Neurophysiology of Movement

The Basis of Motor Control. Integrating the Activity of Muscles, Alpha and Gamma Motoneurons and Their Leading Control Systems. RAGNAR GRANIT. Academic Press, New York, 1970. viii, 346 pp., illus. $14.50.

The award of the Nobel Prize to Granit in 1967 was based on his contributions to an understanding of sensory processes, and it may therefore come as a surprise to nonphysiologists that for the past two decades his major research has dealt with neural control of movement. Granit's work on this problem began in the late '40's, when, as he writes in the preface to this book, he began to study muscle receptors in the context of their functional role in movement, "and not merely as parents of afferent nerves." The muscle receptor which he selected for study (it is a stretch receptor called a "spindle" because of its shape) was one whose existence had long been known but whose true mode of operation was first indicated by a discovery made in Granit's laboratory in 1945. Prior to this discovery (to be described below) the muscle spindle had been known to contain sensory nerve terminals excited by muscle stretch. These sensory nerves pass back to the spinal cord, where they excite the very motor neurons that send axons back out to the stretched muscle. The "knee jerk" elicited by the physician when he taps on a tendon is, in fact, generated by the process just outlined. The physician's hammer indents the tendon and stretches the muscle to which the tendon is attached. This muscle stretch elongates the spindles lying within and parallel to the stretched muscle, and this in turn initiates impulses in the afferent nerves associated with the spindle. These afferent impulses pass back to the spinal cord, where they excite motoneurons, which send impulses back out to induce contraction in the muscle fibers surrounding the spindle. This muscular contraction opposes the stretch and provides for postural stability.

Such was the picture that existed prior to 1945, when Leksell, working in Granit's laboratory, showed that far from being a simple, passive stretch receptor, the spindle is a dynamic receptor with a specialized system for regulation of its own sensitivity so as to compensate for changes in the length of the muscle in which it is situated. Prior to Leksell's work it had been thought that all nerve fibers leaving the spinal cord by way of the ventral root innervated skeletal muscle. Leksell found that the smaller fibers in the ventral root (called gamma fibers) do not terminate on skeletal muscle at all, but instead end in the spindle receptors. Within the spindle, these gamma fibers innervate a specialized type of tiny muscular element whose function is to set the length (and thereby the sensitivity) of the receptor.

This discovery and the many subsequent discoveries by Granit and coworkers, as well as other groups, have had profound implications not only for our understanding of this particular muscle receptor but also for our view of sensorimotor processes generally. Here was a case in which a major part of the "motor output" was devoted not to production of movement but to regulation of sensory input. How might this controlled sensory input be used by the central nervous system? In what order might the two types of motor fibers (alpha fibers to skeletal muscle and gamma fibers to spindles) come into play in the course of movement? These are the sorts of questions that Granit has been working on since the late '40's, and the present volume summarizes and integrates Granit's research with that of other investigators, considering problems such as "How do we employ our muscle spindles in the control of movement and posture, and why do we need this potent and highly differentiated fusimotor-spindle apparatus?"

It is of note that though the spindle itself is present in Amphibia, gamma fibers devoted exclusively to spindle control are absent. In the frog, the same neurons giving rise to contraction of skeletal muscle fibers send branches to the specialized "intrafusal" muscle fibers of the muscle spindle. With the development of two separate control systems for regulating (i) muscular length and (ii) receptor sensitivity, it has been possible for the motor control system of the mammal to operate in a number of different modes, depending on the type of motor activity the system is called upon to emit. The evolutionary development of the spindle and its central control system in mammals has led Granit to explore the way in which supraspinal structures are linked to the spindle, and this exploration has in turn led him to analyze the way in which the brainstem, the cerebellum, and the cerebral sensorimotor cortex control the gamma motoneurons which in turn control the spindle. Thus, starting with a quest to understand a muscle receptor, Granit has been led from the lowest to the highest levels of the nervous system. It is indeed remarkable that he has found it possible to present a lucid coverage of this wide area in less than 300 pages without sacrificing important scientific detail. The volume he has prepared is sufficiently inclusive to serve as a physiological handbook with reference to the muscle spindle, and yet his approach is sufficiently general to allow the volume to serve as a text in neurophysiology or bioengineering seminars, and as interesting reading for the neurologist, physiologist, or psychologist interested in the control of movement.

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Darwin's "Retreat"

Charles Darwin: The Years of Controversy. The *Origin of Species* and Its Critics, 1859–1882. PETER J. VORZIMMER. Temple University Press, Philadelphia, 1970. xx, 300 pp., illus. $12.50.

As I sink "under the whelming tide" generated by Darwin's exegetes, I wonder whether I am being covered by increasing wisdom or by the agent of Dr. No's demise. Can anyone have anything new to say at this point, 11 years after the centennial of the *Origin* opened the floodgates? To the delight of aspiring scholars, the answer remains yes; for Vorzimmer has treated a very important, yet previously unexamined, phase of Darwin's work: he has given us the first detailed account of Darwin's response to his critics through six editions of *Origin of Species* (1859–1872).

Darwin's alterations of the *Origin* have long been the chief battleground of his modern critics: detractors speak of a retreat to impotent confusion while supporters often see no more than a gracious accommodation to criticism of peripheral issues. Darwin's theory, as Vorzimmer and many others