

The Physiology of the Senses

Transformations For Perception and Action

Lecture 5 - The Cerebral Association Cortex

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The 5 main subdivisions of the cerebral cortex.

Frontal, temporal, occipital, parietal and limbic (on medial side).

The primary sensory and motor areas.

This is where most of the sensory information first arrives. Primary motor areas send commands to the muscles. In the rat these areas occupy nearly all the cortex. In humans they occupy only about 20%.

The higher order (secondary) sensory and motor areas.

Higher order visual, somatosensory, and auditory lie near the respective primary areas. This is where sensory information is further processed.

These are also called unimodal association areas.

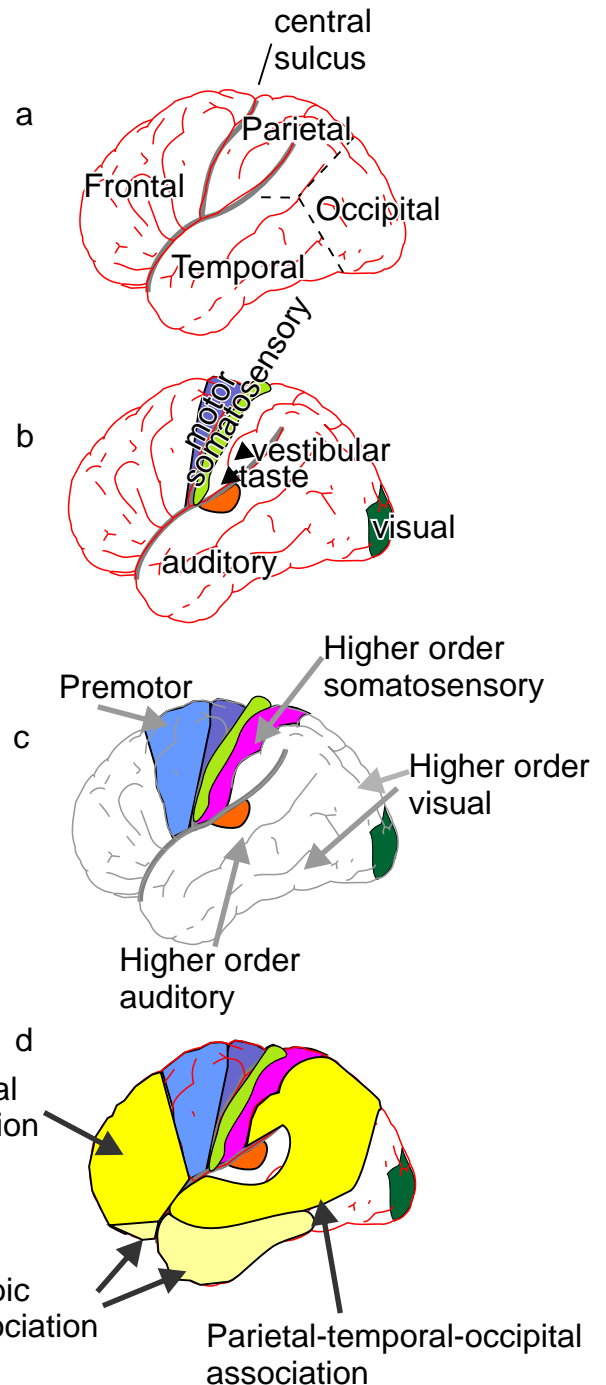
Premotor areas send commands to the motor areas.

The three association areas.

Prefrontal, Limbic, and Parietal-Temporal-Occipital areas

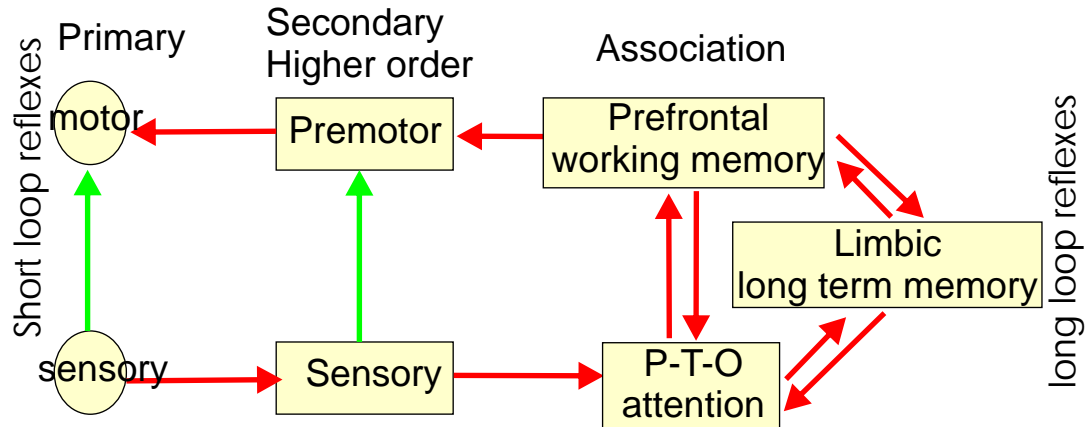
This is where:

- different modalities combine.
- attention is shifted.
- planning occurs.
- things are remembered.



How are the different areas of cortex interconnected?

a) What is the general pattern of connections between primary, secondary, and association areas?



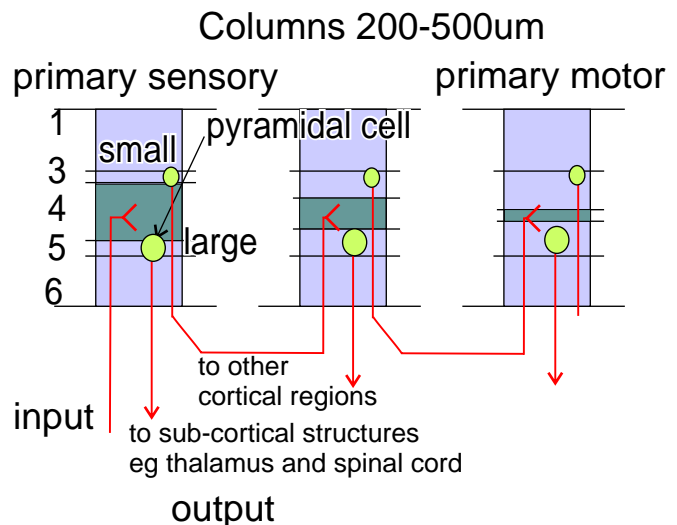
Long loop reflexes, such as writing down the name of a seen object, require the complex processing power of the association regions. Short loop reflexes mediate rapid, but simple, responses, such as swatting a mosquito.

b) How do the input & output layers differ in these areas?

Layer 4 receives input from the thalamus and other cortical regions. It is thickest in primary sensory regions. The striate cortex (primary visual) is so-called because of its thick layer 4.

Layers 3 and 5 send output to other cortical regions, the brain stem, and spinal cord. These layers are thickest in primary motor cortex.

All areas have columns. The bulk of the output from one column is to another column, forming a vast interconnective network.



This feature also predisposes the cortex to epilepsy. A locus of abnormal activity in one area quickly spreads to other regions, leading to a seizure. These interconnections are, as we will see in session 11, where our memory is located.

What are the functions of the different association areas?

a) Are the functions of different cortical areas unique?

There are two opposing theories:

Lashley's equipotential theory: Information on a particular function is spread out over the entire cortex.

Evidence for: The loss of a few cells from a small lesion in one part results in minimal impairment.

Evidence against: The cortex is not uniform. Different regions serve different functions.

Grandmother cell theory: Simple cells connect to complex cells, complex cells connect to hyper-complex cells, and so on, until finally there is one unique cell that fires when you see your grandmother. If you lose that cell, you can no longer recognize your grandmother but have no problems with grandfather.

Evidence for: Some lesions do impair the recognition of faces selectively. Some cells are activated only by a particular face.

Evidence against: Brain cell death is common, yet the memory loss observed is a general fuzziness in remembering faces, not an absolute loss of one face and not of another.

Truth probably lies somewhere between these two extremes.

b) Is the function of a particular cortical area identical in different people?

No. The cortex is very plastic, particularly in early life.

If a particular sensory input is missing.

That area which previously received this input will now receive a different sensory input. This is similar to the competition for cortical representation between the two eyes. If one eye is lost, the remaining eye takes over the missing eye's cortical areas. Similarly, loss of both eyes allows auditory and somatosensory areas to expand. This may explain the very fine acuity of these senses in the blind.

If a particular cortical area is damaged.

The same function becomes organized in a new cortical area. For example language is usually represented on the left. If the left is damaged early in life, the right side develops language function.

How and why do the two sides of the cortex differ in function?

a) Each hemisphere excels in different tasks

Dominant (usually left) - sequential or serial tasks

e.g. language (reading writing speaking signing), analytic (math $A=B$, $B=C$, therefore $A=C$)

Non-dominant (usually right)- tasks requiring parallel processing

e.g. spatial tasks, intuitive (C resembles O as I resembles L), geometry, music

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b) Patients with a section of the corpus callosum.

Sperry received Nobel Prize for these studies.

The subject was shown an apple on the left.

The subject could not name the apple because it is not seen by the language center on the left.

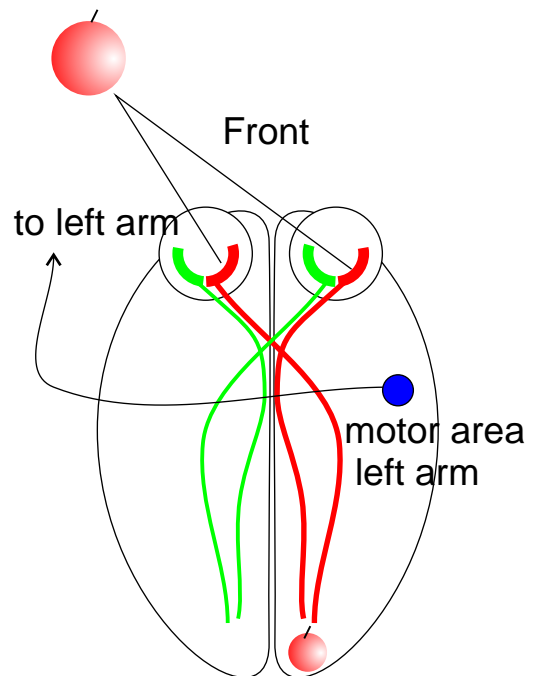
The subject could visually recognize an apple and pick it out from a group of other objects with his left arm (the one controlled by the right side of the brain).

Two independent brains function in one person (e.g. a patient would hug wife with one arm and push her away with the other).

c) What are the advantages and disadvantages of lateralization?

Advantage: Shorter paths to interconnect related regions.

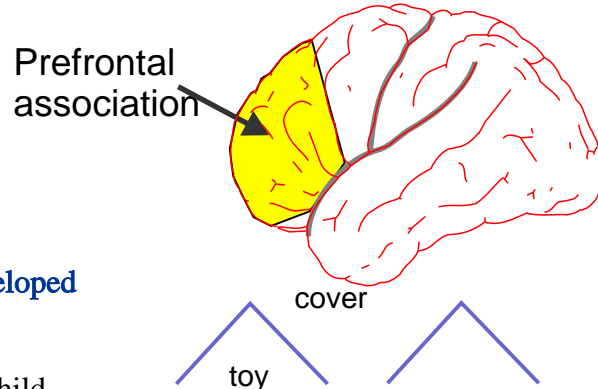
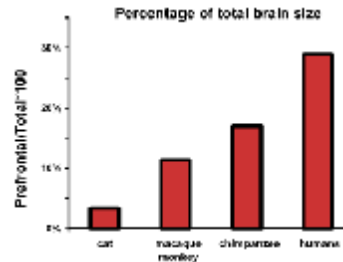
Disadvantage: less redundancy. Redundancy is good if one part breaks down.



Prefrontal association area:

The prefrontal cortex has become larger, as a percentage of total brain size, over the course of evolution. One important function is planning through the use of working memory

Lesions of the prefrontal association area produce deficits in tasks that are spatial and delayed (remembering which of two boxes contains food for few seconds). This is called working memory, a form of short term memory.



Children prior to the age of 1 yr have not developed this working memory.

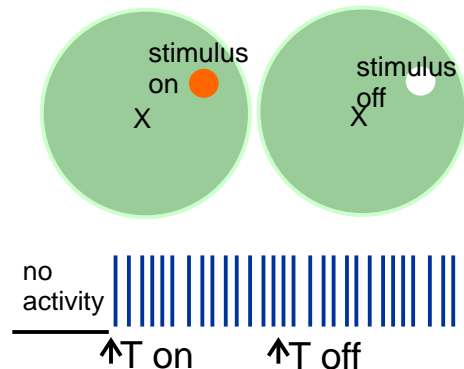
If a toy is covered by one of two covers, the child cannot find it. Out of sight is out of mind.

Neurons in the prefrontal cortex show

- activity which starts when a stimulus appears (T on) in a particular location
- unlike neurons in V1, here activity continues even when the stimulus disappears (T off).

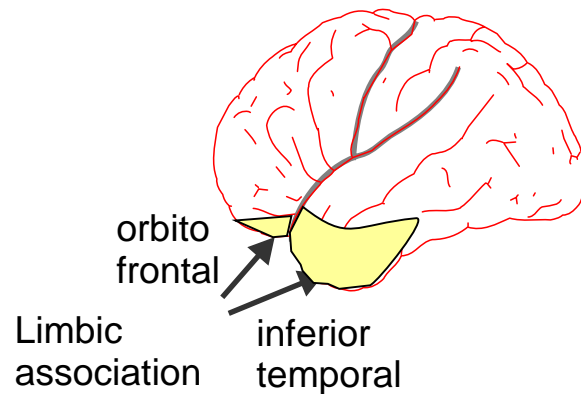
This tonic activity holds the object location in working memory.

Different cells hold the memory of objects in different target locations.



Depletion of dopamine in the prefrontal cortex impairs working memory.

The prefrontal cortex is interconnected with the basal ganglia. Parkinson patients have difficulty in initiating movements to targets in working memory. They need some external stimulus to initiate movement.



Limbic Association Areas

These are large area located on the underside of the cortex.

There are two parts

i) Orbito frontal: Involved in emotion

After lesions, patients display no anger if they make mistakes. Because this has a calming effect, frontal lobotomies used to be a popular cure for aggression. Unfortunately it also destroyed initiative.

ii) Inferior Temporal lobe: Involved in long term memory.

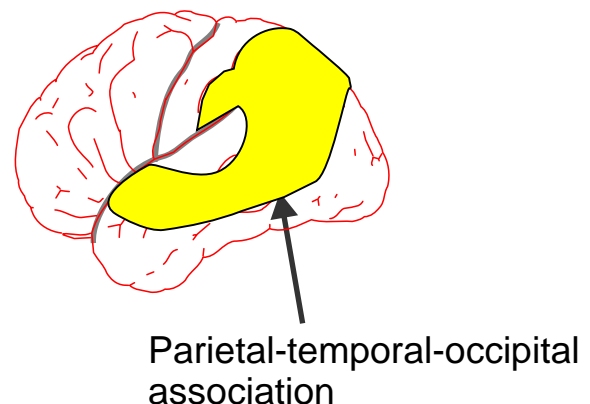
The right side is more involved with pictorial memory (e.g. faces) and the left side, in verbal memory (e.g. names of people).

Parietal- Occipital- Temporal (PTO): Polimodal convergence of senses and attention.

e.g. locating objects in space by touch, sight, sound etc.

e.g. language: sound of words, written words (sight), or Braille (touch)

Attention allows us to focus in on specific stimuli and neglect others, for example a specific voice in a crowd.



The spot light analogy of attention

An analogy that is simple and useful in beginning to understanding attention is that of a flash light that selectively casts light on particular features of a scene.

Attention acts like a bottle neck. It limits what enters the brain. The retina and visual cortex see both the person and the bike but attention limits what gets further down into the what stream. We are blind to what does not get through the bottleneck.

Visual perception is a two stage process

Stage 1) an early stage that performs rapid low level processing of the visual world.

Stage 2) an attention-demanding capacity-limited bottle neck that limits what enters working memory, awareness and consciousness.

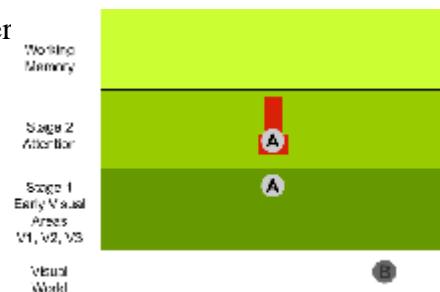
Visual objects compete for your attention. While attention is processing a visual object one is blind to the presence of other objects, even those at the location one is attending to. This is known as the attentional blink.

Attention can be drawn from below by things that pop out from the background. In early visual areas, like or similar objects are inhibited and have a reduced influence while different objects are accentuated and thus drawing attention to themselves.

Or attention can be directed voluntarily from above by areas in the parietal dorsal stream.

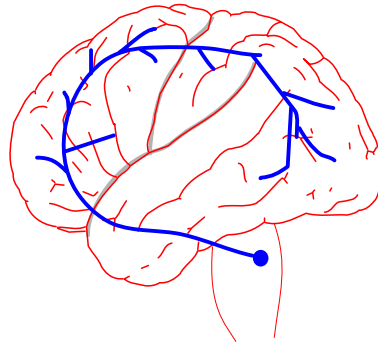
Finding Waldo takes time. This occurs for 3 reasons.

- 1) Because Waldo does not automatically draw your attention to him as does a horizontal line among a background of vertical lines.
- 2) Because it takes time to voluntarily shift your attention and/or make an eye movement from one potential Waldo to another.
- 3) At each location, it takes time to process the image and decide if it is Waldo or not.



Attention is not the same as arousal.

Arousal is general while attention is specific. Arousal is mediated by one of several diffuse systems arising from the brainstem. One of these is the locus coeruleus whose neurons release norepinephrine. One neuron projects to 100,000 cortical neurons. They act like a volume control to increase one's level of alertness.



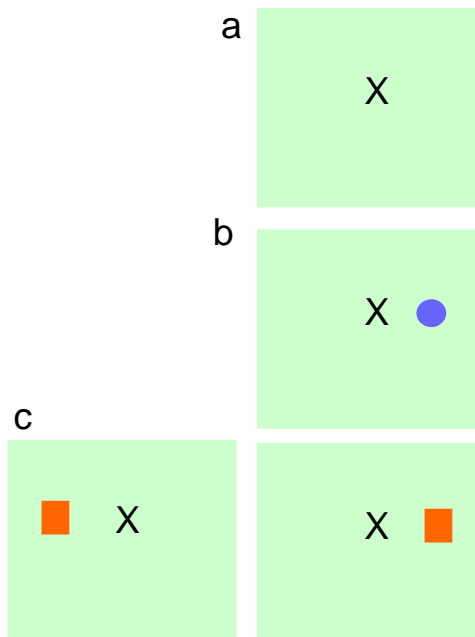
Attention allows us to focus in on a specific location.

This is illustrated by a simple experiment developed by [Posner](#)

- a) Subject is asked to fixate on the X
- b) Subject cued to expect an stimulus on the right
- c) A test stimulus is presented to the left or right

The subject has better sensitivity to the cued side because attention was shifted to it. Sensitivity can be measured by reaction time or the ability to detect a faint stimulus.

Most people, take longer to respond on the trial cue is to one side and the test is to the other. This is because on these trials the cue shifts attention to the wrong place. In trials where the cue and the test are in the same place, one is faster because attention raises the sensitivity of the correct place. This is an example of spatially directed attention.



Attending to different features causes activity in different cortical regions

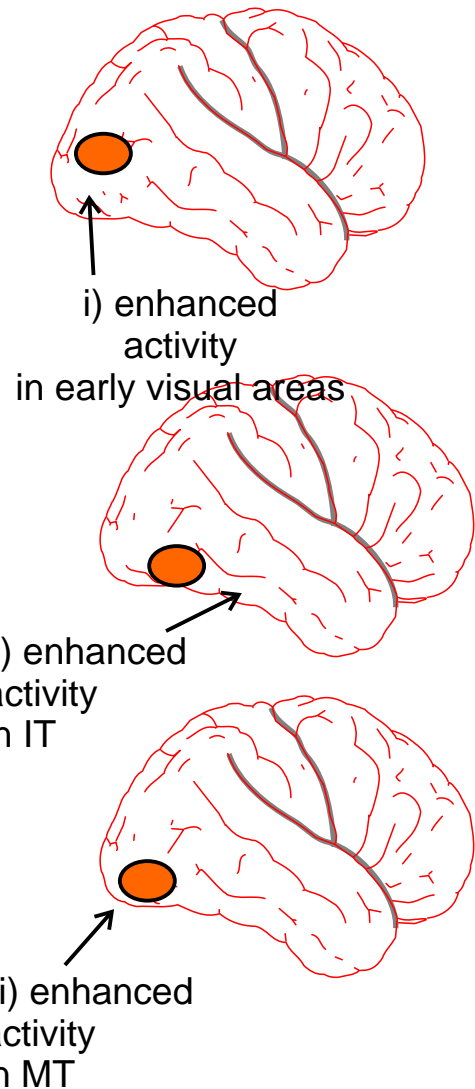
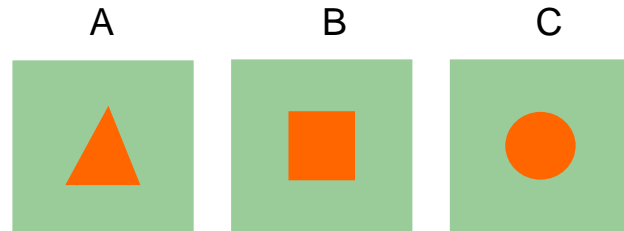
A subject is shown an image A and then, after a delay of .5 sec, image B and then C

Instruction to the subject:

- i) "Indicate when two successive objects have the same color."
- ii) "Indicate when two successive objects have the same shape."
- iii) "Indicate when two successive objects have the same direction of motion."

Attention can be viewed as a flash light that is directed at different aspects of an object

But the big question is: "What directs the flash light?"



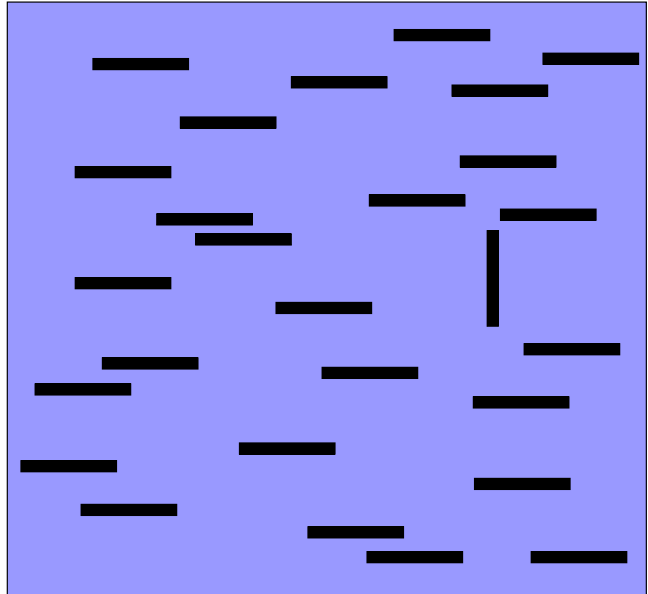
Attention to a particular color or orientation

Find the line that is different.

That was easy because, as we saw in session 3, your early visual areas automatically cause the odd line to pop out and draw your attention to it.

Now find the line that is different in a more complex pattern.

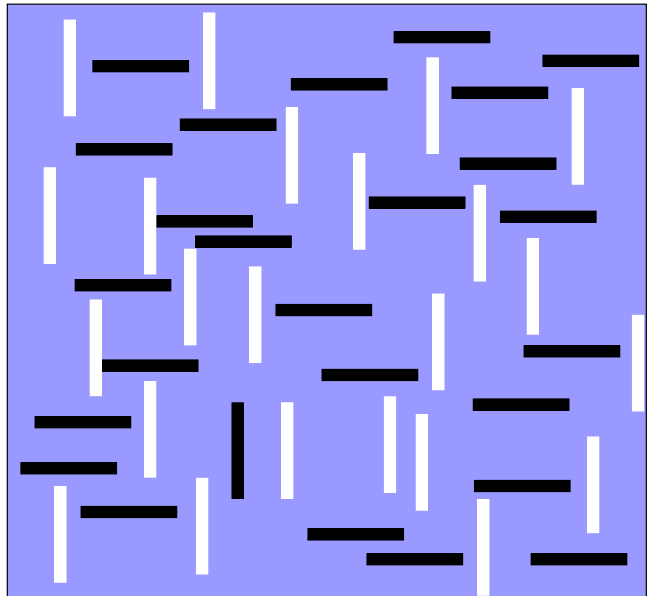
This takes a bit longer. Now the odd line no longer pops out. You need to serially scan the image to find the odd line.



Now try it again but this time focus your attention just to the dark lines. Notice how the odd line pops out again. The same thing happens if one focuses one's attention to just vertical lines, irrespective of color.

Thus attention can selectively enhance the activity of neurons that code a particular color or a particular orientation.

Presumably the selective activation is guided by feedback from higher areas to early visual areas.



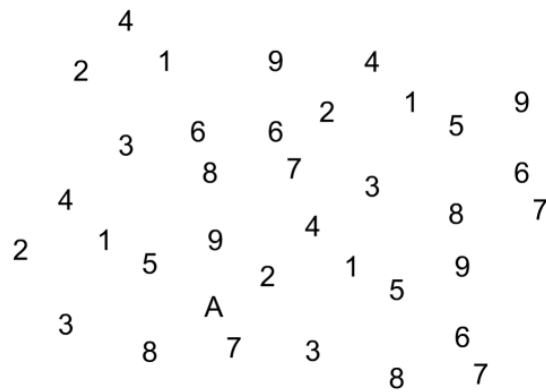
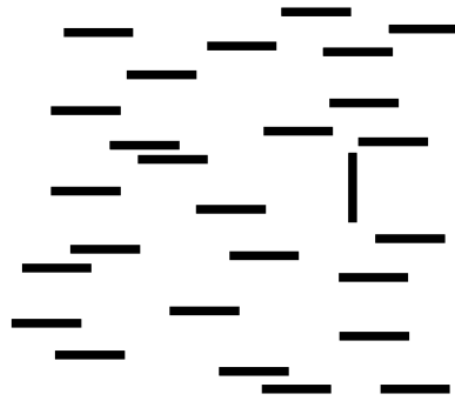
We have seen 2 types of attention:

1. spatial: you can voluntarily direct the spotlight of attention selects a particular location.
2. feature-based: you can voluntarily focus your attention onto a particular attribute such as orientation, color, etc.

In addition there is a 3rd type of attention

Object-based: Objects that stand out from the background automatically attract attention.

This can be a vertical line that pops out when seen in a field of horizontal lines, a letter that pops out when seen in a field of numbers, or thick lines that form a rino pop out when seen against a field of thinner lines.



Neglect

We saw that the PTO is involved in focussing our attention to the spatial location of objects in space and to a particular object.

A lack of attention leads to lack of awareness. A lesion of the right PTO causes neglect of things on the left. The patient is unaware that half the world is gone.

In a right V1 lesion, one is blind to everything to the left of where one's eyes look.

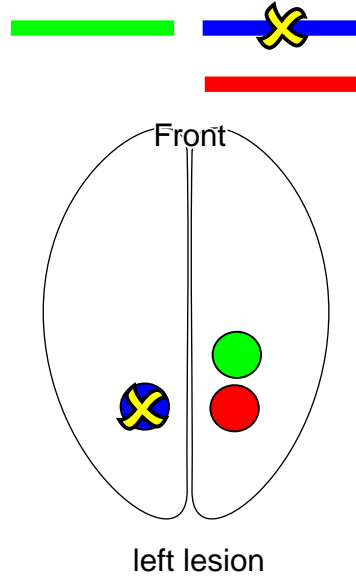
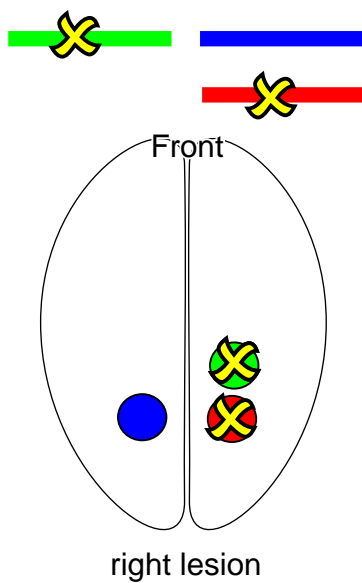
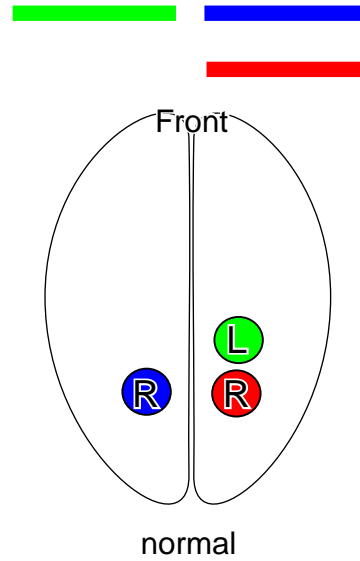
In many right PTO lesions, the left side of the face is neglected independent of whether you look (X) to the right or left of the face.

This is because what is left and right depends on how the brain frames the object.

In objects like faces, the frame is drawn around the face and patients neglect the left side of the frame independent of its position.



You might suppose that a lesion of the left PTO would result in neglect of things on the right. Strangely it does not. One suggested explanation is that the right side contains a representation of things on the left and right while the left contains only a representation of things on the right.



Thus after a lesion on the left, the right side still attends to things on the right (as well as the left). After a lesion on the right, the representation of things on the left is lost.

Coordinate Frames

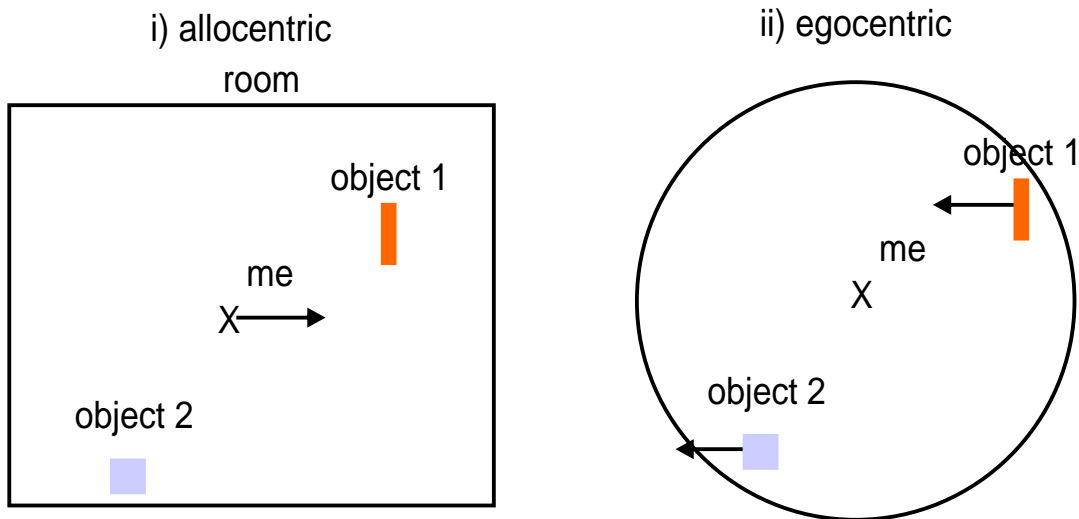
There are many ways of stating an object's location. Two ways are:

i) Allocentric coordinates: State its location with respect to some other object, e.g., a table in terms of its location in a room, or a feature of a face in terms of its location on the face.

Allocentric coordinates can also be thought of as object centered. For example, the room can be thought of as an object.

ii) Egocentric coordinates: State where the object is relative to *you*. (Note *you* can be your body, your head or your eye).

The best way to appreciate the difference between these is to consider what happens when you move (e.g. to the right).



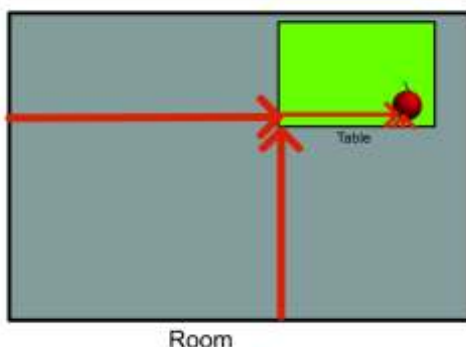
A useful model: Take two transparencies. On one draw an x indicating your location. On the other draw the location of a few objects. Place the two on top of each other.

For allocentric: move the sheet with you on it. See how you re-code your position while the position of all the other objects stay fixed.

For egocentric: move the sheet with the objects on it.

See how you re-code the location of all the objects while your location stays fixed.

Allocentric & egocentric coordinates may have nested frames.



An example of a nested allocentric frame:

Frame 1. The location of the apple may be specified with respect to the table.

Frame 2. The location of the table may be specified with respect to the room.

Coordinate Frames

Areas in the "where" stream tend to encode locations in egocentric coordinates.

Areas in the "what" stream tend to encode locations in allocentric (object centered) coordinates.

If the task is to recognize a face, the "what" stream is involved. The frame of attention is centered on the face. The features of the face are coded in an allocentric frame and you can attend to a feature on the left or right side of the face independent of where the face is on the retina (i.e. relative to the eye).

If you are standing at one end of a square and the task is to walk to restaurant on your left, the "where" stream becomes involved

