

The Eye

September 9, 2019 11:25 AM

Objectives

1. List factors that prevent an image from being clearly focused on the back of the retina
2. Identify how all of the information that is sensed by a relatively large retina can be funneled down a relatively small optic nerve
3. Specify the transformations that are performed by the neural circuits within the retina
4. Specify why the cone receptors in the retina are not adequate for distinguishing '[-colors

Intro

- Course emphasizes the 'why's'
- Cost of a single AP is high - so activating over 10% of your neurons causes you to faint
 - You run out of oxygen in your brain
 - Our brain has evolved to be very efficient
- 3 key building blocks of the eye
 1. Lens focuses the light emitted by objects in world onto retina at back of the eye
 2. Retina - contains light sensitive cells that convert light to electrical activity
 3. Network of neurons collects visual info and transmits it down the optic nerve -> brain

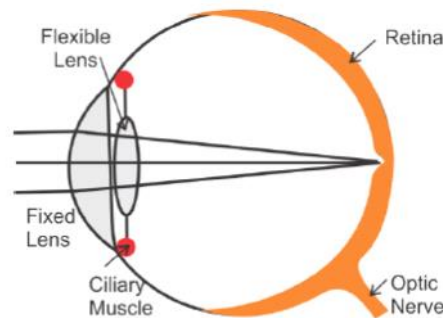


Figure 1.1 Light is focused 1st by the fixed lens and 2nd by the flexible lens onto the retina at the back of the eye. Neurons in the retina project down the optic nerve to the brain.

- Eye = brain's window to world and doctor's window to brain
 - b/c retina is part of cerebral cortex
 - e.g. New techniques developing to use view of retina to spot early signs of dementia (i.e. Alzheimer's)

Accommodation

- Light is focused by curvature of 2 lenses:
 1. Fixed lens (cornea)
 2. Flexible lens - changed by ciliary muscle that encircles the lens
 - The ciliary muscle is attached by springs - muscle contracts toward lens
- Ciliary muscle contracted = diameter decreased = springs less taut = lens more round
 - Close object focused onto retina
- Ciliary muscle relaxed = lens more flat = distant object focused onto retina
- Lens loses elasticity with age and remains too flat even when ciliary muscle is completely contracted
 - Near objects become blurred

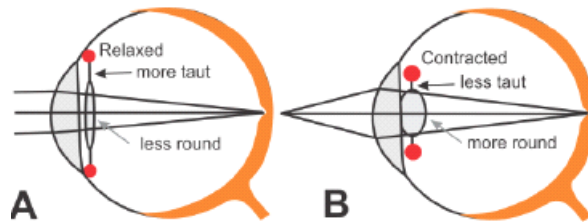
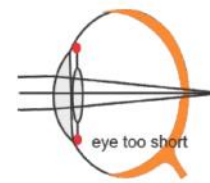
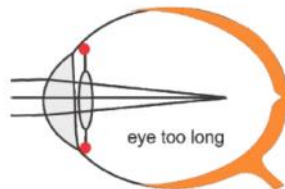


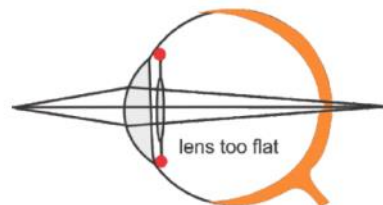
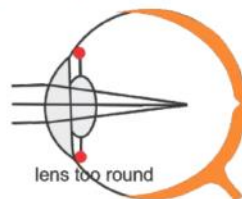
Figure 1.2 The ciliary muscle changes the curvature of the flexible lens. A. To view a far target the muscle relaxes and the springs pull on the lens making it less round. To view a near target the muscle contracts releasing the lens allowing it to return to its normal round shape.

One's ability to clearly focus an image depends on two factors.

1) The shape of the eye ball
(Wallman & Winawer 2004)



2) The shape of the lens



Either of the above produces someone who cannot focus on far targets, is **near-sighted**, and needs a **concave** lens.

Either of the above produces someone who cannot focus on near targets, is **far-sighted**, and needs a **convex** lens.

The Iris

- Iris determines diameter of pupil
 - Restricts amount of light or improve focus of image on retina
- Smaller pupil = less blur on retina

Cells in the Retina

- 5 cell types in retina
 1. Light sensitive receptors (rods and cones)
 - Hyperpolarized by light and depolarized by dark (dark = stimulus)
 2. Ganglion cells - only output from eye
 3. Bipolar cells - connect receptors to ganglion cells
 4. Horizontal cells - converge signals from several receptors
 - Determine how many receptors each ganglion cell 'sees'
 5. Amacrine cells - converge signals from peripheral rods via bipolar cells

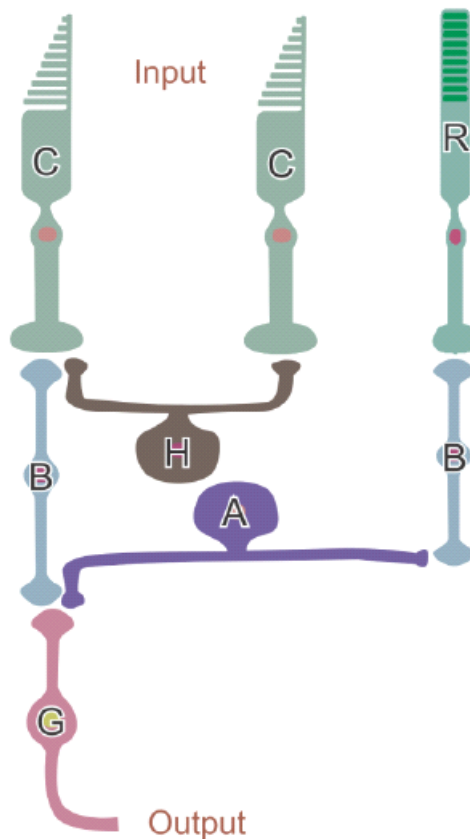


Figure 1.5 The Cell Types in the Retina Light activates the receptors consisting of rods (R) and cones (C). These connect through bipolar (B) cells onto ganglion (G) cells. Horizontal (H) cells and amacrine (A) cells interconnect receptors and bipolar cells.

Which Cells produce APs?

- Some amacrine and all ganglion cells produce APs
- Rods and cones, horizontal cells and bipolar cells only produce graded changes in potential

Why do most cell types in eye show only graded changes in potential?

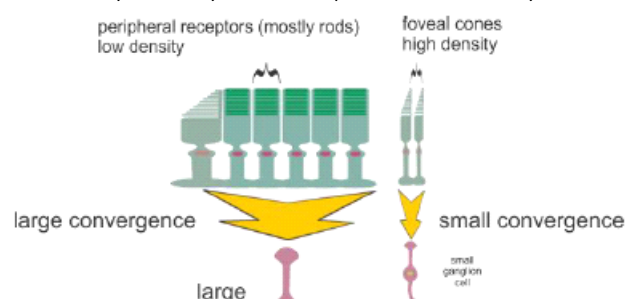
- APs have a relatively small frequency of about 10-1000/s so are slow at info transmission
- Graded changes allow continuous and rapid transmission of information

Why do ganglion cells generate APs?

- They have to transmit info over a long distance to the Lateral Geniculate Nucleus (LGN) and Superior Colliculus - graded changes in potential cannot travel that far
- Ganglion cells must convert visual info, coded by graded potential changes in bipolar cells into a discrete code consisting of APs

Why is reading difficult in low illumination?

1. Retina is not uniform
 - Peripheral retina is primarily rods
 - Center of eye (fovea) = cones
2. Cones are less sensitive to light than rods
 - e.g. at low levels of illumination, we see better in periphery (where rods are)
3. Periphery has poor acuity - rod system has poor visual acuity



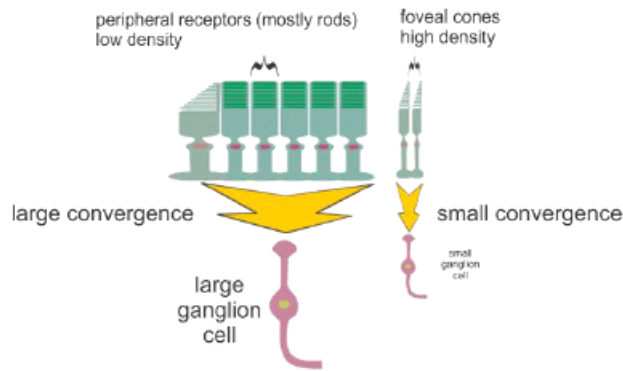
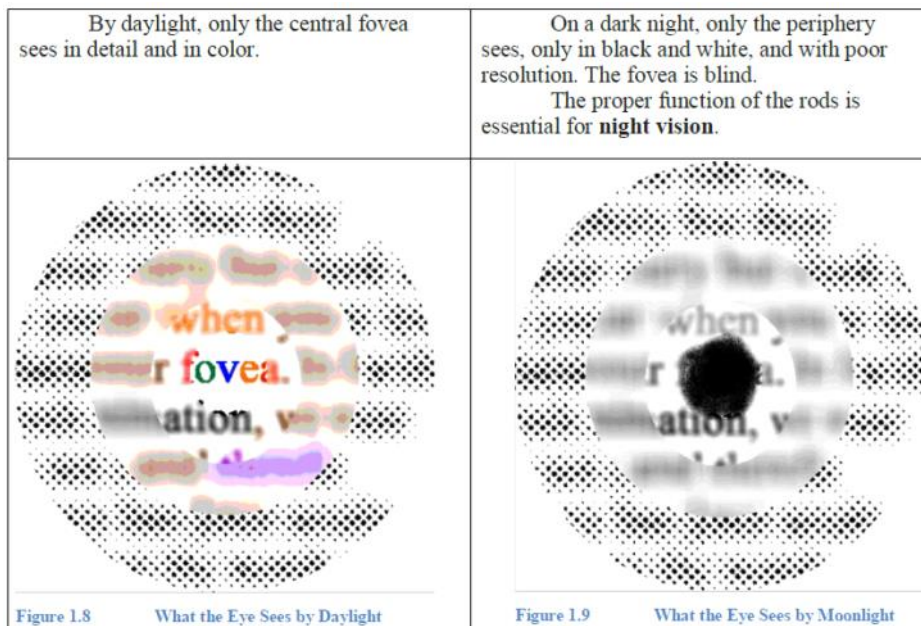


Figure 1.7 A Comparison of the Peripheral and Foveal Retina Large ganglion cells in the peripheral retina have poor acuity because of a large convergence of low-density receptors. Small ganglion cells in the fovea have a high acuity because of a small convergence of dense cones.

- Periphery
 - Large ganglion cells integrate information from a large area of retina
 - Large spacing and large convergence results in low acuity
- Foveal
 - Small ganglion cells integrate info from a small area of retina
 - Small spacing and low convergence results in high acuity
- Retina contains a continuum of ganglion cell sizes

What the eye Sees

- Optic nerve is small compared to retina - so forms an anatomical bottleneck along route from eye to brain
 - Solved by giving preference to foveal fibers and allowing detailed vision in only a small part of the eye
- The fovea sees only the central 2 degrees (1%) of the visual field
 - About twice the width of your thumbnail at arm's length
 - But the fovea takes up about 50% of optic nerve



Receptive Fields

- Receptive field = neuron's window to world
- Receptive field of a ganglionic cell - area of retina over which light stimuli changes the activity of a particular ganglion cell (changes = excitatory or inhibitory)
 - Receptive field shows which rods and cones are connected to the ganglion cell
- To measure receptive field of a ganglion cell:
 1. Record from a ganglion cell
 2. Shine small beam of light over different parts of the retina in a sequence
 3. Map those that produce a change in firing rate
- Note:
 - Same definition applies to all visually responsive cells
 - Shape and other characteristics of the receptive field are very important in categorizing the cell types

and discovering their function

- Similar definition applies to all other sensory modalities
 - e.g. for touch, skin replaces retina

Shape of receptive field of ganglion cells

1. ON center, OFF surround - measure relative brightness
 2. OFF center, ON surround - measure relative darkness
- ON = +, OFF = -
 - Image shows ON center cells (reverse signs for OFF cell)
 - There are an equal numbers of on and off center cells
 - Rapidly adapting or phasic ganglionic cell - good cells for detecting changes (i.e. flashing light)
 - When light is turned on, cell fires rapidly for a short period of time
 - When light is turned off, cell activity is briefly inhibited

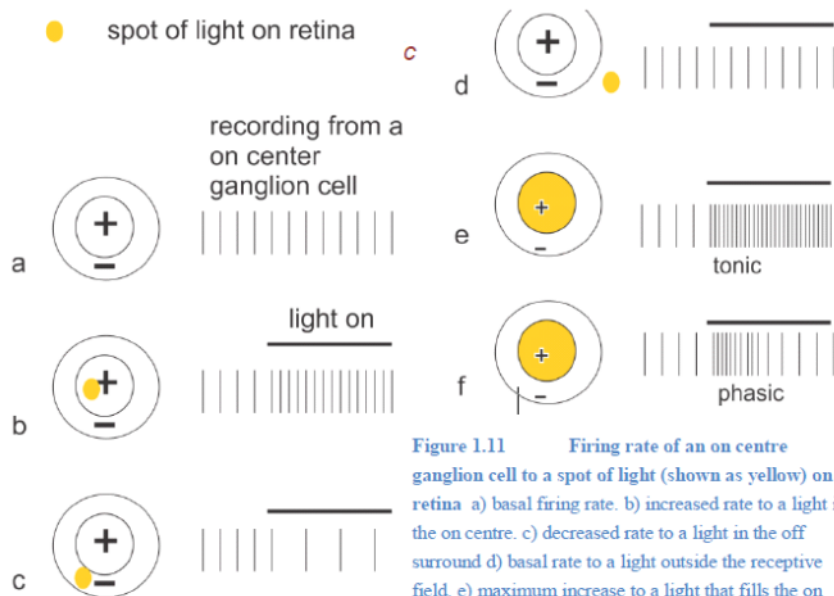


Figure 1.11 Firing rate of an on-center ganglion cell to a spot of light (shown as yellow) on retina a) basal firing rate. b) increased rate to a light in the on centre. c) decreased rate to a light in the off surround d) basal rate to a light outside the receptive field. e) maximum increase to a light that fills the on centre. f) a phasic response to a light stimulus.

How an Antagonistic Surround Receptive Field is Produced

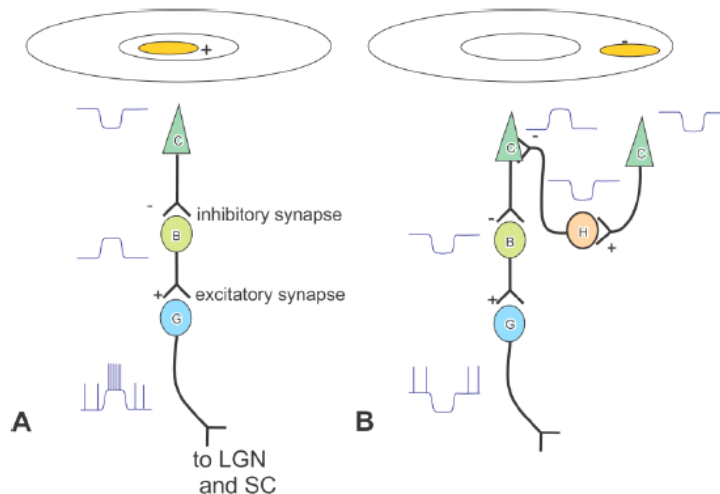


Figure 1.12 Synaptic Connections of an On Center Ganglion cell A) Light to the center produces excitation of the ganglion cell. B) Light to the surround produces inhibition of the ganglion cell.

1. Light to on center, exciting ganglionic cell
 - Light decreases cone voltage and the cone releases less inhibitory transmitter
 - Less inhibition causes the voltage inside the bipolar cell to increase and it releases more transmitter
 - Ganglion cell is excited and it fires more often
2. Light to off surround, inhibiting ganglionic cell
 - Light decreases surround cone's voltage and cone releases less excitatory transmitter
 - Voltage inside horizontal cell decreases and it releases less inhibitory transmitter
 - Voltage inside center cone increases and releases more inhibitory transmitter

- Voltage inside bipolar cell decreases and releases less excitatory transmitter
- Ganglionic cell fires less often
- Note:
 - Horizontal and ON cone cells release inhibitory transmitter
 - Ganglionic, bipolar and OFF cone cells release excitatory transmitter

Function of Ganglion Cell Receptive Fields

- One important function of the ganglion cell's antagonist surround is to accentuate edges
- When eye sees a black/white edge, the activity of ganglion cells far from edge shows a similar low level of activity
 - This is because both centers and surrounds cancel
 - little change in firing rate b/c center and surround experiences the same amount of light
 - Only at the edge is the activity increased or decreased
- How does the brain compute what it must, using so few active neurons?
 - By activating only ganglion cells that sense a change (i.e. the edges)
 - The brain keeps the number of active neurons to a minimum

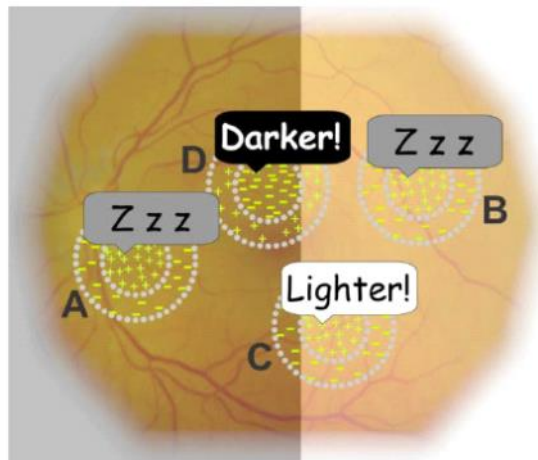


Figure 1.13 A change in response is seen only when the receptive field is near the black/white edge. The eye's ganglion cells A and B fire at their basal rates because the centre and surround responses cancel. Less inhibition from the edge in the dark occurs in C. More excitation from the edge in the light occurs in D producing an increase in firing rate and thus highlighting the edge.

Vision involves extracting key features

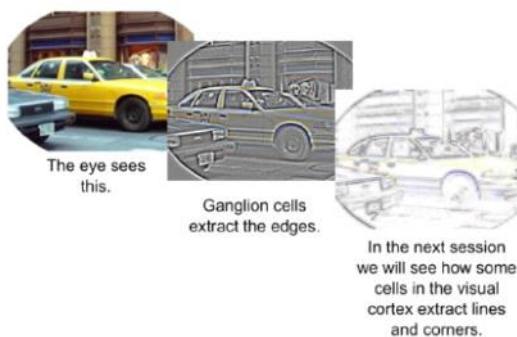
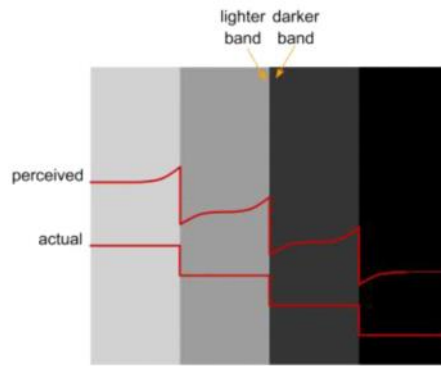


Figure 1.14 The Features Extracted at Various Stages From left the right: What the retina "sees". What the ganglion cells respond to. What the visual cortex extracts.

Consequences of edge extraction

- Inhibitory surround produces illusion of an accentuated edge

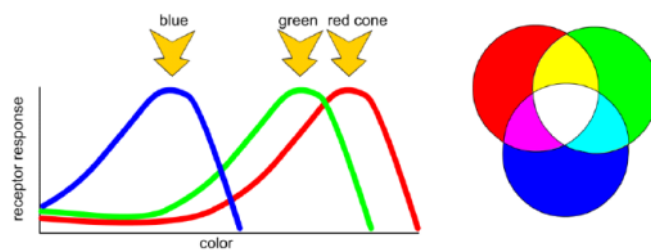


Ganglion cells provide constancy - by measuring change

- Ganglion cells measure change across an edge so a change in light does not change the image
- The contrast, or change in intensity between adjacent bits of an image, remains constant independent of lighting conditions

Advantages of Color Vision

- Sensation of color developed, in part, to allow us to see which fruit is ripe
- Cones respond best to a particular wavelength of light and respond, but less, for a large range of colors
- 3 cone types: blue, green and red color sensitive
 - A 3 color cone system is good at distinguishing an object from its background
 - Most species have evolved at least a 2 cone system
 - But even 3 cones are not very good at distinguishing colors
- Mixing light is not the same as mixing paint
 - Mixing all 3 makes white light



How Cones are Distributed on the Retina

- In the fovea:
 1. The # of each cone type is not equal
 - Usually red cones are most numerous and blue cones least numerous
 2. The relative numbers vary from person to person
 3. The cones of the same type form clusters
- The very center of the fovea has no blue type cones
- Moving away from the fovea
 1. The number of cones drops and the number of rods increases
 2. The size of both rods and cones increases and thus their density decreases

Color blindness

- Each cone type contains a different light sensitive photo pigment
 - Color blindness occurs when there is a defect in the genes that produce these photo pigments
- Various combinations of defects can occur
 1. Missing 1 cone type
 2. Missing 2 cone types
 3. Missing all 3 cone types
 - Vision limited to rods - no foveal vision
 4. A cone type is made with a photo pigment different from normal

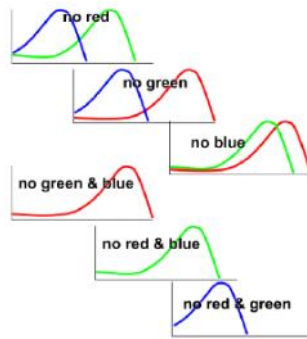


Figure 1.21 Various Types of Color Blindness

How many gradations of color can the human brain distinguish?

1. 200 hues
 - The brain transforms the wavelengths of light seen in a rainbow into a color circle containing 200 distinguishable hues
2. 20 levels of saturation
 - Saturation is the combination of 2 or more wavelengths
 - Hues on opposite sides of the color circle are complementary
 - When complementary wavelengths are combined equally, one gets grey
 - Combining green with its non-complementary shade of red produces yellow
3. 500 brightness levels
 - Any color on the circle can be made brighter or darker
 - b/c very bright or dark colors are more difficult to distinguish, the circle becomes narrower
 - There are 2,000,000 gradations of color



Figure 1.24 Each level of saturation can be made brighter or darker.

Color Adaptation - after image shows complementary colors

- Complementary colors are opposites - they act as push-pull pairs
- Normally white light activates all cones equally, but during prolonged viewing of the dark blue spot, blue cones adapt
- So when you look at the white, the push from adapted blue cones is weaker than the pull from yellow (red-green) cones

Double Opponent Cells

- The cell type needed is the double opponent cell, which is not found in the eye's retina but in the cerebral cortex
- The receptive fields of these single opponent cells (center vs surround) are combined in the cortex to form double opponent cells (center vs surround and center vs center)
- The center has an excitation from blue cones that is equal to the inhibition from red and green cones
 - Thus, white light will not activate this cell
 - Blue light will activate the center and inhibit the surround
 - Yellow light will do the opposite
 - One also finds green-magenta double opponent cells.

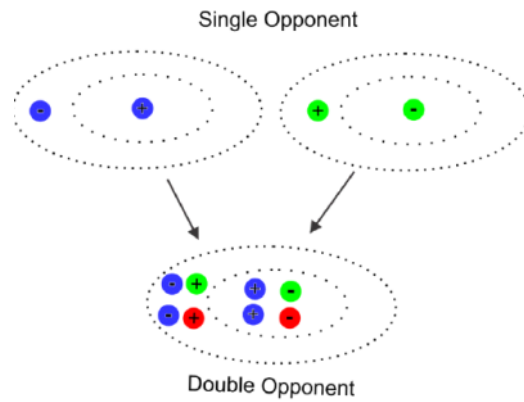


Figure 1.26 The Receptive Field of a Blue-Yellow Double Opponent Cells in the Visual Cortex

Adaptation of double opponent cells

- Recall how prolonged viewing of a yellow spot made its afterimage look blue
 - Prolonged exposure to yellow light in the center will adapt the red and green cones more than the blue cones
 - Now when exposed to white light, the influence of the blue cones will exceed that of the red and green cones and activate the double opponent cell
 - The result is the perception of blue.
- Thus because we have blue-yellow double opponent cells, the after-image of yellow is blue and vice versa
- Similarly, because we have green-magenta double opponent cells, the after-image of magenta is green and vice versa
- In fact if you pick any color around the color wheel you can predict that its after-image color is that on the opposite side of the color wheel, going through the center

Why does a blue object against a yellow background stand out so well?

- A blue spot in the centre activates the double opponent cell
 - A yellow spot (red and green light) in the surround also activates the cell
- A combination of the two gives the maximum response
 - This double opponent cell responds best to the change from blue to yellow
- Other double opponent cells would be maximally activated by a yellow tie against a blue background

What happens when you shine diffuse yellow light over the whole receptive field?

- Diffuse yellow light over the centre activates both red and green receptors
- Yellow light in the surround activates the same receptors cancelling the input from the center
- Diffuse blue light does the same, as does any diffuse color
- This helps maintain color constancy b/c the centre and surround produce opposite responses, a double opponent cell is unaffected by any background color

What happens when you do not adjust the white balance in your camera?

- Your pictures will have a yellow hue from the background incandescent lights
- Cameras measure absolute color and do not have color constancy

Primary Visual Cortex

September 17, 2019 11:41 AM

Objectives

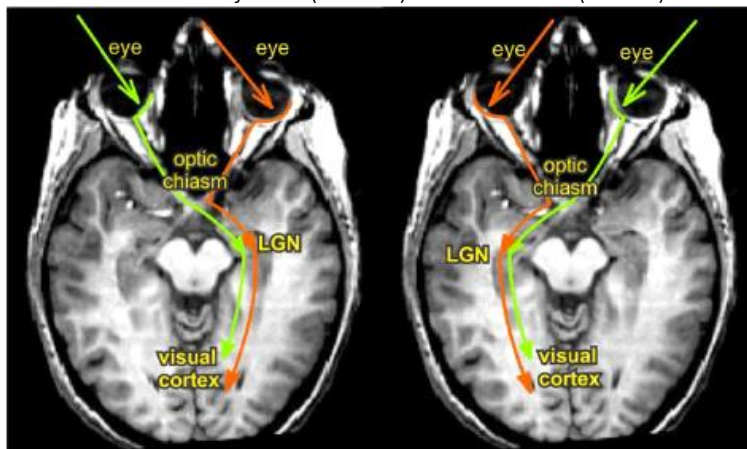
1. Explain how neurons within the visual cortex become tuned to a visual edge of a particular orientation.
2. Predict the long-term deficit that can result from a cloudy lens in one eye of a newborn. Specify how this is different from the deficit in a newborn who exhibits strabismus.
3. Specify where in the visual pathway the signal from the two eyes first comes together. Specify what these neurons do that the preceding neurons cannot.
4. List the feature channels that the primary visual cortex signals to the higher-order areas. Specify from where in the primary visual cortex these channels arise.

Introduction

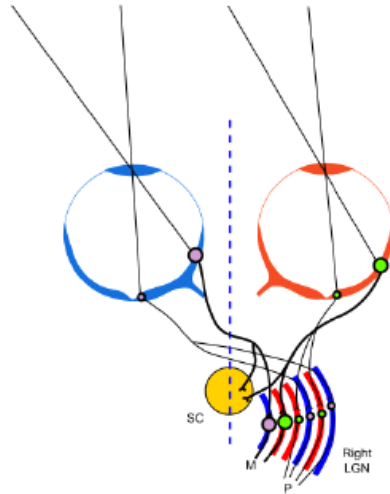
- With visual stimuli, the area around the calcarine sulcus is stimulated
 - The activation is the opposite area from the stimuli (left activates right)

The Ganglion Cells' Projections

- Images seen by one or the other side are processed by the opposite side of the brain
 - Only the ganglion cells on the nasal side of each eye (green) cross at the optic chiasm
- P (Parvocellular; small and slow conducting) ganglion cells
 - Project from fovea to lateral geniculate nucleus (LGN) of thalamus
- M (Magnocellular; large and fast conducting) ganglion cells
 - Project from peripheral retina
 - Code where objects are and project to LGN and structures in the brainstem (including the superior colliculus (SC))
 - SC causes eye and head to turn to an interesting visual object - 'visual grasp reflex'
 - LGN sends info to visual cortex
 - Info to where an object is (M cells) and what it is (P cells)

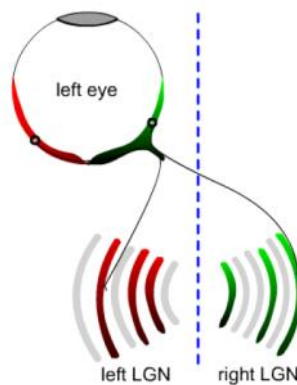


- In the LGN, the 2 eyes maintain their own separate representations in diff layers



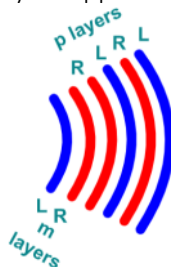
How does a ganglion cell connect to the correct place in the LGN

- Ganglion cell axons grow to specific locations within each LGN layer
 - Neighbouring cells grow to neighbouring locations
- Steps
 1. The eye develops a chemical gradient based on its location in the eye socket (e.g. temporal vs nasal)
 2. Ganglion cells are given a location identity by the position specific chemical gradient in the eye
 3. A similar gradient is set up in each LGN
 4. Axons from the nasal retina are guided by this 'scent' to the correct location in the contralateral LGN
 5. Some time later, axons from the temporal retina are guided to the ipsilateral LGN
- Similar process maps the LGN onto the visual cortex



What don't we know about the LGN

1. Why there are so many layers - 2 of the P layers appear to be redundant

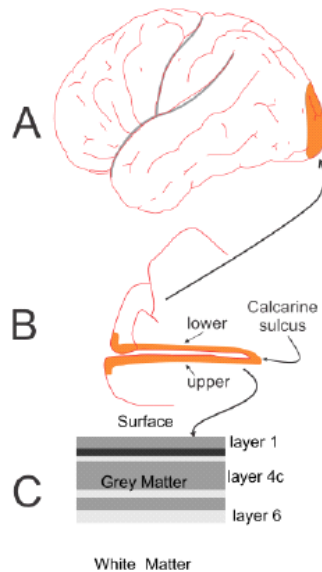


2. 80-90% of the input is not from the retina but from the reticular formation and the primary visual cortex
 - What does this input do??
3. The receptive fields of the LGN neurons are the same as those of ganglion cells
 - So the LGN does not appear to further process visual info - so why synapse?

Primary Visual Cortex (area V1)

- LGN neurons project to the primary visual cortex at the back of the head (mostly on medial side)
- Primary cortex has many names (V1, area 17, and striate cortex)
 - Called striate cortex b/c very thick layer 4c - this is where massive input from LGN ends
- V1 is made up of a folded thin sheet of grey matter near the surface
 - Lots of grey matter = good b/c that's where all the cells and connections are

- Below the grey matter is the white matter
 - Contains the nerve fibers - the 'wiring' interconnecting cells in grey matter
- Gray matter has 6 layers

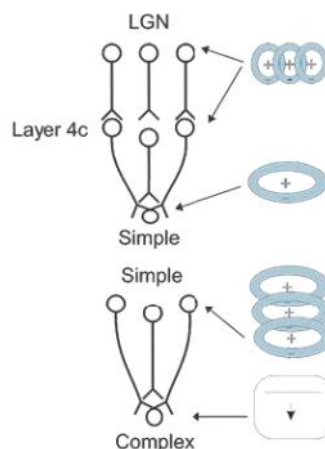


V1 contains 3 main types of cells

1. Layer 4c cells
 - Receptive fields are the same as those of the LGN and ganglion cells
 - Not selective to any particular orientation b/c has circular receptive field
 - where massive input from LGN ends
2. Simple cells with elongated receptive fields
 - So maximally sensitive to a line of particular orientation at a particular location of retina
3. Complex cells whose receptive fields are similar to those of simple cells except the line can lie over a larger area of the retina (positional invariance)
 - Some are sensitive to motion

How are the different receptive fields produced?

- Simple cells - several ganglion cells, whose receptive fields lie along a common line, converge by way of the LGN onto a simple cell
- Complex cells - several simple cells of the same orientation converge onto a complex cell
- End stopped complex cell (aka hypercomplex cell)
 - Receptive fields are similar to complex cells but maximally activated by lines of a particular length
 - The activity is less both for longer lines or shorter lines
 - But other end stopped complex cells fire when a line ends in their receptive field



Why is this important and clinically relevant?

- The simple cell is tuned to a very particular stimulus
- The complex cell generalizes this over a larger area
- Similarly, cells in the temporal lobe respond only to particular faces that are generalized over the whole of the retina
- David Hubel discovered the simple and complex cells

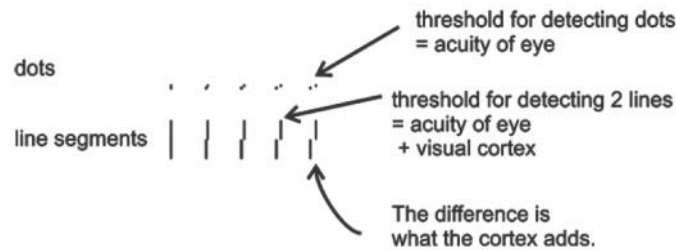
- Changes in the organization of these cell can lead to amblyopia (form of blindness)

Blind Spots

- Patients with damage to their fovea can experience blind spots
 - e.g. seeing only the stripes when seeing a face against a striped background
- This happens b/c no cells in the cortex are activated in the blind spot b/c no input from the retina there
 - But end stopped complex cells outside the blind spot become activated by the end of the lines
 - So the firing of these cells elicit the percept of a line even within the blind spot
- We normally have blind spot in our vision - where the optic nerve leaves the back of the eye
 - Twice the size of the fovea
 - If one part of your retina cannot see, the visual system uses info from adjacent parts to fill in missing info

The visual cortex actually improves on what the eye sees

- Ganglion cells see dots. Simple cells in the cortex see lines
- Hyperacuity - visual cortex improves acuity by analyzing line segments that encompass many ganglion cells
- The smallest line offset that you can detect is smaller than that of the smallest dot offset
- Clinical letter charts test the acuity of both the eye and the hyperacuity of the visual cortex
 - Problem with either causes impaired vision



Why are there many more cells in the visual cortex than in the LGN?

- Cell A in the LGN shares its info with many simple cells in the visual cortex
- By grouping diff LGN neurons, sensitivity to a variety of orientations can be achieved using only a small number of LGN neurons
- e.g. If there were a simple cell for each 5 deg. change in orientation, the same cell A would provide information to 36 simple cells ($180 \text{ deg.} / 5 \text{ deg.} = 36$)

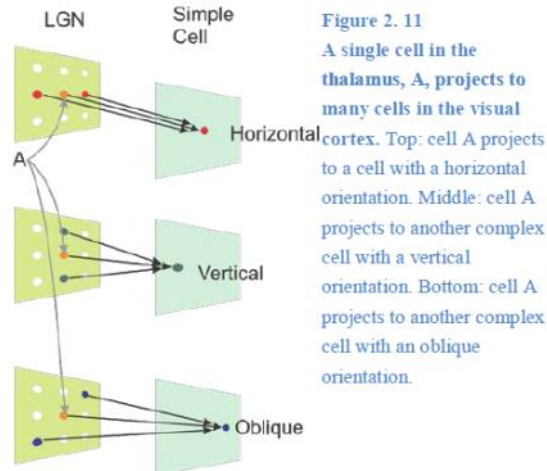
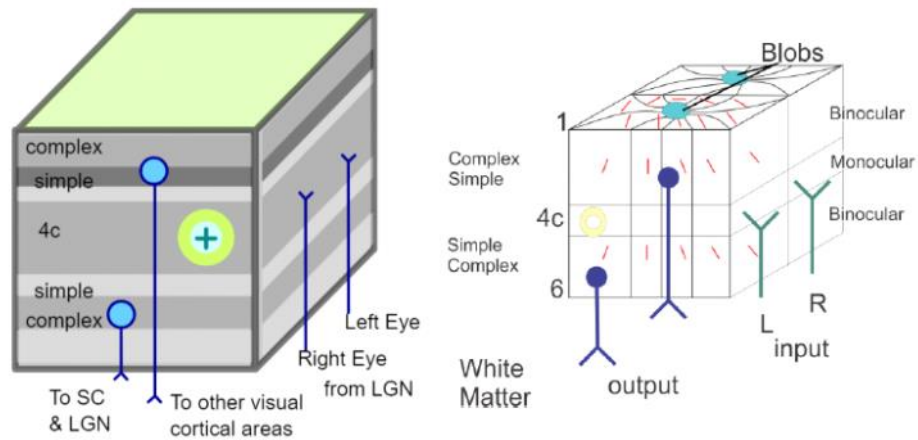


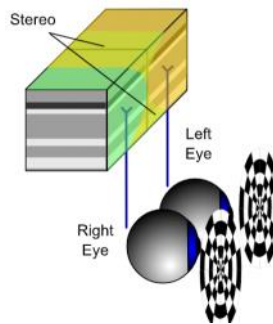
Figure 2. 11
A single cell in the thalamus, A, projects to many cells in the visual cortex. Top: cell A projects to a cell with a horizontal orientation. Middle: cell A projects to another complex cell with a vertical orientation. Bottom: cell A projects to another complex cell with an oblique orientation.

The Columnar Organization of V1

- V1 is composed of a grid (1mm x 1mm) - called hypercolumns
 - Each hypercolumn analyses info from 1 small region of retina
- V1 has a retinotopic representation
 - It forms a map of eye in your brain, with adjacent areas in the eye mapped to adjacent hypercolumns in the brain
 - This map is distorted as the fovea has a very large representation
 - As many columns devoted to fovea as the rest of the retina
- Input from the L and R eyes (via the LGN) enters at layer 4c
 - Cells are driven here by input from one eye or the other (monocular cells)
- Information from both eyes first comes together in binocular simple and complex cells located above and below layer 4c
 - These cells are important b/c they contribute to the sense of visual depth



- Each hypercolumn extracts:
 1. Stereopsis (depth)
 - In each half, one or the other eye dominates
 - One sees in stereo by combining info from 2 eyes in binocular cells above and below the input layer 4c



2. Color
 - In center of each cube there is a column, called a blob, running through all 6 layers except layer 4
 - The blob contains color sensitive double opponent cells with circular surround receptive fields
 - Thus each hypercolumn contains two blobs; one right eye dominant, the other left
 - These color sensitive cells in the blobs make up only 10% of the cells in the column and yet color seems to dominate vision
 - Blob is the only color detecting cell
3. Orientation of line segments
 - Radiating from the blobs, like spokes from the centre of a wheel, one finds simple and complex cells ordered into pinwheels of the same orientation
 - These cells are edge sensitive, but not color sensitive
 - The pinwheel arrangement allows cells with similar orientation sensitivities to be grouped together
 - This is an important organizing principle shared by the entire cortex
 - Neurons like to be near their own kind
 - It minimizes the length and number of axons

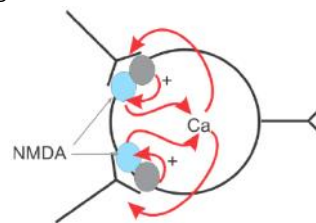
The Effect of Visual Deprivation

- At birth, most simple cells above and below layer 4c receive equal binocular input
 - As adults, side of the column becomes L or R dominant as each eye competes for representation in V1
- Visual deprivation of 1 eye in an infant has a profound effect on the organization of V1
 - b/c this is during the critical period
 - Good eye takes over cortical representation normally occupied by impaired eye
 - Called deprivation amblyopia - permanent cortical blindness in the impaired eye, which persists even if this eye regains normal function
 - Impossible to reverse
- As an adult, visual deprivation has little effect
- Studies in kittens raised in the dark suggest that equal deprivation keeps the critical period dormant
- The visual cortex however retains the capacity for other forms of plasticity, such as learning and recovery from damage throughout one's lifetime

Synaptic Mechanisms for Neural Plasticity

- The basis of the synaptic plasticity is synchronous activity

- The key is the NMDA receptor which opens only when the cell is strongly depolarized
- If two synapses fire synchronously, they strengthen each other at the expense of others that fire asynchronously.
 - Cells that fire together wire together



- This model has been used as a basis for plasticity or learning throughout the central nervous system
- The steps are:
 1. Synchronous activation causes a strong depolarization
 2. The NMDA receptor is activated allowing Ca^{++} to enter the cell
 3. Postsynaptic nerve growth factor is released and taken up only by recently active presynaptic terminals
 4. These particular terminals enlarge at the expense of others
- Synapses are strengthened if the activity from several pre-synaptic afferents occurs in the same time and is weakened if they occur at different times
- Learning is the combination of forming memories and forgetting
- The postsynaptic changes take time
 - The influx of Ca^{++} triggers a cascade of molecular processes some rapid but not long lasting, others taking days and are semi- permanent

How competition Helps Align the Visual Maps of the 2 Eyes

- At birth many simple cells are activated by both eyes - but this mapping is imprecise
 - Only those cells that are simultaneously activated by both eyes, that is, those that have the same retinal correspondence, will retain their connections
- Purpose of critical period - to tune the acuity of the visual system
- Amblyopia (lazy eye) - vision in one of the eyes is reduced because the eye and the brain are not working together properly
- A simple binocular cell is maximally activated by the same optimal line orientations in the two eyes
 - This means that a corresponding line of receptors on the retina of the two eyes must be wired to the same simple cell in the cortex

What happens in a child with strabismus?

- When the 2 eyes are normal, but do not point in the same direction, one sees a double image
- Each eye is stimulated and thus retains its representation in the visual cortex
 - However, binocular cells are never activated simultaneously by the same stimulus
 - These cells eventually become monocularly driven and the child permanently loses stereopsis.
- Because strabismus causes double vision, the image from one eye may be suppressed
 - This suppression may lead to amblyopia

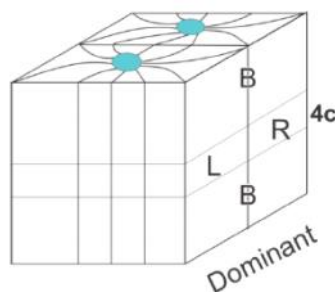


Figure 2.16 In a normal cortex the cells in layer 4C are monocular but binocular in layers above and below layer 4C.

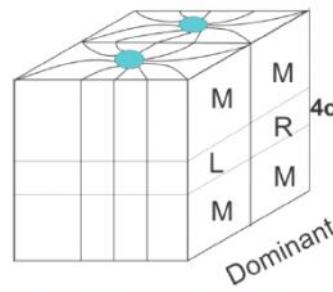
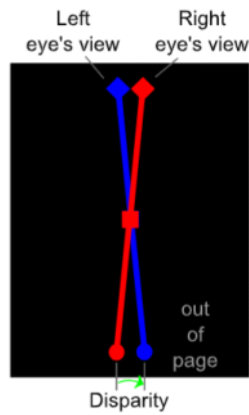


Figure 2.17 If a child is raised with strabismus all the neurons become monocular, with those on one side receiving input from one eye and the others receiving input from the other.

Stereopsis (aka stereo vision)

- Stereopsis - object seems 3D as you see 3 images when you converge your eyes
 - Main reason we have 2 eyes
- Disparity of images gives the illusion of depth



- If you looked at this image with a filter that only allowed red through the right eye and only blue through the left eye, the bottom should appear to be a line coming out of the page
 - The disparity of the top is the reverse and it should appear behind the page

At what level of the visual pathway is binocular disparity 1st analyzed

- Input from the 2 eyes first converges onto cells in V1 (above and below layer 4c) where about 70% are binocularly driven.
- Each cell is only activated by a particular retinal disparity:
 - The 'far' neuron is activated when the images are displaced inward
 - The 'in focus' cell is activated when there is no retinal disparity
 - The 'close' neuron is activated when the images are displaced outward in the two retinas.

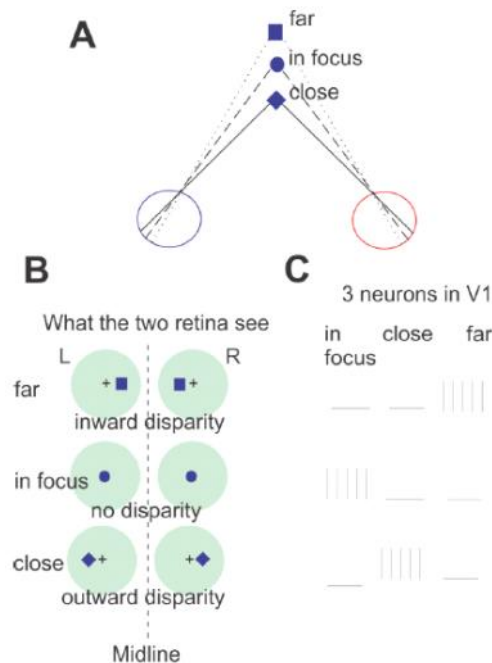


Figure 2.19 Activation of 3 Binocular Neurons in V1

A: The view from above of 3 objects and their projections on the two eyes. B: The view from behind on the two retinas. C: Each of the 3 neurons prefers a different retinal disparity.

Questions

- Lesion of the optic chiasm will cause a loss of vision from both nasal retinas
 - Causes a blind spot
- Lenses for astigmatism improves vision, but does not restore vision to normal
 - Lines of a particular orientation that appeared blurred would be seen more faintly
 - Meridional amblyopia
- Posterior half of V1 correlates with middle of visual field
- Anterior half of V1 correlates with periphery of visual field

Visual Perception of Objects

September 21, 2019 1:10 AM

Objectives

1. Select the key difference in the way the retina is mapped in each of the visual areas V1, V2 and V3
2. Specify the mechanism that allows the features encoded by primary visual cortex to be grouped into objects
3. State the 2 key areas within the ventral stream involved in the coding of objects

What is after V1?

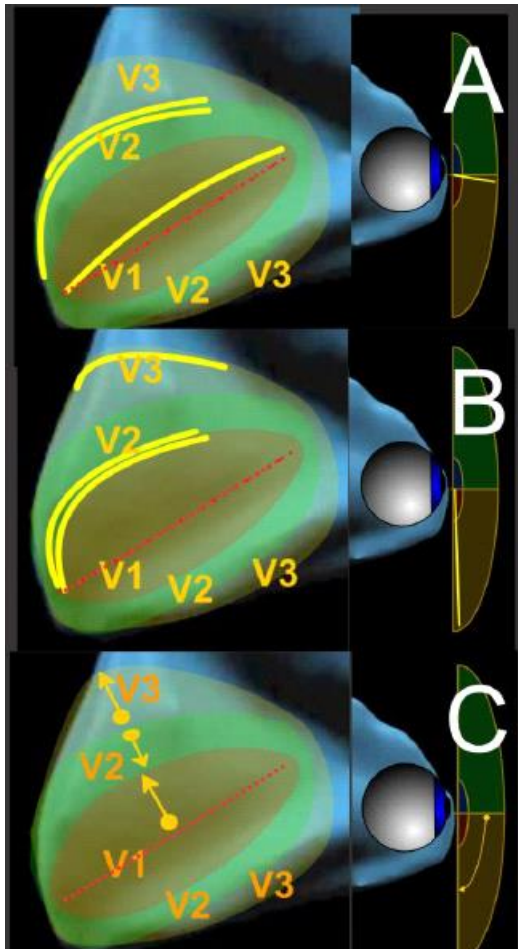


Figure 3.2 The Projection of Lines in the Bottom Right Quadrant of the Visual Field to V1, V2, V3 in the Left Visual Cortex above the Calcarine Sulcus (red dotted line)

- A: The projection of a line on the left horizontal meridian.
- B: The projection of a line on the lower vertical meridian.
- C: The projection of an arrow whose tail starts on the right horizontal meridian and ends on the lower vertical meridian.

- From V1 info is sent to higher order visual areas -> V2 -> V3
 - In each area the retina is re-represented (3 times in total - once in each area)
- Landmarks defining locations of V1, V2 and V3 formed by location of horizontal and vertical lines of visual field
 - Line just below horizontal is mapped first just above the calcarine sulcus in V1 and again along both sides of the border where V2 and V3 meet
 - Also, a near vertical line (Figure 3.2B) is represented at the V1/V2 border and again on the far side of the V3 border
- Mirroring at V1/V2 border and V2/V3 border occurs for everything mapped in V1
- "Like" cells like to be near each other
 - Reduces length of axons and wiring in the brain (as in the length of the black arrows in Figure 3.3)

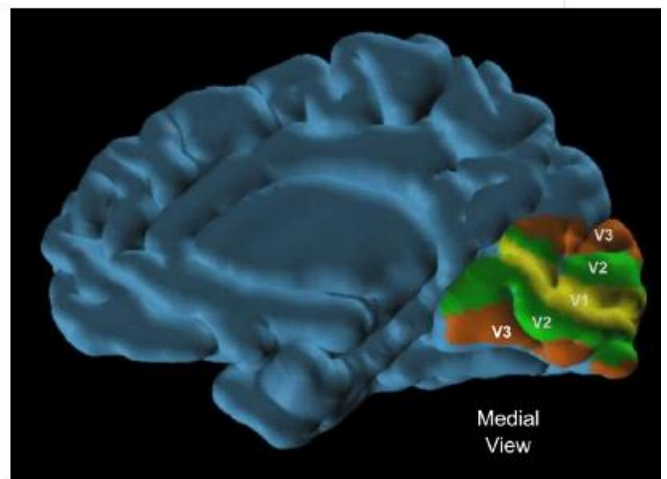


Figure 3.1 Higher Order Visual Areas V1, V2, and V3

The medial view of the right cortex with the calcarine sulcus (yellow) represented at the posterior end.

- During brain's development, axons may act as springs pulling heavily connected areas together
 - forms cortical folds between V1 and V2 as well as elsewhere in the cortex

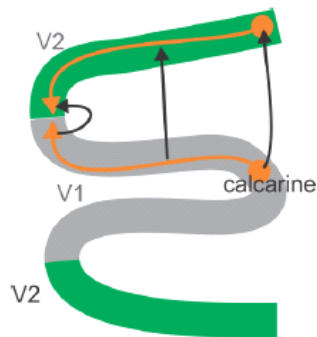


Figure 3.3 A Possible Reason for Mirroring
 The head of the arrow in V1 connects the head of the mirrored arrow in V2. The same holds for the tail and every point in between. The length of these axons is less than if the arrow was not mirrored.

Assembling Simple Features into Objects

- In V2 and V3, visual system starts to assemble objects from lines and edges extracted in V1
- V1 cortex first "sees" elementary features of objects
 - Each line asynchronously activates an orientation-specific V1 simple cell
- Higher areas, such as V2 and V3, begin grouping the features that belong to the same object.
 - This grouping is fed back to V1 producing synchronous and therefore larger activity
 - To allow for this synchronous activity to develop, columns of cells in V1, V2, and V3 have extensive reciprocal interconnections

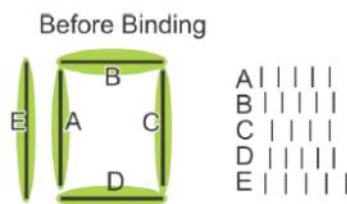


Figure 3.4 Before binding, the neurons representing the 5 lines A, B, C, D and E, fire at different times.

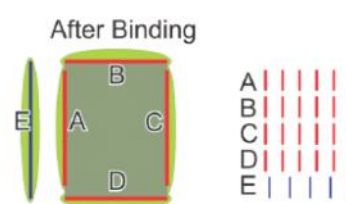


Figure 3.5 After binding the square shown on the left, the action potentials from neuron in the square's receptive field, shown on the right, occur at the same time.

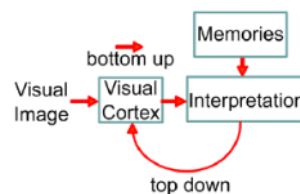
The 'Binding Problem'

- In general, binding involves grouping features into objects
- The visual system uses common color, motion, or form to group features common to an object
- Past experience is another important factor for what features to bind

Illusory Contours

- Cells in V2, and some in V1, are activated by both a real contour and an illusory (or subjective) contour
 - Higher areas fill in the gaps
 - Color in the center of the square is defined from the corners

What we perceive depends on our interpretation of what we see

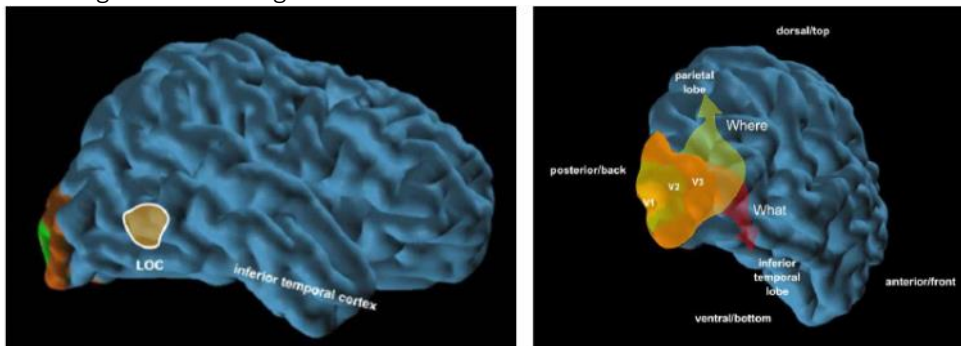


- Interpretation based on our memories modifies what we see
- These top down influences (from higher to earlier areas) can be viewed as predictions
- Ex. If based on our memory of the word "example" we expect to see the letter m in "exanple" and we may not notice that it has been misspelled

Visual Areas Beyond V3

- From V3, information diverges to over 3 dozen higher order visual areas

- Each of these areas processes some special aspect of what we are seeing
- These visual areas are like a multi-screen cinema
 - The main difference is that each of your brain's screens is showing a different attribute of the same movie: some just the motion, others the colors, etc.
- Beyond V3 the two processes separate into:
 1. The dorsal stream (top surface), along intra parietal sulcus - 'Where' stream
 - Directs actions to the spatial locations of objects
 2. The ventral stream (bottom surface), projecting to inferior temporal lobe - 'What' stream
 - Perception and recognition of objects, e.g. faces
- Object perception begins in V1, which extracts simple features that are common to all images, e.g., lines
 - It ends in the inferior temporal cortex (IT) - center for object perception
 - Where cells respond to a particular combination of complex features, that define a particular object (ex. a face)
- In V2 and V3, the upper and lower visual quadrants are separated by V1
 - In V1 lines of the same orientation activate pinwheels of the same orientation
 - So an object centered in the visual field becomes divided into four parts in the cortex
 - In V2 and V3, features that share common cues, such as lines of similar orientations, are bound together
 - In regions such as the fusiform face area (FFA) located in IT, the left and right sides are brought together, and the object is recognized
- Lateral occipital complex (LOC) - combines object parts seen in the contralateral visual field but not, as yet, those in the ipsilateral visual field
 - Elements of objects are extracted from background on the bases of features bound by common color, motion, or form
 - LOC codes that something is an object part, while areas of IT code a particular object (e.g. a rhinoceros)
- Lesions of LOC
 - Lesions of LOC result in visual agnosia - inability to perceive all objects through vision
 - A bilateral lesion of LOC results in an inability to recognize any object including faces
 - Lesions in small areas of IT can result in visual agnosia of a particular class of objects
 - e.g. rhinoceros-agnosia



Evidence for 'What' and 'Where' Pathways

- In a functional imaging experiment - gave subjects 2 tasks:
 1. Press button when face you see now is the same face as that shown just previously
 - This produced activity in early visual areas and a greater activity in the 'what' > "where" stream
 2. Press the button when the face you see now is in the same location as that shown just previously
 - This produced a greater activity in the 'where' stream
 - The stimuli and actions of the two tasks are identical!
 - Remarkably, simply changing the task shifted which areas were most active
- If two streams exist, then one should be able to find patients with selective loss of abilities that are characteristic of each stream - This is indeed the case
- Patients with lesions of the intraparietal sulcus have difficulty in pointing or grasping accurately
 - Ex. a patient will have difficulty grasping a computer mouse with the correct orientation
- Small lesions in the IT produce a particular type of agnosia, ex. Prosopagnosia - specific loss of face recognition
 - A patient with a lesion of LOC will have difficulty seeing the mouse among the other objects, but when directed to it, will reach for the mouse with the correct orientation without knowing that it is a mouse

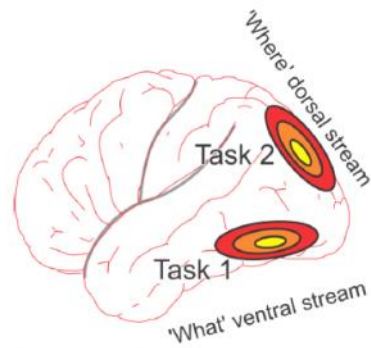


Figure 3.12 Location of Activation to Task 1 and Task 2

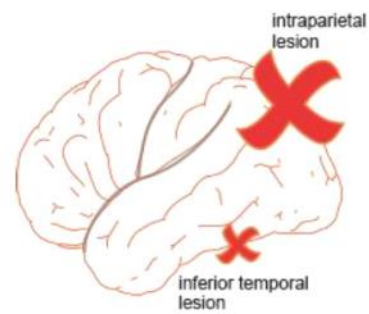


Figure 3.13 Lesions of the "Where" and "What" Streams

The Inferior Temporal Cortex (IT)

- IT - stores the memories of a variety of objects - e.g. animals
- FFA - small region in IT that represents faces
 - All neurons respond preferentially to faces
 - A particular face is stored by a cluster of highly selective neurons
 - A similar visual representation may hold for all objects
- Lesions of the FFA lead to prosopagnosia
 - Patients with prosopagnosia cannot recognize friends from visual clues, or even themselves in a mirror, but can recognize them through other modalities such as their voice or gait
 - Visual acuity and the recognition of colors and movement are not impaired
 - Patients can recognize that a face is a face and features such as eye brows, lips, etc., but cannot recognize that a particular combination of features belongs to a particular person
- In areas of IT that include FFA:
 1. Cells respond selectively to a particular class of objects e.g. faces, body parts, animals, etc.
 - Within each region, some cells are tuned to particular instances of object, e.g. a particular animal
 2. Cells exhibit perceptual constancy
 - Their response is the same independent of:
 - a. location of object's image on retina b/c these cells have large bilateral receptive fields
 - b. size of the image on retina
 - c. cue that defines the object's shape (e.g. lines, color, texture, motion).
- The area involved in the perception of a particular object is also involved in storing its associated visual memories

IT has a columnar organization

- Cells within a column in IT are activated by the same object
- Neighbouring columns (shown from above as squares in Figure 3.16) respond best to images of the same object from different viewpoints or objects of similar shapes, as in a and b

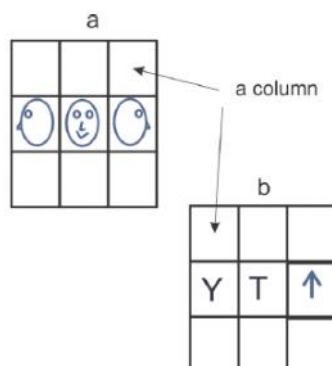


Figure 3.16 Columns in the inferior temporal cortex. a: Three columns respond best to different views to a face. b: columns that respond to similar letter-like features.

When examining an object like a face, the eye scans it

- This is because you see clearly only with the central 2 degrees of the retina, the fovea
- To inspect the features of a face, you scan it with saccades
- Saccades point the fovea to each important feature
- Some yet unknown process reassembles these features into their correct positions when the face is

recognized

An Important Property of the 'What' Stream

- The right yellow line is longer
- “What” stream perceives geometric properties of objects independent of our viewpoint
- This is why drawing, what we see, takes so much practice
 - We have to learn to draw what is viewed, not what we perceive



Figure 3. 18 Our perception of perspective distorts our perception of the length of a line. The rightmost of the two yellow lines added to the window seems shorter. But actually it's the longer of the two.

Notice Anything odd?

- Objects, like faces, are stored in their usual orientation: an object centered representation
 - When we see features like the eyes, we re-map what our eyes see into this representation
 - For reasons that are not fully understood, this re-mapping fails when these features are seen in unusual orientations - Perhaps it is simply a lack of practice

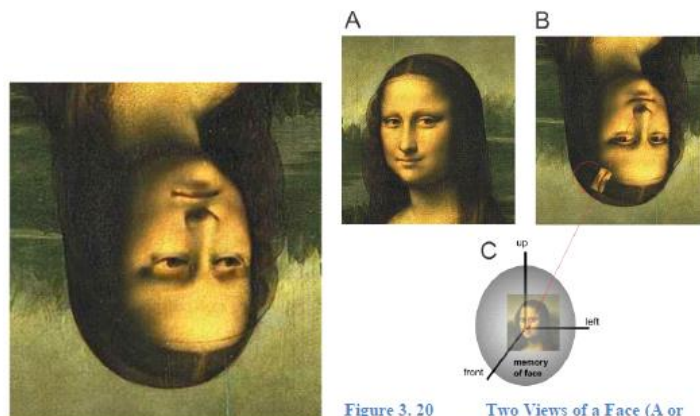


Figure 3. 20 Two Views of a Face (A or B) and its Stored Orientation C In order to compare the viewed orientation A or B to its stored orientation C, processes in the cortex must rotate the viewed features, such as the lips, from the viewed to the stored orientation.

Visual Sense of Motion

October 2, 2019 7:03 PM

Objectives

1. Contrast the differences in function and neural properties of area MT+ and the ventral stream
2. Evaluate the features of the neural circuit that are used to detect motion of a particular direction and speed.
3. Evaluate the evidence that neurons in area MT+, and not those in V1, are required for motion perception.
4. List the different subdivisions of area MT+ and their unique functions.
5. Explain how the perception of depth, offered by motion parallax, differs from that offered by retinal disparity.
6. Specify how corollary discharge helps differentiate the movement of a seen object from the movement of one's eye.
7. Specify how a prolonged motion in the same direction recalibrates the brain's velocity scale.
8. Name a task in which areas MT, LOC, and STS all cooperate

Introduction

- Middle temporal area (MT) - analyzes visual motion
 - First identified at the posterior end of the middle temporal gyrus in the owl monkey - why its called MT
 - In humans the equivalent area is located around the ascending limb of the inferior temporal sulcus
 - MT is part of a larger motion complex, called MT+ -
- MT+ - contains multiple regions, each specialized in different aspects of motion perception
 - Without this region, visual motion becomes a series of stills - hard to gauge speed and direction
 - Only sees in black and white
 - Cannot identify objects - that's for the 'what' stream (and vv, 'what' stream can't perceive motion)
- Neurons in MT+ have large receptive fields, ~10x larger than those in V1
 - Therefore, has poor visual acuity

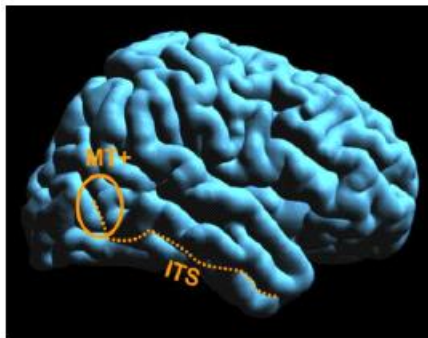


Figure 4.1 The motion complex (MT+) is located on ascending limb of the inferior temporal sulcus.

Motion Area MT and Its Input

- The parvocellular LGN feeds layer 4C which in turn feeds:
 1. Cells in blobs which analyse color and
 2. Orientation sensitive cells which contribute to the extraction of edges
 - Both have high visual acuity
- The motion system gets its input from the magnocellular LGN (low acuity)
 - Here, cells in layer 4C project to cells in layer 4B
 - Cells in layer 4B are also orientation and motion sensitive in particular directions
 - They send their signal both directly to MT and indirectly via V2 and V3
 - Because many cells receive binocular input, these cells signal stereopsis or depth of field

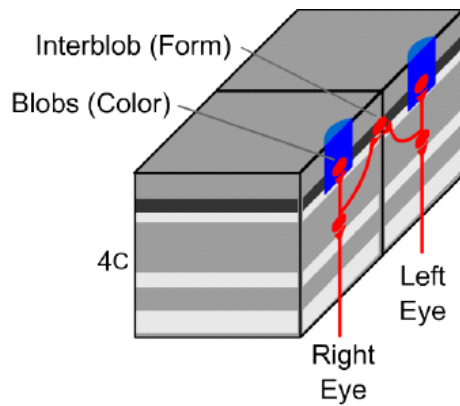


Figure 4.2 From parvocellular LGN, neurons project to layer 4c and provide a detailed signal for color sensitive cells in blobs and the orientation sensitive binocular cells in between.

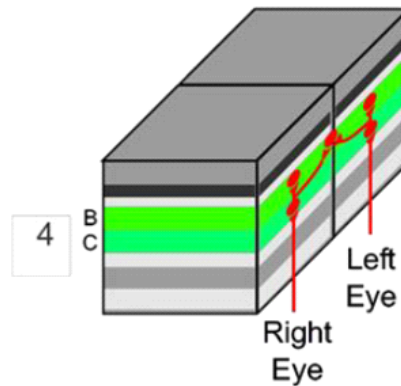


Figure 4.3 From magnocellular LGN, neurons project to layer 4B and provide MT a signal that is binocular, motion sensitive, and orientation sensitive.

Motion Sensitivity of a Neural Circuit

- Light moving in one direction causes synchronous activation so output neuron fires
 - but with asynchronous activation in the opposite direction - output neuron doesn't reach threshold
 - From differences in axon lengths - causes delay in reaching output neuron
- In some species, like birds, this circuit is found in the eye.
- In other species, such as primates, a modified form of this circuit is in V1

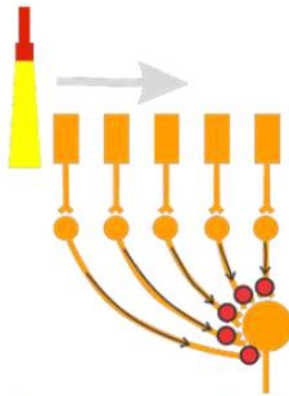


Figure 4.4 Activation of the receptors in this sequence activates the output cell, which signals motion in a particular direction and speed.

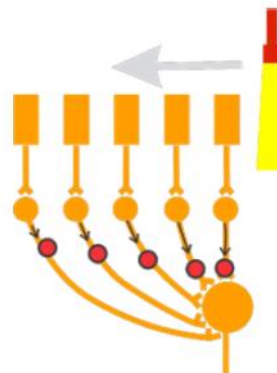


Figure 4.5 Activation of the receptors in this sequence fails to activate the output cell.

The Aperture Problem

- Receptive fields of motion sensitive cells views features through an aperture
 - Cannot see ends of lines and motion of lines become ambiguous
- The motion system makes a best guess.
 1. That motion is perpendicular to line
 - Recall: V1 layer 4B simple and complex cells sense motion of lines
 - Complex cells are maximally activated by lines moving perpendicular to line's orientation

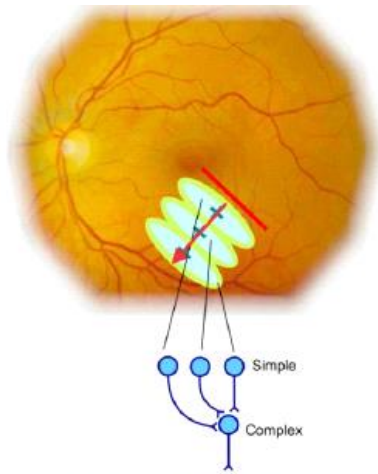


Figure 4.7 Motion of the red line down to the left activates the simple cells in a sequence that produces a synchronous activation of the simple cell.

2. Line is perceived as an object

- When we see the real ends of a line, these ends cue the direction of motion
- With a circular aperture, the visual system automatically computes that the ends are symmetric around the aperture and that motion is perpendicular to the line
- In other cases, it extrapolates motion from the ends of lines
 - In these cases, the motion percept need not be perpendicular to the line's orientation

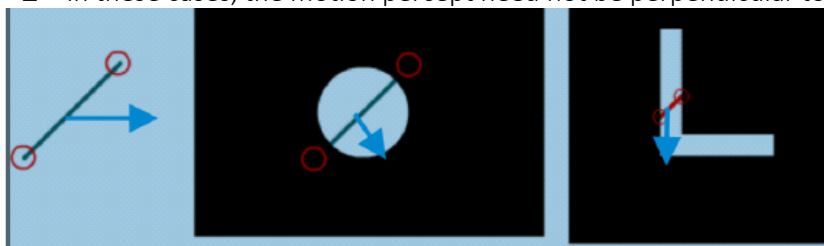
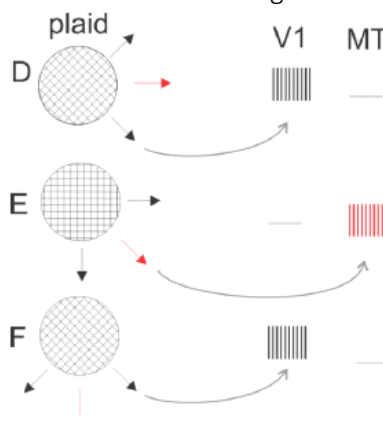


Figure 4.8 The real or imagined ends of a line are important in determining motion direction. Left: The motion of the real line ends signal direction. Middle and Right: The motion of the imagined line ends signal direction.

Does area in MT or V1 perceive motion?

- V1 responds to actual motion
- MT responds to perceived motion
- E.g. for V1 and MT cells sensitive to motion down to right



Activity in area MT is dependent on attention

- Attention is like selective tuning
 - Neuron becomes active when it is tuned to a particular dot AND that dot's motion is in the neuron's preferred direction
 - More significantly, shifting attention to the dot of one color makes you "blind" to other dots (even in receptive field)

The Parts of Area MT+

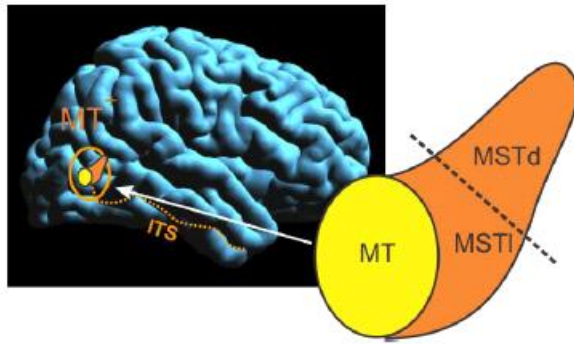


Figure 4.13 MT+ is made up of areas MT and MST.
MST is divided into dorsal and lateral parts.

- Area MT+ = MT + MST
- MST is subdivided into: dorsal (MSTd) and lateral (MSTl) parts
- MT, like V1, is organized into columns
 - Column = input from patch of retina
 - Columns are subdivided into mini-columns = particular direction of motion and a particular depth
 - Neighbouring mini-columns prefer slightly different directions of motion and depths
 - Within a mini-column, different cells prefer different speeds
 - Therefore most active cell within mini-column signals perceived direction, speed and depth from 1 patch of retina
- Area MST analyses two basic types of visual motion.
 1. MSTl - senses when an object moves
 - Often these objects are small, activating small parts of the retina
 - Involved in generating the pursuit eye movement used to follow moving objects with the fovea
 2. MSTd - senses the visual motion produced when you move
 - Movement of the background produces an optic flow pattern on the entire retina
 - Unlike neurons in MT or MSTl whose receptive fields are contralateral, MSTd neurons have receptive fields that are much larger, often integrating motion from almost the entire visual field
 - To achieve these large visual fields, neurons receive input from the ipsilateral and contralateral MT via corpus callosum
 - ◆ These connections are formed early in life as the infant is exposed various patterns of optic flow
 - Each column in MSTd is tuned to a particular pattern of optic flow
- Optic flow can produce a powerful sensation of motion
 - Ex. when you are stopped at a corner and looking at the car beside you, you sense that you are moving when in fact it is the car beside you that has started moving
- Figure 4.18 shows some of the patterns of optic flow produced on your retina when you move in different directions
 - Notice that moving in different directions generates different patterns of flow on the retina
 - Different MSTd neurons are wired to recognize these different patterns.

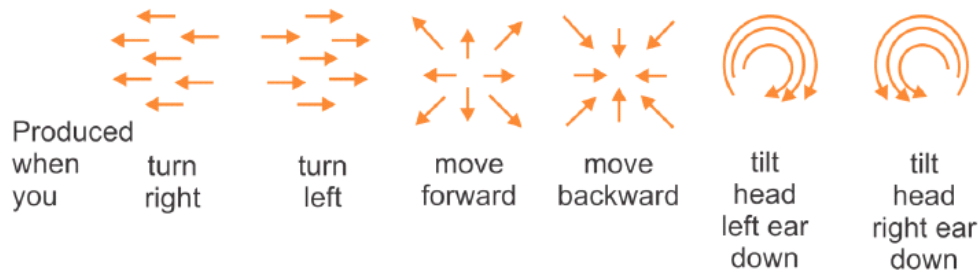


Figure 4.16 Patterns of Optic Flow Produced on the Retina When You Move in Various Directions. All neurons in one MSTd column may be activated by the same pattern.

Motion Parallax

- Motion helps extract the 3D structure of the world
- Recall: stereo vision depends on the disparity in the views of the two eyes
 - This disparity becomes minute for objects located more than an arm length away.
- For more distant objects, the visual system relies on another cue
- Motion parallax - perception of depth

- This is independent of binocular cells
- In retinal disparity, the brain measures distance by comparing the view in each eye
- In motion parallax, it compares one eye's view over time.
- Near objects sweep quickly across your retina, far objects sweep more slowly.

Motion Parallax with Eye Movements

- When you fixate a moving target with a pursuit eye movement, the pattern of optic flow from other objects is changed. If the eye pursues a near object, the motion on the retina (retinal slip) of other near objects is minimized and the motion of far objects is large
- When the eye locks onto a far object, the opposite pattern is observed. It is now the image of the near object that sweeps across the retina.
- Thus to decode the optic flow pattern correctly, the motion of the eye must be taken into account
 - The pattern produced depends on where you are looking

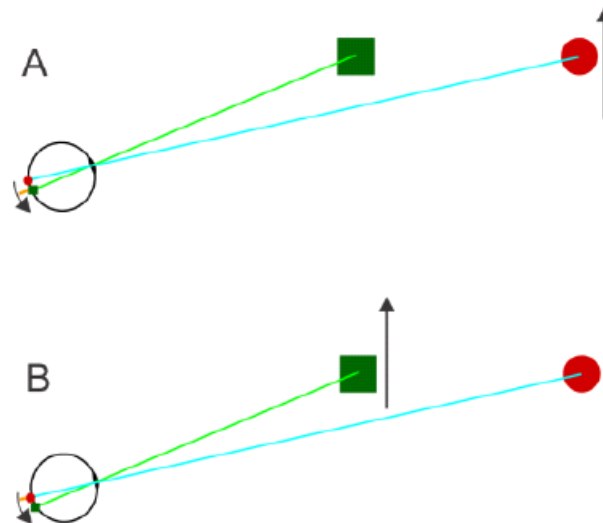


Figure 4.19 Motion Parallax During Pursuit Eye Movements A: Pursuit of a near target (yellow bar on the eye signifies the fovea) causes retinal slip from a far target. B: Pursuit of a far target causes retinal slip from a near target.

An Internal Sense of Motion

- The image of an object moves on the eye for one of 2 reasons:
 1. because object moves
 2. because eye moves
- Retinal slip (image moves on retina) could be combined with internal sense of our eye movements to improve our perception of motion
- Corollary discharge - internal sense of movement that is a copy of the movement command
- If there is retinal slip while the eye is still (corollary discharge = zero), then motion on retina must be from object
- However, if there is retinal slip opposite eye movements, image motion can be attributed to eye motion, not object motion (think object is stationary)
 - If, however, there is no corollary discharge elicited by eye movements due to a lesion, then stationary objects appear to move whenever the eyes move)

The Motion After-Effect

- Motion after-effect - Prolonged viewing of a moving stimulus can cause stationary objects appear to move
 - E.g. A rotating spiral appears to contract
 - E.g. Stationary face appears to expand
- Aka waterfall illusion
 - If one looks at a waterfall for a minute, then at a stationary rock, the rock appears to move upwards
- Effect is produced in part by changes in MT
- One common mis-interpretation is that this effect occurs because neurons fatigue
 - There are two good functional reasons for this effect:
 1. Adaptation

- CNS is not interested in things that are constant - prefers to detect changes
- When a constantly moving stimulus is applied, the system adapts
 - ◆ Then when motion stops, one experiences a rebound.
- 2. Velocity scale becomes recalibrated
 - When travelling at a constant velocity, neurons that represent velocities around that of the constant velocity become more finely tuned to these velocities
 - ◆ This makes them more sensitive to small changes around the constant velocity
 - This also pulls the scale, stretching it for other velocities and giving these other velocities a coarser representation
 - ◆ The activated cell can move to 0 - object seems stationary
 - Result could be percept of motion in opposite direction after motion stops as the scale changed

The 'What' and 'Where' streams share info

- Motion can be used to bind elements of an object, segregating it from the background
 - Suggests that motion is used to define the form of objects and that MT sends information to areas, such as LOC, that analyse form
- Thus MT ('where') and LOC ('what') co-operate by sharing information

Biological Motion

- CNS must decide that deformations observed on 2D screen are actually produced by rotations of a rigid 3D statue
- Biological motion - perception of something living - objects deform
 - e.g. people walking, lips moving
- Motion helps extract 2 things:
 1. Form
 2. Relative motion of the form's parts
- Analysis required for biological motion is sophisticated and requires the superior temporal sulcus (STS)
- STS gets:
 1. input about the object's form from LOC
 2. motion input from MT. STS can, from relatively few fragments, determine remarkable things from motion like the sex of the walking human figure and even its identity

Cerebral Association Cortex

October 8, 2019 4:09 PM

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

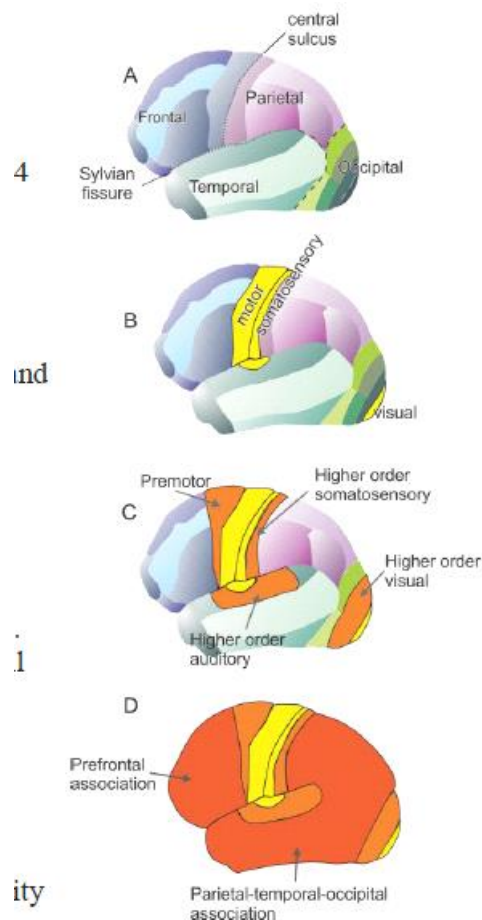


Figure 5.1 The Association Areas

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

4 anatomic subdivisions

- 4 lobes: frontal, temporal, occipital, and parietal

5 functional subdivisions

1. Primary sensory areas
2. Primary motor areas
 - 1 and 2 are where sensory info first arrives
 - In rats, these 2 occupy nearly all the cortex - in humans, 20%
3. Higher order (secondary) sensory areas
 - Higher order visual, somatosensory, and auditory lie near the respective primary areas

- Where each modality of sensory information is further processed for the most part without influence of other modalities
4. Premotor areas
 - Sends commands to the motor areas
 5. Prefrontal and Parietal-Temporal-Occipital association areas - make up over half of cortex
 - Where:
 1. Different modalities combine
 2. Attention is shifted
 3. Planning occurs and decisions are made
 4. 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
- Complex reflexes - require processing power of the association regions

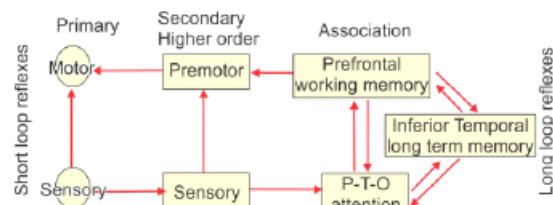


Figure 5.2 Interconnections Between the Different Areas Rapid short loop reflexes are on the left and long loop are on the right.

Some Properties of Cortex

Grey and White Matter

- Brain has extensive interconnections predisposing cortex to epilepsy
 - Abnormal activity in one area quickly spreads to other regions, leading to a seizure
- The grey matter requires more oxygen than white matter
 - To minimize total oxygen supplied, blood is directed preferentially to areas of in-use grey matter
 - This is basis for fMRIs - uses changes in blood flow to measure areas most active in a particular task
 - Measures the delivery of oxygen to ~cubic mm of grey matter containing millions of neurons, over a time span of seconds
 - In comparison, APs of neurons are measured in a fraction of ms
 - adds the brain's functioning to the structure imaged by MRI

The human Brain

- A 3-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

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

- Each neuron connects, on average, to 1,000 other neurons
 - Each neuronal output is dependent on input from a large number of other neurons
 - By comparison, modern PCs with 64 bit processors have an equivalent 64 connections
 - # of connections seems to be crucial difference between brain and computers - at least for now
- Diffusion tensor imaging (DTI) - another new MRI technique that maps brain's connections (axons in white matter)
 - Used to construct the *Human Connectome*: a map of all the neural connections in the human brain

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
- Layers 3 and 5 send output to other cortical regions, the brain stem, and spinal cord
 - These layers are thickest in primary motor cortex
- Over 100 years ago, anatomical differences in layer thickness let K. Brodmann divided cortex into 43 areas
 - Only now are we discovering that perhaps each has a unique function

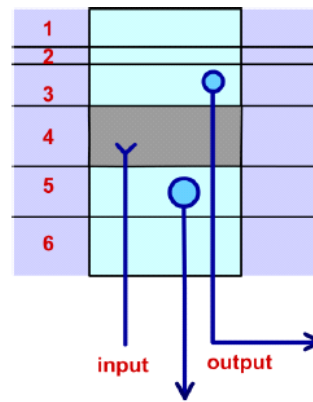


Figure 5.4 The grey matter has 6 layers, layer 4 receives input and layers 3 and 5 send output.

Are the functions of different cortical areas unique?

- 2 opposing theories:
 1. Lashley's equipotential theory - Information on a particular function is spread out over entire cortex
 - Evidence for: Loss of a few cells from a small lesion often results in minimal impairment
 - Evidence against: Cortex is not uniform - Different regions serve different functions
 - Most clearly seen in the primary sensory and motor areas
 2. Grandmother cell theory
 - Simple cells -> complex cells -> hyper-complex cells etc. 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
 - Evidence for: Lesion of the FFA do impair the recognition of faces selectively
 - 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

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

- No because the cortex is very plastic, particularly in early life
- 'Use it or lose it'

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

1. Each hemisphere excels in different tasks.

- The "dominant" side (usually L) - excels in sequential or serial tasks (e.g. language and mathematics)
 - Right hand preference begins in fetus - moves right hand more
 - These asymmetries are common among animals
- The "non-dominant" side (usually R) - excels in tasks requiring parallel processing (e.g. face recognition and geometry)
 - It excels in tasks that are spatial or intuitive, 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

2. Patients with a section of the corpus callosum

- The corpus callosum - large fiber tract that interconnects the 2 hemispheres
 - One extreme treatment for patients with severe epilepsy was to cut the corpus callosum
 - 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)
- 2 independent brains can function in one person - the 2 hemispheres

3. What are the advantages and disadvantages of lateralization (specialization of each side)?

- Advantages:
 - Corpus callosum pathways are long and thus slower
 - Pathways within the same hemisphere are often shorter and thus faster
 - Two halves could do two different things at the same time - duplication is a waste
 - Capacity of the brain could be nearly doubled

- Disadvantage:
 - Less redundancy - Redundancy is good if one part breaks down

Functions of the Prefrontal Association Area

- The prefrontal cortex has become larger, as a percentage of total brain size, over the course of evolution
 - So many believe that it is this area that distinguishes us from other animals
- Brain has high metabolic consumption - 20% oxygen use
 - Humans have evolved to learn to cook food - therefore get more energy
 - Animals larger than humans cannot cook - therefore cannot digest enough calories to fuel a human sized brain
 - So their brains are smaller than humans

Function 1: Planning and working memory

- Both planning and working memory are important functions of the prefrontal association area.
- Children, prior to the age of 1, have not developed working memory
 - If a toy is hidden behind one of two covers, the child cannot find it
- Lesions of the prefrontal association area produce deficits in tasks that are spatial and delayed
- Neurons in the prefrontal cortex:
 1. Show activity, which starts when a stimulus appears in a particular location
 2. Unlike neurons in V1, here activity continues even when the stimulus disappears
 - 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 an actual external stimulus to initiate movement

Function 2: Decision-making

- 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
 - Frontal lobotomies invented in 1949
- 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

1. 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
 - e.g. Locating objects in space by touch, sight, sound etc.
 - e.g. Language involves convergence of the sound of words, written words (sight), or Braille (touch)
2. Function 2: Attention
 - Attention allows us to focus in on specific stimuli and neglect others
3. 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)

The Flashlight of Attention

- In-attention causes blindness
- An analogy to understand attention: flashlight that selectively casts light on particular features of a scene
- One can tell whether one is paying attention and processing the material by an increase in size of their pupil
- Attention acts like a bottleneck - limits what enters the brain
 - The retina and visual cortex sees everything, but attention limits what gets further down
 - We are blind to what does not get through the bottleneck
 - We can't handle paying attention to all the information - we would faint
 - b/c APs are metabolically costly
 - This limits number of active brains cells

- Attention directs activity to particular brain areas that are best suited to process that information

Visual Perception is a 2-stage process

1. An early involuntary stage that automatically performs rapid low level processing of the visual world
 2. A voluntary and attention-demanding capacity-limited bottle neck regulates what enters working memory, awareness and consciousness
- Visual objects compete for your attention
 - Attentional blink - While attention is processing 1 visual object, blind to presence of other objects, even those at the location you had been attending
 - Attention can be drawn from below by objects that pop out from the background
 - In early visual areas, like or similar objects are inhibited while objects that are different are accentuated
 - Areas in the parietal dorsal stream can also direct attention voluntarily, as can areas that direct them

Finding an object in a crowded scene takes time

- It takes time for 3 reasons
 1. Objects don't automatically draw attention to itself
 2. Takes time to voluntarily shift your attention without moving your eyes (covert shift) or make 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 same as arousal

- Arousal is general, 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 NE
 - One locus coeruleus neuron projects to 100,000 cortical neurons
 - These neurons act like a volume control to increase one's level of alertness

Selectivity of Attention

- Attention can be directed at a specific location - increasing sensitivity to that location
- Attention to different features causes activation of particular cortical areas best suited to process that feature
 - For color, early visual areas, V1, V2 V3 are activated
 - For form, area LOC is activated, and for motion, area MT+
- Attention can selectively enhance 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
 - Bottom-up - when image automatically pops out - uses primarily fast connections from early visual areas
 - Top-down - selective attention - uses slower paths

More Types of Attention

1. **Spatial attention:** can voluntarily direct spotlight of attention to a particular location
2. **Feature-based:** can voluntarily focus your attention onto a particular attribute such as orientation, color, etc.
3. **Object-based attention:** objects, which stand out from the background, automatically attract attention

Neglect

- A lack of attention leads to lack of awareness
- A lesion of the right parietal cortex causes neglect of object's left side
 - Independent of what side of the object the patient is looking at
 - Frame of attention is drawn around the face, neglect is independent of frame's position on retina
- In a right V1 lesion, one is blind to everything to the left of where one's eyes look
- But lesion of left parietal doesn't result in neglect of things on object's right
 - Possible explanation: right parietal directs attention to both the left and right side of objects
 - The left parietal directs attention only to the right

Coordinate Frames

- 2 ways of representing an object's location and also of developing neglect:
 1. Allocentric coordinates - give an object's location with respect to some other object
 - Object-centered - your coordinates change
 - e.g. NESW
 2. Egocentric coordinates - state where object is relative to you (e.g. right, above, behind)
 - Patients with this neglect, only recalls objects on one side, but if asked to change vantage point,

recalls objects of objects of opposite side

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).
1. Frame 1: The location of the apple may be specified with respect to the table
 2. Frame 2: The location of the table may be specified with respect to the room

The 'What' and 'Where' Streams

- "where" stream tend to encode locations in egocentric coordinates
- "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
- "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

Visually Guided Actions

October 8, 2019 4:10 PM

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.

Multiple Representations of Space

- Dorsal stream's representations of space used to guide a variety of movements: saccades, grasps, reaches, and feeding
 - The activation of these areas direct one's attention to locations, but selection of the appropriate effector (e.g. which arm) can occur unconsciously
- Recall: Ventral stream is subject to perspective illusions
- Dorsal stream is not subject to perspective illusions
 - b/c you want to direct actions to the precise location
- 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:
 1. The early visual areas code objects with respect to the retina
 2. The ears are mounted in the head - so early auditory areas code locations with respect to head
 3. The location of your finger is coded with respect to your body

These representations surround the Intra-Parietal Sulcus (IPS)

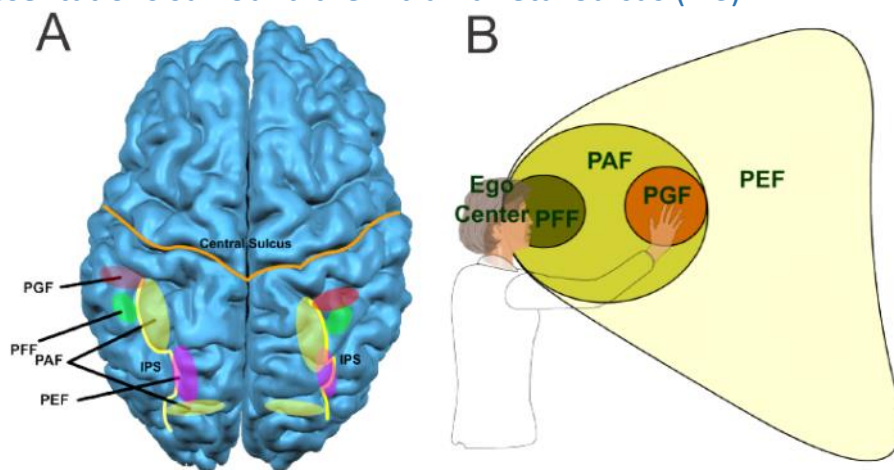


Figure 6.4 Location of various representations of space along the intraparietal sulcus and their extent. A: The Parietal Eye Field (PEF), the Parietal Arm Fields (PAF), the Parietal Grasp Field (PGF), and the Parietal Face Field (PPF). Yellow line is the intraparietal sulcus and orange line is the central sulcus. B: The extents in space of the areas shown in A.

- 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
- Contains several fields each responsible for directing a particular type of movement:
 1. PEF (Parietal Eye Field) - represents the retinotopic locations of objects you intend to look at
 - Neurons respond to visual and auditory stimuli that indicate a location wrt the retina
 - aka human LIP
 2. PAF (Parietal Arm Fields) - represents retinotopic locations in the immediate peripersonal space (where you can reach)
 - 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

3. PGF (Parietal Grasp Field) - represents the shape information required to grasp objects, not location
 - Also important is object info such as "strawberries are soft and should be grasped lightly".
 4. PFF (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
 - PEF - map space that is both near and far
 - PAF
 - Presumably PGF also receives input from the ventral stream of an object's properties such as their allocentric coordinates to grasp a knife by the handle and not the blade

An Example of Activity of 1 Specific Neuron in the Parietal Face Field (PFF)

- Neurons in PFF code specific locations wrt head
- Ex. Looking at a neuron activated by touching the mouth
 - This neuron is also activated by sight of object approaching the mouth from any direction
 - Even when looking up or down
 - But not activated by sight of an object approaching other parts of face (job of another PFF neuron)

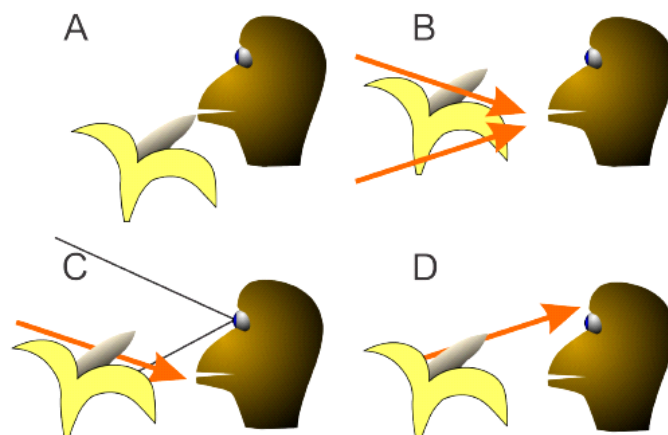


Figure 6.5 Neurons in the Parietal Face Field (PFF) code specific locations with respect to the head A: A neuron is activated by a touch to the lower lip. B: The same neuron is also activated by the sight of an object approaching the lower lip from any direction (Serenó & Huang 2006). C: And by the sight 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

1. Short latency saccades

- Saccades - 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

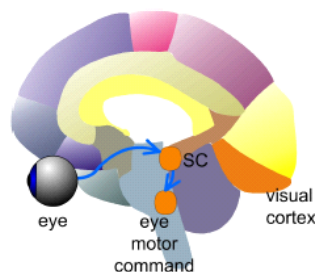


Figure 6.6
The route for short latency saccades

2. Long latency voluntary saccade

- The prefrontal association area - holds locations of remembered targets in working memory and makes the decision that one is of interest
- The PEF directs attention at the one of interest
- The FEF generate a long latency saccade to it.

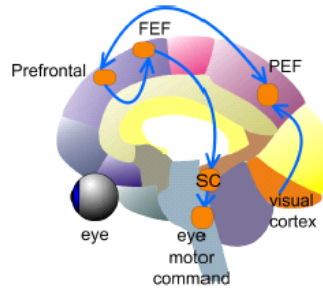


Figure 6.7
The route for long latency voluntary saccades involves the frontal eye fields.

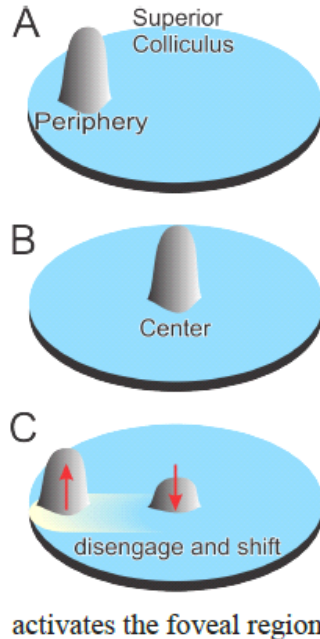
Characteristics of cells in the Superior Colliculus (SC)

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.



- The activity of the SC reflects engaging and disengaging of attention
- Examining how the SC codes location provides important clues as to how the IPS does so as well
- Recall: retinal ganglion cells, which project to 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 - can be viewed as a hill of activity
- SC mediates the visual grasp reflex
- A visual stimulus in a periphery produces activity in a corresponding location in SC
 - Activity at this location generates a motor command, which turns the eye's fovea to visual stimulus
 - This activates the foveal region at the center of the SC
- Before 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

A Comparison of 5 Topographic Areas

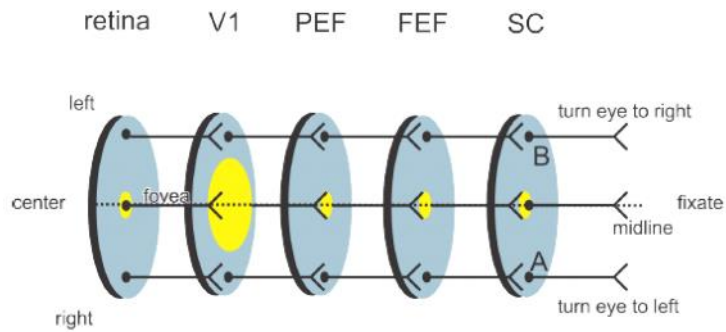
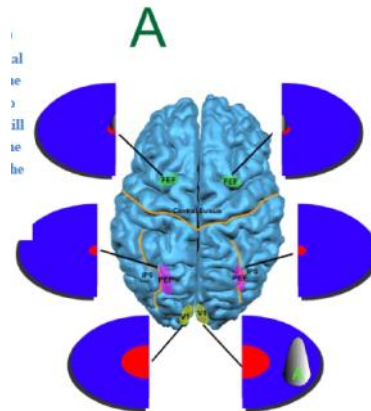


Figure 6.9 Topographic Maps in the Retina, the Primary Visual Cortex (V1), the parietal eye fields (PEF), the frontal eye fields (FEF), and the superior colliculus (SC) Both sides of the brain are shown, with the midline running through the center. Half the foveal (yellow) representation is on one side and half is on the other side.

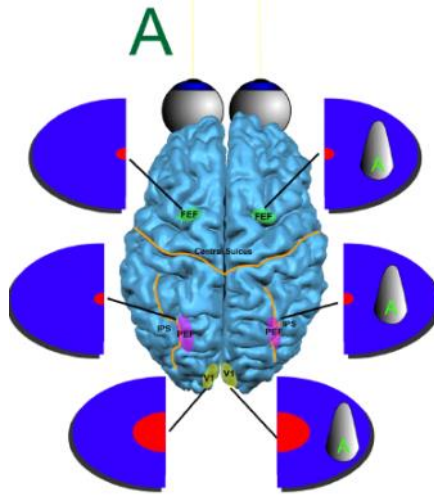
- Like the SC, the retina, V1, PEF, and FEF have topographic maps where the location of a group of active cells indicates the relative location of a target in the visual field
 - This becomes a map for the required size of movements
 - If one electrically stimulates a group of cells in the SC or FEF at location A, the eye would orient towards A
 - Similarly, stimulation at B causes an orientation to B
 - Activity at the center maintains fixation
 - 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 are under the following 4 everyday conditions

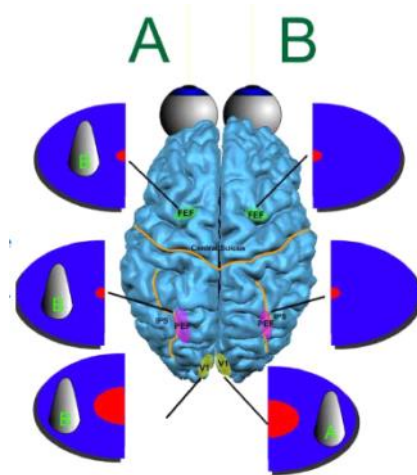
- In each case one is recording from a region that is activated by a light stimulus at location A or B, and the eye is initially pointing forward at center.
1. Condition 1: while looking forward a visual stimulus appears at the peripheral location A but no motor response is required
 - Enhanced activity 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



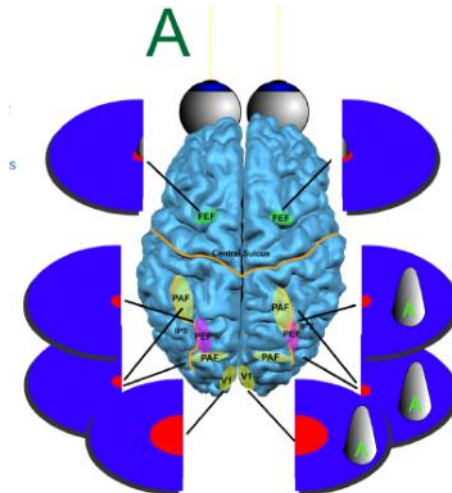
2. Condition 2: the same visual stimulus appears at A but now subject is required to saccade to A
 - In this case activity is the same as condition 1, plus enhanced activity in PEF, FEF, and SC at location A
 - A saccade is generated



3. 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 layers at location B
 - At location A, enhanced activity only occurs in the retina and the right visual cortex
 - A saccade to B is generated



4. Condition 4: a visual stimulus appears at A and 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 on right is associated with shift of attention to A
 - PAF is activated on right to direct a limb movement to A



- 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

4 Properties of the Parietal and Prefrontal Areas

1. These are activated by the memory of target locations

- 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 PEF and in working memory in the prefrontal (PF) cortex.

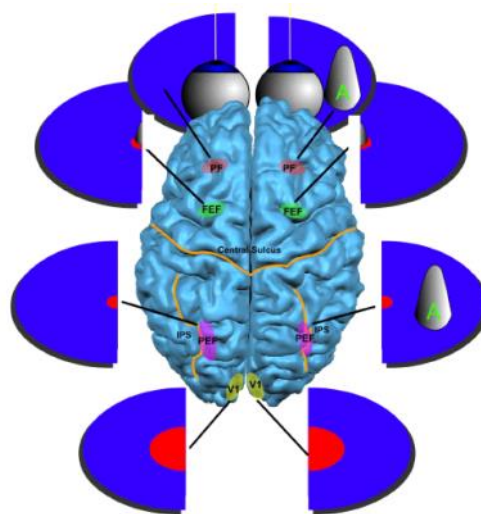
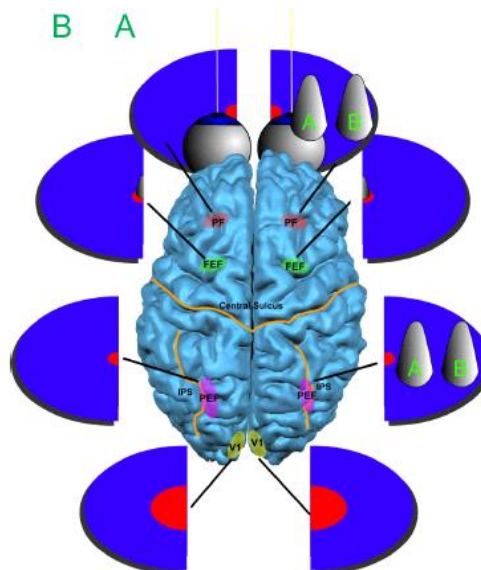


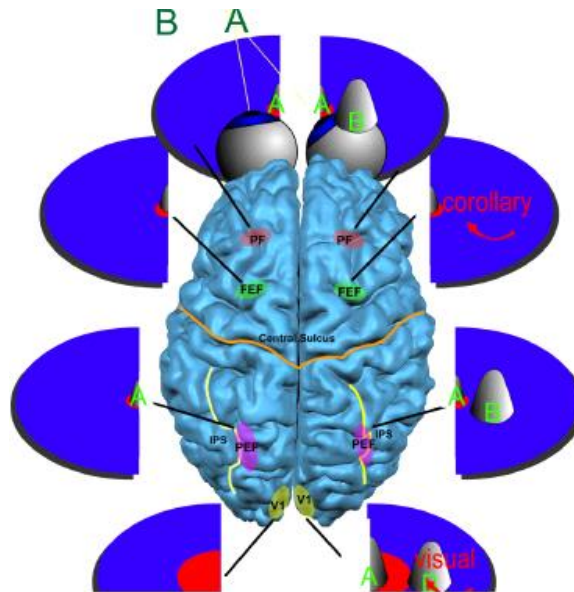
Figure 6.14 The memory of target A in the left visual field produces activity in the right PEF and PF. Activity in the foveal FEF maintains fixation.

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

- Saccade to 2 visual targets, A and B, that are briefly flashed in sequence and then both disappear
 - Activity in V1 while targets are still in sight
 - 2 hills of activity (1 for each target) persists in PEF and prefrontal cortex after visual stimuli disappears
 - In the FEF, the hill is bilateral in the foveal area
 - When the decision is made to saccade to the memory of "A", a hill of activity begins to grow in the FEF at the location of A, eventually overwhelming the hill in the fovea
 - Then a saccade is launched towards A



- 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 (corollary discharge)
 - This corollary discharge originates in the SC and is directed -> FEF (and to PF and PEF)
 - The corollary discharge shifts activity to group of neurons that would have been activated if A and B were still visible
 - When visual targets are continuously visible, the image of objects shifts during each eye movement
 - But sense that these objects are stationary b/c images land where our corollary discharge tells PEF to expect them



3. The Parietal and Prefrontal areas are involved in covert shifts in attention

- PEF through the FEF directs saccades to locations of interest - overt shifts of attention
 - They are also involved in covert shifts of attention
- Covert shifts can redirect attention to a spatial location without moving one's eyes - so 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
 - This in turn helps locate potential targets for a saccade to waldo
 - 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 an overt saccade is as yet not understood
- This cortical control of saccades involves a network of interconnected areas
 - Signals from V1 project along the dorsal stream -> PEF, FEF and PF
 - In turn areas such as 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
 - 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

4. One need not be conscious of covert and overt shifts in attention.

- When searching for Waldo in a picture we are conscious of what Waldo looks like
 - but not conscious of the many covert and overt saccades that we make while searching
- Each activates and shifts hills of neural APs in the parietal and prefrontal areas + visual cortex
- We can consciously direct our attention to some location in the picture, some color or some feature
 - We are also conscious of finding or not finding Waldo

The Representation of Numbers in IPS

- Numerosity - number of items in a group
 - The same number can have a variety of representations, 3 people or voices or the symbol "3"
 - The ability to compare numericities is present in young infants before they have learnt to count and in a variety of animals including birds
 - In humans, lesions of the IPS cause not only impairments in the ability in performing spatial tasks, but also in understanding numbers or quantities and performing calculations
- All regions in IPS have various topological representations, such as retinotopic or head centered
 - Numerosity also has a topographic representation in the IPS
 - The location of activity in IPS determines number size, not the level of activity
 - In this map, small numbers produce activity in medial areas while large numbers in lateral areas
 - It is easier to discriminate between small quantities (2 vs 3), than large quantities (11 vs 12) because a larger area of neurons represent these smaller numbers
- This is remarkable because it suggests that other cortical areas could have topographic maps of yet unidentified abstract values
 - Some humans report a spatial representation of numbers with small and large values located in different

- parts of their visual fields
- Not surprisingly, the frontal lobes are also involved in holding numerosity in working memory