**MULTIPLE VISUAL AREAS**

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**Brodmann 1909**

cytoarchitectonic map
of human cerebral cortex
Brodmann area 4  (characterised by very large ‘Betz’ cells in layer 5)
[or ‘PRIMARY MOTOR CORTEX’, or ‘AGRANULAR FRONTAL CORTEX’ ]
Brodmann’s cytoarchitectonic map of human cortex 1909

MOTOR (area 4)  SPEECH (area 44/45)  VISUAL (area 17)

= “Broca’s area”

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.
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
CORTICAL ARCHITECTURE

Golgi stained cortical pyramidal cells

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

VISUAL PATHWAYS

only nasal fibres cross over = ‘decussation’

optic nerve
chiasm
optic tract
lateral geniculate nucleus
optic radiation
primary visual cortex
Area V1 has a retinotopic map

- '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)

Left visual cortex

Right visual field

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

1 cm
Cells in layer 4C are monocular.

Lateral Geniculate Nucleus

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.

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; e.g. Holmes)

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

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

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

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

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

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

- V5 has a distinct myeloarchitecture

BUT..

The visual map in V5 lacks a high degree of topographic order, and it is therefore difficult to use the map to define the border of V5.
**Felleman & Van Essen 1991**

visual areas in flatmap of macaque cortex

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’).
Functional Magnetic Resonance Imaging (fMRI)

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

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

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).
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).

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;
Schema for the arrangement of maps in areas V1, V2 & V3 of primate visual cortex

Horton & Hoyt 1991 [ref 4] Quadrantanopia from V2 lesion

Horton & Hoyt 1991

Quadrantanopia from V2 lesion
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).

Area V4

Functionally identified areas of human cortex using fMRI

V4 lesion gives rise to achromatopsia

area V4v (found on fusiform gyrus)
HEMI-ACHROMATOPSIA

Functionally identified areas of human cortex using fMRI

Area V5
a.k.a. area MT

The retinotopic organization of the human middle temporal area MT/V5 and its cortical neighbors.

V5 lesion gives rise to a kinetopsia

area V5/MT
BILATERAL LESION OF V5
(akinetopsia, patient LM)

Functionally identified areas of human cortex using fMRI

Area LO

LO lesion gives rise to agnosia

area LO (Lateral Occipital)
Functionally identified areas of human cortex using fMRI

**Areas FFA & PPA**

- **V1**
- **V2**
- **V3**
- **V4d**
- **V4v**
- **LO**
- **V5**
- **V3A**
- **FFA**
- **PPA**
- **V7**

**Functionally identified areas of human cortex using fMRI**

- **Parahippocampal Place Area** [topographic disorientation]
- **Fusiform Face Area** [prosopagnosia]

**Areas VWFA**

- **V1**
- **V2**
- **V3**
- **V4d**
- **V4v**
- **LO**
- **V5**
- **V3A**
- **FFA**
- **PPA**
- **V7**

**Functionally identified areas of human cortex using fMRI**

- **Visual Word Form Area** [alexia or pure word blindness]

**LEFT hemisphere**

- **north**
- **south**
- **east**
- **west**

- **mirror text**
- **normal**
Functionally identified areas of human cortex using fMRI

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

area V6 ('medial motion area')

Human V6: the medial motion area.

Direction-selective motion blindness after unilateral posterior brain damage
Two distinct regions where cortical lesions produce motion deficits.

Motion blind patients: composite reconstruction of lesioned regions across subjects

'Area MT' is an alternative term for V5
Visual field maps in human cortex.

CHARTING VISUAL AREAS WITH fMRI

Visual map in macaque area V1:
- this diagram shows the map of polar angle
4. Why are there multiple areas? A ‘theory’ of vision

Campbell 1905

‘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
Lessons from AI: machine vision

DAVID MARR

‘SEEING’: to know what is where by looking

Three levels of analysis by which to understand any seeing system (natural or artificial)

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

Why are there so many visual areas...?

COLOUR
FORM
STEREOSCOPIC DEPTH
MOTION

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