

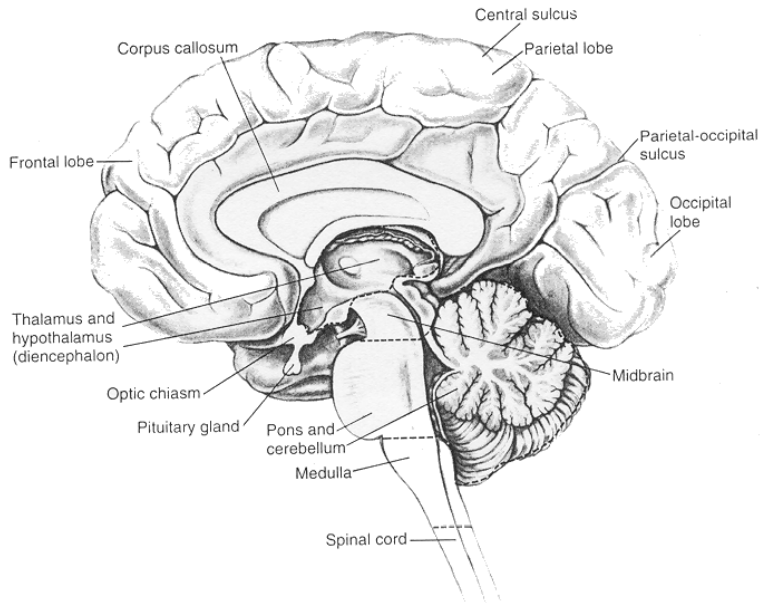
Introduction to Neural Coding

Peter Latham / Maneesh Sahani

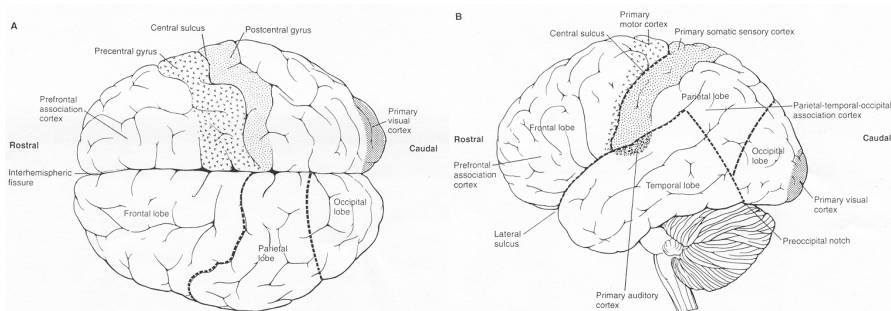
Gatsby Computational Neuroscience Unit
University College London

Term 1, Autumn 2013

The CNS

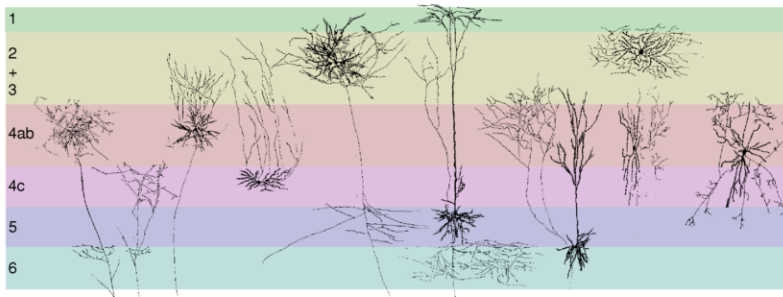


Neocortex

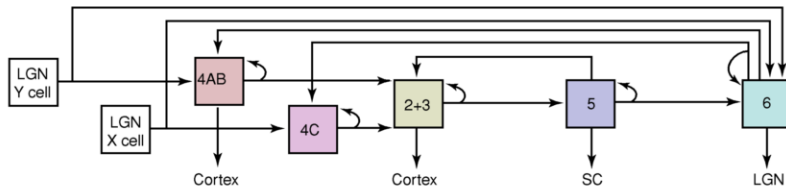


Cortical layers

A



B



Neural signals (in vivo)

Aggregate

- ▶ aggregate fields – EEG, MEG, LFP
- ▶ aggregate membrane voltage – dye imaging (voltage/calcium)
- ▶ metabolism – fMRI, PET, intrinsic imaging

Single neuron

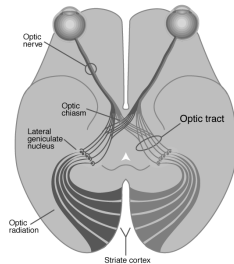
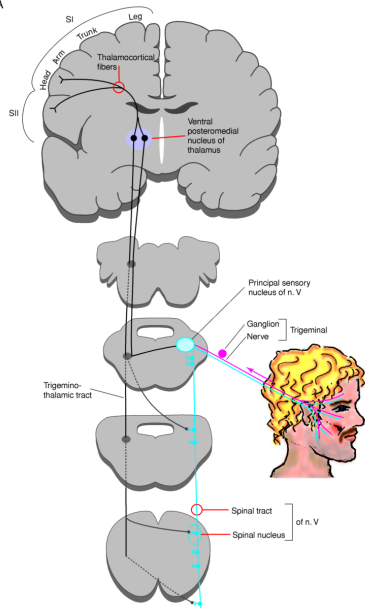
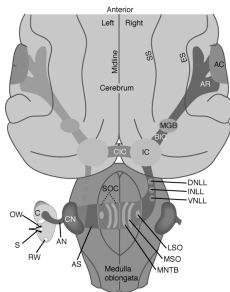
- ▶ extracellular – single neuron, spike sorting, cell attach
- ▶ intracellular – sharp electrode, whole cell
- ▶ imaging – 2-photon calcium (and soon voltage) dyes.

Senses

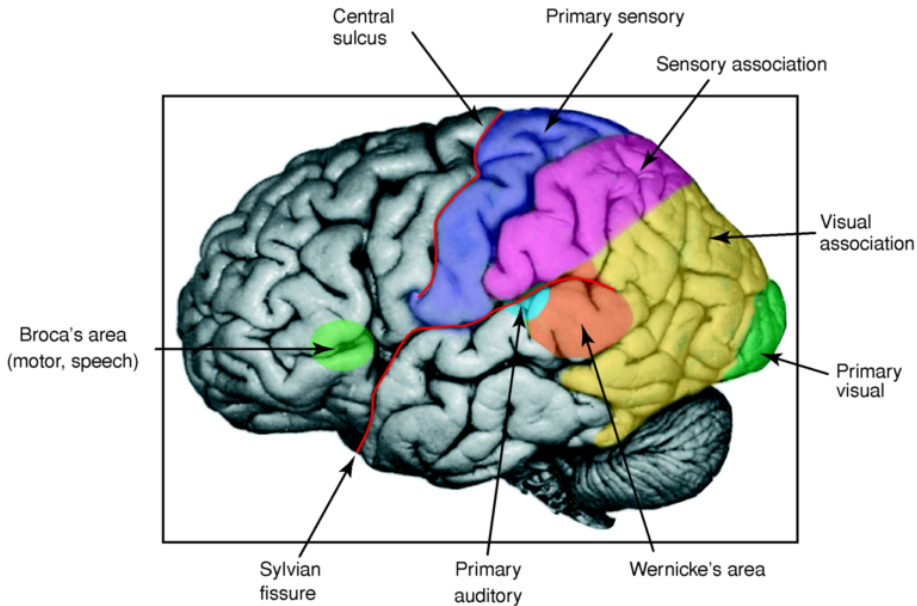
How many senses do you have?

Neocortical senses

A



Sensory areas



Common features of neocortical senses

- ▶ common pathways: receptors – subctx nuclei – thalamus – primary ctx – higher ctx
- ▶ thalamic loops between cortical areas
- ▶ feedback
- ▶ parallel hierarchy
- ▶ alternate pathways – tectal, para-lemniscal

Common processing

- ▶ receptor discretisation – sampling
- ▶ receptive fields
- ▶ centre-surround processing
- ▶ contrast sensitivity – Weber's law
- ▶ adaptation
 - ▶ neural vs. psychological
 - ▶ adaptation to higher features
 - ▶ mismatch negativity
 - ▶ statistical adaptation

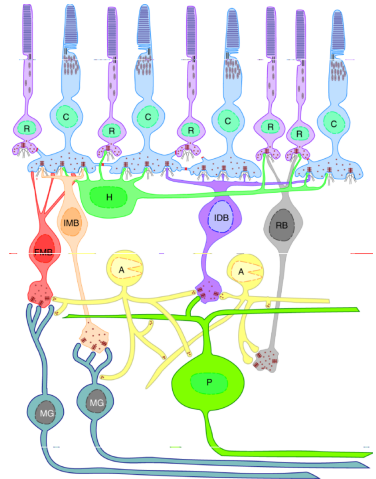
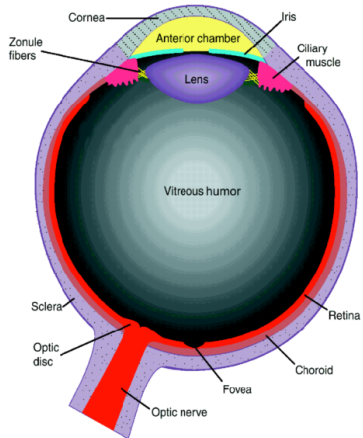
Quantifying responses

- ▶ receptive fields
- ▶ motor fields
- ▶ stimulus-response functions
- ▶ sensory computation and encoded variables
- ▶ tuning curves

Optimality of coding

- ▶ “impedence” matching between different components
- ▶ matching to natural statistics
- ▶ matching to behaviourally relevant features
- ▶ redundancy reduction

The eye and retina



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Centre-surround receptive fields

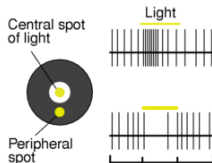
A On center field



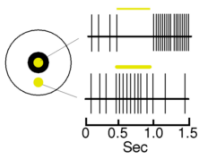
F Off center field



B On center cell responses



G Off center cell responses



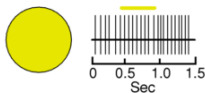
C Central illumination



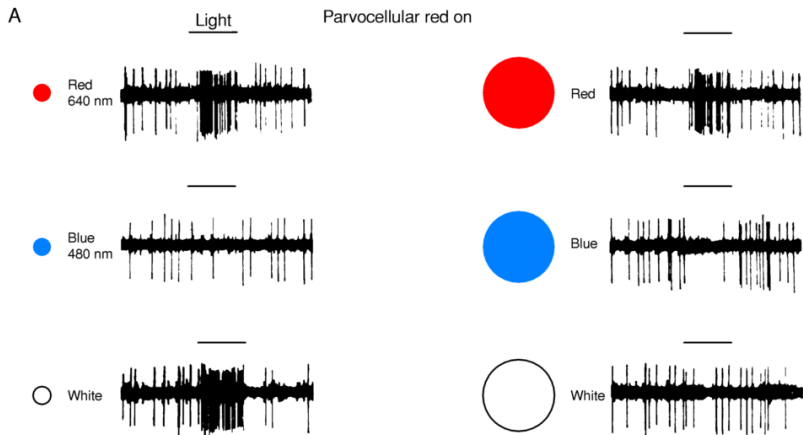
D Annular illumination



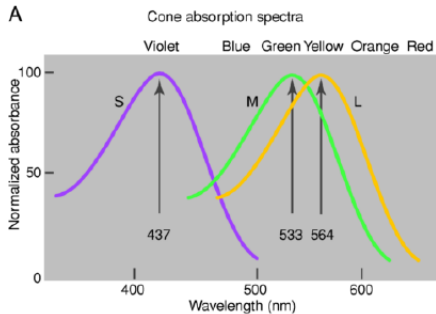
E Diffuse illumination



Colour at the retina

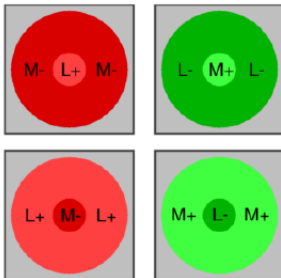


Colour at the retina



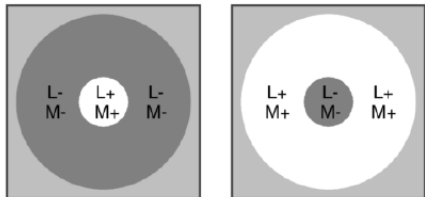
B

Parvocellular receptive fields



C

Magnocellular receptive fields

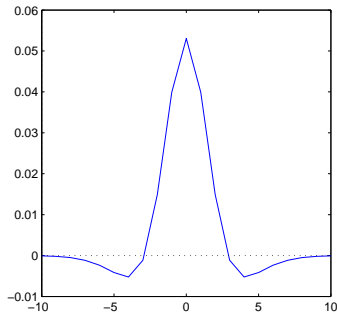
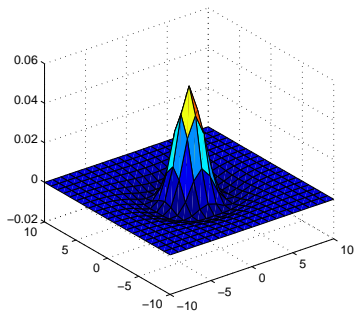


Centre-surround models

Centre-surround receptive fields are commonly described by one of two equations, giving the scaled response to a point of light shone at the retinal location (x, y) .

A difference-of-Gaussians (DoG) model:

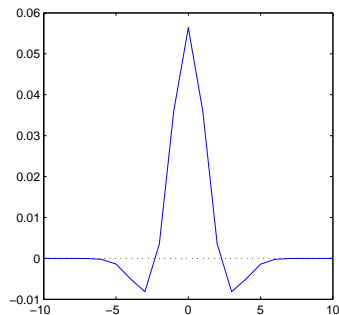
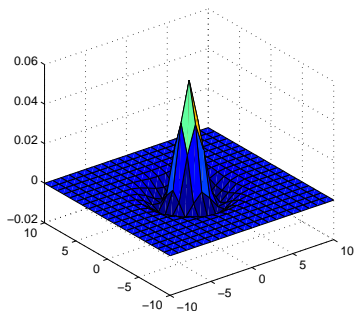
$$D_{\text{DoG}}(x, y) = \frac{1}{2\pi\sigma_c^2} \exp\left(-\frac{(x - c_x)^2 + (y - c_y)^2}{2\sigma_c^2}\right) - \frac{1}{2\pi\sigma_s^2} \exp\left(-\frac{(x - c_x)^2 + (y - c_y)^2}{2\sigma_s^2}\right)$$



Centre-surround models

... or a Laplacian-of-Gaussian (LoG) model:

$$D_{\text{LoG}}(x, y) = -\nabla^2 \left[\frac{1}{2\pi\sigma^2} \exp \left(-\frac{(x - c_x)^2 + (y - c_y)^2}{2\sigma^2} \right) \right]$$



Linear receptive fields

The linear-like response apparent in the prototypical experiments can be generalised to give a predicted firing rate in response to an arbitrary stimulus $s(x, y)$:

$$r(c_x, c_y; s(x, y)) = \int dx dy D_{c_x, c_y}(x, y) s(x, y)$$

The receptive field centres (c_x, c_y) are distributed over visual space.

If we let $D()$ represent the RF function centred at 0, instead of at (c_x, c_y) , we can write:

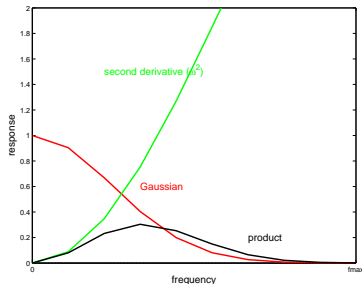
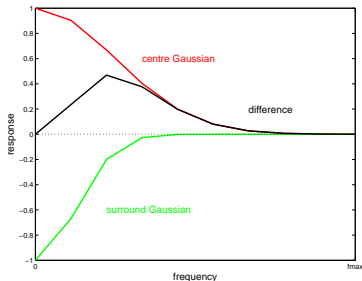
$$r(c_x, c_y; s(x, y)) = \int dx dy D(c_x - x, c_y - y) s(x, y)$$

which looks like a convolution.

Transfer functions

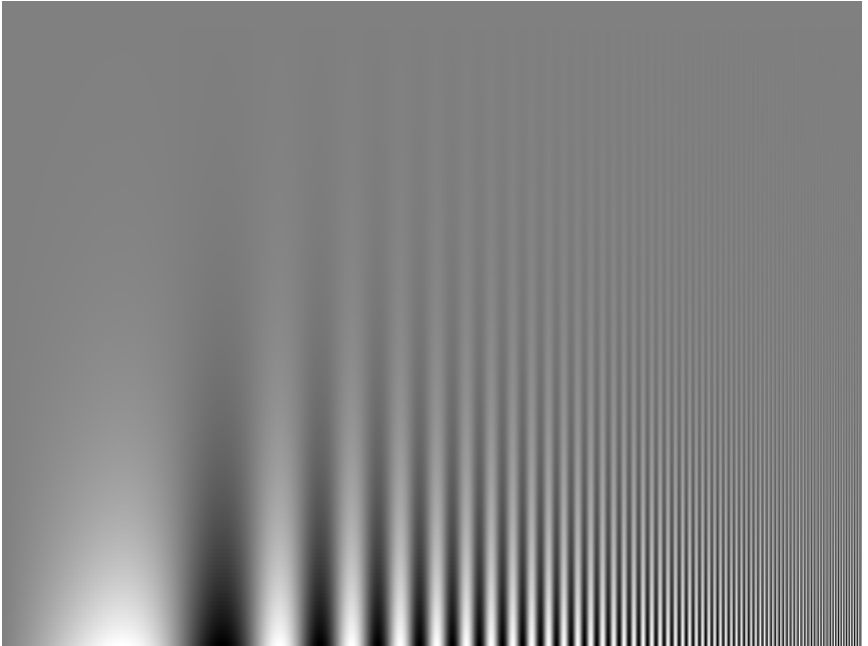
Thus a repeated linear receptive field acts like a spatial filter, and can be characterised by its frequency-domain transfer function. (Indeed, much early visual processing is studied in terms of linear systems theory.)

Transfer functions for both DoG and LoG centre-surround models are **bandpass**. Taking 1D versions:



This accentuates mid-range **spatial** frequencies.

Transfer functions



Edge detection

Bandpass filters emphasise edges:



original image

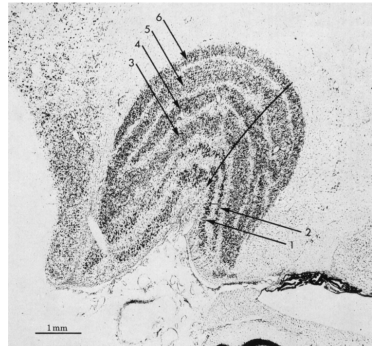
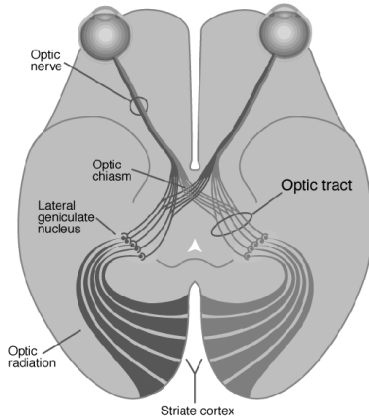


DoG responses



thresholded

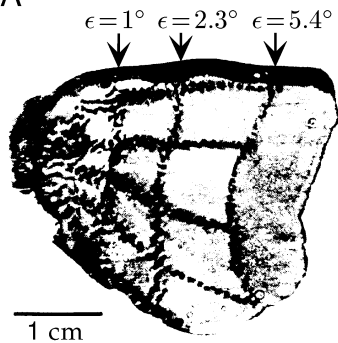
Thalamic relay



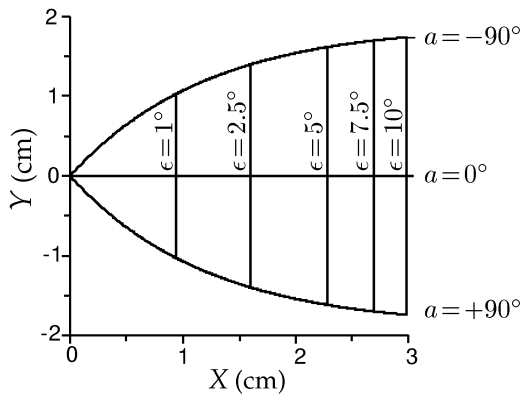
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Visual cortex

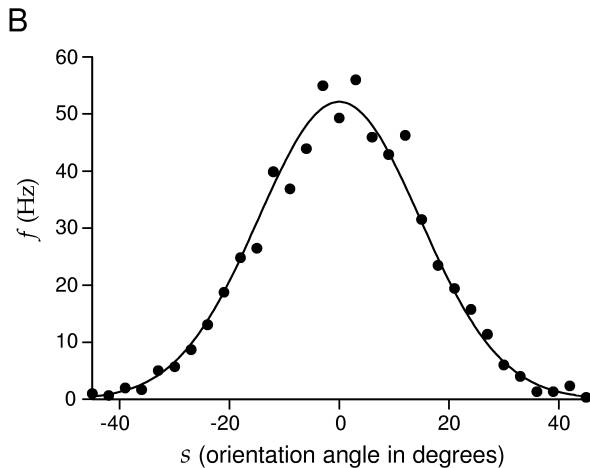
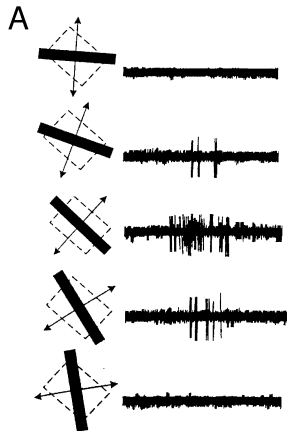
A



B



Orientation selectivity



Linear receptive fields – simple cells

Linear response encoding:

$$r(t_0, s(x, y, t)) = \int_0^\infty d\tau \int dx dy s(x, y, t_0 - \tau) D(x, y, \tau)$$

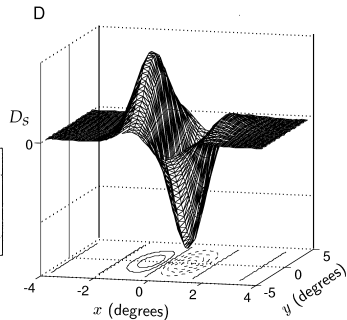
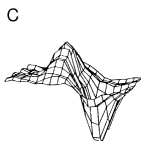
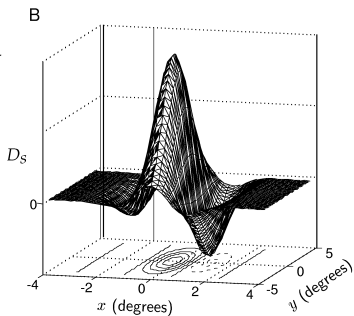
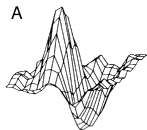
For separable receptive fields:

$$D(x, y, \tau) = D_s(x, y) D_t(\tau)$$

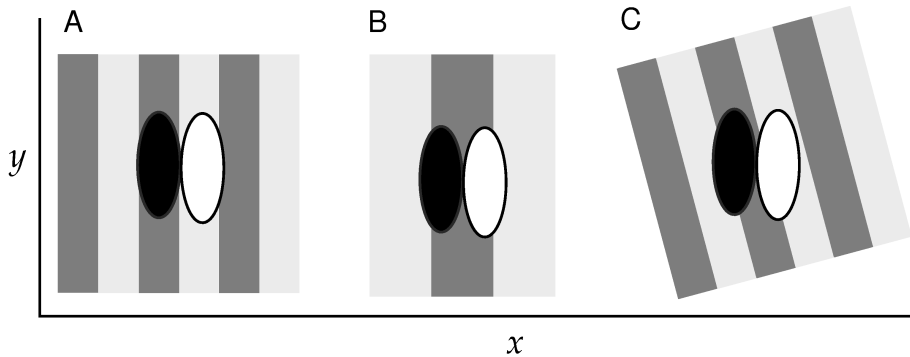
For simple cells:

$$D_s = \exp\left(-\frac{(x - c_x)^2}{2\sigma_x^2} - \frac{(y - c_y)^2}{2\sigma_y^2}\right) \cos(kx - \phi)$$

Linear response functions – simple cells



Simple cell orientation selectivity



2D Fourier Transforms

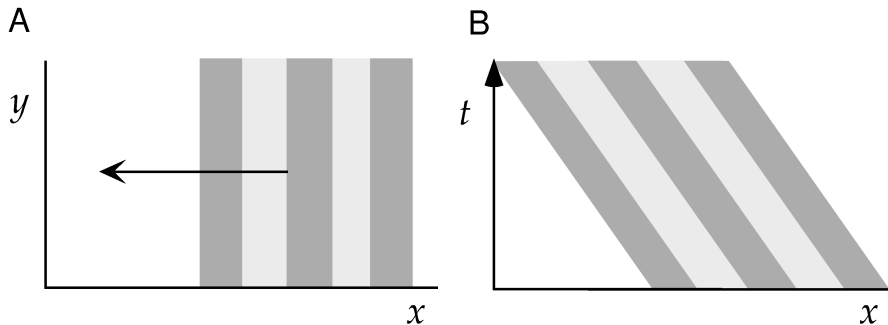
Again, the best way to look at a filter is in the frequency domain, but now we need a 2D transform.

$$D(x, y) = \exp\left(-\frac{x^2}{2\sigma_x^2} - \frac{y^2}{2\sigma_y^2}\right) \cos(kx)$$

$$\begin{aligned}\tilde{D}(\omega_x, \omega_y) &= \int dx dy e^{-i\omega_x x} e^{-i\omega_y y} \exp\left(-\frac{x^2}{2\sigma_x^2} - \frac{y^2}{2\sigma_y^2}\right) \cos(kx - \phi) \\&= \int dx e^{-i\omega_x x} e^{-x^2/2\sigma_x^2} \cos(kx - \phi) \cdot \int dy e^{-i\omega_y y} e^{-y^2/2\sigma_y^2} \\&= \sqrt{2\pi}\sigma_x \left[e^{-\sigma_x^2 \omega_x^2/2} \circ \pi[\delta(\omega_x - k) + \delta(\omega_x + k)] \right] \sqrt{2\pi}\sigma_y e^{-\sigma_y^2 \omega_y^2/2} \\&= 2\pi^2 \sigma_x \sigma_y \left[e^{-\frac{1}{2}[(\omega_x - k)^2 \sigma_x^2 + \omega_y^2 \sigma_y^2]} + e^{-\frac{1}{2}[(\omega_x + k)^2 \sigma_x^2 + \omega_y^2 \sigma_y^2]} \right]\end{aligned}$$

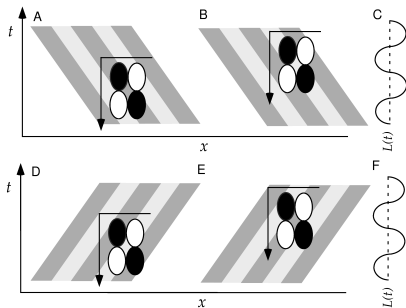
Easy to read spatial frequency tuning, bandwidth; orientation tuning and (for homework) bandwidth.

Drifting gratings

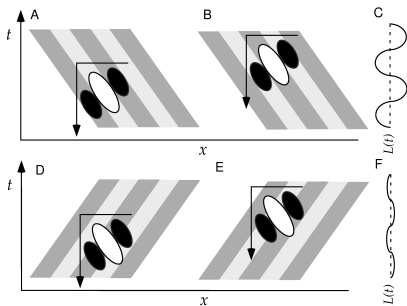


$$s(x, y, t) = G + A \cos(kx - \phi) \cos(\omega t)$$

Separable and inseparable response functions



Separable: motion sensitive;
not direction sensitive



Inseparable: motion sensitive;
and direction sensitive

Complex cells

Complex cells are sensitive to orientation, but, supposedly, not phase.

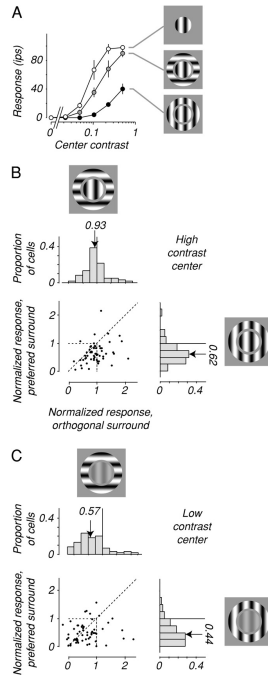
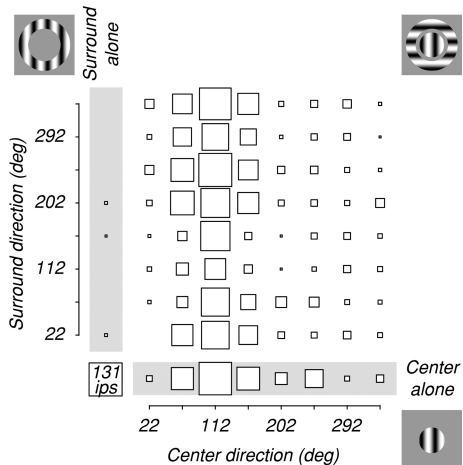
One model might be (neglecting time)

$$r(s(x, y)) = \left[\int dx dy s(x, y) \exp \left(-\frac{(x - c_x)^2}{2\sigma_x^2} - \frac{(y - c_y)^2}{2\sigma_y^2} \right) \cos(kx) \right]^2 \\ + \left[\int dx dy s(x, y) \exp \left(-\frac{(x - c_x)^2}{2\sigma_x^2} - \frac{(y - c_y)^2}{2\sigma_y^2} \right) \cos(kx - \pi/2) \right]^2$$

But many cells do have some residual phase sensitivity. Quantified by (f_1/f_0 ratio).

Stimulus-response functions (and constructive models) for complex cells are still a matter of debate.

Other V1 responses: surround effects

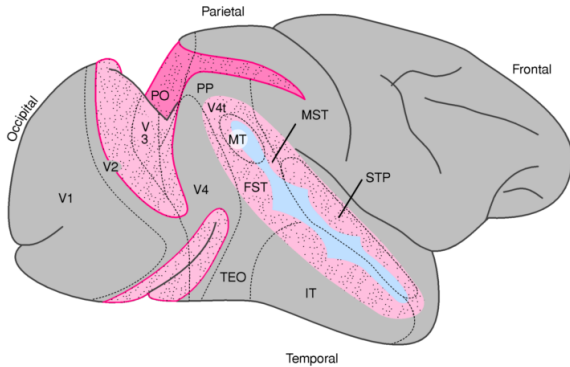


Other V1 responses

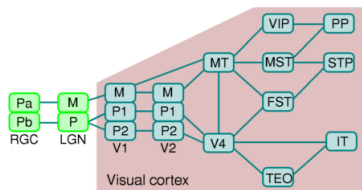
- ▶ end-stopping
- ▶ blobs and colour
- ▶ ...

Higher Visual Areas

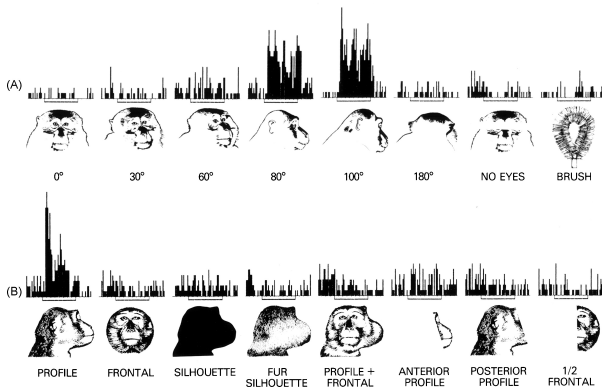
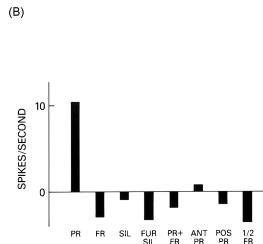
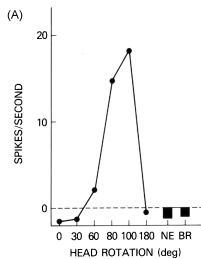
A



B



Object recognition



Grandmother cells (for certain definitions of grandmother)

a

