Book Reviews

The Cerebellum

The Cerebellum and Neural Control. MASAO ITO. Raven, New York, 1984. xviii, 580 pp., illus. $75.

To fully appreciate the contribution Ito makes in this monograph it is important to have a perspective on the region of the brain he has analyzed. The cerebellum is a remarkable neuronal structure. Although its surface topography appears complicated, its internal organization is surprisingly simple and geometrically arranged. There is a basic wiring diagram for the cerebellum that is repeated in a largely constant fashion throughout the structure. The cortex of the cerebellum contains only a limited number of different cell types, each of which has a highly distinctive shape. One of these cell types, the Purkinje cell, has a round cell body with long processes shaped like a deer's antlers extending from it. Purkinje cells are the sole source of output from the cortex. The major inputs to cerebellar cortex, which have been given names like "mossy" fiber and "climbing" fiber, have unique shapes, patterns of connections, and physiological effects.

The contribution of the cerebellum to neural control has been the subject of much speculation. It has long been known that destruction of the cerebellum results in striking disorders, particularly of voluntary movement. Cerebellar damage does not result in the loss of the ability to move; rather, it leads to gross incoordination. When patients with cerebellar lesions reach for an object they tend to oscillate around it. Such oscillations have been termed "intention tremors" and have been likened to the oscillations of a malfunctioning control system.

By 1967, the basic interconnections and physiology of elements within the cerebellum could be described in almost incredible detail. An excellent monograph by Eccles, Ito, and Szentágothai (*The Cerebellum as a Neuronal Machine*) was published, and some believed that the mystery of cerebellar function could be solved. It soon became apparent, however, that knowing the connectivity of the cerebellum was not sufficient to reveal its function. Too little was known about the "behavior" of cerebellar elements during movement to allow complete descriptions of what they contribute to normal motor function.

Some of the missing information began to be provided during the late '60's and early '70's, when techniques for recording the activity of single neurons in awake, behaving animals became available. These new methods allowed the activity of single cerebellar elements to be correlated with ongoing motor behavior. Several groups employed these methods and observed surprising results. One cerebellar element, previously thought to "trigger" movement, displayed a pattern of neural activity entirely inconsistent with such a function. One of the aims of this monograph, which Ito has certainly attained, is to review the new physiological findings and incorporate them, along with updated anatomical information, into a revised view of cerebellar operation. The first sections of the monograph are devoted to this aim.

The '70's also saw important attempts to provide theoretical models of cerebellar networks. One model postulated a special type of synaptic plasticity for the cerebellar cortex (Marr, 1969, and Albus, 1971), and it has important functional implications. The major assumption of the model is that appropriately timed signals to a Purkinje cell from one source of input, the "climbing fiber," lead to a long-term modification in the synaptic efficacy of signals to the same cell from another source of inputs, the "parallel fibers." This assumption endows the neural machinery of the cerebellar cortex with a form of plasticity that could contribute to the adjustment of motor responses and the acquisition of motor skills. Ito and his colleagues have been among the leaders in attempts to experimentally examine the assumption and the synaptic plasticity it would entail. All the data and arguments in support of Ito's position are clearly presented in chapter 10, which examines various features of the cerebellar cortex with reference to various theoretical models. Models and interpretations other than Ito's could have been presented more fully in the chapter.

The core of the monograph is a concise statement of Ito's hypothesis concerning cerebellar operation, a presentation of the data that support it, and an examination of its broader functional implications. This begins in chapters 24 and 25 with a focus on the involvement of one part of the cerebellum (the flocculus) in the vestibulo-ocular reflex. The vestibulo-ocular reflex produces eye movements to compensate for head movements. The function of the reflex is to prevent images in the visual world from moving across the retina when the head moves. According to Ito's "flocculus hypothesis of the vestibulo-ocular reflex control," the flocculus is placed in a "sidepath" off the main neural circuitry responsible for generating the vestibulo-ocular reflex. When the reflex is inadequate, error signals indicating "slip" of images across the retina reach Purkinje cells in the flocculus via climbing fiber inputs. According to the cerebellar network model outlined in chapter 10, the conjunction of climbing fiber input with ongoing parallel fiber activity causes modifications in the parallel fiber synapses on Purkinje cells and alters Purkinje cell output and signal transfer through the flocculus sidepath. The end result, according to the hypothesis, is an adaptive modification of vestibulo-ocular reflex performance. These and other proposals are elegantly presented in the many diagrams displayed throughout the text.

In the remainder of the monograph Ito relates his hypothesis to cerebellar control in other neural systems. This leads to a great deal of speculation, but all of it is relevant. The many ideas presented should generate interesting experiments in the future.

The book is significant from another perspective. The field of neuroscience has become very fragmented, with each group tending to believe that its approach to the analysis of brain function is the only one worth pursuing. Ito's monograph should serve to remind us that there are many levels of analysis. The search for function in regions of the brain as complex as the cerebellum clearly requires a multidisciplinary approach. Each piece of new information, whatever the methodology by which it is derived, is valuable and must be integrated into a whole. This monograph is a model of synthesis worthy of the field's respect and emulation.

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