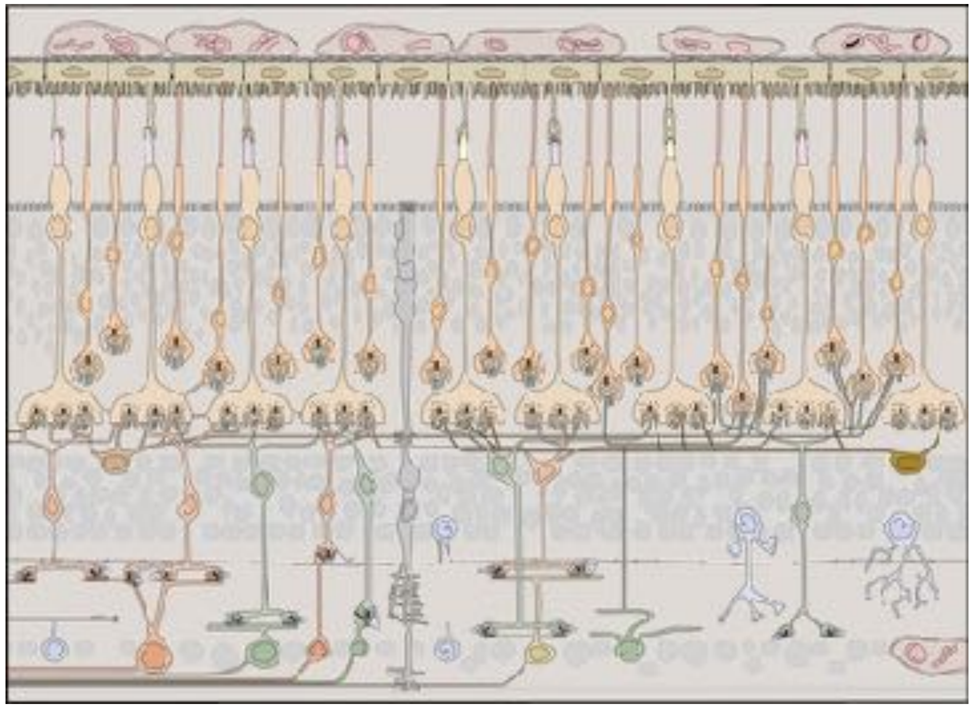
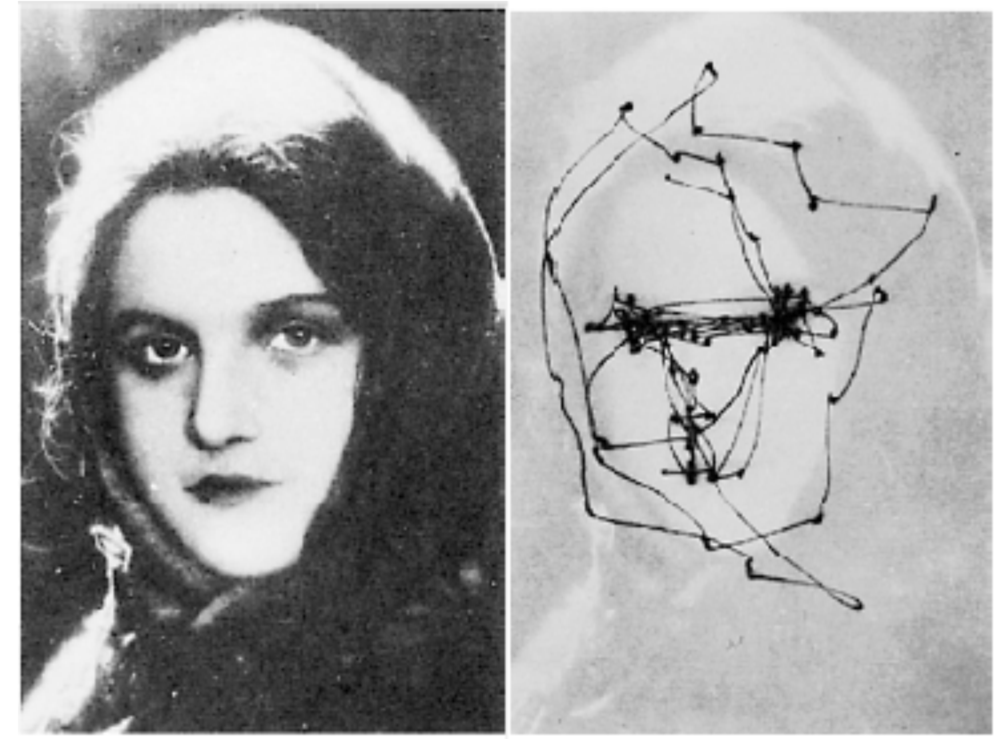
Neural mechanisms of vision

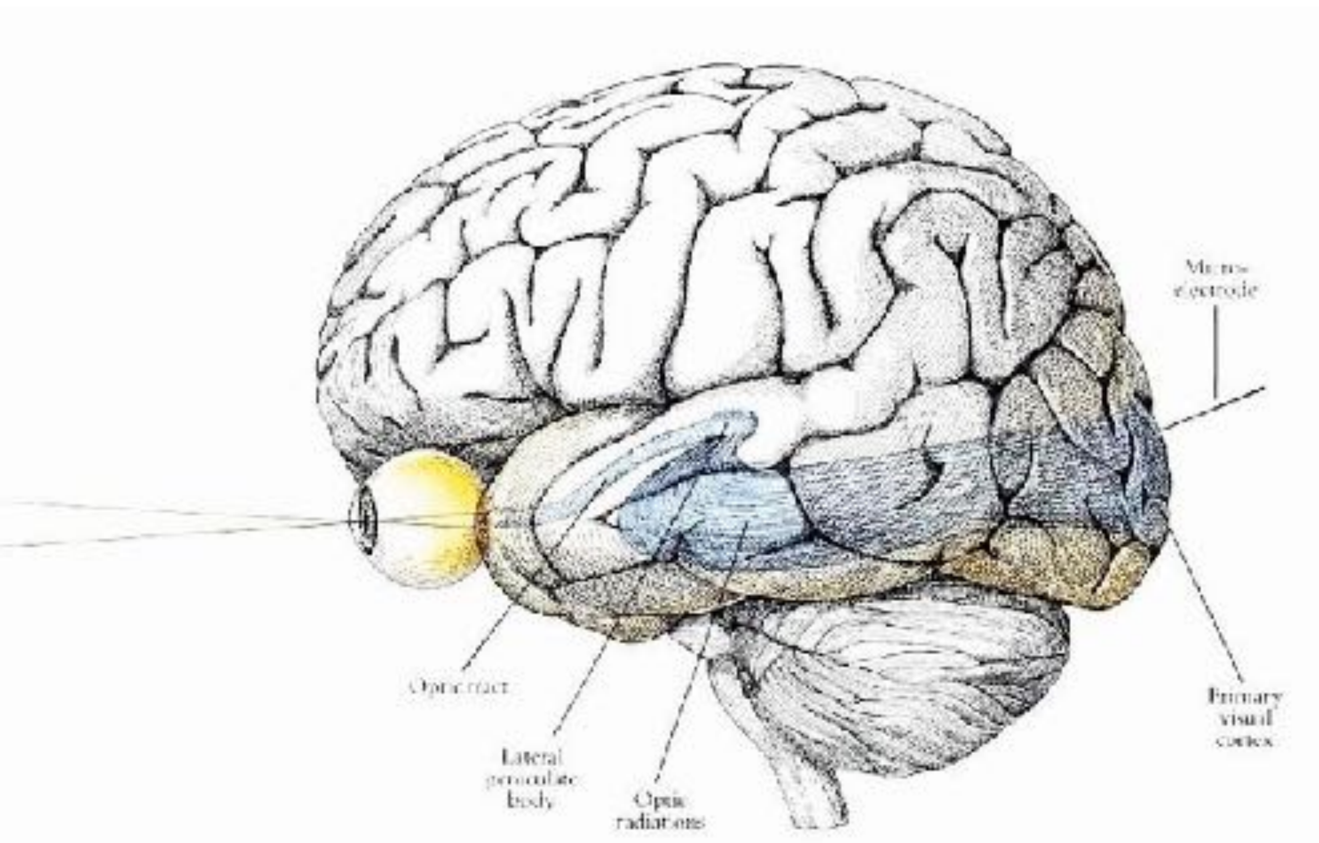
Bruno A. Olshausen
Helen Wills Neuroscience Institute, School of Optometry
and Redwood Center for Theoretical Neuroscience
UC Berkeley



Retina



Eye movements



Cortex

Mystery

Evolution of the eye

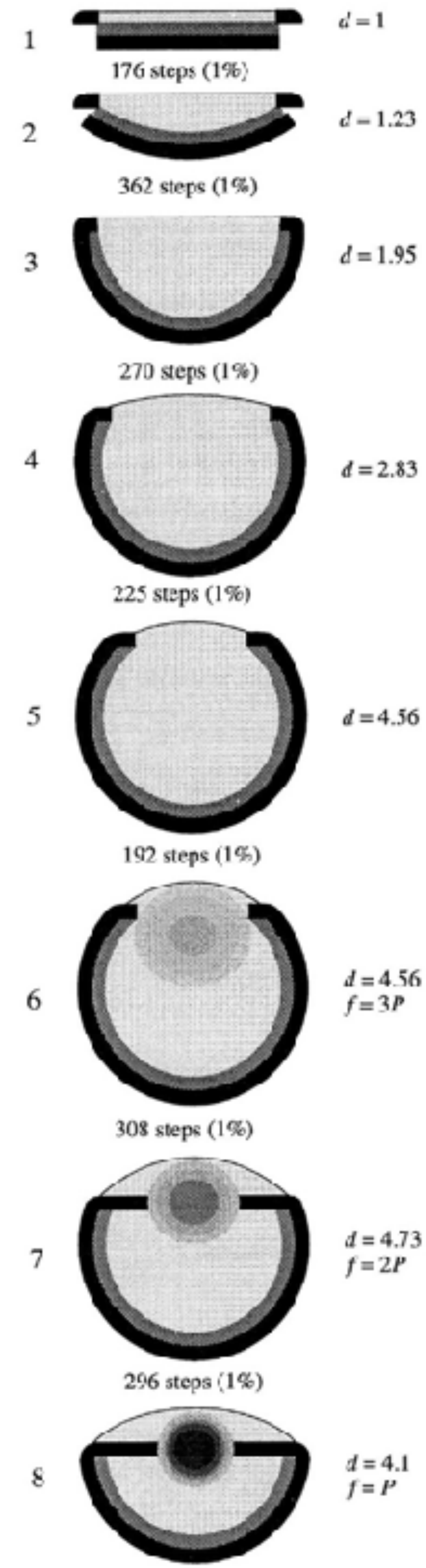
A Pessimistic Estimate of the Time Required for an Eye to Evolve

(500k years)

Nilsson & Pelger (1994)

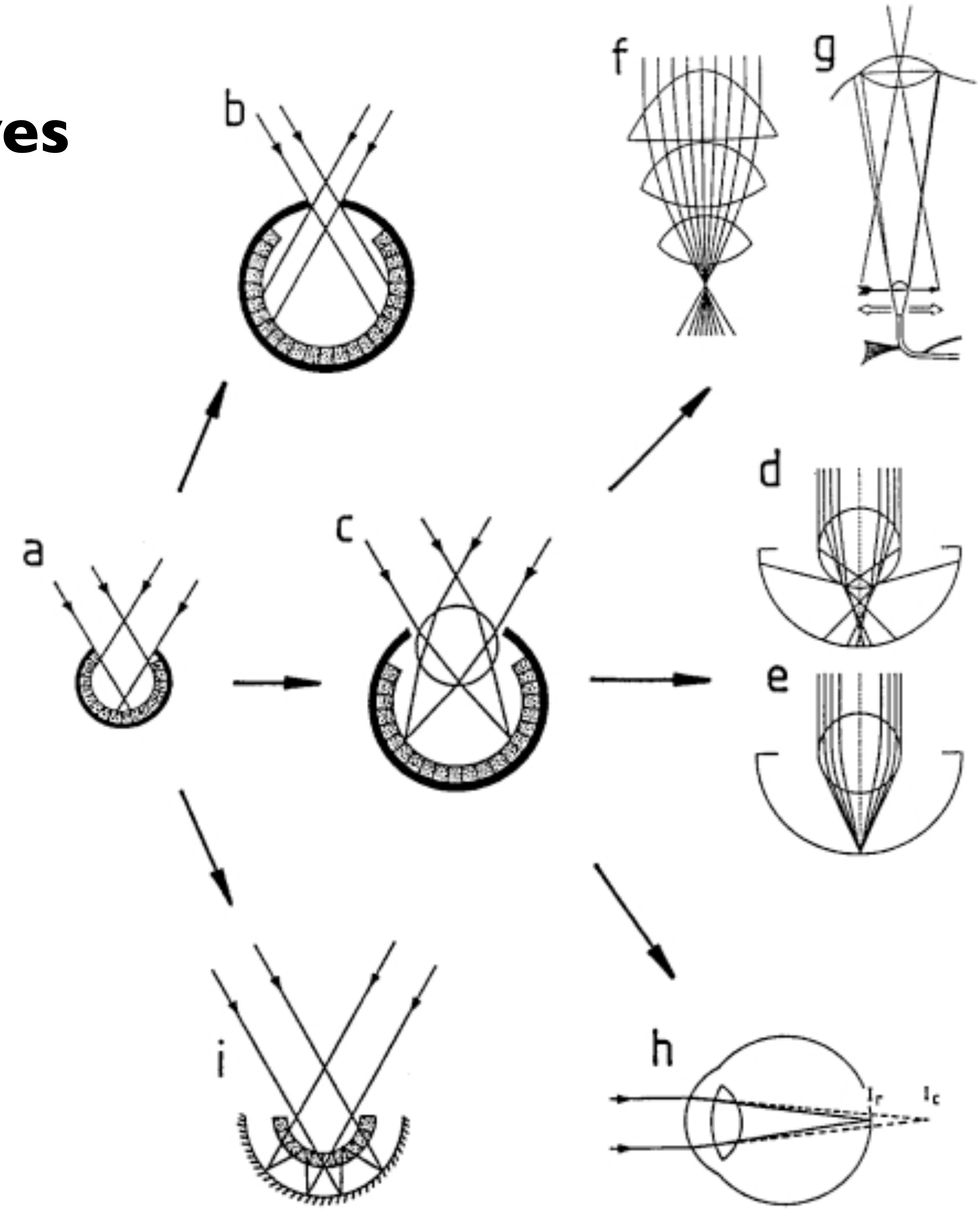
that the eye...could have been formed by natural selection seems, I freely confess, absurd in the highest possible degree.

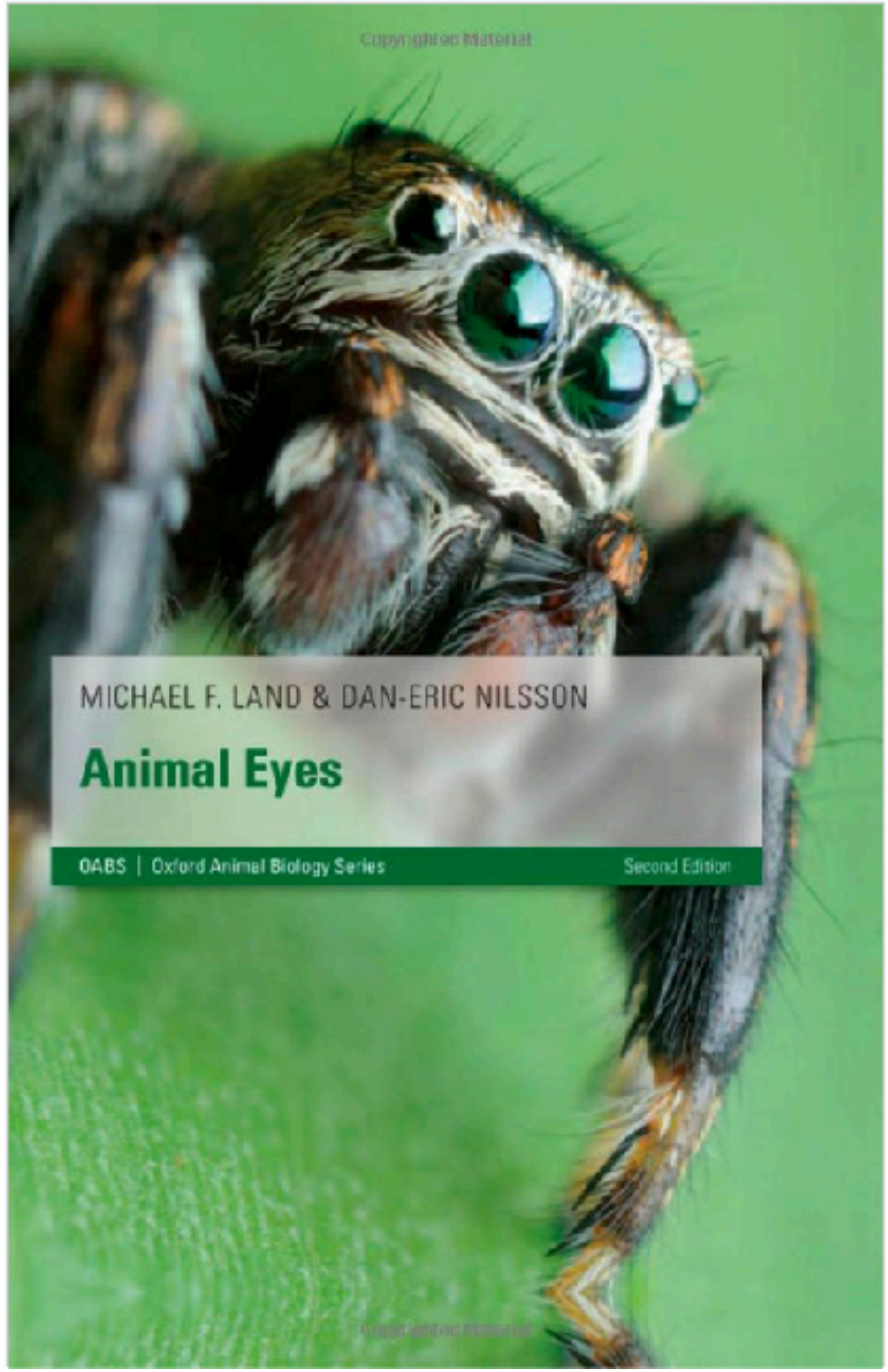
-- Charles Darwin (1859)



The evolution of eyes

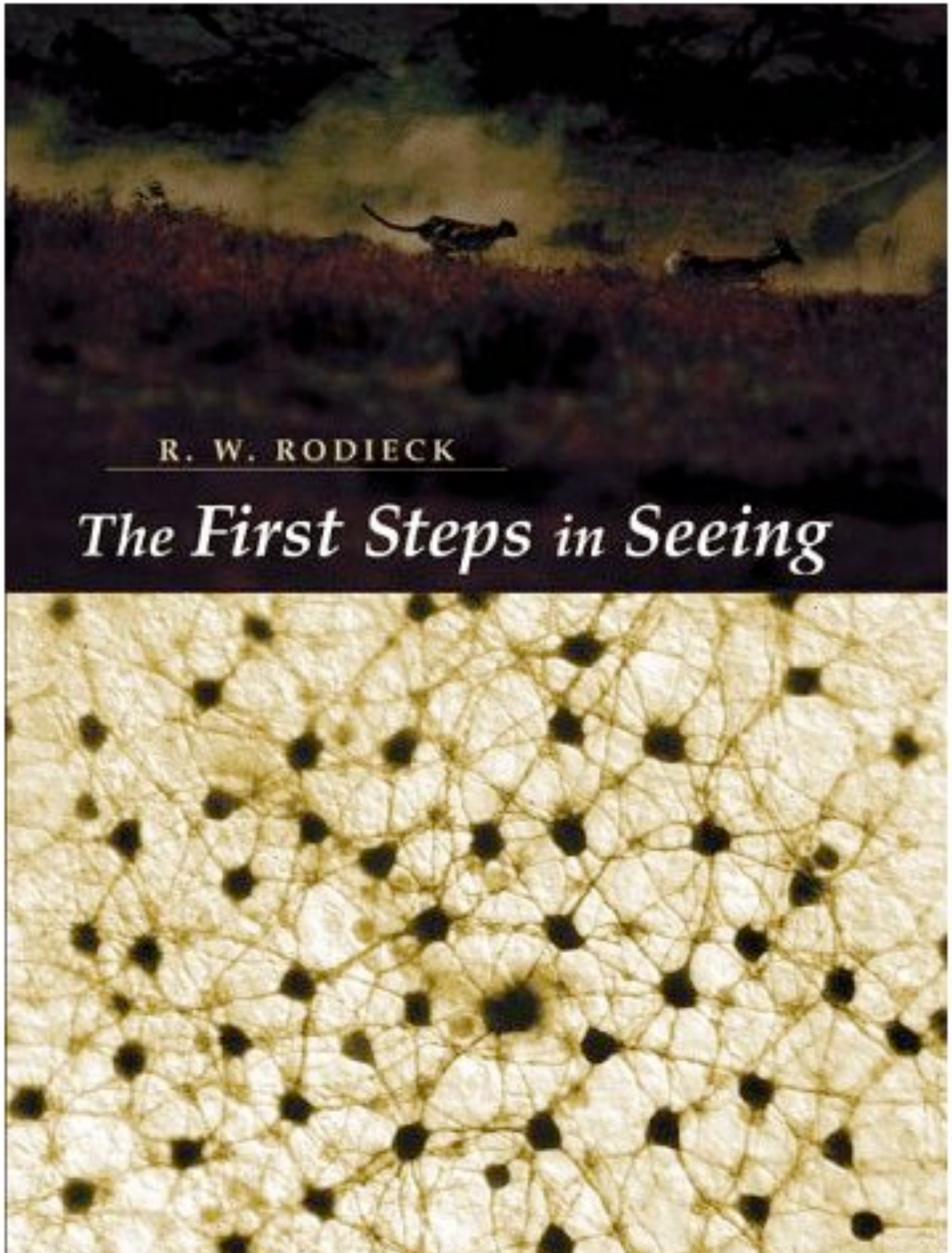
Land & Fernald (1992)

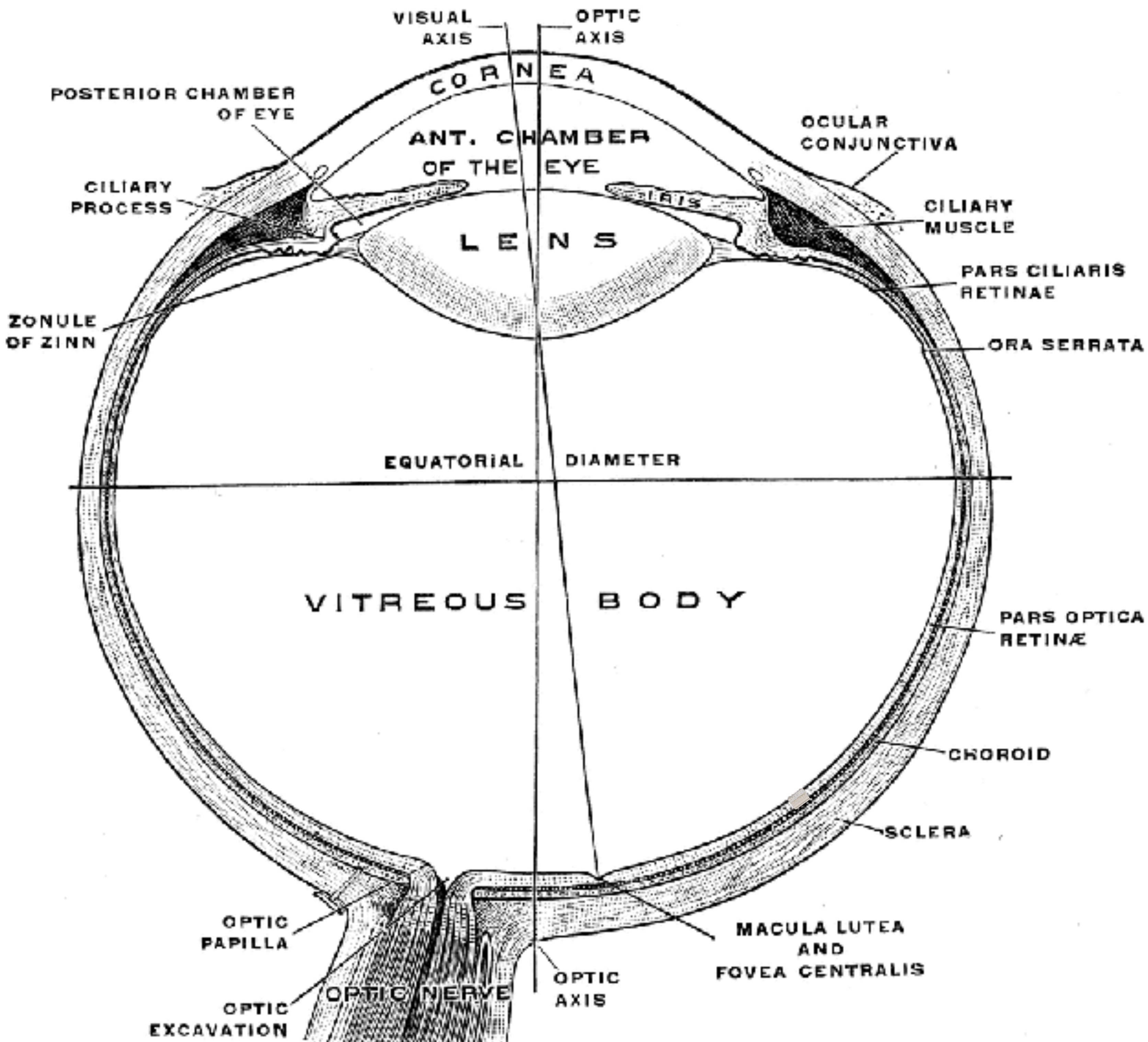


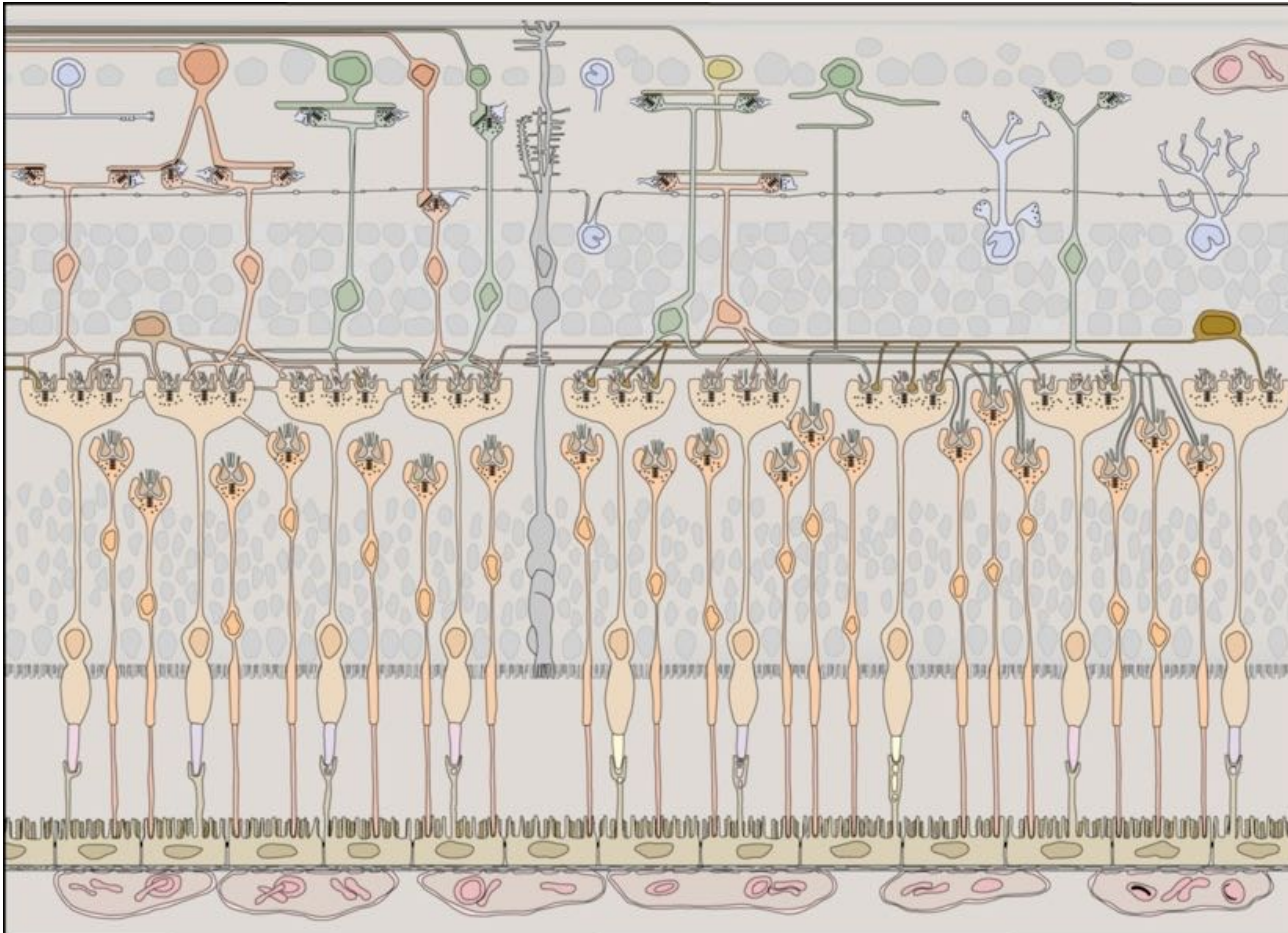


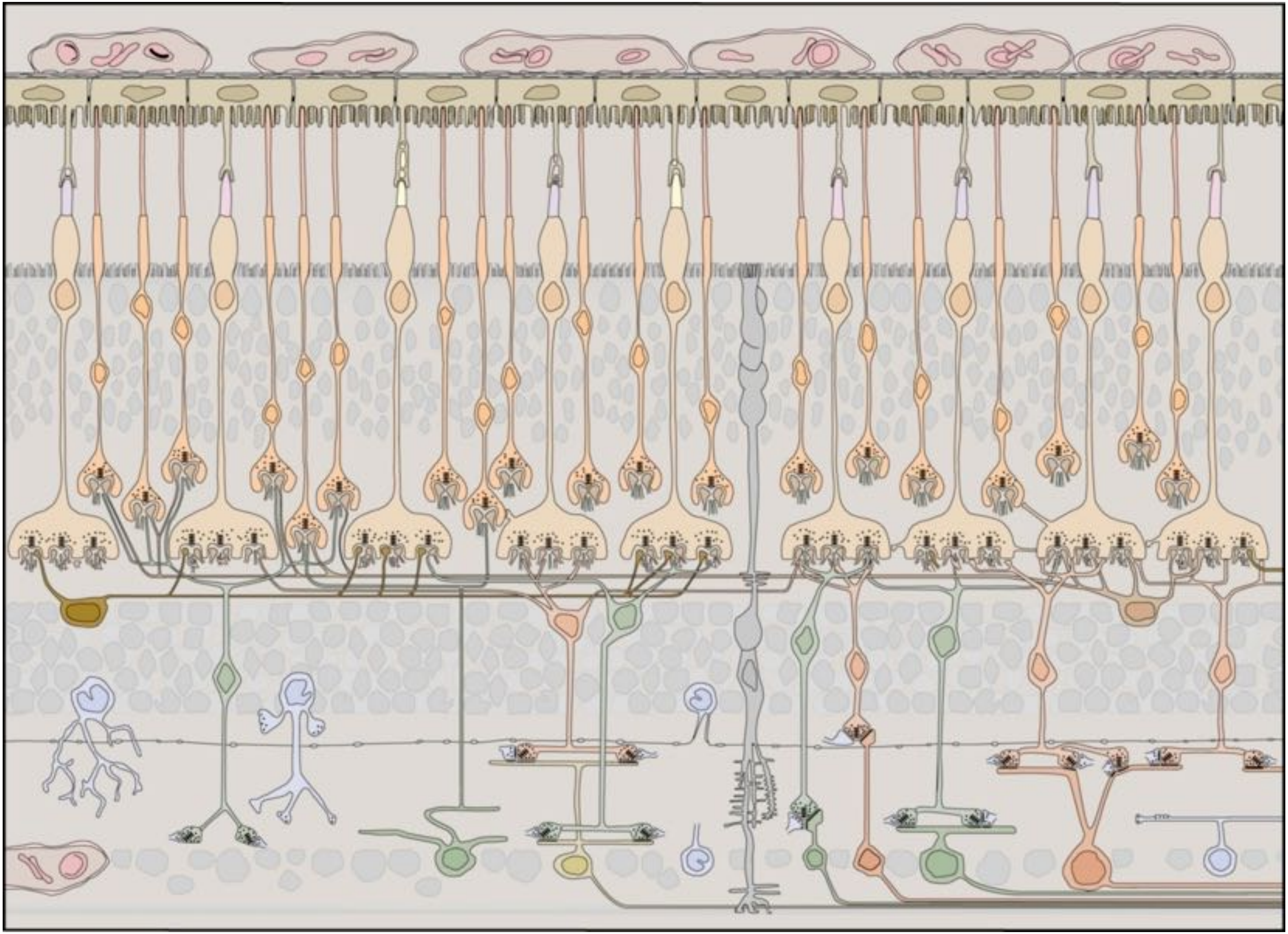
http://redwood.berkeley.edu/wiki/VS298:_Animal_Eyes

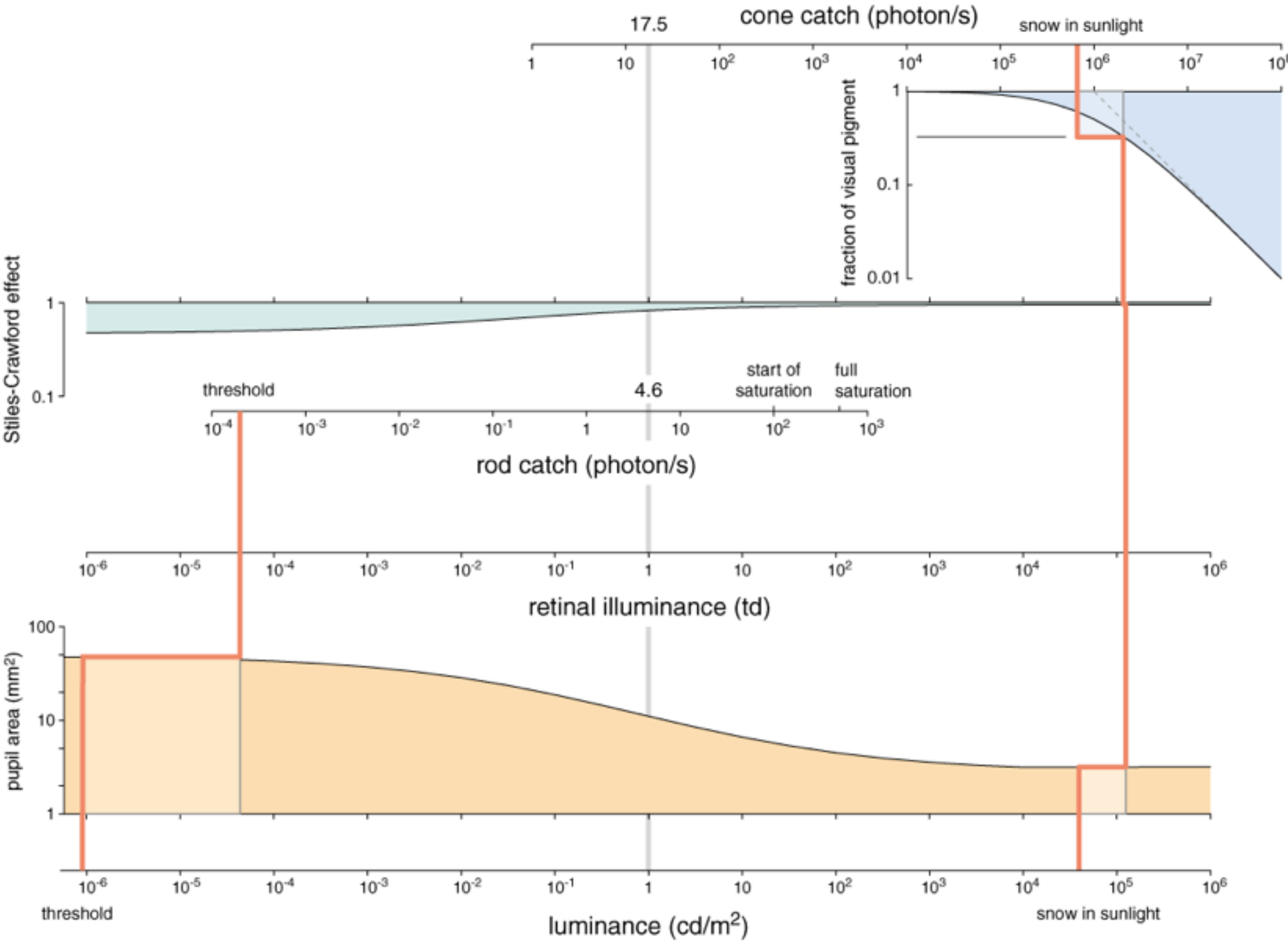
Retina


R. W. RODIECK
The First Steps in Seeing


VISUAL AXIS
OPTIC AXIS
CORNEA
POSTERIOR CHAMBER OF EYE
ANT. CHAMBER OF THE EYE
OCULAR CONJUNCTIVA
CILIARY PROCESS
IRIS
CILIARY MUSCLE
LENS
PARS CILIARIS RETINAE
ZONULE OF ZINN
ORA SERRATA
EQUATORIAL DIAMETER
VITREOUS BODY
PARS OPTICA RETINÆ
CHOROID
SCLERA
OPTIC PAPILLA
MACULA LUTEA AND FOVEA CENTRALIS
OPTIC NERVE
OPTIC AXIS
OPTIC EXCAVATION

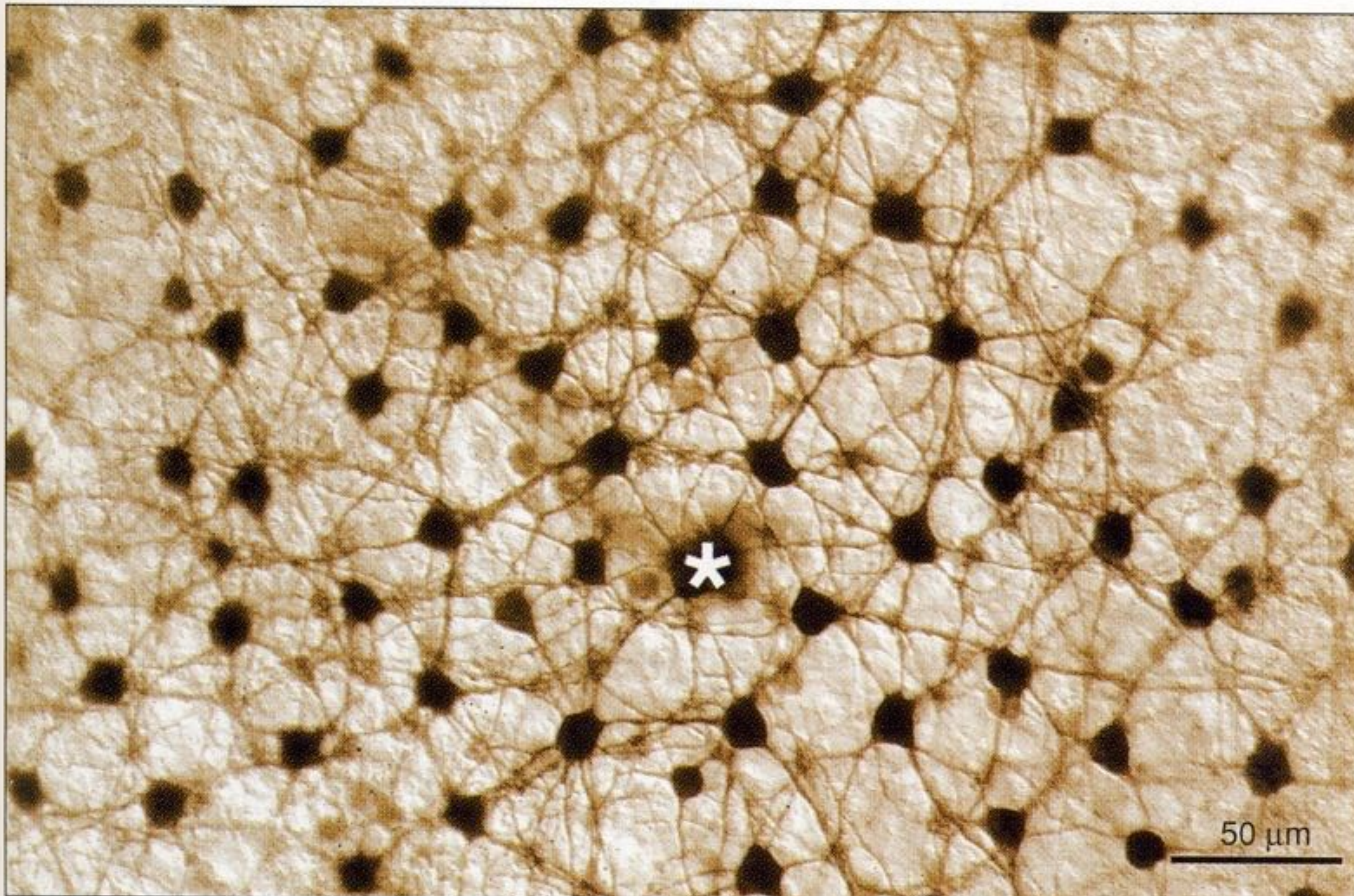






starlight CRT clear blue sky

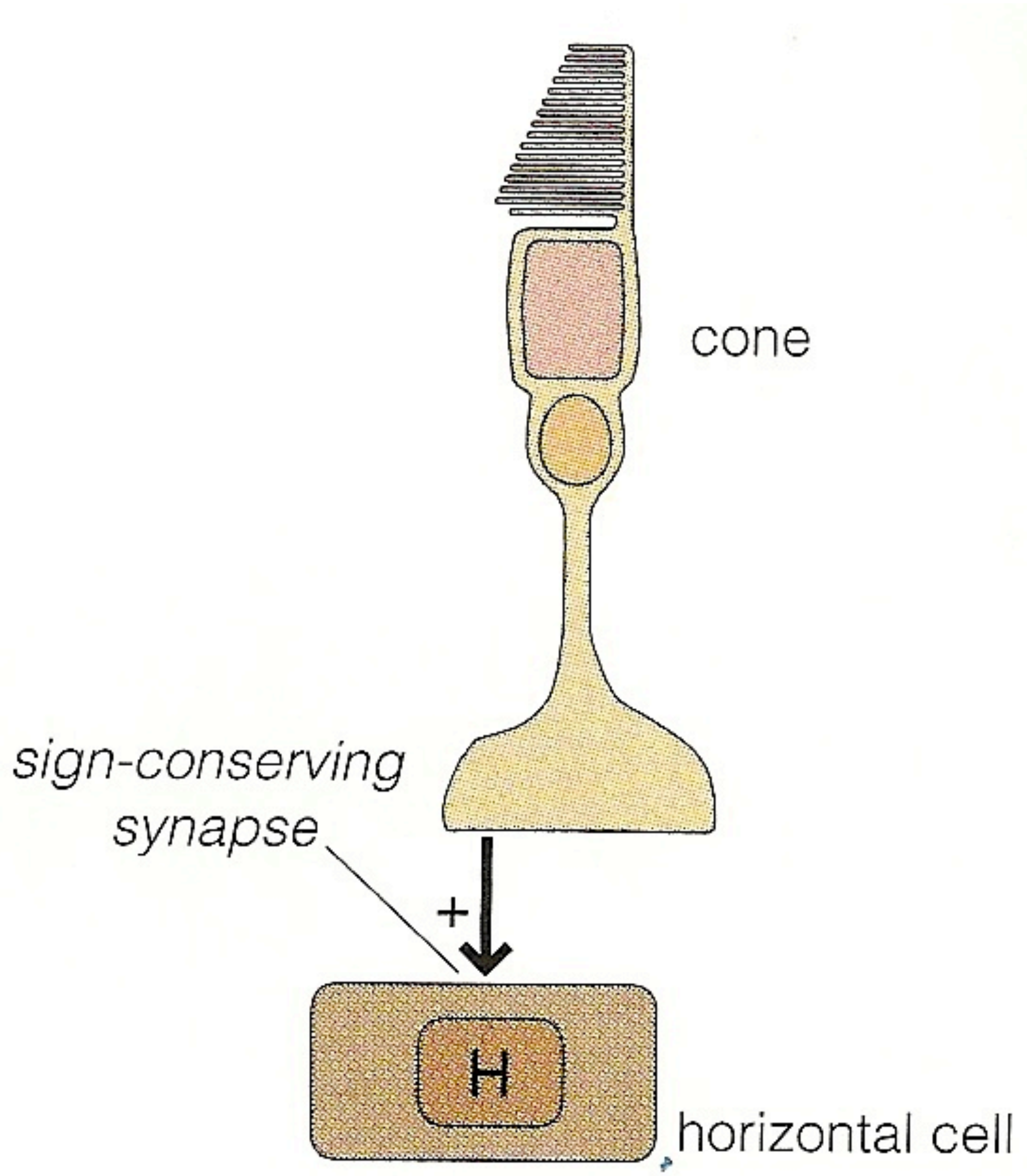
HI horizontal cells connected via gap junctions



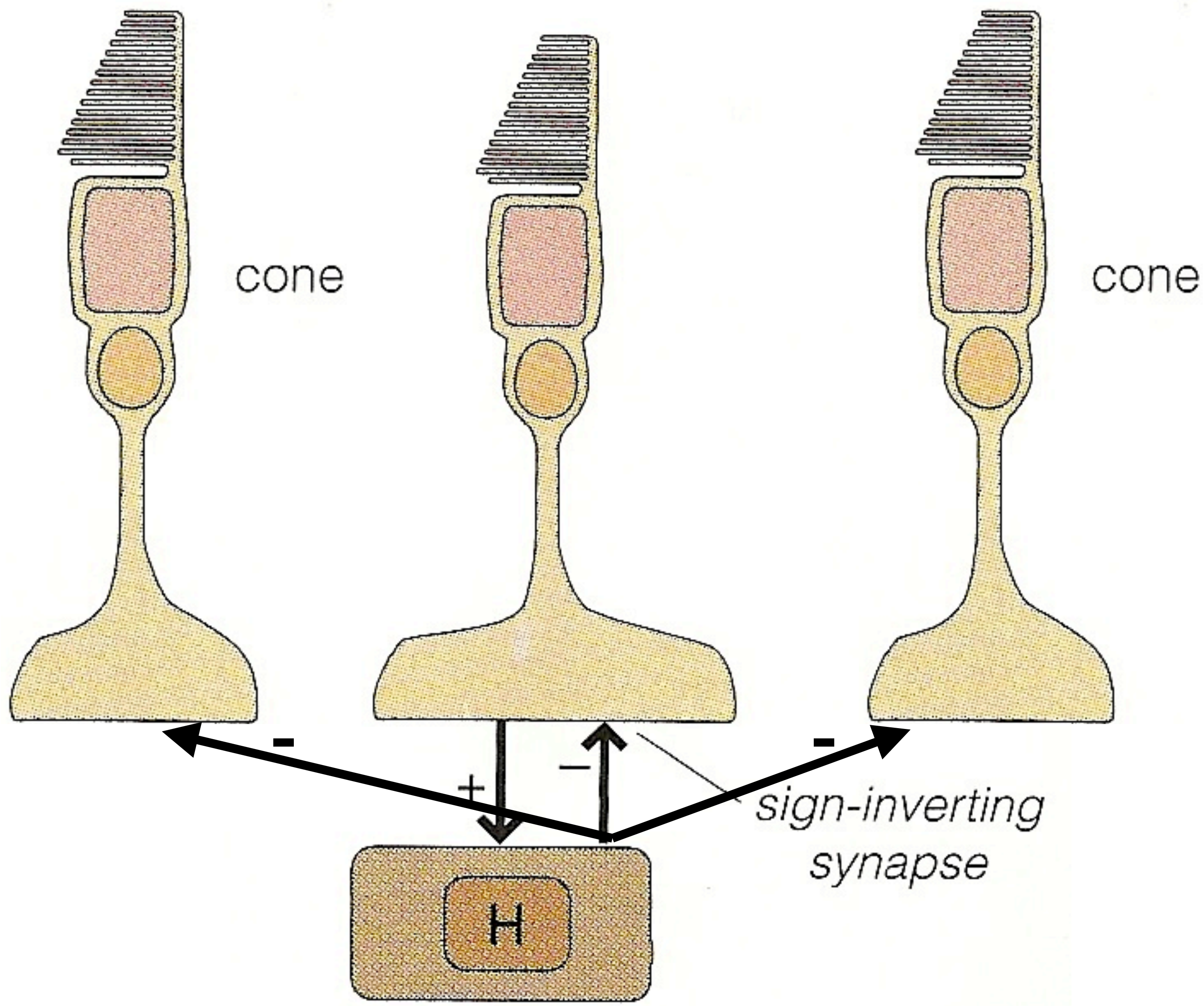
HI horizontal cells labeled following injection of one HI cell (*) ×300

after Dacey, Lee, and Stafford, 1996

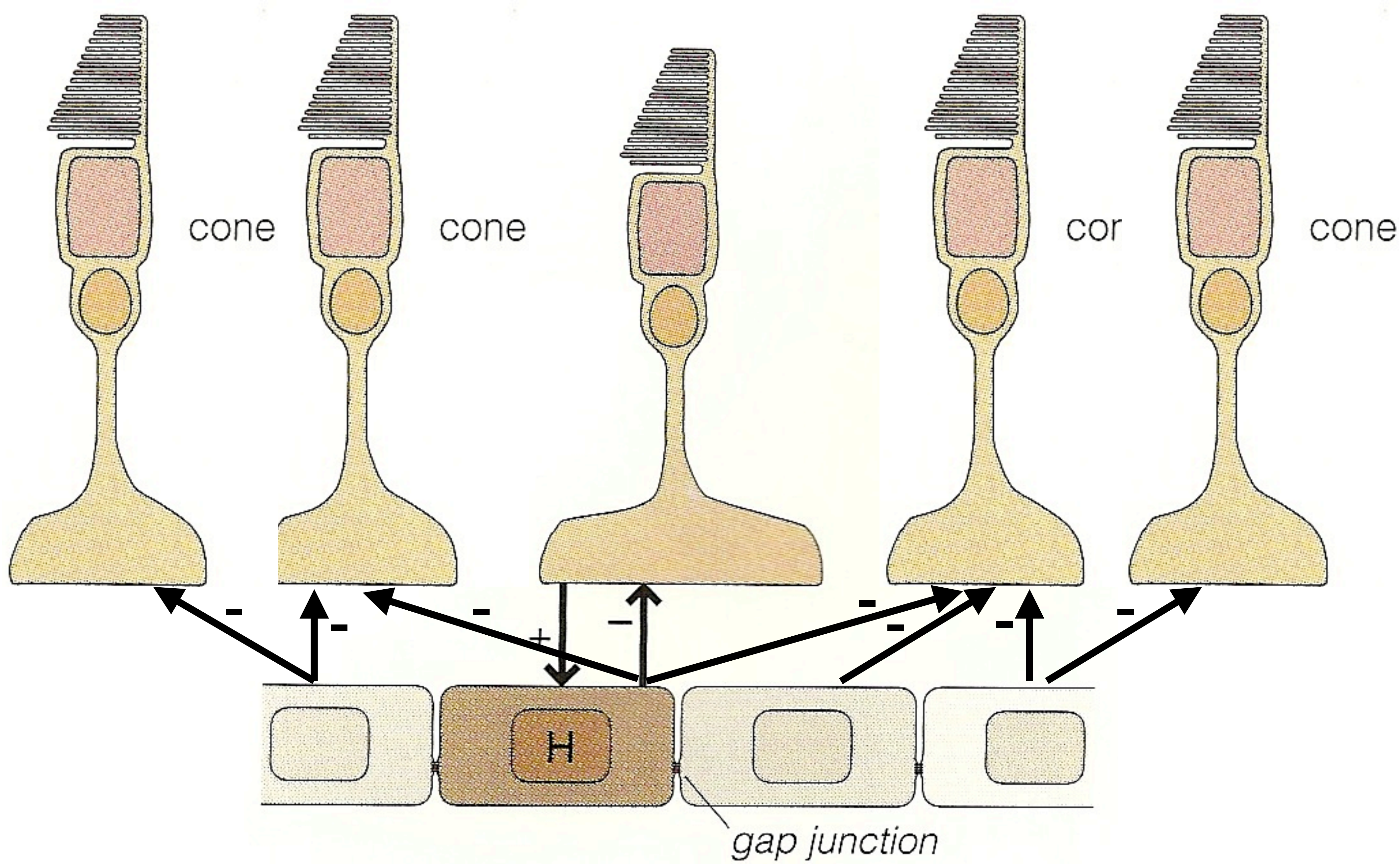
Hyperpolarization of photoreceptor results in *hyperpolarization* of horizontal cells



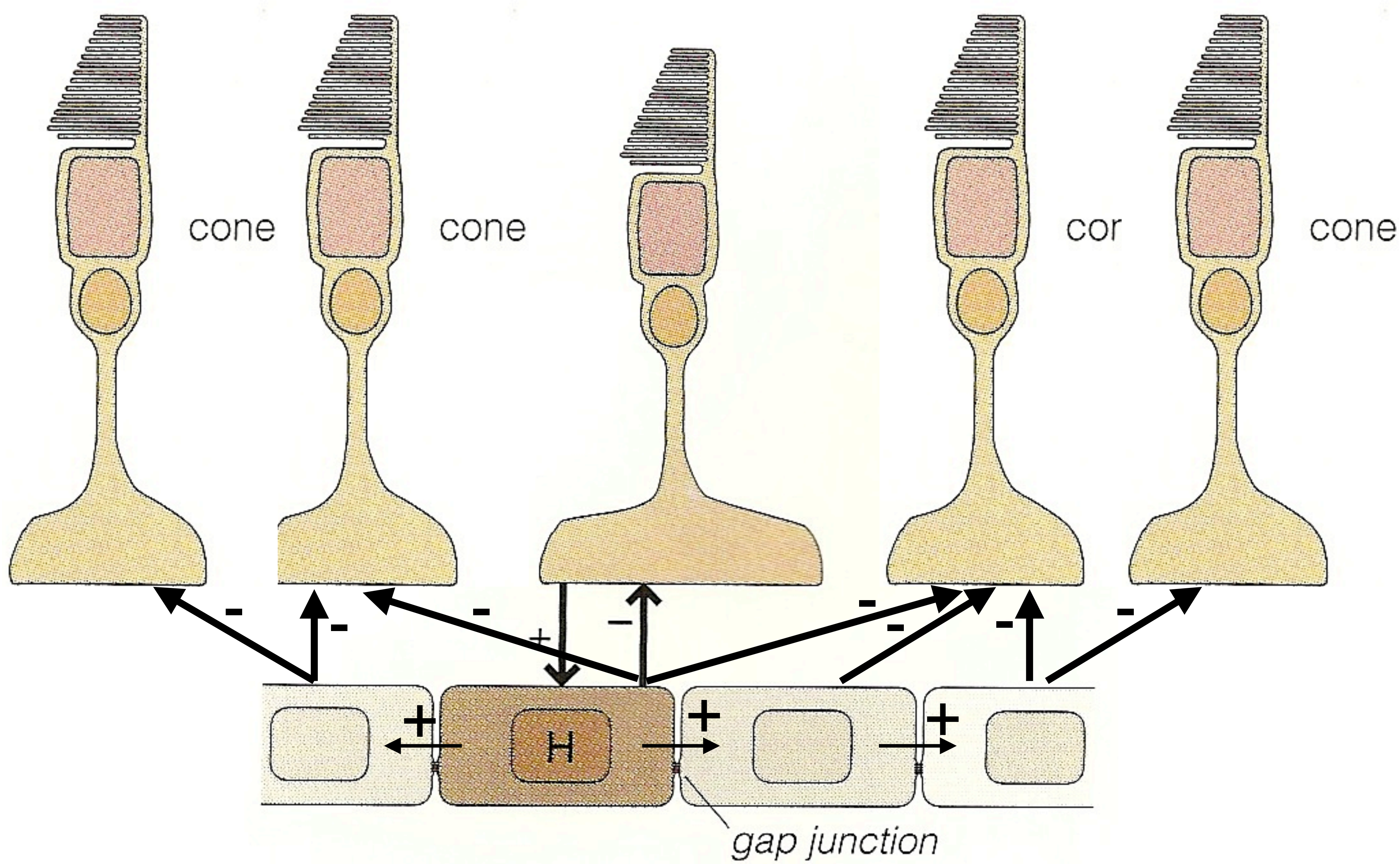
Hyperpolarization of horizontal cell results in *depolarization* of photoreceptors



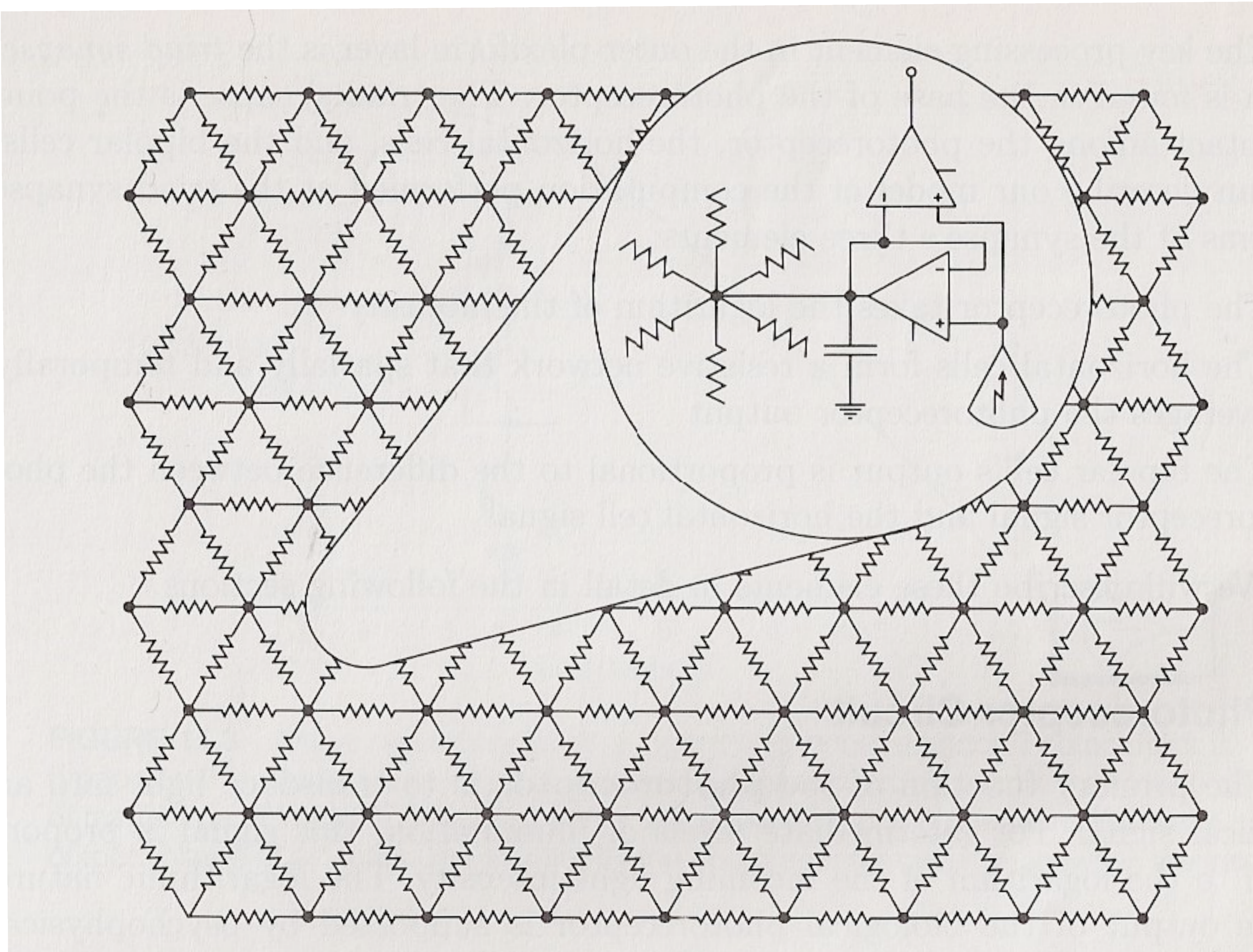
Hyperpolarization of horizontal cell spreads to other horizontal cells via gap junctions



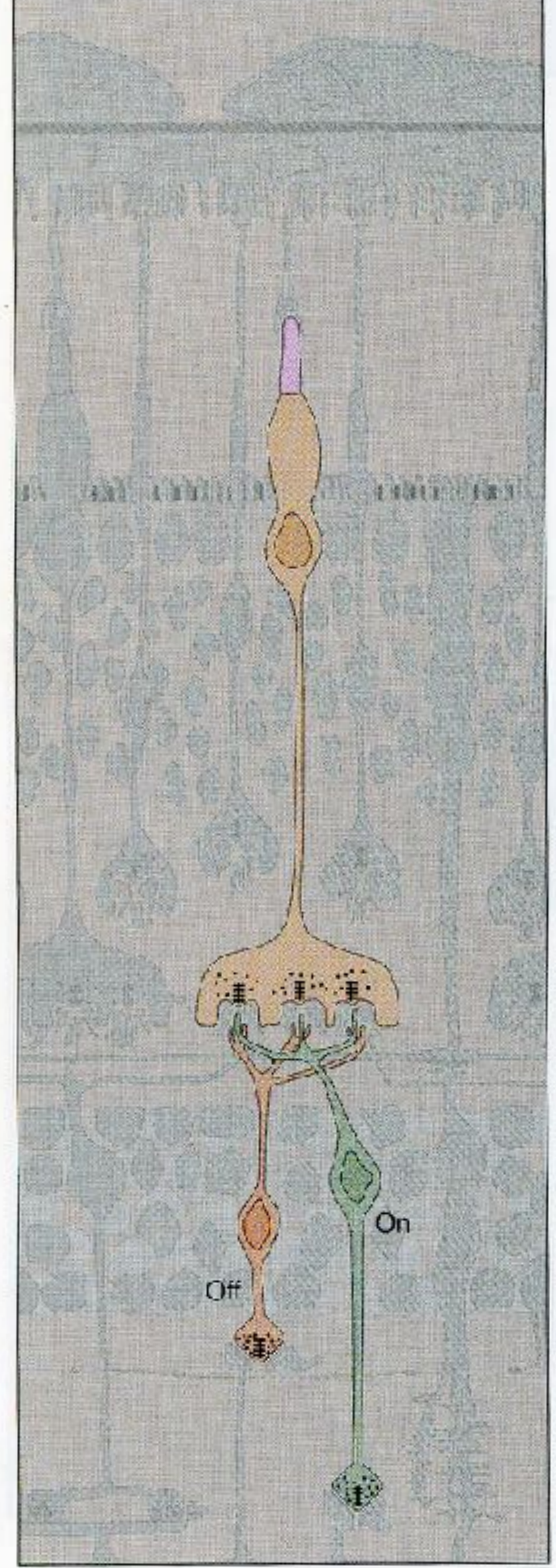
Hyperpolarization of horizontal cell spreads to other horizontal cells via gap junctions

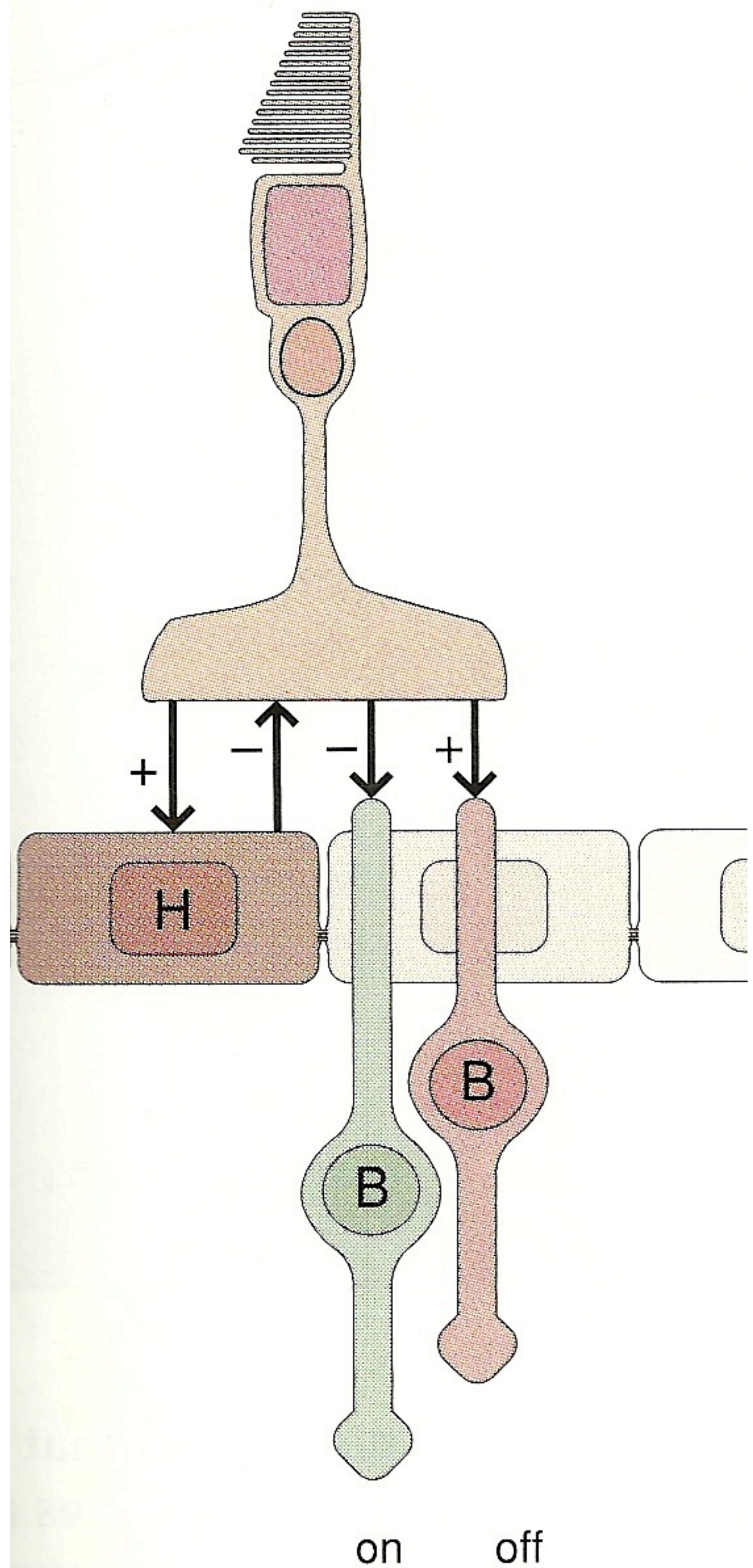


Analog VLSI retina
(Mead & Mahowald, 1989)



On vs. off cone bipolar cells

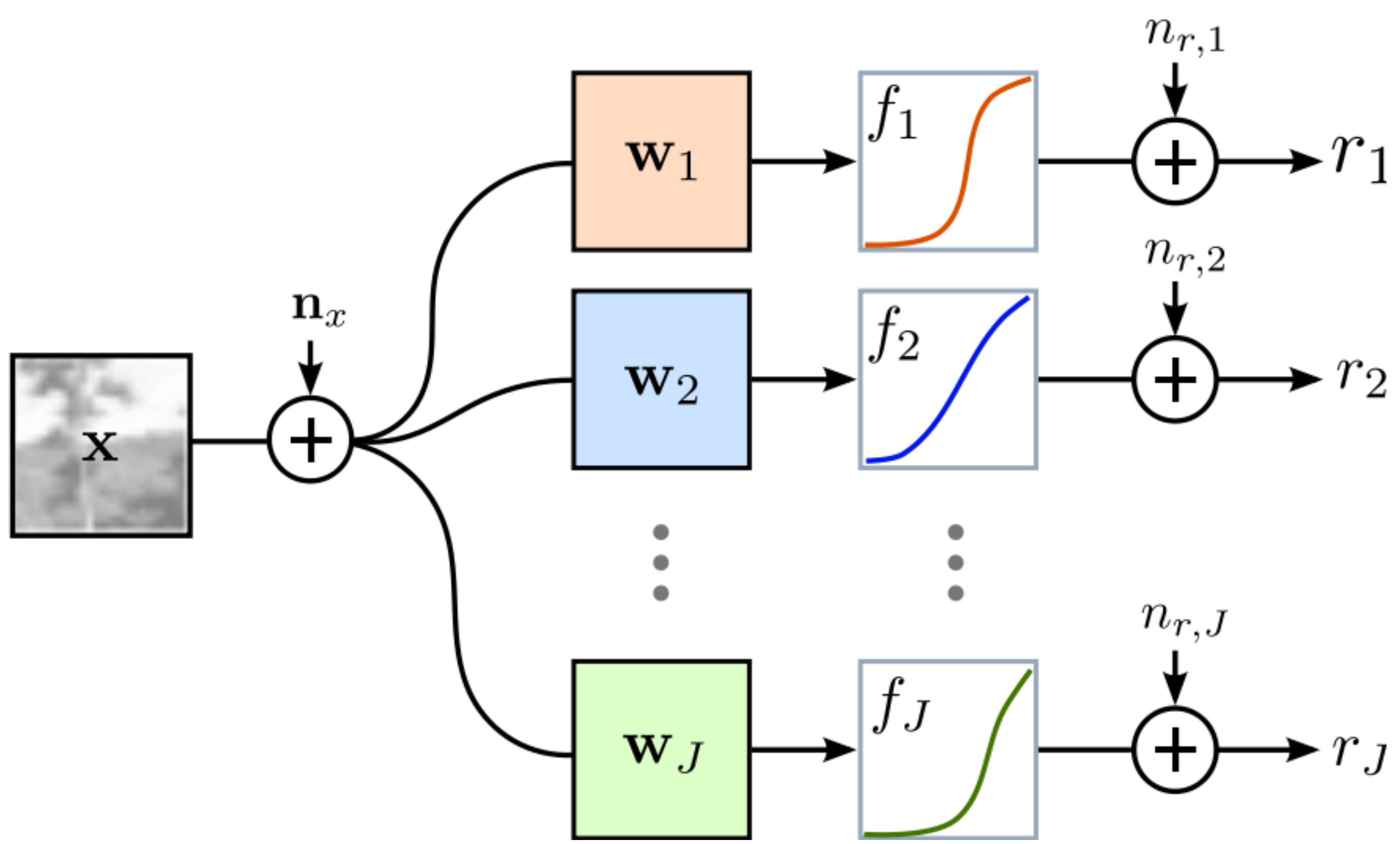




+
−
−
+
H
B
B
on
off

Efficient coding model of retina

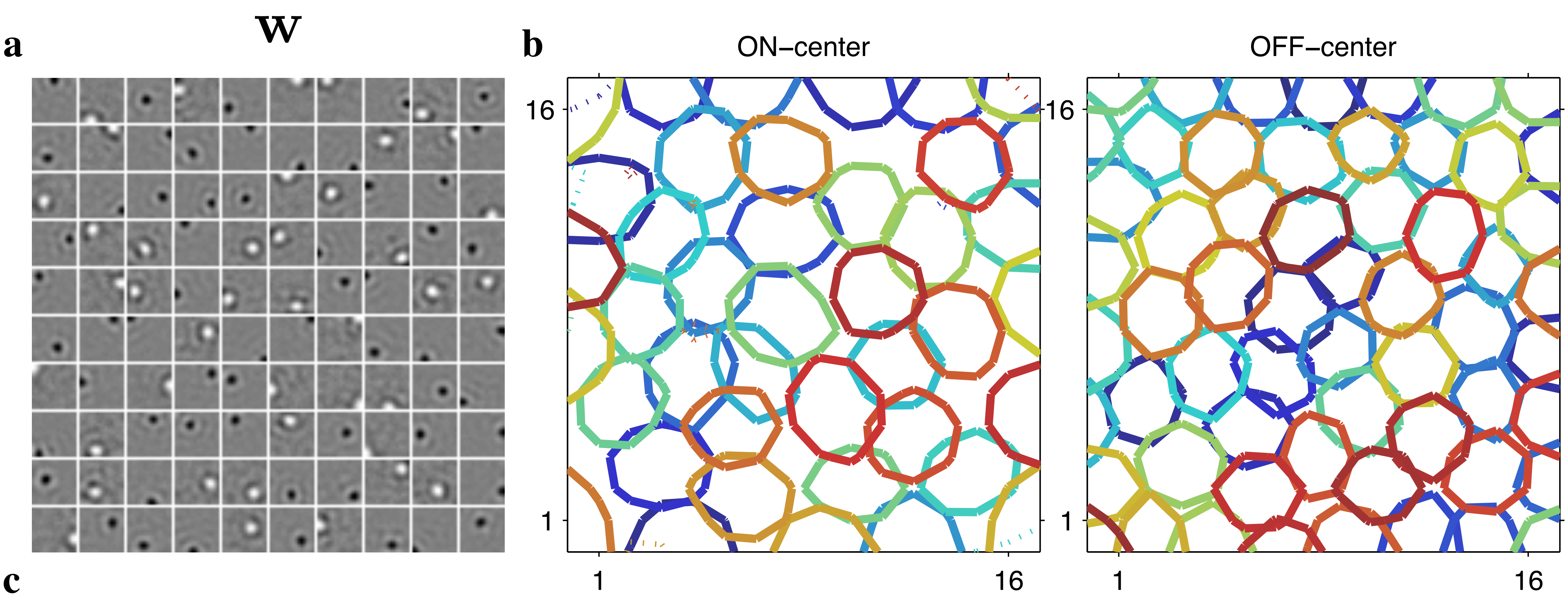
(Karklin & Simoncelli 2012)



Objective function: $I(X;R) - \sum_j \lambda_j \langle r_j \rangle$

Efficient coding model of retina

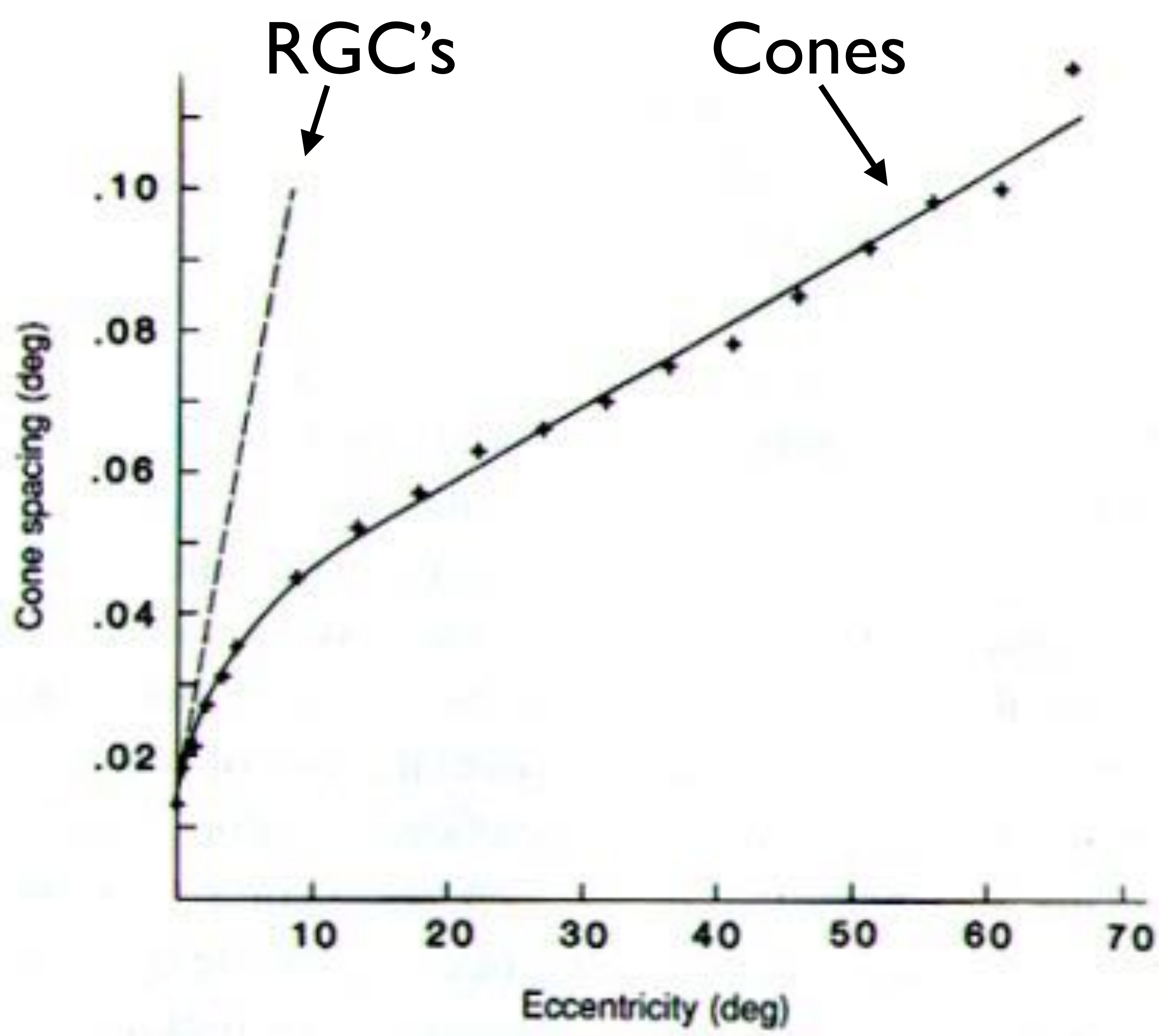
(Karklin & Simoncelli 2012)



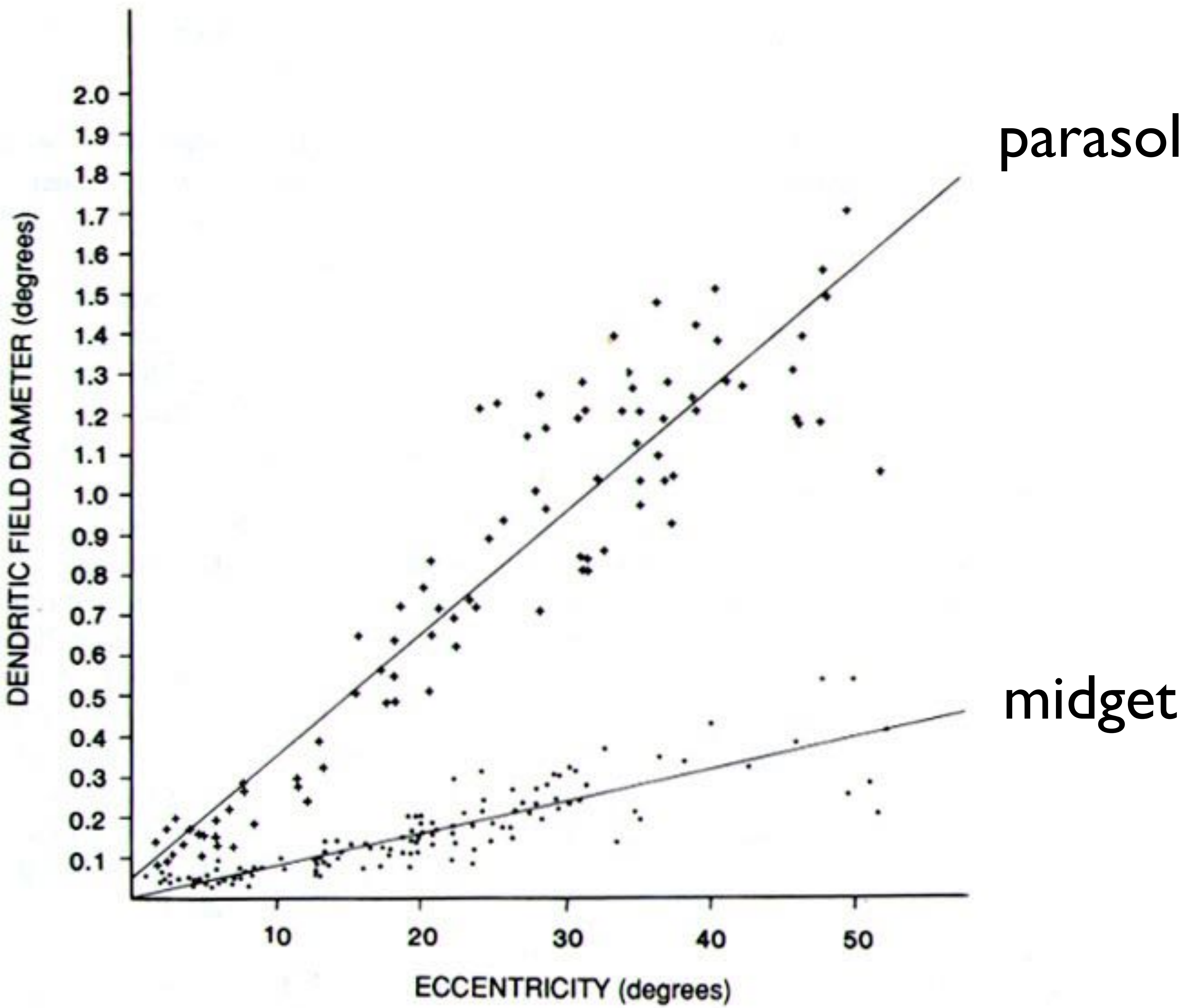
Midget ganglion cells receive input from midget bipolar cells.

Ratio is 1:1 in fovea.

Cone vs. retinal ganglion cell spacing as a function of eccentricity

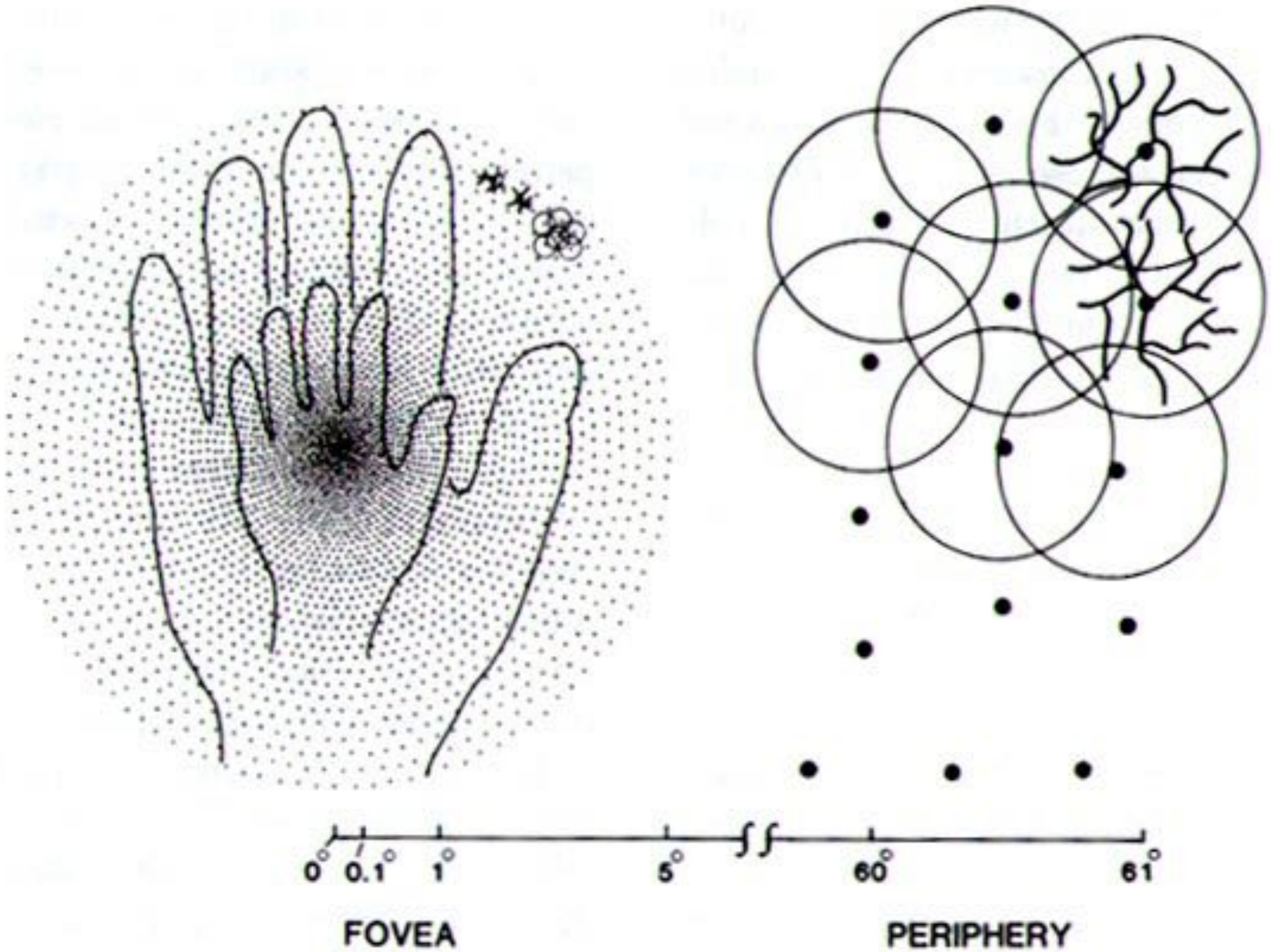


Midget- and Parasol-cell dendritic field diameter as a function of eccentricity



Retinal ganglion cell sampling array

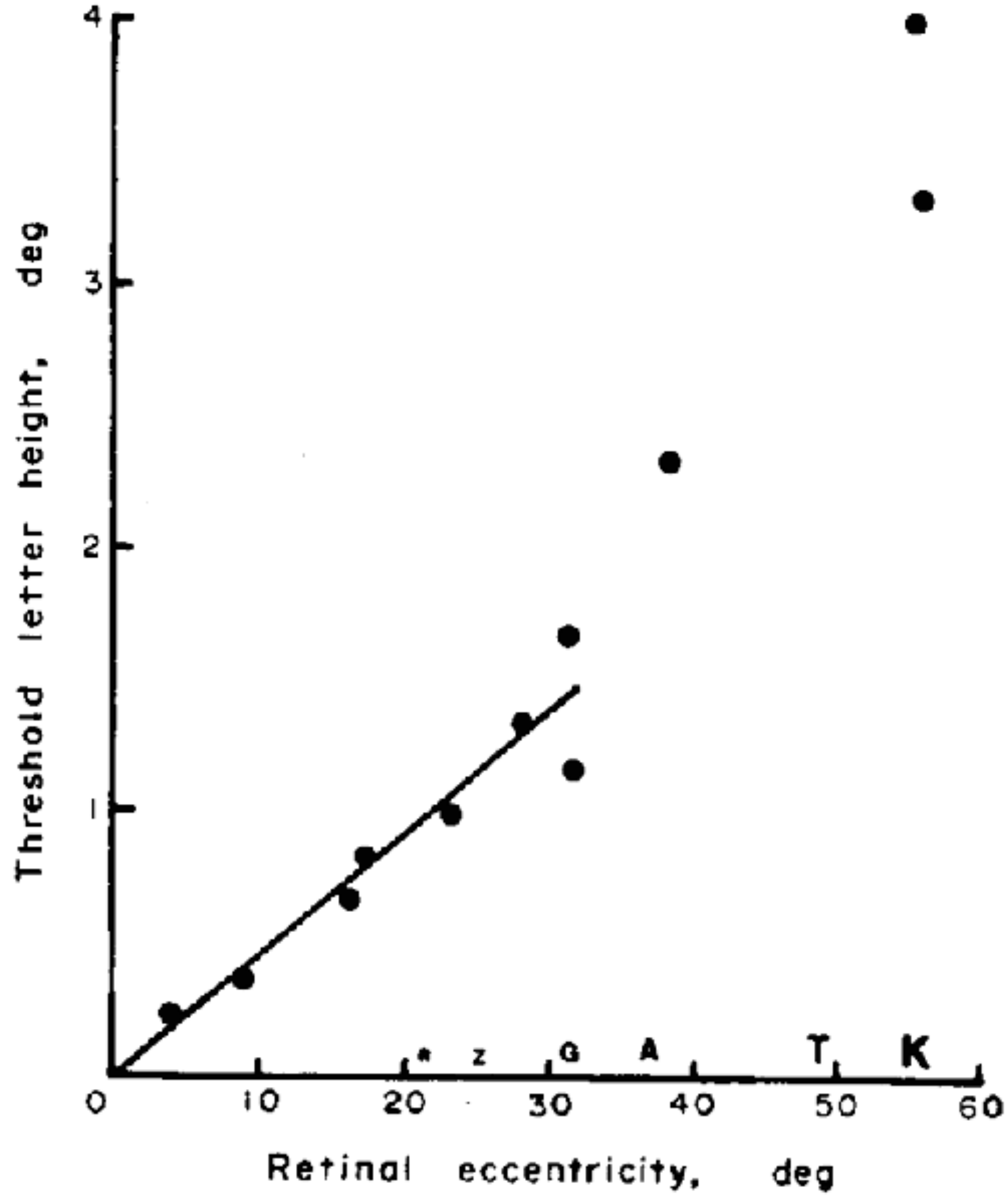
(shown at one dot for every 20 ganglion cells)



$$\Delta \approx .01(|E| + 1)$$

(from Anderson & Van Essen, 1995)

Letter size vs. eccentricity
(Anstis, 1974)



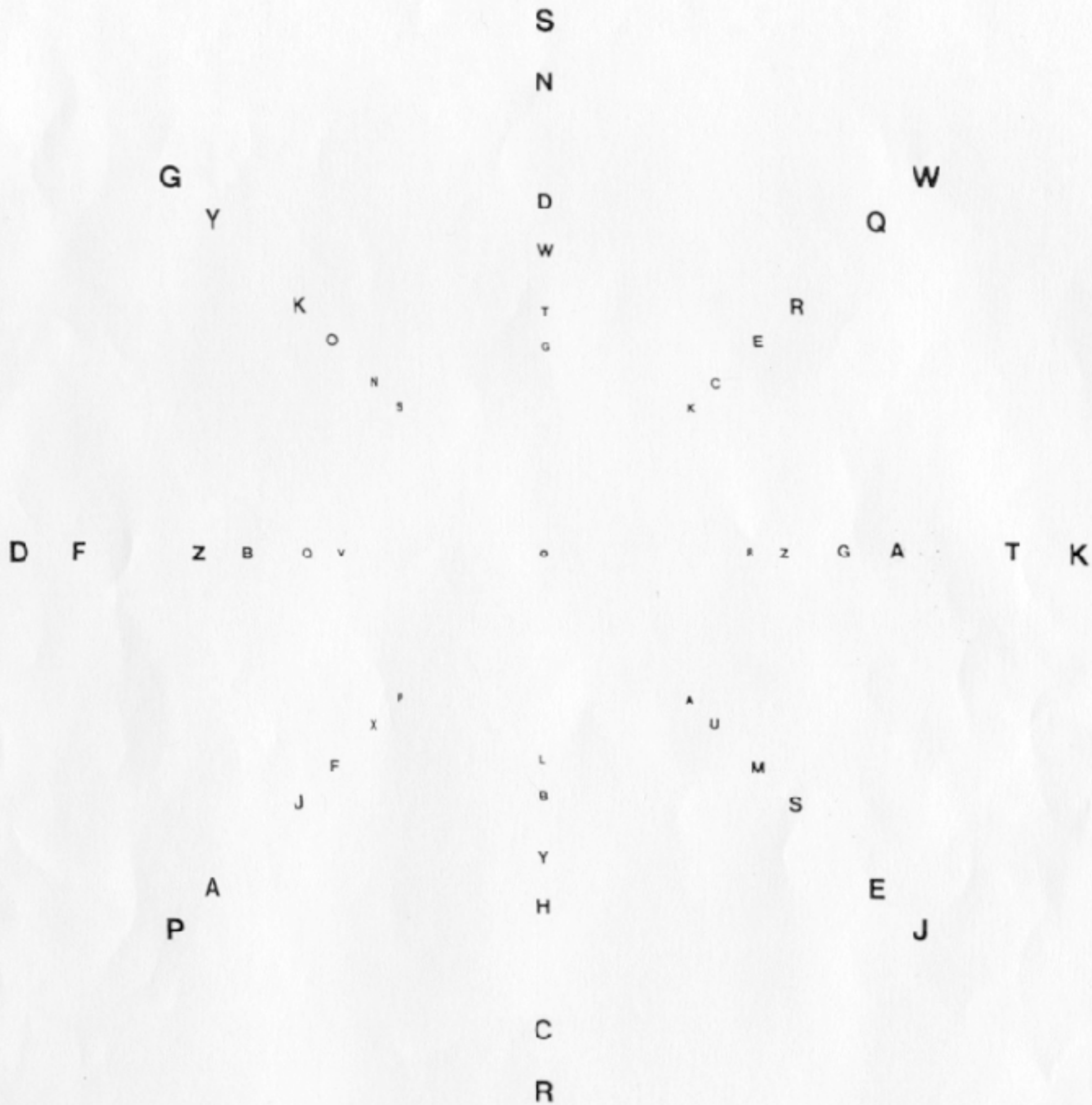


Fig. 2. All letters should lie at threshold when centre of this chart is fixated. Threshold letter size increases linearly with increasing distance from fixation point.

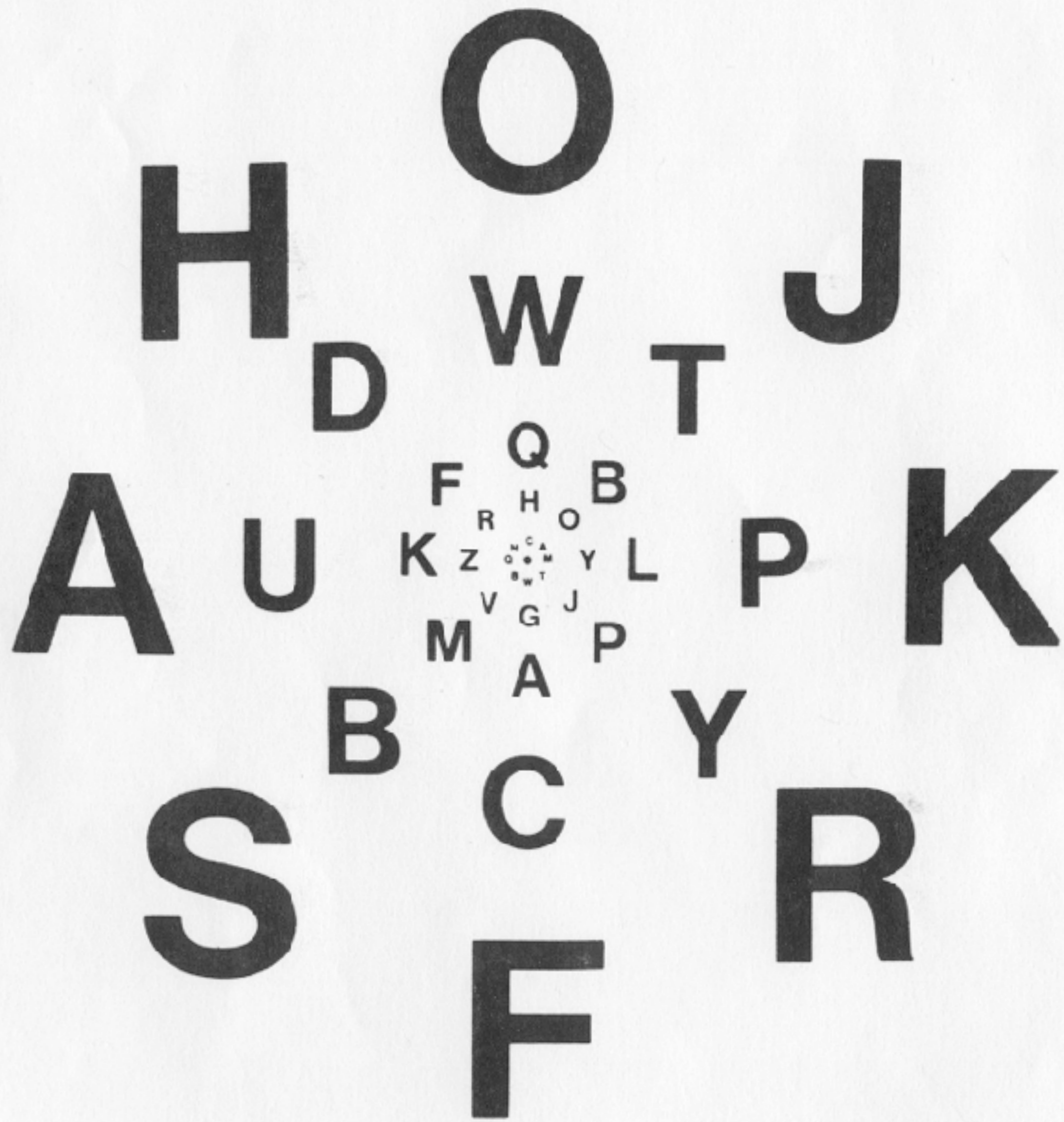
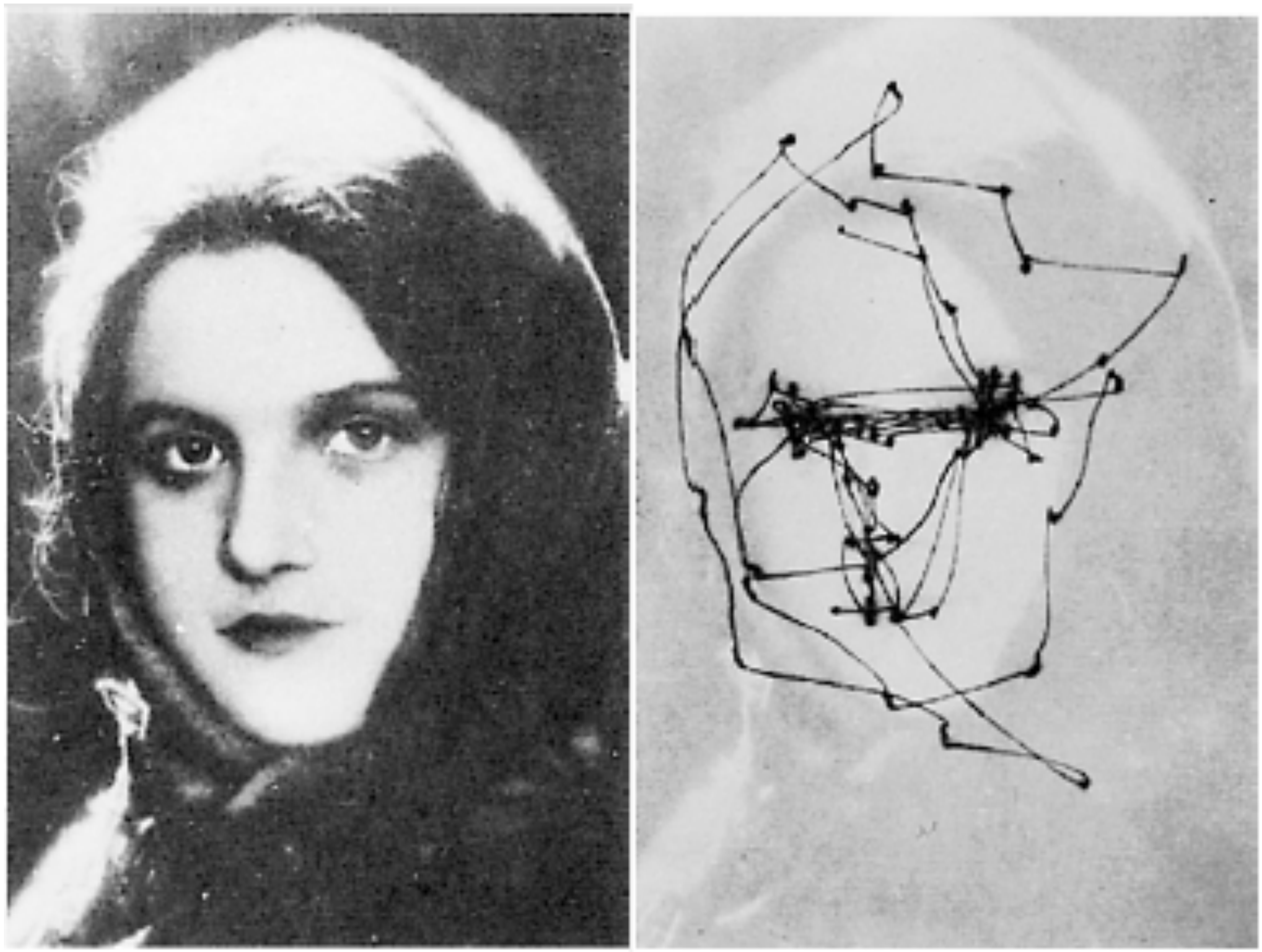


Fig. 3. All letters should be equally readable when centre of this chart is fixated, since each letter is ten times its threshold height.

Eye movements

Human eye movements during viewing of an image



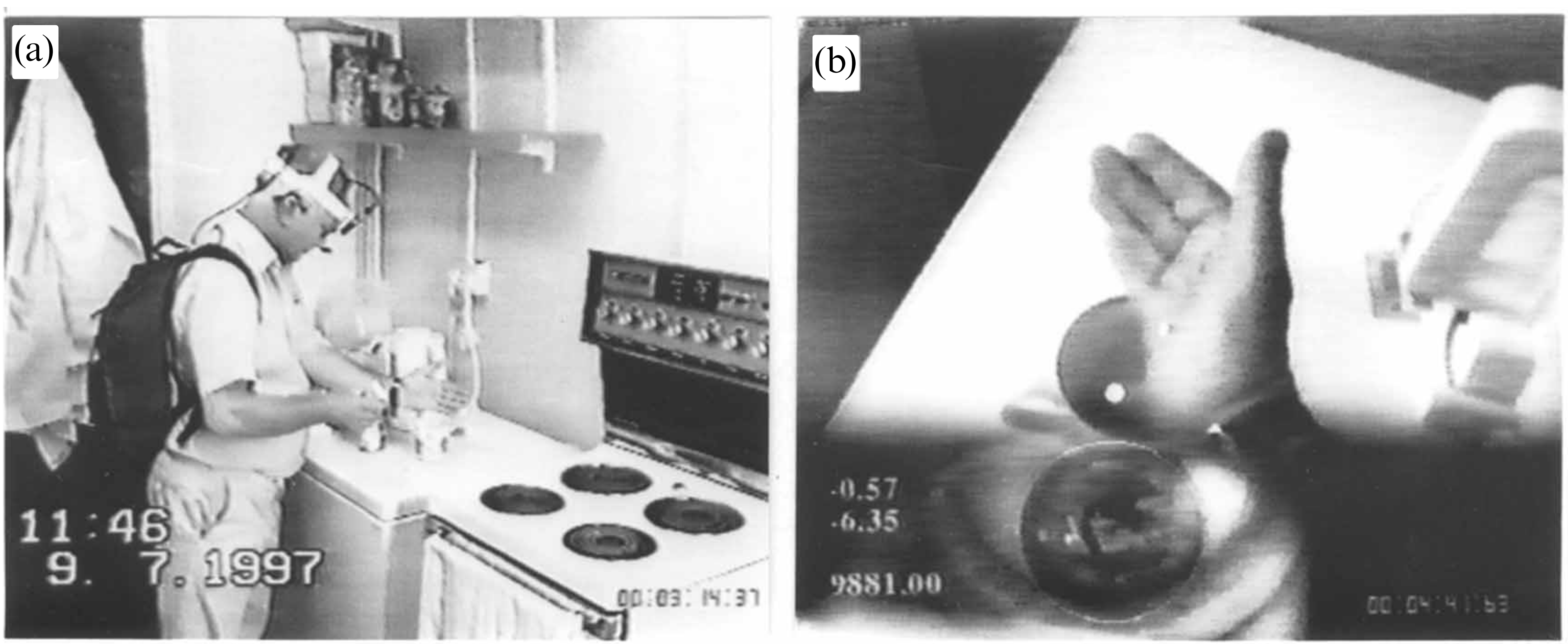
Yarbus (1967)

Perception, 1999, volume 28, pages 1311 – 1328

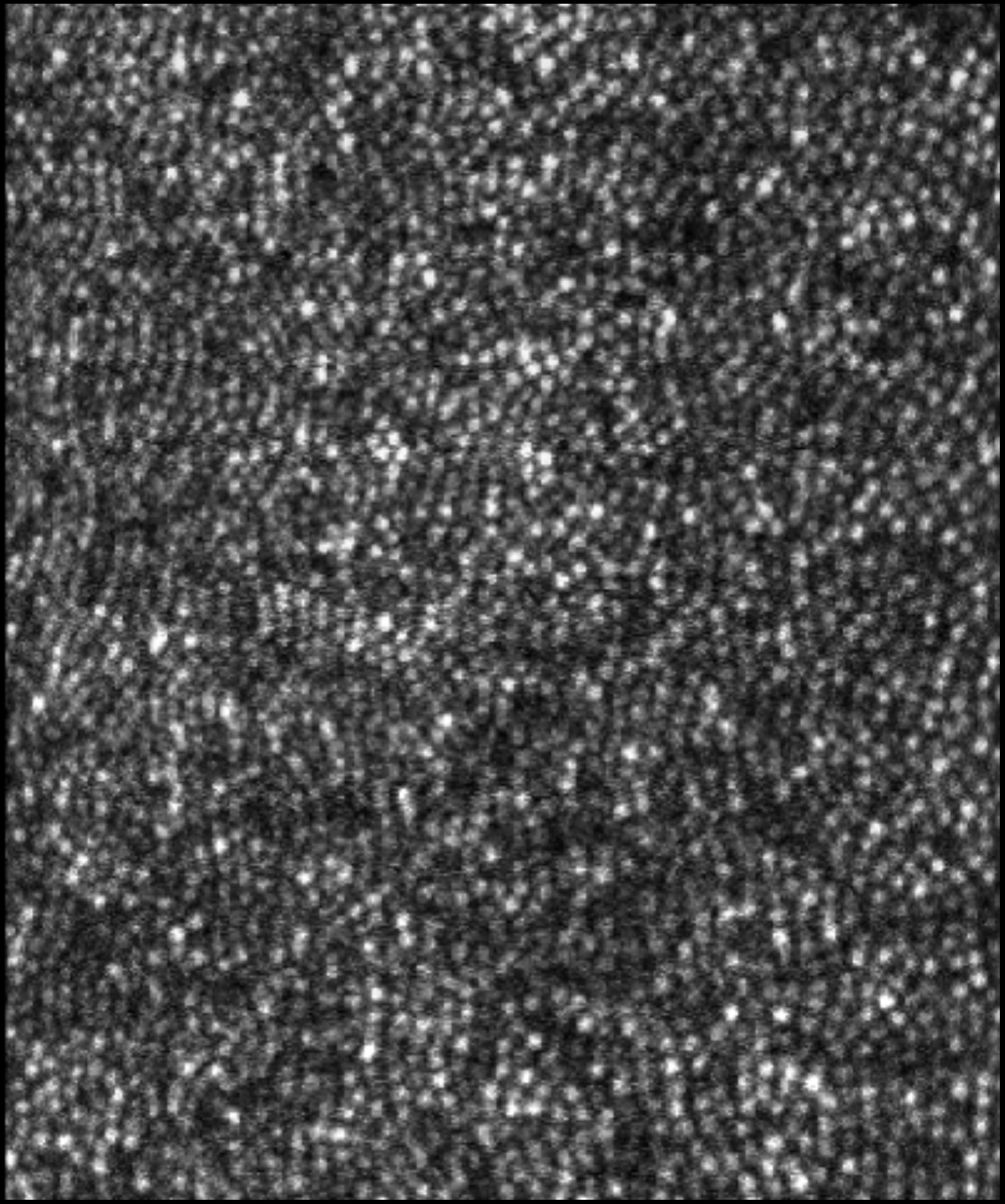
DOI:10.1068/p2935

The roles of vision and eye movements in the control of activities of daily living

Michael Land, Neil Mennie, Jennifer Rusted
Sussex Centre for Neuroscience and Laboratory of Experimental Psychology, School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK; e-mail: M.F.Land@sussex.ac.uk
Received 4 May 1999, in revised form 9 August 1999

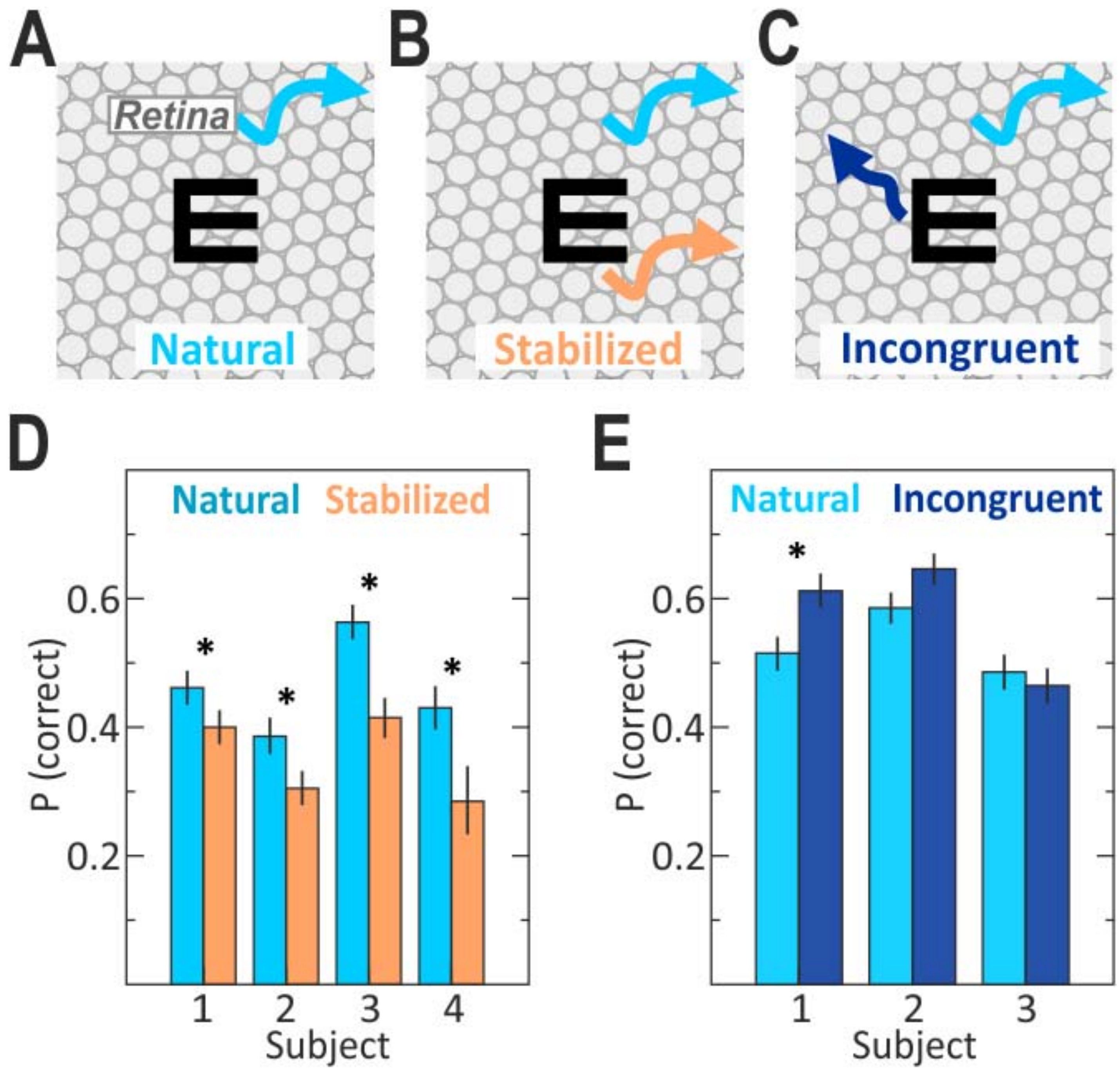


Fixational eye movements (drift)



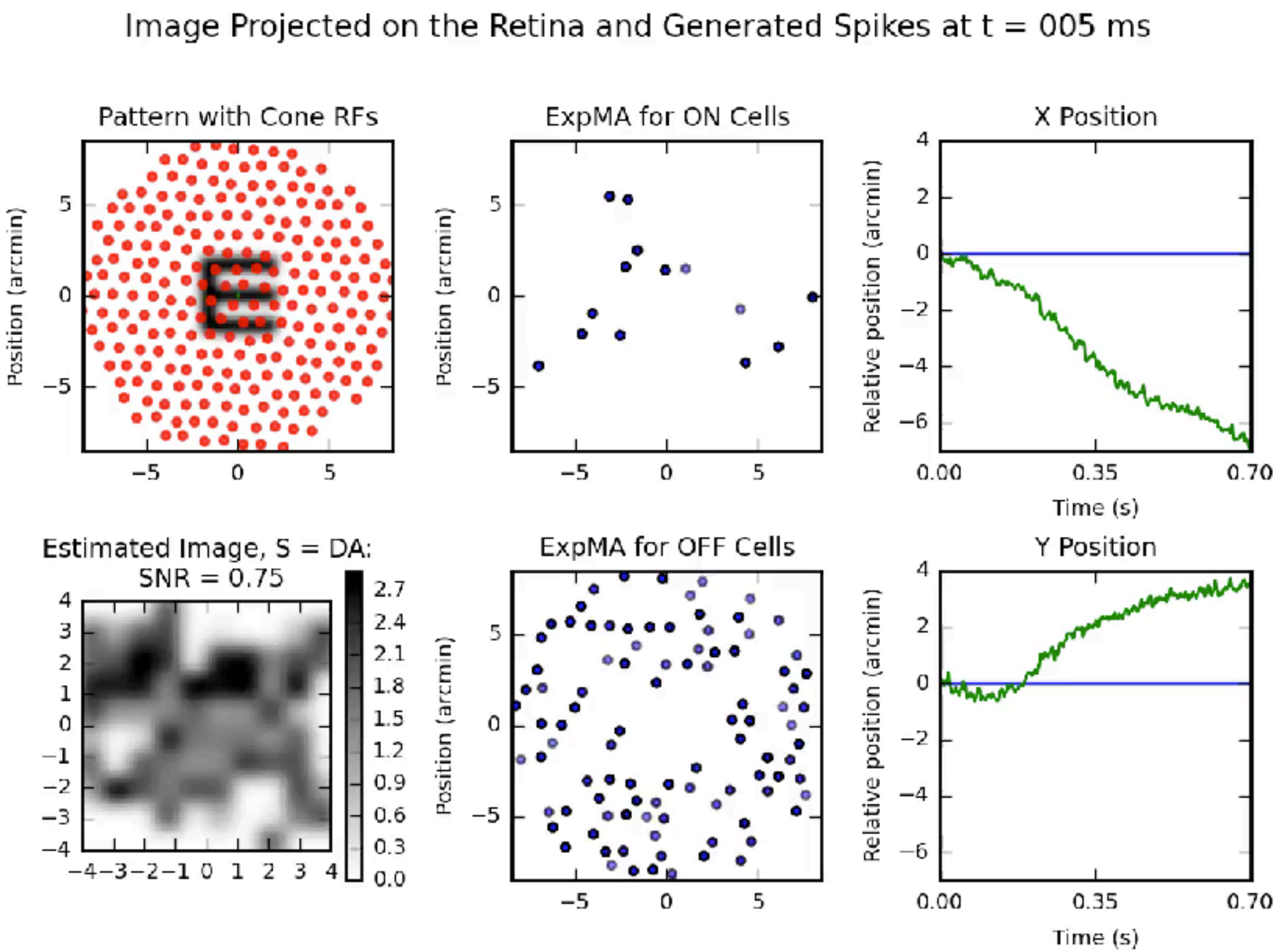
(from Austin Roorda, UC Berkeley)

Retinal image motion helps pattern discrimination

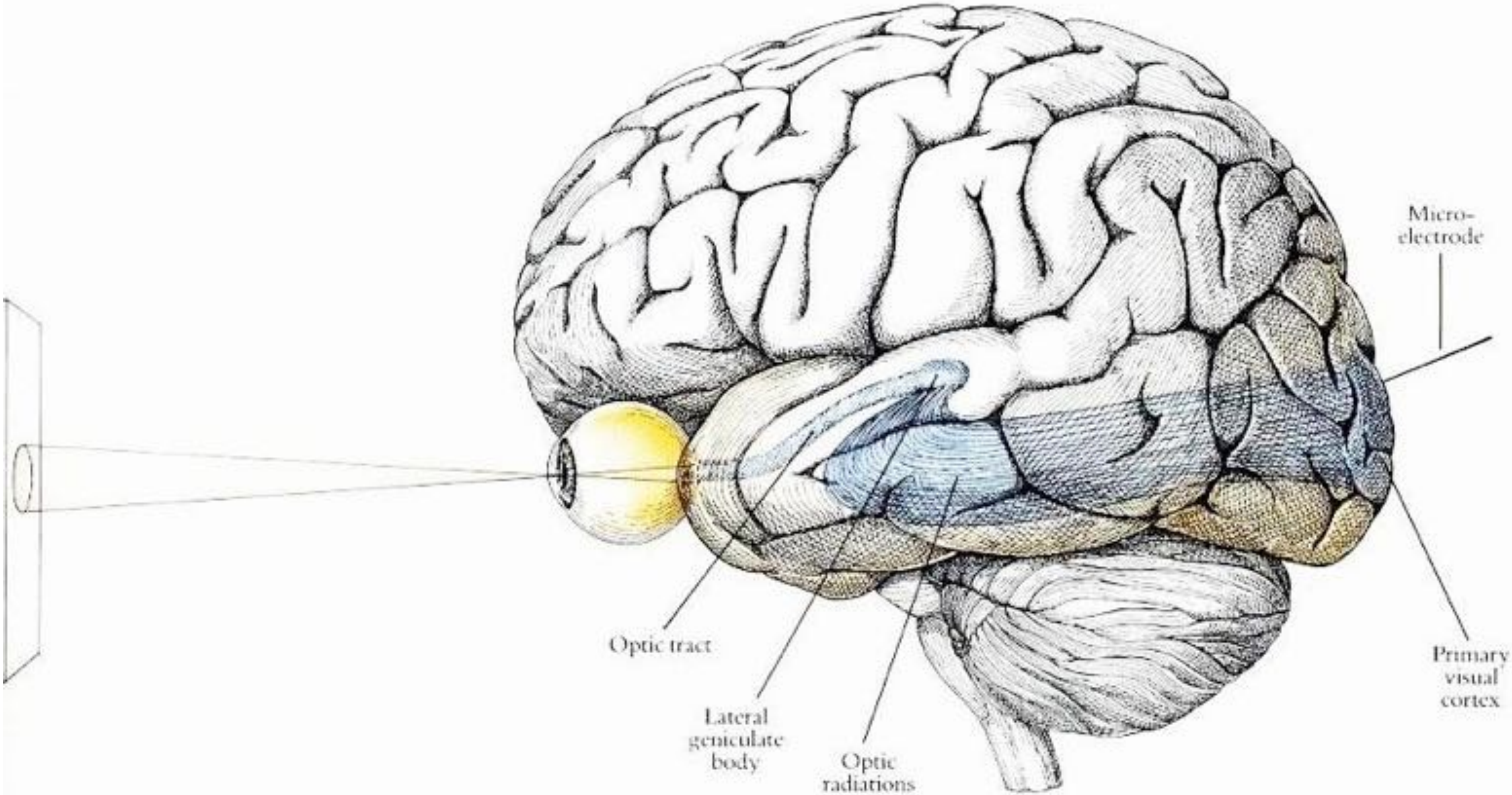


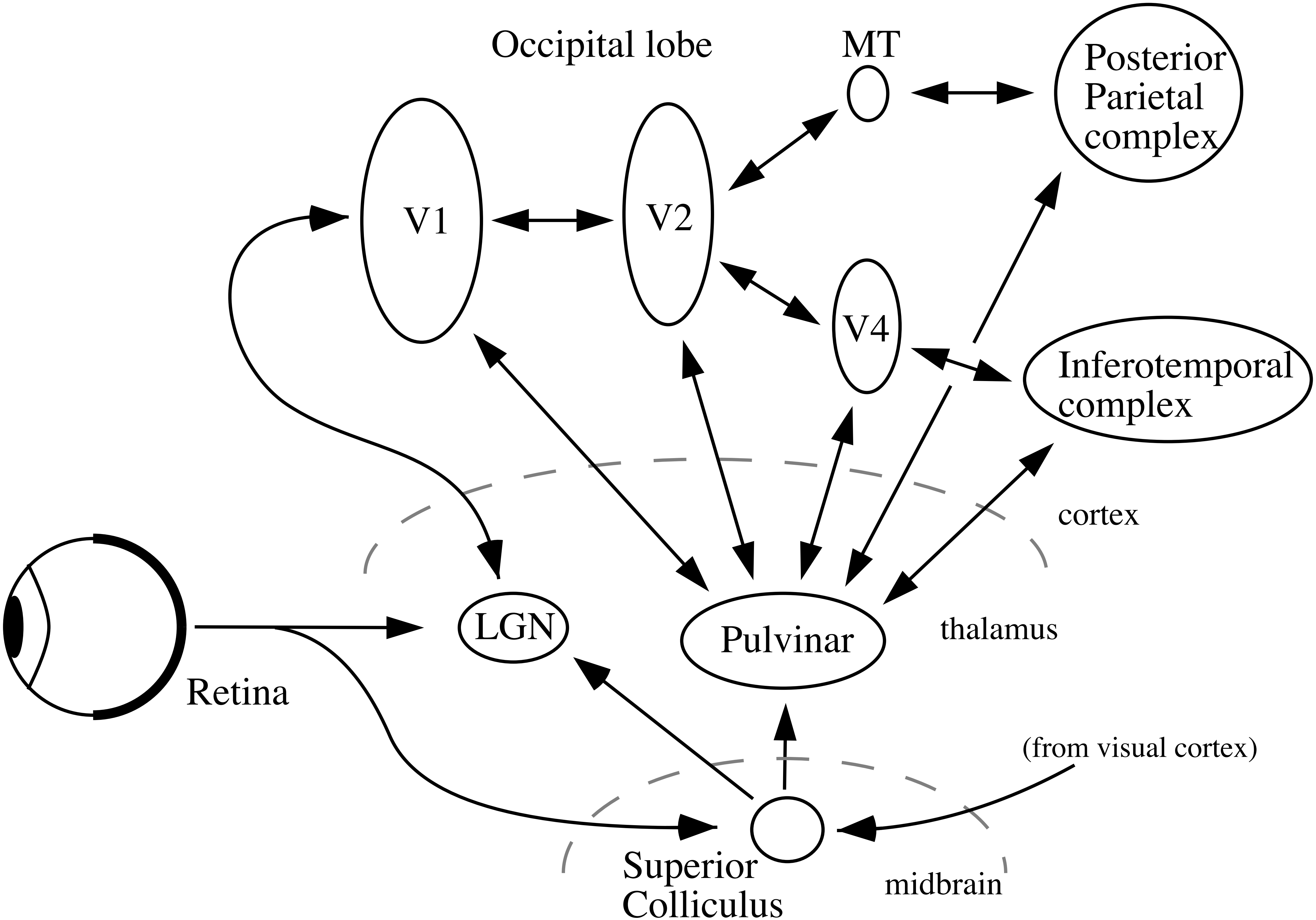
Ratnam, K., Domdei, N., Harmening, W. M., & Roorda, A. (2017). Benefits of retinal image motion at the limits of spatial vision. *Journal of Vision, 17*, 1–11.

Joint estimation of form and motion
(Alex Anderson, Ph.D. thesis)

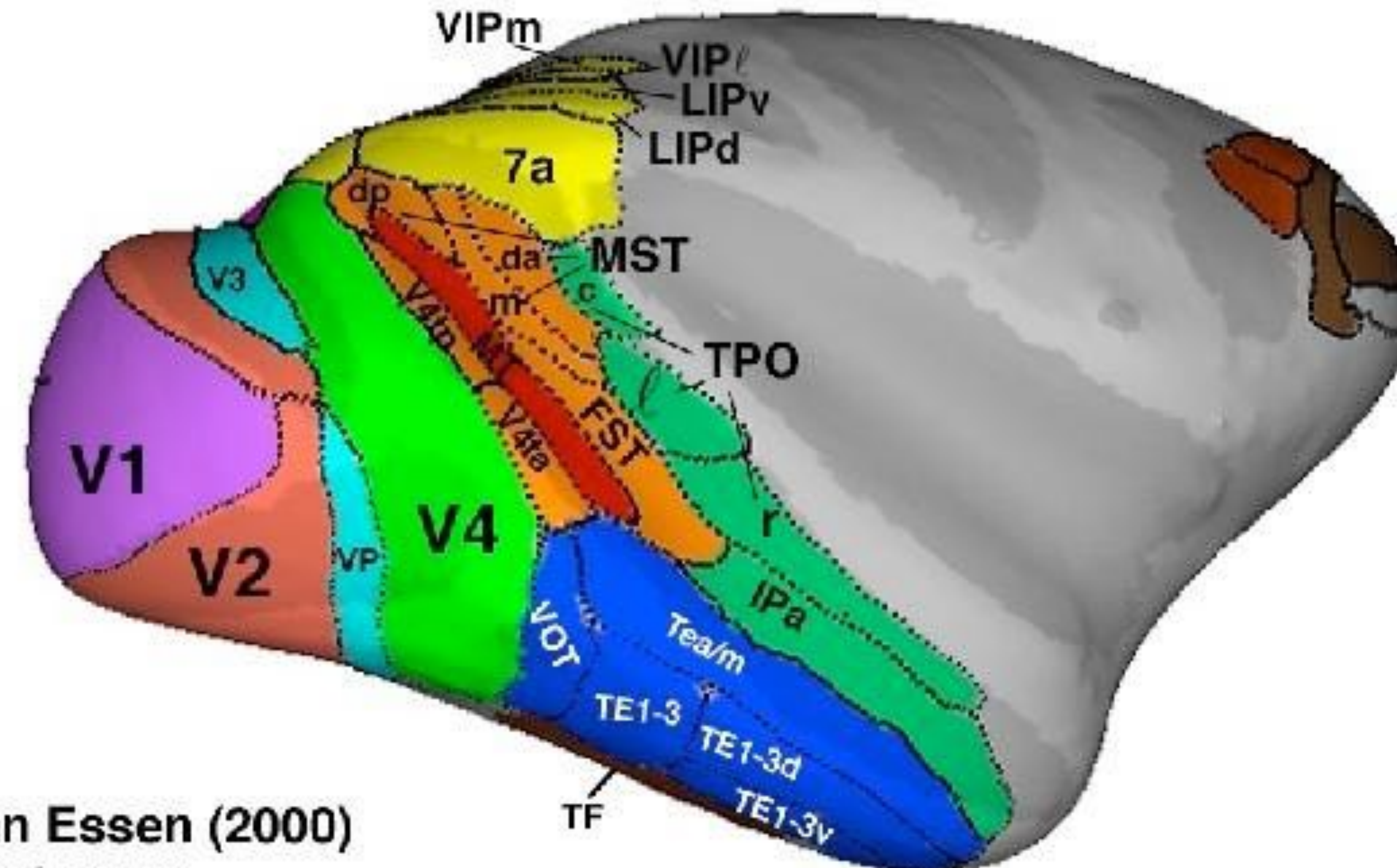


Cortex


Micro-
electrode
Optic tract
Lateral
geniculate
body
Optic
radiations
Primary
visual
cortex

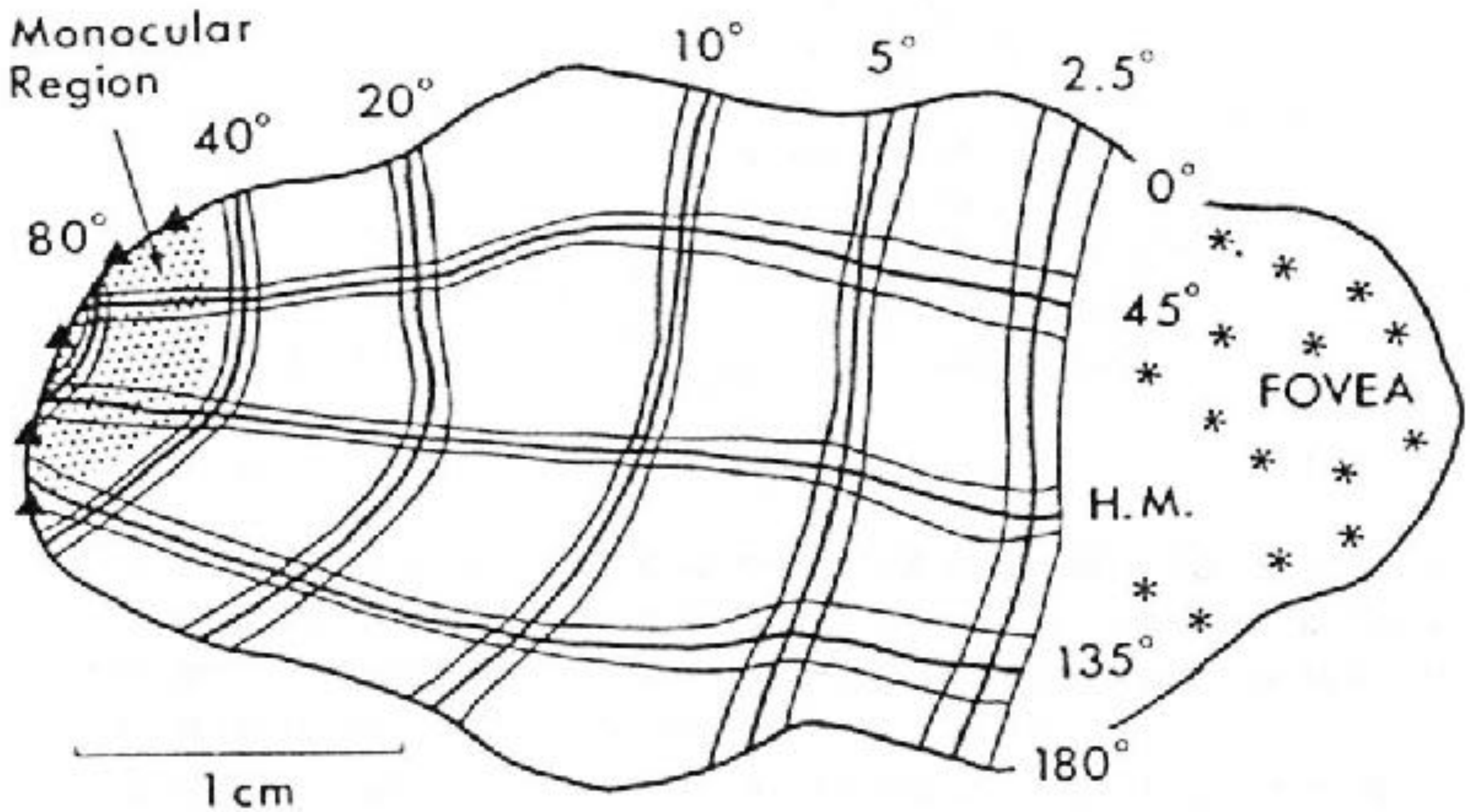

Occipital lobe
MT
Posterior
Parietal
complex
V1
V2
V4
Inferotemporal
complex
cortex
LGN
Pulvinar
thalamus
Retina
(from visual cortex)
Superior
Colliculus
midbrain

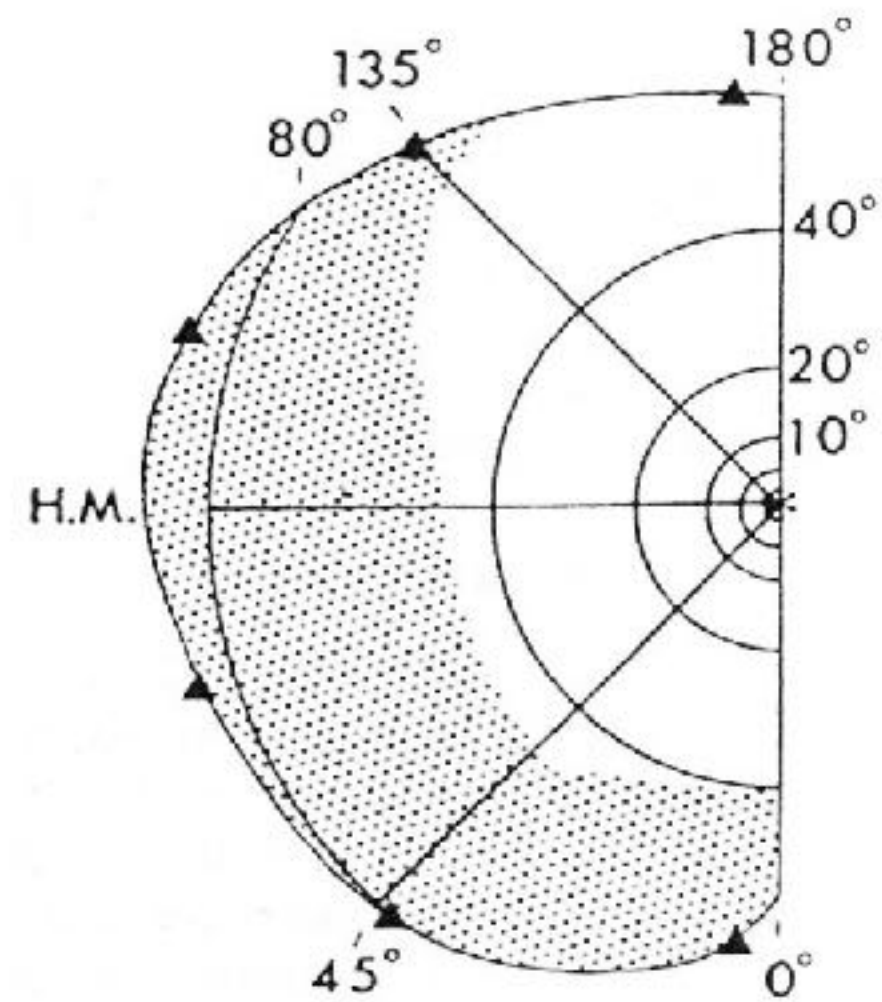
Primate visual cortex



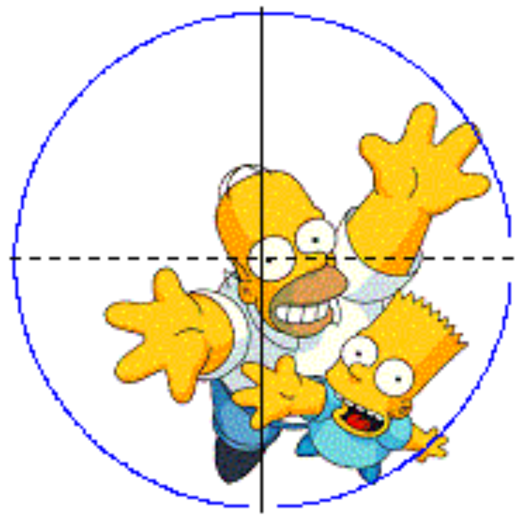
Lewis & Van Essen (2000)
Visual areas

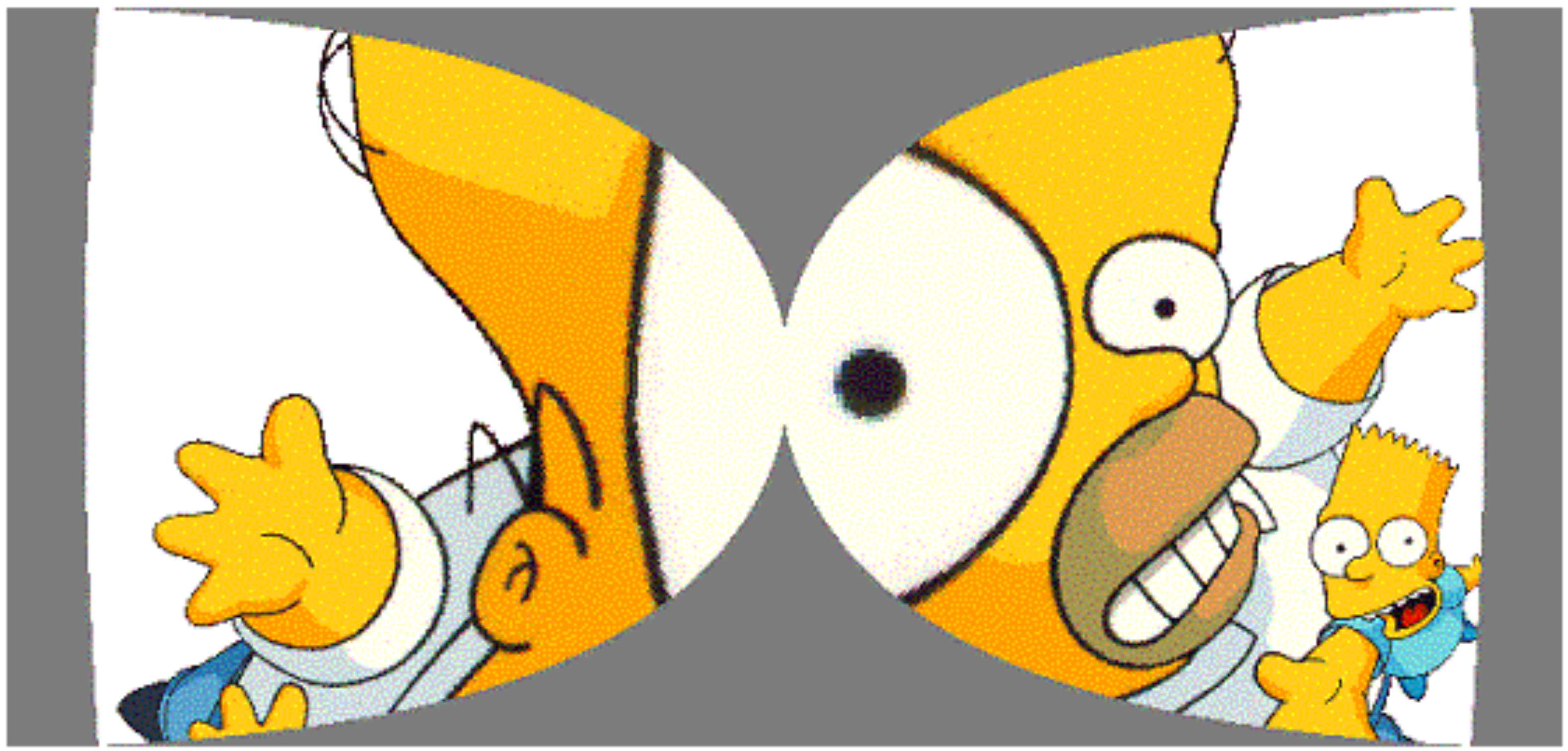
V1 - topographic representation





Cortical magnification

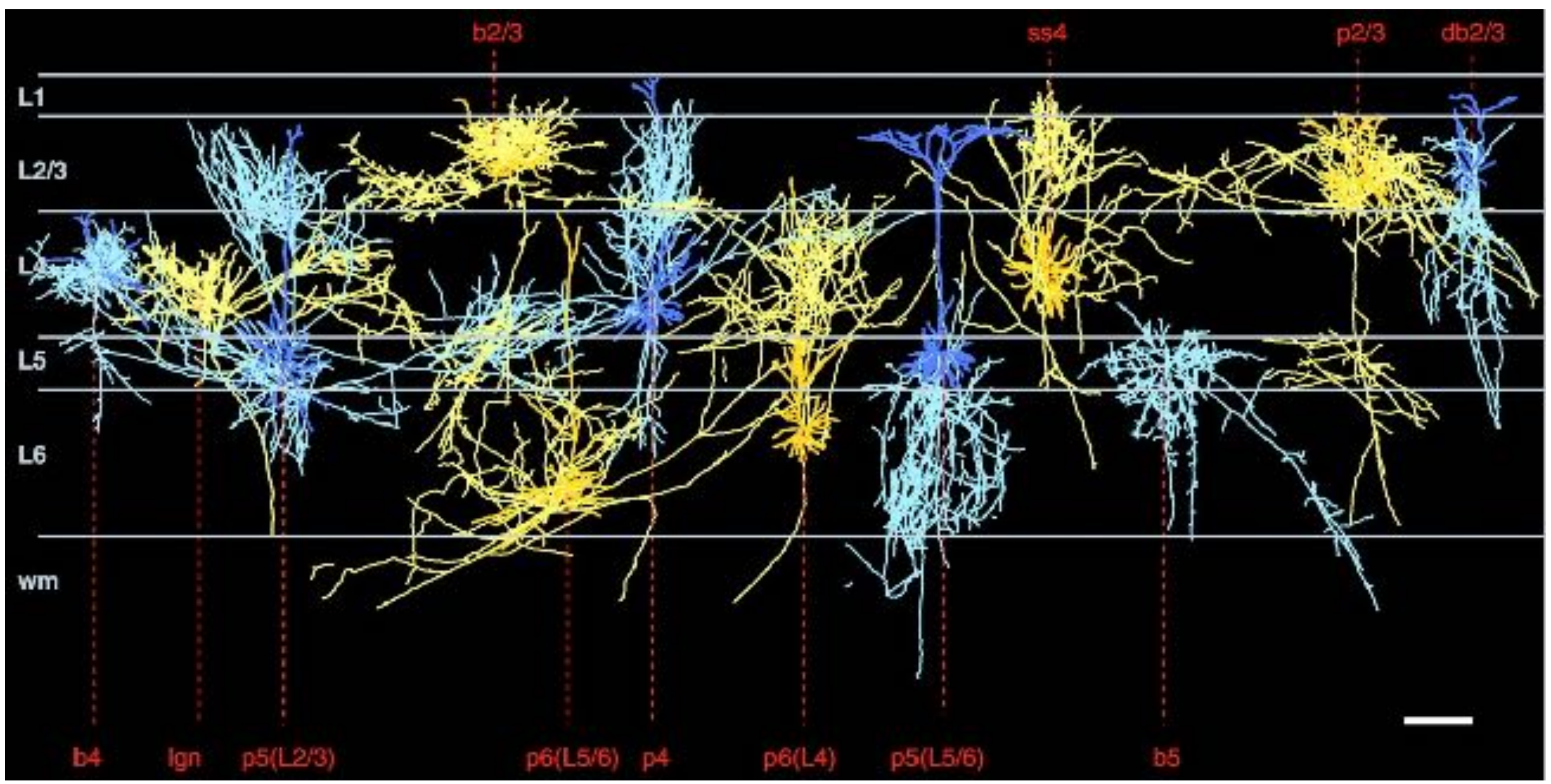


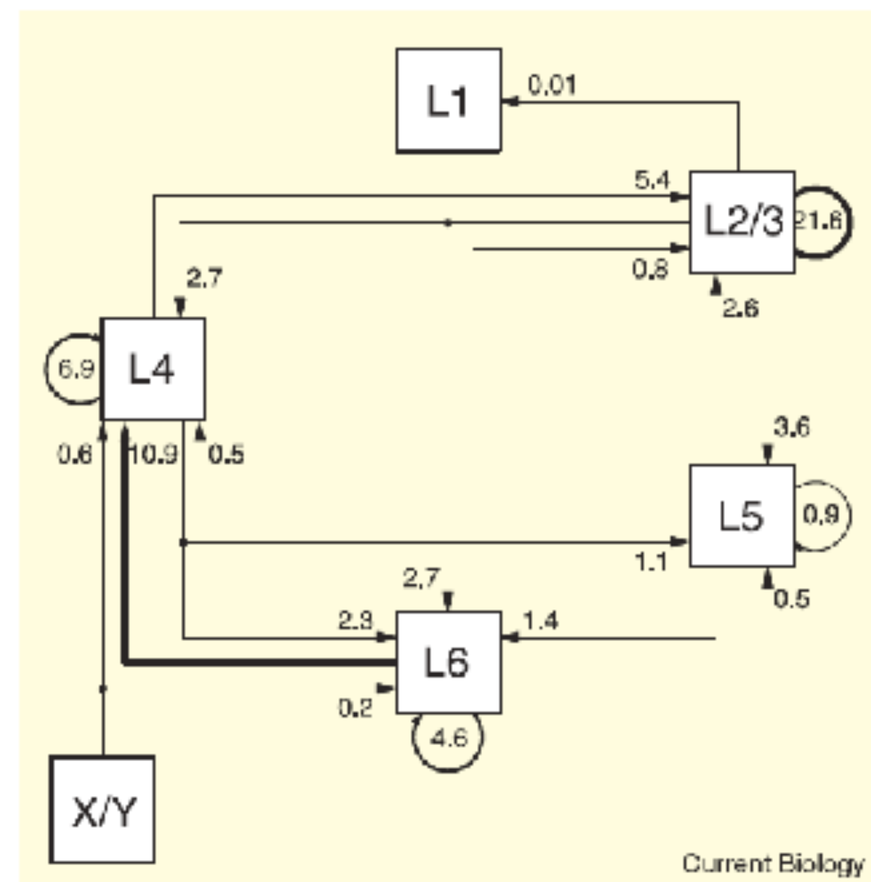


courtesy of Arash Fazl

Cortical neurons

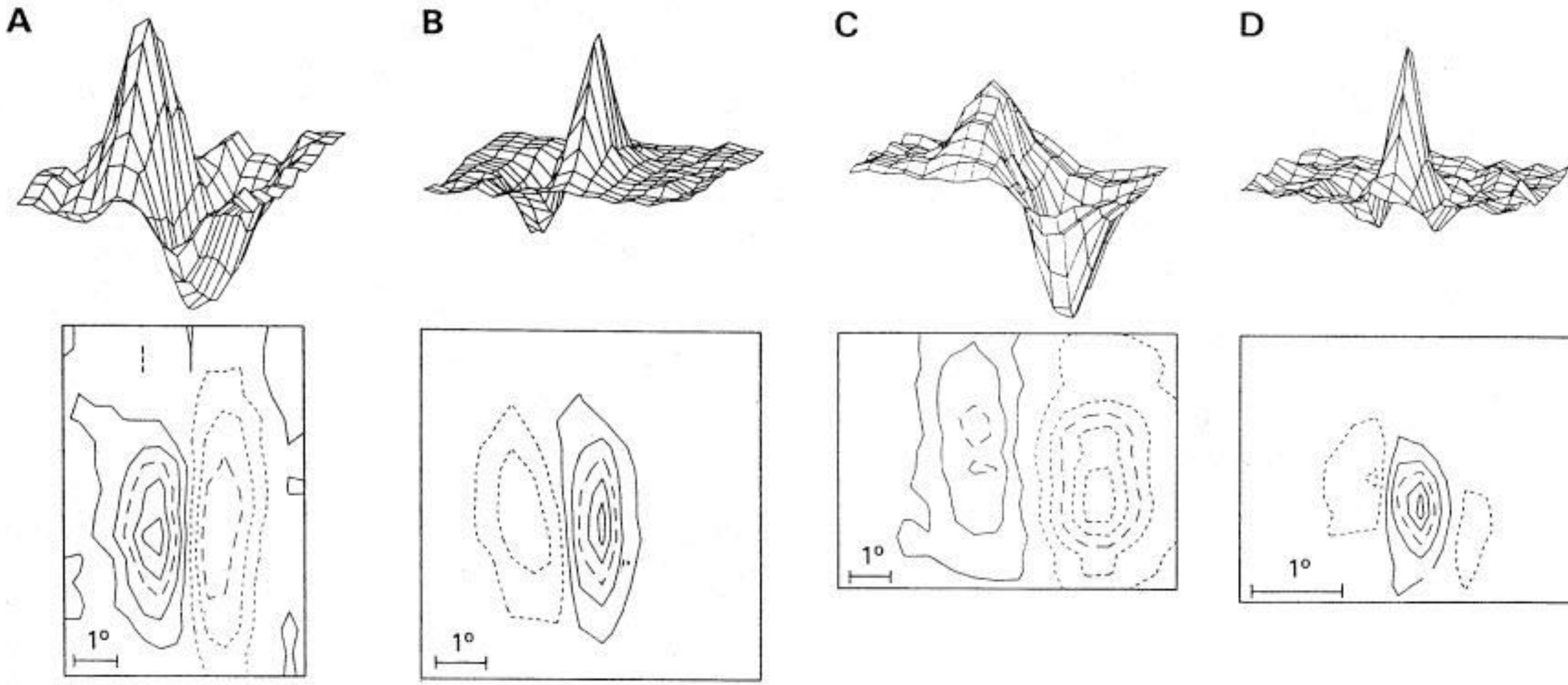
- have elaborate *dendritic* and *axonal* arbors
- are highly organized by layer
- are interconnected in a 'canonical microcircuit'





(Douglas and Martin, 2007)

V1 - simple cell receptive fields



Perception, 1972, volume 1, pages 371-394

Single units and sensation: A neuron doctrine for perceptual psychology?

H B Barlow
Department of Physiology-Anatomy, University of California, Berkeley, California 94720
Received 6 December 1972

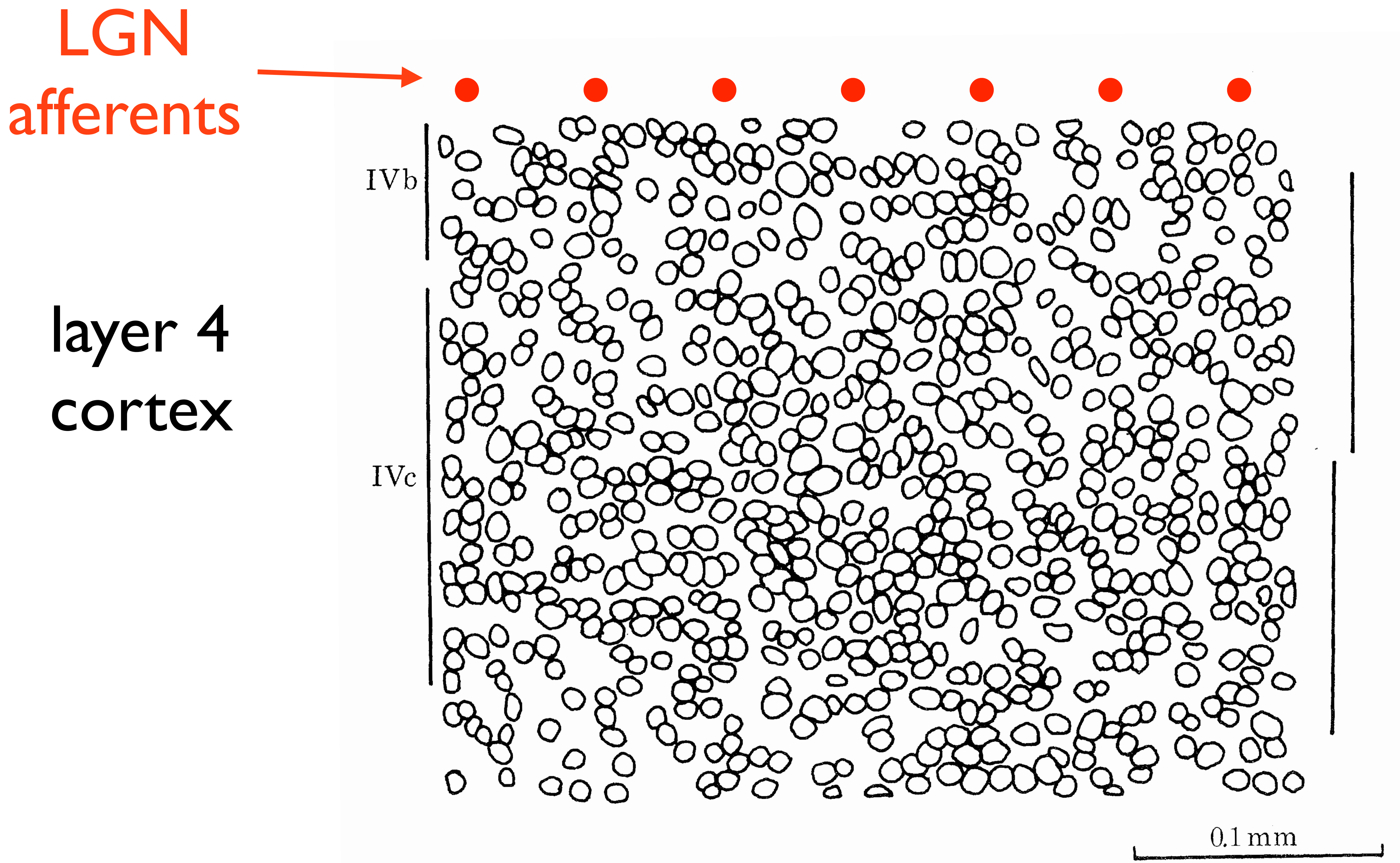
Abstract. The problem discussed is the relationship between the firing of single neurons in sensory pathways and subjectively experienced sensations. The conclusions are formulated as the following five dogmas:
1. To understand nervous function one needs to look at interactions at a cellular level, rather than either a more macroscopic or microscopic level, because behaviour depends upon the organized pattern of these intercellular interactions.

2. The sensory system is organized to achieve as complete a representation of the sensory stimulus as possible with the minimum number of active neurons.

neurons, each of which corresponds to a pattern of external events of the order of complexity of the events symbolized by a word.
5. High impulse frequency in such neurons corresponds to high certainty that the trigger feature is present.

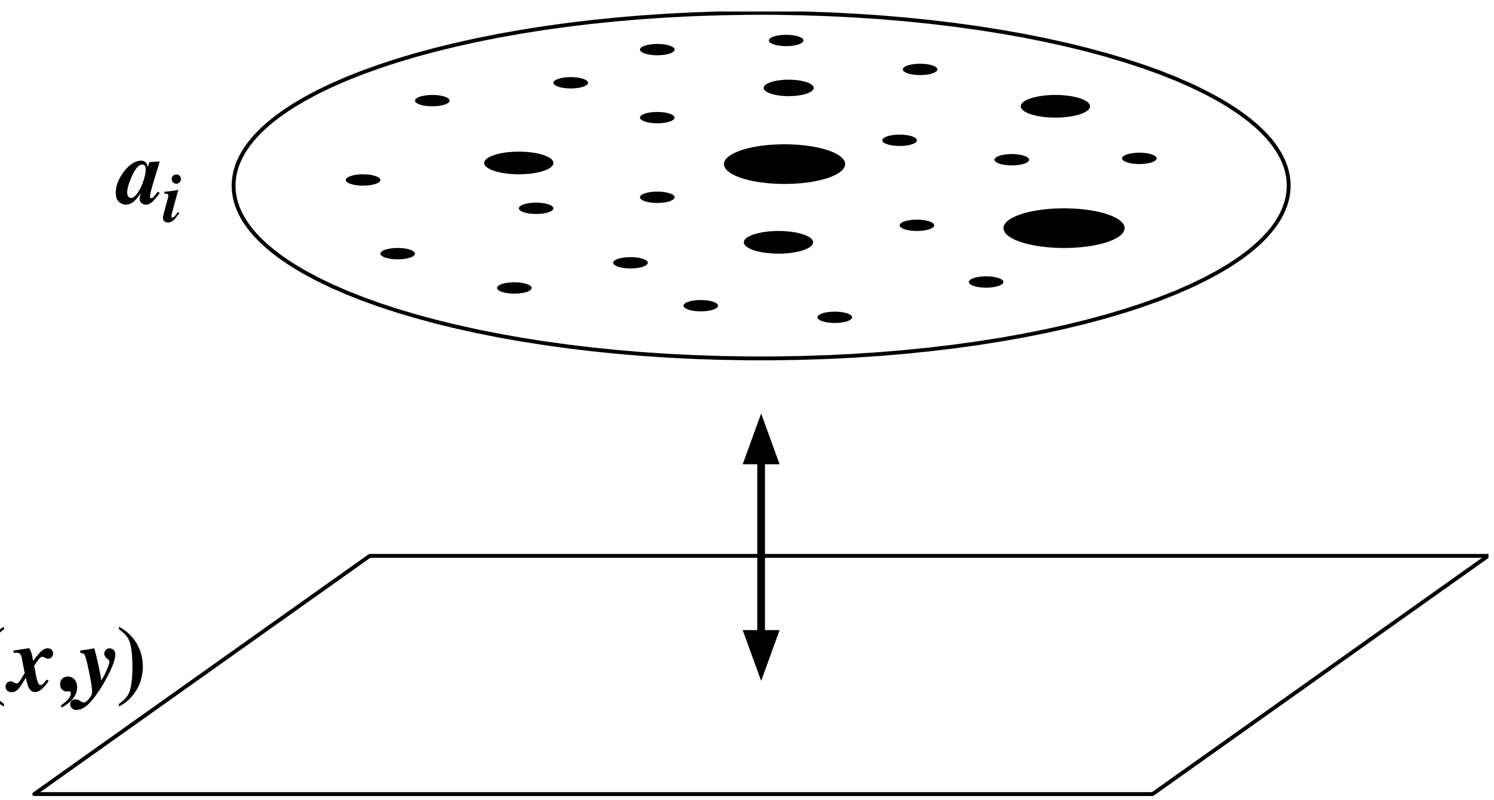
The development of the concepts leading up to these speculative dogmas, their experimental basis, and some of their limitations are discussed.

V1 is highly overcomplete



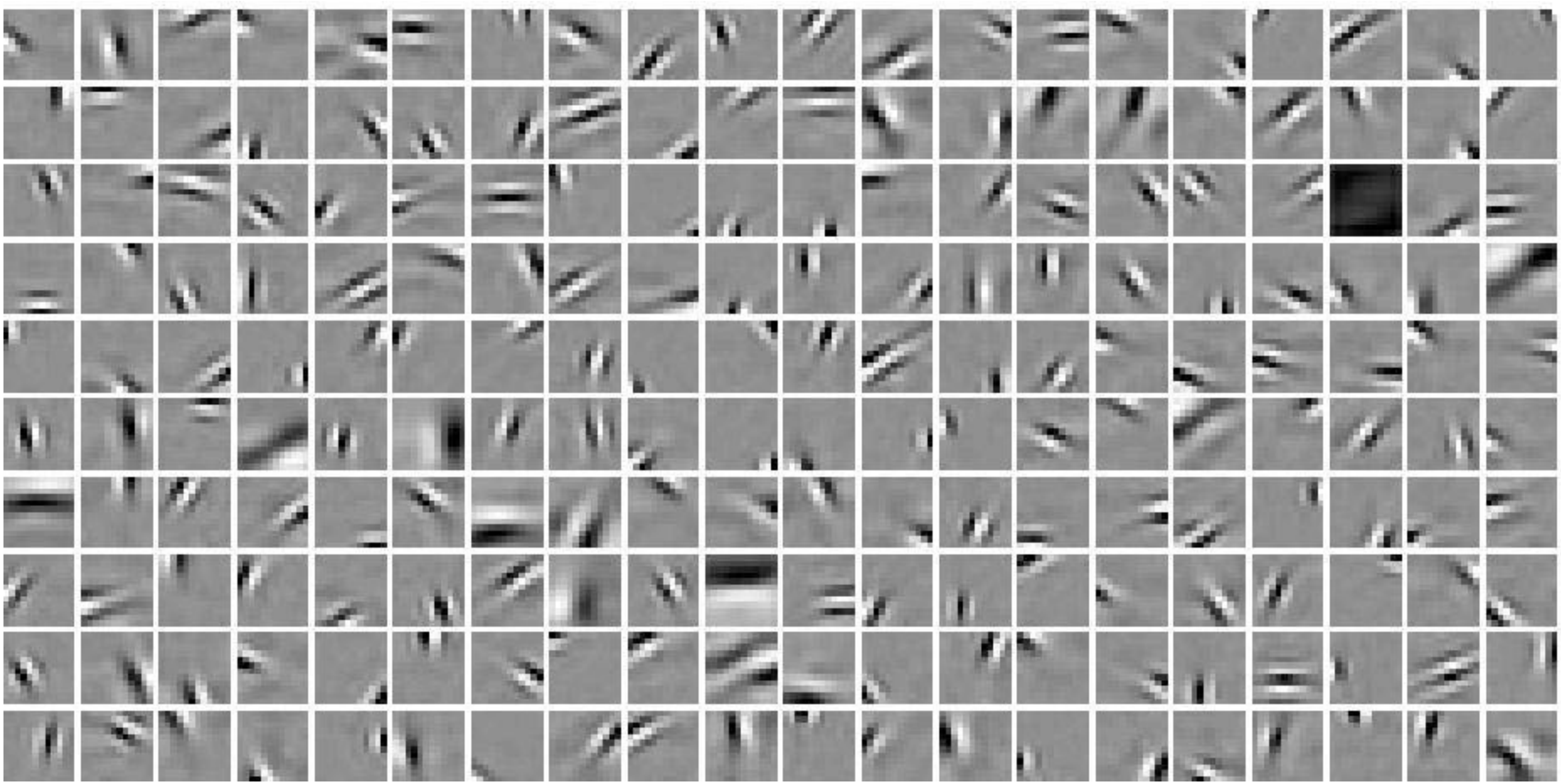
Barlow (1981)

Sparse, distributed representations

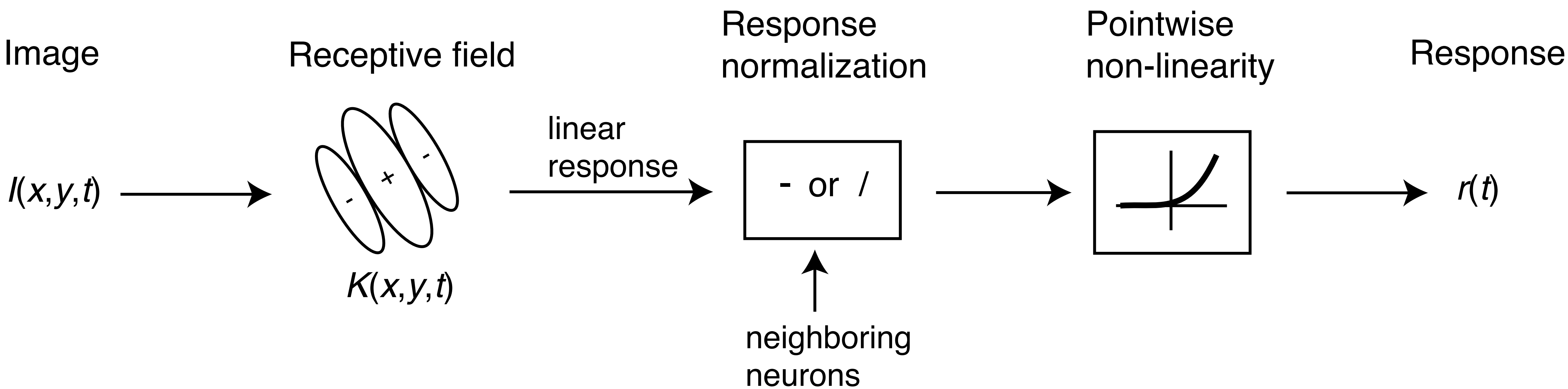


$$I(x,y) = \sum_i a_i\, \phi_i(x,y) + \epsilon(x,y)$$

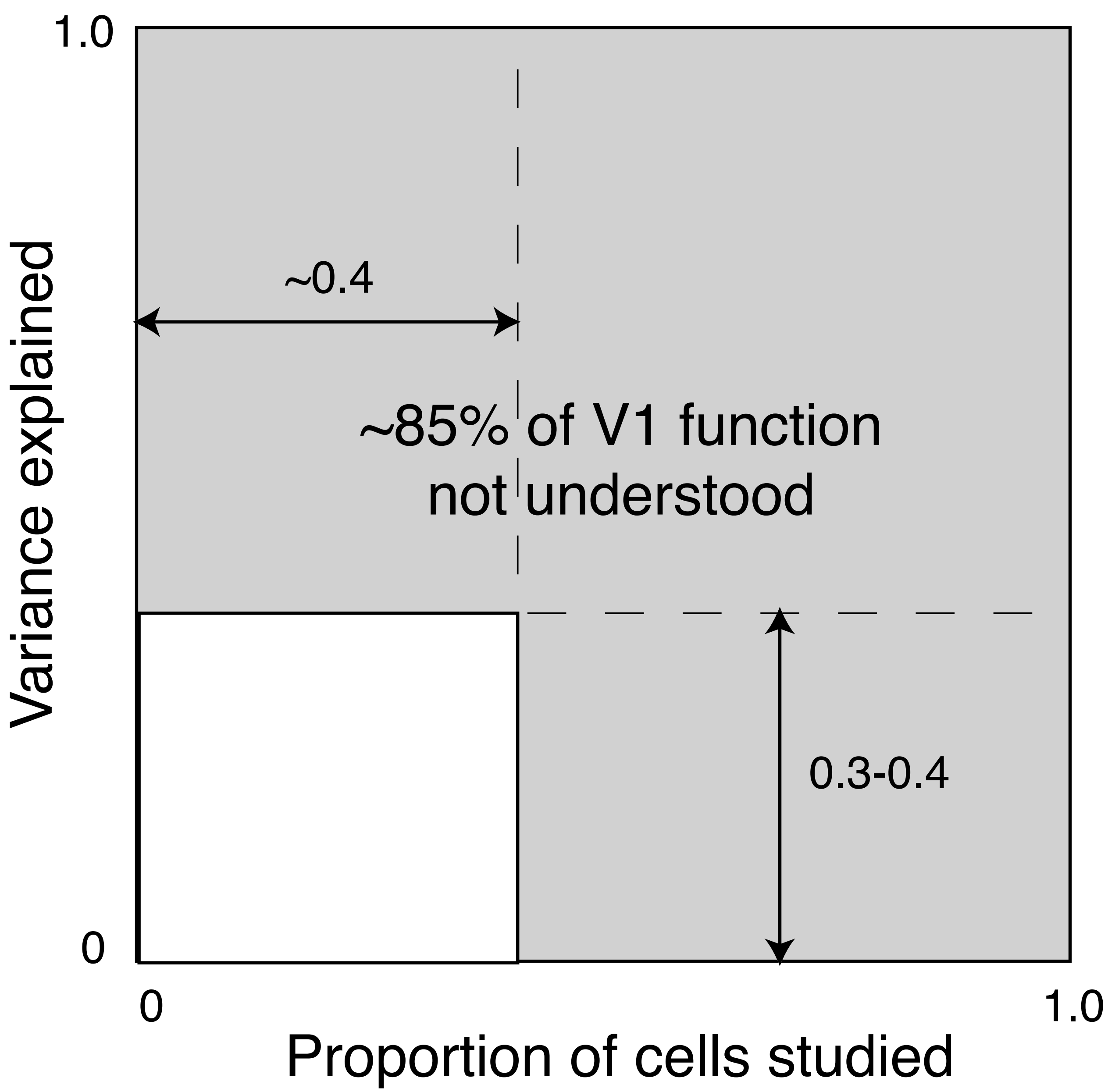
Learned basis functions
(200, 12x12 pixels)



The "standard model" of V1



What is the other 85% of V1 doing?

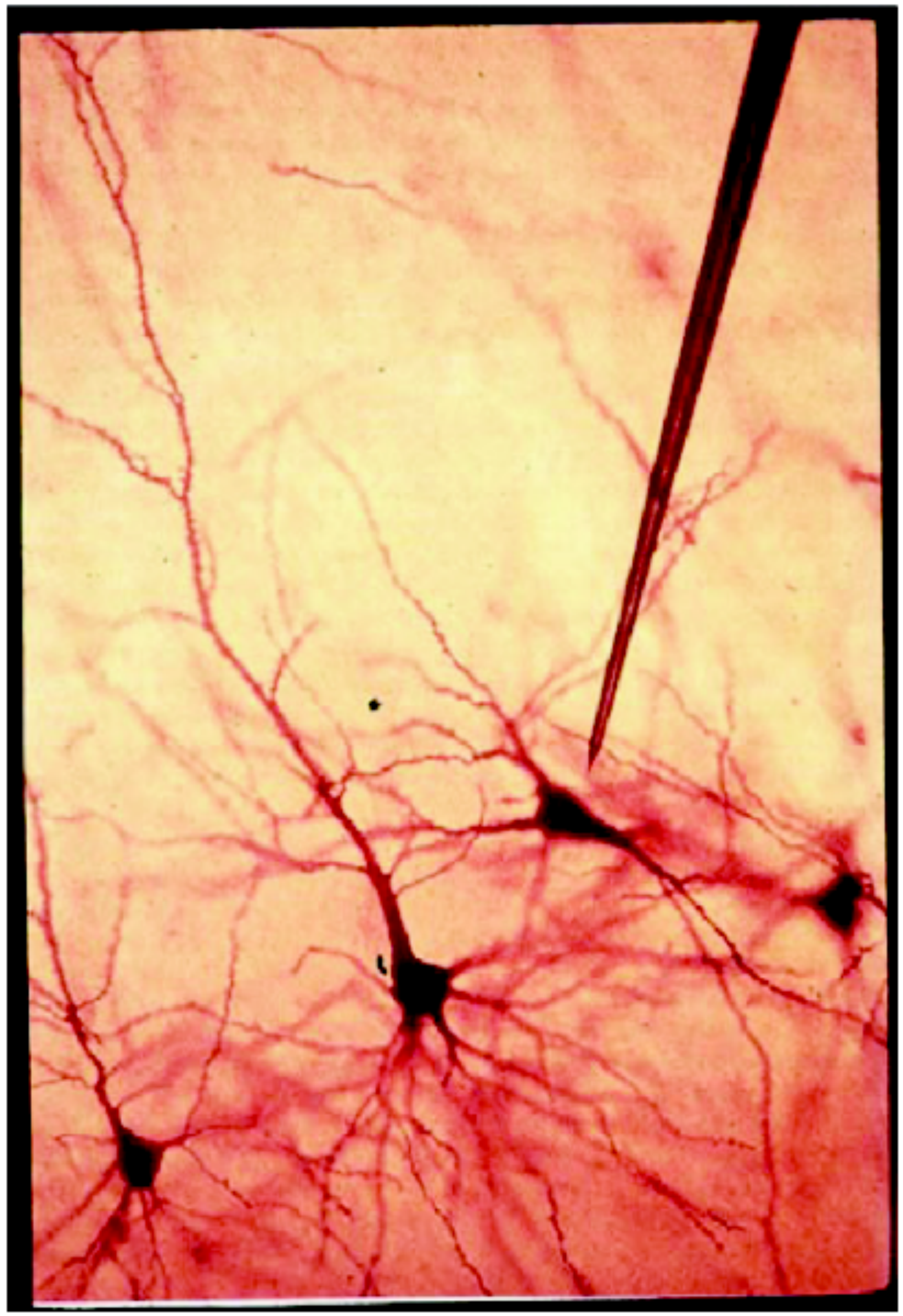


Five problems with the current view:

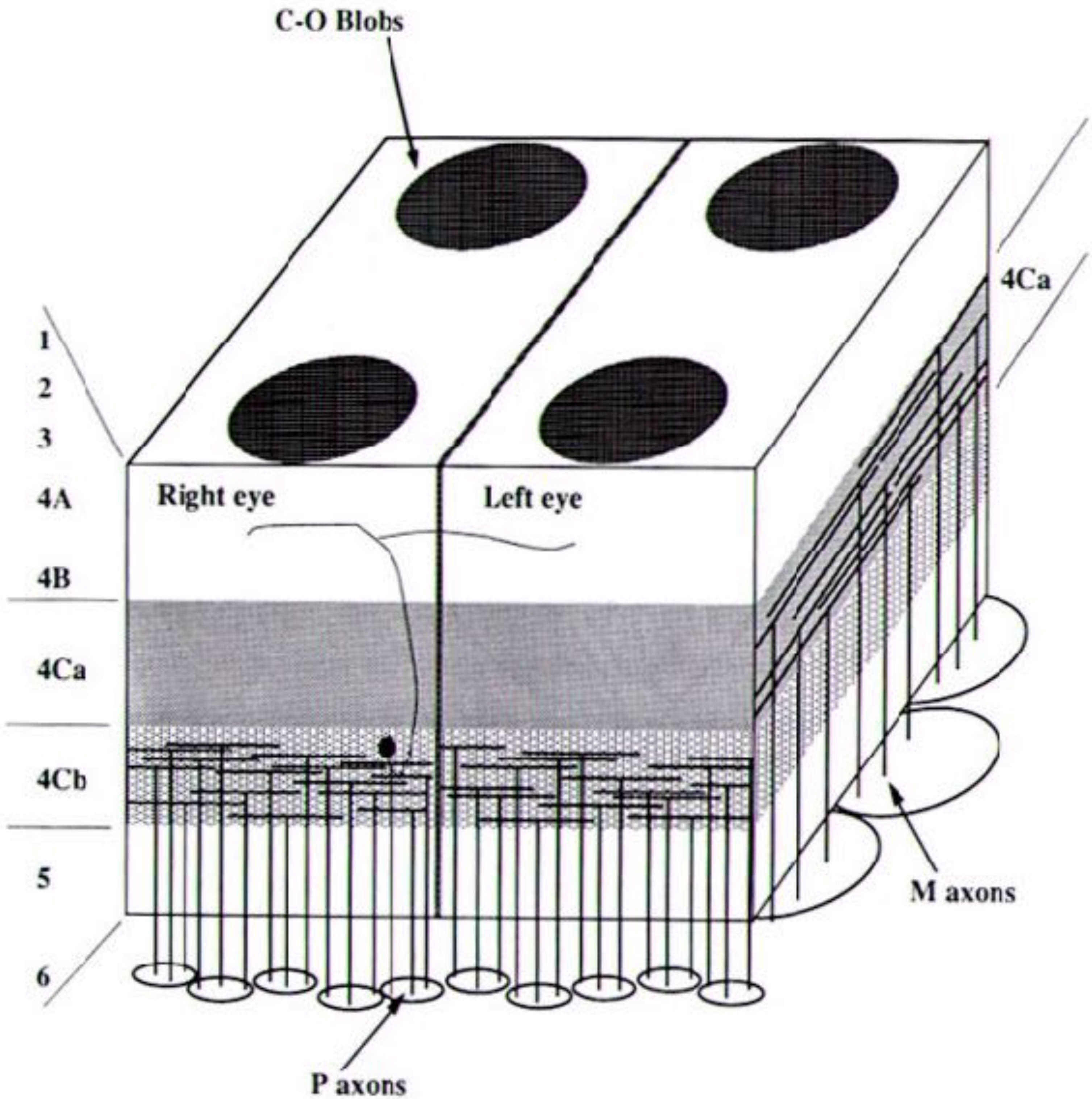
- Biased sampling (single unit recording)
- Biased stimuli (bars, spots, gratings)
- Biased theories (data-driven vs. functional theories)
- Interdependence and context (effect of intra-cortical inputs)
- Ecological deviance

Olshausen BA, Field DJ (2005) How close are we to understanding V1? *Neural Computation, 17*, 1665-1699.

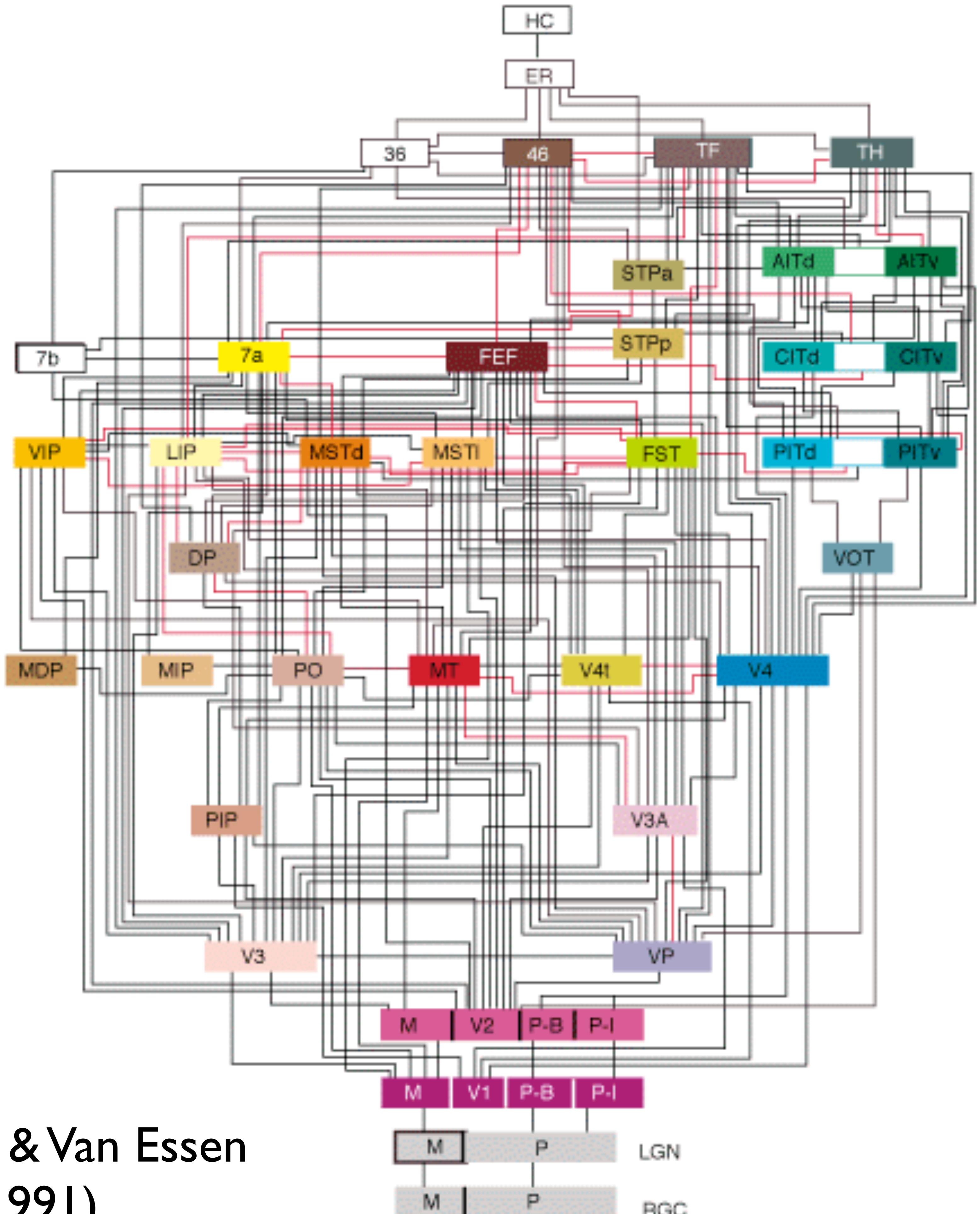
Single-unit electrophysiology



1 mm^2 of cortex analyzes ca. 14 x 14 array of retinal sample nodes and contains 100,000 neurons



1 mm^2 of cortex contains 100,000 neurons

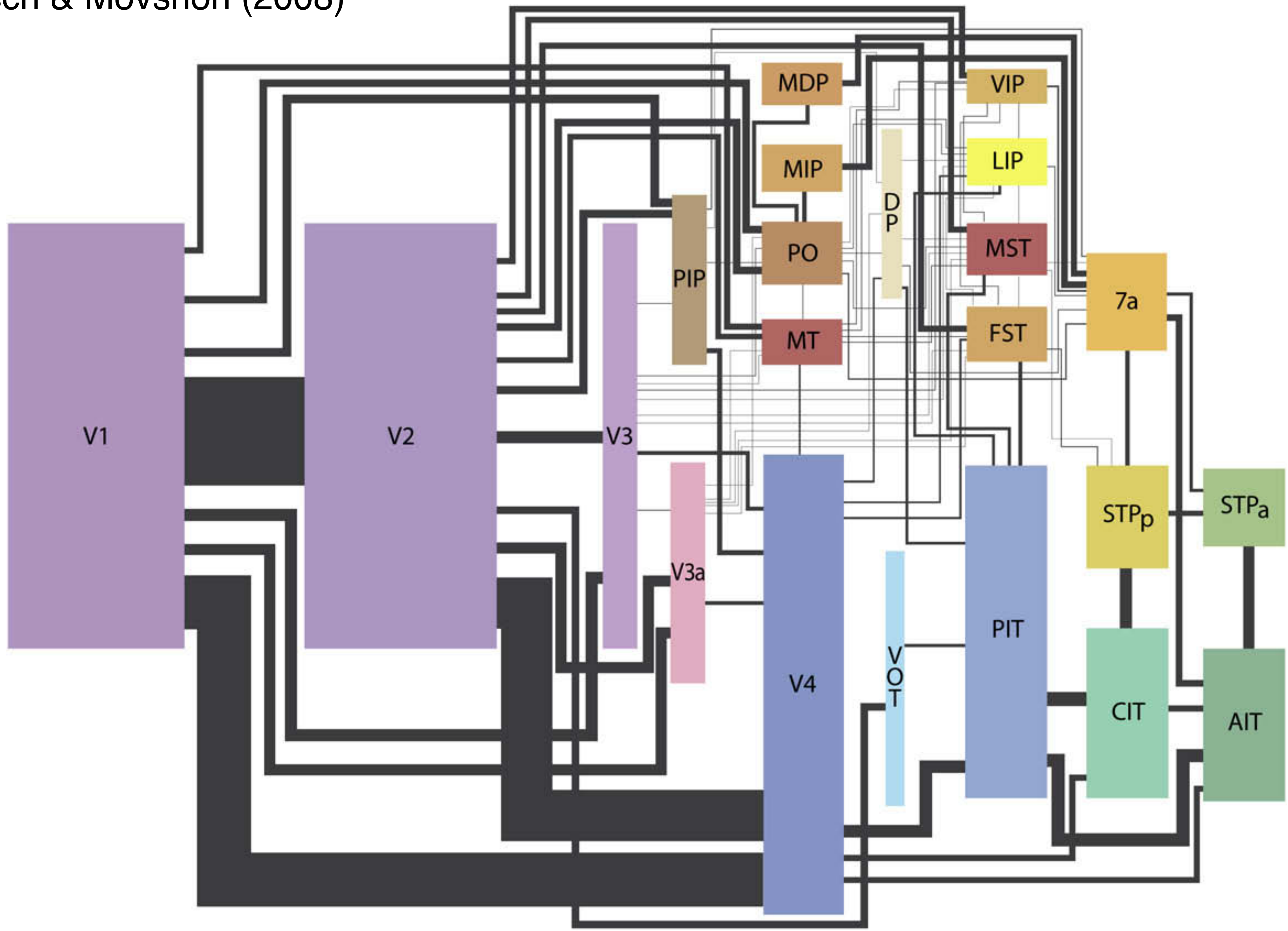


Felleman & Van Essen (1991)

place cells
grid cells
.
.
face cells
.
invariant repr.
complex motion
.
.
?
.
.
.
'Gabor filters'

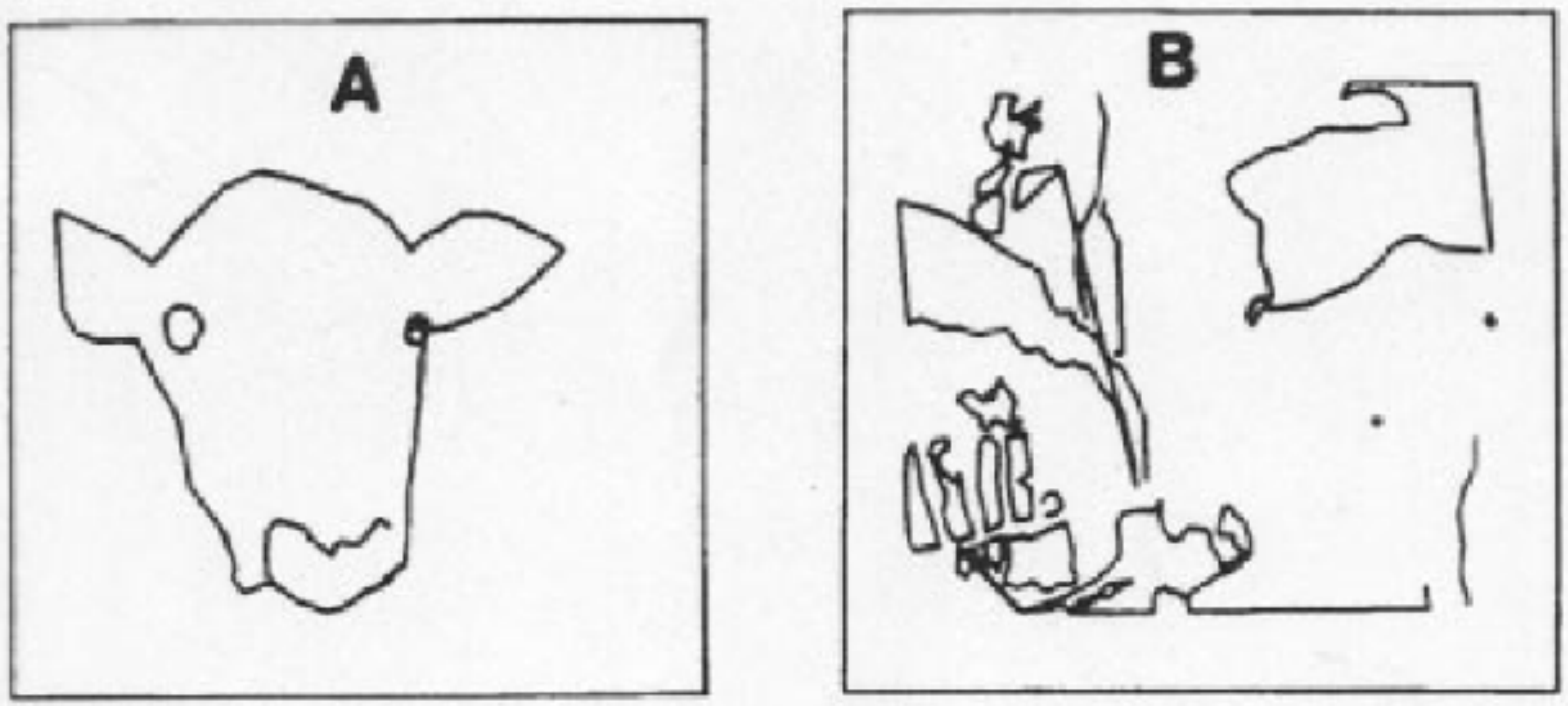
	OCCIPITAL									TEMPORAL														PARIETAL										FRONTAL	
From: \ To:	V1	V2	V3	VP	V3A	V4	VOT	V4t	MT	FST	PITd	PIT	PITv	CITd	CIT	CITv	AITd	AITv	STPp	STP	STPa	TF	TH	MSTd	MSTl	PO	PIP	LIP	VIP	MIP	MDP	DP	7a	FEF	46
V1		+	+	.	+	+	.	NR	+	.	.		.	.		.	.	.	.		.	.	.	.	?	+	+	.	.	.	.	.	.	.	.
V2	+		+	+	+	+	+	+	+	+	.		.	.		.	.	.	.		.	.	.	+	+	+	+	.	+	.	.	.	.	?	.
V3	+	+			+	+	.	+	+	+	.		.	.		.	.	.	.		.	+	.	+	.	+	+	+	+	.	.		.	?	.
VP	.	+	+		+	+	+	.	+	+	.		.	.		.	.	.	.		.	+	.	+	.	+	+		+	.	.		.	?	.
V3A	+	+	+	+		+			+	+	.		.	.		.	.	.	.		.	.	.	+	+	+				.	.	+	.	?	.
V4	+	+	+	+	+			+	+	+	+		+	+		+	.	+	.		.	+	+	.	.	.	+	+	.	.	.	+	.	?	+
VOT	.	+	.	+		+					+		+																						
V4t	+		+	.		+			+	+														NR?	+	+								?	
MT	+	+	+	+	+	+		+		+	.		.	.		.	.	.	.		.	.	.	+	+	?	+	+	+	.	.	.	.	+	?
FST	.	NR?	+	NR?	+	+		+	+			+		.		.	.	.	+			+		+	+	.	.	+	+				+	+	.
PITd	.	.	.	.	.	+			.							+	+	+							.	.	.	.	.				.		
PIT										+														+										+	+
PITv	.	.	.	.	.	+			.							+		+							.	.	.		.				.		
CITd	.	.	.	.	.	+			.				+				+	+						.	.	.	.	.	.				.		
CIT																																		+	+
CITv	.	.	.	.	.	+			.				+				+	+						.	.	.	.	.	.				.		
AITd	.	.	.	.	.	.			.	.			+			+								.	.	.	.	.	.	.	.		+	+	+
AITv	.	.	.	.	.	+			.	.			+			+					.	+	+	.	.	.	.	.	.	.	.				
STPp	.	.	.	.	.	.			.	+					+		.				+	+	+	+	+	.	.	.	.	.	.			+	+
STP																																	+		
STPa	.	.	.	.	.	.			.								+	.	+			+	+			.	.	.	.	.	.				+
TF	.	.	+	+	.	+			.	+			+			+	+	+	+		+			+		.	.		.	.	.		+		+
TH	.	.	.	.	.	+			.				+		+		+	+	+		+			.	.	.	.	.	.	.	.		+		+
MSTd	.	+	+	+	+	.		+	+	+		+		.		.	.	.	+							+		+	+			+	+	+	
MSTl	NR	+	.	.	+	.		NR?	+	+	.	.	.	.		.	.	.	+							+	.		+			NR?	NR?	+	
PO	+					.			+	.	.		.	.		.	.	.	.		.	.	.	+	+			+	+			+	+	?	
PIP	+		+	+		+			+		.		.	.		.	.	.	.		.					+						+	+		
LIP	.		+	+	+	+			+	+	.		+	.		.	.	.				+	.	+	+	+			+			+	+	+	+
VIP	.		+						+	+	.		.	.		.	.	.						+	+	+		+					+	+	
MIP	.	.	.	.	.	.			.	.	.		.	.		.	.	.						.	.	+							+		
MDP	.	.	.	.	.	.			.	.	.		.	.		.	.	.						.	.	+							+		
DP	.	.	.	.	+	+			.	+	.		.	.		.	.	.	.		.	.	.	+	+	+	+	+					+		+
7a	.	.	.	.	.	.			.		.		.	.		.	+			+		+	+	+	?	+		+				+		+	+
FEF	.								?	+					+		+		+					+	+	+		+	+			+	+		+
46	.	.	.	.	.					.					+		+		+		+	+	+	.								+	+	+	

Wallisch & Movshon (2008)



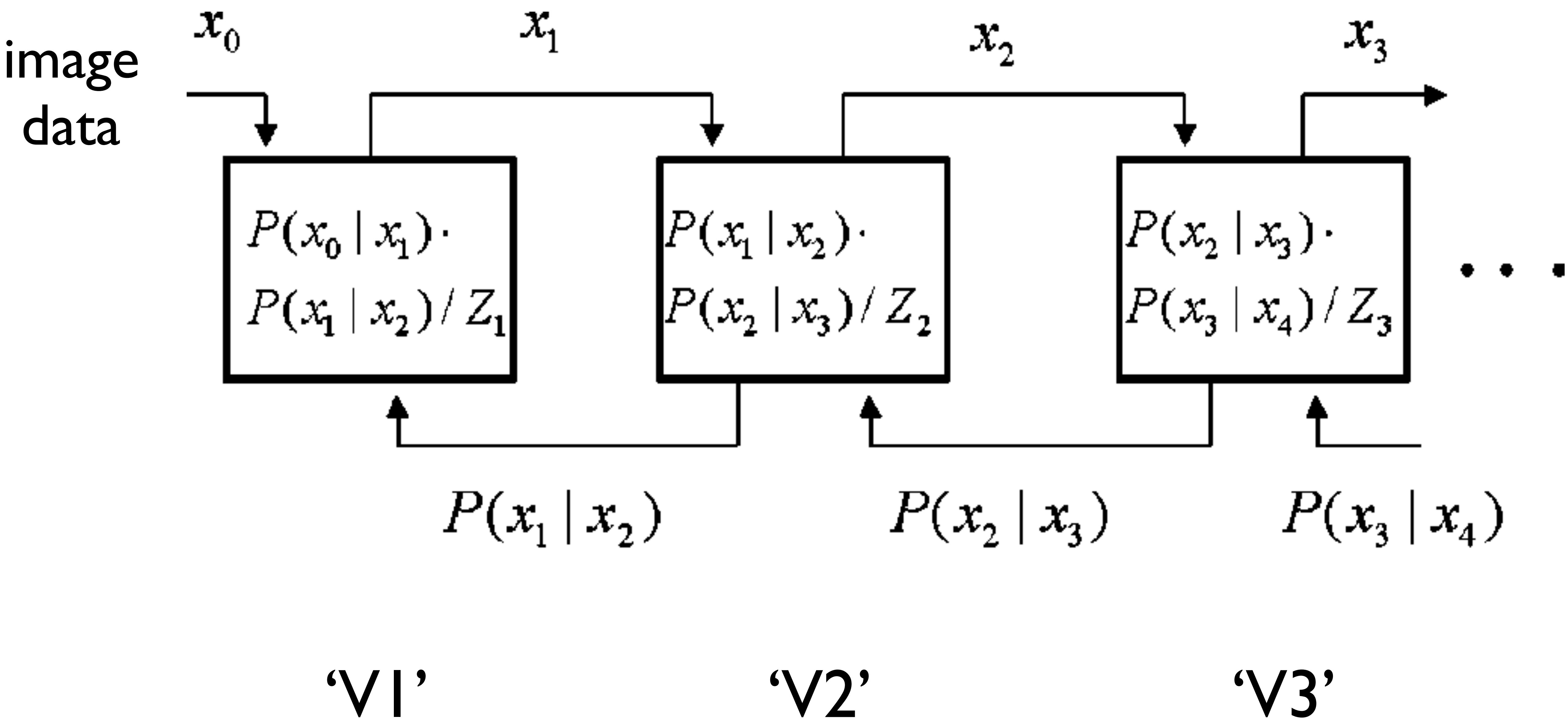
'Gabor filters' . . ? . . objects . faces

b

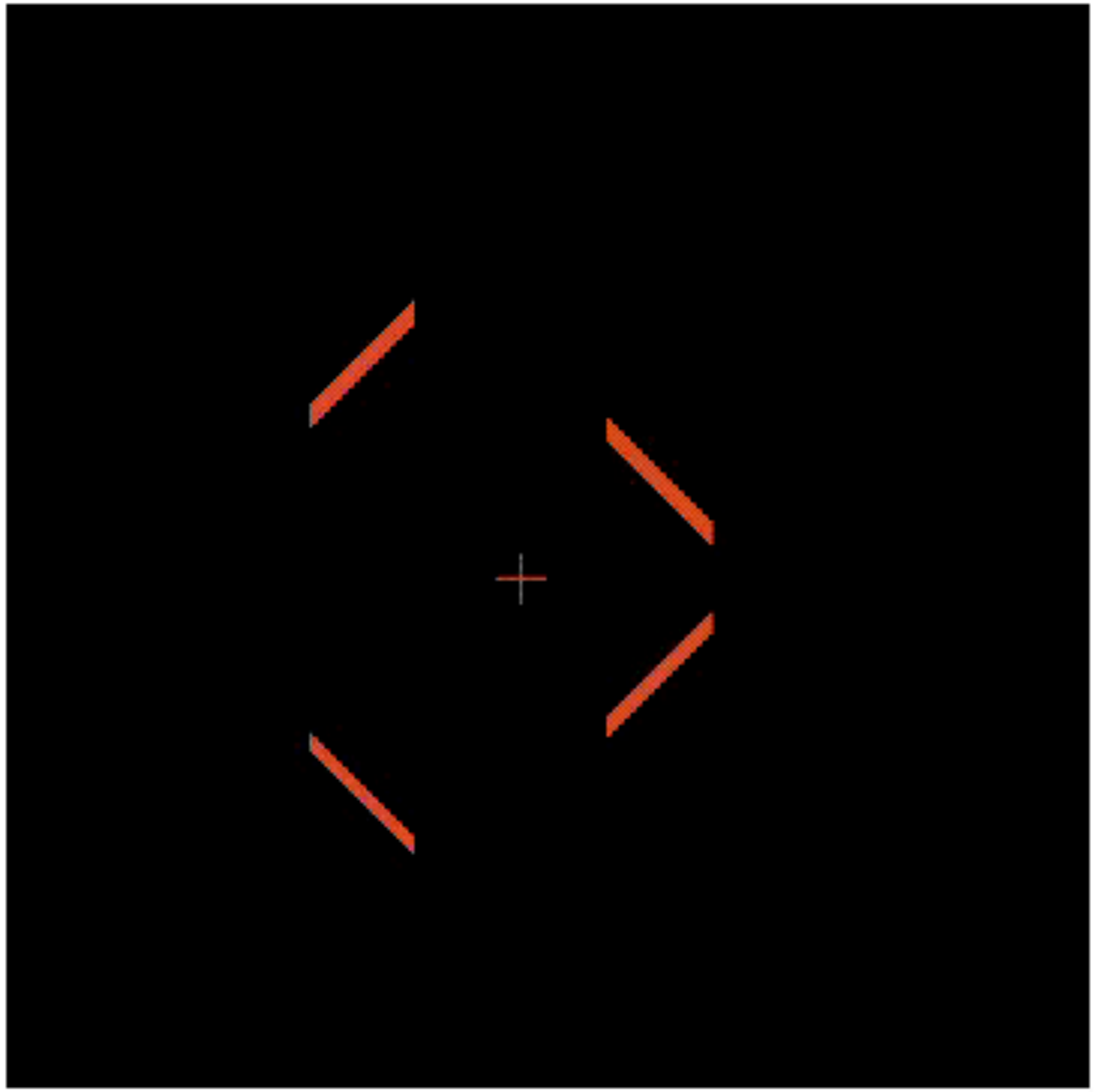


Hierarchical Bayesian inference in visual cortex

(Lee & Mumford, 2003)

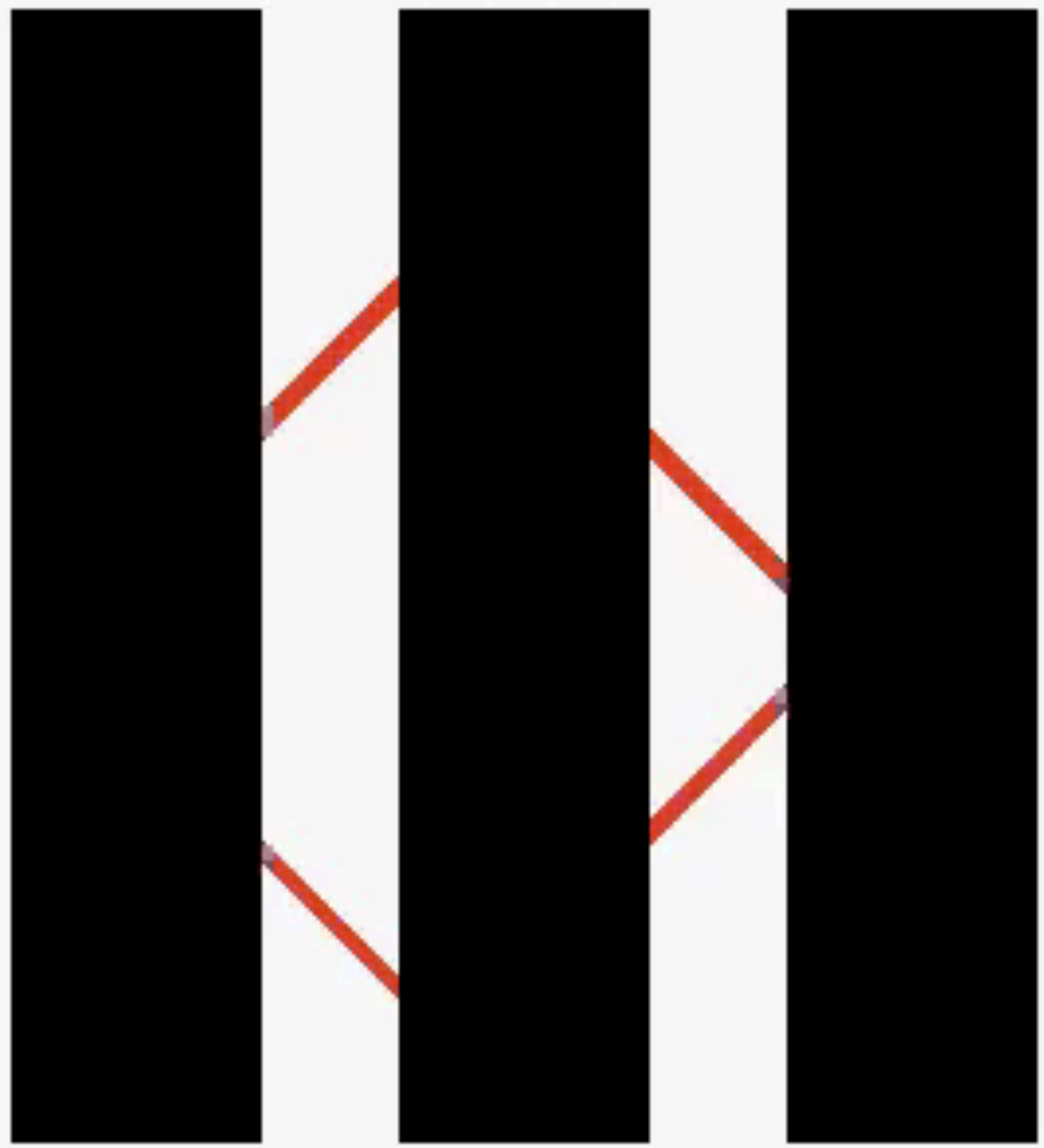


What do you see?

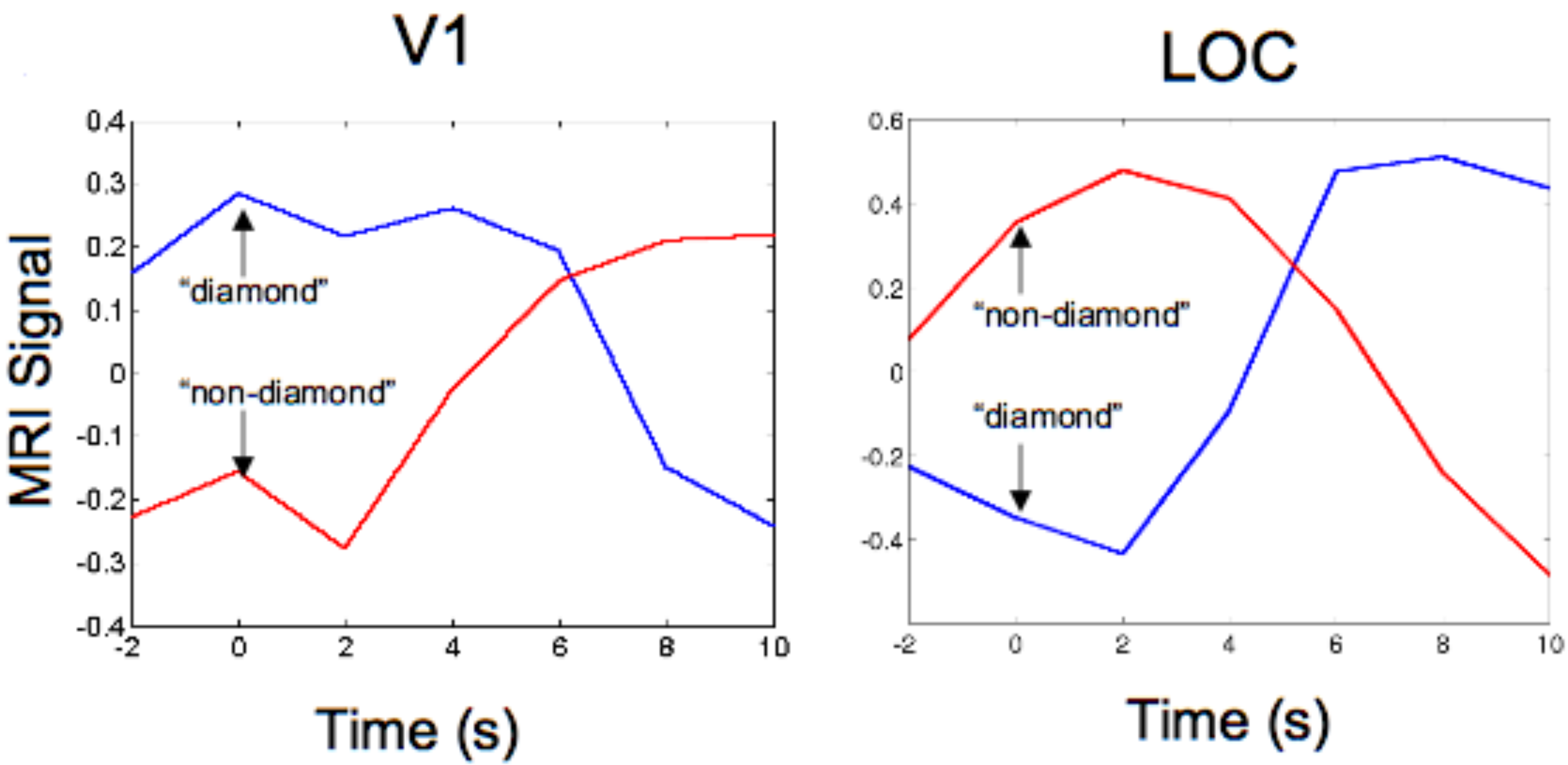


Lorenceau & Shiffrar (1992);
Murray, Kersten, Schrater, Olshausen & Woods (2002)

(easy version)

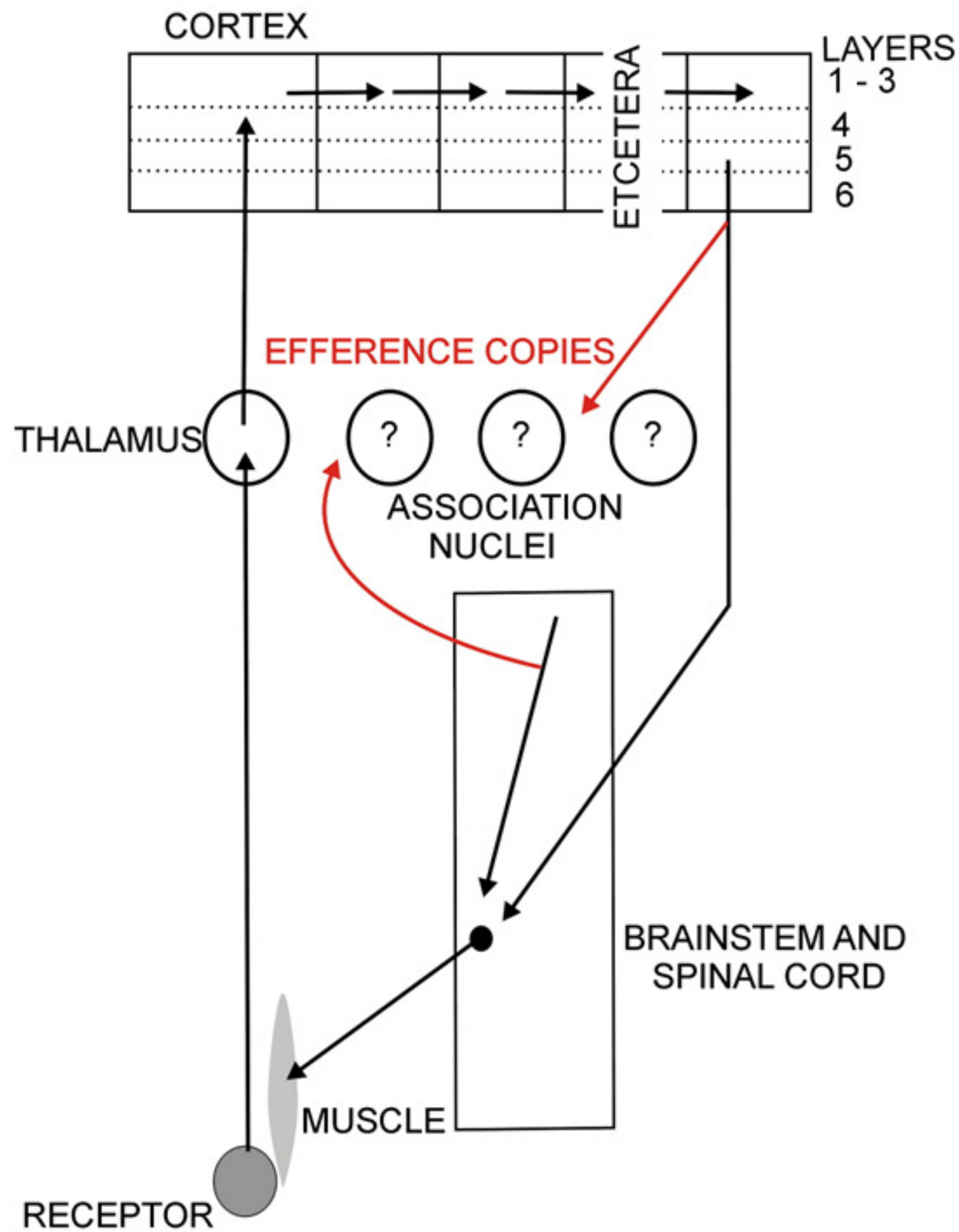


BOLD signal in V1 and LOC



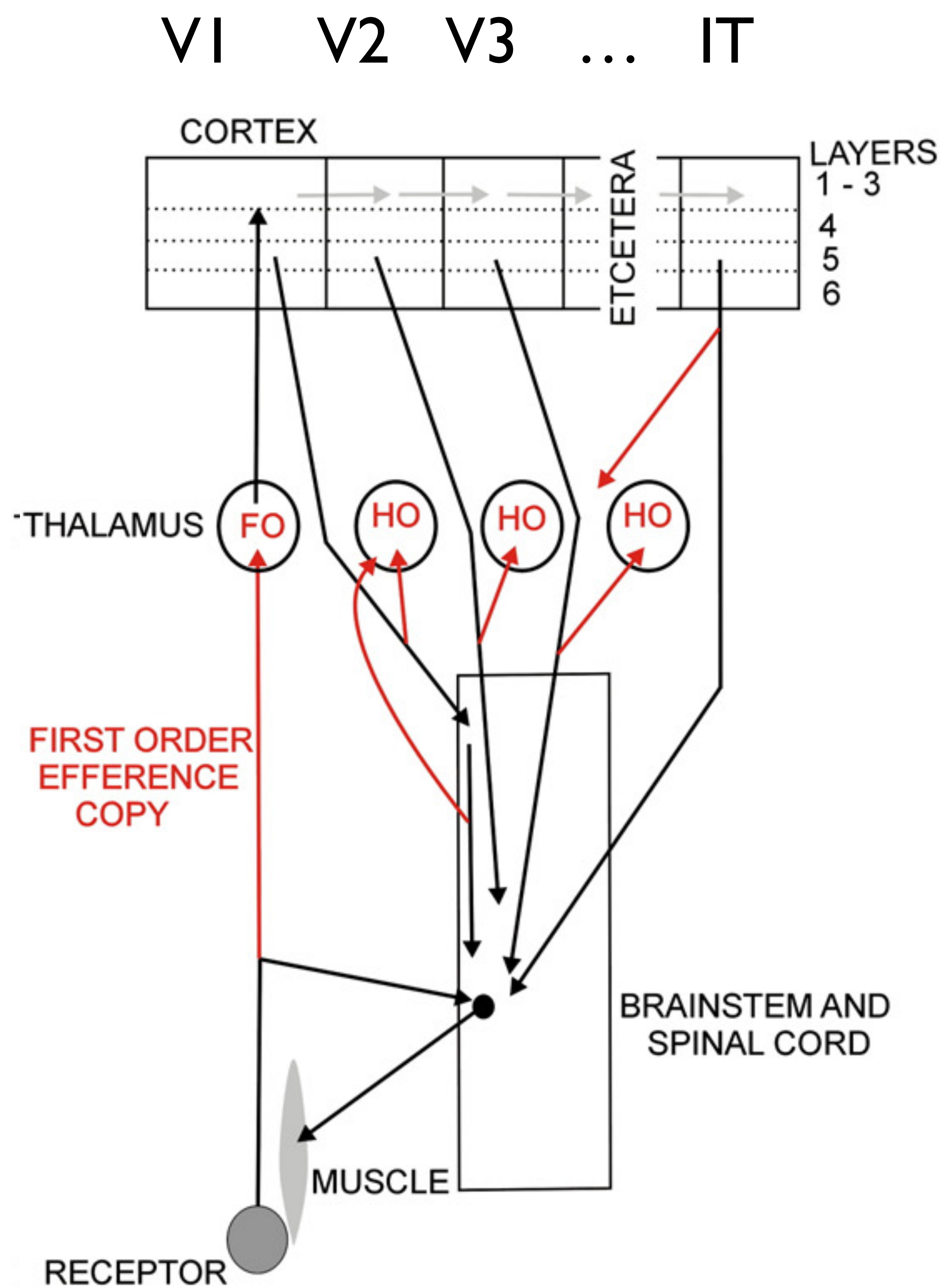
V1 V2 V3 ... IT

The conventional view

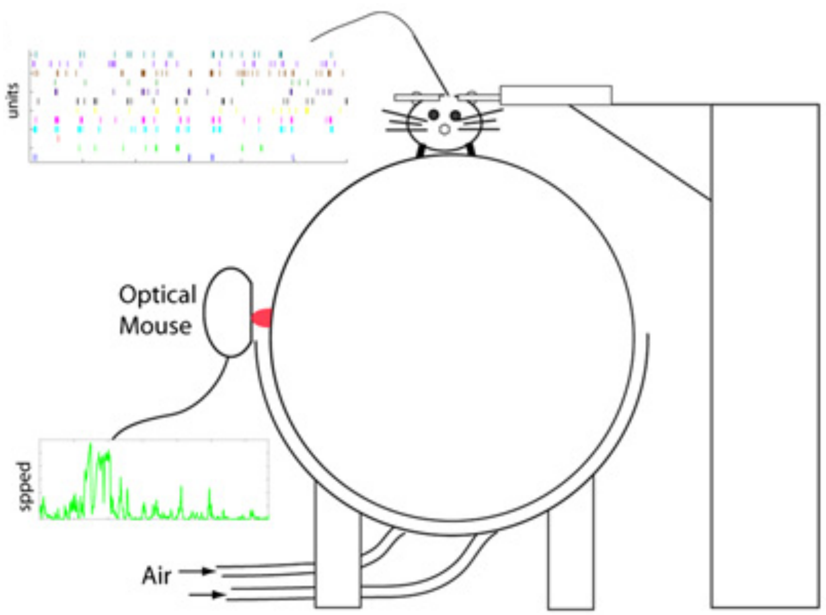


An alternative view

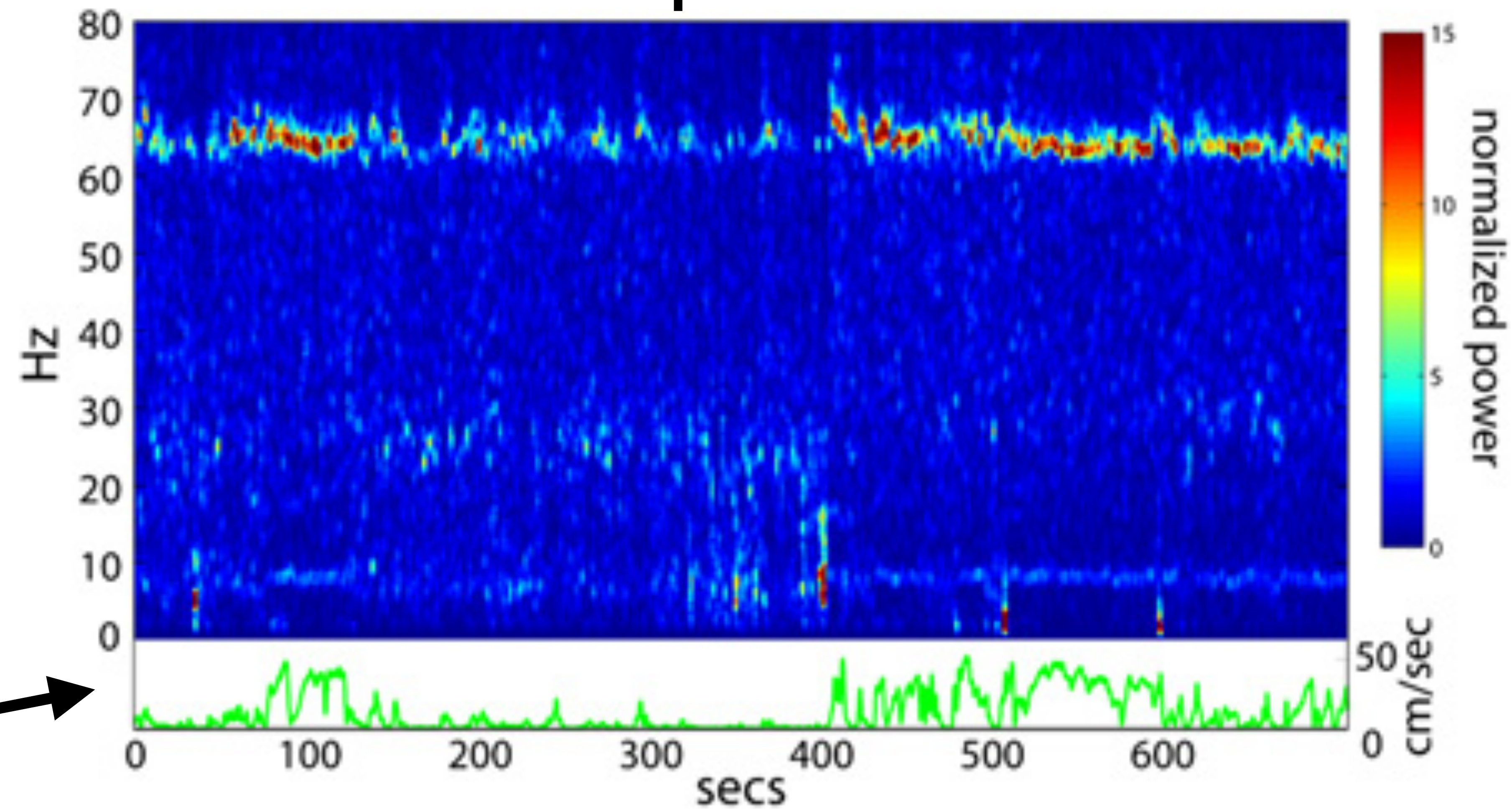
(Guillery & Sherman)



Activity in V1 more than doubles during locomotion



LFP power

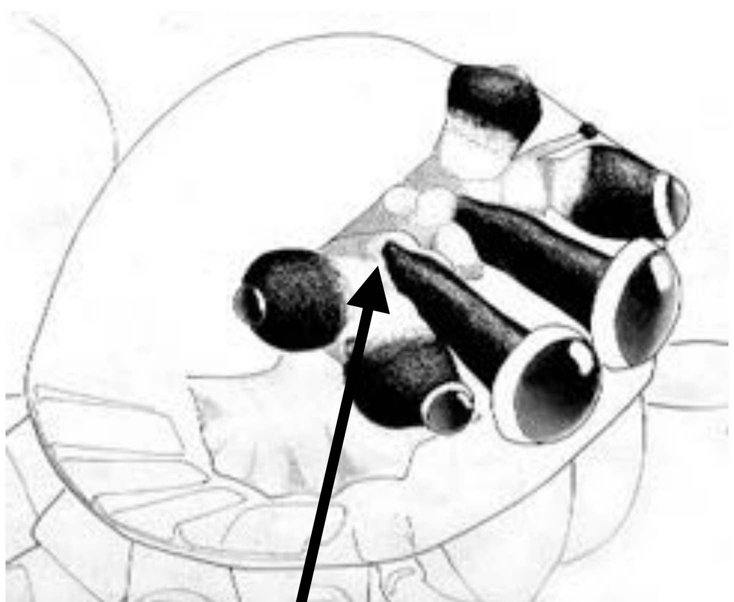


animal's speed

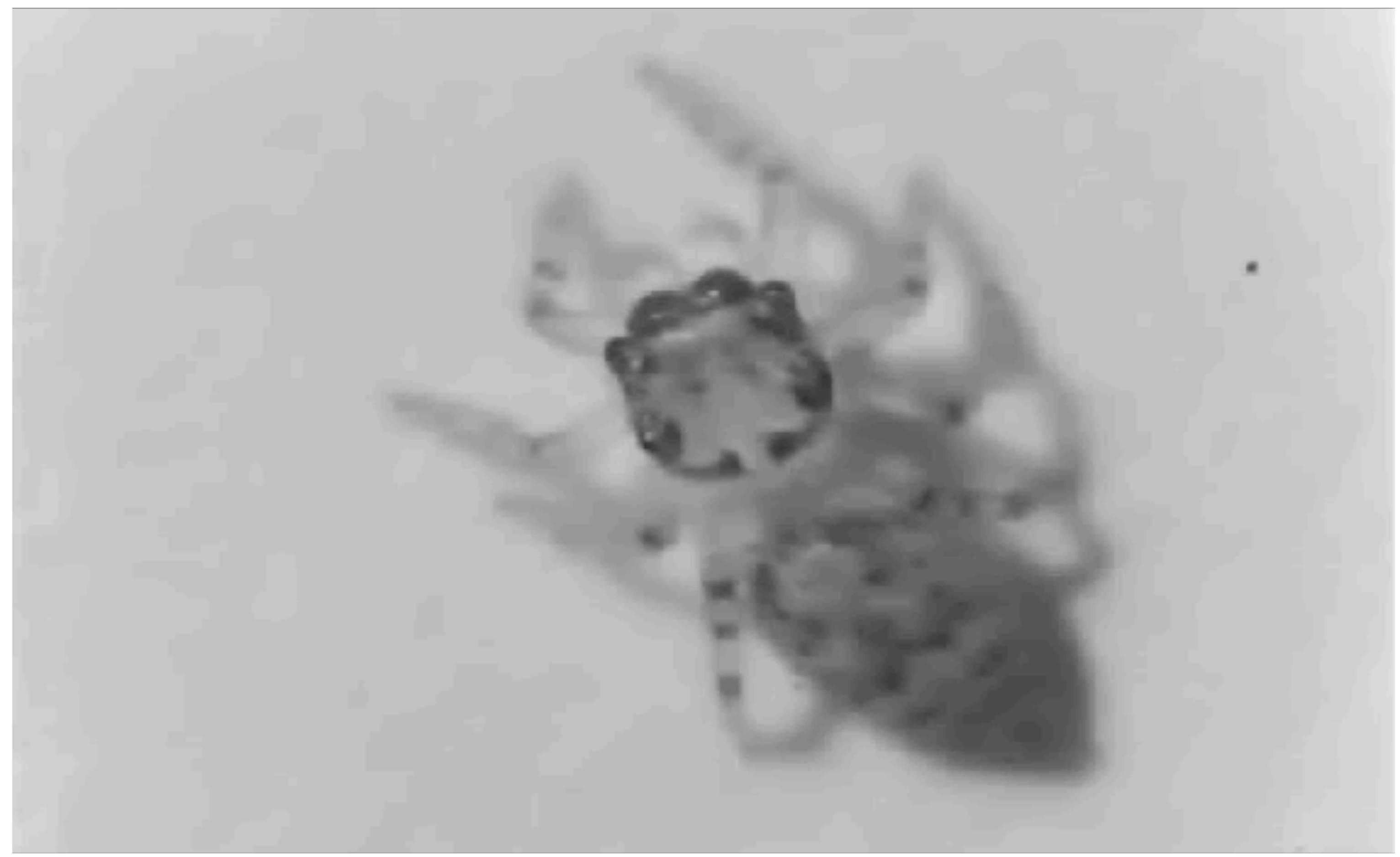
(Neil & Stryker, 2010)

Mystery

Vision in jumping spiders

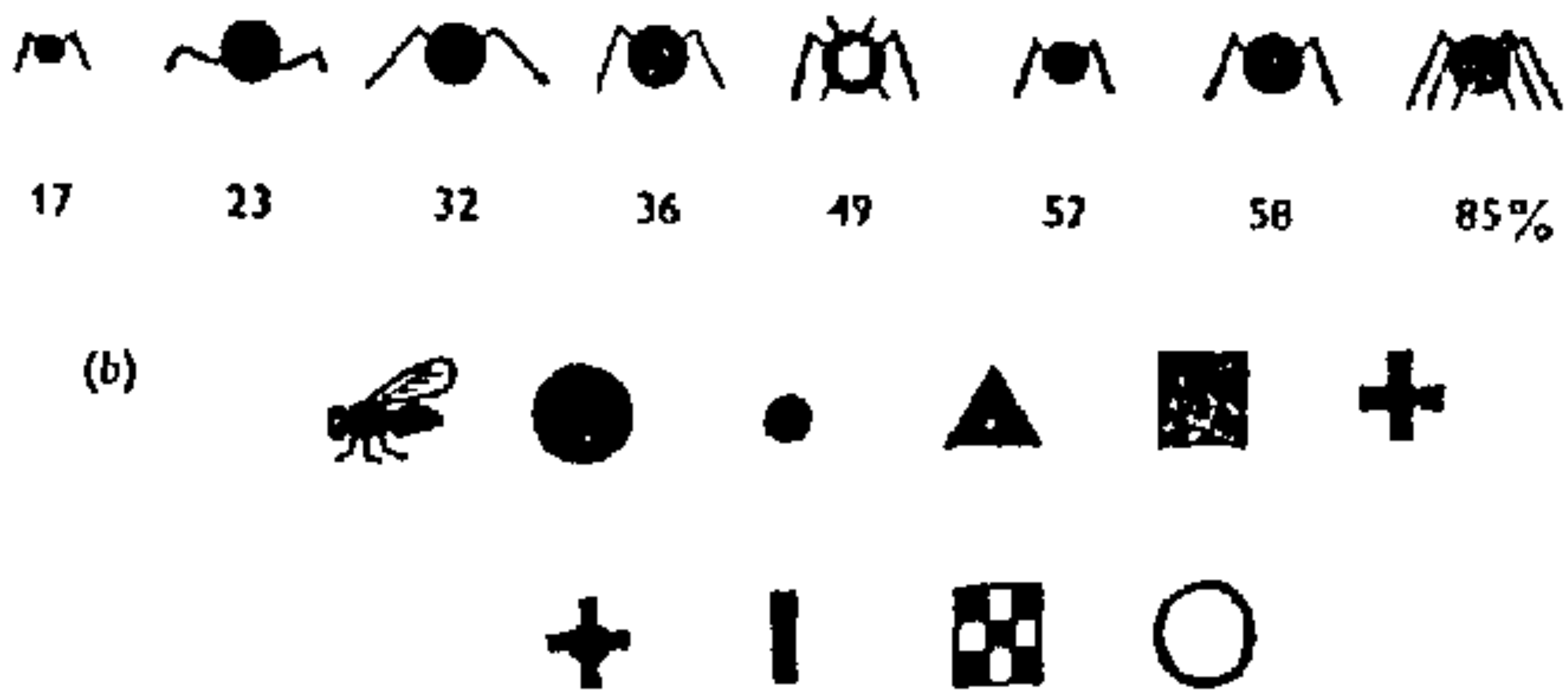


(Wayne Maddison)



(Bair & Olshausen, 1991)

Jumping spiders do object recognition

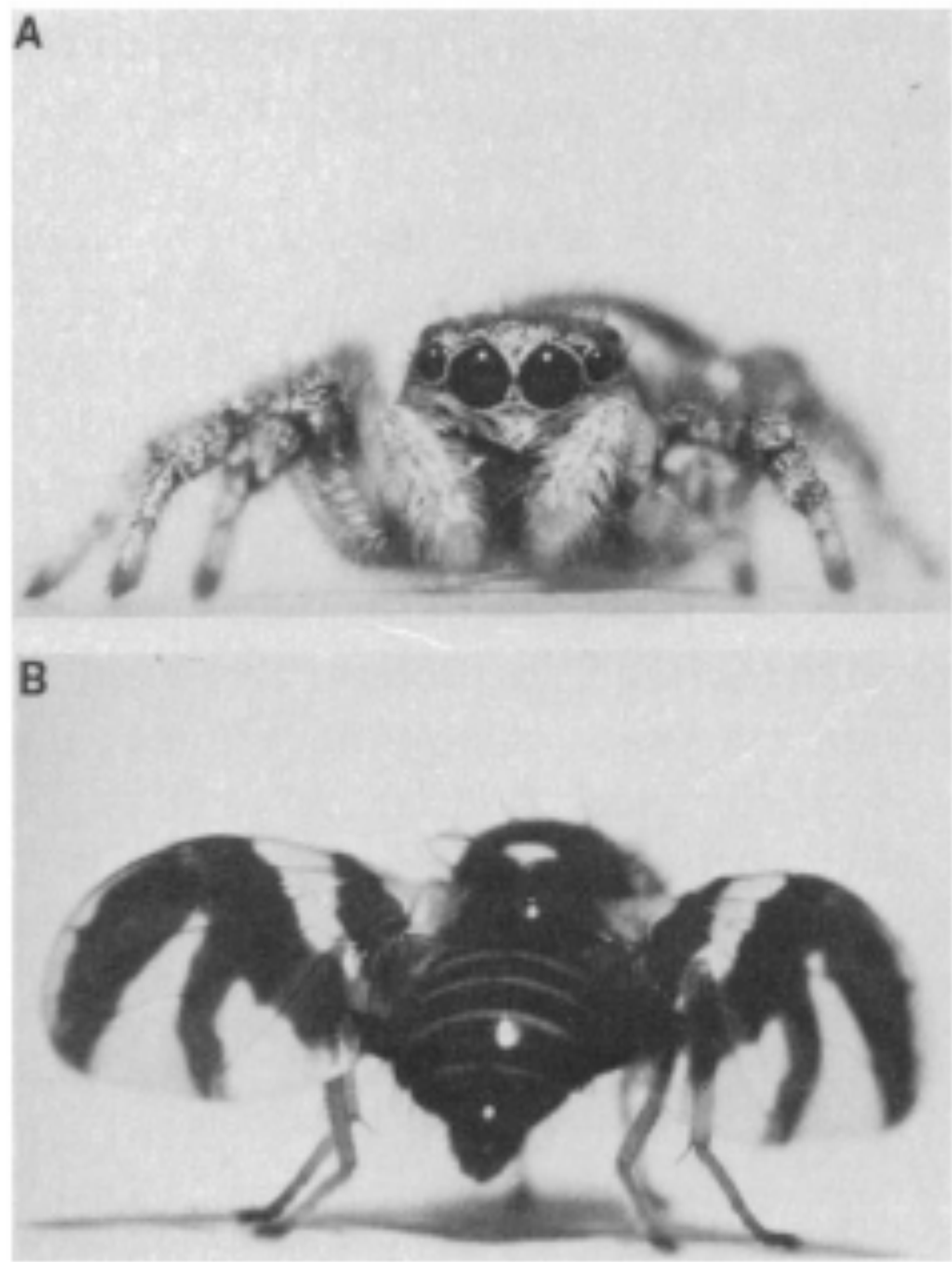


Text-fig. 12. Stimuli found by Drees to evoke courtship (*a*) and prey capture (*b*) in male jumping spiders (*Epiblemum scenicum*). The numbers beneath each figure in (*a*) are the percentage of trials on which courtship was evoked. After Drees (1952).

Spider mimicry in flies

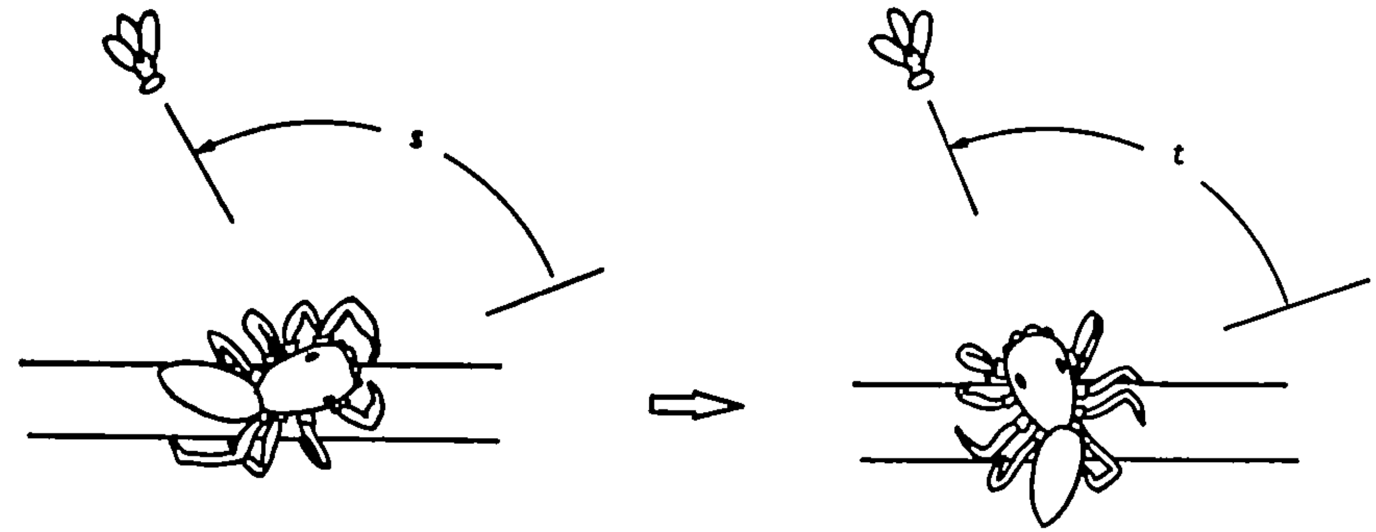
spider

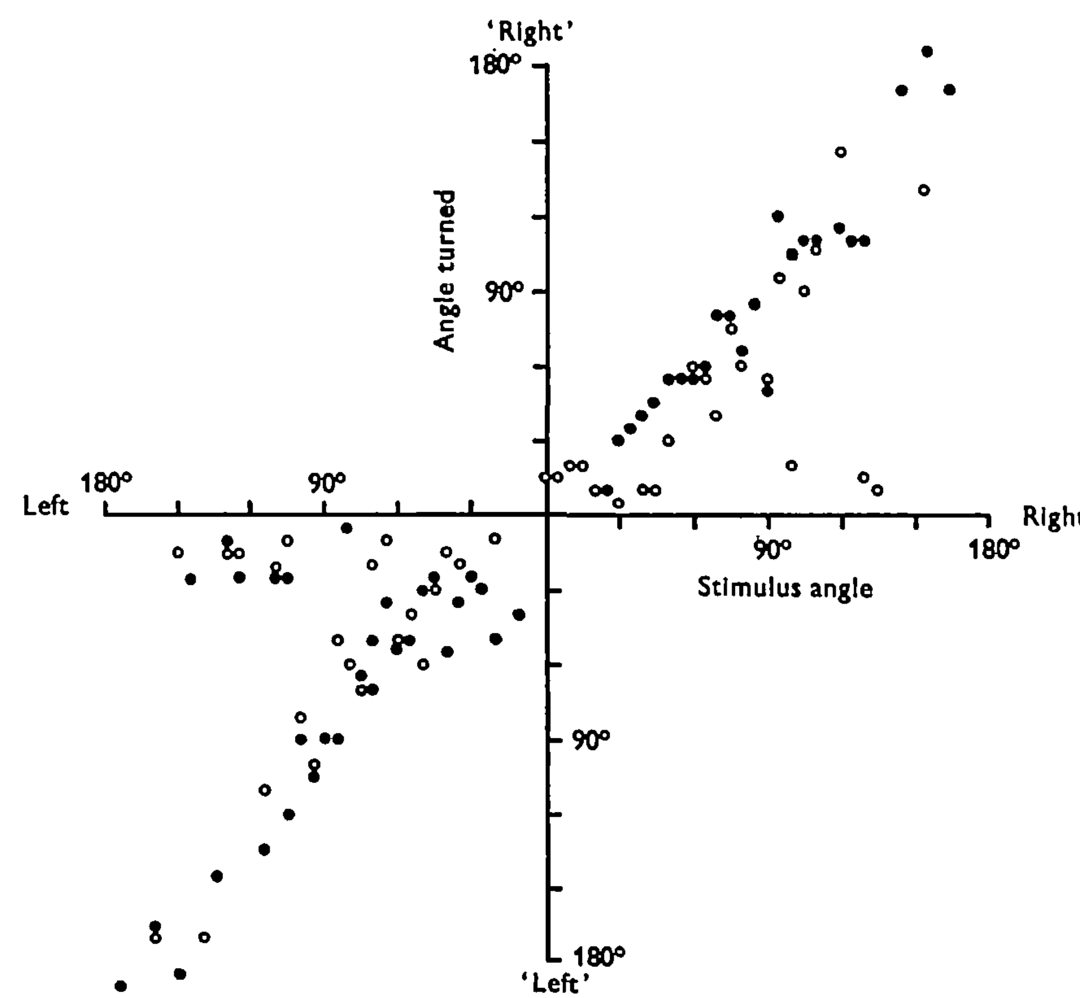
fly



Prey capture

- attention
- orienting
- tracking





Land (1971)

One-day old jumping spider
(filmed in the Bower lab, Caltech 1991)

One-day old jumping spider
(filmed in the Bower lab, Caltech 1991)

Navigation

(Tarsitano & Jackson 1997)

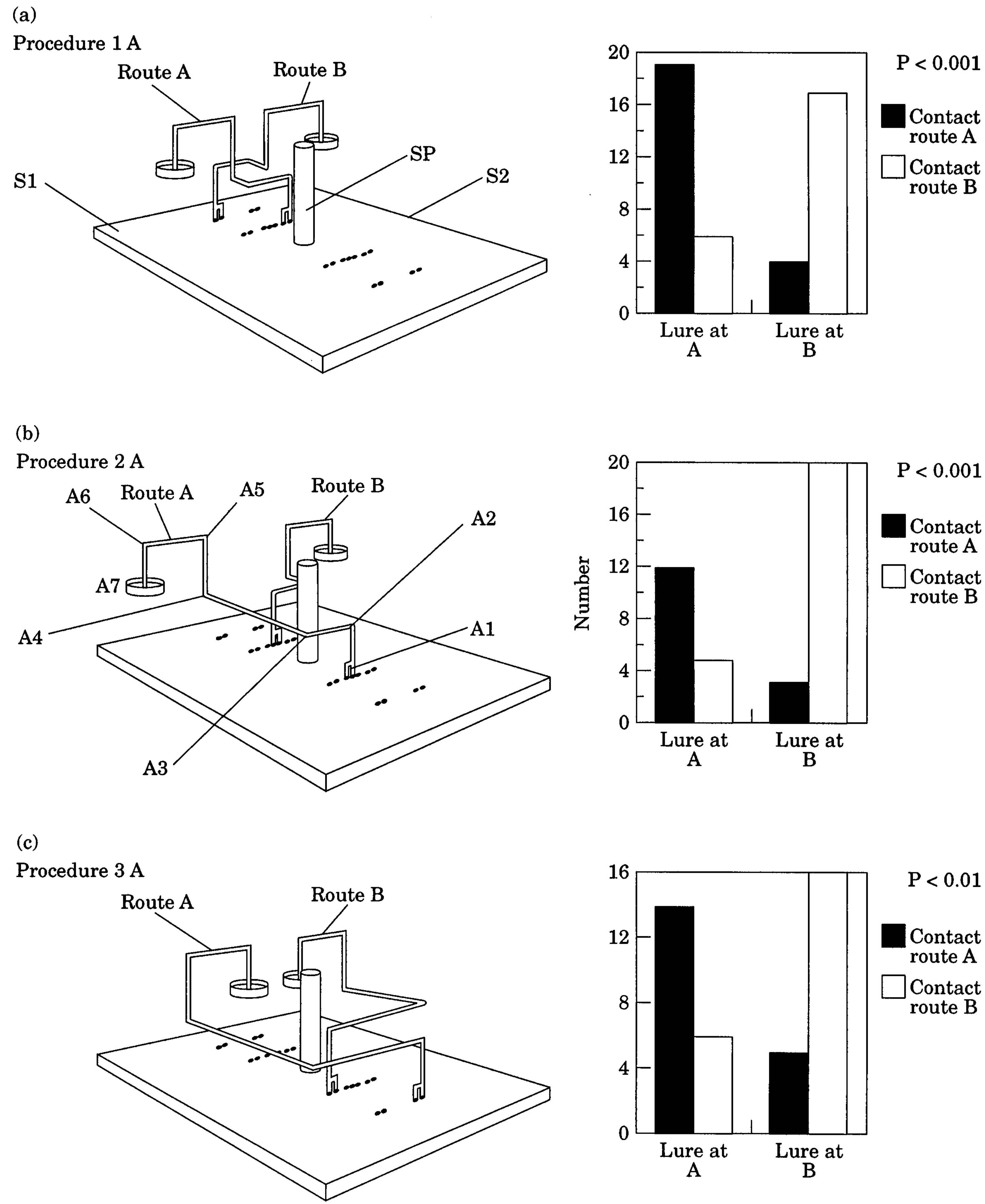


Figure 1 a-c.

…problem solving behavior, language, expert knowledge and application, and reason, are all pretty simple once the essence of being and reacting are available. That essence is the ability to move around in a dynamic environment, sensing the surroundings to a degree sufficient to achieve the necessary maintenance of life and reproduction. This part of intelligence is where evolution has concentrated its time--it is much harder.

— Rodney Brooks, "Intelligence without representation," *Artificial Intelligence* (1991)

...in the 1960s almost no one realized that machine vision was difficult.

… the idea that extracting edges and lines from images might be at all difficult simply did not occur to those who had not tried to do it. It turned out to be an elusive problem.

— David Marr (1982)

20 years of learning about vision: Questions answered, questions unanswered, and questions not yet asked. In: *20 Years of Computational Neuroscience*. J.M. Bower, Ed. (Symposium of the CNS2010 annual meeting)

http://redwood.berkeley.edu/bruno