Cerebellar contributions to rapid semantic processing in reading

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1. Introduction

Clinical and neuroimaging studies alike have indicated an important role for the cerebellum in processing oral and written language, through both motor (e.g., articulation) and non-motor (e.g., reading, semantic processing) functions (Stoodley, 2012 for review). The cerebellum's role in reading is particularly interesting because it is infrequently examined as a core component of the reading network, despite being frequently activated during reading-related tasks. Cerebellar activation is consistently observed in tasks of single-word reading, reading of connected-text, and phonological and semantic processing (e.g., Turkeltaub et al., 2003; Christodoulou et al., 2014; Mariën and Beaton, 2014; D'Mello et al., 2017; Lesage et al., 2017; but see Richlan, Kronbichler, & Wimmer, 2009), but the cerebellum's exact role in reading is still under-specified. Regions of the cerebellum that are engaged during reading-related behaviors (particularly the right posterior cerebellum) connect functionally to cerebral regions recruited for reading, including inferior frontal, temporoparietal, and occipito-temporal regions (Buckner et al., 2011; Alvarez and Fiez, 2018). These functional connections provide relations to the major components of the reading network by which the cerebellum might contribute to reading-related skills. Further, lesions to the cerebellum can result in reading impairments including alexia (Moretti et al., 2002) and cerebellar dysfunction has been proposed to contribute to reading difficulties in individuals with dyslexia (Nicolson et al., 2001).

In the current study, we examined the relations between cerebellar activation and one component of fluent reading, rapid semantic processing. Prior studies have associated the cerebellum with semantic processing (Stoodley 2012; D'Mello et al., 2017) and other aspects of rapid reading (Ang et al., 2020). Specifically, we evaluated whether there are differences in cerebellar activation associated with rapid semantic processing in the context of sentence reading for comprehension. Participants completed an in-scanner reading task wherein they

were shown five sequentially-presented words that formed a sentence and asked to determine whether the sentence was semantically plausible or implausible. To manipulate rate-of-processing demands, words were presented at slow, medium, and fast rates. We assessed whether activation patterns were associated with rate-of-processing, and whether these patterns were sensitive to semantic information. We related variation in activations to variation in out-of-scanner standardized assessments of reading at the sub-lexical, word, and passage level so that we could associate patterns of cerebellar activation to standard measures of reading ability. Further, reading ability develops throughout the lifespan, with cortical regions specialized for print continuing to specialize into adulthood (Centanni, King, Eddy, Whitfield-Gabrieli, & Gabrieli, 2017). We therefore included typically-developing readers from adolescence into adulthood to evaluate whether there are age-related changes in cerebellar activations and their associations with reading abilities.

2. Methods

2.1. Participants

A subset of the participants included in the current study were analyzed in a previous study (Christodoulou et al., 2014). Prior to data-cleaning, the original study sample included thirty-nine right-handed typical readers. Four participants were excluded from analysis due to poor accuracy on the fMRI task, resulting in a final sample of n = 35 typical readers (mean age = 20.05 ± 5.47 years, range = 11–34 years; 15 males). All participants completed a battery of standardized reading-related assessments which included (1) sub-lexical tasks of rapid naming, (2) word-level reading, and (3) passage-level reading. The *Rapid Automatized Naming and Rapid Alternating Stimulus Tests* (RAN/RAS 2-set; Wolf and Denckla, 2005) were used to assess rapid automatized naming speed. The RAN/RAS 2-set requires naming

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of alternating letters and numbers as quickly and as accurately as possible. Raw scores correspond to the time (seconds) it takes each participant to complete the stimulus set. Incorrect responses are not factored into the score (standard scores μ = 100, SD = 15). The *Test of Word Reading Efficiency* (TOWRE) Sight Word Efficiency and Phonemic Decoding Efficiency subtests were used as measures of timed word-level reading (word and pseudoword reading, respectively; Torgesen et al., 1999). The TOWRE sub-tests require reading of real and pseudowords as quickly and accurately as possible in 45 seconds (standard scores μ = 100, SD = 15). Lastly, the *Nelson-Denny Reading Test Reading Rate* (NDRT-R) uses the number of words in a passage read at a normal reading rate after one minute to assess passage-level reading rate (scale score, μ = 200, SD = 25).

As a supplementary analysis, we analyzed brain-behavior relationships on standardized reading-related assessments un-associated with reading speed including measures of (1) untimed single word/pseudo reading, (2) comprehension, and (3) phonological skills. The *Woodcock Reading Mastery Test* (WRMT) Word Identification and Word Attack subtests were used to assess untimed single-word reading ability, and comprehension was measured on the Passage Comprehension sub-test which assess comprehension of a sentence by asking participants to fill in a missing word (standard scores μ = 100, SD = 15) (Woodcock, 1998). The *Comprehensive Test of Phonological Processing* (CTOPP) Elision subtest was used to assess phonological skills. For the CTOPP Elision subtest, participants remove phonological segments of one word, to form a new word (scaled scores μ = 10, SD = 3) (Wagner, et al., 1999).

All participants performed at or above the 25th percentile across four measures of timed and untimed single word reading (TOWRE and WRMT subtests), and demonstrated at least average cognitive performance (score greater than 85 on the *Wechsler Abbreviated Scale of Intelligence, 3rd Edition* (WASI) Performance IQ subtest) (Wechsler, 1999). TOWRE and WRMT composite scores were created by averaging scores on subtests of the TOWRE and the WRMT, respectively. One participant was missing data on the WRMT (Word identification and Word Attack subtests), and six participants were missing data on the NDRT. For analyses on age, adolescents were defined as individuals ≤ 18 years of age, and adults were defined as individuals > 18 years of age (see Table 1). Written consent or assent was acquired from all participants and all procedures were approved by the MIT Committee on the Use of Humans as Experimental Subjects.

2.2. Neuroimaging Task:

Details of the imaging session and reading task used here were previously reported (Christodoulou et al., 2014). Briefly, each trial consisted of a sentence made up of five words presented sequentially, followed by a question mark (Fig. 1A). Participants were asked to determine whether each sentence was *semantically plausible* (e.g., Coaches envy teams with talent) or *semantically implausible* (e.g., Pillows hammer nails in wood). Words were presented at one of three speeds (slow = 400 ms/word; medium = 250 ms/word; fast = 100 ms/word). The slow presentation rate corresponded to the silent reading rate of typical third and fourth grade readers while the fast presentation rate was selected so as to be challenging for typical college-level adult readers. Nouns and verbs were matched across run, condition, and sentence type for number of syllables and written frequency (details of matching procedures reported in Christodoulou et al., 2014.) To account for differences in sentence duration, the question mark duration was varied such that all trials were 4 s long. Stimuli were presented in a jittered event-related design in which sentence conditions were randomly intermingled with rest trials. Participants completed two consecutive 10 min runs of the task (156 total sentences, 26 sentences of each plausibility condition per rate). Accuracy and reaction time were recorded via button press. For each participant, response accuracy was calculated by determining the total number of correct responses divided by the total number of responses offered. No participants omitted more than 30% of trials, and all participants had overall task accuracy greater than 60% in the slow condition. Participants completed two additional fMRI reading tasks in the scanner, which are outside the scope of the current study.

2.3. Imaging data acquisition:

Data acquisition parameters have been previously detailed by Christodoulou et al. (2014). All data were acquired on a Siemens 3T

Table 1
Standardized reading measures in the whole sample and by age group. Table shows means and standard error in parentheses for the whole sample (adults and adolescents) as well as by group. Certain subtests have differing n's due to missing data.

Assessment	Whole Sample		Age Group			
	n	Mean	n	Adolescents	n	Adults
RAN/RAS						
RAN/RAS (raw)	35	20.09 (0.7)	14	21.93 (1.019)	21	18.86 (0.87)
RAN/RAS (standard)	35	112.69 (1.35)	14	111.71 (2.45)	21	113.33 (1.58)
TOWRE						
Sight Word Efficiency (raw)	35	95.54 (1.53)	14	91.57 (2.63)	21	98.19 (1.66)
Sight Word Efficiency (standard)	35	105.71 (1.48)	14	107.43 (2.55)	21	104.57 (1.79)
Phonemic Decoding (raw)	35	53.71 (0.95)	14	51.29 (1.67)	21	55.33 (1.00)
Phonemic Decoding (standard)	35	103.54 (1.28)	14	104.79 (2.19)	21	102.71 (1.58)
TOWRE Composite	35	104.63 (1.05)	14	106.12 (1.87)	21	103.64 (1.21)
WRMT						
Word Attack (raw)	34	39.53 (0.58)	13	38.38 (0.95)	21	40.24 (0.71)
Word Attack (standard)	34	110.44 (1.82)	13	106.85 (2.02)	21	112.67 (2.58)
Word Identification (raw)	34	98.18 (1.08)	13	95.23 (2.19)	21	100 (0.94)
Word Identification (standard)	34	109.29 (1.59)	13	108.69 (2.81)	21	109.67 (1.94)
WRMT Composite	34	109.87 (1.48)	13	107.77 (1.94)	21	111.17 (2.06)
Passage Comprehension (raw)	35	58.89 (1.04)	14	56.64 (2.15)	21	60.38 (0.89)
Passage Comprehension (standard)	35	114.29 (1.72)	14	113.71 (3.13)	21	114.67 (2.03)
Nelson Denny						
Reading Rate (raw)	29	317.24 (21.74)	10	296.7 (52.14)	19	328.05 (19.69)
Reading Rate (standard)	29	222.83 (5.37)	10	224 (12.61)	19	222.21 (5.14)
CTOPP						
Elision (raw)	35	18.77 (0.19)	14	18.36 (0.39)	21	19.05 (0.18)
Elision (standard)	35	11 (0.19)	14	10.86 (0.42)	21	11.1 (0.17)
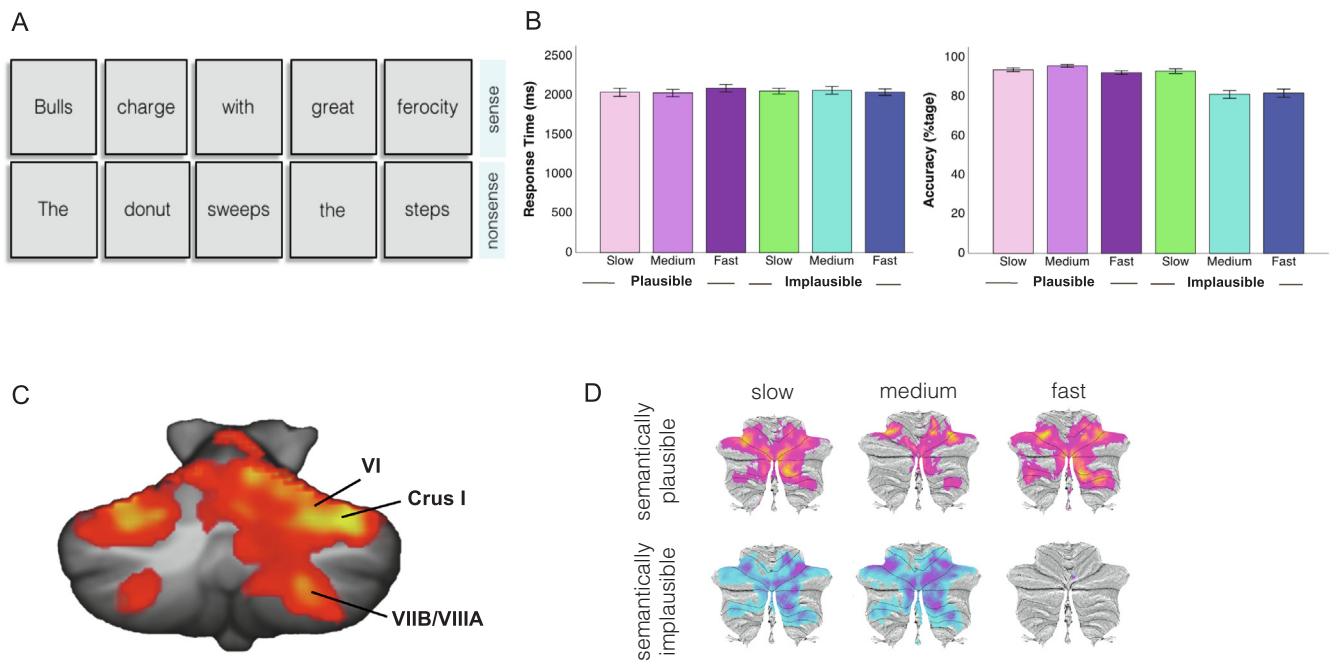
Fig. 1. (A) Task design showing examples of different conditions. (B) Average accuracy and response times for each rate and semantic condition. (C) Averaging across all presentation rates (slow, medium, and fast) showed that sentence reading activated bilateral lobules VI and VIIB/VIIIA, and Crus I/II ($p < 0.001$ uncorrected, FWE cluster $p < 0.05$). (D) Activation patterns for individual rates shown on cerebellar flatmaps.

Tim-Trio using a 12-channel head coil. A high resolution T1-weighted image was acquired and functional images were collected using a gradient echo T2*-weighted EPI sequence (32 slices; $3.1 \times 3.1 \times 4.0$ mm voxels; TR = 2000 ms; TE = 30 ms). All scans were visually inspected to ensure full cerebellar coverage.

2.4. fMRI data analysis

2.4.1. Preprocessing

Data were preprocessed in SPM12. Whole-brain functional images were slice-time corrected, realigned, and coregistered to the T1 MPRAGE. Unsmoothed, realigned, and slice-time corrected images were entered into a general linear model at the first level. Separately, the anterior commissure was set as the origin on each participant's structural image. Structural images were cropped to exclude the cerebral cortex and isolate the cerebellum using the Spatially Unbiased Infratentorial Template (SUIT) toolbox (Diedrichsen, 2006; Diedrichsen et al., 2009). Cropped and isolated structural images were then normalized to a high-resolution cerebellar template. Normalization parameters were then applied to the first-level functional contrast images to bring them into SUIT template space, and images were smoothed with a 6 mm FWHM kernel.

2.4.2. Outlier detection:

Outlier detection was performed using ART Detection implemented in the CONN Toolbox (Whitfield-Gabrieli and Nieto-Castanon, 2012) (outlier = head displacement > 1 mm from the previous frame or global mean intensity > 3 standard deviations from the mean). No participant had greater than 20% of time points flagged as outliers.

2.4.3. Statistical analysis

At the first level, each event was modeled as a 4 s duration (from the start of the first word to the end of the response period). We modelled each rate (slow, medium, fast) crossed with each semantic condition (semantically plausible, semantically implausible) resulting in six conditions per run in the first level design matrix. All trials (correct, incorrect, and omitted responses) were included in first level modeling.

To test for a rate by plausibility interaction, we assessed differences between rates (slow < medium < fast) within subjects at the first-level. These contrasts were brought up to a second level t-test to determine whether there were rate-related differences between semantically plausible and implausible sentences. The interaction was verified using SPSS by extracting parameters from resulting clusters. Results were thresholded at $p < 0.001$ uncorrected voxel threshold, with an FWE corrected cluster threshold to control for multiple comparisons ($p < 0.05$) (Woo et al., 2014). Clusters were visualized on the SUIT template and on gradient maps of the cerebellum using LittleBrain (Guell et al., 2019). LittleBrain plots cerebellar voxels along two axes – each corresponding to a principle functional gradient of cerebellar organization (Guell et al., 2018b). Gradient 1 represents an axis of motor to un-focused task processing, and Gradient 2 represents an axis of task-focused processing. This mapping allows for a more discrete and gradual visualization of cerebellar results than plotting on a template.

2.4.4. Behavioral correlations:

Pearson's R correlations were used to determine whether neural responses correlated with behavioral measures (RAN/RAS, TOWRE, WRMT, and NDRT). When multiple tests were performed, an FDR correction for multiple comparisons was used. Additional supplementary correlations were performed to determine whether neural responses correlated with phonological measures of reading (CTOPP Elision).

3. Results

3.1. Accuracy and response times across presentation rates

Sentences were presented word-by-word at slow, medium, and fast rates. At each rate, half were semantically plausible or implausible (Fig. 1A). Participants designated sentences as plausible or implausible via button press, and accuracy and response times were recorded. We conducted 3×2 ANOVAs to determine how accuracy, response times, and omitted responses differed by rate and semantic plausibility. There were main effects of rate on accuracy (F(2,68) = 65.0, $p < 0.001$) and

reaction time (F(2,68) = 17.8 , $p < 0.001$) whereby participants were less accurate and slower for sentences presented at the fast rate. There were no main effects of semantic condition, or number of omitted responses, and no interactions (Fig. 1B). These findings confirm that increasing the rate of presentation increased the difficulty of task performance.

3.2. A network of cerebellar regions is active during reading

We averaged activation across all conditions and identified cerebellar regions that were activated across all rates (slow, medium, and fast > fixation; Fig. 1C-D) including bilateral lobules VI, Crus I/II, VIIB, and VIIIA ($t = 9.28$, $p = 3.7 \times 10^{-11}$, $k = 8438$). Cerebellar activation for reading was mainly right-lateralized, consistent with previous findings of cerebellar contributions during reading and sentence completion tasks (D'Mello et al., 2017; Lesage et al., 2017; Martin et al., 2015), and with known contralateral connections between the right cerebellum and left cerebral cortex.

3.3. Semantic plausibility interacts with presentation rate to modulate cerebellar activations

There were no main effects of rate or semantic plausibility on cerebellar activations, but there was a rate × semantic condition interaction. As word presentation rates increased, there was greater activation for sentences that were semantically plausible compared to sentences that were semantically implausible in right lobules V-VI

($t = 5.25$, $p = 8.4 \times 10^{-7}$, $k = 620$) and right Crus II/VIIB, VIIIA ($t = 4.33$, $p = 2.5 \times 10^{-5}$, $k = 153$) (Fig. 2A and B).

The interaction was confirmed by a rate-by-semantic condition ANOVA with extracted parameters from these clusters (Fig. 2B). The interaction was driven by significant differences in cerebellar activation to increasing presentation rates between semantically plausible and implausible conditions. Specifically, cerebellar activation increased from both slow and medium to fast presentation rates in the semantically plausible condition, but decreased as presentation rates became faster in the semantically implausible condition. We plotted both clusters on cerebellar gradient maps to assess whether clusters fell into specific cerebellar networks. Both clusters were located in regions at the border of motor and task-positive focused attention networks (Fig. 2C). Supplementary analyses showed that this interaction was also present in right frontal regions, right middle temporal gyrus, right posterior parietal cortex, and the left putamen (Fig. S1).

3.4. Cerebellar activation is associated with individual differences in timed reading tasks

To examine the functional significance of cerebellar activation patterns to reading skills, we examined whether individual differences in cerebellar response patterns were associated with reading measures outside of the scanner including single letter-naming, word-level reading, and passage-level reading. For each cluster, we calculated a difference score between in-scanner cerebellar activation in response to semantically plausible and semantically implausible activation at the
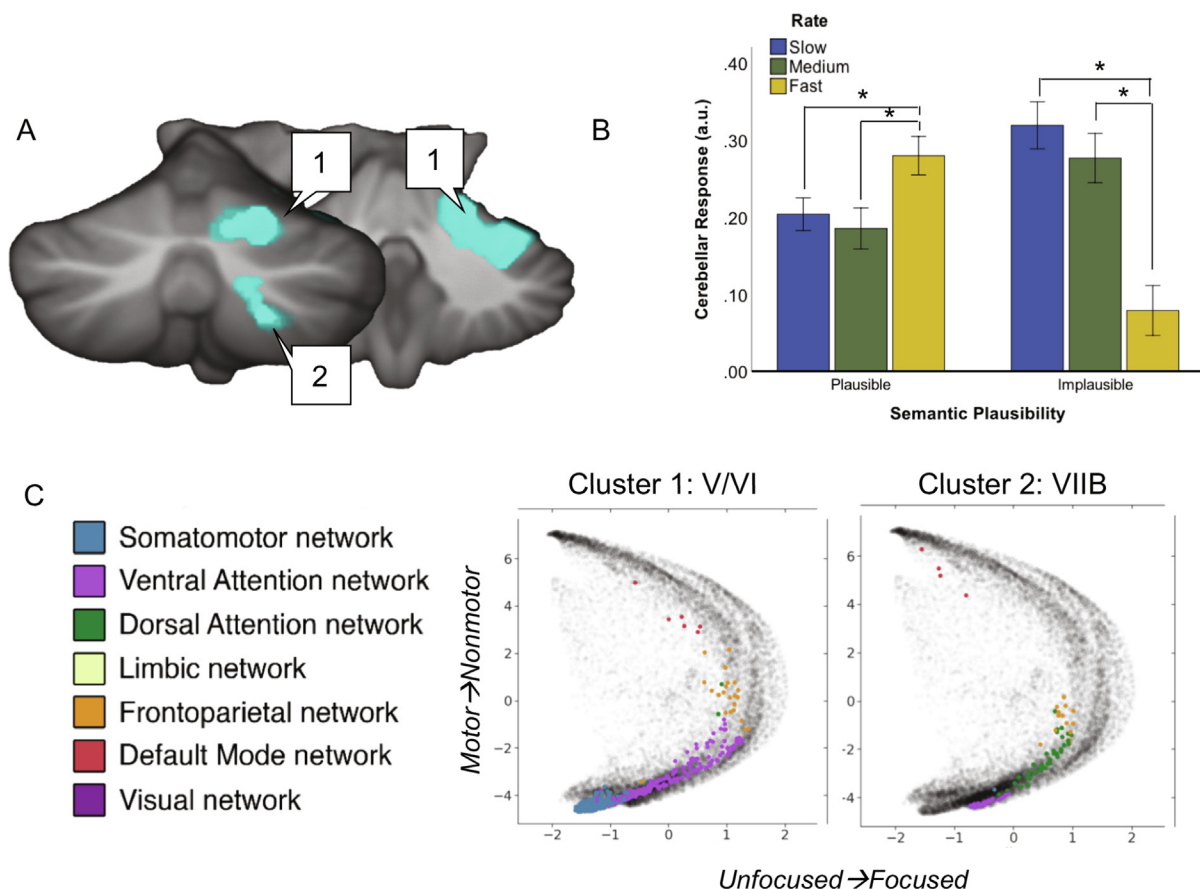
Fig. 2. Effects of semantic processing on cerebellar response to increasing reading rate demands. (A) As speed demands increased, there was greater activation in two cerebellar clusters for sentences that were semantically plausible compared to those that were implausible (Cluster 1 = Right V-VI; Cluster 2 = Crus II, VIIB, VIII; Interaction F = 16.4, $p < 0.001$). (B) Bar graph showing interaction of semantic plausibility and word presentation rate across both clusters. Cerebellar activation (arbitrary units, a.u.) increased from slow and medium to fast presentation rates for semantically plausible sentences, but decreased for semantically implausible sentences. (C) Gradient maps of the cerebellum situating clusters of activation on the two main gradients of cerebellar functional organization (gradient 1 = motor to non-motor; gradient 2 = un-focused to focused). Each dot represents a voxel within the cluster. Dot color corresponds to network colors from Buckner et al. (2011).
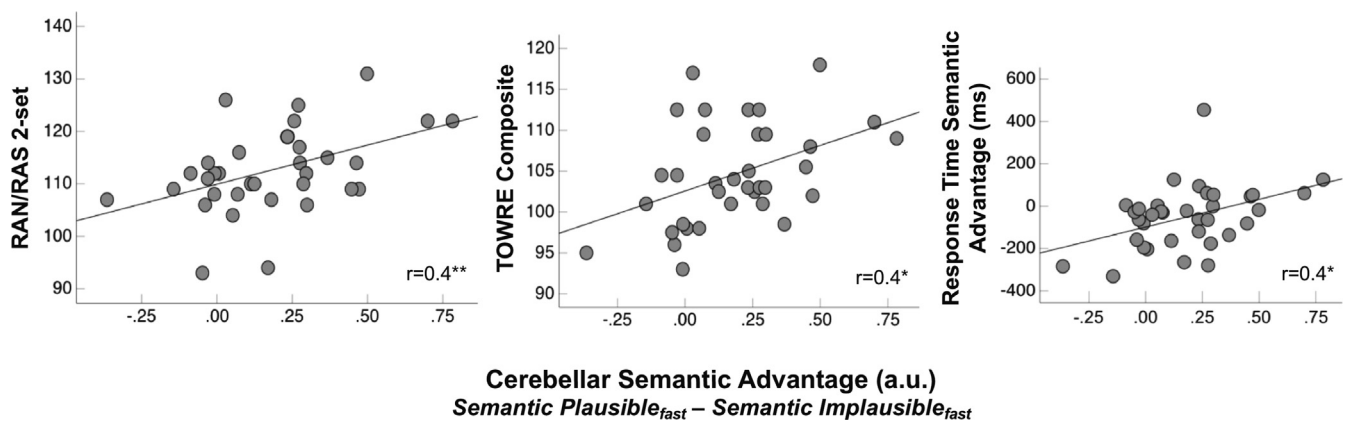
Fig. 3. Increased semantic advantage was associated with performance on standardized measures of rapid automatized naming (RAN/RAS 2-set) and timed word/pseudoword reading (TOWRE composite). Scatterplots show correlations between cerebellar response and RAN/RAS (left), TOWRE composite (middle), and reaction time semantic advantage (right). **$p < 0.01$, *$p < 0.5$.

fastest rate. This difference score reflected the "semantic advantage" at the fastest word presentation rate (semantic advantage = semantically plausible$_{fast}$ – implausible$_{fast}$) for each individual. Readers with larger cerebellar semantic advantages had higher scores on rapid automatized naming (RAN/RAS 2-set, $r = 0.45$, $p = 0.007$) and timed word-level reading (TOWRE composite score, $r = 0.43$, $p = 0.01$) (Fig. 3B). Both correlations remained significant after correcting for multiple-comparisons using an FDR correction ($p < 0.05$). There was no significant correlation with passage-level reading rate (NDRT Reading Rate, $p = 0.21$). We conducted additional supplementary analyses to determine whether the cerebellar semantic advantage was associated with reading skills apart from speeded measures. There were no significant correlations between cerebellar activation and *untimed* measures of reading (WRMT composite, $p = 0.13$), phonological processing (CTOPP Elision, $p = 0.99$), or measures of reading comprehension (WRMT passage comprehension score, $p = 0.17$).

To examine whether differences in activation were related to dissimilarities in processing time (e.g., in case plausible judgments require reading more of the sentence to decide) or other factors that may have differed between conditions, we compared response times, accuracy, and number of omitted responses for semantically plausible and implausible fast sentences. There were no significant differences between conditions for accuracy or omissions ($ps > 0.77$), but there was a trend for a response time difference ($p = 0.054$) such that semantically plausible sentences had longer response times than implausible sentences.

3.5. Cerebellar contributions to reading rate and accuracy are independent of age

Reading skill develops through adolescence and into adulthood. We therefore assessed the effects of age on measures of timed reading and our rate × semantic plausibility interaction. Age was significantly correlated with *raw* scores on all standard measures of timed reading (RAN/RAS raw $r = -0.47$, $p = 0.004$; TOWRE raw composite $r = 0.55$, $p = 0.001$) with adults performing better than adolescents. However, the cerebellar semantic advantage was not correlated with age (Fig. S2), implying that cerebellar activation is a consequence of rapid reading skill exercised through experience, not a result of age. To determine if development of reading skills could account for our results, we further controlled for age in correlations between cerebellar response and RAN/RAS and TOWRE assessments. These findings remained significant when controlling for age.

4. Discussion

To our knowledge, this is the first study to use fMRI to specifically examine cerebellar contributions to rapid semantic processing during sentence reading. Semantic context affected cerebellar activations to changing reading rate demands, and individuals who showed greater cerebellar activation for the most rapidly-presented semantically plausible sentences were also the readers who scored higher on measures of rapid automatized naming and timed real and pseudoword reading. These results suggest that the engagement of distinct cerebellar regions involved in simple sensorimotor adaptation (lobules V, VI), attention (lobules VI, VIIB), and also higher-order semantic prediction (Crus II, VIII) (D'Mello et al., 2017) may support one aspect of reading fluency.

4.1. The cerebellum is sensitive to reading rate and context matters

In the current study, cerebellar activation in response to increased reading rate demands changed depending on the semantic context. In particular, as word presentation rates increased, readers engaged the right posterior cerebellum for semantically plausible sentences and disengaged this region for non-plausible sentences. This finding falls in line with the role of the cerebellum as supporting rapid reading in service of reading comprehension, and disengaging when sentences are rapidly presented but not semantically plausible. These results are consistent with behavioral studies finding that reading-related skills such as rapid naming are aided by semantic and syntactic context (see Wolf & Katzir-Cohen, 2001 for review), which may render certain sentences more predictable and therefore enable faster reading. Although sentences used here differed in *plausibility*, it is possible that these activation patterns reflect heightened prediction processes necessary to correctly distinguish semantically plausible from implausible sentences when reading speed demands were high. Increased activation in similar cerebellar regions has been described for sentences that were semantically predictable over those that are less predictable (D'Mello et al., 2017; Lesage et al., 2017), or nonsensical (Moberget et al., 2014). It has been suggested that increased cerebellar activation may reflect the searching and error correction process necessary when limited word completions exist (Marr, 1969; Desmond et al., 1997), as may be the case in more predictive or semantically plausible sentences. The role of the cerebellum in predictive processing has been examined in both motor (e.g. Bastian, 2006) and linguistic domains (e.g. D'Mello et al., 2017), and may underlie cerebellar contributions to the development of rapid reading in service of comprehension.

Selective activation differences between semantically plausible and implausible sentences in the fastest condition could not be accounted for by other stimulus or response characteristics. Words were presented

serially in a single location, which precluded eye-movement differences across conditions. Word and sentences across conditions were equated for word frequency and numbers of syllables. There were no significant differences in accuracy, or omitted responses in plausible versus implausible conditions, though there was a marginal yet insignificant effect of plausibility on response time.

The activation patterns elicited by the current task fall within regions of the cerebellum that are consistent with known cerebellar functional topography (Stoodley et al., 2012) and cerebellar contributions to reading (Martin et al., 2015). We found increased activation in two distinct cerebellar clusters: one cluster spanning lobule V-VI, and a second cluster spanning Crus II, VIIB, and VIII. Using gradient maps, we found that both clusters fall within regions at the border of motor and task-positive attention networks (see Fig. 3A; Guell et al., 2018b), and are engaged by linguistic tasks. Although lobules V/VI and VIII have often together been considered part of the motor system, more recent research suggests that there may be multiple, distinct representations of task activation within the cerebellum. Further, clinical and neuroimaging research suggests that there may be functionally distinct contributions of these two representations within the cerebellum. For example, although both lobules V-VI and VIIB-VIII are activated for motor tasks, lobules VIIB and VIII are also engaged during complex linguistic tasks, such as verb generation (e.g. Stoodley et al., 2012). Notably, lobule VIIB and VIII are functionally connected with posterior parietal, temporo-parietal junction, and occipito-temporal cortices, regions that are also implicated in reading (Kipping et al., 2013) and both lobules show increases as a product of reading rate (Christodoulou et al., 2014). Lastly, activation in Crus II-VIIB has been associated with context dependent aspects of cognitive control – the process by which individuals decide which actions to choose based on changing context (D'Mello et al., 2020). The localization of cerebellar clusters using gradient maps (Guell et al., 2019) to the border of motor and task-positive attention networks is in-line with increased activation due to increasing reading rates in fronto-parietal regions of the cerebral cortex (Christodoulou et al., 2014). Increased engagement of these cerebellar regions as reading rates increase may therefore contribute to the visual, motor, and auditory rapid adaptive coordination necessary for rapid semantic processing that supports fluency in reading and other language-related functions.

4.2. Cerebellar activation is associated with individual differences in reading rate and accuracy

Activation in specific cerebellar regions (right Crus II/VIIB/VIII) was positively correlated with scores on widely-used assessments of reading measured at sub-lexical and single-word levels (RAN/RAS and TOWRE, respectively), and with a semantic advantage in response time. Crucially, correlations between cerebellar activation and reading performance were specific to assessments that necessitated speed (e.g., timed but not untimed assessments such as the WRMT).

Although the rate by semantic plausibility analysis identified two clusters (Cluster 1 = right lobule V/VI; Cluster 2 = right Crus II, VIIB, VIIA), only the more posterior cluster was associated with reading speed. Unlike Cluster 1, the majority of voxels in Cluster 2 fell within attention and frontoparietal regions of cerebellum that are implicated in non-motor, task-focused attentional processes (Fig. 3 left). This finding is consistent with the proposed functional topography of the cerebellum, whereby multiple representations of task activation and functional networks exist (Buckner et al., 2011; Guell et al., 2018). For example, strokes to lobule V-VI result in classic cerebellar motor symptoms, whereas strokes to lobule VIIB-VIII are associated with both motor and non-motor symptoms including naming, visuo-spatial, and executive-function deficits (Stoodley et al., 2016). In addition, functional connectivity research suggests differing patterns of connectivity from each of these two regions (Kipping et al., 2013). Here, for the first time, we show a *behavioral* distinction between these two regions in

typical readers: Although both clusters show a "semantic advantage," only activation in the more posterior cluster correlated with reading rate and semantic advantage in response time. This is consistent with the suggestion that although both regions are involved in motor/task-positive networks, posterior regions of the cerebellum may play an additional role in higher-order cognitive processing.

4.3. Cerebellar contributions to reading: Adaptive control and rapid semantic processing

A core contribution of the cerebellum is the development of automaticity in both motor and non-motor domains (Ito, 2008; Sokolov , Miall , & Ivry, 2017). Though the term automaticity is used in a variety of contexts, in reference to the cerebellum, automaticity refers to the execution of commonly executed physical or cognitive actions that require minimal attention. The cerebellum is often associated with automaticity in the motor domain. For example, the movement of one arm in a "figure-8" pattern can be maintained even when attentional resources are diverted elsewhere (Lang and Bastian, 2002) because of the automaticity underlying the execution of that motor plan. Reading, and rapid semantic processing in particular, is a skill that, with many years of practice, becomes increasingly automatic in that words presented rapidly are easily recognized and processed without the need for the decoding of each individual letter (Wolf and Katzir-Cohen, 2001; Mani and Huettig, 2012; Kuperberg and Jaeger, 2016), allowing for the diversion of attentional resources to tasks related to comprehension (Katzir et al., 2006). Longitudinal behavioral studies find that measures of automaticity (the effortless matching of letter to sound or name) are associated with reading comprehension abilities and are predictive of future reading ability (e.g., National Institute of Child Health and Human Development, 2000; Fuchs et al., 2001; Riedel, 2007; Roehrig et al., 2008; Kim et al., 2010). Here, we find that cerebellar activation is associated with reading rate and comprehension - skills that require automaticity.

The cerebellum may also contribute to adaptive control and prediction in multiple cortical processes via connectivity with both motor and non-motor regions of the brain (Marek et al., 2018), allowing for optimization of behavior. Networks thought to be important in adaptive control are over-represented in the cerebellum (Buckner et al., 2011; Marek et al., 2018), and damage to the posterior cerebellum can result in loss of adaptive and well-timed cognitive processes or "dysmetria of thought" (Schmahmann, 2010). In the case of rapid semantic processing, cerebellar adaptive control over eye-movements, sensorimotor processing, and attention processes could scaffold early reading development and contribute to later reading skills (Alvarez and Fiez, 2018). Later emerging skills, such as verbal working memory, may rely in part on cerebellar learning and rapid adaptive functions. In the present task, in addition to mechanisms of adaptive control and predictive processing, it is possible that faster word presentation rates taxed verbal working memory mechanisms that are necessary to determine semantic plausibility in the face of increasing reading rate demands. Previous studies have found that cognitive demands and verbal working memory load can increase cerebellar activation in regions such as those reported here (Chen & Desmond, 2005; Küper et al., 2016).

The finding that the semantic advantage correlated with right-hemisphere neocortical activations rather than left-hemisphere neocortical activations was somewhat unexpected, but consistent with some neuroimaging studies. A study using an overlapping sample of participants as assessed here found that increasing rate was associated with increased activation in left-hemisphere language regions important for reading, including the inferior frontal gyrus and superior temporal gyrus (Christodoulou et al., 2014), regions that may also play a role in verbal working memory and increased cognitive demands. Although the current study did not identify canonical left-hemisphere cerebral regions, right-lateralized cerebral regions such as those identified in the current analysis have been associated with semantic

integration and content processing in reading (St George et al., 1999; Vigneau et al., 2011). In particular, the predominantly right-hemisphere results are consistent with previous findings that support a role for the right hemisphere when greater inference or more effortful comprehension was required (St George et al., 1999), as was likely the case in the current study as individuals had to make rapid semantic judgements.

Although the focus of the current study was systems supporting rapid semantic processing, it is important to acknowledge the full range of systems that support reading. Broadly, these include phonological, pragmatic, orthographic, morphological, and syntactic systems; a thorough investigation across these areas was beyond the scope of the current study. Some of these systems, (e.g., phonological processing) have been shown to activate similar cerebellar regions as found here (Fulbright et al., 1999). Crucially, although both the TOWRE (timed) and WRMT (untimed) assessments are associated with phonological processing, only the TOWRE showed significant associations with cerebellar activation. Further, phonological skills were not correlated with cerebellar activation. This suggests that cerebellar engagement was particularly related to comprehension while reading at various speeds. Nonetheless, it possible that activation at the fastest rates was driven more by individual differences in lower-level decoding skills than individual differences in higher-order semantic skills. This may explain why we did not find correlations between passage-level reading rate (NDRT) and cerebellar activation, as performance on these may be less directly reliant on lower-level decoding skills.

4.4. The cerebellum, development of rapid semantic processing, and implications for reading disorders

The development of fluent reading occurs over many years of reading experience. Neuroimaging findings suggests that many aspects of the reading network require a significant amount of time and practice to fully specialize for reading. For example, the visual word form area, a key component of the reading network, does not fully specialize for print until early adulthood (Centanni et al., 2017). Rapid naming skills also develop with age (Cohen et al., 2018). In the current study, we found no relationship between age and cerebellar semantic advantage, and correlations between cerebellar semantic advantage and performance on timed reading measures remained significant when controlling for age. It is therefore possible that cerebellar response is associated with rapid semantic processing *skill* (reflecting experience), independent of age. However, the youngest participants in the current study were adolescents who already exhibited mature reading performance. Future research should examine cerebellar contributions to the development of fluent reading in younger children who are building their mastery of reading.

The cerebellum has also been implicated in disorders of reading. Predictive abilities, similar to those associated with cerebellar processing, may underlie rapid naming speed and impairments in these abilities may contribute to reading difficulty. For example, individuals with dyslexia continue to show difficulties in reading rate even after remediation for phonological processing deficits (Gabrieli, 2009; Stoodley & Stein, 2013). This has led to the suggestion that difficulties with skill automatization in individuals with dyslexia may be associated with cerebellar dysfunction (Alvarez and Fiez, 2018). Neuroimaging studies of individuals with dyslexia find abnormal cerebellar engagement during reading tasks and meta-analyses of dyslexia find that reduced cerebellar gray matter (GM) is one of the most distinctive biomarkers of dyslexia (Stoodley, 2014). One study reported increased left cerebellar activation during reading of non-meaningful sentences relative to single words in children with reading difficulties, and activation was negatively correlated with reading behavioral measures including word-level fluency (Rimrodt et al., 2009). Despite our findings being right-lateralized, these patterns of activation are consistent with our results in which high activation in fast implausible sentences relative to plausible

sentences was associated with slower overall reading rates. Here, we examined cerebellar contribution to rapid semantic processing in typical readers. However, future research should examine these processes in individuals with dyslexia across a wide age range.

The current study has several limitations. In standard assessments of reading, reading rate is commonly based on the reader's adaptation to text, rather than by the experimenter. However, the processes examined here are likely to approximate those involved in reading rate as they show correlations with commonly used reading measures in which readers determine their own reading rate. In addition, given that the purpose of the current study was to assess processes involved in rapid semantic processing during reading, and not accuracy per se, we did not exclude incorrect answers or omissions from the fMRI analysis. Therefore, activation patterns are likely to reflect error-based processes in addition to those underlying correct choice, particularly because accuracy was so high in many conditions. However, the cerebellar semantic advantage did not correlate with accuracy, suggesting that errors did not influence these activation patterns. Further, removing error trials might have confounded analyses of reading rate as it would have resulted in fewer trials in faster conditions (as these had the lowest accuracy). Next, a potential confound is that we found a trend for response time differences between semantically plausible and implausible conditions. Lastly, although we found correlations between rapid automatized naming and timed single-word measures of reading, there were no associations with passage-level reading rate. This may have been the result of lower power in this correlation due to a disproportionately higher rate of missing data for this subtest or may elucidate cerebellar-specific contributions to reading. Alternatively, rate for reading text passages may have been strongly associated with other capacities, such as background knowledge, comprehension, or executive functions, in addition to sub-lexical and lexical processes. Future research should examine the specific cerebellar contributions across sublexical, word-, and passage-levels of reading.

5. Conclusions

We assessed cerebellar contributions to rapid semantic processing by examining whether the cerebellum is engaged in judgments of semantic plausibility over changing reading rates. We found an interaction between reading rate and semantic plausibility, such that increasing reading rate was associated with greater cerebellar engagement only when sentences were comprehensible. These cerebellar regions disengaged for progressively faster presentation rates when sentences did not make sense. Individuals who showed high cerebellar engagement for fast, nonsensical sentences were slower on timed sub-lexical and lexical measures of reading. The cerebellum, therefore, appears to be part of a network of regions throughout the brain important for rapid semantic processing during reading.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bandl.2020.104828.

References

Alvarez, T. A., & Fiez, J. A. (2018). Current perspectives on the cerebellum and reading development. *Neuroscience & Biobehavioral Reviews, 92*, 55–66.

Ang, C., Zhang, J., Chu, M., Li, H., Tian, M., Feng, X., et al. (2020). Intrinsic cerebro-cerebellar functional connectivity reveals the function of cerebellum VI in reading-related skills. *Frontiers in Psychology, 11*.

Bastian, A. J. (2006). Learning to predict the future: The cerebellum adapts feedforward movement control. *Current Opinion in Neurobiology, 16*, 645–649.

Buckner, R. L., Krienen, F. M., Castellanos, A., Diaz, J. C., & Yeo, B. T. T. (2011). The organization of the human cerebellum estimated by intrinsic functional connectivity. *Journal of Neurophysiology, 106*, 2322–2345.

Centanni, T. M., King, L. W., Eddy, M. D., Whitfield-Gabrieli, S., & Gabrieli, J. D. E. (2017). Development of sensitivity versus specificity for print in the visual word form area. *Brain and Language, 170*, 62–70.

Chen, S. H. A., & Desmond, J. E. (2005). Temporal dynamics of cerebro-cerebellar network recruitment during a cognitive task. *Neuropsychologia, 43*, 1227–1237.

Christodoulou, J. A., Del Tufo, S. N., Lymberis, J., Saxler, P. K., Ghosh, S. S., Triantafyllou, C., et al. (2014). Brain bases of reading fluency in typical reading and impaired fluency in dyslexia. *PLoS ONE, 9*, Article e100552.

Cohen M, Mahé G, Laganaro M, Zesiger P (2018) Does the Relation between Rapid Automatized Naming and Reading Depend on Age or on Reading Level? A Behavioral and ERP Study. Front Hum Neurosci 12.

D'Mello AM, Turkeltaub PE, Stoodley CJ (2017) Cerebellar tDCS modulates neural circuits during semantic prediction: A combined tDCS-fMRI study. The Journal of Neuroscience 2818–16.

D'Mello AM, Gabrieli JDE, Nee DE (2020) Evidence for Hierarchical Cognitive Control in the Human Cerebellum. Current Biology. In Press.

Desmond, J. E., Gabrieli, J. D., Wagner, A. D., Ginier, B. L., & Glover, G. H. (1997). Lobular patterns of cerebellar activation in verbal working-memory and finger-tapping tasks as revealed by functional MRI. *Journal of Neuroscience, 17*, 9675–9685.

Diedrichsen, J. (2006). A spatially unbiased atlas template of the human cerebellum. *NeuroImage, 33*, 127–138.

Diedrichsen, J., Balsters, J. H., Flavell, J., Cussans, E., & Ramnani, N. (2009). A probabilistic MR atlas of the human cerebellum. *NeuroImage, 46*, 39–46.

Fuchs, L. S., Fuchs, D., Hosp, M. K., & Jenkins, J. R. (2001). Oral reading fluency as an indicator of reading competence: A theoretical, empirical, and historical analysis. *Scientific Studies of Reading, 5*, 239–256.

Fulbright, R. K., Jenner, A. R., Mencl, W. E., Pugh, K. R., Shaywitz, B. A., Shaywitz, S. E., et al. (1999). The cerebellum's role in reading: A functional MR imaging study. *AJNR. American Journal of Neuroradiology, 20*, 1925–1930.

Guell X, Schmahmann JD, Gabrieli JD, Ghosh SS (2018b) Functional gradients of the cerebellum. eLife Available at: https://elifesciences.org/articles/36652 [Accessed August 23, 2018].

Gabrieli, J. D. E. (2009). Dyslexia: A new synergy between education and cognitive neuroscience. *Science, 325*, 280–283.

Guell, X., Gabrieli, J. D. E., & Schmahmann, J. D. (2018). Triple representation of language, working memory, social and emotion processing in the cerebellum: Convergent evidence from task and seed-based resting-state fMRI analyses in a single large cohort. *NeuroImage, 172*, 437–449.

Guell, X., Goncalves, M., Kaczmarzyk, J. R., Gabrieli, J. D. E., Schmahmann, J. D., & Ghosh, S. S. (2019). LittleBrain: A gradient-based tool for the topographical interpretation of cerebellar neuroimaging findings. *PLoS ONE, 14*, Article e0210028.

Ito, M. (2008). Control of mental activities by internal models in the cerebellum. *Nature Reviews Neuroscience, 9*, 304–313.

Katzir, T., Kim, Y., Wolf, M., O'Brien, B., Kennedy, B., Lovett, M., & Morris, R. (2006). Reading fluency: The whole is more than the parts. *Annals of Dyslexia, 56*, 51–82.

Kim, Y.-S., Petscher, Y., Schatschneider, C., & Foorman, B. (2010). Does growth rate in oral reading fluency matter in predicting reading comprehension achievement? *Journal of Educational Psychology, 102*, 652–667.

Kipping, J. A., Grodd, W., Kumar, V., Taubert, M., Villringer, A., & Margulies, D. S. (2013). Overlapping and parallel cerebello-cerebral networks contributing to sensorimotor control: An intrinsic functional connectivity study. *NeuroImage, 83*, 837–848.

Küper, M., Kaschani, P., Thürling, M., Stefanescu, M. R., Burciu, R. G., Göricke, S., et al. (2016). Cerebellar fMRI Activation Increases with Increasing Working Memory Demands. *Cerebellum, 15*, 322–335.

Kuperberg, G. R., & Jaeger, T. F. (2016). What do we mean by prediction in language comprehension? *Language, Cognition and Neuroscience, 31*, 32–59.

Lang, C. E., & Bastian, A. J. (2002). Cerebellar damage impairs automaticity of a recently practiced movement. *Journal of Neurophysiology, 87*, 1336–1347.

Lesage, E., Hansen, P. C., & Miall, R. C. (2017). Right lateral cerebellum represents linguistic predictability. *Journal of Neuroscience, 37*, 6231–6241.

Mani, N., & Huettig, F. (2012). Prediction during language processing is a piece of cake–but only for skilled producers. *Journal of Experimental Psychology: Human Perception and Performance, 38*, 843–847.

Marek, S., et al. (2018). Spatial and temporal organization of the individual human cerebellum. *Neuron, 100*, 977–993.e7.

Mariën, P., & Beaton, A. (2014). The enigmatic linguistic cerebellum: Clinical relevance and unanswered questions on nonmotor speech and language deficits in cerebellar disorders. *Cerebellum Ataxias, 1*.

Marr, D. (1969). A theory of cerebellar cortex. *Journal of Physiology, 202*(437–470), 1.

Martin, A., Schurz, M., Kronbichler, M., & Richlan, F. (2015). Reading in the brain of children and adults: A meta-analysis of 40 functional magnetic resonance imaging studies. *Human Brain Mapping, 36*, 1963–1981.

Moberget, T., Gullesen, E. H., Andersson, S., Ivry, R. B., & Endestad, T. (2014). Generalized role for the cerebellum in encoding internal models: evidence from semantic processing. *Journal of Neuroscience, 34*, 2871–2878.

Moretti, R., Bava, A., Torre, P., Antonello, R. M., & Cazzato, G. (2002). Reading errors in patients with cerebellar vermis lesions. *Journal Of Neurology, 249*, 461–468.

National Institute of Child Health and Human Development (2000) Report of the National Reading Panel. Teaching children to read: An evidence-based assessment of the scientific research literature on reading and its implications for reading instruction (NIH Publication No. 00-4769).

Nicolson, R. I., Fawcett, A. J., & Dean, P. (2001). Developmental dyslexia: The cerebellar deficit hypothesis. *Trends in Neurosciences, 24*, 508–511.

Richlan, F., Kronbichler, M., & Wimmer, H. (2009). Functional abnormalities in the dyslexic brain: A quantitative meta-analysis of neuroimaging studies. *Human Brain Mapping, 30*, 3299–3308.

Riedel, B. W. (2007). The relation between DIBELS, reading comprehension, and vocabulary in urban first-grade students. *Reading Research Quarterly, 42*, 546–567.

Rimrodt, S. L., Clements-Stephens, A. M., Pugh, K. R., Courtney, S. M., Gaur, P., Pekar, J. J., et al. (2009). Functional MRI of sentence comprehension in children with dyslexia: beyond word recognition. *Cerebral Cortex, 19*, 402–413.

Roehrig, A. D., Petscher, Y., Nettles, S. M., Hudson, R. F., & Torgesen, J. K. (2008). Accuracy of the DIBELS oral reading fluency measure for predicting third grade reading comprehension outcomes. *Journal of School Psychology, 46*, 343–366.

Schmahmann, J. D. (2010). The role of the cerebellum in cognition and emotion: personal reflections since 1982 on the dysmetria of thought hypothesis, and its historical evolution from theory to therapy. *Neuropsychology Review, 20*, 236–260.

Sokolov, A., Miall, C., & Ivry, R. (2017). The cerebellum: Adaptive prediction for movement and cognition. *Trends in Cognitive Sciences, 21*, 313–332.

St George, M., Kutas, M., Martinez, A., & Sereno, M. I. (1999). Semantic integration in reading: Engagement of the right hemisphere during discourse processing. *Brain, 122*, 1317–1325.

Stoodley, C. J., & Stein, JF (2013). Cerebellar function in developmental dyslexia. *Cerebellum, 12*, 267–276.

Stoodley, C. J. (2012). The cerebellum and cognition: Evidence from functional imaging studies. *Cerebellum, 11*, 352–365.

Stoodley, C. J. (2014). Distinct regions of the cerebellum show gray matter decreases in autism, ADHD, and developmental dyslexia. *Frontiers in Systems Neuroscience, 8*, 92.

Stoodley, C. J., MacMore, J. P., Makris, N., Sherman, J. C., & Schmahmann, J. D. (2016). Location of lesion determines motor vs. cognitive consequences in patients with cerebellar stroke. *NeuroImage: Clinical, 12*, 765–775.

Stoodley, C. J., Valera, E. M., & Schmahmann, J. D. (2012). Functional topography of the cerebellum for motor and cognitive tasks: An fMRI study. *NeuroImage, 59*, 1560–1570.

Torgesen J, Wagner R, Rashotte C (1999) Test of Word Reading Efficiency. Austin, Texas: Pro-Ed. Inc.

Turkeltaub, P. E., Gareau, L., Flowers, D. L., Zeffiro, T. A., & Eden, G. F. (2003). Development of neural mechanisms for reading. *Nature Neuroscience, 6*, 767–773.

Vigneau, M., Beaucousin, V., Hervé, P.-Y., Jobard, G., Petit, L., Crivello, F., et al. (2011). What is right-hemisphere contribution to phonological, lexico-semantic, and sentence processing? Insights from a meta-analysis. *Neuroimage, 54*, 577–593.

Wagner, R. K., Torgesen, J. K., & Rashotte, C. A. (1999). *Comprehensive Test of Phonological Processing.* Austin, TX: Pro-Ed. Inc.

Wechsler, D. (1999) Wechsler Abbreviate Scale of Intelligence (WASI). San Antonio, TX: The Psychological Corporation.

Whitfield-Gabrieli, S., & Nieto-Castanon, A. (2012). Conn: A functional connectivity toolbox for correlated and anticorrelated brain networks. *Brain Connectivity, 2*, 125–141.

Wolf M, Denckla M (2005) RAN/RAS: Rapid Automatized Naming and Rapid Alternating Stimulus Tests. Austin, TX: Pro-Ed. Inc.

Wolf, M., & Katzir-Cohen, T. (2001). Reading Fluency and Its Intervention. *Scientific Studies of Reading, 5*, 211–239.

Woo, C.-W., Krishnan, A., & Wager, T. D. (2014). Cluster-extent based thresholding in fMRI analyses: Pitfalls and recommendations. *NeuroImage, 91*, 412–419.

Woodcock, R. (1998). *Woodcock Reading Mastery Tests, Revised Normative Update.* Circle Pines, MN: American Guidance Service.