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REVIEW

Cerebellar Function in Developmental Dyslexia

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Abstract Developmental dyslexia is a genetically based neurobiological syndrome, which is characterized by reading difficulty despite normal or high general intelligence. Even remediated dyslexic readers rarely achieve fast, fluent reading. Some dyslexics also have impairments in attention, short-term memory, sequencing (letters, word sounds, and motor acts), eye movements, poor balance, and general clumsiness. The presence of "cerebellar" motor and fluency symptoms led to the proposal that cerebellar dysfunction contributes to the etiology of dyslexia. Supporting this, functional imaging studies suggest that the cerebellum is part of the neural network supporting reading in typically developing readers, and reading difficulties have been reported in patients with cerebellar damage. Differences in both cerebellar asymmetry and gray matter volume are some of the most consistent structural brain findings in dyslexics compared with good readers. Furthermore, cerebellar functional activation patterns during reading and motor learning can differ in dyslexic readers. Behaviorally, some children and adults with dyslexia show poorer performance on cerebellar motor tasks, including eye movement control, postural stability, and implicit motor learning. However, many dyslexics do not have cerebellar signs, many cerebellar patients do not have reading problems, and differences in dyslexic brains are found throughout the whole reading network, and not isolated to the cerebellum. Therefore, impaired cerebellar function is probably not the primary cause of dyslexia, but rather a more fundamental neurodevelopmental abnormality leads to differences throughout the reading network.

Keywords Cerebellum · Developmental dyslexia · Magnetic resonance imaging · Reading · Implicit learning

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Introduction

Developmental dyslexia is defined as deficient literacy acquisition despite adequate intellectual ability and sufficient educational exposure [1, 2]. Extensive research over the last four decades has firmly established dyslexia as a neurobiological syndrome. It is strongly heritable; many of the susceptibility genes that have been identified have been found to help to control neuronal migration during early brain development [3]. These alleles explain why the dyslexic brain shows anomalous migration patterns such as cortical ectopias and misplaced magnocells in the thalamus [4]. Hence, dyslexia can be considered a neurobiological syndrome that only incidentally affects reading. Consistent with this, while reading disability is the primary diagnostic criterion, dyslexic individuals often experience a variety of other problems. In language and literacy, there is impaired ability to sequence word sounds auditorily and letters visually [5]. In addition, there is poor short-term memory for sequences such as days of the week, months of the year, and telephone numbers, and poor motor sequencing leading to incoordination, clumsiness, poor handwriting, and left/right confusions. Infants at risk of developing dyslexia due to a family history show early differences in processing basic auditory stimuli, and these differences predict later language and literacy skills [6, 7]. Due to this wide range of behavioral symptoms to be accounted for, the etiology of dyslexia has yet to be established conclusively.

More direct evidence for a neurobiological basis to dyslexia comes from a large number of neuroimaging studies, which have detailed differences in symmetry, laterality, gray matter volume, and the integrity of white matter fiber tracts in dyslexics compared with typically developing readers [8]. Eckert [9] concluded that the most consistent regions where structural differences are to be found in dyslexia include the inferior parietal lobule, the inferior frontal gyrus—and the cerebellum. However, the introduction of the cerebellar theory of dyslexia by Nicolson et al. [10] was met with much skepticism: Why would a motor structure be the cause of a reading disorder?

The cerebellum is an extensively connected computational machine. It contains half of all the neurons in the brain: 50 billion granule cells receive input from almost all parts of the rest of the CNS and supply the 20 million output Purkinje cells with enormous amounts of information. These feed highly processed signals back to the rest of the brain, but particularly to the cerebral cortex. Two hundred thousand parallel fibers pass at right angles through the flattened dendritic trees of perfectly aligned rows of Purkinje cells. This highly uniform and regular structure suggests that the processing operation of each Purkinje cell is fundamentally the same whatever connections it has with other parts of the nervous system. This operation is probably to predict future states of the body in detail by generating internal neural "forward" models of the sensorimotor system [11, 12]. These models can then be used to predict the outcome of any set of motor commands [13] and to adjust the motor commands precisely to meet the demands of the moment; hence, these cerebellar forward models can optimize motor programs. In principle, these models could be used to predict likely outcomes of possible behaviors even if no motor programs are generated—in other words, to mediate aspects of cognition. Ito and many others have pointed out that the cerebellar processing operations underlying the optimization of motor performance could equally well be applied to mental operations (e.g., [14–18]). Many would argue that planning and predicting is what cognition is. Thus, this cerebellar role in planning actions and predicting their outcome is likely to be relevant for reading and reading difficulties.

Cerebellar Functional Topography Despite the consistent, repeating circuitry of the cerebellar cortex, different regions of the cerebellum connect with different regions of the cerebral cortex, leading to a functional topography of the cerebellum (Fig. 1) [19–22]. Overt motor tasks engage the sensorimotor homunculi [23] in the anterior lobe (lobules I–V, extending into medial lobule VI for articulation) and lobule VIII. These regions show correlated activity with sensorimotor regions of the cerebral cortex [24–27]. In contrast, the lateral lobes of the posterior cerebellum (lobules VI and VII) are richly interconnected with association cortices, including the prefrontal cortex. Buckner et al. [27] used resting state functional MRI (fMRI) to provide a complete map of the functional topography of the human cerebellum based on functional connectivity with the cerebral cortex, confirming that the sensorimotor networks map to the anterior lobe and lobule VIII, whereas lobules VI and VII contain functional connectivity maps of association cortices, including the cognitive control network and default network.

Most behavioral investigations of cerebellar tasks in developmental dyslexia have focused on motor tasks such as postural stability. However, the regions where there are structural and functional differences in dyslexics do not always correspond to the cerebellar regions involved in motor control. Therefore, cerebellar functional topography can be useful for interpreting cerebellar findings in reading and dyslexia.

Cerebellum and Reading: Typically Developing Readers

As reading requires the coordinated integration of visual, auditory, motor, and language systems, it is mediated by a network interconnected brain regions [28, 29]. The left-hemisphere reading network includes the occipital–temporal cortex, involved in the visual processing of word form; the temporal–parietal cortex, involved in visuo-auditory association and phonological processing; and the inferior frontal gyrus for articulation [28]. All these regions are richly connected with the cerebellum [20, 30].

What could the cerebellum be doing during reading? It is active not only during speech but also during silent reading and passive language processing (see reviews [31–34]) and before and during visually guided movements such as the eye movements required for reading text [35]. Other cerebellar functions potentially relevant to reading include the direction of attention [36–40], error detection [41, 42], and timing/sequencing [43–47]. Finally, the role of the cerebellum in implicit and associative learning (e.g., [48–51]) may be crucial to the acquisition of fluent reading skills.

Neuroimaging studies have shown that the cerebellum is an important part of the reading network in typically developing readers. Reading-related activity tends to be focused in lobules VI and VII and maximal in the right posterolateral cerebellum ([52, 53]; Braille reading [54]), similar cerebellar areas to those activated during language tasks [21]. The localization of the activation patterns depends on the demands of the particular task; for example, reading aloud engages cerebellar regions where the articulatory muscles are represented (bilateral lobules V/VI [55]). It has been suggested that the left cerebellum is involved in processing the morphology of word forms, whereas the right is more active during phonological processing [56]. Supporting this, reading nonwords vs. viewing consonant strings engaged right cerebellar lobules VI and VII [57]. Right lobule VI is

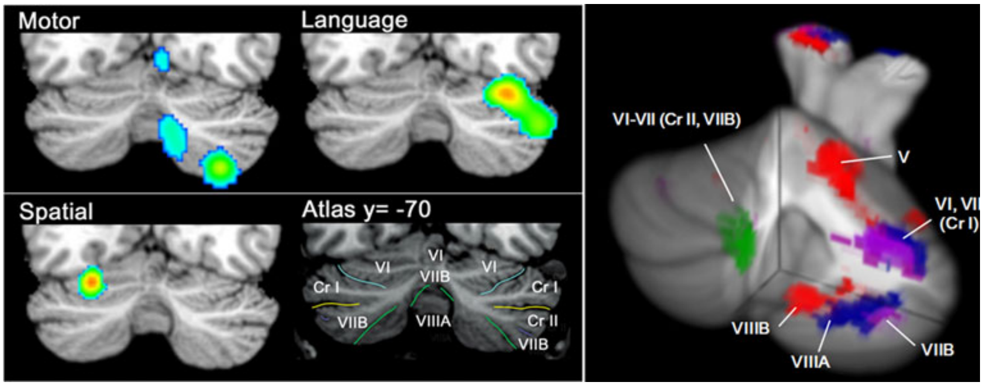

Fig. 1 Functional topography in the human cerebellum. Segregated "motor" (lobules I–V and VIII) and "cognitive" (lobules VI and VII) areas of the cerebellum based on functional MRI data. *Left*, Meta-analysis of functional MRI studies shows converging activation for motor, language and spatial tasks [21]. *Right*, Activation during finger tapping (*red*), verb generation (*blue*), working memory (*purple*), and mental rotation (*green*) in healthy controls [178]

active during lexical decision tasks [55], and right lobule VII is engaged during semantic processing [41, 58]. Reading low-frequency words activated left lobule VII [39, 57]. Two studies have reported cerebellar activation in lobules VI (bilaterally) and right lobule VII during the implicit processing of words [39, 40]. Finally, in a magnetoencephalography study, Kujala and colleagues [59] found that the cerebellum was one of two crucial forward-driving nodes in the reading network (Fig. 2); the other was the left inferior occipitotemporal cortex, the site of the visual word form area, which is involved in early word-specific visual processing.

Do Cerebellar Patients Have Reading Difficulties?

Cerebellar damage can lead to acquired reading difficulties via a variety of processing impairments that have knock-on effects on reading. Patients with lesions of the vermis/paravermis (who did not show language deficits) had difficulties with reading both single words and continuous text due to a variety of oculomotor deficits in fixation, saccadic, and pursuit eye movements [60]. Reading and writing impairments have been shown in patients with olivo-ponto-cerebellar atrophy who had intact performance on problem solving, memory, and abstraction tasks [61]. Vermal lesions can impact the reticular activating system, which can negatively affect focusing of attention [62], which is vital for successful reading [63]. Visual dyslexia and surface dysgraphia have been described in a patient with a right superior cerebellar artery infarct [64]. Consistent with the imaging results in healthy readers, cerebellar patients with difficulties in both language and reading tasks tend to have right-lateralized damage [65]. Cerebellar patients with damage involving lobules I–VII presented with phonological processing deficits on a rhyme judgment task and difficulties in a nonword repetition task (though these patients had no overt reading deficits [66]). The patients' pattern of increased errors in rhyme judgments in which there was a mismatch between orthography and phonology (e.g., fear-bear) was similar to that found in dyslexic participants [67]. Thus, cerebellar dysfunction can impact reading in a variety of ways, from basic oculomotor disruption to more complex impairments in linguistic processing. This leads us to the question: What types of "cerebellar" deficits, if any, are evident in individuals with developmental dyslexia?

Impaired Reading—Developmental Dyslexia

Behaviorally, the majority of dyslexic readers present with difficulties in visuo-phonological processing—difficulty

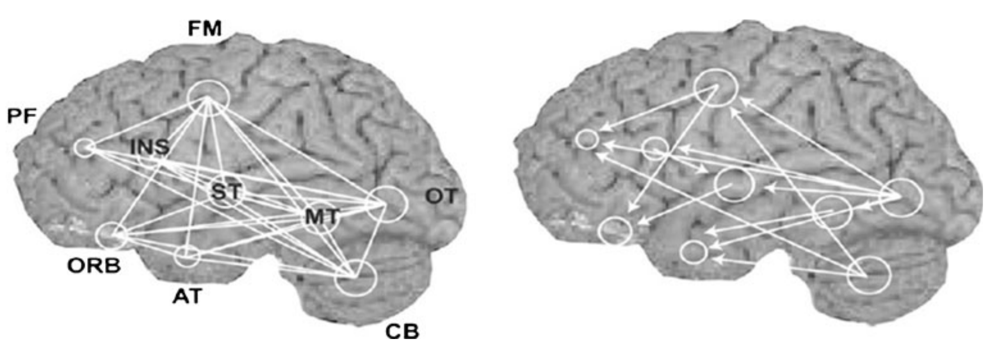

Fig. 2 The reading network as indicated by magnetoencephalography phase-coupling at 8–13 Hz. *OT* inferior occipitotemporal cortex, *MT* medial temporal cortex, *ST* superior temporal cortex, *AT* anterior part of inferior temporal cortex, *FM* face motor cortex, *INS* insula, *CB* cerebellum, *PF* prefrontal cortex, *ORB* orbital cortex. From [59]

with translating letters into the sounds they stand for and problems breaking down spoken words into their constituent phonemes. Although it is suggested that phonological deficits are the main cause of reading problems [68–73], most people now acknowledge that the phonological deficit probably has more fundamental causes to be sought in visual, auditory, and motor domains [5, 29]. In orthographies that are more regular than English, dyslexia is not characterized by phonological errors, but by slower, more laborious reading. Because the phonological relationship between letters and sounds is so consistent in languages such as German or Italian, dyslexic readers can become accurate decoders, but still fail to attain fluent, automatic reading [74].

Deficient phonological processing also fails to explain the poorer performance of dyslexic groups on a range of other sensorimotor tasks, including eye-movement control [75–77], motor coordination and balance [10, 78, 79], information-processing speed [80, 81], motor processing speed [82], implicit motor learning (e.g., [83–87]), and low-level visual and auditory tasks [88–94]. Recently, therefore, there has been a resurgence of interest in the broader neurocognitive profile of dyslexia (e.g., [95]), including differences in visual spatial, attention, and executive functions.

The characteristic of lack of automaticity in dyslexia, coupled with anecdotal evidence of delayed motor milestones, clumsiness, and poor handwriting, led to Nicolson et al. [10] introducing the Cerebellar Deficit Theory of dyslexia. They proposed that cerebellar dysfunction—and particularly impaired procedural learning—can explain both the reading disorder and the nonliteracy symptoms of dyslexia [10, 96]. This theory links cerebellar dysfunction to the phonological difficulties in dyslexia via the articulatory system; visual sequencing problems to the cerebellar role in visual attention and eye movements; incoordination, clumsiness, and poor handwriting to the cerebellar contribution to motor control, and the role of the cerebellum in implicit learning to the slow, laborious learning seen in dyslexic individuals.

Do Dyslexic Children and Adults Show Signs of Cerebellar Dysfunction?

Neuroimaging Differences in the cerebellum are consistently reported in structural imaging studies comparing dyslexic with typically developing readers [9]. Typically developing readers tend to show more right-lateralized cerebellar asymmetry, but dyslexic readers tend to have more symmetrical cerebella [97, 98], and the degree of cerebellar symmetry correlates with phonological processing errors. The right anterior cerebellum is smaller in dyslexic adults [99] and, together with a smaller right pars triangularis, decreased volume in this region correctly classified 72 % of dyslexic subjects [100]. However, reduced cerebellar size and asymmetry may be more generally associated with cognitive deficits and not specific to dyslexia [101]. Voxel-based morphometry (VBM) analyses comparing dyslexic and control groups have shown significantly reduced gray matter bilaterally in the cerebellar nuclei [102], lateral lobule VII [103], and the anterior cerebellum extending into lobule VI [104]. However, VBM studies do not always find cerebellar differences in dyslexia [105, 106].

While the localization of anatomical differences varies across studies, a recent meta-analysis of VBM showed that right lobule VI abnormalities are found consistently [107]. Pernet et al. [108] reported that a region of right cerebellar lobule VI was the most reliable biomarker for dyslexia in a sample of 38 dyslexic adults, and phonological and lexical measures were significantly worse in dyslexics with low gray matter volume in this region. This cerebellar region is consistently activated during language tasks in fMRI studies in healthy controls [21]. Interestingly however, cerebellar differences were not found in prereading children at risk for dyslexia, suggesting that differences in the cerebellum might be a consequence of reading difficulties, rather than pre-existing and causal [109, 110].

Differences in cerebellar activation have been shown in dyslexic readers during a variety of functional imaging paradigms. Reduced cerebellar activation has been shown during phonological tasks [111], and activation differences have been shown in right lobule VI during implicit motor learning paradigms [112, 113]. Dyslexic readers show alterations in functional connectivity between the cerebellum and other regions in the reading network, including the angular and inferior frontal gyri [114, 115]. Baillieux et al. [116] showed that cerebellar activations in dyslexics were more widespread than in controls, which, they suggest, represents impaired information processing in the cerebellum. Consistent with structural findings, the anterior lobe of the cerebellum showed reduced activation in both Chinese and English dyslexics [117, 118]. Beneventi and colleagues found that controls showed greater engagement of the right dentate nucleus and right Crus II during a working memory paradigm than the dyslexic readers [119].

Cerebellar Task Performance in Dyslexic Readers The cerebellar hypothesis of Nicolson and Fawcett spurred studies investigating eye movements, postural stability, classical conditioning tasks (which are known to require cerebellar circuitry, such as eyeblink conditioning, associative learning paradigms), and implicit or procedural learning tasks (serial response time tasks). A more extensive review of cerebellar task performance in dyslexic readers can be found elsewhere [120].

Both the pattern of eye movements and their control differ in dyslexics compared with typically developing readers. Some, but not all [121], studies report that dyslexics have longer and less steady fixations [122], poor binocular control [77, 122–126], and abnormal control of saccades [76, 127–129]. English-speaking dyslexics tend to show a greater number of regressions while reading [130], and English, Italian, and German dyslexics make more fixations and spend a longer time fixating words [128, 131, 132].

As a wide-based stance, staggering gait, and postural instability are clinical hallmarks of cerebellar disease, several studies have investigated balance and postural stability in dyslexia. Most have found that dyslexic participants are less stable during a variety of balancing tasks compared to controls [78, 79, 133–137], but others have shown no group differences [138–142] or they have only found differences during eyes-open balancing [79, 135]. Some have argued that only dyslexics with co-morbid conditions such as ADHD and developmental coordination disorder are likely to have balance difficulties [140, 143, 144], although a recent study found no relationship between balance ability and ADHD symptoms in children with a familial risk of dyslexia [137].

In addition to postural control, the cerebellum is important for the smooth coordination of rapid movements. Evidence for difficulties on speeded motor paradigms in dyslexic children and adults include slower performance on the Annett peg-moving task [82], a worse combined speed–accuracy score during rapid pointing [142], slower performance on a speeded pointing task [145], and slower tapping speed [146].

Classical conditioning and implicit motor learning can be used to test plasticity in cerebellar circuits [147]. Two studies have examined eyeblink conditioning in subjects with developmental dyslexia: One in adults showed poorer tuning of conditioned responses [148], and in the other, dyslexic children failed to learn the conditioned response at all [149]. Studies employing implicit learning paradigms have found that some dyslexic children and adults show less learning than typically developing readers [83–87, 150, 151]. In contrast, explicit learning is intact (e.g., [84, 150, 151]). However, not all studies have reported impaired implicit learning in dyslexia [85, 152–154], and some find that dyslexics are only impaired when the implicit learning task requires sequence learning [85, 151, 155]. The relatively poorer performance on tasks requiring sequencing in dyslexics further suggests cerebellar dysfunction, as it has been proposed that the cerebellum is crucially involved in sequence detection [47]. Poorer implicit phonological representations have been found in dyslexic children [156], which suggests that impaired implicit learning could extend outside the motor domain. Implicit learning deficits in dyslexic children and adults may explain the laborious learning in dyslexia: Impaired implicit learning may lead to over-reliance on (intact) explicit strategies for reading acquisition.

In summary, some (but not all) studies report poorer performance in dyslexic participants on a range of "cerebellar" tasks, including balance, motor, and learning paradigms. Differences in results could be due to differences in tasks, selection criteria, and confounding by comorbid disorders such as developmental coordination disorder or ADHD [157, 158]. In addition, our understanding of the functional topography of the cerebellum suggests that some of the regions in which gray matter differences are reported in dyslexia are part of "cognitive" cerebro-cerebellar loops. Given this, one might not predict that the majority of dyslexic individuals show poorer performance on classical cerebellar motor tasks, but may be more likely to be impaired on tasks that engage these specific cerebellar regions, such as language and working memory paradigms.

Cerebellum, Learning, and Intervention

As suggested above, cerebellar learning mechanisms may be important for acquiring literacy skills. Given that the degree of learning on an implicit motor learning paradigm correlated with size of discrepancy between cognitive and reading scores in adult dyslexic university students [86], we suggested that cerebellar circuits may be particularly important for compensation and remediation of reading difficulties. But even though there are remediation programs designed to improve "cerebellar" function, the specificity and effectiveness of these programs remains highly controversial [159–163].

Beyond specifically training cerebellar function in an attempt to improve literacy skills, few studies have provided data relevant to assessing the potential impact of cerebellar processing on remediation. A recent study reported that in dyslexic children articulatory training combined with purely auditory phonological training yielded significant additional benefit over phonological training alone [164]. They also found that a tapping task was one of the best predictors of response to remediation (along with rapid naming and word recognition, which are more obviously associated with reading outcome). These findings suggest that motor performance is predictive of remediation response. However, using bead threading and postural stability as measures of cerebellar motor performance, Barth et al. [165] found no relationship between performance on these tasks and response to intervention in poor readers (although, postural stability and bead threading may not be the most appropriate "cerebellar" measures for dyslexic children, given the localization of many of the structural findings to the right posterolateral hemisphere).

Studies using functional MRI to measure intervention-related neural changes can also provide insight into whether the cerebellum has a role in remediation. While some remediation studies [166] did not attain cerebellar coverage during scanning, other studies indicate that there are alterations in cerebellar activity during phonological tasks in dyslexic groups post-remediation [167, 168]. In dyslexic children, post-intervention structural changes in cerebellar gray matter were found in the right anterior cerebellum [169], and the degree of gray matter change in this region correlated with improvement in nonword reading scores. That said, the cerebellum was not one of the areas shown to predict future reading gains in dyslexia in a recent study [170]. Therefore, the potential role of the cerebellum in remediation of reading disorders is currently not clear and requires further clarification.

Potential Mechanisms

Possible mechanisms underlying the contribution of cerebellar processing to reading and dyslexia come from the extensive motor control literature [171]. Dyslexia is characterized by poor phonological processing skills [72], often accompanied by difficulties in spelling, writing, and sequencing of information. Relevant to poor spelling and writing skills is the finding that “apraxic agraphia” can result from cerebellar damage (Marien in [171–173]). Several researchers have linked the cerebellum to language and phonological processing via speech, even when there is no overt articulation; Ackermann et al. [174] suggested that the cerebellum produces a “pre-articulatory code” for language. Ivry emphasizes the cerebellar role in timing, including the timing of articulatory movements and the importance of the duration of, for example, silent periods in phonetic contrasts for speech discrimination (Ivry in [171]). These processes could be crucial precursors to the development of phonemic awareness. Supporting a possible link between motor skills and phonemic awareness, children with developmental coordination disorder, which is characterized by poor motor skills, also have a high incidence of phonological difficulties [175]. Both Nicolson and Fawcett [176] and Ben-Yehudah and Fiez [66] have suggested that cerebellar impairment might yield phonological processing difficulties via poorer articulatory monitoring, in the framework of a cerebellar role in error monitoring [66]. This may be particularly important during the acquisition of literacy skills, as compared to the effects of cerebellar damage in formerly competent adult readers, who may only show difficulties when error monitoring is required (e.g., if the task involves unfamiliar or non-words). Molinari et al. [47] emphasize the importance of the cerebellum in sequencing information—be it motor, linguistic, or spatial—which is important when we consider the findings from the implicit learning literature, in which dyslexics seem to have specific difficulties when a learning paradigm involves sequences of information. In a more recent permutation of the cerebellar theory of dyslexia, Nicolson and Fawcett [96] argue that an overarching deficit in procedural learning, via dysfunctional cortico-cerebellar language circuits, could account for the specific impairments in dyslexia.

Conclusion

The cerebellum is probably involved in various aspects of reading, including eye movements, language and spatial processing, working memory, and skill acquisition and automaticity. Some children and adults with developmental dyslexia show impairments on cerebellar tasks—including eye movement control, postural stability, and implicit motor learning—and the cerebellum is now thought to be involved in cognitive processes beyond the motor domain. While cerebellar dysfunction is not likely the primary cause of dyslexia, the cerebellum is clearly involved in the reading process, and there is evidence that it is part of the network of regions disrupted in dyslexia. It is possible that differences in cerebellar structure and function in dyslexia are related to a similar genetically driven developmental process as the differences seen in “higher” cortical areas, such as neural migration abnormalities (e.g., [177]). The lack of cerebellar findings in at-risk children prior to the start of literacy acquisition has led Raschle and colleagues [110] to suggest that cerebellar differences are a result rather than a cause of failure to learn to read, perhaps as part of a network of regions involved in compensation. The cerebellar role in skill acquisition, as well as the finding that gray matter changes in the right cerebellum are related to gains in nonword reading after intervention [169], suggests that this might be the case. Our newer understanding of functional subregions of the cerebellum suggests that the regions involved in developmental dyslexia tend to be those that are engaged during language and working memory paradigms. In this way, our broadening understanding of the role of the cerebellum in higher functions clarifies why the cerebellum might be one of the neural substrates of developmental dyslexia.

Conflict of Interest Statement We confirm that there is no conflict of interest, financial or otherwise, which might bias this work.

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