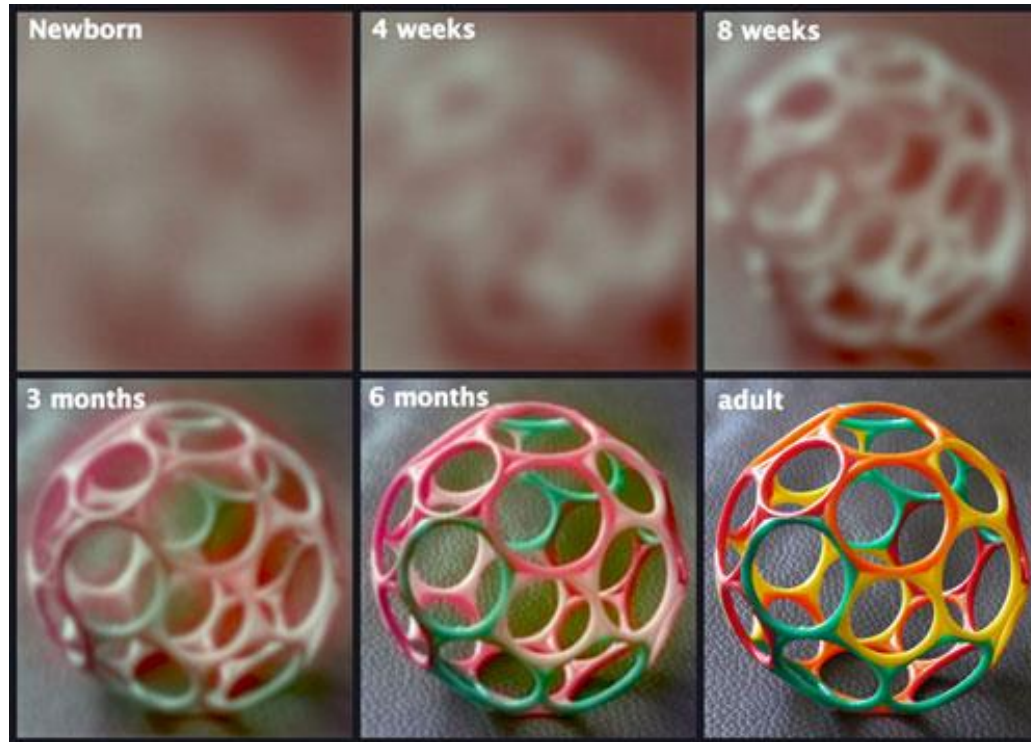


The development of spatial vision in human infants

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Human infants are born (legally) blind



I. Methods of measuring infant vision

Basic overview of methods for infants

- Behaviour: Eye movements
 - Cortical/Saccadic: Preferential looking
 - Reflexive: Optokinetic nystagmus
- Electrophysiology
 - EEG/VEP (Electroencephalography)
 - ERG (Electroretinography)
- Histology
 - *In Vitro*, using staining
 - Non-invasive *In Vivo*, using retinal imaging (OCT, SLO)

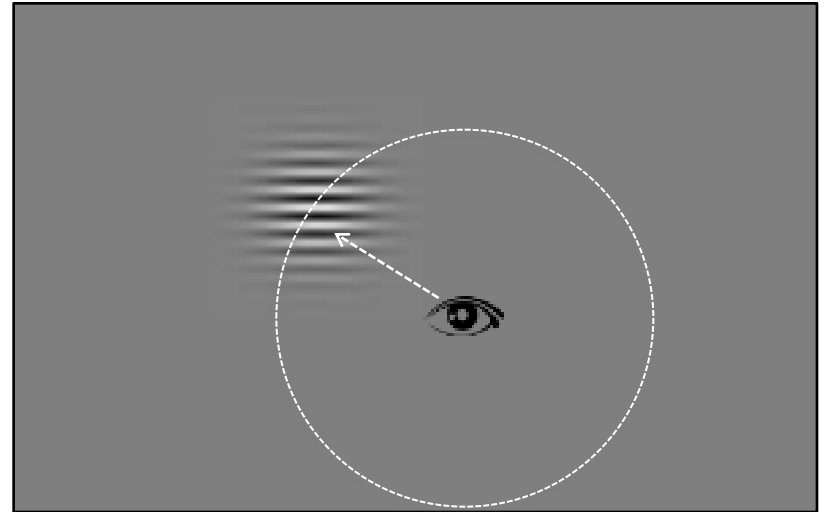
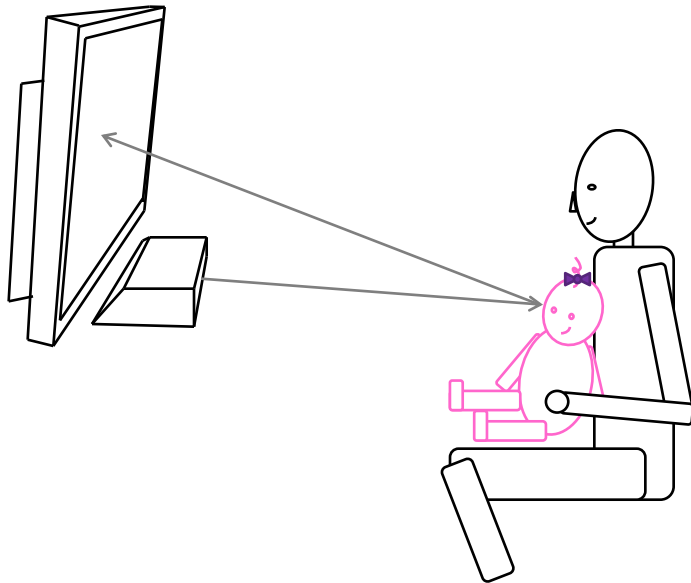
BEHAVIOURAL DATA

Key behavioural task: “**Preferential Looking**”

- “Did the infant see the stripes?”
- Test grating presented against equiluminant background (invisible if not resolved!)
- Position of reference and test randomised
- (Typically) baby’s response classified by human operator
- N.B. not forced choice!



Key behavioural task: “**Preferential Looking**”



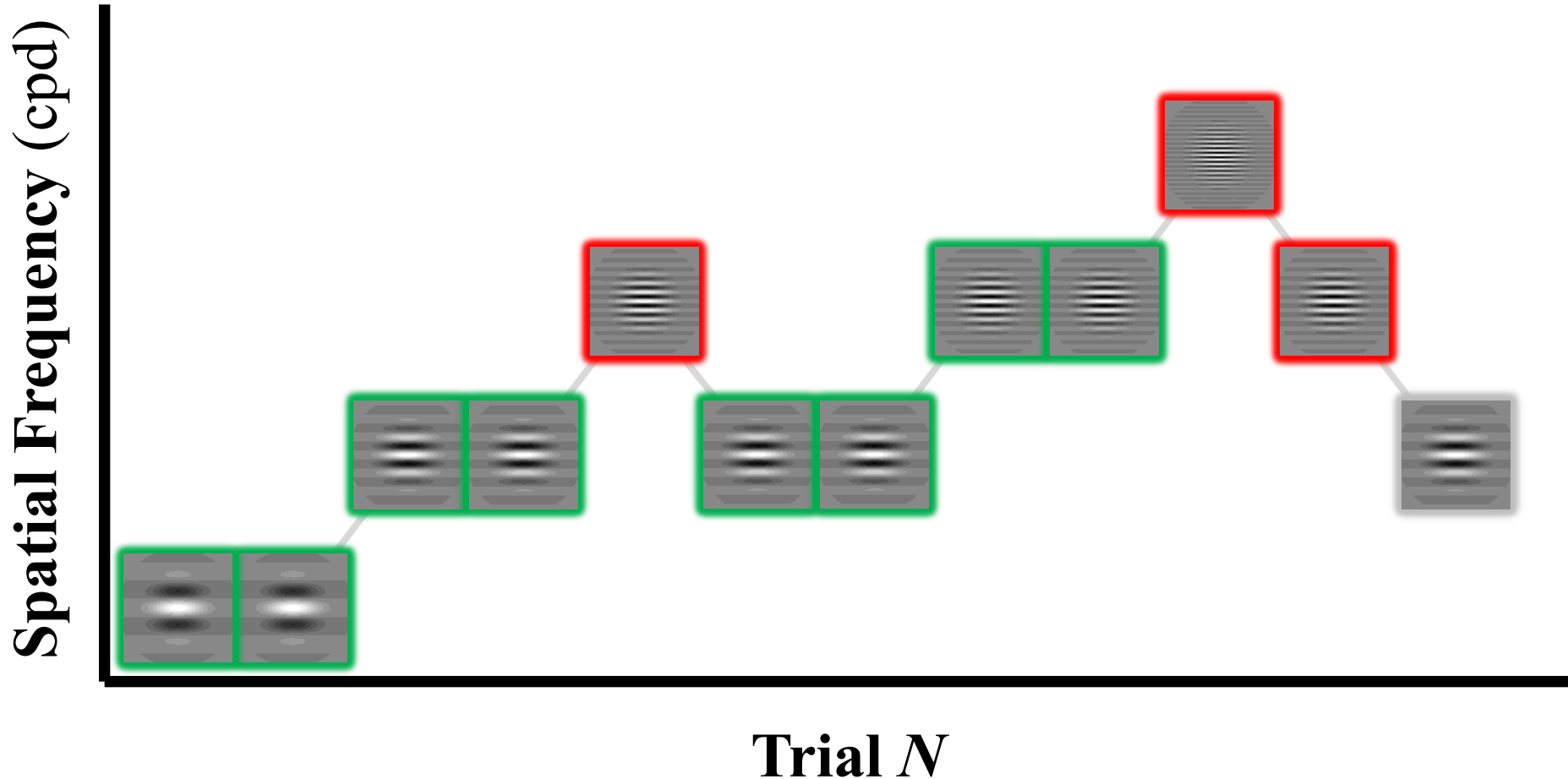
Key behavioural task: “**Optokinetic Nystagmus**” [OKN]

- “Did the stripes elicit OKN?”
- A reflex (in some cases subcortical) – so perhaps less affected by mood/attention (!)
- Requires wide-field presentation (cumbersome, cannot assess local visual-field function)



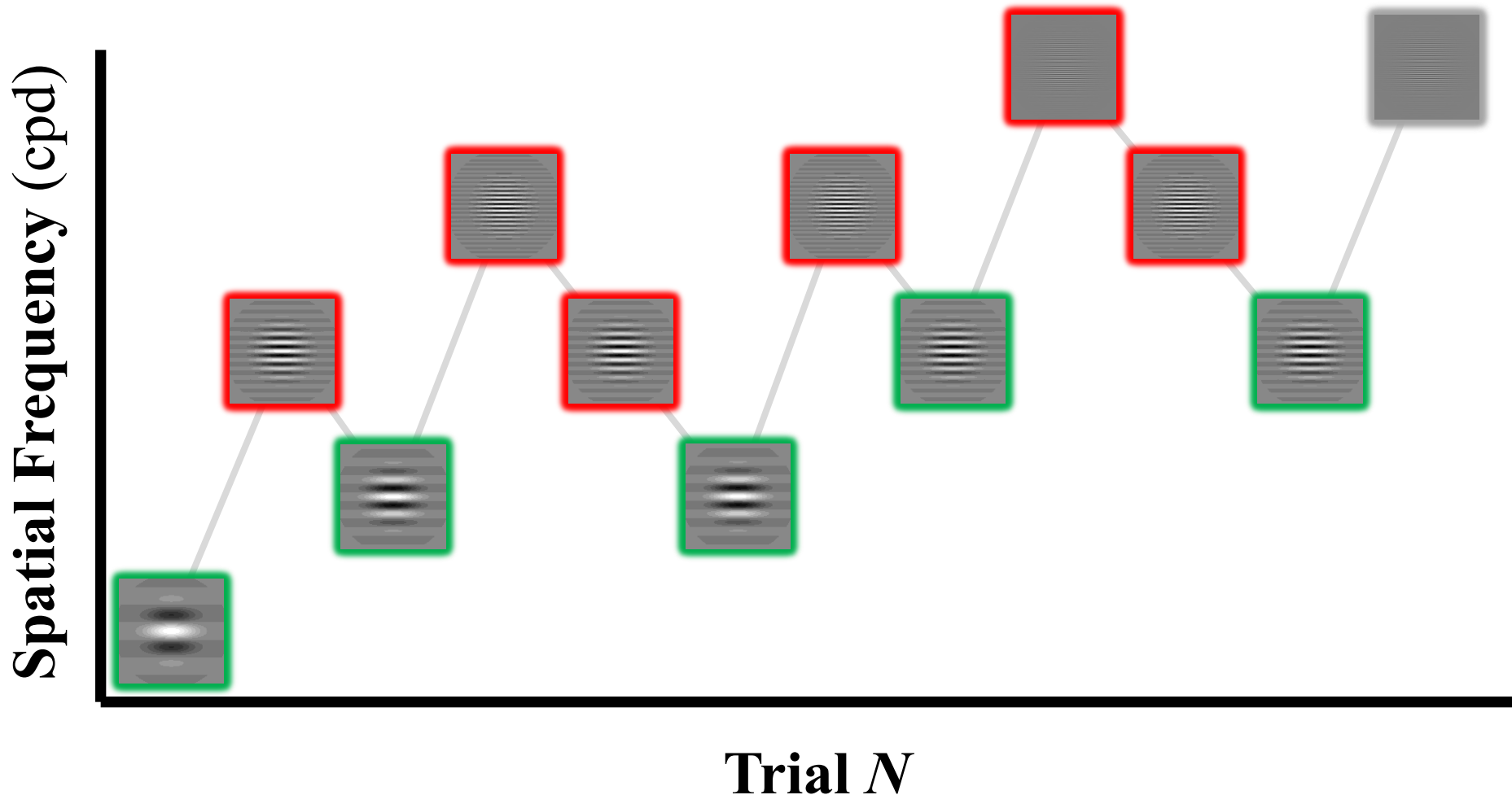
Threshold determined by a staircase

2-Up-1-Down (70.7%) *transformed* staircase (Levitt, 1971)



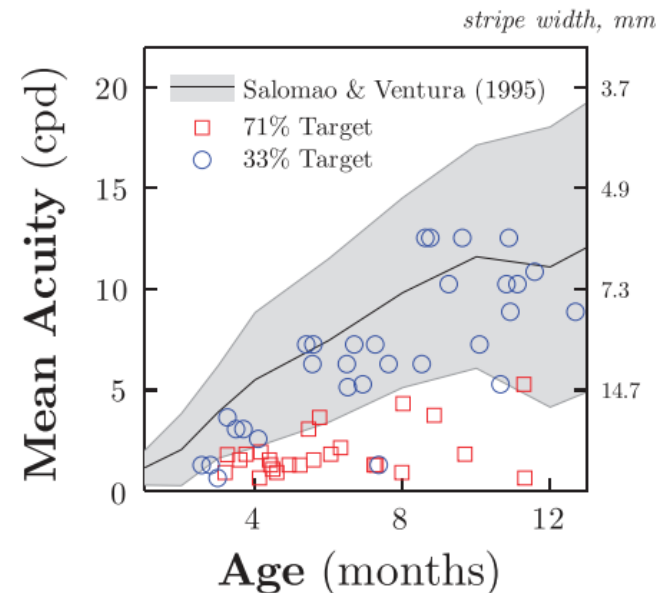
Threshold determined by a staircase

Up-2-Down-1 (33.3%) *weighted* staircase (Kaernbach, 1991)



Threshold determined by a staircase

- Choice of staircase parameters is vital
- Important to not just copy from 'adult' papers, as infants/children behave in qualitatively different ways
- In particular: high lapse rates (as much as 33%!)
- Failure to account for these population-differences can be the difference between a test giving useful results or meaningless noise

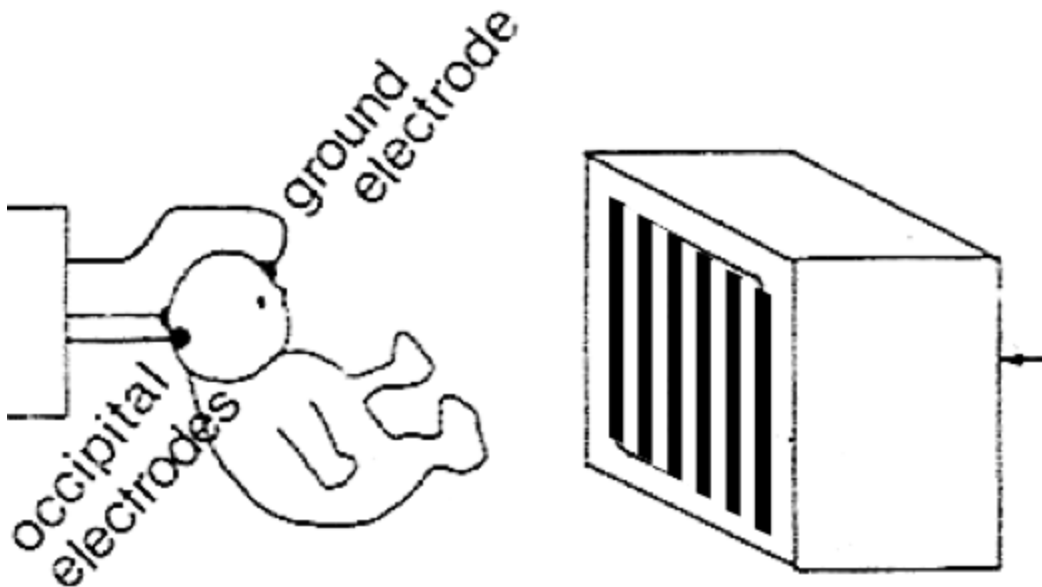


Jones et al, *JoV*, 2015

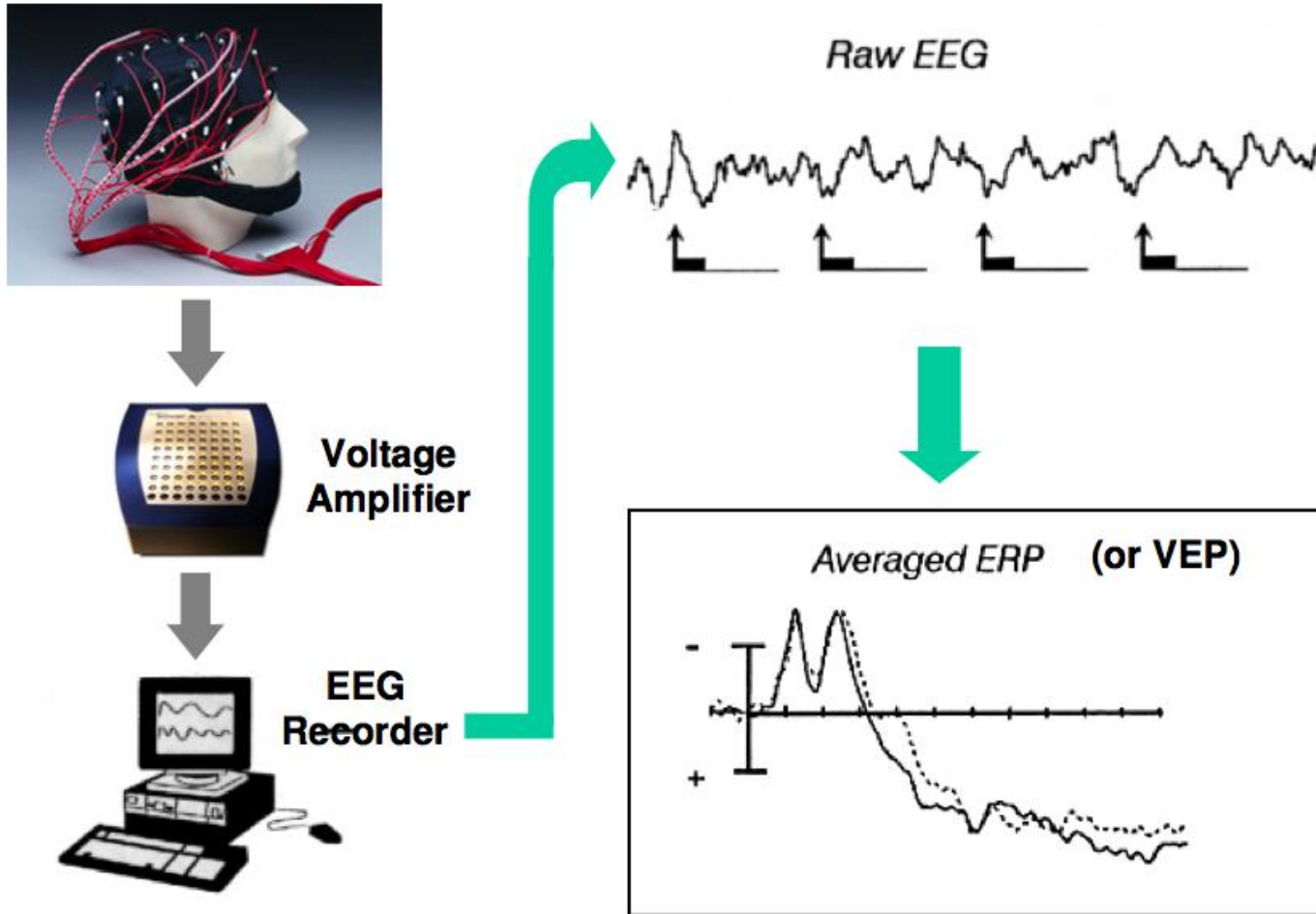
ELECTROPHYSIOLOGY

Key physiological measure: VEP

- Visual-evoked potential
- A vision-specific name for a Event Related Potential [ERP]

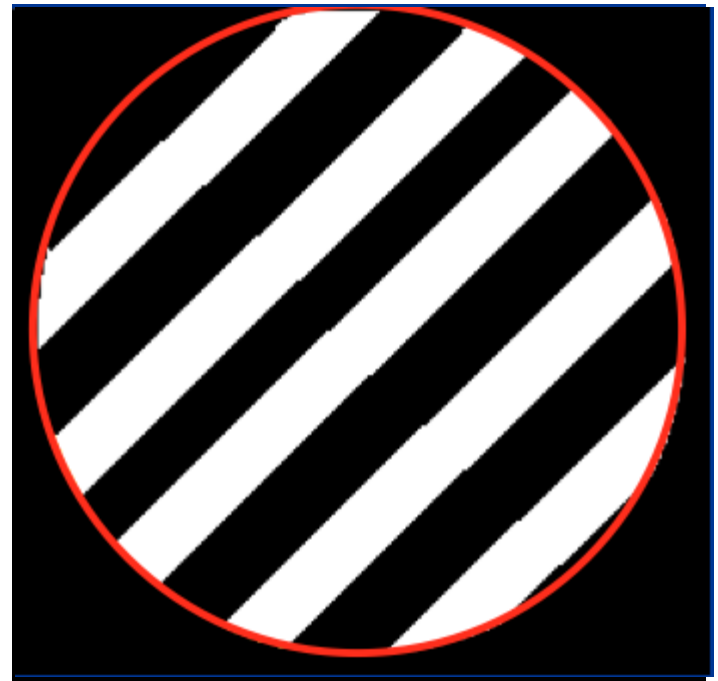


Recording EEG Activity



Steady-state, Phase-reversal, VEP

- Alternate phase of stripes at a fixed rate
- Look for correlated neural activity with the same periodicity



Steady-state, Phase-reversal, VEP

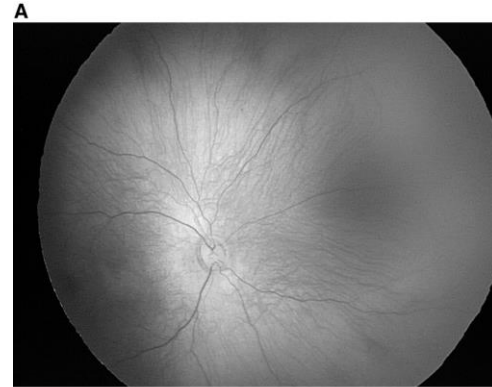
- Alternate phase of stripes at a fixed rate
- Look for correlated neural activity with the same periodicity



HISTOLOGY

Traditional performed in vitro (“in glass”)

- Vasculature
- Thickness of retinal cell layers
- Cell counts / density



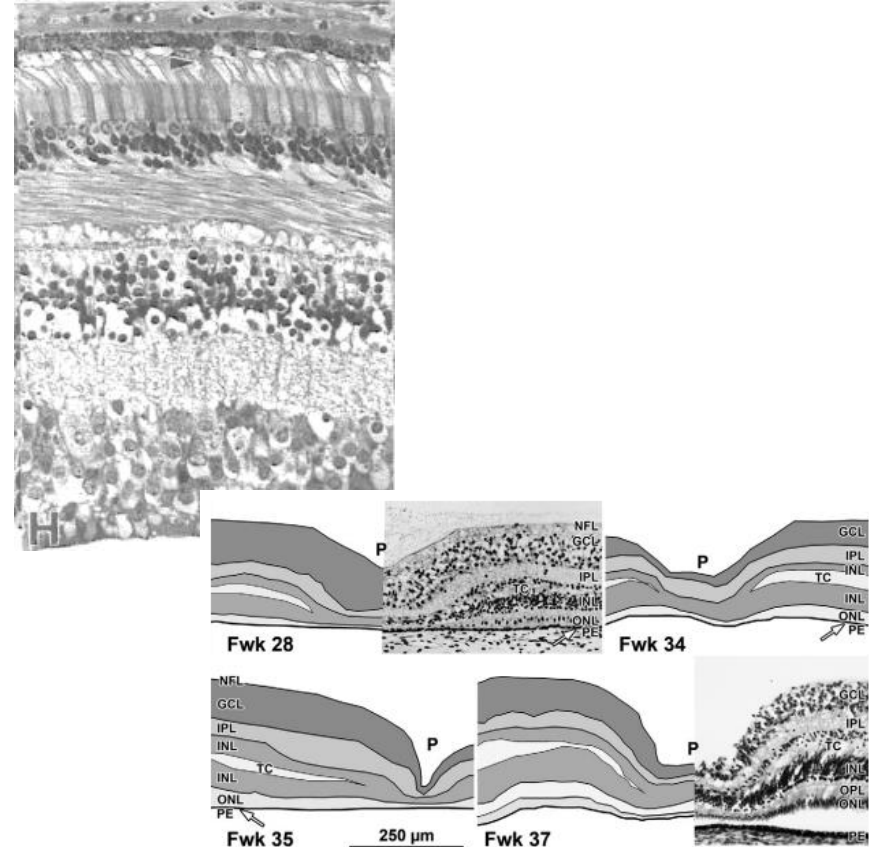
/wo
ROP



/w
ROP

Traditional performed in vitro (“in glass”)

- Vasculature
- Thickness of retinal cell layers
- Cell counts / density



Hendrickson & Drucker, 1992

Hendrickson et al, 2012

Traditional performed in vitro (“in glass”)

- Vasculature
- Thickness of retinal cell layers
- Cell counts / density

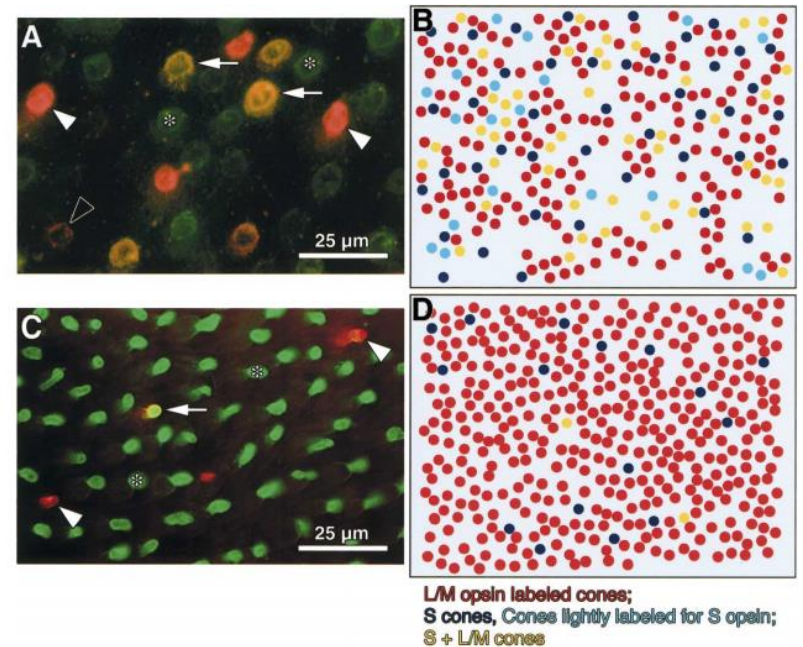


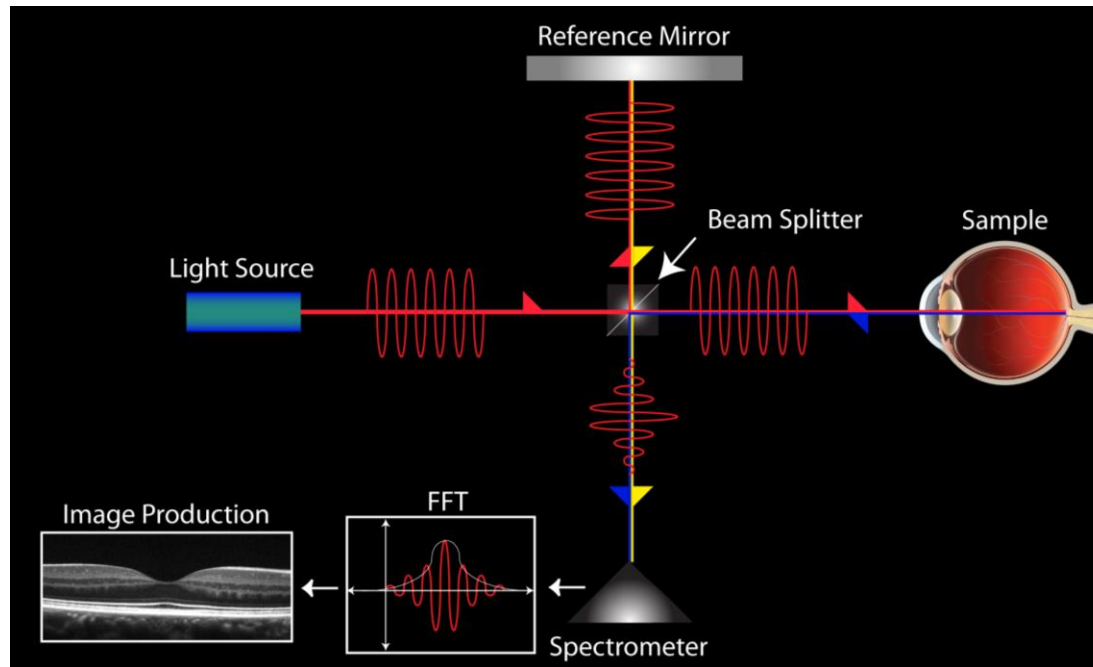
Fig. 3. (A,C) Double exposure photographs of a Fwk22 (A) and a P8 mo (C) human retinal wholemount double labelled for S opsin (red) and L/M opsin (green). The entire cell membrane is labelled at Fwk22, but only the outer segment is labelled at P8mo. Heavily labelled S cones are indicated by a white arrowhead. Cones expressing only L/M opsin are indicated by an asterisk. S + L/M cones are yellow and are indicated by arrows. The open arrowhead in A shows a small cone cell body lightly labelled only for S opsin; these cones were not present in the P8mo retina. (B,D) Diagrammatic reconstructions of cone types near the Fwk24 L/M opsin expression front (B) and in the P8mo peripheral retina (D). These reconstructions show the sharp decrease in S + L/M cones (yellow), the disappearance of lightly labelled S cones (light blue), and the increase in L/M cones (red) with age. Heavily labelled S cones (dark blue) remain constant.

However, increasingly being done in vivo using retinal imaging (!!)

- Retinal imaging allows the cells in the retina to be visualised in awake, behaving humans
- Currently two main 'flavours'
 - Optical Coherence Tomography (OCT)
 - Scanning Laser Ophthalmoscope (SLO)
 - » *And now:* Adaptive Optics SLO (AO-SLO)

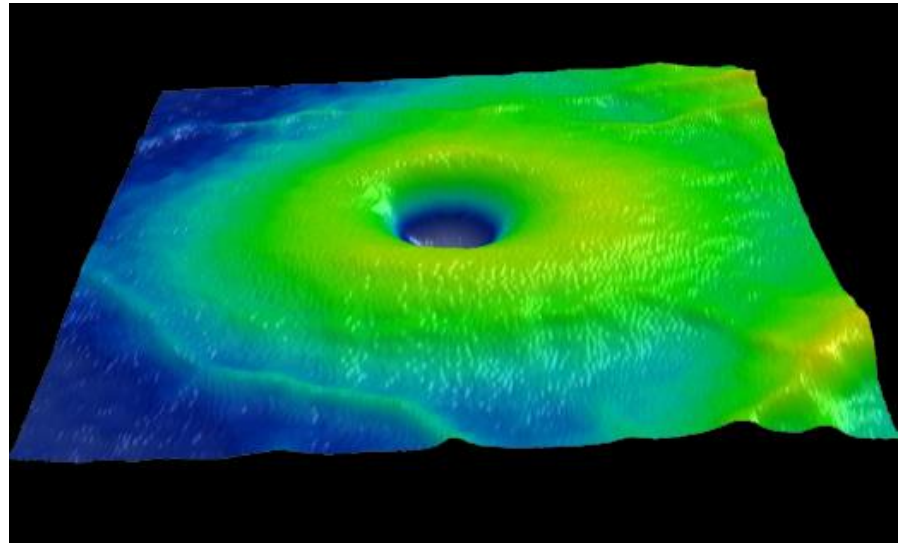
Optical Coherence Tomography (OCT)

- Similar to an ultrasound, except it uses light waves to determine the reflectivity of cells in the retina



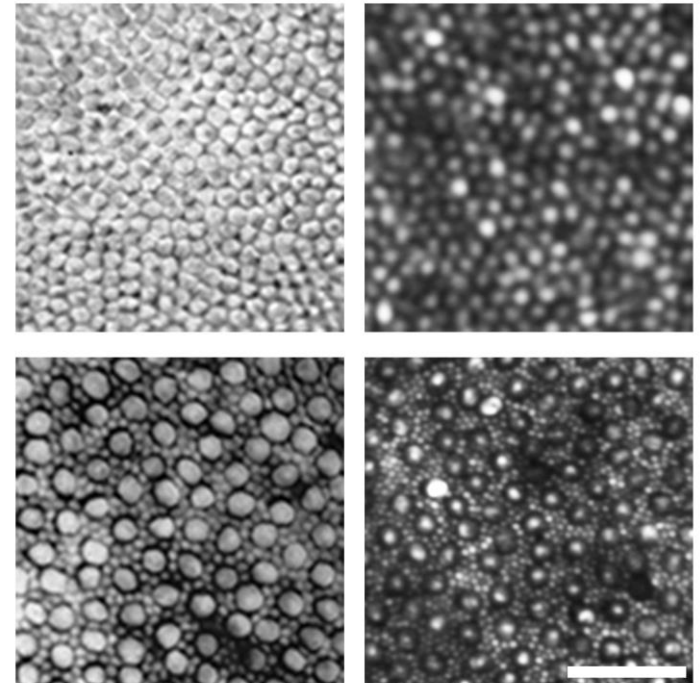
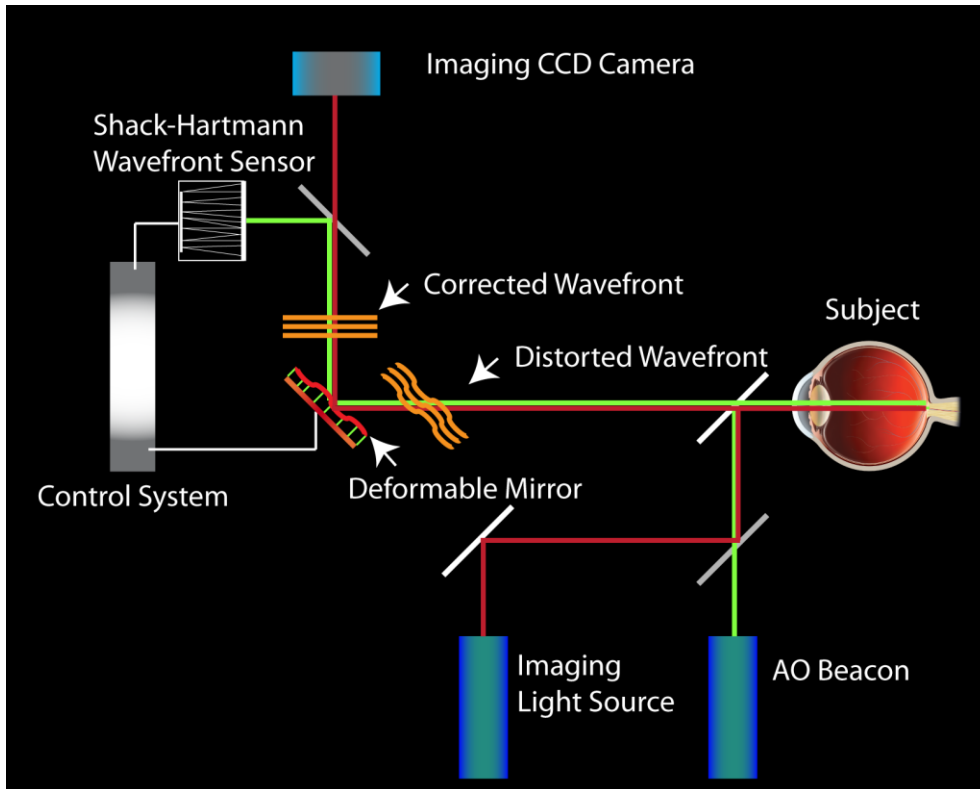
Optical Coherence Tomography (OCT)

- Build up 'slices' to get a full 3D picture of the retina



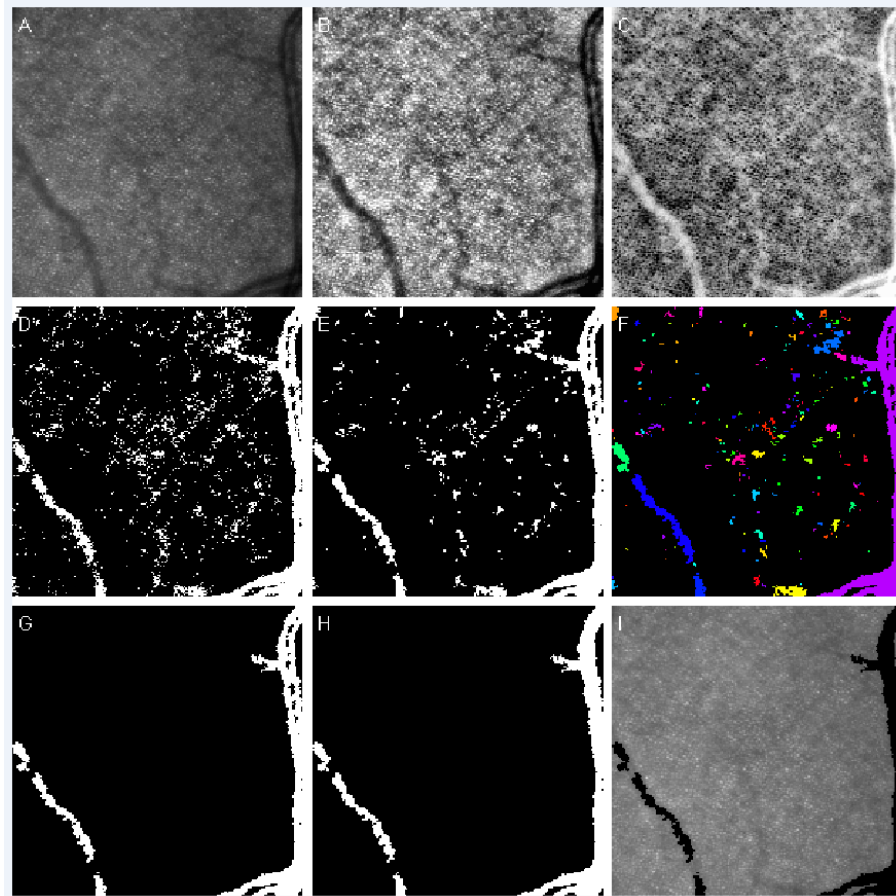
Adaptive Optics SLO (AO-SLO)

- Based on confocal microscopy



Adaptive Optics SLO (AO-SLO)

- ... and a lot of image processing!



III. The development of spatial vision (acuity) during infancy

MEMORY

MOTOR CONTROL

ATTENTION

Recognition

- Objects
- Faces

Visual action

- Reaching
- Locomotion
- Navigation

Visual cognition

- Physics/causality
- Social cognition

Global orientation

Global motion

Orientation

Motion

Depth

Spatial information

Temporal change

Colour

VISION

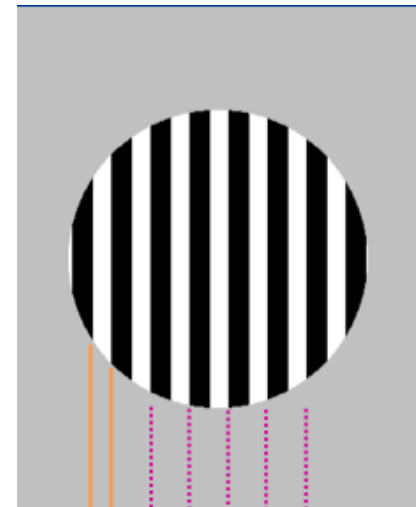
Most basic function of vision: transmitting spatial information

- Acuity is the one key measure
- In adults:

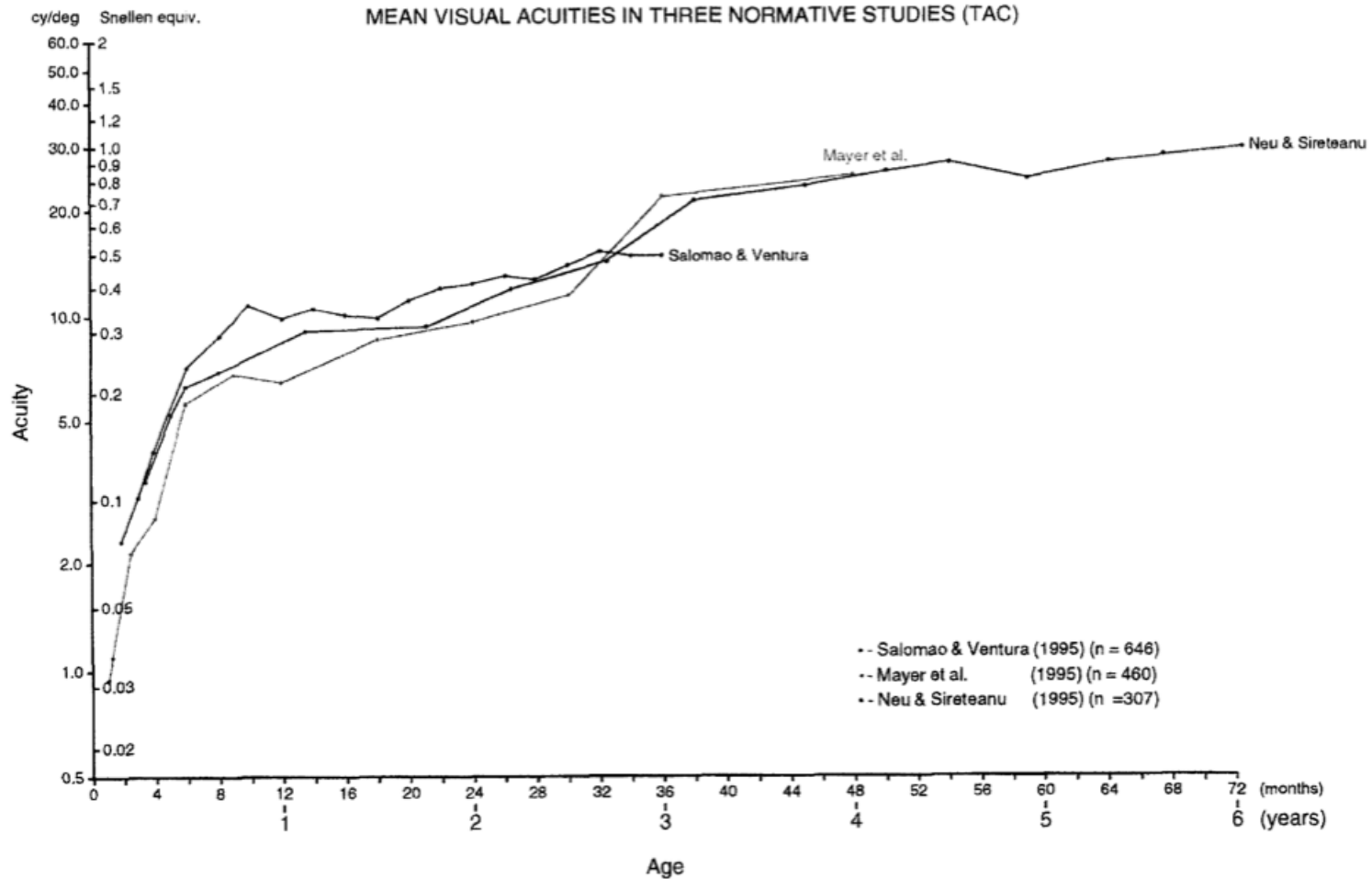
recognition acuity =
6/6 (or 20/20 in USA)



Resolution acuity =
• ~30cycles/deg

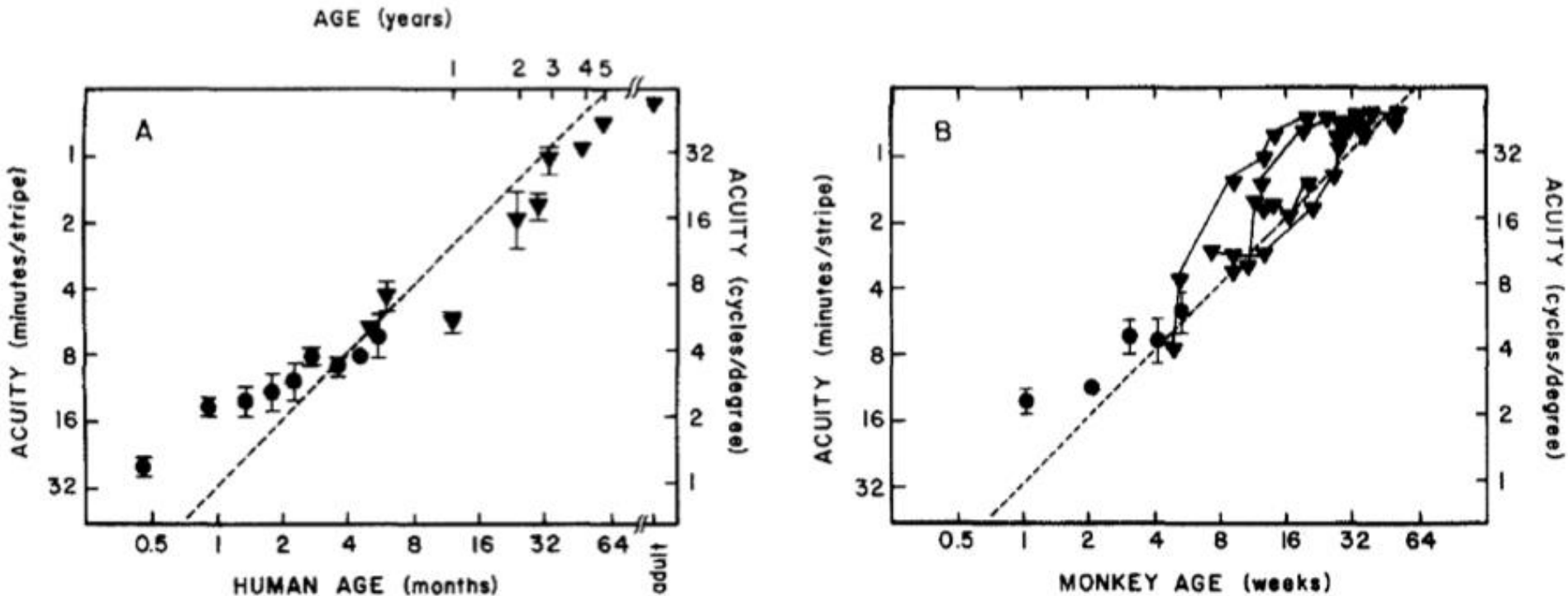


Behavioural data (1/2)



Behavioural data (2/2)

- In first year around ~ 1 cpd per month in humans
- Similar developmental shape, but around ~ 1 cpd per *week* in macaques



Electrophysiological data

- Shows “better” performance than is exhibited behaviourally
- N.B. only shows that there is input to cortex, not whether that information is used/extracted

Rough overlay of Neu & Sireteanu (1997)

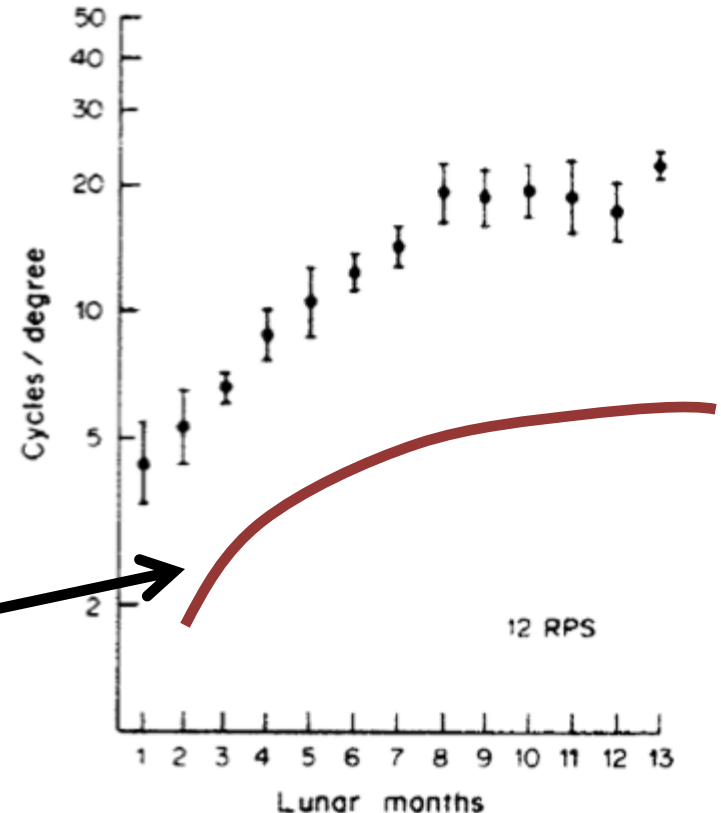
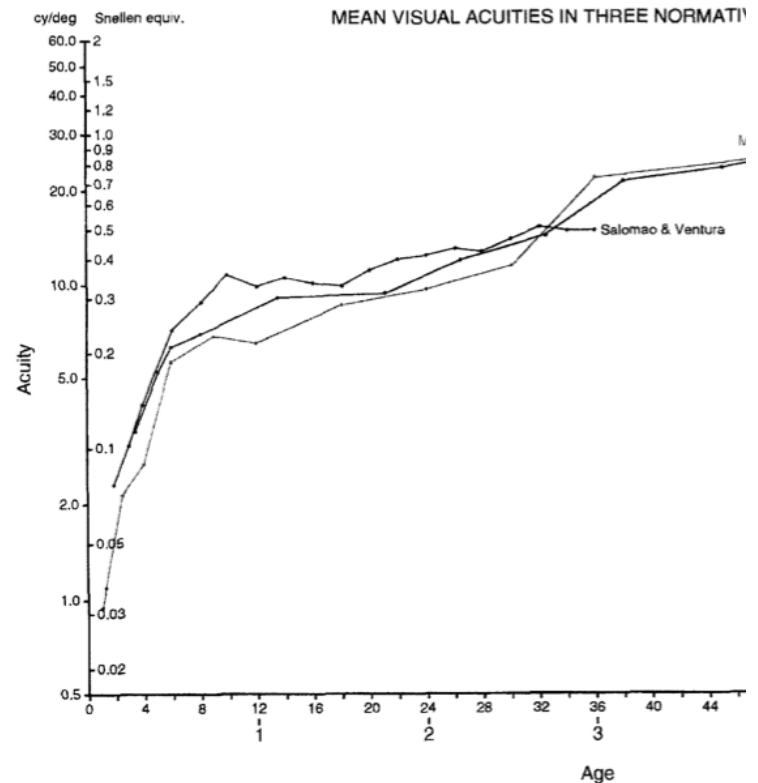


Fig. 7. The mean sweep VEP acuity with 95% confidence bands in 1 month (lunar) increments for the data of Fig. 6.

IV. Limiting factors during development

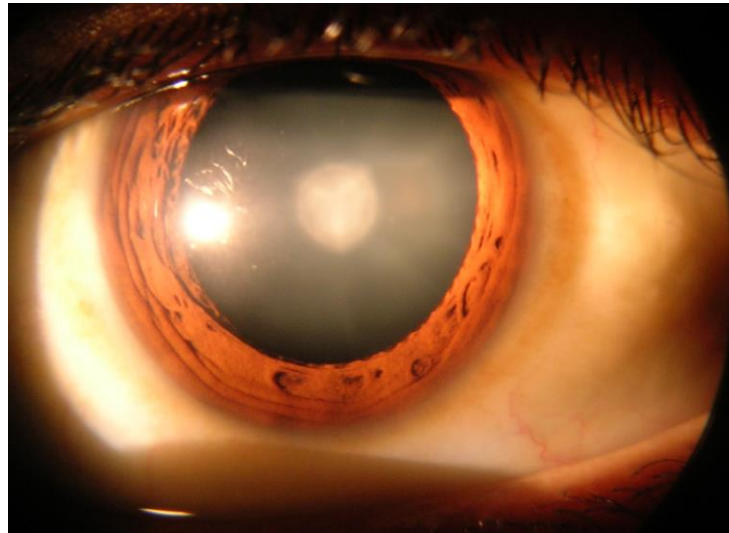
Acuity increases with age – why? What limits the development of VA?

- Optical inefficiency?
- Transduction inefficiency?
- Neural inefficiency?



Optical: Is light falling on the eye being blurred or occluded?

- ***Clarity of ocular media?*** (Cornea, Lens, and Humours)



- Some abnormalities in neonates, and some extreme clinical cases, but generally clear when inspected by ophthalmoscopes (Howland, 1993)

Optical: Is light falling on the eye being blurred or occluded?

- ***Reduced apperture?***
- Pupil size is smaller, and the eyeball is shorter and smaller – smaller area of the retina receives input
- But acuity is mediated by the fovea (centre)

Optical: Is light falling on the eye being blurred or occluded?

- ***Refractive error?*** An inability to accommodate?
- Accommodation not mature at birth (can focus at 75cm but not at 150cm; Braddick et al, 1979)
- But most acuity testing done at < 40cm
- Acuity roughly constant when testing distance manipulated (30–150cm; Salapatek et al, 1976)
- May be the opposite – less VA limits accommodation

Optical: Is light falling on the eye being blurred or occluded?

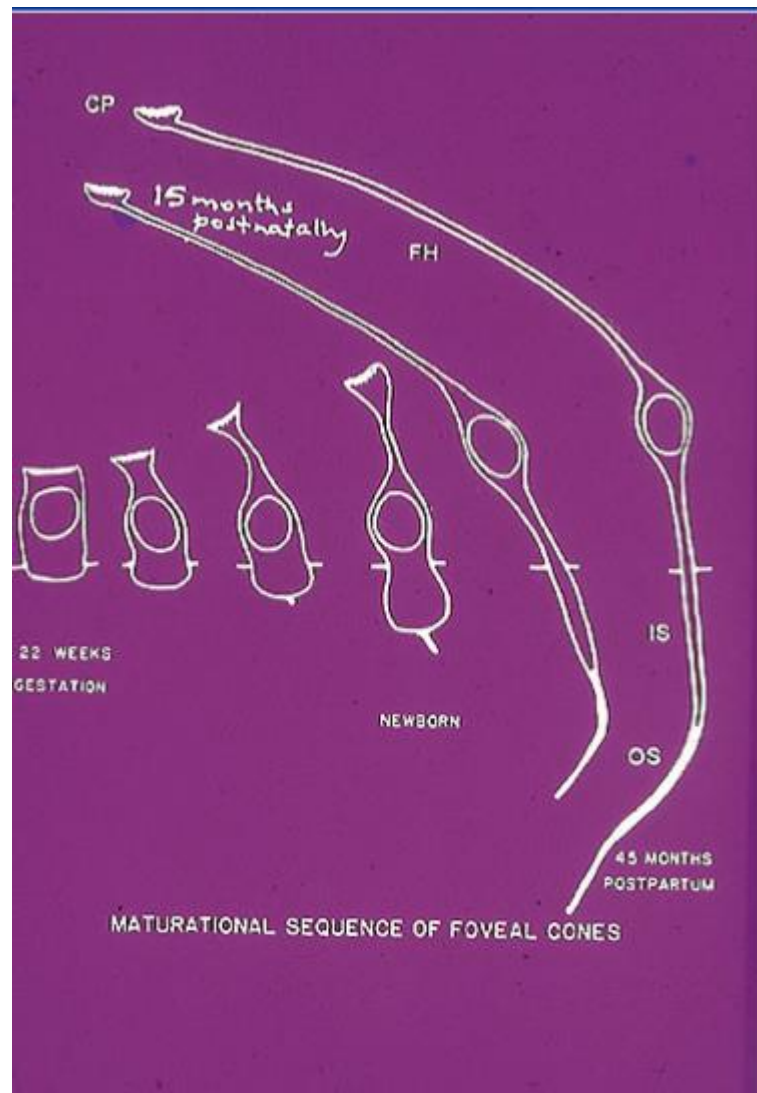
- ***Motor noise?***
- Retinal image can't be too still (Troxler fading), or too variable
- Controlled subcortically (though potentially with top-down inputs)
- Some evidence of immature motor control (slower saccadic onset; poor binocular-yoking in first month), but grossly good from birth.

Optical: Is light falling on the eye being blurred or occluded?

- Unclear ocular media?
 - No
- Reduced aperture?
 - No
- Refractive error?
 - No
- Motor noise?
 - No

Transduction: Is the retina failing to convert light to nerve impulses?

- Cone cells are immature in two key ways.
- Firstly, the outer segment (OS) is shorter
- OS contains the photopigment
- Around 10 times fewer isomerisations per incident quanta



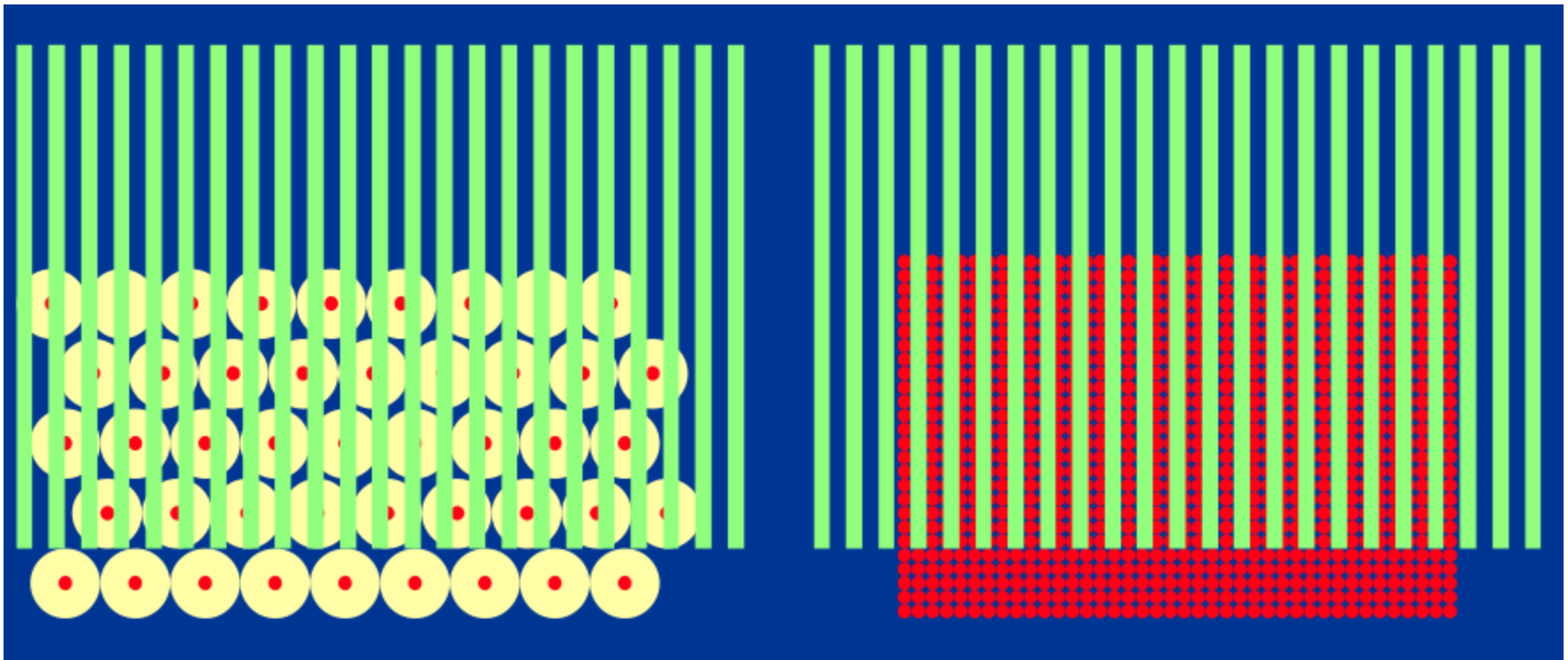
Transduction: Is the retina failing to convert light to nerve impulses?

- Secondly, the inner segment is fatter, allowing for less dense packing

~6 μm at birth

versus

~1.9 μm in adults

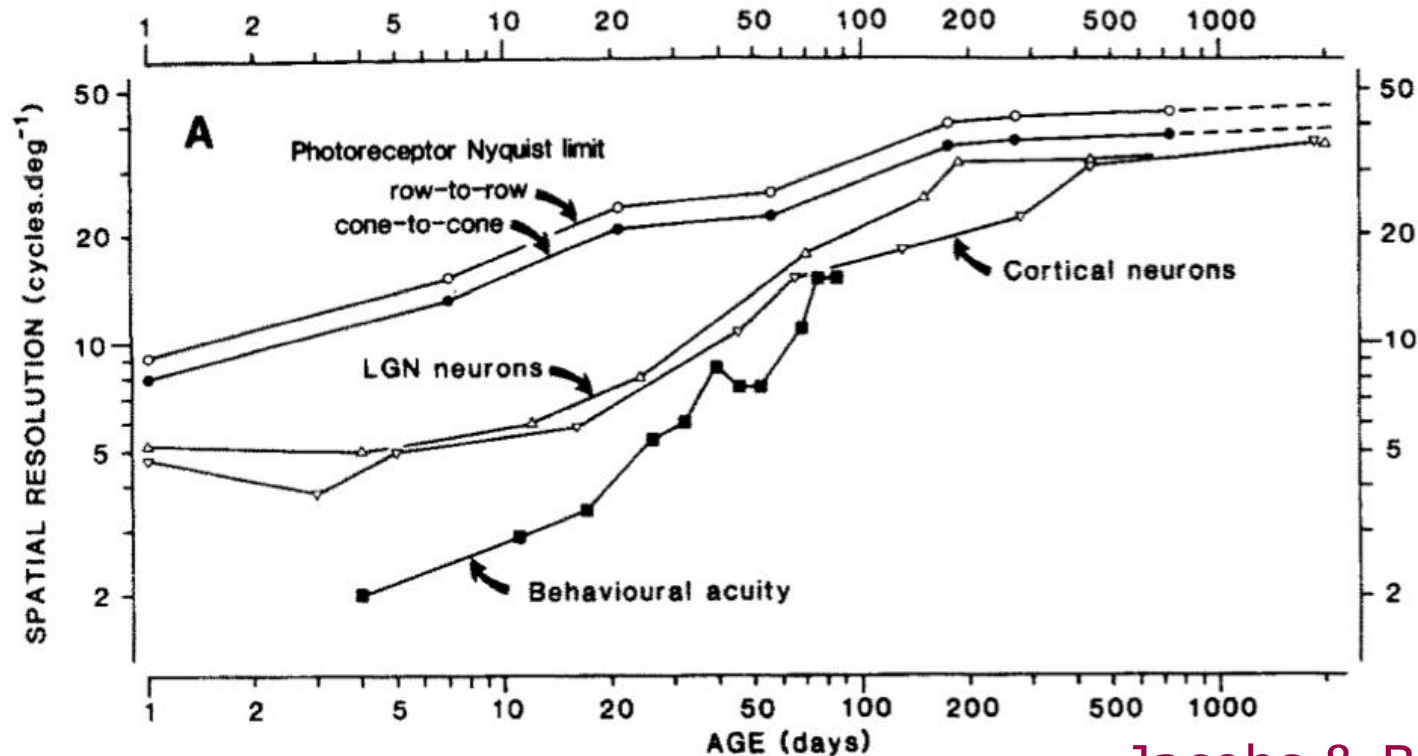


Transduction: Is the retina failing to convert light to nerve impulses?

- When Banks & Bennet (1988) performed an *ideal observer analysis*, they found that a substantial loss of VA is due to preneural factors
- **However:**
 - Only predicts ~2-octave loss of grating acuity (relative to adults), whereas neonates exhibit ~5-octaves
 - The developmental profiles don't match. Kiorpes and Movshon (2004) found changes in monkey photoreceptors were confined to the first four weeks
- Substantial inefficiency unaccounted for...

Cortical development

- Evidence of improving selectivity along the visual hierarchy
- Increased physiological receptive fields (Lack of appropriate excitatory/inhibitory connections?)



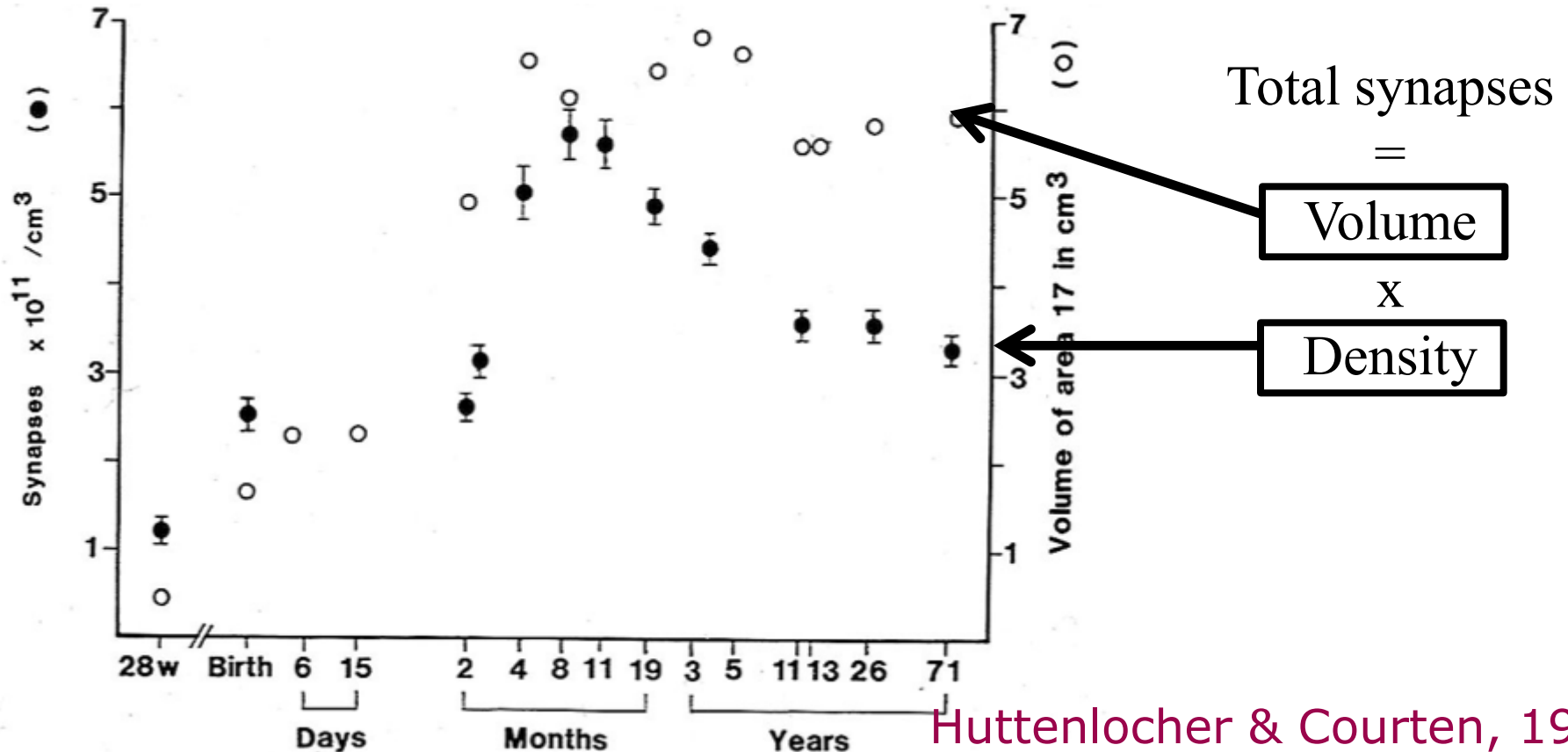
Jacobs & Blakemore, 1988

Cortical development

- Evidence of wide-spread neural development
- The mass of the brain increases postnatally, from 350g to 1350g ($\sim \times 4$)
- Rapid expansion of primary visual cortex (BA17) volume during first four months postnatal (Huttenlocher & Courten, 1987)
- N.B. But neural numbers remain roughly constant (Leuba & Garey, 1987)... what's changing... ?

Cortical development

- Massive increase in synaptic connectivity
- Burst in synaptogenesis correlates with a sudden increase in visual alertness and emergence of binocular interactions



Huttenlocher & Courten, 1987

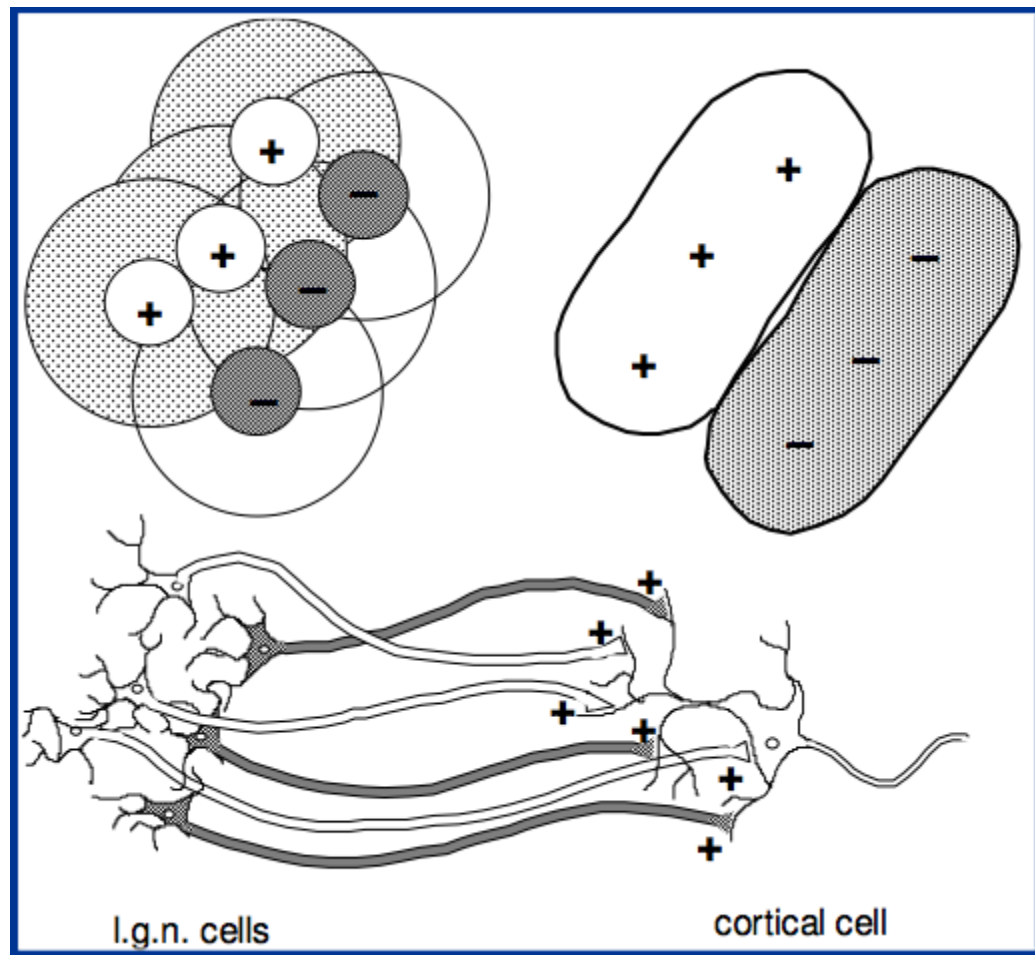
V. Summary

Summary

- Behavioural (FPL), electrophysiological (VEP), in vitro histology, and in vivo retinal imaging methods can all be used to assess infant vision
- Visual acuity shows very rapid development during first few months (1cpd/month), then slower development towards maturity by ~4 years
- The limiting factors driving development are partly retinal (immature and sparse photoreceptors), and partly neural (lack of connectivity and myelination)

Wider context: Higher order spatial function

- Acuity ('visual resolution') is fundamental, but is only one component of spatial vision
- Massive development of higher-order systems (Marr, Hubel & Wiesel, etc.)



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MOTOR CONTROL

ATTENTION

Recognition

- Objects
- Faces

Visual action

- Reaching
- Locomotion
- Navigation

Visual cognition

- Physics/causality
- Social cognition

Global orientation

Global motion

Orientation

Motion

Depth

Spatial information

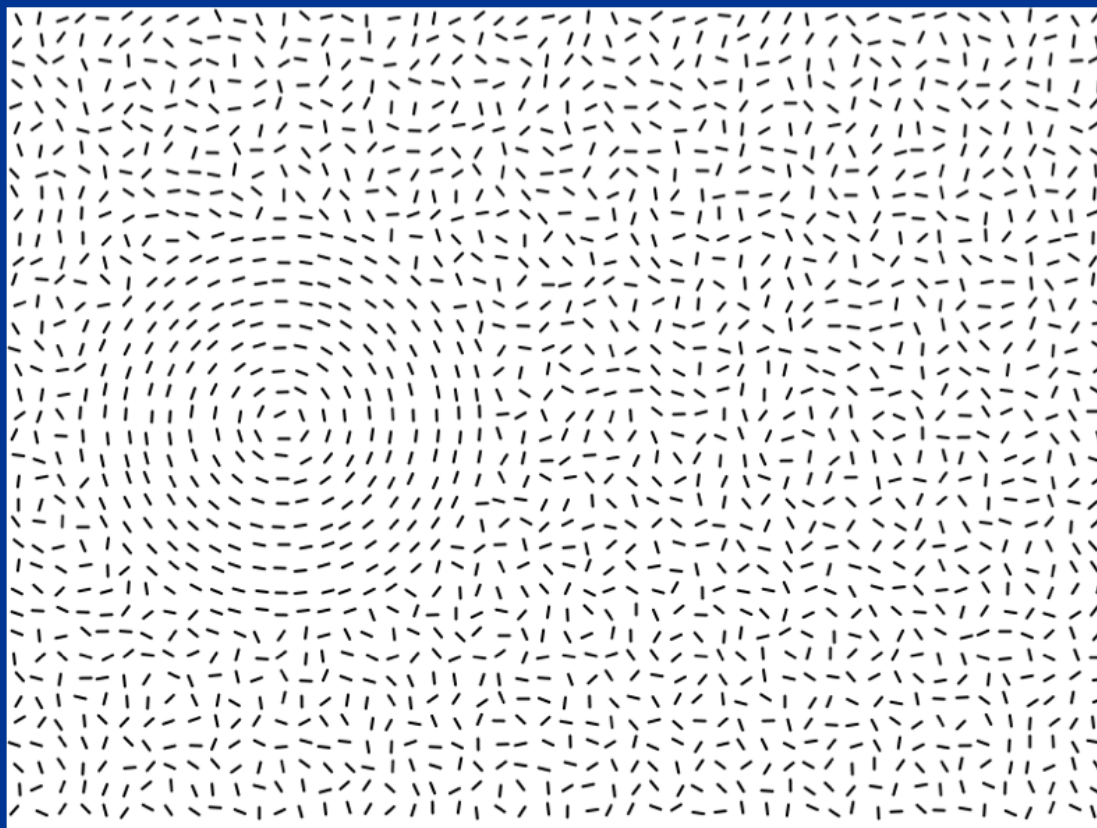
Temporal change

Colour

VISION

Wider context: Higher order spatial function

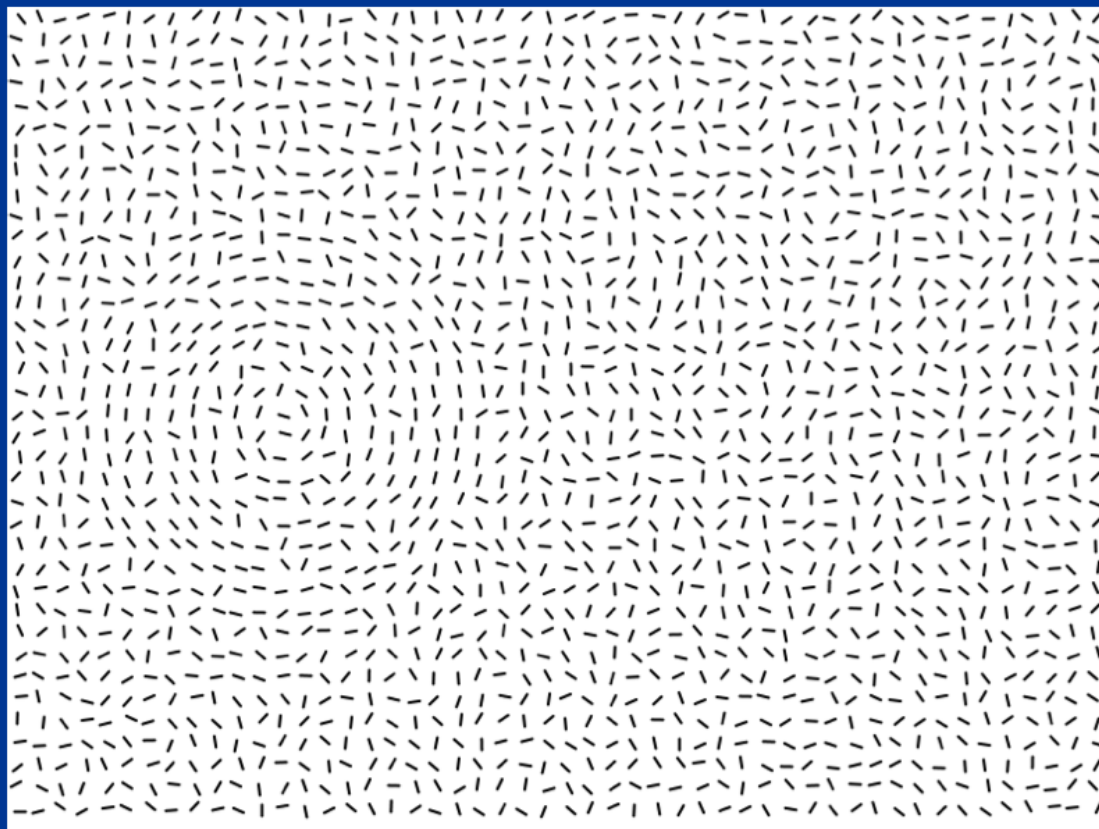
Form coherence



Coherence = 100%

Wider context: Higher order spatial function

Form coherence



coherence = 60%

Wider context: Other visual abilities

