

# CS375 / Psych 249:

## Large-Scale Neural Network Models for Neuroscience

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### Lecture 2: The biological inspiration of CNNs

2025.01.07

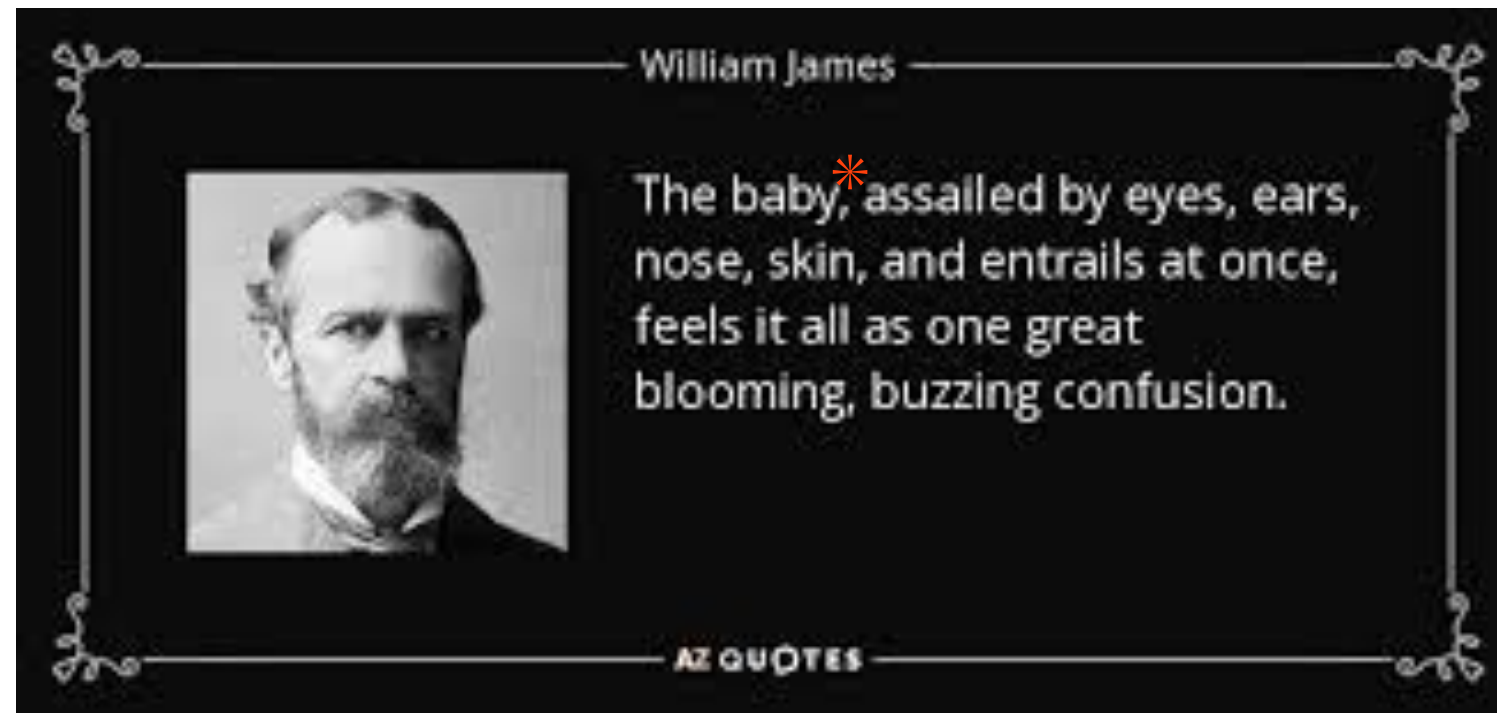
**Daniel Yamins**

Departments of Computer Science and of Psychology  
Stanford Neuroscience and Artificial Intelligence Laboratory  
Wu Tsai Neurosciences Institute  
Stanford University



# Problem: Entity Extraction

Understanding complex, noisy data streams is a critical part of cognition.



Without sophisticated parsing and entity extraction, the world would be “as one great blooming, buzzing confusion” (for babies or otherwise).

\*actually not clearly true for babies ...

# Problem: Entity Extraction

Why is the problem hard computationally?

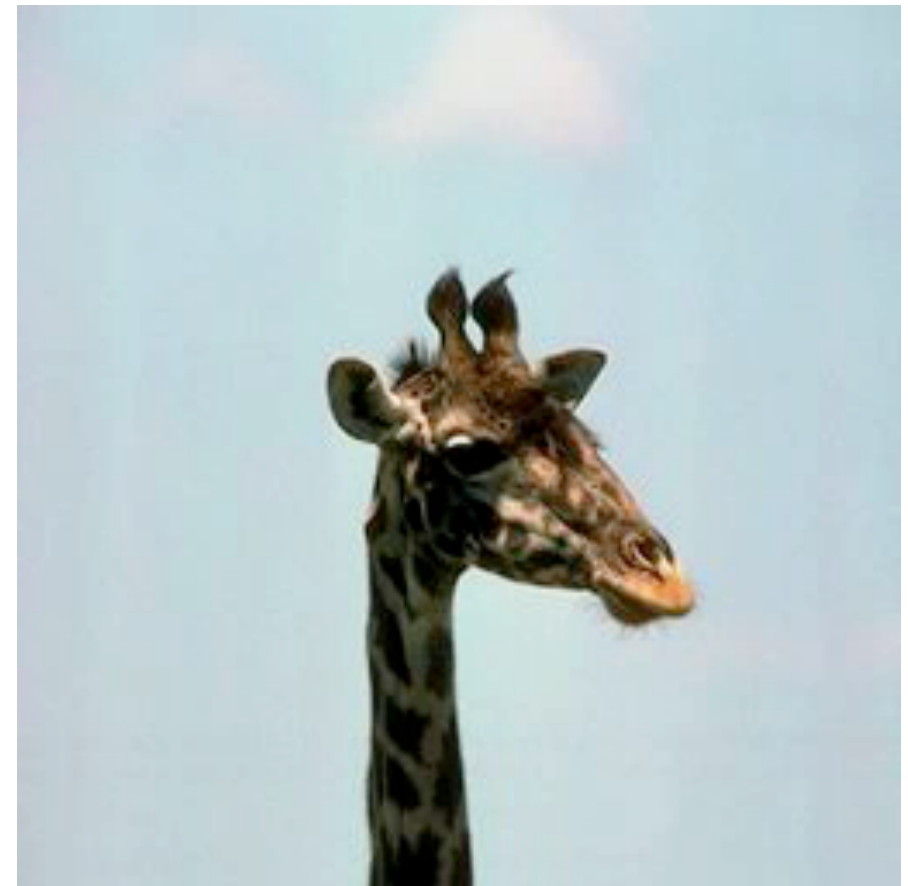
1. Nonlinear misalignment between physical and behavioral dimensions

# Problem: Entity Extraction

Why is the problem hard computationally?

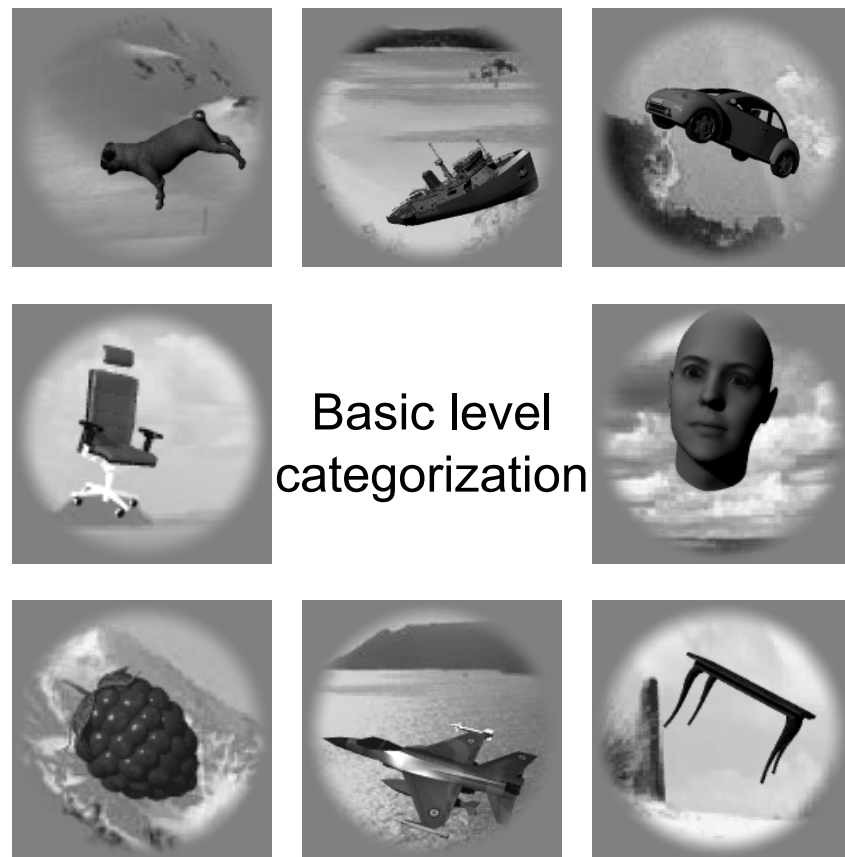
1. Nonlinear misalignment between physical and behavioral dimensions

2. Needs to be done ***\*fast\****, and thus, presumably, massively in parallel

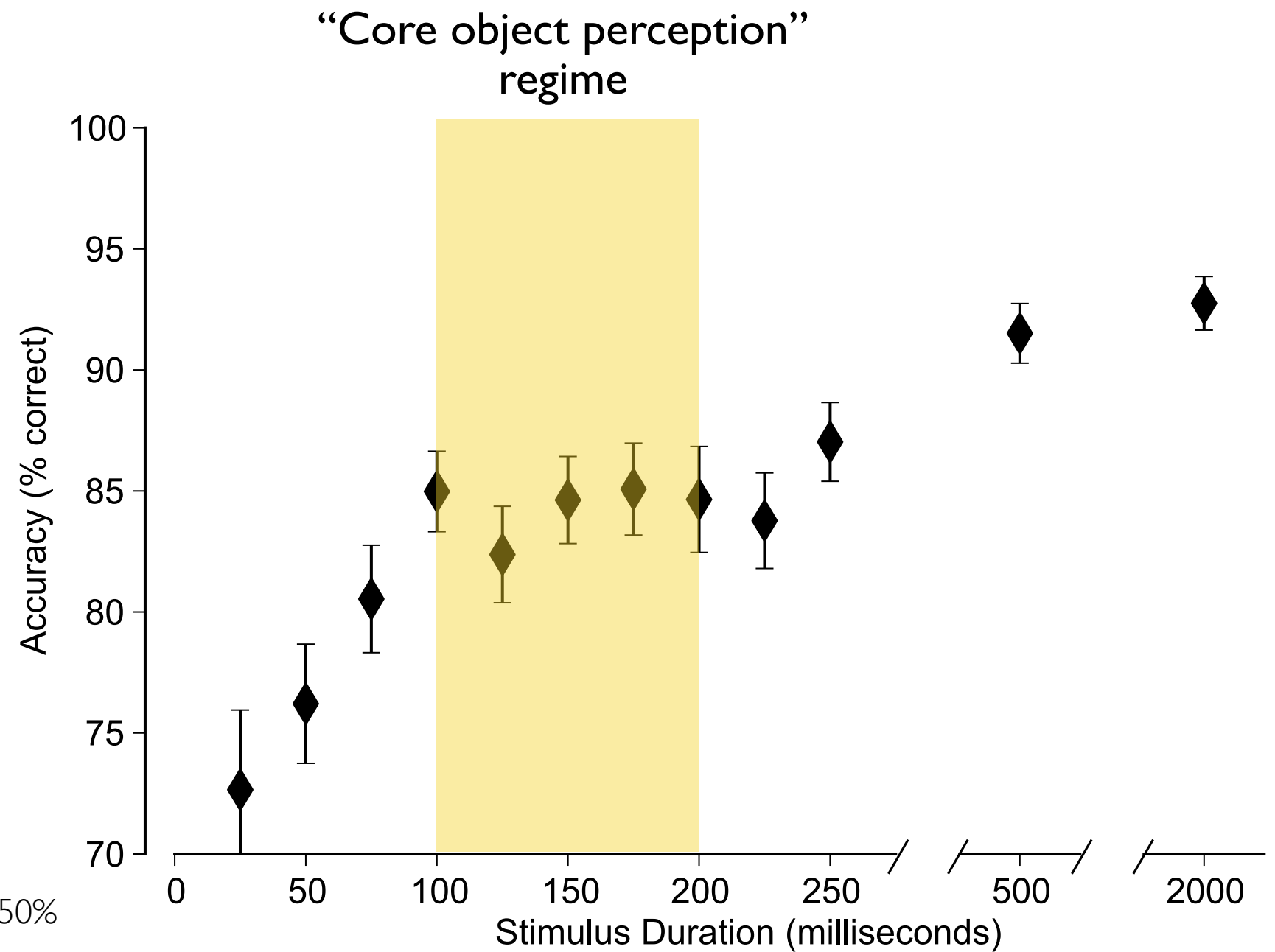




# Problem: Entity Extraction

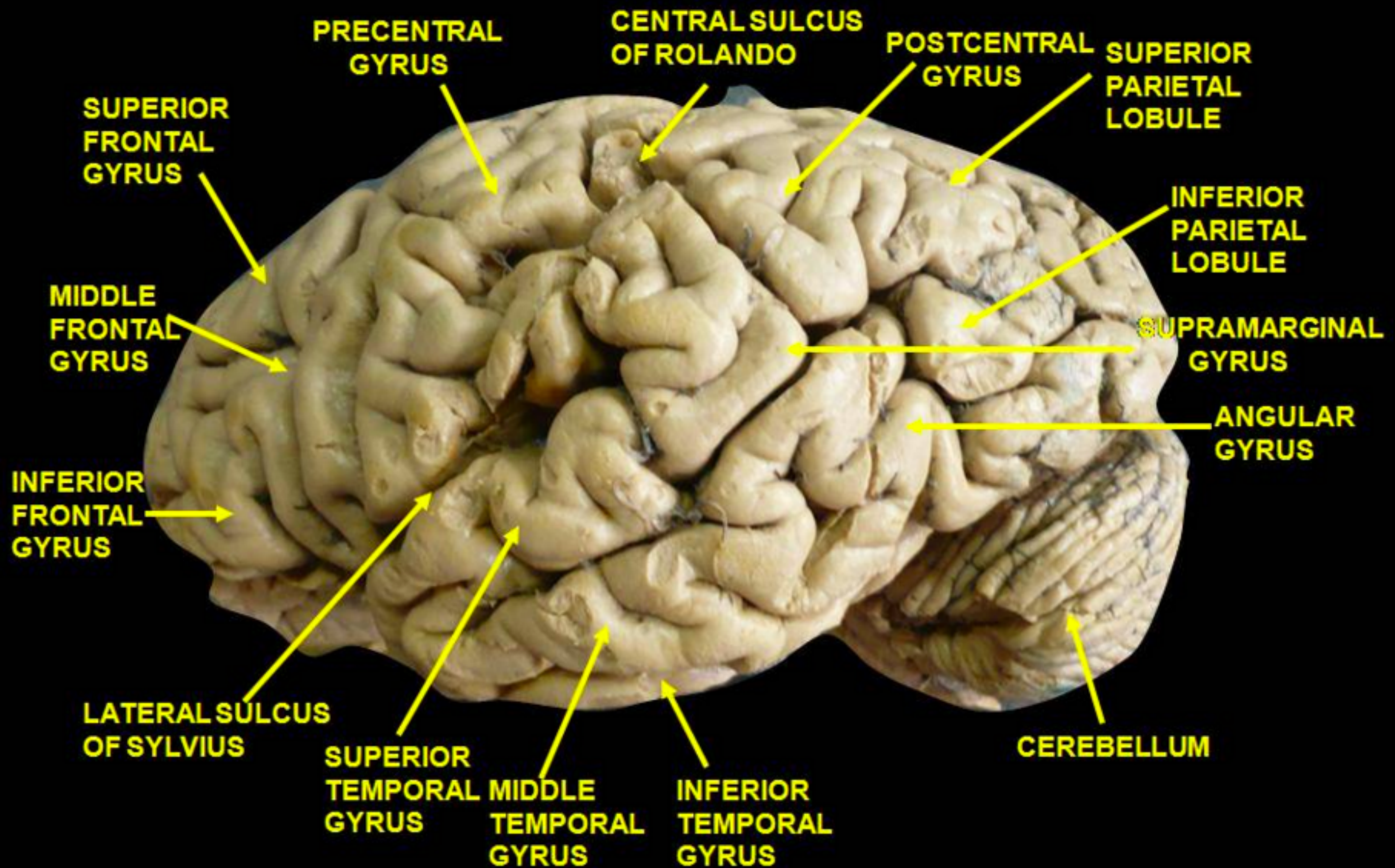


Chance is 50%



↑  
All the data I will show  
you today

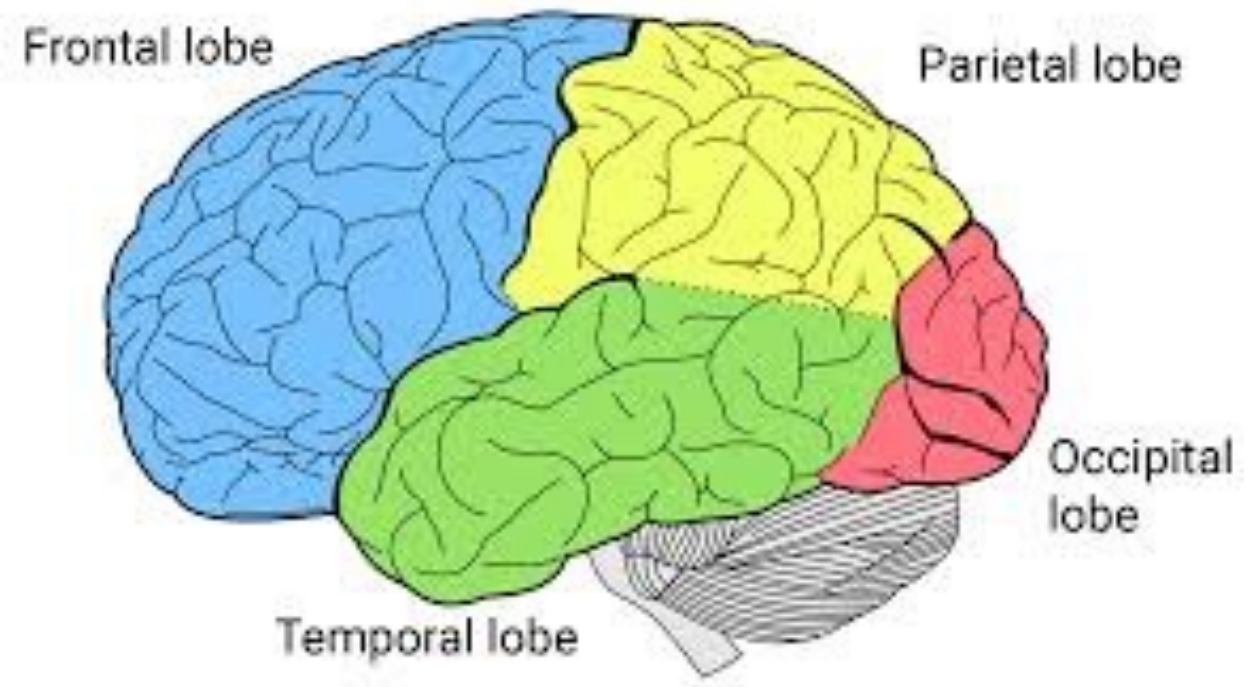
↑  
Typical primate fixation  
duration during natural  
viewing





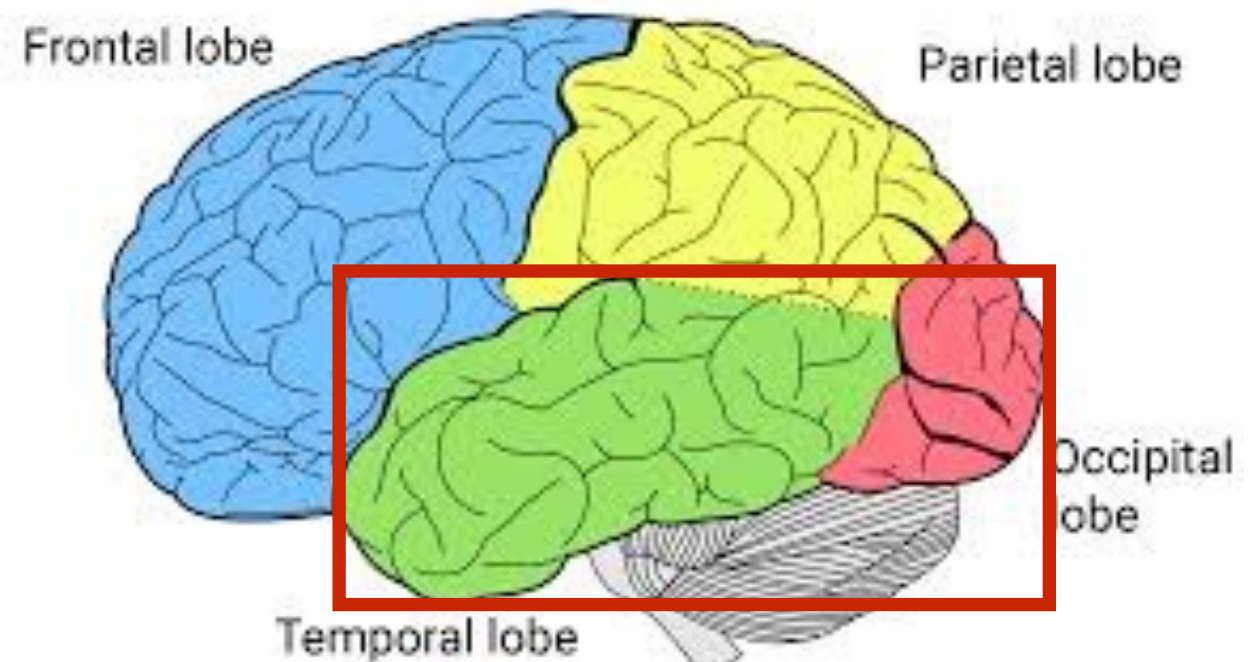
# Many Different Computational Goals

- ▶ Sensory processing
  - visual, auditory, somatosensory recognition (occipital, temporal)
  - navigation (hippocampus?)
- ▶ motor command production & execution (motor cortex)
- ▶ memory, decision making and planning (hippocampus, prefrontal cortex)
- ▶ language
- ▶ emotions, theory-of-mind



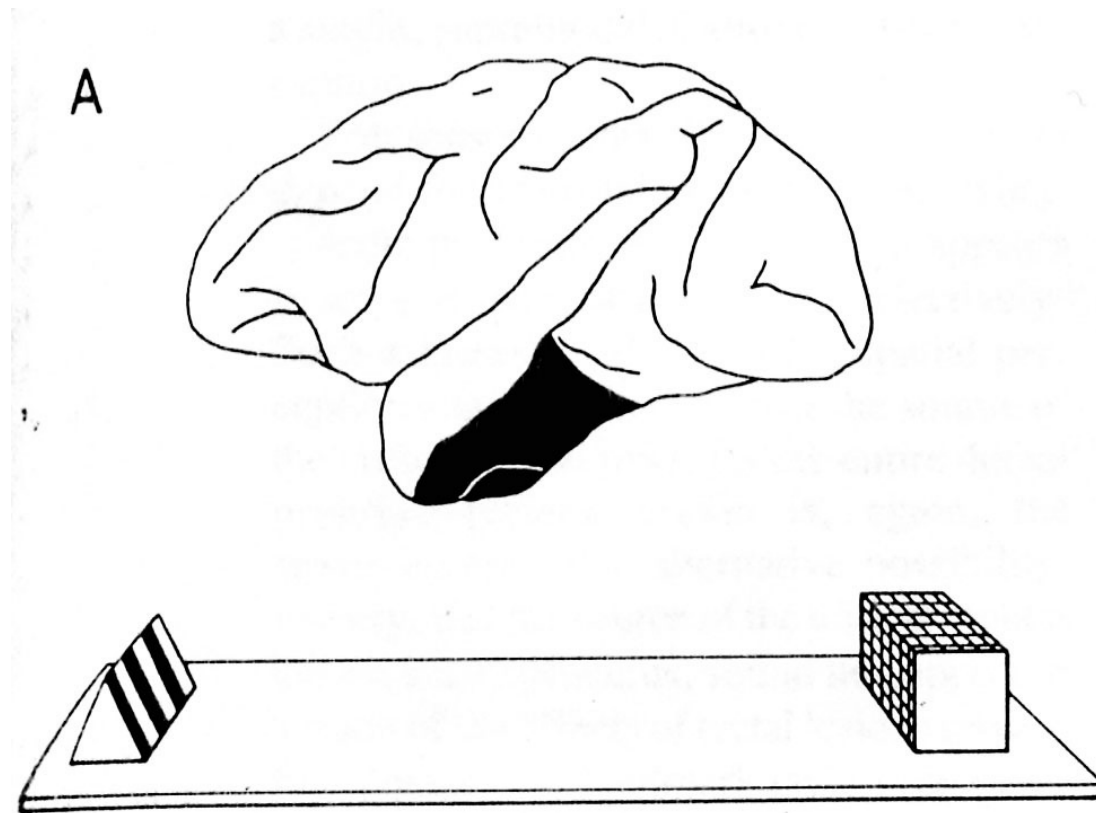
# Many Different Computational Goals

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- ▶ language
- ▶ emotions, theory-of-mind



# Background: Ventral visual stream

*Mishkin & Ungerleider, 1982*



**“what” / ventral / occipitotemporal**

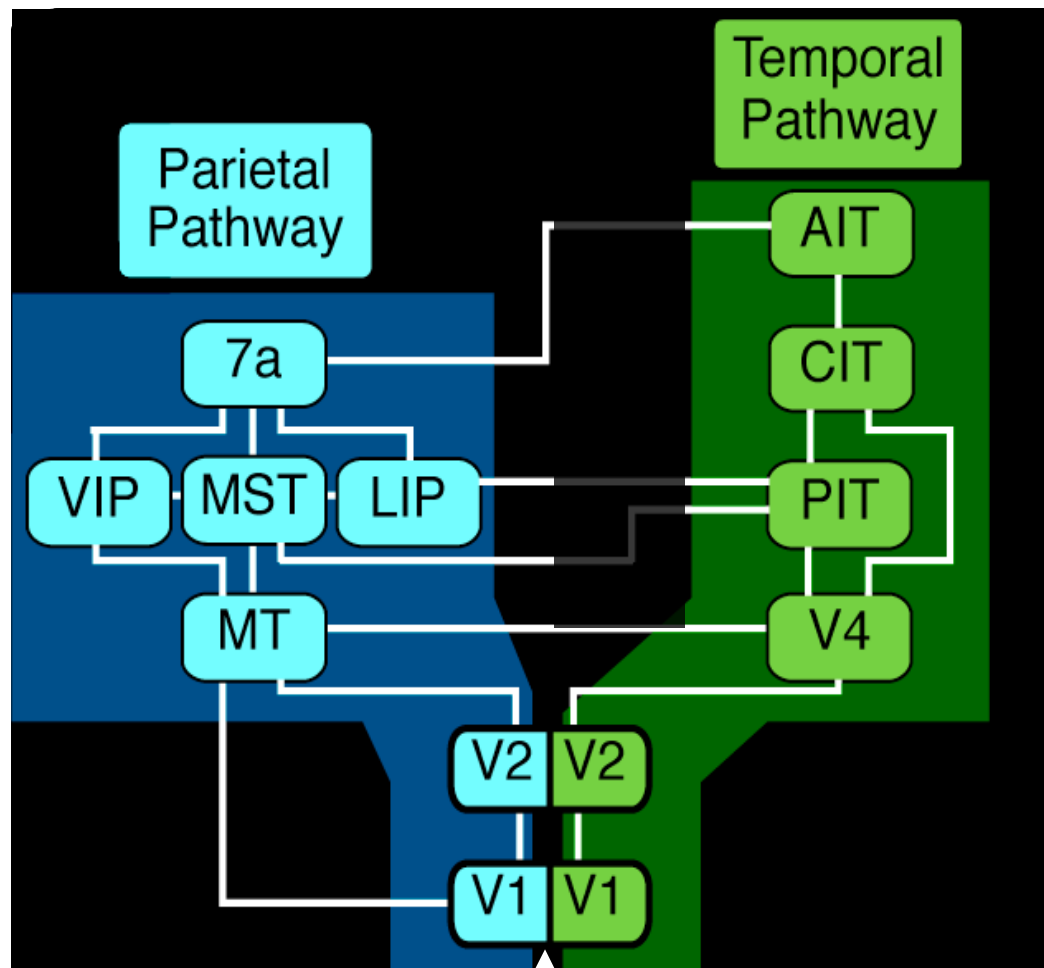
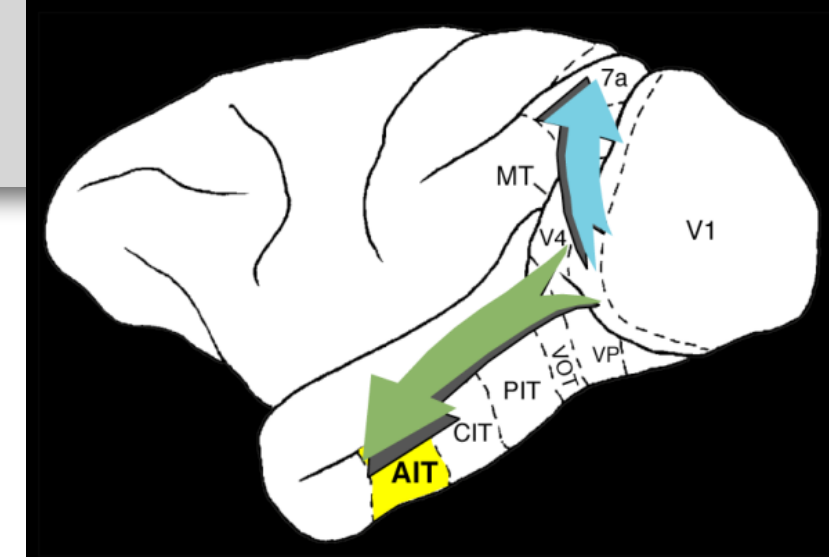
*Lesions in IT cortex produce  
deficits in shape discrimination tasks  
(Gross et al, 1973, Mishkin 1982)*



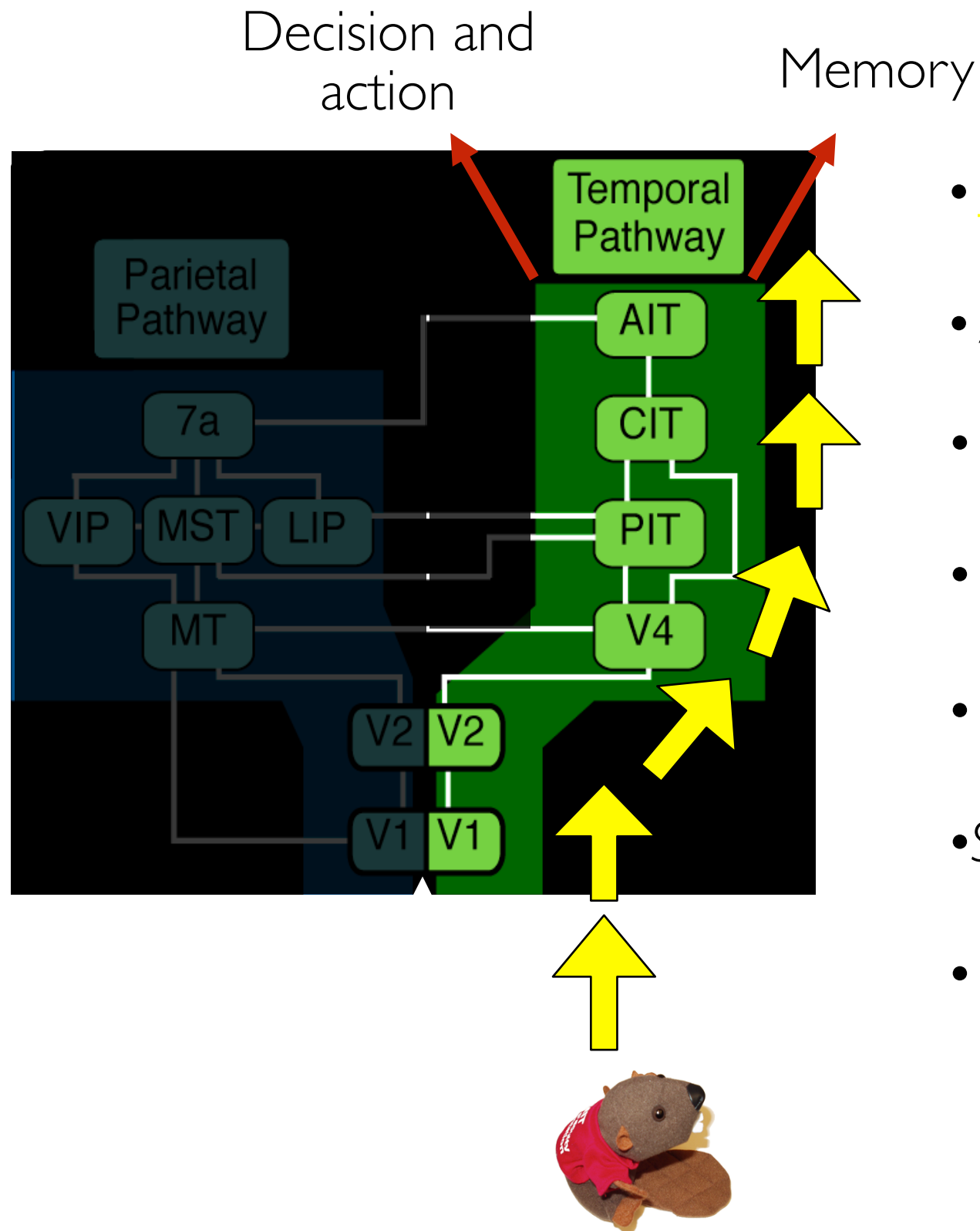
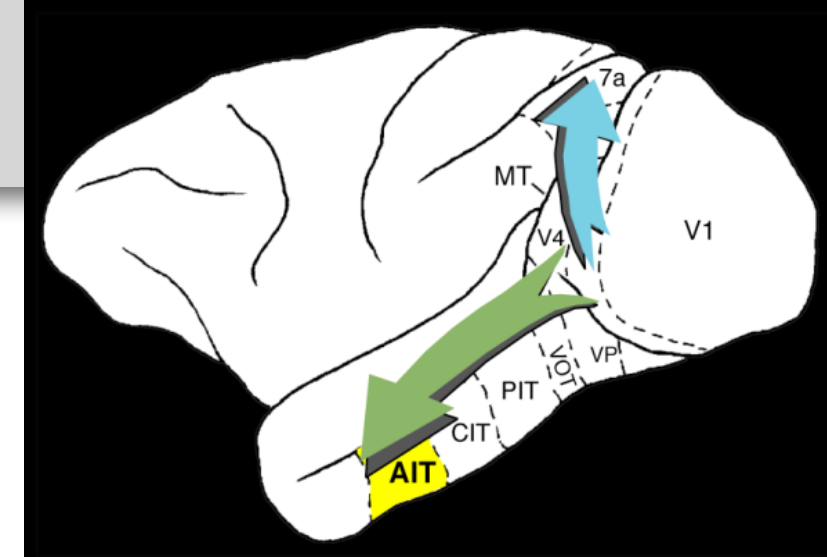
**“where” / dorsal / parietal**

*Lesions in parietal cortex produce  
deficits in landmark task  
(Pohl et al. 1973)*

# Background: Ventral visual stream



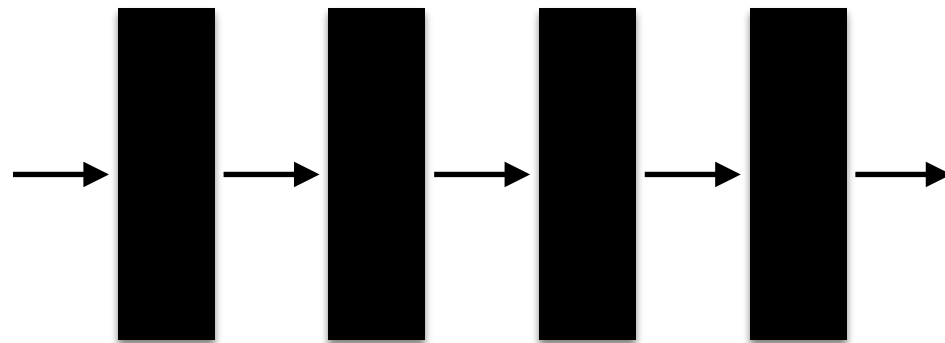
# Background: Ventral visual stream



- Tolerance to identity-preserving transforms
- Ability to support visual recognition
- Correlation with perceptual report
- Sensitivity to behavioral state (e.g. attention)
- Visually-evoked latency
- Selectivity to visual “feature” conjunctions
- Effects of experience (plasticity)

# Sensory cascade

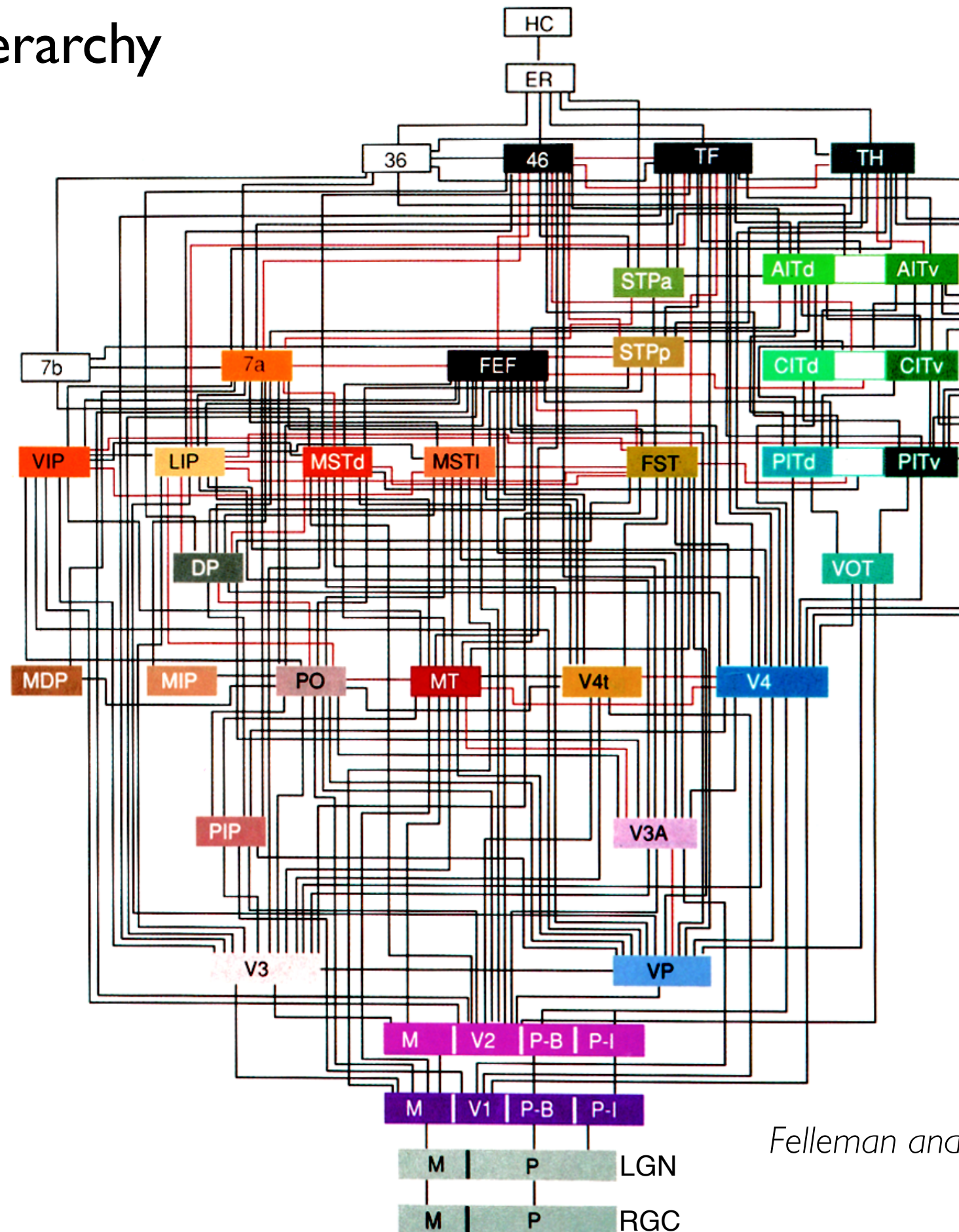
sensory cascade in  
visual (mostly-) cortex



Madame Curie!

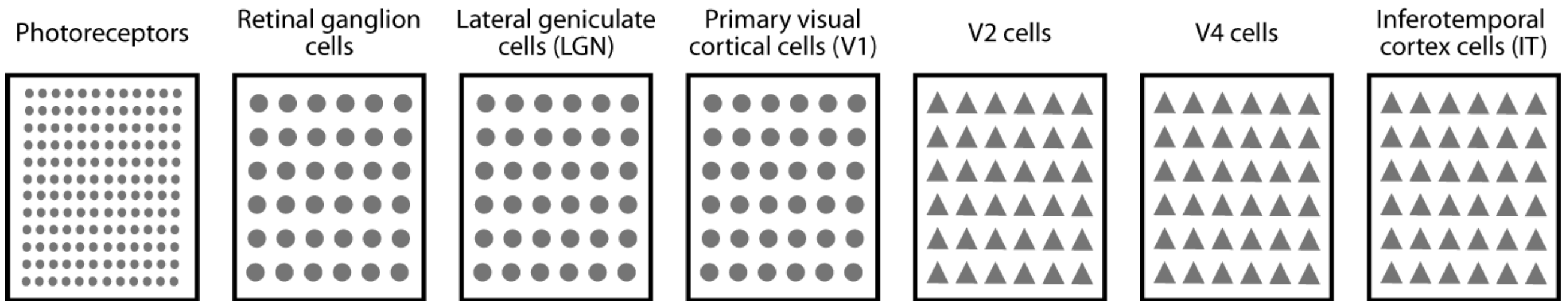


# Visual area hierarchy

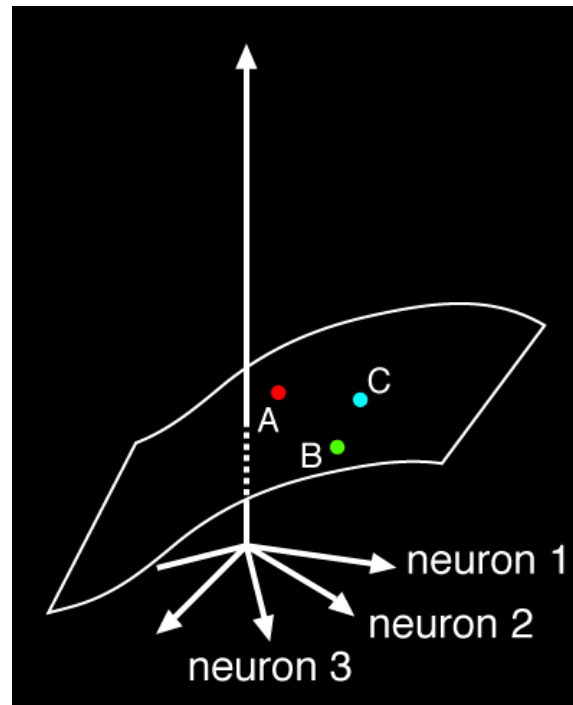


*Felleman and Van Essen, 1991*

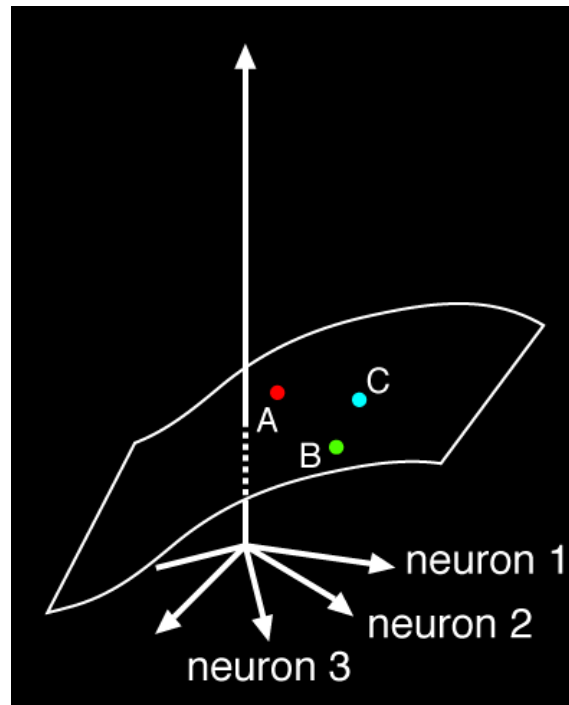
# How does the brain represent the visual world?



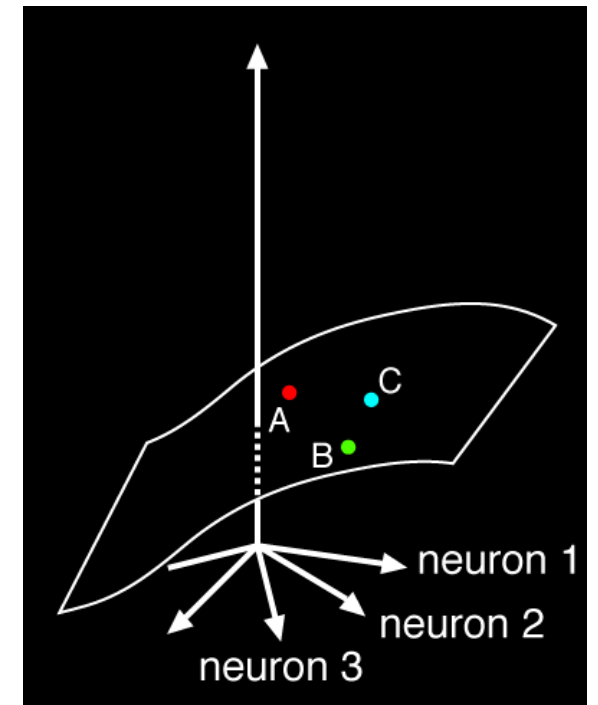
photoreceptor  
representation



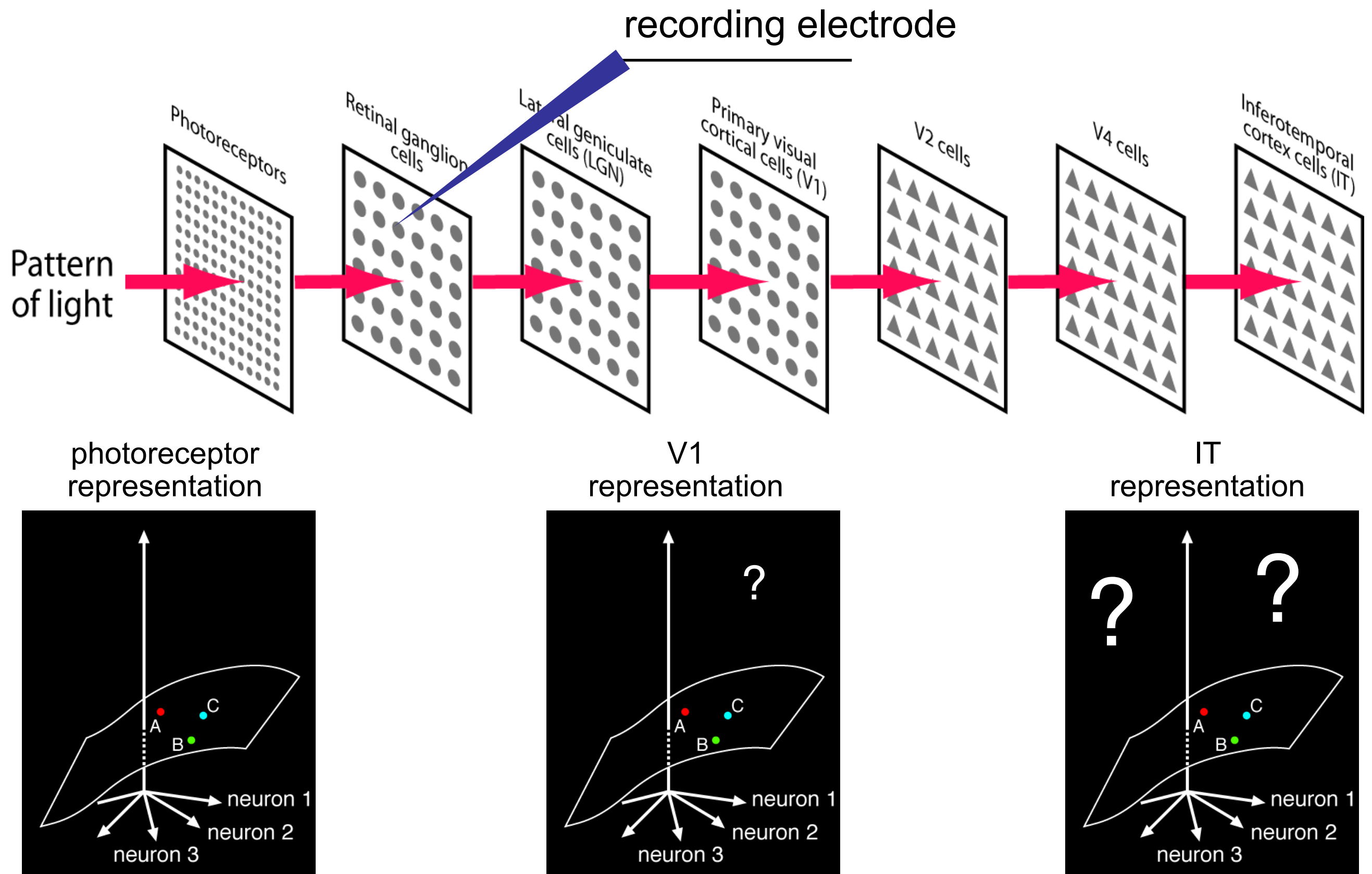
V1  
representation



IT  
representation

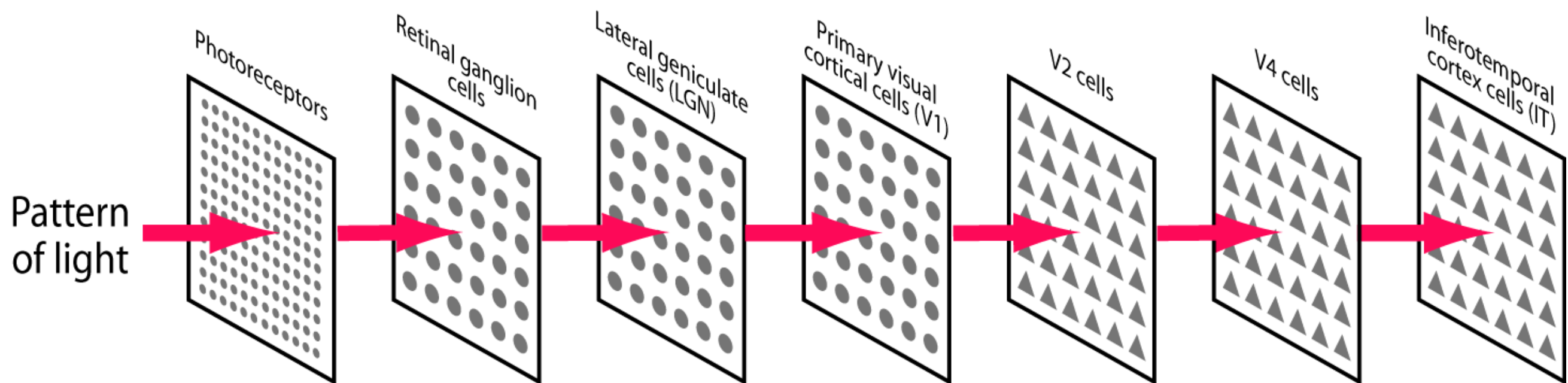


# How does the brain **re-represent** the visual world?

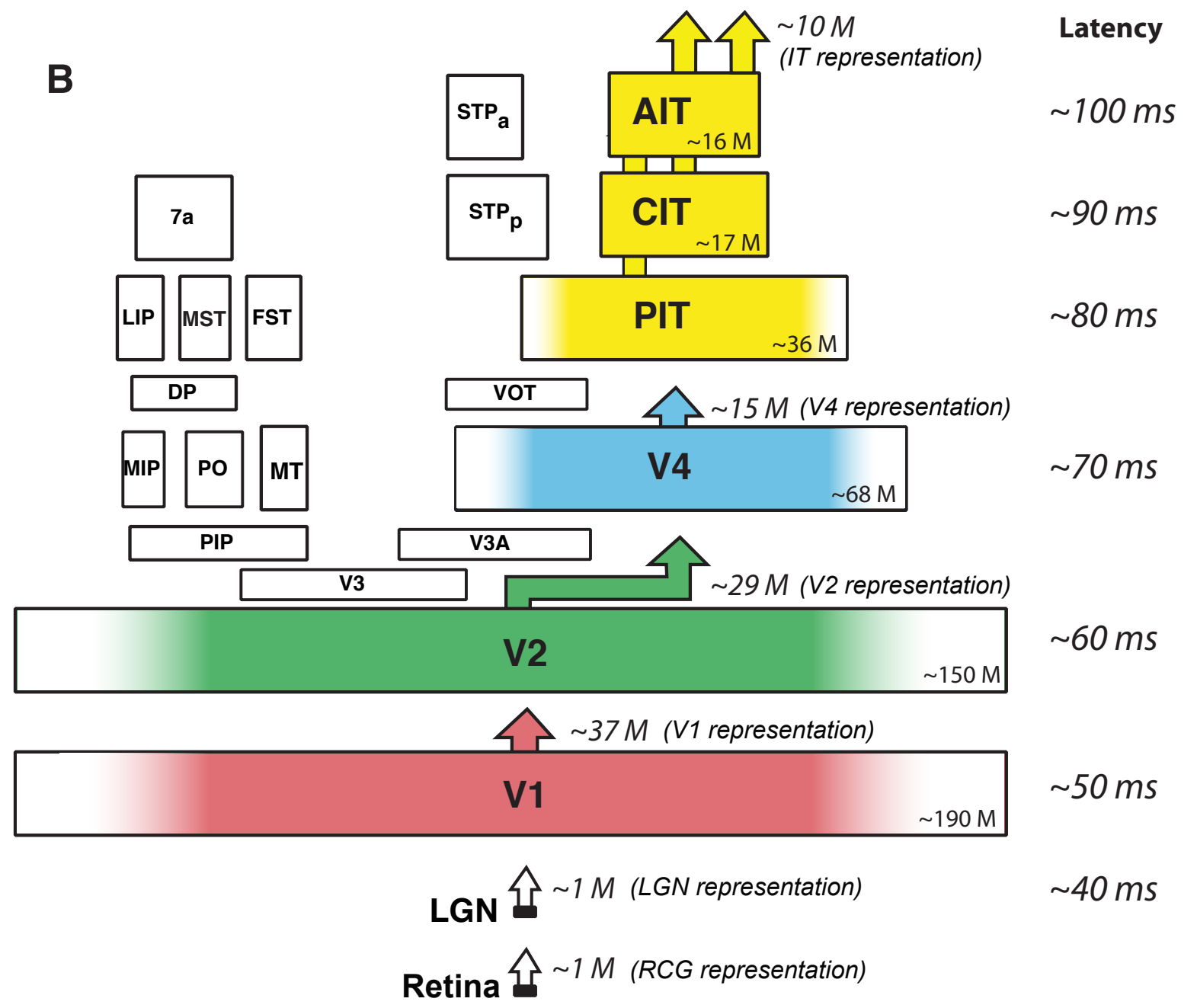
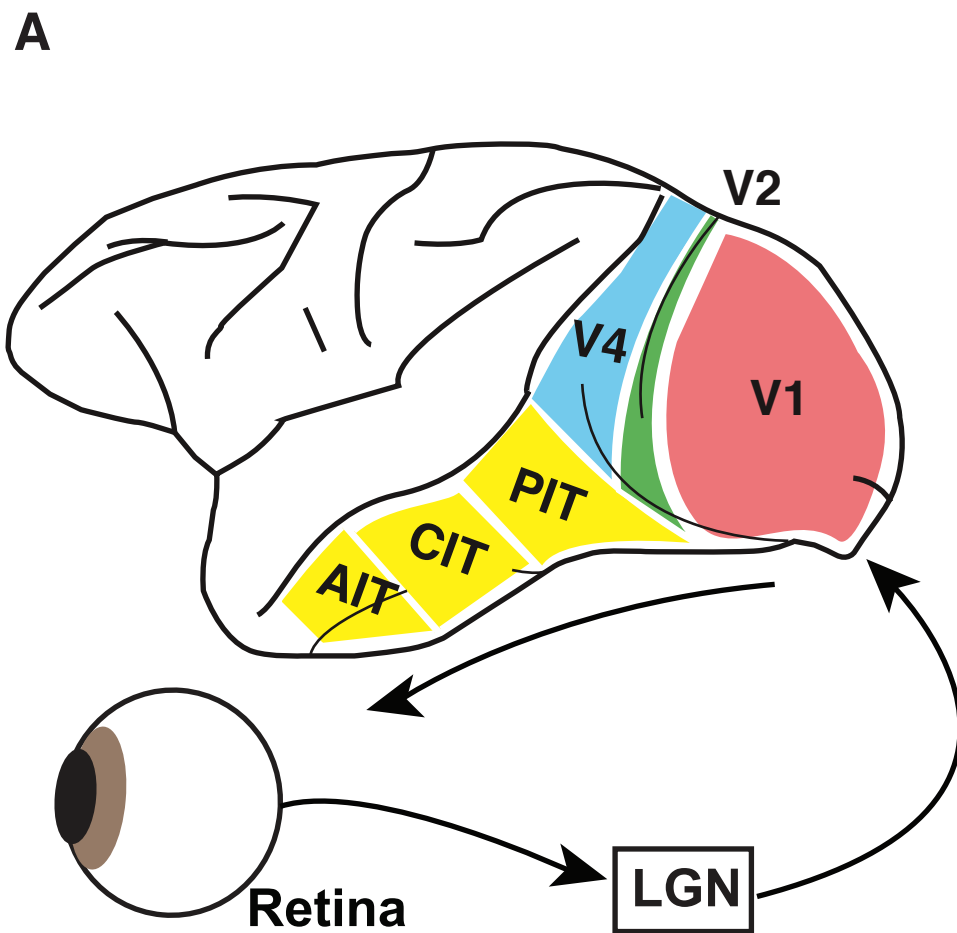


# Four important pieces on information

- 1) Neuronal selectivity generally increases as we move up the cortical hierarchy
- 2) Receptive field (RF) size generally increases as we move up the cortical hierarchy
- 3) Selectivity pattern is typically apparent at the time first spikes are elicited by a visual stimulus (“feedforward” assumption)
- 4) There is hierarchy of times at which first spikes are detected.



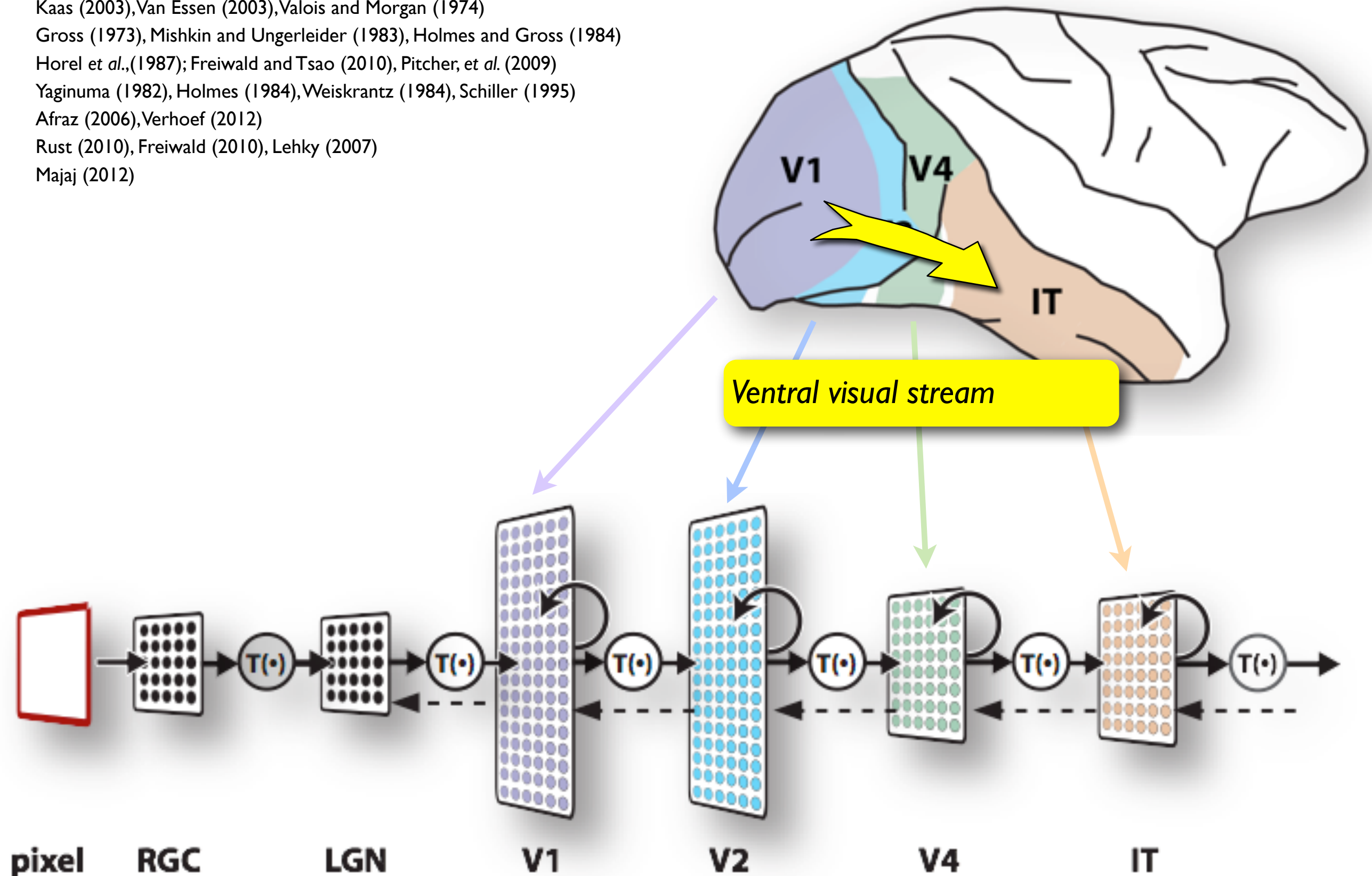




# Background: Ventral visual stream

Kaas (2003), Van Essen (2003), Valois and Morgan (1974)  
Gross (1973), Mishkin and Ungerleider (1983), Holmes and Gross (1984)  
Horel et al., (1987); Freiwald and Tsao (2010), Pitcher, et al. (2009)  
Yaginuma (1982), Holmes (1984), Weiskrantz (1984), Schiller (1995)  
Afraz (2006), Verhoef (2012)  
Rust (2010), Freiwald (2010), Leaky (2007)  
Majaj (2012)

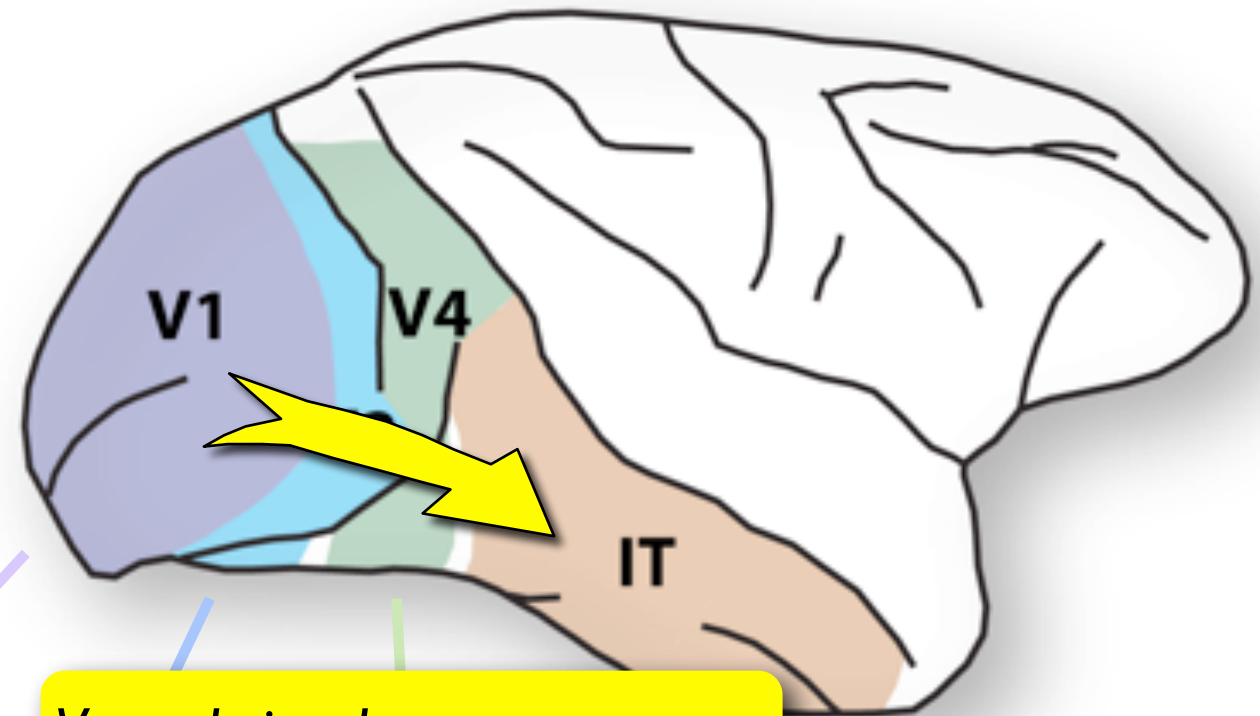
*rhesus macaque (macaca mulatta)*



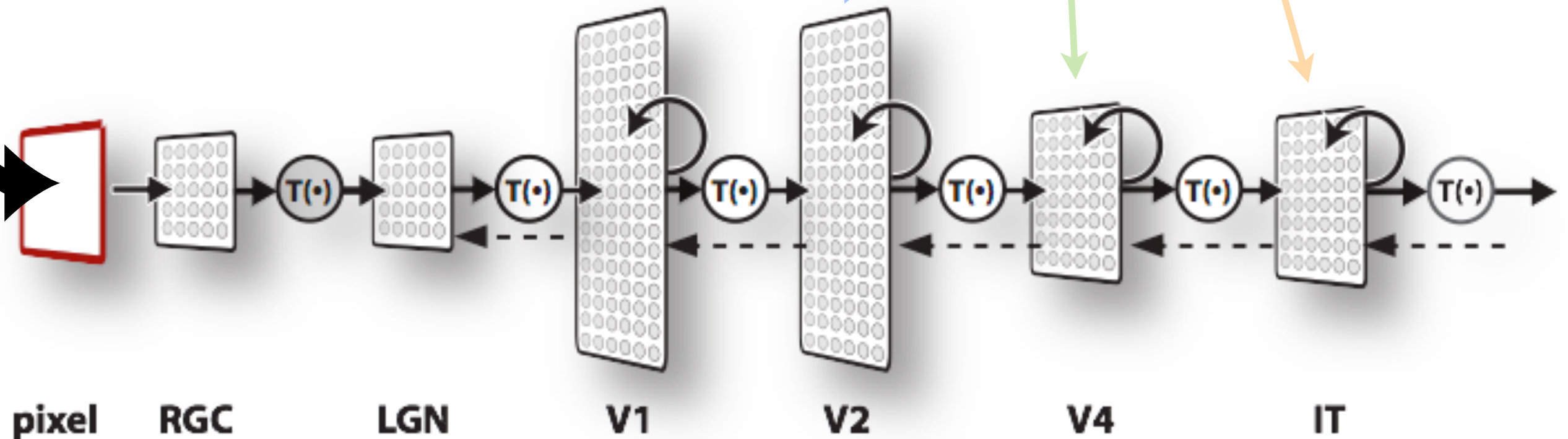
# Background: Ventral visual stream



*rhesus macaque (macaca mulatta)*

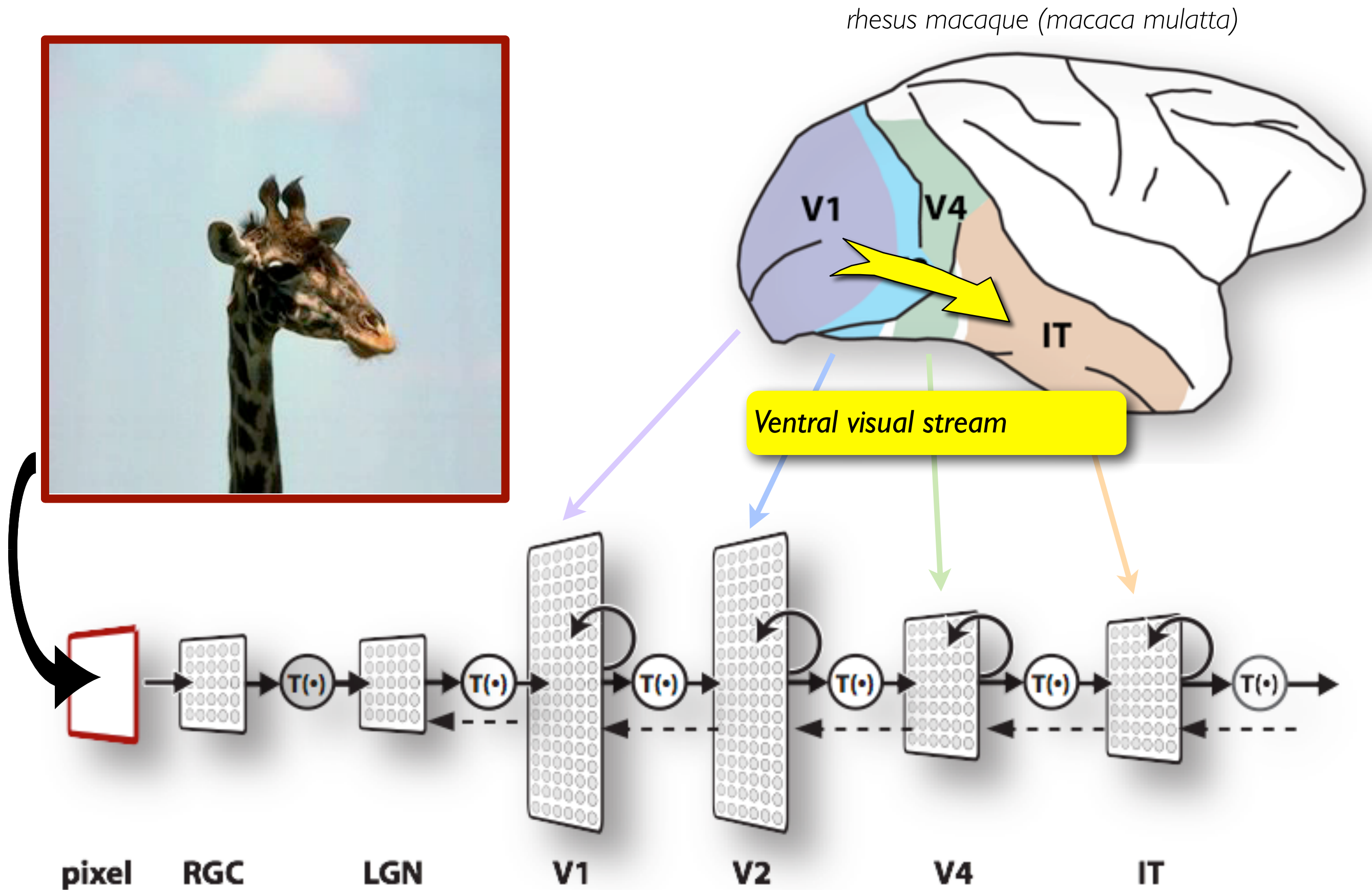


*Ventral visual stream*



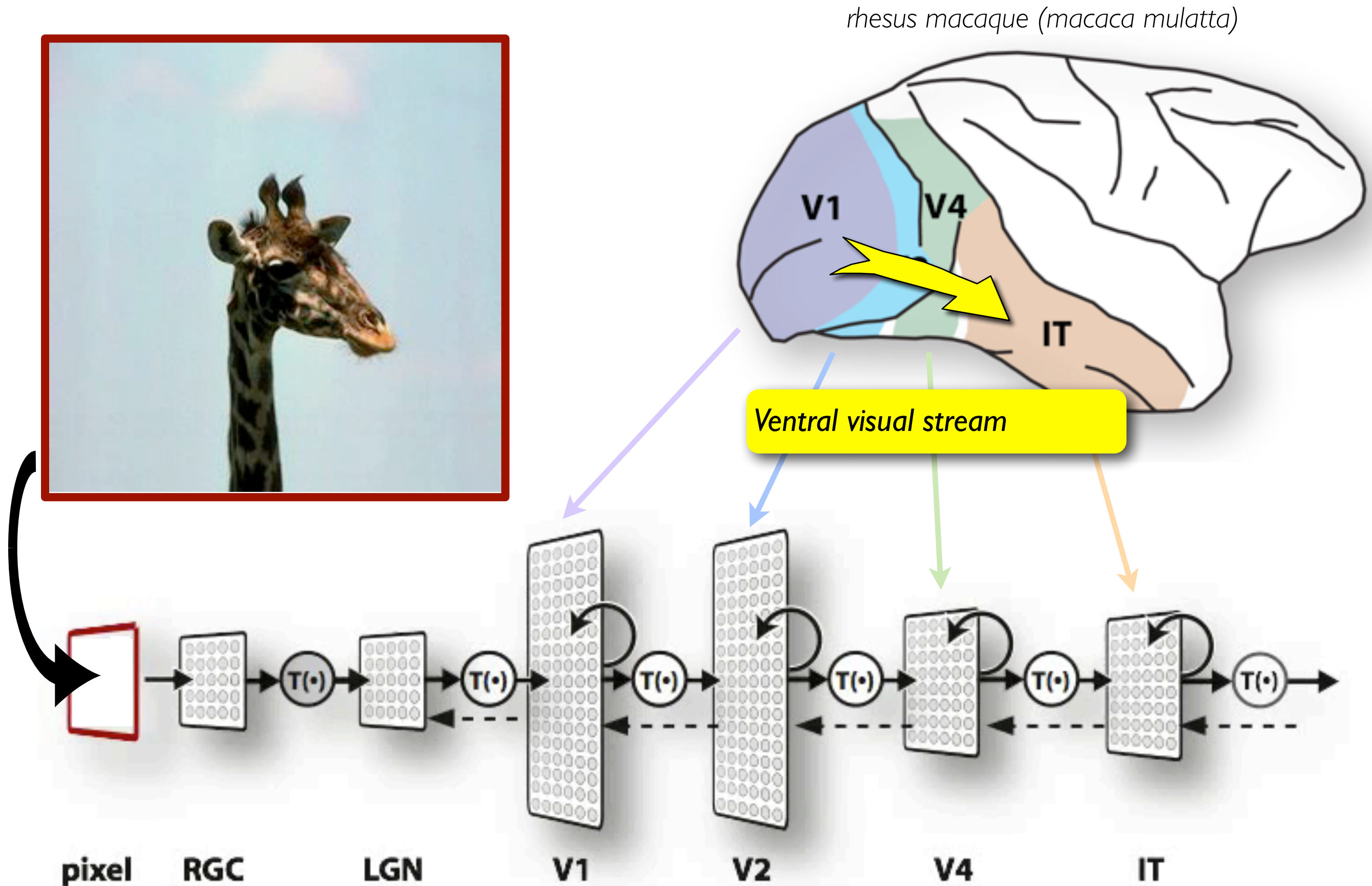


# Background: Ventral visual stream

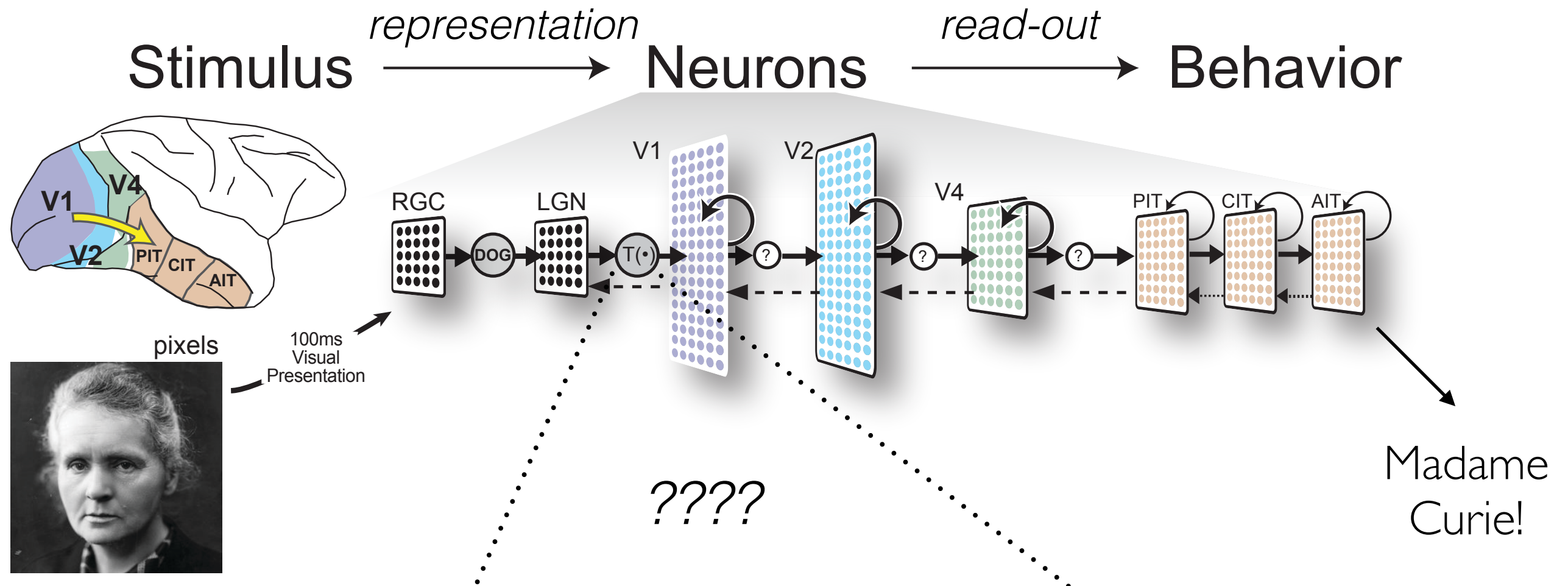




# Background: Ventral visual stream

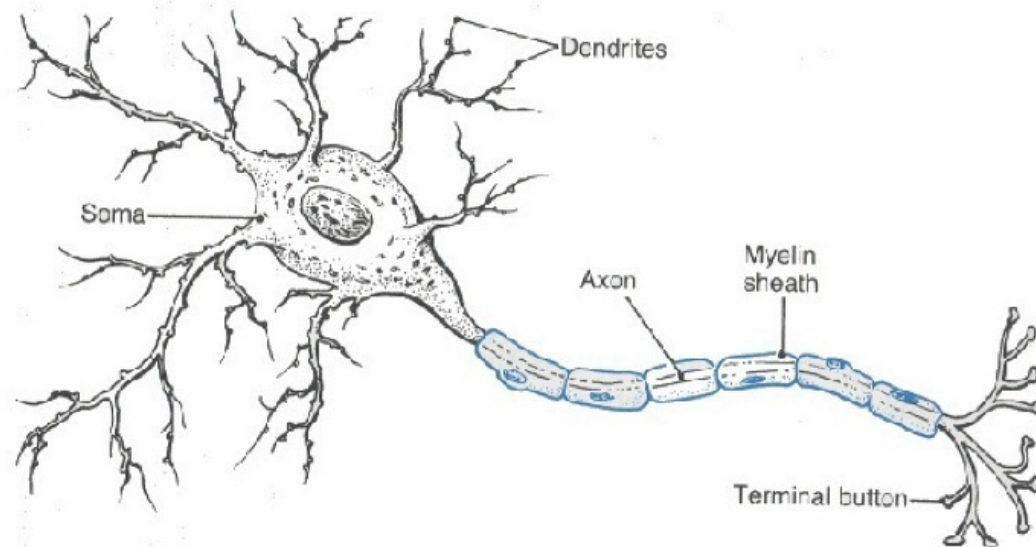


# Ventral Stream = Connected series of brain areas



Recall ...

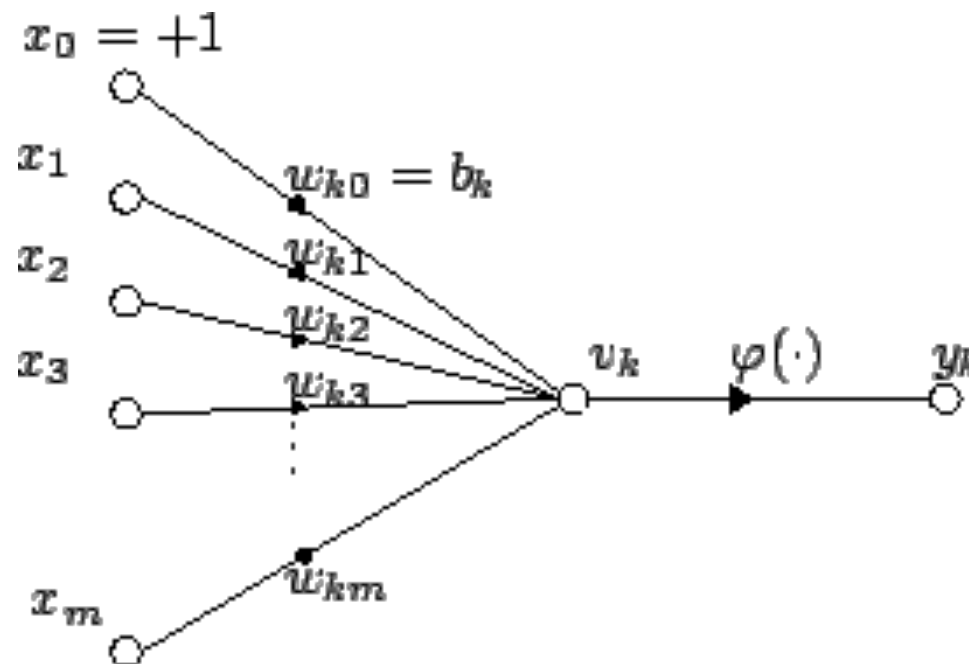
## McCulloch and Pitts (1943)



$$y_k = \phi \left( \sum_{j=0}^m w_{kj} x_j + b_k \right)$$

$$\phi : \mathbb{R} \mapsto \mathbb{R}$$

some nonlinear activation function



$$w_{kj} \in \mathbb{R}^{m+1}$$

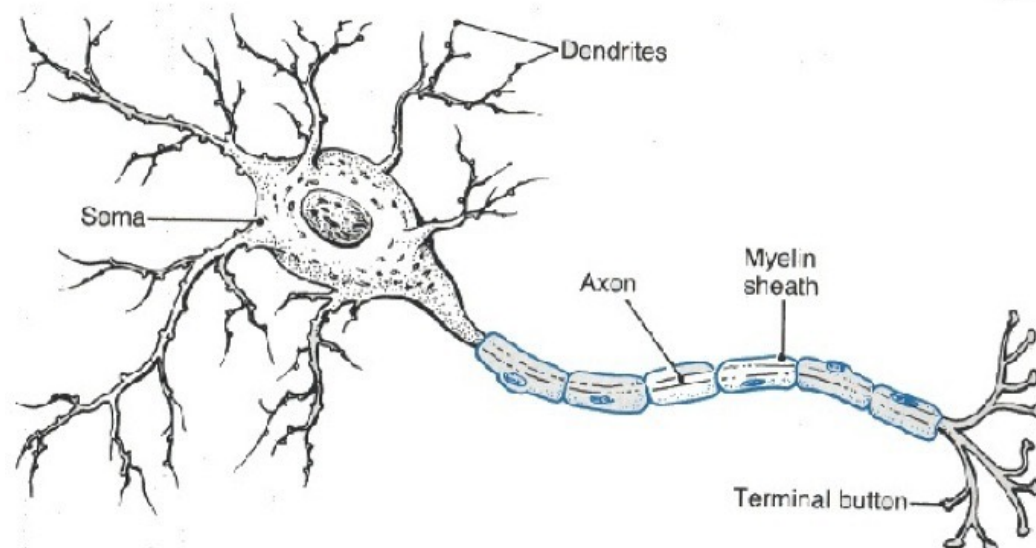
“synaptic strengths”

$$b_j \in \mathbb{R}$$

“biases”

Recall ...

## McCulloch and Pitts (1943)

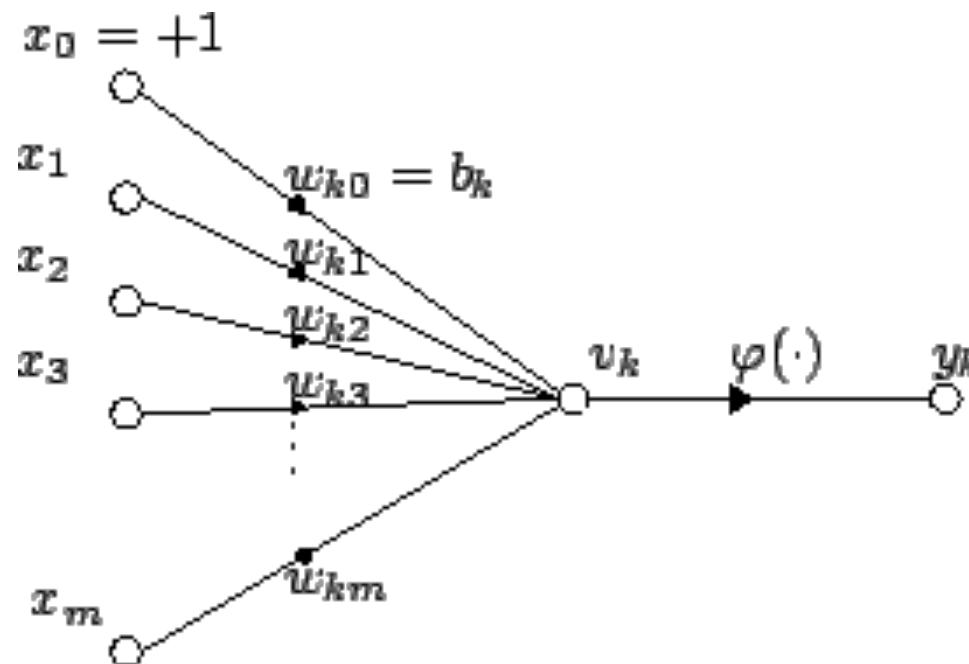


$$y_k = \phi \left( \sum_{j=0}^m w_{kj} x_j + b_k \right)$$

???

$$\phi : \mathbb{R} \mapsto \mathbb{R}$$

some (nonlinear) activation function



???

$$w_{kj} \in \mathbb{R}^{m+1}$$

“synaptic strengths”

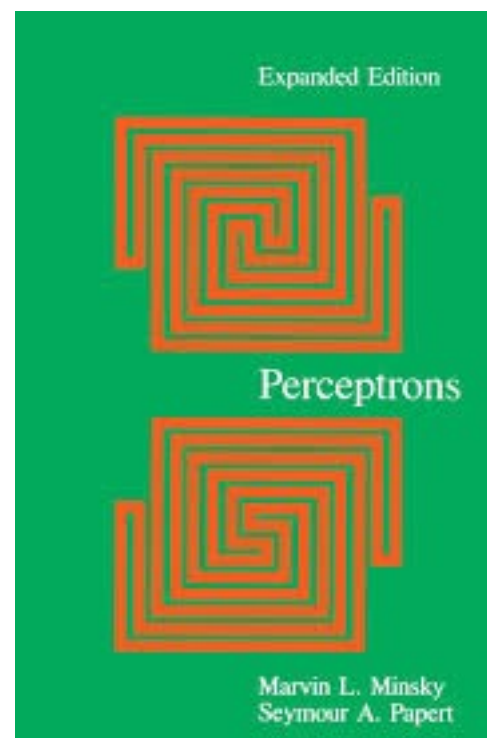
$$b_j \in \mathbb{R}$$

“biases”

**and what's the  
connectivity?**

# Cautionary tale

Minsky & Papert (1969)



$$y_k = \phi \left( \sum_{j=0}^m w_{kj} x_j + b_k \right)$$

$$\phi : \mathbb{R} \mapsto \mathbb{R}$$

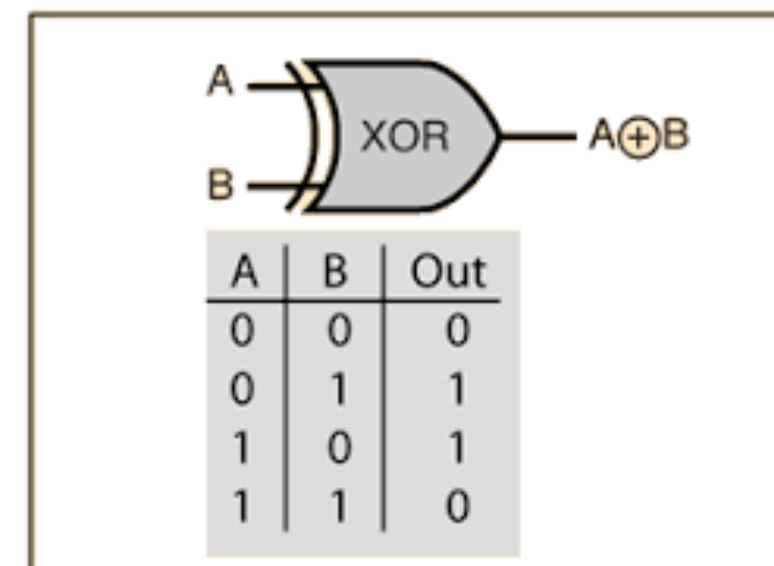
**1. better have more than one layer**

$$\sum_{i=0}^N v_i \phi(w_i^T x + b_i) \text{ at least (and which, according to the UAT, is enough)}$$

**cause otherwise ... ain't no XOR**

**and what's the connectivity?**

**2. better be actually nonlinear**





## Limitations of Perceptrons



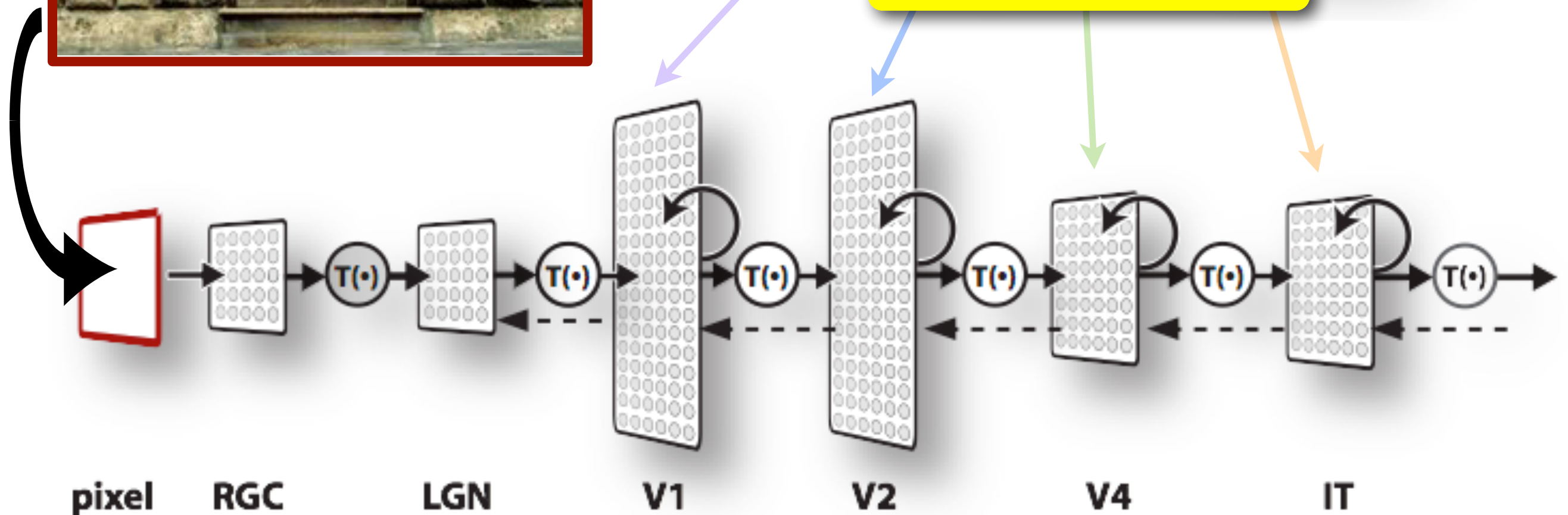
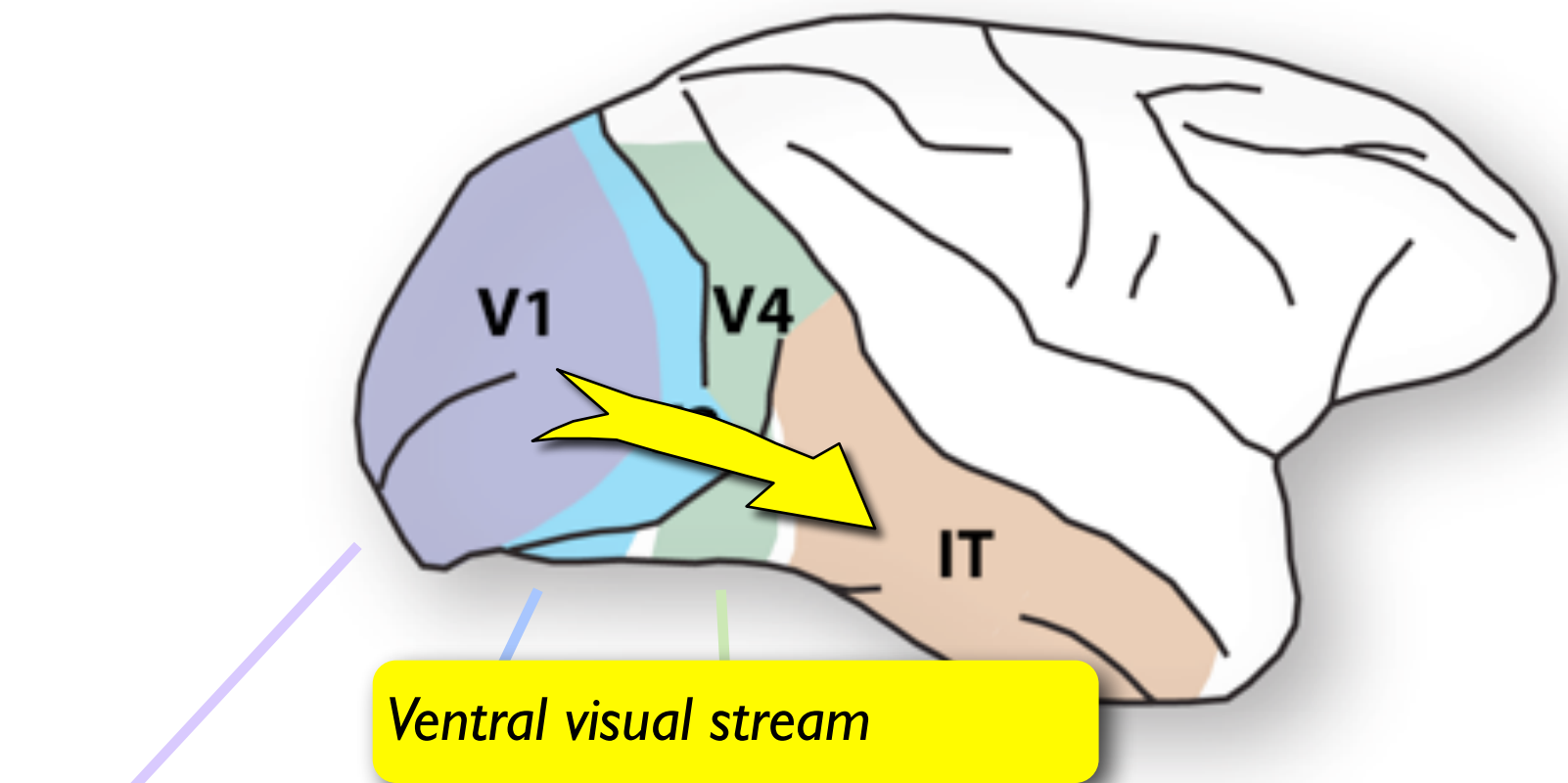
- ***Minsky & Papert published (1969) “Perceptrons” stressing the limitations of perceptrons***
- ***Single-layer perceptrons cannot solve problems that are linearly inseparable (e.g., xor)***
- ***Most interesting problems are linearly inseparable***
- ***Kills funding for neural nets for 12-15 years***

UNIVERSITY  
of VIRGINIA

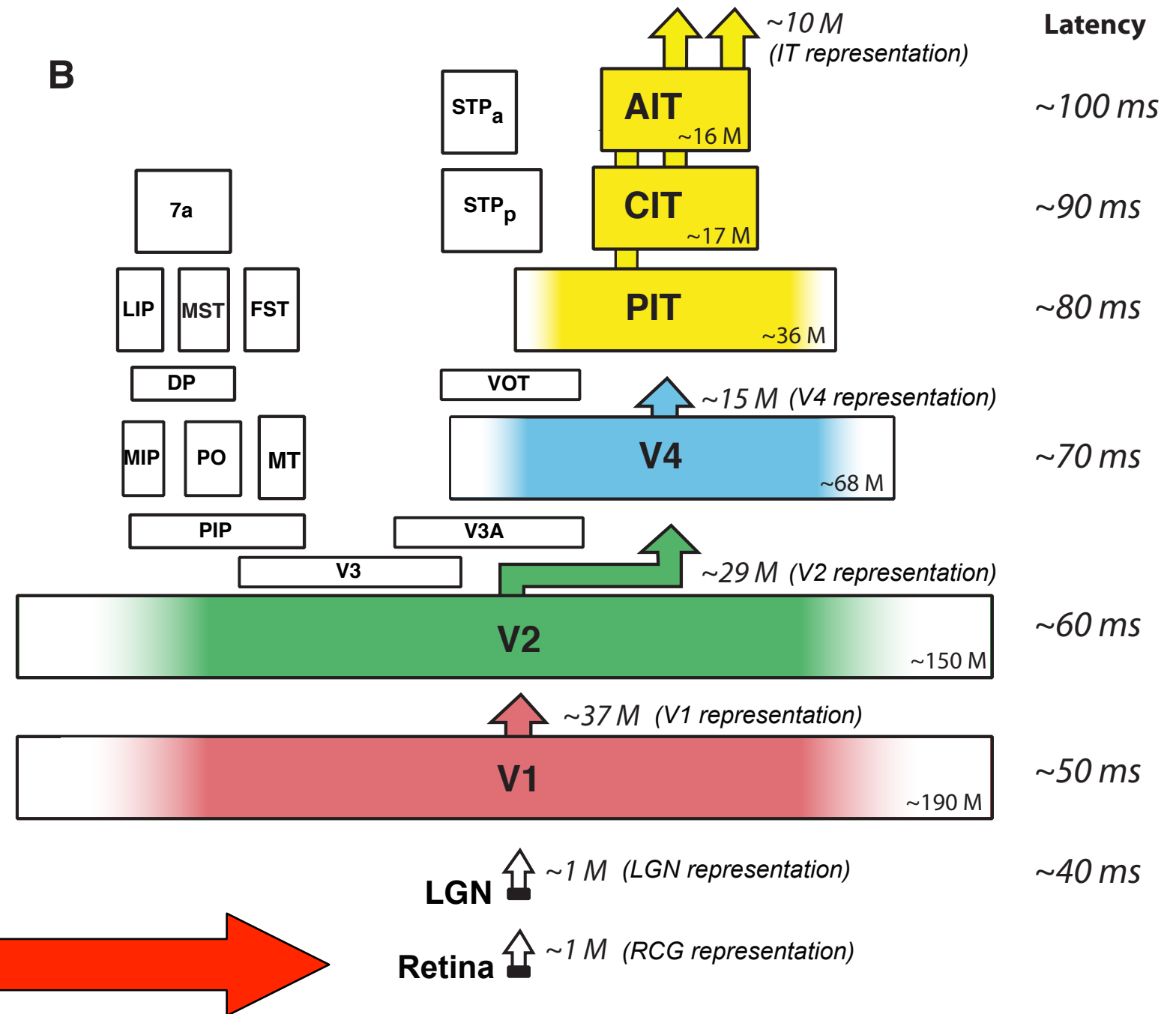
Maybe a bit apocryphal .... but I can definitely say from personal experience that MIT CSAIL felt very “anti-neural networks” as late as 2012

Ventral Stream = Connected series of brain areas

neuroanatomy + neurophysiology tell us:

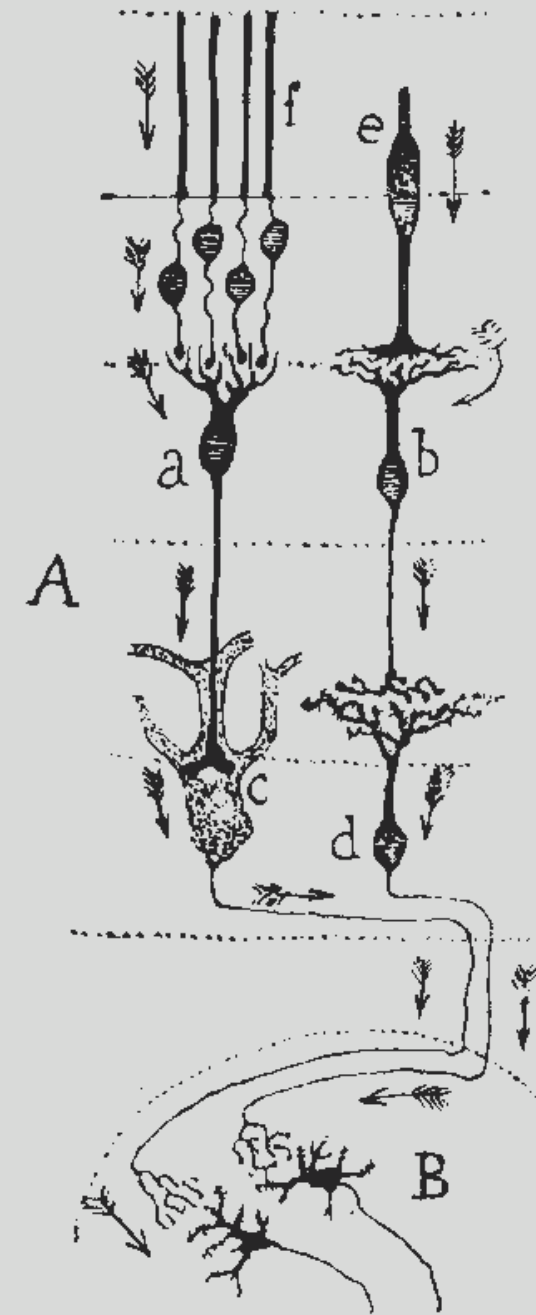


**B**





# Origins in the Retina



**Ramon y Cajal** from Rodieck  
(1973)

# Origins in the Retina

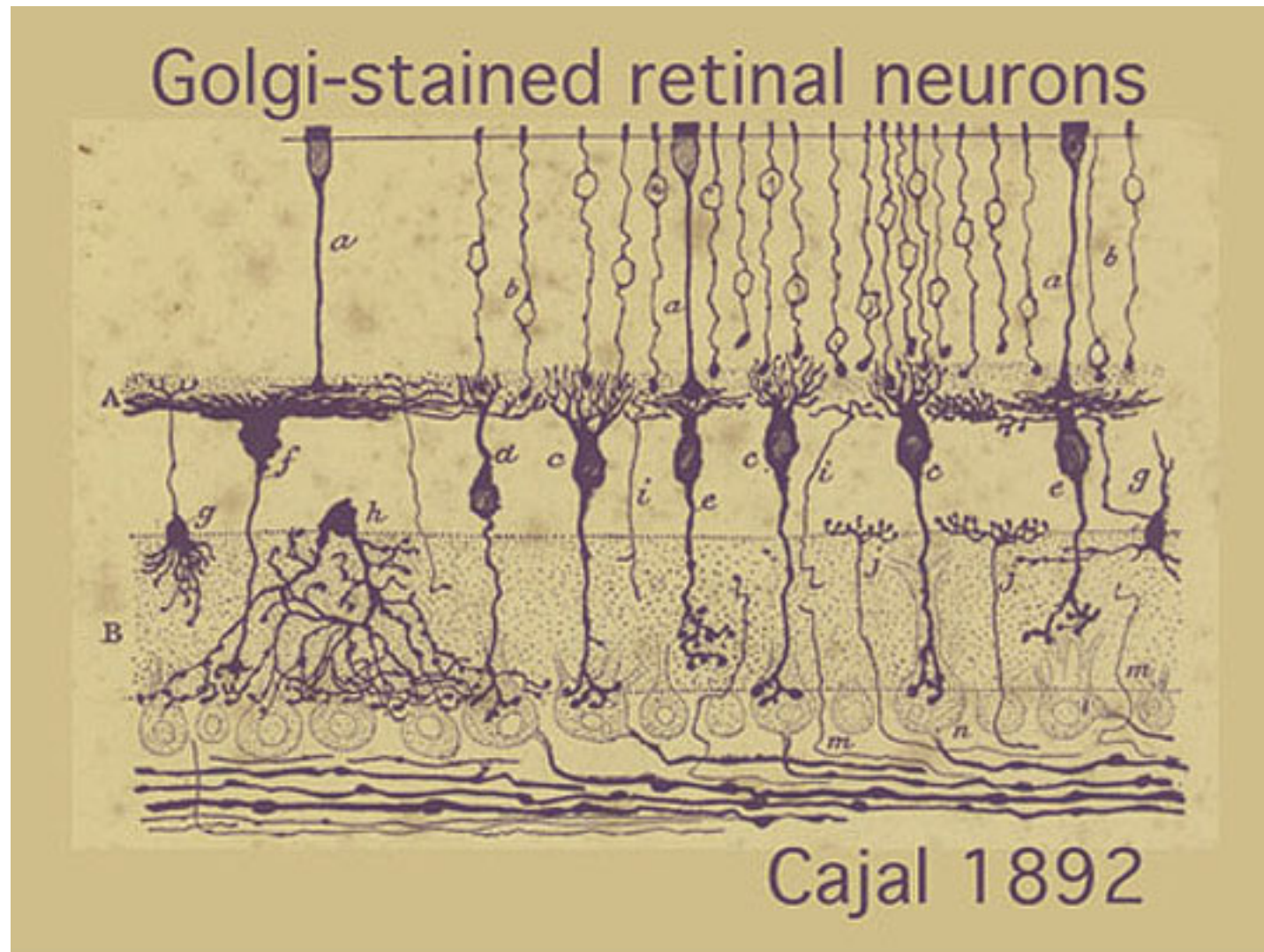
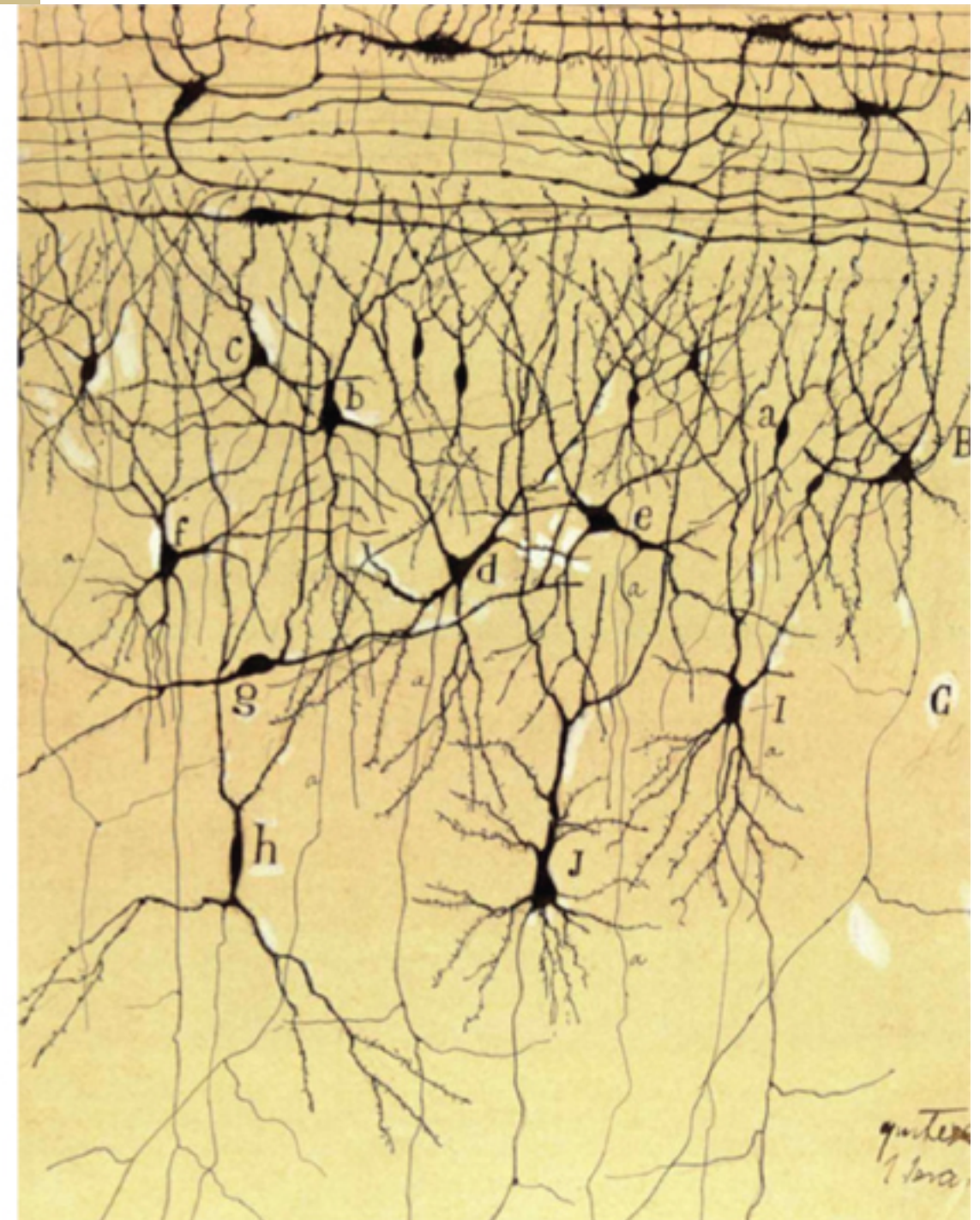


Fig. 2. A drawing done by Cajal to show some of the neurons of the retina in vertical section.

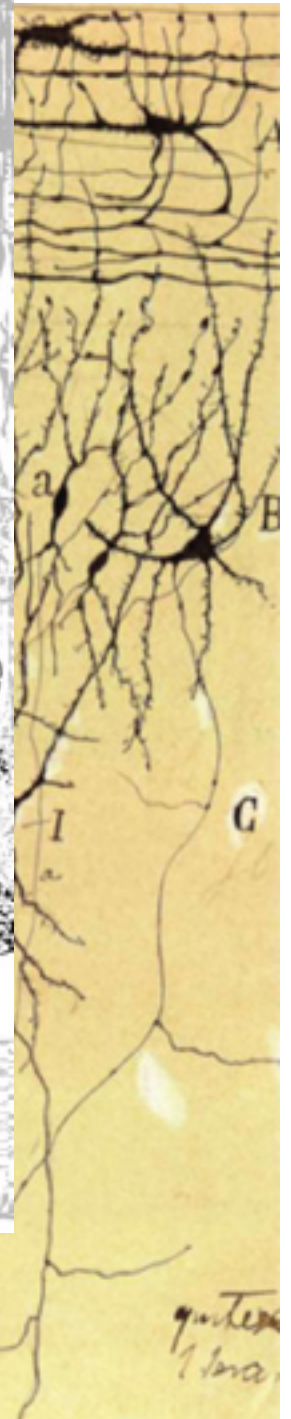
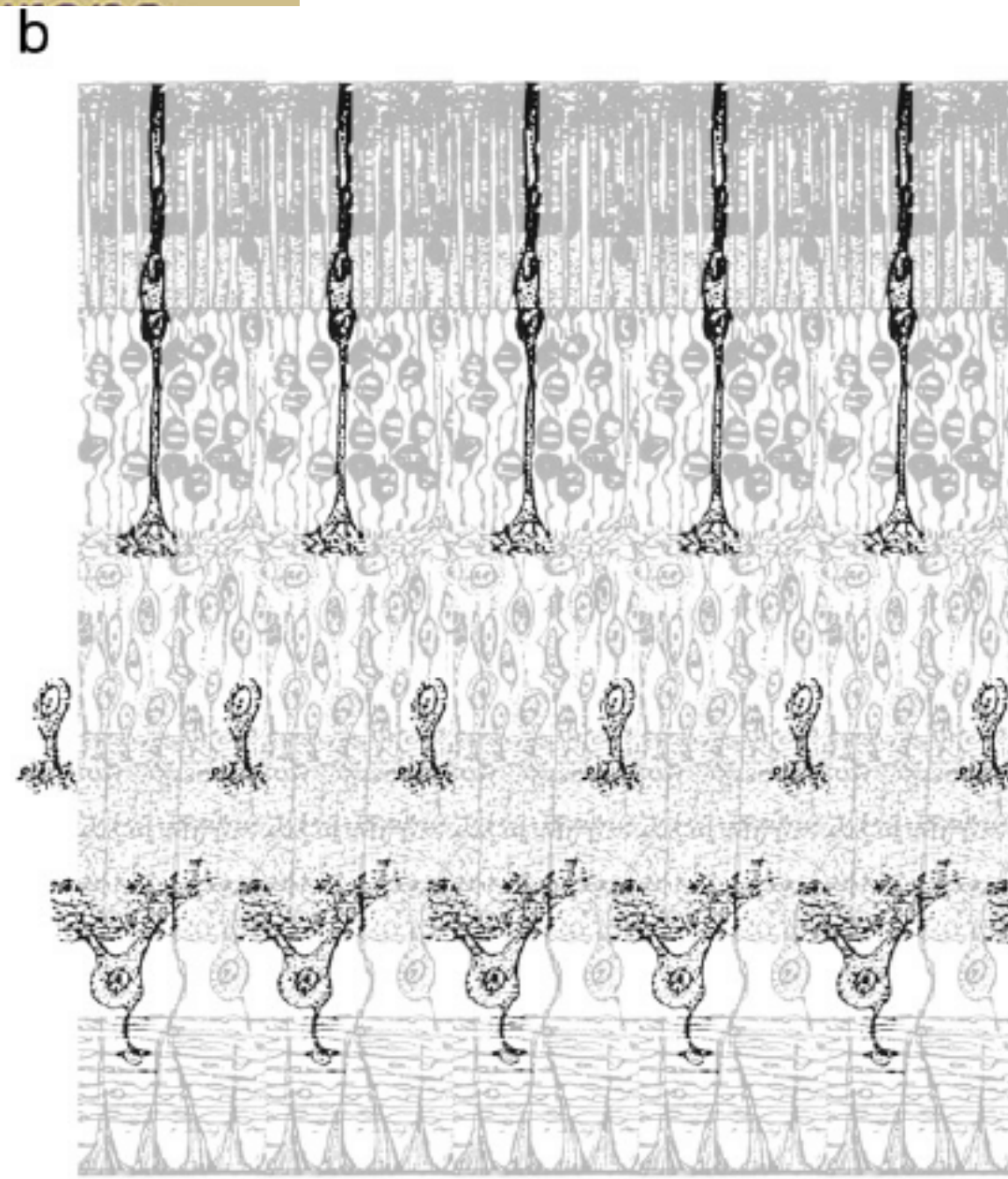
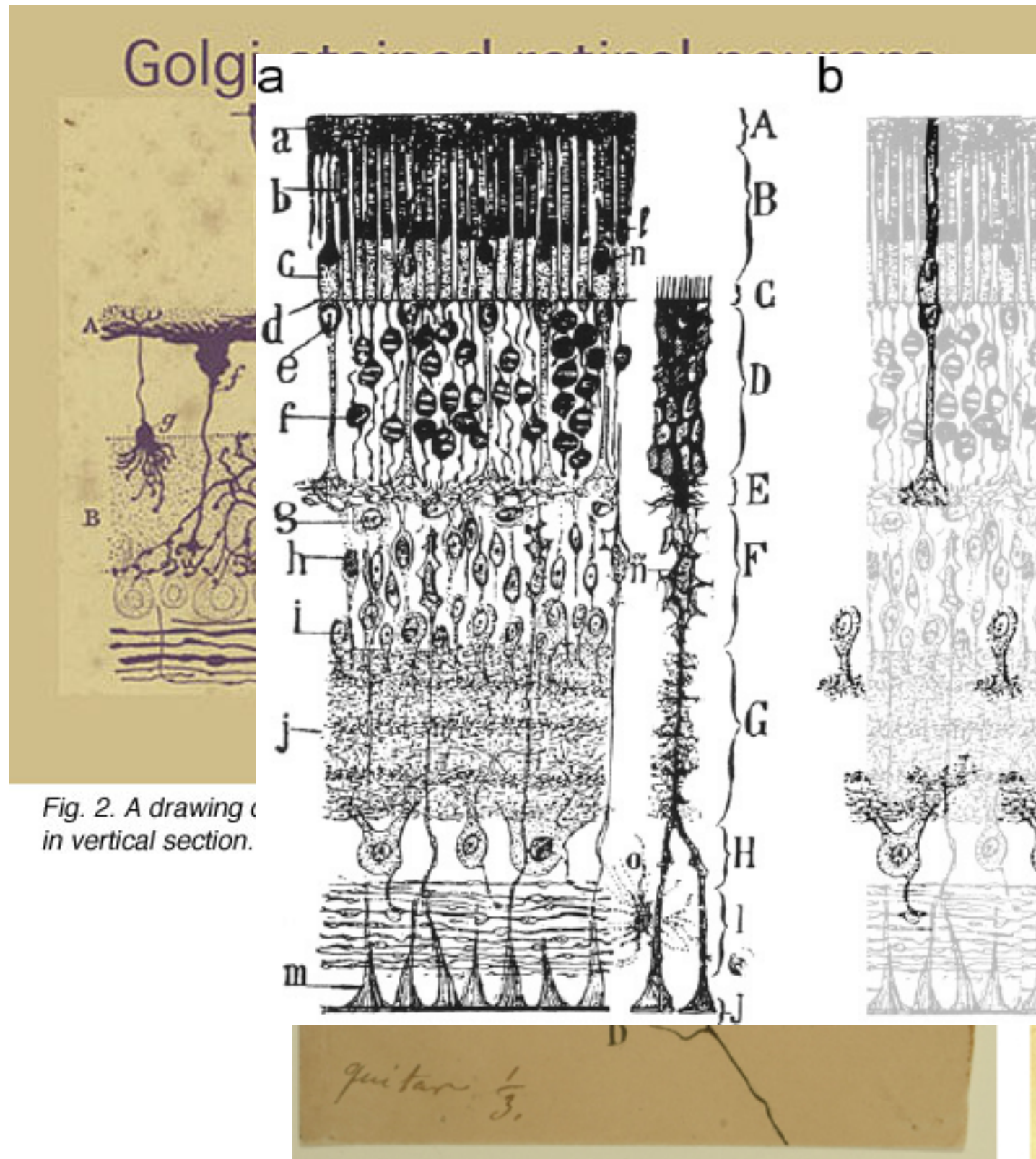


# Origins in the Retina



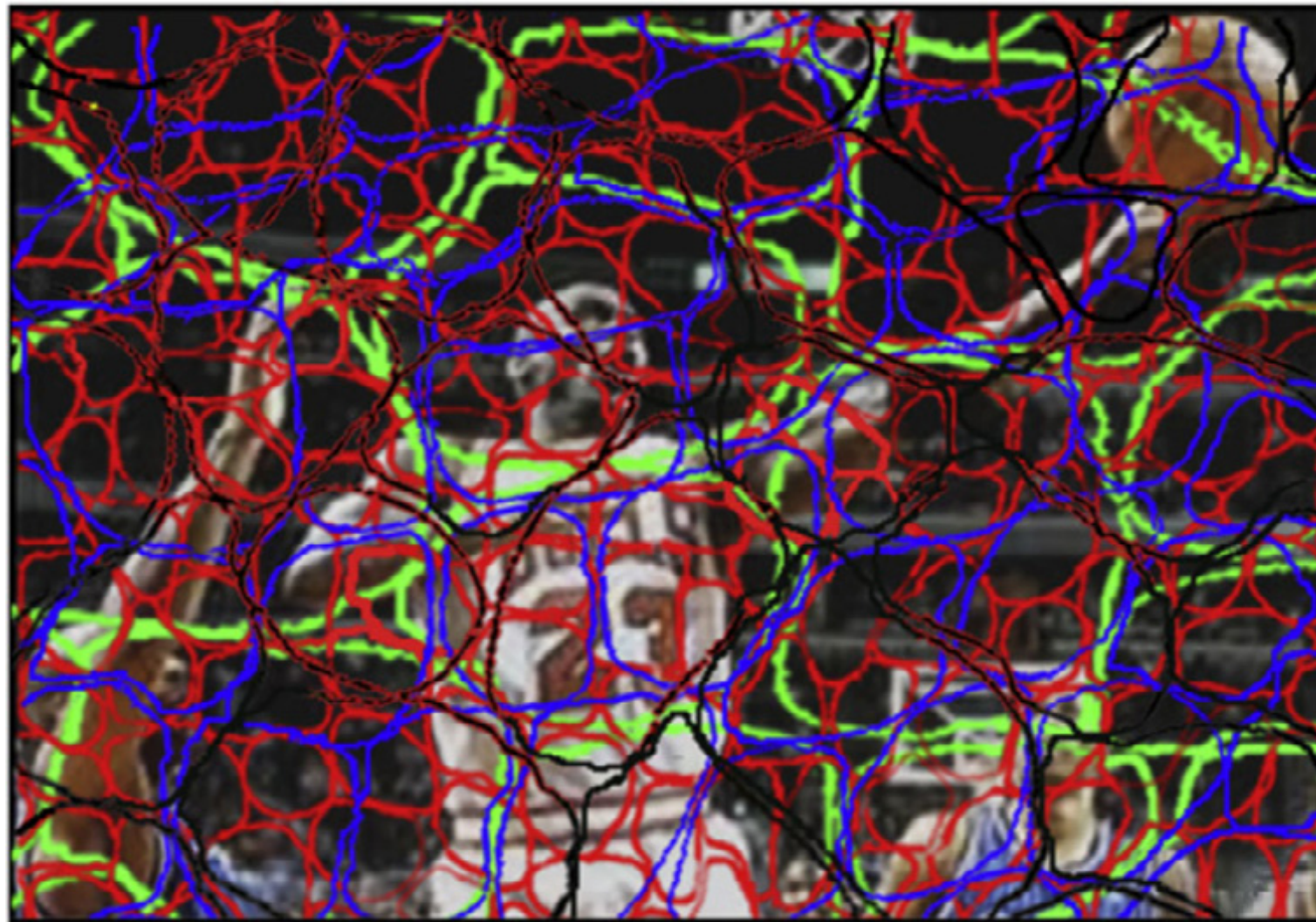


# Origins in the Retina





# Origins in the Retina



(a)



(b)



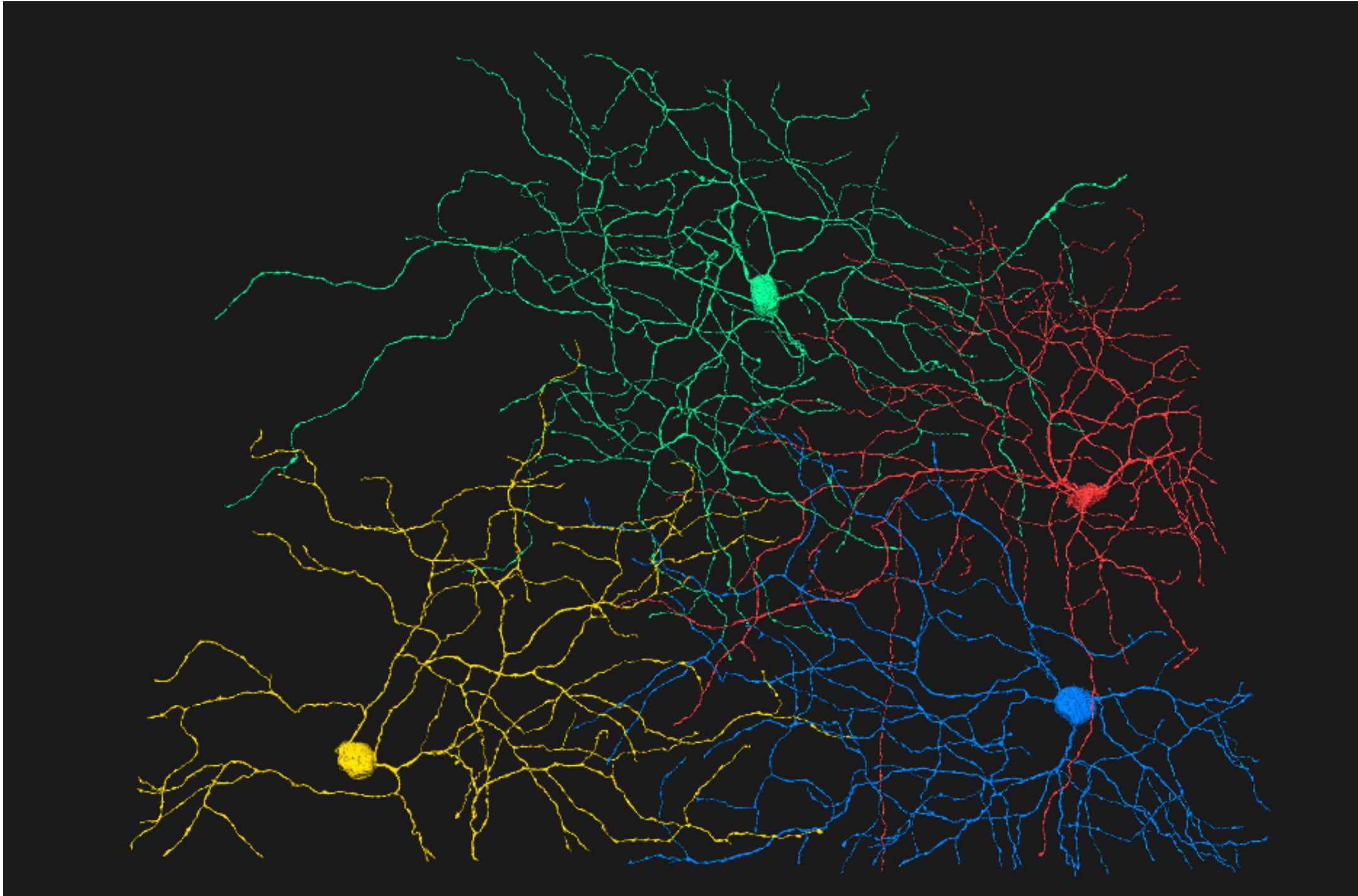
(c)



(d)

*Masland (2012)*

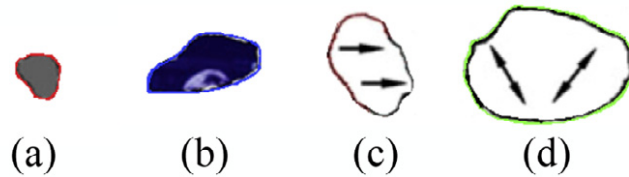
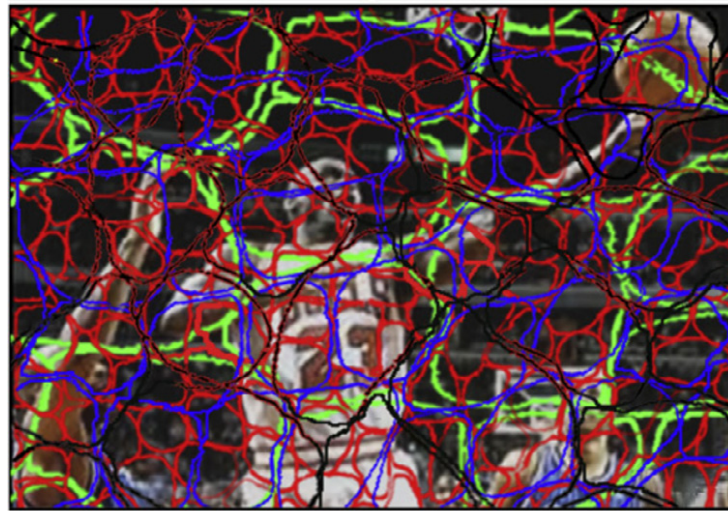
# Origins in the Retina



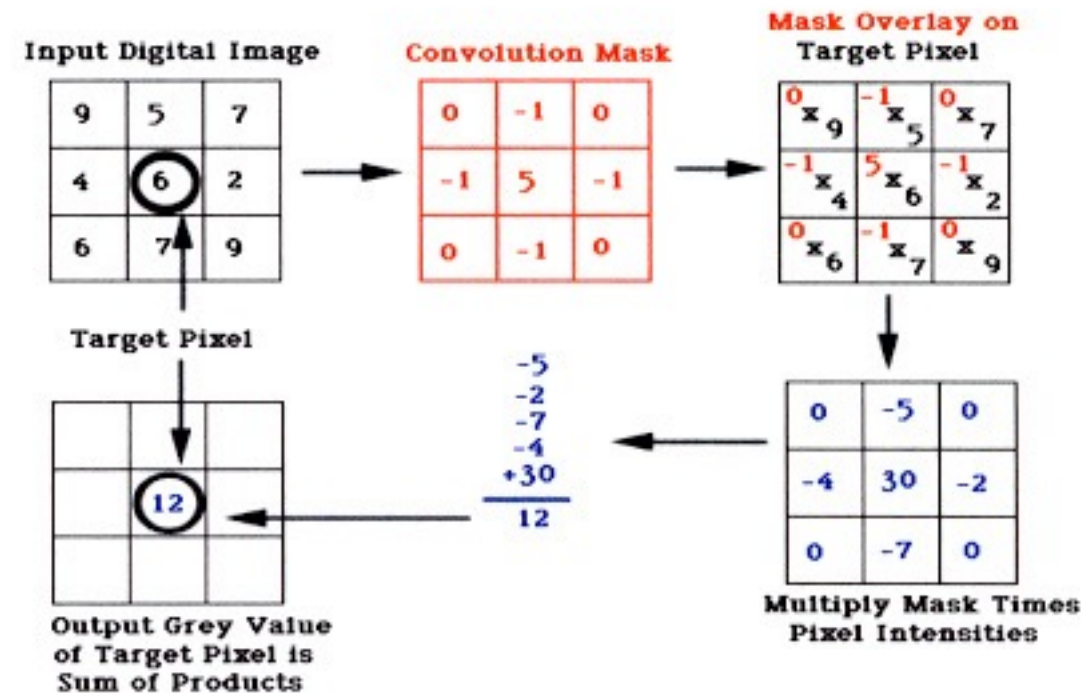
<http://museum.eyewire.org>



# Origins in the Retina



## SPATIAL CONVOLUTION



1. The convolution mask is overlaid on the original image so that the center pixel of the mask is matched with a pixel location on the image (Target Pixel- to be convolved).
2. Each pixel value in the original image is multiplied by the corresponding value in the overlying mask..
3. The grey value of the target pixel is replaced by the sum of all the products in the second step.
4. The operation is repeated for each pixel in the original image (the mask scans the entire image) and each pixel is replaced by the weighted average of its 3 x 3 neighbors.

# Origins in the Retina

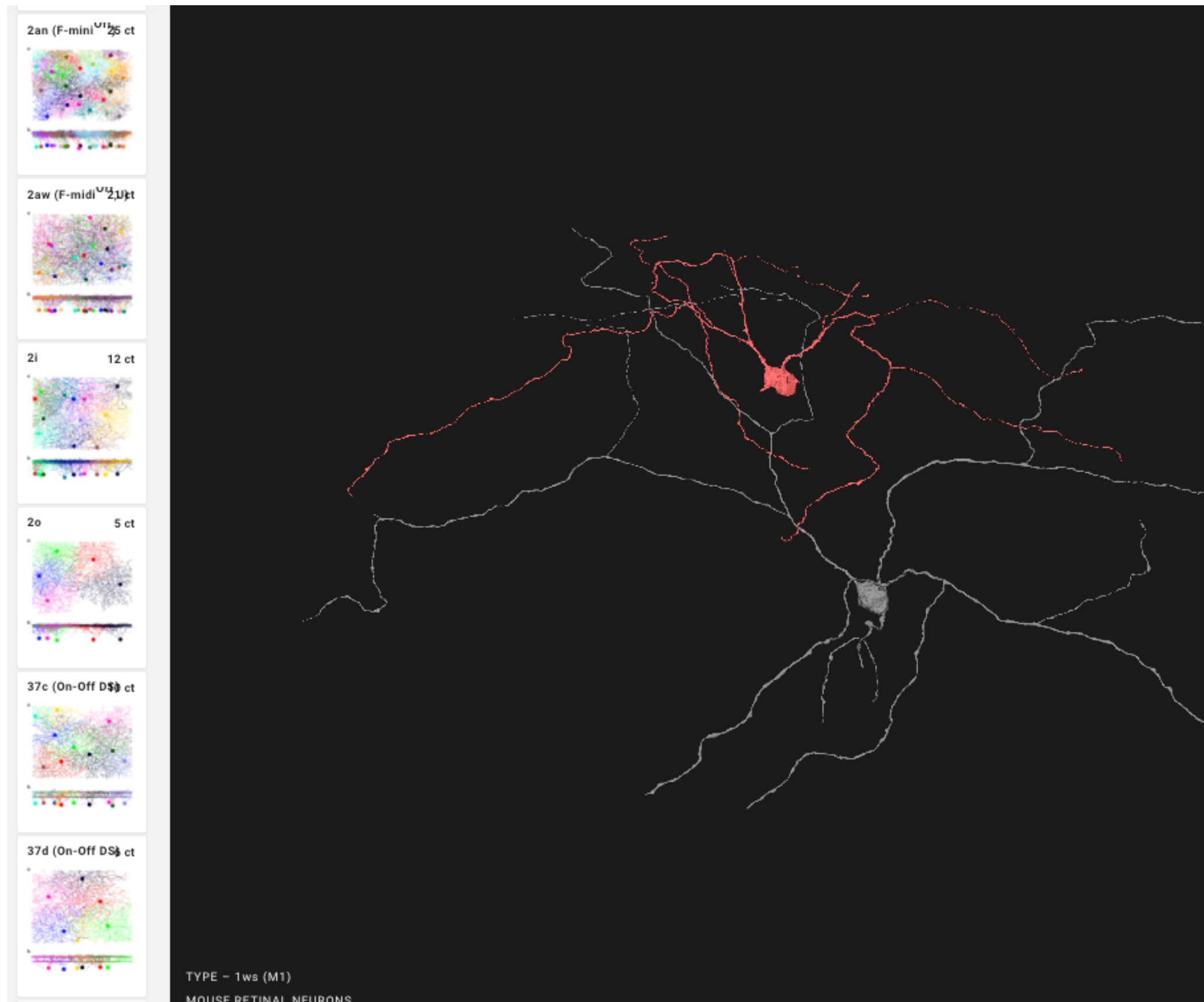
*cell types  
like different  
filters in a  
filterbanks*

.

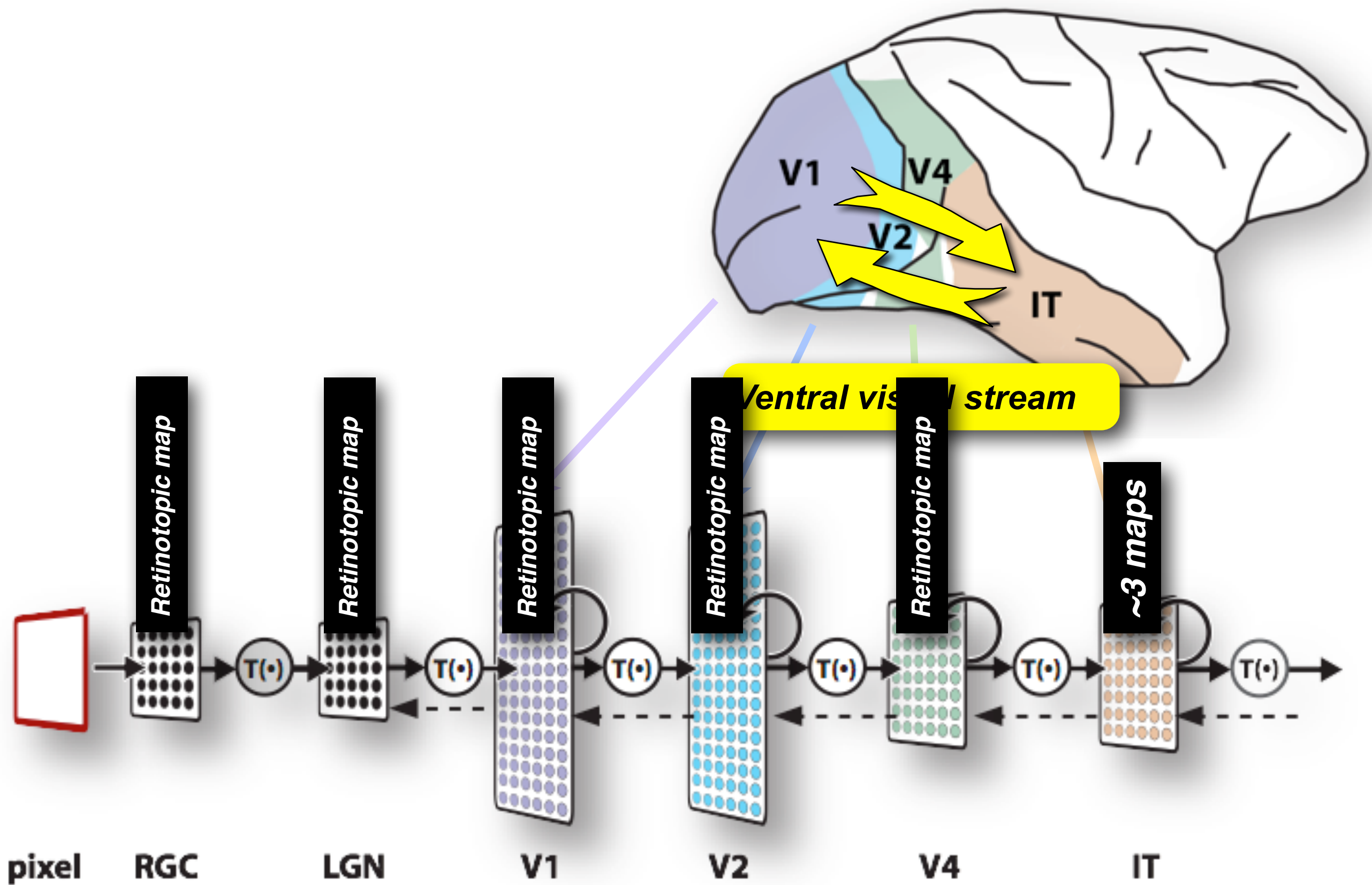
.

.

*but which  
filters?*

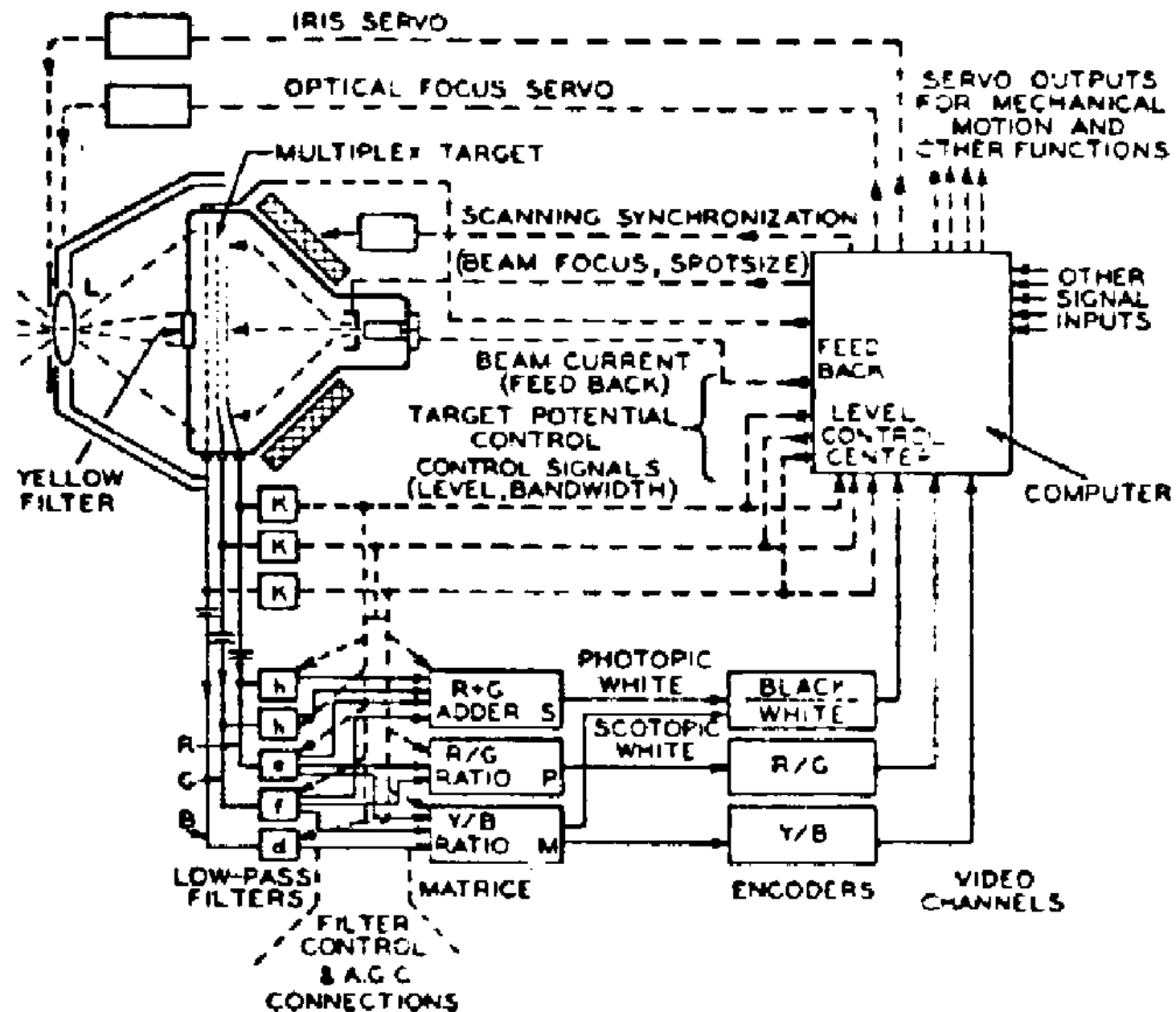






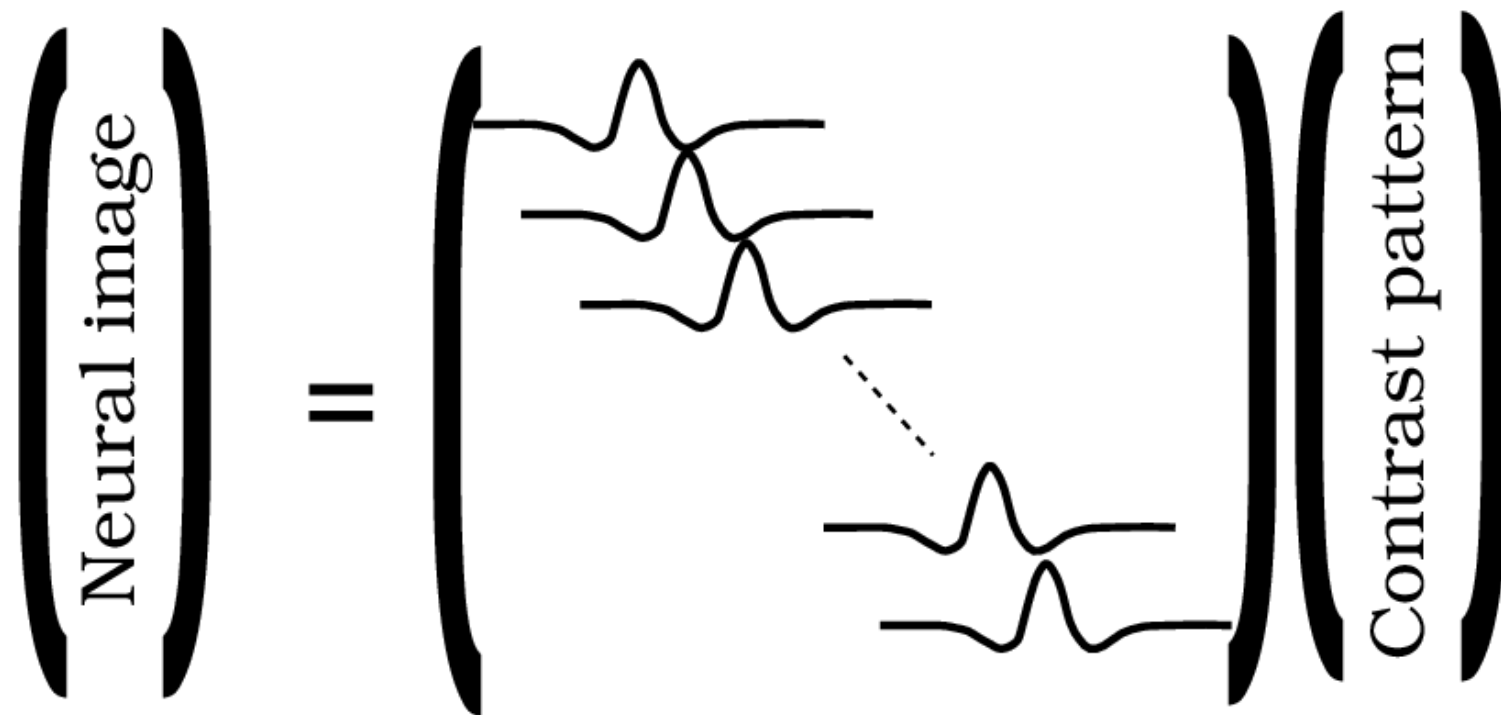
# Origins in the Retina

characterizing a *transfer function* ...



# Origins in the Retina

characterizing a *transfer function* ...



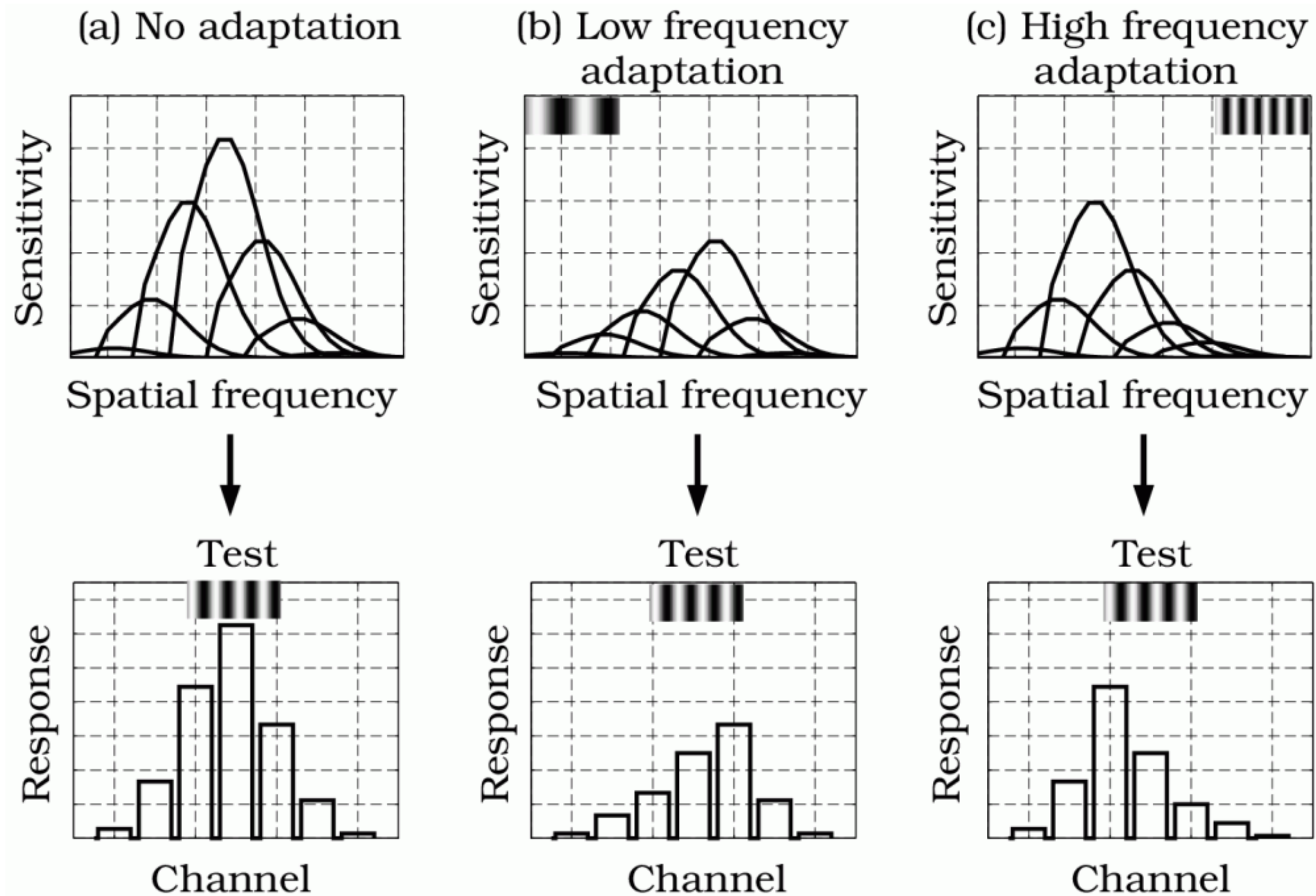
*Christina Enroth-Cugell*



*John Robson*

... and thus, presumably, doing linear systems (e.g fourier) analysis

# Origins in the Retina



*from Wandell 1996*

# Origins in the Retina

## THE CONTRAST SENSITIVITY OF RETINAL GANGLION CELLS OF THE CAT

BY CHRISTINA ENROTH-CUGELL AND J. G. ROBSON\*

*From the Biomedical Engineering Center, Technological Institute,  
Northwestern University, Evanston, Illinois, U.S.A.† and  
the Department of Physiology, Northwestern University  
Medical School, Chicago, U.S.A.*

*(Received 19 April 1966)*

1. Spatial summation within cat retinal receptive fields was studied by recording ... responses of ganglion cells to grating patterns
2. Summation over the receptive fields of some cells (X-cells) was found to be **approximately linear**, while for other cells (Y-cells) summation was **very non-linear**.
3. The mean discharge frequency of Y-cells ... was greatly increased when grating patterns drifted across their receptive fields.
4. In X-cells ... it was found that the contrast sensitivity function, **could be satisfactorily described by the difference of two Gaussian functions**.
5. This finding supports the hypothesis that the sensitivities of the antagonistic centre and surround summing regions of ganglion cell receptive fields fall off as Gaussian functions of the distance from the field centre.



*Christina Enroth-Cugell*



*John Robson*



# Old-School CV: Marr-Hildreth's "Laplacian of Gaussians"

*Proc. R. Soc. Lond. B* **207**, 187–217 (1980)

*Printed in Great Britain*

## Theory of edge detection

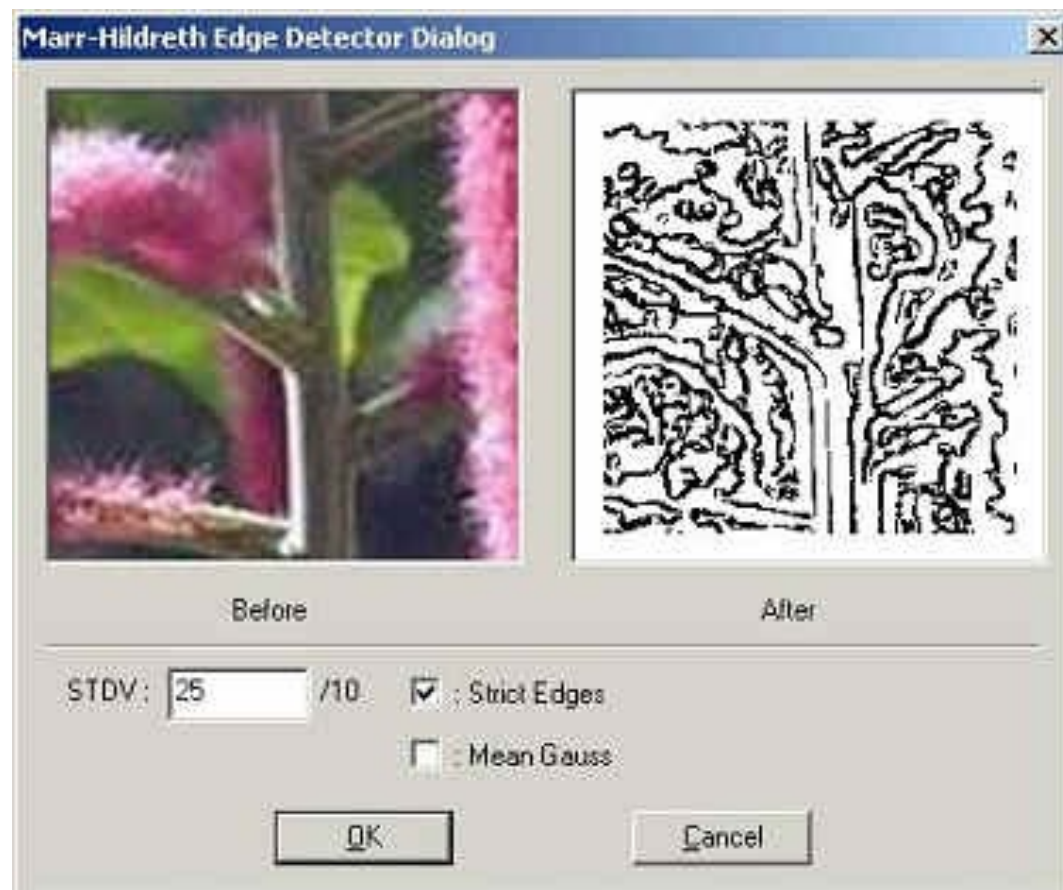
BY D. MARR AND E. HILDRETH

*M.I.T. Psychology Department and Artificial Intelligence Laboratory,  
79 Amherst Street, Cambridge, Massachusetts 02139, U.S.A.*

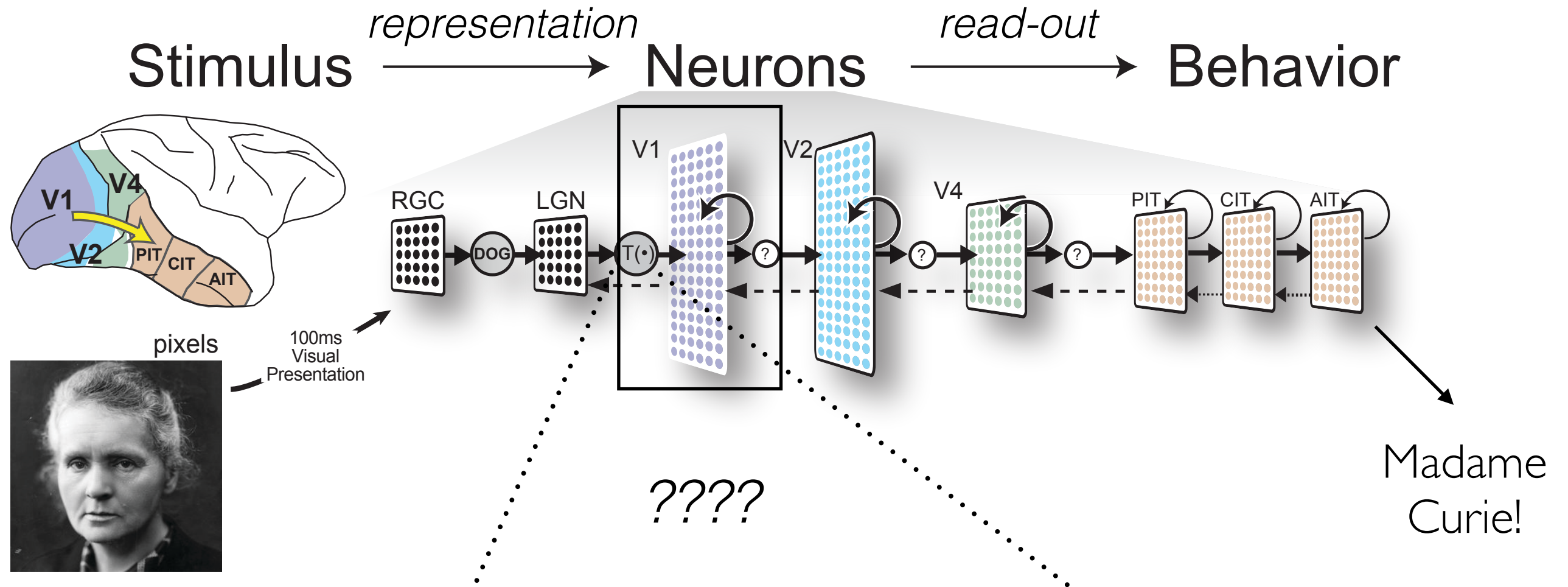
*(Communicated by S. Brenner, F.R.S. – Received 22 February 1979)*

$$\nabla^2 G(x, y) * Im(x, y)$$

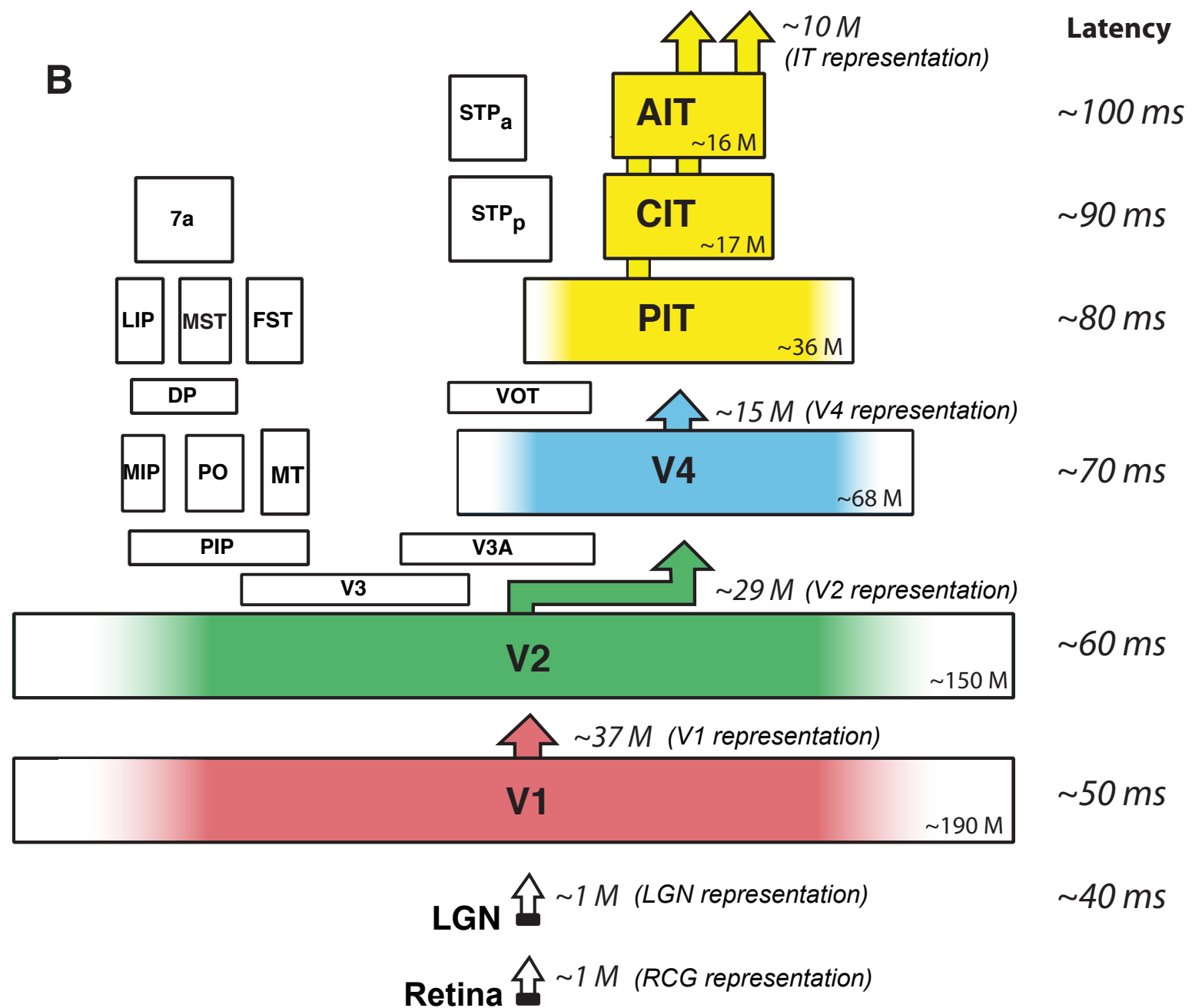
$$\sim DoG$$



# Gabors in V1



You are here.



106

*J. Physiol.* (1962), **160**, pp. 106–154

*With 2 plates and 20 text-figures*

*Printed in Great Britain*

**RECEPTIVE FIELDS, BINOCULAR INTERACTION  
AND FUNCTIONAL ARCHITECTURE IN  
THE CAT'S VISUAL CORTEX**

**BY D. H. HUBEL AND T. N. WIESEL**

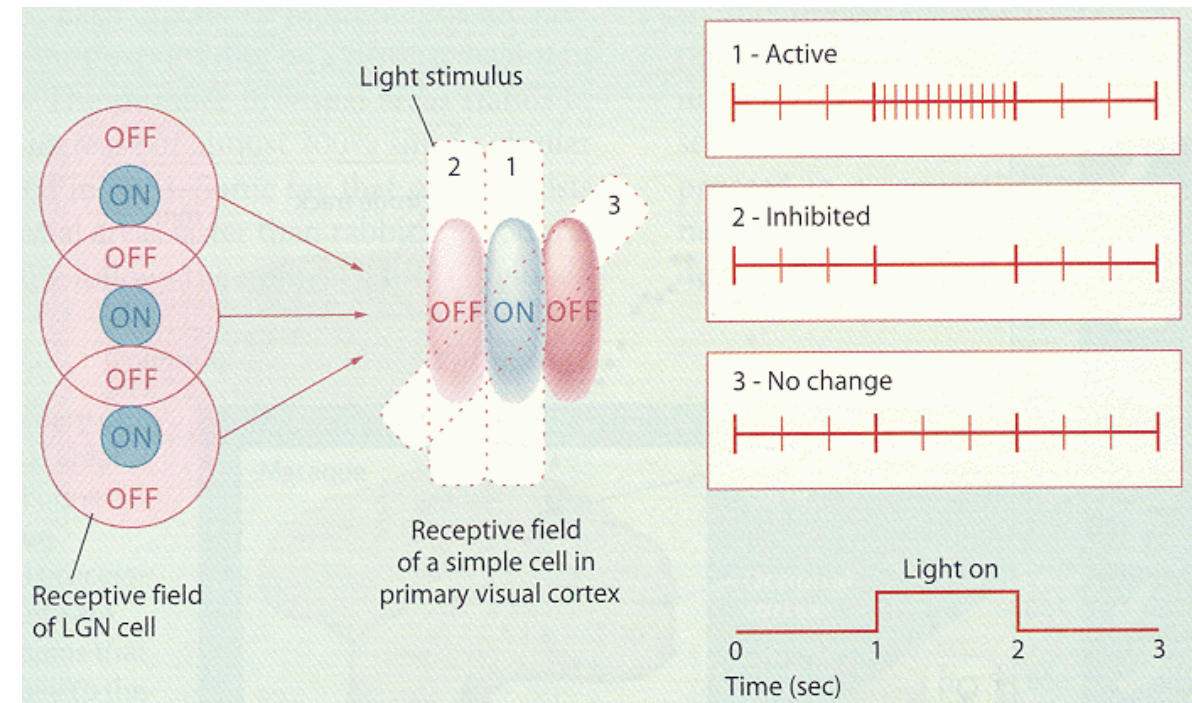
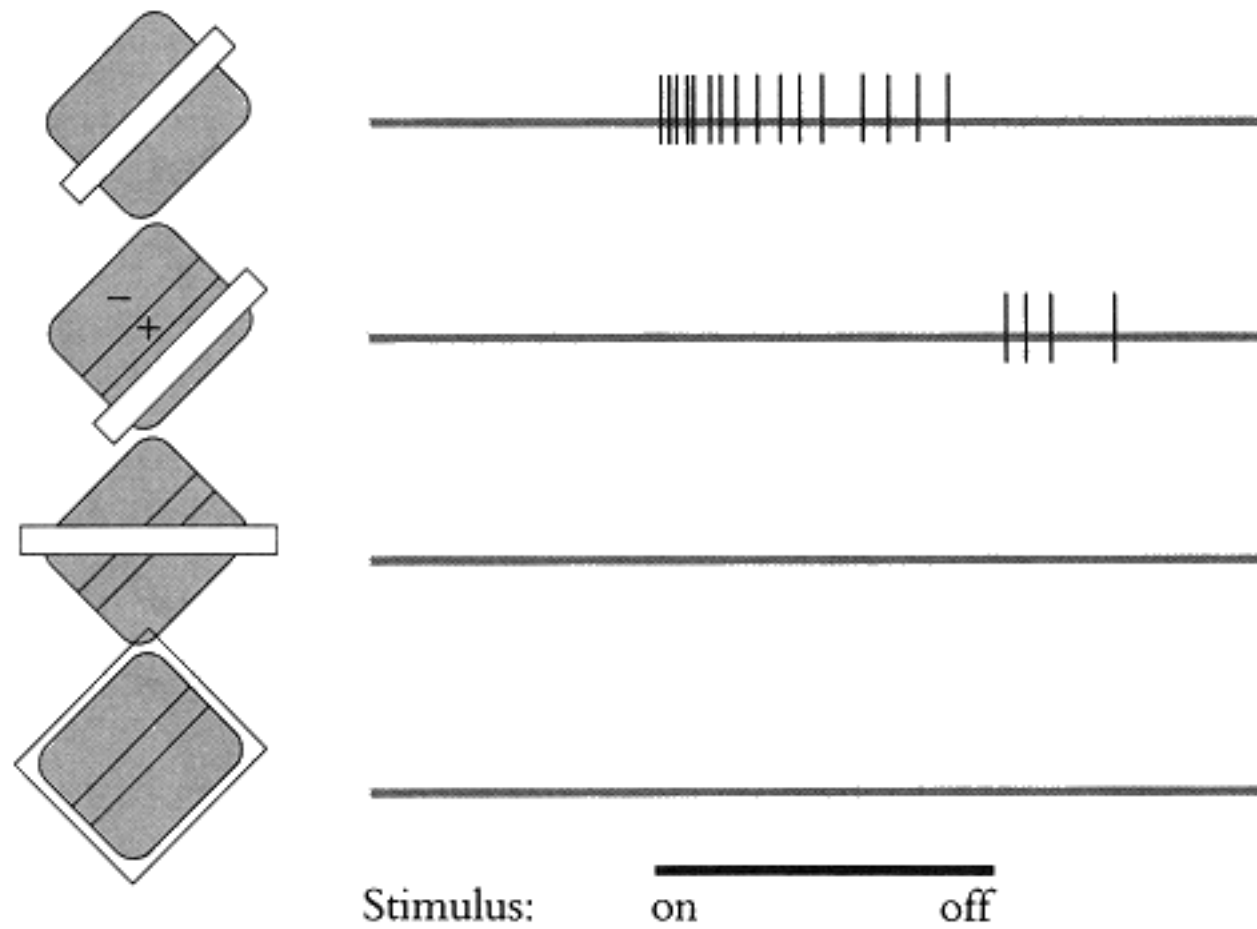
*From the Neurophysiology Laboratory, Department of Pharmacology  
Harvard Medical School, Boston, Massachusetts, U.S.A.*

*(Received 31 July 1961)*

**PART I**

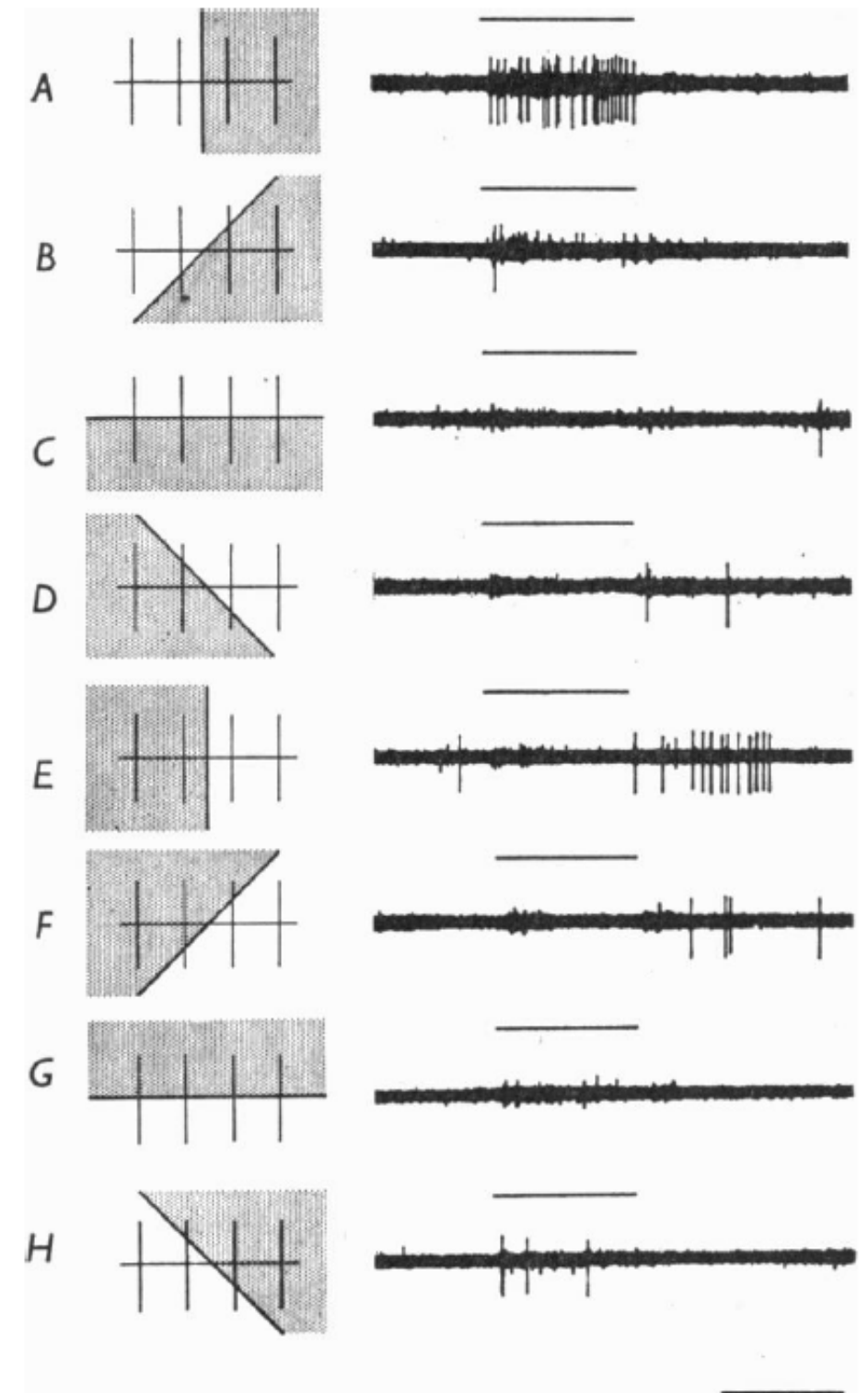
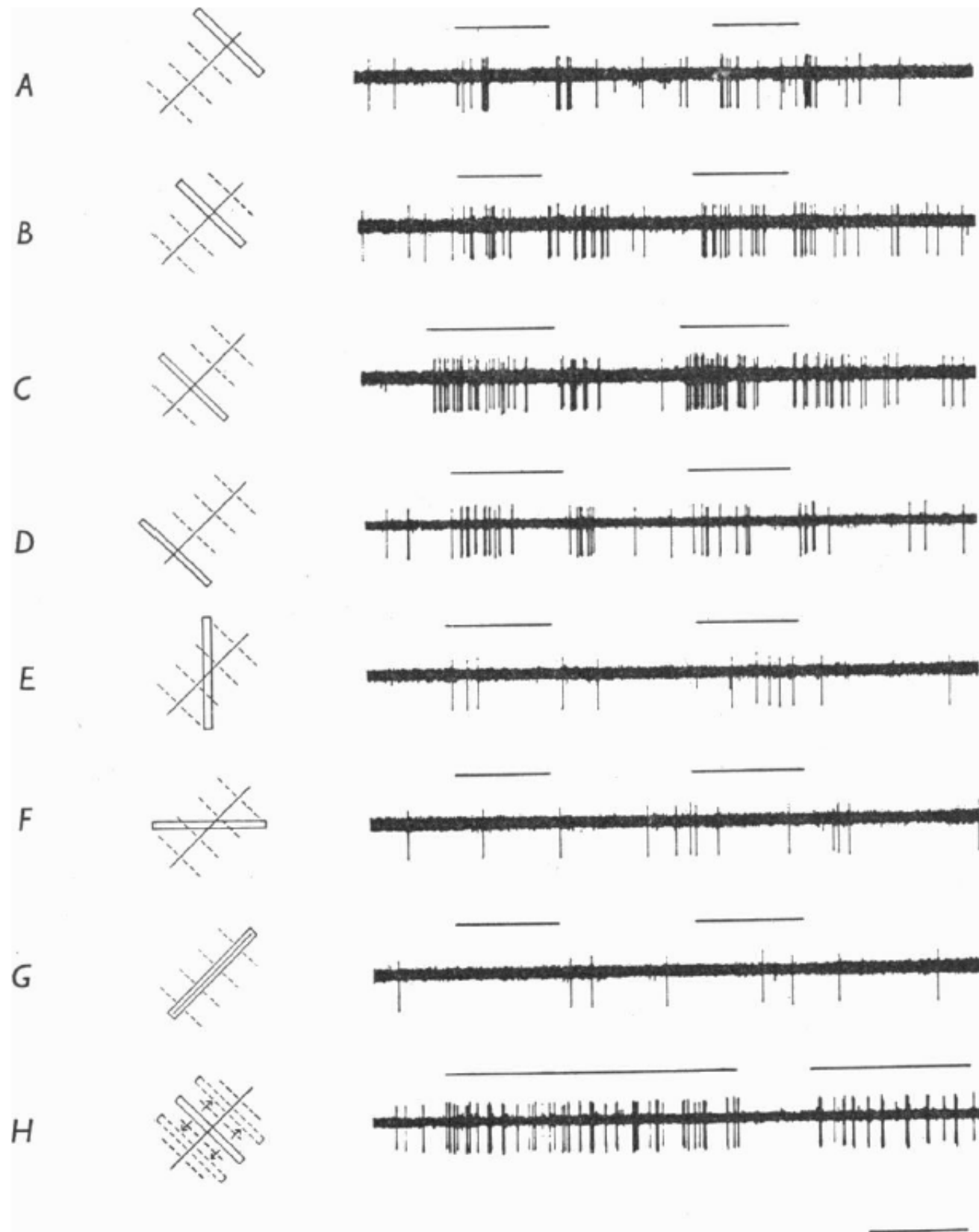
**ORGANIZATION OF RECEPTIVE FIELDS IN CAT'S  
VISUAL CORTEX: PROPERTIES OF 'SIMPLE'  
AND 'COMPLEX' FIELDS**

# Gabors in VI

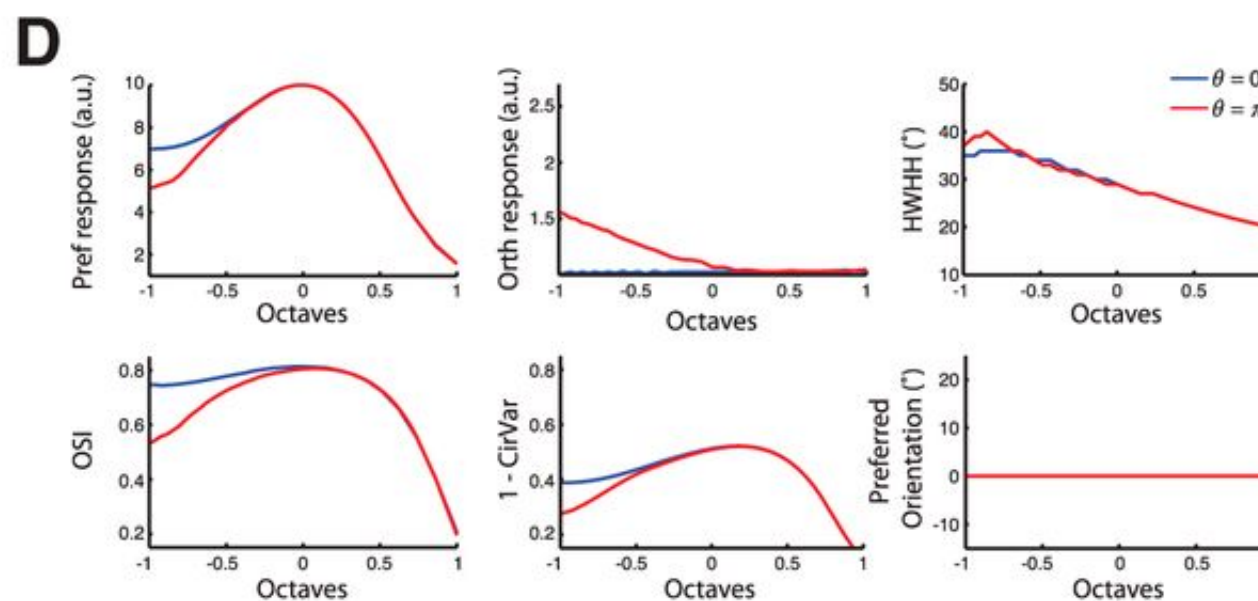
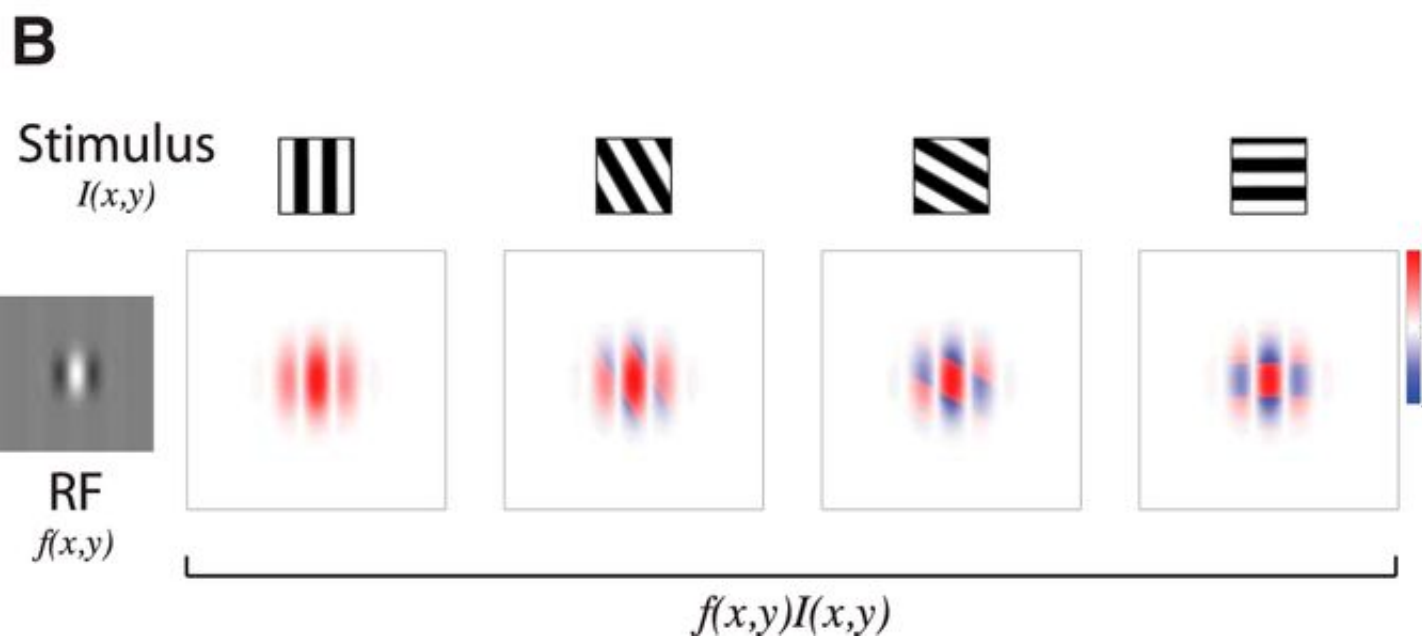
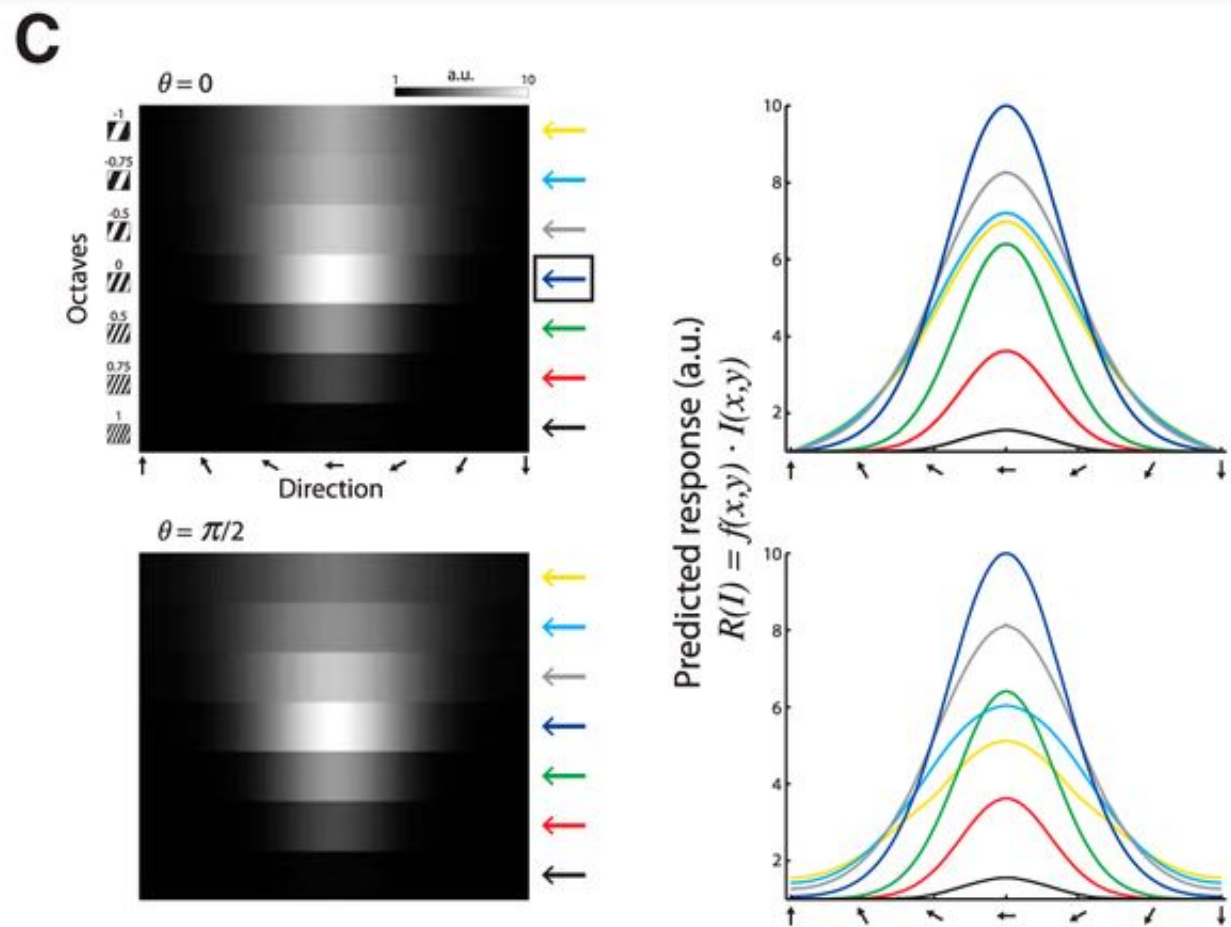
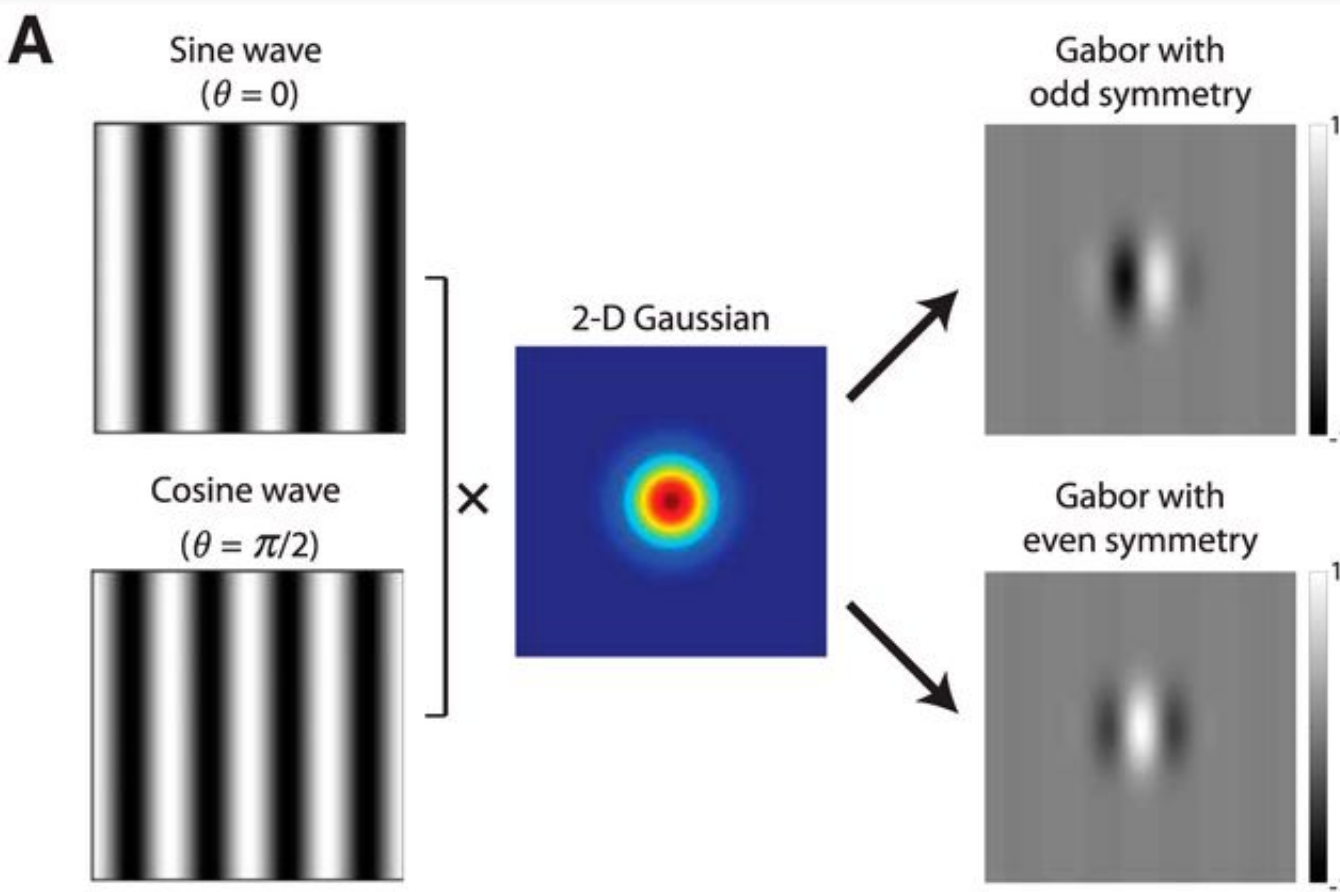




# Gabors in VI

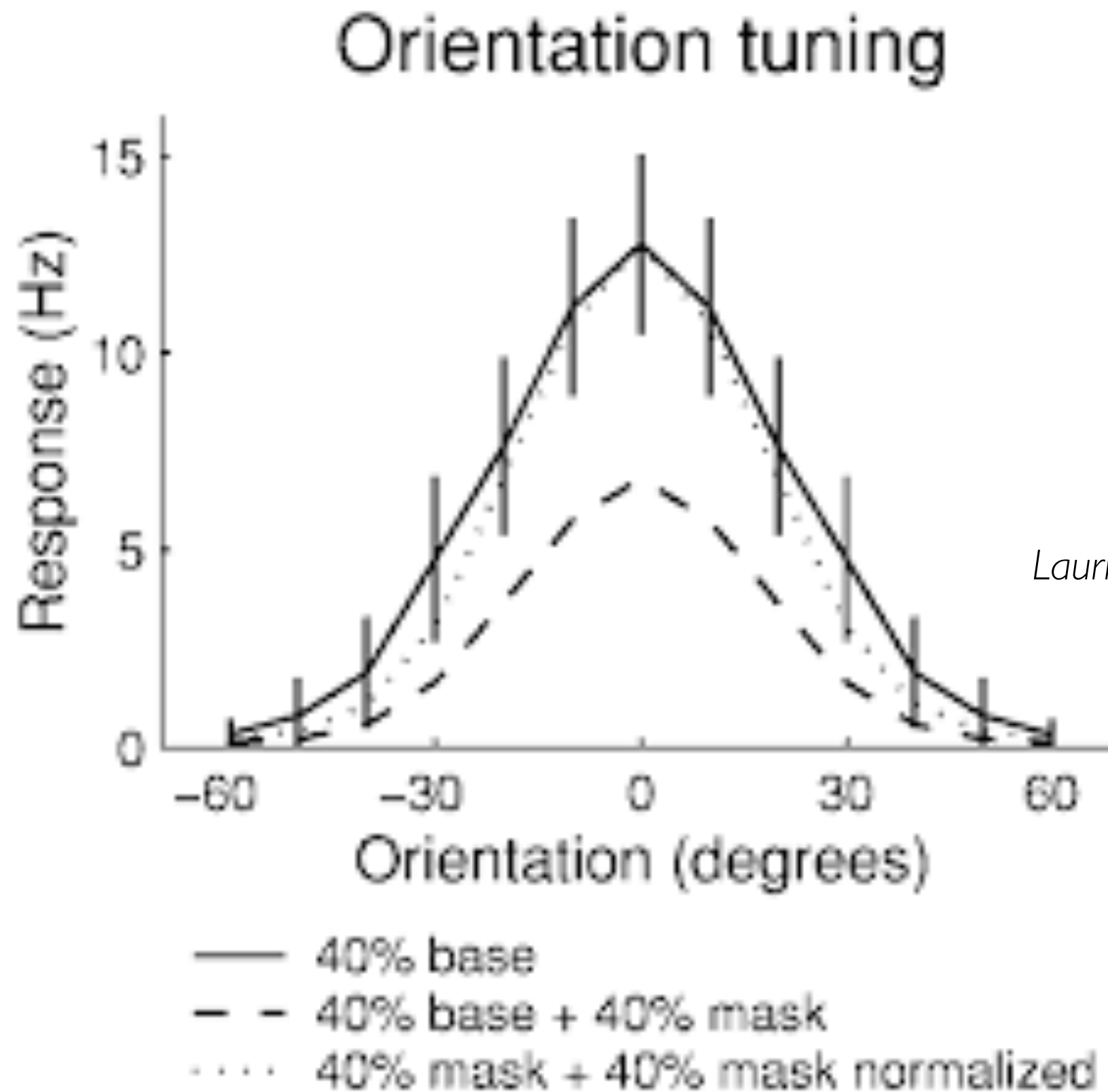


# Orientation Tuning Curves



from Ayzenshtat et al (2016)

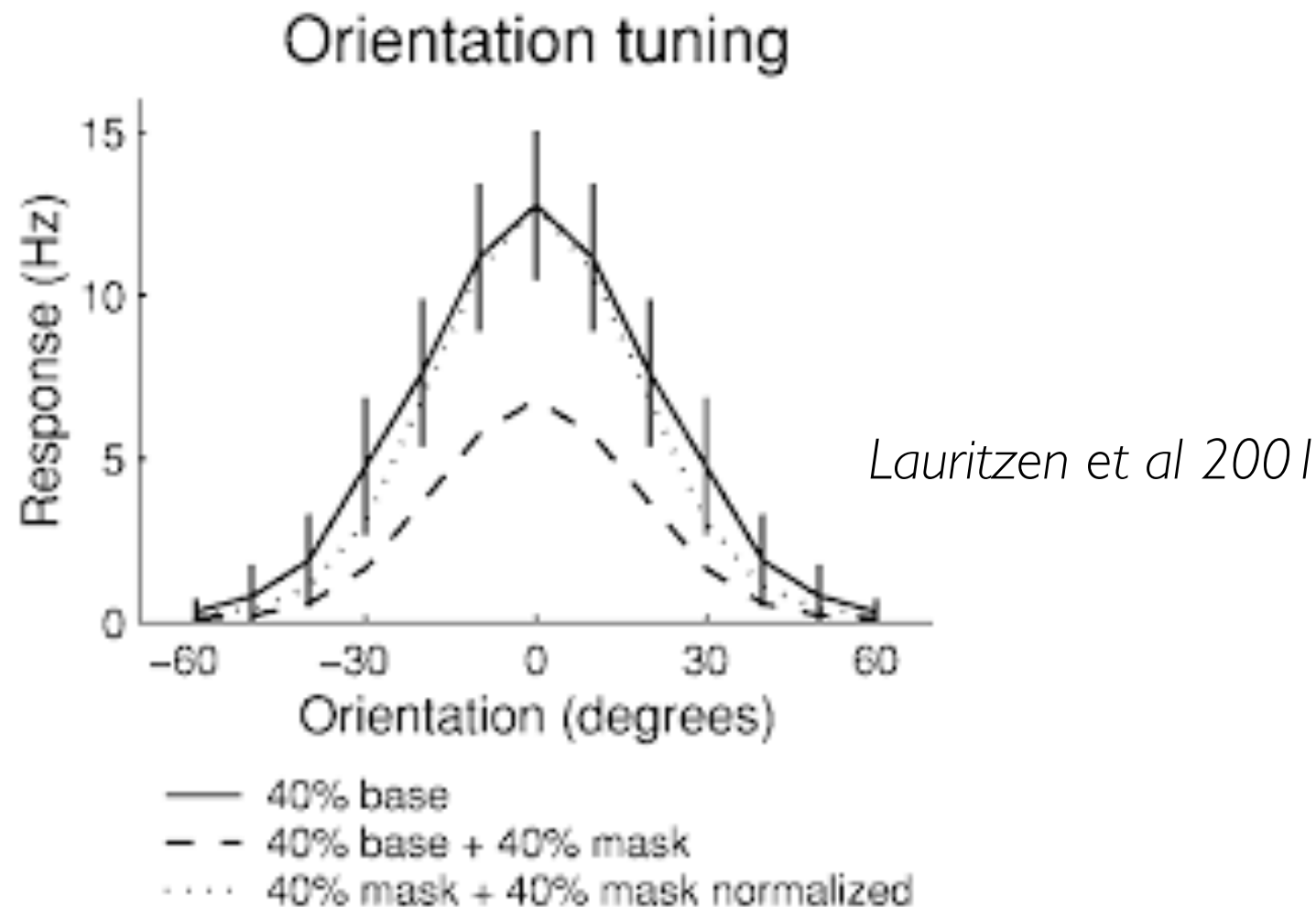
# Orientation Tuning Curves



*Lauritzen et al 2001*



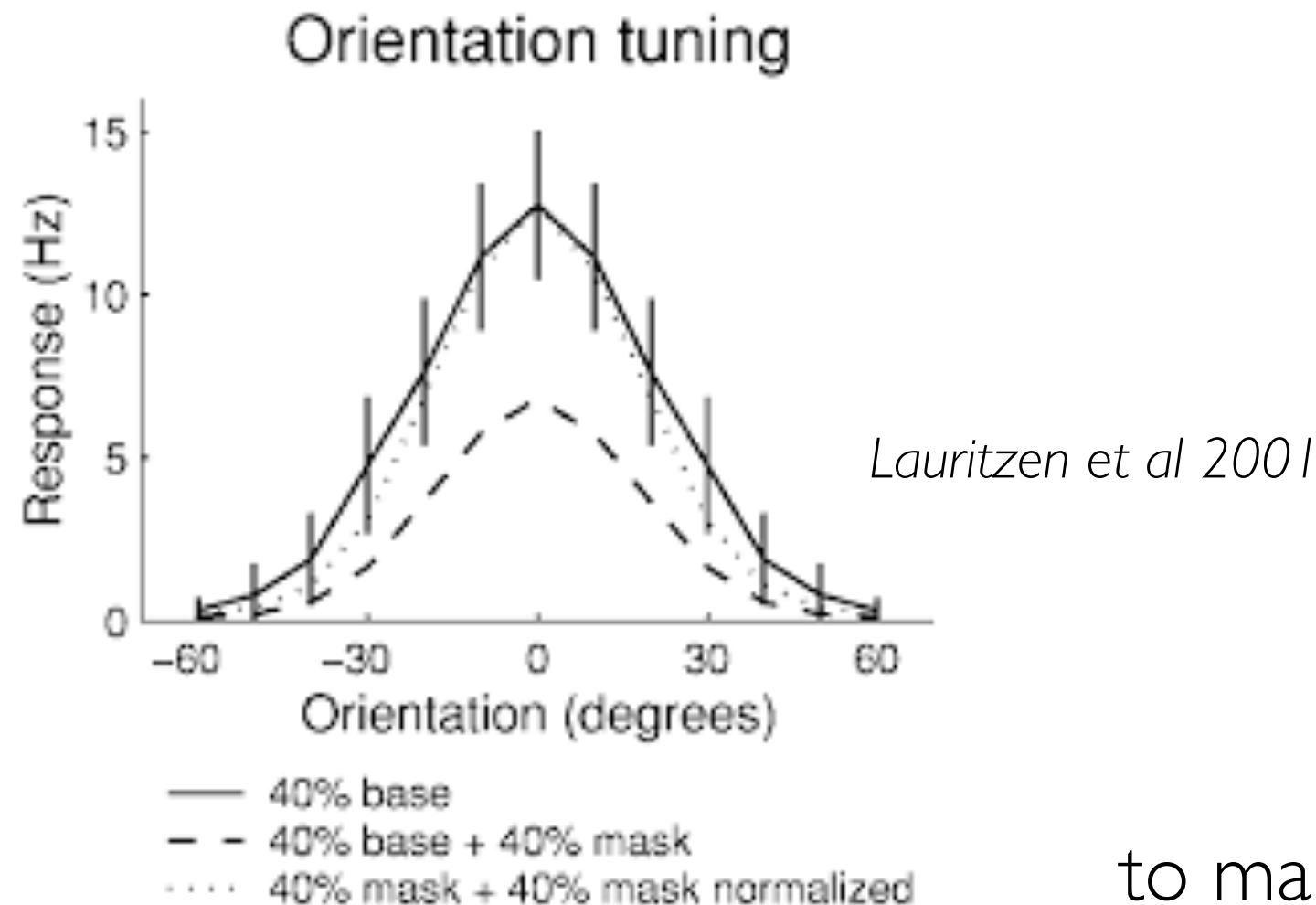
# Orientation Tuning Curves



$$\text{Circular Variance} = 1 - \frac{\sum_k r_k e^{2i\theta_k}}{\sum_k r_k}$$

$r_k$  = neuron  $\mathbf{r}$ 's response to stimulus with pure orientation  $\mathbf{k}$

# Orientation Tuning Curves



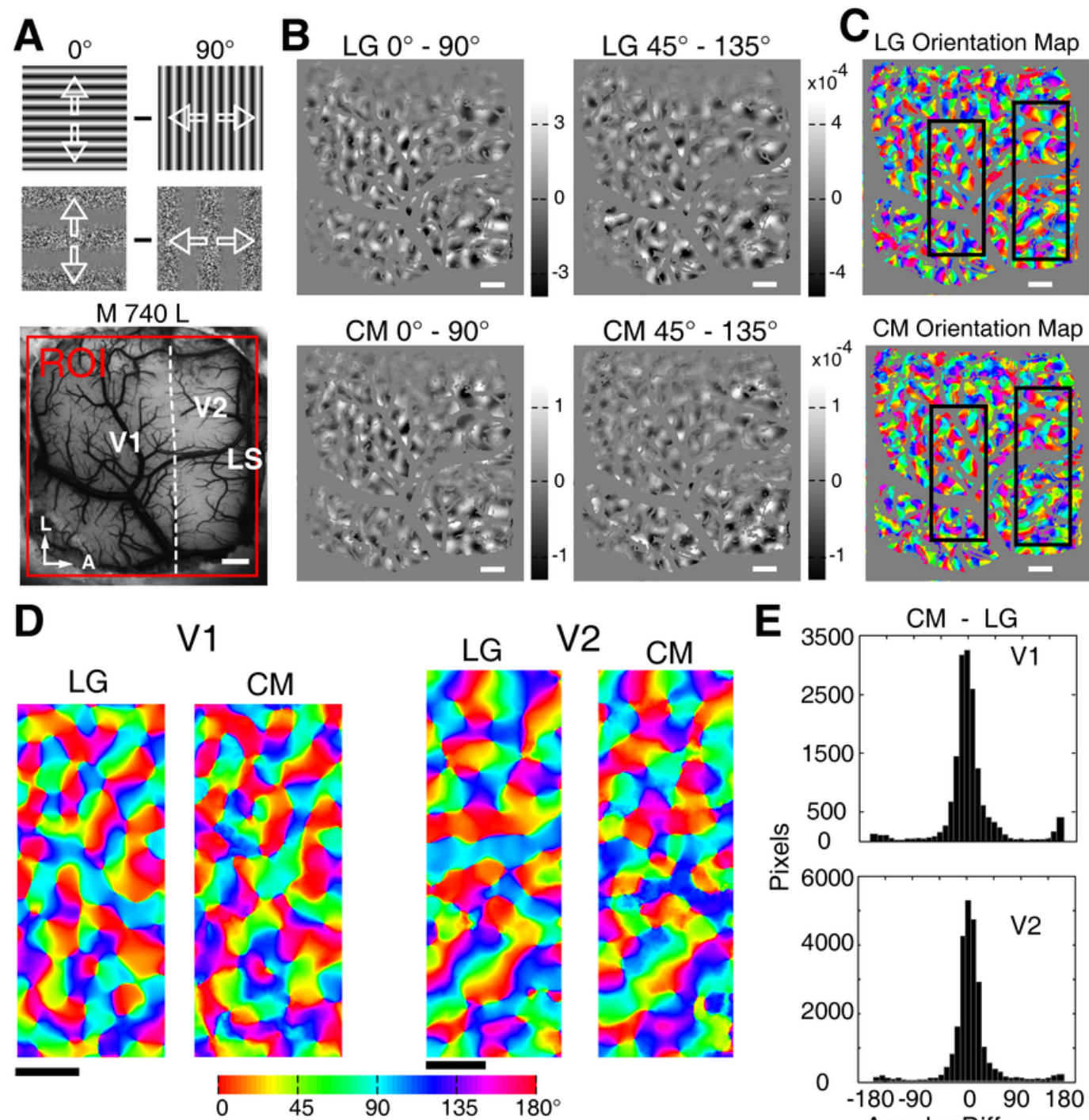
to make it “circular”

$$\text{Circular Variance} = 1 - \frac{\sum_k r_k \boxed{e^{2i\theta_k}}}{\boxed{\sum_k r_k}}$$

total response

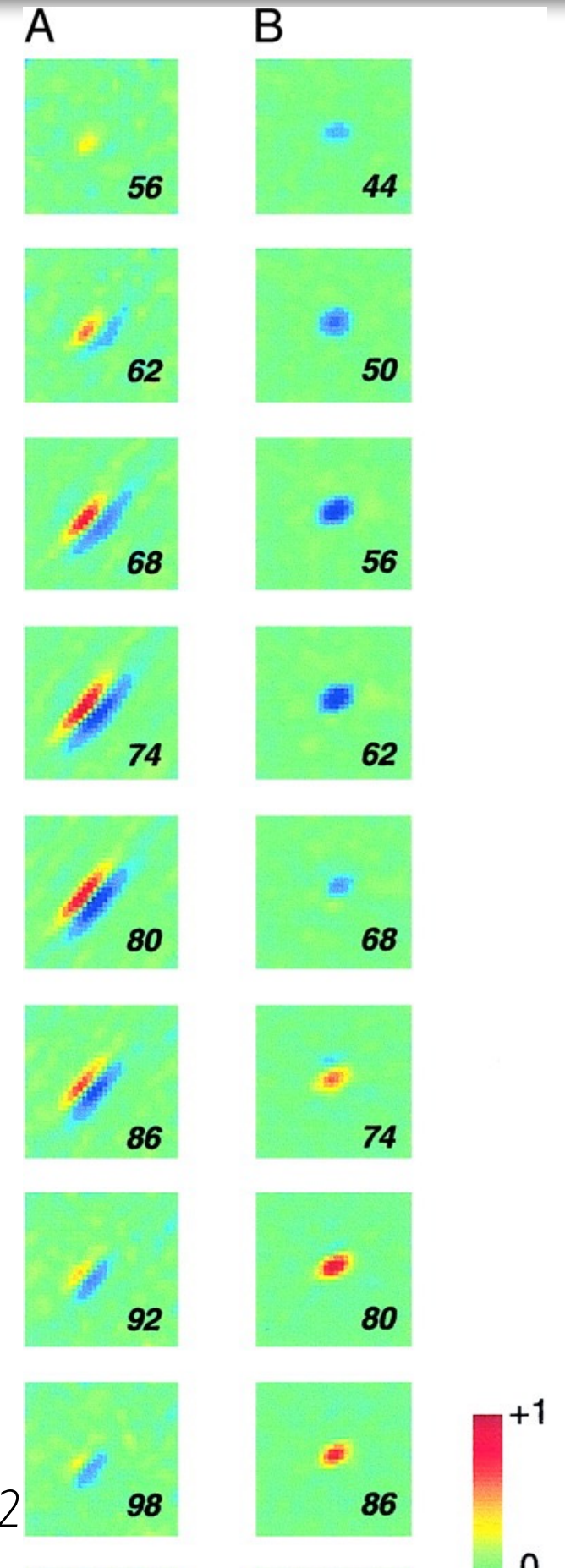
$r_k$  = neuron  $\mathbf{r}$ 's response to stimulus with pure orientation  $\mathbf{k}$

# Gabors in V1



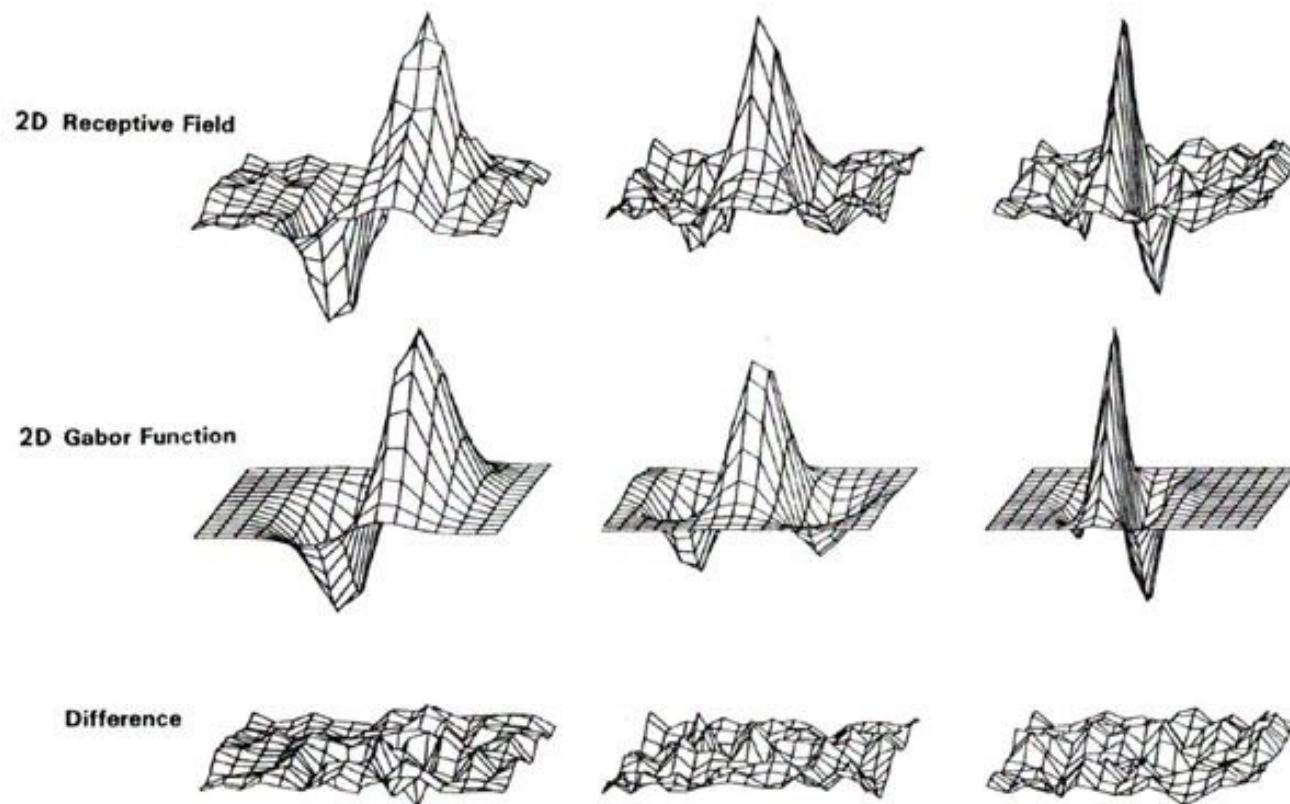
An et al 2015

Ringach 2002





## Simple V1 cells Daugman, 1985



Receptive fields in primary visual cortex (Jones and Palmer, 1987)

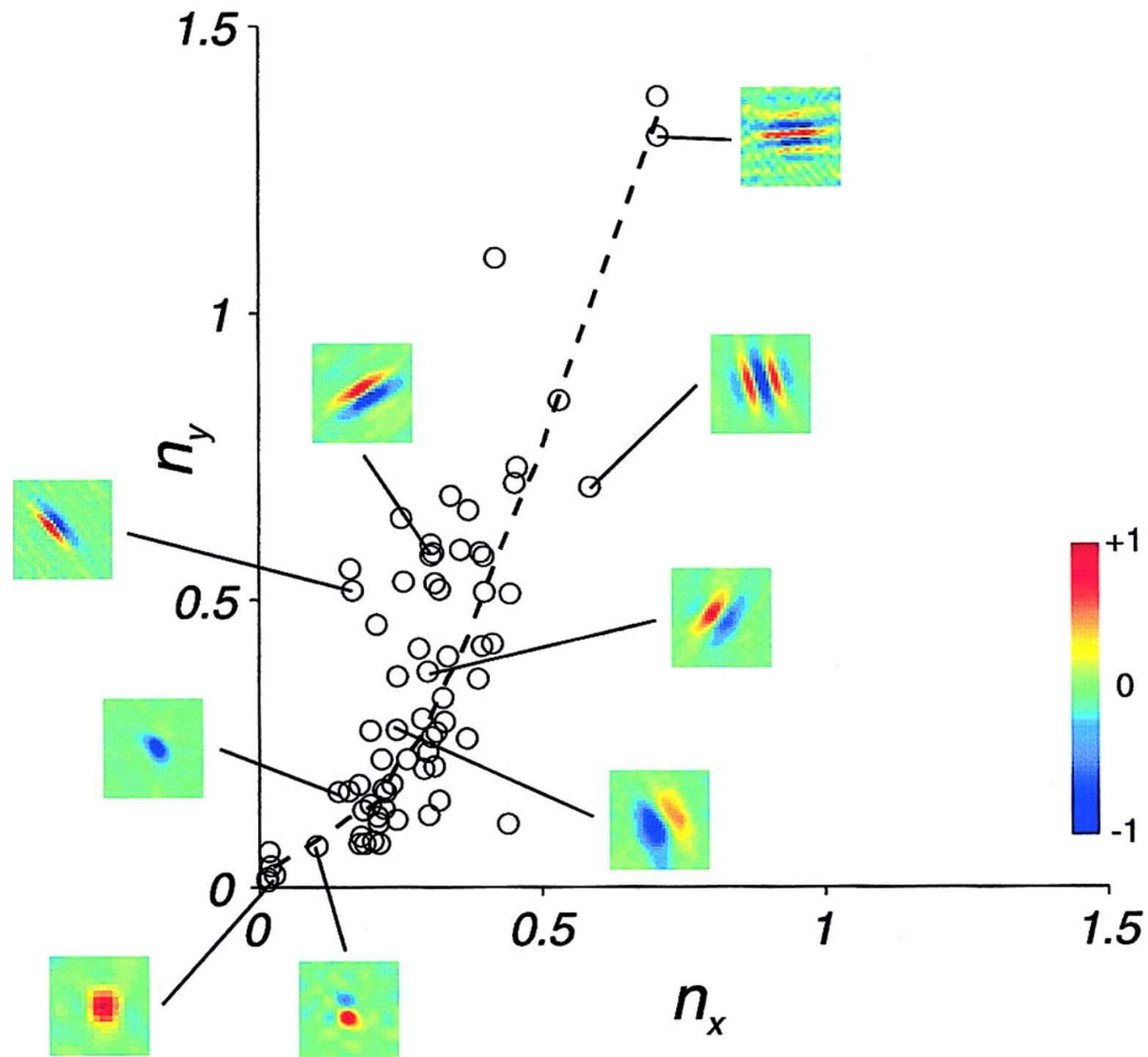
**Gabor wavelets:** localized sine and cosine waves

$$G(x) \propto \exp\left\{-\frac{1}{2}\left[\frac{x_1^2}{\sigma_1^2} + \frac{x_2^2}{\sigma_2^2}\right]\right\} e^{ix_1}$$

Translation, rotation, dilation of the above function

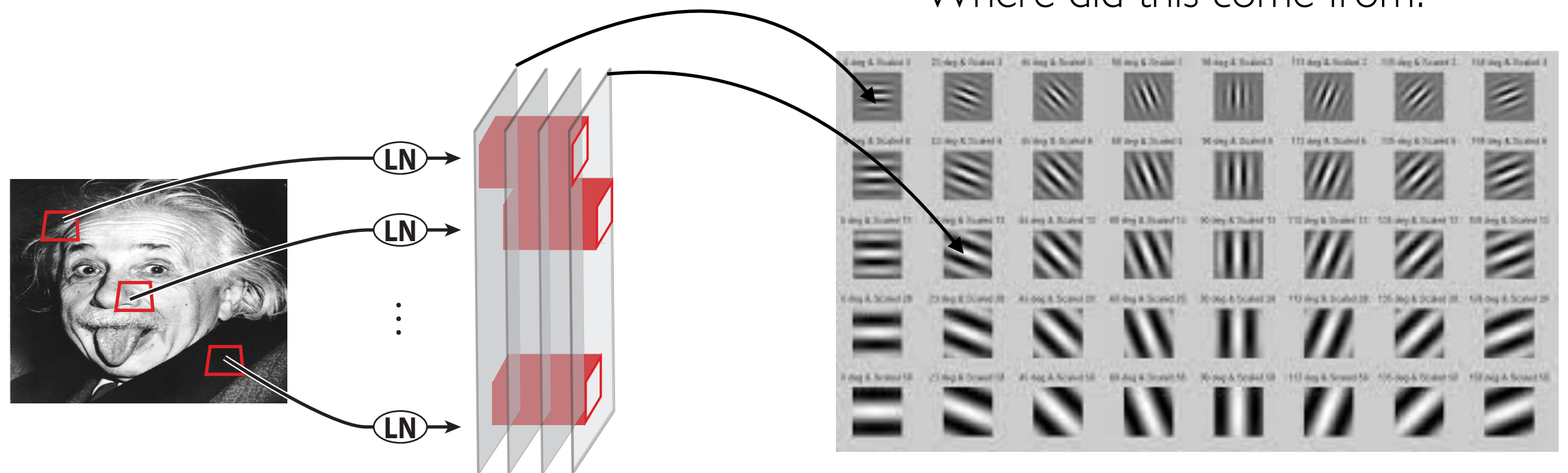
# Gabors in VI

There is a frequency-orientation relationship:



from Ringach 2002

# Models of VI





## **Two strategies to find the correct parameters.**

*less normative theory*

*more normative theory*

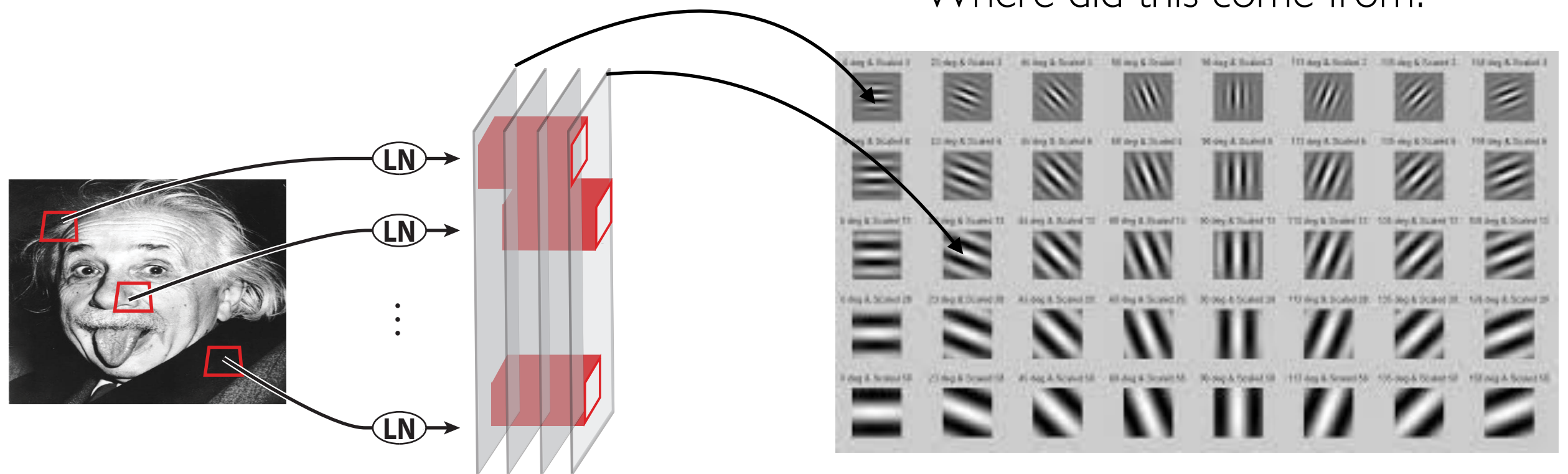
1. Fit neural  
data

2. Solve a high-  
level  
ecological task

...

compare to  
neural data  
*and*  
Turing Test

# Models of VI

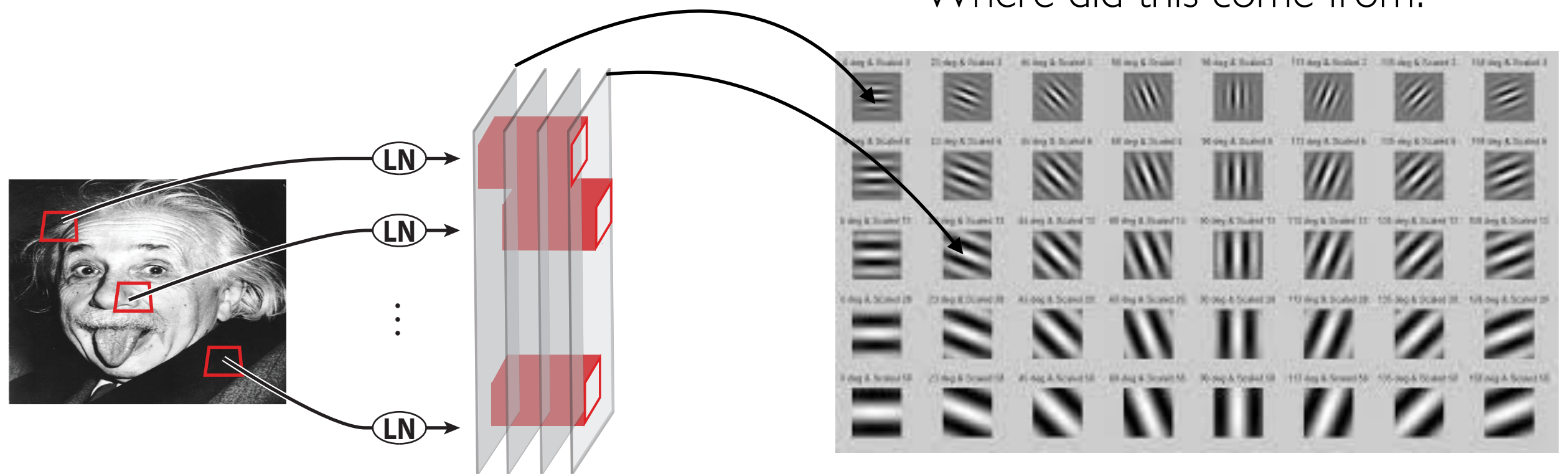


Where did this come from?

(I) “Hubel and Wiesel’s Intuition”  
~1970s and formalized later

→ e.g. there is a “fixed basis set”  
that just “makes sense” if we’re  
smart enough

# Models of VI



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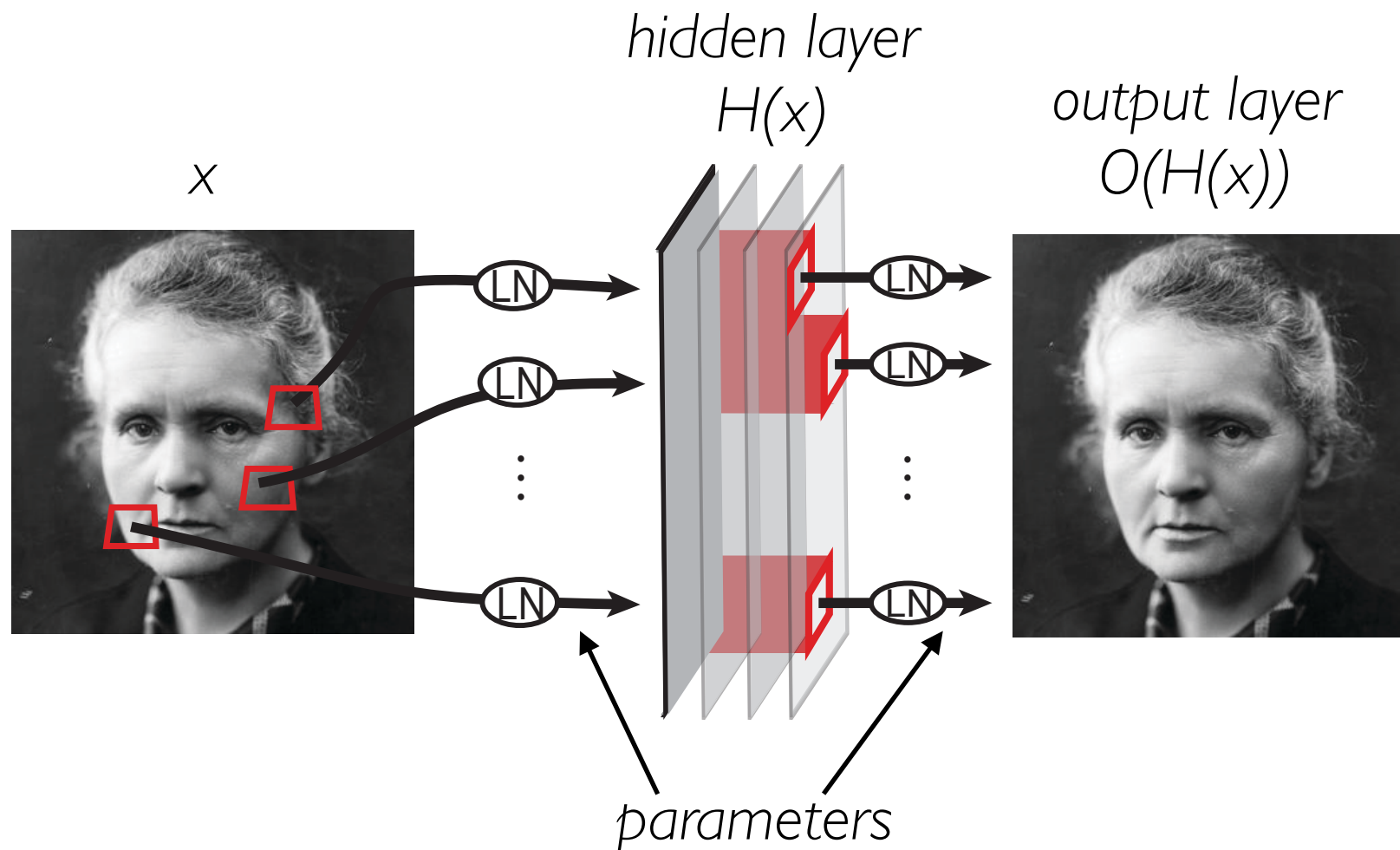
→ e.g. there is a “fixed basis set”  
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(2) Sparse Coding Foldiak, Olshausen,  
mid 1990s

→ neurons have to represent their  
environment, as efficiently as possible



# Models of VI

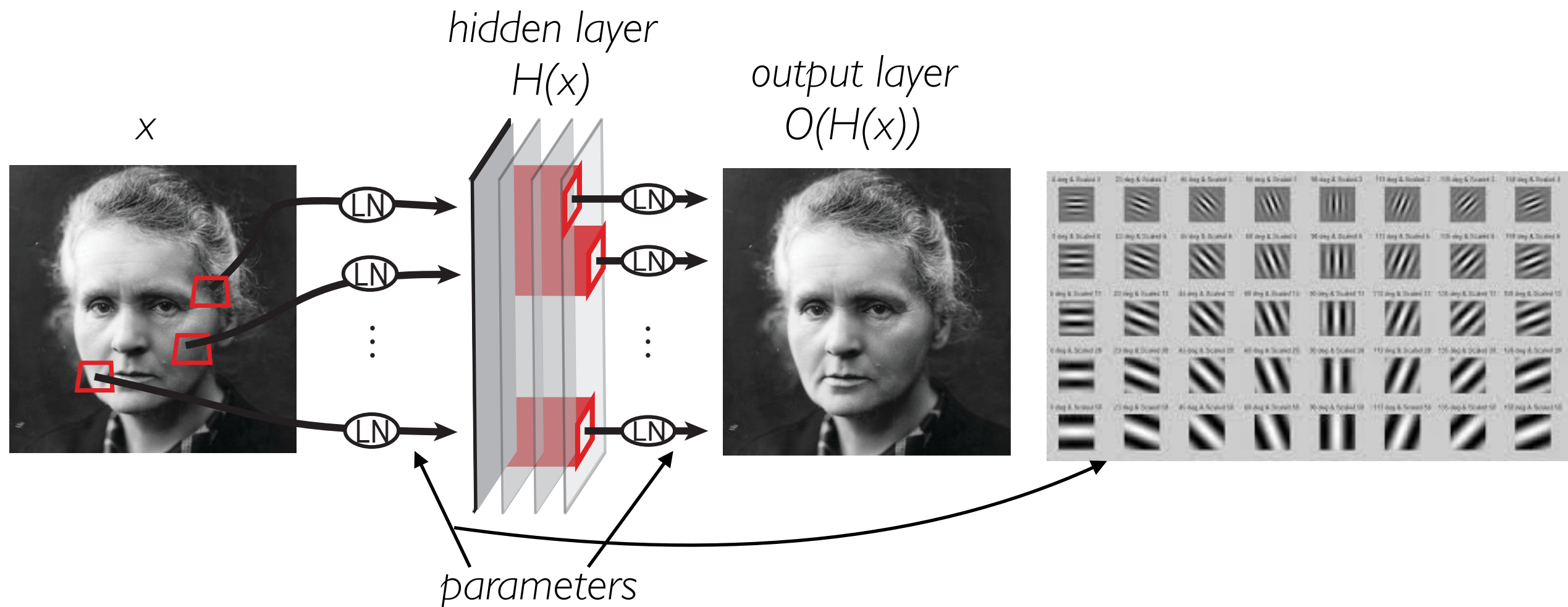


$$L(x) = |x - O(H(x))|^2 + \lambda \cdot |H(x)|$$

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# Models of VI

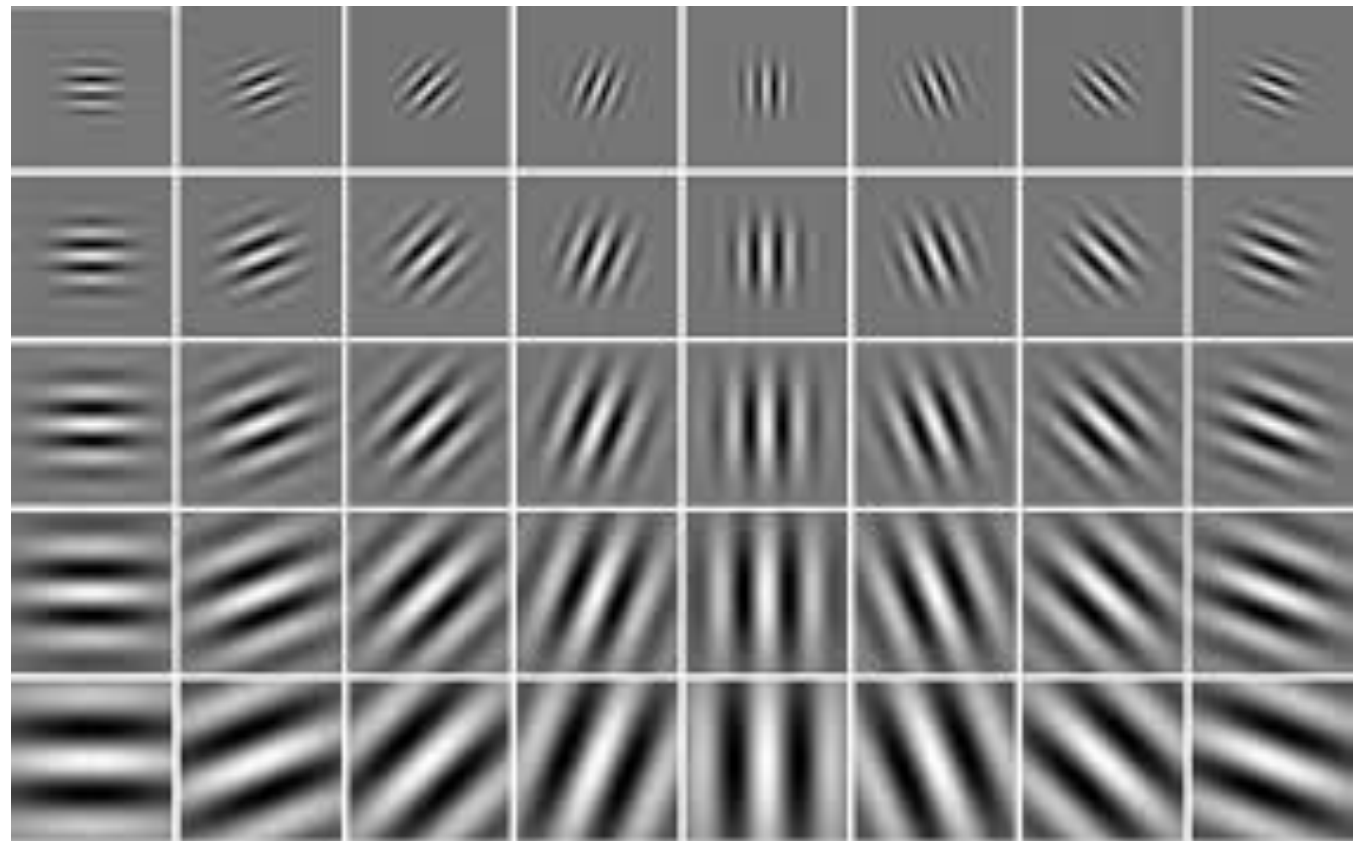
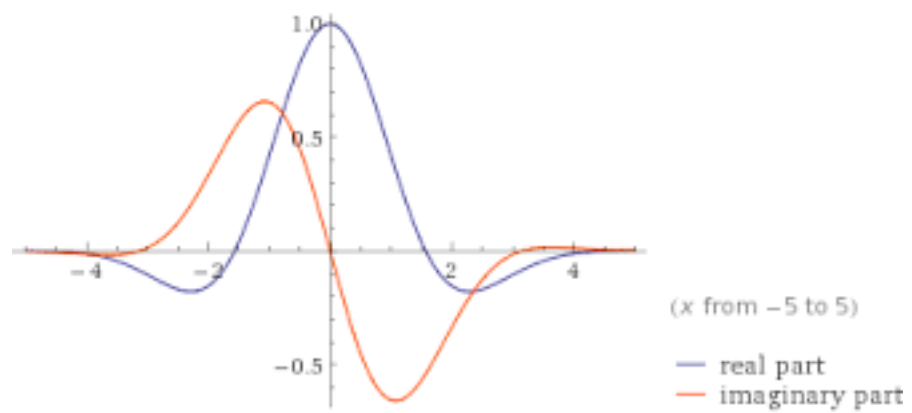


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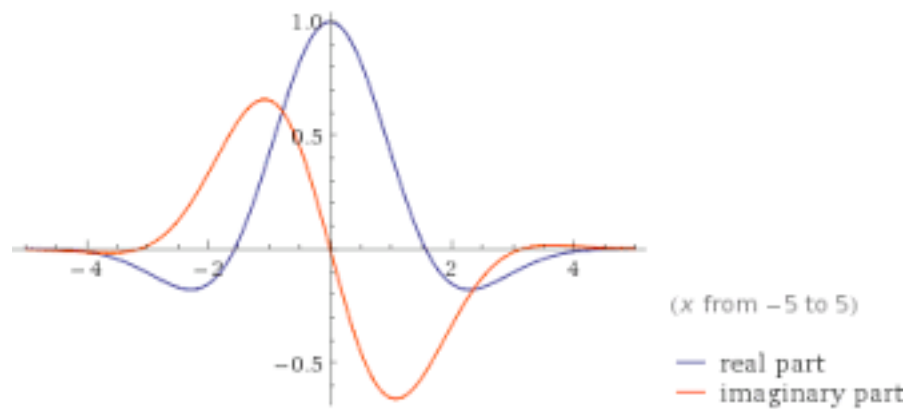
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# Old-School CV part 2: The Wavelet Wave



# Old-School CV part 2: The Wavelet Wave



IEEE TRANSACTIONS ON IMAGE PROCESSING, VOL. 4, NO. 11, NOVEMBER 1995

1549

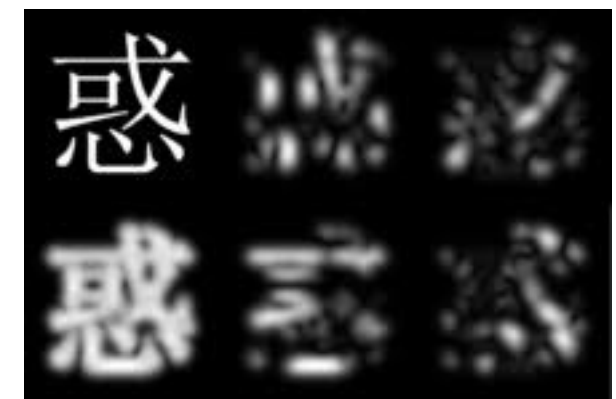
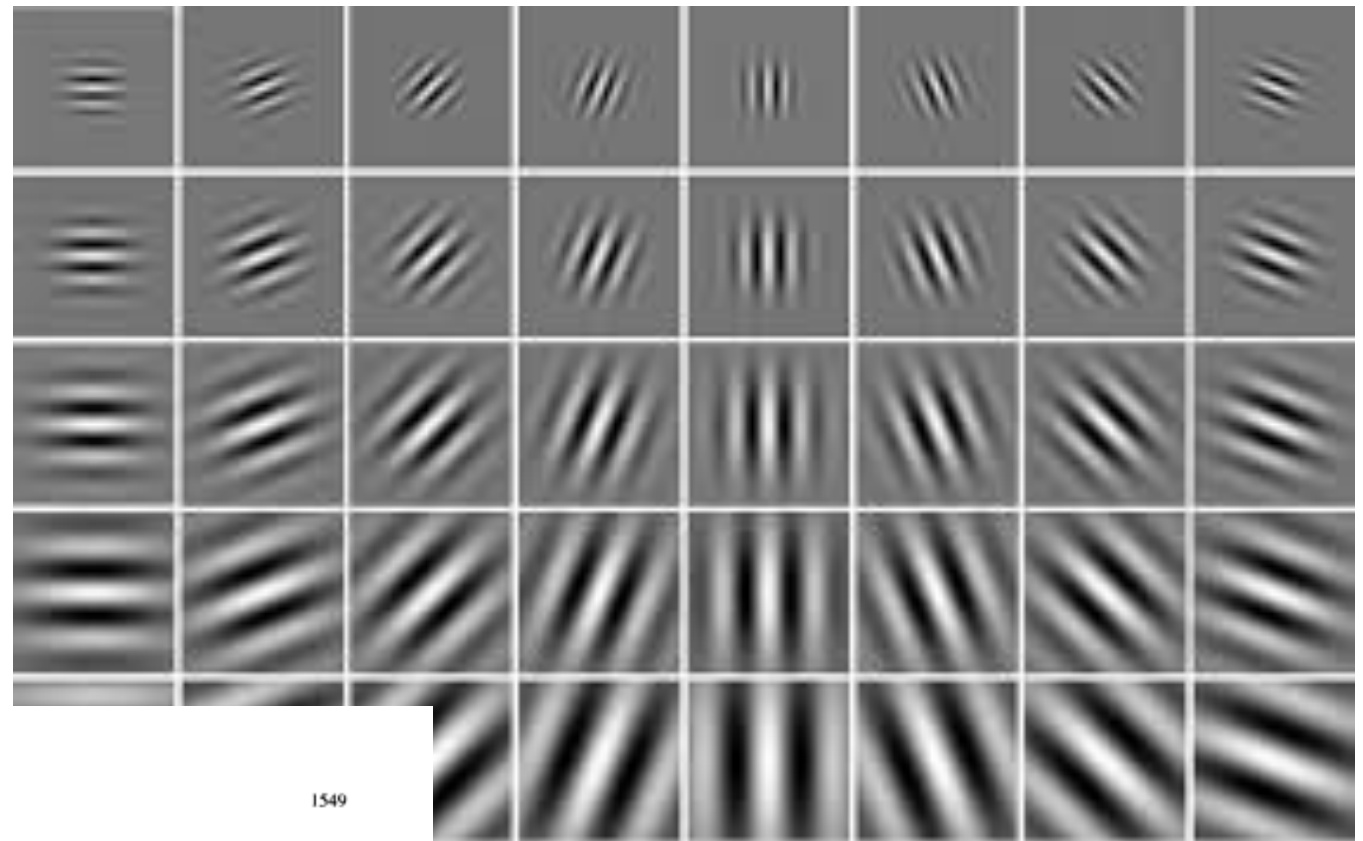
## Texture Classification and Segmentation Using Wavelet Frames

Michael Unser, *Senior Member, IEEE*

**Abstract**—This paper describes a new approach to the characterization of texture properties at multiple scales using the wavelet transform. The analysis uses an overcomplete wavelet decomposition, which yields a description that is translation invariant. It is shown that this representation constitutes a tight frame of  $l_2$  and that it has a fast iterative algorithm. A texture is characterized by a set of channel variances estimated at the output of the corresponding filter bank. Classification experiments with 12 Brodatz textures indicate that the discrete wavelet frame (DWF) approach is superior to a standard (critically sampled) wavelet transform feature extraction. These results also suggest that this approach should perform better than most traditional single resolution techniques (co-occurrences, local linear transform, and the like). A detailed comparison of the classification performance of various orthogonal and biorthogonal wavelet transforms is also provided. Finally, the DWF feature extraction technique is incorporated into a simple multicomponent texture segmentation algorithm, and some illustrative examples are presented.

reversible, which limits their applicability for texture synthesis. Most of these problems can be avoided if one uses the wavelet transform, which provides a precise and unifying framework for the analysis and characterization of a signal at different scales [16]–[19]. The use of a pyramid-structured wavelet transform for texture analysis was first suggested in the pioneering work of Mallat [19]. This initial proposal has been followed by several studies on texture classification with a particular attention to the use of wavelet packets [20], [21], which constitute a multiband extension of the pyramid-structured wavelet transform.

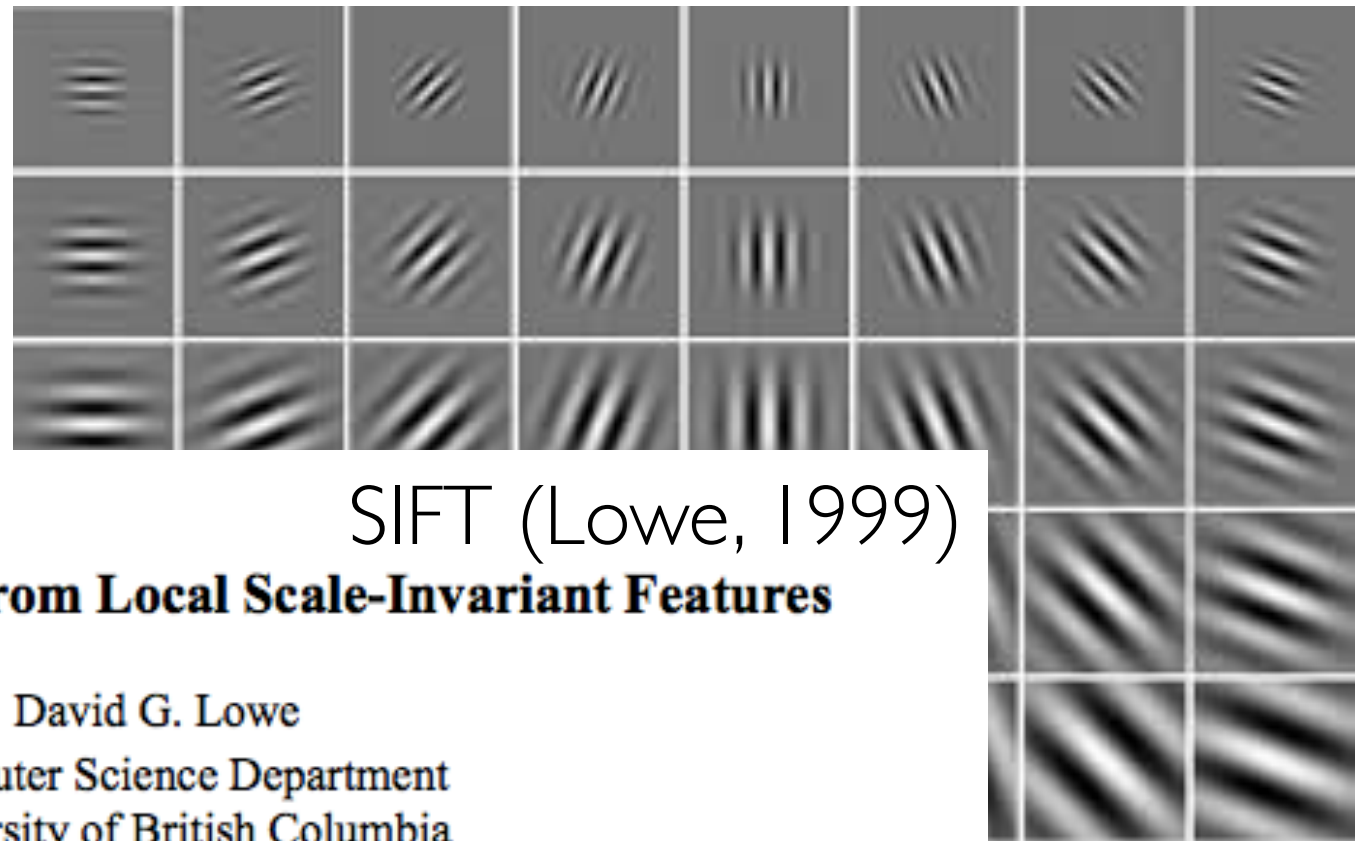
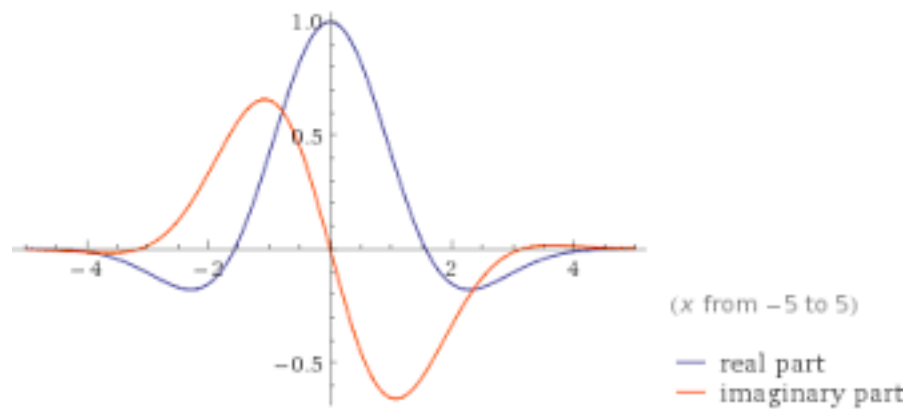
In this paper, a variation of the discrete wavelet transform is introduced for characterizing texture properties. This technique is applied to the problems of texture classification and segmentation. The present analysis method, which is described in Section II, uses an overcomplete wavelet decomposition (the discrete wavelet frame (DWF)) in which the wavelet



Many CV careers made on wavelets.



# Old-School CV part 2: The Wavelet Wave



SIFT (Lowe, 1999)

## Object Recognition from Local Scale-Invariant Features

David G. Lowe

Computer Science Department  
University of British Columbia  
Vancouver, B.C., V6T 1Z4, Canada  
lowe@cs.ubc.ca

IEEE TRANSACTIONS ON IMAGE PROCESSING

Segmentation

Michael Unser, Senior Member, IEEE

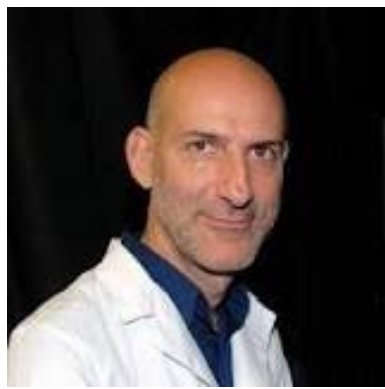


**Abstract**—This paper describes a new approach to the characterization of texture properties at multiple scales using the wavelet transform. The analysis uses an overcomplete wavelet decomposition, which yields a description that is translation invariant. It is shown that this representation constitutes a tight frame of  $l_2$  and that it has a fast iterative algorithm. A texture is characterized by a set of channel variances estimated at the output of the corresponding filter bank. Classification experiments with 12 Brodatz textures indicate that the discrete wavelet frame (DWF) approach is superior to a standard (critically sampled) wavelet transform feature extraction. These results also suggest that this approach should perform better than most traditional single resolution techniques (co-occurrences, local linear transform, and the like). A detailed comparison of the classification performance of various orthogonal and biorthogonal wavelet transforms is also provided. Finally, the DWF feature extraction technique is incorporated into a simple multicomponent texture segmentation algorithm, and some illustrative examples are presented.

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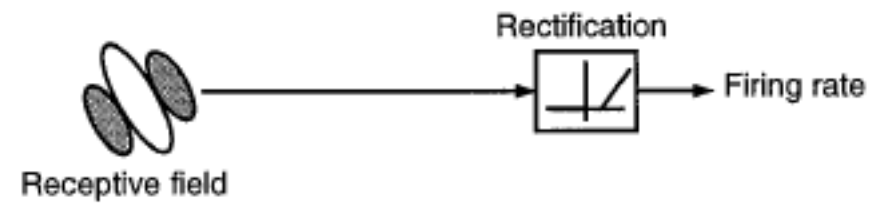
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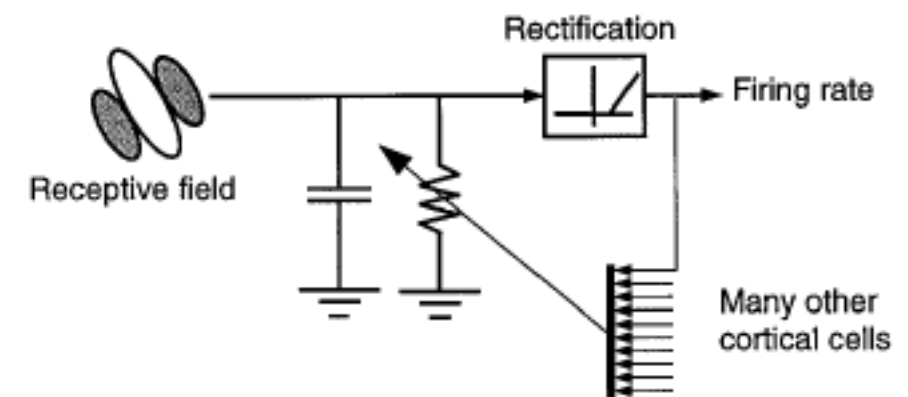


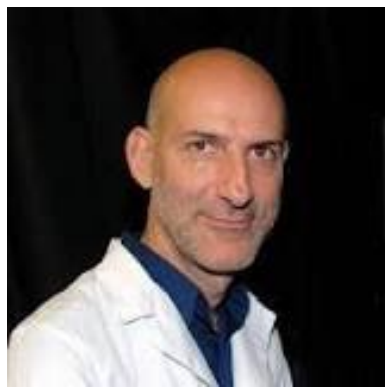
*Carandini, Heeger and Movshon (1997)*

**A** Linear model



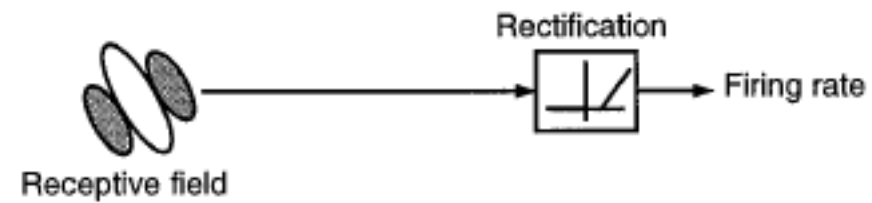
**B** Normalization model



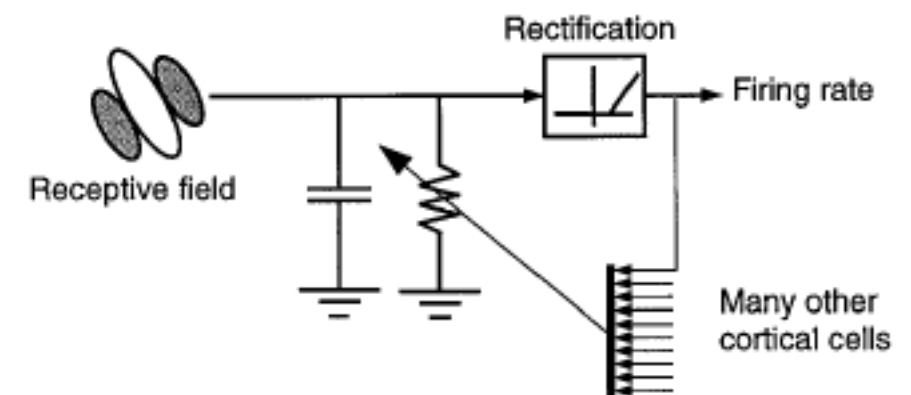


*Carandini, Heeger and Movshon (1997)*

### A Linear model



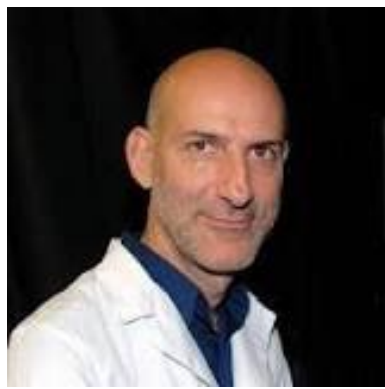
### B Normalization model



$$C \frac{dV}{dt} + gV = I$$

$$g = \frac{g_0}{\sqrt{1 - k \cdot \sum_{r \in R_x} r}}$$

$$R = \max(0, V)$$

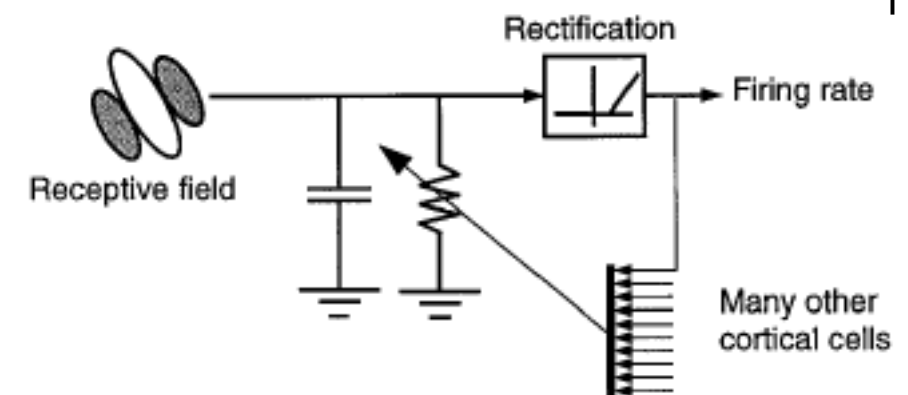


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### A Linear model



### B Normalization model



$$C \frac{dV}{dt} + gV = I$$

$$g = \frac{g_0}{\sqrt{1 - k \cdot \sum_{r \in R_x} r}}$$

$$R = \max(0, V)$$

measure R from neural data

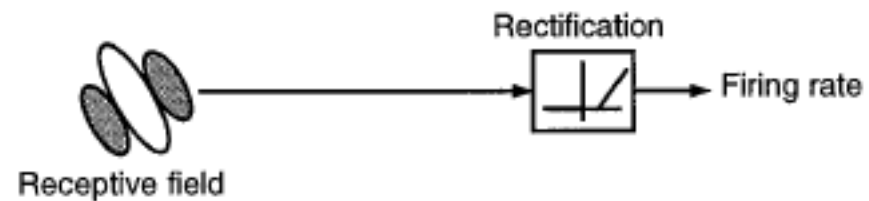
solve diff eq for equilibrium, estimate free parameters: C, k, g0





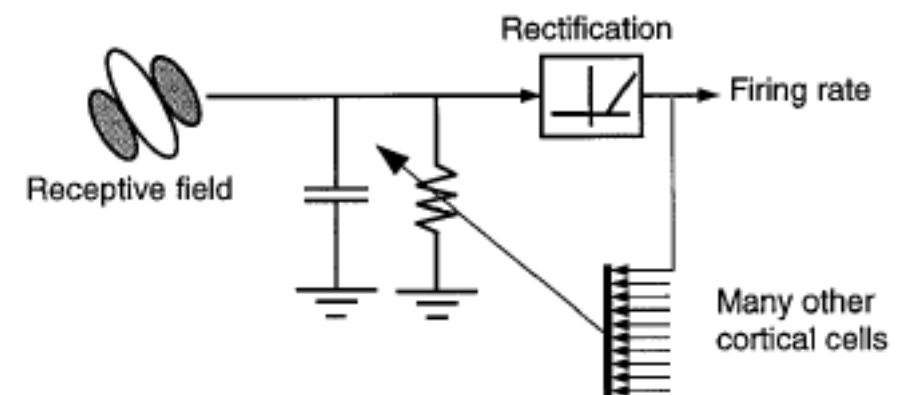
*Carandini, Heeger and Movshon (1997)*

### A Linear model



$$y = R [W * x]$$

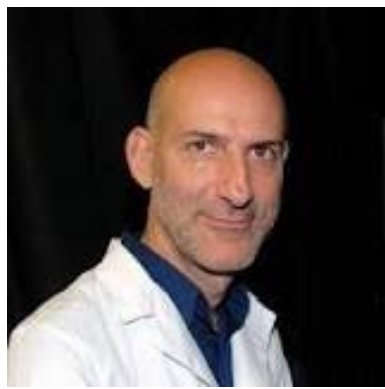
### B Normalization model



$$y = R [ \text{norm}(W * x) ]$$

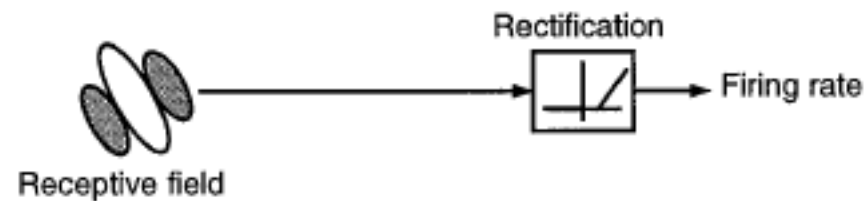
OR: derive this expression: ———>  
(basically)

$$\text{norm}(x) \sim \frac{x}{\left( \gamma + \alpha \cdot \sum_{r \in R_x} x_r^2 \right)^\beta}$$



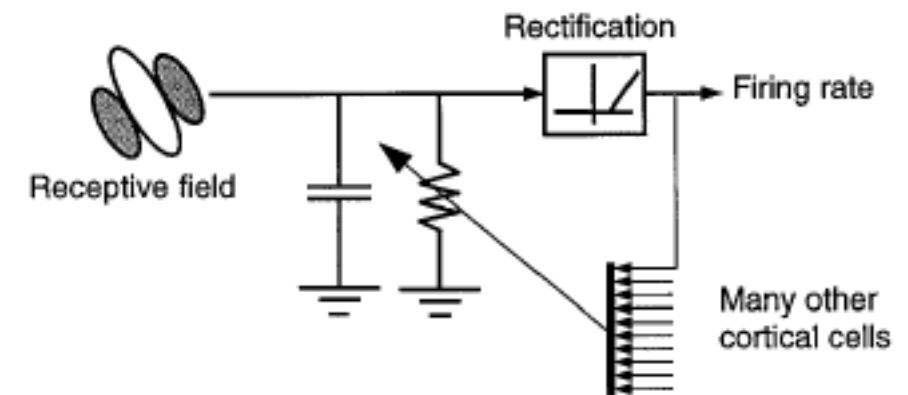
Carandini, Heeger and Movshon (1997)

### A Linear model



$$y = R [W * x]$$

### B Normalization model



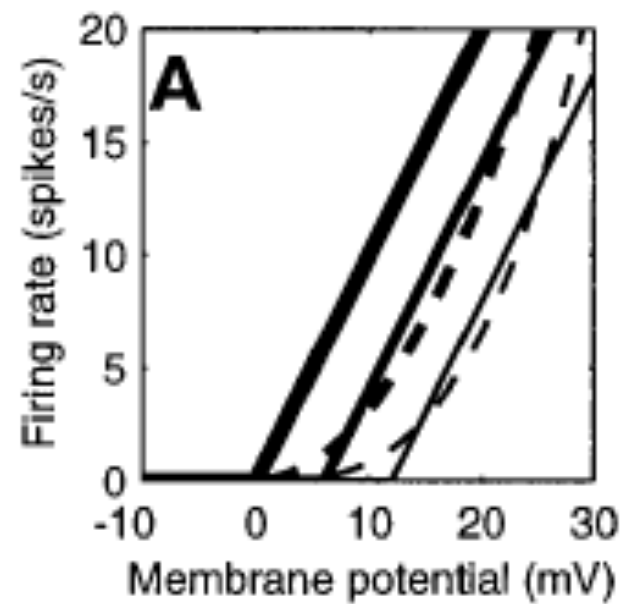
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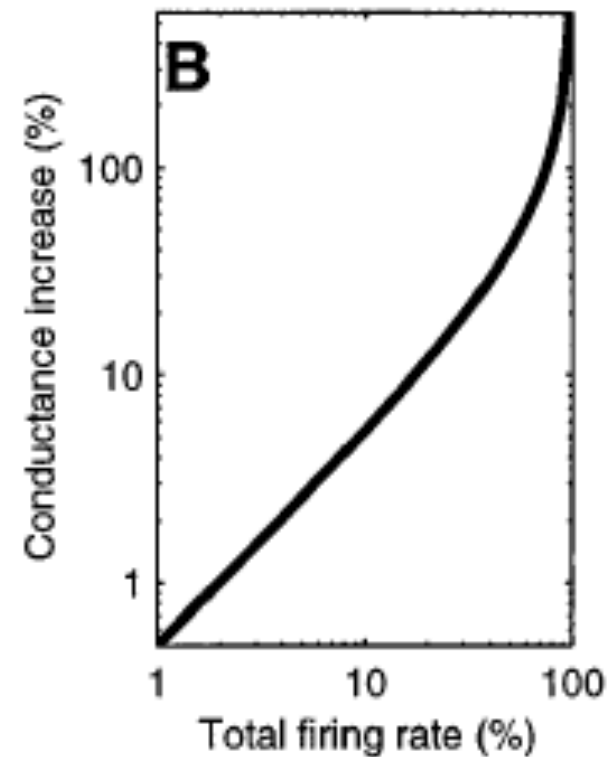
$$\text{norm}(x) \sim \frac{x}{\left( \gamma + \alpha \cdot \sum_{r \in R_x} x_r^2 \right)^\beta}$$

NB: (1) derivation involves “reasonable” assumption that “the normalization pool to contain quadruples of cells with the same amplitude response but with phases 90° apart.” (2) **The above is how we now define local response normalization**

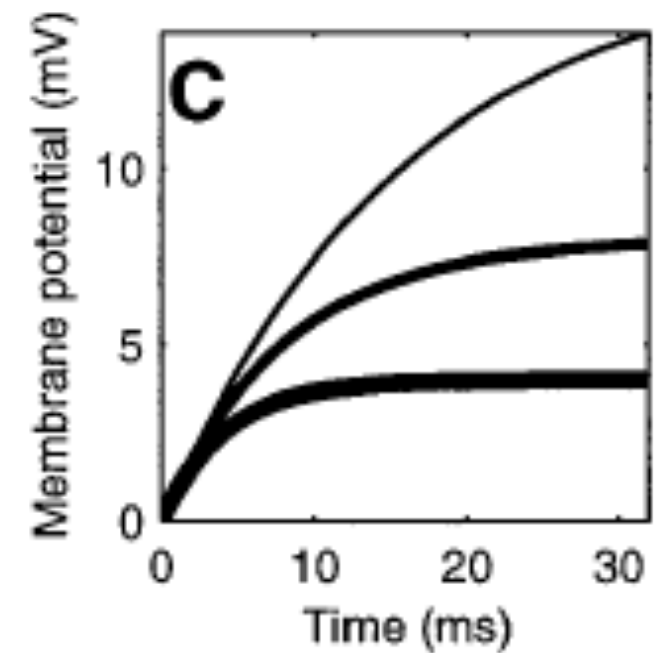
Interrelations and effects of the principal variables in the normalization model.



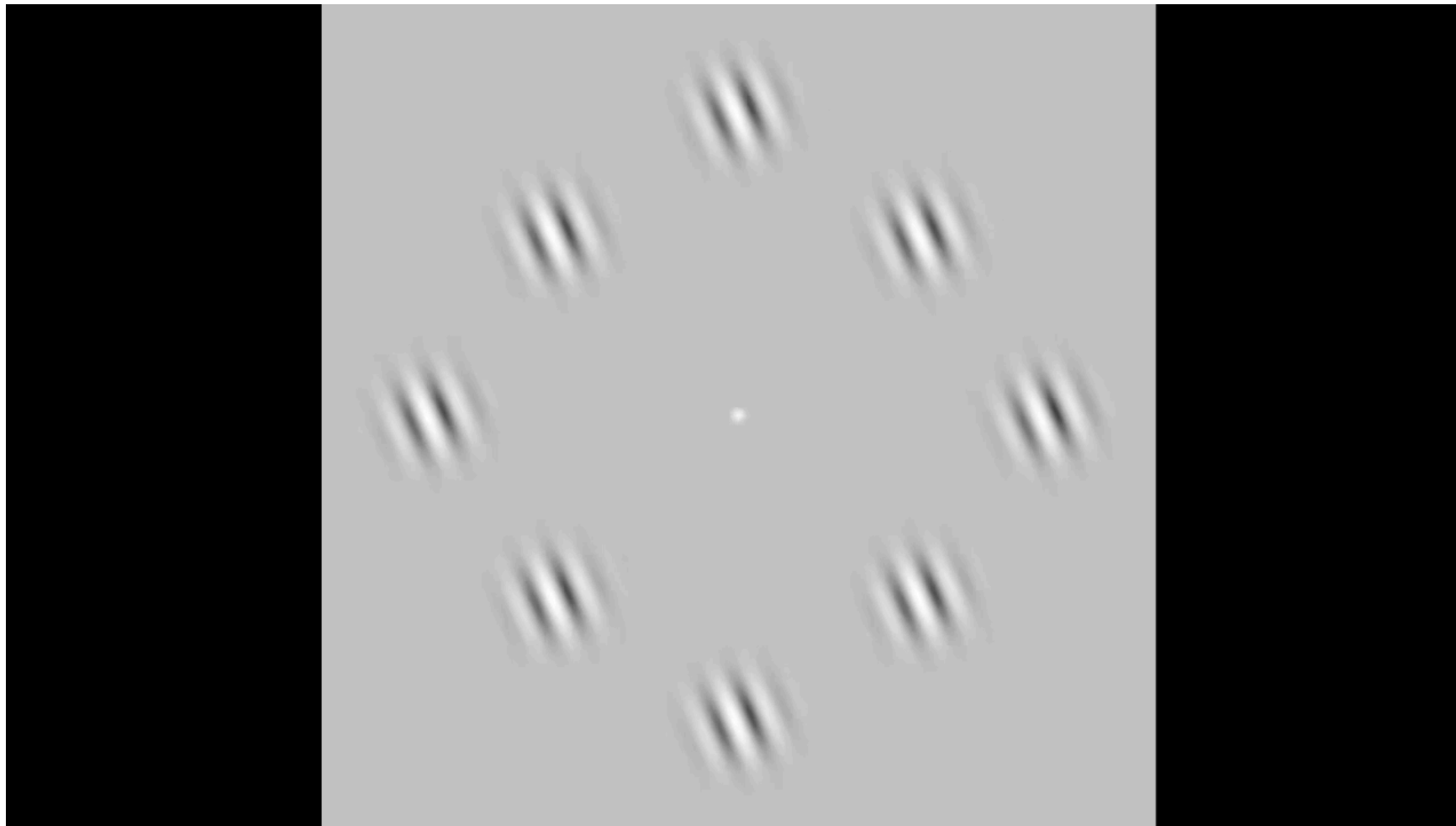
Relation between  
membrane potential  
and  
firing rate.



Relation between  
pool activity and  
membrane  
conductance.



Effects of  
conductance on  
the size and time  
course of the  
membrane  
potential.



The **I** in this equation:

$$C \frac{dV}{dt} + gV = I$$

is a sinusoid

$$\text{neural response} \sim A * \sin (w t + d)$$

A = amplitude of cell

w = frequency of the drift

d = phase of cell

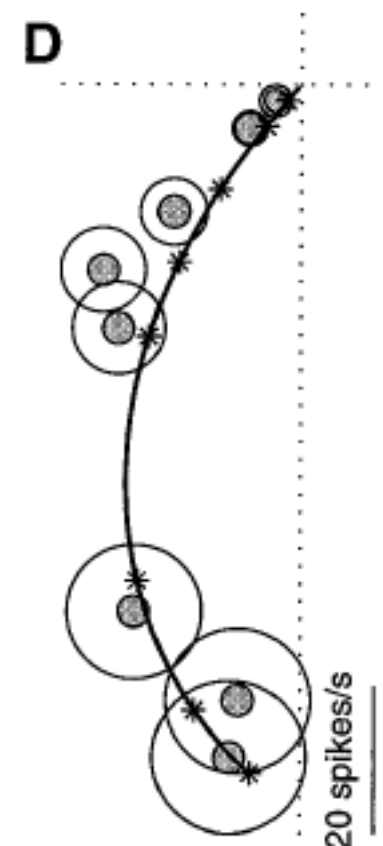
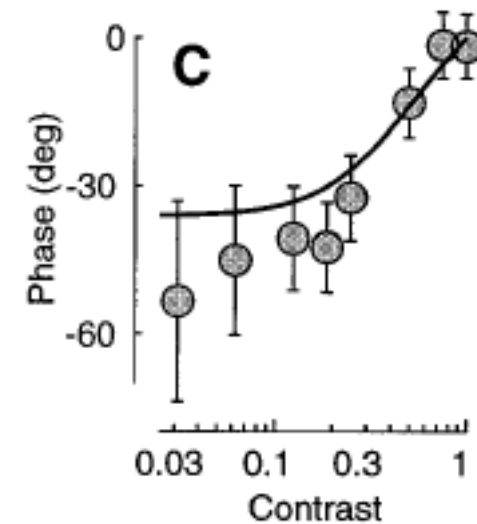
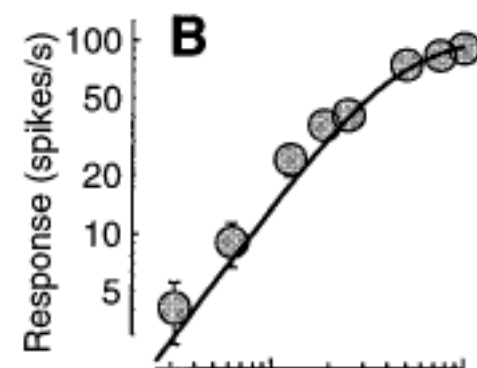
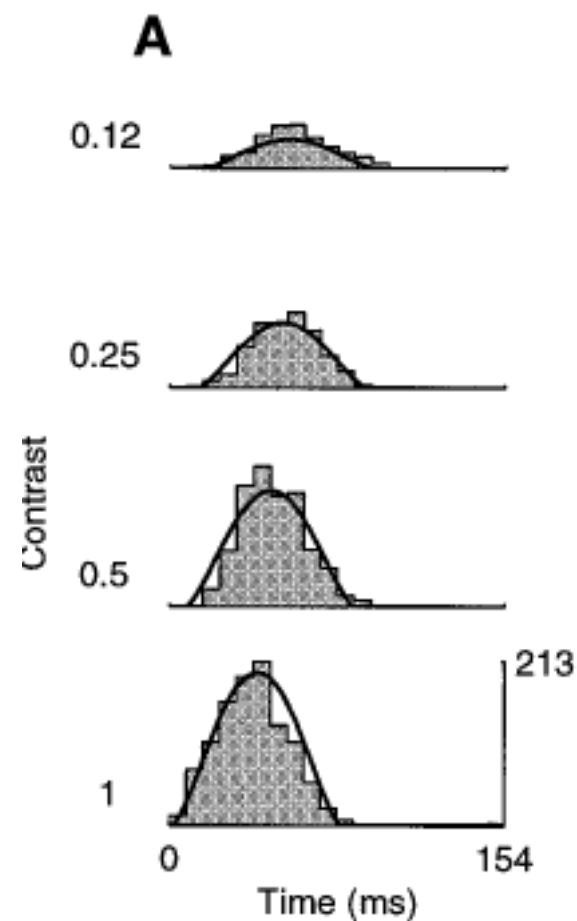
A, d are fit to the data



What functions are  $A$  and  $d$  of a stimulus parameter — contrast?

the parameters **C**, **k**, **A**, **d** (basically) are fit to the neuron over a bunch of stimulus conditions

histogram of responses for different contrasts

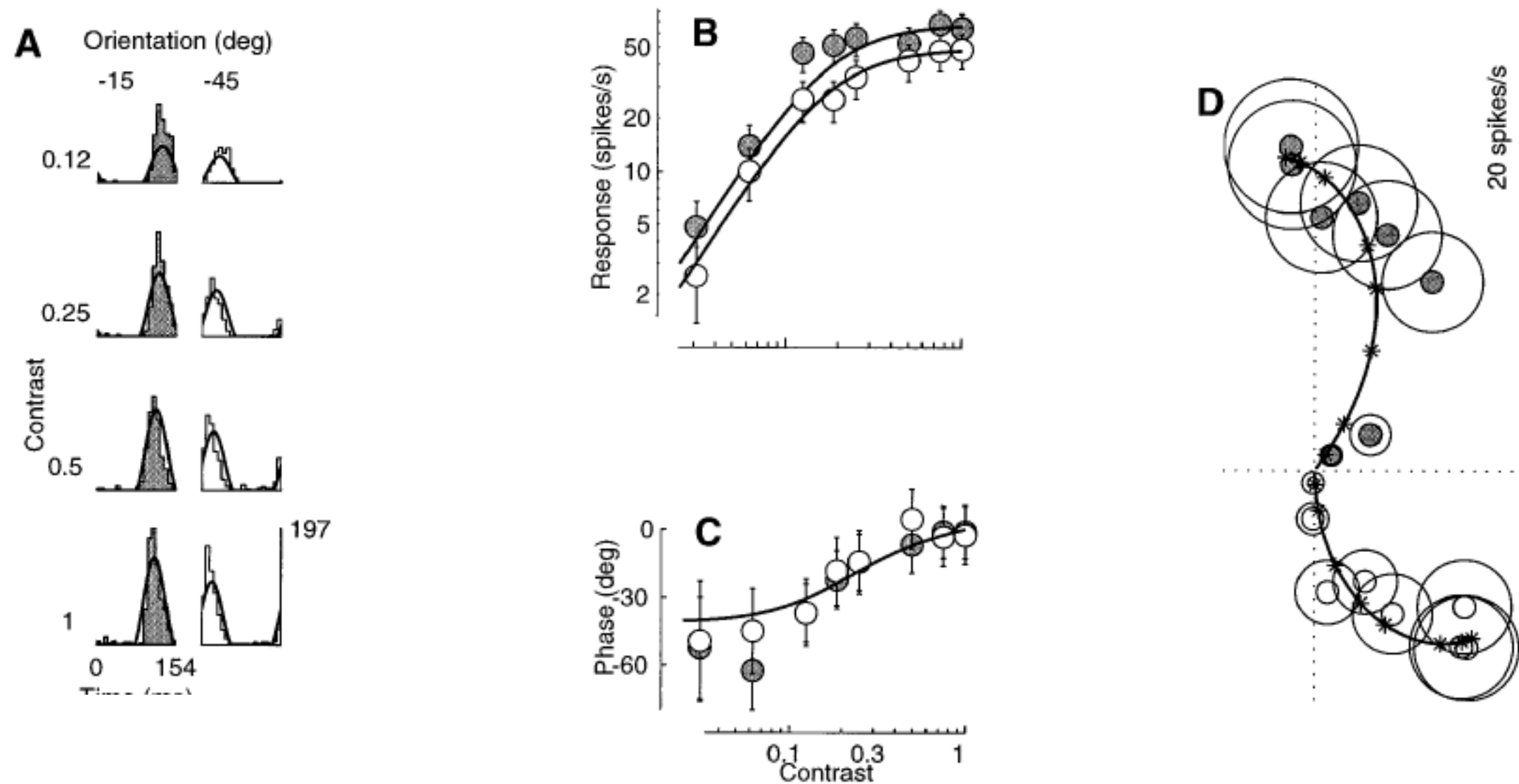


response vs phase

each point is response to a different sinusoid

Now as a function of grating orientation

*Carandini, Heeger and Movshon (1997)*

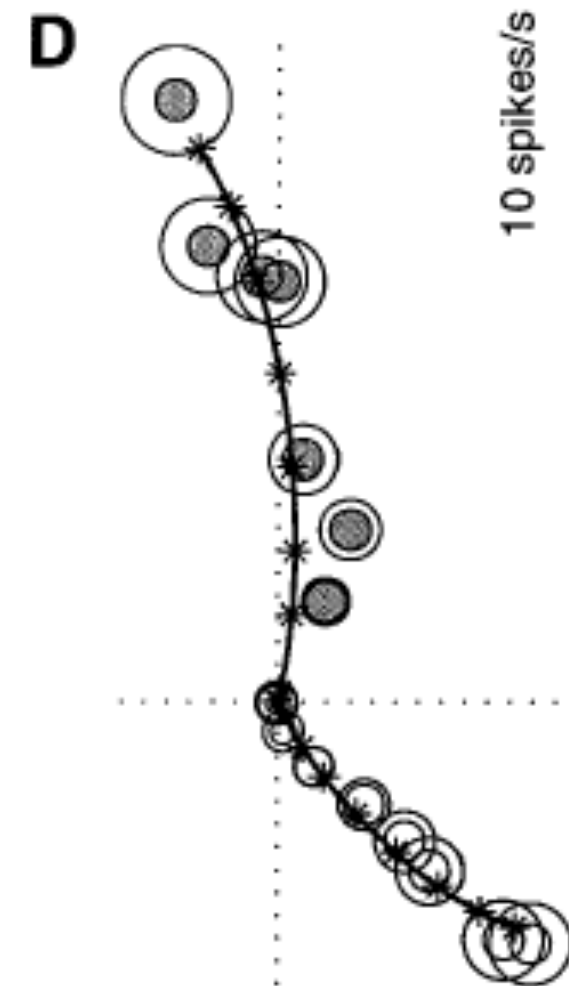
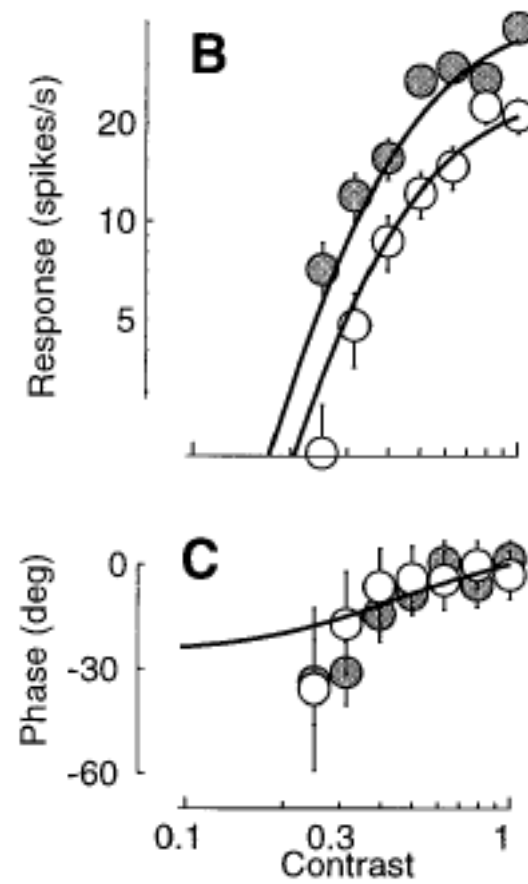
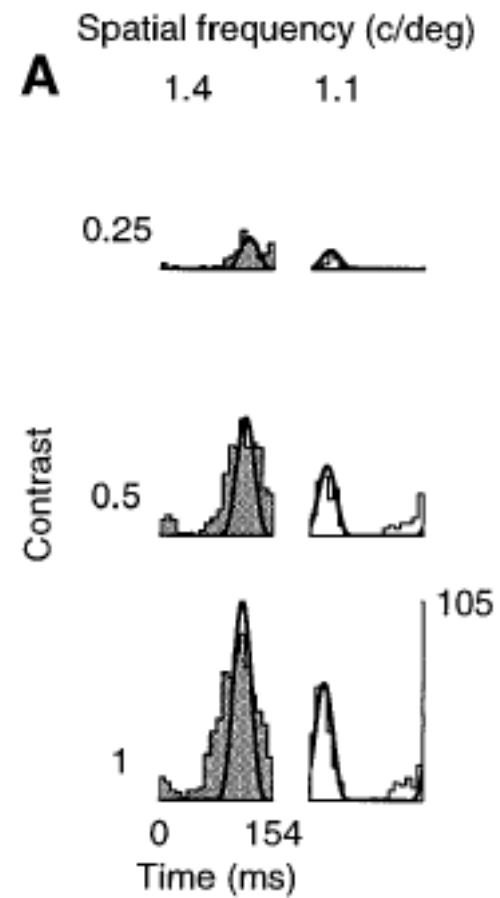


response vs phase

gray = -15deg, white = -45deg

Now as a function of spatial frequency

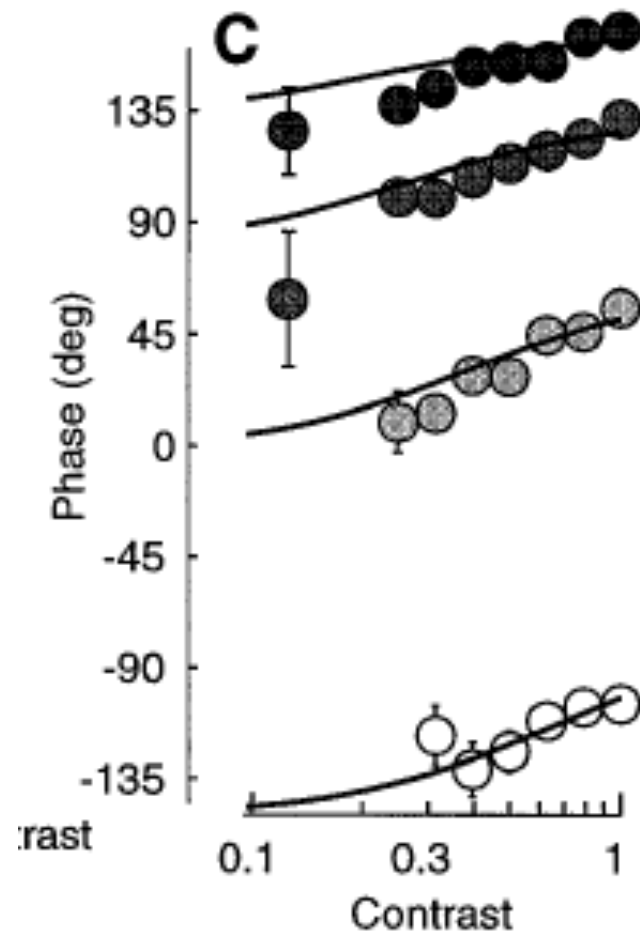
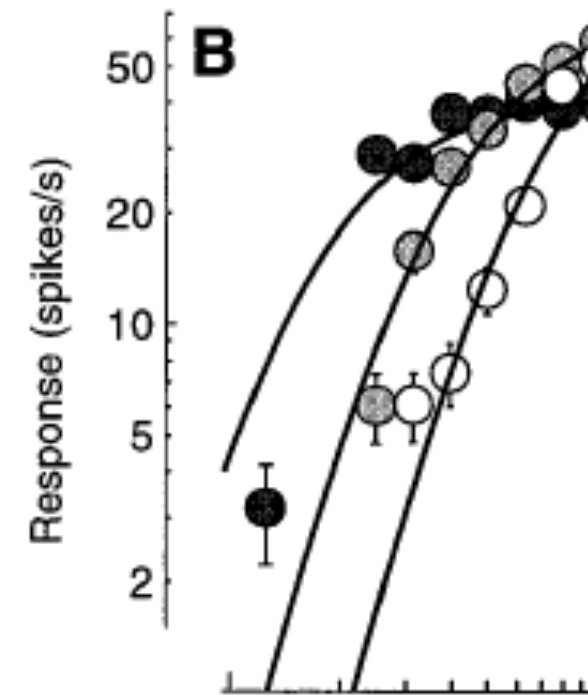
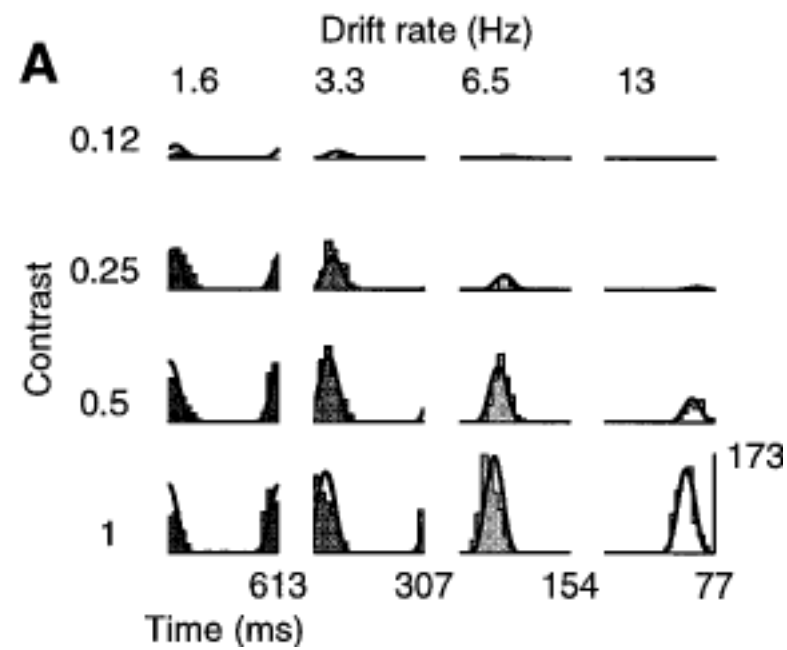
*Carandini, Heeger and Movshon (1997)*



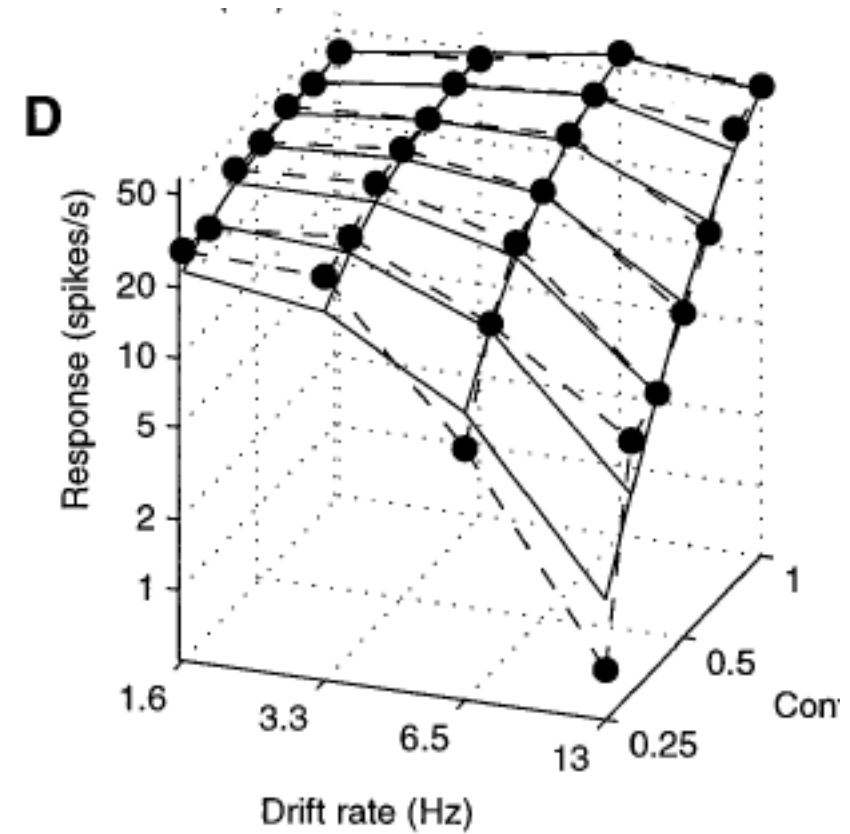
gray = 1.4 cyc/deg, white = 1.1 cyc/deg

Now as a function of temporal frequency

*Carandini, Heeger and Movshon (1997)*

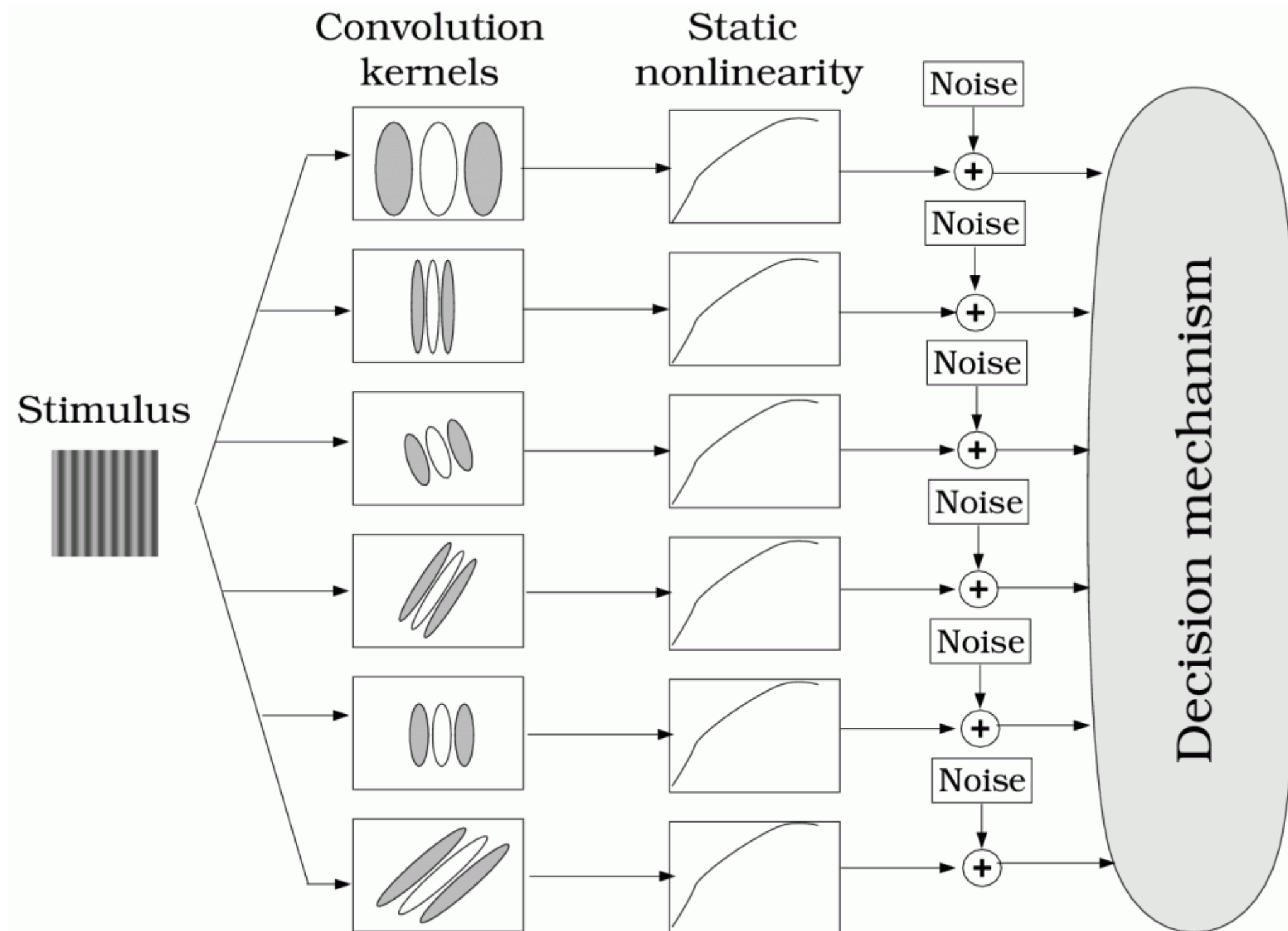


Colors  
as in  
panel **A**





# Goal: Predictive Model of Ventral Stream



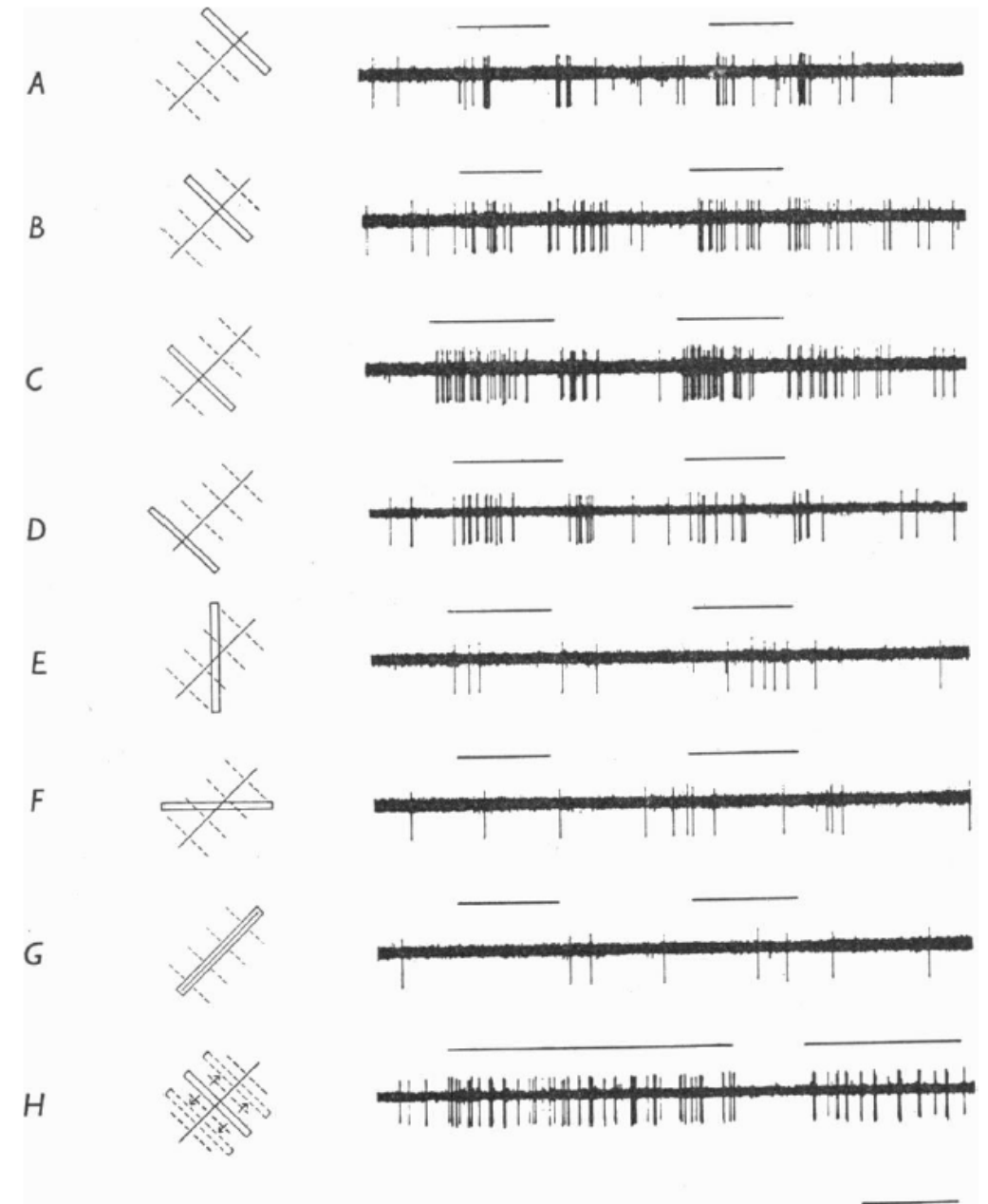
*from Wandell 1996*

# Pooling

More generally, it was realized in computer vision that **pooling** was a good idea.

recall Hubel & Wiesel's complex cell >>

$$y = \left( \frac{1}{|N_r|} \sum_{i \in N_r} x_i^p \right)^{1/p}$$

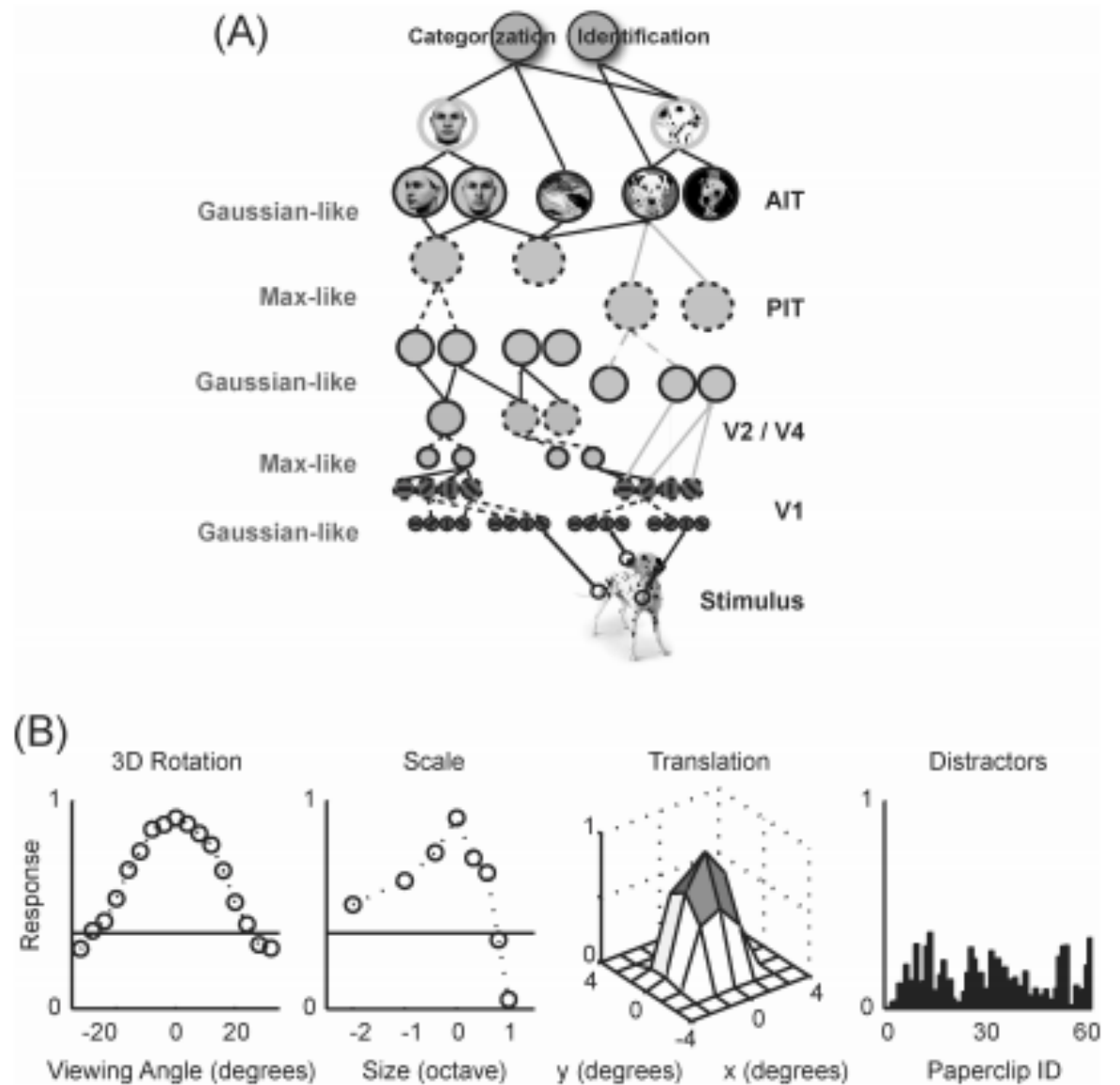


(Actually, if you're running a CNN, you basically *\*have\** to do pooling + downsampling, for memory reasons.)

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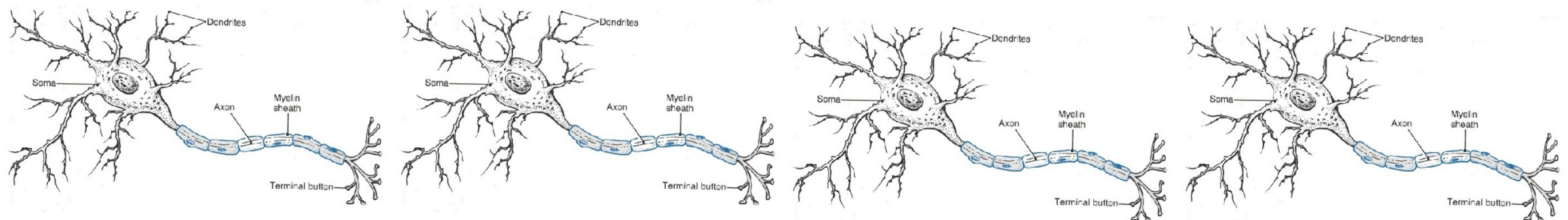
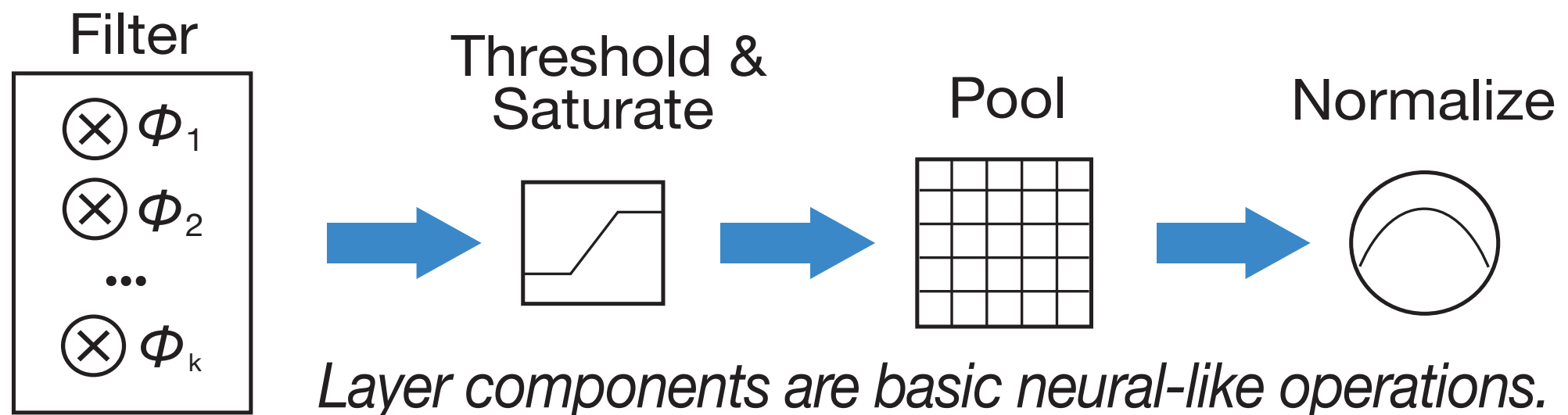


from Kouh and Poggio (2008)

(Actually, if you're running a CNN, you basically *\*have\** to do pooling + downsampling, for memory reasons.)

# Linear-Nonlinear Operations

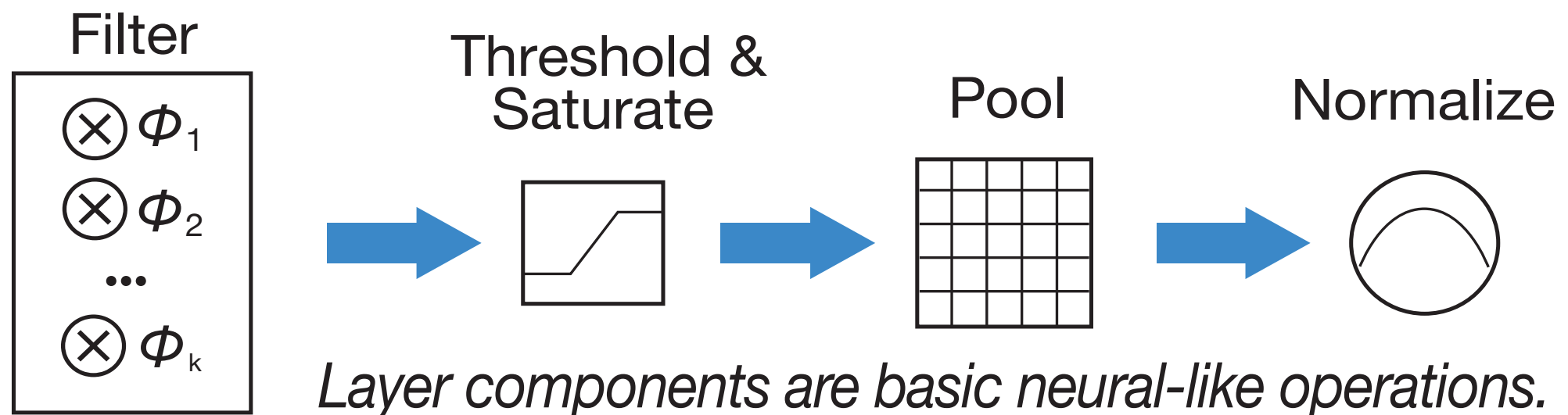
- Linear-Nonlinear neurally-plausible **basic operations** within layer





# Linear-Nonlinear Operations

- ▶ Linear-Nonlinear neurally-plausible **basic operations** within layer

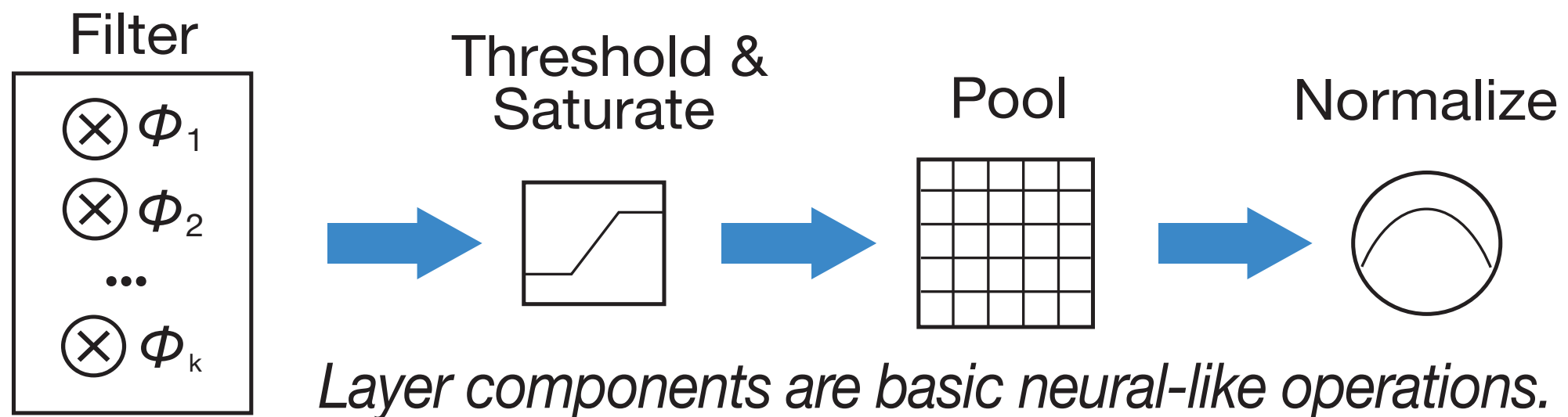


neuro: synaptic  
weights  
patterns

data: untangling  
through  
dimension  
expansion

# Linear-Nonlinear Operations

- ▶ Linear-Nonlinear neurally-plausible **basic operations** within layer



**neuro:** synaptic weights patterns

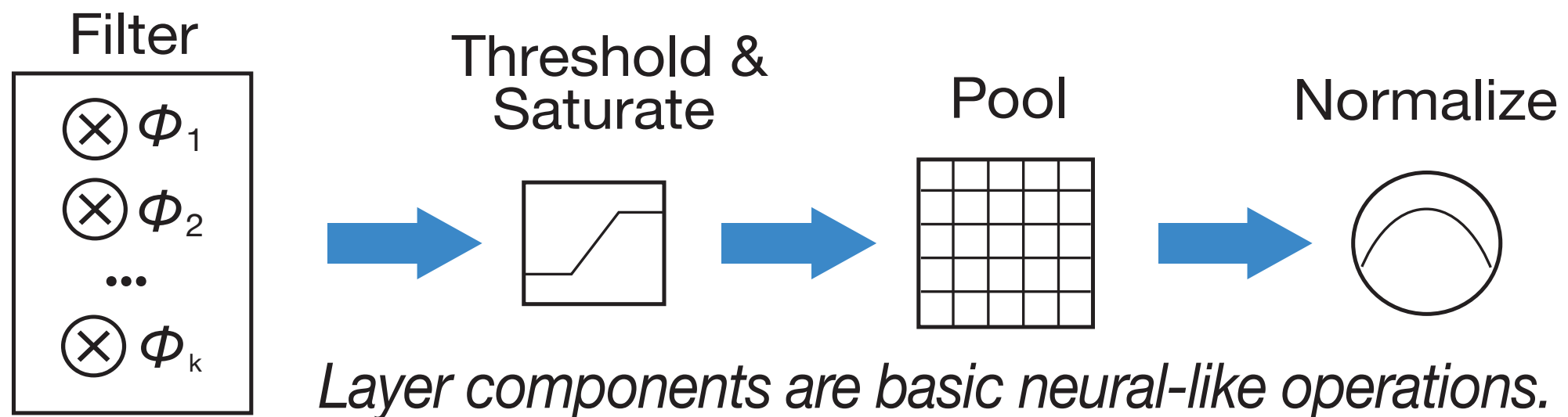
single-unit activations

**data:** untangling through dimension expansion

“AND” operation by limiting dynamic range

# Linear-Nonlinear Operations

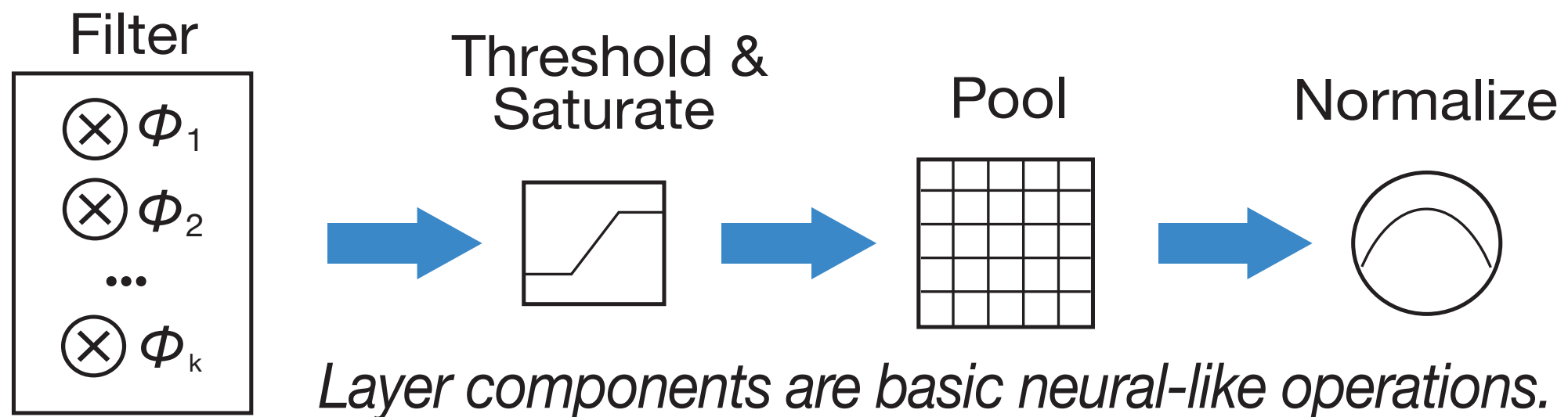
- ▶ Linear-Nonlinear neurally-plausible **basic operations** within layer



<b>neuro:</b>	synaptic weights patterns	single-unit activations	complex cells
<b>data:</b>	untangling through dimension expansion	“AND” operation by limiting dynamic range	adding robustness by dimension reduction

# Linear-Nonlinear Operations

- Linear-Nonlinear neurally-plausible **basic operations** within layer

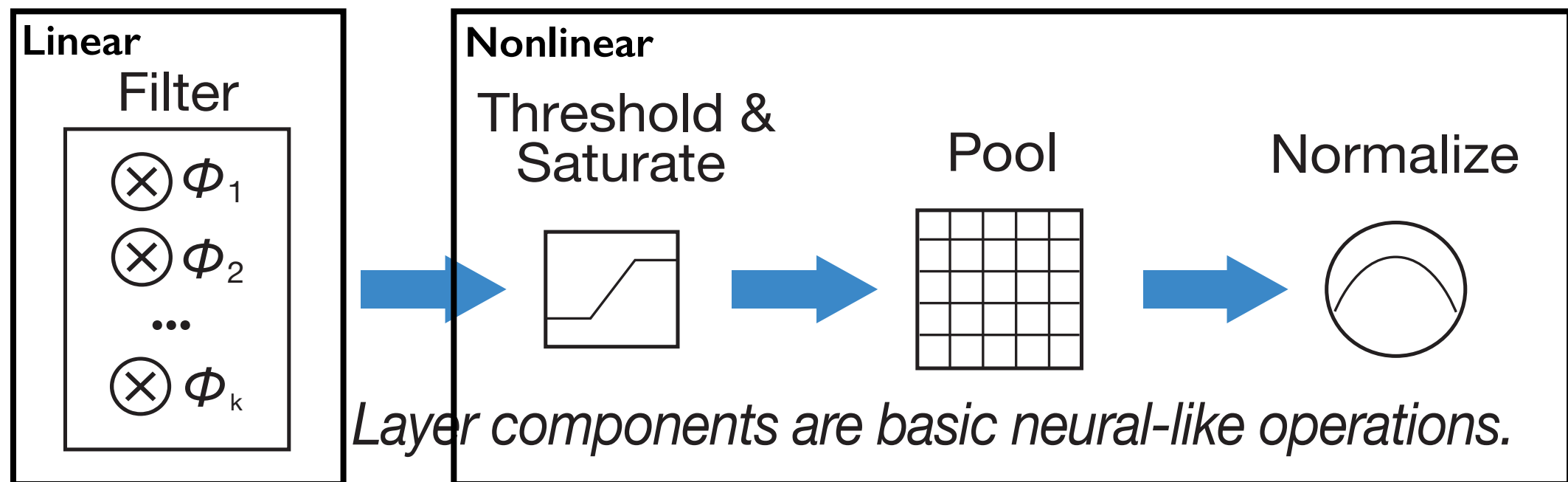


<b>neuro:</b>	synaptic weights patterns	single-unit activations	complex cells	competitive inhibition
<b>data:</b>	untangling through dimension expansion	“AND” operation by limiting dynamic range	adding robustness by dimension reduction	put results back into standard range



# Linear-Nonlinear Operations

- Linear-Nonlinear neurally-plausible **basic operations** within layer



**neuro:** synaptic weights patterns

single-unit activations

complex cells

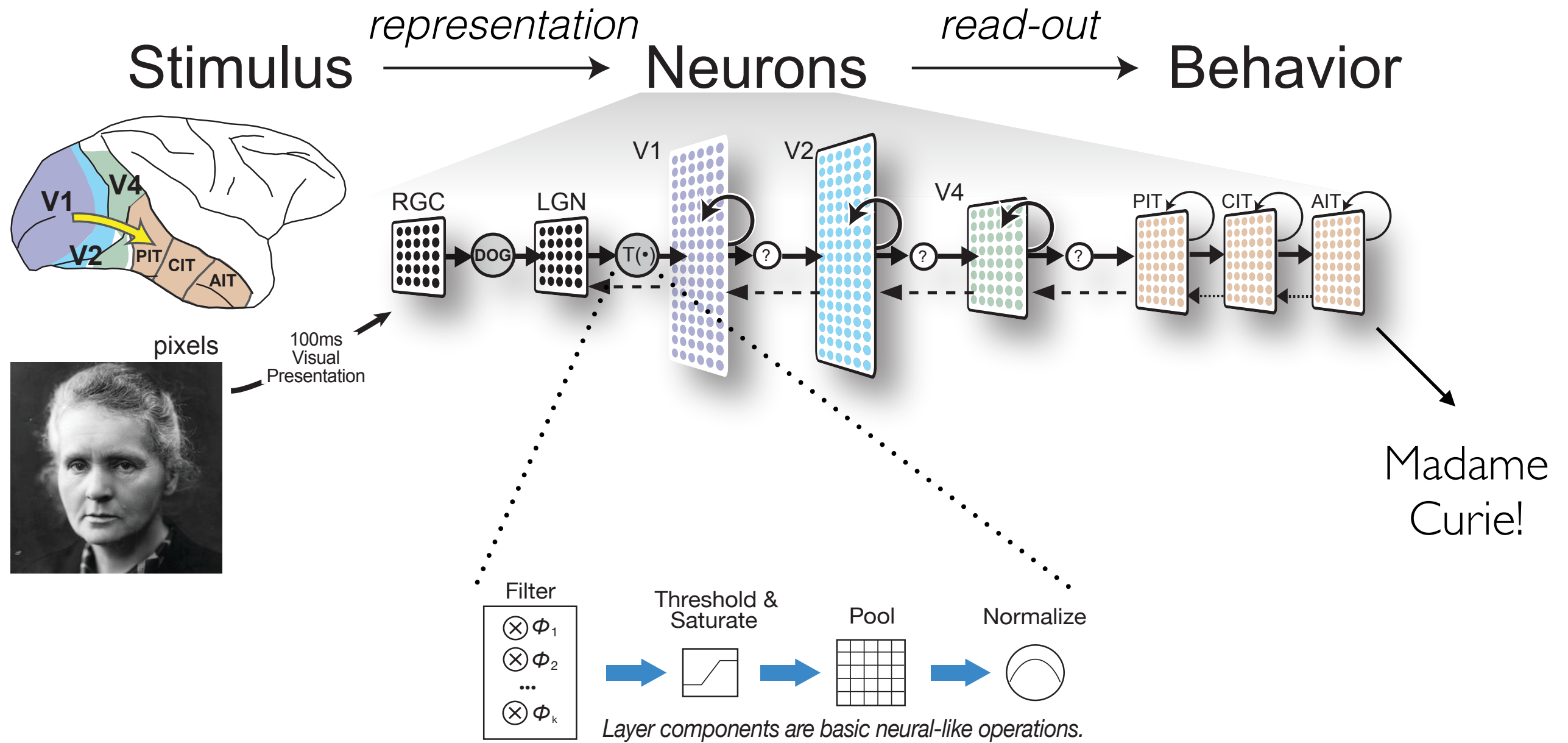
competitive inhibition

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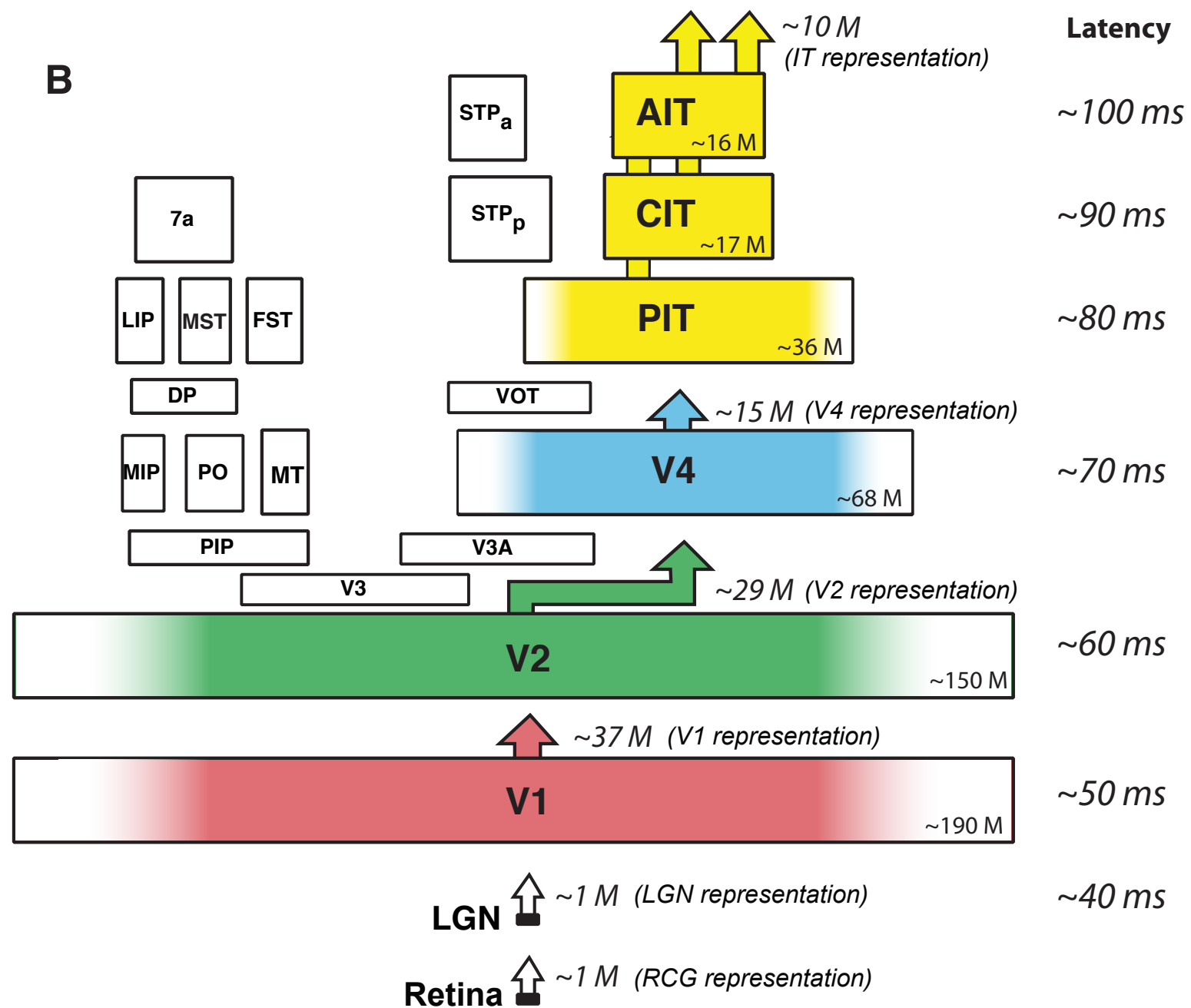
adding robustness by dimension reduction

put results back into standard range

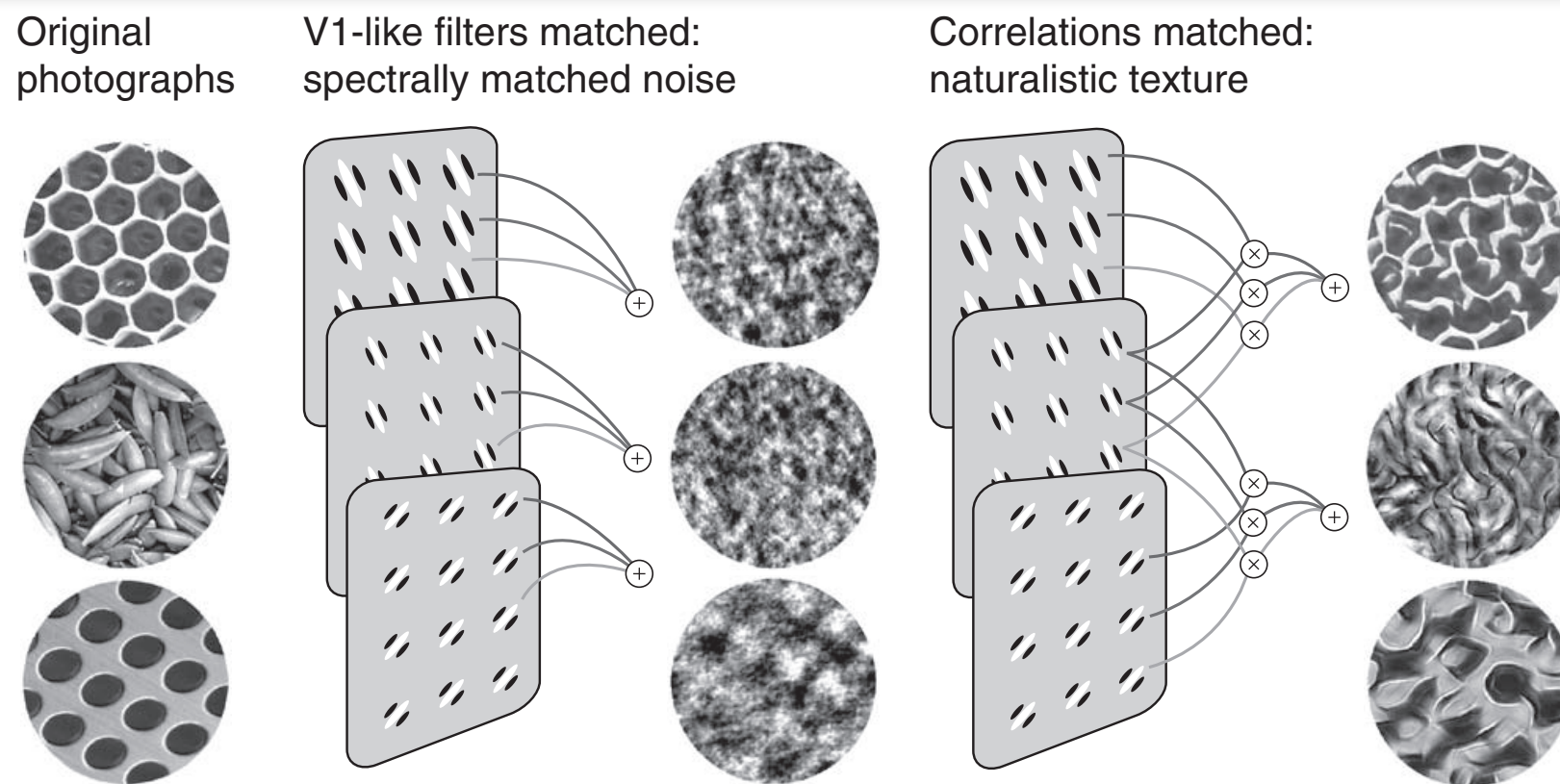


Linear-Nonlinear neurally-plausible **basic operations** within layer

You are here.



# Area V2 (first cortical area after V1):



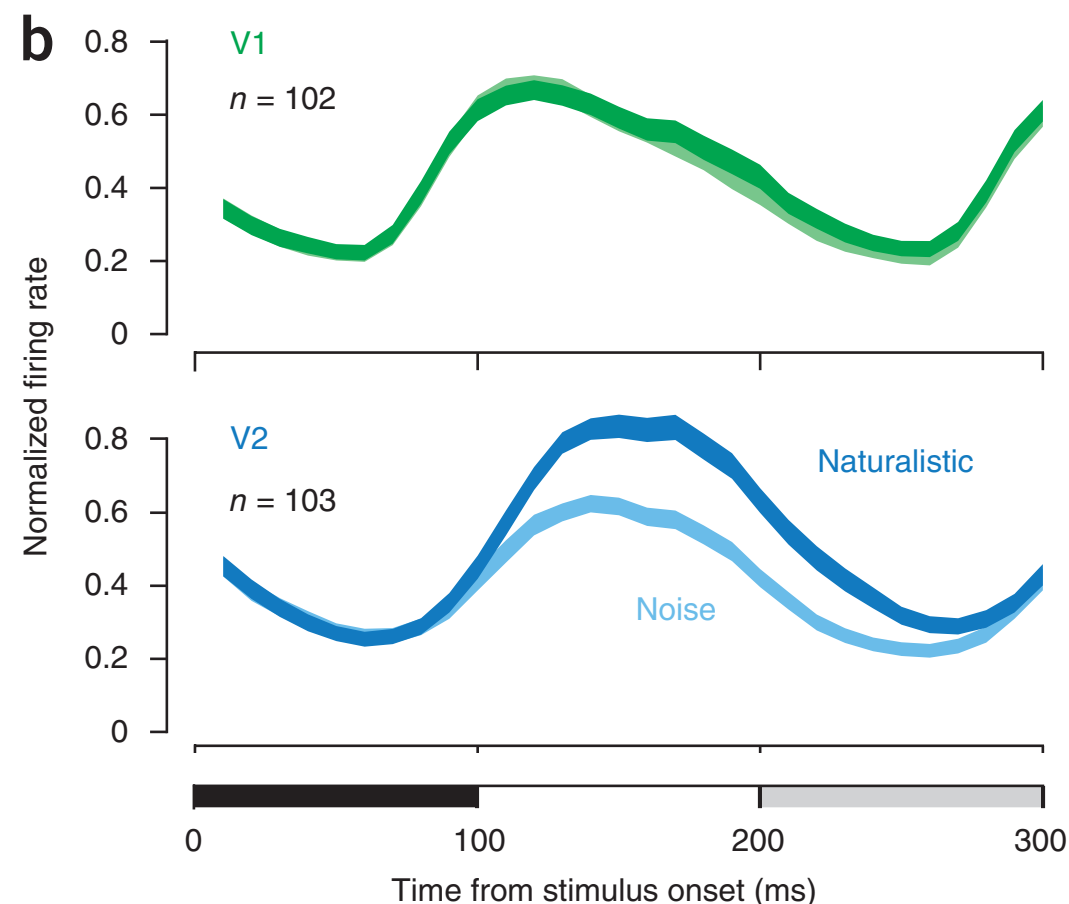
Eero Simoncelli



Tony Movshon



Jeremy Freeman



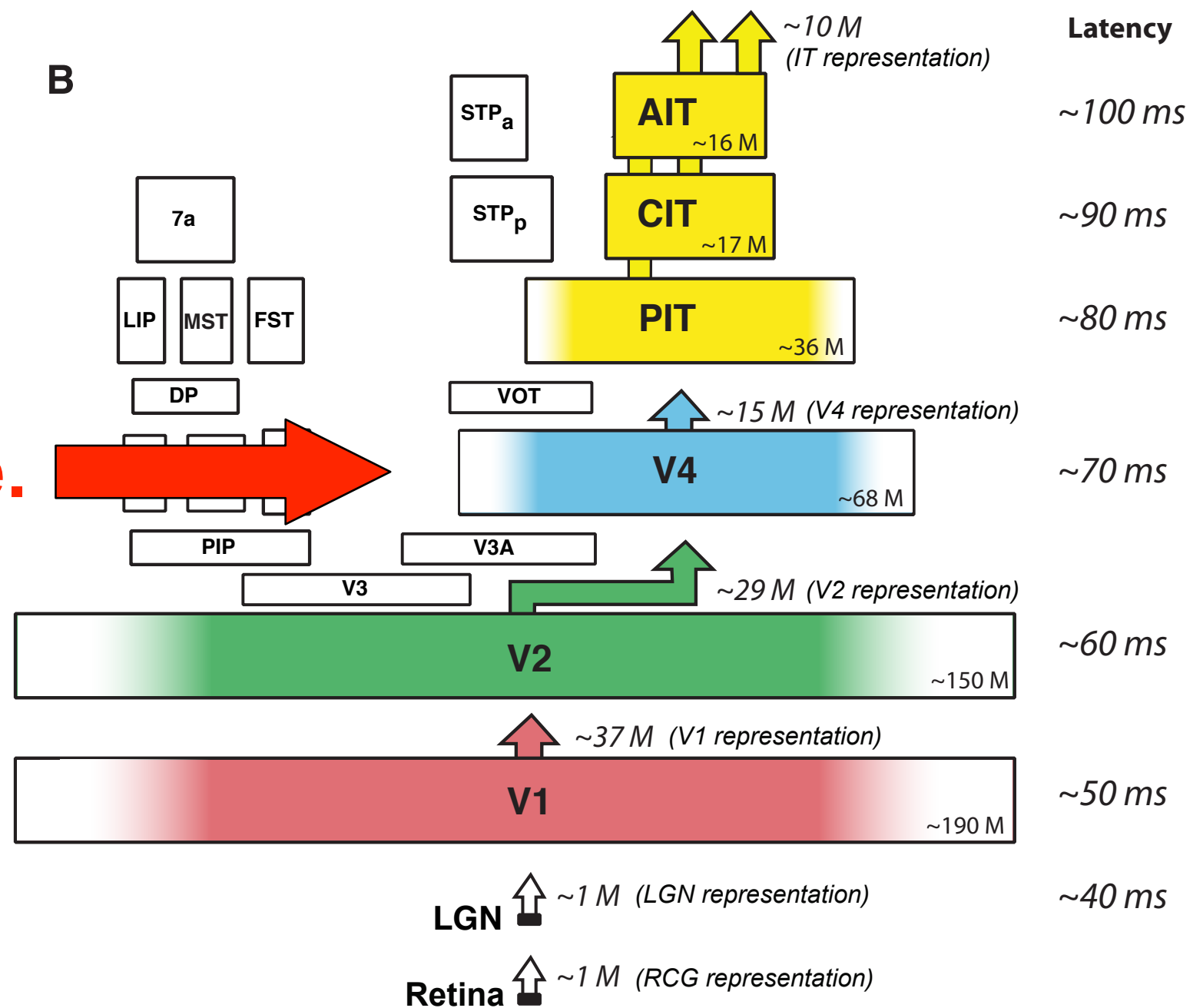
Interpretation:

- V2 neurons apply “and-like” operators on V1 outputs
- those “ands” are tuned toward natural co-occurring V1 statistics

**So, maybe a hierarchically-built sparse auto-encoding in a 2-layer model with max pooling??**



You are here.



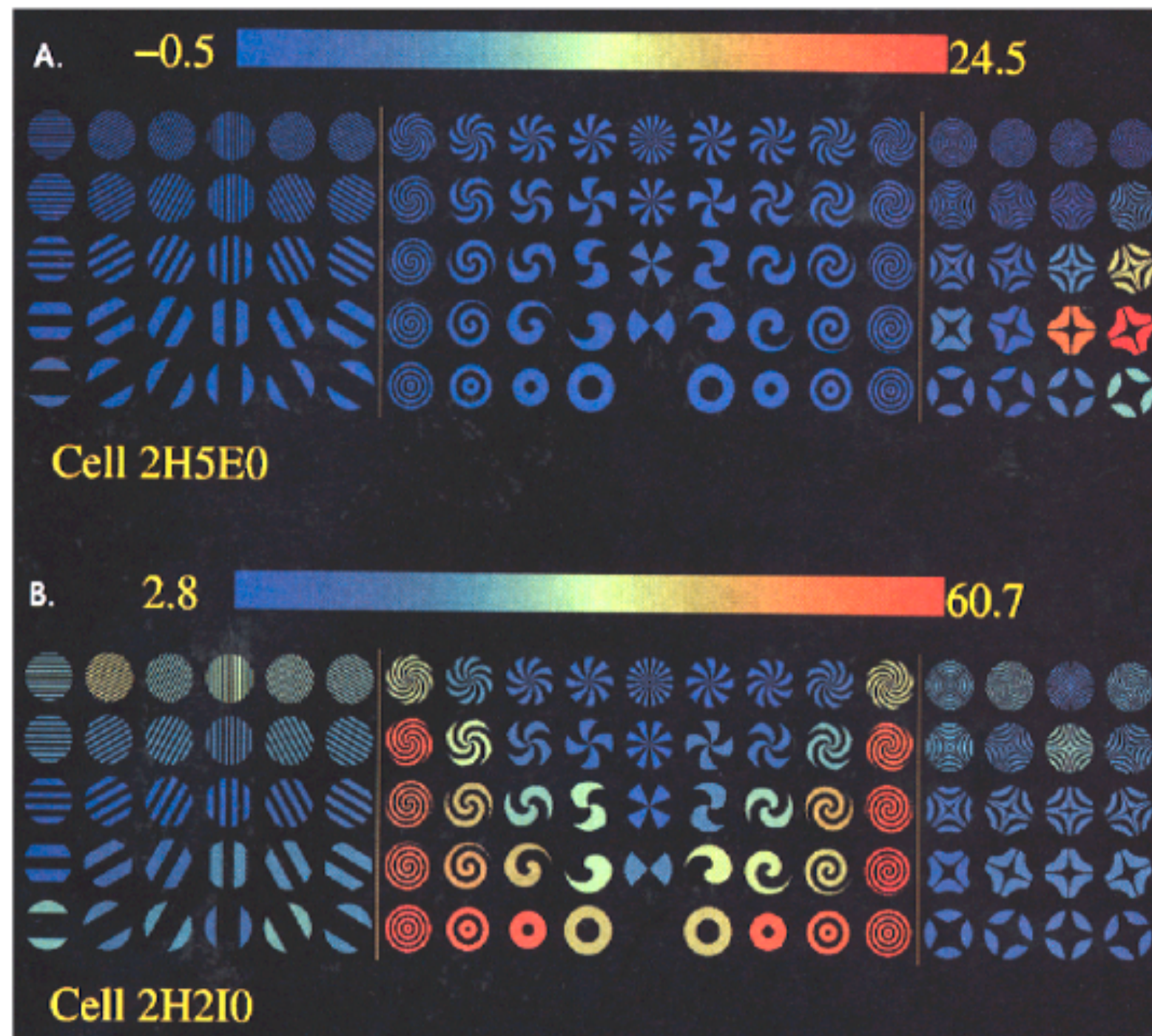
# Area V4 (cortical area after V2):

## V4 Responses to Non-Cartesian Gratings

Gallant et al. 1996



Jack Gallant

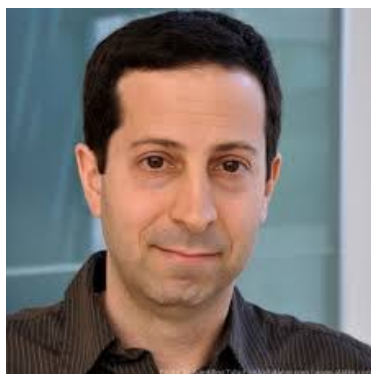




# Area V4 (cortical area after V2):



Anitha Pasupathy



Scott Brincat



Ed Connor

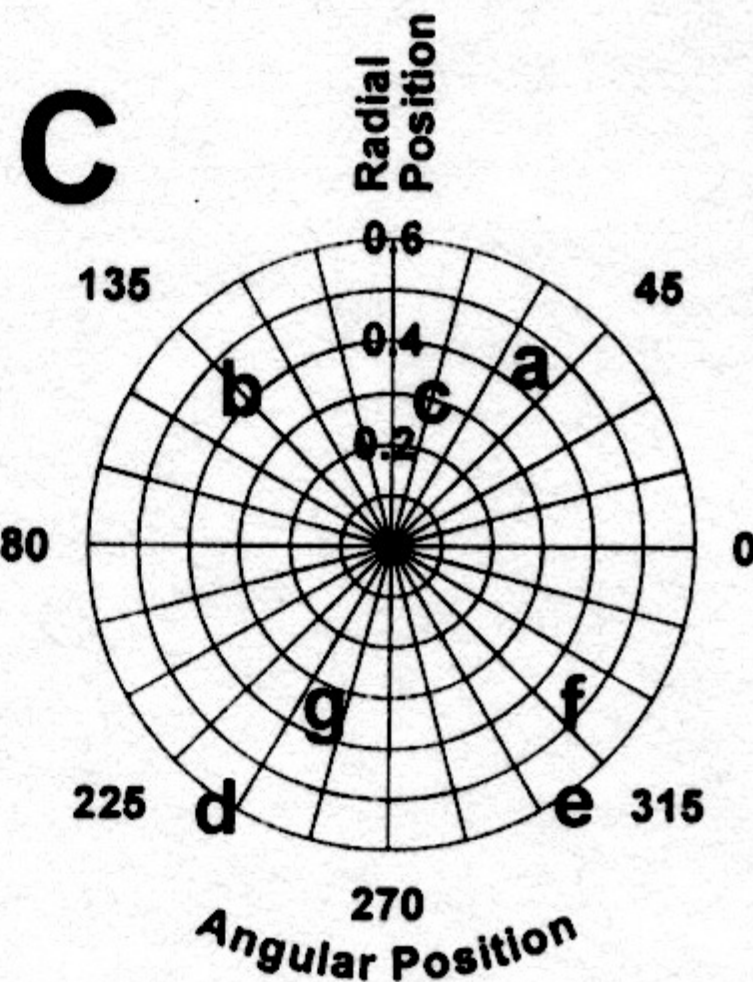
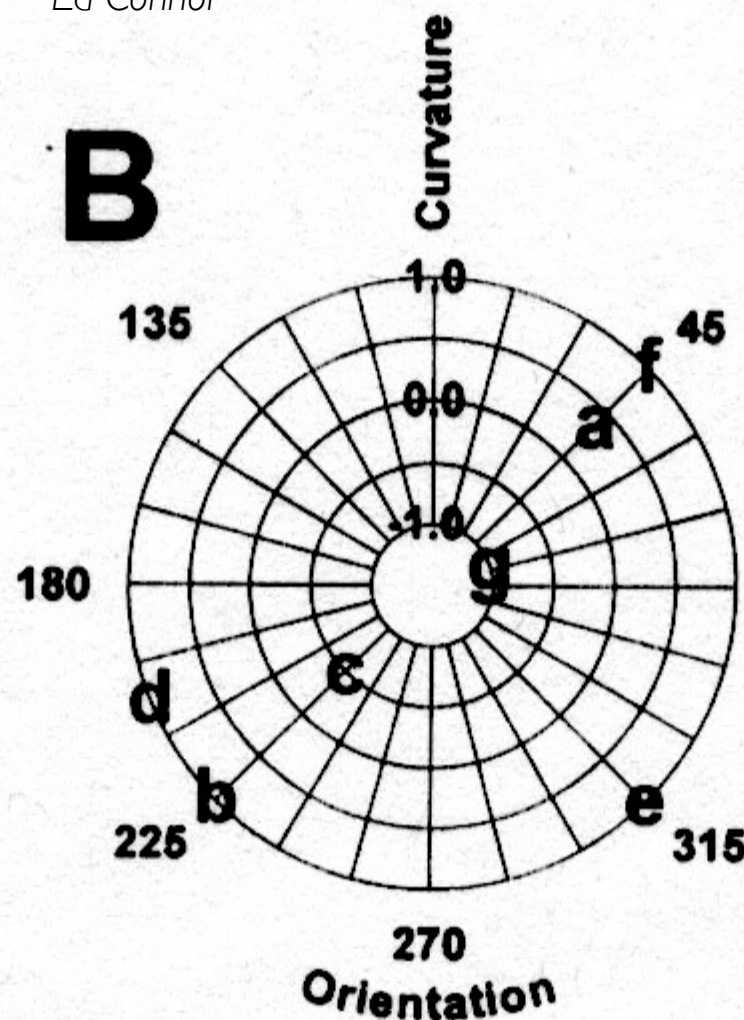
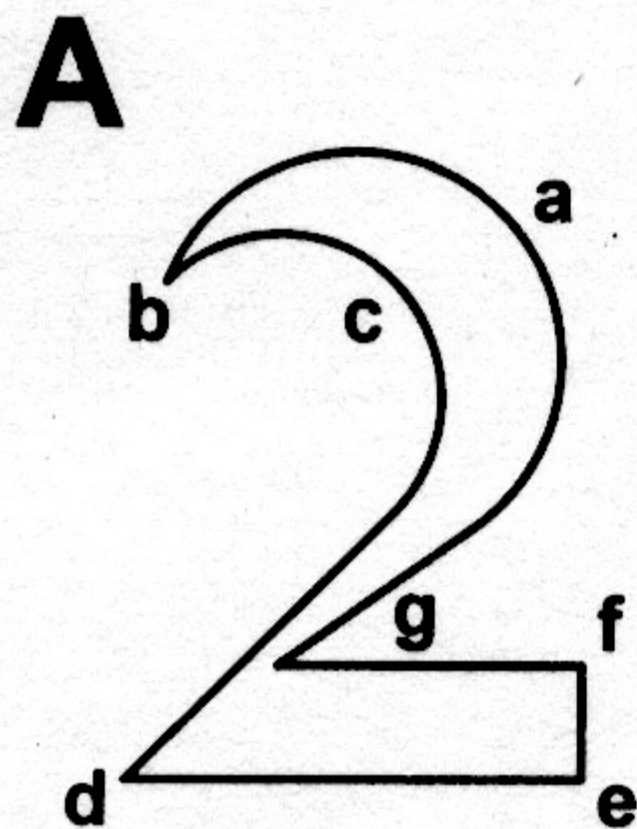
Make a basis for shapes:

each shape = set of curved elements

each element = (ang position, curvature)

Hypothesis:

V4 neurons are tuned in this basis



A structural (parts-based) shape-coding scheme based on contour fragments. *A*, The example shape, a bold numeral 2, can be decomposed into contour fragments (*a-g*) with different curvatures, orientations, and positions. *B*, The curvature and orientation of each contour fragment is plotted on a 2-D domain. *C*, The positions of the contour fragments (relative to the object center) are plotted on a 2-D domain. Together, plots *B* and *C* represent a 4-D domain for describing contour fragments.

# What shape features drive V4 response?

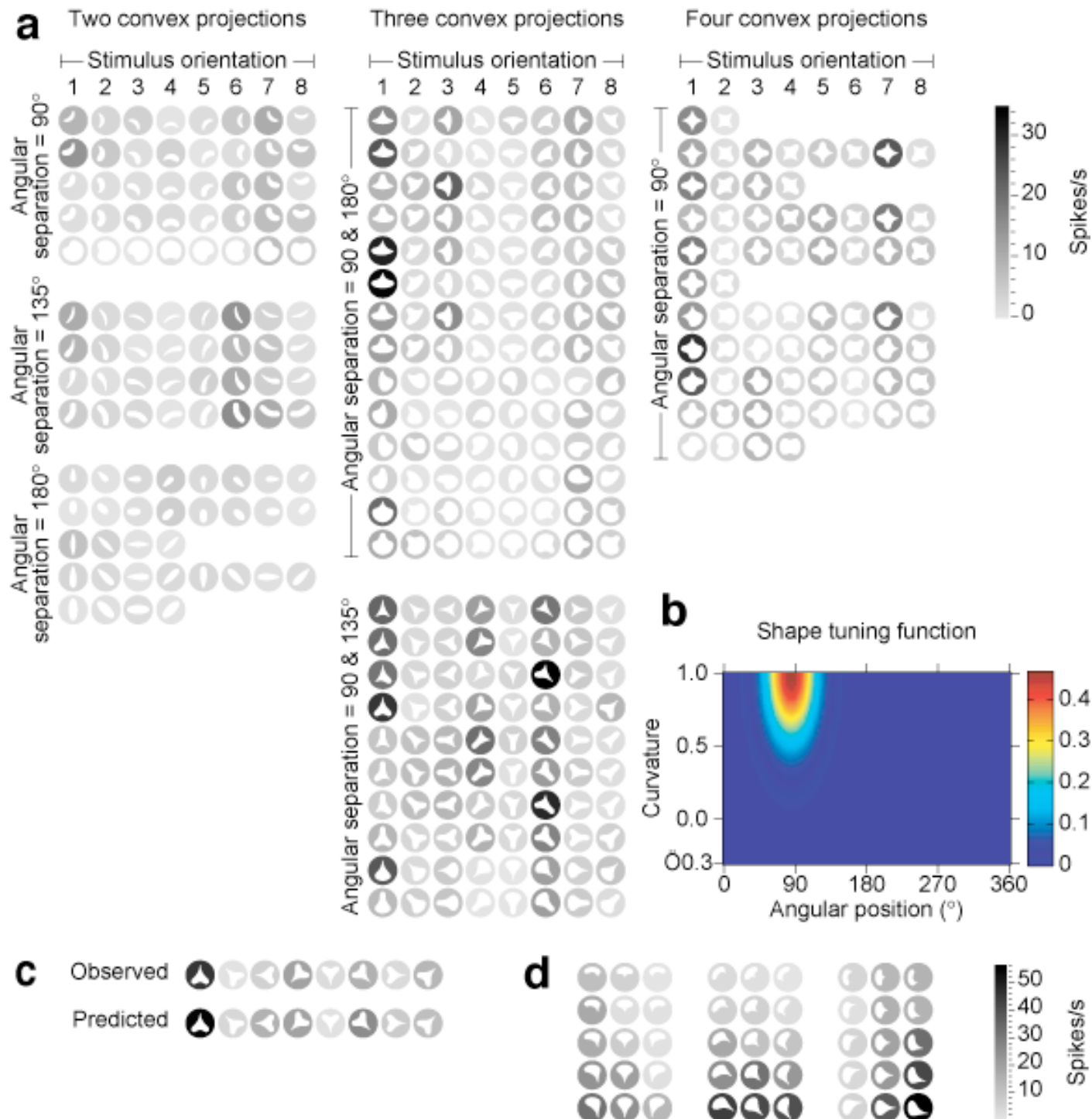
*Adapted from C.E. Connor*

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*Pasupathy and Connor (V4)*  
*Brincat and Connor (PIT)*



# What shape features drive V4 response?

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Make a basis for shapes:

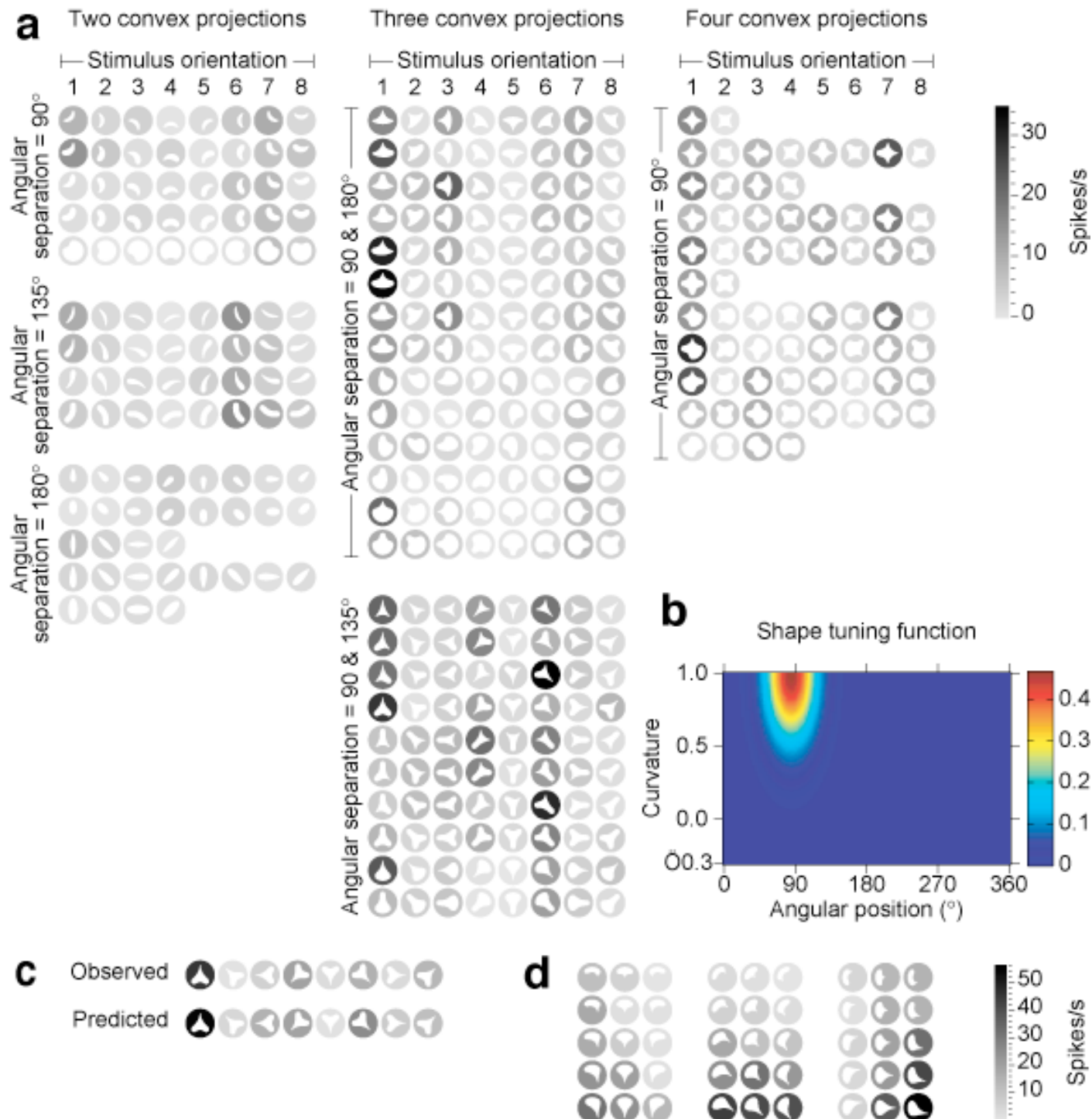
each shape = set of curved elements  
each element = (ang position, curvature)

Hypothesis:

V4 neurons are tuned in this basis

### Experimental result:

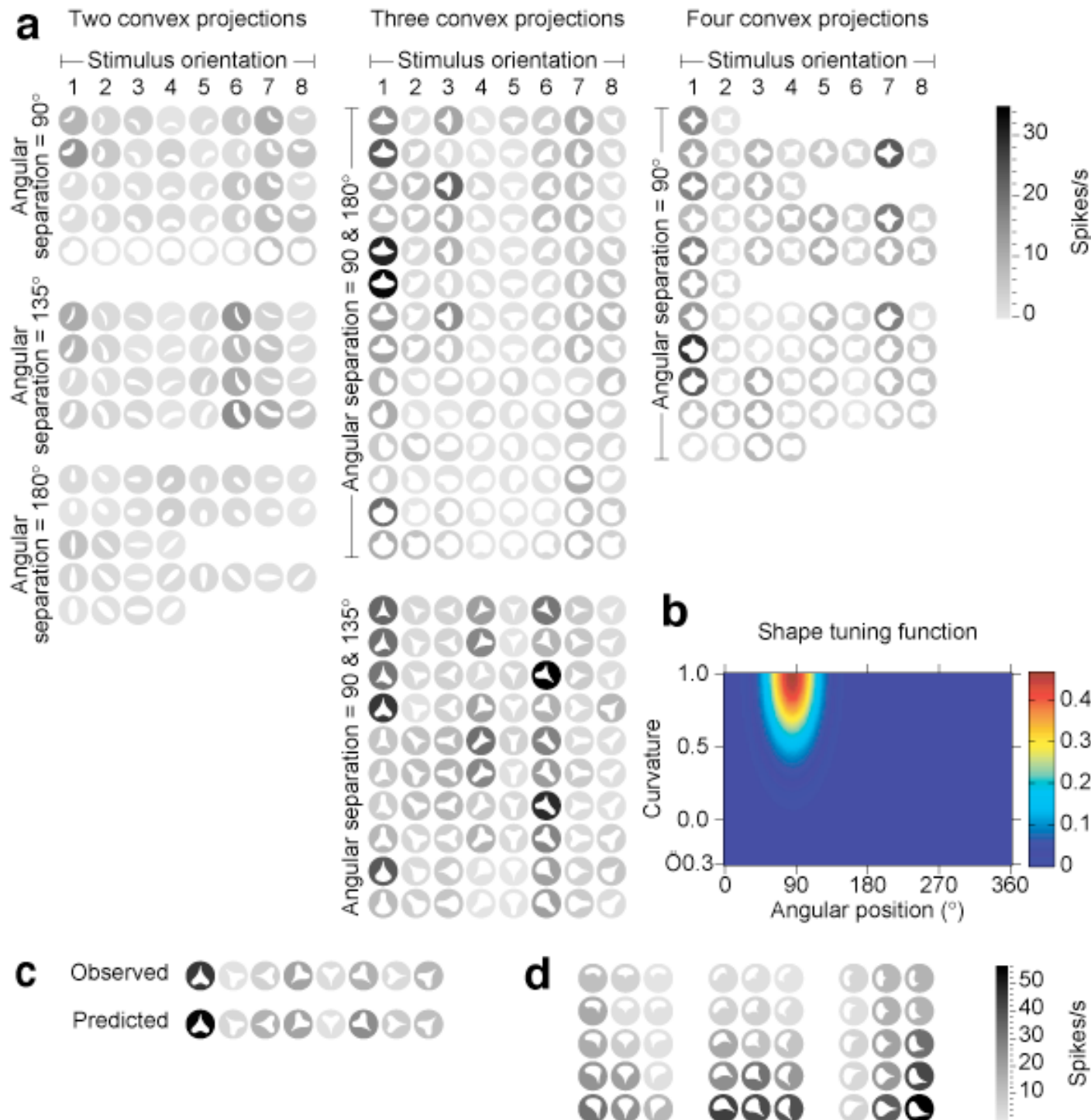
Hypothesis explains ~50% of the explainable response variance for these types of stimuli



Pasupathy and Connor (V4)  
Brincat and Connor (PIT)

# What shape features drive V4 response?

*Adapted from C.E. Connor*



Make a basis for shapes:

each shape = set of curved elements

each element = (ang position, curvature)

Hypothesis:

V4 neurons are tuned in this basis

Experimental result:

Hypothesis explains ~50% of the explainable response variance for these types of stimuli

**Problem:**

**No predictions for any other images.**

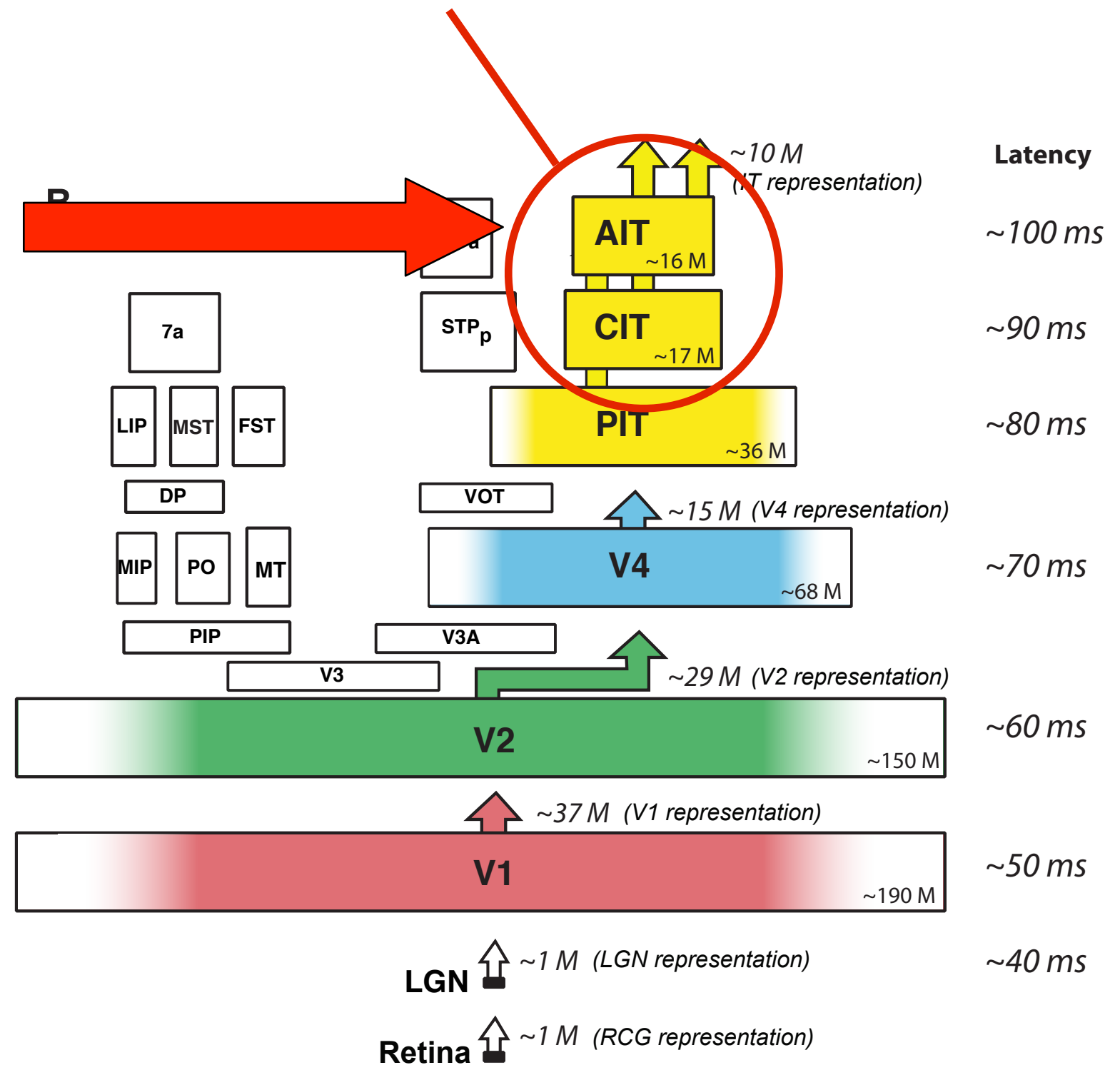
**i.e.**

**is not an “image-computable” model**

*Pasupathy and Connor (V4)*  
*Brincat and Connor (PIT)*

You are here.

“IT” (Inferior temporal cortex)



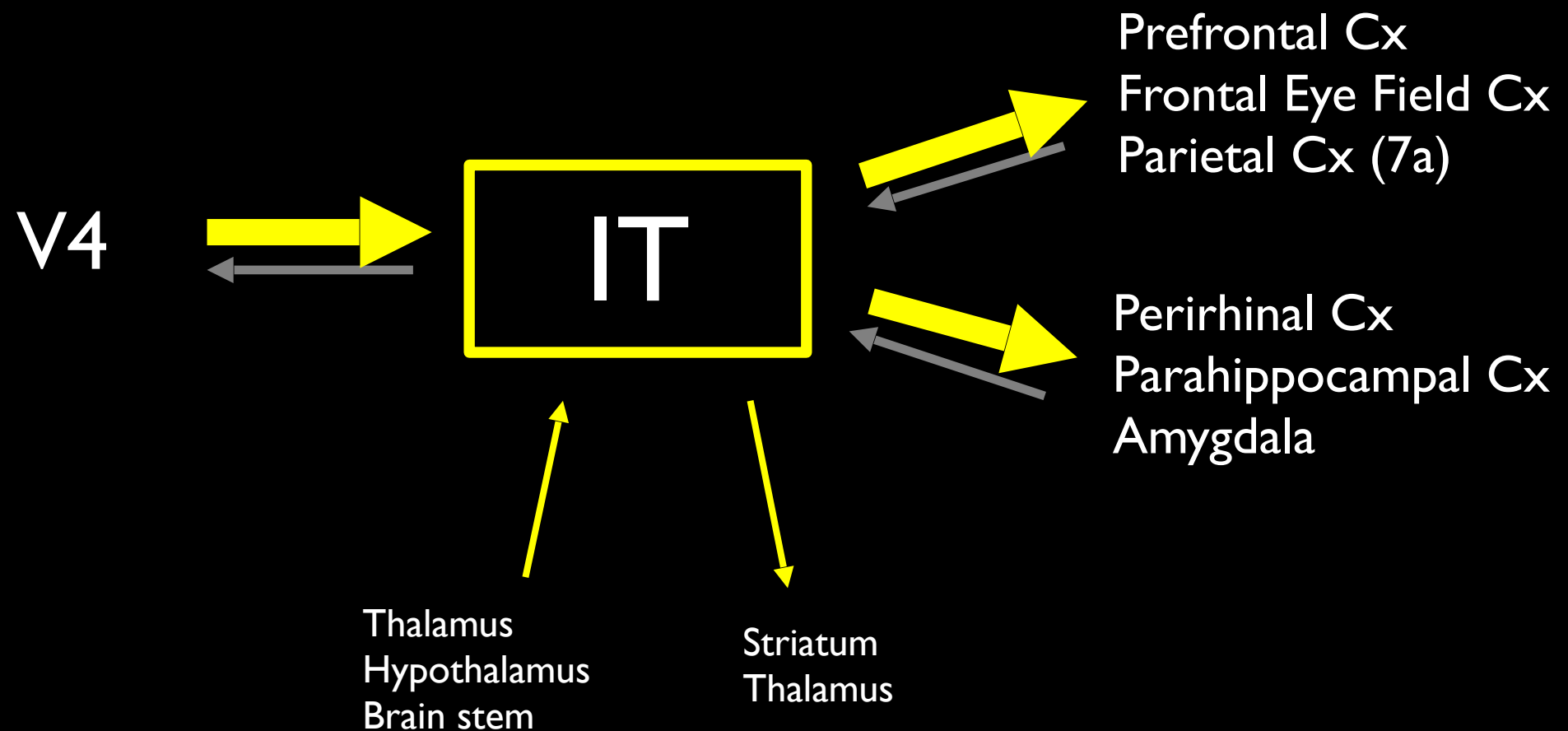
# IT statistics (rhesus monkey)

~ 7.7 cm<sup>2</sup>

~ 8% of neocortex (~ 15% of visual cortex)

~ 90 million neurons

Subregions: (PIT, CIT, AIT) (TEO, TE)





# Stimulus selectivity in inferotemporal cortex

Gross, Rocha-Miranda & Bender 1972



*Increasing ability to drive this IT neuron -->*

*The use of [these] stimuli was begun one day when, having failed to drive a unit with any light stimulus, we waved a hand at the stimulus screen and elicited a very vigorous response from the previously unresponsive neuron...*

*We then spent the next 12 hr testing various paper cutouts in an attempt to find the trigger feature for this unit. When the entire set of stimuli used were ranked according to the strength of the response that they produced, we could not find a simple physical dimension that correlated with this rank order. However, the rank order of adequate stimuli did correlate with similarity (for us) to the shadow of a monkey hand" (Gross et al., 1972).*

# Stimulus selectivity in inferotemporal cortex

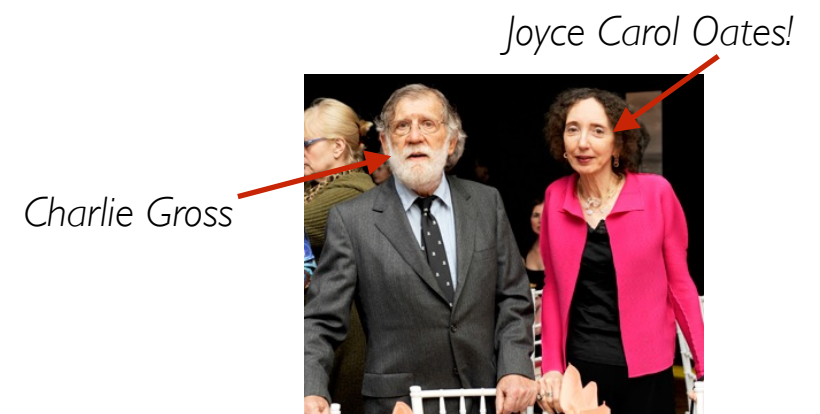
Gross, Rocha-Miranda & Bender 1972



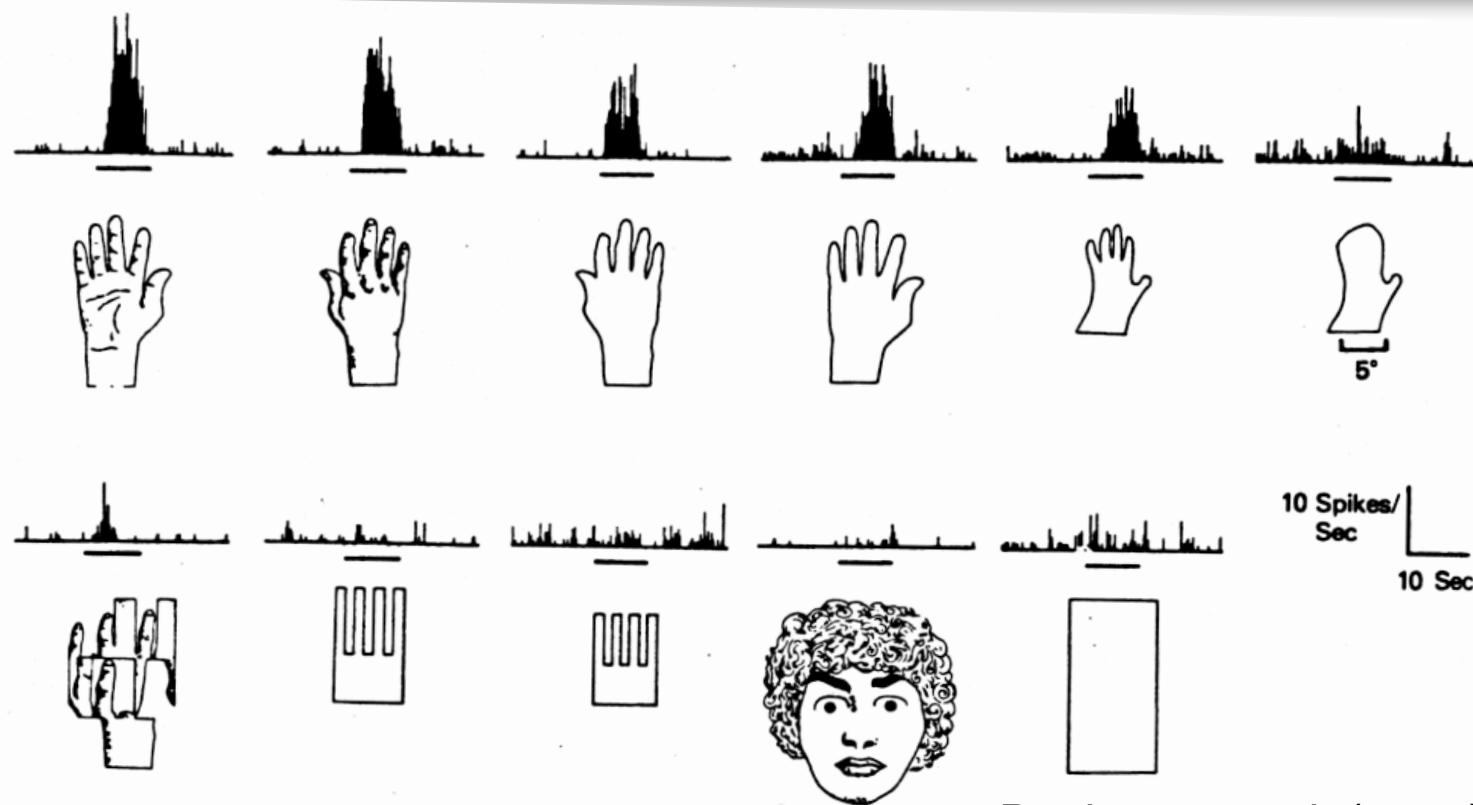
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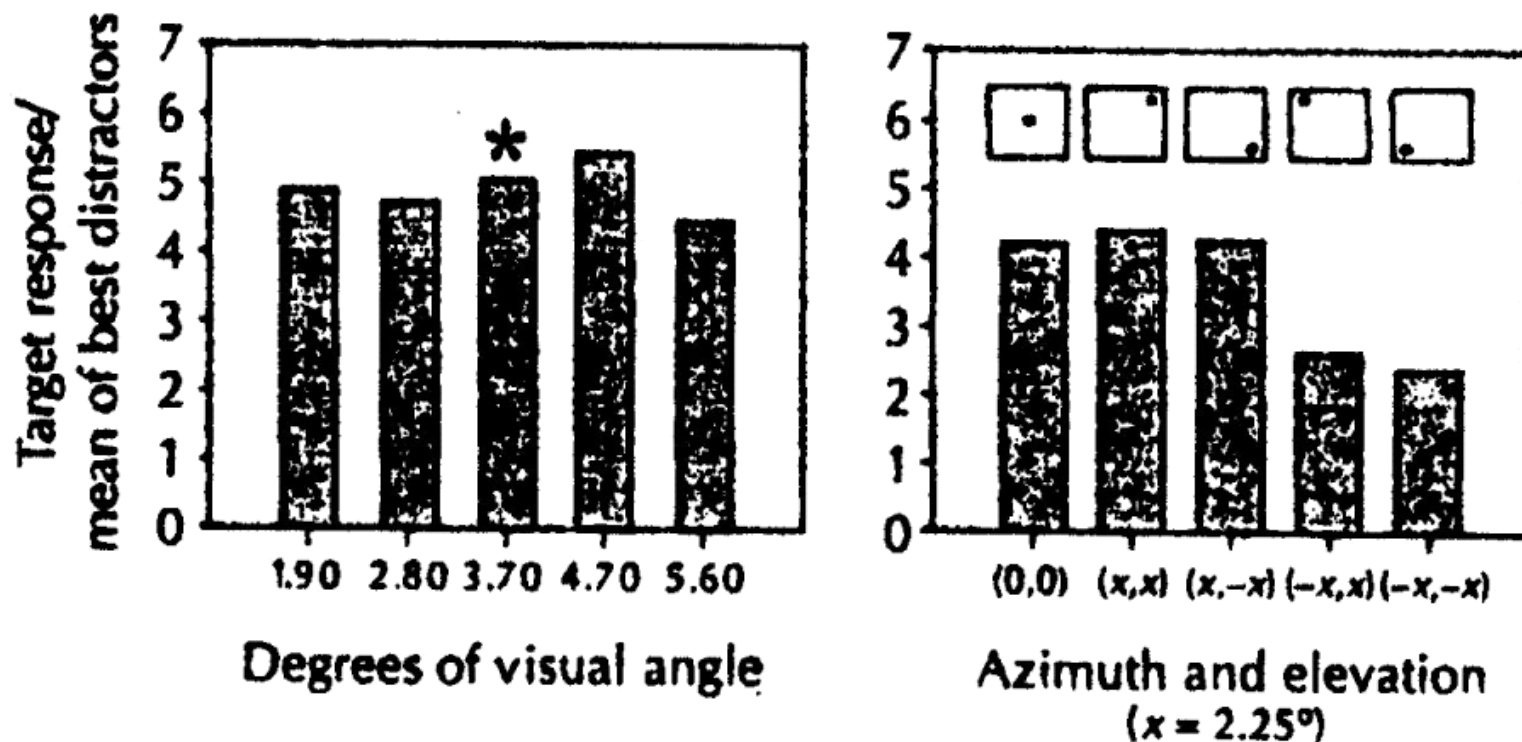


# What stimulus feature are IT neurons actually “tuned” to?



Desimone et al. (1984)

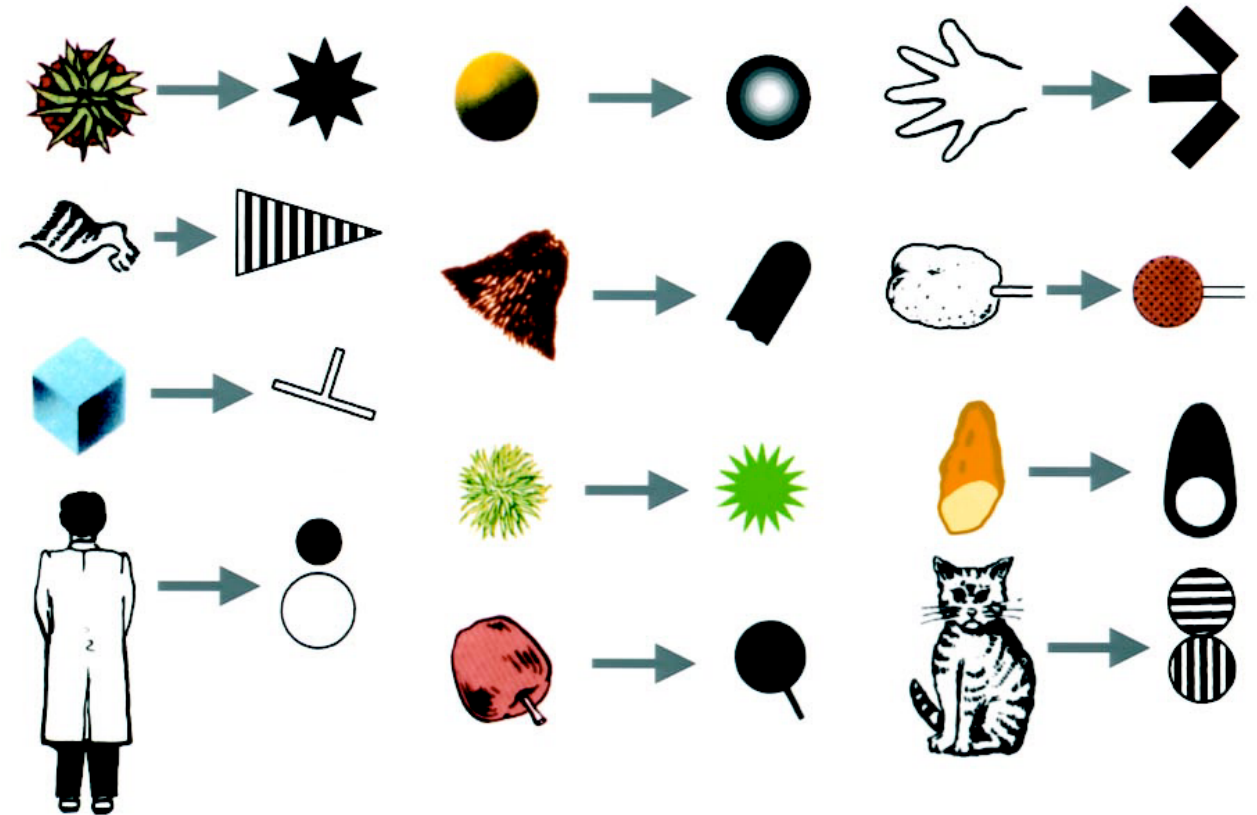
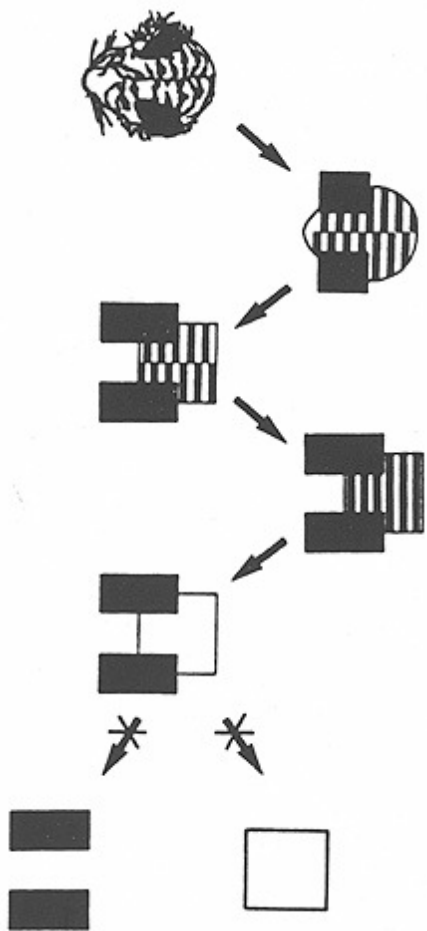
IT neurons can be tuned to specific combinations of features (high “selectivity”)



Logothetis et al. (1995)

That selectivity is tolerant to changes in position and size

# What stimulus feature are IT neurons actually “tuned” to?

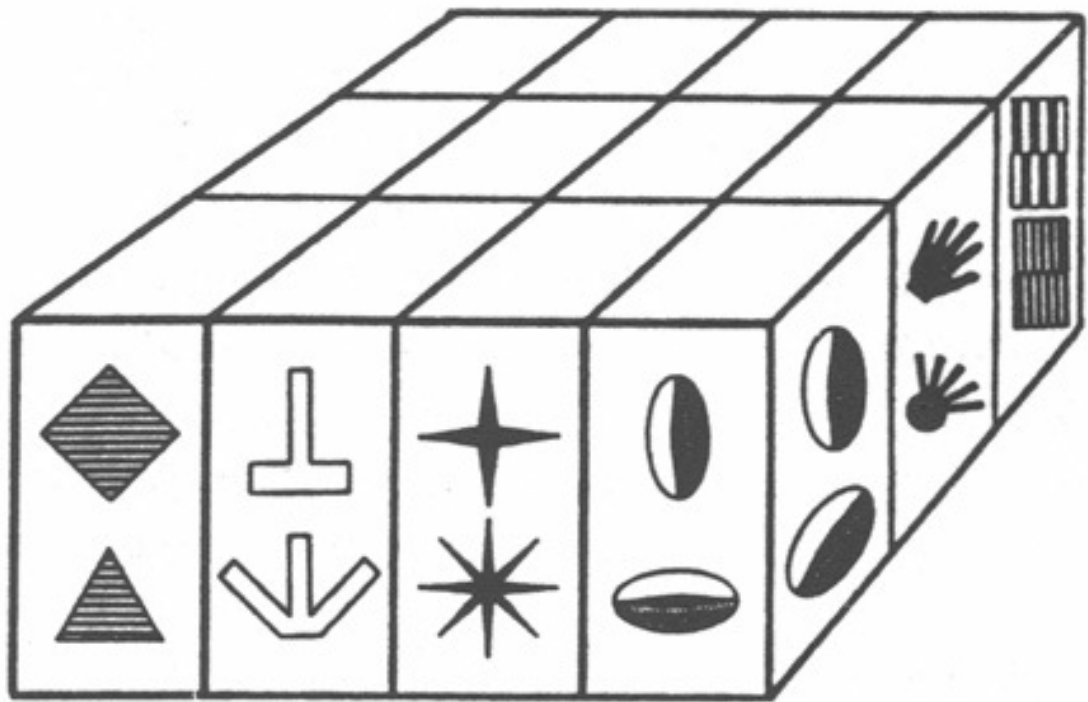


*Tanaka et al.*

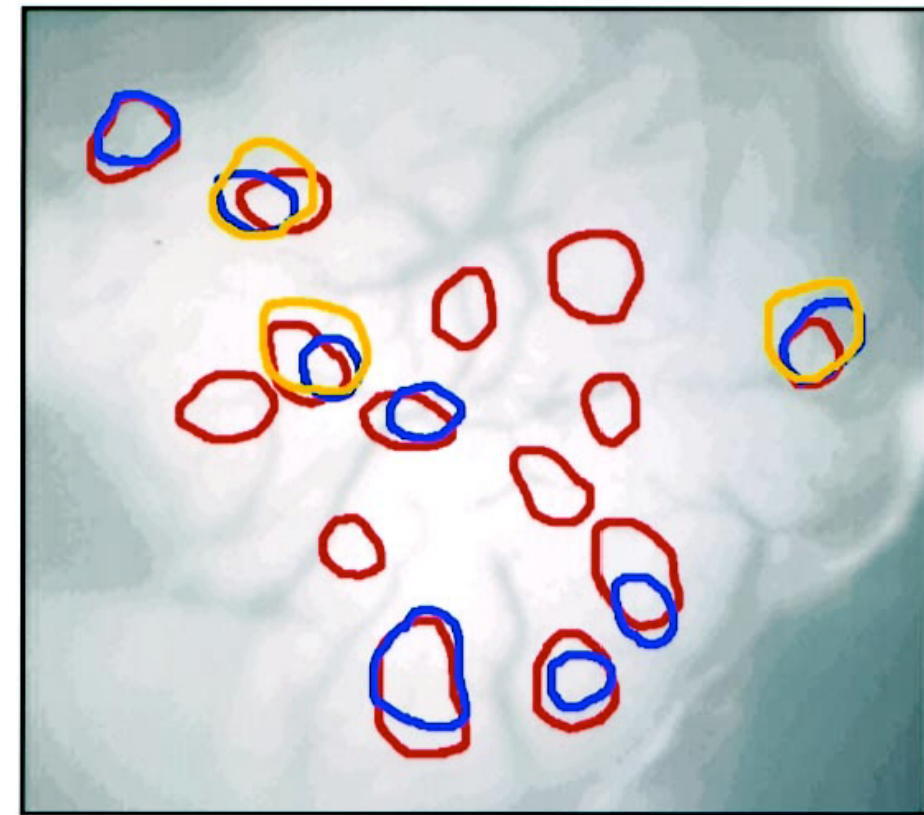




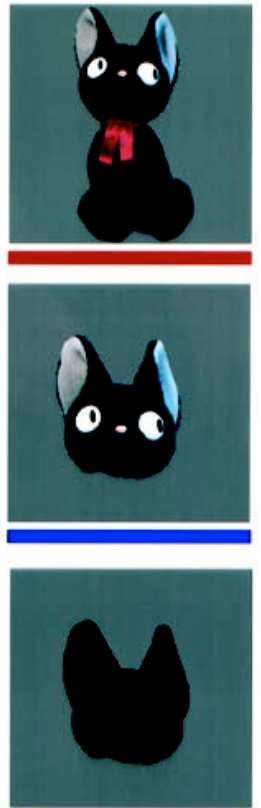
IT has spatial organization at 500  $\mu\text{m}$  - 1 mm scale



*Tanaka et al.*



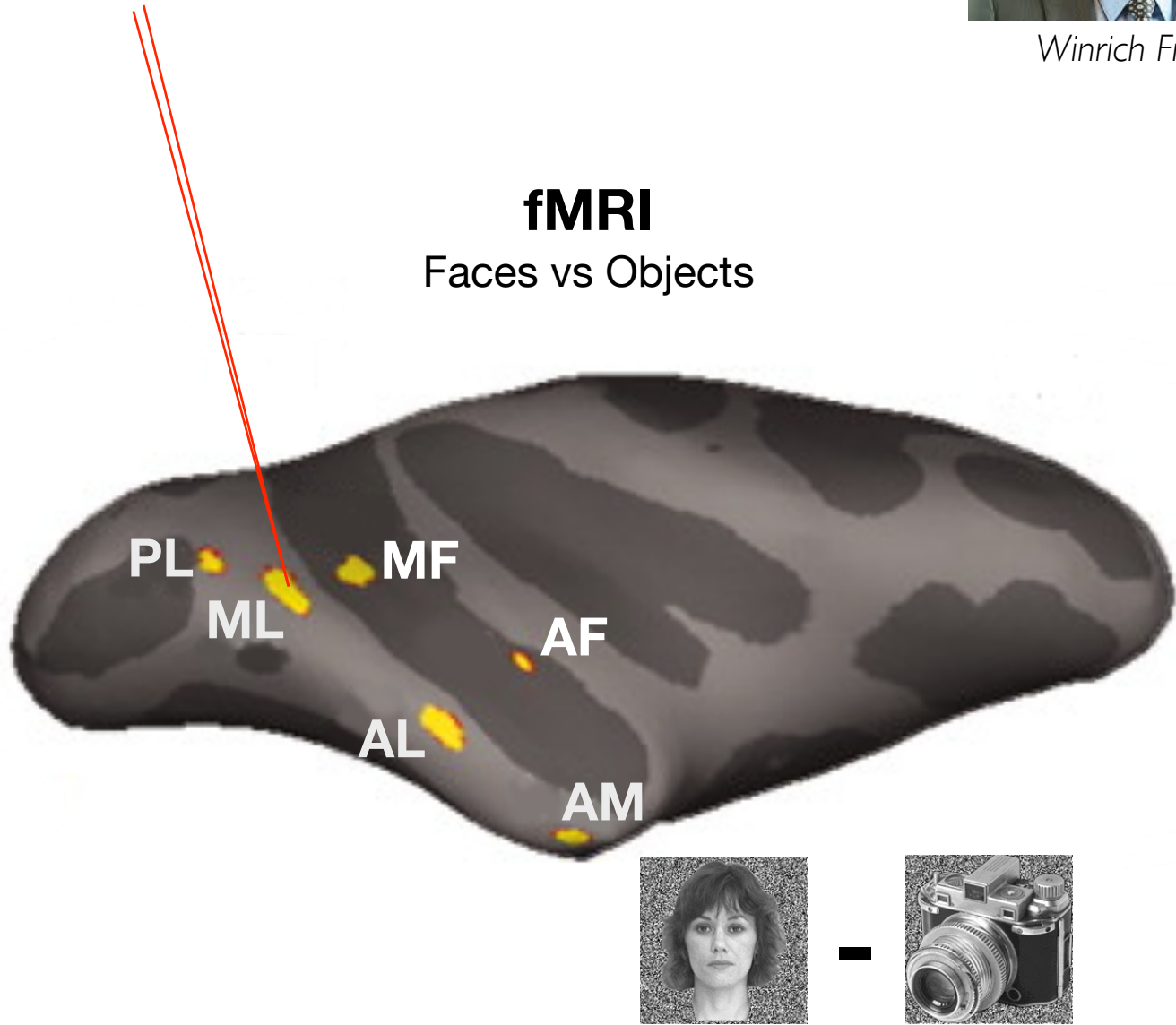
1 mm



*Tsunoda et al.*

# Larger scale (2-6 mm) organization for some image contrasts

## Face Patches in IT



Winrich Freiwald

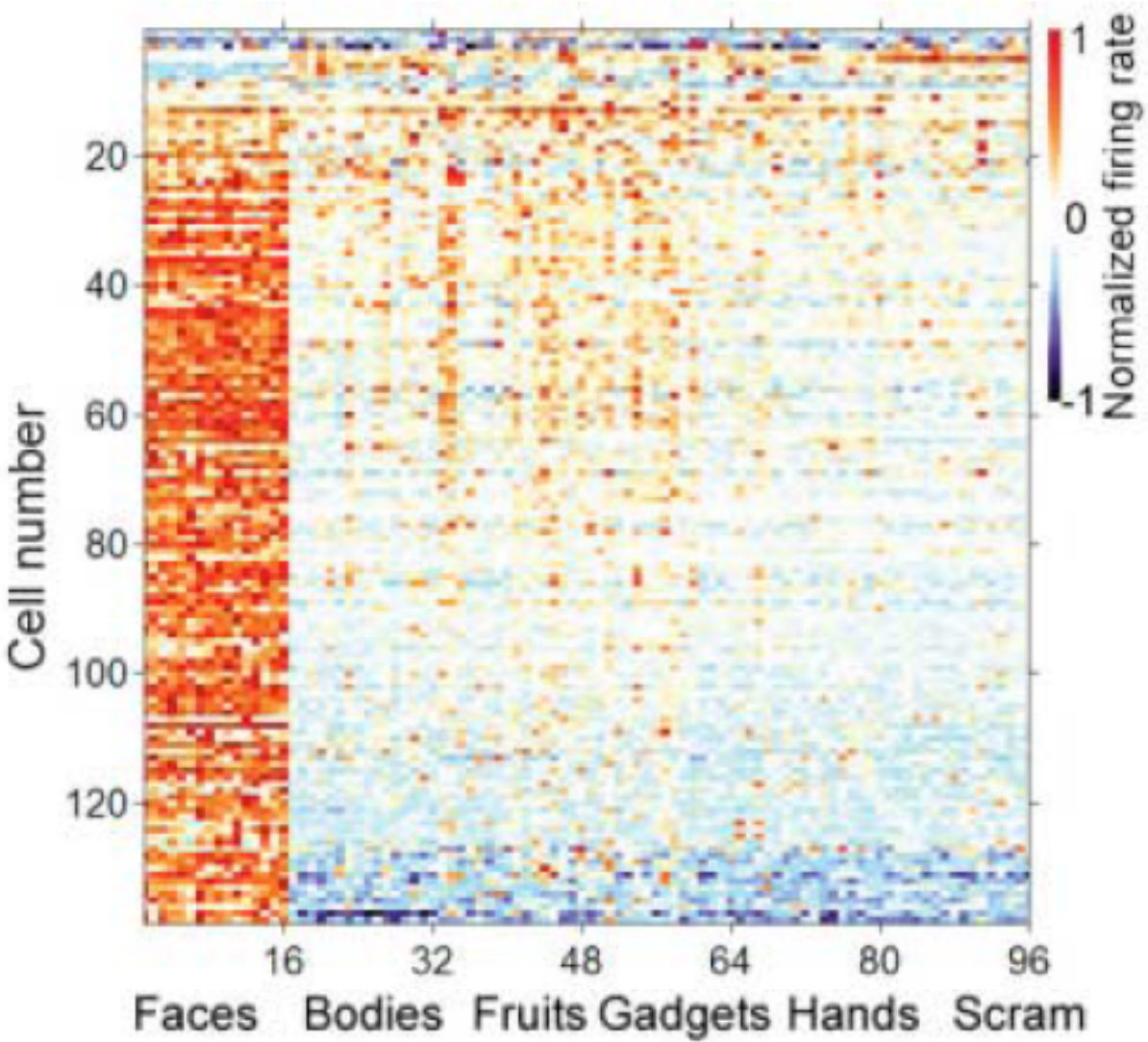


Doris Tsao

ML



Nancy Kanwisher



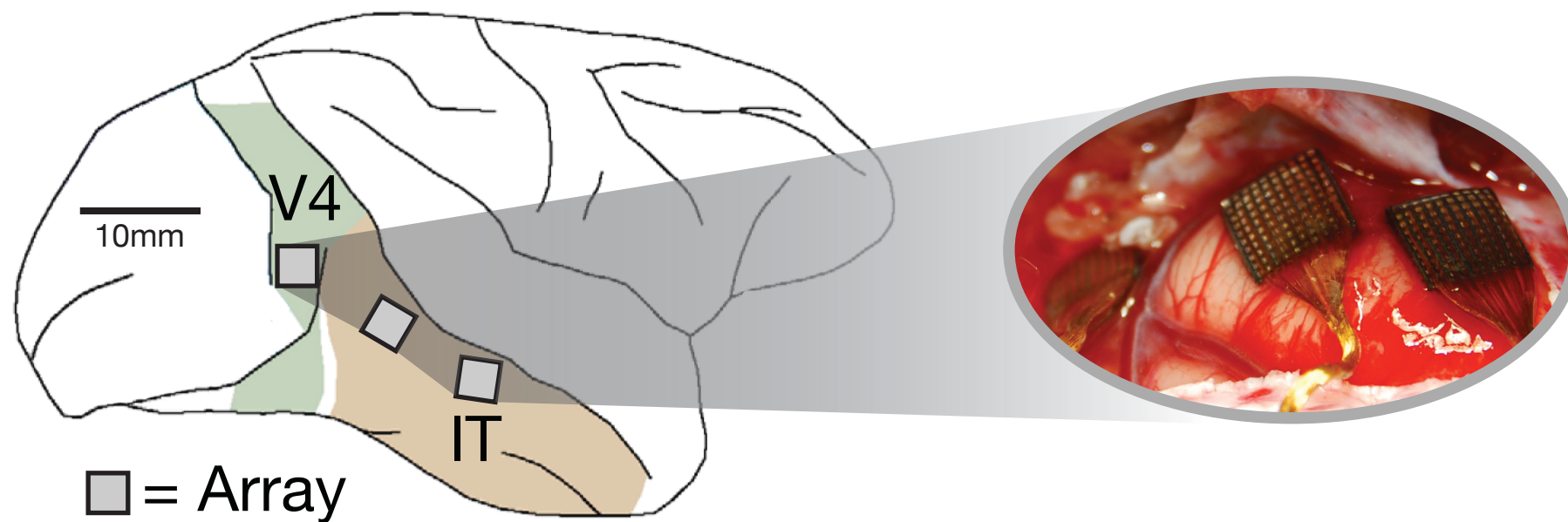
Tsao, Freiwald, and Livingstone used fMRI to reveal a set of face selective regions in macaque IT (aka “face patches”)

Most of the single neurons in these regions showed a preference for frontal faces

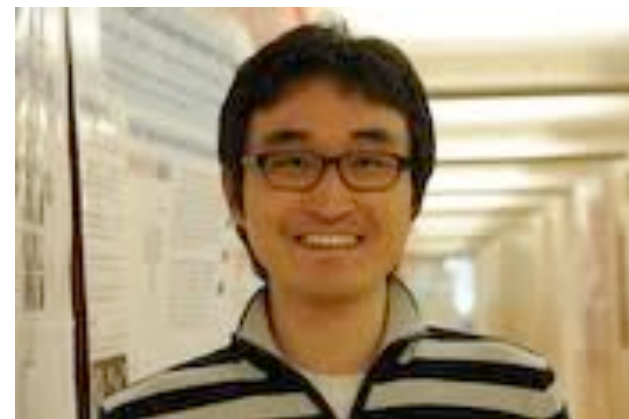


# Multi-array Electrophysiology Experiment

Multi-array electrophysiology in macaque V4 and IT.



About 300 total sites



Ha Hong



Jim DiCarlo

# Multi-array Electrophysiology Experiment

5760 images

64 objects

8 categories

uncorrelated photo backgrounds

Low variation



... 640 images

Medium variation



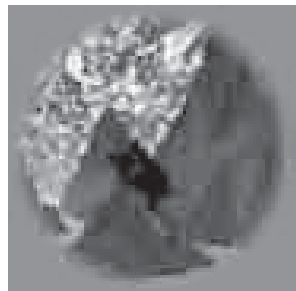
... 2560 images

High variation



... 2560 images

Animals



Boats



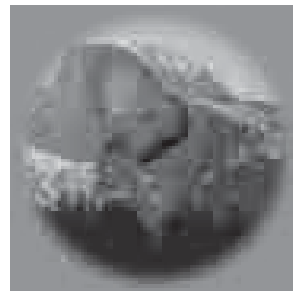
Cars



Chairs



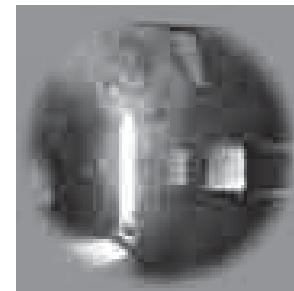
Faces



Fruits



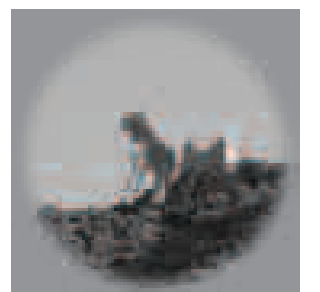
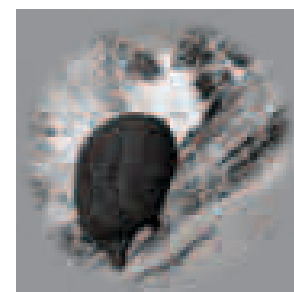
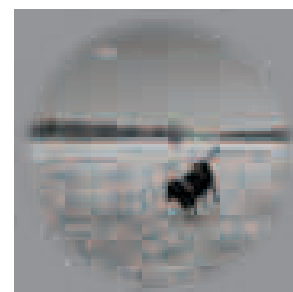
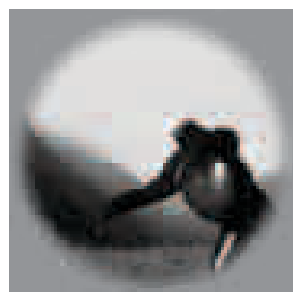
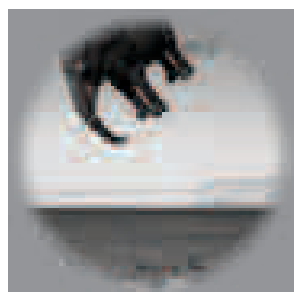
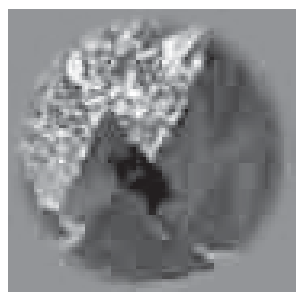
Planes



Tables



Pose, position, scale, and background variation





# Multi-array Electrophysiology Experiment



# Multi-array Electrophysiology Experiment



complex, uncorrelated backgrounds **prevent low-level cheating**

part of what we mean by “complex task”

# Multi-array Electrophysiology Experiment

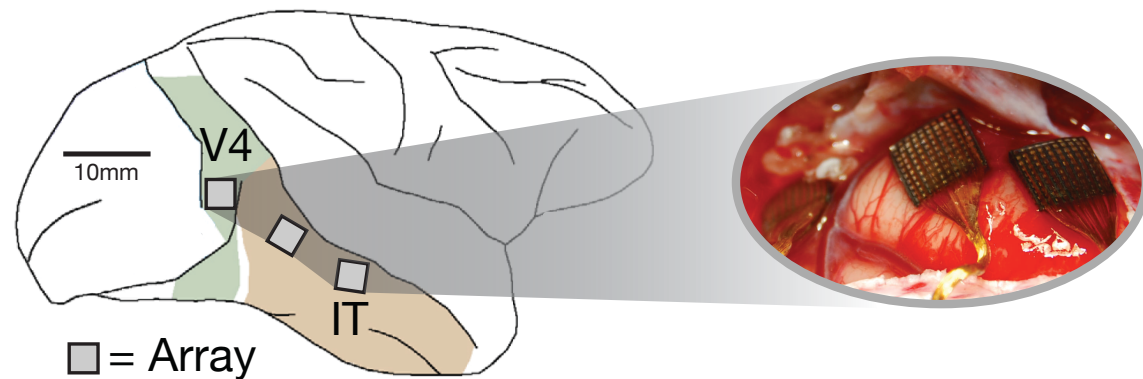


**Ellie.** C. Shay & K. Kar (Winter 2019)

complex, uncorrelated backgrounds **prevent low-level cheating**

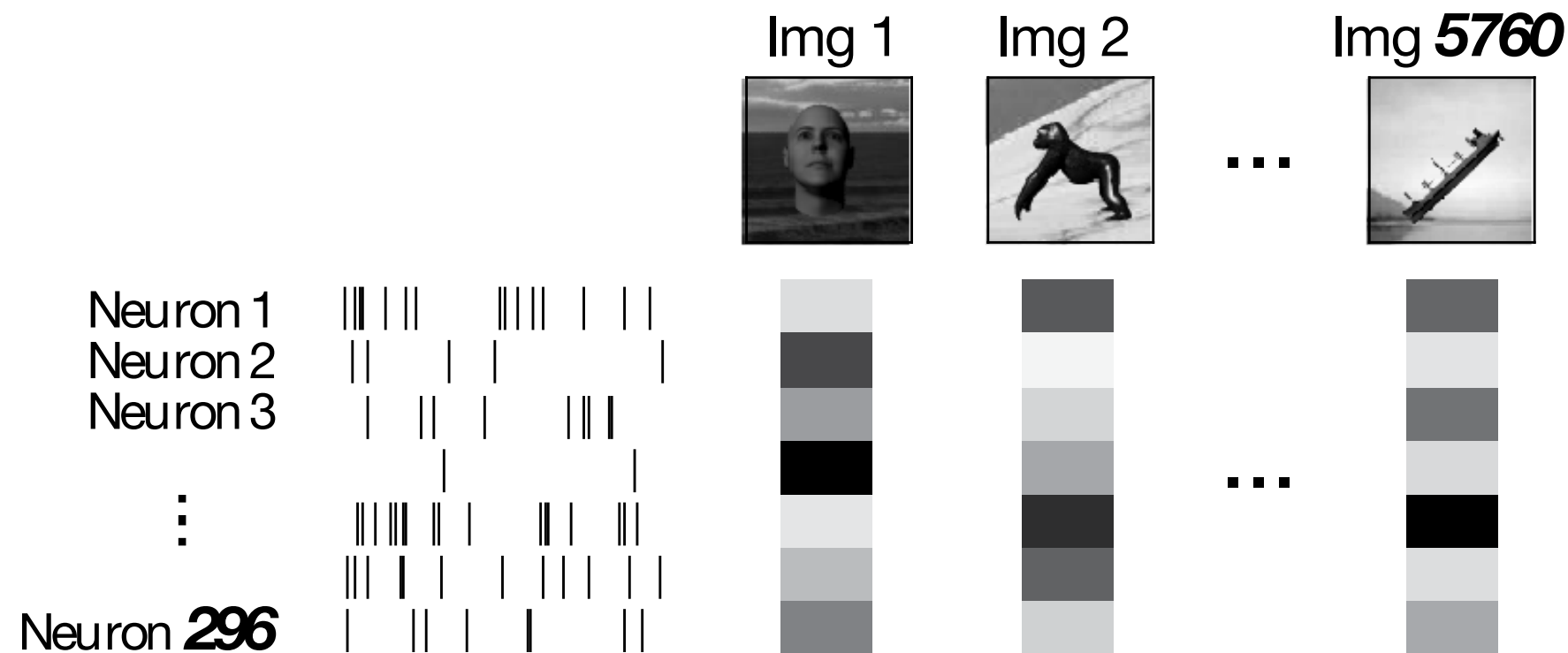
part of what we mean by “complex task”

# Multi-array Electrophysiology Experiment



About 300 total sites

*Output = Binned spike counts 70ms-170ms post stimulus presentation averaged over 25-50 reps of each image.*

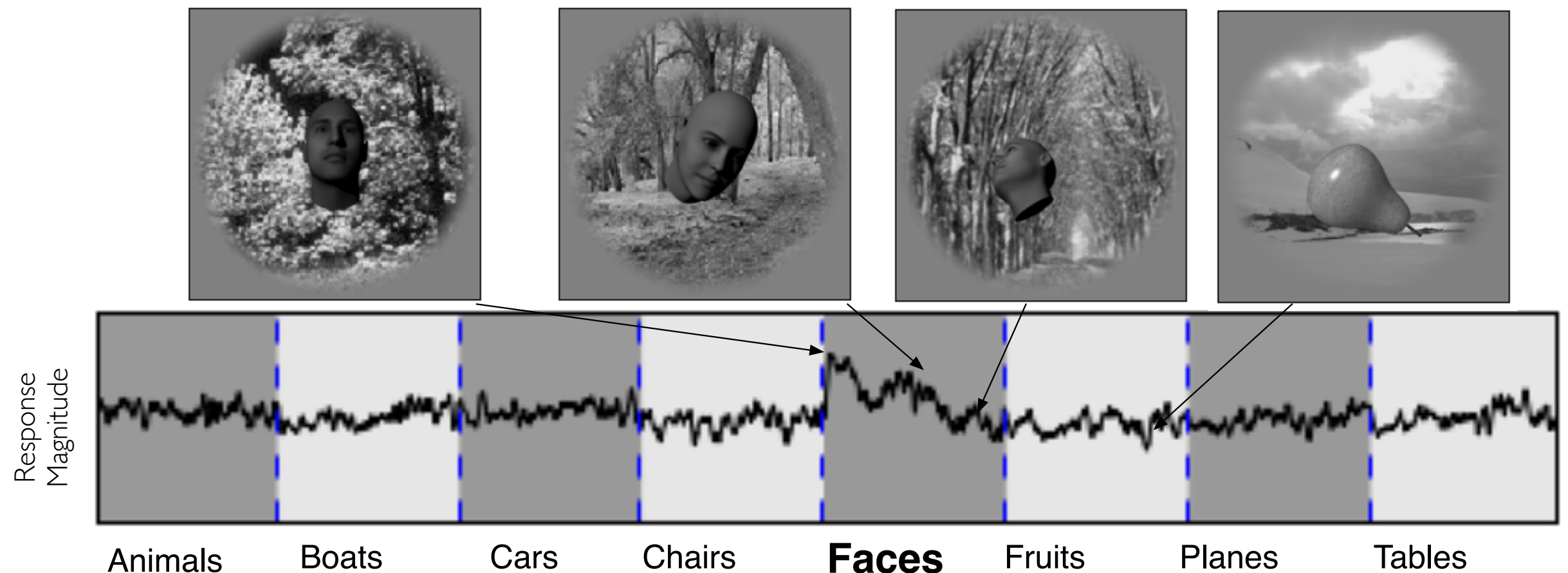




# Multi-array Electrophysiology Experiment

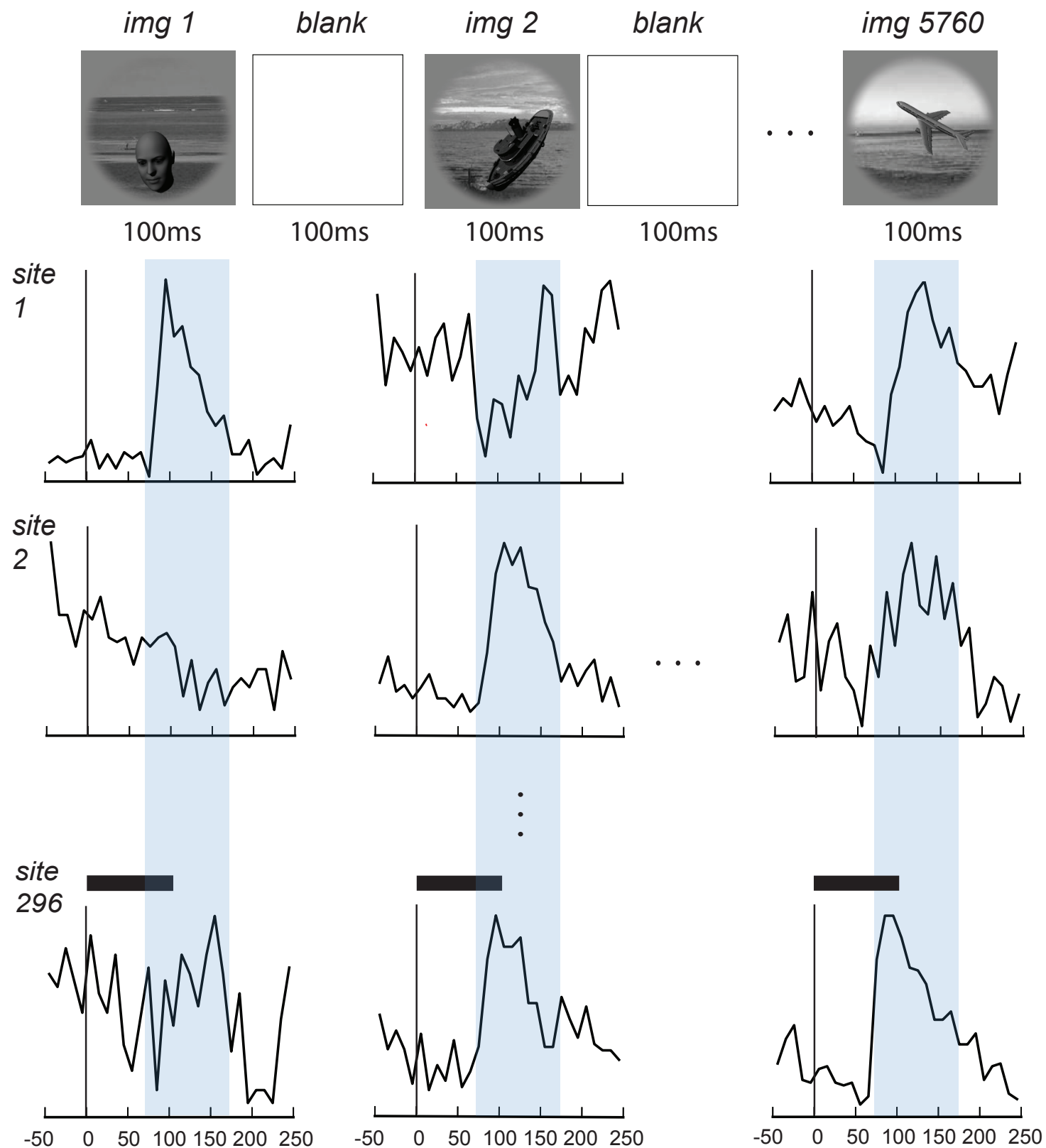
Responses to 1600 test images of two example units

IT unit 53

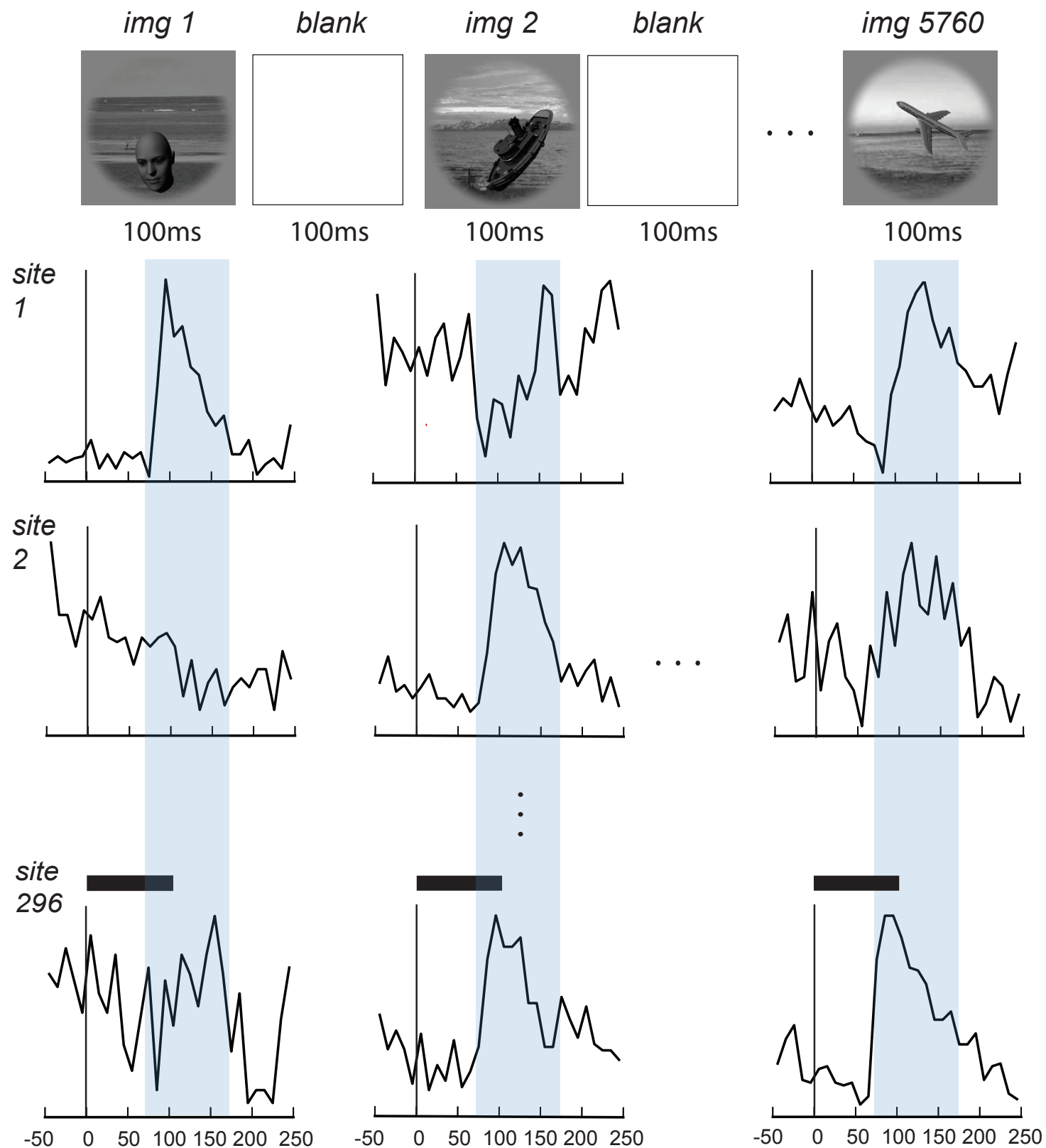


Images sorted first by **category**, then **variation level**.

# Neural-Behavior Decoding

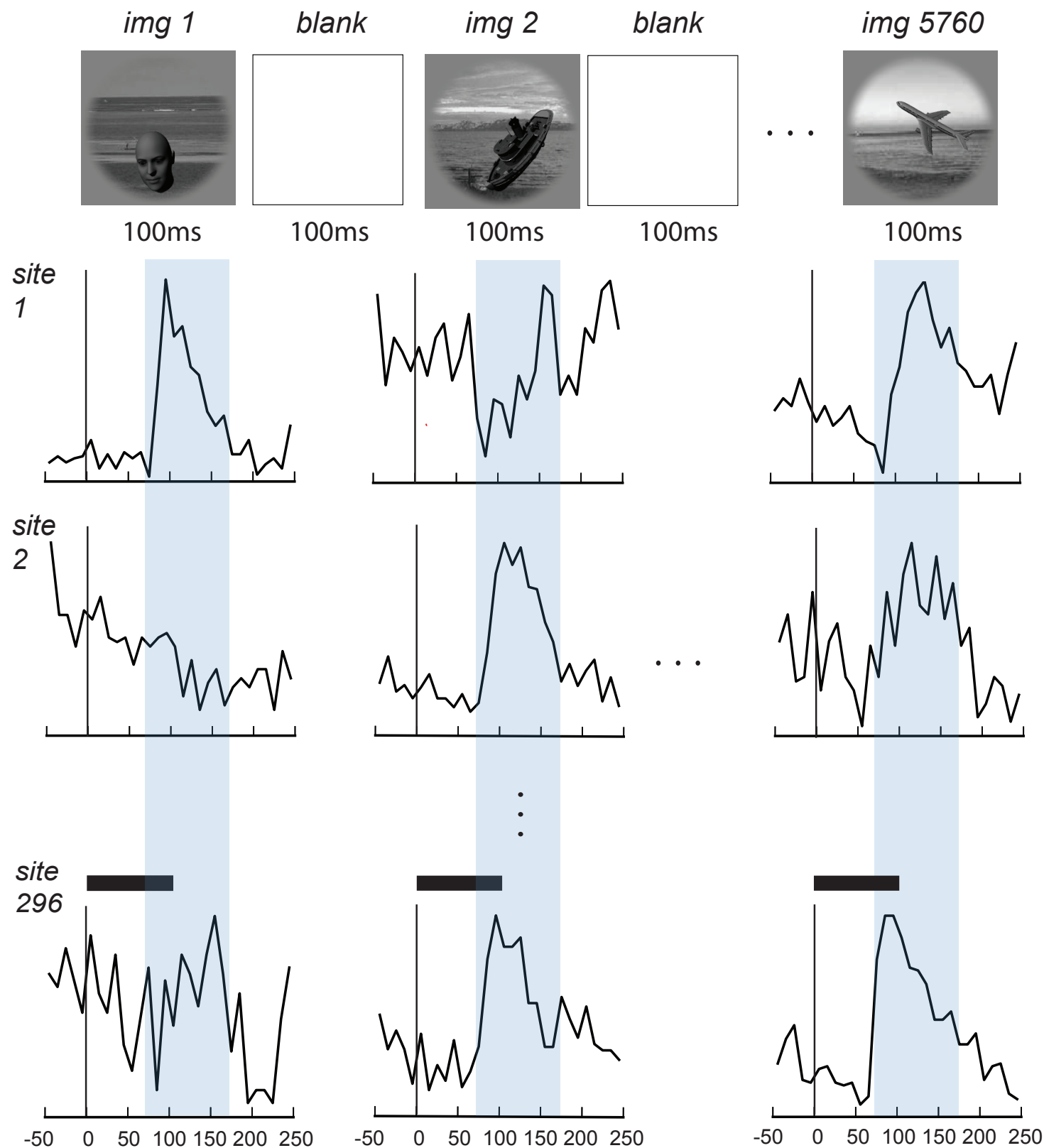


# Neural-Behavior Decoding



linear combination of units

# Neural-Behavior Decoding

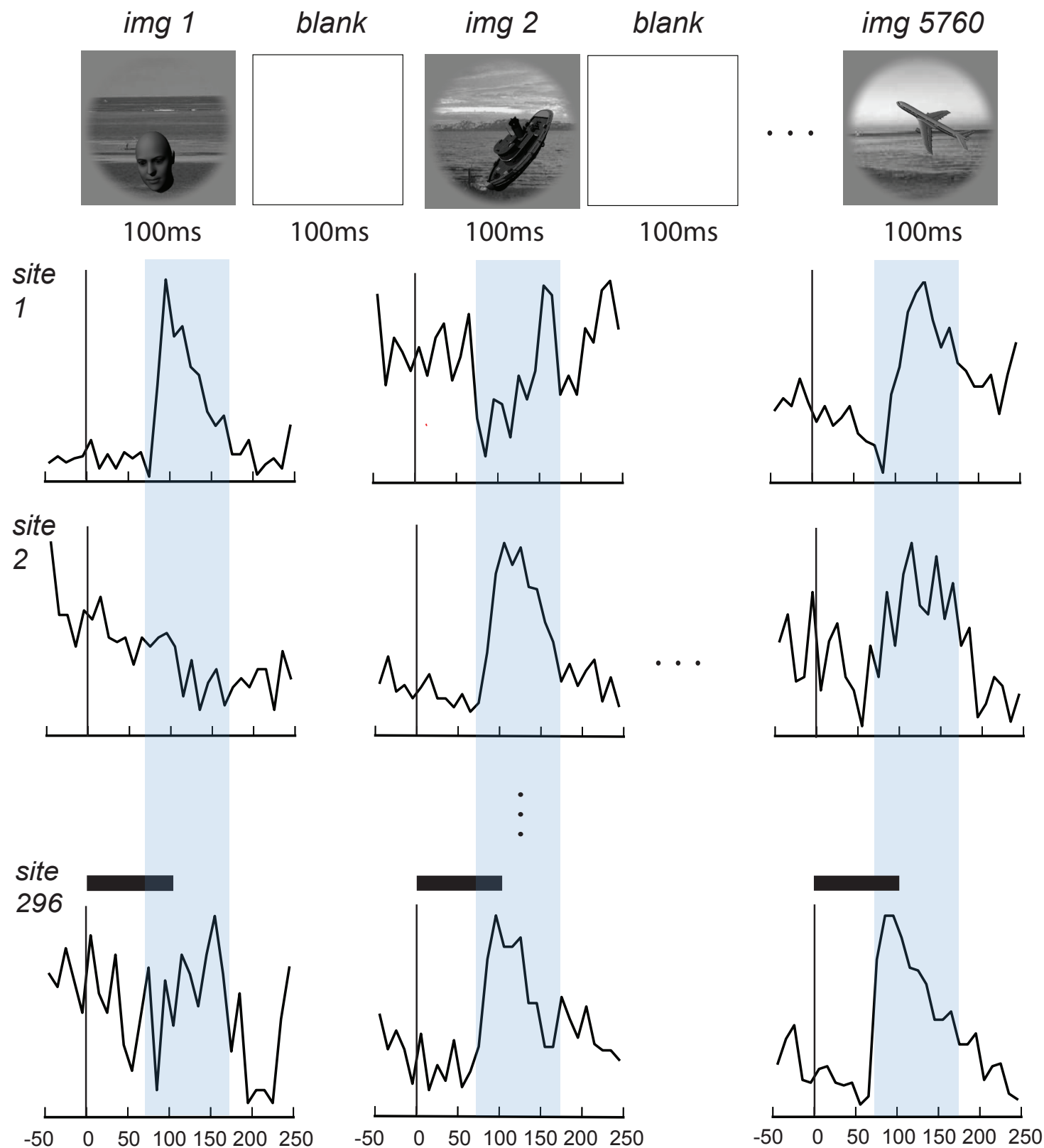


Animal or not?

linear combination of units



# Neural-Behavior Decoding



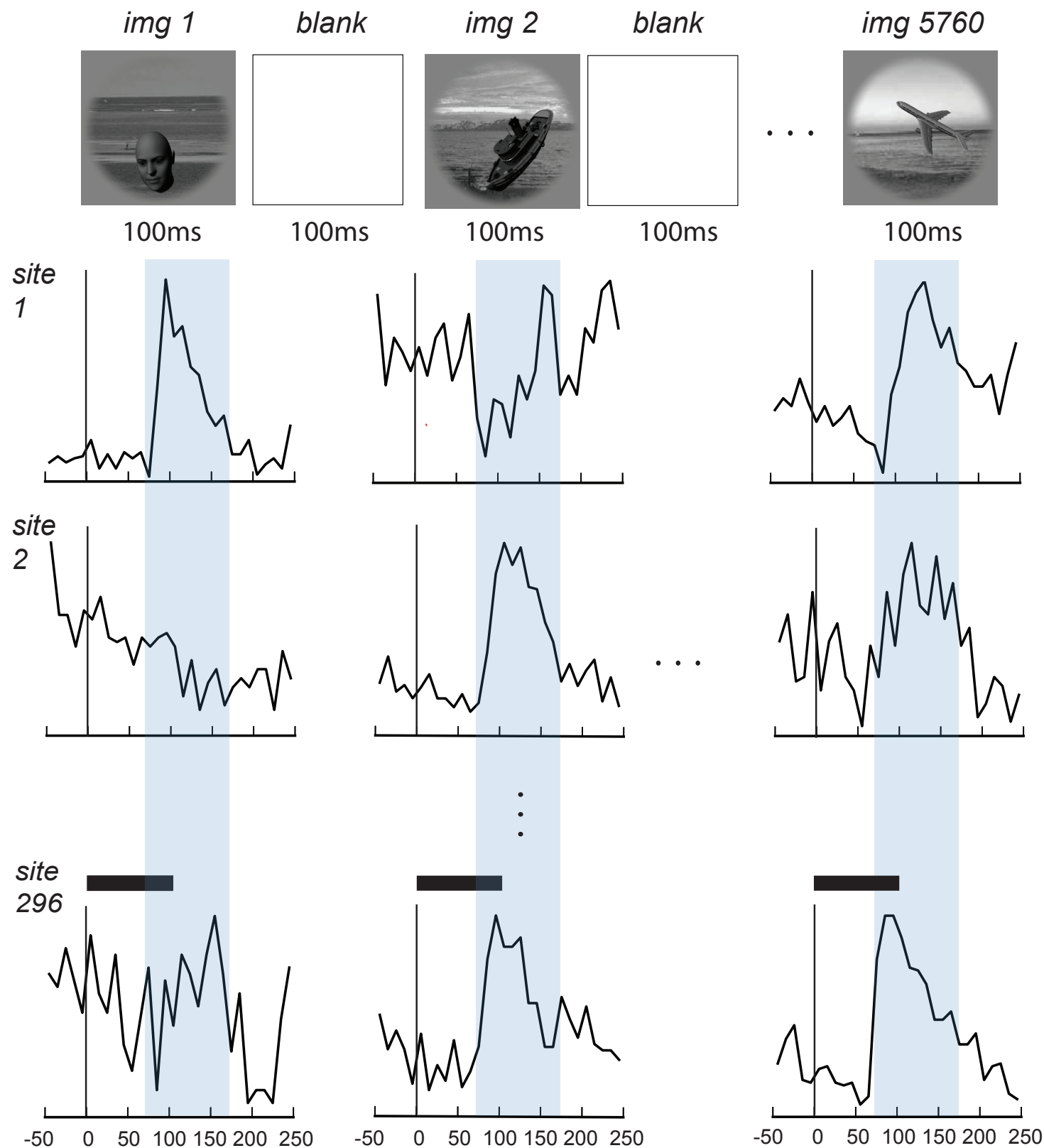
Animal or not?

linear combination of units

different linear combination

Car or not?

# Neural-Behavior Decoding



Animal or not?

linear combination of units

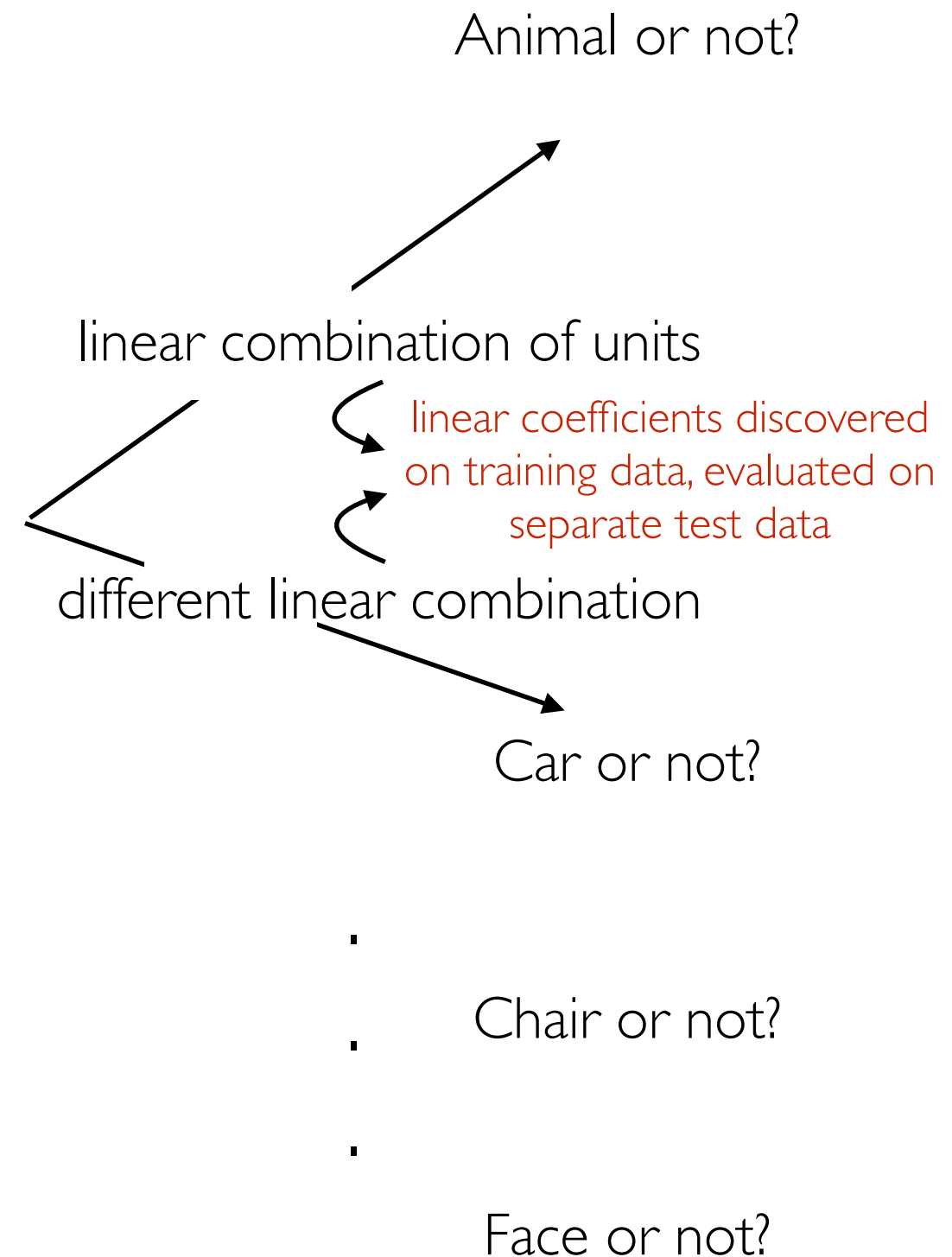
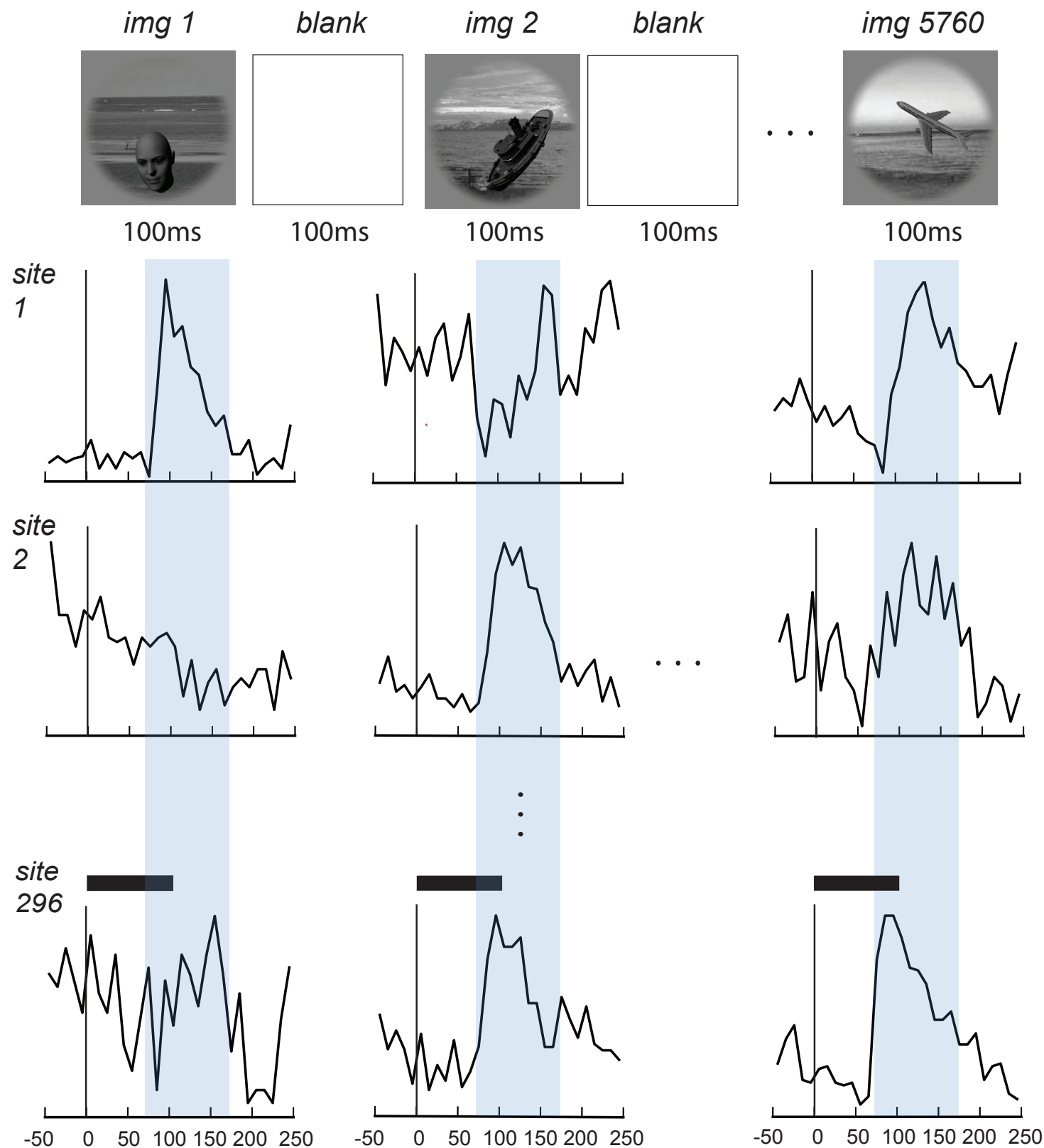
different linear combination

Car or not?

Chair or not?

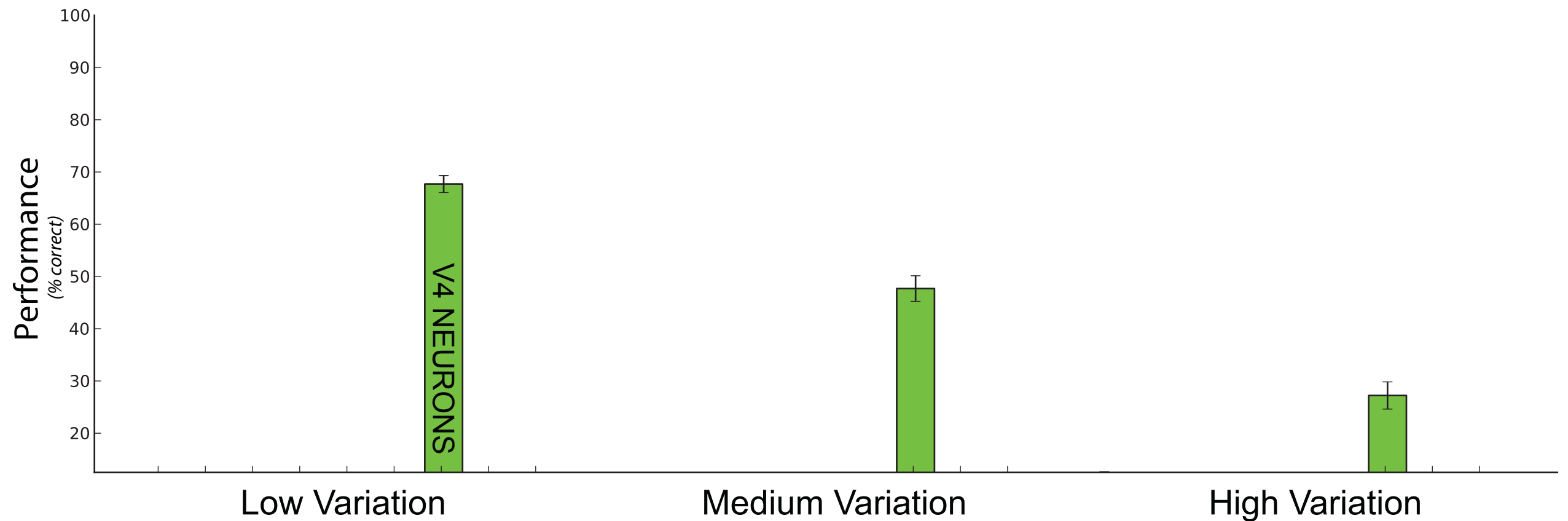
Face or not?

# Neural-Behavior Decoding



# Decoding Behaviorally Output from Neural Populations

V4 loses out at higher variation:





# Range of Human Behavior

at  
ceiling ...

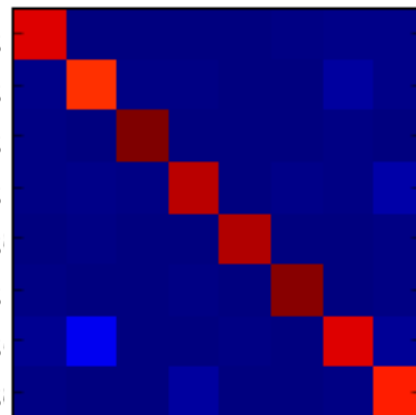
## Variation Level

Low

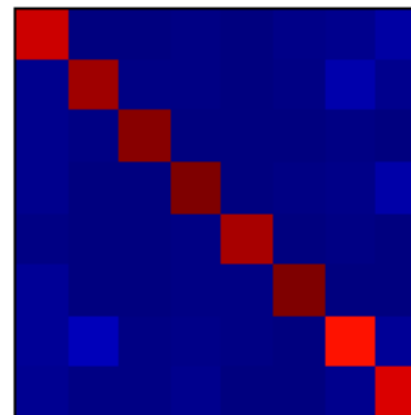
Medium

High

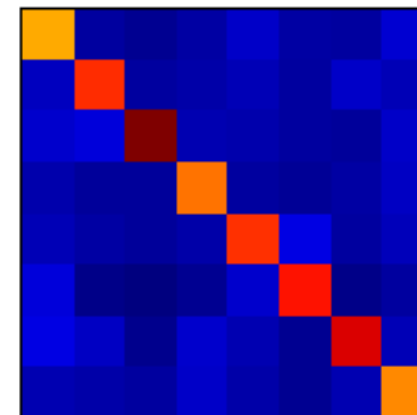
Animals  
Boats  
Cars  
Chairs  
Faces  
Fruits  
Planes  
Tables



Cars Lo var

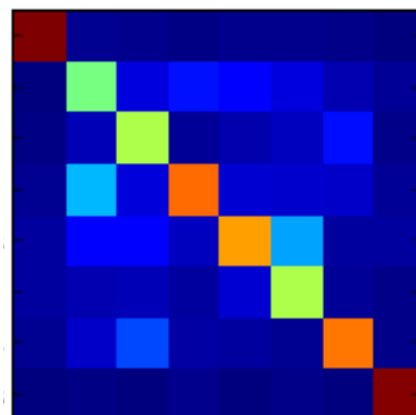


Cars Med var

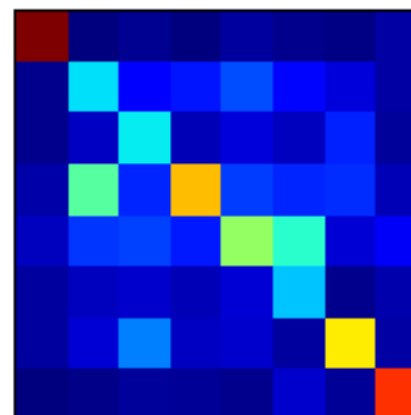


Cars Hi var

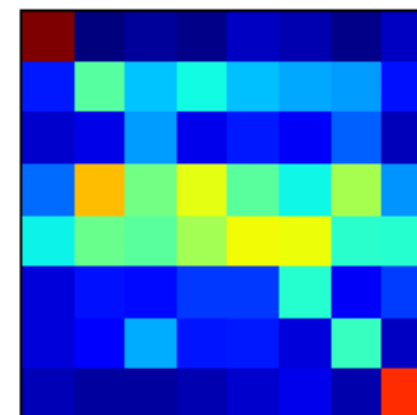
Car 1  
Car 2  
Car 3  
Car 4  
Car 5  
Car 6  
Car 7  
Car 8



Faces Lo var

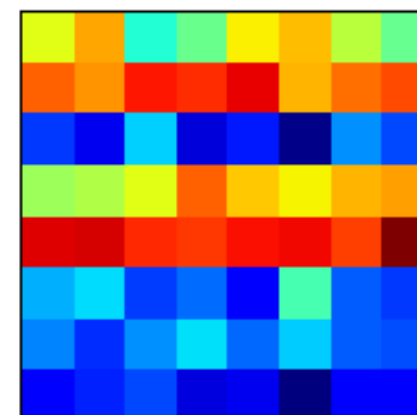
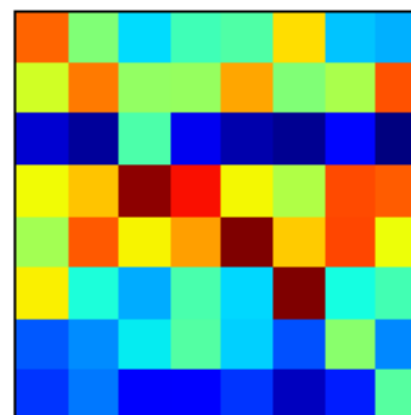
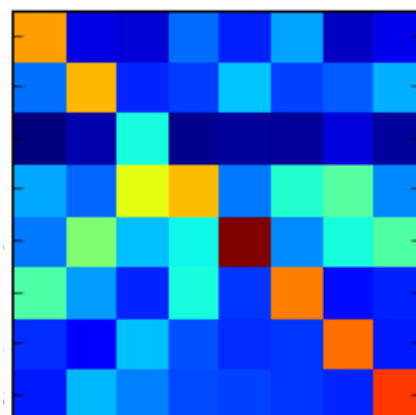


Faces Med var



Faces Hi var

Face 1  
Face 2  
Face 3  
Face 4  
Face 5  
Face 6  
Face 7  
Face 8

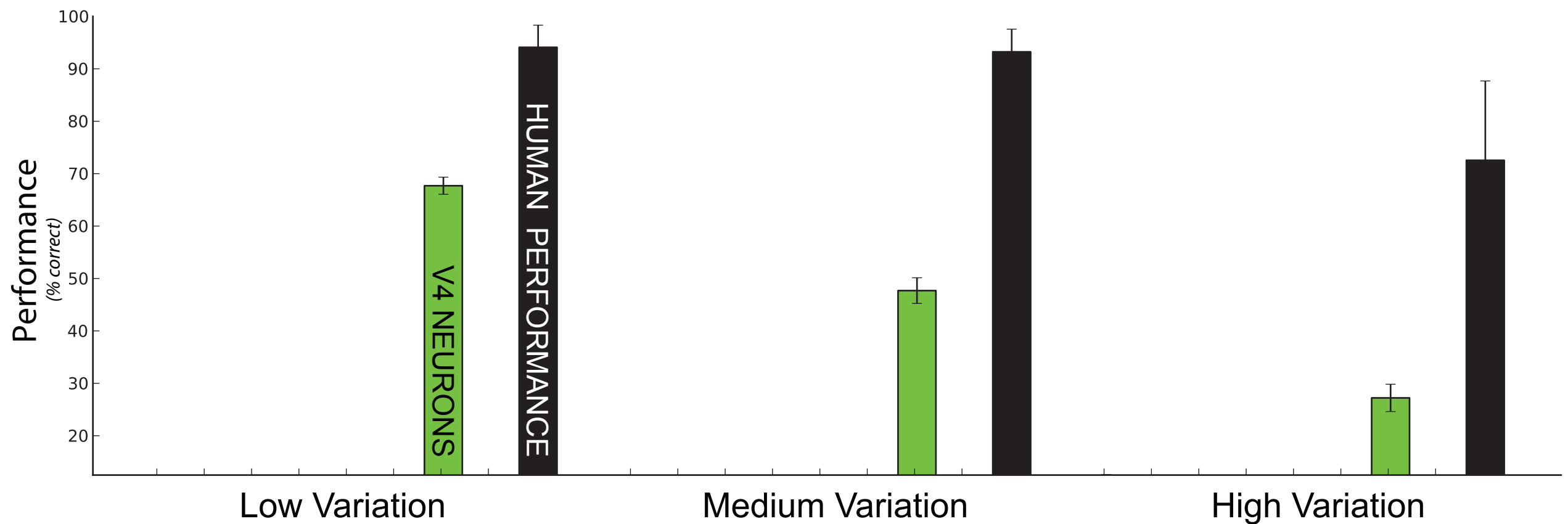
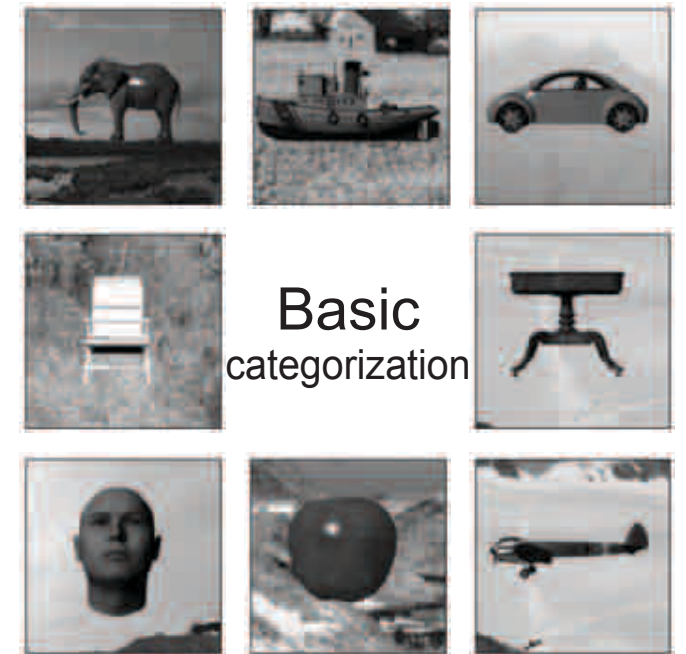


... at  
chance

# Decoding Behaviorally Output from Neural Populations

V4 loses out at higher variation:

... but humans are much less affected.

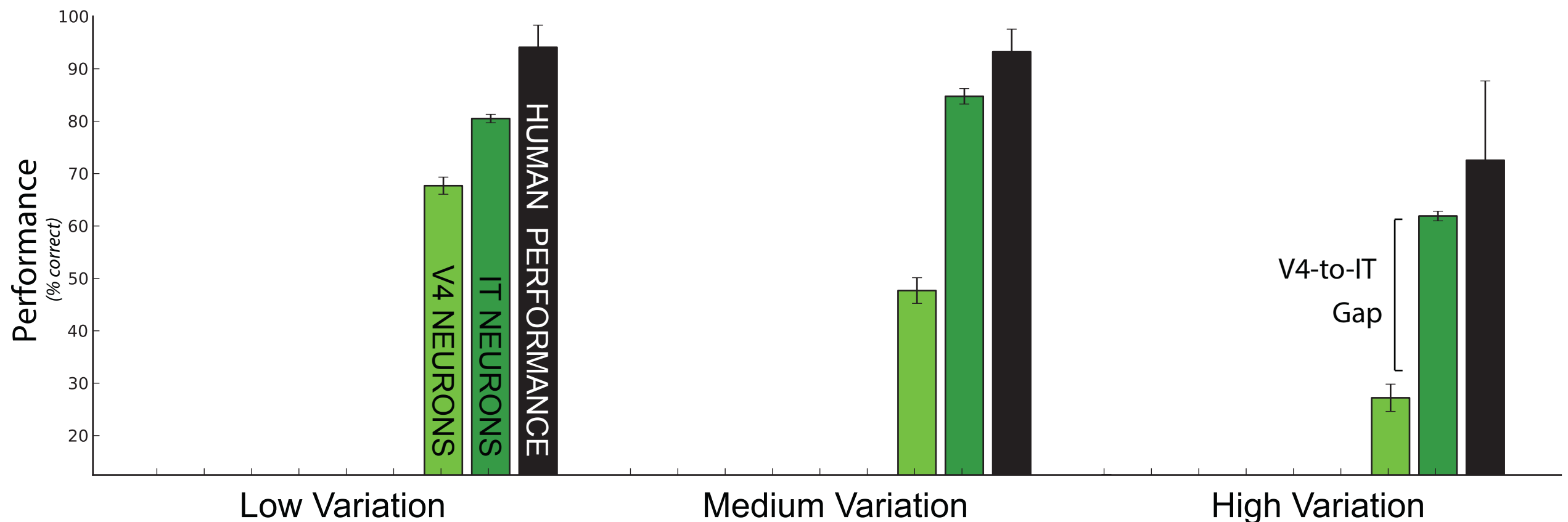
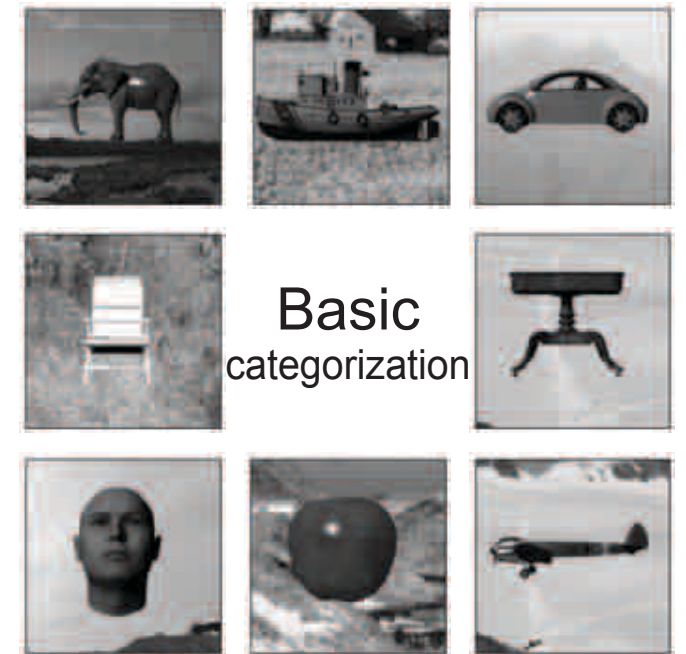


# IT Neurons Track Human Performance

V4 loses out at higher variation:

... but humans are much less affected.

... as is the IT neural population.

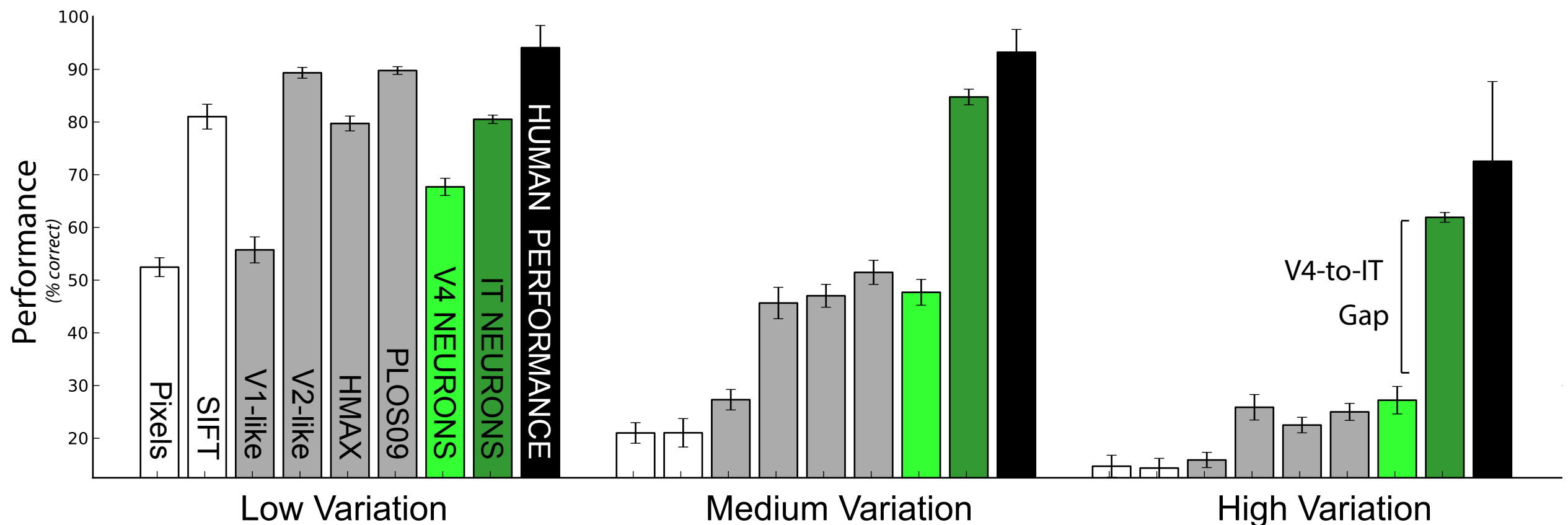
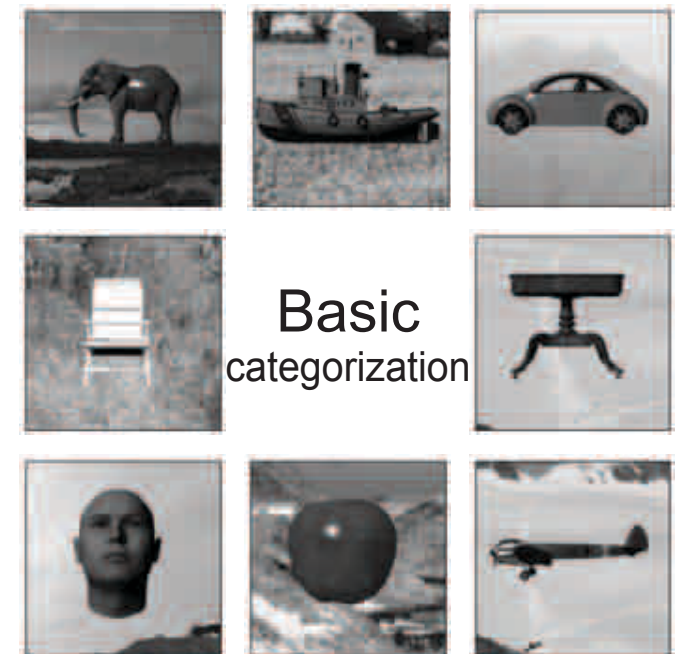


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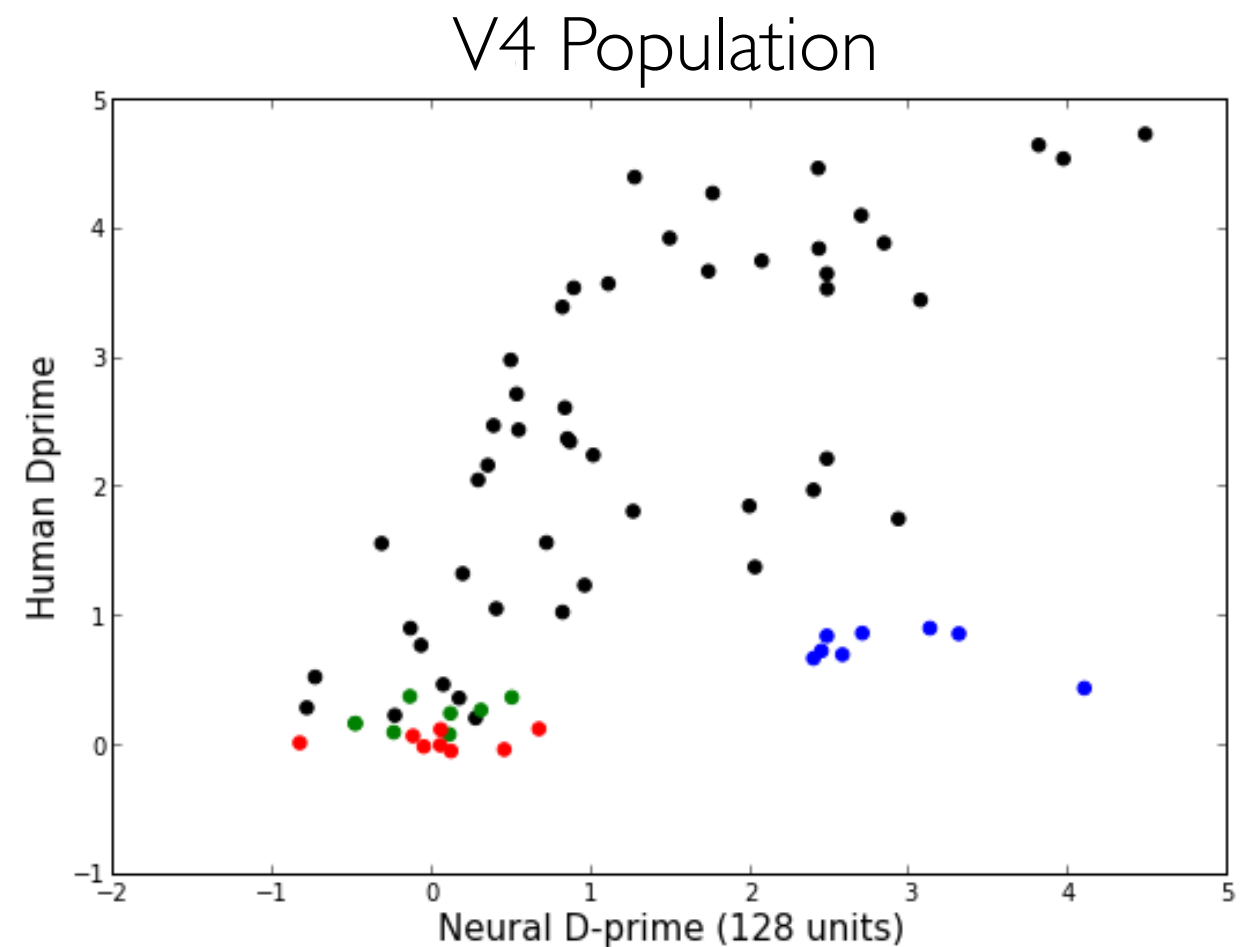
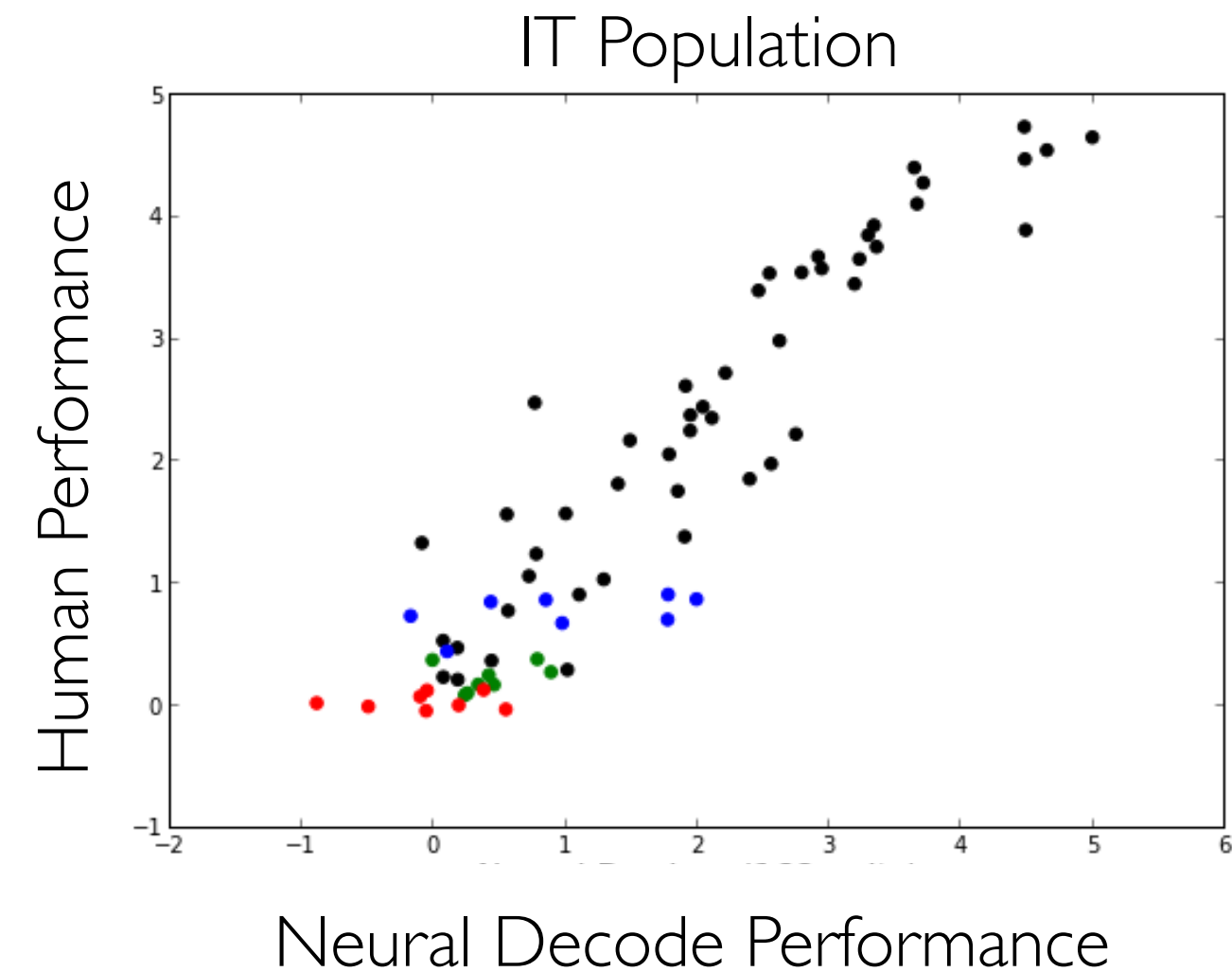
Yamins\* and Hong\* et. al. **PNAS** (2014)

At high variation levels, IT much better than V4 and existing models.



# IT Neurons Track Human Performance

IT matches human error patterns as well as raw performance.

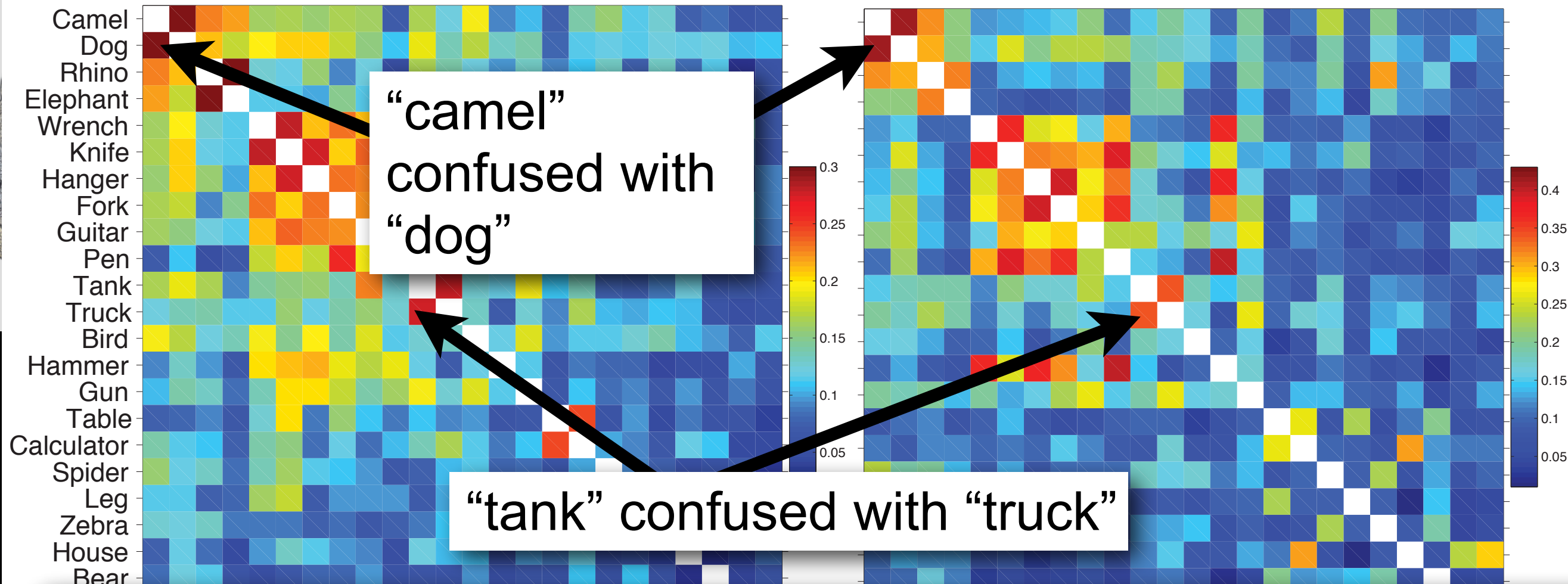


- Low-Variation Face subordinate tasks.

# Human / Monkey similarities

## Human

## Rhesus monkey



**Upshot: human and non-human primate basic level core object perceptual (sp. identification) are indistinguishable**

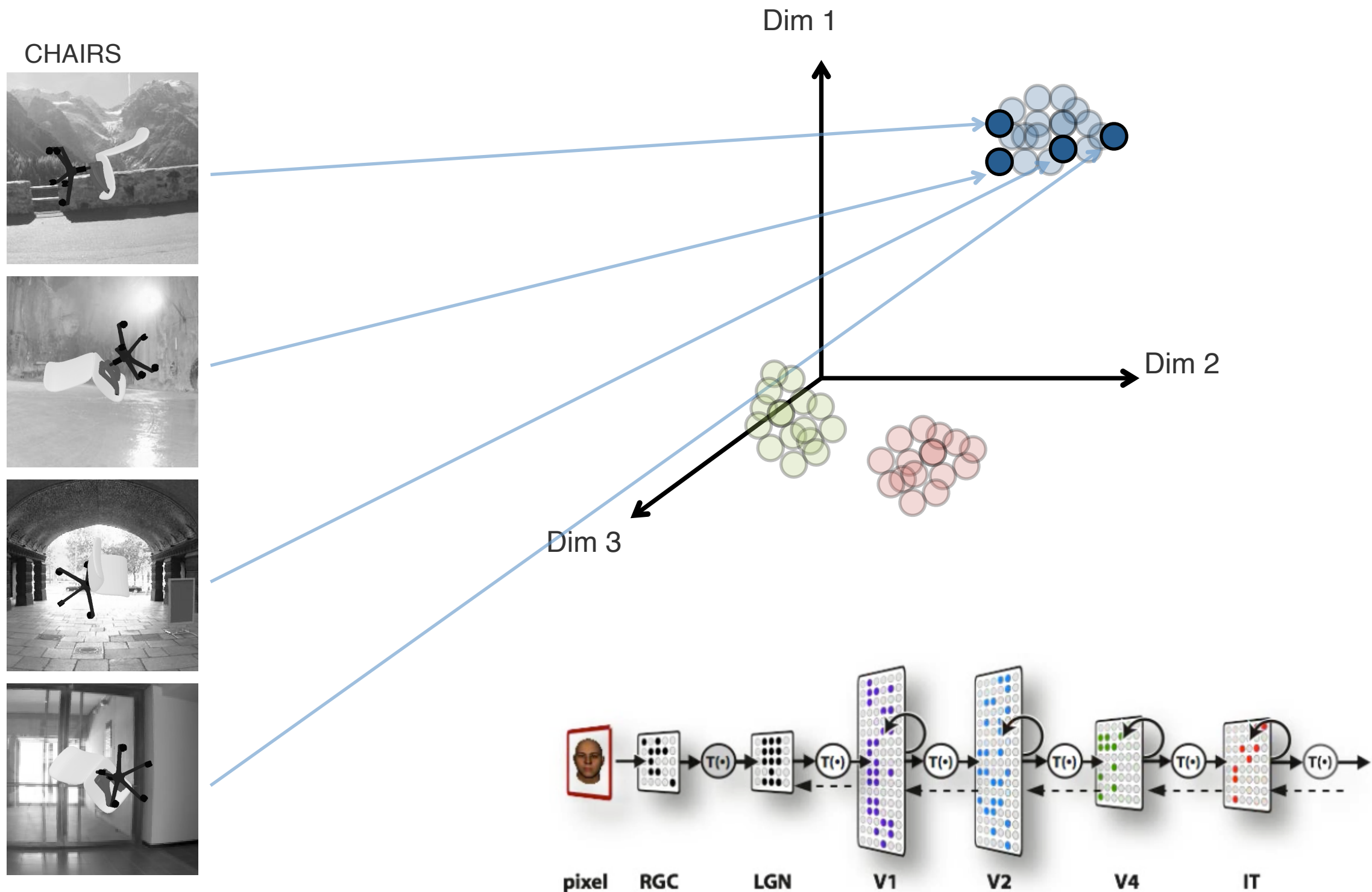
**Does not depend on reporting effector (touch vs. eye movement)**

Comparison of Object Recognition Behavior in Human and Monkey  
R. Rajalingham, K Schmidt, J.J. DiCarlo, **Vision Sciences Society** (2014)  
R. Rajalingham, K Schmidt, J.J. DiCarlo, **J. Neuroscience** (2015)

# Feature Space as Encoding

Pixel space:  $R \sim 10000000$

Feature space:  $R^{4000(?)}$



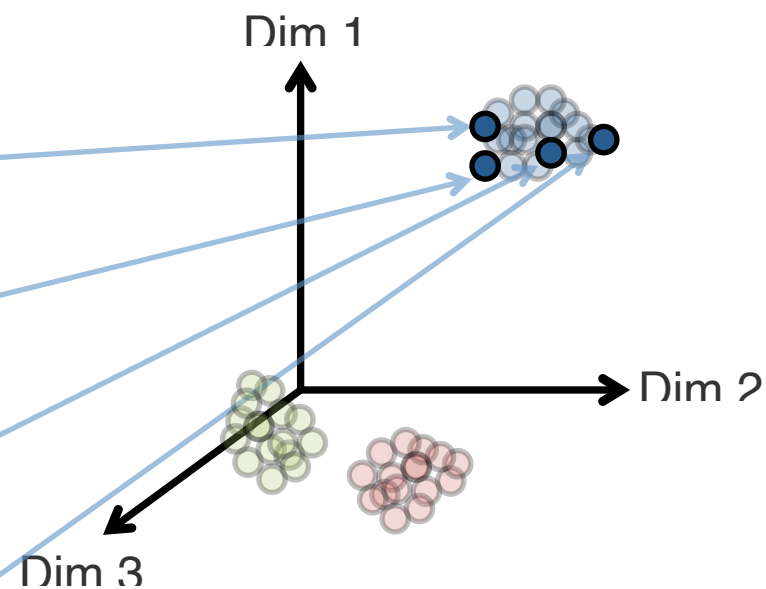
# Feature Space as Encoding

Behavior = Feature space + Simple decision rule  
= encoding + decoding

Pixel space:  $\mathbb{R}^{1000000}$   
Output

Feature space:  $\mathbb{R}^{4000(?)}$

Behavioral



Linear Classifier

Linear Regressor

Distance Function

Category Judgement

Localization

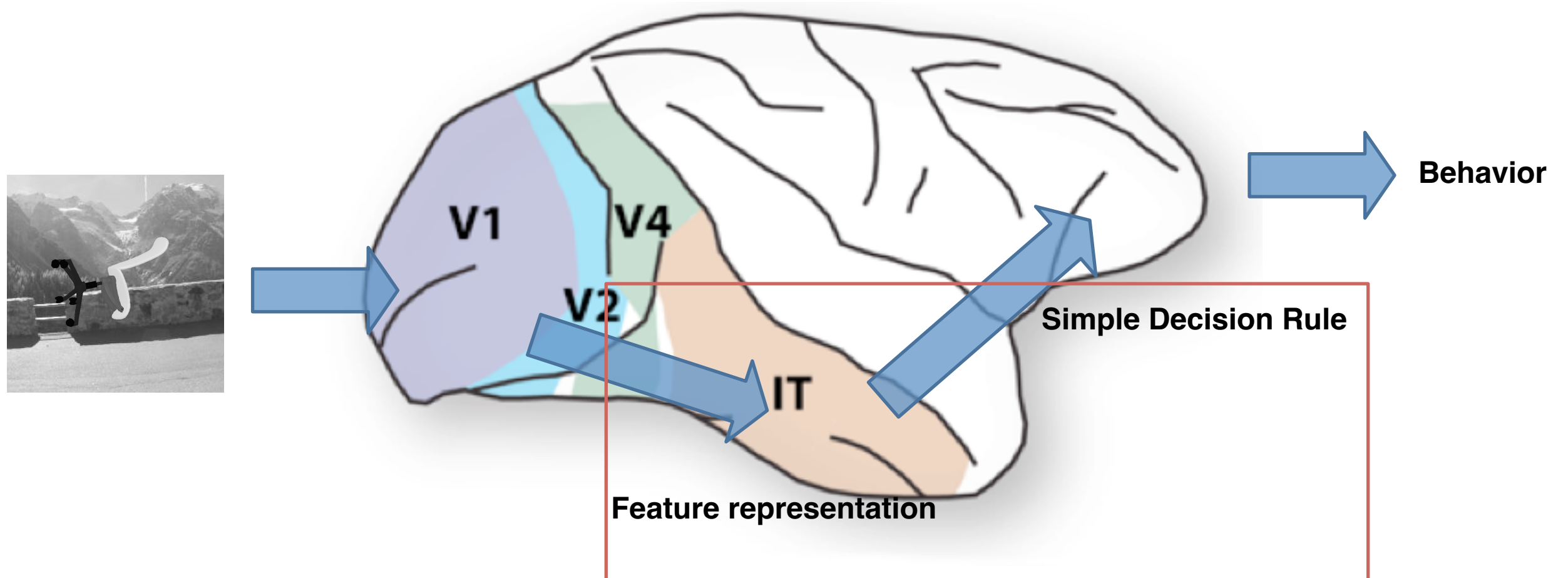
“Subjective” Similarity judgement

⋮  
⋮  
⋮

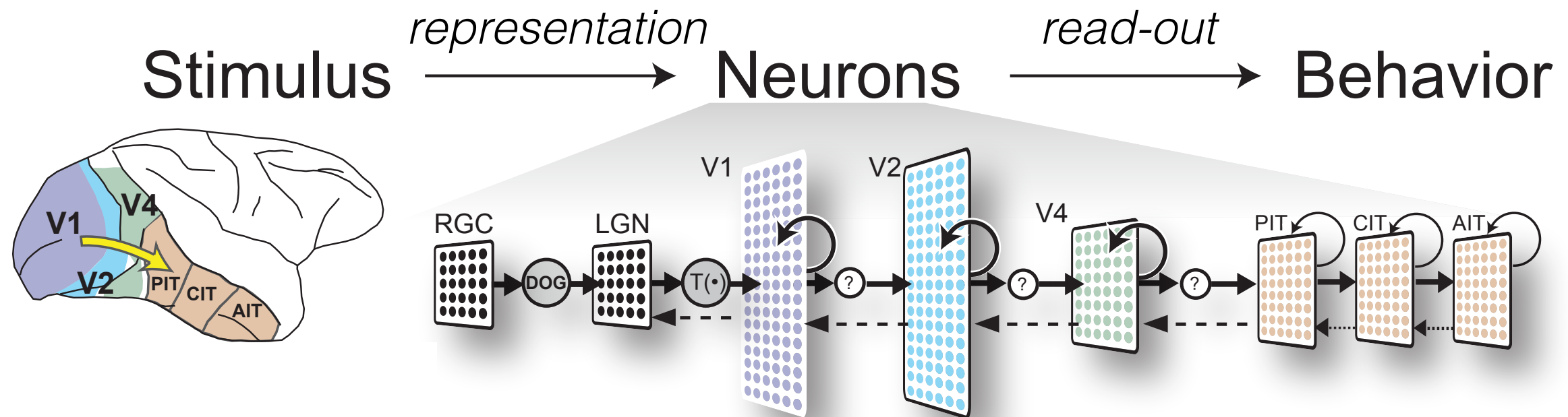


# Encoding & Decoding

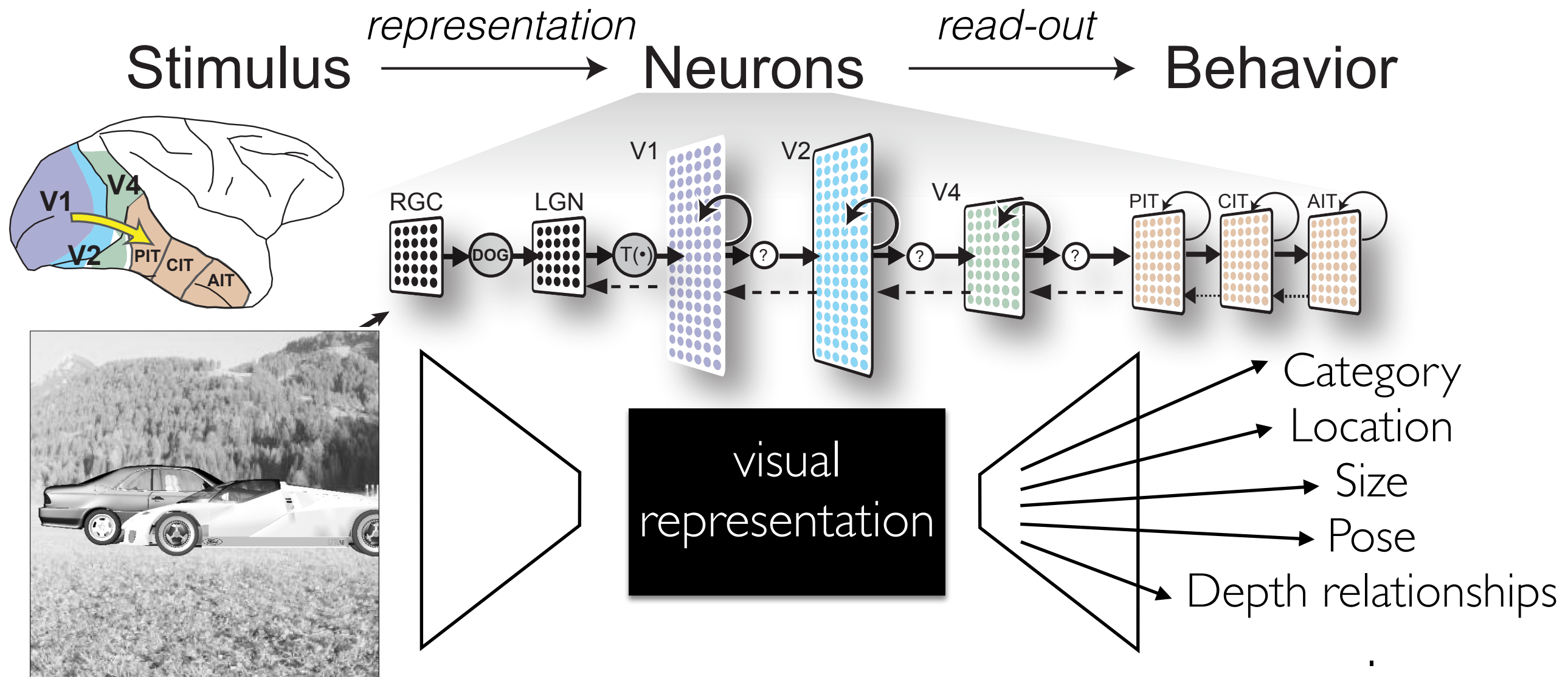
Behavior = Feature space + Simple decision rule  
= encoding + decoding



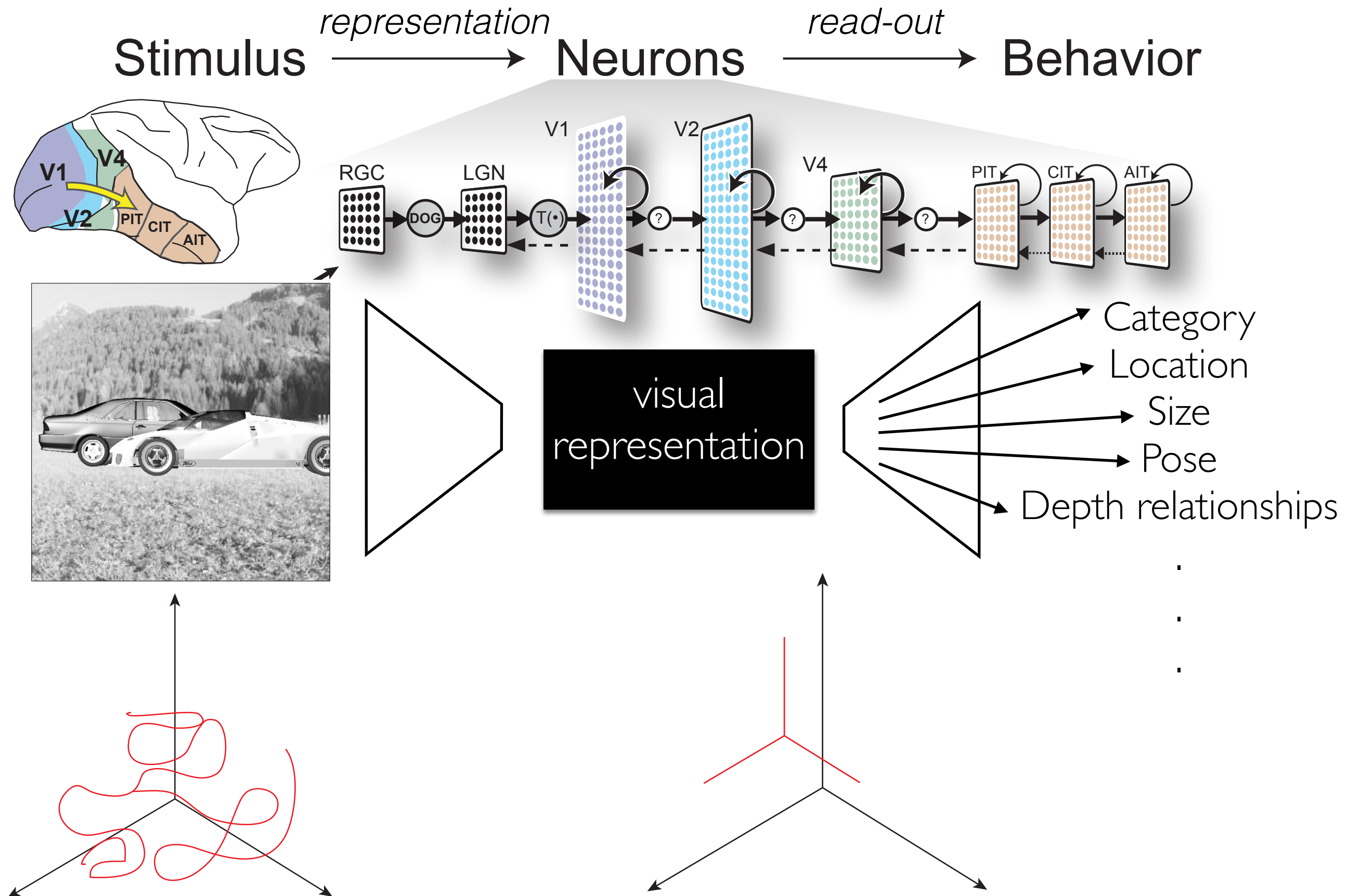
# Encoding & Decoding



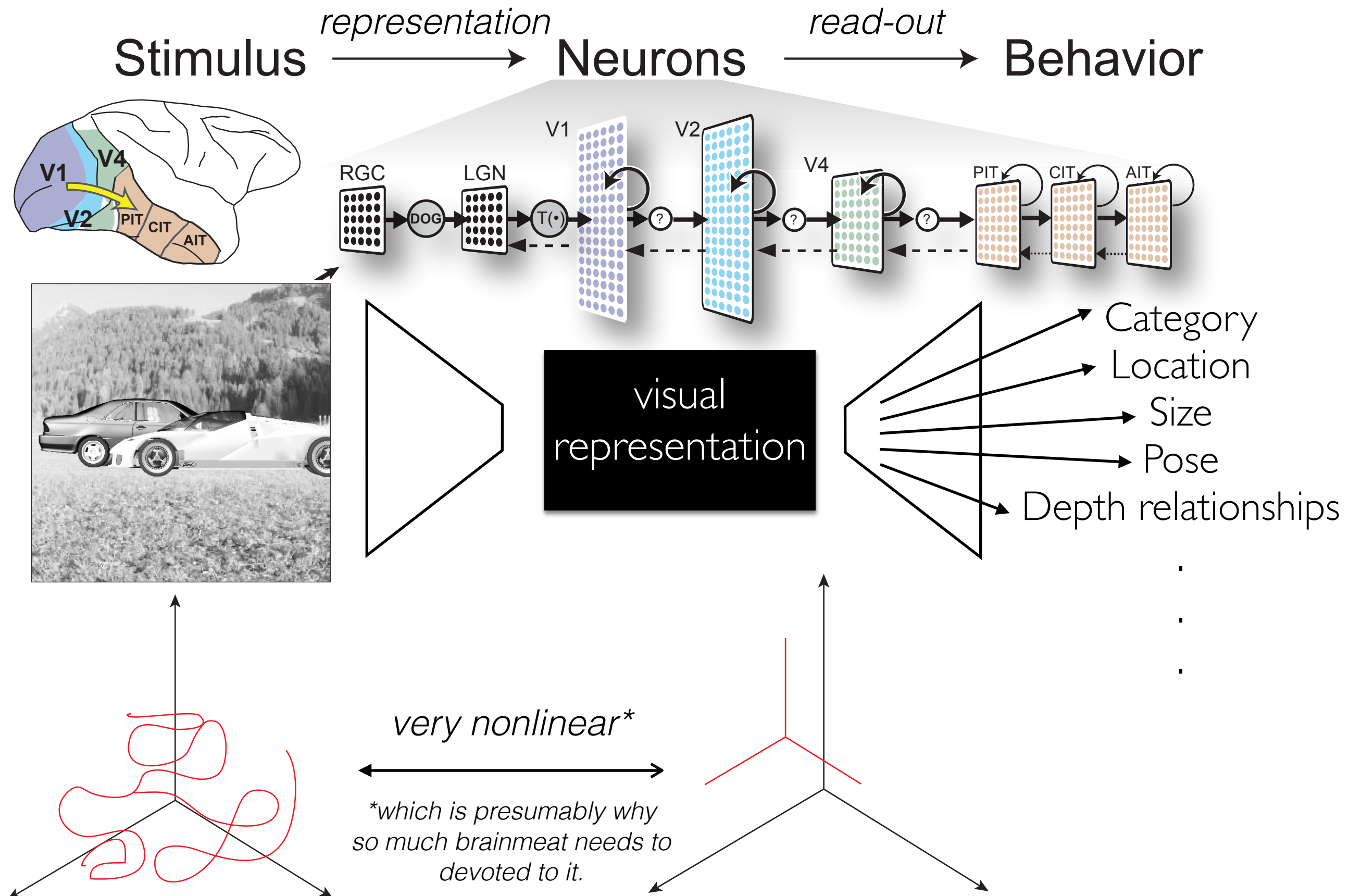
# Encoding & Decoding



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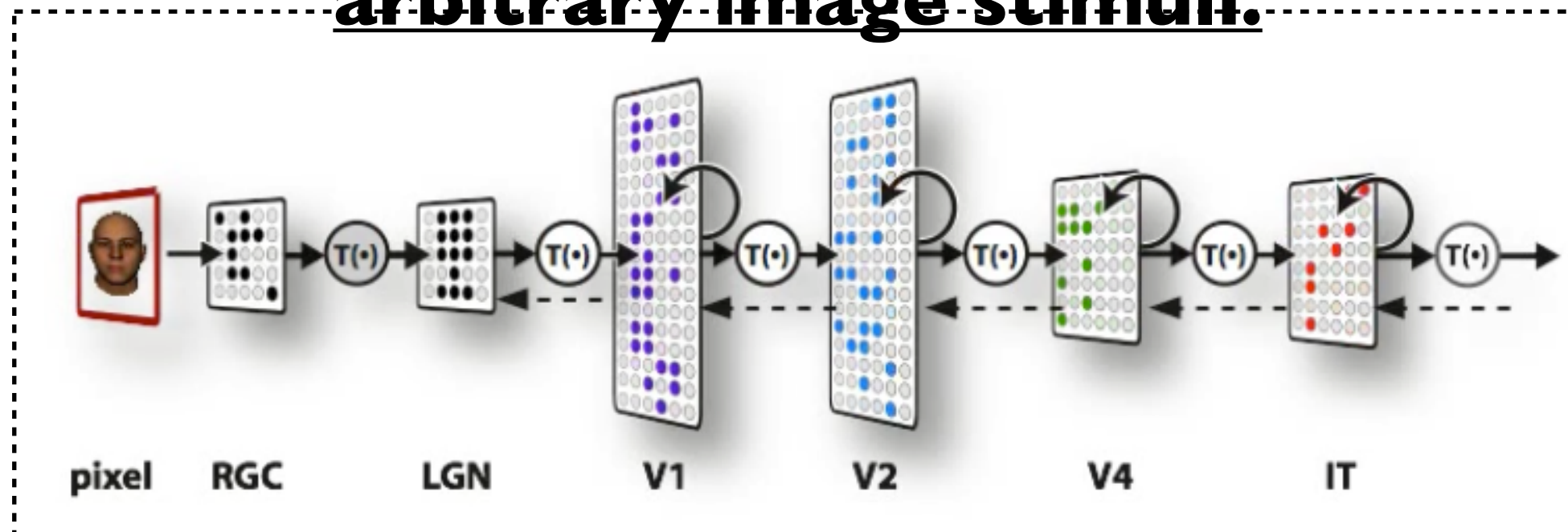


# Encoding & Decoding





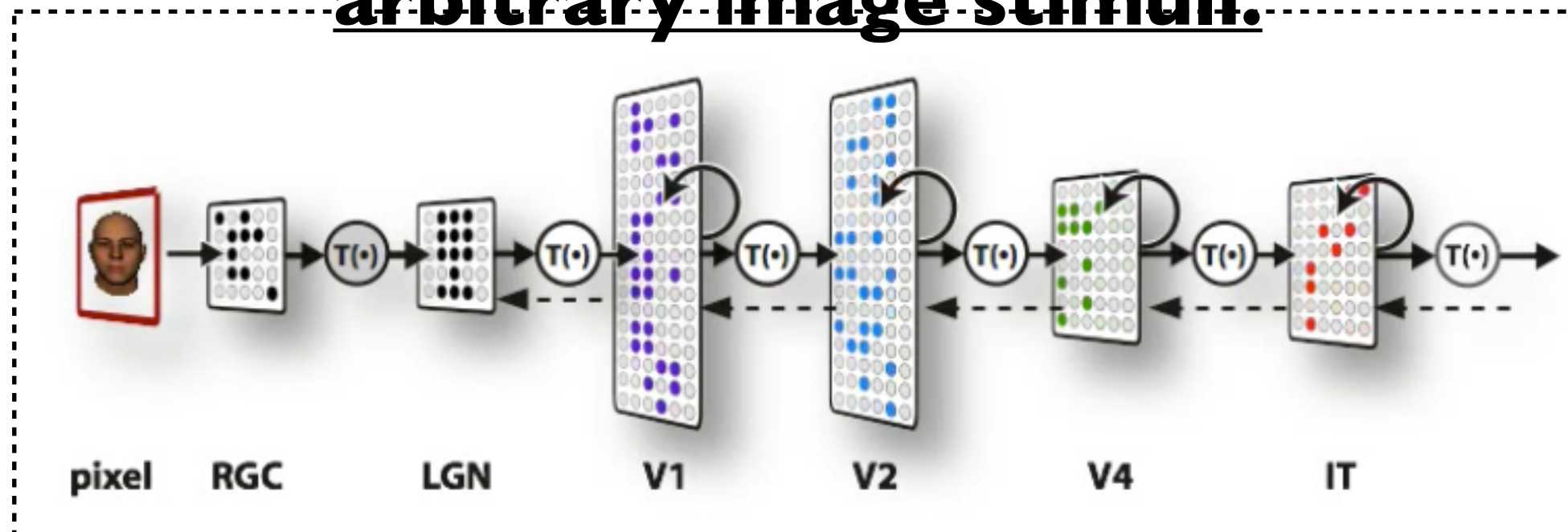
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Key questions:

(a) how many layers?

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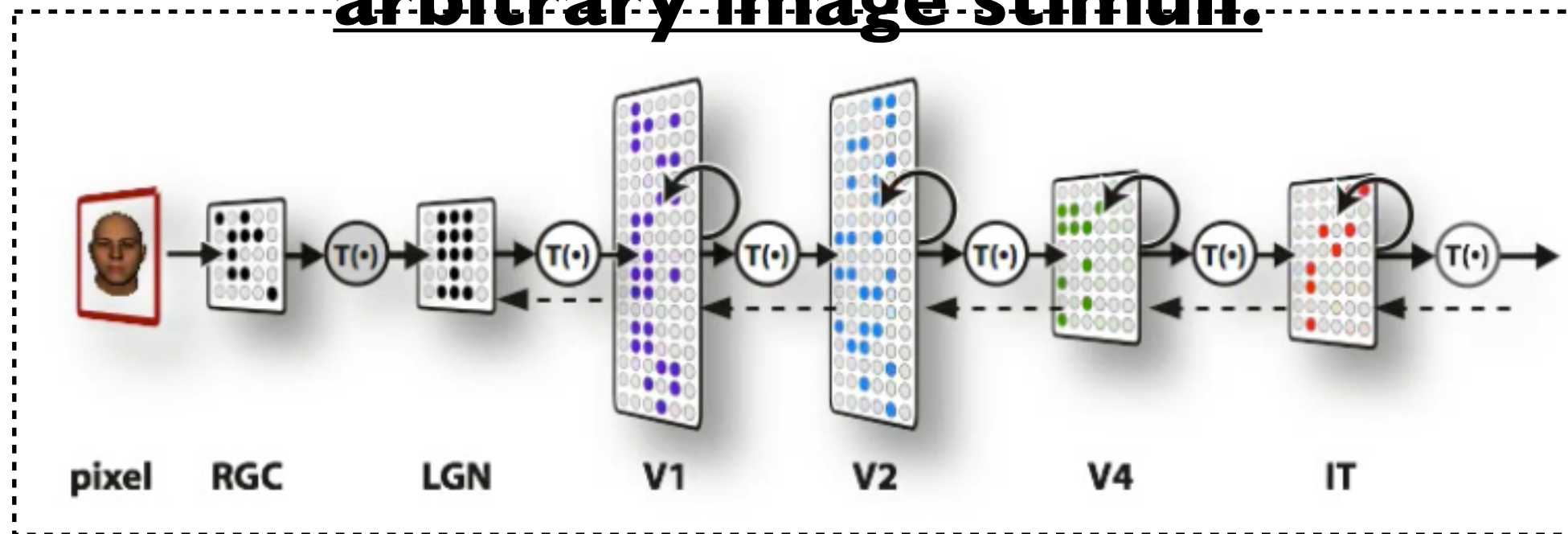


Key questions:

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(b) what's in each layer, specifically?

## **GOAL: Predictive model of single-neuron responses throughout the ventral stream to arbitrary image stimuli.**



Key questions:

- (a) how many layers?
- (b) what's in each layer, specifically?
- (c) what behavioral goals and biophysical facts constrain it to be as it is?

**How are we supposed to use all this hard-won  
(Retina-IT) neuroscience knowledge to make  
an actual model?**