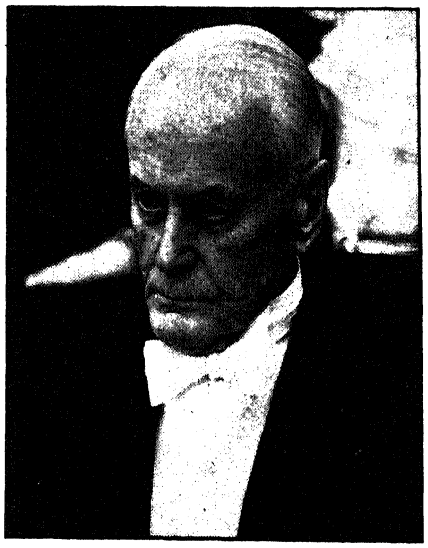
Light on vision and movement

An obituary of Ragnar Arthur Granit

Professor Granit, formerly professor of neurophysiology, Karolinska Institute, Stockholm, and director of the neurophysiology department, The Nobel Institute of Neurophysiology, who died in March this year aged 90, made major and pioneering contributions in vision physiology and motor control by muscular afferents. For his discoveries in vertebrate vision physiology he was awarded the Nobel prize for physiology or medicine in 1967, along with Haldon Keffer Hartline and George Wald.

The perception of light and colour by the visual apparatus involves absorption of radiation energy by chromophores in the sensory cells of the retina, and transduction of this information into nerve impulses, which are directed towards the brain. Ramon y Cajal's histological studies had shown that the retina is a nervous structure. The receptor and horizontal cells in the outer retinal layer are connected to the bipolar cells. The bipolar and amacrine cells in turn are connected to the ganglion cells. Considering the system of retinal interconnections, the ganglion cells convey the information made up by the total contribution of four cell types. It was Granit's idea to study the electrophysiology of the retina, and Ramon y Cajal's histological work on the retina formed the basis. Granit's method, which was later used by others, consisted of removing the cornea and lens and placing glass-insulated wire electrodes on the retinal tissue. His initial studies in 1932 were on the electroretinogram and analysis of its components. He provided evidence in 1934 to suggest that light can produce inhibition of signals in addition to excitation. This was another important contribution in vision physiology.

His foremost contribution for which he was distinguished with the Nobel prize was his work related to colour vision. The basic foundation of Granit's work was provided by the trichromacy theory, which was proposed to explain colour vision by Young and later modified by Helmholtz (the Young–Helmholtz theory). The theory proposed that there are three primary colour receptors in the retina—blue, green and red. Any individual colour in the continuous spectrum of colours is perceived on stimulation of these three hypothetical receptors in different proportions. This was based on Newton's work, which showed that any colour, including white light, can be decomposed into a few simple primary colours, and these mixed back again to give rise to the original colour. Different proportions of the three primary colours, blue (400 nm), green (540 nm) and red (575 nm) can match any given colour. Granit's experimental work on the cat retina using glass-insulated microelectrode studies of neuron activity of the retina



exposed to the spectrum of light frequencies provided the first experimental support for the trichromacy theory. He found that the neural discharges from the retinal units were grouped around three wavelengths, each unit responding to either the blue, green or red part of the spectrum. The recordings made by Granit (1945) were most likely from ganglion cells of the retina. The retinal elements which responded to a narrow band of the spectrum were designated as 'modulators'. In addition, he distinguished retinal elements which showed a broad distribution of spectral sensitivity, designated as 'dominators'.

Granit's research interests subsequently shifted to principles of muscle control and movement by sensory organs in the muscle sensing muscle length (muscle spindles) and tension (tendon organs). The muscle spindles are widely scattered throughout the fleshy parts of the muscle and attached to extrafusal fibres at both ends. Each spindle contains thin muscle fibres known as intrafusal fibres, which are innervated by axons called gamma fibres, whose capacity for making spindles discharge was demonstrated by L. Leskell in Granit's laboratory. Subsequent studies by Granit and his colleagues showed that localized sites in the brain and the cerebellum which excited or inhibited the motor or alpha neurons had parallel actions on the gamma motoneurons. Their experimental work supported the concept of the gamma loop, and the linked alpha and gamma action. Breakdown of this loop was observed after ablation of the cerebellum. The studies led to the clinical differentiation of alpha and gamma rigidities and understanding of the clinical symptoms of dysmetria. Other significant findings were the differentiation of tonic from phasic motoneurons and the phenomenon of recurrent inhibition. He defined the muscle spindles as sensory-motor end organs, whose function was related to both the measurement of muscle length and the control of muscle action.

Granit was born on 30 October 1900 in Helsinge, Finland. He graduated from the Swedish Normal-Lyceum, Helsinki, in 1919, took the M Phil and MD degrees in 1923 and 1927 respectively at Helsinki University, and served there as professor of physiology during 1935–1940. The formative years of his research career were spent in Charles Sherrington's laboratory in Oxford, and at the Johnson Foundation, University of Pennsylvania. It was during this period that his interests in retinal physiology were established. In 1940 he was invited to a research chair in neurophysiology at the Karolinska Institute in Stockholm. From 1945 onwards he was director of the Nobel Institute of Neurophysiology, from where he retired in 1967.