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.

EDWARD V. EVARTS
Laboratory of Neurophysiology, National Institute of Mental Health, Bethesda, Maryland

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

have noted, has two parts: (i) variation occurs, and (ii) favorable variants are accumulated by natural selection, eventually to form new species. Although his theory dealt mainly with the second part, almost all of his trouble arose from the first. Darwin began by attributing most variation to "the indirect effect of the conditions of life" (chapter 1 of Vorzimmer). Such variation would be "random"—that is, it would not occur in any preferred direction. As critics affirmed the limits of variability and doubted the power of natural selection, Darwin granted an increasing role to causes that could produce *directed* variability toward advantageous states (by use and disuse and direct effect of the environment, for example). Almost all changes in the *Origin* refer to this point; it has set the battlefield. Detractors err in claiming that Darwin was driven to "Lamarckism," for they confuse the two parts of Darwin's theory: if favorable variants arise by use, they must still be accumulated by selection. But supporters also err in stating that Darwin did not compromise selection because he altered only his views on the causes of variation; for if variation is inherently directed toward advantageous states, then selection, though it work continuously, plays only the headman's role of removing the unfit.

In this context, Vorzimmer's concentration upon Darwin's concept of variation is appropriate. He begins with a summary of Darwin's ideas, provides an excellent chapter on the study of inheritance up to Darwin, and dissects the issues that troubled Darwin and fired his critics in this pre-Mendelian world (the inheritability of variation, the role of saltations, blending, the limits of variability). The exposition is clear, though not concise, and includes both thorough analysis and occasional gems (on p. 36, for example, we learn that Darwin actually "discovered" the Mendelian 3:1 ratio of hybrid crosses, though he interpreted it as a stage in the decline of "prepotency" from 100 percent in F_1 to an eventual blending). There are some curious omissions (we receive a good account of Darwin's debate with Galton about pangenesis, but no real analysis of why Darwin developed his "provisional hypothesis" in the first place).

My serious criticism of Vorzimmer is that, by virtually confining himself to the critics of Darwin's views on variation, he has artificially sundered a larger subject and rendered an incomplete account of the reasons for Darwin's alterations. Apart from a chapter on sexual selection, he provides no discussion of the debate on Darwin's views of macroevolution (origin of major structures, the history of life through time). We hear nothing of the argument that the fossil record abounds in discrete breaks, rather than gradual transitions—though Darwin had staked his theory on a belief that breaks are the artifacts of an imperfect record: "he who rejects these views on the nature of the geological record, will rightly reject my whole theory" (first edition, p. 342). We are not told of Lord Kelvin's youthful earth, though it troubled Darwin greatly. He referred to Kelvin as an "odious spectre," and his increasing acceptance of directed variability was strongly motivated by a need to "speed up" evolution that it might occur in the time Kelvin allowed. Although Vorzimmer rightly grants Mivart a special place among Darwin's critics, he barely mentions Mivart's primary contention: that the incipient stages of useful structures cannot be selected because they are not of use themselves.

These omissions are doubly serious because they place Darwin's reactions in a biased light. Darwin was most vulnerable on questions of variation. If only these are treated, the belief that he withdrew from his original ideas in increasing confusion becomes credible. Darwin was much more effective in answering critics of his macroevolutionary notions, and here his theory gained strength. Some important breaks in the fossil record were filled (the discovery of *Archaeopteryx*, the sequence of horse evolution that Huxley affirmed in America), and, although these events did not bear upon all aspects of the debate, they at least cast doubt upon various types of saltationism. Moreover, although Darwin was not able to counter Mivart's arguments on variability, he provided a very effective rebuttal of the critique on incipient stages in a special chapter added to the sixth edition of the *Origin*. In explaining Darwin's "retirement" after his sixth *Origin*, Vorzimmer (p. 251) points to Mivart as "the prime instrument in badgering the elderly Darwin into the state of frustrating confusion." I would explain Darwin's subsequent silence more simply: he felt he had answered Mivart's major claim.

Why have we so many Darwins? Ghiselin's (*The Triumph of the Darwinian Method*) is a tower of strength and consistency, a man of uncommon brilliance. Barzun's (*Darwin, Marx, Wagner*) and Himmelfarb's (*Darwin and the Darwinian Revolution*) is a somewhat pedestrian man, reduced to impotence by his critics. Vorzimmer stands between, but his Darwin is far more cowed, more compromised, and more confused than that of most biologists, including myself. Vorzimmer's summary of Darwin's final position (pp. 240–41) seems fair and accurate: it exposes an amplified theory, altered in its emphases, but unchanged in its identification of selection as the primary cause of evolutionary change. Yet, his words portray a more serious retreat. He states, for example (p. 238), that only in the *Descent* (1871) did Darwin first assign a role in evolutionary modification to the Lamarckian factors that he had previously invoked only as producers of variability. Yet Mayr (introduction to facsimile of the first edition of the *Origin*, Harvard University Press, 1964, p. xxvi) cited 13 passages in the first *Origin* that grant to use and disuse the power to produce evolutionary change. Again, Darwin's later alteration was in emphasis, not content.

There is a curious correlation in our literature on Darwin's response to his critics. Humanists and historians (Barzun, Himmelfarb) tend to see a retreat and abandonment where biologists (de Beer, Ghiselin, Mayr) detect smaller compromises and changes of emphasis. In defending the humanists I might argue that biologists, lacking a historical sense, view Darwin in the inappropriate light of his modern vindication. In supporting biologists, I might contend that historians often lack an appreciation for the complexity of biological theory. Perhaps historians are viewing biology falsely, as though it were a "mature" physical science—a body of rigorous theorems limited in flexibility and scaffolded one upon the other. Natural selection "bends" more easily than the Newtonian laws: the test of its importance is its overwhelming, not its universal, occurrence. After all, in this day of its reign, we still recognize minor classes of exceptions (genetic drift, the founder principle).

I have assuaged my initial fear. There is still an untrodden path in Darwin's legacy. What we need now is a history of Darwin's historians.

STEPHEN JAY GOULD
Museum of Comparative Zoology,
Harvard University,
Cambridge, Massachusetts