

6. Perception

Outline

A. Biology of Perception

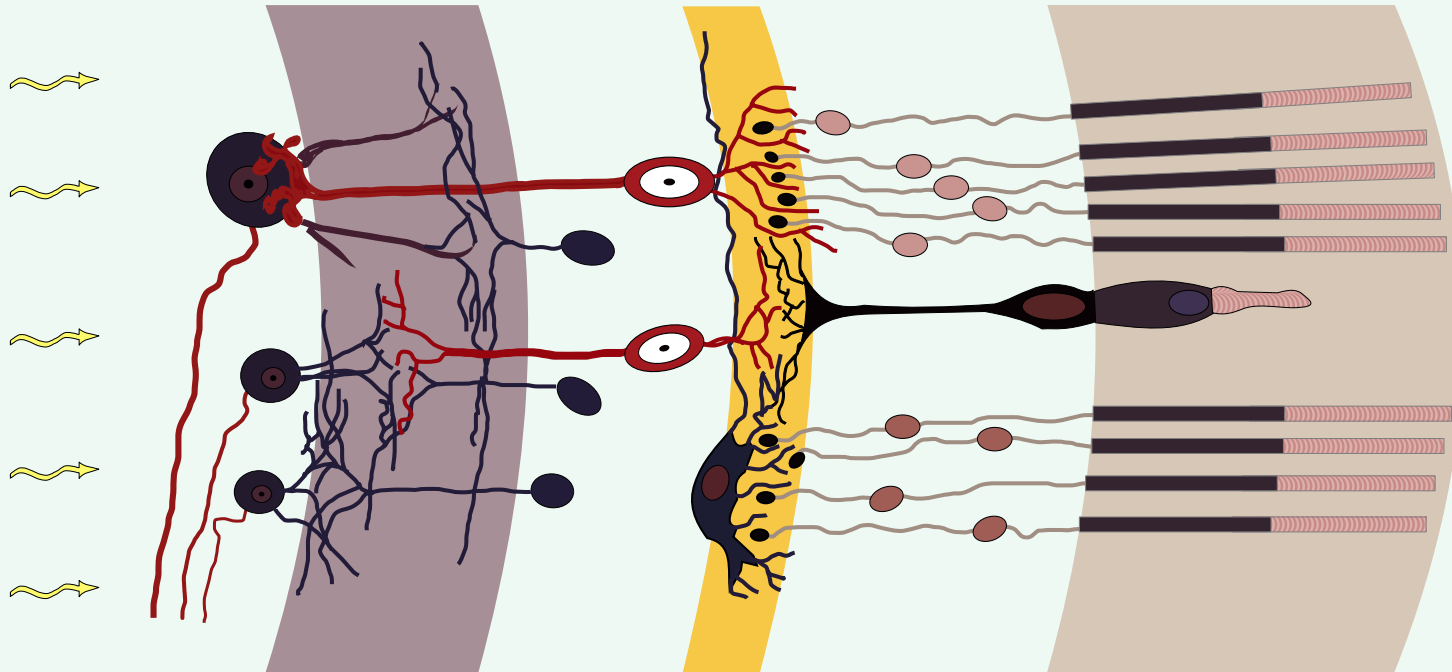
B. Primary Visual Cortex

C. Object Recognition and “What” Pathway

D. Attention and “How” Pathway

A. Biology of Perception

Retinal Layers



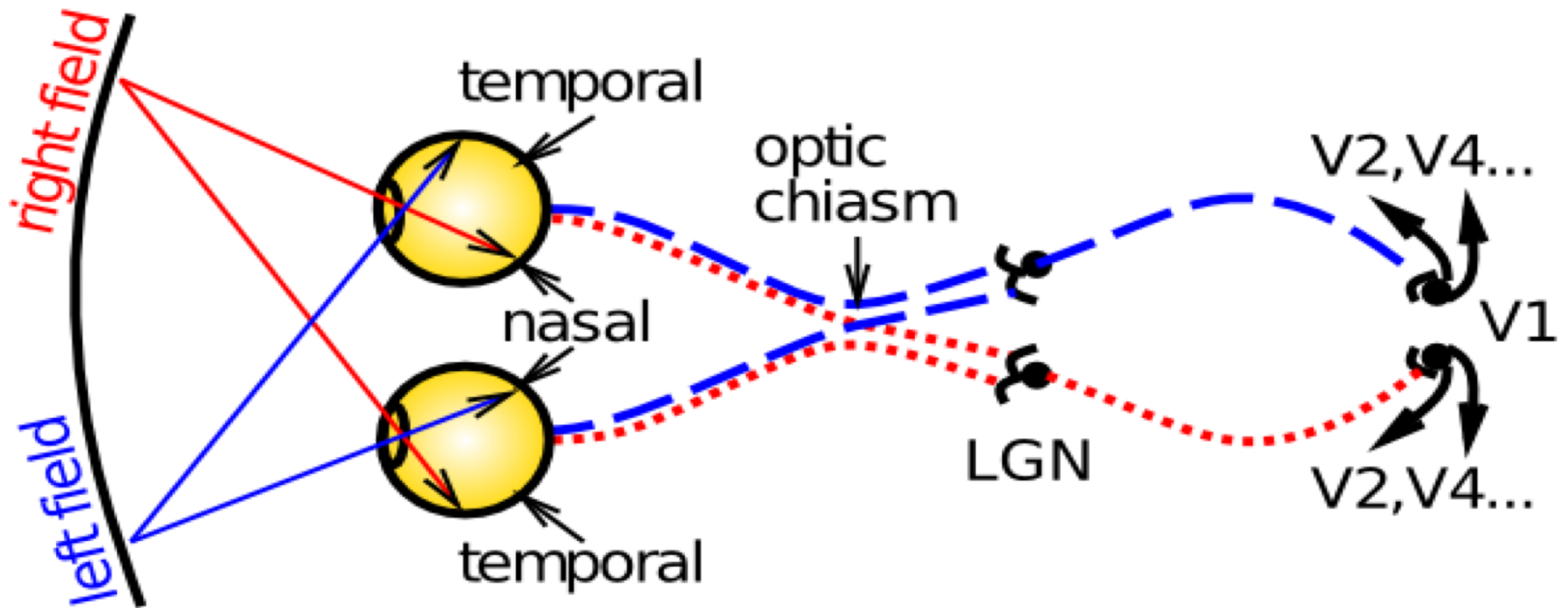
From right:

- (1) rods and cones (tan),
- (2) bipolar and horizontal cells (yellow),
- (3) amacrine and retinal ganglion cells (purple)

Retinal Cells

- Retina is CNS tissue
- Nonuniform distribution of cells
 - rods in periphery specialized for sensitivity and motion
 - cones in macula/fovea specialized for color & form (acuity)
 - humans are *foveating* animals
- Information compression:
 - 120 million rods (low light)
 - huge convergence of rods on bipolars \Rightarrow sensitivity
 - 6 million cones (color and high acuity)
 - 1 million RGC (retinal ganglion cells)
 - estimated to transmit 10^9 bits/sec
 - spontaneously active; information conveyed by change in rate

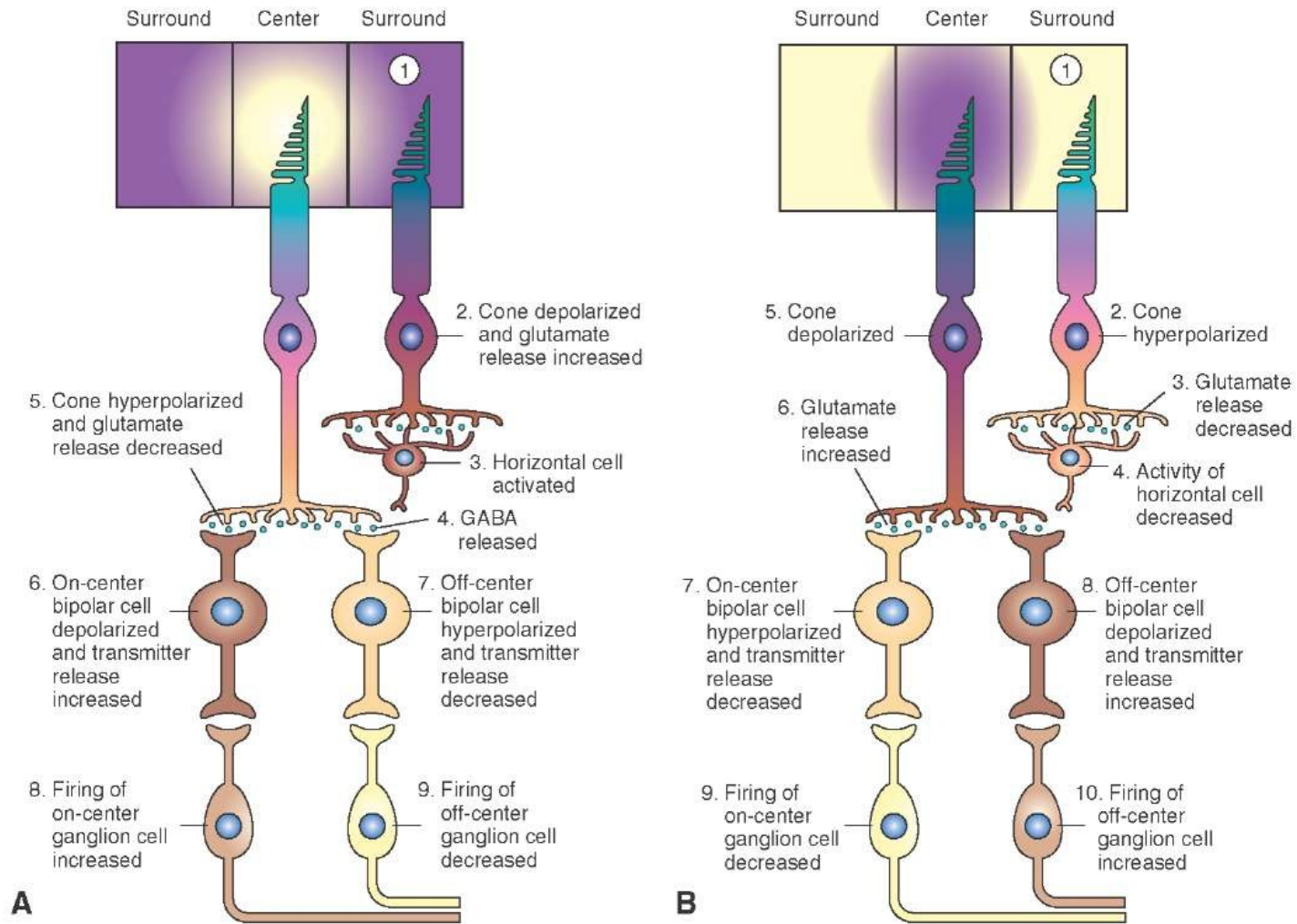
Optic Pathway



Key Organizing Principles

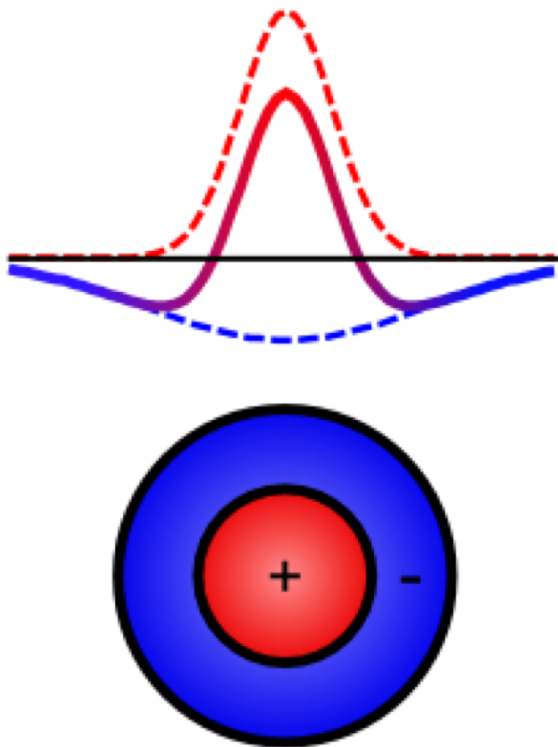
- Transduction of different information
 - wavelength (rods; blue, green, red cones)
 - spatial frequency (resolution)
 - motion
- Topographic organization
 - contrasting similar information
- Filtering to extract relevant information

Retinal Cells

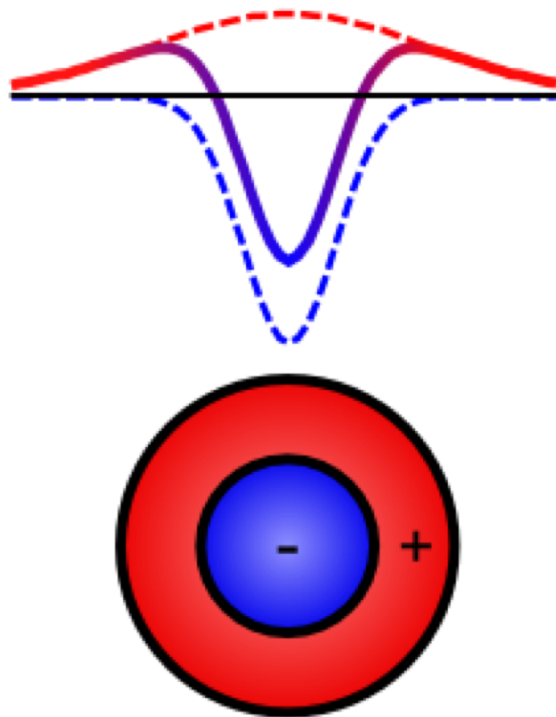


Retinal Contrast Filtering

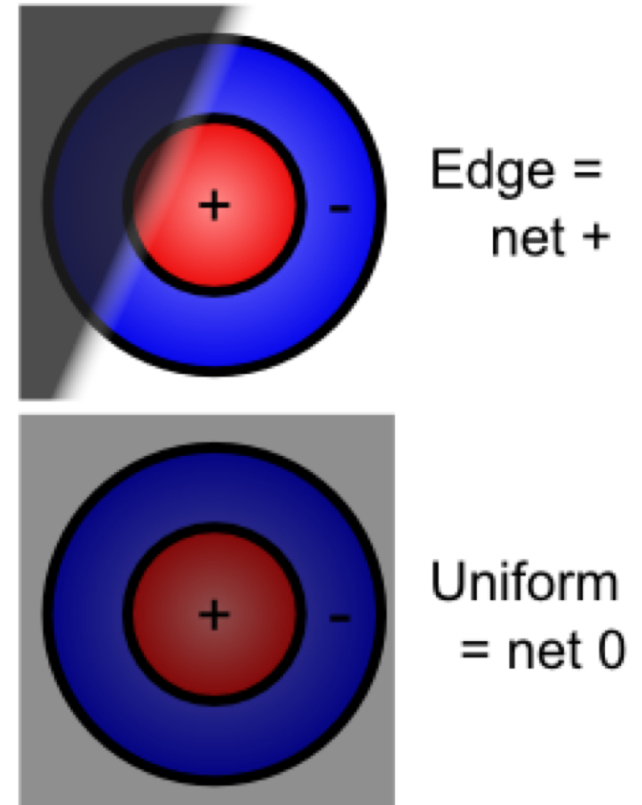
a) On-center



b) Off-center



c) Contrast sensitive



Retinal ganglion cells respond to edges

Input image
(cornea)



“Neural image”
(retinal ganglion cells)



Center-surround receptive fields: emphasize edges.

LGN of the Thalamus

- A “relay station,” but also much more
- Organizes different types of information into different layers with aligned retinotopic maps
- Performs dynamic processing: magnocellular motion processing cells, attentional processing
- On- and off-center information from retina is preserved in LGN

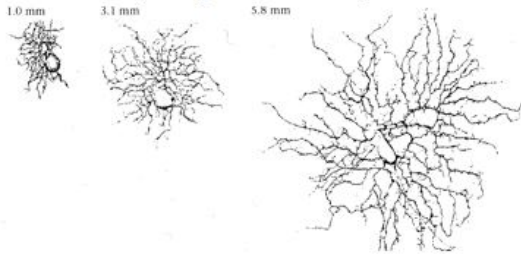
Structure of LGN

Parallel pathways

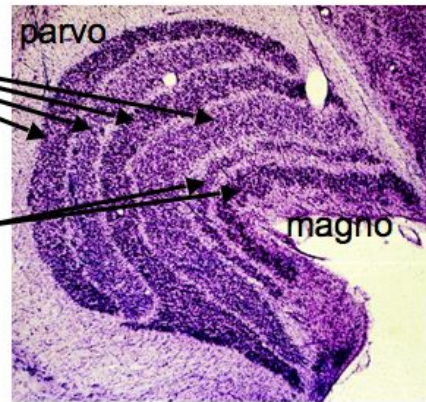
Midget (parvocellular)



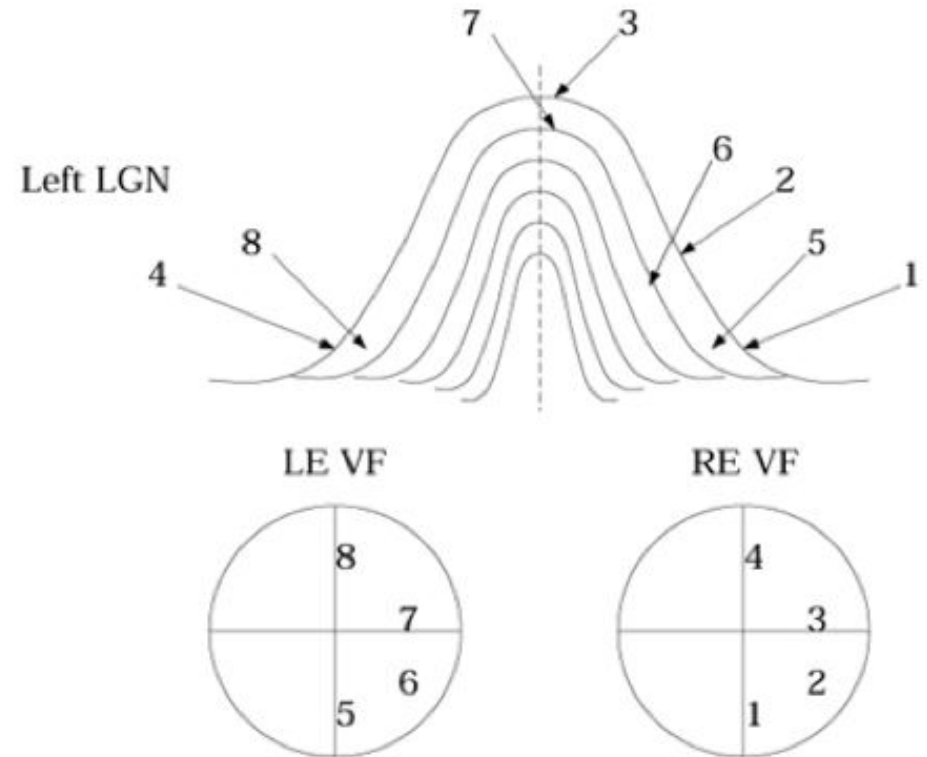
Parasol (magnocellular)



Retina



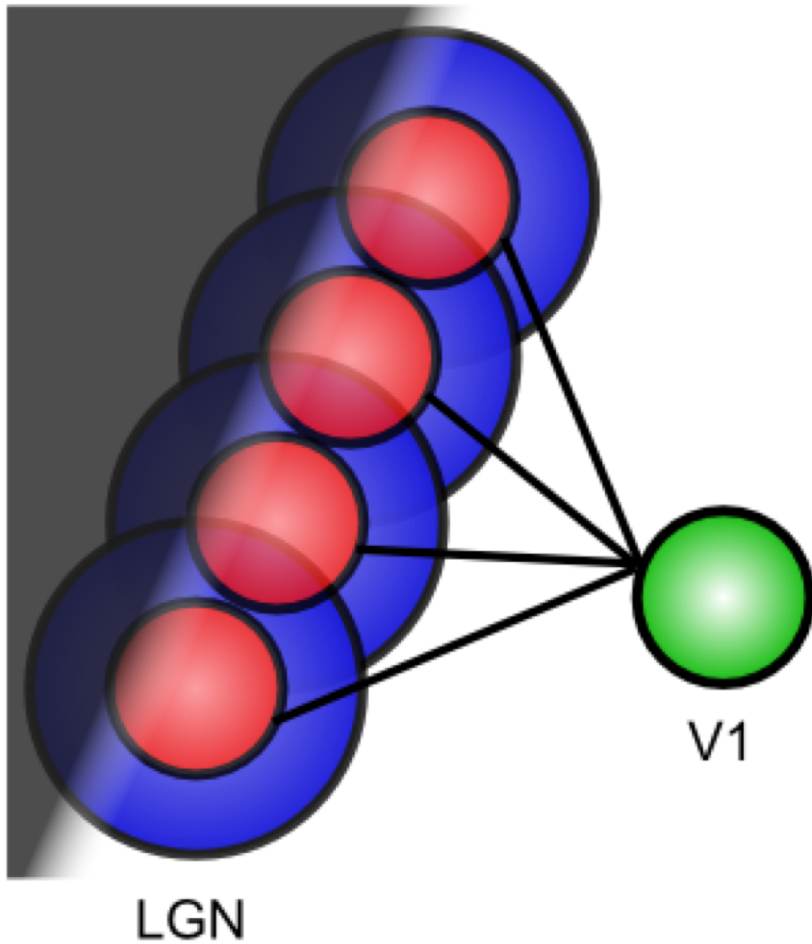
LGN



- Cells have monocular input
- Six layers alternate input from two eyes (RGC)

V1

V1 simple cell edge detector

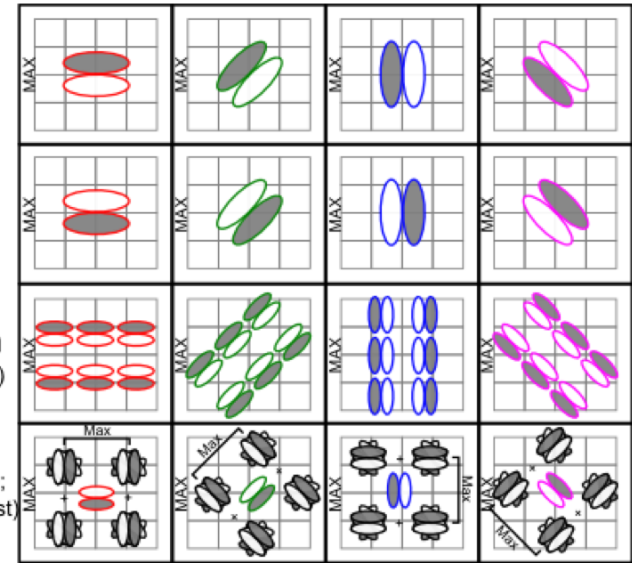


V1 Complex: & MAX over larger spatial RF

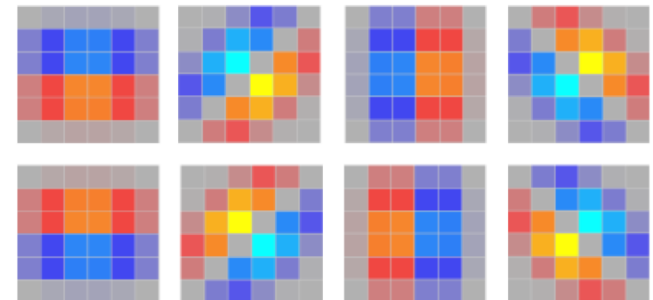
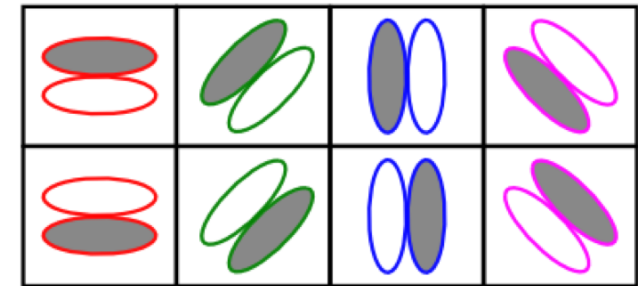
V1-Simple
Max
(V1S with MAX
over spatial RF)

Length-Sum
(max over polarity)

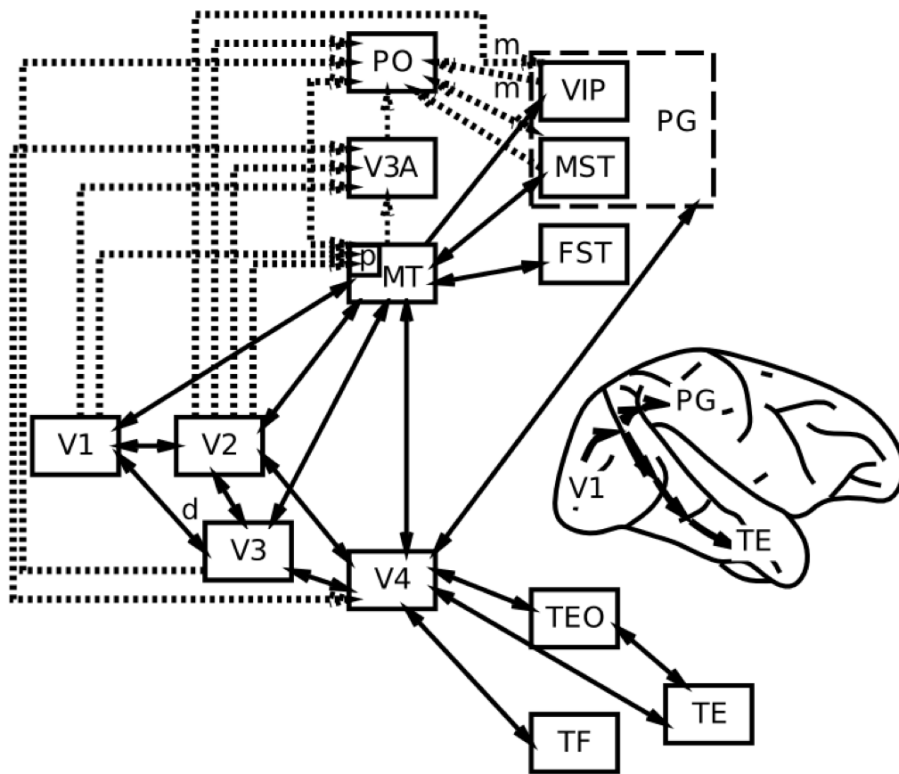
End-Stop
(max over polarity;
orientation contrast)



V1 Simple: Gabor edges

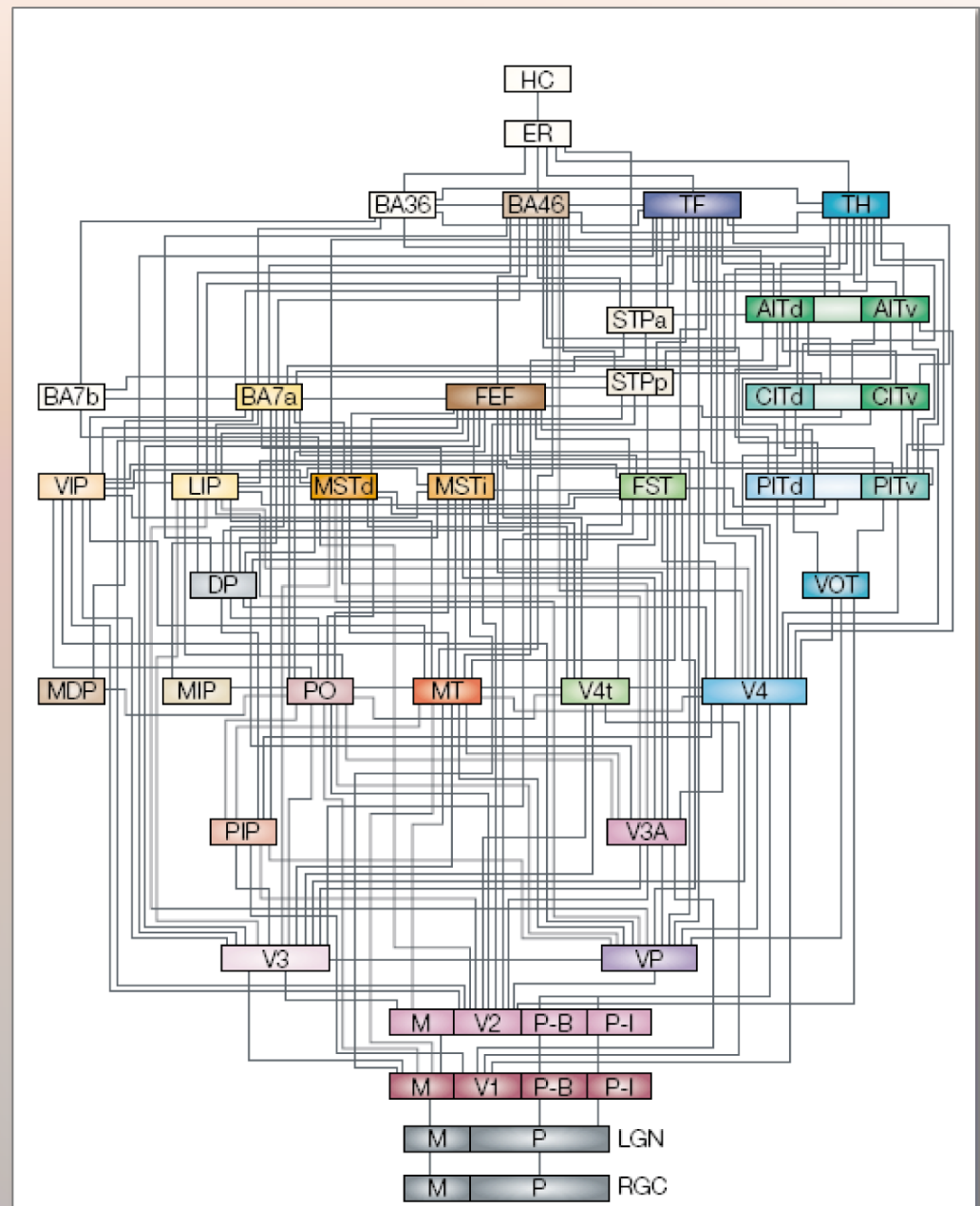


“What” vs. “Where” Pathways



- “What” ignores differences in location, illumination, size, rotation
- “Where” emphasizes location, size, and ignores object identity

Hierarchy of Macaque Visual Areas



Principal Regions in “What” Pathway

Occipital Lobe

V1: Primary visual cortex

- encodes image in terms of oriented edges

V2: Secondary visual cortex

- encodes in terms of intersections & junctions

V4: Third cortical area in ventral stream

- more complex features over wider range of locations
- modulation by attention

Temporal Lobe

PIT: Posterior inferotemporal (IT) cortex

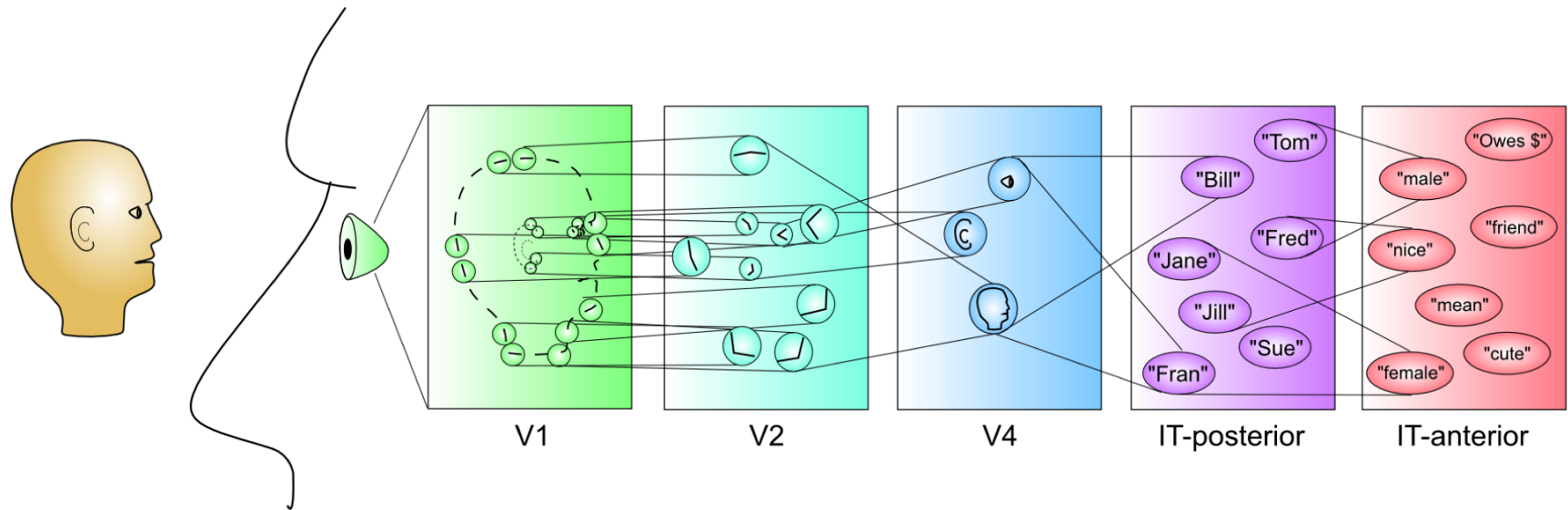
- location & size invariant object recognition

- includes FFA (fusiform face area)

AIT: Anterior IT cortex

- abstract/semantic visual information

Hierarchy of Visual Detectors



B. Primary Visual Cortex

What is the origin of detectors for oriented bars of light?

Self-Organization of V1 Orientation Selective Neurons

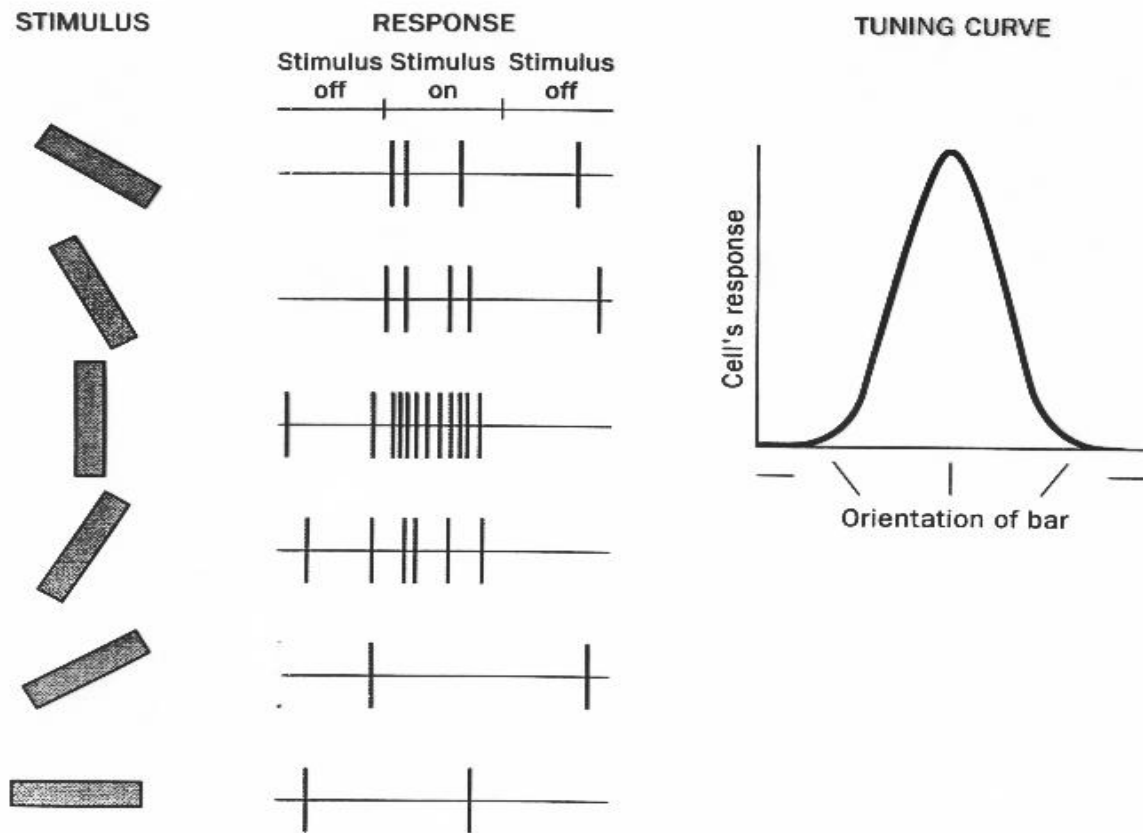
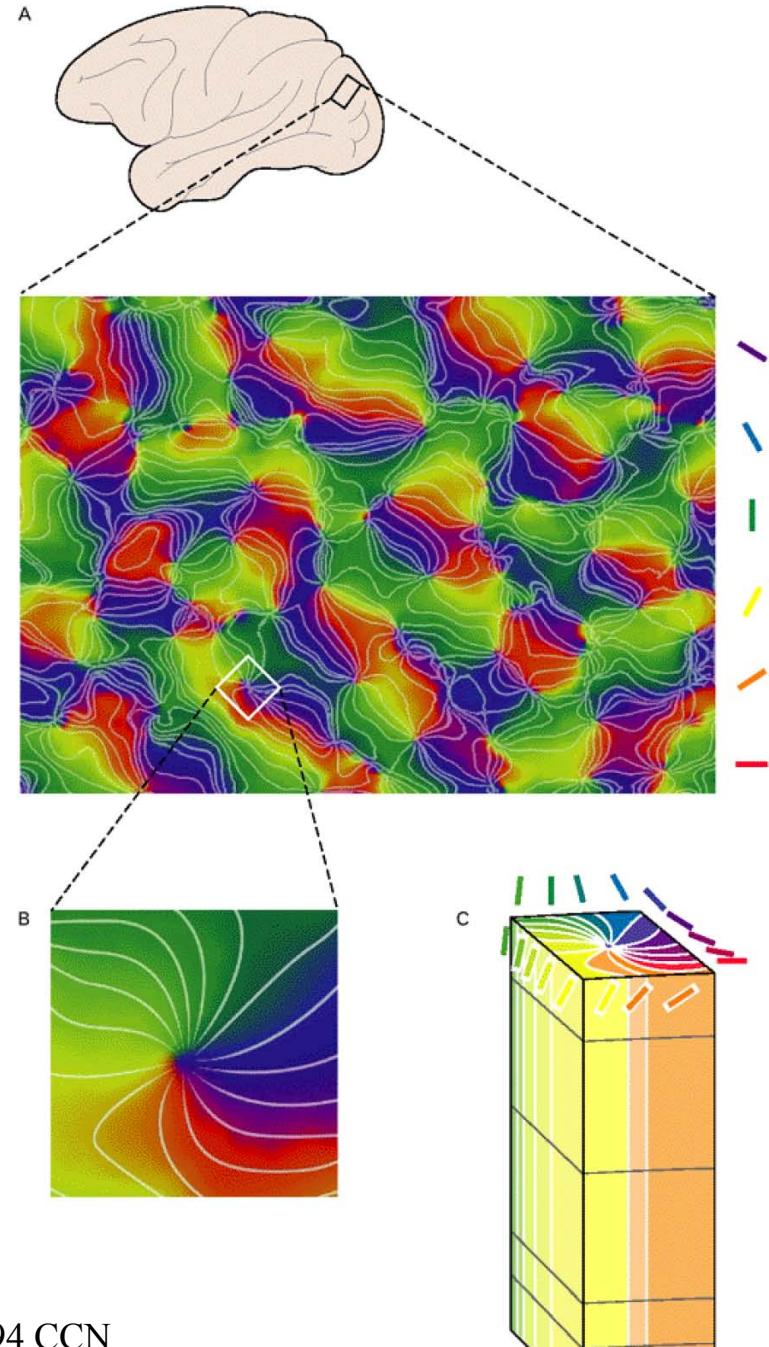


FIGURE 4.8 Response of a single cortical cell to bars presented at various orientations.

Topographic Maps

- Map of orientations
- Hypercolumn: Full set of coding for each position
- Pinwheel can arise from learning and lateral connectivity: not hard-wired!

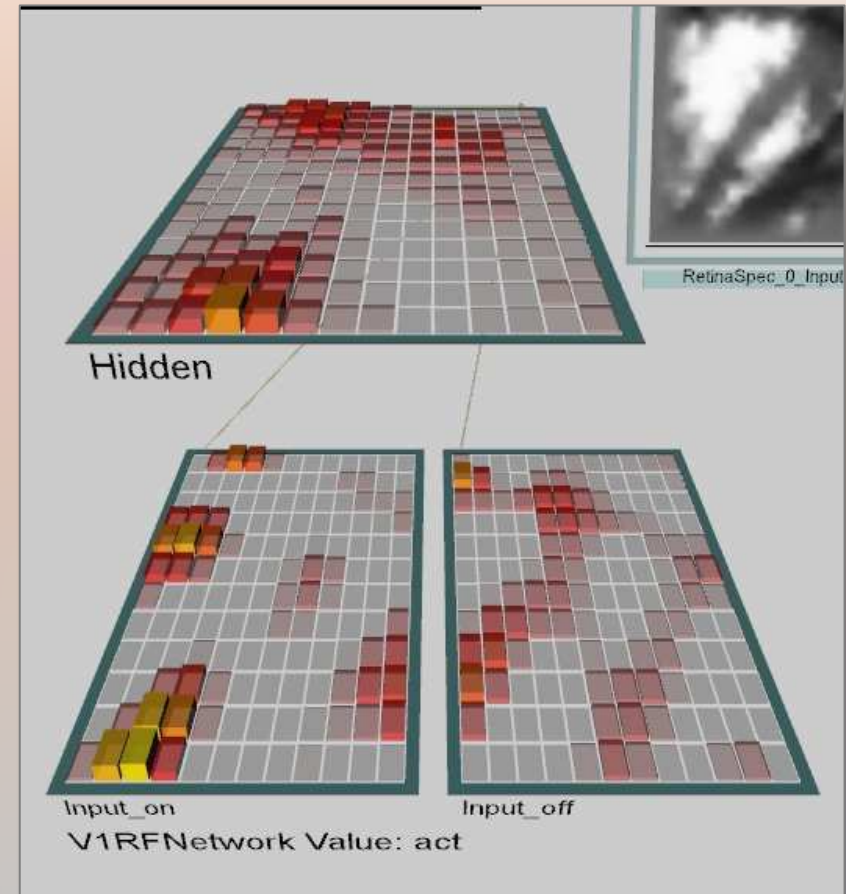


What is Common?



V1Rf: Simulating One Hypercolumn

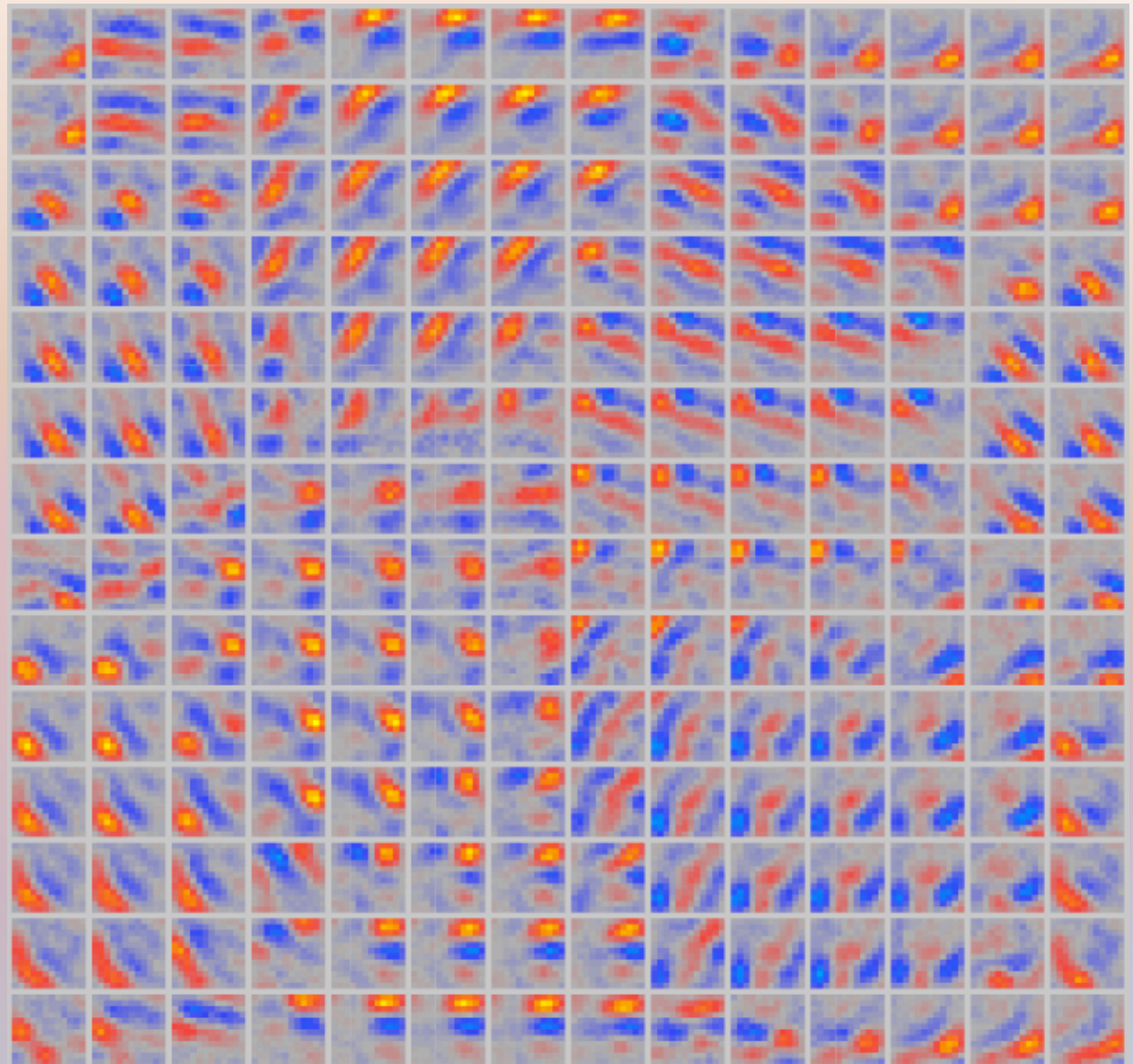
- Natural visual scenes are preprocessed by passing them (separately) through layers of on-center and off-center inputs
- Hidden layer: edge detectors seen in layers 2/3 of V1; Layer 4 (input) just represents unoriented on/off inputs like LGN (but can be modulated by attention)
- Circular neighborhoods of lateral excitatory connectivity in Hidden layer
- Inhibitory competition in Hidden layer



emergent demonstration: V1Rf

Self-Organized Topography

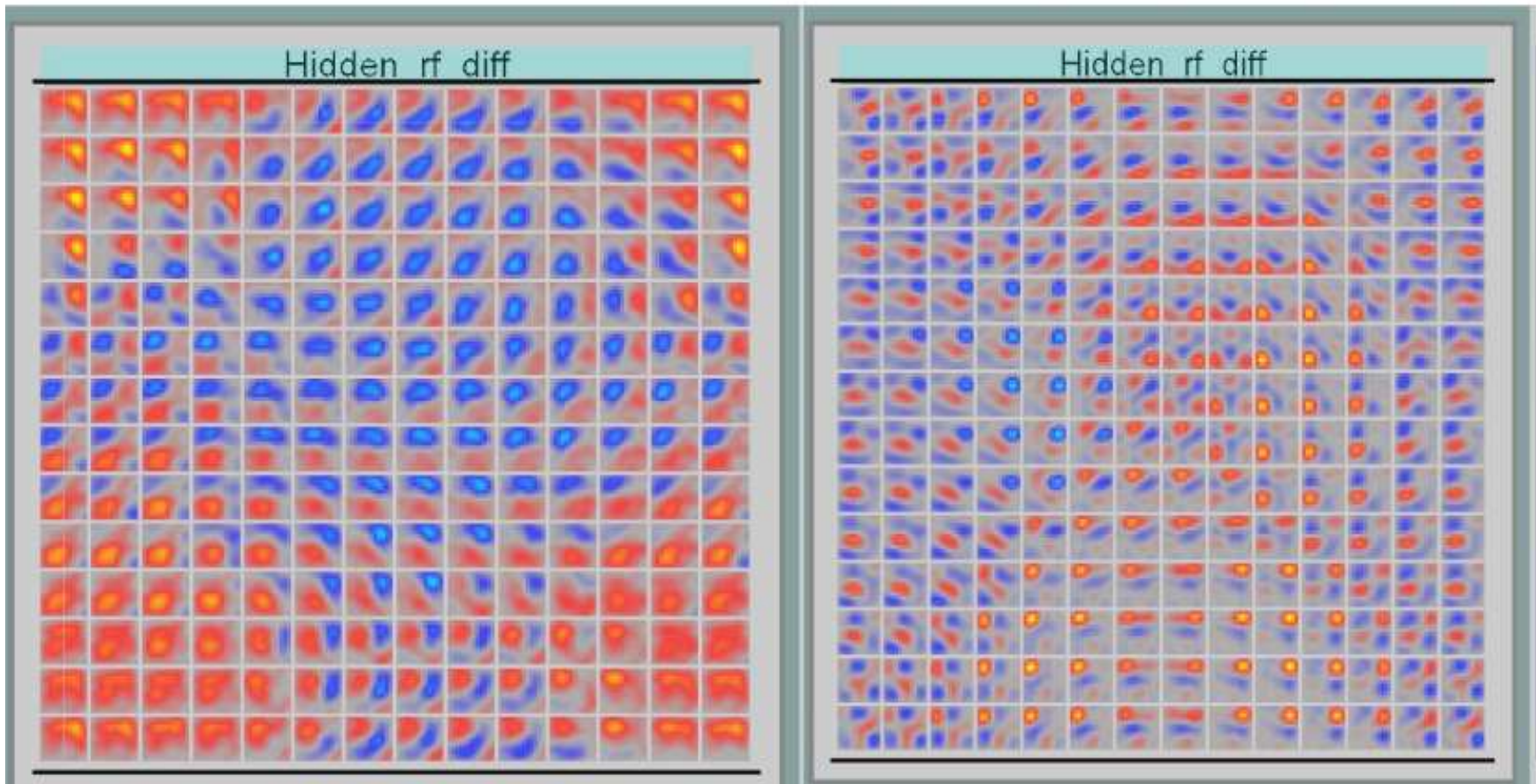
Model shows how documented V1 properties can result from interactions between learning, architecture (connectivity), and structure of environment



Faces vs. Natural Scenes

Faces

Nature Scenes

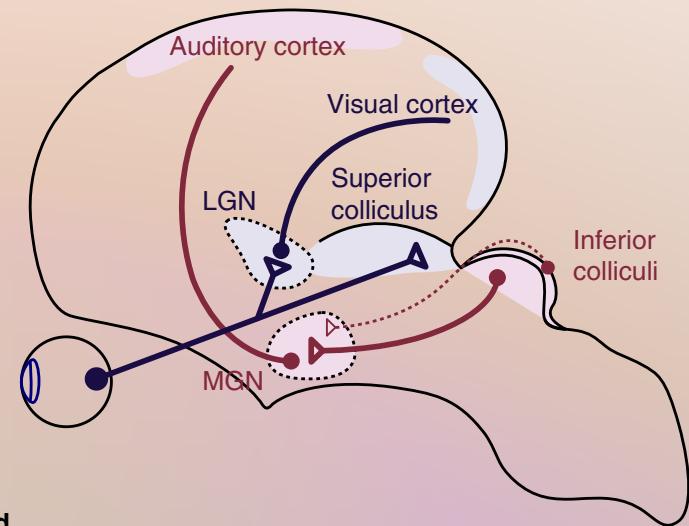


Some differences, but pinwheels still emerge

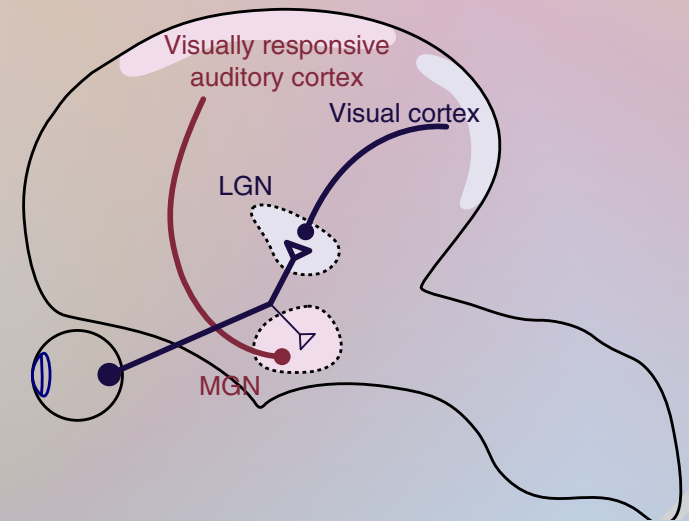
Rewiring Cortex

- Experiments by Mriganka Sur & colleagues (MIT)
- What happens if retinal axons are redirected into auditory thalamus (MGN) instead of its usual inputs?
- Answer: Auditory cortex (A1) develops orientation columns and retinotopic maps similar to V1
- Animals experience activity in A1 as visual perception

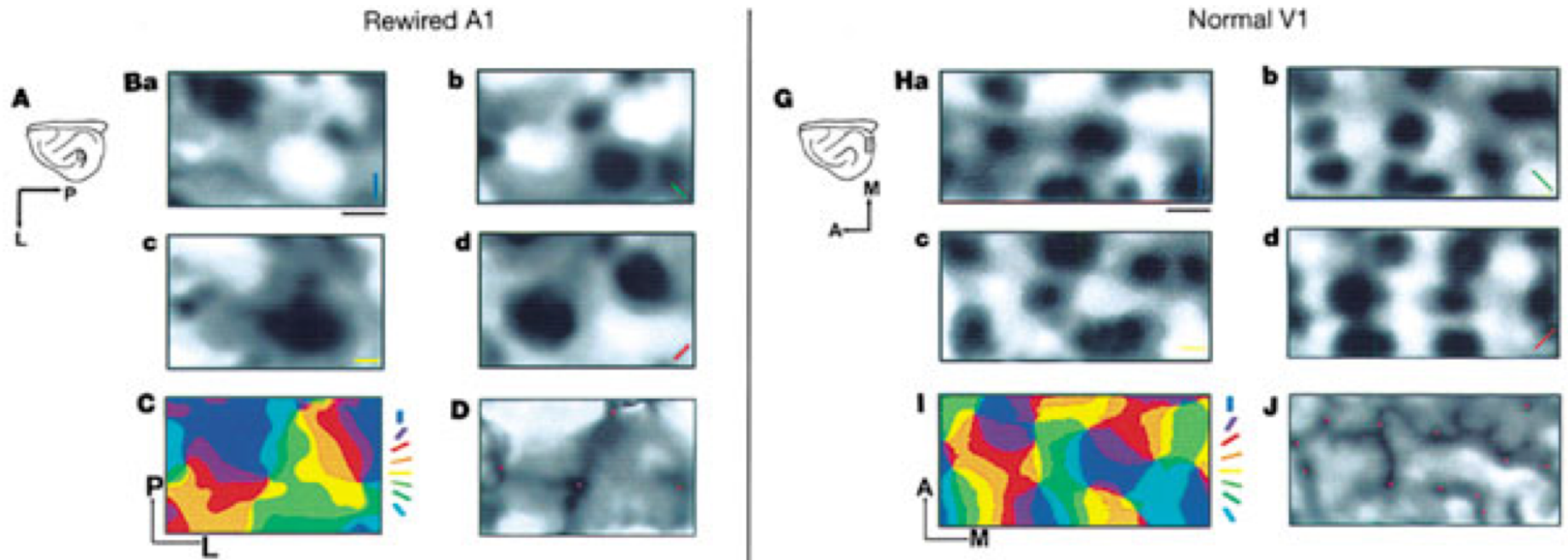
(a) Normal



(b) Rewired

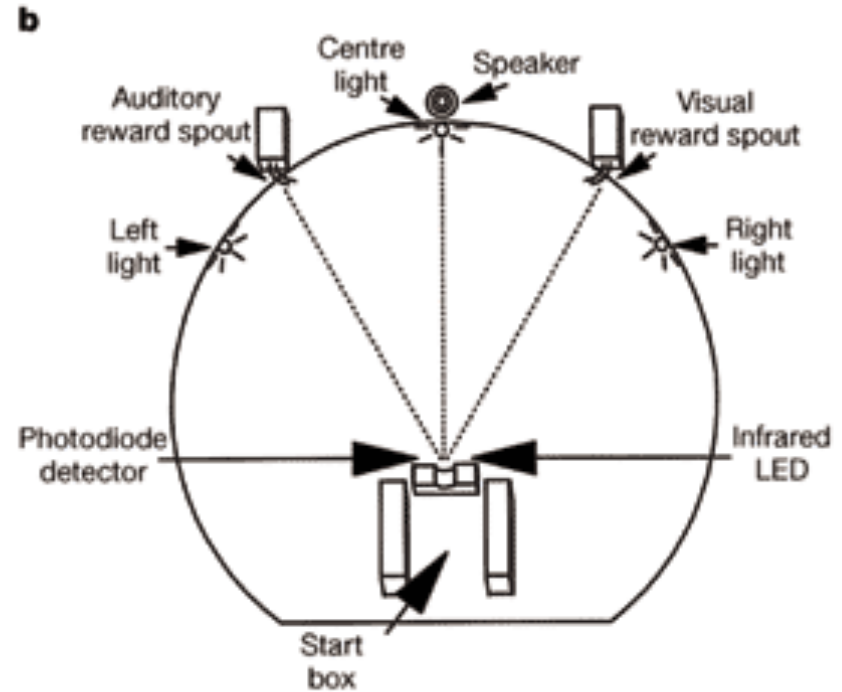
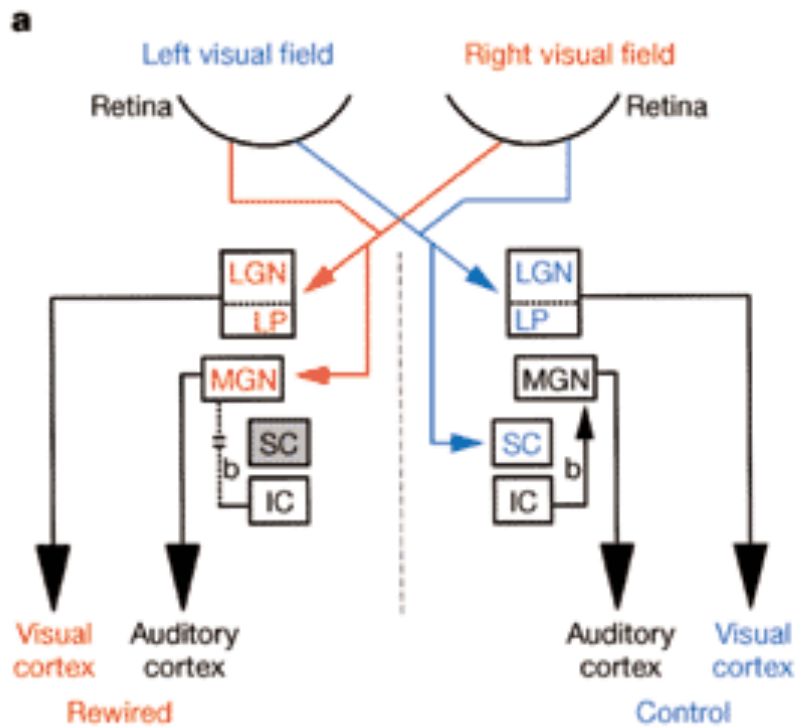


Orientation Columns in A1

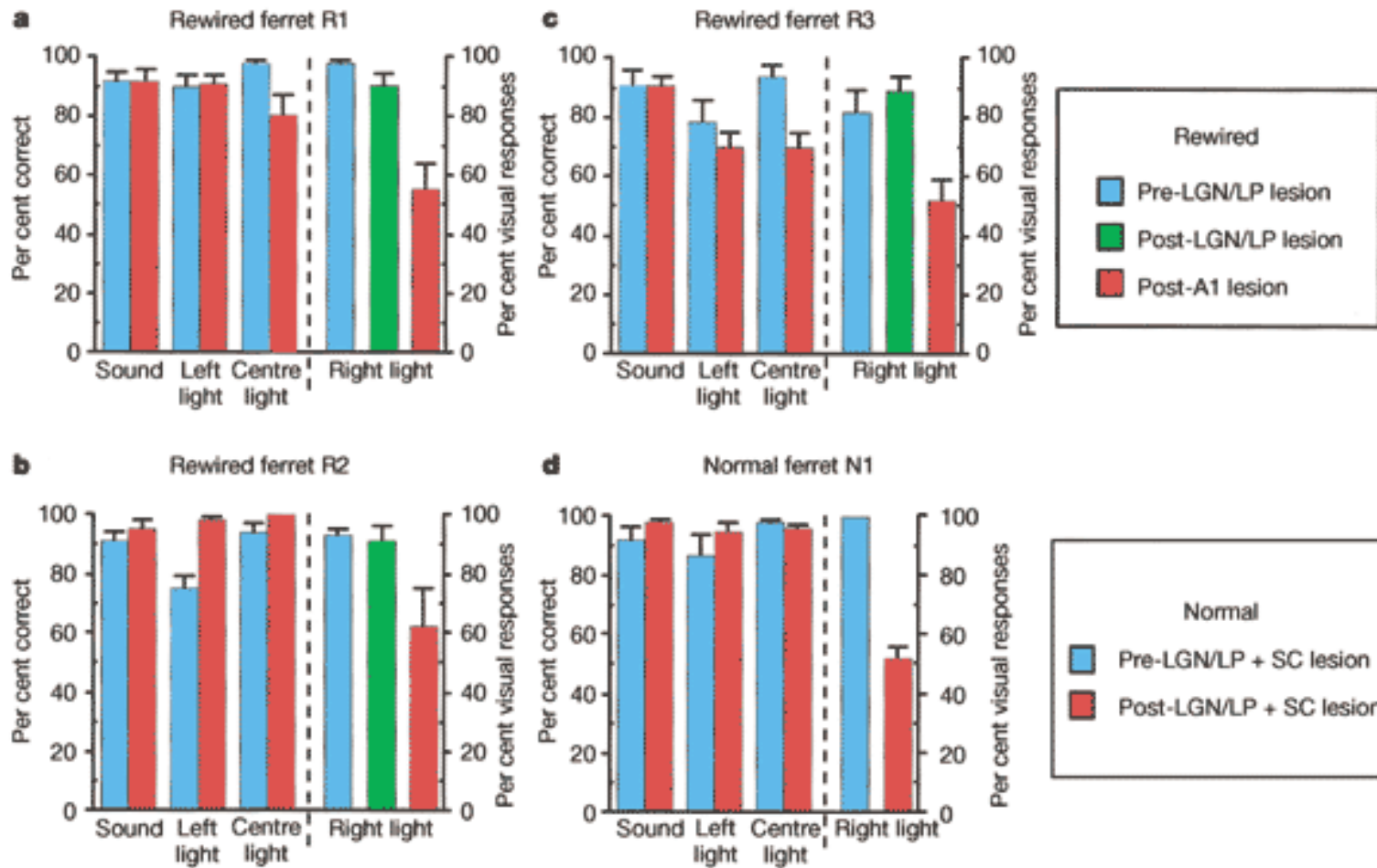


Orientation columns develop in A1 similar to those in V1

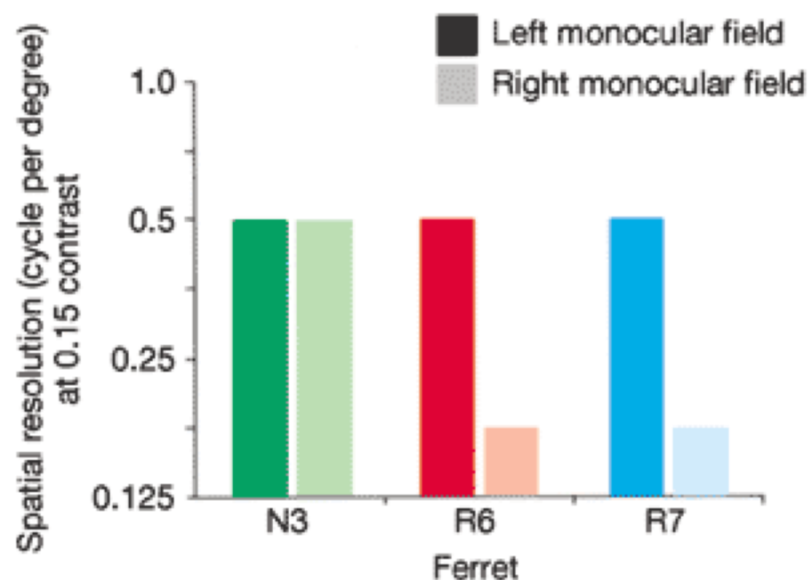
Are They Having Visual Experiences?



They Are Having Visual Experiences



Visual Acuity

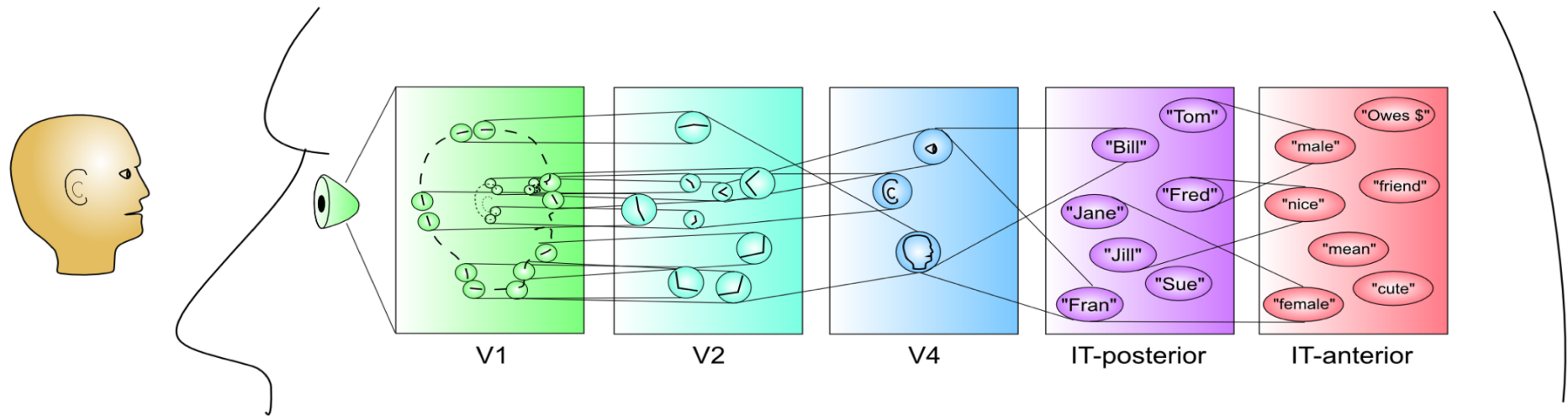


- There is less visual acuity in the rewired pathway
- Suggests there may be intrinsic factors in organization of auditory cortex as well as extrinsic factors

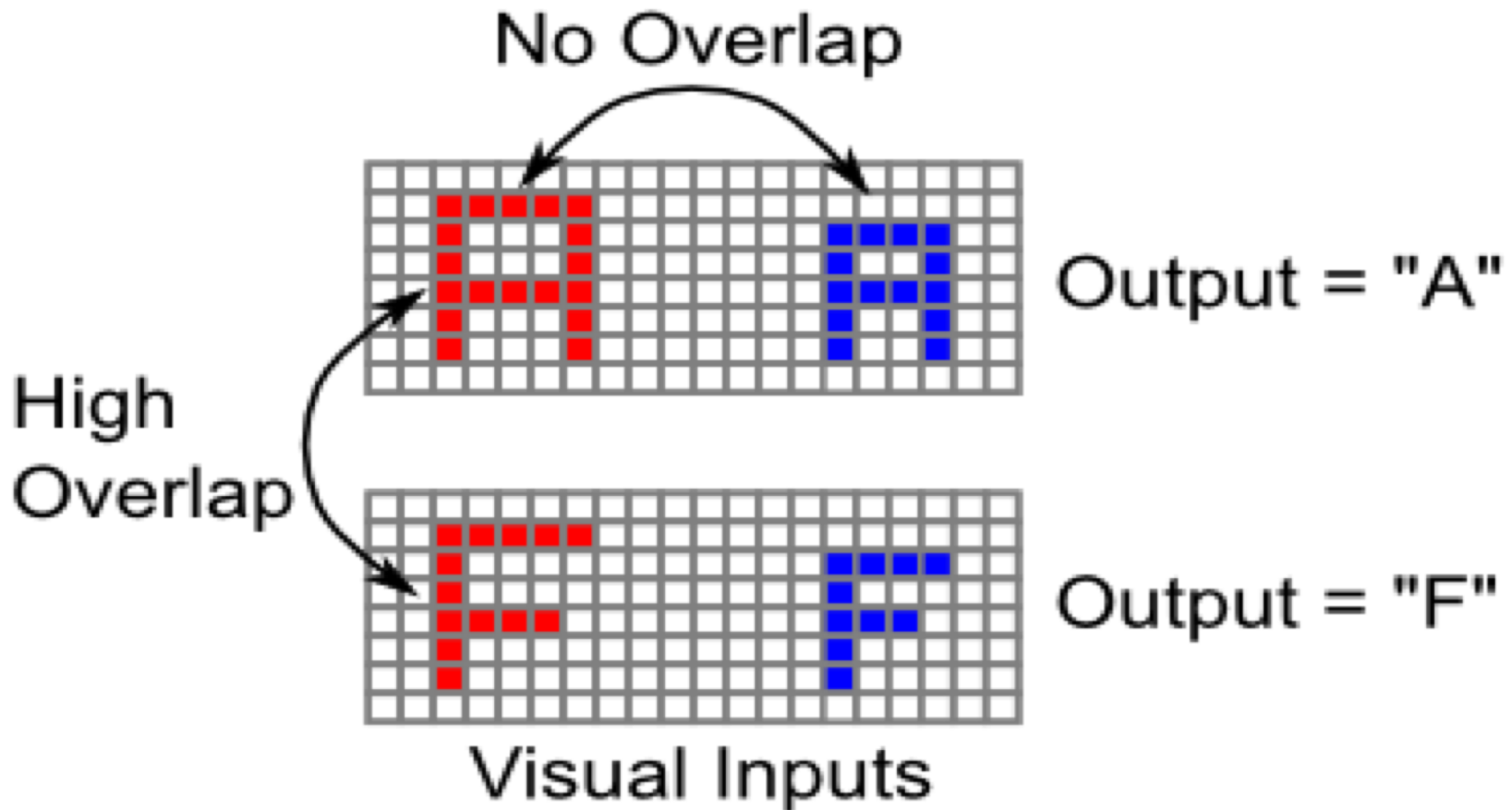
C. Object Recognition and the “What” Pathway

How do we recognize objects (across locations, sizes, rotations with wildly different retinal images)?

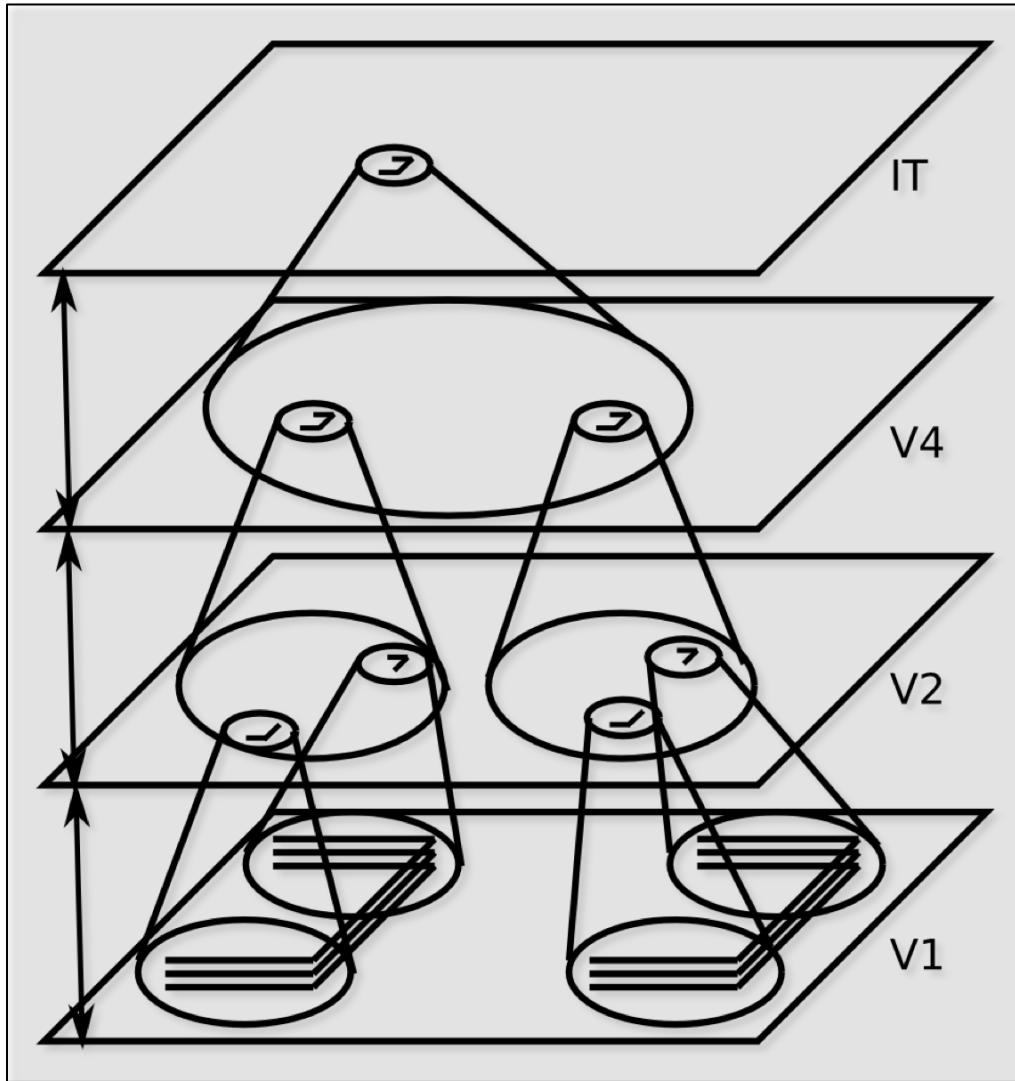
Invariant Object Recognition



It's Hard



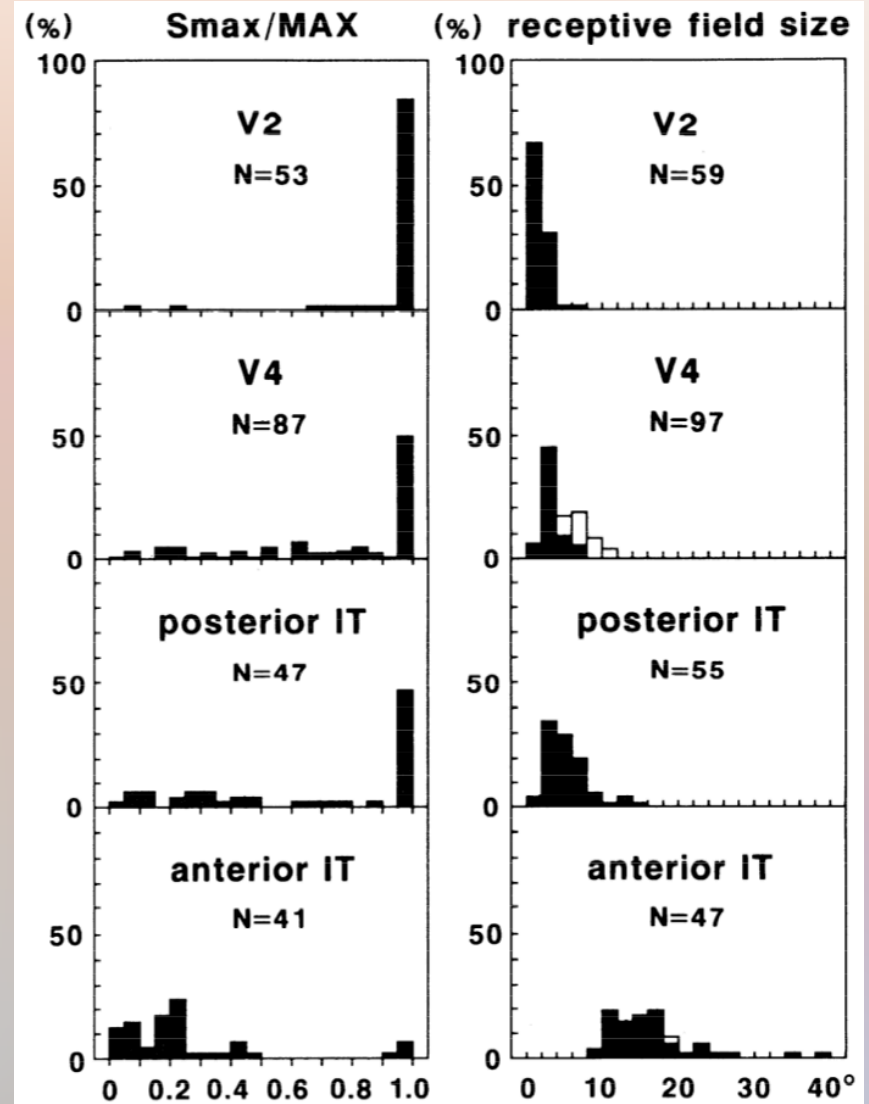
Invariant Object Recognition



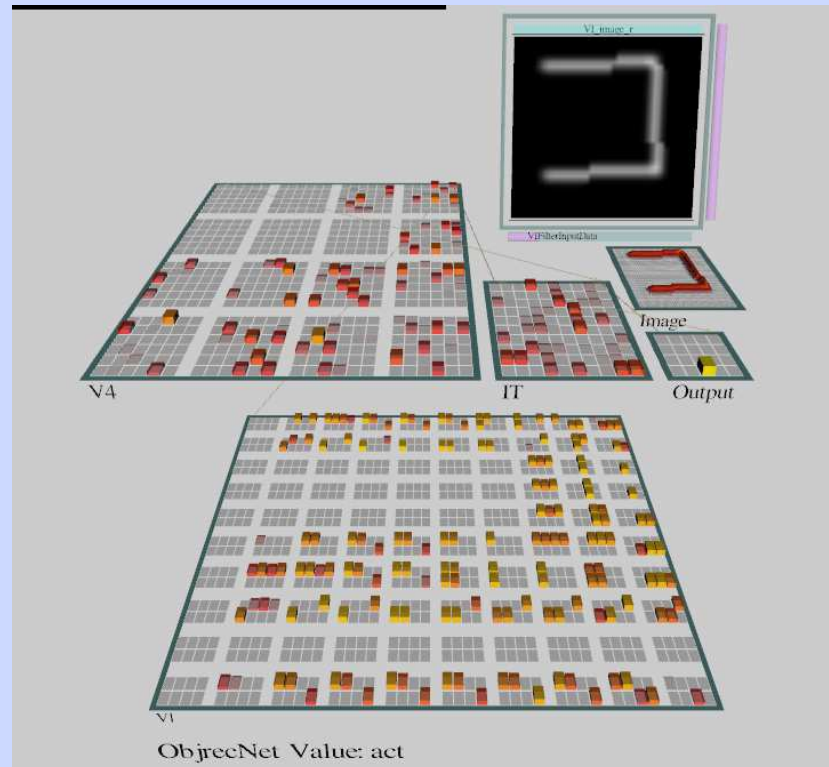
- Hierarchy of increasing:
 - Feature complexity
 - Spatial invariance
- Increasing RF size:
 - Conjunction of features (to form more complex objects)
 - Collapsing over location information (“spatial invariance”)
- Strong match to RF’s in corresponding brain areas

Biological Data: Increasing Complexity and Invariance

V2	V4	posterior IT	anterior IT



The Model: combining Fukushima with convolutional neural nets, bidirectional connectivity and learning!

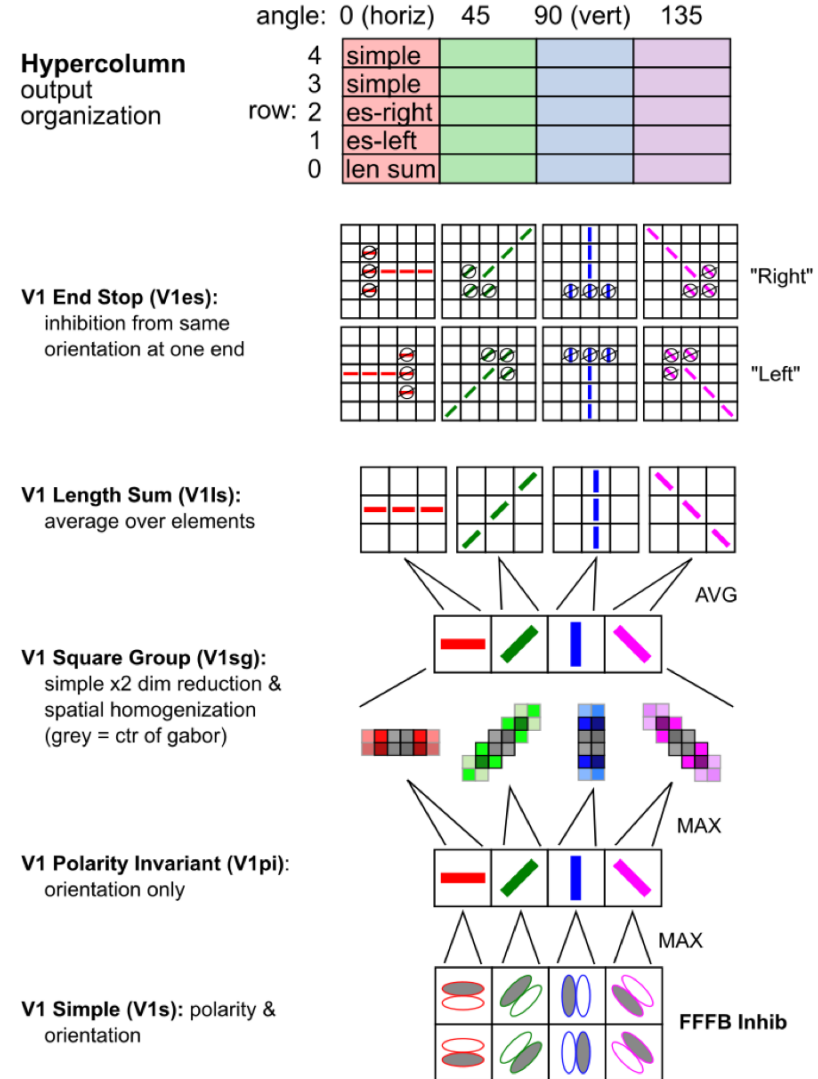


V1 = oriented line (edge) detectors, hard-coded
V4 units encode conjunctions of V1 edges across a subset of space
Each IT unit pays attention to all of V4

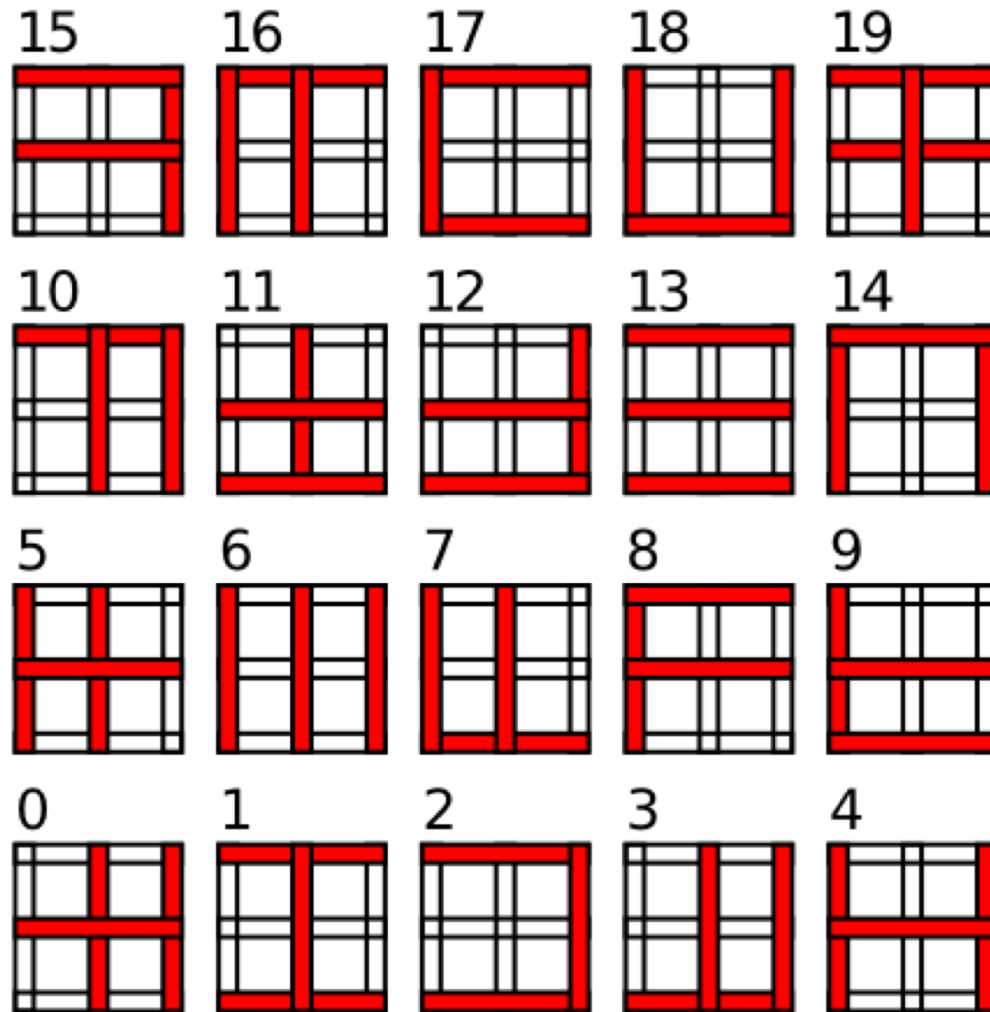
(V2 omitted here, important for figure-ground etc)

V1 Receptive Fields

- 4×5 hypercolumns
- Two rows of simple cells at 4 orientations and two polarities
- Two rows of end-stop complex cells
- One row of length-sum complex cells
- One row of polarity invariant complex cells
- 50% overlap with adjacent hypercolumns



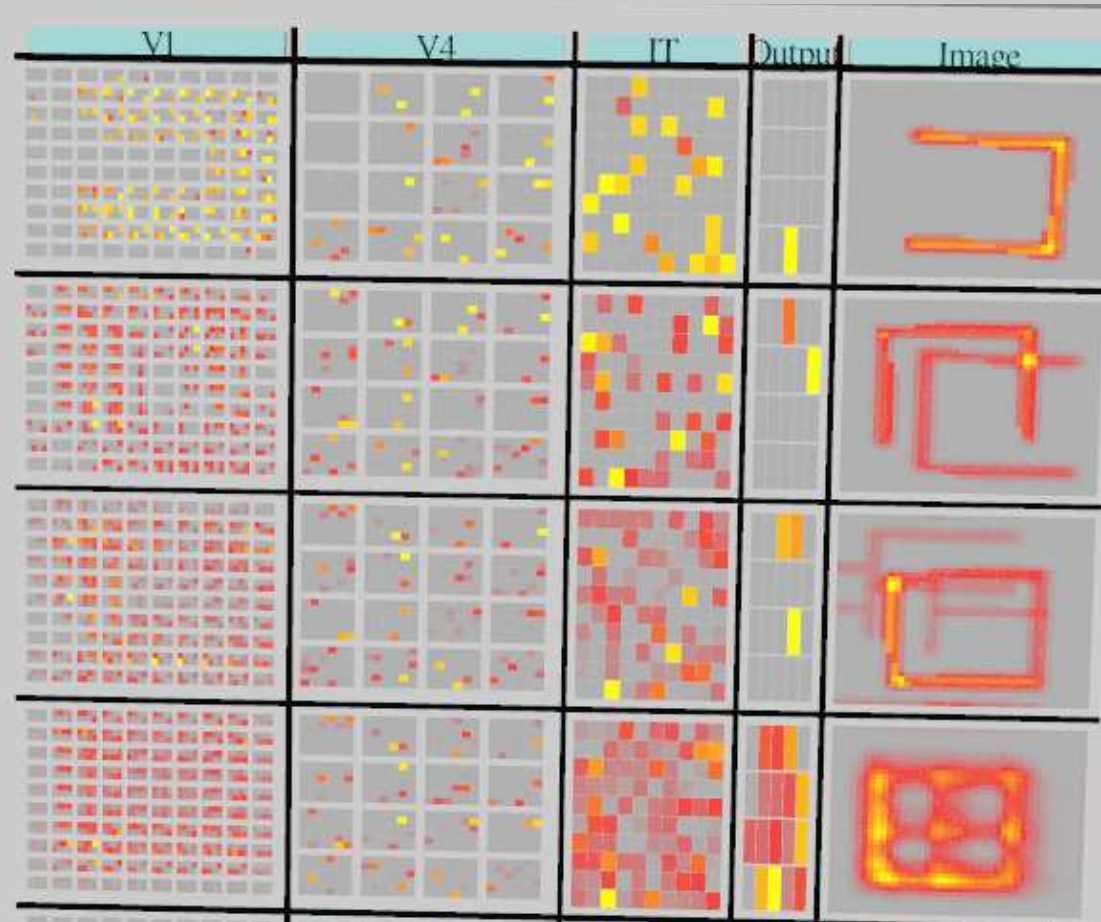
Simple Textbook Test



Activation-Based Receptive Fields

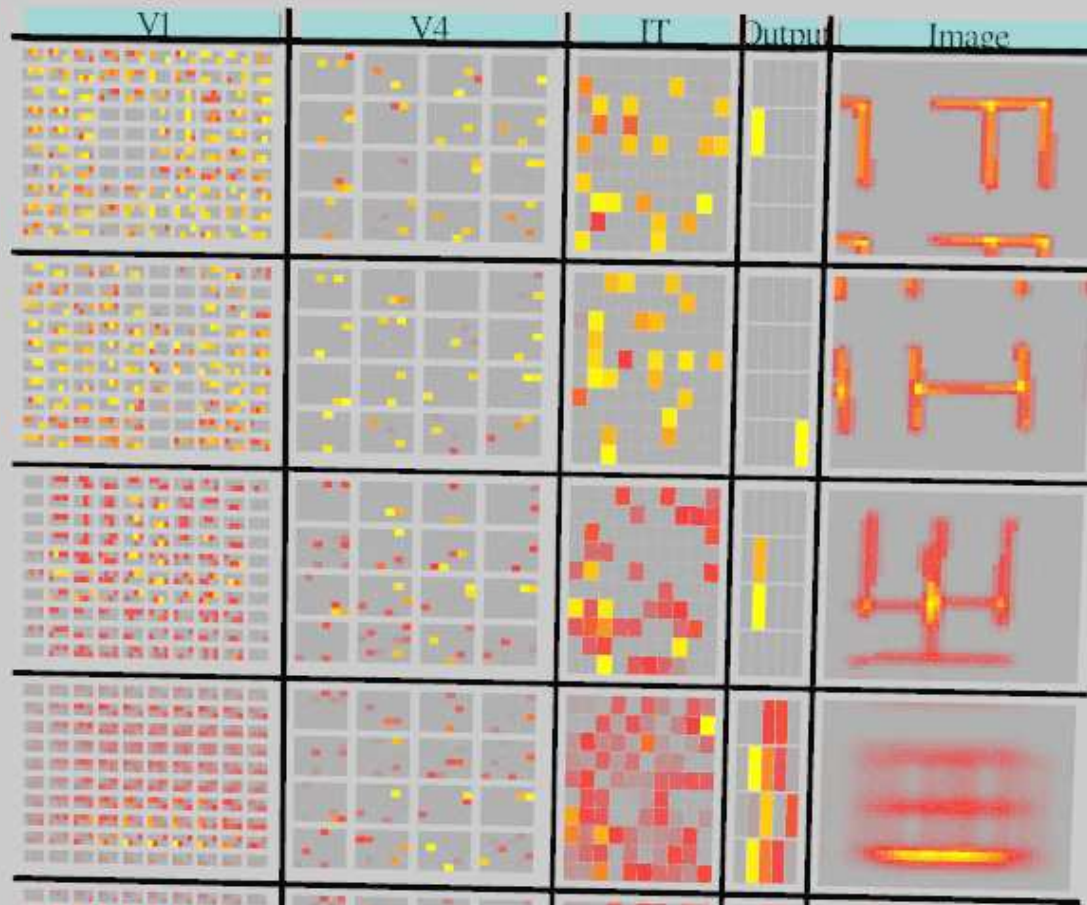
- How do we plot receptive fields for V4?
- Receiving weights show which V1 units a V4 unit responds to, but they don't show what thing in the world the unit responds to
- Solution: Show the network lots of input patterns.
- Then, display a composite of all the input patterns that activate the unit (weighted by activity).

V4 Receptive Fields



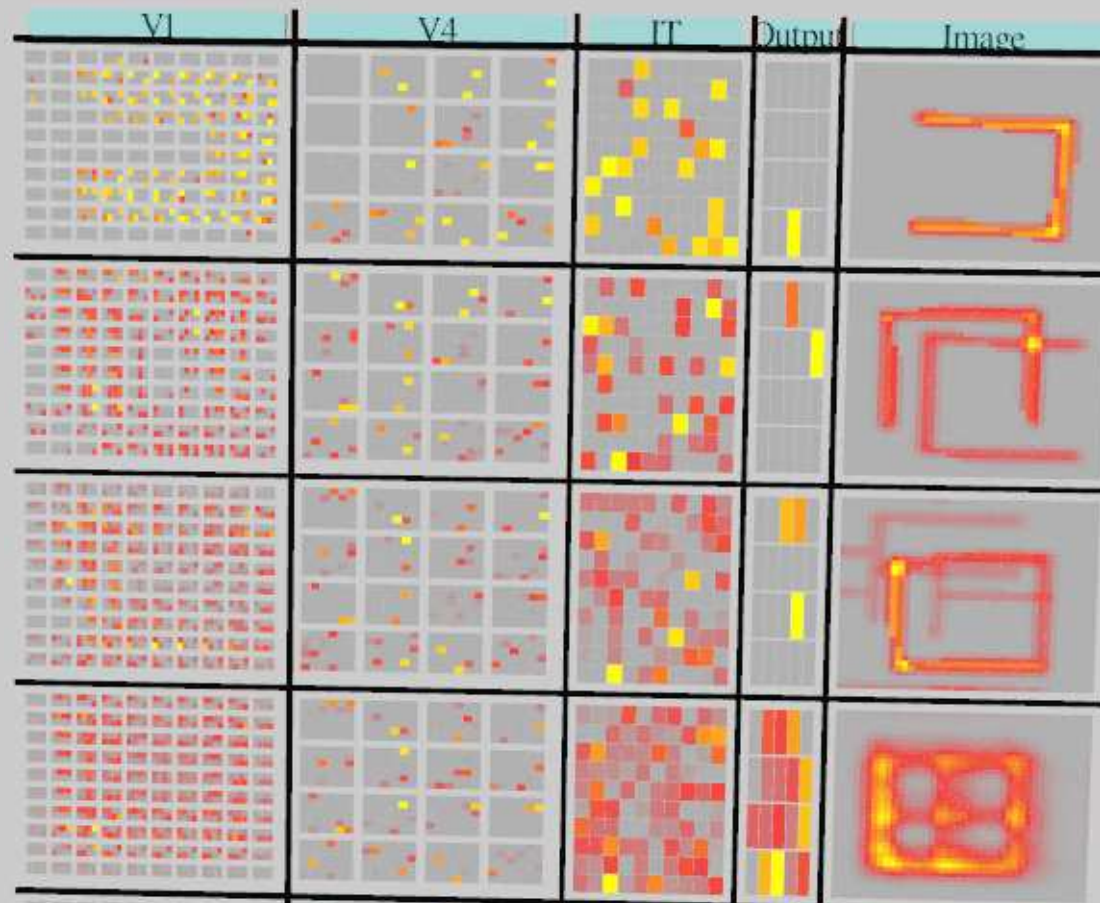
- Some V4 units code for location-specific conjunctions of V1 features
- This will show up as a sharp receptive field for Image input

V4 Receptive Fields



- Some V4 units code for simple features in a location invariant way
- This will show up as smeary parallel lines in Image input

V4 Receptive Fields



- Can also look at which Output units tend to get active for any given V4 unit
- Generally a given V4 unit is associated with multiple objects

3D Object Recognition Test



3D models from Google SketchUp

100 categories

9–10 objects per category

2 objects left out for testing

+/- 20° horiz depth rotation
+ 180° flip

0–30° vertical depth rotation

14° 2D planar rotations

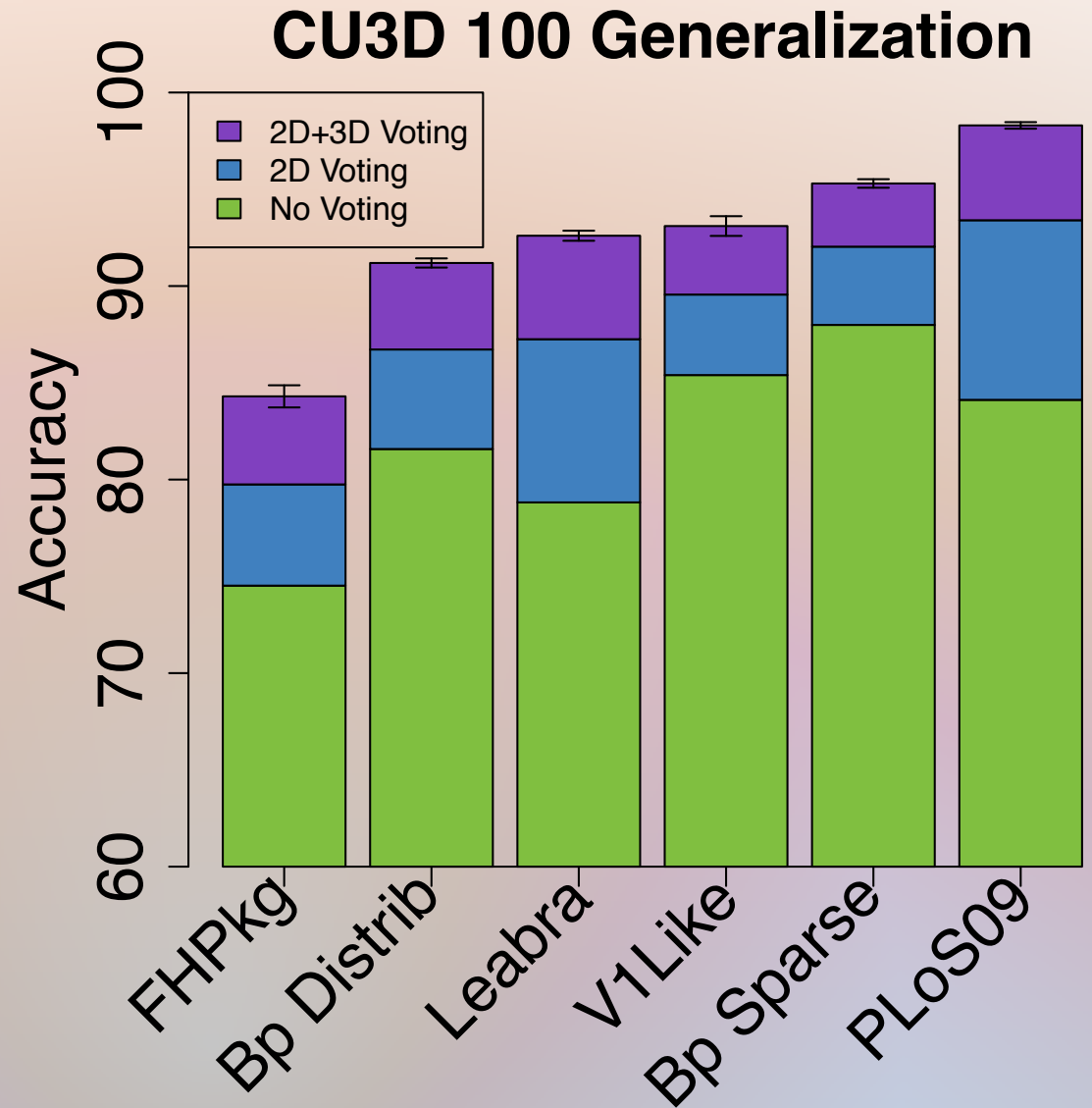
25% scaling

30% planar translations

Depth & Lighting Variations for One Object



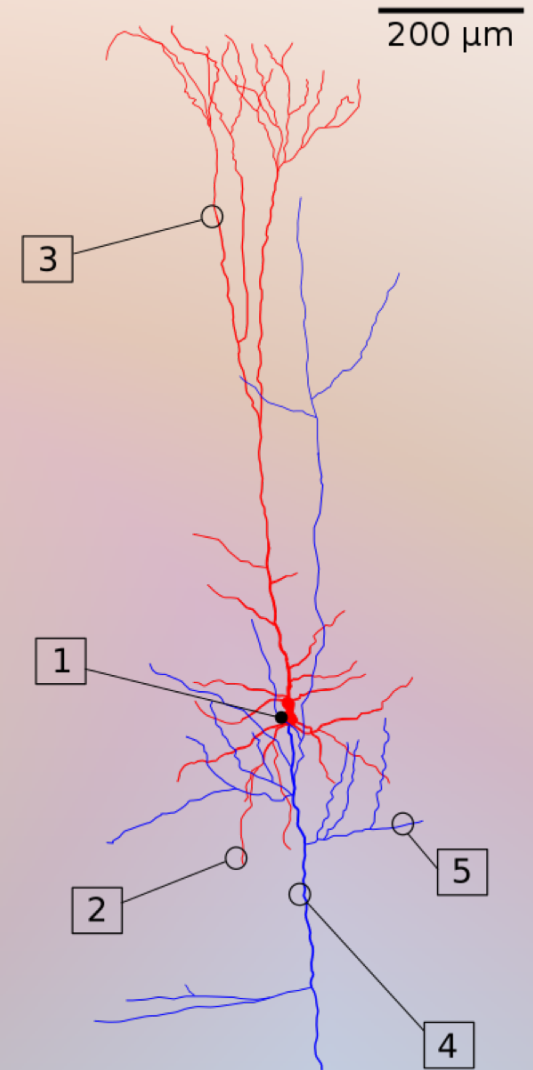
Generalization to
Novel Category
Exemplars –
Better than 90%



emergent demonstration: Objrec

Active Cortical Dendrites Modulate Perception

- Ca^{2+} activity in some L5 pyramidal cells in S1 correlated with perception threshold
- May amplify long-range feedback from other cortical regions to primary sensory areas via superficial layers
- Apical amplification hypothesis: Ca^{2+} activity correlates with subliminal-to-liminal transition
- More generally, apical amplification via dendritic Ca^{2+} currents seems related to cognitive processing & conscious perception
- Takahashi et al., *Science* **354** (2016): 1587.



D. Attention and “How” Pathway

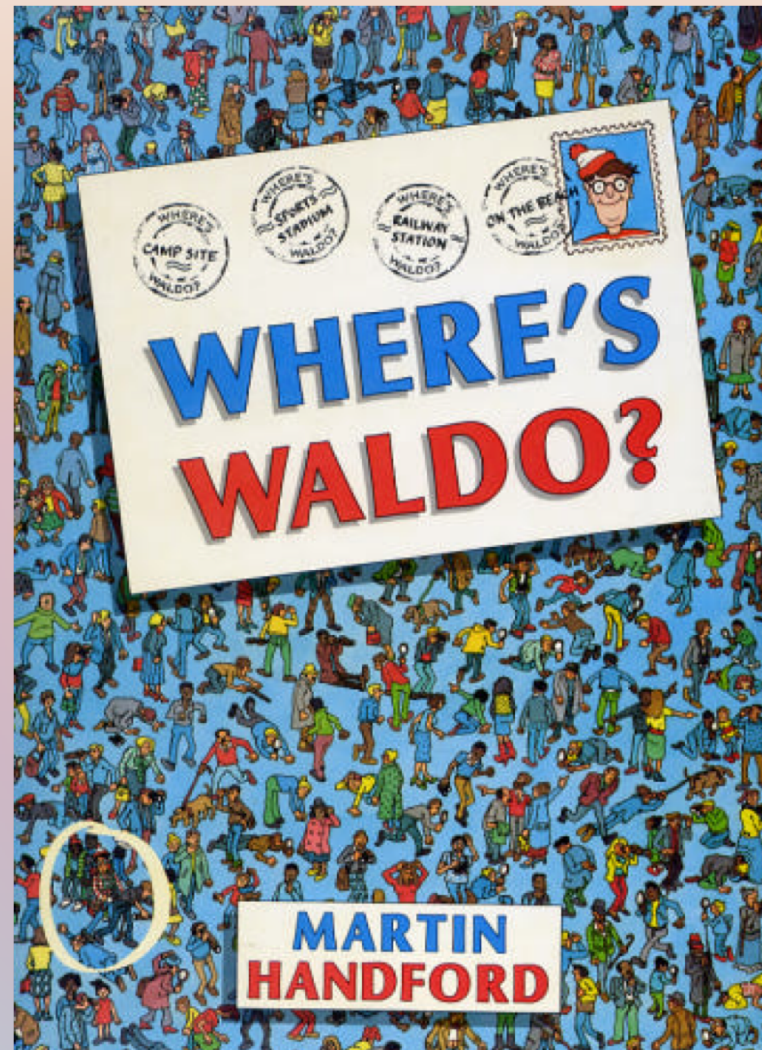
Why is visual system split into what/where pathways?

Why does parietal damage cause attention problems (neglect)?

Some Functions of Dorsal Pathway

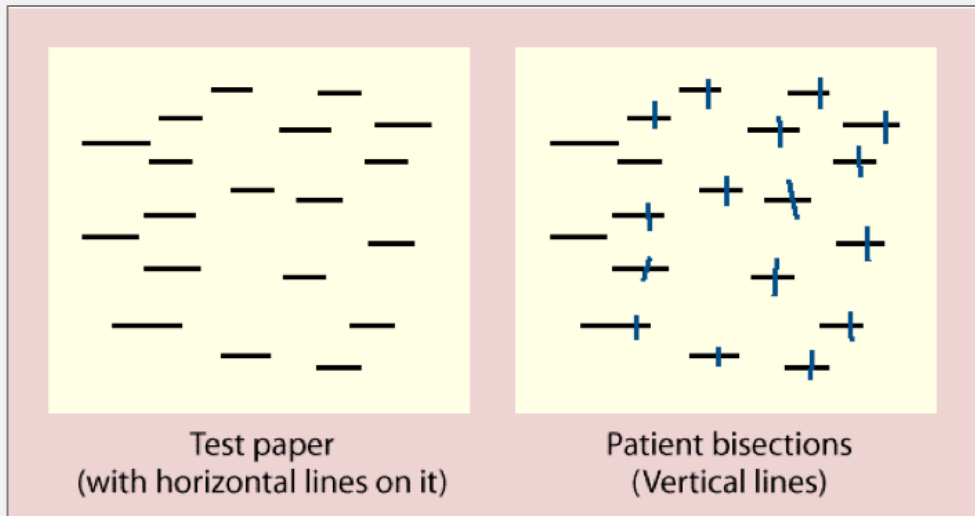
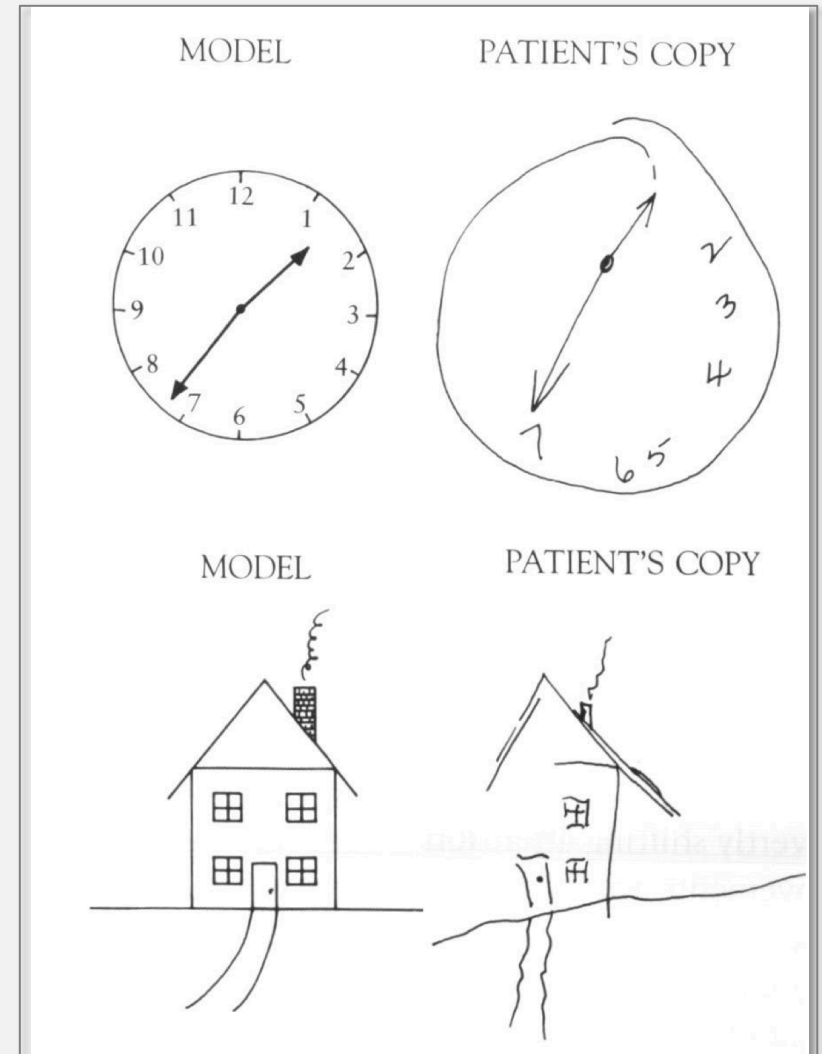
- “Where” pathway (spatial relations)
 - visual attention (this chapter)
- But more broadly “how” pathway
 - maps perception to action (next chapter)
- Numerical and mathematical processing
- Representation of abstract relationships
- Modulation of episodic memory
- Aspects of executive control

Spatial Attention and Neglect



Hemispatial Neglect

Mainly from injuries to right parietal cortex

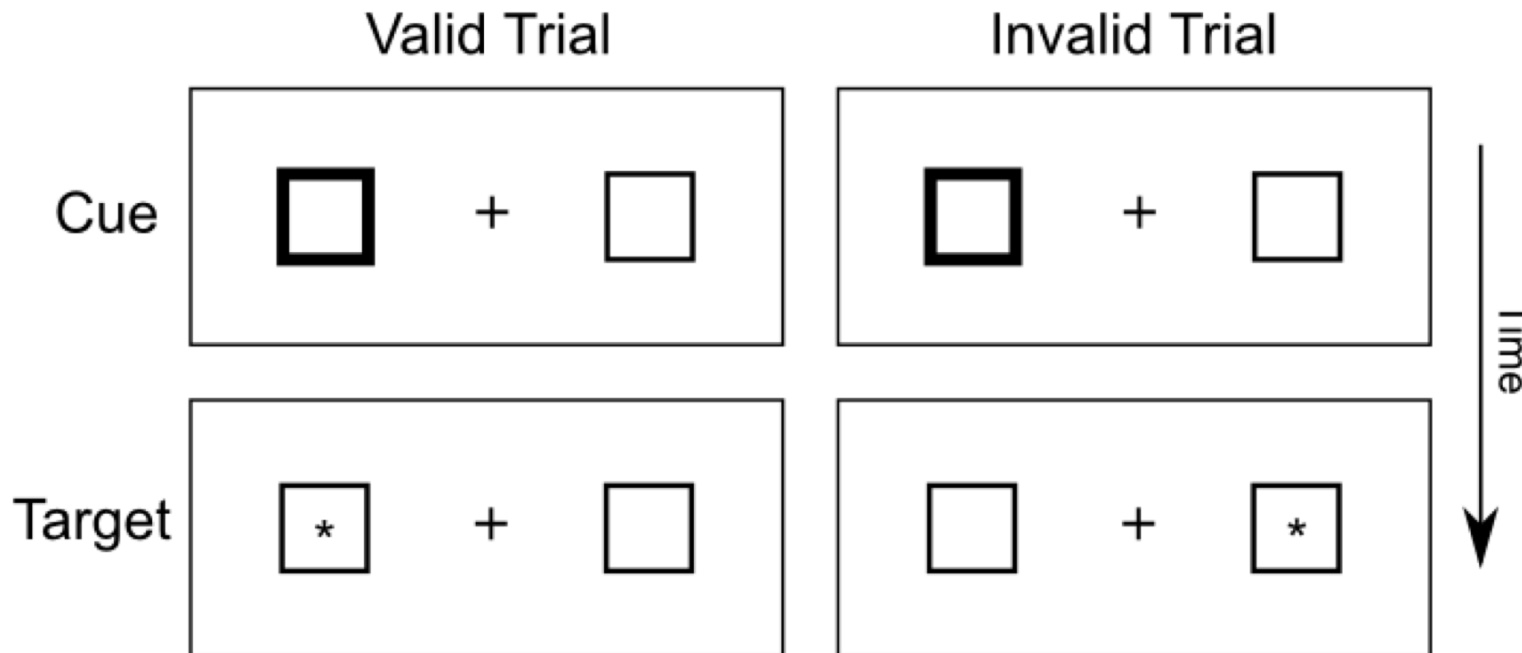
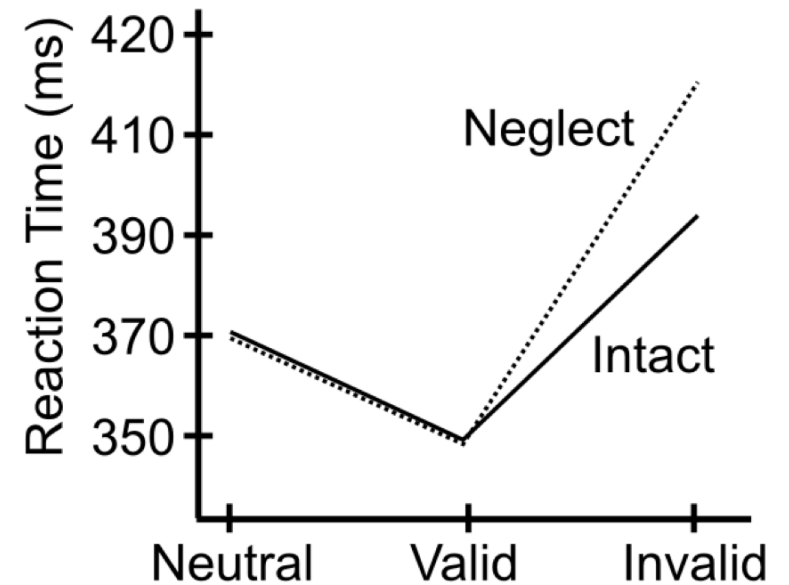


Test paper
(with horizontal lines on it)

Patient bisections
(Vertical lines)

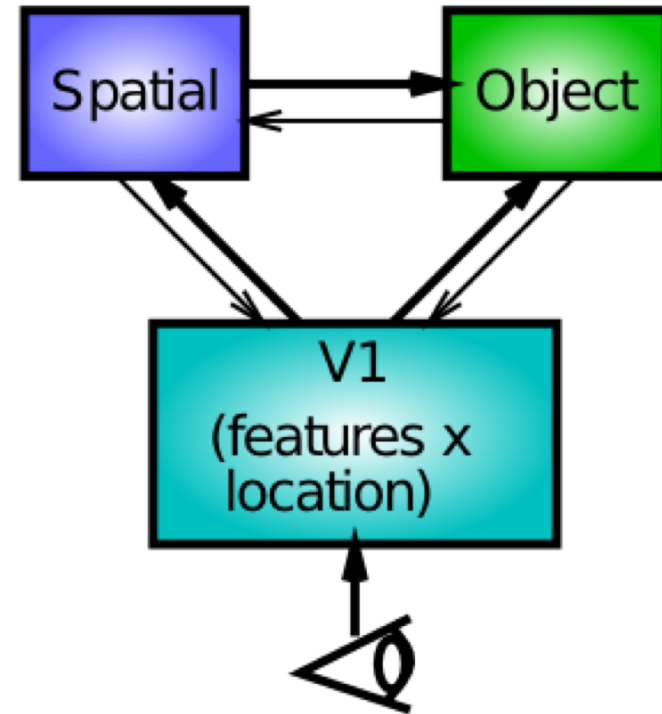
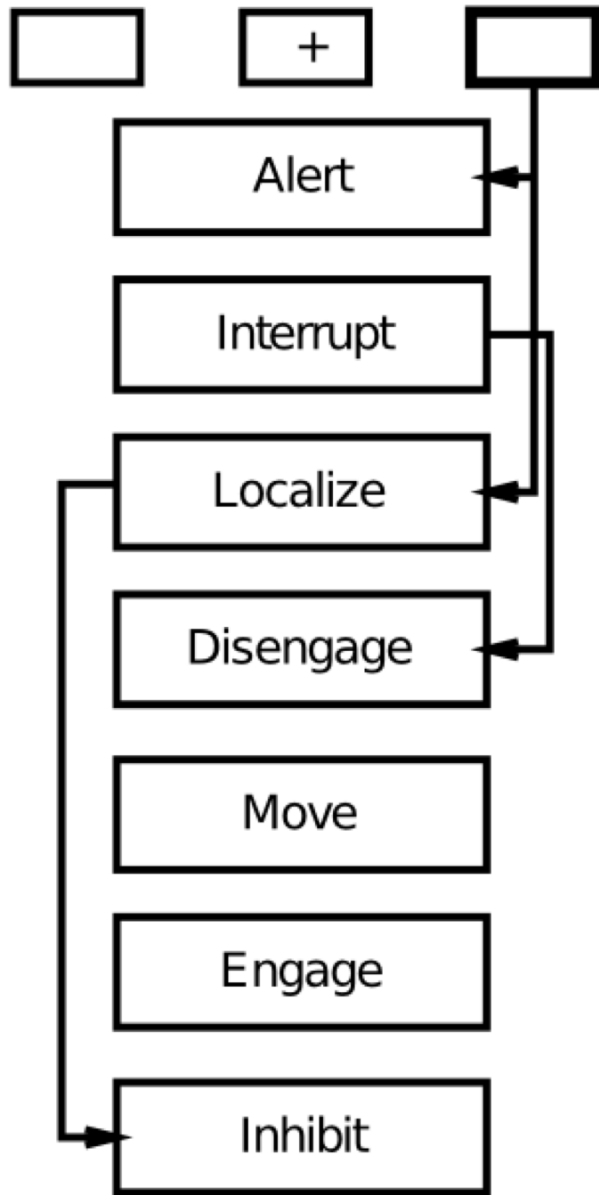
Posner Task

- Valid cues speed performance (relative to “no cue” condition)
- Invalid cues slow performance (relative to “no cue” condition)



- Patients perform normally in the “neutral” (no cue) condition, regardless of where the target is presented
- Patients benefit just as much as controls from valid cues
- Patients are hurt more than controls by invalid cues

Models: Boxology vs. Biology



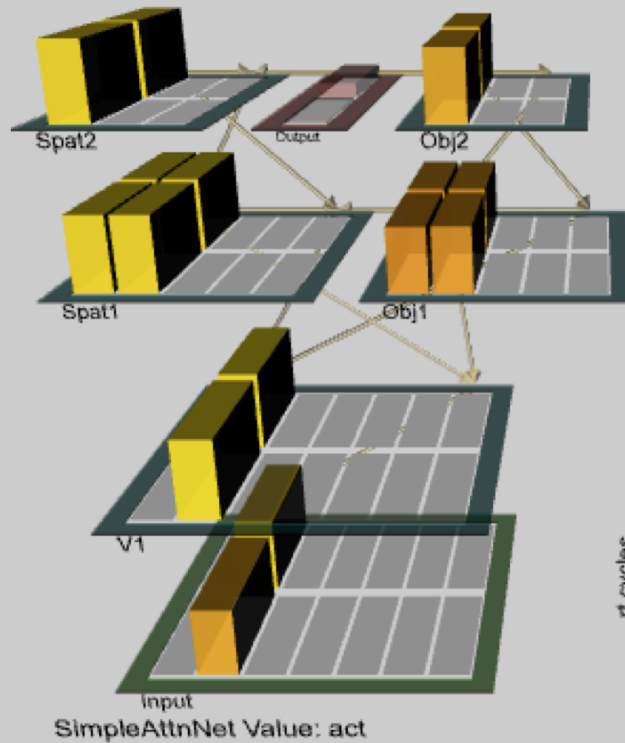
Posner Task Simulation

- Model explains the basic finding that valid cues speed target processing, while invalid cues hurt
- Also explains finding that patients with small unilateral parietal lesions benefit normally from valid cues in ipsilateral field but are disproportionately hurt by invalid cues
- No need to posit “disengage” module
- Also explains finding of **neglect** of contralateral visual field after large, unilateral parietal lesions when some stimulus is present in ipsilateral field (“extinction”)

Balint's Syndrome

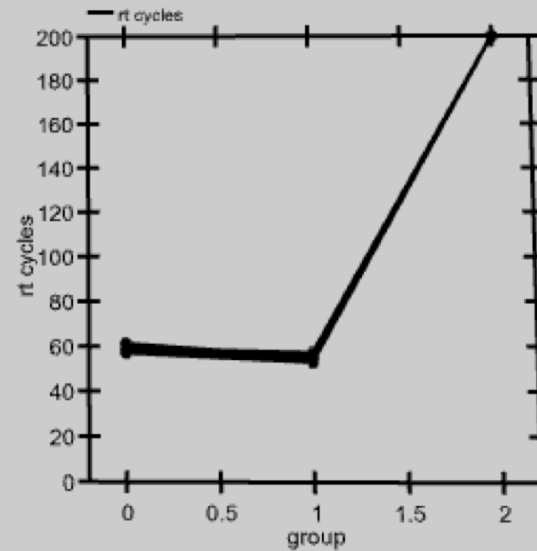
- Bilateral parietal lesions \Rightarrow Balint's syndrome
- \Rightarrow *simultanagnosia* = inability to recognize multiple objects presented simultaneously
- Decreased level of attentional effects on Posner task
- Better explained by competitive model than Posner's disengage theory
 - Latter predicts bilateral slowing for invalid trials (i.e., difficulty disengaging)

Simple Attention Exploration



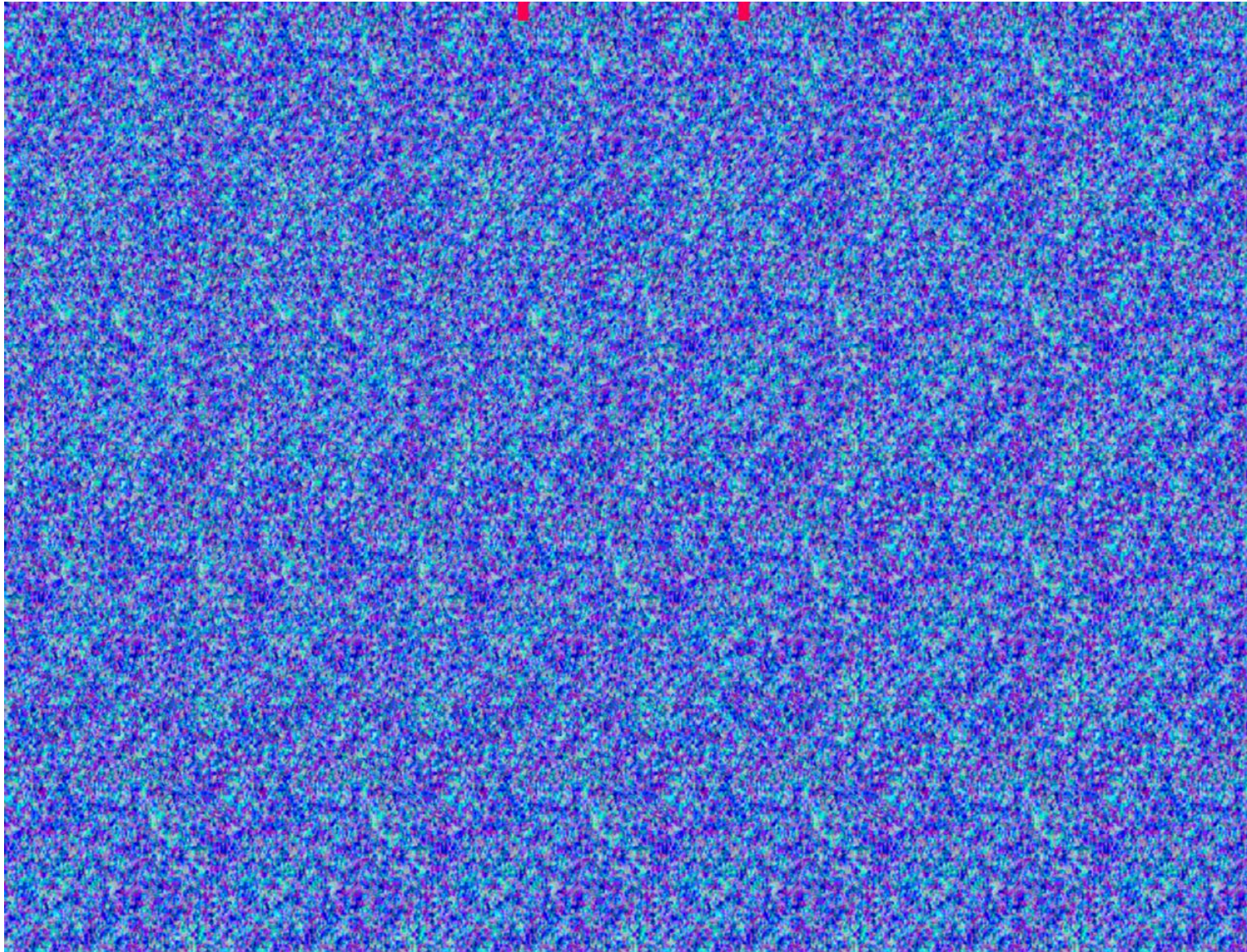
grou ~ name	group	batch	rt cycles
Diff_Ob...	0	9	59.2
Same_Ob...	1	9	54.4
Diff_Ob...	2	9	200

BatchAvgOutputData



GroupOutputData

What's Missing? Lacking Depth..



Supplementary

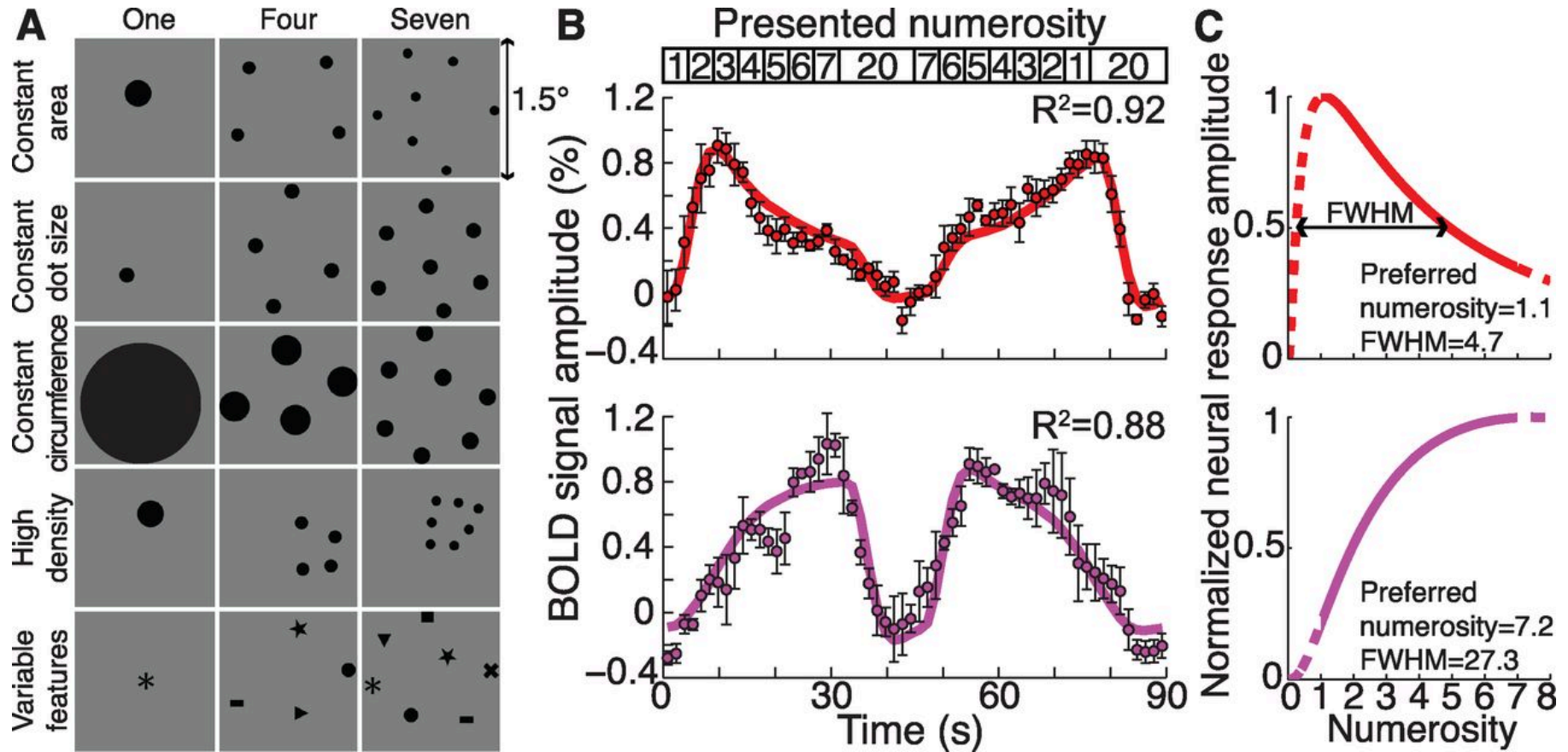
Topographic Representation of Numerosity in the Human Parietal Cortex

B. M. Harvey, B. P. Klein, N. Petridou, S. O. Dumoulin, *Science* 06
Sep 2013:Vol. 341, Issue 6150, pp. 1123–1126

Background

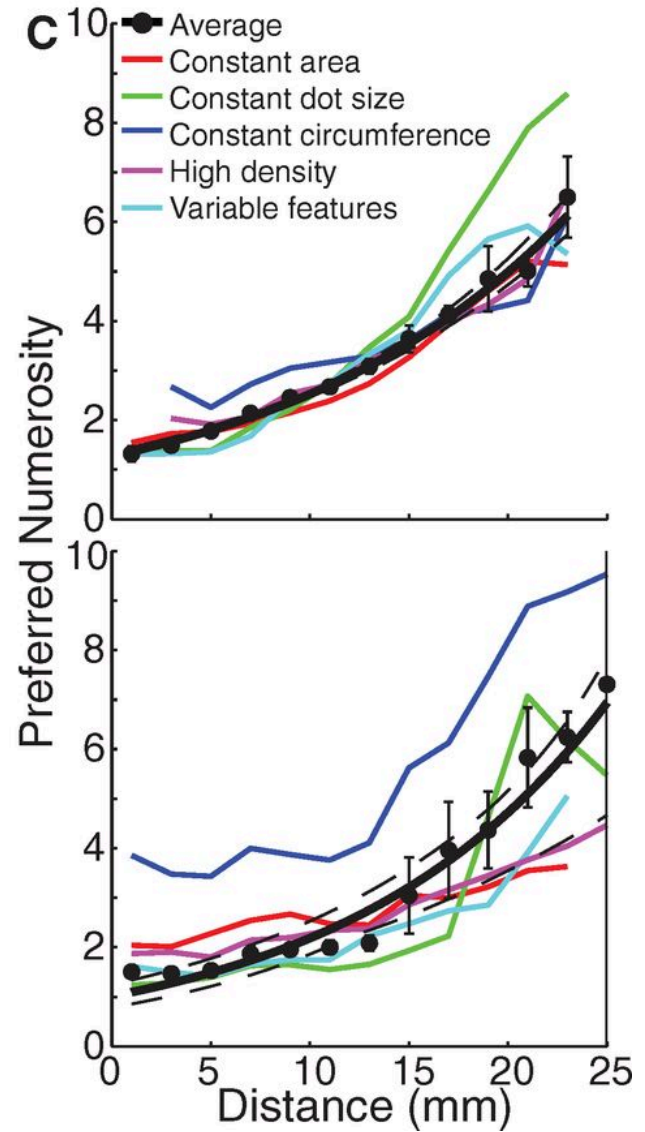
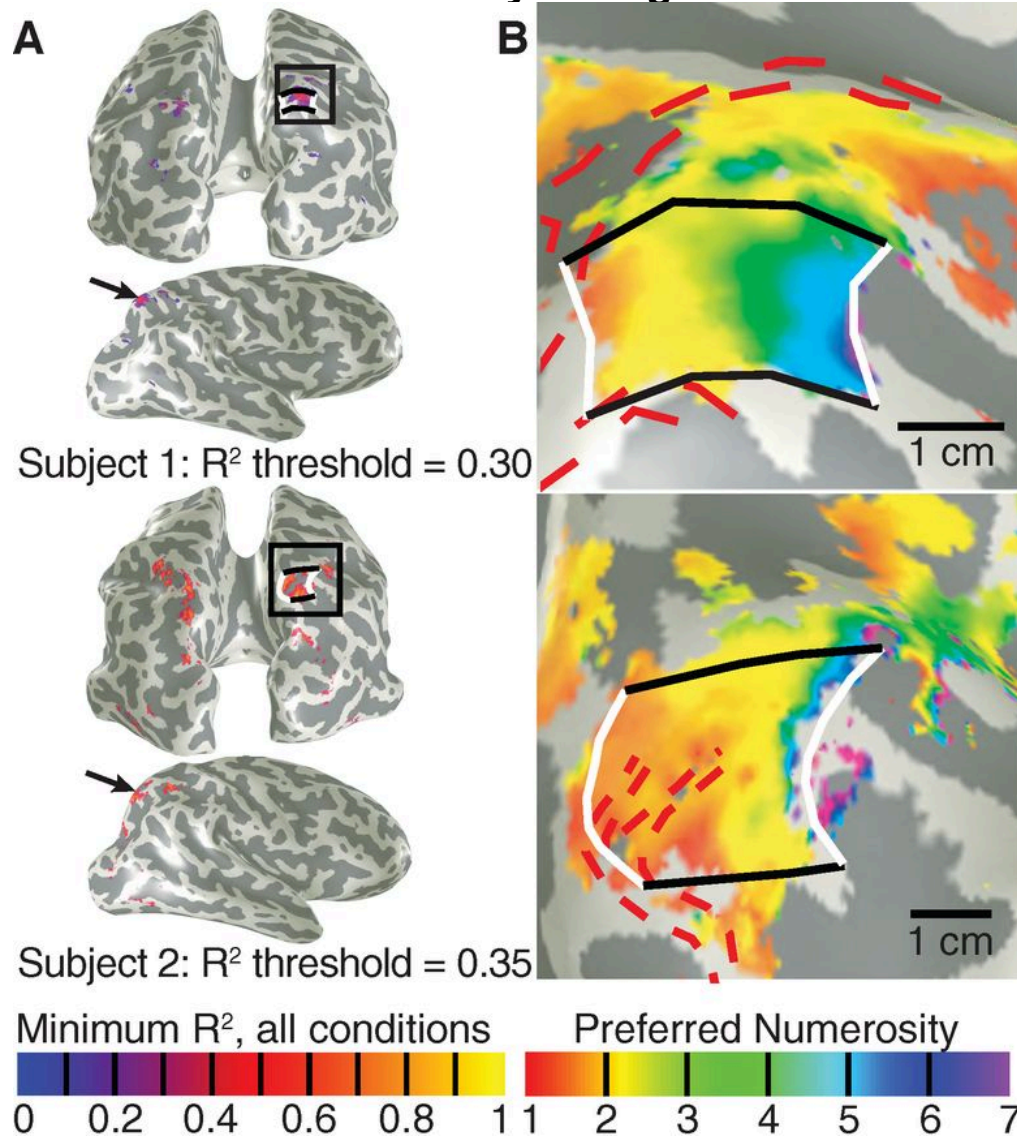
- Humans and many other animals use numerosity to guide behavior and decisions
- Numerosity perception becomes less precise as size of numbers increases
 - particularly effective for small numbers
- Animals, infants, and tribes with no numerical language perceive numerosity
- Hence, numerosity processing is an evolutionarily preserved cognitive function
 - distinct from counting and humans' unique symbolic and mathematical abilities
- Because aspects of numerosity processing mirror primary sensory perception, sometimes referred to as a “number sense”
- Are the cortical representation and processing of numerosity organized topographically, even though no sensory organ has a numerical structure?

Fig. 1 Stimuli, responses, and neural population tuning.(A) Illustration of stimulus conditions, with examples representing different numerosities.



B. M. Harvey et al. Science 2013;341:1123-1126

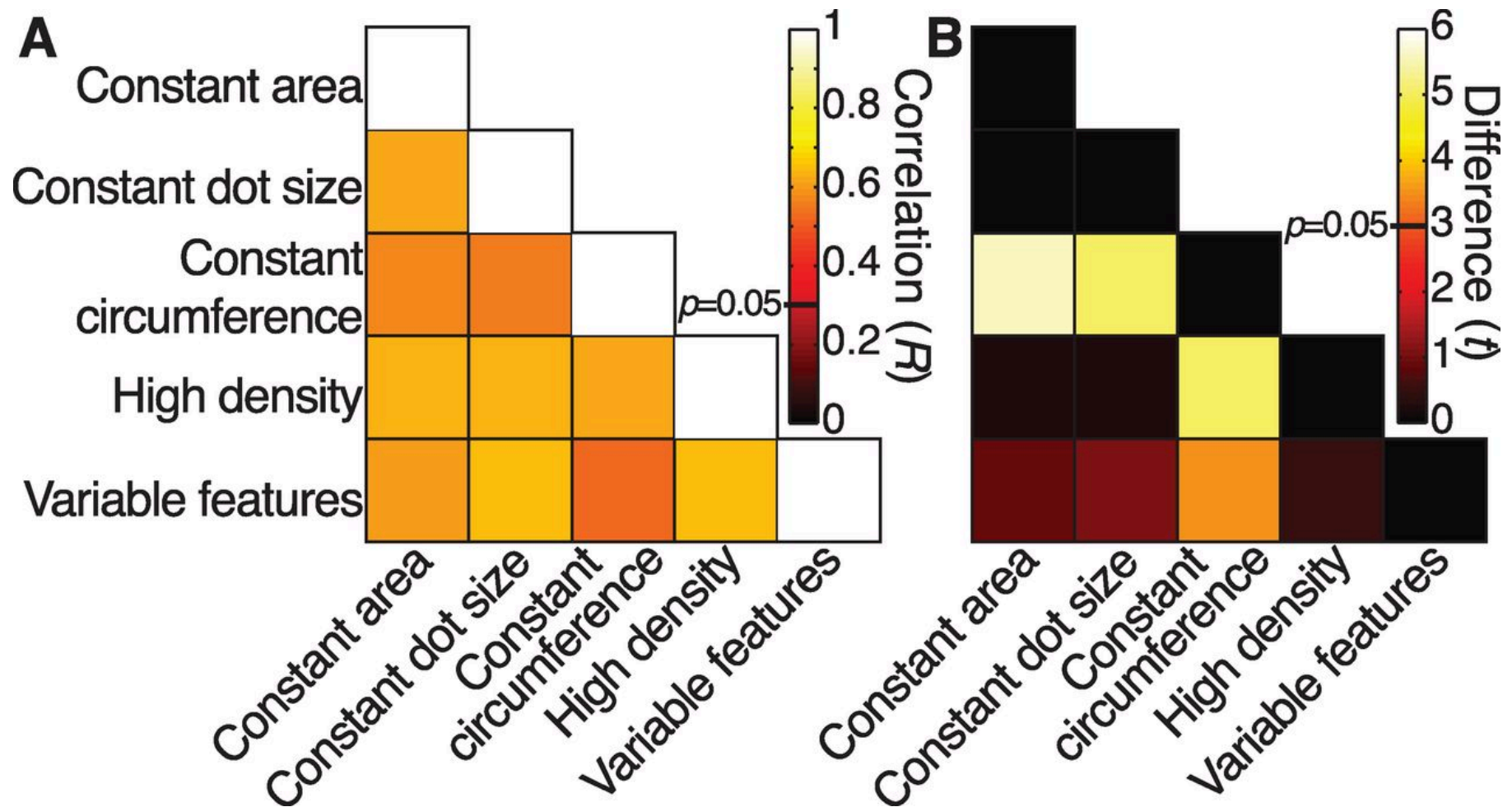
Fig. 2 Topographic representation of numerosity. (A) The variance explained by the model (R^2) highlighted a region in the right parietal cortex where neural populations demonstrated numerosity tuning in all stimulus conditions (Fig. 1A).



B. M. Harvey et al. *Science* 2013;341:1123-1126



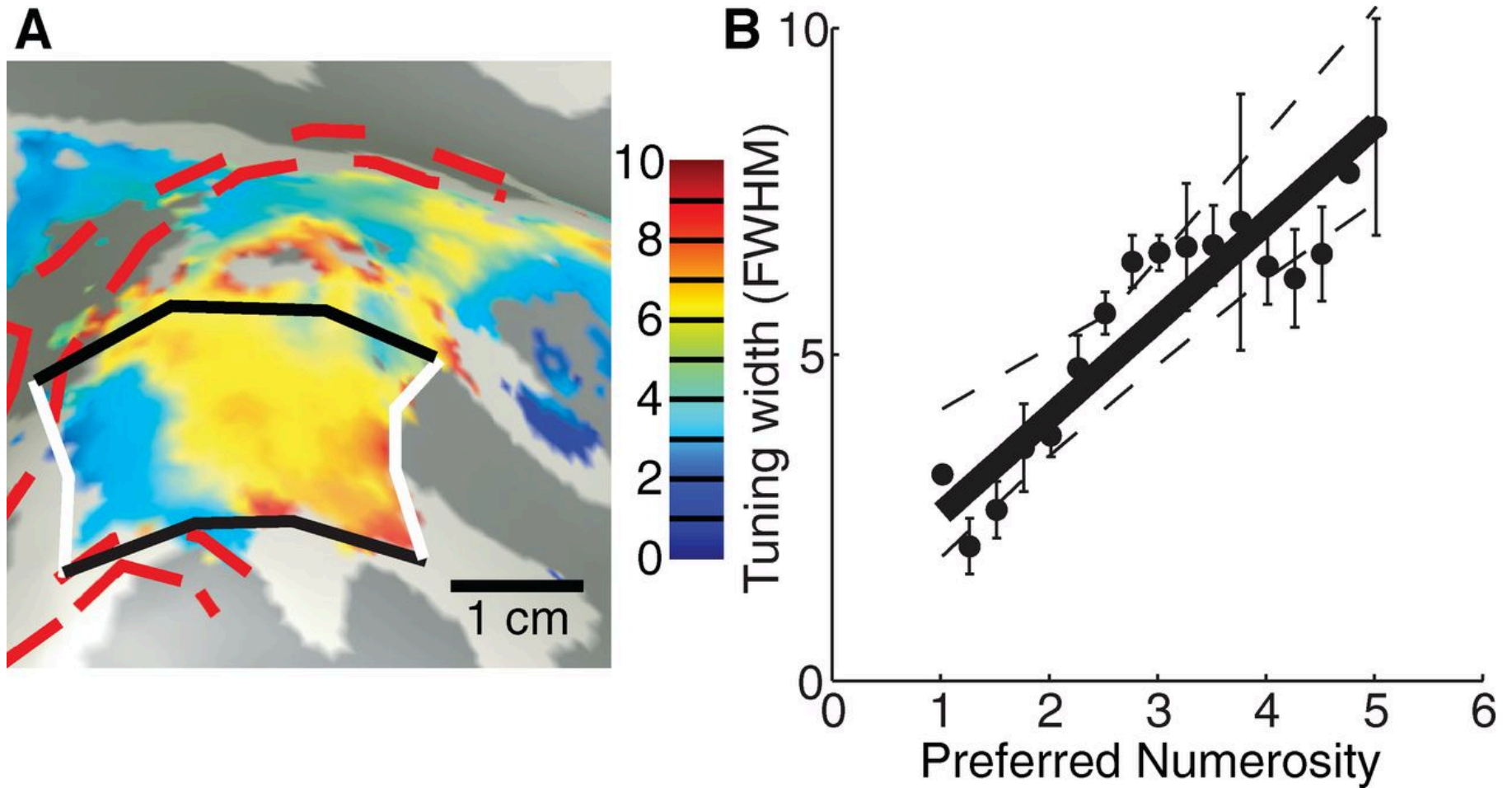
Fig. 3 Comparison of numerosity preferences across recording points in different stimulus conditions, averaged across participants. (A) Because numerosity preferences are topographically organized in all stimulus conditions, they are always correlated.



B. M. Harvey et al. Science 2013;341:1123-1126



Fig. 4 The progression of population tuning width (see Fig. 1C) across the cortical surface (A) and with preferred numerosity (B) for one representative participant. Dots represent mean tuning widths in each preferred numerosity bin, and error bars represent standard errors.



B. M. Harvey et al. *Science* 2013;341:1123-1126



Other Results

- Organization in LH is less clear than seen in RH
- Differences between subjects in map, range of numerosity preferences in map, tuning width, consistency between stimulus conditions, and topographic organization in LH and in right posterior parietal lobe outside region of interest
- No evidence of Arabic numeral-tuned responses in the numerosity map

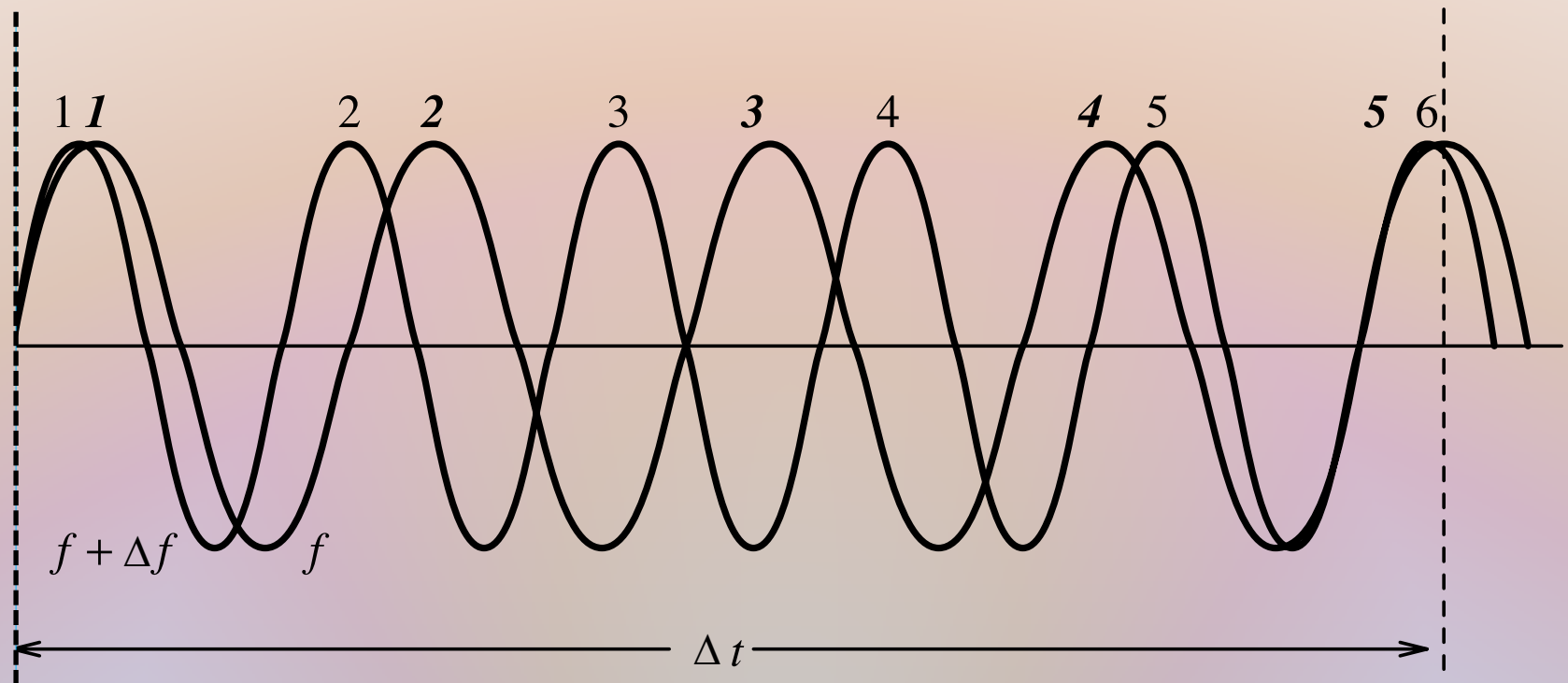
Gabor Uncertainty Principle and Gabor Elementary Functions

MacLennan, B. J. *Gabor Representations of Spatiotemporal Visual Images*. University of Tennessee, Knoxville, Computer Science Department technical report CS-91-144, September 1991

Dennis Gabor

- Dennis Gabor (1900–79) is the father of holography (1947, 1971 Nobel Prize in Physics)
- “the future cannot be predicted, but futures can be invented”
- Developed a theory of information (1946) complementary to Shannon’s theory
- Gabor Uncertainty Principle based on same mathematics as derivation of Heisenberg Uncertainty Principle
- Nearly optimal Gabor representations are used in primary visual cortex

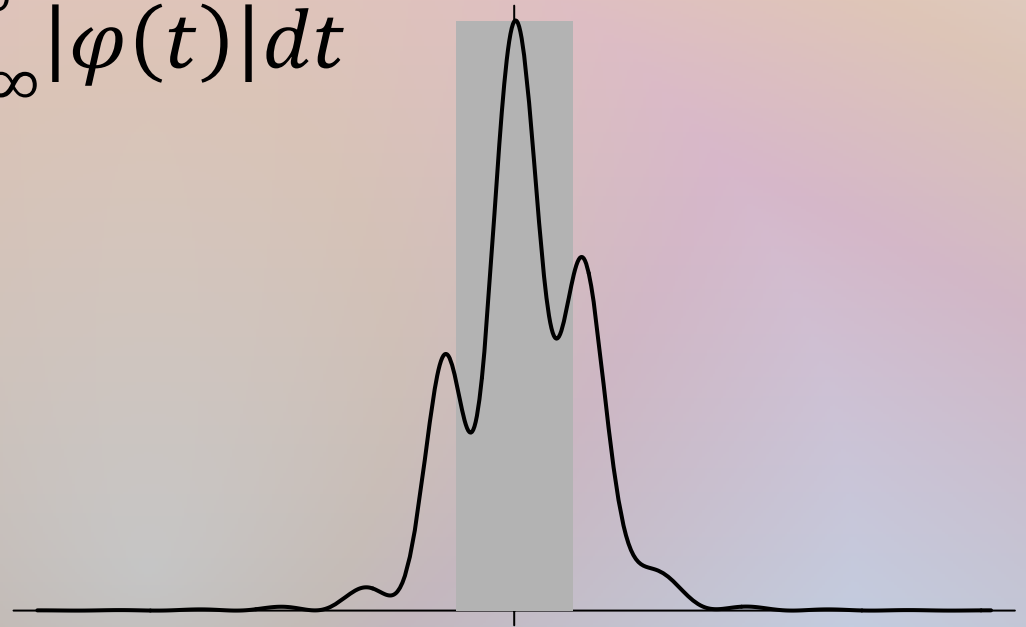
Time to Detect Difference in Frequency



$$\Delta f \Delta t \geq 1$$

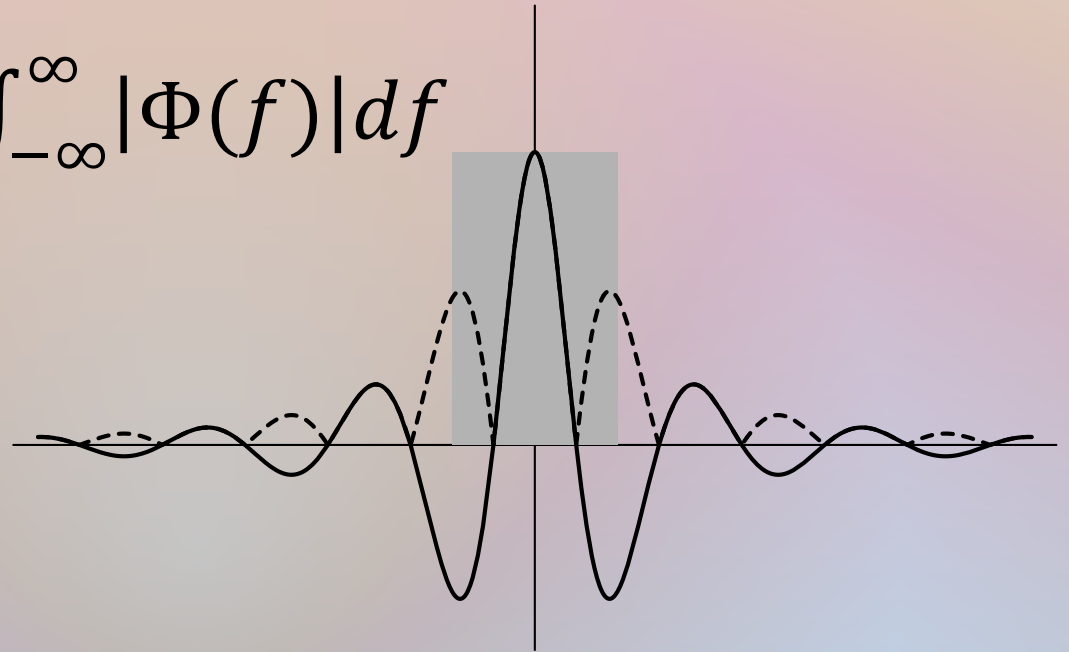
A Little More Formally...

- **Nominal duration** (Δt) = duration of rectangular pulse with same area as signal and height equal to amplitude at origin
- Hence, $\Delta t |\varphi(0)| = \int_{-\infty}^{\infty} |\varphi(t)| dt$
- Some details omitted



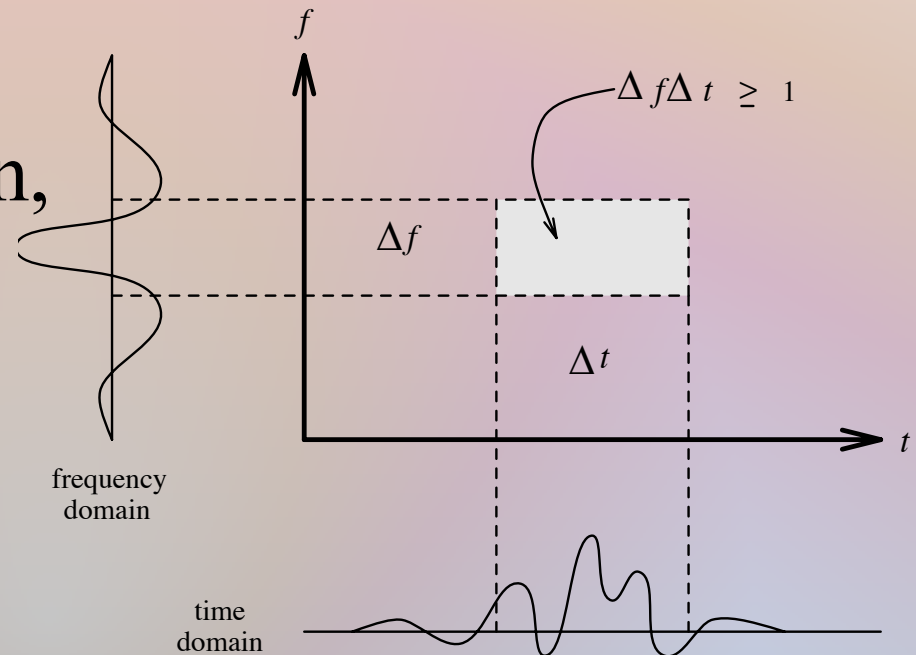
A Little More Formally (2)

- **Nominal bandwidth** (Δf) of spectrum = width of rectangular pulse with height equal to spectrum's amplitude at origin and same area as absolute value of spectrum
- Hence, $\Delta f |\Phi(0)| = \int_{-\infty}^{\infty} |\Phi(f)| df$

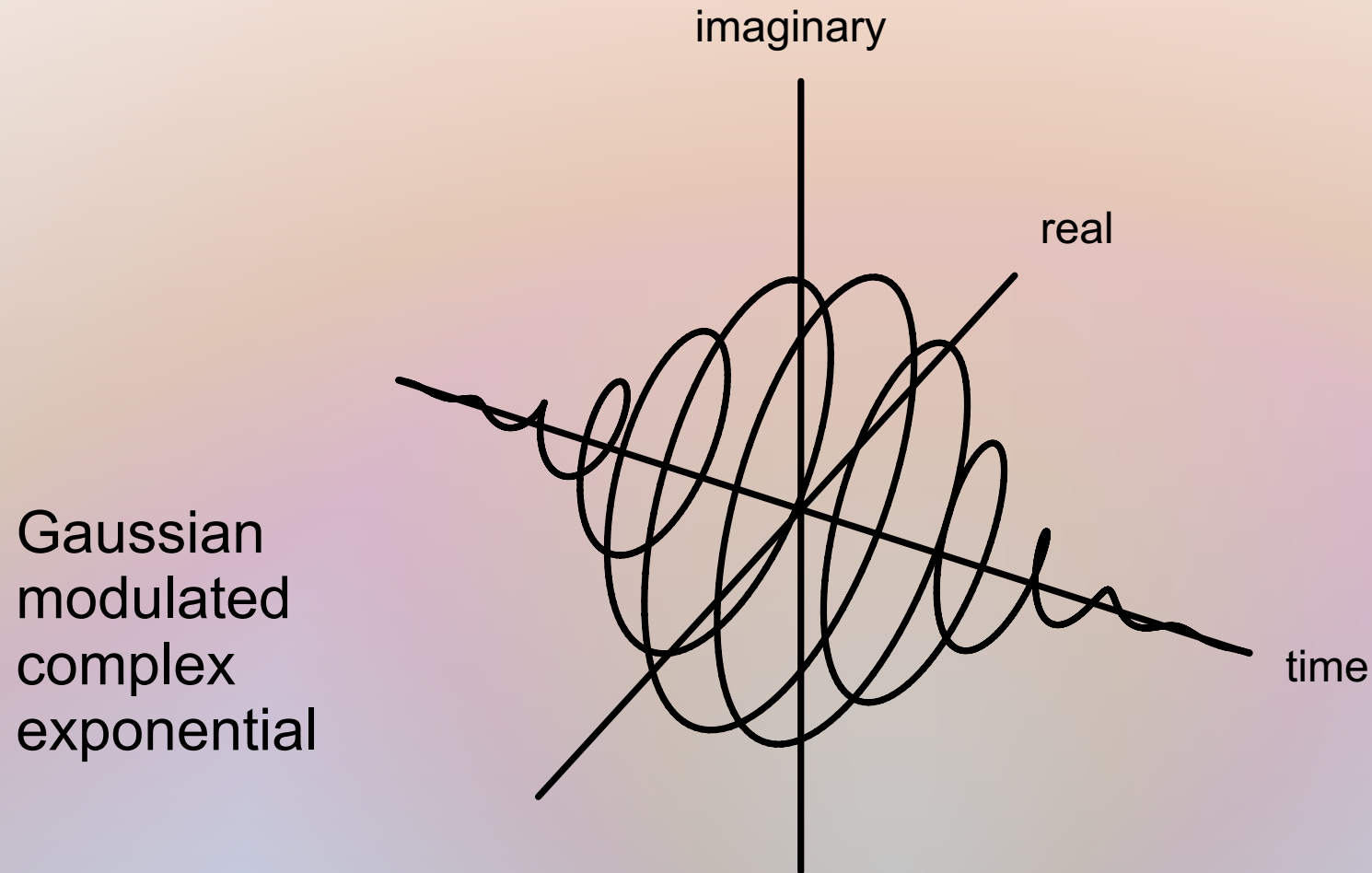


A Little More Formally (3)

- Computing the Fourier transform at origin,
 $|\Phi(0)| \leq \Delta t |\varphi(0)|$
- So $\Delta t \geq |\Phi(0)|/|\varphi(0)|$
- Computing the inverse Fourier transform at origin,
 $|\varphi(0)| \leq \Delta f |\Phi(0)|$
- So $\Delta f \geq |\varphi(0)|/|\Phi(0)|$
- Hence, $\Delta f \Delta t \geq 1$

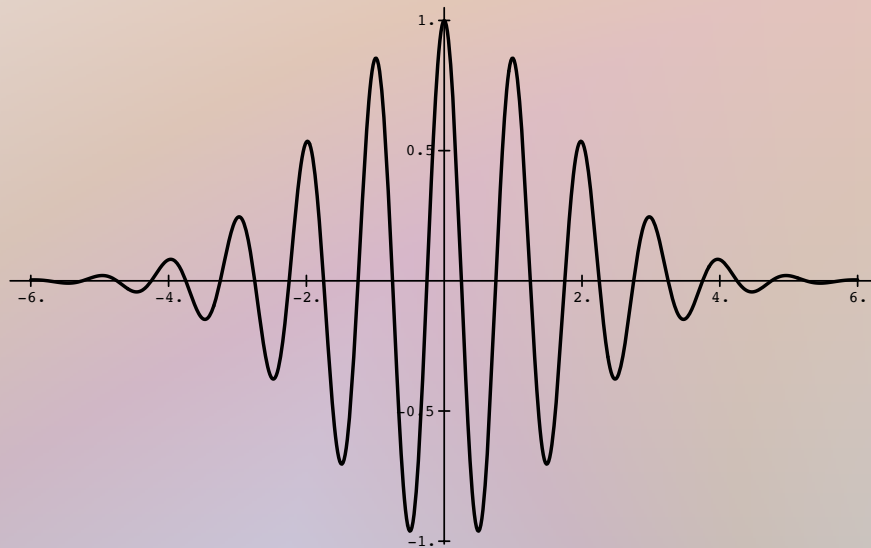


1D Gabor Elementary Function

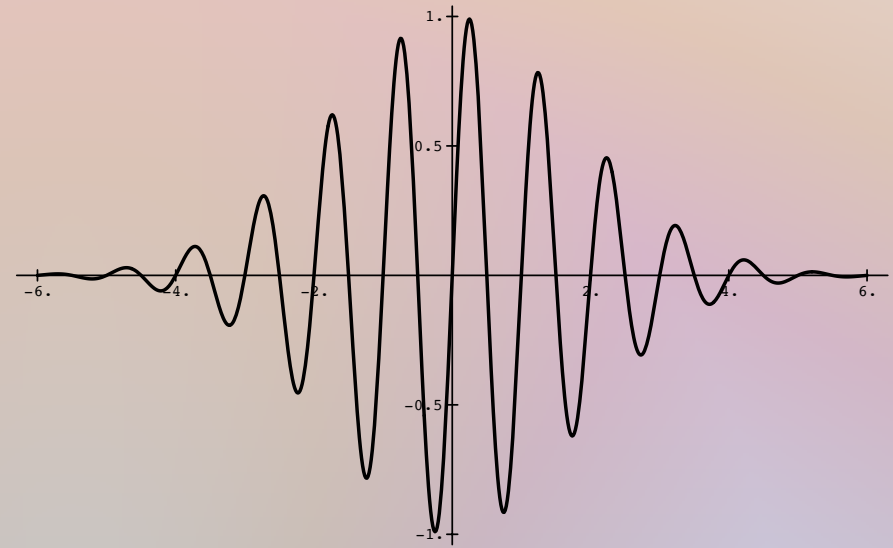


Orthogonal Components of 1D Gabor

Cosine (real)

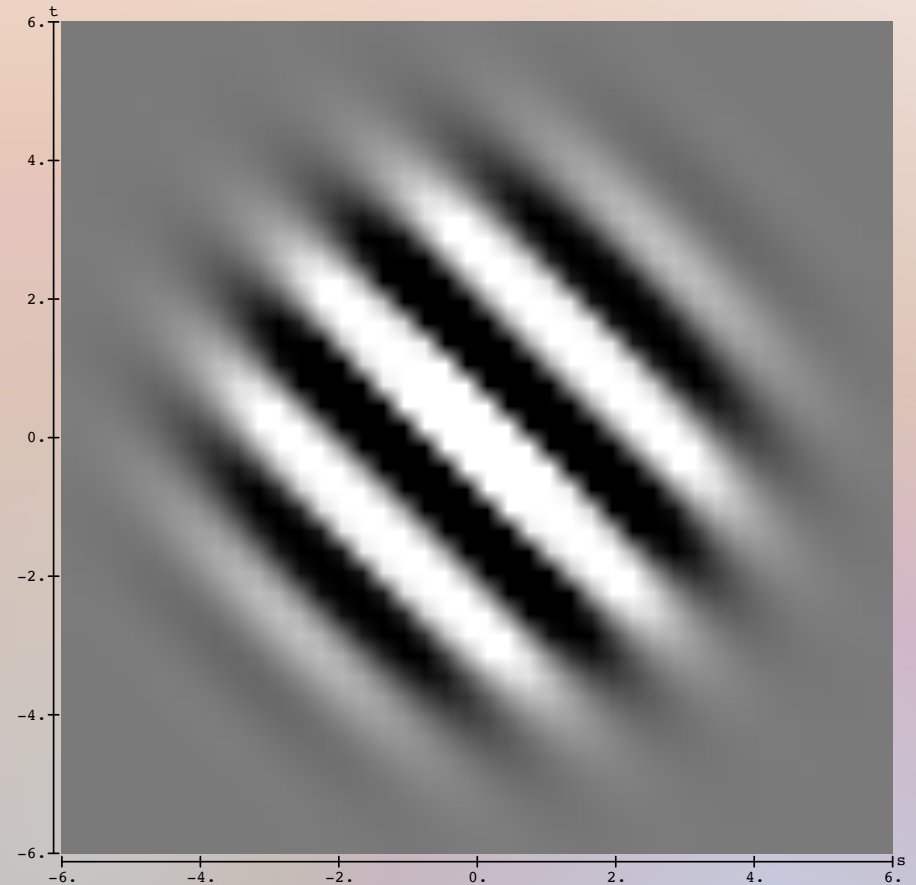
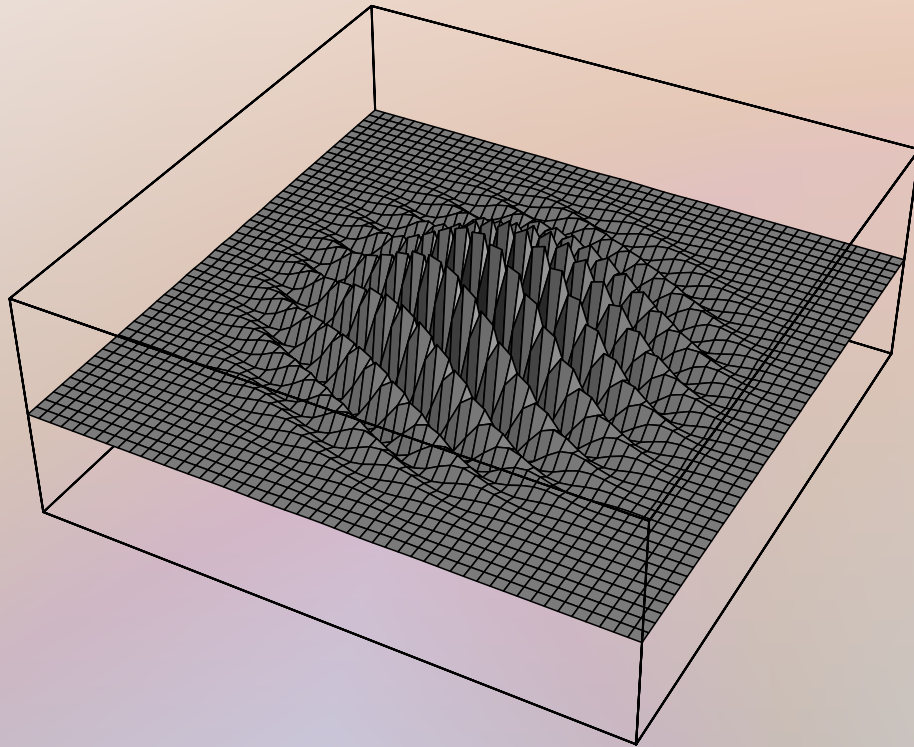


Sine (imaginary)

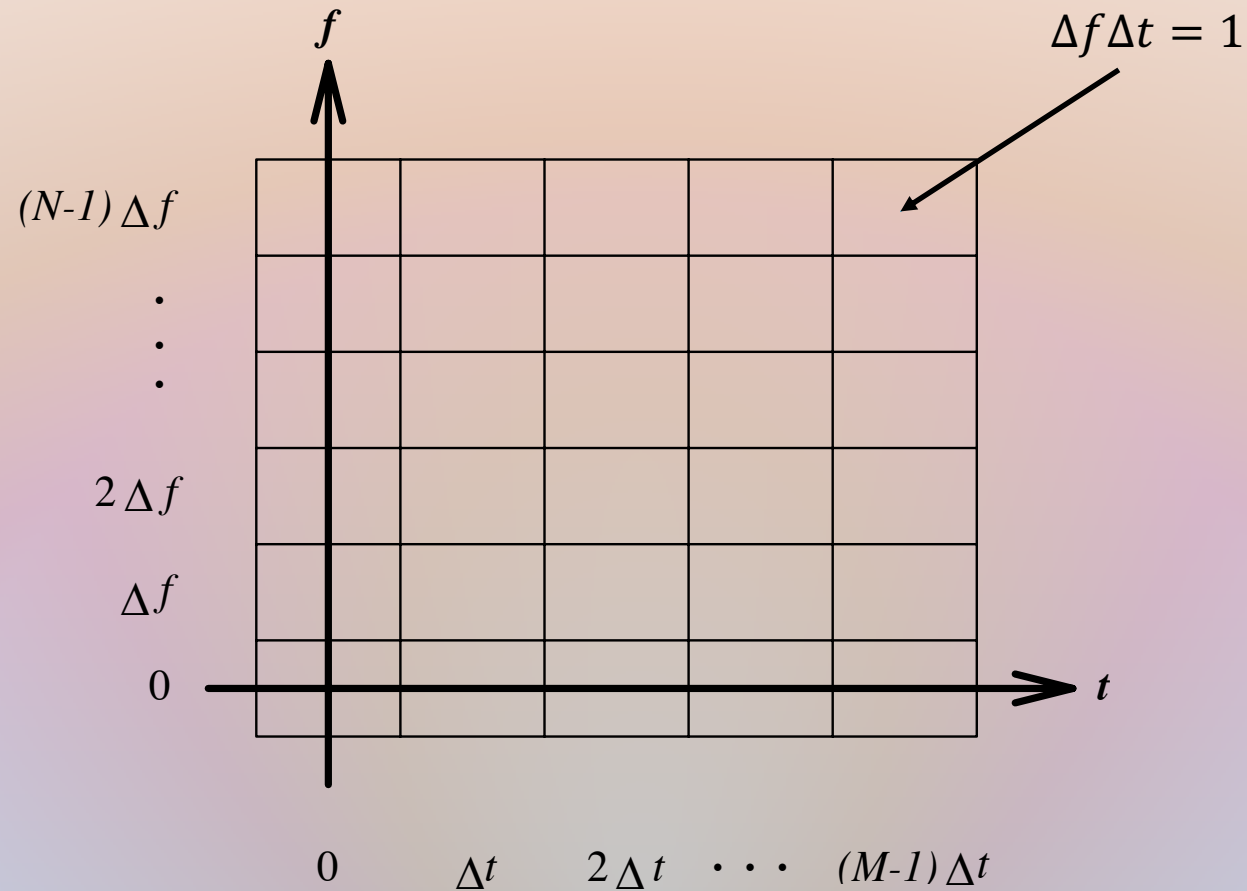


$$e^{ift} = \cos ft + i \sin ft$$

Real Part of 2D Gabor Elem. Function



Maximum Logon Content of Signal



Maximum Logon Content

- If $T = M\Delta t$ is the duration and $F = N\Delta f$ is the bandwidth
- The maximum number of logons MN is achieved when $\Delta t\Delta f = 1$ (i.e., Gabor elementary functions)
- In general, the area doesn't have to be divided into rectangles of the same shape, so long as area is 1
- So the maximum logon content is TF (duration times bandwidth)
- Any such signal can be represented uniquely as a sum of TF Gabor elementary functions

Gabor Representations

- Any “finite energy” function ψ of finite duration T and finite bandwidth F is equal to a linear superposition of Gabor elementary functions:

$$\psi(t) = \sum_{j=0}^{M-1} \sum_{k=0}^{N-1} a_{jk} C_{jk}(t) + b_{jk} S_{jk}(t)$$

where $C_{jk}(t) = e^{-\pi(t-j\Delta t)^2/\alpha^2} \cos[2\pi k\Delta f(t - j\Delta t)]$

and $S_{jk}(t) = e^{-\pi(t-j\Delta t)^2/\alpha^2} \sin[2\pi k\Delta f(t - j\Delta t)]$

- The same applies in higher dimensions.

Gabor Filters in Early Vision

- Measurements of receptive fields of simple cells in cat visual cortex have show them to be like Gaussian-modulated sinusoids (Jones & Palmer, 1987)
- Daugman (1984, 1985, 1993) showed 97% of them are statistically indistinguishable from the odd- or even-symmetric parts of a 2D Gabor elementary function
- Adjacent simple cells have grating patches that are 90° out of phase, but matched in preferred orientation and frequency
- And more... (MacLennan, 1991)