Introduction to The Retina

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With some slides from Zhaoping Li (UCL) and other sources.
The Retina – basic properties

• *Part 1. The Retina as the input to the visual system. The start of the visual hierarchy.*
• *Part 2. Neurons, basic properties.*
• *Part 3. The Purpose of the Retina.*
• *Part 4. Complexity of the Retina and Neurons.*
Part 1: Retina as the input to the visual system

Image formation

3D world

Eye

2D image

Vision (brain)
The Structure of the Eye

• The eye is backwards, Meaning that lights passes by neurons before getting captured by the photoreceptors. *Only a small percentage of the photons that enter the eye reach the photoreceptors.* But the eye is extremely efficient at detecting photons which do.
The Fovea

• The density of cone (color) photoreceptors is peaked at the center and falls off rapidly.
• Rods (night vision) falls off slowly.
• We only have high resolution in a limited region,
• Two main consequences:
  • (1) The need for rapid eye movements.
  • (2) Crowding effects.

Figure from "Understanding Vision: theory, models, and data", by Li Zhaoping, Oxford University Press, 2014
Rapid Eye Movements: saccades & attention

• Eyes are frequently moving (several times a second). Movements take between 20-100 msec (10-3 seconds). Saccades.
• How do humans have consistent perception?
• Related phenomenon: In-attentional blindness – difficult to spot the difference between two images.
• These cause big differences between human vision and computer vision. No need for computer vision systems to have a fovea. No need for them to have in-attentional blindness.
• Presumably the brain is very efficient. It uses a very effective strategy that is often correct, but will occasionally make some errors which a computer would avoid.
Rapid Eye Movements and In-attentional Blindness.

• Eye movements (Zhaoping Li).
Crowding

• Visual crowding—the deleterious effect of clutter on peripheral object recognition—is ubiquitous in natural scenes.

• It seriously impacts virtually all everyday tasks including reading, driving, and interacting with the environment.

• Crowding impairs the ability to recognize and scrutinize objects, but it does not make them disappear. Sometimes it is impossible to recognize the spatial order of objects (or letter).

Crowding.

• A. Fixate at the bull’s-eye, near the construction zone. Observe it is difficult or impossible to recognize the child on the left side of the road, because of the presence of the nearby signs. The child on the right, on the other hand, is relatively easier to recognize.

• B. While fixating the crosses, identifying the middle shape, letter, or line orientation—or even the number of tilted lines—is difficult or impossible on the bottom half of the panel. Crowding impairs the ability to recognize and scrutinize objects, but it does not make them disappear; one can see that some thing is present in panel (A), but it is difficult to identify the thing as a child as opposed to another sign. Crowding defines the spatial resolution of conscious object recognition throughout most of the visual field.
Retinotopy: spatial organization

• Higher visual areas – e.g., V1, V2 in visual cortex also have similar spatial organization to retina. This is called Retinotopy.

Figure from "Understanding Vision: theory, models, and data", by Li Zhaoping, Oxford University Press, 2014
Retina as the start of visual hierarchy (V0?)

- Retina – no top-down input:
  connects to superior colliculus (SC)
SC controls muscles for gaze control.
Part 2: Basic Neurons

• Real neurons and neural circuits.

Figure from "Understanding Vision: theory, models, and data", by Li Zhaoping, Oxford University Press, 2014
Simplest Model of a Neuron

- Simplest model. Integrate and Fire.

Response \( O = \sum_x K(x)S(x) \)

Retinal ganglion cell

Effective filter \( K(x) \) for the receptive field

Photoreceptor input

Figure from "Understanding Vision: theory, models, and data", by Li Zhaoping, Oxford University Press, 2014
Measuring Receptive Fields

• Electrophysiology: Move and vary stimulus until neuron fires.

Figure from "Understanding Vision: theory, models, and data", by Li Zhaoping, Oxford University Press, 2014
Ganglion Cells: Center Surround Receptive Field

- Mathematical models next lecture.

Figure from "Understanding Vision: theory, models, and data", by Li Zhaoping, Oxford University Press, 2014
Sensitivity to Color

- Three colors – but some people have two (color blindness)

Figure from "Understanding Vision: theory, models, and data", by Li Zhaoping, Oxford University Press, 2014
Part 3: Purpose of the Retina

• With about 10 million retinal receptors, the human retina makes on the order of 10 to 100 million measurements per second. These measurements are processed by about a billion plus cortical neurons.

• How sensitive is the eye? What are the limits of vision?

• It can be shown that the retina can be sensitive to a very small number of photons. This is close to theoretical predictions based on the biophysics of neurons (W. Bialek handout).
Purpose of the Retina

- The anatomy and electrophysiology of the retina has been studied extensively – far more deeply than the cortex.
- The main functions of the retina are:
  - (i) To convert image intensity patterns (photons) to patterns of neural activity.
  - (ii) To reduce slow spatial and temporal changes through spatial and temporal filtering of the image (smoothing the input).
  - (iii) To normalize neural responses – gain control -- to encode contrast and deal with the large range of luminance (intensity) from scene to scene. Ranging from faint starlight to bright sunlight (range of 1 to $10^9$).
  - (iv) Encode the intensity so that it can be efficiently transmitted to the LGN and then on the visual cortex.

The next lecture will describe the “standard model of neurons in the retina” based on linear filtering.
Purpose of the Retina

- Zhaoping Li’s conceptual picture. Retina captures image and encodes for transmission to LGN (Thalamus) and then to visual cortex V1.

![Diagram of visual processing stages]

- **Encoding**: (e.g., by retinal neural activities)
- **Selection**: (attentional selection, often by saccading to selected locations)
- **Decoding**: (e.g., face recognition)

For motor action or cognitive decisions
How simple is the human retina?

• Does the retina of humans/monkeys just capture images and transmit them to the visual cortex? Or does it process them – e.g., by extracting edges. (like the retinas of simpler animals – frogs).

• Standard wisdom: “smart animals have dumb retinas and dumb animals have smart retinas.”

• This is questioned by T. Gollitsch and M. Meister (handout). They argue that human/monkey retinas are more complex than current models suggest. That current models of retinal neurons are based on experimental findings using simple stimuli – and the neurons are more complicated when they see natural stimuli. (We will keep returning to this issue).

• Why use so many neurons if the retina is only a smart camera?

• Smart cameras have complex engineering and algorithms – sophisticated gain control (20th century cameras frequently saturated), insensitive to noisy movements (e.g., hand movements). Over the past forty years camera technology has developed much faster than our understanding of the retina!
• Claim: the primate retina is much more complex than standard models.

• List six computations performed by the retina and their underlying microcircuits.
(A) Detection of dim light flashes in the rod-to-rod bipolar pathway. (Left) Rod bipolar cells pool over many rod photoreceptors, which show distinct responses to single-photon activation embedded in noise. Bipolar cell potentials are not swamped by the accumulated noise in all rods, but instead show distinct activations from single photons, as shown by the voltage traces from a simple model simulation. (Right) The important elements of the corresponding retinal microcircuitry. Each photoreceptor output is sent through a band-pass temporal filter followed by a thresholding operation before summation by the rod bipolar cell (Field and Rieke, 2002). Notation for this and all circuit diagrams: triangle, neuron; rectangle, temporal filter function; oval, instantaneous rectifier; closed/open circle, sign-preserving/inverting synapse.
Gollitsch and Meister: (B) Moving Texture.

(B) Sensitivity to texture motion. (Left) Y-type ganglion cells show activation when a fine grating shifts in either direction over the receptive field (circle), even though the average illumination remains constant. (Right) The underlying microcircuit. Each shift of the grating excites some bipolar cells and inhibits others. The bipolar cells have biphasic dynamics (see impulse response in inset) and thus respond transiently. Only the depolarized bipolar cells communicate to the ganglion cell, because of rectification in synaptic transmission. Thus, the ganglion cell fires transiently on every shift (Hochstein and Shapley, 1976).
Detection of differential motion. (Left) An object-motion-sensitive ganglion cell remains silent under global motion of the entire image but fires when the image patch in its receptive field moves differently from the background. (Right) The circuitry behind this computation is based on similar elements as for the Y cell (panel B). Rectification of bipolar cell signals in the receptive field center creates sensitivity to motion. Polyaxonal amacrine cells in the periphery are excited by the same motion-sensitive circuit and send inhibitory inputs to the center. If motion in the periphery is synchronous with that in the center, the excitatory transients will coincide with the inhibitory ones.
Gollitsch and Meister: (D) Approaching Motion

(D) Detection of approaching motion. (Left) A certain type of retinal ganglion cell responds strongly to the visual pattern of an approaching dark object, as indicated by the schematic spike train below, but only weakly to lateral object motion. (Right) The circuit that generates this approach sensitivity is composed of excitation from OFF bipolar cells and inhibition from amacrine cells that are activated by ON bipolar cells, at least partly via gap junction coupling. Importantly, these inputs are nonlinearly rectified before integration by the ganglion cell (Münch et al., 2009).
Gollitsch and Meister: (E) Spatial structures.

(E) Rapid encoding of spatial structures with spike latencies. (Left) Specific retinal ganglion cells encode the structure of a new image by their spike latencies. Cells with receptive fields (circles) in a dark region fire early, those in a bright region fire late. Cells whose receptive fields contain both dark and bright produce intermediate latencies and thus encode the boundary in their synchronous firing. (Right) The responses result from a circuit that combines synaptic inputs from both ON and OFF bipolar cells whose signals are individually rectified. The timing differences in the responses follow from a delay ($\Delta t$) in the ON pathway (Gollisch and Meister, 2008a).
(F) Switching circuit. (Left) A control signal selectively gates one of two potential input signals. (Right) In the retina, such a control signal is driven by certain wide-field amacrine cells (A₁), which are activated during rapid image shifts in the periphery. Their activation leads to a suppression of OFF bipolar signals and, through a putative local amacrine cell (A₂), to disinhibition of ON bipolar signals (Geffen et al., 2007).
What do smart camera do?

• Engineers (and computer vision researchers) develop algorithms to enhance photographs and videos. E.g., to adjust color balance, prevent over- and under-exposure.

• Some of these algorithms are quite complex – requiring many of the retinal operations hypothesized by Gollitsch and Meister. E.g., spatial and temporal grouping.

Part IV: Complexity of the Retina and Neurons

• The structure of the retina is very complex.
• So are the structures of neurons.
The anatomy of the retina is not simple.

- The anatomical structure of the retina gets increasingly complex as scientists study it in detail. S. Seung. Connectonics. (YouTube).

- Many different types of neurons when you consider their detailed anatomy (Masland). Seung recruited volunteers to label the three-dimensional structure of neurons in the retina.

- Scientists who study the visual cortex also find many different types of neurons (hundreds) the more they look into the details. (although many are pyramidal).
The Retina. Complex connections.

- Many different types of neurons – neurons have complex dendritic structure – and complex connections between neurons.
The Retina: Many different types of neurons.

- Neurons: Dendrites, Axons, and Soma (cell body).
The Retina and Connectonics

• How much will wiring diagrams, or even detailed biophysical models, help understanding the brain.

• Scientists understood the wiring and biophysics of C. Elegans (150 neurons) but this failed to give much insight into the computations performed in its brain. And mice and human/monkey brains are more complicated by many orders of magnitude.

• Surely we have to understand the types of computations being performed as well – it would be hard to understand the function of a TV by just analyzing its electrical circuits – and you certainly could not understand what program it was showing.

• “Could a neuroscientist understand a microprocessor”. Eric Jonas and Konrad Kording. PLOS. Handout.

• S. Seung and A. Movshon debate: http://www.youtube.com/watch?v=fRHzkRqGf-g

• But surely understanding the wiring diagrams and the biophysics is a pre-requisite. There are major attempts to understand the wiring diagrams of the mouse brain.
Retina Implants: Artificial Retinas.

- Retinal implants are intended to help blind people see.
- Current implants 10x10 arrays.
- Prosthetic Eyes; Sheila Nirenberg (TED talk).
- But restoring input to the eye may not enable perception (Mike Mays)
Lecture Summary

• This talk gave a brief introduction to the retina. Mathematical models (standard) will follow in the next lecture.
• Part 1. The Retina as the input to the visual system.
• Part 2. Neurons, basic properties.
• Part 3. The Purpose of the Retina.

• Moral: the visual system is very complicated and only partially understood, even the retina.