INVOLVMENT OF THE CEREBELLUM IN VERABL WORKING MEMORY AND PHONOLOGICAL JUDGMENT: EVIDENCE FOR A ROLE IN PREDICTIVE PHONOLOGICAL CODING

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Within recent decades, researchers have found evidence that the cerebellum contributes to language processing, yet exactly *how* it contributes remains a mystery. Researchers have attempted to map functional zones within the cerebellar cortex in an effort to determine precisely how the cerebellum contributes to language with limited success. We predict that the cerebellum's functional zones are not strictly divisible by cognitive domains such as "language" or "executive control" and are instead delineated by task demands not unlike cognitive regions in the cerebral cortex. Prior neuropsychological results indicate that rhyme judgment and verbal working memory tasks impose task demands that require the cerebellum for normal levels of performance. In an effort to localize this shared functional process in the cerebellum, we used a slow event-related design to study the hemodynamic response in participants (N=12) as they performed rhyme judgment task and then compared to the results to separate pool of the subjects who performed a verbal working memory task (N=12). We hypothesized that these two tasks share cognitive processes and thereby neural substrates; in other words, they will engage the same functional regions in the cerebellum. Secondly, we hypothesized that these functional regions would be most

engaged during task components negatively impacted by concurrent articulation, i.e., the encoding period of verbal working memory tasks and judgments involving mismatched non-rhyme pairs, e.g. “tint” and “pint.” We found three potential clusters engaged in both tasks, with one region (located in Crus I) demonstrating the predicted response patterns across different task components. Based upon these findings and the cognitive literature on verbal working memory and rhyme judgments, we suggest that this region contributes to an internal speech-based process that involves phonological error prediction.

TABLE OF CONTENTS

1.0 Introduction 1

2.0 Methods

Participants 5
Experimental design and stimuli 6
Image acquisition 7
Preprocessing 8
SUIT normalization 9
fMRI conjunction analysis 9
fMRI timeseries analysis 11
Neurosynth 11

3.0 Results 13

Behavioral results 13
Functional imaging results 14
Conjunction analysis 14
Timeseries analysis 15
Neurosynth 17

4.0 Discussion

General discussion 19
What does the cerebellum do? 21
Insights from speech production 24
Conclusions 25

Bibliography 26

LIST OF TABLES

Table 1. Regions in the cerebellum that are active for p < 0.005 in at least one task. ..15

LIST OF FIGURES

Figure 1. Average reaction time during each trial type during the rhyme task. 14

Figure 2. Average accuracy for each trial type during the rhyme task. 14

Figure 3. Average percent signal change during each trial type within the Left VI cluster (-7, -65, -17). 16

Figure 4. Average percent signal change during each trial type within the Right Crus II cluster (13, -75, -26). 18

Figure 5. Average percent signal change during each trial type within the Right Crus I cluster (34, -64, -29). 18

Figure 6a. The ten most correlated features with the coordinates in left lobule VI, weighted by z value. 19

Figure 6b. The ten most correlated features with the coordinates in right Crus II, weighted by z value. 18

Figure 6c. The ten most correlated features with the coordinates in right Crus I, weighted by z value. 18

1.0 INTRODUCTION

The cerebellum's involvement in language processing remains an enigma despite nearly three decades of research (for review, see De Smet et al. 2013, Marien et al. 2014). Neuropsychological and functional imaging research have provided strong evidence that the cerebellum is involved in language processing, but have left unanswered the question of *how* is it involved. Theories have been placed forth as how to the cerebellum contributes to language, ranging from timing (Ackermann et al. 2007, Ivry et al., 2004, Keele et al., 1990) to motor planning (Manto et al. 2012), yet little has been done to link these theories to specific neuroanatomical mechanisms. Even after years of research, exactly how the cerebellum contributes to language processing is unknown.

Identifying and mapping functional areas within the cerebellar cortex that contribute to language processing is essential in order to better understand the region's role in language. Language processing in general has been localized to lobule VI, Crus I, and Crus II (Stoodley and Schmahmann, 2009), yet attempts to more finely map the language cerebellum have been largely inconclusive, with lesion studies resulting in conflicting or contradictory deficits and imaging studies demonstrating differing patterns of activation (Marien et al., 2001; De Smet et al., 2007). These conflicting results are likely because previous studies have attempted to divide the cerebellar neuroanatomy into broad categories of function – such as "language" regions and "executive function" regions — but have disregarded indisputable complexities within said categories; for instance,

language processing in the cerebral cortex is known to engage multiple processing streams with differentially weighted activation depending on the focus of the task (Hickok 2009, Stoodley & Schmahmann 2009).

Like in the cerebral cortex, differences in cerebellar activation patterns may arise from differentially weighted task demands. This suggests that to successfully understand the organization of the cerebellum for language, we must gain a better understanding of how specific task components activate specific regions. Therefore, by seeking out language tasks with shared task components, we can begin to outline a more fine-grained map of the human cerebellum and advance our understanding of the cerebellar cortex's contribution to language.

Rhyme judgment and verbal serial recall are two language-based tasks that appear to share a functional and structural link within the cerebellum. This connection was proposed by Ben-Yehudah and Fiez (2008), who found that although participants with cerebellar lesions had normal performance on most language tasks, they struggled with a verbal serial recall task and a rhyme judgment task. In the rhyme judgment task, participants were instructed to determine whether a word pair rhymed (e.g., *cat, bat*) or did not rhyme (*fish, black*). When compared to controls, patients with cerebellar lesions had poorer performance for non-rhyming pairs with mismatching phonology and orthography (e.g. *hint*, *pint*) also known as Hard-No pairs. In the serial recall task, participants had to recall a series of either words or non-words after a brief delay. The participants struggled with this task, especially for non-word lists. Ben-Yehudah

and Fiez concluded that damage to the cerebellum interrupted a phonological process important for processing Hard-No pairs and for phonological verbal working memory. Deficits in verbal working memory have been well documented in patients with cerebellar lesions, with reduced accuracy and increased reaction time on digit span (Silveri et al. 1998, Ravizza et al. 2006, Schmahmann et al., 1998). The deficits caused by cerebellar lesions in both of these tasks point towards a structural-functional link between rhyme judgment and verbal working memory.

The behavioral effects of concurrent articulation bolster the theory that verbal working memory and rhyme judgment call on a shared functional process. When healthy participants are forced to perform rhyme judgment while simultaneously vocalizing repetitive speech (e.g., “the, the, the”), or concurrent articulation, they demonstrate decreased accuracy on Hard-No word pairs, the same pattern of impairment as patients with cerebellar lesions. Judgments about word pairs with mismatching phonology and orthography that *do* rhyme (e.g., *dare, hair*), or Hard-Yes word pairs, are not negatively influenced by concurrent articulation, suggesting that deficits are not simply caused by increased difficulty (Besner 1987, Besner & Daniels 1981). Concurrent articulation has also been found impact serial recall performance in healthy individuals, especially when performed during the encoding phase (Chein & Fiez 2010). Because both a structural lesion and a behavioral task (or a so-called “functional lesion”) result in the same profile of impairment, it seems likely that verbal working memory and rhyme judgment share a task component that involves the cerebellum.

In an effort to illuminate functional subdivisions within the language cerebellum, healthy volunteers performed a rhyme judgment task within an fMRI scanner. Results were then compared to a separate dataset in which healthy participants performed a verbal working memory task within the scanner. A conjunction analysis assessed whether there were any shared regions of activation in the cerebellum. Our hypothesis was that verbal working memory and rhyme judgment not only share a functional component, but that they also draw upon a common subdivision within the language cerebellum. Activity within this subdivision of the cerebellum should be greatest for task components that are disrupted by concurrent articulation — in other words Hard-No word pairs in rhyme judgment and the encoding phase during verbal working memory. By evaluating how the brain reacts to each task — especially the task components that are impaired by cerebellar lesions and concurrent articulation – we sought to identify a functional region within the cerebellum, improving our understanding of how the cerebellum contributes to language processing.

2.0 METHODS

2.1 PARTICIPANTS

Twelve right-handed adults (8 females) with ages between 18 and 22 years (mean age 19.2 years) participated in a neuroimaging study that involved a rhyme judgment task. All participants were native English speakers without a history of a neurological or psychiatric disorder, claustrophobia, or ferrous metal implants. All participants gave written informed consent according to the Institutional Review Board at the University of Pittsburgh and received monetary compensation ($25) for their participation.

Twelve right-handed, native English-speaking adults (six females; mean age 22.8 years) participated in a previously published neuroimaging study (Chein et al., 2001) that involved a verbal working memory task (delayed serial recall). The participants in this previous study were also native English speakers without a history of neurological or psychiatric disorder, claustrophobia, or ferrous metal implants. Participants gave written informed consent according to the Institutional Review Board at the University of Pittsburgh.

2.2 EXPERIMENTAL DESIGN AND STIMULI

Participants performed a rhyme judgment task within the scanner as a part of a larger series of studies; the additional studies will not be discussed here. Participants were required to judge whether or not a presented word pair rhymed while data were acquired using a slow event-related design. Both words in each word pair were presented simultaneously for 600 ms, followed by fixation cross for 13400 ms to allow the hemodynamic response to return to baseline. Words were displayed in capital letters, size 14 Courier font, with one word printed above the other in white on a black background. There were 48 pairs of words of four different types (12 word pairs of each type). Hard-No (*bone, none*) word pairs looked alike but did not rhyme, Easy-Yes (*full, pull*) word pairs looked alike and did rhyme, Easy-No (*chair, reel*) word pairs did not look alike and did not rhyme, and Hard-Yes (*dare, hair*) word pairs did not look alike but did rhyme. Participants indicated whether or not the word pairs rhymed by pressing 1 (yes) or 2 (no) on a response glove compatible with the magnetic resonance environment. Before beginning the tasks, participants were provided with task instructions and practice trials outside of the scanner. Participants completed two 10 m runs of the rhyme task, totaling 20 m.

The Chein et al. (2001) dataset was chosen due to the temporal structure of the verbal working memory task used in this study. Specifically, participants performed a verbal serial recall task characterized by an encoding, maintenance,

and retrieval period. During the encoding period, a sequential list of five word or word-like items were displayed for 1 s with a 600 ms interval between items. Following the presentation of the list, a rehearsal cue (—-) appeared. During the 20 s maintenance period, participants were instructed to covertly rehearse the items. A retrieval cue (###) signaled the end of the maintenance period. Four seconds were provided for participants to overtly recall the items in sequential order. Participants were instructed to say ‘skip’ as a placeholder for items that could not be remembered. Because the maintenance period in this study was particularly long (20s), it allows the hemodynamic response in the encoding period and the maintenance period to be discriminated from one another. Separating the hemodynamic response of the encoding period from the maintenance period is of particular interest because concurrent articulation has a greater effect on encoding period than the maintenance period, and thus activity during the encoding period should be greater in our regions than during the delay (Chein & Fiez, 2010). Participants performed eight blocks of eight trials total, leading to a total scan time of approximately 57 m.

2.3 IMAGE ACQUISITION

The rhyme judgment data were acquired using a 3.0 Tesla Siemens Allegra scanner. The imaging session began with the acquisition of scout images and T2-weighted structural images aligned to the functional imaging slice plane with

the slice prescriptions designed to provide full coverage of the cerebellum. In addition, a high-resolution MPRAGE image volume was acquired. During the functional runs, a 38-slice image volume aligned to the AC/PC plane, with 3.2 mm isotropic voxels, was acquired every 2 s using a EPI sequence (TR = 2000 ms, TE = 25 ms, flip angle = 70°, field of view of 205 mm). Task stimuli were projected via mirror onto a visual display positioned above the subject's chest. Stimulus presentation and the recording of keypad responses were controlled using E-Prime software (Psychology Software Tools, Inc).

The data for the serial recall task were acquired as described by Chein et al. (2001). In brief, serial recall imaging data were acquired on a 1.5 T whole-body GE Sigma magnet. During the functional runs, a 26-slice image volume aligned to the AC/PC plane, with 3.75 x 3.75 x 3.8 mm isotropic voxels, was acquired every 4 s using a T2*-weighted, gradient-echo, two-shot spiral pulse sequence (TR = 2000 ms, TE = 25 ms, flip angle = 70°, field of view of 205 mm).

2.4 PREPROCESSING

Imaging data from the rhyme judgment task were analyzed using the NeuroImaging Software package (NIS 3.8). Structural and functional images were reconstructed and corrected for participant motion with the Automated Image Registration software (AIR 3.08; Woods, Cherry, & Mazziotta, 1992). Runs with head motion that exceeded 4 mm were not used in the analysis. Structural

images (T1) of each participant were stripped to remove the skull. Functional images (T2) were transformed into the same common space, normalized by a mean scaling of each image to match the global mean image intensity across participants, and smoothed using a three-dimensional Gaussian filter (8mm). Serial recall data were analyzed using an earlier version of the NeuroImaging Software package (NIS 3.3), but all structural and functional preprocessing steps remained the same.

2.5 SUIT NORMALIZATION

Structural images of each participant from the rhyme judgment study and verbal working memory study were normalized into the Spatially Unbiased Atlas Template (SUIT) of the cerebellum and brainstem (Diedrichsen, 2006; Diedrichsen et al., 2009) to allow a more accurate localization of activation within the cerebellum using SPM 8 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8). First, the cerebellum was isolated from the remainder of the brain via an automated segmentation algorithm. The isolated cerebellum was then registered using normalization parameters to the SUIT template. These same normalization parameters were used to reslice the smoothed functional images into the new atlas space, allowing a more fine-tuned map of the task-based activation.

2.6 FMRI CONJUNCTION ANALYSIS

Statistical analysis for both rhyme judgment and serial recall was completed using the NIS package 3.7 (University of Pittsburgh, Princeton University). Regions of interest in both tasks were localized via voxel-wise ANOVA using an alpha threshold of $p< 0.05$ (uncorrected).

Concurrent articulation, a task manipulation that causes the behavior of healthy participants to mimic the behavior of patients with cerebellar lesions, impacts Hard-No word pairs more than any other word pair during rhyme judgment (Besner 1987, Besner & Daniels 1981). For this reason, ANOVA factors in the rhyme task were Time (TR) and Problem Type (Hard-No, Hard-Yes, Easy-No, Easy-Yes). During a serial recall task, concurrent articulation significantly affects the encoding period more than the maintenance period (Miles et al. 1991, Chein and Fiez 2010). In the serial recall task, Phase (encoding, maintenance) was used as the factor in the ANOVA in order to highlight regions with greater activity during the encoding period than the maintenance period. For the encoding epoch, the average signal intensity during the last 8 s of stimulus presentation for each trial (TR2 and TR3) was used as the dependent measure. For the maintenance epoch, the average signal intensity during the last 8 s of each 20-sec maintenance period (TR7 and TR8) was used as the dependent measure.

Contrasts from both tasks were converted into masks, which were then overlaid in a conjunction analysis to identify overlapping task clusters. A

conjunction cluster was retained if activation in at least one ANOVA contrast reached a corrected alpha threshold of $p < .05$. This voxel-wise significance threshold was corrected for multiple comparisons using Monte Carlo simulations (i.e., 3dClustSim by AFNI) with a contiguity threshold of 5 voxels.

2.7 FMRI TIMESERIES ANALYSIS

Performing an ANOVA indicates whether or not an effect is present but does not indicate the direction of the effect. To better characterize the neural responses of the regions identified by the conjunction analysis, timeseries of the hemodynamic response were extracted from each region. The percent signal change was calculated for each timepoint during the trial with the first TR as a baseline. Paired t-tests were then performed for each task in order to determine the direction of the effect. In the rhyme task, word pairs that appear to rhyme visually but do not rhyme phonologically (Hard-No) were expected to produce greater hemodynamic response than other word pair types. In the serial recall task, greater activation during the encoding phase than the maintenance phase was expected.

2.8 NEUROSYNTH

To identify cognitive features that have been previously associated with the regions identified in the conjunction analysis, we investigated each conjunction region using NeuroSynth (Yarkoni et al. 2011, version 0.2), a meta-analysis tool that combines data-mining and machine learning to make quantitative associations between keywords (such as “language”) and stereotaxic coordinates. Coordinates and keywords are gathered from over one thousand functional imaging studies, allowing researchers to readily perform both “forward inference” and “reverse inference” analyses. Forward inference is the probability of observing activity in a brain region given the knowledge of the psychological process, whereas “reverse inference” indicates the probability of a psychological process being present given knowledge of activation in a particular brain region. We identified the center of mass in each overlapping cluster and performed reverse inference by inputting the coordinates into Neurosynth. Z values were recorded for the top ten most correlated features. For visualization purposes, features sized in proportion to their z values are pictured in a frequency-based word cloud.

In addition, we used the Neurosynth resting state functional connectivity analysis in order to evaluate the correlations between our regions. Neurosynth uses a sample size of 1000 subjects (Yeo et al. 2011) and reduces blurring of signals across cerebo-cerebellar and cerebro-striatal boundaries by regressing

fMRI signals from the cerebellum and the striatum (Buckner et al. 2011, Choi et al. 2012).

3.0 RESULTS

3.1 BEHAVIORAL RESULTS

We performed an ANOVA in order to determine whether problem type (Hard-No, Hard-Yes, Easy-No, Easy-Yes) significantly affected reaction time (RT) and accuracy. Results were significant for RT, $F(3,12) = 3.287$, $p < 0.03$. In order to determine the direction and origin of the effect, we performed a series of t-tests. As expected, Hard-No trials resulted in significantly greater reaction times (M =

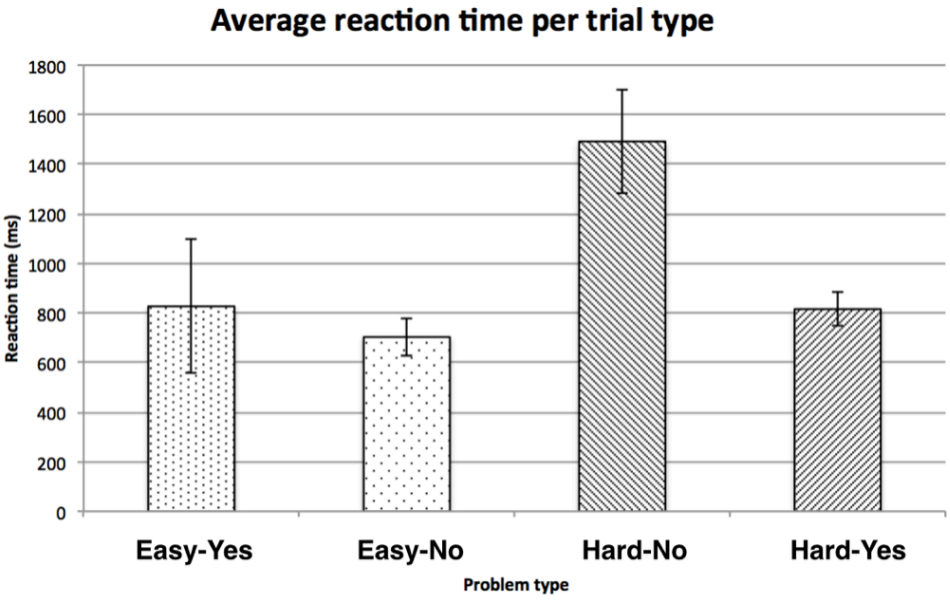

Figure 1. Average reaction time during each trial type during the rhyme task. Error bars mark standard error.

14491.98, SD = 720.71) than Hard-Yes (M = 815.81, SD = 231.27) trials, $t(11) = 2.967$, $p < 0.013$, and Easy-Yes (M = 703.15, SD = 260.88) trials, $t(11) = -2.291$, $p < 0.043$. Hard-No trials, however, where not significantly different from Easy-

No (M = 826.93, SD = 929.08) trials, t(11) = -0.33, p < 0.748. All other comparisons were not significant (Figure 1).

A significant effect of problem type was not observed in accuracy F(3,12) = 0.22, p < 0.88; Hard-No (M = 0.90, SD = 0.08), Hard-Yes (M = 0.92, SD = 0.29), Easy-No (M = 0.99, SD = 0.29) and Easy-Yes (M = 0.96, SD = 0.29) (Figure 2).

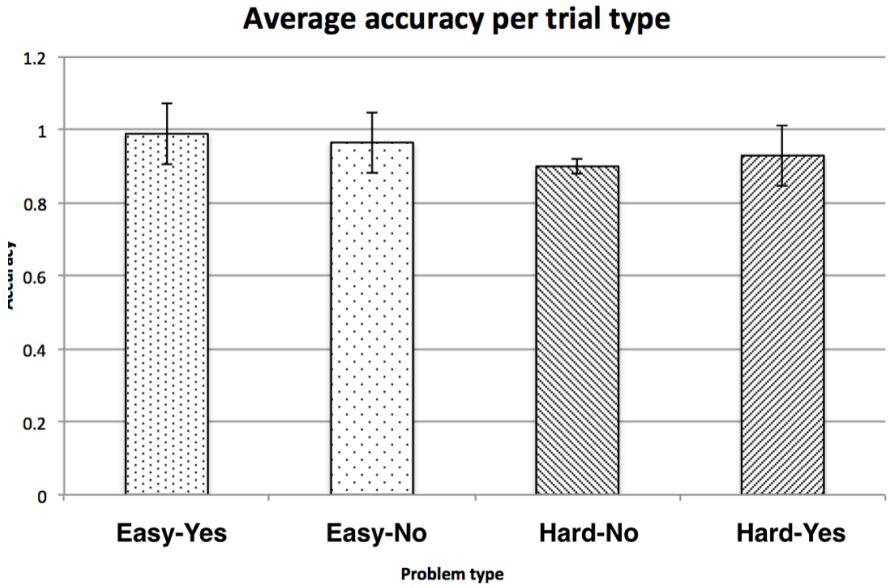

Figure 2. Average accuracy for each trial type during the rhyme task. Error bars mark standard error.

3.2 FUNCTIONAL IMAGING RESULTS

3.2.1 CONJUNCTION ANALYSIS

Individual voxel-wise contrasts were performed for each task condition (rhyme judgment and serial recall) and then overlaid in a conjunction analysis. In the rhyme judgment task, factors were TR and problem type (Hard-No, Hard-Yes, Easy-No, Easy-Yes). In the serial recall task, the factor was phase (encoding, maintenance). Three voxel clusters were identified within the cerebellar cortex

(Table 1).

Table 1. Regions in the cerebellum that are active for $p < 0.005$ in at least one task.

Cerebellar Region	Sector	x	y	z	cluster size
Left VI	Medial	-7	-65	-17	2
Right Crus I	Lateral	34	-64	-29	2
Right Crus II	Medial	13	-75	-26	16

3.2.2 TIMESERIES ANALYSIS

We extracted the timeseries of the hemodynamic response from the three clusters within the cerebellar cortex that met our conjunction criteria in order to further investigate the response to problem type. The voxel cluster within left lobule VI (Figure 3) demonstrated an overall decrease in activity over the course of both tasks. All problem types resulted in deactivation and none differed significantly from another. The second voxel cluster was located within right Crus II (Figure 4). Easy-Yes word pairs were less deactivated than Hard-No, $t(11) = 2.96$. $p < 0.013$, and Hard-Yes pairs, $t(11) = 3.787$, $p < 0.003$. No other comparisons were significant. The final voxel cluster was within right Crus I (Figure 5). This brain region demonstrated significantly greater activation in the Hard-No trials compared to Easy-No, $t(11) = -3.247$, $p < 0.008$, Easy-Yes ($p<0.005$), $t(11) = -5.321$, $p < 0.0001$, and Hard-Yes trials, $t(11) = 3.565$, $p <$

0.004, demonstrating the expected activation patterns. No other comparisons were significant. Timeseries were also extracted from the verbal working memory task. The voxelwise ANOVA indicated that all clusters had significantly different activity during the encoding period (TR 2 – 3) compared to the maintenance period (TR 7- 8). A visual inspection of the hemodynamic response revealed that activity during the encoding period was significantly greater than the hemodynamic response during the maintenance period.

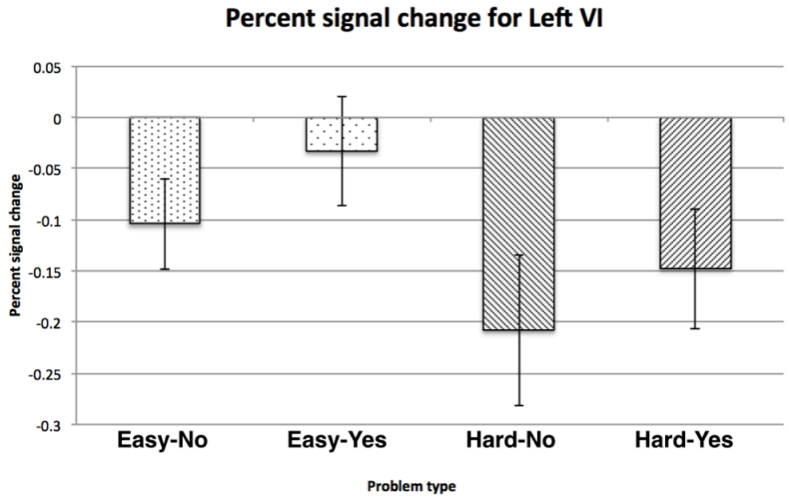

Figure 3. Average percent signal change during each trial type within the Left VI cluster (-7, -65, -17). Error bars mark standard error.

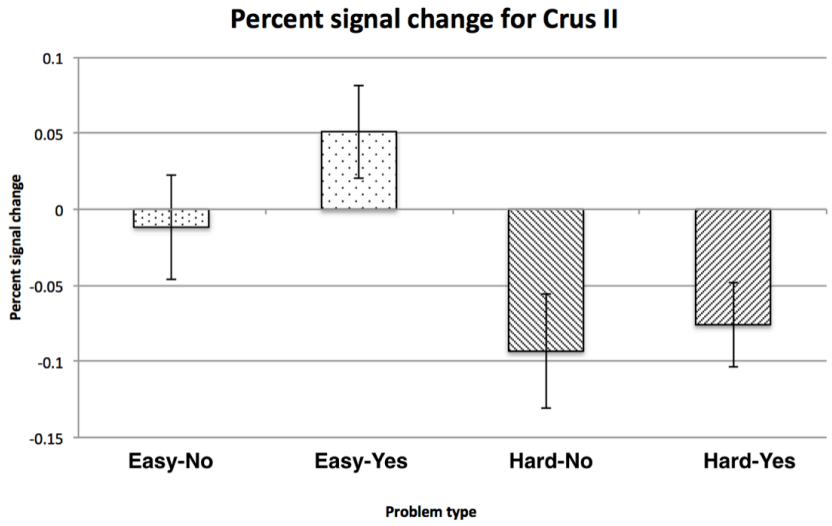

Figure 4. Average percent signal change during each trial type within the Right Crus II cluster (13, -75, -26). Error bars mark standard error.

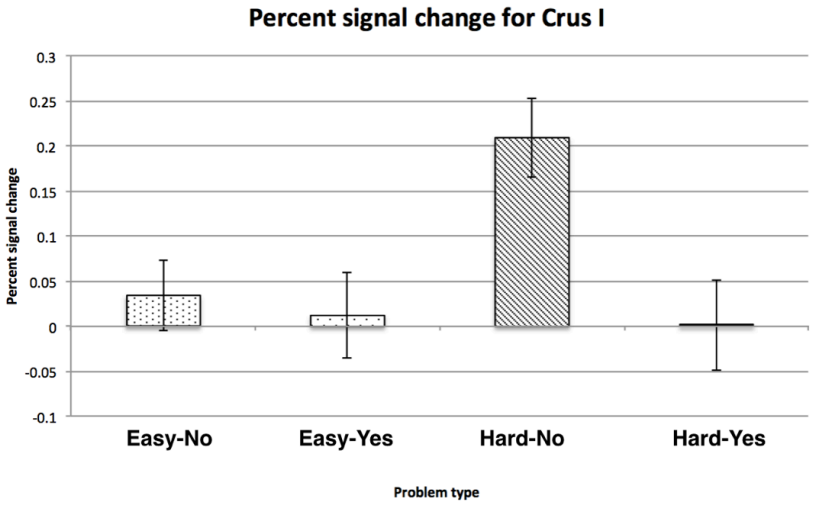

Figure 5. Average percent signal change during each trial type within the Right Crus I cluster (34, -64, -29). Error bars mark standard error.

3.2.3 NEUROSYNTH

The voxel cluster in left lobule VI was heavily associated with motor features, specifically articulatory features (Figure 6a). The voxel cluster in right Crus II was associated with a wide variety of different features (Figure 6b) that included executive functions (e.g. contextual, decisions) and sensation (e.g., pain-related,

heat) among other features. The voxel cluster in right Crus I was associated with features engaged in both working memory (e.g., retrieval, rehearsal) and language (e.g., verbal, overt) (Figure 6c).

Using Neurosynth's resting state functional connectivity feature, we examined correlations between our clusters. This analysis revealed a high correlation between the Crus I cluster and the Crus II cluster (r = 0.39), but weak correlations between Left VI and Crus II (r = 0.04) and Left VI and Crus I (r = 0.06).

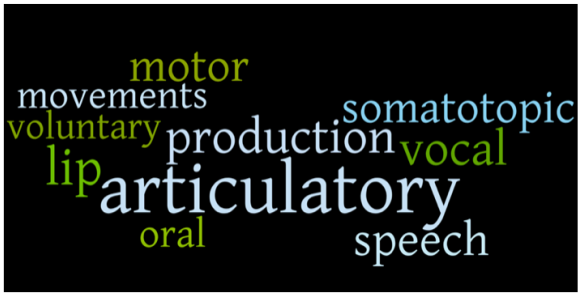

Figure 6a. The ten most correlated features with the coordinates in left lobule VI, weighted by z value.

Figure 6b. The ten most correlated features with the coordinates in right Crus II, weighted by z value.

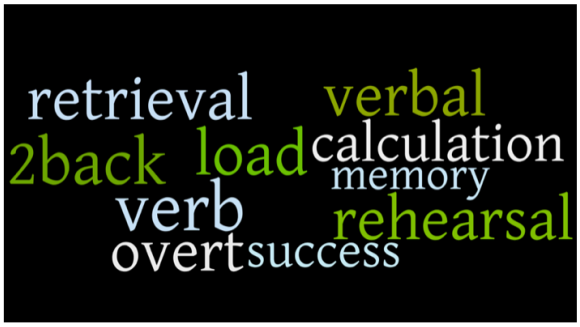

Figure 6c. The ten most correlated features with the coordinates in right Crus I, weighted by z value.

4.0 DISCUSSION

The goal of this study was to improve our understanding of the functional contributions of the cerebellum to language by comparing functional activation results for verbal serial recall and rhyme judgment, two tasks theorized to share a functional and thereby structural link. Our interest in the structural correlates of these two tasks arises from the observation that both cerebellar lesions and concurrent articulation disrupt the tasks in strikingly similar ways, suggesting that the two tasks make a common processing demand that involves the cerebellum. By identifying one or more regions of common cerebellar activation across these two tasks, we would take an important step towards understanding the cerebellum's role in language.

We found three regions within the cerebellar cortex that are potential candidates for a structural/functional link between serial recall and rhyme judgment. The meta-analytic database Neurosynth supported all three regions as potential candidates; keywords associated with the averaged coordinates in two of the regions skewed heavily towards both language and working memory. Although we found three separate regions of activation rather than a single functional zone, our results are no less illuminating; these three structures within the cerebellum may very well work in tandem to support a shared functional component in both phonological processing and verbal working memory.

One functional region we observed was within the anterior cerebellum (Left

VI), also known as the more traditional “motor cerebellum.” Physiological experiments in cats (Adrian, 1943) and functional imaging studies in humans (Grodd et al., 2001) have revealed the presence sensorimotor homunculi within the anterior cerebellum. Activity within a radius of 5 millimeters from our coordinates has been regularly associated with the production of mouth movements (Ackermann et al. 2007, Grabski et al. 2012). This functional region was deactivated during our task rather than activated, perhaps suggesting that overt speech commands were being suppressed.

Another functional region we identified (Crus II) was within the posterior cerebellum, the subdivision of the cerebellum commonly associated with cognitive function. Activity within these coordinates previously been observed during language tasks (Brambati et al. 2006, Booth et al. 2002, Stoodley & Schmahmann 2009), although the nature of its function in our task is harder to pinpoint. Within this region, Easy-Yes word pairs were significantly less deactivated than both Hard-No and Hard-Yes pairs, suggesting a difficulty effect rather than an effect specific to Hard-No word pairs, as anticipated from deficits caused by concurrent articulation and cerebellar lesions. Neurosynth provided further illumination; this conjunction region is strongly correlated with the Crus I conjunction region. Even though the contribution is difficult to pinpoint, it appears to be involved in both verbal working memory and rhyme judgment tasks.

The third functional region we identified (Right Crus I) has been previously observed by Chen and Desmond (2005) during their research on the cerebellum’s role in verbal working memory. Like us, they found that during a

verbal working memory task, activation within right Crus I peaked during the encoding phase and dipped during the maintenance phase (Chen and Desmond 2005). Multiple regions within the cerebral cortex demonstrated similar patterns of activity over the course of the working memory task, including the precentral gyrus and the left inferior frontal gyrus (i.e., Broca's area). Because this region exhibited phase-variant activity that co-varied with motor speech regions in the cerebral cortex, Chen and Desmond proposed that it is responsible for creating an articulatory plan during the encoding phase.

4.1 WHAT DOES THE CEREBELLUM DO?

We localized three regions within the cerebellar cortex that contribute to both rhyme judgment and verbal working memory. One of the identified regions, located in Crus I, demonstrated the expected response pattern in both serial recall and rhyme judgment, i.e., greater activity in the encoding versus maintenance period during serial recall and greater activity for Hard-No trials (e.g., hint, pint) than other rhyme trials during rhyme judgment. Our data as well as conclusions made in previously published studies lead us to believe that the Crus I conjunction region contributes to an aspect of inner speech — specifically a phonological prediction process.

The idea that the cerebellum functions as a wide-reaching prediction and monitoring system was proposed by Ito et al. (2008), who suggested that the

cerebellum's uniform cytoarchitecture combined with its distinct connections with the cerebral cortex placed it in a prime position to produce internal models for motor and non-motor tasks alike. Internal models are neural representations of the dynamic properties of an object (for instance, an arm) that can be used to predict and control actions involving said object (Wolpert et al. 1995, Ito 2006). Discrepancies between the predicted and actual sensory consequences of that action result in a prediction error signal and a subsequent correction. Although this error correction model has been traditionally associated with the cerebellum's role in motor control, Ito's group theorized that this algorithm could extend beyond the motor domain and into more cognitive processes such as language and executive functions, coordinating thoughts not unlike how it coordinates movements.

Recent studies have investigated whether or not the cerebellum uses internal models and prediction errors during language processing. Lesage et al. (2012) used rTMS in order to determine whether or not inhibiting cerebellar activity inhibits predictive language processing on the sentence level. Participants were instructed to look towards the next word in a sentence as quickly as possible. When words were predictable based on the rest of the sentence, cerebellar rTMS significantly slowed reaction time. A more recent study by the Moberget et al. (2014) also concluded that the cerebellum might use internal models in order to perform predictive coding. They observed heightened cerebellar activation when the terminal words in the sentence were predictable (e.g., "two plus two is four"), as well as an even greater activation when terminal words appeared to be

predictable but instead defied expectations (e.g., “[the water] had frozen to cars”). This study as well as the observation that rTMS to the cerebellum disruptions predictive sentence processing suggests that the cerebellum uses internal models during language tasks, at least at the sentence level.

Ben-Yehudah and Fiez (2008) suggested that cerebellar internal models could assist the phonological system during inner speech as well; specifically, to account for the rhyme judgment and verbal working memory impairments that they observed in individuals with cerebellar lesions, they theorized that the cerebellum may use internal models during inner speech in order to simulate the sensory consequences of subvocal articulation and compare these consequences to phonological representations for presented items. Word pairs such as “hint and pint” and “golf and wolf” would be more likely to induce phonological errors, given the mismatch between orthography and phonology in these items, and working memory for unfamiliar words (or non-words) would require articulatory monitoring more than familiar words. The elimination of this phonological monitoring system, whether via structural or functional lesion, would result in increased error rates on the trials that are more inclined for phonological errors.

The suggestion that the cerebellum participates in phonological error prediction is further strengthened by the strikingly similar deficits resulting from cerebellar lesions and concurrent articulation. Concurrent articulation was originally theorized to interrupt inner speech as a whole, but it instead appears to hinder a more specific component of the process. In the rhyme task, concurrent

articulation does not disrupt reading in general but word pairs with mismatching phonology and orthography (Besner et al. 1981, Besner et al. 1987). Similarly, concurrent articulation also does not significantly decrease accuracy or increase reaction times for homophony judgments (e.g., does “fome” sound like “foam?”) (Besner et al. 1987, Tree et al. 2011). Thus, like cerebellar lesions, concurrent articulation impacts phonological judgment trials in which there is a mismatch between phonology and orthography, suggesting that it may interrupt a phonological error prediction process. These similar deficits support the theory that the cerebellum contributes to phonological prediction as a component of inner speech.

4.2 INSIGHTS FROM SPEECH PRODUCTION

To further illuminate the potential contributions of the cerebellum to inner speech, we turn to the behavioral literature on speech production, specifically the flexible abstract model by Oppenheim and Dell (2008). Like other models within the language production literature, the flexible abstract model theorizes that inner speech emerges at a phonological level of representation (Indefrey & Levelt, 2004; Levelt, 1999; Wheeldon & Levelt 1995). Unlike other language production models, however, the flexible abstract model predicts that feedback from articulatory system can bias phoneme selection depending on the motor demands of the task; for instance, when participants are instructed to silently mouth words, they are more likely to rely on the articulatory system (Oppenheim and Dell 2008) and therefore commit more errors influenced by articulation.

Gupta and MacWhinney (1997) pinned a similar role on the articulatory system; they theorized that an efferent copy of planned articulation could “refresh” inner speech during various tasks, allowing a strengthened signal that could help maintain items during working memory as well as word acquisition. Gupta’s model is particularly intriguing, as it implicates articulation in both verbal working memory and phonological processing, the two functions we probed during our study. The articulatory feedback described by both Oppenheimer and Dell (2008) and Gupta and MacWhinney (1997) could feasibly be connected with the cerebellum’s role in error correction.

As suggested in both the Dell and the Gupta models, we propose that feedback from articulatory programming influences speech planning. We take one step further than both models, however, and suggest that an efferent copy of the proposed articulatory plan does more than provide reactivation, it provides information that can be compared to the phonological plan. Discrepancies between the planned production and the efferent copy can be corrected at the phonological level, to reduce errors in phonological representation and speech production.

4.3 CONCLUSIONS

We identified three regions in the cerebellum which activity that modulated in response to task components associated with rhyme judgment and verbal serial recall. One of these regions, located in Crus I, exhibited a pattern of activity predicted by the effects of concurrent articulation on rhyme judgment and verbal working memory. Given our results as well as conclusions made in previous studies, we theorize that this region participates in phonological error prediction.

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