The Eye

Introduction

About half of the human cerebral cortex is involved in analyzing the visual world. The eye is much like a digital camera; the retina is like the digital sensor. Retinal neurons (axons) continue into the optic nerve to distribute information to brain structures:

- Involved in regulating biological rhythms.
- Controlling eye movements and the optics of the eye.
- Constructing visual perceptions (starting with the lateral geniculate nucleus of the thalamus.

Properties of Light

- Light is electromagnetic radiation that varies in wavelength, frequency and amplitude.
- The human visual system detects wavelengths of about 400-700 nm.
- Light can be reflected, absorbed, refracted and diffracted (interfered with).

Structure of the Eye

Layers of the Eye

- Fibrous tunic
  - Cornea – anterior clear structure.
  - Sclera – lateral and posterior "white" of the eye.
- Vascular tunic
  - Iris, Ciliary muscles, Lens – anterior structures.
  - Choroid - lateral and posterior vascular layer.
- Neural tunic
  - Retina – lining of eye.
  - Pigment epithelium – between retina a choroid.
- Fluids
  - Aqueous humor – anterior to lens.
  - Vitreous humor – posterior to lens.

Image Formation

Refraction by cornea

- Refraction is about 42 diopters (d).
- $d = 1/f$; (f = focal distance in meters).

Accomodation by lens

- Refraction ranges from about 7 to 20 diopters.
- Refraction is controlled by contraction of ciliary muscles.
- Contraction of ciliary muscle "fattens lens" (increases diopters).
- Relaxation of ciliary muscle "thins" (decreases diopters).

Pupillary light reflex

- Retina → brainstem → pupillary muscles.
    - Constriction of pupil decreases light, increases depth of field, decreases maximum resolution.
    - Dilation of pupil increase light, decreases depth of field, increases maximum resolution.
- Visual acuity
    - Depends on the spacing of the photoreceptors and the eye's refraction.

Microscopic Anatomy of Retina

- Photoreceptors → Bipolar cells → Retinal ganglion cells.
- Only the photoreceptors are light sensitive.
- Only the axons of the ganglion cells leave the retina.

Photoreceptor Structure

- There are 125 million photoreceptors
- Outer segment contains membranous disk which contain light sensitive photopigments.
- Rod photoreceptors contain many disks and the same photopigment (a single type of opsin).
- Cone photoreceptors contain fewer disks and one of three different photopigments (three different types of opsin).
- Rods are about 1000 times more sensitive to light than cones.

Regional Differences in Retinal Structure

- The central retina (the fovea) contains a high density of cones and few rods.
    - Each retinal ganglion cell of the central retina receives signals from one or only a few photoreceptors.
    - Allows high resolution in well lit situations.
- The peripheral retina (away from the center) contains few cones and a large number of rods.
    - Each retinal ganglion cell of the peripheral retina receives signals from many photoreceptors.
    - Allows low resolution in poorly lit situations.

Phototransduction

Rod Photoreceptors

- Rods come in just one type, each with an opsin most sensitive to blue-green light (peak about 500 nm).
- Rods are very sensitive to light and dominant in nighttime vision.

Cone Photoreceptors

- Cones come in three varieties, each with a different opsin:
  - "Blue" cones are most sensitive to blue light (peak about 430 nm).
  - "Green" cones are most sensitive to green light (peak about 530 nm).
  - "Red" cones are most sensitive to red light (peak about 560 nm).
- Cones are much less sensitive to light and dominant in daytime vision.

Photoreception in rods and cones

Except for the opsins, the machinery for photoreception are the same in rods and cones.

- When not exposed to light:
  - GTP is converted to cGMP by guanylyl cyclase.
  - Specific Na^+ channels are kept <u>open</u> by cGMP.
  - The cell is depolarized (membrane potential about -30 mV).
  - Glutamate is released.
- When exposed to light:
  - The light is absorbed by an opsin, a G-protein coupled receptor.
  - The G-protein is activated.
  - The G-protein in turn activates phosphodiesterase.
  - The phosphodiesterase in turn converts cGMP into <u>inactive GMP</u>.
  - Specific Na^+ channels <u>close</u> in the absence of cGMP.
  - The cell is <u>not</u> depolarized (membrane potential about -65 mV).
  - Glutamate is <u>not</u> released.
- Color detection is dependent on the relative contribution of the three types of cones.

Dark and Light Adaptation

The transition from all-cone daytime vision to all-rod nighttime vision takes time.

- Dark adaptation (getting adjusted to the dark) takes 20-25 minutes.
  - Sensitivity to light increases a million fold or more during this time.
  - Pupil dilation increases light entry by up to 16 fold.
  - Unbleached rhodopsin regenerates.
  - More information from rods is made available to each ganglion cell by functional adjustment of circuitry.
- Light adaptation (getting adjusted to the light) takes 5-10 minutes.
  - Sensitivity to light decreases during this time.
  - Pupil constriction decreases light entry.
  - Less information from rods is made available to each ganglion cell.
  - Ca^{2+} concentration changes within the cones, which allow cones to register relative changes in light levels.

Retinal Processing

- Of the retinal cells, only retinal ganglion cells produce action potentials
- Photoreceptors release more glutamate when exposed to darkness than when exposed to lightness.
- Each photoreceptor is in synaptic contact with bipolar cells and horizontal cells.
- Each bipolar cell is in synaptic contact with retinal ganglion cells and amacrine cells.

Processing by Bipolar Cells

Off-Bipolar Cells

- Off-bipolar cells respond to glutamate from photoreceptors by depolarizing (and to absence of glutamate by not depolarization).
    - Caused by glutamate binding to and opening glutamate gated Na^{+}/Ca^{2+} channels.

On-Bipolar Cells

- On-bipolar cells respond to glutamate from photoreceptors by hyperpolarizing (and to absence of glutamate by depolarization and not hyperpolarization).
    - Caused by glutamate binding to G-protein coupled receptors that open Cl^{-} channels and close Na^{+}/Ca^{2+} channels.

Responses of Photoreceptors, Off-Bipolar Cells, and On-Bipolar Cells to Light On and to Light Off

	Light on	Light-off
Photoreceptor Cells	Less Depolarization	More Depolarization
	Less Glutamate	More Glutamate
Off-Bipolar Cells	Less Depolarization More Hyperpolarization	More Depolarization Less Hyperpolarization
On-Bipolar Cells	Less Hyperpolarization More Depolarization	More Hyperpolarization Less Depolarization

Bipolar Cell Receptive Fields

Each bipolar cell receives direct synaptic input from a cluster of photoreceptors. The number of photoreceptors in a cluster varies from one in the fovea to thousands in the periphery of the retina.

- The receptive field of a bipolar cell is the area of retina, that when stimulated with light, changes the cells membrane potential.
    - The circular part of retina that receives direct photoreceptor input is called the receptive field center
    - The part of the retina that receives indirect input via horizontal cells is called the receptive field surround.

- Responses of bipolar cells to light in the receptive field center are the opposite of the responses of the bipolar cells to light in the receptive field surround.
    - The center surround receptive field organization of the bipolar cells is passed to the retinal ganglion cells

Retinal Output

Retinal ganglion cells are the sole source of output from the retina to the rest of the brain.

Ganglion Cell Receptive Fields

Each retinal ganglion cell receives inputs from bipolar cells and from amacrine cells. There are only about a million ganglion cells in each retina.

- Similar to bipolar cells, retinal ganglion cells have a center surround receptive field organization.
- On-center and off-center ganglion cells receive input from the corresponding type of bipolar cell.
    - An On-center ganglion cells will be depolarized and respond with action potentials when a small spot of light is projected onto the middle of the receptive field.
    - An Off-center ganglion cell will be depolarized and respond with action potentials when a small dark spot is projected onto the middle of the receptive field.
    - However, in contrast to bipolar cells, the responses of both On-center and Off-center ganglion cell stimulation of the center is cancelled by like-stimulation of the surround; and vice versa.
    - Retinal ganglion cells are mainly responsive to differences within a receptive field, and emphasize contrast at light–dark edges.

Types of Ganglion Cells

Most retinal ganglion cells have a center surround receptive field organization with On-center or Off-center organization.

- About 90% are P-type ganglion cells.
    - Small (Parvocellular) neurons.
    - Small receptive fields.
    - Sustained discharge of slowly conducting action potentials.
    - More sensitive to high contrast stimuli.
- About 5% are M-type ganglion cells
    - Large (Magnocellular) neurons.
    - Large receptive fields.
    - Transient bursts of rapidly conducting action potentials
    - action potentials
    - More sensitive to low contrast stimuli
- About 5% are nonM-nonP ganglion cells

- Color-Opponent Ganglion Cells
    - Some P-type and nonM-nonP cells are sensitive to differences in the wavelength of light.
    - Response of to one wavelength in the receptive field center is cancelled by another color in the receptive field surround.
    - Color sensitivity in a receptive field seem to be paired as red/green or blue/yellow

Parallel Processing

Visual information seems to be processed in separate and parallel pathways.

- Information from the two eyes is kept separate.
- Information about light and dark sensitivity is kept separate.
- Information from small and large receptive fields is kept separate.
- Information about red *vs.* green and blue vs. yellow is kept separate.
- These lines of separate information are then forwarded to the brain.