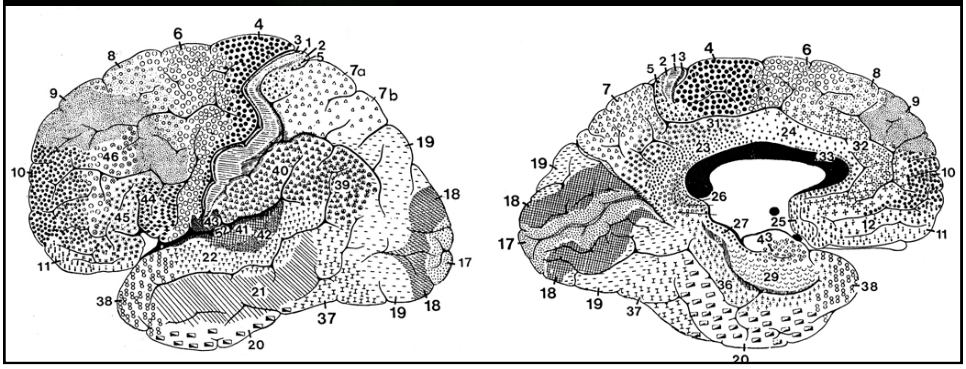
MULTIPLE VISUAL AREAS

1:	Definition of an 'area' of visual cortex
2:	Discovery of areas in monkey visual cortex; functional specialisation
3:	Use of imaging to chart areas in human visual cortex
4:	Why are there multiple areas? A 'theory' of vision.

1

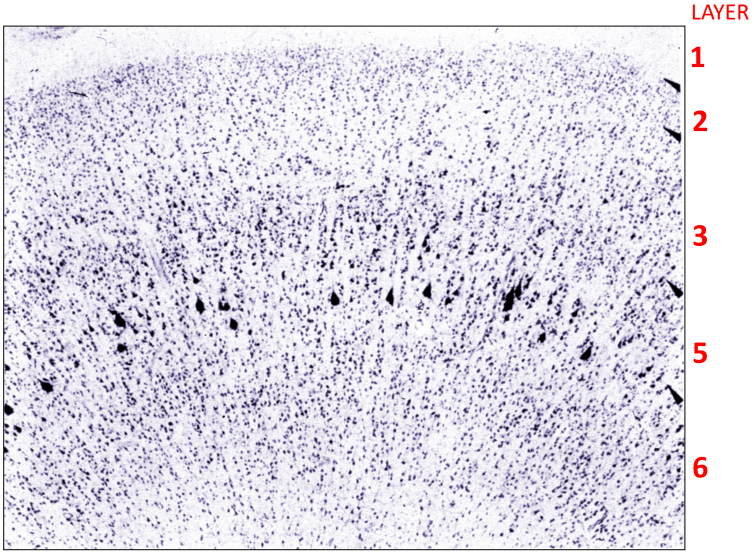
Brodmann 1909

cytoarchitectonic map
of human cerebral cortex



2

Brodmann area 4 (characterised by very large 'Betz' cells in layer 5)
[or 'PRIMARY MOTOR CORTEX', or 'AGRANULAR FRONTAL CORTEX']



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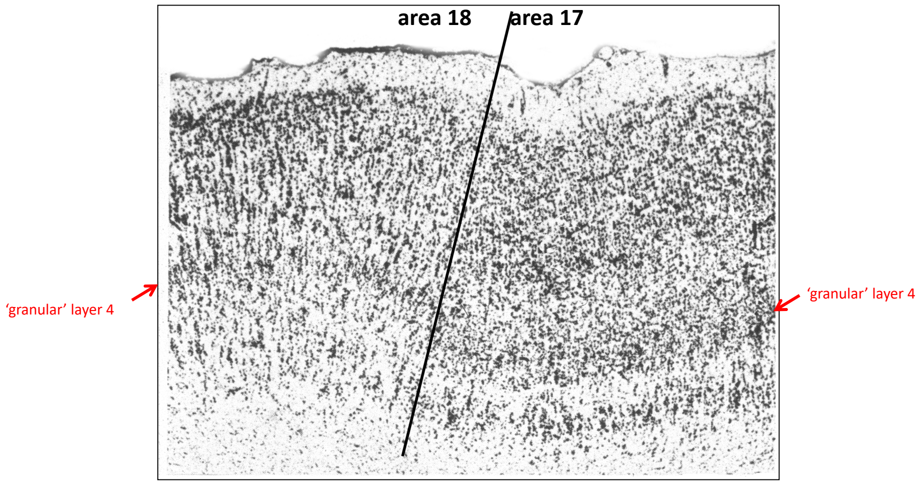
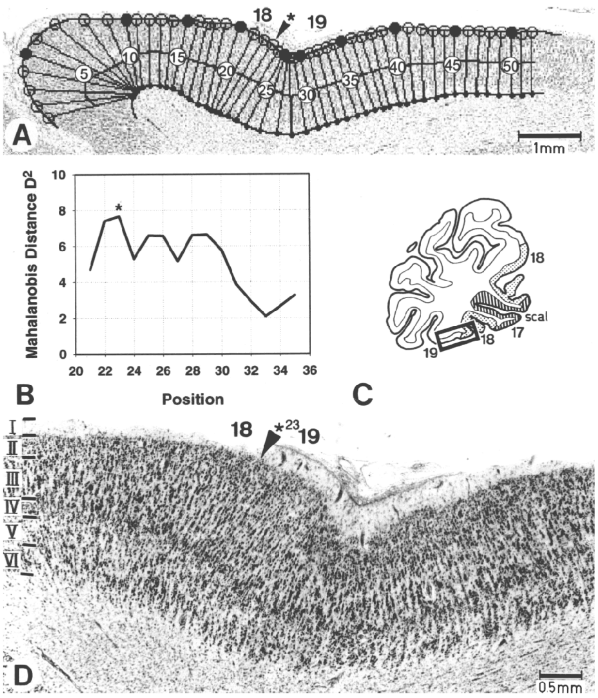


cytoarchitecture

4

Area 18/19 border in human cortex
Amunts, Zilles et al (2000)
[ref. 1]

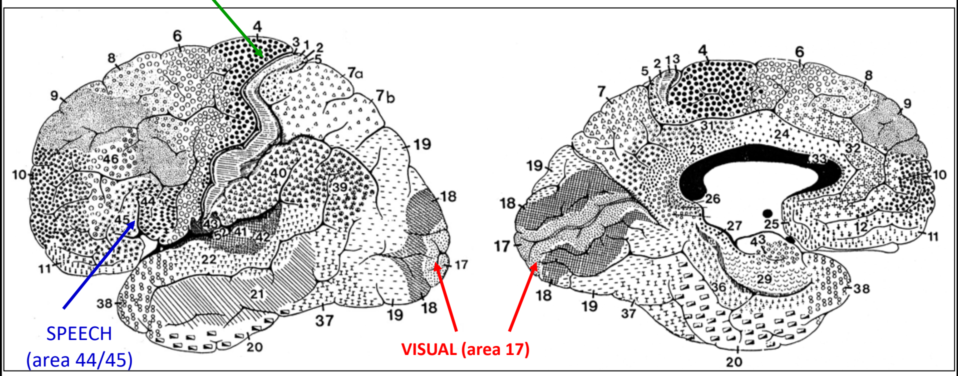
Quantitative versus subjective assessment of architectonic borders



5

Brodmann's cytoarchitectonic map of human cortex 1909

MOTOR (area 4)



SPEECH (area 44/45)
= 'Broca's area'

VISUAL (area 17)

Brodmann's theory: different areas represent 'organs' of the brain…(?)
Localisation of functional modalities, e.g vision, hearing, touch, motor control, speech.

But also (unknown to Brodmann) there are many separate areas specialised for visual sub-modalities (e.g. colour vision) within cyto-architectural areas 18, 19 & 37.

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1. Definition of an 'area' of visual cortex

-- architecture

-- connectivity

-- functional map (e.g. map of retina, or of other sensory surface)

-- specific functional properties

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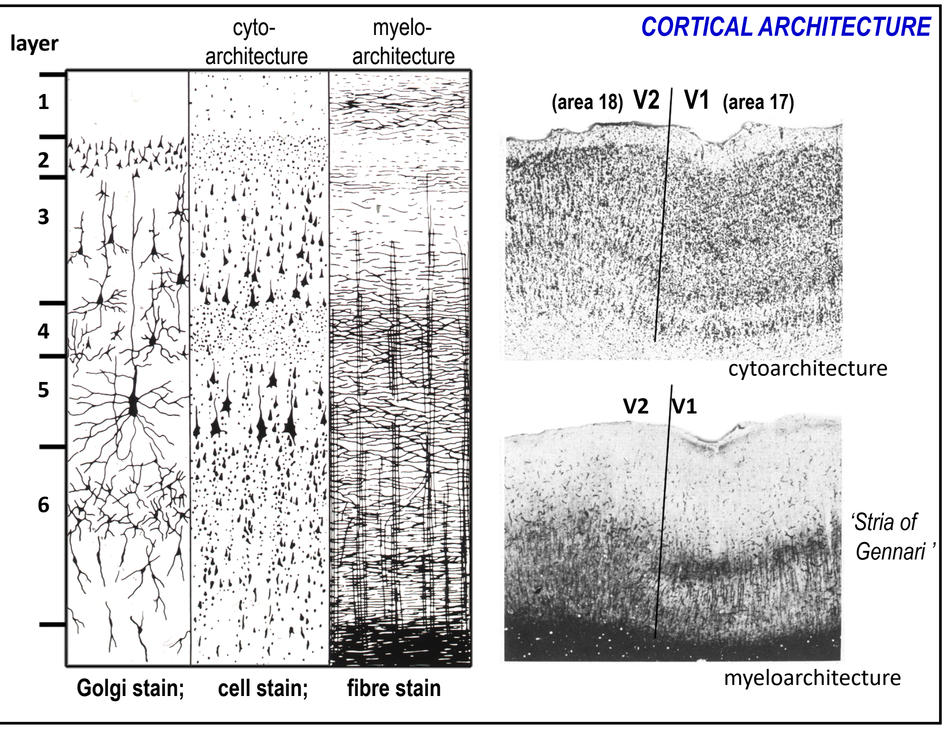
CORTICAL ARCHITECTURE



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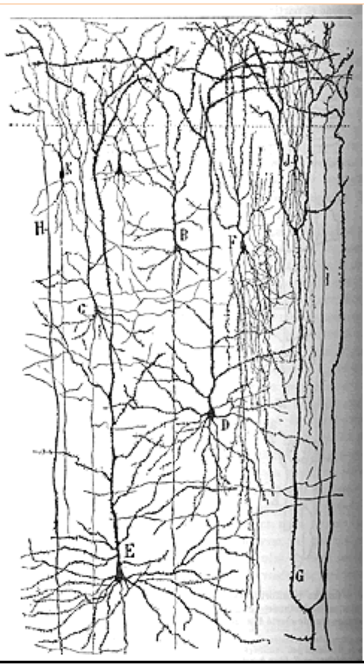
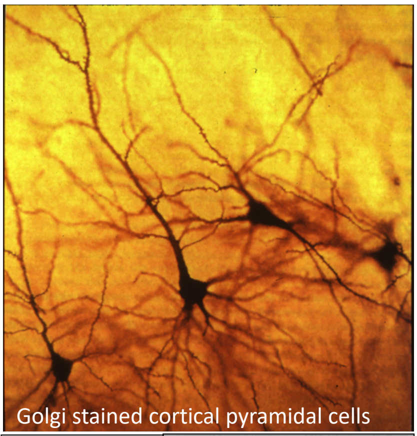
CORTICAL ARCHITECTURE

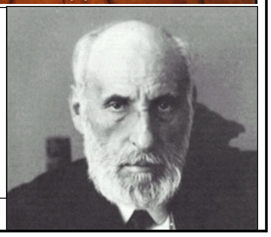
Cajal; L'Histologie du Système Nerveux





Golgi stained cortical pyramidal cells

- as studied by Spanish neuroanatomist Ramon y Cajal (Nobel Laureate 1906), giving rise to the 'neuron doctrine'.



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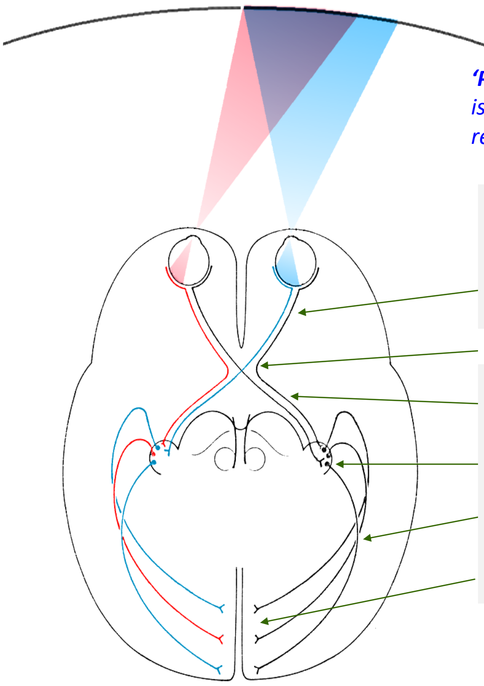
CONNECTIVITY

'Primary visual cortex'
is defined as the cortical field in receipt of the optic radiation.



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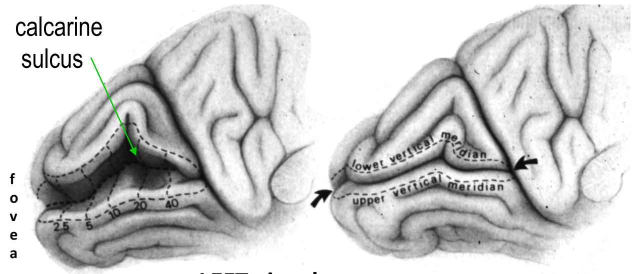
Area V1 has a retinotopic map



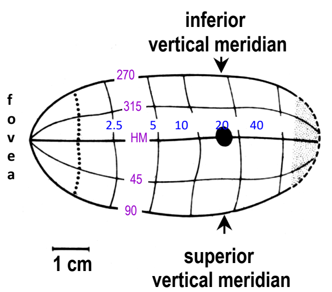
LEFT visual cortex

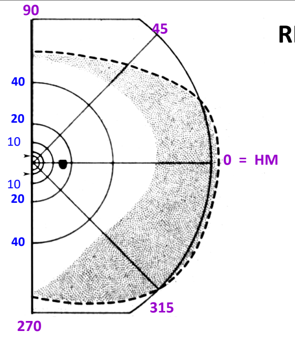
'scotoma'
-a circumscribed region of visual field loss, caused by punctate damage to a small region of area V1;
- e.g. as caused by a bullet wound.

- First accurate map of V1 produced by Gordon Holmes, studying casualties of WW I.

- Also Tatsuji Inouye for the Russo-Japanese war (1904-5)

*





RIGHT visual hemifield

'magnification factor'
=
mm cortex per
degree of visual field

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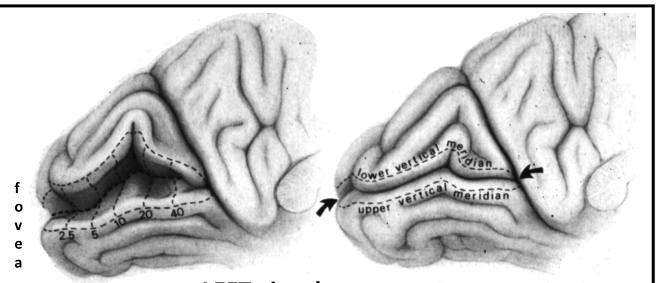
Area V1 has a retinotopic map



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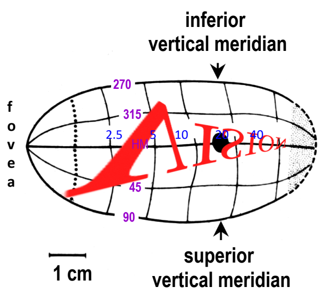

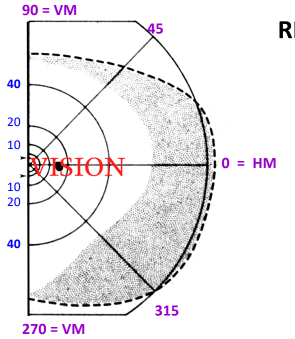

RIGHT visual hemifield

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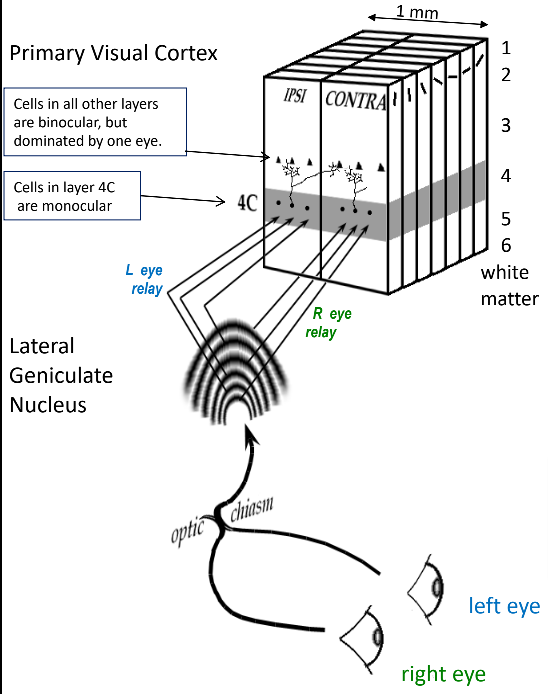
12



FUNCTIONAL ARCHITECTURE OF PRIMARY VISUAL CORTEX

David **Hubel** & Torsten **Wiesel**

V1 ***(left)***
two independent modular subsystems:
- ocular dominance columns
- orientation columns

LGN ***(left)***
6 monocular layers;
- each layer maps a right, or a left eye half-retina

The possession of monocular neurons is a unique feature of V1, that helps to confirm its identity as a discrete area of cortex ...
- although, historically, this feature was never used as an operational means of defining V1.

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To recap: multiple terminology reflects historical convergence of separate concepts:

striate cortex (myeloarchitecture; stria of Gennari)

= ***area 17*** (cytoarchitecture; e.g. Brodmann)

= ***primary visual cortex*** (connectivity, i.e. area of distribution of optic radiation)

= ***area V1*** (first map of visual field)

Extrastriate cortex:

Definition of other, non-primary visual areas depends on similar combinations of separate criteria;

- experimental aim is to find congruent evidence for borders between neighbouring areas.

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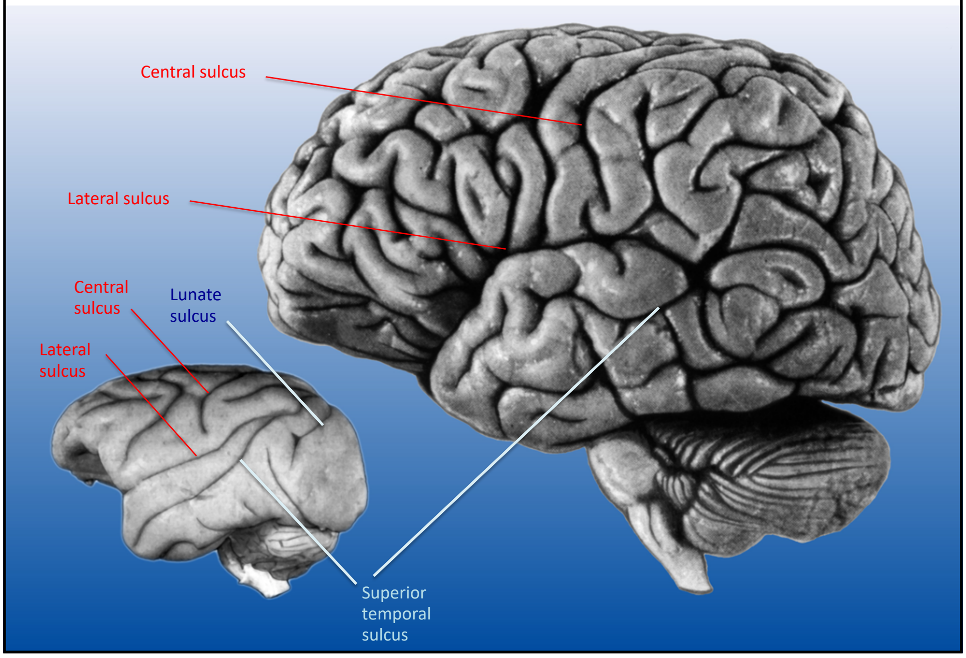
2. Discovery of areas in monkey visual cortex; functional specialisation



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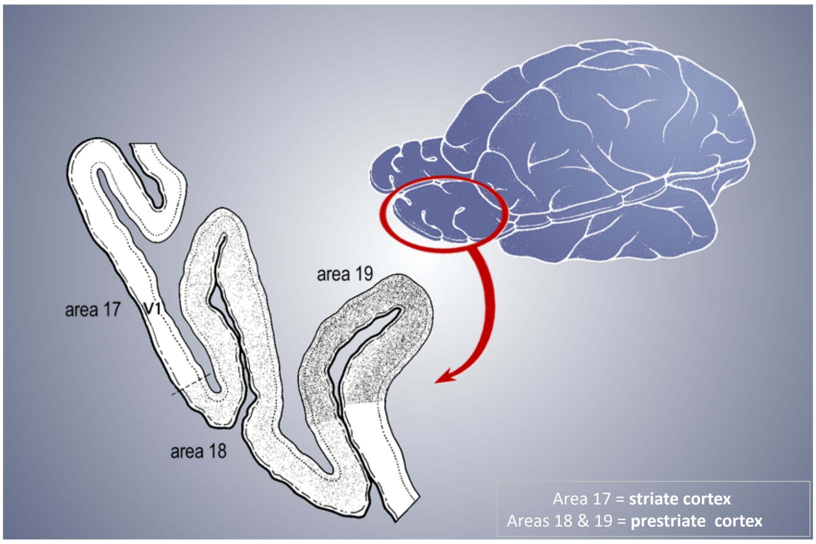
Brodmann cytoarchitectonic areas in macaque monkey



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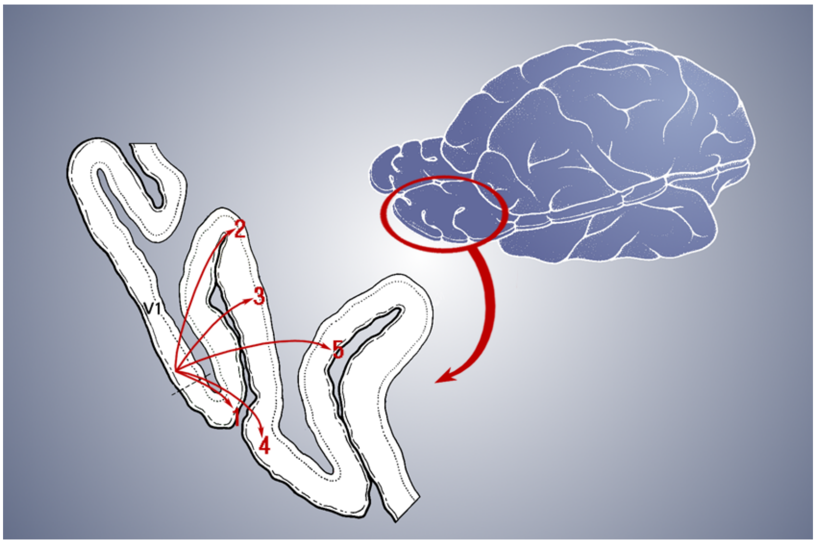
Multiple outputs from V1 to sites in prestriate cortex of macaque monkey
-implies parallel pathways & multiple visual maps (Zeki, 1969)



Early, 'lesion-degeneration' method for tracing connectivity; here a small lesion in V1 was followed, after 1 week post-operative recovery, by silver stain histology for anterograde axonal degeneration.

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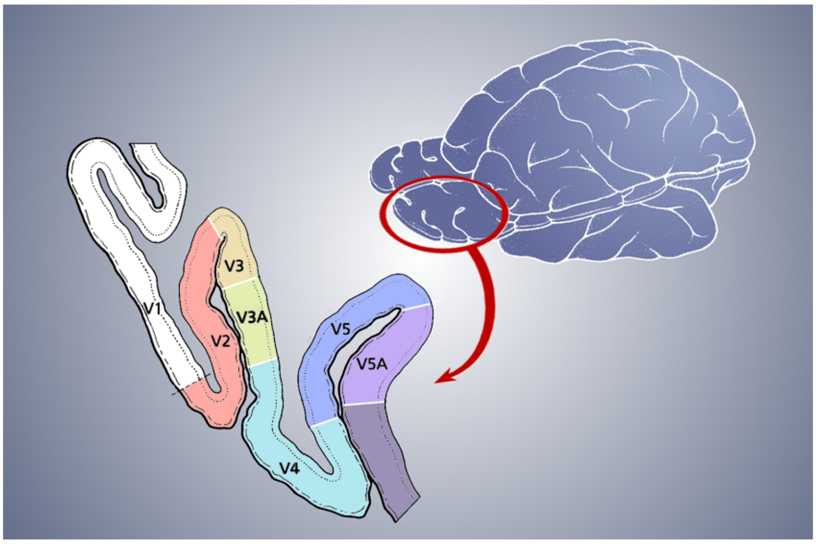
Multiple visual areas in prestriate cortex of macaque monkey
(Zeki 1978)



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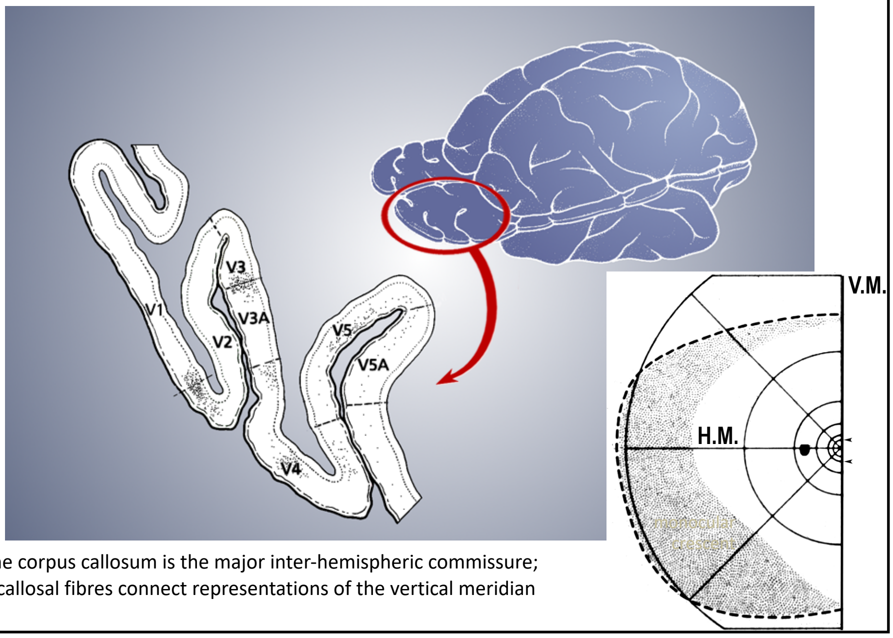
Using callosal connections to chart the borders of visual areas (Zeki 1978)



The corpus callosum is the major inter-hemispheric commissure;
– callosal fibres connect representations of the vertical meridian

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Using callosal connections to define borders between separate visual areas

The chain of reasoning runs as follows:

1. Neighboring loci within a visual field map communicate by short-range intrinisic connections;
2. Loci close to the the mapped representation of the vertical meridian must communicate with symmetrical loci on the other side of the vertical meridian through interhemispheric (callosal) connections;
3. Callosal connections are conveniently revealed by surgical transection of the corpus callsoum, followed 1 week later by silver stain histology for degenerating axons (the portion of the callosal axon in the hemisphere opposite to its parent cell body undergoes degeneration);
4. This degeneration is observed to appear in several discrete patches;
5. Each patch is inferred to be at a site of representation of the vertical meridian;
6. These sites are also inferred to mark (part of) the boundaries of maps of the visual hemifield;
7. On the basis of the hypothesis that each visual area corresponds to a separate visual map, the callosal patches also define area borders (often where adjacent areas share a common representation of the vertical meridian, e.g. V1/V2).

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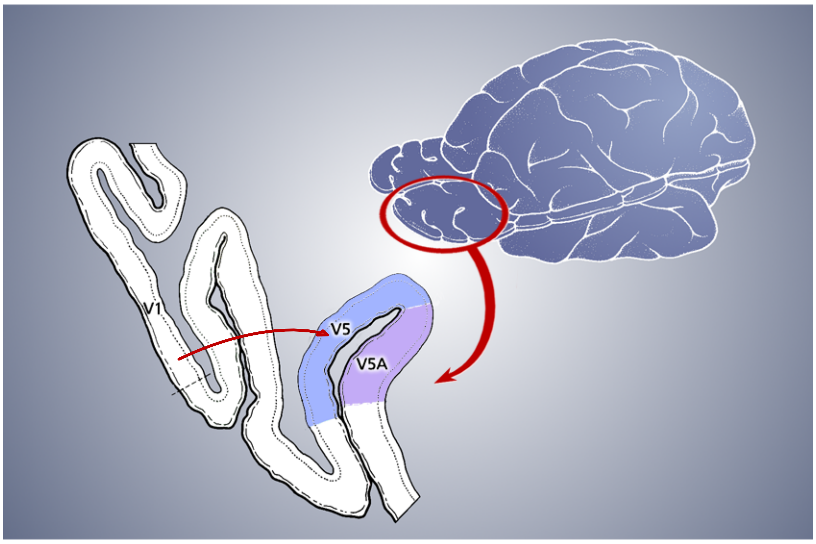
Prestriate areas have varying specialised functions
e.g. areas V5 & V5A (or MT, MST & FST) are motion areas



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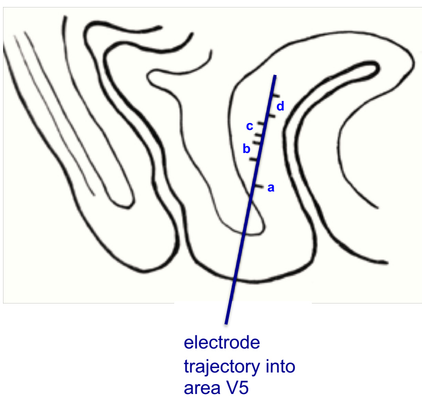
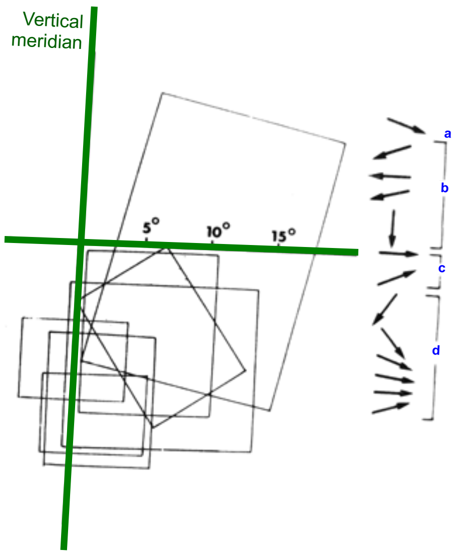
The discovery of directional selectivity in area V5 (Zeki, 1974)





Early recording from area V5

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Criteria for area definition : V5/MT (alternative terminology for homologous areas across species)

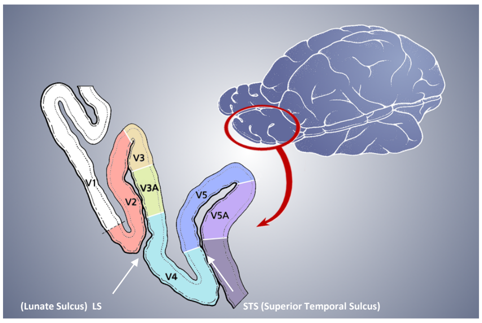
- V5 is an isolated projection field of V1 (Zeki 1969);
  (neighbouring cortex within STS does not receive input from V1). **Connectivity**

- V5 has a very high proportion of direction-selective cells (Zeki 1974) ; **Functionality**
  V4 has little direction tuning;
  V5A also has many direction-selective cells, but they have larger receptive fields than V5 cells.

- area MT has a distinct myeloarchitecture (Allman & Kaas 1971); **Architecture**
  - as determined in the owl monkey (Aotus)
  - MT = 'middle temporal'

- area MT has a unitary visual hemifield map (Allman & Kaas 1971) **Map of sensorium**
  - as determined in the owl monkey (Aotus)

	colour	motion	form
V5		+	
V4	+		+
V3/A		+	+
V2	+	+	+



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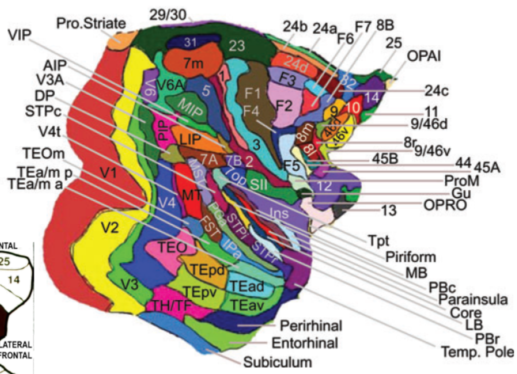
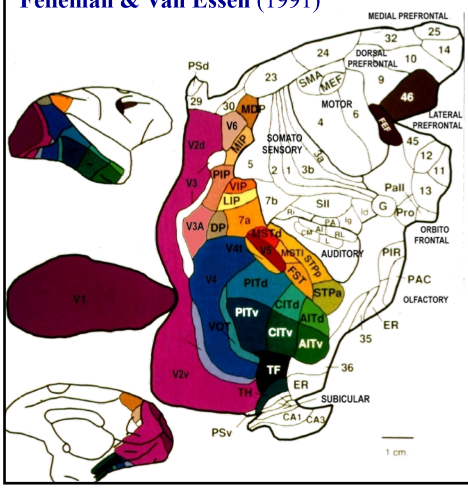
Visual areas
in flatmap of macaque cortex



Markov *et al.* (2014)[ref 6]

Felleman & Van Essen (1991)[ref 5]



The 'area hypothesis':
- that all cortex is composed of discrete areas.

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Can we use the same methods to identify human visual areas?

- Invasive methods for tract-tracing are impermissible;
- Single unit physiology is only obtainable under special circumstances;
- Post-mortem cortical architecture cannot be correlated with other criteria;

- BUT...

3: Use of imaging to chart areas in human visual cortex

- *Functional magnetic resonance imaging (fMRI) can:*
    - obtain retinotopic maps;
    - examine functional specialisation;
    - trace fibre bundles through white matter = DTI ('diffusion tensor imaging').

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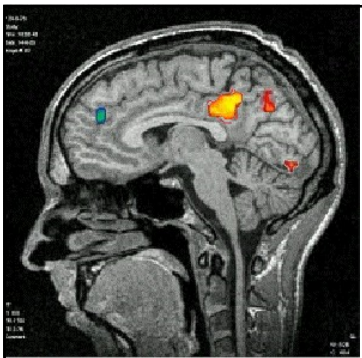

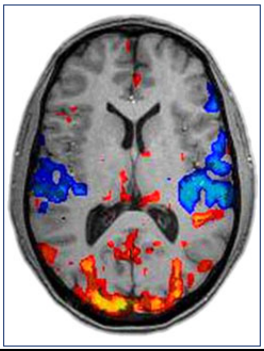

Functional Magnetic Resonance Imaging (fMRI)

Detects BOLD signal (Blood Oxygenation Level Dependent): oxyhaemoglobin gives higher signal than de-oxyhaemoglobin.

NB. BOLD signal <u>increases</u> in active regions of the brain, because increased blood supply overcompensates for increased tissue oxygen demand.

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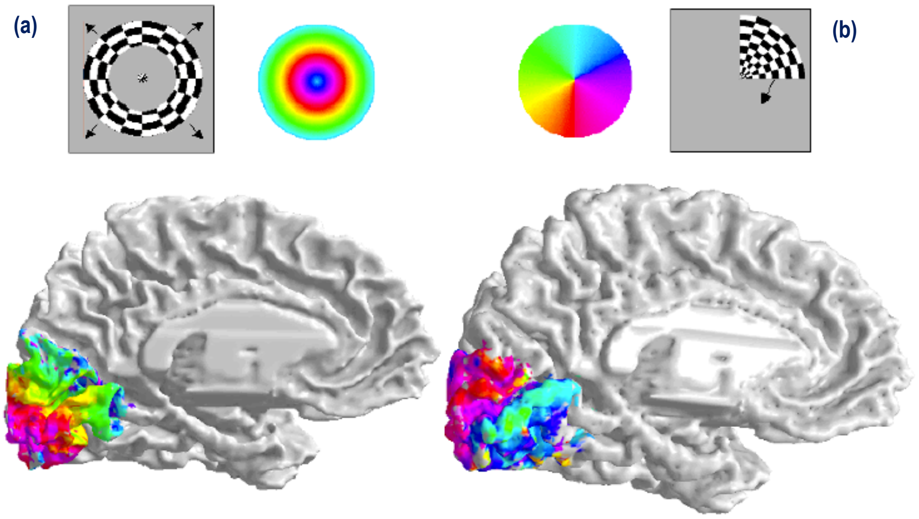
CHARTING VISUAL AREAS WITH fMRI [ref 3]



'Travelling wave' technique

Checkerboard stimuli, formed as an alternately expanding and contracting annulus **(a)**, or a slowly revolving quadrant (or octant) **(b)**.
Phase mapping BOLD signal analysis to reconstruct map of eccentricity **(a)**, and polar angle **(b)**.

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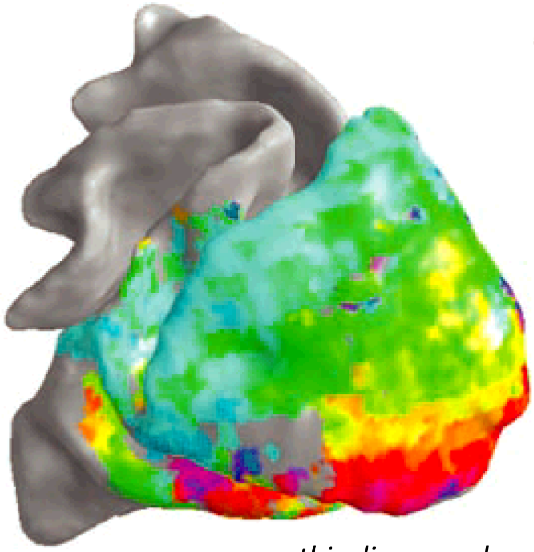
…also in monkeys

CHARTING VISUAL AREAS WITH fMRI

Visual areas in macaque cortex measured using functional magnetic resonance imaging.
Brewer *et al.* (2002) J Neurosci, **22**: 10416-10426.



Visual map in macaque area V1:

- this diagram shows the map of polar angle

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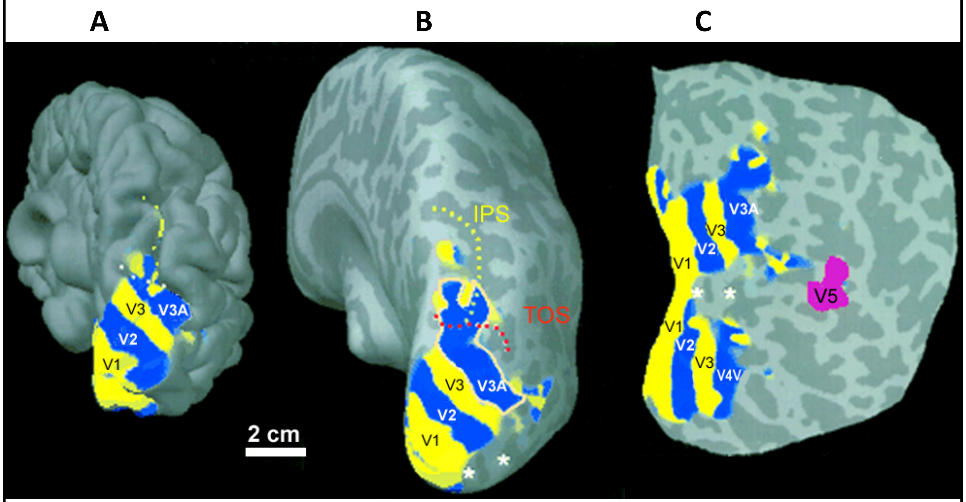
CHARTING VISUAL AREAS WITH fMRI [ref 2]



Determine separate visual areas by charting visual field maps and determining 'local sign'. These can be rendered:

(A) on brain surface image;

(B) on brain 'balloons' (inflate volume to flatten out sulci, shown in dark grey;

(C) on totally flattened 2D surface (NB this requires 'tearing' part of the surface to minimise distortion).

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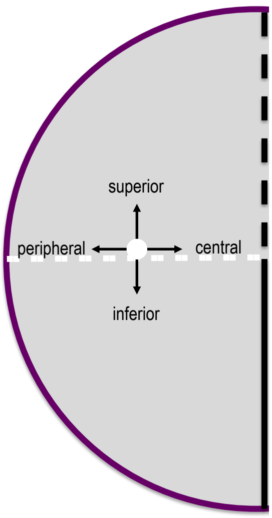
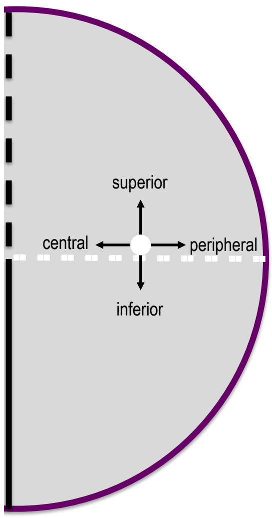
Maps, and mirror-image maps are distinguished by their 'local sign', which refers to the configuration of their bi-dimensional axes, as sampled at any local point within a map.



– e.g. as shown in the map at left, the central direction is 90° clockwise of the superior direction, whereas it is 90° anti-clockwise from superior in the mirror-image map at right.



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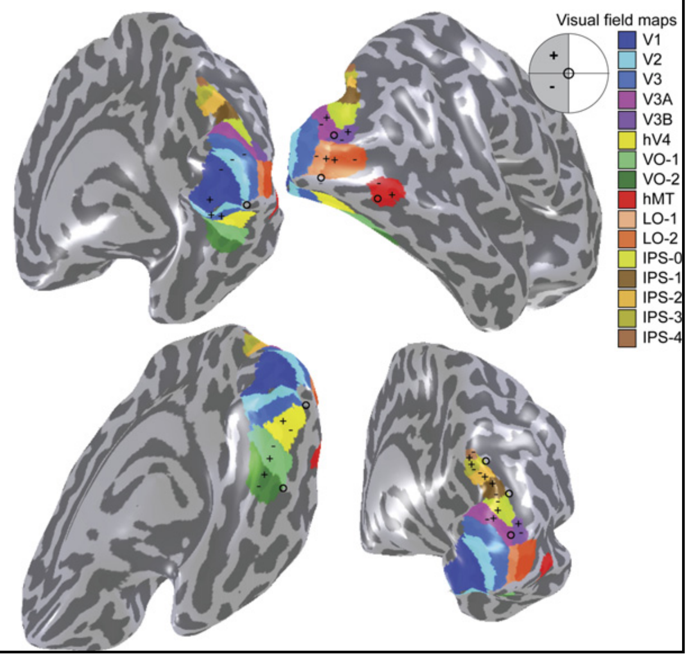
Wandell *et al.* (2007) Neuron 56:366-383 *Visual field maps in human cortex.*



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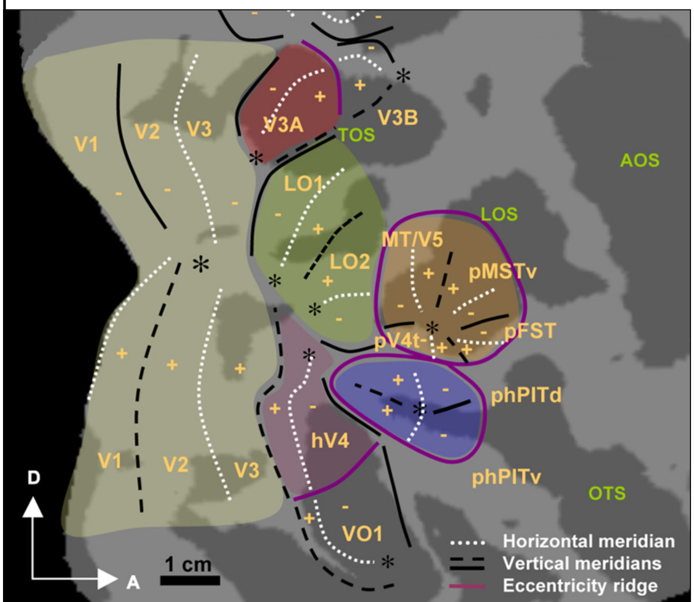
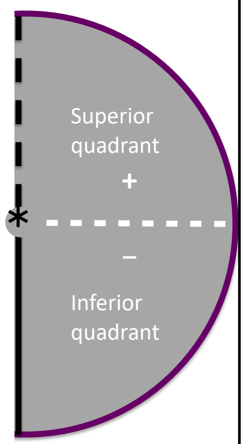
Multiple visual field maps in human cortex



Visual hemifield chart



TOS = transverse occipital sulcus
LOS = lateral occipital sulcus
AOS = anterior occipital sulcus
OTS = occipito-temporal sulcus

The retinotopic organization of the human middle temporal area MT/V5 and its cortical neighbors.
Kolster *et al.* (2010) **[ref 7]**

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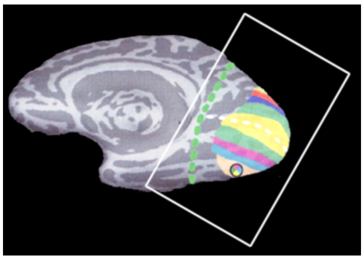
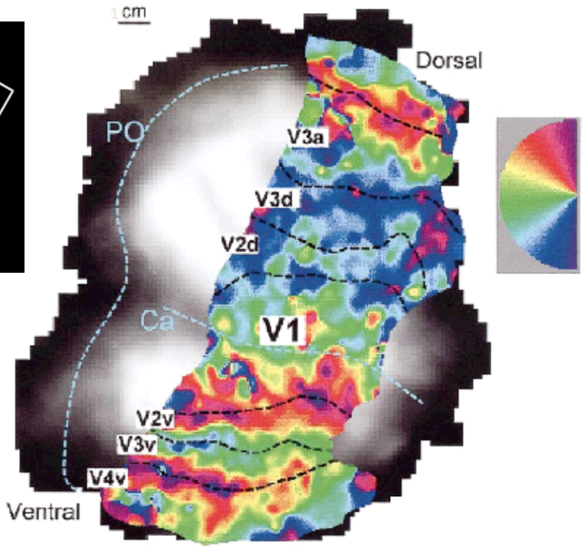
CHARTING VISUAL AREAS WITH fMRI





this chart shows:
a representation of the inferior VM at the borders between V1 / V2d & V3d / V3A;
a representation of the superior VM at the borders between V1 / V2v & V3v / V4v;
a representation of the HM at the borders between V2v / V3v & V2d / V3d;

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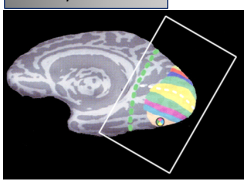
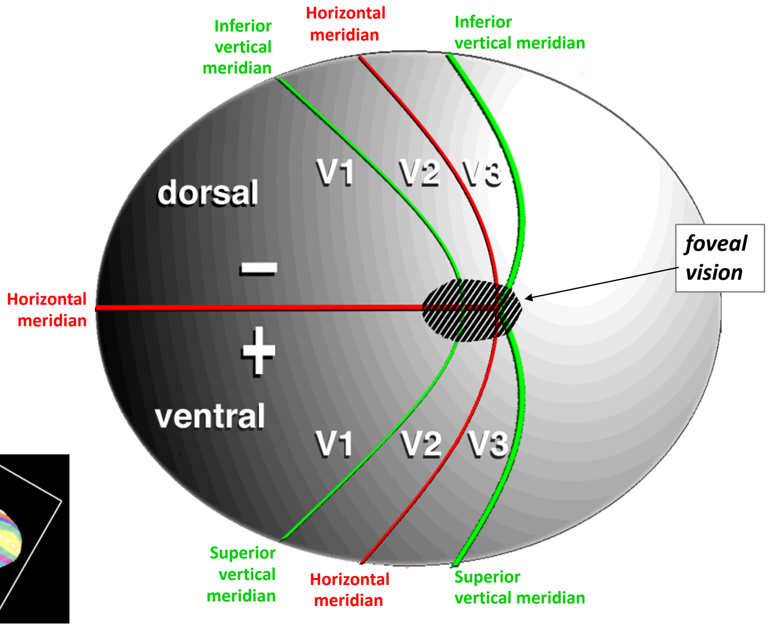
Schema for the arrangement of maps in areas V1, V2 & V3 of primate visual cortex:
- split representation of the horizontal meridian (HM)

Schematic view of occipital pole of 'inflated' right hemisphere





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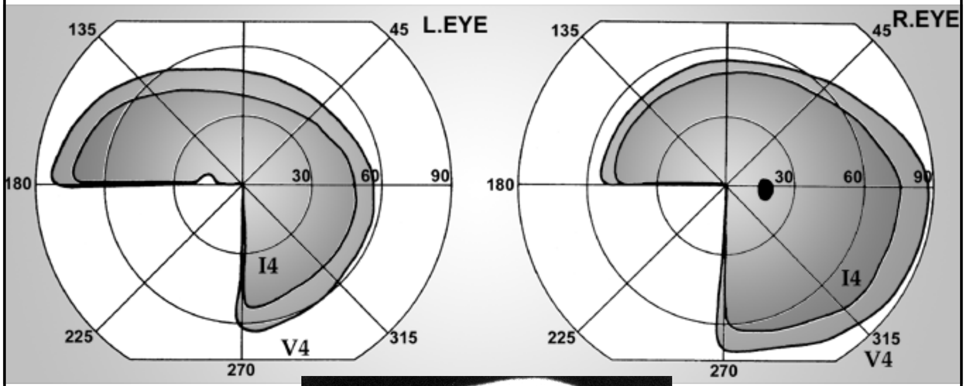
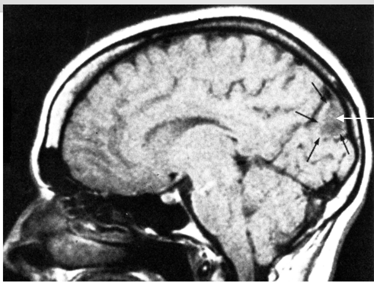
Horton & Hoyt (1991) [ref 4]

Quadrantanopia from V2 lesion



RIGHT hemisphere



tumour

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Use of fMRI to determine areas in human visual cortex

(i) By charting retinotopic maps;

(ii) By identifying regions with specific function (e.g. 'face' area).

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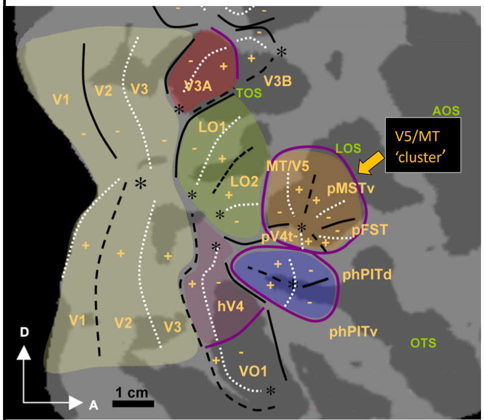
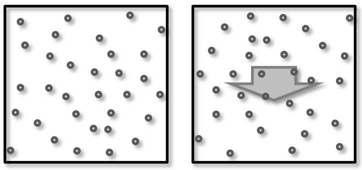
Area V5
a.k.a. area MT

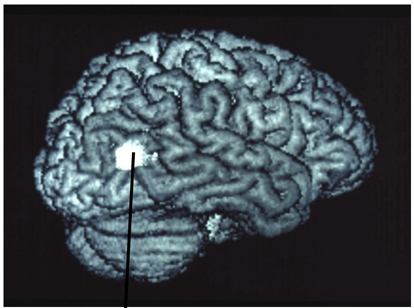
Functionally identified areas of human cortex using fMRI





static v *dynamic*

V5 lesion gives rise to *akinetopsia*



area V5/MT *posterior bank, ascending limb of inferior temporal sulcus*

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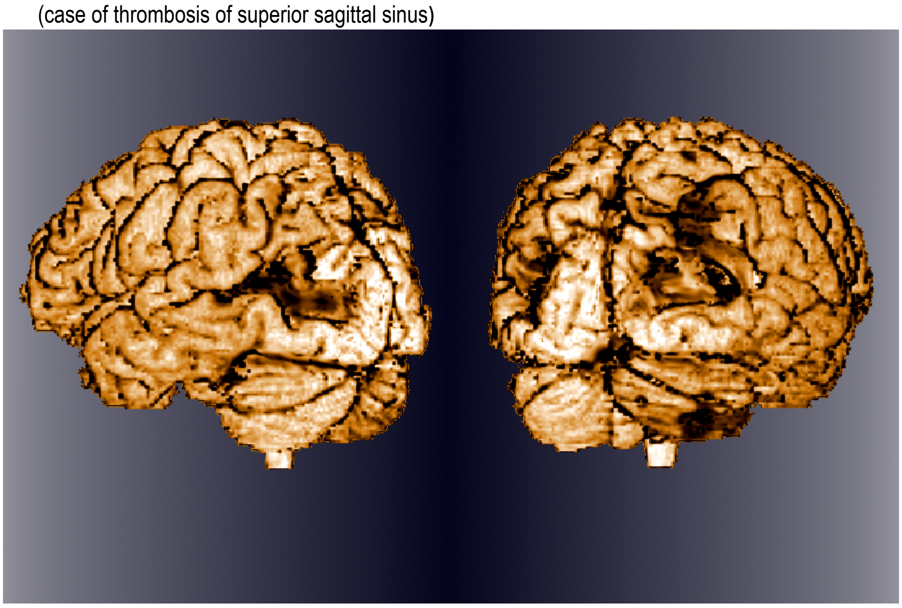
BILATERAL LESION OF V5
(akinetopsia, patient LM)

(case of thrombosis of superior sagittal sinus)



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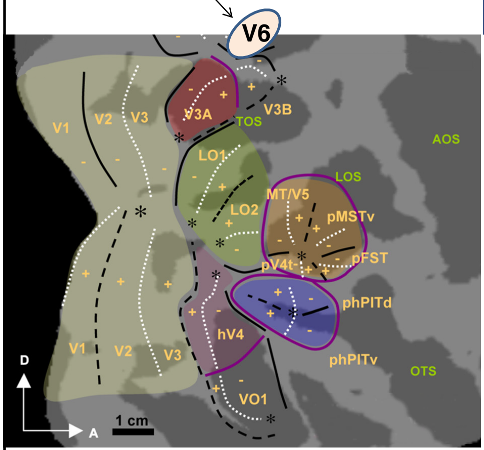
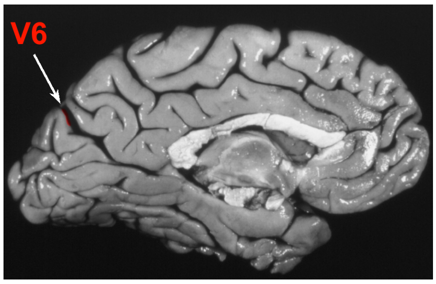
Area V6

Functionally identified areas of human cortex using fMRI

- **V6**:
- a relative emphasis on *peripheral* visual field;
- strong response to 'optic flow';
- initiates a visual pathway to premotor cortex.



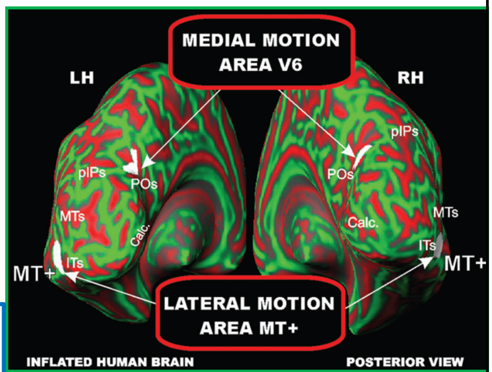


area V6 ('medial motion area')

posterior bank of parieto-occipital sulcus

Functionally identified areas of human cortex using fMRI

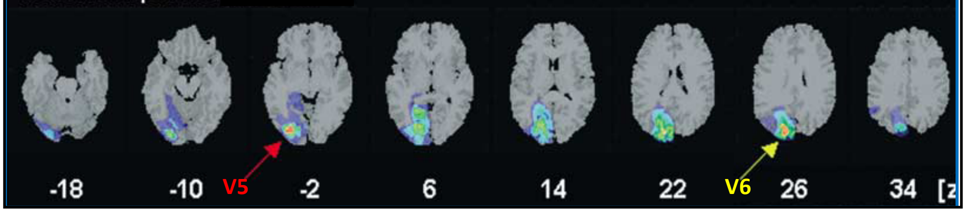
Human V6: the medial motion area.
Pitzalis et al. *(2010)* *ref 9*



N.B. 'area MT' is an alternative term for V5

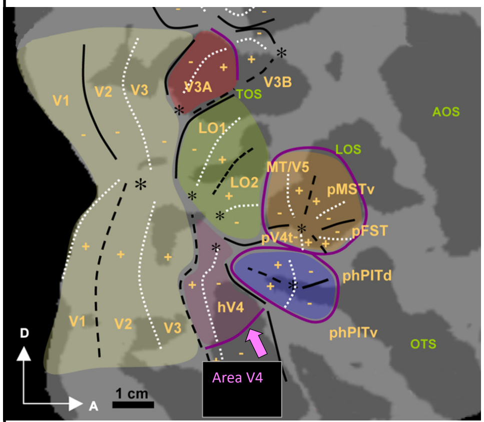
Direction-selective motion blindness after unilateral posterior brain damage
Blanke C. et al.. *(2003) Eur. J. Neurosci. 18, 709-722*
Two distinct regions where cortical lesions produce motion deficits

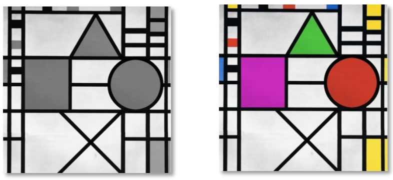
Motion blind patients: composite reconstruction of lesioned regions across subjects



Area V4

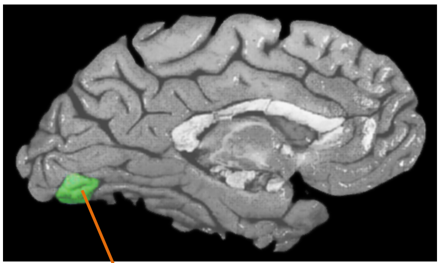
Functionally identified areas of human cortex using fMRI





greyscale v *colour*

V4 lesion gives rise to *achromatopsia*



area V4 *(found on fusiform gyrus)*

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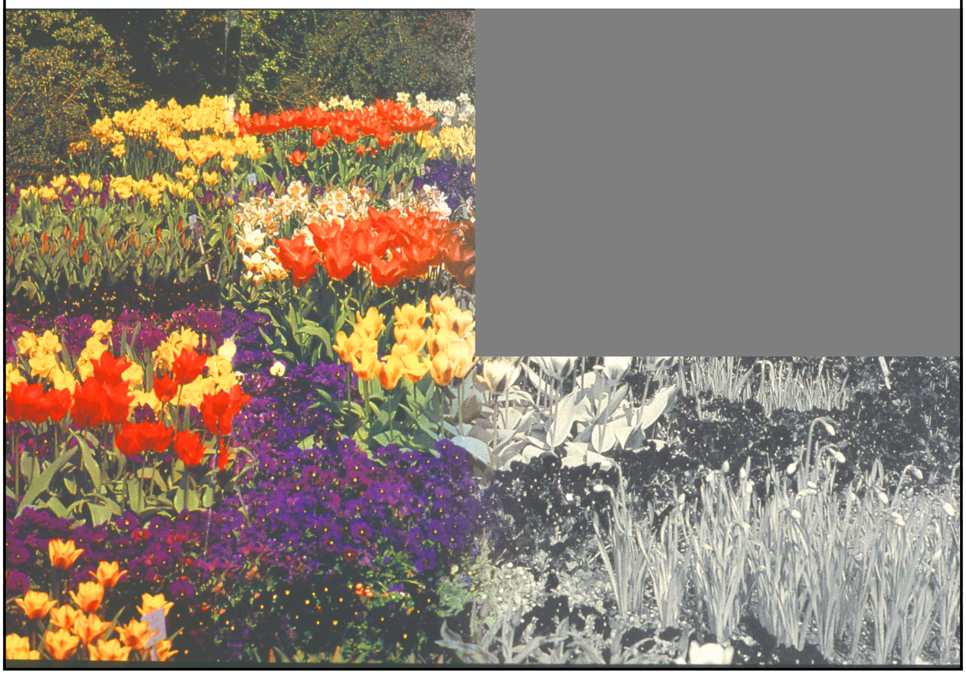
HEMI-ACHROMATOPSIA plus SUPERIOR QUADRANTANOPIA



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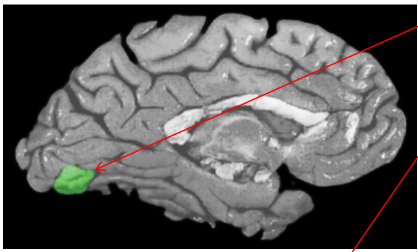
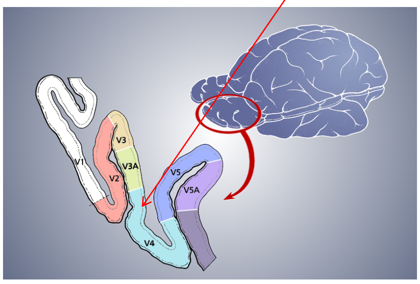
Macaca/Homo homology : area V4 ?

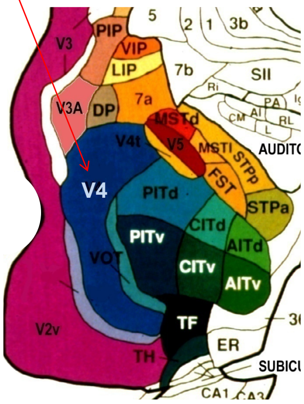


Human V4 is located in ventral occipital cortex (fusiform gyrus) and is separate from area V5;

macaque area V4 is located within the prelunate gyrus, neighbours area V5 and has a crescent shape extending between dorsal cortex and ventral cortex. Are these two areas really homologous?

- *Apparently yes: see next slide.*





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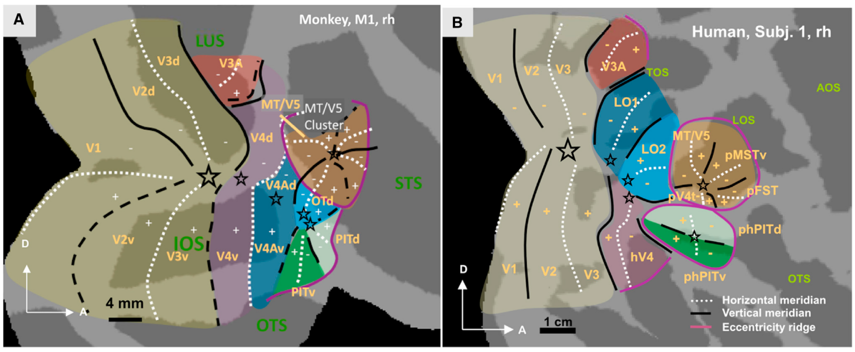
Kolster *et al.* (2014) [ref 8] **Macaca/Homo homology : area V4 ?**

Macaque cortex | Human cortex



macaque area V4 = human area V4
macaque area V4a = human area LO1
macaque area OTd = human area LO2

As ascertained by using identical ‘Motion v Static’ & ‘Intact v Scrambled Object’ tests in fMRI studies conducted in both species.

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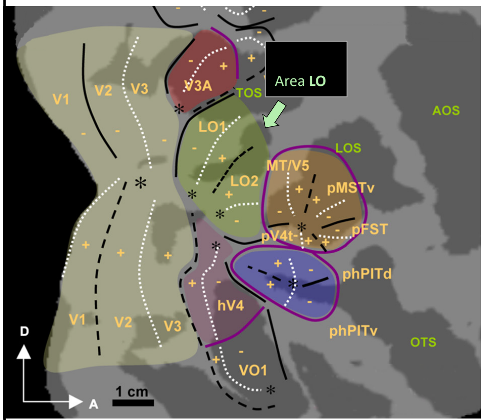
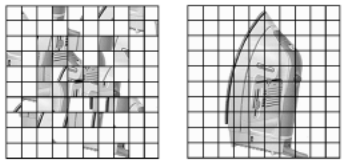
Area LO

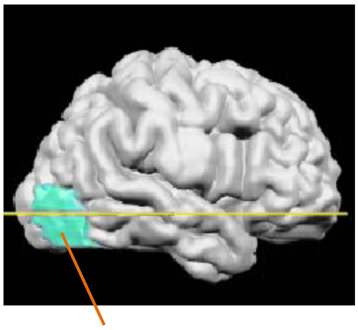
Functionally identified areas of human cortex using fMRI





scrambled non-object v *object*

LO lesion gives rise to *agnosia*



area LO (Lateral Occipital)

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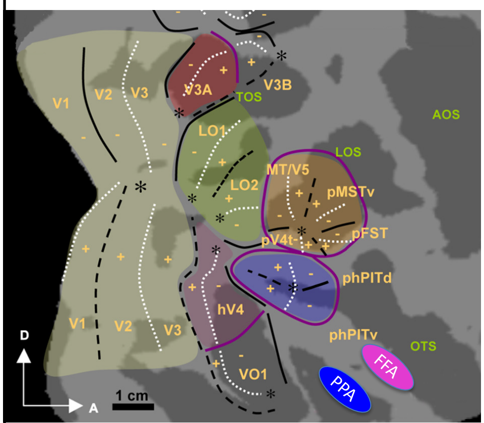
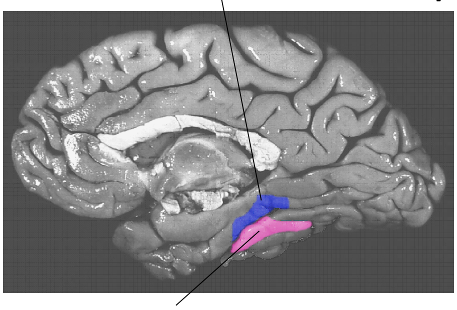
Areas FFA & PPA

Functionally identified areas of human cortex using fMRI



attend face v *attend house*

Parahippocampal Place Area, [topographic disorientation]



Fusiform Face Area [prosopagnosia]

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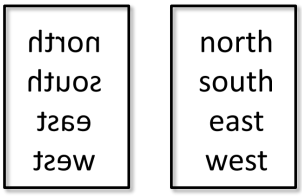
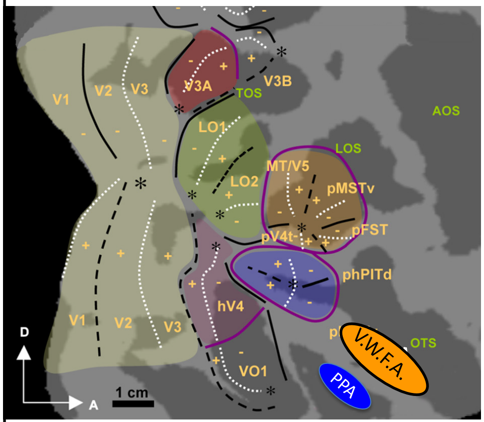
Area VWFA

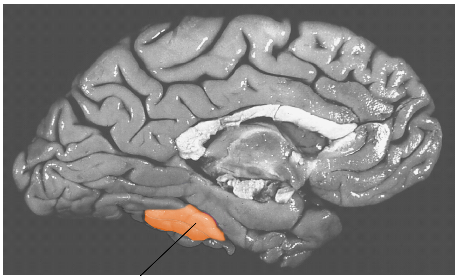
Functionally identified areas of human cortex using fMRI



mirror text v *normal*



LEFT hemisphere



Visual Word Form Area [alexia or pure word blindness]

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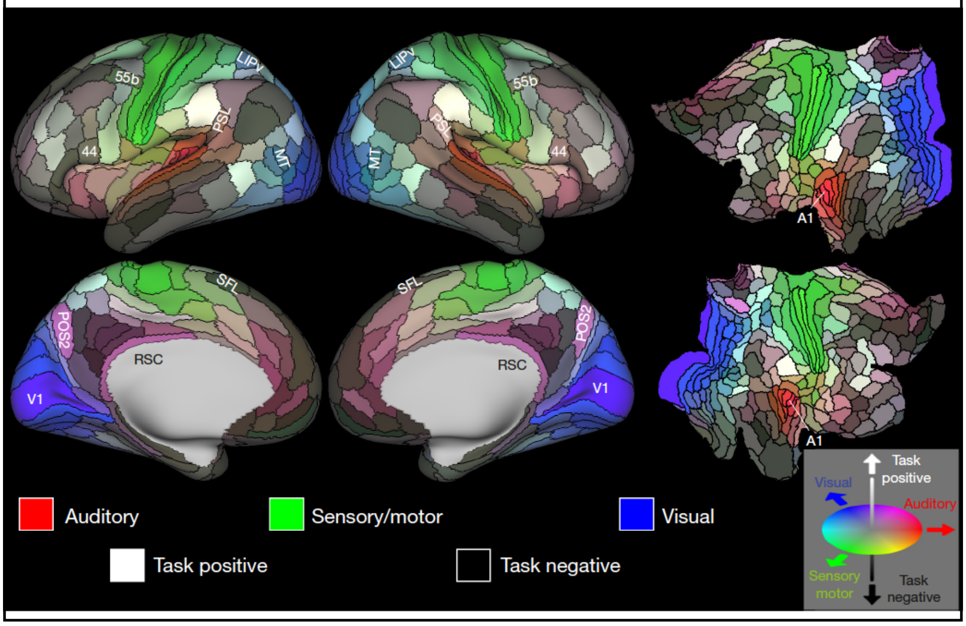
Glasser *et al.* (2016) Multi-modal parcellation of human cerebral cortex
Nature 536: 171-178.



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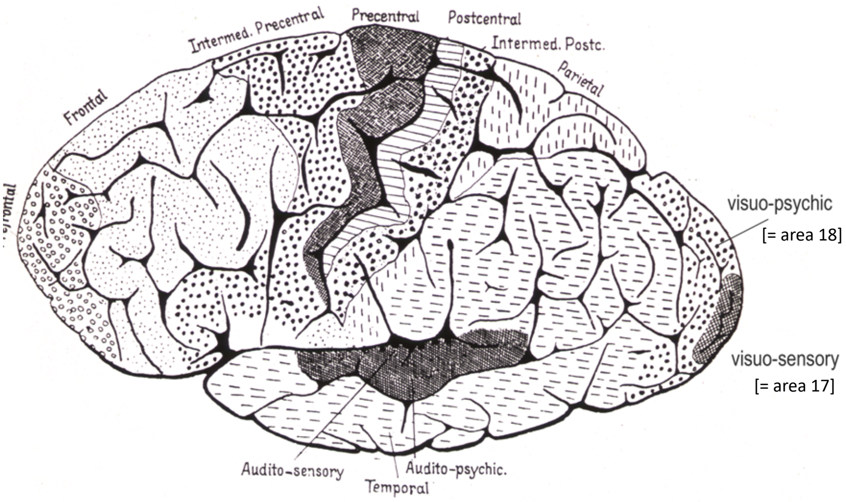
4. Why are there multiple areas? A ‘theory’ of vision



Campbell 1905

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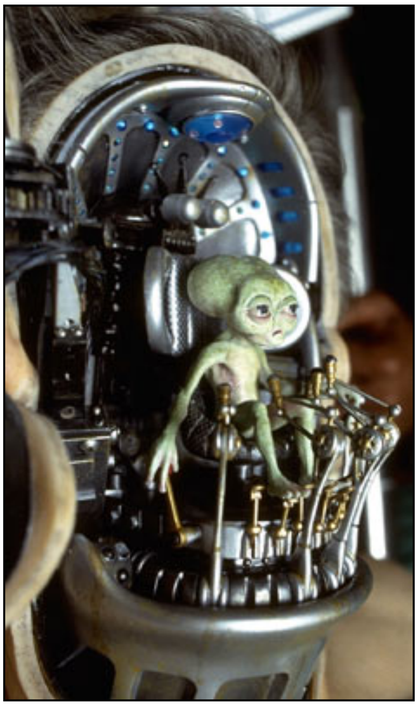

~~‘homunculus’ theory of vision & brain function~~

visual processing requires active synthesis of ‘feature detectors’

- colour
- form/edges
- motion
- stereo depth

+

hierarchical analysis of feature combinations

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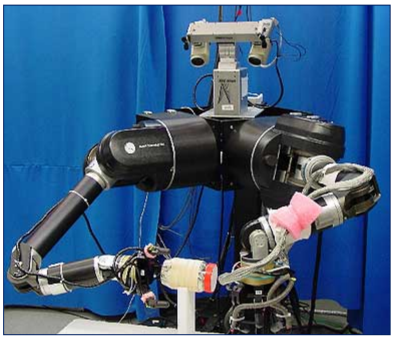
Lessons from AI: machine vision

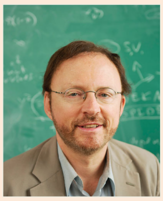


DAVID MARR

'SEEING': to know what is where by looking

Marr's 3 levels of analysis by which to understand any seeing system (natural or artificial):

1. **Computational goal**
2. **Algorithm**
2. **Physical implementation by computational hardware (biological or electronic)**



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Why are there so many visual areas... ?

COLOUR
FORM
STEREOSCOPIC DEPTH
MOTION

All require very different processing strategies
- most efficient if performed separately

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The logic of functional specialisation:

- Multiple areas enable more efficient visual computation;
- Different computational goals are implemented most efficiently by separate, specialised subsets of neural circuitry.

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