

# The Physiology of the Senses

## Lecture 5 - The Cerebral Association Cortex

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### Contents

|   |    |
|---|----|
| Objectives .....  | 1  |
| The Main Subdivisions of the Cerebral Cortex .....            | 2  |
| Some Properties of the Cortex .....                           | 3  |
| Functions of the Prefrontal Association Area.....             | 15 |
| Functions of the Parietal-Occipital-Temporal (PTO) Area ..... | 17 |
| Neglect.....  | 22 |
| Coordinate Frames.....  | 23 |
| See problems and answers posted on .....                      | 24 |

### Objectives

- 1) List the 5 main functional cortical subdivisions.
- 2) Contrast the 2 opposing theories as to whether different cortical areas have unique functions.
- 3) Specify what a patient with a section of the corpus callosum cannot do when an apple is shown in the left visual field.
- 4) Compare the 2 functions of the Prefrontal Association areas.
- 5) Describe 3 functions of the Parietal Temporal Occipital Association areas.
- 6) Contrast the 3 different types of attention.
- 7) Suggest a hypothesis that explains why left-sided lesions of area PTO do not cause neglect.
- 8) Specify how the coordinate frames of the "what" and "where" streams differ.

## The Main Subdivisions of the Cerebral Cortex

We began in Chapter 1 with the story of how light is converted into electrical activity by the eye. In chapter 2 we examined how the cortex then extracts features which in chapter 3 were assembled into visual objects and in chapter 4 led to the perception of motion. In this chapter we will examine the functions of the remaining cortex, those in the association areas.

### The 4 anatomic subdivisions (Figure 5.1A)

The cortex has 4 lobes: frontal, temporal, occipital, and parietal.

### The 5 functional subdivisions

#### 1) primary sensory and 2) motor areas (Figure 5.1B)

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

#### 3) higher order (secondary) sensory and 4) premotor areas (Figure 5.1C)

Higher order visual, somatosensory, and auditory lie near the respective primary areas. This is where each modality of sensory information is further processed for the most part without the influence of the other modalities.

Premotor areas send commands to the motor areas.

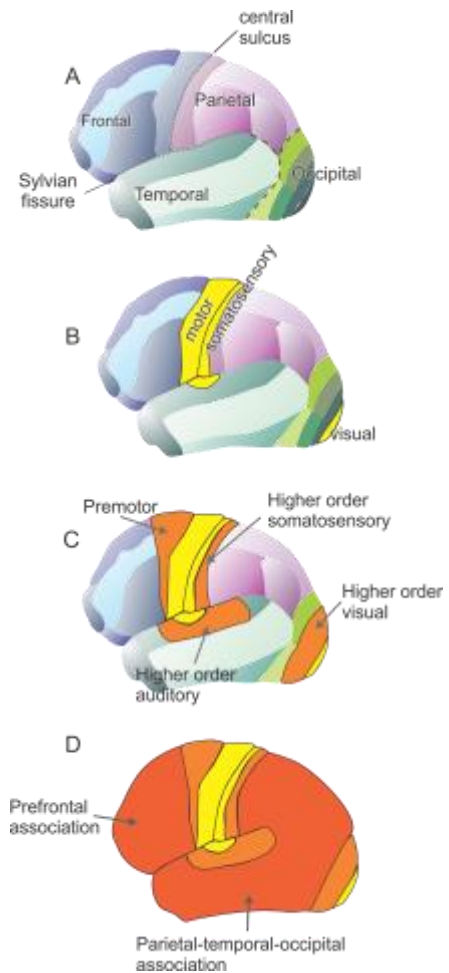
#### 5) the Prefrontal and Parietal-Temporal-Occipital association areas (Figure 5.1D)

These make up over half of the cortex. It is where:

- different modalities combine,
- attention is shifted,
- planning occurs and decisions are made,
- things are remembered.

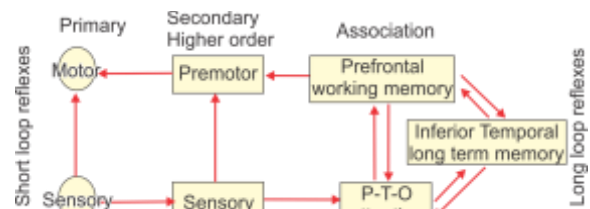
### How are the different areas of cortex interconnected?

Much of what we do can be considered a motor response to sensory input, a reflex. Short loop reflexes mediate rapid but simple responses, such as swatting a mosquito (Figure 5.2). Complex reflexes, such as writing down the name of a seen object, require the processing power of the association regions.



**Figure 5.1 The Association Areas**

**A:** the anatomic subdivisions. **B:** primary sensory and motor areas. **C:** higher order areas. **D:** association areas.



**Figure 5.2 Interconnections Between the Different Areas** Rapid short loop reflexes are on the left and long loop are on the right.

## Some Properties of the Cortex

### Grey and White Matter

The neurons in all areas of the cortex are confined to a thin sheet called the grey matter. This sheet is extensively folded to minimize the size of our skulls while maximizing the area of the cortical sheet. In the mature brain this sheet contains 100 billion neurons.

All areas of cortex are extensively interconnected through fiber tracts that form the white matter of the cortex. This white matter contains several million miles of axons. The extensive interconnections predispose the cortex to epilepsy. Abnormal activity in one area quickly spreads to other regions, leading to a seizure. These interconnections are also, as we will see later, where our memory is. Our grey matter contains an amazing thousand trillion connections (synapses).

The grey matter requires more oxygen than the white matter. To minimize the total oxygen supplied, blood is directed preferentially to areas of the grey matter that are in use. This is the basis for functional magnetic resonance imaging, fMRI, which reveals which areas of the cortex are most active in a particular task. fMRI measures the delivery of oxygen to approximately a cubic mm of grey matter containing millions of neurons, over a time span of seconds. In comparison, action potentials of neurons are measured in a fraction of milliseconds. fMRI adds the brain's functioning to the structure imaged by MRI. fMRI has exploded in popularity for research and in all likelihood will become very popular clinically.

*Connectivity is very important for the human brain's processing speed.*

Each neuron connects on average to 1,000 other neurons. In turn each neuron's output is dependent on the input from a large number of other neurons. By comparison, modern PCs with 64 bit processors have an equivalent 64 connections. The number of connections seems to be the crucial difference between the brain and computers, at least for now.

Diffusion tensor imaging (DTI) is another new MRI technique that maps the brain's connections, the axons in the brain's white matter. DTI is being used to construct the [Human Connectome](#): a map of all the neural connections in the human brain. DTI is also used to map the nerve fibers in this [amazing video](#) which shows neurons on the grey matter in one area communicating with others.

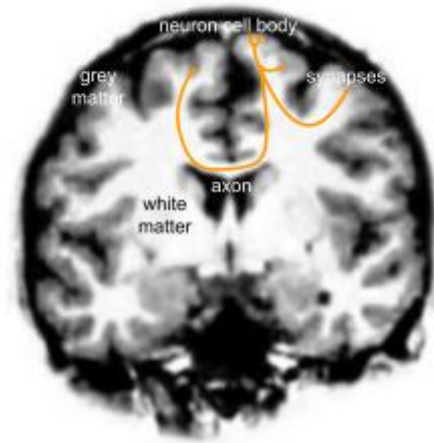


Figure 5.3 The Grey and White Matter

#### The Human Brain Is

A three-pound ball.

100 billion neurons joined by 100 trillion (100,000,000,000,000) connections

100 billion neurons is 10% of a 1 terabyte computer disk that costs a few \$100

No computer understands "a rope is for pulling not pushing", but a 6-year-old human brain can.

*Grey matter consists of six, anatomically distinct, layers.*

Information arrives in layer 4, spreads to more superficial and deeper layers, and is finally integrated by output cells whose bodies are located in layers 3 and 5.

Layer 4 receives input from the thalamus. For this reason it is thickest in primary sensory regions. The primary visual cortex is also called the striate cortex because the thick layer 4 here distinguishes it from adjacent areas.

Layers 3 and 5 send output to other cortical regions, the brain stem, and spinal cord. These layers are thickest in primary motor cortex, which sends axons down the spinal cord to contract the body's muscles.

More than 100 years ago, such anatomical differences in layer thickness allowed K. Brodmann to divide the cortex into 43 areas in the human brain. Only now are we discovering that perhaps each has a unique function.

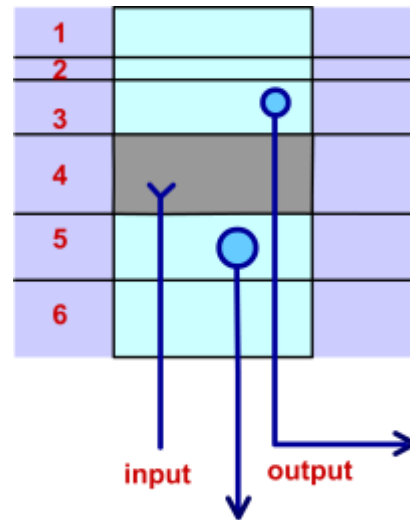


Figure 5.4 The grey matter has 6 layers, layer 4 receives input and layers 3 and 5 send output.

### *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 often results in minimal impairment.

*Evidence against:* The cortex is not uniform. Different regions serve different functions. This is most clearly seen in the primary sensory and motor areas.

**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 problem recognizing grandfather.

*Evidence for:* Lesion of the FFA 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 (e.g. of grandmother but not of aunt Jane).

Truth probably lies somewhere between these two extremes.

### *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, the area which normally 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 may become organized in a new cortical area. For example, language is usually represented more strongly on the left. If the left cortex is damaged early in life, the right side develops stronger language function.

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

### a) Each hemisphere excels in different tasks.

The “dominant” side (usually the left) excels in sequential or serial tasks such as language (reading, writing, speaking, signing) and mathematics (algebra  $A=B$ ,  $B=C$ , therefore  $A=C$ ).

The “non-dominant” side (usually the right) excels in tasks requiring parallel processing such as face recognition and geometry. It excels in tasks that are spatial or intuitive, (C resembles O as I resembles L), and music.

Although one side may dominate for a particular function, recent evidence suggests that the other cortex is also activated, although less, in the same function.

### b) Patients with a section of the corpus callosum

The corpus callosum is the large fiber tract that interconnects the two hemispheres. One extreme treatment for patients with severe epilepsy was to cut the corpus callosum. This limited the epilepsy to one hemisphere and reduced its severity.

When a patient with a cut corpus callosum is shown an apple in his left visual field, the patient cannot name the apple because it is not seen by the language center on the left.

The patient can 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 can function in one person. One patient was reported to have hugged his wife with one arm and push her away with the other.

### c) What are the advantages and disadvantages of lateralization (specialization of each side)?

#### Advantages:

Corpus callosum pathways are long. Pathways within the same hemisphere that interconnect related regions are often shorter and thus faster.

Duplication would be a waste of one hemisphere. By having different specializations in each hemisphere, the capacity of the brain could be nearly doubled. Two halves could do two different things at the same time.

#### Disadvantage:

Less redundancy. Redundancy is good if one part breaks down.

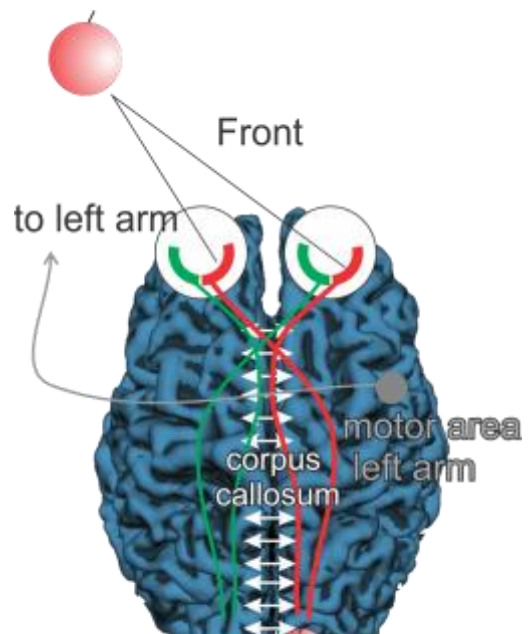


Figure 5.5 A patient whose corpus callosum, the connection between the two sides, has been cut, is shown an apple in his left visual field and asked to reach to it with his left arm or name what he sees.

## Functions of the Prefrontal Association Area

The prefrontal cortex has become larger, as a percentage of total brain size, over the course of evolution (Figure 5.7). As a consequence, many believe that it is this area that distinguishes us from other animals.

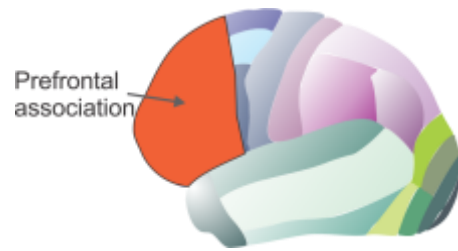


Figure 5.6 The Prefrontal Association Area

Gorillas are far bigger than humans. Why are not their brains bigger than ours? The answer is that they could not digest enough calories to fuel a human sized brain. The most important factor in our brain's growth and development was homo-sapiens' learning to cook food. As mentioned before, thinking is expensive process. The brain which is only 2% of body weight uses up 20% of its oxygen and metabolic consumption. Without cooking we would have to be eating 24 hours a day just to provide enough energy for our brains. There would be no time for thinking.

### Function 1: Planning and working memory

Imagine playing checkers and planning your next move. To do this you have to go through different moves and then compare them to decide which is the better. This in turn requires a short-term memory called working memory. Both planning and working memory are important functions of the prefrontal association area.

Close your eyes, wait, and then point to a particular object that you remember being in the room. Your ability to remember the location of an object is another example of working memory, in this case spatial.

Children, prior to the age of 1 yr., have not developed this working memory. If a toy is hidden behind one of two covers, the child cannot find it. Out of sight is out of mind.

Lesions of the prefrontal association area produce deficits in tasks that are spatial and delayed (remembering for few seconds which of two boxes contains food).

Neurons in the prefrontal cortex  
 a) show activity, which starts when a stimulus appears in a particular location (Figure 5.8, T on) and  
 b) 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.

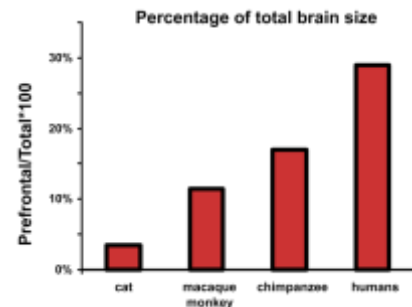


Figure 5.7 The size of the prefrontal association area, as a percentage of total brain size, is largest in humans.

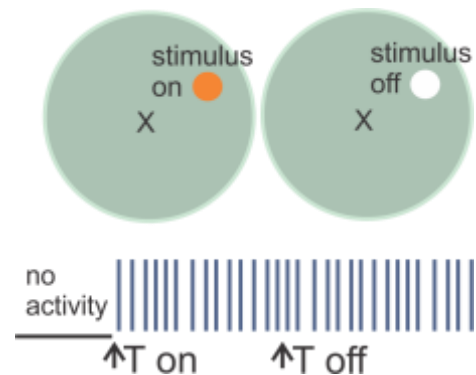


Figure 5.8 A visual stimulus, up and to the right, is turned on, orange dot, and then off. The neuron in the prefrontal association remains on even after the stimulus goes off (working memory).

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 an actual external stimulus to initiate movement.

### *Function 2: Decision-making*

Having compared a variety of checker moves, the next step is to make the decision to move. This is a second important function of the prefrontal association area. After lesions of this area little frustration is displayed when the patient makes mistakes in every day decisions. One might expect that a destruction of the tools to plan and decide would make one less prone to become frustrated. But at what cost! Surprisingly neurologist António Egas Moniz won the Nobel Prize for medicine in 1949 for inventing frontal lobotomies. Later Dr. Walter Freeman performed these lobotomies in minutes using an ice pick hammered through the back of the eye socket into the brain. He performed thousands of lobotomies in minutes from his office. His patients included Rosemary Kennedy, the sister of John F. Kennedy.

Have our techniques for tinkering with the function of such a complex organism as the brain become less blunt? Perhaps not. The pharmaceutical industry typically screens anti-depressants by injecting a laboratory rat with potential drugs, putting the rat in a beaker of water, and measuring how long the rat continues to swim trying to escape. Perhaps this behavioural test is not for anti-depressants but for one that tests against the wise rat that decides it is useless to try.



## Functions of the Parietal-Occipital-Temporal (PTO) Area

**Function 1: Polimodal convergence of senses:** This area is near visual, somatosensory, and auditory our primary sensory areas and thus ideal for tasks that may require these senses. Locating objects in space can be done by touch, sight, sound etc. Language involves convergence of the sound of words, written words (sight), or Braille (touch). These topics will be covered in the next chapter and in chapter 9.

**Function 2: Attention:** Attention allows us to focus in on specific stimuli and neglect others, for example a specific voice in a crowd. Both attention and neglect will be covered in detail here in this chapter.

**Function 3: Memory:** The inferior and medial portions of the temporal lobe are large areas, located on the underside of the cortex, that are 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). We will look at memory in detail in the last chapter.

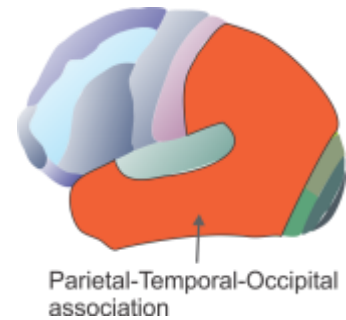


Figure 5.9 The Parietal Temporal-Occipital-Temporal Association Area

### The Flashlight of Attention

Researchers at Western Washington University questioned students who walked past a unicycling clown while talking on their cell phones. Those using their phones were twice as likely of not noticing the clown as those that were not. Drivers who are texting are as impaired as those who are drunk. In-attention causes blindness. This is true whether you are walking, driving a car or listening to a lecture.

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

Attention acts like a bottleneck. 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. We are blind to what does not get through the bottleneck. But why is a bottle neck required?

"The amount of information that is potentially available through our sense organs is far greater than our brains can handle." (Tootell & Hadjikhani 2000). Were it not for the small flashlight of attention the brain would fry!

Is this true? No, you would faint. Recall how metabolically costly action potentials are. Attention is another method the brain uses to limit the number of active brain cells. Attention directs activity to particular brain areas that are best suited to process that information.



Figure 5.10 The "spotlight" of attention casts light on only a small part of what one sees.

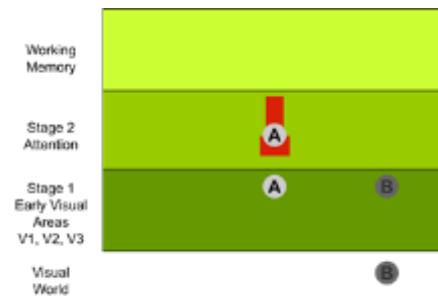
### *Visual perception is a two-stage process.*

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

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

Visual objects compete for your attention. While attention is processing one visual object, you are blind to the presence of other objects, even those at the location you had been attending. This is known as the attentional blink. We behave as if our eyes are closed while attention is processing an object.

Attention can be drawn from below by objects that pop out from the background. In early visual areas, like or similar objects are inhibited and have a reduced influence while objects that are different are accentuated and thus draw attention to themselves. Areas in the parietal dorsal stream can also direct attention voluntarily, as can areas that direct them.



**Figure 5. 11** An image A appears in V1, V2, and V3 and is captured in stage 2 by the “spotlight” of attention. If an image B appears in V1, V2, and V3 it is neglected until the processing of image A is complete.

### *Finding an object in a crowded scene takes time.*

**Figure 5. 12** Can you find the fallen skater in this painting completed at the end of the little ice age? The one with a hockey stick? “Ice Skating near a Village” 17th-century Dutch artist, Hendrick Avercamp



It takes time for 3 reasons.

- 1) Because the object does not automatically draw your attention to itself as does a horizontal line among a background of vertical lines.
- 2) Because it takes time to voluntarily shift your attention without moving your eyes (covert shift) or make an eye movement from one potential object to another (overt shift).
- 3) At each location, it takes time to process the image and decide if it is desired object 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 locus coeruleus neuron projects to 100,000 cortical neurons. These neurons act like a volume control to increase one's level of alertness.

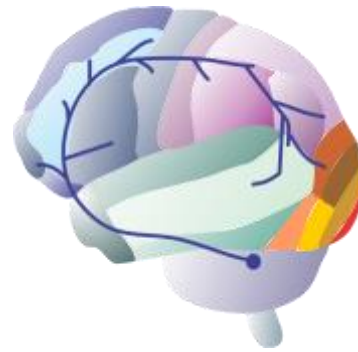


Figure 5.13 One Circuit for Arousal, that from the Locus Coeruleus

*Attention can be directed at a specific location.*

This is illustrated by a simple experiment developed by Posner (Figure 5.14):

A) The subject is instructed to fixate on the X and to watch for a trigger, a circle.

B) The subject is cued, with a square, to expect the circle at a particular location.

C) A trigger circle is presented at the expected location (right) or some other (left).

The subject has better sensitivity to the cued side, in this case the right, because attention was shifted to that location. Sensitivity can be measured by reaction time or the ability to detect a faint stimulus.

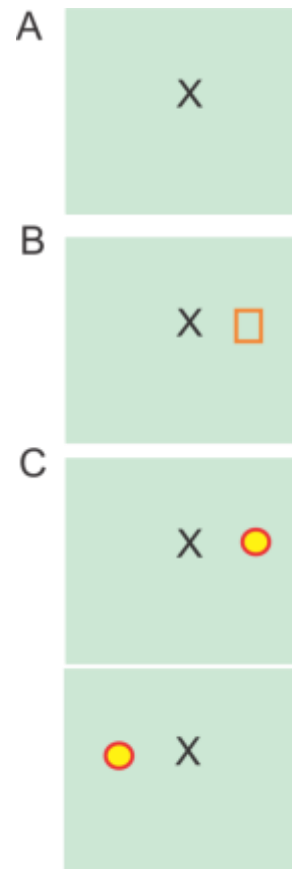
Figure 5.14

Posner's Experiment on Attention.

A: Fixate X

B: Cue appears on right.

C: Target for saccade appears on the right (expected) or left (unexpected) position.



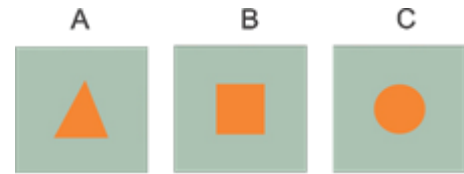
*Attending to different features causes activity in different cortical regions.*

A subject is shown an image A and then, after a delay of .5 sec, image B and then C, each in different colors and moving in different directions.

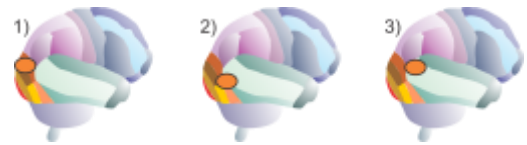
The subject is instructed to perform one of three tasks:

- 1) “Indicate when two successive objects have the same color.”
- 2) “Indicate when two successive objects have the same shape.”
- 3) “Indicate when two successive objects have the same direction of motion.”

In each of these tasks, attention is focused at a different feature, color, shape, or motion. This in turn requires activation of particular cortical areas that are best suited to processing that feature. For color, early visual areas, V1, V2 V3 are activated. For form, area LOC is activated, and for motion, area MT+ (Figure 5.15).



**Figure 5.15** An Experiment in Attending to Different Features After instructions that focus attention to 1) color 2) shape, or 3) direction of motion three shapes (A, B, or C) are presented in sequence.

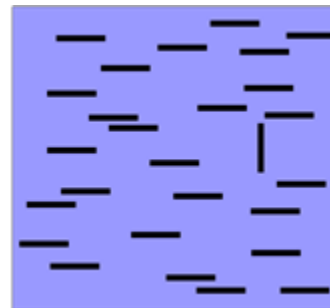


**Figure 5.16** Areas with Enhanced Attention

Attention to 1): color enhances activity in early visual areas, 2): shape in area LOC or 3): motion direction in area MT+.

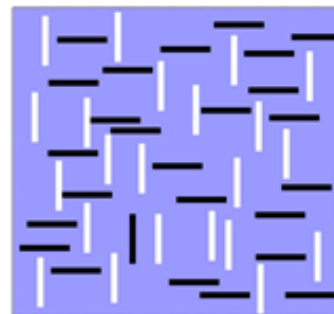
*Attention to Color and Orientation*

In the Figure 5.17 find the line that is different. That is easy because, as we saw in Chapter 3, your early visual areas automatically cause the odd line to pop out and draw your attention to it.



**Figure 5.17** An example of an object, the vertical line that automatically draws attention to itself.

In Figure 5.18 finding the odd line is more difficult. It takes a bit longer because now the odd line no longer pops out. It takes time to search through each line using either covert or overt shifts in attention.



**Figure 5.18** In this more complex figure it takes longer to find the odd line. This speeds up if you search only for the odd *black* line, ignoring those that are white.

Now try again to find the odd line, 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. When, in Figure 5.17 the odd line automatically pops out, one uses primarily fast

connections from early visual areas (bottom-up). When, in the bottom set of lines, you use attention to select the dark lines, slower paths (top-down) become involved.

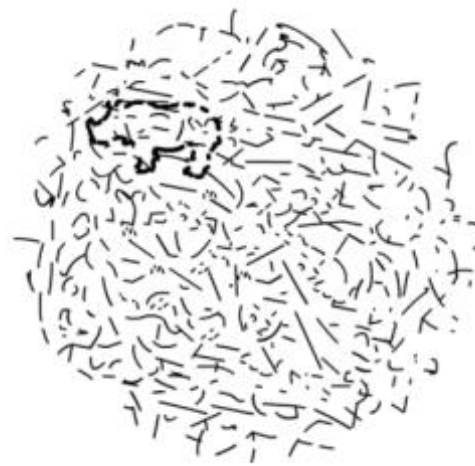
### *More Types of Attention*

*We have seen 2 types of attention:*

1. Spatial attention: you can voluntarily direct the spotlight of attention to 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 3<sup>rd</sup> type of attention.*

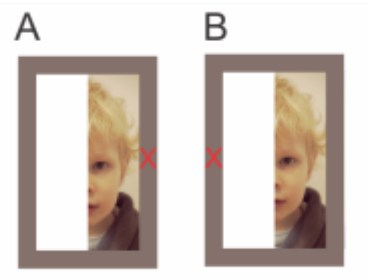
Object-based attention: objects, which stand out from the background, automatically attract attention. This can be a vertical line that pops out when seen in a field of horizontal lines (Figure 5.17), or thick lines that form a rhinoceros which pop out when seen against a field of thinner lines (Figure 5.19).



**Figure 5. 19** The thicker lines forming the rhinoceros are bound together into an object.

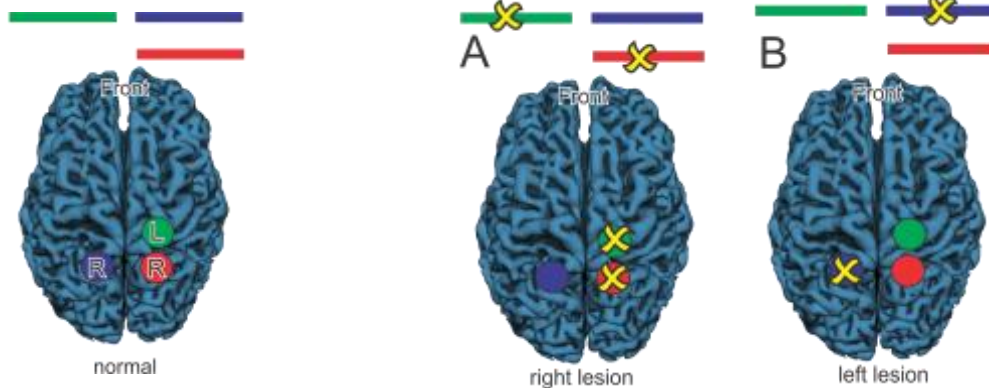
## Neglect

We saw that the parietal cortex is involved in directing our attention on the spatial location or on a particular object. A lack of attention leads to lack of awareness. A lesion of the right parietal cortex causes neglect of object's left side. Such a patient would be unaware that the left half of her own face is missing when drawing a portrait of herself from a mirror.



**Figure 5.20** Neglect produced by a lesion of the right parietal cortex results in a lack of awareness of the left half of a face, independent of where the face appears. X (red) is where the subject fixates. **A:** Face is in the left visual field. **B:** Face is in the right visual field.

In a right V1 lesion, one is blind to everything to the left of where one's eyes look. In many right parietal lesions, the left side of the face is neglected independent of whether the patient looked (X) to the right or left of the face (Figure 5.20). In objects like faces, the frame of attention is drawn around the face and patients neglect the left side of the frame independent of the frame's position on the retina.



**Figure 5.22** The right parietal cortex allows for awareness of features to the object's left (green) and right (red). The left parietal cortex allows for awareness of features only to the object's right (purple).

**Figure 5.21** Lesions of the parietal cortex produce neglect.

**A)** Lesions of the right parietal cortex produce a lack of awareness of features on the object's left.

**B)** Lesions of the left parietal produce little lack of awareness because both object sides are represented in the right parietal cortex.

You might suppose that a lesion of the left parietal would result in neglect of things on the object's right. Strangely it does not. One suggested explanation is that the right parietal directs attention to both the left and right side of objects. The left parietal directs attention only to the right (Figure 5.22). Thus after a lesion in the left parietal, the right parietal still attends to the right as well as the left side of objects (Figure 5,21B). After a lesion in the right parietal, one is not able to attend to the left side (Figure 5,21A).

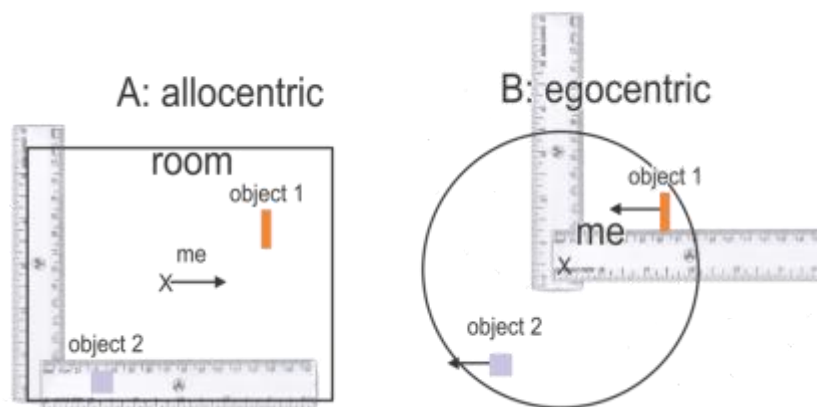
## Coordinate Frames

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

A) **Allocentric** coordinates give an object's 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.

B) **Egocentric** coordinates state where the object is relative to **you** (e.g. right, above, behind). **You** can be your body, your head or your eye. When giving the direction as "north", the direction is in allocentric coordinates as opposed to "right" which is egocentric.

To construct a useful model take two transparencies. On one draw an x indicating your location (me in Figure 5.23B). On the other, draw the location of a few objects (Figure 5.23A). Place the two on top of each other. The best way to appreciate the difference between these is to consider what happens when either moves.



**Figure 5.23** Coordinates **A**: Allocentric coordinates code locations with respect to objects in the world such as the location of objects with respect to a room. **B**: Egocentric coordinates code the location of objects with respect to some part of yourself such as the location of object in your visual field with respect to the fovea.

For allocentric, move the sheet with you on it. The ruler is on the room. See how you re-code your position in the room while the position of all the other objects stay fixed.

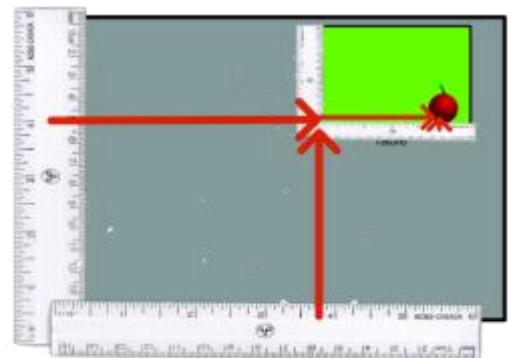
For egocentric, move the sheet with the objects on it. The ruler is on you. See how you re-code the location of all the objects with respect to you while your location stays fixed.

### *Allocentric and egocentric coordinates may have nested frames.*

An example of a **nested** allocentric frame is an apple sitting on a table that in turn is located in the corner of a room (Figure 5.24).

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.



**Figure 5.24** Nested Allocentric Coordinates

## The “What” and “Where” Streams

Cortical areas in the "where" stream tend to encode locations in egocentric coordinates. Areas in the "what" stream 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).

The "where" stream becomes involved when you are standing at one end of a square and the task is to walk to the restaurant on your left. It codes the location of the restaurant relative to you, i.e. in an egocentric frame. We will cover these and other egocentric frames in more detail in the next lecture on Visually Guided Actions.

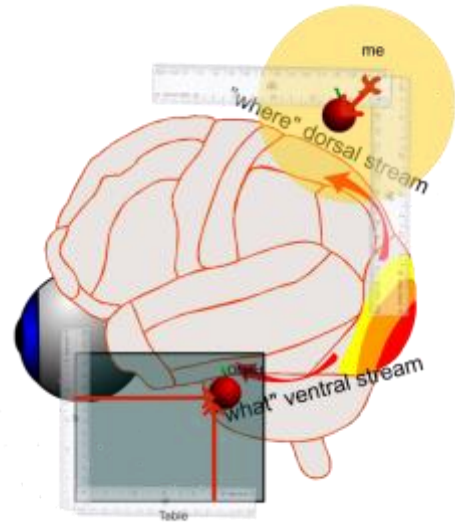


Figure 5. 25 Areas in the “what” stream code visually perceived objects in allocentric coordinates while areas in the “where” stream code target locations in egocentric frames.

See problems and answers posted on

<http://www.tutis.ca/Senses/L5Association/L5AssociationProb.swf>