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2 The cerebellum is sensitive to the lexical properties of words during spoken language

3 comprehension

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5 Abbreviated title: Effects of lexical properties in cerebellum

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Abstract

Over the past few decades, research into the function of the cerebellum has expanded far beyond the motor domain. A growing number of studies are probing the role of specific cerebellar subregions, such as Crus I and Crus II, in higher-order cognitive functions including receptive language processing. In the current fMRI study, we show evidence for the cerebellum's sensitivity to variation in two well-studied psycholinguistic properties of words— lexical frequency and phonological neighborhood density—during passive, continuous listening of a podcast. To determine whether, and how, activity in the cerebellum correlates with these lexical properties, we modeled each word separately using an amplitude-modulated regressor, time-locked to the onset of each word. At the group level, significant effects of both lexical properties landed in expected cerebellar subregions: Crus I and Crus II. The BOLD signal correlated with variation in each lexical property; patterns consistent with both language-specific and domain-general mechanisms. Activation patterns at the individual level also showed that effects of phonological neighborhood and lexical frequency landed in Crus I and Crus II as the most probable sites, though there was activation seen in other lobules (especially for frequency). Although the exact cerebellar mechanisms used during speech and language processing are not yet evident, these findings highlight the cerebellum's role in word-level processing during continuous listening.

Introduction

During spoken language perception, the brain performs a breathtaking array of functions to transform the incoming speech signal into a meaningful message. From segmenting the continuous speech signal into discrete words to assigning each speech stream to the correct talker—all while simultaneously building a coherent narrative—it is no wonder that this process engages interacting brain networks comprising cortical and subcortical structures. Despite evidence that subcortical areas and the cerebellum are recruited for higher-order cognitive processing (Ackermann et al., 2007; Ashida et al., 2019; Guediche et al., 2015; Stoodley & Schmahmann, 2010), neuroanatomical research of speech and language has almost entirely focused on the cerebral cortex (e.g., Hickok & Poeppel, 2007). Although the cerebellum is relatively well-studied in the sensorimotor domain (for review, see Ohyama et al., 2003), it remains a neural underdog in the language domain. Due in part to significant developments in understanding the cerebellum's neural circuitry and it's connections to cortical and subcortical areas (Alvarez & Fiez, 2018; Balsters et al., 2013; Bostan et al., 2013; Buckner, 2013; Diedrichsen, 2006; Fiez et al., 1992; Kelly & Strick, 2003; Leiner et al., 1994; Marek et al., 2018; Middleton & Strick, 2000; Ramnani, 2012; Stoodley & Schmahmann, 2009; Xue et al., 2021), and insight into its contributions to the perception and production of language (Argyropoulos, 2016; Booth et al., 2007; Guediche et al., 2015; Kotz & Schwartze, 2010; Manto & Mariën, 2015; Marek et al., 2018; Mariën et al., 2014; Moberget & Ivry, 2019; Pleger & Timmann, 2018; Van Dun et al., 2016), interest in the role of the cerebellum in mapping the speech signal to phonetic and lexical units has grown over the past few decades.

The uniform microarchitecture of the cerebellum has led to the hypothesis that a single (or multiple) universal cerebellar mechanism(s) are adaptable to motor and non-motor domains (Diedrichsen et al., 2019; Ito, 2008), perhaps achieved through unique structural and functional connections with cortex (Booth et al., 2007; Guell et al., 2018; Xue et al., 2021). The

cerebellum has a remarkable amount of functional diversity in non-motor language-related tasks (Desmond et al., 1997; Desmond & Fiez, 1998; D'Mello et al., 2017; Durisko & Fiez, 2010; Moberget & Ivry, 2016; Stoodley et al., 2012; Stoodley & Schmahmann, 2009; Van Dun et al., 2016), inspiring calls to determine a potential cerebellar system perhaps comprised of one or multiple adaptable mechanisms that contribute to language processing (Argyropoulos, 2016; Ito, 2005, 2008; Moberget & Ivry, 2016; Skipper & Lametti, 2021; Sokolov et al., 2017). If the cerebellum recruits spatially segregated regions, then characterizing its contributions to higher-order language processes can be informed by precisely defining the specific loci for processing the basic properties of language, including the lexical properties of words.

Although recent work suggests that the cerebellum may be involved in word-level conceptual processing (LeBel et al., 2021), no studies to date have directly measured cerebellar responses to lexical frequency and phonological neighborhood density—two properties known to influence word recognition during speech perception. Examining the cerebellar response to these two fundamental properties of the lexicon allows for the exploration into the potential roles of the cerebellum during the dynamic process of lexical retrieval. One potential mechanism is that the cerebellum encodes and adjusts internal models (Argyropoulos, 2016; E et al., 2012; Ishikawa et al., 2016) which can serve as the basis for generating and adjusting linguistic predictions. Put simply, an internal model is an adaptive, context-specific representation that allows for efficient processing of an incoming sensory experience (Moberget et al., 2014). A critical affordance of internal models, both in the motor and cognitive domains, is the ability to predict what will happen next and to calculate prediction errors that capture the unexpected (Ito, 2008). An increasing number of empirical studies have tested hypotheses related to the cerebellum's role in linguistic predictions (Guediche et al., 2015; Lesage et al., 2012, 2016; Moberget et al., 2014) prompting a number of review articles on the topic (e.g., Pleger & Timmann, 2018; Skipper & Lametti, 2021).

111   Another proposed role for the cerebellum concerns semantic integration. Focal

112   disruption of the right posterior cerebellum interrupts judgments on the semantic relatedness

113   of word pairs (Gatti et al., 2020). Further, in studies of continuous listening, the cerebellum is

114   shown to be sensitive to dissociable conceptual feature dimensions of single words (LeBel et

115   al., 2021). Prediction and integration—the proposed cerebellar roles sketched here—are both

116   connected to the dynamic process of lexical retrieval, though we note that the current study is

117   unable to fully distinguish between them during continuous listening. Rather, here, we focus

118   on identifying the spatial loci of cerebellar sensitivity to lexical frequency and phonological

119   neighborhood density during task-free continuous listening; conditions that best approximate

120   natural lexical processing.

121   Lexical frequency and phonological neighborhood density have shaped theoretical and

122   computational accounts of lexical processing (Benkí, 2003; Besner & Young, 2022; Brysbaert

123   et al., 2018; Chen & Mirman, 2015; Dahan et al., 2001; Luce & Pisoni, 1998; Savin, 1963).

124   Lexical frequency is a measure of the commonness of a word, while phonological

125   neighborhood density refers to the number of words that differ from a target word by one

126   phoneme—whether added, subtracted, or changed (Vitevitch & Luce, 2016; Vitevitch et al.,

127   1999). The lexical frequency effect describes the impact of frequency on the ease of word

128   recognition. Less frequent words tend to slow access to a word's form (Dahan et al., 2001).

129   This effect emerges in a variety of active tasks including word naming, lexical decision, and

130   priming (for reviews, see Brysbaert et al., 2011, 2018). Studies of phonological neighborhood

131   density have generally shown that word recognition is slowed for words occupying denser

132   neighborhoods compared to sparser ones (for review, see Vitevitch & Luce, 2016) though this

133   effect is not monotonic (Chen & Mirman, 2015). Beyond recognition, these properties are also

134   likely to affect a word's integration into the broader context (Cibelli et al., 2015). Taken

together, a word's frequency and number of phonological neighbors likely modulates online word recognition as well as integrative processing.

In the cerebral cortex, word frequency and phonological neighborhood density modulate activity in canonical language regions including the middle temporal gyrus and supramarginal gyrus (Gow, 2012; Peramunage et al., 2011; Prabhakaran et al., 2006; Zhuang et al., 2011). Frontal lobe activation associated with these two properties has also led to domain-general arguments regarding differences in cognitive control demands such as those associated with challenges to lexical selection (Binder et al., 2004; Luthra et al., 2019; Righi et al., 2010; Zhuang et al., 2011). While the effects of frequency and neighborhood density have emerged in the cerebral cortex, of interest is whether activity in the cerebellum is also modulated by lexical-level properties during continuous listening.

The current fMRI study was passive in nature; participants only listened to a podcast without any additional task. The vast majority of studies (behavioral and neural) examining lexical frequency and phonological neighborhood density effects have used artificial active tasks that involve making decisions about words presented in isolation (e.g., lexical decision in Dahan et al., 2001); leaving open whether these effects emerge in more ecologically valid contexts, such as when listening to a podcast. Recent studies using fMRI have shown substantial success in modeling semantic, syntactic, and lexical-level properties of continuous speech and text (Brennan, 2016; Brennan et al., 2016; LeBel et al., 2021; Wehbe et al., 2014) despite the sluggish nature of the hemodynamic response in relation to the rapid nature of conversational speech. The potential for fMRI to capture these rapidly occurring lexically modulated effects, in the cerebellum, is especially appealing as other neuroimaging techniques are not as well-suited for capturing responses in such deep-seated structures. Thus, we follow the precedent set by other studies and model words (verbs, nouns, adjectives, adverbs, and function words) using individual, canonical hemodynamic response functions to assess how

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160 word-level processing modulates cerebellar activity during continuous listening (Brennan et

161 al., 2016). Critically, we chose an analysis approach—amplitude modulated regression—that

162 allows us to model the relationship between activity in the cerebellum with variation in each

163 lexical property over time. This allows us to look for regions for which by-item differences in

164 the BOLD signal correlates with by-item variation in each lexical property above and beyond

165 activity associated with the timecourse alone (see Mechtenberg et al., 2021; Xie & Myers,

166 2018). For example, a positive correlation reflects that for each step that lexical frequency

167 increases, activity in the cerebellum also increases proportionally.

168   We hypothesize that the effects of both lexical frequency and phonological

169 neighborhood density should emerge in the postero-lateral cerebellar cortex—Crus I and/or

170 Crus II. Meta-analyses of cerebellar activation across a range of tasks—language, motor,

171 spatial processing, working memory, executive control, and emotion—shows Crus I, Crus II,

172 and Lobule VI (see Fig. 1A for labelled cerebellar atlas) emerging as the most likely regions to

173 support receptive language processing (Mariën et al., 2014; Pleger & Timmann, 2018;

174 Schmahmann, 2019; Stoodley et al., 2012). Highly relevant to the current paper, activation

175 differences associated with lexical predictability have been observed in Crus I and Crus II.

176 When semantic predictability and sentence-final target-word congruency were systematically

177 manipulated, a region in Crus I/Crus II was activated when final words could be predicted

178 based on context (compared to scrambled sentences) and had even greater activation when final

179 words violated predictions, thought to reflect both predictive processing and cerebellar

180 involvement in error processing (Moberget et al., 2014). The Crus I/Crus II response to lexical

181 prediction also co-occurs with changes in the cortical language network (D'Mello et al., 2017),

182 supporting its contribution (at least in part) to language processes. Further, during continuous

183 listening, Crus I/Crus II (as well as Lobules VIIIA and VIIIB) showed sensitivity to conceptual

184 feature dimensions at the word-level (LeBel et al., 2021).

185   Despite some confidence in where we expect to find cerebellar sensitivity, studies

186   report variability in regards to other subregions—such as Lobule VII, VIII, and IX—that may

187   be recruited for language processing due to additional cognitive demands (e.g., working

188   memory and executive control) that are not a result of processing speech or lexical information

189   specifically (Balsters et al., 2013; Schmahmann, 2019). If effects are observed in these regions,

190   they may reflect differences in domain-general cognitive demands associated with variation in

191   frequency and phonological neighborhood density. Activity in Lobules IV and V (and even

192   portions of Lobule VI; see Fig. 1A for a labeled cerebellar atlas) has been correlated with

193   language production tasks that engage motor output such as writing and speaking (Manto &

194   Mariën, 2015; Pleger & Timmann, 2018; Schmahmann, 2019; Stoodley et al., 2012). As our

195   "task" is entirely passive and does not require any motor output it would be unexpected, but

196   interesting, if we observed activity in these regions (Galantucci et al., 2006). Finally, it is worth

197   noting that activity in Crus I/Crus II has not exclusively been associated with language-related

198   tasks. For instance, other cognitive functions also reliably activate different subregions of Crus

199   I/Crus II including tasks requiring executive control and working memory (Ashida et al., 2019;

200   Balsters et al., 2013; D'Mello et al., 2020; Habas, 2021). The design of the present study does

201   not allow us to untangle what is language-specific or not during naturalistic listening. As such,

202   our interpretation of potential effects of lexical information will also consider domain-general

203   explanations.

204   Precise localization of cerebellar effects at the group level can be challenging due to

205   considerable individual variability in cerebellar anatomy (Diedrichsen, 2006; Kong et al., 2021;

206   Kozlova, 1984). For this reason, in addition to group-level analyses, we also report the results

207   of individual-level analyses, which are spatially aligned to a probabilistic atlas of the

208   cerebellum (Diedrichsen, 2006). The individual-level analyses allow for a more precise spatial

209   localization tailored to each individual. Similar approaches have been used in auditory cortex

(see Okada & Hickok, 2006), where variability in the precise location of activity seen at the individual level would have been obscured at the group level. Reporting the individual-level spatial maps also helps to verify that group-level results were not driven by only a few participants.

In the current study, we scanned 79 adults via fMRI while they passively listened to 10 minutes of a popular podcast. We aim to provide insight into cerebellar involvement in word-level processing by modeling the effects of lexical frequency and phonological neighborhood density during continuous listening at the group and at the individual level. We interpret these findings through both language-specific and domain-general mechanisms.

Materials and Methods

Participants

Seventy-nine participants (male = 17, female = 61, other = 1) were recruited from the University of Connecticut community as part of a larger project from our group (Heffner & Myers, 2021). All reported that they were native speakers of American English, had no hearing loss or neurological disorders, and were over 18 years of age (M = 23.94, range: 18-43). Participants provided written consent based on the University of Connecticut's Institutional Review Board guidelines and were screened for MRI safety. Each participant was compensated $30/hour.

Podcast

All participants listened to the same clip of the first 10 minutes of an episode of National Public Radio's podcast *Fresh Air with Terry Gross* called "A Science Writer Explores The 'Perversions And Potential' Of Genetic Tests," with interviewee Dr. Carl Zimmer (Gross, 2018). The use of this podcast in a research context falls under Fair Use

235 Laws. Please visit https://www.copyright.gov/fair-use/more-info.html for more information.

236 The podcast features a female host and a male interviewee in an interview-style turn-taking

237 discourse. Both talkers spoke in their native language, American English.

238   Word boundaries were identified by the Penn Forced Aligner (Yuan & Liberman,

239 2008), and were manually checked for good fit. Word boundaries were adjusted when

240 appropriate. Our two lexical dimensions of interest, lexical frequency (SUBTLWF$_{US,}$ Brysbaert

241 & New, 2009) and phonological neighborhood density (complete lexicon, no homophones)

242 were determined for each word within the 10-minute segment using the English Lexicon

243 Project (Balota et al., 2007). Excluded words included personal names (e.g., Terry Gross and

244 Carl Zimmer), acronyms (e.g., DNA), and the word "epigenetic" as it did not appear in the

245 SUBTLWF$_{US}$ corpus. Values of lexical frequency and phonological neighborhood density

246 were log-transformed and then z-scored. There was a statistically significant correlation

247 between lexical frequency and phonological neighborhood density ($R^2 = 0.37$, $p < 0.01$). We

248 checked the severity of the collinearity by calculating the Variance Inflation Factor (VIF)

249 which came to 1.587. VIF values below five are considered to be of low concern (O'Brien,

250 2007). Thus, the relationship between the lexical factors is unlikely to limit our ability to

251 accurately model word frequency and neighborhood density. The timing for each word's onset

252 was extracted using the software Praat (Boersma & Weenink, 2022). These were used as the

253 stimulus onset times in the amplitude-modulated regression which is described in detail in the

254 data analysis section.

255

256 *MRI Procedure*

257   After obtaining high-resolution structural scans, each participant was told that they

258 were going to listen to 10 minutes of a podcast. The podcast audio was delivered via MRI-

259 compatible earbuds (Avotech Silent Scan SS3300, Stuart, FL) during a single functional run.

260   There was no visual (i.e., fixation cross) or behavioral component; participants merely listened

261   to the podcast and were instructed to keep their eyes open and listen attentively.

262

263   *fMRI Acquisition*

264   Structural and functional MRI images were acquired from a 3-T Prisma Scanner

265   (Erlanger, Germany). T1-weighted structural images were acquired using a magnetization

266   prepared rapid gradient echo (MPRAGE) sequence (repetition time (TR) = 2400ms, echo time

267   (TE) = 2.22ms, inversion time = 1000ms, flip angle = 8°, 300 × 320 matrix, voxel size = 0.8 ×

268   0.8 × 0.8 mm3). Functional volumes were collected every 1000ms (TR = 1000ms, echo time

269   (TE) = 25ms) in an ascending, interleaved order with an accelerated multiband sequence

270   (multi-band factor = 4, 52 slices, 2.5-mm thick, 110 × 110 acquisition matrix, flip angle = 62°).

271

272   *fMRI data analysis*

273   All analyses were completed using AFNI (Cox, 1996). Functional images were

274   preprocessed using a standard pipeline. Images were de-obliqued, outlier volumes were

275   censored, motion corrected via a six-parameter rigid body transform and the aligned functional

276   images to each participant's skull-stripped anatomical images. Initial normalization used the

277   Talairach atlas (Talairach & Tournoux, 1988), but for the purpose of mapping to the MNI-

278   transformed cerebellar atlas, output of the first-level regression was then warped to MNI space.

279   After normalization, images were smoothed using a 4-mm Gaussian kernel and all motion and

280   signal outliers were removed following standard AFNI procedures. As the current study is

281   exclusively concerned with patterns of activity within the cerebellum, we created individual

282   participant masks using a native AFNI cerebellum mask to restrict the analysis of the functional

283   data to the cerebellum. We then combined the individual masks to create a group cerebellum

284   mask with overlapping voxels for at least 75 out of 79 participants. To do this, we first created

285 by-participant masks (generated during AFNI pre-processing) to identify all voxels with

286 functional data that fell within the cerebellum. These masks were aligned and overlaid, and we

287 excluded any voxel for which there was not usable functional data for at least 75 participants.

288 This procedure ensures that each voxel will have representation from the majority of

289 participants, and also avoids shrinking the size of the group mask unduly if a few participants

290 have atypical anatomy.

291   To assess word-level sensitivity to variation in lexical frequency and phonological

292 neighborhood density, we used amplitude-modulated regression. For this approach, we created

293 a single time-series vector containing the onset of each word in the podcast together with both

294 the corresponding lexical frequency and phonological neighborhood density values. The

295 participant-level regression using this time-series vector was implemented using the "-

296 stim_times_AM2" flag in the *3dDeconvolve* function in AFNI. The vector was convolved with

297 a canonical HRF function and further regressed with the six movement parameters generated

298 during preprocessing. The output, for each participant, was two amplitude-modulated by-voxel

299 fit coefficients—one modeling sensitivity to lexical frequency and the other to phonological

300 neighborhood density. As this was a simultaneous regression, we were able to evaluate the

301 cerebellar sensitivity to lexical frequency while controlling for phonological neighborhood

302 density and vice versa.

303   We ran two group-level analyses, each estimating the main effects of BOLD signal

304 changes to lexical frequency and phonological neighborhood density (separately) versus an

305 implicit baseline (see Fig. 1B and D). Group-level comparisons were done with a t-test using

306 the *3dttest++* function in AFNI. Outputs of each test were constrained to the group-level

307 cerebellum mask described above and cluster thresholded. Cluster thresholding was

308 determined using the *3dClustSim* function via a mixed autocorrelation function that used

309 10,000 Monte Carlo simulations (Cox et al., 2017) on the group mask. We estimated the group-

level spatial smoothness by averaging across all participants' noise smoothness values by extracting their ACF parameters using *3dFWHMx* and including the "-acf" flag within *3dClustSim*. This approach to thresholding fMRI data has been shown to address the concerns associated with Type I error rates in fMRI analyses (Eklund et al., 2016). The corrected group-level threshold was set at a voxelwise threshold of $p < 0.001$ with an alpha value of 0.01, used a 2-sided thresholding, and an extant cluster size of 32 voxels.

To visualize individual differences and capture variability in the localization of the effect of our regressors of interest, we constructed a heat map (limited to the bounds of the cerebellum) that layered individual activation clusters by combining the betas from the first-level regression. For individual-level activation thresholds, we set the cluster threshold to a voxelwise threshold of $p < 0.01$ at an alpha of 0.05, using 2-sided thresholding, extant cluster size: 78 voxels). At this threshold, eight participants did not have any significant clusters for lexical frequency (Fig 2A; n = 71) and nine participants did not have any significant clusters for phonological neighborhood density (Fig 2B; n = 69). The heat maps are additionally constrained depicting only voxels that were shared by at least six participants.
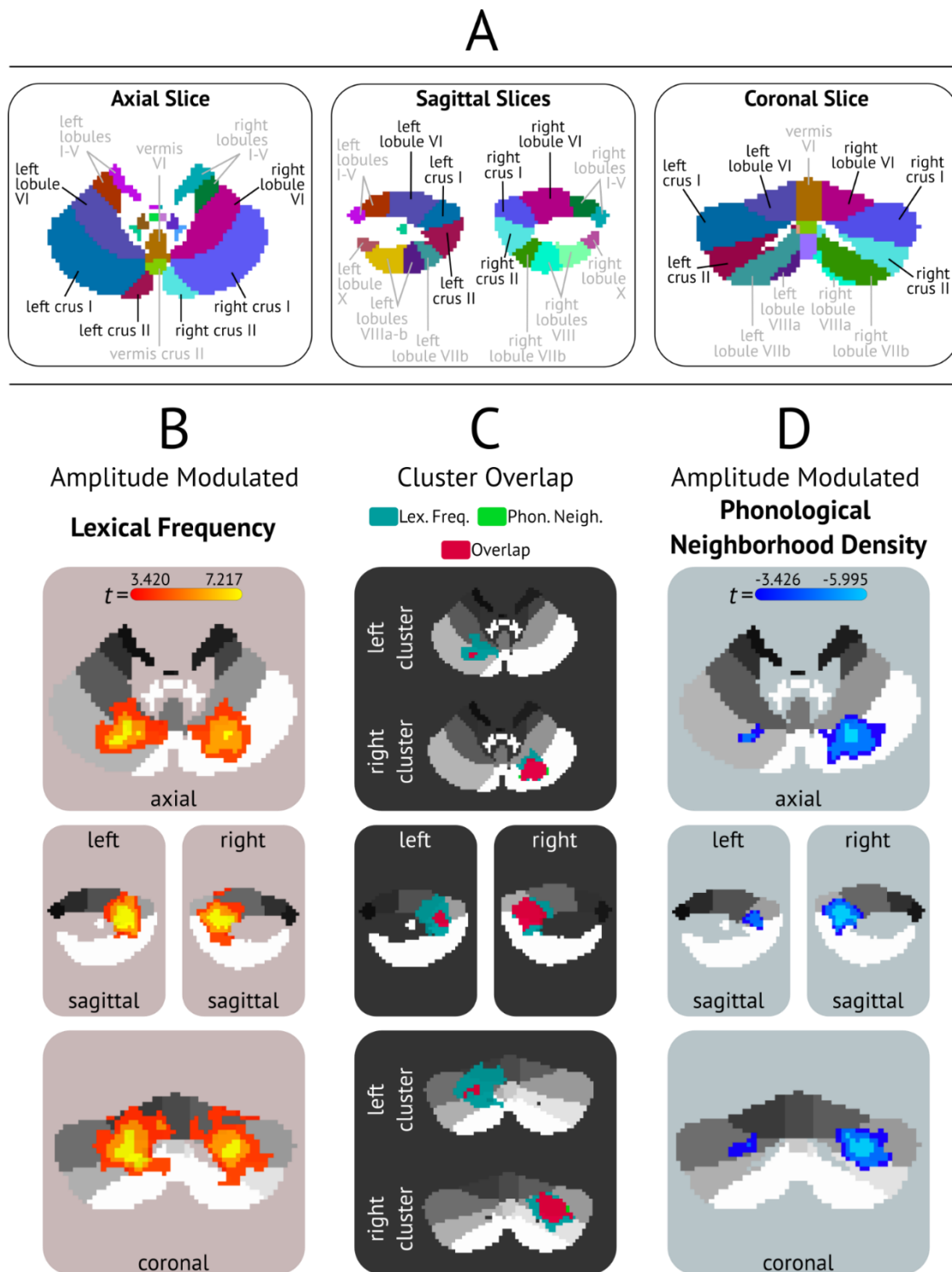
Fig. 1. (A) MNI cerebellar atlas, labeled with anatomical names. All slices numbers are identical to the slices used to depict the functional results. Slice coordinates are at: axial (z) = 22, left sagittal (x) = 35, right sagittal (x) = 57, coronal (y) = 81. (B) Results of the amplitude-modulated activation for lexical frequency versus implicit baseline, with all regions patterning positively with lexical frequency. Clusters corrected at $p < 0.01$

(voxelwise $p < 0.001$, alpha = 0.01, 32 voxel cluster threshold). (C) Depiction of the amount of overlap of the

left and right Crus I/Crus II lexical frequency and phonological neighborhood density clusters. Voxels sensitive

to only lexical frequency are shown in teal, voxels sensitive to only phonological neighborhood density are

shown in neon green. Overlapping voxels are shown in pink. (D) Results of the amplitude-modulated activation

for phonological neighborhood density versus implicit baseline, with activity in all regions negatively

correlating with phonological neighborhood density. Clusters corrected at voxelwise $p < 0.001$, alpha = 0.01, 32

voxel cluster threshold).

Results

Group-level effects of Lexical Frequency and Phonological Neighborhood Density

At the group-level, a significant effect of lexical frequency emerged in three cerebellar

clusters (corrected at a threshold of $p < 0.01$; voxelwise threshold of $p < 0.001$, 32 voxel

minimum cluster size). Each cluster showed a positive correlation with lexical frequency such

that increased lexical frequency was associated with increased activation in these regions. As

shown in Fig. 1B, the two largest clusters were in right and left Crus I—extending into inferior

and lateral portions of Crus II—and superior parts of Lobule VI (see Fig. 1A for labeled

cerebellar atlas). A small cluster was also found in Lobule IX (see Table 1).

Phonological neighborhood density effects emerged in two bilateral clusters—located

in Crus I and extended into Crus II (see Fig. 1D). The size of the two clusters differed, however,

showing a right-hemisphere bias with the right cluster spanning 463 voxels and the left cluster

with only 77 voxels (see Table 1, lower panel). Phonological neighborhood measures were

negatively correlated with changes in BOLD (i.e., words with sparse neighborhoods were

associated with greater activity in both clusters).

To facilitate spatial comparison of the two bilateral Crus I/Crus II clusters for each

lexical factor, we computed the overlap using *3dcalc* and *3dABoverlap*—with the resulting

overlap shown in Fig 1B. There was a remarkable degree of overlap. For the left cluster, the

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358 overlap encompassed an extensive area with only two voxels uniquely sensitive to

359 phonological neighborhood density. In the right cerebellar cluster, 41 voxels were uniquely

360 sensitive to phonological neighborhood density.
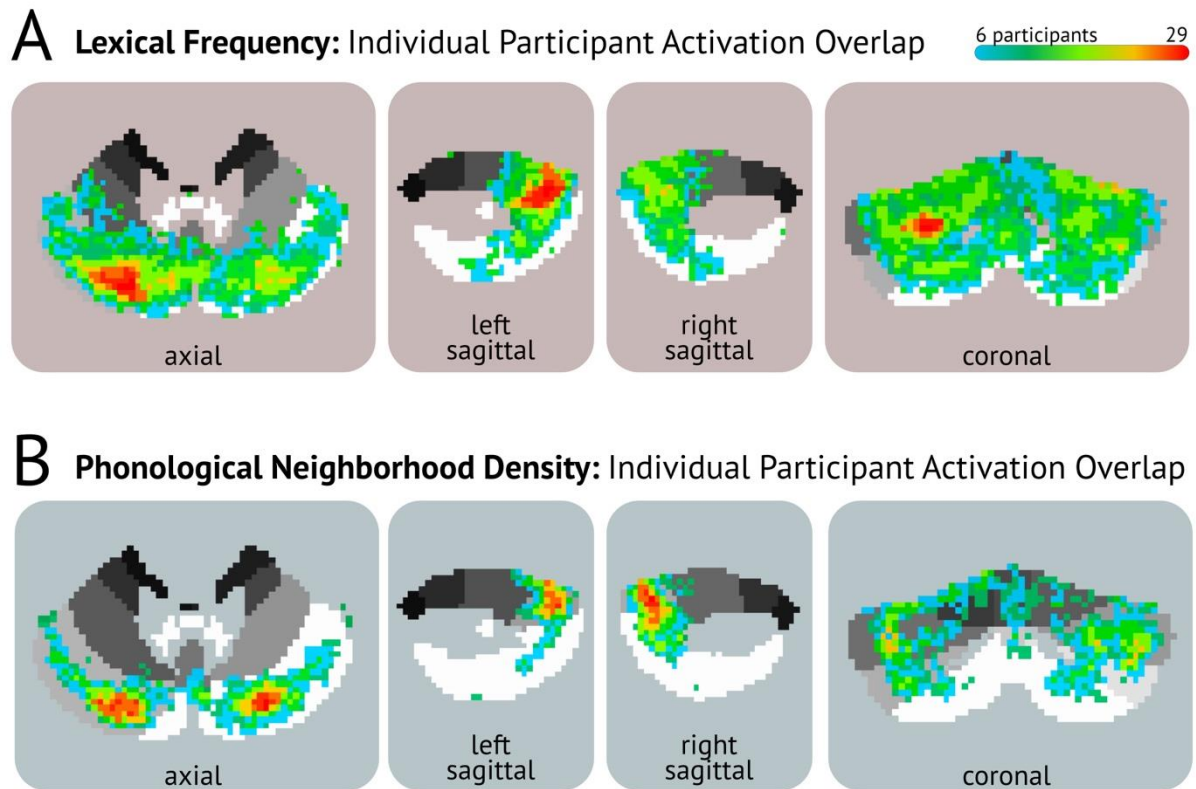
361
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363

Table 1

Results of Group Amplitude-Modulated Analyses

Area	Cluster Size in Voxels	Maximum Intensity Coordinates (mm)			Maximum t Value
		x	*y*	*z*	
Lexical Frequency					
Left Crus I/Crus II	941	-19	-75	-34	6.81
Right Crus I/Crus II	727	25	-71	-34	6.81
Lobule IX	163	5	-53	-40	3.68
Phonological Neighborhood Density					
Right Crus I/Crus II	463	29	-75	-34	-5.19
Left Crus I/Crus II	77	-21	-77	-34	-4.25

364

365

A Lexical Frequency: Individual Participant Activation Overlap

6 participants ████ 29

axial   left sagittal   right sagittal   coronal

B Phonological Neighborhood Density: Individual Participant Activation Overlap

axial   left sagittal   right sagittal   coronal

Fig. 2. Slice levels are identical to those in Fig. 1. Individual clusters thresholded at $p < 0.01$ (voxelwise $p < 0.01$, 78 contiguous voxels) and voxels must be shared by at least six other participants. (A) Heat map showing individual-level voxel overlap for sensitivity to lexical frequency. Hotter colors indicate greater overlap, with a maximum of 29 participants activating the same voxel. (B) Heat map showing individual-level voxel overlap for sensitivity to phonological neighborhood density.

Individual Variability

To explore potential variability in the localization of lexical sensitivity in the cerebellum, we mapped clusters sensitive to lexical frequency (see Fig. 2A) and phonological neighborhood density (see Fig. 2B) for each participant. Overlap across participants is shown qualitatively via a heat map, with hotter colors indicating a greater number of participants activating the same voxel. For lexical frequency, the greatest overlap was found primarily in a region corresponding to the left cerebellar Crus I/Crus II cluster, which also emerged in the group results. There was less consistency in the activation pattern in the right cerebellar hemisphere. Overall, there were widespread effects of lexical frequency. Across individuals, effects of

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382 frequency were additionally observed in Lobules V, VII, VIII, and IX. Activation associated

383 with phonological neighborhood density was more focal across participants and landed mostly

384 in Crus I/Crus II. For phonological neighborhood density, the hottest regions were similar to

385 those found at the group-level. However, there seemed to be less of a right-hemisphere bias

386 observed in the group-level results.

387

388 **Discussion**

389 The current study's aims were two-fold. First, we built on existing fMRI studies of

390 naturalistic continuous speech processing (Brennan et al., 2016; LeBel et al., 2021). We

391 modeled word-by-word variation in two lexical statistics that have been pivotal in our

392 understanding of language processing while participants passively listened to 10 minutes of a

393 popular podcast. As evident in the results, an amplitude-modulated regression approach

394 identified variation of the BOLD signal in the cerebellum associated with these lexical

395 properties during continuous listening. Our second aim was concerned with the nature of the

396 cerebellum's response to variation in lexical frequency and phonological neighborhood

397 density. At the group level, functional sensitivity to both lexical frequency and phonological

398 neighborhood density fell in predicted subregions—primarily bilateral Crus I and Crus II which

399 extended somewhat into Lobule IX. At the individual level, there was a considerable amount

400 of variability in the location and degree of activation to both factors.

401 There was a positive relationship between activation and lexical frequency and a

402 negative relationship between activation and phonological neighborhood density. The

403 correlations between cerebellar activity and each lexical measure were in a consistent direction,

404 suggesting that the cerebellum is sensitive to lexical-level properties that are known to affect

405 word recognition. Of further interest is whether sensitivity to phonological neighborhood

406 density and lexical frequency in Crus I/Crus II emerged in common voxels. Figure 1 shows the

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407   extent of the overlap; the majority of the voxels sensitive to phonological neighborhood density

408   were shared with those activated for frequency effects. Since both factors are known to impact

409   lexical processing, this naturally leads to the question: what role might the cerebellum play in

410   online language comprehension?

411   When listening to spoken language, the statistical distributions of the incoming speech

412   signal are tracked at multiple levels of processing (e.g., Luthra et al., 2021; Theodore & Miller,

413   2008). However, much of what we know about the neural responses associated with these

414   distributions has almost exclusively been restricted to the cerebral cortex. With a growing

415   consensus that the cerebellum is integral to the neural architecture that supports spoken

416   language comprehension (Bonhage et al., 2015; Geva et al., 2021; Moberget & Ivry, 2016;

417   Stoodley & Schmahmann, 2009), we focus on how the cerebellum might rely on internal

418   models (Ito, 2005; R. Ivry, 1997; Ivry & Keele, 1989; Wolpert et al., 1998) that represent word-

419   sound relationships. The cerebellum has been proposed to generate perceptual and linguistic

420   predictions, and also to integrate single words with the broader linguistic context, by "tracking"

421   word-level behaviorally relevant distributions.

422   The work on the cerebellum and language-based internal models has focused primarily

423   on the role of the cerebellum in generating linguistic predictions; for example, investigating

424   the cerebellum's role in semantically-generated lexical predictions from a preceding sentence

425   context (Moberget et al., 2014). While there is strong evidence for cerebellar involvement in

426   this process, there is debate regarding the nature of these linguistic predictions; whether they

427   are generated from motor processes (Pickering & Gambi, 2018), involve associative semantic

428   relationships (e.g., Argyropoulos, 2011), or occur at multiple levels (Skipper & Lametti, 2021).

429   Our finding of a common area that is sensitive to both lexical frequency and phonological

430   neighborhood density suggests that phonological-lexical statistics are tracked by the

431   cerebellum and may help in generating predictions and/or encoding prediction errors at

432   multiple levels of processing. Importantly, the clusters associated with lexical variation were

433   located in Crus I/Crus II. These subregions are not associated with motor processing (Stoodley

434   et al., 2012), suggesting that the predictions generated during listening and comprehension are

435   not limited to motor-based processes.

436   The current study used a natural, continuous speech stimulus. Continuous speech

437   contains rich context cues, at the sentential and the conversational level, motivating a more

438   active listening experience that is conducive for generating predictions about upcoming

439   linguistic elements and for integrating words into the broader context. There is little dispute

440   that predictions are beneficial when deciphering ambiguous speech and listening in noisy

441   environments (for review, see Mattys et al., 2012). In noise, prediction accuracy is modulated

442   by lexical frequency; high frequency words are more easily and accurately predicted than low

443   frequency words (Benkí, 2003; Besner & Young, 2022; Huizeling et al., 2022). Words with

444   denser phonological neighborhoods are likely to generate a greater number of potential

445   candidates (or predictions) compatible at different timepoints of the unfolding speech signal

446   (Luce & Pisoni, 1998). Thus, our findings are broadly consistent with a prediction

447   interpretation in which lexical knowledge contributes to predictions about what we hear. In

448   particular, the voxels sensitive to both frequency and neighborhood density in Crus I/Crus II

449   may be due to their involvement in lexically-generated phonological predictions as has been

450   previously suggested (Guediche et al., 2014, 2015; Lesage et al., 2017).

451   Prediction is only one possible framework for interpreting the cerebellum's role in

452   speech comprehension that fits with the current results. For instance, semantic integration of a

453   given word with surrounding words—and the entire discourse—is also affected by the word's

454   properties. Evidence points to higher frequency words being processed faster than lower

455   frequency words (reviewed in Huizeling et al., 2022). If higher frequency words are accessed

456   more easily and more rapidly, we might expect that these same words are easier to integrate in

457 with previously heard context (Ferreira & Chantavarin, 2018; Roodenrys et al., 2002). Further,

458 frequency effects tap into retrieval and integration mechanisms at multiple levels of processing

459 including the word's phonological form (Fox, 1984) and discourse-level context (Brodbeck et

460 al., 2022). Phonological neighborhood density may also affect word recognition as it unfolds

461 over time. Since the relatedness of a preceding semantic context is also known to modulate the

462 magnitude of neighborhood density effects (Chen & Mirman, 2015), phonological

463 neighborhood density may also impact ease of contextual semantic integration.

464   It may be that the cerebellum reflects the ease of processing individual words as

465 modulated *solely* by a given word's lexical properties (either in terms of prediction, integration,

466 or both); an interpretation that cannot be disentangled from the ease of processing words that

467 vary in their demands on domain-general resources (e.g., working memory demands). To this

468 point, the Crus I/Crus II subregions that emerged in the current study are also implicated in

469 domain-general processes via functional connectivity with cortex. Resting state functional

470 connectivity studies have shown that portions of Crus I/Crus II are associated with the default

471 mode network (Buckner et al., 2011; Xue et al., 2021) as well as fronto-parietal executive

472 control networks (Habas, 2021; Habas et al., 2009). Resting state approaches, however, speak

473 to whether certain regions pattern together at rest. Thus, they are limited in their interpretation

474 regarding their connectivity in response to specific tasks. Studies that have used task-based

475 functional connectivity analyses for language processes tend to show Crus I/Crus II patterning

476 with the canonical cortical language network (Ashida et al., 2019; King et al., 2023; Xue et al.,

477 2021). There does appear to be some overlap between language-specific and more domain-

478 general functional networks in cognitive cerebellar regions (Ashida et al., 2019), and there is

479 growing evidence that domain-general networks might contribute to various aspects of

480 language processing. Concerning the default mode network specifically, the traditional view

481 was that it supported task disengagement functions such as mind-wandering (for review, see

482   Raichle, 2015). More recently, the default mode network is shown to have potential

483   involvement in language-related tasks such as narrative comprehension and semantic access

484   (Chang et al., 2022; Simony et al., 2016), as well as direct overlap with the semantic network

485   (Binder et al., 2009). Interestingly, the default mode network (including the cerebellum) can

486   be subdivided into multiple networks, some of which are implicated in language processing

487   (Buckner & DiNicola, 2019; Gordon et al., 2020). Regardless of whether sensitivity to word-

488   level information in the cerebellum is due to domain-general or language-specific mechanisms,

489   there is mounting evidence pointing towards the cerebellum's involvement in language

490   processing (Schmahmann, 2019) that cannot be discounted. Differences in connectivity

491   findings may indicate that traditional boundaries between online language processing and

492   domain-general functions are rather artificial (Binder et al., 2009; Dohmatob et al., 2020).

493   Further work is needed to carefully parcellate the cortical functional networks in specific

494   subregions of the cerebellum across a wide range of tasks including continuous listening.

495   On the issue of specificity, group-level effects do not necessarily capture what emerges

496   at the individual level, especially if there is some degree of functional and/or structural

497   variability (e.g., Okada & Hickok, 2006). In the current study, we observed a considerable

498   amount of overlap at the individual level in location and degree of activation to both factors,

499   and also variation across individuals (see Figure 2). Individual activation maps indicate that

500   articulatory (Lobule V), perceptual (Lobule VI), and other cognitive processes (Lobules VII

501   and VIII, and IX) might also contribute to the emergence of lexical frequency effects in the

502   cerebellum. Individual variation in sensitivity to neighborhood density was not as widespread

503   as that of lexical frequency nor was it as variable across individuals. Density effects were more

504   restricted to Crus I/Crus II and to closely surrounding areas and was more right lateralized.

505   Since cerebellar connections to cerebral cortex are contralateral, the right-lateralized effects of

506   phonological neighborhood density in the cerebellum are consistent with the involvement of

507 the more dominant left-hemisphere language network (Murdoch, 2010). These findings suggest

508 a potential cascading influence of frequency and neighborhood density across the language

509 system that varies across individuals. Despite this variability, Crus I/Crus II remained the most

510 probable sites of activation across participants for both factors, supporting the group level

511 results. Visualizing the individual-level data helps to confirm the group-level results, lending

512 confidence to the patterns and functional loci of activity in the cerebellum reported in the

513 current study.

514

515 **Conclusion**

516 We add to mounting evidence that calls for including the cerebellum (especially Crus

517 I/Crus II) into neuroanatomical accounts of language processing as a critical part of the

518 underlying functional architecture, and for investigating the cerebellum's role during language

519 processing more broadly. While our findings cannot identify the specific cerebellar

520 mechanisms involved in spoken language processing, as they are consistent with many possible

521 interpretations, they do highlight the cerebellum's role in word-level processing. Importantly,

522 future work can further tease apart the contributions of specific subregions in different aspects

523 of language processing by using targeted manipulations of stimulus features, analyses methods

524 (including connectivity), and other methodological tools that improve localization precision

525 and accuracy.

526

527 **Code and Data Availability Statement**

528 The data and code that support the findings of this study are openly available on GitHub at

529 https://github.com/Hannah-r-Mechtenberg/cerebellum-podcast-fmri. At the moment of

530 publication, we are sharing the downstream statistical data files that directly support the current

531 study. We have provided the scripts that these statistical files were derived from (including the

532 regression script and associated timing file), as well as the group-level statistics script and the

533 script to compute functional cluster overlap.

534   The raw, whole-brain data files (structural and functional) will be available upon

535 request while our group is currently working on several lines of research drawing from these

536 data. Pending publication of these in-progress projects, we will update the repository with

537 whole brain files as well as any additional files or scripts requested by interested parties.

538

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542

543 **Author Contributions**

544 Data collection was done by C.C.H. Data analysis and graphs were completed by H.R.M. The

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548

549 **Conflicts of Interest**

550 The authors report no conflict of interest

551

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556

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