The Cerebellum
https://doi.org/10.1007/s12311-021-01279-y

ORIGINAL ARTICLE

Cerebro-Cerebellar Response to Sequence Violation in a Cognitive Task: an fMRI Study

Yi-Shin Sheu[1] · John E. Desmond[1]

Accepted: 11 May 2021

Abstract

The phonological loop is part of Baddeley's verbal working memory (VWM) model that stores phonological information and refreshes its contents through an articulatory process. Many studies have reported the cerebellum's involvement during VWM tasks. In the motor literature, the cerebellum is thought to support smooth and rapid movement sequences through internal models that simulate the action of motor commands, then use the error signals generating from the discrepancy between the predicted and actual sensory consequences to adjust the motor system. Here, we hypothesize that a similar monitoring and error-driven adjustment process can be extended to VWM; specifically, the cerebellum checks for discrepancies between the predicted and actual articulatory process to ensure the accuracy and fluency of articulatory rehearsal. During neuroimaging, participants rehearsed a sequence of letters in sync with the presentation of a visual pacing stimulus (#) that was terminated by the occurrence of a probe letter. Participants judged whether the probe was the correct letter in the sequence (i.e., match trial), or deviated from the sequence (i.e., mismatch trial). Detection of sequence violation was not only associated with prolonged reaction time but also an increased activation in a left executive control network. Psychophysiological interaction was used to investigate whether the cerebellum interacts with the cerebral cortex for error monitoring and adjustments. We found increased functional connectivity between the right cerebellum and the cerebral cortex during mismatch relative to match probes, indicating sequence violation resulting in greater cerebellar connectivity with areas in the cerebral cortex involved in phonological sequencing.

Keywords Cerebellum · Sequence violation · Phonological loop · Working memory · Forward models · fMRI

Introduction

Verbal working memory (VWM) refers to the ability to store and manipulate verbal information for short periods of time in service of a task [1]. For example, it might be necessary to remember a license plate (e.g., 7LHC252) as a witness in a car accident. A typical strategy would be to repeat the sequence of characters serially in one's mind until they can be written down. This ability of flexibly encoding and maintaining novel sequences, particularly when the verbal items are presented in an arbitrary serial order, underlies core human faculties such as language acquisition and production [2], sentence comprehension [3], and numerical calculation [4–6]. Despite serial order information being a critical element in our success in everyday tasks, scientists have yet to provide a clear understanding of how serial-order coding is achieved in verbal working memory.

In Baddeley and Hitch [7] working memory model, verbal working memory is supported by a phonological loop that exclusively deals with phonological representations and has two parts: (1) a phonological store that holds speech-based (phonological) information for 1–2 s, and (2) an articulatory control system that first translates verbalizable material into phonological codes and then maintains these codes in the store through subvocal rehearsal. Because smooth rehearsal requires a rapid updating of the phonological loop, it has been proposed that the cerebellum provides predictive control in VWM by forming a forward internal model of the predicted articulatory trajectory based on the sequence of phonemes it receives [8]. This hypothesis that the cerebellum engages in forward model predictions received support in our recent verbal working memory transcranial magnetic stimulation (TMS)

✉ Yi-Shin Sheu
yishin.sheu@gmail.com

[1] Department of Neurology, Johns Hopkins University School of Medicine, Baltimore, MD, USA

Published online: 22 May 2021

experiment [9]. We showed that cerebellar TMS, administered prior to the probe presentation during covert rehearsal of a memorized sequence of letters, caused errors in judging which letter was next in the sequence in a manner that was predicted by a forward model. This pattern was not observed when TMS was administered to an occipital control region.

In motor control, this feedforward computation of the cerebellum has also been linked to error-driven adjustments [10]. In this feedforward model, the predicted sensory consequences of motor command are compared to the actual consequences by the cerebellum, resulting in a sensory prediction error, which may be used for online adjustments, or alerting specific neural system about a potential execution error [11, 12]. For instance, neuroimaging studies have shown increased cerebellar activation following unexpected presence or absence of a sensory stimulus [13–15] or during the initial motor learning phase when errors are mostly prevalent [16]. Also, the detection of deviant somatosensory stimuli in a predicted sequence is impaired in cerebellar patients [17]. Furthermore, the cerebellum has a facilitatory effect on excitability of the contralateral cortical area, such as M1, through cerebello-thalamo-cortical pathways [18–20]. Together, these studies suggest that the cerebellum is involved in the implementation of adaptive control of movements by (1) constantly monitoring sequence violation between predicted and actual sensory consequences; and (2) providing feedforward, putatively excitatory, input to the cortical areas when sequence violation is detected.

Since the cerebellum has shown to be involved in a number of non-motor domains including verbal working memory [8, 21–23] and an increasing amount of evidence suggests that the cerebellum plays a predictive role in both motor and cognitive function [for a review see 24], it is plausible that a similar monitoring and error-driven adjustment process that occurs in motor control may be extended to verbal working memory. Therefore, in the current study, we proposed that the cerebellum enhances the integrity of the phonological loop by first computing an articulatory trajectory based on the phonemes it receives during the encoding phase, then comparing this predicted articulatory trajectory with the incoming phonemes during the rehearsal phase. If the incoming phoneme matches the predicted phoneme, then expectancy is realized and the cerebellar feedforward control to the cerebral cortex would be minimal. However, if a sequence violation or mismatch were detected, then the cerebellar feedforward control to the cerebral cortex would increase to reflect prediction errors. In turn, this would result in greater excitability of those feedforward brain areas participating in the task at hand.

To test our hypotheses, we used functional magnetic resonance imaging (fMRI) and a guided verbal working memory rehearsal task in which participants were asked to memorize a sequence of six letters and covertly rehearsed them in sync with each presentation of a # sign. This guided rehearsal feature created an articulatory trajectory with known temporal occurrence for each letter in the sequence, allowing the participants to form an expectation about the next incoming letter. When the probe letter finally appeared, the participants' task was to indicate whether it matched the letter in the sequence. On half of the trials, the probe was the correct letter in its predicted position within a sequence (i.e., Match Probe condition), and on the other half, the probe was a letter that was either one position earlier or later in the sequence (i.e., Mismatch Probe condition). Because a mismatch probe represents a letter from the encoded sequence but in an incorrect serial order position, it is hypothesized that such violation of sequential order would result in an increase of the cerebellar feedforward inputs to the cerebral cortex. In particular, we predicted greater activation in the cerebro-cerebellar circuit typically involving verbal working memory for mismatch compared to match probes.

To test the hypothesis that the cerebellum provides feedforward input to the cerebral cortex for monitoring and error-driven adjustments, we employed a psychophysiological interaction (PPI) [25] analysis to investigate the context-dependent connectivity changes between the match and mismatch trials in terms of the functional interaction between the cerebellum and the cerebral cortex. Right posterior inferior cerebellum (cerebellar lobule VIIb and VIIIa) was selected as a seed region for the PPI analysis, as it has consistently implicated in language [26, 27] and verbal working memory processing [8, 28], and has reciprocal connections with non-motor regions, including the prefrontal and posterior parietal cortices [29, 30]. We predicted increased functional integration between the right cerebellar seed region and cerebral cortex during mismatch trials relative to match trials, as this connectivity would reflect a prediction error signal from the cerebellum to the cerebral cortex to indicate discrepancy between the predicted letter and the actual visual input. Specifically, we predicted a left-lateralized neocortical network, including lateral and medial premotor regions as well as subcortical areas in the basal ganglia, to be functionally connected with the right cerebellum, based on the previously identified neural networks in speech production [31–33] and primate anatomical studies showing that the cerebral cortex and the cerebellum are contralaterally connected via the thalamus [34–37].

Methods

Participants

A total of 19 healthy adults (7 males/12 females) between the ages of 19–30 participated in the study. All participants were native English speakers with educational attainment of at least 8 years, no history of neurological, psychiatric disorder, or

stroke, and were not on any anxiolytic, antidepressant, neuroleptic, or sedative medication at the time of the study. All participants provided written informed consent and were compensated for their time. The study procedures were approved by Institutional Review Board of the Johns Hopkins University School of Medicine.

Task Paradigm

Participants were asked to covertly memorize an array of six uppercase letters (3 letters on the first row, and 3 letters on the second row) presented centrally on a screen, which were then removed from sight after 2 s. They were instructed to read the letters (selected randomly from a pool of consonants, excluding vowels A, E, I, O, U, Y) from left to right, first row then second row, as a single sequence. After a short delay (0.5 s), 2 to 4 # signs appeared on the screen one at a time (0.4 s in duration for each # sign with a 0.15-s blank screen in separation), followed by a probe letter for 3 s (presented in lowercase with a question mark next to it) and a 1.8-s inter-trial-interval. Participants were instructed that each # sign represents a letter in order from the six-letter sequence, and they were to press button 1 (right index finger) to indicate "match" if the identity of the probe letter matches to the letter from the sequence in the correct order, and press button 2 (right middle finger) to indicate "mismatch" if the identity of the probe letter did not match the correct letter in the sequence (Fig. 1). The identity of the probe letter was manipulated so that in half of the trials, the probe letter was either one letter before or after the correct letter in the sequence (i.e., 50% mismatch trials), and in the remaining half, the probe letter was in the correct order position (i.e., 50% match trials). In order to make the timing of the probe letter unpredictable, the probe letter could appear either at the third, fourth, or fifth position. However, the shorter trials (third and fourth position) were not included in the analysis because a previous pilot behavioral study in our lab showed a ceiling effect for these shorter trials due to low VWM demands. A total of 96 trials were given and divided evenly between two runs for scanning purpose. Eighty out of the 96 trials where the probes appeared in the 5th position were included in the analysis, which yielded 40 match and 40 mismatch trials for the current experiment.

Follow-up Behavioral Task

In a follow-up behavioral study, an additional 14 participants (4 males/10 females) between the ages of 19–30 participated in a modified behavioral version of the serial rehearsal VWM task. Half of the probes in the mismatch trials were replaced with novel probes, i.e., randomly selected letters from the pool of consonants outside of the current 6-letter encoding sequence. For novel probes, the letter identity is neither a predicted letter like the match probes, nor a sequential deviant, like the mismatch probes. The goal of this follow-up experiment was to investigate whether the robust RT difference between the Mismatch and Match Probe condition in the fMRI study was either due to more efficient processing of the match probes or to less efficient processing of the mismatch probes. We reasoned that if the faster RT observed in Match Probe condition was a result of the predicted stimulus (i.e., match probes) being processed more efficiently, then we should expect the RTs for both Novel and Mismatch Probe conditions to be significantly slower than the Match Probe condition (match < novel = mismatch), because neither the Novel nor the Mismatch probe identities can be predicted from the memorized encoding sequence. On the other hand, if the slower RT in Mismatch Probe condition is a result of additional processing required to resolve the sequential violations, then we should expect the RTs for both Novel and Match Probe conditions to be significantly faster than the Mismatch Probe condition (match = novel < mismatch), because neither the Match nor the Novel probe represent a sequential deviant. Finally, if

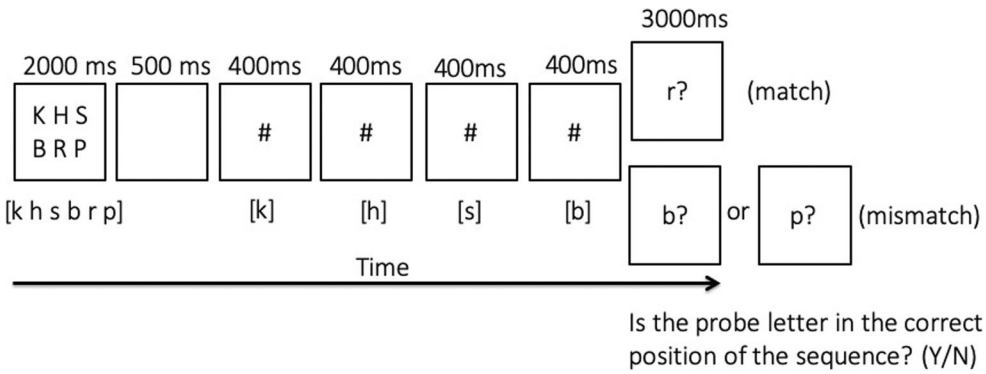

Fig. 1 An example of trial events progression in the verbal working memory task. Participants were asked to encode 6 letters presented on the screen and to covertly rehearse the letters in sync with the appearance of # symbols. Between each # presentation, a 150-ms blank screen was included to visually separate the adjacent # presentation. The letter(s) listed in [ ] indicates the correct content for rehearsal. When a probe letter appeared, the participants were to press button 1 to indicate "match" if the identity of the probe letter matches to the letter from the sequence in the correct order, and press button 2 to indicate "mismatch" if the identity of the probe letter does not match to the correct letter in the sequence

the RT for the Novel Probe condition falls somewhere between the Match and Mismatch Probe condition (match < novel < mismatch), then additive effects from both accounts (prediction and sequential violation) may be at work.

In this follow-up behavioral experiment, the timing of stimuli and structure of the task paradigm were identical to the fMRI version, with number of trials adjusted for each of the 3 conditions. A total of 80 trials were given, and 64 out of the 80 trials in which the probe appeared in the 5th position were included in the analysis, which yielded 32 match trials, 16 mismatch trials, and 16 novel trials. Since the correct response for a novel probe was "mismatch," this ratio kept the current behavioral task free from response bias.

fMRI Scanning Protocol

Participants were given a short practice of the task outside of the scanner room approximately 20 min before the scan began. fMRI scanning was conducted at the F. M. Kirby Research Center for Functional Brain Imaging in Kennedy Krieger Institute (Baltimore, MD) on a Philips 3T Achieva scanner with 32-channel SENSE head coil. High-resolution T1-weighted anatomical images were collected using a MPRAGE scanner sequence (170 sagittal slices, FOV = 240 × 240 × 170, TR = 7 ms, TE = 3.2 ms, flip angle = 8°, voxel size of 0.83 × 0.83 × 1 mm^3). Whole brain T2*-weighted functional images were collected in an ascending sequential order, using an echo-planer imaging sequence (44 axial slices, FOV = 96 × 96 × 44, TR = 2.3 s, TE = 30 ms, flip angle = 61°, voxel size of 2.3 × 2.3 × 3 mm^3). A total of 250 volumes were acquired for each of the two runs.

The stimuli were presented using E-Prime Professional 2.0 on a Dell Optiplex computer with Intel Core i7 (Quad Core, 8 MB, 3.4 GHz) and 8 GB SDRAM. The participant viewed the projected image displays on a rear projection screen via a front-silvered, 45° inclined mirror attached to the top of the head coil. This mirror provided a 23.5° horizontal and 17.7° vertical field of view with the projector zoomed to give maximum image size. At the beginning of each experiment, we had each participant verbally confirmed that they could clearly see the 6-letter encoding array.

Physiological variables such as heart rate and breathing have shown to influence blood-oxygenated-level-dependent (BOLD) response [38–41], with stronger artifact present in the cerebellum [14] and brainstem areas [42]. Furthermore, heart rate deceleration has been observed following prediction errors, which has been shown to artificially decrease cerebellar BOLD signals if they are not properly corrected for physiological factors [14]. Thus, to properly estimate BOLD signal changes in mismatch and match trials, cardiac and respiration rates were recorded during the functional runs at 496 Hz (wireless) using a peripheral pulse unit and a respiratory belt built in with the Philips MR scanner. The physiological recordings were processed using model-based noise correction method implemented in PhysIO Toolbox [43], which resulted in multiple regressors encoding components of physiological noise that can be later incorporated into a general linear model (GLM).

Finally, the participants were asked to respond as quickly and accurately as possible with a button press, using the fingers of their right hand. They were instructed to press the left button with their index finger to indicate a "match" response, and to press the right button with their middle finger to indicate a "mismatch" response (same configuration as their previous practice). Their responses were sent to a Cedrus RB-830 response box (Cedrus, San Pedro, CA) via fiber optic cables and recorded by the E-Prime program.

Behavioral Analyses

Accuracy (% correct) and reaction time (RT) were analyzed using SPSS version 27 (IBM Corp, Armonk, NY, USA). Paired *t*-tests were used to determine whether there were any behavioral differences between match and mismatch trials, for either RT or Accuracy. Two RT analyses were performed — the first included all the trials available regardless of whether the subject answered correctly or not, and the second only included trials that were answered correctly. The statistical threshold was set at $p < 0.025$ (alpha = 0.05, two-tailed) for all behavioral analyses.

fMRI Data Pre-processing

All preprocessing and statistical analyses were performed using SPM12 (Wellcome Trust Centre for Neuroimaging, UCL, London, UK). The functional images were corrected for slice timing, realigned to the first volume for motion correction, and coregistered to the anatomical image. The anatomical image then was segmented, bias corrected, and spatially normalized to the tissue probability maps in MNI space. The resulting forward deformation field then was used to transform functional images to the standard MNI space. The normalized functional images were re-sampled to 2 × 2 × 2 mm and smoothed with a 6-mm full-width at half-maximum (FWHM) Gaussian kernel.

fMRI Data Analysis

Task-dependent changes in BOLD signal were modeled by 7 regressors, representing "encoding phase for both match and mismatch trials," "probe phase match trials," "probe phase mismatch trials," "encoding phase for short trials (probe position at 3rd and 4th), "probe phase for short trials," "encoding phase for error trials (participants answered incorrectly)," and "probe phase for error trials." The first 3 are regressors of interest, while the last 4, as well as the PhysIO Toolbox

outputs (a multiple-regressor-matrix combined with motion parameters), are regressors of no interest. All the encoding-related regressors were time-locked to the onset of the encoding array, and all the probe-related regressors were time-locked to the onset of the probe letter. All regressors, except the physiological and motion ones, were modeled by a stick function (i.e., duration = 0) and convolved with SPM's canonical hemodynamic response function. The GLM model was estimated for each participant in a first-level analysis. The primary contrast of interest was *Mismatch* > *Match* during the probe phase. All first-level contrasts were entered into a group-level random-effects analysis using a one-sample *t*-test with a contrast value of 1. The statistical maps were corrected for multiple comparisons at a threshold of $p < 0.05$ after applying either the cluster-wise family-wise error rate (FWE) or the cluster-wise false discovery rate (FDR) correction methods. The size of the significant clusters, measured in units of contiguous voxels (k), was based on a voxel-wise local maxima threshold of uncorrected $p = 0.005$.

Psychophysiological Interaction Analysis

Psychophysiological interaction (PPI) are based on regression models, such that a direction of functional influence between two regions is inferred from the hypothesis itself. Given our *a priori* hypothesis that the cerebellum provides a feedforward input to the cortical areas when a sequence violation is detected, we investigated if the cerebellar seed region shows context-dependent (mismatch > match) increments in functional coupling with the cerebral cortex. The cerebellar region of interest (ROI) was identified within the right posterior inferior cerebellum using the significant cluster ($p < 0.05$, cluster-wise FDR correction) from the *Mismatch* > *Match* contrast during the probe phase in the group-level GLM (Fig. 3a). For each participant, the eigenvalues for each ROI were extracted from the preprocessed data and adjusted for effects of interest against an *F*-contrast. This step resulted in 2 eigenvalues representing run 1 and run 2.

To generate the proper interaction term (source signal × experimental contexts) in the PPI analysis, SPM's internal PPI algorithm was used, which provided robust deconvolution of the HRF to derive the interaction term. The experimental contexts of interest included the "probe phase match trials" (weight = − 1) and "probe phase mismatch trials" (weight = + 1). This step resulted in 2 PPI models, given that there are 2 runs in the fMRI study, and each model entailed a psychological variable (mismatch > match), a physiological variable (eigenvalues from that ROI), and an interaction variable derived from the multiplication of the psychological and physiological variables. A first-level GLM model containing these 2 PPI models from run 1 and run 2 (each PPI model contains 3 PPI regressors and 6 motion parameters) was estimated for each participant. A contrast of + 1 for the two interaction terms (interaction term from run 1 and from run 2) was used to obtain the average effect of the PPI interaction terms over runs. First-level contrasts from all participants were then entered into a group-level random-effect analysis using one-sample *t*-test with a contrast value of 1. The statistical maps were corrected for multiple comparisons at a cluster-level of $p < 0.05$ (either FWE or FDR corrected), based on a voxel-level threshold of uncorrected $p = 0.005$ and a cluster-level extent threshold measured in units of contiguous voxels (k), calculated by SPM.

Results

Behavioral Data Results During fMRI Scan

In terms of accuracy, the match trials ranged from 80% correct to 100%, with a mean of 90.13% (SE = 1.46%). In comparison, the accuracy for mismatch trials ranged from 85 to 100%, with a mean of 94.47% (SE = 1.06%). The paired *t*-test revealed that our participants were significantly more accurate on mismatch trials compared to match trials ($t_{(18)} = 2.661$, $p = 0.016$). However, the pattern of results should not be entirely explained in the context of speed-accuracy trade off, as the correlation between correct-trials-only RT and Accuracy was not significant ($r = -0.272$, $p = 0.260$).

Because the accuracy was significantly higher for mismatch trials compared to match trials, we ran two RT analyses, one with just the correct trials and the other one with all trials, to show that the RT effect was fairly consistent, regardless of the accuracy difference. The RT difference between Mismatch (mean = 767.077 ms, SE = 48.795 ms) minus Match trials (mean = 612.799 ms, SE = 36.697 ms) was calculated for each of the 19 participants. All 19 participants showed slower RTs for Mismatch trials with no exception, with the RT differences ranging from 16.4 to 394.7 ms with a mean of 154.278 ms (SE = 24.069 ms) for the correct trials only calculation. When including all trials, regardless of whether the participant answered it correctly, the mean difference between Mismatch (mean = 768.953 ms, SE = 48.323 ms) versus Match trials (mean = 635.983 ms, SE = 40.037 ms) was 132.969 ms (SE = 20.859 ms). The paired *t*-test confirmed that the participants were significantly slower during the mismatch trials compared to match trials, in their overall RT ($t_{(18)} = 6.375$, $p < 0.001$) and in the correct-trials-only RT ($t_{(18)} = 6.410$, $p < 0.001$)

Follow-up Behavioral Data Results

In a follow-up behavioral study, we included novel probes as a third probe type. The novel probe was randomly selected from an array of consonants that was not included in the current encoding array. In terms of RT, there is a difference among the three conditions ($F_{(2, 26)} = 11.224$, $p < 0.001$). Upon closer

examination, participants responded to the novel probes (mean = 609.546 ms, SE = 43.387 ms) just as quickly as the match probes (mean = 605.009 ms, SE = 37.618 ms) as indicated by the non-significance results in the post hoc paired t comparison ($t_{(13)} = 0.291$, $p = 0.776$). However, participants responded significantly longer to mismatch probes (mean = 687.497 ms, SE = 53.126 ms) compared to novel probes, as indicated by post hoc paired t comparison ($t_{(13)} = 4.049$, $p < 0.001$).

In terms of accuracy, there is an overall difference among the three conditions ($F_{(2, 26)} = 11.034$, $p < 0.001$). Participants responded to the novel probes (mean = 96.88%, SE = 1.99%) significantly more accurately compared to the match probes (mean = 86.83%, SE = 1.96%) as indicated by the post hoc paired t comparison ($t_{(13)} = 4.707$, $p < 0.001$). However, there was no significant difference between novel versus mismatch probes (mean = 95.09%, SE = 1.30%), as indicated by post-hoc paired t comparison ($t_{(13)} = 0.7$, $p = 0.497$).

Given that the Novel Probe condition showed a pattern of faster RT (novel = match < mismatch) while retaining a high level of accuracy, it appears that the slower RT in Mismatch Probe > Match Probe condition was a result of additional processing required to resolve sequential violations in verbal working memory.

Task-Related Activations

As a first step, we examined the brain activations for the probe phase (probe > baseline), during which the participant made a "match" or "mismatch" judgment based on the probe presented. This contrast revealed a brain network composed of cortical and subcortical structures, including the superior and inferior cerebellum, insula, basal ganglia (caudate, putamen, globus pallidus), thalamus, superior and inferior parietal lobules as well as areas in the frontal lobe (middle and inferior frontal gyri, premotor, supplemental motor areas) (Fig. 2a).

Next, we examined regions exhibiting activation difference when the presented probe letter on the screen was a mismatch compared to a match to the letter being anticipated in working memory. The activity in those regions was hypothesized to reflect a sequence prediction error based on the discrepancy between the visual input of the letter on the screen and the self-

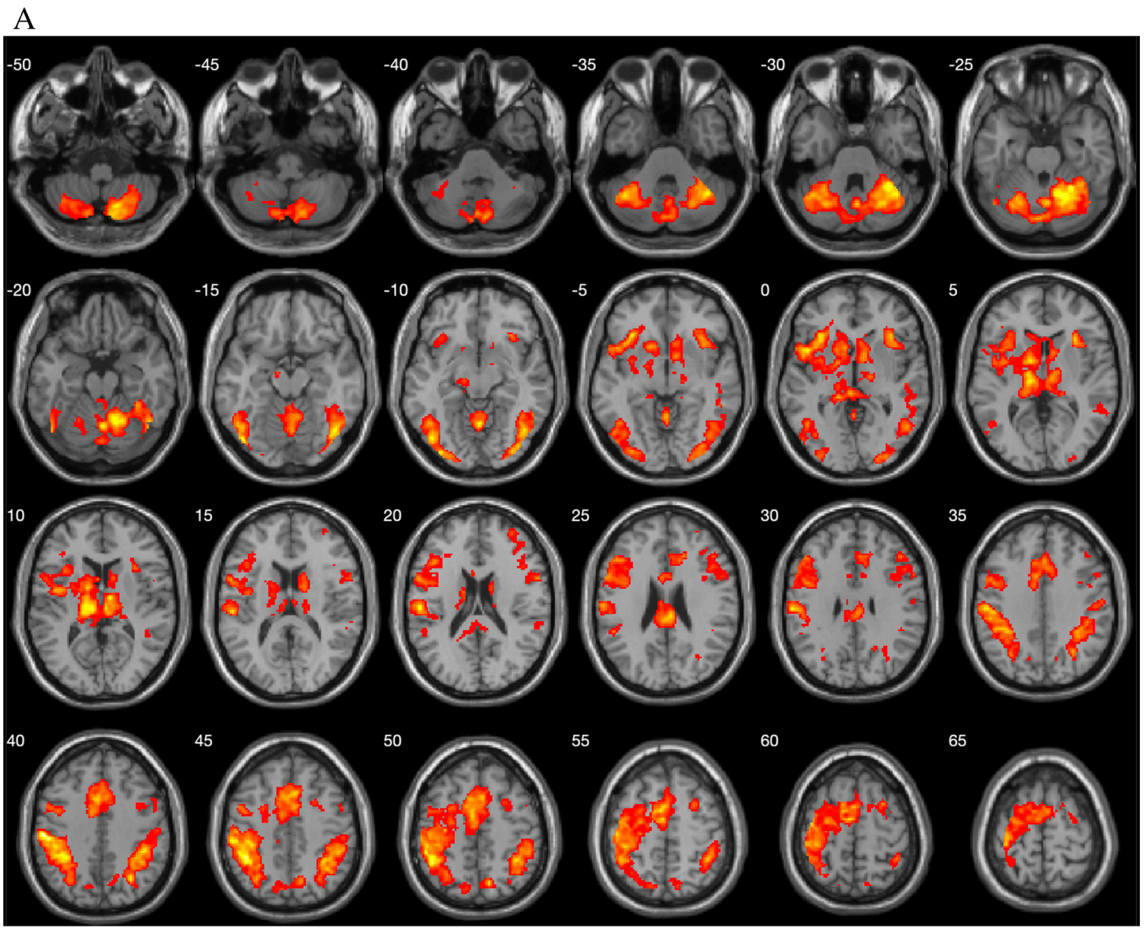

Fig. 2 **a** Activations for Probe phase > Baseline. Only positive activations are shown. **b** Brain correlates of detecting sequential deviants in verbal working memory (mismatch vs. match probe). Positive activations (mismatch > match) are shown in red; negative activations (match > mismatch) are shown in blue

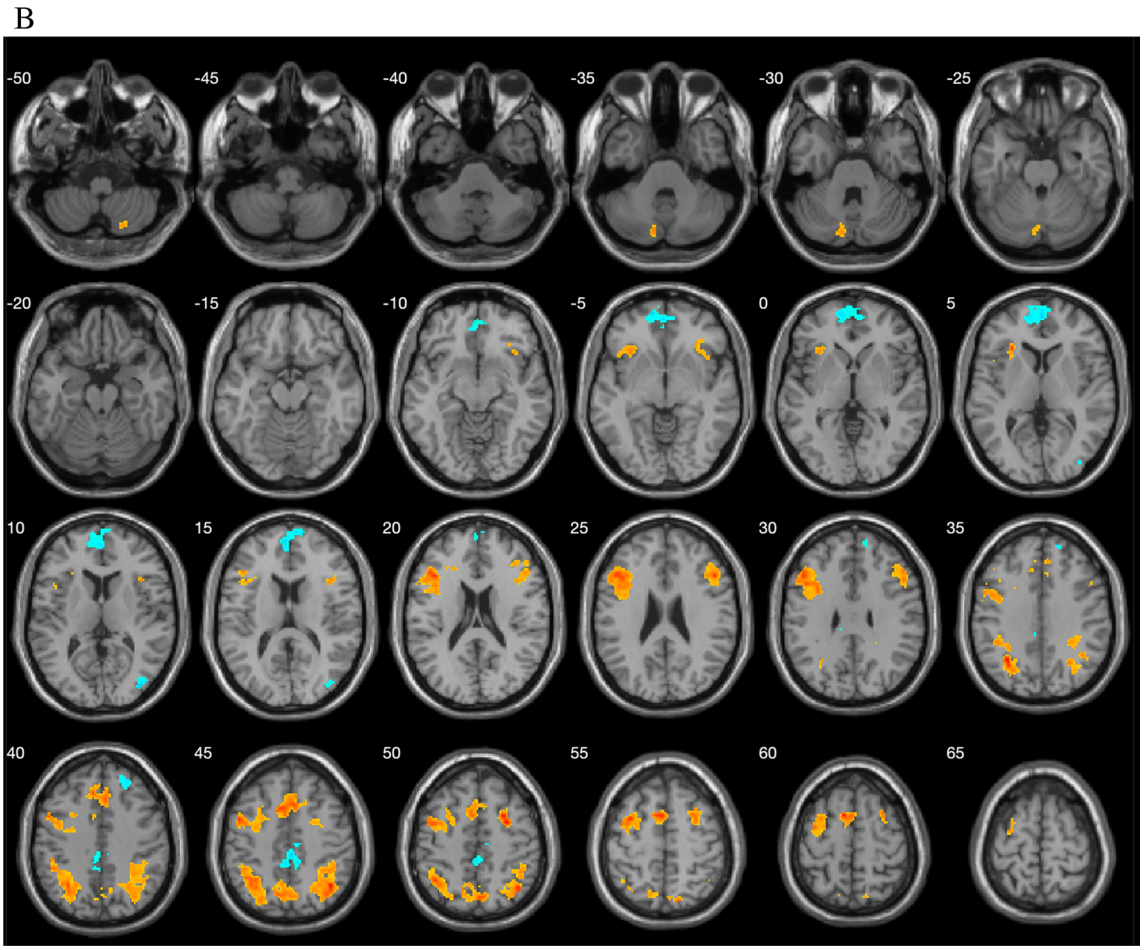

Fig. 2 continued.

generated expected/predicted letter. As seen in Fig. 2b and Table 1a, the *Mismatch* > *Match* contrast during the probe phase revealed cortical areas in the bilateral middle and inferior frontal gyrus, bilateral inferior parietal lobule, supplemental motor area, insula, and the precuneus in the midline, as well as cerebellar areas in the right lobule VIIb and VIIIa, and left Crus II. The opposite contrast (*Match* > *Mismatch*) showed medial frontal gyrus in BA10 and posterior cingulate cortex in BA 31.

Voxel-Wise PPI Results

The PPI analysis allows us to assess if the cerebellum displayed context-dependent increments in functional connectivity with regions in the cerebral cortex when a sequence violation is detected compared to when there is no sequence violation. Given our *a priori* hypothesis regarding the functional role of right posterior inferior cerebellum in language and verbal working memory based on prior studies [8, 9, 22], we first identified an activation in the right posterior inferior cerebellum within lobule VIIb using the Mismatch > Match contrast from the group results (Fig. 3a, Table 1a). Next, PPI analysis was performed, searching for voxels in the whole brain for which functional connectivity was enhanced on mismatch relative to match trials (Mismatch > Match).

An increase of functional connectivity was found in areas predominantly within the left fronto-parietal network during mismatch trials compared to match trials (Fig. 3b, Table 1b). This includes a large cluster encompassing left precentral and postcentral gyrus (BA6/BA8) and clusters in left inferior parietal lobule (BA40), supplemental motor area (SMA), and both sides of the thalamus. Smaller clusters were also found in the right postcentral gyrus, insula, and transverse temporal gyrus. No region was found in the opposite pattern of PPI interaction, i.e., Match > Mismatch. This pattern of results is consistent with our hypothesis that the right posterior inferior cerebellum engages a mostly left-lateralized network that is known for speech planning and production, including sensorimotor, parietal, and supplementary motor areas, via the thalamus bilaterally [31, 32].

Discussion

We used functional neuroimaging and a serial VWM rehearsal task to further elucidate how the cerebellum contributes to

Table 1 Anatomical brain area, MNI coordinates (x, y, z), maximal *t*-statics and *z*-score, size of significant activations, and corrected p values after applying FWE and FDR. (A) Group-level activation results. (B) Group-level PPI results

Brain region	x y z (mm)	t	SPM {z}	Size (voxels)	pFWE-corr	qFDR-corr
(A) Group-level activation results						
Significant activations for mismatch > match during probe phase						
Right middle frontal gyrus (BA6)	28 8 52	7.19	4.88	249	p = 0.003	p < 0.001
Right inferior frontal gyrus (BA46)	48 24 24	6.91	4.77	470	p < 0.001	p < 0.001
Right inferior parietal lobule (BA40)	42 − 60 48	6.19	4.48	1137	p < 0.001	p < 0.001
Left middle frontal gyrus/precentral gyrus	− 44 24 28	5.87	4.33	2043	p < 0.001	p < 0.001
Left inferior parietal lobule (BA40)	− 30 − 60 38	5.85	4.33	1105	p < 0.001	p < 0.001
Left/right supplemental motor area	− 8 10 58	5.81	4.30	786	p < 0.001	p < 0.001
Left insula	− 26 26 6	5.47	4.14	190	p = 0.015	p < 0.001
Left/right precuneus (BA7)	4 − 70 50	5.11	3.96	512	p < 0.001	p < 0.001
Right posterior cerebellum (lobule VIIb/VIII)	32 − 70 − 58	5.39	4.11	99	p = 0.287	p = 0.033
Right insula	34 32 − 6	4.37	3.56	89	p = 0.394	p = 0.044
Left posterior cerebellum (Crus II)	− 10 − 80 − 32	4.24	3.48	142	p = 0.069	p = 0.008
Significant activations for match > mismatch during probe phase						
Left/right medial frontal gyrus (BA10)	− 6 52 10	− 2.88	− 0.33	874	p < 0.001	p < 0.001
Left/right posterior cingulate cortex (BA31)	− 4 40 48	− 2.88	− 0.33	256	p = 0.002	p < 0.001
(B) Group-level PPI results with posterior inferior cerebellum as seed region						
Significant connectivity with seed region using mismatch > match context						
Left precentral and postcentral gyri gyri (BA6)	− 58 − 16 14	8.2	5.23	2803	p < 0.001	p < 0.001
Left and right thalamus	− 2 − 24 6	6.04	4.41	211	p = 0 004	p = 0.002
Left and right supplemental motor area	− 2 − 4 52	5.15	3.98	231	p = 0.002	p = 0.001
Right transverse temporal gyrus (BA 41)	64 − 14 20	4.87	3.84	181	p = 0.011	p = 0.004
Right postcentral gyrus (BA3)	22 − 30 56	5.57	4.19	104	p = 0.177	p = 0.043
Right insula (BA 13)	40 − 10 4	4.86	3.84	125	p = 0.081	p = 0.022

VWM. Because the serial rehearsal task is guided by the known sequential occurrence of the letters obtained during the encoding phase, participants can predict the identity of each letter during rehearsal by keeping track of the letters as well as their sequential position relative to one another in working memory. Previous motor [44–47] and non-motor [9, 26, 48] studies have converged on the view of the cerebro-cerebellum network as the loci of internal forward models. In the motor literature, an internal forward model is thought to predict the sensory consequence of a movement over time that is then used to compare with the actual consequences of that movement. If the predicted and actual signals match, then the sensory effect of a movement is canceled [49, 50]. If not, the discrepancy constitutes a sensory prediction error, which provides a mean to adjust movement sequence or to update a state estimation of the motor system [for a review: 51]. In the current study, we presented evidence that such monitoring and error-driven adjustment processes that occur in motor control can be used to explain the cerebellum's involvement in cognitive functions, particularly in the context of verbal working memory. Specifically, our findings support the idea that, analogous to the forward models in motor control, the cerebellum computes a predicted articulatory trajectory representing phonemes in the encoded sequence, from which the predicted phoneme is then compared to the incoming phoneme during rehearsal. Any discrepancies between the two would result in an alert to the cognitive system about the potential error within the phonological loop, leading to a corrective adjustment in the articulatory trajectory. This monitoring and error-driven adjustment process is supported by the behavioral and neural evidence discussed below.

When a mismatch between the expected and presented letter occurs during rehearsal, analogous to the sensory prediction error in motor control, participants were significantly slower (154 ms, on average) to respond, compared to the match condition where the expected and presented letter agreed. This behavioral effect, longer RT for mismatch compared to match probe, was consistently observed in all participants in the current study. Using functional neuroimaging, we also demonstrated that the behavioral effect was accompanied by an increase of BOLD activity in a myriad of frontal and parietal regions typically referred to as the left executive control network [52, 53]. Because the mismatch probe represents a letter from the encoded letters but is in an incorrect sequential position, it can

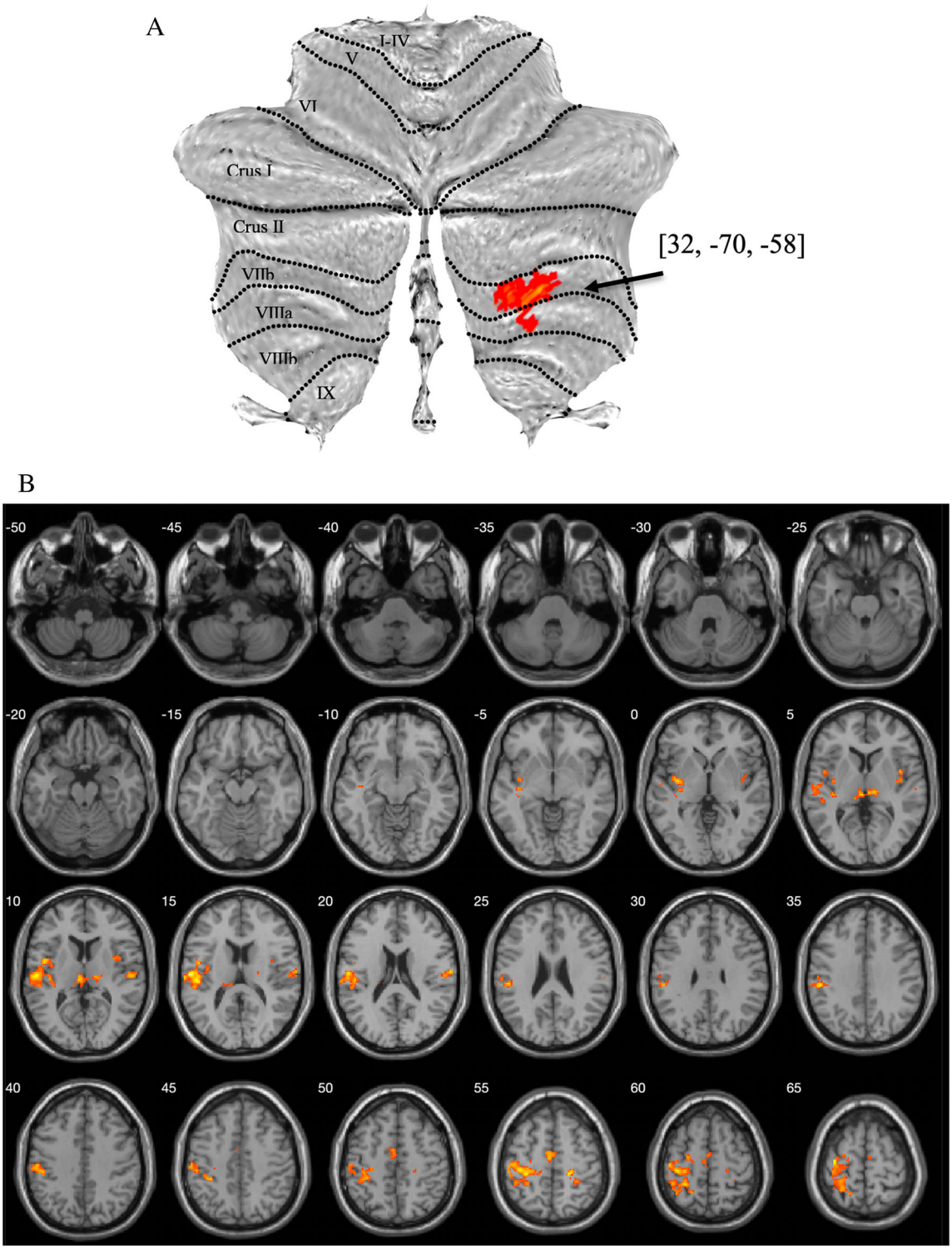

Fig. 3 **a** Cerebellar seed region for PPI analysis overlaid onto a cerebellar flatmap. The seed region was identified using the *Mismatch* > *Match* Contrast from the group GLM activation map (cluster-wise FDR corrected at $p < 0.05$), and is located mainly within lobule VIIb. **b** Areas in cerebral cortex showing increased connectivity with the seed region as a function of sequence violation (Mismatch > Match)

be considered to reflect a violation of sequential order. In this context, the increased behavioral and neural responses to the mismatch probes may indicate higher demands in working memory and attentional control to process a sequential deviant in the phonological loop. Alternatively, it is also likely that the predicted stimuli (match probes) are processed more efficiently than the unpredicted stimuli (mismatch probes), leading to less neural response and faster RT. The latter explanation would be

consistent with a predictive coding model in vision literature, showing that visual cortices learn statistical regularities of the world and stimuli with higher predictability, reducing activity in the early visual areas through feedback from the higher-level area [54].

Here, we argue that our results might be best understood in terms of a violation of sequential order ("sequential deviant") that led to greater demands in working memory and attentional control. First, the accuracy is significantly lower for match compared to mismatch trials, suggesting the match probes were not processed more "efficiently," just "faster" and perhaps more "hastily." If prediction were to facilitate processing of the match probes, then we should expect equal, if not better, performance compared to mismatch probes. Second, by including a 3rd probe type – novel probe – in a follow-up behavioral study, we were able to demonstrate the source of RT difference between mismatch and match probes was likely due to the increased demands of processing of the mismatch probes, rather than the decreased demands of processing the match probes. We reason that, since the novel probes were chosen from letters outside of the encoding sequence, their identity could not be predicted like they could be for match probes, nor did they represent sequential deviants like they did for mismatch probes. From the results for the novel probes, it seems unlikely that shorter RTs for match relative to mismatch probes resulted from facilitation for predicted stimuli given that participants response times to unpredicted novel probes were not significantly different from those to match probes. Rather, the behavioral results showing that the participants responded to the novel probes just as quickly as to the match probes but significantly faster when comparing to mismatch probes provide additional support for an account of sequential violations leading to greater cognitive demands in verbal working memory. By the same logic, the increased activation in the left executive control network during mismatch compared to match trials likely reflects greater demands in working memory and cognitive control needed to process sequential violation associated with the mismatch probes, rather than greater neural efficiency associated with the processing of match probes. Furthermore, this increase of response within the left executive control network may indicate a more general response to sequence violation which is not restricted to a specific task, rather than a task-specific response to sequence violation occurred in the verbal domain. In order to examine sequence violation more specific to the phonological information in VWM, PPI analysis was conducted to examine a task- or context-specific changes in the relationship between two brain regions. Mathematically, the PPI model accounts for variance explained by the interaction term over and above what can be explained by the shared main effects of task and physiological correlation [55]. Therefore, it can rule out non-task-related changes in the relationship between brain regions whenever a sequence violation is detected.

A PPI analysis was thus performed to assess context-dependent (mismatch > match) functional connectivity changes using the right posterior inferior cerebellum as a seed region. We were able to further elucidate the functional interaction between the cerebellum and cerebral cortex when a sequence violation was detected during rehearsal. Specifically, we found that presentation of a sequential deviant was associated with greater functional coupling between the right cerebellum and the left premotor-parietal network, with increased connectivity also found in the bilateral thalamus. Together with other neuroimaging studies showing cerebellar involvement for the encoding of sensory prediction errors during motor task [14, 16], our findings provide additional evidence for cerebellar involvement in the encoding of prediction errors using a cognitive task. Moreover, this increased functional connectivity observed between the cerebellum and the premotor-parietal cortices during mismatch relative to match condition indicate a monitoring and error-driven adjustment process occurring when the incoming stimulus represented a sequential deviant.

The right posterior inferior cerebellum, the chosen seed in our PPI analysis, has long been implicated in language processing and verbal working memory. We have shown previously that right cerebellar TMS disrupts the prediction of upcoming letter in verbal working memory [9]. In other neuromodulation studies, rTMS over right cerebellar regions has shown to disrupt internal prediction of upcoming speech [56] and prediction of upcoming sentence content in a language comprehension task [48]. Previous fMRI studies also indicate the right cerebellar region involve in linguistic prediction [57, 58] and its activity is modulated by the predictability of upcoming sentence content [26]. Anatomically, viral tracing studies in primates revealed that the motor, premotor, prefrontal, and parietal cortices receive input from the posterior cerebellar lobules through the thalamus [30, 59], with reciprocal connections projected from the cerebral cortex to the cerebellum through the pontine nuclei [60, 61]. Resting-state functional connectivity studies in humans also confirmed widespread cortico-cerebellar interconnections between the posterior cerebellar lobule and higher-order association areas involving working memory, language, and emotional task processing [62–65]. Thus, the observed PPI functional connectivity pattern in the current study not only fits the known neural pathways but also suggests a cerebellar feedforward input to the contralateral cerebral cortex via the thalamus, engaging cerebral regions in the left premotor and parietal cortex when a sequence violation is detected, in order to keep the integrity of the phonological loop. However, it is also important to keep in mind that a PPI analysis is unable to determine directionality or causality between functionally connected brain areas. Therefore, an alternative interpretation would be that the functional connectivity observed represents an input from the cerebral cortex to the cerebellum, or a reciprocal exchange of information between them.

Interestingly, in the perceptual domain, detection of sequential deviants has shown to trigger an increase of activation in a very similar, but mostly right-lateralized network, including the middle frontal gyrus (BA9/46), premotor, pre-SMA, cerebellum, and thalamus [13]. The recruitment of a common sensorimotor "sequencing" network, across motor, perceptual, and cognitive domains, suggests that the ability of the cerebellum to predict incoming stimuli and to alert specific neural systems for sequential deviants can be considered a supramodal function [for a review, see 66]. Given that the present task reflects left hemisphere dominance for language and verbal working memory [67], while perceptual sequential tasks invoke right hemisphere dominance for visual target and distractor detection [68–70], the comparable pattern of cerebro-cerebellar networks recruited in opposite hemispheres in both domains is also in line with the idea that the intricate cerebellar neuronal circuit operates on a common computational principle, with differences in function derived from the local input-output connections with the cerebral cortex [24, 59, 71–73]. This suggests that sequence deviation-related activation found in the present study is specific to the verbal domain, rather than a general attentional response to any sequence violation, but more research on this is needed.

The ability to encode and maintain speech-related novel sequences in verbal working memory for short periods of time is important for many core human faculties related to language acquisition, speech comprehension, verbal reasoning, and numerical calculations. Previous studies, both from our lab and others [see Consensus paper: 74], have supported the idea of cerebellar involvement in language, as well as cerebellar internal models in aid of language-related processes and verbal working memory by predicting upcoming verbal stimuli. Our current findings further implicate a monitoring process that relies on the interaction between the cerebellum and the cerebral cortex, which engages error-driven adjustments of the articulatory trajectory when a mismatch between the predicted and actual incoming stimuli is detected. We argue that the incorporation of a monitoring process that detects errors and provides feedback to update the cerebellar internal models would not only ensure the integrity of the phonological loop but also support cognitive learning, similarly to the idea of motor learning through an adaptive control system [75]. Baddeley and his colleagues have reviewed evidence and proposed that the primary function of phonological loop is not to remember familiar words, but to help learn new words [76]. According to their view, the phonological loop provides temporary storage of novel phonological forms while permanent memory representations are being constructed [77]. Thus, our results could be informative about the neural mechanism of learning new words, which are essentially sequences of phonemes, and we speculate that large increases in cerebro-cerebellar connectivity when violations of expected phoneme sequences occur could be vital to neocortical adjustments and the language learning process.

Author Contribution YS conceived the presented idea, analyzed the data, and took the lead in writing. JD developed the task and contributed to the writing of the manuscript.

Funding This work was funded by the National Institutes of Health (NIH/NIMH; grant number R01MH104588 to J.E.D.) and was also supported by NIH/NICHD Award Number P50 HD103538. The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health.

Data Availability The datasets generated for this study are available on request to the corresponding author.

Declarations

Ethics Approval All procedures performed in this study involving human participants adhere to the tenants of the Declaration of Helsinki. The study was approved by the Institutional Review Board of the Johns Hopkins University School of Medicine.

Conflict of Interest The authors declare no competing interests.

References

1. Baddeley A. Working memory. Science. 1992;255:556–9.
2. Acheson DJ, MacDonald MC. Verbal working memory and language production: common approaches to the serial ordering of verbal information. Psychol Bull. 2009;135:50–68.
3. Lewis RL, Vasishth S, Van Dyke JA. Computational principles of working memory in sentence comprehension. Trends Cogn Sci. 2006;10:447–54.
4. Attout L, Majerus S. Serial order working memory and numerical ordinal processing share common processes and predict arithmetic abilities. Br J Dev Psychol. 2018;36:285–98.
5. Attout L, Noël MP, Majerus S. The relationship between working memory for serial order and numerical development: a longitudinal study. Dev Psychol. 2014;50:1667–79.
6. Attout L, Noël MP, Nassogne MC, Rousselle L. The role of short-term memory and visuo-spatial skills in numerical magnitude processing: evidence from Turner syndrome. PLoS One. 2017;12:e0171454.
7. Baddeley AD, Hitch G. Working memory. New York: Academic Press; 1974.
8. Desmond JE, Gabrieli JD, Wagner AD, Ginier BL, Glover GH. Lobular patterns of cerebellar activation in verbal working-memory and finger-tapping tasks as revealed by functional MRI. J Neurosci. 1997;17:9675–85.
9. Sheu YS, Liang Y, Desmond JE. Disruption of cerebellar prediction in verbal working memory. Front Hum Neurosci. 2019;13:61.
10. Wolpert DM, Miall RC, Kawato M. Internal models in the cerebellum. Trends Cogn Sci. 1998;2:338–47.
11. Shadmehr R, Smith MA, Krakauer JW. Error correction, sensory prediction, and adaptation in motor control. Annu Rev Neurosci. 2010;33:89–108.
12. Wolpert DM, Ghahramani Z. Computational principles of movement neuroscience. Nat Neurosci. 2000;3 Suppl:1212–7.
13. Bubic A, von Cramon DY, Jacobsen T, Schröger E, Schubotz RI. Violation of expectation: neural correlates reflect bases of prediction. J Cogn Neurosci. 2009;21:155–68.
14. Schlerf J, Ivry RB, Diedrichsen J. Encoding of sensory prediction errors in the human cerebellum. J Neurosci. 2012;32:4913–22.

15. Tesche CD, Karhu JJ. Anticipatory cerebellar responses during somatosensory omission in man. Hum Brain Mapp. 2000;9:119–42.
16. Imamizu H, Miyauchi S, Tamada T, Sasaki Y, Takino R, Pütz B, et al. Human cerebellar activity reflecting an acquired internal model of a new tool. Nature. 2000;403:192–5.
17. Restuccia D, Della Marca G, Valeriani M, Leggio MG, Molinari M. Cerebellar damage impairs detection of somatosensory input changes. A somatosensory mismatch-negativity study. Brain. 2007;130:276–87.
18. Daskalakis ZJ, Paradiso GO, Christensen BK, Fitzgerald PB, Gunraj C, Chen R. Exploring the connectivity between the cerebellum and motor cortex in humans. J Physiol. 2004;557:689–700.
19. Galea JM, Jayaram G, Ajagbe L, Celnik P. Modulation of cerebellar excitability by polarity-specific noninvasive direct current stimulation. J Neurosci. 2009;29:9115–22.
20. Holdefer RN, Miller LE, Chen LL, Houk JC. Functional connectivity between cerebellum and primary motor cortex in the awake monkey. J Neurophysiol. 2000;84:585–90.
21. Chein JM, Fiez JA. Dissociation of verbal working memory system components using a delayed serial recall task. Cereb Cortex. 2001;11:1003–14.
22. Chen SH, Desmond JE. Cerebrocerebellar networks during articulatory rehearsal and verbal working memory tasks. NeuroImage. 2005;24:332–8.
23. Peterburs J, Blevins LC, Sheu YS, Desmond JE. Cerebellar contributions to sequence prediction in verbal working memory. Brain Struct Funct. 2019;224:485–99.
24. Ito M. Control of mental activities by internal models in the cerebellum. Nat Rev Neurosci. 2008;9:304–13.
25. Friston KJ, Buechel C, Fink GR, Morris J, Rolls E, Dolan RJ. Psychophysiological and modulatory interactions in neuroimaging. NeuroImage. 1997;6:218–29.
26. Lesage E, Hansen PC, Miall RC. Right lateral cerebellum represents linguistic predictability. J Neurosci. 2017;37:6231–41.
27. Stoodley CJ, Schmahmann JD. Evidence for topographic organization in the cerebellum of motor control versus cognitive and affective processing. Cortex. 2010;46:831–44.
28. Stoodley CJ, Schmahmann JD. Functional topography in the human cerebellum: a meta-analysis of neuroimaging studies. NeuroImage. 2009;44:489–501.
29. Hoover JE, Strick PL. The organization of cerebellar and basal ganglia outputs to primary motor cortex as revealed by retrograde transneuronal transport of herpes simplex virus type 1. J Neurosci. 1999;19:1446–63.
30. Kelly RM, Strick PL. Cerebellar loops with motor cortex and prefrontal cortex of a nonhuman primate. J Neurosci. 2003;23:8432–44.
31. Ackermann H. Cerebellar contributions to speech production and speech perception: psycholinguistic and neurobiological perspectives. Trends Neurosci. 2008;31:265–72.
32. Jürgens U. Neural pathways underlying vocal control. Neurosci Biobehav Rev. 2002;26:235–58.
33. Riecker A, Mathiak K, Wildgruber D, Erb M, Hertrich I, Grodd W, et al. fMRI reveals two distinct cerebral networks subserving speech motor control. Neurology. 2005;64:700–6.
34. Clower DM, West RA, Lynch JC, Strick PL. The inferior parietal lobule is the target of output from the superior colliculus, hippocampus, and cerebellum. J Neurosci. 2001;21:6283–91.
35. Dum RP, Strick PL. An unfolded map of the cerebellar dentate nucleus and its projections to the cerebral cortex. J Neurophysiol. 2003;89:634–9.
36. Middleton FA, Strick PL. The cerebellum: an overview. Trends Cogn Sci. 1998;2:305–6.
37. Sasaki K, Jinnai K, Gemba H, Hashimoto S, Mizuno N. Projection of the cerebellar dentate nucleus onto the frontal association cortex in monkeys. Exp Brain Res. 1979;37:193–8.
38. Birn RM, Smith MA, Jones TB, Bandettini PA. The respiration response function: the temporal dynamics of fMRI signal fluctuations related to changes in respiration. NeuroImage. 2008;40:644–54.
39. Chang C, Cunningham JP, Glover GH. Influence of heart rate on the BOLD signal: the cardiac response function. NeuroImage. 2009;44:857–69.
40. Glover GH, Li TQ, Ress D. Image-based method for retrospective correction of physiological motion effects in fMRI: RETROICOR. Magn Reson Med. 2000;44:162–7.
41. Shmueli K, van Gelderen P, de Zwart JA, Horovitz SG, Fukunaga M, Jansma JM, et al. Low-frequency fluctuations in the cardiac rate as a source of variance in the resting-state fMRI BOLD signal. NeuroImage. 2007;38:306–20.
42. Harvey AK, Pattinson KT, Brooks JC, Mayhew SD, Jenkinson M, Wise RG. Brainstem functional magnetic resonance imaging: disentangling signal from physiological noise. J Magn Reson Imaging. 2008;28:1337–44.
43. Kasper L, Bollmann S, Diaconescu AO, Hutton C, Heinzle J, Iglesias S, et al. The PhysIO toolbox for modeling physiological noise in fMRI data. J Neurosci Methods. 2017;276:56–72.
44. Bastian AJ. Learning to predict the future: the cerebellum adapts feedforward movement control. Curr Opin Neurobiol. 2006;16:645–9.
45. Nowak DA, Topka H, Timmann D, Boecker H, Hermsdörfer J. The role of the cerebellum for predictive control of grasping. Cerebellum. 2007;6:7–17.
46. Morton SM, Bastian AJ. Cerebellar control of balance and locomotion. Neuroscientist. 2004;10:247–59.
47. Tseng YW, Diedrichsen J, Krakauer JW, Shadmehr R, Bastian AJ. Sensory prediction errors drive cerebellum-dependent adaptation of reaching. J Neurophysiol. 2007;98:54–62.
48. Lesage E, Morgan BE, Olson AC, Meyer AS, Miall RC. Cerebellar rTMS disrupts predictive language processing. Curr Biol. 2012;22:R794–5.
49. Blakemore SJ, Rees G, Frith CD. How do we predict the consequences of our actions? A functional imaging study. Neuropsychologia. 1998;36:521–9.
50. Blakemore SJ, Wolpert DM, Frith CD. Central cancellation of self-produced tickle sensation. Nat Neurosci. 1998;1:635–40.
51. Sokolov AA, Miall RC, Ivry RB. The cerebellum: adaptive prediction for movement and cognition. Trends Cogn Sci. 2017;21:313–32.
52. Bressler SL, Menon V. Large-scale brain networks in cognition: emerging methods and principles. Trends Cogn Sci. 2010;14:277–90.
53. Seeley WW, Menon V, Schatzberg AF, Keller J, Glover GH, Kenna H, et al. Dissociable intrinsic connectivity networks for salience processing and executive control. J Neurosci. 2007;27:2349–56.
54. Rao RP, Ballard DH. Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. Nat Neurosci. 1999;2:79–87.
55. O'Reilly JX, Woolrich MW, Behrens TEJ, Smith SM, Johansen-Berg H. Tools of the trade: psychophysiological interactions and functional connectivity. Soc Cogn Affect Neurosci. 2012;7:604–9.
56. Runnqvist E, Bonnard M, Gauvin HS, Attarian S, Trébuchon A, Hartsuiker RJ, et al. Internal modeling of upcoming speech: a causal role of the right posterior cerebellum in non-motor aspects of language production. Cortex. 2016;81:203–14.
57. Desmond JE, Fiez JA. Neuroimaging studies of the cerebellum: language, learning and memory. Trends Cogn Sci. 1998;2:355–62.
58. Moberget T, Gullesen EH, Andersson S, Ivry RB, Endestad T. Generalized role for the cerebellum in encoding internal models: evidence from semantic processing. J Neurosci. 2014;34:2871–8.

59. Strick PL, Dum RP, Fiez JA. Cerebellum and nonmotor function. Annu Rev Neurosci. 2009;32:413–34.
60. Schmahmann JD, Pandya DN. Anatomic organization of the basilar pontine projections from prefrontal cortices in rhesus monkey. J Neurosci. 1997;17:438–58.
61. Wiesendanger R, Wiesendanger M, Rüegg DG. An anatomical investigation of the corticopontaine projection in the primate (Macaca fascicularis and Saimiri sciureus)–II. The projection from frontal and parental association areas. Neuroscience. 1979;4:747–65.
62. Bernard JA, Seidler RD, Hassevoort KM, Benson BL, Welsh RC, Wiggins JL, et al. Resting state cortico-cerebellar functional connectivity networks: a comparison of anatomical and self-organizing map approaches. Front Neuroanat. 2012;6:31.
63. Buckner RL. The cerebellum and cognitive function: 25 years of insight from anatomy and neuroimaging. Neuron. 2013;80:807–15.
64. Buckner RL, Krienen FM, Castellanos A, Diaz JC, Yeo BT. The organization of the human cerebellum estimated by intrinsic functional connectivity. J Neurophysiol. 2011;106:2322–45.
65. Wang D, Buckner RL, Liu H. Cerebellar asymmetry and its relation to cerebral asymmetry estimated by intrinsic functional connectivity. J Neurophysiol. 2013;109:46–57.
66. Molinari M, Masciullo M. The implementation of predictions during sequencing. Front Cell Neurosci. 2019;13:439.
67. Riès SK, Dronkers NF, Knight RT. Choosing words: left hemisphere, right hemisphere, or both? Perspective on the lateralization of word retrieval. Ann N Y Acad Sci. 2016;1369:111–31.
68. Bledowski C, Prvulovic D, Goebel R, Zanella FE, Linden DE. Attentional systems in target and distractor processing: a combined ERP and fMRI study. NeuroImage. 2004;22:530–40.
69. Bledowski C, Prvulovic D, Hoechstetter K, Scherg M, Wibral M, Goebel R, et al. Localizing P300 generators in visual target and distractor processing: a combined event-related potential and functional magnetic resonance imaging study. J Neurosci. 2004;24:9353–60.
70. Huettel SA, Mack PB, McCarthy G. Perceiving patterns in random series: dynamic processing of sequence in prefrontal cortex. Nat Neurosci. 2002;5:485–90.
71. Bellebaum C, Daum I, Suchan B. Mechanisms of cerebellar contributions to cognition in humans. Wiley Interdiscip Rev Cogn Sci. 2012;3:171–84.
72. Ishikawa T, Tomatsu S, Izawa J, Kakei S. The cerebro-cerebellum: Could it be loci of forward models? Neurosci Res. 2016;104:72–9.
73. Ramnani N. The primate cortico-cerebellar system: anatomy and function. Nat Rev Neurosci. 2006;7:511–22.
74. Mariën P, Ackermann H, Adamaszek M, Barwood CHS, Beaton A, Desmond J, et al. Consensus paper: Language and the cerebellum: an ongoing enigma. Cerebellum. 2014;13:386–410.
75. Barlow J. The cerebellum and adaptive control. Cambridge: Cambridge University Press; 2002.
76. Baddeley A, Gathercole S, Papagno C. The phonological loop as a language learning device. Psychol Rev. 1998;105:158–73.
77. Gathercole SE, Baddeley AD. Phonological working memory: a critical building block for reading development and vocabulary acquisition? Eur J Psychol Educ. 1993;8:259–72.