

# The Human Eye and Vision

Is the eye a camera?

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Gresham College: 30/9/09





Early morning on 8th September 1888, Just before 6am John Davis, an elderly resident of 29 Hanbury Street came downstairs, passing along a narrow passage he opened the back door. The sight awaiting him was truly shocking. Running to the front door he staggered onto the street startling two workmen, shouting "Men! Come here." They followed him into the passageway to the backyard where they saw...



# Is the eye a camera?

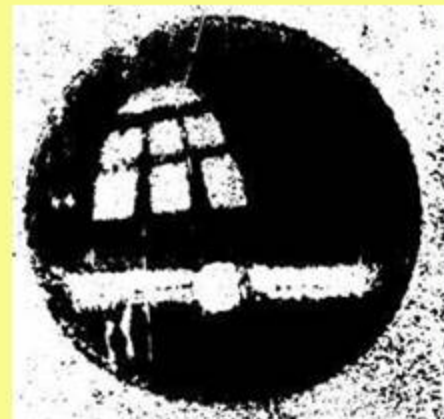
- The jury foreman at the inquest of Annie Chapman asked the police surgeon whether any photographs of the eyes had been taken “in case they should retain any impression of the murderer”. (Daily Telegraph tues sept 11<sup>th</sup> 1888)
- 1888 Walter Dew, detective recalled in his memoirs that photos of the eyes of Mary Kelly had been taken
- Heinrich Müller: 1851 found a reddish pigment in the retinas of frogs.
- Franz Boll: 1876 located these rods, noted it bleached away post-mortem unless the eyes were kept in the dark. 20 secs yellow, 60 secs gone. Dying age 30 his work was continued by
- Willy Kühne, renamed the pigment visual purple. Fixing the eye of a freshly sacrificed rabbit produced an image of the window it faced in life “optogram”. Also claimed to have obtained an image from the retina of executed criminal 1880. Became the stuff of detective fiction and fable.
- "few ophthalmologists have seen the vivid color of living unbleached retina, as the living fundus is dominated by hemoglobin and melanin."



They looked. Murderer's ground. It passed darkly. Shuttered, tenantless, unweeded garden. Whole place gone to hell. Wrongfully condemned. Murder. The murderer's image in the eye of the murdered. They love reading about it.—

James Joyce, *Ulysses*

*Standard Bodley Head 1937 p92*



# Light

The Sun: Black body 6000K emits a spectrum of EM. Not hot enough to generate x-rays. But corona is.

1:2 billionths of sun's EM radiation  $\sim 1,368 \text{ Wm}^2$ .  
Scattering of blue, reflection by clouds, distributed over spherical surface weaker at poles so on the ground  $\sim 120 \text{ Wm}^2$  varies.

We are immersed in a sea of electromagnetic radiation waves which interact with each other and objects to present a cacophony of electromagnetic signals (Feynman). Through a tiny aperture the eye selects a small fraction of the energy (400-700nm).  $\sim 10\%$  of photons are captured, 3% reflected, rest miss the target and absorbed by non-seeing structures. Captured photons converted via chemical reactions to stereotypical electrical signals which travel to the brain: data needed for survival; reconstruction of the world.

The result is scene, form, depth, movement, colour, texture.

How we came to understand this complex process, called vision, is a fascinating story of 2,300 years of human endeavour.





# Ancient theories of vision

Ancient optics was not concerned with the physics of light but with the process of sight (Mark Smith). The ray was a line of sight not a pathway for light energy.

**Optics:** appearances of unbroken line of sight,

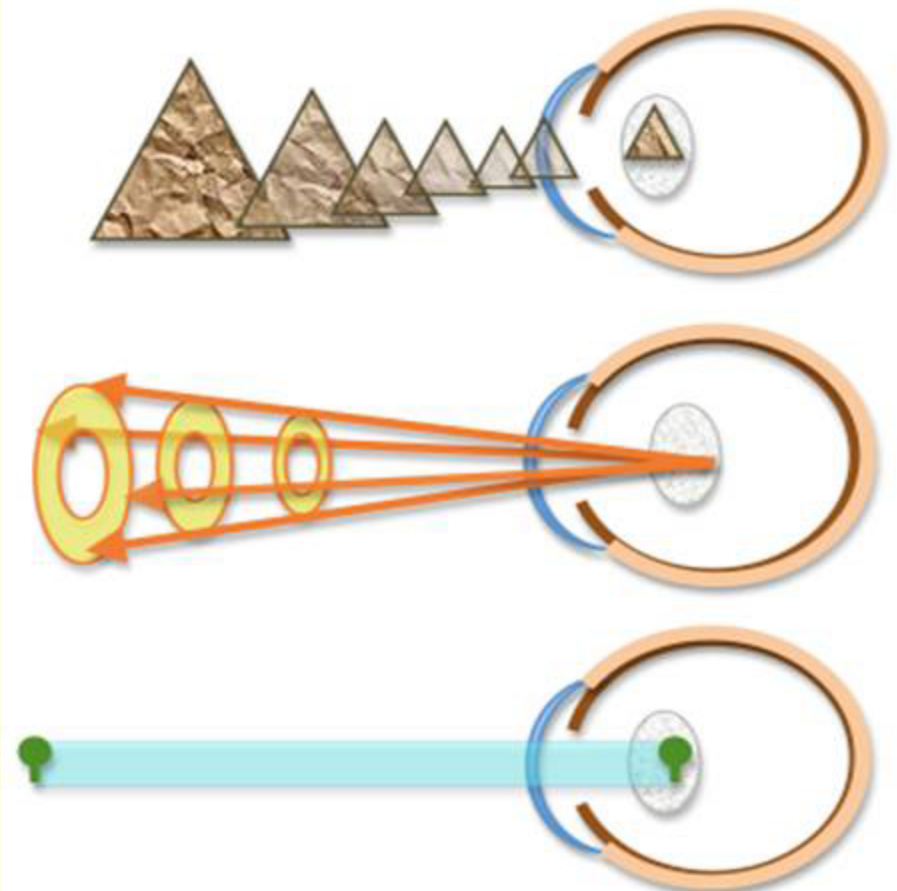
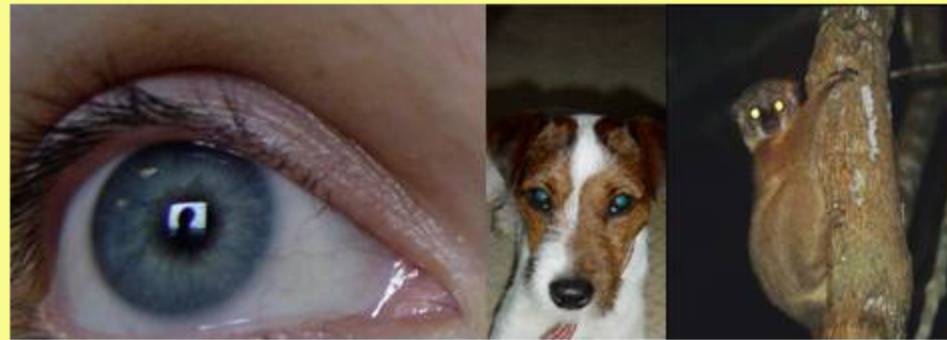
**Catoptrics:** a broken line of sight, mirror or images,

**Dioptrics:** partially broken line of sight.

Theories of vision in antiquity: (Lindberg)

Based on connection between the object and the visual organ. Like touch. Three ways in which contact could be established.

1. The object could send its image through the intervening space. Atomists (Leucippus, Democritus, Epicurus). Thin films (eidola Gk, simulacra Latin). Lucretius: Shedding locusts, calves, or skin of a snake. Coagulated convoys of atoms, which transport the visible qualities. As detected by mirror image of scene on cornea
2. The eye could send out a ray to the object. Proposed by Plato, Euclid, developed by Ptolemy.
3. Contact could be made through the medium (usually air) that intervened. Aristotle "colour sets in motion what is transparent-and lies between air-and every colour has in it the power to set in motion what lies in-between". The colour of the object shapes and moves the medium into the eye where the humours assume the qualities of the object as it is being seen. Air needs to be lit





# Ancient theories of vision: Limited Sources:

Thrasyllus in 1stC AD lists 70 treatises by Democritus 460-357BC. Many of them devoted to optical matters. None survive.

## The 4 primary texts.

**Euclid: Optics:** Theon's edition was the main source. Oldest copy 888AD in Bodleian. However a C10<sup>th</sup> copy from an older source in Vatican Excerpts transl in Cohen & Drabkin Source book in Greek Science.

**Hero of Alexandria: Catoptrics.** Latin translation by William of Moerbeke 1269. Hero formulated the Principle of the Shortest Path of Light: If a ray of light propagates from point A to point B within the same medium, the path-length followed is the shortest possible

**Pseudo-Euclidian Catoptrics:** Attrib by Heiberg to Theon of Alexandria. More recently arguments to propose Euclid. French transl Ver Eecke

**Ptolemy: Optics** Translated into Arabic 10thC now lost only surviving as a 12thC Latin translation by the Byzantine Eugene in Sicily. Eng trans by Mark Smith 1996.

## Supplementary sources

**Aristotle:** Meteorology, on the Soul, Sense and Sensibilia

**Diocles:** c 240BC: On burning mirrors

**Galen:** On the usefulness of parts of the body, On the Opinions of Hippocrates and Plato

**Lucretius:** epic philosophical poem on Epicureanism *De rerum natura* On the nature of things. Attempts to explain the full range of natural phenomena on the basis of atoms.

**Plato: Timaeus** dialogue, includes an extensive account of sensation including vision.

**Theophrastus:** c320BC 230 works, 4 about optics, only one survives **On the senses.** a critique on the theories of predecessors including Democritus



Euclid Duke of Urbino 1458



# Alexandria 300BC

## **EUCCLID 300BCE** Ευκλείδης ο Αλεξανδρεύς

- Purely mathematical analysis of vision: Wrote **Elements of Geometry** and **Optics** the earliest surviving treatise concerning optics and light
- develop a geometrical theory of the perception of space. Formulation of the ray concept.
- Radiation emanates in form of a cone of rectilinear rays proceeding from the eyes diverge indefinitely. Observer only sees object if it intersects on of these rays in the cone. The apparent size depends on how many rays it intersects. **KL** appears longer than **GD**
- Platonic tradition that vision is caused by rays that emanate from the eye, but also offers an analysis of the eye's perception of distant objects and defines the laws of reflection of light from smooth surfaces.
- EXTRAMMISSION THEORY

Rays linear proceed from eye diverge infinitely

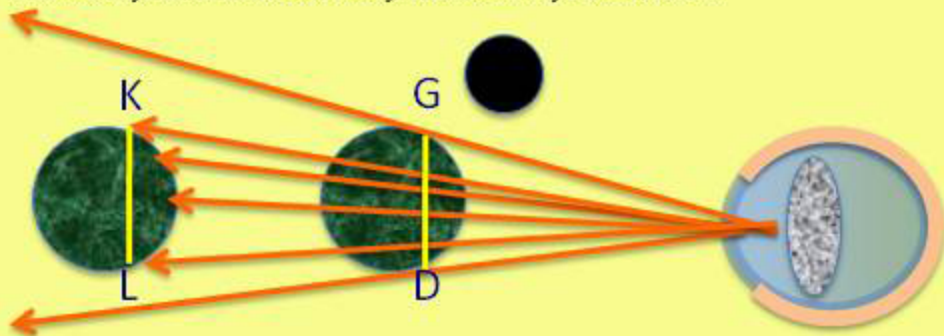
The figure contained is a cone of rays, base is surface of object

Things seen are those on which rays fall, those not seen upon which no rays fall

Things seen under a larger angle appear bigger

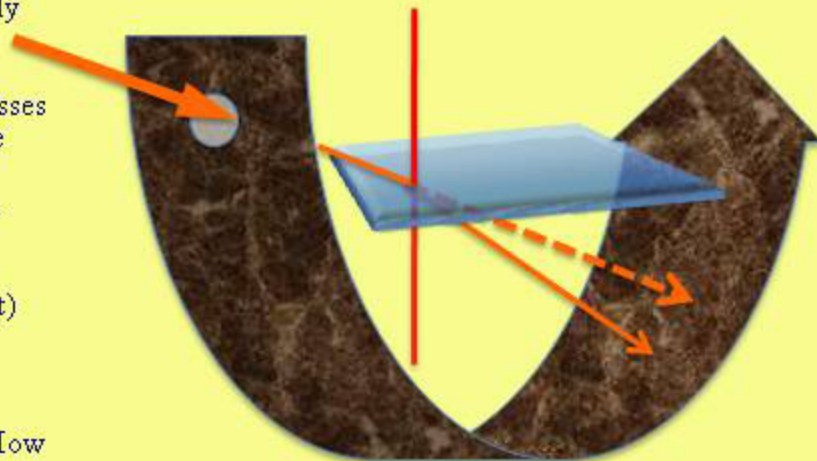
Things seen by higher rays higher, by rays to right appear further to right

Nearer objects seen more clearly The more rays seen clearer



## **PTOLEMY Claudius c100AD**

- Greco-Egyptian, perhaps a roman citizen (hence incongruous 1<sup>st</sup> name). lived into reign of Marcus Aurelius. Describes the Moon Illusion, initially incorrectly (Almagest) then correctly as a psychological effect in **Optics**.
- Only surviving text of Optics is a poor version 12thC translation of an Arabic translation by Eugene of Sicily. Misses 1<sup>st</sup> book and ends abruptly in middle of 5<sup>th</sup>. intellectual elite associated with William 1<sup>st</sup> 1154-1166.
- However earlier version in Arabic cited by Ibn al-Haythem. Angle of incidence and **reflection** are equal. Angle of incidence and **refraction** are not.
- Describes the Moon Illusion, initially incorrectly (Almagest) then correctly as a psychological effect in **Optics**.
- Proposed visual rays were not discrete with spaces but a continuous cone.
- Describes need for external light to make vision possible. How is not explained.





# Other traditions



## China

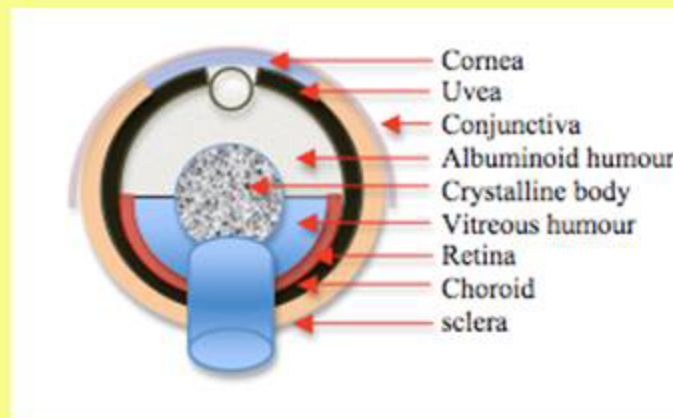
- **Mo Ti** or **Mozi** 5thC BC. Engineer founded school of thought, Mohism, flourished during the Warring States era (479-221 BC). Understood principles of pin hole camera.
- **Shen Kuo** (1031-1095 AD) *Mengxi bitan* Dream Pool Essays of 1088, Shen Kuo experimented with the camera obscura
- **Zhāng Zé duān** 张择端 (1085-1145 AD): Painting of daily life of the Song Dynasty capital Kaifeng geometrically accurate. Techniques: shading and foreshortening, later abandoned and not developed further.
- Euclid's elements translated into chinese in 1606: Christian convert **Xu Guang-qi** scientist: but 1617 Emperor Wanli evicts Jesuits
- **India:** Astronomy and optics: angle of incidence equals angle of reflection. Cataract surgery: Sankhya: One of the 6 orthodox systems of Hindu Philosophy. Light is 1 of 5 subtle elements out of which grow gross elements.
- Vaisheshika: Atomic theory. Basic atoms are earth (prithvi) water apas, fire teg and air vayu. Light is a stream of fast tejas fire atoms.
- Sushruta mentions the lens has the form of a pea and is the organ of sight.





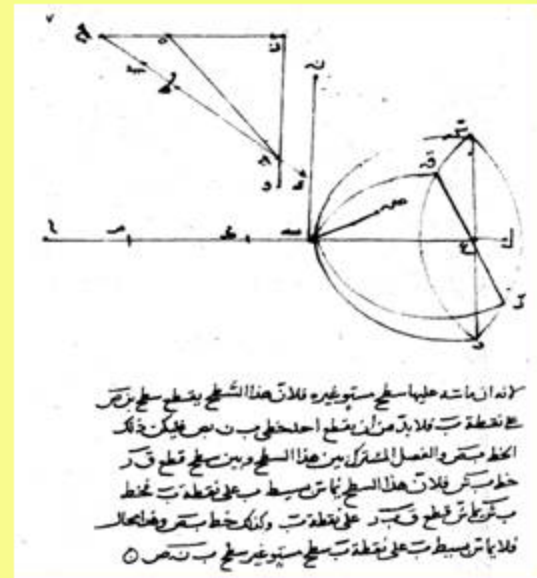
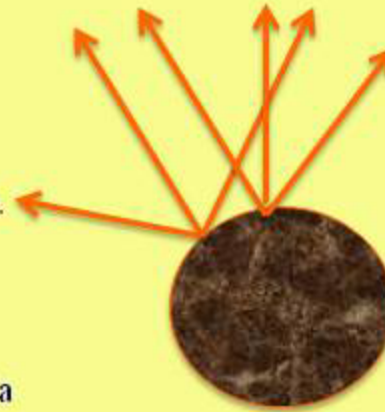
# Early concepts of Eye Anatomy

- Pre-Hippocratic anatomy: transparent cornea and opaque wall, lined by a layer with a perforation which formed the pupil enclosing a fluid thought to be seat of vision. Tube connecting eye and the brain, allowed movement of visual substance
- **Aristotle** dissected animal eye. Three layers instead of two are recognized. internal structure poor. ocular fluid changed on exposure to air; lens regarded as a post-mortem manifestation.
- **Herophilus** wrote treatise on the eye. no manuscripts survive so **Celsus** poor understanding. Recognition of the lens, *crystalloides*.
- **Galen**: *De usu partium* based on predecessors animal dissection. After this, until Versalius 1,000 yrs later no re-examination.
- **Yuhanna ibn Masawaih** (777-857) Christian Court Physician Baghdad. **Daghal al-'ayn**. (The Alteration of the Eye). Earliest treatise on the eye
- **Hunain ibn Is-hâq's** (808-873) **Johannitus**: A Nestorian Christian from Hira. Translator. Adopted Galenic theory of vision
- **Book of Questions on the eye: Book of the Ten Treatises on the Eye**. Written when imprisoned for refusing to poison an enemy of the Caliph "because of my religion and my profession". First diagram of eye. Central place of lens. Because it is transparent it cannot receive nutrient from the blood so requires an intermediary, the vitreous. Behind this are three tunics, the **retina** (vascular), **choroid** nourishes retina and **sclera** protective. One humour glass-like (vitreous)
- In front symmetrically are three tunics (**Uvea**, **cornea** and **conjunctiva**) and one humour (albinoid).





# Muslim golden age



- The Baghdad-centered Abbasid dynasty, which replaced the Damascus-centered Umayyad dynasty after AD 750. Closer to Persian culture. Influenced by the (pre-Islamic) Sassanid Zoroastrian practice of translating works and creating great libraries
- **Al-Kindi** (d c866 Baghdad): formulated new concept of radiation. Individual small points of a luminous body send out rays independently of each other in all directions. (Incoherent radiation). Defender of intromission.
- 902 translation of Gk text on burning mirrors Kuwait library (Prof Rashid)
- **Ibn Sahl** (c940-1000) mathematician with Abbasid court Baghdad. Burning mirrors Discovered law of refraction rediscovered by Harriot 1602 in correspondence with Kepler. Snell's law.
- the ratio of the length of the smaller hypotenuse to the larger =  $1/\text{refractive index of the crystal}$
- Intromission theory of Aristotle supported in C10th by the Persians **al-Rhazi (Rhazes)**, and **al-Farabi**. And in 11thC **Abū Alī Sīnā** Avicenna 980-1037.
- C12th **Ibn Rushd Averroes (1126-1198)** Cordoban polymath



# Ibn al-Haythem (Alhacen) c965-1049

Born Iraq summoned to Egypt by the Fatimid Khalif, al-Hakim (996-1021)

**Kitab al-Manazir (De aspectibus)** (a1030) "Book of Optics" written whilst under house arrest in Cairo. theory of vision based on Gk. Correct model of vision: the passive reception of light reflected from other objects, vs extramission of Ptolemy, Al Kindi etc.

Not appreciated and evidence of his books being burned.

Translated during the late C12th/early C13th prob in Spain by the Lombard; Gerard of Cremona (ca. 1114–1187)

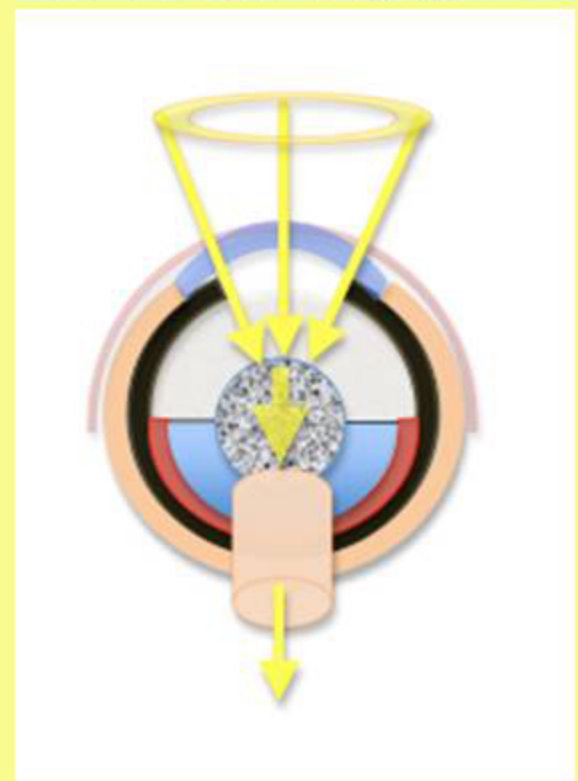
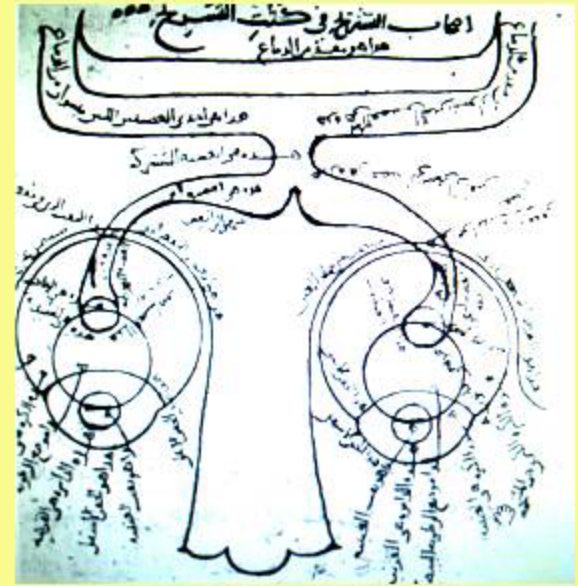
7 books, 3 analyse visual perception, next 3 reflection last study on refraction. A critique of Ptolemy's Optics, challenging supposition that the eye emits a visual flux in a radial bundle forming a cone.

1. ability of bright objects to injure eye (from without)
2. How can enough be emitted from eye to fill up the space when we observe the stars

Adopted the visual cone BUT with intromission theory. Major advance.

How can an incoherent radiation allow for coherent visual perception? If the eye receives radiation from every point in the visual field then confusion not clear perception should be the outcome. There must be one-one correspondence between the pattern of receiving points replicating the radiating points in the visual field.

Not every point in the visual field is vision-producing. Only rays perpendicular to the primary sense organ are used forming a cone with the base being the visual field, the vertex at the centre of the eye.





# Robert Grosseteste c1168-1253

## Grosted, Bishop of Lincoln

- Aristotelian in a Platonist world (Aristotle's vision of the dual path of scientific reasoning: generalizing from particular observations into a universal law, and then back again from universal laws to prediction of particulars): living a very strict monastic life in reign of Henry III. talent for scientific observation. He looked for God's perfection, but he did so in the physical world. (JH. Lienhard)
- Augustine of Hippo 354-430 used optical imagery to describe theology. God was light. Understanding light meant understanding God, since light followed the rules of Euclid, the way to light and to God was through geometry.
- *Timaeus* (Τίμαιος) Plato a theoretical treatise as Socratic dialogue, c360 BC speculation on the nature of the physical world. Chartres School, understood the dialogue to refer to a creatio ex nihilo also newly translated, Euclid De speculis and Catoptrica, Aristotle Meteorologica and Al-kindī De aspectibus
- Learned optical questions could be analysed mathematically.
- From 1220 to 1235 wrote 200 works including:
- *De sphaera*. An introductory text on astronomy.
- *De luce*. On the "metaphysics of light".
- *De iride*. On the rainbow.
- Belief universe started as point of light expanding as spheres. So optics was the fundamental science of nature.
- rainbow not reflected but refracted light. bent in the mists that form rainbows as it bends in a pool of water.

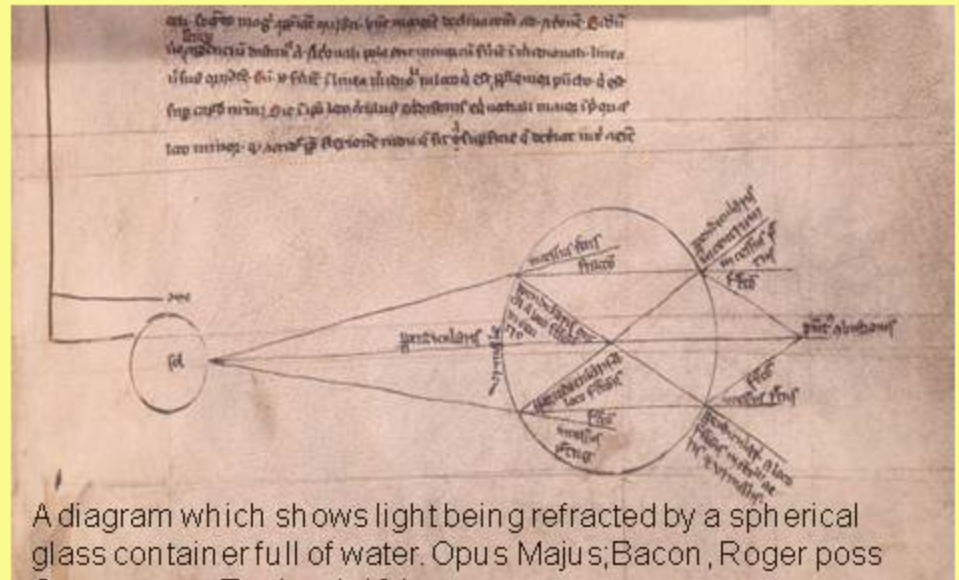


Calcidius' Latin translation Timaeus. C10th



# Bacon c1220-1292

- Inspired by Grosseteste but had the advantage of optical literature of greek antiquity and medieval Islam. Adopted Alhacen's intromission theory. Influenced by the mathematical analysis of light and vision. *Et harum scientiarum porta et clavis est Mathematica. Mathematics is the door and key to the sciences: Opus Majus*
- Champions Grosseteste's ideas. Persuades Papacy that science and math were a proper arm of theology.
- Predicts: self-propelled vehicles, lamps that wouldn't burn out, flying machines, explosive powders, better medicine, longer life, high-yield agriculture.
- Mainly interested in optics. He predicted telescopes and spectacles, first made in Italy a few years before he died.
- Visual realism.** Images of saints were to stimulate thought of the deeds. Not realistic. Bacon believes religion should be represented as realistically as possible. Perspectival drawing gives a 3-D realism, bringing saints to life on church walls.
- New Basilica of St. Francis, at Assisi, perspective paintings. The most popular tourist attractions of its age. Another one and half centuries before Florentine Brunelleschi





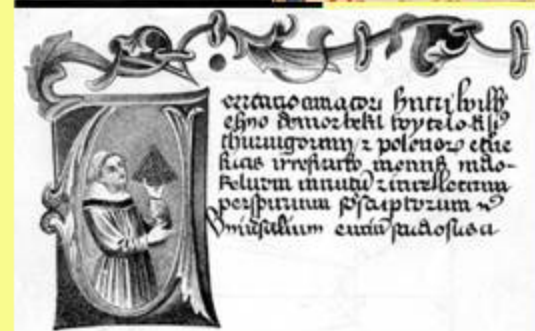
# Bacon followers.

## John Peckham (c1230–1292),

- Educated Lewes Priory, Franciscan friar c1250. Studied Paris, taught theology, debated with St. Thomas Aquinas twice, opposing views on nature of the soul. studied optics and astronomy, influenced by Bacon. Archbishop of Canterbury 1279–1292.
- **Perspectiva communis** (1277-9) written whilst at the Papal Curia. Most influential book of optics for three hundred years.
- Book I: theory of vision: propagation of rays, colour, anatomy, visual perception, psychology of vision, and errors of direct vision.
- Book II analysis of image formation by reflection. by plane, spherical, cylindrical, and conical mirrors; understanding of the nature of the focal point of a concave mirror
- Book III refraction, the rainbow, and the Milky Way.

## Erazmus Witelo

- Polish Mother, German father "Turingorum et Polonorum filius" a son of Poland and Thuringia. He studied at Padua University about 1260, then went on to Papal Court at Viterbo. **Perspectiva**, completed 1270–78, dedicated to William of Moerbeke, the translator of Aristotle. Similar to the Alhacen's *Perspectivae* and influenced by Bacon:  $42^\circ$  for sum of altitudes of sun and rainbow. In 1267 Bacon sent his work to the papal court at Viterbo. A new work appeared a decade later Witelo!





# Medieval interest in perspectiva

**Peter Auriol:** French Franciscan philosopher and theologian called "Doctor Facundus," lectures 1316-1318 he asks how we are able to see and know the world around us. He begins by considering perceptual error. (Dallas Denery). If we look at the sun then close our eyes we still see a circle of light. When a straight stick is partially submerged it appears to be broken. He believed these experiences of perceptual error held the key to understanding vision itself.

Alhacen's 'De aspectibus', Witelo's 'Perspectiva', and John Pecham's 'Perspectiva communis' all served as university texts, primarily for the instruction of mathematics within the Arts curriculum." In the Sorbonne library before 1338. Lectured on at Würzburg till 1595.

**Albrecht Dürer** (1471-1528), **Underweysung der Messung**, first text on Euclidian geometry and perspective written in Vernacular (German), accessible to craftsmen and artists

16thC revival of perspectivist tradition. 30 printed editions of books.

**Francesco Maurolico** (Messina 1494) Benedictine Abbott of S. Maria del Parto. Recognised crystalline humour was a convex lens transmitting and refracting light so Bacon and Pecham were wrong by asserting that only vision only occurs from perpendicular rays.

**Giovanni Battista Della Porta:** 1535 Neopolitan Nobility. De refractione optices parte libri novem. Traditional perspectivist view. Had outlined importance of lens in camera obscura but failed to develop this theory for the eye believing crystal lens was the screen for the image.



Canterbury Tales of 1387–1400: **Squire's Tale**  
And some much wondered on the mirror's po

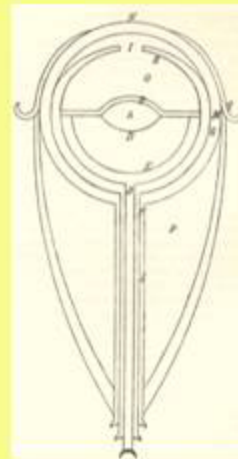
That had been borne up to the donjon tower  
how men in it such strange things could see.  
answered, saying it might be Quite natural,  
oddly spaced And sly reflections thus within

And said, at Rome was such a one, men kn  
spoke of Alhacen and Witelo And Aristotle, v  
wrote, in their lives, On mirrors strange and  
perspectives, As all they know who've read  
published word.



# Renaissance

- **Vesalius**, anatomy theoretical to observational. However for the eye he is inferior to Galen.
- **Fallopian** rediscovered the greater curvature of the cornea. disproved the existence of the retractor bulbi in man.
- **Felix Platter** 1536-1614 De corporis humani structura et usu. Retina not lens is seat of vision
- **Fabricius** correct position of the lens (A.D. 1600),
- **Christoph Scheiner** 1573-1650. Jesuit mathematician and astronomer dispute with Galilei. Measures radius of cornea by reflectance and shows optic nerve exits nasally. First accurate diagram of the eye. Optical image on wall of eyeball 1625
- Time of religious wars. Rising neo-platonism and Augustinian philosophy. Reality a mixture of matter (corrupt) and spirit (good). The human body was unique, a micro-version of the cosmos and therefore influenced astrologically. Mars correlated with bravery, fortitude. Its correlate on earth is iron/ore, red and the strongest metal. So if you have anaemia-lassitude-not enough Martian influence. Phillip von Hohenheim (Paracelsus) (1493-1541) treats you with iron and you get better. Fleeting rash of syphilis, Rx with Mercury.
- **Francis Bacon** in the New Atlantis 1620 reacts against the self-serving University Aristotelians, and secretive magicians and music of the spheres and celestial harmonies.
- For an educated person something new was required. That was mechanical philosophy. C17th machines had no internal power. Automata constructed with levers/pulleys. The creator was Divine Engineer. Gassendi a priest, Descartes a practicing catholic, Hobbes a protestant.





# Johannes Kepler (1571-1630)

Born in Baden-Wuerttemberg teacher then assistant to astronomer **Tycho Brahe**, whom he succeeded as Imperial Mathematician. **Ad Vitellionem paralipomena** (a supplement to Witelo)

Kepler showed how cones of rays from each point in the visual field are focused into a point-to-point correspondence on the retina. Image not caught by lens but focused and painted on the retina. Like the pinhole camera the image was inverted and reversed. How this is perceived "I leave to the natural philosophers to argue about". in the hollows of the brain" due to the "activity of the Soul."

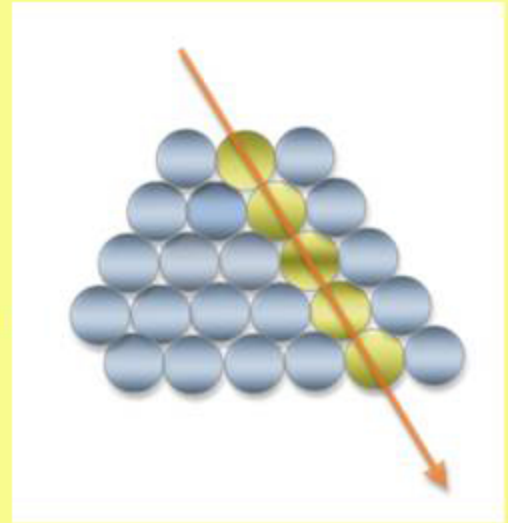
Jan 1604, manuscript for Emperor published as **Astronomiae Pars Optica** (The Optical Part of Astronomy). reconstruction of the theory of light, the physiology of vision, and the mathematics of refraction. Describes inverse-square law of intensity of light, reflection by flat and curved mirrors, and principles of pinhole cameras, as well as the astronomical implications of optics





# Descartes (1596-1650)

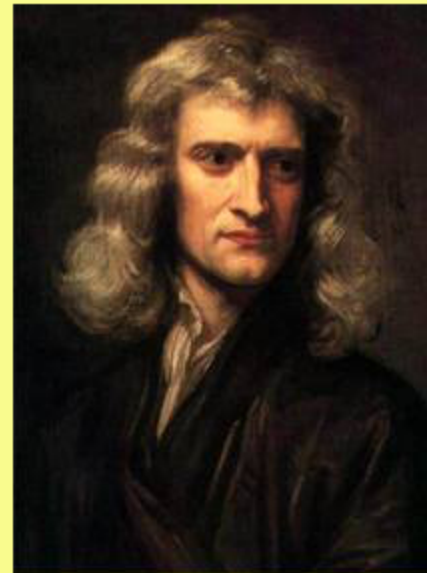
- 1619 military mission in Bavaria, series of dreams. Only thought and reason are beyond doubt. The body works on mechanical principles. The mind has different properties. Dualism persists, "its only in the mind". Whoever does not exist cannot be deceived, and so I exist if I am deceived. Therefore, since I exist if I am deceived, how can I be deceived about my existing when it is certain that I exist if I am deceived?
- Connection between Cartesian and Scholastic thought? Not all dreamt up in a wood oven in Bavaria then. Learned corpuscular theory from friend Beeckman
- Everything is one of 3 things, God, Mind or atoms (corpuscles to avoid trouble with Church). Corpuscles have few properties, size/shape/moveable/impenetrable. So they bounce off each other and to understand the laws explains nature. Since C17th some other properties added, Newton Mass and gravitational force, C19th energy (electrical, mechanical) C20th charm, spin.
- two parts: one mechanical (matter in motion), one perceptual (the world we see). He connects the 'world we see' to the body machine by means of 'many tiny threads.' Distinguishes how visual stimulus reaches eye (matter in motion) from how it was represented (signs), vision is completed by the subject's innate capacity (nativism) to 'read' natural signs not to 'see' pictures.
- "Considering that this bow appears not only in the sky, but also in the air near us, whenever there are drops of water illuminated by the sun, as we can see in certain fountains, I readily decided that it arose only from the way in which the rays of light act on these drops and pass from them to our eyes. Further, knowing that the drops are round, as has been formerly proved, and seeing that whether they are larger or smaller, the appearance of the bow is not changed in any way, I had the idea of making a very large one, so that I could examine it better.



- St. Augustine (De civitate Dei XI, 26: Smith)



# Newton



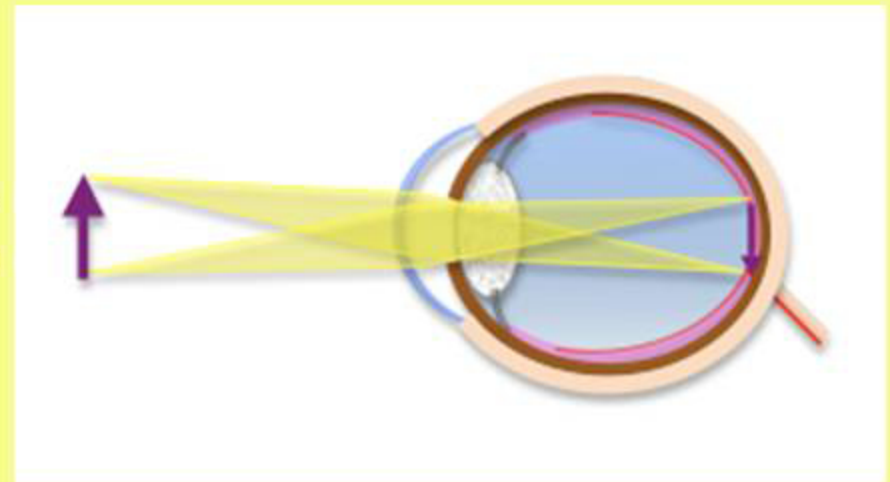
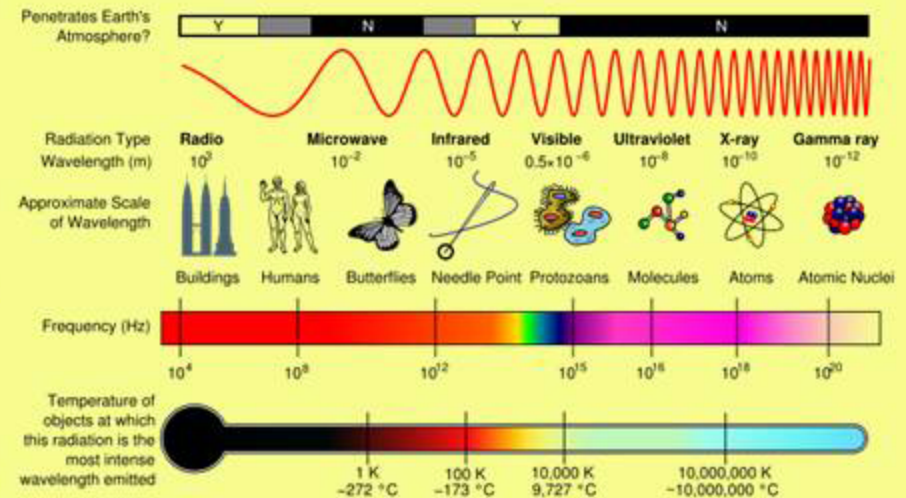
- Since Aristotle it had been believed that light was a single entity. chromatic aberration - lenses tend to act as prisms, means telescopes made from 2 lenses (Galileo) will be flawed. Newton invents the shorter reflecting telescope.
- 1666. Using double prisms discovers white light is combination of other colours which cannot themselves be changed.
- "The oddest if not the most considerable detection yet made in the operations of nature."
- 1672 Philosophical transactions: "Light itself is a Heterogeneous mixture of differently coloured rays... colours are not qualifications of light, derived from refractions, or reflections from natural bodies... but original and connate properties."
- Colour is therefore not rotation of the corpuscles. Annotates Descartes' book with "Error"
- **Particle theory of light.**
- "Blue rays are reflected more than red rays, because they are slower. Each colour is caused by uniformly moving globuli. The uniform motion which gives the sensation of one colour is different from the motion which gives the sensation of any other colour."
- Disagreement with Hooke and Huygens and others proposing a wave theory of light. Light travels in straight lines, sound and water waves do not. You can hear a cannon over the hill but not see it. Newton backs down, proposing his account of the experiment was neutral between wave and particle theories.
- "To speak of light in general terms, considering it abstractly, as something or other propagated every way in straight lines from luminous bodies, without determining what that thing is."
- He formulates another theory, where light is particulate, but excites waves in the aether as it passes through it. Disagrees with Cartesian plenum of pressure waves.





# The contemporary view

- Electromagnetic radiation is a spectrum. Dual nature.
- Light is the bit of the spectrum we see.
- Using lenses is refracted to be focused onto retina
- Absorbed by coloured molecules (photo-pigment)
- Chemical reactions convert light energy to electrical signals
- Summated in retina and passed to output (ganglion cells)
- Processing of information begins in the retina to enhance borders and wavelength information.
- Visual information transmitted to brain by ganglion cells as digital (on/off) responses called action potentials.
- The brain the interprets the signals to create the visual scene.



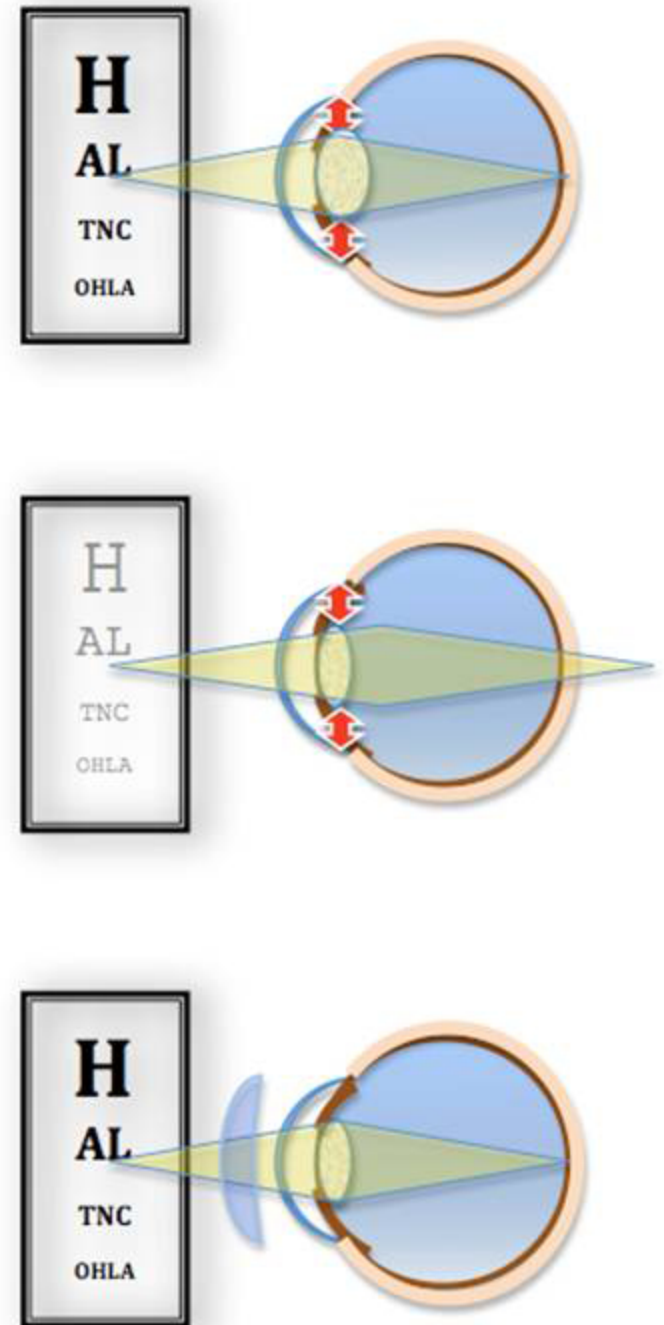


# Lenses of the eye

- Cornea: Fixed. Steeper radius of curvature than sclera
- Crystalline Lens: ciliary muscle control (accommodation)



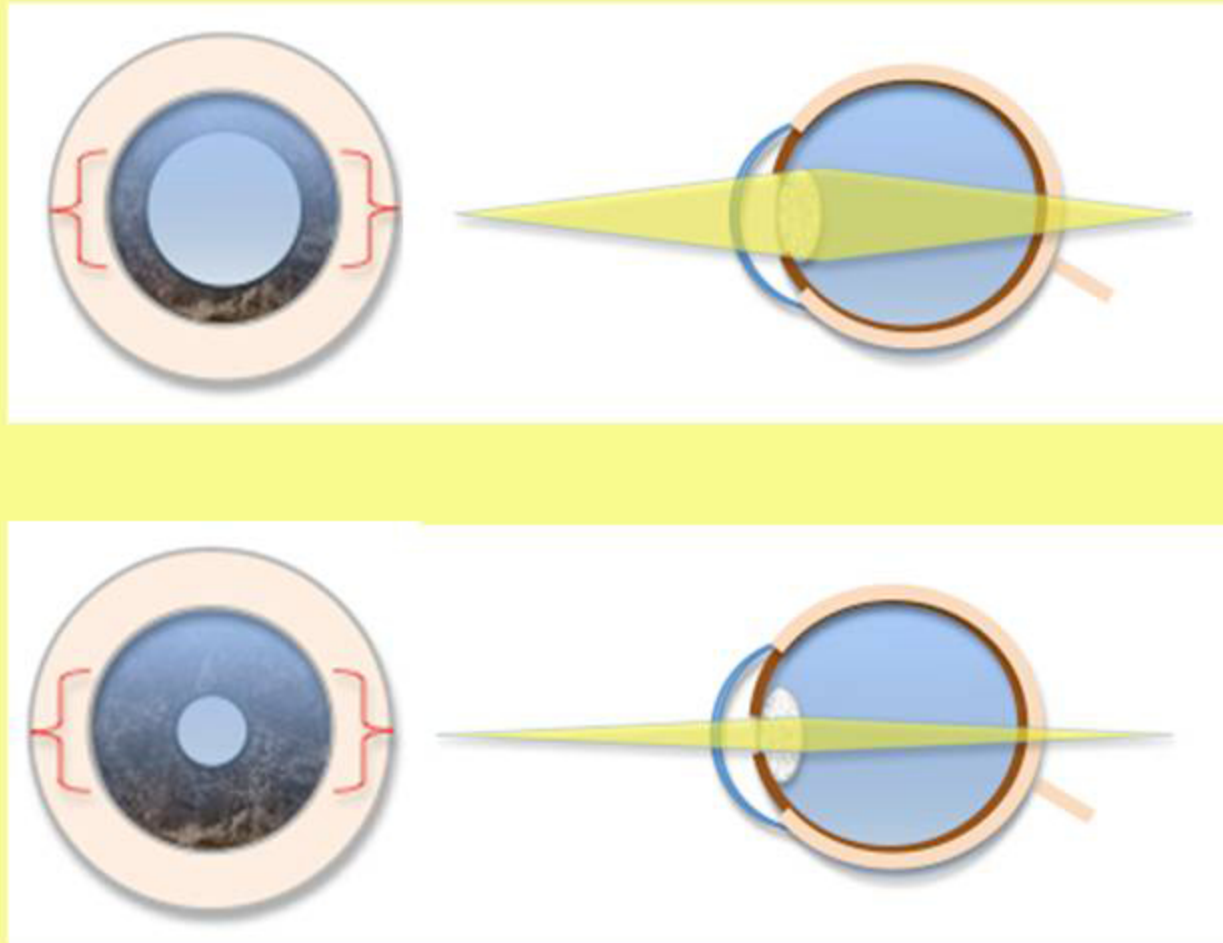
Jan van Eyck 1436  
Madonna met Kanunnik Joris Van der Paele





# Iris

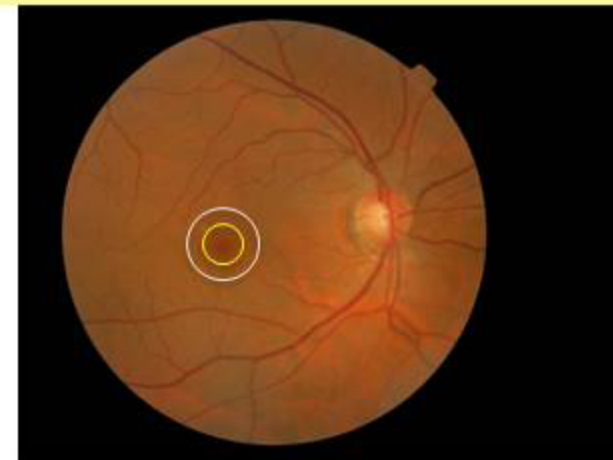
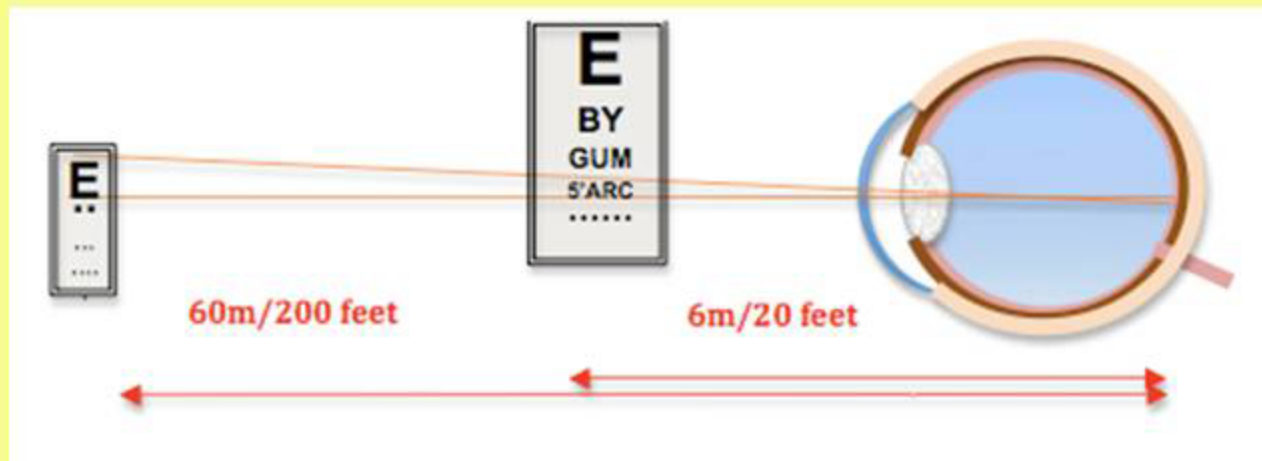
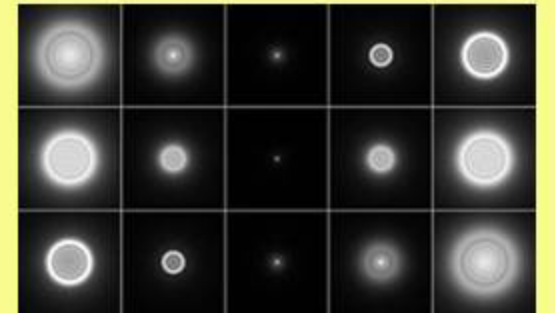
- Muscular aperture.
- Size changes according to light
- Autonomic reflex. Affected by arousal, drugs
- Doesn't keep light intensity constant but optimises acuity for a given light level. Acts as F stop ( "sunny 16 rule").
- f-number ( focal ratio, relative aperture) of an optical is the focal length divided by the "effective" aperture diameter. Smaller aperture, larger f.stop less light. The f-number of the human eye varies from about *f/8.3 in a very brightly lit place to about f/2.1 in the dark*
- Also affects depth of focus





# Acuity: The ability to discriminate 2 objects

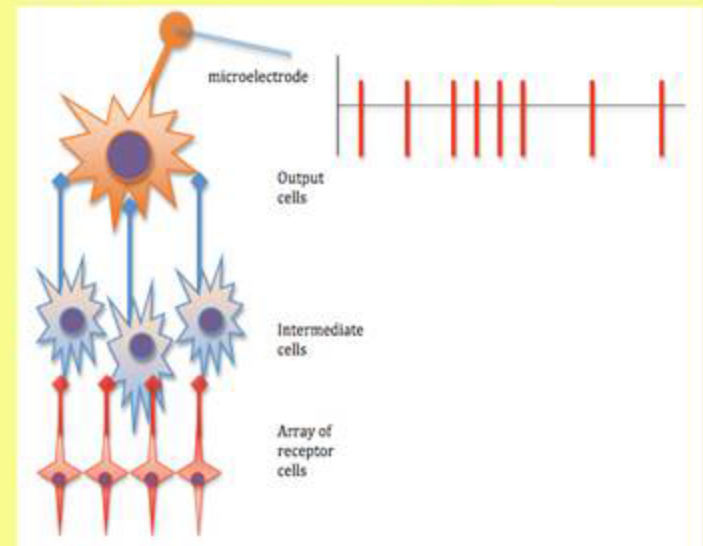
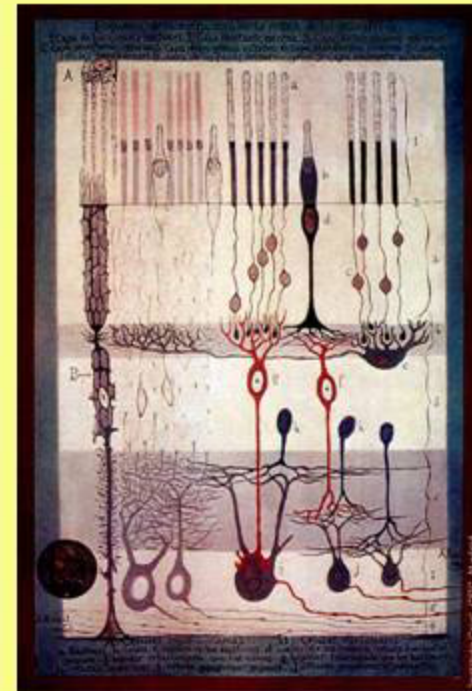
- 0.5 $\mu$ m Wavelength orange light
- 1-3 $\mu$ m: Diameter of cone:
- 1' arc 5 $\mu$ m on retina: discrimination of 2 points
- 12' arc Mizar and Alcor (Giovanni Battista Riccioli 1650 14")
- 20' arc Foveola
- 30' arc (1/2<sup>0</sup>) diameter of sun/moon
- 1<sup>0</sup> 288 $\mu$ m
- 1-2<sup>0</sup> Rod free area
- 2<sup>0</sup> thumb at arms length
- 3.5<sup>0</sup> 1,000 $\mu$ m (1mm)
- 5<sup>0</sup> Headlines at arms length 50% acuity loss  
1.5mm





# The retina: part of the nervous system

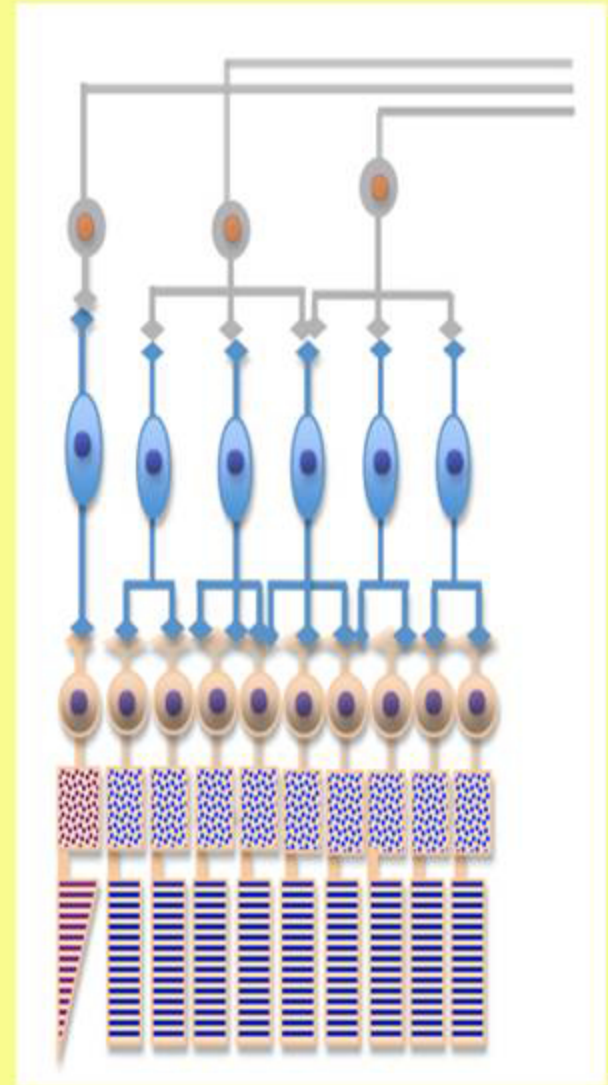
- nerve cells connect to other neurons using tiny 20nm chemical junctions called synapses.
- released chemicals open ion channels in the next neuron which can either hyperpolarise the membrane (stabilising and inhibiting the cell) or depolarise it causing excitation.
- The cell adds up all this information. If there is enough depolarisation beyond a threshold, an electrical signal is generated (action potential)
- AP travels down the axon to terminal synapses.
- rate of firing: one every few seconds to 1000 per second.
- determined by information received from feeding cells.
- rate transfers information to next cells it synapses with.
- nerve cells arranged in a structure (plates or globs).
- Retina has 3 layers of cells and 2 synaptic relays.
- Not all cells develop impulses. Graded potentials can produce enough depolarisation at the synaptic terminals to cause a release of transmitter. Several cell type in the retina





# The retina

- converts light to electrical (nerve) signals, enables vision from night to midday, differentiates wavelength for colour perception by the brain, has acuity to distinguish 2 stars 0.5' arc apart but also pick nits in hair close up. The retina is part of the brain, connected by optic nerve. Constructed like a plate, 1/4mm thick consistency of wet tissue paper. 3 layers of nerve-cell bodies 2 layers of cell connections
- **Pigment epithelium**, mops up scattered light and is needed to chemically restore the PR after bleaching.
- Inner layer: fine mosaic of densely packed  $125 \times 10^6$  **Photoreceptors**. Inner layer so light has to pass through other cell layers. Two retinas, rods and Cones are present throughout the retina. The central 0.5mm contains only cones. Here the overlying cell layers are displaced forming a pit (fovea).
- Middle layer: 3 types of cells. **Bipolar Cells**, connect receptors to ganglion cells **Horizontal Cells** link **receptors** and **BPC** by long connections, **Amacrine Cells** link **BPC** and Ganglion Cells
- **Ganglion cells**.  $1 \times 10^6$ . Pass visual information to brain as bursts of nerve impulses. On/off. Typically each ganglion cell is fed into by 10 to 1000 BPC. Each may receive input from one to dozens of receptors.



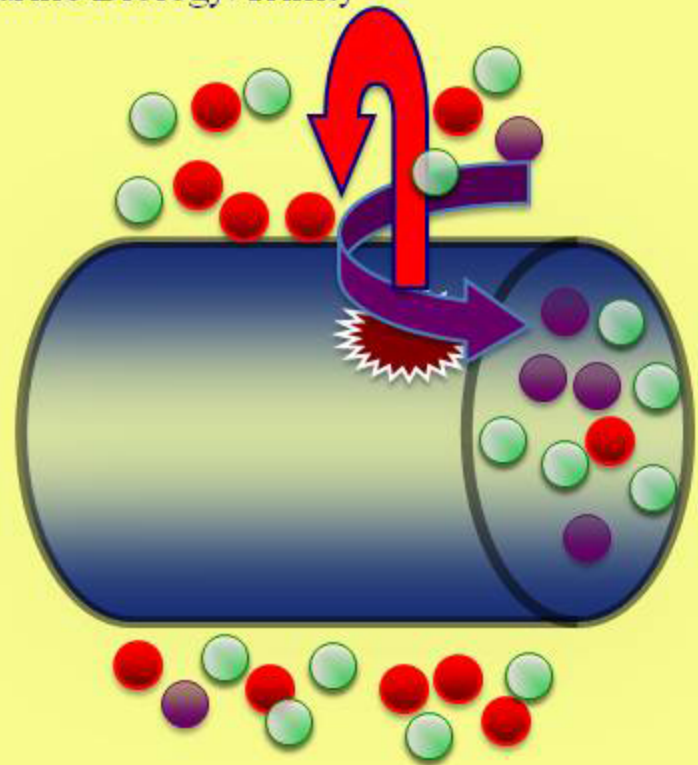
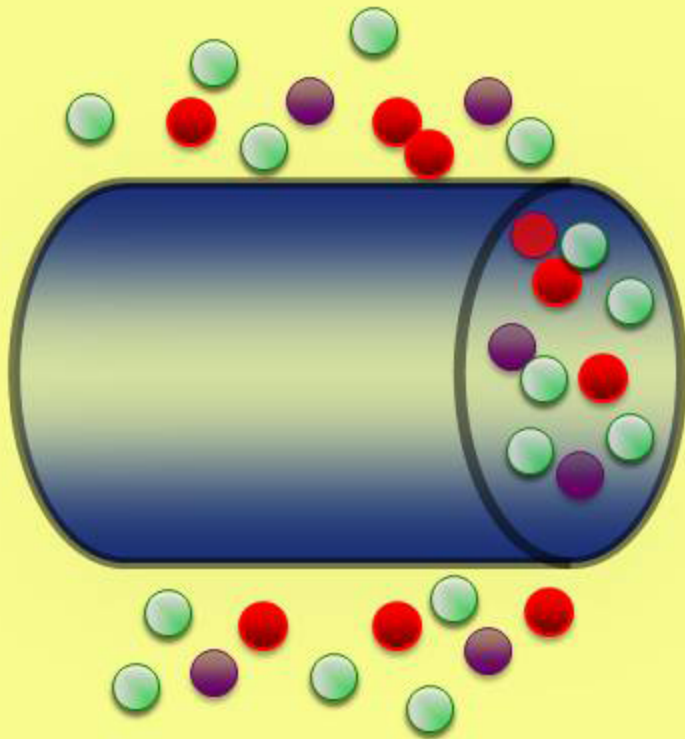


# Generation of resting potential

Decartes, Newton question animal spirit.

Galvani discovers animal electricity.

Hodgkin & Huxley Plymouth Marine Biology/Trinity



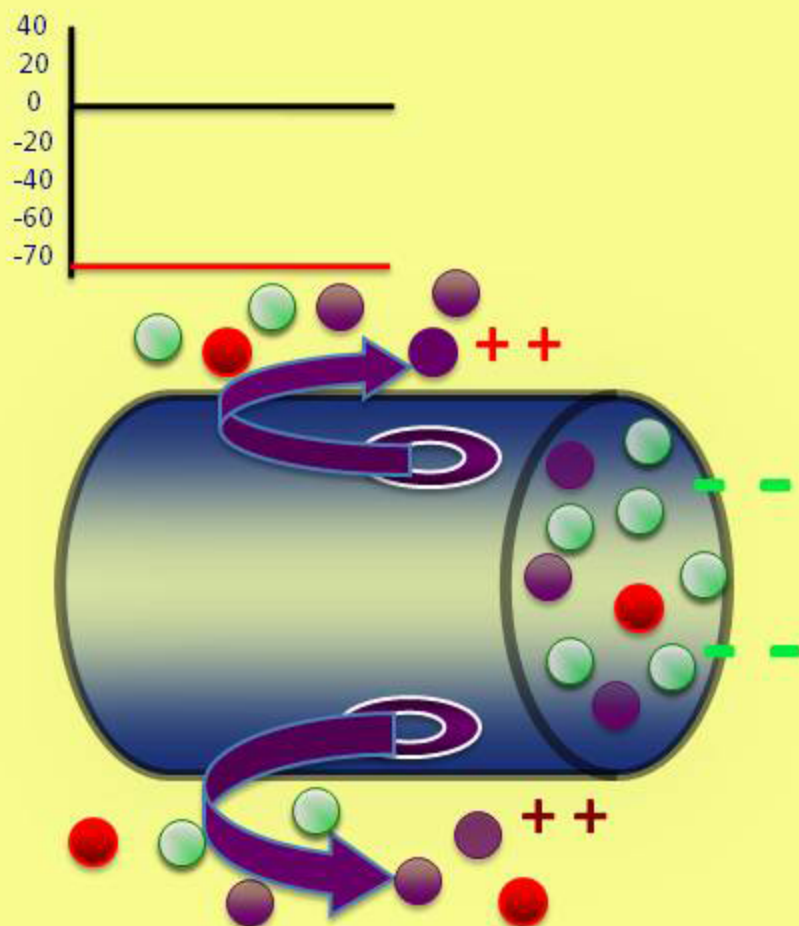
Nerve cell contains and is bathed in salt solution.  $\text{Na}^+/\text{K}^+/\text{Ca}^{2+}$  and  $\text{Cl}^-$ . Active ATP-fuelled pump exchanges  $\text{Na}^+$  for  $\text{K}^+$ . Develops an ionic gradient



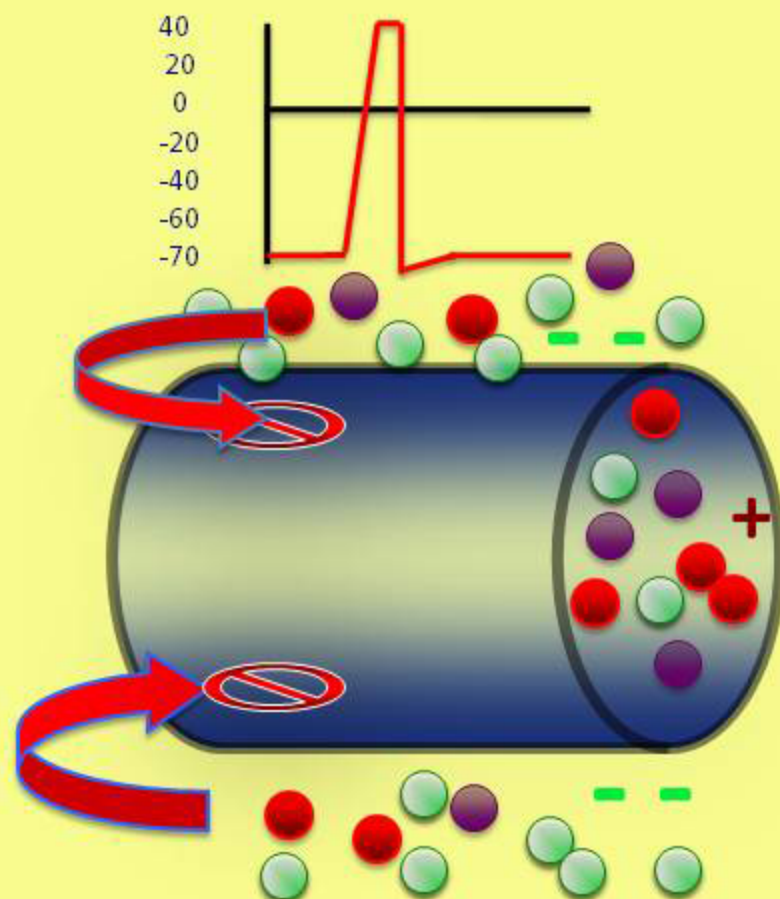
| Ion     | $\text{K}^+$ | $\text{Na}^+$ | $\text{Ca}^{2+}$ | $\text{Cl}^-$ |
|---------|--------------|---------------|------------------|---------------|
| Outside | 5            | 150           | 2                | 150           |
| Inside  | 100          | 15            | 0.0002           | 13            |
| Ratio   | 1:20         | 10:1          | 10,000:1         | 12:1          |



# Generation of action potential



$K^+$  leaks out along ionic gradient  
negative charge inside (resting potential)  
Inside and outside of cell differ  
by about  $1/10^{th}$  volt (70mV) -ve inside

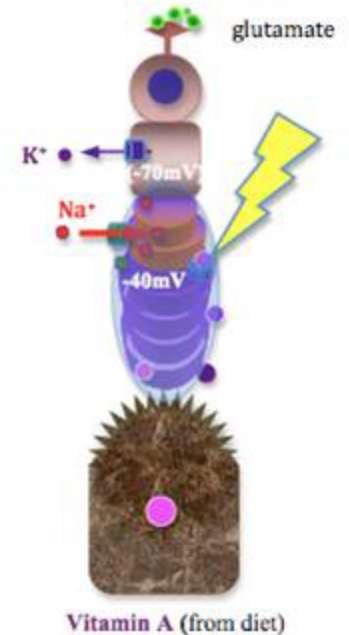
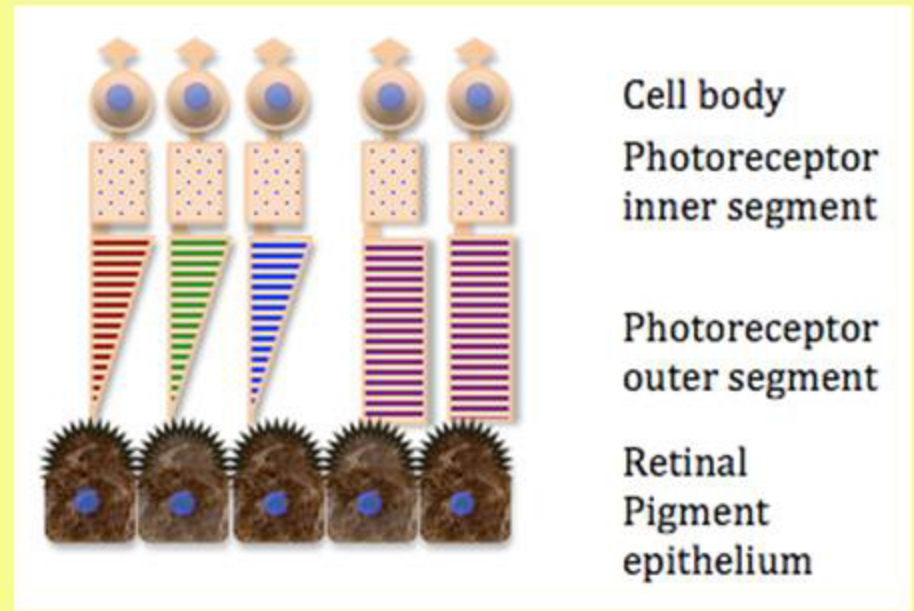


Sudden opening of  $Na^+$  channels allows  
 $Na^+$  to flood in: Reversing the membrane  
Potential.  $1/1000^{th}$  second. Then close  
Then more  $K^+$  pores open restoring balance



# Photoreceptors

- Rods: 120 million. Long slender cells sensitive to dim light. 1 type of pigment
- Cones: 6 million. short and tapered. Present in centre of retina. 3 types of pigment
- Electrical responses of cells technically difficult to measure, so animals with large cells and no arterial pulsation used (often invertebrates, squids etc). Tomita (sound engineer lab destroyed) 1964 electrode into a cone of fish. The potential was unexpectedly low 50mV. When illuminated this increased (hyperpolarized) the opposite of what would be expected.
- So in the dark the depolarized cell is constantly releasing transmitter. light turns this off. In dark the cell is leaky and  $\text{Na}^+$  flows in. Dark current (Hagins, Penn & Yoshikami 1970).
- George Wald: Harvard 1950's:
- Light energy photons captured by Vitamin A-protein complex. Visual purple
- How does a single flash absorbed by a single protein change the membrane potential? By closing millions of channels?





# The conversion of light to electricity

Photoreceptors, have leaky pores.  $K^+$  leaks out. A pump for inward  $Na^+$  is active in dark, needs energy (**cGMP**), keeps the cell partially depolarized (-40mV *cf* -70mV of other nerve cells). Constant glutamate release into synapse.

conversion of photon to electrical signal, stabilizes cell membrane, reducing release. i.e. Light turns the cell OFF. Although a single photon can generate a signal, 20-50 give half maximal response and in order to **see** a flash about 6 rods need be stimulated at the same time. For cone min quantal catch is 5

Visual pigment: Protein called opsin wrapping aldehyde derivative of vitamin A (**11-cis retinal**). Packaged in the membranes of discs

Absorbs light and converts to **all-trans retinal**. Opsin changes shape to Metarhodopsin II which activates a cascade of enzymes: **transducin** activates **phosphodiesterase** which breaks down **cGMP**.

Metarhodopsin II is unstable so breaks up to opsin and **all-trans retinal**, reduced to **all-trans retinol** for transport to the pigment epithelium for recycling.



# Cells of the middle layer

## BIPOLAR CELLS:

Pass information from receptors to Ganglion cells

Cones interact with 2 types. One excited when cone absorbs more light on centre (invaginating), the other excited when cone absorbs less light off centre (flat contact).

**metabotropic glutamate receptors**, G-protein coupling mechanism, close cation channels; hyperpolarizing the bipolar cell. **ionotropic glutamate receptors**: inward cation current that depolarizes the bipolar cell.

**Rod BPC**: Finer bushier dendrites. Connect to 20-50 rods. Always depolarise. Via **amacrine cells** hitch hike onto the cone pathway.

## HORIZONTAL CELLS

Large cells, with both pre and post-synaptic processes (no axons). Turned off (hyperpolarised) by light. Responsible for **Centre Surround** receptive field. (center is supplied by *direct* input from receptors; the surround arises from an *indirect* path from a surrounding receptors that feed into horizontal cells, which feed into the bipolars). Feed back sharpens edge detection.

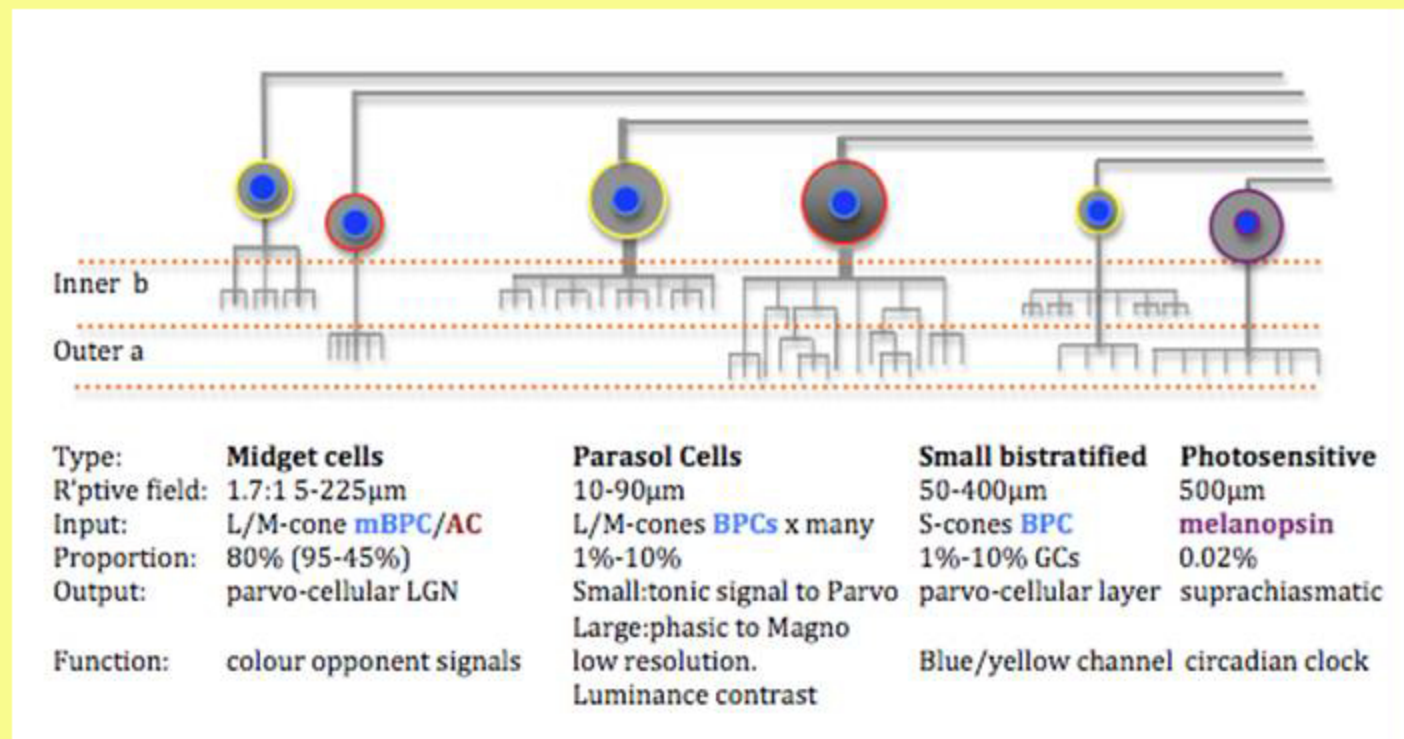
## AMACRINE CELLS

Outnumber **HC** by 10:1. come in a variety of shapes, use several neurotransmitters. There may be twenty or more different types. **AII** type links **rod BPC** to cone ganglion cell output 70% of Large GC input and 50% of midget GC input is from amacrine.



# Ganglion cells: The output from the eye

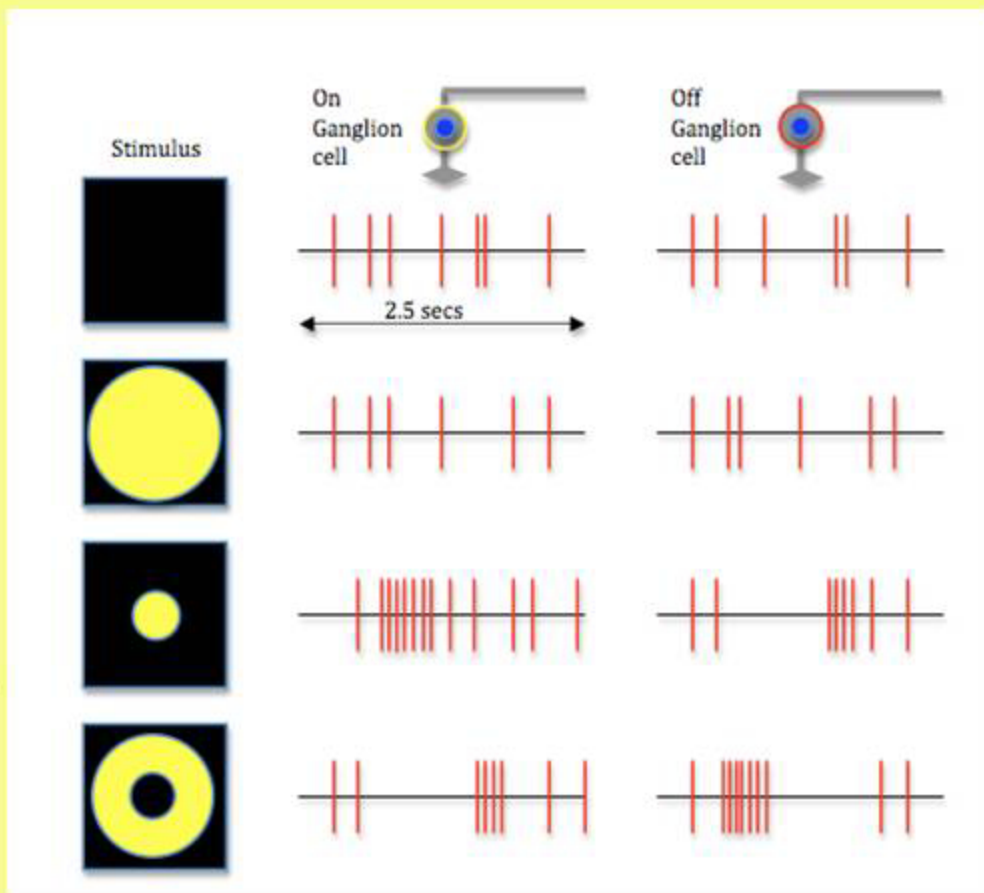
- Final output neurons of the retina
- Collect information from visual world delivered in chemical packages by interneurons **BPC** and **amacrine cells**.
- The various signals are summated and either stimulate or inhibit firing of Action Potentials, the digital on/off signaling which transport information long distances, from eye to brain.
- The optic nerve contains the ganglion cell axons on their way to the first relay stations in the brain.
- The input (dendritic field size) increases with distance from fovea (10x between 2-6mm eccentricity).
- Large (M) 5% transient burst rapid movement sensitive response
- Small (P) 90% sustained discharge. Wavelength sensitive. Concentrated in fovea
- Non M-P
- Light sensitive Ganglion cells: 1% slow reacting to the illumination of the dawn sky. Large receptive fields 500 $\mu$ m
- Project to hypothalamus circadian clock and to pre-tectal pupil control





# Receptive fields

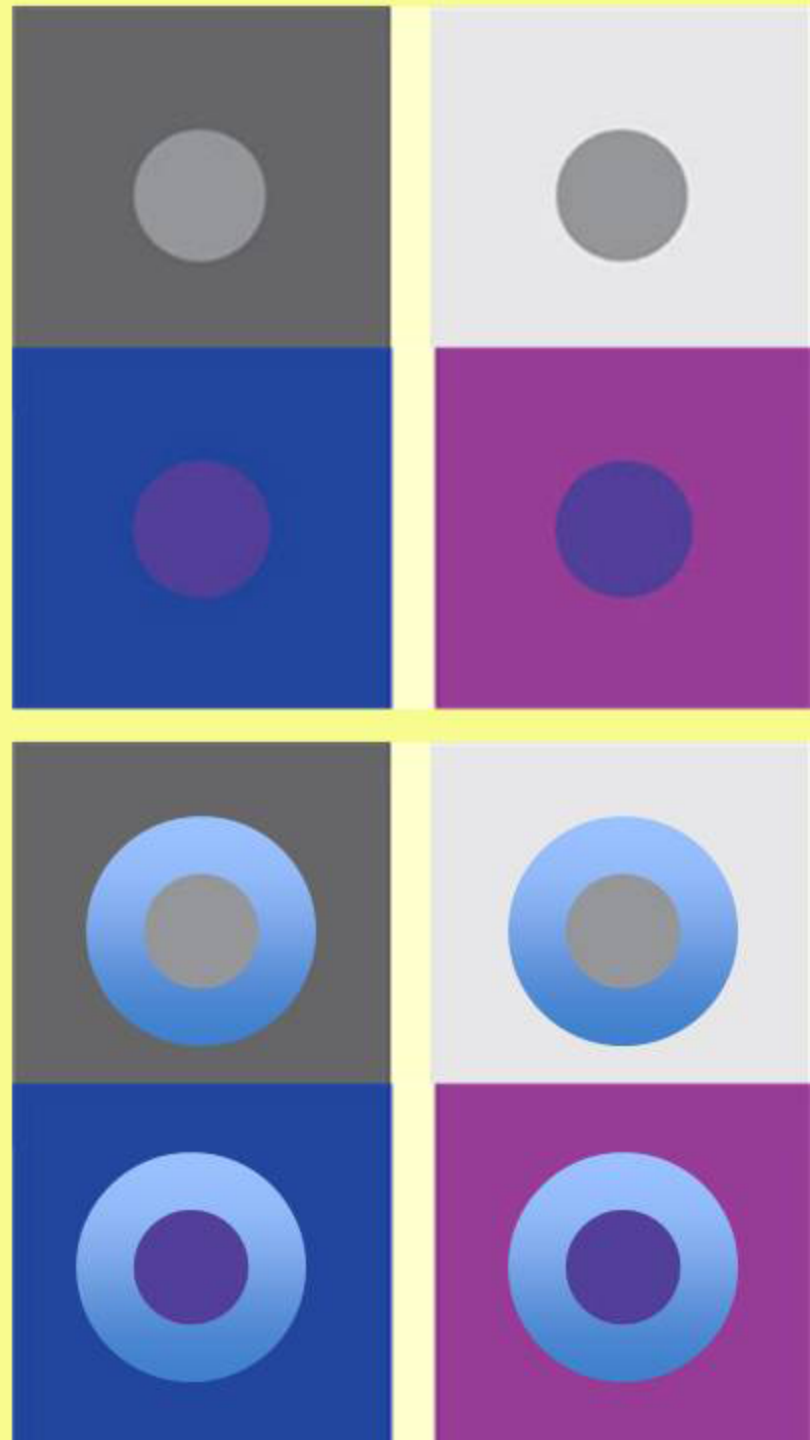
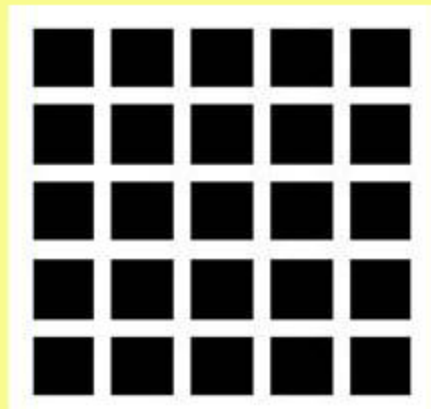
- Hartline: limulus crab axon: Stimulating receptors inhibited neighbouring axons.
- 1950: Setphen Kuffler (Wilmer, Jhophkins) records from cat retina with electrodes inserted through sclera. In dark steady irregular firing 2-20/sec! In diffuse light?...
- Shining small spots: areas were found that increased rate, others that decreased rate. About equally distributed.
- Moving away from on centre the spontaneous rate was inhibited. Turning light off a quick burst. Centre surround.
- LETTVIN bug detector
- An **on-center** cell fires at increased rate when a small spot was shone in the center of the receptive field. moving the spot of light a small distance away from the center of the receptive field, suppressed the spontaneous firing of the cell.
- An **off-center** cell does the opposite: small center from which off responses were obtained, and a surround that gave on responses.
- In nature, dark objects are as common as light ones, (like this text). The eye developed both on-center cells and off-center cells to pass on this information.





# Consequence of processing

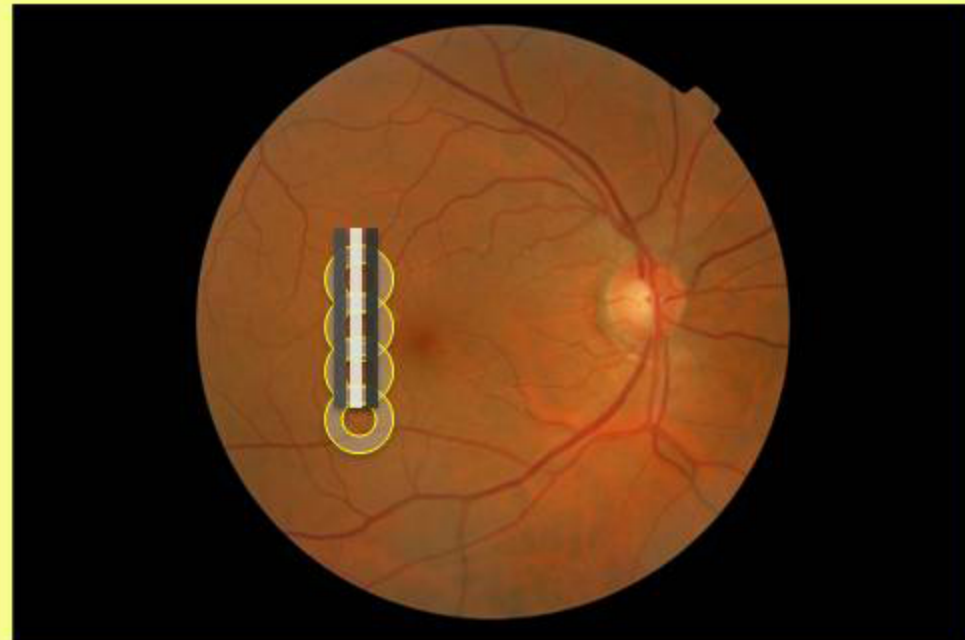
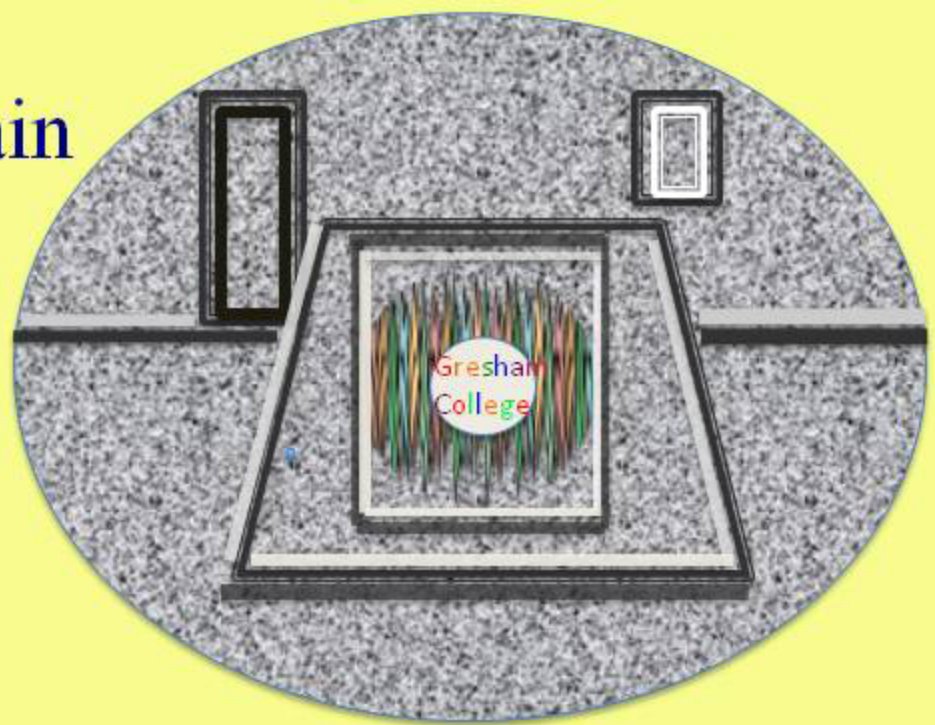
- Consequence of processing is that by the time the visual signal leaves the eye it has been stripped of absolute illumination and replaced with a map of differences, where light abuts dark.
- Most optical illusions result from processes in the cortex, but some do originate in the retina. One such illusion is the Hermann grid shown here a phenomenon called lateral retinal inhibition
- Context influences perceptions, the surround affect perception of that object. As artists know. Similarly the apparent brightness of a surface, depends both on its own luminance and the luminance of the areas surrounding it.





# What the eye tells the brain

- Retina detects edges. Diffuse illumination in centre of field does nothing. The output of the eye, after two or three synapses, contains information that is far more sophisticated than the point representation of the world encoded in the rods and cones.
- It does this by responding to relative difference in brightness.
- Black print outdoors sends twice as much light to the retina as the white paper does indoors! However still seen as black on white. The appearance of black and white is not a function of the amount of light an object reflects, but the amount of light relative to the amount reflected by surrounding objects. "black" and "white" are more than physical concepts; they are biological terms, the result of a computation done by our retina and brain on the visual scene.
- Darkness is absence of light. It still seems real because we have receptors for light.
- Similarly cold is the absence of heat, silence the absence of sound.
- A TV screen appears grey. If we turn it on we can get many shades of black, but the screen cannot get darker!
- The reflectance of the moon is the same as that of coal. Appears white.





# Summary: Is the eye a camera?

- In ancient times sophisticated mathematical analysis had worked out the basics of how light behaves. How the eye worked took longer to establish. Anatomy improved with microscope C19th then astounding electrophysiological experiments in C20th. C21st is looking at the processing pathways.
- Light from the sun or other source is collected by the focusing mechanism of the eye and illuminates the retina.
- Photons are converted to electrical signals.
- Electrical signals are sorted into channels enhancing border detection
- The channels are tuned up by horizontal and amacrine cells to sharpen edge detection and wavelength discrimination.
- These parallel channels pass the information to the output pathway to the brain (ganglion cells)
- The eye passes interpreted information to the brain- not just transmitting a copy of the map of light distribution of the observed scene.
- So is the eye a camera like Kepler and Willi Kuhne thought? It is but not as we know it Spock.
- more appropriate to compare eye to a digital video camera attached to an automatically tracking tripod, is self-focusing, adjusts automatically for light intensity, has a self-cleaning lens, and image enhancement with parallel-processing capabilities so advanced engineers cannot mimic them.



# Thank you

A little learning is a dangerous thing, but none at all is fatal. Francis Bacon

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