

**Seminar: Modern Classics in Visual Perception, Visual Science, and Visual Neuroscience:**

**Psychology W3255  
Prof. Leonard Matin  
Dept. of Psychology**

**Psychology G4255y.  
Spring, 2013, 6:10-8:00 pm, Thursday  
Room 405, Schermerhorn Hall**

The specifics of this sequence will be modified to fit especially interesting directions as we proceed. For example, as I'm making up the syllabus (below) for this semester, it's clear that we will be spending most, if not all, of Jan. 31 and some of Feb. 7 on readings related to the 'Two Visual Systems' story and a piece of 'Nature/Nurture' before making a significant shift to some classic work on retinal receptive fields and Egocentric Space Perception.

1. Jan. 24 Organization & Introduction to Visual Perception, and Visual Neuroscience
2. Jan. 31 Two Visual Systems: What/Where and/or Perception/Action?
3. Feb. 7 Nature/nurture: visual development
4. Feb. 14 Retinal receptive fields
5. Feb. 21 Egocentric Spatial Perception
6. Feb. 28 Psychophysics & the visual stimulus in relation to threshold detection and intensity discrimination: Light and dark adaptation
7. Mar. 7 The physical quantum and threshold
8. Mar. 14 Lateral inhibition: neural and psychophysical  
*Mar. 21: Spring Holiday*
9. Mar. 28 Opponency and trivariance in color vision
10. Apr. 4 Temporal frequency: the de Lange function
11. Apr. 11 Spatial frequency and multiple channels
12. Apr. 18 Stereovision: A Computational Model for the Perception of Depth
13. Apr. 25 Audition and Auditory Localization: The missing fundamental --  
Auditory Pitch independent
14. May 2 Perception of Motion and Visual Orientation -- Projection System models

**Some References Useful for Basic Background**

**1. Basic Visual Information:**

Wolfe, J. M., Kluender, K R. Levi D. M. Sensation and Perception. (2<sup>nd</sup> ed. 2008, 1<sup>st</sup> ed. 2005)

Goldstein, B. Sensation and Perception (either 7th edition, 2007 or earlier), or any other sensation and/or perception text. Authors of some such texts: R. Sekuler & R. Blake; M. Levine; B. Wandell; R V. Bruce, P. Green & M. Georgeson.

**2. Useful Additional References on Vision:**

Graham, C.H. Vision and Visual Perception, 1965

Cornsweet, T. Visual Perception, 1970

Rodieck, R.W. The First Steps in Seeing, 1998

Zeki, S., A Vision of the Brain, 1993

Hubel, D. Eye, Brain, and Vision, 1988, 1995

Readings from Scientific American: Perception: Mechanisms and Models (R. Held & W. Richards, [eds]), 1971.

Readings from Scientific American: Recent Progress in Perception (R. Held & W. Richards), 1964, 1975.

Dowling, J. E. The Retina, 1987

**3. Any elementary physics book (Light, Optics, etc. ).**

**4. Some Additional Books to be used during the Semester**

1. Nijhawan, R. & Khurana, B. (eds.) Problems of Space and Time in Perception and Action, 2010, Cambridge University Press.

2. Marr, D. Vision. 1982

3. Howard, I. Human Visual Orientation, 1982

4. Howard, I. and Templeton, Human Spatial Orientation, 1966

5. Hein, A. & Jeannerod, M. Spatially Oriented Behavior, 1983

6. Barlow, H. and Mollen, J. [eds], The Senses, 1982

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7. Hubel, D. & Wiesel, T. Brain and Visual Perception. 2005, Oxford
8. Cohen, B., Tomko, D. and Guedry, F. [eds.], Symposium on Sensing and Controlling Motion: Vestibular and Sensorimotor Function, Annals of the New York Academy of Sciences. **656**, 1992.
9. Howard, I. & Rogers, B. Seeing in Depth, Vol 1, Vol. 2, 2002

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**THE FOLLOWING PAGES PROVIDE A PRELIMINARY LIST  
OF ASSIGNED READINGS FOR DISCUSSION DURING THE FIRST 8 MEETINGS**

**Readings For Class Meetings on Jan 24, Jan 31, and Feb. 7, 2013**

**TOPIC: Two Visual Systems**

**Books with Initial Readings:** (This list Will Grow)

1. Milner, A.D., and Goodale, M.A. The Visual Brain in Action. 1995
2. Gazzaniga, M. (ed). The Cognitive Neurosciences. 1995

**First Reading: Twos Visual Systems**

- \*1. Milner & Goodale (book 1). (ch. 1, pp. 1-24)

**Human Pathology**

- \*2. Goodale, et al., A neurological dissociation between perceiving objects and grasping them.  
*Nature*, 1991, 349, 154-156 (3 pages; folder)

**Normal Human: Two Systems (Dissociated Perception/Action)**

- \*3. Aglioti, S., Goodale, M., & DeSouza, J., *Curr. Biol.*, 1995, 5, 679-85.

**More Reading on DF**

4. Goodale, Jakobson, Milner, Perrett, Benson, and Hietanen, The nature and limits of orientation and pattern processing supporting visuomotor control in a visual form agnostic. *J. Cogn. Neurosci.*, 1994, 6, 46-56

**Two Visual Systems: Some Basic Orienting Questions**

1. What is the “two visual systems concept?”
2. What is the neuroanatomy that underlies the “two visual systems concept”
3. What is the behavioral evidence from animals that underlies the view that the two systems subserve “what” and “where”, respectively? (ONLY sec 1.3.3, pp. 20-24 in Milner & Goodale, chapter.)
4. What is the behavioral evidence from humans that underlies the view that two systems subserve “perception” and “action”, respectively? **Readings 1-4**

**TOPIC: Nature/Nurture**

**Basis in Neuroanatomy and “Heredity” for Spatial Localization and Orientation**

**Sperry and Jumping Frogs**

- \*1. Sperry, The Eye and the Brain (5 pages)

**Ingle, Behavioral Goals & Neuroanatomy**

- \*2. Ingle Two Visual Systems in the frog. *Science*, 1973, 14, 1053-55. (3pages)

**First Pass at Visual Development**

- \*3. Held, R. & Hein, A. Movement-produced stimulation in the development of visually guided behavior. *J. Comp. & Physiol. Psych.*, 1963, 56, 872-876.

- \*4. Blakemore, C. & Cooper, G. Development of the Brain depends on the visual environment. *Nature*, 1970, 228, 477-478.

**Nature/Nurture: Some Orienting Questions**

1. What are the two kinds of experimental changes that were made on the frog's visual system that led to changes in the frog's behavior (or to no changes)?
2. What are the significant things that Sperry's experiments tell us? What is the biggest surprise?
3. Why is Ingle's experiment important vis-a-vis behavioral goals?
4. Held and Hein's article was the first to make convincing case for the influence of experience on sensorimotor development. Given 50 more years of science since they did it, how would you improve on it?
5. Today we hear a lot about plasticity in the brain. This Blakemore & Cooper experiment was one of the very first to show aninfluence due to experience. Why was it surprising?

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**TOPIC: Retinal Receptive Fields: Probably by Feb. 14, 2013**

There are a few classics on the initial work on retinal receptive fields that are worth reading. These that constitute the early history here: two are by Hartline, and another by Kuffler. But the first two listed below are important openers. The third article presents a model that is essential to the thinking of much, if not most, subsequent work. But, at this stage in the course it will provide too many difficulties for full presentation. I'll try to find a way for us to work with it later in the semester.

The fourth article (Maturana, et al., 1959) shows the development of the Sperry work in an age when it was possible to do microelectrode recording from single neurons in the optic nerve and in the tectum in the frog following regeneration. The three functionally different kinds of neurons discovered by Hartline (maintained on, on/off, and off) are shown to reside in different tectal layers, and a fourth functionally different kind of neuron was found to terminate in a fourth tectal layer.

- \*1. **Hartline, H.K. (1938)**, The response of single optic nerve fibers of the vertebrate eye to illumination of the retina. *Amer. J. Physiol.*, **121**, 400-415.
- \*2. **Kuffler, S. W.** Neurons in the retina: organization, inhibition, and excitation problems. **Cold Spring Harbor Symposia in Quantitative Biology**, **17**, 281-292.
3. **Rodieck, R.W. (1965)**, Quantitative analysis of cat retinal ganglion cell response to visual stimuli. **Vision Research**, **5**, 583-601).
4. **Maturana J. Y. Lettvin, W. S. McCulloch, W. H. Pitts**, Evidence That Cut Optic Nerve. Fibers in a Frog Regenerate to Their Proper Places in the Tectum. **Science**, 1959. 1709-10.

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**TOPIC: Egocentric Space Perception I: Perception of the Vertical**

I've selected two classic articles that really opened the modern era for egocentric space perception. The first two are the 2nd and 4th of a series of four articles that were awarded "best article in the journal for that year", and received other awards as well. The number of references to them is huge. They continue to be referred to as centerpieces for numerous research programs. Surprisingly, as we'll see in the third article (a *Scientific American* article in 1959) the work also opened an entire field in "Personality" concerned with "Cognitive Styles" that was one of the most significant fields during the 50s to the 70s.

Witkin's work was well-supported by ONR, and there is an interesting historical background to that. We had invaded the above-ground and below-ground three-dimensional world with airplanes and submarines and some peculiar things happen to humans when we go there -- we are not adapted to either above or below ground. In the twenties, as story would have it (I've not checked on much of this directly), pilots flying solo or with a second person in a second cockpit, would emerge from a cloud bank upside down and not be aware of it, on some occasions, until it was too late when they hit the ground. So, a great deal of concern was obviously raised.

There was an interesting intellectual background to Witkin's work also. There was controversy about whether vision or our sensing the direction of gravity was more significant in our perception of spatial orientation. In 1937, Gibson and Mowrer published an article that took the strong position that sensing the direction of gravity was more significant. However, Witkin's work made it clear that they were wrong, and that vision was the dominant sense modality as the picture has remained ever since. This early position of Gibson on this matter is historically particularly interesting since he has become well-known for a phenomenological approach to perception, emphasizing vision to the point of referring to some aspect of our egocentric space perception as "Visual Kinesthesia".

1. **Asch, S.E. and Witkin, H.A. (1948).** Studies in space orientation II. Perception of the upright with displaced visual fields and the body tilted. **J. Exp. Psychol.**, **38**, 455-477.
2. **Witkin, H.A. and Asch, S.E. (1948).** Studies in space orientation IV. Further experiments on perception of the upright with displaced visual fields. **J. Exp. Psychol.**, **38**, 762-782.
3. **H. A. Witkin (Mar., 1959).** Perception of the upright. *Scientific American*, 49-56.

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**TOPIC: Egocentric Space Perception II: Perception Of Elevation**

These two articles will take us into work in my lab. We'll visit the lab and see some surprising perceptual phenomena. that were first described in the second reading. How these phenomena in normal human observers relate to phenomena measured with experimentally paralyzed observers (first reading) will be a subject for our discussion. That discussion will also tie together some of what we had dealt with in our earlier treatment relating eye movements and spatial localization. Numerous studies have employed "pointing to a visual target" as a means of studying spatial localization, often neglecting the possibility that manual behavior had properties of its own that did not allow for identifying results with those obtained by psychophysical measurement or verbal report. If time permits, I will raise questions about what you would expect when pointing or heightmatching to perceptually mislocalized targets, and tell you about some surprising differences and similarities with the psychophysical measurements of the elevation of perceptually mislocalized visual targets resulting from induction by visual pitch.

The first article describes the first systematic psychophysical measurements on people whose extraocular muscles had been weakened (efficiency of the neuromuscular junction reduced) by paralytic agents. The mislocalizations we discovered there led to the construction of the pitchroom and psychophysical measurements of the perception of elevation in the presence of visual pitch (second article).

**Primary Reading**

1. **Matin, L., Picoult, E., Stevens, J. K., Edwards, M. W. Jr., Young, D., & MacArthur, R. (1982).** Oculoparalytic illusion: visual-field dependent mislocalizations by humans partially paralyzed with curare. *Science*, **216**, 198-201.
2. **Matin, L., & Fox, C. R. (1989).** Visually perceived eye level and perceived elevation of objects: linearly additive influences from visual field pitch and from gravity. *Vision Research*, **29**, 315-324.

**TOPIC : Egocentric Space Perception III: MultiModal Neurons, Bimodal Neurons**

- \*1. Graziano & Gross, Mapping space with neurons. *Curr. Dir. in Psychol. Sci.*, 1994, 3, 164-167 (4 pages)
2. Graziano, M. and Gross, C. (book 2), Ch. 67, pp. 1021-1034.

**Basic questions: further into the dorsal system:**

1. Distinguish retinotopic, head-centered, arm-centered. (big-toe-centered?)
2. How would an arm-centered neural network with visual input from V1 be constructed (Black box style)?

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**COMPUTATIONAL MODELING: INTRODUCTION**

Mathematical modeling is an important approach to the study of space perception and sensorimotor behavior. I've chosen four very diverse examples of modeling from several very large literatures.

1. The Hartline/Ratliff Nobel Prize work on inhibitory interaction in the compound eye of the horseshoe crab in the late 1950s is probably the first really tight connection between neurophysiology and perception to have been made where the work at both ends (neuro, perception) was mature and substantial. The mathematics is of the simplest kind, but contains profound consequences. It remains as very important.
2. The Hecht work on quantum requirements really opened a new era in vision in terms of analysis of the stimulus.
3. The Marr binocular model was a true masterpiece of analysis and synthesis in computational modeling. The first chapter in Marr's book (also on the list) provides a basic statement of philosophy about how neuroscience needed to proceed and has actually proceeded when it is at its best.
4. The Georopolou model on motor control of the arm is a computational model dealing with the motor system whose *raison d'être* here will be stated *in situ* when we take it up.

**COMPUTATIONAL MODELING I:  
INHIBITORY INTERACTION IN LIMULUS, THE HORSESHOE CRAB'S EYE,  
MACH BANDS AND LATERAL INHIBITION**

The human retina contains 6 kinds of neurons: The rods and cones contain photopigment. When a molecule of photopigment absorbs a quantum of light, the first step in seeing occurs. The photoreceptors send signals to the bipolar cells, and the bipolar cells send signals to the ganglion cells whose axons converge and exit the back of the eye as the optic nerve. However, lateral interaction is an important feature of communication in the retina (mainly mediated by the horizontal and amacrine cells).

In 1932, when Hartline and Graham first recorded individual nerve impulses from single fibers in the horseshoe crab's eye, the simplicity of the firing pattern that was elicited suggested to them that there was no interaction among the different optic nerve fibers each of which came from a different ommatidium. However, subsequent work nearly 20 years later disclosed that there was indeed interaction between single optic nerve fibers. And in fact, all of the interaction was wholly inhibitory. The modeling of the interaction was linear and of the simplest kind (i.e.,  $Y = aX + b$  where Y and X are response frequencies of two different neurons, A is an inhibitory coefficient (negative value) for interaction, and b the threshold for influence of one neuron on the other. By bringing in distance across the eye, several very important consequences are derived: (1) disinhibition -- could be mistaken for excitatory interaction; (2) generation of Mach bands; (3) If the spatial distribution of intensities is given and a table of inhibitory coefficients for the eye stimulated, the responses of fibers in the area represented can be predicted; nothing more is needed for the steady state response.

**MAIN READINGS**

F. Ratliff, W. H. Miller, and H. K. Hartline, "Neural Interaction in the Eye and the Integration of Receptor Activity," *Ann. N. Y. Acad. Sci.* 74, 210-222 (1958).

Ratliff, F. (1972). Contour and contrast. *Scientific American*, 226, 90-101.

**ALSO SEE**

Mach Bands: *Quantitative Studies on Neural Networks in the Retina*. Floyd Ratliff. Holden-Day, San Francisco, 1965, Chapters 2-4.

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### **COMPUTATIONAL MODELING II:**

#### **THE PSYCHOMETRIC FUNCTION AND QUANTUM REQUIREMENTS FOR DETECTION OF LIGHT AT THE ABSOLUTE VISUAL THRESHOLD:**

Prior to 1942 the major theory that was employed to explain most of the major phenomena of visual function was called the “photochemical theory”. Selig Hecht was its main developer and proponent. The photochemical theory was developed mathematically, employing a simple idea along with some equations from photochemistry. The simple idea is simply expressed: Exposure of the retina to a steady bright adapting light led to absorption of the light by the photopigment  $t$  in the photoreceptors, and absorption led to breakdown of the photopigment in the retina as the first step in seeing. The more light that was absorbed from the adapting light, the more photopigment was broken down, and thus, the less photopigment remained available to absorb light from a subsequent test flash whose presence or absence was to be reported on by a subject. This reduction in available photopigment by more intense adapting illumination meant that in order for the test flash to be seen under more intense illumination, the test light itself needed to be more intense. Thus, the intensity threshold for a flash of light increased with increased level of the adapting light. This simple idea of photochemical availability was used quantitatively to explain the form of the light and dark adaptation growth functions, intensity discrimination, critical flicker frequency, visual acuity, and the equations that it led to did extremely well in fitting much of the available experimental data.

In 1942, Hecht carried things to another level and published an important article in which he made use of the known fact that successive flashes of light of fixed duration from a “constant” source contained different numbers of quanta, and thus the successive flashes were not really constant. In fact successive flashes varied statistically as does a poisson distribution. With the sources of light available at that time, this poisson variability was an irreducible phenomenon.

Of particular interest here is the fact that when a subject is required to report the presence or absence of a light flash under “constant conditions”, on some trials the subject will report seeing and on other trials the subject will report that the flash is not seen. With increase in the light intensity, the frequency of reports of seeing increases systematically. This uncertainty at a given intensity level, and the systematic variation in frequency of seeing with intensity goes by the name of the “psychometric function”. The intensity range that produces between 0% seeing and 100% seeing is known as the uncertainty range, and prior to Hecht’s work, the uncertainty itself was attributed to subjective variables, such as moment to moment fluctuations in attention, eye movements, and motivation,

However, Hecht recognized that the physical flash-to-flash fluctuation in numbers of quanta presented to the subject’s eye could play a role in generating the uncertainty of the subject’s report of seeing or not seeing. And this recognition led to the 1942 classic.

I emphasize that a brilliant idea is not sufficient. What makes the HECHT, SHLAER, AND PIRENNE article a classic is the way in which the authors followed through. I will say no more here, but let us all read it and discuss it. There is a lot to discuss.

#### **THE KEY READING:**

Hecht, S., Shlaer, S., and Pirenne, M.H., (1942). Energy, Quanta, And Vision. *J Gen Physiol.* 25(6): 819–840.

**(Also, An Excellent Secondary Reading: CORNSWEET’S BOOK, “Visual Perception”, 1970, CHAPTERS 2 AND 4**



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### **COMPUTATIONAL MODELING: III. BINOCULAR STEREOVISION**

There are three terms that are central to the introduction to stereovision: (1) horizontal binocular retinal disparity, (2) corresponding points in the two eyes, (3) and the Vieth-Muller horopter. Once we've got that bit under our belts, we can go on to see how Marr attacks the problem of how the visual system derives the perception of depth (=distance from the observer) from the fact that the two eyes have slightly different perspectives on the world. I have found that a couple of very elementary demos clears the way for treating

### **COMPUTATIONAL MODELING IV: NEURAL CONTROL OF ARM MOVEMENT**

The neural control of arm movement is

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**COMPUTATIONAL MODELING: V. PERCEPTION OF ORIENTATION**

**(THE TILT ADAPTATION MODEL AS AN EXAMPLE OF OTHER MODALITIES)**