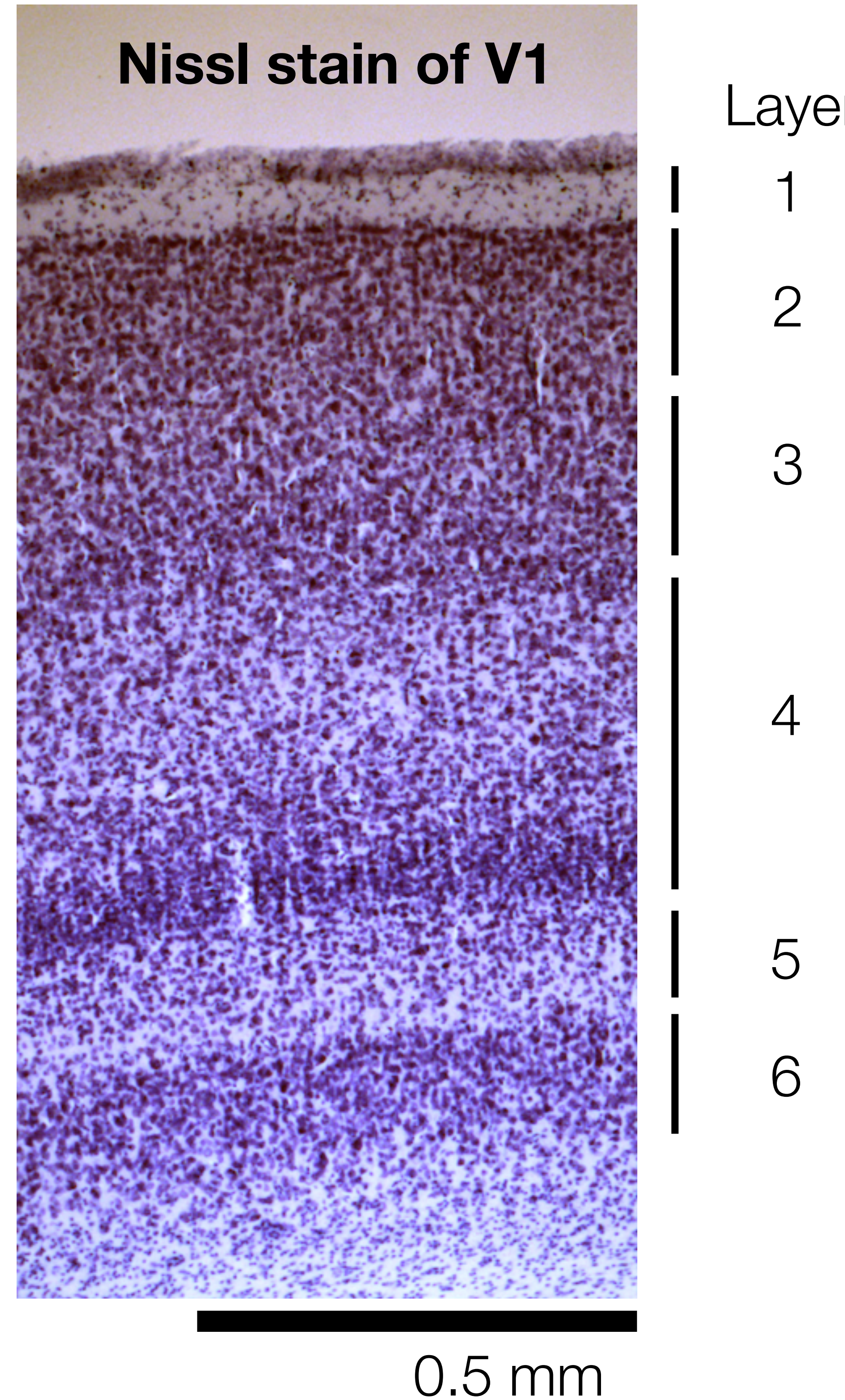
The complex circuitry of the cortex

Anatomy and physiology

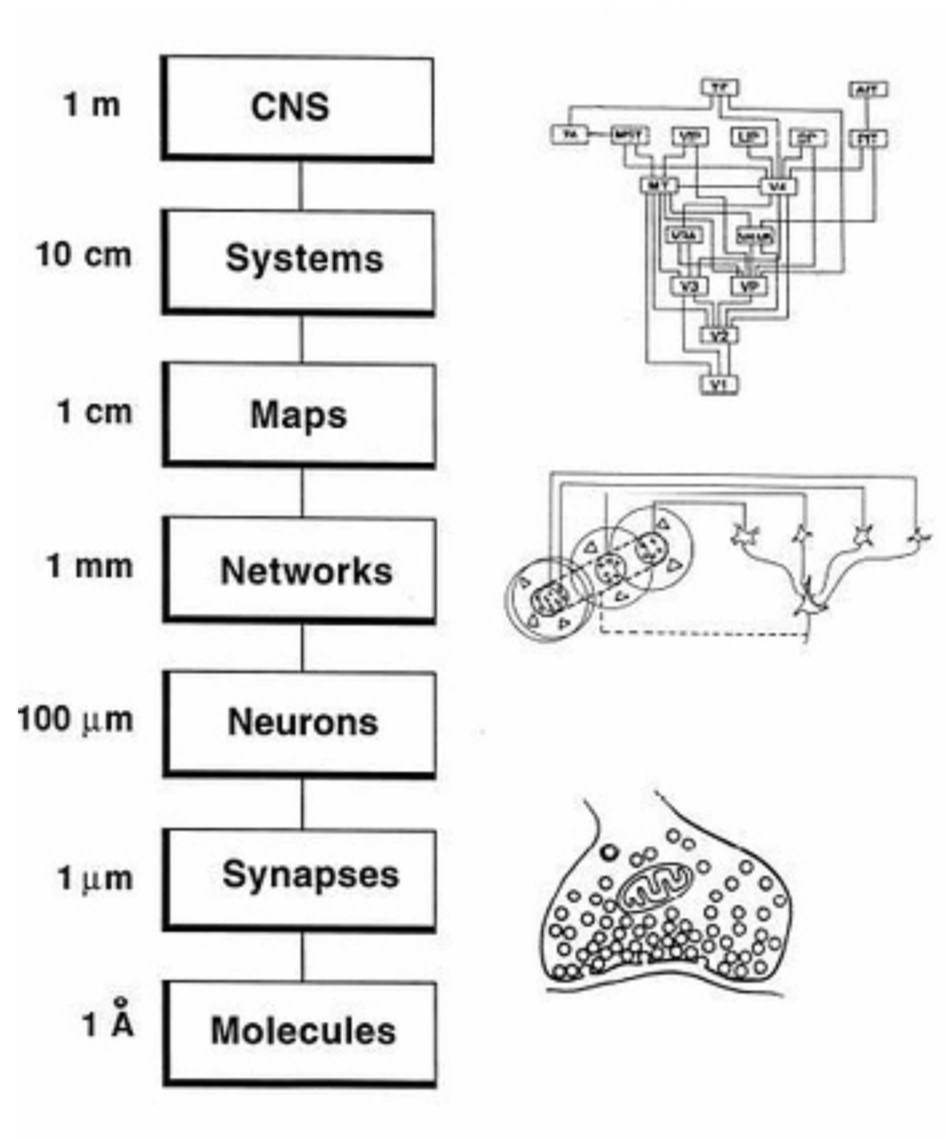
Ramón y Cajal (1852–1934)



GOLGI-STAINED NERVE TISSUE from the visual cortex of a rat was sketched by Cajal in 1888. The numbers along the right-hand margin identify cellular layers; the capital letters label individual neurons. One of Cajal's most important contributions to neurobiology was to establish the neuron as a discrete, well-defined cell rather than as part of a continuous network.



Spatial scales of the nervous system



Churchland and Sejnowski, 1992

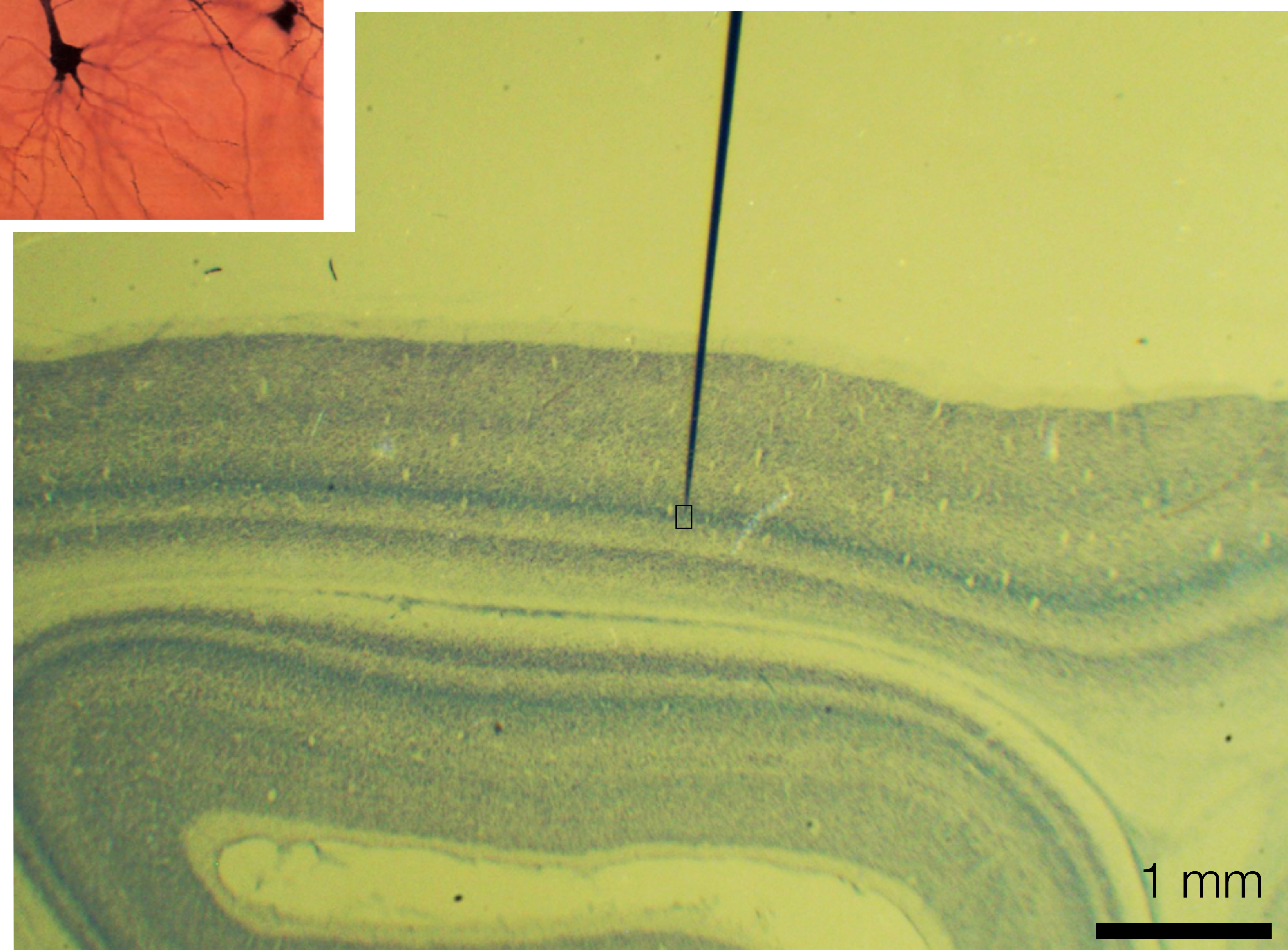
Physiological access using the microelectrode

Edgar Adrian 1926

Neuronal resolution
Sub-millisecond temporal resolution
Direct examination of action potentials

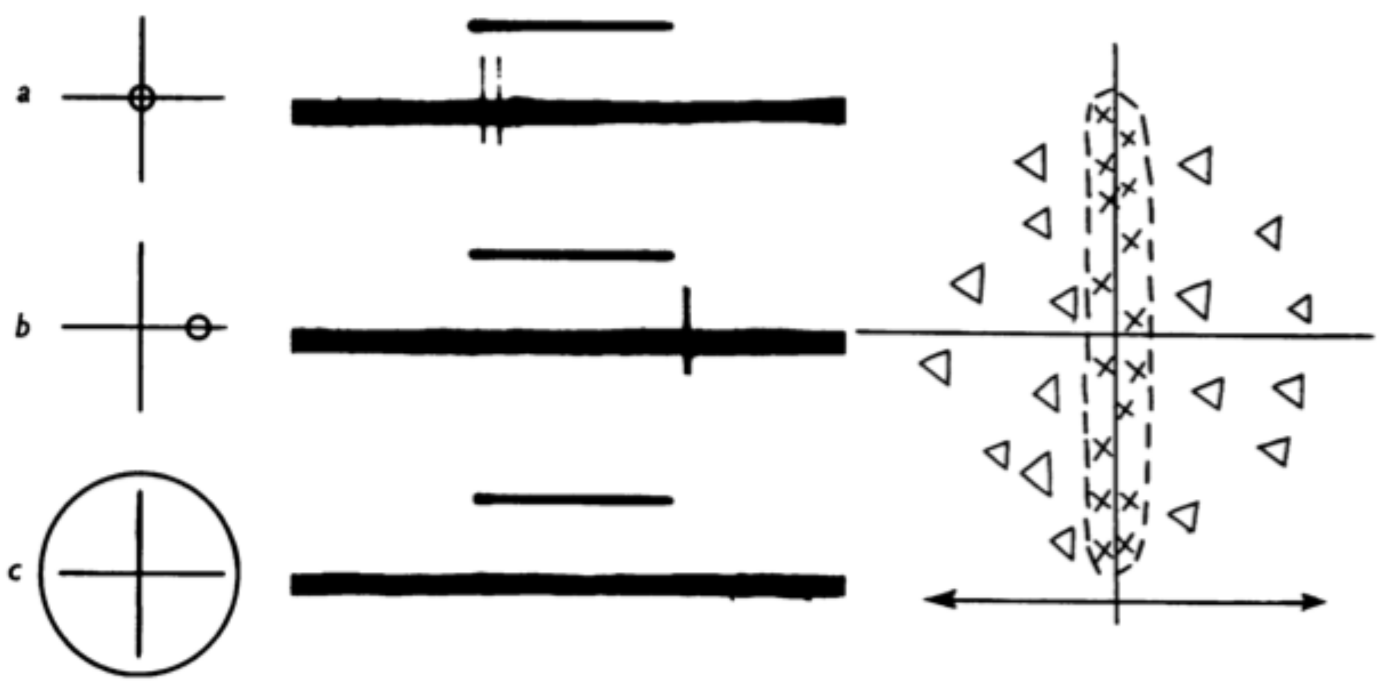
Hubel, D. (1979). The Visual Brain. SCIENTIFIC AMERICAN 241, 45-53.

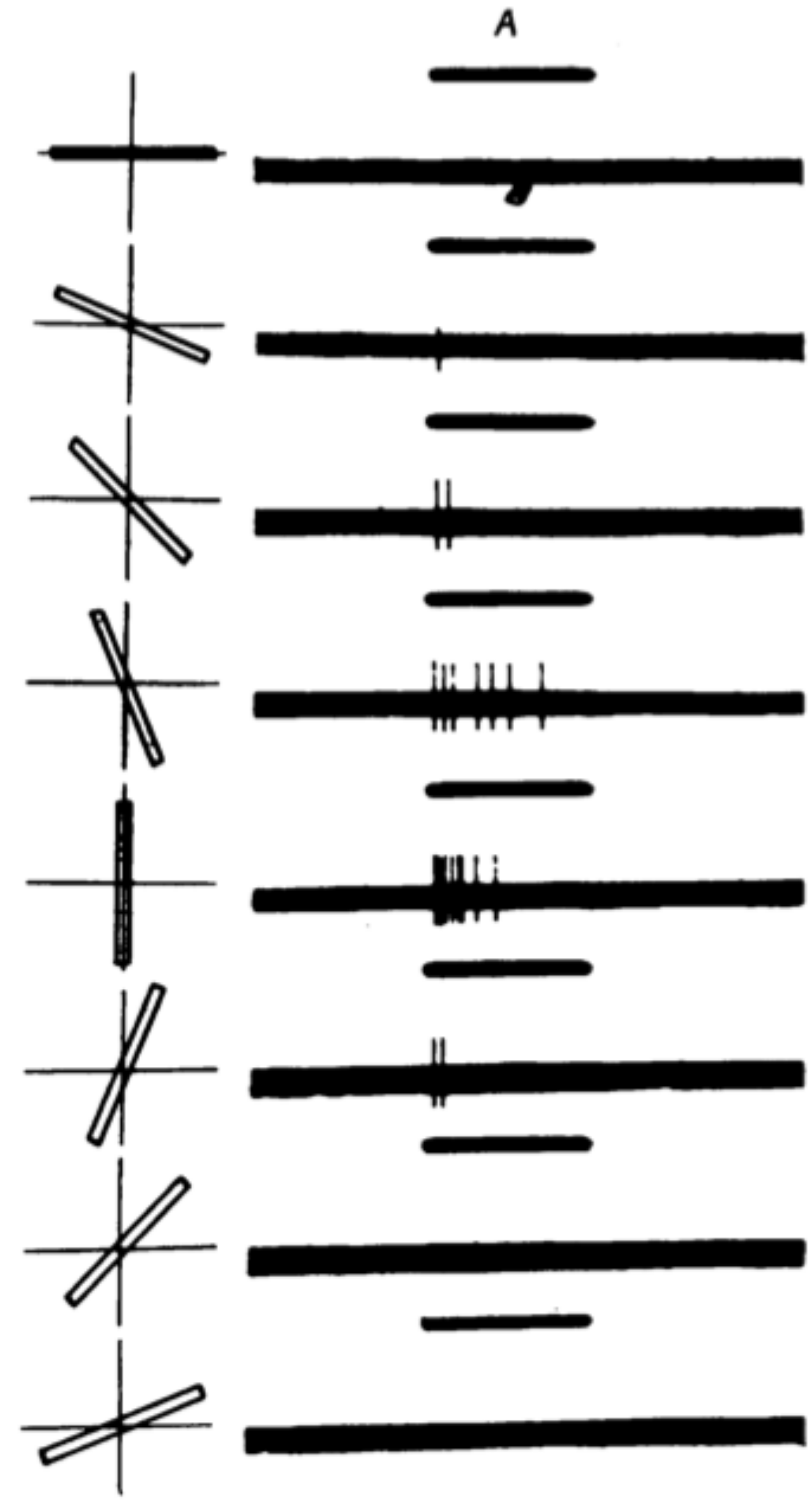
Hubel Wiesel



Electrophysiological recordings from V1

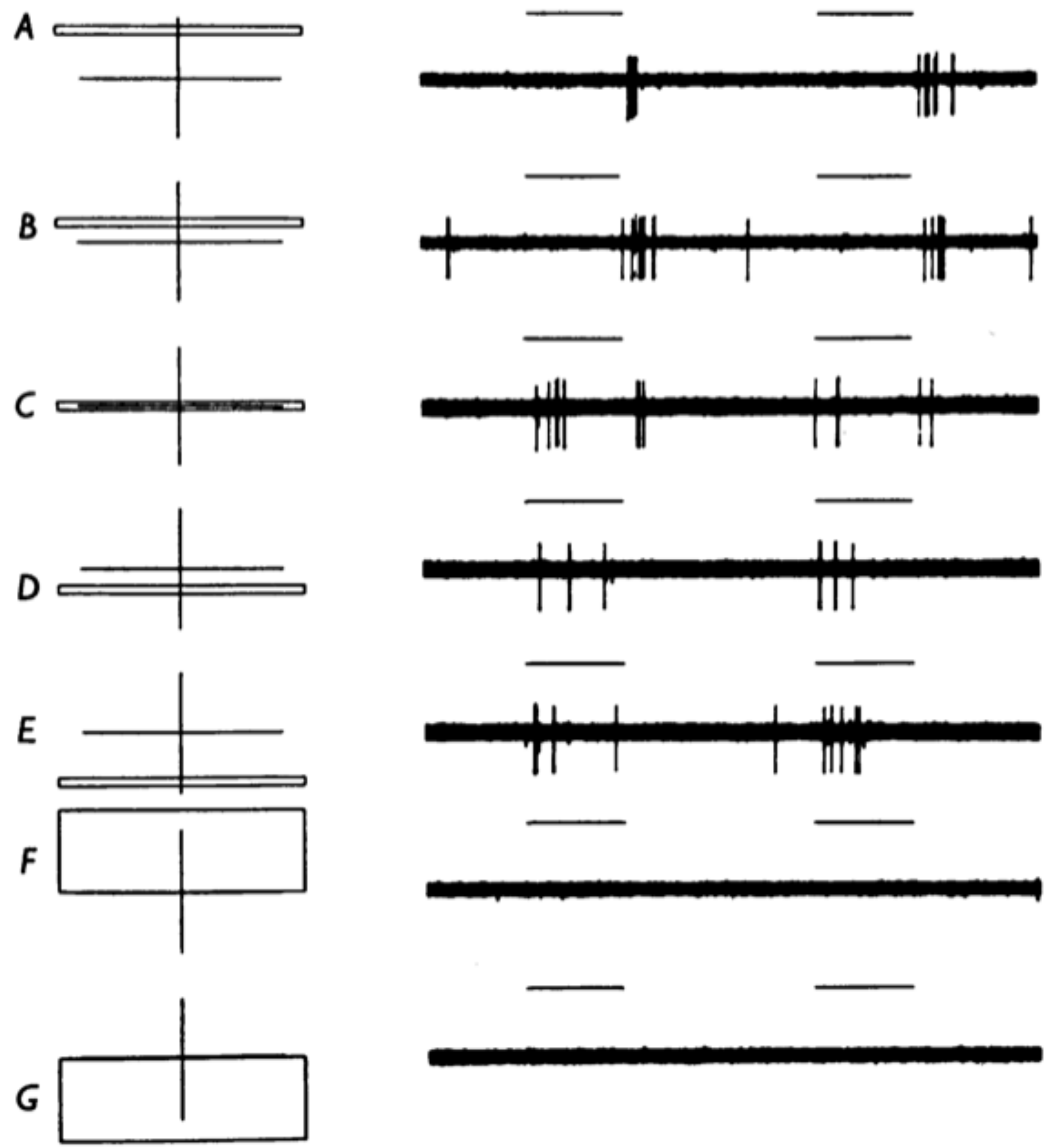
Orientation selectivity of simple fields





Hubel & Wiesel, *J. Physiol.*, 1959

Selectivity and tolerance of complex fields



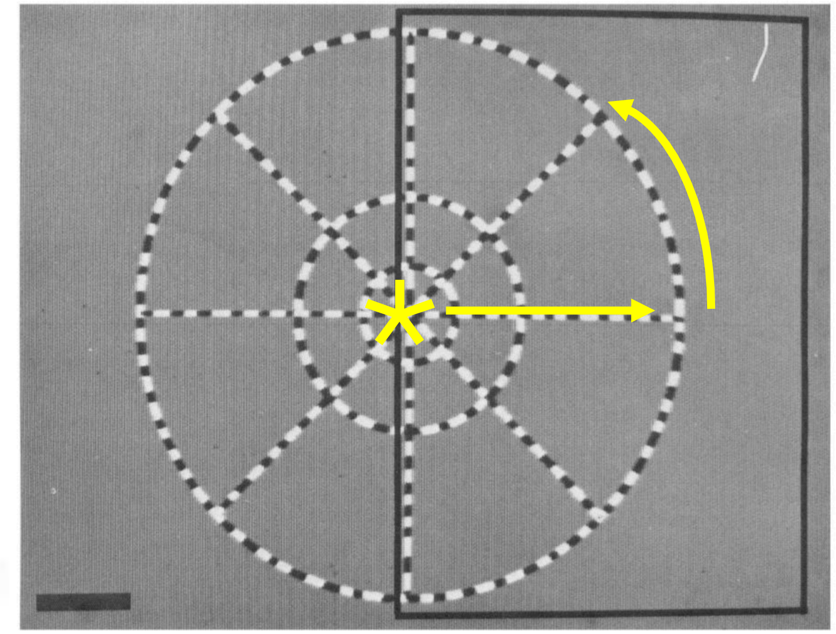
Hubel & Wiesel, *J. Physiol.*, 1962

Hubel and Wiesel mapping V1 neurons

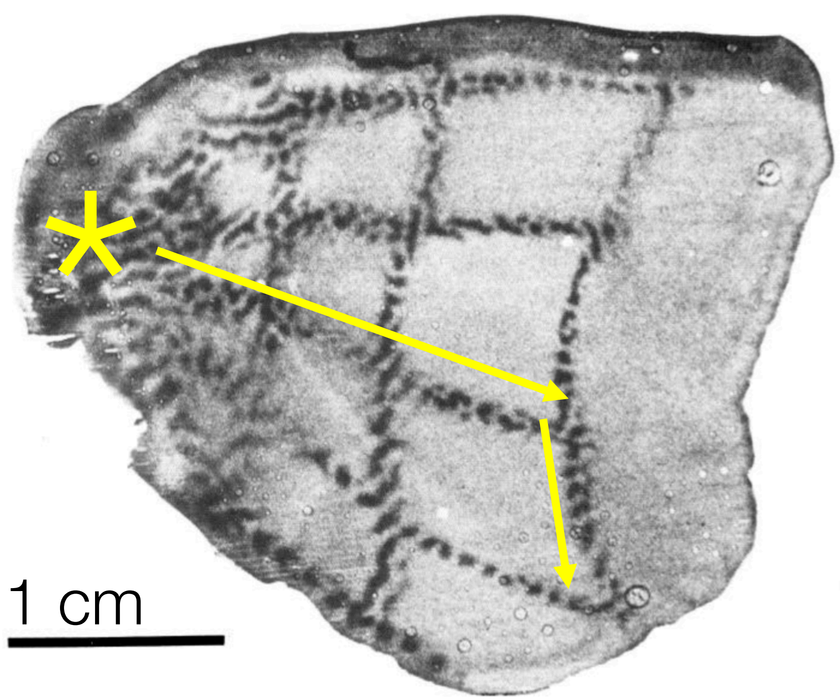
www.youtube.com/watch?v=8VdFf3egwfg

Functional organization

Retinotopical map in the cortex

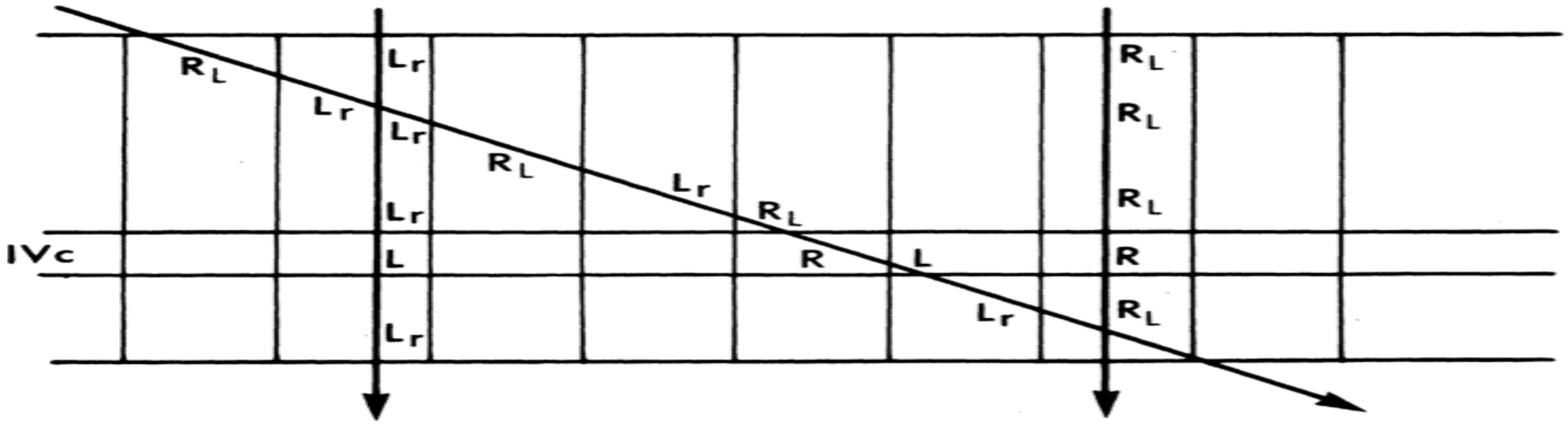


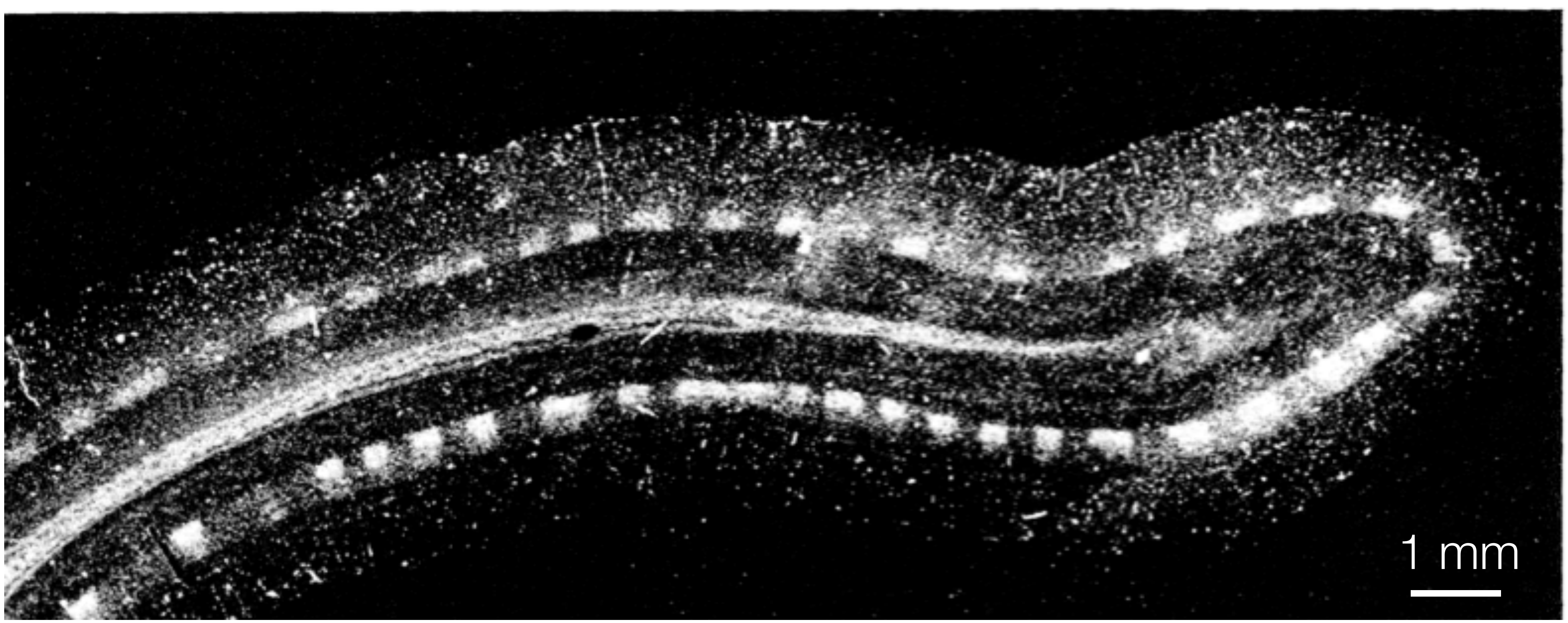
Left hemisphere V1



Tootell et al., *J. Neurosci.*, 1988

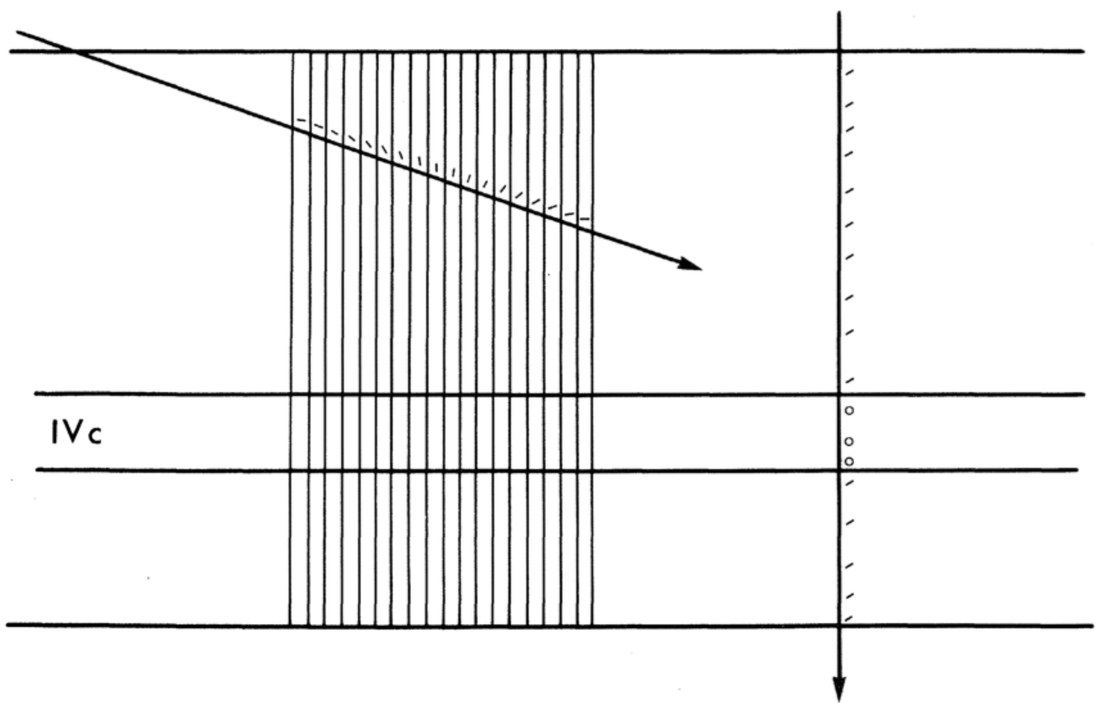
Ocular dominance columns

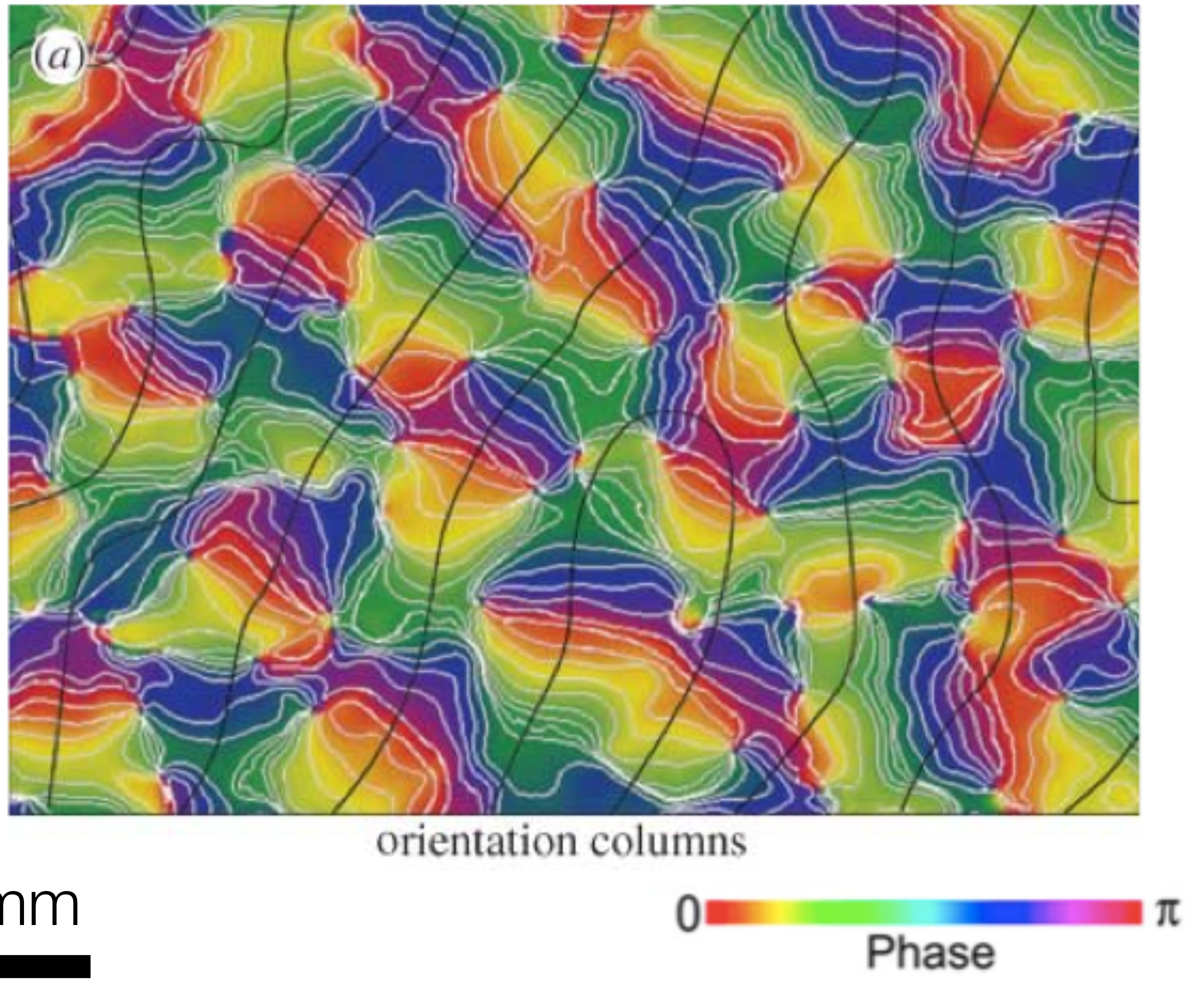




Hubel & Wiesel, *Proc. R. Soc. Lond. B*, 1977

Visual orientation columns



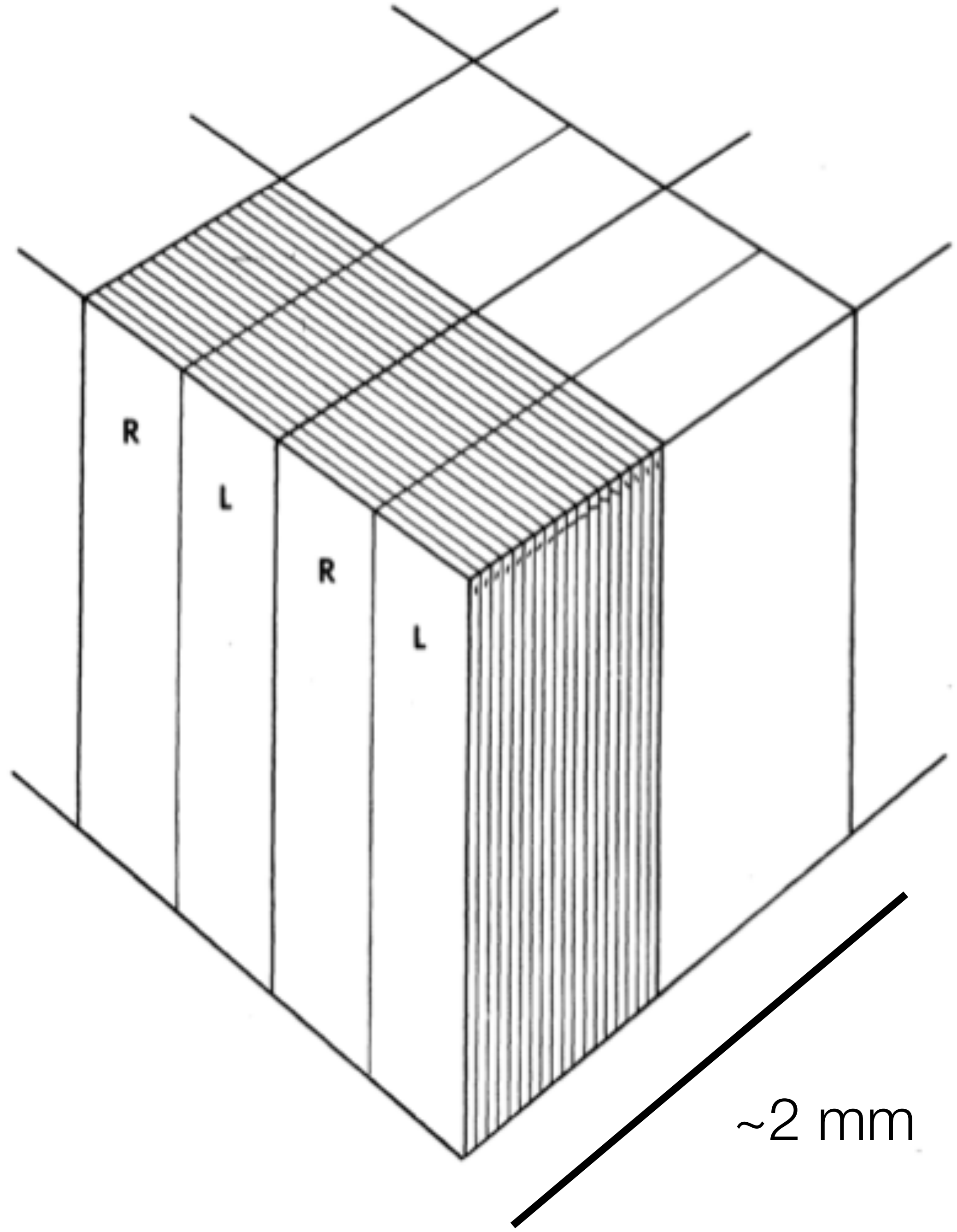


1 mm

Hubel & Wiesel, *Proc. R. Soc. Lond. B*, 1977

Horton & Adams, *Phil. Trans. R. Soc. B*, 2005

Putting it all* together: the “hypercolumn”



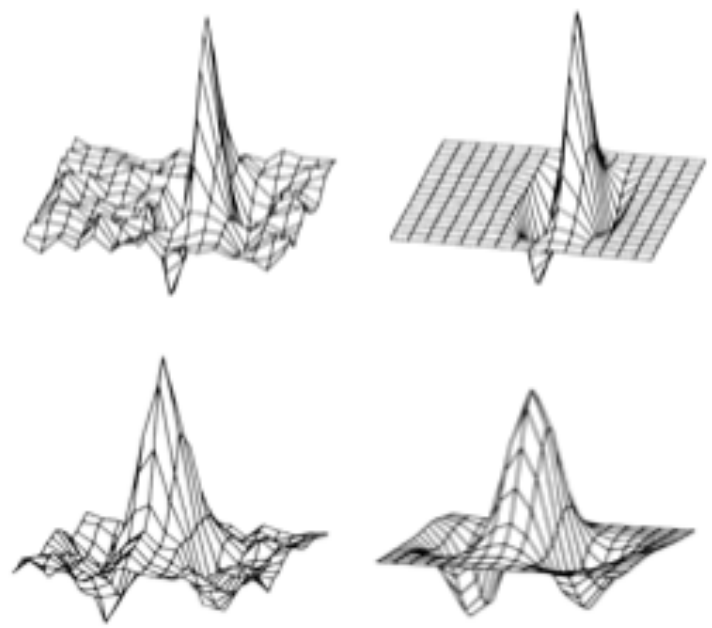
*all is more than ocularity and orientation. Many V1 neurons are also selective for:

- Direction & speed
- Depth
- Color

Hubel & Wiesel, *Proc. R. Soc. Lond. B*, 1977

Mathematical description of a receptive field

Spatial receptive field Gabor fit



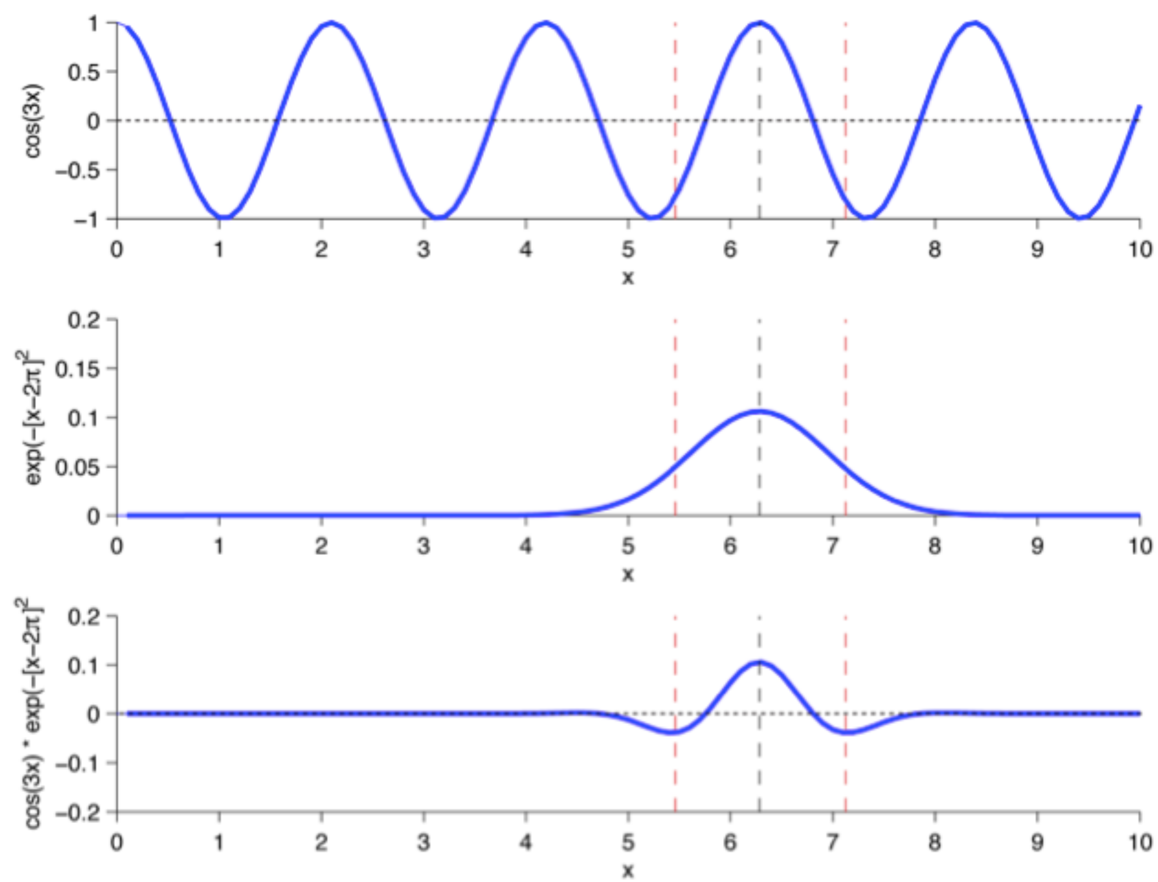
Cell 1

Cell 2

Spatial receptive field
Cat primary visual cortex (area 17)
Jones and Palmer 1987

Gabor function

$$D(x,y) = \frac{1}{2\pi\sigma_x\sigma_y}\exp\left[-\frac{x^2}{2\sigma_x^2}-\frac{y^2}{2\sigma_y^2}\right]\cos(kx-\phi)$$



[Time permitting]

Interlude : MATLAB

An easy way to write computer code

- http://www.mathworks.com/index.html
- "High-level" computer programming language
- Quite powerful!

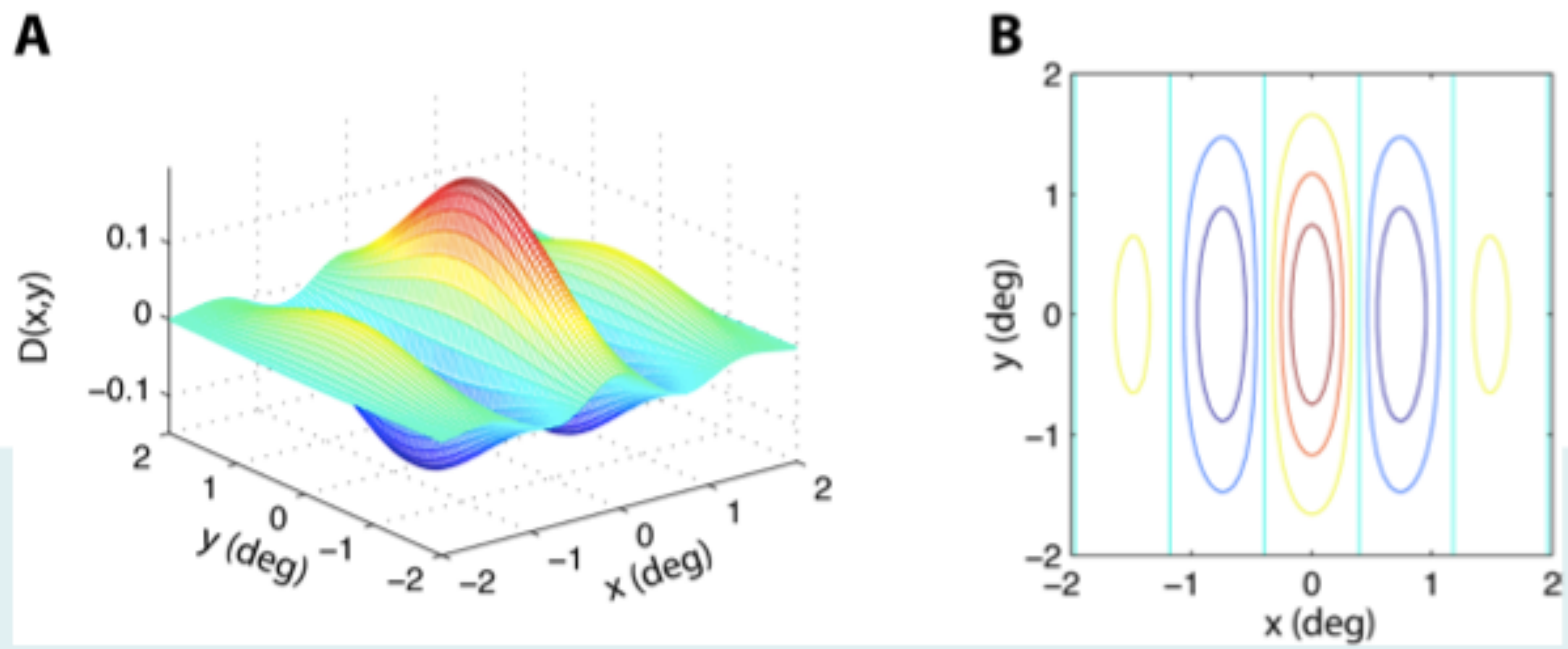
```
theta_rad=(2*pi/360)*theta;                          % theta angle in radians
x=(-2*sigma_x):bin:(2*sigma_x);nx=length(x);         % define x axis
y=(-2*sigma_y):bin:(2*sigma_y);ny=length(y);         % define y axis

factor1=1/(2*pi*sigma_x*sigma_y);
for i=1:nx
    for j=1:ny
        curr_x=x(i)*cos(theta_rad)+y(j)*sin(theta_rad);
        curr_y=y(j)*cos(theta_rad)-x(i)*sin(theta_rad);
        factor2=exp(-curr_x^2/(2*sigma_x^2)-curr_y^2/(2*sigma_y^2));
        factor3=cos(k*curr_x-phi);
        Ds(i,j)=factor1*factor2*factor3;
    end
end
```

$$D(x,y) = \frac{1}{2\pi\sigma_x\sigma_y}\exp\left[-\frac{x^2}{2\sigma_x^2}-\frac{y^2}{2\sigma_y^2}\right]\cos(kx-\phi)$$

Interlude : MATLAB

An easy way to make plots



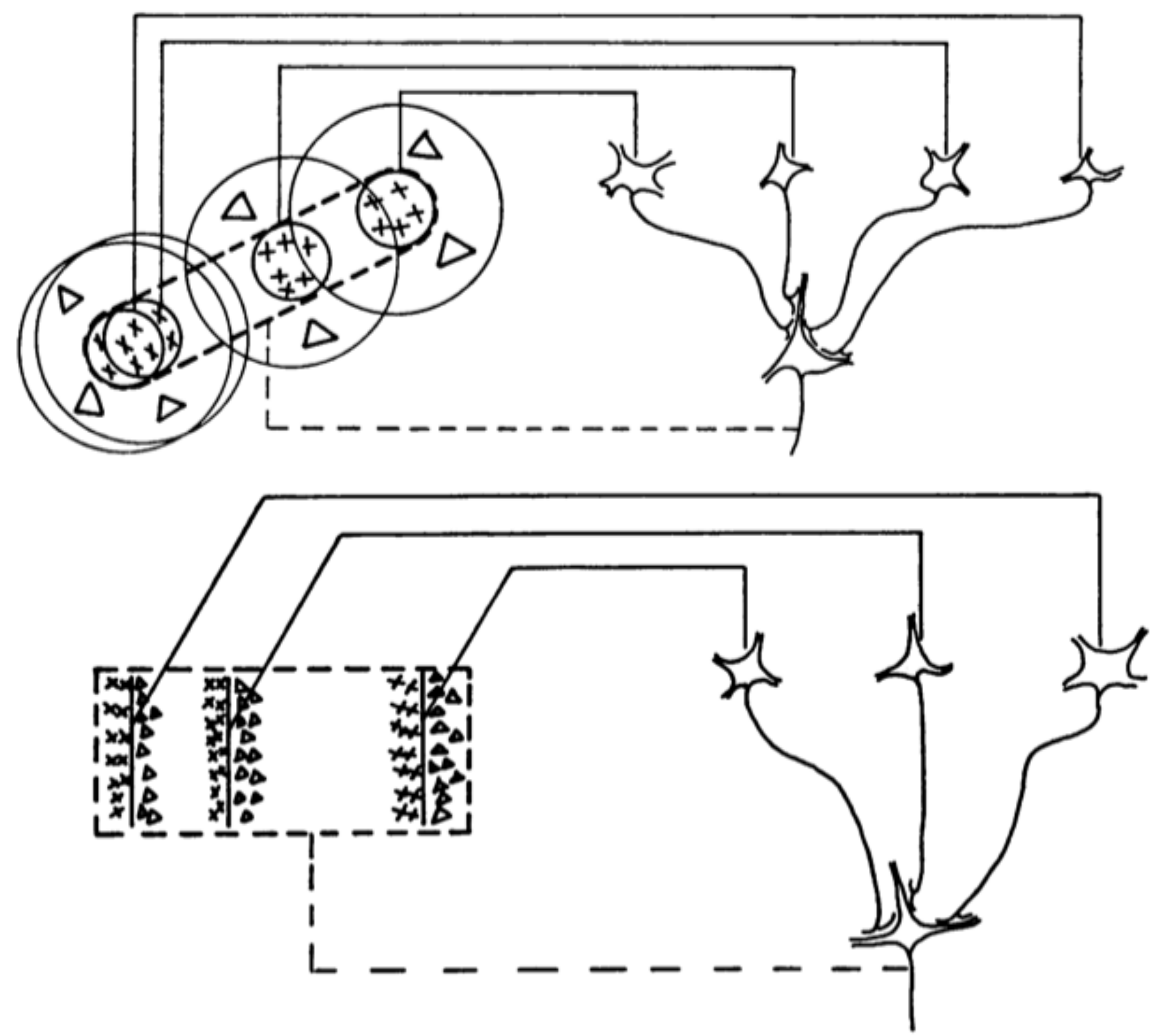
$$D(x,y) = \frac{1}{2\pi\sigma_x\sigma_y}\exp\left[-\frac{x^2}{2\sigma_x^2}-\frac{y^2}{2\sigma_y^2}\right]\cos(kx-\phi)$$

```
sigma_x=1;
sigma_y=1;
bin=0.05;
k=1/0.25;
theta=0;
i=0;
phi=0;
[Ds,x,y]=mygabor1(sigma_x,sigma_y,k,phi,theta,bin);
subplot(2,2,1);
mesh(x,y,Ds');
axis([min(x) max(x) min(y) max(y) min(Ds(:)) max(Ds(:))]);
subplot(2,2,2);
contour(x,y,Ds');
axis square;
```

Stimulus “selectivity” and “tolerance”

Orientation selectivity of a simple cell:
boolean ‘AND’ operation over circular ON fields with *different positions*

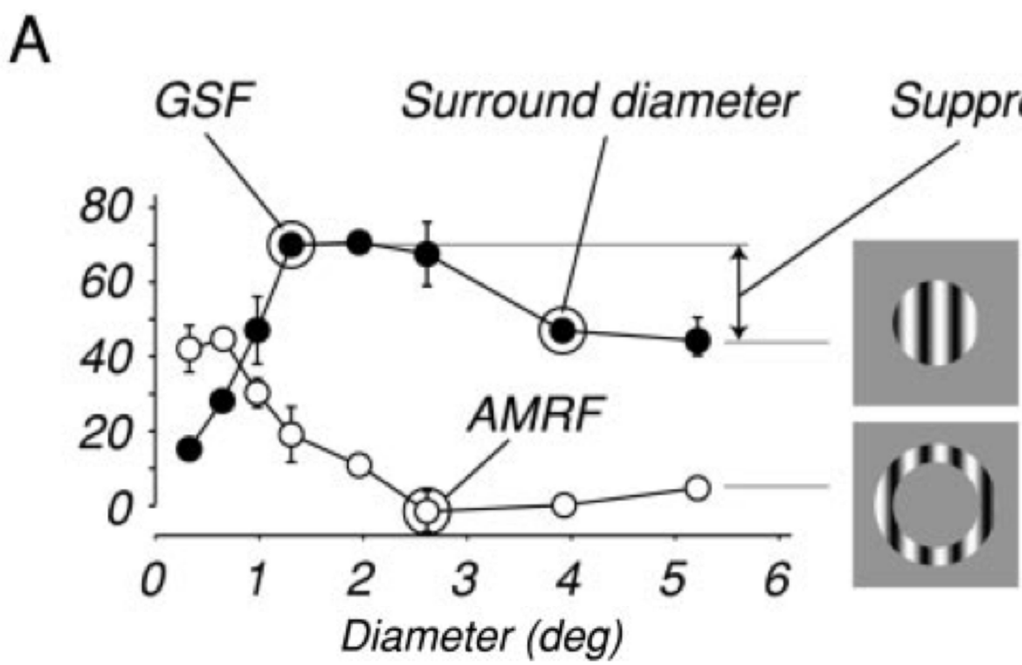
Position tolerance of a complex cell:
boolean ‘OR’ operation over simple fields with *same orientation preference*



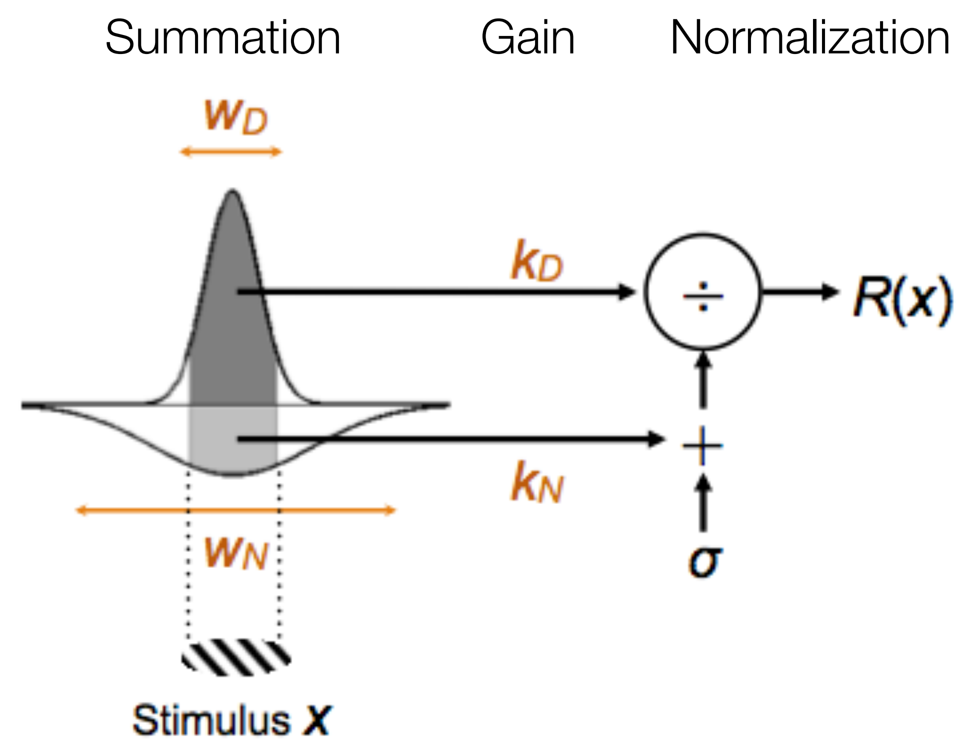
Hubel & Wiesel, *J. Physiol.*, 1962

Question: The circuits are essentially identical, so why call one ‘AND’ and the other ‘OR’?

More is not always better: the surround can suppress the responses of neurons in V1



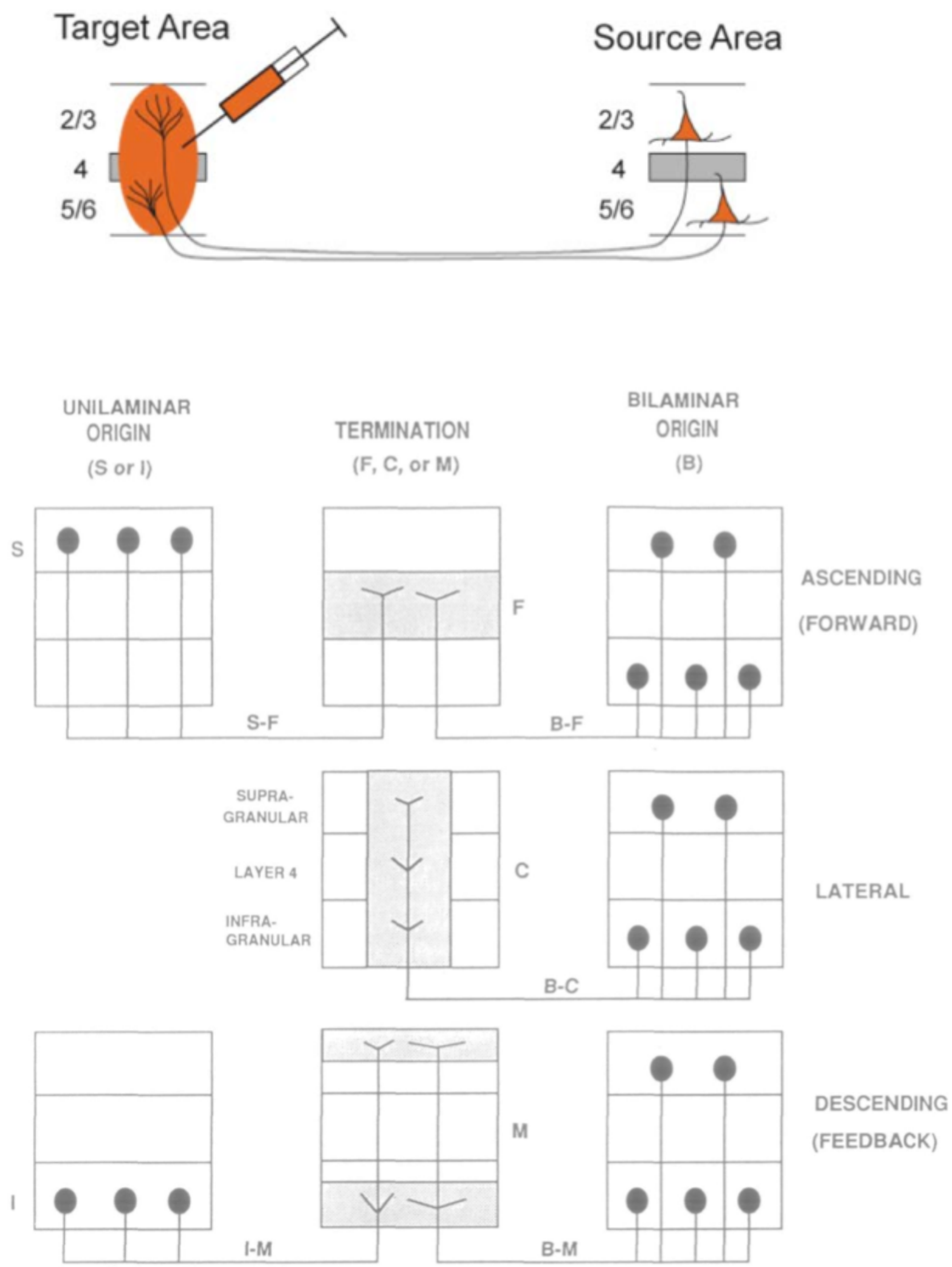
Cavanaugh et al., *J. Neurophysiol.*, 2002



$$R_{\mathrm{ROG}}(x) = R_0 + \frac{k_D\,[w_D\,\mathrm{erf}(x/2w_D)]^2}{\sigma + k_N\,[w_N\,\mathrm{erf}(x/2w_N)]^2}$$

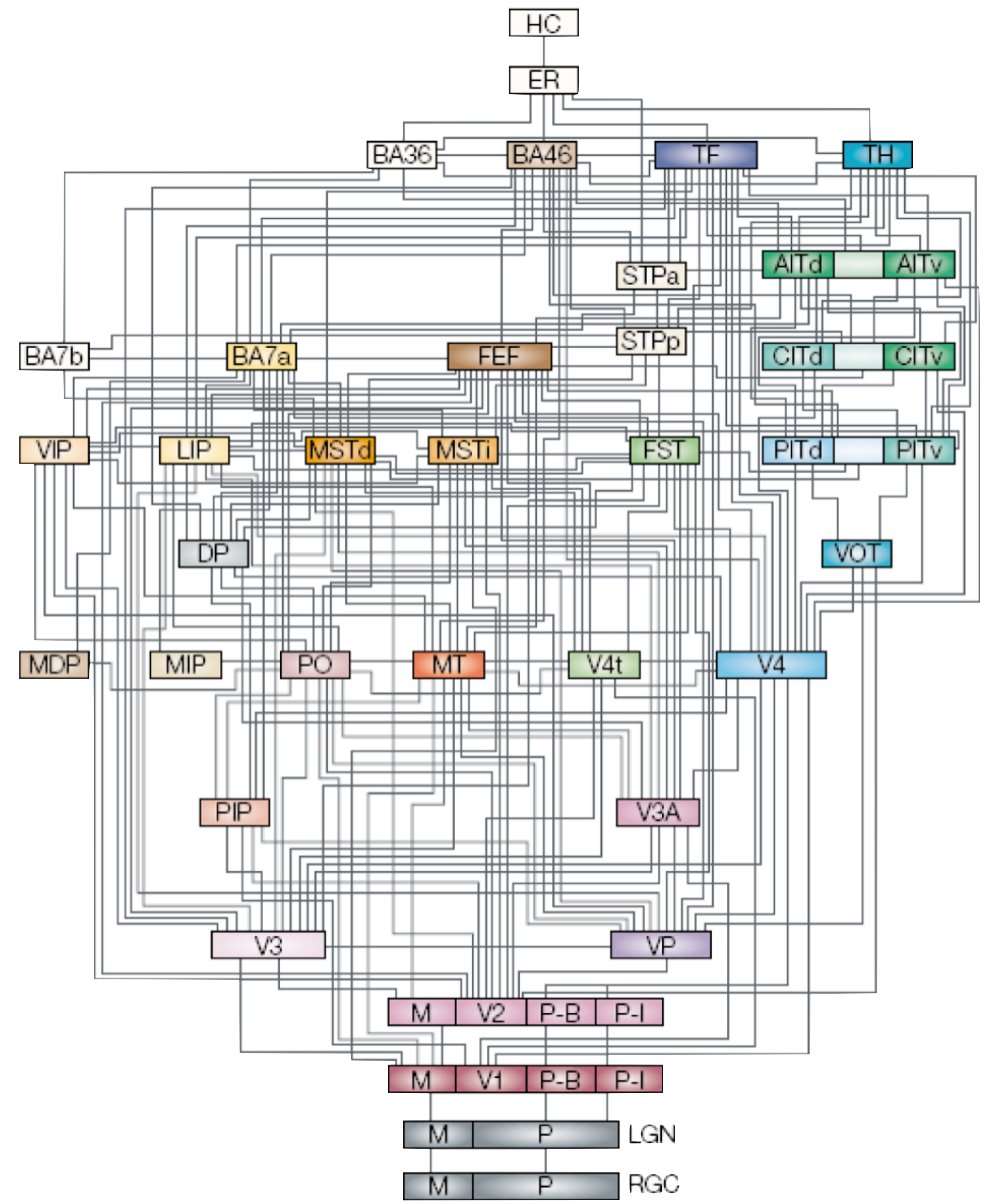
Nassi et al., *Front. Syst. Neurosci.*, 2014

Neurons “work” together!



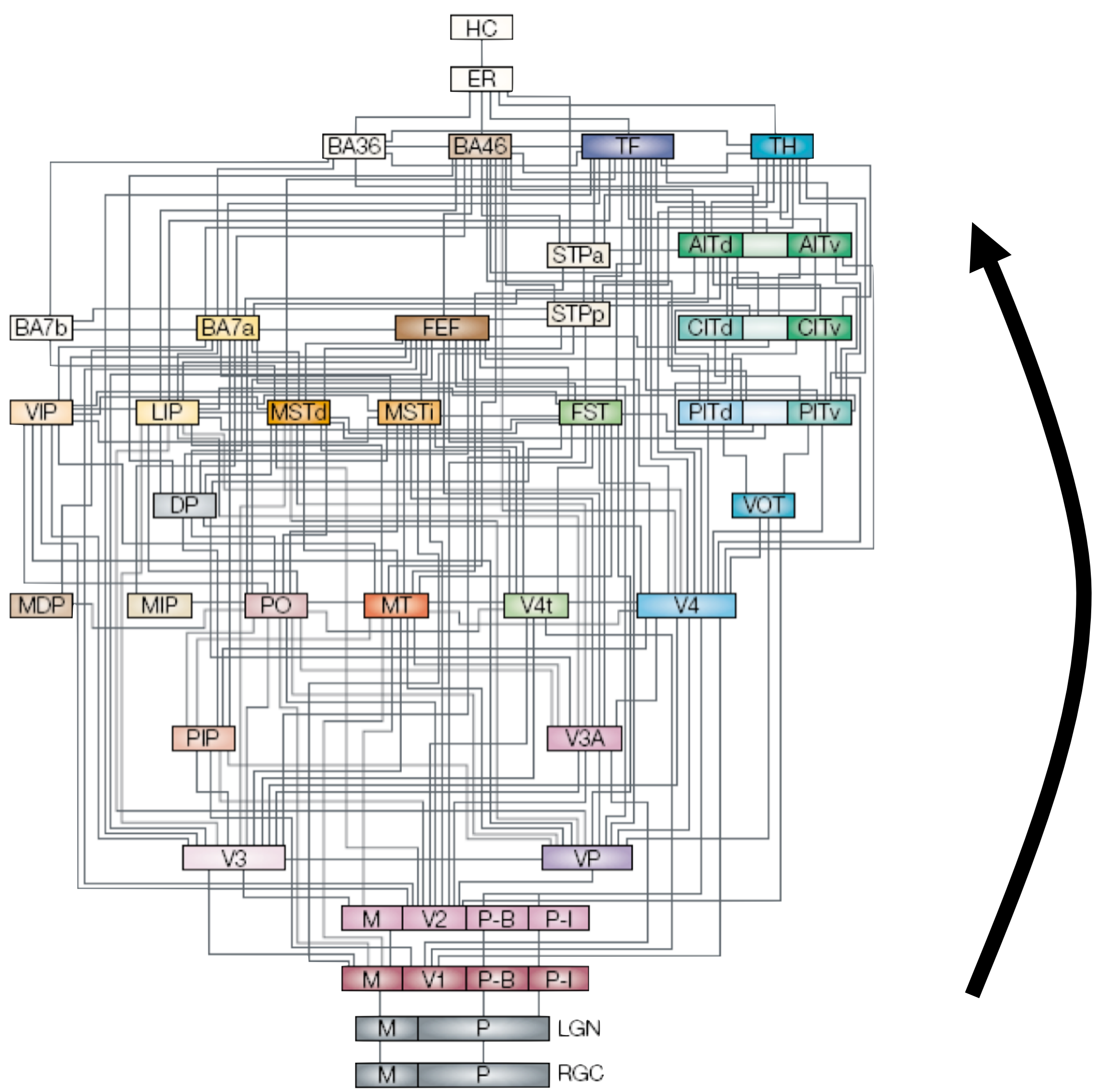
Maunsell & Van Essen, *J. Neurosci.*, 1983

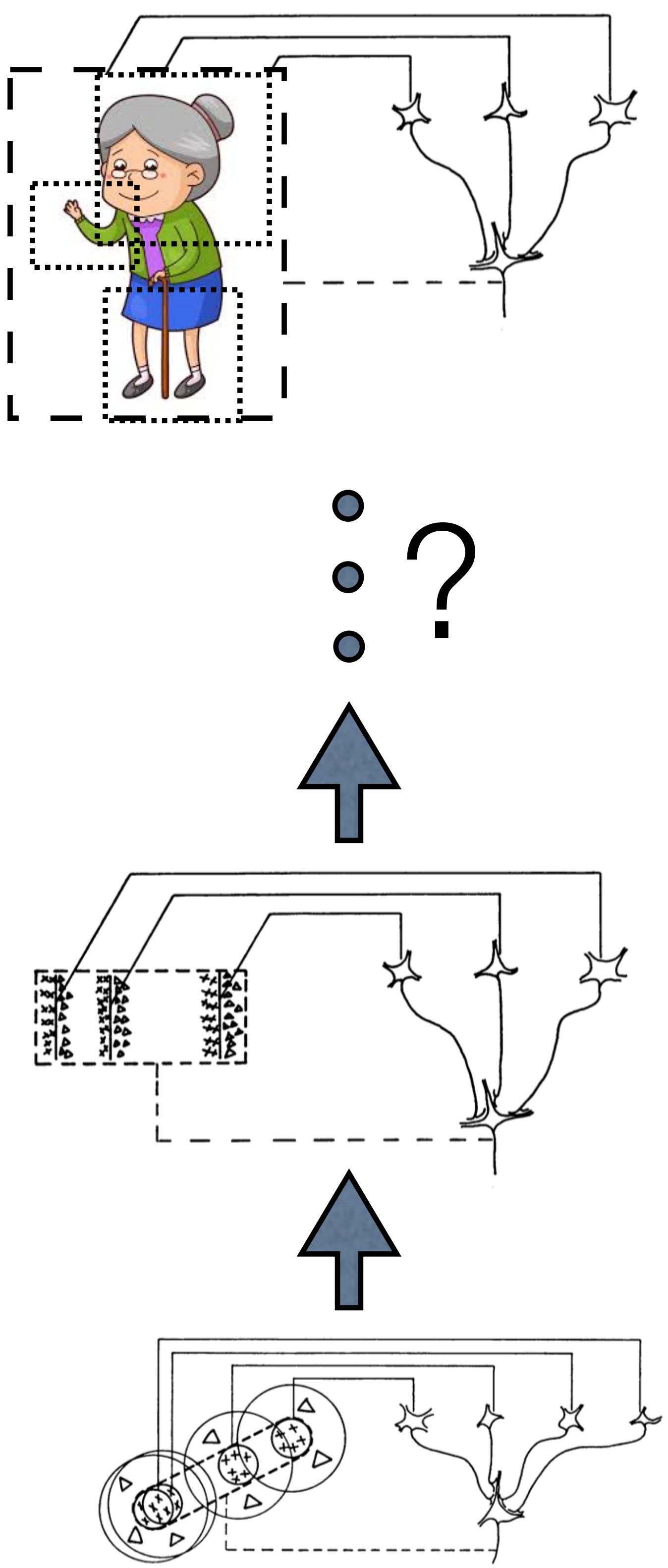
Cortical areas are hierarchically organized



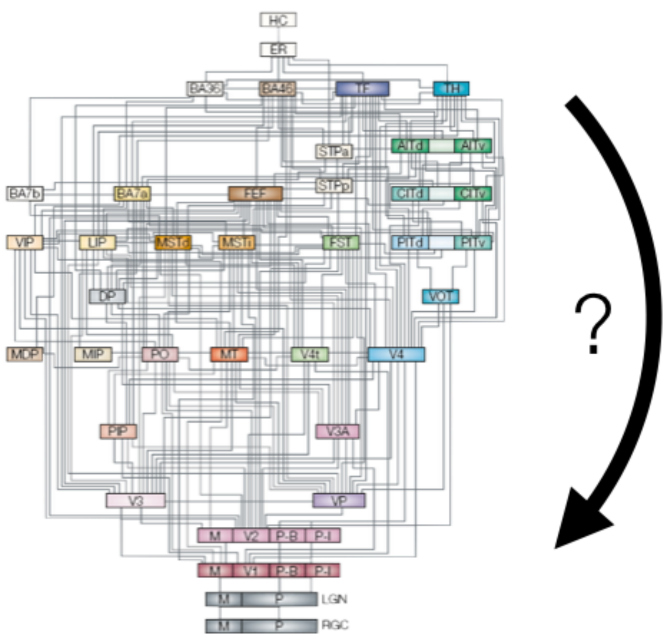
Felleman & Van Essen, *Cereb. Cortex*, 1991

Feedforward connectivity can enable highly selective (and tolerant) neurons

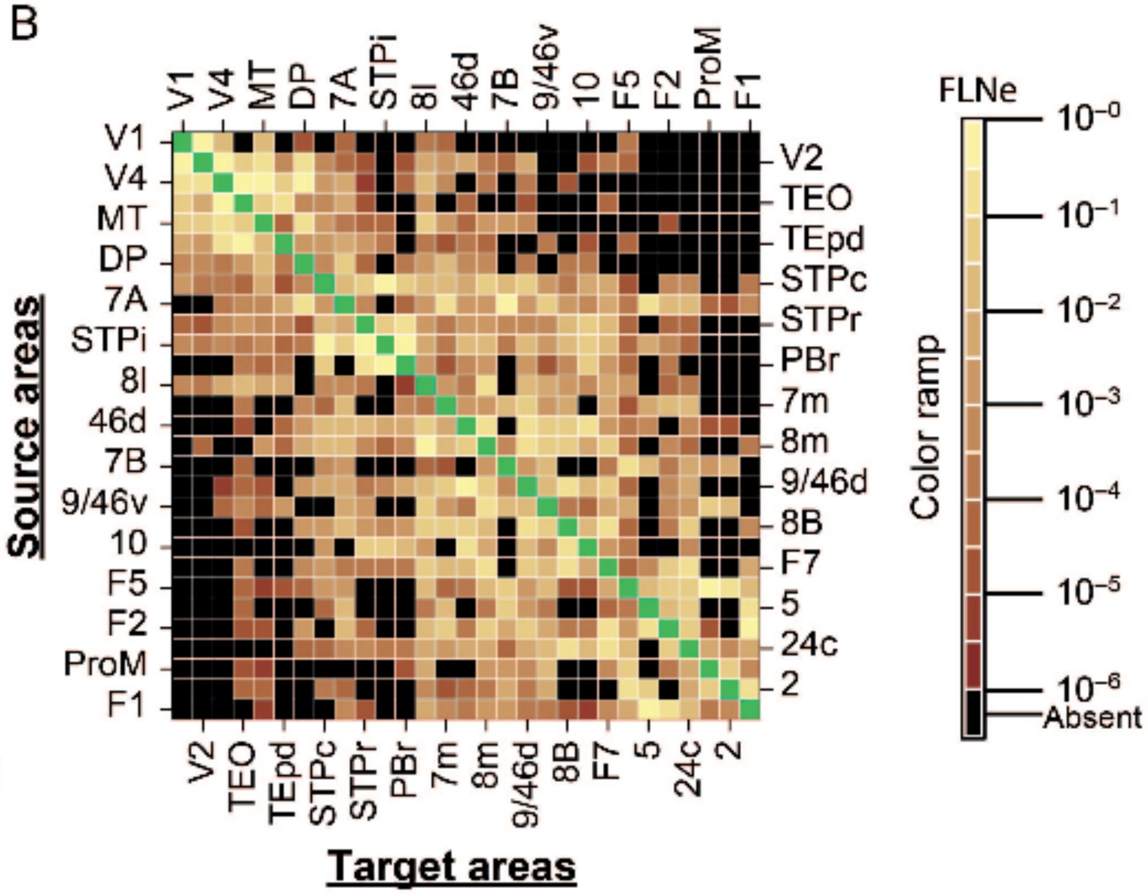




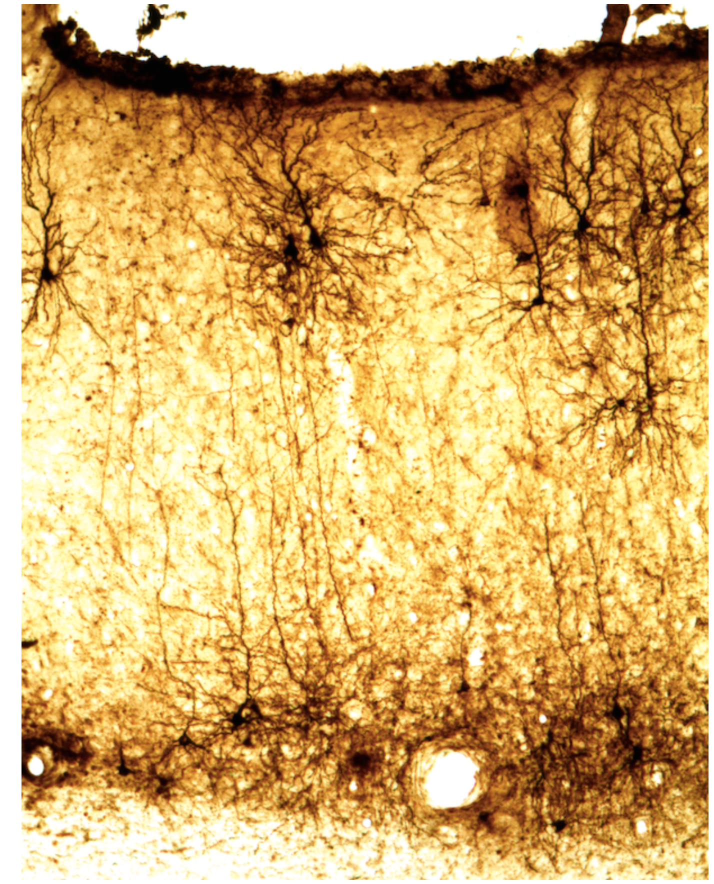
So, what does cortical feedback do?

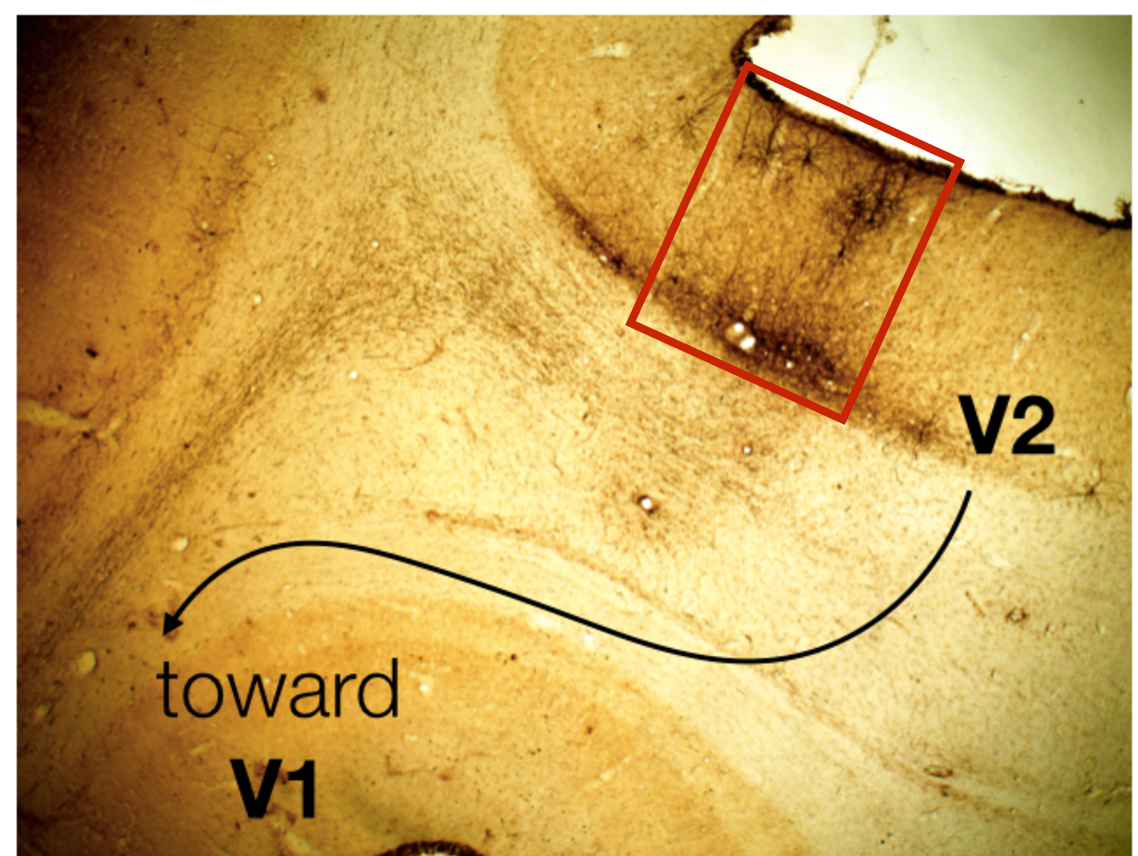


B



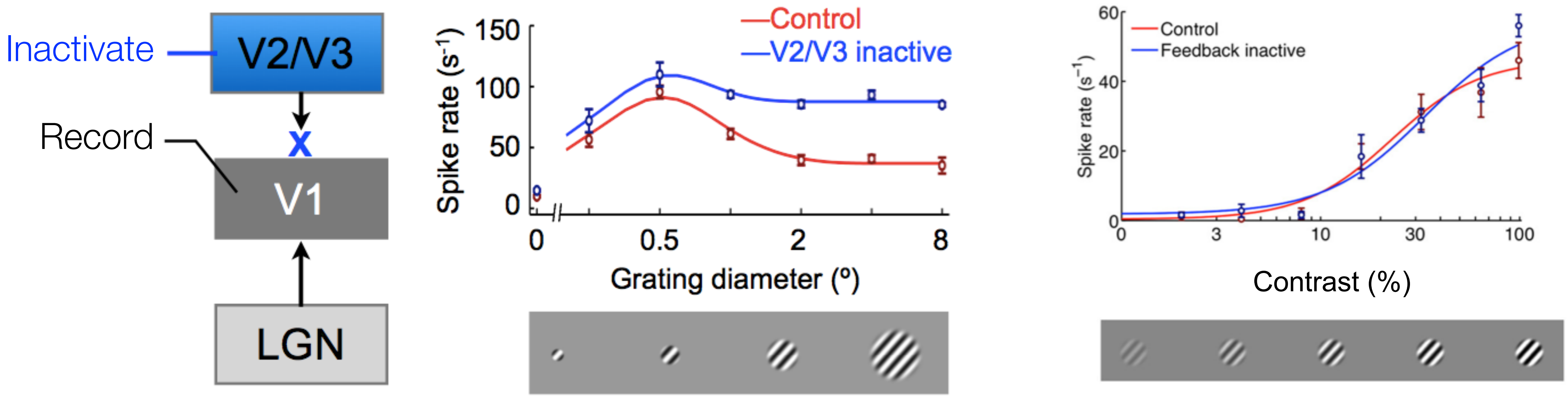
Markov et al., *Cereb. Cortex*, 2014





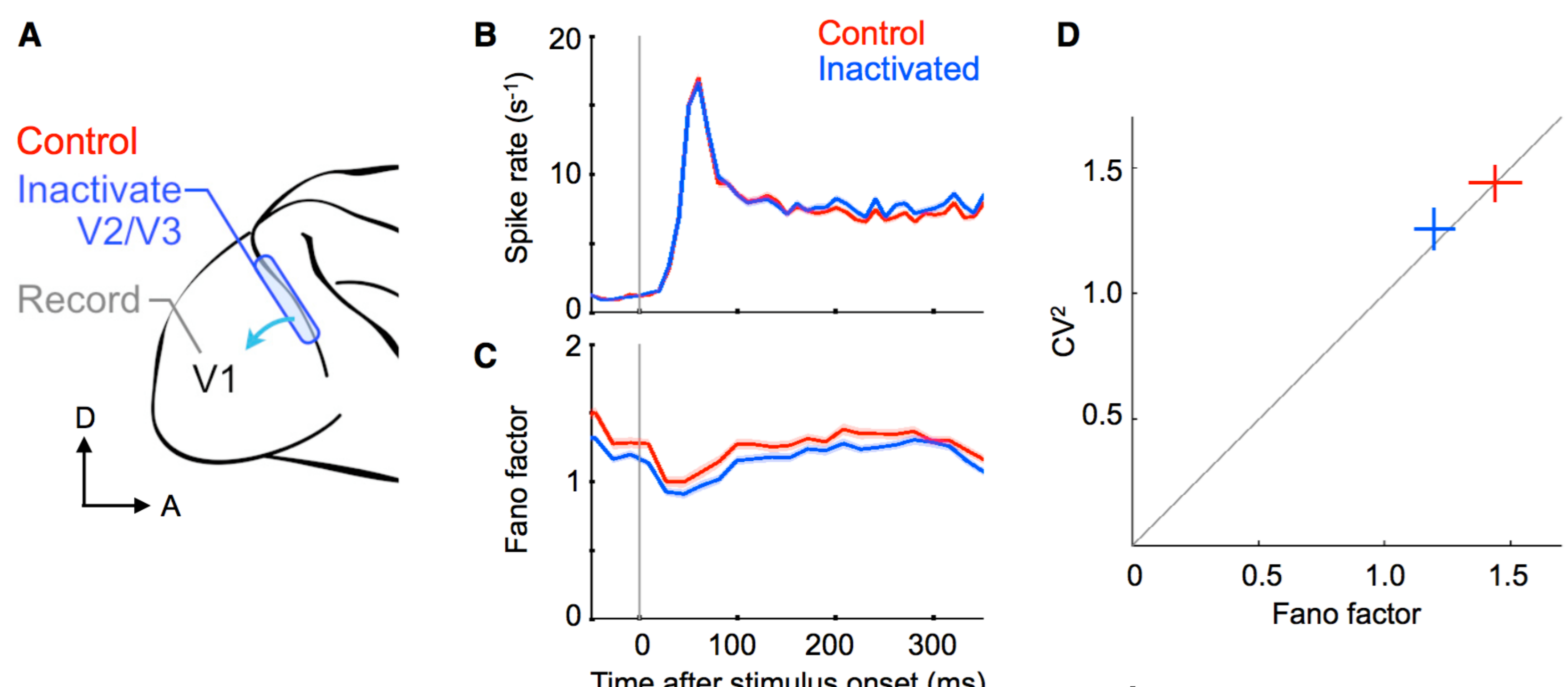
Two basic things we've learned about feedback:

Cortical feedback increases surround suppression to V1 neurons



Nassi et al., *Front. Syst. Neurosci.*, 2014

Cortical feedback increases the **trial-to-trial variability** of V1 neurons



Gómez-Laberge et al., *Neuron*, 2016

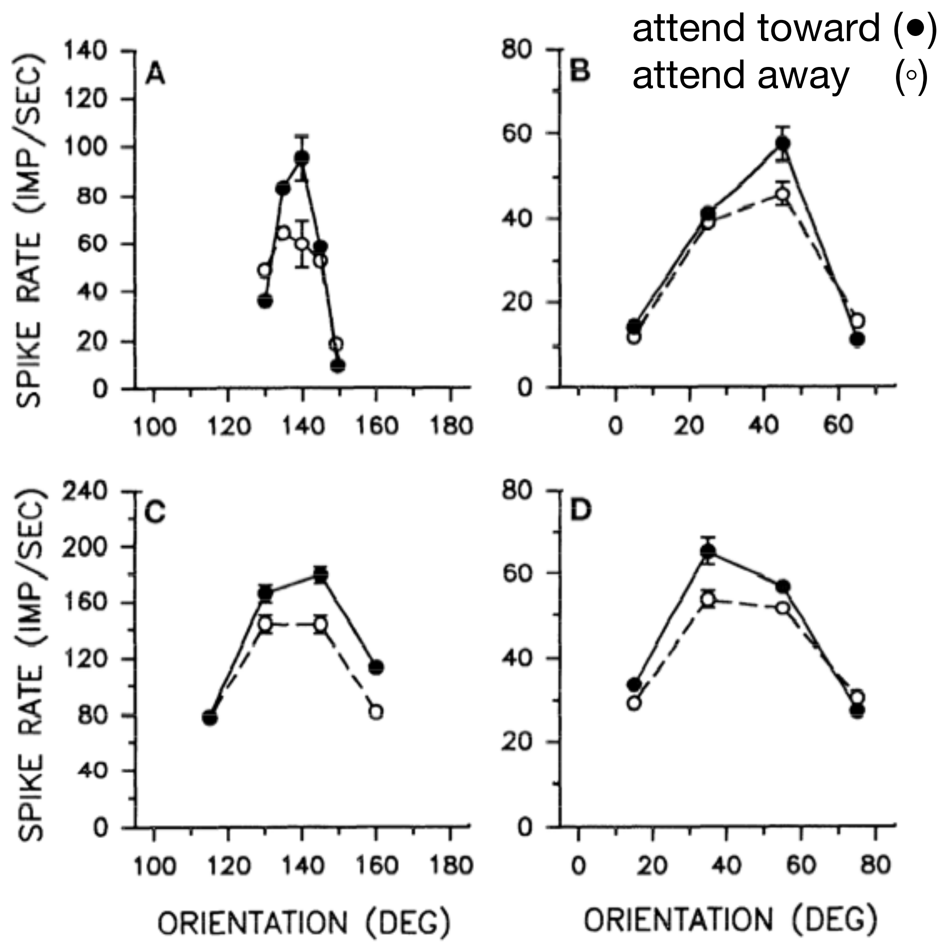
Four orders of magnitude: from neuron to organism

Neural correlates of behavior

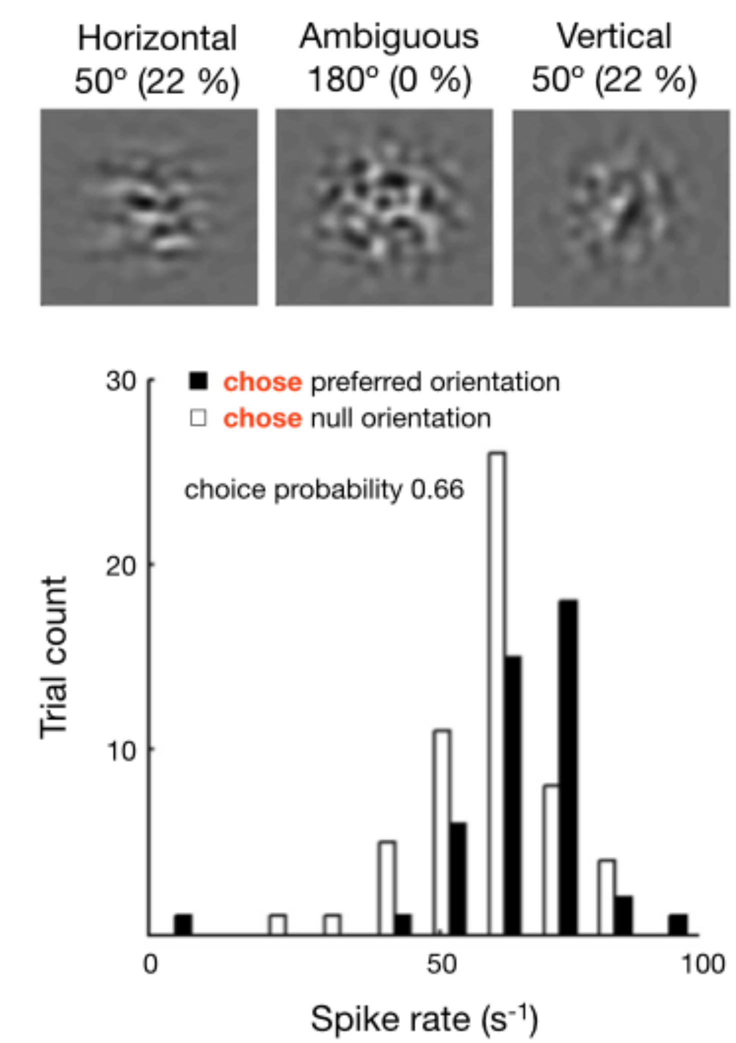
The Emergence of a Neurobiology of Perception

The ready ability to record neuronal activity in alert nonhuman primates has allowed one of the most notable achievements of modern neuroscience: the establishment of direct links between the behavior of single neurons and that of the whole organism (e.g., Mountcastle et al. 1972, Newsome et al. 1989; see also Barlow 1972).

Albright & Stoner, *Annu. Rev. Neurosci.*, 2002



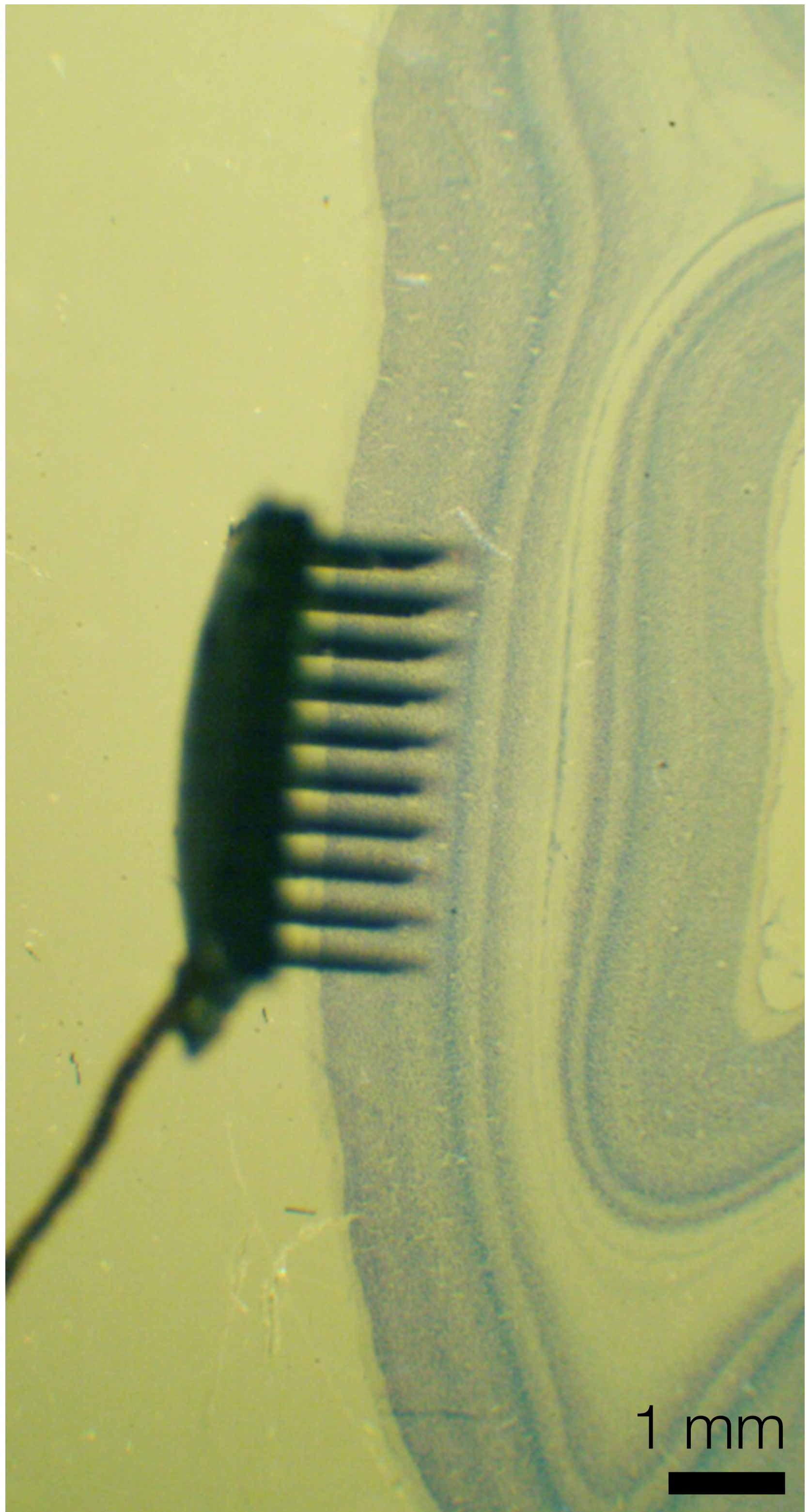
Motter, *J. Neurophysiol.*, 1993



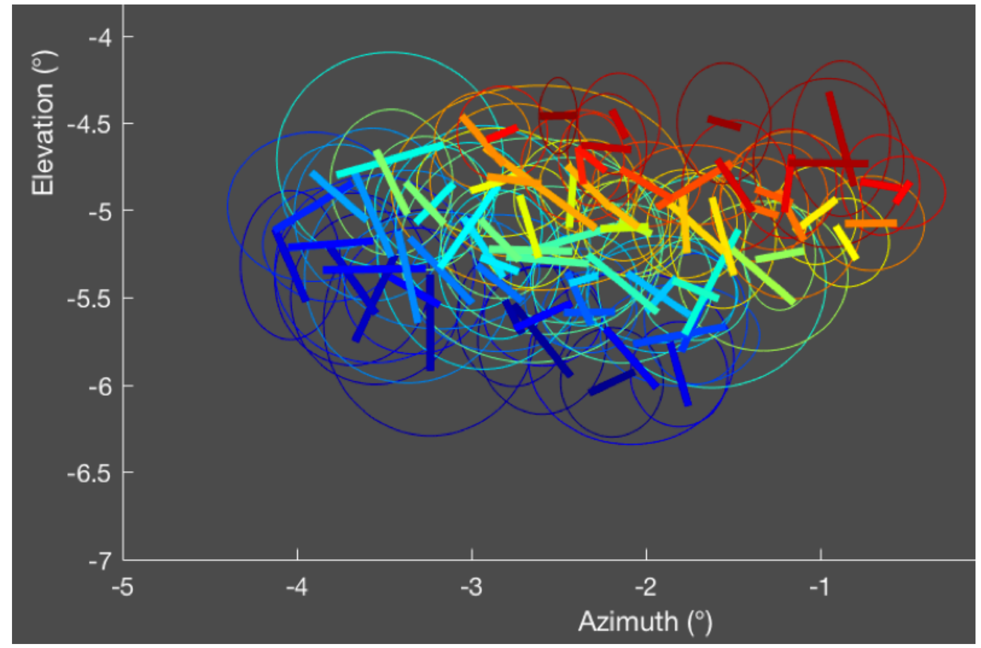
Nienborg & Cumming, *J. Neurosci.*, 2014

Behavioral context is also related to neural co-variability...

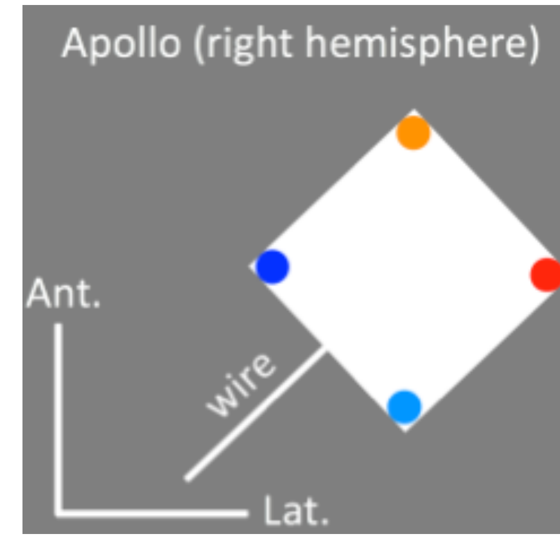
10 x 10 multi-electrode array



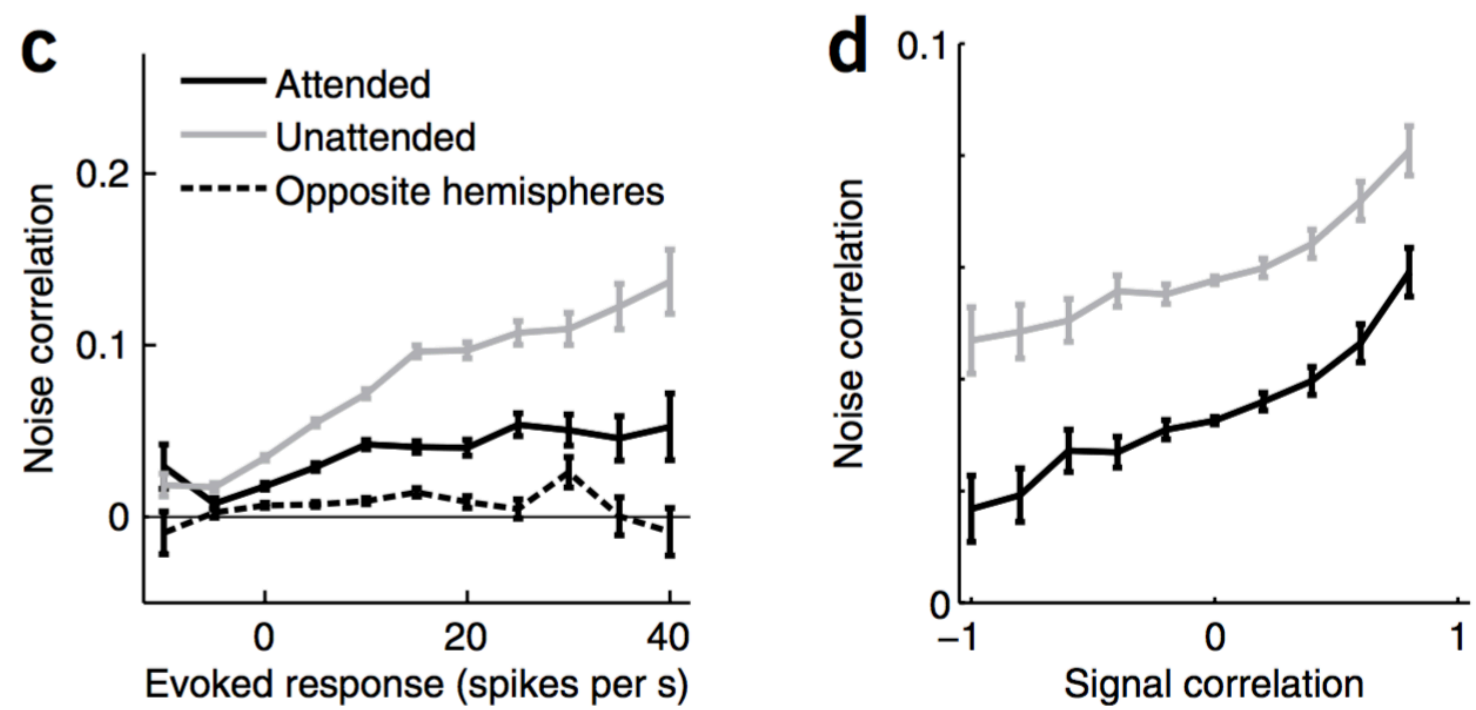
receptive field and preferred orientation



array placement in brain



correlated activity between neurons is prevalent in cortex



Cohen & Maunsell, *Nat. Neurosci.*, 2009

... which leads us to a unifying hypothesis (to be tested): <u>feedback provides behavioral context to visual cortex</u>

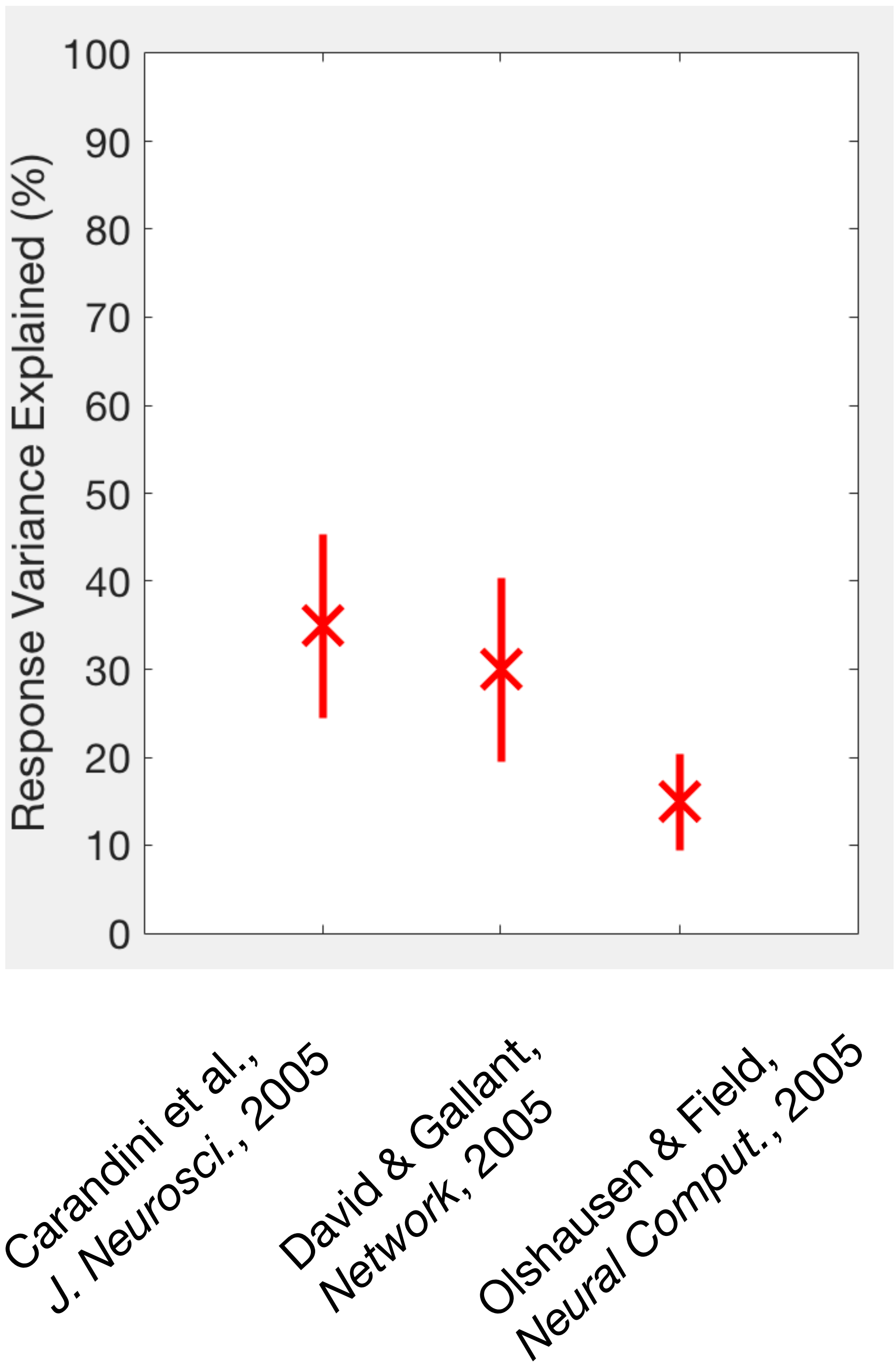
[Some unpublished work will appear on this slide during the lecture]

A grain (perhaps a block) of salt: But do we even *really* know what V1 does?

The Unknown

What we currently understand is subject to important limitations:

- Biased sampling of neurons
- Biased visual stimuli
- Biased theories
- Contextual effects
- Internal connections and feedback



Further reading

- **Wandell B. Foundations of Vision. Sinauer Books1995.**
- **Dayan and Abbott. Theoretical Neuroscience. MIT Press 2001.**

Papers cited in these slides (not exhaustive list):

1. Hubel DH, Wiesel TN (1959) Receptive fields of single neurones in the cat's striate cortex. J Physiol (Lond) 148:574–591.
2. Hubel DH, Wiesel TN (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. J Physiol (Lond) 160:106–154.
3. Hubel DH, Wiesel TN (1977) Functional architectureof macaque monkey visual cortex. Proc R Soc Lond B 198:1–59.
4. Horton JC, Adams DL (2005) The cortical column: a structure without a function. Philos Trans R Soc Lond, B, Biol Sci 360:837–862.
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7. Maunsell JHR, van Essen DC (1983) The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. J Neurosci 3:2563–2586.
8. Felleman DJ, van Essen DC (1991) Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex 1:1–47.
9. Markov NT et al. (2014) A weighted and directed interareal connectivity matrix for macaque cerebral cortex. Cereb Cortex 24:17–36.
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11. Smith MA, Kohn A (2008) Spatial and temporal scales of neuronal correlation in primary visual cortex. J Neurosci 28:12591–12603.
12. Motter BC (1993) Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. J Neurophysiol 70:909–919.
13. Albright TD, Stoner GR (2002) Contextual influences on visual processing. Annu Rev Neurosci 25:339–379.
14. Nienborg H, Cumming BG (2014) Decision-related activity in sensory neurons may depend on the columnar architecture of cerebral cortex. J Neurosci 34:3579–3585.
15. Cohen MR, Maunsell JHR (2009) Attention improves performance primarily by reducing interneuronal correlations. Nat Neurosci 12:1594–1600.
16. Lange RD, Haefner RM (2016) Inferring the brain's internal model from sensory responses in a probabilistic inference framework. bioRxiv. doi: 10.1101/081661