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Jeremy Nathans' Lecture Part 1B:
The Vertebrate Retina

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Contents

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1. Keywords and Terms

eye, retina, visual cortex, fovea, eye movements, photoreceptor topography, ganglion cell receptive field, center-surround receptive field, Hering illusion, motion detector, Ouchi illusion, stereoscopic depth perception, depth from shading, figure-ground organization, visual art

2. Lecture Notes

Photoreceptors and Image Processing:

The human retina has a specialized central region, the fovea, which has a high cone density and is used for high acuity vision.

Fixational eye movements serve to bring the image of the object of interest onto the fovea. Monitoring these eye movements reveals the visual search strategy associated with a given visual task. Eye movements also largely compensate for head and body motion.

The antagonistic center-surround spatial organization of many retinal ganglion cell receptive fields enhances the detection of spatial contrast and accounts for the Hering illusion. This organization, and its elaboration at higher levels within the visual system, probably accounts for the effectiveness of simple line drawings and portraits, which, in essence, are creating an image that mimics the brain's processed representation of the scene.

Other retinal ganglion cells respond selectively to motion in a particular direction, and some of these cells respond only to local motion. Retinal ganglion cells that are direction-selective motion detectors mediate the Ouchi illusion.

Binocular vision (i.e. vision with two eyes) serves as the anatomic basis of stereoscopic depth perception. Charles Wheatstone, a British engineer, first recognized this phenomenon in the early 19th century. Because of the different locations of the two eyes within the head, the images projected onto the left and right retinas differ, and those differences allow the brain to calculate the relative depths of objects within the scene. How and where in the brain this calculation takes place is still not entirely clear.

A variety of simple perceptual effects that are both subconscious and effortless appear to involve learned responses. For example, judgments about three-dimensionality based on shading are made with the hidden assumption that the source of illumination is from above (a generally correct assumption for the real world); and judgments about absolute size are strongly biased by our assessment of how far away the objects are.

Perception in the context of ambiguous or competing ways of organizing the scene suggest that the visual system attempts to synthesize a single, unifying, and consistent perceptual explanation for any given scene.

We can extend the theme summarized above regarding simple line drawings. Thus, abstraction in visual art probably works because it mimics some of the perceptual strategies used in the brain's higher visual centers.

3. Recommended Reading

1. **Kandel, E.R., and Wurtz, R.H. (2001) Constructing the Visual Image (chapter 25), in Principles of Neural Science (fourth edition). Kandel, E.R., Schwartz, J.H., Jessell, T.M., editors. New York: Elsevier.**
2. **Livingstone, M. (2002) Vision and Art, the Biology of Seeing. New York: Harry Abrams.**
3. **Wurtz, R.H., and Kandel, E.R. (2001) Perception of Motion, Depth, and Form (chapter 28), in Principles of Neural Science (fourth edition). Kandel, E.R., Schwartz, J.H., Jessell, T.M., editors. New York: Elsevier.**

4. Review Questions

1. **In humans and other primates, how does the central retina differ from the peripheral retina?**
2. **What types of eye movements occur during reading?**
3. **What types of eye movements occur when viewing a face?**
4. **What is a retinal ganglion cell receptive field?**
5. **Define center-surround receptive field.**
6. **What features of an image does a system of center-surround receptive fields emphasize?**
7. **What is the utility of retinal ganglion cells that are activated by local but not global motion?**
8. **In judging shape from shading – that is, the pattern of shadows – what hidden assumption does the observer typically make?**

5. Answers to Review Questions

1. **The central retina (the fovea) is characterized by a high concentration of cones. This is the only region of the retina that mediates high acuity vision.**
2. **There are periods of steady fixation interrupted by rapid movements (saccades) that bring the direction of gaze to a new fixation point.**
3. **The eyes move so that those facial features that are of special interest are imaged on the fovea where they can be seen with high acuity. These features include the eyes, mouth, and the contours of the head.**
4. **It is the region of the retina where light either activates or inhibits the response of the retinal ganglion cell.**
5. **In this type of retinal ganglion cell receptive field, light that falls on a central zone stimulates the cell, while light falling on a surrounding annulus inhibits the cell. There are also center surround retinal ganglion cells in which the polarity of this response is reversed: the center is inhibitory and the surround is excitatory.**
6. **It emphasizes spatial differences in light intensity, as seen with edges and lines.**
7. **These cells are sensitive to the motions of objects relative to their surroundings: for example, a bird flying in front of a stand of trees. Importantly, the uniform image motion that arises from eye or head movements does not activate local motion detectors.**
8. **We generally assume that lighting is from above, as it is when the sun illuminates a scene.**

6. Discussion Questions

1. **In the lecture, examples were shown of human eye movements during reading or while viewing faces. How are such eye movements measured?**
2. **As Newton observed when passing light through a glass prism, differently colored lights are bent to different extents. The same phenomenon occurs when light is focused by refraction by the cornea and lens. This phenomenon, referred to as chromatic aberration, produces an image on the retina which will be optimally**

focused for one particular wavelength of light and progressively out of focus for wavelengths that are progressively further from the one for which the focus is optimal. How has the problem of chromatic aberration been solved for optical instruments such as telescopes and microscopes?

3. **The center-surround receptive field organization of retinal ganglion cells serves as a way of comparing light intensity at different locations on the retina. Why has the retina evolved to have this organization? Is this general principle used in other contexts within the visual system or in other sensory systems?**

7. Answers to Discussion Questions

1. **The most common method is to use an infrared light and an infrared video camera to record eye movement. Infrared is used because it is invisible to the subject. A second method uses a blank (i.e. nonrefracting) contact lens that has a very fine ring of magnetic material around its periphery. The orientation of this magnet can be measured by a set of magnetic sensors around the subject.**

2. **The original solution for telescopes - invented by Isaac Newton - was to use a parabolic mirror rather than a glass lens to focus the light. When light is reflected from a surface, the angle of incidence equals the angle of reflection and this is independent of wavelength. Microscopes generally use refraction rather than reflection to focus light, and the current approach to correcting the problem of chromatic aberration is to use "achromatic" lenses, glass lenses that have been manufactured with an inhomogeneous composition that largely compensates for the chromatic aberration that occurs at the air/glass interface.**

3. **Cells with center-surround receptive fields are activated by relative differences in intensity at different locations on the retina, and, as such, they are less concerned with absolute intensities. This abstraction is useful to the organism because the absolute brightness of objects within a scene, which is highly dependent on the intensity of the light source, is generally of little interest compared to relative intensities. Relative brightnesses reflect differences in the intrinsic properties of the objects – for example, the lower reflectance of black ink compared to white paper. Consider the following example. If we suppose that a particular type of ink on white paper reflects 1% as much light as the paper, then the ratio of light reflected from printed letters compared to the surrounding paper will remain 100:1, regardless of the intensity of illumination. If we are reading a book outside on a sunny afternoon**

when the light is 1,000 times brighter than inside under a dim light bulb, the letters will still appear as black objects against the white background in both situations even though the absolute amount of light reflected from the black ink under direct sunlight is ten times greater than the amount reflected by the white paper under a dim light bulb.

4. **A similar "normalization" of the image occurs with color information, with the result that our perception of the colors of different objects within a scene remains remarkably constant even as the wavelength composition of the illumination changes. Other sensory systems employ similar principles to detect small stimulus differences. For example, two sounds that differ subtly in pitch can be reliably distinguished, but identifying the absolute pitch of a sound is far more difficult.**

8. Explain or Teach These Concepts to a Friend

1. **What is the physiologic basis for the Hering Illusion (the illusory black dots that are located at the white intersections between large black squares)?**
2. **What is physiologic basis of the Ouchi Illusion (the apparent motion and segregation of the central panel of vertical black and white rectangles from a surround of horizontal black and white rectangles)?**

9. Research the Literature on Your Own

1. **Investigate the different types of human eye movements. For example, what is the difference between smooth pursuit eye movements and fixational eye movements? What is the arrangement of extra-ocular muscles and how do they work together to generate eye movements?**
2. **What types of visual information is relayed to the brain by the different classes of retinal ganglion cells?**
3. **What is the mechanism of stereoscopic depth perception? What are some other cues to depth perception that do not depend on binocular viewing? Historical note: Leonardo Da Vinci and other painters figured out most of them, and have used them in their paintings.**