The Cerebellum and Adaptive Control

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CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
40 West 20th Street, New York, NY 10011-4211, USA

CAMBRIDGE UNIVERSITY PRESS
The Pitt Building, Trumpington Street, Cambridge, United Kingdom
The Edinburgh Building, Cambridge CB2 2RU, UK
477 Williamstown Road, Port Melbourne, VIC 3207, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain
Dock House, The Waterfront, Cape Town 8001, South Africa

http://www.cambridge.org

First published 2002

Printed in the United States of America

Typeface Times Ten 10/13 pt. *System* LaTeX 2ε [TB]

Library of Congress Cataloging in Publication Data
Barlow, John S., 1925–
The cerebellum and adaptive control / John S. Barlow.
p. cm.
Includes bibliographical references and index.
ISBN 0-521-80842-1
1. Cerebellum. 2. Adaptive control systems. I. Title.
QP379 .B37 2002
573.8′6 – dc21 2002023394

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Introduction

1.1. History

In the introductory chapter of his magnificent three-volume monograph, *The Comparative Anatomy and Histology of the Cerebellum*, Olof Larsell (1967; Larsell and Jansen, 1972) provides a history of the cerebellum in its gross aspects, which reads in part as follows (additional historical details can be found in Clarke and O'Malley 1968):

> Herophilus (335–280 B.C.) is usually credited with recognition of the human cerebellum as a distinct division of the brain. Aristotle (384–322 B.C.), however, calls it parencephalis, indicating that he did not regard it as part of the principal mass of the brain. The great Galen (A.D. 131–200) designated the vermis cerebelli "the worm-like outgrowth" (epiphysis scolexoides). The arbor vitae [the treelike set of outlines of white substance seen on a median section of the cerebellum] was described by Thomas Willis (1664) in his *Cerebri Anatome* as "ramificatio cerebelli ad foramen arboris." The latter author also suggested that the cerebellum presides over the involuntary movement of the body, whereas the cerebrum controls those movements brought about by volition. The first good drawing of the vermis was publishes by Heister (1717), but Vesalius (1543) had already included in his *Fabrica* rather crude illustrations of the entire cerebellum which are in striking contrast to his beautiful figures of muscles, bones, and other structures. Haller (1777) described the cerebellar hemispheres under the name lobi, and Malacarne (1780) gave a detailed description of the entire organ. Many of the terms which Malacarne introduced are still in use. He also described the surface folia or "laminette," giving their total number as 500 to 780. In the cerebellum of an idiot, he found only 340 folia, leading him to conclude that intelligence depends on the number of cerebellar folds. . . .
>
> The earlier studies of the cerebellum in animals were largely experimental in execution. Rolando (1809) removed the cerebellum in fishes, reptiles, and mammals, described the disturbances of voluntary movements that resulted, and

pointed out that cerebellar ablation does not affect sensation. Flourens (1844) confirmed and extended Rolando's observations, emphasizing the exaggeration of tendon and antigravity reflexes and the curious stiff-legged locomotion, with retraction of the head that followed ablation of the cerebellum in birds. [Purkinje's original description of the pear-shaped cell somata was made in Prague in 1837; see also Brazier 1988]. Ferrier (1876) reported his observations on the responses of the eyes, head, and neck to electrical stimulation of the cerebellum in dogs. Luciani (1891) described the results in the dog of complete removal of the organ, and Sherrington (1900) defined the cerebellum as the "head ganglion of the proprioceptive system," holding that it functions as a whole because it deals with the musculature of the body as a whole rather than with individual muscles. This concept was the dominating influence in cerebellar physiology for more than forty years.

During the last decade of the nineteenth century a new approach toward an understanding of the organ was begun by studies on its comparative anatomy and its embryonic development. The first article to appear in the *Journal of Comparative Neurology* was a comparative paper on the cerebellum by C. L. Herrick (1891).

There have been many attempts in the past to characterize the essential function of the cerebellum, of which the one by C. J. Herrick (1924b; the two Herricks were brothers) can serve as an example:

> The cerebellum is primarily the balancing brain, controlling posture, regulating and coordinating all movements of precision of the skeletal musculature, and maintaining muscular tone. Its stabilizing influence may be compared with the action of a gyroscope on a large steamship, ensuring the steady progress of the vessel in its course by compensating the buffeting of wind and waves. The role of the cerebellum is that of proprioceptive adjustor.

According to Dow and Moruzzi (1958 p. 4), it was Flourens (1824, 1842) who introduced the concept of the function of the cerebellum as coordinating movements. Thus, after cerebellar ablation, the possibility of executing movements remained, but the coordination of these movements was lost.

1.2. The Cerebellum at Present

Ito (1984) published a magnificent, comprehensive, treatment of the cerebellum, which was preceded by that of Eccles, Ito, and Szentágothai (1967), and before that, by the book of Dow and Moruzzi (1958). Subsequently, a vast additional literature on the cerebellum has emerged and continues to appear, seemingly at an ever-increasing rate. For example, eight full papers, 43 open peer commentaries, and the responses to the latter by the authors of the full papers, under the general topic, "Controversies in neuroscience IV: Motor learning and synaptic plasticity in the cerebellum" (Bell, Cordo, and Harnad 1996), are included in the September 1966 issue of *Behavioral and Brain Sciences* (Vol. 19, No. 3). Two issues of *Learning and Memory* (Vol. 3, No. 6, and Vol. 4, No. 1) were devoted to the cerebellum as were paired issues of

Trends in Neurosciences (Vol. 21, No. 9, Sept. 1998), and *Trends in Cognitive Sciences* (Vol. 2, No. 9, Sept. 1998). In an interesting short autobiographical note, Ito (1999) briefly traced the history of the discovery of the inhibitory action of the cerebellum, the evolution of the concept of synaptic plasticity, and its demonstration experimentally.

1.3. The Perspective of This Book

The present work, the focus of which is the question of the cerebellum as an adaptive controller, has a relatively narrow perspective. Correspondingly, in the background to this main theme, only the most directly relevant aspects are considered, for the most part. In no way is a comprehensive treatment of the cerebellum intended or attempted. Some repetition can be found; this is partly intentional, to emphasize important points, and partly unintentional.

In Part I (Anatomy and Physiology of the Cerebellar System – a term used here to include the cerebellum itself, its nuclei, and the inferior olive), a brief treatment of the evolutionary or comparative anatomical aspects (Chapter 2) of the cerebellum is given. In the chapter on anatomy and physiology of the cerebellar cortex itself (Chapter 3), somewhat greater emphasis is placed on the former than on the latter. In subsequent chapters, emphasis is placed on those connections and components of the cerebellar system that appear to be of particular importance in relation to the question of cerebellar mechanisms (e.g., the mossy fibers; Chapter 4), the inferior olive and associated climbing fibers (e.g., the mossy fiber and climbing fibers constituting the major input systems to the cerebellar cortex; Chapter 5), the cerebellar nuclei (Chapter 6), which together with the vestibular nuclei constitute the output system of the cerebellar cortex, and the nucleocortical and nucleo-olivary pathways (Chapter 6).

In Part II (Cerebellar Functions), limited aspects of cerebellar mechanisms are discussed, including synaptic plasticity (Chapter 7) as a specific mechanism of cerebellar adaptability (adaptive control), the vestibulocerebellum (Chapter 8) as the simplest form of cerebellar function, cognition and imaging studies (Chapter 9), and conditioning and timing (Chapter 10). To include human disease in the survey of actual or presumed cerebellar function, aspects of cerebellar pathology and pathophysiology and their clinical manifestation are included (Chapter 11). Specialized cerebellar-like structures in certain fish (i.e., the valvula and the electroreceptive lateral lobe and the mammalian dorsal cochlear nucleus), which are found in these animal groups in addition to a true cerebellum, are included (Chapter 12) because of their resemblance in certain respects to the cerebellum itself, even if the functions of these organs and their relationship to the cerebellum remains unclear in part.

In Part III (Models and Theories), as background to the consideration of adaptive control models of the cerebellum, a relatively limited survey of a number of nonadaptive theories and models (the two terms are used more or less interchangeably) of cerebellar function are discussed (Chapter 13). A review of the closely related topics of adaptive control and neural nets (Chapter 14) follows. Several specific features of adaptive controllers are next illustrated in an adaptive controller (adaptive signal processor) of the author's own design and construction (Chapter 15). A survey of several adaptive control models of the cerebellum then follows (Chapter 16).

In Part IV (Summary and Conclusions), a selective recapitulation of material in earlier chapters is presented, together with a detailed comparison between an adaptive signal processor and the vestibulo-ocular reflex as an example of the operation of the cerebellar system (Chapter 17). Some remaining questions are also discussed. In sum, the marshalled evidence that the cerebellum can be considered at least in part as an adaptive controller appears to be very strong. At the same time, however, the cerebellar system itself appears to lack the capability of true prediction, for which a specific time mechanism would be required. The site of the latter capability, perhaps distributed in location, remains unclear.