OSA and the Early Days of Vision Research

Patricia Daukantas

By the second decade of the twentieth century, scientists studying human vision had come a long way from the days of the ancient Greeks, who debated whether light rays shot themselves out of the eyeball or emanated from objects in the visual field [1]. Nevertheless, the whole area of vision, especially the retina's reaction to light, remained an important topic of research as The Optical Society (OSA) was organizing itself.

In the early days of the OSA, scientists had come to realize that vision sat at the intersection of three fields: physiology, for the anatomy of the eye; physics, for the action of stimuli on the eye; and psychology, governing how the conscious brain interprets the eye's sensations [2]. Reflecting the interdisciplinary nature of the subject, vision-related articles published in 1920 were distributed among 58 different journals from fields ranging from physics and engineering to zoology and pathology.

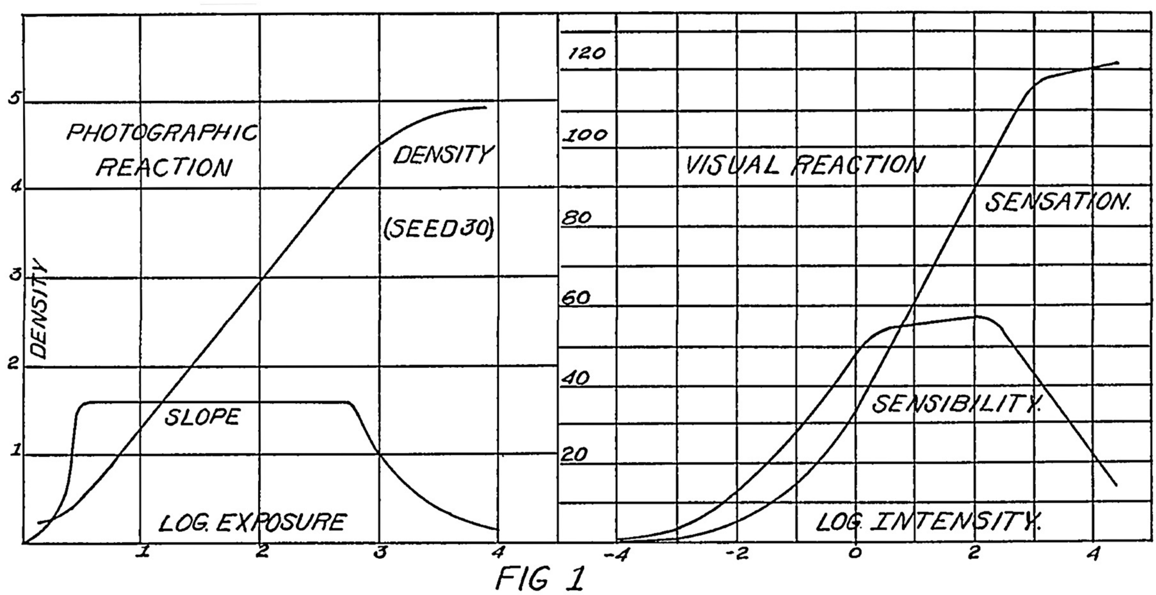
Between the two world wars, the scientists studying photochemistry—including two who would become OSA Honorary Members—progressed from the simple eyes of sea creatures to the complexities of the human visual system. Researchers learned that the retina contains vitamin A, leading to generations of parents telling their children, "Eat your carrots—they're good for your eyesight!" The new understanding of the eye paved the way for advances in vision correction and optical instruments.

Visual Reception and Photochemical Theory

In the very first issue of the *Journal of The Optical Society of America* (JOSA), two OSA presidents addressed some of the fundamental questions associated with human vision. Leonard Thompson Troland (1889–1932) published his theory of how the eye responds to light [3]. Perley G. Nutting (1873–1949) explored the status of a general photochemical theory that would apply to both the eye and photography and noted the similarities in the characteristic curves of photographic film and the eye's response to light [4] (see Fig. 1).

Nutting, who had tried to start an optical society several years before OSA's founding, served as the new organization's president through 1917. In his later years his focus shifted to geophysics. Troland (Fig. 2), who served as OSA president in 1922 and 1923, died in the prime of life when he fell off a cliff on Mount Wilson in California. Though he was never elected to the U.S. National Academy of Sciences, the academy gives an annual award in his name to young researchers who study the relationship between consciousness and the physical world. In photometry, the troland is a cgs unit for physical stimulation of the eye by light.

By 1919, OSA was becoming a leader in defining standards of visibility. That year, the Society's standards committee on visual sensitometry, led by Nutting, summarized [5] the extent of scientists' quantitative knowledge of the visibility of radiation, detection thresholds of intensity and contrast, color vision, rates of adaptation to changes in light, and "absolute sensibility," which takes into account the area of the retina exposed to light. For example, it was already well established that the human cone is most sensitive to light with a wavelength of 556 nm.



▲ **Fig. 1.** P. G. Nutting's comparison of the sensitivity of photographic film (left) and human vision (right) to light [4]. For film, optical density is plotted against the logarithm of exposure; for vision, reaction is plotted against the logarithm of light intensity. The lower curve on the vision graph, "photometric sensibility," was determined experimentally, according to Nutting, whereas the upper curve, "sensation," was determined "by integration."

Photochemistry: Hecht, Hartline, and Wald

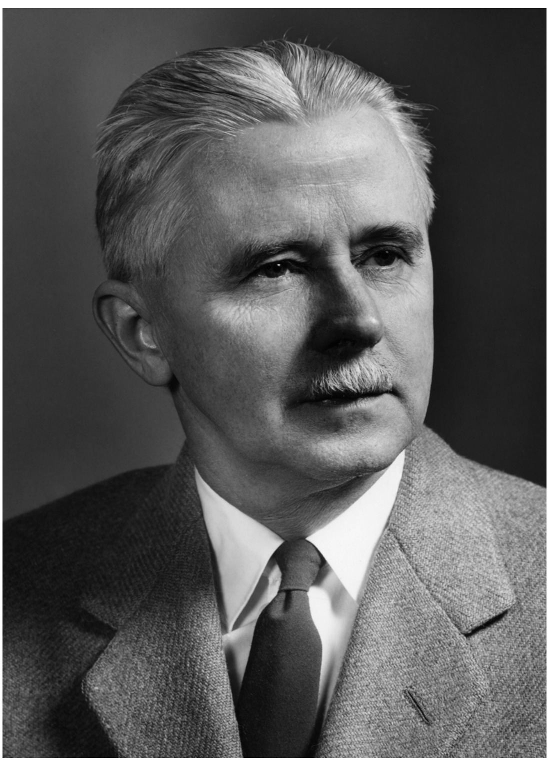
During the 1920s and 1930s, three scientists whose talents bridged the fields of physics, chemistry, and biology made invaluable contributions to our understanding of the molecules that react in the presence or absence of light.

Born in an Austrian town now part of Poland, but raised in the United States, Selig Hecht (1892–1947) (Fig. 3) explored the photochemistry of vision by studying animals whose visual systems are much simpler than those of humans: the worm *Ciona* and the clam *Mya*. Those organisms' reactions to light were slow enough that they could be measured without sophisticated apparatus [6].

Hecht began his studies of the photoreceptor process immediately after receiving his Ph.D., when he spent a summer at the facility now known as the Scripps Institution of Oceanography. There he investigated the sensitivity of *Ciona* to light. As he moved among several institutions in the United States and England, he studied the rate at which visual purple (now known as rhodopsin) decomposes upon exposure to light [7], the bleaching of rhodopsin in solution [6], and (with Robert E. Williams) the spectral sensitivity of human rod vision [8]. Hecht ended up at Columbia University, where, with his frequent collaborator Simon Shlaer, he built an instrument for

▲ **Fig. 2.** Leonard Thompson Troland, OSA president from 1922 to 1924. (AIP Emilio Segre Visual Archives.)

▲ **Fig. 3.** Selig Hecht. (AIP Emilio Segre Visual Archives, Physics Today Collection.)



▲ **Fig. 4.** Haldan Keffer Hartline. (Eugene N. Kone, Rockefeller Institute, courtesy AIP Emilio Segre Visual Archives, Physics Today Collection.)

measuring the dark adaptation of the human eye, leading to one of the classic experiments in eye sensitivity, still taught today [9].

Hecht considered himself a physiologist, but he served a term as an OSA director at large and another term on JOSA's editorial board [6]. In 1941, OSA awarded him the Frederic Ives Medal for overall distinction in optics.

Trained as a physician, Haldan Keffer Hartline (1903–1983) (Fig. 4) never practiced medicine. Indeed, after receiving his M.D. from Johns Hopkins, he spent a year Europe studying mathematics and physics under Arnold Sommerfeld and Werner Heisenberg. He was disappointed that he lacked the background to keep up with the pioneering physicists, but his quantitative bent served him well in his research career.

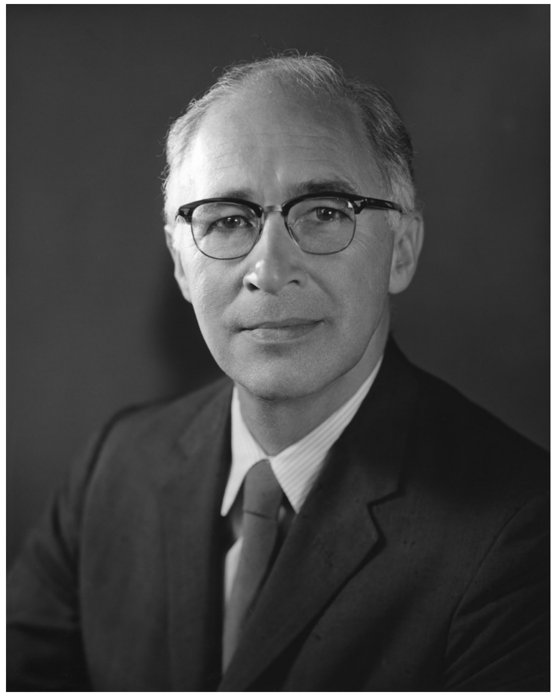
Hartline spent the 1930s as a medical physicist at the University of Pennsylvania, where he investigated the visual systems of the horseshoe crab (*Limulus polyphemus*). In 1932, he and colleague Clarence H. Graham made the first recording of the electrical activity of a single fiber taken from the optic nerve of a horseshoe crab. (Five years earlier, another team had studied the electrical pulses of the trunk of an eel's optic nerve, but could not separate the fibers.) Their work revealed that the intensity of the light falling on the photoreceptor is reflected in the rate of discharge of the nerve's electrical pulses [10,11].

Subsequently, Hartline progressed to studies of single optic-nerve cells from vertebrate retinas and measured their varying responses to light: some signaled during steady illumination, whereas others responded to the initiation or cessation of light [10,12]. By 1940, he came to realize that the ganglion cells in the retina received exciting and inhibiting stimuli through various pathways from different photoreceptors, and the optic nerve fiber, attached to the ganglion, serves as the final pipeline to transmit the signals to the brain [13]. Finally, Hartline discovered the effect now known as lateral inhibition in the *Limulus* compound eye sometime during the late 1930s, although he did not publish a report on it until 1949 [10].

George Wald (1906–1997) (Fig. 5), one of Hecht's graduate students at Columbia University, took his mentor's work further. As a student, Wald worked on the visual functioning of the *Drosophila* fruit fly and participated in Hecht's photoreceptor research. After he completed his doctorate in 1932, Wald identified the substance known as vitamin A—which was itself discovered only in 1931—in the retina.

The German scientist Franz Christian Boll had discovered rhodopsin, the primary light-sensitive pigment in the retina's rod cells, back in 1876, but nobody before Wald knew the exact chemical mechanism that made the substance react to light. During postdoctoral research in the laboratory of German biochemist Otto Warburg, Wald took the absorption spectrum of rhodopsin and found that the pigment contains carotenoids, which he found intriguing, because physicians had already connected nutritional night blindness with vitamin A deficiency [14].

Working with a Swiss researcher, Paul Karrer, Wald extracted vitamin A from the retinas of cattle, sheep, and pigs, and then moved to the Heidelberg lab of another Nobel laureate, Otto Meyerhof. With the clock ticking down on his time in Europe—after Adolf Hitler came to power, the U.S. National Research Council recalled the young Jewish postdoc home—Wald used a shipment of frogs, delivered while everyone else was vacationing, to gain a revolutionary insight. Since dark-adapted retinas contained a carotenoid slightly different from the vitamin A found in light-adapted retinas, he reasoned that the carotenoid, which he initially called retinene, was bound to the protein in rhodopsin and was released upon exposure to light, then gradually recombined to the rhodopsin protein to reverse the process [14]. (Later scientists changed retinene's name to retinal.)



▲ **Fig. 5.** George Wald. (Photo by Bachrach.)

Wald moved to Harvard University in 1934 and continued studying the chemical reactions within the retina both at Harvard and the Marine Biological Laboratory at Woods Hole, Massachusetts. He began investigating pigment molecules in the retina's cone cells, but World War II duties interrupted that line of work, so the important research he and his co-workers conducted on the red-sensitive pigment of the cones was not completed until the mid-1950s.

Hartline and Wald, along with Finnish–Swedish scientist Ragnar Granit (1900–1991), shared the 1967 Nobel Prize in Physiology or Medicine for their studies of vision systems. Hartline's 1940 JOSA paper was cited as one of the works for which he won the Nobel [15]. Hartline and Wald also were named OSA Honorary Members, the former in 1980, the latter in 1992.

Lasting Consequences

Many of the discoveries about the eye as a visual system did not bear practical fruit until after the interwar (1916–1940) period. The studies of sensitivity performance and contrast thresholds of the human eye formed the basis of everything from television and computer displays to the design of highway signs, which must be read in mere milliseconds for safety's sake [16,17]. That early twentieth century work continues to enhance many aspects of our twenty-first century life.

References

1. J. P. C. Southall, "Early pioneers in physiological optics," J. Opt. Sci. Am. **6**, 827–842 (1922).
2. L. T. Troland, *The Present Status of Visual Science*, Bulletin of the National Research Council of the National Academy of Sciences (U.S.A.) (1922), Vol. **5**, No. 27, pp. 1–2.

3. L. T. Troland, “The nature of the visual receptor process,” J. Opt. Sci. Am. **1**, 3–14 (1917).
4. P. G. Nutting, “A photochemical theory of vision and photographic action,” J. Opt. Sci. Am. **1**(1), 31–36 (1917).
5. P. G. Nutting, “1919 report of standards committee on visual sensitometry,” J. Opt. Sci. Am. **4**(2), 55–79 (1919).
6. G. Wald, “Selig Hecht, 1892–1947: a biographical memoir,” in *Biographical Memoirs* (The National Academy Press, 1991), Vol. **60**, pp. 80–101.
7. S. Hecht, “Photochemistry of visual purple: I. The kinetics of the decomposition of visual purple by light,” J. Gen. Physiol. **3**(1), 1–13 (1920).
8. S. Hecht and R. E. Williams, “The visibility of monochromatic radiation and the absorption spectrum of visual purple,” J. Gen. Physiol. **5**(1), 1–33 (1922).
9. S. Hecht and S. Shlaer, “An adaptometer for measuring human dark adaptation,” J. Opt. Sci. Am. **28**, 269 (1938).
10. F. Ratliff, “Haldan Keffer Hartline, 1903–1983: a biographical memoir” in *Biographical Memoirs* (The National Academy Press, 1990), Vol. **59**, pp. 196–213.
11. H. K. Hartline and C. H. Graham, “Nerve impulses from single receptors in the eye, “J. Cell. Comp. Physiol. **1**, 277–295 (1932).
12. H. K. Hartline, “Intensity and duration in the excitation of single photoreceptor units,” J. Cell. Comp. Physiol. **5**, 229–247 (1934).
13. H. K. Hartline, “The nerve messages in the fibers of the visual pathway,” J. Opt. Sci. Am. **30**, 239–247 (1940).
14. J. E. Dowling, “George Wald, 1906–1997: a biographical memoir” in *Biographical Memoirs* (The National Academy Press, 2000), Vol. **78**, pp. 298–317.
15. J. N. Howard, “Milestone JOSA articles from 1917–1973,” Opt. Photon. News **18**(11), 20–21 (2007).
16. A. Rose, “The sensitivity performance of the human eye on an absolute scale,” J. Opt. Sci. Am. **38**, 196–208 (1948).
17. H. R. Blackwell, “Contrast thresholds of the human eye,” J. Opt. Sci. Am. **36**, 624–632 (1946).