

# The Cerebellum and Cognitive Function: 25 Years of Insight from Anatomy and Neuroimaging

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Twenty-five years ago the first human functional neuroimaging studies of cognition discovered a surprising response in the cerebellum that could not be attributed to motor demands. This controversial observation challenged the well-entrenched view that the cerebellum solely contributes to the planning and execution of movement. Recurring neuroimaging findings combined with key insights from anatomy and case studies of neurological patients motivated a reconsideration of the traditional model of cerebellar organization and function. The majority of the human cerebellum maps to cerebral association networks in an orderly manner that includes a mirroring of the prominent cerebral asymmetries for language and attention. These findings inspire exploration of the cerebellum's contributions to a diverse array of functional domains and neuropsychiatric disorders.

A shift in the understanding of the cerebellum has taken place over the past 25 years. The majority of the human cerebellum is associated with cerebral networks involved in cognition, which is an astonishing finding given that, until quite recently, the cerebellum was thought to contribute primarily to the planning and execution of movements (Strick et al., 2009; Schmahmann, 2010; Leiner, 2010). The focus on motor function arose early in the 19<sup>th</sup> century following careful observations in animal models of cerebellar damage (Ito, 1984). The cerebellum's anatomical positioning atop the spinal cord and deficits observed in neurological patients led Charles Sherrington (1906) to refer to the cerebellum as the "head ganglion of the proprioceptive system." Despite sporadic findings supporting a more general role of the cerebellum in nonmotor functions, often conducted by eminent neurophysiologists (Schmahmann, 1997), the overwhelming emphasis of the literature did not waiver from focus on motor control. The motor emphasis was partly driven by a peculiar feature of cerebrocerebellar circuitry that has prevented traditional anatomical techniques from discovering the cerebellum's full organizational properties (Figure 1).

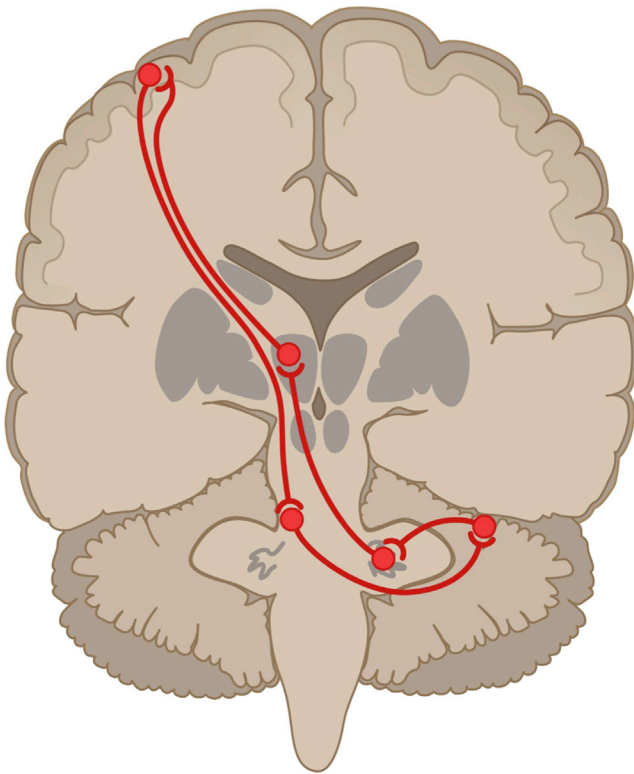
The cerebellum is interconnected with the contralateral cerebrum primarily through two polysynaptic circuits—an input channel that synapses in the pons and then crosses to the cerebellum and an output channel that projects first to the deep cerebellar nuclei, then to the thalamus, and finally to the cerebral cortex (Evarts and Thach, 1969; Kemp and Powell, 1971; Strick, 1985; Schmahmann and Pandya, 1997a). This polysynaptic circuitry is a major contributor to the controversy surrounding the organization of the cerebellum. Because there are no monosynaptic projections between the cerebral cortex and the cerebellum, the organization of the cerebellum could not be unraveled using conventional anterograde and retrograde tracing techniques that do not cross the synapse. Foundational questions including whether portions of the cerebellum map to

domains of the cortex involved in nonmotor function were left unanswered. In the absence of clear anatomical evidence that the cerebellum projects to nonmotor structures and the emphasis on motor deficits in clinical settings, early influential models of the cerebellum focused exclusively on motor function (e.g., Evarts and Thach, 1969). The past 25 years have witnessed a major revision in our understanding of the cerebellum.

## Emergence of a New Perspective

Discoveries beginning in the 1980s set the stage for reframing the role of the cerebellum in cognition. The initial impetus was an incisive review by the interdisciplinary team of Henrietta Leiner, Alan Leiner, and Robert Dow. Leiner et al. (1986) (see also Leiner et al., 1989, 1993) summarized extensive evidence to suggest that the human cerebellum contains regions linked to cerebral association areas. Their review, which initially met resistance (Leiner, 2010), was based on the observation that the lateral output nucleus of the cerebellum (the dentate) is expanded in apes and humans relative to other species. The expansion is accounted for by preferential of the newer ventrolateral portion of the dentate and, by their estimates, occurred in parallel with expansion of prefrontal cortex. By comparing the topography of the dentatohthalamic and thalamocortical projections, they deduced that the output channel from the cerebellum contains substantial projections to cerebral association areas including those within the prefrontal cortex. Foreshadowing research to appear over the next several decades, they further suggested that human neuroimaging methods could be used to confirm their hypothesis.

Human neuroimaging techniques emerged in the mid-1980s as a revolutionary tool to indirectly map brain function in humans (Raichle, 1987). Early studies were conducted using positron emission tomography (PET). fMRI first appeared in the early 1990s (Kwong et al., 1992; Ogawa et al., 1992) and became



**Figure 1. The Cerebrotocerebellar Circuit**

The cerebellum possesses complex connectivity with multiple subcortical structures including vestibular nuclei and the basal ganglia. The focus of this review is on circuits connecting the cerebellum to the cerebral cortex. A schematic diagram depicts the major input and output cerebrotocerebellar circuits. Input projections from the cerebral cortex first synapse on the ipsilateral pons and then cross to the contralateral cerebellar cortex. Output projections first synapse on the dentate then cross to synapse in the contralateral thalamus and finally project to the cerebral cortex. Because there are no monosynaptic connections between the cerebral cortex and the cerebellum, conventional tract tracing techniques have been unable to map the relationship between the cortex and its projection zones in the cerebellum.

widely available within a few years. PET and fMRI both measure brain activity indirectly through the coupling of neuronal activity to increases in blood flow, often called the hemodynamic response. The approaches are frustratingly indirect, causing uncertainty about the neuronal origins of the recorded signals (Heeger and Ress, 2002; Logothetis, 2008; Kim and Ogawa, 2012). Despite this limitation, the approaches are powerful because brain activity can be surveyed in living individuals performing cognitive tasks. Critically, many studies broadly survey activity across the full brain (or nearly so) including the cerebellum because the field of view is large compared to other invasive physiological techniques. The ability of neuroimaging to survey regional responses in the cerebellum led to an unexpected discovery when human neuroimaging was first directed toward the study of cognition.

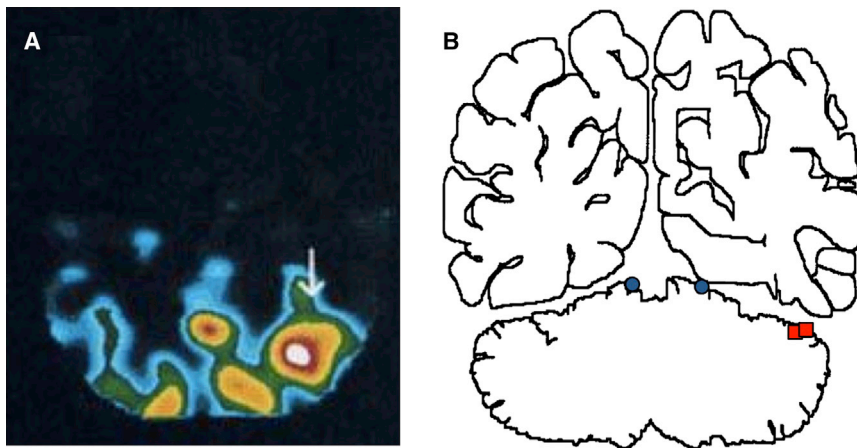
In 1988, Petersen and colleagues published a landmark paper on the functional anatomy of single-word processing (Petersen et al., 1988; see also Petersen et al., 1989). Their strategy was simple: measure brain function using PET while people viewed words and engaged in progressively more elaborate tasks. At

the most basic task level, participants passively viewed the words (e.g., nouns like *cake*, *dog*, and *tree*). A second-level task evoked motor control demands by asking the participants to read the words aloud. At the most demanding level, the participants generated action verbs that were meaningfully related to the words (e.g., *eat*, *walk*, and *climb*). It was this last condition that yielded an extraordinary result. When participants generated words, a robust response was observed in the right lateral cerebellum (Figure 2). The response was distinct from the expected motor response present in the anterior lobe of the cerebellum, leading the authors to conclude that “The different response locale from cerebellar motor activation and the presence of the activation to the generate use subtractions argue for a ‘cognitive,’ rather than a sensory or motor computation being related to this activation” (Petersen et al., 1989). The right lateralization in the cerebellum was consistent with strong responses in the left cerebral association regions presumably activated by the controlled semantic processing demands of the task.

Anchoring from this initial observation, a number of studies soon found that the “cognitive” cerebellar response could be attenuated by keeping the motor response demands constant but automating the task (Raichle et al., 1994) and modified by making features of the cognitive demands easier (Desmond et al., 1998). An early high-resolution fMRI study further revealed that the dentate, the output nucleus of the cerebellum, could be activated by cognitive processing—in this case, completion of a puzzle (Kim et al., 1994). Directly motivated by the neuroimaging findings, Fiez et al. (1992) conducted a detailed assessment of the cognitive capabilities of a patient with cerebellar damage and found evidence of deficits further fueling interest. The nature of the tasks used in these initial studies—in particular the requirement to generate action verbs to presented nouns—lent the findings to alternative interpretations, including the possibility that motor imagery was a critical component of the tasks. However, the growing availability of human functional neuroimaging using fMRI quickly produced a large number of cerebellar activations to many domains of cognitive tasks, leaving little doubt that the origins of the responses were nonmotor. Two recent meta-analyses capture the current state of the field, so I will not recount the results here (Stoodley and Schmahmann, 2009a; Keren-Happuch et al., 2012; see also Stoodley, 2012). It is sufficient to note that, without setting out to do so, the vast community of researchers conducting functional human neuroimaging studies generated compelling evidence that the human cerebellum responds to cognitive task demands.

### Anatomical Breakthroughs

The recurring observation that the cerebellum is active during cognitive tasks remained an enigma for many years because there was still widespread belief that the cerebellum predominantly influenced motor areas. Recall that cerebrotocerebellar circuits are polysynaptic and therefore cannot be delineated with conventional tract tracing techniques. The seminal review of Leiner et al. (1986) suggesting a role for the cerebellum in cognition was based on indirect arguments and therefore open to alternative interpretations. What was required to solidify a revision in thinking about the cerebellum’s contribution to nonmotor function was direct anatomical evidence.



**Figure 2. PET Activation of the Cerebellum during a Cognitive Task**

(A) A transverse section displays a robust PET activation of the right lateral cerebellum (arrow) while subjects generated verbs to nouns in one of the first human neuroimaging studies of cognition. The response was present when the motor demands of the task, evoked by simple word reading, were subtracted.

(B) A summary diagram from the original publication highlights the “cognitive” cerebellar response (shown by red squares). The location of the cognitive cerebellar response was anatomically distinct from the motor zones (shown by blue circles). Adapted with permission from Petersen et al. (1989).

Two bodies of anatomical work in the monkey met this challenge—one body of work from Jeremy Schmahmann and colleagues and the other from Peter Strick and colleagues. The development of sensitive anterograde tracing methods made it possible to inject specific cerebral areas and determine whether their projections terminate in the pons. The presence of pontine-labeled neurons indicates that cerebrocerebellar input to the cerebellum exists without specifying where the projections terminate within the cerebellar cortex. Using anterograde tracing techniques, Schmahmann and Pandya (1989, 1991, 1997b) demonstrated that specific regions of prefrontal cortex linked to cognitive networks project to the cerebellum. Prior studies using retrograde tracers had noted widespread cerebral input but relatively modest involvement of prefrontal areas typically associated with cognitive function (e.g., Glickstein et al., 1985). However, the clear observation of anatomic input to the cerebellum from multiple prefrontal regions left open the possibility that cerebrocerebellar circuits form a type of anatomical siphon: the cerebellum might integrate incoming information from widespread cortical regions via the pons but then project exclusively to motor areas.

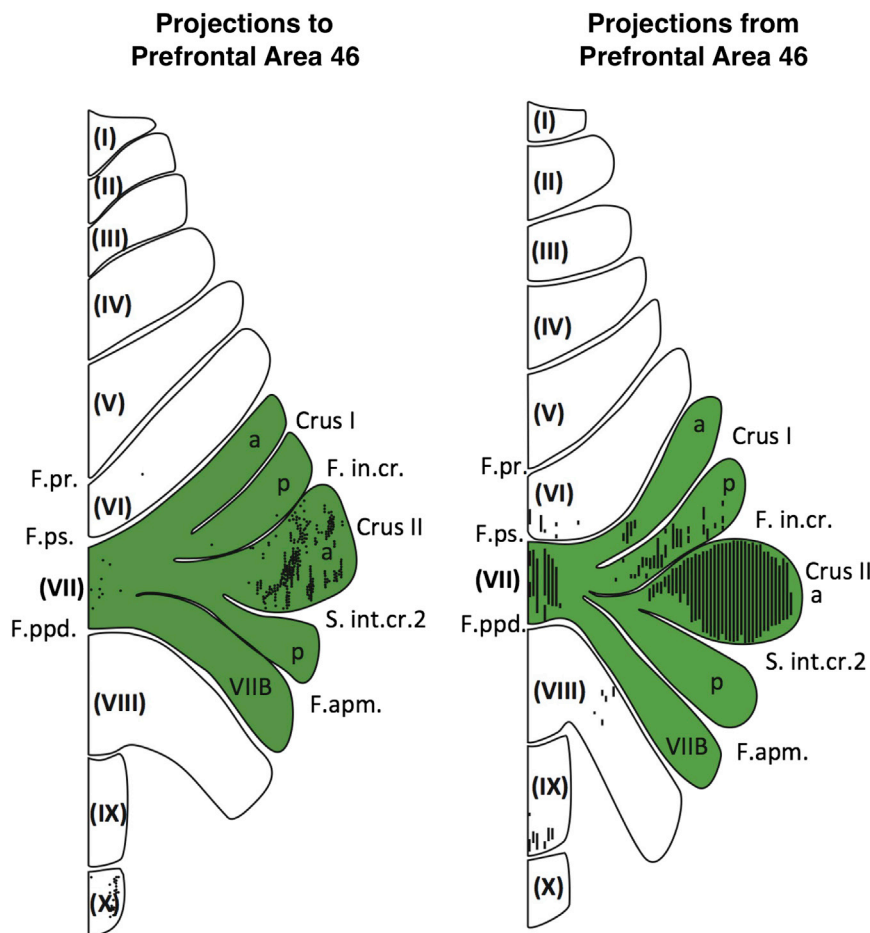
Strick and colleagues resolved the issue by using transneuronal tracing to observe both input and output projections between the cerebellum and cerebral association cortex (Middleton and Strick, 1994, 2001; Kelly and Strick, 2003; see Bostan et al., 2013 for review). Transneuronal tracing techniques use viruses that spread across synapses to map polysynaptic circuits, thereby overcoming the limitations of traditional tracing techniques. Middleton and Strick (1994, 2001) first used transneuronal retrograde tracing to show that prefrontal areas receive projections from the dentate (output) nucleus. Further advances in viral tracing techniques provided a means to explore how cerebellar input and output is organized (e.g., Kelly and Strick, 2003). Critically, they discovered that a large region near Crus I and Crus II both sends and receives projections from prefrontal cortex area 46, forming a closed-loop circuit (Figure 3). The cerebellar region participating in prefrontal circuitry was nonoverlapping with distinct cerebellar regions that formed motor circuits.

These collective observations reveal an anatomical substrate for contributions of the cerebellum to cognition. Despite earlier assumptions, the cerebellum receives and sends information to nonmotor cortical regions including prefrontal areas involved

in higher cognition. The topographic relationship between the cerebellar motor zones and the newly discovered association zones provides an interesting clue to the broader organization of the cerebellum. The cerebellar association zones in Crus I/II fall between motor zones of the anterior and posterior lobes that possess mirrored motor maps. The cerebellum’s motor topography was first described by British physiologist Edgar Adrian, who stimulated the cerebral motor areas and recorded cerebellar discharges (Adrian, 1943). He discovered an inverted somatomotor representation in the anterior lobe of the cerebellum (Figure 4A). The hind-limb (foot) was represented within the central lobule (HIII) and the fore-limb (hand) in adjacent lobule HIV. Snider and Stowell (1944) made a similar observation in the cat but additionally observed a second, upright body map in the posterior lobe. The transneuronal viral tracing results of Strick and colleagues suggest that the cerebellar regions connected to association cortex fall between the mirrored motor representations. An open question is whether there are multiple cerebellar representations of cerebral association areas within the in-between zone and, if so, whether they possess a mirrored topography that parallels the motor representations. Comprehensive mapping of the human cerebellum using neuroimaging approaches answered this question and revealed a simple topography that connects the long-known motor representations to the newly discovered cerebellar association zones.

### Mapping the Human Cerebellum

The anatomical work reviewed above demonstrates that major portions of the cerebellum are connected to cerebral association regions. The transneuronal viral tracing results further reveal that extensive cerebellar association zones fall in between the primary and secondary motor maps. But how are the association zones and motor zones related? And is there a parsimonious principle that explains the global topography of cerebrocerebellar circuits? A surprisingly powerful approach able to comprehensively map the organization of cerebellar cortex in the human has recently provided insight into these two questions. The approach derives from the observation that brain organization can be inferred by measuring spontaneous low-frequency fluctuations in intrinsic activity (Biswal et al., 1995; for review see Fox and Raichle, 2007).



**Figure 3. Input-Output Organization of Cerebellar Loops Revealed by Transneuronal Anatomical Tracing**

(Left) Purkinje cells that send output to prefrontal area 46 are displayed. These neurons were labeled using retrograde transport of a modified rabies virus injected into area 46.

(Right) Granule cells that receive input from prefrontal area 46 are displayed. These neurons were labeled using anterograde transport of a HSV1 virus strain injected into area 46. The shaded green region illustrates the zone of Crus I/II that forms a closed-loop circuit with prefrontal cortex. The topography of the projections is specific and distinct from the motor zones. Adapted with permission from Bostan et al. (2013).

2009; Krienen and Buckner 2009; O'Reilly et al., 2010; Lu et al., 2011; Bernard et al., 2012; Kipping et al., 2013).

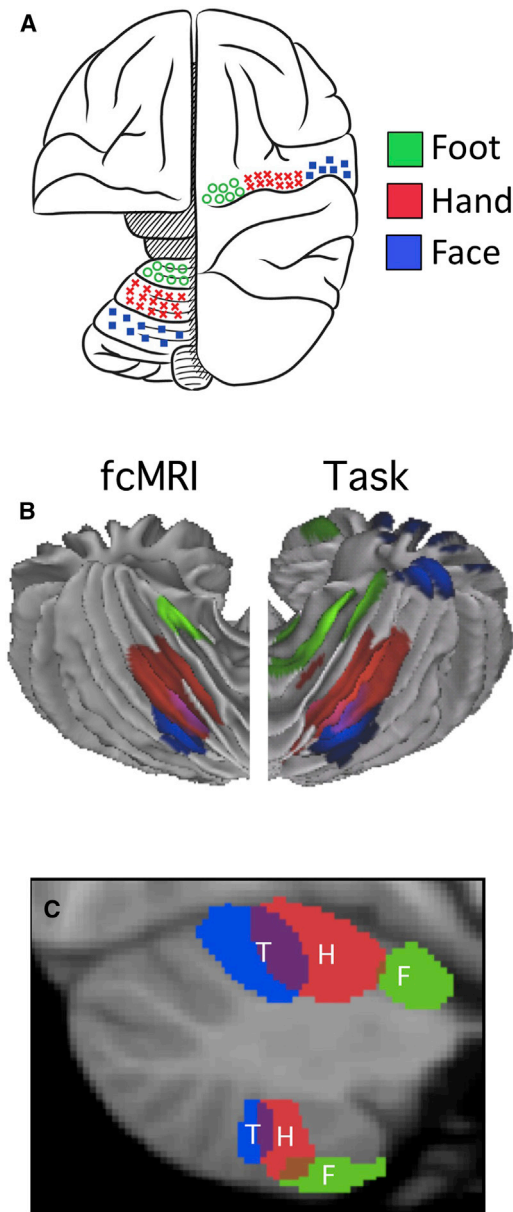
The usefulness of the approach can be appreciated by examining motor topography in the cerebellum, which, as described above, is well established from studies in the cat and monkey (Adrian, 1943; Snider and Stowell, 1944) and also from neuroimaging studies of active movements in the human (Nitschke et al., 1996; Rijntjes et al., 1999; Grodd et al., 2001). In a particularly detailed exploration of human motor topography using actual motor movements, Grodd et al. (2001) found that the body maps in the human cerebellum converge closely with the monkey in

When individuals are imaged at rest in an MRI scanner there is a tremendous amount of spontaneous activity that exhibits spatial and temporal structure. Marcus Raichle notes that the brain's energy budget is directed more toward these spontaneous activity events than toward activity changes transiently evoked by the immediate task at hand (Raichle, 2011). The precise physiological origin of the slow fluctuations is presently unclear but several lines of evidence suggest that, while there are multiple determinants of the spontaneous activity fluctuations, regions that show monosynaptic or polysynaptic connections tend to fluctuate together (Leopold and Maier, 2012; Buckner et al., 2013; Hutchison et al., 2013). This means that anatomically connected regions can be inferred, with many caveats, by measuring correlations among brain regions (for discussion of caveats as they pertain to mapping the cerebellum, see Buckner et al., 2011). In a seminal proof-of-concept, Biswal and colleagues (1995) demonstrated that fluctuations in primary motor cortex measured while subjects rested were correlated with the contralateral motor cortex and midline motor regions. While this initial study surveyed only a small portion of the brain that did not include the cerebellum, later work subsequently showed that correlated fluctuations can be detected between the cerebral cortex and the cerebellum with preferential coupling to the contralateral cerebellum (Allen et al., 2005; Habas et al.,

both the anterior and posterior lobes (see also Wiestler et al., 2011). Critically, studies using intrinsic functional coupling also detect both the inverted body representation in the anterior lobe and the upright body representation in the posterior lobe (Buckner et al., 2011; Figures 4B and 4C). The responses are strongly lateralized as expected with the left cerebrum preferentially coupled to the right cerebellum and can be detected in individual participants as well as group-averaged data (Krienen and Buckner, 2009). Demonstrating that the functional coupling depends on intact anatomical connectivity, patients with focal infarcts to the hemispheres, which disconnect the cerebrum from the contralateral cerebellum, display selectively disrupted functional coupling between the cerebrum and contralateral cerebellum (Lu et al., 2011). These results suggest that measures of intrinsic functional coupling reveal details of cerebellar organization with a high degree of precision.

What maps to the extensive zones between the cerebral motor representations in the human? Three independent studies examining coupling with cerebral association cortex, including prefrontal regions, all demonstrated that extensive portions of the cerebellum map to association cortex (Habas et al., 2009; Krienen and Buckner, 2009; O'Reilly et al., 2010). For example, Habas et al. (2009) showed that major portions of Crus I/II are linked to association networks involved with executive control.





**Figure 4. Somatomotor Topography of the Cerebellum**

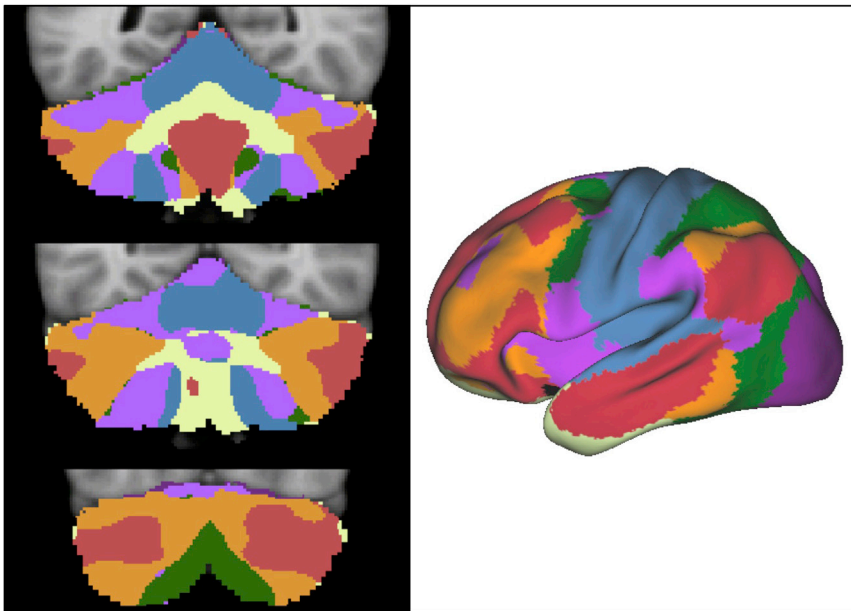
(A) The cerebral (right) and cerebellar (left) locations of the foot (green), hand (red), and face (blue) representation are shown for the monkey. Adapted from [Adrian \(1943\)](#). Note that the body representation in the cerebellum is inverted (meaning the feet are anterior and the face is posterior).  
(B) Cerebellar locations of the foot, hand, and tongue representation in the human measured by fMRI. In the left cerebellar hemisphere, labeled fMRI, results based on intrinsic functional connectivity are displayed. In the right cerebellar hemisphere, labeled Task, results based on actual foot (green), hand (red), and tongue (blue) movements are displayed.  
(C) Cerebellar locations of the foot (F), hand (H), and tongue (T) representations from fMRI are shown in a sagittal section. This view demonstrates the anterior lobe (top) and posterior lobe (bottom) somatomotor representations. Note that they are mirror images of one another—the anterior lobe representation is inverted, while the posterior lobe representation is upright. In addition to informing motor topography, these findings illustrate that the human cerebellum can be mapped using functional connectivity. Further details of these data are illustrated in [Figures 5 and 6](#), which comprehensively map association zones of the cerebellum. Adapted from [Buckner et al. \(2011\)](#).

Given that association cortex is disproportionately expanded in humans relative to monkeys and apes ([Preuss, 2004](#); [Van Essen and Dierker, 2007](#); [Hill et al., 2010](#); [Sherwood et al., 2012](#)), it is possible that a majority of the human cerebellum is connected to association cortex. To explore this possibility in greater detail, [Buckner et al. \(2011\)](#) used an approach to comprehensively map the cerebellum. In a group of 1,000 individuals, each voxel within the cerebellum, which represents 2 blurred cubic mm of tissue volume, was mapped to its most strongly associated cortical network. Three findings resulted from this winner-take-all approach.

First, the majority of the human cerebellum falling between the anterior and posterior motor representations maps to cerebral association networks ([Figure 5](#)). Second, with a few notable exceptions, the proportion of the cerebellum dedicated to a cerebral network was about as large as the extent of that network in the cerebrum. That is, cerebral networks that are large display coupling to correspondingly large cerebellar territories. Thus, the cerebellum, at least insofar as representation of the cerebrum is concerned, displays a roughly homotopic representation of the full cerebral mantle. The few notable exceptions include the primary visual and auditory cortex, which are not represented within the cerebellum of the human. Finally, cerebral association networks displayed multiple anterior and posterior representations in the cerebellum paralleling the long-established double representation of the body motor map. This last finding is particularly revealing as it suggests that there may be parsimony to the overall organization of the cerebellum.

Viewing the organization of the cerebellum in the sagittal (side view) plane suggests one possible broad organizing principle ([Figure 6](#)). The anterior lobe motor representation, which is inverted with respect to body orientation (foot, hand, tongue), is sequentially followed by representations of premotor networks, association networks related to executive control, and then finally the limbic-association network, sometimes called the default network. At Crus I/II the entire sequential ordering reverses and progresses through the cerebellum with a flipped representation ending with the upright body map (tongue, hand, foot). Thus, the major cerebellar representation of the cerebral cortex may comprise two maps (and possibly a smaller third map) of the cortical mantle oriented as mirror images of each another. The established body maps in the anterior and posterior lobes may be continuous with cortical association maps.

A final interesting property of cerebellar organization that has been revealed by human neuroimaging concerns its asymmetry. Asymmetry here refers to the relative dominance of one hemisphere over the other hemisphere for a specific network or function, not simply that the cerebrum projects preferentially to the contralateral cerebellum. As noted above, the “cognitive” response first noted by [Petersen et al. \(1989\)](#) was right lateralized in the cerebellum consistent with the left dominance of language. Meta-analysis of task responses in the cerebellum indicates strong asymmetry as expected from notions of cerebral lateralization (e.g., [Stoodley and Schmahmann, 2009a](#)). In a recent exploration of functional coupling, [Wang et al. \(2013\)](#) reported that the asymmetrically organized networks in the cerebral cortex, meaning functional coupling on one side of the brain is stronger than the other, show a parallel but reversed asymmetry in the



**Figure 5. The Majority of the Human Cerebellum Maps to Association Cortex**

Multiple coronal sections are displayed through various levels of the cerebellum. The colored parcellation of the cerebellum represents the most strongly functionally coupled networks of the cerebral cortex (illustrated on right). The blue cerebellar region corresponds to cerebral somatomotor cortex. Note that the cerebellum possesses regions in the anterior and posterior lobes strongly coupled to the somatomotor cortex as expected (see Figure 4). However, most of the human cerebellum is linked to cerebral association networks including an executive control network (shown in orange) and the default network (shown in red). Also note that the association networks each have multiple representations in the cerebellum. Similar maps have been converged upon by multiple, independent studies.

cerebellum. These functional asymmetries were preferential for association as compared to sensorimotor networks and varied across individuals in a predictable manner. Those individuals displaying the strongest cerebral functional asymmetries also possessed the strongest cerebellar asymmetries. By all measures the cerebellum appears to possess a roughly homotopic map of the cerebral cortex including its asymmetrical functional organization.

### The Unsolved Mysteries of Origin and Function

A striking feature of the cerebellum is the beautifully regular and simple cellular organization that is repeated across its cortex (Ito, 1984; Ramnani, 2006). The progress in mapping the topography of the cerebellum suggests that the cerebellum is functionally heterogeneous because the repeating cerebellar modules (microcomplexes) process distinct information dependent upon the location of the cortical input. The prevailing view, based partly on the uniformity of the cerebellar cortex, is that the processing contribution the cerebellum performs on inputs from motor areas generalizes to inputs from association cortex (see Schmahmann [1991] for an early articulation of this idea).

For example, Ito (2008) suggested that the cerebellum's contribution to cognitive function parallels its role in the control of movement (Ito, 1984). Within this theory, the cerebellum forms an internal model through repeated performance and feedback. As a movement is repeated, the cerebellum allows the movement to be executed skillfully without dynamic feedback. Analogous processes are postulated to support the skillful execution of mental acts. Prefrontal control of cognitive objects—the mental models that represent imagined scenes and constructed thoughts—are operated upon by feedback mechanisms and internal models supported by the cerebellum. A similar evolution of ideas is present in the proposal of Thach (1998, 2007), who suggested that a postulated role of the cerebellum in coordinating and temporally synchronizing multimuscle movements

might find a parallel whereby the cerebellum links cognitive units of thought.

Motivated by behavioral disturbances in patients with cerebellar abnormalities, Jeremy Schmahmann was among the

earliest modern proponents for a role of the cerebellum in nonmotor functions including neuropsychiatric illness (e.g., Schmahmann, 1991). He hypothesized, “It may also transpire that in the same way as the cerebellum regulates the rate, force, rhythm, and accuracy of movements, so may it regulate the speed, capacity, consistency, and appropriateness of mental or cognitive processes,” further noting “the overshoot and inability in the motor system to check parameters of movement may thus be equated, in the cognitive realm, with a mismatch between reality and perceived reality, and the erratic attempts to correct the errors of thought or behavior. Hence, perhaps, a dysmetria of thought.” The concept of dysmetria of thought has been expanded considerably in recent years with observations of patients with cerebellar abnormalities (e.g., Schmahmann and Sherman, 1998; Tavano et al., 2007; Schmahmann, 2010) and psychosis (e.g., Andreasen et al., 1998).

Despite these ideas and other examples of cognitive impairments in patients with cerebellar lesions (e.g., Fiez et al., 1992; Grafman et al., 1992; Courchesne et al., 1994; Stoodley and Schmahmann, 2009b; see also Tomlinson et al., 2013), there remains a general belief among neurologists that cerebellar lesions do not typically produce marked cognitive impairment, at least as contrasted to the severe motor disturbances that are obvious. It is difficult to know where the gap lies between clinical impressions and the impairments that have now been documented in several studies. One possibility is that clinicians are not testing appropriately for cognitive and affective disturbances in patients with cerebellar damage. Another possibility is that, in the end, the cognitive deficits are relatively subtle even in many cases of large cerebellar lesions. Several explorations of deficits in patients with cerebellar lesions have found minimal cognitive impairment (e.g., Helmuth et al., 1997). This raises an interesting paradox: how can the majority of the human cerebellum be linked to cerebral association networks important to cognition yet the deficits following cerebellar



damage be so subtle as to be missed by many clinicians and traditional tests of function?

Evolution of brain structures is powerfully limited by rules of embryonic development, birth orders of neurons, and size scaling relations among brain regions. In considering the large size of the cerebellum in primates and humans, adaptive arguments have been put forward in the context of motor function leaning on the dexterous hands of primates and consequences of full bipedalism in humans (e.g., [Holmes, 1939](#); [Glickstein, 2007](#)) or, in the context of cognitive function, the extraordinary mental abilities of apes and humans ([Leiner et al., 1986](#)). These notions assume that there has been direct selection for an increase in the size of the cerebellum. An alternative is that the selection has been for an overall increase in brain size and the cerebellum comes along as a byproduct.

One possibility is that an ancient ancestor may have possessed a small cortex largely devoted to sensory-motor functions with pervasive connectivity between the cerebral cortex and the cerebellum. That general circuit organization may have carried forward with relatively little modification into the primate lineage and later into the hominin lineage, leading to the large cerebellum and organization that we see today in our brains (Buckner and Krienen, 2013). I do not think this is likely to be the complete explanation for the large cerebellar association zones or even the major part of the explanation, but this alternative is a reminder that all possibilities should be considered as we further explore the functional role of the cerebellum in cognition.

Twenty-five years of discovery have converged to suggest that the majority of the human cerebellum is connected to cerebral association networks. The revelation that the cerebellum possesses prominent association zones has far-reaching implications for how we explore its function and also view mental disturbances that arise from network disruptions. The recognition of the cerebellum's importance to cognition is also a remarkable story of scientific discovery. Initial insights arose from the unconventional thoughts of a unique interdisciplinary team (Henrietta Leiner, Alan Leiner, and Robert Dow) and an observation made serendipitously during an early neuroimaging study of human cognition. Modern anatomical techniques were necessary to give traction to the discovery while neuroimaging techniques able to broadly survey the brain were best suited to reveal a parsimonious map that connects the motor zones of the cerebellum to the newly discovered association zones.



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