**Week 1 Lecture 1: Introduction and Colour**

**A statement:** *Even the simplest visual task involving coloured stimuli cannot be explained by what we currently know about the visual system, let alone the more complex observations we make all the time*

- Why?
- What evidence do I have to say this?

Colour itself and the sense of colour itself is a result of the interpretation of your brain; not product of environment

- Photons of different wavelengths, absorbed during daylight by three different photoreceptors in order to reconstruct the colours you eventually see
- However, contact with the image projected on to the retina is lost almost immediately and the world we perceive is indeed a construct of the operation of the system
- Colour is context-specific
- In fact, vision and all the brain's activity is context-specific
- The outcome these is that things result in the experience you have

**Issac Newton** – showed that white light was made up of all visible colours

**Young and Helmholtz** – our visual system constitutes just three receptors at the outset and by somehow comparing the output of these receptors we are able to reconstruct all colours seen. Trichromacy.

**Ewald Hering** – suggest our visual system has four, rather than three receptors wired into pairs in opposition to one another: red-green and blue-yellow. Showed that prolonged exposure to a stimulus produced an afterimage, a complement of that stimulus. Later stated that the first stage of colour vision could be a trichromatic stage and then an opponent stage.

**The detection of colour:** what we know and what we don' t know

- What are the behavioural properties of basic colour detection?
    - Krauskopf, J., Williams, D. R. & Heeley, D. W. (1982). Cardinal directions of colour space. *Vision Research*, *22*, 1123-1131.
- What is the neural substrate? (A **neural substrate** is a term used in neuroscience to indicate a part of the nervous system that underlies a specific behaviour or psychological state)

**Stimuli and methods (Krauskopf 1982)**

Interested in simple colour detection; you could detect the presence of a stimuli without really knowing what it is.

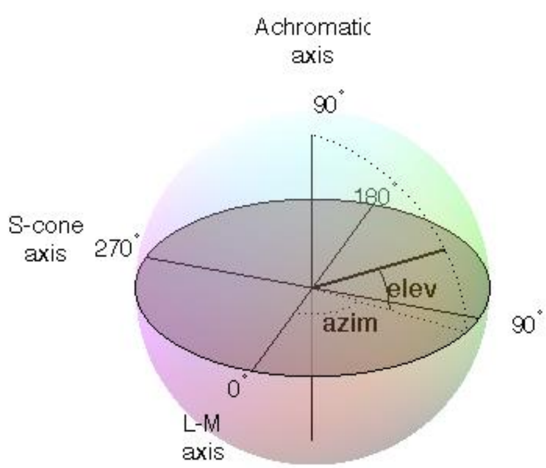
- Small (4deg) discs whose colour varied in time along an axis of opponent colour space

    - Accurate representation of the space requires careful and extensive calibration; an absolute essential of psychophysical experiments - define the input absolutely
- Observers required to indicate whether a test pulse was visible before and after prolonged exposure (30 secs + 5 secs) to a similar stimulus modulated along given axis
    - Contrast (visibility) of the pulse varied according to the observer's response until a "threshold" is reached
- Threshold taken as the 75% correct point in the task
    - This is the detection threshold of the system (observer) to the described stimulus and measures the effect of prolonged exposure to the same and different stimuli as subsequently detected

### Colour space pictured and animated (Derrington, Krauskopf and Lennie)

A colour space is a method by which a particular light and colour may be represented such that its definition is unique and replicable.

L cones vs. M cones and S cone axis (Also known as Cardinal Space; relates to the 'excitation' stage of processing)




The translation of the level of the retina is at three opponent deflections along these three axes

*The Derrington, Krauskopf and Lennie (1984) colour space is based on the Macleod-Boynton (1979) chromaticity diagram. Colours are represented in 3 dimensions using spherical coordinates that specify the elevation from the isoluminant plane, the azimuth (the hue) and the contrast (as a fraction of the maximal modulations long the cardinal axes of the spaces).*

The cardinal colour space consists of two chromatic axes (colour) and one achromatic axis (luminance).

It's easier for me to think of a colour in Cartesian DKL coordinates with the dimensions:

- Luminance or L+M, sum of the L and M cones response (bluish, yellowish stimulus)
- L-M, difference of L and M cone response (reddish, greenish stimulus) [output of Long wavelength-sensitive L cones]
- S-(L+M), S cone responses minus sum of L and M cone response (black and white stimulus) [output of short wave-length S cones only]

*note when modulating the output of one axis should not modulate the output of the other axes; they are independent mechanisms*

The three classes of cones respond a bit to almost all colours, but some reds excite L cones the most, some greens M cones the most, and come blues S cones the most.

They don't look red and green and yellow due to our understanding of those colours. They don't appear to be *good* examples of red green blue and yellow.

In between these stimuli there are intermediate colours; orange, purple etc. You can move across all spaces and produce all kinds of colours

**Results (Krauskopf 1982)** : *Adapted – Unadapted threshold = Distance from centre*

Plotted the threshold difference between pre-adaption and post-adaption stimulus

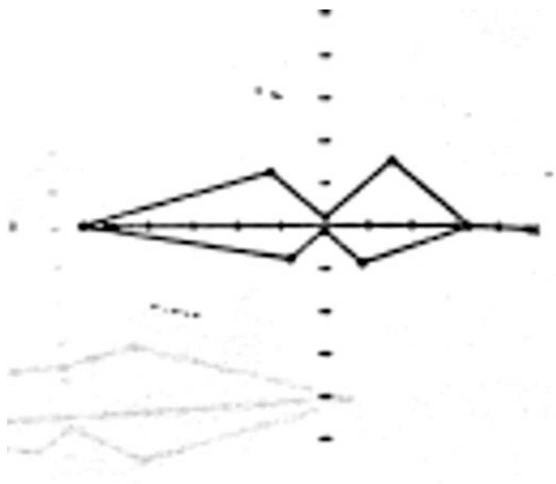
Means that the adapted stimuli had an effect on how you perceive

The further away the data point is from the origin, the bigger the adapting effect.

In order to explain our ability to detect and pass that information on to the rest of the system, we have three mechanisms:

1. It is sensitive to modulation of L and M output
2. It is sensitive to modulation of S cone as opposed to L and M output
3. It is sensitive to photon principally contributed by L and M because there are far more of them than there are S cones; a luminant-sensitive mechanism

*Distance from centre = Difference in contrast threshold before and after adaption. Arrows indicates axis of adapting stimulus*



### Results (Kraskopf 1982)

- Each axis shows independent adaptability
    - Threshold is only raised by adapting to a stimulus along the same axis; threshold is unaffected by adapting to other two axes
    - This shows psychophysical orthogonality of the space and strongly suggests three independent detection mechanisms mediate the transmission of spatio-chromatic information from retina to cortex
    - The three mechanisms are only sensitive to modulation along one of each of the three axes…..just like the cells in the LGN

- This is the basis of the Cardinal Colour Space

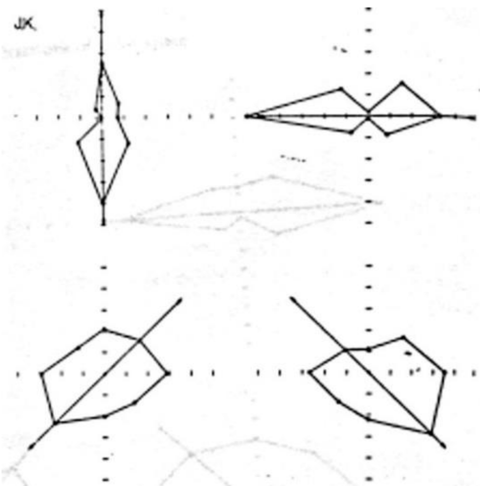



Fig. 5. (Upper) changes in thresholds resulting from viewing fields varying along the provisional cardinal axes. See text for details. Observer—J.K. (Lower) Changes in thresholds resulting from viewing fields varying along directions halfway between the provisional cardinal axes.

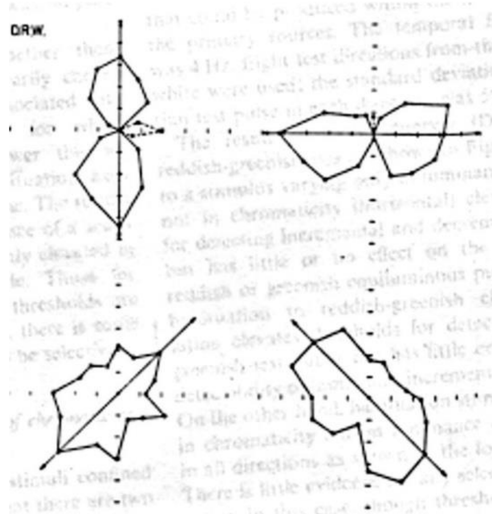



Fig. 6. Effects of chromatic habituating stimuli on detectability of chromatic test pulses for observer D.R.W.

The simplest thing we can possibly do with our visual system is being able to detect some kind of variation in the environment (is something there or not?): which is mediated by three mechanisms

- Three independent primary detection mechanisms which is all you need as the start of everything you see to identify just the presence of a stimuli

**Colour space theory:**

The system has developed to represent what happens at the retina in a very efficient way

- Coding different colours and only needing 3 numbers to make of what you perceive
- Relate to each of the three opponent mechanisms; a prophecy of the early visual system theories

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**Week 1 Lecture 2: Colour 2**

**In conclusion**

According to Krauskopf:

- You can explain every brightness and every colour we are able o see when we are asked just to detect the stimulus in terms of three mechanisms: black-white; red-green; blue-yellow

- His experiment quantified the ideas of Hering in relation to opponency and linked it to Helmholtz idea of how the cones might initiate the first stage of vision. There is opponency but it is at a level prior to sensation, but excitation. This doesn't correspond to what you actually see and perceive.

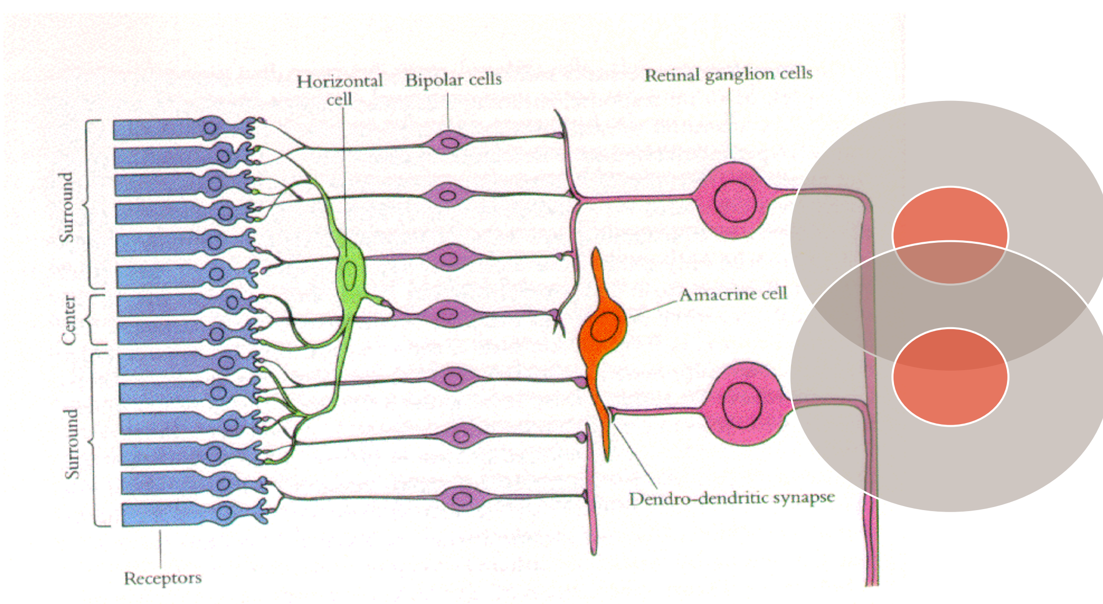
### Hinton's "Lilac Chaser"

- Shows deflection along an axis of the colour space. When we modulate along this axis it gets translated into a model of colour.
- By focusing on the centre of the circle (fixation point) when a lilac dot is removed we perceive a green dot moving around the circle. This is a visual representation of the adaptation experience of the visual system. According to opponency theory, the visual system overcompensated such that prolonged exposure causes the system o overcompensate when the colour (or stimulus) disappears leaving an opponent colour present ie. Green.

### What are the cardinal neurones?

- Considering the basic and simple nature of the task we might expect to find some group of neurons that can explain our behaviour
- Properties:
  - Chromatic sensitivities clustered along cardinal axes (needed to get the pattern of independent adaptability that Hering showed in his experiments)
  - Change in output after prolonged exposure (opponency; adapt and reduce their sensitivity when exposed to that stimulus)

### The retina



## Retina – LGN – cortex

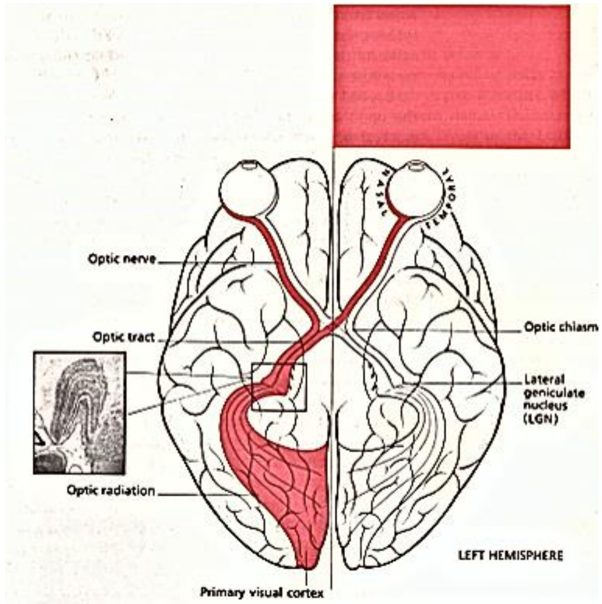
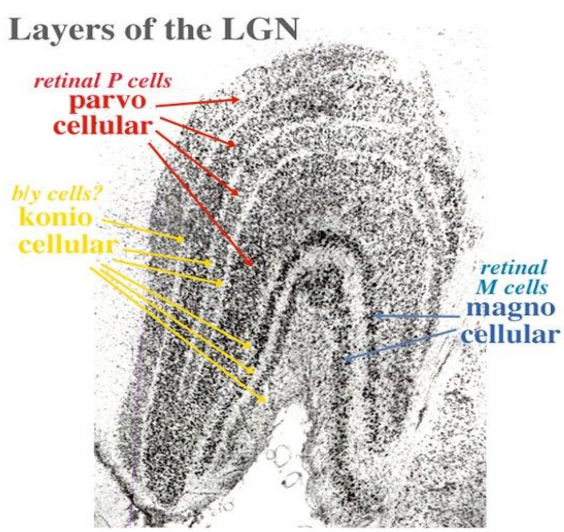



**Fig. 3.3** The connections from the retina to the cerebral hemispheres. For details, see text. Inset to the left shows the multi-layered lateral geniculate nucleus [LGN].

## Dorsal LGN




## Receptive fields of dLGN neurons

Derrington, A.M., Krauskopf, J. & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of maaque. *Journal of Physiology (London), 357,* 241-265

## Stimuli and methods (Derrington et al. 1984)

- Recording of discharges of single macaque dLGN neurons
- Receptive field locations established with coloured spot stimuli then analysed with full-field stimuli modulated sinusoidally in time
  - Colour and luminance properties of the gratings described in opponent colour space
  - Stimuli modulated within three orthogonal planes of the space until a minimum of "null" response found
    - "silent substitution" – two coloured lights may be exchanged (or modulated between) with no effect on the output of the neurons
  - The preferred stimuli of each cell taken as that plane orthogonal to the null plane in the 3D space

## Results

Three "Cardinal" planes

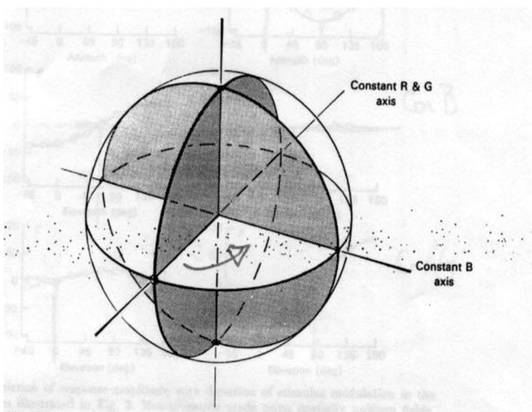



Fig. 3. Schematic representation of the three cardinal planes within which stimuli were modulated in the experiments to establish the position of the null plane for each cell. Within each plane stimuli were modulated along vectors that passed through the white point and were spaced at 22·5 deg intervals.

Peristimulus time histograms to uniform field modulated along axis in equiluminant plane →

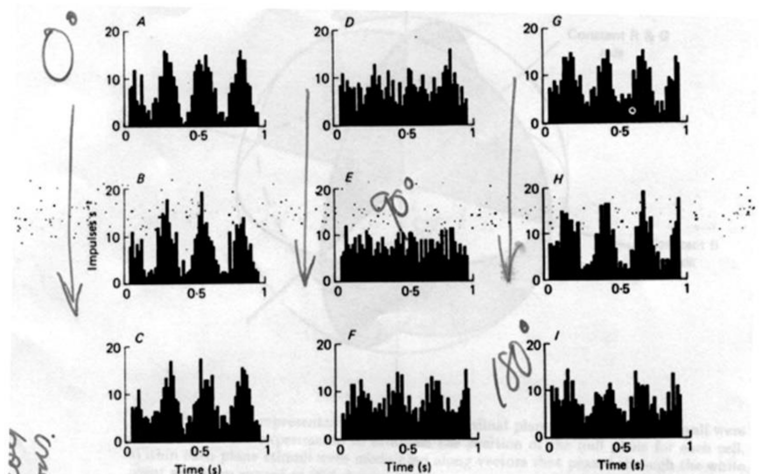



Fig. 2. Peristimulus time-histograms (p.s.t.h.s) of responses to temporal modulation of the chromaticity of a spatially uniform field. For all responses drawn here the modulation was confined to the isoluminant plane (elevation 0 deg); successive records show the effect of changing the azimuth of the direction along which chromaticity was modulated, from 0 deg (A) to 180 deg (I) in steps of 22·5 deg. Note the change in phase of the response as it passes through the null near 90 deg. Temporal frequency 3·75 Hz; bin width, 16·7 ms: thirty responses accumulated per histogram.

## LGN colour neurophysiology – summary

- Cells fall into three distinct subgroups in terms of their chromatic signature which correspond well to the three opponent axes
  - Neurons "chromatic signature" fell into three distinct subgroups (cf. Wiesel & Hubel) clustered along each of the opponent aces
  - Magnocellular units very sensitive to luminance modulation: but weak colour sensitivity (M cones)
  - Parvocellular units less sensitive to luminance; specific chromatic sensitivity to either RG or BY stimuli

## So the Cardinal directions are a property of the LGN?

- So can the link between behaviour and neurophysiology be made directly at this early stage of the system?
    - Arguably the most simple psychophysical task – detection
- Not unless the properties of the geniculate neurons can explain a drop in threshold after prolonged exposure…
    - Which they cannot… (Derrington et al 1984)
    - …but cortical neurons do 'adapt', are they similarly clustered?

## Receptive fields – chromatic selectivity

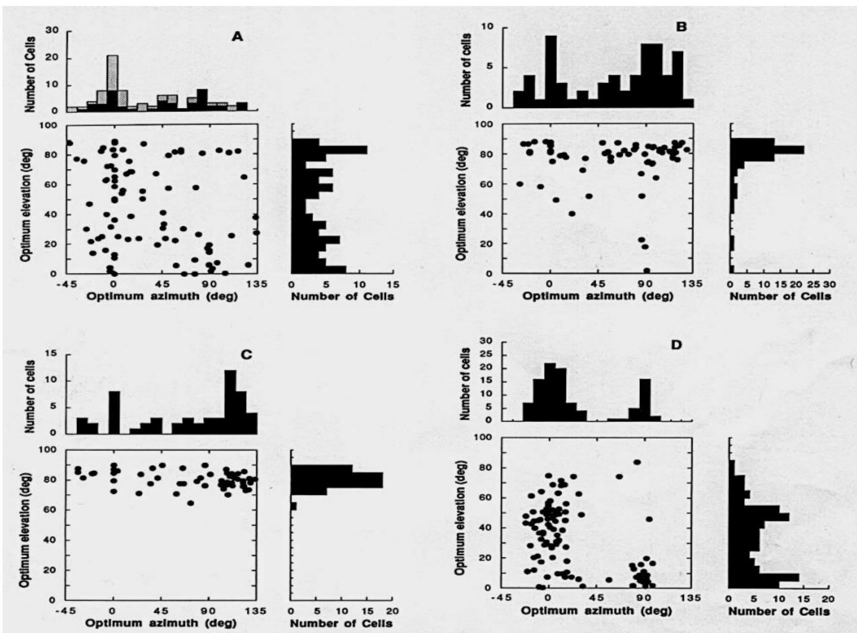



*Figure 11.* Distribution of azimuth ($\theta_m$) and elevation ($\phi_m$) of maximal response. *A,* Nonoriented cells (48). The histogram *above* the scatter plot shows the distribution of $\phi_m$; that to the *right,* the distribution of $\theta_m$. In the histogram of $\phi_m$, *solid* components denote cells with $\theta_m$ <45°; *shaded* components denote cells with $\theta_m$ >45°. *B,* Simple cells (48); other details as for *A. C,* Complex cells (56); other details as for *A. D,* Neurons in parvocellular l.g.n. (from Derrington et al., 1984); other details as for *A.*


## Summary

- Chromatic sensitivity of LGN neurons align with the axes of a behaviourally defined space
- The basis of the definition (independent adaption) is not supported by other properties of the individual neurons in either LGN or cortex
- Cardinal behaviour (independent adaptability) can only be explained on the basis of a combination of LGN and cortical properties
    - LGN neurones have cardinal colour signatures but don't adapt
    - V1 neurones do not have cardinal signatures but do adapt

## The problem

- We cannot even explain the ability to see a red dot on the basis of a simple neural substrate, let alone explain why we call it "red"

- Maybe we need to change the way we think about the system from the beginning

If we had local processing the cardinal neurones would be in the retina and the LGN. They would be adapting nicely and they would be clustered along the axis and you would call that pinkish colour the red and greenish colour green but we don't.

If we have completely distributed processing we would have a lot of problems defining fine motions as well as we do. Having a distributed visual system for pace and time would not be good for the detection of motion.

What does this mean for the argument overall?