

Neuroimaging studies of the cerebellum: language, learning and memory

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During the decade following a functional neuroimaging study of language that showed cerebellar involvement in a cognitive task, PET and fMRI studies have continued to provide evidence that the role of the cerebellum extends beyond that of motor control and that this structure contributes in some way to cognitive operations. In this review, we describe neuroimaging evidence for cerebellar involvement in working memory, implicit and explicit learning and memory, and language, and we discuss some of the problems and limitations faced by researchers who use neuroimaging to investigate cerebellar function. We also raise a set of outstanding questions that need to be addressed through further neuroimaging and behavioral experiments before differing functional accounts of cerebellar involvement in cognition can be resolved.

The notion that the cerebellum is exclusively involved in motor control has been challenged by studies of cerebellar-damaged patients and by functional neuroimaging results. Although patient studies are important for understanding cerebellar function, they are not without complications and controversy. For example, positive results showing an association between cerebellar damage and cognitive deficits might reflect encroachment of pathology onto brainstem structures¹. Conversely, negative results could be due to differences in the location of cerebellar damage. For example, Ivry *et al.*² have shown a dissociation between medial and lateral cerebellar lesions on timing perception and performance in cerebellar patients.

An additional approach for correlating structure and function is through functional brain imaging methods. Measures of brain activation from positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have enhanced our understanding of brain-behavior relationships. Interpreted in conjunction with patient studies, functional imaging can provide a powerful tool for understanding the anatomical substrates for specific behavioral phenomena. For example, the types of tasks that elicit changes in cerebellar functional activation and the locations of these changes can serve as hypotheses regarding the types of computations the cerebellum is performing and where in the cerebellum they are being performed; these hypotheses can then be tested with cerebellar patient studies.

A number of functional imaging studies have reported changes in cerebellar activation during a variety of cognitive tasks (see Fig. 1), suggesting that this structure is involved in

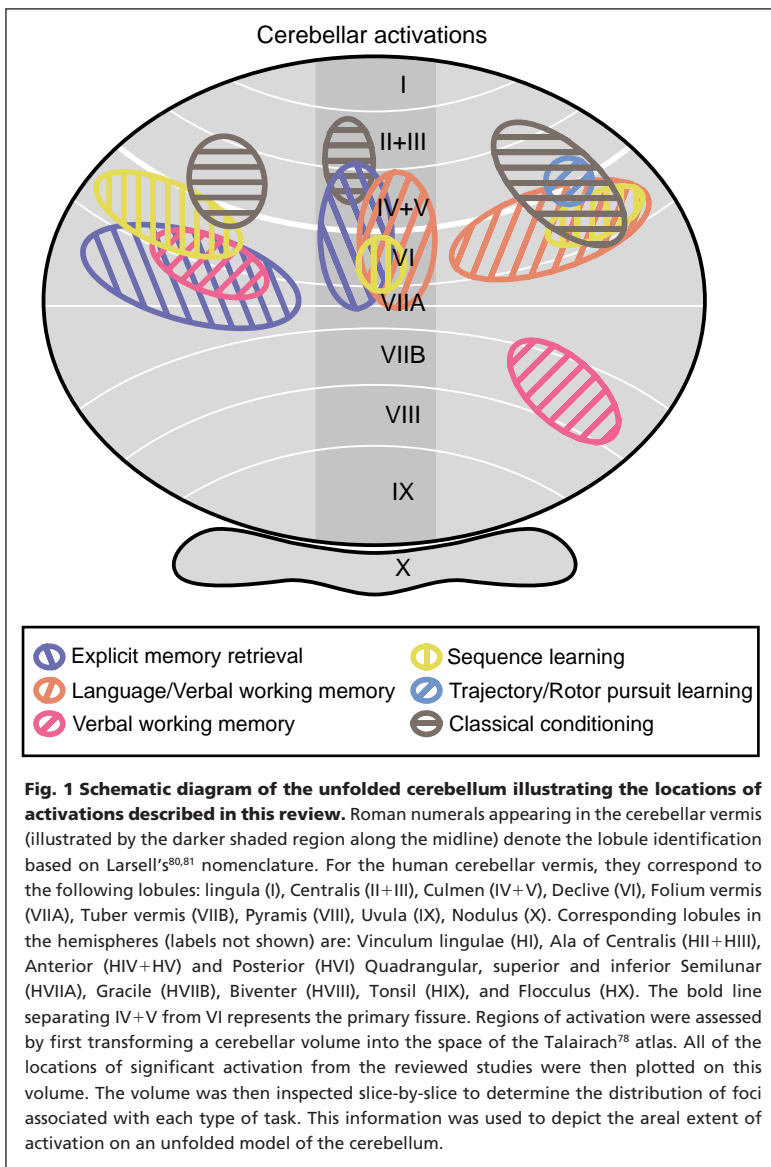
basic cognitive processes, such as working memory, implicit and explicit learning and memory, and language. Here we review functional imaging evidence for cerebellar participation in these processes. We will focus on outlining the general pattern of results and the critical issues in each topic area. We will not develop a theoretical framework to account for all of the existing results, nor will we evaluate existing theories of cerebellar contributions to cognition (for reviews of this type, see Schmahmann³ and Ivry and Fiez⁴). We will, however, review the outstanding questions that make theoretical accounts of cerebellar involvement in cognition incomplete and open to debate.

Working memory

Working memory can be broadly defined as the ability to maintain and manipulate information 'on-line.' Models of working memory have postulated that it involves a central process (the 'central executive') that operates in conjunction with rehearsal systems specialized for the maintenance of different types of information. Verbal information (letters, words, digit names) appears to be maintained using a silent rehearsal strategy that involves articulatory processes also involved in overt speech production⁵. Comparisons across neuroimaging studies of working memory reveal a set of areas that is active during verbal working memory studies, but not spatial working memory studies: left Brodmann areas 44/45 (Broca's area), the supplementary motor area (SMA), and the cerebellum (for review, see Ref. 6). This pattern of selective activation, coupled with the fact that all three areas have been associated with aspects of speech

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production, has led to numerous suggestions that they constitute at least part of the neuroanatomical substrate of verbal rehearsal (for example, see Refs 7–9).

While the neuroimaging results are in accord with the basic notion of an articulatory rehearsal system that supports the maintenance of verbal information, the results also pose challenges for the predominant model of this system. As proposed by Baddeley⁵, the rehearsal system is conceived as a continuous loop in which a covert articulatory process, modelled as a single component, serves to refresh acoustically based phonological representations. As described above, the neuroimaging evidence implicates at least three broad regions – Broca's area, the SMA and the cerebellum – in an articulatory process, and within some of these areas multiple foci of activation are often reported. It is unclear how to map the set of activated areas onto a single conceptual component, especially as converging evidence from other tasks and methodologies indicates that the different areas make distinct contributions to speech production (for review, see Fiez and Raichle⁶).

A related issue is the nature of the interactions between the areas. One possibility is that information 'loops' through

the areas, perhaps from high-level phonologically based representations in Broca's area to lower-level movement-based representations in the cerebellum and SMA, to acoustically based representations corresponding to the predicted outcome of these motor plans. If this were true, damage to any component of the loop should 'break' the loop and result in dramatic impairments in verbal working memory. However, subjects with cerebellar damage generally appear to have intact verbal working memory¹⁰, although typically it is assessed as part of a standard neuropsychological battery and not as a focus of experimental investigation. A second possibility is that the cerebellum serves to enhance working memory performance, perhaps becoming more important as the memory load increases and the need for more accurate and efficient rehearsal becomes more critical. For instance, Desmond *et al.*¹¹ hypothesized that the function of the cerebellum during verbal working memory is to compare, via distinct cerebellar subregions, the output of sub-vocal articulation with acoustically based phonological representations in a short-term store. Discrepancies between actual versus intended motor trajectories are hypothesized to result in an error-correction that would serve to maintain the integrity of the rehearsed items. A third possibility is that Broca's area and the cerebellum can independently support the maintenance of verbal information. For instance, based upon neuropsychological evidence, Cubelli and colleagues¹² hypothesized that the cerebellum contributes to an articulatory rehearsal process, whereas Broca's area might be important for recoding visual information into speech-specific articulatory representations.

A final issue is that the articulatory rehearsal system is generally assumed to be a 'slave' system to a central executive. As a consequence it is thought to be driven by a simple covert articulation task in the same way as it is by a verbal working memory task. This hypothesis was tested in three neuroimaging studies, in which subjects performed both a verbal working memory task and an articulatory rehearsal task that did not impose a significant memory load (the latter was either: silently counting from one to five repeatedly⁸, silently reading 1–6 letters¹¹, or silently repeat a single letter⁷). In all cases, greater cerebellar activation was found in the verbal working memory task than in the silent rehearsal task. These findings reveal a complex relationship between covert articulation and articulatory rehearsal that is not accounted for by current models of verbal working memory.

Implicit learning and memory

The term 'implicit' is applied to learning when experience-dependent changes in performance do not require the subject to recollect the circumstances under which improvement occurred¹³. This form of learning and memory is thought to be independent of medial temporal/hippocampal structures and includes phenomena such as classical conditioning, motor skill learning, and priming¹⁴. Given the devastating effects that cerebellar damage can have on motor behavior, the cerebellum has long been suspected as a possible site for motor learning, although this is still a matter of controversy.

One difficulty in using functional imaging to investigate learning is the challenge of separating learning from

performance changes. For example, as a subject learns to finger-press keys in a repeating sequence (a skill that would be acquired when learning to play the piano), reaction times tend to decrease and the subject tends to make more finger movements per unit time. Greater functional activation in the cerebellum following learning could be due to learning or to the fact that there is more movement. Conversely, in a joystick-controlled trajectory-tracking task, a reduction of movement occurs as the subject acquires greater skill in moving a cursor toward a target. Decreases in functional activation could reflect learning or an overall reduction in movement. In some cases this problem can be addressed by pacing movements so that the overall number of movements remains constant across conditions.

A second difficulty is that non-specific order effects can contaminate measurements of learning. That is, if activation is obtained initially during a naive state and is then obtained later during a learned state, global or regional activation drifts upward or downward could lead to erroneous conclusions of learning-related increases or decreases in activation. This problem can be addressed by taking multiple measurements of a neutral (or resting) condition before and after learning to insure that no such nonspecific changes have occurred.

Classical eyeblink conditioning

Although eyeblink conditioning might seem far removed from human cognition, the mechanisms for simple forms of associative learning might generalize to associations between words or between concepts, and thus could be relevant to human cognitive processes. Lesion evidence from both animals and humans have demonstrated that cerebellar circuitry is essential for eyeblink conditioning^{15–22}. Given that lesions of nucleus interpositus have the most detrimental effect on classically conditioned responding¹⁸, it is perhaps surprising that in four PET studies of eyeblink conditioning^{23–26} only one has reported changes in deep nuclear activation for conditioning relative to pseudoconditioning training²³. Whether the paucity of activation reflects possible limitations in imaging resolution on the one hand, or complex firing patterns of deep nuclear neurons that attenuate measurable changes in blood flow on the other hand, is unknown. Cerebellar cortical activation was observed, and consistent with rabbit lesion literature, most of these were superior activations in the vicinity of HVI (see Fig. 1). Two studies reported decreased activation for conditioning relative to pseudoconditioning^{24,25}, one study reported both increases and decreases in different portions of the hemisphere²³, and one reported only increases²⁶. As will be described below, the discrepancy in results for the latter study might be due to the fact that training occurred over days rather than in a single session.

Motor skill learning

Three types of tasks have been used to investigate possible cerebellar contributions to motor skill learning. The first two, rotor pursuit learning and trajectory tasks, require learning sensorimotor coordination. The third type of task, sequence learning, can be performed either with or without visual input.

(1) *Rotor pursuit learning*: in the rotor pursuit task, the subject tries to keep the tip of a stylus on a target located on the edge of a rotating disk. Learning is measured by the duration of time the stylus is kept on the target. Grafton *et al.*²⁷ found that during early acquisition, right anterior superior portions of cerebellar cortex exhibited increased activation during later compared to earlier periods of training. However, the cerebellum was not activated at all after extended performance of the task, suggesting a net decrease in activation after learning had reached an asymptote.

(2) *Trajectory learning*: trajectory tasks require sensory-guided hand/arm manipulation of a tracking device with the goal of following a defined path or reaching a specific target. For example, Shadmehr and Holcomb²⁸ observed increased activation in right anterior superior cerebellar cortex after subjects learned to track a target by moving a robot arm under visual guidance. The increase in activation required a period of consolidation of 5.5 hours, and occurred while total movement remained constant. In contrast to these results, other studies have observed decreased activation in well-trained subjects relative to early learning conditions. Seitz *et al.*²⁹ measured cerebral blood flow while subjects learned to draw novel two-dimensional ideograms on a digitizer pad. Interestingly, the right dentate nucleus showed the greatest increase relative to a resting baseline condition when first learning to draw a new ideogram. Movement velocity was lowest during this phase of learning. Dentate activation was sharply lower when subjects were asked to draw a familiar ideogram (the letter 'r') very accurately. Similar results were found in a study by Flament *et al.*³⁰, in which subjects manipulated a joystick to guide a cursor to a target under standard (normal tracking) and reversed (cursor moves in direction opposite to imposed joystick motion) conditions. A wide distribution of cerebellar cortical activation (relative to a resting baseline) was observed initially during the reversed condition. As performance improved, the extent and magnitude of the activation decreased. Finally, Petersen *et al.*³¹ observed decreased activation in left cerebellar cortex as subjects learned a maze-tracing task, which consisted of tactile guidance of a digitizing pen through cut-out cardboard designs. Left cerebellar change was observed regardless of which hand was used to trace through the maze, and learning-dependent changes appeared to be unrelated to differences in movement velocity.

(3) *Sequence learning*: sequence learning has been studied by a number of investigators under a variety of conditions, but all required subjects to perform a sequence of motor responses using one or more fingers. Early investigations of this task employed sequences of finger-to-thumb movements of the right hand^{32,33}. Subsequent studies have used sequences of key or touch-pad presses paced by an auditory or visual cue^{34–36}, with learning assessed by the decrease in reaction time from cue onset to finger press. In most cases, decreases in activation have been observed bilaterally in superior cerebellar cortex and deep nuclear regions as subjects' performance improved. However, a different conclusion was reached by Doyon *et al.*³⁶ who observed increased activation in the right dentate nucleus during highly-learned relative to newly-learned sequences.

Table 1. Studies of implicit learning and memory in the cerebellum

Study	Visually-guided movement	Explicit instructions or error feedback	Consolidation hours to days	Activation change from new learning to well-learned	Net movement change from new learning to well-learned
Classical conditioning					
Blaxton <i>et al.</i> ²³				↑↓	–
Logan <i>et al.</i> ²⁶			✓	↑	–
Molchan <i>et al.</i> ²⁴				↓	–
Schreurs <i>et al.</i> ²⁵				↓	–
Rotor pursuit learning					
Grafton <i>et al.</i> ²⁷	✓	✓	✓	↓ (a) (b)	?
Trajectory learning					
Flament <i>et al.</i> ³⁰	✓	✓		↓	↓
Petersen <i>et al.</i> ³¹		✓		↓	↓ (c)
Seitz <i>et al.</i> ²⁹	✓	✓		↓	↑
Shadmehr <i>et al.</i> ²⁸	✓	✓	✓	↑ (b)	–
Sequence learning					
Doyon <i>et al.</i> ³⁶	✓			↑	– (d)
Friston <i>et al.</i> ³³		✓		↓	– (d)
Jenkins <i>et al.</i> ³⁴		✓		↓ (b)	– (d)
Jueptner <i>et al.</i> ³⁵		✓		↓	– (d)
Seitz <i>et al.</i> ³²		✓		↓ (e)	↑

Abbreviations: ✓ = condition present; ↑ = increase; ↓ = decrease; – = no change

(a) increased activation was observed between the first and third trial of the new learning period

(b) order effects tested with control scans

(c) additional controls ruled out the possibility that decreased activation was due to changes in velocity or the number of error stops encountered while learning the maze

(d) finger movements were paced with auditory or visual cue to equate number of movements across conditions

(e) decrease inferred by virtue of the fact that activation remained constant despite increased frequency of movement after subjects became well-trained

Increased or decreased cerebellar activation after motor skill learning?

The different patterns of increased or decreased activation in motor skill learning could be attributable to several factors that varied across studies (see Table 1). One factor is the potential role of feedback. In the sequence learning study of Doyon *et al.*³⁶ learning occurred under completely implicit conditions; that is, subjects were unaware of the sequence and were given no feedback. In contrast, other sequence learning studies have either provided explicit training of the sequence^{32,33}, or correct/incorrect feedback signals during training^{34,35,37}. In support of this explanation, Doyon *et al.*³⁶ observed that if subjects are given explicit training on the sequence, right dentate activation is significantly lower than it is during completely implicit conditions, even though reaction times are not significantly different.

Other explanations for the discrepancies are possible, however. For example, subject proficiency at the time of scanning and differences between control conditions could be important factors. In addition, in the task used by Doyon *et al.*³⁶, subjects moved their arms and hands in order to press one of four screen locations. In contrast, the other sequence learning studies were conducted with eyes closed and used multiple finger movements. It is likely that

more sensorimotor integration was required for the Doyon *et al.*³⁶ task than the other sequence learning tasks. In the somatosensory domain, it has been shown that such integration can result in significantly more dentate activation than would occur under movement conditions alone^{38,39}.

Finally, the results of the trajectory learning study of Shadmehr and Holcomb²⁸ suggest that the degree to which consolidation occurs might also influence whether or not increased cerebellar activation occurs after learning. In this regard it is relevant to note that the only imaging study of classical eyeblink conditioning to observe only increases in cerebellar activation after learning used a training protocol that extended over days, in contrast to the typical single-session protocol²⁶. Although there are no obvious temporal factors that differ between Doyon *et al.*³⁶ and other sequence learning studies, other differences in experimental procedures might have contributed to differential rates of consolidation.

Explicit memory

Explicit memory refers to memory for specific events or experiences that can be intentionally recalled. The formation of such memories is thought to be dependent on medial temporal lobe structures^{40–43}, and thus it is not surprising that explicit memory is generally found to be unimpaired in

patients with cerebellar damage^{1,10,44–46}. However, it is possible that the cerebellum is involved in the circuitry normally invoked by explicit memory processes.

Tulving has postulated a ‘Hemispheric Encoding Retrieval Asymmetry’ (HERA) model⁴⁷ in which left prefrontal cortical regions are proposed to be involved in retrieving information from semantic memory (the latter consisting of generic factual knowledge, such as the meanings of words) and in simultaneously encoding the retrieved information into explicit memory. In support of this notion is the observation that tasks that tend to involve elaborate semantic retrieval, such as generating verbs to presented nouns^{48,49} or deciding whether a word is abstract or concrete^{50,51}, tend to produce increased activation in left prefrontal areas and lead to superior memory for those words⁵². Right prefrontal cortical regions, on the other hand, are proposed to be more involved in explicit memory retrieval.

Given the contralateral connections between cerebellar and frontal structures, including cognitive prefrontal areas⁵³, the HERA model would predict reversed cerebellar laterality for explicit encoding and retrieval processes. Imaging studies appear generally to support this prediction. As reviewed below, semantic tasks that elicit left prefrontal activation often produce increases in right cerebellar activation. Conversely, retrieval of explicit information produces, in many cases, increased activation in the left cerebellum as well as in right prefrontal structures. This phenomenon has been observed under a variety of explicit retrieval conditions, including during the recognition of previously seen⁵⁴ or heard⁵⁵ words, the recognition of previously seen faces^{56,57}, the retrieval of autobiographical information^{58,59}, the completion of three-letter stems with previously studied words^{60,61}, and the recall of words that had been paired with other words⁶². The regions of activation in these studies often involve lateral posterior portions of cerebellar cortex (see Fig. 1). Right frontal lobe areas that are often simultaneously activated include Brodmann areas 9, 10, 45, 46 and 47.

The role of the cerebellar activation in explicit memory retrieval is unknown, but it has been proposed that right frontal activation reflects the effort of retrieving, rather than the successful retrieval of information *per se*. If so, cerebellar activation might complement this operation; for example, Backman *et al.*⁶⁰ suggest that the cerebellum contributes to self-initiated retrieval. Alternatively, Cabeza *et al.*⁶² have proposed that the cerebellum could be involved in generation of ‘candidate responses’ during retrieval, a hypothesis that is similar to the one proposed by Desmond *et al.*⁶³ who observed a dissociation of right cerebellar and left frontal activation during a semantic retrieval task. In this last study, subjects completed stems that had either few or many possible completions. The right cerebellum showed greater activation when there were few possibilities, perhaps reflecting the search for a valid response, whereas left frontal areas exhibited greater activation when there were many possible completions, perhaps reflecting the selection of response (see also Ref. 64). It is possible that analogous processes of search and selection are reflected in fronto-cerebellar networks for explicit as well as semantic retrieval operations.

Language

One of the first examples of cerebellar activation during a clearly cognitive task came from a PET study of language processing reported by Petersen *et al.*⁴⁸. As part of this study, subjects were asked to think of and say aloud appropriate verbs for presented nouns. During the control scan, subjects were asked to merely read aloud or repeat auditorily presented nouns. Unexpectedly, activation of an area within the right lateral cerebellum was found when subjects generated verbs, but not when they read or repeated nouns. In addition to the cerebellar activation, a set of left-lateralized frontal cortical regions was selectively activated during the verb-generation task. This correspondence (the cerebellar hemispheres communicate with contralateral neocortex), as well as the lack of lateral cerebellar activation during simpler verbal output tasks, made it difficult to account for the cerebellar activation on a purely motor basis⁴⁸. Subsequent studies have replicated this initial finding and extended the results to include other types of generation tasks (e.g. Refs 65–67).

The verb-generation task is one of the most-cited instances of cerebellar involvement in language processing. It thus serves as a useful example of how the cerebellum might contribute to language processing (for discussion of other tasks, see Ref. 68). Unlike damage to left hemisphere perisylvian regions, damage to the cerebellum is not strongly tied to central disturbances of language and reading (acquired aphasias and dyslexias). This fact suggests that the cerebellum is not integral to the access and representation of orthographic, phonological, semantic and syntactic information, but instead that it exerts a more indirect influence.

Indirect cerebellar influences on the performance of language tasks might be best understood by highlighting the interfaces between language and other domains of cognition. Examining a language task from an alternative perspective could yield theoretical explanations applicable to both language and non-language tasks. For instance, the verb-generation task has features associated with implicit learning tasks: performance improves rapidly with practice, improvement does not depend upon conscious awareness of previous responses, and the learning is mostly item-specific^{49,69}. Similarly to the findings reported for other implicit learning tasks, the patterns of cortical and cerebellar activation associated with the verb-generation task change following practice, and cerebellar damage has also been associated with impaired learning on the task^{45,49}. The verb-generation task also has features of an explicit memory task, such as requiring the retrieval of information from semantic memory⁷⁰. As discussed in the preceding section, the cerebellum might participate in the search for valid responses from semantic memory. Potentially, this participation could form the basis for the improved performance observed with repeated exposure to the same items. Finally, the verb-generation task might have features of an articulatory rehearsal task: for instance, it has been suggested that cerebellar activation during the verb-generation task reflects the preparation of a set of potential responses, in order to facilitate rapid production of a selected response⁷¹. These prepared responses might take the form of internal articulatory

Outstanding questions

- To what extent could non-cognitive factors be affecting cerebellar activations reported in cognitive experiments? Most experiments include controls for motoric differences across conditions, but sometimes this is difficult. For instance, studies of learning might necessarily involve changes in motor output, and the difficulty of introducing electrical devices into the MRI environment might preclude monitoring for eye movements, etc. Even when overt components of movement are well-matched, other task differences can be interpreted from a motoric perspective. For instance, differences in reaction time could be interpreted as evidence for differences in motor planning.
- In cognitive operations, does the cerebellum simply mirror what is going on in neocortical structures, or does it provide a unique contribution to cognition? To the extent that neocortical and cerebellar activations can be dissociated⁶³, unique contributions of the cerebellum to cognition might be identifiable.
- Can a unified theory of cerebellar 'computation' be developed? Different investigators have theorized that cerebellar cognitive operations involve processes such as attention^{72,73}, timing⁷¹, context-response linkage⁷⁴, sensory acquisition^{38,39,75} and state estimation⁷⁶. Each of these theoretical frameworks can account for a diverse set of imaging and neuropsychological results at a qualitative level of description, giving rise to much debate about which, if any, most accurately characterize the contributions of the cerebellum. We would pose an additional question: at what level of description will a unified theory be useful? For instance, even if there is agreement that the cerebellum contributes to 'cognitive coordination,' similarly to how the frontal cortex might be viewed as important for 'executive control,' or parietal cortex for 'visuospatial processing,' where does this get us in terms of understanding the specific contributions of the cerebellum to a given task?
- Are cerebellar cognitive 'computations' fundamentally similar to those used in motor control? Interpretations of cerebellar involvement in cognition often draw upon analogies to cerebellar involvement in motor tasks. For instance, one finds discussions of motor and cognitive skill learning, motor and cognitive error detection, motor and cognitive timing, motor and cognitive coordination, and overt and covert speech production. It has been questioned whether a distinction between cognitive and motor domains is even useful, because "there is not movement without cognition, and there is not cognition without movement"⁷⁷.
- Does it make sense to treat the cerebellum as a single structure? As illustrated in Fig. 1, there is anatomical specificity in the patterns of cerebellar activation for different tasks, with some overlap between tasks. However, our current state of knowledge precludes a detailed explanation of how each area of the cerebellum uniquely contributes to cognitive function. Furthermore, it is unclear how such specificity bears upon general theoretical accounts of cerebellar function. A single theoretical account of cerebellar function that lumps together different regions might be no more informative than a single theoretical account of the cerebral cortex that seeks to explain the role of regions as diverse as primary visual cortex and dorsolateral prefrontal cortex. On the other hand, the cytoarchitectonic structure of the cerebellum is strikingly consistent, and this might indicate a singularity in function, with regional specialization arising purely from differences in afferent input.
- What is happening in the inferior cerebellum? In most imaging studies data are not acquired from the entire brain. This is because of field-of-view limitations in early generations of PET scanners, and trade-offs between the covered volume, temporal resolution, and the signal-to-noise ratio in fMRI. Coverage of the cerebellum is often deliberately limited in order to sample the cortex more completely, resulting in a sampling bias across studies for superior portions of the cerebellum. Another problem is that the stereotaxic atlas used for reporting the majority of functional imaging results⁷⁸ contains only sparse anatomical detail for the hindbrain. Recent studies have begun to address this problem through the use of cerebellar-lobular-based techniques for reporting activation¹¹ and the development of a Talairach stereotaxic atlas for the cerebellum⁷⁹.

representations that are similar to those hypothesized to support verbal rehearsal.

Conclusion

Neuroimaging studies have demonstrated that the cerebellum exhibits changes in activation during a wide variety of cognitive tasks that involve implicit and explicit learning and memory processes, working memory, and language. This somewhat surprising result is consistent with the equally surprising observations from neuropsychological studies that demonstrate cognitive impairments in cerebellar-damaged patients. This review has focused on describing the general patterns of cerebellar activation observed across different cognitive domains, but there is still considerable debate as to whether a unified theory of cerebellar function can account for these observations (see Outstanding questions). Answers to these questions will require the results from neuroimaging experiments to be integrated with what is known about cerebellar architecture, cerebro-cerebellar connectivity, and patterns of cognitive and motor deficits after cerebellar damage. Such integration remains a challenging but necessary task for investigators desiring to understand the role of the cerebellum in cognition.

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Dysmetria of thought: clinical consequences of cerebellar dysfunction on cognition and affect

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Cognitive and emotional changes might be prominent or even principal manifestations of cerebellar lesions. This realization supports evidence suggesting that the cerebellum is an important part of a set of distributed neural circuits that subserve higher-order processing. Early anecdotal clinical accounts described aberrant mental or intellectual functions in the setting of cerebellar atrophy. Later systematic analyses showed that the cerebellum is able to influence autonomic, vasomotor, and emotional behaviors, and further studies revealed neuropsychological deficits in patients with degenerative diseases. Current descriptions of behavioral changes in adults and children with acquired cerebellar lesions bring the debate about the cerebellar role in neural function within the realm of clinically relevant cognitive neuroscience. The activation of focal cerebellar regions by cognitive tasks on functional neuroimaging studies, and morphologic abnormalities of cerebellum in psychiatric diseases such as autism and schizophrenia further support this view. Anatomical substrates have been elucidated that could support a cerebellar role in cognition and emotion. Our concept of 'dysmetria of thought' draws an analogy with the motor system to describe and explain the impairments of higher-order behavior that result when the distributed neural circuits subserving cognitive operations are deprived of cerebellar modulation.

The possible role of the cerebellum in sensory, cognitive and affective processing has long been overshadowed by interest in the cerebellar coordination of voluntary movement. Cerebellar motor disturbances are characterized by incoordination of the limbs (dysmetria), wide based, un-

steady, and lurching gait (ataxia), speech impairment (dysarthria), and a variety of disturbances of eye movements (such as nystagmus, and overshoot and undershoot with attempted volitionally directed gaze). Midline lesions are characteristically associated with truncal ataxia, and lesions

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