Pseudocerebellum

Pentti Kanerva, Jeff Teeters, Bruno Olshausen

Nov 03, 2021

CONTENTS:

| 1 | About the Pseudocerebellum project | 3 | | | | |
|---|---|------|--|--|--|--|
| | 1.1 Synopsis | . 3 | | | | |
| | 1.2 Why the Cerebellum? | . 3 | | | | |
| | 1.3 Models of the Cerebellum | . 4 | | | | |
| | 1.4 Computing with Vectors | . 5 | | | | |
| | 1.5 The Pseudocerebellum Project | . 5 | | | | |
| | 1.6 Looking to Be Efficient | . 5 | | | | |
| | 1.7 Digital Implementation | . 6 | | | | |
| | 1.8 Resources | . 6 | | | | |
| 2 | ORGANIZING THE WEBSITE | 9 | | | | |
| 3 | Abbreviations | 11 | | | | |
| 4 | Tables | 13 | | | | |
| | 4.1 Cell counts in different species | . 13 | | | | |
| | 4.2 Cells and connections in cat | . 13 | | | | |
| | 4.3 Cell and fiber counts in human from TomaschJ-1968 | . 14 | | | | |
| 5 | Properties | 17 | | | | |
| | 5.1 Connections to / from the cerebellum | . 17 | | | | |
| | 5.2 Microcircuit of Cerebellar cortex | . 21 | | | | |
| | 5.3 Cell counts in cortical loop | . 23 | | | | |
| 6 | Data | 25 | | | | |
| | 6.1 Mossy Fibers | . 25 | | | | |
| | 6.2 Glomeruli | . 27 | | | | |
| | 6.3 Granule | . 29 | | | | |
| | 6.4 Golgi cells | . 32 | | | | |
| | 6.5 Stellate | . 33 | | | | |
| | 6.6 Basket cells | . 34 | | | | |
| | 6.7 Purkinje | . 37 | | | | |
| | 6.8 Inferior Olive | . 39 | | | | |
| | 6.9 Deep Cerebellar Nuclei | . 41 | | | | |
| 7 | Questions | | | | | |
| | 7.1 How would Loebner fig 2 be changed to take into account more recent data? | . 43 | | | | |
| | 7.2 Anatomy of microzone circuits | . 44 | | | | |
| 8 | Notes | 45 | | | | |

| | 8.1 | AndersonBB+2-1992 - A quantitative study of the human cerebellum with unbiased stereological tech- | | | | |
|-----|-----------------|--|----|--|--|--|
| | 0 7 | niques | 45 | | | |
| | 0.2 | Anna D - Hawkee D 2000 | 40 | | | |
| | 0.5 | Appsx+nawkesk-2009 | 47 | | | |
| | 0.4 | $DimingSO + 4 - 2014 \qquad \dots \qquad $ | 49 | | | |
| | 0.5 | CesanaE+0-2013 | 51 | | | |
| | 8.0 9.7 | DAngeloE+3-2013 | 51 | | | |
| | 8./ | DezeeuwCI+2-2021 | 52 | | | |
| | 8.8 | EcclesJC+2-1967 | 54 | | | |
| | 8.9 | GlicksteinM-200/ | 54 | | | |
| | 8.10 | | 54 | | | |
| | 8.11 | HullC+RegehrWG-2012 | 55 | | | |
| | 8.12 | KorboL+3-1993 | 56 | | | |
| | 8.13 | LangeW-19/5 | 57 | | | |
| | 8.14 | LoebnerEE-1989 | 57 | | | |
| | 8.15 | PalkovitsM+2-1971a | 57 | | | |
| | 8.16 | PalkovitsM+2-1971b | 58 | | | |
| | 8.17 | PalkovitsM+2-1971c | 59 | | | |
| | 8.18 | PalkovitsM+2-1972 | 60 | | | |
| | 8.19 | PalkovitsM+3-1977 | 61 | | | |
| | 8.20 | RahimiA+3-2019 | 62 | | | |
| | 8.21 | RieublandS+2-2014 | 63 | | | |
| | 8.22 | SudhakarSK+8-2017 | 63 | | | |
| | 8.23 | TomaschJ-1968 | 64 | | | |
| | 8.24 | WitterL+4-2016 | 66 | | | |
| 9 | Refer | ences | 69 | | | |
| 10 | Bibliography 71 | | | | | |
| Bil | Sibliography 7. | | | | | |

9

Pentti Kanerva, Jeff Teeters and Bruno Olshausen

pseudocerebellum@berkeley.edu

Editors' note, Oct 11, 2021: This website is under construction, your comments are welcome.

ABOUT THE PSEUDOCEREBELLUM PROJECT

1.1 Synopsis

Our lives depend on remembering a myriad of things learned over a lifetime. Learning and remembering is what brains do, but how? If we understood it in theory, we could begin to build artificial systems with traits somewhat like ours.

The aim of this project is to gather information about the cerebellum that could lead to the engineering of an efficient, high-capacity memory for artificial systems. By "memory" we mean a physical structure for storing information–in the humanities "memory" is something more abstract: a mental state or image recalled from the past. The project is organized around a website that collects and abstracts information about the cerebellum as an associative memory. The website is meant to be a community effort. Ideally, it will build a table with an entry for each neuron type in the cerebellum, its location, the number of neurons of that type, what neurons they connect to with what fan-ins and fan-outs, nature of the connections (excitatory, inhibitory), and firing rate (typical, range). The table is referred to as "Cerebellum Facts." Each "fact" is accompanied by a reference to the source and a page number. Information of this kind was compiled already in the 1980s by Loebner (1989) [LoebnerEE-1989]; see his Figure 2 below. In addition to the "wiring," we want the information to be sufficient for a realistic estimation of the cerebellum's energy use.

In addition to the list of references, the website will include an annotated bibliography, to help viewers navigate the material. The annotations are informal, more like comments. They are written by us who want to participate in the website and are meant to point out particulars about a paper that have struck us as significant and likely to be helpful to others.

1.2 Why the Cerebellum?

The simple answer is its very size: the human cerebellum has many more neurons than the rest of the brain (Llinas, 1975) [LlinasRR-1975]. The cerebellum's importance for motor control was established long ago. We can therefore expect that understanding it will help us build more agile robots. There is increasing evidence that the cerebellum is involved also in mental functions, including language. With its huge numbers of neurons and synapses, the cerebellum would have the capacity to store a lifetime of learning. A relatively simple neural structure with over half the brain's neurons deserves a major role in our models of brain function.

Human and animal memory works by association. Among the brain's circuits, the cerebellum's looks the most like an associative memory. A small number of neuron types is organized in a uniform three-dimensional structure that has been modeled mathematically since Marr's theory of cerebellar cortex (Marr, 1969) [MarrD-1969]. Among mathematical models of the brain's circuits, the cerebellum's is perhaps the most compelling.



Fig. 1: Figure 2 in Loebner (1989) [LoebnerEE-1989].

1.3 Models of the Cerebellum

Three mathematical models of the cerebellum interpret it as an associative memory: Marr's (1969) [MarrD-1969] from a neuroscience point of view, Albus' (1971) [AlbusJS-1971] from an engineering point of view, and Kanerva's (1988) [KanervaP-1988] from computer and cognitive science points of view. All three assign identical functions to two prominent cell types, the Granule Cells and the Purkinje Cells, and to two main kinds of input, the Mossy Fibers and the Climbing Fibers. The mossy fibers bring in information from the rest of the nervous system–they represent the system's sensory state–the granule cells distribute it within the cerebellar cortex, information is stored in the Purkinje-cell synapses with granule-cell axons, the Purkinje cells provide the sole output, and the climbing fibers provide an error signal when the output differs from the desired output. This is known as the Marr-Albus model.

When the cerebellum is viewed as a memory and is compared to the memory of a computer, each granule cell represents a memory location. The contents of a location are along its axon, called the parallel fiber, which intersects multiple Purkinje-cell dendrites that lie in planes perpendicular to the parallel fibers. Climbing fibers are a telltale feature of the circuit, as each Purkinje cell is paired with a single climbing fiber which is ideally situated for "training" the Purkinje cell; see Figs. 1 and 2 of D'Angelo and Casali (2013) [DAngeloE+CasaliS-2013]. See also Kandel, Schwartz & Jessell (2000) Chapter 42 on the cerebellum [KandelER+2-2000] and images that Google returns for "cerebellar circuitry." The layout is basically the same as in the three-dimensional magnetic-core memory of the 1960s.

The cerebellum "memory" differs from computer memory in two important aspects: whereas computer memory is accessed one location at a time, to reach the data specific to that location, a single "read" and "write" action activates multiple locations (granule cells) of the cerebellum. The data are distributed and superposed with other data in the activated locations. The cerebellum differs also from most neural-net models in that granule-cell activation is all-ornone and only a tiny fraction of all possible granule cells is active at once: activation is exceedingly sparse (perhaps one in a 1,000), learning is fast (can take fewer than 10 trials), and the number of modifiable synapses is very large (could be a million millions or more).

Even if the cerebellum were not exactly an associative memory we have envisaged, understanding it as an engineering object can be of value to fields such as robotics. Cerebellum's importance for motor learning and control is undisputed.

1.4 Computing with Vectors

A significant new development in computing began with Plate's Holographic Reduced Representation (HRR) in the 1990s [PlateT-1991]. It addressed the shortcomings of artificial neural systems and rule-based AI, namely, neural nets struggled with compositional structure such as in language, and rule-based AI struggled with statistical learning from data. The new idea is to compute with high-dimensional vectors (e.g., D = 10,000) in a style familiar to us from computing with numbers: the addition and multiplication of vectors produce vectors of the same high dimensionality. The idea is covered thoroughly in the book Holographic Reduced Representation (Plate 2003) [PlateTA-2003], it is summarized in a paper on "hyperdimensional" computing (Kanerva 2009) [KanervaP-2009], and it is also called Vector Symbolic Architecture (VSA; Gayler, 2003) [GaylerRW-2003]. In analog to computing with numbers, computing with high-dimensional vectors, a large "high-D RAM."

1.5 The Pseudocerebellum Project

Building a large associative memory for high-dimensional vectors is a major engineering challenge. Since nature appears to have solved it by evolving the cerebellum, we want to understand its principles of operation, hence the Pseudocerebellum Project. This work was began in the 1980s and was cited above (Loebner, 1989) [LoebnerEE-1989]. It is all the more relevant now, after the advent of computing with high-dimensional vectors.

The project website collects information about the cerebellum starting with neuroanatomy. Where do inputs to the cerebellum come from and in what numbers? Where do outputs go and in what numbers? What connections are internal to the cerebellum, and again in what numbers? How does the circuit vary from one area of the cortex to another? The paper by Loebner serves as a model. It pertains to the the cerebellum of the cat; we want those connections and numbers also for the human brain.

In addition to cerebellum facts and references, the website will have comments written by us highlighting the reasons for including the paper in the website. Please tell us in your comment what caught your attention, what did you learn, what might be helpful for someone else?

1.6 Looking to Be Efficient

We think of autonomous robots as artificial animals with silicon brains-that's what "bio-inspired" often means-and we want robot brains to match real brains in their function and energy efficiency. Computing with high-dimensional vectors is expected to provide some of the functionality, and it relies fundamentally on an associative memory. The activation algorithm has a crucial role in making the memory work.

Activation of the Sparse Distributed Memory (SDM; Kanerva 1988) [KanervaP-1988] requires the computing of Hamming distances between high-dimensional vectors, implying that the granule cells should have hundreds or thousands of inputs when, in fact, they have only 3-6. Two models by Jaeckel (1989a, 1989b) [JaeckelLA-1989a] [JaeckelLA-1989b] deal with this discrepancy, the Selected-Coordinate Design when the high-dimensional cue vectors are dense, and the Hyperplane Design when they are sparse. In both designs a location is activated if its "address" matches the cue in a small subset of coordinates that are specific to the location. Jaeckel's designs should interest engineers by being energy efficient. Of the two, the hyperplane design is closer to the cerebellum's. The point is, when our models imply things not seen in nature, we need to keep on looking for more realistic alternatives.

1.7 Digital Implementation

By digital we mean an ordinary computer. Associative memory can then be realized as a table that stores every vector known to the system. The cue vectors are noisy, and finding the most similar vector or vectors in the table becomes the problem to solve. However, comparing a high-dimensional cue to every vector in the table is practical only when the number of stored vectors is small, and so we need an efficient algorithm for nearest-neighbor search of large data sets. An algorithm by Li and Malik (2017) [LiK+MalikJ-2017] may provide a solution.

Karlsson's (2001) [KarlssonR-2001] Fast Activation Mechanisms is an efficient realization of Jaeckel's selected-coordinate design.

1.8 Resources

1.8.1 Projects and Websites

1. CEREBELLAR PLATFORM is a Japanese collection of references to cerebellar research up to 2018:

https://cerebellum.neuroinf.jp/

2. HUMAN BRAIN PROJECT includes a section on the cerebellum

https://www.humanbrainproject.eu/en/brain-simulation/cerebellum/

They gather information about the cerebellum with the aim of building a biologically faithful simulation (D'Angelo et al., 2016) [DAngeloE+11-2016]. Much of the information is of interest also to us.

3. COGNITIVE CONSILIENCE provides an interactive graphical interface for tracing connections between neurons in different parts of the brain (Solari & Stoner, 2011a,b) [SolariSVH+StonerR-2011a][SolariSVH+StonerR-2011b]

4. CEREBELLAR ATLAS VIEWER displays the activity (functional MRI) of different parts of the cerebellum in a variety of tasks (King et al., 2019a,b) [KingM+4-2019a][KingM+4-2019b].

1.8.2 Review Articles

http://www.scholarpedia.org/article/Cerebellum

1.8.3 Mathematical Models Other than Associative Memory

- Fujita M (1982). Adaptive filter model of the cerebellum. Biological Cybernetics 45(3):195-206. https://doi.org/ 10.1007/BF00336192
- Miyashita Y and Paulin M (1989). A Kalman filter theory of the cerebellum. Dynamic interactions in neural networks. pp. 239-259. Berlin, Heidelberg: Springer-Verlag. https://doi.org/10.1007/978-1-4612-4536-0_15
- Pellionisz A and Llinas R (1980). Tensor approach to the geometry of brain function: Cerebellar coordination metric tensor. Neuroscience 5:1125-1136. https://doi.org/10.1016/0306-4522(80)90191-8

1.8.4 Recent reviews of Associative Memory Models

[KawatoM+3-2021].

ORGANIZING THE WEBSITE

We are new to making a website like this. For collecting, organizing and sharing information over the Internet, we have used Stanford Encyclopedia of Philosophy https://plato.stanford.edu/ as a model, although our effort is small in comparison, and more focused. The data for the "Van Essen Diagram" of the hierarchy of visual areas (Fig. 4 of Felleman & Van Essen, 1991 [FellemanDJ+VanEssenDC-1991]) is another example we have followed, although they emphasize connections between brain areas while we, as circuit designers, are much more concerned with actual numbers. A more recent example, specific to the cerebellum, comes from a collaboration within Europe's Human Brain Project (Table 1 of D'Angelo et al., 2016 [DAngeloE+11-2016]).

We hope to make the website into a useful source of information about the cerebellum that is easy to navigate and to contribute to. It is focused narrowly on the cerebellum as an associative memory. When you have information that you see missing or in need of updating, please pass it on to us for inclusion in the website–email it to

pseudocerebellum@berkeley.edu

We plan to make submitting to the website more automatic as traffic on the website warrants. Your ideas for making the website more effective are welcome.

The pseudocerebellum project is housed at UC Berkeley's Redwood Center for Theoretical Neuroscience and is funded from grants from the Air Force Office of Scientific Research (Engineering and Information Science/Cognitive and Computational Neuroscience) and DARPA Defense Science Office (Artificial Intelligence Exploration/Virtual Intelligence Processing).

CHAPTER

THREE

ABBREVIATIONS

Following are abbreviations used in the data pages about each source (cell or region).

FO - Fan-out (target per source).

FI - Fan-in (source per target)

DCN - Deep Cerebellar Nucleus

Connections - *output* connections

CHAPTER

FOUR

TABLES

This page contains tables of data which may be compiled from multiple sources. The link next to value in each table go to a page giving the source reference.

The following tables are available:

4.1 Cell counts in different species

The following table provides the count of cerebellum cells types in different species.

Values are the number of cells of the given type in the specified species.

| Cell type | Species | | | | |
|-----------------|---------------------|-------------------------|------------------|--|--|
| | human | cat | rat | | |
| purkinje | 30.5 x 10^6 [d1] | 1.25 x 10^6 <i>[p1]</i> | 0.61 x 10^6 [r1] | | |
| golgi | 81.3 x 10^6 [d4] | 417,000 [pb2] | 0.64 x 10^6 [r2] | | |
| grannule | 101,000 x 10^6 [d2] | 2.2 x 10^9 [pb1] | 265 x 10^6 [r3] | | |
| basket | | 7.5 x 10^6 <i>[pb1]</i> | | | |
| stellate | | 20.9x 10^6 [pb2] | | | |
| dentate nucleus | 5.01 x 10^6 [d3] | | | | |

4.2 Cells and connections in cat

The following table provides counts of cells and connections in the cat cerebellum. The first two columns (*Source cell* and *Cell count*) are respectively a cell type and the count (number) of cells of that type. The values in the rest of the table give the number of connections from the Source cell to Target cells. These are specified as a pair of numbers: FO,FI. FO is fan-out (number of target cells each source cell contacts) and FI is fan-in (number of source cells going to each target cell). Data is from Figure 2 in [LoebnerEE-1989].

Values are either a Cell count, or FO,FI where FO is *fan-out* (number of target cells each source cell contacts) and FI is *fan-in* (number of source cells going to each target cell).

| Source cell | Cell | Target cell | | | | | |
|-------------|----------|-------------|-----------|-----------|-------------------|-------------|--------------------|
| | count | basket | golgi | granule | purkinje | stellate | dcn |
| basket | 7.5x10^6 | | | | 9, 50 [b2] | | |
| | [b1] | | | | | | |
| golgi | 4.2x10^5 | | ?, ? [g2] | 5.2x10^3, | | | |
| | [g1] | | | ? [g3] | | | |
| granule | 2.2x10^9 | ?, | ?, | | 200x10^3, | ?, 3.6x10^3 | |
| | [r1] | 3.7x10^3 | 5.2x10^3 | | 8.5x10^4 | [r5] | |
| | | [r2] | [r3] | | [r4] | | |
| purkinje | 1.3x10^6 | | | ?,? [p2] | | | 35,860 |
| | [p1] | | | | | | [p3]; |
| | | | | | | | 35,700 <i>[p4]</i> |
| stellate | 2.1x10^7 | | | | 3, 26 <i>[s2]</i> | | |
| | [s1] | | | | | | |
| dcn | 4.6x10^4 | | | | | | |
| | [d1] | | | | | | |

The table above was made using the sphinxcontrib-filltableref. Sphinx extension. See that link for documentation about the extension.

Original version of Cells and connections in cat table

The following version of the table was a prototype created using straight html. Using html made it difficult to write and does not allow specifying the data on different pages as is done using the sphinxcontrib-filltableref Sphinx extension. This prototype is being kept on the page (at least temporarily) to allow viewing the difference in the methods for creating the tables (html method, vs Sphinx extension method). To see the differences in the methods click on the "Page source" link on the lower right. That will show the source of the page ("rst" code).

Each row in the following table lists source cells on the left and destination cells on the top. The first column with numeric values gives the number of source cells. The other entries gives FO, FI. FO is fan-out (number of target cells each source contacts) and FI is fan-in (number source cells going to each target). All values are for the cat.

4.3 Cell and fiber counts in human from TomaschJ-1968

The following table provides the count of cerebellum cell and fiber counts in human, from [TomaschJ-1968].

| Cell or fiber | Description | Quantity | |
|------------------------------|--|--------------------------------|--|
| purkinje | Total number both hemispheres | 15 million | |
| cortico-pontine | # fibers from cerebral cortex to pons | 19.14 million (for one side) | |
| ponto-cerebellar | # cells in pons, same as number from pons to | 23.085 million | |
| | cerebellum | | |
| inferior olive | # fibers entering cerebellum from inferior olive | 0.5 million | |
| | (one side) | | |
| Inferior cerebeller peduncle | number of axons | 0.52 million (one side) | |
| cerebellar nuclei | total number neurons (one side) | 311,404 | |
| dentate nucleus | total number neurons (one side) | 284,000 | |
| nucleus globosus | total number neurons (one side) | 16,153 | |
| emboliforme nucleus | total number neurons (one side) | 10,381 | |
| fastigii nucleus | total number neurons (one side) | 5210 | |
| superior cerebellar peduncle | number of axons (one side) | 0.782 million | |
| superior cerebellar peduncle | number axons into cerebellum through superior | less than 1/2 number of fibers | |
| afferents (one side) | cerebellar peduncle | (0.782/2) | |
| superior cerebellar peduncle | number axons leaving cerebellum through supe- | about 311,000 (total number | |
| efferents (one side) | rior cerebellar peduncle | nuclei, 311,404; maybe less | |
| | | number fastigii nuclei, 5201) | |

CHAPTER

PROPERTIES

This section describes properties about the cerebellum which are likely to be important for the creation of models of the cerebellum.

5.1 Connections to / from the cerebellum





Magnocellular visual pathway provides input to cerebellum but not parvocellular pathway. [GlicksteinM-2007]. Below text from [KandelER+4-2013].

5.1.1 Vestibulocerebellum

The Vestibulocerebellum Regulates Balance and Eye Movements

Inputs:

semicircular canals and the otolith organs, which sense the head's motion and its position relative to gravity. Most of this vestibular input arises from the vestibular nuclei in the brain stem. The vestibulocerebellum also receives mossy fiber visual input, both from pretectal nuclei that lie deep in the midbrain beneath the superior colliculus and from the primary and secondary visual cortex through the pontine and pretectal nuclei.

Outputs:

The vestibulocerebellum is unique in that its output bypasses the deep cerebellar nuclei and proceeds directly to the vestibular nuclei in the brain stem. Purkinje cells in the midline parts of the vestibulocerebellum project to the lateral vestibular nucleus to modulate the lateral and medial vestibulospinal tracts, which predominantly control axial muscles and limb extensors to assure balance during stance and gait. Disruption of these projections through lesions or disease impairs equilibrium. Purkinje neurons in the lateral parts of the vestibulocerebellum project to the medial vestibular nucleus to control eye movements and coordinate movements of the head and eyes. Interestingly, this ancient part of



Fig. 2: Figure 2. Projections from cerebellum to cortex. From [StrickPL+2-2009].

the cerebellum has been co-opted in more recent phylogeny by visual guidance of eye movements. In fact, the most striking deficits following lesions of the lateral vestibulocerebellum are in smooth-pursuit eye movement toward the side of the lesion.

5.1.2 Spinocerebellum

The Spinocerebellum Regulates Body and Limb Movements.

The spinocerebellum comprises the vermis and intermediate parts of the cerebellar hemispheres.

Inputs:

The spinocerebellum receives extensive sensory input from the spinal cord, mainly from somatosensory receptors conveying information about touch, pressure, and limb position, through several direct and indirect pathways. This input provides the cerebellum with different reports of the changing state of the organism and its environment and permit comparisons between the two.

Direct pathways originate from interneurons in the spinal gray matter and terminate as mossy fibers in the vermis or spinocerebellum. Indirect pathways from the spinal cord to the cerebellum terminate first on neurons in one of several precerebellar nuclei in the brain stem reticular formation: the lateral reticular nucleus, reticularis tegmenti pontis, and paramedian reticular nucleus.

One fundamental principle of cerebellar operation can be appreciated on the basis of two important pathways from the spinal interneurons. The ventral and dorsal spinocerebellar tracts both transmit signals from the spinal cord directly to the cerebellar cortex but convey two different kinds of information. The dorsal spinocerebellar tract conveys so-matosensory information from muscle and joint receptors, providing the cerebellum with sensory feedback about the consequences of the movement. This information flows whether the limbs are moved passively or voluntarily. In contrast, the ventral spinocerebellar tract is active only during active movements. Its cells of origin receive the same inputs



Origin of projections from the cerebral cortex to the cerebellum. (*Dp*) The relative density of corticopontine neurons is indicated by the dots on lateral and medial views of the macaque brain. (*Bottom*) Histogram of relative density of corticopontine cells in different cytoarchitectonic areas of the monkey. Ai, As, inferior and superior limbs of arcuate sulcus, respectively; CA, calcarine fissure; CgS, cingulate sulcus; CS, central sulcus; IP, intraparietal sulcus; LS, lateral sulcus; Lu, lunate sulcus; IO, inferior occipital sulcus; PO, parietal-occipital sulcus; PS, principal sulcus; STS, superior temporal sulcus. Adapted from Glickstein et al. 1985, published in *The Journal of Comparative Neurology*, Vol. 235, No. 3, 1985, pp. 343–59. Copyright © 1985. Alan R. Liss, Inc. Reprinted with permission of John Wiley & Sons, Inc.

Fig. 3: Figure 3. Projections from cortex to cerebellum. From [StrickPL+2-2009].

as spinal motor neurons and interneurons, and it transmits an efference copy or corollary discharge of spinal motor neuron activity that informs the cerebellum about the movement commands assembled at the spinal cord. The cerebellum is thought to compare this information on planned movement with the actual movement reported by the dorsal spinocerebellar tract in order to determine whether the motor command must be modified to achieve the desired movement. The dorsal and ventral spinocerebellar tracts provide inputs from the hind limbs, whereas the cuneocerebellar and rostral spinocerebellar tracts provide similar inputs from more rostral body parts.

Outputs:

The Spinocerebellum Modulates the Descending Motor Systems Purkinje neurons in the spinocerebellum project somatotopically to different deep nuclei that control vari- ous components of the descending motor pathways. Neurons in the vermis of both the anterior and pos- terior lobes send axons to the fastigial nucleus. The fastigial nucleus projects bilaterally to the brain stem reticular formation and lateral vestibular nuclei, which in turn project directly to the spinal cord (Figure 42–7).

Purkinje neurons in the intermediate part of the cerebellar hemispheres project to the interposed nucleus. Some axons of the interposed nucleus exit through the superior cerebellar peduncle and cross to the contralateral side of the brain to terminate in the magnocellular portion of the red nucleus. Axons from the red nucleus cross the midline again and descend to the spinal cord (Figure 42–9). Other axons from the interposed nucleus continue rostrally and terminate in the ventrolateral nucleus of the thalamus. Neurons in the ventrolateral nucleus project to the limb control areas of the primary motor cortex. page 1021 (970)

The vermis may be the only area of the cerebellum responsible for saccades, but it seems to share responsibility for smooth pursuit with the lateral part of the flocculonodular lobe. The outputs from neurons of the vermis concerned with saccades are transmitted through a very small region of the caudal fastigial nucleus to the saccade generator in the reticular formation. The exact neural pathways for guidance of pursuit by the vermis are not known, but they involve more synaptic relays than the outputs from the lateral part of the flocculonodular lobe, which reach extraocular motor neurons through two intervening synapses. One idea currently being explored is that the vermis also plays a role in motor learning that corrects errors in saccades and smooth-pursuit movements.

5.1.3 Cerebrocerebellum

The CerebrocerebellumIs Involved in Planning Movement

The Cerebrocerebellum Is Part of a High-Level Internal Feedback Circuit That Plans Movement and Regulates Cortical Motor Programs

Input:

In contrast to other regions of the cerebellum, which receive sensory information more directly from the spinal cord, the lateral hemispheres receive input exclusively from the cerebral cortex. This cortical input is transmitted through the pontine nuclei and through the middle cerebellar peduncle to the contralateral dentate nucleus and lateral hemisphere (see Figure 42–3).

Output:

Purkinje neurons in the lateral hemisphere project to the dentate nucleus. Most dentate axons exit the cerebellum through the superior cerebellar peduncle and terminate in two main sites. One terminus is an area of the contralateral ventrolateral thalamus that also receives input from the interposed nucleus. These thalamic cells project to premotor and primary motor cortex (see Figure 42–9). The second principal terminus of dentate neurons is the contralateral red nucleus, specifically a portion of the parvocellular area of the nucleus distinct from that which receives input from the interposed nucleus. These neurons project to the inferior olivary nucleus, which in turn projects back to the contralateral cerebellum as climbing fibers, thus forming a recurrent loop (see Figure 42–6). Neurons in the parvocellular portion of the red nucleus, in addition to receiving input from the dentate nucleus, also receive input from the lateral premotor areas. On the basis of brain imaging, the intriguing suggestion has been made that this loop involving the premotor cortex, lateral cerebellum, and rubrocerebellar tract participates in the mental rehearsal of movements and perhaps in motor learning (see Chapter 33).

Interestingly, the active area of the dentate nucleus is the area that receives input from the part of the cerebral cortex (area 46) involved in working memory. The dentate nucleus appears to be particularly important in processing sensory information for tasks that require complex spatial and temporal judgments, which are essential for com- plex motor actions and sequences of movements.



5.2 Microcircuit of Cerebellar cortex

Fig. 4: Figure 1. Cells in Circuit in cerebellar cortex



Fig. 5: Figure 2. Circuit diagram cerebellar cortex

5.3 Cell counts in cortical loop



Fig. 6: Figure 1. Cell counts in loop between cortex to cerebellum. From [DiedrichsenJ+4-2019] (figure 42.2).

CHAPTER

SIX

DATA

Data about the following cells or regions are provided:

6.1 Mossy Fibers

6.1.1 Overview

Adapted from: https://en.wikipedia.org/wiki/Mossy_fiber_(cerebellum):

Mossy fibers are one of the major inputs to cerebellum. There are many sources of this pathway, the largest of which is the cerebral cortex, which sends input to the cerebellum via the pontocerebellar pathway. Other contributors include the vestibular nerve and nuclei, the spinal cord, the reticular formation, and feedback from deep cerebellar nuclei. Axons enter the cerebellum via the middle and inferior cerebellar peduncles, where some branch to make contact with deep cerebellar nuclei. They ascend into the white matter of the cerebellum, where each axon branches to innervate granule cells in several cerebellar folia.

See Microcircuit of Cerebellar cortex for a diagram of mossy fibers.

6.1.2 Quantity

In cat:

So far, I have not found an explicit estimate of the total number of mossy fibers in cat. Instead, the numerical values provided are based on the divergence and convergence between cell types within a folium. The unknown factor is the number of folia which are innervated by each mossy fiber. Statements related to the quantity are below.

Following from [ItoM-1984], page 86:

Mossy fiber-Purkinje cell ratio within the folia is 4:1 [PalkovitsM+2-1972]. If each mossy fiber afferent innervates two folis by branching in the white matter, there will be 2.4×10^{6} mossy fibers in the whole cat cerebellum (a total number of Purkinje cells is assumed to be 1.2×10^{6} ; [PalkovitsM+2-1971a]. However, this is an overestimate if the mossy fibers branch more abundantly.

"According to earlier data [PalkovitsM+2-1971b] the granule cell-glomerulus ratio is 27-28:1, the mossy fiber-granule cell ratio is therefore 1:460." [PalkovitsM+2-1972].

The granular layer contributed to 29.09% of the total cerebellar volume, their absolute number being 2.2 $x 10^{9}$. [PalkovitsM+2-1971b] p. 29.

The above two would mean 4.78 x 10⁶ mossy fibers (2.2 x 10⁹ granule cells / 460);

6.1.3 Structure

"Within a folium, a mossy fiber branches along the plane perpendicular to the long axis of the folium. Therefore, the cascade arborization of mossy fibers (Cajal, 1911) tends to be parallel with the dendritic arborization of Purkinje cells." [ItoM-1984], p. 87.

6.1.4 Connection to glomeruli

Divergence

"One mossy fiber breaks up (within a given folium) into about 16-17 mossy rosettes" (which glomeruli form around). [PalkovitsM+2-1972]. From [ItoM-1984], page 86: "If each mossy fiber afferent innervates two folis by branching in the white matter, ..." (Comment:: Would this mean about 32 glomeruli per mossy fiber)?

Convergence

1? (Comment: I think each glomeruli is associated with just one mossy fiber rosette. However, in a table of properties used for a computational model ([DAngeloE+11-2016] Table 2) it says that both the convergence and divergence from mossy fibers to glomeruli is "not known" (row 2 of Table 2)).

6.1.5 Connection to grannule cells

Divergence

Cat: 1.7 x 10³ (from [LoebnerEE-1989], fig 2).

From [PalkovitsM+2-1972], p. 26: "Four mossy fibers entering a folium give rise to 16 rosettes each, hence a total of 64 glomeruli. Since one glomerulus has synaptic contacts with an average of 28 granule cells, the total number of granule cells reached by the 4 mossy fibers will be 1,792. Each granule cell is presumed to pick up excitatory impulses from 4 glomeruli belonging to different mossy fibers by as many dendrites."

but also, from the same paper, page 28: "The granule cells have 4.17 dendrites, on average; *the average mossy rosette is contacted by 112 granule dendrites*. The number of postsynaptic units (dendrite digits) is 10.2/dendrite and 1,142/glomerulus."

At first, this seems contradictory, (28 granule cells vs 112 granule dendrites per glomerulus). As described in the section of Golomeruli to granule connection *Connection to granule cells* I think the fan out is 1,792 per mossy fiber (as given in [LoebnerEE-1989], fig 2).

Convergence

Cat:

4 (from [LoebnerEE-1989], fig 2); 4.17 (from [PalkovitsM+2-1972], p. 28).

Mouse and in general:

About 4. Analysis of why 4 is optimal in: [BillingsG+4-2014].

6.1.6 Connection to Golgi cells

Divergence

Cat:

Unknown ([LoebnerEE-1989], fig 2).

Convergence

Cat:

Unknown ([LoebnerEE-1989], fig 2).

6.1.7 Connection to DCN (Deep Cerebellar Nuclei)

Divergence

Cat:

Unknown ([LoebnerEE-1989], fig 2).

Convergence

Cat:

Unknown ([LoebnerEE-1989], fig 2).

6.2 Glomeruli

6.2.1 Overview

From: https://en.wikipedia.org/wiki/Glomerulus_(cerebellum):

The cerebellar glomerulus is a small, intertwined mass of nerve fiber terminals in the granular layer of the cerebellar cortex. It consists of post-synaptic granule cell dendrites and pre-synaptic Golgi cell axon terminals surrounding the pre-synaptic terminals of mossy fibers. (from: http://neurolex.org/wiki/Category: Cerebellar_glomerulus)

6.2.2 Density

In cat:

In 1 cu.mm of the granular layer 98,800 glomeruli are found on average. citation?

"With direct counting of the glomeruli the corrected density was found to be 98,879 +/- 4,065/cu.mm; ..." [PalkovitsM+2-1972], p. 23.

6.2.3 Quantity

In cat:

The granule cell-glomerulus ratio is 27-28:1. [PalkovitsM+2-1972] The density of granule cells was found earlier 1° to be 2,800,000/cu.mm (for the living), hence the glomerulus-granule cell ratio is 1:28.32. [PalkovitsM+2-1972], p. 23.

"According to earlier data [PalkovitsM+2-1971b] the granule cell-glomerulus ratio is 27-28:1, the mossy fiber-granule cell ratio is therefore 1:460." [PalkovitsM+2-1972], p. 28.

The granular layer contributed to 29.09% of the total cerebellar volume, their absolute number being 2.2 $x 10^{9}$. [PalkovitsM+2-1971b] p. 29.

6.2.4 Connection to grannule cells

Divergence

Cat:

From [PalkovitsM+2-1972], p. 26: "Four mossy fibers entering a folium give rise to 16 rosettes each, hence a total of 64 glomeruli. Since *one glomerulus has synaptic contacts with an average of 28 granule cells*, the total number of granule cells reached by the 4 mossy fibers will be 1,792. Each granule cell is presumed to pick up excitatory impulses from 4 glomeruli belonging to different mossy fibers by as many dendrites."

but also, from the same paper, page 28: "The granule cells have 4.17 dendrites, on average; *the average mossy rosette is contacted by 112 granule dendrites*. The number of postsynaptic units (dendrite digits) is 10.2/dendrite and 1,142/glomerulus."

This seems contradictory, (28 granule cells vs 112 granule dendrites). I think the "dendrite digits" refers to a dendrite having multiple protrusions as shown in [EcclesJC+2-1967] Fig. 75 (see note for this paper), so those can be ignored for the purpose of calculating the divergence.

So, the question is whether the divergence from glomeruli is 28 or 112? I think it is 112, and that the value of 28 is calculated by taking into account the convergence of 4 (112/4) = 28. This seems compatable with the divergence:convergence from mossy fibers to granule cells given in the [LoebnerEE-1989] fig 2 which is $1.7x10^3$:4 because 1,792 is given as the number of granule cells reached by 4 mossy fibers on average (quote above from [PalkovitsM+2-1972], p. 26) and Loebner is using that as the number reached by one mossy fiber, which means that mossy fiber has 4x the divergence than that given by one mossy fiber.

Another potential contradiction is the total number of mossy fibers. In the Loebner paper, the divergence: convergence from mossy fibers to granule cells is given as $1.7x10^{3:4}$ and the number of granule cells is given as 2.2×10^{9} . From this, the number of mossy fibers would be about $(2.2x10^{9} * 4 / 1.7x10^{3}) = 5.2x10^{6}$ mossy fibers. This is more than the estimated number of 2.4×10^{6} mossy fibers, which might already be an overestimate.

Rat: From [JakabRL+HamoriJ-1988], abstract The results demonstrate that, in the rat cerebellum, there is a high degree of convergence of granule cells at a glomerulus (53 to 1); and that there is a rich inhibitory input to about 60% of all granule cell dendrites.

Convergence

In our Golgi-Kopsch stained material the number of dendrites ranged from 2 to 7. 61.6% of cells had 4 dendrites, 22.4% had 5 dendrites and 15.2% had 3 dendrites. *The average dendrite number was calculated as 4.17.* [PalkovitsM+2-1972] p. 24.

6.3 Granule

6.3.1 Overview

(adapted from: https://en.wikipedia.org/wiki/Cerebellar_granule_cell):

Cerebellar granule cells form the thick granular layer of the cerebellar cortex and are among the smallest neurons in the brain. (The term granule cell is used for several unrelated types of small neurons in various parts of the brain.) Cerebellar granule cells are also the most numerous neurons in the brain: in humans, estimates of their total number average around 50 billion, which means that they constitute about 3/4 of the brain's neurons.

The cell bodies are packed into a thick granular layer at the bottom of the cerebellar cortex. A granule cell emits only four to five dendrites, each of which ends in an enlargement called a dendritic claw. These enlargements are sites of excitatory input from mossy fibers and inhibitory input from Golgi cells.

The thin, unmyelinated axons of granule cells rise vertically to the upper (molecular) layer of the cortex, where they split in two, with each branch traveling horizontally to form a parallel fiber; the splitting of the vertical branch into two horizontal branches gives rise to a distinctive "T" shape. In humans, a parallel fiber runs for an average of 3 mm in each direction from the split, for a total length of about 6 mm (about 1/10 of the total width of the cortical layer). As they run along, the parallel fibers pass through the dendritic trees of Purkinje cells, contacting one of every 3–5 that they pass, making a total of 80–100 synaptic connections with Purkinje cell dendritic spines.[1] Granule cells use glutamate as their neurotransmitter, and therefore exert excitatory effects on their targets.

See *Microcircuit of Cerebellar cortex* for a diagram of grannule cells.

6.3.2 Density

In cat:

A percentage of 41.85% of the total volume of the granular substance was occupied by the granule cells (bodies), their density calculated for the living state being 2.8 x 10^{6} /cu.mm. [PalkovitsM+2-1971b] p. 29.

In rat:

Using morphological measurements, it can be calculated that the rat cerebellar granular layer has a cell density of 4×10^{6} /mm³ for granule cells and 9300/mm³ for Golgi cells, with a Golgi cell : granule cell ratio of 1:430 (Korbo et al., 1993). Moreover, the density of the glomeruli is 3×10^{5} /mm³, and each glomerulus is composed of one mossy fiber terminal, about 53 dendrites from separate granule cells (Jakaband Hamori, 1988), and one or more dendrites from Golgi cells. [DAngeloE+5-2013] p. 9-10.

6.3.3 Quantity

In cat:

The granular layer contributed to 29.09% of the total cerebellar volume, their absolute number being 2.2 $x 10^{9}$. [PalkovitsM+2-1971b] p. 29.

This value is used in [LoebnerEE-1989] (the value is probably from the same source, e.g. [PalkovitsM+2-1971b]).

The granule cell : Purkinje cell ratio was 1700-1800. [PalkovitsM+2-1971b] p. 29.

See Table 2 in note for [LangeW-1975] for granule cell : Purkinje cell ratio for different species.

6.3.4 Connection to Purkinje Cells

Structure

In cat:

From: [PalkovitsM+2-1972]:

Numerically, the granule cells belonging to one Purkinje cell (1,792) are capable of transmitting impulses from 4 mossy fibers and their 68 rosettes (glomeruli), while the parallel fibers, being 2 mm long, penetrate the dendrite trees of 225 Purkinje cells. Since they establish synapses with only every fifth of these Purkinje cells, the calculated number of parallel fibers-Purkinje spine synapses would be 80,550/ Purkinje cell 11. This calculated value agrees reasonably well with the counted number of Purkinje cell dendritic spines = 91,600.

Each granule call split to form a "T" to form parallel fibers that extend 1 mm (2 mm total) in a direction parallel to the longititudional access of the folium (that is in a direction perpendicular to the Purkinje cells).

Divergence

Cat: 45.

From: [PalkovitsM+2-1972], p. 27: The parallel fibers divide in T-fashion and run in both directions for an average distance of 1 mm, i.e. they are 2 mm long n. They establish synapses with only about every fifth Purkinje cell whose dendritic tree they cross. With 225 Purkinje cell dendritic trees accommodated in 2 mm along the longitudinal axis of the folium 9, *each parallel fiber may contact synaptically 45* Purkinje cells.

This is different from the value given in Fig. 2 of [LoebnerEE-1989], which is 200×10^3 . I'm not sure what that figure is referring to.

Convergence

Cat: 80,550

From: [PalkovitsM+2-1972] Since they establish synapses with only every fifth of these Purkinje cells, the calculated number of parallel fibers-Purkinje spine synapses would be 80,550/ Purkinje cell [PalkovitsM+2-1971c]. This calculated value agrees reasonably well with the counted number of Purkinje cell dendritic spines = 91,600.

This is similar to the value in [LoebnerEE-1989] Fig. 2 (8.5×10^{4}). I'm not sure what the source is of that value.

6.3.5 Connection to Golgi Cells

Divergence

Unknown ([LoebnerEE-1989], Fig. 2)

Convergence

5.2 x 10³ ([LoebnerEE-1989], Fig. 2)

6.3.6 Connection to Basket Cells

Divergence

Unknown ([LoebnerEE-1989], Fig. 2)

Convergence

3.7 x 10³ ([LoebnerEE-1989], Fig. 2)

6.3.7 Connection to Stellate Cells

Divergence

Unknown ([LoebnerEE-1989], Fig. 2)

Convergence

3.6 x 10^3 ([LoebnerEE-1989], Fig. 2)

Data for table Cells and connections in cat

The following table has data and references for table *Cells and connections in cat*. Values are either a Cell count, or FO,FI where FO is *fan-out* (number of target cells each source cell contacts) and FI is *fan-in* (number of source cells going to each target cell).

| ld | Source cell | Target cell | Value | Reference |
|----|-------------|-------------|--------------------|-------------------------------|
| r1 | granule | Cell count | 2.2x10^9 | [LoebnerEE-1989] ¹ |
| r2 | granule | basket | ?, 3.7x10^3 | [LoebnerEE-1989]? |
| r3 | granule | golgi | ?, 5.2x10^3 | [LoebnerEE-1989]? |
| r4 | granule | purkinje | 200x10^3, 8.5x10^4 | [LoebnerEE-1989]? |
| r5 | granule | stellate | ?, 3.6x10^3 | [LoebnerEE-1989]? |

¹ EE Loebner. Intelligent network management and functional cerebellum synthesis. In Raugh MR, editor, *Cerebellar Models of Associative Memory: Three papers from IEEE COMPCON SPRING* '89, pages 14–19. Research Institute for Advanced Computer Science, NASA Ames Research Center, 1989. PDF: LoebnerEE-1989.pdf, Notes: LoebnerEE-1989.html.

6.4 Golgi cells

Overview (adapted from: http://www.scholarpedia.org/article/Cerebellum#Neuronal_types):

Golgi cells are inhibitory interneurons. There are two sizes of Golgi cells: (I) large ones (somata 9-16 μ m in diameter), which are found mainly in the upper part of the granular cell layer, and (2) smaller ones (somata 6-11 μ m in diameter), which are found in the lower half of the granular layer. They have extensive radial dendritic trees that extend through all layers of the cortex. They receive input from the parallel fibers in the molecular layer and from climbing and mossy fiber collaterals in the granular layer. Their axons branch repeatedly in the granular layer, where they terminate on granule cell dendrites in the cerebellar glomeruli. There are approximately as many Golgi cells as Purkinje cells.

See Microcircuit of Cerebellar cortex for a diagram of Golgi Cells.

In addition to the connections described above (input from parallel fibers and climbing and mossy fiber collaterals) Golgi cells are also connected to each other via gap junctions [DeZeeuwCI+2-2021] and inhibit each other by synaptic connections [HullC+RegehrWG-2012]. Also, some Golgi cells receive inhibition from deep Cerebellar Nuclei [AnkriL+5-2015].

[LoebnerEE-1989] Fig 2 *About the Pseudocerebellum project* has arrows for connections between Golgi cells and Basket cells. But according to [DeZeeuwCI+2-2021] connections between Golgi Cells and molecular layer interneuronshave been ruled out. So removing these connections would be an update to the figure to account for more recent data.

Some additional connections needed for [LoebnerEE-1989] Fig 2 are between Golgi cells (both gap junctions and synaptic connections).

6.4.1 Quantity

Cat:

4.2x10^5 [LoebnerEE-1989] Fig 2

The numerical ratio of Golgi cells : Purkinje cells was 1 : 3 [PalkovitsM+2-1971b], p. 30. The total number of Purkinje ceils was 1.2-1.3 million. [PalkovitsM+2-1971a]. These two quantities would mean that the number of Golgi cells would be about 1.25 million / 3, or about 4.17 x 10^5. This is probably the source of data in LoebnerEE-1989 Fig. 2.

6.4.2 Connection to Granule Cells

Divergence

Cat:

5.2x10^3 [LoebnerEE-1989] Fig 2
Convergence

Cat: Unknown. [LoebnerEE-1989] Fig 2.

6.4.3 Gap junctions between Golgi Cells

Described in: [DugueGP-2009+8].

6.4.4 Synaptic inhibition between Golgi Cells

Described in: [HullC+RegehrWG-2012]

Data for table Cells and connections in cat

The following table has data and references for table *Cells and connections in cat*. Values are either a Cell count, or FO,FI where FO is *fan-out* (number of target cells each source cell contacts) and FI is *fan-in* (number of source cells going to each target cell).

| ld | Source cell | Cell count or Target | Value | Reference |
|----|-------------|----------------------|-------------|-------------------------------|
| | | cell | | |
| g1 | golgi | Cell count | 4.2x10^5 | [LoebnerEE-1989] ¹ |
| g2 | golgi | golgi | ?, ? | [HullC+RegehrWG-2012] |
| g3 | golgi | granule | 5.2x10^3, ? | [LoebnerEE-1989]? |

6.5 Stellate

Overview (adapted from: http://www.scholarpedia.org/article/Cerebellum#Neuronal_types):

Basket and Stellate cells: Are interneurons present in the molecular layer. They are both inhibitory (GABAergic) on to Purkinje cells. Their axons run in the same direction as the dendrites of the Purkinje cells are electrically coupled and receive both climbing fiber collaterals as well as parallel fibers originating in the granule layer.

6.5.1 Quantity

In Cat:

2.1x10^7 [LoebnerEE-1989]

The Purkinje cell-stellate cell ratio 1 : 16-17.5 [PalkovitsM+2-1971c].

¹ EE Loebner. Intelligent network management and functional cerebellum synthesis. In Raugh MR, editor, *Cerebellar Models of Associative Memory: Three papers from IEEE COMPCON SPRING* '89, pages 14–19. Research Institute for Advanced Computer Science, NASA Ames Research Center, 1989. PDF: LoebnerEE-1989.pdf, Notes: LoebnerEE-1989.html.

² Court Hull and Wade G. Regehr. Identification of an Inhibitory Circuit that Regulates Cerebellar Golgi Cell Activity. *Neuron*, 73(1):149–158, January 2012. URL: https://linkinghub.elsevier.com/retrieve/pii/S0896627311009949, doi:10.1016/j.neuron.2011.10.030, Notes: HullC+RegehrWG-2012.html.

6.5.2 Synapse to Purkinje cells

Divergence

In cat:

3 [LoebnerEE-1989]

Convergence

In cat:

26 [LoebnerEE-1989]

6.5.3 Gap junctions and synapses between stellate cells

From: [RieublandS+2-2014]

By recording from multiple molecular layer interneurons in the cerebellar cortex, we reveal specific, nonrandom connectivity patterns in both GABAergic chemical and electrical interneuron networks.

Chemical connections exhibit a preference for transitive patterns, such as feedforward triplet motifs. This structured connectivity is supported by a characteristic spatial organization: transitivity of chemical connectivity is directed vertically in the sagittal plane, and electrical synapses appear strictly confined to the sagittal plane.

Data for table Cells and connections in cat

The following table has data and references for table *Cells and connections in cat*. Values are either a Cell count, or FO,FI where FO is *fan-out* (number of target cells each source cell contacts) and FI is *fan-in* (number of source cells going to each target cell).

| ld | Source cell | Target cell | Value | Reference |
|----|-------------|-------------|----------|-------------------------------|
| s1 | stellate | Cell count | 2.1x10^7 | [LoebnerEE-1989] ¹ |
| s2 | stellate | purkinje | 3, 26 | [LoebnerEE-1989]? |

Some text about Stellate cells.

6.6 Basket cells

Overview (adapted from: http://www.scholarpedia.org/article/Cerebellum#Neuronal_types):

Basket cells are interneurons found in the lower molecular layer which are inhibitory (GABAergic) on to Purkinje cells. Their axons run in the same direction as the dendrites of the Purkinje cells, are electrically coupled, and receive both climbing fiber collaterals as well as parallel fibers originating in the granule layer.

Their axons extend along the Purkinje cell layer at right angles to the direction of the parallel fibers. They may spread over a distance equal to 20 Purkinje cell widths and 6 deep and may contact as many as 150 Purkinje cell bodies. During its course, the horizontal segment of a basket cell axon sends off groups of collaterals that

¹ EE Loebner. Intelligent network management and functional cerebellum synthesis. In Raugh MR, editor, *Cerebellar Models of Associative Memory: Three papers from IEEE COMPCON SPRING* '89, pages 14–19. Research Institute for Advanced Computer Science, NASA Ames Research Center, 1989. PDF: LoebnerEE-1989.pdf, Notes: LoebnerEE-1989.html.

descend and embrace the Purkinje cell soma and initial segment. As many as 50 different basket cells are thought to wrap their axon terminals around each Purkinje cell soma, forming a basket-like meshwork resembling that on an old Chianti bottle (Hamori & Szentagothai, 1966). Basket cell axons also ascend to contact the Purkinje cell dendritic tree. There are about six times as many basket cells as Purkinje cells.



Fig. 1: Basket cell arrangement in cerebellar cortex. From [LlinasRR-1975].

6.6.1 Quantity

In Cat:

About 6x number of Purkinje cells. For cat, this is 7.5x10^6. See note for [PalkovitsM+2-1971c].

6.6.2 Synapse with purkinje cells:

Divergence

In cat:

[PalkovitsM+2-1971c] states that:

"Calculations of the average number of Purkinje cell baskets in which the basket axon participates gave unexpectedly low values: 8-9 baskets per axon."

This is a "fan-out" (divergence) of about 8-9. However, the scholarpedia article (exerpt above) states up to 150 Purkinje cell bodies may be contacted. That may be for a different species, perhaps human. Some other sources of data (referenced in [DAngeloE+11-2016], Table 1 for mouse) specify a divergence of 1:30 and convergence of 7:1.



Fig. 2: Stimulation and inhibition of Purkinje cells. From [LlinasRR-1975].

Convergence

In cat: 50 [LoebnerEE-1989].

6.6.3 Gap junctions and synapses between basket cells

There are also synaptic gap junctions between molecular layer interneurons which are oriented along the sagittal plane (same direction as the basket cell axons, perpendicular to the parallel fibers). Described in note for: [RieublandS+2-2014].

Data for table Cells and connections in cat

The following table has data and references for table *Cells and connections in cat*. Values are either a Cell count, or FO,FI where FO is *fan-out* (number of target cells each source cell contacts) and FI is *fan-in* (number of source cells going to each target cell).

| ld | Source cell | Cell count or Target | Value | Reference |
|----|-------------|----------------------|----------|-------------------------------|
| b1 | basket | Cell count | 7.5x10^6 | [LoebnerEE-1989] ¹ |
| b2 | basket | purkinje | 9, 50 | [LoebnerEE-1989]? |

¹ EE Loebner. Intelligent network management and functional cerebellum synthesis. In Raugh MR, editor, *Cerebellar Models of Associative Memory: Three papers from IEEE COMPCON SPRING* '89, pages 14–19. Research Institute for Advanced Computer Science, NASA Ames Research Center, 1989. PDF: LoebnerEE-1989.pdf, Notes: LoebnerEE-1989.html.

6.7.1 Overview

Adapted from: https://en.wikipedia.org/wiki/Purkinje_cell:

Purkinje cells are some of the largest neurons in the human brain with an intricately elaborate dendritic arbor, characterized by a large number of dendritic spines. Purkinje cells are found within the Purkinje layer in the cerebellum. Purkinje cells are aligned like dominos stacked one in front of the other. Their large dendritic arbors form nearly two-dimensional layers through which parallel fibers from the deeper-layers pass. These parallel fibers make relatively weaker excitatory (glutamatergic) synapses to spines in the Purkinje cell dendrite, whereas climbing fibers originating from the inferior olivary nucleus in the medulla provide very powerful excitatory input to the proximal dendrites and cell soma. Parallel fibers forming a Granule-cell-Purkinje-cell synapse with a single Purkinje cell. Each Purkinje cell receives approximately 500 climbing fiber synapses, all originating from a single climbing fiber. Both basket and stellate cells (found in the cerebellar molecular layer) provide inhibitory (GABAergic) input to the Purkinje cell, with basket cells synapsing on the Purkinje cell axon initial segment and stellate cells onto the dendrites.

Purkinje cells send inhibitory projections to the deep cerebellar nuclei, and constitute the sole output of all motor coordination in the cerebellar cortex.

See Microcircuit of Cerebellar cortex for a diagram of Purkinje cells.

6.7.2 Quantity

Cat: The total number of Purkinje ceils was 1.2-1.3 million. [PalkovitsM+2-1971a].

The granule cell : Purkinje cell ratio was 1700-1800. [PalkovitsM+2-1971b] p. 29.

Human: 15 million (total number both hemispheres) [TomaschJ-1968].

See Table 2 in note for [LangeW-1975] for granule cell : Purkinje cell ratio for different species.

6.7.3 Connection to Golgi Cells

Divergence

Unknown [LoebnerEE-1989]

Convergence

Unknown [LoebnerEE-1989]

6.7.4 Connection to Basket Cells

Divergence

Unknown [LoebnerEE-1989]

Convergence

Unknown [LoebnerEE-1989]

6.7.5 Connection to Purkinje Cells

Purkinje cells have inhibitory synaptic connections to other Purkinje cells through axon collaterals [WitterL+4-2016].

Structure

In mice:

Collaterals were confined to a narrow sagittal plane but extended hundreds of micrometers within that plane. [WitterL+4-2016]

Divergence and convergence

In mice:

5 to 10 [WitterL+4-2016]

6.7.6 Connection to Granule cells

[GuoC+5-2016] shows that Purkinje cells directly inhibit granule cells. "... non-canonical feedback is region specific: it is most prominent in lobules that regulate eye movement and process vestibular information"

Divergence and convergence

Unknown

6.7.7 Connection to DCN

Divergence

In cat:

35 "one Purkinje axon may reach potentially 35 nuclear cells." [PalkovitsM+3-1977]. Also, [PalkovitsM+3-1977] Fig 2 (probably from the same source).

Convergence

In cat:

Around 860 "the probable convergence of Purkinje axons upon nuclear cells can be deduced as being numerically somewhere around 860" [PalkovitsM+3-1977].

700 [LoebnerEE-1989] Fig 2.

Data for table Cells and connections in cat

The following table has data and references for table *Cells and connections in cat*. Values are either a Cell count, or FO,FI where FO is *fan-out* (number of target cells each source cell contacts) and FI is *fan-in* (number of source cells going to each target cell).

| ld | Source cell | Target cell | Value | Reference |
|----|-------------|-------------|----------|-------------------------------|
| p1 | purkinje | Cell count | 1.3x10^6 | [LoebnerEE-1989] ¹ |
| p2 | purkinje | granule | ?,? | [GuoC+5-2016] ² |
| p3 | purkinje | dcn | 35,860 | $[PalkovitsM+3-1977]^3$ |
| p4 | purkinje | dcn | 35,700 | [LoebnerEE-1989]? |

6.8 Inferior Olive

Oveview:

Adapted from https://en.wikipedia.org/wiki/Inferior_olivary_nucleus:

The inferior olivary nucleus (ION) house the cell bodies of the olivocerebellar fibers. These neurons are the major input source for the cerebellum (the climbing fibers). Each climbing fiber targets a single climbing fiber. There are three major components of the IO.

- Primary olivary nucleus (PO) This is the major laminar structure. It receives signals from other components of the brainstem, such as the red nucleus and the N. Darkschewitsch. The PO also receives signals from the cerebral cortex. The PO targets the intermediate cerebellum as well as the cerebellar hemispheres.
- Medial accessory olivary nucleus (MAO) The MAO receives signals from the tectum and the pretectum. Climbing fibers from the MAO synapse with the vermis, the flocculus, and the cerebellar hemispheres.
- Dorsal accessory olivary nucleus (DAO) It is the smallest nucleus in the IO. It receives signals from the spinal cord and the dorsal column nuclei. The DAO synapses with vermis.

¹ EE Loebner. Intelligent network management and functional cerebellum synthesis. In Raugh MR, editor, *Cerebellar Models of Associative Memory: Three papers from IEEE COMPCON SPRING* '89, pages 14–19. Research Institute for Advanced Computer Science, NASA Ames Research Center, 1989. PDF: LoebnerEE-1989.pdf, Notes: LoebnerEE-1989.html.

² Chong Guo, Laurens Witter, Stephanie Rudolph, Hunter L. Elliott, Katelin A. Ennis, and Wade G. Regehr. Purkinje Cells Directly Inhibit Granule Cells in Specialized Regions of the Cerebellar Cortex. *Neuron*, 91(6):1330–1341, September 2016. URL: https://linkinghub.elsevier.com/retrieve/pii/S0896627316305037, doi:10.1016/j.neuron.2016.08.011, Notes: GuoC+5-2016.html.

³ M. Palkovits, Eva Mezey, J. Hamori, and J. Szentagothai. Quantitative histological analysis of the cerebellar nuclei in the cat. I. Numerical data on cells and on synapses. *Experimental Brain Research*, May 1977. URL: http://link.springer.com/10.1007/BF00237096, doi:10.1007/BF00237096, Notes: PalkovitsM+3-1977.html.

6.8.1 Synapse with Purkinje cells

Divergence

10 [LoebnerEE-1989], Fig. 2

Convergence

1 [LoebnerEE-1989], Fig. 2

6.8.2 Synapse with DCN

Divergence

Unknown [LoebnerEE-1989], Fig. 2

Convergence

Unknown [LoebnerEE-1989], Fig. 2

6.8.3 Synapse with Golgi cells

Divergence

Unknown [LoebnerEE-1989], Fig. 2

Convergence

Unknown [LoebnerEE-1989], Fig. 2

6.8.4 Synapse with Basket cells

Divergence

Unknown [LoebnerEE-1989], Fig. 2

Convergence

Unknown [LoebnerEE-1989], Fig. 2

6.8.5 Synapse with Stellate cells

Divergence

Unknown [LoebnerEE-1989], Fig. 2

Convergence

Unknown [LoebnerEE-1989], Fig. 2

6.9 Deep Cerebellar Nuclei

6.9.1 Overview

From: https://en.wikipedia.org/wiki/Deep_cerebellar_nuclei:

The cerebellum has four deep cerebellar nuclei embedded in the white matter in its center. These nuclei receive inhibitory (GABAergic) inputs from Purkinje cells in the cerebellar cortex and excitatory (glutamatergic) inputs from mossy fiber and climbing fiber pathways. Most output fibers of the cerebellum originate from these nuclei. One exception is that fibers from the flocculonodular lobe synapse directly on vestibular nuclei without first passing through the deep cerebellar nuclei. The vestibular nuclei in the brainstem are analogous structures to the deep nuclei, since they receive both mossy fiber and Purkinje cell inputs. From lateral to medial, the four deep cerebellar nuclei are the dentate, emboliform, globose, and fastigii. Some animals, including humans, do not have distinct emboliform and globose nuclei, instead having a single, fused interposed nucleus. In animals with distinct emboliform and globose nuclei, the term interposed nucleus is often used to refer collectively to these two nuclei.

6.9.2 Quantity

Cat:

The total number of the cerebellar nuclear cells was found to be 4.6×10^{4} . On the basis of karyometric studies the medial and interpositus nuclei appear to contain two, the lateral nucleus probably three different neuron populations. The over-all numerical ratio between Purkinje and nuclear cells is 26:1. [PalkovitsM+3-1977].

4.8x10^4, [LoebnerEE-1989] Fig 2

6.9.3 Excitatory connection to Granule and Golgi Cells

From [AnkriL+5-2015]:

A less-known nucleo-cortical circuit is formed by the glutamatergic neurons of the CN which, in addition to projecting to various premotor and associative regions of the brain ... send axonal collaterals to the cerebellar granule cell layer (GrCL; Houck and Person, 2015). These collateral fibers form MF-like terminals contacting granule cell (GrC) and Golgi cell dendrites The functional significance of this excitatory nucleo-cortical (eNC) pathway, loosely following the modular arrangement of the cerebellum ... is likely related to efference copying of motor commands to the cerebellar cortex (Sommer and Wurtz, 2008; Houck and Person, 2015).

6.9.4 Inhibitory connection to Golgi Cells

Some Golgi cells receive inhibition from deep Cerebellar Nuclei [AnkriL+5-2015]. From abstract: (data from mice):

The cerebellum, a crucial center for motor coordination, is composed of a cortex and several nuclei. The main mode of interaction between these two parts is considered to be formed by the inhibitory control of the nuclei by cortical Purkinje neurons. We now amend this view by showing that inhibitory GABA-glycinergic neurons of the cerebellar nuclei (CN) project profusely into the cerebellar cortex, where they make synaptic contacts on a GABAergic subpopulation of cerebellar Golgi cells. These spontaneously firing Golgi cells are inhibited by optogenetic activation of the inhibitory nucleo-cortical fibers both in vitro and in vivo. Our data suggest that the CN may contribute to the functional recruitment of the cerebellar cortex by decreasing Golgi cell inhibition onto granule cells.

6.9.5 Inhibitory connection to Inferior Olive

From [AnkriL+5-2015]:

Currently, the cerebellar cortex and the CN are known to interact through two circuits. The best known is the nucleo-olivary (NO) circuit (...) where the small GABAergic CN cells, subject to PN inhibition (Najac and Raman, 2015), project to the contralateral IO (Fredette and Mugnaini, 1991). This pathway regulates olivary activity (...) and thereby complex spike activity in the PNs and cerebellar cortical plasticity (...).

Data for table Cells and connections in cat

The following table has data and references for table *Cells and connections in cat*. Values are either a Cell count, or FO,FI where FO is *fan-out* (number of target cells each source cell contacts) and FI is *fan-in* (number of source cells going to each target cell).

| ld | Source cell | Target cell | Value | Reference |
|----|-------------|-------------|----------|----------------------------------|
| d1 | dcn | Cell count | 4.6x10^4 | [PalkovitsM+3-1977] ¹ |

¹ M. Palkovits, Eva Mezey, J. Hamori, and J. Szentagothai. Quantitative histological analysis of the cerebellar nuclei in the cat. I. Numerical data on cells and on synapses. *Experimental Brain Research*, May 1977. URL: http://link.springer.com/10.1007/BF00237096, doi:10.1007/BF00237096, Notes: PalkovitsM+3-1977.html.

CHAPTER

SEVEN

QUESTIONS

Some questions for which we are trying to find answers:

7.1 How would Loebner fig 2 be changed to take into account more recent data?

Figure 2 in Loebner 1989 (see *About the Pseudocerebellum project*) is one of the main starting points for this website. How would that figure be updated to given more recent data? Some papers that may provide updates:

- Paper [DeZeeuwCI+2-2021] gives a summary of multiple updates. From text: The discovery of several new connections (Fig. 1, red) highlights a previously unappreciated level of recurrence in the cerebellar circuit. Mutual inhibition of like cell types is common: Purkinje cells inhibit other Purkinje cells¹, molecular layer interneurons inhibit other molecular layer interneurons in a way that is spatially highly structured²,³, and Golgi cells inhibit other Golgi cells⁴. At the same time, previously hypothesized connections between molecular layer interneurons and Golgi cells have been ruled out[?]. There also is electrical coupling among molecular layer interneurons5 and among Golgi cells⁵. Circuitry in the granule cell layer has the potential to filter and even reverse the sign of the input from mossy fibers, especially if it incorporates the unipolar brush cells7. In some regions, collaterals from Purkinje cells contact (inhibit) granule cells and create an additional recurrent connection in the input layer⁶. Finally, neurons in the cerebellar nuclei provide feedback to the cerebellar cortex, via a mossy fiber-like projection that is subject to plastic changes during learning9,10.
- Inhibitory neurons of the cerebellar nuclei (CN) project profusely into the cerebellar cortex, where they make synaptic contacts on a GABAergic subpopulation of cerebellar Golgi cells. [AnkriL+5-2015],⁷.

¹ Laurens Witter, Stephanie Rudolph, R. Todd Pressler, Safiya I. Lahlaf, and Wade G. Regehr. Purkinje Cell Collaterals Enable Output Signals from the Cerebellar Cortex to Feed Back to Purkinje Cells and Interneurons. *Neuron*, 91(2):312–319, July 2016. URL: https://linkinghub.elsevier. com/retrieve/pii/S0896627316302483, doi:10.1016/j.neuron.2016.05.037, Notes: WitterL+4-2016.html.

² Sarah Rieubland, Arnd Roth, and Michael Häusser. Structured Connectivity in Cerebellar Inhibitory Networks. *Neuron*, 81(4):913–929, February 2014. URL: https://linkinghub.elsevier.com/retrieve/pii/S0896627313011902, doi:10.1016/j.neuron.2013.12.029, Notes: RieublandS+2-2014.html.

³ Charlotte Arlt and Michael Häusser. Microcircuit Rules Governing Impact of Single Interneurons on Purkinje Cell Output In Vivo. *Cell Reports*, 30(9):3020–3035.e3, March 2020. URL: https://linkinghub.elsevier.com/retrieve/pii/S2211124720301637, doi:10.1016/j.celrep.2020.02.009.

⁴ Court Hull and Wade G. Regehr. Identification of an Inhibitory Circuit that Regulates Cerebellar Golgi Cell Activity. *Neuron*, 73(1):149–158, January 2012. URL: https://linkinghub.elsevier.com/retrieve/pii/S0896627311009949, doi:10.1016/j.neuron.2011.10.030, Notes: HullC+RegehrWG-2012.html.

⁵ Guillaume P. Dugué, Nicolas Brunel, Vincent Hakim, Eric Schwartz, Mireille Chat, Maxime Lévesque, Richard Courtemanche, Clément Léna, and Stéphane Dieudonné. Electrical Coupling Mediates Tunable Low-Frequency Oscillations and Resonance in the Cerebellar Golgi Cell Network. *Neuron*, 61(1):126–139, January 2009. URL: https://linkinghub.elsevier.com/retrieve/pii/S0896627308010210, doi:10.1016/j.neuron.2008.11.028.

⁶ Chong Guo, Laurens Witter, Stephanie Rudolph, Hunter L. Elliott, Katelin A. Ennis, and Wade G. Regehr. Purkinje Cells Directly Inhibit Granule Cells in Specialized Regions of the Cerebellar Cortex. *Neuron*, 91(6):1330–1341, September 2016. URL: https://linkinghub.elsevier.com/ retrieve/pii/S0896627316305037, doi:10.1016/j.neuron.2016.08.011, Notes: GuoC+5-2016.html.

⁷ Lea Ankri, Zoé Husson, Katarzyna Pietrajtis, Rémi Proville, Clément Léna, Yosef Yarom, Stéphane Dieudonné, and Marylka Yoe Uusisaari. A novel inhibitory nucleo-cortical circuit controls cerebellar Golgi cell activity. *eLife*, 4:e06262, May 2015. URL: https://elifesciences.org/articles/ 06262, doi:10.7554/eLife.06262, Notes: AnkriL+5-2015.html.

Cited references:

7.2 Anatomy of microzone circuits

The cerebellum is organized into thousands of microzones or modules. What is the specific anatomy (size, connections, fan-in fan-out) of a microzone? A starting point for reference is [AppsR+HawkesR-2009]¹.

¹ Richard Apps and Richard Hawkes. Cerebellar cortical organization: a one-map hypothesis. *Nature Reviews Neuroscience*, 10:670–681, 9 2009. doi:10.1038/nrn2698, Notes: AppsR+HawkesR-2009.html.

CHAPTER

EIGHT

NOTES

Notes about the following papers are available:

8.1 AndersonBB+2-1992 - A quantitative study of the human cerebellum with unbiased stereological techniques

Notes about [AndersonBB+2-1992]¹.

This paper has data giving the counts of some cell types in the human cerebellum. The data is given in Table 2 of the paper.

| 16 A 10 20 10 20 | TABLE 4. Total Cell Number in Five Human Cerebella (10 ⁶) ¹ | | | | | | |
|------------------|--|-------------|--------------|--------------|--------------|--------------|---------------|
| Brain No. | Granule | Purkinje | Golgi/g | Glial/g | Glial/m | Neurons/m | Dentate nucle |
| 1 | 80,900 (0.12) | 24.6 (0.13) | 56.3 (0.15) | 1,130 (0.16) | 1 160 (0.06) | 1 270 (0 14) | 5.24 (0.08) |
| 2 | 97,400 (0.09) | 34.2 (0.21) | 115.3 (0.16) | 1.170 (0.18) | 900 (0.08) | 1.320 (0.07) | 6.87 (0.04) |
| 3 | 108,700 (0.10) | 31.2 (0.18) | 80.6 (0.27) | 1.260 (0.12) | 1.020 (0.06) | 1 460 (0 07) | 3 98 (0.05) |
| 4 | 102,700 (0.12) | 33.4 (0.30) | 86.3 (0.11) | 1.750 (0.11) | 540 (0.25) | 2.090 (0.10) | 0.00 (0.00) |
| 5 | 116,100 (0.21) | 29.1 (0.08) | 68.1 (0.10) | 1,330 (0.19) | 1.540(0.11) | 2.020 (0.20) | 3 94 (0.08) |
| Mean | 101,100 (0.13) | 30.5 (0.13) | 81.3 (0.27) | 1,330 (0.19) | 1,030 (0.36) | 1,630 (0.24) | 5.01 (0.28) |

Coefficient of error (SEM/mean) is shown in parentheses after individual values. Coefficient of variation (SD/mean) between cerebella is shown in parentheses after the mean value for each column and / gand /m refers to cells in either granular or molecular layer. The granular layer is the reference volume for granule, Purkinje, Golgi/g, glial/g cells; and the molecular layer is the reference volume for glial/m and neurons/m.

| 112.11 1000 ± 11 1000 ± 2 1772 11000 ± 2 1772 | Fig. 1: Ta | ble 4 in Anderson | BB+2-1992 | [AndersonBB+2 | -1992]. |
|---|------------|-------------------|-----------|---------------|---------|
|---|------------|-------------------|-----------|---------------|---------|

Data for table Cell counts in different species

The following table has data and references for table *Cell counts in different species*. Values are the number of cells of the given type in the specified species.

| ld | Cell type | Species | Value | Reference |
|----|-----------------|---------|----------------|----------------------|
| d1 | purkinje | human | 30.5 x 10^6 | [AndersonBB+2-1992]? |
| d2 | grannule | human | 101,000 x 10^6 | [AndersonBB+2-1992]? |
| d3 | dentate nucleus | human | 5.01 x 10^6 | [AndersonBB+2-1992]? |
| d4 | golgi | human | 81.3 x 10^6 | [AndersonBB+2-1992]? |

¹ Andersen BB, Korbo L, and Pakkenberg B. A quantitative study of the human cerebellum with unbiased stereological techniques. *J Comp Neurol*, 326(4):549–60, 1992. doi:10.1002/cne.903260405, Notes: AndersonBB+2-1992.html (this file).

8.2 AnkriL+5-2015

Notes about $[AnkriL+5-2015]^1$.

This paper shows that cerebellar nuclei (CN) neurons inhibit some Golgi cells.

Abstract:

The cerebellum, a crucial center for motor coordination, is composed of a cortex and several nuclei. The main mode of interaction between these two parts is considered to be formed by the inhibitory control of the nuclei by cortical Purkinje neurons. We now amend this view by showing that inhibitory GABA-glycinergic neurons of the cerebellar nuclei (CN) project profusely into the cerebellar cortex, where they make synaptic contacts on a GABAergic subpopulation of cerebellar Golgi cells. These spontaneously firing Golgi cells are inhibited by optogenetic activation of the inhibitory nucleo-cortical fibers both in vitro and in vivo. Our data suggest that the CN may contribute to the functional recruitment of the cerebellar cortex by decreasing Golgi cell inhibition onto granule cells.

Other quotes from paper:

Page 1:

Currently, the cerebellar cortex and the CN are known to interact through two circuits. The best known is the nucleo-olivary (NO) circuit (Apps and Garwicz, 2005; Apps and Hawkes, 2009; Chaumont et al., 2013), where the small GABAergic CN cells, subject to PN inhibition (Najac and Raman, 2015), project to the contralateral IO (Fredette and Mugnaini, 1991). This pathway regulates olivary activity (Chen et al., 2010; Bazzigaluppi et al., 2012; Chaumont et al., 2013; Lefler et al., 2014) and thereby complex spike activity in the PNs and cerebellar cortical plasticity (Hansel and Linden, 2000; Coesmans et al., 2004; Bengtsson and Hesslow, 2006; Medina and Lisberger, 2008).

A less-known nucleo-cortical circuit is formed by the glutamatergic neurons of the CN which, in addition to projecting to various premotor and associative regions of the brain (Tsukahara and Bando, 1970; Asanuma et al., 1980; Angaut et al., 1985; Sultan et al., 2012; Ruigrok and Teune, 2014), send axonal collaterals to the cerebellar granule cell layer (GrCL; Houck and Person, 2015). These collateral fibers form MF-like terminals contacting granule cell (GrC) and Golgi cell dendrites (see also Tolbert et al., 1976, 1977, 1978; Ha'mori et al., 1980; Payne, 1983). The functional significance of this excitatory nucleo-cortical (eNC) pathway, loosely following the modular arrangement of the cerebellum (Dietrichs and Walberg, 1979; Gould, 1979; Haines and Pearson, 1979; Tolbert and Bantli, 1979; Buisseret-Delmas, 1988; Provini et al., 1998; Ruigrok, 2010 ; reviewed by Houck and Person, 2013), is likely related to efference copying of motor commands to the cerebellar cortex (Sommer and Wurtz, 2008; Houck and Person, 2015).

In addition to the pathways linking the CN with the cerebellar cortex mentioned above, evidence has occasionally emerged for an inhibitory nucleo-cortical (iNC) pathway. GABAergic neurons have been shown to be labeled in the CN by retrograde tracing from the cerebellar cortex (Batini et al., 1989), and nucleocortical terminals with non-glutamatergic ultrastructural features have been found to contact putative Golgi cell dendrites (Tolbert et al., 1980). More recently, it was demonstrated that GlyT2-expressing CN neurons extend axons toward the cerebellar cortex (Uusisaari and Kno[°]pfel, 2010), suggesting that the iNC pathway might be identifiable by its glycinergic phenotype. While the iNC projection is likely to have significant impact on cerebellar computation, its postsynaptic targets and its functional organization remain unknown.

¹ Lea Ankri, Zoé Husson, Katarzyna Pietrajtis, Rémi Proville, Clément Léna, Yosef Yarom, Stéphane Dieudonné, and Marylka Yoe Uusisaari. A novel inhibitory nucleo-cortical circuit controls cerebellar Golgi cell activity. *eLife*, 4:e06262, May 2015. URL: https://elifesciences.org/articles/ 06262, doi:10.7554/eLife.06262, Notes: AnkriL+5-2015.html (this file).

8.3 AppsR+HawkesR-2009

Notes about [AppsR+HawkesR-2009]¹.

This paper describes different zones of the cerebellum.

| Table 1 Different o | erebellar nomenclatures | |
|-------------------------------|--|--------------------------|
| Topographical unit | Description | Experimental basis |
| Longitudinal zone | A rostrocaudally extended array of Purkinje cells within the cerebellar cortex with specific olivocerebellar and cortico-nuclear connections and climbing fibre input relayed through a common set of olivocerebellar pathways | Anatomy and physiology |
| Module | A longitudinal zone of Purkinje cells together with its olivo-cortico-nuclear connections and associated recurrent pathways | Anatomy |
| Microzone | Subdivision of a longitudinal zone in which Purkinje cells have similar climbing fibre receptive fields | Physiology |
| Transverse zone | Region of cerebellar cortex identified by mediolateral gene expression boundaries | Gene expression patterns |
| Purkinje cell stripe/ band | Longitudinally oriented subregion of a transverse zone in which Purkinje cells have the same phenotype | Gene expression patterns |
| Patch | Region of cerebellar cortex with similar mossy fibre receptive fields in the granular layer | Physiology |
| | | |

Fig. 2: Table 1 in AppsR+HawkesR-2009 [AppsR+HawkesR-2009].

p. 671

Transverse zones Although anatomical, physiological and behavioural studies have emphasised a longitudinal organization within the cerebellar cortex (see later), developmental studies 17,18 suggest that the development of the fundamental cerebellar architecture begins with the subdivision of the cerebellar cortex into five (or six in birds) transverse zones 17 (FIG. 2)

Stripes Every transverse zone is subdivided into a series of stripes (or 'bands') oriented along the rostrocaudal axis and which are defined by the restricted expression of molecular markers (FIG. 2). The most comprehensively studied molecular marker is zebrin II22, which cloning studies revealed to be the metabolic enzyme aldolase C23,24. Zebrin II is expressed by a subset of Purkinje cells (zebrin II+) that alternate with Purkinje cells that do not express this marker (zebrin II–), thus forming zebrin II+/– stripes (FIG. 2). The zebrin II+/– stripes are symmetrically distributed across the midline, highly reproducible between individuals22,25,26 and conserved across species (reviewed in REF. 27).

p. 673:

Longitudinal zones Numerous pathway tracing studies have revealed 'longitudinal zones' within the cerebellar cortex: narrow, rostrocaudally elongated regions that run perpendicular to the long axis of the lobules3,78–80 (FIG. 4). Longitudinal zones were originally defined by their topographically organized Purkinje cell output to different territories within the cerebellar and vestibular nuclei (the socalled A, b, C1, C2, C3, D1 and D2 longitudinal zones of Voogd; for a review of the earlier literature see REF. 2); additional longitudinal zones have subsequently been added, for example, X, CX and D0 (FIG. 4). A longitudinal zonal arrangement also holds true for the anatomy of olivocerebellar climbing fibre projections81 and for the pattern of termination of physiologically characterised spino-olivocerebellar connections defined by anatomical and physiological methods coincide, for example, see REF. 83.

p. 674-675

Modules and microzones.

Anatomical tract tracing has also been used to describe the way in which olivocerebellar (climbing fibre) afferents and corticonuclear (Purkinje cell) efferents are linked to form discrete complexes, the cortical component of each of these 'modules' being a longitudinal zone of Purkinje cells2,79. Anatomically defined modules have been extended to include other connections, notably the nucleo-olivary and reciprocal

¹ Richard Apps and Richard Hawkes. Cerebellar cortical organization: a one-map hypothesis. *Nature Reviews Neuroscience*, 10:670–681, 9 2009. doi:10.1038/nrn2698, Notes: AppsR+HawkesR-2009.html (this file).



Figure 2 | **Transverse zones and stripes.** The mouse cerebellar cortex is divided into transverse zones, and each zone is subdivided into parasogittal stripes. Zones and stripes are clearly seen in the expression patterns of multiple Purkinje cell antigens. a | The distribution of Purkinje cells that are immunoreactive to zebrinl lin the cerebellum of the adult mouse, seen from anterior (top panel), dorsal (middle panel) and posterior (bottom panel) views¹¹. The expression of zebrin II reveals a complex cytoarchitecture comprising four transverse zones in the vermis in both hemispheres: the striped anterior zone (PZ) alternating with the uniformy zebrin II stripe cerebellum of the adult mouse, line the gosterior zone (PZ) alternating with the uniformy zebrin II stripes cells are referred to as P1+ to P7+ (numbered in the figure as 1-7 for calrity) from the midline laterally, and the intervening zebrin II stripes (beige in the figure as 1-6 for calrity) from the midline laterally, and the intervening zebrin II-stripes (beige in the figure as the intervening zebrin II-stripes (beige in the figure as the intervening zebrin II-stripes (beige in the figure as the intervening zebrin II-stripes (beige in the figure) are numbered with reference to the neighbouring (medial) zebrin II+stripe (that is, P1- lies immediately lateral to P1+ etc.²¹²³). Lobules in the vermis are indicated by Roman numerals. D I wo specific examples of stripes. In the top panel, heat shock protein 25 (15P2) immunocytochemistry on a transverse section through the mouse cerebellum reveals Purkinje cell stripes of PLC34 reveals stripes of Purkinje cells. In Ac Z (for example, lobule VII) but not in the CZ (for example, lobule VIb) or NZ (for example, lobule IX), Part a reproduced, with permission, from REF. 9 (0200) Histochemical Society. The top panel of part b is reproduced, with permission, from REF. 9 (0200) Histochemical society. The top panel of part b is reproduced, with permission, from REF. 9 (0200) Histochemical society. The top pan



Fig. 3: Fig 2 in AppsR+HawkesR-2009 [AppsR+HawkesR-2009].

Figure 4| Longitudinal zones. Dorso-posterior view of the rat cerebellum, indicating the approximate location of different longitudinal zones on the cerebellar surface on the left hand side. Each longitudinal zone is defined by its inferior olive climbing fibre input and Purkinje corticonuclear output. From the medial to the lateral plane (right to left in the figure) are shown: the A.AX, X B and A2 zones (in the vermis), the C1, CX, C2 and C3 zones (in the paravermis), and the D1, D0 and D2 zones (in the hemisphere). Longitudinal zones in the parafloculus and floctuus are not shown. In the simplified block diagrams below, matching colours show, for individual cerebellar cortical zones, the sites of origin of climbing fibres in the contralateral inferior olive, and the corresponding Purkinje cell corticonuclear output targets in the ippliateral cerebellar and vestibular nuclei. Note that some longitudinal zones are not necessarily present in all cerebellar lobules in the adult animal (for example, the X and B zones). Figure is based on data from REFS 14.7380.944, 97, 149, 150. cMAO (subnuc a), subnucleus a of caudal medial accessory olive; cMAO (subnuc less bol facudal medial accessory olive; cMAO (subnuc b'/c), subnucleus b' and c of caudal medial accessory olive; COP; coupla pyramidis; dIPAO, dorsal lamella of the principal olive; iMAO (absounce and hum; DLP) dorsolared in purclubarance of medial nucleus; dIPAO, dorsal lamella of the principal olive; iMAO (absounce); MAO (med), medial part of intermediate nedial accessory olive; IVN, lateral part of intermediate interpositus anterior; NIR; nucleus interpositus posterior; NL (magno), magnocellular part of interal vestibular nucleus; LS, lobulus simplex; MeAN (med), lateral part of medial nucleus; MeAN (med), magnocellular part of medial nucleus; NLA, nucleus interpositus anterior; NIR; nucleus interpositus posterior; NL, magnod, magnocellular part of medial nucleus; MAO, ventral fold of orsal accessory olive; vPO, ventral lamella of the princip

Fig. 4: Fig 4 in AppsR+HawkesR-2009 [AppsR+HawkesR-2009].

olivo-nuclear projections86. In the same way that Purkinje cell stripes are evolutionarily conserved, cerebellar modules are remarkably similar in a range of species (see Supplementary information S1 (table)). S1 (table) The behavioural significance of these modules is beyond the scope of this Review but their conservation implies that each subserves a similar function in different species (for example, regulation of spinal reflexes and limb movements by the paravermal modules87; and control of compensatory eye movements by modules in the flocculus88).

Some longitudinal zones can be further split into smaller units called 'microzones'82,89. In particular, high resolution electrophysiological mapping from medial to lateral across the width of the vermal b zone or the paravermal C3 zone shows small groups of Purkinje cells with distinct climbing fibre receptive fields that arise from different body parts. Each Purkinje cell group typically occupies a narrow, rostrocaudally oriented strip of cortex within the broader longitudinal zone (each zone ~1 mm and each microzone \sim 100–300 m wide). microzones mapped in the vermal b zone form a regular array of olivo-cortico-nuclear 'microcomplexes' that are thought to control different aspects of the motor functions handled by the broader module82. However, the most extensively studied microzones lie within a small part of the C3 longitudinal zone in the paravermis of lobule V in cats, and their organization seems to be rather different89. Whereas individual microzones in the b zone are thought to extend the entire rostrocaudal length of the zone (more than 100 mm in cat)82, microzones in C3 tend to be much shorter, usually extending across no more than a few adjacent cerebellar folia. In addition, microzones located in different parts of the paravermal cortex can have the same climbing fibre receptive field characteristics (for example, there are at least four separate 'eyeblink' microzones in each paravermis90). This has led to the concept that spatially separated collections of microzones with common climbing fibre input — termed 'multizonal microcomplexes' — may be important for the parallel processing and integration of information from mossy fibre inputs derived from multiple sources3,89.

Some anatomical data are consistent with such a possibility (for example, see REF. 91), but physiological studies to fully test this hypothesis are currently lacking. Anatomical tracer studies have also revealed a correspondingly detailed map within the inferior olive, with subgroups of olivary cells providing climbing fibres to different parts of the same longitudinal zone (for example, see REF. 92 and FIG. 4). In some cases the resolution of the anatomical mapping has been sufficient to reveal this connectivity at a level that might correspond to microzones93,94. Longitudinal zones are therefore most probably composite entities, and the basic operational unit of the cerebellar cortex is narrower, possibly an individual microzone or, in the case of the paravermis, an assembly of microzones forming a multizonal microcomplex3.

8.4 BillingsG+4-2014

Notes about [BillingsG+4-2014]¹.

This paper has data about the connections between mossy fibers and granule cells in mouse and analysis showing that a small number of inputs to granule cells (about 4) is most efficient for transmitting information from mossy fibers to granule cells.

¹ Guy Billings, Eugenio Piasini, Andrea Lőrincz, Zoltan Nusser, and R. Angus Silver. Network Structure within the Cerebellar Input Layer Enables Lossless Sparse Encoding. *Neuron*, 83(4):960–974, August 2014. URL: https://linkinghub.elsevier.com/retrieve/pii/S089662731400631X, doi:10.1016/j.neuron.2014.07.020, Notes: BillingsG+4-2014.html (this file).



Fig. 5: Figure 2 in BillingsG+4-2014 [BillingsG+4-2014].



Figure 3. Number of synaptic Connections per Neuron and Infestion Determine the Transmission and Infansionmation of information in a Uniform Binary Network Model (A) Top: schematic illustration of mossy fibers (MF, red) and granule cells (GCs) (blue) for a binary network with one MF synaptic connection per GC (*d* = 1; blue) lines, shown for 3 GCs only). Middle: GC activation probability (*p*(/GC)) as a function of MF activation probability (*p*(/MF)); red line for a threshold of 1. Gray dashed line indicates p(G) = p(MF). Bottom: information (entropy) in GC population as a function of p(MF) for one billion events. Vertical dashed lines indicate range of p(MF) where >99% of the information is encoded by the GC population. (G) Same as for (A) but for a network with *d* = 3 and all possible threshold values (1-3 red-blue). (C) Same as for (B) but for *d* = 7 (1-7 red-cyan).

Fig. 6: Fig 3 in BillingsG+4-2014 [BillingsG+4-2014].

8.5 CesanaE+6-2013

Notes about [CesanaE+6-2013]¹.

This paper is cited by [SudhakarSK+8-2017] for the convergence and divergence between (i) mossy fibers to golgi cells and (ii) grannule cells to golgi cells through acending axons and parallel fibers.

| Connectivity name | Convergence | Divergence |
|-------------------|-------------|------------|
| MF-GoC | 13.65 | 12.5 |
| GrC-GoC | 554 | 1.36 |
| GrC-GoC | 4759 | 11.34 |

The full table is here

8.6 DAngeloE+5-2013

Notes about [DAngeloE+5-2013]¹.

This paper has data about of grannule cells and Golgi cells in rat cerebellum. p. 9:

Quantitative Golgi Cell Connection Scheme

On the basis of current knowledge it is possible to generate a quantitative connection scheme for the Golgi cell, which is unique both for its high level of precision and for the quantity of available experimental data. Using morphological measurements, it can be calculated that the rat cerebellar granular layer has a cell density of 4×10^{6} /mm³ for granule cells and 9300/mm³ for Golgi cells, with a Golgi cell : granule cell ratio of 1:430 (Korbo et al., 1993). Moreover, the density of the glomeruli is 3×10^{5} /mm³, and each glomerulus is composed of one mossy fiber terminal, about 53 dendrites from separate granule cells (Jakaband Hamori, 1988), and one or more dendrites from Golgi cells. Network connections can be reconstructed by applying simple rules, most of which can be directly extracted from original works on cerebellar architecture (e.g., see Eccles et al., 1967).

Granule cell connection rules are quite simple and can be summarized as follows: granule cell dendrites cannot reach glomeruli located more than 40 m away (meanden dritic length : 13.6 m) and a single granule cell cannot send more than one dendrite into the same glomerulus. Conversely, Golgi cell connection rules are more complex. It can be assumed that only one Golgi cell axon enters a glomerulus, forming inhibitory synapses on all the afferent granule cell dendrites, and that a Golgi cell axon entering a glomerulus cannot access the neighboring glomeruli if they share granule cells with the first one. This should prevent a granule cell from being inhibited twice by the same Golgi cell (see above and Solinas et al., 2010). Each Golgi cell can inhibit as many as 40 different glomeruli and atotal of about 2000 granule cells, accounting for the 1:430 Golgi cell:granule cell ratio and the aforementioned convergence and divergence ratios (see above). Recent calculations seem to indicate a specific organization of excitatory connectivity. Golgi cells were suggested to receive excitatory inputs from about 40 mossy fibers on basal dendrites (Kanichay and Silver, 2008). Moreover, a specific organization is emerging for granule cell inputs through the ascending axons and parallel fibers (Cesana et al., 2010). Golgi cells could receive about 400 connections from the ascending axons of local granule cells on the basal dendrites and another 400 connections through the parallel fibers of local granule cells,

¹ E. Cesana, K. Pietrajtis, C. Bidoret, P. Isope, E. D'Angelo, S. Dieudonne, and L. Forti. Granule Cell Ascending Axon Excitatory Synapses onto Golgi Cells Implement a Potent Feedback Circuit in the Cerebellar Granular Layer. *Journal of Neuroscience*, 33(30):12430–12446, July 2013. URL: https://www.jneurosci.org/lookup/doi/10.1523/JNEUROSCI.4897-11.2013, doi:10.1523/JNEUROSCI.4897-11.2013, Notes: CesanaE+6-2013.html (this file).

¹ Egidio D'Angelo, Sergio Solinas, Jonathan Mapelli, Daniela Gandolfi, Lisa Mapelli, and Francesca Prestori. The cerebellar Golgi cell and spatiotemporal organization of granular layer activity. *Frontiers in Neural Circuits*, 2013. URL: http://journal.frontiersin.org/article/10.3389/fncir. 2013.00093/abstract, doi:10.3389/fncir.2013.00093, Notes: DAngeloE+5-2013.html (this file).

which would provide the basis for a powerful feedback circuit. In addition, Golgi cells receive about 1200 parallel fiber contacts on the apical dendrites from transversely organized granular layer fields. It has been calculated that the effectiveness of local granule cells is about 10 times greater than that of an equivalent population located outside the direct afferent field and forming only parallel fiber contacts toward the Golgi cell.

8.7 DeZeeuwCI+2-2021

Notes about [DeZeeuwCI+2-2021]¹.

This paper describes some recently discovered connections and changes to the cortical circuit. Specifically:

The discovery of several new connections (Fig. 1, red) highlights a previously unappreciated level of recurrence in the cerebellar circuit. Mutual inhibition of like cell types is common: Purkinje cells inhibit other Purkinje cells², molecular layer interneurons inhibit other molecular layer interneurons in a way that is spatially highly structured³,⁴, and Golgi cells inhibit other Golgi cells⁵. At the same time, previously hypothesized connections between molecular layer interneurons and Golgi cells have been ruled out². There also is electrical coupling among molecular layer interneurons5 and among Golgi cells⁶. Circuitry in the granule cell layer has the potential to filter and even reverse the sign of the input from mossy fibers, especially if it incorporates the unipolar brush cells7. In some regions, collaterals from Purkinje cells contact (inhibit) granule cells and create an additional recurrent connection in the input layer⁷. Finally, neurons in the cerebellar nuclei provide feedback to the cerebellar cortex, via a mossy fiber-like projection that is subject to plastic changes during learning9,10.

x The newly discovered recurrent pathways may endow the cerebellar cortex with an exceptional capacity for dynamic processing and has led to suggestions of several new and previously unappreciated neural computations. Electrical coupling, along with synaptic inputs, could regulate the synchrony of functionally related clusters of interneurons11,12 or could perform local functions for individual neurons, such as linearization of dendritic integration13. The mossy fiber feedback from the cerebellar nucleus could serve to organize the different components of a movement sequence14 or relay a corollary discharge that amplifies learned responses10.

¹ Chris I. De Zeeuw, Stephen G. Lisberger, and Jennifer L. Raymond. Diversity and dynamism in the cerebellum. *Nature Neuroscience*, 24(2):160–167, February 2021. URL: http://www.nature.com/articles/s41593-020-00754-9, doi:10.1038/s41593-020-00754-9, Notes: DeZeeuwCI+2-2021.html (this file).

² Laurens Witter, Stephanie Rudolph, R. Todd Pressler, Safiya I. Lahlaf, and Wade G. Regehr. Purkinje Cell Collaterals Enable Output Signals from the Cerebellar Cortex to Feed Back to Purkinje Cells and Interneurons. *Neuron*, 91(2):312–319, July 2016. URL: https://linkinghub.elsevier. com/retrieve/pii/S0896627316302483, doi:10.1016/j.neuron.2016.05.037, Notes: WitterL+4-2016.html.

³ Sarah Rieubland, Arnd Roth, and Michael Häusser. Structured Connectivity in Cerebellar Inhibitory Networks. *Neuron*, 81(4):913–929, February 2014. URL: https://linkinghub.elsevier.com/retrieve/pii/S0896627313011902, doi:10.1016/j.neuron.2013.12.029, Notes: RieublandS+2-2014.html.

⁴ Charlotte Arlt and Michael Häusser. Microcircuit Rules Governing Impact of Single Interneurons on Purkinje Cell Output In Vivo. *Cell Reports*, 30(9):3020–3035.e3, March 2020. URL: https://linkinghub.elsevier.com/retrieve/pii/S2211124720301637, doi:10.1016/j.celrep.2020.02.009.

⁵ Court Hull and Wade G. Regehr. Identification of an Inhibitory Circuit that Regulates Cerebellar Golgi Cell Activity. *Neuron*, 73(1):149–158, January 2012. URL: https://linkinghub.elsevier.com/retrieve/pii/S0896627311009949, doi:10.1016/j.neuron.2011.10.030, Notes: HullC+RegehrWG-2012.html.

⁶ Guillaume P. Dugué, Nicolas Brunel, Vincent Hakim, Eric Schwartz, Mireille Chat, Maxime Lévesque, Richard Courtemanche, Clément Léna, and Stéphane Dieudonné. Electrical Coupling Mediates Tunable Low-Frequency Oscillations and Resonance in the Cerebellar Golgi Cell Network. *Neuron*, 61(1):126–139, January 2009. URL: https://linkinghub.elsevier.com/retrieve/pii/S0896627308010210, doi:10.1016/j.neuron.2008.11.028.

⁷ Chong Guo, Laurens Witter, Stephanie Rudolph, Hunter L. Elliott, Katelin A. Ennis, and Wade G. Regehr. Purkinje Cells Directly Inhibit Granule Cells in Specialized Regions of the Cerebellar Cortex. *Neuron*, 91(6):1330–1341, September 2016. URL: https://linkinghub.elsevier.com/ retrieve/pii/S0896627316305037, doi:10.1016/j.neuron.2016.08.011, Notes: GuoC+5-2016.html.



Fig. 1 | Intricacies of the cerebellar circuit. Red arrows show novel synaptic connections and dashed red circles show novel electrical connections. Open and filled presynaptic terminals and cell bodies represent excitatory and inhibitory cell bodies or terminals, respectively. Open and filled arrows point to newly discovered excitatory and inhibitory connections. PC, Purkinje cell; Go, Golgi cell; GC, granule cell; UBC, unipolar brush cell; CF, climbing fiber input; CN, cerebellar nucleus; IO, Inferior olive; MF, mossy fiber input; ML, molecular layer interneurons; PFs, parallel fiber inputs.

Fig. 7: Figure 1 in De Zeeuw CI (2021) [DeZeeuwCI+2-2021].

8.8 EcclesJC+2-1967

Notes about [EcclesJC+2-1967]¹.

This book has extensive data about the cerebellum.



Fig. 8: Figure 75 in [EcclesJC+2-1967].

8.9 GlicksteinM-2007

Notes about [GlicksteinM-2007]¹.

States that:

The cerebellum is probably the single most important link between visual and motor areas of the cerebral cortex. What sort of visual information reaches the cerebellum? In monkeys there are two groups of cortical areas that process visual information beyond the primary visual cortex. A dorsal, medially located group that is dominated by cells that are responsive primarily to moving stimuli, and a ventral group involved in visual recognition. Ungerleider and Mishkin [14] based their suggested grouping of visual areas — "where is it?" versus "what is it?" — on the behavioural effects of lesions. Jack May and I [15] based our distinction between a medial and a lateral group on the difference in the pontine projections of the two groups. The dorsal group is connected to the cerebellum by way of the pons; the lateral, more ventrally placed group is not. Information on movement of objects and of the body in relation to its surroundings is sent continuously to the cerebellum by cells in the dorsal cortical visual areas. Lesions of the dorsal group, including the cortex within the angular gyrus in monkeys [16] and a similar cortical area in humans [17] produce a lasting deficit in visual guidance of movement of the arms and fingers. Lesions of the ventral group do not.

8.10 GuoC+5-2016

Notes about $[GuoC+5-2016]^1$.

This paper shows that Purkinje Cell Collaterals inhibit granule cells in some regions.

From abstract:

¹ John C. Eccles, Masao Ito, and János Szentágothai. *The Cerebellum as a Neuronal Machine*. Springer Berlin Heidelberg, 1967. doi:10.1007/978-3-662-13147-3, Notes: EcclesJC+2-1967.html (this file).

¹ Mitch Glickstein. What does the cerebellum really do? *Current Biology*, 17(19):4, 2007. doi:10.1016/j.cub.2007.08.009, Notes: GlicksteinM-2007.html (this file).

¹ Chong Guo, Laurens Witter, Stephanie Rudolph, Hunter L. Elliott, Katelin A. Ennis, and Wade G. Regehr. Purkinje Cells Directly Inhibit Granule Cells in Specialized Regions of the Cerebellar Cortex. *Neuron*, 91(6):1330–1341, September 2016. URL: https://linkinghub.elsevier.com/ retrieve/pii/S0896627316305037, doi:10.1016/j.neuron.2016.08.011, Notes: GuoC+5-2016.html (this file).

Inhibition of granule cells plays a key role in gating the flow of signals into the cerebellum, and it is thought that Golgi cells are the only interneurons that inhibit granule cells. Here we show that Purkinje cells, the sole output neurons of the cerebellar cortex, also directly inhibit granule cells via their axon collaterals. Anatomical and optogenetic studies indicate that this non-canonical feedback is region specific: it is most prominent in lobules that regulate eye movement and process vestibular information. Collaterals provide fast, slow, and tonic inhibition to granule cells, and thus allow Purkinje cells to regulate granule cell excitability on multiple timescales. We propose that this feedback mechanism could regulate excitability of the input layer, contribute to sparse coding, and mediate temporal integration.



Fig. 9: Figure 2 in GuoC+5-2016 [GuoC+5-2016].

Comment: I don't understand why the purkinje cell firing rates are decreasing in figure 5c. I thought excitatory input from mossy fibers would increase the firing of purkinje cells.

8.11 HullC+RegehrWG-2012

Notes about [HullC+RegehrWG-2012]¹.

This paper shows that Molecular Layer Interneurons do not inhibit Golgi cells and that Golgi cells inhibit each other through synaptic inhibition.

From abstract:

In contrast to current thought, we find that Golgi cells, not MLIs, make inhibitory GABAergic synapses onto other Golgi cells. As a result, MLI feedback does not regulate the Golgi cell network, and Golgi cells are inhibited approximately 2 ms before Purkinje cells, following a mossy fiber input. Hence, Golgi cells and Purkinje cells receive unique sources of inhibition and can differentially process shared granule cell inputs.

¹ Court Hull and Wade G. Regehr. Identification of an Inhibitory Circuit that Regulates Cerebellar Golgi Cell Activity. *Neuron*, 73(1):149–158, January 2012. URL: https://linkinghub.elsevier.com/retrieve/pii/S0896627311009949, doi:10.1016/j.neuron.2011.10.030, Notes: HullC+RegehrWG-2012.html (this file).



Figure 8. The Timing of Golgi Cell Inhibition Matches the Timing of Granule Cell Excitation

All Schematic depicting our revision of the cerebellar circuit diagram. Golgi cells make GABAergic inhibitory synapses onto each other (red circle), and MLIs do not make synapses onto Golgi cells (red X).

(B) Light activation (0.2 ms, 473 nm) evoked an excitatory current onto a Golgi cell with two distinct components (EPSC1 and EPSC2) in control (black). EPSC2 was reduced in the presence of the type 1 cannabinoid receptor (CB1R) agonist WN (3 μ M; light gray) and recovered by the additional application of the CB1R antagonist AM251 (3 μ M; dark gray). (C) The effects of the CB1R agonist and antagonist on EPSC1 and EPSC2 are

(c) The effects of the CBT H agonist and antagonist on EPSC2 are summarized, and each component is normalized to its initial value in control conditions.
(D) Left: example Golgi cell recording in which the same light stimulus

produces a dual component EPSC at the IPSC reversal potential and a disynaptic IPSC at the EPSC reversal potential. Right, top: the same recording



8.12 KorboL+3-1993

Notes about [KorboL+3-1993]¹.

This paper has data giving counts of some cell types in rat cerebellum.

Data for table Cell counts in different species

The following table has data and references for table *Cell counts in different species*. Values are the number of cells of the given type in the specified species.

| ld | Cell type | Species | Value | Reference |
|----|-----------|---------|-------------|------------------|
| r1 | purkinje | rat | 0.61 x 10^6 | [KorboL+3-1993]? |
| r2 | golgi | rat | 0.64 x 10^6 | [KorboL+3-1993]? |
| r3 | grannule | rat | 265 x 10^6 | [KorboL+3-1993]? |

¹ Korbo L, Andersen BB, Ladefoged O, and Møller A. Total numbers of various cell types in rat cerebellar cortex estimated using an unbiased stereological method. *Brain Res*, 609(1-2):262–268, April 1993. doi:10.1016/0006-8993(93)90881-m, Notes: KorboL+3-1993.html (this file).

8.13 LangeW-1975

Notes about [LangeW-1975]¹.

This paper has data on the Purkinje and granule cell ratio in different species.

| Table 2. Ratio of Purkinje cells to granule cell in man and some other mammals | | | | |
|--|--------|------------------------------------|--------|--|
| Man (Homo sapiens) | 1:2991 | Cat (Felis domestica) | 1:1580 | |
| Vervet monkey (Cercopithecus aethiops) | 1:2128 | Sheep (Ovis aries) | 1:1568 | |
| Rhesus monkey (Macaca mulatta) | 1:1898 | Bull (Bos taurus) | 1:1508 | |
| Elephant (Loxodonta africana) | 1:1866 | Guinea pig (Cavia cobaya) | 1: 959 | |
| Squirrel monkey (Saimiri sciureus) | 1:1864 | Opossum (Didelphys virginiana) | 1: 952 | |
| Bottle-nose dolphin (Tursiops truncatus) | 1:1812 | Rabbit (Oryctolagus cuniculus) | 1: 931 | |
| Pilot whale (Globicephala macrorhyncha) | 1:1790 | Rat (Rattus norvegicus) | 1: 897 | |
| Common porpoise (Phocaena phocaena) | 1:1762 | Mouse (Mus musculus domesticus) | 1: 778 | |
| Fox (Vulpes vulpes) | 1:1739 | Mole (Talpa europaea) | 1: 706 | |
| Horse (Equus caballus) | 1:1612 | Hedgehog (Erinaceus europaeus) | 1: 609 | |

Fig. 11: Table 2 in LangeW-1975 [LangeW-1975].

8.14 LoebnerEE-1989

Notes about [LoebnerEE-1989]¹.

This paper has some data for cat in Figure 2.

8.15 PalkovitsM+2-1971a

Notes about [PalkovitsM+2-1971a]¹.

This paper has data about the Purkinje cells in the cat cerebellum.

From page 9: Quantitative parameters are as follows: (a) the Purkinje cell density in the flat part of the folium is 384/sq.mm and the cortical surface area/Purkinje cell is 2604 sq.um; (b) the width of the Purkinje cell dendritic tree (including the spaces between neighbouring dendritic arborizations) is 8.9/um and the dendritic spread is 292.5 um; and (c) the mean distance between Purkinje cells (centre of perikarya) is 51 /um.

From Summary:

¹ W. Lange. Cell number and cell density in the cerebellar cortex of man and some other mammals. *Cell and Tissue Research*, March 1975. URL: http://link.springer.com/10.1007/BF00223234, doi:10.1007/BF00223234, Notes: LangeW-1975.html (this file).

¹ EE Loebner. Intelligent network management and functional cerebellum synthesis. In Raugh MR, editor, *Cerebellar Models of Associative Memory: Three papers from IEEE COMPCON SPRING* '89, pages 14–19. Research Institute for Advanced Computer Science, NASA Ames Research Center, 1989. PDF: LoebnerEE-1989.pdf, Notes: LoebnerEE-1989.html (this file).

¹ M Palkovits, P. Magyar, and J. Szentagothai. Quantitative histological analysis of the cerebellar cortex in the cat. i. number and arrangement in the space of the purkinje cells. *Brain Research*, pages 13, 1971. Notes: PalkovitsM+2-1971a.html (this file).



Fig. 4. Idealized model of Purkinje cell arrangement (drawn to scale) in plan view of the cerebellar cortex. Corresponding cell bodies (circles) and dendritic trees (oblongs) are shown in the same pattern (hatching and stippling). Arrow indicates longitudinal axis of the folium.

Brain Research, 32 (1971) 1-13

Fig. 12: Figure 4 in PalkovitsM+2-1971a [PalkovitsM+2-1971a].

Purkinje cell numbers, densities and arrangement in space were studied by quantitative histology in the cerebella of adult cats. Calculated for the living state the density of the Purkinje cells was 373/sq.mm in entire folia (lobus paramedianus); the density in flattened parts of these folia was 384/sq.mm. The mean density calculated for the total living cerebellum was 330/sq.mm. The total number of Purkinje cells was 1.2-1.3 million. On the basis of the known general principles of shape and arrangement in this study a new space arrangement model is suggested. Purkinje cells are placed in a rhomboid pattern. In reality certain distortions of this pattern occur, in consequence of a flexibility in the relations of cell bodies to dendritic trees, but the essential correctness of the model can be proved statistically by distance measurements of Purkinje cells in randomly and in geometrically determined directions.

Data for table Cell counts in different species

The following table has data and references for table *Cell counts in different species*. Values are the number of cells of the given type in the specified species.

| ld | Cell type | Species | Value | Reference |
|----|-----------|---------|-------------|-----------------------|
| p1 | purkinje | cat | 1.25 x 10^6 | [PalkovitsM+2-1971a]? |

Range specified in the paper was 1.2-1.3 million. 1.25 million is the average.

8.16 PalkovitsM+2-1971b

Notes about [PalkovitsM+2-1971b]¹.

This paper has data about of grannule cells and Golgi cells in cat cerebellum.

Data for table Cell counts in different species

The following table has data and references for table *Cell counts in different species*. Values are the number of cells of the given type in the specified species.

¹ M Palkovits. Quantitative histological analysis of the cerebellar cortex in the cat. II. Cell numbers and densities in the granular layer. *Brain Research*, pages 16, 1971. Notes: PalkovitsM+2-1971b.html (this file).

| ld | Cell type | Species | Value | Reference |
|-----|-----------|---------|------------|-----------------------|
| pb1 | grannule | cat | 2.2 x 10^9 | [PalkovitsM+2-1971b]? |
| pb2 | golgi | cat | 417,000 | [PalkovitsM+2-1971b]? |

Figure is given on page 29 (summary section). Also states that the The granule cell : Purkinje cell ratio was 1700-1800 : 1.

Paper also states that the ratio of Golgi cells to Purkinje cells is 1 : 3. This means, that if there are 1.25×10^{6} Purkinje cells, then there are about 416,666 Golgi cells (rounded, about 417,000).

p. 30:

This density of the Golgi cells – assuming non-overlap between dendrites and axons – would require a compartmentation of the space available to the Golgi cells in an idealized model into hexagonal prisms of around 100 #m diameter. The prisms would cut vertically through all 3 layers of the cortex, and the volume of the part corresponding to the granular layer would be approximately 0.002 cu.mm (calculated for the living cat), containing about 200 glomeruli.

If 200 glomeruli are contacted by each Golgi cell, then the number of granule cells potentiall connected by each Golgi cell would be $200 \times 112 = 2.24 \times 10^{4}$. This is different than the figure of 5.2×10^{4} in [LoebnerEE-1989] Fig 2. If the average was 28 granule cells per glomeruli, the figure would be $200 \times 28 = 5.6 \times 10^{4}$ which is closer to the figure in [LoebnerEE-1989] Fig 2.

8.17 PalkovitsM+2-1971c

Notes about [PalkovitsM+2-1971c]¹.

This paper has data about basket and stellate cells and parallel fibers in cat cerebellum.

Data for table *Cell counts in different species*

The following table has data and references for table *Cell counts in different species*. Values are the number of cells of the given type in the specified species.

| ld | Cell type | Species | Value | Reference |
|-----|-----------|---------|------------|-----------------------|
| pb1 | basket | cat | 7.5 x 10^6 | [PalkovitsM+2-1971c]? |
| pb2 | stellate | cat | 20.9x 10^6 | [PalkovitsM+2-1971c]? |

The cell counts above are calculated from the data using the Figure is given on page 29 (summary section). Also states that the The granule cell : Purkinje cell ratio was 1700-1800 : 1.

The previous paper in the series [PalkovitsM+2-1971b] states that there are about 1.25 x 10⁶ purkinje cells. This paper estimates that the Purkinje cell-basket cell ratio is 1 : 6; the Purkinje cell-stellate cell ratio 1 : 16-17.5. Based on that, there would be about 7.5×10^{6} basket cells and 20.9×10^{6} stellate cells.

Summary section of paper:

Cell density in the molecular layer of the cat cerebellar cortex calculated for the living state is 43,700/cu.mm. Of these 15% are basket cells, 42.8% stellate cells and 41.2% are glial elements (including endothelial cells, pericytes, etc.). The Purkinje cell-basket cell ratio is 1 : 6; the Purkinje cell-stellate cell ratio 1 : 16-17.5. Of the basket cells 21% are located in the ganglionic layer and 79.9% in the molecular layer. Of the molecular layer basket cells 95% are situated in the deeper half of this stratum. The average

¹ M. Palkovits, P. Magyar, and J. Szentágothai. Quantitative histological analysis of the cerebellar cortex in the cat. III. Structural organization of the molecular layer. *Brain Research*, 34(1):1–18, November 1971. URL: https://linkinghub.elsevier.com/retrieve/pii/0006899371903477, doi:10.1016/0006-8993(71)90347-7, Notes: PalkovitsM+2-1971c.html (this file).

length of the basket axons in the transverse plane of the folium is 500-550 um (a distance of 10 Purkinje cells). The average span of their descending side branches in the longitudinal plane of the folium is 300-320 um (a distance of 3-3 Purkinje cell bodies in both directions). Calculations of the average number of Purkinje cell baskets in which the basket axon participates gave unexpectedly low values: 8-9 baskets per axon.

Statistical evaluation of systematic measurements performed on electron micrographs of the molecular layer yielded the following quantitative data for the parallel fibers: the average length of the parallel fibers is 2 mm, their average diameter 0.197 um and in a 1 mm wide longitudinal prism of the molecular layer in the living animal there are 1,374,000 parallel fibers. The average diameter of parallel fibers is slightly greater in the deeper palt of the molecular layer; the difference, although statistically significant, is hardly relevant biologically. The average number of parallel fibers crossing the whole dendritic arborization of a Purkinje cell is roughly 400,000. Calculation based on the average lengths and densities of parallel fiber synaptic thickenings showed that the parallel fiber makes synaptic contact with, on an average, only every fifth (allowing for correction, every 5.5th) Purkinje dendrite arborization which it penetrates during its course. The average parallel fiber would thus contact, in its entire course of 2 mm, 45 Purkinje cells (after correction, 42.5). The number of dendritic spines per Purkinje cells is calculated to be 80,000.

8.18 PalkovitsM+2-1972

Notes about [PalkovitsM+2-1972]¹.

This paper give the ratio between mossy fibers, climbing fibers and purkinje cells in the cat cerebellum and a circuit diagram showing the connections.



Fig. 13: Figure 4 in PalkovitsM+2-1972 [PalkovitsM+2-1972].

"The mossy fiber-Purkinje cell ratio within the folium is thus 4:1."

¹ Miklos Palkovits, Pal Magyar, and Janos Szentagothai. Quantitative histological analysis of the cerebellar cortex in the cat. IV. Mossy fiber-purkinje cell numerical transfer. *Brain Research*, 45(1):15–29, October 1972. URL: https://linkinghub.elsevier.com/retrieve/pii/0006899372902132, doi:10.1016/0006-8993(72)90213-2, Notes: PalkovitsM+2-1972.html (this file).

From summary:

About 96,000 fibers/sq.mm cross-sectional area enter through the medullary lamina at the base of cerebellar folia in the adult cat. Of these one-sixth are Purkinje axons, one-sixth climbing fibers and the remaining four-sixths of the total number of fibers crossing the base can be assumed to be mossy fibers. The mossy fiber-Purkinje cell ratio within the folium is thus 4:1.

In 1 cu.mm of the granular layer 98,800 glomeruli are found on average (calculated for the living state) in homogeneous distribution and arranged isotropically in space. One mossy fiber breaks up (within a given folium) into about 16-17 mossy rosettes (glomeruli). According to earlier data [10] the granule cell-glomerulus ratio is 27-28:1, the mossy fiber-granule cell ratio is therefore 1:460. The granule cells have 4.17 dendrites, on average; the average mossy rosette is contacted by 112 granule dendrites. The number of postsynaptic units (dendrite digits) is 10.2/dendrite and 1,142/glomerulus. Numerically, the granule cells belonging to one Purkinje cell (1,792) are capable of transmitting impulses from 4 mossy fibers and their 68 rosettes (glomeruli), while the parallel fibers, being 2 mm long, penetrate the dendrite trees of 225 Purkinje cells. Since they establish synapses with only every fifth of these Purkinje cells, the calculated number of parallel fibers-Purkinje spine synapses would be 80,550/Purkinje cell 11. This calculated value agrees reasonably well with the counted number of Purkinje cell dendritic spines = 91,600.

On the basis of this study series the numerical transfer model of the mossy fiber- Purkinje cell neuron chain can be constructed according to an all-over input-output ratio of 4:1. Further, the numerical, metrical and topological parameters of the divergence from mossy fibers through granule cells and parallel fibers, as well as those of the convergence at granule cell and Purkinje cell level can be established with reasonable accuracy. Since both the numerical and connectivity aspects of the entire neuron model are consistent with one another, and are based on numerous counts and measurements performed using a variety of independent approaches (either on the whole cerebellum or on representative parts), the connectivity model presented is suitable for realistic computer simulation models of the cerebellar cortex.

8.19 PalkovitsM+3-1977

Notes about [PalkovitsM+3-1977]¹.

This paper give information about nuclear cells (Deep Cerebellar Nuceli) in cat.

From summary:

Summary. The tissue volume, cell number, cell density, as well as the numbers and densities of various kinds of synaptic terminals were determined in the cerebellar nuclei of adult cats by means of stereological procedures both on the light and electron microscopic levels. The total number of the cerebellar nuclear cells was found to be 4.6×10^{4} . On the basis of karyometric studies the medial and interpositus nuclei appear to contain two, the lateral nucleus probably three different neuron populations. The over-all numerical ratio between Purkinje and nuc/ear cells is 26: 1. On the basis of simplified cytological and size criteria five different types of synaptic terminals were distinguished and counted separately. The total number of synaptic boutons was found to be 9.2×10^{8} , 62% of which (5.7×10^{8}) belong to Purkinje axons. The average number of synaptic boutorns per nuclear cell is 2×10^{4} with systematic differences in the several nuclei (medial = 27500; interpositus = 18000; lateral = 13900). The number of boutons of Purkinje cell origin is 11600 per nuclear cell, on the average.

The average number of synaptic bontons per Purkinje axon is 474, which are distributed in a space of about 13.5×10^{6} um³. In view of the density of the nuclear cells and the metric parameters of their dendrites, the number of nuclear cells with which synapses might be established is 35. This is a direct

¹ M. Palkovits, Eva Mezey, J. Hamori, and J. Szentagothai. Quantitative histological analysis of the cerebellar nuclei in the cat. I. Numerical data on cells and on synapses. *Experimental Brain Research*, May 1977. URL: http://link.springer.com/10.1007/BF00237096, doi:10.1007/BF00237096, Notes: PalkovitsM+3-1977.html (this file).

measure for the divergence; i.e. one Purkinje axon may reach potentially 35 nuclear cells. The number on any nuclear cell of boutons that originate from the same Purkinje axon would be mathematically 13.5 as an average, but may vary excessively between 1 and around 50 boutons. From these data the probable convergence of Purkinje axons upon nuclear cells can be deduced as being numerically somewhere around 860, however, this apparently excessive value is mitigated by the Golgi observation that a single Purkinje axon may contribute to the same nuclear cell as many as 50 somatic synapses. The dendritic synapses - forming the vast majority of all contacts - are probably more evenly distributed among the great majority of the converging Purkinje axons but with correspondingly fewer individual contacts.



Fig. 5. Diagram summarizing the interpretation of the quantitative data obtained in the study in terms of divergence and convergence. The rationale of this interpretation is to place one nuclear cell (center, drawn in outlines) into the center of its dendritic sphere (with 400 µm radius) and to consider how many other cells might participate in the same sphere either with their bodies or with their dendrites. Purknip axons are assumed — on the basis of Golg pictures – to arborize in narrow sagitatly oriented cylinders of approximately estimated volume. The number of Purknip axon terminals per cell having been estimated on the basis of cell density and Purknip axon terminal density, and knowing additionally the number of Purknip cells, and of nuclear cells this geometrical reasoning leads to an estimate of the probable divergence from the average Purknipie axon 35 different nuclear cells and a convergence of buotons belonging to about 860 different Purknip axons upon the average nuclear cells.

Fig. 14: Figure 5 in PalkovitsM+3-1977 [PalkovitsM+3-1977].

8.20 RahimiA+3-2019

Title: Efficient Biosignal Processing Using Hyperdimensional Computing: Network Templates for Combined Learning and Classification of ExG Signals

Authors: Abbas Rahimi ; Pentti Kanerva ; Luca Benini ; Jan M. Rabaey

DOI: 10.1109/JPROC.2018.2871163

PDF of paper is at: https://iis-people.ee.ethz.ch/~arahimi/papers/PROC18.pdf

8.21 RieublandS+2-2014

Notes about [RieublandS+2-2014]¹.

This paper shows the difference between sagittal and transverse inhibition from molecular interneurons in rat.

From Abstract:

By recording from multiple molecular layer interneurons in the cerebellar cortex, we reveal specific, nonrandom connectivity patterns in both GABAergic chemical and electrical interneuron networks. Both networks contain clustered motifs and show specific overlap between them. Chemical connections exhibit a preference for transitive patterns, such as feedforward triplet motifs. This structured connectivity is supported by a characteristic spatial organization: transitivity of chemical connectivity is directed vertically in the sagittal plane, and electrical synapses appear strictly confined to the sagittal plane. The specific, highly structured connectivity rules suggest that these motifs are essential for the function of the cerebellar network.

From p. 923:

Although classically MLIs have been divided into basket and stellate cells, our data support the accumulating evidence suggesting that these cells constitute a single population with a continuum of morphological properties with their position in the ML as main parameter: their dendrite length becomes gradually shorter the higher the interneuron is located in the ML



Fig. 15: Figure 2 in RieublandS+2-2014 [RieublandS+2-2014].

8.22 SudhakarSK+8-2017

Notes about [SudhakarSK+8-2017]¹.

This paper describes a computational model of the cerebellum and has a table of connection properties used in the model and references.

The full table is here.

¹ Sarah Rieubland, Arnd Roth, and Michael Häusser. Structured Connectivity in Cerebellar Inhibitory Networks. *Neuron*, 81(4):913–929, February 2014. URL: https://linkinghub.elsevier.com/retrieve/pii/S0896627313011902, doi:10.1016/j.neuron.2013.12.029, Notes: RieublandS+2-2014.html (this file).

¹ Shyam Kumar Sudhakar, Sungho Hong, Ivan Raikov, Rodrigo Publio, Claus Lang, Thomas Close, Daqing Guo, Mario Negrello, and Erik De Schutter. Spatiotemporal network coding of physiological mossy fiber inputs by the cerebellar granular layer. *PLOS Computational Biology*, 13(9):1–35, September 2017. URL: https://dx.plos.org/10.1371/journal.pcbi.1005754, doi:10.1371/journal.pcbi.1005754, Notes: SudhakarSK+8-2017.html (this file).

8.23 TomaschJ-1968

Notes about [TomaschJ-1968]¹.

This paper has lots of data about number of efferent and afferent fibers cell counts in human cerebellum.

Summary of data in this paper:

| A H H | | A |
|------------------------------|--|--------------------------------|
| Cell or fiber | Description | Quantity |
| purkinje | Total number both hemispheres | 15 million |
| cortico-pontine | # fibers from cerebral cortex to pons | 19.14 million (for one side) |
| ponto-cerebellar | # cells in pons, same as number from pons to | 23.085 million |
| | cerebellum | |
| inferior olive | # fibers entering cerebellum from inferior olive | 0.5 million |
| | (one side) | |
| Inferior cerebeller peduncle | number of axons | 0.52 million (one side) |
| cerebellar nuclei | total number neurons (one side) | 311,404 |
| dentate nucleus | total number neurons (one side) | 284,000 |
| nucleus globosus | total number neurons (one side) | 16,153 |
| emboliforme nucleus | total number neurons (one side) | 10,381 |
| fastigii nucleus | total number neurons (one side) | 5210 |
| superior cerebellar peduncle | number of axons (one side) | 0.782 million |
| superior cerebellar peduncle | number axons into cerebellum through superior | less than 1/2 number of fibers |
| afferents (one side) | cerebellar peduncle | (0.782/2) |
| superior cerebellar peduncle | number axons leaving cerebellum through supe- | about 311,000 (total number |
| efferents (one side) | rior cerebellar peduncle | nuclei, 311,404; maybe less |
| | | number fastigii nuclei, 5201) |

| Table 1: TomaschJ-1968 cell | and fiber counts in human |
|-----------------------------|---------------------------|
|-----------------------------|---------------------------|

Excerpts from the paper:

cortico-pontine (From cerebral cortex to pons). 19.14 million axons (for one side).

- **ponto-cerebellar (from pons to cerebellum).** Total of 23.085 million nerve cells within the pontine grey. May range from 17 to 25 million neurons.
- **Ratio of ponto-cerebellar to cortico-pontine** From 1:1.37 to 1:2.25. "This overall convergence ratio may not be uniform for every individual circuit, it indicates a definite reduction, however, in the number of unit-elements involved from the peduncular to the pontine level."
- Number of purkinje cells. "A range of from 14-25 million Purkinje-cells [in the whole cerebellum] seems, therefore, well established. Estimates for the number of granular cells in the cerebellar cortex range front 10 to 100 billion cells (Braitenberg and Atwood). According to Fox and Barnard (1957), there are in the macaque 960 granular cells for 1 Purkinje cell."
- **Ratio of mossy fibers to purkinje cells** "From the granular cells a re-convergence of the same overall ratio is taking place, the number of Purkinje-cells, according to the figures of Lojda being of the same order of magnitude as the estimate for the number of pontine nerve cells. In other words, there is a 1:1 relationship between the numbers of pontine nerve cells and of Purkinje-cells."
- Number of fibers from inferior olive "The inferior olivary nuclear complex provides the second largest source of cerebellar afferents. Among four male subjects, including the 56 year old male refered to above, Moatamed (1966) counted and estimated a figure of 0.5 million cells for the nuclei of one side. This range of cell frequencies

¹ J. Tomasch. The overall information carrying capacity of the major afferent and efferent cerebellar cell and fiber systems. *Stereotactic and Functional Neurosurgery*, 30(5-6):359–367, 1968. URL: https://www.karger.com/Article/FullText/103549, doi:10.1159/000103549, Notes: TomaschJ-1968.html (this file).

was confirmed by Escobar et al. who found in one human subject, age and sex not stated, 0.45 million cells in the dentate olivary nucleus alone. Thus with 1 million neurites entering the cerebellum from this source, this inflow is only 1/23 that of pontine origin. After decussating, these neurites enter the cerebellum via the inferior cerebellar peduncle."

- **Number fibers in inferior cerebeller peduncle** "The estimate comes to 0.52 million axons and 0.45 million of these are myelinated. [One side]. The difference accounting for un-myelinated axons is 7.4%."
- Number of pinal and vestibular afferents into the cerebellum "An estimate of both spino-cerebellar tracts at the level above the pyramidal decussation, renders a figure of 0.204 million axons: of these 0.147 million are myelinated."
- **Number of vestibular nucleus cells** "The number of vestibular nuclear cells is 0.245 million according to Blinkov and Ponomarev (1965). No information is available at present about the proportion from this source for cerebellum and for spinal cord."
- Number of cerebellar deep nuclei cells. "The number of cells in the cerebellar nuclei of man was counted and estimated in 3 male subjects (Heidary and Tomasch, 1969). Cell-frequencies in all nuclei of one hemisphere are 311,404+ 3,835 neurons. Of this total, 284,000 cells belong to the dentate nucleus, 16,153 to the nucleus globosus, 10,381 to the emboliforme nucleus and only 5210 to the nucleus fastigii."
- **Variability in counts for inferior olive and nuclei** "... yet detailed counts and estimates carried out in our laboratory and covering in several instances an age range from the new-born to the pre-senescent age resulted in the case of the olivary nucleus in a coefficient of variation of only 1.5 %. For the three subjects in whom the cerebellar nuclear cells were counted, the coefficient of variation is 1.9%"
- **Number fibers in superior cerebellar peduncle** "There is general agreement that the large majority of axons arising form the cells of the cerebellar nuclei, leave the cerebellum via the superior cerebellar peduncle, the exception being the fastigio-bulbar tract that leaves via the juxta-restiforme body. In the 56 year old subject, the cross-sectional area of the superior peduncle is 19.51 0.41 mm2. The estimate for the number of fibers found over this area rendered a figure of 0.782 million axons; of this total 0.761 million are myelinated. The percentage of un-myelinated axons is the lowest found for any of the fiber tracts associated with the cerebellum."
- Number fibers leaving and entering via superior cerebellar peduncle "Although 311,000 cerebellar nuclear cells were found in one hemisphere, the number of axons in one superior cerebellar peduncle was found to be more than twice this figure. This discrepancy may be caused either by the branching of the outgoing axons, as was actually demonstrated in the brachium conjunctivum of sub-primates by Cajal, or it may be due to fibers entering the cerebellum via this tract. The latter occurrence was demonstrated by Brodal and Gogstad (1954) who found extensive rubro-cerebellar connections entering the cerebellum. Thus indirectly a measure is also obtained for this additional source of cerebellar afferents. It would seem that their number should not be higher than about half of the number of axons estimated in the superior cerebellar peduncle. Some cerebellar nuclear cells are said to project to vestibular and reticular nuclei of the brain stem via the juxta-restiforme body, in the form of the fastigio-bulbar tract. As the number of cells in one fastigial nucleus is only 5210, their proportion can not be very high."
- **Convergence of cerebellar input to output** "There is a convergence ratio of about 1:25 to 1:38 from the Purkinjecells to the cells of the cerebellar nuclei. If the overall capacity of cerebellar outflow is gauged by the number of cells found in the cerebellar nuclei, there is a proportion of about 1:40 between cerebellar afferent and of efferent circuits."
- **Range in fiber diameters** "Since different speeds of conduction are related to differences in fiber diameters, it would seem significant that the cerebellar afferent and efferent fiber systems show a considerable range in fiber diameters. While fibers in the cortico-pontine system are so fine as to permit 21.85 to be accommodated in a 100 micrometer^2 area, in the inferior cerebellar peduncle only 2.71 are found over the same area. The differential composition of these pathways as to their fiberspectrum would seem to offer some as yet untapped avenues for research with structural as well as functional aims."
- Cerebellar convergence compared to other areas "Considering that all motor functions are under the constant regulatory influence of the cerebellum, one might have expected the ratio between the number of incoming and

out-going fibers to be much lower than 40:1. The overall ratio between afferent and efferent fibers in all spinal roots of one side is only 4.83:1 (Arnell, 1933)."

- **Possible reason for crebocerebellum connections** "The vast capacity of the cortico-ponto-cerebellar system, 40 times over that of all other afferent sources combined, might find an explanation, if it is assumed, that it is largely to function to retrieve stored information from many different areas of the cerebral cortex, while the other afferent systems seem to be concerned with current stimuli. Thus a correlation between the numerical size of a fiber system and its mode of functioning is implied. Whether and to what extent the numerical size of a fiber-system might vary among individuals, being correlated to development of special skills for instance, remains to be studied."
- **Summary of paper** "A survey is presented of quantitative data dealing with the numeri cal sizes of the major extrinsic and intrinsic cerebellar cell and fiber systems. Except for the granular cells, which may by a factor of ten (Brait-enberg et al., 1958) exceed the routinely quoted figure of 1010, said to comprise the total neuron capacity of the human nervous system at all levels, other cerebellar systems range within more finite limits. Purkinje cells 14-25 million (Kreuzfuchs, 1902, Lojda, 1955), pontine nuclear cells 17-25 million, inferior olivary nuclear complex, bilaterally 0.9 to 1 million neurons (Moatamed, 1966, Escobar et al., 1968), cerebellar nuclei, bilaterally 0.6 million cells (Heidary et al., 1968). Fiber systems range, hemilaterally, the corticopontine system from 20 million axons, down to 0.7 million neurites in the brachium conjuuctivum. There is an overall ratio of 40:1 of afferent to efferent neurites."

8.24 WitterL+4-2016

Notes about [WitterL+4-2016]¹.

This paper shows that Purkinje cell collaterals Feed Back to Purkinje Cells and Interneurons. Experiments were done using mice.

p. 317:

Collaterals were confined to a narrow sagittal plane but extended hundreds of micrometers within that plane.

... we estimate that each PC receives input from five to ten other PCs (Figure 4). This is in good agreement with our estimates of convergence from our synaptic labeling experiments in which each PC forms synaptic contacts near approximately six to eight PCs (Figure 2). PC axon collateral synapses onto PCs and MLIs could regulate activity in narrow parasagittal strips, which are likely contained within broader zebrin bands that constitute functional units (Apps and Hawkes, 2009). Both PC collaterals and MLI axons are restricted to narrow parasagittal planes (Gao et al., 2006; Hawkes and Leclerc, 1989). Therefore, PC feedback regulates cerebellar activity at the output stage in these functionally delimited zones, and could potentially act to regulate the rate or timing of firing of PCs and MLIs.

PC collaterals could allow the output of the cerebellar cortex to feed back and control the gain of the cerebellar cortex. Gain control by inhibitory feedback is a common mechanism to maintain the dynamic range of neural circuits. When principal output neurons are excitatory, inhibitory feedback requires interneurons as in the cerebral cortex (Olsen et al., 2012) and hippocampus (Freund and Buzsa ki, 1996). When output neurons are GABAergic, as in the basal ganglia and as described here for the cerebellum, gain control can be achieved by connections between the output cells (Brown et

¹ Laurens Witter, Stephanie Rudolph, R. Todd Pressler, Safiya I. Lahlaf, and Wade G. Regehr. Purkinje Cell Collaterals Enable Output Signals from the Cerebellar Cortex to Feed Back to Purkinje Cells and Interneurons. *Neuron*, 91(2):312–319, July 2016. URL: https://linkinghub.elsevier. com/retrieve/pii/S0896627316302483, doi:10.1016/j.neuron.2016.05.037, Notes: WitterL+4-2016.html (this file).

al., 2014). If PC collaterals control the firing rate of their targets, then PC-to-PC connections allow PC activity to suppress the output of the cerebellar cortex. In contrast, PC-to-MLI synapses would have the opposite effect and would suppress inhibition of MLIs to PCs, thereby providing positive feedback. The time course and extent of feedback on PC firing rates will thus depend on collateral con- nectivity and the balance of direct inhibition and indirect disinhibition.



Fig. 16: Figure 2 in WitterL+4-2016 [WitterL+4-2016].
CHAPTER

NINE

REFERENCES

CHAPTER

TEN

BIBLIOGRAPHY

The bibliography (below) contains sources of information which may not be included in the *References*. (Most of the items listed below are not explicitly cited in text on the website).

BIBLIOGRAPHY

- [AlbusJS-1971] JS Albus. A theory of cerebellar function. Mathematical Biosciences, 10(1-2):25–61, 1971. URL: https://robotictechnologyinc.com/images/upload/file/Albus%20Theory%20Of%20Cerebellar% 20Function.pdf, PDF: AlbusJS-1971.pdf.
- [AlbusJS-1981] JS Albus. Brains, Behavior and Robotics. McGraw-Hill, New York, NY, 1981.
- [AnkriL+5-2015] Lea Ankri, Zoé Husson, Katarzyna Pietrajtis, Rémi Proville, Clément Léna, Yosef Yarom, Stéphane Dieudonné, and Marylka Yoe Uusisaari. A novel inhibitory nucleo-cortical circuit controls cerebellar Golgi cell activity. *eLife*, 4:e06262, May 2015. URL: https://elifesciences.org/articles/06262, doi:10.7554/eLife.06262, Notes: AnkriL+5-2015.html.
- [AppsR+HawkesR-2009] Richard Apps and Richard Hawkes. Cerebellar cortical organization: a one-map hypothesis. *Nature Reviews Neuroscience*, 10:670–681, 9 2009. doi:10.1038/nrn2698, Notes: AppsR+HawkesR-2009.html.
- [ArltC+HausserM-2020] Charlotte Arlt and Michael Häusser. Microcircuit Rules Governing Impact of Single Interneurons on Purkinje Cell Output In Vivo. *Cell Reports*, 30(9):3020–3035.e3, March 2020. URL: https://linkinghub.elsevier.com/retrieve/pii/S2211124720301637, doi:10.1016/j.celrep.2020.02.009.
- [AndersonBB+2-1992] Andersen BB, Korbo L, and Pakkenberg B. A quantitative study of the human cerebellum with unbiased stereological techniques. *J Comp Neurol*, 326(4):549–60, 1992. doi:10.1002/cne.903260405, Notes: AndersonBB+2-1992.html.
- [BillingsG+4-2014] Guy Billings, Eugenio Piasini, Andrea Lőrincz, Zoltan Nusser, and R. Angus Silver. Network Structure within the Cerebellar Input Layer Enables Lossless Sparse Encoding. *Neuron*, 83(4):960–974, August 2014. URL: https://linkinghub.elsevier.com/retrieve/pii/S089662731400631X, doi:10.1016/j.neuron.2014.07.020, Notes: BillingsG+4-2014.html.
- [CesanaE+6-2013] E. Cesana, K. Pietrajtis, C. Bidoret, P. Isope, E. D'Angelo, S. Dieudonne, and L. Forti. Granule Cell Ascending Axon Excitatory Synapses onto Golgi Cells Implement a Potent Feedback Circuit in the Cerebellar Granular Layer. *Journal of Neuroscience*, 33(30):12430–12446, July 2013. URL: https://www. jneurosci.org/lookup/doi/10.1523/JNEUROSCI.4897-11.2013, doi:10.1523/JNEUROSCI.4897-11.2013, Notes: CesanaE+6-2013.html.
- [DAngeloE+CasaliS-2013] E D'Angelo and S Casali. Seeking a unified framework for cerebellar function and dysfunction: from circuit operations to cognition. *Frontiers in Neural Circuits*, 2013. URL: https://www. frontiersin.org/articles/10.3389/fncir.2012.00116/full#B220, PDF: DAngeloE+CasaliS-2013.pdf.
- [DAngeloE+5-2013] Egidio D'Angelo, Sergio Solinas, Jonathan Mapelli, Daniela Gandolfi, Lisa Mapelli, and Francesca Prestori. The cerebellar Golgi cell and spatiotemporal organization of granular layer activity. *Frontiers in Neural Circuits*, 2013. URL: http://journal.frontiersin.org/article/10.3389/fncir.2013.00093/ abstract, doi:10.3389/fncir.2013.00093, Notes: DAngeloE+5-2013.html.

- [DeZeeuwCI+2-2021] Chris I. De Zeeuw, Stephen G. Lisberger, and Jennifer L. Raymond. Diversity and dynamism in the cerebellum. *Nature Neuroscience*, 24(2):160–167, February 2021. URL: http://www.nature.com/ articles/s41593-020-00754-9, doi:10.1038/s41593-020-00754-9, Notes: DeZeeuwCI+2-2021.html.
- [DiedrichsenJ+4-2019] Jörn Diedrichsen, Maedbh King, Carlos Hernandez-Castillo, Marty Sereno, and Richard B. Ivry. Universal transform or multiple functionality? understanding the contribution of the human cerebellum across task domains. *Neuron*, 102(5):918–928, June 2019. URL: https://linkinghub.elsevier.com/ retrieve/pii/S0896627319303782, doi:10.1016/j.neuron.2019.04.021.
- [DugueGP-2009+8] Guillaume P. Dugué, Nicolas Brunel, Vincent Hakim, Eric Schwartz, Mireille Chat, Maxime Lévesque, Richard Courtemanche, Clément Léna, and Stéphane Dieudonné. Electrical Coupling Mediates Tunable Low-Frequency Oscillations and Resonance in the Cerebellar Golgi Cell Network. *Neuron*, 61(1):126–139, January 2009. URL: https://linkinghub.elsevier.com/retrieve/pii/S0896627308010210, doi:10.1016/j.neuron.2008.11.028.
- [DAngeloE+11-2016] Egidio D'Angelo, Alberto Antonietti, Stefano Casali, Claudia Casellato, Jesus A. Garrido, Niceto Rafael Luque, Lisa Mapelli, Stefano Masoli, Alessandra Pedrocchi, Francesca Prestori, Martina Francesca Rizza, and Eduardo Ros. Modeling the Cerebellar Microcircuit: New Strategies for a Long-Standing Issue. *Frontiers in Cellular Neuroscience*, July 2016. URL: http://journal.frontiersin.org/Article/ 10.3389/fncel.2016.00176/abstract, doi:10.3389/fncel.2016.00176, PDF: DAngeloE+11-2016.pdf.
- [EcclesJC+2-1967] John C. Eccles, Masao Ito, and János Szentágothai. *The Cerebellum as a Neuronal Machine*. Springer Berlin Heidelberg, 1967. doi:10.1007/978-3-662-13147-3, Notes: EcclesJC+2-1967.html.
- [FellemanDJ+VanEssenDC-1991] DJ Felleman and DC Van Essen. Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1(1):1–47, Jan/Feb 1991. URL: https://www.cns.nyu.edu/~tony/ vns/readings/felleman-vanessen-1991.pdf, PDF: FellemanDJ+VanEssenDC-1991.pdf.
- [GaylerRW-2003] RW Gayler. Vector symbolic architectures answer jackendoff's challenges for cognitive neuroscience. In Peter Slezak, editor, *Proceedings of the ICCS/ASCS Joint International Conference on Cognitive Science (ICCS/ASCS 2003)*, 133–138. Sydney, NSW, AU, July 2003. University of New South Wales. URL: http://arxiv.org/abs/cs/0412059, arXiv:0412059v1, PDF: GaylerRW-2003.pdf.
- [GlicksteinM-2007] Mitch Glickstein. What does the cerebellum really do? *Current Biology*, 17(19):4, 2007. doi:10.1016/j.cub.2007.08.009, Notes: GlicksteinM-2007.html.
- [GuoC+5-2016] Chong Guo, Laurens Witter, Stephanie Rudolph, Hunter L. Elliott, Katelin A. Ennis, and Wade G. Regehr. Purkinje Cells Directly Inhibit Granule Cells in Specialized Regions of the Cerebellar Cortex. *Neuron*, 91(6):1330–1341, September 2016. URL: https://linkinghub.elsevier.com/retrieve/pii/ S0896627316305037, doi:10.1016/j.neuron.2016.08.011, Notes: GuoC+5-2016.html.
- [HullC+RegehrWG-2012] Court Hull and Wade G. Regehr. Identification of an Inhibitory Circuit that Regulates Cerebellar Golgi Cell Activity. *Neuron*, 73(1):149–158, January 2012. URL: https://linkinghub.elsevier. com/retrieve/pii/S0896627311009949, doi:10.1016/j.neuron.2011.10.030, Notes: HullC+RegehrWG-2012.html.
- [ItoM-1984] M Ito. The Cerebellum and Neural Control. Raven Press, New York, NY, 1984.
- [JaeckelLA-1989b] LA Jaeckel. A class of designs for a sparse distributed memory. Technical Report 89.29, NASA Ames Research Center, 1989. URL: https://ntrs.nasa.gov/archive/nasa/casi.ntrs.nasa.gov/19920002426. pdf, PDF: JaeckelLA-1989b.pdf.
- [JaeckelLA-1989a] LA Jaeckel. An alternative design for a sparse distributed memory. Technical Report 89.28, NASA Ames Research Center, 1989. PDF: JaeckelLA-1989a.pdf.
- [JakabRL+HamoriJ-1988] R. L. Jakab and J. Hamori. Quantitative morphology and synaptology of cerebellar glomeruli in the rat. Anatomy and Embryology, 179(1):81–88, October 1988. URL: http://link.springer. com/10.1007/BF00305102, doi:10.1007/BF00305102.
- [KandelER+2-2000] ER Kandel, JH Schwartz, and TM Jessell. The cerebellum. In ER Kandel, JH Schwartz, and TM Jessell, editors, *Principles of Neural Science*, chapter 42, pages 201–213. McGrae-Hill, New

York, fourth edition, 2000. URL: https://www.cs.cmu.edu/afs/cs/academic/class/15883-f17/readings/ghez-2000.pdf.

- [KandelER+4-2013] ER Kandel, JH Schwartz, TM Jessell, SA Siegelbaum, and Hudspeth AJ. The cerebellum. In ER Kandel, JH Schwartz, and TM Jessell, editors, *Principles of Neural Science*, chapter 42, pages 960–981. McGrae-Hill, New York, fifth edition, 2013.
- [KanervaP-1988] P Kanerva. Sparse Distributed Memory. MIT Press, Cambridge, MA, 1988.
- [KanervaP-1989] P Kanerva. A cerebellar-model associative memory as a generalized random-access memory. In Proc. 34th IEEE Computer Society Int'l Conference (COMPCON Spring '89, San Francisco), 570–576. 1989. URL: https://pdfs.semanticscholar.org/65f7/e9bc99f27cd24226e74ba3bc673d69175e5e.pdf?_ga= 2.145552822.361059761.1574023399-1910310255.1574023399, PDF: KanervaP-1989.pdf.
- [KanervaP-1993] P Kanerva. Sparse distributed memory and related models. In M.H. Hassoun, editor, Associative Neural Memories: Theory and Implementation, chapter 3, pages 50–76. Oxford University Press, New York, 1993. PDF: KanervaP-1993.pdf.
- [KanervaP-2009] P Kanerva. Hyperdimensional computing: an introduction to computing in distributed representation with high-dimensional random vectors. *Cognitive Computation*, 1(2):139–159, 2009. URL: https: //redwood.berkeley.edu/wp-content/uploads/2018/01/kanerva2009hyperdimensional.pdf.
- [KarlssonR-2001] R Karlsson. A fast activation mechanism for the kanerva sdm memory. In Kanerva P Uesaka Y and Asoh H, editors, *Foundations of Real-World Intelligence*, pages 289–293. CSLI Publications, Stanford, CA, 2001. URL: http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.44.5112&rep=rep1&type=pdf.
- [KawatoM+3-2021] Mitsuo Kawato, Shogo Ohmae, Huu Hoang, and Terry Sanger. 50 Years Since the Marr, Ito, and Albus Models of the Cerebellum. *Neuroscience*, 462:151–174, May 2021. URL: https://linkinghub.elsevier.com/retrieve/pii/S0306452220303961, doi:10.1016/j.neuroscience.2020.06.019.
- [KenyonGT-1997] GT Kenyon. A model of long-term memory storage in the cerebellar cortex: a possible role for plasticity at parallel fiber synapses onto stellate/basket interneurons. *Proc. Natl. Acad. Sci. USA (Psychology)*, 94:14200–14205, December 1997. URL: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC28457/ pdf/pq014200.pdf, PDF: KenyonGT-1997.pdf.
- [KingM+4-2019b] M King, CR Hernandez-Castillo, RA Poldrack, RB Ivry, and J Diedrichsen. Cerebellar atlas viewer. Website with interactive graphics, 2019. URL: http://www.diedrichsenlab.org/imaging/AtlasViewer/.
- [KingM+4-2019a] M King, CR Hernandez-Castillo, RA Poldrack, RB Ivry, and J Diedrichsen. Functional boundaries in the human cerebellum revealed by a multi-domain task battery. *Nature Neuroscience*, 22:1371–1378, July 2019. URL: http://www.diedrichsenlab.org/pubs/King_NatureNeuro_2019.pdf.
- [KorboL+3-1993] Korbo L, Andersen BB, Ladefoged O, and Møller A. Total numbers of various cell types in rat cerebellar cortex estimated using an unbiased stereological method. *Brain Res*, 609(1-2):262–268, April 1993. doi:10.1016/0006-8993(93)90881-m, Notes: KorboL+3-1993.html.
- [LangeW-1975] W. Lange. Cell number and cell density in the cerebellar cortex of man and some other mammals. *Cell and Tissue Research*, March 1975. URL: http://link.springer.com/10.1007/BF00223234, doi:10.1007/BF00223234, Notes: LangeW-1975.html.
- [LiK+MalikJ-2017] K Li and J Malik. Fast k-nearest neighbour search via dynamic continuous indexing. 2017. URL: https://arxiv.org/abs/1512.00442, PDF: LiK+MalikJ-2017.pdf.
- [Litwin-KumarA+4-2017] A Litwin-Kumar, KD Harris, R Axel, H Sompolinsky, and LF Abbott. Optimal degrees of synaptic connectivity. *Neuron*, 93(5):1153–1164, March 2017. URL: https://www.ncbi.nlm.nih. gov/pmc/articles/PMC5379477/pdf/nihms849288.pdf, doi:10.1016/j.neuron.2017.01.030, PDF: Litwin-KumarA+4-2017.pdf.
- [LlinasRR-1975] RR Llinas. The cortex of the cerebellum. *Scientific American*, 232(1):56–71, 1975. URL: https://www.scientificamerican.com/article/the-cortex-of-the-cerebellum/, PDF: LlinasRR-1975.pdf.

- [LoebnerEE-1989] EE Loebner. Intelligent network management and functional cerebellum synthesis. In Raugh MR, editor, *Cerebellar Models of Associative Memory: Three papers from IEEE COMPCON SPRING* '89, pages 14–19. Research Institute for Advanced Computer Science, NASA Ames Research Center, 1989. PDF: LoebnerEE-1989.pdf, Notes: LoebnerEE-1989.html.
- [MarrD-1969] D Marr. A theory of cerebellar cortex. *Journal of Physiology*, 1969. URL: https://pdfs.semanticscholar. org/3c6f/34131ad83fda26a3d8ca9892a6705fd40d11.pdf, PDF: MarrD-1969.pdf.
- [PalkovitsM+2-1971b] M Palkovits. Quantitative histological analysis of the cerebellar cortex in the cat. II. Cell numbers and densities in the granular layer. *Brain Research*, pages 16, 1971. Notes: PalkovitsM+2-1971b.html.
- [PalkovitsM+2-1971a] M Palkovits, P. Magyar, and J. Szentagothai. Quantitative histological analysis of the cerebellar cortex in the cat. i. number and arrangement in the space of the purkinje cells. *Brain Research*, pages 13, 1971. Notes: PalkovitsM+2-1971a.html.
- [PalkovitsM+2-1971c] M. Palkovits, P. Magyar, and J. Szentágothai. Quantitative histological analysis of the cerebellar cortex in the cat. III. Structural organization of the molecular layer. *Brain Research*, 34(1):1–18, November 1971. URL: https://linkinghub.elsevier.com/retrieve/pii/0006899371903477, doi:10.1016/0006-8993(71)90347-7, Notes: PalkovitsM+2-1971c.html.
- [PalkovitsM+3-1977] M. Palkovits, Eva Mezey, J. Hamori, and J. Szentagothai. Quantitative histological analysis of the cerebellar nuclei in the cat. I. Numerical data on cells and on synapses. *Experimental Brain Research*, May 1977. URL: http://link.springer.com/10.1007/BF00237096, doi:10.1007/BF00237096, Notes: PalkovitsM+3-1977.html.
- [PalkovitsM+2-1972] Miklos Palkovits, Pal Magyar, and Janos Szentagothai. Quantitative histological analysis of the cerebellar cortex in the cat. IV. Mossy fiber-purkinje cell numerical transfer. *Brain Research*, 45(1):15–29, October 1972. URL: https://linkinghub.elsevier.com/retrieve/pii/0006899372902132, doi:10.1016/0006-8993(72)90213-2, Notes: PalkovitsM+2-1972.html.
- [PlateT-1991] T Plate. Holographic reduced representations: convolution algebra for compositional distributed representations. In John Mylopoulos and Ray Reiter, editors, *Proceedings of the 12th International Joint Conference on Artificial Intelligence (IJCAI)*, pages 30–35. Morgan Kaufmann, San Mateo, CA, 1991. URL: http://d-reps.org/papers/plate.ijcai91.pdf, PDF: PlateT-1991.pdf.
- [PlateTA-2003] TA Plate. *Holographic Reduced Representation: Distributed Representation of cognitive structure*. CSLI Publications, Stanford, CA, 2003.
- [RahimiA+3-2019] A Rahimi, P Kanerva, L Benini, and JM Rabaey. Efficient biosignal processing using hyperdimensional computing: network templates for combined learning and classification of exg signals. *Proceedings of the IEEE*, 107(1):123–143, 2019. URL: https://doi.org/10.1109/JPROC.2018.2871163, Notes: RahimiA+3-2019.html.
- [RaughMR-ed-1989] ed. Raugh MR. Cerebellar models of associative memory: three papers from ieee compcon spring '89. Technical Report, NASA Ames Research Center, 1989. URL: https: //pdfs.semanticscholar.org/65f7/e9bc99f27cd24226e74ba3bc673d69175e5e.pdf?_ga=2.145552822. 361059761.1574023399-1910310255.1574023399, PDF: RaughMR-ed-1989.pdf.
- [RieublandS+2-2014] Sarah Rieubland, Arnd Roth, and Michael Häusser. Structured Connectivity in Cerebellar Inhibitory Networks. *Neuron*, 81(4):913–929, February 2014. URL: https://linkinghub.elsevier.com/retrieve/ pii/S0896627313011902, doi:10.1016/j.neuron.2013.12.029, Notes: RieublandS+2-2014.html.
- [SolariSVH+StonerR-2011a] SVH Solari and R Stoner. Cognitive consilience: primate non-primary neuroanatomical circuits underlying cognition. *Frontiers in Neuroanatomy*, December 2011. URL: https://www.frontiersin. org/articles/10.3389/fnana.2011.00065/full.
- [SolariSVH+StonerR-2011b] SVH Solari and R Stoner. Cognitive consilience: visualization. Website with interactive graphics, 2011. URL: http://www.frontiersin.org/files/cognitiveconsilience/index.html.
- [SolinasS+2-2010] Sergio Solinas, Thierry Nieus, and Egidio D'Angelo. A realistic large-scale model of the cerebellum granular layer predicts circuit spatio-temporal filtering properties. *Frontiers in Cel*-

lular Neuroscience, 4:12, 2010. URL: https://www.frontiersin.org/article/10.3389/fncel.2010.00012, doi:10.3389/fncel.2010.00012.

- [StewartTC+2-2011] TC Stewart, Y Tang, and Eliasmith C. A biologically realistic cleanup memory: autoassociation in spiking neurons. *Cognitive Systems Research*, 12:84–92, 2011. URL: http://compneuro.uwaterloo.ca/ files/publications/stewart.2011.pdf, PDF: StewartTC+2-2011.pdf.
- [StrickPL+2-2009] Peter L. Strick, Richard P. Dum, and Julie A. Fiez. Cerebellum and nonmotor function. *Annual Review of Neuroscience*, 32:413–434, 6 2009. doi:10.1146/annurev.neuro.31.060407.125606.
- [SudhakarSK+8-2017] Shyam Kumar Sudhakar, Sungho Hong, Ivan Raikov, Rodrigo Publio, Claus Lang, Thomas Close, Daqing Guo, Mario Negrello, and Erik De Schutter. Spatiotemporal network coding of physiological mossy fiber inputs by the cerebellar granular layer. *PLOS Computational Biology*, 13(9):1–35, September 2017. URL: https://dx.plos.org/10.1371/journal.pcbi.1005754, doi:10.1371/journal.pcbi.1005754, Notes: SudhakarSK+8-2017.html.
- [TomaschJ-1968] J. Tomasch. The overall information carrying capacity of the major afferent and efferent cerebellar cell and fiber systems. *Stereotactic and Functional Neurosurgery*, 30(5-6):359–367, 1968. URL: https: //www.karger.com/Article/FullText/103549, doi:10.1159/000103549, Notes: TomaschJ-1968.html.
- [TyrrellT+WillshawD-1992] T Tyrrell and Willshaw D. Cerebellar cortex: its simulation and the relevance of marr's theory. *Philosophical Transactions of Royal Society of London, B: Biological Sciences*, 336(1277):239–257, May 1992. URL: https://royalsocietypublishing.org/doi/pdf/10.1098/rstb.1992.0059, PDF: TyrrellT+WillshawD-1992.pdf.
- [VanEssenDC-2002] DC Van Essen. Surface-based atlas of cerebellar cortex in human, macaque, and mouse. Annals of the New York Academy of Sciences, 978:468–479, December 2002. URL: http://brainvis.wustl.edu/ resources/VE_ANYAS02.pdf, PDF: VanEssenDC-2002.pdf.
- [WitterL+4-2016] Laurens Witter, Stephanie Rudolph, R. Todd Pressler, Safiya I. Lahlaf, and Wade G. Regehr. Purkinje Cell Collaterals Enable Output Signals from the Cerebellar Cortex to Feed Back to Purkinje Cells and Interneurons. *Neuron*, 91(2):312–319, July 2016. URL: https://linkinghub.elsevier.com/retrieve/pii/ S0896627316302483, doi:10.1016/j.neuron.2016.05.037, Notes: WitterL+4-2016.html.
- [Abdelgabar2019] Abdel R. Abdelgabar, Judith Suttrup, Robin Broersen, Ritu Bhandari, Samuel Picard, Christian Keysers, Chris I. De Zeeuw, and Valeria Gazzola. Action perception recruits the cerebellum and is impaired in patients with spinocerebellar ataxia. *Brain*, 142:3791–3805, 12 2019. doi:10.1093/brain/awz337.
- [Albus1971] James S Albus. A theory of cerebellar function. Mathematical Biosciences, 1971.
- [Amemiya2019] Kaoru Amemiya, Tomoyo Morita, Daisuke N. Saito, Midori Ban, Koji Shimada, Yuko Okamoto, Hirotaka Kosaka, Hidehiko Okazawa, Minoru Asada, and Eiichi Naito. Local-to-distant development of the cerebrocerebellar sensorimotor network in the typically developing human brain: a functional and diffusion mri study. *Brain Structure and Function*, 224:1359–1375, 4 2019. doi:10.1007/s00429-018-01821-5.
- [Apps2005] Richard Apps and Martin Garwicz. Anatomical and physiological foundations of cerebellar information processing. *Nature Reviews Neuroscience*, 6:297–311, 4 2005. doi:10.1038/nrn1646.
- [Apps2013] Richard Apps and Thomas C. Watson. Cerebro-cerebellar connections. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1131–1154, 1 2013. doi:10.1007/978-94-007-1333-8_48.
- [Ashida2018] Reiko Ashida, Nadia L. Cerminara, Jon Brooks, and Richard Apps. Principles of organization of the human cerebellum: macro- and microanatomy. *Handbook of Clinical Neurology*, 154:45–58, 1 2018. doi:10.1016/B978-0-444-63956-1.00003-5.
- [Bagnall2013] Martha Bagnall, Sascha du Lac, and Michael Mauk. Chapter 31 cerebellum. Fundamental Neuroscience (Fourth Edition), 2013. doi:http://dx.doi.org/10.1016/B978-0-12-385870-2.00031-7.
- [Barmack2013] Neal H. Barmack and Vadim Yakhnitsa. Vestibulocerebellar connections. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 357–376, 1 2013. doi:10.1007/978-94-007-1333-8_18.

- [Beckinghausen2019] Jaclyn Beckinghausen and Roy V. Sillitoe. Insights into cerebellar development and connectivity. *Neuroscience Letters*, 688:2–13, 1 2019. doi:10.1016/j.neulet.2018.05.013.
- [Benagiano2018] Vincenzo Benagiano, Anna Rizzi, Loredana Lorusso, Paolo Flace, Matteo Saccia, Raffaele Cagiano, Domenico Ribatti, Luisa Roncali, and Glauco Ambrosi. The functional anatomy of the cerebrocerebellar circuit: a review and new concepts. *Journal of Comparative Neurology*, 526:769–789, 4 2018. doi:10.1002/cne.24361.
- [Bengtsson2013] Fredrik Bengtsson and Germund Hesslow. Feedback control in the olivo-cerebellar loop. *Handbook* of the Cerebellum and Cerebellar Disorders, pages 1079–1100, 1 2013. doi:10.1007/978-94-007-1333-8_45.
- [Bengtsson2019] Fredrik Bengtsson, Anders Rasmussen, and Germund Hesslow. Feedback control in the olivocerebellar loop. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1–24, 2019. doi:10.1007/978-3-319-97911-3_45-2.
- [Billings2014] Guy Billings, Eugenio Piasini, Andrea Lorincz, Zoltan Nusser, and R. Angus Silver. Network structure within the cerebellar input layer enables lossless sparse encoding. *Neuron*, 83:960–974, 8 2014. doi:10.1016/j.neuron.2014.07.020.
- [Birnstiel2009] S. Birnstiel, N. T. Slater, D. R. McCrimmon, E. Mugnaini, and N. A. Hartell. Voltagedependent calcium signaling in rat cerebellar unipolar brush cells. *Neuroscience*, 162:702–712, 9 2009. doi:10.1016/j.neuroscience.2009.01.051.
- [Bjaalie1992] Jan G Bjaalie. Organization of the pontine nuclei. Neuroscience Research, 13:83–118, 1992.
- [Bjaalie1997] Jan G Bjaalie. Cat pontocerebellar network: numerical capacity and axonal collateral branching of neurones in the pontine nuclei projecting to individual parafloccular folia. *Neuroscience Research*, 27:199–210, 1997.
- [Blatt2013] Gene J. Blatt, Adrian L. Oblak, and Jeremy D. Schmahmann. Cerebellar connections with limbic circuits: anatomy and functional implications. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 479–496, 1 2013. doi:10.1007/978-94-007-1333-8_22.
- [BlazqezPaPastorAM2013] Pablo M. Blázquez and Angel M. Pastor. Cerebellar control of eye movements. *Handbook* of the Cerebellum and Cerebellar Disorders, pages 1155–1174, 1 2013. doi:10.1007/978-94-007-1333-8_49.
- [Boele2016] H. J. Boele, M. M. Ten Brinke, and C. I. De Zeeuw. Classical conditioning of timed motor responses: neural coding in cerebellar cortex and cerebellar nuclei. *The Neuronal Codes of the Cerebellum*, pages 53–96, 2016. doi:10.1016/B978-0-12-801386-1.00003-4.
- [Bosman2009] L. W.J. Bosman and A. Konnerth. Activity-dependent plasticity of developing climbing fiber-purkinje cell synapses. *Neuroscience*, 162:612–623, 9 2009. doi:10.1016/j.neuroscience.2009.01.032.
- [Bostan2013] Andreea C. Bostan, Richard P. Dum, and Peter L. Strick. Cerebellar networks with the cerebral cortex and basal ganglia. *Trends in Cognitive Sciences*, 17:241–254, 5 2013. doi:10.1016/j.tics.2013.03.003.
- [Bostan+StrickPL-2013] Andreea C. Bostan and Peter L. Strick. Cerebellar outputs in non-human primates: an anatomical perspective using transsynaptic tracers. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 549–570, 1 2013. doi:10.1007/978-94-007-1333-8_25.
- [Bower2013] James M. Bower. Computational structure of the cerebellar molecular layer. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1359–1380, 1 2013. doi:10.1007/978-94-007-1333-8_60.
- [Bracha2009] V. Bracha, S. Zbarska, K. Parker, A. Carrel, G. Zenitsky, and J. R. Bloedel. The cerebellum and eyeblink conditioning: learning versus network performance hypotheses. *Neuroscience*, 162:787–796, 9 2009. doi:10.1016/j.neuroscience.2008.12.042.
- [Brissenden2018] James A. Brissenden, Sean M. Tobyne, David E. Osher, Emily J. Levin, Mark A. Halko, and David C. Somers. Topographic cortico-cerebellar networks revealed by visual attention and working memory. *Current Biology*, 28:3364–3372.e5, 11 2018. doi:10.1016/j.cub.2018.08.059.

- [Buckner2013] Randy L. Buckner. The cerebellum and cognitive function: 25 years of insight from anatomy and neuroimaging. *Neuron*, 80:807–815, 10 2013. doi:10.1016/j.neuron.2013.10.044.
- [Cengiz2016] Bülent Cengiz and H. Evren Boran. The role of the cerebellum in motor imagery. *Neuroscience Letters*, 617:156–159, 3 2016. doi:10.1016/j.neulet.2016.01.045.
- [Cerminara2005] N. L. Cerminara, A. L. Edge, D. E. Marple-Horvat, and R. Apps. The lateral cerebellum and visuomotor control. *Progress in Brain Research*, 148:213–226, 2005. doi:10.1016/S0079-6123(04)48018-2.
- [Cerminara2013] Nadia L. Cerminara, Hanako Aoki, Michaela Loft, Izumi Sugihara, and Richard Apps. Structural basis of cerebellar microcircuits in the rat. *Journal of Neuroscience*, 33:16427–16442, 2013. doi:10.1523/JNEUROSCI.0861-13.2013.
- [Cerminara2015] Nadia L. Cerminara, Eric J. Lang, Roy V. Sillitoe, and Richard Apps. Redefining the cerebellar cortex as an assembly of non-uniform purkinje cell microcircuits. *Nature Reviews Neuroscience*, 16:79–93, 1 2015. doi:10.1038/nrn3886.
- [Cesa2009] R. Cesa and P. Strata. Axonal competition in the synaptic wiring of the cerebellar cortex during development and in the mature cerebellum. *Neuroscience*, 162:624–632, 9 2009. doi:10.1016/j.neuroscience.2009.02.061.
- [CesaRaStrataP2005] Roberta Cesa and Piergiorgio Strata. Axonal and synaptic remodeling in the mature cerebellar cortex. *Progress in Brain Research*, 2005. doi:10.1016/S0079-6123(04)480005-4.
- [Chabrol2019] Francois P. Chabrol, Antonin Blot, and Thomas D. Mrsic-Flogel. Cerebellar contribution to preparatory activity in motor neocortex. *Neuron*, 103:506–519.e4, 8 2019. doi:10.1016/j.neuron.2019.05.022.
- [Chaisanguanthum2014] Kris S. Chaisanguanthum, Mati Joshua, Javier F. Medina, William Bialek, and Stephen G. Lisberger. The neural code for motor control in the cerebellum and oculomotor brainstem. *eNeuro*, 11 2014. doi:10.1523/ENEURO.0004-14.2014.
- [Chandler2013] Daniel J. Chandler, Shevon E. Nicholson, Gerard Zitnik, and Barry D. Waterhouse. Norepinephrine and synaptic transmission in the cerebellum. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 895–914, 1 2013. doi:10.1007/978-94-007-1333-8_37.
- [Cicirata2005] Federico Cicirata, Maria Francesca Serapide, Rosalba Parenti, Maria Rosita Pantò, Agata Zappalà, Annalisa Nicotra, and Deborah Cicero. The basilar pontine nuclei and the nucleus reticularis tegmenti pontis subserve distinct cerebrocerebellar pathways. *Progress in Brain Research*, 148:259–282, 2005. doi:10.1016/S0079-6123(04)48021-2.
- [Coombs2009] I. D. Coombs and S. G. Cull-Candy. Transmembrane ampa receptor regulatory proteins and ampa receptor function in the cerebellum. *Neuroscience*, 162:656–665, 9 2009. doi:10.1016/j.neuroscience.2009.01.004.
- [Cooper2010] Richard P Cooper. Forward and inverse models in motor control and cognitive control. *Proceedings of the International Symposium on AI-Inspired Biology*, 2010.
- [Courtemanche2016] Richard Courtemanche and Ariana Frederick. A spatiotemporal hypothesis on the role of 4to 25-hz field potential oscillations in cerebellar cortex. *The Neuronal Codes of the Cerebellum*, pages 219–238, 2016. doi:10.1016/B978-0-12-801386-1.00010-1.
- [ReegDG+2-1971] 'D G R egg, J J S guin, and M Wiesendanger'. Effects of electrical stimulation of somatosensory and motor areas of the cerebral cortex on neurones of the pontine nuclei in squirrel monkeys. *Nuuro.wunw*, 2:923–927, 1971.
- [DAngeloEp6y2009] E. D'Angelo, S. K.E. Koekkoek, P. Lombardo, S. Solinas, E. Ros, J. Garrido, M. Schonewille, and C. I. De Zeeuw. Timing in the cerebellum: oscillations and resonance in the granular layer. *Neuroscience*, 162:805–815, 9 2009. doi:10.1016/j.neuroscience.2009.01.048.
- [DAngeloED+5-2009] E. D'Angelo, S. K.E. Koekkoek, P. Lombardo, S. Solinas, E. Ros, J. Garrido, M. Schonewille, and C. I. De Zeeuw. Timing in the cerebellum: oscillations and resonance in the granular layer. *Neuro-science*, 162:805–815, 9 2009. doi:10.1016/j.neuroscience.2009.01.048.

- [DAngeloEp8y2011] E. D'Angelo, P. Mazzarello, F. Prestori, J. Mapelli, S. Solinas, P. Lombardo, E. Cesana, D. Gandolfi, and L. Congi. The cerebellar network: from structure to function and dynamics. *Brain Research Reviews*, 66:5–15, 1 2011. doi:10.1016/j.brainresrev.2010.10.002.
- [DAngeloE2014] Egidio D'Angelo. The organization of plasticity in the cerebellar cortex: from synapses to control. *Progress in Brain Research*, 210:31–58, 2014. doi:10.1016/B978-0-444-63356-9.00002-9.
- [DAngeloE2018] Egidio D'Angelo. Physiology of the cerebellum. *Handbook of Clinical Neurology*, 154:85–108, 1 2018. doi:10.1016/B978-0-444-63956-1.00006-0.
- [DAngeloE-2018] Egidio D'Angelo. Physiology of the cerebellum. *Handbook of Clinical Neurology*, 154:85–108, 1 2018. doi:10.1016/B978-0-444-63956-1.00006-0.
- [DAngeloEp32016] Egidio D'Angelo, Stefano Masoli, Martina Rizza, and Stefano Casali. Single-neuron and network computation in realistic models of the cerebellar cortex. *The Neuronal Codes of the Cerebellum*, pages 239–260, 2016. doi:10.1016/B978-0-12-801386-1.00011-3.
- [DMelloAMp3y2020] Anila M. D'Mello, Tracy M. Centanni, John D.E. Gabrieli, and Joanna A. Christodoulou. Cerebellar contributions to rapid semantic processing in reading. *Brain and Language*, 9 2020. doi:10.1016/j.bandl.2020.104828.
- [Daniel2013] Hervé Daniel and F. Crepel. Purkinje neurons: synaptic plasticy. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 793–808, 1 2013. doi:10.1007/978-94-007-1333-8_32.
- [DashS+ThierP-2014] Survadeep Dash and Peter Thier. Cerebellum-dependent motor learning. lessons from adaptation of eye movements in primates. *Progress in Brain Research*, 210:121–155, 2014. doi:10.1016/B978-0-444-63356-9.00006-6.
- [Dash2014] Suryadeep Dash and Peter Thier. Cerebellum-dependent motor learning. lessons from adaptation of eye movements in primates. *Progress in Brain Research*, 210:121–155, 2014. doi:10.1016/B978-0-444-63356-9.00006-6.
- [deGruijlJR+2-2009] J. R. de Gruijl, P. van der Smagt, and C. I. De Zeeuw. Anticipatory grip force control using a cerebellar model. *Neuroscience*, 162:777–786, 9 2009. doi:10.1016/j.neuroscience.2009.02.041.
- [Dean2013] Paul Dean, Henrik Jörntell, and John Porrill. Adaptive filter models. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1315–1336, 1 2013. doi:10.1007/978-94-007-1333-8_58.
- [Dean2019] Paul Dean, Henrik Jörntell, and John Porrill. Adaptive filter models. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1–12, 2019. doi:10.1007/978-3-319-97911-3_58-2.
- [Dean2014] Paul Dean and John Porrill. Decorrelation learning in the cerebellum. computational analysis and experimental questions. *Progress in Brain Research*, 210:157–192, 2014. doi:10.1016/B978-0-444-63356-9.00007-8.
- [Dean2010] Paul Dean, John Porrill, Carl Fredrik Ekerot, and Henrik Jörntell. The cerebellar microcircuit as an adaptive filter: experimental and computational evidence. *Nature Reviews Neuroscience*, 11:30–43, 1 2010. doi:10.1038/nrn2756.
- [Decety1990] Jean Decety, Hans Sjfholm, Erik Ryding, Georg Stenberg, and David H Ingvar. The cerebellum participates in mental activity: tomographic measurements of regional cerebral blood flow. *Brain Research*, 535:313–317, 1990.
- [Diedrichsen2019] Jörn Diedrichsen, Maedbh King, Carlos Hernandez-Castillo, Marty Sereno, and Richard B. Ivry. Universal transform or multiple functionality? understanding the contribution of the human cerebellum across task domains. *Neuron*, 102:918–928, 6 2019. doi:10.1016/j.neuron.2019.04.021.
- [Dum2003] Richard P. Dum and Peter L. Strick. An unfolded map of the cerebellar dentate nucleus and its projections to the cerebral cortex. *Journal of Neurophysiology*, 89:634–639, 1 2003. doi:10.1152/jn.00626.2002.
- [DangeloE2013] Egidio D'angelo. Cerebellar granule cell. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 767–792, 1 2013. doi:10.1007/978-94-007-1333-8_31.

- [DMelloAMaRozenkrantL2020] Anila M. D'Mello and Liron Rozenkrantz. Neural mechanisms for prediction: from action to higher-order cognition. *Journal of Neuroscience*, 40:5158–5160, 7 2020. doi:10.1523/JNEUROSCI.0732-20.2020.
- [Eagleman2004] David M. Eagleman, John E. Jacobson, and Terrence J. Sejnowski. Perceived luminance depends on temporal context. *Nature*, 428:854–856, 4 2004. doi:10.1038/nature02467.
- [Ebner2013] Timothy J. Ebner. Cerebellum and internal models. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1281–1296, 1 2013. doi:10.1007/978-94-007-1333-8_56.
- [Francis1976] B. A. Francis and W. M. Wonham. The internal model principle of control theory. *Automatica*, 12:457–465, 1976. doi:10.1016/0005-1098(76)90006-6.
- [Fujita1982] M Fujita. Adaptive filter model of the cerebellum. *Biol. Cybern*, 45:195–206, 1982.
- [Fujita1982b] M Fujita. Biological cybernetics simulation of adaptive modification of the vestibulo-ocular reflex with an adaptive filter model of the cerebellum. *Biol. Cybern*, 45:207–214, 1982.
- [Galliano2013] Elisa Galliano, Zhenyu Gao, Martijn Schonewille, Boyan Todorov, Esther Simons, Andreea S. Pop, Egidio D'Angelo, Arn M.J.M. Van Den Maagdenberg, Freek E. Hoebeek, and Chris I. De Zeeuw. Silencing the majority of cerebellar granule cells uncovers their essential role in motor learning and consolidation. *Cell Reports*, 3:1239–1251, 4 2013. doi:10.1016/j.celrep.2013.03.023.
- [Galliano2014] Elisa Galliano and Chris I. De Zeeuw. Questioning the cerebellar doctrine. *Progress in Brain Research*, 210:59–77, 2014. doi:10.1016/B978-0-444-63356-9.00003-0.
- [Gao2006] Wangcai Gao, Gang Chen, Kenneth C. Reinert, and Timothy J. Ebner. Cerebellar cortical molecular layer inhibition is organized in parasagittal zones. *Journal of Neuroscience*, 26:8377–8387, 8 2006. doi:10.1523/JNEUROSCI.2434-06.2006.
- [Gao2018] Zhenyu Gao, Courtney Davis, Alyse M. Thomas, Michael N. Economo, Amada M. Abrego, Karel Svoboda, Chris I. De Zeeuw, and Nuo Li. A cortico-cerebellar loop for motor planning. *Nature*, 563:113–116, 11 2018. doi:10.1038/s41586-018-0633-x.
- [Glickstein2009] M. Glickstein, P. Strata, and J. Voogd. Cerebellum: history. *Neuroscience*, 162:549–559, 9 2009. doi:10.1016/j.neuroscience.2009.02.054.
- [Glickstein2007] Mitch Glickstein. What does the cerebellum really do? *Current Biology*, 10 2007. doi:10.1016/j.cub.2007.08.009.
- [Glickstein2013] Mitchell Glickstein. Visual circuits from cerebral cortex to cerebellum; the link through pons. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 469–478, 1 2013. doi:10.1007/978-94-007-1333-8_21.
- [Glickstein2008] Mitchell Glickstein and Karl Doron. Cerebellum: connections and functions. *Cerebellum*, 7:589–594, 12 2008. doi:10.1007/s12311-008-0074-4.
- [Glickstein1985] Mitchell Glickstein, Jack G May, and Barbara E Mercier. Corticopontine projection in the macaque: the distribution of labelled cortical cells after large injections of horseradish peroxidase in the pontine nuclei. *THE JOURNAL OF COMPARATIVE NEUROLOGY*, 235:343–359, 1985.
- [Grewe2011] Jan Grewe, Thomas Wachtler, and Jan Benda. A bottom-up approach to data annotation in neurophysiology. *Frontiers in neuroinformatics*, 5:16, 8 2011. URL: http://www.ncbi.nlm.nih.gov/pubmed/21941477, doi:10.3389/fninf.2011.00016.
- [DeGruijlJRa4y2013] J. R. De Gruijl, L. W.J. Bosman, Chris I. De Zeeuw, and M. T.G. De Jeu. Inferior olive: all ins and outs. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1013–1058, 1 2013. doi:10.1007/978-94-007-1333-8_43.
- [GuellX+2-2018] Xavier Guell, John D.E. Gabrieli, and Jeremy D. Schmahmann. Embodied cognition and the cerebellum: perspectives from the dysmetria of thought and the universal cerebellar transform theories. *Cortex*, 100:140–148, 3 2018. doi:10.1016/j.cortex.2017.07.005.

- [Guell2018] Xavier Guell, John D.E. Gabrieli, and Jeremy D. Schmahmann. Triple representation of language, working memory, social and emotion processing in the cerebellum: convergent evidence from task and seed-based resting-state fmri analyses in a single large cohort. *NeuroImage*, 172:437–449, 5 2018. doi:10.1016/j.neuroimage.2018.01.082.
- [Guillaume2018] Alain Guillaume, Jason R Fuller, Riju Srimal, and Clayton E Curtis. Cortico-cerebellar network involved in saccade adaptation. J Neurophysiol, 120:2583–2594, 2018. URL: www.jn.org, doi:10.1152/jn.00392.2018.-Saccade.
- [Habas2009] Christophe Habas, Nirav Kamdar, Daniel Nguyen, Katherine Prater, Christian F. Beckmann, Vinod Menon, and Michael D. Greicius. Distinct cerebellar contributions to intrinsic connectivity networks. *Journal of Neuroscience*, 29:8586–8594, 7 2009. doi:10.1523/JNEUROSCI.1868-09.2009.
- [Habas2018] Christophe Habas and Mario Manto. Probing the neuroanatomy of the cerebellum using tractography. *Handbook of Clinical Neurology*, 154:235–249, 1 2018. doi:10.1016/B978-0-444-63956-1.00014-X.
- [Habas2013] Christophe Habas, William R. Shirer, and Michael D. Greicius. Delineation of cerebrocerebellar networks with mri measures of functional and structural connectivity. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 571–586, 1 2013. doi:10.1007/978-94-007-1333-8_26.
- [Habas2019] Christophe Habas, William R. Shirer, and Michael D. Greicius. Delineation of cerebrocerebellar networks with mri measures of functional and structural connectivity. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1–17, 2019. doi:10.1007/978-3-319-97911-3_26-2.
- [Hardwick2013] Robert M. Hardwick, Maria Dagioglou, and R. Chris Miall. State estimation and the cerebellum. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1297–1314, 1 2013. doi:10.1007/978-94-007-1333-8_57.
- [Hariri2019] Ahmad R. Hariri. The emerging importance of the cerebellum in broad risk for psychopathology. *Neuron*, 102:17–20, 4 2019. doi:10.1016/j.neuron.2019.02.031.
- [Hashimoto2009] K. Hashimoto, T. Yoshida, K. Sakimura, M. Mishina, M. Watanabe, and M. Kano. Influence of parallel fiber-purkinje cell synapse formation on postnatal development of climbing fiber-purkinje cell synapses in the cerebellum. *Neuroscience*, 162:601–611, 9 2009. doi:10.1016/j.neuroscience.2008.12.037.
- [Hashimoto2004] Mitsuhiro Hashimoto and Katsuhiko Mikoshiba. Neuronal birthdate-specific gene transfer with adenoviral vectors. *Journal of Neuroscience*, 24:286–296, 1 2004. doi:10.1523/JNEUROSCI.2529-03.2004.
- [Heck2013] Detlef H. Heck, Chris I. De Zeeuw, Dieter Jaeger, Kamran Khodakhah, and Abigail L. Person. The neuronal code(s) of the cerebellum. *Journal of Neuroscience*, 33:17603–17609, 2013. doi:10.1523/JNEUROSCI.2759-13.2013.
- [Herzfeld2018] David J. Herzfeld, Yoshiko Kojima, Robijanto Soetedjo, and Reza Shadmehr. Encoding of error and learning to correct that error by the purkinje cells of the cerebellum. *Nature Neuroscience*, 21:736–743, 5 2018. doi:10.1038/s41593-018-0136-y.
- [Hesslow2020] Germund Hesslow, Dan-Anders Jirenhed, and Fredrik Johansson. Purkinje neurons during eye blink conditioning and new mechanisms of cerebellar learning and timing. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1–10, 2020. doi:10.1007/978-3-319-97911-3_115-1.
- [Huang2013] C. Huang and Robert E. Ricklefs. Cerebellum and human evolution: a comparative and information theory perspective. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1337–1358, 1 2013. doi:10.1007/978-94-007-1333-8_59.
- [Ioffe2013] M. E. Ioffe. Cerebellar control of posture. Handbook of the Cerebellum and Cerebellar Disorders, pages 1221–1240, 1 2013. doi:10.1007/978-94-007-1333-8_53.
- [Ito2009] M. Ito. Functional roles of neuropeptides in cerebellar circuits. *Neuroscience*, 162:666–672, 9 2009. doi:10.1016/j.neuroscience.2009.01.019.
- [Ito2001] Masao Ito. Cerebellar long-term depression: characterization, signal transduction, and functional roles. *Pyhsrev*, 2001. URL: http://physrev.physiology.org.

- [Ito2002] Masao Ito. The molecular organization of cerebellar long-term depression. *Nature Reviews Neuroscience*, 3:896–902, 2002. doi:10.1038/nrn962.
- [Ito2005] Masao Ito. Bases and implications of learning in the cerebellum adaptive control and internal model mechanism. *Progress in Brain Research*, 148:95–109, 2005. doi:10.1016/S0079-6123(04)48009-1.
- [Ito2006] Masao Ito. Cerebellar circuitry as a neuronal machine. *Progress in Neurobiology*, 78:272–303, 2 2006. doi:10.1016/j.pneurobio.2006.02.006.
- [Ito2014] Masao Ito, Kazuhiko Yamaguchi, Soichi Nagao, and Tadashi Yamazaki. Long-term depression as a model of cerebellar plasticity. *Progress in Brain Research*, 210:1–30, 2014. doi:10.1016/B978-0-444-63356-9.00001-7.
- [Ito1997] Mcsco Ito. Cerebellar microcomplexes. Int Rev Neurobiol, 1997.
- [IvryR1997] Richard Ivry. Cerebellar timing systems. Int Rev Neurobiol, 1997.
- [Jaeger2013] Dieter Jaeger. Cerebellar nuclei and cerebellar learning. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1111–1130, 1 2013. doi:10.1007/978-94-007-1333-8_47.
- [Jaeger2019] Dieter Jaeger. Cerebellar nuclei and cerebellar learning. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1–24, 2019. doi:10.1007/978-3-319-97911-3_47-2.
- [JorntellH2016] Henrik Jörntell. Cerebellar neuronal codes-perspectives from intracellular analysis in vivo. *The Neuronal Codes of the Cerebellum*, pages 155–172, 2016. doi:10.1016/B978-0-12-801386-1.00007-1.
- [Kavalali2018] Ege T. Kavalali and Lisa M. Monteggia. The ketamine metabolite 2r,6r-hydroxynorketamine blocks nmda receptors and impacts downstream signaling linked to antidepressant effects. *Neuropsychopharmacology*, 43:221–222, 1 2018. doi:10.1038/npp.2017.210.
- [Kawato1987] M Kawato, Kazunori Furukawa ', and R Suzuki. Biological cybernetics a hierarchical neural-network model-for control and learning of voluntary movement. *Biol. Cybern*, 57:169–185, 1987.
- [KawatoM1999] Mitsuo Kawato. Internal models for motor control and trajectory planning. *erato atr*, 1999. URL: http://www.erato.atr.co.jp/DB/.
- [Kawato2020] Mitsuo Kawato, Shogo Ohmae, Huu Hoang, and Terry Sanger. 50 years since the marr, ito, and albus models of the cerebellum. *Neuroscience*, 2020. doi:10.1016/j.neuroscience.2020.06.019.
- [Kelly2003] Roberta M Kelly and Peter L Strick. Behavioral/systems/cognitive cerebellar loops with motor cortex and prefrontal cortex of a nonhuman primate. *J. of Neuroscience*, 2003.
- [Kilteni2020] Konstantina Kilteni and H. Henrik Ehrsson. Functional connectivity between the cerebellum and somatosensory areas implements the attenuation of self-generated touch. *Journal of Neuroscience*, 40:894–906, 1 2020. doi:10.1523/JNEUROSCI.1732-19.2019.
- [Koeppen2018] Arnulf H. Koeppen. The neuropathology of the adult cerebellum. *Handbook of Clinical Neurology*, 154:129–149, 1 2018. doi:10.1016/B978-0-444-63956-1.00008-4.
- [Kostadinov2019] Dimitar Kostadinov, Alexandre Mathy, and Beverley A. Clark. Dynamics of the inferior olive oscillator and cerebellar function. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1–21, 2019. doi:10.1007/978-3-319-97911-3_44-2.
- [Krageloh_Mann2010] Ingeborg Krägeloh-mann. Lesions in early cerebellar development do they matter? *Developmental Medicine and Child Neurology*, 52:694–694, 8 2010. doi:10.1111/j.1469-8749.2009.03549.x.
- [Lang2016] Eric J. Lang. Coordination of reaching movements: cerebellar interactions with motor cortex. *The Neuronal Codes of the Cerebellum*, pages 197–217, 2016. doi:10.1016/B978-0-12-801386-1.00009-5.
- [Laurens2016] Jean Laurens and Dora E. Angelaki. How the vestibulocerebellum builds an internal model of selfmotion. *The Neuronal Codes of the Cerebellum*, pages 97–115, 2016. doi:10.1016/B978-0-12-801386-1.00004-6.

- [LeinerHC+LeinerAL1997] Henrietta C Leiner and Alan L Leiner. How fibers subserve computing capabilities: similarities between brains and machines. *International Review of Neurobiology*, 1997.
- [Leiner1991] Henrietta C Leiner, Alan L Leiner, and Robert S Dow. The human cerebro-cerebellar system: its computing, cognitive, and language skills. *Behavioural Brabt Research*, 44:113–128, 1991.
- [Leiner1986] Henrietta C Leiner, Alan L Leiner, Charming House, Palo Alto, California Robert, and S Dow. Does the cerebellum contribute to mental skills? *Behavioral Neuroscience*, 100:443–454, 1986.
- [Leiner2010] Henrietta C. Leiner. Solving the mystery of the human cerebellum. *Neuropsychology Review*, 20:229–235, 9 2010. doi:10.1007/s11065-010-9140-z.
- [Leitner2015] Yael Leitner, Katherine E. Travis, Michal Ben-Shachar, Kristen W. Yeom, and Heidi M. Feldman. Tract profiles of the cerebellar white matter pathways in children and adolescents. *Cerebellum*, 14:613–623, 12 2015. doi:10.1007/s12311-015-0652-1.
- [LevRamVp3y2003] Varda Lev-Ram, Samar B Mehta, David Kleinfeld, and Roger Y Tsien. Reversing cerebellar long-term depression. PNAS, 2003. URL: www.pnas.orgcgidoi10.1073pnas.2636935100.
- [LevRamVp3y2002] Varda Lev-Ram, Scott T Wong, Daniel R Storm, and Roger Y Tsien. A new form of cerebellar long-term potentiation is postsynaptic and depends on nitric oxide but not camp. *pnas*, 2002. URL: www. pnas.orgcgidoi10.1073pnas.122206399.
- [Lindquist2013] Derick H. Lindquist, Joseph E. Steinmetz, and Richard F. Thompson. Cerebellum and eyeblink conditioning. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1175–1190, 1 2013. doi:10.1007/978-94-007-1333-8_50.
- [Lisberger2009] S. G. Lisberger. Internal models of eye movement in the floccular complex of the monkey cerebellum. *Neuroscience*, 162:763–776, 9 2009. doi:10.1016/j.neuroscience.2009.03.059.
- [Liu2013] Siqiong June Liu. Stellate cells: synaptic processing and plasticity. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 809–828, 1 2013. doi:10.1007/978-94-007-1333-8_33.
- [Lixenberg2020] Adi Lixenberg, Merav Yarkoni, Yehudit Botschko, and Mati Joshua. Encoding of eye movements explains reward-related activity in cerebellar simple spikes. *J Neurophysiol*, 123:786–799, 2020. URL: www.jn.org, doi:10.1152/jn.00363.2019.-The.
- [LlinasRR-2009] R. R. Llinás. Inferior olive oscillation as the temporal basis for motricity and oscillatory reset as the basis for motor error correction. *Neuroscience*, 162:797–804, 9 2009. doi:10.1016/j.neuroscience.2009.04.045.
- [Longley2014] Michael Longley and Christopher H. Yeo. Distribution of neural plasticity in cerebellum-dependent motor learning. *Progress in Brain Research*, 210:79–101, 2014. doi:10.1016/B978-0-444-63356-9.00004-2.
- [Luo2014] Yuanjun Luo and Izumi Sugihara. Cerebellar afferents originating from the medullary reticular formation that are different from mossy, climbing or monoaminergic fibers in the rat. *Brain Research*, 1566:31–46, 5 2014. doi:10.1016/j.brainres.2014.04.020.
- [LenaCandPopaD2016] Clément Léna and Daniela Popa. Cerebrocerebellar loops in the rodent brain. *The Neuronal Codes of the Cerebellum*, pages 135–153, 2016. doi:10.1016/B978-0-12-801386-1.00006-X.
- [MacLeod2012] Carol MacLeod. The missing link. evolution of the primate cerebellum. *Progress in Brain Research*, 195:165–187, 2012. doi:10.1016/B978-0-444-53860-4.00008-8.
- [Magal2013] Ari Magal. A hypothetical universal model of cerebellar function: reconsideration of the current dogma. *Cerebellum*, 12:758–772, 10 2013. doi:10.1007/s12311-013-0477-8.
- [Mannarelli2019] Daniela Mannarelli, Caterina Pauletti, Antonio Currà, Lucio Marinelli, Alessandra Corrado, Roberto Delle Chiaie, and Francesco Fattapposta. The cerebellum modulates attention network functioning: evidence from a cerebellar transcranial direct current stimulation and attention network test study. *Cerebellum*, 18:457–468, 6 2019. doi:10.1007/s12311-019-01014-8.

- [Manto2018] Mario Manto. Cerebellar motor syndrome from children to the elderly. *Handbook of Clinical Neurology*, 154:151–166, 1 2018. doi:10.1016/B978-0-444-63956-1.00009-6.
- [MarienPaBorgattiR2018] Peter Mariën and Renato Borgatti. Language and the cerebellum. *Handbook of Clinical Neurology*, 154:181–202, 1 2018. doi:10.1016/B978-0-444-63956-1.00011-4.
- [Markov2014] N. T. Markov, M. M. Ercsey-Ravasz, A. R. Ribeiro Gomes, C. Lamy, L. Magrou, J. Vezoli, P. Misery, A. Falchier, R. Quilodran, M. A. Gariel, J. Sallet, R. Gamanut, C. Huissoud, S. Clavagnier, P. Giroud, D. Sappey-Marinier, P. Barone, C. Dehay, Z. Toroczkai, K. Knoblauch, D. C. Van Essen, and H. Kennedy. A weighted and directed interareal connectivity matrix for macaque cerebral cortex. *Cerebral Cortex*, 24:17–36, 1 2014. doi:10.1093/cercor/bhs270.
- [Mathy2013] Alexandre Mathy and Beverley A. Clark. Dynamics of the inferior olive oscillator and cerebellar function. Handbook of the Cerebellum and Cerebellar Disorders, pages 1059–1078, 1 2013. doi:10.1007/978-94-007-1333-8_44.
- [McElvain2010] Lauren E. McElvain, Martha W. Bagnall, Alexandra Sakatos, and Sascha Du Lac. Bidirectional plasticity gated by hyperpolarization controls the gain of postsynaptic firing responses at central vestibular nerve synapses. *Neuron*, 68:763–775, 11 2010. doi:10.1016/j.neuron.2010.09.025.
- [Medina2000] Javier F Medina and Michael D Mauk. Computer simulation of cerebellar information processing. *nature neuroscience*, 2000. URL: http://neurosci.nature.com.
- [Medina2011] Javier F. Medina. The multiple roles of purkinje cells in sensori-motor calibration: to predict, teach and command. *Current Opinion in Neurobiology*, 21:616–622, 8 2011. doi:10.1016/j.conb.2011.05.025.
- [MiddletonFAaStrickPL1997] Frank A Middleton and Peter L Strick. Cerebellar output channels. *Int Rev Neurobiol*, 1997.
- [Middleton2001] Frank A Middleton and Peter L Strick. Cerebellar projections to the prefrontal cortex of the primate. *J of Neuroscience*, 2001.
- [Middleton1998] Frank A. Middleton and Peter L. Strick. Cerebellar output: motor and cognitive channels. *Trends in Cognitive Sciences*, 1998. doi:10.1016/S1364-6613(98)01220-0.
- [Miterko2019] Lauren N. Miterko, Roy V. Sillitoe, and Richard Hawkes. Zones and stripes: development of cerebellar topography. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1–23, 2019. doi:10.1007/978-3-319-97911-3_3-2.
- [Moberget2016] Torgeir Moberget and Richard B. Ivry. Cerebellar contributions to motor control and language comprehension: searching for common computational principles. *Annals of the New York Academy of Sciences*, 1369:154–171, 4 2016. doi:10.1111/nyas.13094.
- [Molinari2013] Marco Molinari and Maria G. Leggio. Cerebellar sequencing for cognitive processing. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1701–1716, 1 2013. doi:10.1007/978-94-007-1333-8_76.
- [Molinari2018] Marco Molinari, Marcella Masciullo, Sara Bulgheroni, Stefano D'Arrigo, and Daria Riva. Cognitive aspects: sequencing, behavior, and executive functions. *Handbook of Clinical Neurology*, 154:167–180, 1 2018. doi:10.1016/B978-0-444-63956-1.00010-2.
- [Molinari2005] Marco Molinari, Domenico Restuccia, and Maria G. Leggio. Cerebellar information flow in the thalamus: implications for cortical functions. *Thalamus and Related Systems*, 2005. doi:10.1017/S1472928807000143.
- [MorenoRiusJ-2018] Josep Moreno-Rius. The cerebellum in fear and anxiety-related disorders. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, 85:23–32, 7 2018. doi:10.1016/j.pnpbp.2018.04.002.
- [Mugnaini2011] Enrico Mugnaini, Gabriella Sekerková, and Marco Martina. The unipolar brush cell: a remarkable neuron finally receiving deserved attention. *Brain Research Reviews*, 66:220–245, 1 2011. doi:10.1016/j.brainresrev.2010.10.001.

- [Nakanishi2009] S. Nakanishi. Genetic manipulation study of information processing in the cerebellum. *Neuroscience*, 162:723–731, 9 2009. doi:10.1016/j.neuroscience.2009.01.028.
- [Narain2018] Devika Narain, Evan D. Remington, Chris I.De Zeeuw, and Mehrdad Jazayeri. A cerebellar mechanism for learning prior distributions of time intervals. *Nature Communications*, 12 2018. doi:10.1038/s41467-017-02516-x.
- [Neubauer2018] Simon Neubauer, Jean-Jacques Hublin, and Philipp Gunz. P a l e o n t o l o g y the evolution of modern human brain shape. *Science*, 2018. URL: http://advances.sciencemag.org/.
- [Nitschke2005] M. F. Nitschke, T. Arp, G. Stavrou, C. Erdmann, and W. Heide. The cerebellum in the cerebrocerebellar network for the control of eye and hand movements - an fmri study. *Progress in Brain Research*, 148:151–164, 2005. doi:10.1016/S0079-6123(04)48013-3.
- [NemecP+OstenP-2020] Pavel Němec and Pavel Osten. The evolution of brain structure captured in stereotyped cell count and cell type distributions. *Current Opinion in Neurobiology*, 60:176–183, 2 2020. doi:10.1016/j.conb.2019.12.005.
- [Overby1989] S E Overby, J G Bjaalie, and P Brodal. Experimental brain research uneven densities of corticopontine neurons in the somatosensory cortex: a quantitative experimental study in the cat. *Exp Brain Res*, 77:653–665, 1989.
- [VanOverwalleFp32017] Frank Van Overwalle, Elien Heleven, Ning Ma, and Peter Mariën. Tell me twice: a multistudy analysis of the functional connectivity between the cerebrum and cerebellum after repeated trait information. *NeuroImage*, 144:241–252, 1 2017. doi:10.1016/j.neuroimage.2016.08.046.
- [VanOverwalleF+10-2020] Frank Van Overwalle, Mario Manto, Zaira Cattaneo, Silvia Clausi, Chiara Ferrari, John D.E. Gabrieli, Xavier Guell, Elien Heleven, Michela Lupo, Qianying Ma, Marco Michelutti, Giusy Olivito, Min Pu, Laura C. Rice, Jeremy D. Schmahmann, Libera Siciliano, Arseny A. Sokolov, Catherine J. Stoodley, Kim van Dun, Larry Vandervert, and Maria Leggio. Consensus paper: cerebellum and social cognition. *Cerebellum*, 2020. doi:10.1007/s12311-020-01155-1.
- [VanOverwalleF+3-2019] Frank Van Overwalle, Mario Manto, Maria Leggio, and José María Delgado-García. The sequencing process generated by the cerebellum crucially contributes to social interactions. *Medical Hypotheses*, 128:33–42, 7 2019. doi:10.1016/j.mehy.2019.05.014.
- [Palay1974] Sanford L Palay, Victoria Chan-Palay, and Springer-Verlag Berlin' Heidelberg. *Cerebellar Cortex Cytology and Organization With 267 Figures including 203 Plates*. Springer-Verlag, 1974.
- [PayneHL+5] Hannah L Payne, Ranran L French, Christine C Guo, Barbara Nguyen-Vu, Tiina Manninen, and Jennifer L Raymond. Cerebellar purkinje cells control eye movements with a rapid rate code that is invariant to spike irregularity. *elife science*, 2019. URL: https://doi.org/10.7554/eLife.37102.001, doi:10.7554/eLife.37102.001.
- [PersonAL+RamanIM-2012] Abigail L. Person and Indira M. Raman. Synchrony and neural coding in cerebellar circuits. *Frontiers in Neural Circuits*, 2012. URL: http://journal.frontiersin.org/article/10.3389/fncir.2012. 00097/abstract, doi:10.3389/fncir.2012.00097.
- [Pietrajtis2013] Katarzyna Pietrajtis and Stéphane Dieudonné. Golgi neurons. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 829–852, 1 2013. doi:10.1007/978-94-007-1333-8_34.
- [Pleger2018] Burkhard Pleger and Dagmar Timmann. The role of the human cerebellum in linguistic prediction, word generation and verbal working memory: evidence from brain imaging, non-invasive cerebellar stimulation and lesion studies. *Neuropsychologia*, 115:204–210, 7 2018. doi:10.1016/j.neuropsychologia.2018.03.012.
- [Popa2019] Laurentiu S. Popa and Timothy J. Ebner. Cerebellum and internal models. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1–25, 2019. doi:10.1007/978-3-319-97911-3_56-2.
- [Popa2014] Laurentiu S. Popa, Angela L. Hewitt, and Timothy J. Ebner. The cerebellum for jocks and nerds alike. *Frontiers in Systems Neuroscience*, 6 2014. doi:10.3389/fnsys.2014.00113.

- [Popa2016] Laurentiu S. Popa, Martha L. Streng, and Timothy J. Ebner. Signaling of predictive and feedback information in purkinje cell simple spike activity. *The Neuronal Codes of the Cerebellum*, pages 1–25, 2016. doi:10.1016/B978-0-12-801386-1.00001-0.
- [PopaLS+3-2016] Laurentiu S. Popa, Martha L. Streng, Angela L. Hewitt, and Timothy J. Ebner. The errors of our ways: understanding error representations in cerebellar-dependent motor learning. *Cerebellum*, 15:93–103, 4 2016. doi:10.1007/s12311-015-0685-5.
- [Poretti2010] Andrea Poretti, Catherine Limperopoulos, Eliane Roulet-Perez, Nicole I. Wolf, Christian Rauscher, Daniela Prayer, Anita MÜller, Markus A. Weissert, Urania Kotzaeridou, Adre J. Du Plessis, Thierry A.G.M. Huisman, and Eugen Boltshauser. Outcome of severe unilateral cerebellar hypoplasia. *Developmental Medicine and Child Neurology*, 52:718–724, 8 2010. doi:10.1111/j.1469-8749.2009.03522.x.
- [Prestori2020] Francesca Prestori, Ileana Montagna, Egidio D'angelo, and Lisa Mapelli. The optogenetic revolution in cerebellar investigations. *International Journal of Molecular Sciences*, 4 2020. doi:10.3390/ijms21072494.
- [Rahimi2019] Abbas Rahimi, Pentti Kanerva, Luca Benini, and Jan M. Rabaey. Efficient biosignal processing using hyperdimensional computing: network templates for combined learning and classification of exg signals. *Proceedings of the IEEE*, 107:123–143, 1 2019. doi:10.1109/JPROC.2018.2871163.
- [Ramnani2014] Narender Ramnani. Automatic and controlled processing in the corticocerebellar system. *Progress in Brain Research*, 210:255–285, 2014. doi:10.1016/B978-0-444-63356-9.00010-8.
- [Rasmussen2014] Anders Rasmussen and Germund Hesslow. Feedback control of learning by the cerebello-olivary pathway. *Progress in Brain Research*, 210:103–119, 2014. doi:10.1016/B978-0-444-63356-9.00005-4.
- [Raymond2018] Jennifer L Raymond and Javier F Medina. Computational principles of supervised learning in the cerebellum. Annu Rev Neurosci, 2018. URL: https://doi.org/10.1146/annurev-neuro-080317-, doi:10.1146/annurev-neuro-080317.
- [Reato2016] Davide Reato, Esra Tara, and Kamran Khodakhah. Deep cerebellar nuclei rebound firing in vivo: much ado about almost nothing? *The Neuronal Codes of the Cerebellum*, pages 27–51, 2016. doi:10.1016/B978-0-12-801386-1.00002-2.
- [Rokni2009] D. Rokni and Y. Yarom. State-dependence of climbing fiber-driven calcium transients in purkinje cells. *Neuroscience*, 162:694–701, 9 2009. doi:10.1016/j.neuroscience.2008.12.044.
- [RondiReigL+4-2014] Laure Rondi-Reig, Anne Lise Paradis, Julie M. Lefort, Benedicte M. Babayan, and Christine Tobin. How the cerebellum may monitor sensory information for spatial representation. *Frontiers in Sys*tems Neuroscience, 11 2014. doi:10.3389/fnsys.2014.00205.
- [Ruigrok2013] Tom J.H. Ruigrok. Cerebellar influences on descending spinal motor systems. Handbook of the Cerebellum and Cerebellar Disorders, pages 497–528, 1 2013. doi:10.1007/978-94-007-1333-8_23.
- [Sabes2011] Philip N. Sabes. Sensory integration for reaching. models of optimality in the context of behavior and the underlying neural circuits. *Progress in Brain Research*, 191:195–209, 2011. doi:10.1016/B978-0-444-53752-2.00004-7.
- [Sacchetti2009] B. Sacchetti, B. Scelfo, and P. Strata. Cerebellum and emotional behavior. *Neuroscience*, 162:756–762, 9 2009. doi:10.1016/j.neuroscience.2009.01.064.
- [Sakai2013] Sharleen T. Sakai. Cerebellar thalamic and thalamocortical projections. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 529–548, 1 2013. doi:10.1007/978-94-007-1333-8_24.
- [Salmi2010] Juha Salmi, Karen Johanne Pallesen, Tuomas Neuvonen, Elvira Brattico, Antti Korvenoja, Oili Salonen, and Synnöve Carlson. Cognitive and motor loops of the human cerebro-cerebellar system. *Journal of Cognitive Neuroscience*, 22:2663–2676, 2010. doi:10.1162/jocn.2009.21382.
- [Sanger2020] Terence D. Sanger, Okito Yamashita, and Mitsuo Kawato. Expansion coding and computation in the cerebellum: 50 years after the marr-albus codon theory. *Journal of Physiology*, 598:913–928, 3 2020. doi:10.1113/JP278745.

- [Sarnat2018] Harvey B. Sarnat. Cerebellar networks and neuropathology of cerebellar developmental disorders. *Handbook of Clinical Neurology*, 154:109–128, 1 2018. doi:10.1016/B978-0-444-63956-1.00007-2.
- [Sawtell2013] Nathaniel B. Sawtell and Curtis C. Bell. Cerebellum-like structures. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1257–1278, 1 2013. doi:10.1007/978-94-007-1333-8_55.
- [Schmahmann2009] J. D. Schmahmann, J. MacMore, and M. Vangel. Cerebellar stroke without motor deficit: clinical evidence for motor and non-motor domains within the human cerebellum. *Neuroscience*, 162:852–861, 9 2009. doi:10.1016/j.neuroscience.2009.06.023.
- [SchmahmannJD+PandyaDN-1991] Jeremy D Schmahmann and and Deepak N Pandya. Projections to the basis pontis from the superior temporal sulcus and superior temporal region in the rhesus monkey. *THE JOURNAL OF COMPARATIVE NEUROLOGY*, 1991.
- [SchmahmannJD+PandyaDN-1993] Jeremy D Schmahmann and and Deepak N Pandya. Prelunate, occipitotemporal, and parahippocampal projections to the basis pontis in rhesus monkey. *THE JOURNAL OF COMPARA-TIVE NEUROLOGY*, 337:94–112, 1993.
- [Schmahmann1999] Jeremy D Schmahmann, Julien Doyon, David Mcdonald, Colin Holmes, Karyne Lavoie, Amy S Hurwitz, Noor Kabani, Arthur Toga, Alan Evans, and Michael Petrides. Three-dimensional mri atlas of the human cerebellum in proportional stereotaxic space. *Neuroimage*, 1999. URL: http://www.idealibrary. com.
- [Schmahmann2019] Jeremy D Schmahmann, Xavier Guell, Catherine J Stoodley, and Mark A Halko. The theory and neuroscience of cerebellar cognition. *Annual Reviews of Neuroscience*, 2019. URL: https://doi.org/10. 1146/annurev-neuro-070918-, doi:10.1146/annurev-neuro-070918.
- [Schmahmann1958] Jeremy D Schmahmann and Deepak N Pandya. Anatomic organization of the basilar pontine projections from prefrontal cortices in rhesus monkey. *J. of Neuroscience*, 1997.
- [Schmahmann1997] Jeremy D Schmahmann and Deepak N Pandyat. The cerebrocerebellar system. *Int Rev Neurobiol*, 1997.
- [Schmahmann2013] Jeremy D. Schmahmann. Cerebellar cognitive affective syndrome and the neuropsychiatry of the cerebellum. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1717–1752, 1 2013. doi:10.1007/978-94-007-1333-8_77.
- [Schutter2013] Dennis J.L.G. Schutter. Human cerebellum in motivation and emotion. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1771–1782, 1 2013. doi:10.1007/978-94-007-1333-8_79.
- [DeSchutterE+SteuberV-2009] E. De Schutter and V. Steuber. Patterns and pauses in purkinje cell simple spike trains: experiments, modeling and theory. *Neuroscience*, 162:816–826, 9 2009. doi:10.1016/j.neuroscience.2009.02.040.
- [Scott2012] Stephen H. Scott. The computational and neural basis of voluntary motor control and planning. *Trends in Cognitive Sciences*, 16:541–549, 11 2012. doi:10.1016/j.tics.2012.09.008.
- [Serrao2018] Mariano Serrao, Alberto Ranavolo, and Carlo Casali. Neurophysiology of gait. *Handbook of Clinical Neurology*, 154:299–303, 1 2018. doi:10.1016/B978-0-444-63956-1.00018-7.
- [Shadmehr2010] Reza Shadmehr, Maurice A. Smith, and John W. Krakauer. Error correction, sensory prediction, and adaptation in motor control. *Annual Review of Neuroscience*, 33:89–108, 2010. doi:10.1146/annurev-neuro-060909-153135.
- [Shinoda2013] Yoshikazu Shinoda and Izumi Sugihara. Axonal trajectories of single climbing and mossy fiber neurons in the cerebellar cortex and nucleus. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 437–468, 1 2013. doi:10.1007/978-94-007-1333-8_20.
- [Sillitoe2008] Roy V. Sillitoe, Seung Hyuk Chung, Jean Marc Fritschy, Monica Hoy, and Richard Hawkes. Golgi cell dendrites are restricted by purkinje cell stripe boundaries in the adult mouse cerebellar cortex. *Journal of Neuroscience*, 28:2820–2826, 3 2008. doi:10.1523/JNEUROSCI.4145-07.2008.

- [Sillitoe2013] Roy V. Sillitoe and Richard Hawkes. Zones and stripes: development of cerebellar topography. Handbook of the Cerebellum and Cerebellar Disorders, pages 43–60, 1 2013. doi:10.1007/978-94-007-1333-8_3.
- [Sillitoe2005] Roy V. Sillitoe, Hassan Marzban, Matt Larouche, Sepehr Zahedi, Jorge Affanni, and Richard Hawkes. Conservation of the architecture of the anterior lobe vermis of the cerebellum across mammalian species. *Progress in Brain Research*, 148:283–297, 2005. doi:10.1016/S0079-6123(04)48022-4.
- [Simpson2005] J. I. Simpson, H. C. Hulscher, E. Sabel-Goedknegt, and T. J.H. Ruigrok. Between in and out: linking morphology and physiology of cerebellar cortical interneurons. *Progress in Brain Research*, 148:329–340, 2005. doi:10.1016/S0079-6123(04)48026-1.
- [Sims2005] Robert E. Sims and Nicholas A. Hartell. Differences in transmission properties and susceptibility to longterm depression reveal functional specialization of ascending axon and parallel fiber synapses to purkinje cells. *Journal of Neuroscience*, 25:3246–3257, 3 2005. doi:10.1523/JNEUROSCI.0073-05.2005.
- [Smaers2014] Jeroen B. Smaers. Modeling the evolution of the cerebellum. from macroevolution to function. *Progress in Brain Research*, 210:193–216, 2014. doi:10.1016/B978-0-444-63356-9.00008-X.
- [Sokolov2017] Arseny A. Sokolov, R. Chris Miall, and Richard B. Ivry. The cerebellum: adaptive prediction for movement and cognition. *Trends in Cognitive Sciences*, 21:313–332, 5 2017. doi:10.1016/j.tics.2017.02.005.
- [Sotelo2009] C. Sotelo and I. Dusart. Intrinsic versus extrinsic determinants during the development of purkinje cell dendrites. *Neuroscience*, 162:589–600, 9 2009. doi:10.1016/j.neuroscience.2008.12.035.
- [Sotelo2011] Constantino Sotelo. Camillo golgi and santiago ramon y cajal: the anatomical organization of the cortex of the cerebellum. can the neuron doctrine still support our actual knowledge on the cerebellar structural arrangement? *Brain Research Reviews*, 66:16–34, 1 2011. doi:10.1016/j.brainresrev.2010.05.004.
- [Spencer2013] Rebecca M.C. Spencer and Richard B. Ivry. Cerebellum and timing. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1201–1220, 1 2013. doi:10.1007/978-94-007-1333-8_52.
- [Steinlin2013] Maja Steinlin and Kevin Wingeier. Cerebellum and cognition. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1687–1700, 1 2013. doi:10.1007/978-94-007-1333-8_75.
- [Steuber2016] Volker Steuber. Modeling the generation of cerebellar nuclear spike output. *The Neuronal Codes of the Cerebellum*, pages 117–133, 2016. doi:10.1016/B978-0-12-801386-1.00005-8.
- [Stoodley2013] Catherine J. Stoodley, John E. Desmond, and Jeremy D. Schmahmann. Functional topography of the human cerebellum revealed by functional neuroimaging studies. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 735–764, 1 2013. doi:10.1007/978-94-007-1333-8_30.
- [Stoodley2016] Catherine J. Stoodley and Catherine Limperopoulos. Structure–function relationships in the developing cerebellum: evidence from early-life cerebellar injury and neurodevelopmental disorders. *Seminars in Fetal and Neonatal Medicine*, 21:356–364, 10 2016. doi:10.1016/j.siny.2016.04.010.
- [Stoodley2018] Catherine J. Stoodley and Jeremy D. Schmahmann. Functional topography of the human cerebellum. *Handbook of Clinical Neurology*, 154:59–70, 1 2018. doi:10.1016/B978-0-444-63956-1.00004-7.
- [Stoodley2012] Catherine J. Stoodley, Eve M. Valera, and Jeremy D. Schmahmann. Functional topography of the cerebellum for motor and cognitive tasks: an fmri study. *NeuroImage*, 59:1560–1570, 1 2012. doi:10.1016/j.neuroimage.2011.08.065.
- [Strata2009] P. Strata, W. T. Thach, and O. P. Ottersen. New insights in cerebellar function. *Neuroscience*, 162:545–548, 9 2009. doi:10.1016/j.neuroscience.2009.06.047.
- [Strick2009] Peter L. Strick, Richard P. Dum, and Julie A. Fiez. Cerebellum and nonmotor function. *Annual Review of Neuroscience*, 32:413–434, 6 2009. doi:10.1146/annurev.neuro.31.060407.125606.
- [Sultan2003] Fahad Sultan and Detlef Heck. Detection of sequences in the cerebellar cortex: numerical estimate of the possible number of tidal-wave inducing sequences represented. *Journal of Physiology Paris*, 97:591–600, 7 2003. doi:10.1016/j.jphysparis.2004.01.016.

- [Sun2016] Zong Peng Sun, Shabtai Barash, and Peter Thier. The role of the cerebellum in optimizing saccades. *The Neuronal Codes of the Cerebellum*, pages 173–196, 2016. doi:10.1016/B978-0-12-801386-1.00008-3.
- [Suvrathan2016] Aparna Suvrathan, Hannah L. Payne, and Jennifer L. Raymond. Timing rules for synaptic plasticity matched to behavioral function. *Neuron*, 92:959–967, 12 2016. doi:10.1016/j.neuron.2016.10.022.
- [Szapiro2009] G. Szapiro and B. Barbour. Parasynaptic signalling by fast neurotransmitters: the cerebellar cortex. *Neuroscience*, 162:644–655, 9 2009. doi:10.1016/j.neuroscience.2009.03.077.
- [Takamuku2015] Shinya Takamuku and Hiroaki Gomi. What you feel is what you see: inverse dynamics estimation underlies the resistive sensation of a delayed cursor. *Proceedings of the Royal Society B: Biological Sci*ences, 7 2015. doi:10.1098/rspb.2015.0864.
- [Tanaka2020] Hirokazu Tanaka, Takahiro Ishikawa, Jongho Lee, and Shinji Kakei. The cerebro-cerebellum as a locus of forward model: a review. *Frontiers in Systems Neuroscience*, 4 2020. doi:10.3389/fnsys.2020.00019.
- [Taylor2014] Jordan A. Taylor and Richard B. Ivry. Cerebellar and prefrontal cortex contributions to adaptation, strategies, and reinforcement learning. *Progress in Brain Research*, 210:217–253, 2014. doi:10.1016/B978-0-444-63356-9.00009-1.
- [Thier1988] P Thier, W Koehler, and U W Buettner. Experimental brain research neuronal activity in the dorsolateral pontine nucleus of the alert monkey modulated by visual stimuli and eye movements. *Exp Brain Res*, 70:496–512, 1988.
- [Thompson2009] R. F. Thompson and J. E. Steinmetz. The role of the cerebellum in classical conditioning of discrete behavioral responses. *Neuroscience*, 162:732–755, 9 2009. doi:10.1016/j.neuroscience.2009.01.041.
- [Timmann2009] D. Timmann, J. Konczak, W. Ilg, O. Donchin, J. Hermsdörfer, E. R. Gizewski, and B. Schoch. Current advances in lesion-symptom mapping of the human cerebellum. *Neuroscience*, 162:836–851, 9 2009. doi:10.1016/j.neuroscience.2009.01.040.
- [Timmann2013] Dagmar Timmann, Michael Küuper, Elke R. Gizewski, Beate Schoch, and Opher Donchin. Lesionsymptom mapping of the human cerebellum. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1627–1656, 1 2013. doi:10.1007/978-94-007-1333-8_72.
- [Tomasch1969] Joseph Tomasch. The numerical capacity of the human cortico-ponto-cerebellar system*. *Brain Research*, 13:476–484, 1969.
- [Tseng2007] Ya Weng Tseng, Jörn Diedrichsen, John W. Krakauer, Reza Shadmehr, and Amy J. Bastian. Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *Journal of Neurophysiology*, 98:54–62, 7 2007. doi:10.1152/jn.00266.2007.
- [Ugolini1986] G Ugolini and H G J M Kuypers. Collaterals of corticospinal and pyramidal fibres to the pontine grey demonstrated by a new application of the fluorescent fibre labelling technique. *Brain Research*, 365:211–227, 1986.
- [Uusisaari2013] Marylka Yoe Uusisaari and Thomas Knöpfel. Neurons of the deep cerebellar nuclei. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1101–1110, 1 2013. doi:10.1007/978-94-007-1333-8_46.
- [vandenBergN+4-2020] Nils S. van den Berg, Rients B. Huitema, Jacoba M. Spikman, Gert Jan Luijckx, and Edward H.F. de Haan. Impairments in emotion recognition and risk-taking behavior after isolated, cerebellar stroke. *Cerebellum*, 19:419–425, 6 2020. doi:10.1007/s12311-020-01121-x.
- [Vella2018] Alessandra Vella and Mario Mascalchi. Nuclear medicine of the cerebellum. Handbook of Clinical Neurology, 154:251–266, 1 2018. doi:10.1016/B978-0-444-63956-1.00015-1.
- [Viscomi2020] M. T. Viscomi, M. G. Leggio, and M. Molinari. Hemicerebellectomy. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1–18, 2020. doi:10.1007/978-3-319-97911-3_70-2.
- [Voogd2011] Jan Voogd. Cerebellar zones: a personal history. *Cerebellum*, 10:334–350, 9 2011. doi:10.1007/s12311-010-0221-6.

- [Voogd2018] Jan Voogd and Peter J. Koehler. Historic notes on anatomic, physiologic, and clinical research on the cerebellum. *Handbook of Clinical Neurology*, 154:3–26, 1 2018. doi:10.1016/B978-0-444-63956-1.00001-1.
- [Voogd2013] Jan Voogd, Yoshikazu Shinoda, Tom J.H. Ruigrok, and Izumi Sugihara. Cerebellar nuclei and the inferior olivary nuclei: organization and connections. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 377–436, 1 2013. doi:10.1007/978-94-007-1333-8_19.
- [Wagner2017] Mark J. Wagner, Tony Hyun Kim, Joan Savall, Mark J. Schnitzer, and Liqun Luo. Cerebellar granule cells encode the expectation of reward. *Nature*, 544:96–100, 4 2017. doi:10.1038/nature21726.
- [Wagner2020] Mark J. Wagner and Liqun Luo. Neocortex–cerebellum circuits for cognitive processing. *Trends in Neurosciences*, 43:42–54, 1 2020. doi:10.1016/j.tins.2019.11.002.
- [Wall2013] Mark J. Wall and Boris P. Klyuch. Purinergic signaling in the cerebellum. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 947–970, 1 2013. doi:10.1007/978-94-007-1333-8_40.
- [Wallisch2008] Pascal Wallisch and J. Anthony Movshon. Structure and function come unglued in the visual cortex. *Neuron*, 60:195–197, 10 2008. doi:10.1016/j.neuron.2008.10.008.
- [Watson2019] Thomas C. Watson and Richard Apps. Cerebro-cerebellar connections. *Handbook of the Cerebellum and Cerebellar Disorders*, pages 1–26, 2019. doi:10.1007/978-3-319-97911-3_48-3.
- [WolpertDM+KawatoM-1998] D M Wolpert and M Kawato. 998 special issue multiple paired forward and inverse models for motor control. *Neural Networks*, 1998.
- [Xiao2018] Le Xiao, Caroline Bornmann, Laetitia Hatstatt-Burklé, and Peter Scheiffele. Regulation of striatal cells and goal-directed behavior by cerebellar outputs. *Nature Communications*, 12 2018. doi:10.1038/s41467-018-05565-y.
- [Zang2019] Yunliang Zang and Erik De Schutter. Climbing fibers provide graded error signals in cerebellar learning. *Frontiers in Systems Neuroscience*, 9 2019. doi:10.3389/fnsys.2019.00046.
- [DeZeeuwCip5y2011] Chris I. De Zeeuw, Freek E. Hoebeek, Laurens W.J. Bosman, Martijn Schonewille, Laurens Witter, and Sebastiaan K. Koekkoek. Spatiotemporal firing patterns in the cerebellum. *Nature Reviews Neuroscience*, 12:327–344, 6 2011. doi:10.1038/nrn3011.
- [Zehl2016] Lyuba Zehl, Florent Jaillet, Adrian Stoewer, Jan Grewe, Andrey Sobolev, Thomas Wachtler, Thomas G. Brochier, Alexa Riehle, Michael Denker, and Sonja Grün. Handling metadata in a neurophysiology laboratory. *Frontiers in Neuroinformatics*, 2016. doi:10.3389/fninf.2016.00026.