What is the other 85% of V1 doing?

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Book chapter

Olshausen BA, Field DJ (2004) What is the other 85% of V1 doing? In: *Problems in Systems Neuroscience*, T.J. Sejnowski, L. van Hemmen, Eds. Oxford University Press. (in press)

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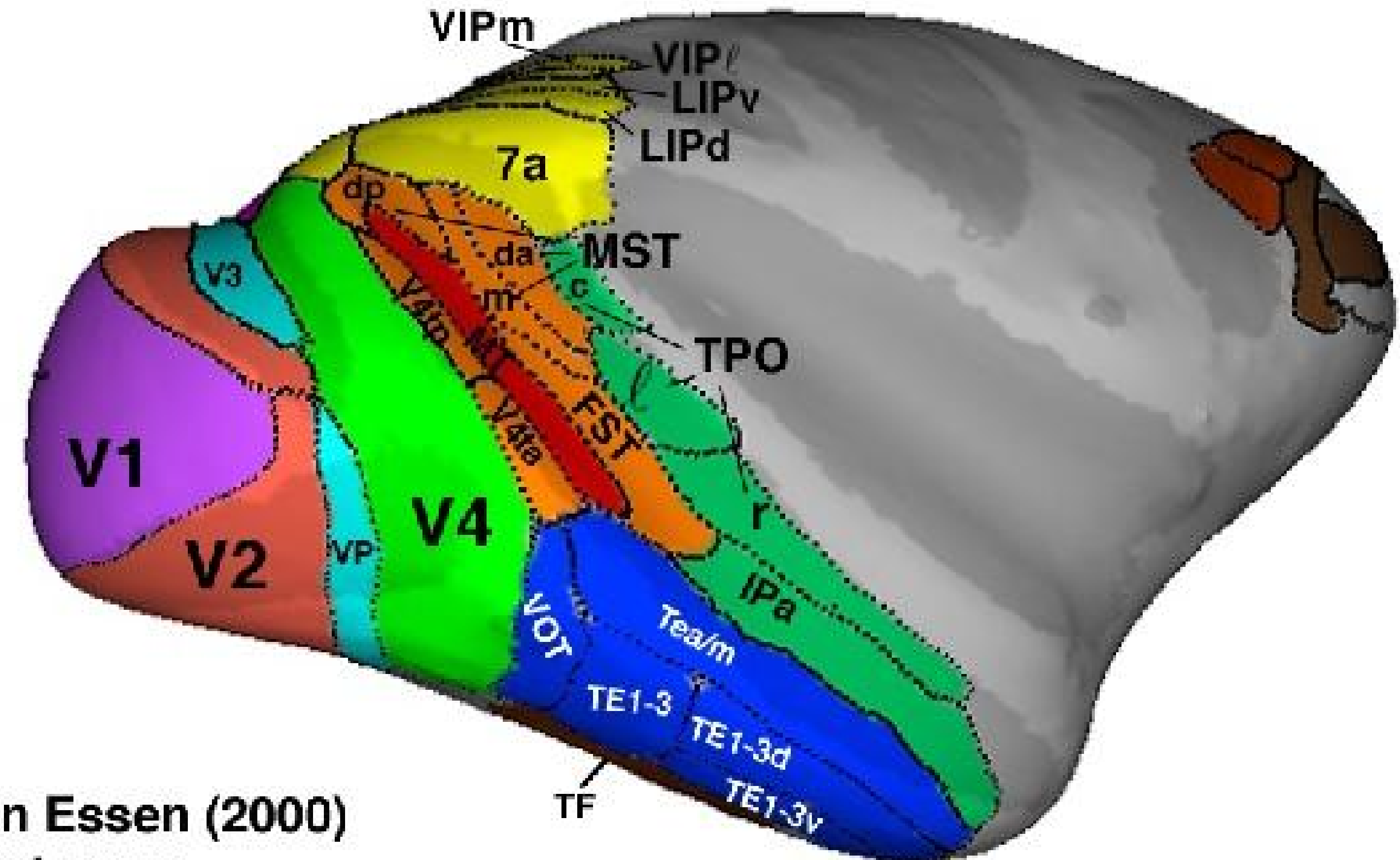
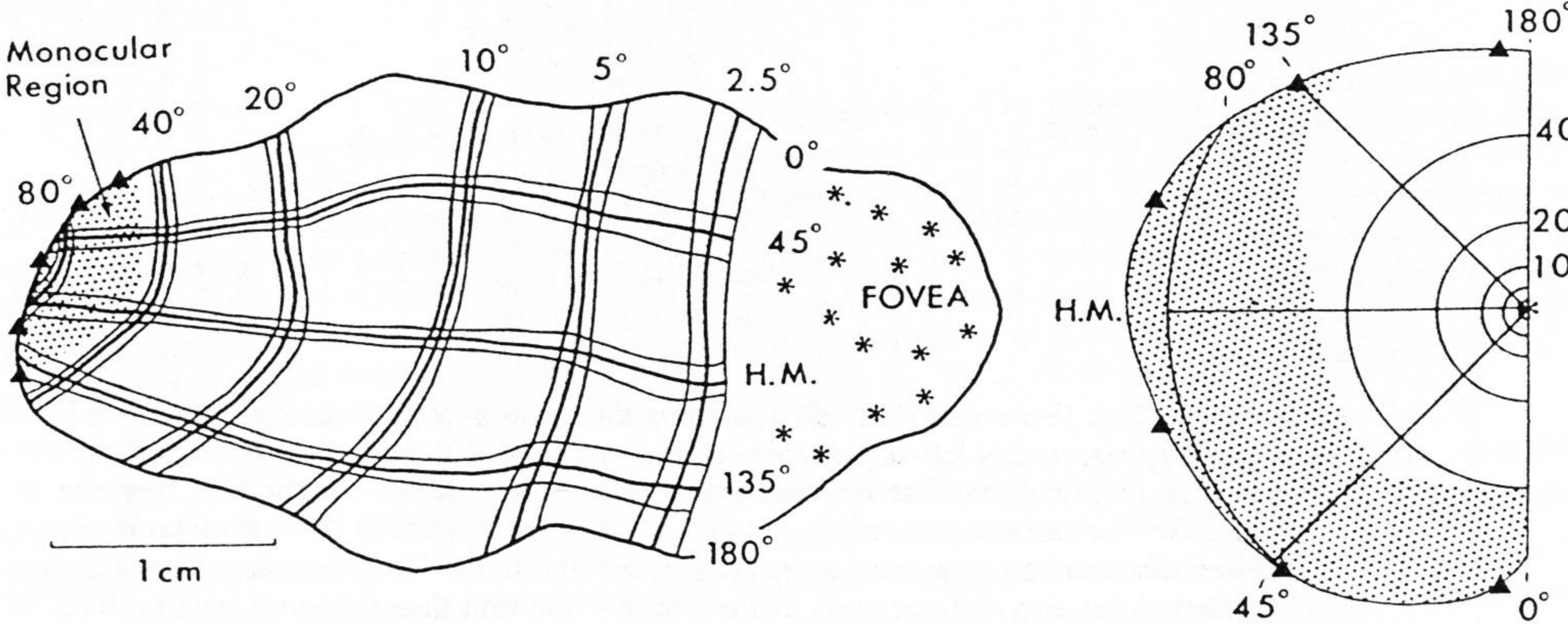
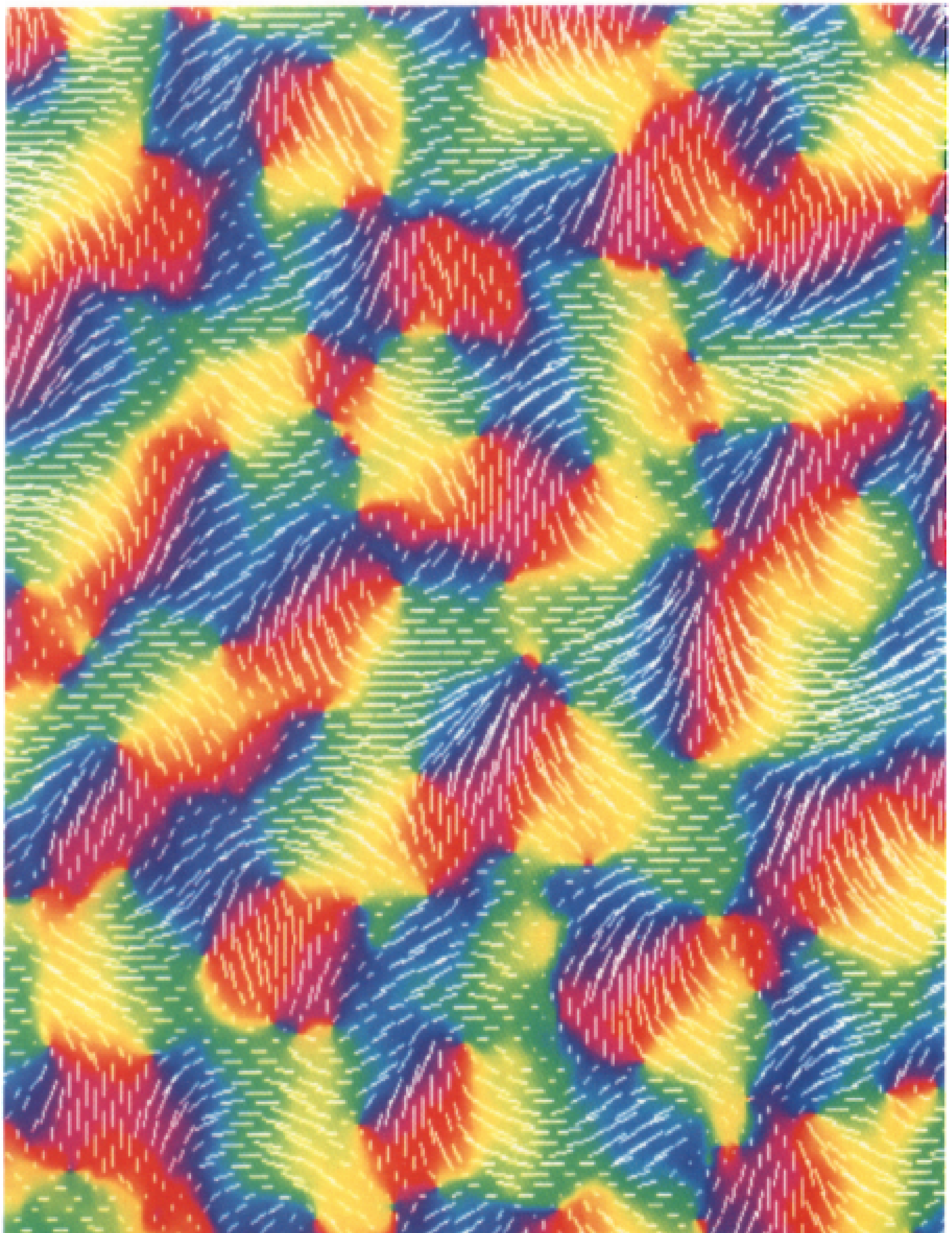
Main Points

- There is still much that we do not understand about V1 function.
- Acknowledging this fact opens the door to new theories.

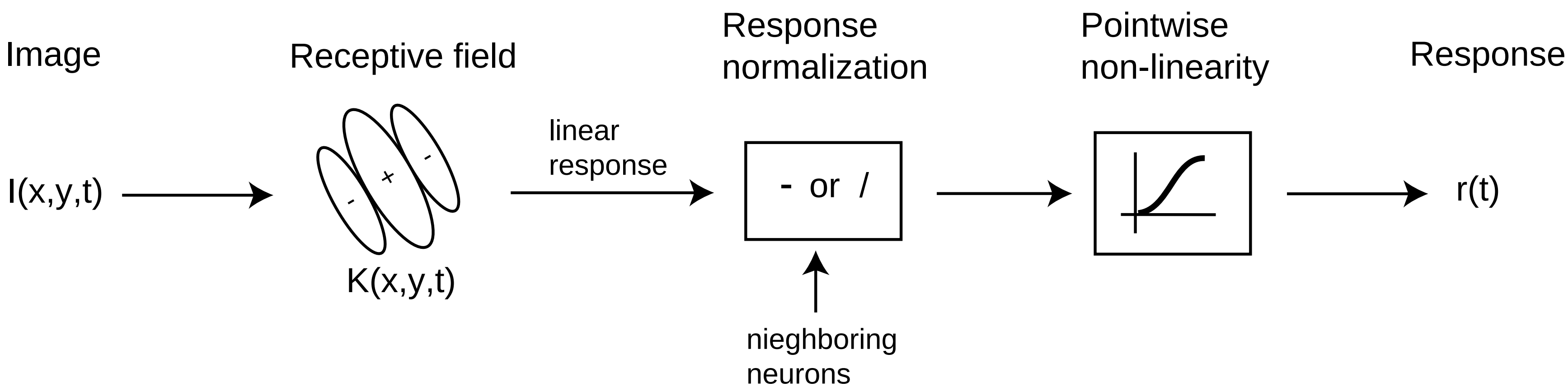


Lewis & Van Essen (2000)
Visual areas


Monocular Region
80°
40°
20°
10°
5°
2.5°
0°
45°
FOVEA
H.M.
135°
180°
1 cm
180°
135°
80°
40°
20°
10°
H.M.
45°
0°

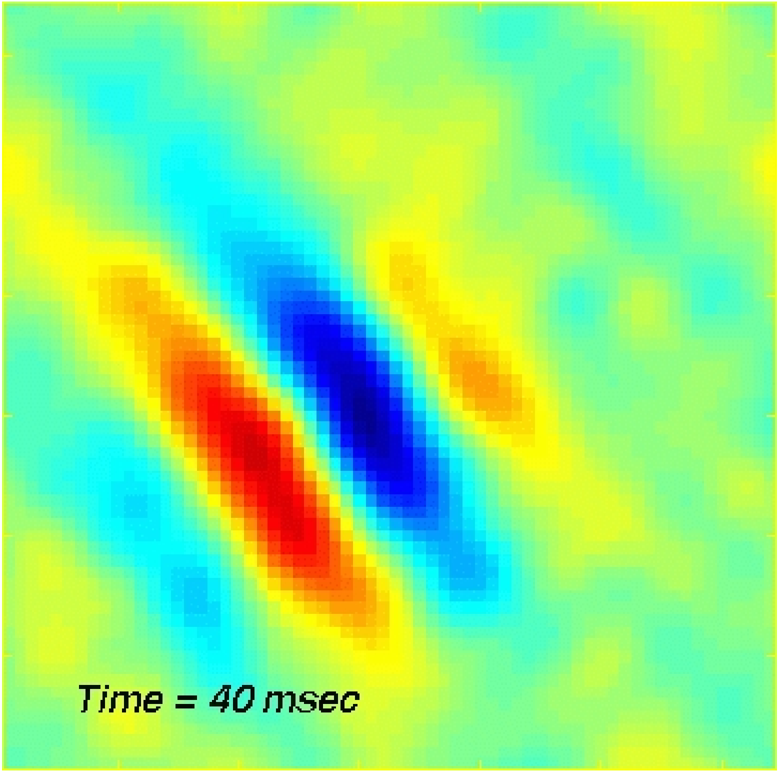


The “standard model”



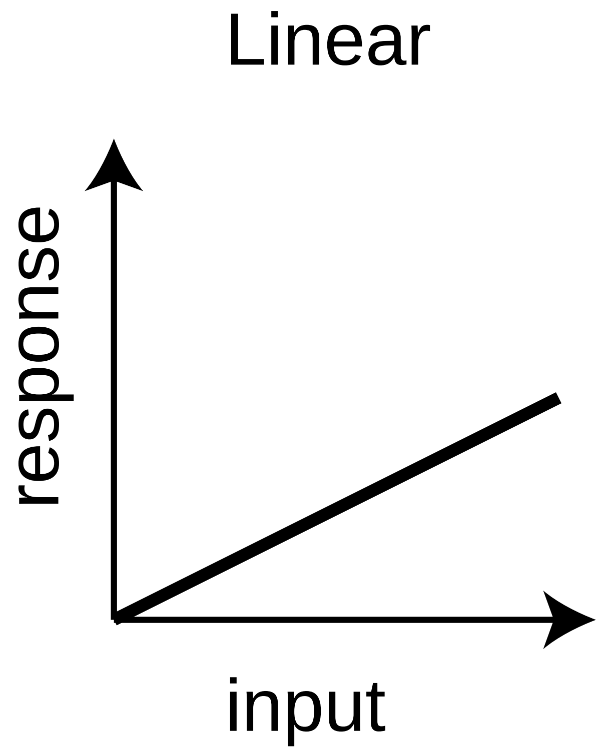
V1 space-time receptive field

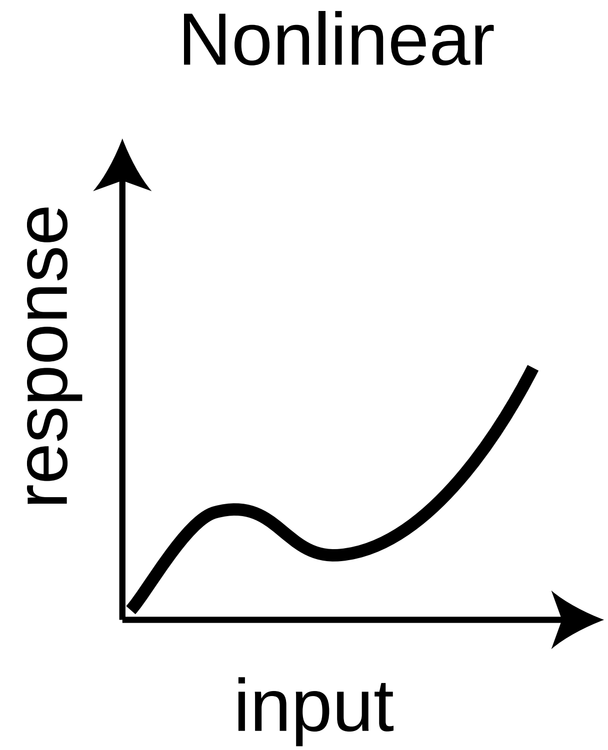
(Courtesy of Dario Ringach)



The problem

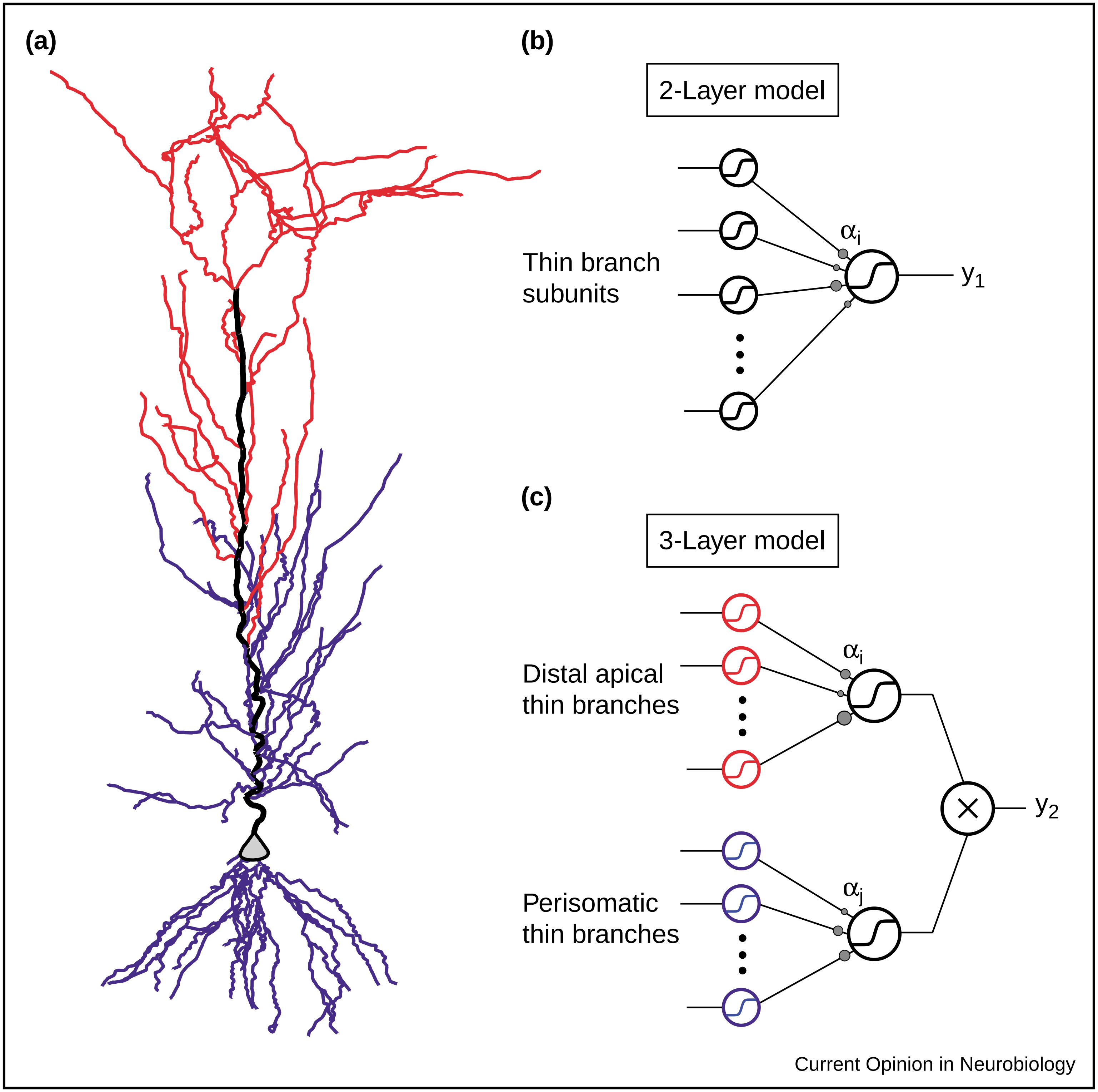
- Neurons are highly nonlinear
- Recurrent circuits of neurons are even more nonlinear
- There is no general method for characterizing nonlinear systems


Linear
response
input


Nonlinear
response
input

Nonlinearities

- Action potentials
- Adaptation
- Dendritic trees



Hausser & Mel (2003) *Current Opinion in Neurobiology, 13*: 372-383

The reductionist approach

- Use simple, “controlled” stimuli (bars, spots, gratings)
- Record from one neuron at a time

Five problems with the current view of V1

1. Biased sampling

2. Biased stimuli

3. Biased theories

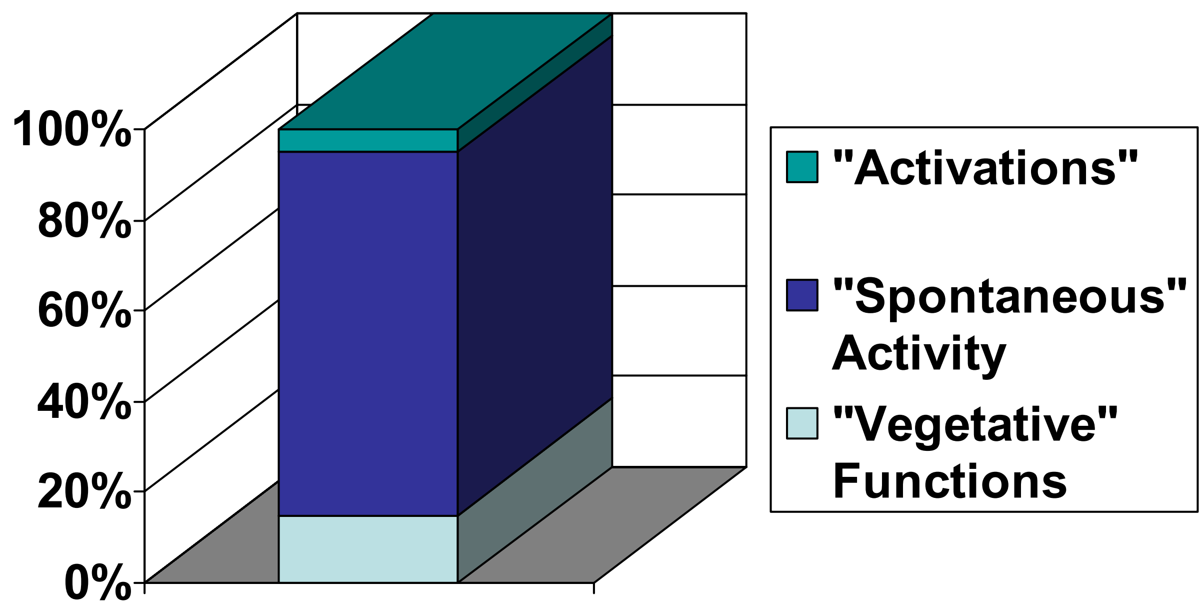
4. Interdependence and context

5. Ecological deviance

1. Biased sampling

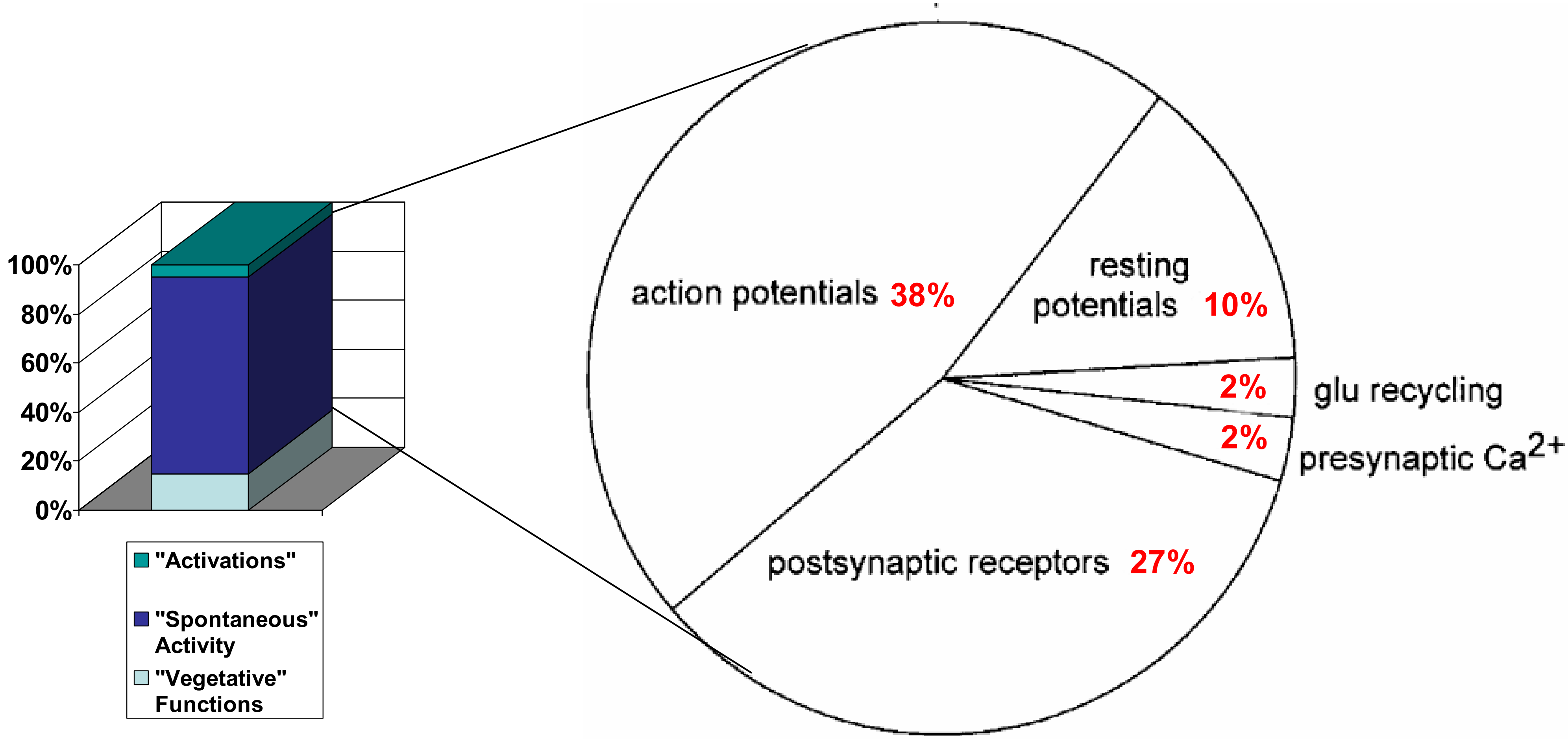
- Neurons with large (extracellular) action potentials
- "Visually responsive" neurons
- Neurons with high firing rates

Distribution of the Brain's Energy Budget



Brain Signaling-Related Energy Expenditure

Distribution of ATP consumption for a mean action potential rate of 4 Hz



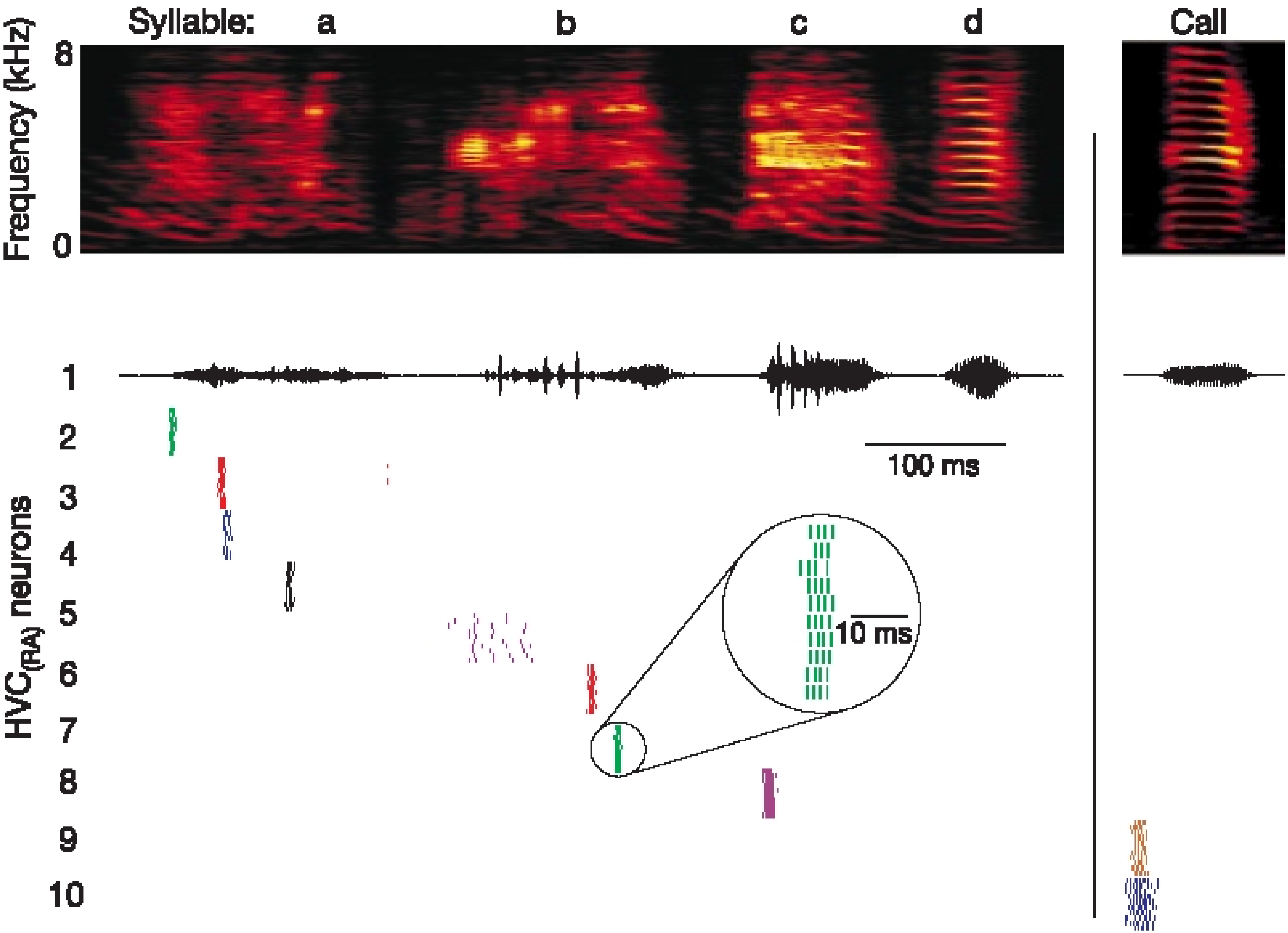
(Ignores the energy expenditure unrelated to signaling as well as glial glycolysis associated with transient increases in activity)

Adapted From Attwell & Laughlin
JCBF&M 21:1133-1145, 2001

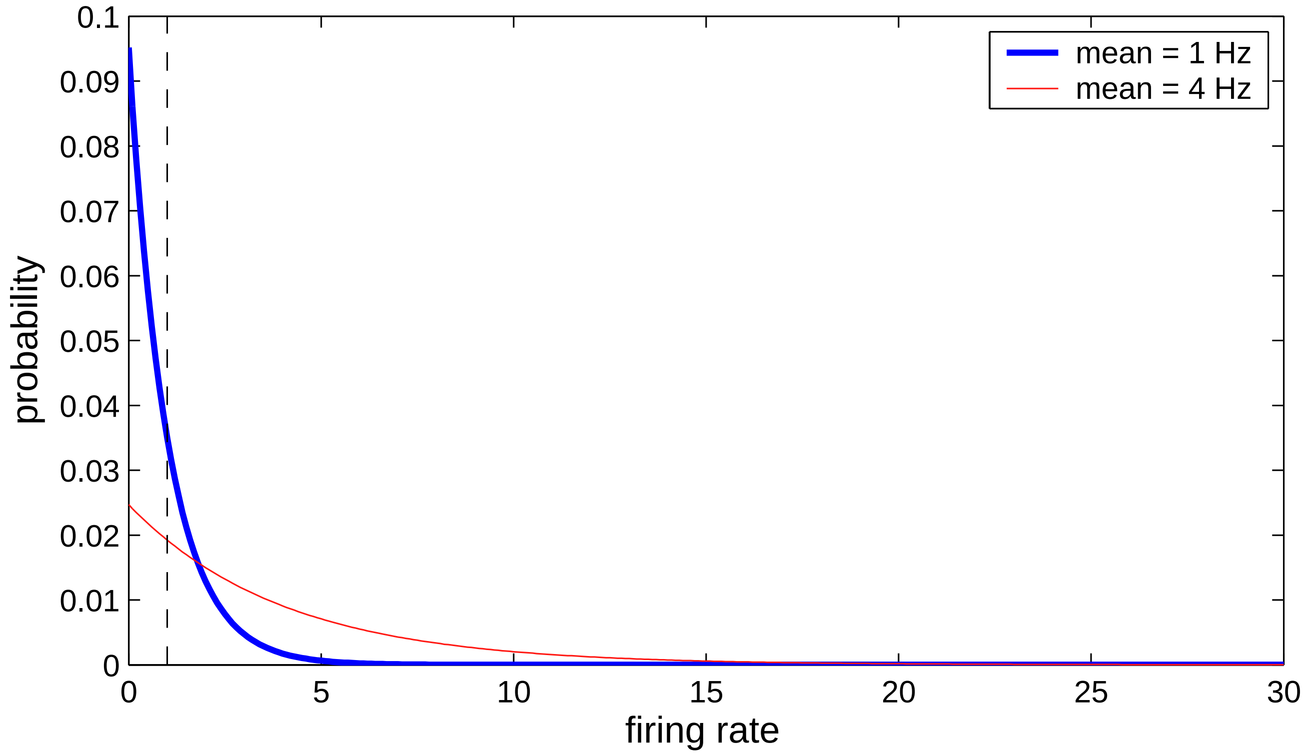
Extreme sparse coding

- Gilles Laurent - mushroom body, insect
- Michael Fee - HVC, zebra finch
- Tony Zador - auditory cortex, mouse
- Bill Skaggs - hippocampus, primate
- Harvey Swadow - motor cortex, rabbit
- Michael Brecht - barrel cortex, rat
- Christof Koch - inferotemportal cortex, human

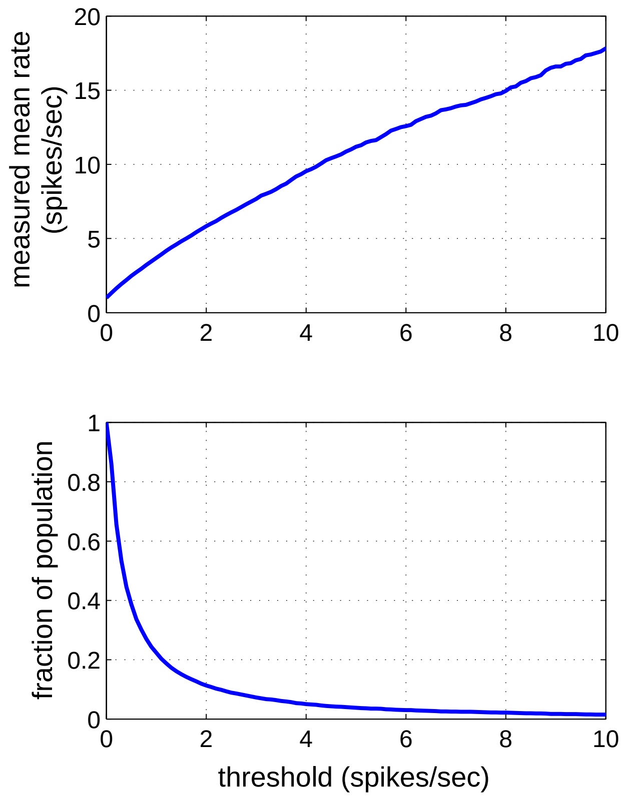
Hahnloser RHR, Kozhevnikov AA, Fee MS (2002) An ultra-sparse code underlies the generation of neural sequences in a songbird. *Nature, 419*, 65-70.



Exponential firing rate distribution



Sampling bias

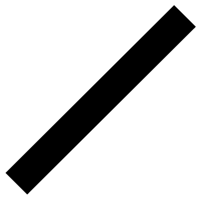


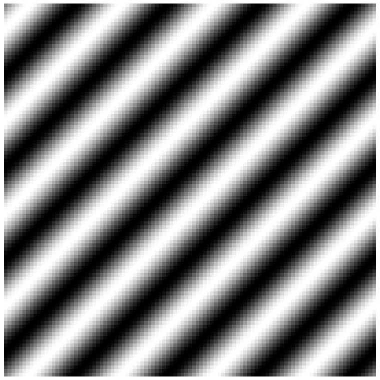
Estimated fraction of population characterized

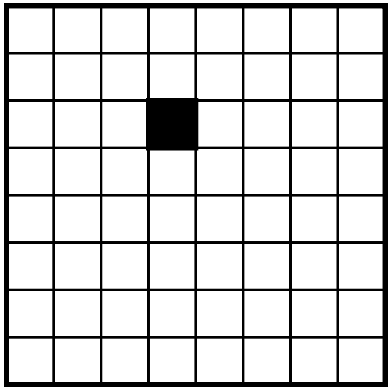
- Missed neurons due to small action potentials (5-10%)
- Missed neurons due to unresponsiveness (5-10%)
- Missed neurons due to low firing rates (50-60%)

Even allowing for some overlap among these populations would yield the generous estimate that 40% of the population has been adequately sampled.

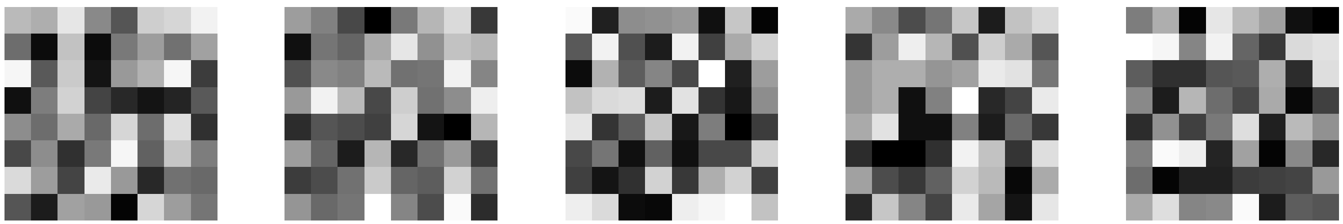
2. Biased stimuli







Searching the entire stimulus space is impossible



…

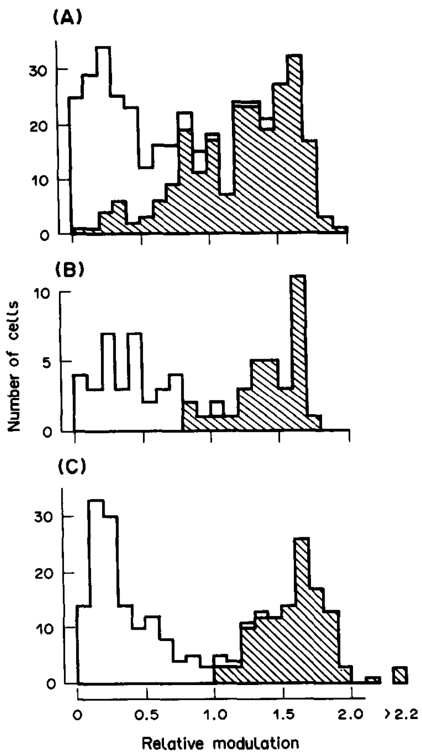
8×8 patch with 6 bits of gray level $= 2^{384} > 10^{100}$ possible combinations.

3. Biased theories

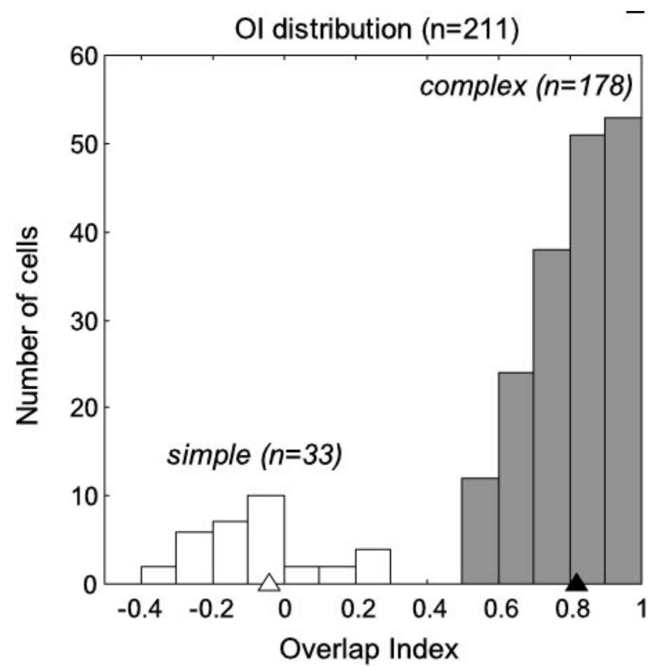
- Emphasis on “telling a story” encourages investigators to demonstrate when a theory explains data, not when a theory provides a poor model.
- Data-driven vs. functional theories (e.g., spatial-frequency tuning).
- Simple/complex/hypercomplex - are these categories real, or the result of the way neurons were stimulated with bars of light?

How do you classify simple vs. complex?

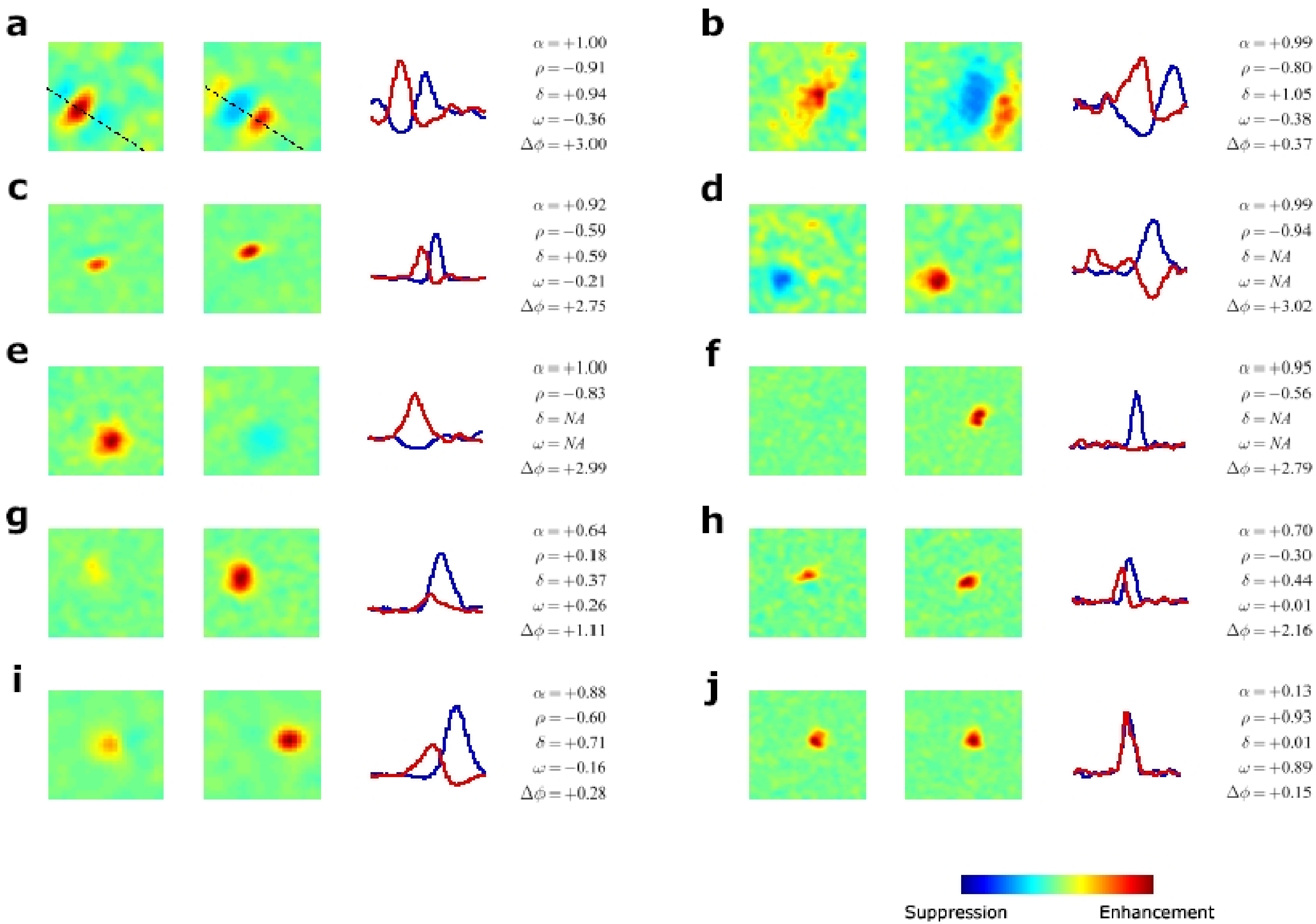
Skottun et al. (1991)



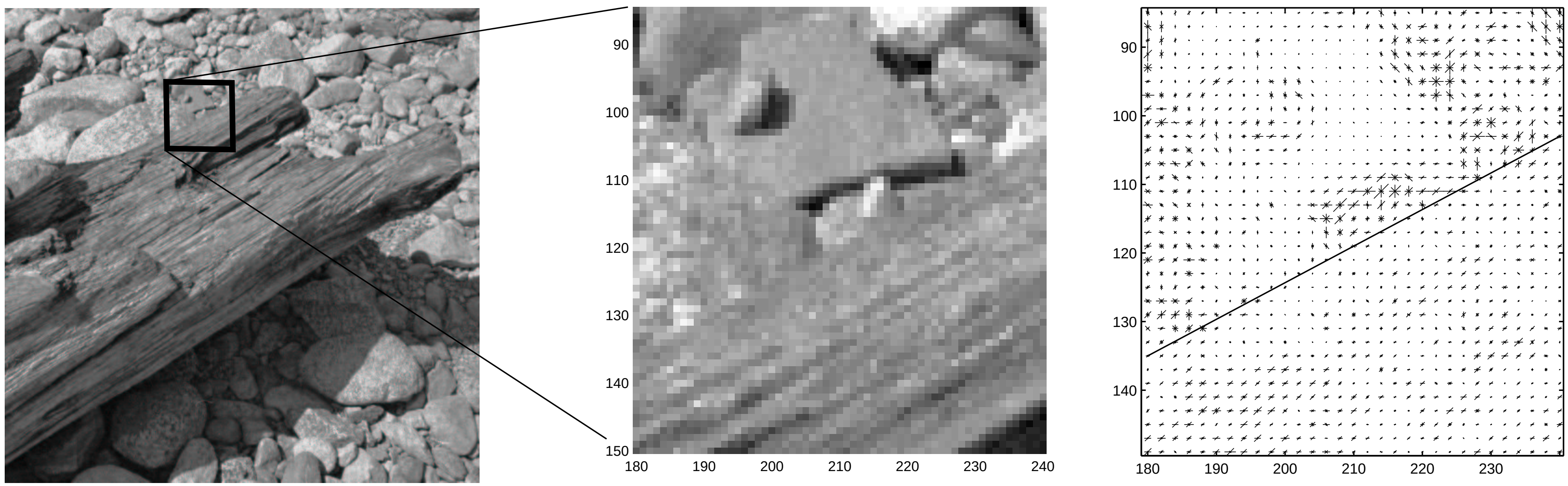
Kagan et al. (2002)



Mata & Ringach (2004)



Do V1 neurons act as feature detectors?



Vision is a difficult problem.

Good theories need to be functionally driven as well as data driven.

Surface representation

- We live in a three-dimensional world.
- The fundamental causes of images are *surfaces* reflecting light, not two-dimensional features such as spots, bars, edges or gratings.
- We rarely see the surface of an object in its entirety.

Nakayama K, He ZJ, and Shimojo S. (1995) **Visual surface representation: a critical link between lower-level and higher level vision.** In: S.M. Kosslyn and D.N. Osherson, Eds, *An Invitation to Cognitive Science*. MIT Press, pp. 1-70.

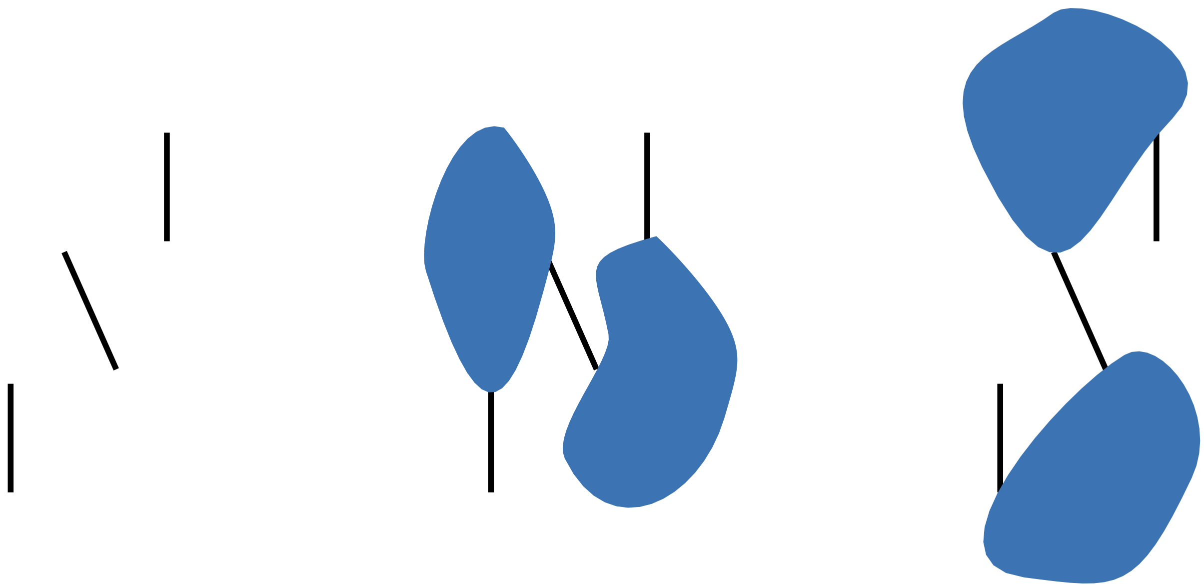
Example: ‘Mooney faces’

Example: ‘Mooney faces’

Completion depends upon occlusion



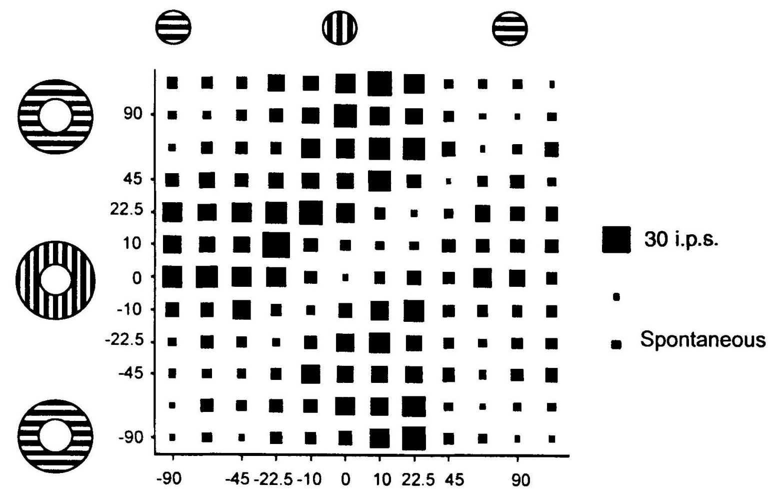
4. Interdependence and context

- $< 5\%$ of the excitatory input in layer 4 arises from LGN (Peters & Payne, 1993).
- Geniculate input is responsible for $< 35\%$ of a V1 neuron's response (Chung & Ferster, 1998).
- Ongoing population activity can account for 80% of an individual V1 neuron's response variance (Arieli et al., 1996).

How to study effects of context?

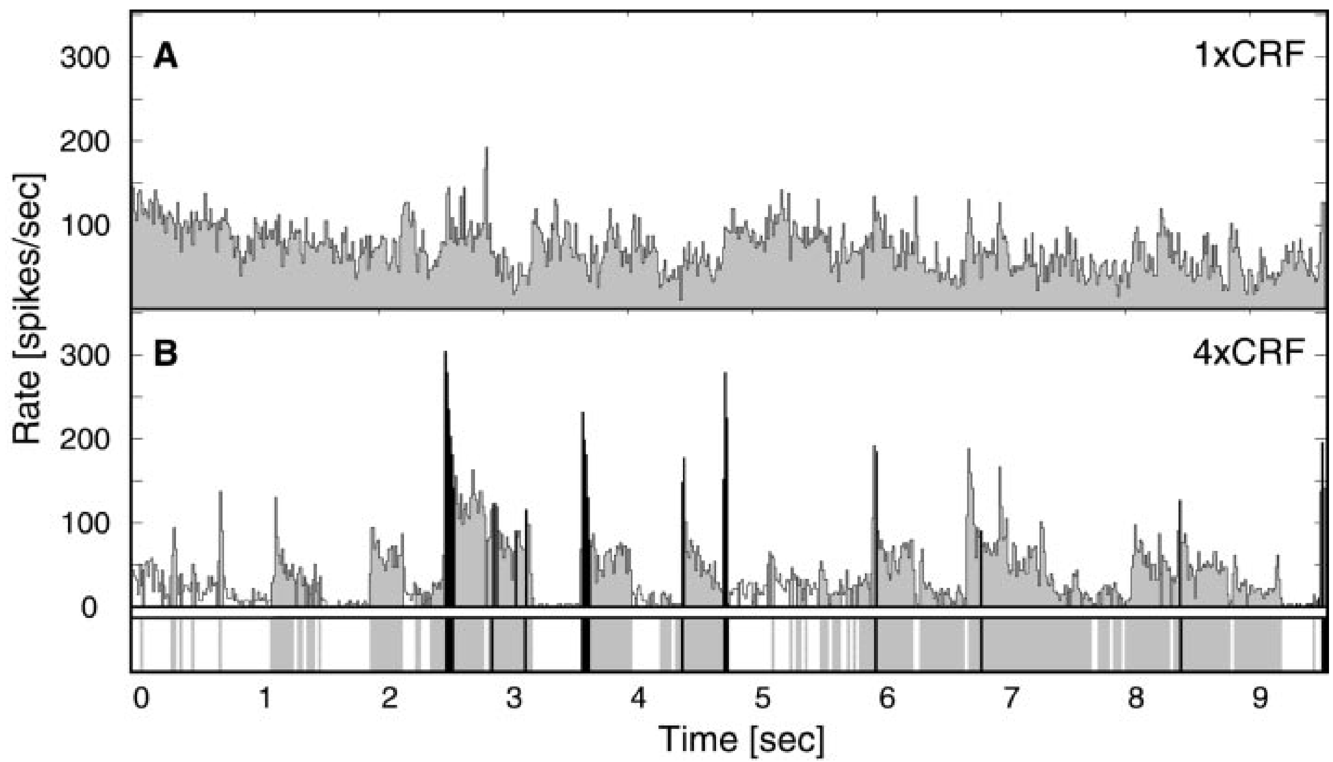
Knierim & Van Essen (1992)

Sillito et al. (1995)

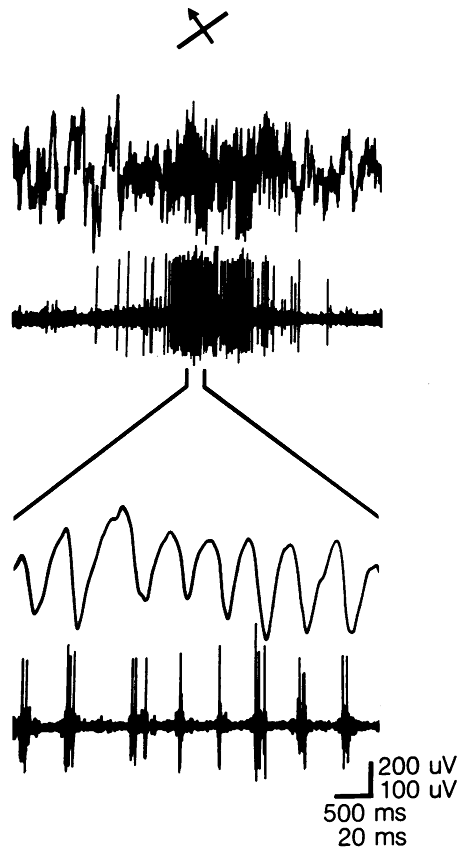


Context in natural scenes sparsifies responses

Vinje & Gallant (2000, 2002)

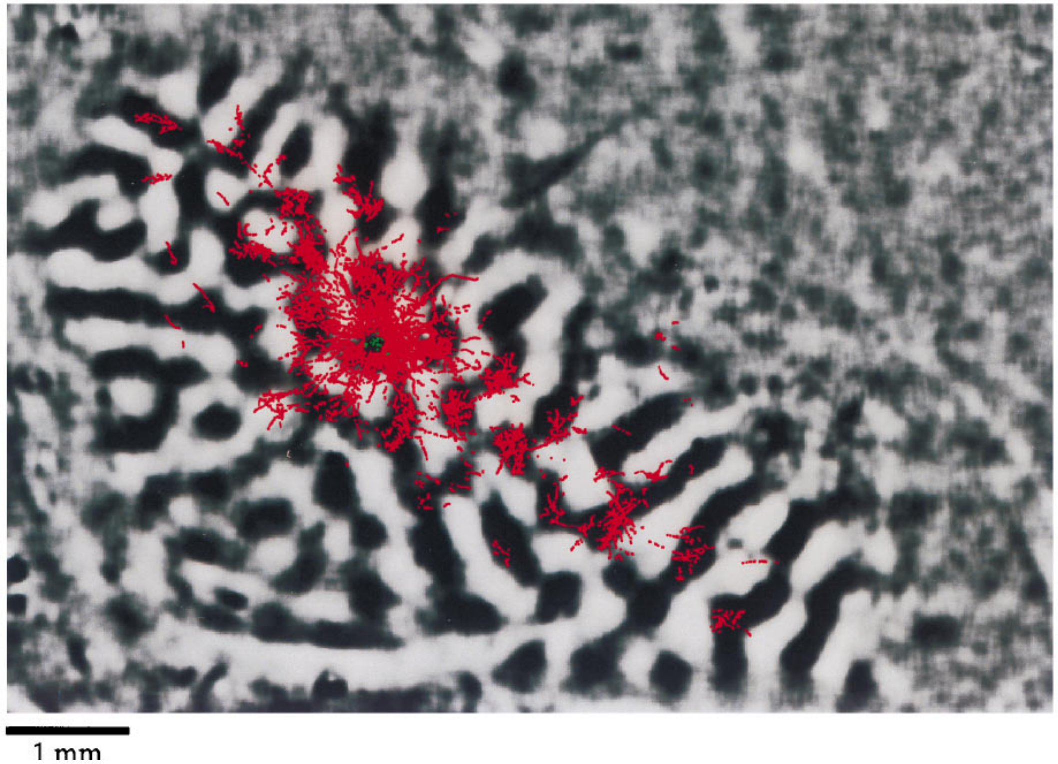


Synchrony



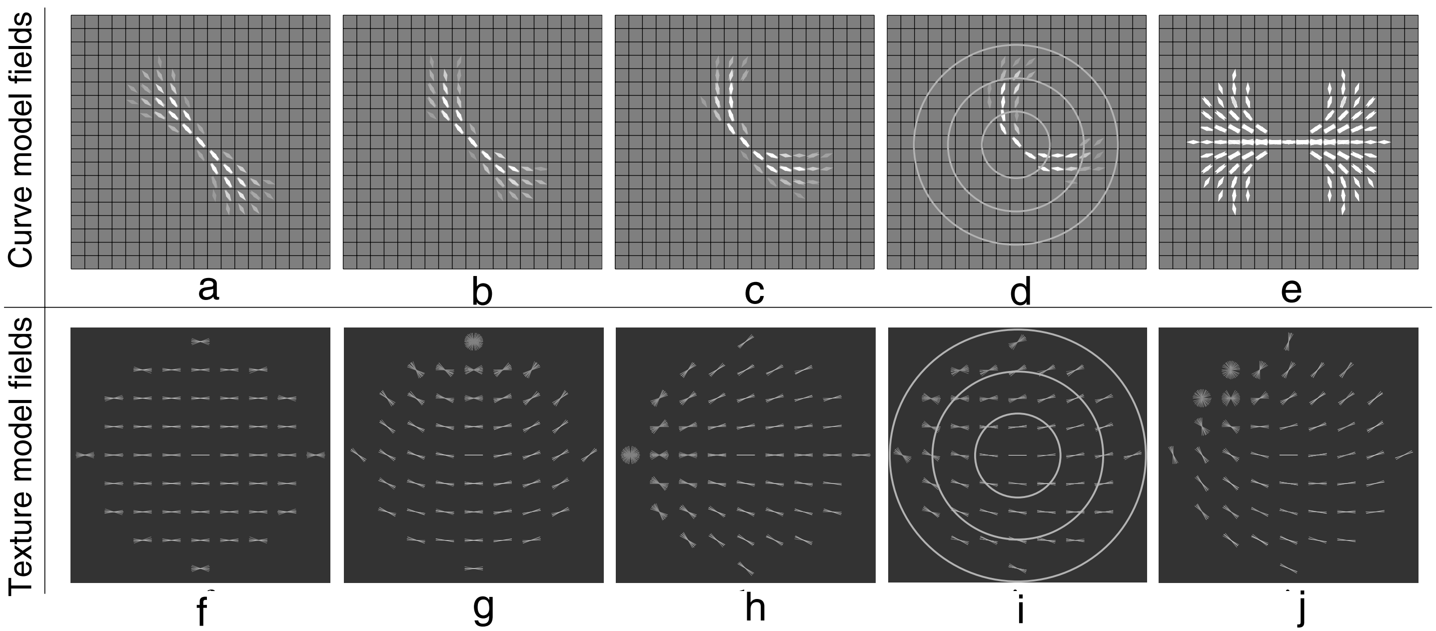
Contour integration

Bosking, Zhang, Schofield & Fitzpatrick (1997)



Models of contour integration

Ben-shahar & Zucker (2004)



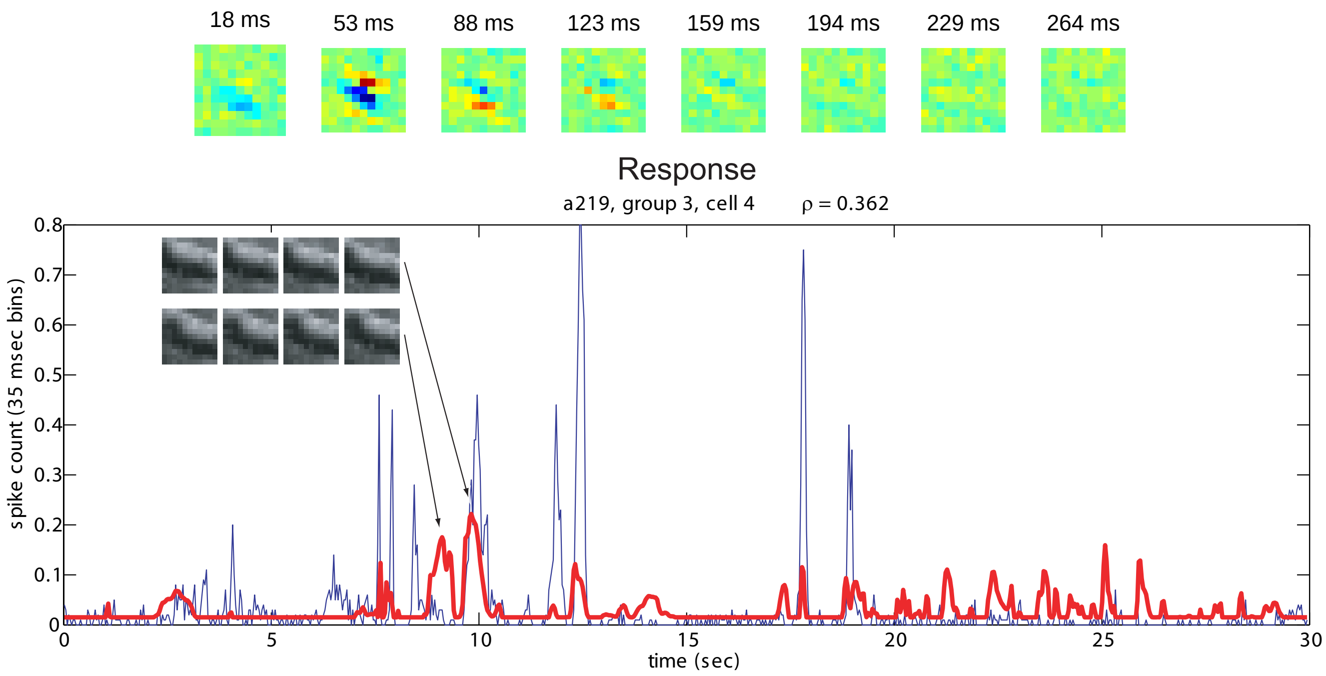
5. Ecological deviance

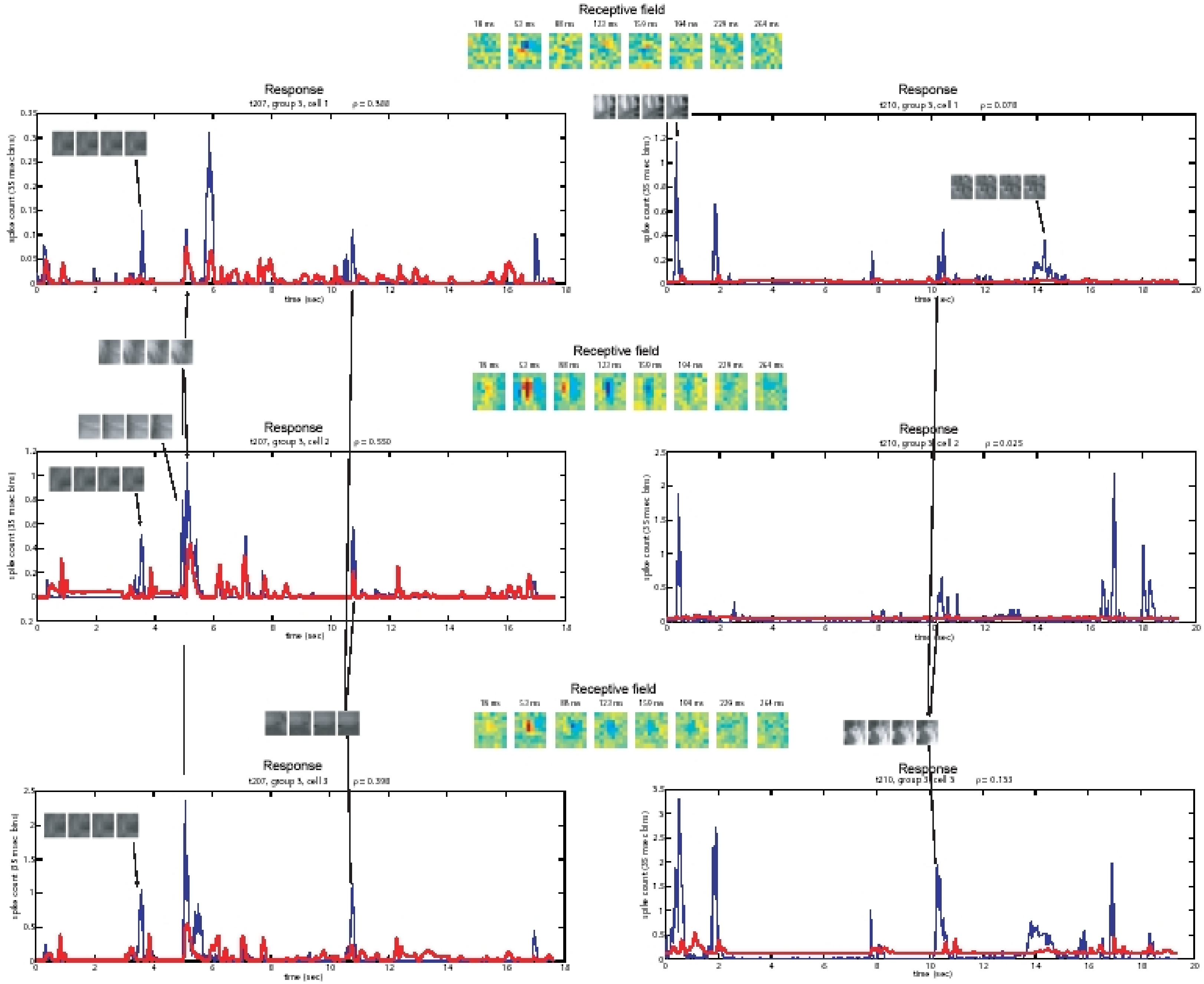
Neural responses to time-varying natural scenes deviate significantly from the predictions of current models.

- David, Vinje & Gallant (1999) - can account for 20-30% of response variance with current models.
- Gray & Baker (unpublished observations) - responses to natural movies are often not predicted by simple receptive field models.
- Machens, Wehr & Zador (2004) - can account for 11 % of response variance in A1 using STRF models.

V1 neural responses to natural scenes deviate from predictions of simple receptive field models

Data from Gray lab (J. Baker)

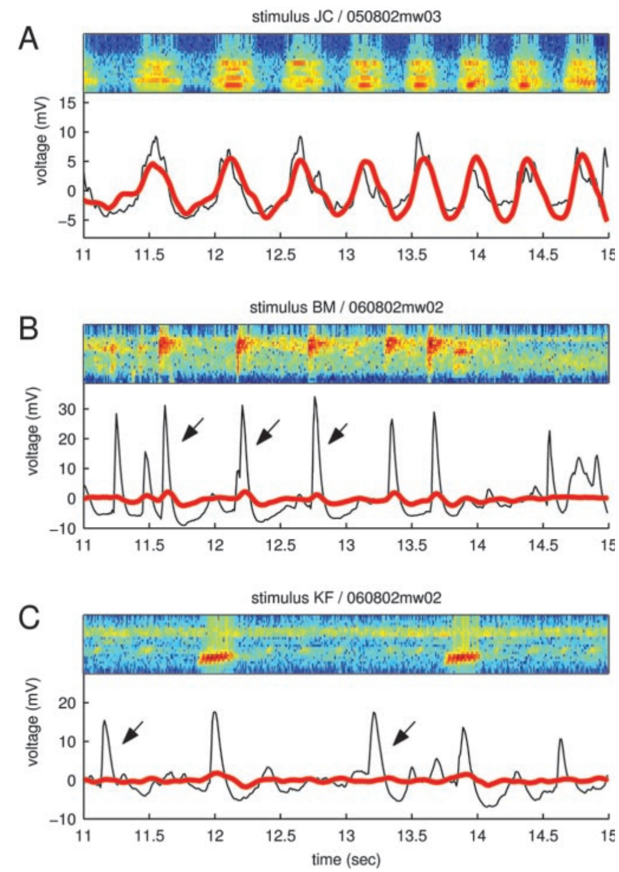




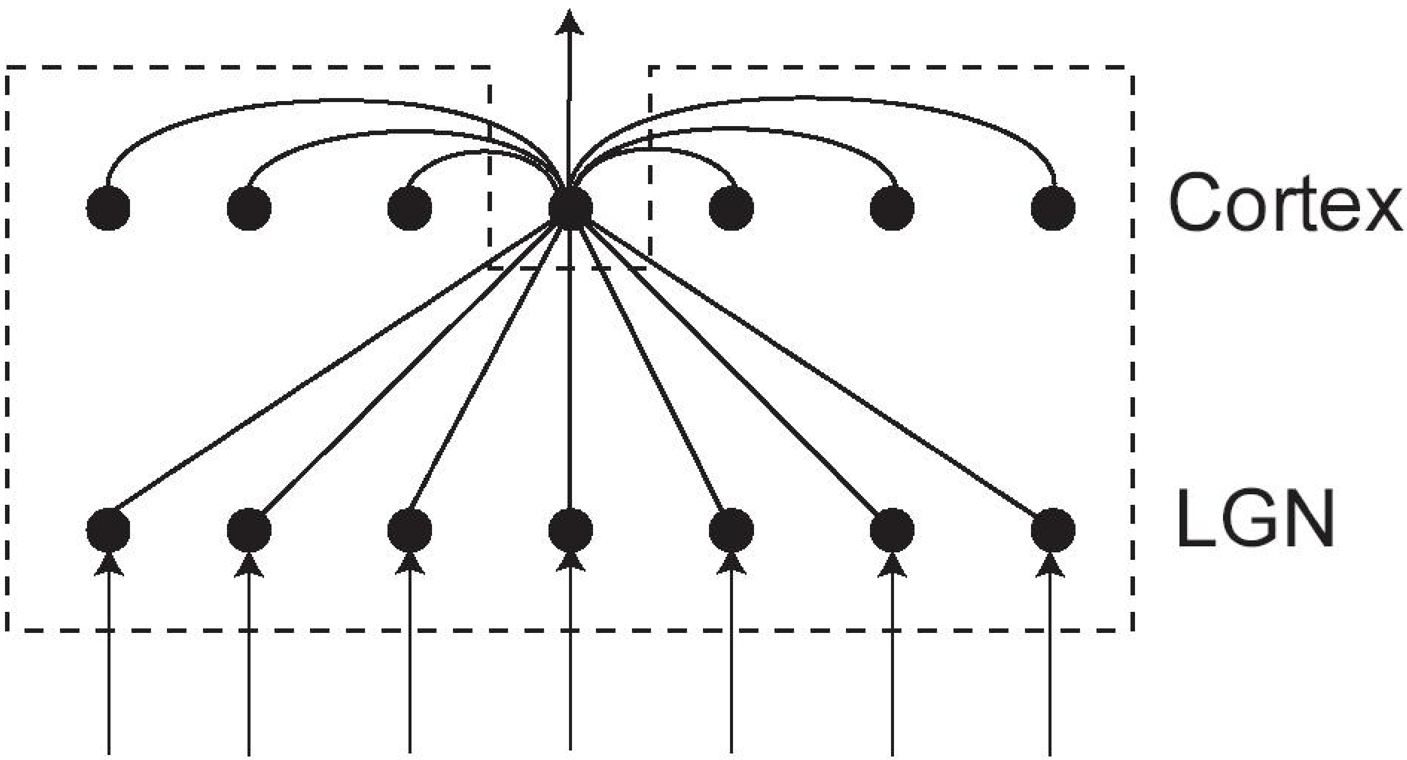
Receptive field
Response
Response
Receptive field
Response
Response
Receptive field
Response
Response
time (sec)

Same thing in A1

Machens, Wehr & Zador (2004)



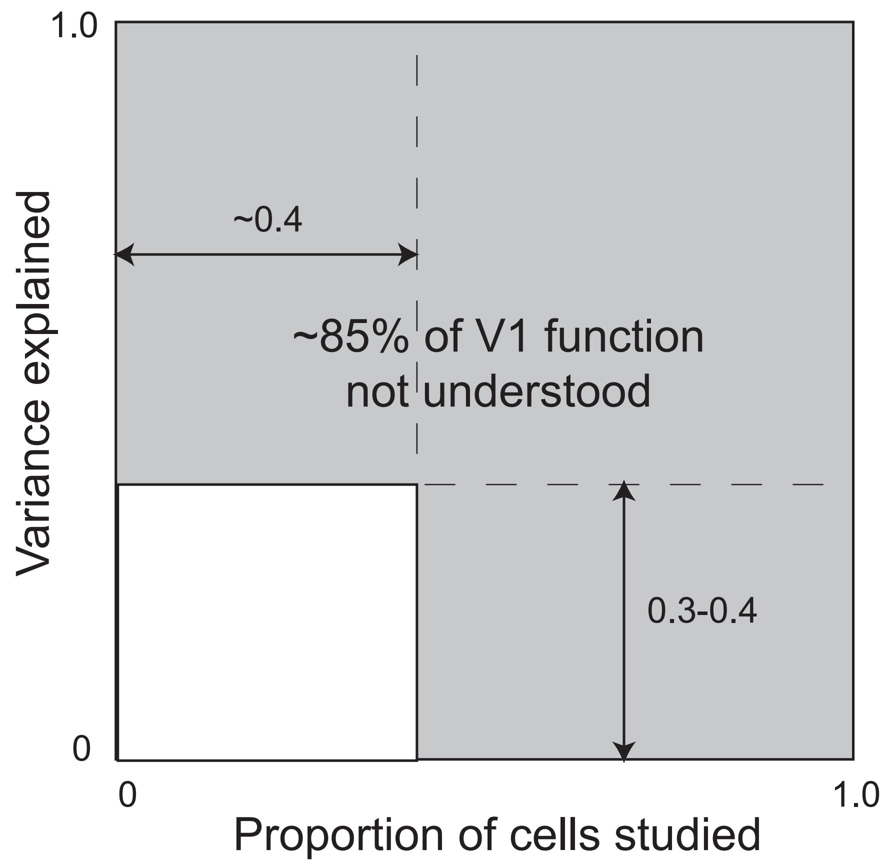
Single unit recording



Summary

	Biased sampling	Biased stimuli	Biased theories	Interdep. & context	Ecological deviance
Problem	large neurons; visually respon-sive neurons; neurons with high firing-rates	use of reduced stimuli such as bars, spots, & gratings	simple/complex cells; data-driven theories	influence of intra-cortical input; effect of context; synchrony	responses to natural scenes deviate from predictions of standard models
Solution	chronically implanted electrodes; parallel recording arrays	use natural scenes, ecologically relevant stimuli	consider more functional/ computational theories that solve problems of vision	examine how context affects responses in natural scenes	develop models that can account for responses to natural images

Bottom line


1.0
~0.4
~85% of V1 function
not understood
Variance explained
0.3-0.4
0
0
1.0
Proportion of cells studied

Conclusions

- We still do not understand the vast majority of what V1 is doing under natural conditions.
- What is needed:
  - Natural scenes, surfaces
  - Simultaneous recordings from large populations of neurons
- We should be prepared for some surprises.