

# Vision Scientists of the Last Two Centuries with Appendages to Antiquity

*Collected by Lothar Spillmann in 2024-25  
edited by Christopher W. Tyler*

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For precious friends hid in death's dateless night. (W. Shakespeare)

If you don't understand the history of your field, you don't understand your field.  
(Mitchell Glickstein)

The trouble with dead men is that they keep talking to you. But if you ask them a question, they no longer answer. (Giovanni B. Vicario)

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*Note, however, that the information in this collection has not been verified by independent peer review. It comes from various sources. Use it at your discretion.*

*Also, kindly report any omissions, inaccuracies, mistakes, and errors to me. Individual scientists may be subsumed under more than one heading. German nobility is listed under "von" (e.g., von Helmholtz). All capsules are liable to change. Your help in filling in the gaps would be much appreciated and would serve us all.*

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## Contents

Brightness and Contrast Perception	Page 3
Color Vision	Page 14
Motion / Flicker	Page 29
Depth Perception	Page 36
Gestalt Psychology / Shape Perception / Object Recognition	Page 39
Visual Illusions	Page 47
Visual Attention	Page 53
Eye Movements / Image Stabilization	Page 54
Visual Development	Page 58
Disarrangement and Rearrangement	Page 62
Neurophysiology and Neuroanatomy	Page 64
Neuropsychology	Page 82
Clinical, Perimetry, ERG	Page 88
Comparative Vision Studies	Page 97
Models	Page 102
Applied & Machine Vision	Page 105
Vision from Antiquity to the 19th Century	Page 108
Visual Science before 1600 (Jack Yellott)	Page 109
Visual Science from 1600 to 1960 (Jack Yellott)	Page 110
Literature	Page 116

## Brightness and Contrast Vision

### **Aguilar, Mariano – 1923-2019, Instituto de Óptica, Valencia**

Spanish physicist dedicated to the physics of vision. First psychophysical demonstration of rod saturation at photopic luminance levels with W. Stiles (1954). Organized ECVF 1985.

### **Arnulf, Albert – 1898-1984, Centre Nationale de la Recherche Scientifique**

French physicist, first to determine the point-spread function of the human eye with F. Flamant and O. Dupuy (1955).

### **Barlow, Horace Basil – 1921-2020, University of Cambridge**

Highly influential British neuroscientist, psychophysicist, and theorist. Proposed that the number of light quanta required to reach threshold is elevated by the presence of background noise, which he attributed to thermal noise. Published seminal psychophysical studies on spatial and temporal integration, the role of microsaccades, and the computational efficiency of neural processing.

See also under [Neurophysiology and Neuroanatomy](#)

### **Bartlett, Neil Riley – 1917-2008, University of Arizona**

Authored studies on visual discrimination and reaction time. Co-author of the important textbook *Vision and Visual Perception* edited by C. Graham (1965).

### **Bergmann, Carl Georg Lucas Christian – 1814-1865, Universität Göttingen**

German anatomist and physiologist, first to report distortions of high-spatial frequency gratings attributable to photoreceptor aliasing (1857). Translation into English: C. Bergmann (1814–1865) and the discovery of the anatomical site in the retina where vision is initiated, DOI: 10.1080/0964704X.2023.2286991

### **Blackwell, H. Richard – 1921-1995, Ohio State University**

Worked on military aspects of visual perception. Collected large amounts of data on visual acuity in the landscape of Northern Michigan. Changed to non-

military research, such as improving highway safety by researching the visual requirements of drivers and providing for proper road lighting. Fellow of the American Academy of Optometry, Recipient of the Adolph Lomb Medal.

**Blakemore, Colin Brian, Sir – 1944-2022, University of Oxford**

World-renowned British neuroscientist. Worked with F. Campbell as an undergraduate to develop the Fourier theory of vision by demonstrating the existence in humans of orientation- and spatial-frequency tuned mechanisms, in a paper that has been cited more than 2000 times. Blakemore also championed lateral inhibition as crucial for explaining the angle expansion illusion (Zöllner, Wundt, Hering). Demonstrated strong adaptation effects to orientation and spatial frequency in grating patterns. Blakemore was a Fellow of the Royal Society of London and won numerous awards, including its Michael Faraday prize for public communication.

See also under [Visual Development](#)

**Bloch, Adolphe-Moïse – 1842-1920, Asile de Vincennes (Paris region)**

French physician who developed Bloch's law (1885), which states that at threshold, the product of luminance and duration is constant up to a limiting value.

**Boll, Franz Christian – 1849-1879, Università la Sapienza di Roma**

German physiologist who discovered rhodopsin in the outer segments of the frog retina. The pigment looked red (not purple) and faded when illuminated by light. He therefore concluded that it initiates the visual process (1876).

**Bouman, Maarten Anne – 1919-2011, Universiteit Utrecht**

Dutch physicist, widely known for his pioneering research on the absolute and differential thresholds of perception. Specified the number of light quanta required to elicit a sensation and to perceive a difference in light intensity ( $\Delta I$ ) over space and time. Seminal paper by F. van Nes and M. Bouman (1967) on the visibility of temporal, spatial, and spatiotemporal sinusoidal variations, which provided an enduring foundation for subsequent studies of contrast sensitivity. Organized ECVF 1979 with Hans Vos. Book: *Limits in Perception Essays in Honour of Maarten A. Bouman*, edited by A. van Doorn, W. van de Grind, & J. Koenderink (1984).

**Campbell, Fergus William – 1924-1993, University of Cambridge**

Brilliant Scottish vision scientist, beloved for his hospitality and sarcastic jokes. Pioneered research into the optics of the human eye and human spatial vision. Most closely identified with the *Fourier theory of vision* and the existence of putative spatial frequency channels in the visual cortex. This approach fostered a revolution in thinking by applying linear-systems theory to the detectability of spatially and temporally modulated sinusoidal gratings. Fourier analysis was regarded as providing new insights into how the visual system processes the retinal image. Campbell's paper (with J. Robson, 1968) entitled *Application of Fourier analysis to the visibility of gratings* has been cited over 4,400 times. Fellow of the Royal Society of London and recipient of the Edgar D. Tillyer Award. Mentored a stream of brilliant PhD students and postdocs.

### **De Lange Dzn, Hendrik – 1901-1974, Philips Telecommunications Hilversum**

Dutch communication engineer who pioneered the systems analytical approach to vision by measuring the sensitivity of the human eye as a function of temporal frequency and intensity. Did experiments on sinusoidal flicker and applied systems analysis to his results (1958). Worked on flicker fusion. Thesis 1957, U. Delft.

### **De Vries, Hessel – 1916-1959, Universiteit Groningen**

Brilliant Dutch physicist who studied the quantum nature of vision and the effect of temperature on sensitivity. Proposed in 1943, the De Vries-Rose Law, which states that contrast sensitivity is proportional to the square root of background luminance. Introduced the field-additivity test and measured increment thresholds as a function of background luminance for various target diameters.

### **Enoch, Jay Martin – 1929-2025, University of California, Berkeley**

Leading researcher in the field of physiological optics. Studied retinal receptor optics using the Stiles-Crawford effect and linked anomalies of directional photoreceptor orientation and alignment to eye diseases. Suggested that photoreceptors are waveguides. Developed layer-by-layer perimetry using the Westheimer function in eye patients and investigated the effect of image blur on perimetric thresholds. Demonstrated that Vernier acuity (the degree of offset from a straight scale) is relatively unaffected by age and ocular media opacities, including dense cataracts. Long-term Dean of the UC Berkeley School of Optometry. Played a major role in the formation of the National Eye Institute of the NIH and the Association for Research in Vision and Ophthalmology. Co-founder of the Elite School of Optometry in India. Received the Charles F. Prentice Medal, the Francis I. Proctor Medal, and the

PISART Award. Published 8 books. Laudation by Gerald Westheimer 2008  
<https://doi.org/10.1098/rspb.2008.0712>

**Fechner, Gustav Theodor – 1801-1887, Universität Leipzig**

German physicist, philosopher, and founder of the field of psychophysics, which explores the quantitative relationship between stimulus and sensation. Distinguished inner from outer psychophysics, the former being concerned with the relationship between the stimulus and sensation, while the latter concerns the relationship between sensation and brain processes. Proposed three methods for measuring thresholds: The method of limits, of constant stimuli, and of adjustment. The Weber-Fechner Law states that brightness is proportional to the logarithm of stimulus intensity. Discovered, in 1838, subjective colors (Fechner Farben) by rapidly rotating a disk with a periodic black and white radial pattern on it. Member of the Prussian Academy of Sciences, of the German National Academy of Sciences Leopoldina, and of the Viennese Academy of Sciences. Books: *Elemente der Psychophysik* (2 vols., 1860), transl. *Elements of Psychophysics* (1966)

**Fiorentini, Adriana – 1926-2016, Laboratorio di Neurofisiologia del C.N.R., Pisa**

Much admired Grande Dame of Italian neuroscience. Was trained as a physicist. Studied grating contrast, contrast perception in night vision, and the effect of lateral inhibition on perception. Introduced subthreshold summation to measure the center-surround profile of perceptive fields in humans. The first to measure the development of contrast sensitivity in infants. Trained generations of optometrists. Organized ECVF 1983 in Il Ciocco. Books: Chapters on Mach Bands in the *Handbook of Sensory Physiology* (1972), and on The Perception of Brightness and Darkness – Relations to Neuronal Receptive Fields in *Visual Perception: The Neurophysiological Foundations* (1990). *Arte e Cervello* (2008) with L. Maffei.

See also under [Neurophysiology and Neuroanatomy](#)

**Flamant, Françoise – 1931-2015, Institute d'Optique, Paris**

French. First to measure the point-spread function of the human eye (1955) with A. Arnulf (1898-1984) and O. Dupuy.

**Gelb, Adhémar Maximilian Maurice – 1887-1936, Universität Halle**

German neuropsychologist who worked with C. Stumpf in Berlin, M. Wertheimer in Frankfurt/M, and K. Goldstein in Frankfurt/M. Close to Gestalt

thinking. The *Gelb Effect* refers to the change of brightness of a black card when illuminated by a spotlight on a black background. When the card is illuminated in isolation, it appears white. When a dark grey card is added next to it, and both cards are illuminated together, the formerly black card now appears in a light grey, and the dark grey card as white. When a medium grey card is added, it appears white, whereas the other two cards now appear light grey and medium grey, respectively, suggesting that brightness perception is relative, depending on the context. In 1933, Gelb lost his professorship under Nazi rule and emigrated to the Netherlands and Sweden. Book: *Psychological Analyses of Brain Pathological Cases* with K. Goldstein and W. Fuchs (1920).

### **Gorea, Andrei – 1953-2019, Université René Descartes, Paris**

Romanian psychologist working in France. Did research in visual perception, sensorimotor processes, and decision-making. Published papers on unifying visual space across the left and right hemifields, the perception of motion and time, awareness and decision, and the relation between perception and action. Reviewed Bloch's Law. Organized ECVF 1990 and 2003 and edited the resulting book: *Representations of Vision. Trends and Tacit Assumptions in Vision Research* (2009). Andrei Gorea died of cancer, on the 7th of January 2019, aged 66 years.

### **Graham, Clarence Henry – 1906-1971, Columbia University**

Founded a highly respected school of experimental psychology and electrophysiology. Participated in neurophysiological experiments by H. Hartline and R. Granit in *Limulus*, who dissected individual fibers of the optic nerve by hand to study neural interactions in the retina. Recorded the electroretinogram (ERG) in the rat, pigeon, and frog. Studied form, depth, and motion perception, and performed extensive studies of color discrimination in color normals and color-blind subjects. Among his 60 PhD students were M. Akita, J. Foley, B. Gillam, H. Leibowitz, L. Matin, C. Mueller, C. McCullough, J. Pokorny, V. Smith, and H. Sperling. Member of the US National Academy of Sciences, and recipient of the Presidential Certificate of Merit, the Howard Crosby Warren Medal, the Edgar D. Tillyer Award, and others. Edited an influential book on *Vision and Visual Perception* (1965). Obituary: Clarence Henry Graham 1906–1971, *A Biographical Memoir* by Lorrin A. Riggs <http://biographicalmemoirs.org/pdfs/graham-clarence.pdf>.

### **Gullstrand, Alvar – 1862-1930, Uppsala Universitet**

Swedish ophthalmologist. Worked on the optical properties of the human eye (dioptrics) to develop the Gullstrand Model Eye. His ophthalmoscope and slit lamp for the clinical study of the eye were used throughout the world. Formulated the equation for the refraction of the human eye. Member of three

Swedish Academies and the Prussian Academies of Science. Nobel Prize in Medicine/Physiology (1911).

**Hecht, Selig – 1892-1947, Columbia University**

Distinguished physiologist who studied visual sensitivity in relation to the time course of the photochemical reactions, initiated by light in the photoreceptors. Contributed importantly to the knowledge of dark adaptation, visual acuity, brightness discrimination, color vision, and the mechanism underlying the visual threshold. A famous landmark study with S. Shlaer, and M. Pirenne (1942) demonstrated that the absolute threshold of human vision is limited by quantal fluctuations (noise) whose effects can be determined psychophysically. Member of the US National Academy of Sciences. Obituary: *Selig Hecht 1892–1947, A Biographical Memoir* by George Wald <http://biographicalmemoirs.org/pdfs/hecht-selig.pdf>

**Kelly, Donald Horton – 1923-1997, Stanford Research Institute International**

Best known for his linear systems analysis of retinal processing (1961, 1966, 1971). Brilliant analyst of spatial, temporal, and chromatic responses of the human visual system, often obtained under stabilized image conditions. Analysis of temporal flicker sensitivity. Received the Edgar D. Tillyer Award.

**Kühne, Wilhelm Friedrich – 1837-1900, Universität Heidelberg**

German scientist trained in physiological chemistry. Followed up on H. Boll's discovery of the photopigment rhodopsin (*Sehpurpur*) in retinal rods. Observed that the pigment is bleached by light and regenerates in the dark in repeated cycles, thereby providing light sensation (1878). Showed that the rate of bleaching was dependent on the intensity as well as the wavelength of the light. No visual purple was found in the fovea. Described the retina as behaving like a photographic plate, which is continually renewed. Member of the Royal Society of London, the Swedish Society of Sciences, Corresponding Member of the Prussian Academy of Sciences, and Member of the American Academy of Sciences.

**Le Grand, Yves – 1908-1986, Muséum National d'Histoire Naturelle, Paris**

French physicist who specialized in optics, photometry of punctiform sources, colorimetry, and photobiology. Studied peripheral flicker thresholds, night myopia, protanopic and deuteranopic vision, the Stiles-Crawford effect, the effect of glare on visual acuity, of blur and lens fluorescence, spherical and chromatic aberrations, and vision with polarized light. Trained many French and foreign students. Was Vice President of the *International Commission on*

*Illumination* (CIE). Recipient of the Edgar D. Tillyer Award and Charles F. Prentice Award. Books: *Light, Colour and Vision* (1957); *Form and Space Vision* (1966); *Physiological Optics* (1980). His *Traité d'Optique Physiologique* (1946-56) has been said to have been as important in the 20th century as Helmholtz's Handbook was in the 19th century.

**Lythgoe, Richard James – 1896-1940, Medical Research Council, London**

Measured visual acuity and critical flicker frequency as a function of adaptation of the eye. Other important work dealt with the photochemistry of visual purple. Held public lectures on the physiology of vision with instructions and demonstrations.

**Manahilov, Velitchko – 1954-2014, Glasgow Caledonian University**

Bulgarian vision scientist. Made theoretical contributions that focus on the temporal dynamics of visual processing, particularly discovering and modeling triphasic temporal impulse responses in the visual system, analogous to spatial Mach bands. Explored visual impairments, suggesting increased neural noise and imbalances between excitation and inhibition in the cortex. A significant contribution is the development of the D Chart software for quantitative metamorphopsia assessment.

**Müller, Heinrich – 1820-1864, Universität Würzburg**

German anatomist. One of the discoverers (in 1851) of visual purple in the rod photopigment, and also of retinal neuroglia, known as *Müller cells*. Concluded from entoptic perception of the vascular structure on the inner wall of the eye (Purkinje tree) that vision is initiated in the photoreceptors located in the back of the retina (1854). Established microscopically that the photoreceptors were pointing away from the incoming light, i.e., towards the pigment epithelium (oriented backwards).

**Nachmias, Jacob – 1928-2019, University of Pennsylvania**

Though legally blind, Nachmias made fundamental contributions to our understanding of vision, most notably through the study of eye movements, signal detection theory, forced-choice psychophysical methods, and the psychophysical characterization of spatial-frequency-selective visual channels. Member of the US National Academy of Sciences, recipient of the Edgar D. Tillyer Award.

**Nagel, Willibald Arnold – 1870-1911, Universität Rostock**

German sensory physiologist, famous for bringing quantitative function tests to the eye clinic. Invented an adaptometer to measure the light sense, night blindness, and the time course of dark adaptation. Also invented the Nagel anomaloscope (1907) to characterize color vision deficiencies. See J. Rayleigh. Ed.: *Handbook of Physiology*, 5 vols. (1904-1909).

**Olzak, Lynn Adrienne – 1951-2016, Miami University**

Worked on constraints of Fourier models of human pattern recognition. Lynn Olzak passed away on October 13, 2016, after falling ill on a trip to Europe.

**Parinaud, Henri – 1844-1905, Hôpital de la Pitié-Salpêtrière, Paris**

Influential French neuro-ophthalmologist who worked on the physiology of vision, the visual receptors, the light sense, night blindness, and color vision. Suggested that changes in visual sensitivity were due to variation in the amount of rhodopsin.

**Piéron, Louis Charles Henri – 1881-1964, University de Paris, Sorbonne**

French sensory physiologist. Founded the Laboratoire de Psychologie de l'Université de Paris. Worked on temporal and spatial summation. Trained generations of French psychologists. Founded several professional journals.

**Piper, Hans Edmund – 1877-1915, Friedrich-Wilhelms-Universität Bonn**

German electrophysiologist. Established Piper's Law (1903), which states that the threshold for luminance is inversely proportional to the square root of the stimulus area,  $\sqrt{A} \times I = C$ . Book: *Elektrophysiologie menschlicher Muskeln* (Electrophysiology of Human Muscles (1912). Died aged 38 in WW I while serving as a staff surgeon.

**Pirenne, Maurice Henri Léonard – 1912-1978, University of Oxford**

Belgian biophysicist. Worked at Columbia University on the biophysics of vision. Well-known for measuring, with S. Hecht, and S. Shlaer (1942) the minimum number of photons that the human eye can detect at absolute threshold. This paper highlighted that the perceived variability of light stemmed from physical fluctuations in the small quantity of light quanta absorbed by the visual photopigment. Pirenne's subsequent research revolved around the visual threshold and its correlation with visual acuity. Wrote *Vision and the Eye* (1948), an influential overview of vision with an

emphasis on the ecological optics of perspective. Foreign Member of the Royal Belgian Academy of Sciences.

**Rayleigh, 3rd Baron, John William Strutt – 1842-1919, University of Cambridge**

British physicist with wide-ranging interests who made numerous discoveries in optics and other fields and defined the measurement criteria for many important physical variables. Developed the Rayleigh anomaloscope (1881) to determine color anomalies and color blindness. Defined the Rayleigh criterion for the optical resolution of two points. Member of numerous academies; Nobel Prize in Physics, 1904.

**Riccò, Annibale – 1844-1919, Università di Catania**

Italian. Determined Riccò's law (1877) that the product of threshold intensity and stimulus area equals a constant up to a limiting size, known as Riccò's area.

**Riggs, Lorrin Andrews – 1912-2008, Brown University**

Leading scholar in the field of visual psychophysics and electrophysiology. Worked with H. Hartline and C. Graham and adopted their emphasis for objective measurement and physiologically based explanations. Research topics included sensitivity to light, color discrimination, dark and light adaptation, stereoscopic vision, depth perception, eye movements, night blindness, pattern vision, color aftereffects, and eye saccades. Most of his work involved human observers, but occasionally he used rats, frogs, pigeons, and horseshoe crabs. A prolific writer who published numerous books and book chapters. Soft-spoken and mild-mannered, he mentored 37 successful doctoral students and a dozen postdoctoral associates, all of whom became internationally known, among them: F. Ratliff, R. Boynton, J. Armington, T. Cornsweet, U. Tulunay-Keesey, F. Volkman, C. Cavonius, W. Makous, D. Hood, B. Wooten, R. Beauchamp, H. Petry, and S. Stevenson; and postdocs, among them: O. Braddick, K. Brown, R. Day, L. Ganz, E. King-Smith, J. Krauskopf, A. Norcia, C. Sternheim, J. Thomas, and P. Whittle. Next to C. Graham's laboratory at Columbia, the Walter S. Hunter Laboratory at Brown University was the most highly sought-after address for vision research from the 50s to 70s. Recipient of many prestigious honors: Member of the US National Academy of Sciences, William James Fellow, Howard Crosby Warren Medal, Jonas Friedenwald Award, Edgar D. Tillyer Medal, Charles F. Prentice Medal, Frederick Ives Medal, and Craik Award from Cambridge U.

See also under [Eye Movements / Image Stabilization](#)

**Röhler, Rainer – 1927-2013, Universität München**

Worked on the visual transfer properties based on linear system theory. (1976). Book: *Sehen und Erkennen, Psychophysik des Gesichtssinnes* (1995).

**Rushton, William Albert Hugh – 1901-1980, University of Cambridge**

Outstanding British researcher of color vision. Formulated the Principle of Univariance: *The output of a receptor depends upon its quantum catch, but not upon what quanta are caught*. Performed the first study of rhodopsin regeneration in the living human retina by retinal densitometry (with F. Campbell, W. Hagins, and G. Brindley, 1955) and later, of cone pigments. Established that the log of the threshold rise was proportional to the pigment bleach. Identified two human cone pigments, named 'chlorolabe' for absorbing middle-wavelength light, and 'erythrolabe' for absorbing long-wavelength light (1955). Provided evidence that protanopia and deuteranopia are each due to the absence of one or the other of the two photosensitive pigments. Correlated increment thresholds during dark adaptation with the equivalent background derived from the Crawford transform. Was fond of pointing out that his initials spelled out WAHR, the German word for truth. Fellow of the Royal Society of London. Received the Proctor Award. Obituaries: M. Alpern (1983), F. Campbell (1983), D. MacLeod, see Rushton Memorial Lecture (1986), and H. Barlow: W. Rushton (1986).

**Schade, Otto H. – 1903 –1981, Radio Corporation of America**

German television pioneer. First measurement (in 1956) of human spatial modulation transfer function (MTF), defined as the ratio of the image contrast to the target contrast, as a function of the spatial frequency of the stimulus. Received numerous honors and awards.

**Schultze, Max Johann Sigismund – 1825–1874, Friedrich-Wilhelms-Universität Bonn**

German anatomist and histologist. Distinguished (in 1865) between two types of retinal photoreceptors, rods and cones and suggested that they have different functions for vision under bright and dim light. This distinction resulted in the *Duplicity Theory*, according to which foveal cones provide color vision and high visual acuity in day light, whereas rods in the periphery of the retina provide colorless vision at night. Book: *Zur Anatomie und Physiologie der Retina* (1866).

**Stevens, Stanley Smith – 1906-1973, Harvard University**

Experimented mainly in vision and hearing, he originated *Stevens' power law* of apparent stimulus intensity, which was found to apply widely with different scaling parameters across all sensory modalities. He also came up with the important idea of *levels of measurement* (i.e., the distinction between nominal, ordinal, interval, and ratio scales), and in 1951 edited the massive *Handbook of Experimental Psychology* (1951, 1988). Received many honors and fellowships, and at Harvard became the world's first Professor of Psychophysics.

**Swets, John A. – 1928-2016, Massachusetts Institute of Technology**

Applied (in 1954) the theory of signal detectability to human sensation, with W. Tanner. Introduced the term *Receiver Operating Characteristic* (ROC). Built the first computer-based laboratory for experiments in perception. See: *A decision-making theory of visual detection*. Psychol. Rev., 1954, 1961; *Signal detection and recognition by human observers*, 1964. Member of the US National Academy of Sciences.

**Tansley, Katherine – 1904-1980, University College London**

Demonstrated that the time course of rhodopsin regeneration in the albino rat and the human dark adaptation curve were similar, suggesting that the sensitivity in the dark was proportional to the amount of rhodopsin present (1931). Did research on night blindness. Book: *Vision in Vertebrates* (1965).

**Troland, Leonard Thompson – 1889-1932, Technicolor**

The Troland (Td) is a unit for retinal illuminance, the light impinging on the retina corrected for pupil size. Was the president of the Optical Society of America.

**Vos, Hans J. – unk-unk, Institute for Perception, TNO Soesterberg**

Dutch vision scientist. Performed psychophysical studies in color vision, light perception, and ocular media. Organized ECVP 1979, with Maarten Bouman.

**Weber, Ernst Heinrich – 1795-1878, Universität Leipzig**

Renowned German physiologist and anatomist. Weber's Law (also known as Weber-Fechner Law) states that the just noticeable difference in a stimulus is a constant fraction of the background luminance ( $\Delta I / I = C$ ) (1832). The law

was first discovered in the domain of weight-lifting. Weber suggested that a constant fraction is applied for all senses, but is different for each sense. See: S.S. Stevens.

### **Whittle, Paul – 1938-2009, University of Cambridge**

Measured threshold vs. contrast functions for increment and decrement stimuli as a function of background luminance and coined the influential contrast metric  $W = \Delta L / L_{min}$ . Discovered the “crispening effect” of relatively enhanced perceived contrast when a target luminance is close to its background luminance. Studied hue change in contrast colors as a function of surround chromaticity. Member of the *Trieste group of Experimental Phenomenology* with A. Gilchrist, L. Arend, W. Gerbino, and S. Bergström.

## Color Vision

### **Abney, William de Wiveleslie, Sir – 1843-1920, Chatham School of Military Engineering**

British pioneer of spectroscopy and color photography. Found the Abney effect, the change in hue of spectrum colors by dilution with white light (1909). Member of the Royal Society of London, President of the Royal Astronomical Society, the Royal Photographic Society, and the Physical Society of London.

### **Akita, Munehira – 1930-2006, Kyoto Institute of Technology**

Japanese professor of psychology and color science who traveled widely and was at home in the East and West. Trained at the University of Michigan (under M. Alpern) and subsequently at Columbia University (under C. Graham), where he obtained his Ph.D. Contributed greatly to the advancement of vision science and color vision in Japan. Educated generations of Japanese scientists and mentored many students and postdocs by encouraging them to study abroad. Best remembered for hosting the Meeting of the *Association Internationale de la Couleur* in 1997, which drew more than 500 attendees from 29 countries to Kyoto. A cosmopolitan and ambassador of vision science, making friends with people wherever he went.

### **Albers, Josef – 1888-1976, Yale University**

Highly influential lecturer and mentor, originally from Germany, in the field of art and color perception. Influenced by Goethe's *Die Farbenlehre* (1810), the Bauhaus, and Gestalt psychology. Defined color as a property of the observer. Albers taught his students how to make opaque colors look transparent, heavy colors turn light, colorless colors become colorful, warm colors look cool, and vice versa. He also demonstrated how to make equal colors look different, and different colors look alike. His credo was that in visual perception, a color is rarely seen as it is in isolation. By placing color samples next to each other, he studied emergent properties such as assimilation, simultaneous and successive contrast, consistent with Max Wertheimer's statement that the whole is different from the sum of its parts. Albers' studies demonstrate that our brain does not "care" about absolutes, such as the exact wavelength or luminance of a given light; what it cares about is the "relationships with others." Demonstrated an effect on vision by sound. Seminal book on the *Interaction of Color* (1963), translated into many languages. See also B. Conway, *Color Consilience: Color through the Lens of Art, Practice, History, Philosophy, and Neuroscience*, *Annals of the New York Academy of Sciences*, 1251 (2012): 77–94.

#### **Alpern, Mathew – 1920-1996, University of Michigan**

Physiologist known for his research on color vision and color blindness. Worked on the polymorphism of human color vision and the distribution of the spectral loci of unique hues in the population. Long-standing collaboration with W. Rushton. Member of the US National Academy of Sciences and recipient of the Jonas Friedenwald Award

#### **Autrum, Hansjochem – 1907-2003, Universität München**

Prominent German zoologist who studied color vision in insects. Discovered the ultra-violet receptor in bees, which acts as a nectar and pollen guide. Editor of the *Journal of Comparative Physiology* and co-editor of the *Handbook of Sensory Physiology*. Numerous Awards. Recipient of the order Pour le Mérite für Wissenschaften und Künste. Books:

- *Human Behavior as a Biological Problem* (1976)
- *Human Biology* (1983)
- *Foundations of Sensory Science* (1984)
- *From Natural Research to Natural Science* (1986)
- *Inventive Nature and Problems of Ecology* (1989)
- *Animal Orientation* (1996)

#### **Bartleson, Clifford James – 1929-1987, Rochester Institute of Technology**

Made important contributions to colorimetry and visual science.

**Bergström, Sten-Sture – 1926-2008, Umeå Universitet**

Swedish psychologist, contributed to color perception, color constancy, chromatic induction, and shape-from-shading. Member of the *Trieste group of Experimental Phenomenology* with A. Gilchrist, L. Arend, and W. Gerbino.

**Bongard, Mikhail Moiseevich – 1924–1971, Institute of Biophysics, Moscow**

Russian physicist. Reported (with M. Smirnov) that extra-foveal human vision was tetrachromatic when tested by the silent-substitution method. This method replaces a light of one wavelength by light of another and determines the energy of the second for which there is no change in the response. The result shows what energies are equivalent to each other at different wavelengths. Suggested an analogy between the tetrachromacy of the parafovea and the weak tetrachromacy of heterozygotes for anomalous color vision whose trichromatic matches are not stable with chromatic adaptation. Well-known in computer science for ‘Bongard Problems’, which were introduced as a challenge for AI programs. Book: *Pattern Recognition* (1970).

**Boynton, Robert Merrill – 1924-2006, University of California, San Diego**

Highly respected and influential vision scientist. Studied color vision, light adaptation, and temporal sensitivity, using methods from visual psychophysics, physiological optics, and electrophysiology. Introduced the minimally distinct border technique for adjusting equiluminance and the minimal fusion frequency for equal brightness. Founded the *Center for Visual Science* at the University of Rochester. Recipient of the Edgar D. Tillyer Award, the Frederic Ives Medal, and the Charles F. Prentice Medal. Member of the National Academy of Sciences. Influential book on *Human Color Vision* (1979), 2nd ed. with P. Kaiser (1996).

**Cavonius, Carl Richard – 1932-2003, Universität Dortmund**

American physicist of Finnish-Swedish descent and long-time resident of Germany. Conducted color studies in Bethesda, Munich, Cambridge, and Amsterdam, on the spatiotemporal properties of human cones, chromatic discrimination, and color space. Co-founder of the *European Conference of Visual Perception* (ECVP) in Marburg in 1978. Obituary Professor C.R. Cavonius (1932-2003) *Perception*, 2005, vol. 34, DOI:10.1068/p3402ob. The Cavonius Centre at Gonville & Caius, University of Cambridge, was built from a family donation. Richard Cavonius died of cancer on January 20, 2003, at the age of 70.

**Chevreul, Michel Eugène – 1786-1889, Gobelins Tapestry Works, Paris**

French chemist working on perceived color changes of textile dyes in gobelins. Demonstrated (in 1829) that a given hue changed in appearance when placed next to another hue (simultaneous contrast, color assimilation). His study led to color theories that provided the scientific basis for Impressionist and Neo-Impressionist painting. Member of the French Academy of Sciences, Foreign Member of the Royal Society of London, recipient of the Copley Medal, Foreign Member of the Royal Swedish Academy of Sciences, and Foreign Honorary Member of the American Academy of Arts and Sciences.

**Crawford, Brian Hewson – 1906-1991, National Physical Laboratory**

British physicist who made important contributions to the science of vision, colorimetry, lighting, and color rendering. The *Stiles-Crawford effect* states that light entering the eye near the edge of the pupil produces a weaker visual response than light entering the eye in the center. This effect has been interpreted to suggest that photoreceptors are waveguides that reduce the effect of optical aberration and diffraction due to their orientation and thereby improve visual acuity. The *Crawford transform* enables the indirect measurement of dark light (i.e., the equivalent background), which is responsible for the decrease of increment thresholds during dark adaptation.

**Dartnall, Herbert – 1936-1998, London Institute of Ophthalmology**

British eye researcher famous for doing microspectrophotometry on the retina. Best known for investigating (with J. Bowmaker and J. Mollon) the spectral sensitivities of individual cone photoreceptors. Did quantitative spectroscopy of visual pigments from coelacanths, pandas, and humans. Introduced the Dartnall nomogram showing that all visual pigments had similar spectral shapes when plotted on a frequency rather than a wavelength basis. The shapes of the absorption spectra are constant when expressed in terms of the logarithm of the frequency of the light. Measured pigment absorption in individual rods and cones from primate and human retina. Book: *The Visual Pigments* (1957). Ed. *Photochemistry of Vision. Handbook of Sensory Physiology* (1972). Founding Editor of *Vision Research*.

**Farnsworth, Dean – 1902-1959, Commander of the United States Navy**

Developed the *Farnsworth–Munsell 100 Hue Color Vision Test* for revealing color deficiencies and color blindness. Tests the ability to arrange small Munsell paper “cups” differing in hue but not in value and chroma according to perceived similarity. The targets cover all the hues described by

the Munsell color system. There are two variations of the test featuring 100 color hues and 15 color hues. The Farnsworth–Munsell 100 Hue Test is more sensitive than the Ishihara plates. Mandatory reading: R. Laskowski: *Procedures for Testing Color Vision* (1981).

### **Grassmann, Hermann Günther – 1809-1877, Stettin Gymnasium**

German polymath. Proposed (in 1853) four laws to encapsulate the results of additive and subtractive color mixtures. The laws are used to predict color matches to a good approximation under photopic and mesopic vision.

### **Hartridge, Hamilton – 1886-1976, Medical Research Council, London**

British eye physiologist. Used an achromatizing lens to study color appearance without chromatic aberration. Postulated a polychromatic theory of colour vision with seven kinds of cones. In 1946, he delivered the Royal Institution Christmas Lecture entitled *Colours and how we see them*. Fellow of the Royal Society.

### **Helson, Harry – 1898-1977, Kansas State University**

Best known for his adaptation-level theory describing the effect of past experience and spatial background on present perception. Book: *Adaptation-level theory: an experimental and systematic approach to behavior* (1964).

### **Hering, Karl Ewald Konstantin – 1834-1918, Universität Leipzig**

German physiologist, considered to be one of the founders of modern visual science. Proposed the opponent-process theory of color vision, thereby causing a life-long controversy with H. von Helmholtz. Instead of three colors, it postulates that there are two pairs of opponent colors (plus black and white), the perception of which is mediated by opponent processes in the nervous system. The theory is supported by the phenomena of simultaneous and successive color contrast. Meanwhile, it has been shown that neurons in the retina and the visual pathway are capable of opponent-type responses and that Hering's and Helmholtz's color theories can be reconciled with each other. Hering further proposed that brightness and color appearance of adjacent surfaces can be explained in terms of reciprocal interactions between neurons in the retina. In 1899, he studied the limits of visual acuity as exhibited by Vernier acuity, which is higher than predicted by the densest spacing of cone photoreceptors. He was also interested in eye movements and visual illusions. Books: *Die Lehre vom binokularen Sehen* (1868). *Zur Lehre vom Lichtsinne* (1878). *Ueber die Grenzen der Sehschärfe* (1899). Translation by L.M. Hurvich and D. Jameson.

**Hsia, Yun – unk-unk, Columbia University**

Studied, with C. Graham, a woman with normal color vision in one eye and dichromatic vision in the other. In her dichromatic eye, she saw only two hues: wavelengths shorter than 502 nm were seen as a blue that matched 470 nm as seen by the normal eye, while wavelengths longer than 502 nm were seen as yellow, matching a wavelength of 570 nm. The 502-nm wavelength could therefore be regarded as a neutral point, appearing white to the subject and separating the two basic receptor systems that were present in her dichromatic eye.

**Hubbard, Ruth – 1924-2016, Harvard University**

Made important contributions to the understanding of the photochemistry of vision in vertebrates and invertebrates. Found that visual excitation is initiated by a chemical rearrangement of the visual pigment rhodopsin, called cis-trans isomerization. Close collaborator of George Wald. First woman to hold a tenured professorship at Harvard's Biology Department.

**Hunt, Robert William Gainer – 1923-2018, University of Leeds**

Director of Kodak Research Laboratories. Published a classic book on *The Reproduction of Colour* (2004), revised (2011).

**Hurvich, Leo Maurice – 1910-2009, University of Pennsylvania**

Distinguished color researcher, first at Eastman Kodak, then New York University, before he settled at U. Penn. Conducted research into human color vision and, together with his wife D. Jameson, quantified the *opponent process theory* of color vision. Outspoken conference participant. Stood up at ARVO in 1970 and condemned the shooting of students at the Kent State University massacre on May 4. Member of the National Academy of Sciences and recipient of the Edgar D. Tillyer Award. Translation of E. Hering's *Outlines of a Theory of the Light Sense* (1964). Book on *Color Vision* (1981),

**Indow, Tarow – 1923-2007, University of California, Irvine**

Published the first systematic application of multidimensional scaling to color perception.

**Ingling, Carl Raymond – 1936-2010, Ohio State University**

Published outstanding work on the fundamental mechanisms of color vision. Developed a highly cited opponent vector model of color vision capable of describing many aspects of vision from threshold to suprathreshold appearance. Also made early and significant contributions to the understanding of how the responses of individual cone classes are related to both spatial vision and color vision.

**Ishihara, Shinobu – 1879-1963, Imperial University of Tokyo**

Japanese ophthalmologist who designed the *pseudoisochromatic color plates* named after him for the testing of color deficiencies and color blindness. In this, he was aided by a color-blind physician who helped him to test the plates on soldiers. The first charts were hand-painted in watercolor. Also developed a Japanese visual acuity chart that is still in use. Made significant contributions to the study of myopia.

**Izmailov, Chingis – 1944-2011, Lomonosov Moscow State University**

Russian psychophysicist and psychophysicist who developed (together with E. Sokolov) a four-dimensional sphere as a model for subjective color differences. Proposed that the Euclidean distance between two color points is the chord length rather than the arc length, implicating the principle of diminishing returns. Suprathreshold color differences are perceived as less than the integral of just noticeable differences between colors. Two “chromatic” axes correspond to the perceptual color-opponent channels (red-green, blue-yellow). The other two axes represent the achromatic “whiteness” and “darkness” channels, which he distinguished from brightness. Demonstrated that equally bright lights are not coplanar in an Euclidean space; the brightness code is not linear in such a space. The model allows one to quantitatively describe luminance contrast and the Bezold–Brücke effect, as well as individual differences; also, it provides a way of quantifying the type and degree of color vision abnormality from mild anomalous dichromatic variations. Studied the emergence of saturation, as a “composite” attribute, from more basic circular color spaces.

**Jameson, Dorothy – 1920-1998, University of Pennsylvania**

Contributed greatly to the field of color vision. Together with L. Hurvich, she provided quantitative data for Hering's *opponent process color theory* using the hue cancellation method (1955). Recipient of the Edgar D. Tillyer Award.

**Judd, Deane Brewster – 1900-1972. National Bureau of Standards, Washington, D.C.**

Distinguished physicist, known for making important contributions to the science of colorimetry and the standardization of color space. Defended the standard color constancy explanation of the Land effect of perceiving a large color gamut from images encoded with just white and red color channels. The AIC Judd Award is a prestigious award given every two years to recognize outstanding work in the field of color science. Books: *Contributions to Color Science*, ed. by D.L. MacAdam (1979); *Color in Business, Science and Industry* (1959), 2nd and 3rd eds. with G. Wyszecki (1963, 1975).

**Katz, David – 1884-1953, Stockholm Universitet**

Noted German psychologist who did research in perception, hearing, and touch. Studied the modes of color appearance and the phenomenology of illumination. Organized, in 1928, a conference in Rostock, which was attended by the Gestalt psychologists: F. Heider, K. Lewin, H. Werner, W. Köhler, A. Michotte, E. Rubin, and M. Wertheimer. Lost his professorship under Nazi rule (in 1933) and moved to London, later Stockholm, before he could resettle in Hamburg. Books: *The World of Colour* (1935), *Gestalt Psychologie* (1944).

**König, Arthur Peter – 1856 -1901, Universität Berlin**

Distinguished physicist and assistant of H. von Helmholtz. Published groundbreaking studies on the spectral sensitivities of trichromats, dichromats, and monochromats. Provided evidence that dichromacy is due to the absence of one type of cone in the eye. Demonstrated agreement between the absorption spectrum of rhodopsin and scotopic spectral sensitivity (1886, 1894). Papers on physiological optics. Ed. Second edition of Helmholtz's *Treatise on Physiological Optics* (1896).

**Krauskopf, John – 1928-2016, New York University**

Highly respected research psychologist and mentor who studied human color discrimination and color-defined motion. Throughout his career, Krauskopf held positions at Brown University, the Walter Reed Army Institute of Research, Bell Laboratories, Rutgers University, Cambridge University, the University of Rochester, and New York University. Best known for identifying the cardinal axes of a spherical color space to analyze the chromatic channels in the lateral geniculate nucleus and striate cortex of macaques. Recipient of the Edgar D. Tillyer Award.

See also under [Eye Movements / Image Stabilization](#)

**Kravkov, Sergei Vasilyevich – 1893-1951, Lomonosov Moscow State University**

A founder of Soviet physiological optics. His research embraces a wide spectrum of color vision aspects, such as color contrast, afterimages, the relationship between the central and peripheral retina, electrophysiology (ERG), and color vision abnormalities. His book: *The Eye and Its Function* (1932; English translation: 1961) was considered the most comprehensive review of the psychophysiology of vision at his time in Russia.

**Ladd-Franklin, Christine – 1847-1930, John-Hopkins University**

Psychologist, logician, and mathematician. Worked with G.E. Müller and H. von Helmholtz. Developed a theory of color vision on evolutionary grounds. Among the first women to become a Member of the Optical Society of America, together with D. Nickerson, G. Rand, and L. Sloan.

**Land, Edwin Herbert – 1909-1991, Polaroid Corporation, Cambridge, MA**

Ingenious American scientist and inventor, co-founder of the Polaroid Corporation. Invented inexpensive filters for polarizing light, introduced instant photography. Discovered a system for projecting a full spectrum of hues with only two colors of projecting light. Known for impressive demonstrations of color constancy in Mondrian-type patterns, which prevailed despite large changes of the illuminant (1959). Formulated *The Retinex Theory of Color Vision* (1977).

**Lanthony, Philippe – 1929-2004, Centre Hospitalier National d’Ophtalmologie, Paris**

Specialized in the physiology and pathology of color vision. Designed the *Lanthony Desaturated D15* and the *New Color Test* for acquired dyschromatopsia. Books: *Art and Ophthalmology* (2009), *A Natural History of Color Vision* (2012), and *History of Color Blindness* (2013).

**MacAdam, David Lewis – 1910-1998, Eastman Kodak, University of Rochester**

American physicist who made important contributions to color science and technology in the fields of colorimetry, color discrimination, color photography, television, and color order. Introduced the MacAdam ellipses of the color discrimination limit around points in equiluminant color space. Contributed to the *Handbook of Colorimetry* (1936). Long-time Editor-in-Chief

of the *Journal of the Optical Society of America* who read and revised every manuscript, even when he was on vacation.

**McCollough, Celeste (later Howard) – 1926-2023, Air Force Laboratory, Texas**

Best known for her discovery of the contingent aftereffect, known as the *McCollough effect*. Demonstrated that the color of the negative afterimage perceived after adaptation to the stripes of a colored grating is *contingent* on the orientation of the stripes of the adapting grating. For example, after alternately looking at a red horizontal grating and a green vertical grating for a few minutes, a black-and-white horizontal test grating will then look greenish, whereas a black-and-white vertical test grating will look pinkish. This phenomenon gave rise to the assumption of both double-duty neurons coding color and orientation and produced hundreds of research papers.

**Nickerson, Dorothy – 1900-1985, Rochester Institute of Technology**

Color scientist and technologist. Made important contributions to the fields of color and color quality control, colorimetry, color perception, standardization of light sources, and color tolerance specification. Received the Gold Medal of the Illuminating Engineering Society of North America, the Judd Award of the International Colour Association, and had the Nickerson Service Award of the International Colour Association named in her honor.

**Ostwald, Wilhelm – 1853-1932, Universität Leipzig**

Eminent German-Baltic chemist, philosopher, and sociologist, interested in the systematization of colors. Recipient of the Exner Medal, Member of the US National Academy of Sciences. Nobel Prize in Chemistry, 1909. Books: *The Color Primer* (1916), *The Color Atlas* (1918). Published a total of 45 books.

**Rand, Marie Gertrude – 1886-1970, Columbia University**

Highly accomplished researcher who did extensive work on color perception, including the mapping of the central and peripheral retina for light detection and color discrimination (Ferree-Rand perimetric map). Developed new instruments and lamps for ophthalmologists and studied (with C. Ferree) the effect of illumination on the perception of color. Designed, with L. Hardy and C. Rittler, the pseudoisochromatic HRR color plates to diagnose color deficiency and color blindness. Worked on vision standards for pilots and ship guards and made recommendations for a glare-free illumination of the Holland Tunnel. Numerous awards. First woman to receive the Edgar D. Tillyer Medal.

**Rautian, Gleb Nicolajewitsch – 1889-1963, All-Union Research Institute of Metrology, Leningrad**

Did research on colorimetry, testing 3000 observers in the USSR. Served as an expert on colorimetry for the *International Commission on Illumination*. As chairman of the permanent colorimetric commission at the VNIIM (All-Union Research Institute of Metrology), he played a key role in coordinating research and standardization of colorimetry. For his contributions to Soviet science and industry, he received multiple awards, including the Order of Lenin and the Order of Merit.

**Richter, Manfred – 1905-1990, Deutsches Farben-Zentrum, Berlin**

Invented a tristimulus colorimeter and worked on color standardization and color metrics. Published *Bibliographie der Farbenlehre* and the DIN-Farbenkarte of the CIE. Received the Judd Award of the International Color Association.

**Ronchi-Rositani, Lucia – 1928-2020, Giorgio Ronchi Foundation, Florence**

Italian physicist with a degree in physiological optics. Authored a series of monographs and reviews dedicated to vision research from her laboratory in the journal *Atti della Fondazione Giorgio Ronchi*. Mentored numerous collaborators. Organized the Wyszecki-Stiles Memorial Symposium on Color Vision Models (1987). Initiated a study group on the Language of Colour (2009).

**Schrödinger, Erwin – 1887-1961, Universität Wien**

Renowned German physicist. Published influential papers on color, which helped to reconcile the trichromatic theory of Helmholtz with the Opponent Color Theory of Hering. Also published a theory of binocular summation. Nobel Prize in Physics for Quantum Theory.

**Sloan, Louise Littig – 1898-1982, Johns Hopkins University**

Ophthalmologist and vision scientist. Worked on physiological optics and color vision. Made important contributions to visual acuity testing. The standard letter chart is named after her, "Sloan Letters". Directed the Wilmer Laboratory of Physiological Optics for 44 years and contributed to the creation of the First International Standard for Visual Field Testing. The second woman to receive the Edgar D. Tillyer Award.

**Smirnov, Mikhail Sergeevich – 1921-2008, Institute of Biophysics, Moscow**

Pioneered the measurement of ocular aberrations. Used a vernier task to measure the retinal misalignment of rays entering through different parts of the pupil, allowing third- and fourth-order aberrations to be estimated. Concluded that it would be possible to construct a contact lens that compensated for the aberrations. Bongard and Smirnov (1956) reported that extrafoveal vision is four-dimensional (tetrachromatic). This kindled renewed interest today in novel types of photoreceptors, owing to the possibility that melanopsin-containing ganglion cells contribute to the perception of peripheral stimuli.

**Sokolov, Evgeny Nicolaevich – 1920-2008, Lomonosov Moscow State University**

Elaborated a general model of sensory processes within his programmatic approach termed “Human being–Neuron–Model”. It united evidence from human psychophysics, animal electrophysiological studies, and mathematical modeling on color processing. This approach was implemented in his multidimensional spherical model of color vision developed together with C. Izmailov. Theoretical insights provided by the spherical model have attracted great attention from the international color vision community, especially the two-dimensionality of achromatic vision and the non-Euclidean relationship between threshold and suprathreshold measurements of color discrimination.

**Sperling, Harry George – 1924-2023, University of Texas, Houston**

Worked on the visual perception of color and the physiological basis of color vision in humans and monkeys. Obtained threshold spectral sensitivity data from rhesus monkeys and found strong similarities with data from humans. Investigated intense light effects in rhesus monkeys that involved experimental color-blinding. Pioneered chromatic mapping of retinal cones. Proposed that all color processing is implemented through opponent interactions in the retina.

**Stiles, Walter Stanley – 1901-1985, National Physical Laboratory, Teddington**

Hailed as one of the most distinguished visual scientists of the 20th century, he made significant contributions to the field of colorimetry and visual science. Favored thresholds and matches (Class A experiments) over descriptions of sensations (Class B). Proposed the concept of the equivalent background (1932), measured rod saturation (1954, with M. Aguilar), demonstrated (with R. M. Boynton and M. Ikeda) inhibitory interactions between test flashes of different wavelengths, and measured large-field color matches in over 50

observers, which became the CIE 10-deg standard. Discovered the directional selectivity of cone photoreceptors (1933, 1939, Stiles-Crawford Effect) and the color change when a monochromatic stimulus enters the pupil off-center (Stiles-Crawford Effect of the 2<sup>nd</sup> order, 1937). Identified the Pi-mechanisms of differential spectral sensitivity in human vision (1939). Recipient of the Edgar D. Tillyer Award. Wrote *Color Science* (1967, 1982), in collaboration with G. Wyszecki. A symposium dedicated to W.S. Stiles was held at the 1985 ECVF in Peniscola, Spain. Obituary by J. Mollon: *Perception* (1986).

### **Trościanko, Tom (Tomasz) Stanislaw – 1953-2011, University of Bristol**

Polish-British collaborator of R. Gregory. Interested in the perception, psychobiology, and ecology of vision. Used isoluminant stimuli to attribute color percepts to the motion-blind Area V4. Traveled to Uganda to study the spatial and spectral properties of apes and birds in the African rainforest where monkeys forage for food. Went to extraordinary effort to “rescue” a busload of Russian researchers stranded at Heathrow Airport and bring them to the ECVF 1988 in Bristol. He also arranged for the participants to enjoy a cruise on the MV Balmoral into the stormy waters of the Bristol Channel. Long-time Editor-in-Chief of *Perception*. Published the textbook: *Basic Vision: An Introduction to Visual Perception* (2006, revised 2011) jointly with R. Snowden and P. Thompson. Tom Trościanko died of heart failure on November 16, 2011, in Amsterdam, on his way to give lectures in Germany. The Tom Troscianko Memorial Award enables young adventurous vision scientists to attend ECVF.

### **Valberg, Arne – 1938-2022, Norwegian University of Science and Technology, Trondheim**

Norwegian physicist from Oslo who did major research in Switzerland, the United States, and Germany. A leading figure in color metrics, color psychophysics, the neurophysiology of color vision, and technical aspects of color science. Worked with goldfish, monkeys, and human observers. Measured color induction as a function of luminance, purity, and wavelength of the inducing stimulus. Worked (with R. Boynton) on minimally distinct borders. Studied the long-range shift (periphery) effect. Involved in *Aid for Children* suffering from low vision. Books: *From Pigments to Perception* (1991) with B. Lee; *Light Vision Color* (2005). Received the Judd Award of the International Color Association. Fellow of OSA. Member of the International Society for Low Vision Research and Rehabilitation.

### **von Brücke, Ernst Wilhelm – 1819-1892, Universität Berlin**

Noted German physiologist. Studied the reflective tapetum lucidum layer of the vertebrate retina and the action of the ciliary muscle. In 1866, Brücke and

W. von Bezold noticed that the color of a stimulus changes slightly as its luminance increases. The hue of stimuli of a constant spectral distribution shifts towards blue if its dominant wavelength is below 500 nm; and towards yellow if above 500 nm. As the intensity is decreased, the hue shifts towards red or green. This phenomenon is called the Bezold-Brücke hue shift.

"Invariant hues" such as unique red, yellow, blue, and green retain their perceived color despite changes in luminance. Aside from his work on color, Brücke's work in optics was instrumental towards Helmholtz's invention of the ophthalmoscope.

### **von Kries, Johannes – 1853-1928, Universität Freiburg**

Renowned sensory physiologist. Following up on Max Schultze, he formulated the Duplicity Theory of rod vision at scotopic light levels and cone vision at photopic light levels. Published on color blindness of the peripheral retina. Proposed a *Zone Theory* of color vision, which combined the three-color theory of H.v. Helmholtz with the opponent-color theory of E. Hering. The theory accounts for color constancy, in which each cone type adapts in proportion to its stimulation level (von Kries adaptation) despite large changes of the prevailing illumination. Member of the Prussian Academy of Sciences, the German National Academy of Sciences Leopoldina, and recipient of the order Pour le Mérite für Wissenschaften und Künste. Book: *Allgemeine Sinnesphysiologie* (1923).

### **Wald, George – 1906-1997, Harvard University**

A towering figure in visual physiology, a student of Selig Hecht, Wald unraveled the nature of the light-sensing molecules found in photoreceptor cells. Spent his *Wanderjahre* as a biochemist mostly in Europe (with Otto Warburg in Berlin, Paul Karrer in Zürich, Otto Meyerhof in Heidelberg), where he discovered (in 1933) the role of vitamin A in rhodopsin as a precursor to the chromophore in photoreceptors that absorbs the light. Studied the effect of vitamin A deficiency on night blindness. Isolated the photopigments of rods and cones, rhodopsin, and iodopsin. Determined the spectral sensitivity functions of the long (560 nm), middle (535 nm), and short (415 nm) wavelength-sensitive cones in normal and color-blind (498 nm) human subjects and measured the absorption spectrum of the human fovea and then of single cones, using microspectrophotometry. Terrific speaker, drawing droves of students to his lectures. Numerous honors, including the Proctor Award and the Nobel Prize in Medicine/Physiology in 1967. Forceful spokesperson against the Vietnam War, nuclear arms proliferation, and the military-industrial complex. Participated in a teach-in at the Massachusetts Institute of Technology and gave a celebrated speech called *A Generation in Search of a Future*.

**Walraven, Pieter L. – 1930-2013, Institute for Perception, TNO Soesterberg**

Contributed significantly to our understanding of how the three types of cones are combined to create three channels for color vision (2 for color and 1 for luminance). Also did seminal work on spatial frequency sensitivity. Published *A zone theory of colour vision* (1966); and *On the derivation of the foveal receptor primaries* (1966).

**Wehrhahn, Christian – 1940-2024, The Salk Institute**

Studied the spatial distribution of light in the eyes of *drosophila*. Showed that the resulting retinal cell activity contains much information on the structure of the environment and funnels it into cortical neuronal networks tuned to detect motion stimuli. Demonstrated the effects of genetic mutation on visual function. Studied the neural mechanisms underlying spatial and motion vision in monkeys and investigated visual processing of color in human and non-human primates. Worked on Vernier acuity in humans (with G. Westheimer).

**Willmer, Edward Neville – 1902-2001, University of Cambridge**

British histologist. Studied human foveal color vision and fish cellular physiology and evolution. Fellow of the Royal Society of London. Book: *Retinal Structure and Colour Vision: A Restatement and an Hypothesis* (1946) coauthored with S. Polyak.

**Wright, William David – 1906-1997, Imperial College, London**

British physicist who specialized in color vision. Made important contributions to colorimetry, visual science, and the development of color television. Wright is regarded as one of the fathers of colorimetry. Provided (with J. Guild) improved spectral sensitivity functions, which resulted in the recommendation of a standard observer by the International Commission on Illumination (CIE). Identified the rare condition of 'blue cone' monochromacy. Recipient of the Newton Medal, the Judd Award of the International Color Association, and the Godlove Award. Obituary: [www.colour.org.uk/w-d-wright-obituary](http://www.colour.org.uk/w-d-wright-obituary).

**Wuerger, Sophie – 1960-2024, University of Liverpool**

Studied neural color mechanisms of color appearance, such as the cortical origin of unique hues and of color constancy across the life span. Here, she proposed that invariant color perception despite yellowing of the ocular lens is due to a compensatory mechanism in the visual brain. She also contributed to cross-sensory perception, e.g., the effect of smell on color perception and of sound on motion perception. In her later work, she dedicated herself to

advanced color display technologies as related to skin imaging. Co-organized ECVF 2015. Translated, with R. Shapley and N. Rubin, H. Wallach's 1935 article: "*On the visually perceived direction of motion*" (1996). Sophie Wuergler passed away on the 3<sup>rd</sup> of January 2024 with cancer.

**Wyszecki, Günter – 1925-1985, National Research Council, Ottawa**

German-Canadian physicist. Made important contributions to the fields of colorimetry, color discrimination, color order, and color vision. Published with D.B. Judd, *Color in Business, Science and Industry*, 2nd and 3rd eds. (1963, 1975); and with W.S. Stiles, the authoritative manual: *Color Science: Concepts and Methods, Quantitative Data and Formulae* (1982).

**Yustova, Elizaveta Nicolaevna – 1910-2008, D.I. Mendeleev Institute of Metrology, Leningrad / St. Petersburg**

Introduced colorimetry based on spectral measurements of pigment colors. Developed a unique system of colors for hue, brightness, and saturation. Her *Atlas of Colors*, with 1,000 color samples, helped to standardize color measurements in the Soviet Union. Beyond this, Yustova conducted research on the physiology and spectral sensitivity of photoreceptors. She also designed original pseudoisochromatic plates for color vision diagnostics.

## Motion / Flicker

**Addams, Robert – 1789-1875**

Rediscovered the motion aftereffect after looking at the Waterfall of Foyers in 1834. The effect was probably first described by Aristotle in his treatise on dreams, and then again by J. Purkinje in 1825 after having looked at a cavalry parade. Wade, N.J.: *Pursuing paradoxes posed by the Waterfall Illusion*. *Perception*, 47, 689-693 (2018).

**Bartley, Samuel Howard – 1901-1988, Memphis State University**

Leading expert on human vision and noted author and researcher, working on a wide range of multisensory perceptual phenomena. Quantified the brightness enhancement or Brücke-Bartley-effect, a visual nonlinearity in which a flickering light appears brighter at an intermediate frequency than the

same light when fused, i.e., a steady light with the same average luminance. Textbook on *Principles on Perception* (1969).

**Benussi, Vittorio – 1878-1927, Università degli Studi di Trieste**

Freudian psychologist in the Graz School, regarded as the founder of Gestalt psychology in Italy. Conducted numerous studies on optical illusions, spatial, and motion perception. Benussi developed serious depression and committed suicide at the age of forty-nine.

**Braddick, Oliver John – 1944-2022, University of Oxford**

Directed research laboratories in Cambridge, London, and Oxford. “Ol” (as he was known in the vision community) and his wife Janette (“Jane”) Atkinson, were omnipresent at conferences and touched the scientific life of many. Braddick performed studies on the Ternus apparent motion effect or element vs. group motion, put forward a two-process theory of apparent motion: a low-level short-range process that depends on directionally selective neurons and responds to discontinuous stimulation, and a long-range higher-level process that interprets the input as a smoothly moving object.

See also under [Visual Development](#)

**De Bruyn, Bart – 1960-2014, University of Surrey**

Belgian. Worked on the brain mechanisms and psychophysics of motion perception and stereopsis. Did research on illusions, and later the development of drawing skills in children.

**Duncker, Karl – 1903-1940, New School for Social Research, New York**

German psychologist of great promise, trained by M. Wertheimer and W. Köhler, emigrated to the United States. Studied induced motion, an illusion in which a stationary stimulus appears to move due to the movement of its surroundings. An example is the moon that appears to race against the clouds. Although we know that the moon is stationary, the induced movement is compelling. Another example is the movement experienced in one’s train if the train on the neighboring track starts moving. Also published a book on *Productive Thinking* (1935). Duncker committed suicide at 37 years of age having suffered from professionally treated depression for some time.

**Eagle, Richard – 1969-1999, University of Oxford**

Demonstrated the factors that underlie the analysis of optic flow in extracting object depth, structure, size from perspective, stereo correspondence, motion direction, velocity, and acceleration, and their dependence on stimulus orientation, spatial frequency, and contrast. The results were explained with quantitative models showing the channels at work in each case and how these vary with the task. Was on the organizing committee for the ECVF 1998 in Oxford. Richard Eagle died of a heart attack just before his 30th birthday.

### **Exner, Sigmund – 1846-1926, Universität Wien**

Brilliant Austrian scientist who pioneered the study of perception from a physiological standpoint. Investigated color contrast and color adaptation. Examined linear motion in two orthogonal directions, presented behind a circular aperture. Reported that the motion seen was in a diagonal direction, with a motion aftereffect in the opposite diagonal. He also explored stroboscopic motion and found that two slightly separated light sparks, one appearing more than 50 ms after the other, appeared as a single light, moving from one location to the other. Based on this observation, Exner contended that motion was a fundamental sensation, thereby preceding M. Wertheimer. Member of the German National Academy of Sciences Leopoldina.

### **Hassenstein, Bernhard – 1922-2016, Universität Freiburg**

Ethologist, co-founder of biocybernetics. Studied (with W. Reichardt) motion perception of the beetle *chlorophanus*. The beetle was attached to a stem while holding a globe made from straw (*Spangenglobus*) with its feet. When a striped carousel was set in motion, the beetle “walked” on the globe to keep its position relative to the moving stripes constant. Contributions to human color vision. An advocate of the child. Book: *Verhaltensbiologie des Kindes* (2001). Had brilliant students who became successful in different walks of life. Member of the Academy of Science Heidelberg and German National Academy of Sciences Leopoldina.

### **Johansson, Gunnar – 1911-1998, Uppsala Universitet**

Highly original Swedish psychologist carried out pioneering experiments to demonstrate biological motion. Attached small lamps to the major body joints of subjects and filmed them while they were moving around, dancing, and climbing stairs in the dark. To perceive biological movement, only a few visible points on the body were needed. Demonstrated that a lamp on the rim of a rotating wheel describes half-circles, but in conjunction with a lamp on the hub appeared to rotate through a full circle. This is an emergent property. Book: Symposium in Honor of Gunnar Johansson: *Perceiving Events and Objects*

by G. Jansson, S.-S. Bergström and W. Epstein (1994). Film by James B. Maas (1991)

**Kolers, Paul – 1926-1986, University of Toronto**

Studied with M. von Grünau the colored phi phenomenon. The object changed its color midway along the apparent motion path say from blue to red before the second stimulus was presented. This is analogous to the perception of the direction of apparent motion, which is also seen before the second stimulus is exposed. Book: *Aspects of Motion Perception* (1972).

**Levinson, John Zebulon – 1924-1992, University of Maryland**

Early investigator of the application of Fourier analysis to flicker sensitivity. *Perception* (1972).

**Lee, David N. – 1939-2025, University of Edinburgh**

Scottish professor of perception/action who studied the programming, monitoring, and performing of purposeful movements. Known for his pioneering work on time-to-contact (cited over 3,000 times) and for his video on visual and vestibular contributions to balance.  
<https://www.bing.com/videos/riverview/relatedvideo?q=video+on+visual+and+vestibular+contributions+to+balance&&mid=0A1928A200FDC389FBED0A1928A200FDC389FBED&FORM=VAMGZC>

**Michotte, Albert Edouard Baron van den Berck – 1881-1965, Katholieke Universiteit Leuven (Université Catholique de Louvain)**

Highly imaginative Belgian psychologist who studied apparent causality in perception, using a disk with a pair of concentric / excentric tracks rotating behind a small cardboard window. Demonstrated that causality can be perceived when two visual events are shown in the appropriate temporal and spatial relationship. From observing the spatio-temporal interaction of the tracks, he described five kinds of apparent causality: launching, push or shoving, pick-up or entrainment, repulsion, and overtaking.

**Musatti, Cesare – 1897-1989, Università degli Studi di Milano Statale**

Important representative of the *Italian School of Experimental Psychology*. Introduced the stereokinetic effect of a figure of eccentric rings spun slowly around its center to elicit the perception of vivid rotation of a 3D cone. Thus, motion provides vivid depth structure of the figure. This demonstration

triggered the interest of the artist M. Duchamps who created depth from motion in his *rotoreliefs*.

### **Ogasawara, Jiei – 1909-1995, University of Tokyo**

Tested Korte's third law of apparent movement, which specifies that an increase in the spatial separation between two successive events must be accompanied by an increase in the length of the pause to produce optimal apparent movement. Ogasawara asked: Is the spatial separation underlying Korte's law the retinal separation or the apparent separation? The results favored the apparent rather than the retinal separation.

### **Plateau, Joseph Antoine Ferdinand – 1801-1883, Rijksuniversiteit Gent**

Belgian physicist and mathematician. Studied flicker perception, discovered stroboscopic movement, and invented motion pictures (with the "phenakistoscope", 1829). Adapted to a rotating spiral to elicit apparent shrinkage and expansion of a static stimulus pattern – the motion aftereffect. The Talbot-Plateau Law asserts that the perceived brightness of a light stimulus flickering above the critical fusion frequency (CFF) matches the brightness of a steady-state stimulus of equal flux. Plateau lost his eyesight in 1842 from gazing directly into the sun for 25 seconds. Foreign Member of the Royal Netherlands Academy of Arts and Sciences.

### **Reichardt, Werner – 1924-1992, Max-Planck-Institut, Tübingen**

Brilliant physicist and founder of the *Max-Planck-Institute for Biological Cybernetics* in Tübingen. Proposed (in 1957 with B. Hassenstein) an autocorrelation model of motion detection in the Limulus eye that consists of two mirror-symmetric subunits, one for each opponent motion direction. The subunits are stimulated by continuous motion, or two discrete flashes presented in nearby locations. In each subunit, the detector input signals (A, B) are multiplied by each other after one of them has been delayed by a time interval ( $*t$ ). The subunit outputs are then subtracted from each other to give the final output signal of the detector. Member of Akademie der Wissenschaften und der Literatur Mainz, American Academy of Arts and Sciences, German National Academy of Sciences Leopoldina, and US National Academy of Sciences. Recipient of the order Pour le Mérite für Wissenschaften und Künste. Werner Reichardt died of heart failure, aged 68, at a symposium organized in his honor.

### **Stumpf, Pleikart – 1888-1965, Munich**

Described the perceived direction of a moving line at right angles to its extent. Determined the influence of temporal, spatial, and luminance variables on the strength of perceived motion and its negative aftereffect. With equally bright achromatic–chromatic or chromatic–chromatic stimuli, the perception of motion ceased, whereas with dotted stimuli, motion was seen veridically. Stumpf also found that the spatial limit of motion perception,  $D_{max}$ , was greater than the separation of retinal receptors.

**Ternus, S. Josef – 1892–1959, Universität Berlin**

PhD Student of Max Wertheimer. Described ambiguous motion elicited by two pairs of equidistant dots that are alternately presented at the diagonal corners of an invisible square. When this stimulus pattern is viewed, the direction of motion between each pair of dots switches spontaneously from vertical to horizontal and back. The question arises: what determines the direction of bistable movement? There is considerable hysteresis when the square is elongated to a rectangle, defying the Gestalt factor of proximity

**von Grünau, Michael Werner – 1944-2011, Concordia University**

German-Canadian psychologist. Conducted research into the color phi phenomenon (with P. Kolars). Studied the fluttering heart phenomenon. Investigated higher-order motion aftereffects, visual flow fields, eye movements, visual search, and attention in the real world. At the ECVF 1988 in Bristol, he unveiled, with P. Cavanagh and S. Peters, a large, folded Canadian Dollar note, picturing the Queen of England. With a slight bending of the note, rigidity failure changed her facial expression to demonic. Michael von Grünau died on 22 December 2011, of cancer.

**von Holst, Erich Walter – 1908-1962, Max-Planck-Institut, Seewiesen**

Brilliant German biophysicist and neuroscientist. Founded the Max-Planck-Institute for Behavioral Physiology at Seewiesen. Developed the *reafference principle* to account for the stability of the outer world during visually guided eye movements. The model proposes that the brain retains a copy of the intended and executed eye movement (efference copy). This copy is matched against the resulting displacement of the retinal image and signaled back to the brain (re-afference). If the efference copy and the re-afferent signal cancel each other, the brain interprets the null signal as stability of the outer world. By comparison, a difference (ex-afference) is attributed to an object's movement in the outer world.

**Wallach, Hans – 1904-1998, Swarthmore College**

An important German-American Gestalt psychologist, originally from Berlin. Wallach's studies of achromatic surface color laid the groundwork for subsequent theories of lightness constancy. Discovered aperture motion, coherent motion, and motion transparency. Although Wallach himself avoided neurophysiological explanations for these perceptual phenomena, his observations became cornerstones for neurophysiological studies on perceived motion. Studied figural aftereffects (with W. Koehler). Member of the US National Academy of Sciences, Guggenheim Fellow, and recipient of the Howard Crosby Warren Medal. Papers translated from the German by S. Wuerger, R. Shapley, & N. Rubin (1996).

### **Weisstein, Naomi – 1939-2015, State University of New York**

Charismatic neuroscientist and cognitive psychologist. Reports have it that she was discriminated against when she became a feminist political activist and was harassed at Harvard, the University of Chicago, and State University New York. Came down with chronic fatigue syndrome and was bedridden for the remainder of her life. Did research in the areas of visual and cognitive neuroscience. One of the first to study phantom motion in orthogonally moving grating stimuli that were masked in the middle. Brilliant speaker at conferences. Would initiate a talk, shouting: "Hey, you spatial frequency freaks, would you mind if I take my shoes off?" Died on March 26, 2015, of cancer at the age of 76.

### **Wertheimer, Max – 1880-1943, New School for Social Research**

Charismatic founder of Gestalt psychology. Following up on Exner's earlier observations, he greatly expanded the study of apparent motion to a paradigm that started *Gestalt* psychology (1912). Distinguished between optimal motion (object or beta motion) and phi motion (pure motion). Established *phi* as a phenomenon *sui generis* or a *Gestalt*. Apparent motion started the movie industry and is best exemplified by the wagon wheel illusion, where the perceived direction of stroboscopic movement changes with changing speed, according to the Gestalt factor of proximity. Depending on the shortest available path between two successive frames, one perceives either clockwise rotation, standstill, or counterclockwise rotation. Left Germany on the morning after one of Hitler's hate speeches for Prague, and then New York.

See also under [Gestalt Psychology / Shape Perception / Object Perception](#)

## **[Depth Perception](#)**

**Brewster, David, Sir – 1781-1868, University of St Andrews and University of Edinburgh**

Scottish physicist, known as “the father of modern physical optics”, he authored over 300 papers, including the description of the kaleidoscope, the prism stereoscope, and the wallpaper phenomenon perceived in a repetitive pattern whose depth appears to shift to a plane near the convergence plane. Fellow of the Royal Society of London and recipient of the Copley Medal.

**Bradshaw, Markland Frederick – 1961-2004, University of Surrey**

Studied the cues by which we see the three-dimensional structure of objects and surfaces. Showed that information from stereoscopic disparity and the observer’s motion interact in ways that depend on the estimated viewing distance. In a widely cited paper in *Nature* (with Brian Rogers), he proved that vertical disparities play an important role in the perception of depth. Studied how cues from stereopsis and motion guide grasping movements of the hand towards objects, and how these abilities develop during childhood. Mark Bradshaw died of cancer at the age of 43.

**Braunstein, Myron – 1939-2024, University of California, Irvine**

His work included studies on depth, distance, and 3D-shape perception from motion, motion parallax, texture, binocular disparity, and perspective. His theory of depth perception is best highlighted by his *Psychological Review* paper in 1971 on the rotation of trapezoids (i.e., the trapezoid illusion) and his 1983 chapter entitled *Contrasts between human and machine vision: Should technology recapitulate phylogeny?* Book: *Depth Perception through Motion* (1976).

**Festinger, Leon – 1919-1989, New School for Social Research, New York**

Although best known as a social psychologist who created the foundational *theory of cognitive dissonance*, he later turned his efforts to vision science. Proposed an innovative efference theory of visual perception, in which eye movements form the organizational basis for contour perception, object shape, and distance.

**Fox, Robert – 1932-2018, Vanderbilt University**

Studied animal vision and human visual perception, both in infants and adults. Perhaps best known for his work on binocular rivalry and for establishing the visual acuity of the falcon.

### **Gibson, James Jerome – 1904-1979, Cornell University**

Eminent psychologist who left a lasting impact on the way that psychologists and philosophers conceptualize perception and action. Demonstrated that the perceived orientation of a test line or grating is shifted away by the presence of a surrounding line or grating with a different orientation → tilt illusion; and that after prolonged adaptation to an oriented line, a subsequently presented line appears to be tilted away from the adapting orientation → tilt aftereffect. Gibson rejected the behaviorists' assumption that learning involves the formation of associations between stimuli and responses but argued instead that the perceived environment is made up of meaningful arrays. Specifically, he maintained that the perception of space and motion is based on the increasing density of optical elements afforded by a receding surface and other gradients. This structural information specifies the distance of objects precisely. The corresponding cue is *ordinal stimulation*, enabling us to see depth structure *in a single step* without any intervening process, or *direct perception* (naïve realism). Gibson proposed that perceptions are veridical to the extent that they enable us to navigate in the environment (vision and action). Perception is not the processing of sensory input, but the *extraction of invariants* from the stimulus flux, which undergo lawful transformations with the movement of the observer. Although the eye moves relative to the head, and the head moves relative to the body, with the body moving relative to the ground, we nevertheless experience the visual world as stable. Gibson accounts for the stability of the world in a way similar to the reafference principle by von Holst & Mittelstaedt (1950). Gibson's ecological approach requires neither cognitive inferences (H. von Helmholtz, R. Gregory) nor the processing of information by figural or Gestalt grouping factors (M. Wertheimer, K. Koffka, W. Metzger). It also excludes the visual brain. President of the American Psychological Association, Member of the US National Academy of Sciences, Fellow at Oxford, Princeton, and Stanford. Books: *The Perception of the Visual World* (1950), *The Senses Considered as Perceptual Systems* (1966), and *The Ecological Approach to Visual Perception* (1979).

### **Gogel, Walter – 1918-2006, University of California, Santa Barbara**

Identified the underlying principles of the perception of space and the relationships between size, distance, and egocentric motion. Devised cue conflict situations resulting in illusions and elucidations of how we weigh perceptual cues. Developed a theory of the phenomenal geometry of visual perception.

**Julesz, Bela – 1928-2003, Bell Laboratories and Rutgers University**

Hungarian telecommunication engineer and visionary who famously pivoted to vision science with his invention of the random-dot stereogram (1960). A stereogram is a probe of binocular vision mechanisms that dissociates the random monocular information presented to each eye from the binocular correlations between the eyes, which carry the depth structure information. This innovation initiated the investigation of the purely binocular, or cyclopean, spatiotemporal processing characteristics of depth perception. Also developed a magnetic dipole model of the long-range interactions involved in resolving these depth structures from the ambiguous local information available in such multi-element stimuli. Went on to extend the power of random-dot texture probes to the study of perceptual processing of bilateral symmetry and the elements making up the discriminable features of textures. He called these features *textons* under the criterion that they were discriminable preattentively (i.e., without attentional scrutiny). Working together with I. Kovacs, he elucidated the role of medial-axis shape descriptors in determining the perceptual organization of outline shapes. Through these creative approaches, he took the study of mid-level vision to the next level of sophistication.

**Ogle, Kenneth Neil – 1902-1968, Dartmouth Eye Institute and Mayo Graduate School of Medicine of the University of Minnesota**

Worked on stereoscopic vision, binocular space perception, and physiological optics. Numerous research papers on the horopter, stereopsis, and aniseikonic effects on space perception. Received the Proctor Gold Medal and Tillyer Medal. Book: *Researches in Binocular Vision* (1964).

**Panum, Peter Ludvig – 1820-1885, University of Copenhagen**

Danish physiologist and pathologist. Measured the area on the retina within which stereoscopic fusion occurs. Introduced orthogonal gratings to study binocular rivalry. Book: *Monograph on Binocular Vision* (1858).

**Shipley, Thorne – 1927-2009, University of Miami**

Studied binocular vision, color vision, pattern recognition, and visual space perception, using electroretinography and evoked brain potentials. Produced data supporting H.M. Traquair's contention that all color isopters would be equivalent if hue, saturation, and intensity were equated. Investigated tetrachromacy in human females. Founding Editor-in-Chief and long-time editor of *Vision Research*.

**Wheatstone, Charles, Sir – 1802-1875, Kings College, London**

British inventor and physicist. Invented (in 1838) the mirror stereoscope that permitted the perception of depth from two stimuli slightly displaced by lateral disparity (stereograms). The instrument enabled the observer to localize whether a certain phenomenon arises before (in the retina) or after the fusion of the two ocular inputs (in the brain). Fellow of the Royal Society of London.

## Gestalt Psychology / Shape Perception / Object Recognition

**Attneave, Fred – 1919-1989, Stanford University**

Developed a guessing test where subjects had to say “black” or “white” to complete a partially given shape on a matrix of  $x$  times  $y$  cells. Attempted to account for some of the figural Gestalt factors, such as symmetry, closure, and smooth continuation, by Information Theory.

**Beck, Jacob – 1929-2003, University of Oregon**

Made pioneering studies on lightness perception, texture segregation, perceptual grouping, and figural organization. Demonstrated that T's and L's group together, whereas T's of different orientation do not. His studies of *linking* and *emergent features* in texture and contour perception inspired subsequent computational treatments and helped to foster the current revival of interest in Gestalt psychology.

**Biederman, Irving – 1939-2022, University of Southern California, Los Angeles**

Much beloved professor of psychology and computer sciences. Advanced the field of shape, object, scene, and face recognition. According to his recognition-by-components theory, we recognize objects by separating them into *geons* (the object's main component parts). Showed that geons are based on basic 3-dimensional shapes (solids such as cylinders, cones, etc.) that can be assembled in various arrangements to form a virtually unlimited number of objects.

**Ehrenstein, Walter – 1950-2009, Universität Dortmund**

German psychologist with wide-ranging interests and friends in many countries. Combined phenomenological observation with psychophysical measurement, neurophysiological interpretation, and clinical application. Showed that brief light flashes could be more easily discerned than equally long dark pauses, thereby suggesting an asymmetry between the neuronal subsystems for brightness and darkness. Used the Pulfrich effect for the psychophysical diagnosis of multiple sclerosis. Developed (jointly with Wist & Schrauf) a dynamic visual acuity test based on form-from-motion, which was applied to large populations of all ages. Worked on the Munker-White effect and the scintillating Hermann grid illusion (with B. Lingelbach). Studied motion estimation behind a tunnel. Published (with L. Spillmann & V. Sarris) on the neurophysiological correlates of Gestalt phenomena. Academic ties with the universities in Sofia, Bulgaria, Kyoto (KIT), Tokushima, and Sassari, Italy. Walter Ehrenstein died at age 59, of cancer.

### **Held, Richard Marx – 1922-2016, Massachusetts Institute of Technology**

A towering figure in the Gestalt tradition. Demonstrated figural deformation after adapting to curved or tilted geometrical patterns. For example, a pattern of rightward curved lines produced a percept of leftward curved lines when tested with a straight line. Similarly, a pattern of straight lines produced an elliptically deformed circle when tested with a real circle, while a square became a rectangle. Predates Blakemore's celebrated demonstration of adaptation to orientation and spatial frequency in gratings patterns. Reported in H.-L. Teuber's (1960) chapter on visual perception in the *Handbook of the American Psychological Society*.

See also under [Visual Development and Disarrangement and Rearrangement](#)

### **Hochberg, Julian – 1923-2022, Columbia University**

Leading experimentalist and theoretician in visual perception. Among his many contributions, he pioneered work on how we integrate the snapshot views of the world with individual visual fixations into fully-formed percepts of the world *in the mind's eye*. He led research and thinking on the Gestalt problem and how our percepts are structured to maximize both the likelihood of their being accurate and simple. Beyond his explorations of form and motion perception, he extended his research into the perception of pictures, film, and dance. Book: *Perception* (1965)

### **Gottschaltdt, Kurt – 1902-1991, Universität Göttingen**

Major representative of the second generation of German Gestalt psychologists. Studied the visibility of a figure (the part) that had previously

been exposed in isolation, when embedded in a complex figure (the whole) that favored the perception of good continuation. With no instruction to look for, the simple figure "jumped out" in only a few presentations. Even when searched for, it remained hidden in the majority of cases. Thus, the complex figure concealed the part, and past experience was of little consequence. The Gottschaldt Hidden Figures test became an important diagnostic for autism. The results on figural concealment were later exploited by the German, British, and US military in camouflage. Dissertation: *Über den Einfluss der Erfahrung auf die Wahrnehmung von Figuren* (1926).

### **Kardos, Lajos – 1899-1986, Eötvös Loránd University, Budapest**

Hungarian Gestalt psychologist who contributed major studies on shadows in object perception, mathematical models of perceptual constancy, neural Information, processing through cognitive maps, and perception and action. Journal chapter: *Ding und Schatten. Eine experimentelle Untersuchung über die Grundlagen des Farbensehens* (1934). The Lajos Kardos Prize of the Hungarian Psychological Society is named in his honor.

### **Kaufman, Lloyd – 1927-2024, New York University**

Made multiple contributions to vision science and neuroscience. Performed real world and simulated world experiments (with Irvin Rock) on the Moon illusion (1962), and ingenious experiments on binocular vision, binocular fusion, and single vision. Made (with S. Williamson) pioneering studies of neuromagnetism and contributed significantly to the development of clinical magnetoencephalography. Books:

- *Sight and Mind: An Introduction to Visual Perception* (1974),
- co-edited (with D. Brenner and S.J. Williamson)
- *Visually Evoked Magnetic Fields of the Human Brain* (1975),
- *Perception: The World Transformed* (1979),
- co-edited (with K. Boff and J. Thomas) the monumental *Handbook of Perception and Human Performance* (1986).

### **Köhler, Wolfgang – 1887-1967, Swarthmore College**

Eminent German theoretician who focused on the link between physics and psychology. Influenced by Max Planck and Carl Stumpf. Famous for his studies of insightful problem-solving by chimpanzees. With M. Wertheimer and K. Koffka, founder of the School of Gestalt psychology in Frankfurt and Berlin. Proposed that percepts tended to structural simplicity and balance or *Prägnanz*. Also proposed that visual patterns give rise to neural substrates (DC-currents) in the brain, which he attempted to record from human observers, using scalp electrodes over the occipital cortex (With R. Held: *The cortical correlate of pattern vision*. Science 110, 1949). Of primary interest in

this endeavor were figural aftereffects of spatial displacement, observed after prolonged inspection of a particular figure when a second figure was presented thereafter. Köhler interpreted these results in support of the hypothesis of psychophysical isomorphism. President of the American Psychological Association in 1959, Member of the US National Academy of Sciences, recipient of the Warren Medal by the Society of Experimental Psychologists, and the Wundt Medal by the German Society for Psychology. Retired to Dartmouth College. Books:

- *Die physischen Gestalten in Ruhe und im stationären Zustand* (1920).
- *Gestalt Psychology* (1929).
- *The Place of Value in a World of Facts* (1938)
- *Dynamics in Psychology* (1940)
- *The Task of Gestalt Psychology* (1969)

### **Koffka, Kurt – 1886-1941, Smith College**

Founding Member of the first generation of Gestalt psychologists (with M. Wertheimer and W. Köhler), left Germany early. Described a striking simultaneous contrast effect on a uniformly grey ring when superimposed onto a bisected bright and dark background. When a black line is drawn to separate the ring along the black-and-white background border, the half that lies on the black background looks brighter, whereas the half that lies on the bright background looks darker. The same effect can be obtained by sliding the two halves of the ring out of register. When the halves are realigned, the ring looks uniformly grey again, testifying to the strength of figural coherence, inner homogeneity, and belongingness. Book: *Principles of Gestalt Psychology* (1935).

### **Kopfermann, Herta – 1902-1987, Universität Berlin**

Student of W. Metzger. Demonstrated that the tendency for a *good Gestalt* can overrule lateral disparity in *binocular* vision. Using glass slides stacked behind each other, she presented the components of a regular symmetrical figure in different depth planes and observed that they combined into a plane figure, despite the difference in disparity. Thus, the tendency for a good Gestalt won over binocular disparity. Hochberg and McAllister (1953), and Hochberg and Brooks (1962) replicated these experiments.

### **Kubovy, Michael – 1940-2025, University of Virginia**

Distinguished Israeli American psychologist, and leader in the rebirth of Gestalt Psychology. student of Daniel Kahneman and Amos Tversky. Recipient of numerous national and international awards, including a Guggenheim Fellowship, and the Bozzi Prize. Book: *Perceptual Organization* (with J.R. Pomeranz), 1981.

### **Leibowitz, Herschel Weldon – 1925-2011, Pennsylvania State University**

Blended basic and applied research in a wide range of studies, such as perception of size, distance, and motion, peripheral vision, and oculomotor functioning. He also studied problems of aviation, traffic safety, motion sickness, postural instability, and the effects of stress on perception. Investigated railroad crossing accidents, pointing out experimentally that an approaching train is perceived to move more slowly than it actually does. Studied dynamic visual acuity in the periphery of the visual field. Built a laser optometer to measure the accommodative state of the eye and found that the mean resting focus of his subjects was a little over 1 m. This explained three previously “unrelated” phenomena: Darkfield myopia, empty field myopia, and instrument myopia. Performed experiments on visual illusions when the field of reference was pitched, rolled, and/or yawed, suggesting two visual systems: one for detecting and identifying objects (focal) and one for locating the body relative to other objects (ambient). Found out that at night, we drive faster than the illumination from car headlights should allow. Also studied motion sickness. Received the American Psychological Association’s *Distinguished Scientific Award for the Applications of Psychology* and numerous other awards. Festschrift: *Visual Perception* (1965).

### **Liebmann, Susanne – 1897-1990, Universität Berlin**

The first to reveal the curious phenomena that arise when colors are equated for luminance. Perceived space suffers the most. Depth loses its magnitude, becomes fully indeterminate, and finally vanishes. Also, the object character of a figure is affected, appearing incorporeal or becoming completely lost. Equiluminant stimuli have later been used by neurophysiologists to demonstrate that the neural mechanism supporting color vision (in visual area V4) is motion-blind. Equiluminant percepts are liable to perceptual fading (Troxler effect).

### **Massironi, Manfredo – 1937-2011, Università degli Studi di Verona**

Combined the study of visual perception and cognition with the practice and theory of visual art. Founding Member of the Gruppo ENNE, a frequent exhibitor in exhibits of programmed, kinetic, and optical art. Committed to an experimental phenomenological approach, both empirically and theoretically, he was intrigued by spatial organization phenomena. Contributed to the study of the perception of spatial structures with oblique viewing, concave surfaces, and anamorphosis. Made substantial contributions to the understanding of amodal completion by studying the perception of surface folding in static and animated displays and in flat knots. Also analyzed the relationship between perception and imagery, spatial representation, and spatial verbal description,

and championed the special status of graphic images in perception and cognition.

**Metelli, Fabio – 1907-1987, Università degli Studi di Padova**

Important representative of the *Italian School of Experimental Psychology*. Developed the laws of visual transparency (1970). Take a bisected disk with the left half light gray (P) and the right half dark gray (Q) placed on a white (A) and black (B) bisected background. When the difference in brightness between the outer regions A and B is slightly greater than the difference between the inner regions P and Q, transparency is high. When region A is brighter than region P, and region B is brighter than region Q, the transparent layer is dark. When P is brighter than A and Q is brighter than B, the transparent layer is bright. Other topics investigated by Metelli were the perception of movement and causal connections between perceptual events. Obituary: Stagner, R. (1989). Fabio Metelli (1907-1987).

**Metzger, Wolfgang – 1899-1979, Universität Münster**

Undisputed authority of the second generation of Gestalt psychologists. Described the phenomenology of the homogeneous or structureless *Ganzfeld* (or whole field), which is characterized as a "sea of light", that has no figure-ground separation, causes a mild disorientation of the observer, and a fluctuating state of accommodation. In a *Ganzfeld*, distance cannot be faithfully determined (the empty field myopia of H. Leibowitz). Lost an eye in World War I and developed an intense interest in the monocular factors of depth perception. Also investigated phenomenal identity and perceived depth in moving patterns (see the motion chapter translation by R. Sekuler). In his book: *Laws of Seeing* (2006), he described phenomena from everyday perception in a non-technical style from the point of Gestalt psychology. Specifically, he proposed that a stimulus pattern becomes perceptually organized in the simplest, most symmetrical, and balanced manner, consistent with the principle of *Prägnanz* or good Gestalt. Gestalt factors are phenomenological categories that are self-evident, persuasive, and allow predictions. They are effective in early infancy and the animal kingdom and cannot be overridden by better knowledge. Frequent interactions with the ethologist K. Lorenz, the zoologist B. Rentsch, and the psychologists A. Michotte, R. Canestrari, G. Kanizsa, F. Metelli, and G. Johansson. Their observations are described in the 2nd edition of his *Laws of Seeing* (1954), long before they became known to English-speaking readers. His book: *Psychologie* (1941) is considered the bible of Gestalt psychology.

**Noguchi, Kaoru – 1935-2006, Chiba University**

Japanese psychologist. Studied the relationship between visual illusions and aesthetic preference with the goal of unifying experimental phenomenology and empirical aesthetics. Experimental phenomenology has demonstrated that perception is much richer than a mere stimulus. For example, in color vision, the same stimulus provides several modes of appearance. Similarly, there are various perceptual dimensions in form perception. Even a simple geometrical figure, inducing a visual illusion, elicits not only a perceptual impression of size, shape, slant, depth, and orientation but also an aesthetic impression. This is also true for an anomalous surface, neon color spreading, and transparency. Subjects made both psychophysical and aesthetic judgments of the same test pattern and found that a strong aesthetic appeal and a strong parametric effect are correlated. Book: *Psychology of Beauty and Kansei: New Horizons of Gestalt Perception* (2007); Review (with A. Kitaoka and M. Takashima: *Gestalt-oriented perceptual research in Japan: Past and present* (2008)).

### **Oyama, Tadasu – 1928-2019, University of Tokyo**

Made outstanding contributions to experimental psychology, psychometric methods, and the history of psychology. Approached subjective perceptual phenomena using psychological techniques to measure them objectively and elucidate their determining factors. Focused on figural after-effects, visual illusions, transparency, color appearance, perceptual constancy, perceptual grouping, and affective meanings. Applied various measurement and analysis methods, including psychophysical techniques, reaction time, the method of transposition, semantic differential techniques, factor analysis, multidimensional scaling, and analysis of causal relations. Mentored many psychology students.

### **Palmer, Steven Erwin – 1948-2023, University of California, Berkeley**

Brilliant psychologist of Gestalt heritage. Focused on behavioral studies of perceptual organization in vision, contextual effects on local processing, the aesthetics of color and spatial arrangement, and the nature and order of visual processing. Made ground-breaking contributions to fundamental problems in perceptual organization, color preference, spatial aesthetics, and cross-modal correspondence. Introduced new Gestalt factors: common region, element connectedness, synchrony, and edge region grouping. These factors describe a tendency towards perceptual grouping when elements are tied together within the same bounded area, are connected, change at the same time, and exhibit different edge groupings. Palmer proposed that all of the above factors can be subsumed under the criterion of similarity and called them *ceteris paribus* rules, implying that everything else being equal, grouping is favored by a given factor, for example, by proximity. Monumental textbook: *Vision Science: Photons to Phenomenology* (1999).

### **Rock, Irvin – 1922-1995, Rutgers University**

Leading advocate of unconscious inferences in perception and brilliant experimentalist who worked on the Moon illusion (with Lloyd Kaufman), object orientation (square vs. diamond), and apparent motion. Showed that it is the perceived distance, not the distance on the retina, that matters for grouping. Studied inattention blindness, which occurs when an individual fails to perceive an unexpected stimulus in plain sight, purely as a result of a lack of attention rather than any vision deficit. A famous study that demonstrated inattention blindness asked participants whether or not they noticed a person in a gorilla costume walking through a dynamic scene of students playing basketball. Inattention blindness is related to, but is distinct from, other failures of visual awareness, such as change blindness, repetition blindness, visual masking, and attentional blink. Longstanding vision editor of *Science* journal. Books:

- *The Logic of Perception* (1983)
- *Perception* (1985)
- *Inattention Blindness* (with A. Mack, 1998)

### **Rubin, Edgar – 1886-1951, Københavns Universitet (Copenhagen)**

Danish psychologist. Made groundbreaking observations on the problem of figure-ground organization in visual perception (1915, 1921). Stated: The contour is unilateral and belongs to the figure (Nakayama's border ownership).

### **Tjan, Siaufung 'Bosco' – 1966-2016, University of Southern California**

Chinese American Psychologist. Studied visual pattern recognition, object, and face recognition, using psychophysical, brain imaging, and computational techniques. Advanced our knowledge of visual processing and cortical reorganization in individuals with central vision loss. His work had significant real-world implications, especially for those suffering from impaired vision. Siaufung Tjan was killed on campus on December 2, 2016.

### **Vicario, Giovanni Bruno – 1932-2020, Università degli Studi di Padova**

Exponent of experimental phenomenology as a field in its own right, independently of quantitative psychophysics. Studied a wide range of perceptual illusions of motion. Wolfgang-Metzger Preis (1999) with Y. Kiritani on the slow-motion tunnel effect. Book: *Illusioni ottico-geometriche: una rassegna di problemi* (2011).

**von Ehrenfels, Maria Christian Julius Leopold – 1859-1932, Universität Prag**

Austrian philosopher. One of the predecessors of Gestalt psychology. Stated that the whole is different from the sum of its parts. Introduced the principles of *supersummativity*, i.e., an emergent property, and *transposition*, i.e., a melody, for Gestalt perception. Had radical views on polygamy and race. Article: *Über Gestaltqualitäten (On the Qualities of Form, 1890)*. Inspired by Mach's work *Beiträge zur Analyse der Empfindungen (Contributions to the Analysis of the Sensations, 1886)*.

**von Fieandt, Kai Victor Johannes – 1909-2000, University of Helsinki**

In *Das phänomenologische Problem von Licht und Schatten (1949)*, he reviews experiments on the perception of images that are ambiguous with respect to illumination and figure-ground articulation, arguing that the visual percept favors simplicity in a process of hierarchical integration. His phenomenological approach is presented in the edited volume *The Perceptual World (1977)* with I.K. Moustgaard.

**Wertheimer, Max – 1880-1943, Frankfurt University and New School for Social Research, New York**

Charismatic founder of Gestalt psychology. Proposed the Gestalt laws of figural organization and grouping, according to which scenes, figures, and elements are segmented, segregated, and grouped, thereby becoming foreground and background. Common to these intrinsic principles is the claim that the whole is different from the sum of its parts (*i.e., an emergent property*) and that it follows the law of good Gestalt or *Prägnanz*. These ideas were tested and expanded in numerous experiments in vision as well as other sense modalities. They have lately been correlated with neurophysiological response patterns to account for the *emergent properties* observed in motion and contour perception. Book: *On Perceived Motion and Figural Organization (2012)*.

See also under [Motion / Flicker](#)

## [Visual Illusions](#)

**Akishige, Yoshiharu – 1904-1979, Kyushu University**

Japanese psychologist. Wrote an English review on perceptual constancy, which summarized approximately 60 studies on size constancy until the 1950s. Investigated (with T. Ibuki and J. Ogasawara) the effects of distance cues, space structure, reality of stimulus objects, and observers' size constancy. Studied a 17-year-old man who had lost sight in his left eye 200 days after birth (1932). Concluded that neither binocular parallax nor convergence is essential for size constancy and that spatial articulation is more important for it.

### **Ames Jr., Adelbert – 1880-1955, Dartmouth Eye Institute**

Contributed to physics, physiology, ophthalmology, psychology, and philosophy. Pioneered the study of physiological optics. Famous for demonstrating a size illusion in a distorted room. In the Ames room, the distance on the left is longer than on the right. The far wall of the Ames room is trapezoidal. The person standing on the left side looks smaller because her retinal image is smaller, and because she is seen at the same distance as the person on the right. There is no information to the contrary (tiled floor). The common assumption that rooms are rectangular is not questioned. Therefore, perception goes wrong. Also developed a Leaf Room densely lined with leaves to mask the perspective cues, showing that binocular stereopsis was a sufficient cue to depth structure.

### **Bozzi, Paolo – 1930-2003, Università degli Studi di Trieste**

Assistant to G. Kanizsa at the *Trieste School of Experimental Phenomenology*. Carried out the first experiments in *Naive Physics*, studying the phenomenology of pendular harmonic motion and falling bodies. Described the law of perceptual organization of directionality. Studied transparency phenomena and chromatic aftereffects. Theoretical discourses on tertiary qualities and phenomenal causality. Discussed the epistemological foundations of experimental phenomenology.

### **Day, Ross – 1927-2018, Monash University**

Influential Australian psychologist. Well-known for his research on geometrical optical illusions, spatial distortions of orientation, size, and alignment, induced motion, kinetic depth effects, and illusory contours. Studied aftereffects of motion adaptation and discovered that viewing unidirectional moving patterns in an otherwise dark room does not induce a negative motion aftereffect. This suggested that relative motion is required and challenged the prevailing explanation by adapted motion detectors in the visual brain. Did research on prism-induced distortions and cross-modal transfer of spatial aftereffects. Fellow of the Australian Academy of Sciences. Book: *Human Perception* (1968).

### **Escher, Maurits Cornelis – 1898-1972, Hilversum**

World-famous Dutch graphic artist. Created “impossible” objects, two-dimensional figures that represent three-dimensional objects that cannot exist as a solid object. Examples: The impossible Necker cube and the endlessly rising staircase. Influenced by L. and R. Penrose. Film: *M.C. Escher, Journey to Infinity* (2018).

### **Gregory, Richard Langton – 1923-2010, University of Bristol**

British psychologist, larger-than-life aficionado of visual illusions in everyday perception, nature, and art. Author of one of the most popular textbooks on visual perception. Editor of the comprehensive *Compendium of the Mind*. Advocated a theory according to which our perception is guided by top-down problem-solving strategies and perceptual postulates, by which we seek to resolve ambiguities in the stimulus in the most plausible manner. An example is the Kanizsa triangle, the illusory contours of which are interpreted as an example of cognitive completion by perceptual occlusion. The perception of illusory brightness is seen as the result of an active attempt by the brain to organize a seemingly incomplete stimulus to best account for the ‘missing’ parts. His theory can be seen as a precursor of both top-down approaches and Bayesian analysis of perceptual processing. Visual illusions (“when the system gets it wrong”) remained one of Gregory’s enduring interests throughout his life. His studies of misapplied size constancy, vision under isoluminant color conditions, and the so-called café wall illusion (in the tradition of H. Münsterberg and S. Liebmann) are well known. So is his groundbreaking work on perceptual filling-in of artificial scotomata (with V.S. Ramachandran) and his classifications of visual illusions. Gregory was the Founder and Editor-in-Chief of the journal *Perception* and for many years wrote an editorial for each of the monthly issues. He founded The Exploratory, a hands-on science center in Bristol. A strong supporter of the European Conference on Visual Perception. Books exhibiting his wide range of interests and profound writing abilities include:

- *Recovery from Early Blindness: A Case Study (with J.G. Wallace)* (1963)
- *Eye and Brain: The Psychology of Seeing* (1966, many editions)
- *The Intelligent Eye* (1970)
- *Illusion in Nature and Art* (1973)
- *Concepts and Mechanisms of Perception* (1974)
- *Oxford Companion to the Mind* (1987)
- *The Artful Eye* (1995)
- *Seeing Through Illusions* (2009)

[See also under Visual Development](#)

**Kanizsa, Gaetano – 1913-1993, Università degli Studi di Trieste**

Leading representative of the *Italian School of Experimental Psychology*. Did research in visual perception (phenomenal transparency, apparent motion, amodal completion, figure/ground organization). Known mainly for his celebrated triangle and related figures bounded by illusory (subjective, quasi-perceptual, or “anomalous”) contours. Advocated a clear distinction between primary (perceptual organization) and secondary (recognition, categorization) processes. Published *Organization in Vision* (1979), *Grammatica del Vedere* (“Grammar of Vision”, 1980) and *Vedere e Pensare* (“Seeing and Thinking”, 1990). Also, S. Petry & G.E. Meyer, Eds. *The Perception of Illusory Contours* (1987). Recipient of the Wolfgang- Metzger Preis in 1987, together with R. Luccio, for their work on *Prägnanz*. Editor of the *Giornale Italiano di Psicologia* (1974-1993).

**Luckiesh, Matthew – 1883-1967, Nela Park National Lamps Works**

Physicist, known as the *Father of the Science of Seeing*. Developed several theories on color and its physiological effect on people. He was also interested in determining the conditions under which optimal visibility was achieved, and in examining the relationship between light and seeing, in order to design better types of lamps. During World War I, he studied camouflage and later invented artificial sunlight and germicidal lamps. Luckiesh held eleven U.S. patents, published 28 books, and several hundred scientific and technical articles between 1911 and 1960. Books: *Visual illusions, their Causes, Characteristics, and Applications* (1922); *Light, Vision, and Seeing* (1944).

**MacKay, Donald MacCrimmon – 1922-1987, Keele University**

Highly visible British physicist, known for his contributions to information theory and the theory of brain organization. Wrote the seminal paper *Visual Noise as a Tool of Research* (1966). Described *complementary* streaming motion and flicker in a noise field after adapting to a redundant spatial pattern. Radial streaming motion was observed after adapting to a pattern of densely spaced concentric circles (bull’s eye), while circular streaming motion followed adaptation to a pattern of densely packed radial rays (star figure, Leviant’s Enigma illusion). The effect has been associated with cross-orientation inhibition. Streaming motion also occurred in a cortical scotoma after previous adaptation to a noise field. Using a moving frame, it could be captured. MacKay also studied split-brain patients and proposed a theory of corollary discharge similar to R. Sperry and H.L. Teuber. Associate and frequent attendee at F.O. Schmitt’s *Neurosciences Research Program* at MIT and the *Oxyopia* seminars at UC Berkeley. Member of the Royal Netherlands Academy of Arts and Sciences and recipient of the Hermann von Helmholtz

Prize for Distinguished Research in the Cognitive Neurosciences. Co-editor of *The Handbook of Sensory Physiology*. Donald MacKay died at age 65 of cancer, within a year of giving the 1986 Gifford Lectures at the University of Glasgow.

**Matin, Leonard – 1928-2017, Columbia University**

Studied egocentric space perception and visually-guided sensorimotor behavior using psychophysical experiments on the perception of space and manual behavior in conjunction with neuro-mathematical modeling. Investigated several large-field visually induced spatial illusions produced by pitched and roll-tilted visual fields, which lead to a large mislocalization of both perception and motor behavior (e.g., the eye level perceived at the hip; people perceived to have grown or shrunk, a vertical appearing tilted). Also utilized centrifuges to vary the relative influence of signals for eye position, head position, and bodily motion while measuring perception, motor behavior, and eye position.

**Morinaga, Shiro – 1908-1964, Chiba University**

Japanese psychologist, worked under W. Metzger and E. Rubin. Introduced the Gestalt factor of *Ebenbreite* (equal width) and discovered the figural after-effect of the Delboeuf (concentric circle) illusion. Also studied the Poggendorf and Zöllner illusions, visual transparency, perceptual constancies, and aesthetic arrangement. The apparent misalignment of the apexes of oppositely facing angles is called Morinaga's paradox. Also worked on perception and performance in brain-injured veterans. Many of his former students became active researchers.

**Münsterberg, Hugo – 1863-1916, Harvard University**

Prolific German American philosopher and psychologist. Founded the Psychological Laboratories at Freiburg University and Harvard University. Assembled in Cambridge, the largest collection of psychophysical instruments for the study of the senses. Observed on a tram ticket two rows of phase-shifted black squares, separated by a straight line, which appeared slanted due to the phase shift. This effect became known as the Café Wall Illusion (R.L. Gregory & P. Heard). Drifted into industrial psychology and became the best-known applied psychologist of his time. Prolific writer who authored numerous books. Article by J. Spillmann & L. Spillmann: The rise and fall of Hugo Münsterberg. *J. Hist. Behav. Sci.*, 29 (4), 322–338 (1993).

**Obonai, Torao – 1899-1968, Tokyo University of Education**

Measured the effect of illusions in various stimulus patterns including the Oppel-Kundt (divided lines), Müller-Lyer (different lengths), and Delboeuf (concentric circles) illusion, and proposed that optical illusions, as well as brightness contrast, color contrast and assimilation, are due to psychophysiological induction and are the net result of physiological excitation and inhibition.

**Ouchi, Hajime – 1945-2025, Osaka**

Japanese graphic designer. Known for a celebrated illusion, demonstrating that the perception of relative motion can arise in the absence of a motion cue. The stimulus consists of a center-surround pattern of phase-locked short horizontal vs. vertical bars. With circular movements of the eyes or the stimulus pattern, the central disk appears to float relative to the surrounding annulus. Up to nine hypotheses were proposed to account for this illusion, with different motion vectors offering the most likely explanation. Ouchi's identity was disclosed in 2014 by K. Saito and H. Komatsu, when they located him in Osaka. Guest Editorial: *Hajime Ouchi – a mystery resolved*. Perception 2016, Vol. 45(4) 371–374. DOI: 10.1177/0301006616637433

**Thayer, Abbott Handerson – 1849 -1921, Thayer Studio, New Hampshire**

American painter, naturalist, and teacher. Displayed and interpreted protective coloration in nature in a book entitled *Concealing-Coloration in the Animal Kingdom*. Proposed military camouflage during World War I through disruptive patterning, distractive markings, and countershading to break up a ship's or plane's outlines. His son G. H. Thayer is the author.

**von Szily, Adolf – 1848-1920, Universität Budapest**

Hungarian ophthalmologist. Demonstrated subjective contours, amodal completion, and depth from half-occlusion in silhouettes. In all-black figures, certain monocular appendages link to form subjective contours in front of the binocular shape. See the article by N.J. Wade et al.: *Adolf von Szily (1848-1920)* for these and other discoveries, made by von Szily before 1921,

**Wenderoth, Peter – 1942-2014, Macquarie University**

Investigated numerous aspects of spatial perception, including illusions and aftereffects, symmetry, and binocular rivalry, always with reference to their neurophysiological underpinnings. Editorial board member of both Perception and Psychological Science. A regular attendee at ECVF.

## Visual Attention

### **Corballis, Michael – 1936-2021, University of Auckland**

New Zealand and Canadian psychologist. Performed incisive studies on cortical laterality, handedness, evolutionary brain specialization for language, symmetry perception, mental rotation, attention, and memory. Fellow of the Royal Society of New Zealand, and recipient of its Rutherford Medal.

### **Driver, Jonathon Stevens – 1962-2011, University College, London**

Focused on selective attention, spatial cognition, and multisensory integration in the healthy and damaged human brain (e.g., in hemispatial neglect). Combined psychophysical, neuropsychological, neuroimaging, and transcranial magnetic stimulation (TMS). Was one of the first to perform concurrent TMS-fMRI, to study how dynamic interactions between brain regions can support cognitive functions, for example, on face processing. Jon Driver took his own life in London on 28 November 2011, aged 49, ten months after shattering his knee in a motorcycle accident which left him in debilitating chronic pain.

### **Neisser, Ulric Richard Gustav – 1928-2012, Cornell University**

German American psychologist. Invented (with O. Selfridge) the groundbreaking *Pandemonium Model* of pattern recognition in 1950, which spawned generations of improved approaches to computer vision. Known as the *Father of cognitive psychology*, he inaugurated the field with his celebrated book, *Cognitive Psychology* (1967), which elevated the visual search paradigm as a laboratory tool. He later criticized this approach in *Cognition and Reality* (1976) for failing to address the complexity of visual information of the real world.

### **Pylyshyn, Zenon Walter – 1937-2022, University of Western Ontario**

Developed the ground-breaking multiple object tracking paradigm of divided attention and a visual indexing theory to account for it. On a larger scale, developed a propositional theory for the structure of visual memory, as opposed to a pictorial concept of mental imagery. Fellow of the Royal Society of Canada.

**Treisman, Anne Marie – 1935-2018, University of British Columbia, University of California, Berkeley, and Princeton University**

Highly influential British perceptual scientist known for introducing the *Feature Integration Theory*. FIT describes object perception as the parallel encoding of basic features—such as color, form, and orientation—which are instantly detectable. In her experiments, she pitted primary properties of the stimulus against each other and determined the time required to find a target embedded in a number of distraction stimuli. Independence of the search time from the number of distractors argued for parallel (Julesz: preattentive) stimulus processing (*primitives*), whereas dependence of the search time pointed in favor of serial processing. Disjunctive stimuli, which differed from each other only by one feature (e.g., orientation), were distinguished from conjunctive stimuli, which differed from each other in terms of several characteristics (such as orientation and size or color). Recipient of the National Medal of Science. Member of the Royal Society of London, the US National Academy of Sciences, and the American Academy of Arts and Sciences. Received the University of Louisville Grawemeyer Award in Psychology.

**Yantis, Steven – 1955-2014, Johns Hopkins University**

Focused on the neural mechanisms of attentional switching and perception, and the use of functional magnetic resonance imaging to supplement behavioral methods. Developed the thesis that visual attention is both bottom-up (attentional capture by visual transients) and top-down (value-driven attention based on past rewards and learning history). Received the Troland Research Award. Book: *Sensation and Perception* (2014). Steven Yantis died at age 58 of cancer.

## [Eye movements / Image Stabilization](#)

**Bridgeman, Bruce – 1944-2016, University of California, Santa Cruz**

A leading figure in the neuroscientific study of spatial orientation. Made significant contributions to the understanding of visual stabilization of the outer world, perception-action interactions, and the neural basis of consciousness. His research on visual stabilization through a reafference mechanism highlights how the brain enables stability of perception despite eye and body movements, and how spatial relocations of stimuli escape awareness during such movements. Senior scientist of the Alexander von Humboldt-Stiftung,

guest professor at the Max-Planck-Institut in München, and the University of Padova. Collaborated widely with international colleagues and served as Editor-in-Chief of the journal *Consciousness and Cognition*. Textbook: *Psychology and Evolution: The Origins of Mind* (2003). Bruce Bridgeman was tragically killed in an accident on July 10, 2016 while in Taipei.

### **Carpenter, Roger Hugh Steven – 1945-2017, University of Cambridge**

An international authority on oculomotor physiology who derived a computational model predicting saccadic latency distributions and developed the saccadic latency paradigm for the experimental analysis of decision-making processes. Book: *Movements of the Eyes* (1988).

### **Ditchburn, Robert William – 1903-1087, University of Reading**

British physicist, among the first to demonstrate the disappearance of stabilized retinal images within a few seconds (with B.L. Ginsborg, 1952), suggesting that small eye movements (microsaccades) are needed to sustain vision and prevent it from fading. Member of the Royal Irish Academy, Fellow of the Royal Society of London. Book: *Eye Movements and Visual Perception* (1973).

### **Gerrits, Henk – 1924-1986, Radboud Universiteit, Nijmegen**

Enthusiastic Dutch engineer who developed a system that enabled him to present stimulus patterns via an optical fiber cable and contact lens to the eye and view them without image slip. Studied perceptual disappearance (Troxler fading) of images thus stabilized on the retina and postulated a neural filling-in process to account for it. Destabilized part of the contour and observed its influence on the perception of the enclosed surface area. Extended this work to patients with retinal and cortical scotomata. His research stimulated many studies in normal observers as well as in eye and brain patients who were tested with brightness, color, and texture fading. It also triggered studies of the physiological blind spot. Neurophysiologists developed a model for filling-in of a scotoma based on recording from visual area V1. Henk Gerrits died at age 62 of cancer.

### **Hebb, Donald Olding – 1904-1989, McGill University**

Called the Father of neuropsychology and neural networks. Postulated the Hebb synapse, which enables neural plasticity and affords perceptual learning. Famous for Hebb's rule: Neurons that fire together wire together, suggesting neural plasticity based on experience. Fellow of the Royal Society of London. Influential paper with R.M. Pritchard in *Scientific American* on

stabilized images on the retina. Question: Do perceptual stimuli disappear (fade) and reappear according to the rules proposed by Gestalt psychology? Influential book: *The Organization of Behavior: A Neuropsychological Theory* (1949).

**Keller, Edward Lowell – 1939-2025, Smith-Kettlewell Eye Research Institute**

Focused on how the brain converts sensory inputs into signals for generating saccadic and smooth pursuit eye movements.

**Kowler, Eileen – 1952-2024, Rutgers University**

A brilliant scientist whose work on eye movements, attention, and visual perception was creative, far-ranging, and rigorous. She was a preeminent authority on eye movements and vision. Kowler's work was critical for showing how eye movement control is connected to a range of cognitive processes such as attention, reading, memory, prediction, planning, and scene understanding. Her work made it clear that eye movements were not just reflexive responses to low-level image properties. For example, she showed how expectations influenced something as basic as a pursuit eye movement. One of Eileen's greatest passions was mentorship, especially of graduate students. Her efforts in this area were recognized in 2013 when VSS awarded her the inaugural Davida Teller award in recognition of both scholarship and mentorship. Eileen Kowler died of cancer on December 30, 2024, at the age of 72.

**Krauskopf, John – 1928-2016, New York University**

Did early work on eye movement stabilization at Brown University under the supervision of L. Riggs. Demonstrated that a shallow contour (e.g., a ramp) facilitates fading. This is presumably because a gradient contour attenuates the temporal onset signal and, therefore, is less effective in sustaining and restoring the enclosed surface. The chromatic stimulus used by Krauskopf was employed many years later in the study by R. von der Heydt, H. Friedman, and H. Zhou (2003) who trained monkeys to signal the perceptual filling-in of a red disk surrounded by a green ring. Unexpectedly, the neuronal response recorded from single neurons during steady fixation did not change when filling-in occurred. Rather, the response was correlated with the (physical) wavelength of the disk, not the perceived change of color. Developed, with A. Derrington and P. Lennie (1984), a convenient spherical metric for human color space that is widely used in the field.

See also under [Color Vision](#)

**Nagy, Allen Louis – 1947-2022, Wright State University**

Contributed importantly to the understanding of visual search and attention, especially on the role of color in these functions, as well as to information visualization and display applications.

**Poggio, Gian Franco – 1927-2007, Johns Hopkins University**

Italian neurophysiologist from Genua. Pioneered the natural study of the visual cortex by recording single-neuron activity in the awake monkey, rather than in anesthetized, paralyzed animals. Demonstrated that in the awake state, many neurons in the primary visual cortex show virtually no spontaneous activity. Best known for his studies on the cortical mechanisms that underlie depth perception based on disparities between the two eyes, i.e., stereo vision. Whereas previous studies had reported neurons that are tuned to disparity, Poggio's studies demonstrated that apparently monocular cells are "near cells" and "far cells", which are active over a wide range of disparities, either on the crossed or uncrossed side. He also studied, for the first time, neuron responses with Julesz-type random-dot stereograms, which enabled him to separate stereoscopic selectivity from ordinary feature selectivity. Received the Golden Brain Award of the Minerva Foundation in 1986 and the Lashley Prize of the American Philosophical Society.

**Riggs, Lorrin Andrews – 1912-2008, Brown University**

Ingenious experimental psychologist, Riggs recorded microsaccades, using a light beam reflected off a small mirror embedded in a tightly-fitting contact lens. With the same technique used in reverse, he stabilized the retinal image, resulting in Troxler-type fading (with F. Ratliff, T. Cornsweet, and J. Cornsweet, 1952). This demonstrated that fixational eye movements are necessary to maintain the activation of retinal cells and sustain the perception of contours that delineate surfaces (Krauskopf and Riggs, 1957).

See also under [Brightness and Contrast Perception](#)

**Robinson, David Anthony – 1924-2016, Johns Hopkins University**

Influential oculomotor pioneer who adapted Faraday magnetic coils into contact lenses for the high-precision measurement of eye rotation, a technique referred to as search coils. Applied this tool to the measurement and mathematical modeling of eye rotation, including the physics of the oculomotor control system, the actions of individual muscles, and the motor and pre-motor neural circuits that produce pursuit, saccadic, and vestibular eye movements.

### **Troxler, Ignaz Paul Vital – 1780-1866, Universität Bern**

Swiss physician. Observed that a peripheral target gradually faded and became invisible during fixation to reappear after a saccade. Troxler fading was subsequently studied using retinal image stabilization by A. Yarbus, R. Ditchburn, L. Riggs, H. Gerrits and others. These studies demonstrated that stabilized stimuli disappeared within seconds, suggesting that microsaccades are needed to preserve vision (Martinez-Conde et al, 2000, 2004; Troncoso et al, 2008). The Troxler effect gave rise to numerous studies on filling-in of brightness, color, and texture, suggesting that uniform surfaces are sustained by lateral information from the surround.

### **Yarbus, Alfred Lukyanovich – 1914-1986, Institute for Information Transmission Problems, Russian Academy of Sciences, Moscow**

Soviet psychologist, best known for his pioneering experiments on eye movements and image stabilization. By recording fixational landing sites, he demonstrated that the fovea is attracted by conspicuous features in the stimulus pattern, such as a girl's eyes, nose, and mouth. His investigation of the effect of attention on eye movements stimulated much research. With a novel suction-type contact lens, he achieved near-complete stabilization of the retinal image, as a consequence of which the target remained visible for only a few seconds, before disappearing permanently. The results were reported in his book: *Eye Movements and Vision* (1967). In collaboration with A. Luria, Yarbus examined impairments of visual perception in patients with simultanagnosia and frontal lobe lesions. He also investigated simultaneous and successive contrast.

## **Visual Development**

### **Blakemore, Colin Brian, Sir – 1944-2022, University of Oxford**

World-renowned neuroscientist and highly influential and much-admired member of the vision community. Is best remembered for his studies on the development of the visual brain in kittens and the demonstration of neural plasticity. Worked with H. Barlow and J. Pettigrew to discover neurons encoding binocular disparity in the cat. Demonstrated that a kitten, reared in complete darkness since birth and then exposed to a vertically striped cylinder for 5 hr daily, when tested half a year later, behaved as if it was blind to a horizontal line. This experiment triggered numerous studies under the

umbrella of *Nature vs. Nurture*. By surgically closing the lids of one eye, Blakemore (with R. van Sluyters) also showed that the normal binocular dominance of cortical neurons shifted to the other eye, a finding that is important for the timely treatment of congenital squint and amblyopia in patients. Further, when kittens were reared with a diffuser in front of their eyes, cortical cells became unresponsive, which is crucial for the timely treatment of congenital cataract. Charismatic speaker who was the first physiologist to give the BBC Reith Lectures on the state of the culture, at age 32, and gave the Royal Institution Christmas Lectures. Longstanding Chair of the Department of Physiology/Neuroscience at Oxford University, and subsequently reformist Head of the Medical Research Council of Britain, the primary body for medical grant awards. In this capacity, he had to testify in parliament on measures to ameliorate animal cruelty in neurophysiological experiments. Received numerous honors from many academies and societies, was elected Fellow of the Royal Society of London and knighted by the Queen in 2014. Colin Blakemore died from Amyotrophic lateral sclerosis (Lou Gehrig's disease) on 27 June 2022, at the age of 78.

See also under [Brightness and Contrast Perception](#)

### **Braddick, Oliver John – 1944-2020, University of Oxford**

Acclaimed developmental psychologist. Established the Visual Development Unit in Cambridge and studied (with his wife J. Atkinson) visual perception in infancy and early childhood. Studied the development of the dorsal and ventral streams in infancy and developed the neurological theory of asymmetric nystagmus in the absence of binocular vision. Pioneered work on contrast sensitivity, the development of motion perception, and form perception in newborns. Developed the *isotropic video refractor*, which projected images of the infant's eye on a video screen and enabled instant measurement of accommodation, astigmatism, and refractive error at any age. Infants under 12 months of age had significant astigmatism, decreasing to adult levels by 2 years of age. Of the over 5000 infants screened at 8 months of age, around 5-6% had visual problems, mostly from hyperopia, and were at risk of developing strabismus (squint) later in life. Contrast sensitivity in babies aged between 1 to 10 days, measured with the visual evoked potential (VEP), was poor but improved with age. Most infants had binocular vision by 3-4 months of age (measured with random dot stereograms) and responded to the orientation of the stimulus at 6 weeks of age (measured with the VEP). Mechanisms underlying optokinetic asymmetries were also studied. Fellow of the Academy of Medical Sciences and of the British Academy. Organized ECVF 1984. Review on the development of human visual function (Vision Research, 13, 1588-1609, 2011).

See also under [Brightness and Contrast Perception](#)

**Dobson, Margaret Velma – 1949-2010, Arizona State University**

Documented improvement in visual function following optical treatment of astigmatism-related amblyopia, such as meridional amblyopia. Showed that astigmatic children are at risk for deficits across a range of visual functions. Treatment effects occurred by 6 weeks. However, astigmatic children never quite attained normal levels of visual function. Velma Dobson died on April 9, 2010 at the age of 61, following complications from Amyotrophic lateral sclerosis (Lou Gehrig's disease).

**Fantz, Robert Lowell – 1925-1981, Case Western Reserve University**

Developmental psychologist. Introduced the preferential-looking paradigm for the study of infant perception. Using this procedure, an observer looks through a peephole at the baby's eyes and judges the location of the target based on the direction of the infant's gaze. Discovered that infants look first and longer at patterned images than on uniform images. Showed that after multiple exposures to the same image, the infant gradually exhibited a preference for a novel stimulus. The paradigm was combined with the analysis of eye movements and pupil dilation.

**Gibson, Eleanor J. (née Jack) – 1910-2002, Cornell University**

Prominent experimental psychologist in the field of development of perception and action, Widely known for her experiment using a visual cliff to test for depth perception in babies and kittens. Babies crawling on a glass plate that enabled a view of a checkerboard pattern one foot beneath would stop crawling, suggesting that they appreciated the change in depth level. Her research led to a new understanding of perceptual development in human infants and children. She was elected to the US National Academy of Sciences, and, in 1992, was awarded the National Medal of Science, the highest scientific honor in the United States. Was denied a professorship at Cornell due to anti-nepotism policies.

**Gregory, Richard Langton – 1923-2010, University of Bristol**

A giant in the field of perceptual psychology, Gregory was also keenly interested in the brain mechanisms underlying perception. His book, *Eye and Brain*, which appeared in five editions and was translated into twelve languages, contains many references to single-cell neurophysiology and their relation to perception. In this book, he described the study of a rare case of a 52-year-old man who had become blind at the age of 10 months and, following corneal transplant surgery, recovered part of his color and motion vision. Sadly, he was so confused by the lack of form vision that he wanted to

be blind again. Gregory also reported on the primitive raster scanning with a single photoreceptor in the copepod *Copilia quadrata*. The Handbook volume *Evolution of the Eye and Visual System* (1991), edited jointly with J. Cronly-Dillon, testifies to his interest in developmental aspects and cross-species comparisons.

See also under [Visual Illusions and Disarrangement and Rearrangement](#)

### **Held, Richard Marx – 1922-2016, Massachusetts Institute of Technology**

Directed one of the foremost laboratories for studying accommodation, astigmatism, myopia, strabismus, stereo acuity, and optokinetic nystagmus in human infants. Among other results, they demonstrated that a baby's ability to see in three dimensions first appears at the age of 16 weeks. With P. Sinha, Held traveled to India to find an answer to the famous question posed by W. Molyneux to the philosopher J. Locke: Could a person born blind who by touch could distinguish between a cube and a sphere, upon gaining sight immediately and without touching, tell the difference between the two objects by sight alone? Studying the sight of congenitally blind children within *Project Prakash* and researching the subsequent development of vision, Held and Sinha, in 2007, reported that newly sighted subjects who sensed objects with their hands could not initially identify them by sight. However, after a week with sight, their abilities rapidly improved. The findings forced a reconsideration of the conventional view that if children lack sight in early childhood, they will never be able to make visual sense of the world. The rapidity of improvement suggested that the visual system is, in some sense, pre-wired, but relies importantly on the feedback between sight and touch that is gained by experience.

See also under [Gestalt Psychology and Disarrangement and Rearrangement](#)

### **Mohn, Gesine – 1953-1989, Universität Tübingen**

Examined visual development in babies from preterm to 12 months of age, finding that preterm infants experience accelerated visual development, implying an environmental influence in the developmental time-course. Assessed visual acuity, visual fields, optokinetic nystagmus, and visual threat response. Gesine Mohn died of cancer, at the age of 36.

### **Sireteanu, Ruxandra – 1945-2008, Max-Planck-Institut, Frankfurt**

Biophysicist and neuroscientist from Romania. Her research centered on the human visual system as it develops from a newborn into adulthood, especially for those with disorders of their binocular vision, such as from deprivation amblyopia. Employed psychophysical, electrophysiological, and clinical

techniques. Used results from deprivation in cats as a model for human amblyopia. Ruxandra Sireteanu died from a fall in her home on 8 September 2008, at the age of 62.

**Teller, Davida Young – 1938-2011, University of Washington, Seattle**

Charismatic leader and pioneering researcher of infant visual development. Extended the preferential looking procedure, developed by R. Fantz, to the two-alternative forced choice measurement of infant visual acuity and color perception. The level of correct guesses obtained with the Teller Acuity Cards indicates a visual acuity of about 20/200 at birth, reaching adult levels by about 3 years of age. Color discrimination is rudimentary at birth, with full color vision present by about 6 months. Teller constrained the relationship between visual phenomena and their presumed neural correlates in terms of "psychophysical linking hypotheses" (G. Brindley). Advocated extensively for equality of women in science. The Davida Teller Award of the Vision Sciences Society is named in her honor. Teller was an excellent speaker and received the Glenn A. Fry Medal, the Jonas Friedenwald Award, and was a Fellow of the Optical Society of America.

## Disarrangement and Rearrangement

**Held, Richard – 1922-2016, Massachusetts Institute of Technology**

Highly supportive professor and a beacon of fairness and modesty at MIT's psychology department. Recorded (with W. Köhler) electrical potentials from the back of the head to find evidence for figural aftereffects. With Alan Hein, Held studied the development of visually controlled movements of the hand and foot in monkeys, using deprivation and selective exposure during rearing. He also studied temporary visual disarrangement and rearrangement in both humans and monkeys, by making subjects wear prism goggles and measuring how long it took for the visual and motor systems to adapt to the spatial displacement. In a famous experiment with A. Hein, each of a pair of kittens raised in the dark was placed in a basket suspended from a rotating carousel, and only one kitten was allowed to walk, whereas the other sat passively in the basket. Although both kittens were exposed to the same visual scenes, only the active kitten adapted to the prism-induced shift of the environment, whereas the passive kitten did not. This work revealed the importance of self-produced movement for visual development. The results were replicated in human observers, using a wheelchair, in which only the active student pushing the wheelchair adapted to the prism-induced right-left reversal, whereas the passive student sitting in the wheelchair did not.

Evidently, self-produced movement and proprioceptive feedback were crucial for visual rearrangement. These experiments suggested cortical remapping and plasticity. – Demonstrated (with E. Pöppel) that patients who were cortically blind had residual vision, presumably from using the colliculo-pulvinar–MT pathway. Elected to the US National Academy of Sciences; received the Glenn A. Fry Medal and the Kenneth Craik Award. Edited (with W. Richards) a valuable compilation of key articles from *Scientific American*. Edited *Perception* – the 8th volume of the *Handbook of Sensory Physiology* (1978).

See also under [Gestalt Psychology and Visual Development](#)

### **Howard, Ian Porteus – 1927-2013, York University, Toronto**

Highly imaginative hands-on vision scientist who constructed his own large-scale apparatus rather than using computer displays. That equipment included (i) an eye movement monitoring system equipped with scleral contact lenses and Ian's own hand-wound field coils, (ii) a 10 ft diameter spherical room that could rotate around the three major axes to measure vection, and (iii) a 10ft x 10ft x10ft furnished cuboid room that could rotate around the three major axes. It was used to measure the extent of tumbling in response to whole-field motion. Future NASA astronauts who would later experience weightlessness in the International Space Station, reported that the feeling of tumbling was more powerful in the furnished cuboid room than in the spherical room. This observation suggests that perceived self-motion is not simply a consequence of motion in the visual field but also depends on the features of the room, as they indicate what is up and what is down.

Outstanding research volumes:

- *Human Spatial Orientation* (with B. Templeton, 1966)
- *Human Visual Orientation* (1982)
- *Binocular Vision and Stereopsis* (with B. Rogers, 1995)
- *Seeing in Depth* (2 volumes, vol. 2 with B. Rogers, 2008)
- *Perceiving in Depth* (2 volumes, vol. 2 with B. Rogers, 2012)

### **Kohler, Ivo – 1915-1985, Universität Innsbruck**

Highly original and skilled assistant of T. Erismann. Conducted experiments using prism and mirror goggles in the tradition of G. Stratton and W. Stern to study the adaptation to a distorted visual input and the ensuing reorganization in the visuomotor system. A broad inventory of inverting spectacles, prism goggles, half-prism goggles, and bichromatic glasses was used. A monograph entitled *Über Aufbau und Wandlungen der Wahrnehmungswelt* (1951) describes in detail the problems encountered in daily life while wearing the binocular reversing goggles. Kohler's experiment, lasting for 124 consecutive days and involving fencing and bicycle riding, triggered a wave of similar experiments in many countries. Book: Translation into German of J.J.

Gibson's *Evolution of the Eye, Visual Evolution of the Eye, and The Senses Considered as Perceptual Systems* (1966). Festschrift edited by L. Spillmann and B. Wooten: *Sensory Experience, Adaptation, and Perception* (1983). Films by Anton Hajos and Nico Troje.

### **Stratton, George Malcolm – 1865-1957, University of California, Berkeley**

Conducted experiments on perception, stereoscopic acuity, eye movements, visual illusions, the limits of the peripheral visual field, and apparent motion. Was the first to wear special glasses that inverted images up / down and left / right (1896). Found himself reaching out with the right hand when he should have used the left, and the other way around, but eventually adapted to the reversal and was able to ride a bicycle. His studies influenced T. Erismann and I. Kohler in Innsbruck. Member of the US National Academy of Sciences.

## Neurophysiology and Neuroanatomy

### **Adrian, Edgar Douglas, 1st Baron Adrian of Cambridge – 1889-1977, University of Cambridge**

Called the Father of modern sensory neuroscience, Adrian was the first to record the responses of single optic nerve fibers to simple visual stimuli. Established the rate code of neural impulses, according to which the frequency of action potentials increases with stimulus intensity, while the amplitude remains constant (all-or-none principle). Studied the electroencephalogram (EEG), discovered by H. Berger in 1933, and showed that the alpha rhythm arises principally in the visual cortex. Recipient of the Nobel Prize in Physiology/Medicine, 1932. Was President of the Royal Society of London (1950-1955); President of the Royal Society of Medicine (1960-1962); Chancellor of the University of Cambridge (1967-1975); and Chancellor of the University of Leicester (1957-1971).

### **Barlow, Horace Basil – 1921-2020, University of Cambridge**

Highly influential British neuroscientist, psychophysicist, and theorist, interested in information redundancy, predictive coding, Bayesian inference, unsupervised learning, and development. Measured threshold as a function of stimulus area in the frog and discovered (with S. Kuffler) lateral inhibition in the surround of the receptive field, which disappeared with dark adaptation. Discovered a feature detector in the fly; (with R. Hill and W. Levick) motion-

sensitive cells in the rabbit retina; and (with C. Blakemore and J. Pettigrew) cells in cat primary visual cortex that were selective to binocular disparity. Proposed a relationship between the firing of single neurons in sensory pathways and perception. His *single-unit doctrine* incorporates efficient coding, statistical inference, and redundancy. Proposed dark light as the background against which increment, and absolute thresholds are measured during dark adaptation. Fellow of the Royal Society of London, recipient of the Ferrier Medal, the Australia Prize, the Schwartz Prize, and the Ken Nakayama Prize. Obituaries by C. Blakemore and by D. Burr & S. Laughlin.

See also under [Brightness and Contrast Perception](#)

**Barlow, Robert B., Jr. – 1939-2009, SUNY Upstate Medical University, Syracuse NY**

Known for his research on the Limulus eye. Discovered that the strength of inhibition between two receptors is nonlinear. Found that the Limulus eye is modulated by efferent optic nerve signals from a circadian clock in the animal's brain. Developed a computational model showing how the spatiotemporal properties of the Limulus eye are tuned to detect moving objects, resembling a potential mate. Studied effects of metabolic stress on the visual sensitivity of mice and its possible role in degenerative eye diseases. Key paper: *What the brain tells the eye* (1990).

**Baumgartner, Günter – 1924-1991, Universität Zürich**

Much beloved physician, researcher, and mentor. Advocated the correlation between neuronal activity and sensory perception. Recorded from optic nerve fibers, geniculate, and cortex neurons of the cat and studied their responses to moving light and dark spots. Described concentric receptive fields in the visual cortex but narrowly missed the orientation specificity found by D. Hubel and T. Wiesel in 1959. Attributed the perceptual phenomenon of border contrast to the receptive field organization of ON- and OFF-neurons and interpreted the Hermann grid illusion as evidence for contrast enhancement through lateral inhibition (later disproven). Used the illusion for a subjective estimate of receptive field size in foveal vision. He also inspired neurophysiological research on illusory contours in the Kanizsa triangle by R. von der Heydt and E. Peterhans and asked: "Where do visual signals become a perception?" His work influenced a whole generation of neurophysiologists and neurologists. Received the Hans Berger Prize and the prestigious Otto Nägeli Prize for promoting clinical sciences and basic research and was a Member of the German National Academy of Sciences Leopoldina. Günter Baumgartner died of cancer on September 11, 1991, at the age of 66.

**Baylor, Denis Aristide – 1940-2022, Stanford University**

Incisive work on early steps in vision, in particular the mechanism by which light energy is converted to neural signals within the rod and cone photoreceptor cells of the eye. Recorded for the first time the response of retinal rods to single quanta of light. Co-developer with J. Schnapf of the suction electrode technique for the measurement of electrical signals from single photoreceptor outer segments. Established the time course and light adaptation characteristics of human and macaque monkey cone photoreceptors. Member of the American Academy of Arts and Sciences, the US National Academy of Sciences, and the Royal Society of London. Received the Proctor Award.

### **Bishop, Peter Orlebar – 1917-2012, Australian National University**

Renowned for his ingenious quantitative approach to the study of the mammalian visual system and his ability to attract a large number of talented people to visual research, first at the University of Sydney and then at the Australian National University in Canberra. His research was based on specially designed, precise instrumentation and data quantification applied to the analysis of the response properties of single neurons in the dorsal thalamic visual relay nucleus, the dorsal lateral geniculate nucleus (LGNd), and the primary visual cortex. Did extensive work on end-stopped (hypercomplex) neurons receiving input from beyond the classical receptive field. Described (with J. Pettigrew) the neural mechanisms of binocular vision. Received the Australia Prize together with H. Barlow and V. Mountcastle. Became Doctor of Science from the University of Sydney and was elected Fellow of the Australian Academy of Science and Fellow of the Royal Society of London.

### **Blum, Baruch – 1926-2007, Tel Aviv**

Israeli physiologist. Organized ECVF 1989. Book (ed.): *Channels in the Visual Nervous System: Neurophysiology, Psychophysics and Models* (London: Freund, 1991)

### **Boycott, Brian Blundell – 1924-2000, Kings College, London**

Outstanding zoologist and neurobiologist. Laid the foundation for our modern understanding of the cell types and synaptic connections that form the basis of parallel processing in the retina. Depicted the different nerve cells in "whole mount" preparations by applying Golgi staining and electron microscopy. Identified the different types of horizontal cells, bipolar cells, and ganglion cells and studied their variation from the central (fovea) to the peripheral retina. By applying quantitative staining methods, Boycott together with L. Peichl and H. Wässle subsequently succeeded in determining the sampling

density of the different retinal cells. They further showed that the light signal in the eye is pre-processed in many parallel circuits before it is transmitted to the brain. Literature: B. Boycott (2001). In *The History of Neuroscience in Autobiography* (ed. L. Squire). Obituary by H. Wässle in: *Biographical Memoirs of Fellows of the Royal Society*. (2002). Received the Proctor Award.

**Byzov, Alexei Leontyevich – 1926–1998, Institute for Information Transmission Problems, Moscow**

Studied electrophysiological mechanisms of visual signal processing in vertebrates (fish, frog, turtle) and invertebrates. Developed an electrode marking method to explore the role of horizontal cells as regulators of synaptic transmission. Modeled photoreceptor coupling and post-receptor interactions in the retina. Demonstrated electrical feedback in synapses in the outer plexiform layers of the retina. Most current Russian electrophysiologists who use intracellular recordings are either his students or students of his students.

**Cajal, Santiago Ramón y – 1852-1934, University of Madrid**

Highly acclaimed Spanish neuroscientist, pathologist, and histologist specializing in neuroanatomy and the central nervous system. Explored the insect visual nervous system with his colleague D. Sánchez. Discovered the axonal growth cone. Provided the first complete histological description of retinal neurons, including amacrine and horizontal cells, as revealed by the Golgi stain. Advocated a point-by-point representation of the retinal image in the visual brain. Demonstrated experimentally that the relationship between nerve cells was not continuous, but rather contiguous. Made the first random pattern stereograms (around 1870). Member of the Academy of Sciences in Göttingen, Foreign Member of the Royal Society of London, Member of the Academy de Sciences in Paris, Member of the US National Academy of Sciences. Nobel Prize in Medicine/Physiology with C. Golgi, 1906. Books: *La rétine des vertébrés* (1893). *Advice for a Young Investigator*. His work on the retina is reprinted in the Supplement to R. Rodieck's book: *The Vertebrate Retina* (1974).

**Creutzfeldt, Otto Detlev – 1927-1992, Max-Planck-Institut, Göttingen**

Sage of German neuroscience at the Max-Planck-Institutes in Munich (1962-71) and Göttingen (1971-92). A central theme of his work was the elaboration of receptive fields at different stations along the visual pathway, and the way this organization relates to perceptual phenomena. In particular, he supported the idea of specific afferent connections from one level to the next, with receptive fields elaborated through local inhibitory processes, rather than by afferent convergence and interaction. This concept has received substantial

support in the past decades. Had brilliant students, including B. Sakmann (Nobel Prize in Medicine/Physiology, 1991), W. Singer, H. Waessle, H. Scheich, S. Kastner, and C. v.d. Malsburg. Member of the Göttingen Academy of Sciences. Book: *Cortex Cerebri* (1983). Otto Creutzfeldt died of cancer on 23 Januar 1992 at the age of 64.

**Daw, Nigel Warwick – 1933-2022, Yale University**

Contributed fundamentally to our understanding of the organization of color vision in the retina, geniculate nucleus, and visual cortex. Uncovered essential physiological and pharmacological properties of retinal receptive fields and their role in direction selectivity and orientation sensitivity. Made important contributions to our understanding of developmental plasticity, critical periods, and amblyopia. Received the Jonas Friedenwald Award, Member of the American Academy of Arts and Science. Textbook: *Visual Development, and How Vision Works: The Physiological Mechanisms Behind What We See* (2012).

**DeValois, Russell Lee – 1926-2003, University of California, Berkeley**

Known to visitors for his hospitality, relaxation, and cheerfulness. Proposed a 'multi-stage color model' to explain how the cortex deconfounds the responses of neurons receiving input from three types of cones to produce separate red-green and blue-yellow systems, as well as luminance percepts (black-white) from color. This model extended the biological implementation of L. Hurvich and D. Jameson's Opponent-Process Theory of color vision. It also attempts to satisfy the long-remaining question of how the visual system separates luminance information from color. The model predicts that human red-green colorblindness can be cured using a retinal gene therapy approach to add the missing photopigment without any additional changes to the post-synaptic circuitry. Russel DeValois died on September 20, 2003, from injuries suffered in an automobile accident in Colorado.

**Donner, Kai Otto – 1922-1995, University of Helsinki**

Founding father of the present physiological vision research community in Finland. Brought single-cell recording "back home" to Helsinki, where it had first been developed by R. Granit and G. Svaetichin in 1939. Suggested that cat retinal ganglion cells may multiplex information about light intensity and wavelength in their spike discharges. Published three papers (with W. Rushton) on rod-cone signal integration in frog ganglion cells. Measured the recovery of retinal sensitivity after bleaching exposures. Studied frog retinas together with Tom Reuter to challenge the then-dominant view that dark adaptation mainly depends on post-receptoral processes. Studied visual acuity of several passerine birds and the spectral sensitivities of pigeon

ganglion cells in relation to oil droplets in the cones. Researched the visual ecology of a tiny crustacean, living at great depths in the Baltic Sea.

**Dreher, Bogdan – 1941-2019, University of Sydney**

Polish immigrant to Australia during the anti-Semitic and anti-intellectual purges in 1968, Professor of Visual Neuroscience from 1995 to 2013. His most frequently cited work was on monkey retinal ganglion cells and their central projections. His analysis of hypercomplex cells in the visual cortex challenged the view that hypercomplexity was at the top of a neuronal hierarchy, progressing from simple to complex to hypercomplex cells.

**Enroth-Cugell, Christina Alma Elisabeth – 1919-2016, Northwestern University**

Renowned vision scientist, mentor, and compassionate colleague, yet feared for her sharp comments. Originally from Scandinavia. Studied at the Karolinska Institute in Stockholm under Nobel Prize-laureate R. Granit, and did seminal research on the function of the retina. Her 1966 paper co-authored with John G. Robson, on X- and Y-retinal ganglion cells and retinal receptive fields, has been cited over 3,400 times. She was one of the first to use systems analysis in visual neuroscience and helped launch the idea of parallel pathways in the visual system. Recipient of the Jonas Friedenwald Award, and Ludwig von Sallmann Prize.

**Fiorentini, Adriana – 1926-2016, Laboratorio di Neurofisiologia del C.N.R., Pisa**

Much admired Grande Dame of Italian neuroscience, admired for her dedication to science, enthusiasm for research, as well as her generosity and humility. Published numerous works on physiological optics and perception. Pursued topics in psychophysics, neurophysiology, electrophysiology, visual development, and plasticity, even neuropharmacology, and art. Characteristic of her work was the integrated approach that took the study of visual phenomena and threshold measurement to the analysis of neuronal mechanisms, and vice versa. Fiorentini worked closely with the neurophysiologist L. Maffei, asking “the same questions to human perception and mammalian single cortical cells,” in an attempt to uncover, where possible, the neural substrate of visual perception. Was among the first to provide evidence of the visual cortex as a spatial frequency analyzer (Maffei & Fiorentini, 1973). Collaborated with F. Campbell and P. Bishop.

See also under [Brightness and Contrast Perception](#)

**Flechsig, Paul Emil – 1847-1929, Universität Leipzig**

German neuroanatomist and neuropathologist who contributed significantly to the understanding of the brain's structure and function. Described the course of the optic radiation from the lateral geniculate nucleus to the striate area of the cortex, based on myelogenesis (1896). Member of the German National Academy of Sciences Leopoldina.

**Frégnac, Yves – 1951-2024, École Polytechnique, Paris**

Influential and visionary French neuroscience researcher who specialized in visual neuroscience and neural plasticity. Known for his pioneering work in systems neuroscience and his integration of experimental and theoretical approaches in studying the visual cortex. Pioneered the use of intracellular recordings in the visual cortex during the 1990s. Advanced the understanding of how neurons develop and modify their response properties to visual stimuli. Created comprehensive multi-scale models of the primary visual cortex that integrated anatomical, statistical, and functional constraints. Developed the understanding of push-pull receptive field organization and synaptic depression in V1, demonstrating mechanisms for the reliable encoding of natural stimuli. Influential voice on the future of neuroscience research in France. Awarded the Grand Prix scientifique de la Fondation Louis D. of the Institut de France.

**Glezer, Vadim Davydovich – 1923-2014, Pavlov Institute of Physiology**

Russian neuroscientist. Did research into visual pattern recognition, luminosity, and receptive field reconfiguration. Developed a mathematical theory of vision. Books: *Information and Vision* (1961), discusses neurophysiological, behavioral, and model research into vision. *Visual Identification and its Neurophysiological Mechanisms* (with K. Dudkin, 1975), includes pattern recognition, object recognition, and neurophysiological mechanisms of visual identification. *Visual Perception and Memory* (1985, with K. Dudkin), includes physiological mechanisms of iconic, short-term, and long-term memory, and the role of these mechanisms in visual perception. *Vision and Thought* (1985), defines vision as “objective thought” and discusses the results of neurophysiological, behavioral, and model research into vision. Proposes a four-level model of the visual process that can be applied to the development of automatic pattern recognition systems. Honored by a centenary symposium at the Russian Academy of Sciences in 2023.

**Glickstein, Mitchell – 1932-2017, University College, London**

US American neuroanatomist interested in the role of the structure and function of the pathways that link the cerebral cortex and the superior colliculus to the cerebellum. Identified the cells of origin of the cortico-pontine

fibers in the cerebral cortex and recorded their visual response properties. He also determined the distribution of fiber size in that pathway in an attempt to relate differences in size to differences in function. Book: *Neuroscience: A Historical Introduction* (2014).

### **Gouras, Peter – 1930-2021, Columbia University**

Captivating Greek neuroscientist and ophthalmologist. Enthusiastic speaker. Described rod and cone signals and the processing of chromatic information in the retinal circuitry. The first to demonstrate spreading depression. Provided evidence that retinal horizontal cells are forming an electrical syncytium. Advocated the use of clinical electroretinography in the study of retinal diseases. Conducted cellular electrophysiology to identify the responses of parvo-, magno- and S-cone systems in the primate retina. Studied isolated arterially perfused eyes and monkey striate cortex. Suggested the transplantation of cultured human retinal cells to slow or stop progressive retinal degeneration. Wrote (with E. Zrenner) *Color Vision: A Review from a Neurophysiological Perspective* (1981).

### **Granit, Ragnar Arthur – 1900-1991, Karolinska Institutet, Stockholm**

Finnish-Swedish pioneer in neurophysiology. Recorded the first electronically amplified human electroretinogram, or ERG (1933), and identified its component contributions from the outer and inner retinal layers. Studied the nerve action potentials of the mammalian retina and the optic nerve in response to light. Demonstrated that light could excite as well as inhibit nervous impulses, thereby giving plausibility to E. Hering's opponent process theory. Known for his dominator-modulator theory of color vision. Distinguished (in 1947) between sustained and transient ganglion cells. Nobel Prize in Medicine/Physiology, 1967 along with H. Hartline and G. Wald. Member of the US National Academy of Sciences and American Academy of Arts and Sciences. Books: *Sensory Mechanisms of the Retina* (1949), *Receptors and Sensory Perception* (1955).

### **Grinvald, Amiram – 1945 – 2021, Weizman Institute of Science Rehovot**

Famous Israeli neurobiologist. Introduced functional optical imaging, based on voltage-sensitive dyes, to enable visualization of electrical activity in the living brain in real time. The method has unprecedented temporal and spatial resolution for imaging cortical processing and higher brain functions. Specifically, it reveals the functional architecture of the visual cortex. The high resolution achieved by optical imaging enables researchers to fully map individual cortical columns, the brain's so-called "microprocessors" for shape, color, and motion perception. It thus constitutes an all-optical physiology parallel to microelectrode neurophysiology. Optical imaging also affords

noninvasive angiography in ophthalmology, offering early diagnoses and treatment for blindness prevention. Foreign director of the Max Planck Institute in Heidelberg and Guest staff member at Riken, Japan. Recipient of the Körber European Science Prize and the Dan David Prize.

**Grüsser, Otto-Joachim – 1932-1995, Freie Universität, Berlin**

German neurophysiologist with wide-ranging interests in the neurophysiology, neuropsychology, and psychophysics of the visual and vestibular systems. Known for his contagious enthusiasm and forceful discussions. Together with R. Jung, G. Baumgartner, and O. Creutzfeldt, he laid the foundation for post-war visual neurophysiology in Germany. Advocated the correlation of single neuron responses with psychophysical thresholds (e.g., brightness as a function of log luminance) and perceptual phenomena (Brücke-Bartley Effect, positive and negative afterimages, critical flicker frequency). In 1957, he was the first to record intracellularly from single horizontal cells in the cat retina. Important papers on pressure and migraine phosphenes and the retino-cortical magnification factor. Conducted EEG studies on face recognition in normal, schizophrenic, and brain-lesioned subjects. Did groundbreaking research on a vestibular-visual area in the parietal cortex of monkeys. Frequent collaboration with Wim van de Grind on motion. Also excelled in the history of medicine, for example, in publications on *J. Purkyně's contributions to the physiology of the visual, vestibular, and oculomotor systems* (1984), a monograph of *Justinus Kerner* (1987), and a book (with T. Landis) on *Visual Agnosias and Other Disturbances of Visual Perception and Cognition* (1991). Authored a chapter (with his wife U. Grüsser-Cornehls) on *Neuronal mechanisms of visual movement perception and some psychophysical and behavioral correlations*. In R. Jung, (Ed.), *Handbook of Sensory Physiology* (1973). Otto-Joachim Grüsser died on 17 October 1995, at the age of 63.

**Hartline, Haldan Keffer – 1903-1983, Rockefeller University**

Pioneer in electrophysiological studies of vision. The first person to record (with Graham, 1932) the activity of single optic nerve fibers in the eye of the horseshoe crab, *Limulus polyphemus*. Mapped the activity of visual receptive fields of retinal ganglion cells in the vertebrate retina. Discovered (with H. Barlow) lateral inhibition in the Limulus eye, and (with F. Ratliff) described the integrative activity of recurrent inhibitory networks using the Hartline-Ratliff equations. Member of the US National Academy of Sciences, the American Philosophical Society, and a Foreign Member of the Royal Society of London. Shared the Nobel Prize in Medicine/Physiology, 1967, with G. Wald and R. Granit.

**Henry, Geoffrey Herbert – 1929-2010, Australian National University**

Noted Australian optometrist and neuroscientist. Focused on tritan color vision defects and the recognition of colored road signal lights by people with abnormal color vision. Furthered our understanding of the visual cortex using the striate cortex of the cat as a model. Studied orientation-specific receptive fields. Recipient of the Glenn A. Fry Medal, and the Rimpac Award. Elected to Honorary Life Membership of the Victorian College of Optometry (1968).

**Holmes, Gordon Morgan, Sir – 1876-1965, National Hospital for Nervous Diseases, Queen Square, London**

Distinguished Irish neurologist. Collaborated with Sir H. Head and published, in 1911, the first accurate account of the functions of the optic thalamus and its relation to the cerebral cortex. Mapped, in 1918, the visual scotomata of brain-lesioned soldiers and correlated their perimetric location with the site of the lesion in the striate cortex. Described the symptoms of cerebellar lesions in his *Croonian Lectures* to the Royal College of Physicians, 1922. Fellow of the Royal Society of London and of the German National Academy of Sciences Leopoldina.

**Hubel, David Hunter – 1926-2013, Harvard University**

Brilliant Canadian neurophysiologist, taught us most of what we know today about the early time of receptive field research. Identified (with T. Wiesel) different kinds of receptive fields: Concentric receptive fields of On-center and Off-center neurons in the retina and LGN, and elongated fields in area V1, characterized by an excitatory axis and inhibitory flanks or vice versa. Showed that these receptive fields are optimally suited for processing certain stimulus parameters, such as orientation, line length, and motion direction. According to Hubel and Wiesel's classification (1959), *Simple cells* respond to a long, narrow slit of light, or a dark bar against a bright background, or a straight edge. Their receptive fields are orientation-specific and position-specific. *Complex cells* respond best to the length of a line up to a certain value and then asymptote. They are orientation-specific but not position-specific. Such cells also respond to movement in one direction, but not in the other. *Hypercomplex cells* respond specifically to a line of a certain length and have therefore been called *endstopped*. The various kinds of cells are systematically arranged in the cortex as illustrated by Hubel & Wiesel's *Ice Cube model*, which has vertical columns for orientation on the right of the cube, ocular dominance columns alternating for the right and left eye in front, and blobs containing cells for color on top. Landmark papers by Hubel & M. Livingstone (1987) and M. Livingstone and Hubel (1987) on separate channels for the perception of form, color, movement, and depth. Member of the US National Academy of Sciences, American Academy of Arts and Sciences, Royal Society of London and the German National Academy of Sciences Leopoldina. Recipient of the Karl Spencer Lashley Prize, Glenn A. Fry Medal, Jonas Friedenwald Award, and Charles F. Prentice Medal. Nobel

Prize in Medicine/Physiology, 1981 with Torsten Wiesel. Brilliant postdocs and research associates, including M. Stryker, M. Livingstone, S. LeVay, C. Shatz., B. Conway, and C. Gilbert. Book: *Eye, Brain, and Vision* (1988).

### **Jung, Richard – 1911-1986, Universität Freiburg**

Most highly acclaimed German neurologist and neurophysiologist of his generation. Pioneered single-cell recording from cat cortex with von Baumgarten and Baumgartner in 1951, when they recorded, for the first time, light-induced action potentials from cortical cells in the cat (published in 1952). In follow-up studies, Freiburg researchers O. Creutzfeldt, O.-J. Grüsser, and G. Baumgartner investigated the neuronal activity of individual cells in the optic nerve, LGN, and visual cortex with luminance, contrast, and flicker stimuli and correlated the discharge rates with subjective perceptual phenomena in humans. These results were presented at the celebrated symposium on the *Neurophysiology and Psychophysics of the Visual System* in 1960. In detailed reviews, Jung (1961, 1973) described the correlation between neuronal findings and perceptual phenomena and explained contrast vision, light and dark vision, as well as afterimages by the reciprocal interaction of B- and D-neurons. He called the psychophysical correlate of the neuronal receptive field in human perception a *perceptual field*. Had numerous scientific and clinical descendants in high-ranking positions all over Germany. Editor-in-Chief: *Handbook of Sensory Physiology* (1973), Co-founder of *Experimental Brain Research*, Article on *Sensory research in historical perspective: Philosophical foundations of perception* in *Handbook of Physiology* (1984). Member of the Mainz Academy of Sciences and Literature and the German National Academy of Sciences Leopoldina. Honored with the Erb Commemorative Coin.

### **Kaplan, Ehud – 1942-2023, Rockefeller University**

Israeli neurophysiologist. Kaplan (with R. Barlow) at SUNY developed a technique for recording from single nerve fibers in the optic nerve of behaving horseshoe crabs (*Limulus polyphemus*). Worked at Rockefeller University (with R. Shapley) on parallel processing of contrast and color in the P and M pathways of the retina and LGN of monkeys and cats. His research at Mt. Sinai was about sensory maps in the visual cortex and population coding of sensory signals. Was one of the first to use multi-unit electrodes and intrinsic optical imaging and found that neurons responded more strongly to natural stimuli, such as those taken in the woods, than to laboratory stimuli. Influential publication with R. Shapley entitled *The primate retina contains two types of ganglion cells, with high and low contrast sensitivity* (1986).

### **Kuffler, Steven William – 1913-1980, Harvard University**

Highly influential, much beloved, and admired Hungarian-American neurophysiologist. One of the Fathers of modern neuroscience. Early contacts with Sir J. Eccles and B. Katz. Founded the Harvard Neurobiology Department and made numerous seminal contributions to our understanding of vision, neural coding, and the neural implementation of behavior. In a paper entitled *Discharge patterns and functional organization of mammalian retina* (1953), he described the antagonistic center-surround organization for on-center and off-center receptive fields in the cat (as follows). When recording from an optic nerve fiber, the response was vigorous for a light spot in the center of the receptive field, but much reduced for more peripheral stimuli. This suggests that the sensitivity within the receptive field center was not uniform but fell off towards the edge. For a light spot placed even further away from the center, the response was inhibited, suggesting a lateral zone that is inhibited by light. In a later paper (with H. Barlow and R. Fitzhugh), he characterized the drop of the inhibitory surround during dark adaptation as evidence for the absence of contrast enhancement at twilight. Member of the American Academy of Arts and Sciences, the US National Academy of Sciences, the Royal Society of London as a Foreign Member, and the American Philosophical Society. Book: *From Neuron to Brain* (with J. Nicholls) (1984, 2020).

### **Kulikowski, Janus Joseph – 1935-2023, Manchester Institute of Science and Technology**

Neuroscientist originally from Poland. While working in F. Campbell's laboratory in Cambridge, he published a famous paper (with D. Tolhurst) on sustained and transient mechanisms in human vision. Used psychophysics, neurophysiology, and mathematical modeling to understand how the retina and visual cortex process spatial, temporal, and chromatic stimuli. Ablated area V4, to study how the cortex enables the perception of color constancy despite substantial differences in ambient illumination. Classic paper with E. King-Smith and Carden on the existence of colour-opponent pathways. Collaborated with P. Bishop in Canberra to study the Gabor formalism of receptive field organization in a series of papers with M. Kato, and S. Marcelja.

### **Lettvin, Jerome Ysroael – 1920-2011, Massachusetts Institute of Technology**

Best known as the lead author of the paper, *What the Frog's Eye Tells the Frog's Brain* (1959), co-authored by H. Maturana, W. McCulloch, and W. Pitts. It is one of the most cited papers in neuroscience. Recording from the frog's tectum opticum, they found four types of neuronal "detectors": sustained contrast detectors, convexity or "bug perceivers," moving edge detectors, and dimming or "enemy detectors." Bug perceivers have small receptive fields and respond to short convex boundaries that move intermittently (stop and go) in the visual field. This suggests that these neurons may be selective to fly-

shaped objects, i.e., potential prey to feed on. In contrast, enemy detectors have a large receptive field and respond to the dimming of a large object, implying that they may be useful for signaling predators. These discoveries in the frog, along with H. Barlow's feature detector in the fly, marked an important step in vision research, suggesting that receptive fields may play a key role in biologically significant behavior. Enormously popular on the MIT campus and in the Cambridge area for his forceful debates against the use of LSD and the war in Vietnam.

**Levick, William Russell – 1931-2022, Australian National University**

One of Australia's most distinguished neuroscientists, making fundamental contributions to the understanding of the neural circuitry of the retina and the visual pathways. Levick and H.B. Barlow's pioneering work on directional selectivity (1965) is one of the most influential papers in visual physiology, inspiring hundreds of subsequent studies in various fields. It has been cited more than 2000 times. The 'Barlow-Levick-model' of motion detection is based on the responses of rabbit retinal ganglion cells that were stimulated by a sequence of two light flashes in neighboring locations, similar to Wertheimer's apparent motion paradigm. Barlow and Levick found that the response to the preferred motion direction of the cell was roughly equal to the sum of the two individual responses, whereas the response to the opposite (null) direction sequence was significantly reduced. Fellow of the Royal Society of London.

**Lund, Jennifer Suzanne – 1940-2025, University of Washington**

Distinguished British neuroanatomist who tried to understand cortical circuitry as related to visual function. Using retrograde neuroanatomical tracers, she provided the first schematics of functional microcircuits in the macaque primary visual cortex. Showed that feedback projections from V1 to the LGN arise from neurons in layer 6, while those to the superior colliculus and pulvinar nucleus arise from layer 5. Discovered that cortical columns, long thought to process visual information independently, were linked into a cooperative network by a system of long-range horizontal connections. She was a Fellow of the Academy of Medical Sciences and won the Krieg Cortical Discoverer Medal in 1992 for her investigations of the cerebral cortex and its connections.

**Masland, Richard Harry – 1942–2019, Harvard Medical School**

Distinguished neuroanatomist and David Cogan Professor of Ophthalmology. Studied the mammalian retina. Devised a method to keep the excised retina alive for 20 hours. Studied information processing by small neural ensembles, especially amacrine cells. His work on the cellular basis of direction-selective

light responses of ganglion cells is considered just as important as W. Reichardt's models on this topic, or the physiological findings of Barlow, Hill, and Levick. The network for directionality in the retina was only "cracked" by W. Denk and colleagues using serial electron microscopy (*Nature* 471, 183-188, 2011). In a review entitled "The Fundamental Plan of the Retina" (2001), Masland established that, in a random sample of several hundred amacrine cells, there were at least 20 distinct types (today, many more). Recipient of the Proctor Medal. Book: *We Know It When We See It: What the Neurobiology of Vision Tells Us About How We Think* (2020). Died of cancer, December 13, 2019, at the age of 77.

**Maximov, Vadim V. – 1937-2015, Institute for Information Transmission Problems, Moscow**

Russian physiologist, morphologist, and model builder. Did behavioral and electrophysiological experiments for studying color vision in monkeys, cats, dogs, birds, ground squirrels, geckos, toads, and frogs. His favorite topic was color vision. He hand-painted hundreds of paper samples and measured their reflectance by spectrophotometry until the desired reflectance was achieved. Suggested that color vision could have arisen as a mechanism for canceling the effect of the spotty illumination patterns produced by ripples on the water's surface. He further developed N. Nyberg's concept of a color solid as part of the color space occupied by the colors of all physically realizable objects. Book: *Transformation of colours under changing illumination* (in Russian, 1984), dedicated to the problem of color constancy in humans and animals. Also worked on the neurons of the visual system in fish. Editorial Board member of *Integrative Neuroscience*.

**Meynert, Theodor Hermann – 1833-1892, Universität Wien**

German-Austrian psychiatrist who made many contributions to the study of the cellular architecture of the brain and is a founder of cerebral cortex cytoarchitectonics. Showed that the optic radiation terminates in the striate area of the visual cortex (1870). Discovered the eponymous Meynert cells, layer V pyramidal cells in the calcarine sulcus. Had many famous students, including S. Freud, J. Breuer, S. Korsakoff, C. Wernicke, and P. Flechsig.

**Minkowski, Mieczyław – 1884-1972, Universität Zürich**

Polish-Swiss neurologist. Demonstrated, in 1910, a point-to-point projection of the retina onto the striate visual cortex in dogs. In 1913, he demonstrated separate laminar terminations of the left and right optic nerve fibers in the lateral geniculate nucleus.

### **Mountcastle, Vernon Benjamin – 1918-2015, Johns Hopkins University**

An eminent figure in brain research whose discovery of the columnar structure of the cerebral cortex was a turning point in investigations of the brain. In 1957, he discovered the columnar organization of the somatosensory cortex, which was subsequently confirmed for all sensory and motor functions of the cerebral cortex. He pioneered the neuroscience of perception when he recorded, in non-anesthetized animals, the firing of single neurons while monkeys were carrying out complex behavioral tasks. Additionally, in the posterior parietal cortex, he found that neurons responded to visual stimuli only if the animal attended to them. Member of the US National Academy of Sciences, recipient of the Louisa Gross Horwitz Prize, and the Albert Lasker Award for Basic Medical Research. He also received the US National Medal of Science and the NAS Award in the Neurosciences from the US National Academy of Sciences. His laboratory was famous for producing future leaders of neuroscience, including R.A. Andersen, M. Merzenich, G. Poggio, and R.v.d. Heydt. Textbook: *Medical Physiology* (1980)

### **Munk, Hermann – 1839-1912, Universität Berlin**

Found that removing parts of the occipital lobe in dogs and monkeys produced blind spots when the corresponding areas of the retina were stimulated. This suggested a topographic projection of the retina onto the cortex (1879).

### **Østerberg, Gustav – 1899–1974**

Danish histologist. Made the first cell count of rods and cones in the human retina (*Acta Ophthalmol [Suppl]* 13:6,1–102,1935). Showed that the greatest density of cones occurred in the fovea, consistent with the highest visual acuity. By comparison, the greatest density of rods is found between 10 and 20 degrees eccentricity, thus straddling the optic disk. Note, however, that the overwhelming majority of cones span the peripheral retina, thus providing the basis for color vision across the entire retina. See: Jonas, J.B., Schneider, U. & Naumann, G.O.H. Count and density of human retinal photoreceptors. *Graefe's Arch Clin Exp Ophthalmol* **230**, 505–510 (1992). <https://doi.org/10.1007/BF00181769>

### **Polyak, Stephen Lucian – 1889-1955, University of Chicago**

Born Stjepan Lucian Poljak. Most prominent visual neuroanatomist of the 20th century. Studied the functional structure of the retina and visual pathways. Epochal books: *The Retina* (1941). *The Vertebrate Visual System* (1957). H. Klüwer had promised Polyak on his deathbed to finish the work.

**Regan, David Martin – 1935-2025, York University, Toronto**

Distinguished neuroscientist and prolific speaker who contributed greatly to the understanding of motion, depth, and depth motion perception. Showed that neurons in monkeys and perceptual channels in humans are tuned to specific directions of motion in depth. An early exponent of the power of steady state visual evoked potentials for the analysis of visual processing of luminance and color. Also studied the effects of neurological disorders such as multiple sclerosis, Parkinson's disease, glaucoma, amblyopia, and cataract, as well as their effects on safety in driving, flying, and sports. Published an influential text on *Human Brain Electrophysiology: Evoked Potentials and Evoked Magnetic Fields in Science and Medicine* (1989) about how the brain responds to sight, sound, and other stimuli. Member of the Royal Netherlands Academy of Science. Received the Donald O. Hebb Award, the Proctor Medal, and the Charles F. Prentice Medal.

**Rodieck, Robert – 1937-2003, University of Washington, Seattle**

Australian neuroscientist. Worked with W. Rushton on rod-cone interaction in single receptive fields. By exchanging two spectrally distinct light spots of controlled intensity projected onto the receptive field center, they were able to change the photon catch rate for cones without changing the photon catch for the rods (the rod isolept). Conversely, they could change the photon catch for rods, while keeping the catch for cones constant (the cone isolept). In this way, they demonstrated that rod and cone dark adaptation proceeded separately after the same bleach and also showed that rod and cone signals could cancel each other. Demonstrated parallel visual processing in the primate visual system, an important step for the understanding of human vision. Books: *The Vertebrate Retina: Principles of Structure and Function* (1973) and *The First Steps in Seeing* (1998).

**Sakata, Hideo – 1934-2013, Nihon University**

Made important contributions to the role of the parietal cortex in spatial perception by recording from single units in the macaque. Found visual fixation neurons sensitive to the depth of the fixation target. Furthermore, found neurons representing visual features of a 3D object in the parietal cortex of the dorsal visual stream. Studied function of the parietal cortex related to visuomotor control of hand manipulation that required 3D information of objects. Made an important contribution to the cerebral study of visual-motor control of hand grasping, in collaboration with M. Arbib, M. Jeannerod, and G. Rizzolatti. Worked on the neural correlate of spatial navigation in a virtual environment.

**Schiller, Peter Harkai – 1931-2023, Massachusetts Institute of Technology**

Outstanding American neurophysiologist of German-Hungarian descent. Integrated the methods of psychology, neurophysiology, pharmacology, and anatomy to solve fundamental problems of vision and fixation. Identified and characterized two parallel neural pathways involved in the generation of visually guided saccadic eye movements: the superior colliculus (for foveation) and the frontal eye fields (for target selection). By administering *2-amino-4-phosphono-butyrates* to the eye, he was able to inactivate the ON-retinal pathway reversibly and demonstrate that the On- and Off-pathways remain segregated from the retina to the striate cortex. Following a selective block of the On-pathway, monkeys could no longer detect a light spot on a gray background but had no problem in detecting the appearance of a dark spot on the same background. This suggests that there exist specific neural circuitries for perceiving brightness and darkness, an idea first proposed by E. Hering and R. Jung. Schiller also proposed that individual neurons in the primate visual cortex, in addition to being feature detectors, are multifunctional and have contextual receptive fields. Charismatic opponent, formidable speaker. His many outstanding PhD students and postdoctoral fellows included M. Cynader, S. Hochstein, A. Hurlbert, V. Lamme, N. Logothetis, J. Maunsell, S. Schein, L. Squire, M. Stryker, R. Vogels, and K. Zipser. Member of the US National Academy of Sciences and the Magyar Tudományos Akadémia. Book: *Vision and the Visual System* (with E.J. Tehovnik, 2015)

**Shevelev, Igor Alexandrovich – 1932-2010, Institute of Higher Nervous Activity and Neurophysiology, Moscow**

Prominent Russian neurophysiologist who studied mechanisms of information processing in the cortex of humans and animals. Developed original concepts of spatio-temporal coding of visual information, adaptation, and neuroplasticity of receptive fields. Discovered intracortical inhibition to account for responses to X- and Y-like figures and orientation tuning in cat striate cortex. Member of the Russian Academy of Sciences.

**Sillito, Adam Murdin – 1944-2023, University College, London**

Powerful British neuroscientist. Studied the effect of pharmacological agents on neuron responses. Discovered that bicuculline abolishes or reduces orientation selectivity, direction selectivity, and size tuning of receptive fields. Bicuculline also turns some monocular cells into binocular cells. Found that many cells in the lateral geniculate nucleus receive binocular input, which he attributed to feedback pathways. Studied contextual neurons that respond to an oriented stimulus outside their classical receptive field, especially orientation discontinuities. Arranged for the move of the London Institute of Ophthalmology from Judd to Bath Street and arranged for a merger of Moorfields Eye Hospital with University College London.

**Spekreijse, Henk – 1940-2006, Universiteit van Amsterdam**

Long-term Editor-in-Chief of Vision Research (1991-2004). Researched fundamental properties of the visual system, including parallel visual pathways, face perception, attention, and the neural correlates of conscious perception. Developed non-invasive diagnostic techniques for visual disorders in young children. Introduced non-linear analysis into vision research, leading to insights into the functional organization of the visual system in mammals, especially humans, and later practical applications in diagnosing visual disorders in clinical settings. Recorded from single units visually evoked response to sinewave-modulated light (flicker) from the human and monkey cortex. Worked on fish retinae. Member of the Royal Netherlands Academy of Arts and Sciences (KNAW). Upon retirement, appointed Knight in the Order of the Netherlands Lion. Organized ARVO symposia. Died on October 20, 2006, of a fatal heart attack, at the age of 65.

**Svaetichin, Gunnar Nils Toivo – 1915-1981, University of Venezuela**

Finnish physiologist working in Caracas. Recorded, in 1953, S-potentials from horizontal cells in fish retinas. Found that electroretinograms were specifically sensitive to three different groups of wavelengths in the areas of blue, green, and red. This provided the first biological demonstration in support of the Young-Helmholtz trichromatic theory. The discovery of neural color opponency is said to rank with the most significant findings in color vision in the 20th century.

**Szentágothai, János – 1912-1994, Semmelweis University, Budapest**

Internationally renowned Hungarian neuroanatomist. Started the department of electron microscopy in brain research in Hungary (1961). Member of the Hungarian Academy of Sciences, the German National Academy of Sciences Leopoldina, American Academy of Arts and Sciences, and Académie des Sciences. Fellow of the Royal Society of London. Member of Parliament, and President of the Hungarian Academy of Sciences. Honorary Member of the American Association for Anatomy. Recipient of the Karl Spencer Lashley Award (1973), and the Kossuth Award (1950). Book: *Synaptology of the visual cortex. Visual Centers in the Brain* (1973).

**Tomita, Tsuneo – 1908-1991, Keio University**

Distinguished Japanese visual physiologist. Established that the basic mechanism of vertebrate photoreceptors' response to light is by hyperpolarization without spikes. Intracellular recordings from cone

photoreceptors provided strong evidence that trichromatic color vision starts at the retinal photoreceptor level. Received many honors, including the Proctor Award, the Japan Academy Prize, and the Ludwig von Sallmann Prize.

**Ts'o, Daniel Y. – 1956-2025, SUNY Upstate Medical University, Syracuse**

Graduate student and collaborator of Nobel laureate T. Wiesel. Developed the intrinsic imaging technique of using a CCD digital camera to map the functional connectivity and architecture of the cortical surface through optical reflectance changes. With A. Roe, he showed that the cortex is organized in a patchwork of local areas coding orientation, color, and depth. These discoveries paralleled and complemented the emergence of fMRI BOLD imaging. Together, this work helped shape the field of modern functional neural imaging.

**Van de Grind, Willem (Wim) Alexander – 1936-2024, Universiteit Utrecht**

Dutch electrical engineer, best known for his psychophysical work on human motion perception, optic flow, structure from motion, and movement aftereffects, in collaboration with J. Koenderink and A. van Doorn; also, for his research on binocular neurons in cat visual cortex, and the psychophysics of binocular vision in humans. Held positions at the University of Amsterdam, the Free University of Berlin (with O.-J. Grüsser), and Utrecht University. Humboldt Prize Winner at Freiburg University. Also studied the temporal properties, color, and motion vision of birds, and electroreception in catfish. Invited lecturer at the ECVF in Edinburgh (1993) and Perception lecturer at the ECVF in Groningen (2000). Had outstanding doctoral students. Review chapter on the temporal properties of the visual system of vertebrates in the *Handbook of Sensory Physiology* (1973).

**von Monakov, Konstantin Nikolajewitsch – 1853-1930, Universität Zürich**

Russian-Swiss neurologist. Demonstrated that the afference from the retina to the primary visual cortex is relayed through the lateral geniculate nucleus (1882). Founded the Institute for Brain Research in Zürich.

**Whitteridge, Daniel – 1912-1994, University of Edinburgh**

British physiologist. Mapped with P. Daniel (in 1961), the way the visual field is represented in the primary visual cortex of the non-human primate, with the fovea being overrepresented relative to the periphery. Introduced the term cortical magnification and demonstrated that there is a precise relationship between cortical magnification and visual acuity.

## Neuropsychology

### **Cowey, Alan – 1935-2012, University of Oxford**

British neuropsychologist with wide research interests, covering color vision, attention, visual neglect, and residual vision after brain lesions. Demonstrated that following an incomplete lesion in the primary visual cortex, macaque monkeys could still respond to stimuli in the 'blind' part of their visual field, though less accurately than non-lesioned animals. This is similar to the ability of some patients who, despite V1 lesions, can guess the location of a stimulus or the direction in which it moves, although they are not aware of it. For two patients, Cowey reported correct guesses about stimuli that they could not see. His colleague, L. Weiskrantz, in his monograph *Blindsight*, pointed out that they may have received visual input from the retina to extrastriate area V5/MT through the superior colliculus (the second visual system). Lesion studies of MT in monkeys and fMRI scans in a patient confirmed this interpretation. Further experiments with P. Stoerig seem to support the existence of blindsight, depending on whether it is based on pointing or awareness. Cowey also showed that central vision and peripheral vision are mapped onto different parts of visual areas V1 and V2. Here, the area of central vision is overrepresented relative to peripheral vision to maximize visual acuity. → Cortical magnification. Fellow of the Royal Society of London, presented the 2004 Royal Society Ferrier Lecture.

### **Flourens, Marie-Jean-Pierre – 1794-1867, Collège de France, Paris**

French physiologist, using ablation in rabbits and pigeons, demonstrated loss of vision following cortical lesions, thereby showing that the cortex is involved in vision. Member of numerous societies and academies.

### **Goldstein, Kurt – 1878-1965, Columbia University**

Internationally known German American psychiatrist. Published with A. Gelb on color perception and color amnesia in brain-injured WWI veterans. Held the William James Lecture at Harvard University (1938/1939).

### **Gratiolet, Louis Pierre – 1815-1865, University de Paris (Sorbonne)**

Did extensive research in the field of comparative anatomy, and performed important studies on human and primate brains. Introduced a demarcation of the brain's cortical surface into five lobes (frontal, temporal, parietal, occipital, and insular). Traced (in 1854) the visual radiation (*radiatio optica*) from lateral geniculate body of the thalamus to the occipital cortex. Founding Member of the Société d'Anthropologie de Paris.

**Gross, Charles Gordon – 1936-2019, Princeton University**

One of the founders of cognitive neuroscience. His discoveries, in the primate visual cortex of cells that are tuned to faces and hands, led to an entirely new field of research. This research was pivotal to the work of his student David Perret and started a cascade of biologically based computational models of recognition. Fellow of the American Academy of Arts and Sciences. Books include *Brain, Vision, Memory: Tales in the History of Neuroscience* (1998), and *A Hole in the Head: More Tales in the History of Neuroscience* (2009).

**Kuroda, Ryo – 1890-1947, Keijo Imperial University**

Studied a girl who had been blind from early cataract. Saw Y.T. first 40 days after the operation, then 5 days later, and lastly 2 months after the first interview. The main results obtained were as follows: (a) the extents of the Hering and Müller-Lyer illusions were similar to those of normally sighted children; (b) seeing perspective geometrical figures such as the Necker cube and the Mach card in depth was extremely difficult; (c) retinal rivalry and binocular stereoscopic vision could not be observed; (d) eye-hand coordination was close to the lowest level of development; (e) named the principal colors, but had no preference among colors; and (f) could not readily interpret facial expression when presented with pictures of familiar movie actresses.

**Mishkin, Mortimer – 1926-2021, National Institutes of Health, Bethesda**

Pioneer neuroscientist who researched neurobiological mechanisms of perception and memory. Contributed significantly to the understanding of the neural basis of visual perception. In the wake of G. Schneider's distinction of two visual pathways in the superior colliculus of the hamster, responsible for exploration and examination, Mishkin proposed two anatomically and functionally separate pathways in the brain of the rhesus monkey, a ventral (occipito-temporal) and a dorsal (occipito-parietal) one. Together with L. Ungerleider he showed that the first deals with color and object recognition (ventral route), whereas the second subserves spatial localization and direction of motion (dorsal route). These two streams thus encode the "what" and the "where" of an object. They receive their inputs predominantly from the parvocellular and magnocellular systems of the retina, lateral geniculate

nucleus, and visual cortex, respectively. Whereas the parvocellular system projects from striate and prestriate cortex to the inferotemporal lobe, the magnocellular system projects to the inferoparietal lobe.

### **Motokawa, Koichi – 1903-1971, Tohoku University, Sendai**

Japanese biologist and physiologist. Studied the neural mechanisms of color vision by electrically stimulating the eye after a brief flash of light at various wavelengths. Found (with K. Iwama) that the time course of the electrical excitability depends on the wavelength of the light used for stimulation. After developing new methods of electrical stimulation of the human retina, they applied it to problems of color vision and of other psychophysical phenomena, such as optical illusions, figural after-effects, stereoscopic vision, etc. This work was compiled into the monograph *Physiology of Color and Pattern Vision* (1970).

### **Nordby, Knut – 1942-2005, Oslo Universitet**

The world's most carefully studied rod monochromat. An entire series of experimental papers from the Oslo, Freiburg, and Cambridge vision laboratories reports, in detail, the properties of K.N.'s isolated rod photoreceptor system. Nordby joined O. Sacks on a trip to a Micronesian island with a high prevalence of achromatopsia, as described in their book: *The Island of the Color Blind* (1997). Autobiography: *Vision in a complete achromat: a personal account* In R. F. Hess, L. T. Sharpe & K. Nordby, *Night Vision: Basic, Clinical and Applied Aspects*. Cambridge University Press (1990) <http://www.achromatopsia.info/knut-nordbys-story/>  
Knut Nordby passed away on April 19, 2005, from Amyotrophic lateral sclerosis (Lou Gehrig's disease), at the age of 62.

### **Penfield, Wilder Graves – 1891-1976, McGill University**

Pioneering brain surgeon. First to electrically stimulate the human visual cortex (with O. Foerster, 1929) from the open skull. Founder of the Montreal Neurological Institute. Expanded brain surgery's methods and techniques, including mapping the functions of various regions of the brain, such as the cortical homunculus. Contributions on neural stimulation included hallucinations, illusions, dissociation, and déjà vu. Devoted much of his thinking to mental processes, including contemplation of whether there was any scientific basis for the existence of the human soul. Books:

- *Epilepsy and the Functional Anatomy of the Human Brain* (1951, 1954).
- *Speech and Brain Mechanisms* (with L. Roberts, 1959),
- *The Mystery of the Mind: A Critical Study of Consciousness and the Human Brain* (1975).

- Designated a National Historic Person by the government of Canada in 1988.

### **Poppelreuter, Walter – 1886-1939, Universität Bonn**

Co-founder of the fields of neuropsychology and psychotechnique. His clinical interest was in the therapy of neuropsychological dysfunctions. Published a book: *The Psychological Damage caused by Head Shot in the War of 1914/17*. Volume 1: *The Disorders of Lower and Higher Visual Performance Caused by Injuries of the Occipital Brain* (1917–1918).

### **Ruddock, Keith Harry – 1939-1996, Imperial College, London**

Welsh biophysicist and successor to W.D. Wright at Imperial College. Carried out extensive studies of color vision in relation to the effects of macular pigment in the eye. Studied visual abnormalities exhibited by clinical patients, many of whom had suffered brain damage as a result of a stroke or tumor. Contributed to studies of 'blindsight' and the mapping of the spatiotemporal properties of subcortical pathways. Collaborated with G. Svaetichin on S-potentials in the mixed rod / cone retina of teleost fish. Keith Ruddock died on 20th December 1996, at an age of 57 years, from a road traffic accident.

### **Saade-Sergent, Justine – 1950-1994, McGill University**

Canadian cognitive neuroscientist. Provided evidence for the functional neuroanatomy of face processing. Described in 1992, the fusiform face area (or FFA, N. Kanwisher) when responding to either faces or objects. Her suicide at 44 years of age included a note citing that it was due to the significant stress caused by an inquiry into research ethics violations. Three years after her death, the inquiry failed to come up with any evidence of fraud.

### **Siegel, Ralph Mitchell – 1958-2011, Rutgers University**

Neurophysiologist whose research ranged from system neurophysiology to psychophysics to computational models of visual processing. Was interested in the mechanisms underlying visual motion and spatial perception with the goal to assist people who have visual processing disorders and neurological injuries. Employed precise psychophysical methods to understand visual motion perception at the level of neuronal activity. Performed pioneering work on parietal neurons and the influence of eye position and attention on perception. His laboratory became the first to perform optical imaging of the parietal cortex in behaving non-human primates. Developed tools that enabled optical monitoring of activity from neurons in behaving animals. Book:

A Memoir (with Oliver Sacks) entitled: *Another Day in the Monkey's Brain* (2012). Ralph Siegel died at the age of 43.

### **Sperry, Roger Wolcott – 1913-1994, California Institute of Technology**

Brilliant neuropsychologist, neurobiologist, and cognitive scientist who asked whether sensory and motor actions are due to nature or nurture. Sectioned the optic nerves of salamanders and rotated the eyes by 180 degrees. The animals behaved as though they experienced the world as upside down and right-left reversed. No amount of training could change the response, and they starved next to their food. – In a famous experiment, with J. Bogen and M. Gazzaniga, he severed the corpus callosum, which connects the two hemispheres in patients, undergoing surgery for epilepsy. Neuropsychological tests led Sperry to believe that the left and right hemispheres function separately when not connected by the corpus callosum, and only the left side of the brain could articulate speech. It has been claimed that in some of the patients, "while their left hand was unbuttoning their shirt, their right hand would .... button it again." This research drew numerous follow-up studies. Today, callosotomy is rarely performed. Elected to the US National Academy of Sciences, the American Academy of Arts and Sciences, and the American Philosophical Society. Shared the Nobel Prize in Medicine/Physiology, 1981, with D. Hubel and T. Wiesel for his work with "split-brain" patients.

### **Teuber, Hans-Lukas – 1916-1977, Massachusetts Institute of Technology**

One of the world's leading authorities on the relationship between brain and behavior. Charismatic and much-beloved founder of the Department of Psychology at MIT, today's *Brain and Cognitive Sciences*, who made the MIT department a mandatory stopover point for brain scientists from all over the world. Combined brain science (neurophysiology, neuroanatomy, and neuropsychology), experimental psychology (perception and perceptuomotor coordination); and language and language learning (psycholinguistics) in his concept of three prongs. Said: "Blindness can illuminate sight; paralysis could tell us about movement; and forgetfulness can suggest directions in which the answers to the riddle of memory may be sought". Studied the effects of penetrating gunshot wounds of the brain in Korean war veterans by plotting their scotomata to find out whether their size changed in time. Applied tests to neuropsychological patients in the tradition of E. Poppelreuter and K. Goldstein. Characterized differences between the two hemispheres and their role in spatial orientation and pattern perception. Coined the term *Double Dissociation* and introduced the term *Corollary Discharge*. Wrote an influential chapter (1960) on visual perception in the *Handbook of the American Physiological Society*. Member of the US National Academy of Sciences, and the National Academy of Arts and Sciences, Recipient of the Karl Spencer Lashley Award and Kenneth Craik Award. Co-Founder of the *Journal of Neuropsychology*. Obituary, *H.L. Teuber (1916-1977)*. *Vision Research* 18

(1978). Hans-Lukas Teuber died at the age of 60 on January 4 1977 from drowning in the Virgin Islands.

### **Ungerleider, Lesley Gail – 1946-2020, National Institutes of Health, Bethesda**

Distinguished neuroscientist. Made major contributions to our understanding of the functional organization of the visual cortex in humans and nonhuman primates, using a combination of neuroanatomical, neurophysiological, neuroimaging, and behavioral methods. Following G. Schneider's observations in the hamster, she demonstrated (with M. Mishkin) that the primate visual cortex contains separate neural systems for perceiving "what" (object identity) and "where" (spatial relation). These two functionally dissociated cortical pathways, namely an occipitotemporal (ventral) pathway for the 'what' and an occipitoparietal (dorsal) pathway for the 'where' were later found in other sensory domains. This concept was also linked to the syndromes of agnosia, ataxia, and neglect in man. Spatial localization and object identification both required an intact striate cortex but were preserved after superior colliculus lesions in monkeys. William James Fellow, Member of the US National Academy of Sciences, the American Academy of Arts and Sciences, and the National Academy of Medicine; won the Grawemeyer Award.

### **Virsu, Veiju Vesa Elias – 1941-2018, University of Helsinki**

Finnish neuropsychologist. Introduced the cortical magnification factor, which decreases toward the peripheral retina to model pan-retinal psychophysical functions. Perceptive fields of retinal neurons subtend only a few arcmin in the fovea, but increase to several degrees in the periphery. A foveal hypercolumn in the cortex thus "looks" at a much smaller area than a hypercolumn in the periphery. This difference in neuronal convergence, combined with the decreasing density of retinal receptors and ganglion cells away from the fovea, is a major reason for the decrease in visual acuity towards the periphery. When retinal stimuli are chosen ("normalized") to map to the same size on the visual cortex, the fall-off of the psychophysical threshold towards the periphery disappears. For example, color can be perceived all the way to the periphery of the visual field when the targets are large enough.

### **von Senden, Marius – 1884-1966**

German. Studied the recovery of vision in sixty-five persons with congenital cataracts. Although in some cases there was considerable residual vision before the operation, progress in using postoperative perception was generally slow, laborious, and imperfect. In addition, "sighted" patients were liable to emotional "crises". More specific information on the visual experience after the operation became available from a case study by R. Gregory and

J.G. Wallace (1963). In their study, these authors emphasized the extent of crossmodal transfer of information from touch to vision, the so-called Molyneux Problem. For more on this topic, see R. Held and P. Sinha. Book: *Space and Sight, The Perception of Space and Shape in the Congenitally Blind Before and After Operation* (1960), originally in German (1932).

**Weiskrantz, Lawrence – 1926-2018, University of Oxford**

Distinguished British neuropsychologist. Discovered the phenomenon of blindsight, where a cortically (V1) blind patient, usually a hemianope, can point approximately towards a target presented within the large scotoma. Tentatively explained by the second visual system delivering visual information via the colliculus to area MT. Fellow of the Royal Society of London. Member of the US National Academy of Sciences. (See A. Cowey)

**Clinical, Perimetry, ERG, EEG**

**Adams, Anthony J. – 1940-2021, University of California, Berkeley**

Much admired Australian optometrist and visual scientist with wide-ranging research interests. Studied chromatic adaptation, color discrimination, blue cone sensitivity, spatial summation, dark adaptation, rod-cone interaction, glare recovery, and contrast sensitivity in normal, color-defective, and diseased eyes. Also worked on retinal mechanisms of lateral interaction in the goldfish retina. Involved in studies on the effects of alcohol, marijuana, and other drugs on visual, ocular, and oculomotor functions. Studied changes in vision from diabetes and issued a report entitled *Myopia, Progression, and Prevalence*, which triggered the Orinda Longitudinal Study on 900 students and was the most extensive longitudinal study of myopia ever undertaken. Served as Dean of the UC Berkeley School of Optometry. Fellow of the American Academy of Optometry.

**Arden, Geoffrey Bernard – 1930-2018, Institute of Ophthalmology, London**

British professor of ophthalmology and visual science, renowned for his extensive research in electrophysiology and retinal diseases. Developed the *Arden Index*, a standardized method for interpreting the electro-oculogram (EOG) to evaluate the health of the retinal pigment epithelium. Developed clinical tests such as the Arden Gratings to detect early signs of vision loss in conditions like glaucoma and age-related macular degeneration. Interim

Editor-in-Chief of Vision Research. Book: *Principles and Practice of Clinical Electrophysiology of Vision* (2006).

### **Aubert, Hermann Rudolph – 1826-1892, Universität Rostock**

German ophthalmologist and one of the towering figures of 19<sup>th</sup>-century physiological optics. Demonstrated with C. Foerster the fall-off of visual acuity with retinal eccentricity (1857) and studied the time course of dark adaptation. Established boundaries for color vision within the visual field. Described, in 1861, that a vertical line in a dark room appeared to be tilted in the opposite direction to the head, when the latter was inclined → the Aubert phenomenon. He also found that the velocity of a moving target was underestimated when it was tracked → the Aubert-Fleischl phenomenon. Book: *Physiology of the Retina* (1865).

### **Aulhorn, Elfriede – 1923-1991, Universität Tübingen**

First woman in Germany to hold a tenured professorship (ordinaria) in ophthalmology. Much beloved and admired for her lectures, research, organizational talent (conferences) and instrument development. Represented physiology and pathophysiology of vision as well as neuro-ophthalmology. Studied the relationship between the light sense, visual acuity, and glare; wrote (with H. Harms) on simultaneous border contrast; and the mutual influence of corresponding retinal sites in normal and disturbed binocular vision. Published numerous papers on visual field defects in glaucoma. Developed the foremost manual perimeter for static and kinetic perimetry, the adoptometer, the mesoptometer, the phase difference haploscope, and the flicker test. Made the Tübingen Eye Clinic the most innovative, research-oriented Eye Hospital in Germany. Member of the German National Academy of Sciences Leopoldina. Chapter (with H. Harms) on *Visual Perimetry. Handbook of Sensory Physiology*. Vol. VII/4 *Visual Psychophysics* (1972). Elfriede Aulhorn died of cancer on 14 March 1991, at the age of 68.

### **Bielschowsky, Alfred – 1871-1940, Dartmouth Eye Institute**

German ophthalmologist and best known strabismologist of his generation. Treated numerous soldiers who had become blind in WWI. Founded the *Deutsche Blindenanstalt* in Marburg. Authored: *Die Motilitätsstörungen der Augen* (1907) in the Handbook by A. von Graefe-Saemisch. Highly decorated by the German government. During a visit to the United States in 1934, Professor Ames recruited Bielschowsky as director of the newly founded Dartmouth Eye Institute that later also recruited H. Burian as his successor.

### **Burian, Hermann Martin – 1906-1974, University of Iowa**

Internationally renowned Austrian strabismologist, left Europe in 1936 after internships in Leipzig, Bern, and Prague, and joined the Dartmouth Eye Institute, where he succeeded A. Bielschowsky. In 1945, he moved on to Boston for private practice and, in 1951, to Iowa City, where he founded a nationally acclaimed center for the treatment of squinting children. Multilingual. Co-inventor of the Burian-Allen scleral electrode for electroretinography. Book: *Binocular Vision and Ocular Motility* with G. van Noorden (1974).

**Cornsweet, Tom Norman – 1929-2017, University of California, Irvine**

Ingenious and versatile experimentalist in vision and ophthalmology. Trained under L. Riggs at Brown University, before he became affiliated with Yale U., UC Berkeley, Stanford U., Baylor College of Medicine, and UC Irvine. Is best known for his pioneering work in visual perception, e.g., the Craik-O'Brien-Cornsweet illusion, and the invention of numerous ophthalmic instruments such as the Stanford eye tracker (with H. Crane), the highly successful autorefractor, and others. He held 40 patents and was the author of the frequently-cited textbook: *Visual Perception* (1970).

**Donders, Frans Cornelis – 1818-1889, Rijksuniversiteit Utrecht**

One of the founders of modern ophthalmoscopy, together with H. von Helmholtz and A. von Graefe. Studied the rotation of the eye in the presence of head tilts. Published the influential book *On the Anomalies of Accommodation and Refraction of the Eye* (1864). Founded the first eye hospital in the Netherlands. Numerous memberships in academic societies.

**Duke-Elder, William Stewart, Sir – 1898-1978, London Institute of Ophthalmology**

Most highly respected ophthalmologist of his time. Best known for his 7-volume *Textbook of Ophthalmology* (1954) and his monumental 15-volume *System of Ophthalmology*. Served for many years as editor of the *British Journal of Ophthalmology and Ophthalmic Literature*. Instrumental in the formation and research direction of the Institute of Ophthalmology, now part of the University College London. Knighted in 1933 and upgraded to the rank of Knight Grand Cross of the Royal Victorian Order (GCVO) in 1958. Served as Surgeon-Oculist to King Edward VIII, George VI, and Queen Elizabeth II. Awarded the 1957 Lister Medal for his contributions to surgical science, and the 1961 Proctor Medal of ARVO. The International Duke Elder Medal is named in his honor.

**Fahle, Manfred – 1950-2020, Universität Bremen**

Conducted research into hyperacuity and perceptual learning, using psychophysics, EEG, eye-tracking, and fMRI. Hyperacuity implies that the retina can resolve detail finer than its photoreceptor grain, e.g., a fraction of the inter-cone distance. A study by Westheimer revealed that the threshold for depth discrimination can be improved by repeated stimulus presentation, resulting in hyperacuity from learning. Fahle also did clinical vision studies and organized ECVF 1995. Awarded the Max-Planck-Research Prize with T. Poggio. Book: *Perceptual Learning* (2002). Manfred Fahle died of cancer on February 26 2020 at the age of 69.

**Flom, Merton Clyde – 1926-2010, University of California, Berkeley**

Clinician, vision scientist, and visionary optometrist. Made significant contributions toward research in binocular vision and space perception. Studied amblyopia and strabismus. Dean of Optometry at UC Berkeley, and President of the American Academy of Optometry.

**Fry, Glenn Ansel – 1908-1996, Ohio State University**

One of the most respected optometrists of his time. The Glenn A. Fry Medal is named in his honor. Conducted extensive experimental analyses on the accommodation/ convergence linkage. Developed new methods for measuring retinal image blur, which is critical for understanding visual acuity and lens design. Quantified the impact of intraocular stray light on contrast sensitivity and vision quality. Explored the effects of intermittent light patterns on color sensation. Studied how the effects of vertical divergence and image size differences affect binocular stereopsis. In 1935, Fry established a graduate course in physiological optics and in 1937 a School of Optometry at Ohio State University. In 1949, he became co-director of the Institute of Research in Vision at the University. Received the Charles F. Prentice Medal and Edgar D. Tillyer Award.

**Goldmann, Hans – 1899-1991, Universität Bern**

One of the most respected figures in 20th-century ophthalmology. Developed the Haag-Streit slit-lamp and the ubiquitous Goldmann perimeter among several other clinical instruments for the evaluation of the eye. These inventions had a world-wide impact on modern-day ophthalmic practice. Received the Gonin Medal of the International Council of Ophthalmology.

**Harms, Heinrich – 1908-2003, Universität Tübingen**

Distinguished German ophthalmologist. Introduced the microscope for ophthalmic surgery, which became the gold standard for ophthalmologists worldwide. Applied methods from sensory physiology to visual field examination (e.g., glaucoma scotoma). Helped develop the Tübingen perimeter for quantitative perimetry, using dynamic and static targets. Tested operators of traffic vehicles under mesopic and scotopic conditions. Close collaboration with E. Aulhorn. Received the von Graefe Prize, Member of the German National Academy of Sciences Leopoldina.

**Köllner, Hans – 1881-1924, Universität Berlin**

German ophthalmologist. Köllner's rule: Outer retinal diseases result in blue-yellow color defects, whereas diseases of the inner retina, optic nerve, visual pathways, and visual cortex result in red-green defects. Book: *Die Störungen des Farbennsinnes* (1912); and *Die Störungen des Farbennsinnes ihre klinische Bedeutung und ihre Diagnose* (1912).

**Landolt, Edmund Jacques Rodolphe – 1846-1926, Laboratoire d'Ophthalmologie, Paris**

Swiss ophthalmologist. Developed the Landolt C as the standard optotype for the examination of visual acuity. It consists of a ring that has a gap (opening) in one of 8 locations. The Landolt C is superior to the Snellen letters for use in alphabetic patients and children.

**Laskowski, Romuald – 1926-2013, University of British Columbia**

Originally from Poland. Covered the design and evaluation of color vision tests, the effect of aging on color perception, and the study of acquired color vision deficiencies. Established the link between changes in color vision and the onset of diabetic retinopathy. His double paper in the *British Journal of Industrial Medicine* (1969) is a classic. He was the first to undertake a detailed colorimetric analysis of pseudoisochromatic plates, such as the Ishihara. Founding Member of the IRGCVD.

**Marg, Elwin – 1918-2010, University of California, Berkeley**

Physiological optometrist. Co-developed with R. Mackay, the Mackay-Marg Tonometer for measuring intraocular pressure, which did not require an anesthetic. He also described and named the electrooculogram as a technique for measuring the resting potential of the retina in the human eye. Attempted to record and plot receptive fields from a human subject. Received the Charles F. Prentice Medal.

**Mariotte, Edme (de Chazeuil) – 1620-1684, Académie des Sciences, Paris**

French physicist. Discovered the blind spot (1681) and wrote on numerous physical and optical phenomena. Founding Member of the *Académie Royale des Sciences*.

**Pickford, Ralph William – 1903-1986, University of Glasgow**

English psychologist. Worked on acquired color vision changes in glaucoma. Developed the Pickford Anomaloscope for diagnosing color deficiencies.

**Purkinje, Jan Evangelista – 1787-1869, Karls-Universität Prag**

Eminent Czech scientist and founder of experimental sensory physiology. Described (in 1819 and 1825) optokinetic nystagmus, entopic visualization of retinal blood vessels (Purkinje tree), the blue arcs of the retina, the shift in brightness from red to green and blue during dark adaptation (Purkinje shift), the reflections from the anterior and posterior surfaces of the cornea and lens (Purkinje images), the negative afterimage (Purkinje afterimage), and motion aftereffects. Member of the German National Academy of Sciences Leopoldina and 37 scientific societies. Dissertation: *Beiträge zur Kenntniss des Sehens in subjectiver Hinsicht* (1819).

**Riggs, Lorrin Andrews – 1912-2008, Brown University**

His work on electroretinography with an improved electrode triggered many clinical studies into eye diseases, such as retinitis pigmentosa and age-related macular degeneration.

**Ripps, Harris – 1927-2014, University of Illinois at Chicago**

Engaging retinal physiologist who made many contributions to the understanding of retinal processing and metabolism in a range of species. He also explored the biophysical mechanisms of blinding eye diseases such as diabetic retinopathy and retinitis pigmentosa. Book: *Night Blindness Revisited: From Man to Molecule* (1982). Recipient of the Proctor Award.

**Schober, Herbert – 1905-1975, Universität München**

Renowned Austrian-German physicist and eye doctor interested in physical optics. Studied human vision under artificial lighting, with a focus on night myopia and glare. Measured the resolution of optical instruments, the

reflection and polarization properties of road surfaces, and the visibility of visual signs. Invented a dark adaptometer for the study of twilight, and established the Landolt ring as a standard visual acuity test. Investigated binocular vision and chromatic aberration of the human eye and developed an examination method that is used in strabismology for the testing of fusion, the Schober test. Visiting professorships in the United States, Australia, India, Malaysia, and Japan. Book: *Das Sehen, Seeing* (2 vols, 1957).

**Steinbach, Martin Jeffrey – 1941-2017, York University, Toronto**

American vision researcher working in Canada. Studied eye movements, eye muscle proprioception, spatial and motion perception, stereoscopic vision, central vision loss, strabismus, and visual illusions. Demonstrated eye movements in the barn owl. Demonstrated (in his dissertation) smooth pursuit movement to a finger moving underneath the tabletop. Found lowered contrast thresholds in the partner eye after monocular enucleation. Also examined visual direction and egocentric location in enucleated and strabismic children and adults. Studied central vision loss produced by age-related macular degeneration and developed effective techniques to improve reading in the presence of partial loss of foveal acuity. Founding Member of the Centre for Vision Research (CVR), York University. Had a great impact on eye research and vision health care in Canada. Recipient of the Carl Kupfer Award.

**van der Tweel, Louis Henk – 1915-1997, Universiteit van Amsterdam**

Influential Dutch physicist known for his great hospitality. Proposed systems analysis of vision. Studied the influence of a surrounding field on the frequency response for sinewave-modulated light. Applied the frequency analysis of sinusoidally modulated light to analyze the electroretinogram (ERG) and the electroencephalogram (EEG). President of the International ERG-Society.

**van Noorden, Gunter Klaus – 1928-2017, Baylor College and University of Texas, Houston**

Eminent German American researcher and surgeon in the field of pediatric strabismus and the neurophysiology of amblyopia in primates. Published (posthumously) H. Burian's book *Binocular Vision and Ocular Motility* (1974) and several editions of *Binocular Vision and Ocular Motility. Theory and Management of Strabismus*. Numerous honors.

**Verriest, Guy – 1927-1988, University Ghent**

Belgian ophthalmologist. Worked on color vision deficiencies, spatial summation, disability glare, equivalent veiling luminance, visual field defects, and color vision tests in children. Started the International Research Group for Color Vision Deficiencies (IRGCVD) in 1971, since 1991 International Color Vision Society, whose Verriest Medal is named in his honor.

**von Graefe, Friedrich Wilhelm Ernst Albrecht – 1828-1870, Universität Berlin**

German ophthalmologist of great fame. Founded (in 1856) ophthalmology in Germany as an independent academic discipline and founded the Deutsche Ophthalmologische Gesellschaft in 1863. Introduced clinical perimetry. Member of the German National Academy of Sciences Leopoldina, Foreign member of the Royal Swedish Academy of Sciences.

**von Helmholtz, Hermann Ludwig Ferdinand – 1821-1894, Universität Heidelberg**

Eminent physiologist and physicist. One of the most outstanding scientists of the 19<sup>th</sup> century across many disciplines. Founded the field of neurophysiology by measuring the speed of conduction of the nerve impulse in his own forearm while an army physician on the eastern front in 1850. Invented the ophthalmoscope (*Augenspiegel*, 1850). Formulated the Trichromatic Color Theory (1850), according to which human color vision can be explained by the mixture of three primaries of appropriate hue, saturation, and brightness. This theory is based on earlier work of Thomas Young and Grassmann and has received support by the discovery of three kinds of retinal receptors (cones), which are sensitive to long, medium, and short wavelengths. Helmholtz also analyzed the form of the vertical horopter, or null-point of binocular disparity, and determined its backward slant (1909), explained accommodation (1856), and measured stereoscopic acuity (1865). Famous quote: "Now it is not too much to say that if an optician wanted to sell me an instrument which had all these defects, I should think myself quite justified in blaming his carelessness in the strongest terms and giving him back his instrument. Of course, I shall not do this with my eyes." Member of the American Academy of Arts and Sciences and the US National Academy of Sciences. Books: *Handbuch der Physiologischen Optik*, 3 vols. (1856, 1860, 1866). The most important work ever produced in the field of physiological optics. Volumes I and II discuss the dioptrics of the eye and the sensations of vision; Volume III examines the perceptions of vision (with extensive supplementary matter by Nagel, Gullstrand, and von Kries). Third edition: 1909, 1911, 1910.

**von Hess, Carl Ludwig Adolf – 1863-1923, Universität München**

German ophthalmologist. Studied color vision, color blindness, simultaneous contrast, afterimages, and light and dark adaptation. The Hess afterimage, following the Hering and Purkinje afterimages, bears his name. Studied light and color vision in vertebrates and invertebrates.

**Wallman, Joshua – 1943-2012, City College of New York**

Neurobiologist Wallman's work spanned multiple systems, species, and topics. His largest contribution was the investigation of myopia and emmetropization in animal models. He also worked on the oculomotor system, saccadic adaptation, and the psychophysics of visual attention. His myopia work incorporated a wide range of ideas, from circadian rhythms to optics and from chromatic aberration to genetics and molecular biology. One major discovery in his myopia research is that the choroid is part of the emmetropization system. It can thicken or thin, pushing the retina toward or away from the cornea, to compensate for defocus. Recipient of the Jonas Friedenwald Award. Joshua Wallman died on March 3, 2012, at the age of 68.

**Walls, Gordon Lynn – 1905-1962, University of California, Berkeley**

Distinguished professor of physiological optics and optometry. Described a diversity of cone cells in the animal world and suggested that the cone cell evolved from an early rod cell. Described the Nocturnal Bottleneck hypothesis, according to which placental mammals were mainly nocturnal through most of their evolution. Chapter in *The Eye in Evolution* (vol. 1) in Duke-Elder's *System of Ophthalmology*. Book: *The Vertebrate Eye and its Adaptive Radiation* (1943), a classic on eye physiology and the evolution of the eye across the full range of species.

**Weale, Robert Alexander – 1922-2013, London Institute of Ophthalmology**

Ophthalmic vision scientist originally from Czechia. Published on the spectral sensitivity of the human retina with age, the effect of light scatter of the lens, and the anatomy of ocular optics. Developed fundus reflection densitometry to measure human cone photopigments in the living eye. Also measured changes of absorption in extracted lenses and in living eyes, using Purkinje images. Modelled age-related changes in color vision. Books:

- *The Eye and Its Function* (1960)
- *The Aging Eye* (1963)
- *From Sight to Light* (1967)
- *A Biology of the Eye – Development, Growth, Age* (1982)
- *The Senescence of Human Vision* (1992).

## Comparative Vision Studies

### **Casagrande, Vivien Alice – 1942-2017, Vanderbilt University**

Employed a comparative approach to study the evolution, development, function, and plasticity of visual areas in the brain in monkeys, galagos, tree shrews, and ferrets. Applied anatomical, electrophysiological, and/or behavioral techniques, adding optical imaging and multi-electrode recordings. Discovered the koniocellular or “k-cell” pathway – a third visual pathway from LGN to cortex in primates. Studied the electrophysiological response properties and anatomical connections of visual neurons in the retina, thalamus, and cortex, and conducted studies of the effect of experimentally induced myopia on the central visual system. Superb and supportive mentor to many graduate and post-doctoral students.

### **Crescitelli, Frederick Nicholas – 1909-1992, University of California, Los Angeles**

International scholar on the physiology of the eye. Worked on the physiology and biochemistry of vision and color vision. Extracted and examined with J. Dartnall, the human visual pigment, rhodopsin. Established the properties of many different visual pigments in various fishes, reptiles, and rodents and related them to the operation of the eyes in these organisms.

### **Dotz, Eberhard – 1923-1994, Max-Planck-Institut, Bad Nauheim**

Studied retinal functions of the salamander with P. Gouras. Discovered the sensitivity of the pineal gland to light. Worked on practical applications of electro-ophthalmology in patients. Organized ECVF 1986, with C.R. Cavonius.

### **Frost, Barrie James – 1938-2018, Kingston, Ontario**

New Zealand-born Canadian psychologist and neuroscientist. Explained anomalous contours and anisotropic visual acuity in humans and birds in terms of visual ecology. Published, with J.I. Nelson, a paper on orientation-selective inhibition from beyond the classic visual receptive field (1978). This paper was the first of its kind reporting input from outside the classically defined receptive field before contextual responses became widely known. He also studied the mechanism of migration in birds and butterflies, and the encoding of luminance, color, motion, and time-to-collision of looming stimuli in the nucleus rotundus of pigeons.

**Govardovskii, Viktor Ivanovich – 1939-2020, Sechenov Institute of Evolutionary Physiology, St. Petersburg**

Prominent in the field of comparative color vision. Studied the Cottoid fish in Lake Baikal and the Lamprey in the Neva River. Made microspectrophotometric measurements of rod and cone spectral sensitivities.

**Horridge, George Adrian – 1927-2024, Australian National University**

Pre-eminent, British-born expert in the field of comparative physiology of vision, working in Australia. Founded the Research School of Biological Sciences and the Centre for Excellence in Vision Science. Investigated (with I. Meinertzhagen) the neural connections of insect photoreceptors and (with A. Snyder) light guides in insect eyes. Initiated a program on optic flow in insect vision (with M. Srinivasan). Showed that bees detect simple features, not shapes. Worked on insect photoreceptor optics, crab perception of the sun's movement, and crab eye movements. Fellow of the Royal Society of London and the Australian Academy of Science. Of 50 PhD students, half became professors, and 8 from his group are Fellows of the Royal Society of London. Books: *Nervous Systems of Invertebrates* (1965) (with T.H. Bullock) and *What Does the Honeybee See?* (2009).

**Ingle, David Joyce – 1934-2006, Massachusetts Institute of Technology**

Tested color constancy in goldfish with a Mondrian pattern under conditions used by E. Land in human observers. Goldfish were trained to approach a particular color within a richly colored Mondrian background. They retained the ability to swim toward that color even when the spectral illuminant was radically changed. Discounting the illuminant thus seems to hold for goldfish as well as for humans. Died from multiple sclerosis on January 14, 2006, at the age of 71.

**Ittelson, William H. – 1920-2017, University of Arizona**

Considered the founder of environmental psychology. Addressed two fundamental questions: "What is the nature of environmental perception?" and "What is the relationship between perceived environmental change and environmental action?" The questions are approached by analyzing the dimensions of environmental experience into four major categories: the environment as an external object, as the representation of self, as the embodiment of value, and as an arena for action. Books: *The Ames Demonstrations in Perception* (1952), *Visual Space Perception* (1960), and *Perceptual Changes in Psychopathology* (with S.B. Kutash, 1961).

**Jacobs, Gerald Haskins – 1934-2025, University of California, Santa Barbara**

Psychologist. Investigated the biological bases of mammalian vision using behavioral, electrophysiological, and genetic tools.

**Land, Michael Francis – 1942-2020, University of Sussex**

British neurobiologist. Studied animal and human vision, especially the optics of the eyes of marine animals, including scallops, shrimps, and deep-water crustaceans. Also studied visual behavior in spiders and insects, particularly during pursuit. Developed, with A. Snyder, the ophthalmoscopic technique of imaging individual photoreceptors in the living vertebrate retina. Studied how spiders and flies use eye and body movements to track, and intercept moving targets and applied similar principles to human visuo-motor behavior. Described how eye movements are tailored top-down to look at critical locations a fraction of a second before each action and suggested how behaviour and awareness are anchored to an internal representation that incorporates egocentric and allocentric frames of reference. Fellow of the Royal Society of London and recipient of the Fink Medal of the Zoological Society of London, and the Alcon Prize. Books:

- *Animal Eyes* (with D. Nilsson (2012)
- *Looking and Acting: Vision and Eye Movements in Natural Behaviour* (2009)
- *The Eye: A Very Short Introduction* (2014)
- *Eyes to See: The Astonishing Variety of Vision in Nature* (2019)

**Müller, Johannes Peter – 1801-1858, Universität Berlin**

Outstanding German physiologist of the 19<sup>th</sup> century. Formulated the *Law of specific nerve energies*. Proposed, in 1826, an explanation of the optics of compound eyes (also see S. Exner). Member of the German National Academy of Sciences Leopoldina, and the American Academy of Arts and Sciences. Recipient of the Copley Medal of the Royal Society of London. Books: *Handbuch der Physiologie* (1833, 1840).

**Pettigrew, John Douglas – 1943-2019, University of Queensland**

Comparative neuroscientist. Tackled, with P.O. Bishop, the neurobiological basis of stereopsis by describing neurons sensitive to binocular disparity. Subsequently studied these neurons, with C. Blakemore and H.B. Barlow, at UC Berkeley. Did ground-breaking work on the physiology of binocular vision and the slant of the horopter in a variety of animals, including cats and owls. Studied a variety of different

birds and mammals with modern neuronal tracing techniques to unravel principles of brain organization. Fellow of the Royal Society of London.

**Schwab, Ivan Roy – 1948-2025, University of California, Davis**

Renowned ophthalmologist interested in the visual system of maritime animals, spiders, birds, and mammals. Won the Ig Nobel prize (Ornithology) for his paper on the effect of wood pecking on the retina. Book: *Evolution's Witness: How Eyes Evolved* (2012).

**Sutherland, Stuart – 1927-1998, University of Sussex**

Well-known for his work in pattern recognition and shape discrimination in rat and octopus. Book: *The Psychology of Vision* (1980).

**Varjú, Dezső – 1932-2013, Universität Tübingen**

Hungarian physicist with an interest in biological cybernetics and neuroethology. Worked on the mechanisms of motion vision in animals, the human pupil response, and the control of eye movements. Studied the optomotor response of flour beetles, shore crabs, pond snails, houseflies, stingless bees, waterstriders, and hawkmoths. Textbook: *Systems Theory for Biologists* (in German, 1977); *Seeing with the Ears and Hearing with the Legs* (in German, 1998); *Polarized Light and Animal Vision* (with G. Horváth, 2003).

**Vassilev, Angel Georgiev – 1935-2021, Institute of Neurobiology, Sofia**

Bulgarian neurobiologist. Studied the latency of visual mechanisms responding to low and high spatial frequency, using both reaction time and visual evoked potential methods. His works in this area received hundreds of citations and had a significant impact on our understanding of the temporal dynamics in visual perception. His work also advanced our knowledge of the spatial characteristics of the S-cone pathway. It made significant contributions to contrast sensitivity, reaction time, and flicker perimetry. Organized the ECVF 1987 in Varna, affording many young scientists in East Block Bulgaria their first opportunity to meet vision scientists from Western Europe and beyond.

**Vogt, Klaus – 1945-2008, Universität Freiburg**

Comparative neurobiologist. Discovered that image formation in the facet eye of the crayfish is achieved by a lattice with a 90-degree angle between the ommatidial walls, instead of the 60-degree hexagonal lattice of insect eyes.

Another major discovery by Vogt is the new photopigment, 3-hydroxy-retinal, in fly eyes.

**von Frisch, Karl Ritter – 1886-1982, Universität München**

Austrian zoologist and ethologist of great renown. Studied color discrimination in the honey bee. Showed that the color perception of bees is comparable to that of humans but shifted away from red to ultraviolet. Bees can distinguish white, yellow, blue, and purple but cannot distinguish red from black. Color pigments that reflect UV expand the bee color spectrum by two. Also demonstrated that fish can see colors. Founded *Zeitschrift für vergleichende Physiologie (Journal of Comparative Physiology)*. Member of the German National Academy of Sciences Leopoldina; of the Academy of Sciences, Göttingen; Royal Dutch Academy of Sciences; and American Academy of Arts and Sciences; Recipient of the order Pour le Mérite für Wissenschaften und Künste; Nobel Prize in Medicine/Physiology, 1973 (with K. Lorenz and N. Tinbergen).

**Yager, Dean – unk-2009, State University of New York**

Studied photopic and scotopic spectral sensitivity in the goldfish for different conditions of adaptation and saturation discrimination. Died early from West Nile Virus.

**Zanforlin, Mario – 1934-2016, Università degli Studi di Padova (Padua)**

Italian comparative and perceptual psychologist. Provided evidence that domestic chicks can perceive illusory contours (e.g., in the Kanizsa triangle), studied stereopsis in humans, and developed a mathematical theory to explain stereokinetic phenomena (such as described by C. Musatti) based on a minimum principle (minimization of velocities).

## Models

**Craik, Kenneth James William – 1914-1945, University of Cambridge**

Scottish psychologist who lost his eyesight, hundred years after Plateau, from gazing directly into the sun. Paper on dark adaptation with M. Vernon. Book: *The Nature of Psychology: A Selection of Papers, Essays and Other Writings by Kenneth J. W. Craik* (ed. S. Sherwood. 1947). Kenneth Craik died from a

road accident on the evening of V.E.-Day at the age of 31. The Kenneth Craik Club is named in his tribute.

**Dobson, Vernon George – 1944-1992, University of Oxford**

British psychologist. Promoted inhibition as important for establishing cortical receptive field selectivity during visual development. Demonstrated how inhibitory networks are more efficient than excitatory ones for pattern recognition and learning, attention, and psychophysical performance. Patented microchip designs for AI pattern analysis. Vernon Dobson tragically drowned on the last day of the Pisa ECVF.

**Knill, David Carl – 1960-2014, University Rochester**

Leader in the application of Bayesian statistics to the study of perception. His work focused on the importance of prior knowledge in visual perception and how humans use vision to guide physical actions. Studied probabilistic modeling, spatial vision, active sensing, and multisensory perception. Book: *Perception as Bayesian Inference* (with W. Richards) (2012). David Knill died on October 6 2014 at the age of 53.

**Mach, Ernst Waldfried Josef Wenzel – 1838-1916, Universität Wien**

Highly influential Austrian physicist, philosopher, and sensory psychologist, using the tools of mathematics to explain visual perception. Best known for his study (in 1865) of "Mach bands" perceived on a staircase of uniform luminance steps, and of simultaneous contrast at borders and edges. Proposed that each region of the retina interacts with neighboring regions in the visual field through reciprocal inhibition in the retina ("Wechselwirkung der Sehfeldstellen"). Direct evidence for this idea came from studies of the neural circuitry of the horseshoe crab retina, carried out by H. Hartline and F. Ratliff (1954) and Ratliff (1965). Mach's theory was one of the first attempts to link perception and psychophysics to physiology. He influenced C. von Ehrenfels and helped bring Gestalt theory into existence (e.g., Mach square). Books: *Über die Wirkung der räumlichen Vertheilung des Lichtreizes auf die Netzhaut* (1885), and *Die Analyse der Empfindungen* (1886), transl. by L. Hurvich and D. Jameson as *Outlines of a Theory of the Light Sense*. Member of the German National Academy of Sciences Leopoldina and Academy of Sciences, Göttingen.

**Marr, David Courtenay – 1945-1980, Massachusetts Institute of Technology**

Highly influential British neurobiologist, physiologist, and computational neuroscientist. Integrated results from psychology, artificial intelligence, and

neurophysiology into a new model of visual processing. Distinguished the computational level, the algorithmic level, and the implementational level. His three stages of vision include: A *primal sketch* of the scene, based on feature extraction of fundamental components of the scene, including edges, and regions; a *2.5D sketch* of the scene, including textures, shades, stereopsis, optic flow, and motion parallax; and a *3D model*, where the scene is visualized in a continuous, 3-dimensional map. Book: *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information* (1982, 2010). David Marr died from leukemia on 17 November 1980 at the age of 35.

### **Raman, Chandrasekhara Venkata, Sir – 1888-1970, University of Calcutta**

Discovered (with his student K.S. Krishnan) that, when light traverses a transparent material, the deflected light changes its wavelength. This phenomenon was subsequently termed Raman scattering. He also worked on the role of the retina in the perception of light and colour.

### **Ratliff, Floyd – 1919-1999, Rockefeller University**

Received his Ph.D. at Brown University under L. Riggs, where he worked on stabilized retinal images. To explain visual perception in terms of fundamental neural mechanisms, he did experiments with H. Hartline to quantify the lateral inhibitory effects in the visual system of the horseshoe crab (*Limulus*). That work led to the formulation of equations, which enabled one to predict the steady-state response of any neuron in the *Limulus* eye, based upon the distribution of light falling on that neuron's ommatidium and its neighbors. First quantitative description of information processing in the visual nervous system. Discovered disinhibition. Demonstrated how neural networks in the retina can explain phenomena of brightness and contrast. His laboratory was the first to use a general-purpose digital computer for online real-time recording of neuronal responses. Received the Warren Medal, the Edgar D. Tillyer Award, and the PISART Vision Award. Books:

- *Mach Bands: Quantitative Studies of Neural Networks in the Retina* (1965), in the tradition of Ernst Mach;
- *Studies on Excitation and Inhibition in the Retina* (1975), a compilation of the key publications at Rockefeller;
- *Paul Signac and Color in Neo-Impressionism* (1992), concepts from visual science and visual art.

### **Richards, Whitman Albin – 1932-2016, Massachusetts Institute of Technology**

Marr-inspired principal investigator in the MIT Computer Science and Artificial Intelligence Laboratory. Important paper on the fortification illusions of migraines in *Scientific American*, 1971, **224**, 88–96. Studied perception as a

complex system of semi-autonomous modules. Focused on understanding the minimal conditions that should be satisfied for a vision system "to work." Computational studies that met Marr's criteria. Asked what it means for a machine to perceive. Invented a new scaling technique, "Trajectory Mapping", which overcomes some of the limitations of traditional multi-dimensional scaling methods, and allows one to explore the "paths" that link elements in conceptual spaces. Books: *Perception as Bayesian inference* (with D. Knill, eds, 1996); *Natural computation* (ed., 1988); *Image understanding*. (with S. Ullman, eds., 1984).

### **Rosenfeld, Azriel – 1931-2004, University of Maryland**

Leading computer image analysis researcher, with many fundamental and pioneering contributions to nearly every area of the field, including writing the first textbook, *Picture Processing by Computer* (1969). Founding editor of the journal *Computer Graphics and Image Processing* (1972). Extensive research on digital image analysis (specifically on digital geometry and digital topology). His early studies on the accurate measurement of statistical features of digital images later found widespread applications in industry and are now integrated into many defense electronics systems (target recognition and guidance systems), remote sensing systems, and biomedical image analysis systems for automated diagnostic procedures and medical research.

### **Stark, Lawrence Walter – 1926-2004, University of California, Berkeley**

Recognized authority in the field of engineering analysis to characterize neurological systems. Best known for his research on the control of eye movements. Pioneered the application of Control Theory to neurological systems with his study of the pupillary light reflex in terms of a linear control system. He also developed the scan path theory of eye movements by studying the way people view the world. Analyzed the vast number of eye movements people make and noticed specific sequences in how they glimpsed at a room, face, or other scene. Suggested that those sequences provide clues to the importance of pictures generated by the brain. Books: *The Artistic Brain Beyond the Eye* (with W. Zangemeister, 2007). And *Presbyopia Research: From Molecular Biology to Visual Adaptation* (with G. Obrecht, eds 2010).

### **Yellott, John Ingle “Jack” – 1938-2019, University of California, Irvine**

Focused on mathematical models of human information processing. Worked on photosensitivity sampling, texture statistics, image processing, metacontrast masking, reaction time, and ranking. Attempted to correct printed text for ocular blur and demonstrated that after correcting these distortions, the legibility of defocused text was greatly improved.

## Applied & Machine Vision

### **Ballard, Dana Harry – 1946-2022, University of Texas, Austin**

Did research on artificial intelligence, human cognition and perception, with an emphasis on the human visual system. Proponent of active vision techniques for computer vision systems. Popularized the use of the generalized Hough transform in computer vision. Helped spark the rise of predictive coding as an influential framework for thinking about the brain and vision (1999, with R. Rao). Books: *Computer Vision* (with C. M. Brown, 1982); *An Introduction to Natural Computation* (1997); and *Brain Computation as Hierarchical Abstraction* (2015), a multilevel approach to understanding neural computation.

### **Bonds, Alfred Bryan III – 1945-2022, Vanderbilt University**

Focused on electrical engineering, computer engineering, and biomedical engineering to improve the understanding of information processing in the visual cortex. Recognized for his work on spatial filtering, contrast processing, and communication within organized, multicellular structures.

### **McConkie, George Wilson IV – 1946-2021, University of Illinois**

Pioneered the use of several eye-movement measures and paradigms that are now widely used in studies of reading, scene perception, and visual search. Helped develop the gaze-contingent methodology that revolutionized our understanding of the processes of reading. Showed that the theory of the visual integrative buffer could not explain perceptual stability across fixations. Introduced the concept of change blindness (with C. Currie, 1996). Worked on the Saccade Target Theory of perceptual stability across saccades.

### **Menendez, Arthur R. – 1953-1992, Armstrong Laboratory, Brooks Air Force Base, Texas**

Studied vision and its application to problems in aviation, laser safety, and aircrew vision. Advanced our knowledge of the visual response to intense light, particularly the effects of light adaptation on target detection and recognition, and the adaptation of pilots to sudden changes in ambient luminance. Felt strongly that computational models of light adaptation and spatial vision could be invaluable tools for addressing applied problems in

aviation, medicine, and defense. Disappeared while scuba diving off the Dutch Antilles on July 5, 1992.

**Prazdny, Kvetoslav "Slava" – 1948-1987, Stanford University**

Czech. An internationally recognized expert on human and machine perception, including stereo vision, image processing, robotics, adaptive neural networks, and psychophysics. His work on transparent random-dot stereograms challenged widely held theories of stereopsis. Influential articles include *The interpretation of a moving retinal image* (1980), and *Detection of binocular disparities* (1987). Kvetoslav Prazdny died in a hang-gliding accident, Saturday, September 19th, 1987, in the California mountains.

**Sullivan, Geoff – 1944-1996, University of Reading (UK)**

Worked with intelligent systems, image processing, and computer vision. Founding Member of the British Machine Vision Association (BMVA). Work on model-based vision influenced the development of the algorithms used in recognizing objects in natural scenes. Helped formulate the Integrated Machine Vision programme. Publications (with K. Baker) include *Model-based vehicle detection and classification using orthographic approximations* (1997), and *Model-based localization and recognition of road vehicles* (1998).

**Wilding, Ludwig – 1927-2010, Kunsthochschule Hamburg**

German painter and representative of Kinetic art and Op-art. Used optical line interference patterns, or moires, to elicit enhanced perceptual experiences of self-generated apparent motion and vivid stereoscopic depth. Also exhibited anamorphoses. Had close ties to Freiburg psychologists and neurophysiologists working in the field of visual perception. Exhibited at ECVPs in Marburg (1978), Bad Nauheim (1986), and Badenweiler (1986).

## **Vision from Antiquity to the 19th Century**

**Aristotle**, 384-322 BC

**Euclid**, -300 BC

**Lucretius, Titus Carius**, 99-55 BC

**Ibn al-Haitham**, 965-1040

**Bacon, Roger**, ~1219-`1292

**Aquinas, Thomas**, 1225-1274

**Alberti, Leon Battista**, 1404-1472

**Leonardo da Vinci**, 1452-1519

**Aguilonius, Franciscus**, 1567-1617

**Descartes, Rene**, 1596-1650

**Boyle, Robert**, 1627-1691

**Newton, Isaac**, 1642-1726

**Lambert, Johann Heinrich**, 1728-1777

**Palmer, George**, 1746-1826

**Von Goethe, Johann Wolfgang**, 1749-1832 *1810*

**Monge, Gaspard, Comte de Peluse**, 1746-1818

**Thompson, Benjamin, Count Rumford**, 1753-1814

**Dalton, John**, 1766-1844.

**Young, Thomas**, 1773-1829

**Runge, Philipp Otto**, 1777-1810

## **Visual Science before 1600 (From Jack Yellott)☺**

The roots of modern visual science reach back twenty-five centuries to the earliest Greek writers: **Polyak's** (1957) account of this history is especially recommended. (See also **Borin**, 1942, and **Duke-Elder**, 1958, 1961, 1968, 1971). From antiquity to the early 17th century the outstanding problem was the nature of the physical connection between eyes and objects. Many classical writers (including **Euclid** and Claudius **Ptolemy**) conceived of this in terms of rays emanating from the eye, so that vision could be understood as a form of touch. This idea persisted for a very long time, and vestiges of it survive even today in popular thought. For many purposes it is optically equivalent to the correct interpretation, and consequently not entirely useless: **Brunelleschi** and **Alberti** were able to work out the theory of perspective pictures early in the 15th century, nearly two-hundred years before emanationist notions were finally laid to rest. It is also worth noting that spectacles were in common use by that time, notwithstanding the complete absence of any theory to explain why they worked.

The alternative (and of course ultimately correct) view was that objects send out copies of themselves, which travel to the eye and are there somehow incorporated into the

body. Under this hypothesis the important questions had to do with the physical nature of these copies, and the anatomical site of their incorporation. On the latter point, classical opinion (e.g., **Galen**) favored the lens, perhaps simply because its striking appearance suggests a miraculous function. This notion persisted until late in the 16th century, despite a growing familiarity with the image forming properties of convex lenses: it was accepted even by Giovanni **della Porta** who first added a lens to the pinhole camera and thereby invented the modern camera (1589). However, it could not long survive Felix **Platter's** demonstration (1583) that vision continues after the lens has been isolated by cutting its suspensory ligament. Platter believed photoreception occurred in the retina, but lacked an optical basis for this hypothesis, as well as experimental verification.

The problem was finally resolved in the early part of the 17th century by Kepler's theoretical explanation of the optics of the eye (1604), followed by Christopher **Scheiner's** direct experimental demonstration that an optical image is indeed formed on the inside rear wall of the eyeball (1625). These two events mark the beginning of modern visual science, and lead directly to the questions that have subsequently occupied the field: How is the retinal image kept in focus? What anatomical structures actually capture the light, and how is this accomplished? What sort of physiological signal does this give rise to? How is this signal processed within the eye? How is it transmitted up the optic nerve? What is its destination in the brain? And the fundamental underlying question: How are these physical processes related to visual perception?

The dates in the chronology of major events in visual science from 1600 to 1960 are taken from a number of secondary sources (which sometimes disagree), and should probably be regarded as accurate to within roughly a decade. Sometimes a discovery evolves over many years and many publications; in this case I try to use the earliest. In addition, there are always disputes about priority: I try to use the name of the investigator most closely associated with an achievement in preference to one who might have suggested an idea in a more or less casual fashion, unrelated to subsequent developments within the field. For instance, I credit Helmholtz rather than Babbage with the ophthalmoscope. Besides the references cited at the beginning, dates have been taken from **Pledge, 1950; Brindley, 1970; Blackwell, 1972; Baumgardt, 1972; Kelly, 1972; Westheimer, 1972; and Davson, 1976.** I thank T.N. **Cornsweet** and B. **Wandell** for helpful comments.

## Visual Science 1600-1960 (From Jack Yellott)☺

- **1604**
  - Kepler's *Ad Vitellionem Paralipomena*: First explanation of the optics of the eye.
- **1610**
  - Galileo publishes the *Siderial Messenger*. First scientific look at the sky through a telescope.
- **1611**
  - Kepler's *Dioptrice*: First explanation of the optics of myopia. Projection theory of stereoscopic vision.
- **1619**
  - Scheiner's *Oculus*: First demonstration that accommodation is an active process. First use of fixatives to preserve the eye for anatomical study. First accurate diagrams of the human eye. Discovery of the pupillary "near reflex."
- **1621**

- Snell's law. (Kepler's optical analysis of the eye was based on a small angle, linear approximation to Snell's law.)
- **1625**
  - Scheiner: First direct observation of the retinal image.
- **1637**
  - Descartes' *La Dioptrique*. Corpuscular theory of light. First suggestion of point to point projection of retina onto brain (in his view, onto the walls of the ventricles).
- **1664**
  - Willis traces the optic tract to the thalamus.
- **1665**
  - Grimaldi describes diffraction (posthumously).
- **1666**
  - Newton's prism experiments begin color science.
- **1675**
  - Roemer measures the speed of light.
- **1678**
  - Briggs describes fibers in the retina.
- **1681**
  - Mariotte discovers the blind spot; articulates trichromacy of human color vision.
- **1682**
  - Newton proposes partial decussation at the optic chiasm.
- **1684**
  - First microscopic observation of the retina: Leeuwenhoek notices structures now known to be the rods and cones.
- **1684**
  - Briggs describes night blindness.
- **1690**
  - Huygens: Longitudinal wave model of light; discovery of polarization .
- **1700**
  - Ruysch describes ocular circulatory system.
- **1704**
  - Newton's *Optics*.
- **1705**
  - Hooke reports (posthumously) 1/2' limit of visual acuity.
- **1719**
  - Morgani describes homonymous hemianopia.
- **1751**
  - Whytt explains neurology of pupillary light reflex.
- **1755**
  - LeRoy demonstrates electrical phosphenes in blind observers: First hint of a relationship between electricity and vision.
- **1757**
  - Lomonosov suggests three-"particle" basis of color vision.
- **1760**
  - Bouguer measures luminance contrast thresholds, prediscovers Weber's Law.
- **1776**
  - Gennari describes striate area of occipital cortex.
- **1789**

- Maskelyne describes night myopia.
- **1798**
  - Dalton describes color blindness (his own deuteranopia).
- **1800**
  - Herschel discovers infrared light.
- **1801**
  - Young discovers astigmatism and proves that accommodation is not due to changes in the length of the eye or in the curvature of the cornea.
  - Young proposes three receptor theory of color vision.
  - Ritter discovers ultraviolet light.
- **1802**
  - Young discovers interference.
- **1804**
  - Troxler describes loss of color in the periphery of the visual field.
- **1807**
  - Gall proposes concept of localization of mental functions in the cortex.
- **1808**
  - French Academy refuses to admit Gall on grounds that the cortex has nothing to do with thinking.
- **1817**
  - Young proposes transverse wave model of light.
  - Josef Fraunhofer discovers the "Fraunhofer lines" in the spectrum of sunlight.
- **1818**
  - Vieth-Muller horopter.
- **1824**
  - Wollaston explains homonymous hemianopia in terms of partial decussation at the chiasm.
  - Flourens demonstrates loss of vision following cortical lesions (first proof that the cortex is involved in vision).
- **1825**
  - Purkinje describes optokinetic nystagmus, entopic visualization of retina blood vessels, "Purkinje shift" in spectral luminosity during dark adaptation, blue arcs of the retina, "Purkinje images" (reflections from surfaces of cornea, lens), and motion aftereffects.
- **1826**
  - Niepce makes the first photograph.
  - J. Muller proposes doctrine of specific energy of nerves, explains optics of compound eyes.
- **1829**
  - Plateau initiates study of flicker, discovers stroboscopic movement, invents motion pictures (the "phenakistoscope")
- **1832**
  - Chevreul describes simultaneous color contrast.
  - Weber measures increment thresholds; Weber's law.
- **1833**
  - Wheatstone invents the stereoscope.
- **1834**
  - Plateau-Talbot law.

- Robert Addams rediscovers the motion aftereffect after looking at the Waterfall of Foyers in Scotland: an illusory motion that notwithstanding the fact that there were at least three earlier reports on this effect, still became known as the Waterfall Illusion. The effect was probably first described by Aristotle in his treatise on dreams. The direction of this illusory motion was first described by Lucretius, a couple of centuries later. In 1825 Johann Evangelista Purkyne also described the phenomenon after having looked at a cavalry parade.
- **1838**
  - Fechner discovers subjective color.
- **1841**
  - Dove shows that stereopsis does not depend on eye movements.
- **1844**
  - Haidinger's brushes.
- **1845**
  - Masson shows that Weber's law fails at low luminances.
- **1847**
  - Donders' law of ocular movements.
- **1849**
  - Du Bois Reymond discovers the resting potential of the eye.
- **1851**
  - H. Muller notices visual purple in rods.
  - Helmholtz invents the ophthalmoscope.
- **1853**
  - Grassman formulates laws of trichromacy.
- **1854**
  - H. Müller proves that photoreception occurs in the rods and cones.
  - Gratiolet traces visual radiation from thalamus to occipital cortex.
  - Listing's law of ocular movements.
- **1856**
  - Maxwell tests validity of Grassman's laws; c"
  - Helmholtz proves that accommodation is effected by a reshaping of the lens.
  - Von Graefe introduces clinical perimetry.
  - Helmholtz' *Handbuch der Physiologischen Optik*.
- **1857**
  - Aubert and Forster demonstrate extrafoveal falloff in acuity.
  - Bergmann reports distorted percepts of high frequency gratings attributable to photoreceptor aliasing.
- **1858**
  - Panum measures areas of stereoscopic fusion.
- **1860**
  - Fechner's *Elemente der Psychophysik*.
- **1862**
  - Maxwell's theory of electromagnetic radiation.
- **1864**
  - Donders explains principles of clinical refraction and prescription.
- **1865**
  - Aubert: First quantitative studies of absolute threshold and dark adaptation.
  - Mach describes "Mach bands," suggests lateral inhibition in the retina.
  - First measurements of stereoscopic acuity (Hering, Helmholtz).

- **1866**
  - Holmgren discovers the electroretinogram.
  - Schultz distinguishes rods and cones; proposes duplicity theory of the retina.
- **1867**
  - Helmholtz discovers the Bezold-Brucke effect.
- **1870**
  - Meynert shows that optic radiation terminates in striate area.
- **1875**
  - Golgi stain.
  - von Gudden establishes partial decussation at the chiasm.
  - Hering proposes opponent process theory of color vision.
  - Exner describes apparent motion.
- **1876**
  - Boll discovers that "visual purple" is bleached by light.
- **1877**
  - Ricco's law.
- **1878**
  - Kuehne isolates rhodopsin.
- **1879**
  - Munk formulates concept of topographic projection of retina onto occipital cortex.
- **1880**
  - Kuehne and Steiner measure gross electrical response of isolated retina.
- **1881**
  - Rayleigh's anomaloscope.
- **1885**
  - Bloch's law.
- **1886**
  - Konig "Fundamentals."
- **1890**
  - Willbrand proposes point to point projection of retina onto striate area.
- **1892**
  - Ferry-Porter law.
- **1892**
  - Wulffing measures vernier acuity.
- **1893**
  - Cajal's *La retina des vertebres*: first complete description of retinal neuroanatomy as revealed by Golgi stain.
  - Abbe initiates Fourier optics (first informed manipulations of image spectrum).
- **1894**
  - Konig demonstrates agreement between absorption spectrum of rhodopsin and scotopic spectral sensitivity.
- **1896**
  - Flechsig describes course of visual radiation from lateral geniculate nucleus to striate area (based on myelogenesis).
  - Stratton experiments with inverted retinal images.
- **1900**
  - Planck introduces quantum concept.
- **1903**

- Piper's law.
- **1905**
  - Einstein's photon theory.
- **1910**
  - Minkowski demonstrates point to point projection onto striate area in dogs via behavioral methods.
  - Stigler describes metacontrast.
- **1911**
  - Gullstrand invents the slit lamp.
- **1912**
  - Wertheimer's studies of apparent motion.
- **1913**
  - Abney's law.
  - Minkowski demonstrates separate laminar terminations of left and right optic nerve fibers in lateral geniculate nucleus.
- **1918**
  - Holmes presents first map of striate cortical projection of the visual field in man.
- **1920**
  - First anatomical demonstration of point to point projection of retina onto lateral geniculate nucleus (Minkowski, Brouwer and Zeeman).
- **1922**
  - First application of Fourier analysis to flicker sensitivity (Ives).
- **1924**
  - First C. I. E. photopic luminosity function.
- **1925**
  - Holm demonstrates that vitamin A deficiency causes night blindness.
- **1927**
  - First recording of electrical activity in optic nerve (Adrian and Matthews)
- **1929**
  - Berger discovers alpha component of the EEG.
- **1929**
  - First electrical stimulation of human visual cortex (Foerster and Penfield).
- **1931**
  - C. I. E. standardizes colorimetry (Guild-Wright primaries).
  - First measurement of rhodopsin regeneration in vivo (Tansley)
- **1932**
  - First recording of electrical activity in single optic nerve fibers (in *limulus*; Hartline and Graham).
- **1933**
  - Stiles and Crawford demonstrate directional sensitivity of cones.
  - Wald finds vitamin A in rhodopsin.
  - First electronically amplified human ERG (Cooper, Creed, and Granit)
- **1935**
  - Osterberg: First cell count of rods and cones in human retina.
  - LeGrand measures visual acuity bypassing the optics of the eye.
- **1939**
  - Stiles introduces Pi mechanism analysis of increment thresholds.
- **1941**

- First mapping of the cortical projection of the retina based on electrical responses (Talbot and Marshall).
- **1942**
  - Hecht, Shlaer, and Pirenne show that rods respond to single quanta.
- **1943**
  - DeVries-Rose law.
- **1947**
  - Granit distinguishes sustained and transient ganglion cells.
- **1948**
  - Gabor describes principles of holography.
  - Rose introduces the concept of detection quantum efficiency
- **1949**
  - Transient VEP first reported by C. C. Evans
- **1951**
  - C. I. E. standardizes scotopic luminosity function.
- **1952**
  - First electrical recording from individual mammalian retinal ganglion cells: Discovery of antagonistic center-surround organization of receptive fields (Kuffler).
  - First demonstration of disappearance of stabilized retinal images (Ditchburn and Ginsborg; Riggs, Ratcliff, Cornsweet and Cornsweet).
- **1953**
  - First recording from horizontal cells (Svaetichin's S potential).
- **1954**
  - First psychophysical demonstration of rod saturation (Aguilar and Stiles).
  - Peterson, Birdsall and Fox present the theory of signal detectability.
  - Tanner and Swets apply the theory of signal detectability to human sensation.
- **1955**
  - Photoreversal (Hagins, Hubbard, and Kropf).
  - Jameson and Hurvich use hue cancellation to infer opponent color codes.
  - First study of rhodopsin regeneration in living human retina by ophthalmic densitometry by Rushton, Campbell, Hagins, and Brindley.
  - Rushton demonstrates light induced changes in human cone pigments; identifies chlorolabe and erythrolabe.
  - Flament makes the first measurement of the line-spread function of the human eye.
  - Kanizsa describes subjective contours.
- **1956**
  - First measurement of human spatial modulation transfer function by Schade.
  - Barlow demonstrates the existence of dark light at absolute threshold.
- **1957**
  - Reichardt presents an autocorrelation model for motion detection.
- **1959**
  - Land's color demonstrations.
  - First electrical recording from individual visual cortical neurons; discovery of simple, complex, hypercomplex receptive fields by Hubel and Wiesel.
  - Lettvin, Maturana, McCulloch and Pitt examine feature detectors in the frog visual system.
- **1960**
  - Publication of first random dot stereogram by Julesz.

- Sperling uses partial report to measure iconic memory.

## Literature

**Jung, R.** (1984): Sensory research in historical perspective: Philosophical foundations of perception. In: Darian-Smith, I. (Ed.) *Handbook of Physiology*, Section 1, *The Nervous System*, vol. III/1, *Sensory Processes*, pp. 1-74. Washington, DC: American Physiological Society.

**Osborne, R.:** Books on Color

**Spillmann, J., & Spillmann, L.** (1993). The rise and fall of Hugo Münsterberg. *Journal of the History of the Behavioral Sciences*, 29(4), 322-338.  
[https://doi.org/10.1002/15206696\(199310\)29:4<322::AIDJHBS2300290403>3.0.CO;2-1](https://doi.org/10.1002/15206696(199310)29:4<322::AIDJHBS2300290403>3.0.CO;2-1)

**Spillmann, L.:** Artists and vision scientists can learn a lot from each other, but do they? *Gestalt Theory*, 29, 13-39 (2007)

**Spillmann, L. et al:** The historical psychological instruments at National Taiwan University. *Chinese Journal of Psychology*, 59, No.4, 213-250 (2017)

**Wade, N.:** <https://neuroportraits.uk/portrait/luigi-rolando.htm>

**Wooten, B.R. & Hammond, B.R. (2025):** Properly speaking, Sir Isaac Newton was the first perceptual psychologist and, therefore, the first psychologist. *Color Research and Application*