A Century After Cajal

The Cerebellum Revisited. RODOLFO LLINÁS and CONSTANTINO SOTELO, Eds. Springer-Verlag, New York, 1992. xiv, 339 pp., illus., + plates. $89. From a meeting, Barcelona, 1988.

The title of this book is derived from a symposium held in 1988 to celebrate the centenary of Ramon y Cajal's "neuron doctrine." The neuron doctrine, it will be recalled, was the germinal idea that individual nerve cells communicate with one another, and this once-speculative notion has now become the basis of all modern neuroscience. Like Cajal's pioneering work, the present collection of research papers deals with the cerebellum and its related structures. The editors admit in the preface that the selection of which papers to include was a "personal choice of topics and an incomplete one at that." They may be readily forgiven for the incompleteness, since the enormous quantity of recent cerebellar research would easily have surpassed the confines of a single volume. Both Llinás and Sotelo are well-known figures in cerebellar research, and I for one was very curious to know which papers they had selected.

The papers are grouped under three broad categories; morphological organization, the electrophysiology of the olivocerebellar system, and movement-related activity changes. Each section is given a brief introduction highlighting the important recent advances. In all there are seven chapters on morphology, three on the olivocerebellar system, and six on neuronal activity related to movement. Given the prodigious rate of change in the neurosciences, one might wonder whether these papers presented five years ago are still of value. Surprisingly, most of them do remain timely, and their bibliographies have been updated to contain references as recent as 1991. For this reader, though, the real appeal of this book is the convenience of having a guided tour of important regions of interesting cerebellar research, in many of which I consider myself a somewhat provincial tourist.

Once a decade, a book about the cerebellum appears that becomes a must-read for everyone in the neurosciences: Eccles *et al.*'s *The Cerebellum as a Neuronal Machine* (1967), Palay and Chan-Palay's *Cerebellar Cortex* (1974), Ito's *The Cerebellum and Neuronal Control* (1984). Although *The Cerebellum Revisited* does not attain this exalted status, the editors do deliver, as they promise, "a book to please both the specialist and the generalist." Among the non-aficionados of the cerebellum who I suspect will find this book the most appealing are those interested in neural development, a field in which the cerebellum has been a key model for some time.

Particularly interesting in this regard are the chapters by Hawkes and Sotelo. For example, Hawkes and his colleagues, using a family of monoclonal antibodies called Zebrins, are able to distinguish 14 alternating labeled and unlabeled parasagittal bands of previously undifferentiated Purkinje cells. The outstanding precision of this organization is demonstrated by the fact that the narrowest Zebrin-positive band, straddling the midline, is sometimes only one or two cells wide. Although the functional interpretation of this startling revelation remains elusive, Hawkes points out that, because the parasagittal compartments are present before afferent connections are established, the system does not need to develop in a linear temporal se-

quence. This avoids the problem associated with coordinating simultaneous growth in different regions of the nervous system and prevents errors of topography among higher-order cells like Purkinje neurons from disrupting the topographic organization at all lower levels. Sotelo and collaborators have successfully grafted genetically normal embryonic Purkinje cells into the adult cerebellum of an adult neurological mutant mouse (PCD) in which all Purkinje cells degenerate. Sotelo demonstrates that the grafted cells carry their own agenda for orientation, growth, and differentiation and follow an "internal clock that regulates all their developmental programs independently of environmental agents."

A highlight of the section of the book devoted to the electrophysiology of Purkinje cells and inferior olivary neurons is the chapter by Llinás and Sugimori. The authors not only summarize much of their work on calcium conductance in Purkinje cells but, perhaps more significant for the non-specialist, offer some functional interpretations of the results. That specialized voltage-dependent conductance channels for sodium or calcium can be triggered by either parallel-fiber or climbing-fiber excitation to produce simple or complex spikes respectively has been well documented by these authors. However, the additional bewildering variety of calcium conductances means that different parts of the dendritic tree are independently responsive and that Purkinje cells can generate as many as six different all-or-none potentials in addition to the plateau potential. Moreover, the dendritic spikes and the plateau potentials differ only in that they are generated at different regions of the dendrites with different complements of potassium channel types. Some dramatic color images of calcium conductance changes after intracellular application of the voltage-sensitive dye fura-2 are used to document the plateau potentials in in vitro cerebellar slices. The illustrations are of excellent quality throughout the book, and the anatomical figures are especially noteworthy, although I noted a few discordances between legends and figures.

The final section of the book deals with cerebellar activity in movement and more particularly with learned movements. The perpetual riddle of the role of the climbing fibers is posed once again, but the varied answers failed to generate the heat and passion that characterized the debate on the same issue at a similar symposium in Turin a year earlier. Alas, there still appears to be no agreement in sight. Even the consensus that complex spikes diminish Purkinje cell responsiveness to parallel fiber excitation appears to some extent equivocal according to Bloedel and collaborators. Although more than half the book is devoted to elaborating the organization of Purkinje cells into narrow rostrocaudal bands, Thach adds evidence to support an old hypothesis that runs counter to the parasagittal bands both literally and figuratively. He suggests that in addition to the rostrocaudal organization, the long parallel fibers running mediolaterally serve to link the functionally different parasagittal bands of the cerebellum together to create specific muscle synergies for multijoint movements.

In some ways we have come full circle with this book since Cajal's pioneering demonstration of the simple geometric arrangement of cerebellar neurons. Neuroscientists expecting that the simple geometric structure would soon be followed by a similarly simple and elegant explanation of its function have been disappointed. Rather ironically, it appears clear from this excellent collection of papers that, after one hundred years of impressive progress, we have developed an elaborate neuron doctrine of the whole brain, but a simple explanation of cerebellar function has yet to be achieved.

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