C84LCN
1. Review of cognitive neuroscience: Vision

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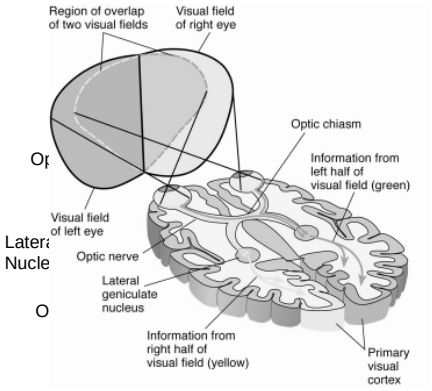
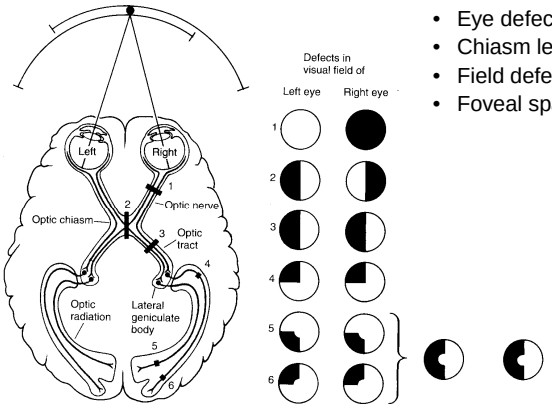
Visual pathways from eye to occipital lobe



Effects of damage at different levels of visual pathway



- Eye defect
- Chiasm lesion
- Field defects
- Foveal sparing

Types of visual cell

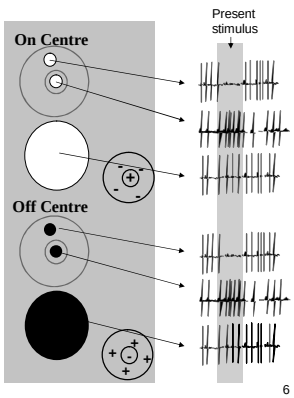
- Photoreceptors (non-spiking)
  - Rods
  - Cones (Long, Medium, Short wavelengths)
- Retinal Ganglion cells (spiking)
- Lateral Geniculate Nucleus (LGN) cells
  - Just like ganglion cells!
- Primary visual cortex (V1). Also called ‘striate cortex’
  - Simple cells
  - Complex cells
  - Tuning

Photoreceptors

- Rods
  - No colour discrimination
  - Sensitive in low light levels
  - Higher density in periphery (don’t look *directly* at dim stars)
  - Will track changes to high rate (see flicker of 60Hz monitor)
- Cones
  - 3 types allow discrimination of different wavelengths (L,M,S)
  - Higher concentration in fovea
  - Less sensitive to low light
  - Can’t follow such rapid changes (can’t see flicker of 60Hz)
- Photoreceptors vary their **voltage** as they are stimulated (analogue signal), whereas all subsequent cells vary spike rate (all-or-nothing, digital signal)
  - Spikes are fast and less susceptible to noise, but simply varying voltage is easy to ‘decode’

Retinal Ganglion neurons

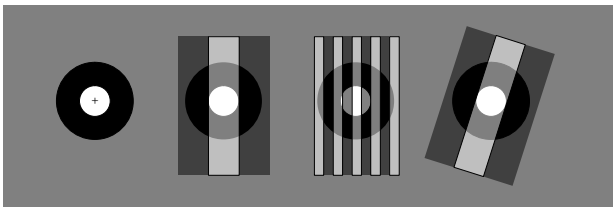
- These are still in the retina but take input from multiple photoreceptors
- They can have ‘On’ regions and ‘Off’ regions, sensitive to the presence of light and the absence
- The response **rate** of the cell is based on the sum of stimulation in the ‘on’ region minus the stimulation in the ‘off’ region
- They generally have a centre-surround opponent organisation



Ganglion and LGN cells like contrast

- Because of their centre-surround configuration these cells like **changes** in luminance (ie **contrast**) rather than just luminance
- They care about **spatial frequency** (thickness of bars) and position of bars but not orientation

e.g., for an on-centre cell:



(No stim) Good stim Bad stim Good stim

Why code for things like that?

- The world has lots of things that stay constant and we don't need to keep responding to them
- So responding to **changes** is better and emphasises boundaries (edges) which are useful
- But, as a result luminance is represented relative to other nearby features, which can result in illusions:

Ganglion and LGN cells (often) like colour

- As well as having centre-surround opponency to luminance, ganglion and LGN cells often are opponent to colour
- The colour opponency comes in only a few types:

L-cone centre, **M**-cone surround (and vice-versa)
Often referred to as Red/Green.

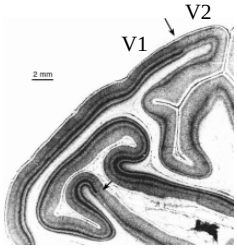
S-cone centre, **L+M** cone surround (and vice versa)
Often referred to as blue/yellow.

Results of colour opponency

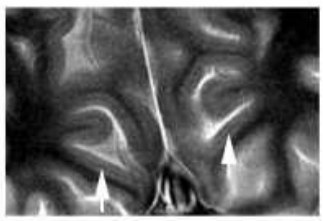
Results of colour opponency

Visual cortex

- After LGN the signals go to the cortex
- They land in layer 4 of Primary Visual Cortex
- Aka: V1; Striate Cortex (meaning stripey)



In monkey (post-mortem)

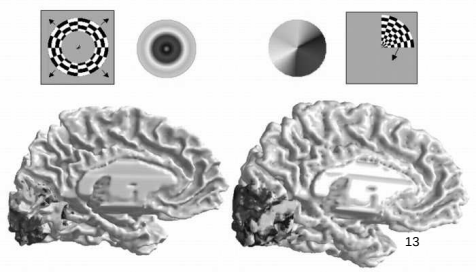


In human (MRI scan)

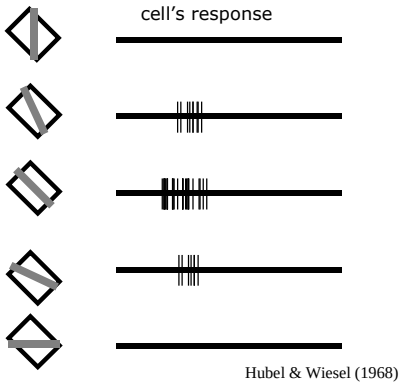
Retinotopic maps

- Retinal ganglion cells cover all locations in the retina
- These project to particular places in the LGN forming a map of the retina
- These, in turn, project to particular places in V1, maintaining the retinotopic map

e.g. visual cortex retinotopy (from Dougherty et al 2003)



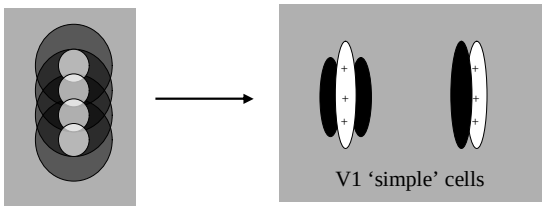
V1 cells are orientation-selective



Hubel & Wiesel (1968)

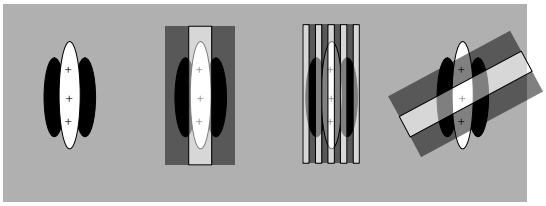
V1 neurons

- Neurons in primary visual cortex also do some combining of the signals (from LGN) to form more elaborate receptive fields:



V1 cells selectivity

- **Simple** cells in V1 respond to changes in luminance of a particular
  - Spatial frequency
  - Bar position (phase)
  - **Orientation**



V1 cells selectivity

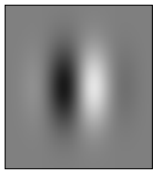
- **Complex cells** combine the outputs of several simple cells V1. They respond to changes in luminance of a particular…
  - Spatial frequency
  - Orientation
  - But **don't care** about bar position within their receptive field
- **End-stop cells** are also sensitive to the **length** of the bars in the stimulus. They have an 'inhibitory surround'
- Some cells are also **direction selective.** ie. they respond best to stimuli in one orientation and spatial frequency **moving in a particular direction**!

V1 cells selectivity

- Each V1 cell has a different preference in the various properties (location, orientation, spatial frequency, colour etc…)
- By identifying which cells are firing, we can see what edges (what Fourier energies) are currently in front of us
- So, basically, the job of V1 is to determine the location and positions of edges

Simple Cells - Linear Filters

Hubel and Wiesel refer to excitatory and inhibitory fields of simple cells:



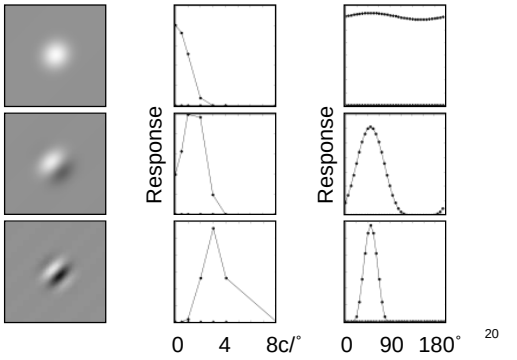
We can also characterise them using mathematical filters, such as Gabors

From these we can potentially deduce a neuron's response to a given stimulus at any point in space/time

Model Cells - Spatial Tuning

SF tuning falls out naturally from the Gabor filter…

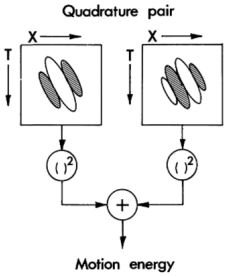
…so does orientation tuning



Modelling complex cells

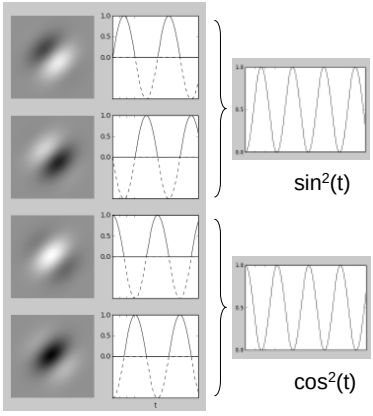
Biophysically complex cells (probably) result from the summing (or mutual excitation) of many cells that differ in phase

Mathematically perfect phase insensitivity can result from 4 (or 2 whose outputs are squared)



Adelsen & Bergen (1985), *JOSA* 2(2):284-299

Filters in quadrature



4 model neurons with carrier phases separated by π/2

None can respond negatively

If each has an output nonlinearity that approaches squaring then the sum of the 4 responses

Then we can use the fact that

$\sin^2(t) + \cos^2(t) = 1$

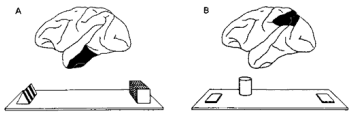
Other additions to the model

- So far we have modeled V1 tuning to
  - Orientation
  - Spatial frequency
  - Phase of the stimulus
- With some simple additions we can add
  - Non-linear contrast response (and cross-orientation suppression)
  - Size tuning

Adaptation

- Adaptation also occurs in V1 and above, but the effects are more complex
- Our perceptions of spatial frequency and orientation of a whole image can change:

Visual Streams – what/where



Ungerleider & Mishkin (1982)

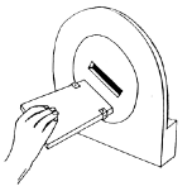
A. Monkeys with lesions to TE or TEO are impaired at discriminating objects (e.g. fail to consistently pick out the pyramidal object for reward). =>The 'what' pathway (ventral stream)

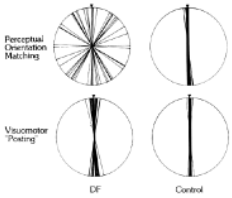
B. With Posterior Parietal Lesions they fail to perform on location tasks (e.g. pick the object near to the post) => The 'where' pathway (dorsal stream)

Visual Streams – what/how

Milner and Goodale 1991

- Worked with a patient, D.F. with extensive bilateral ventral-stream lesions since 1991.
- D.F. has profound visual form agnosia
- But some interesting spared abilities…





It's the need to act on the stimulus that allows her to perform. She still doesn't know **what** it is or (maybe) **where** it but knows **how** to post something into it

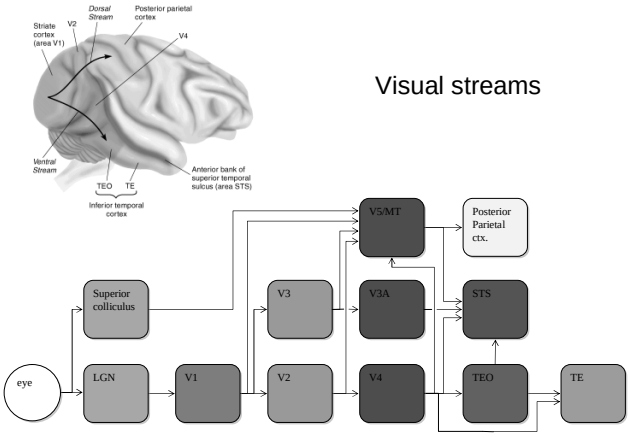
Visual Streams – what/how

- Balint's syndrome – dorsal lesions
  - Optic apraxia (poor control of eye-movements)
  - Optic ataxia (poor visually-guided other movements)
  - Simultanagnosia (inability to identify 2 objects at once)

e.g. of optic ataxia
The patient (right) is trying to touch the doctor's finger

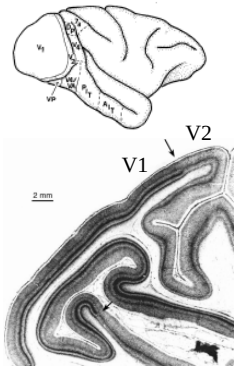
Rizzo, M et al. J Neurol Neurosurg Psychiatry 2002;72:162-178

Visual streams



Other visual areas: V2

- Meets V1 and is anatomically quite visible (at least in macaque and cat)
- They meet at the 'vertical meridian' of the retinotopic map
- Dorsal V2 represents lower visual field and ventral V2 represents upper
- Retinotopic map of each quarter field is a mirror of the V1 map



Other visual areas: V2

- Cells are very similar to V1
  - Orientation- and SF-tuned
  - Greater tendency to be 'complex'
  - Greater tendency to be binocularly driven
  - Slightly larger receptive fields
- Possibly cells here are more involved in detecting 'contours' rather than Fourier energies (gratings)
  - Respond to 'illusory' contours as well as regular contours? (e.g. von der Heydt R *et al* (1984))

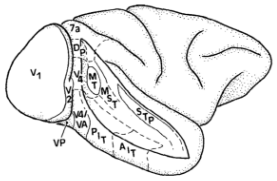
Other visual areas: V3

V3 is the most enigmatic of the occipital areas, because its cells generally lack distinctive visual characteristics, and because its outputs are directed principally towards regions (V4 and MT) that already receive much of their input from V2. The characteristics of receptive fields in the upper and lower parts of the representation are similar, but cells with different sorts of visual preferences occur with different frequencies. Orientation-selective cells are common in both divisions, though they appear to be less selective than neurons in V2 (Baizer 1982); directionally selective cells are common in the lower field representation (Zeki 1978c; Felleman and Van Essen 1987; Gegenfurtner et al 1997) but not in the upper field map. This difference can be readily explained by supposing that the map of the lower field receives much more direct input from layer 4B of V1. Color-selective cells are relatively frequent (Burkhalter and Van Essen 1986; Felleman and Van Essen 1987; Gegenfurtner et al 1997); the population of neurons that are both color-selective and direction-selective seems to be distinctive (Gegenfurtner et al 1997). Many neurons appear to be sensitive to binocular disparity (Felleman and Van Essen 1987; Poggio et al 1988).

On the whole, single-unit work tells us little about what V3 does, and it might be more profitable to try to understand it by considering some of its gross properties and by analyzing the flow of information to it and from it. Although we can say little about the details, its relatively small size and large receptive fields imply a coarse analysis. The intermediate position of V3 also makes it likely that signals from it reach V4 and MT later than do signals from V2. These observations, coupled with the fact that V3 apparently provides only a small fraction of the input to V4 and MT suggests that its role might be to provide a spatially coarse, and perhaps relatively slow, modulation of information transmission in the principal pathways connecting V1 and V2 to the parietal and temporal lobes. A better appreciation of the role of V3 might have to await studies that explore the effects of damage confined to it.

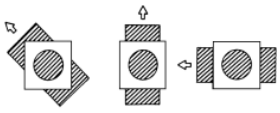
Other visual areas: MT/V5

- Called MT because in the monkey it lies in the Medial Temporal (especially US)
- Called V5 because… it makes sense (mainly UK)
- Rather small area, anatomically
- Good evidence that this is involved in motion perception
  - Plaids
  - Random dot stimuli



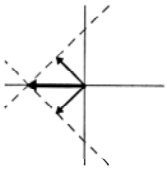
From Maunsell and Newsome 1987

Plaid motion detection



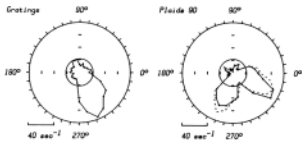
The aperture problem: when viewed through an aperture (like a receptive field) direction of grating motion is ambiguous

When two gratings are moving, the perception is a plaid, moving in a single direction

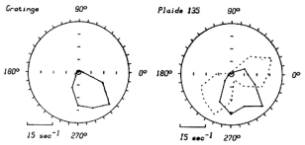


Plaid motion detection

- Cells in V1, always respond to the direction of the component gratings ('component motion')

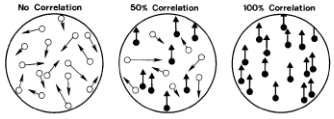


- Cells in MT often respond to the direction of the plaid ('pattern motion')

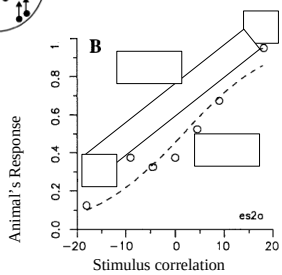


Dot motion in MT

Salzman, Murasugi, Britten & Newsome(1992)

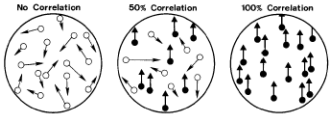


Train a macaque to report the direction of motion of moving dot displays of various degrees of coherence



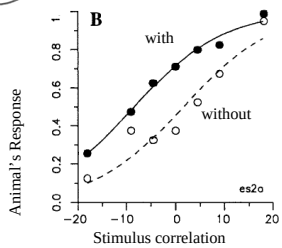
Dot motion in MT

Salzman, Murasugi, Britten & Newsome(1992)



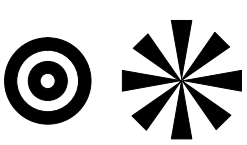
Train a macaque to report the direction of motion of moving dot displays of various degrees of coherence

Then 'micro-stimulate' using the same electrode

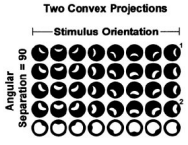


Other visual areas: V4

- Many people still claim that V4 is for colour perception
- Little evidence has confirmed that (although there is a condition called *achromatopsia*)
- Probably important mid-stage in object recognition, given position anatomically
- Cells here seem selective/tuned for more complex visual characteristics (like curvature?)



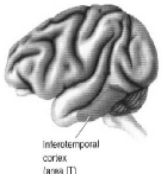
Gallant and van Essen

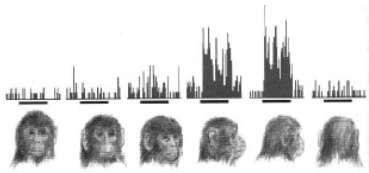


Pasupathy and Connor

Other visual areas: IT

- Infero-temporal cortex (IT) contains cells that respond to very complex visual objects
- In TE they have larger receptive fields and more complex preferences than TEO
- Famous for 'face' cells (like the profile-selective cell below)





Face recognition in humans

- In humans there is also an area that responds selectively to faces – the Fusiform Face Area (named because it lives on the Fusiform Gyrus) shown using PET and fMRI
- In humans there is also a selective deficit in recognising faces (prosopagnosia)

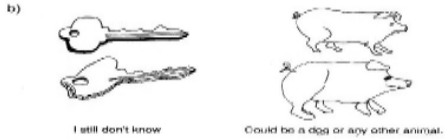
Agnosias

- What happens when our higher-level perceptual systems are damaged?
  - Apperceptive agnosia (like D.F.)
    - Tyically ventral anterior lesions
  - Associative agnosia
    - Typically more posterior temporal ctx.
  - Balint's syndrome – dorsal lesions
    - Optic apraxia (poor control of eye-movements)
    - Optic ataxia (poor visually-guided other movements)
    - Simultanagnosia (inability to identify 2 objects at once)
  - Also other selective deficits (akinetopsia, achromatopsia…)

Examples

Apperceptive agnosia (visual form agnosia)

Associative agnosia



Modules versus increasing complexity

- Some people say that there are areas for particular aspects of the image (colour, depth, shape, motion…)
- Maybe these things are processed in multiple areas, but with increasing complexity
- MT – seems clear evidence from electrophys/stimulation, fMRI, TMS that MT is involved in motion
- V4 – probably not a specialised colour area
- No idea what V2 and V3 do in the modularity scheme
- IT/FFA – easy/robust to localise, but is it special for faces, or just a particular type of processing?

Summary and general principles

- As we progress through the visual system we get an increasingly complex representation of the visual scene
- This is based on a Fourier representation in V1
- The system attempts to 'reduce redundancy' – cells stop firing when they don't need to fire (e.g. coding by contrast, adaptation effects…)
- Gets very mysterious after V1!

- Further reading:
  - *Basic Vision.* Snowden, Thompson, & Troscianko. Oxford University Press.
  - Lennie. Single units and visual cortical organization. Perception (1998) vol. 27 (8) pp. 889-935

- Basic Reading
  - Carlson chapter 6
- Detailed reading
  - Lennie. Single units and visual cortical organization. Perception (1998) vol. 27 (8) pp. 889-935

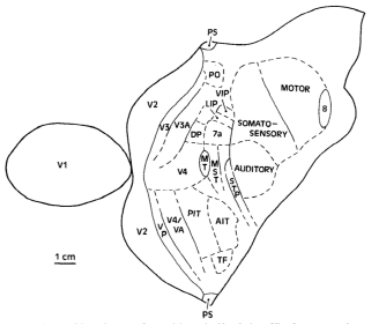


Figure 3 A map of the entire cortex from a right cerebeal hemisphere. Visual cortex occupies the left (posterior) side of the map and comprises more than half of cortex. In this flattened representation it is possible to see the relative dimensions of the different cortical areas. Individual areas have not been drawn for other modalities, with the exception of area 8 (the frontal eye fields).