

Go configure

Can PCT model the cerebellum?

Introduction.

My interest in understanding the cerebellum builds upon the proposal by Bill Powers¹ that its function is at Level 3 of the (postulated) perceptual hierarchy—specifically, configurations of body parts. We may understand this also to include the orientation and location of the body as a whole in the environment. He defined

a configuration as an invariant function of a set of sensation vectors, [with] particular computing properties common to these different input functions: They abstract invariant relationships so that the third-order signals will change only if sensation vectors on which they are based change in certain ways. (*B:CP* 122)

The cerebellum (‘little brain’ in Latin) is a very complicated place. Its unique ‘crystalline’ structure (Delgado-García 2001) is a highly repetitive matrix with complex nuances of selective excitation and inhibition. Its functions have been deduced from the effects of injuring it. Because the most obvious effects of lesions have been deficits of motor control, standard textbook descriptions still say that the

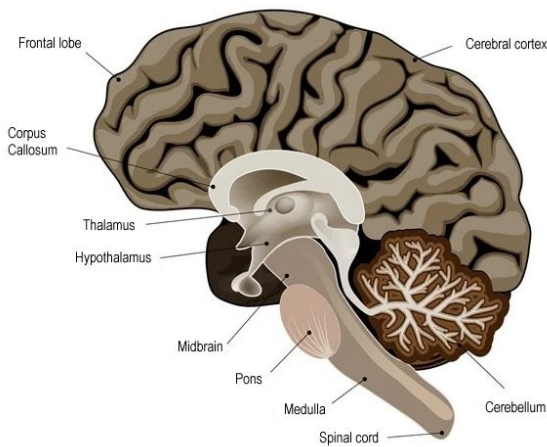


Figure 1: Location of the cerebellum

function of the cerebellum is to smooth motor control, and this was Bill’s understanding as he revised *B:CP* for publication in 1973. However, the role of the cerebellum in ‘cognitive’, emotional, and social functions has become generally accepted since about 2015.² The role of the cerebellum in learning is well established, and its involvement with limbic systems is not surprising (e.g. Blatt et al. 2021).

These diverse functions of the cerebellum are all served by a neuroanatomical organization of cells and connectivity which is invariant across all parts of the cerebellum. Whatever serves motor control, kinesthetics, and proprioception in the cerebellum also serves the higher functions. What is the cerebellum doing?

My conjecture is that the cerebellar system provides perceptual input functions and possibly reference output functions linking not only between configurations at level 3 and sensations at level 2, but also between higher adjacent pairs of levels. To my knowledge, there has been very little research into how these many-one and one-many interconnection systems are structured, beyond a mostly heuristic working-out of computational details to implement the PCT model in simulations of specific, experimentally constrained behavioral situations.

¹ See Chapter 9 of *Behavior: The control of perception (B:CP)*.

² Van Overwalle et al. (2020), Leiner et al. (1986), Barton & Venditti (2014), Rice et al. (2021). Many in the field put ‘cognitive’ in scare quotes because it is ill defined, and I accept that caveat.

If my conjecture that the cerebellum is a kind of general-purpose I/O function is wrong, then it is in some other way that the cerebellar system is implicated in such a wide range of perception and control. No matter the outcome, it behooves us to build a better understanding of the structure and function of the cerebellar system. That is the present purpose.

It seems odd to me to have to plead the case to a PCT audience that PCT researchers ought to study findings of neuroscience. PCT makes the claim that the organism is a black box and that a PCT simulation which replicates its behavior is a white box, such that the robust accuracy of the replication predicts that known control structures within the simulation correspond to control structures in the organism which are difficult to observe, or impossible by presently available means. In this way, PCT promises to provide guidance for specific lines of neuroscience research. Maybe more importantly, as an organizing framework PCT can help integrate and explain neuroscience findings. Neuroscience research and publications are almost universally way down in the weeds, and a larger context for each myopic close-up is usually framed in terms of plans and execution, with occasionally some talk of feedback and feedforward, information and (no kidding) ‘outformation’. As Bill said to Henry Yin in 2010 ([t.ly/te1X](#)), “The biggest problem here is that neuroscientists are applying their own perceptual categories to the data they are getting about the brain, and their categories were not formed out of a theory that correctly represents what the brain does and how it does it.” They are also encumbered by vocabulary assigned by early anatomists (olive, dentate nucleus, flocculus, glomurulus) which is naively descriptive rather than functional. This in turn thickens the hedge we have to work through to understand what they’re writing about. To be fair, figuring out functions is precisely the problem at hand.

Didn't Bill already model the cerebellum?

The first chapters of *Behavior: The control of perception* (Powers 1973) show some results of Bill’s efforts to fulfil this requirement to correlate the PCT model with neuroscience. Later chapters dealing with higher levels in the hierarchy are increasingly speculative, and necessarily so.

Neurophysiological understanding has advanced greatly since Powers (1973) proposed that the cerebellum controls configurations (perceptions of the third order), and sketched a circuit for motor control as control of the configurations of the body and its limbs. While suggestive, this chapter based on neuroscience of the late 1960s cannot be seriously presented to neuroscientists today without substantial revision. Within the decade after this was published it was known that the major inputs to Purkinje cells were all excitatory, the cerebral cortical signals through the parallel fibers as well as the sensory signals through the climbing fibers, so the suggestion of comparators here does not hold.³

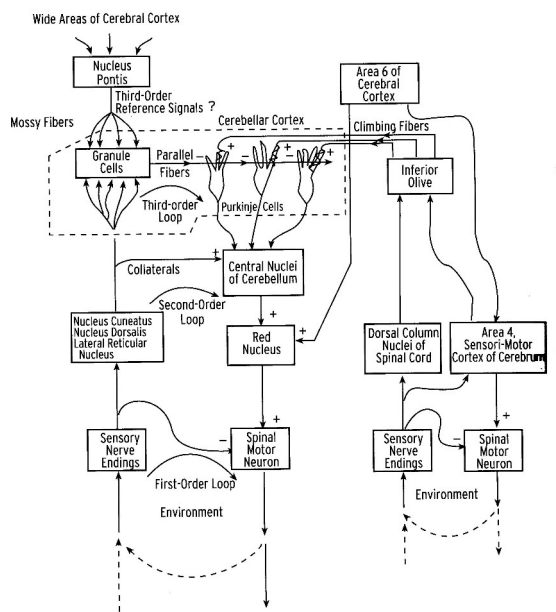


Figure 2: Bill's mapping of anatomy to control loops (B:CP fig. 9.1)

3 There are inhibitory inputs modulating these principal excitatory signals, as we shall see, and it is possible that Bill misread the literature which he cites. His main source, John Eccles, was one of three joint winners of a Nobel Prize in

Instead of random-walk (e. coli) reorganization, Bill's 'artificial cerebellum' is an implementation of the convolution theorem, a method that he was familiar with for sharpening visual images in astronomy. He used it to stabilize the control systems in the 'Little Man' simulation. In its favor (sort of), Dean et al. (2010) have advanced the notion that the cerebellum functions as an [adaptive filter](#). We will return to this at a later point.

Bill later decided that it was not his business to follow developments in neuroscience, applying his gifts instead to the PCT modeling side of the relationship and (fortunately for us) to helping others gain a grasp of PCT. One consequence, however, is that the 2005 reissue of *B:CP* was not brought up to date, and this model of cerebellar function cannot be seriously presented to neuroscientists.

Three sets of control loops for motor control

The structures and functions in the cerebellum, and in its connectivity to other parts of the brain, are increasingly well known. However, to map the cerebellar system to the control-loop block diagrams which are familiar in PCT appears to call for combinations of diagrams, and aggregate behaviors of them, which are decidedly unfamiliar. The burden of this presentation is to lay out a coherent overview of the cerebellum, pulled together from publications that too often either focus myopically or impose systemic preconceptions that are inimical to a control-theoretic analysis.

Figure 2 shows three distinct groups of control loops in the cerebellar system. Somewhat simplified, they are:

- Spinal loop: Motor control through the spinal cord via the inferior olive (IO)
- Brainstem loop: Somatic control through the brainstem
- Cerebral loop: 'Cognitive' control through the cerebral cortex via nuclei in the pons (Latin 'bridge') above the brainstem

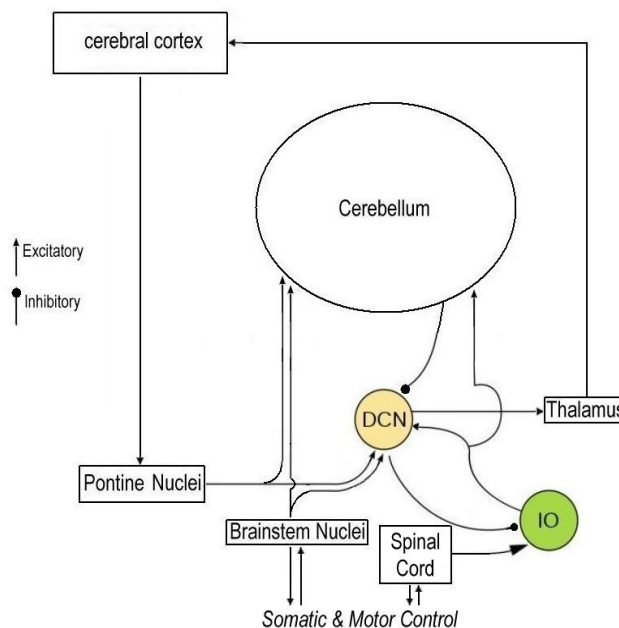


Figure 3: Three sets of control loops in the cerebellar system

Each loop passes through the deep cerebellar nuclei (DCN). These neural complexes are functionally distinct. The largest, the dentate nucleus, is devoted to the cerebral loop. Figure 2 shows that signals from each loop are copied both to the DCN and to the cerebellum.⁴

For the moment, detail of structures within the cerebellum is omitted in Figure 2. Suffice to say that the cerebellum receives copies of all of these inputs to the DCN, subjects them to considerable transformation, and returns inhibitory signals to the DCN. The only outputs of the cerebellum are from the Purkinje cells (which we will come to presently), and each such axon inhibits precisely one neuron in the DCN. I have not found detail about synapses in the DCN. These nuclei could be collections of

1963 for his finding that some synapses are inhibitory. Before the 'both are true' resolution of the 'war of the soups and the sparks' (memorialized by Valenstein 2005) Eccles championed the electrical transmission view.

4 To limit visual clutter, outputs of the DCN to the brainstem loop and spinal loop are not shown, except for the inhibitory DCN output to the IO.

comparators, one for each perceptual signal. It is possible in addition that these inhibitory signals, applied to signals of level n , leave only ‘differences that make a difference’ for a signal at level $n+1$, so that the DCN is also a collection of perceptual input functions, or the initial stages of perceptual input functions, with further processing in the thalamus and/or cerebral cortex.

Evolutionary expansion

This investigation began for me at our meeting in Manchester, when I asked Frans Plooij How he thought our brains accomplish the obvious continuation of cognitive development in humans after the entire perceptual control hierarchy is in place, at about 1.5 years of age. His answer was to point to the expansion of the cerebellum in the evolution of primates and humans.

In humans, the cerebellum is only 10% or 11% of the whole brain (whether by mass or volume), developmentally doubling from about 5% in infants,⁵ yet it has about 80% of the brain’s surface area, due to its deeply fractal surface, and comprises an estimated 80% of neurons in the whole brain.

In Figure 2, the sagittal view shows that the archaic parts of the cerebellum are the anterior lobe at the top and the inferior posterior lobe and the flocculus (Latin: ‘tuft of cotton’) at the bottom. The dorsal view in the bottom part of the figure shows that the connective vermis (Latin ‘worm’), and those portions of the two hemispheres which are closest to it, are also labeled ‘old’. These archaic parts shared with all vertebrates are devoted to kinaesthesia, balance, orientation, and motor control.

The great bulge of the superior posterior lobe, both to the rear of the skull and laterally in each hemisphere, is devoted to higher cerebral functions. It is these portions which are expanded in primates, and greatly expanded in humans.

The cerebellum is folded, like the little shrimp in the upper corner of Figure 4. Until you understand this, the relationship of the more anatomical sagittal view above to the more schematic ‘flattened’ dorsal view below may be obscure. This folding keeps the more archaic functions in the head and tail close to their connections through the pons and brainstem. Later developments did not disturb the more immediate connections that the archaic parts of the cerebellum had previously established.

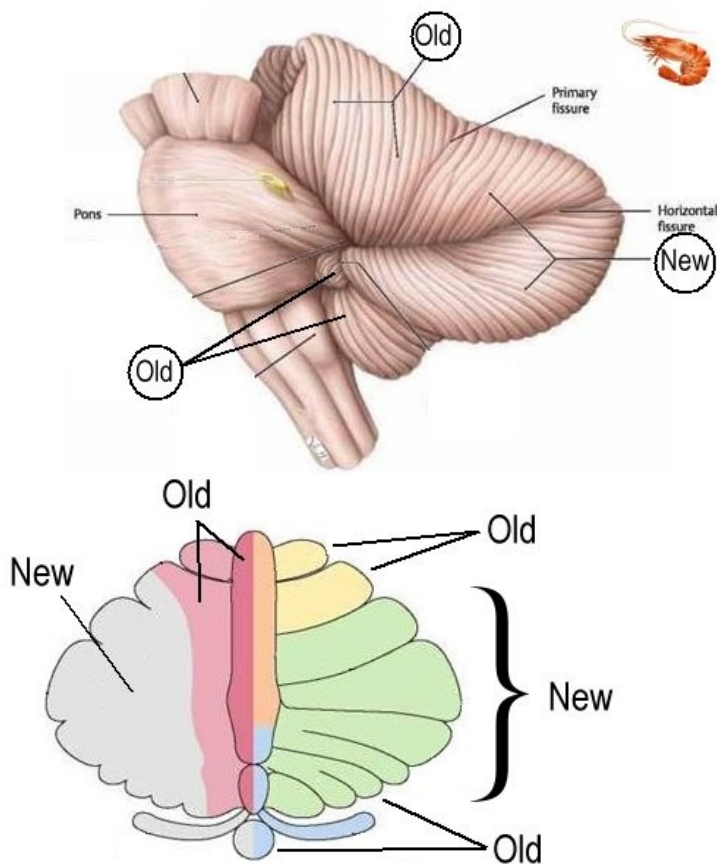


Figure 4: Evolutionary expansion of the cerebellum

⁵ Since the perceptual hierarchy is in place by about 75 weeks (17 months), it would be valuable to know the ratio at that stage, but I have not found that datum.

The unique matrix structure found in the archaic motor regions of the cerebellum is uniform throughout these evolutionary extensions. If we can understand how the neural mechanisms in those regions function in control of posture, balance, eye direction, and motor control, it should illuminate how structurally identical mechanisms in newer parts of the cerebellum serve control of diverse emotional, social, and ‘cognitive’ perceptions (Ramnani 2006). This has suggested to me the conjecture that these higher perceptions are all analogous to the configurations that we perceive to be ‘physical’ and amenable to motor control. Subjectively, ‘abstract’ configurations underlie significant gesture, music, language, and culture. (See e.g. Vandevort (2016) and discussion at t.ly/A6bz.) This could account for the role of analogy and metaphor in cognition.

Expanded levels of control

Each of the cerebral loop entities identified in Figure 4 has expanded in parallel with the cerebellum. The cerebellum is most clearly divided into functionally distinct regions. The functional anatomy of the cerebral cortex (especially the prefrontal cortex) is less well understood, and the fine internal detail of the nuclei and thalamus least.

Within the cerebellum, each Purkinje cell has one axon which inhibits precisely one neuron in the DCN. It bears repeating that these precisely targeted inhibitory signals are the only outputs of the cerebellum.

Above the spinal cord, the brainstem comprises (from bottom to top) the medulla oblongata, pons, and midbrain (Figure 6). In the pons, the pontine nuclei bring signals from the cerebral cortex to the DCN and the cerebellum. The other brainstem nuclei transform signals in autonomic and somatic control loops.

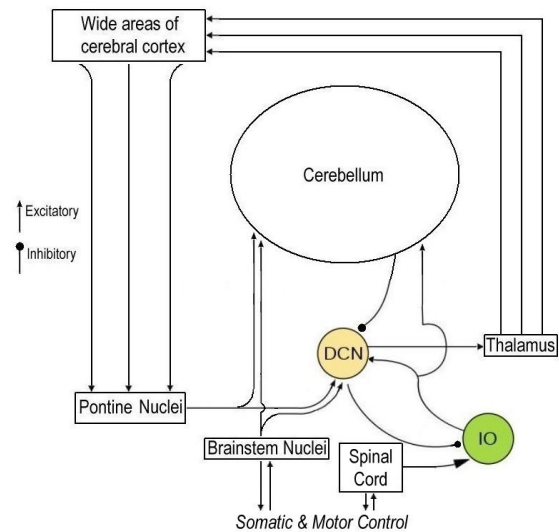


Figure 5: Additional loops through the cerebral cortex

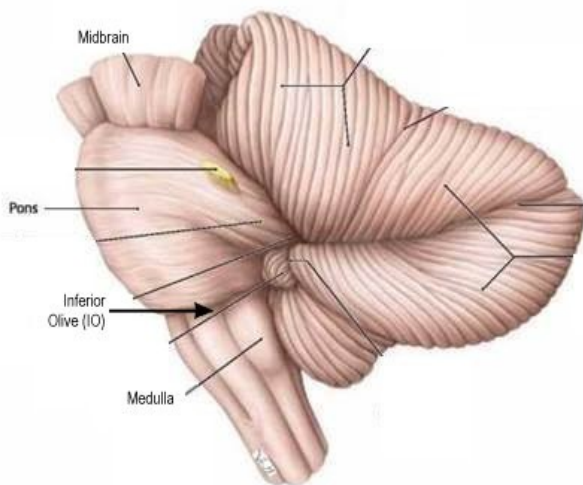
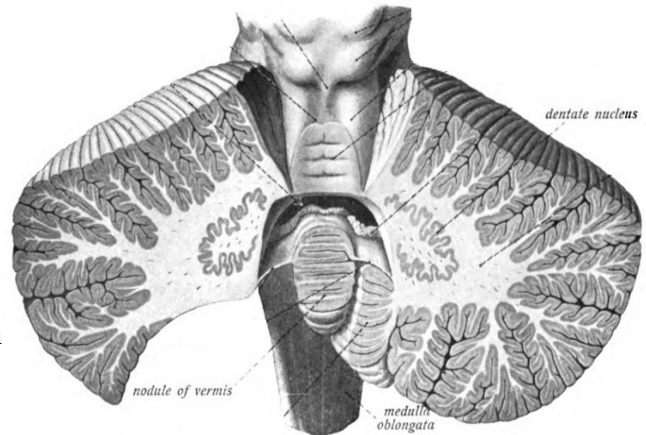


Figure 6: The brainstem, above the spinal cord, comprises the medulla, the pons, and (here truncated) the midbrain

Uniform matrix architecture

From the outside, the surface of the cerebellum presents the appearance of parallel grooves separating laminae (Latin ‘leaves’). The grooves descend deep into the cerebellum, replicating a separation into laminae along their sides (Figure 7). The arrangement is symmetrical in the two ‘hemispheres’ of the cerebellum to the left and right behind the brainstem. Joining the hemispheres at their ventral surfaces, farthest from the laminae, and connecting them to the brainstem is the vermis (Latin ‘worm’, see the lower part of Figure 4, above).



The deep cerebellar nuclei (DCN) are in the white matter between the laminae and the vermis. The largest of these, the dentate (‘toothy’) nucleus is shown in Figure 7.

Figure 7: The fractal surface of the cerebellum, and of the dentate nucleus

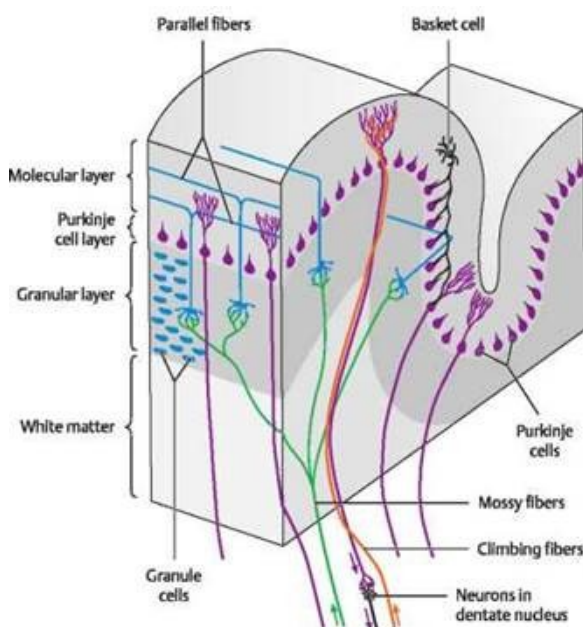


Figure 8: Internal structure of a lamina

Each lamina contains long rows of Purkinje cells linked together by parallel fibers which extend through their dendrites like telephone wires. In Figure 8, dendrites are shown with only a few Purkinje cells. Purkinje cells spread their dendrites like a tree grown espalier against a wall (Figure 9), in a plane transverse to the long axis of the lamina, so that they present a maximum number of dendrites to the parallel fibers.

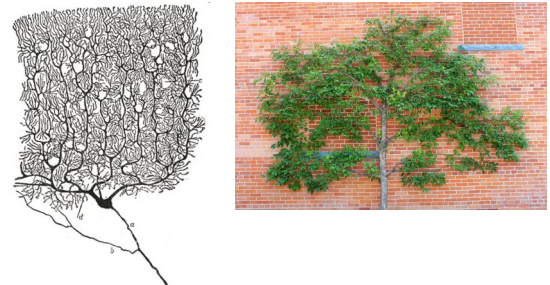


Figure 9: Dendritic tree of a Purkinje cell, flat like a tree grown espalier

‘Interneurons’ in the Purkinje layer include basket cells and (not shown in Figure 8) stellar cells.

Below the Purkinje layer, the granular layer is densely packed with tiny granule cells, the smallest and most numerous in the nervous system, which (together with certain interneurons) collectively modulate the signals from the cerebral cortex by selective inhibition. The mossy fibers (a descriptive term also used elsewhere in the brain) bring these signals from the pontine nuclei in the pons (Figure 5).

Motor and somatic signals from the spinal cord and brainstem ascend through the climbing fibers.

Inputs from the spinal cord ascend by the climbing fibers (CF), which wrap through the dendrites of Purkinje cells (PC). Each CF excites about 30,000 synapses in one PC, producing ‘complex spikes’ at a rate of about one per second. These begin with a large spike, among the strongest in the nervous system, followed by a couple of successively lesser spikes. An analogy to an earthquake and aftershocks is picturesque but may not be valid.

Mossy fibers (MF) carry cerebral signals from the pons to be modulated in the granular layer, whence arise the parallel fibers (PF). These bifurcate in the Purkinje layer, extending in opposite directions along the length of a lamina. Each PF excites about 150,000 PCs, making about 175,000 synapses on each PC, at a rate of about 50 to 100 ‘simple spikes’ per second. The parallel fibers are unmyelinated. Myelin functions as electrical insulation, so fibers close to one another may synchronize by ephaptic communication (electrical transmission without synapses).

The axons of Purkinje cells are the only outputs of the cerebellum.

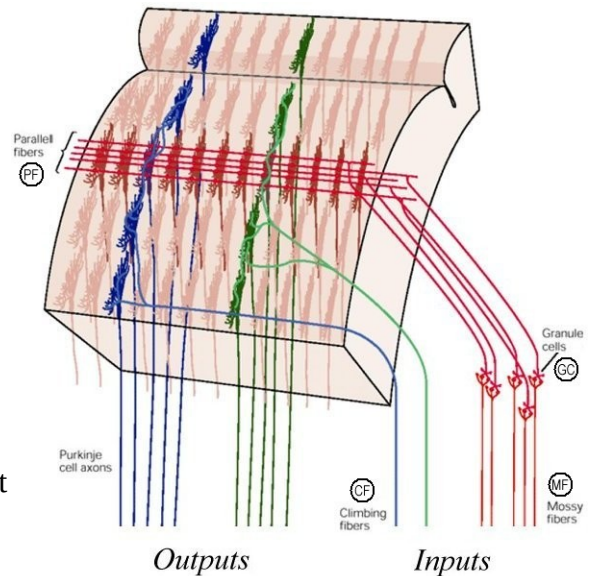


Figure 10: Purkinje cell inputs and outputs

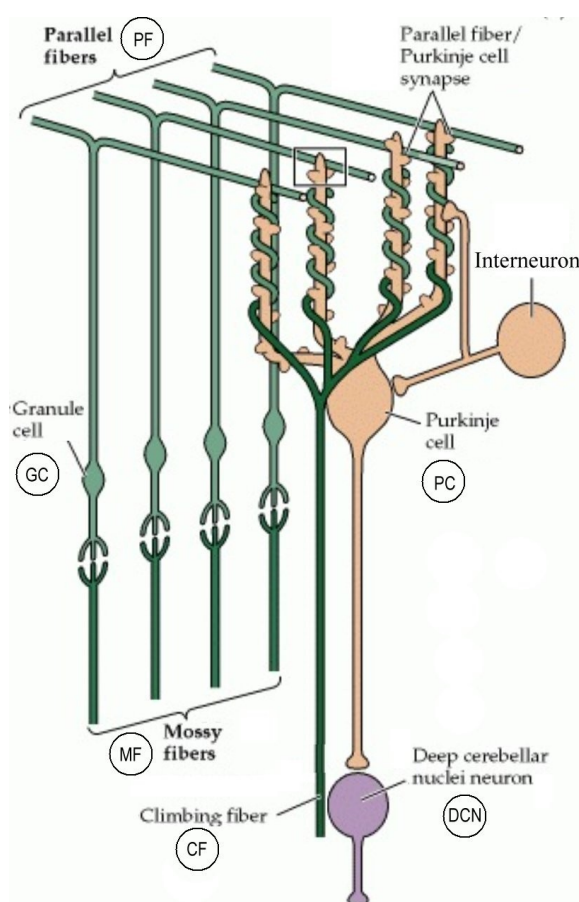


Figure 11: Schematic view of Purkinje cell (PC) inputs and outputs

In Figure 10 we can begin to discern the matrix structure of the cerebellum. Figure 11 shows these connections in a more schematic way.

The parallel fibers lay out one dimension of the matrix, along the length of the laminae. Each lamina is functionally distinct from its neighbors. Within the lobes shown in Figures 4 and 6 above, anatomists conventionally divide the cerebellum into ten functionally distinct lobules or zones comprising parallel groups of laminae. These are suggested by the interior groupings of laminae shown in Figure 7, but I have not included an illustration of them as such.

The granular layer imposes functionally distinct ‘stripes’ crossing the laminae and lobules at right angles to the parallel fibers (Holloway & Lerner 2019). These appear to be implicated especially in learning processes. They provide obvious avenues for analogical parallels between motor, kinesthetic, and ‘cognitive’ kinds of perceptual control. Mastery of control of one kind apparently serves as a scaffold to support gaining control of another kind.

Interneurons and learning

In the Purkinje layer, interneurons receive input from multiple parallel fibers and inhibit specific Purkinje cells.

- A basket cell (BC) receives input from multiple parallel fibers and inhibits one Purkinje cell by synapsing directly on the soma.
- A stellate cell (SC) receives input from multiple parallel fibers and inhibits some of the parallel fiber excitation of one Purkinje cell by synapsing within its dendritic tree.

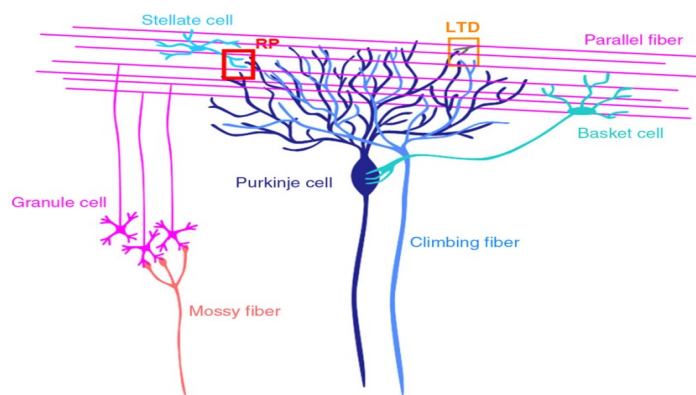


Figure 13: basket cells and stellate cells (Hirano1 & Kawaguchi 2014)

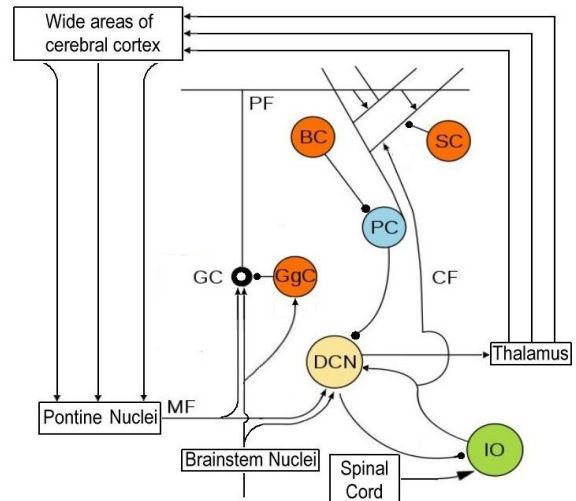


Figure 12: Interneurons are instrumental in learning

These interneurons are instrumental in two cellular mechanisms of learning in which the state of Purkinje cell synapses is stabilized.

- Long-term depression (LTP) follows from repeated strong activation of parallel fibers (PF) and climbing fibers (CF) together. Purkinje cell synapses become less responsive to (excitatory) glutamate.
- Rebound potentiation (RP) is a long-lasting potentiation of GABAergic (i.e. inhibitory) synaptic transmission induced by postsynaptic depolarization.

The output of a given PC through its axon inhibits a specific neuron in the DCN. Inhibiting a particular Purkinje cell therefore enables the specific loop signal in that neuron to pass through the DCN uninhibited.

On the input side of the PCs, each Golgi cell (GgC) inhibits about a thousand granule cells (GC) in the granular layer, so that the MF & PF inputs to those GCs proceed uninhibited to PCs in the Purkinje layer.

Implications

It is remarkable and highly suggestive that the ‘cognitive’, emotional, and social functions of the cerebellum are served by evolutionarily recent anatomical extensions of the very same arrangements of neurological structures that serve motor control.⁶ These expansions may be seen in mammalian evolution, more pronouncedly in primates, and greatly so in humans (see e.g. MacLeod et al. 2003). Because so great a proportion of the relevant research is not on primates and humans, but rather on monkeys, cats, rats, and mice (among others) direct experimental data on these aspects are relatively sparse, and rely mostly on relatively wide-view imaging.

Yet the unique matrix structure found in the archaic motor regions of the cerebellum is uniform throughout these evolutionary extensions. The neural mechanisms by which the cerebellum is involved in control of posture, balance, eye direction, and motor control generally also serve control of diverse emotional, social, and ‘cognitive’ perceptions. This has suggested to me the conjecture that these higher perceptions are all analogous to the configurations that we perceive to be ‘physical’ and amenable to motor control. Progressively more and more ‘abstract’ configurations underlie significant gesture, dance, music, language, and culture.⁷

In the cerebellar system, the deep cerebellar nuclei (DCN) look something like collections of comparators, where each inhibitory signal from a Purkinje cell is subtracted from the excitatory signal traversing one of the three loops that pass through the DCN.

However, that assumes that the relation of signals is simply 1-1, an inhibitory signal affecting a corresponding perceptual signal in the loop. We do not know how much branching there may be, how much copying of signals within the essentially unmapped complexity of the DCN (and of the other nuclei and the thalamus). And we do know that complex patterns of inhibition are jostled into form in the even more obscure complexities of the granular layer.

In addition to (or instead of) what may seem an obvious comparator function, the DCN may provide a stage in transforming many signals at one perceptual level to one signal at another, inhibiting irrelevant detail. And if

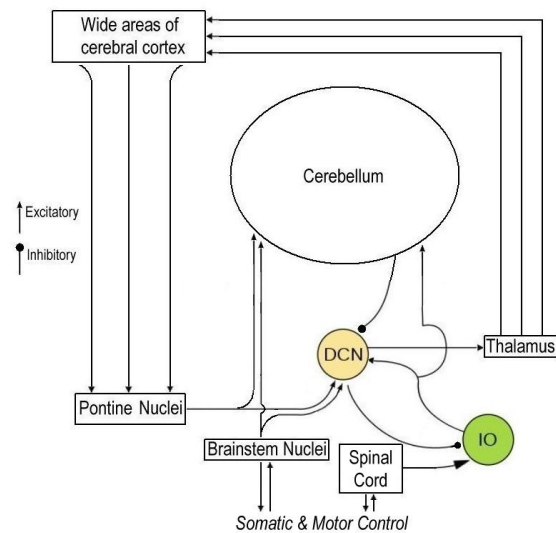
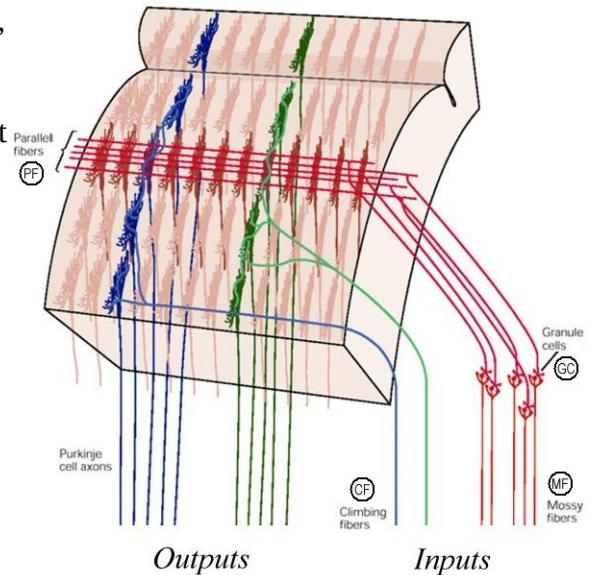


Figure 14: Are the deep cerebellar nuclei (DCN) collections of comparators? Or PIF functions transforming between levels?

6 See e.g. Ramnani (2006), van Essen et al. (2018).

7 See e.g. Vandevort (2016), Taylor (forthcoming), and discussion at t.ly/A6bz.

it can do that, it could also transform an error signal into many reference signals sent to the brainstem and spinal cord.

The learning mechanisms in the cerebellum would then be much more general than learning routine motor behavior. (Cerebellar control of motor intentions is thought to be too slow.)

Conjectures

The ‘traditional’ conjecture is that the cerebellum stabilizes motor control. This is inferred from the effects of lesions. Bill showed how impairment of configuration control should result in the observed gestural impairments.

A conjecture that is currently popular among neuroscientists is that the cerebellum learns routine stereotyped behavior, and that this is important because planning and executing behaviors from the cerebellum is too slow. One possible (unstated?) basis for this is a misinterpretation of the slowness of ‘conscious control’ while learning vs. the speed of practiced control after it is well integrated into the hierarchy (M. Taylor, forthcoming). Apparently, there is too little awareness of failures to implement and test model of plan-and-execute vs the successes of cascading hierarchical control in the HPCT model.

Bill’s conjecture was that the cerebellum performs pattern recognition to create perceptions at the configuration level. It “abstracts invariant relations among lower-level signals.” He assumed that a higher value (faster rate of neural firing) corresponds to ‘more of’ the given configuration, in some sense: ‘more of’ the bend-in-the-elbow relation or ‘more of’ a head-turn relation, where the configuration itself is ‘invariant’ through these lower-level changes. A configuration is invariantly *that configuration* while it undergoes rotation, translation, is partly obscured, and perhaps even while it undergoes some limited topological transformations. (Note in passing that this is categorial.)

When we consider that inhibitory cerebellar (PC axon) signals synapse originate from signals in the loop and make inhibitory synapses with copies of those loop signals suggests that the DCN may contain collections of comparators. If the signals passing through the DCN are already configuration signals, then this is consistent with identifying the cerebellum with configuration control. However, the constructing of configuration signals would have to happen prior to entry into the DCN, and it would have to happen severally in the three different loops that pass through the DCN. The notion that the DCN contain comparators is incompatible with Bill’s conjecture.

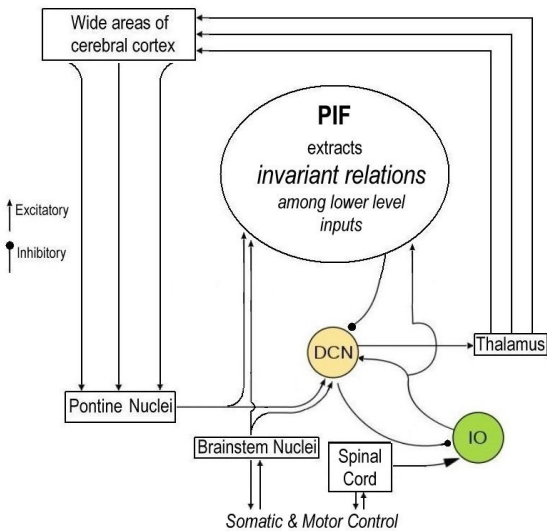


Figure 15: Transforming signals between levels

My conjecture is that the cerebellar system began life, in evolutionary terms and to a degree in developmental terms, as a system of neural functions that transform sensation signals into configuration signals. Subsequently, this same extremely flexible system, with its capacity for reorganization and learning, became employed to transform configuration signals into higher-level atemporal perceptual signals. (For ‘atemporal’ see the digression about transitions in the Appendix.) It became a generalized perceptual input function (PIF), or the primary stage of one: it is now recognized that the thalamus provides more than ‘relays’ that transmit signals from the DCN to the cerebral cortex.

At each transition between levels, up to the category level (if that is required), a pattern-recognition function that “extracts invariant relations among lower level inputs” suffices to create signals for those ‘invariant relations’, which thereupon are constituted as signals at the next level up. Relationships are particular ‘invariant relations’ among configurations. Categories are complex relationships among entities which are perceptually disparate, in the sense that not all need be configurations, or none.

Table 1: Transformations between atemporal levels

Enter DCN (2x)	Exit Thalamus
Sensations	→ Configuration
Configurations	→ Relationship
Relationships	→ Category
Imagined configurations, relationships, etc. → Abstract concepts	
Concepts	→ Principles
Principles	→ System concepts

The cerebellar system provides a capacity for analogy which enables control of imagined perceptions for which environmental input is lacking. These ‘mental concepts’ can be juxtaposed, inverted, assembled (synthesized) into more complex mental objects, disassembled (analyzed), and so on. Invariant (complex) relations extracted from them are perceived as principles, among which invariant (complex) relations are perceived as system concepts.

This accords with the observed facts of species evolution and individual development. Especially, it accounts for the continuation of cognitive development after the System Concept level has emerged in the child at about 75 weeks, and it admits that further cognitive development is open ended for individuals and for our species, to the degree that we choose to participate.

The development of higher levels of the hierarchy, and the existence of reference values at the top of the hierarchy without infinite regress of levels, is usually attributed in the HPCT model to control of intrinsic variables by the reorganization system. First, we now can recognize that the cerebellum is very good at reorganizing. Secondly, collective control strongly influences the formation of perceptual input

functions and the learning of viable reference values for them. The effects of collective control are patently manifest within a family, in a community, and (increasingly in today's world) more widely. These influences are strongest and most difficult to resist the higher we go in the hierarchy, but they can reach even to lower levels.

Appendix: A digression about transitions

I have used the word ‘atemporal’ to exempt events and transitions, which seem to be perceptions of relationship between a current perception and prior values of that perception stored in short-term memory. Memory is stored at every synapse. Learning mechanisms in the cerebellum involve longer-term memory (see the discussion of LTP and RP in reference to Figure 12). Longer-term consolidation of memory is generally understood to involve the hippocampus and related regions of the brain which are not shown in the figures in this paper.

The bending of an arm is variation in the ‘amount’ of the elbow configuration, resulting in a transition perception even as the configuration perception remains ‘invariant’. The invariant configuration signal p_c has sensation inputs $\{p_s \dots p_s\}$ which may change through time. While e.g. that arm flexes, is the transition perception of flexing a *varying* relationship between the present values of some inputs in the set $\{p_s \dots p_s\}$ and prior values of those inputs?

Bill elaborated this conceptual apparatus of ‘the amount of’ a configuration in context of motor control involving one degree of freedom. How well does it apply to recognizing a visual shape from different angles or as it changes its orientation, with more than one degree of freedom?

Such questions are beyond the scope of this paper. I introduce them only to explain the omission of ‘temporal’ perceptions in Table 1 and the associated discussion.

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