HHS Public Access
Author manuscript
Neuropsychologia. Author manuscript; available in PMC 2021 November 01.

Published in final edited form as:
Neuropsychologia. 2020 November ; 148: 107630. doi:10.1016/j.neuropsychologia.2020.107630.

Functional parcellation of the right cerebellar lobule VI in children with normal or impaired reading

Hehui Li[a], **James R. Booth**[b], **Xiaoxia Feng**[a], **Na Wei**[a], **Manli Zhang**[c], **Jia Zhang**[a], **Hejing Zhong**[a], **Chunming Lu**[a], **Li Liu**[a], **Xiangzhi Meng**[c,d,*], **Guosheng Ding**[a,*]

[a]State Key Laboratory of Cognitive Neuroscience and Learning & IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing, 100875, P.R. China

[b]Department of Psychology and Human Development, Vanderbilt University, Nashville, TN 37203-5721, USA

[c]School of Psychological and Cognitive Sciences, Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing, 100871, P.R. China

[d]PekingU-PolyU Center for Child Development and Learning, Peking University, Beijing, 100871, P.R. China

Abstract

Neuroimaging studies have reported that the right cerebellar lobule VI is engaged in reading, but its role is unclear. The goal of our study was to identify functionally-dissociable subregions in the right lobule VI and how these subregions contribute to reading in children with normal or impaired reading. In Experiment I, typically developing children performed an orthographic task and a phonological task during functional magnetic resonance imaging (fMRI). We classified the voxels in the right lobule VI into seven zones based on the patterns of functional connectivity with the cerebrum across both tasks. In Experiment II, we compared the brain activation and cerebro-cerebellar connectivities of each subregion between children readers with different reading levels. We did not find significant group differences in cerebellar activation. However, we found that impaired readers had considerably higher functional connectivity between R1 and the right angular gyrus and the right precuneus compared to the control group in the phonological task. These

*Corresponding Author: Guosheng Ding, State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing, 100875, P. R. China. Work: 86-13552929824, Fax: 86-10-58806154, dinggsh@bnu.edu.cn; Xiangzhi Meng, School of Psychological and Cognitive Sciences, Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing, 100871, P. R. China, Work: 86-18210920692, Fax: 86-10-62761081, mengxzh@pku.edu.cn.

Author contribution statement

Experiment I. Conceptualization and Methodology: Guosheng Ding, Xiangzhi Meng, Wei Na; Investigation: Wei Na; Formal analysis: Hehui Li; Original Draft: Hehui Li, Guosheng, Ding; Review & Editing: Guosheng Ding, Xiangzhi Meng, James Booth, Liu Li, Chunming Lu; Supervision: Guosheng Ding, Xiangzhi Meng.

Experiment II. Conceptualization and Methodology: Guosheng Ding, Xiangzhi, Meng; Investigation: Xiaoxia Feng, Hehui Li, Jia Zhang, Hejing Zhong; Formal analysis: Hehui Li; Original Draft: Hehui Li, Guosheng, Ding; Review & Editing: Guosheng Ding, Xiangzhi Meng, James Booth, Liu Li, Chunming Lu; Supervision: Guosheng Ding, Xiangzhi Meng.

Declarations of interest

The authors have no conflicts of interest to declare.

findings show that the right cerebellar lobule VI is functionally parceled and its subregions might be differentially connected with the cerebrum between children with normal reading abilities and those with impaired reading.

Keywords

the cerebellum; right cerebellar lobule VI; reading impairment; phonological; functional connectivity

1. Introduction

Increasing evidence has shown that successful reading relies not only on the cerebrum, but also on the cerebellum (Alvarez & Fiez, 2018; van Kemenade, et al., 2018). For example, consistent activation in the cerebellum, especially the right cerebellar lobule VI, has been observed during reading (Martin, Schurz, Kronbichler, & Richlan, 2015; Turkeltaub, Eden, Jones, & Zeffiro, 2002). In addition, structural or functional abnormalities in the right cerebellar lobule VI were associated with reading impairment (Eckert, et al., 2016; Feng, et al., 2017; Richlan, et al., 2010). Gray matter volume in the right lobule VI could also be used as a biomarker to differentiate dyslexic readers and typical readers (Pernet, Poline, Demonet, & Rousselet, 2009). Although the engagement of the right cerebellar lobule VI in reading is convincing, how its contributions to reading remains unclear.

Reading is a multifaceted process, which requires integration of both domain-general cognitive processes (e.g., sensory-motor processing) and linguistic specific processes (e.g., orthographic, phonological, and semantic processing) (Achal, Hoeft, & Bray, 2015). Given that the right cerebellar lobular VI was also engaged in working memory (Ashida, Cerminara, Edwards, Apps, & Brooks, 2019; Rottschy, et al., 2012) and sensorimotor processing (Yuan & Brown, 2015), its function in reading could be associated with domain general processes rather than linguistic specific processing. On the other hand, it was found that the right cerebellar lobule VI was still significantly activated in the verb generation task after controlling the articulatory process. It may suggest that this region was integral to linguistic processes, such as semantic processing (Ashida, et al., 2019; Frings, et al., 2006). Therefore, it is to be determined whether it is engaged in domain general processes or linguistic specific processing.

Controversies also exist in the studies of reading disability. The cerebellar deficit hypothesis proposed that the cerebellum impacts reading via either motor/automatization processing or linguistic specific processing, such as articulation skill or phonological skill (Nicolson, Fawcett, & Dean, 2001). Consistent with this theory, dysfunction of the right cerebellar lobule VI in dyslexic readers has been reported in both motor sequence learning tasks (Menghini, Hagberg, Caltagirone, Petrosini, & Vicari, 2006; Nicolson, et al., 1999) and rhyming tasks (Meng, et al., 2016; Richlan, et al., 2010). A recent study compared the cerebral neural activities between impaired readers and typical readers in motor-related regions and language-related regions (Crus I and Crus II), and found that impaired readers showed reduced activation only in the motor-related regions compared to typical readers in the silent word reading task, suggesting that cerebellar aberrance is associated with motor process (Cullum, Hodgetts, Milburn, & Cummine, 2019). However, language-related regions in Cullum et al. (2019) did not include the right cerebellar lobule VI, which could be a reason for the absence of group effect in language areas. Ashburn, Flowers, Napoliello, and Eden (2020) took the right lobule VI as cerebellar language areas and compared the functional connectivity between the right lobule VI and cerebral regions in typical and impaired readers. However, no significant group differences were observed. In that study, they used the whole right lobule VI as a seed to identify its connected cerebral regions, which was probably not sensitive enough, considering that this lobule is likely a functional heterogeneous region.

Several studies suggest that the right cerebellar lobule VI may consist of functionally specialized areas (Buckner, Krienen, Castellanos, Diaz, & Yeo, 2011; Ji, et al., 2019). Based on the intrinsic functional connectivity patterns between the cerebrum and cerebellum, Buckner et al. (2011) divided the cerebellum into different functional networks, and the right cerebellar lobule VI included several subregions which belong to different functional networks such as the sensorimotor, attention, frontoparietal, and default mode networks. Notably, subregions obtained based on resting-state data might not be able to depict how the cerebrum and the cerebellum work together during reading tasks. King et al. (2019) defined a functional atlas in the cerebellum with a multiple domain task battery. In their study, the right cerebellar lobule VI consisted of subregions specifically activated in motor processing, visual working memory, visual letter recognition, and verbal fluency (King, Hernandez-Castillo, Poldrack, Ivry, & Diedrichsen, 2019). However, they did not employ reading specific tasks in their study.

In the current study, we examined the functional parcellation of the right cerebellar lobule VI during reading tasks. We addressed two issues: 1) whether the right cerebellar lobule VI could be segregated into subregions associated with different cognitive processing, either domain general processing or linguistic specific processing; 2) how the subregions of the right lobule VI, if they could be segregated, are associated with reading impairment. We focused on the right lobule VI because this region of the cerebellum was most often reported in neuroimaging studies of reading and impairment (Eckert et al., 2016; Linkersdörfer et al., 2012; Stoodley et al., 2013; Booth et al., 2007). In addition, previous research has been inconclusive of how the right lobule VI is engaged in reading. Both increased and decreased activation have been found in dyslexic readers compared to typical readers in reading or reading-related tasks (Feng et al., 2017; Richlan et al., 2010; Meng et al., 2016), so our study attempted to resolve some of the inconsistencies.

We conducted two fMRI experiments. In Experiment I, we categorized the selected cerebellar voxels into different subregions according to their connectivity profiles with cerebral regions during typically developing children performing reading tasks. We hypothesized that connectivity with certain cerebral region(s) could provide a clue on how each subregion is associated with different processing during reading, given that it is relatively clear how different cerebral regions take part in reading. Specifically, we supposed that some subregions were involved in domain-general processes, namely sensorimotor processing, and others were involved in linguistic processes, namely orthographic and phonological processing, which could be determined with which cerebral region(s) they connect to during reading. In Experiment II, we compared the neural activation and cerebro-cerebellar functional connectivities of each subregion between typically developing children and reading-impaired children. We hypothesized that the subregions of the right lobule VI responsible for linguistic processing would show alterations in impaired readers, as deficits in orthographic and phonological processing are frequently associated with reading impairment (D'Mello & Gabrieli, 2018).

2. Experiment I

2.1 Methods

2.1.1 Participants—Sixteen typically developing Chinese children (mean age = 10.0 years, age range = 8.9 - 11.2 years, 3 males, Table 2) participated in Experiment I. All of them were right-handed according to self-report (Edinburgh Handedness Inventory, Oldfield, 1971), and had normal or corrected-to-normal vision. None of the children had head injuries or a history of neurological or psychiatric disorders. Parents' reports and ratings were used to verify that the children recruited in the experiment had no attention deficit hyperactivity disorder (ADHD, Feng et al., 2017). This study was approved by the Ethical Review Board of Beijing Normal University. Written consent was obtained from each participant and his/her guardian(s) before the experiment.

2.1.2 Behavioral measures—The Raven's Standard Progressive Matrices was administered to measure the children's abstract reasoning, considered as an estimation of the nonverbal IQ (Raven and Court., 1998). A standardized Chinese Character Recognition Test and a Reading Comprehension Test were administered to measure the participants' reading ability.

The standardized Chinese Character Recognition Test consisted of 210 single Chinese characters, which were divided into ten groups based on their difficulty (Wang & Tao, 1993). The participants were asked to generate a word or phrase which contains the given character/morpheme. For example, 池/chi2/ (meaning pool) could be used in the word '池塘/chi2tang2/ (meaning pond)'. The number of correct answers was recorded as the raw score. Participants who scored above one standard deviation (SD) below the mean were recruited as typical readers for the study.

The Reading Comprehension Test included 95 simple sentences, each paired with five multiple-choice pictures (Feng, et al., 2017; Li, et al., 2018; You, et al., 2011). The children were required to read each sentence and select the picture that best matched the meaning of that sentence. The participants were encouraged to complete as many sentences as possible within seven minutes.

2.1.3 fMRI tasks—Before the experiment, the children were allowed to play in a mock scanner so that they could get familiar with the MRI environment and be comfortable when entering the real scanner. During the scanning, they were asked not to move their head while performing the tasks. If they felt uncomfortable for any reason, they could squeeze a rubber alarm ball to stop the experiment.

Two reading tasks, orthographic (Chinese character-spelling) and phonological (Chinese character-homophone) task, were designed. There were two scanning runs, one for each task. Each run included six task blocks and seven fixation blocks, lasting for nearly six minutes. The character and fixation blocks were presented alternately. All fixation blocks had a duration of 24 s, whereas the length of each character block was randomized from 24 s to 36 s, with an average time of 30 s containing ten trials. The duration of each trial was 3000 ms, including a 2500 ms character presentation followed by a 500 ms blank screen.

In the fixation blocks, participants passively viewed a central asterisk. In the character-spelling task, they were required to determine whether the two characters had similar shapes or not (Fig. 1; materials can be found in Table. S1). The strokes, frequency, structural, and tone information of those characters in the "yes" and "no" conditions were well matched. Structural information included single component, top-bottom, left-right, enclosed, top-middle-bottom. For the character rhyming task, they were asked to determine whether the two simultaneously presented characters sound the same or not by pressing a button (Fig. 1; Table. S1). The strokes and structural as well as tone information of those characters in the "yes" and "no" condition were well matched. However, the word frequency was higher in the "yes" response condition compared to the "no" condition ($t = 2.27$, $p = 0.024$). The response hand in the two tasks was counterbalanced across participants. Stimuli were projected onto a screen placed in front of the MR scanner and viewed using a mirror mounted to the head coil. Stimuli were presented, and responses were recorded with E-prime software (Psychology Software Tools, Inc.).

2.1.4 Scan acquisition—Whole-brain images were acquired with a 3T Siemens Trio Scanner at MRI center of Beijing Normal University, using a T2*-weighted echo planar imaging (EPI) sequence. The parameters were as follows: flip angle = 90°; echo time (TE) = 30 ms; repetition time (TR) = 3000 ms; field of view (FOV) = 200 mm; voxel size = 3.1×3.1×4.0 mm, 30 slices (4 mm). T1-weighted images were also acquired using the following parameters: flip angle= 7°; TE = 3.39 ms; TR = 2530 ms; FOV = 256 mm; voxel size = 1.3×1.0×1.3 mm, 128 slices (1.33 mm).

2.1.5 fMRI preprocessing—Functional image preprocessing was conducted with Data Processing Assistant for Resting-State fMRI (DPARSFA software http://www.restfmri.net/forum/DPARSF) in MATLAB 14a. The procedures were as follows: (1) image data first underwent slice timing correction and then were realigned to the middle scan in the functional series; (2) each participant's high-resolution structural image was motion-corrected and co-registered to its mean functional image as well as spatially normalized to the Montreal Neurological Institute (MNI); (3) normalized images were smoothed with a 6 mm full-width half-max (FWHM) Gaussian kernel; and (4) high-pass filtering with a cutoff of 1/128 Hz was used and the linear trends were removed.

2.1.6 Determining the functional subregions of the right lobule VI—Language processing is right lateralized in the cerebellum (Hubrich-Ungureanu, Kaemmerer, Henn, & Braus, 2002; Jansen, et al., 2005; Sokolov Arseny, Miall R, & Ivry Richard, 2017), which could be due to the contralateral anatomical connections between the cerebellum and the cerebrum (Booth, Wood, Lu, Houk, & Bitan, 2007; Pleger & Timmann, 2018). Thus, here we focused on the right cerebellum VI and explored its role in typical and atypical reading.

Two brain masks were defined. One was the right cerebellar lobule VI andextracted from a specific cerebellar template in the SUIT toolbox (http://www.diedrichsenlab.org/imaging/suit.htm). Then it was resampled in MNI space with a voxel size of 2*2*2 (Fig. 2A). Notably, after being resliced, the mask slightly extended to the Crus I (Fig. 2A). The other mask was the bilateral cerebrum, which was made via the Wake Forest University PickAtlas tool (https://www.nitrc.org/projects/wfu_pickatlas). Previous studies have reported contralateral (Alvarez & Fiez, 2018; Sokolov Arseny, et al., 2017) and ipsilateral (Buckner, et al., 2011) cerebral-cerebellar connections. Therefore, in the current study, bilateral cerebrum rather than only the left was used to depict the functional relations between the right lobule VI and the cerebrum.

For each participant, the functional connectivity between each voxel in the right cerebellar lobule VI and each voxel in bilateral cerebrum was calculated and organized into a matrix. Functional connectivity analysis between each pair was performed after removing the time series of the fixation blocks. Temporal correlations of the BOLD signal were calculated across all concatenated task periods(Cole, Bassett, Power, Braver, & Petersen, 2014; Krienen, Yeo, & Buckner, 2014; Liu, et al., 2016). The matrix consisted of rows indicating voxels within the right cerebellar lobule VI and columns representing voxels within bilateral cerebrum. Values in the matrix represented the index of the functional connectivity (FC) and were normalized into standard scores as well as averaged across subjects. Two separate matrices were obtained for the phonological and orthographic tasks, respectively.

K-means clustering was used to group the voxels into the same cluster in the right cerebellar lobule VI with homogenous FC to the cerebrum. To determine the appropriate number of clusters, the k value varied from 2 to 10. For each k, the k-means clustering was repeated 100 times to find the minimal total within-cluster sum of squares (WSS). The ratio of WSS divided by the total sum-of-squares was characterized as the unexplained variance associated with each k value. The total sum-of-squares indicated the Euclidean distance between each voxel and the central voxel. The within-category sum-of-squares indicated the sum of squares of the Euclidean distance between each voxel and the central voxel of the corresponding cluster. As Fig. 2 shows, the unexplained variance decreased with increasing k. In addition, the percentage of the overlapping area across two tasks was calculated. Subregions obtained in two tasks largely overlapped (Fig.2C), suggesting that functional parcellation was stable across different tasks.

The voxels within the mask of the right cerebellar lobule VI was finally grouped into seven clusters, in which the unexplained variances in the orthographic and phonological tasks were both lower than 40%. Voxels extending to Crus I were assembled into a separate cluster (Fig. 3), so we could examine FC confined to lobule VI.

2.1.7 Statistical analysis—After identifying seven subregions in the right cerebellar lobule VI, the following analyses were performed. First, we extracted the overlap regions (labeled R1, R2, R3, R4, R5, R6, and R7) defined by FC in the two reading tasks for further analysis. Second, each subregion was used as a seed to identify the FC patterns that divided these subregions, during which a winner-take-all approach was used (Buckner, et al., 2011; Marek, et al., 2018). Specifically, the FC pattern specific to a subregion referred to the voxels in the cerebrum that have a higher FC with this subregion compared with other subregions. A threshold of voxel-level $p < 0.001$ with a FWE corrected cluster-level $p < 0.05$ was used.

We compared the FC pattern corresponding to each subregion with that of Buckner et al., (2011). The cerebro-cerebellar functional relations have been integrated into Neurosynth so that regions functionally connected with a specific location can be assessed (https://www.neurosynth.org/locations/). Here, we used the central coordinates of each subregion to identify its connected cerebral regions.

Finally, to quantitatively and interactively decode each FC statistical map specific to each subregion, the Neurosynth image decoder was used (Gorgolewski, et al., 2015; Huckins, et al., 2019; Krieger-Redwood, et al., 2016; Rubin, et al., 2017), during which the correlation between the unthresholded FC statistical map and keywords related meta-maps in the Neurosynth database was calculated. The correlation coefficients were then used to generate a ranking of keywords associated with these statistical maps.

2.2 Results

2.2.1 Demographics and behavioral results—The demographic information is presented in Table 2.

Two paired-sample t-tests were performed, with two tasks (phonological and orthographic task) as the within-subject factor and accuracy or reaction time as the dependent variables. The results showed that reaction time was significantly higher ($t(1, 15) = 7.49$, $p < 0.000$) and accuracy was numerically lower ($t(1, 15) = -2.05$, $p = 0.058$) in the phonological task compared to the orthographic task, suggesting that the phonological task was more difficult than the orthographic task.

2.2.2 Seven subregions in the cerebellar lobule VI—Based on the FC pattern between the right cerebellar lobule VI and bilateral cerebrum under the phonological and orthographic tasks, the lobule VI was divided into seven subregions. The overlapping regions (Fig. 3 & Table 3) account for 78% of the area of the right lobule VI. To explore whether the high overlapping ratio was due to the clustering number or not, we calculated the ratio where k value varied from 2 to 10. The result showed that all of the overlapping ratios were larger than 70% (Fig. 2C), suggesting that the high overlapping ratio was less likely to be influenced by the clustering number. Then, we extracted the overlapping voxels in each subregion defined in the two reading tasks. These subregions were shown in Fig. 3 and were named R1 (dark blue region), R2 (light blue region), R3 (cyan region) R4 (yellow region), R5 (bright red region), R6 (dark red region), and R7 (orange region). Notably, R6 extends to right Crus I, whereas R7 was on the edge. These seven overlapping regions were used for further analysis.

2.2.3 FC between subregions and the cerebral cortex—Each subregion showed similar FC patterns with the cerebrum across tasks. Specifically, compared to the other regions, R1 was connected with the left pre- and post-central gyri, the supplementary motor area, along with subcortical regions including the thalamus and para-hippocampal gyrus (Fig.4; Table, S3). R2 was connected with bilateral inferior frontal gyri, the postcentral gyrus, and insula (Fig.4; Table, S3). R3 was connected with bilateral inferior occipital gyri and regions around the supplementary motor area. R4 was connected with bilateral fusiform gyri, bilateral inferior occipital gyri, and bilateral parietal lobules (Fig.4; Table S3). R5 was connected with bilateral medial fusiform gyri and postcentral gyrus (Fig.4; Table S3). R6 was connected with inferior frontal gyrus, parietal lobule, and middle occipital gyrus. No cerebral regions showed significantly higher FC with R7 compared to the other subregions. We also compared functional connectivity across tasks, but no significant task effect was observed. These results indicate that functional parcellation might be independent of tasks.

We then compared the FC pattern with Buckner et al. (2011). Interestingly, we found that the FC pattern specific to R1, R2, and R6 was similar to this previous study. The remaining regions R3, R4, and R5 also showed a similar FC pattern with that of Buckner et al. (2011), except in the current study, these subregions were also strongly connected with visual areas. Two reading tasks in our study relied heavily on visual-orthographic processing, which might contribute to the connection between the cerebellum and visual regions.

Neurosynth was used to decipher each FC image corresponding to each subregion (Table 4). The results suggest that the FC map specific to R1 was associated with sensorimotor processing or finger tapping. The FC map specific to R2 is linked to speech production. The FC map specific to R3 was associated with visual processing. The FC map specific to R4 was linked to visual and orthographic processing. The FC map specific to R5 was related to visual processing, orthographic processing, and auditory processing. The FC map specific to R6 was associated with higher-level cognitive processing, including semantic processing, phonological processing, and working memory.

These results indicate that functional parcellation exists in the right cerebellar lobule VI. Specifically, R1 and R3 were implicated in domain general cognitive processing, responsible for sensorimotor and visual processing, respectively. Whereas R2 and R6 were responsible for linguistic specific processes, such as articulation and phonological processing. R4 and R5 might be responsible for multiple roles, such as visual-orthographic processing and visual-auditory integration.

3. Experiment II

In Experiment I, we identified seven subregions engaged in reading in typical readers. In Experiment II, we further compared brain activation and functional connectivity between impaired readers and typical readers during two reading tasks.

3.1 Materials and method

3.1.1 Participants—Experiment II recruited another two groups of participants, 20 typical readers (7 boys, mean age = 10.3 years, age range = 8.7 – 11.6 years) and 14 impaired readers (9 boys, mean age = 10.2, age-range = 8.9 – 11.4 years). This dataset has no overlap with that in Experiment I. All of the participants were right-handed, with normal or corrected-to-normal vision, and had no head injuries or a history of neurological or psychiatric disorders. Parents' reports and ratings were used to verify that the participants had no attention deficit hyperactivity disorder (ADHD). Written consent was obtained from each participant and his/her guardians before the experiment.

3.1.2 Behavioral measures—The Raven's Standard Progressive Matrices test was used to measure nonverbal IQ. A standardized Chinese Character Recognition Test and a Reading Comprehension Test were administered to measure the participants' Chinese reading ability. In addition, we used Chinese phonological awareness test to tap into phonological manipulation ability (Shu et al., 2006; Shu et al.,2008) and a digit cancellation test (Mirsky et al., 1991) to assess attention level as well as a rapid naming test to index automatization ability (Feng et al., 2017).

The Chinese phonological awareness test consisted of four subtests, including phoneme deletion, tone detection, onset detection, and rhyme detection. In the phoneme deletion test, participants were asked to say the remaining part (for example, "an2") of a spoken word (for example,"tan2") after the omission of a given phoneme (for example,"t") (Shu et al., 2006). There were 16 items. In the tone detection, onset detection, and rhyme detection test, participants were required to indicate which tone, or initial or final sound, of the four spoken single-syllable real words was distinct from the other three. Each subtest contained 20 items (Shu et al., 2008). A composite score for Chinese phonological awareness was calculated by averaging the standard scores of these four tests for each participant.

The rapid naming test was a paper-pencil test requiring participants to read numbers one by one as fast and accurately as possible (Feng et al., 2017). Task performance was indexed by the average time to read all of the numbers twice.

The digit cancellation test was a paper-pencil test and consisted of 25 rows of 40 digits each. In each row, digits from "0" to "9" were arranged in random order. The participants were required to cross out all occurrences of '3' row by row in three minutes.

All of the participants were from the same cohort as Li et al. (2018). We first conducted a large-scale screening procedure in 2554 children who were from several primary schools, during which children were asked to perform the Chinese Character Recognition Test, the Reading Comprehension Test, the Raven's Standard Progressive Matrices test as well as the digit cancellation tests. Raw scores of the Raven's were transformed to percentiles based on the Chinese norm (Zhang & Wang, 1985), whereas raw scores of the other tests were transformed to standard scores with a mean of 100 and a standard deviation of 15. 103 children with percentiles equal or above the 50th percentile in the Raven's Standard Progressive Matrices test took part in the second stage of the experiment. In this step, they performed the Chinese phonological awareness test and the rapid naming test. As above, raw scores of these two tests were transformed to standard scores based on 103 children.

Finally, Children were classified as impaired readers if (1) their standard scores were 1.5 SDs below-average in the Chinese Character Recognition Test or (2) one SD below-average in the Chinese Character Recognition Test and 1.5 SDs below average in a Chinese phonological awareness test (Feng et al., 2017). Based on these criteria, 14 participants were identified as impaired readers. The typical readers all scored above one SD below-average on the Chinese Character Recognition Test and the Chinese phonological awareness test. 20 children were identified as typical readers, with age and IQ matched to the impaired readers.

3.1.3 fMRI tasks—The two reading tasks and the associated procedures were similar to that in Experiment I. However, there were differences in the number of blocks and trials. In Experiment II, there were four task blocks with a number of trials ranging from 8 to 12 and five fixation blocks with 10 trials each. In Experiment I, the phonological task was a homophone judgment task, whereas in Experiment II, the phonological task was a rhyme judgment task, during which the participant was required to judge whether the two presented characters rhymed with each other or not. The strokes, frequency, structural as well as tone information of those characters in the "yes" and "no" condition were well matched in both the phonological task and orthographic task (Table. S2).

3.1.4 Scan acquisition—Whole-brain images were acquired with a 3T Siemens Trio Scanner at MRI center of Beijing Normal University. The parameters were as follows: flip angle = 81°; TE = 30 ms; TR = 2400 ms; slice thickness = 3 mm; in-plane resolution = 3×3 mm, matrix = 64×64, 40 slices (3 mm). T1-weighted images were also acquired using the following parameters: flip angle = 9°; TE = 4.18 ms; TR = 2300 ms; FOV = 256 mm; slice thickness = 1 mm; in-plane resolution = 1×1 mm, axial slices = 176.

3.1.5 fMRI preprocessing—Functional image preprocessing was the same as in Experiment I.

3.1.6 Statistical analysis—Two steps were conducted in Experiment II. First, voxel-based FC analyses seeded with each subregion were conducted, during which regions specifically connected with each subregion identified by Experiment I were used as masks (Fig.5). Statistical images were thresholded at voxel-level $p < 0.001$ and cluster-level FWE $p < 0.05$. To further investigate which region was involved in reading, activation of each subregion in the two tasks was then compared, contrast images in the character-spelling task (orthographic task, OT) or character-rhyming task (phonological task, PT) versus the fixation were generated using the general linear model. Mean β values of the voxels in each subregion in the two reading tasks were extracted and analyzed with one-sample t-tests. Activation analysis was corrected using the False Discovery Rate (FDR) procedure with a = 0.05. Given that R7 was on the edge of the right cerebellum VI and was not significantly connected with cerebral regions, we only focused on the first six subregions in the following analysis.

Second, 1) In terms of activation, two-way repeated analysis of variance (ANOVA) was calculated in each subregion, with task as the within-subject factor, group as the between-subject factor, and activation of each subregion as the dependent variable (Fig.5). The statistical significance of each analysis was corrected with FDR, a = 0.05. 2) In terms of FC with the cerebral areas, two-way repeated ANOVAs were also calculated in each voxel within two masks: the cerebral cortical areas that showed specific FC with the corresponding subregion of right lobule VI (Fig.5, Mask 1) and the rest of the cerebral cortex (Fig.5, Mask 2). For example, the cerebral areas showing higher FC with R1 in the two tasks (identified in Experiment I) were combined and defined as Mask 1 (Fig.5) and the remaining cerebral areas served as Mask 2. Statistical maps were thresholded at voxel-level $p < 0.001$ and cluster-level was adjusted to FWE $p < 0.004$ (the commonly used alpha level of 0.05 was divided by 12 because we had two masks and six subregions). 3) Analyses on FC were limited to the reading network. Based on a recent meta-analysis on single-word reading, we defined 11 regions of interest (ROIs) in the cerebral reading network (Table 5; Murphy et al., 2019). The FC between each ROI and each subregion in each task was calculated and used as the dependent variable, separately. Two-way ANOVAs (Group * Task) were conducted for the FC between each subregion and ROI. The significance of each analysis was corrected with FDR, a = 0.05 for multiple comparisons.

3.2 Results

3.2.1 Demographic and behavioral results—The behavior measures showed that impaired readers scored significantly lower than typical readers on the Chinese Character Recognition Test, the Reading Comprehension Test, and the Chinese phonological task, indicating that impaired readers had deficits in reading abilities and phonological processing abilities.

For the two tasks in the scanner, the phonological task (PT) was significantly more difficult than the orthographic task (OT), with a higher reaction time ($t = 8.9$, $p < 0.001$; PT, mean = 1927 ms, SD = 264; OT, mean = 1133 ms, SD = 212) and a lower accuracy ($t = 8.2$, $p < 0.001$; PT, mean = 0.68, SD = 0.05; OT, mean = 0.94, SD = 0.15, $p < 0.000$). However, we did not observe significant group difference between the typical and impaired readers either in the orthographic or phonological task (Table 4).

3.2.2 FC pattern and activation in all readers—To validate the results obtained in Experiment I, we conducted a similar FC analysis in all readers in Experiment II. The results showed that the main FC patterns observed in Experiment I were repeated. Specifically, R1 was connected with bilateral post- and pre-central gyri. R2 was connected with bilateral post-central gyri. R3 was connected with bilateral inferior occipital gyri. R4 was connected with bilateral inferior occipital gyri, bilateral fusiform gyri, and bilateral parietal lobules. R5 was connected with medial occipital gyrus and pre- and post-central gyri. R6 was connected with temporal gyrus, parietal lobule, and frontal gyrus (Fig.1S). This verified the FC patterns observed in Experiment I.

As to the activation of each subregion, one-sample t-tests were first conducted on each subregion in the two reading tasks. The results showed that all subregions were significantly activated. For the orthographic task, R1 ($t = 8.2$, $p < 0.001$, FDR corrected), R2 ($t = 3.7$, $p < 0.001$, FDR corrected), R3 ($t = 8.9$, $p < 0.001$, FDR corrected), R4 ($t = 10.0$, $p < 0.001$, FDR corrected), R5 ($t = 4.0$, $p < 0.001$, FDR corrected), R6 ($t = 6.0$, $p < 0.001$, FDR corrected), R7 ($t = 4.3$, $p < 0.001$, FDR correlated). For the phonological task, R1 ($t = 7.5$, $p < 0.001$, FDR corrected), R2 ($t = 5.8$, $p < 0.001$, FDR corrected), R3 ($t = 6.9$, $p < 0.001$, FDR corrected), R4 ($t = 8.6$, $p < 0.001$, FDR corrected), R5 ($t = 4.7$, $p < 0.001$, FDR corrected), R6 ($t = 7.9$, $p < 0.001$, FDR corrected), R7 ($t = 3.0$, $p < 0.005$, FDR corrected).

Given the results of Experiment I suggest that R2 might be responsible for speech production and R6 might be responsible for phonological processing, it is expected that these two regions were more likely to be engaged in phonological tasks. Two-sample t-tests were then conducted in each subregion to examine task effects. As expected, activation in R2 ($t = -2.8$, $p = 0.008$; FDR uncorrected) and R6 ($t = -2.2$, $p = 0.037$; FDR uncorrected) were higher in the phonological task than that in the orthographic task, and such difference was not observed in other subregions. But this effect did not survive after multiple comparisons.

3.2.3 Differences between the typical and impaired readers in terms of activation—We then conducted two-way ANOVA analyses in each ROI, with groups and tasks as the independent variables and activation as the dependent variable. No interaction effect (*ps* > 0.5) or main effect of group was observed (*ps* > 0.3). We only observed main effect of task in R2 ($F_{(1,32)} = -7.4$, $p = 0.01$, uncorrected) and R6 ($F_{(1,32)} = -4.7$, $p = 0.037$, uncorrected), with higher activation in the phonological task compared to the orthographic task. However, these results did not survive after multiple comparison correction.

Two-sample t-tests were further conducted between typical and impaired readers in each ROI and each task. However, no significant group effect was observed in any of these ROIs (*ps* > 0.2). We also used the functional subregions in the right lobule VI obtained by Buckner et al. (2011) (five subregions), Ji et al. (2019) (eight subregions), and King et al. (2019) (six subregions). Only one region in Ji et al. (2019) showed significantly higher activation in the phonological tasks compared to the orthographic task ($F_{(1,32)} = -4.5$, $p = 0.031$, FDR uncorrected), which did not survive after multiple comparison correction.

Notably, in our previous study, Feng et al. (2017) observed significantly higher activation in impaired readers in the anterior part of the cerebellar lobule VI in the orthographic task. This region partly overlapped with R1 (Fig. 6B), suggesting that R1 might be associated with reading impairment.

3.2.4 Differences between the typical and impaired readers in terms of FC—In Experiment I, cerebral regions that showed specific FC with each subregion were identified. In Experiment II, within these regions (see data analyses pipeline in Fig. 5, Mask 1), two-way ANOVAs were conducted, with group and task as the independent variables and voxel-based FC seeded by each subregion as the dependent variables. However, no significant effects were observed.

Then we conducted two-way ANOVAs within the rest of the cerebral areas (Fig.5, Mask 2). We found that FC between R1 and the right angular gyrus (MNI coordinate: x = 60, y = −54, z = 38, Z value = 4.82, cluster size = 517, voxel-level $p < 0.001$, cluster-level FWE $p = 0.0002$) and the right precuneus (MNI coordinate: x = 4, y = −68, z = 24, Z value = 4.40, cluster size = 563, voxel-level $p < 0.001$, cluster-level FWE $p = 0.0001$) showed significant interaction effects. Given that there was a marginal group difference in IQ, we used IQ score as a covariate and these interaction effects were still significant. The follow-up analyses showed that group difference between typical and impaired readers was only observed in the phonological task. Specifically, impaired readers had higher FC between R1 and the right angular gyrus (MNI coordinate: x = 56, y = −42, z = 32, Z value = 3.56, cluster size = 33, voxel-level $p < 0.001$) and between R1 and the right precuneus (MNI coordinate: x = −10, y = −58, z = 22, Z value = 3.79, cluster size = 21, voxel-level $p < 0.001$), as compared to typical readers in only the phonological task but not the orthographic task.

Task differences were also observed, reflecting higher FC in the phonological task compared to the orthographic task. The higher FC was mainly with the bilateral frontal regions and the left motor areas. Specifically, R2 had higher FC with the left precentral gyrus, the right superior frontal gyrus, the right middle cingulum, and the right inferior frontal gyrus in the phonological task compared to the orthographic task. R3 had higher FC with the left superior frontal gyrus, the left anterior cingulum, and the right superior medial frontal gyrus; R4 had higher FC with the left postcentral gyrus and the left superior frontal gyrus; R5 had higher FC with the left supplementary motor area, the left postcentral gyrus, and the right middle frontal gyrus; and R6 had FC with the left inferior frontal gyrus and the right superior frontal gyrus. After controlling for IQ, these task effects were still significant.

3.2.5 FC analyses specific to reading network—

When examining regions in the reading network, we found that FC between R1 and right inferior frontal gyrus ($F(1, 32) = 14.25$, $p = 0.001$, $\eta^2 = 0.31$, FDR correlated, Fig.7B) and between R2 and right superior parietal lobule ($F(1, 32) = 12.74$, $p = 0.001$, $\eta^2 = 0.31$, FDR correlated, Fig.7B) showed significant main effects of group, with a higher FC in impaired readers compared to typical readers. Main effects of task were also observed, with the left postcentral gyrus having higher FC with R2, R3, R4, R5, and R6 in the phonological task compared to the orthographic task (Fig.7B). After controlling for IQ, these significant group or task effects were still significant. No interaction effects or main effects of group were observed in any other subregions.

4. Discussion

In the current study, we investigated the function of the right cerebellar lobule VI in typical and impaired reading. In Experiment I, typical readers performed a character matching task and a rhyming task, and seven subregions within the right lobule VI were identified based on their functional connectivity (FC) patterns with the cerebrum. These subregions were connected with certain cerebral areas in both tasks. In Experiment II, group comparisons were conducted between typical and impaired readers. No significant group or interaction effects were observed for the activation of any subregion. However, functional connections between the cerebrum and R1 were significantly higher in impaired readers compared to typical readers when they performed the phonological task. These results deepen our understanding of the role of the right cerebellar lobule VI in reading in several ways.

4.1 Functional segregation of the right cerebellar lobule VI in reading

Established neural models of reading have mainly focused on the contributions of the cerebral regions (Dehaene, 2009; Perfetti, Cao, & Booth, 2013). Emerging evidence has suggested that the cerebellum is also important for reading (Stoodley & Stein, 2013). For example, previous studies have reported significant activation in the right lobule VI during the visually presented rhyming task (Gao, et al., 2015), the auditorily presented rhyming task (Meng, et al., 2016), character processing tasks (Krafnick, et al., 2016; Peng, et al., 2003), the single-word reading task (Cullum, et al., 2019). However, it remains unclear how this region is involved in reading. Some have suggested that the cerebellar contributions to reading mainly via motor processing (Danelli, et al., 2013; Fawcett, Nicolson, & Dean, 1996; Nicolson, et al., 1999). Meanwhile research also revealed that the relationship between the cerebellum and reading was associated with linguistic processing, such as speech production or phonological processing (Cullum, et al., 2019; Mariën, et al., 2014). In the current study, we hypothesized that the right cerebellar lobule VI might be multi-functional during reading, consisting of regions responsible for both motor and language processing.

To this end, we first explored functional segregation of the right cerebellar lobule VI in performing both phonological and orthographic tasks, and seven subregions were identified. Then we deciphered the FC patterns specific to each subregion to infer the contribution of these subregions to reading. The results showed that the subregions in the lobule VI identified by the orthographic and phonological tasks largely overlapped and showed similar FC with the cerebrum. Specifically, we observed that R1 was connected with left pre-and post-central gyri and left the supplementary motor area, suggesting that this region is associated with sensorimotor processing. R2 was connected with bilateral post-central gyri and insula, suggesting an association with speech production. R3 was connected with bilateral lingual gyri and regions around the supplementary motor area, suggesting that it is involved in visual processing. R4 was connected with bilateral fusiform gyri, bilateral inferior occipital gyri, and bilateral inferior parietal lobules; R5 was connected with bilateral medial occipital and pre-central gyri. R4 and R5 might be involved in orthographic and orthographic-phonological processing. R6 was connected with inferior frontal gyrus, superior temporal gyrus, and fusiform gyrus, suggesting it plays a role in semantic processing, phonological processing, and working memory. This FC pattern was replicated in Experiment II with an independent sample.

Buckner et al. (2011) examined functional parcellation of the cerebellum with cerebro-cerebellar connections during resting-state. In the current study, we used functional connectivity during two reading tasks to divide the right cerebellar lobule VI. We found that the FC patterns specific to R1, R2, and R6 in our study were similar to those reported by Buckner et al. (2011). The functional connection patterns in the other three regions (R3, R4, and R5) in our study were different from Buckner et al. (2011), as only we found significant connections with visual regions. This difference could be attributed to the fact that visual orthographic processing is heavily reliant on in the two reading tasks in the current study, but not for resting state in Buckner et al. (2011).

Recently, King et al. (2019) examined the functional parcellation of the whole cerebellum, based on brain activation in 26 diverse tasks. As to the function of the right lobule VI, our results were not completely consistent with King et al. (2019). For example, R1 connecting with the left sensorimotor cortex in the current study overla*ps* with the regions responsible for motor planning in King et al. (2019). R2 connecting with regions involved in speech production in the current study corresponds to areas engaged in working memory and letter recognition in King et al. (2019). The R3, R4, and R5 regions connecting with bilateral occipital gyri, bilateral fusiform gyri, and bilateral inferior parietal lobules were probably involved in visual-orthographic processing or visual-auditory integration, but in King et al. (2019) this region corresponds to the areas engaged in verbal fluency, attention and active maintenance. Inconsistent subregions resulting from different methods warrant further investigation.

Notably, although we assumed that the functional parcellation might be influenced by tasks, and designed two tasks to investigate task effect, we found that the subregions obtained across tasks highly overlapped in Experiment I. To explore whether this pattern is tied to certain k value(s), we calculated the total overlapping voxels of the corresponding subregions across tasks with cluster numbers varying from 2 to 10. The overlapping ratios were all larger than or equal to 70% (99%, 93%, 86%, 70%, 70%, 78%, 76%, 79%, 74%). In contrast, in Experiment II we observed significant task effects of FC between the cerebellar subregions and the cerebral areas, especially in the frontal and motor cortex, indicating that as the tasks get harder, communication between the cerebellum and cerebrum becomes stronger. Differences in task effects across experiments might be related to differences in sample sizes. The sample size of Experiment II is almost twice that in Experiment I.

4.2 Abnormality of functional connectivity in impaired readers

Functional contributions of the right lobule VI to reading disability remains inconclusive. Both increased and decreased neural activation have been reported in impaired readers compared to typical readers (Feng, et al., 2017; Linkersdörfer, Lonnemann, Lindberg, Hasselhorn, & Fiebach, 2012; Meng, et al., 2016; Richlan, et al., 2010). The discrepancy across previous studies could be due to the heterogeneity of the right lobule VI. To help resolve these inconsistencies, we compared the neural activity of each subregion (R1~R6) between the typical and impaired readers. No significant main effect or interaction effect involving group was found. However, the voxel-based FC analyses showed significant interaction effects, with higher FC between R1 and two cerebral regions, the right angular gyrus and the right precuneus, in impaired readers as compared to typical readers. These effects were found in the phonological task but not in the orthographic task. Increased FC in impaired readers was also observed in the ROI-based FC analyses, in which we found that R1 had greater FC with the right inferior frontal gyrus in impaired readers compared to typical readers irrespective of task. Overall, FC results indicated that the anterior part of the right lobule VI (i.e., R1) is involved in impaired reading.

A recent study compared intrinsic FCs across groups, in which they observed higher FC in impaired readers than typical readers between the right lobule VI and the right lateral occipital cortex (Greeley et al., 2020). However, this result was not necessarily associated with reading abilities in that the observed group difference was based on resting state imaging data. Different from this study, the current study, Feng et al. (2017), and Ashburn et al. (2020) performed reading tasks.

Our result is partially consistent with Feng et al., (2017), in which they found that the anterior part of the right lobule VI, an area partly overlapping with R1 in our study, showed higher activation and higher FC with the left fusiform gyrus in dyslexic readers compared to typical readers. These two studies jointly suggest that the right anterior lobule VI might be associated with reading impairment. However, Feng et al., (2017) found increased FC with the left fusiform gyrus, but we found increased FCs with the right angular gyrus and the right precuneus. The reasons for these differences might be twofold. First, Feng et al., (2017) conducted 24 ROI-based FC analyses without multiple comparison corrections. In our study, all 66 ROI-based FC analyses went through FDR (a = 0.05) correction. This strict threshold criterion may have limited the observation of significant results in the left hemisphere. Second, the ROIs selected by Feng et al., (2017) were all in the left cerebrum. Converging evidence suggests that the reading network involves both hemispheres (Cattinelli, et al., 2013; Martin, et al., 2015; Murphy, Jogia, & Talcott, 2019; Turkeltaub, et al., 2002). In the current study, based on a recent meta-analytic study on single-word reading (Murphy, Jogia, & Talcott, 2019), we selected nine ROIs from the left hemisphere and two from the right hemisphere. FC analyses between these ROIs and the subregions in right lobule VI offer a relatively more comprehensive picture across the hemispheres.

The present study also extended the analytical approach of Feng et al., (2017). The right lobule VI in our study was divided into functional subregions, with roles in reading inferred via the functional connectivity pattern. The R1 region sensitive to reading impairment is likely related to sensorimotor processing rather than linguistic processing. In addition, the cerebral regions showing abnormal FC with R1 in poor readers in Experiment II were not the cerebral regions that connected with R1 for the typical readers in Experiment I. This suggests that instead of damaging the typical cerebro-cerebellar connections, reading impairment might increase the other cerebro-cerebellar connections.

Ashburn et al. (2020) investigated the FC pattern of the right lobule VI with the cerebrum between typical readers and impaired readers too; however, they did not observe significant group differences. This discrepancy could be due to different tasks across studies. Ashburn et al. (2020) used an implicit reading task that required participants to make a response based on word visual features. In the current study, we used a rhyming task, requiring children to judge whether two presented characters sound alike, which relies on explicitly phonological decoding. Greater demand for phonological processing might in turn contribute to the increased cerebro-cerebellar connections in impaired readers. In addition, Ashburn et al. (2020) used the whole right lobule VI as their ROI. In the current study, stronger FC in impaired readers was only observed in R1, which was just a subregion. Compared to a subregion, the whole lobule VI might not be sensitive enough to detect the cerebro-cerebellar connection patterns because of the potential functional parcellation within an antomical region.

Another important consideration concerns language differences. We studied native Chinese speakers, whereas Ashburn et al. (2020) studied native English speakers. The writing systems of these two languages differ from each other (Cao, et al., 2013; Cao, et al., 2017; Ramus, Altarelli, Jednoróg, Zhao, & di Covella, 2017). For English readers, phonological information is extracted by assembling the decoded phonemes, whereas, for Chinese, it is usually directly addressed from long term memory based on orthographic information (Tan, Laird, Li, & Fox, 2005; Xia, Hancock, & Hoeft, 2017). As a result, reading in English relies heavily on phonological analysis, while reading in Chinese relies more on visual analysis (Ramus, et al., 2017; Xia, et al., 2017). In addition, Chinese characters are learned with writing, so that motor systems aid in character recognition (Cao, et al., 2013). In Experiment I, we found that the posterior parts of right lobule VI were implicated in phonological processing; whereas the anterior parts of right lobule VI were implicated in motor and visual processing. Therefore, the posterior and anterior parts might be preferentially engaged in reading in English and Chinese, respectively. In support of this, several studies have observed a reduced gray matter volume and activation in the posterior parts of right lobule VI in native English speakers (Eckert et al., 2016; Meng et al., 2017; Linkersdörfer et al., 2012; Richlan, et al., 2010). For Chinese, Feng et al. (2017) observed hyperactivation of the anterior part of right lobule VI in dyslexic readers. Yang et al. (2013) also reported increased activation in the lobule IV/V, a motor-related region. In the current study, R1, also a motor-related region, shows an increased connection with the cerebral areas in dyslexic readers. Taken together, the posterior parts of right lobule VI (and/or the surrounding regions, i.e., Crus I) might be selectively impaired in English dyslexic readers, whereas the anterior parts of right lobule VI (and/or the surrounding regions, i.e, lobule IV/V) might be abnormal in Chinese dyslexic readers.

What is the functional significance of increased FC of R1 with the right angular gyrus and the right precuneus in impaired readers in the phonological task? Stronger activation in the right angular gyrus has been observed in the processing of pseudowords compared to real words (Cattinelli, et al., 2013). In contrast, processing real words is associated with greater activation in bilateral precuneus compared to pseudoword processing (Cattinelli, et al., 2013; Taylor, Rastle, & Davis, 2013). Without a lexical representation, pseudowords can only rely on grapheme to phoneme mapping principles and the brain regions engaged in phonological processing. Therefore, greater activation in the right angular gyrus might be associated with increased reliance on phonological processing. Real words can activate semantic information which is absent in pseudowords. Greater activation in precuneus for impaired readers suggests increased reliance on semantic processing. Therefore, the current results indicate that impaired readers tend to increase FC between the cerebellum and the phonological or semantic regions during the phonological task. In the ROI-based FC analysis, the right inferior frontal gyrus showed significant group effect, with a higher FC between this region and R1 in impaired readers compared to typical readers. The right inferior frontal gyrus was frequently reported to be hyper-activated in readers with reading difficulties (Aylward, et al., 2003; Rumsey, et al., 1992; S. E. Shaywitz, et al., 1998). Moreover, activation in this region increased with the age of impaired readers (B. A. Shaywitz, et al., 2002) and could predict their future reading gain (Hoeft, et al., 2011; B. A. Shaywitz, et al., 2004). As reported, the right inferior frontal gyrus showed consistently greater activation in pseudoword processing compared to real word processing (Taylor et a., 2013), suggesting that this region was implicated in phonological processing. Stronger activation in this region might be caused by the compensation for the functional disruption of the posterior phonological-related regions, such as the left temporoparietal junction (Hoeft, et al., 2011).

The hyper-FC observed in the current study might also be a compensatory mechanism for impaired readers. First, we observed higher FC rather than lower in impaired compared to typical readers. Second, the regions in the cerebrum showing higher FC with R1 were outside of the cerebellar-subregions identified in Experiment I in typical readers. Third, regions showing higher FC with R1 were all in the right cerebral hemisphere. Language processing is left-lateralized in the cerebrum (Cao, 2016; Frost, et al., 1999). Impaired readers rely more on the right hemisphere compared to typical readers (Di Liberto, et al., 2018; Kovelman, et al., 2012; Milne, Syngeniotis, Jackson, & Corballis, 2002; B. A. Shaywitz, et al., 2002; Waldie, Haigh, Badzakova-Trajkov, Buckley, & Kirk, 2013). Homogeneous regions in the right hemisphere have been regarded as potential compensatory regions in impaired reading (Cao, et al., 2017; Eden, et al., 2004; Li, Tao, Peng, & Ding, 2017).

No significant group effects were observed for performance in the scanner. The lack of difference could be due to the low sensitivity of the experimental tasks. The orthographic task was relatively easy and resulted in high accuracy, as children were only required to make a visual judgment. In contrast, the rhyming task was relatively difficult, as children needed to access to phonological information from orthographic information, which may have resulted in a floor effect. An alternative explanation for the lack of performance differences in the scanner could be due to the increased cerebro-cerebellar connection in dyslexic readers. This compensatory mechanism might facilitate phonological access for dyslexic readers.

4.3 Limitations

An obvious limitation of the current study is the small sample size in both experiments, 16 typically developing readers were recruited in Experiment I, and 34 participants (20 typically developing readers and 14 impaired readers) were recruited in Experiment II. However, the FC patterns were replicated in the two experiments, suggesting that these effects are reliable. Notably, the IQ score was higher in impaired readers than typical readers. However, after we regressed out the IQ score, the main effects or interaction effects were still significant. Finally, we only focused on functional parcellation of the right cerebellar lobule VI during orthographic and phonological processing. Future studies are required to verify whether these functional subdivisions are replicable in other reading-related tasks, such as semantic processing.

5. Conclusion

Our results show functional segregation in the right cerebellar lobule VI, which consists of subregions that are engaged in either domain general processes or linguistic specific processing. Specifically, the anterior part (R1) appears to be involved in domain-general sensorimotor processing. The postero-medial (R2) appears to be responsible for speech production. The postero -lateral part (R3, R4, and R5) appears to be important for visual processing. The region (R6) extending to the lobule Crus I seems to be engaged in semantic and phonological processing. When comparing reading impaired children with typically developing children, we did not observe any functional deficits in R6. But we observed that the functional connection between cerebral regions and R1 increased in impaired readers, suggesting alterations in sensorimotor processing and reliance on the right cerebral hemisphere for compensation.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

This work was supported by grants from the National Natural Science Foundation of China (NSFC: 31971039, 31971036). It was also supported by a grant from the National Institute of Child Health and Human Development (HD042049) awarded to James R. Booth.

References

Achal S, Hoeft F, & Bray S (2015). Individual Differences in Adult Reading Are Associated with Left Temporo-parietal to Dorsal Striatal Functional Connectivity. Cerebral Cortex, 26, 4069–4081. [PubMed: 26400921]

Alvarez TA, & Fiez JA (2018). Current Perspectives on the Cerebellum and Reading Development. Neuroscience & Biobehavioral Reviews, 92, 55–66. [PubMed: 29730484]

Ashburn SM, Flowers DL, Napoliello EM, & Eden GF (2020). Cerebellar function in children with and without dyslexia during single word processing. Human brain mapping, 41, 120–138. [PubMed: 31597004]

Ashida R, Cerminara NL, Edwards RJ, Apps R, & Brooks JC (2019). Sensorimotor, language, and working memory representation within the human cerebellum. Human brain mapping.

Aylward EH, Richards TL, Berninger VW, Nagy WE, Field KM, Grimme AC, Richards AL, Thomson J, & Cramer SC (2003). Instructional treatment associated with changes in brain activation in children with dyslexia. Neurology, 61, 212–219. [PubMed: 12874401]

Booth JR, Wood L, Lu D, Houk JC, & Bitan T (2007). The role of the basal ganglia and cerebellum in language processing. Brain research, 1133, 136–144. [PubMed: 17189619]

Buckner RL, Krienen FM, Castellanos A, Diaz JC, & Yeo BT (2011). The organization of the human cerebellum estimated by intrinsic functional connectivity. American Journal of Physiology-Heart and Circulatory Physiology, 106, 2322–2345.

Cao F (2016). Neuroimaging studies of reading in bilinguals. Bilingualism: Language and Cognition, 19, 683–688.

Cao F, Vu M, Lung Chan DH, Lawrence JM, Harris LN, Guan Q, Xu Y, & Perfetti CA (2013). Writing affects the brain network of reading in Chinese: A functional magnetic resonance imaging study. Human brain mapping, 34, 1670–1684. [PubMed: 22378588]

Cao F, Yan X, Wang Z, Liu Y, Wang J, Spray GJ, & Deng Y (2017). Neural signatures of phonological deficits in Chinese developmental dyslexia. NeuroImage, 146, 301–311. [PubMed: 27890803]

Cattinelli I, Borghese NA, Gallucci M, & Paulesu E (2013). Reading the reading brain: A new meta-analysis of functional imaging data on reading. Journal of neurolinguistics, 26, 214–238.

Cole MW, Bassett DS, Power JD, Braver TS, & Petersen SE (2014). Intrinsic and task-evoked network architectures of the human brain. Neuron, 83, 238–251. [PubMed: 24991964]

Cullum A, Hodgetts WE, Milburn TF, & Cummine J (2019). Cerebellar Activation During Reading Tasks: Exploring the Dichotomy Between Motor vs. Language Functions in Adults of Varying Reading Proficiency. The Cerebellum, 1–17.

D'Mello AM, & Gabrieli JD (2018). Cognitive neuroscience of dyslexia. Language, speech, and hearing services in schools, 49, 798–809.

Danelli L, Berlingeri M, Bottini G, Ferri F, Vacchi L, Sberna M, & Paulesu E (2013). Neural intersections of the phonological, visual magnocellular and motor/cerebellar systems in normal readers: Implications for imaging studies on dyslexia. Human brain mapping, 34, 2669–2687. [PubMed: 22736513]

Dehaene S (2009). Reading in the brain: The new science of how we read: Penguin.

Di Liberto GM, Peter V, Kalashnikova M, Goswami U, Burnham D, & Lalor EC (2018). Atypical cortical entrainment to speech in the right hemisphere underpins phonemic deficits in dyslexia. NeuroImage, 175, 70–79. [PubMed: 29609008]

Eckert MA, Berninger VW, Vaden KI, Gebregziabher M, Tsu L, & Consortium DD (2016). Gray Matter Features of Reading Disability: A Combined Meta-Analytic and Direct Analysis Approach. eneuro, 3, ENEURO.0103-0115.2015.

Eden GF, Jones KM, Cappell K, Gareau L, Wood FB, Zeffiro TA, Dietz NA, Agnew JA, & Flowers DL (2004). Neural changes following remediation in adult developmental dyslexia. Neuron, 44, 411–422. [PubMed: 15504323]

Fawcett AJ, Nicolson RI, & Dean P (1996). Impaired performance of children with dyslexia on a range of cerebellar tasks. Annals of Dyslexia, 46, 259–283. [PubMed: 24234275]

Feng XX, Li L, Zhang ML, Yang XJ, Tian MY, Xie WY, Lu Y, Liu L, Belanger NN, Meng XZ, & Ding GS (2017). Dyslexic Children Show Atypical Cerebellar Activation and Cerebro-Cerebellar Functional Connectivity in Orthographic and Phonological Processing. Cerebellum, 16, 496–507. [PubMed: 27785760]

Frings M, Dimitrova A, Schorn CF, Elles H-G, Hein-Kropp C, Gizewski ER, Diener HC, & Timmann D (2006). Cerebellar involvement in verb generation: an fMRI study. Neuroscience letters, 409, 19–23. [PubMed: 17046160]

Frost JA, Binder JR, Springer JA, Hammeke TA, Bellgowan PS, Rao SM, & Cox RW (1999). Language processing is strongly left lateralized in both sexes: Evidence from functional MRI. Brain, 122, 199–208. [PubMed: 10071049]

Gao y., Wei N, Wang Z, Jian J, Ding G, Meng X, & Liu L (2015). Interaction between native and second language processing: Evidence from a functional magnetic resonance imaging study of Chinese-English bilingual children. Acta Psychologica Sinica, 47, 1419–1432.

Gorgolewski KJ, Varoquaux G, Rivera G, Schwarz Y, Ghosh SS, Maumet C, Sochat VV, Nichols TE, Poldrack RA, & Poline J-B (2015). NeuroVault. org: a web-based repository for collecting and sharing unthresholded statistical maps of the human brain. Frontiers in neuroinformatics, 9, 8. [PubMed: 25914639]

Hancock R, Richlan F, & Hoeft F (2017). Possible roles for fronto-striatal circuits in reading disorder. Neuroscience & Biobehavioral Reviews, 72, 243–260. [PubMed: 27826071]

Hoeft F, McCandliss BD, Black JM, Gantman A, Zakerani N, Hulme C, Lyytinen H, Whitfield-Gabrieli S, Glover GH, & Reiss AL (2011). Neural systems predicting long-term outcome in dyslexia. Proceedings of the National Academy of Sciences, 108, 361–366.

Hubrich-Ungureanu P, Kaemmerer N, Henn FA, & Braus DF (2002). Lateralized organization of the cerebellum in a silent verbal fluency task: a functional magnetic resonance imaging study in healthy volunteers. Neuroscience letters, 319, 91–94. [PubMed: 11825678]

Huckins JF, Adeyemo B, Miezin FM, Power JD, Gordon EM, Laumann TO, Heatherton TF, Petersen SE, & Kelley WM (2019). Reward - related regions form a preferentially coupled system at rest. Human brain mapping, 40, 361–376. [PubMed: 30251766]

Jansen A, Flöel A, Van Randenborgh J, Konrad C, Rotte M, Förster AF, Deppe M, & Knecht S (2005). Crossed cerebro–cerebellar language dominance. Human brain mapping, 24, 165–172. [PubMed: 15486988]

Ji JL, Spronk M, Kulkarni K, Repovš G, Anticevic A, & Cole MW (2019). Mapping the human brain's cortical-subcortical functional network organization. NeuroImage, 185, 35–57. [PubMed: 30291974]

King M, Hernandez-Castillo C, Poldrack R, Ivry R, & Diedrichsen J (2019). Functional boundaries in the human cerebellum revealed by a multi-domain task battery. Nature neuroscience.

Kovelman I, Norton ES, Christodoulou JA, Gaab N, Lieberman DA, Triantafyllou C, Wolf M, Whitfield-Gabrieli S, & Gabrieli JD (2012). Brain basis of phonological awareness for spoken language in children and its disruption in dyslexia. Cerebral Cortex, 22, 754–764. [PubMed: 21693783]

Krafnick AJ, Tan L-H, Flowers DL, Luetje MM, Napoliello EM, Siok W-T, Perfetti C, & Eden GF (2016). Chinese Character and English Word processing in children's ventral occipitotemporal cortex: fMRI evidence for script invariance. NeuroImage, 133, 302–312. [PubMed: 27012502]

Krieger-Redwood K, Jefferies E, Karapanagiotidis T, Seymour R, Nunes A, Ang JWA, Majernikova V, Mollo G, & Smallwood J (2016). Down but not out in posterior cingulate cortex: Deactivation yet functional coupling with prefrontal cortex during demanding semantic cognition. NeuroImage, 141, 366–377. [PubMed: 27485753]

Krienen FM, Yeo BT, & Buckner RL (2014). Reconfigurable task-dependent functional coupling modes cluster around a core functional architecture. Philosophical Transactions of the Royal Society B: Biological Sciences, 369, 20130526.

Li H, Booth JR, Bélanger NN, Feng X, Tian M, Xie W, Zhang M, Gao Y, Ang C, Yang X, Liu L, Meng X, & Ding G (2018). Structural correlates of literacy difficulties in the second language: Evidence from Mandarin-speaking children learning English. NeuroImage, 179, 288–297. [PubMed: 29902587]

Li H, Tao W, Peng D, & Ding G (2017). The Causal Relationship between Developmental Dyslexia and Abnormal Brain Regions:Research Paradigms and the Relevant Findings. Psychological Development and Education, 33, 631–640.

Linkersdörfer J, Lonnemann J, Lindberg S, Hasselhorn M, & Fiebach CJ (2012). Grey matter alterations co-localize with functional abnormalities in developmental dyslexia: an ALE meta-analysis. PloS One, 7, e43122. [PubMed: 22916214]

Liu L, Li H, Zhang M, Wang Z, Wei N, Liu L, Meng X, & Ding G (2016). Aberrant topologies and reconfiguration pattern of functional brain network in children with second language reading impairment. Developmental science, 19, 657–672. [PubMed: 27321248]

Marek S, Siegel JS, Gordon EM, Raut RV, Gratton C, Newbold DJ, Ortega M, Laumann TO, Adeyemo B, & Miller DB (2018). Spatial and Temporal Organization of the Individual Human Cerebellum. Neuron.

Mariën P, Ackermann H, Adamaszek M, Barwood CH, Beaton A, Desmond J, De Witte E, Fawcett AJ, Hertrich I, & Küper M (2014). Consensus paper: language and the cerebellum: an ongoing enigma. The Cerebellum, 13, 386–410. [PubMed: 24318484]

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. [PubMed: 25628041]

Meng XZ, You HL, Song MX, Desroches AS, Wang ZK, Wei N, Tian MY, Gaab N, & Ding GS (2016). Neural deficits in auditory phonological processing in Chinese children with English reading impairment. Bilingualism-Language and Cognition, 19, 331–346.

Menghini D, Hagberg GE, Caltagirone C, Petrosini L, & Vicari S (2006). Implicit learning deficits in dyslexic adults: An fMRI study. NeuroImage, 33, 1218–1226. [PubMed: 17035046]

Milne RD, Syngeniotis A, Jackson G, & Corballis MC (2002). Mixed lateralization of phonological assembly in developmental dyslexia. Neurocase, 8, 209–209.

Murphy K, Jogia J, & Talcott J (2019). On the neural basis of word reading: A meta-analysis of fMRI evidence using activation likelihood estimation. Journal of neurolinguistics, 49, 71–83.

Nicolson RI, Fawcett AJ, Berry EL, Jenkins IH, Dean P, & Brooks DJ (1999). Association of abnormal cerebellar activation with motor learning difficulties in dyslexic adults. The Lancet, 353, 1662–1667.

Nicolson RI, Fawcett AJ, & Dean P (2001). Developmental dyslexia: the cerebellar deficit hypothesis. Trends in Neurosciences, 24, 508–511. [PubMed: 11506881]

Oldfield. (1971). The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia, 9, 97–113. [PubMed: 5146491]

Peng D. l., Xu D, Jin Z, Luo Q, Ding G. s., Perry C, Zhang L, & Liu Y (2003). Neural basis of the non - attentional processing of briefly presented words. Human brain mapping, 18, 215–221. [PubMed: 12599280]

Perfetti C, Cao F, & Booth J (2013). Specialization and universals in the development of reading skill: How Chinese research informs a universal science of reading. Scientific studies of reading, 17, 5–21. [PubMed: 24744605]

Pernet CR, Poline JB, Demonet JF, & Rousselet GA (2009). Brain classification reveals the right cerebellum as the best biomarker of dyslexia. BMC neuroscience, 10, 67. [PubMed: 19555471]

Pleger B, & Timmann D (2018). The role of the human cerebellum in linguistic prediction, word generation and verbal working memory: evidence from brain imaging, non-invasive cerebellar stimulation and lesion studies. Neuropsychologia.

Ramus F, Altarelli I, Jednoróg K, Zhao J, & di Covella LS (2017). Neuroanatomy of developmental dyslexia: pitfalls and promise. Neuroscience & Biobehavioral Reviews.

Richlan F, Sturm D, Schurz M, Kronbichler M, Ladurner G, & Wimmer H (2010). A common left occipito-temporal dysfunction in developmental dyslexia and acquired letter-by-letter reading? PloS one, 5, e12073. [PubMed: 20711448]

Rottschy C, Langner R, Dogan I, Reetz K, Laird AR, Schulz JB, Fox PT, & Eickhoff SB (2012). Modelling neural correlates of working memory: a coordinate-based meta-analysis. NeuroImage, 60, 830–846. [PubMed: 22178808]

Rubin TN, Koyejo O, Gorgolewski KJ, Jones MN, Poldrack RA, & Yarkoni T (2017). Decoding brain activity using a large-scale probabilistic functional-anatomical atlas of human cognition. PLoS computational biology, 13, e1005649. [PubMed: 29059185]

Rumsey JM, Andreason P, Zametkin AJ, Aquino T, King AC, Hamburger SD, Pikus A, Rapoport JL, & Cohen RM (1992). Failure to activate the left temporoparietal cortex in dyslexia: An oxygen 15 positron emission tomographic study. Archives of Neurology, 49, 527–534. [PubMed: 1580816]

Shaywitz BA, Shaywitz SE, Blachman BA, Pugh KR, Fulbright RK, Skudlarski P, Mencl WE, Constable RT, Holahan JM, & Marchione KE (2004). Development of left occipitotemporal systems for skilled reading in children after a phonologically-based intervention. Biological psychiatry, 55, 926–933. [PubMed: 15110736]

Shaywitz BA, Shaywitz SE, Pugh KR, Mencl WE, Fulbright RK, Skudlarski P, Constable RT, Marchione KE, Fletcher JM, & Lyon GR (2002). Disruption of posterior brain systems for reading in children with developmental dyslexia. Biological psychiatry, 52, 101–110. [PubMed: 12114001]

Shaywitz SE, Shaywitz BA, Pugh KR, Fulbright RK, Constable RT, Mencl WE, Shankweiler DP, Liberman AM, Skudlarski P, & Fletcher JM (1998). Functional disruption in the organization of the brain for reading in dyslexia. Proceedings of the National Academy of Sciences, 95, 2636–2641.

Sokolov Arseny A, Miall R C, & Ivry Richard B (2017). The Cerebellum: Adaptive Prediction for Movement and Cognition. Trends in cognitive sciences, 21, 313–332. [PubMed: 28385461]

Stoodley CJ, & Stein JF (2013). Cerebellar function in developmental dyslexia. The Cerebellum, 12, 267–276. [PubMed: 22851215]

Tan LH, Laird AR, Li K, & Fox PT (2005). Neuroanatomical correlates of phonological processing of Chinese characters and alphabetic words: A meta - analysis. Human brain mapping, 25, 83–91. [PubMed: 15846817]

Taylor J, Rastle K, & Davis MH (2013). Can cognitive models explain brain activation during word and pseudoword reading? A meta-analysis of 36 neuroimaging studies. In: American Psychological Association.

Turkeltaub PE, Eden GF, Jones KM, & Zeffiro TA (2002). Meta-analysis of the functional neuroanatomy of single-word reading: method and validation. NeuroImage, 16, 765–780. [PubMed: 12169260]

van Kemenade BM, Arikan BE, Podranski K, Steinsträter O, Kircher T, & Straube B (2018). Distinct Roles for the Cerebellum, Angular Gyrus, and Middle Temporal Gyrus in Action-Feedback Monitoring. Cerebral Cortex.

Waldie KE, Haigh CE, Badzakova-Trajkov G, Buckley J, & Kirk IJ (2013). Reading the wrong way with the right hemisphere. Brain Sciences, 3, 1060–1075. [PubMed: 24961521]

Wang X, & Tao B (1993). Chinese character recognition test battery and assessment scale for primary school children. In: Shanghai, China: Shanghai Education Press.

Xia Z, Hancock R, & Hoeft F (2017). Neurobiological bases of reading disorder Part I: Etiological investigations. Language and Linguistics Compass, 11.

You H, Gaab N, Wei N, Cheng-Lai A, Wang Z, Jian J, Song M, Meng X, & Ding G (2011). Neural deficits in second language reading: fMRI evidence from Chinese children with English reading impairment. NeuroImage, 57, 760–770. [PubMed: 21146615]

Yuan Y, & Brown S (2015). Drawing and writing: An ALE meta-analysis of sensorimotor activations. Brain and cognition, 98, 15–26. [PubMed: 26051526]

Highlights

1. We investigated functional parcellation of the right cerebellar lobule VI in reading.
2. Seven subregions were identified based on the FC patterns during tasks.
3. The subregions suggest to be implicated in domain-general and language processing.
4. Impaired reading was associated with abnormality of the sensorimotor zone.

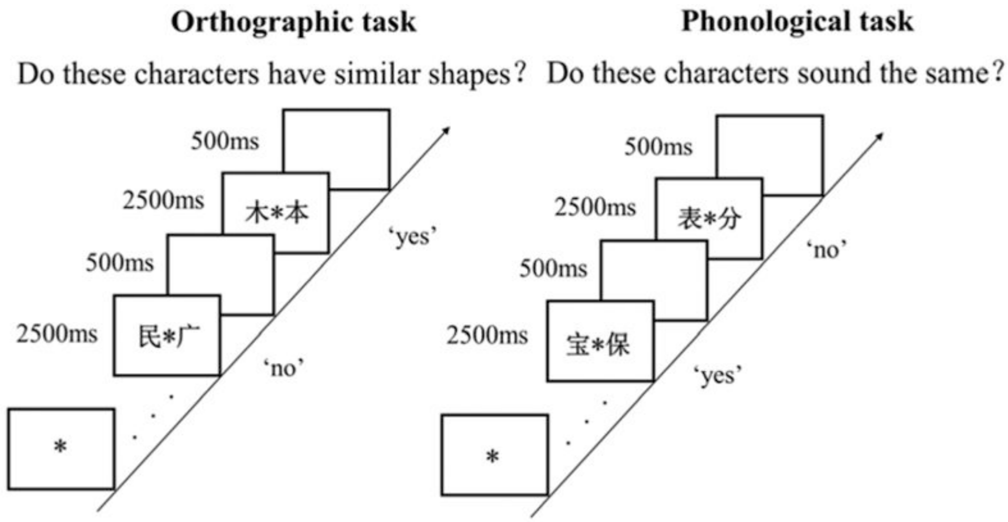

Fig. 1.

Procedures for two tasks: orthographic (left) and phonological (right) tasks.

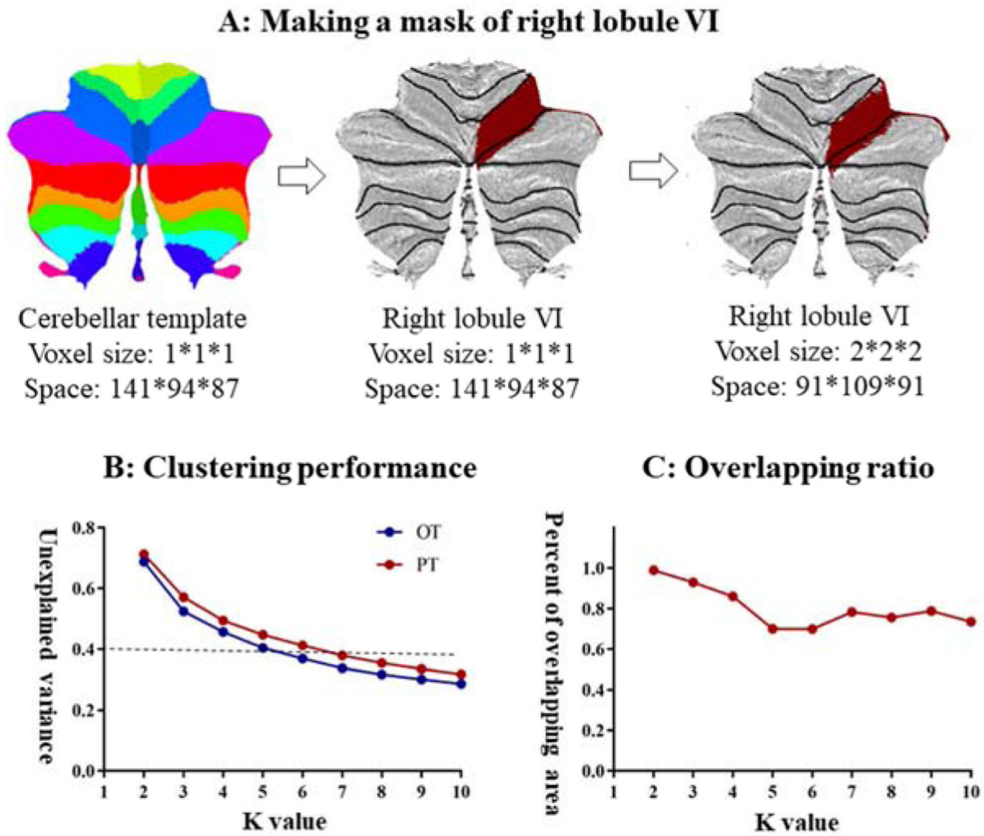

Fig. 2.

A mask of the right cerebellar lobule VI, clustering performance, and overlapping ratio. A: depicts the mask of right lobule VI. B: represents clustering performance, indicating the unexplained variance as a function of the number of clusters (k value). C: indicates the percentage of the overlapping area of the corresponding subregions across tasks. OT = orthographic task; PT = phonological task.

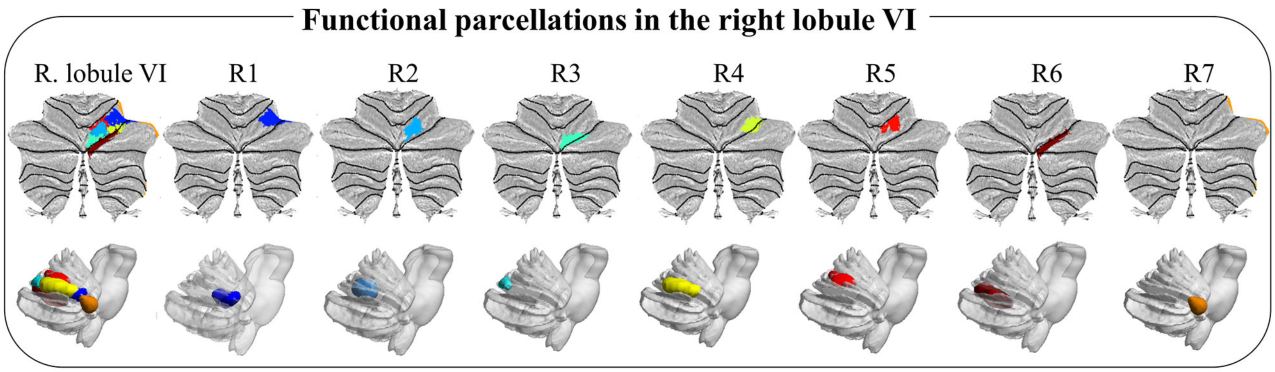

Fig. 3.

Topographic organization of the seven subregions in the right cerebellar lobule VI. The dark blue region was named R1, the light blue region was named R2, the cyan region was named R3, the yellow region was named R4, and the bright red region was named R5, the dark red was named R6, the orange region was named R7.

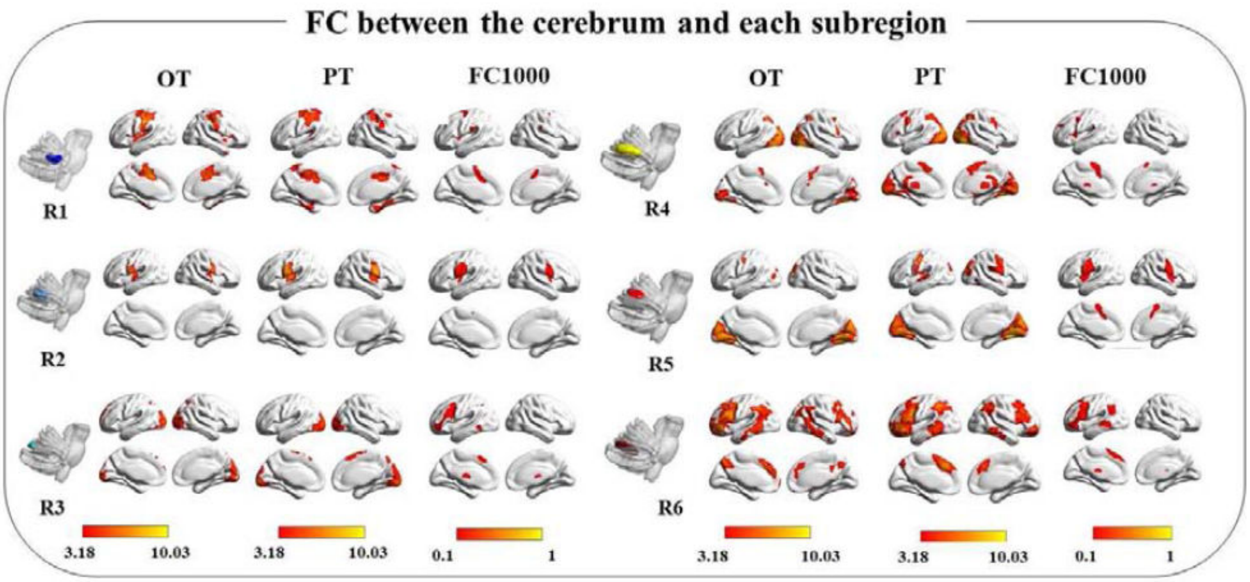

Fig. 4.

The relative strength of functional connectivity (FC) with the cerebrum in each subregion compared to the other subregions. OT = the orthographic task, PT = the phonological task. FC1000 means regions that were identified via Neurosynth based on the study of Buckner, et al. (2011). Voxels with $r > 0.1$ were displayed.

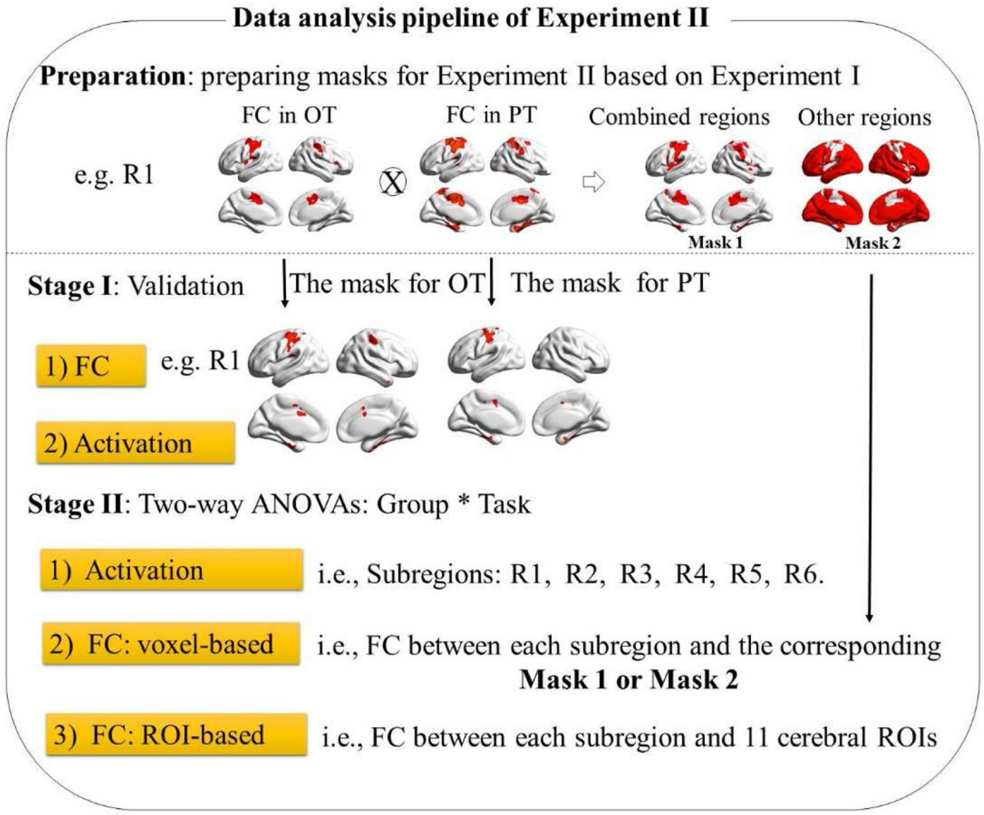

Fig. 5.

Data analysis pipeline of Experiment II.

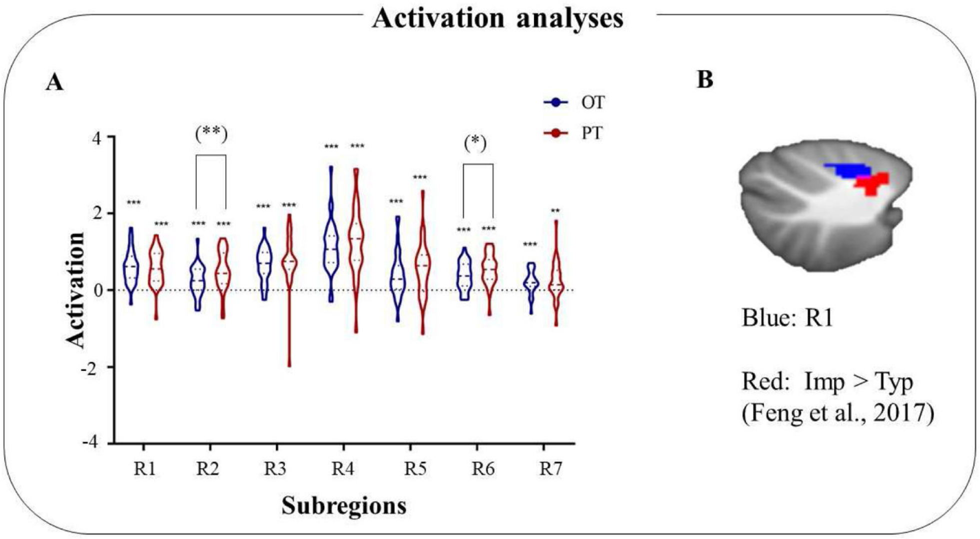

Fig. 6.

Activation in each subregion in the two reading tasks (A), and the comparison of R1's location with Feng et al., 2017 (B). PT = phonological task; OT = orthographic task. *** $p < 0.001$. ** $p < 0.01$, * $p < 0.05$. (**) $p < 0.01$, FDR uncorrected; (*) $p < 0.05$, FDR uncorrected. Imp = impaired readers; Typ = typical readers.

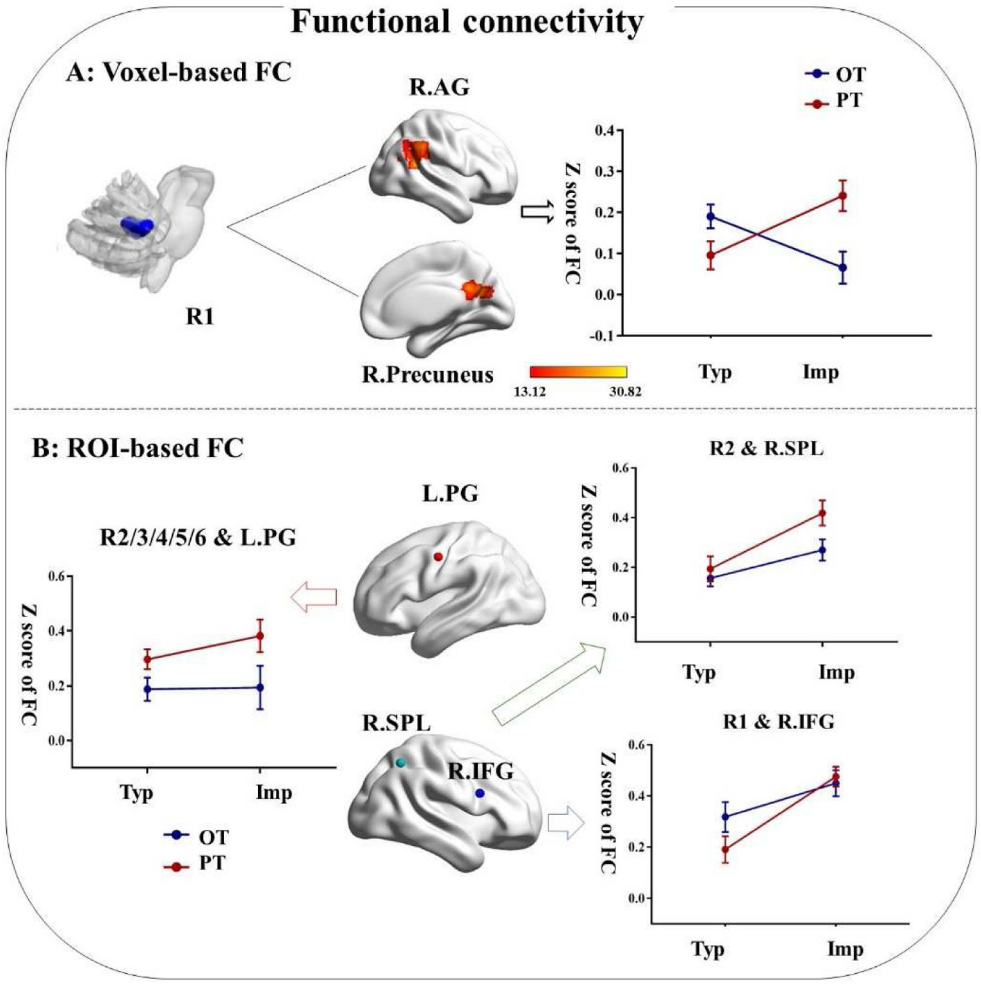

Fig.7.

Comparison of functional connectivity across groups and tasks. OT = orthographic task; PT = phonological task.

Table 2.

Demographics and behavioral results in experiment I

	Mean	SD	Mean	SD
Age (years)	9.9	0.6		
Sex (M/F)	3/13			
Handedness (L/R)	0/16			
Task performance outside scanner				
Ravens' IQ[b]	76.5	12.8		
Chinese Character Recognition Test[a]	110.5	12.4		
Reading Comprehension Test[a]	117.9	17.3		
Task performance during scanning	**Reaction time (ms)**		**Accuracy (%)**	
Orthographic task[c]	674	119	98.0	0.2
Phonological task[c]	1097	293	91.0	1.4

Note:

[a]Standardized score, with a mean of 100 and a standard deviation of 15.

[b]Percentiles.

[c]Raw scores.

Table 3.

Coordinates of the central voxel in each subregion

MNI	R1	R2	R3	R4	R5	R6	R7
X	31	16	16	33	20	21	35
Y	−49	−63	−74	−61	−62	−67	−40
Z	−29	−24	−22	−25	−19	−29	−36

Table 4:

The first seven keywords associated with the FC pattern specific to each subregion decoded by Neurosynth

Sub-regions	FC pattern on OT condition	FC pattern on PT condition
R1	Somatosensory/motor/hand/finger/sensori-motor/movement/ execution	Hand/somatosensory/finger/movement/motor/sensori-motor/ finger movements
R2	Somatosensory/speech/speech production/auditory/sounds/ listening/acoustic	Speech production/somatosensory/speech/vocal/pitch/auditory/ sounds
R3	Visual, early visual, sighted, objects/reading/vision/face	Visual/early visual/reading/tasks/orthographic/working memory/Chinese
R4	Visual/objects/face/reading/task/orthographic/viewing	Visual/objects/face/reading/early viewing/sighted/motion/
R5	Visual/sighted/navigation/vocal/motor/sensory/auditory/	visual/sighted/speech production/pitch/motor/auditory/ navigation
R6	Working memory/semantic/tasks/demands/word/language/ phonological	Semantic/working memory/retrieval/language/sentence/ demands/word

Table 5:

ROIs in the reading network (Murphy et a., 2019).

ROIs	BA	MNI coordinates X	Y	Z
Left middle frontal gyrus (L.MFGa)	9	−40	28	24
Left middle frontal gyrus (L.MFGb)	6	−4	−2	56
Left inferior frontal gyrus (L.IFG)	9	−44	6	26
Right inferior frontal gyrus (R.IFG)	9	48	12	24
Left postcentral gyrus (L.PostG)	4	−50	−8	44
Left superior parietal lobule (L.SPL)	7	−22	−68	48
Right superior parietal lobule (R.SPL)	7	34	−56	50
Left superior temporal gyrus (L.STG)	41	−54	−16	8
Left fusiform gyrus ($L.FG_a$)	37	−50	−48	−8
Left fusiform gyrus ($L.FG_b$)	37	−42	−54	−18
Left inferior occipital gyrus (L.IOG)	17	−24	−98	−4

Table 6.

Demographics and behavioral results in Experiment II.

	Typical readers	Impaired readers	t	p
Age (years)	10.3(1.0)	10.2(0.7)	0.38	N.S
Sex (M/F)	7/13	9/5	$X^2=2.8$	0.092
Handedness (L/R)	0/20	0/14		
Task performance outside the scanner				
Raven IQ[b]	73.3(15.8)	82.9(12.7)	−1.89	0.07
Chinese Character Recognition Test[c]	2279(292)	1324(345)	8.69	<0.001
Reading Comprehension Test[c]	64.3(17.4)	36.9(10.0)	5.82	<0.001
Chinese phonological test[c]	49.8(16.0)	28.3(20.6)	3.31	<0.01
Rapid naming test[c]	13.7(3.0)	14.6(3.9)	0.88	N.S
Digit cancelation test[c]	62.8(11.0)	53.5(20.3)	1.56	N.S
Task performance during scanning				
Orthographic task				
Reaction Time (ms)	1083 (230)	1195 (184)	−2.6	N.S
Accuracy (%)	95 (7)	94 (5)	1.1	N.S
Phonological task				
Reaction Time (ms)	1920 (319)	1933 (228)	−0.1	N.S
Accuracy (%)	72 (18)	64 (11)	−1.0	N.S

Note:

[b]Percentiles

[c]Raw score; Standard deviation in parentheses