Design of Peripheral Sensory Mechanisms

We have no *direct* experience of the world; what we perceive is determined by the trains of action potentials from our peripheral sensory apparatus. To understand perception, we need to know how it is limited by peripheral mechanisms.

Sensory periphery is exquisitely engineered to overcome enormous information processing demands.

Example:

\[
\begin{align*}
2000 \times 2000 \text{ pixels} &= 4 \times 10^6 \text{ pixels/frame} \\
x 24 \text{ bits/pixel} &= 10^8 \text{ bits/frame} \\
x 100 \text{ frames/s} &= 10^{10} \text{ bits/s} \\
\text{Gigabit Ethernet} &= 10^9 \text{ bits/s (theoretical maximum)} \\
\end{align*}
\]

\[
\frac{1}{\sim 10^6 \text{ optic nerve fibers}} = 10,000 \text{ bits/s/fiber}
\]

-> roughly 100-1000 fold too much information to cram down the optic nerve! Design of retina can be understood as a solution to this problem.
1. Visual Pathways

- dominant pathway from retina -> lateral geniculate nucleus (LGN) -> primary visual cortex (V1) -> extrastriate cortices

- minor pathways from retina to pretectum (accessory optic system), superior colliculus (orienting), and suprachiasmatic nucleus (circadian)

- partial decussation at optic chiasm
Appreciating the complexity…
in monkeys, roughly 30 regions of cerebral cortex involved in vision
-These regions collectively comprise about 50% of the cortex, contain billions of neurons, and are extensively connected. Both feedforward and feedback connections.
2. Basics of Visual Transduction

- Light is focused onto the retina (what 2 ways?) and strikes photoreceptors at the back of the eye. Absorption of light by the photopigment sets off a cascade of events leading to change in membrane potential (which way?)

- Outside fovea, light passes through other cell types before arriving at photoreceptors. What are consequences? Why built this way?

- In fovea, other cell types are pushed aside.
Signal flow in retina:

- vertical pathway from photoreceptors to bipolar cells to ganglion cells (spiking output cells)

- horizontal pathway involving horizontal and amacrine cells.

- ganglion (output) cells are only spiking neurons
3. Design Principles of the Retina

3.1. Two classes of specialized Photoreceptors

CONES (~5 million)
- mediate vision under well-lit conditions
- 3 types of photopigments: like short (S), medium (M), and long (L) wavelengths. Relative responses of 3 types underlie color vision.
- cones are responsible for high visual acuity. In fovea, bipolar cells get input from a single cone

RODS (~120 million)
- very sensitive to light, can respond to a single photon
- mediate vision under low-light conditions
- contain a single photopigment -> do not mediate color vision (why everything looks B&W in very dim light)
- many rods converge onto a single bipolar cell: low spatial resolution

- Cone response to a brief pulse of light is biphasic lasting 200-300ms. This limits temporal resolution of vision to ~55 Hz. Rods are much more sluggish (~12 Hz).
In dim light, we throw away color and fast temporal information to increase sensitivity.

Cones have varied sensitivities to spectral wavelength (L, M, S cones). Their relative activities form the basis for color vision. Coding based on relative activities allows us to sense the color of objects as the spectral content of the light source changes.
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3.2. Non-uniform sampling and the moveable eye

- unlike a camera, the retina does not have uniform spatial resolution across the visual field (right). Hence the need for a moveable eye.

- cones are abundant near fovea and rods absent; rods are plentiful in periphery (star gazing).

- in the fovea, cones are densely packed into a regular array. Cone separation \( \approx 0.0084 \) deg. This corresponds to a spatial sampling frequency of \( (1/0.0084) = 120 \) samples/deg.

- this sampling frequency is tightly matched to the optics of the eye, as measured by the modulation transfer function (right). Sampling frequency is 2x the highest spatial frequency in the image (Nyquist theorem).
3.3. Light (dark) adaptation

- We can see well across 10 orders of magnitude of the intensity of light.

- This presents a major problem for receptor neurons that have a limited dynamic range of responses (define threshold, dynamic range, saturation).

- Note the tradeoff between slope and coding range.

Which coding scheme below is best? Why?
3.3. Light (dark) adaptation (cont.)

- to code a very large range of light levels efficiently, the retina has mechanisms for light/dark adaptation

- We all have experienced light/dark adaptation. Adaptation serves to remove the effect of average light level on visual perception.

- This requires the retina to transmit less information about light levels to the rest of the brain

- Behaviorally, the dark adaptation curve has two phases due to cones and rods. How could you separate them?
A neural mechanism of light adaptation:

- cones and ganglion cells adjust their operating range according to the mean light level (curves shift horizontally, on a log luminance axis).

- as a result, change in response is proportional to change in light level around the ambient level: \( \Delta R = \Delta L/L \)

  Equivalently, the slope (or sensitivity) is given by: \( \Delta R/\Delta L = 1/L \)

  Note that \( \log(\Delta L/L) = \log(\Delta L) - \log(L) \), so changing \( L \) shifts curve on a log x-axis

- the form of this relationship also holds for many other types of perceptual tasks: WEBER’S LAW

- why is this useful (scale analogy)?
- How does this help with the tradeoff between sensitivity and coding range?
3.4. Lateral Inhibition and coding of contrast

- lateral connections in the retina subserve an important function: coding of contrast

- Horizontal cells mediate lateral inhibition between photoreceptors and bipolar cells

- Amacrine cells mediate lateral inhibition between bipolar cells and ganglion cells

- 2 types of synapses between PRs and bipolars help to create two classes of bipolars: depolarizing and hyperpolarizing

- These two types of bipolars provide input to ON and OFF ganglion cells, which have a characteristic center-surround receptive field organization

Receptive field = region of visual space in which stimuli influence firing rate
ON-center cells: excited by light (inhibited by dark) in the center, inhibited by light (excited by dark) in the surround

OFF-center cells: opposite pattern

- little response to uniform luminance over the receptive field -> code the difference in light between center and surround, CONTRAST

- Why is this useful?

- Lateral inhibition is widely used in sensory systems of the brain.
- Effect of filtering an image with a ‘receptive field’ resembling an ON-center ganglion cell

- What does this do to the information content of the image?
Some Coding Principles in the Sensory Periphery

1) Specialized receptor types: e.g., rods and cones. Each receptor type is sensitive to different portions of the input spectrum.

2) Convergence: e.g., many photoreceptors feeding into a single ganglion cell in the periphery -> removes high-frequency information ("low-pass") and boosts sensitivity

3) Adaptation: e.g., to luminance (or contrast). Allows neurons to shift their dynamic range to encode the range of inputs that is currently relevant to behavior.

4) Lateral Inhibition: e.g., horizontal connections making up the surrounds of ganglion cells -> removes low-frequency information ("high-pass") and enhances discontinuities