The Physiology of the Senses
Lecture 6 Visually Guided Actions

http://www.tutis.ca/Senses/

Contents

Objectives

1. Compare the maps that are coded in the dorsal stream in terms of their similarities and their differences.
2. Contrast the pathways and functions of two types of saccadic eye movements.
3. Contrast the activation observed in the dorsal stream while one is passively viewing a TV show and when one is actively playing the Wii video game on the TV screen.
4. Describe the site of action and function of corollary discharge.
5. Contrast covert and overt shifts of attention.

revised 11/10/2016

Multiple Representations of Space

Recall that visual information from V1 divides along two streams:

1) a dorsal “Action" or “Where" stream to the posterior parietal cortex which contains several representations of space for the guidance movements, and

2) a ventral “What" stream to the inferior temporal cortex which is concerned the perception and recognition of objects.

The dorsal stream’s representations of space are used to guide a variety of movements: rapid eye movements (saccades), grasps, reaches, and feeding.

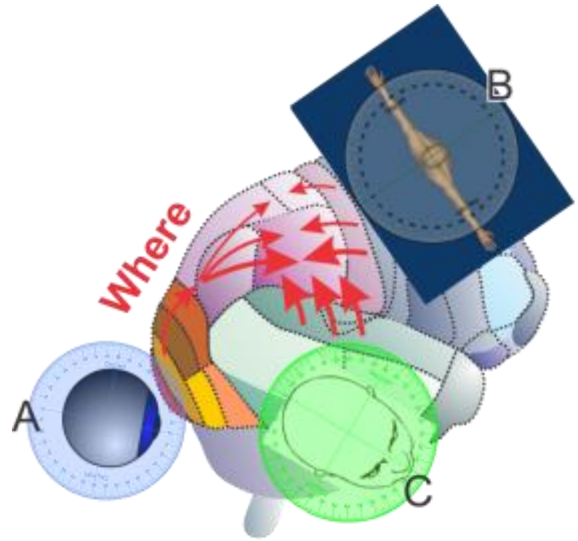


Figure 6. 1 Convergence of the “Where” Streams in the Posterior Parietal Cortex A: The visual information is initially coded in a retinotopic (eye centered) frame of reference. **B:** Proprioceptive sense of limb position is initially coded in a somatotopic frame. **C:** The auditory system initially codes sound location in a head centered frame.

The activation of these areas direct one's attention to locations, but the selection of the appropriate effector (e.g. which arm to reach with) can occur unconsciously.

Recall that the ventral stream is subject to **perspective illusions**. The length of line may not be what we perceive them to be. The dorsal stream is not subject to these illusions. This makes sense because you want to direct actions to the precise location of objects. In Figure 6.2 notice that bottom yellow bar looks shorter than the top one. But as you can see in the Figure 6.3 this is an illusion of the ventral stream. They are actually the same length. If using the dorsal stream, you were to throw a dart at the right most edge of this bar, your action would, most likely, be accurate and not subject to this illusion.

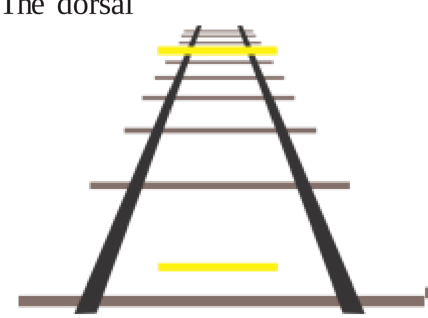


Figure 6. 3 The “What” stream is subject to perspective illusions. Notice that the bottom yellow line seems longer than the top one.

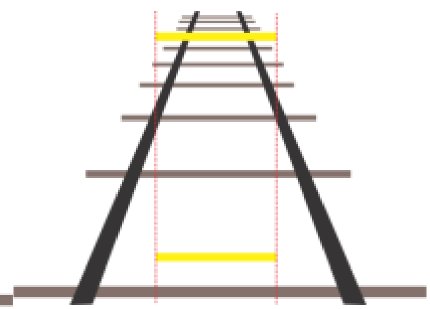


Figure 6. 2 The “Where” Stream is not subject to perspective illusions. Notice that the length of the yellow lines is actually the same. Your pointing movement to these ends should be accurate.

Another distinguishing feature between the dorsal and ventral streams is its **frame of reference**. The ventral stream uses an object-centered frame. The dorsal stream uses various forms of **egocentric frames**, some of which are the following (Figure 6.1).

1. The early visual areas code objects with respect to the retina.
2. The ears are mounted in the head, and so it is not surprising to find that the early auditory areas code locations with respect to the head.
3. The location of your finger is coded with respect to your body.

Patients with lesions in the dorsal stream have difficulty in making saccades, grasps, reaches, and feeding accurately.

These representations surround the Intra Parietal Sulcus (IPS).

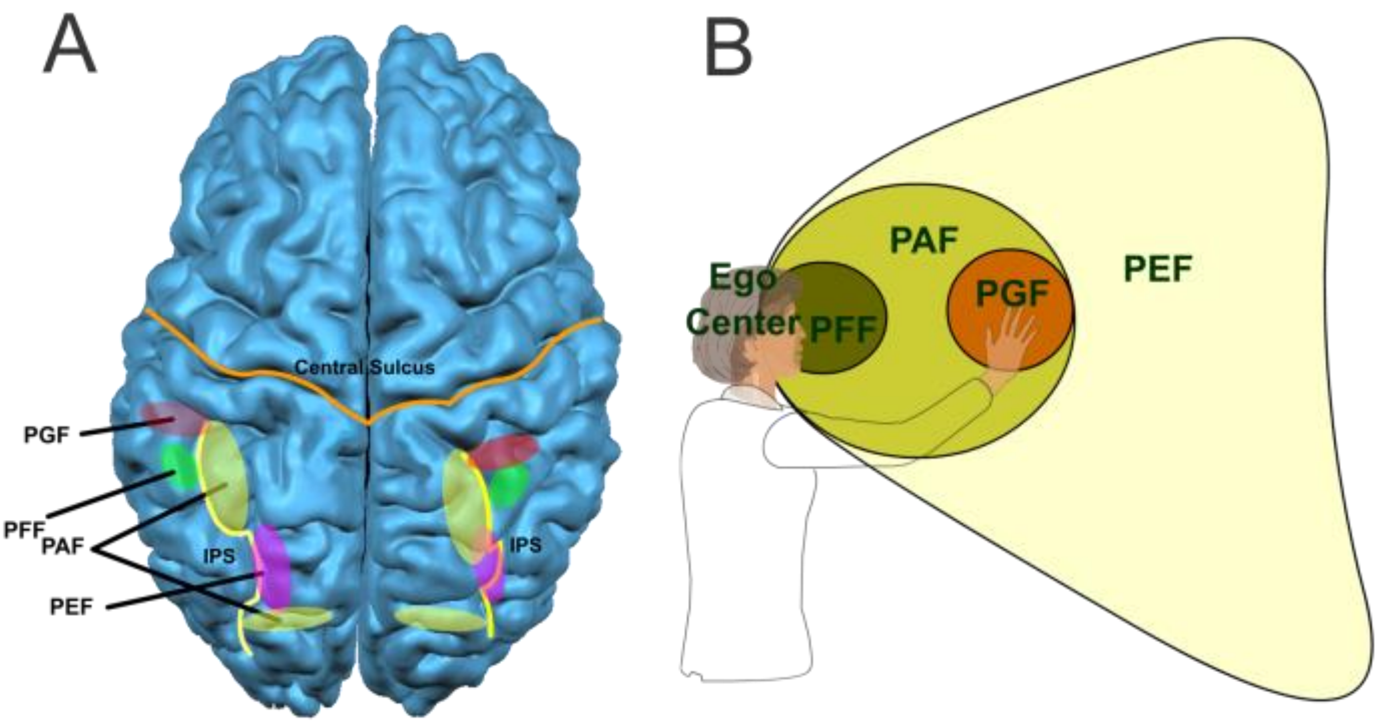


Figure 6. 4 Location of various representations of space along the intraparietal sulcus and their extent. A: The Parietal Eye Field (PEF), the Parietal Arm Fields (PAF), the Parietal Grasp Field (PGF), and the Parietal Face Field (PFF). Yellow line is the intraparietal sulcus and orange line is the central sulcus. **B:** The extents in space of the areas shown in A.

The **Intra Parietal Sulcus** (IPS) is ideally located to integrate the representations of space that are derived from several modalities of sensory information: visual, somatosensory, and auditory. Locations can be seen, felt, or heard. The IPS contains several fields each responsible for directing a particular type of movement.

PEF, the Parietal Eye Field, represents the retinotopic locations of objects that you intend to look at. Here neurons respond to visual and auditory stimuli that indicate a location.

PAF, the Parietal Arm Fields, represents retinotopic locations in the immediate peripersonal space, the region of space one can reach to. PAF is used to direct arm movements. Neurons receive both visual and somatosensory information. Lesions here cause optic ataxia, (visually directed reaching errors even though the vision and arm's motor systems are functioning correctly).

PGF, the Parietal Grasp Field, represents not the location of objects, but the shape information required to grasp objects. Also important is object information such as "strawberries are soft and should be grasped lightly".

PFF, the Parietal Face Field, represents the ultra near space that is used to guide the head, mouth, and lips during feeding or kissing. Neurons receive visual input and tactile input from the face.

Some of these egocentric regions, like PFF, map space that is near while others, like PEF, map space that is both near and far. Presumably PGF also receives input from the ventral stream of an object's properties such as their allocentric co-ordinates in order to grasp a knife by the handle and not the blade.

An Example of Activity of One Specific Neuron in the Parietal Face Field (PFF)

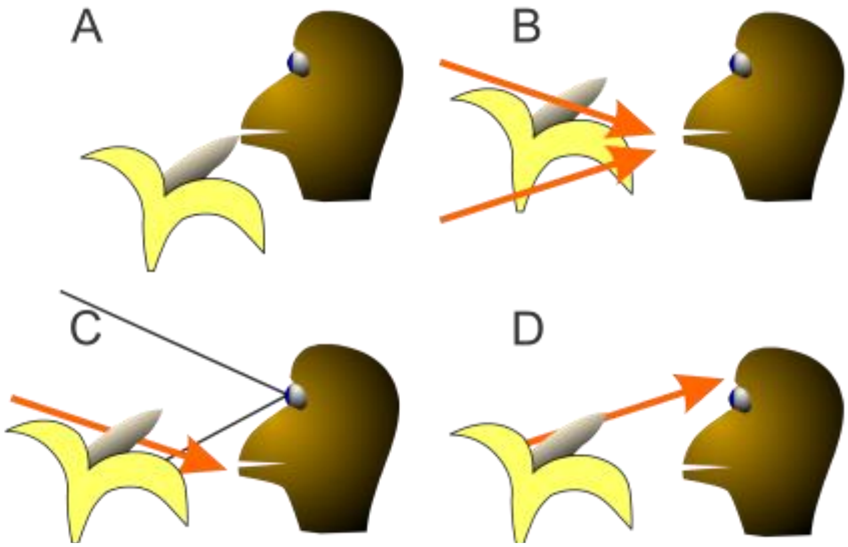


Figure 6. 5 Neurons in the Parietal Face Field (PFF) code specific locations with respect to the head
A: A neuron is activated by a touch to the lower lip. **B:** The same neuron is also activated by the sight of an object approaching the lower lip from any direction. **C:** And by the sight of an object approaching the lower lip independent of gaze direction. **D:** But this neuron is not activated by the sight of an object approaching the brow. That is the job of some other PFF neurons.

Visually Directed Saccadic Eye Movements

a) Express saccades

Saccades are rapid eye movements. Saccades to a novel peripheral stimulus (e.g. flashing/moving) involve the superior colliculus (SC). This stimulus generates short latency or "express" saccades.

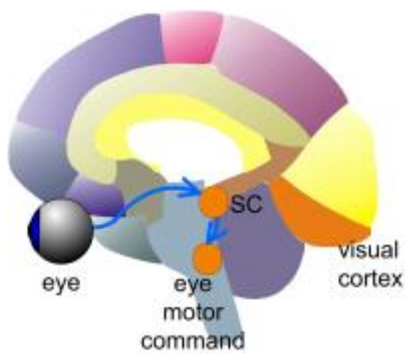


Figure 6. 6 The route for express saccades

b) Long latency voluntary saccade

The prefrontal association area holds the locations of remembered targets in working memory and makes the decision that one is of interest. The parietal eye field (PEF) directs attention at the one of interest. And the frontal eye fields (FEF) generate a longer latency saccade to it.

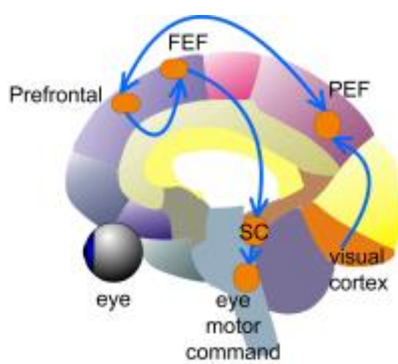


Figure 6. 7 The route for long latency voluntary saccades involves the frontal eye fields.

The activity of the superior colliculus reflects the engaging and disengaging of attention.

You may recall that the retinal ganglion cells, which project to the SC, have large receptive fields. Because of this, the activity is not localized to a point but to an area. The activity of cells in the center of the area has the highest activity. This can be viewed as a hill of activity. How the SC codes location provides important clues as to how the IPS codes location as well.

As we have seen, the superior colliculus mediates the visual grasp reflex. A visual stimulus in a periphery produces activity in a corresponding location in the SC (Figure 6.8A). Activity at this location generates a motor command, which turns the eye's fovea to the visual stimulus. This activates the foveal region at the center of the SC (Figure 6.8B).

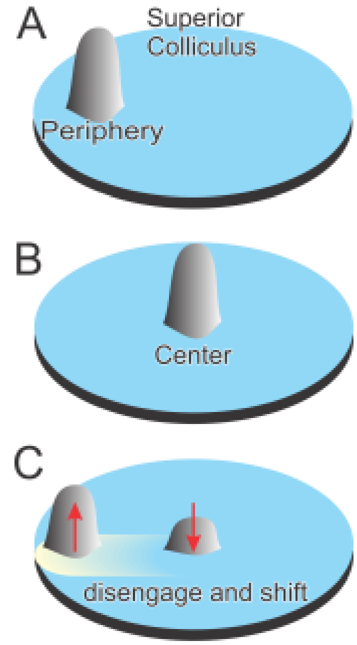


Figure 6. 8 The hills of activity in the superior colliculus (SC)

A: The visual stimulus in the retina's periphery activates the corresponding region of the (SC).

B: During fixation of the visual target a hill of activity in the foveal SC suppresses the generation of saccades.

C: To generate a saccade the activity at the center must be suppressed and that at the periphery enhanced.

Before the next saccade can begin, the hill of activity at SC's foveal region must be removed. This hill of activity projects to neurons in the brain stem and keeps the eyes fixating at the current location by inhibiting the generation of saccades. Thus not moving your eyes, fixation, is an active process.

To remove the activity at SC's foveal region, a strong visual stimulus must appear at the peripheral SC or the PEF must disengage one's attention from the center and then shift it to the periphery (Figure 6.8C).

A Comparison of Five Topographic Areas

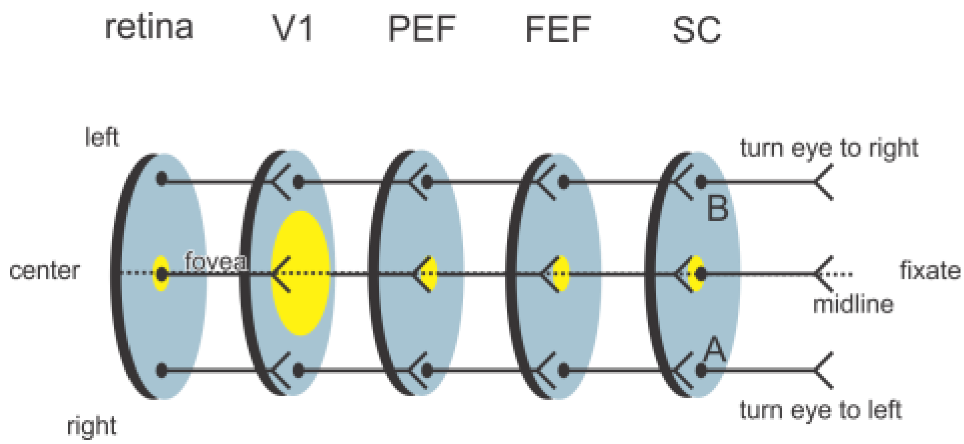


Figure 6. 9 Topographic Maps in the Retina, the Primary Visual Cortex (V1), the parietal eye fields (PEF), the frontal eye fields (FEF), and the superior colliculus (SC) Both sides of the brain are shown, with the midline running through the center. Half the foveal (yellow) representation is on one side and half is on the other side.

Like the superior colliculus (SC), the retina the primary visual cortex (V1), the parietal eye fields (PEF), and the frontal eye fields (FEF) have topographic maps where the location of a group of active cells indicates the relative location of a target in the visual field. This becomes a map for the required size of movements. If one electrically stimulates a group of cells in the superior colliculus or FEF at location A (Figure 6.9), the eye would orient towards A. Similarly, stimulation at B causes an orientation to B. Activity at the center maintains fixation. Also if you electrically stimulate at A and B at the same time, the commands would cancel and no movement occurs.

Area V1 has a large foveal representation, as do other areas in the ventral "what" stream. In contrast, areas PEF, FEF, and SC have large peripheral and small foveal representations, as do other areas in the dorsal "where" stream.

Compare the activity in each area under the following four everyday conditions:

In each case one is recording from a region that is activated by a light stimulus at location A or B, and the eye is initially pointing forward at center.

Condition 1: while looking forward a visual stimulus appears at the peripheral location A but no motor response is required.

In this case enhanced activity is restricted to location A of the retina and visual cortex.

The foveal activity in the FEF (and SC) maintains the forward fixation (i.e. prevents saccades). Because attention is limited to the forward direction the FEF and PEF are blind to stimulus A.

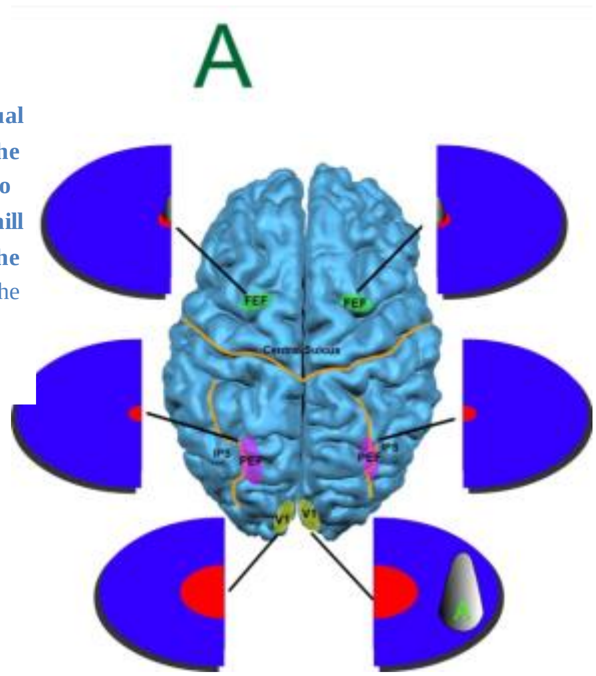


Figure 6. 10
When a visual stimulus appears in the left visual field, but no action is required, a hill of activity occurs in the right V1. Activity in the foveal FEF maintains fixation.

Condition 2: the same visual stimulus appears at A but now subject is required to saccade to A.

In this case activity is the same as condition 1, plus enhanced activity in PEF, FEF, and SC at location A.

A saccade is generated.

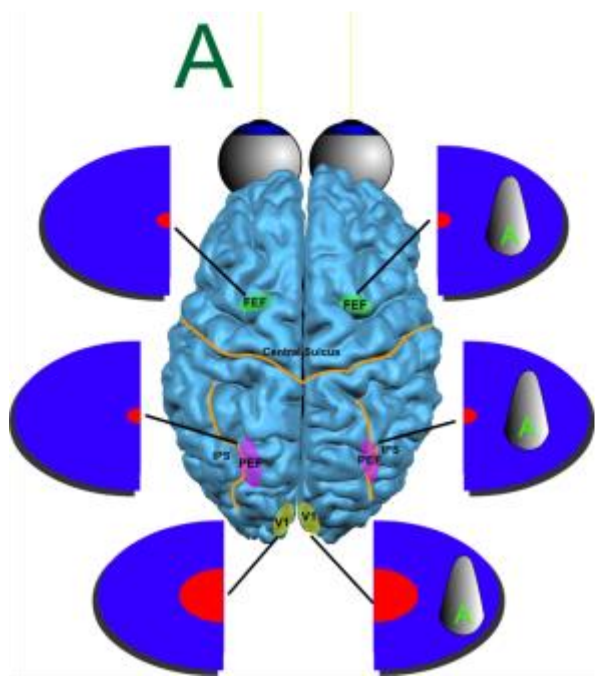


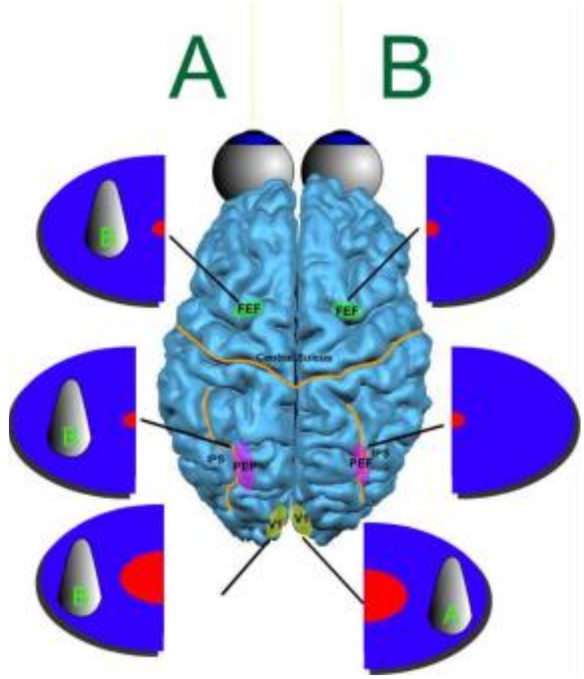
Figure 6. 11
When a visual stimulus appears in the left visual field and a saccade to the stimulus is required, a hill of activity occurs in the right V1, PEF and FEF. Activity in the right FEF initiates a saccade to the stimulus.

Condition 3: a visual stimulus appears at A and B, and the subject is instructed to saccade to B not A.

In this case enhanced activity is observed in the left side of all areas at location B. At location A, enhanced activity only occurs in the retina and the right visual cortex.

A saccade to B is generated.

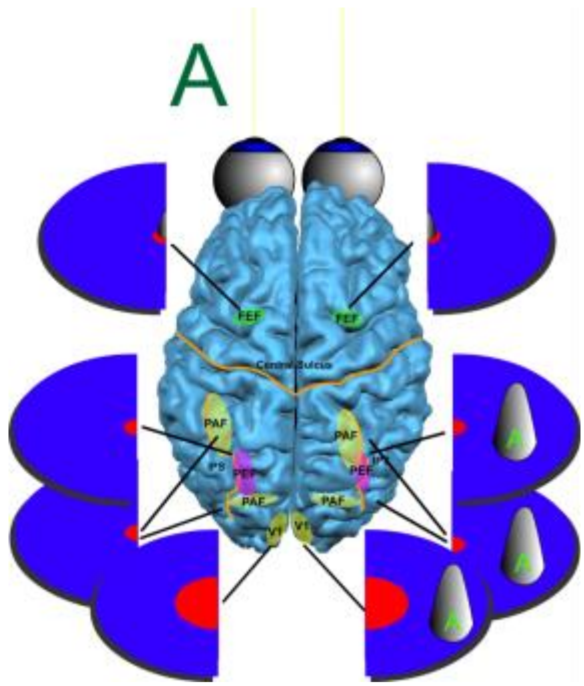
Figure 6. 12 When a visual stimulus appears in both visual fields a saccade to the stimulus on the right is required, a hill of activity occurs in the left V1, PEF and FEF. Activity in the left FEF initiates a saccade to the stimulus. Activity also occurs in the right V1.



Condition 4: a visual stimulus appears at A and the subject is required to make an arm movement to A while still fixating the center.

Because no saccade is required, little enhanced activity is observed in the FEF or SC at location A. Enhanced activity at location A of areas PEF and PAF on the right leads to activation of appropriate limb motor areas to direct limb movement to A.

Figure 6. 13 When a visual stimulus appears in the left visual field and arm movement to the stimulus is required, a hill of activity occurs in the right V1 and PEF. Activity in the right PAF initiates an arm movement to the stimulus.



Conclusion:

In the retina and visual cortex, activity requires a visual stimulus.

In the PEF, activity requires a visual stimulus and attention. Attention selects the target for a movement.

In the FEF and SC, activity occurs when an orienting response of the eyes is required. In contrast activity is directed to PAF if movement of the arm is required.

Three Properties of the Parietal and Prefrontal Areas

1) These are activated by the memory of target locations.

In figure 6.14 a target is shown briefly at location A, and one is asked to attend to it but not look at it. After the visual stimulus disappears, activity is maintained in the parietal eye fields (PEF) and in working memory in the prefrontal (PF) cortex.

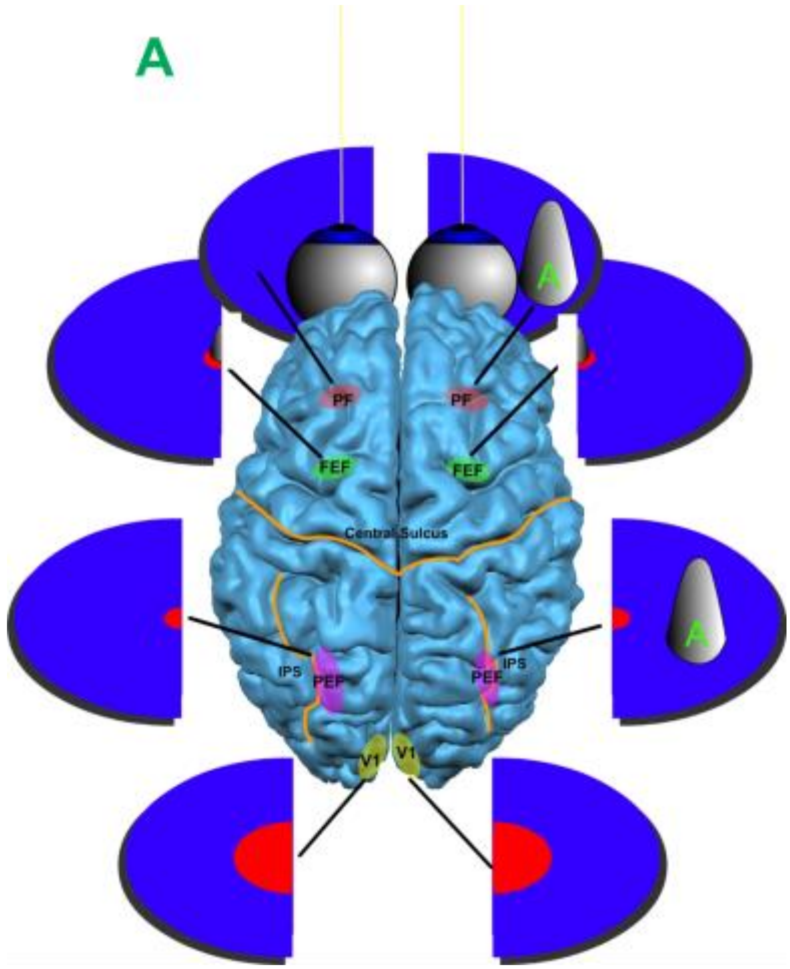


Figure 6. 14 The memory of a target in the left visual field produces activity in the right PEF and PF. Activity in the foveal FEF maintains fixation.

2) Their spatial representations are updated after saccades in the parietal and prefrontal areas.

Suppose two visual targets, A and B, are **briefly** flashed in sequence and then both disappear. The instruction is to saccade to A and then to B.

Figure 6.15 shows the areas activated immediately after the visual stimuli are presented.

Two hills of activity persist in the PEF and the prefrontal cortex (PF), one for target A and another for B. In the FEF, the hill is bilateral in the foveal area.

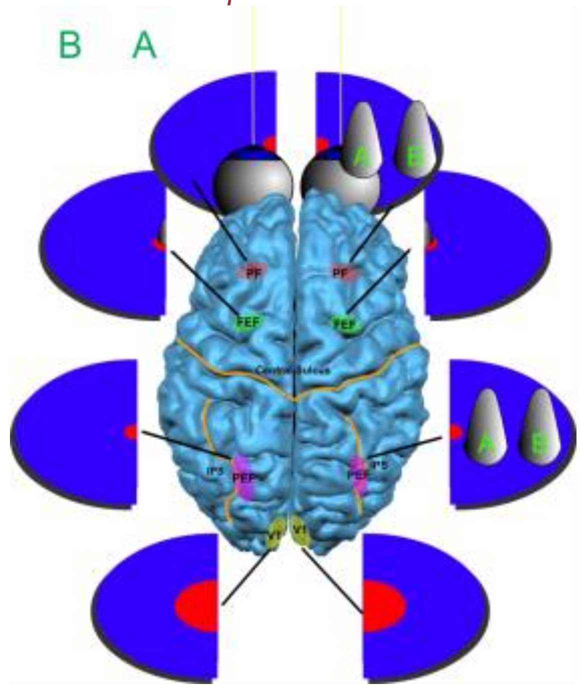


Figure 6. 15 Two visual targets are shown in sequence in the left visual field in sequence, A then B. Before a saccade in initiated two hills of activity are seen in the right PEF and PF as well as foveal FEF.

After a saccade to the memory of "A", the activity in parietal and prefrontal cortex jumps, or shifts. "A" now appears in the foveal region.

It is thought that activity is shifted from one set of neurons to another by a copy of the saccadic eye movement. The copy command is known as the **corollary discharge**. This corollary discharge originates in the SC and is directed to the FEF (and to PF and PEF). The corollary discharge shifts the activity to the group of neurons that would have been activated if A and B were still visible.

In the normal world in which visual targets are continuously visible, the image of objects shifts during each eye movement (as shown on the right). Yet we sense that these objects are stationary. This is because the images land where our corollary discharge tells the PEF to expect them. The activity shifted by corollary discharge in PEF matches that arriving from visual cortex.

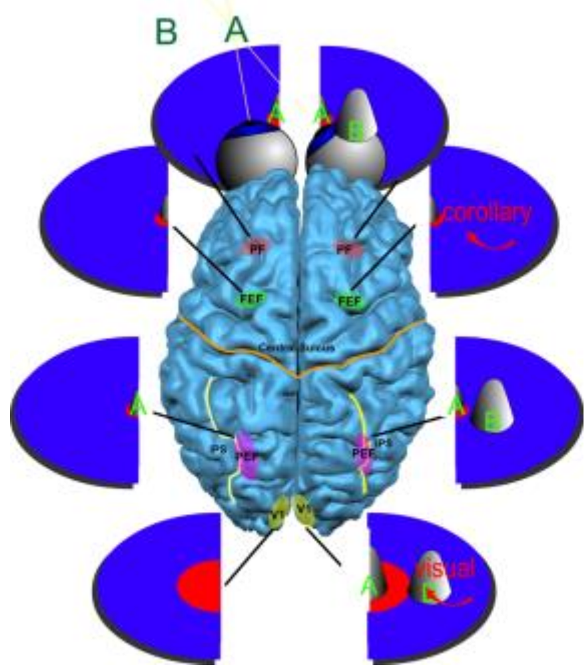


Figure 6. 16 Saccades shift the activity through corollary discharge. After a saccade to the remembered location of A, the activity in PEF and PF is shifted to the foveal location and B to a less peripheral location. In V1 this is where B would have been coded were it visible.

3) *The parietal and prefrontal areas are involved in covert shifts in attention.*

As we have seen, the PEF through the FEF directs saccades to locations of interest. These are overt shifts of attention. The two areas are also involved in covert shifts of attention.

Because covert shifts can redirect attention to a spatial location without moving one's eyes, they are much faster than saccades.

These covert shifts of attention selectively enhance the neural activity of the corresponding retinotopic locations in early visual areas including V1. This in turn enhances the visual object's contrast, suppresses that of surrounding images, and helps locate potential targets for a saccade to the object (Figure 6.17). How these covert activations in the peripheral FEF and PEF become large enough to cause suppression of activity in the FEF foveal region, and thus in overt saccades, is as yet not understood.

Figure 6. 17 When fixating at the center, covert attention enhances the possible location of the object that one is searching for (inside orange circle in the upper left quadrant).

This cortical control of saccades involves a network of interconnected areas. As we have seen in Figure 6.7, signals from V1 project along the dorsal stream to PEF, FEF and PF. In turn areas such PF exert a positive influence on FEF, PEF and V1. This selectively tunes V1 to enhance one's perception of the features that are relevant at the moment (i.e. is this Waldo?). The enhanced signal is passed back to PF and the feedback process is repeated continuously. Thus there is ongoing communication within this network between higher and lower areas as one patch of retina is examined and then an adjacent patch.

In Conclusion

We will learn in the next session that the sensation of touch from your skin is mapped onto a strip of cortex behind the central gyrus. As in any map, adjacent points on the skin are mapped to adjacent points on this cortical strip.

Another strip, just in front of this one, maps the sensed locations of all your body parts.

We have seen in this session that the parietal cortex contains many more maps. These code the locations of objects that one can act on, for example the location of a ball to kick.

One of these maps the locations one can reach either with the arms, legs, or even one's head. This is called the peripersonal space.

These maps are elastic. They expand when one uses tools such as a stick, a baseball bat, or even a car. Over time one's map of the exterior surface of one's car becomes almost as familiar as one's skin and one can park in the tightest of spots without a scratch.

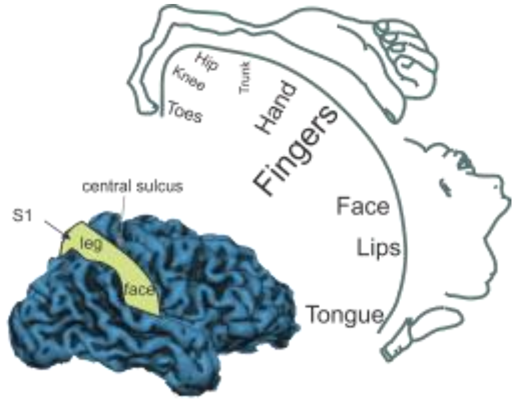


Figure 6. 18

The sensation from the body is mapped onto strips behind the central sulcus.

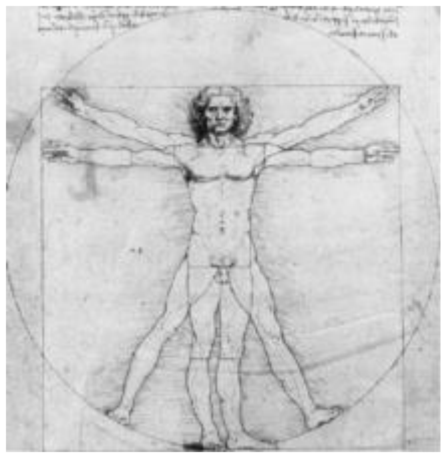


Figure 6. 19

The Circle of Peripersonal Space

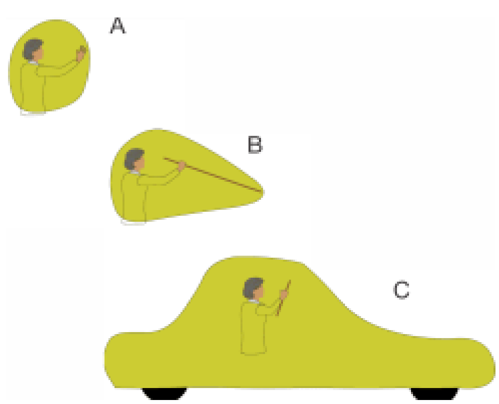


Figure 6. 20

The Elastic Nature of Peripersonal Space.

A: Normal extent.

B: Extent when holding a stick

C: When driving a car.

See problems and answers posted on

http://www.tutis.ca/Senses/L6StreamAction/L6ActionProb.swf