SENSATION AND PERCEPTION

Part 1

2220 3.0B

Laurence Harris

2016

SENSATION AND PERCEPTION

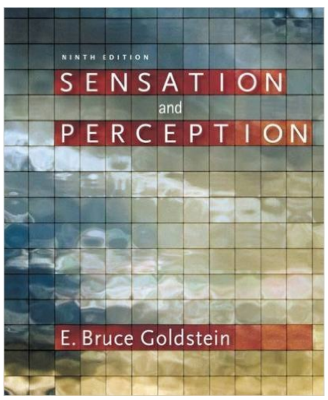
2220 3.0

(2016 edition)

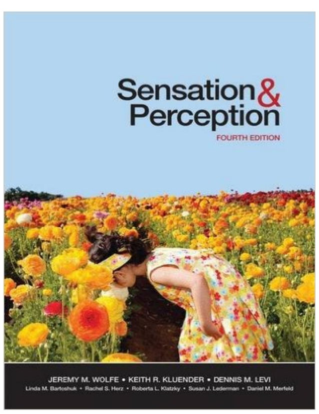
CONTENTS

INTRODUCTION

You are expected to come to the lectures and use these notes as a guide through the course. This material is covered in many textbooks that mostly share the name “Sensation and Perception”. If you would like to see how these textbooks cover the material, ones that I recommend are listed below. Do not feel the need to buy the latest edition. They are all pretty much the same and do not change much from edition to edition. Please note that they go into the material in quite some depth (and with reference to many scientific articles). You do not need this information to get a perfect mark in this course. However, some of their pictures are clearer than mine.



Sensation and Perception by Goldstein



Sensation and Perception by Wolfe, Kluender, Levi and others

I (and next year’s class) would appreciate feedback on these notes. If you spot errors or see ways that the notes could be improved please let me know.

Laurence Harris

SOME WEB PAGES

Administration

The webpage for this course is the MOODLE
https://moodle.yorku.ca/
Here I will post various things of interest including powerpoints of the lectures.

Interest

The web offers many interesting things with many pages devoted to perception and perceptual phenomena. Surfing can find you lots of interesting things, none of which you need to get a perfect mark in PSYC 2220!

Here are some sites I recommend:

Seeing, hearing, and smelling the world
http://www.physics.uci.edu/~tritz/senses/senses.pdf

The Joy of Visual Perception
http://www.yorku.ca/eye/

The York University Vision Group
http://cvr.yorku.ca/

A sensory adventure
http://psylux.psych.tu-dresden.de/i1/kaw/diverses%20Material/www.illusionworks.com/html/jump_page.html

Optical Illusions and Visual Phenomena
http://www.michaelbach.de/ot/

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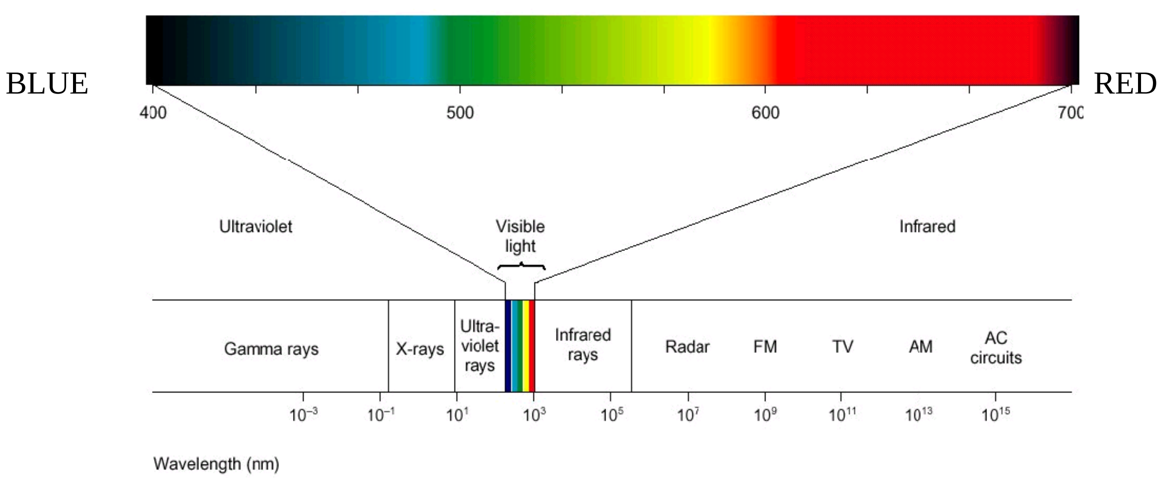
Aug 2016

A table putting the senses into context:

ENERGY			EXAMPLES
Electro-Magnetic Radiation		Ultra-violet	*some insects*
		visible light	*human vision*
		infra-red	*pit viper*
Mechanical	airwaves	Ultra-sound	*bats, dolphins, rats*
		medium frequencies	*human hearing*
		very-low frequencies	*whales, frogs*
	pressure	from outside	*touch, pain*
		from inside	*lateral line of fishes* *vestibular organ* *proprioception*
Chemical	in air	from same species	*pheromones, smell*
		from outside	*smell*
	in mouth	from inside	*taste*

THE ELECTROMAGNETIC SPECTRUM

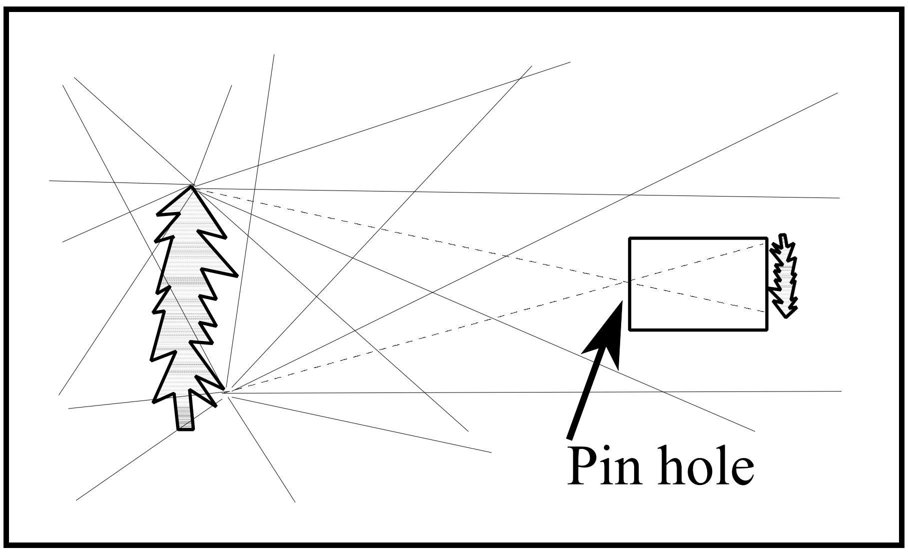


G ENERAL SCHEMA

Physical Energy → Sense organs → BRAIN → PERCEPTION

IN VISION	ACHIEVED BY
1 point the eyes to the right place	EYE MOVEMENTS
2 Focus	ACCOMMODATION
3 Adjust for the light level	PUPILS LIGHT ADAPTATION
4 Convert light energy to activity in cells	TRANSDUCTION

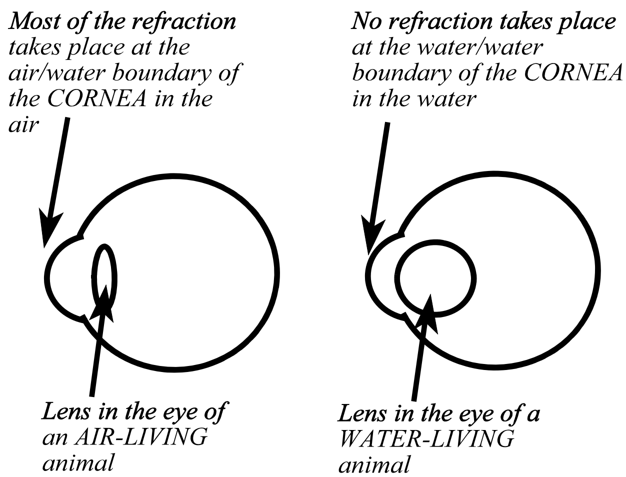
THE EYE AND ITS OPTICS



The lines coming from the fir tree represent some of the reflected light from two points on the tree. The dotted ones are the only rays that happen to pass through the hole in the camera. The smaller the aperture of the camera, the greater the ***depth of focus***. A pin-hole camera that lets through just a single ray from each point has an infinite depth of focus (everything is in focus, no matter how far away).

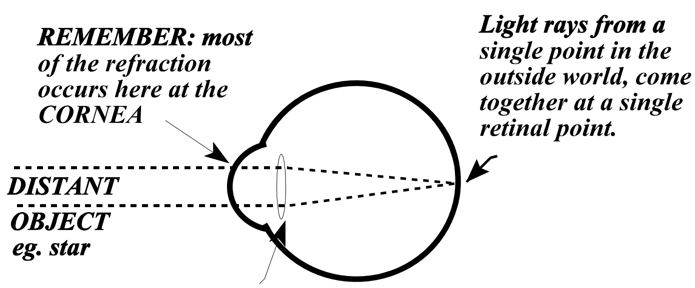
IMAGE FOCUSING

In the human eye, focusing is achieved mostly by REFRACTION at the air/water boundary at the front of the eye (the CORNEA). The LENS only does the fine tuning and some vision is possible without the lens at all. In water-living animals, the lens has to do all the work because there is no air/water boundary, only a water/water boundary which causes no refraction. Therefore the lens of water-living animals is much stronger than the lens of air-living animals.

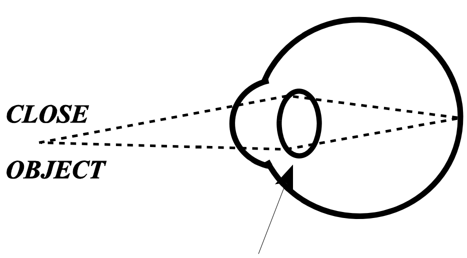


ACCOMMODATION

fine tuning of focus by the lens



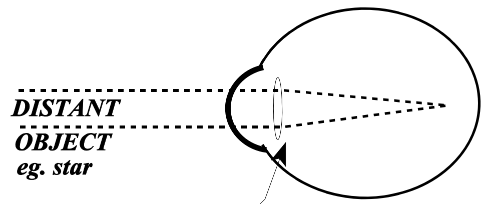
When looking at a distant object, the lens is RELAXED. The relaxed state is THIN. A thin lens does not refract light as much as a FAT lens.



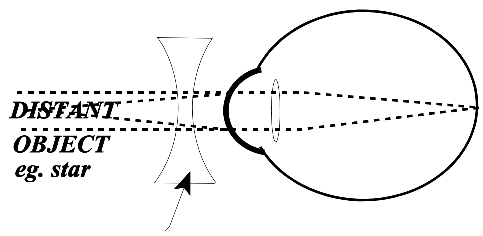
When looking at a close object, light rays need to be bent more to come together in focus at the retina. The lens CONTRACTS and becomes FATTER, thus bending the light more.

SHORT SIGHTED
(Myopia)

If the eye is too LONG, the light rays need to be bent less. This is not a problem for CLOSE OBJECTS because it is easy to make a FAT lens not-so fat. But it IS a problem for DISTANT objects, because the lens cannot relax enough. It's difficult to go thinner than thin!



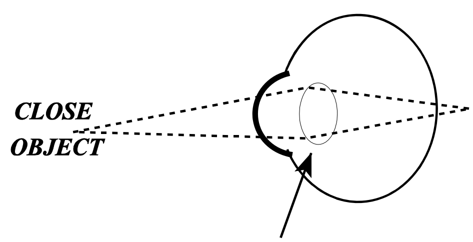
Even the relaxed lens is too strong. The rays are focused in front of the retina!



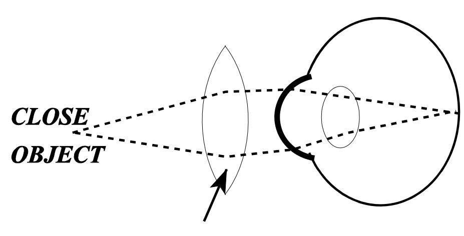
The CONCAVE lens makes the rays DIVERGE, thus compensating for the unwanted strength of the eye's optics.

LONG SIGHTED
(Hyperopia)

If the eye is too SHORT, the light rays need to be bent more. This is not a problem for DISTANT OBJECTS because it is easy to make a THIN lens a little bit fatter. But it IS a problem for CLOSE objects, because the lens just cannot get fat enough.



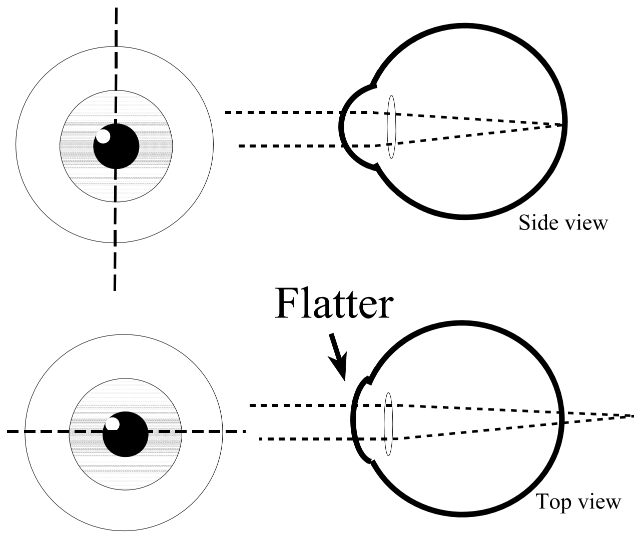
The fully-contracted lens cannot get strong enough. The rays are focused behind the retina!



The CONVEX lens helps the rays CONVERGE, thus assisting the inadequate strength of the eye's optics.

With age, the lens becomes less flexible and accommodation becomes fixed at some distance. This fixing of the focal length of the lens is called **PRESBYOPIA**.

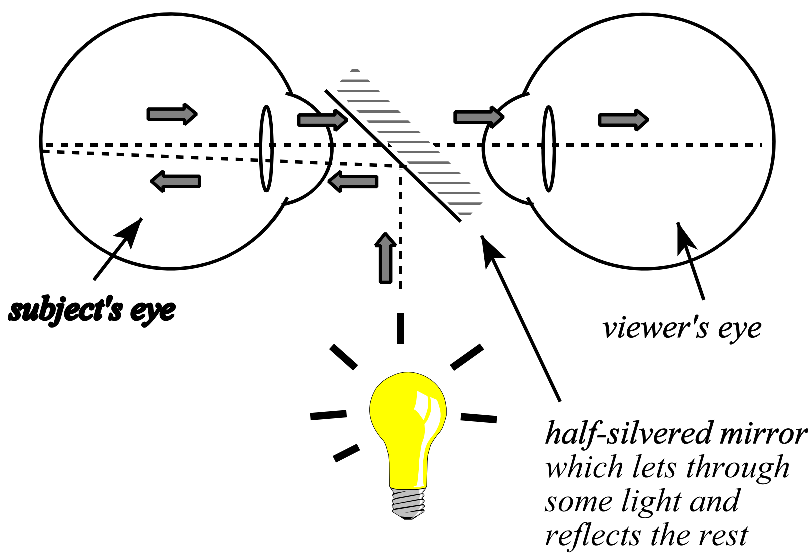
The refracting power of the eye may not be the same in all dimensions. This is called **ASTIGMATISM**.



For this person, the cornea is flatter from left to right than it is from top-to-bottom. Therefore, for this **astigmatic** person, vertical lines would be better in focus than horizontals.

THE OPHTHALMOSCOPE

(spelling hint: note the two H's)



DIVING ANIMALS

The life-style of some animals requires that they can see both in and out of water. When an animal moves between AIR and WATER, it has a problem as the cornea works sometimes (when it is in the air) and not other times (when it is in the water). At least five solutions are found:

1 Put on a mask that keeps an area of air in front of the cornea even when under water. EXAMPLE: only humans, of course!

2 Rely on a strong lens that is flexible enough to change between the WATER-LIVING style and the AIR-LIVING style. EXAMPLE: otter

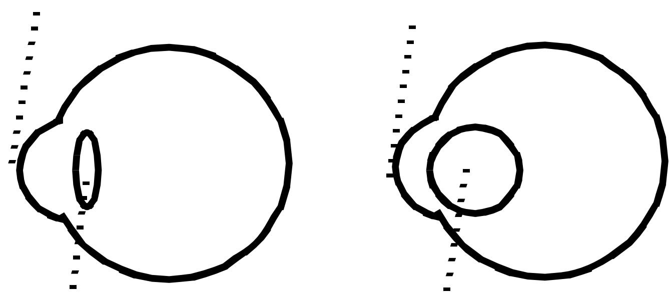
3 Have a flat cornea (to remove its contribution at all times - even in the air) and then use a WATER-LIVING-STYLE lens at all times. EXAMPLES: penguins, flying fish

4 Have TWO PAIRS of eyes, one for each environment. EXAMPLE: the four-eyed fish

5 Use a WATER-LIVING style lens in the water but by-pass the contribution of the cornea AND lens in the air by using a PIN-HOLE style pupil on land. EXAMPLE: seal

Most of the refraction takes place at the air/water boundary of the CORNEA in the air

No refraction takes place at the water/water boundary of the CORNEA in the water

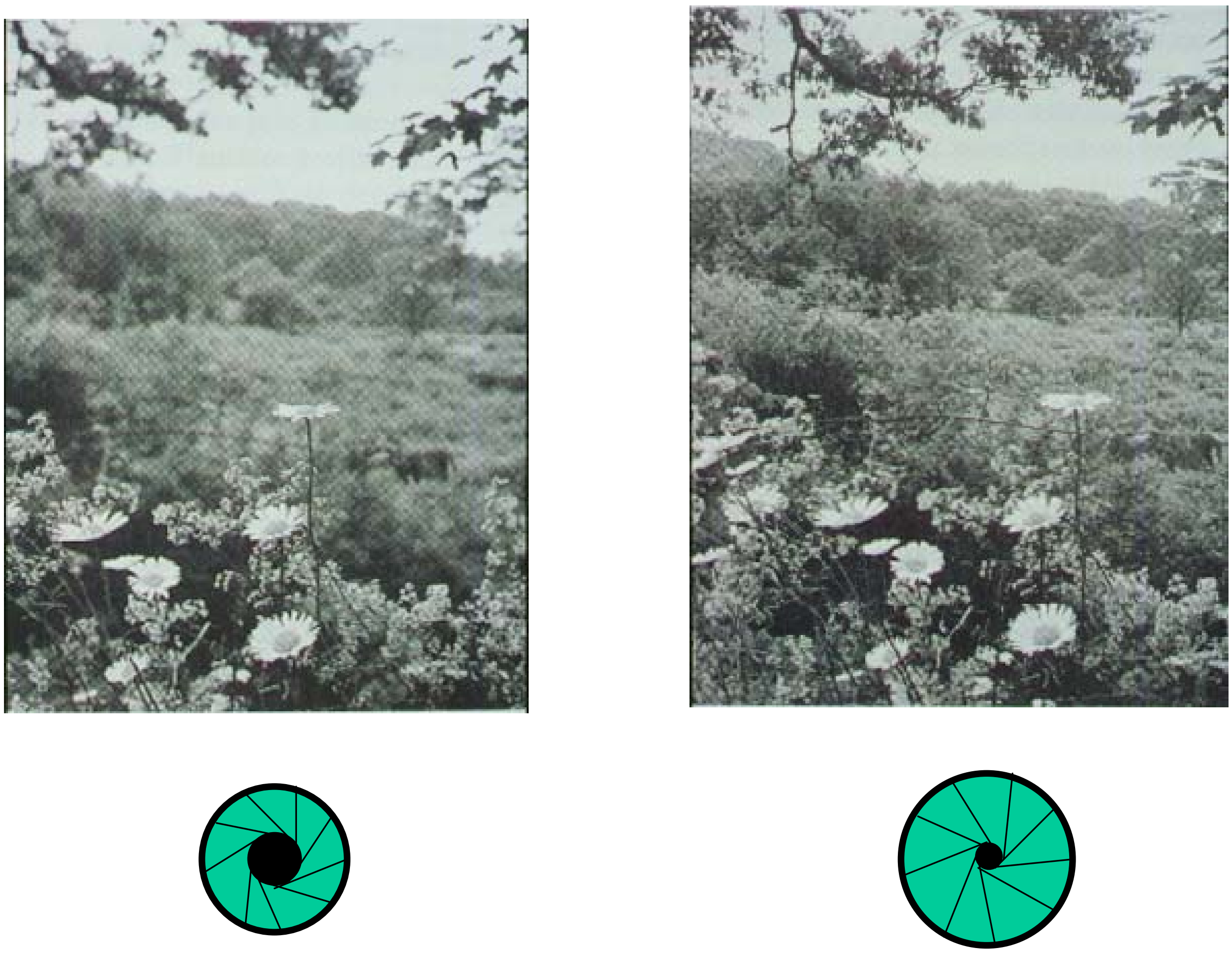


Lens in the eye of an AIR-LIVING animal

Lens in the eye of a WATER-LIVING animal

AIR LIVING

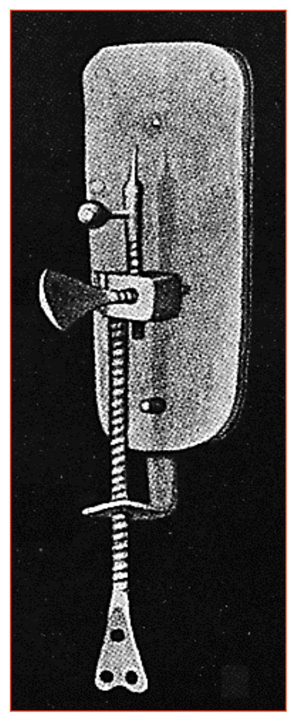
WATER LIVING



The effect of **pupil size** on **depth of field**. A large pupil (left) allows objects at one particular distance to be well focused (here the flowers in the foreground). This is a small depth of field. Whereas a small pupil (right) allows objects over a range of distances to be in focus at the same time, a large depth of field.

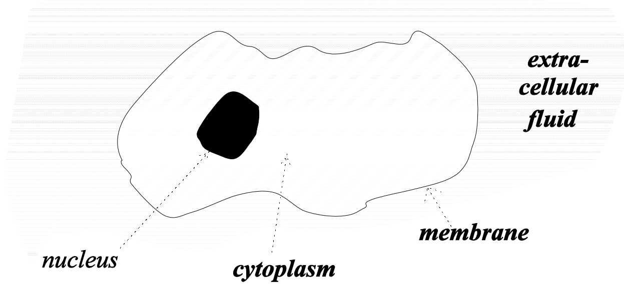
THE CELL CONCEPT

Antony van Leeuwenhoek (1632-1723)
and his microscope



THE CELL CONCEPT

Leeuwenhoek discovered cells shortly after inventing the microscope. All animals and plants can be divided into cells. Cells initially are *undifferentiated*, that is they are unspecialized.



The nucleus contains the chemical that has the information to make this undifferentiated cell into any cell in that particular organism. The cells we will encounter in detail in this course are specialized nerve cells, but notice that the CORNEA is also specialized, transparent cells and so is the LENS.

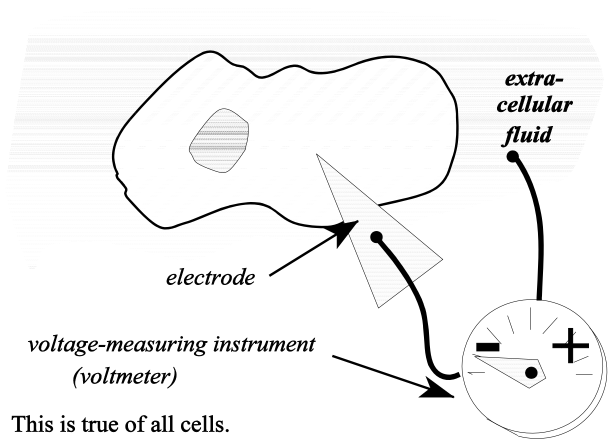
Cells contain a liquid called CYTOPLASM that is kept in a bag called a membrane. The membrane means that the cytoplasm can have a different concentration of chemicals from the fluid outside. The fluids contain salts.

CELLS HAVE ELECTRIC CHARGES

Salts are made up of IONS which are collections of atoms that have an electric charge. For example, table salt is SODIUM CHLORIDE and is made up of SODIUM (Na^+) and CHLORIDI (Cl^-) ions. There is a lot of salt in mammalian bodies.

The membrane of cells keeps the number of positive (+) ions different on the inside of cells from the outside. There are more +'s outside. Therefore if you put a measuring device (electrode) into a cell, you will see it is negative (-ve) with respect to the outside.

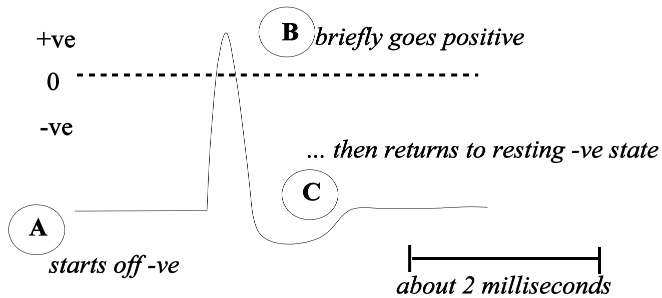
The different concentrations are achieved by specialized **channels** in the membrane that each only let one type of ion through.



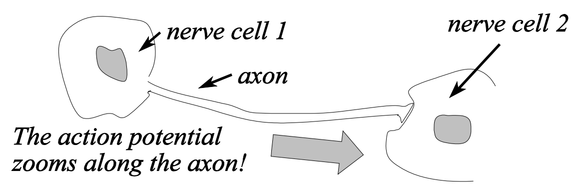
This is true of all cells.

SPECIAL PROPERTIES of NERVE CELLS (neurones)

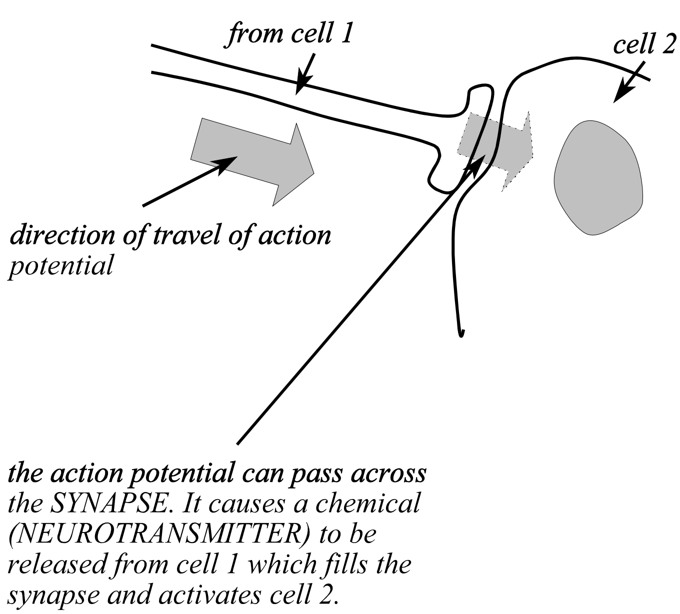
Nerve cells have an elecric voltage between their insides and outsides like other cells. But the unusual feature of nerve cells is that they can briefly reverse this voltage. Thus they change from negative inside to positive inside. They can use this voltage reversal to send information to other nerve cells. The pulse of voltage reversal is called an ACTION POTENTIAL.



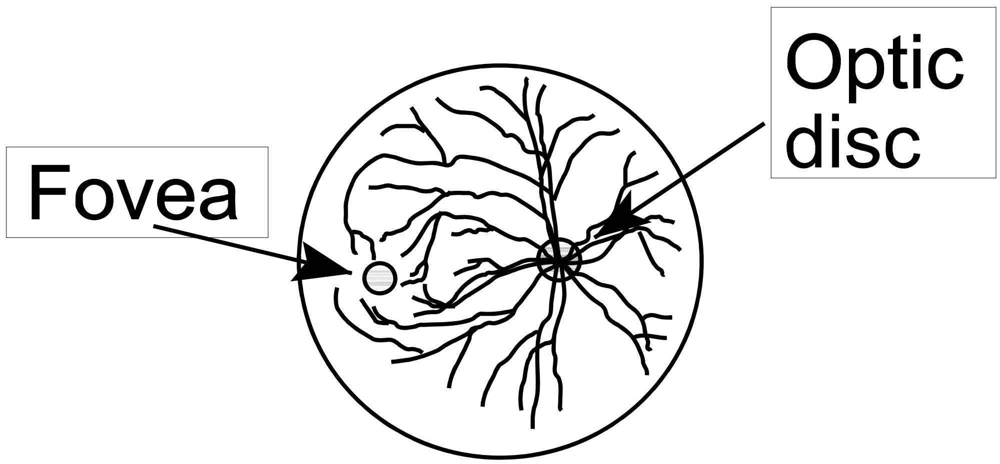
Nerve cells have long processes called AXONS which connect one cell to another. Action potentials are like blips of information or code and pass along these axons.

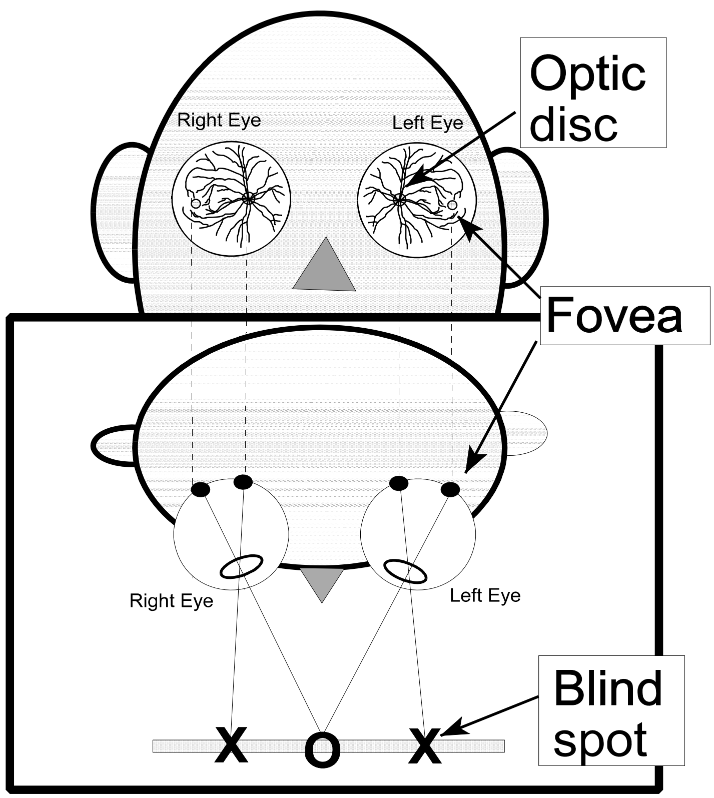


Action potentials pass from one cell to the next across a one-way junction called a SYNAPSE. Synapses act as valves and allow the action potential to go only one way.



THE RETINA

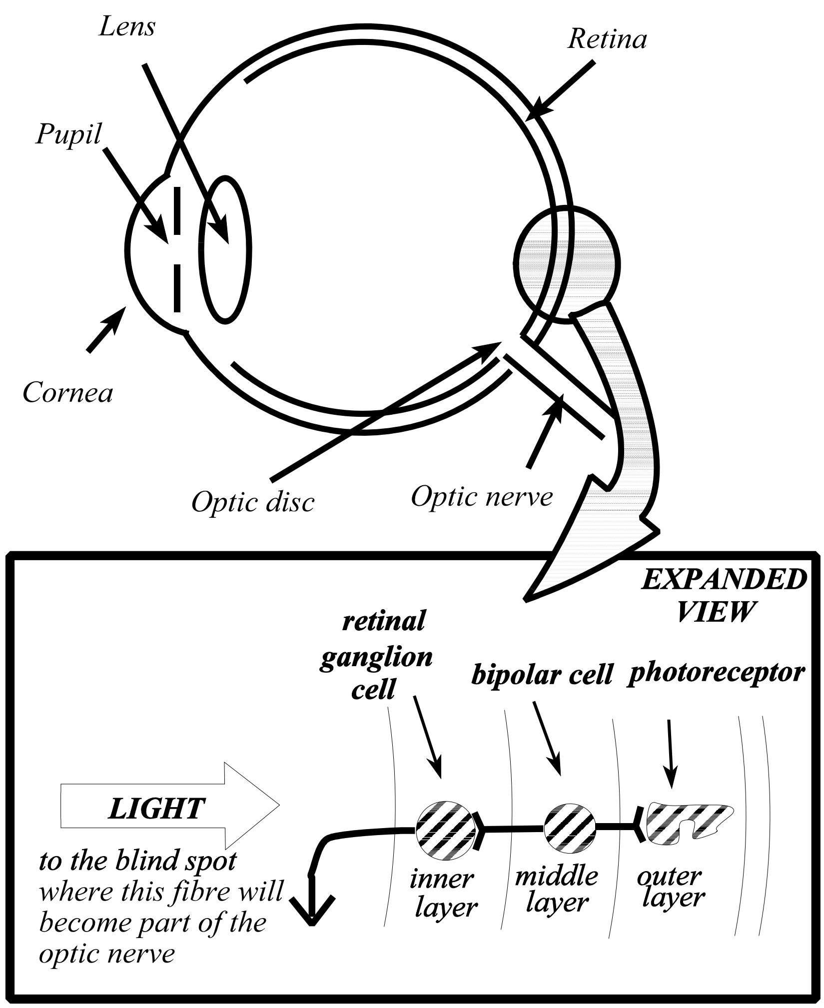




X O

RETINAL PROPERTY		PERCEPTION
1 image is upside down	→	1 world seen right way up
2 image is very small	→	2 world seen as actual size
3 image is on curved surface	→	3 no curve seen
4 TWO retinas	→	4 only ONE world seen
5 blood supply forms a "tree" below which there are no receptors	→	5 definitely no tree seen in front of everything!
6 the BLIND spot (where the nerve comes in) has no receptors	→	6 no black hole seen
7 only the CENTRAL part of the retina is very sensitive; the peripheral part cannot resolve detail	→	7 no difference in clarity between vision in different parts of the visual field

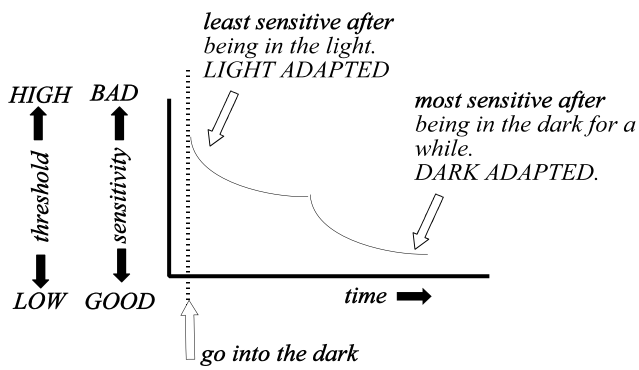
STRUCTURE OF THE EYE



DARK AND LIGHT ADAPTATION

1 **You can measure your visual SENSITIVITY by seeing how** bright the dimmest spot you can just see is. When you can just see the spot, its brightness is said to be at your DETECTION THRESHOLD. The more sensitive you are, the lower your threshold.

2 **Your threshold to light changes if you sit in a dark room.** You become ADAPTED to that light level. Your threshold can be measured at regular intervals after you enter the dark.

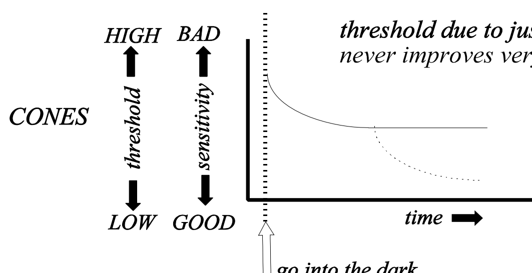


3 **The two-part nature of the curve is due to their being two** kinds of photoreceptors in the retina: rods and cones.

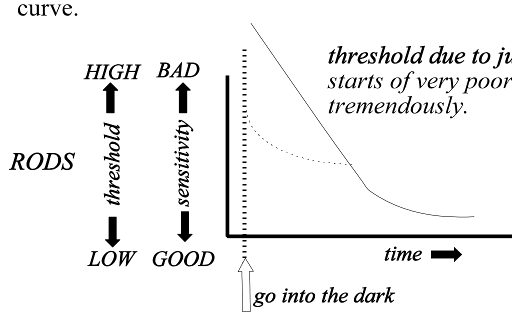
4 **When you are light adapted (PHOTOPIC), your cones are** more sensitive than your rods.

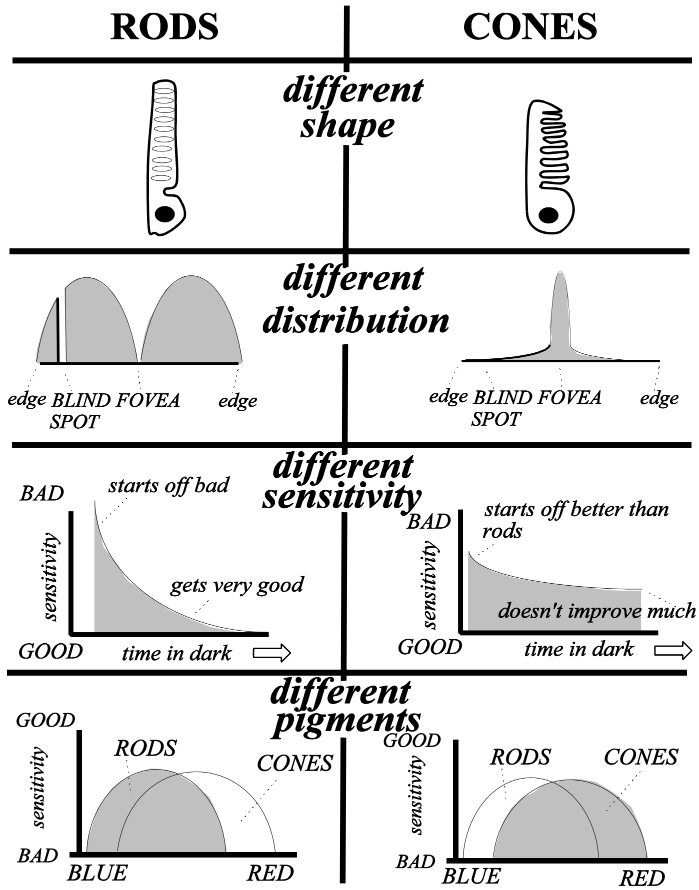
5 When you are dark adapted (SCOTOPIC), your rods are more sensitive than your cones.

6 If we carefully test just cones (by using the foveal region), we can see their contribution.

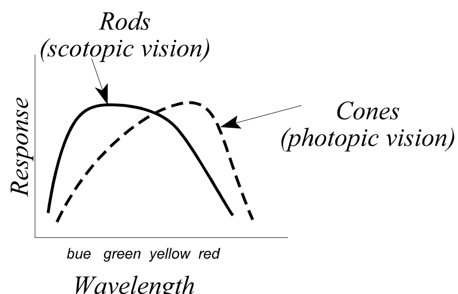


7 If we carefully test just rods (by using the peripheral region of the retina), we can see their contribution to the dark adaptation curve.

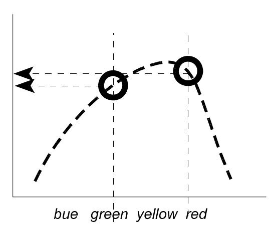




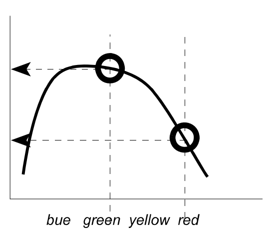
An explanation for **the Purkinje Shift** in which the relative brightness of different coloured objects changes at dusk.



1 Rods and cones have different pigments.

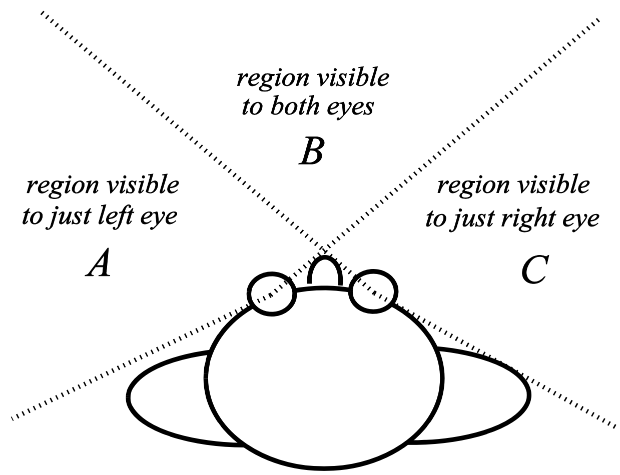


2 When using cones (photopic), red causes a bigger response than green....



3 When using rods (scotopic), red causes a smaller response than green....

THE VISUAL FIELDS OF THE EYES

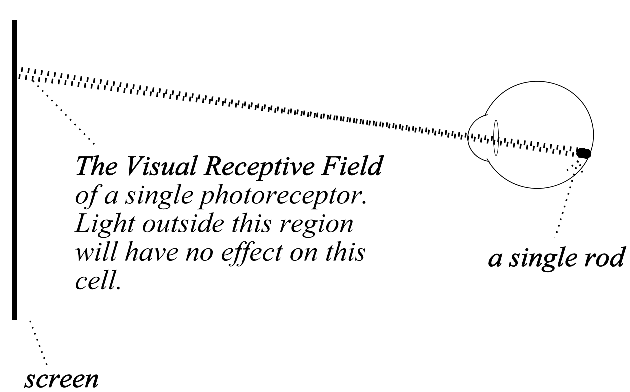


This diagram shows the left eye's visual field (A+B), the right eye's visual field (B+C) and the person's visual field (A+B+C).

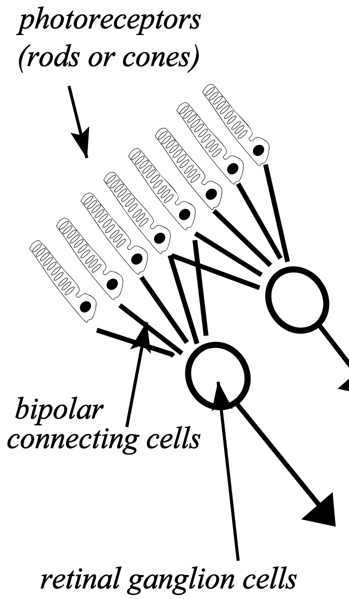
VISUAL RECEPTIVE FIELD

> "The visual receptive field of something is that area of the outside world from which light will have an effect."

THE VISUAL RECEPTIVE FIELD OF A SINGLE PHOTORECEPTOR



RETINAL GANGLION CELLS:



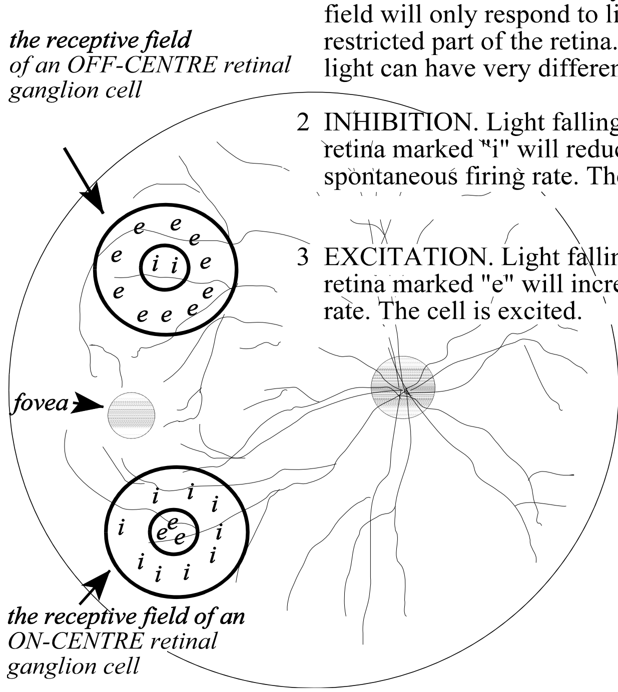
1 **have larger receptive fields than** photoreceptors because the signals from several photoreceptors CONVERGE onto each retinal ganglion cell.

2 have a SPONTANEOUS level of neural activity. Action potentials are produced even if nothing is happening.

3 in the foveal region have smaller receptive fields than those in the peripheral region.

4 have concentrically arranged receptive field structures.

CONCENTRICALLY ORGANIZED RECEPTIVE FIELDS

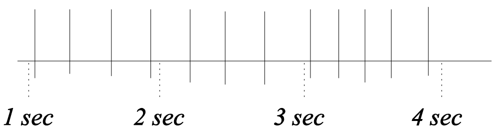


1 **A cell with a concentrically-organized receptive** field will only respond to light coming from a restricted part of the retina. But within that area, light can have very different effects.

2 INHIBITION. Light falling on that part of the retina marked "i" will reduce the cell's spontaneous firing rate. The cell is inhibited.

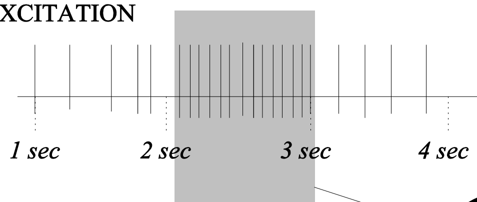
3 EXCITATION. Light falling on that part of the retina marked "e" will increase the cell's firing rate. The cell is excited.

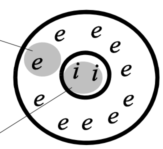
4a SPONTANEOUS



These are action potentials. They are squashed up in time and that's why they look like vertical lines. This cell has an average spontaneous rate of four action potentials per second.

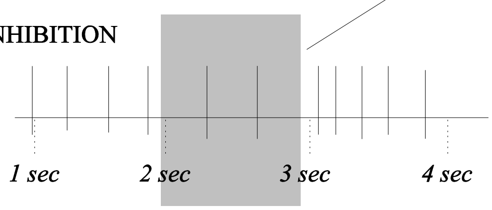
4b EXCITATION



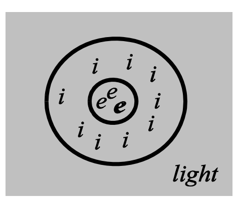


The effect of shining light on the excitatory ('e') or inhibitory ('i') areas of the cell's receptive field.

4c INHIBITION

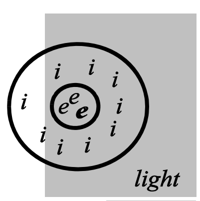


5 If the same amount of light falls on the excitatory and inhibitory regions of the retinal ganglion cell's receptive field, the cell will be excited and inhibited at the same time! These effects will cancel out and the cell will not respond at all but will stay at its spontaneous rate.

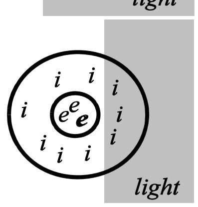


The excitatory region is maximally excited since it is covered with light. The inhibitory region is also maximally inhibited. The activity from the two regions will therefore cancel.

6 If different levels of light fall on different parts of the receptive field then the excitation and inhibition will not cancel out and the cell WILL respond:

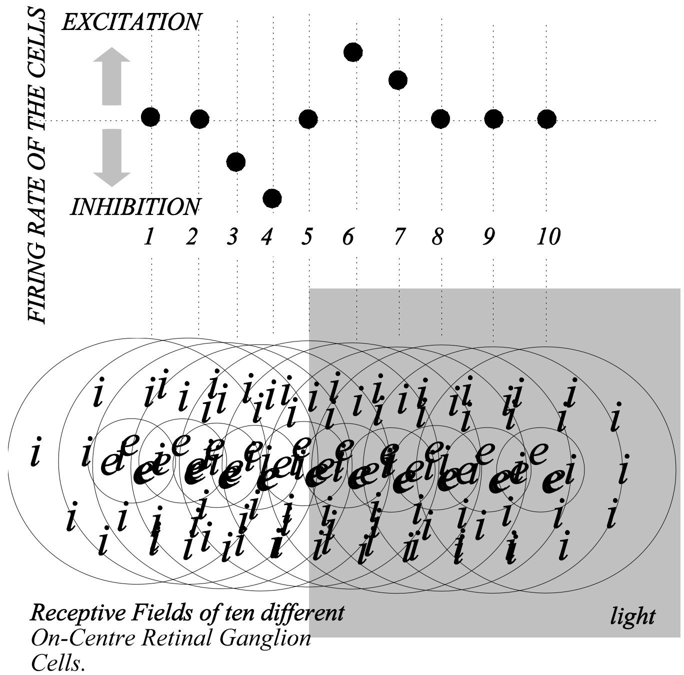


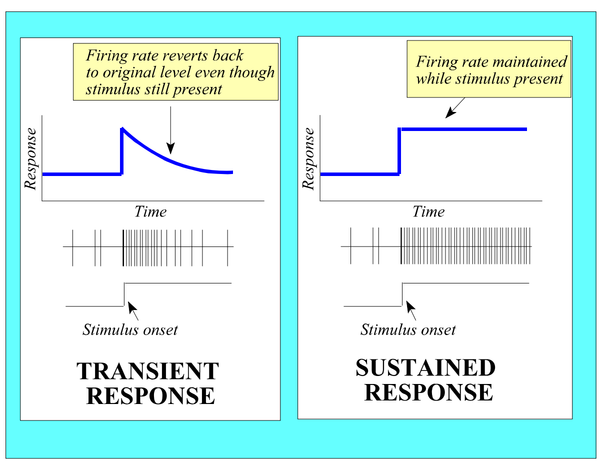
The excitatory region is maximally excited since it is covered with light. The inhibitory region is not maximally inhibited since there is an area where no light is falling. The activity from the two regions will therefore not cancel and there will be an overall EXCITATION.



The excitatory region is not excited at all since there is no light in that region. The inhibitory region is partially inhibited since there is an area where light is falling. The activity from the two regions will not cancel and there will be an overall INHIBITION.

7 **The consequence of the concentric organization of visual** receptive fields in retinal ganglion cells is that any one cell will only be active when a FEATURE of some kind - a change in light level - falls within that cell's receptive field. Here the feature is the edge of a patch of light.

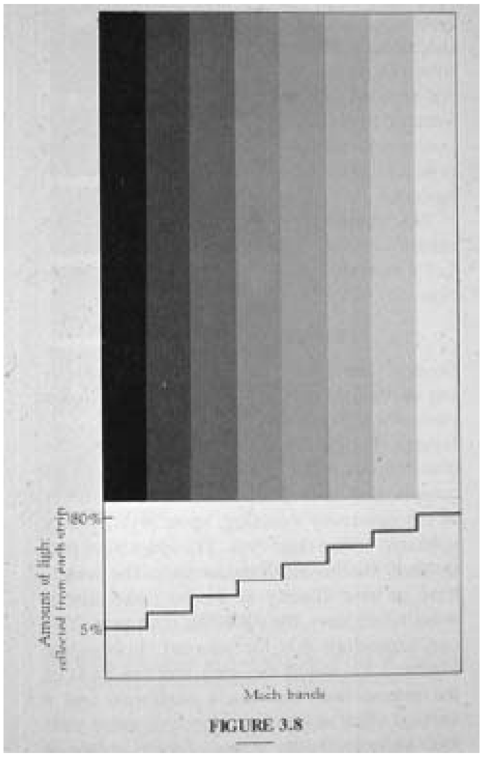




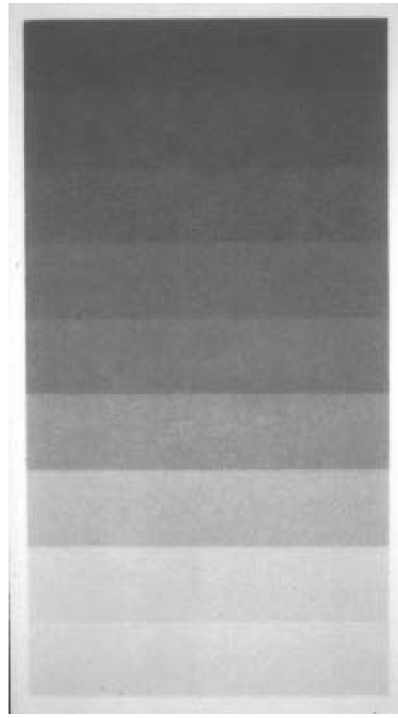
There are two types of on-centre and off-centre retinal ganglion cells. One type has sustained responses and the other type has transient responses. Thus there are four basic types of retinal ganglion cells.

Transient responses are useful for coding things that change with time, for example moving objects.

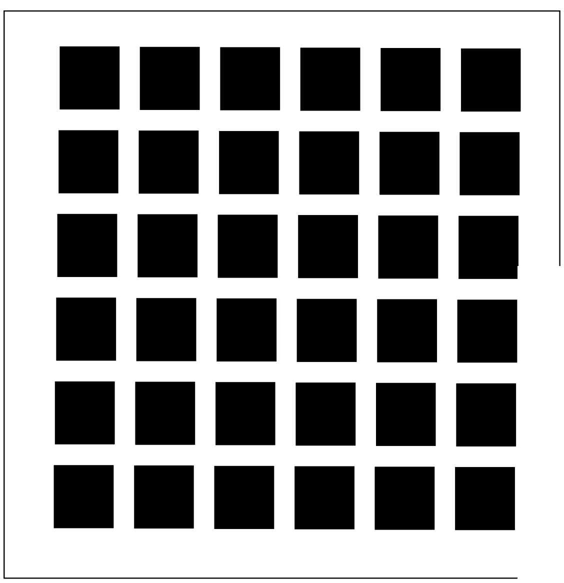
Sustained responses are useful for coding pattern information.



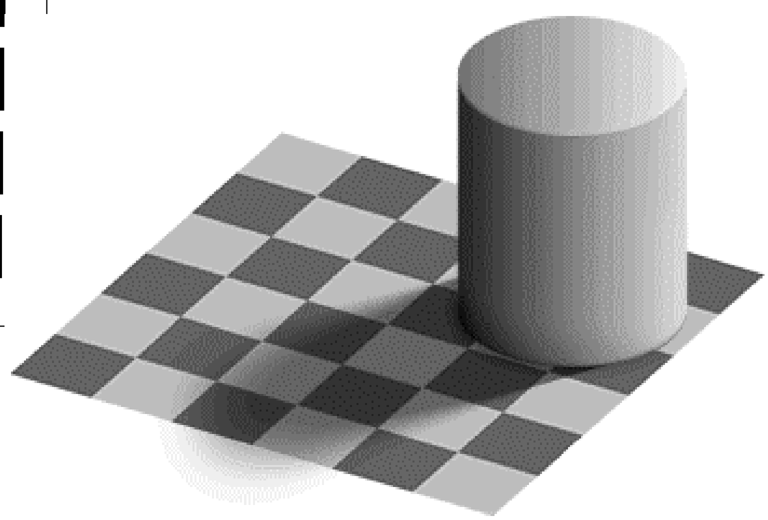
Mach Bands



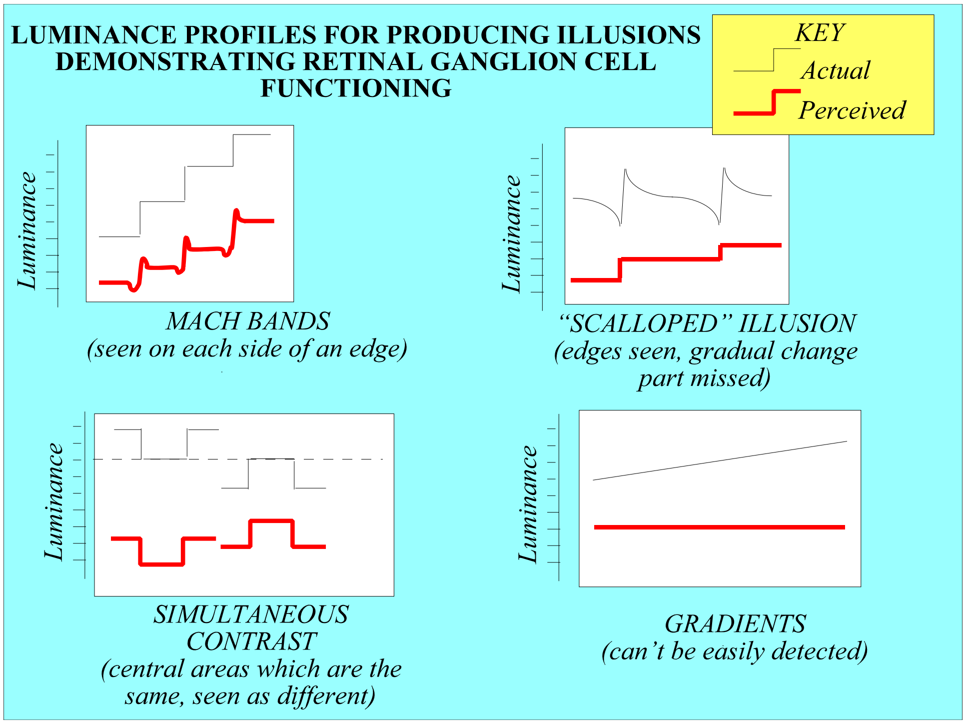
Scalloped Illusion



Hermann Grid

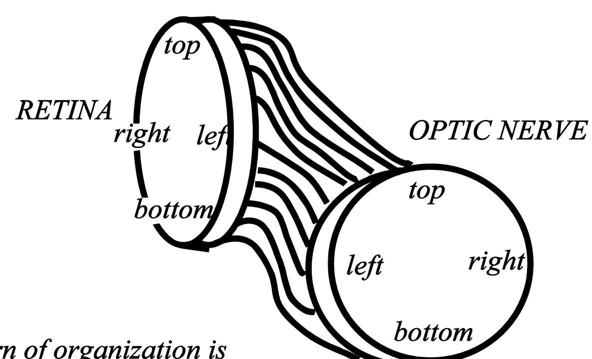


Simultaneous contrast



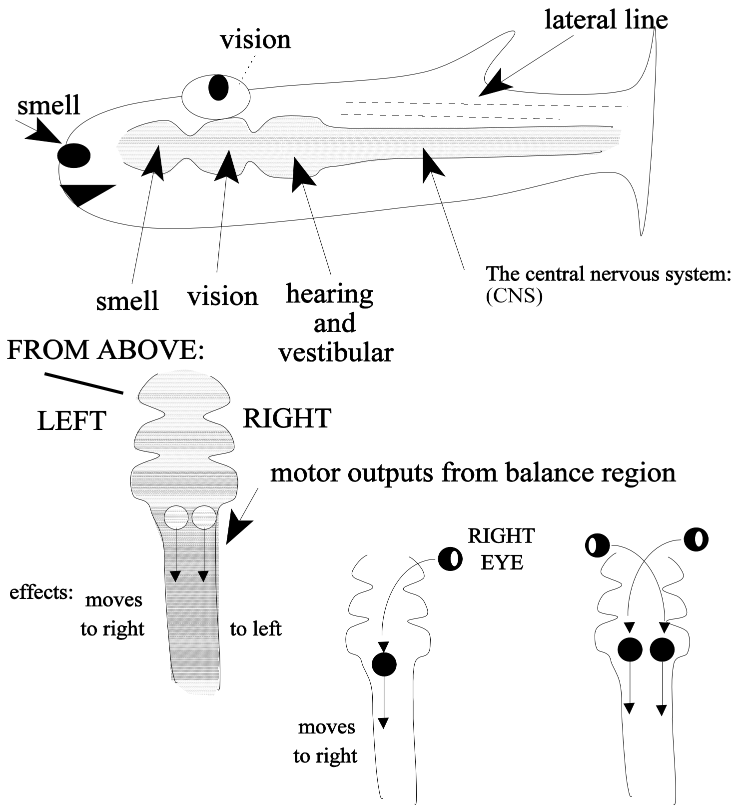
INFORMATION THAT IS CARRIED BY THE OPTIC NERVE:

1. is in the form of action potentials
2. has more detail about the image falling on the fovea that about the periphery
3. has information mainly about CHANGES in light level around the image.
4. is organized so that the optic nerve fibres are in the same order as they are in the retina.

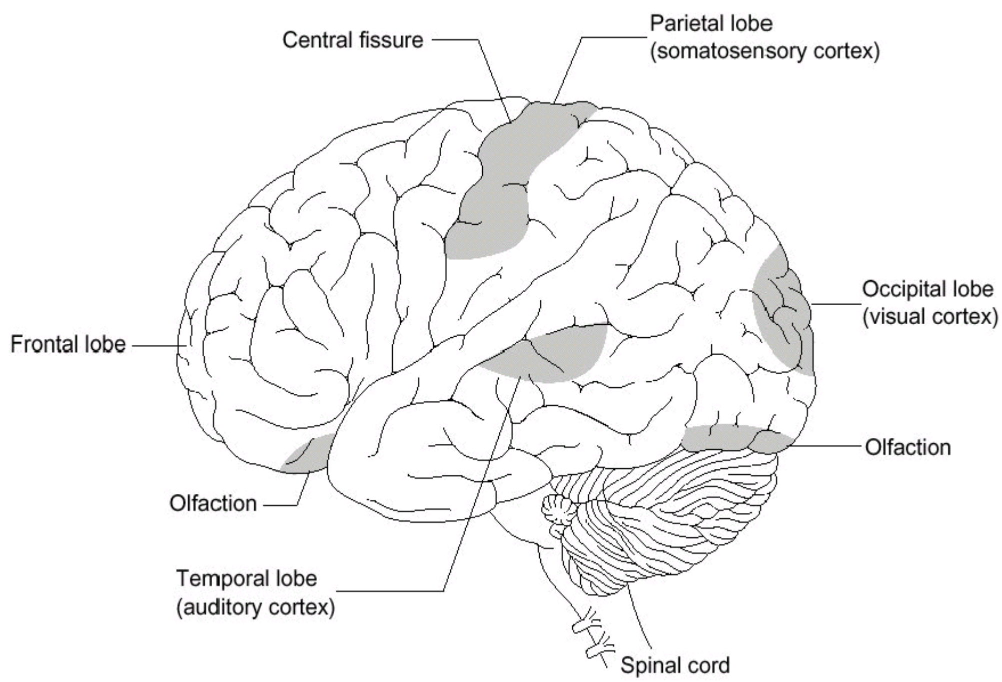


This pattern of organization is called RETINOTOPIC.

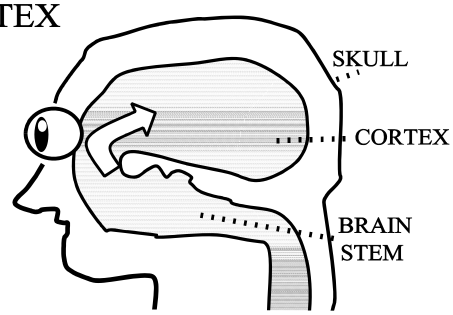
BASIC NEUROANATOMY



The connections from the eyes to the motor control systems on the other side of the body are appropriate for orienting movements.

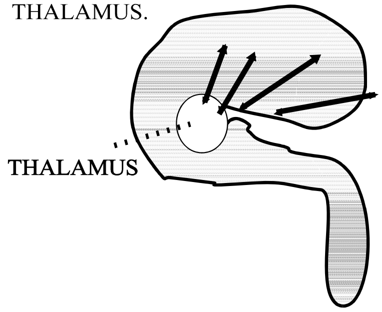


THE CORTEX

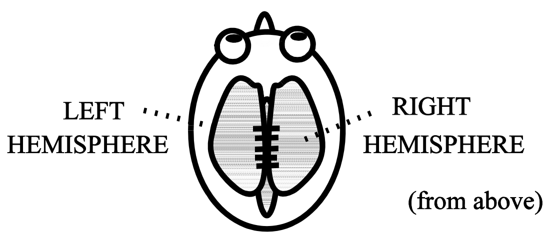


1 **In the course of evolution, the front of the brain has** grown forwards and has come to cover all the rest of the brain. If you look at a brain taken out of the skull, all you can see is the cortex. This new (in terms of evolution) part of the brain is called the CORTEX - in contrast to the more ancient BRAIN STEM.

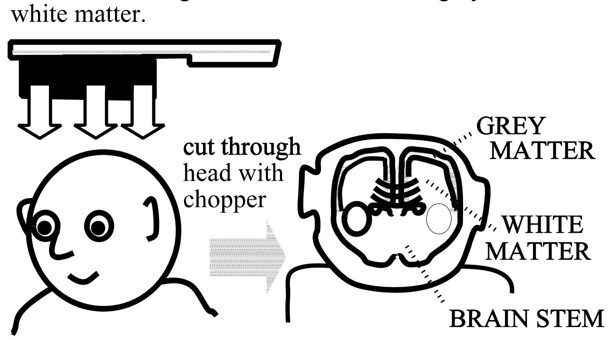
2 **A relay station has developed to channel information** into and out of the cortex: this is called the THALAMUS.



3 **The brain is symmetrical with one hemisphere of cortex** on one side and one on the other.



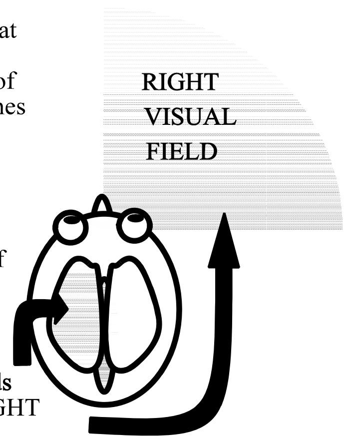
4 **If we slice through the cortex we can see grey and** white matter.



5 **The white matter looks white because it is made up** of nerves. Nerves are insulated by a layer of fatty cells called Schwann cells that wrap around the axons. The grey matter is grey because of the cytoplasm of the cell bodies. Cytoplasm is grey in appearance.

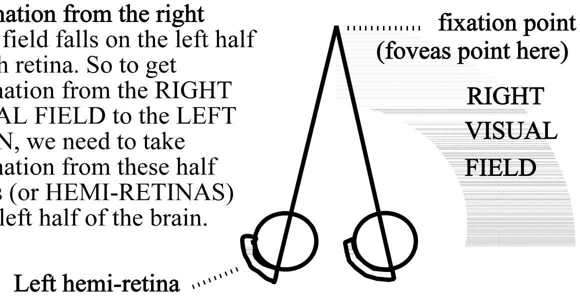
THE OPTIC CHIASM

Since human eyes are at the front, they can see both sides at once. That is, each eye receives information from left, right and straight ahead of the nose. This is different from fishes or other animals with their eyes on the sides of their heads. In order to make proper connections with the motor system, it is important that each half of the brain receives information about the opposite half of the visual field.

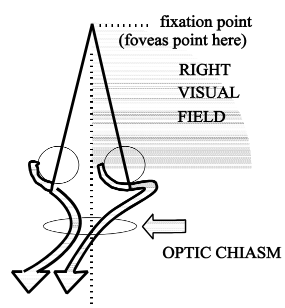


Left half of the brain needs information about the RIGHT half of the visual field.

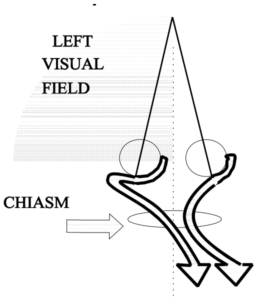
Information from the right visual field falls on the left half of each retina. So to get information from the RIGHT VISUAL FIELD to the LEFT BRAIN, we need to take information from these half retinas (or HEMI-RETINAS) to the left half of the brain.



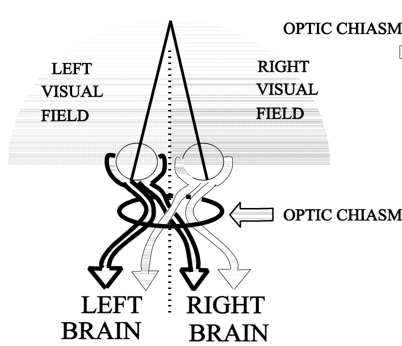
1 **Information from the** right visual field is carried to the left half of the brain. Fibres from the NASAL retina (nearest the nose) cross. Fibres from the TEMPORAL retina (nearest the temples) do not cross.



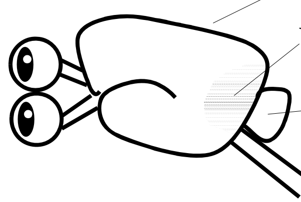
2 **Information from the left** visual field is divided in the same way.



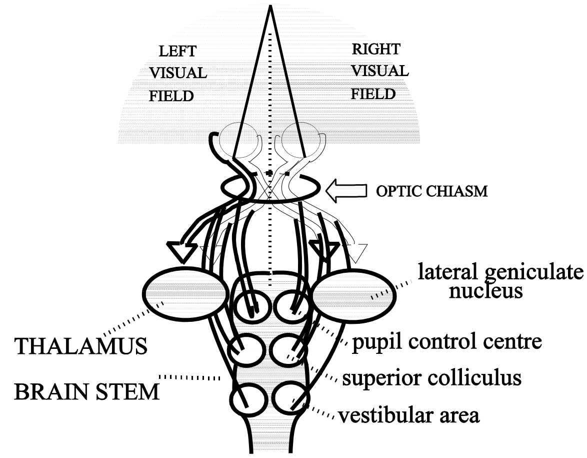
3 **So the arrangement within** the optic chiasm is as follows:



4 The part of the cortex that receives visual information is at the back.



5 Summary of these visual pathways:



DESTINATIONS OF THE VISUAL PATHWAYS

1 Visual information is required for VISUAL REFLEXES as well as PERCEPTION.

2 Three examples of visual reflexes are:

FUNCTION	*PURPOSE*	*SITE IN BRAIN*
i PUPIL CONTROL	regulates the amount of light in the eye	pupil control center in brain stem (Edinger-Westphal Nucleus)
ii FAST EYE MOVEMENT	changes where you are looking from one place to another	superior colliculus (swelling in the middle of brain stem)
iii SLOW EYE MOVEMENT	keeps the image stable during head movements and walking	vestibular area (swelling at back of brain stem)

3 Perceptual pathway goes to the visual cortex via the thalamus (relay). The part of the thalamus that relays visual information to the visual part of the cortex is called the LATERAL GENICULATE NUCLEUS.

LATERAL GENICULATE NUCLEUS

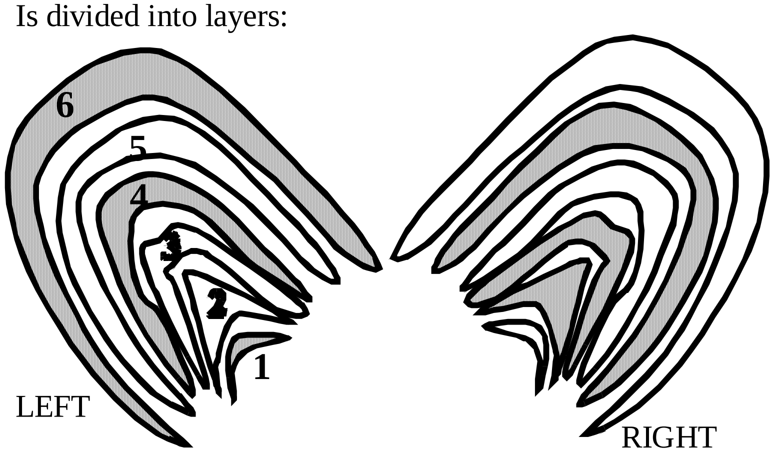
1 Acts as a relay to the cortex

2 Keeps information from the two eyes separate

3 Has visual receptive fields that look just like the retina

4 Is retinotopically arranged

5 Is divided into layers:



gets input from RIGHT eye

gets input from LEFT eye

1,2 *Magnocellular layers*
(Magno = big)
From TRANSIENT cells

3-6 *Parvocellular layers*
(Parvo = small)
From SUSTAINED cells

CELLS IN THE VISUAL CORTEX:

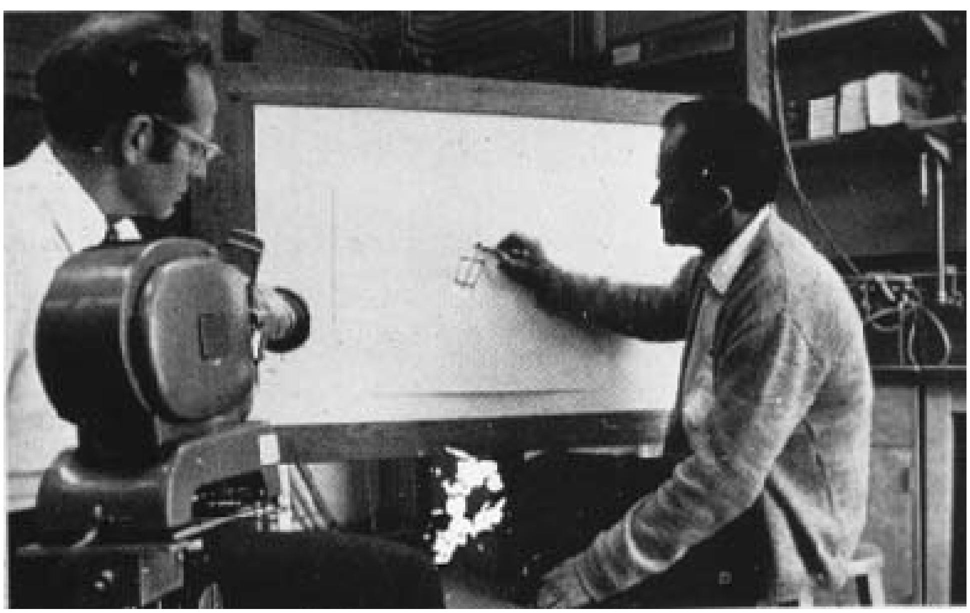
1 Have response properties different from retinal ganglion cells

2 Have been investigated by Nobel Prize Winners David Hubel and Torsten Wiesel.

3 Can be divided into
   i SIMPLE CELLS
   ii COMPLEX CELLS
   iii HYPERCOMPLEX CELLS

4 Are binocular (they get information from BOTH eyes).

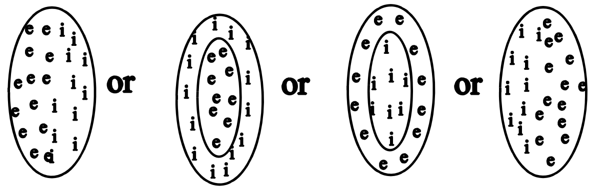
5 Have receptive fields that are arranged *retinotopically* over the surface of the cortex. That is, there is a *map* over the surface of the cortex which preserves the arrangement of the retina. If you could see the activity in the primary visual cortex like a television screen, you would see a recognizable image (all the parts would be in the right order - not jumbled up) although it would be *very* distorted.



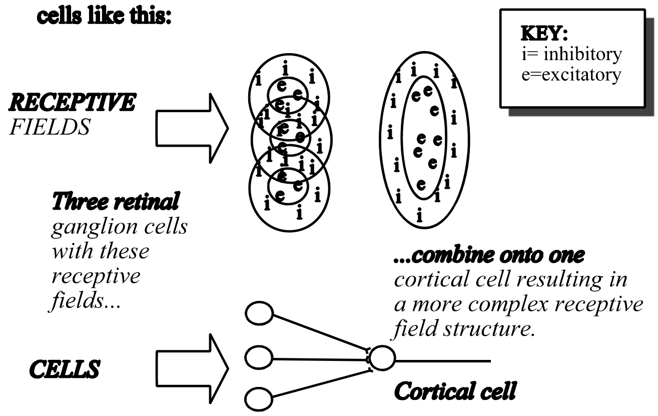
CELL TYPES IN THE PRIMARY CORTEX:

SIMPLE CELLS...

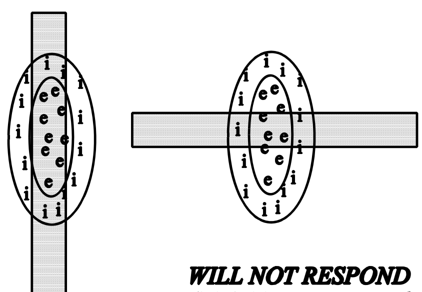
1 ... have receptive fields like this.



2 These fields could be made up from retinal cells like this:



3 These cells will respond best to stimuli of a particular ORIENTATION.



WILL RESPOND

WILL NOT RESPOND
('e' & 'i' regions stimulated).

4 They are therefore selective to particular features (here a vertical line).

5 The cells are binocular and respond best to a stimulus that comes through both eyes at once.

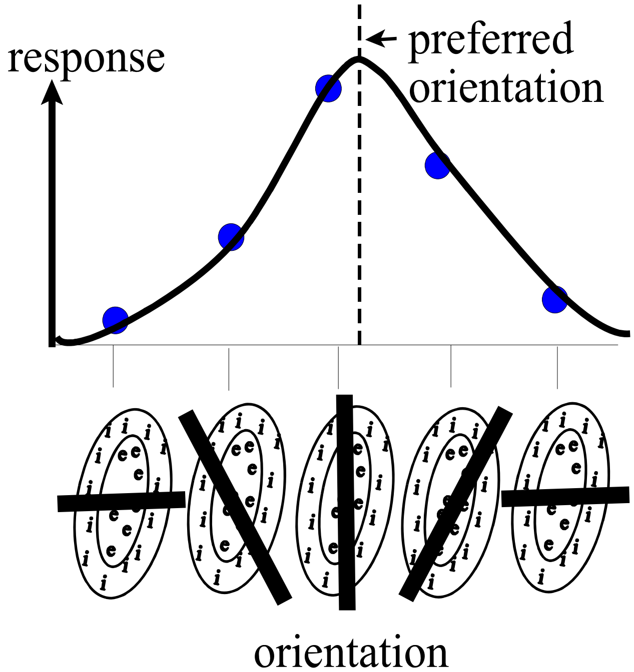
6 The cells are tuned to particular disparities.

TRANSLATION:
"respond best to"

"where the same image falls on different parts of the two retinas"

TUNING CURVE

A simple cell's response varies systematically with orientation. One orientation evokes the biggest response from that cell. The cell is said to be tuned to that orientation.

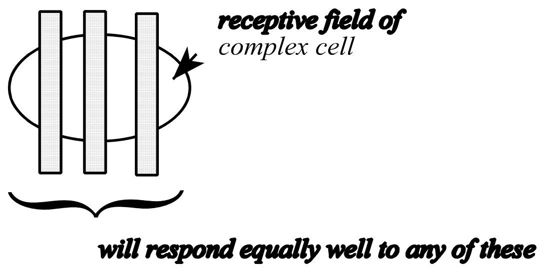


COMPLEX CELLS:

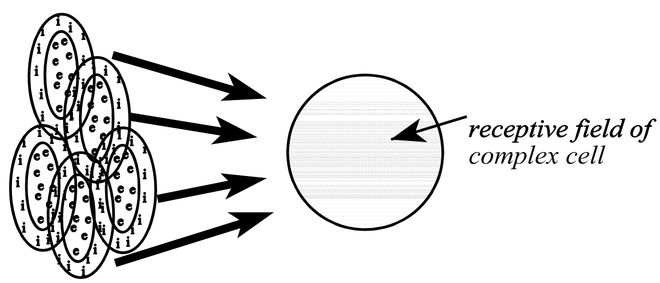
1 have receptive fields that cannot easily be divided up into excitatory and inhibitory areas.

2 are orientation tuned (*translation: respond best to a stimulus of a particular orientation).*

3 respond equally well to a bar put anywhere in their field.

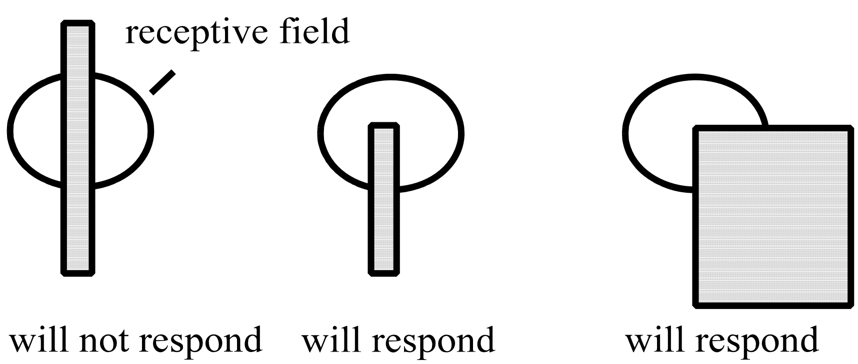


4 could be viewed as being built up from several simple cells.



HYPERCOMPLEX CELLS:
(also known as: end-stopped complex cells)

1 are similar to complex cells but respond best to a STOPPED edge that falls in their receptive field.



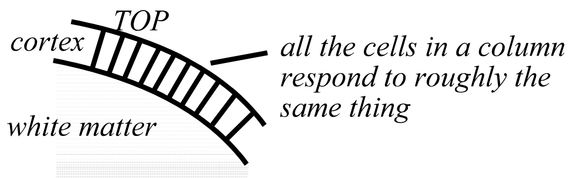
2 Hypercomplex cells have suitable properties to detect such features as CORNERS in an image.

COLUMNS AND HYPERCOLUMNS IN THE CORTEX

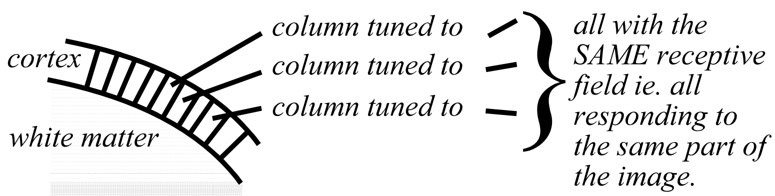
1 Each part of the visual cortex receives information about one part of the image.

2 There is an orderly, retinotopically-arranged map of the image over the surface of the cortex.

3 At each point, cells tuned to a particular orientation form a column.

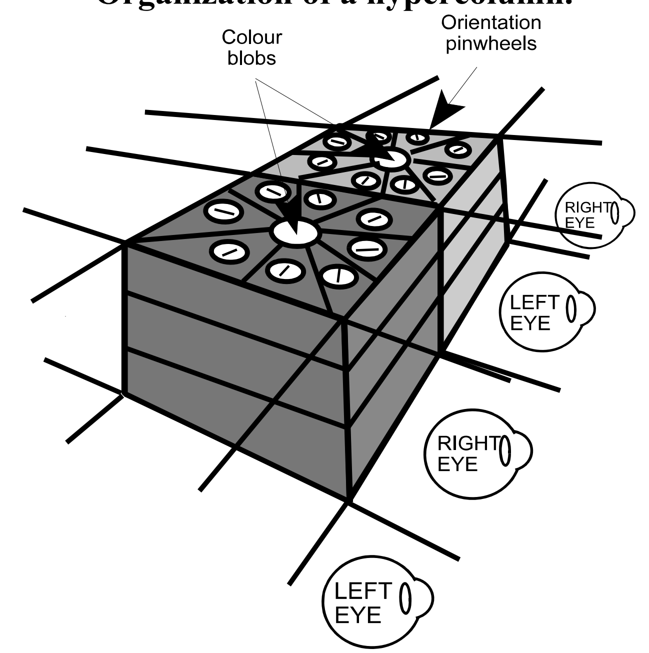


4 ALL orientations need to be represented for each part of the image. This is achieved by having clusters of these columns, all responding to the SAME part of the image, but responding to DIFFERENT orientations.

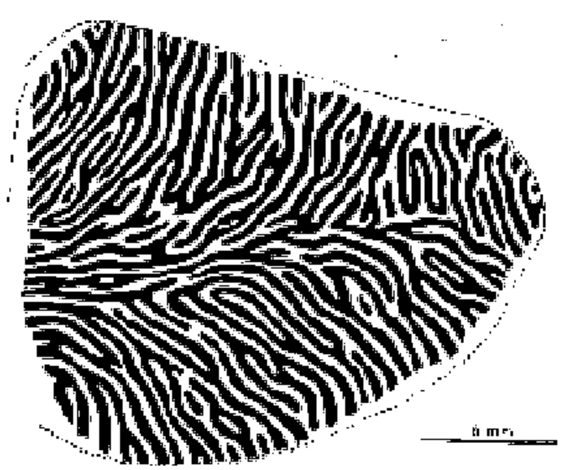


5 A cluster of columns responding to different features in the same part of the image is called a hypercolumn.

Organization of a hypercolumn.



Ocular Dominance Bands



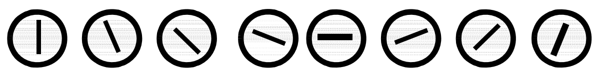
HOW TO REVEAL YOUR OWN ORIENTATION DETECTORS

THE TECHNIQUE OF ADAPTATION

1 For the next stage in the processing system to decide which orientation was present in the receptive field of a particular hypercolumn, the outputs of each column must be compared.

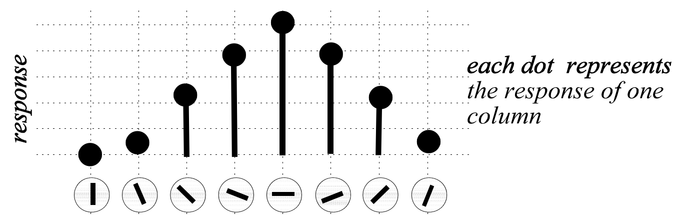
2 i If a particular orientation is present, then detectors tuned to that orientation will be stimulated more.

ii Here is an imaginary hypercolumn with eight member columns.



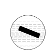
iii They are all "looking at" the same area of the retina, ie the same area of space.

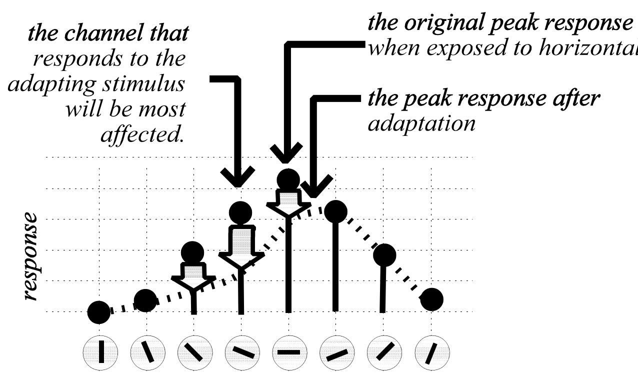
iv Here is their response to a horizontal bar:



v A comparison is required to determine which is the most active channel and hence what the stimulus was.

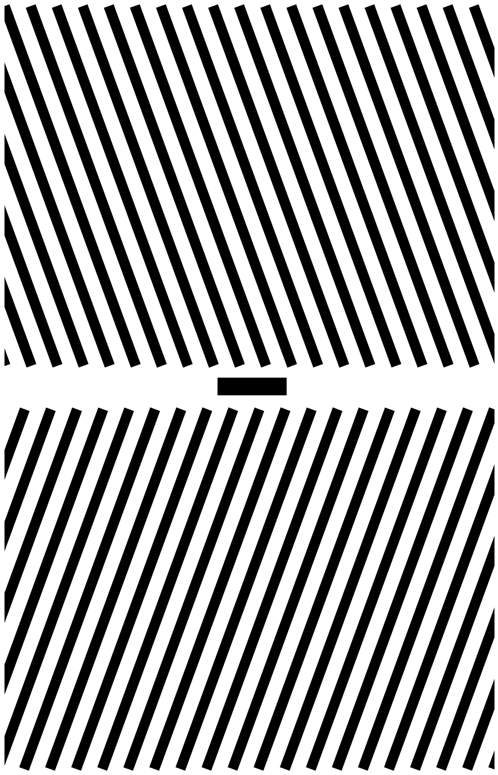
3 If you look at a stimulus of a particular orientation for a while, those detectors most activated by this *adapting stimulus* will *adapt*. That is they will "get tired" and subsequently give a smaller response, even to the *same* stimulus. The amount by which they tire depends how active they were.

4 The response to our horizontal stimulus, after adapting to this stimulus  will be distorted like this:

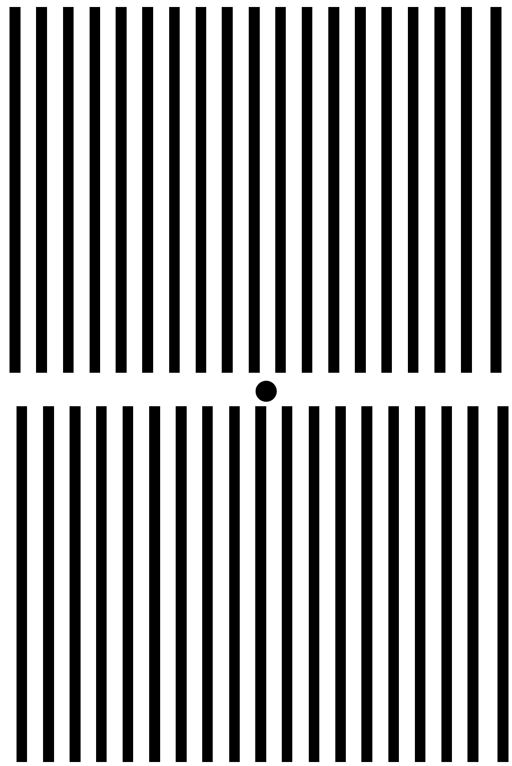


5 If you tell what you have seen by looking for the peak and the peak has been shifted by adaptation, then your perception should be altered after adaptation. Such a shift is proof that your brains contain orientation-tuned channels.

TILT AFTER EFFECT



adapting stimulus



test stimulus

INSTRUCTIONS

1. *Check out the* test stimulus *and make sure that the two halves are the same and vertical. See what it looks like when you fixate the dot in the middle.*
2. *wander your eyes back and forth along the little horizontal bar in the middle of the* adapting stimulus *for about a minute.*
3. *fixate the little dot in the centre of the* test stimulus *again.*

VISUALISING COLUMNS

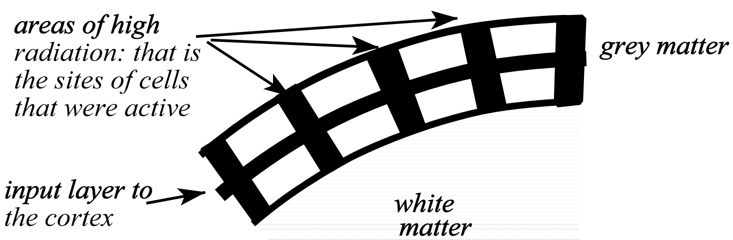
1 In the same way as active cells will adapt, they also use more energy. This energy is obtained from sugars, especially glucose, therefore active cells will use more glucose.

2 If we use *radioactive* glucose and alter it so that it does not leave cells easily (deoxyglucose), then we can selectively label those cells that are active at any time.

3 Injections of radioactive deoxyglucose while an animal is viewing, for example, horizontal stripes, will cause those cells that are activated by that stimulus to become more radioactive because they will take up more sugar.

4 The radioactivity can then be visualised by lying very thin slices of tissue on a photographic plate sensitive to radiation. This is called an *autoradiogram* because it takes a picture of itself with its own energy (the radioactivity).

5 This is what you see:



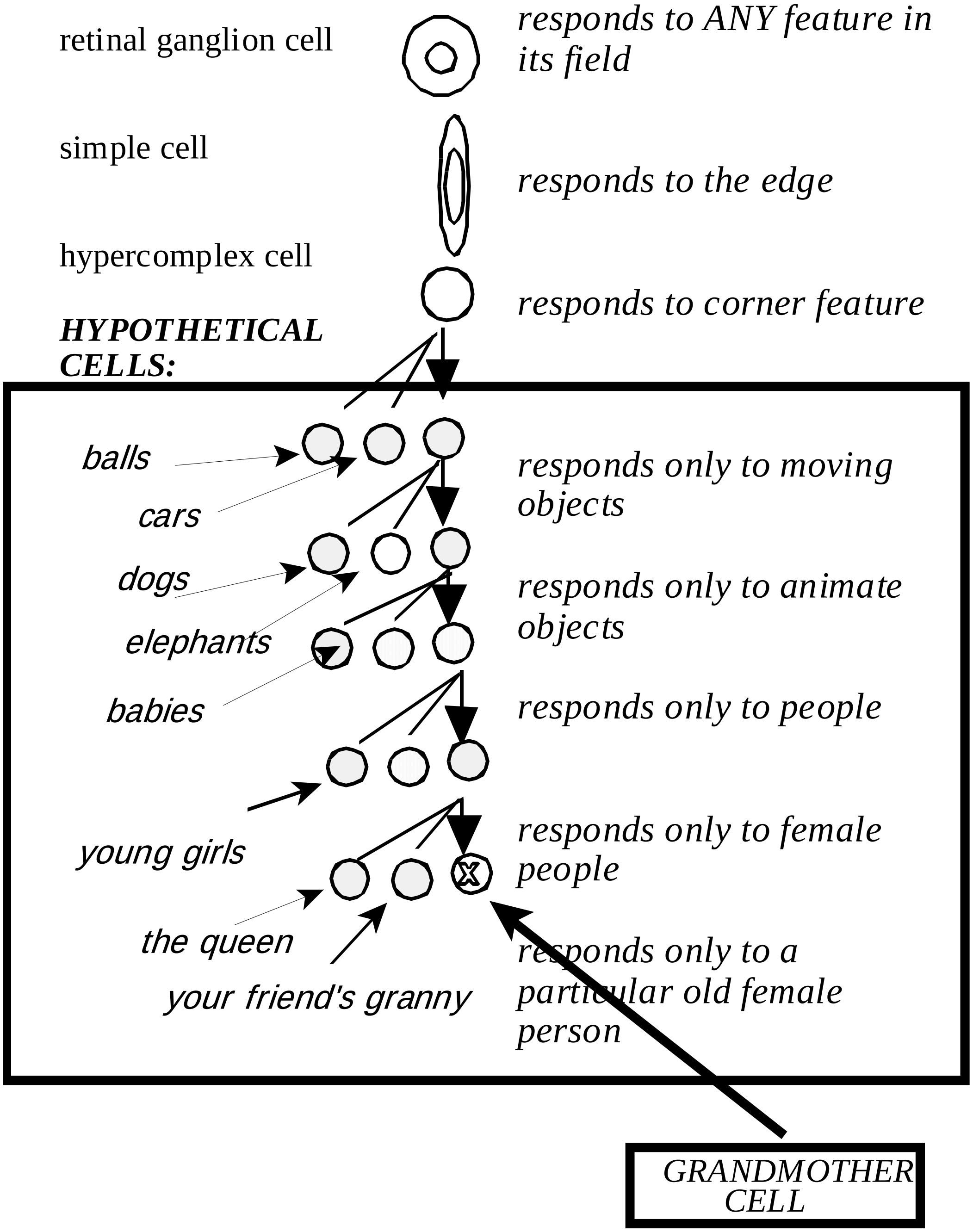
WHAT HAPPENS BEYOND THE HYPERCOMPLEX CELLS?

If cell's properties are built up from simpler cells, then we could expect them to get increasingly complex in their requirements: increasingly fussy about what they will respond to. Thus the retinal ganglion cells respond to any change of luminance within their receptive field. Simple cortical cells require that the image contains an oriented edge, hypercomplex cells need a particular feature (a corner) to fall in their receptive field. Taking this to its LOGICAL conclusion leads us to predict that some cells might respond only to very complex stimuli indeed - perhaps even a level of complexity corresponding to an individual object. Such cells could form the basis of visual recognition: their firing indicating the presence of the object to which they are tuned. This hypothesis has been called the GRANDMOTHER CELL hypothesis since it would predict hierarchies of cells feeding ultimate object detectors. Thus there would be a hierarchy of cells responding to features that indicated the presence of a grandmother (for example). When they ALL (or some fraction of them) were active, they would activate the cell at the top of the hierarchy whose firing would indicate "grandmother detected". All that would be needed for this perception would be the firing of the cell: it is not "looked at" by any higher system.

There are some reports that some cells in the inferotemporal path through the monkey cortex might respond only to such complex objects (eg. a monkey's hand).

There are also some clinical conditions involving damage to the inferotemporal region in which only high-level recognition is lost (eg. PROSOPAGNOSIA: the inability to recognize faces).

THE GRANDMOTHER CELL HYPOTHESIS



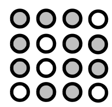
PROBLEMS WITH THE GRANDMOTHER CELL HYPOTHESIS

1 Is it possible to equate a perception with a cell's activity?

2 We know a lot more about any object than just that it is there. For example, we can notice that a car is red as well as recognizing it as a friend's car. Information about such extra features must be carried by the activity of more than one cell!

3 Although there are a LOT of cells in the brain, there are just not enough cells to code every object you have ever or will ever be able to recognize.

4 A modification of the grandmother cell hypothesis that addresses points 2 & 3, is to hypothesize the coding of an object not by the activity of a single cell but by a GROUP of cells: that is a unique pattern of activity across several cells:

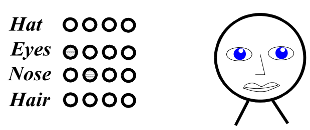


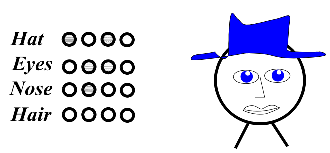
A group of sixteen cells, for example, could code 2^{16} (65,536) patterns even if each cell could only be OFF or ON.

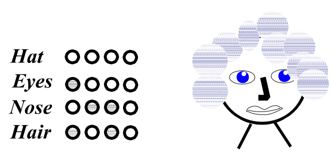
5 If the activity of each cell , or perhaps a subgroup of cells, represented an ATTRIBUTE (eg, wearing glasses, wearing a hat, nose length, age, etc....), then perception could be coded in a PARALLEL DISTRIBUTED NETWORK.

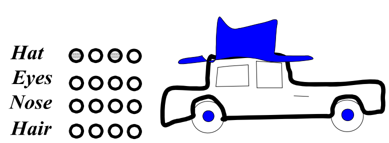
PARALLEL: because each subgroup is working in at the same time, independent of the other subgroups

DISTRIBUTED: because no one subgroup has all he information needed to identify the object.









6 The activity of each of these sets of cells is unique. It allows you distinguish the objects just by looking at the cell activity.

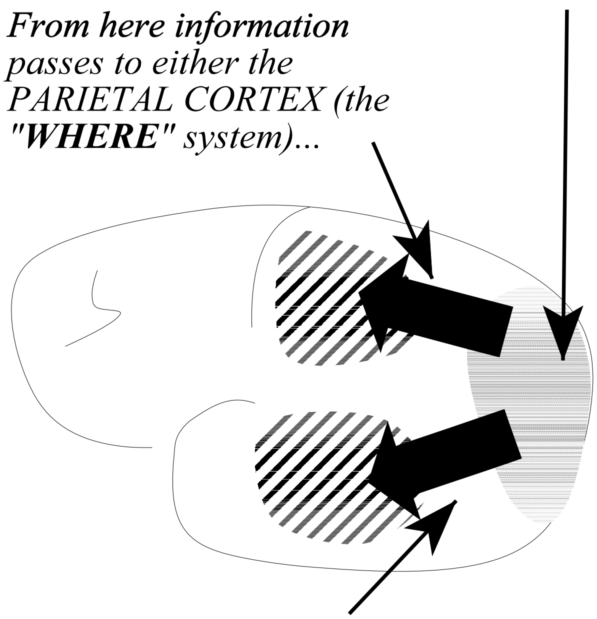
7 So this sort of mechanism COULD underlie the coding of objects in the brain.

8 But usually lots of objects are perceived at once. How do you know which GROUPS of cells should go together? This is called the BINDING PROBLEM.

TWO STREAMS OF VISUAL PROCESSING WITHIN THE CORTEX OF THE BRAIN:

This is the primary visual cortex.

***From here information** passes to either the PARIETAL CORTEX (the "**WHERE**" system)...*



*... or to the INFEROTEMPORAL CORTEX (the "**WHAT**" system).*

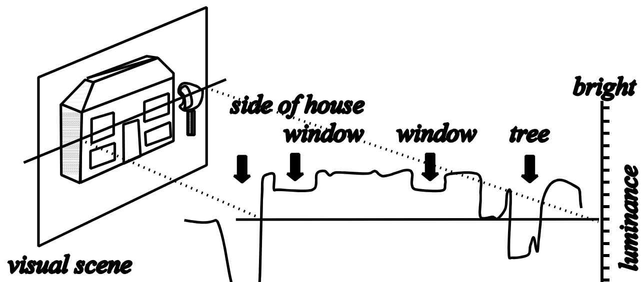
KEY:

INFEROTEMPORAL: "below the temples"
PARIETAL: "on the wall"

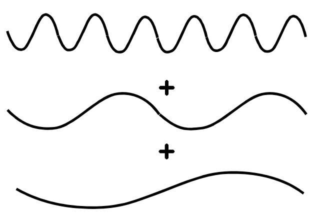
SPATIAL VISION AND PATTERN PERCEPTION

1 Any complex visual pattern can be mathematically broken down into its components.

2 If we measure the luminance of a scene along a cross section we get a complicated looking squiggly line.



3 **Fourier's theorem:** All such complicated lines, can mathematically be expressed as the sum of a set of simple sine waves.



***this is just to give you an** idea - to reproduce a particular pattern needs lots of carefully chosen sine waves.*

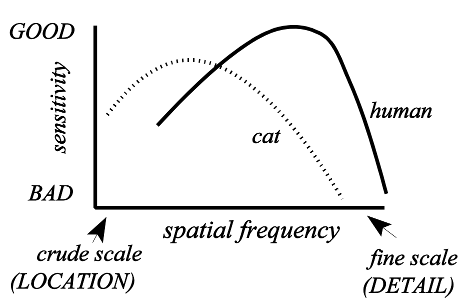
4 The component sinewaves have differing numbers of cycles across the visual field. They are said to be of different SPATIAL FREQUENCIES.

5 Components with low spatial frequencies have few cycles across the scene. They correspond to a crude scale, coding just areas of light and dark.

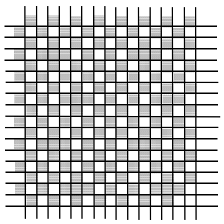
6 Components with high spatial frequencies have many cycles closely packed across the scene. They correspond to the detailed information in the scene.

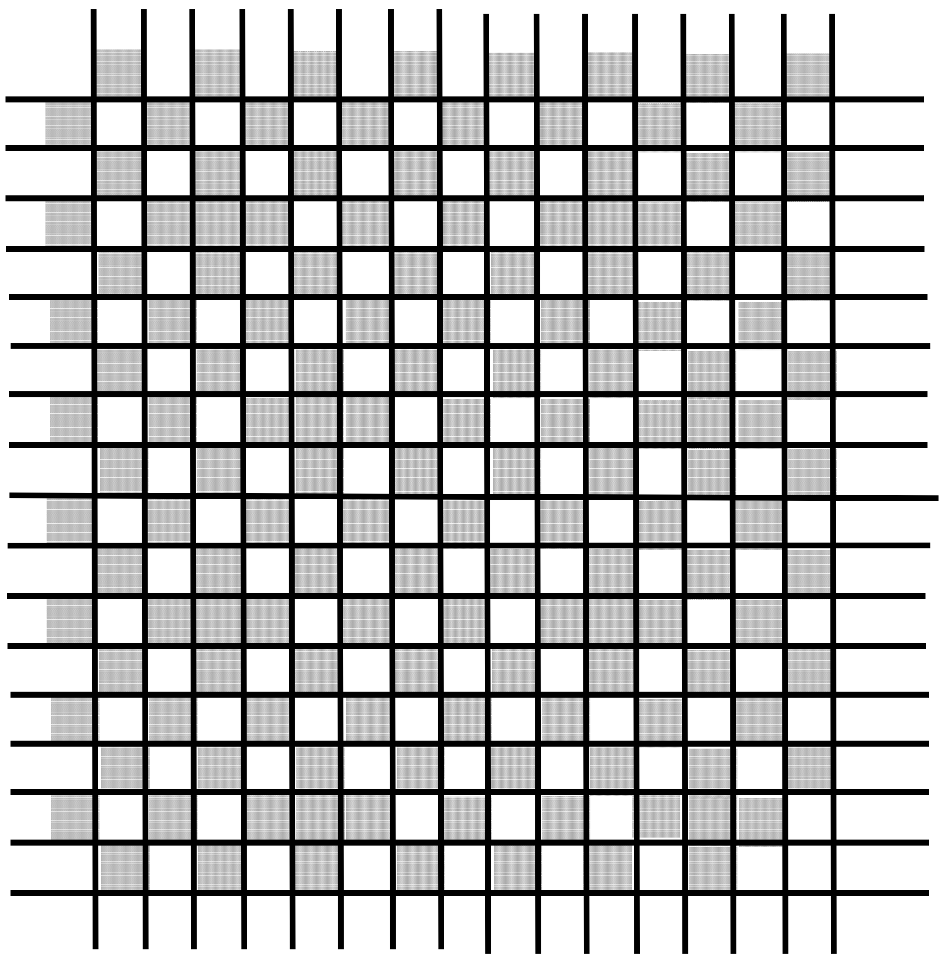
7 Many visual cells, by virtue of having receptive fields of a particular size and orientation, can extract these components from the image. They can decompose the image into its constituent parts.

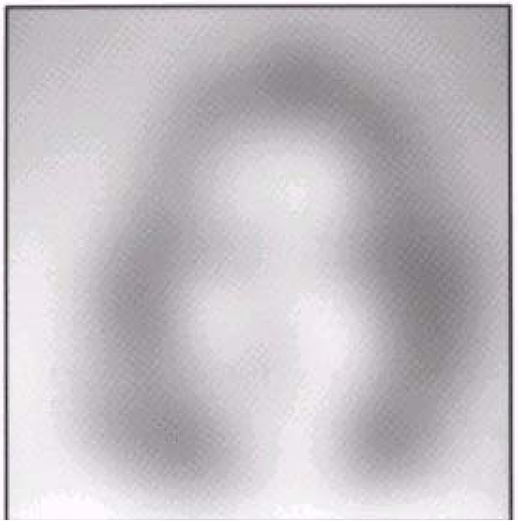
8 The sensitivity to each of these components can be measured separately to produce a CONTRAST SENSITIVITY FUNCTION that describes the performance of the visual system over a variety of scales.



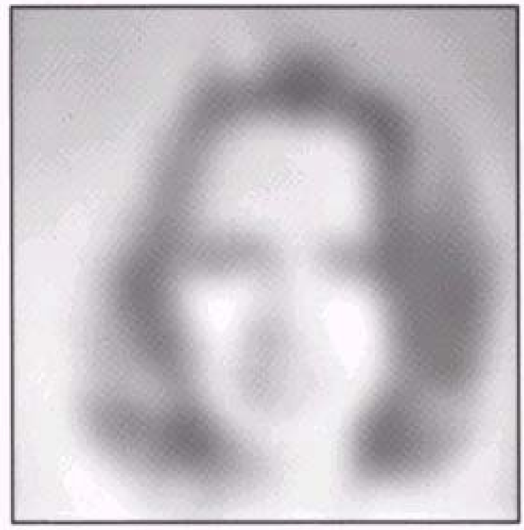
9 The different channels, corresponding to the representation of different spatial scales, interfere with each other. In this grid the crude-scale information (where are the areas with more dark?) is interfered with by the fine detail of the grid. Squinting up your eyes while looking at the picture blurs the fine detail out and makes the cruder information easier to see.



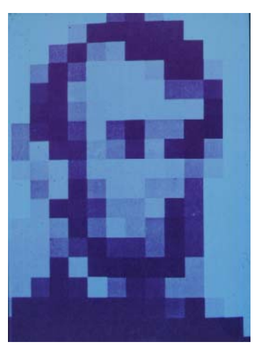


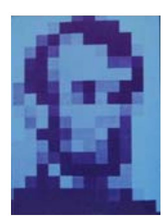


Just low frequencies



all frequencies

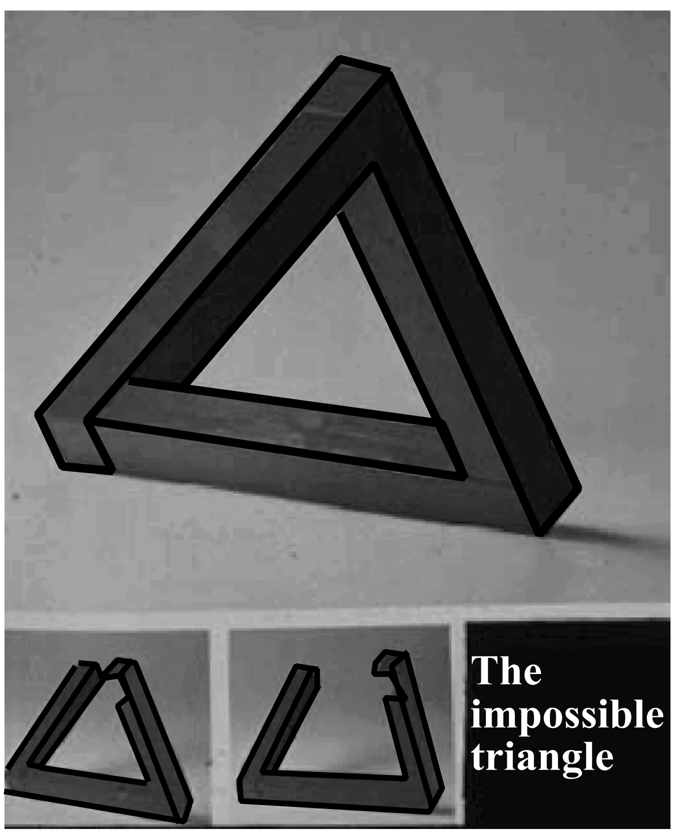




CLUES ABOUT DEPTH

Depth refers to the distance from the viewer of an object in the visual field. There are many cues to distance, but are they used? Here is a list of candidates:

STEREOPSIS	the two eye's views of the world are different
PARALLAX	close things move faster than distance things when you move your head
PERSPECTIVE	parallel lines converge
SIZE	things get smaller when they are further away
OVERLAY	things in front of other things are closer than the things they occlude
TEXTURE GRADIENT	you can see more detail on closer surfaces
ACCOMMODATION	if you know how fat your lens is then at lens means you are focused on a close object and a thin lens means a more distant object



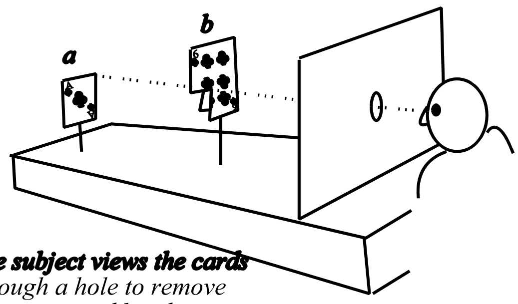
The impossible triangle

This demonstration shows that overlay is more important than perspective.

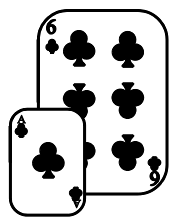
THE PLAYING CARD ILLUSION

This optical illusion demonstrates the relative role of some distance cues (size and overlay).

When a distant playing card (a) is carefully lined up with a gap in a closer card (b), it looks as though the distant card (a) is overlaying the nearer one. This illusion opposes the overlay cue with other cues to distance such as size.

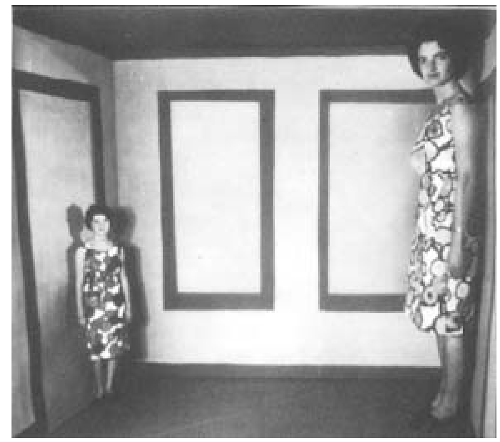


The subject views the cards *through a hole to remove stereopsis and head movements.*



This is what the subject sees: *it looks like a little Ace in front of a big six, even though the playing cards are from the same deck.*

This demonstration shows that overlay is more important than knowledge about the size of objects.

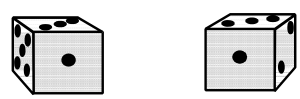


The Ames Room Illusion

Perspective makes you see two people are different sizes. This demonstration shows that perspective is more important than knowledge about size of objects.

STEREOPSIS

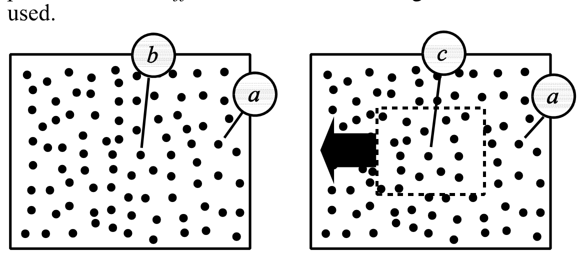
1 A single 3D object presents different views to the two eyes:



left eye's view *of a cube* ***right eye's view of*** *the same cube*

2 The two images, given the distance between your two eyes, contain all the information you need to describe the object in three dimensions.

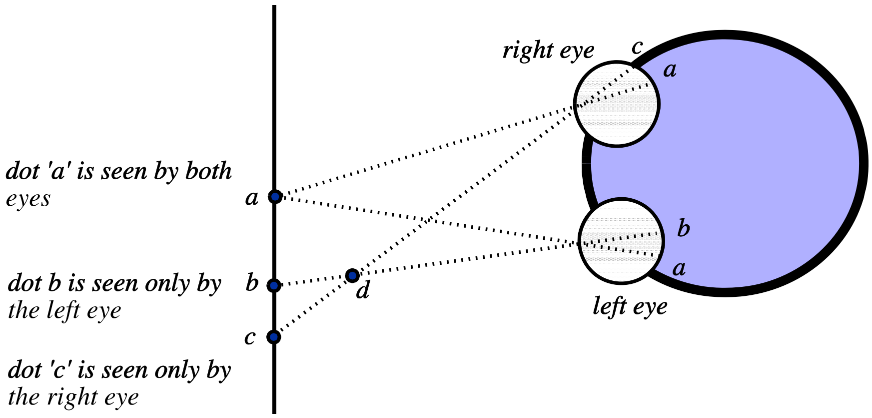
3 By presenting a separate image to each eye, Bella Julesz proved that this *difference* between the images could be used.



left eye's image

the right eye's image is exactly *the same except that a central block has been shifted a little to the left.*

4 When you look at this *stereogram* in a *stereoscope* you see a square at a different distance from the background.

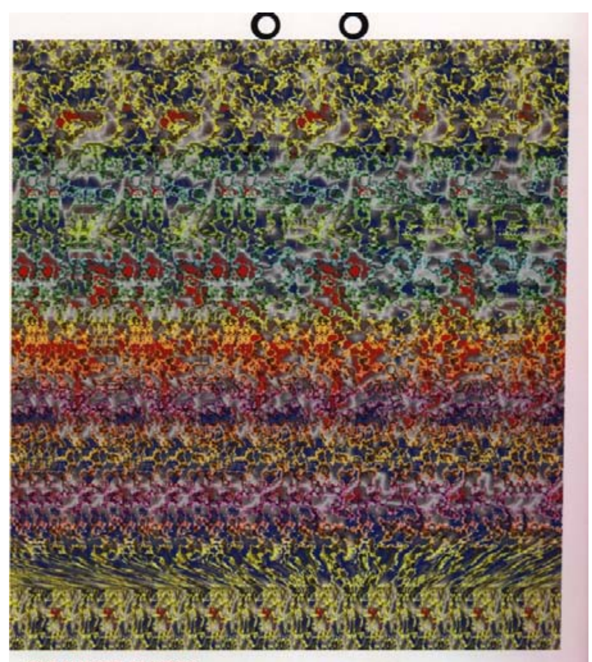


5 i The distances between a and b in the left eye and a and c in the right eye are not the same. The difference is called a *disparity*.

ii The only spot in the real world that could have produced image b in the left eye and image c in the right eye, is at point d.

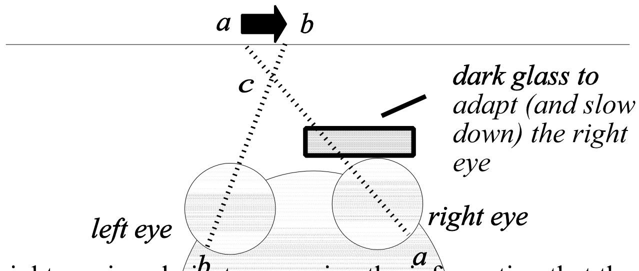
iii The brain can calculate this point d from the disparity and this is what is seen: a single dot floating in front of point a at point d.

6 By shifting the image in the right eye to the *right* (instead of to the left as in the example above) the effect is reversed and the dot is seen as further away than a.


THE AUTHOR AT WORK
With his faithful Macintosh, and a cup of tea.

7 **AUTOSTEREOGRAM** Stereograms are created by putting one pattern into one eye and another into the other eye. The brain is able to detect common features and disparities between these two images and create a sense of depth. The images can be separated by lenses (as in a conventional stereoscope), by colour (wearing glasses that only allow, say, the red image to one eye and the green image to the other eye), by polarization or by pointing your eyes in different directions. The autostereogram works by using this last trick. Dots (or other features) are arranged so that when those from one area of a picture are FUSED with dots from another area OF THE SAME PICTURE -- hence the name AUTO (or self) stereogram, the disparities between the two regions create a sensation of depth as described above.

8 Another way of shifting the images to the two eyes was discovered by Pulfrich. When the eye is dark adapted it takes longer to process information than when it is light adapted. So if one eye is dark adapted and the other is not, that eye will still be processing a moving object after the other eye has finished the job.

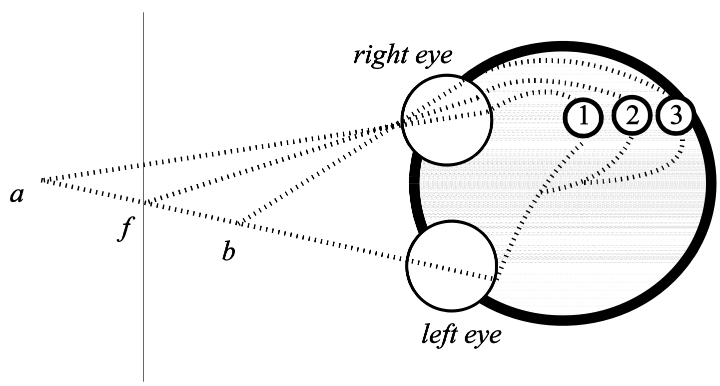


The right eye is only just processing the information that the dot is at point a even though it has already reached point b. The left eye sees the object as being at point b. The only point that could give these two images at the same time would have been at point c.

As for the random dot stereogram, this is what is seen, a single dot closer to the viewer than it really is.

If the dot moves from right to left (away from the dark adapted eye), the geometry is reversed and the dot is seen as further away than it really is.

9 i The visual cortex has cells that can pick up differences in the images of the two eyes. These cells are sensitive to *disparity*. This can be achieved by the wiring arrangement.



ii In the diagram, the eyes are looking at point f: the fixation point. Point a is further away, point b is closer. All the points in this example fall on the same part of the left eye's retina.

iii Because of their different distances, points a and b fall on different points in the right eye.

iv Cells in the visual cortex will respond best if the inputs to them from both eyes are active at the same time.

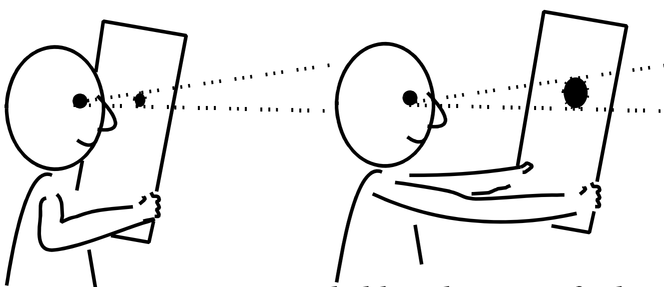
v Cell 1 will thus respond most to a point at a.
Cell 2 will respond best to a point at f.
Cell 3 will respond best to a point at b.
These cells can carry information about depth (distance from the observer).

SIZE CONSTANCY

Things in the real world are seen as staying the same size even though they change their *retinal* size all the time. This is called size constancy and shows that distance from the observer is taken into account when interpreting the retinal image.

If an object keeps the *same* retinal size as it changes its distance from you, then it must be changing its physical size at the same time. This doesn't usually happen in the real world, but can be made to happen in the laboratory by looking at an after image.

An *after image* is obtained by viewing a brief flash. This bleaches the part of the retina on which the image falls and the photoreceptors continue signalling the presence of the image for several seconds after the flash. Of course its retinal size doesn't change. If an after-image is superimposed on a screen at different distances, it seems to change its size.



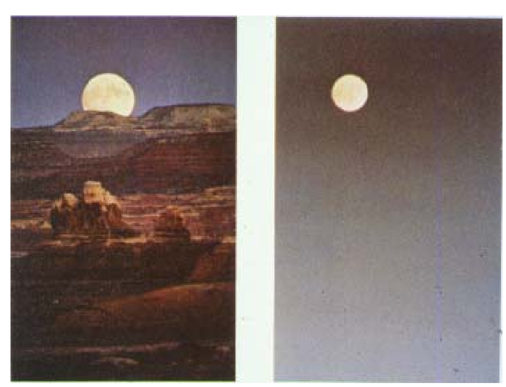
holding the screen closer *makes the after image look smaller*

holding the screen further *away makes the after image look bigger*

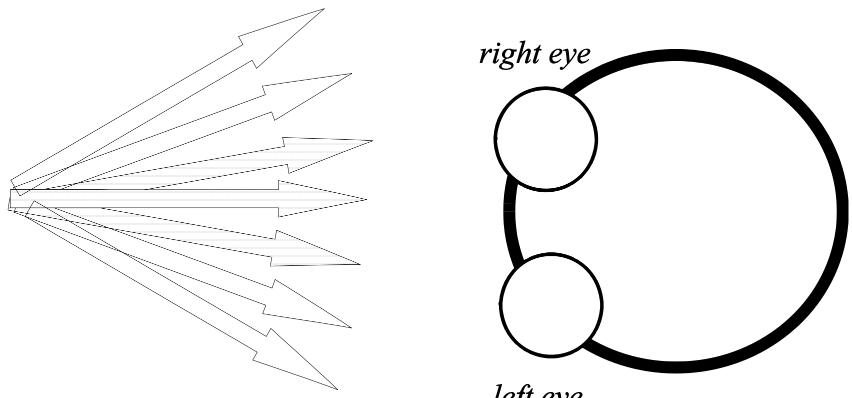
Of course the retinal image stays the same size all the time. This illusion demonstrates that perceived size is CALCULATED or DEDUCED from other information including retinal image size and perceived distance.

Moon Illusion 1: The size-of-the-moon

The moon (which has the same retinal image size wherever it is) appears to be smaller when it is straight above and larger when it is near the horizon. *(Note that in neither position does it appear the correct size: 3,500km across!)* This moon illusion can be explained if you regard the moon as CLOSER (nearer to you) when it is straight above you. Size must be deduced from retinal image and perceived distance. Retinal image size is the same in both cases and therefore presumed distance must be varying.



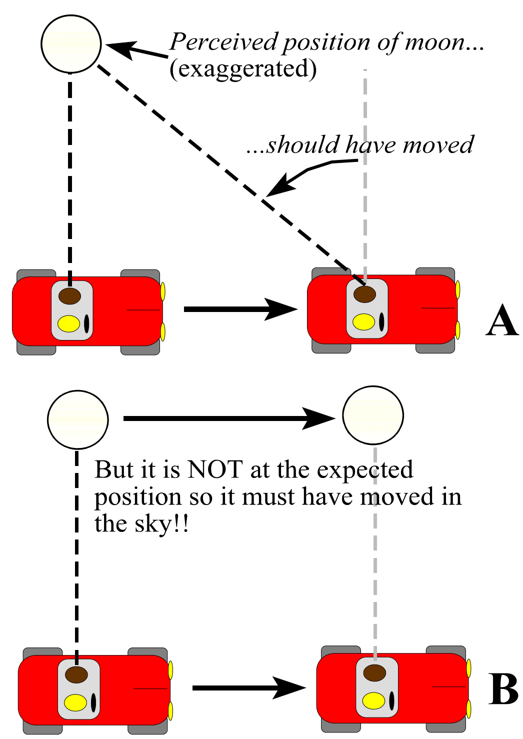
MOVEMENT IN DEPTH: There are even cells in the visual cortex that respond best to *movement in depth*. For example, a spot moving from point a to b in the picture on the previous page. Some cells will respond only if the object is on a course to hit the viewer!



some cells will respond to movement in the direction of the filled arrows, but not in the direction of the open arrows.

Moon Ilusion 2: Moon seems to move with you

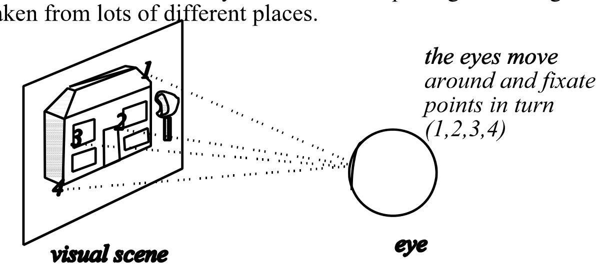
This is where the moon appears to move with you as you move. Because you perceive the moon to be much closer than it really is (see moon illusion 1), you expect it to change in position with respect to you when you move. But because it is so far away, it does not in fact change its position with respect to you when you move. How can your brain explain why it doesn't move? Either (a) you could adjust your estimate of how far away the moon is or (b) you could assume the moon really has changed its position.

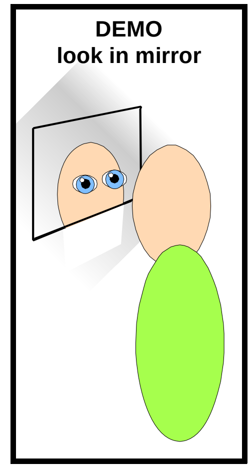


VISUAL MOVEMENT

1 **The brain needs to know whether visual movement was** produced by an eye movement or real movement. During eye movements vision is suppressed (**saccadic suppression**).

2 It needs to know about eye movements to put together images taken from lots of different places.





3 Two major theories about how the perceptual part of the brain knows about eye movements are:

INFLOW: information about eye movements is sent from sensors in the eye muscles themselves.

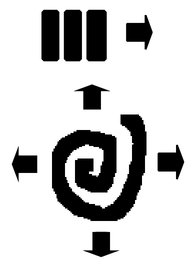
OUTFLOW: copies of the commands ***(corollary discharges)*** sent to the eye muscles are also sent to the perceptual parts of the brain.

EXPERIMENTS	PREDICTIONS		
	INFLOW	OUTFLOW	DATA
Active motion of real image	**No movement**	**No movement**	**No movement**
Passive motion of real image	**No movement**	**YES movement**	**YES movement**
Active motion of after image	**YES movement**	**YES movement**	**YES movement**
Passive motion of after image	**YES movement**	**No movement**	**No movement**
Attempt to move paralyzed eye	**No movement**	**YES movement**	**YES movement**

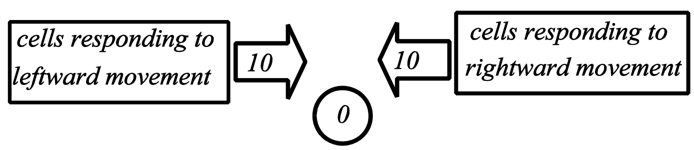
4 Evidence supporting the outflow theory:
- i when you push the eye passively, the world seems to move
- ii viewing an after-image during an eye movement shows no movement if it is a passive movement
- iii the after image *does* seem to move if it is an active movement (ie. voluntary, self-made move).
- iv if you try to make an eye movement under paralysis, the world seems to move whenever you try to make an eye movement

5 Cells in the visual cortex respond well to moving stimuli. They are usually direction selective, that is they prefer movement in a particular direction.

6 i viewing continuous movement either in one direction or in several directions at once, produces an AFTER EFFECT in which movement in the opposite direction is seen if a target that is actually stationary is looked at. This is because of adaptation.

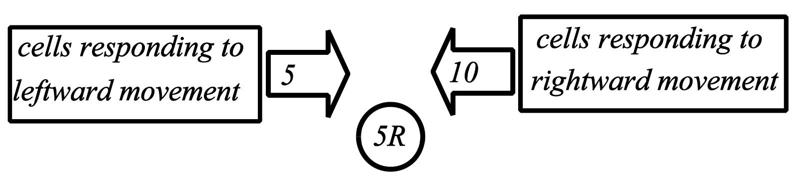


ii normally, when an object is stationary, the spontaneous output of these two opposing groups of cells balances.



iii After looking at, say, leftward movement at one place on the retina for a while, the leftward movement sensitive cells adapt (get tired).

iv Adaptation of some but not others will alter their balance at rest (when not looking at anything moving).



The unadapted cells will dominate.

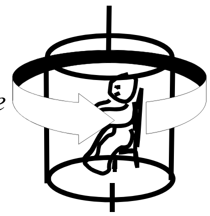
7 AUTOKINESIS is where a small, dim light seen in a dark room,seems to move on it own. It is probably due to inaccuracies in the corollary discharge system.

8 i World movement can be wrongly felt during DRUNKENNESS. This is because the balance organs of the inner ear are accidentally stimulated and this is wrongly interpreted as a head movement.

ii Normally head movements are detected by two systems: vision and the inner ear. Their contributions can be looked at separately in the laboratory.

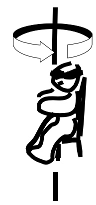
iii VISION ALONE (optokinetic stimulation)

subject feels they are moving to right (opposite direction of visual motion)



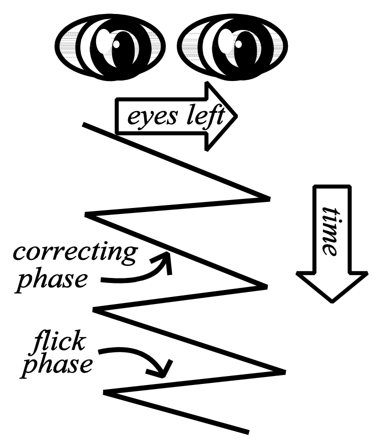
iv INNER EAR ALONE (vestibular stimulation)

subject rotated in the dark.

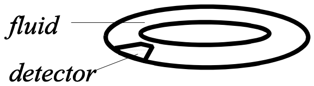


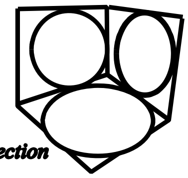
v The vestibular stimulation or the optokinetic stimulation both produce a) a sensation of movement and b) corrective eye movements called "nystagmus".

nystagmus: in which the eyes correct for the head movement for a while and then flick to another point

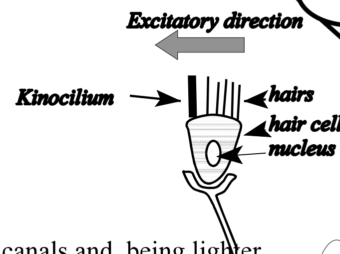


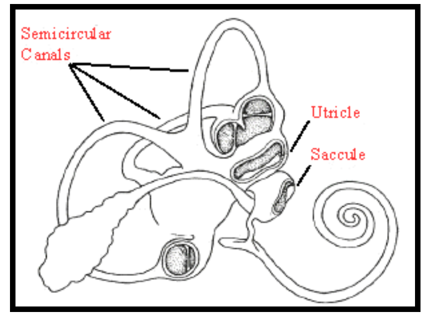
vi The vestibular system consists of canals full of fluid



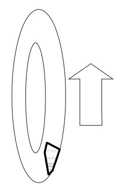


with a detector in that detects movement. The canals are in two sets of three (one on each side of the head) arranged 90° to each other. The detectors are hair cells.

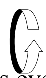




vii Alcohol enters the canals and, being lighter than water, rises to the top, creating movement of the fluid.



viii The fluid movement is detected and interpreted as movement.



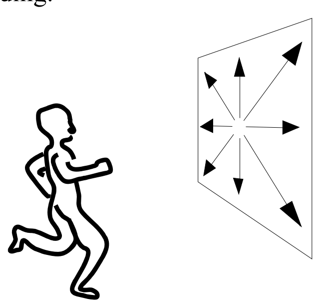
ix The perceived movement evokes eye movements that WOULD be appropriate for that head movement (eg, leftward eye movements to compensate for a rightward head movement).

x These eye movements then sweep the eyes past a stationary world and make it look as though the world is moving.

9 **Visual movement is important for picking out an object** from its background (imagine a camouflaged frog suddenly moving).

10 Visual movement is important to avoid things (cf. movement in depth).

11 Visual movement is important in planning your own movements. Visual movement can indicate where you are heading.

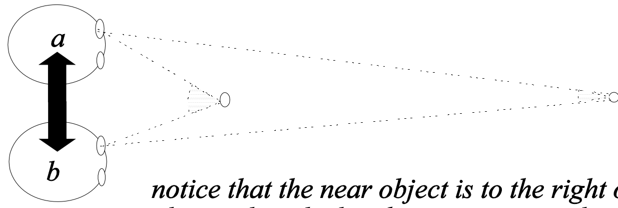


visual flow will radiate out *from the point you are heading towards*

12 Visual movement is important in depth perception (PARALLAX)

i Things closer to you will move over the retina faster than further-away objects when you move your head.

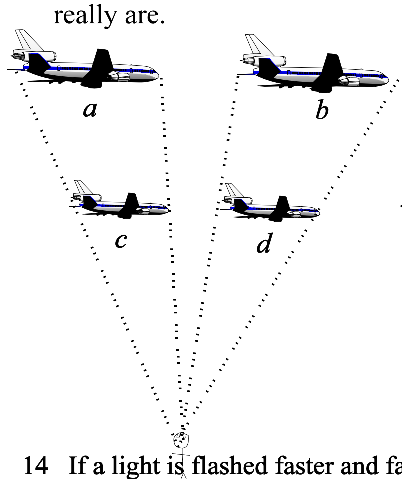
ii This relative movement can tell you the relative distances.



notice that the near object is to the right of the far *object when the head is at position a, but to the left of the far object when the head is at position b. The near object has moved more than the far object during the head movement.*

13**If objects are thought of as being at the wrong distance,** they will be judged as having the wrong speed.

Airplanes are often seen as closer than they really are and this makes them seem to be moving slower than they really are.

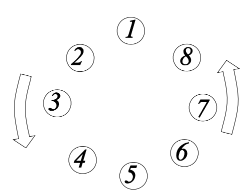


If the plane was judged at the *further distance, then it would have to go through the distance a-to-b. If on the other hand it was judged to be closer, then it would only have to go through the distance c-to-d (a shorter distance) in the same time.*

14 **If a light is flashed faster and faster, the individual flashes** will eventually *fuse* and be seen as a single light. The point at which this happens is called the CRITICAL FLICKER FUSION FREQUENCY (CFFF).

The CFFF is approximately:
50 Hz (cycles/second) for the fovea,
100 Hz for peripheral vision
and 200 Hz for cats.

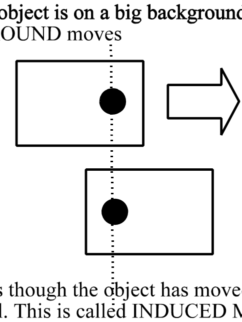
15 If, when one light goes out, another comes on within a short interval, it is seen as a single light jumping. This is called APPARENT MOVEMENT or PHI MOVEMENT. It is used in lots of street displays:



If these lights are lit sequentially, a single light going round in a circle is seen.

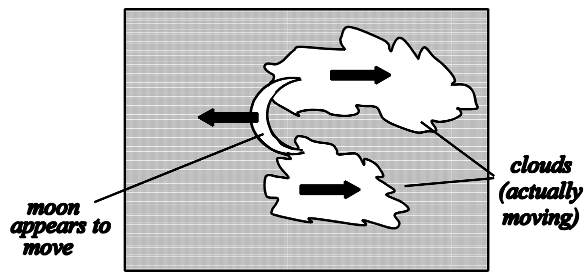
16 CINEMA and television combine FUSION and APPARENT MOTION effects.
a) Images are flashed too fast to see them as separate and
b) Successive images (or frames) are slightly different so that you see apparent movement of the image.

17 **If a small object is on a big background and the** BACKGROUND moves



it looks as though the object has moved and the background has stayed still. This is called INDUCED MOVEMENT.

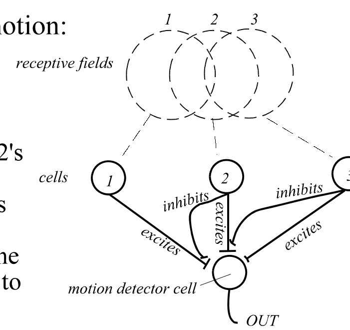
Moon illusion 3: An example of INDUCED MOVEMENT can be seen when the moon appears to move when clouds are blown in front of it



18 How the brain might detect motion:

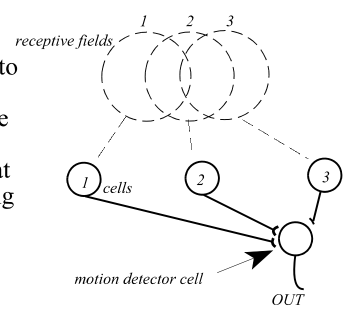
Inhibition model

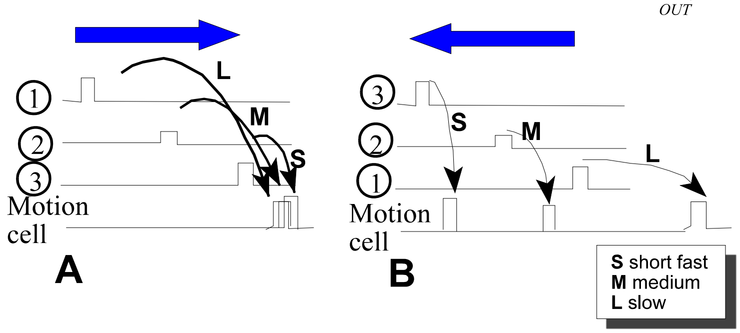
If an object passes through the receptive field of cell 3 *before* it passes through cell 2's, then cell 2's activity cannot get through to the "motion detector cell" because its connection is blocked by the inhibitory activity of cell 3. So the motion detector will not respond to motion 3 ➔ 2 ➔ 1. The motion detector cell will only respond to motion in the direction 1 ➔ 2 ➔ 3.



Delay model

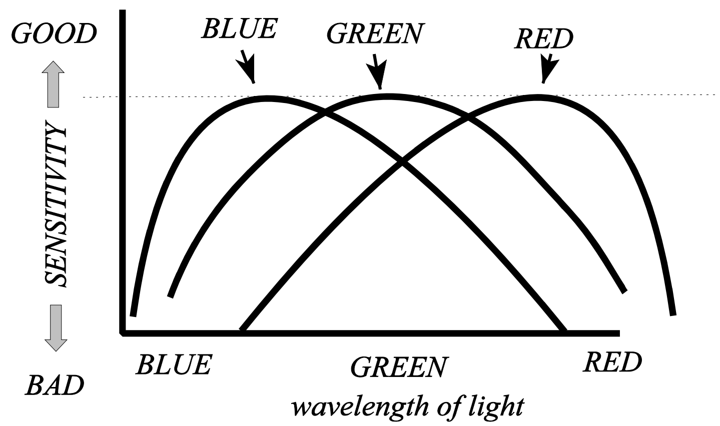
Cells 1, 2 and 3 have connections to the "motion cell" with different delays. When an object excites the cells in the order 1 ➔ 2 ➔ 3 the activity reaches the 'motion cell' at roughly the same time (A) allowing enhancement. When the objects travels the other way, the delays spread out the response (B)





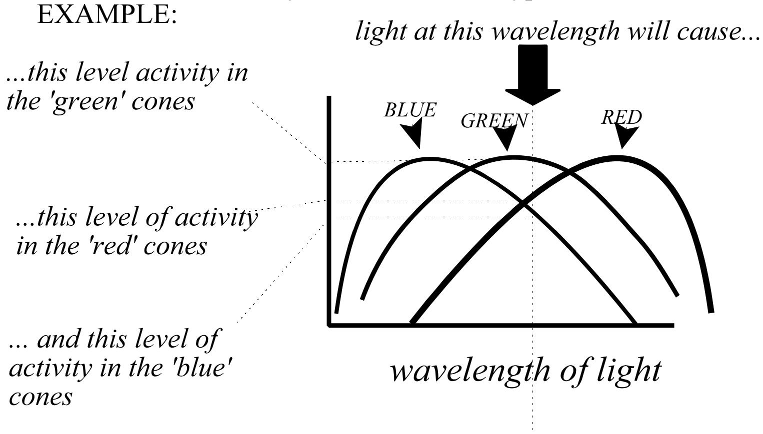
COLOUR VISION

There are three types of CONES:



1 **These curves are the sensitivities of each of the three types** of cones in the human retina. They are different because they each contain a slightly different PHOTOPIGMENT.

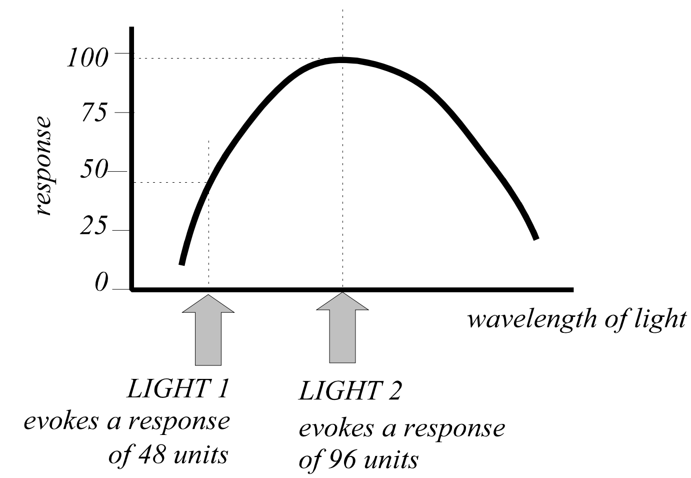
2 Light of any wavelength will produce a particular combination of activity in the three cone types. FOR EXAMPLE:



3 This ratio of activity in the three cone types is unique for light of a single wavelength (MONOCHROMATIC LIGHT), but can be mimicked by mixing together a set of three other lights. Thus we can 'fool the system' by mixing separate lights. This is what is done to produce a colour television picture. In fact the picture there is only three colours!

4 A Martian with FOUR cone types would not be fooled by earthling television. The pattern of activity of their FOUR cone types would not be the same when looking at the real object (with its particular spectral content) and looking at the mixture of blue, green and red light provided by the television.

5 COLOUR BLINDNESS: A person who has only TWO types of cone (ie. who is missing one type) can be fooled by a mixture of only TWO lights. Such a person is called a DICHROMAT. A person with only ONE type of cone (called a MONOCHROMAT) can always match any two lights, no matter what their wavelength, by adjusting their intensity alone.

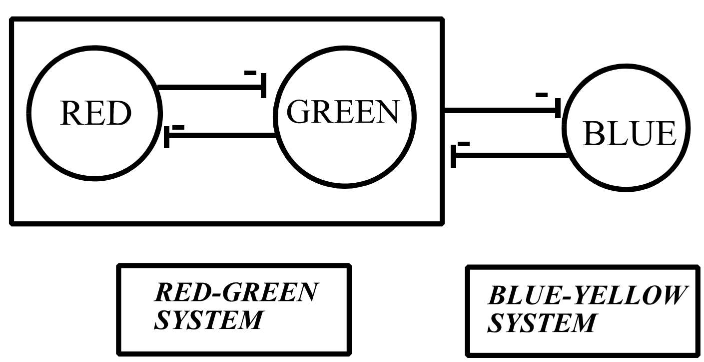


This graph represents the sensitivity of a person with only one cone type. Light 1 can be matched to Light 2 by simply doubling its intensity. This will double the response so that the response becomes the same as Light 2 at the initial intensity.

6 Normal colour vision is said to be TRICHROMATIC because phenomena such as colour matching (3 above) and colour blindness (5 above) can be explained by postulating three cone types. The trichromacy theory was arrived at long before the anatomy of the retina was understood and PREDICTED the existence of the three cone types which have since been found.

7 However the trichromacy theory cannot on its own explain COLOUR AFTER-EFFECTS. After looking at RED a white screen appears GREEN (actually CYAN); after looking at BLUE, white appears YELLOW; and visa versa.

8 The phenomenon of colour after-effects can be explained by the OPPONENCY theory which postulates that



9 Such opponency between cone types has been found in the arrangement of retinal ganglion cells.

VISUAL ILLUSIONS

Although visual illusions have some inherent appeal, they are usually designed to test or prove some hypothesis or theory.

A CLASSIFICATION SYSTEM FOR ILLUSIONS

I will consider visual illusions in these arbitrary four classes. The illusions mentioned so far could be fitted in too!

1 ADAPTATION ILLUSIONS

Illusions in which the balance of the nervous system has been upset by previous exposure

examples: vertical bars look tilted after viewing tilted bars
movement after effect
after staring at RED, things look GREEN

2 SIMULATION ILLUSIONS

Illusions in which the brain has no choice but to signal that a particular event has occurred

examples alcohol simulates the effect of a head movement
apparent movement
mixing colours simulates the effects of a particular wavelength
stereograms simulate depth

3 INCOMPATIBLE CUES ILLUSIONS

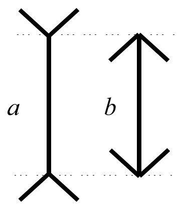
Illusions where some key information (eg, stereopsis) is missing.

examples playing card illusion
many of Escher's famous drawings

4 GEOMETRIC ILLUSIONS

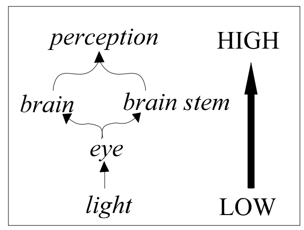
THE MÜLLER-LYER ILLUSION:
AN EXAMPLE OF A GEOMETRIC ILLUSION

There is no "right answer" to explain this, or any other illusion. Probably many processes are contributing. "Explanations" can be either *bottom up* or *top down.*

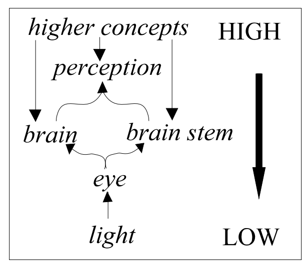


"a" looks longer than "b"

BOTTOM UP
A *bottom up* explanation states that a phenomenon arises from the processing of information as it passes through the chain from the lower levels (eg. retina) up to the higher levels.



TOP DOWN
A *top down* explanation involves calling on higher processes eg. memory, at the top of the chain of events, influencing the flow of information.



Here are some examples of theories, or groups of theories that have been proposed to "explain" the Müller-Lyer illusion. They can be divided into bottom up and top down types.

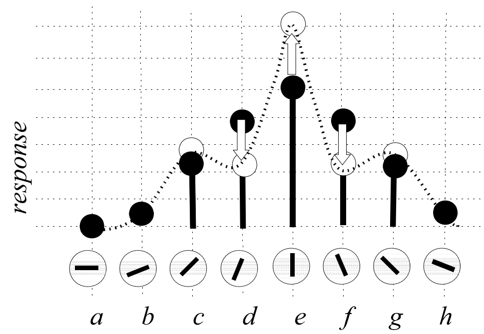
BOTTOM UP

1	EYE MOVEMENTS	signals from eye movements during scanning are inaccurate
2	LIMITED ACUITY	the ends are blurred and pulled into the centres of the terminal triangles
3	PHYSIOLOGICAL CONFUSION	some properties of cells in the visual system are responsible

TOP DOWN

4	EMPATHY	"a" looks open & excited "b" looks closed & depressed
5	"GOOD FIGURE"	grouping into "wholes" (Gestalts) exaggeration of the distance of features that stand apart
6	PERSPECTIVE	the lines are interpreted as features in the real world

A POSSIBLE PHYSIOLOGICAL BASIS FOR THE MÜLLER-LYER ILLUSION



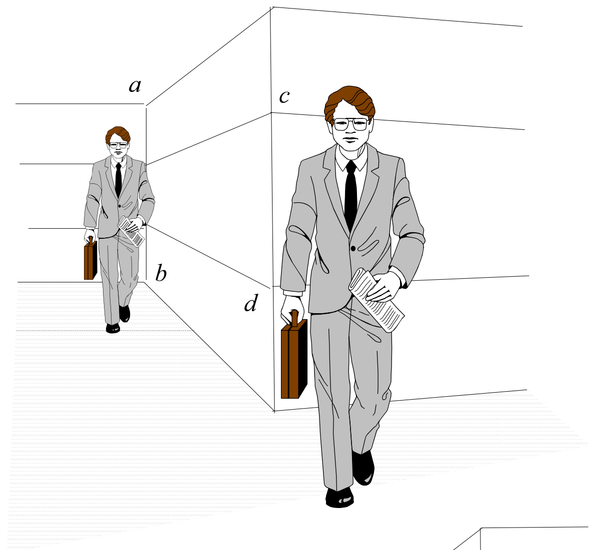
● *the response of one cell without lateral inhibition*

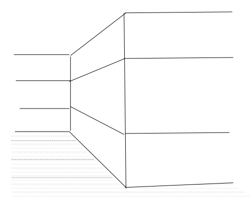
○ *the response of one cell with lateral inhibition*

If each cell inhibits its neighbours, then, if cell "e" is active, it will inhibit its neighbours "d" and "f". This in turn will reduce their inhibitory influence on cell "e". The result is that cell "e" has more activity and its neighbours have less, which should make it easier to see which is the most active.

If cells d, e and f are *all* stimulated (as by the arrow head in the Müller-Lyer) then cell "e" cannot be released from inhibition and its response will be less than usual (ie. less than the response to the Y-head of the illusion).

A PERSPECTIVE OR ECOLOGICAL EXPLANATION FOR THE MÜLLER-LYER ILLUSION



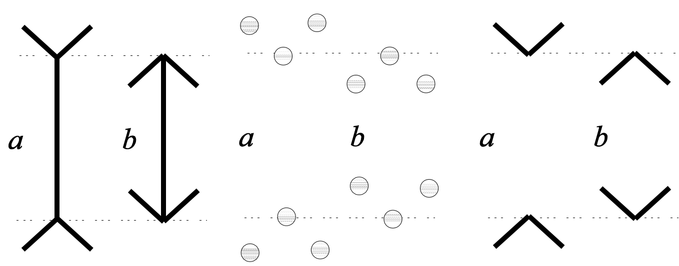


The distance between points a and b and between c and d are the same. They represent a "real-life" version of the Müller-Lyer.

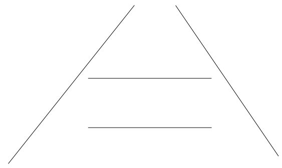
The perspective explanation of the Müller- Lyer is that the features at the end of the longer bar make it appear to be a distant, background feature. The features of the shorter bar make it appear closer.

Now, size constancy states that if two objects are indeed the same size, then, if one is closer, it will have an appropriately larger retinal image. If two objects are at different distances, but have the same retinal image size, then they must be different real sizes.

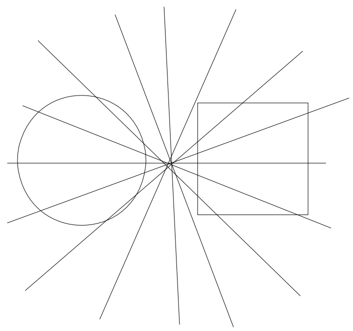
SO INTERPRETATION (TOP DOWN INFLUENCES) CAN CAUSE ILLUSIONS. And often physiological effects are too small, and too specific. An explanation based on edges could not expand to cover these versions of the illusion for example.



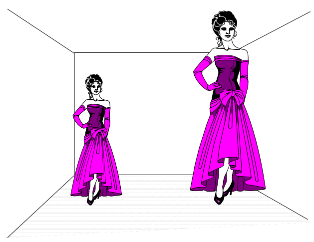
Examples of each of these types of explanations can also be generated for the following illusions.



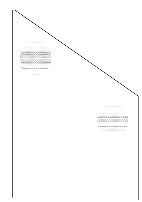
Is this illusiondue to the influence of the closeness of the horizontal lines to the obliques? Or the obliques being seen as railway lines laid out in three dimensions?



Can this be explained in terms of the complex junctions or do the radiating lines imply depth?



The Ames Room



The floor plan of the Ames Room. This illusion seems to imply knowledge of rooms and must be TOP DOWN.

DO YOU NEED TO LEARN TO SEE?

EITHER "All knowledge starts from experience"
ie. you can't know or do anything without experience.
EMPIRICIST APPROACH

OR "knowledge is a priori"
ie. everything is present (in potential) at birth.
NATIVIST APPROACH

CLASSES OF EVIDENCE	*suggest*:
1 Animal behaviour	*nativist*
2 Blind people recovering sight	*both*
3 Babies' visual development	*both*
4 Adaptation experiments	*empiricist*
5 Controlled rearing experiments	*empiricist*

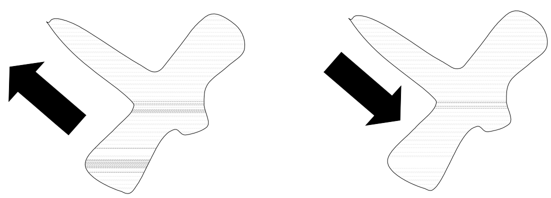
CONCLUSION *both are important*

Photograph by R.C. James

ANIMAL BEHAVIOUR

There are many examples of innate, inborn, instinctive behaviours, many of which clearly require sophisticated visual processes.

For example, ducklings avoid this shape but only when it is moving in the direction that makes it look like a hawk. They don't react to it when it moves in the opposite direction when it looks like a goose or swan.



harmless flying goose *duck-eating hawk*

Birds and other animals are able to migrate over huge distances without guidance.

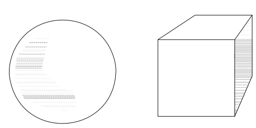
Chimpanzees, even zoo bred, instinctively fear snakes.

Many other examples.......

BLIND PEOPLE RECOVERING SIGHT

In the seventeenth century Molyneux asked a famous question:

"could a man born blind distinguish a sphere and a cube by sight alone?"



Surprisingly actual case studies give a mixed response.

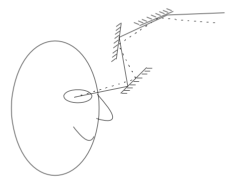
There are serious problems in interpreting these clinical data:

- patient's visual history is rarely known exactly, for example, how blind is the patient? When did they first go blind?
- the patients have had other experience: they are not fossilized baby visual systems

References: "Eye and Brain" by R Gregory
"Molyneux's Question" by MJ Morgan

ADAPTATION EXPERIMENTS

1 wearing inverting lenses (or mirrors) makes the world appear upside down at first. Within a few days you *adapt* and then things look normal again. When you take the glasses off, you need to readapt to the normal state.



2 It is thought that the amount of adaptation was exaggerated by early experimenters. However, there is no doubt that some adaptation takes place.

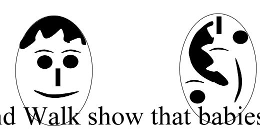
3 Hens and amphibians shown less adaptation than adult humans when given this sort of lens. Hens cannot peck accurately, for example.

CONCLUSION

The visual system *is* able to learn.

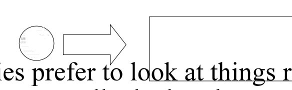
BABY VISUAL DEVELOPMENT

1 Fantz showed babies ordered and disordered faces. The babies spent twice as long looking at the ordered ones, suggesting they could see the difference.

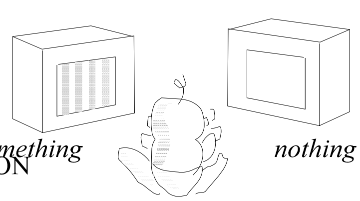


2 Gibson and Walk show that babies will not crawl over a visual cliff (even when protected by glass).

3 Babies expect objects to reappear if they go behind a screen suggesting knowledge about objects (object persistence).



4 Since babies prefer to look at things rather than blank screens, you can tell whether they can see something by giving them a choice (preferential looking technique).

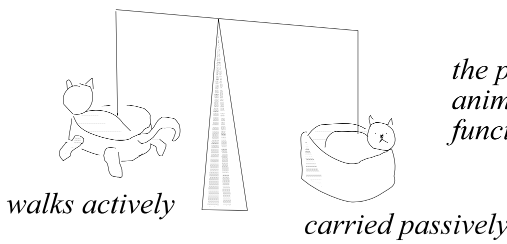


CONCLUSION

Babies have some visual abilities very early on. But probably only low-level ability ie. that information required for visual reflexes.

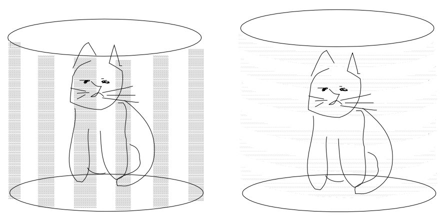
CONTROLLED REARING EXPERIMENTS

1 kittens brought up either: able to walk around in the light
or passively carried around



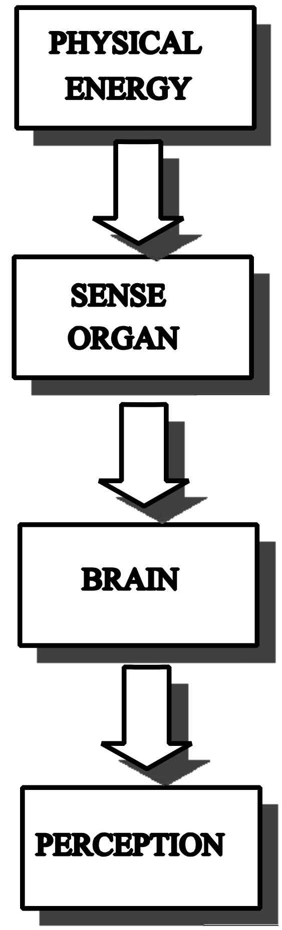
the passively carried animal grows up functionally blind.

2 kittens brought up in environments with only stripes of a certain orientation have more cells in their visual cortex tuned to the exposed direction. They are functionally blind to the other orientation.



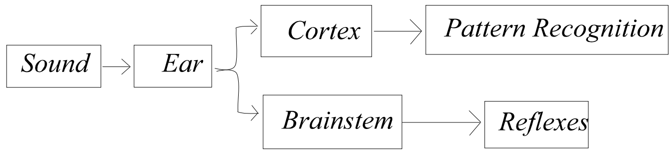
3 There is a critical period during which such environments have an effect (the first month for cats) after which exposure has no effect.

HEARING



THE GENERAL SCHEMA of the hearing system is the same as vision:

STAGES IN HEARING	ACHIEVED BY
1 point the ears at the right place	HEAD MOVEMENTS
2 Focus	PINNA (outer ears)
3 Adjust for the difference in pressure between air and fluid	bones of the inner ear relative size of membranes
4 Convert physical energy to activity in cells	TRANSDUCTION



ORGANIZATION OF THE AUDITORY SYSTEM

The arrangement of the auditory system is conceptually the same for hearing as for vision.

Patterns in hearing are patterns in time made up of different frequencies and changes of frequencies with time. This compares with visual patterns which are made up of different light levels and changes of light levels across space.

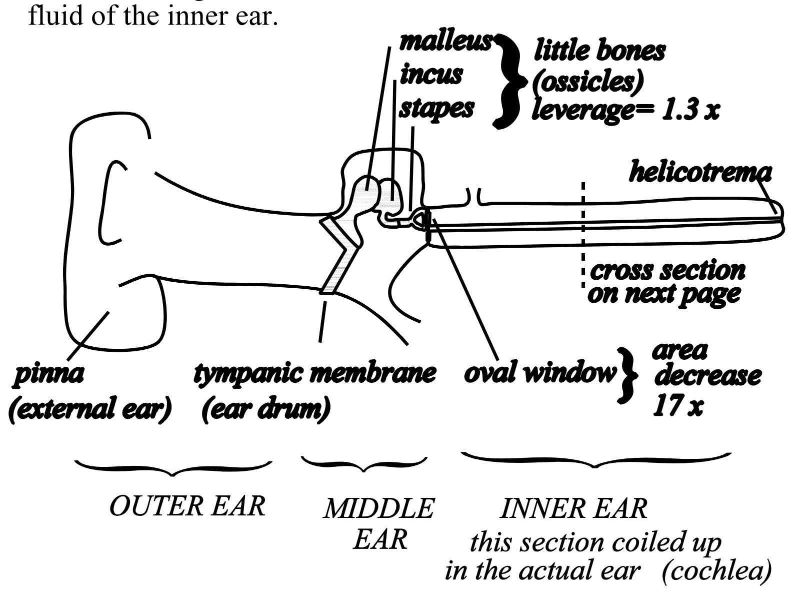
Reflexes are similar for hearing and vision, too. Either lights or sounds (or better, both) evoke orientation movements. To orient to something, you need to know where something is. The ability to know where a sound came from is called AUDITORY LOCALIZATION.

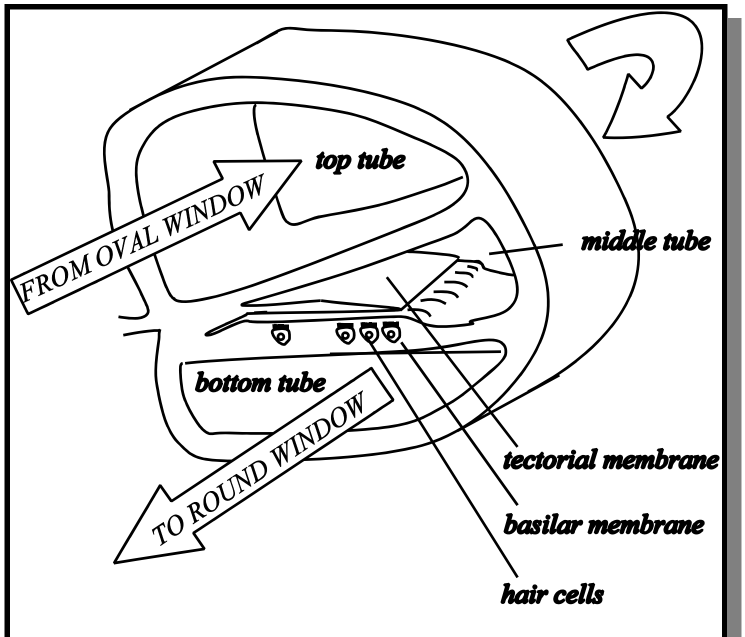
Sound waves in the air are not forceful enough to cause vibrations in the fluid of the inner ear. The force of the sounds waves is amplified by two mechanisms:

1 The three little bones that connect the tympanic membrane (ear drum) to the oval window (cover of the entrance to the inner ear) act as levers. The increase the force by 1.3 times.

2 The tympanic membrane is 17 times as big as the oval window. This increases the force by 17 times.

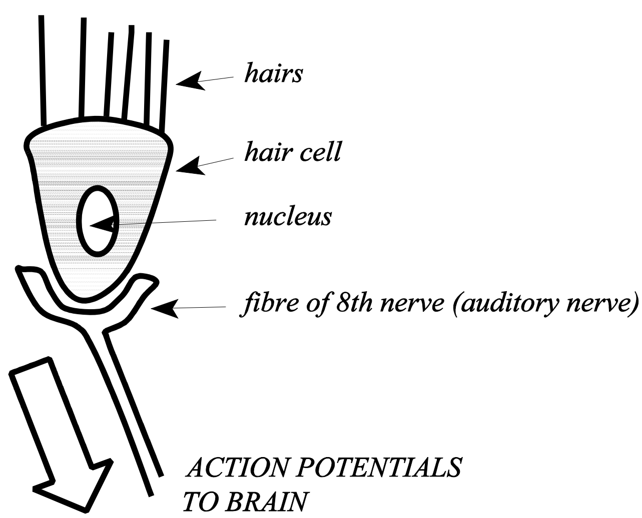
So together, the force is increased by 17 x 1.3 = 22 times which is enough for sound waves to cause vibrations in the fluid of the inner ear.





vibrations pass down the top tube to the end (the HELICOTREMA) and then back down the bottom tube.

The vibration in the fluid sets up a TRAVELLING WAVE in the BASILAR MEMBRANE in between the top and bottom tubes. This membrane supports HAIR CELLS who sit between the BASILAR and TECTORIAL MEMBRANES. When the hairs of these hair cells are vibrated, it causes electrical events within the cells (TRANSDUCTION).



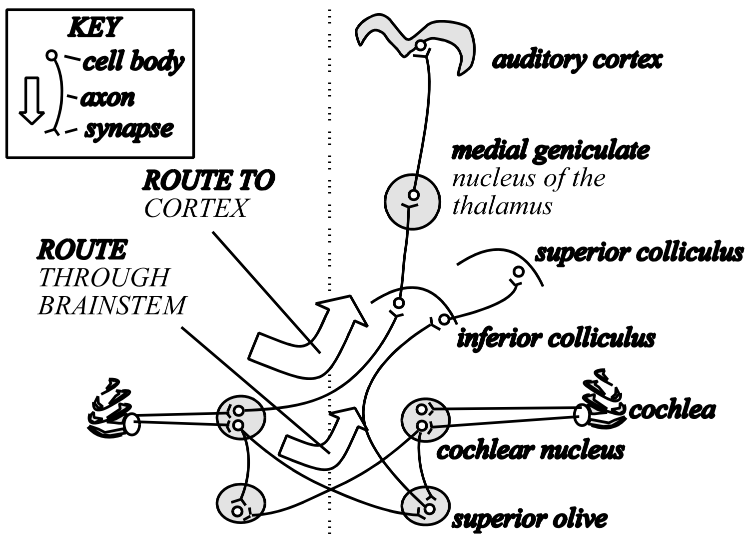
The electrical events in the hair cells can lead to action potentials in the nerve cells connected to them. These action potentials travel along the auditory nerve to the brain.

THE AUDITORY PATHWAY IN THE BRAIN

Comparison with the visual system:

Similarity: two routes: one to the cortex via the thalamus that underlies *perception*; and one to the brainstem that controls unconscious *reflexes*

Difference: there are more connections in the retina than in the cochlea. The cochlear nucleus can be regarded as equivalent to the retinal ganglion cells.



CHARACTERISTICS OF THE CELLS IN THE AUDITORY SYSTEM

AUDITORY NERVE

Nerve fibres respond best to particular frequencies, depending on which part of the basilar membrane their hair cells are located.

COCHLEAR NUCLEUS

Two groups: one, which forms part of the route to the cortex, is more "fussy" and needs an auditory "feature" such as a change in frequency to respond. The other, which forms part of the route through the brainstem, is just like the auditory nerve.

SUPERIOR OLIVE

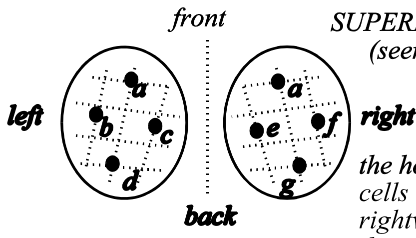
responds best to sounds arriving through both ears with a small time of arrival difference. The superior olive is the first part of the auditory system where information from the two ears comes together. In the visual system, information from the two eyes don't come together until the level of the cortex.

INFERIOR COLLICULUS

is a relay site for both parts of the auditory pathway

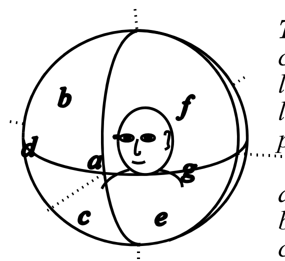
SUPERIOR COLLICULUS

responds best to sounds coming from a particular direction. It has a map of space over its surface and responds best when a light and sound appear at the same place at the same time.



SUPERIOR COLLICULI
(seen from above)

the horizontal lines join cells with similar left or rightward receptive fields; the vertical lines join cells with similar up/down fields.



The sites on the superior colliculi labelled a-g are the locations of cells responding to lights and/or sounds at the points in space shown below.

a straight ahead
b right and up
c right and down
d right
e left and down
f left and up
g left

The cells of the superior colliculus, like those of other sensory areas, carry information about the opposite side of space: the left colliculus carries information about the right side of space. The cells are connected to the appropriate musculature to allow orientation movements of the eye and head towards stimuli appearing at the location that they respond to.

MEDIAL GENICULATE NUCLEUS (of thalamus)
and
AUDITORY CORTEX

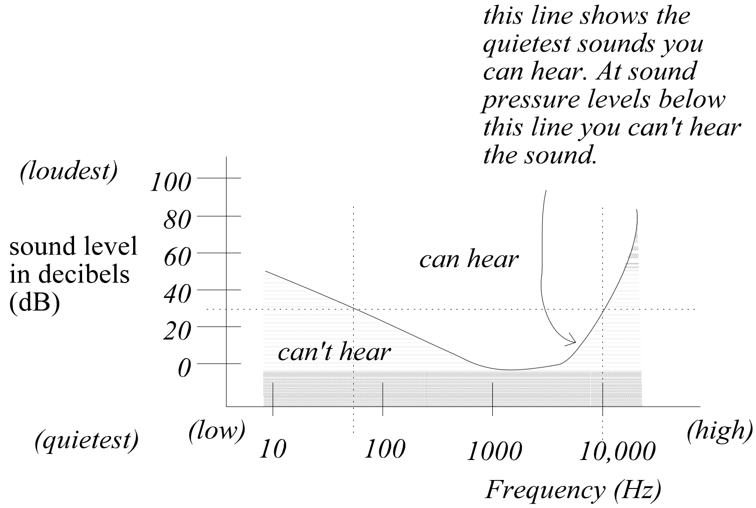
As you get closer to the cortex, the cells get more and more fussy about what they will respond to. This is similar to the situation for the visual system. In the auditory system they require patterns in frequency instead of patterns in space. An example of a specific auditory pattern would be a sound that started at 1,000 Hz and went to 3,000 Hz. Fussy cells might respond to this change only as it went up and not as it came down.

Cortical cells are selective for features in the auditory pattern, rather like the cells of the visual cortex. A visual cell might look for a feature but not be too concerned about where that feature occurred in space. An auditory cell might look for a feature and not be too concerned about where it occurs in the frequency range. Thus a cell might respond to a sound changing from 500 to 1,000 Hz and be equally responsive to a change from 2,000 to 4,000 Hz.

Auditory features are what is important to an animal. Different features are important to different animals and cells are found in the cortex of particular species that look for auditory features that are important to that species. Thus cells have been found in the auditory cortex of the squirrel monkey that are selective for features of the squirrel monkey's distinctive call. Human cortex might be expected to have cells that respond best to the features that are important in comprehending spoken language.

HEARING THRESHOLDS

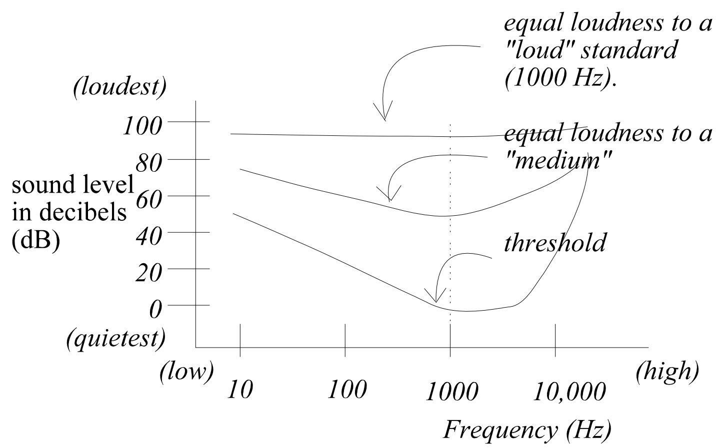
By playing PURE TONES (perfect sine waves) through head phones, we can determine the quietest sound you can hear for a given frequency.



For sounds played at, for example 30 dB, the lowest frequency you could hear would be about 60 Hz, and the highest about 10,000 Hz according to this graph.

EQUAL LOUDNESS

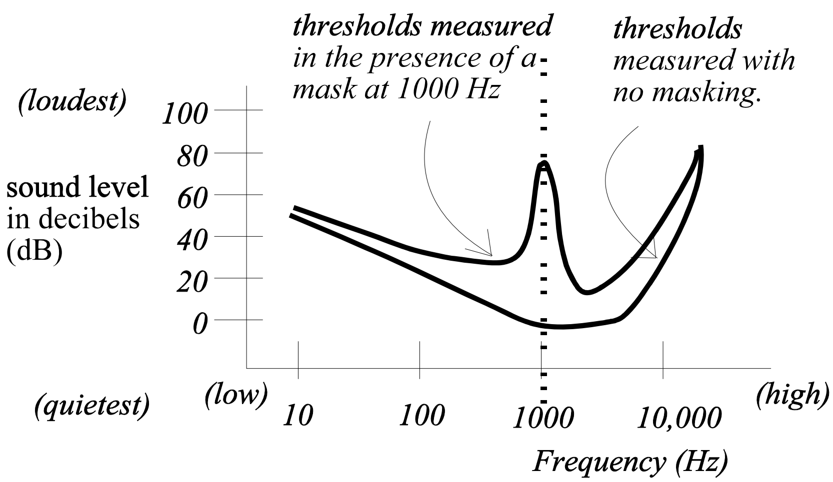
If sounds are compared to a standard (eg. 1000Hz) at a particular loudness, then curves of equal loudness can be obtained. For example, when the standard is at threshold (can just be heard), then all the others will be set to "can just be heard", too. But if the standard is "quite loud" then, all the other frequencies can also be set to sounding that level.



For quiet sounds, low and high frequency sounds need more "sound level" to be heard as equal to a 1000Hz standard. For louder sounds, this is no longer true. That is the equal loudness curves flatten out for louder sounds. Sounds recorded LOUD and played back QUIET, need to be adjusted by boosting the low and high frequencies selectively. This is what the LOUDNESS switch on your hi-fi does.

MASKING

If two tones are played at the SAME TIME, then one interfers with the other, such that they need to be played louder to be heard. The tones MASK each other. The extent to which they mask each other depends on how close in frequency they are.

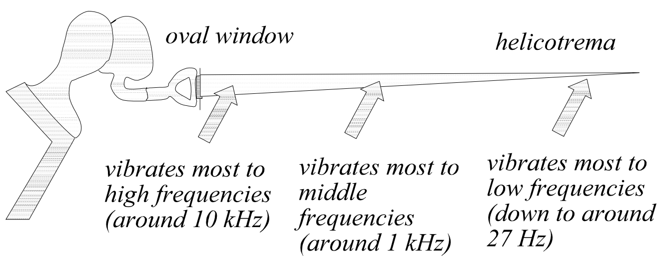


MECHANISMS OF PITCH PERCEPTION

You can hear notes of particular pitches and you can tell them apart. Extracting the content of speech and music, for example, requires you to do this. How can it be done? There are two competing theories, place theory and periodicity theory.

PLACE THEORY

1 The basilar membrane has a "stiffness" that varies along its length. The resonant frequency - the frequency that causes the maximum response in the membrane - depends on the stiffness. Thus the resonant frequency varies along the membrane. It is most stiff at the oval window end. High stiffness means it will vibrate best to high frequencies. It is least stiff at the helicotrema: at this end, it will vibrate best to low frequency sounds.



2 The place theory states that the brain is able to analyse which frequencies were present in a sound by seeing which *places* on the membrane were most active.

3 To identify which places on the membrane were most active, the brain would have to identify which nerve fibres were active. If an active fibre came from hair cells at the helicotrema, for example, then it must have been activated by a low frequency sound, and so forth for all fibres.

4 A coding system in which the identity of a tone is represented by its place, is similar to the coding of the visual signal in which the spatial relationship between all the optic fibres is maintained. In the visual system, the spatial coding of the retina was called RETINOTOPIC coding, in the auditory system the spatial coding of tones is called TONOTOPIC coding.

5 Notice that the whole membrane vibrates for most sounds - it just vibrates more at some places that at others. So all sounds must generate some activity in all hair cells, its just that some will be more active than others.

THE PERIODICITY OR TELEPHONE THEORY

In this theory it is not which fibres are active that is important, it is the pattern of activation in each fibre. If a fibre has action potentials at 200 Hz (200 spikes/sec) then it doesn't matter what part of the membrane it is connected to, it always signals the presence of that frequency. Periodicity theory requires that pitch discrimination is done neurally at a later stage since each fibre would carry information about all frequencies.

EVIDENCE AGAINST PLACE THEORY

The case of the Missing Fundamental

1 Complex tones (eg. a piano note) contain several different frequencies in a harmonic series. For example, the note middle C contains frequencies at 262 Hz, 524 Hz, 786 Hz, 1048 Hz, 1310 Hz etc...

2 If asked to match the middle C piano note with a pure tone whose frequency you could set, you would match it with 262 Hz: the lowest frequency in the series. The note is said to have a PITCH of 262 Hz. The lowest frequency in the series determines the pitch and is called the fundamental frequency.

3 The presence of the other harmonics in the piano note gives it its special piano quality or *timbre*. The other harmonics are also present when middle C is played on any other instrument, but their sizes would vary giving each instrument its distinctive *timbre*.

4 The fundamental frequency 262 Hz can be experimentally removed from the note by

either: a) playing it so quietly that the fundamental frequency is below threshold

or b) by removing it with an electronic device

5 Amazingly, the pitch of the note still sounds the same at 262 Hz, even though there is no actusl vibration at that frequency any longer.

6 The Place Theory could only explain the phenomenon of the missing fundamental by suggesting that the membrane was somehow distorted by the presence of the higher harmonics such that it actually vibrated strongly at the 262 Hz location, even in the ABSENCE of this particular frequency.

7 This can be tested. If the membrane WAS being distorted in this way, then the note should be masked by a low frequency noise (around and including the 262 Hz target) just like an ordinary tone of 262 Hz would be.

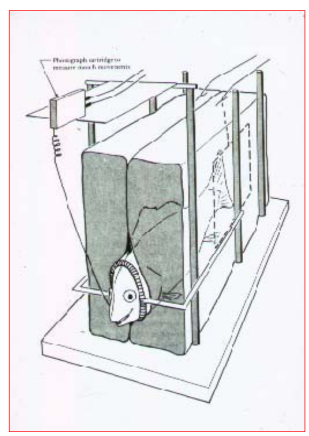
8 The noise does mask a real tone at 262 Hz, but does NOT mask the illusory, missing fundamental. The complex tone still has a pitch of 262 Hz, even though a REAL tone of 262 Hz would not be heard!

9 Furthermore, the missing fundamental can still be heard (although more faintly) if some of the harmonic series are put into one ear and others are put into the other.

10 The missing fundamental seems to require a neural explanation.

ANIMALS WITHOUT A BASILAR MEMBRANE

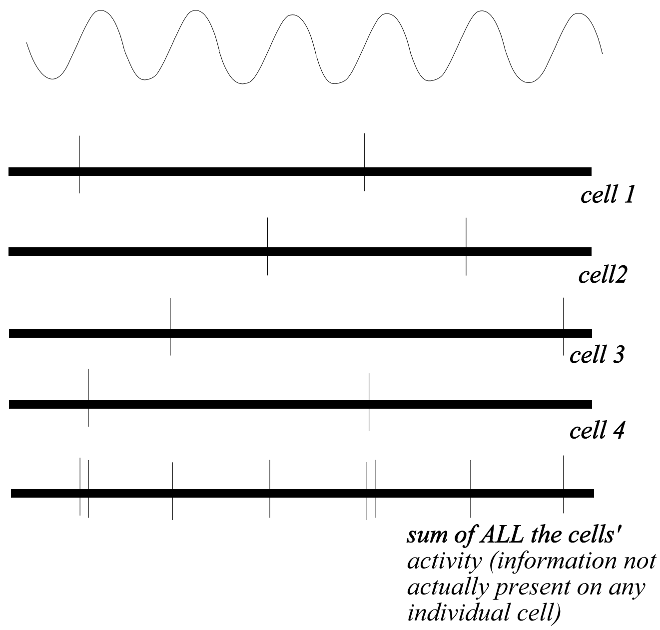
Animals without a basilar membrane can still distinguish tones. Goldfishes for example, can be conditioned (a type of learning involving punishment and reinforcement) to respond if two notes are different. They (in common with most fish) have no basilar membrane. Thus the place theory is not essential to being able to distinguish tones.



EVIDENCE AGAINST PERIODICITY THEORY

1 Nerve cells cannot fire above about 300 Hz but we can hear up to 20,000 Hz or thereabouts, depending on age.

COUNTER-ARGUMENT: Perhaps neural processing could allow the higher frequencies to be carried in a population of many cells instead of by a single cell.



2 DIPLACUSIS is the clinical condition in which when the same tone played to each ear in turn, it is heard as having different pitches.

It is difficult (but not impossible) to explain this in neural terms. It is easy to imagine the basilar membranes in the two ears having different stiffnesses as a result of a clinical condition. Thus a place on the membrane that had been associated with a particular frequency now resonates to a different frequency. That new resonant frequency is thus identified as being the old frequency: the one that used to excite that area of the membrane.

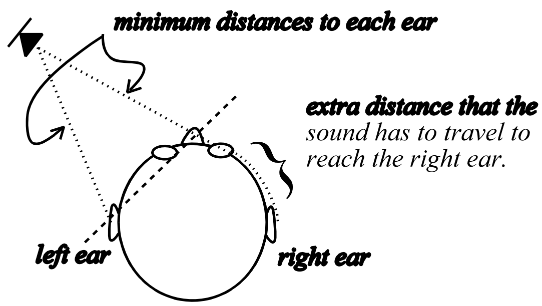
IN CONCLUSION:

PLACE VERSUS PERIODICITY THEORIES

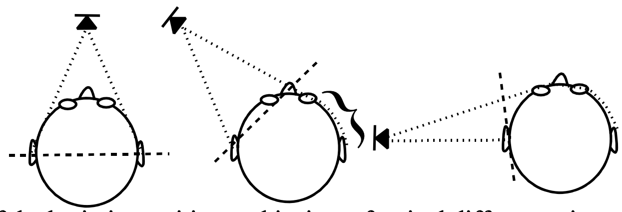
Probably both processes (place and periodicity) play a role in interpretting the auditory stimulus. This is the DUPLICITY theory meaning both are right! Probably the periodicity theory best describes the response to low frequencies (below 1 kHz) where variations in the places of peak membrane response are difficult to identify. But the place theory best describes the analysis of high frequencies (above 1 kHz), where the stimulus frequency is so much above the ability of a single nerve to code the temporal pattern. So over most of the important part of the frequency range, tonotopic coding is found, comparable to retinotopic coding in the visual system.

PRINCIPLES OF AUDITORY LOCALIZATION

1 INTER-AURAL TIME OF ARRIVAL DIFFERENCES
Sound travels at 332 m/s or 1200 kph. Under most circumstances, the difference in time of arrival in the two ears will therefore be significant. Light on the other hand travels at 300,000,000 m/s and the difference in time of arrival at the two eyes is likely to be insignificant.



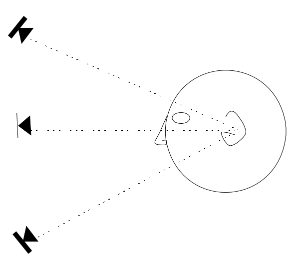
The extra distance is longer, the further the sound source is to one side.



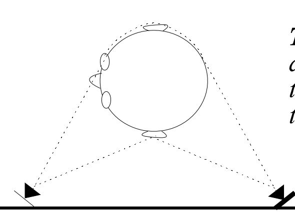
If the brain is sensitive to this time of arrival difference, it could work out the direction of the sound source.

Experiments using head phones (to reduce other cues about where something is) have shown that humans can detect time differences of 10-20 μ secs (μ = micro = 1/1,000,000 = 10^{-6}). For an average size head, a time of arrival difference of 10-20 μ secs corresponds to about a 2° displacement from the straight ahead.

NOTE: A) this system cannot tell you about how high a sound is.

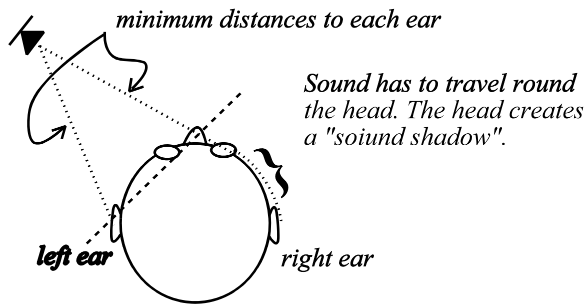


B) This system cannot tell you front from back.



2 INTER-AURAL INTENSITY DIFFERENCES

For a sound source that is not directly ahead the intensity of the sound arriving at the two ears will be different. This is because a) the sound has to travel further to get to one ear and b) the head gets in the way and casts a "sound shadow".

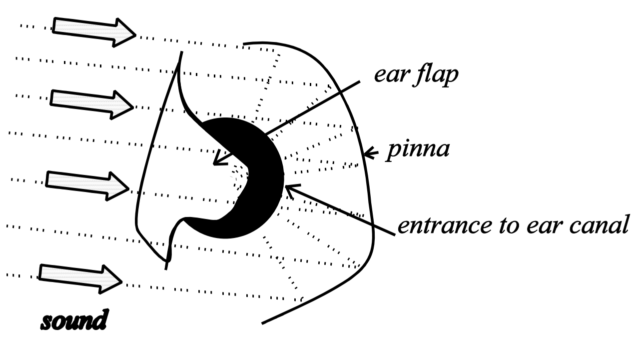


Experiments with head phones, where any confounding time of arrival difference can be removed, reveals that the auditory system is sensitive to inter-aural intensity differences as an indicator of direction of a sound source. However this cue is not so sensitive as the time of arrival difference.

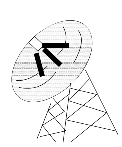
Notice that this cue, like the time of arrival difference, cannot tell how high a stimulus is. In some complex way, the intensity difference *might* be able to distinguish front and back because of the shadowing effects of the pinnae.

3 THE ROLE OF THE PINNAE

Sound reflection around the pinna is complex as you can imagine from its complex and varied shape in humans. It acts as a collector to "focus" sound waves into the ear canal.

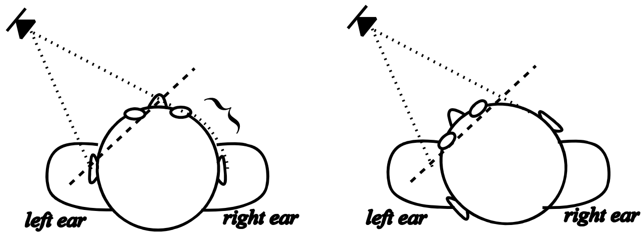


This is similar to the principle of a radio telescope. It is directional. It can also distinguish sounds coming from above from sounds coming from straight ahead or from below. It can also distinguish sounds coming from the front from sounds coming from the back. The directional properties of the pinna are especially useful if the head moves.



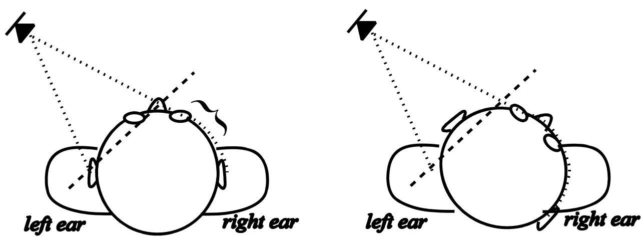
4 THE ROLE OF HEAD MOVEMENTS

a) If you move your head *towards* a sound source, the time of arrival differences and intensity differences between the two ears will get less.



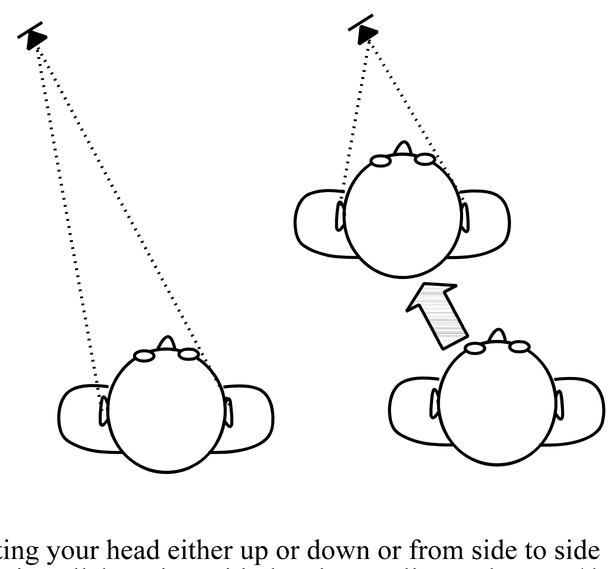
time of arrival and intensity *differences LARGE*   ***differences much smaller***

b) If you move your head *away* from a sound source, these differences will get larger.



c) In conjunction with the other cues to auditory localization, head movements can be very useful.

d) Also physically moving closer to or further away from a a sound source will increase or decrease the intensity. This cue would work even if you only have one ear!



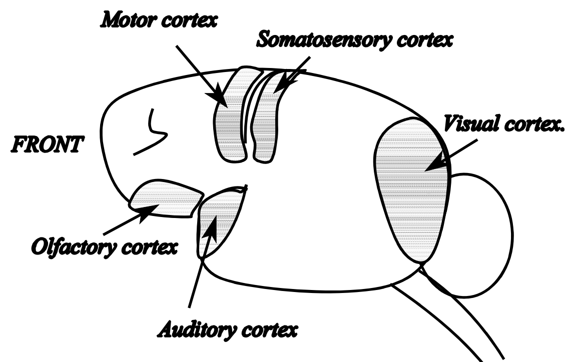
e) Tilting your head either up or down or from side to side can, in collaboration with the pinna, tell you about up/down position. Without a pinna, such head tilts would have less effect.

LOCALIZATION OF FUNCTION IN THE CORTEX

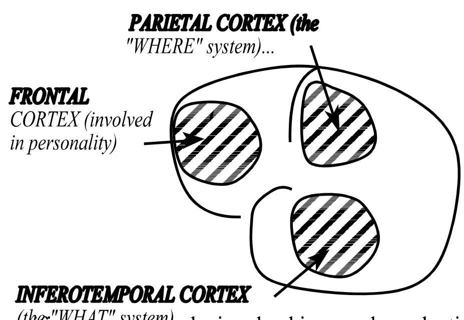
1 The following techniques.....

electrical stimulation (in people and animals)
anatomy
lesions (accidental in humans, carefully controlled in animals)
recording (of single cell activity or tissue activity)

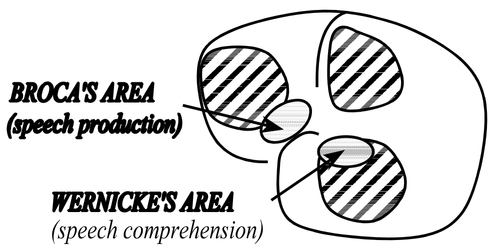
.... have revealed that some areas of the cortex are specialized for specific functions. These areas are called the PRIMARY CORTICAL AREAS.



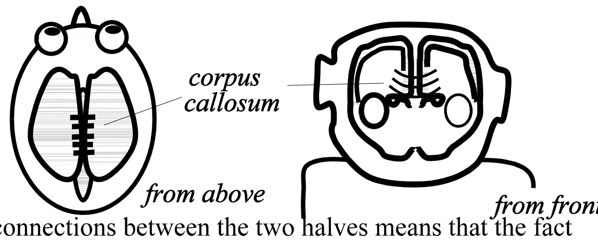
2 The other areas of the cortex have much less well understood functions. They are often called the ASSOCIATION AREAS.



3 Two specific areas seem to be involved in speech production and understanding. These are best developed in most people on the left hand side of the brain. BROCA'S area is near the motor control areas for the mouth and is involved in speech production. WERNICKE'S area is near the auditory cortex and the pattern areas of the ASSOCIATION AREAS and is involved in speech comprehension.



4 Normally the two halves of the cortex are connected by a huge bundle of fibres called the corpus callosum.



5 The connections between the two halves means that the fact that half the visual world goes to one half of the brain and the other half of the visual world goes to the other half of the brain doesn't normally matter, since the information is passed between the two sides.

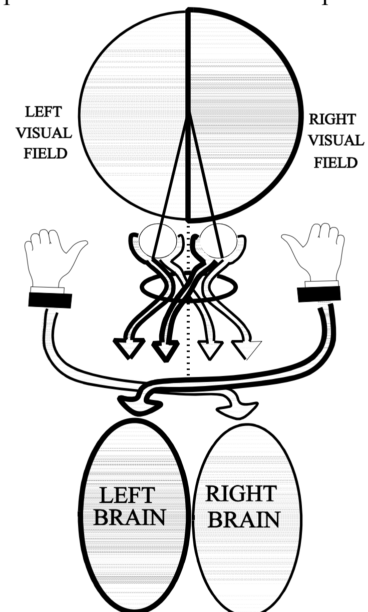
6 Thus both hemispheres normally get access to the "speech centres" even though the speech centres are located on the left side of the brain. Information that goes to the left half of the brain (eg. from the right side of visual space) gets there directly, information from the other side goes through the corpus callosum.

7 Normally also, eye and head movements ensure that most of the visual world falls, at one time or another on both halves of the retina and therefore passes to both hemispheres.

8 But some people have had their corpus callosum cut in an operation to try to stop the spread of epileptic fits from one side of the brain to the other. Normally the operation has no adverse effect because of eye and head movements that ensure that information gets to both hemispheres directly.

9 Touch information from the hands crosses over before arriving at the brain. Thus information felt by the left hand is sent first to the right side of the brain.

10 If, in the laboratory, people with a cut corpus callosum are asked to keep their eyes still and are prevented from seeing their hands, then we can present information separately to each hemisphere of these SPLIT BRAIN patients.

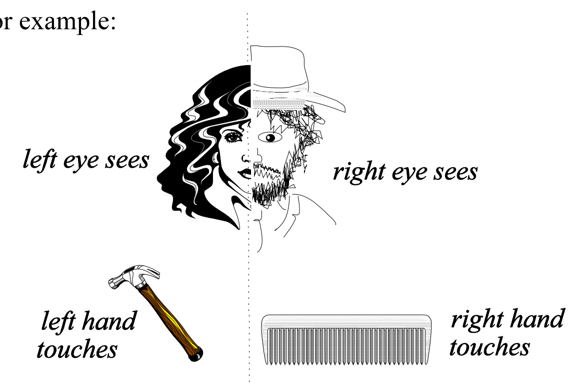


Information from the right visual world and right hand will go only to the left hemisphere and *visa versa*.

11 When asked what they see or hold, subjects will only report verbally about stimuli in the right half field or held in their right hands.

12 However, when asked to point, the left hand can point to what it was holding and what was in the left half visual field.

For example:



Subjects report seeing a man and holding a comb but the left hand can point to the hammer and chooses a picture of a woman.

13 The subject is *unaware* of seeing just half a face. The rest of the face is filled in by the brain, presumably in the same way as
you are unaware of the blind spot (where the optic nerve leav the retina). Normal people are also, of course, unaware that only a tiny part of the visual world is seen clearly at any one time.

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