Our Wonderful Cerebellum

An Insight into the Organ of Tomorrow

prepared for

6.891: Cognition and Embodiment

by

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on

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"Precise and concise... how many more cises could you want?"
—*Purkinje Press Review*

"Always tangy, never tart...
I love it!"
—Emilio Lugaro
Little Venice Daily Reader

"A gem."
—Woodrow P. Ecker
AMAZING Magazine

Contents

List of Figures

Chapter 1

Cerebellum ≡ Goodness

This paper is a very basic account of the cerebellum, the human cerebellum in particular. It is certainly not intended to be a classical tome on neurophysiology; rather, it is a convenient starting place for anyone who, like myself, knows little neuroscience but wants to get some insight into the workings of the cerebellum. My personal reason for writing this paper (aside from capping off a thoroughly rewarding second semester of graduate school) is to get a jump start on my own master's thesis research. I am thinking of designing a cerebellar control system for Cog[1], and I figured it would be good to know just what the cerebellum does before I get started.

Introduction

For those readers who are completely new to the field of neuroscience, the cerebellum is a part of the brain. It is found in all vertebrates, somewhere between the top of the brain stem and the base of the cerebrum. The size and outward structure varies considerably between species, but all cerebellums have similar neural structures and functions.

In man, the universally recognized cerebellar functions are all related to motor control, although some current research gives evidence of sensory and cognitive roles as well (see Section 3.2). The view of the cerebellum as a motor control system is for the most part due to the pioneering work of Holmes (1917), who carefully catalogued the effects of gunshot wounds to the heads of soldiers in World War I. Fifty years later, (Eccles et al. 1967) published their similarly complete account of cerebellar physiology.

Classical Clinical Effects of Cerebellar Dysfunction

The cerebellum is usually viewed as a motor subsystem because cerebellar lesions and deficits have a multitude of obvious effects on motor performance. Unlike damage to the cerebral motor cortex, damage to the cerebellum does not prevent voluntary activity, but rather reduces its quality. This is traditionally attributed to a release of motor pathways from supervisory control after damage occurs. Hence, many cerebellar dysfunctions are marked by excessive, undesired motion.

Lesions of the archicerebellum and paleocerebellum, the evolutionarily oldest portions of the cerebellum, produce a loss of posture: reduced muscle tone in the trunk and neck, or a staggering, drunken gait.

Lesions of the neocerebellum, the newer region of the cerebellum, yield a number of complex motor deficits (Dichgans & Diener 1985):

- diminished tendon reflexes (*hypotonia*)
- weak, easily tired muscles (*asthenia*, attributed to inefficient muscular control)
- decomposition of movements into component parts
- inability to gauge distance of movements correctly (*dysmetria*)

[1] The first of several humanoid robots envisioned by Professor Rodney Brooks of the MIT Artificial Intelligence Lab.

- inability to perform smooth alternating, repetitive movements (*dysdiadochokinesia*)
- oscillation in voluntary motion (*intention tremor*)
- ataxic gait (drunken walk; note that the cerebellum is sensitive to alcohol)
- slow, explosive, slurred speech (*scanning speech*)

The dysfunctions due to partial damage of the cerebellar cortex usually get better as time goes on, lending credence to theories of cerebellar plasticity. Damage to the deep, inner regions of the cerebellum, however, is never undone.

Chapter 2

Basic Cerebellar Physiology

2.1 Macroscopic Structure

The human cerebellum is a deeply folded cue ball of neurons hanging off the back of the brain at the junction between the brainstem and the cerebrum (Figure 2.1). The cerebellum is connected to the rest of the brain via three *peduncles*, or pillars of nerves, which join to the medulla, pons, and thalamus.

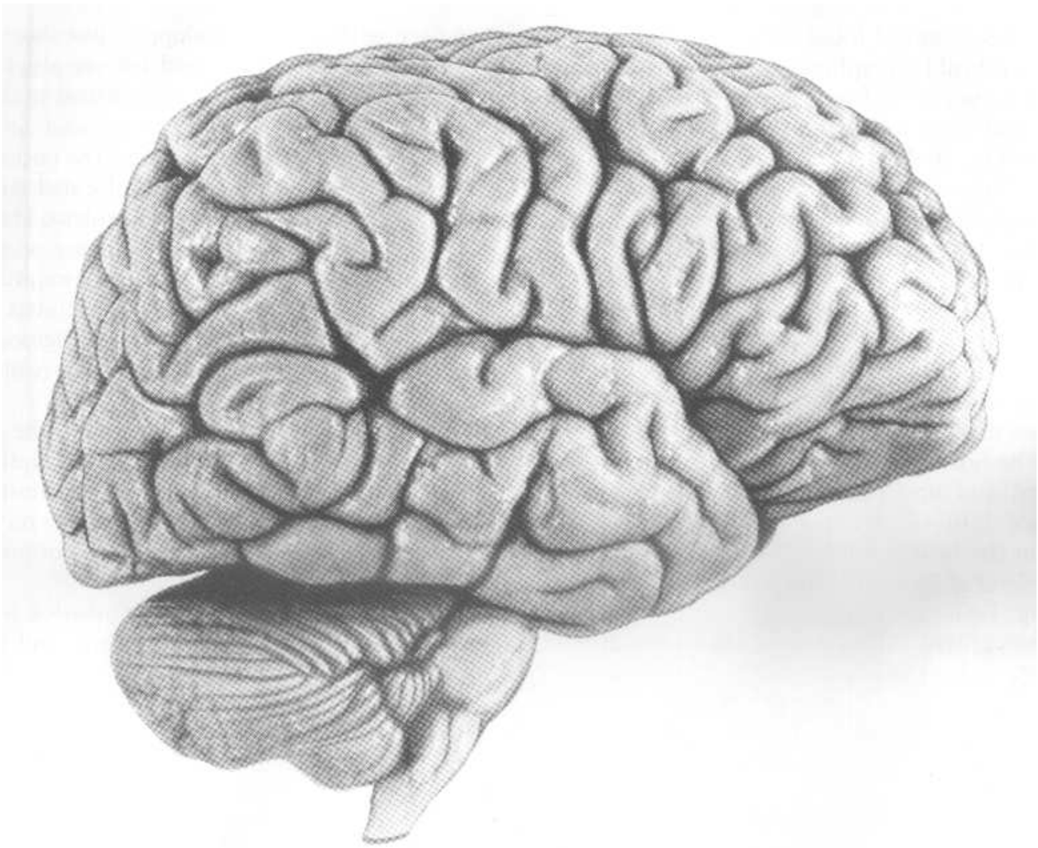

Figure 2.1: Sagittal view of the brain. The cerebellum is the more finely folded structure in the lower left (Noback 1981, p.3).

Like the cerebrum, the cerebellum has a *medulla* of white matter covered by a thin, folded *cortex* of gray matter. However, unlike the cerebrum, the cerebellar cortex is connected across the midline; there is no fissure between the hemispheres.

The cerebellar medulla contains four pairs of *deep cerebellar nuclei* (DCN) —fastigial, emboliform, globose, and dentate— which serve as the clearinghouse between the cerebellum and the rest of the brain. Except for connections to the vestibular nuclei, there are no direct output connections between the cerebellar cortex and the cerebrum or the brainstem.

2.1.1 Divisions of the Cerebellum

The unfolded cerebellum is commonly divided into several sagittal (vertical) and transverse (horizontal) sections (Noback 1981, p.322f). (Refer to Figure 2.2.)

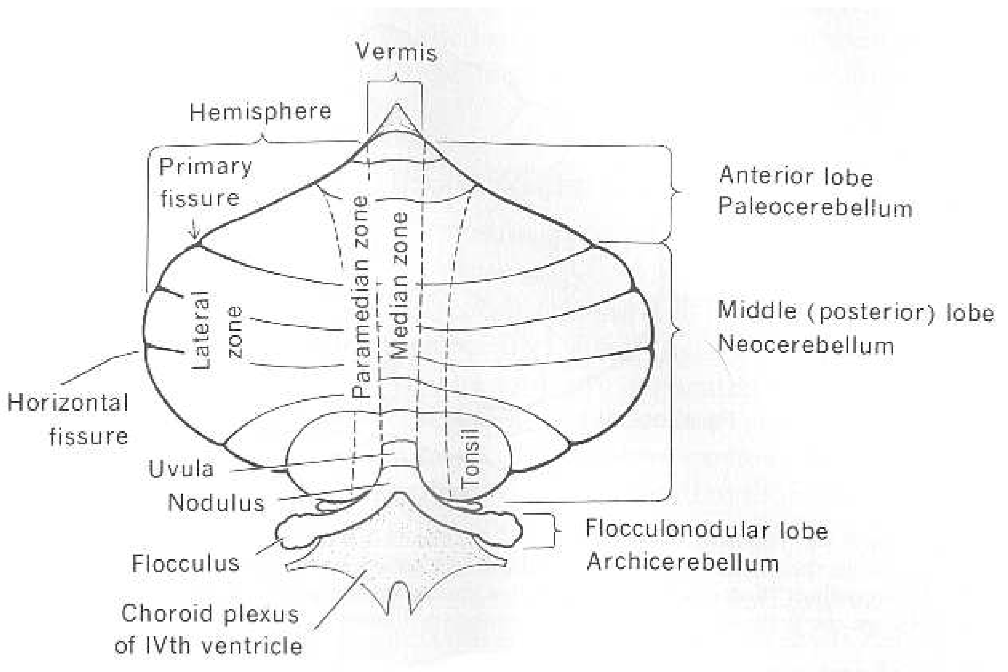

Figure 2.2: Sagittal and transverse division of the unfolded cerebellum (Noback 1981, p.323).

Sagittal Divisions

The cerebellum has three major sagittal divisions: median, paramedian, and lateral.

The median zone contains the *vermis*, the strip of cortex which joins the two hemispheres. The vermis connects to the vestibular and fastigial DCN, and is known to be involved with automatic motor actions, such as balance, gait, and the vestibulo-ocular response (VOR).

The paramedian zone is the border region between the vermis and the hemispheres. It projects to the emboliform and globose nuclei, and influences other automatic actions, such as posture and stance.

The lateral zone, comprising the two hemispheres, is the largest portion of the human cerebellum. Through the dentate nucleus, the hemispheres send and receive signals to and from the medulla, thalamus, and red nucleus. The lateral zone influences voluntary, complex motor skills, although the exact nature of that influence is an open question.

Transverse Divisions

The cerebellum is also divided into three major transverse divisions: archicerebellum, paleocerebellum, and neocerebellum.

The archicerebellum, also referred to as the *flocculonodular lobe*, is evolutionarily the oldest part of the cerebellum. This section has direct connections to the vestibular apparatus, and as such it is devoted to vestibular reflexes, balance, and posture.

The paleocerebellum, also an old section, is involved in the regulation of various forms of muscle tone.

The neocerebellum is the newest portion of the cerebellum, on an evolutionary par with the cerebral neocortex. It receives input from all of the senses and is known to be necessary for the coordination of fine motor skills. This is the portion of the cerebellum that may also contribute to cognitive skills.

2.1.2 Cerebellar Cortex

The cerebellar cortex comprises the outermost $1mm$ of the cerebellar surface. This surface is deeply folded, first into *lobes*, then smaller *lobules*, then *sublobules*, and finally into *folia* (see Figure 2.3). All of the folds and resulting folia run horizontally, parallel to each other (Fahle & Braitenberg 1985, p.186); unfolded, the cortex is actually a strip of tissue measuring approximately $15cm \times 100cm$. This strip is so deeply folded that only 15 percent of it is exposed to the outer surface.

In fact, although the cerebellar cortex contains only 10 percent of the brain by weight, its area ($> 100,000mm^2$) is a full three-quarters of the area of the cerebral cortex (Noback 1981, p.325). In addition, the cerebellar cortex contains nearly half of the total number of neurons in the brain (Keeler 1990, p.396).

The cerebellar cortex is composed of six types of unmyelinated neurons: Purkinje, granule, basket, stellate, Golgi, and Lugaro (see Section 2.2). These neurons are arranged in a uniform geometric structure not found anywhere else in the brain. Inputs to the cortex come from the *mossy fibers* and *climbing fibers*, axons which project up from nuclei in the brainstem and spinal cord. The output of the cortex is provided solely by the Purkinje cells, which project back to the deep cerebellar nuclei and to the vestibular nuclei.

2.2 Microscopic Structure

The cerebellar cortex has an amazingly regular microscopic structure, a structure found in the cerebellums all vertebrates. The cortex is divided into three layers, determined by the cell bodies which each contains. The *inner* or *granule layer* ($200 - 300\mu m$ thick) contains the granule cells and the axon terminations of the mossy fibers. The *middle* or *Purkinje cell layer* contains the Purkinje cell bodies. The *outer* or *molecular layer* ($\sim 400\mu m$ thick) contains the stellate and basket cells, as well as the axonal network of the granule cells. Throughout the cortex, these fibers and cells are interconnected as shown in Figure 2.4.

2.2.1 Mossy Fibers

Mossy fibers are axons from neurons in spinal and brainstem nuclei; they form the primary input path to the cerebellar cortex. As each fiber enters a folium, it branches in a plane parallel to the long axis of the folium, yielding around 16 terminals. These terminals are called *rosettes*, and each rosette is the centerpiece of a *glomerulus*, or "island." A glomerulus is composed of a rosette surrounded by ~ 25 granule cell dendrites and a few Golgi cell axons (Chauvet 1986, p.202).

The mossy fibers form excitatory synapses with the granule cell dendrites. Mossy fibers also have collateral branches which synapse with Golgi cell bodies, and which terminate in the DCN.

2.2.2 Granule Cells

The granule cells are the smallest and most numerous cells in the cerebellar cortex: each cell is $5 - 8\mu m$ in diameter and there are an estimated total of $10^{10} - 10^{11}$ such cells in the cortex (Ito 1984, p.74). Granule cells have $2-7$ dendrites apiece, which terminate at separate glomeruli in the granular layer, and thus receive input from mossy fibers and Golgi cells.

Figure 2.3: Sagittal section of the cerebellum, through the midline. Folding down to the level of lobules is visible. Note the thinness of the white matter, and the continuity of the cerebellum through the midline (Noback 1981, p.9).

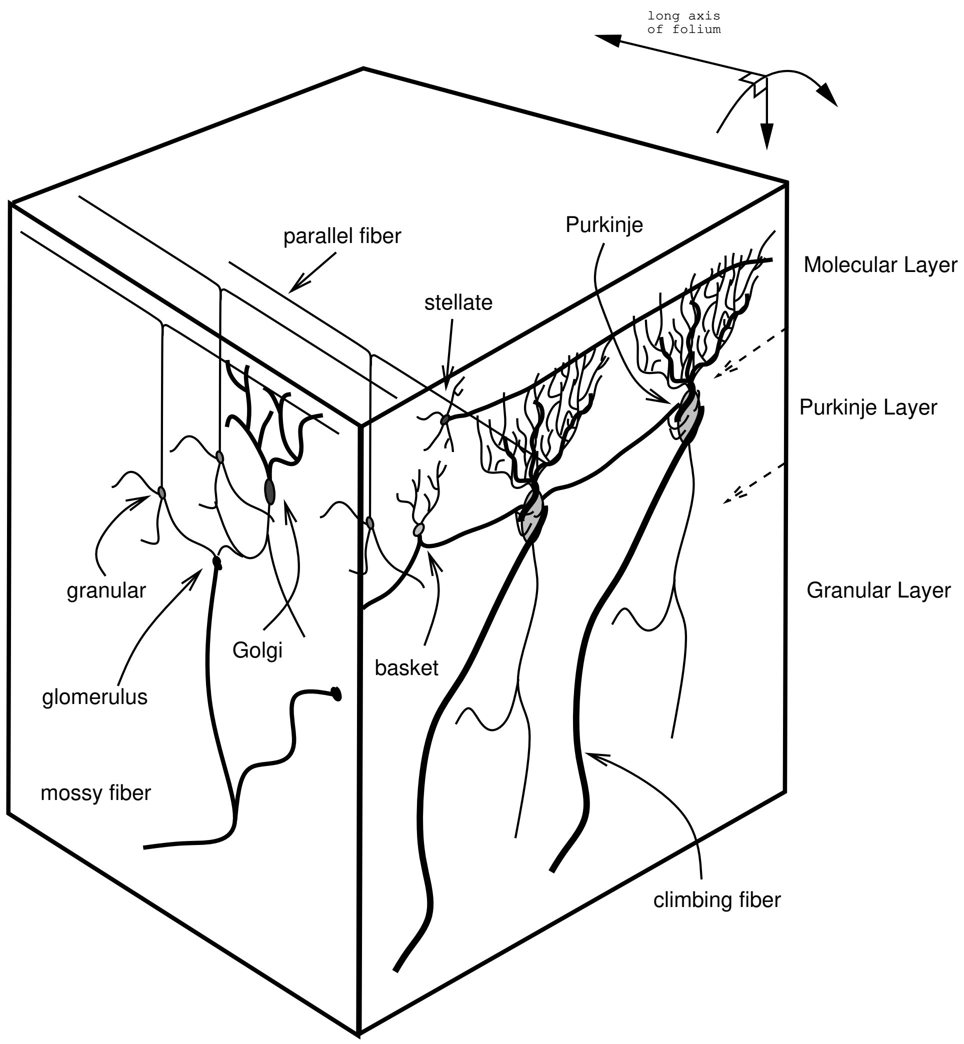

Figure 2.4: Neural connections in the cerebellar cortex. Note that parallel fibers are perpendicular to Purkinje dendritic fans and stellate cell axons.

The unmyelinated axon of a granule cell projects radially through the middle layer of the cortex into the molecular layer, where it bifurcates into a "T" parallel to the long axis of the folium, forming a *parallel fiber*. Each fiber is $\sim 2mm$ long and runs parallel to the others and to the plane of the molecular layer. These fibers form excitatory synapses with Purkinje cell dendrites *en passant* (that is, at intervals along the fiber as well as its end). The parallel fibers also form synapses with the dendrites of stellate, basket, and Golgi cells in the molecular layer.

Granule cells are the only excitatory neurons native to the cerebellar cortex.

2.2.3 Purkinje Cells

Purkinje cells are the large ($21 - 40\mu m$ long) pear-shaped output neurons of the cerebellar cortex. All of the Purkinje cell bodies lie in a single sheet, one cell thick — the middle layer. There are approximately 15 million Purkinje cells in the human cerebellum, one for every $3000 - 9000$ granule cells (Ito 1984, p.21,p.74).

Purkinje cell axons descend into the white matter where they have an inhibitory effect on DCN neurons mediated by γ-aminobutyric acid (GABA).[1] Each axon contacts about 35 nuclear cells. The axons also always have collaterals which ascend back from the white matter into the middle layer to synapse with stellate, basket, Golgi, and other Purkinje cells.

The dendrites of Purkinje cells extend outward into the molecular layer where they branch into a fan ($\sim 350 \times 350 \times 35\mu m$) perpendicular to the long axis of the folium (*i.e.* perpendicular to the parallel fibers). Roughly 300,000 parallel fibers pass through the dendritic tree of each Purkinje cell, although only $60,000 - 120,000$ form synapses. Viewed from the other side, each parallel fiber passes through ~ 500 dendritic planes, but forms only ~ 45 synapses. The synapses are formed by spiny projections on the Purkinje cell dendrites which contact the passing parallel fibers.

Purkinje cells are unusual in that the dendrites have local action potentials: stimuli to dendrites are summed at branch points and generate thresholded "baby action potentials" (Noback 1981, p.326) which then travel down to further branch points. The dendrites have considerable internal structure, and in some sense act like networks of neurons in themselves.

2.2.4 Climbing Fibers

Climbing fibers, like mossy fibers, are input axons originating in cells in the spinal and brainstem nuclei. However, in mammals, climbing fibers originate exclusively from a brainstem structure called the inferior olivary nuclei.

Climbing fibers are unique to the cerebellum. Every Purkinje cell has a single climbing fiber which wraps around its cell body and branches out into its dendritic fan. These fibers have a powerful direct excitatory effect on the Purkinje cells. Because of the 1-1 map of Purkinje cells to climbing fibers, these fibers are often championed as being the mediators of synaptic plasticity and programming in the Purkinje cells (see Section 3.1.2). Climbing fibers are also often associated with long-term changes in the cerebellum because their spontaneous activity is at the rate of $1 - 3Hz$, which seems to be too slow to contribute to immediate motor coordination.

Each climbing fiber branches out and contacts about 15 Purkinje cells, and also sends collaterals to Golgi and Lugaro cell bodies, as well as to granule cell dendrites (in the form of climbing fiber glomeruli).

2.2.5 Golgi Cells

Golgi cells are interneurons which reside in the granular layer. They receive input from parallel fibers, climbing fibers, and Purkinje cell collaterals, and send an inhibitory output to thousands of glomeruli. The general view is that Golgi cells serve as a feedback loop to modulate granule cell excitation (Keeler 1990). They may also have a role in restructuring the synapses between mossy fibers and granule dendrites (Chauvet 1986).

[1] As a matter of fact, all of the inhibitory synapses in the cortex appear to be mediated by GABA.

2.2.6 Basket and Stellate Cells

Basket and stellate cells are similar in form and function. Both are inhibitory interneurons with cell bodies in the molecular layer which receive input from climbing fibers, parallel fibers, and Purkinje collaterals. The dendrites and axons of these cells project across the cortex perpendicular to the long axis of the folium.

Axons of both cells synapse with Purkinje dendrites, but basket cells also have arborizations around Purkinje cell bodies in the form of a basket-like structures of 50 or so axons (hence the name). Each basket cell forms baskets with $8-9$ Purkinje cell bodies, in a line perpendicular to the parallel fibers.

Incidentally, basket cells are found exclusively in birds and mammals (Ito 1984, p.108).

2.2.7 Lugaro Cells

Lugaro cells are found sparsely in the granular layer, near the middle layer. They have elongated cell bodies, they receive input from Purkinje collaterals along horizontal dendrites, and they have axons which extend mostly horizontally in the molecular layer. Other than that, no one is sure of what they do.

That last statement actually does a fair job of summarizing the entire cerebellar cortex. Even though the cortex has a well-known regular, three-dimensional structure, the meaning and intent of this structure is still the subject of speculation. A lot of this speculation comes from computer scientists, mathematicians, and physicists who are attracted to the cerebellum by the relative simplicity and accessibility of its cortical topology. However, the cerebellar cortex contains many significant complexities, such as the sophistication of Purkinje cell dendrites, or even just the sheer number of neurons in the network.

Chapter 3

Theories of Cerebellar Function

Although the structure of the cerebellum has come to be very well-understood over the past thirty years, researchers are still at a loss in trying to explain how that structure implements cerebellar functions. In fact, researchers still don't fully understand what those functions are.

In this chapter I will touch on some aspects of the question "What does the cerebellum do, and how does it do it?" There are roughly two camps of thought on this issue: those who think of the cerebellum as a sophisticated motor controller, and those who think of it as something more.

3.1 Traditional Approaches

The traditional approach is to view the cerebellum as a sophisticated control subsystem which mediates the body's motor activities. The cerebellum does not instigate actions, but takes motor commands from the cerebral cortex and translates them into smooth, efficient motor programs for the musculature.

This approach is motivated by the clinical definitions of cerebellar dysfunction. The obvious and well-recognized behavioral deficits due to damage to the cerebellum are all motor control problems. Following the standard (and arguably simplistic) line of reasoning of lesion studies, if motor control breaks down when the cerebellum breaks down, then the cerebellum must do motor control.

The theories of how the cerebellum accomplishes this control have become much more sophisticated over the decades. Stein (1986) points out that these theories tend to track the latest innovations in control theory:

> ...in the early nineteenth century the cerebellum was thought to be a voltaic battery; in the early 1900s it became a proprioceptive telephone exchange; in the 1950s it was a collection of transistor delay lines; and today it is a computer.

Indeed, most of today's theories model the cerebellum as some type of adaptive neural network controller which forms extensive feedback and feedforward control loops between the cerebrum and the brainstem. This is the current state of the art in electromechanical controllers.

3.1.1 Three Modes of Interaction

Assuming that the cerebellum is a sophisticated motor controller, it must fit into the motor control pathways of the brain somewhere. Ito (1984, pp.326-331) discusses three possible modes of interaction between the cerebellum and the rest of the brain's motor areas: the side-path, loop, and lateral interaction models.

Side-Path

In the side-path model, the cerebrum provides direct, primary control of a motor pathway (G_1 in Figure 3.1). However, the cerebellum monitors motor commands, and adds its own contribution (S) to the signal sent to the brain stem. The motor output is $T = (G_1 - S)G_2$, the result of the raw motor command embellished or corrected by the cerebellum.

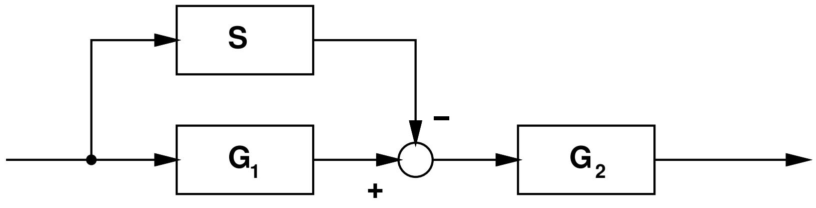

Figure 3.1: Basic side-path control system.

The VOR is a classic example of side-path interaction. Between the vestibular apparatus and the eye muscles is a short (few neuron) reflex arc which causes your eyes to keep pointing toward the same target when you turn your head. A side-path connection joining the flocculus of the cerebellum to the vestibular apparatus and the vestibular nuclei modulates this reflex, keeping it precise in lieu of changes in the ocular musculature or vestibular senses.

Note that side-path control is a feedforward system; the cerebellum may correct a motor command, but it does so without direct knowledge of the final effect.

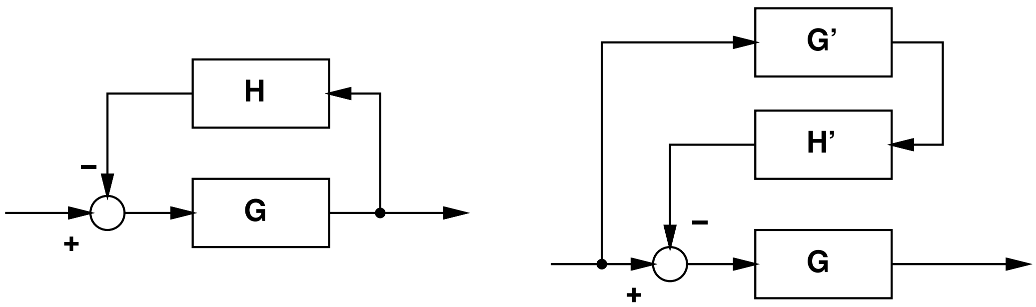

Figure 3.2: Two loop control systems: closed-loop (*left*), and closed-loop simulator (*right*).

Loop

In the typical closed loop system of Figure 3.2(left), the cerebellum resides somewhere in H, the feedback path between motor output (perhaps through the real world and some sensory input), and the motor cortex. This is the standard closed-loop controller which budding electrical engineers are familiar with. Closed loops like this have been found in the brain. For example, there are known connections from motor cortex to the pontine nuclei, to the *pars intermedia* of the cerebellum, to thalamus, and back to the motor cortex.

An interesting variation on loop control is shown in Figure 3.2(right). This is an open-loop system, *i.e.* no feedback from the outside world, in which the cerebellum produces G' and H'. If the cerebellum can be trained so that G' and H' approximate G and H —that is, so that the cerebellum models both the motor control circuitry and feedback from the real-world— then this open-loop design will simulate the standard closed-loop design. The advantage to this is that a quick simulation loop could replace a slower real feedback path, especially if the real path involves a complex sensory modality such as vision.

Lateral Interaction

The lateral interaction model (Figure 3.3) captures the idea that a part of the cerebellum in some control path A may inject a signal into another control path B to compensate for some effect caused by A. An

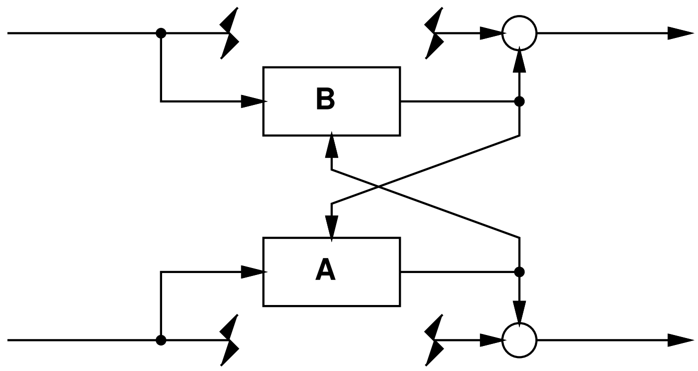

Figure 3.3: Lateral-interaction control.

example would be to cancel out the sensory feedback to one motor center resulting from unrelated movement caused by another motor center.

Out of the motor control pathways traced through the cerebellum up to now, the side-path mode of interaction appears to be the most prevalent. Side-path models also reflect the notion that the cerebellum is not required for movement, but does make it smooth and precise.

3.1.2 Motor Learning and Cerebellar Plasticity

The first two "modern" theories of the cerebellum were the very similar neural network models of Marr (1969) and Albus (1971). Both of these models used a three-layer network of perceptrons which roughly resembled the cerebellar circuitry: mossy input fibers, granule association cells, and Purkinje output cells. These networks acted as associative memory systems which translated patterns of sensory input into coordinated (or rather, coordinat*ing*) motor-domain outputs (Keeler 1990).

Marr introduced the concept of a codon representation by the granule cells. Although each mossy fiber synapses with many granule cells, each granule cell synapses with around five mossy fibers. Marr suggested that if a granule cell required some minimum number of mossy fiber inputs for activation, then those mossy fibers would form a *codon*, or coded input, to the granule cell. If several groups of mossy fibers fire at once, it is easier to separate the groups if they are coded by sets of multiple fibers. Keeler (1990) notes that a codon representation has the effect of decomposing a high-dimensional input space into a covering by many low-dimensional slices.

In the Marr and Albus models, the "weights" between granule and Purkinje cells were programmed by some mechanism which implemented a Hebbian learning principle, presumably by modifying the synapses between parallel fibers and Purkinje dendrites.[1] This learning was to be mediated by the climbing fibers, which have a special $1-1$ relationship with the Purkinje cells.

Evidence of such cerebellar plasticity did not come forth for over a decade, and even now the mechanisms behind it are not understood. Stein (1986) suggests that complex spike patterns produced on a climbing fiber serve to directly program which parallel fibers a Purkinje cell will be sensitive to. Strata (1985) presents a theory that the climbing fibers may transport some crucial substance directly to sites on the Purkinje dendrites. He notes that a complete lesion of the inferior olive, the source of the climbing fibers, results in severe degeneration of Purkinje dendritic fans, but no such effect occurs when only the electrical activity of the olive is halted.

[1] The primary difference between the two models was simply that Marr rewarded Purkinje cells for correct output, and Albus punished Purkinje cells for incorrect output.

3.2 Contemporary Alternatives

Within the last decade, several theories of cerebellar function have surfaced (and resurfaced) which grant the cerebellum a greater role in the function of the brain than just motor control. These theories suggest that the cerebellum may be a more general-purpose mechanism, which aids in sensory and cognitive activities as well as motor activities.

3.2.1 Cerebellum as a Predictive Modeler or Tracking System

Perhaps the cerebellum is more than just a Marr-Albus retrieval service for libraries of motor commands. Keeler (1990) makes the claim that the cerebellum performs predictive state modeling. He shows how the three-layer neural network topologies proposed by Marr and Albus can be used to predict trajectories in a high-dimensional phase space.

Paulin (1993) posits that the cerebellum may in fact be a sophisticated motion tracking system which has the actual function of modeling internal and external dynamics. He points out that the same body of evidence which supports the theory that the cerebellum is a motor controller also supports the theory of the cerebellum as a dynamic systems modeler which happens to feed some of its results to the motor pathways.

Paulin shows this is plausible by comparing cerebellar morphology and function in several classes of vertebrates. The weakly electric Mormyrid fish, which use electrolocation, have relatively huge cerebellums, yet they have very simple motor activities. Activity in the enlarged portions of the mormyrid cerebellum has been tied to electrodetection of external stimuli. Also, the electrosensory system in the mormyrids bears a histological and structural resemblance to the cerebellum; developmentally, they are probably offshoots of the same system. In a similar vein, the platypus, with an electrosensitive beak, also has an enlargement of its cerebellum, which is connected to rich sensory input from the beak.

Both insect-feeding bats and dolphins have similar highly-developed lobules in the cerebellum which bare no particular relation to either the wings or the fins (important motor outputs), but rather to the auditory system. These lobules are smaller in species of bats and cetaceans which do not rely as extensively on echolocation.

Finally, Paulin notes that expanded parts of the cerebellum in primates (including man) are related to the hands, which not only perform complex mechanical tasks, but also receive rich tactile sensory input.

There are many more cases of species in which the rich sensory inervation of the cerebellum is not explained by a motor control theory. Paulin suggests that the true role of the cerebellum may be similar to a Kalman filter —a mechanism which tracks, encodes, and predicts the states of dynamic systems. This operation may be used to model limb dynamics for motion control, or to decode and extract spatial information from complex sensory data.

3.2.2 Cerebellum as a Cognitive Mechanism

Only in the last decade have researchers begun to put a concerted effort into exploring cerebellar activity which is not directly related to motor skills. Daum et al. (1993) cites several reports which connect cerebellar damage to:

- impairments in visuo-spatial recall and manipulation in three dimensions
- changes in visuo-spatial organization ability
- deficits in anticipatory planning
- deficits in verbal learning,

She also describes her own experiment, in which she tested patients with cerebellar damage for deficiencies in a couple of perceptual and cognitive skills (mirror-reading of words and the Tower of Hanoi puzzle). However, she contends that her own study was inconclusive.

A recent study by Akshoomoff & Courchesne (1992) shows that the neocerebellum is involved in shifting attention between sensory modalities. In their experiment, patients with neocerebellar damage were given two skill tests, in which they viewed a computer screen showing a small red or green square, and listened to a $1kHz$ or $2kHz$ tone. For the first test, subjects were told to respond to a change in color of the square, but not a change in pitch of the tone. For the second test, subjects were told to respond to a change in color, then respond to the following change in pitch, alternating pitch and color as the session went on.

The first set of trials measured a subject's ability to focus and hold attention on one sensory modality; the second tested the ability to shift attention from one modality to the other. The results showed that both the experimental group and a control group fared equally well at the focusing task. However, the experimental group showed a significant impairment in shifting attention if the new stimulus came less than 2.5 seconds after the cue to shift (the first stimulus). This impairment was not due to poor motor skills: the only motor skill involved was pressing a button, and the mean difference in reaction time was only $77ms$ between control and test groups. The subjects with cerebellar damage actually missed their cues.

The results of this experiment are odd in that they point to a function of the cerebellum which is not involved in motor control, nor particularly involved in spatio-temporal modeling. But, this function *is* related to modulation of sensory input.

Chapter 4

Cerebellum $\equiv$ Enigma

What does the cerebellum do, and how does it do it?

This paper barely scratches the surface of that question, but I hope that it has provided an intriguing glimpse into the intricacies involved. My own hunch is that such a large and evolutionarily old part of the brain must be involved in more than just motor control. That might be the human cerebellum's most significant function, but there could easily be many other sublime cognitive and subcognitive functions which have been missed up to now simply because no one has looked for them.

Suggestions For Further Reading

(Eccles et al. 1967) is the seminal work on the physiology of the cerebellum. (Marr 1969) and (Albus 1971) are classic papers from the computational side of the field. (Ito 1984) is a heavy book, pretty much everything you always wanted to know about the cerebellum, up to 1984.

I find (Paulin 1993) and (Akshoomoff & Courchesne 1992), and related works which they cite, to be the most intriguing.

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