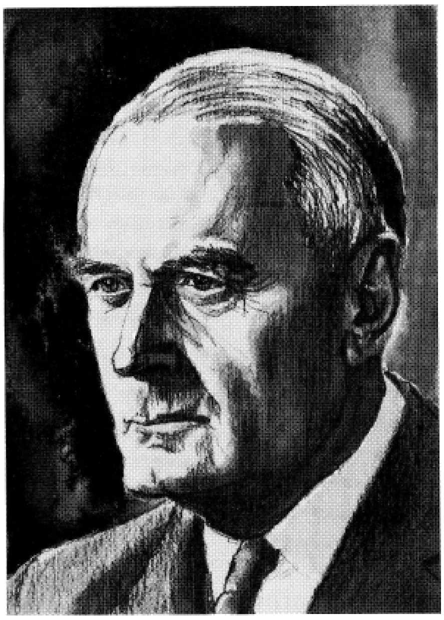
the Society of Experimental Psychologists in 1941 and the Tillyer Award of the Optical Society of America in 1963. He was elected to the National Academy of Sciences in 1946.

Graham edited, and wrote many of the chapters in, *Vision and Visual Perception* (1965).

For background information *see* COLOR VISION in the McGraw-Hill Encyclopedia of Science and Technology. ■



GRANIT, RAGNAR ARTHUR

★ Swedish physiologist

***Born** Oct. 30, 1900, Helsinge, Finland*

Granit is best known for his work in vision and in the field of motor control by muscular afferents; for the former he received the 1967 Nobel Prize in medicine or physiology. During his medical studies he became interested in the psychophysics of vision but soon concluded that a physiological approach was needed. E. D. Adrian had demonstrated the value of this approach in pioneer work with the eye of the conger eel. Granit's leading idea was that since the retina had been shown by S. Ramón y Cajal to be a nervous center, it should be studied as such. He acquired the necessary background during 2 years in Sir Charles Sherrington's laboratory in Oxford. The idea was first tested psychophysically by the flicker method during 2 years at the Johnson Foundation, University of Pennsylvania. The so-called Granit-Harper law of summation was thus established.

Granit began electrophysiological work by developing his well-known analysis of the components of the electroretinogram in 1932. The question of whether light could inhibit, as well as elicit, impulses in the optic nerve seemed fundamental at the time. In 1934 he produced evidence for inhibition, and this fact is today a cornerstone in visual physiology. Also unknown was the relation between amount of rhodopsin (visual purple) and retinal sensitivity. Granit, with T. Holmberg and M. Zewi, studied this quantitatively. It was further shown that intensities of spectral green which failed to bleach rhodopsin caused very large reductions of retinal sensitivity. The explanation may lie in the later discovery, by K. O. Donner and T. Reuter, of a strong feedback inhibition of sensitivity by small quantities of the photoproducts called metarhodopsins.

Thomas Young's conception of three types of fiber in the optic nerve for the three fundamental colors had been interpreted psychophysically by S. Hecht on the theory of three types of receptors (cones) with almost wholly overlapping spectral distributions of sensitivity. Granit's first tests with the electroretinogram in 1937 clearly indicated greater spectral differentiation. A microelectrode technique developed by Granit and G. Svaetichin in 1939 was the first ever used for sensory work. The technique soon showed that some optic nerve fibers (the dominators) responded to the whole spectrum, while others, being narrow-banded "modulators," were color-specific and occurred with slightly varying location within three main regions of the spectrum. This work was extended to a large number of species with variable cone populations. Finally, selective adaptation was used to isolate in a mammal (cat) the three basic spectral sensitivity curves for red, green, and blue. Other researchers have since demonstrated, in training experiments, color sensitivity in the cat. Granit concluded this phase of activity with a summary of his color work in his Thomas Young Oration in 1945, and he covered the whole of retinal electrophysiology in *Sensory Mechanisms of the Retina* in 1947.

Granit next turned to the length meters and tension meters in the muscles known as muscle spindles and tendon organs, respectively. The spindles are extremely complex organs with a motor innervation by special fibers, the gamma fibers, whose capacity for making spindles discharge had been demonstrated in his laboratory by L. Leksell. Granit found that sites in the brain and the cerebellum which excite or inhibit the muscles' motor or alpha neurons had parallel actions on the gamma motoneurons. The concept of the gamma loop through the length-measuring spindles, serving as a second motor system, was then developed experimentally, and it led to a differentiation of alpha and gamma rigidities in neuropathology. The concept of linked alpha and gamma action and its significance was elaborated. Breakdown of this linkage was observed after cerebellar ablation, and this was held to explain the clinical symptoms of dysmetria. Expanding this work to a circuit analysis of the components of the alpha and gamma reflex arcs, Granit differentiated tonic from phasic motoneurons; he studied, by extra- and intracellular recording, the effects of tendon organs and muscle spindles on motoneurons, the role of inhibition, including recurrent or feedback inhibition through fibers which return to the motoneurons from the outgoing axons, and so on. He maintained throughout this experimentation strong emphasis on the organizational aspects and the principles of motor control by the muscles' sense organs. In particular, the spindles were defined as sensory-motor end organs, at the same time measuring and controlling motor action. Finally, feeling the need for precise information on impulse frequency as an instrument of communication, Granit set out to establish by intra- and extracellular recording the rules by which excitation and inhibition balance out quantitatively at the membrane of single cells. He chose motoneurons as his prototype.

Granit graduated from the Swedish Normal-lyceum, Helsinki, in 1919, took Mag.Phil. and M.D. degrees at the University of Helsinki, and served there as professor of physiology during 1935–40. He was invited to a personal research chair in neurophysiology at the Royal Caroline Institute of Stockholm in 1940. In 1945 the Caroline Institute approved a building program for the Medical Nobel Institute, which was to be provided with three departments, one to be devoted to neurophysiology with Granit as director. A special chair of neurophysiology was erected for him by the Swedish government for this purpose. In 1945 Granit delivered the Thomas Young Oration of the Physical Society, London, and in 1960 he was elected a foreign member of the Royal Society of London. In 1967 he gave the Sherrington Lecture of the Royal Society of Medicine, London; in 1972 the Sherrington Lecture of the University of Liverpool; and in 1975 the Hughlings Jackson Lecture of McGill University. He was appointed resident scholar of the Fogarty International Center, Bethesda, MD, for 1971–72 and 1974. Granit was elected a foreign member of the National Academy of Sciences, Washington, and of the Accademia dei Lincei, Rome. He was awarded the Donders, Purkinje, Retzius, and Sherrington medals and seven honorary degrees.

Granit wrote *Sensory Mechanisms of the Retina* (1947; 2d ed. 1963). He delivered the Silliman Lectures at Yale University in 1954, published as *Receptors and Sensory Perception: A Discussion of Aims, Means and Results of Electrophysiological Research into the Process of Reception* (1955). In 1965 Granit organized Nobel Symposium I for the Nobel Foundation. He edited the proceedings under the subtitle *Muscular Afferents and Motor Control* (1966). For the series "British Men of Science" he wrote *Charles Scott Sherrington: An Appraisal* (1966). Other books are *The Basis of Motor Control* (1970) and *The Purposive Brain* (1977). In the Swedish language he published a collection of essays on the scientific life, *Ung Mans Väg till Minerva* (1941; 2d ed. 1958).

For background information *see* COLOR VISION; EYE (VERTEBRATE); MOTOR SYSTEMS; PSYCHOPHYSICAL METHODS in the McGraw-Hill Encyclopedia of Science and Technology. ■

GRAY, HARRY

★ American chemist

***Born** Nov. 14, 1935, Woodburn, KY, U.S.A.*

Gray's early interest in transition metal compounds led him to investigate their electronic structures after he joined the chemistry faculty of Columbia University in 1961. His training at Northwestern University with Fred Basolo and Ralph Pearson and later at Copenhagen University with Carl Ballhausen allowed him to interpret the visible and ultraviolet absorptions of compounds containing metal-to-carbon bonds. In 1963 Gray was able to explain why molecules containing nickel, palladium, platinum, rhodium, and iridium bonded to four other groups in a planar arrangement absorb near-ultraviolet light so strongly, and in 1969 he interpreted for the first time the intense near-ultraviolet absorptions of compounds containing two metal atoms directly bonded together. Both investigations played a major role in laying the foundation for his later work in solar energy conversion. *See* BASOLO, FRED; PEARSON, RALPH GOTTFRID.

In the 1960s during frequent visits to the Rockefeller University, Gray became interested in the role of transition metal ions in living systems. With Harvey Schugar, he investigated the nature of tripositive iron ions in aqueous solutions, and he used the results of this work in interpreting the structures of several iron-containing proteins. At the California Institute of Technology in the late 1960s and early 1970s, he started a major study of the pathways by which electrons are transferred in iron and copper proteins. At about the same time, he became interested in photochemistry, and with George Hammond and Mark Wrighton, he elucidated the ways in which transition metal compounds react when raised to high energy levels by irradiation with visible and ultraviolet light. *See* HAMMOND, GEORGE SIMMS.

Gray's work on the electron transfer reactions of metalloproteins and his interests in photochemistry led him in the mid-1970s to try experiments in the area of solar energy conversion. Utilizing his knowledge of the electronic energy levels of metal complexes, he, Kent Mann, and Nate Lewis began to investigate the photochemistry of molecules in which two rhodium atoms are held together by isocyanide (NC) groups at the ends of carbon chains. As it turned out, these molecules were able both to trap the energy in sunlight and to perform the necessary catalytic steps to store this energy by transferring electrons to protons in water to make hydrogen gas.

In 1977 the first solar energy storage reaction involving hydrogen production in homogeneous solutions was discovered by Gray and his coworkers. The photocatalyst was a blue rhodium compound, called rhodium bridge, which was shown in work in the next 2 years to contain four rhodium atoms in its light-active form. The four-rhodium molecule split apart when it absorbed sunlight, and one two-rhodium fragment carried the two electrons needed to reduce two protons to one diatomic hydrogen molecule. Further work by Gray and his coworkers in 1979 suggested several ways of improving the quantum efficiencies of solar energy storage reactions of this type.

Gray received his B.S. in chemistry at Western Kentucky University in 1957 and his Ph.D. at Northwestern University in 1960. The following year he was a National Science Foundation postdoctoral fellow at the University of Copenhagen, where he collaborated with Ballhausen on studies of the electronic structures of metal complexes. From Copenhagen he went to Columbia University, where he became a full professor in 1965. In 1966 he was appointed professor of chemistry at the California Institute of Technology. For his work Gray received two American Chemical Society awards, in Pure Chemistry (1970) and Inorganic Chemistry (1978). He was elected to the National Academy of Sciences in 1971.

Gray wrote *Electrons and Chemical Bonding* (1964); *Molecular Orbital Theory*, with C. J. Ballhausen (1964); *Ligand Substitution Processes*, with C. H. Langford (1966); *Basic Principles of Chemistry*, with G. P. Haight (1967); *Chemical Dynamics*, with J. B. Dence and G. S. Hammond (1968); *Chemical Principles*, with R. E. Dickerson and Haight (1970, 1974); *Models in Chemical Science*, with Hammond, J. Osteryoung, and T. H. Crawford (1971); *Project Acac: An Experimental Investigation in Synthesis and Structure*, with J. G. Swanson and Crawford (1972); and *Chemical Bonds* (1973).