Principles of Neuroscience: January 9, 2008

Visual routes to perception and action

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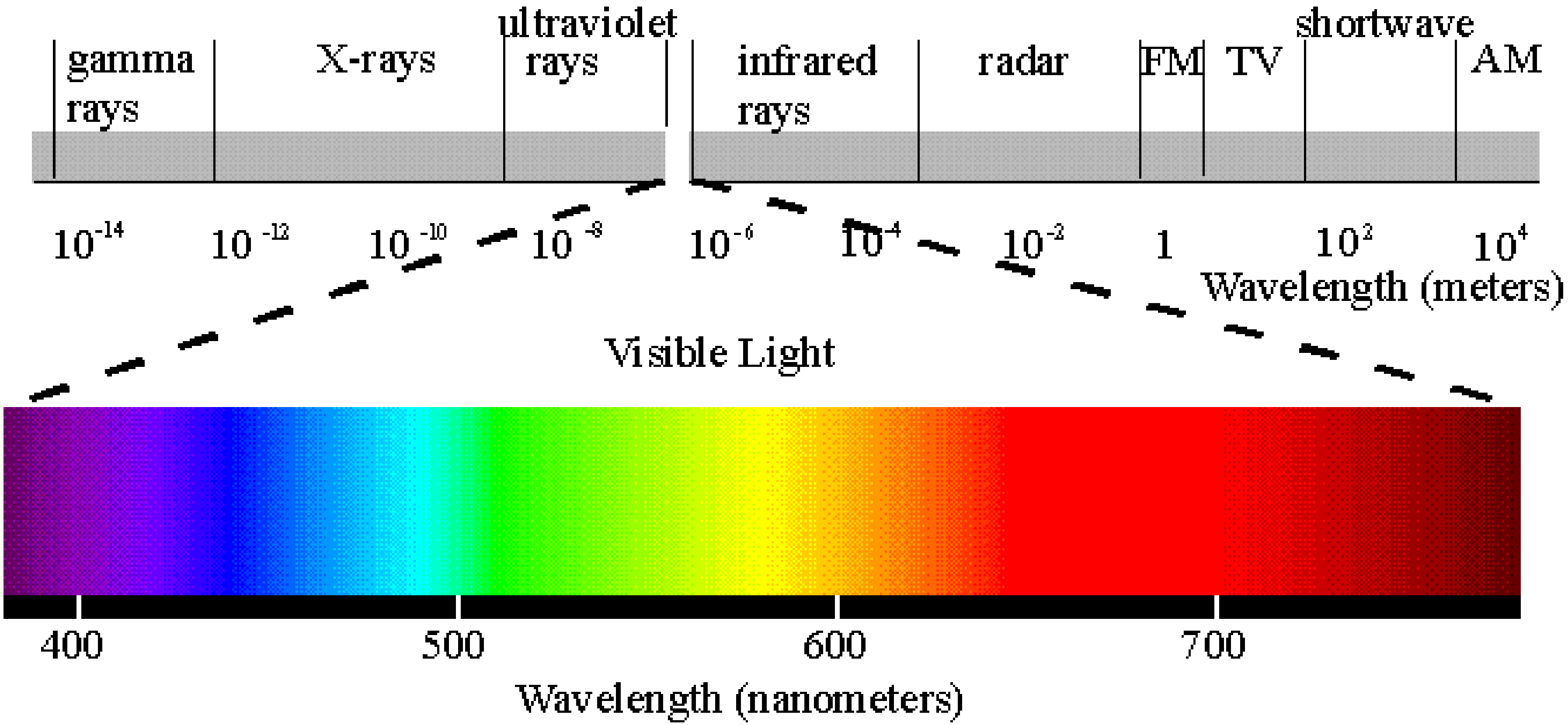
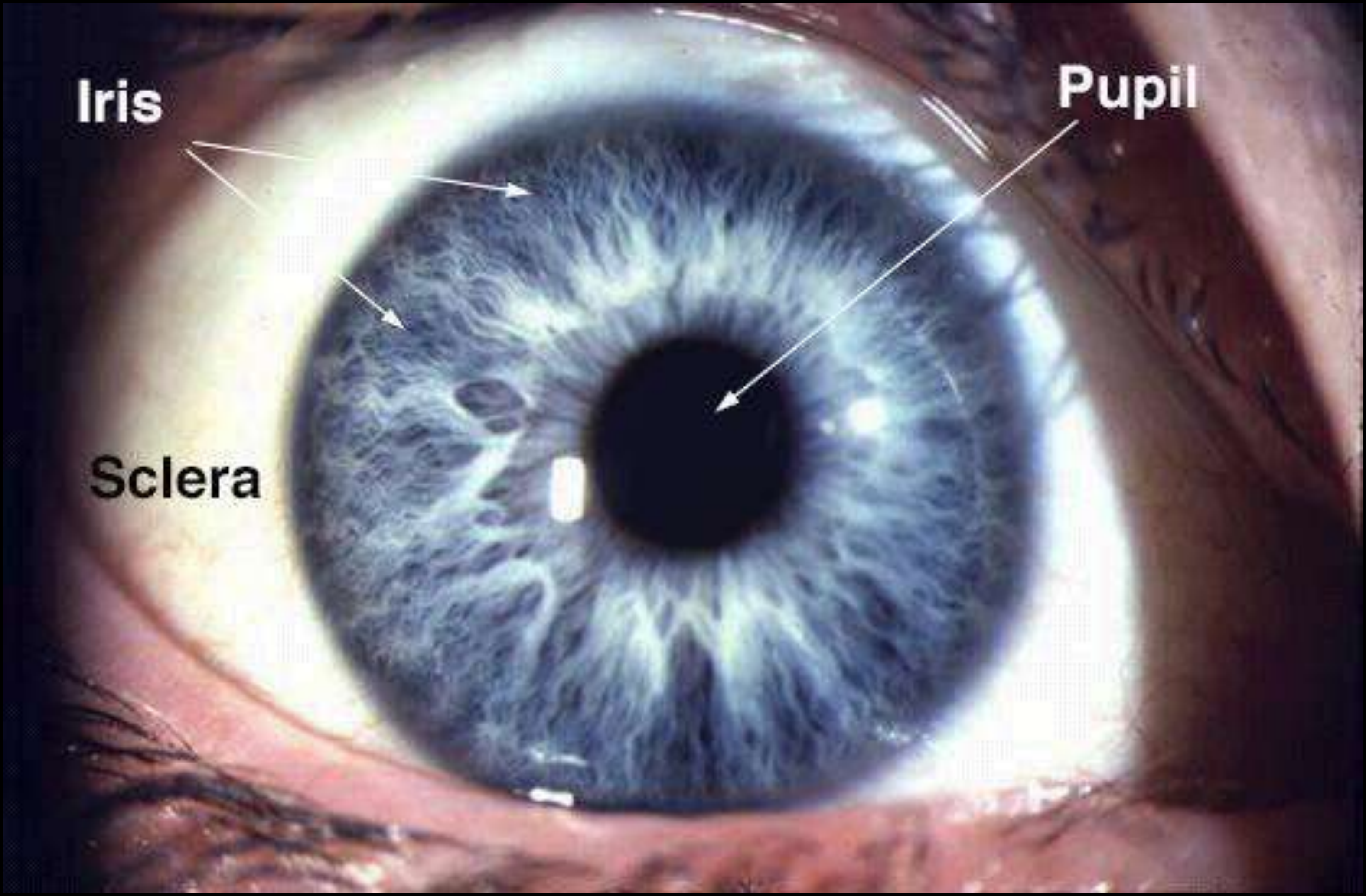
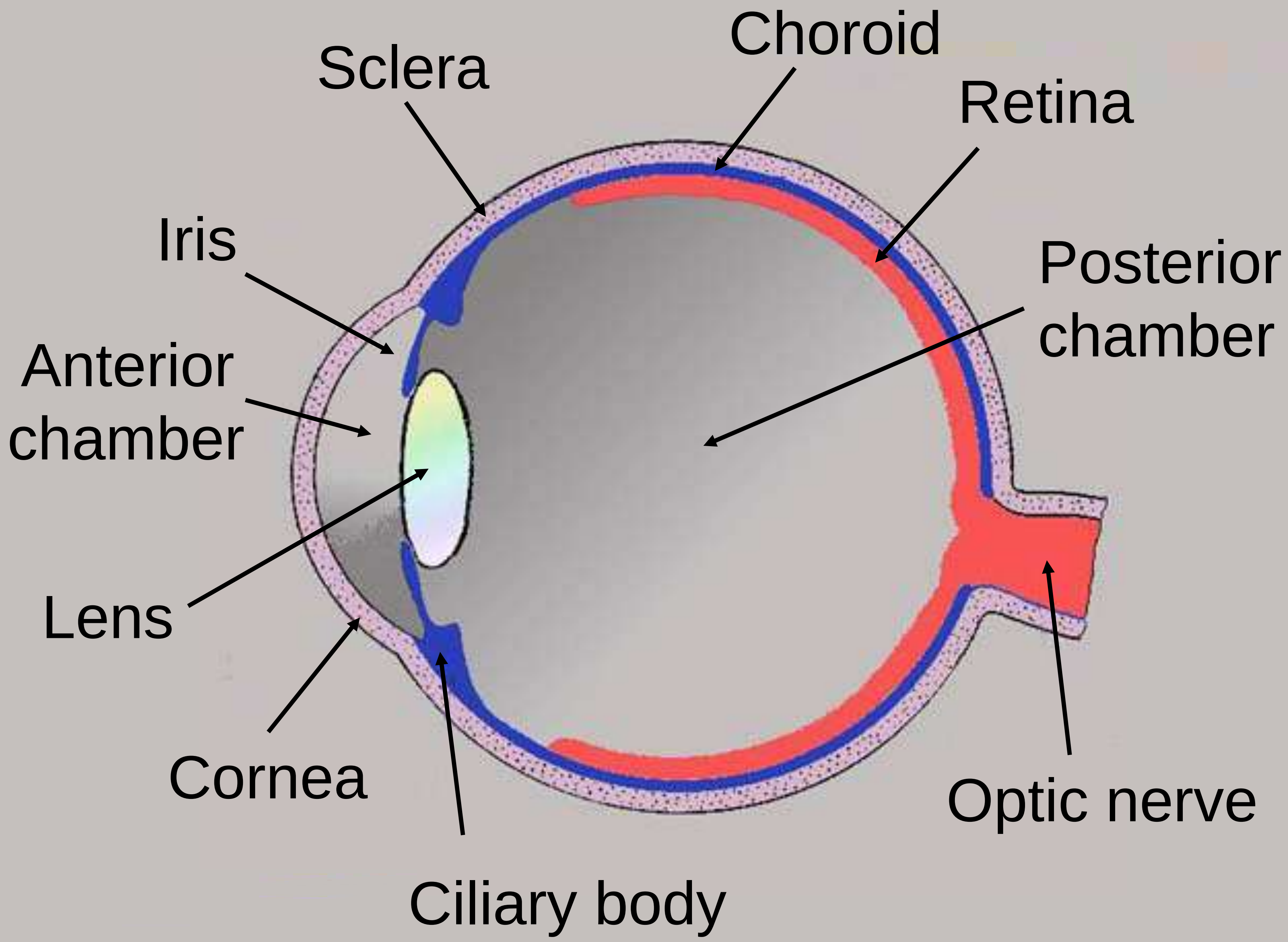
The Visible Spectrum



One nm = one billionth of a meter

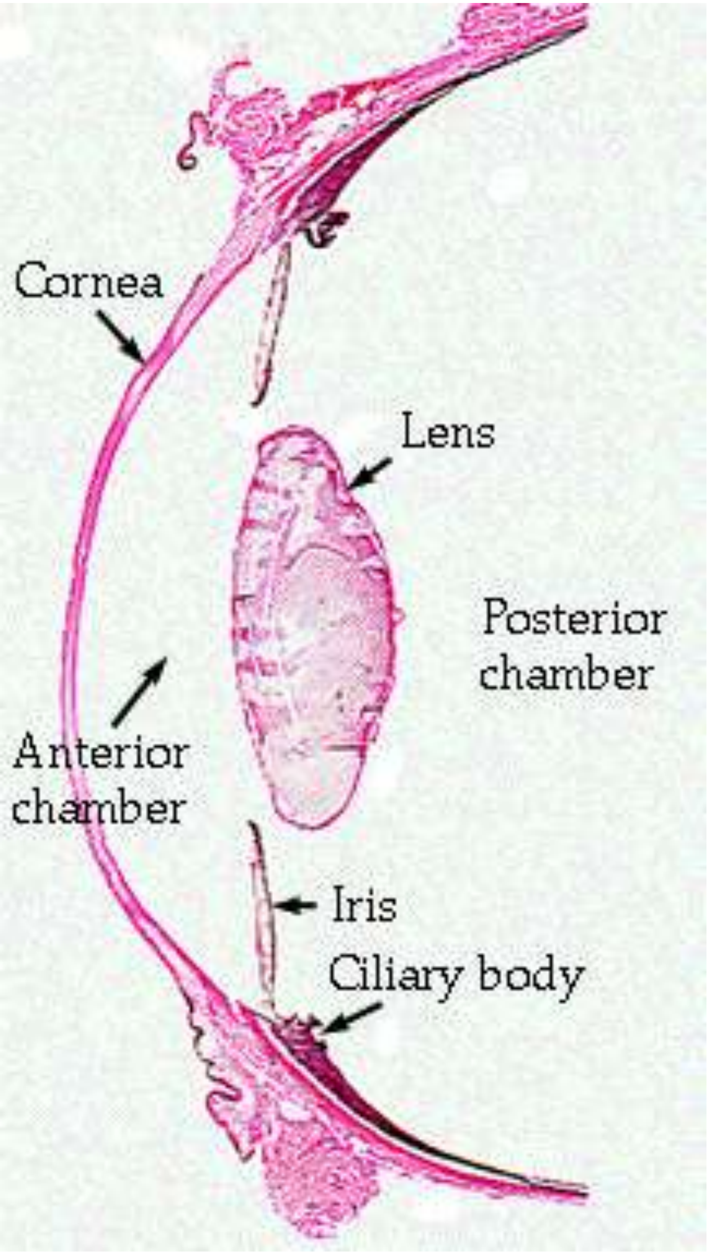
The Human Eye




Choroid
Sclera
Retina
Iris
Posterior chamber
Anterior chamber
Lens
Cornea
Ciliary body
Optic nerve

The cornea does most of the refraction (bending) of the light that strikes the eye

The lens provides some adjustment to the refraction so that we can focus on things that are close or far away

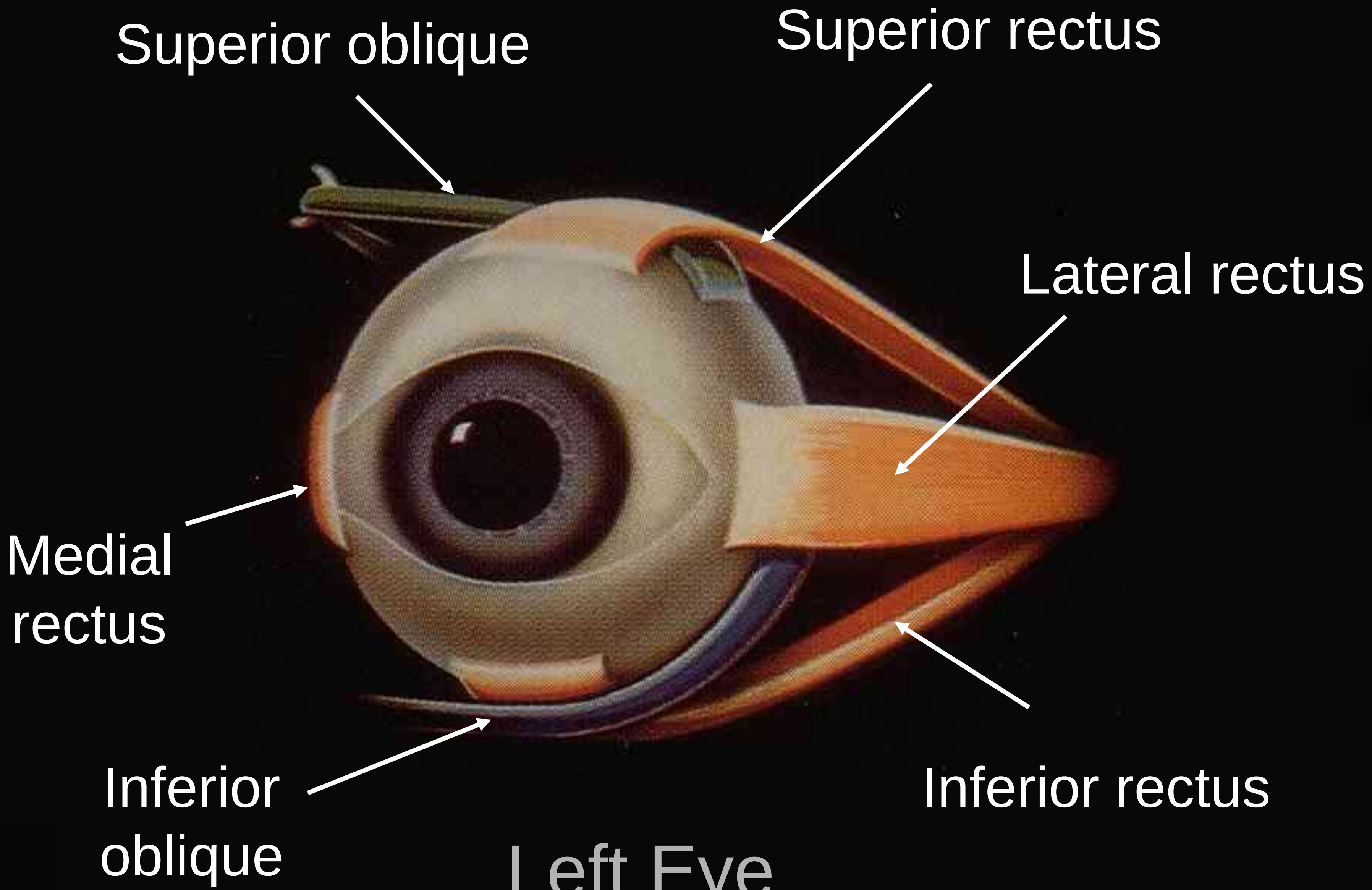


MRI Scan of Eyes

Lens

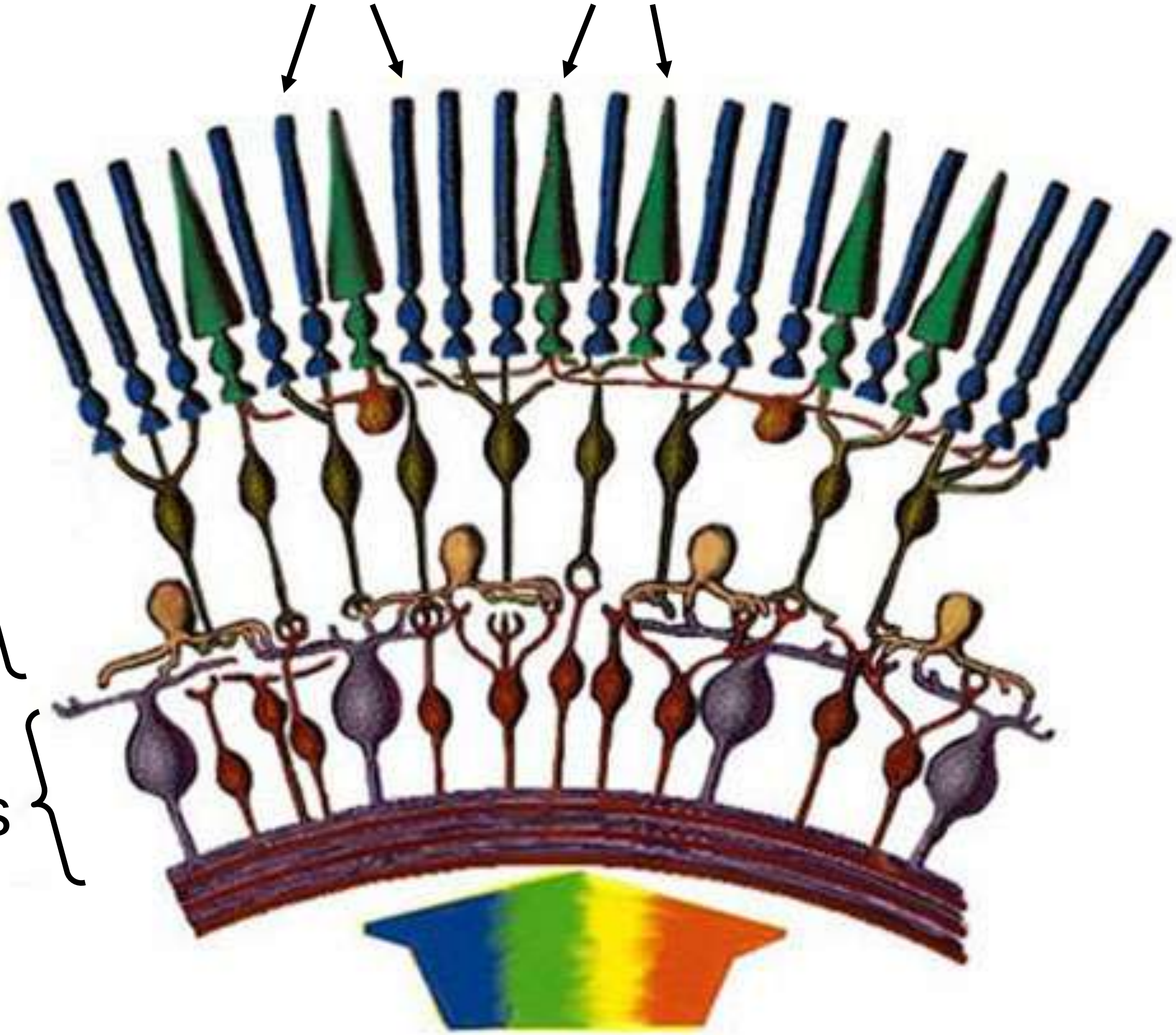
Brain

Extra-ocular Muscles


Superior oblique
Superior rectus
Lateral rectus
Medial rectus
Inferior oblique
Inferior rectus

Left Eye

Retinal Layers



Rods

Cones

Receptors

Bipolar cells

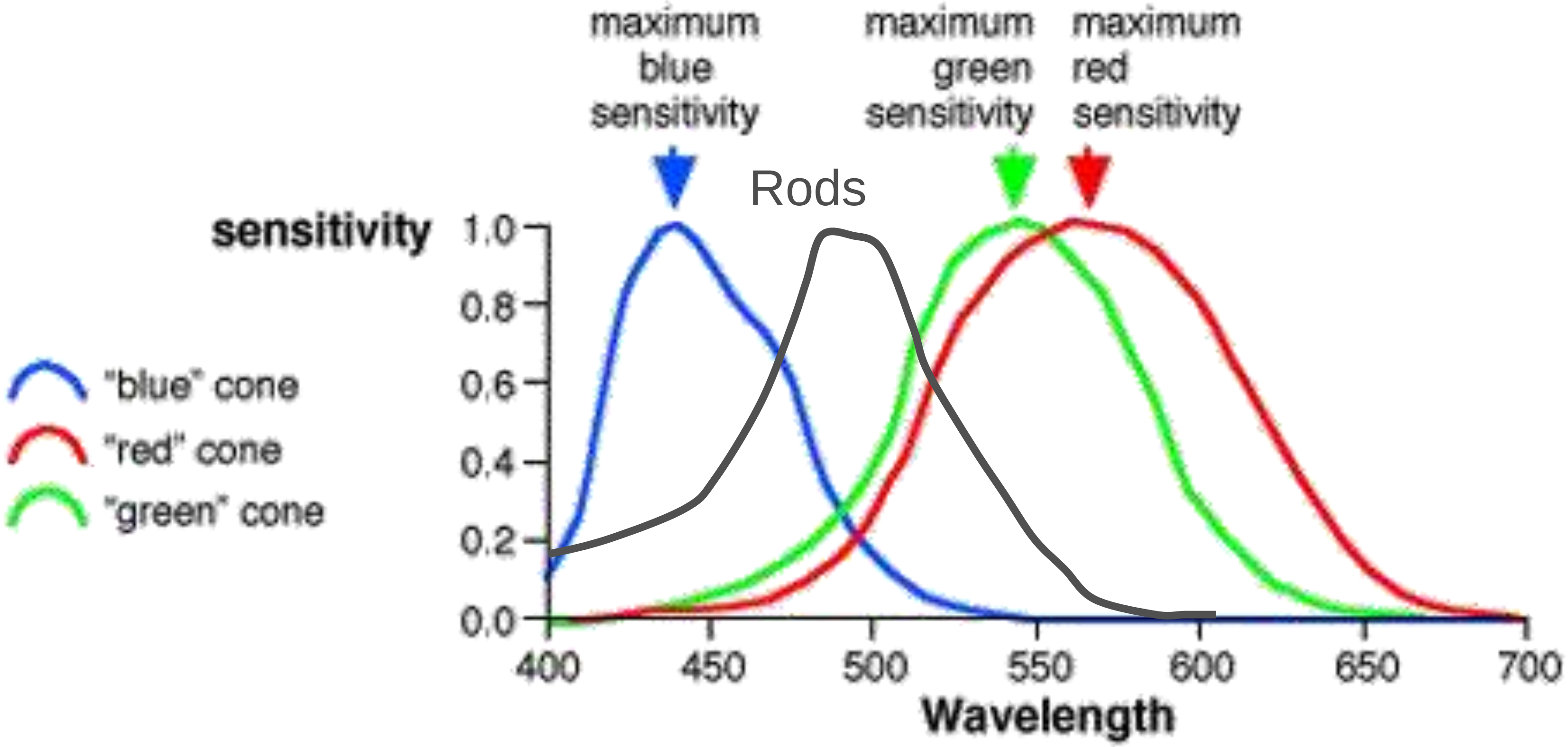
Ganglion cells

Light

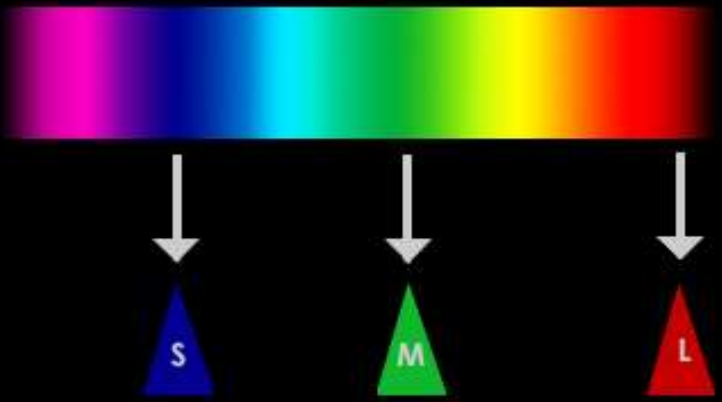
When light strikes the photochemicals in the receptor cells, a change in the membrane potential of the receptor occurs which in turn regulates the release of transmitter substance from the terminal endings of the receptor.

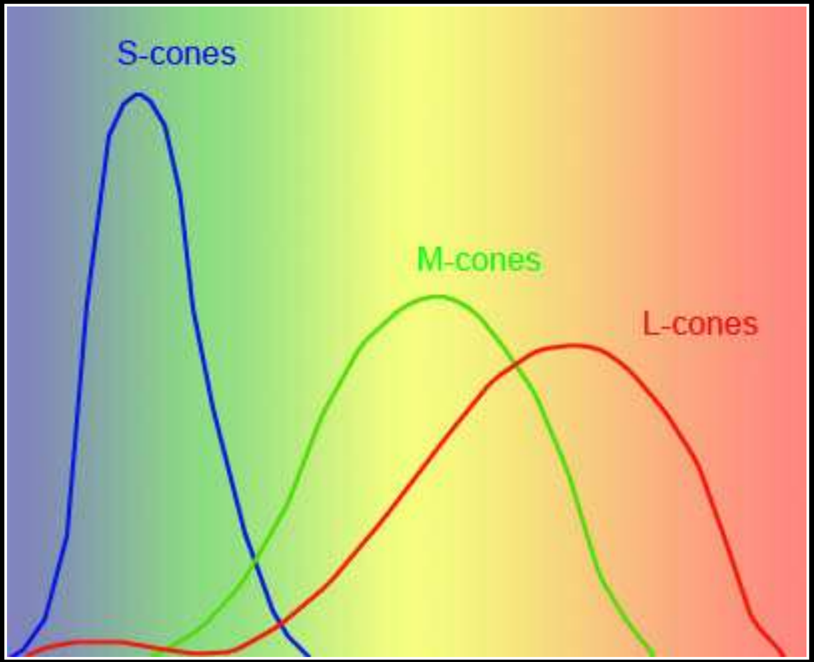
The photochemical in the rods is called rhodopsin. There are three different kinds of cones, each of which has a slightly different photochemical.

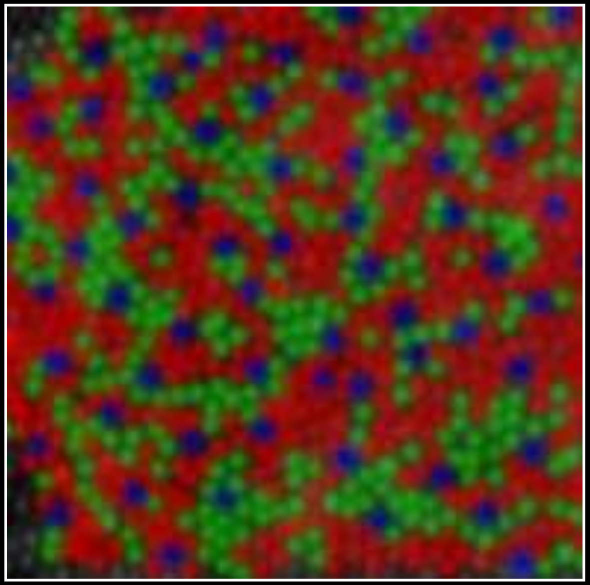
Trichromatic Spectral Sensitivity



Trichromatic Spectral Sensitivity





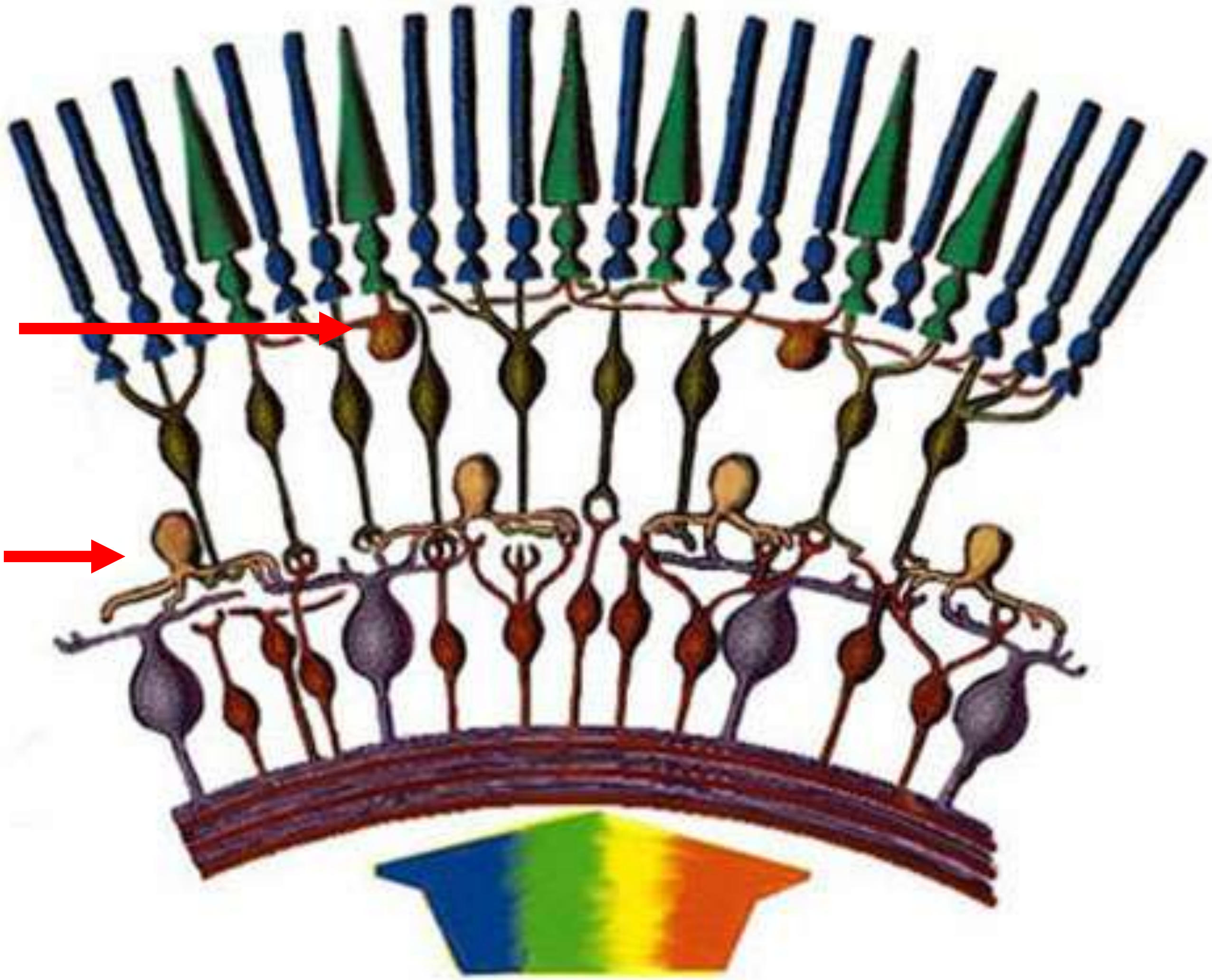


Trichromatic
cone mosaic

The rods and cones hyperpolarize to light but do not generate action potentials.

Some bipolar cells hyperpolarize to light; others depolarize -- but they also do not produce action potentials.

Ganglions cells do produce action potentials: some fire to light onset; others fire to light offset.



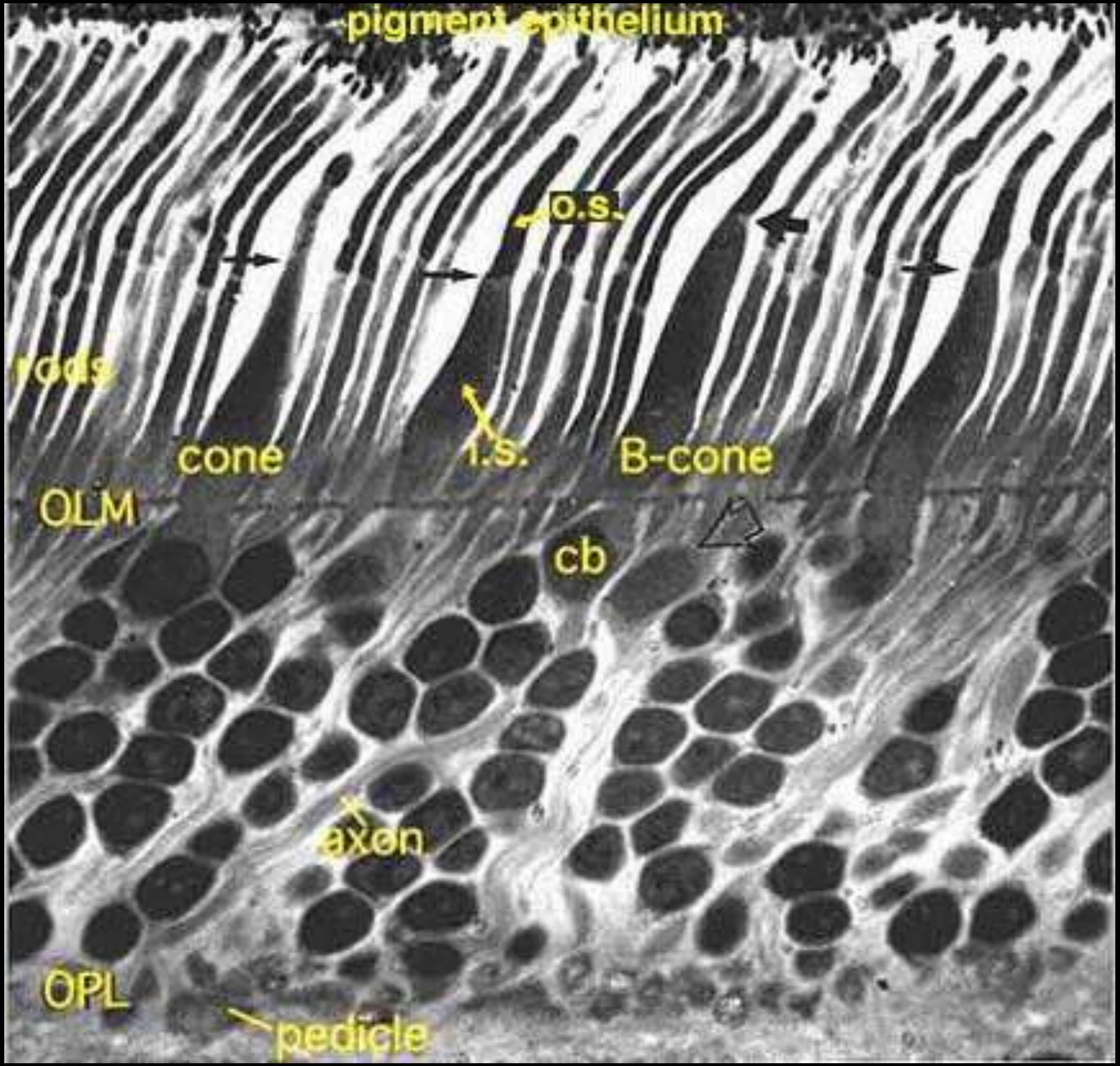
Horizontal cells

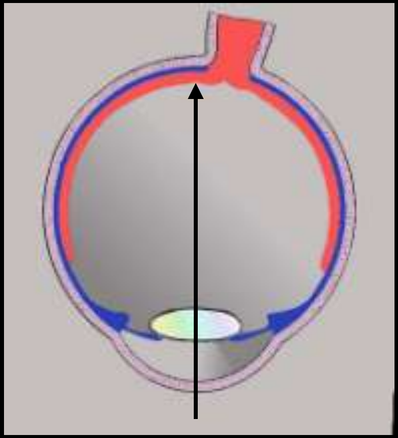
Amacrine cells

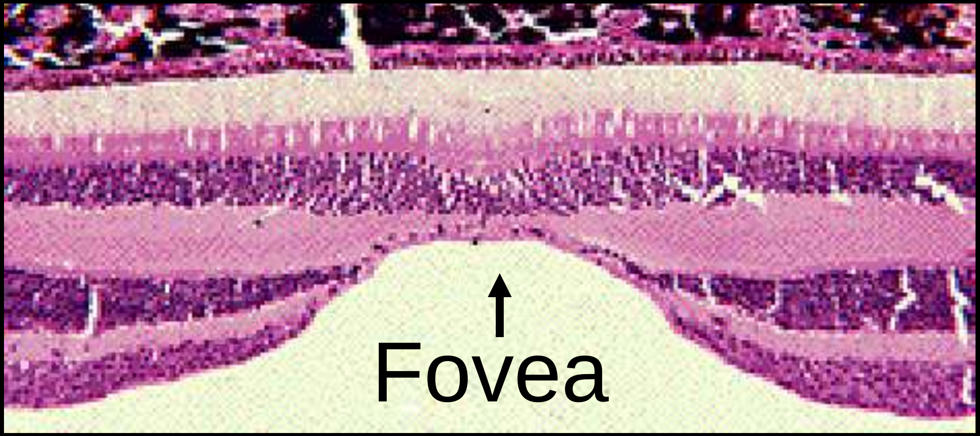
Horizontal cells help neighbouring receptor cells to communicate and participate in the creation of a ganglion cell’s receptive field.

The amacrine cells modulate the communication between bipolar cells and ganglion cells.

Semi-thin section through human retina

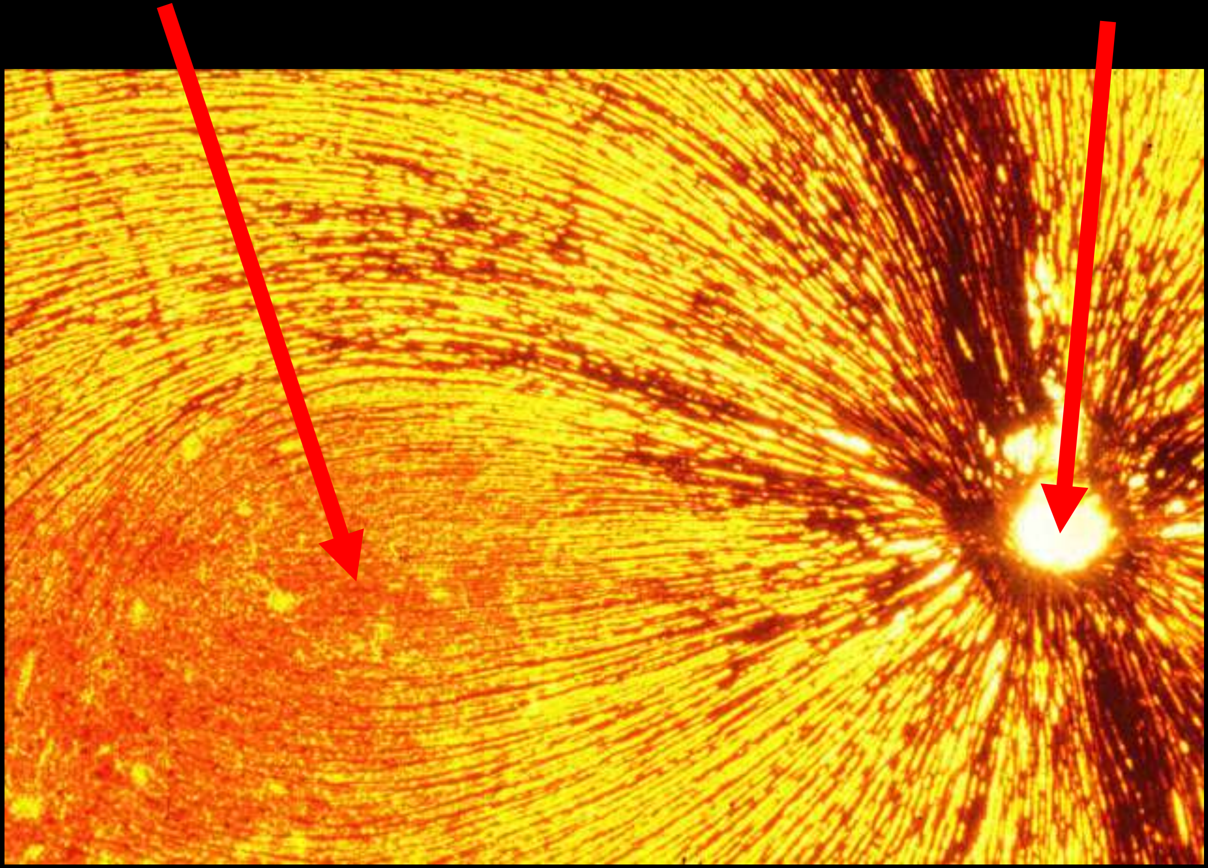






The fovea, which is directly behind the pupil, is the most sensitive part of the retina.

There are no ganglion cells or bipolar cells in front of the photoreceptors to block the light.

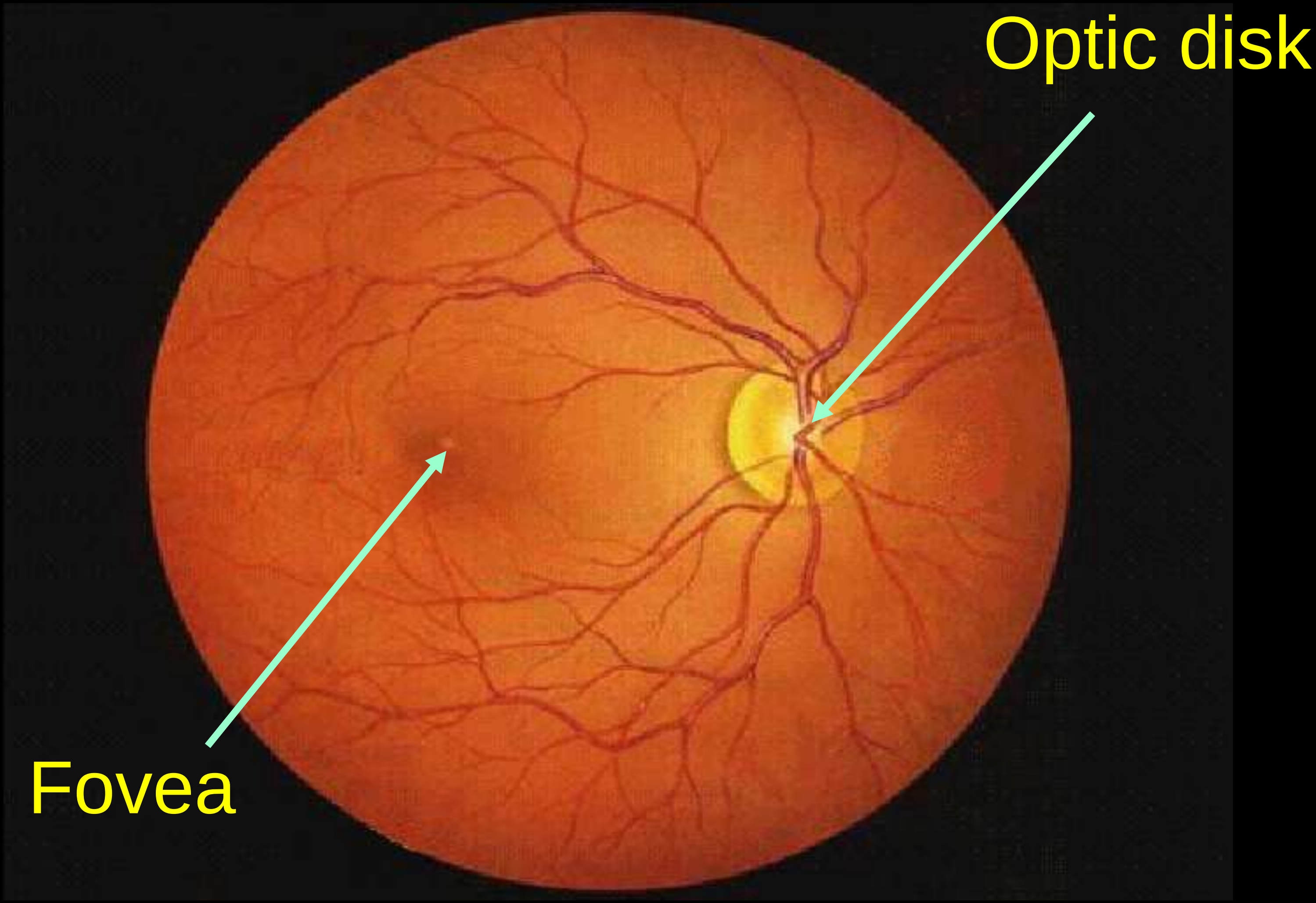


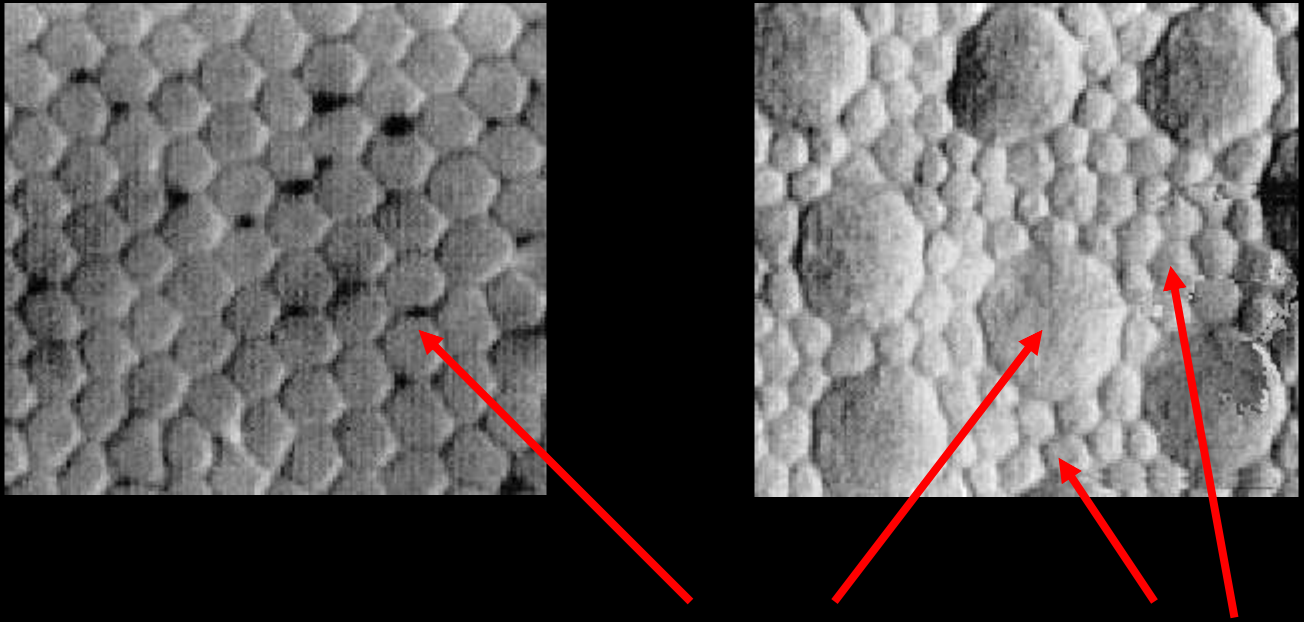
Fovea

Optic nerve

Notice how the axons of the ganglion cells avoid crossing in front of the fovea

Blood Vessels in Retina





Fovea

Periphery

Cones

Rods

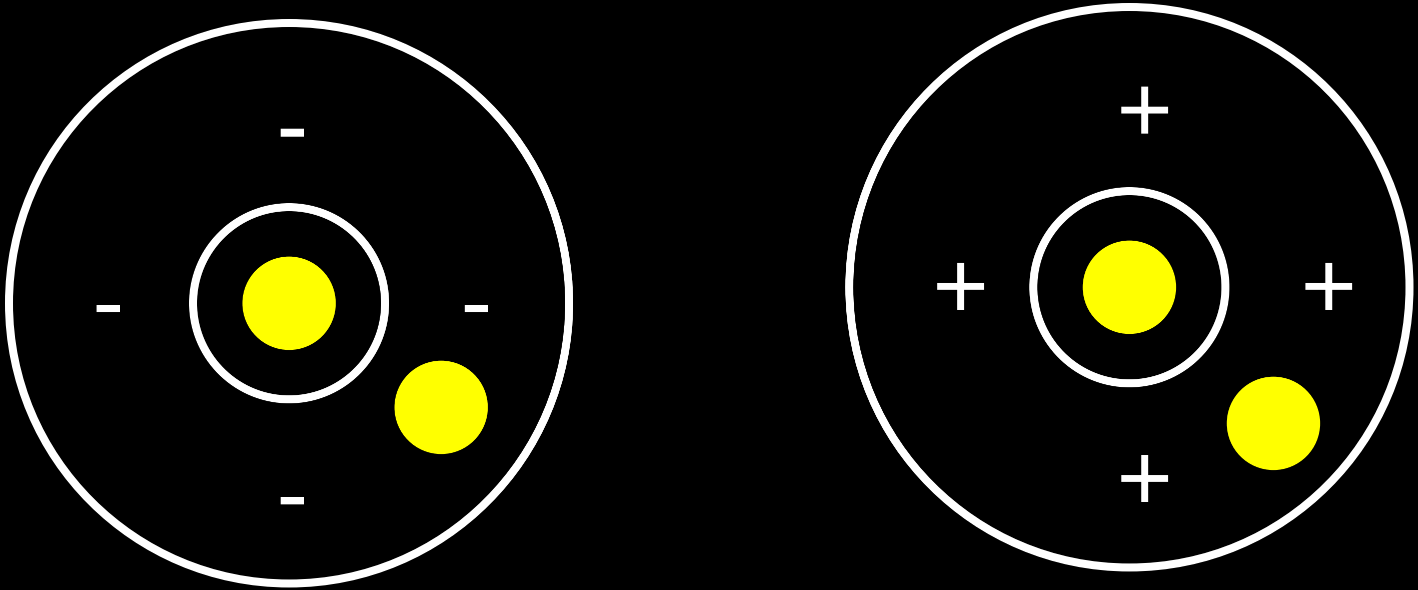
In the fovea, there are only cones (small ones) that are packed in a hexagonal pattern. In the periphery, there are large cones and lots of rods.

Recording from Ganglion Cells

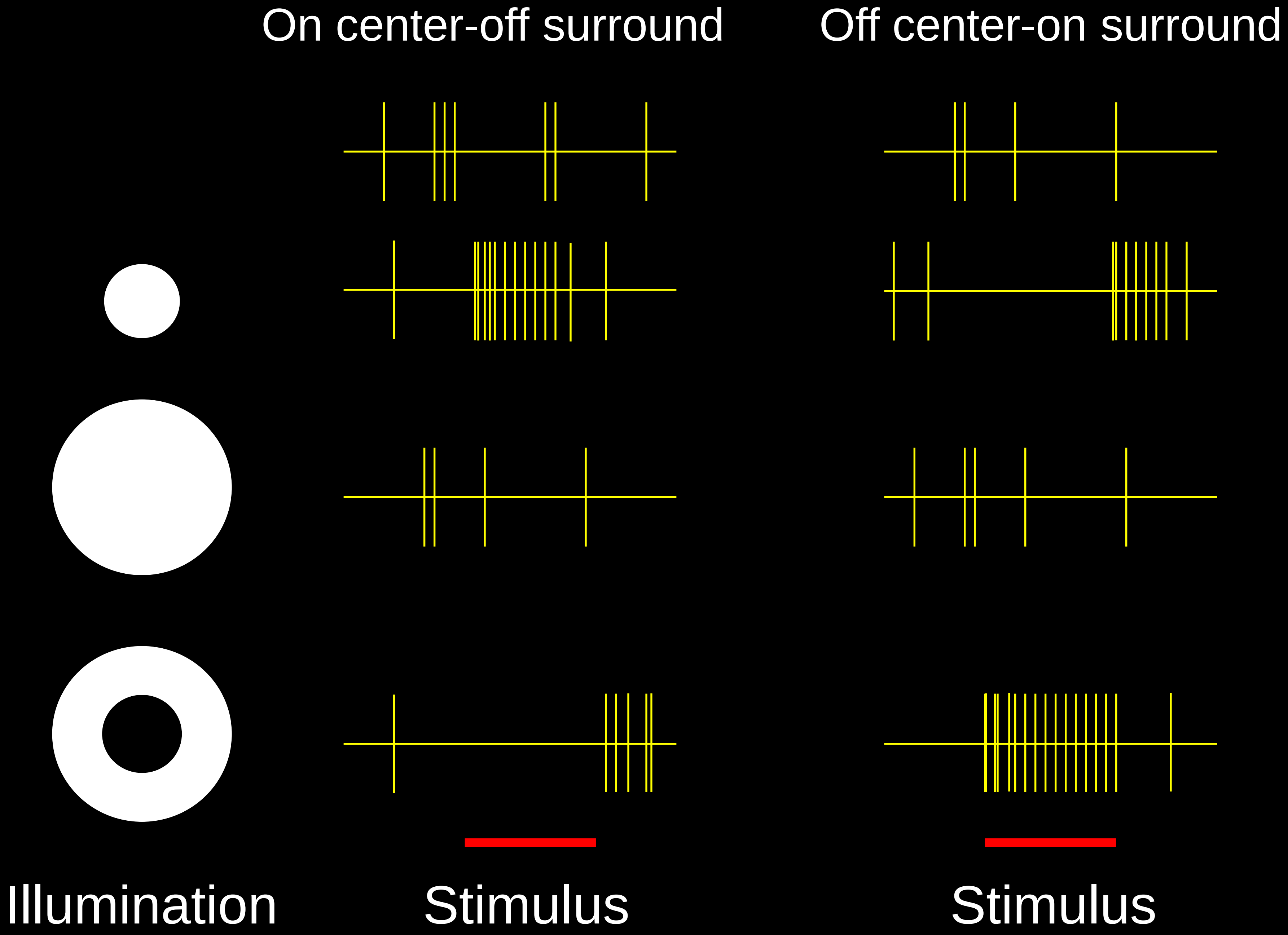
They do not respond well to illumination across whole retina

They respond best when light is presented to a small part of the visual field, each cell responding to a specific locus in the visual field.

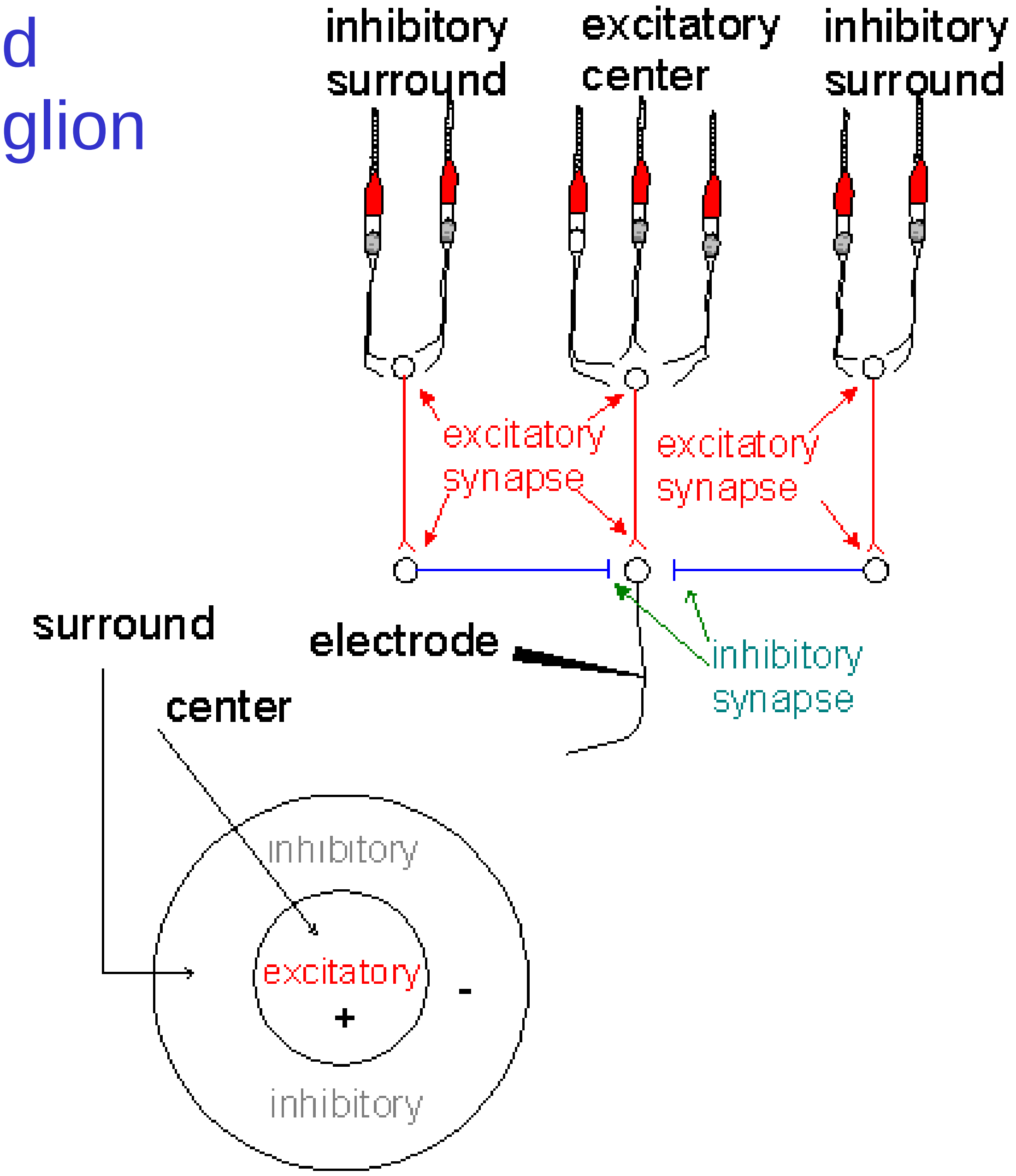
These receptive fields have a circular organization, with a center and a surrounding annulus.

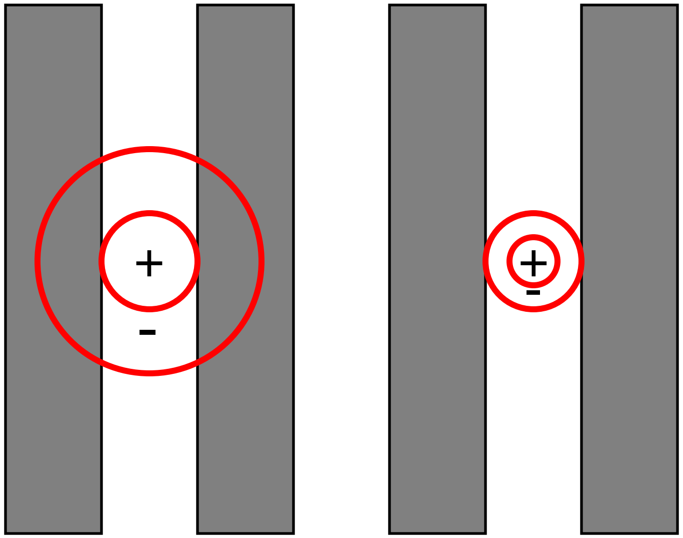


Structure of Receptive Fields

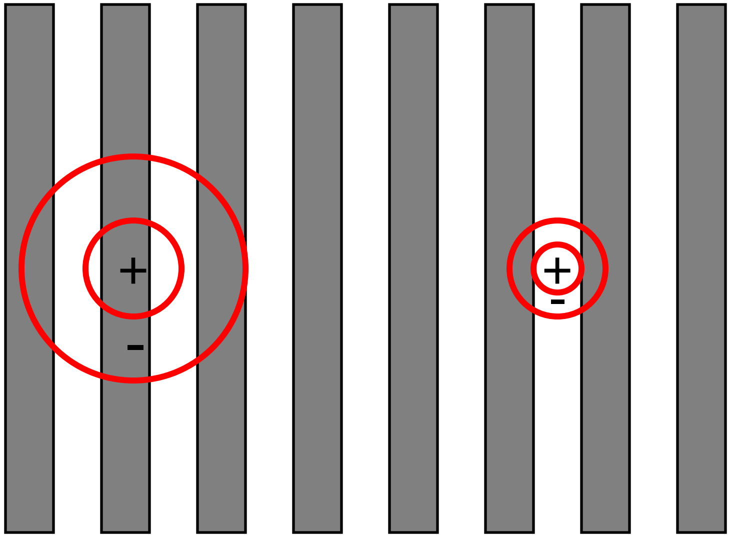

On center-off surround
Off center-on surround
Illumination
Stimulus
Stimulus

The center-surround organization of ganglion receptive fields depends on lateral inhibition by neighbouring cells.

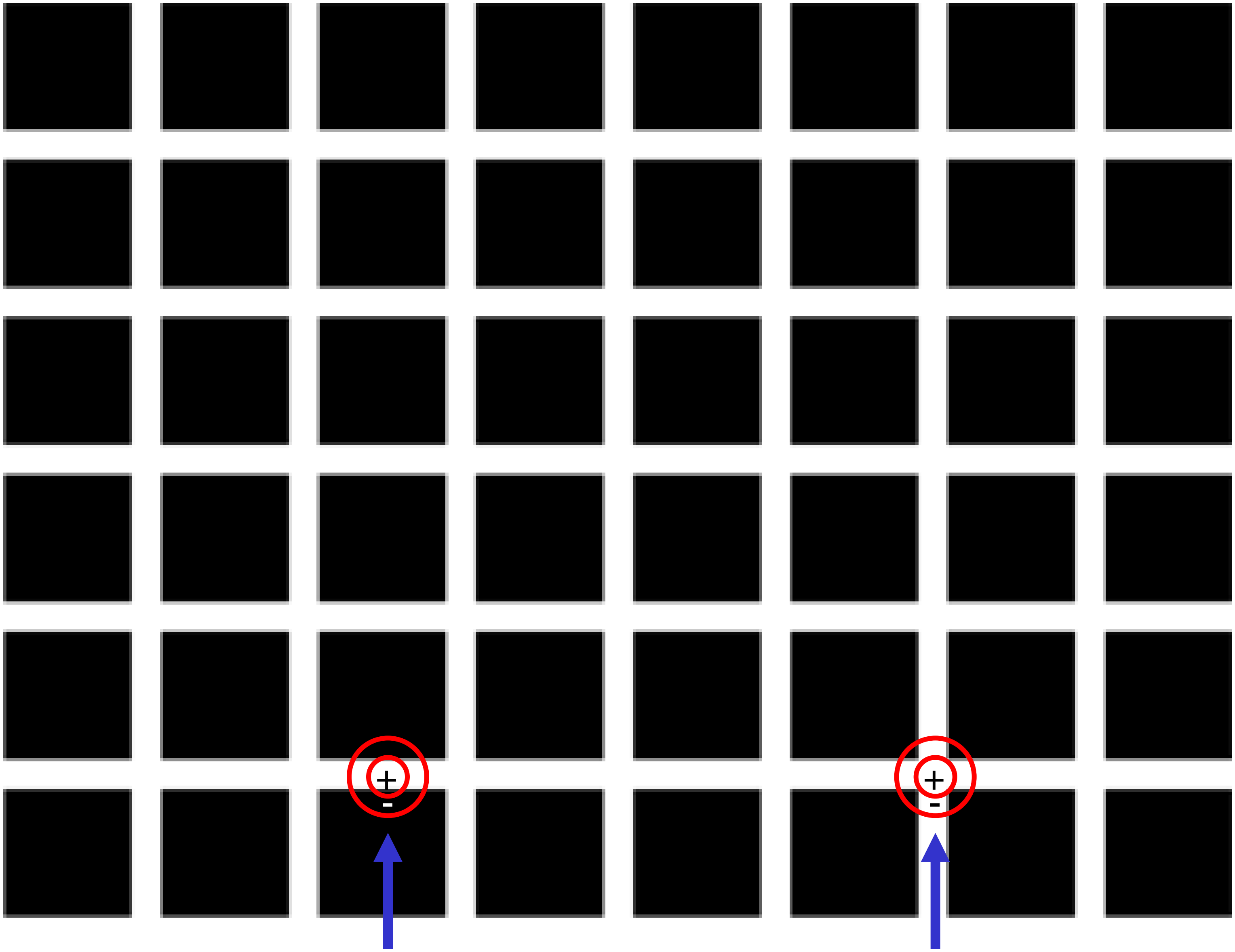




Cell with large receptive field fires more than cell with small receptive field



Cell with small receptive field fires more than cell with large receptive field

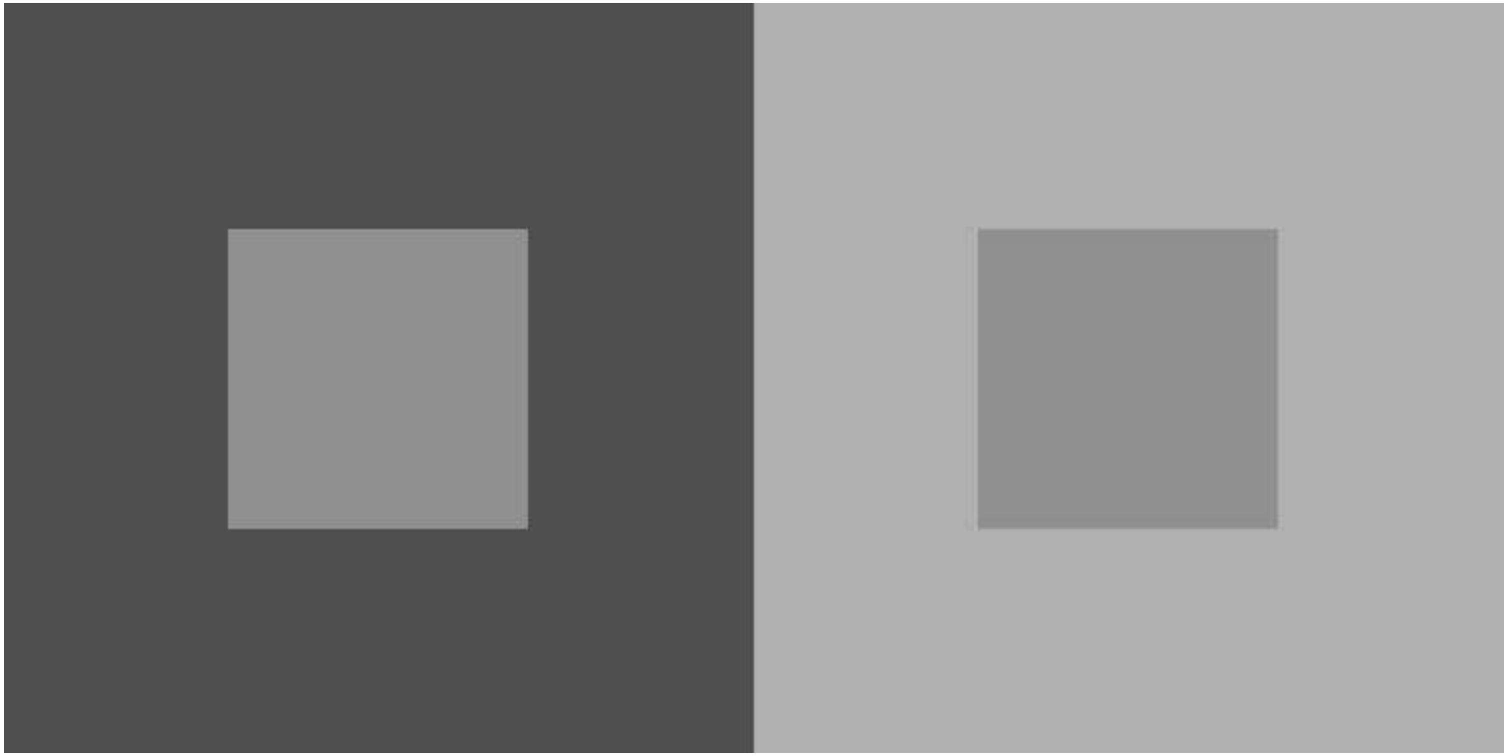


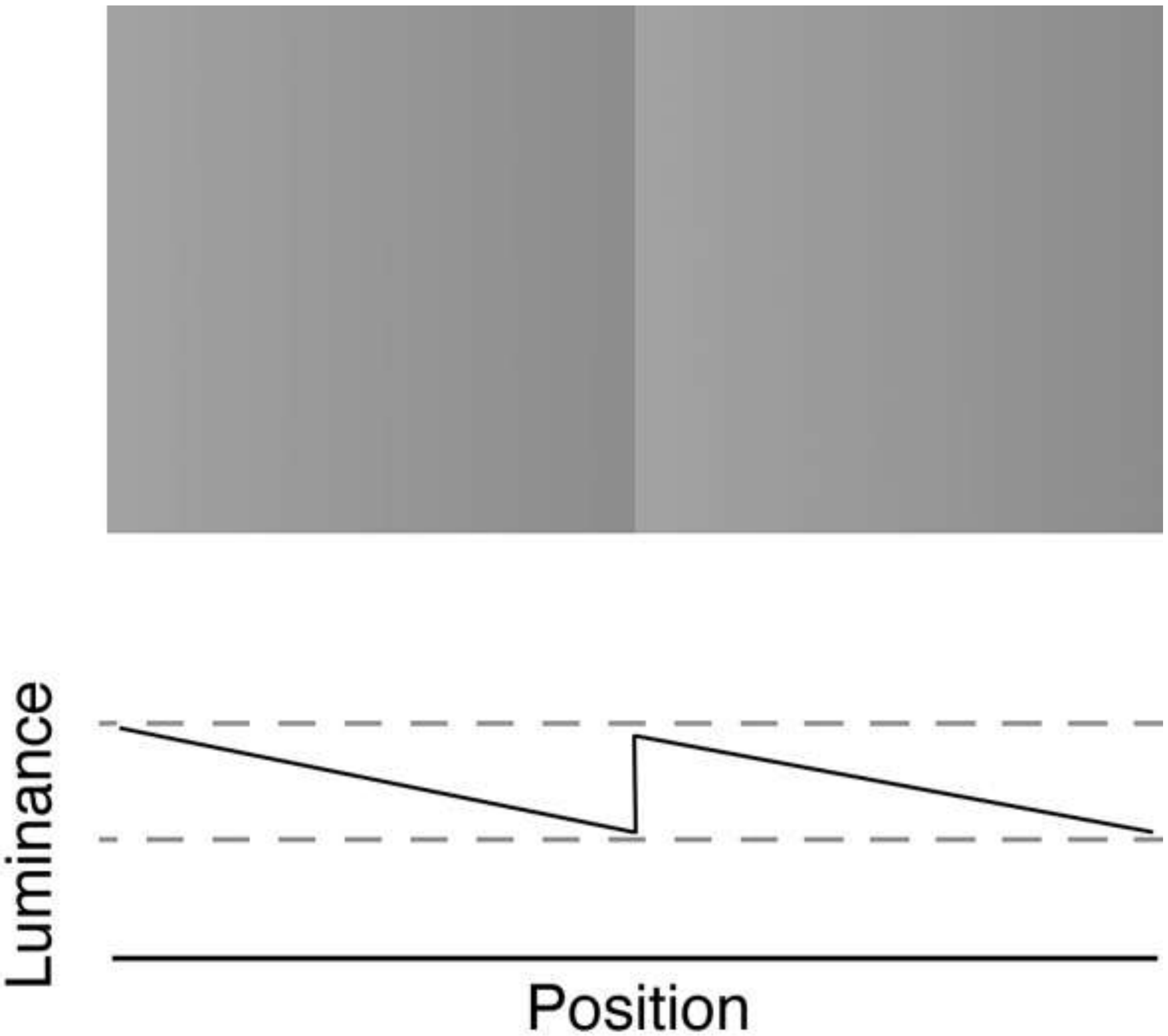
Cell A

Cell B

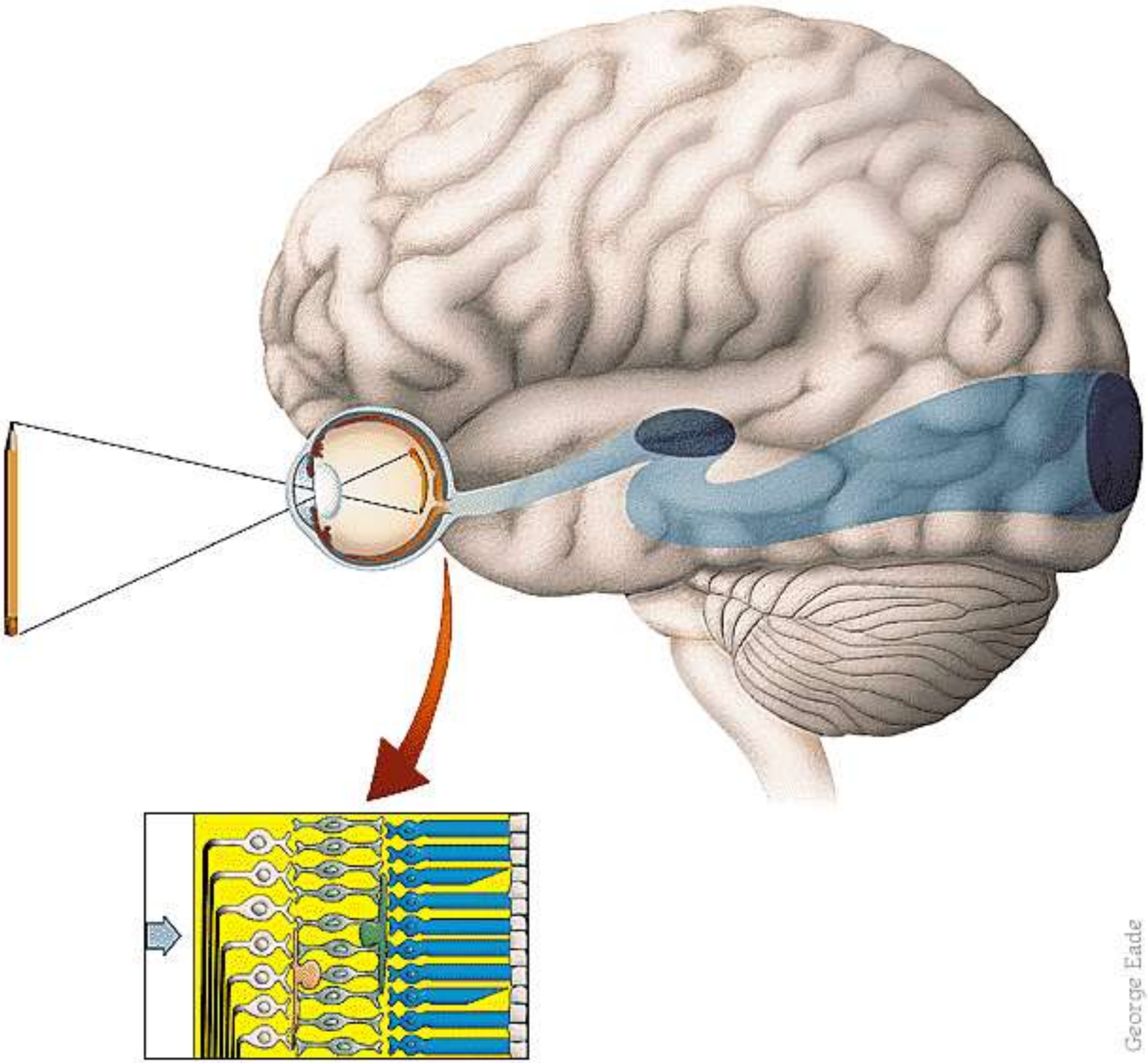
Cell A is stimulated more optimally than Cell B

Visual system in general is sensitive to contrast between light intensities, not absolute light intensity.

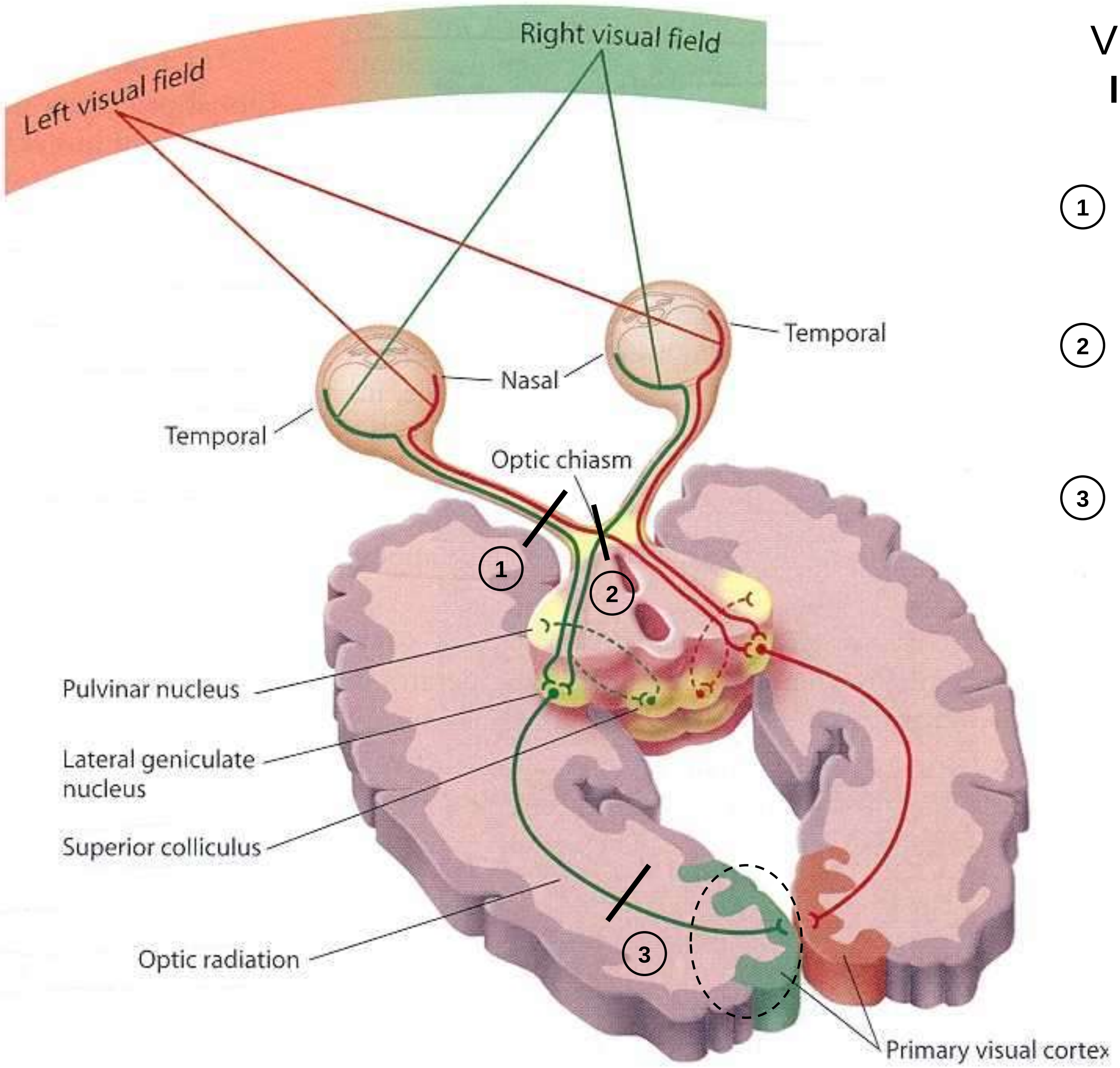



Luminance
Position

Visual Projections to Cortex

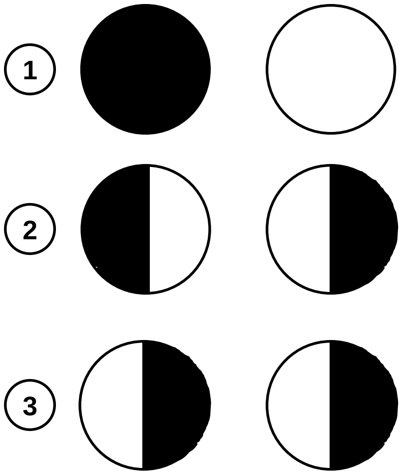


George Eade



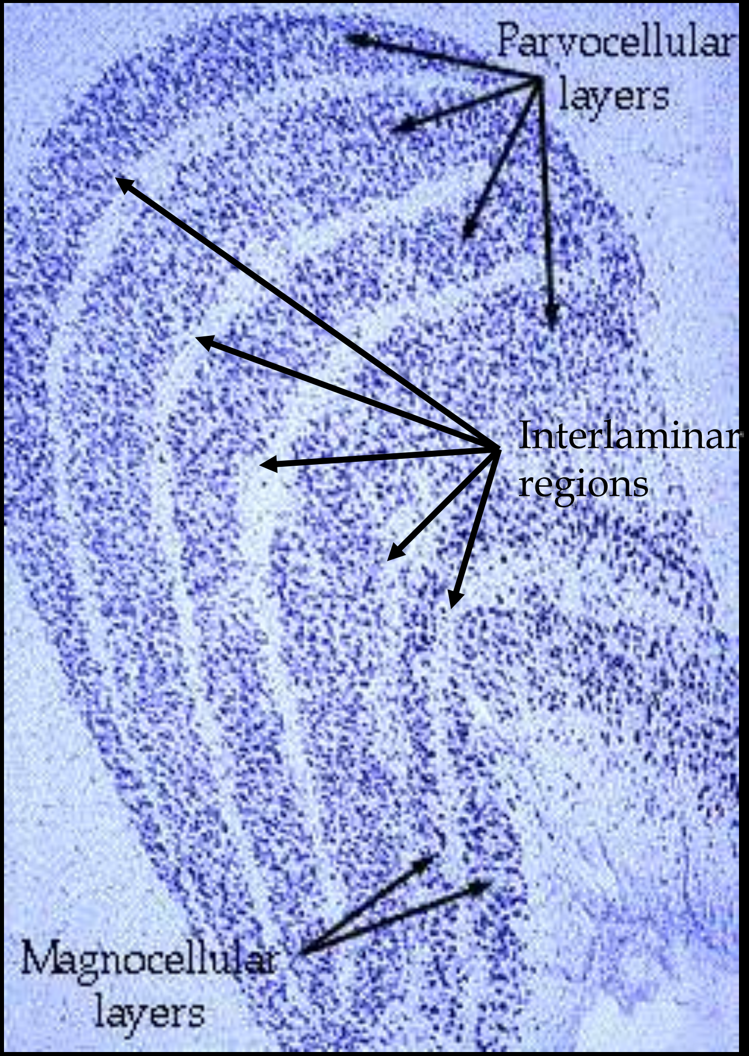
Visual field defects

left eye **right eye**



The LGNd has six layers each of which gets independent input from either the left or the right eye but not both.

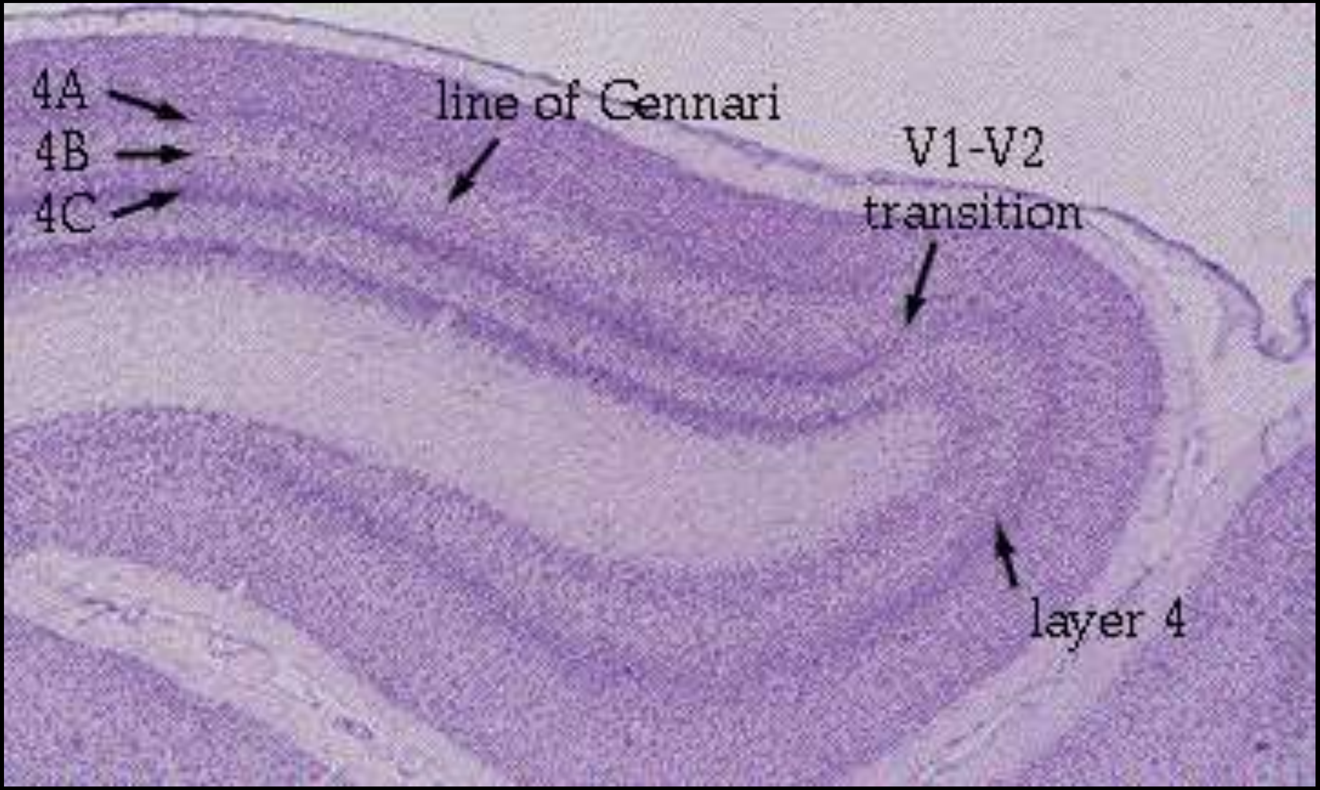
There are two major classes of projections, parvocellular (small) and magnocellular (large) projections.



Lateral Geniculate Nucleus

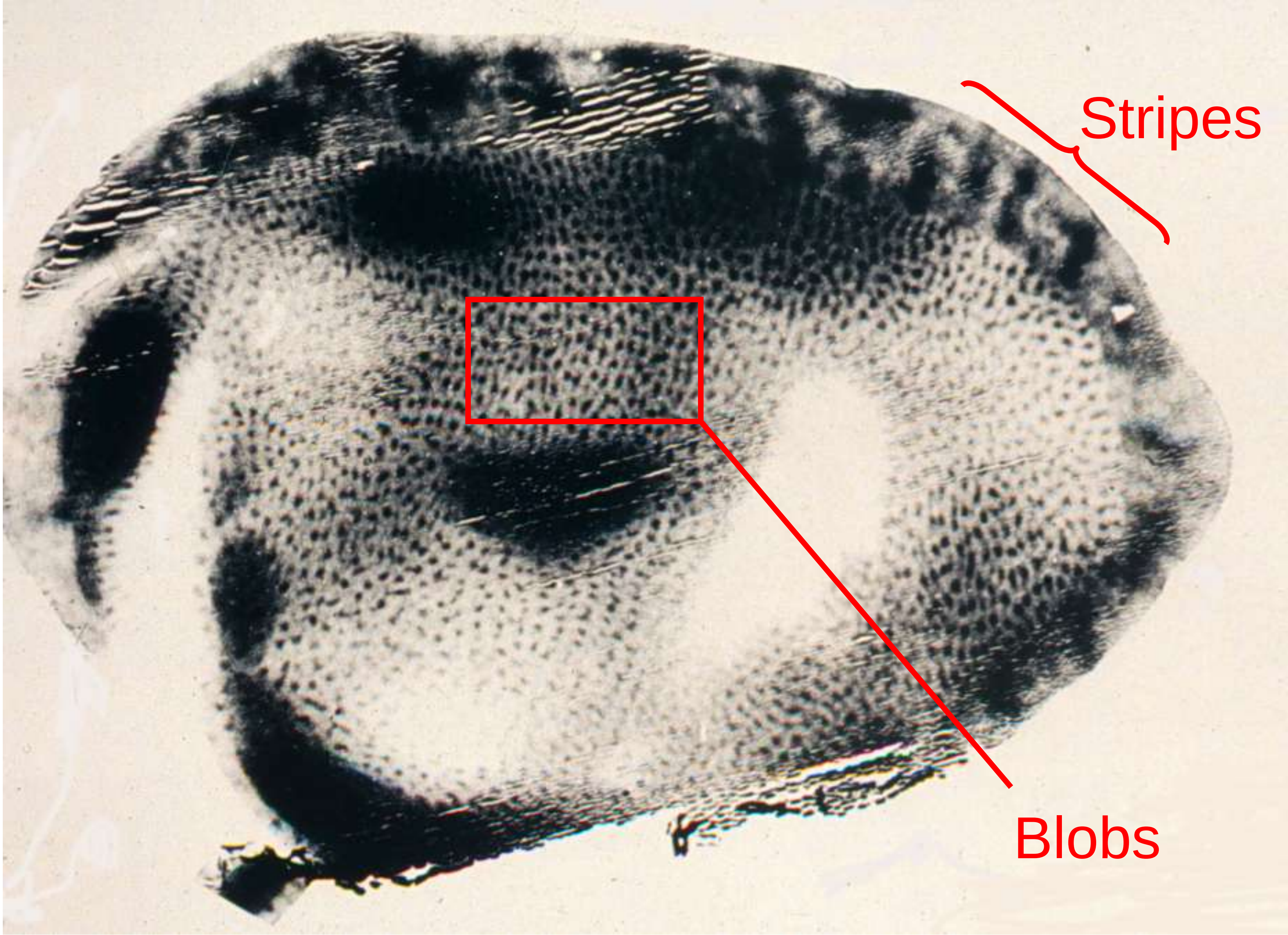
Magnocellular	Parvocellular
Large ganglion cells	Small ganglion cells
Centre/Surround	Centre/Surround
Colour insensitive	Colour sensitive
Large RFs	Small RFs
Fast, transient	Slow, sustained
More sensitive at low contrast	More sensitive at high contrast

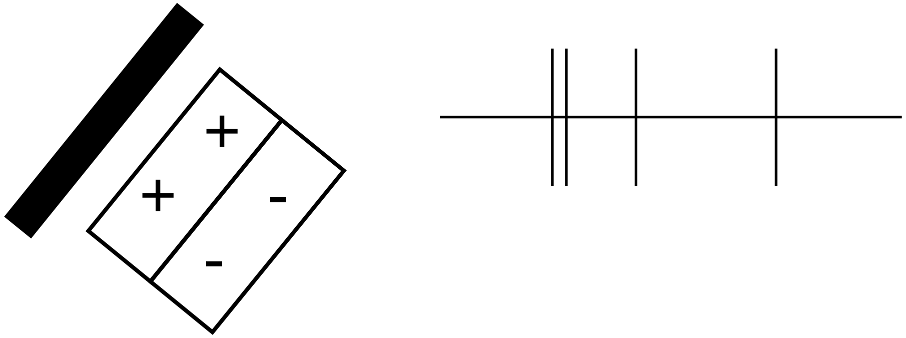
Primary Visual Cortex

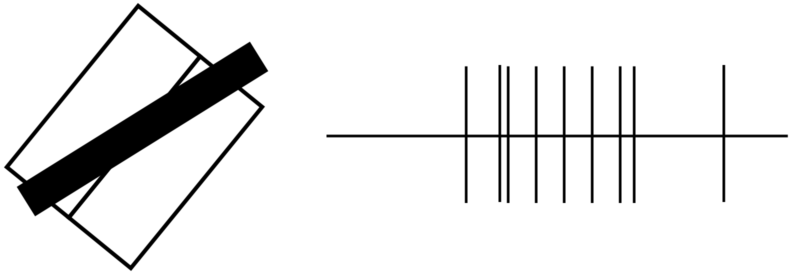


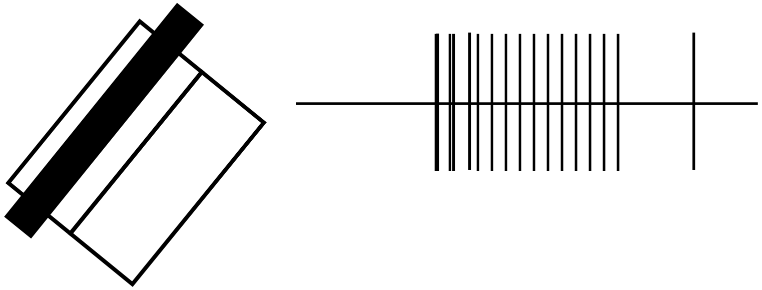
The LGNd projects to primary visual cortex (striate cortex or area V1) in the occipital lobe.

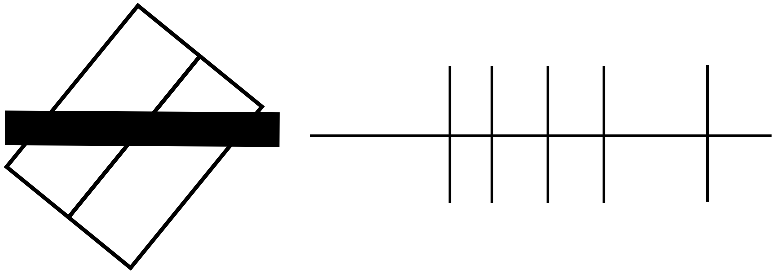
The magno and parvo projections are still somewhat segregated in V1.

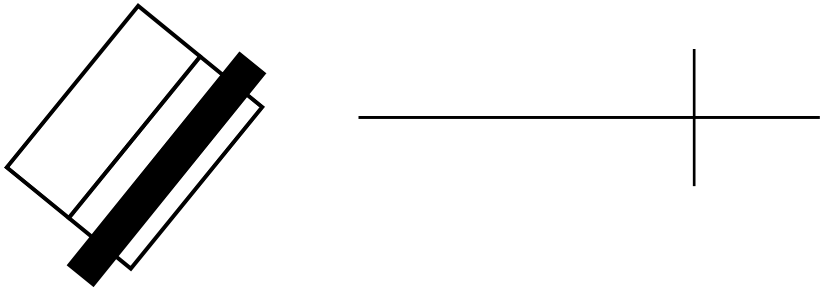

Stripes
Blobs

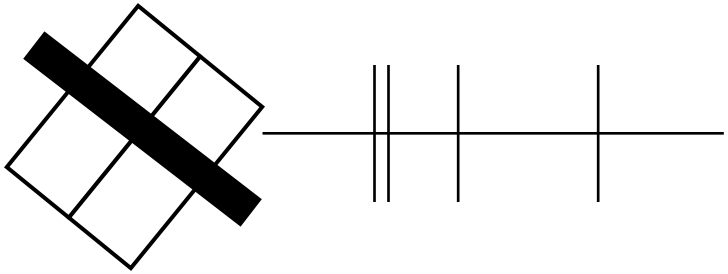


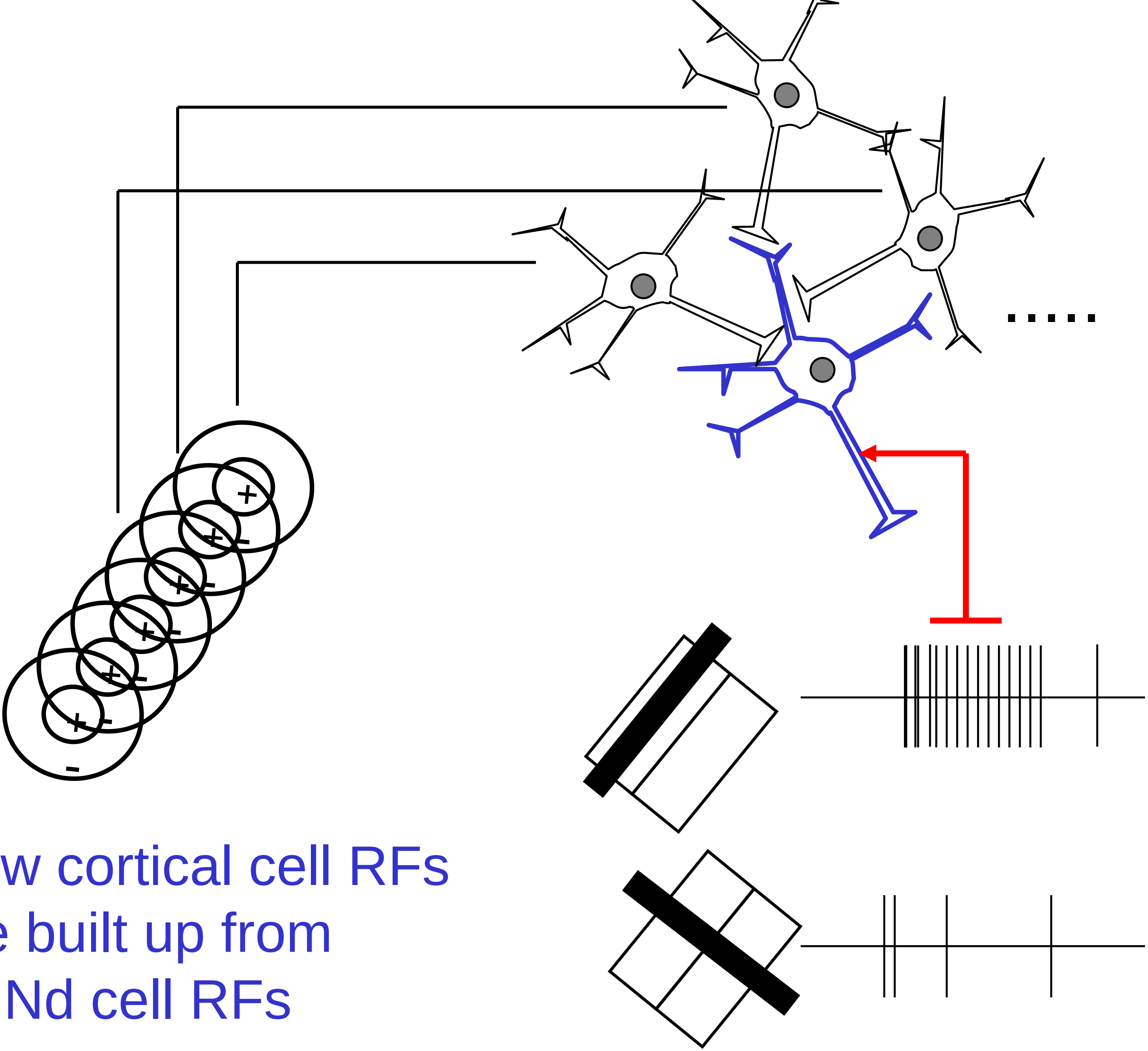








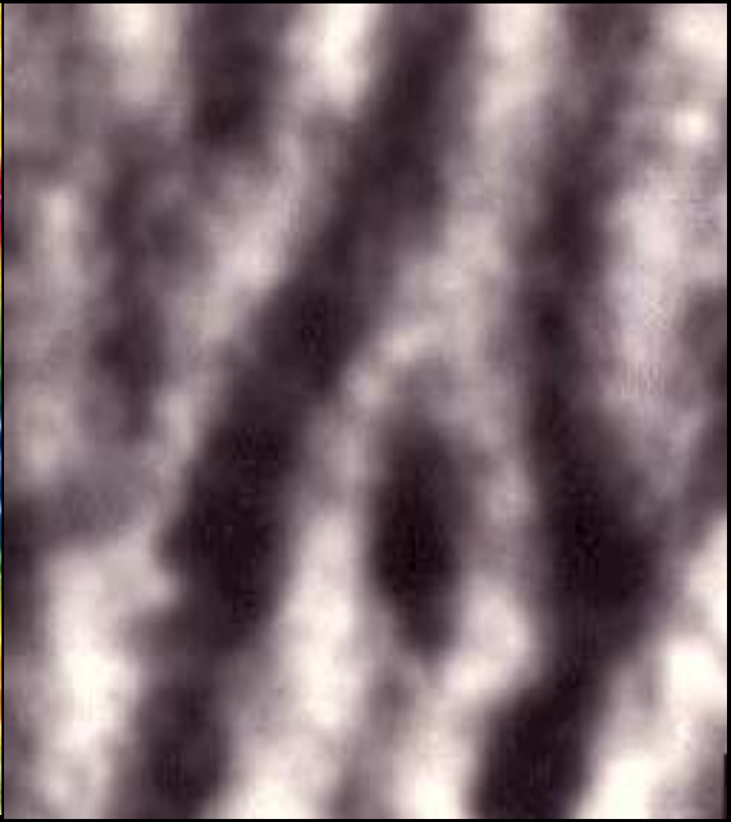




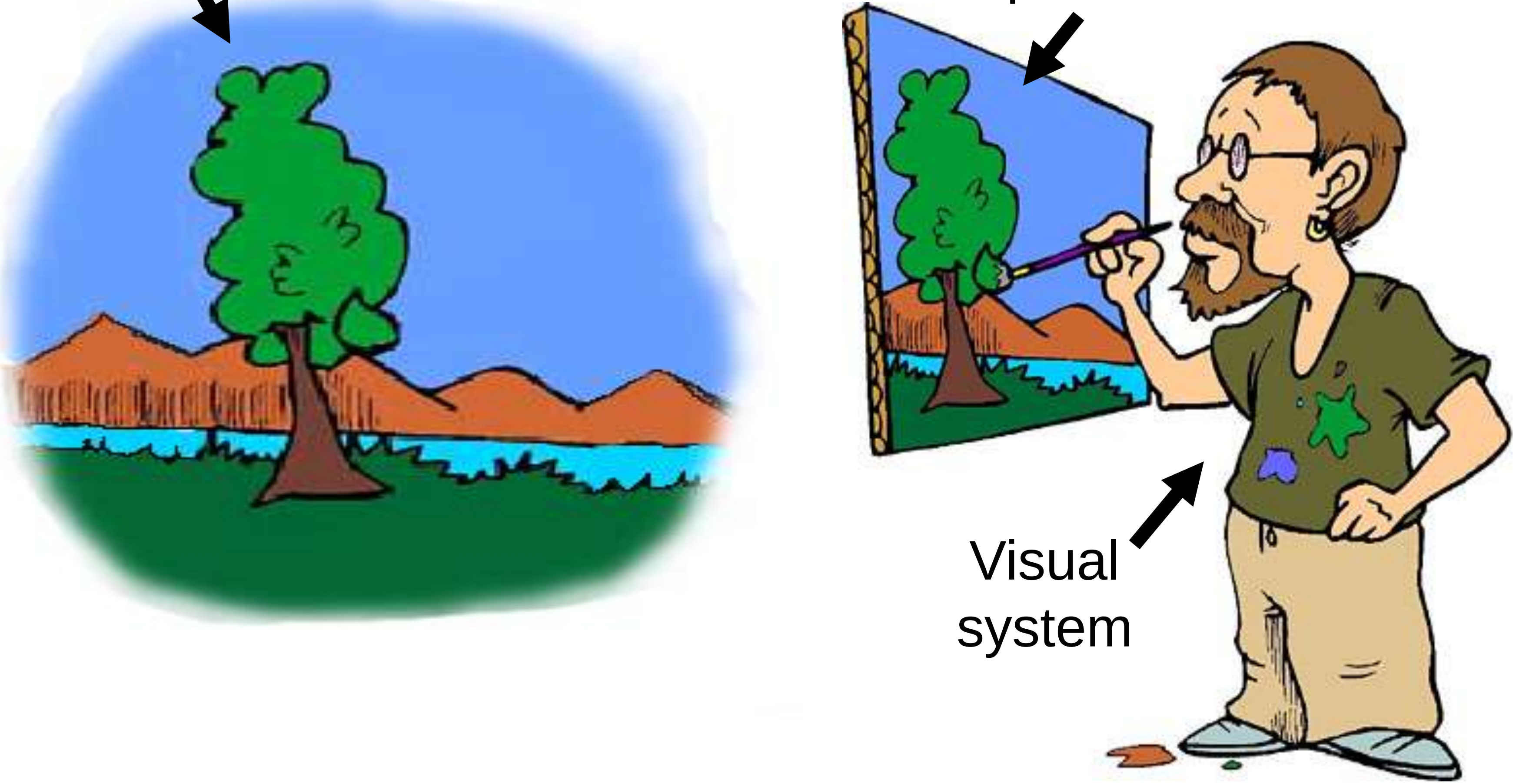
How cortical cell RFs are built up from LGNd cell RFs

Primary visual cortex is organized into hypercolumns

Orientation and spatial frequency columns



Ocular dominance columns



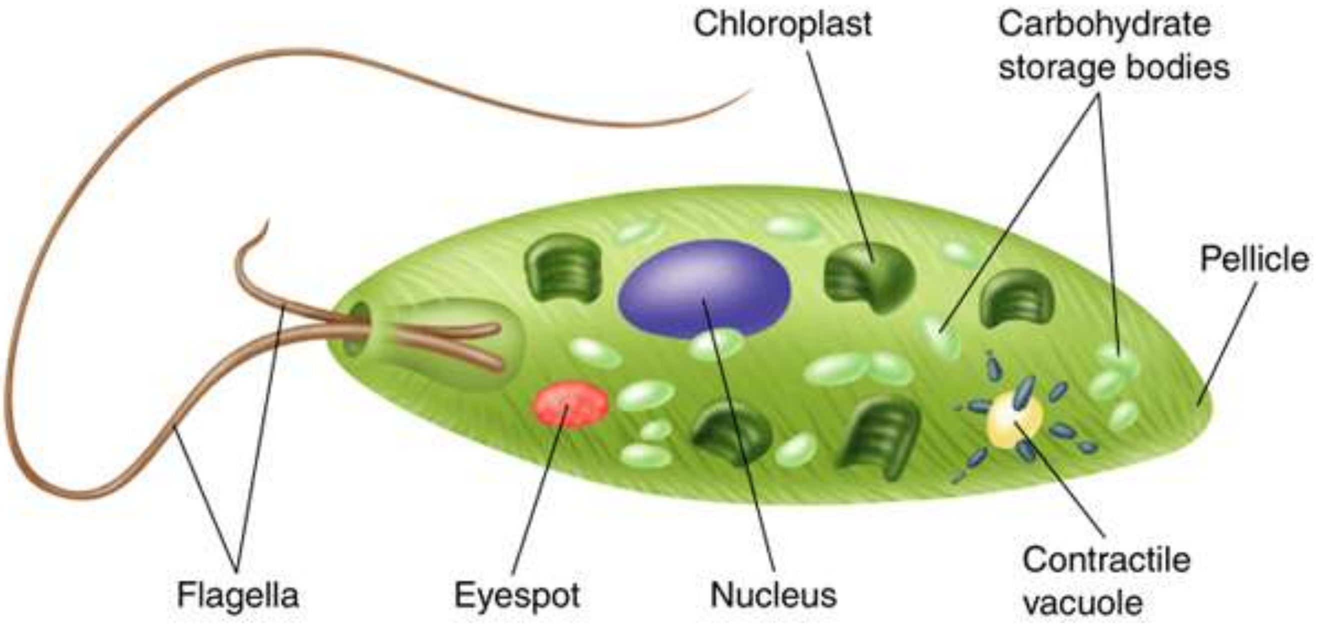
Real world

Internal representation

Visual system

A metaphor for vision?

Euglena


Chloroplast
Carbohydrate storage bodies
Pellicle
Flagella
Eyespot
Nucleus
Contractile vacuole

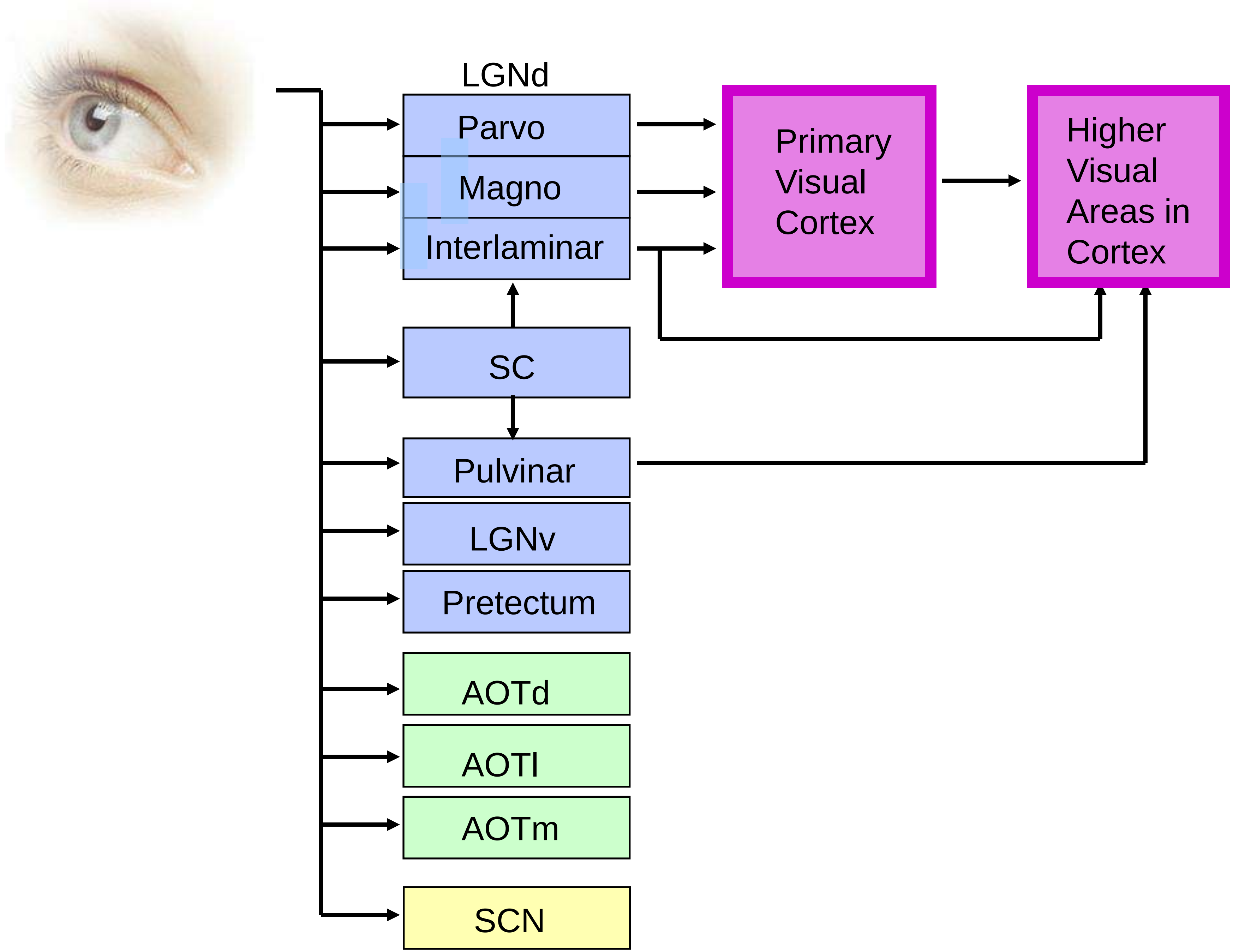
Goodale, M.A. & Milner, A.D. (1992).
Trends in Neurosciences 15: 20-25.

For most of us (including many philosophers and scientists), it seems self-evident the actions we perform on visible objects make use of the same visual representation that allows us to perceive those objects.

This incorrect assumption is sometimes called the:

Assumption of Experience-based Control

Andy Clark (2002). Is seeing all it seems? Action, reason and the grand illusion. *Journal of Consciousness Studies* 9: 181-202.



LGNd

Parvo

Magno

Interlaminar

Primary Visual Cortex

Higher Visual Areas in Cortex

SC

Pulvinar

LGNv

Pretectum

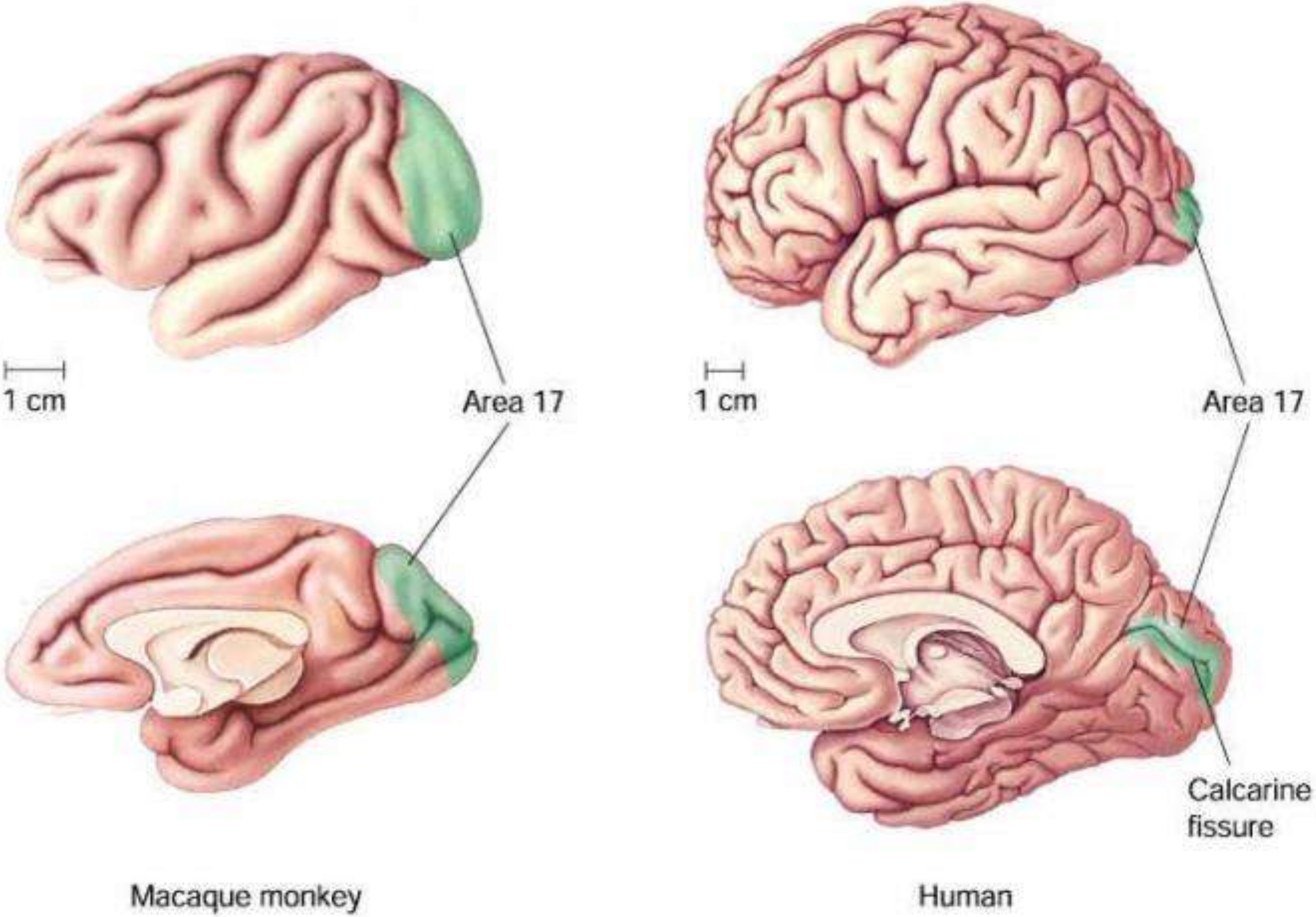
AOTd

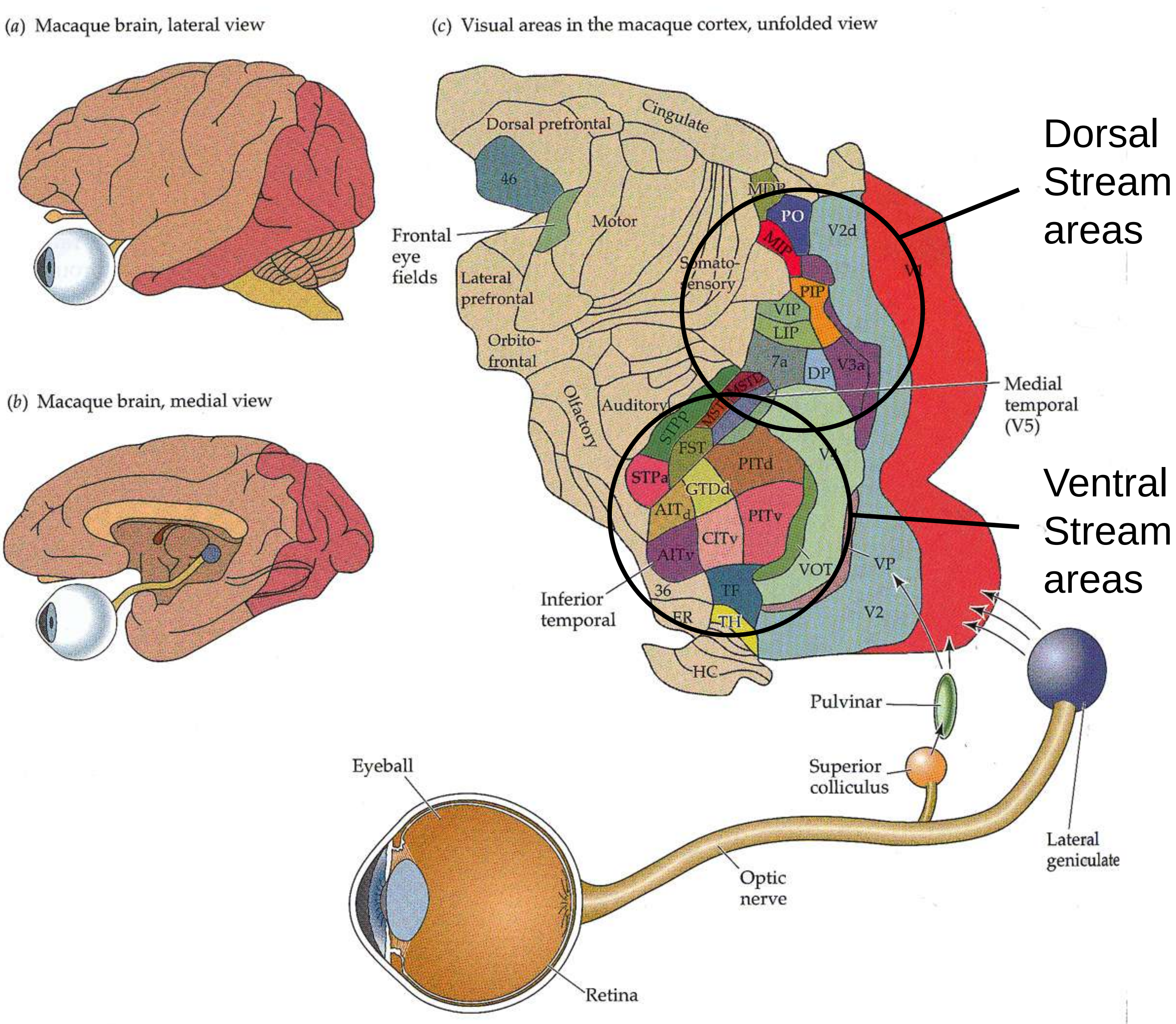
AOTl

AOTm

SCN

Two Visual Pathways in Primate Cerebral Cortex


1 cm
Area 17
1 cm
Area 17
Calcarine fissure
Macaque monkey
Human



(*a*) Macaque brain, lateral view

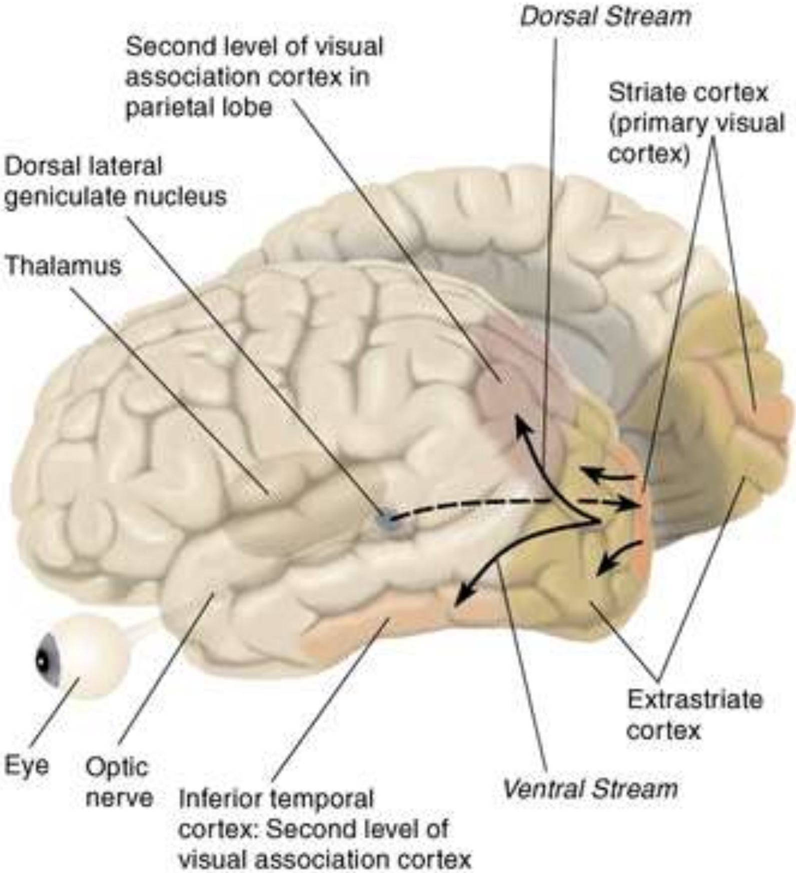
(*b*) Macaque brain, medial view

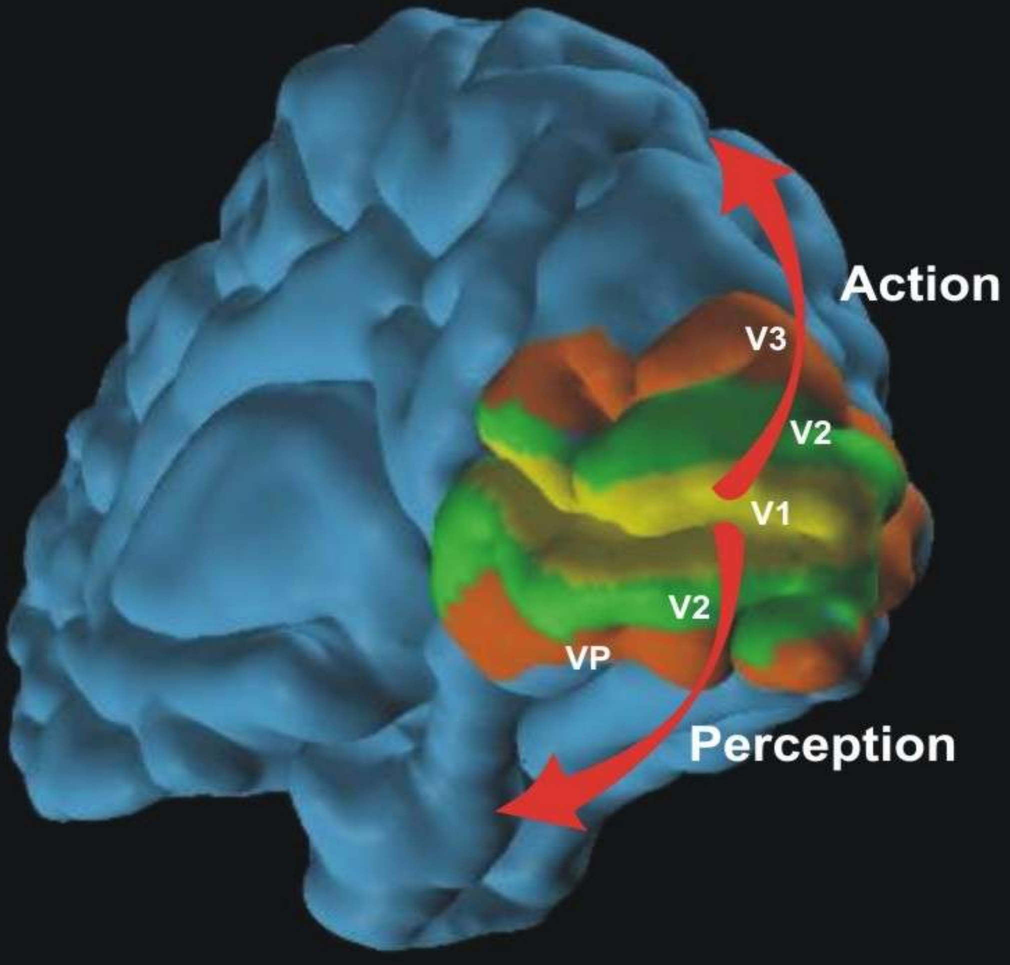
(*c*) Visual areas in the macaque cortex, unfolded view

Dorsal Stream areas

Ventral Stream areas

▸ The Human Visual System





Goodale, M.A. & Milner, A.D. (1992).
Trends in Neurosciences 15: 20-25.

Vision for Perception	Vision for Action
Ventral Stream	Dorsal Stream
Inferotemporal Cortex	Posterior Parietal Cortex
Object-based	Viewer-based
Object identification	Movements
‘Conscious’	‘Automatic’

Goodale, M.A. & Milner, A.D. (2004).
Sight Unseen. Oxford University Press

Neuropsychological Studies

“It is not so much the injury that should capture our attention, but how, through injury or disease, normal function is laid bare.”

H Head, “*Aphasia and the Kindred Disorders of Speech*”, 1926

Damage to the dorsal stream:

Optic Ataxia

Seelenlähmung des Schauens, optische Ataxie, räumliche Störung der Aufmerksamkeit

[Psychic paralysis of gaze, optic ataxia, and spatial disorder of attention.]

Rudolph Bálint 1909

Monatsschrift für Psychiatrie und Neurologie (1909) 25: 51-81

Disturbances of visual orientation

Gordon Holmes 1918

British Journal of Ophthalmology (1918) 2: 449-468.

“Thus, when asked to grasp a presented object with his right hand, he would miss it regularly and would find it only when his hand knocked against it.”

“... the motor rather than the visual disorder was the dominant one [since] all the movements performed deficiently with the right hand were executed perfectly or with very little error with the left hand.”

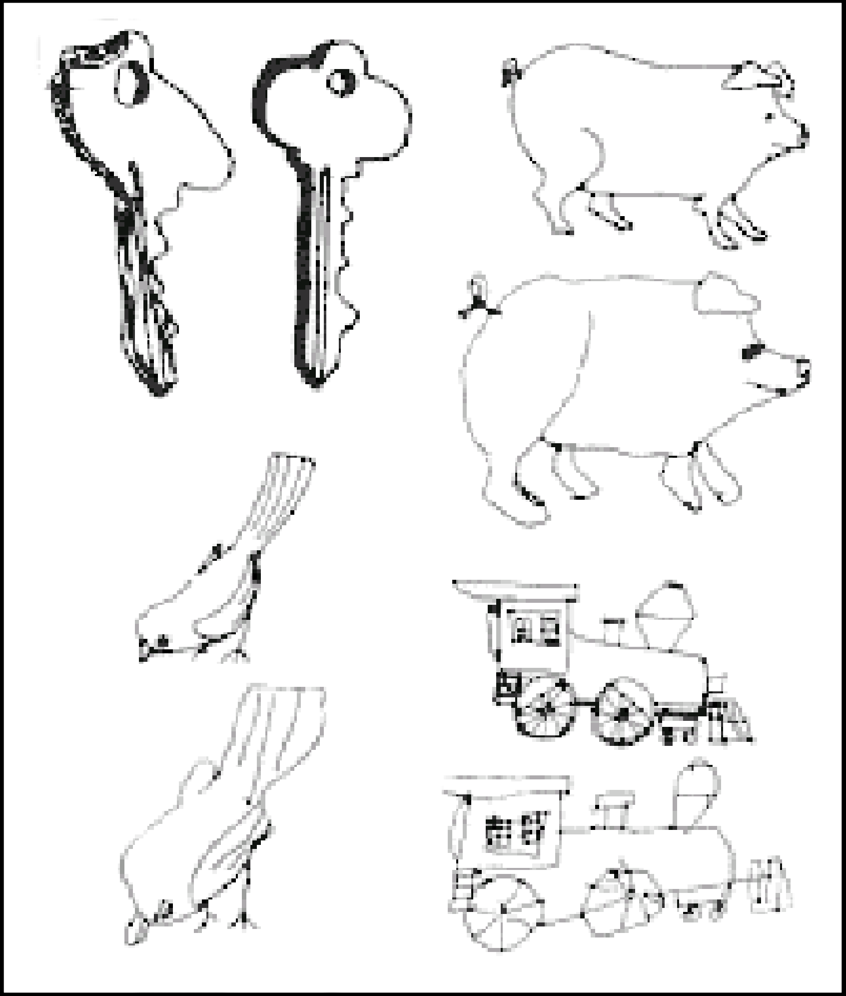
“... only movements which required visual control were faulty.”

Rudolf Balint 1909

[translated by Monika Harvey 1995]

Damage to the ventral stream:

Visual Agnosia



Associative Agnosia

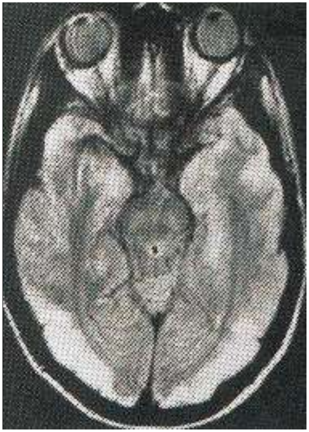
Apperceptive Agnosia

Lissauer, 1889

Associative agnosia patients typically have damage, usually from a stroke, beyond occipital cortex in inferior temporal regions.

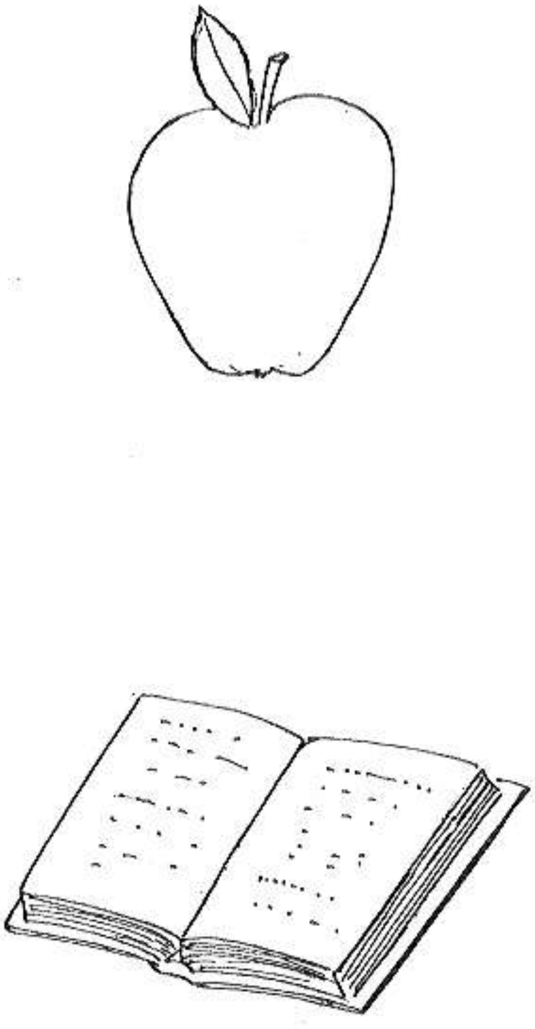
Apperceptive agnosia patients typically have damage lateral occipital areas, usually from anoxia (e.g. carbon monoxide poisoning). Apperceptive agnosia is sometimes called visual form agnosia.

Patient DF



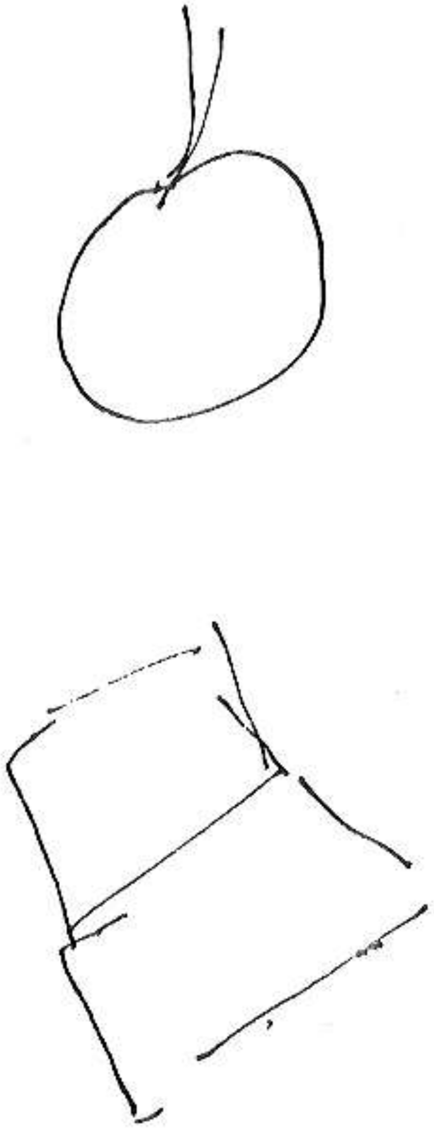
- Hypoxia from carbon monoxide poisoning
- MRI in 1989 showed diffuse brain damage with lesions in the ventral stream, sparing primary visual cortex
- Most obvious symptom was visual form agnosia
- Clinical and low-level visual testing was largely in the normal range

Model



Copy

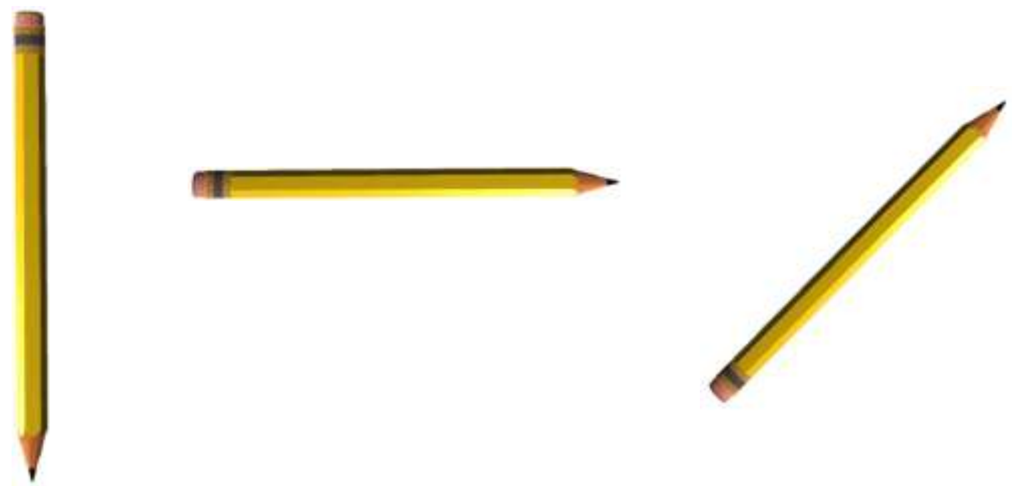
Memory

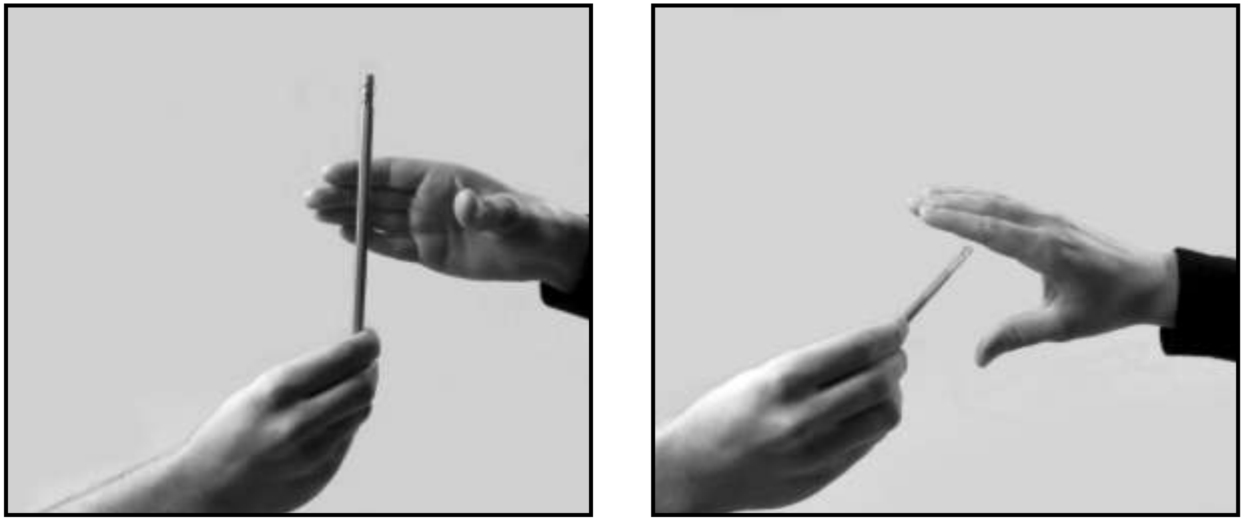


“It’s made out of metal – is it aluminum?
It’s got red plastic on it.”

“Is it some sort of kitchen utensil?”

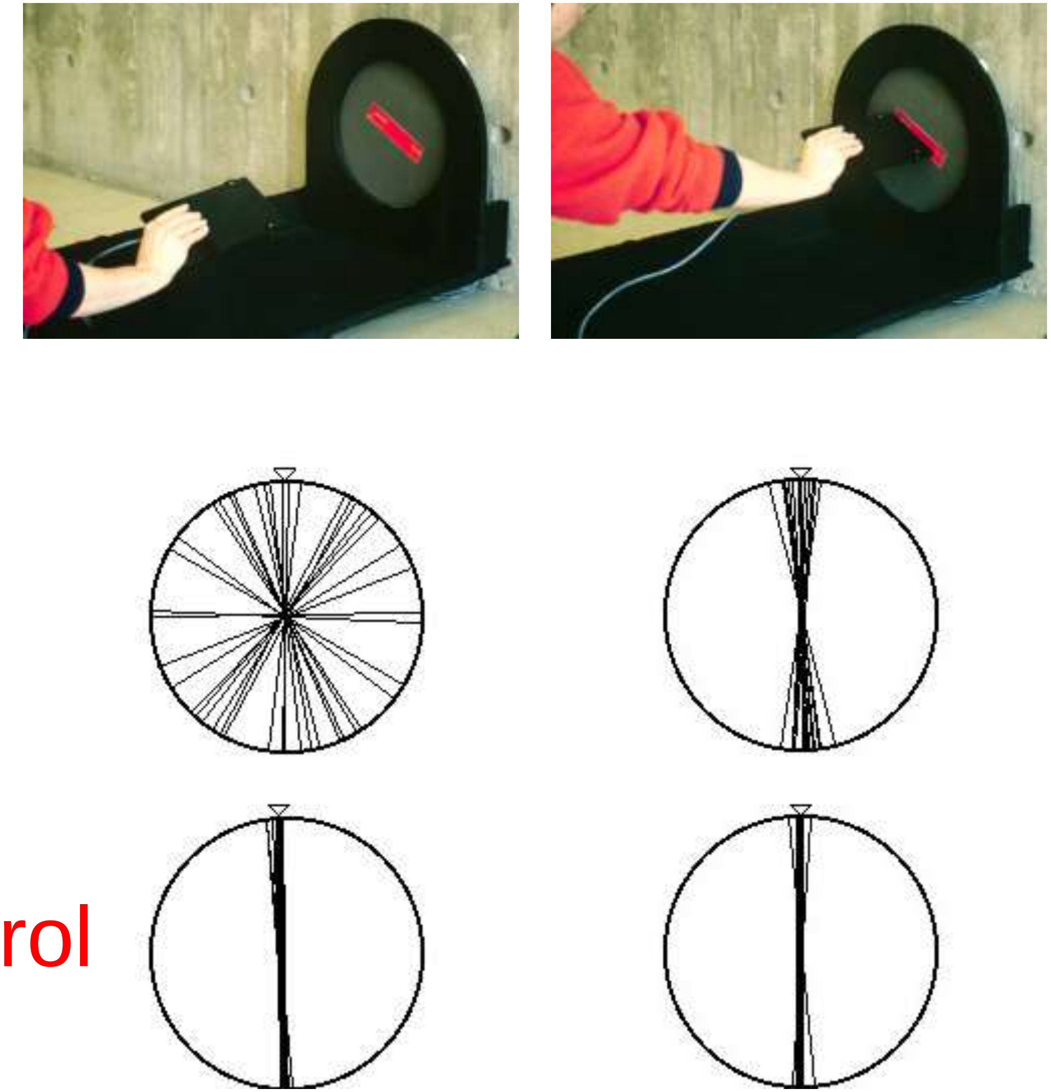
Humphrey, Goodale, Jakobson, & Servos (1994). *Perception*





Slot Task

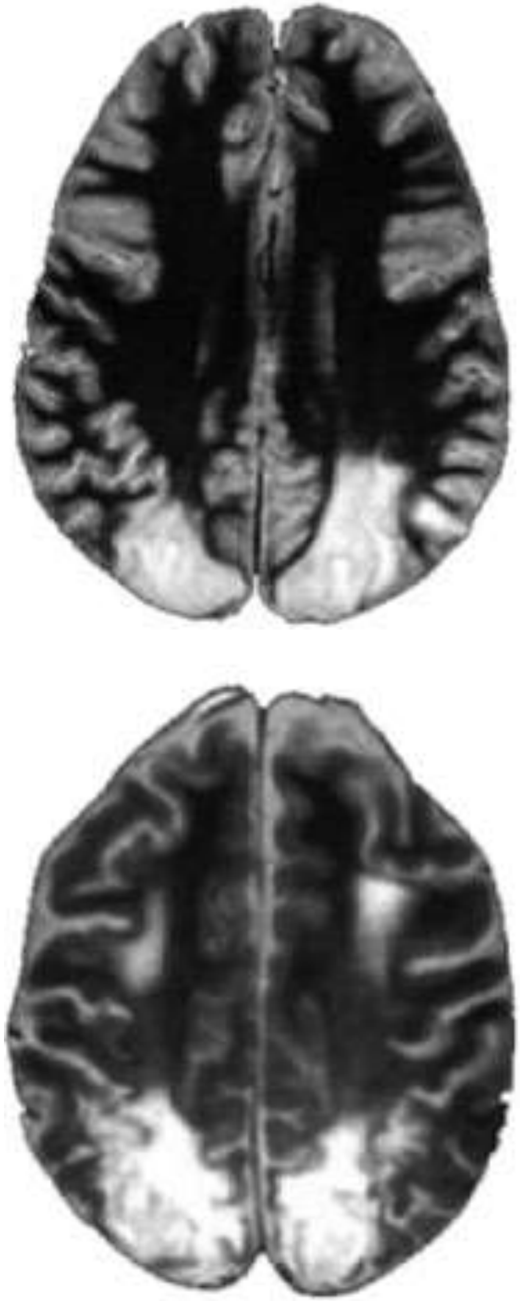
Matching Posting



DF

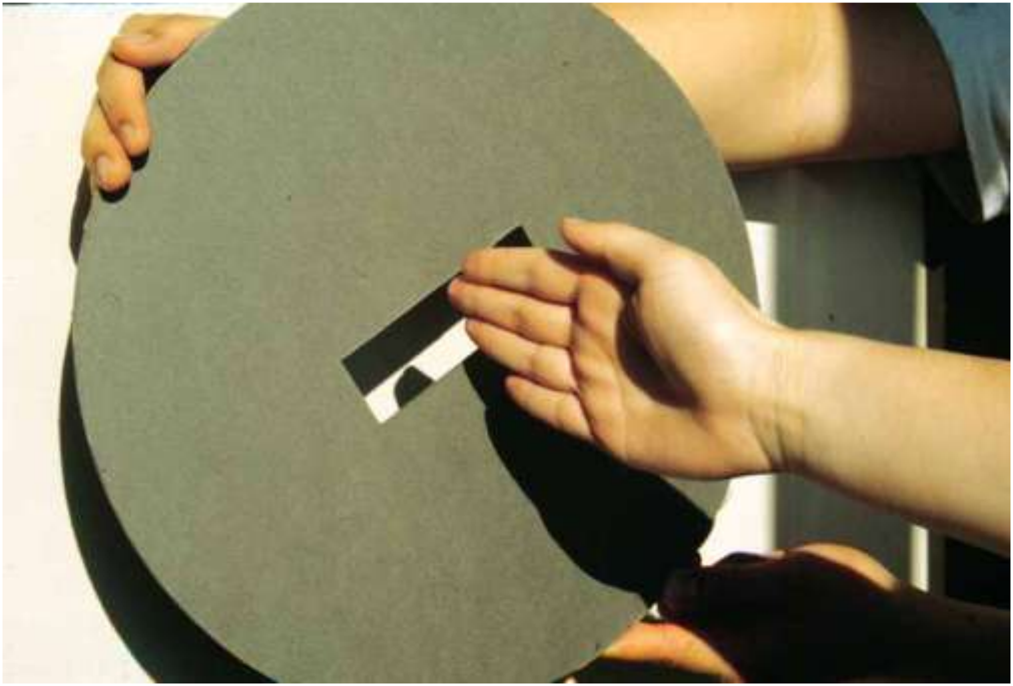
Control

Goodale et al. (1991) *Nature*



What about patients with lesions of the dorsal stream?

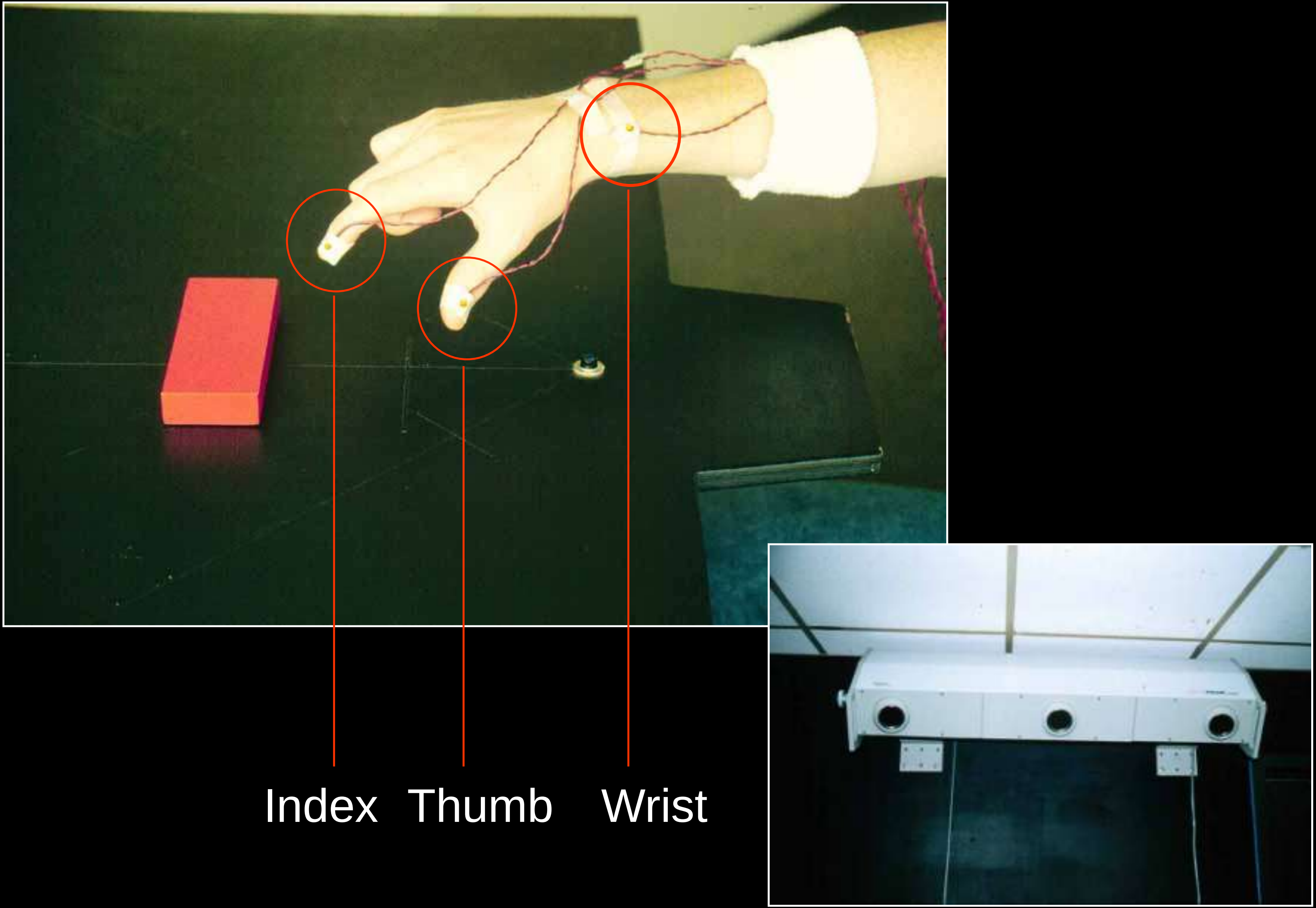
Optic ataxic patient
(posterior parietal lesion)

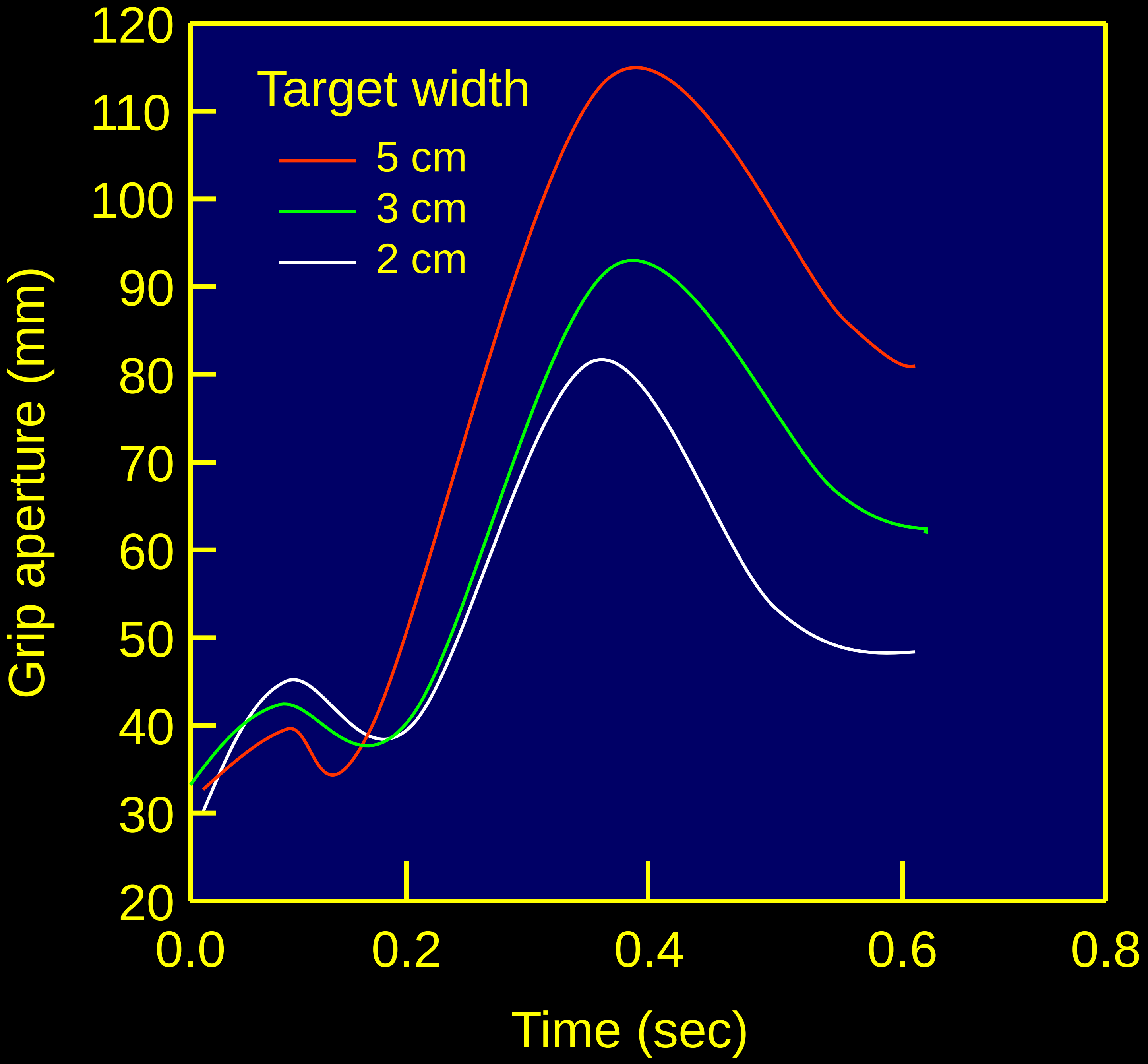


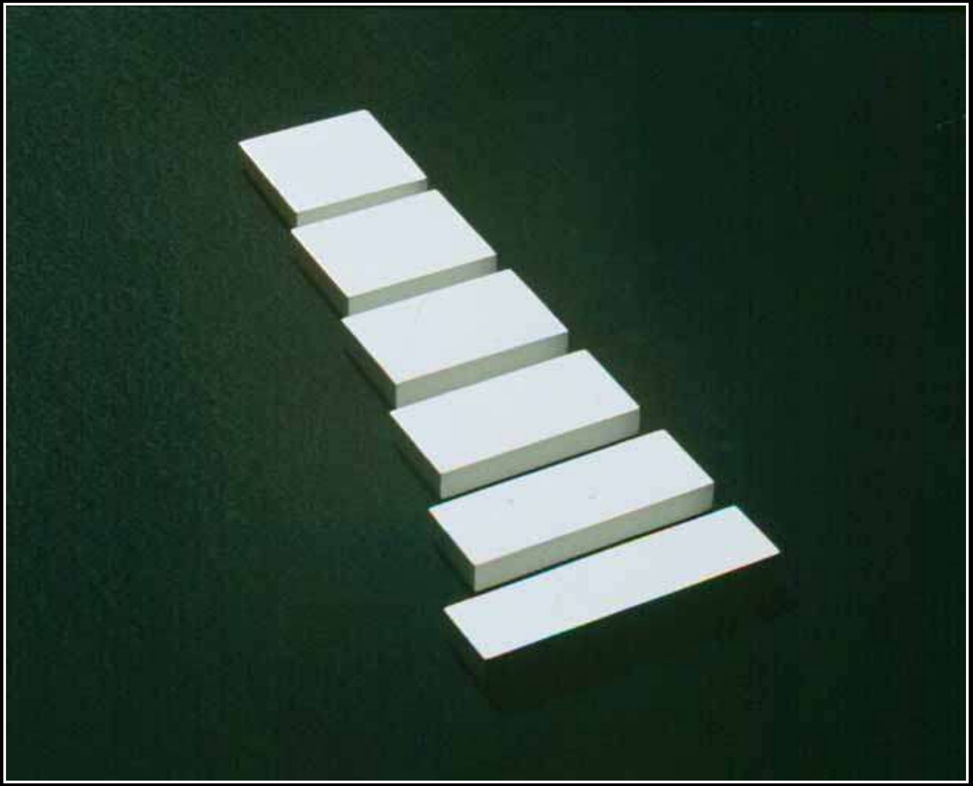
Perenin, M.–T., & Vighetto, A. (1988).
Brain, *111*, 643–674.

Small hand-aperture

Large hand-aperture

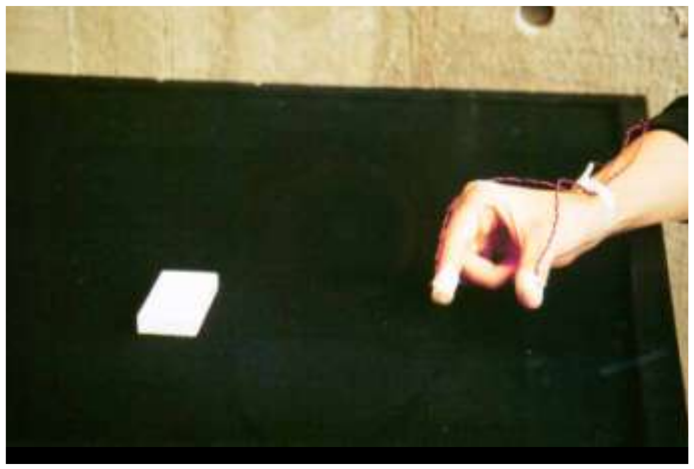

Index
Thumb
Wrist


Target width
5 cm
3 cm
2 cm
Grip aperture (mm)
120
110
100
90
80
70
60
50
40
30
20
0.0
0.2
0.4
0.6
0.8
Time (sec)



‘Efron’ Blocks

Object size

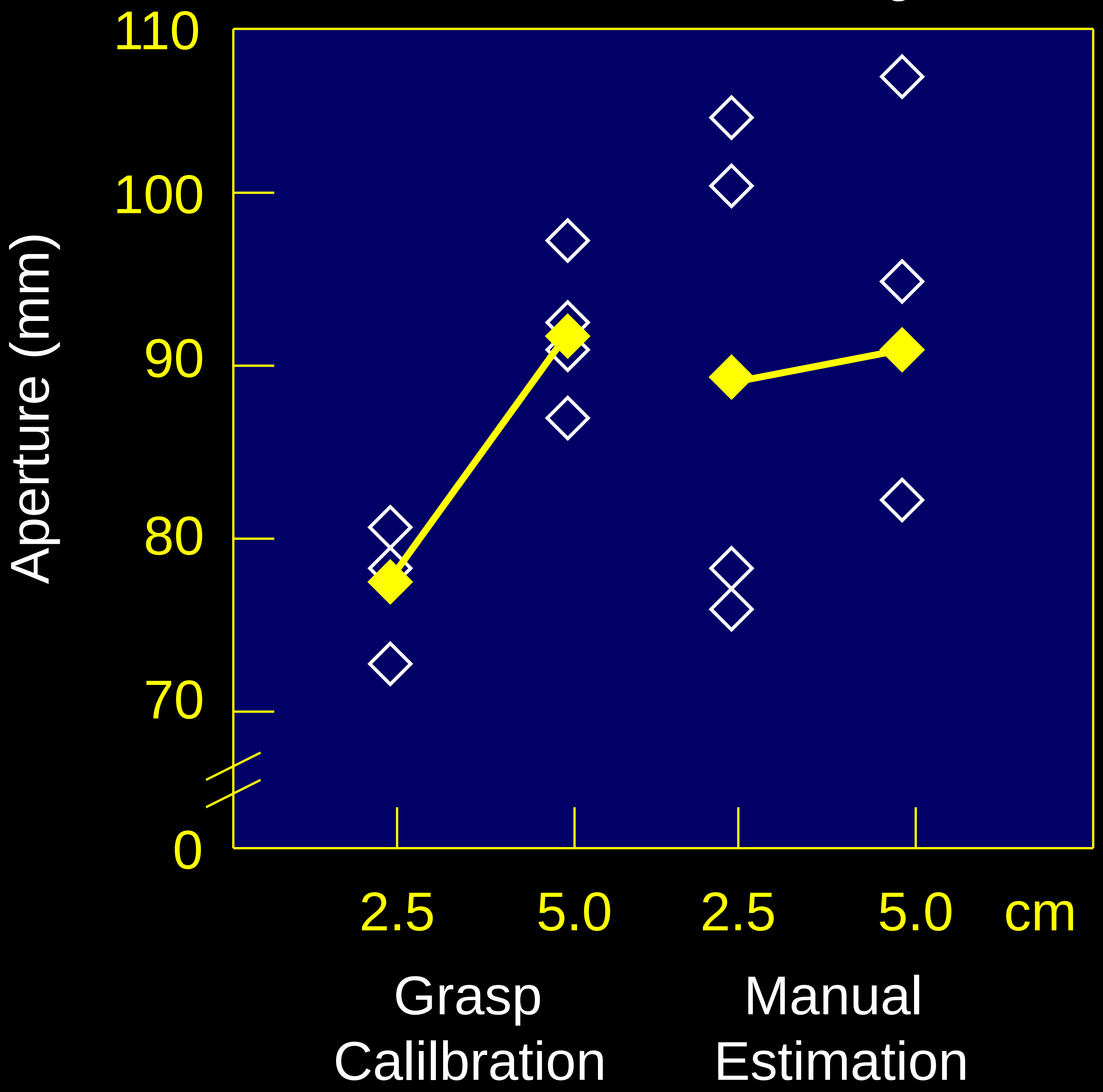


Manual
Estimation

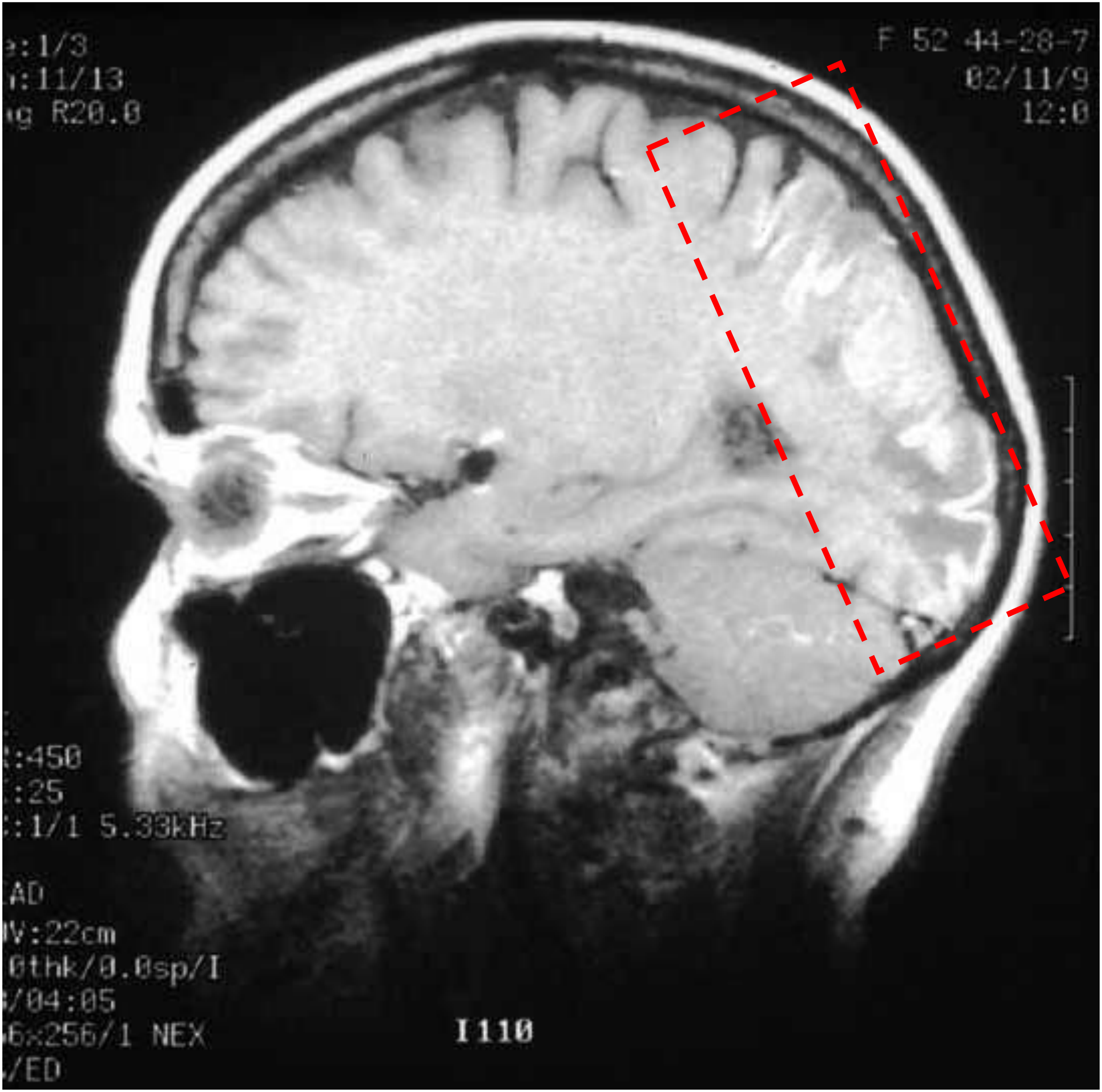
Grasp

Goodale et al. (1991) *Nature*

Patient DF: Visual Form Agnosia

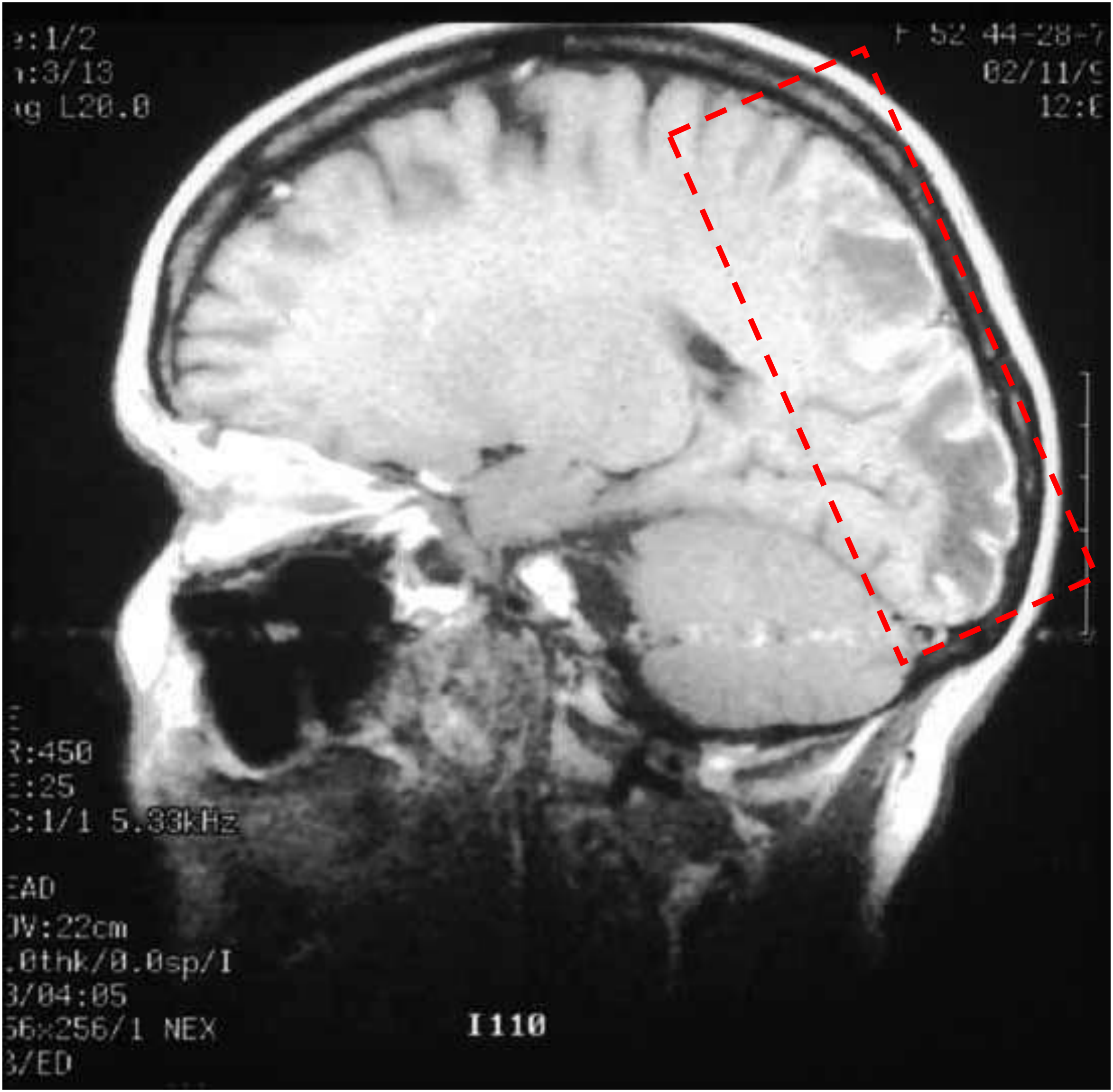


Patient RV: Damage to dorsal stream



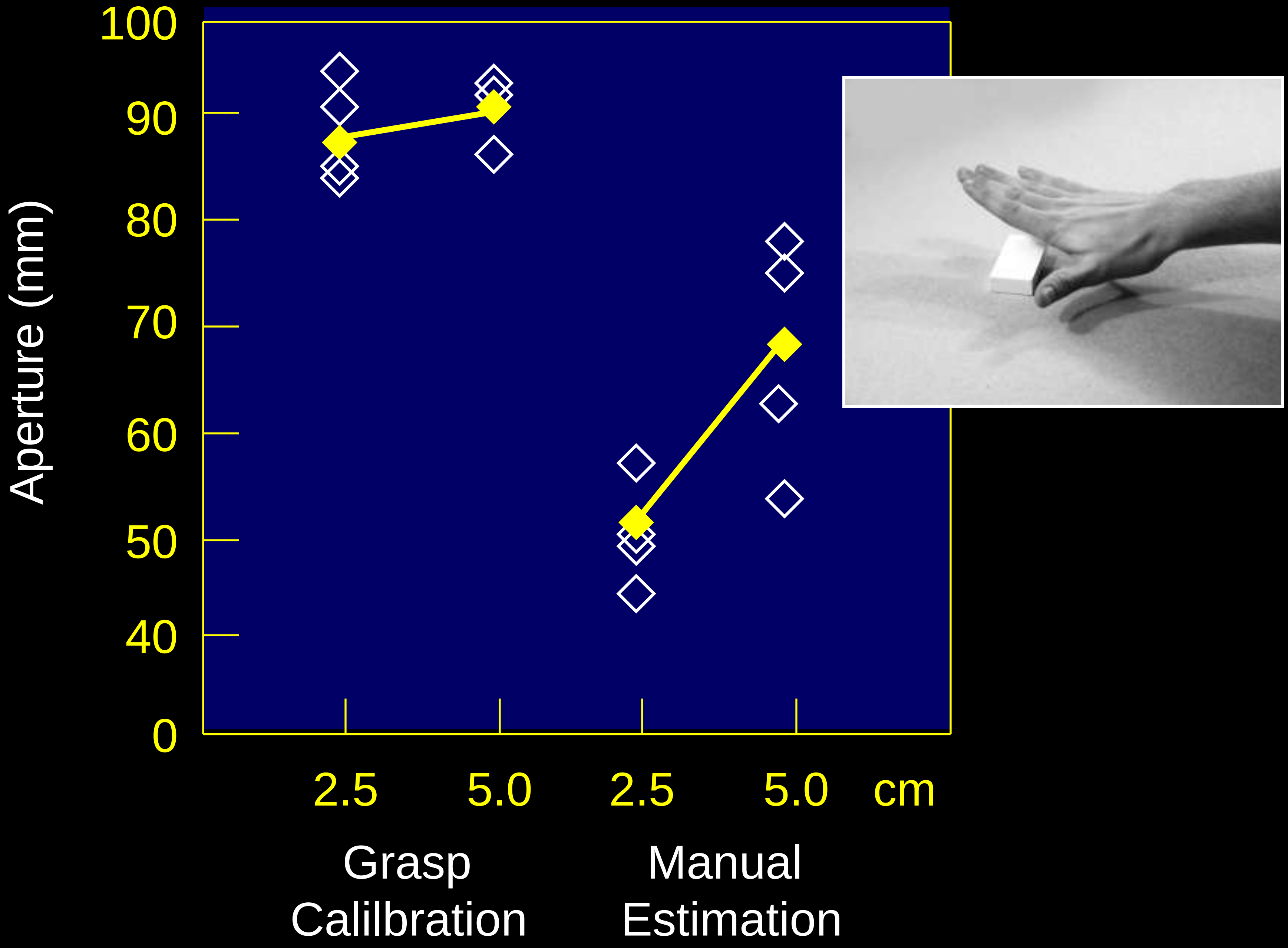
Right Hemisphere

Patient RV: Damage to dorsal stream

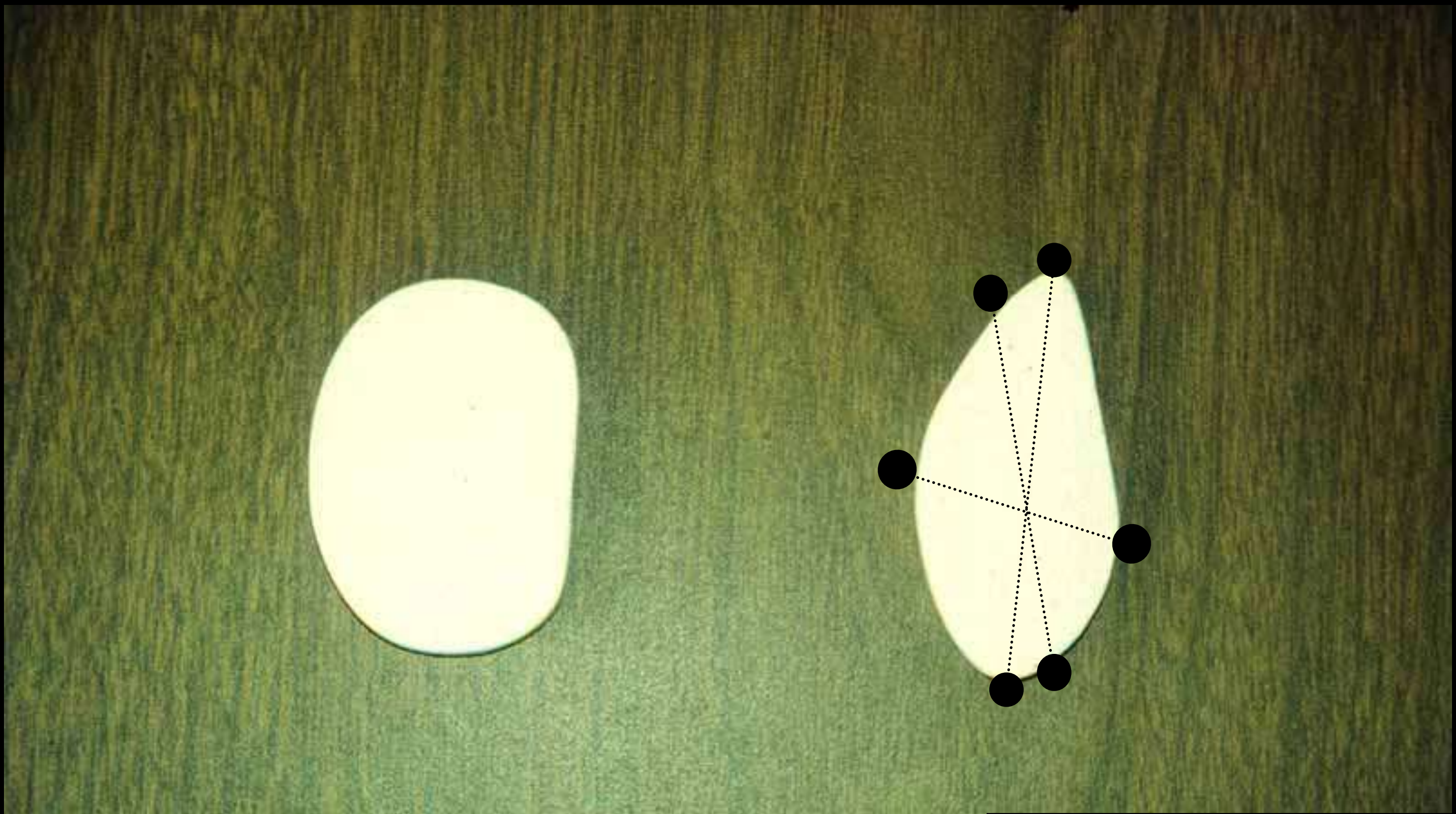


Left Hemisphere

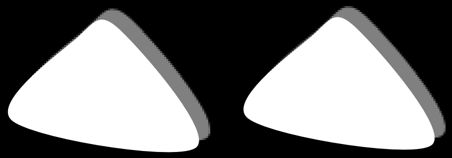
Patient RV: Optic Ataxia



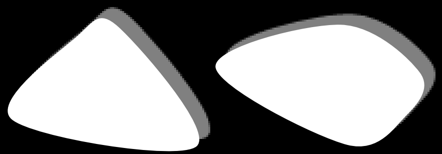
What about object shape?



“Blake” shapes

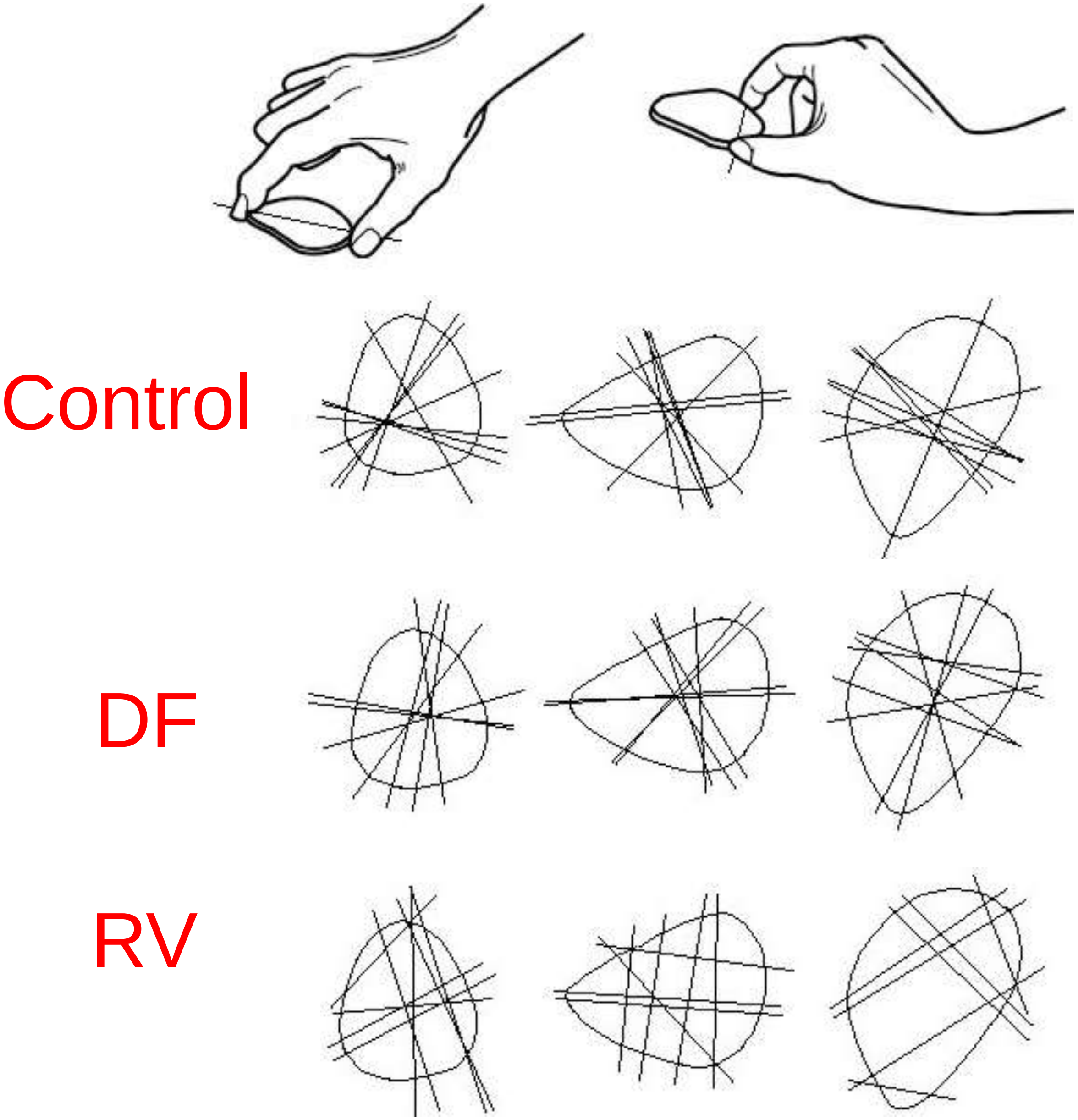


Same



Different

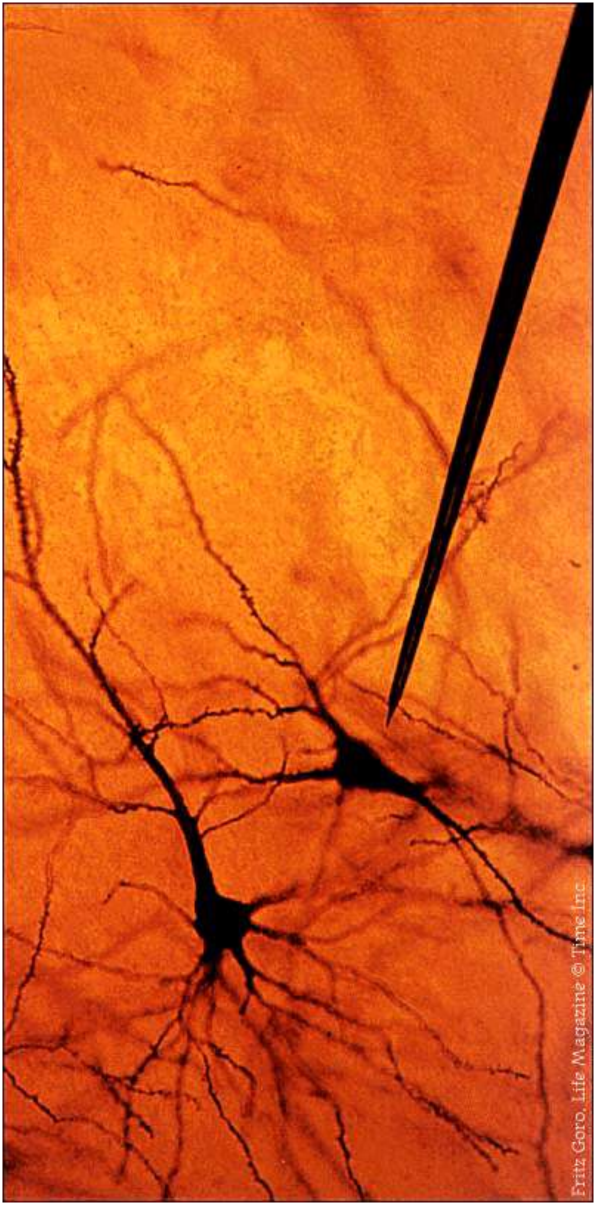
DF	52%
RV	90%



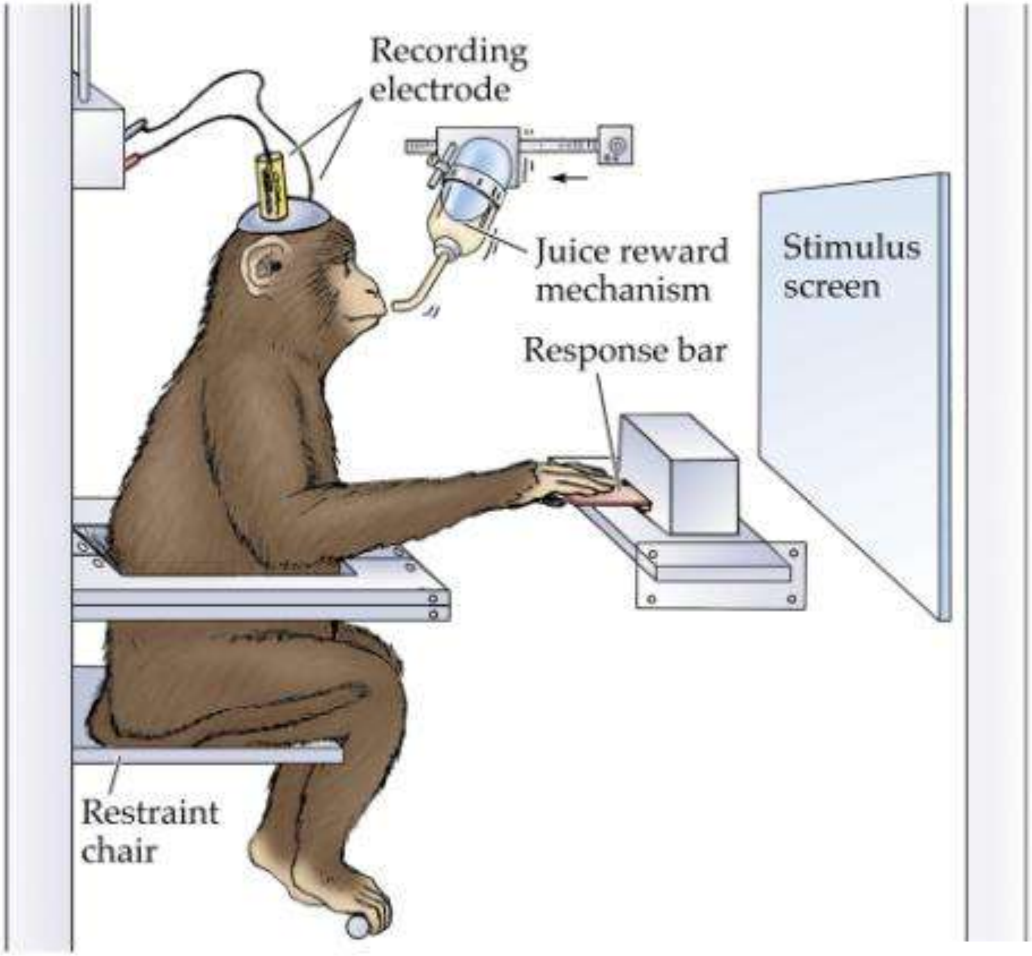
Goodale et al. (1994). *Current Biology*

	Perception	Action	Site of Damage
Visual form agnosia	✗	✓	Ventral Stream
Optic Ataxia	✓	✗	Dorsal Stream

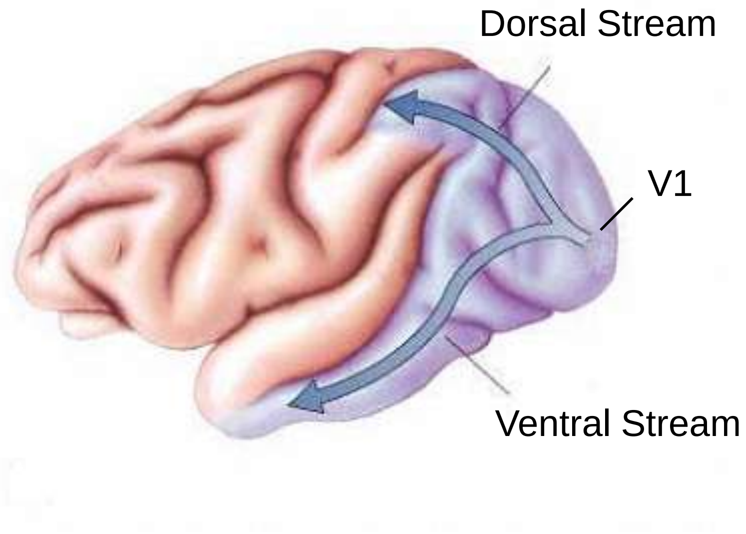
Single-unit recording in the monkey



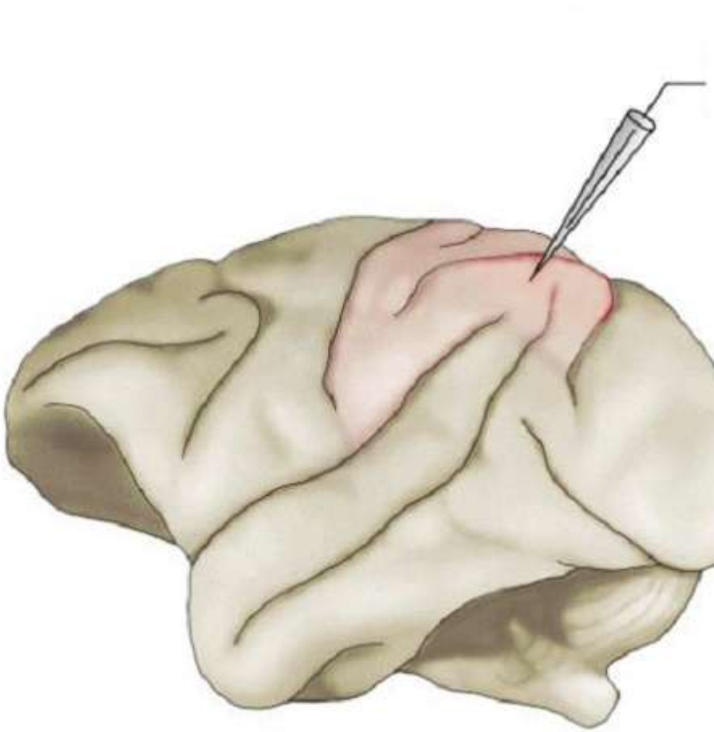
Fritz Goro, Life Magazine © Time Inc.

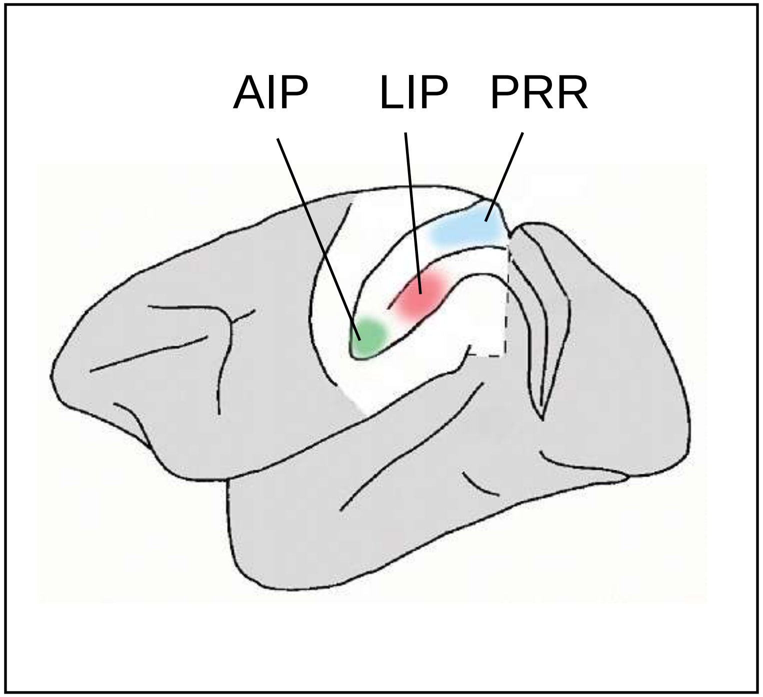

Recording electrode
Juice reward mechanism
Stimulus screen
Response bar
Restraint chair

Macaque Monkey Brain

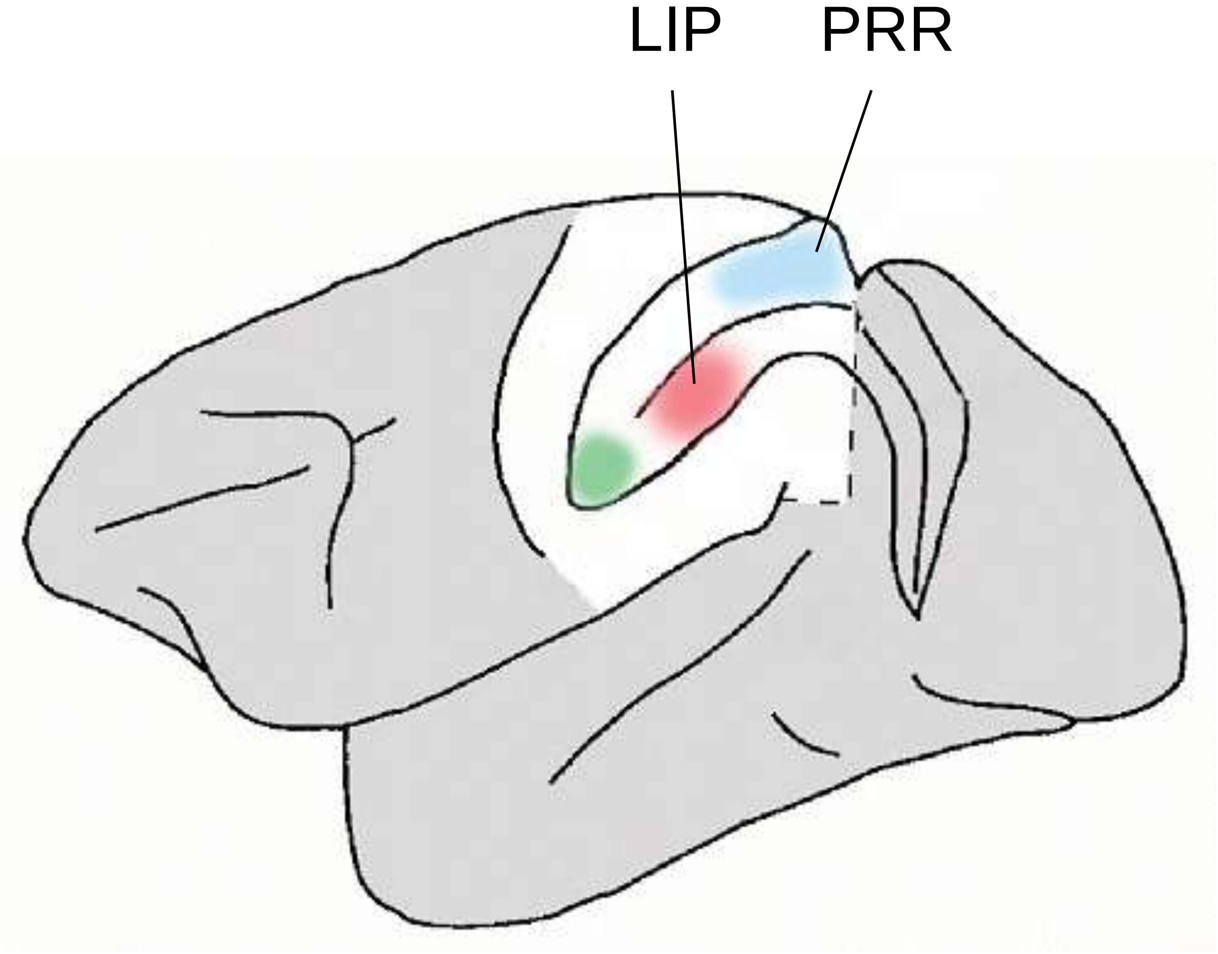


Recording from the Dorsal Stream

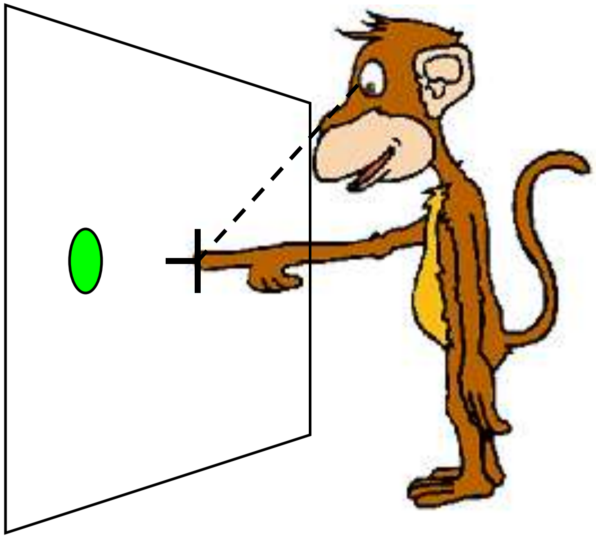


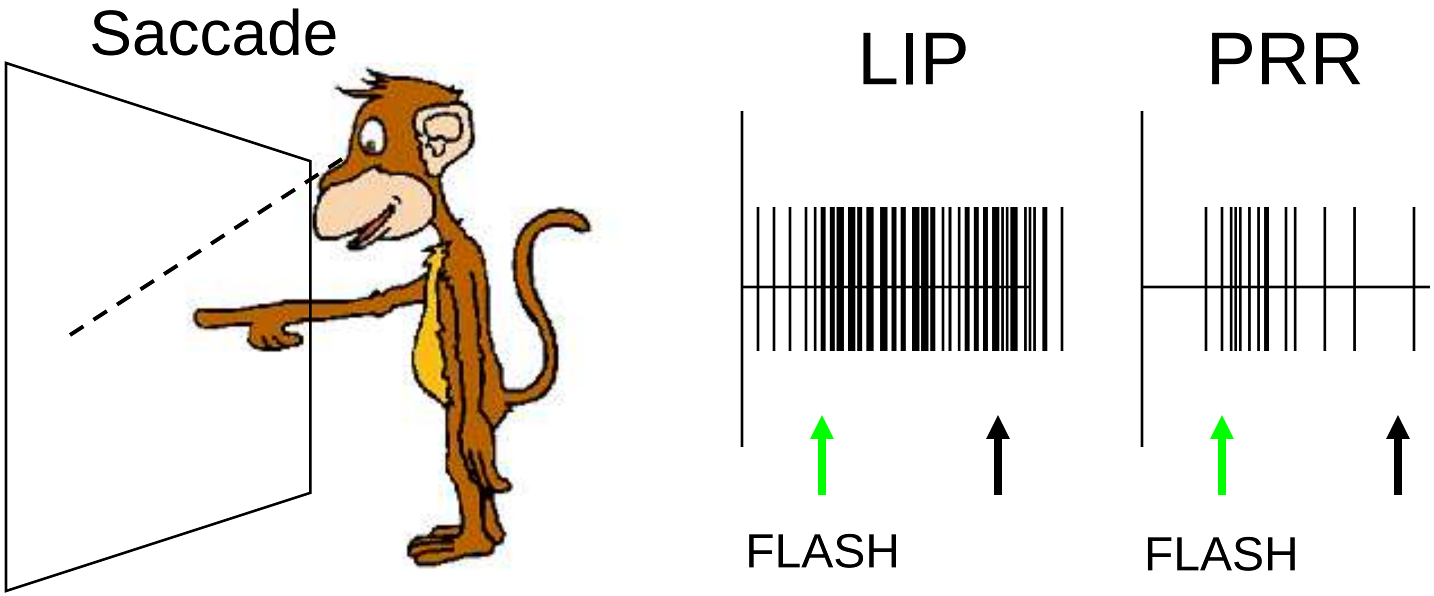


Recording from lateral intraparietal sulcus (LIP) and the parietal reach region (PRR)

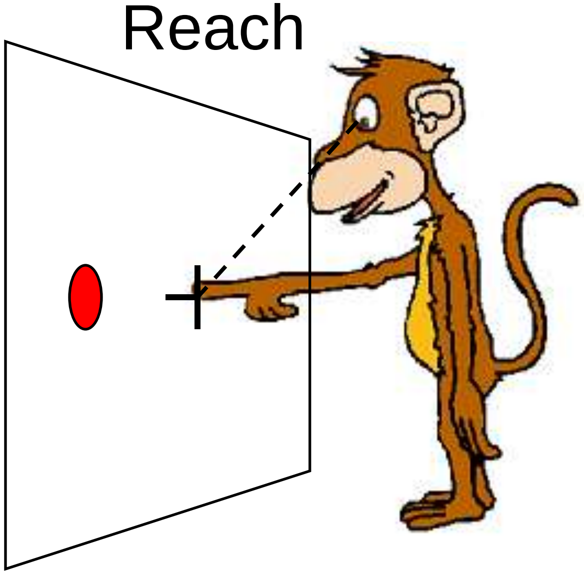


Saccade

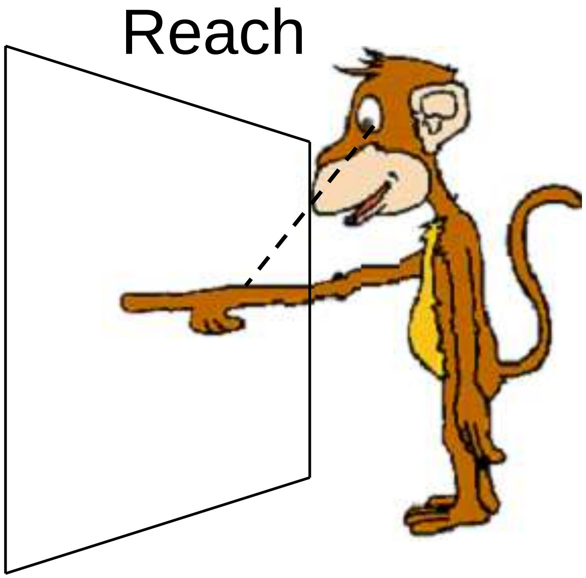


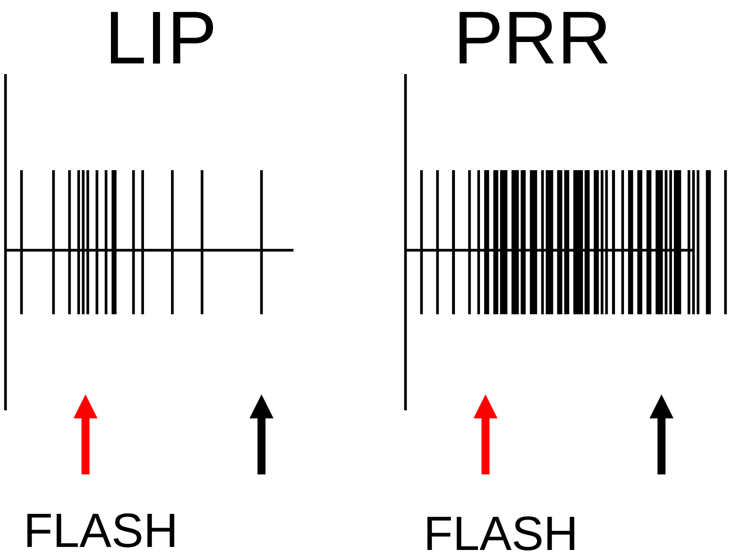


Snyder, Batista and Andersen, 1997

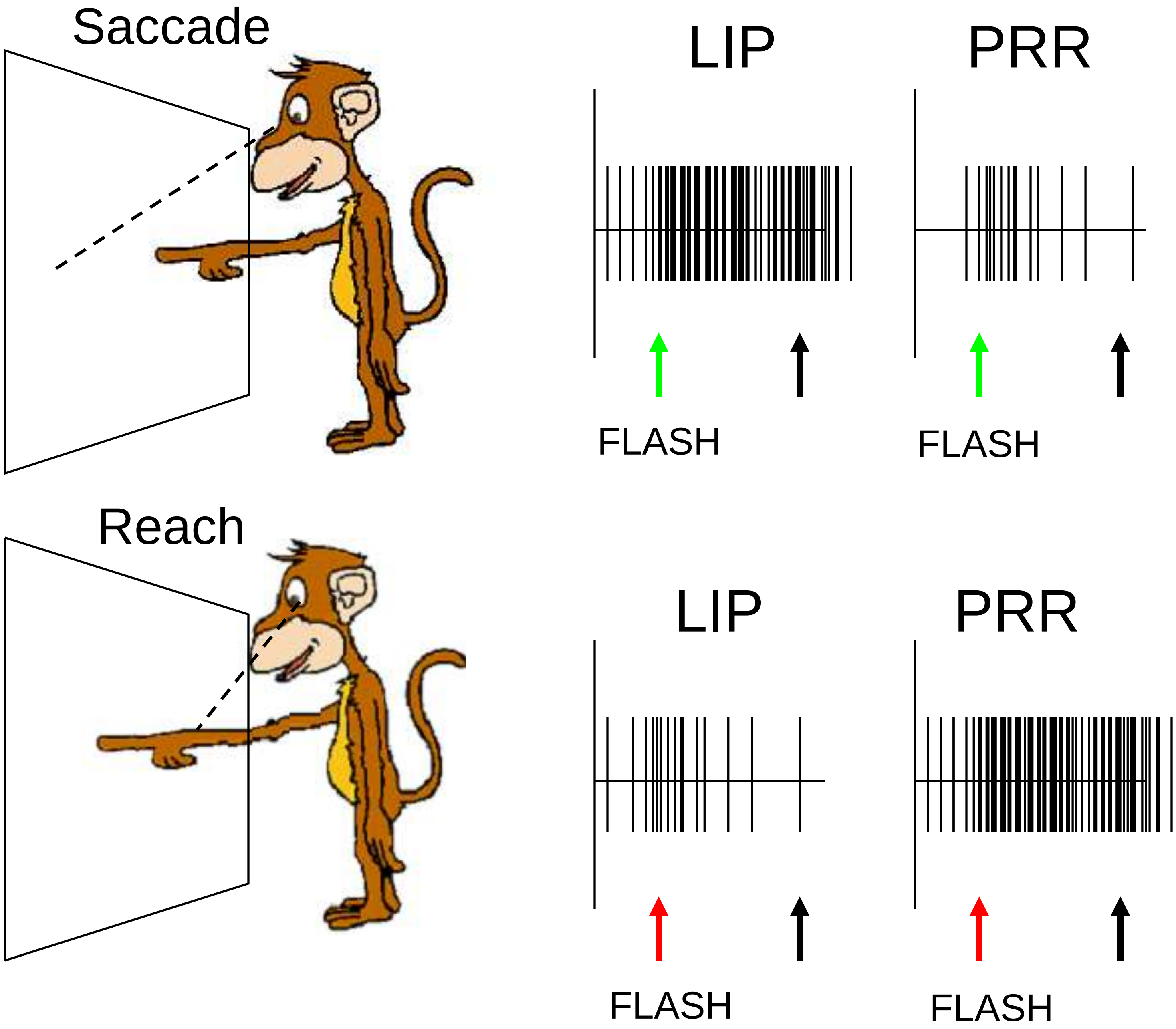


Snyder, Batista and Andersen, 1997





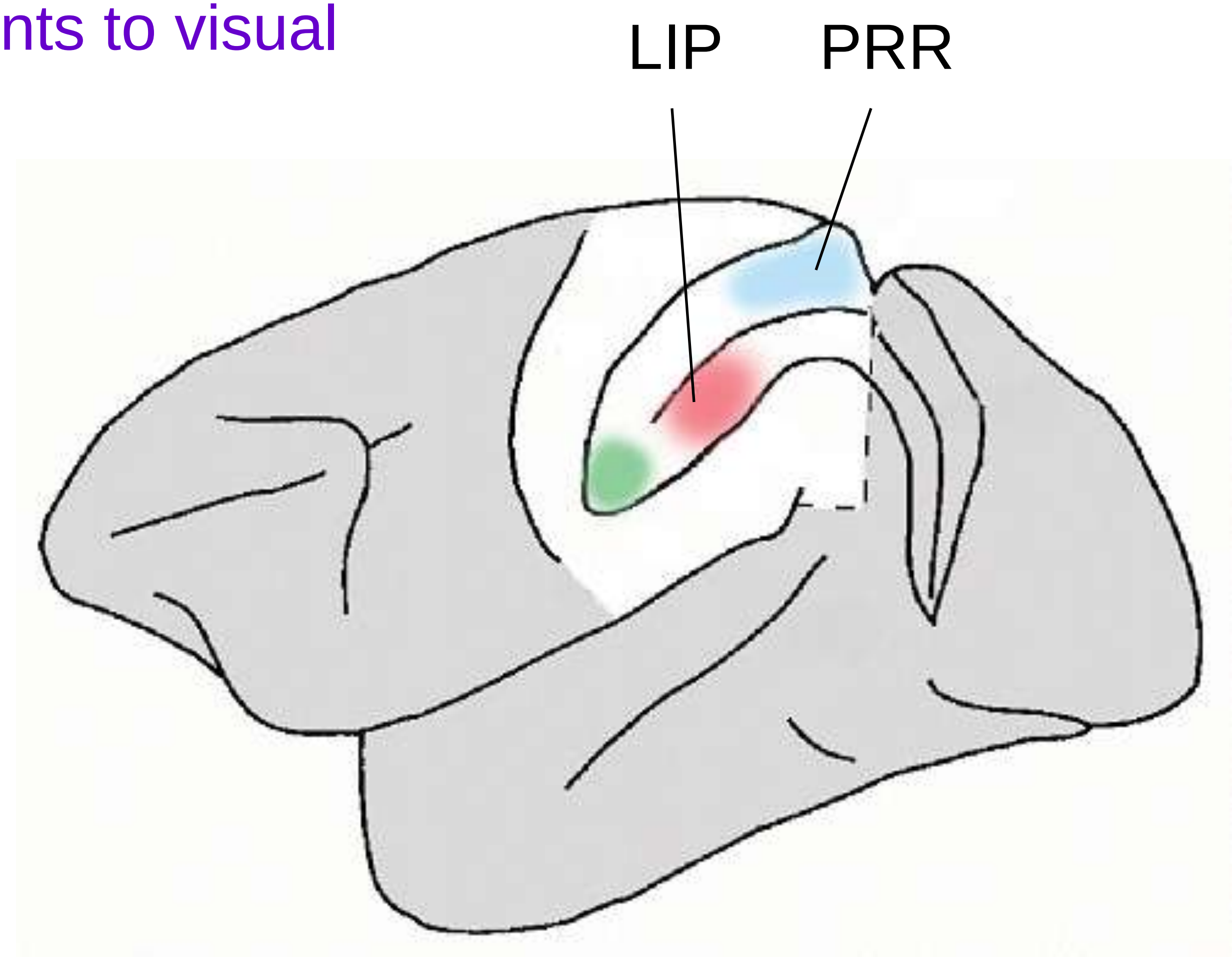
Snyder, Batista and Andersen, 1997



Snyder, Batista and Andersen, 1997

LIP plays a role in the initiation of voluntary saccades to visual targets

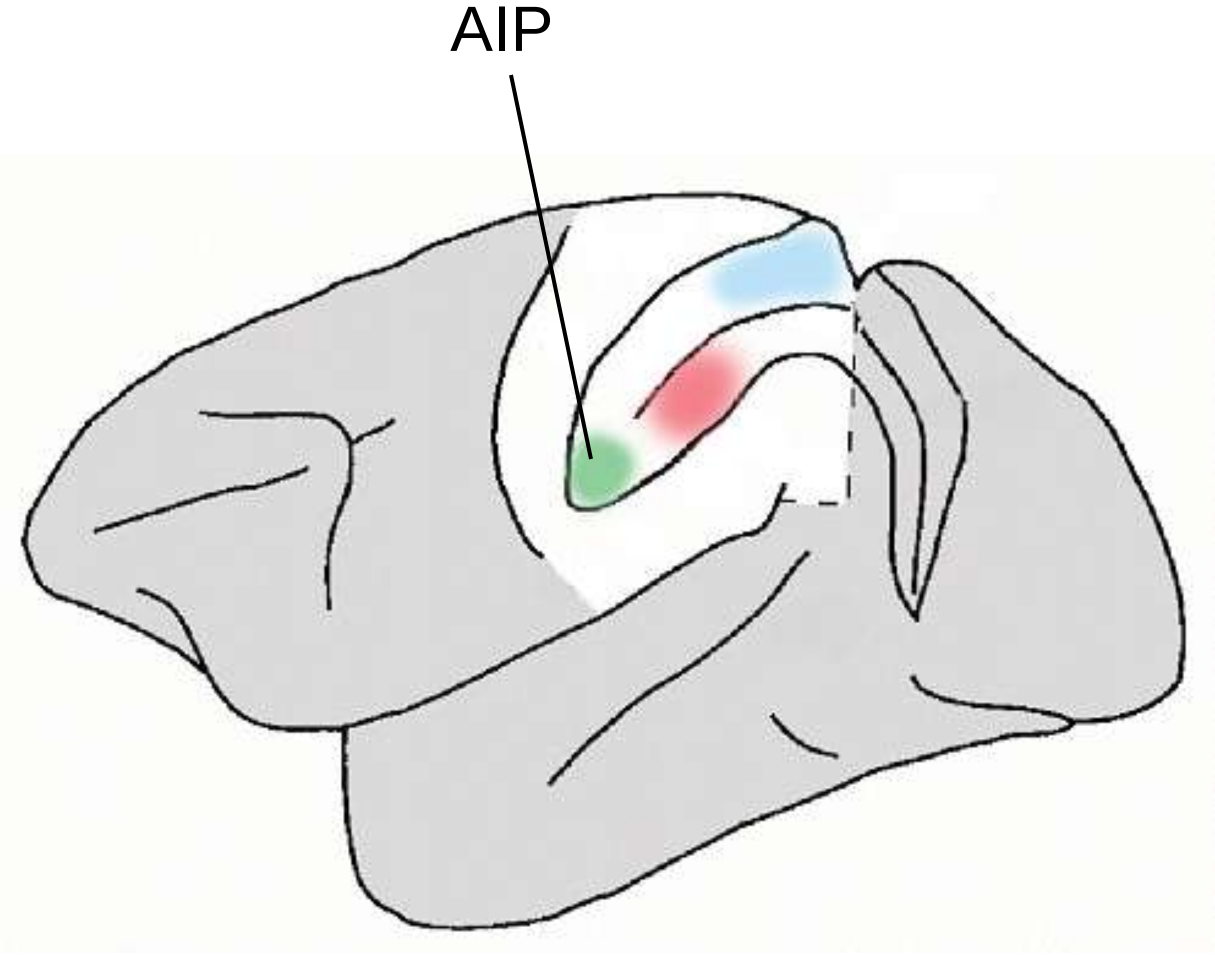
PRR plays a role in the initiation of reaching movements to visual targets

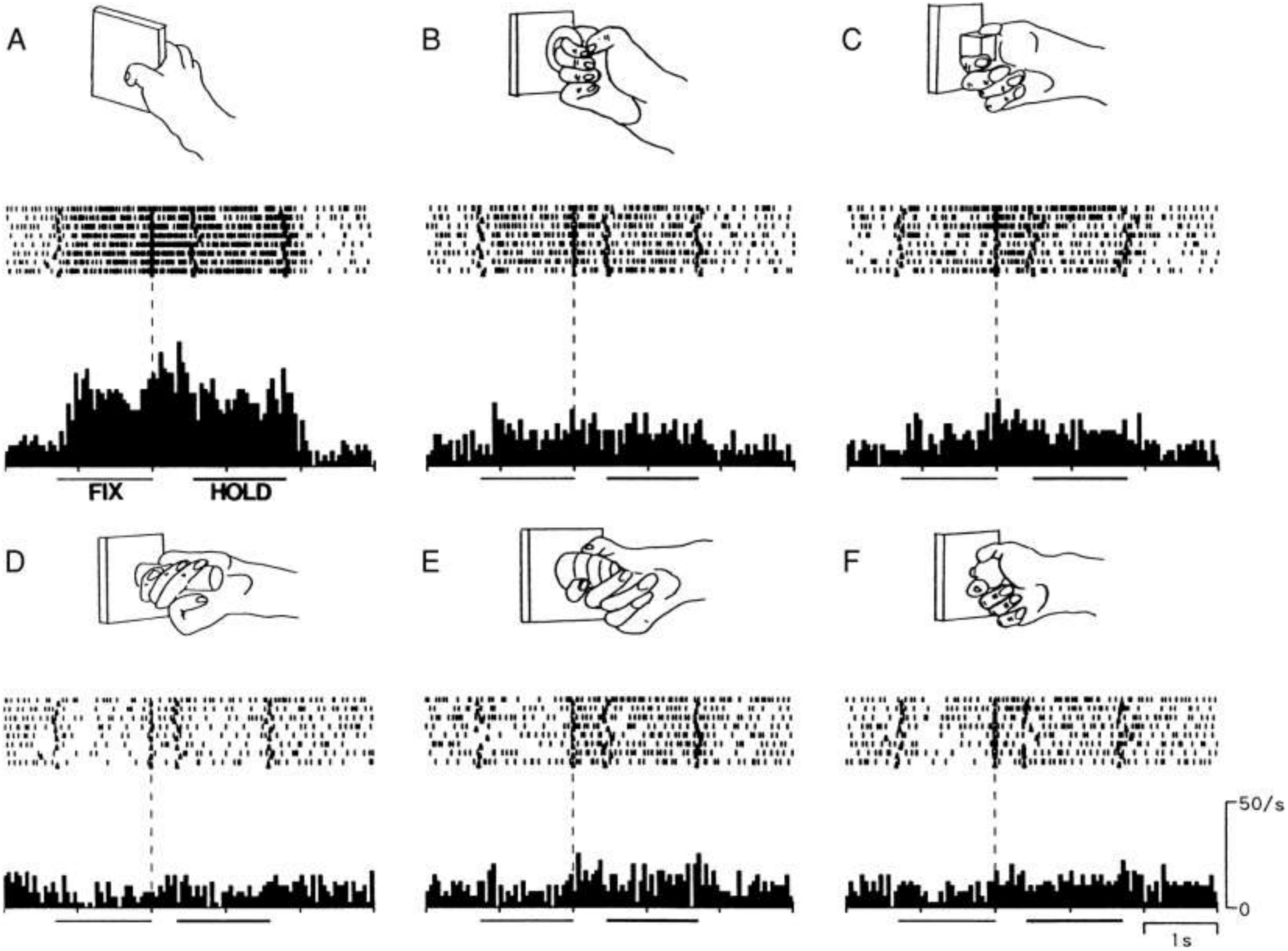


Snyder, Batista and Andersen, 1997

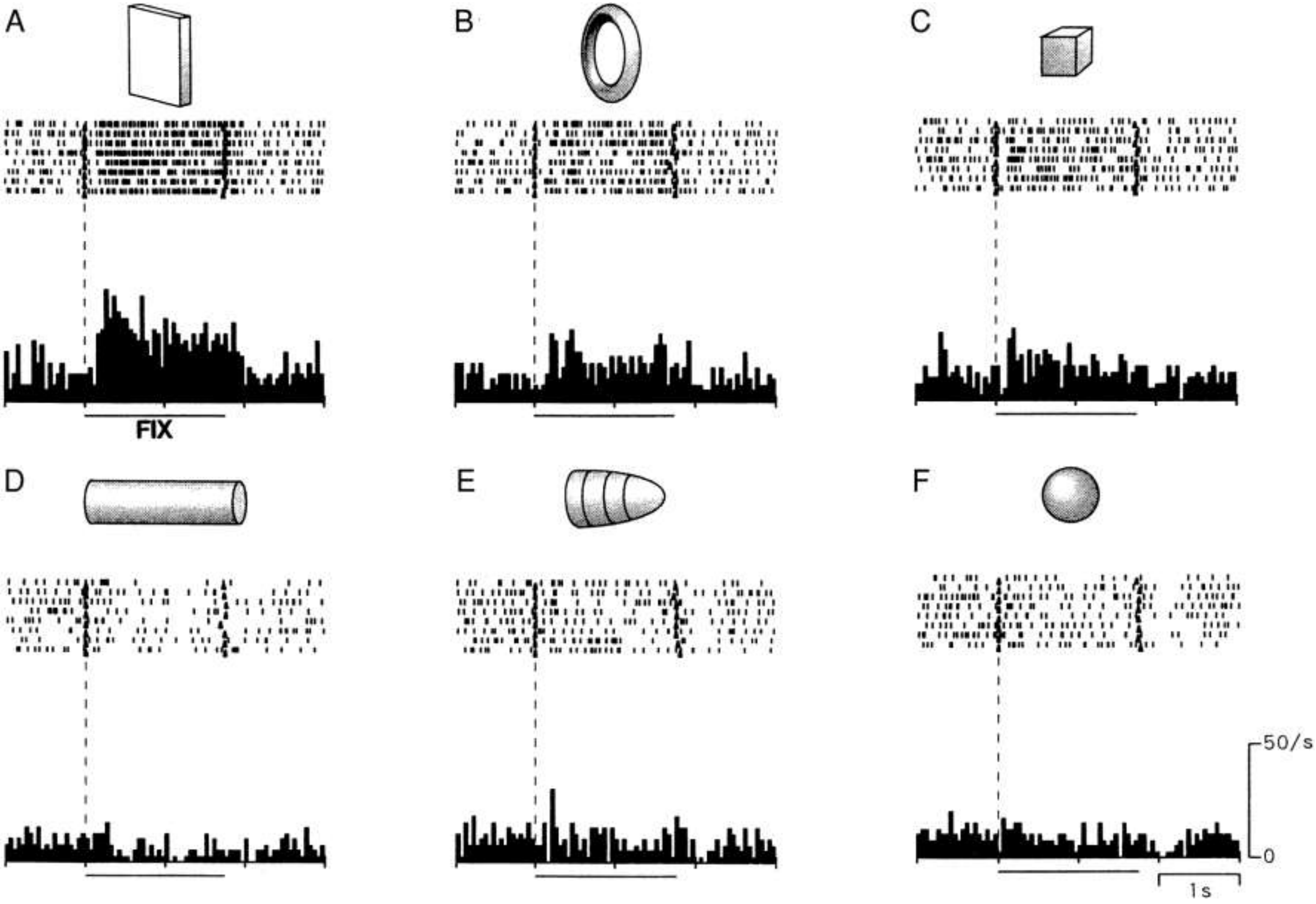
Parietal areas involved in the visual control of grasping

Recording from anterior intraparietal sulcus (AIP)



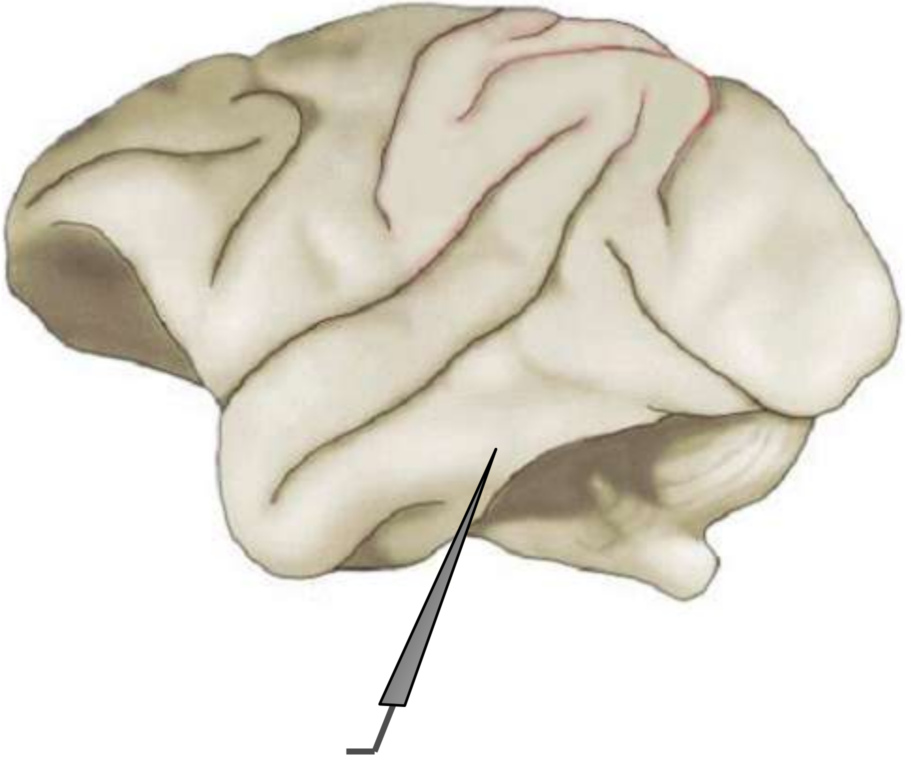


Gallese et al. (2000)



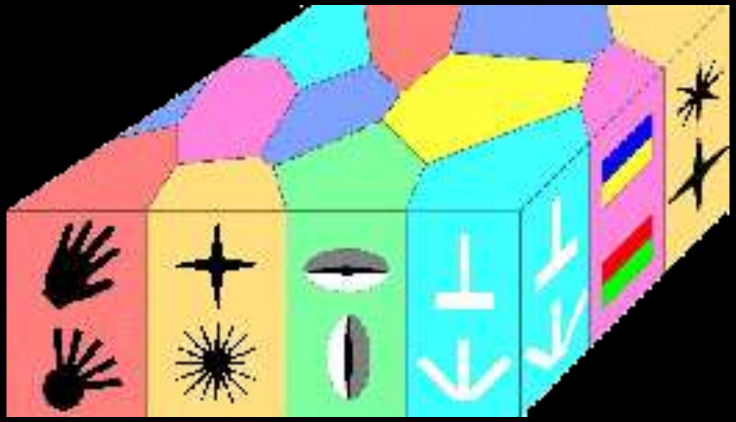
Gallese et al. (2000)

Recording from the Ventral Stream in Monkeys



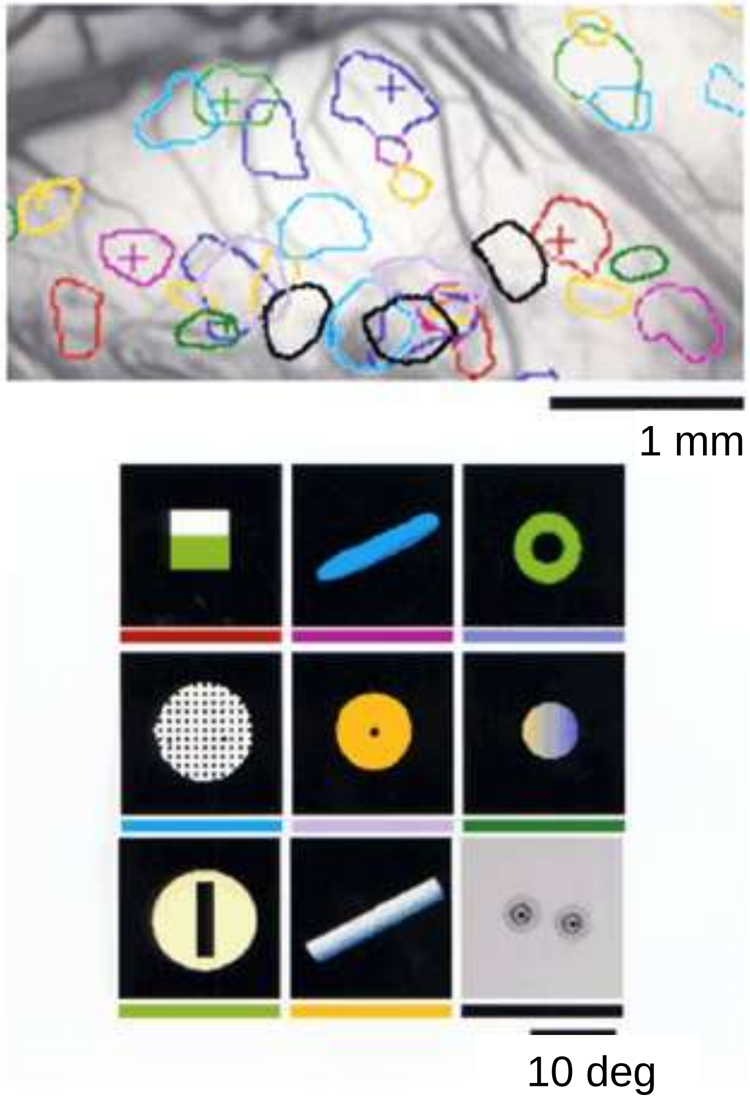
Cells in inferotemporal cortex code for objects and object features

Neurons that code for similar objects or object features are organized in columns in inferotemporal cortex

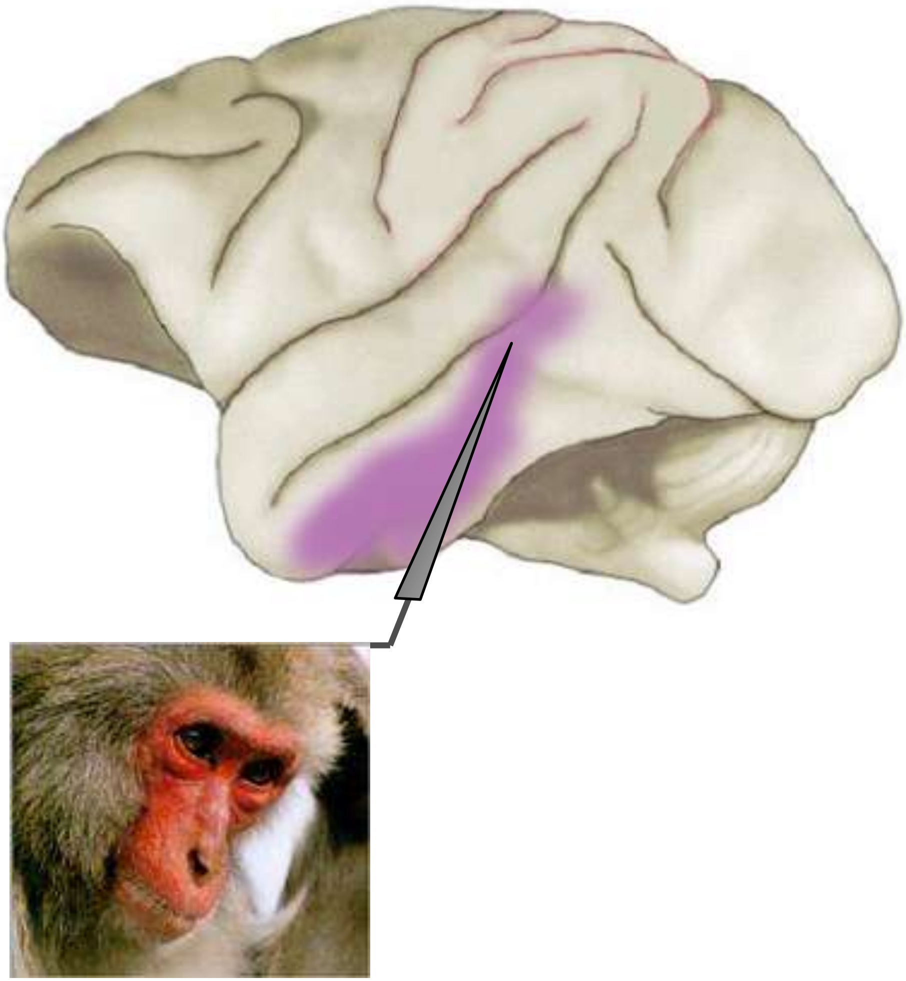


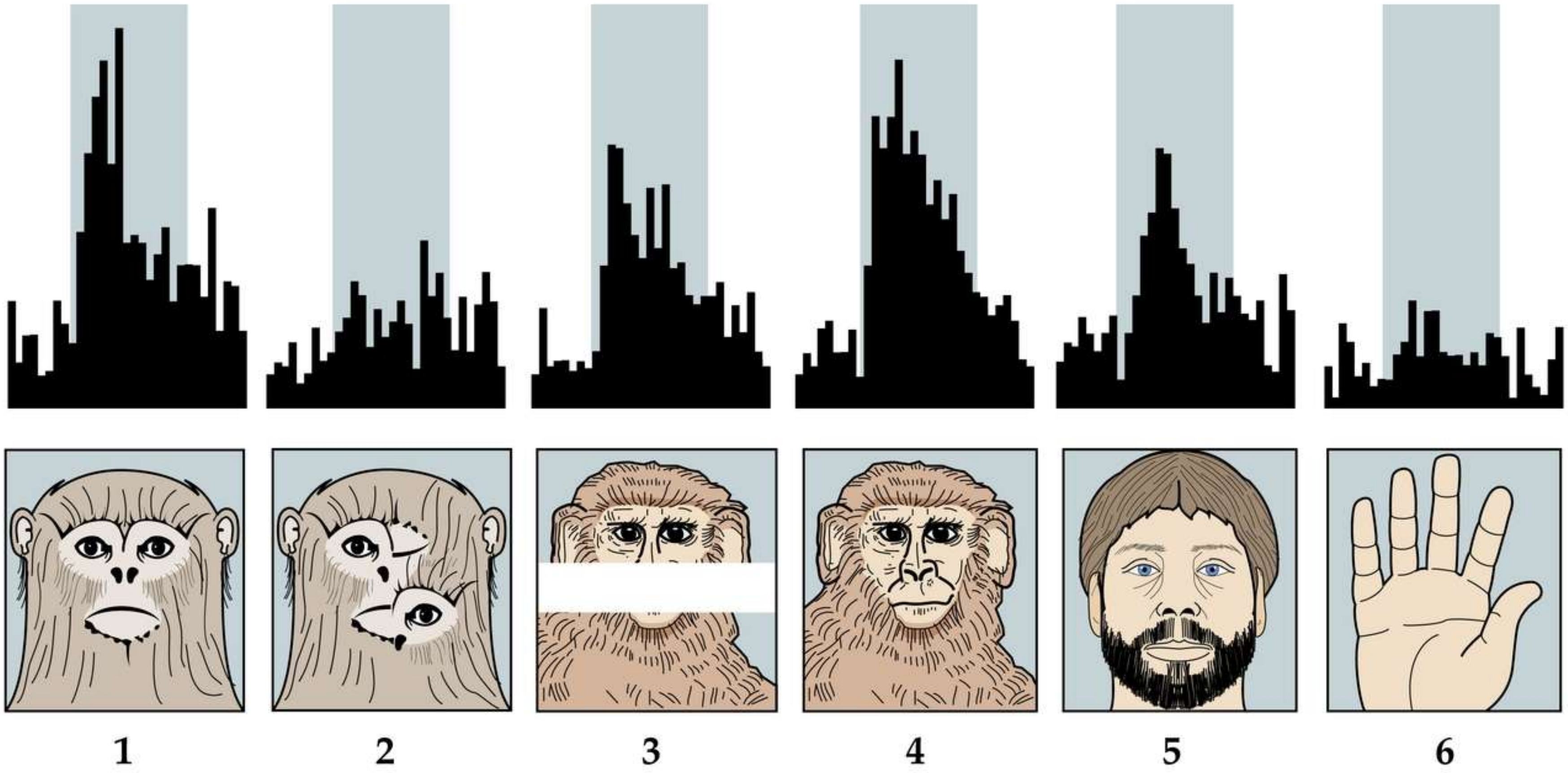
Optical Imaging

Optical imaging of monkey inferotemporal cortex has also shown patches (columns) that are tuned to specific object features



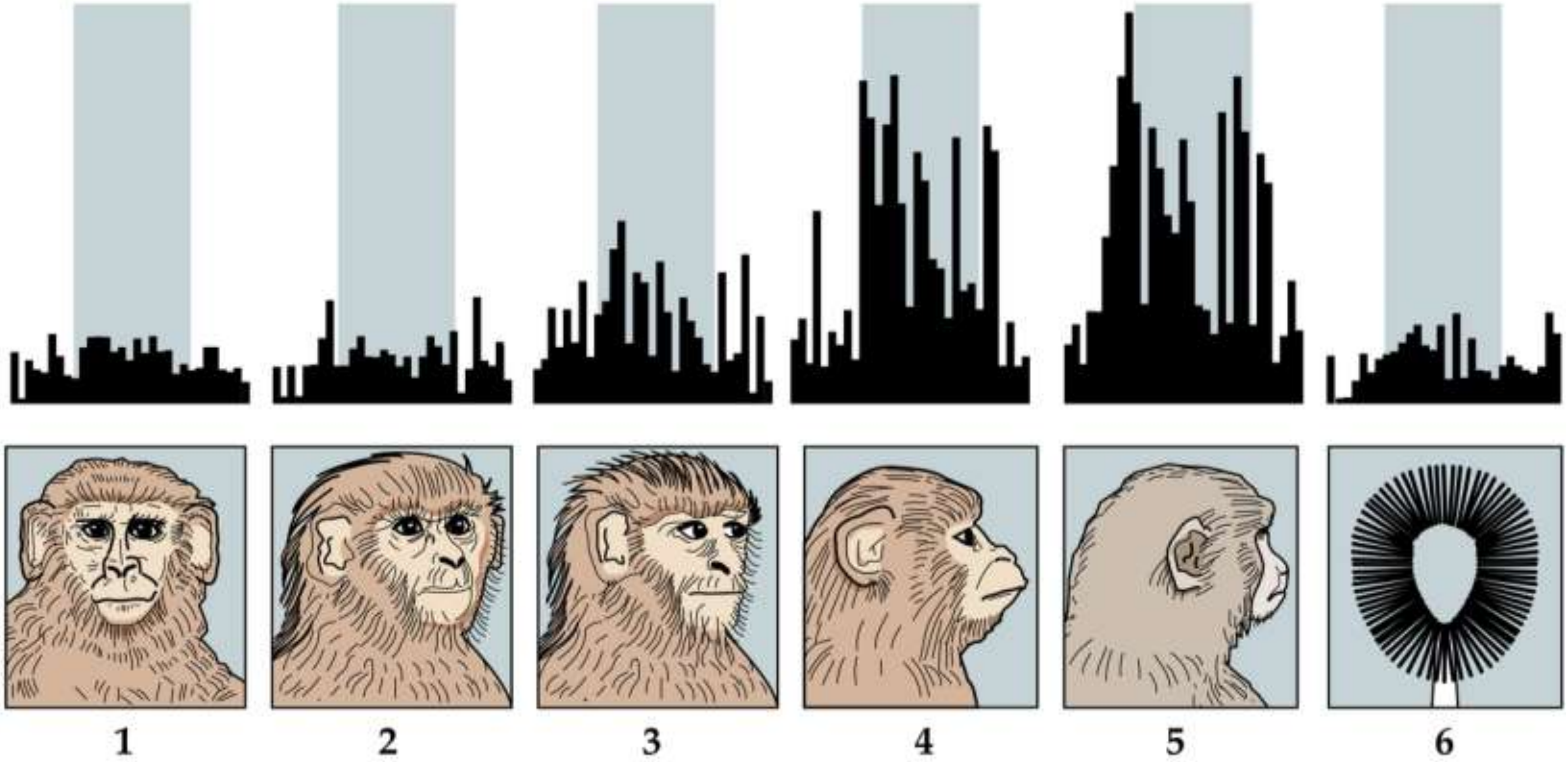
‘Face’ cells in the ventral stream



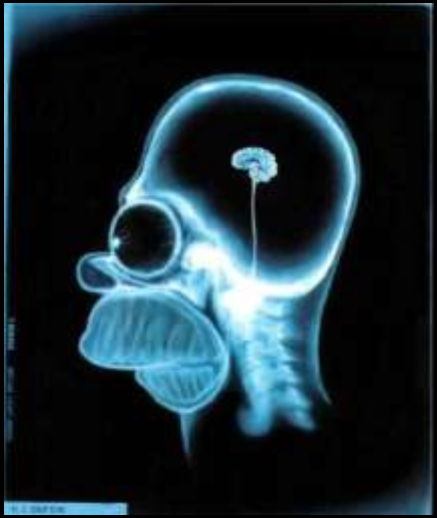


Face selective cells

‘Face’ sensitive cells are often viewpoint dependent



Neuroimaging Studies of the Human Visual System

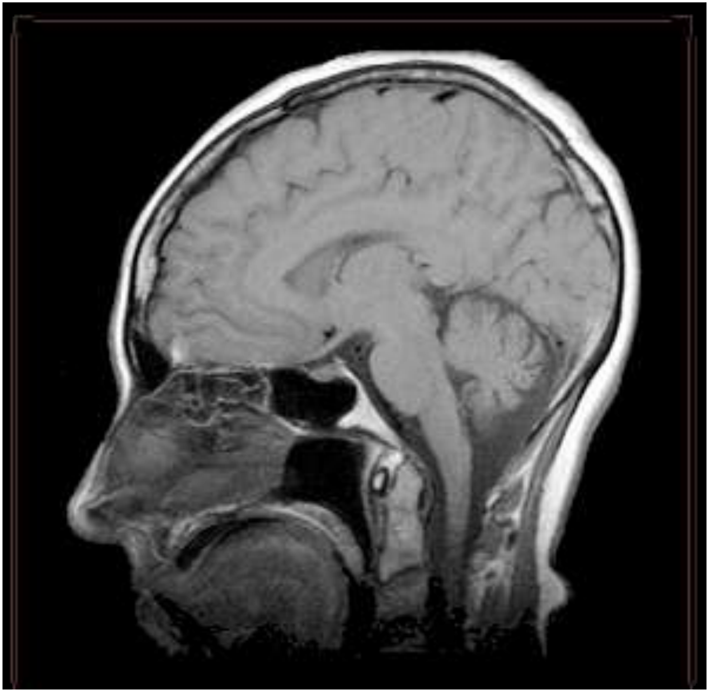


MRI

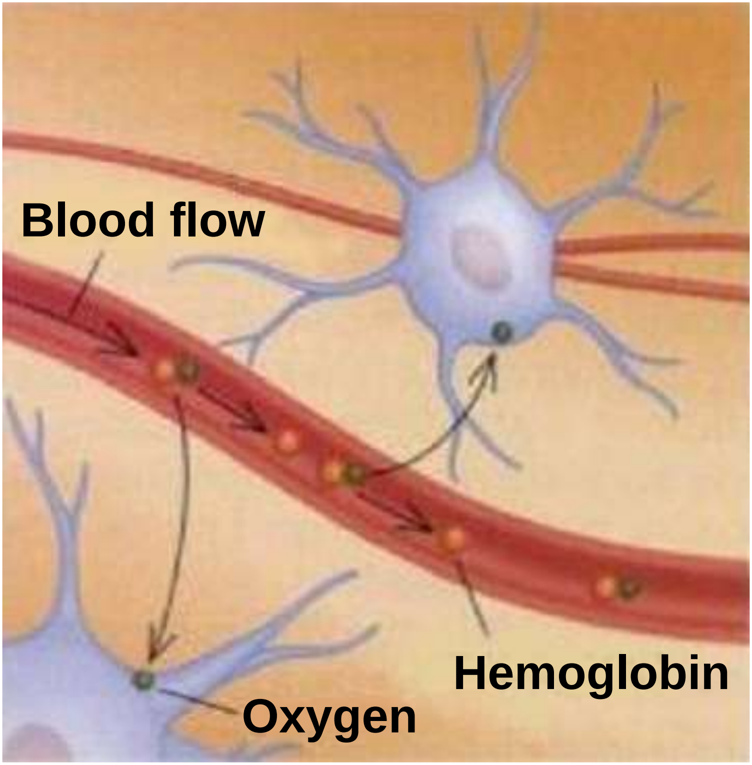
Magnetic
Resonance Imaging

fMRI

4 Tesla Magnet at the
Centre for Brain and Mind

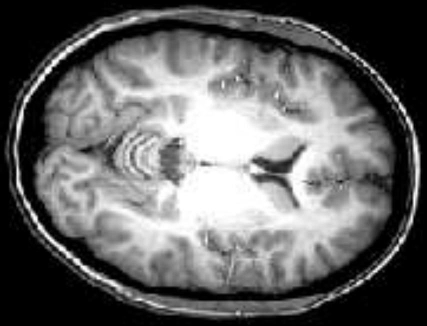


Blood flow increases as a function of neural activity



The fMRI signal depends on the difference in the magnetic properties of oxygenated and de-oxygenated hemoglobin.

Anatomical image



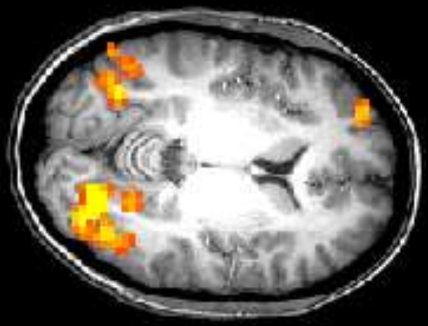
Functional images

Condition 1

minus

Condition 2

Superimposed images

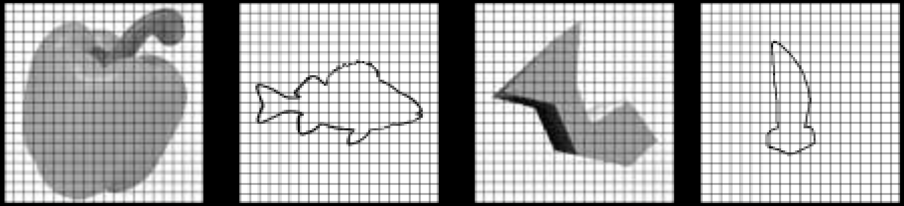


Functional images are subtracted from one another.

The differences in the two images are then superimposed on the anatomical image.

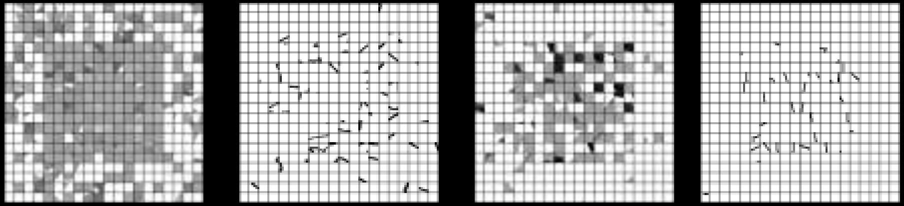
fMRI studies of Object Recognition

Intact Objects

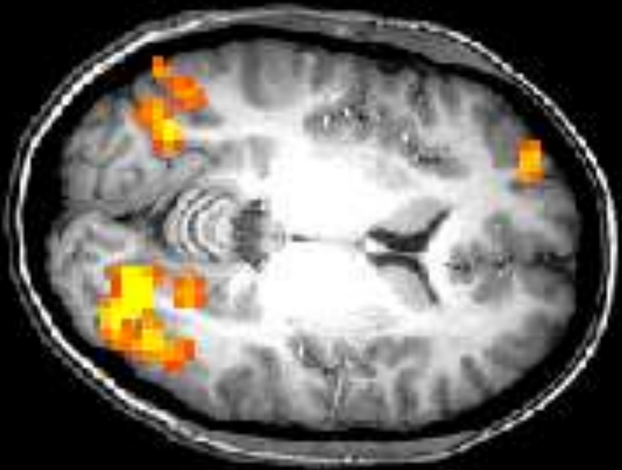


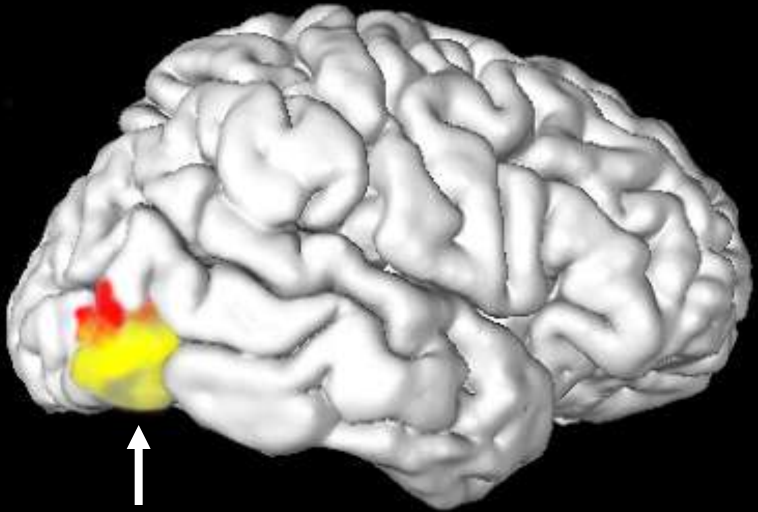
minus

Scrambled Objects



James, Culham, Humphrey, Milner, & Goodale (2003) *Brain*

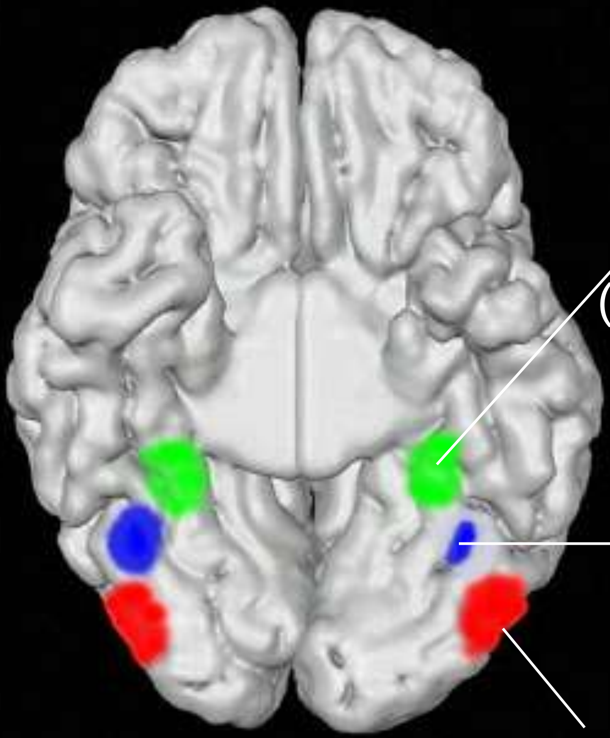




Lateral Occipital area (area LO) activation

Ventral ‘perception’ stream

front



Underside
of brain

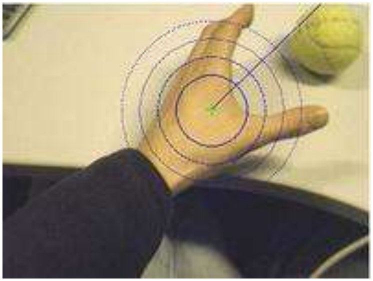
PPA
(places)

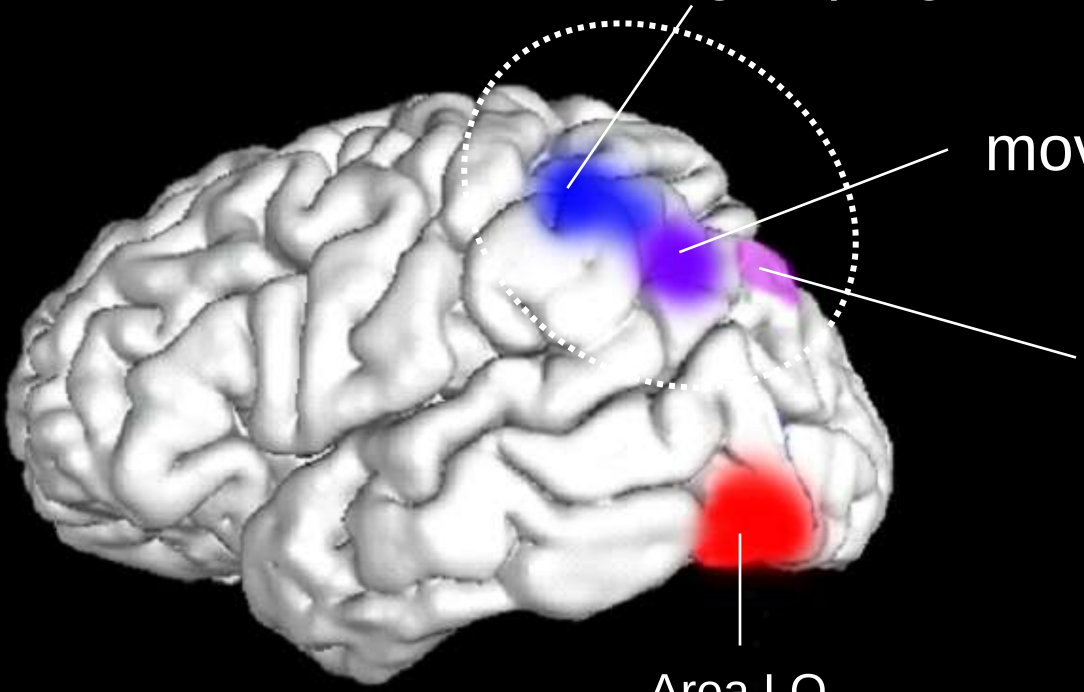
FFA
(faces)

area LO
(objects)

back

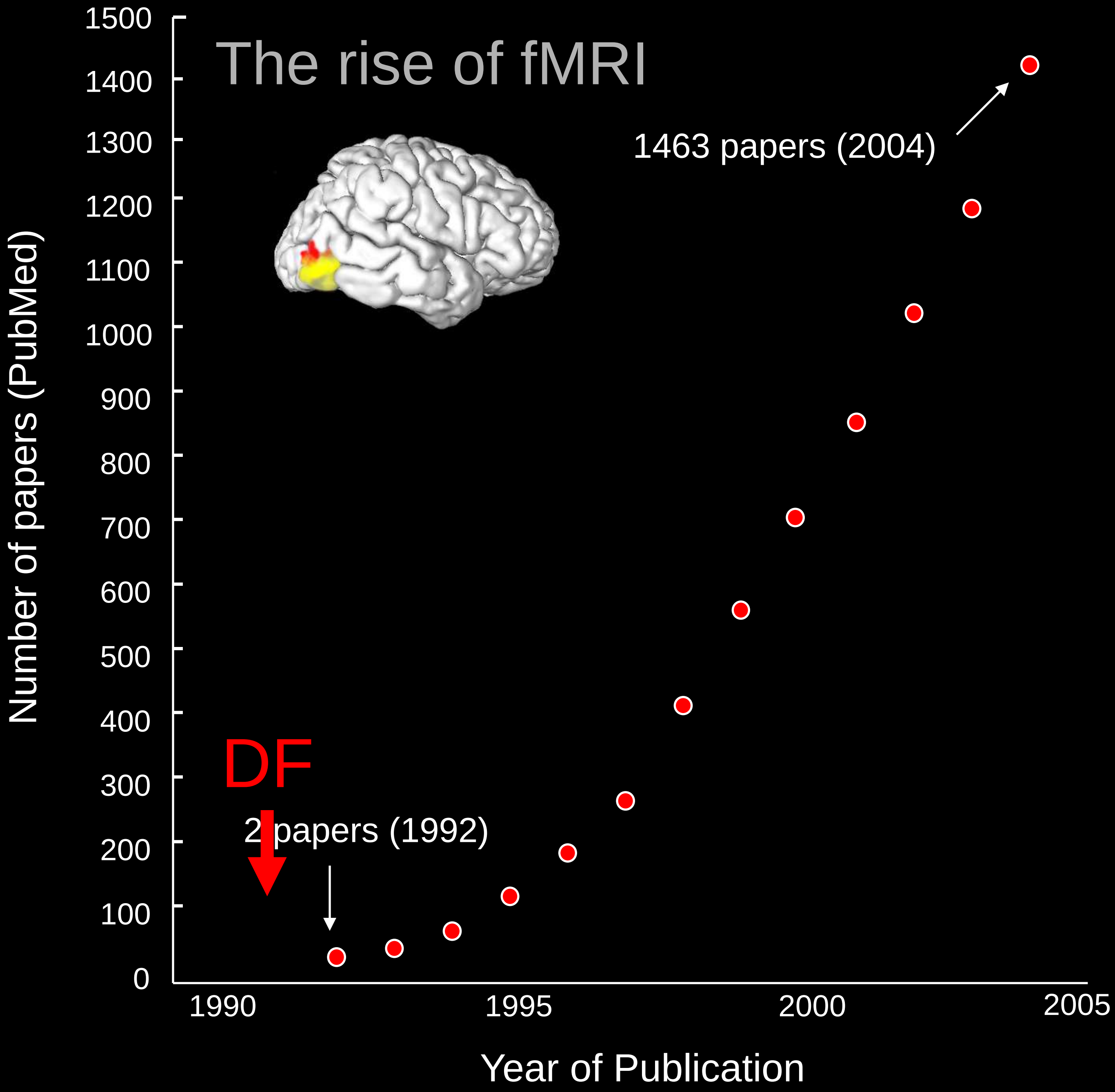
Dorsal ‘action’ stream





Connolly, Goodale, Menon, & Munoz (2002) *Nature Neuroscience*
Connolly, Andersen, & Goodale (2003) *EBR*
Culham, Danckert, Menon, Gati, & Goodale (2003) *EBR*

The rise of fMRI



FMRI investigation of DF’s ventral stream during object recognition

4 T whole body scanner (Varian/Siemens)

13 coronal slices

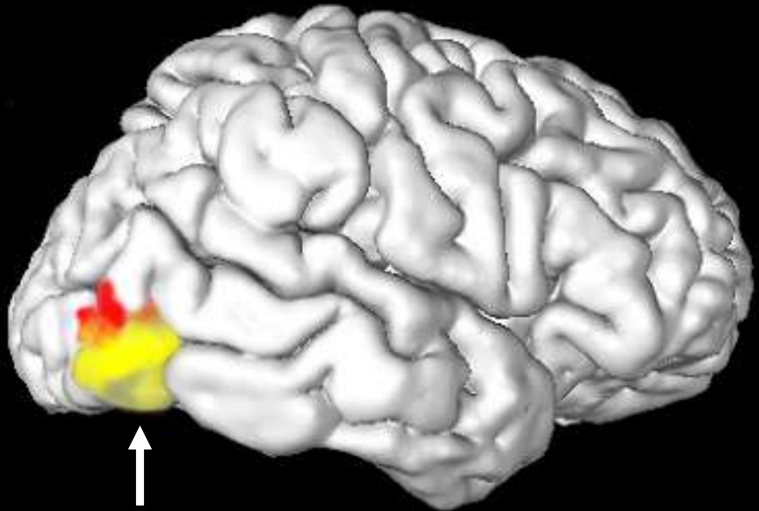
Voxel size: 3.0 x 3.0 x 6.0 mm

Event-related design

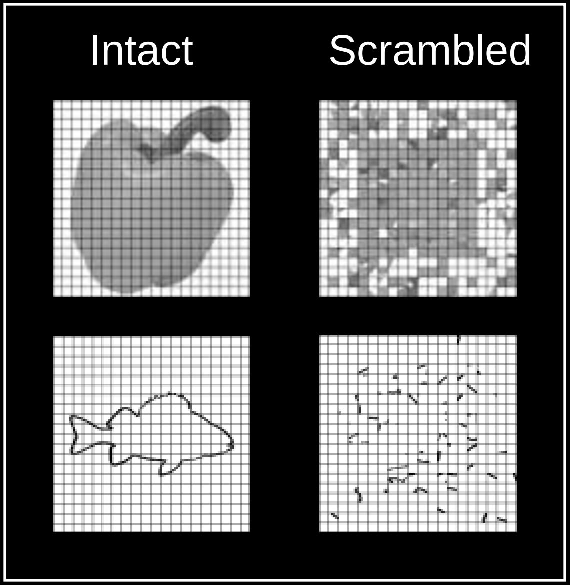
James, Culham, Humphrey, Milner, & Goodale (2003) *Brain*

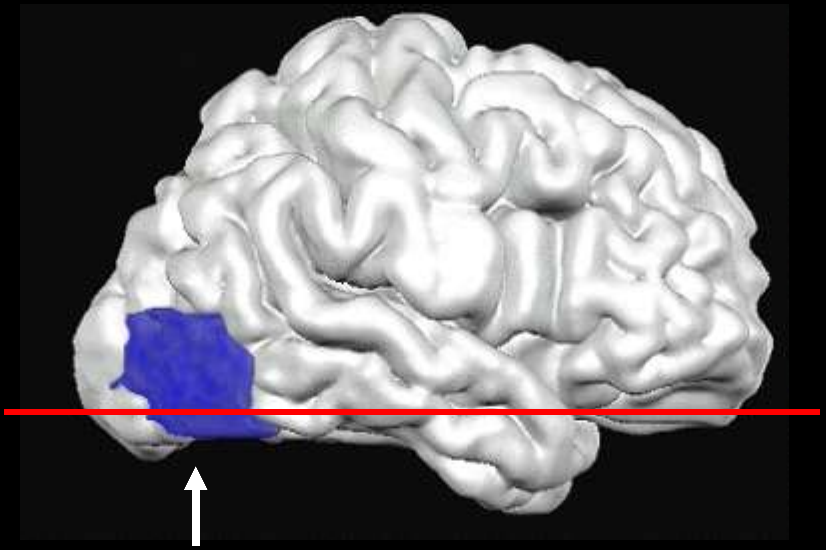
Normal observer’s brain

DF’s brain

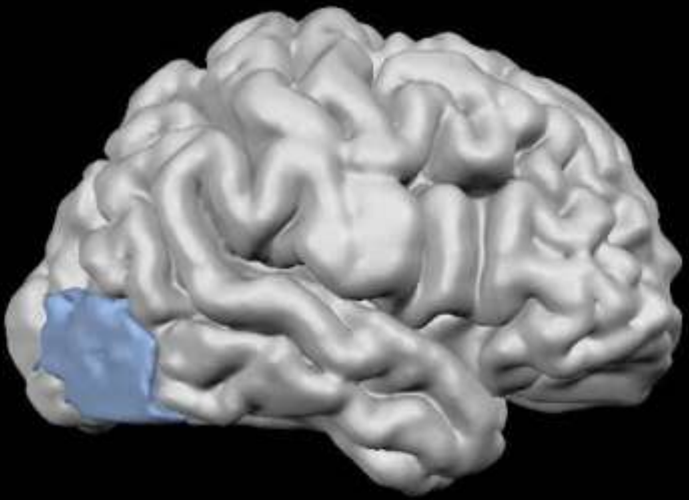


Lateral Occipital area (area LO) activation

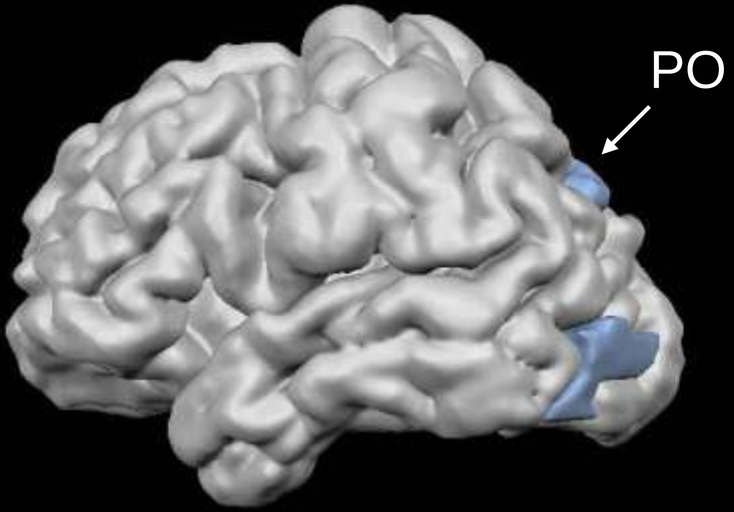




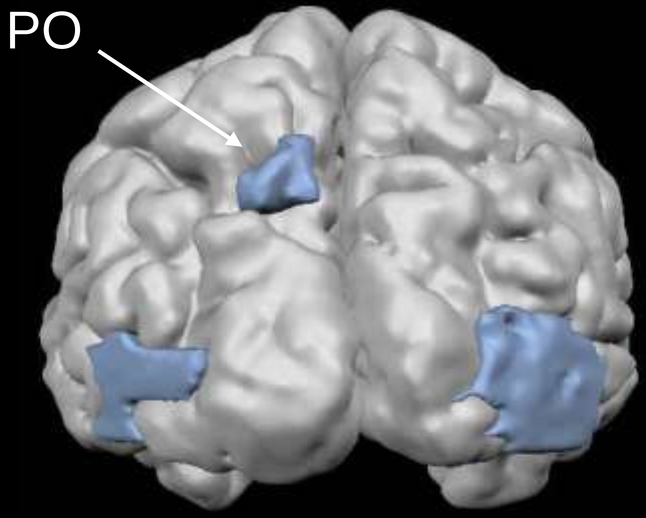
area LO lesion



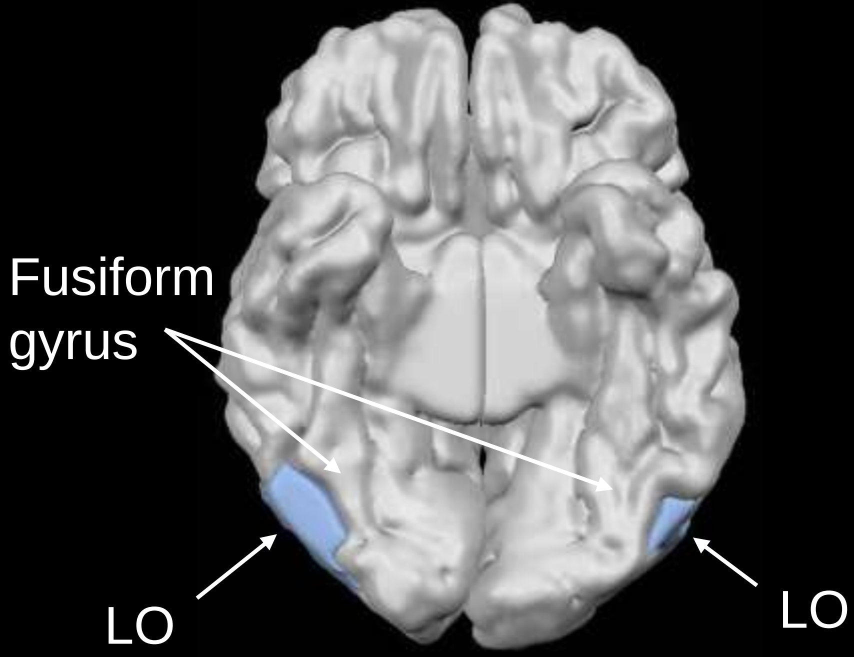
Right lateral



Left lateral

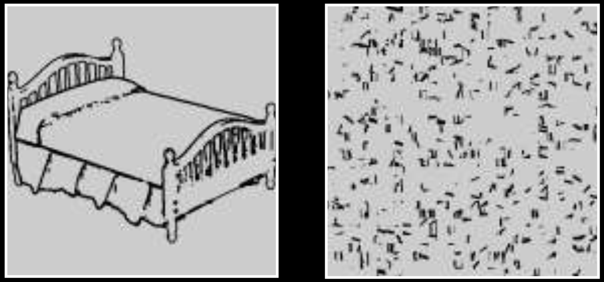


Posterior

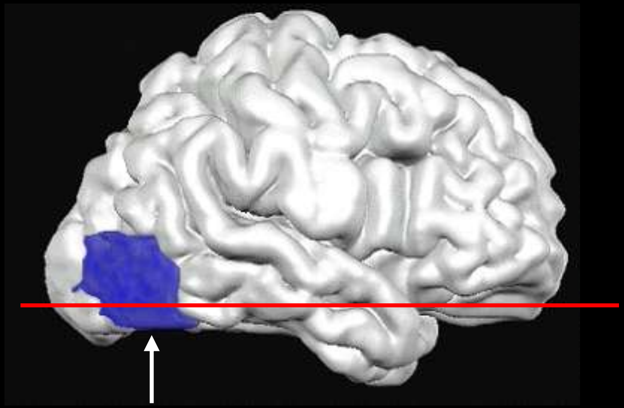


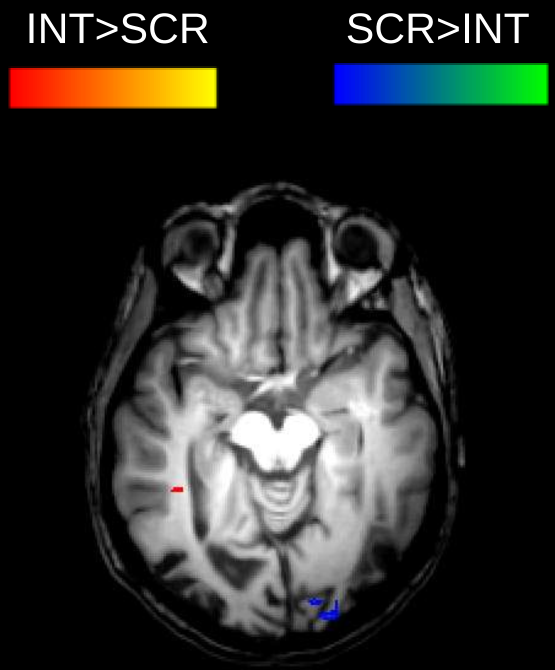
Ventral

Intact Line Drawings
versus scrambled

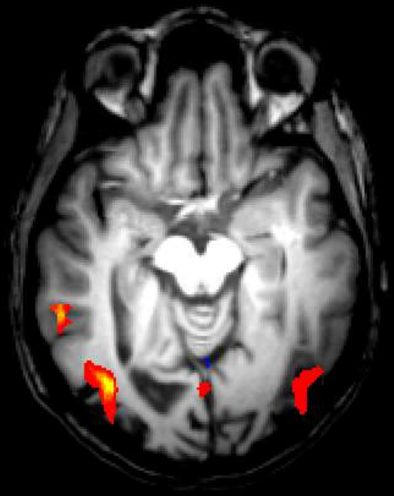


Each image presented
for 4 s with 12-s ISI


LO
lesion



DF

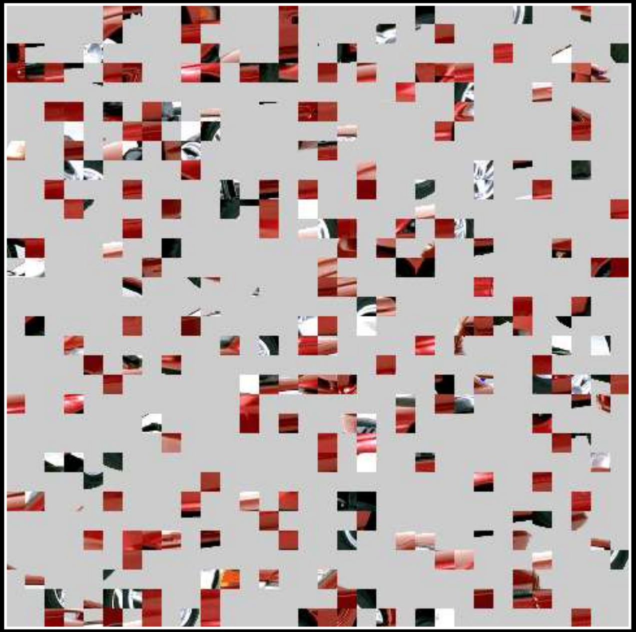


Control

(activation plotted
on DF’s brain)

Intact Colored Picture

Scrambled Picture

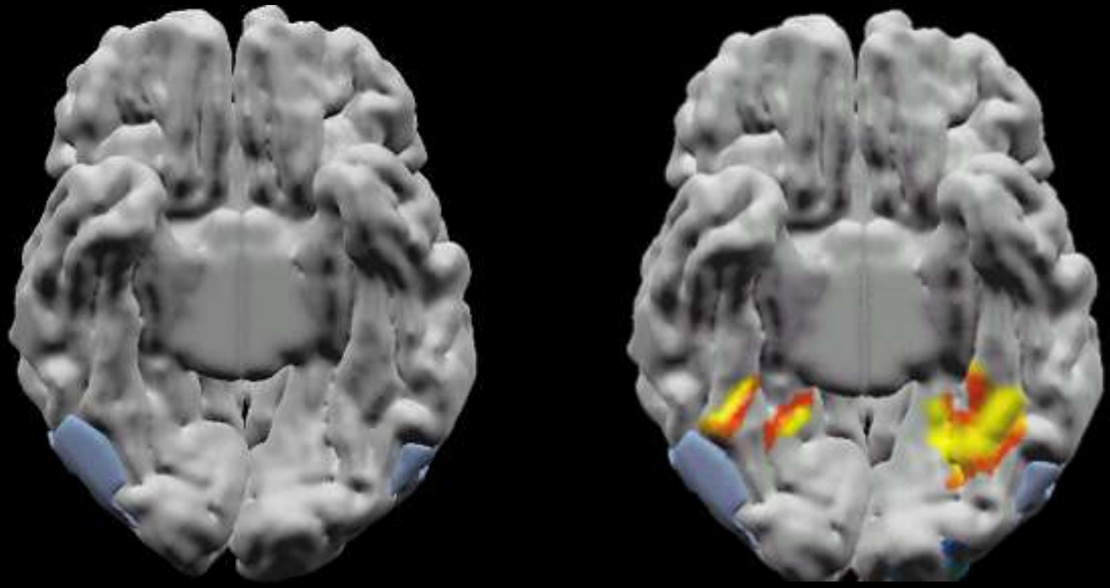


Each image presented
for 4 s with 12-s ISI

Ventral surface of DF’s cerebral cortex

INT>SCR 🟥

SCR>INT 🟦



Intact Line Drawings minus scrambled

Intact Colored Pictures minus scrambled

FMRI studies of DF’s dorsal stream

13 slices parallel to calcarine through parietal cortex

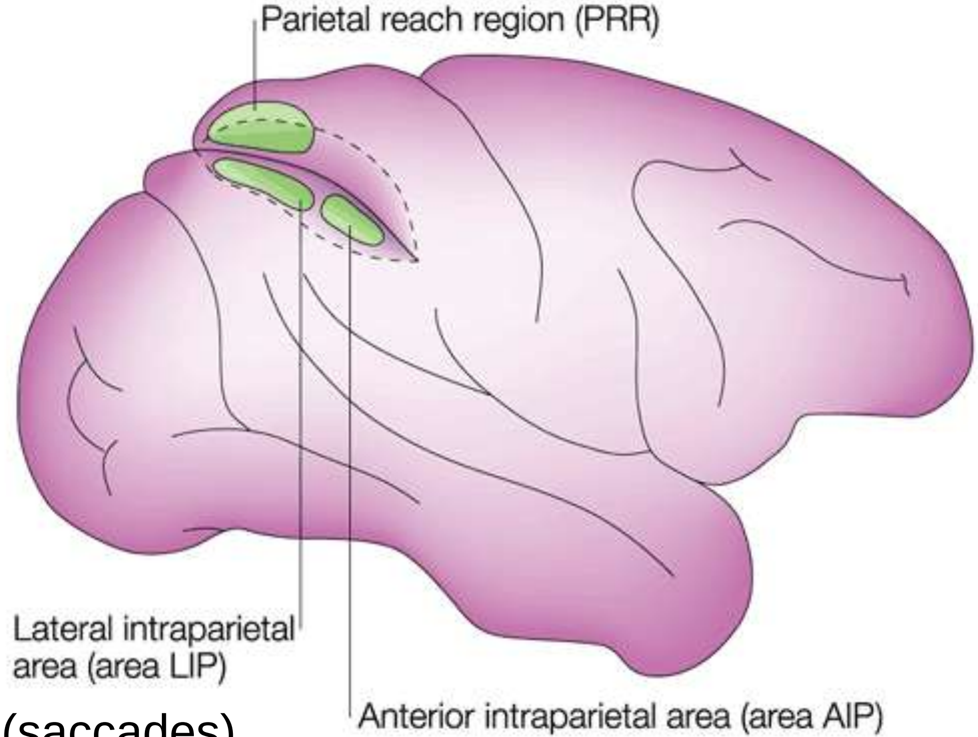
Voxel size: 3.13 x 3.13 x 6.0 mm

Event-related design

James, Culham, Humphrey, Milner, & Goodale (2003) *Brain*

Macaque Monkey
(single-unit studies)

(reaching)

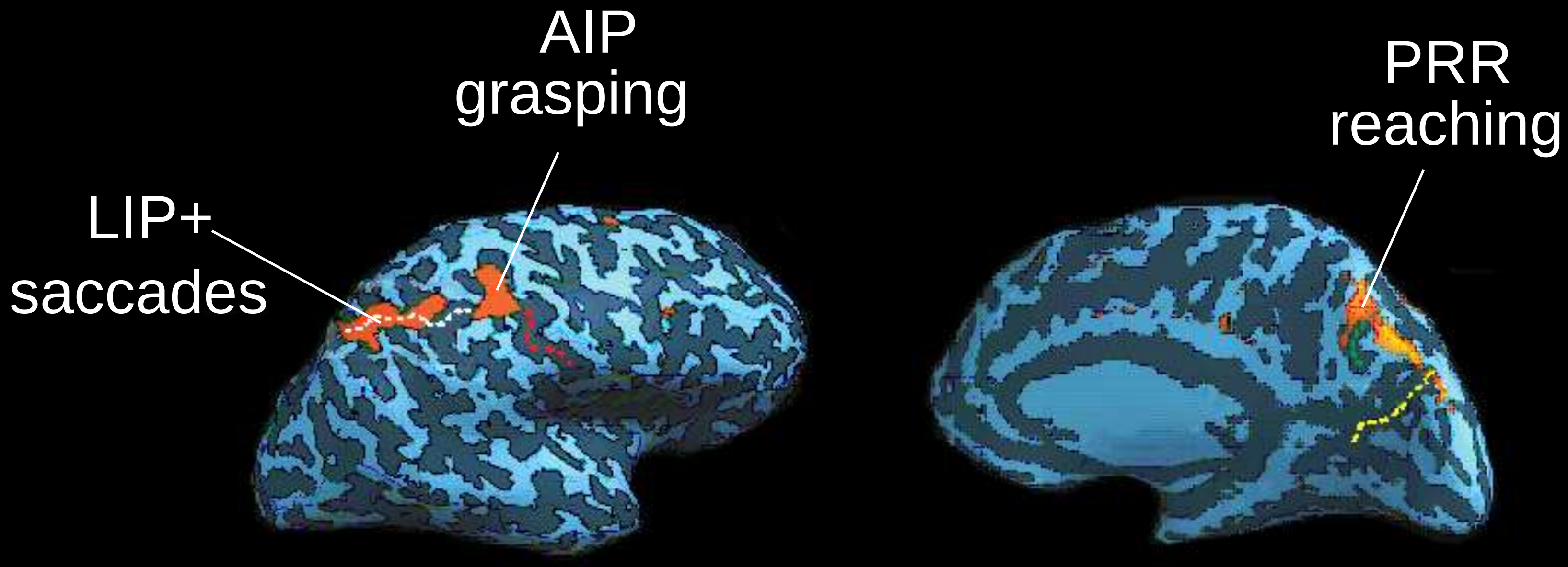


(saccades)

(grasping)

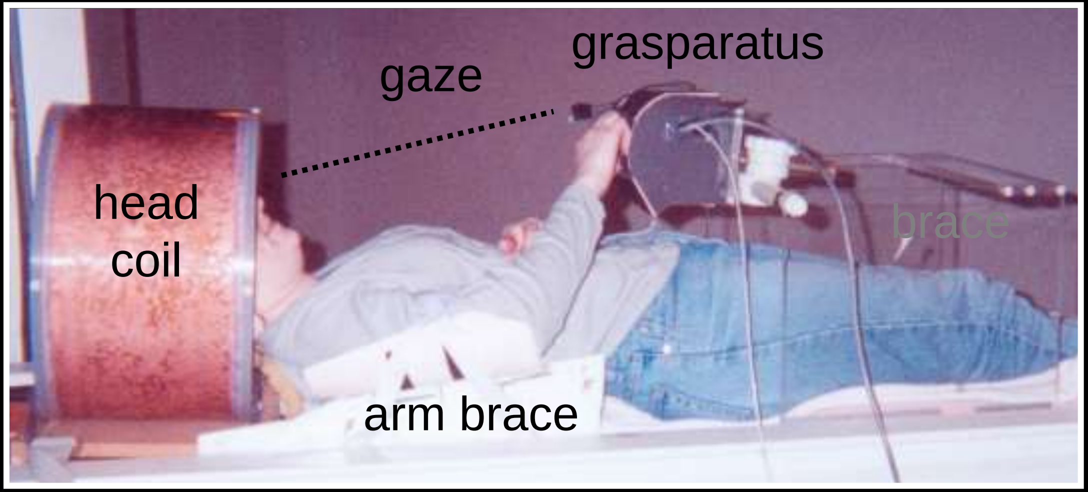
Cohen & Andersen (2002) Nature Reviews Neuroscience

fMRI studies of Visuomotor Control



Connolly, Goodale, Menon, & Munoz (2002) *Nature Neuroscience*
Connolly, Andersen, & Goodale (2003) *EBR*
Culham, Danckert, DeSouza, Gati, Menon & Goodale (2003). *EBR*

Grasping in the magnet




Grasping

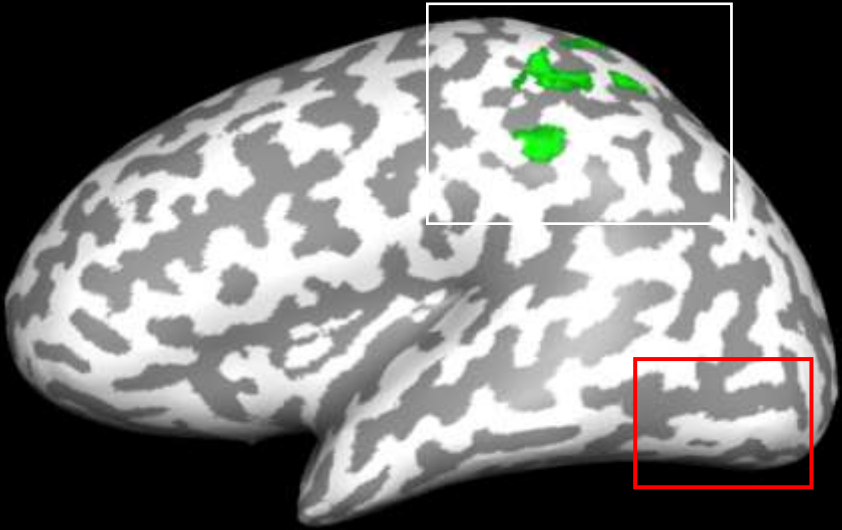

Reaching

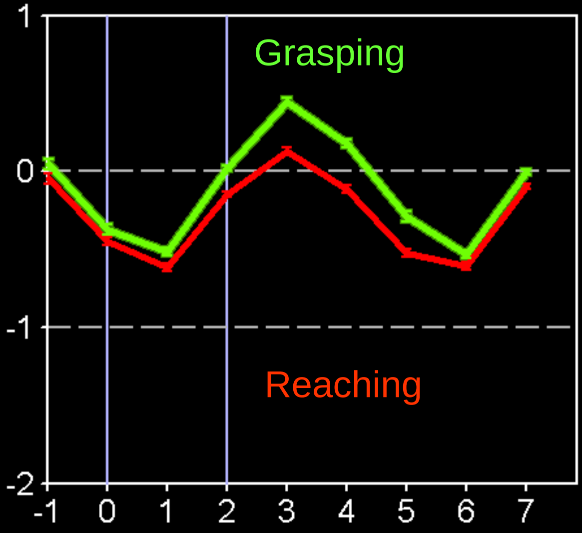
Culham, Danckert, DeSouza, Gati, Menon & Goodale (2003). *Experimental Brain Research*

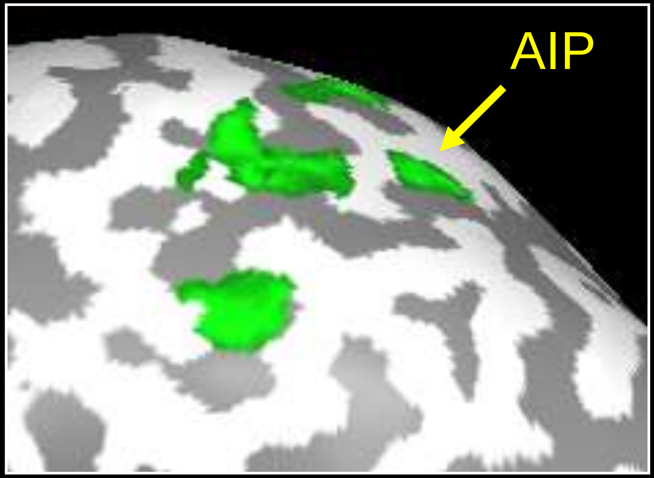
FMRI studies of grasping in normal subjects

Grasping

Reaching

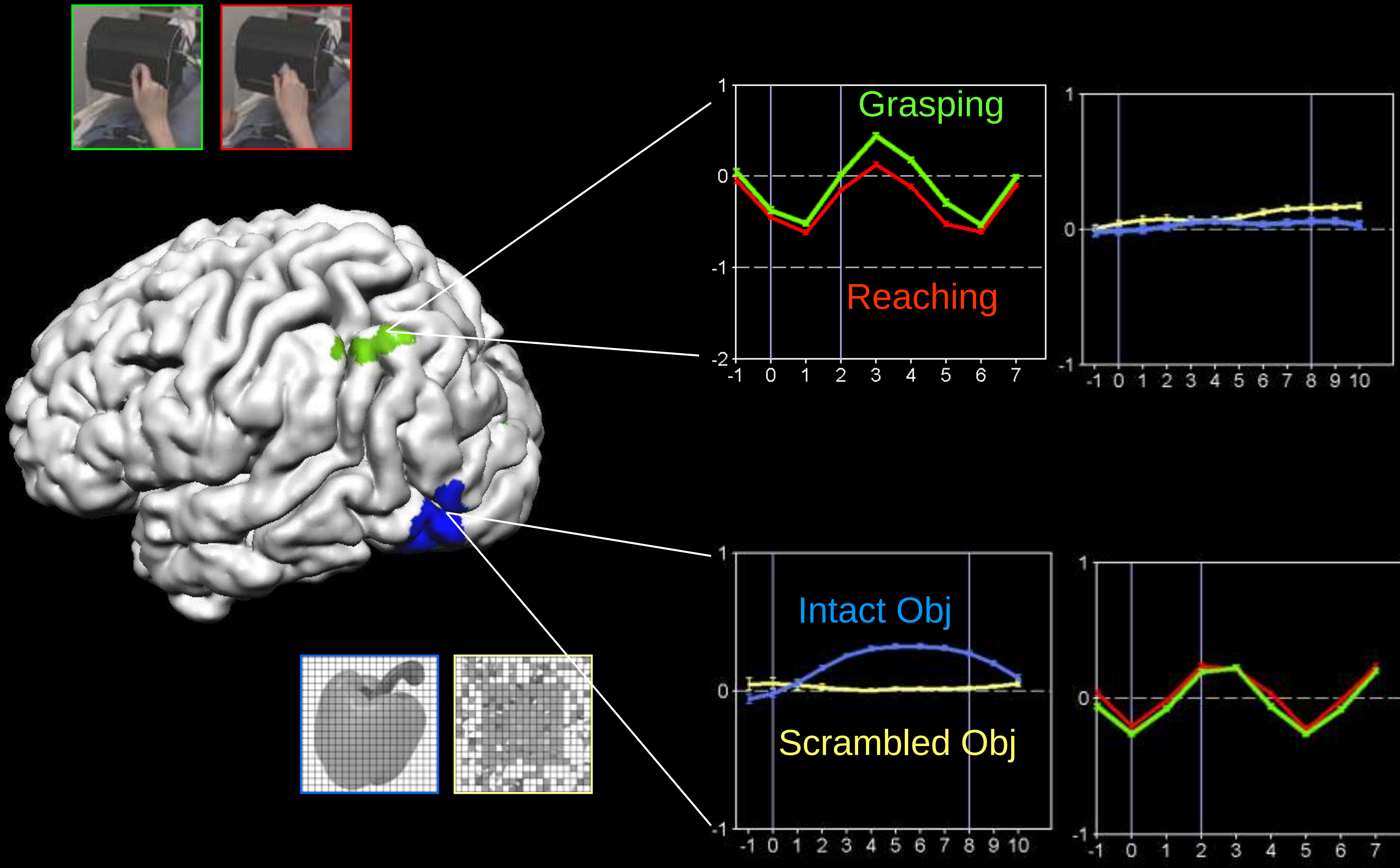






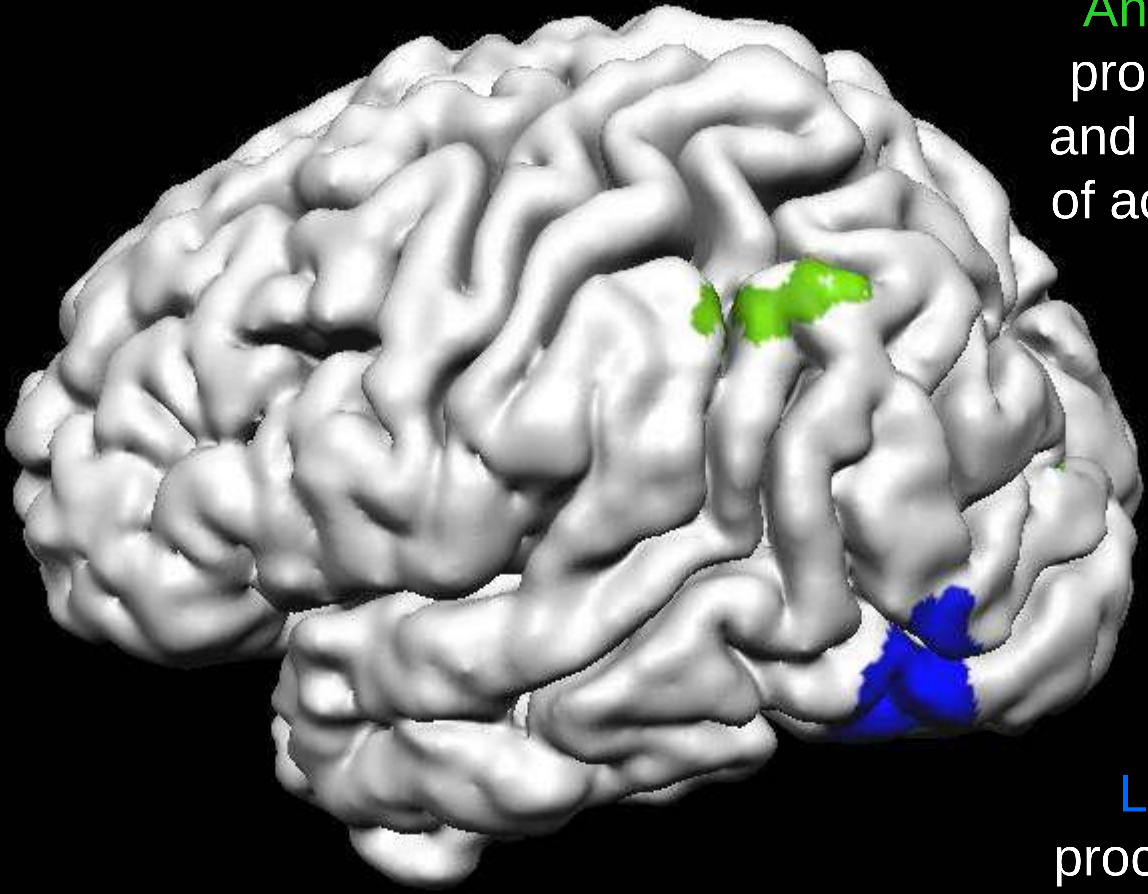
Culham, Danckert, De Souza, Gati, Menon, & Goodale (2003) *EBR*

Grasping vs. Object Recognition



Culham, Danckert, DeSouza, Gati,
Menon & Goodale (2003). *EBR*

Object Grasping vs. Recognition



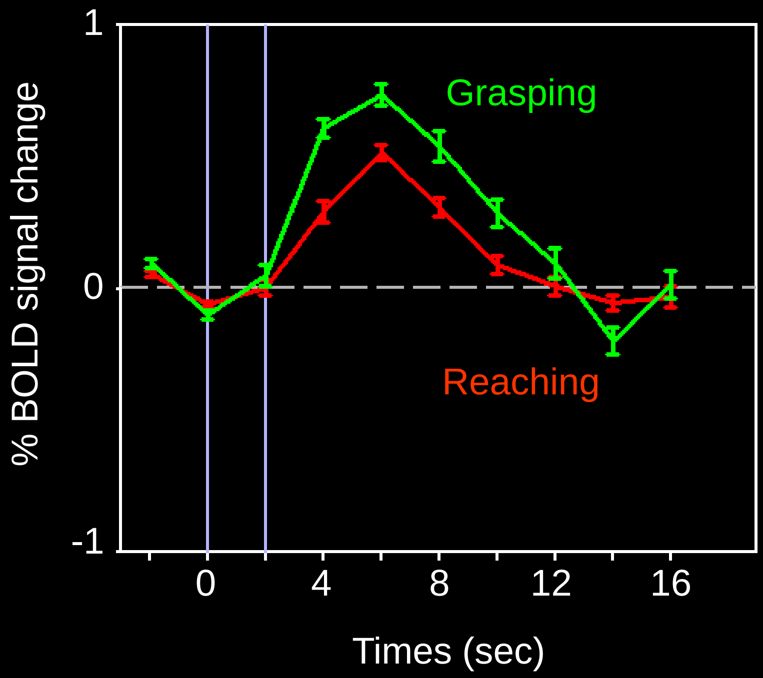
Anterior Intraparietal Sulcus
processes object shape, size
and orientation for the purpose
of actions such as GRASPING

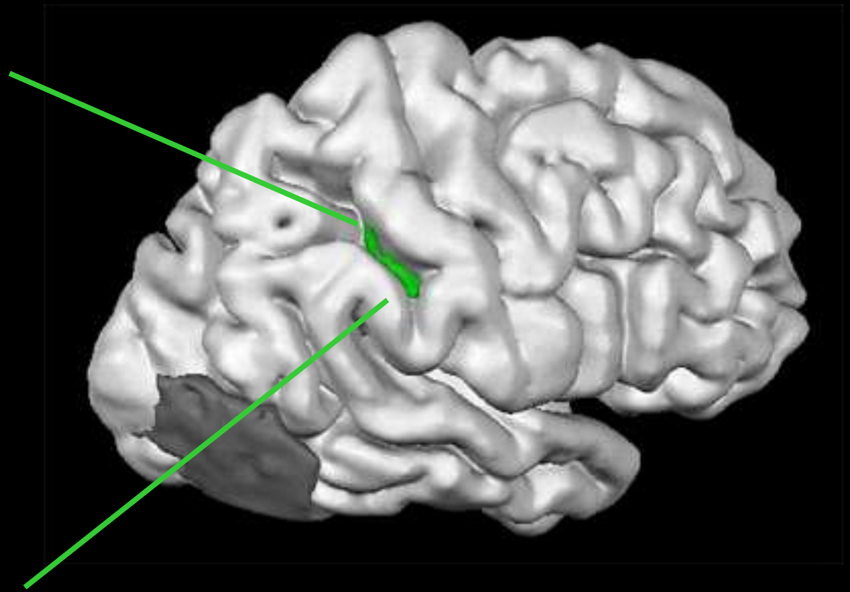
Lateral Occipital Cortex
processes object shape, size
and orientation for the purpose
of RECOGNITION

Patient DF: spared grasping is mediated by intact AIP

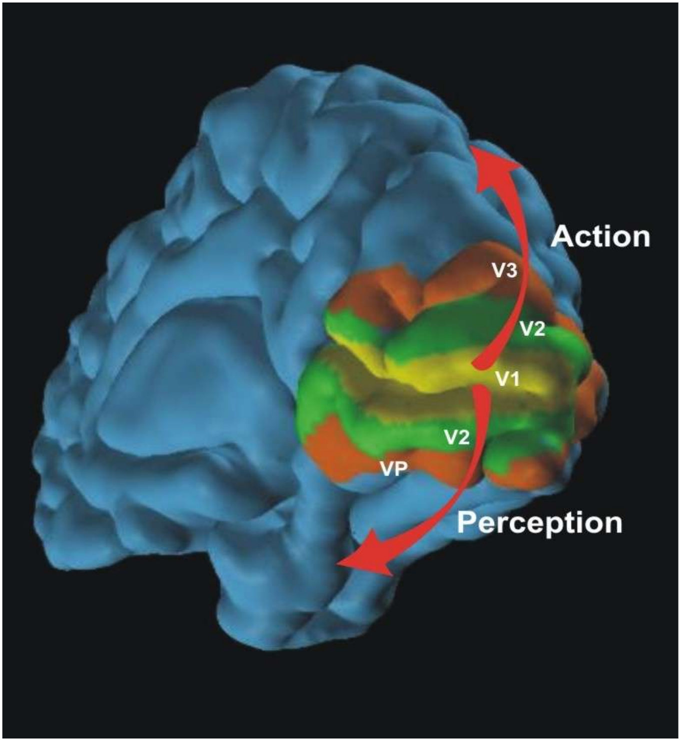

Grasping


Reaching





James, Culham, Humphrey, Milner & Goodale (2003). *Brain*

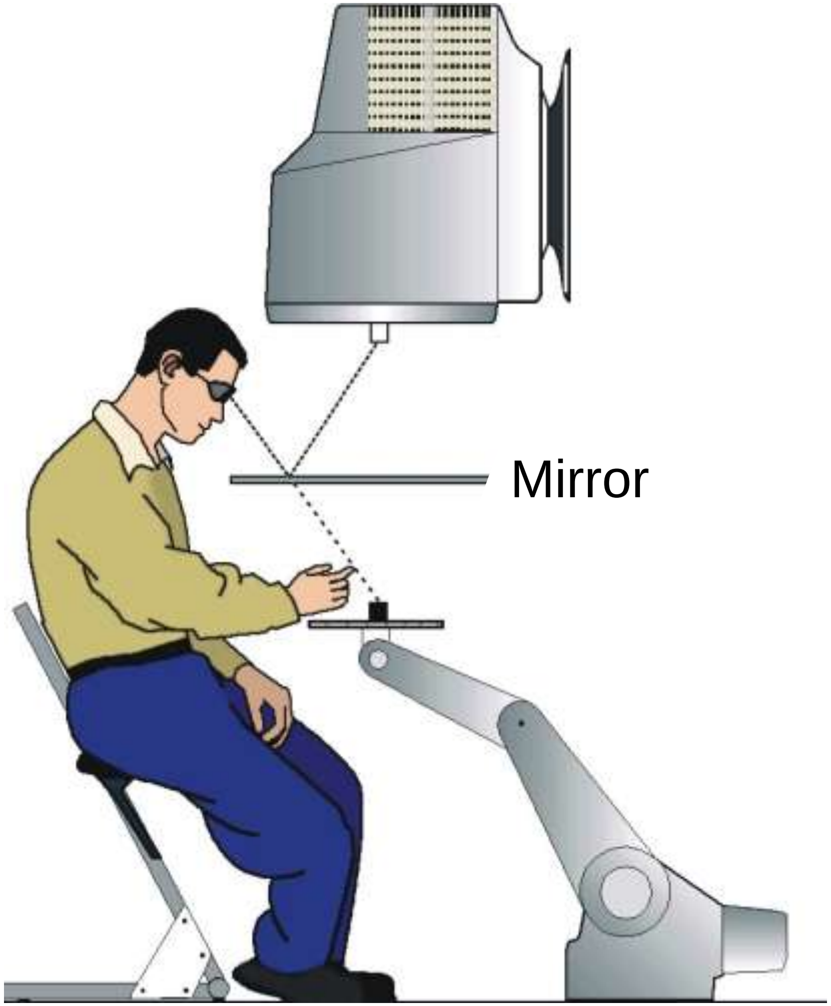


But why are there two separate visual systems?

Ventral Stream	Dorsal Stream
Scene-parsing and object identification	Visual control of motor output
Scene-based frame of reference	Effector-based frames of reference
Relational metrics	Absolute metrics
Long-term representations	Moment-to-moment computations
Contents of visual consciousness	Visuomotor transformations for (un)conscious acts

Goodale, M.A. & Humphrey, G.K. (1998). *Cognition.*

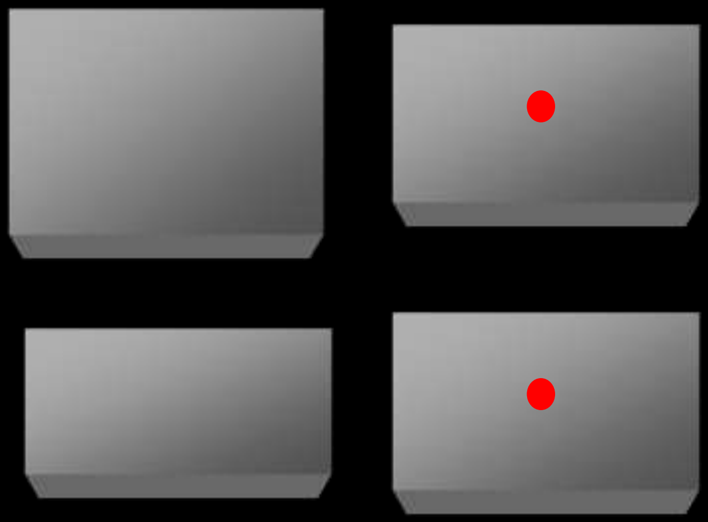
Virtual Workbench



Hu, Y. & Goodale, M.A.
(2000). *J. Cogn. Neurosci.*

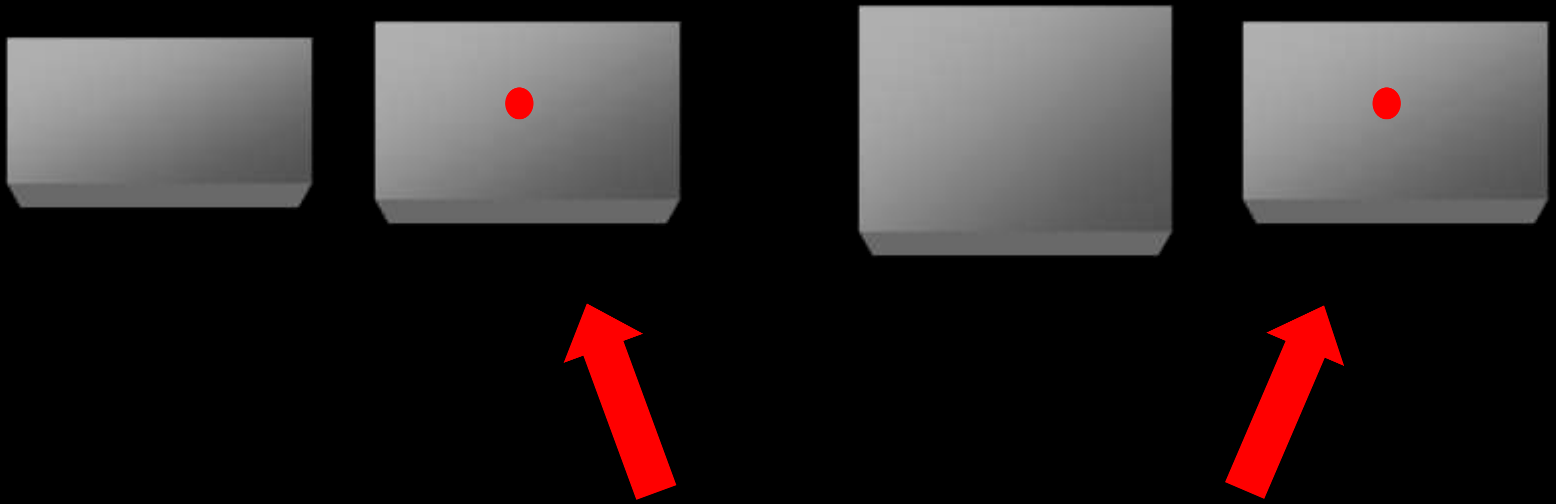
Real-time vs. Delayed Estimation

“Show me how big the one with the dot is”

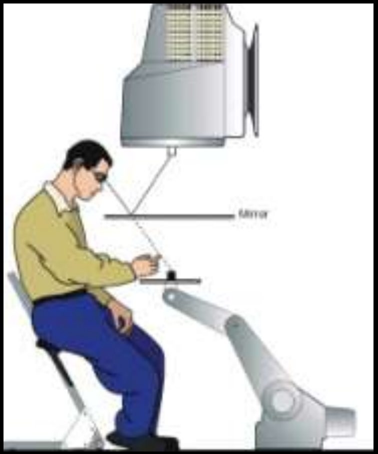


Two conditions: No delay vs. 5s delay

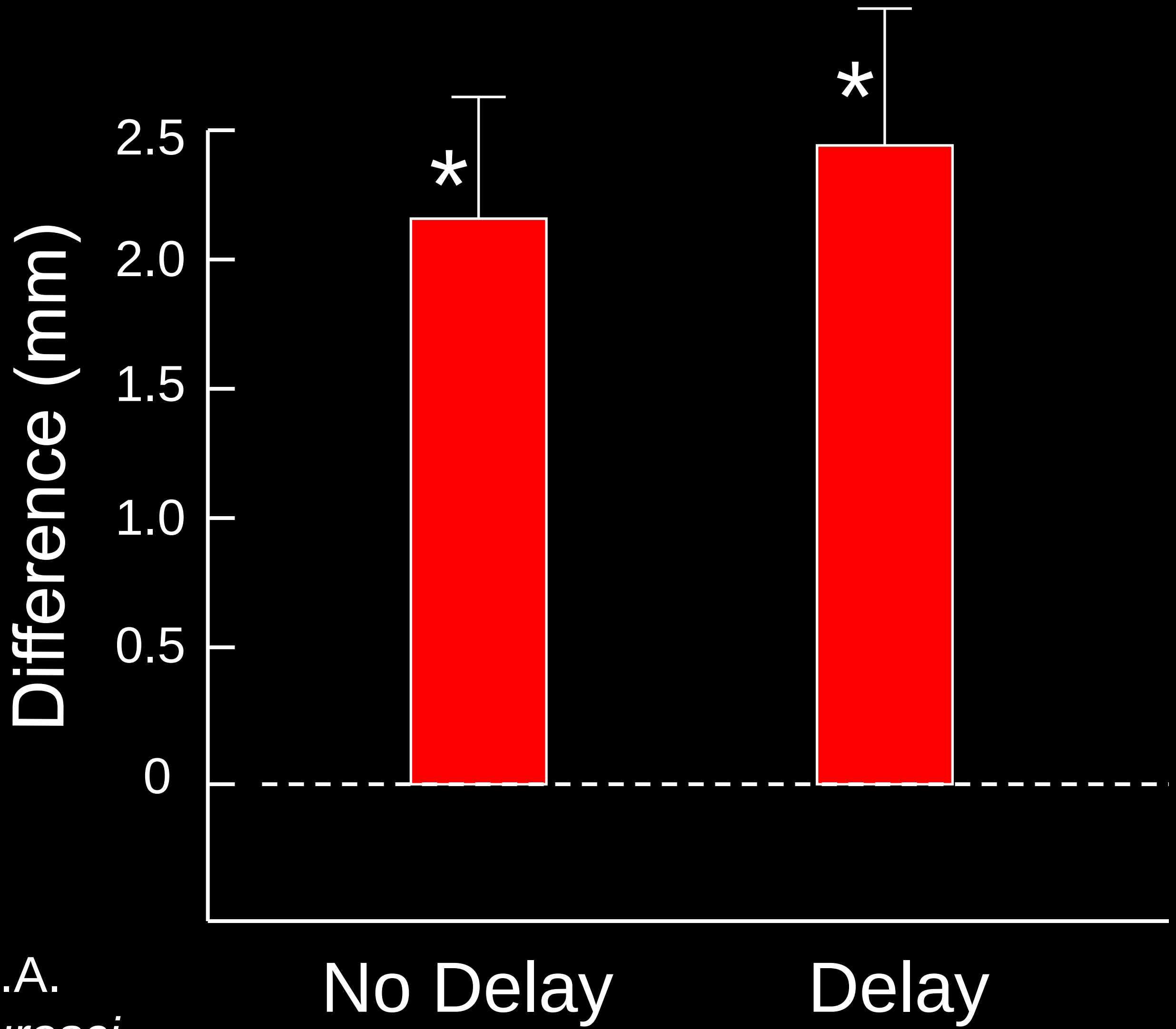
Measuring the Size-contrast Effect



Difference Score = “Larger” - “Smaller



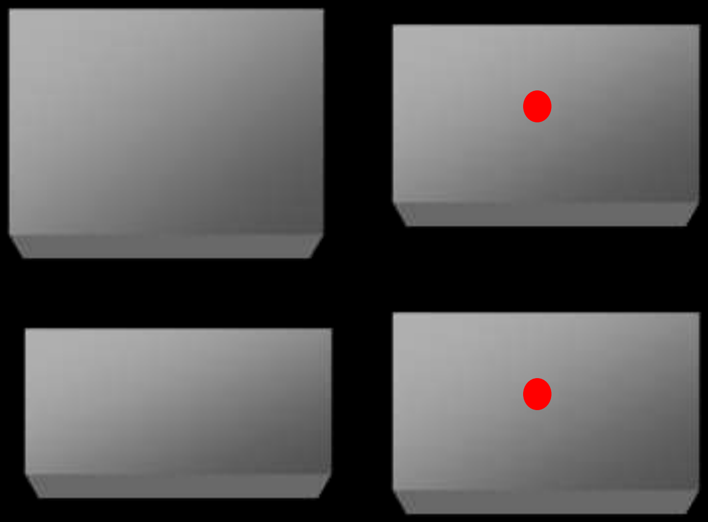
Size-contrast Effect: Estimation



Hu, Y. & Goodale, M.A. (2000). *J. Cogn. Neurosci.*

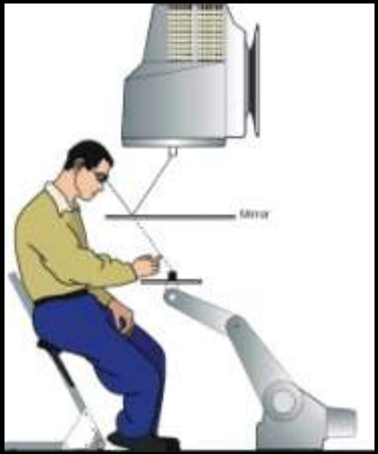
Real-time vs. Delayed Grasping

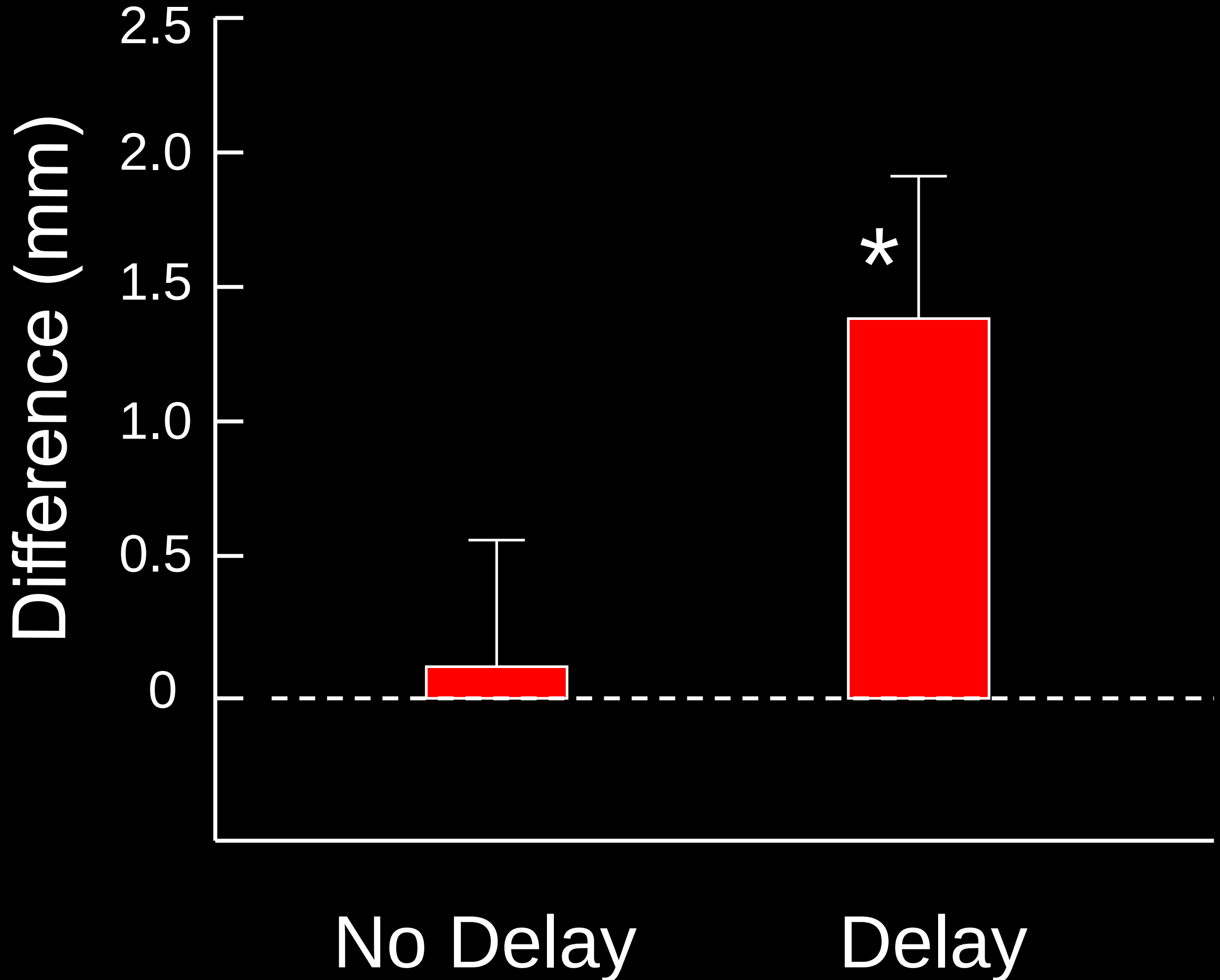
“Pick up the one with the dot”



Two conditions: No delay vs. 5s delay

Size-contrast Effect: Grasping





Hu, Y. & Goodale, M.A.
(2000). *J. Cogn. Neurosci.*

Normal Grasping

Object viewing

Automatic visuomotor response

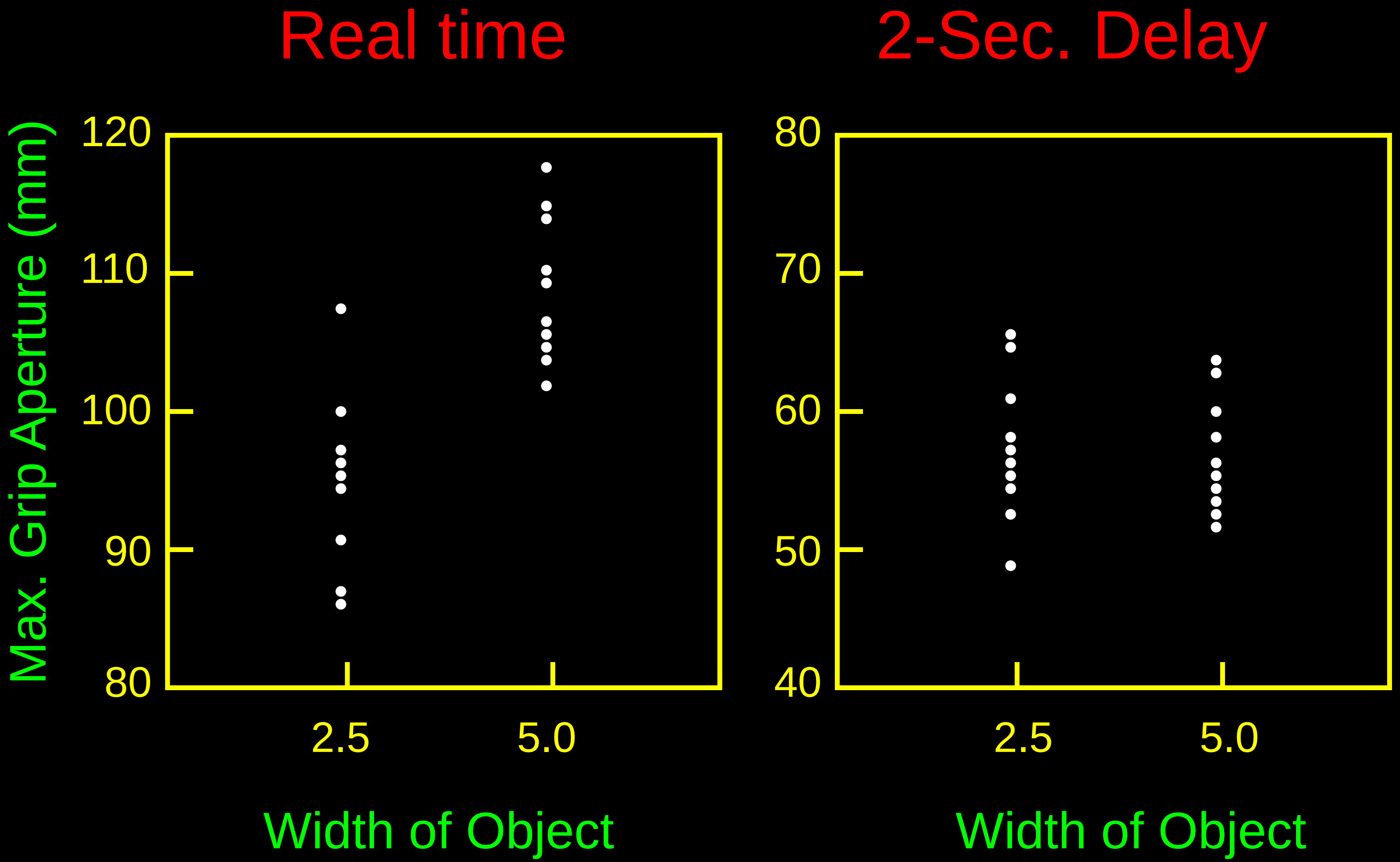
Pantomimed Grasping

Object viewing

Delay Period:
Visuomotor program decays or is never formed.
Image generation takes place

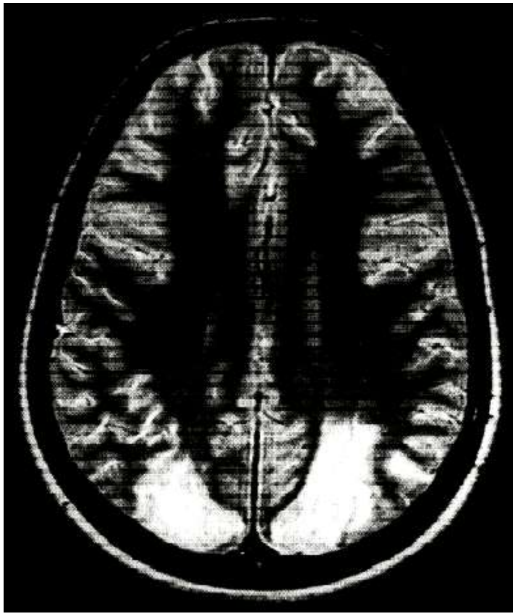
Perceptually driven pantomimed response

DF



Goodale, Jakobson, & Keillor(1994) Neuropsychologia

Optic ataxia patient (IG)

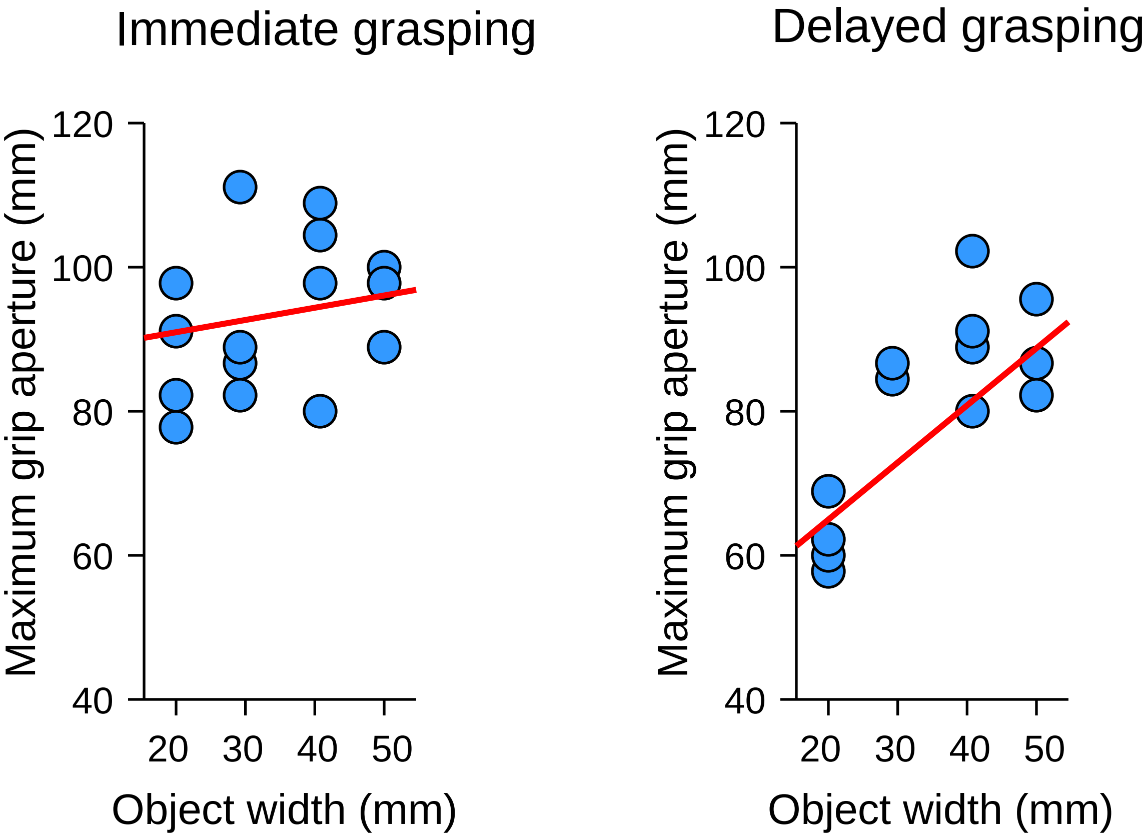


Lesion to posterior parietal cortex bilaterally

Conscious form perception *intact*

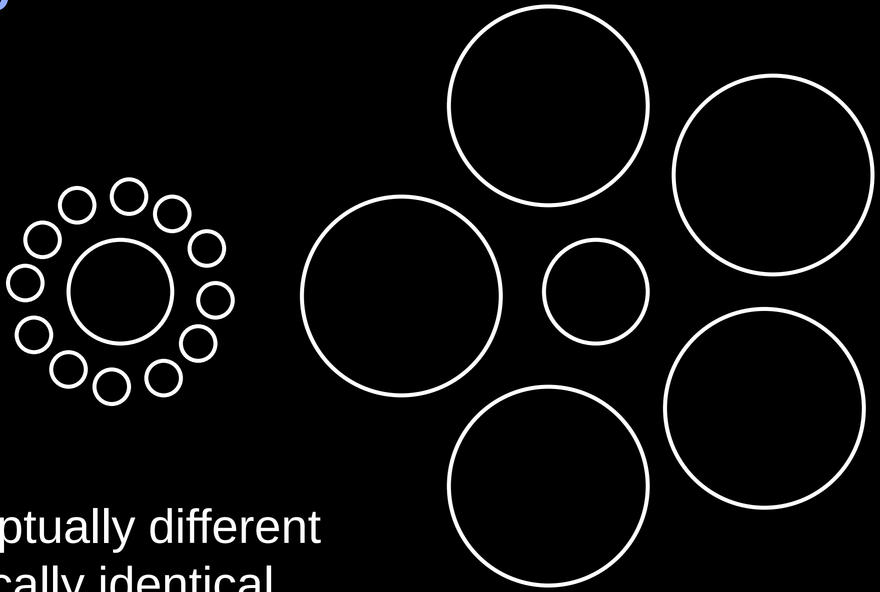
Grasping visible objects: poor grip scaling

Patient IG

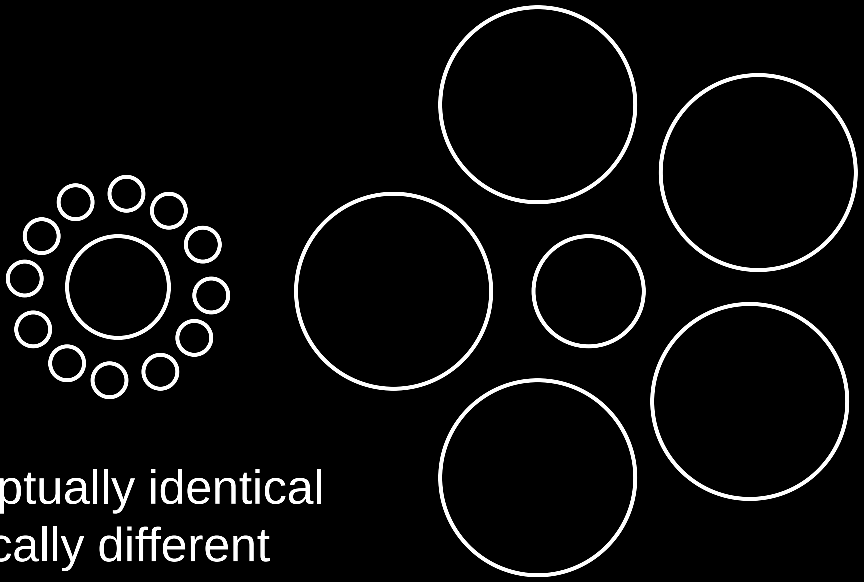


Milner et al. (2001) *Current Biology*

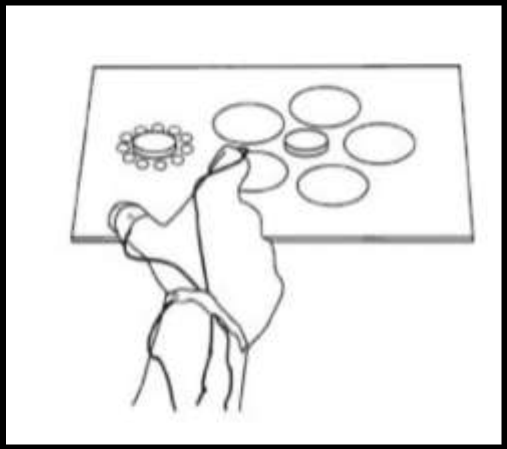
Acting on illusions



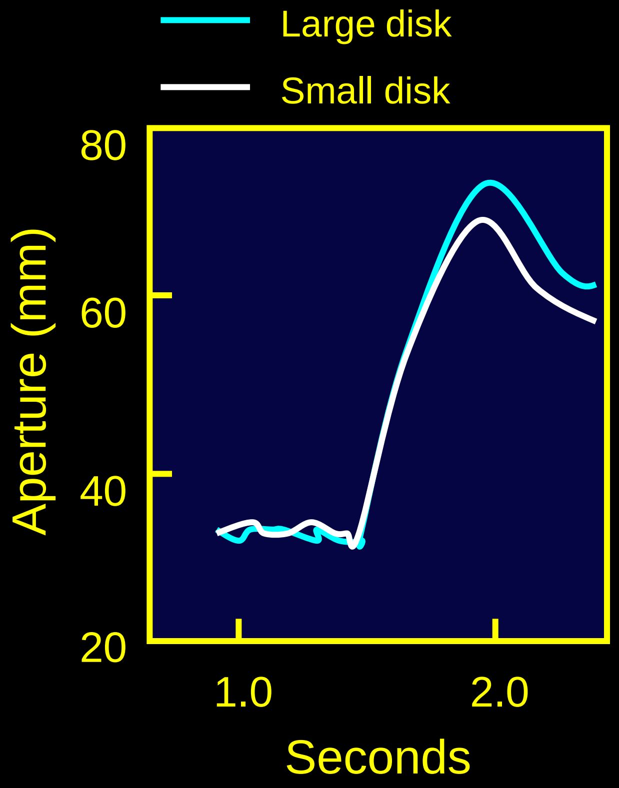
Perceptually different
Physically identical



Perceptually identical
Physically different



Perceptually Identical Trials

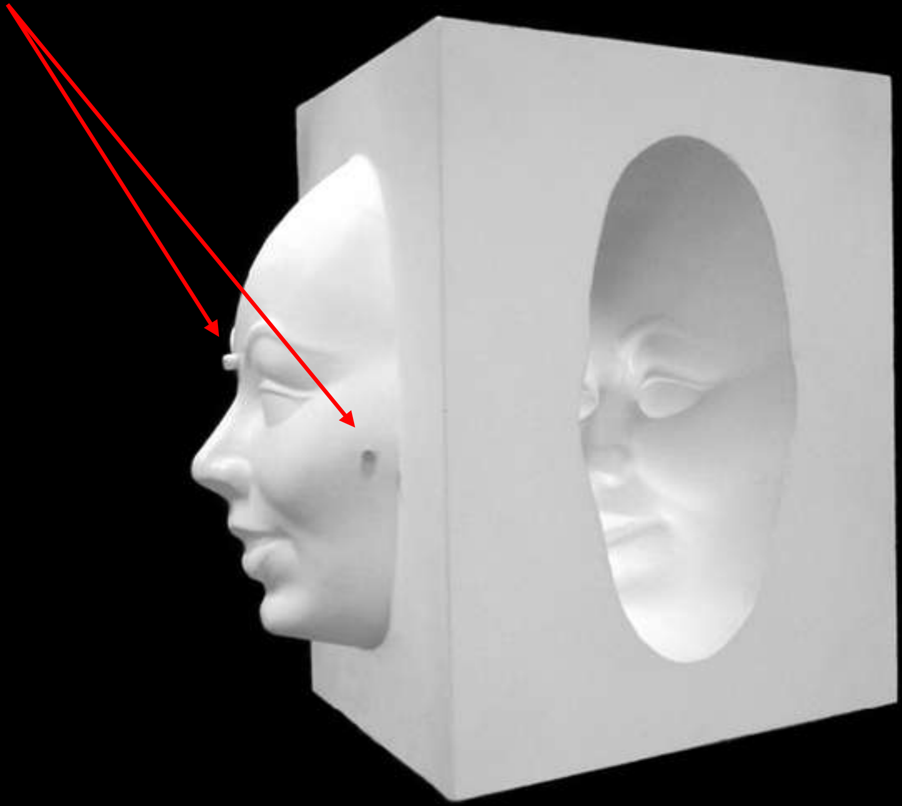


Aglioti, DeSouza, & Goodale (1995) *Current Biology*

Hollow face Illusion

courtesy of Richard Gregory

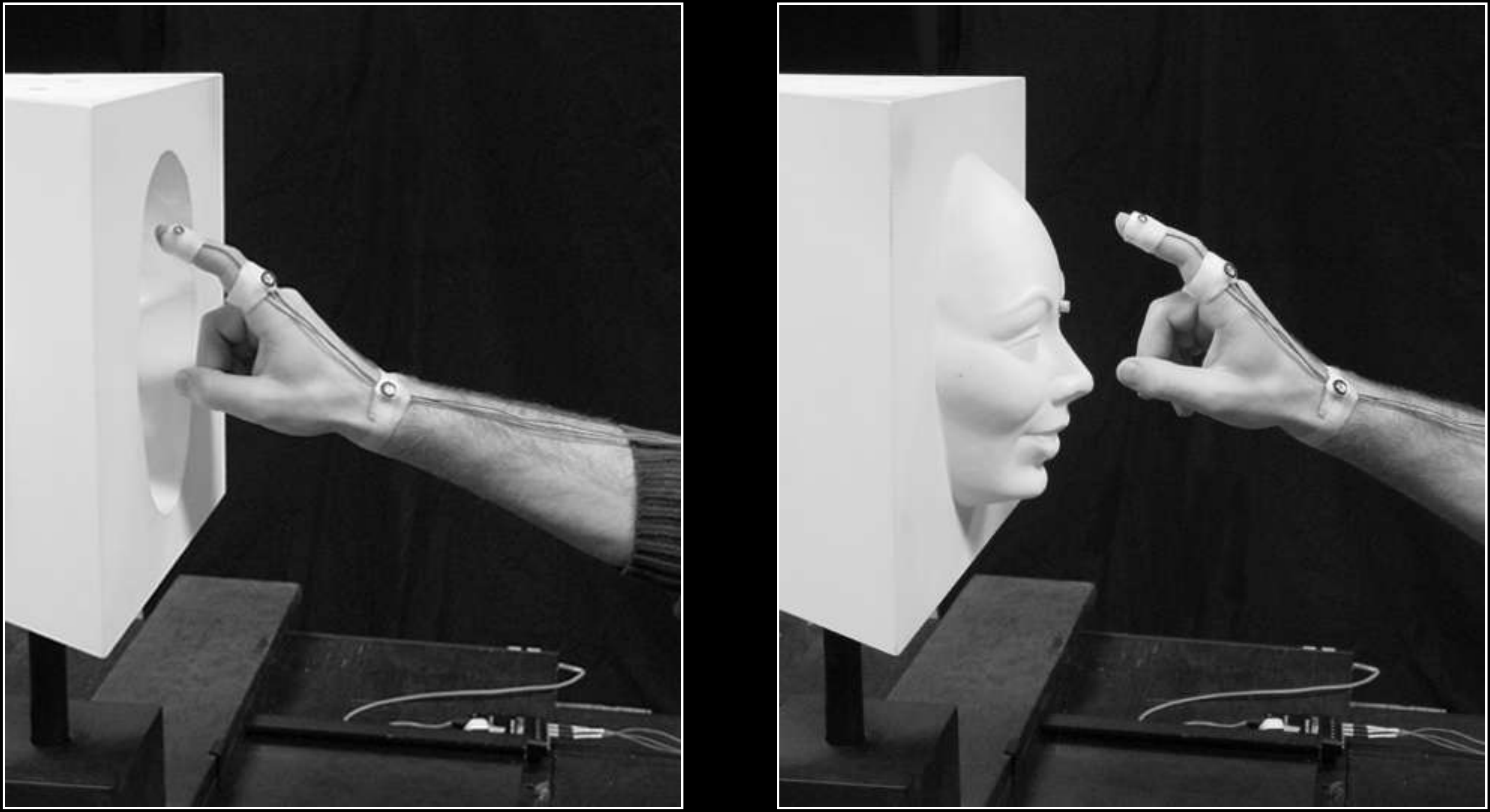
Hollow-face illusion: Perception and action



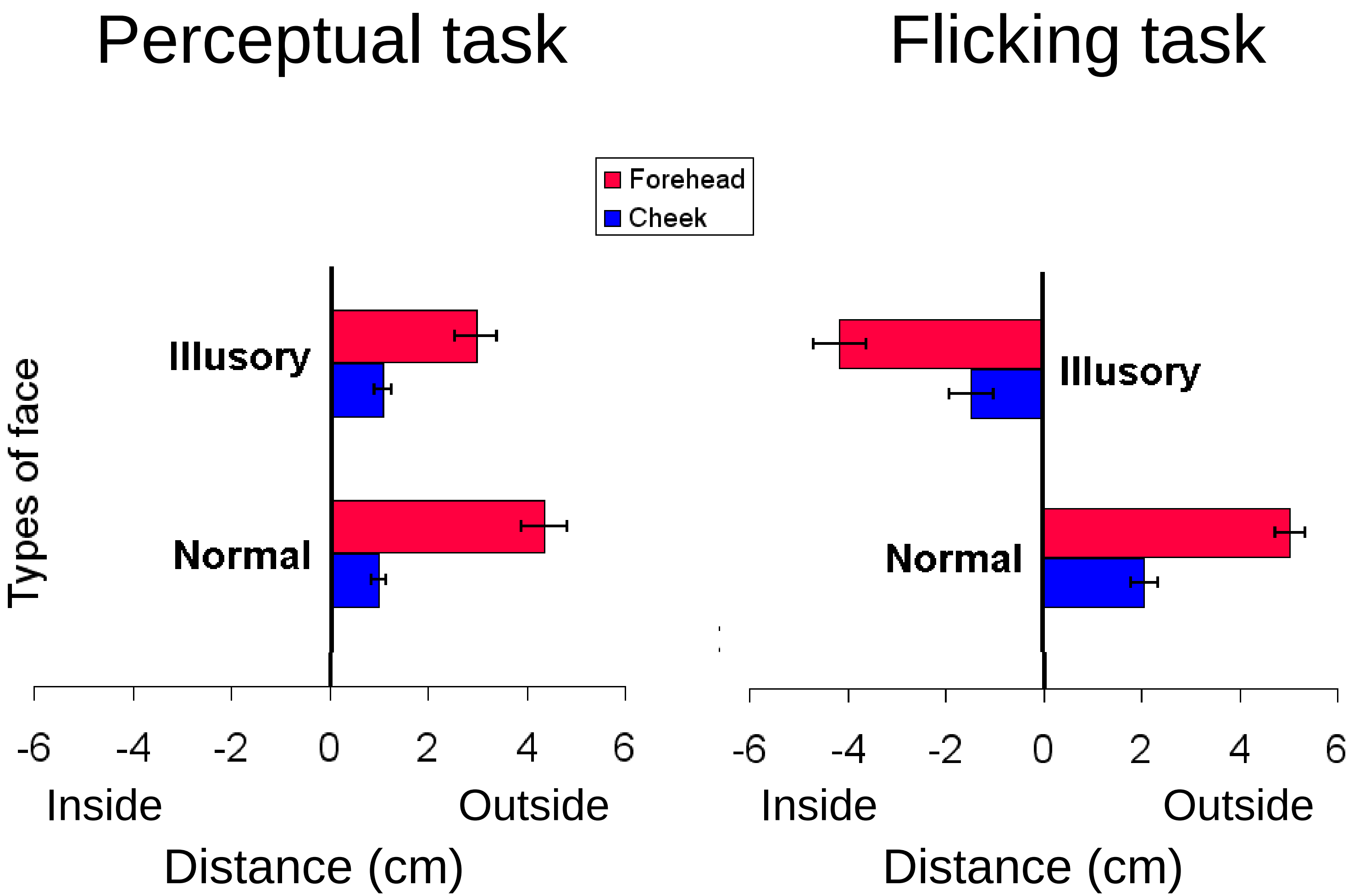
1. Perceptual estimates
2. Fast object-directed ‘flicking’

Króliczak, Heard, Goodale & Gregory (2006) *Brain Research*

The flicking task



Króliczak, Heard, Goodale & Gregory (2006) *Brain Research*

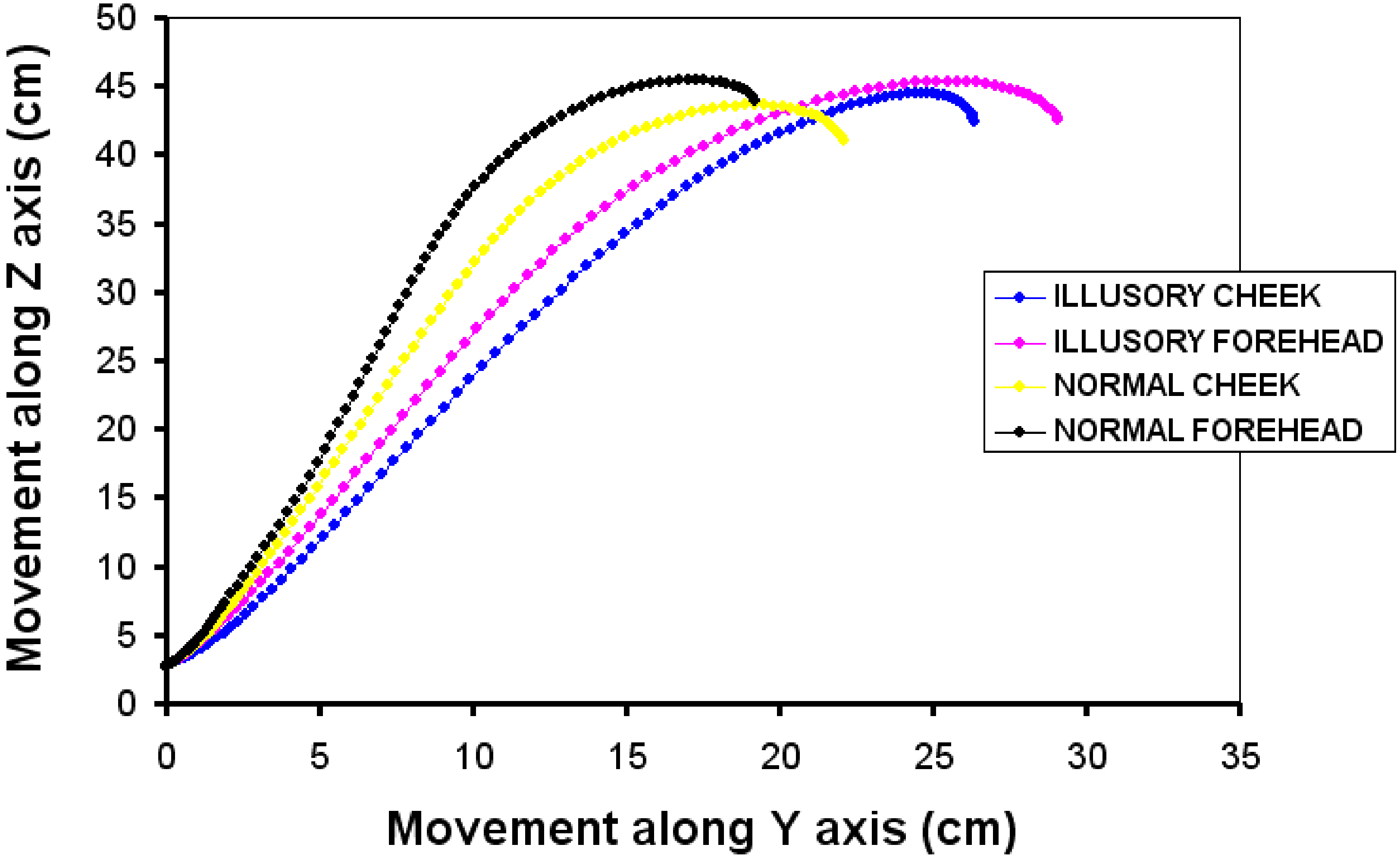


Perceptual task

Flicking task

Króliczak, Heard, Goodale & Gregory (2006) *Brain Research*

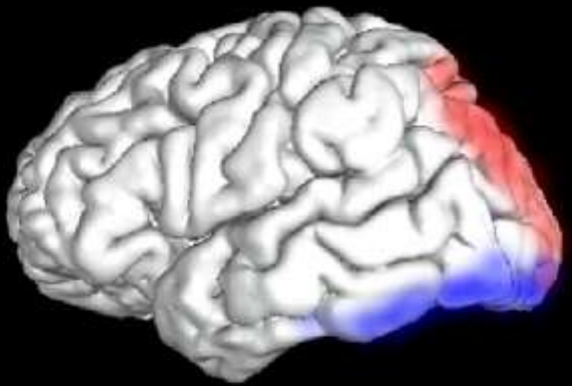
Flicking Profiles (side view)



Króliczak, Heard, Goodale & Gregory (2006) *Brain Research*

The visuomotor system can use bottom-up input about the veridical locations of targets despite the presence of a powerful top-down illusion of depth

Vision-for-action



Vision-for-perception

With thanks to Alex Colville

“To Prince Edward Island” 1965

“Berlin Bus” 1978

But how do the two streams work together in the production of adaptive behaviour?

“Picking Grapes”
Eugene De Blass

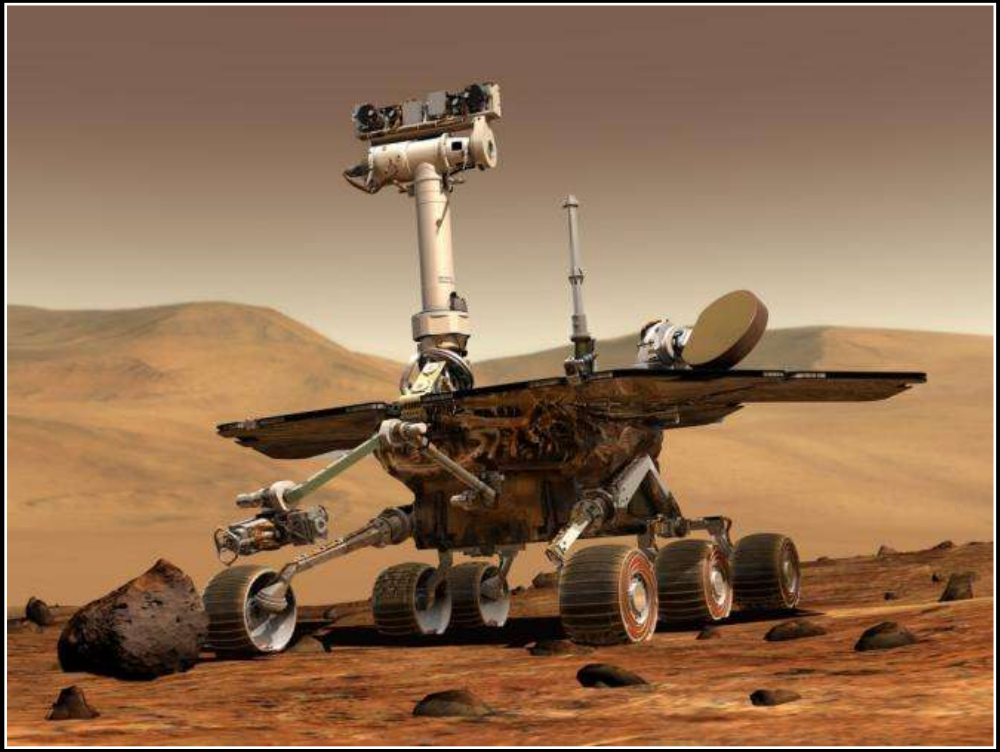
The primary division of labour between the ventral and dorsal streams

- The ventral stream identifies goals and (together with prefrontal cortical areas) plans an appropriate action

- The dorsal stream (in conjunction with related circuits in premotor cortex, basal ganglia, and brainstem) programs and controls those actions.

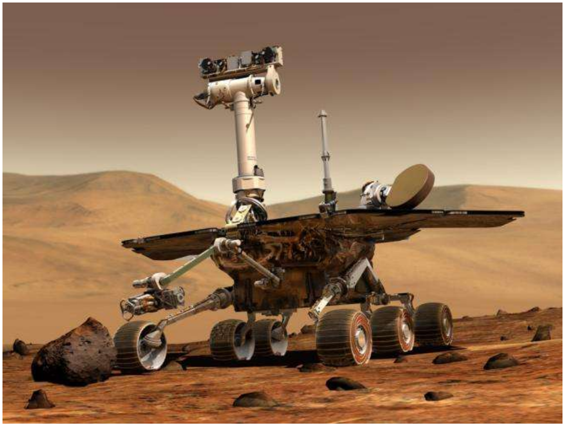
…an engineering metaphor

Autonomous Robot



Tele-operation

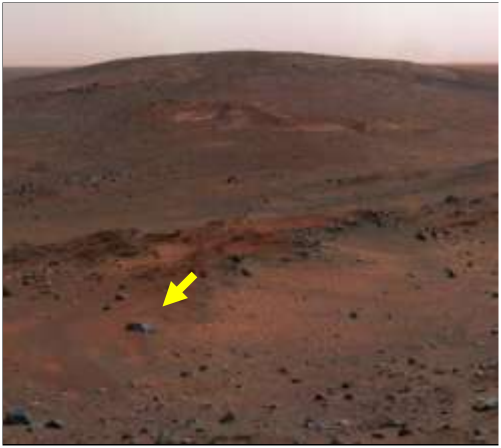
Human Operator



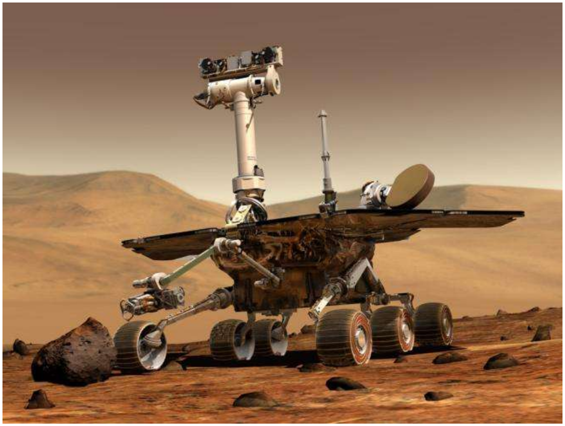
Slave Robot

Tele-assistance

Human Operator

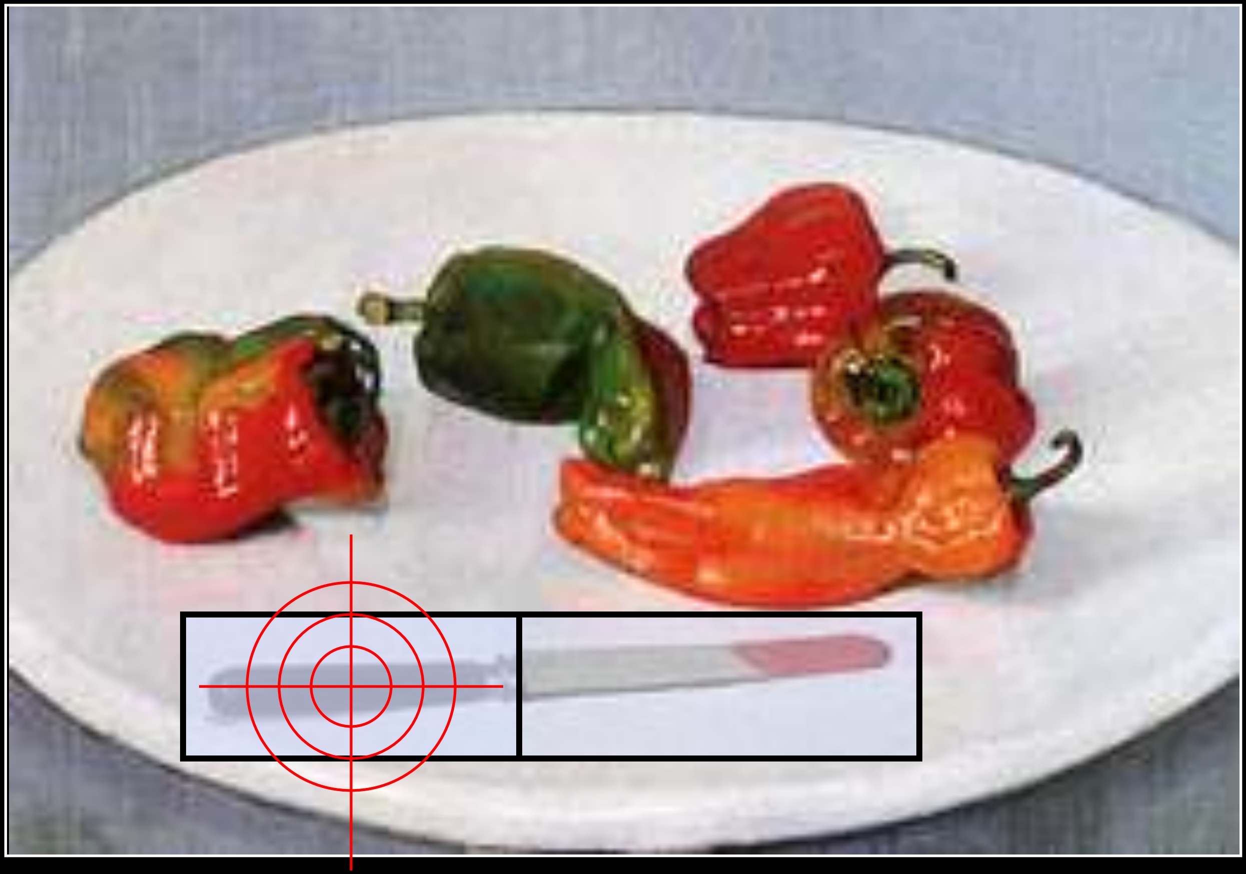


‘Flagged’ Object



Semi-autonomous
Robot

Biological tele-assistance



The great end of life is not knowledge but action.

Thomas H. Huxley

1825-1895