

**Granit R.** *Receptors and sensory perception: a discussion of aims, means, and results of electrophysiological research into the process of reception.* New Haven, CT: Yale University Press, 1955. 369 p.  
[Nobel Institute for Neurophysiology and Karolinska Institutet, Stockholm, Sweden]

My book, *Receptors and Sensory Perception*, with the subtitle, *A Discussion of Aims, Means, and Results of Electrophysiological Research into the Process of Reception*, contained the 1954 Silliman Memorial Lectures of Yale University, expanding my earlier work on the retina to general sensory and motor physiology. [The *SCI*® and *SSCI*® indicate that this book has been cited in over 850 publications.]

## A Love of Psychophysics

Ragnar Granit  
Eriksbergsgatan 14  
S-114 30 Stockholm  
Sweden

January 11, 1990

I was chosen for the Silliman Lectures not only to present my work in this field, but also because Yale wanted to celebrate the 50th anniversary of Sir Charles S. Sherrington's classical lectures, *The Integrative Action of the Nervous System*.<sup>1</sup> I was a pupil of Sherrington.

The advent of the early amplifiers in the 1920s did away with all restrictions on sensitivity and speed of recording that had hampered progress. From 1920 I had been interested in the special senses and consequently in psychophysics. I can well remember how deeply stirred I was when E.D. Adrian's first contributions<sup>2</sup> began to appear.

My own experimental experience derived from two fields, retina and muscular end organs, particularly stretch receptors. I began in psychophysics at the Eldridge R. Johnson Foundation in Philadelphia trying to study retinal interactions by using the flicker-fusion point as an absolute measure of excitability. On this line I continued work at the Johnson Foundation for two years.

The results obtained evoked my desire to be closer to my preparations than I could be in psychophysics, so I went to electrophysiology and remained there for the rest of my active life. I built myself a DC amplifier at Helsingfors University and then went for a second time to Oxford as a Fellow of the Rockefeller Foundation. My leading paper there consisted of producing decisive experimental evidence for a

minimum of three components (PI, PII, PIII) in the electroretinogram and correlating them to the discharge in the optic nerve.<sup>3</sup> Sherrington liked this paper very much, but I said to him: "I am sure there must be inhibitions in the retinal center, but I don't know how to go about to prove it." He replied: "Don't you worry, within a few years you will have proved it yourself."

Returning to Helsingfors, my alma mater, in 1932 I recalled some old observations by W. Einthoven and W.A. Jolly,<sup>4</sup> which in terms of my component analysis meant that a fairly pure PIII-response could be obtained by reilluminating the eye on top of the off-effect. This proved to give a powerful inhibition of the mass discharge in the optic nerve. Probably I have never been equally elated by anything else in my experimental life. I was a young man and very happy to have found something fundamental for the science of vision: that light could both excite and inhibit and that the two opposite processes were antagonistic. I sent a preliminary note to the Physiological Society with my coworker P.O. Therman in 1934.<sup>5</sup>

Around 1945, having spent 25 years with the eye, I decided that the time had come for doing something else. The late Lars Leksell<sup>6</sup> had shown at the Nobel Institute that the thin fibers in the ventral roots conducting at gamma rate were specific for the intrafusal musculature at the ends of the sense organ long known as muscle spindles. Suspecting that the main role of the gamma system was to be at the disposal for higher centers, I asked B.R. Kaada from the famous Anatomical Institute in Oslo to come over and test this notion. Success was immediate.<sup>7</sup> Every cortical or subcortical site known to have excitatory or inhibitory motor effects had the corresponding effect on the spindles. This was named alpha-gamma linkage. For the Silliman Lectures it necessitated a chapter on the spinal cord containing the recent work of Renshaw, Lloyd, Eccles, and us.

The Silliman Lectures were well received and went into several editions. While in vision my earlier *Sensory Mechanisms of the Retina*<sup>8</sup> had given the details of my own work with full historical background, the Silliman Lectures were rather brief on vision but expanded the historical section widely into general sensory and some motor physiology. Its actualities are now history, and today the book can be described as a first coherent history of the entry of electronics into the physiology of the central nervous system.

1. Sherrington C S. *The integrative action of the nervous system*. New Haven, CT: Yale University Press, 1906. 412 p. (Cited 950 times since 1945.)
2. Adrian E D. *The basis of sensation: the action of sense organs*. London: Christophers, 1928. 122 p. (Cited 150 times since 1945.)
3. Granit R. The components of the retinal action potential and their relation to the discharge in the optic nerve. *J. Physiology* 77:207-40, 1933. (Cited 195 times since 1945.)
4. Einthoven W & Jolly W A. The form and magnitude of the electrical response of the eye to stimulation by light at various intensities. *Quart. J. Exp. Physiol.* 1:373-416, 1908.
5. Granit R & Therman P O. Inhibition of the off-effect in the optic nerve and its relation to the equivalent phase of the retinal response. *J. Physiology* 81:47P-48P, 1934. (Cited 95 times since 1945.)
6. Leksell L. The action potential and excitatory effects of the small ventral root fibres to skeletal muscle. *Acta Physiol. Scand.* 10(Supp. 31), 1945. (Cited 200 times.)
7. Granit R & Kaada B R. Influence of stimulation of central nervous structures on muscle spindles in cat. *Acta Physiol. Scand.* 27:130-60, 1952. (Cited 310 times.)
8. Granit R. *Sensory mechanisms of the retina*. Oxford, England: Oxford University Press, 1947. 412 p. (Cited 640 times.)