Brain and Language 186 (2018) 32–43

Contents lists available at ScienceDirect

Brain and Language

journal homepage: www.elsevier.com/locate/b&l

Cortical regions supporting reading comprehension skill for single words and discourse

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ARTICLE INFO

Keywords:
Reading comprehension
fMRI
Modality
Processing level
Partial Least Squares Correlation (PLSC)
Naturalistic design

ABSTRACT

A substantial amount of variation in reading comprehension skill is explained by listening comprehension skill, suggesting tight links between printed and spoken discourse processing. In addition, both word level (e.g., vocabulary) and discourse–level sub-skills (e.g., inference-making) support overall comprehension. However, while these contributions to variation in comprehension skill have been well-studied behaviorally, the underlying neurobiological basis of these relationships is less well understood. In order to examine the neural bases of individual differences in reading comprehension as a function of input modality and processing level, we examined functional neural activation to both spoken and printed single words and passages in adolescents with a range of comprehension skill. Data driven Partial Least Squares Correlation (PLSC) analyses revealed that comprehension skill was positively related to activation in a number of regions associated with discourse comprehension and negatively related to activation in regions associated with executive function and memory across processing levels and input modalities.

1. Introduction

While the contributors to variation in reading comprehension ability in both children and adults have been well-studied behaviorally, the underlying neurobiological basis of this variation is less well understood. Progress in this area has been hindered by a reliance on off-line measures of reading comprehension, such as standardized assessments or comprehension questions, which do not support the investigation of comprehension processes as they unfold. In addition, such measures likely recruit other strategic test-taking or problem solving skills which may not be intrinsic to comprehension processes themselves. The current study addresses this gap by tracking neural activity (BOLD signal) during natural text comprehension in a task-free environment so that task processing demands cannot artificially drive relations among the dimensions of interest.

Research on variability in reading comprehension skill has been heavily influenced by the Simple View of Reading (Gough & Tunmer, 1986), which suggests that reading comprehension is the product of decoding (word and non-word reading) and listening comprehension. Indeed, regression models testing the Simple View have been found to account for as much as 77% of variance in reading comprehension (e.g., Adlof, Catts, & Little, 2006; Braze, Tabor, Shankweiler, & Mencl, 2007; García & Cain, 2014; Joshi, Ji, Breznitz, Amiel, & Yulia, 2015; Sparks & Patton, 2016; Tunmer & Chapman, 2012). A natural extension of this view is the notion that once word decoding is mastered, reading comprehension ability will be solely determined by an individual's oral language ability (i.e., listening comprehension). This is consistent with high correlations observed between reading and oral language comprehension ($r = .50–.75$; Braze et al., 2007; Diakidoy, Stylianou, Karefillidou, & Papageorgiou, 2005; Tighe & Schatschneider, 2014; Tunmer & Chapman, 2012; Wise, Sevcik, Morris, Lovett, & Wolf, 2007).

A wealth of behavioral evidence supports this approach. To begin with, listening comprehension has a strong influence on reading comprehension ability throughout development (Hogan, Adlof, & Alonzo,

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https://doi.org/10.1016/j.bandl.2018.08.001
Received 30 May 2017; Received in revised form 16 July 2018; Accepted 2 August 2018

2014). It is related to reading comprehension over and above reading fluency in first grade, a time when word reading skill is still developing (Kim, Park, & Wagner, 2014). Reading and listening comprehension are highly correlated and the skills important for both are largely overlapping (Adams, Bourke, & Willis, 1999; Verhoeven & van Leeuwe, 2008). These include both word-level processing skills (phonological and lexical-semantic processing) and higher-level linguistic skills such as word-to-text integration, parsing, and inference making (Babayigit & Stainthorp, 2014; Diakidoy, et al., 2005). In addition, a few studies suggest that functional activation during comprehension is largely modality-independent, especially for complex sentences or passages (Braze et al., 2011; Constable et al., 2004). Despite these findings, there has only been one exploration of the relationship between reading comprehension skill and neural activation as a function of processing modality (spoken versus printed).

Shankweiler et al. (2008) examined how activation during listening and reading comprehension relates to many different reading-related skills. Their participants listened to or read sentences in the scanner. They found that convergence in activation across modalities increased with reading comprehension skill in dorsal IFG, such that more-skilled comprehenders showed similar activation while reading and listening while less-skilled comprehenders showed more modality-specific activation in this region. This effect persisted even after taking into account individual differences in listening comprehension, decoding, and vocabulary. However, another goal of this study was to investigate effects related to processing syntactically and pragmatically anomalous sentences. Thus, the stimuli were somewhat artificial in nature. In the present study, we seek to replicate and extend this study by examining how reading comprehension skill relates to neural activation during comprehension of naturalistic spoken and printed texts.

An important component in any such investigation is examining the multiple different levels at which variation may occur. Many skills at multiple levels of processing contribute to reading comprehension ability. For example, decoding skill often explains significant variance in reading comprehension ability, especially in young readers (Kendeou, van den Broek, White, & Lynch, 2009; Perfetti & Hogaboam, 1975). However, even after decoding has been taken into account, many other skills make significant contributions to reading comprehension ability. These include other word-level abilities, such as vocabulary (Braze et al., 2007; Cain & Oakhill, 2014) and morphosyntax (Chik, man, Ho, C. S. han, Yeung, P. sze, Wong, Y. kai, Chan, D. W. ock, Chung, K. K. hoa, & Lo, L. yan. , 2012) as well as higher-level and domain-general skills such as inference-making (Cain, Oakhill, & Bryant, 2004) and executive function (Sesma, Mahone, Levine, Eason, & Cutting, 2009). These skills each account for unique variance in reading comprehension across the distribution of comprehension ability (Language and Reading Research Consortium, & Logan, 2017), suggesting that individual differences in reading comprehension could be related to processing ability at any or all of these different levels. Consequently, the goal of the current study is twofold. First, we seek to identify common and distinct neural bases for comprehension across modalities (speech versus print) and processing levels (single words vs. passages). Second, we explore how individual differences in reading comprehension (measured offline) are associated with activation as a function of these processing levels and modalities.

Multiple regions support passage comprehension. Comparisons of text comprehension to rest, a simple perceptual baseline, or to unconnected text (e.g., word lists) most consistently show activation in bilateral middle and superior temporal gyri (MTG/STG) and bilateral anterior temporal lobe (ATL) across studies (Ferstl, Neumann, Bogler, & von Cramon, 2008). A meta-analysis of studies looking at semantic and syntactic comprehension in spoken and written tasks found that studies most often showed activation in regions in and around the left inferior frontal gyrus (IFG), including pars opercularis, pars triangularis, and precentral gyrus, This study also found activation in left MTG extending into the left STG (Rodd, Vitello, Woollams, & Adank, 2015). These two meta-analyses indicate that comprehension across modalities includes temporal and frontal regions, with text comprehension showing more bilateral activation.

Similarly, recent meta-analyses indicate overlapping regions for comprehension of language across processing levels. Houdé et al., (2010) conducted a meta-analysis on 16 studies where participants completed a variety of reading-related tasks at various levels of processing while in the scanner. These studies revealed many regions consistently activated during reading in the left frontal, temporoparietal, and occipitotemporal regions. Specifically, the putative Visual Word Form Area (VWFA) in left occipitotemporal (OT) cortex was consistently activated across all studies. In addition, IFG and precentral gyrus were implicated. Regions in the inferior, middle, and superior temporal gyri as well as inferior parietal gyrus show consistent activation, as does a cluster in bilateral supplementary motor area (SMA). A later meta-analysis looking at activation during various reading tasks at the word and sentence levels in both adults and children showed similar consistency in patterns of activation (Martin, Schurz, Kronbichler, & Richlan, 2015). Studies of both adults and children exhibited convergent activation in left OT, left IFG (specifically pars opercularis and pars triangularis), bilateral SMA, and left posterior parietal cortex. Temporal activation was seen more in children than adults, specifically in STG. Adults showed more convergence than children in left frontal regions, left middle occipital gyrus, cerebellum, and ventral OT. These results indicate that word and sentence/passage reading involves activation in left OT, left IFG, bilateral SMA, and left posterior parietal cortex.

Despite the wealth of behavioral studies investigating individual differences in reading comprehension and recent studies looking at the neural bases of comprehension, relatively few studies have explored the neural bases of individual differences in reading comprehension skill. However, some existing work supports the view that variation in spoken language processing skill and variation in reading comprehension skill are linked at the neurological level. For example, amount of activation in regions that have been associated with language processing (e.g., IFG, STG, MTG) during both listening and reading comprehension tasks is related to overall reading comprehension ability. In particular, reading comprehension skill has been shown to be related to print-speech activation overlap in IFG (Shankweiler et al., 2008). Activation during spoken narrative comprehension in left inferior frontal gyrus (IFG) is correlated with reading comprehension ability (Horowitz-Kraus, Vannest, & Holland, 2013). Reading comprehension skill is also associated with activation in left middle and superior temporal gyri (MTG/STG) during printed sentence and passage processing (Aboud, Bailey, Petrill, & Cutting, 2016; Van Ettinger-Veenstra, McAllister, Lundberg, Karlsson, & Engström, 2016; Yarkoni, Speer, & Zacks, 2008). These neural findings converge with behavioral results showing great overlap between spoken and printed comprehension at the passage level.

Studies of brain-behavior relationships for single word processing have identified similar regions, suggesting that individual differences in reading comprehension skill similarly modulate neural activation across the sentence, passage, and word levels. For example, one study found that reading comprehension is negatively related to activation in left IFG and left fusiform gyrus when processing semantically-related printed words (Malins et al., 2016). In addition, Welcome and Joanisse (2012) found that during word reading, activation in the left MTG is negatively related to reading comprehension skill. Further, individuals with particularly poor reading comprehension despite typical decoding skill have been found to have atypical functional connectivity between IFG and parahippocampal regions during a lexical decision task (Cutting et al., 2013). Thus, across studies, the regions that link offline reading comprehension skill and online single word and passage comprehension are largely overlapping.

The studies summarized here implicate associations between reading comprehension skill and neural activation during both word and passage processing in regions that are important for language processing, but not specifically linked to reading. However, untangling the relationships between reading comprehension skill and activation across processing level (word versus passage) and modality (speech versus print) currently requires cross-study comparisons. Only one study to date has directly compared activation for both single words and passages in relation to reading comprehension skill, and another has compared input modalities in relation to reading comprehension skill (Shankweiler et al., 2008). To address the first contrast, Aboud et al. (2016) found that connectivity was greater between left dorsolateral prefrontal cortex (DLPFC; a region involved in executive function) and left angular gyrus (AG; a key region for semantic processing) during passage relative to single word processing. This relationship was stronger in more-skilled comprehenders. By directly comparing word- and passage-level processing, this approach revealed a tighter link between executive and semantic regions for better comprehenders, specifically for passage-level comprehension (Aboud et al., 2016). Thus, direct comparisons of processing level can show relationships that may not be found by comparing across studies. The current research builds upon this work by comparing processing levels as well as modality using a data-driven, whole-brain approach to compare activation modulated by both modality and processing level in relation to reading comprehension skill.

The goal of the current work is to determine whether individual differences in reading comprehension, listening comprehension, and word-level processing have a common neural basis. To address this goal, we use a naturalistic, task-free design to examine the relationship between reading comprehension skill (assessed offline) and functional neural activation to spoken and printed single words and passages. Naturalistic reading and story listening paradigms have recently been adopted across a number of studies to explore the neural circuitry for comprehension. These paradigms, and the analyses associated with them, provide more ecological validity as well as the ability to probe multiple aspects of discourse without the need for highly constrained contrasting stimuli. Studies using naturalistic designs have been able to separate regions responsible for semantic and syntactic processing (Wehbe et al., 2014) and to investigate the relationship between syntactic constructions and activation over time (Brennan, Stabler, Van Wagenen, Luh, & Hale, 2016; Hale, Lutz, Luh, Brennan, & Arbor, 2015). Other studies have used naturalistic designs to investigate regions involved in strategy use during text reading (Moss & Schunn, 2015). Thus, naturalistic designs are ideal for revealing the relationship between neural activation during comprehension and individual differences in reading comprehension skill. One reason for this is that participants are able to engage in passage comprehension without unnatural breaks due to task demands. Thus, our naturalistic and task-free passage task allows us to measure brain function that is as similar as possible to what occurs during passage comprehension in the real world. To complement our passage task, we developed a task-free single word processing task. Previous reports note that comparing word- and passage-level processing across studies presents confounds due to differing task demands (Wang et al., 2015). Thus, our single word processing task is passive and task-free to allow for the most valid comparison of processing level between our passage and word processing tasks.

While our primary goal is to use a data-driven partial least squares correlation (PLSC) approach to identify common and distinct sets of regions for these processes as well as their relations to reading comprehension skill, we also test some specific hypotheses. First, given strong correlations between listening comprehension and reading comprehension, we predict substantial overlap in activation for these two processes regardless of reading comprehension skill. We expect to see activation in frontal and temporal regions associated with passage comprehension, including bilateral STG, MTG, and left IFG. Second, we predict that reading comprehension skill will be associated with similar patterns of activation for spoken and printed passages. We expect to see that activation in STG, MTG, and IFG is related to reading comprehension skill, indicating differential use of the regions typically associated with passage-level processing as comprehension skill varies. Finally, given that individuals who struggle with reading comprehension tend also to have word-level weaknesses in vocabulary and other lexical-semantic processing tasks (e.g., semantic priming; Catts, Adlof, & Weismer, 2006; Nation & Snowling, 1999; Silva & Cain, 2015), we predict that the relationship between comprehension skill and activation will be similar for both single word and passage processing. Thus, we predict that activation will be related to reading comprehension skill similarly for both single word and passage processing.

2. Methods

2.1. Participants

A total of 32 adolescent monolingual English participants were included in this study (M Age = 17, SD = 1.62, range = 13.75–18.75, 14 males, 72% right-handed). Six subjects not included in the final 32 analyzed here had unusable fMRI data due to movement artifact, defined below. In accordance to the Yale University Human Investigation Committee, all participants over 18 gave informed consent. Written consent of a parent or guardian was also provided for participants under 18.

2.2. Behavioral assessments of skill

Sensory testing confirmed that all participants had normal hearing and vision. Participants completed assessments of reading comprehension, nonword decoding, and performance IQ. The Kaufman Test of Educational Achievement Second Edition (KTEA-II) reading comprehension test (Kaufman & Kaufman, 2004) was used as the primary measure of reading comprehension. This task assesses comprehension as a whole and cannot differentiate between comprehension component processes. Participants read short passages and answered comprehension questions about them. The Word Attack (WA) subtest of the Woodcock-Johnson III (Woodcock, McGrew, Mather, & Schrank, 2001) was the measure of nonword decoding and the Wechsler Abbreviated Scale of Intelligence II (WASI; Wechsler & Hsiao-pin, 2011) provided a measure of performance IQ.

In order to isolate variability in reading comprehension above and beyond the influence of decoding or general cognitive ability, we ran only participants with normal decoding ability (defined here as at or above a standard score of 95 on WA) and normal cognitive function (defined here as at or above standard score of 80 on WASI). Our participants had a mean standardized reading comprehension score of 105.3 (SD = 18.91), ranging from 76 to 146. The distribution of reading comprehension ability was normal, as confirmed by a D'Agostino normality test (omnibus $\chi^2 = 3.21$, p = .20). Mean decoding skill was 108.3 (SD = 9.02, range = 96–124). Finally, mean performance IQ was 107.9 (SD = 17.84, range = 81–142).

2.3. fMRI tasks

2.3.1. Passage task

Participants completed a modified version of the story task described in Wang et al. (2015). In the scanner, participants passively read or listened to four stories by Hans Christian Andersen across four scan runs. We used unusual and relatively unpopular stories, chosen so that participants would not have prior experience with them. Each run was divided into blocks of printed and spoken conditions. During the printed condition (PPass), story portions were presented phrase by phrase in the center of the screen. For the spoken condition (SPass), portions of the stories were narrated to the participants through headphones.

This experiment utilized a mini-block design paradigm. Each run lasted about 372 s and consisted of 6 blocks: 2 printed condition blocks, 2 spoken condition blocks, and 2 blocks of rest. Each block had a mean duration of 52 s. During PPass, each phrase was presented for 2 s, with an average of 96 phrases and 12 words per phrase. Each phrase appeared on the screen for 2000 ms. The rate of presentation of the stimuli within SPass blocks was matched to the rate of presentation in PPass. Spoken stimuli were presented in a continuous speech stream. Presentation of PPass and SPass alternated within the story, such that some sentences were spoken and some were printed. The average word frequency in this task was 10.61 (log-transformed, Lund & Burgess, 1996).

2.3.2. *Word task*

Participants passively read or listened to four conditions of rapidly presented visual and auditory stimuli. The conditions included printed real words (PWord), printed false font tokens (FalseFont), spoken real words (SWord), and vocoded spoken words (Vocod; stimulus details are provided below).

An event-related design was used for this experiment. In each trial, subjects received a group of 4 different tokens from the same condition (tetrads), rapidly presented at a rate of 450 ms per stimulus. There was a jittered ITI of 4–7 s between trials, with occasional “null” trials up to 13 s long. Participants received two runs of this task while in the scanner, for a total duration of 302 s. Each run had 12 trials of each condition randomly presented, for a total of 48 trials per run and 24 trials per condition.

All stimuli in PWord and SWord were one-syllable medium- to high-frequency words. Word frequency was established by the English Lexicon Project (Balota et al., 2007). Average word frequency was 10.59 (log-transformed; Lund & Burgess, 1996). There was no significant difference in log-transformed word frequency between the Passage and Word task, $t(653) = 0.14$, $p = .88$. FalseFont stimuli were real words presented using the Wingdings typeface, making them appear as a string of unrelated symbols; any letter-like symbols were not used. Vocod stimuli was created using Praat (Boersma & van Heuven, 2001). Stimuli were first divided into three bands: 0.14–3.13 Bark; 3.13–6.12 Bark; 6.12–9.11 Bark. For each band, root mean square intensity was computed and those intensity values were used to modulate Gaussian noise. We then replaced the original signal in each band with the noise to create 3-channel vocoded speech. Three channels were utilized to ensure that the speech was unintelligible.

2.4. *fMRI acquisition*

Anatomical and functional imaging was performed on a Siemens 3.0T Trio Tim System at the Yale University School of Medicine. Scanning sessions utilized a 12-channel coil. Functional activation images were acquired at thirty-two axial-oblique anatomic images prescribed parallel to the intercommissural line using single shot, gradient echo, echo planar sequence with the following parameters: FA = 80∘; TE = 30 ms; TR = 2000 ms; FOV = 220; 4 mm slice thickness, no gap; matrix size 64 × 64; 3.4 mm in-plane resolution. High resolution, 1 mm isotropic, T1-weighted MP-RAGE structural images were also gathered for registration with the following parameters: FA = 7∘; TE = 3.66; TR = 2530 ms; FOV = 256; 1 mm slice thickness, no gap; matrix size 256 × 256.

2.5. *fMRI analysis*

2.5.1. *Image processing*

Single subject data were processed using the AFNI suite of programs (Cox, 1996). Anatomic images were skull stripped. The first six TRs from each run were removed to allow for scanner stabilization. Functional images were then corrected for slice acquisition time, motion corrected, normalized into standard Talairach space, and then smoothed with an 8 mm FWHM Gaussian filter. Any TRs with greater than 10% outlier voxels or more than 3 mm of movement were removed and not included in our analyses. Data were submitted to a multiple regression analysis (3dDeconvolve) with explanatory variables representing conditions of interest (stimulus types); and nuisance regressors representing movement (3 rotation and 3 translation parameters) and drift (1st and 2nd order polynomial). The hemodynamic response was modeled using a gamma function for the word task and a duration-modulated BLOCK function for the passage task. This resulted in two sets of activation maps from each subject (beta images): two maps from the Passage Task (SPass minus rest, and PPass minus rest) and four maps from the Word Task: (simple evoked response to SWord, to PWord, to Vocod, and to FalseFont).

2.5.2. *Group analysis*

Scans from each subject were normalized into the N27 standard space template (Talairach & Tournoux, 1988) for subsequent group analysis. Group analysis used 3dttest + + to apply one-sample *t*-tests on each condition in the two tasks to find regions of significant activation across all subjects ($p = .001$, FDR corrected).

2.5.3. *Partial least squares correlation analysis (PLSC)*

We utilized PLSC analysis to investigate the relationships between patterns of brain activation, our experimental manipulations, and comprehension skill. PLSC is a multivariate approach that allows for the analysis of complex relationships between brain and behavior by using data from the whole brain across conditions simultaneously (Krishnan, Williams, McIntosh, & Abdi, 2011; McIntosh, Bookstein, Haxby, & Grady, 1996). In addition, PLSC is a bottom-up, data-driven approach that can identify relationships between brain and experimental design as well as brain and behavior without requiring *a priori* contrasts to be built into the model. PLSC can be compared conceptually to principal components analysis (PCA), in that both techniques look for shared variance across sets of data. In the case of PLSC, the relevant data types are brain activation, behavioral measures, and experimental conditions. Specifically, we used two types of PLSC: task and behavioral. Task PLSC was used to determine the relationship between brain activation and the experimental conditions of the word and passage tasks. Behavioral PLSC was used to determine how reading comprehension skill relates to activation across conditions.

PLSC results are reported in the form of latent variables that account for the maximum amount of covariance between two data matrices (X and Y), similar to the factors produced by a PCA. The X matrix corresponds to brain activation values; here, the subject activation maps (pre-processed beta images, containing beta weights rather than raw activation data for each voxel). Each subject contributes a beta image for each condition. The Y matrix varies according to the type of analysis being done. In task PLSC, the Y matrix represents the experimental conditions. In behavioral PLSC, the Y matrix represents behavioral performance (i.e., participants’ scores on the KTEA). For behavioral PLSC, the X matrix (containing brain activation values) is organized into condition-wise sub-matrices representing experimental conditions (e.g. speech followed by print). Crucially, *a priori* relationships between conditions are not present in the matrices (e.g. PWord and FalseFont, both printed conditions, are not explicitly linked). The resulting covariance matrix is created by crossing the X and Y matrices and is subsequently decomposed into orthogonal latent variables (LVs) using singular value decomposition. In both task and behavioral PLSC, the latent variable loadings to the brain activity maps (in the X matrix) are called brain scores. Again, brain scores can be related to the factor loadings found in a PCA; both indicate how strongly a measure or voxel expresses a given factor or LV. In PLSC, the actual value of the brain scores matters less than its direction. Brain scores going in the same direction indicate that within a given voxel, different experimental conditions or behavioral measures relate to brain activation in the same way.

Each LV accounts for some amount of the covariance between the brain data and the behavioral or design information. Significance of the

LVs is determined using permutation tests in which the Y matrix is randomly reordered and the analysis is re-run. The significance of the original LV comes from the probability that a singular value from the permuted data is larger than that of the original analysis. Bootstrap resampling is used to determine standard error. Bootstrapping also provides confidence intervals (CIs) for brain scores that can be used to compare conditions.

We used the Partial Least Squares software for our PLSC analyses (McIntosh & Bookstein, 2015). We used mean-centered PLSC. Significance of LVs was determined by 1000 permutations and 1000 bootstraps using the process described above. Significant voxels for each LV had a bootstrap ratio with an absolute value of greater than or equal to 3. Bootstrap ratios are the ratios of each voxel's brain score to its standard error. This threshold is standard in PLSC analyses. Cluster correction was not used because the multivariate methods used in PLSC (specifically, resampling at the whole-brain level) make it inappropriate.

3. Results

3.1. Basic contrasts

While our primary analyses consist of our multivariate PLSC reported below, we first report activations to speech and print across the word and passage tasks using conventional analyses to verify that our tasks were accurately tapping spoken and printed language processing regions (see Supplemental Fig. 1).

Passage Task: One-sample t-tests were performed to determine significant activation in the passage comprehension task for PPass or SPass minus rest (see Supplemental Table 1). Both PPass and SPass activated many regions bilaterally. Across subjects, PPass elicited significant activation ($p = .001$, FDR corrected) in bilateral fusiform and lingual gyri, while SPass elicited significant activation ($p = .001$, FDR corrected) bilaterally in the STG. Both PPass and SPass showed significant activation ($p = .001$, FDR corrected) in the bilateral MTG, left IFG, and bilateral superior frontal gyrus. Deactivations were largely similar across the two conditions, with significance ($p = .001$, FDR corrected) bilaterally in cuneus, cingulate gyrus, supramarginal gyrus, superior frontal gyrus, and insula.

Word Task: One-sample t-tests were also performed to determine significant activation in the word task (see Supplemental Table 1). PWord elicited significant activation ($p = .001$, FDR corrected) in bilateral fusiform and extrastriate cortex, inferior and middle occipital gyri, bilateral precentral gyrus, and bilateral IFG. SWord showed significant activation ($p = .001$, FDR corrected) in bilateral STG, bilateral lingual gyrus, and bilateral cuneus. Both PWord and SWord showed significant activation ($p = .001$, FDR corrected) in precuneus, and bilateral middle frontal gyrus. While SWord showed very little deactivation, the PWord showed significant deactivation ($p = .001$, FDR corrected) in bilateral STG.

3.2. PLSC analyses

3.2.1. Task PLSC

To analyze the relationships between brain activity and task conditions, we used a mean-centered task PLSC. The task PLSC examined how whole brain activation covaried with the six experimental conditions (PPass, SPass, PWord, SWord, FalseFont, and Vocod). Three LVs were significant. The first LV had a singular value of 351.3 and accounted for 50.93% of the covariance ($p < .001$). This LV dissociated printed conditions from spoken conditions (see Fig. 1a for design score plots). Print conditions (PWord, FalseFont, PPass) showed more activation in bilateral fusiform and extrastriate cortex. Speech conditions (SWord, Vocod, SPass) showed more activation in bilateral STG (Fig. 1b). 95% confidence intervals indicate that PPass [−237.7, −184.8] expresses the LV more strongly than PWord [−112.8, −84.8] and false font [−118.6, −90.9], which are equivalent. SPass [135.4, 192.4], SWord [117.8, 142.8], and Vocod [112.6, 136.8] express the pattern equally.

The second significant LV had a singular value of 311.5 and accounted for 41.33% of the covariance ($p < .001$). It differentiated passage conditions from word conditions (see Fig. 1c). Both PPass and SPass showed more activation in bilateral MTG and left inferior frontal gyrus (IFG) pars orbitalis. 95% CIs reveal that SPass [168.6, 223.2] and PPass [146.8, 208.2] show the pattern to the same extent. All word conditions (SWord, PWord, FalseFont, and Vocod) showed more activation in anterior and posterior cingulate cortex (ACC, PCC; Fig. 1d). PWord [−125.2, −94.5] and FalseFont [−130.7, −97.8] conditions express the LV more strongly than SWord [−91.6, −51.3] and Vocod [−89.7, −63.0].

The third significant LV had a singular value of 123.3 and accounted for 6.28% of the covariance ($p = .001$) (see Supplemental Fig. 2a). This LV dissociated SPass, PWord, and FalseFont from PPass, SWord, and Vocod. While this LV is significant, it appears as though the word conditions are driving the effect. Areas showing more activation for SPass, PWord, and FalseFont include bilateral fusiform and extrastriate cortex, whereas areas showing more activation for PPass, SWord, and Vocod include bilateral STG (see Supplemental Fig. 2b). Because the first two LVs already account for 91% of the covariance, leaving only a small percentage of the covariance for this LV, we will limit our interpretation.

The results of the task PLSC suggest that the tasks are indeed picking up on the differential processing that tasks place for words vs. texts and spoken vs. printed stimuli. Much of the covariance between brain activation and experimental design was explained by latent variables that reflect our main experimental manipulations: modality (spoken vs. written) and processing level (word vs. passage). The experimental design matrix in a task PLSC only tells the analysis which trials belong to each condition without any *a priori* information about how the conditions relate (e.g. the three auditory conditions are not linked). Thus, the analysis looks for similar activation patterns across conditions without the need for prespecified contrasts. The analysis' production of latent variables dissociating between modality and processing level supports the validity of these tasks' ability to evoke processing at different levels and in different modalities. For more detailed information on the results of the task PLSC analysis, see Table 1.

3.2.2. Behavioral PLSC

Two behavioral PLSC analyses were conducted. We used non-rotated behavioral PLSC analyses, coding the conditions of interest as 1 and the others as 0. Unlike mean-centered PLSC, non-rotated PLSC allows you to investigate specific contrasts while also taking into account all conditions of an experiment. In this investigation, we were able to look at the covariance between specific conditions of primary interest without removing the other task conditions. Since both of our non-rotated task PLSC analyses had only one contrast, percent of covariance accounted for is not relevant; there is only one source of covariance. The first non-rotated behavioral PLSC analysis determined how reading comprehension scores covaried with the two passage task conditions (SPass and PPass) to test whether the modality of the material affected the modulation of regions used for comprehension (see Table 2). Because the number of latent variables in non-rotated behavioral PLS analyses is equal to the number of contrasts, we found one LV. This LV had a singular value of 70.8. This LV did not dissociate between the two passage conditions; comprehension ability was related to similar patterns of neural activation across both modalities, which was confirmed by 95% CIs [spoken: .72, .92; printed: .68, .91] (see Fig. 2a). That is, the same distinct sets of brain regions were associated with lower or higher comprehension skill for *both* SPass and PPass. SWord also showed the same pattern, although to a lesser extent. Specifically, across both modalities, activation related to higher reading comprehension skill was seen in bilateral MTG and left IFG pars orbitalis and pars

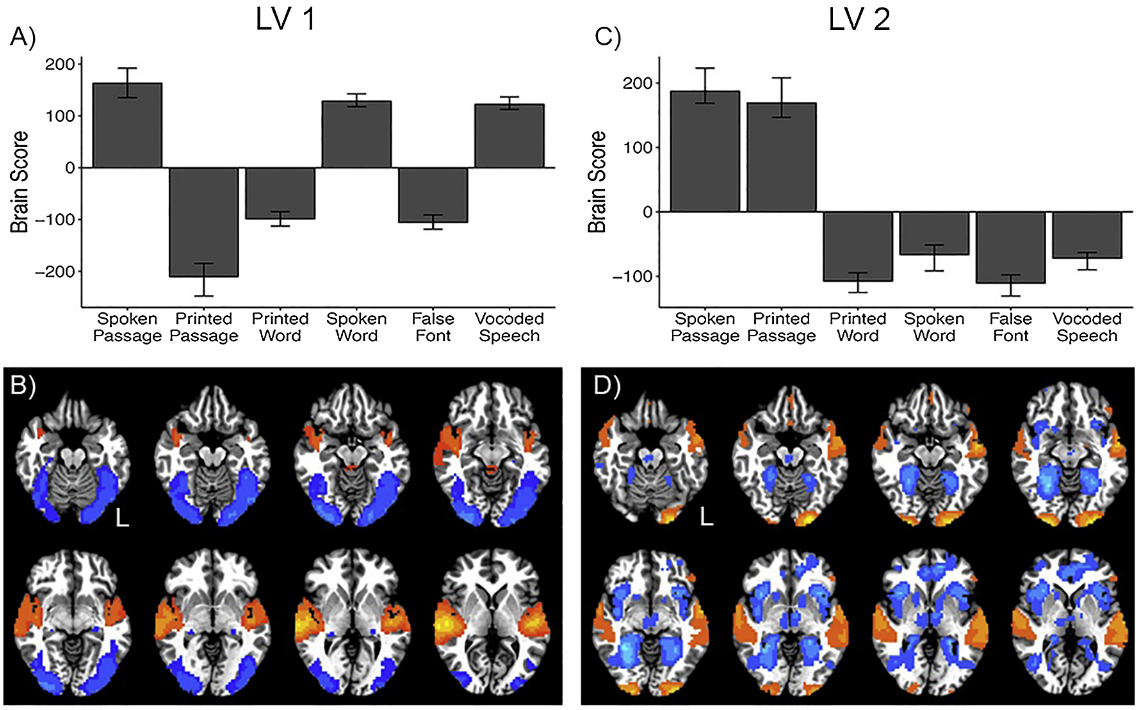

Fig. 1. Task PLS results. (A) Brain score plot for LV1. The brain score indicates how a condition is related to the pattern shown in B. Error bars indicate 95% CIs from bootstrapping. (B) Bootstrap ratio plot for LV1. Regions shaded in red showed more activation to conditions with a positive brain score and regions shaded in blue showed more activation to a negative brain score. (C) Brain score plot for LV2. The brain score indicates how a condition is related to the pattern shown in D. Error bars indicate 95% CIs from bootstrapping. (D) Bootstrap ratio plot for LV2. Regions shaded in red showed more activation to conditions with a positive brain score and regions shaded in blue showed more activation to a negative brain score. (L = R). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

triangularis. Activation associated with lower reading comprehension skill was seen in the ACC, insula, and parahippocampal gyrus (Fig. 2b).

The second behavioral PLSC assessed the covariance between activation in PPass, PWord, and reading comprehension skill in order to test whether comprehension ability similarly modulated the regions used for word and text processing (see Table 3). Our LV found covariation between the two printed conditions and comprehension ability (Fig. 2c). It had a singular value of 51.6. 95% CIs show that both PWord [.51, .71] and PPass [.51, .87] conditions expressed the LV equally. We also saw that the spoken passage and false font conditions also expressed the same pattern, although to a lesser extent. For both printed word- and passage-level processing, skilled comprehenders showed more activation in visual areas, including the inferior and middle occipital gyri, and the left occipitotemporal area. Skilled comprehenders also showed more activation in left IFG pars triangularis and bilateral MTG (Fig. 2d). In contrast, less-skilled comprehenders showed greater activation in ACC, DLPFC, and anterior insula.

Because our sample had a rather wide age range, we conducted an additional analysis to see if age was driving any of the effects seen in the behavioral PLSC analyses. To do this, we correlated the brain scores for each condition within each behavioral PLSC with age. The correlation between age and brain scores was not significant for each condition in the first (PPass and age: $r = -.014$, $p = .94$; SPass and age: $r = .13$, $p = .47$) and second (PPass and age: $r = .18$, $p = .34$; PWord and age: $r = -.057$, $p = .76$) behavioral PLSC analyses. This suggests that age was not related to the results found in these analyses. In addition, age and reading comprehension ability are not correlated in our sample ($r = -.08$, $p = .65$).

4. Discussion

The current study investigated how neural activation during processing of spoken and printed words and passages is related to reading comprehension skill in individuals with adequate decoding ability. To this end, participants read or listened to passages, single real words, or nonsense sounds/font in a naturalistic, task-free design. Predictions from theoretical models as well as empirical evidence suggest that individual differences in reading comprehension beyond decoding are related to many higher-level language and domain-general processes, including semantic processing, inference-making, executive function, and motivation. As such, comprehension ability in good decoders should modulate activation in regions that subserve these processes during comprehension of single words and text across modalities.

4.1. Modality- and task-specific activation patterns

Our initial task PLSC analysis revealed two interpretable latent variables that confirmed the validity of our experimental manipulations. The first latent variable discriminated visual presentation of printed text and text-like stimuli from auditory presentation of speech and speech-like stimuli, irrespective of their linguistic or discourse content. Modality-specific activity fell in typical sensory areas, such as primary and associative auditory regions for speech. For print, activation was found in visual cortex and occipitotemporal regions often implicated in visual word recognition (McCandliss, Cohen, & Dehaene, 2003). This pattern of modality specificity was largely consistent with simple task vs. rest contrasts for spoken and printed stimuli presented here (Supplemental Fig. 1) and in prior research (e.g., Rueckl et al., 2015).

The second latent variable discriminated presentation of a continuous, coherent discourse from presentation of words and word-like stimuli. Specifically, the passage task more strongly engaged regions shown to be consistently engaged by complex language processing, including bilateral temporal cortex (STG, MTG, ATP; Rogers et al., 2006; Spitsyna, Warren, Scott, Turkheimer, & Wise, 2006; Visser, Jefferies, Lambon Ralph, et al., 2010) and left IFG pars orbitalis and

Table 1
Results from task PLS analyses.

X coord	Y coord	Z coord	Peak BSR	Cluster Size	Hemisphere	Areas in this cluster	BA
LV 1							
Activation greater for spoken tasks							
−49.5	19.5	8.5	19.918	1218	R	Superior temporal gyrus	BA 22
43.5	25.5	11.5	21.913	951	L	Superior temporal gyrus	BA 22
10.5	70.5	29.5	9.246	61	L	Precuneus, cuneus	BA 7, 31
22.5	52.5	−48.5	7.807	47	L	Cerebellar tonsil	
10.5	52.5	50.5	7.144	31	L	Precuneus	BA 7
Activation greater for printed tasks							
37.5	43.5	−12.5	−11.413	1112	L	Fusiform gyrus, middle occipital gyrus, inferior occipital gyrus	BA 18, 19
−25.5	91.5	−6.5	−12.921	910	R	Fusiform gyrus, middle occipital gyrus, inferior occipital gyrus	BA 18. 19
40.5	−1.5	47.5	−7.297	135	L	Middle frontal gyrus, precentral gyrus	BA 6
−28.5	61.5	47.5	−8.616	96	R	Superior parietal lobule, precuneus	BA 7
25.5	55.5	44.5	−6.493	35	L	Superior parietal lobule, precuneus	BA 7
1.5	73.5	−21.5	−6.21	30	B	Declive of Vermis	
LV 2							
Activation greater for passages							
55.5	7.5	−6.5	8.629	708	L	Middle temporal gyrus, superior temporal gyrus	
−58.5	13.5	5.5	8.817	431	R	Middle temporal gyrus, superior temporal gyrus	
25.5	94.5	−6.5	10.207	396	L	Inferior occipital gyrus	
−13.5	79.5	−30.5	9.03	318	R	Uvula	
−22.5	94.5	−6.5	9.913	125	R	Inferior occipital gyrus	BA 17
49.5	61.5	26.5	7.687	122	L	Middle temporal gyrus	BA 39
46.5	−31.5	−6.5	5.542	53	L	Inferior frontal gyrus p. orbitalis/triangularis	
10.5	−34.5	50.5	5.788	38	L	Superior frontal gyrus	
−55.5	58.5	23.5	6.607	36	R	Superior temporal gyrus	BA 39
Activation greater for single words							
4.5	22.5	32.5	−11.361	5882	B	Cingulate gyrus (anterior to posterior), cuneus, precuneus, inferior parietal lobule, middle frontal gyrus, right parahippocampus	BA 9
16.5	70.5	32.5	−11.843	1046	L	Cuneus, posterior cingulate gyrus, parahippocampal gyrus	
−31.5	−37.5	35.5	−9.464	1022	R	Middle frontal gyrus, insula	
7.5	7.5	2.5	−7.53	177	B	Thalamus	
31.5	40.5	−30.5	−5.772	71	L	Cerebellar tonsil	
−16.5	−13.5	−0.5	−5.596	45	R	Putamen	
−43.5	4.5	23.5	−4.884	30	R	Precentral gyrus	
LV 3							
Activation greater for spoken passages, printed single words and false fonts							
−34.5	40.5	−9.5	6.756	1362	R	Parahippocampal gyrus, fusiform gyrus, insula	
31.5	49.5	−9.5	6.873	226	L	Parahippocampal gyrus, fusiform gyrus	
40.5	1.5	11.5	4.667	139	L	Insula	BA 13
−19.5	58.5	65.5	4.021	134	R	Superior parietal lobule	
−46.5	−37.5	−9.5	4.378	91	R	Middle frontal gyrus	BA 47
−55.5	−10.5	−3.5	3.997	64	R	Superior temporal gyrus	BA 22
43.5	−37.5	−9.5	5.448	62	L	Middle frontal gyrus	BA 47
10.5	55.5	56.5	4.124	53	L	Precuneus	
19.5	4.5	−27.5	3.416	43	L	Parahippocampal gyrus, uncus	
40.5	43.5	53.5	3.651	30	L	Inferior parietal lobule	BA 40
52.5	58.5	−0.5	3.515	30	L	Middle temporal gyrus	BA 37
−58.5	22.5	38.5	3.173	28	R	Postcentral gyrus	BA 3
Activation greater for printed passages, spoken words and vocoded words							
16.5	82.5	−9.5	−9.617	10,448	B	Lingual gyrus, cuneus, thalamus, insula, superior temporal gyrus, posterior cingulate gyrus, anterior cingulate gyrus, medial frontal gyrus, middle frontal gyrus,	BA 18, 10
1.5	28.5	−33.5	−5.613	197	B	Brainstem	
4.5	4.5	59.5	−4.528	107	L	Medial frontal gyrus	BA 6

All results come from the three significant LVs of the task PLS.

triangularis (Ferstl et al., 2008; Friederici, Rüschemeyer, Hahne, & Fiebach, 2003; Liakakis, Nickel, & Seitz, 2011; Newman, Ikuta, and Burns Jr., 2010). The IFG has also been linked to social-emotional processing as well as working memory, which are known to be components of narrative comprehension (Keuken et al., 2011; Rota et al., 2009; Tops & Boksem, 2011). These regions were also similar to those found to be activated for both printed and spoken passage comprehension in our basic GLM contrasts.

The single-word level task more strongly engaged the hippocampal regions as well as the anterior cingulate, thalamus, and insula. These findings are consistent with studies directly contrasting single words and passages (Wang et al., 2015). This suggests that these regions support single-word processing specifically when compared to passage comprehension. Other regions typically isolated by word processing, such as anterior fusiform, left inferior frontal gyrus, and left middle temporal gyrus, seem to be involved in processing words both in isolation and in connected text (Crepaldi et al., 2013; Taylor, Rastle, & Davis, 2013). Further, the regions more strongly activated by the word tasks in this LV may partially reflect processing specific to this task, such as comprehending unrelated lists of words and quickly switching

Table 2
Results from the first behavioral PLS.

X coord	Y Coord	Z Coord	Peak BSR	Cluster Size	Side	Areas in this cluster	BA
Activation greater for more-skilled comprehenders							
43.5	−34.5	−9.5	5.36	49	L	Inferior frontal gyrus pars orbitalis	BA 11
−4.5	52.5	29.5	4.92	58	B	Cingulate gyrus	
−1.5	−46.5	−9.5	3.74	59	B	Medial frontal gyrus	
−22.5	85.5	−9.5	4.78	73	R	Middle occipital gyrus	BA 18
34.5	31.5	−15.5	4.04	101	L	Fusiform gyrus	
52.5	−28.5	14.5	9.19	157	L	Inferior frontal gyrus pars triangularis	BA 46
−61.5	37.5	−0.5	3.76	170	R	Middle temporal gyrus	BA 21
−19.5	76.5	−36.5	4.8	183	R	Cerebellum	
4.5	−37.5	44.5	4.76	202	B	Superior frontal gyrus	BA 8
31.5	70.5	−33.5	7.81	203	L	Cerebellum	
−58.5	4.5	−6.5	6.08	227	B	Middle temporal gyrus	
58.5	31.5	5.5	6.78	754	L	Middle temporal gyrus	BA 22
Activation greater for less-skilled comprehenders							
4.5	−28.5	17.5	−9.14	1718	B	Anterior cingulate cortex	BA 24
10.5	52.5	−12.5	−8.77	1302	B	Cerebellum	
25.5	37.5	2.5	−8.55	1020	B	Posterior cingulate cortex, parahippocampus, insula, inferior parietal lobule	
−31.5	−34.5	26.5	−6.54	195	R	Middle frontal gyrus	
−13.5	70.5	26.5	−3.8	57	R	Precuneus	
−40.5	−4.5	14.5	−4.31	47	R	Insula	
4.5	−7.5	−0.5	−3.81	33	L	Caudate	
−16.5	49.5	−45.5	−3.78	30	R	Cerebellum	

Areas where activity during printed and spoken conditions of the passage task is related to reading comprehension. Activity in regions with a positive bootstrap ratio (BSR) is associated with higher reading comprehension skill. Activity in regions with a negative bootstrap ratio (BSR) is associated with lower reading comprehension skill.

between conditions.

Thus, at the group level, the task PLSC successfully identifies important task-related variability in brain activity that aligns well with results found from basic contrasts. Critically, the task PLSC analysis uses an unsupervised approach, where similarities are extracted without the experimenter inputting specific contrasts. The overlap between task PLSC and contrast-based analyses confirm the validity of the modality and processing level experimental manipulations. We now turn to analyses applying the same approach to explore brain activity associated with individual differences in comprehension ability.

4.2. *Activity associated with individual variability in comprehension*

Extant research finds tight links between reading and listening comprehension ability (Adams et al., 1999; Verhoeven & van Leeuwe, 2008). Thus, we hypothesized that individual differences may be related to activation during comprehension similarly across modalities. To test this hypothesis, our first brain-behavior analysis (behavioral PLSC) examined the relationship between comprehension skill and passage-level processing across the spoken and printed modalities, contrasted against other conditions. In line with our hypothesis, this analysis identified regions that were modulated by comprehension skill similarly for both modalities, suggesting that some reading comprehension skill associated differences in neural response are modality-independent. This result is in line with Shankweiler et al. (2008), which also found that activation during both print and speech in some regions was related to comprehension ability.

Additionally, research has also identified relations between reading comprehension skill and word level processing (Henderson, Snowling, & Clarke, 2013; Nation & Snowling, 1999; Oakhill & Cain, 2012; Oakhill, Hartt, & Samols, 2005). More specifically, performance in tasks that tap word-level semantic processing (Henderson et al., 2013; Nation & Snowling, 1999), as well as tasks that tap higher-level word to text integration (Silva & Cain, 2015) have been correlated with comprehension skill and impaired in those with S-RCD. Thus, we hypothesized that reading comprehension skill would be related to neural activation during processing of words in addition to processing of passages. Our second brain-behavior analysis tested this hypothesis by analyzing the relationship between reading comprehension skill and printed single-word and passage processing, contrasted against the other conditions. Findings from this second brain-behavior analysis show that the relationship between neural activation and reading comprehension skill was similar for both the single-word and passage conditions.

Across both passage and word processing tasks and spoken and printed modalities, we observed that reading comprehension skill was positively associated with activation in bilateral STG/MTG, the inferior parietal lobe (including AG), the anterior temporal pole, and portions of the left IFG (pars triangularis and orbitalis). Meta-analyses show that these regions are consistently activated in both print and speech for word- and passage-level processing (Crepaldi et al., 2013; Ferstl et al., 2008; Martin et al., 2015; Rodd et al., 2015). In addition, studies find positive relationships between reading comprehension ability and activation during sentence comprehension in left AG and left STG (Van Ettinger-Veenstra et al., 2016) and during passage comprehension in left IFG as well as bilateral STG and inferior parietal lobe (Aboud et al., 2016; Horowitz-Kraus et al., 2013). Thus, these regions seem to support comprehension across modalities and processing levels.

Reading comprehension skill was negatively associated with activation in ACC, DLPFC, and hippocampal areas. DLPFC and ACC have been shown to be involved in a variety of executive functions, including cognitive control, performance monitoring, flexibility, inhibition, and effortful control (MacDonald, Cohen, Stenger, & Carter, 2000; Niendam et al., 2012; Nouchi et al., 2016). Thus, during comprehension of spoken and written passages and words, poorer comprehenders show more activation in executive function regions. Prior research has found that connectivity for passages relative to words between left DLPFC and left ventral AG is positively correlated with reading comprehension (Aboud et al., 2016). This study also found that left DLPFC was activated during both word and passage reading. The authors suggest that left DLPFC may be involved in word-to-text integration, supporting communication between networks involved in word-level and passage-level reading. However, our findings show that activation in DLPFC is negatively related to reading comprehension ability, perhaps suggesting atypical use of DLPFC in poorer comprehenders for both word- and passage-level comprehension. In addition, activation in ACC and anterior insula have been shown to be related to task difficulty (Barch et al., 1997; Edward, James, Ross, William, & Therese, 2013). As such, it is possible that poorer comprehenders found our tasks more difficult.

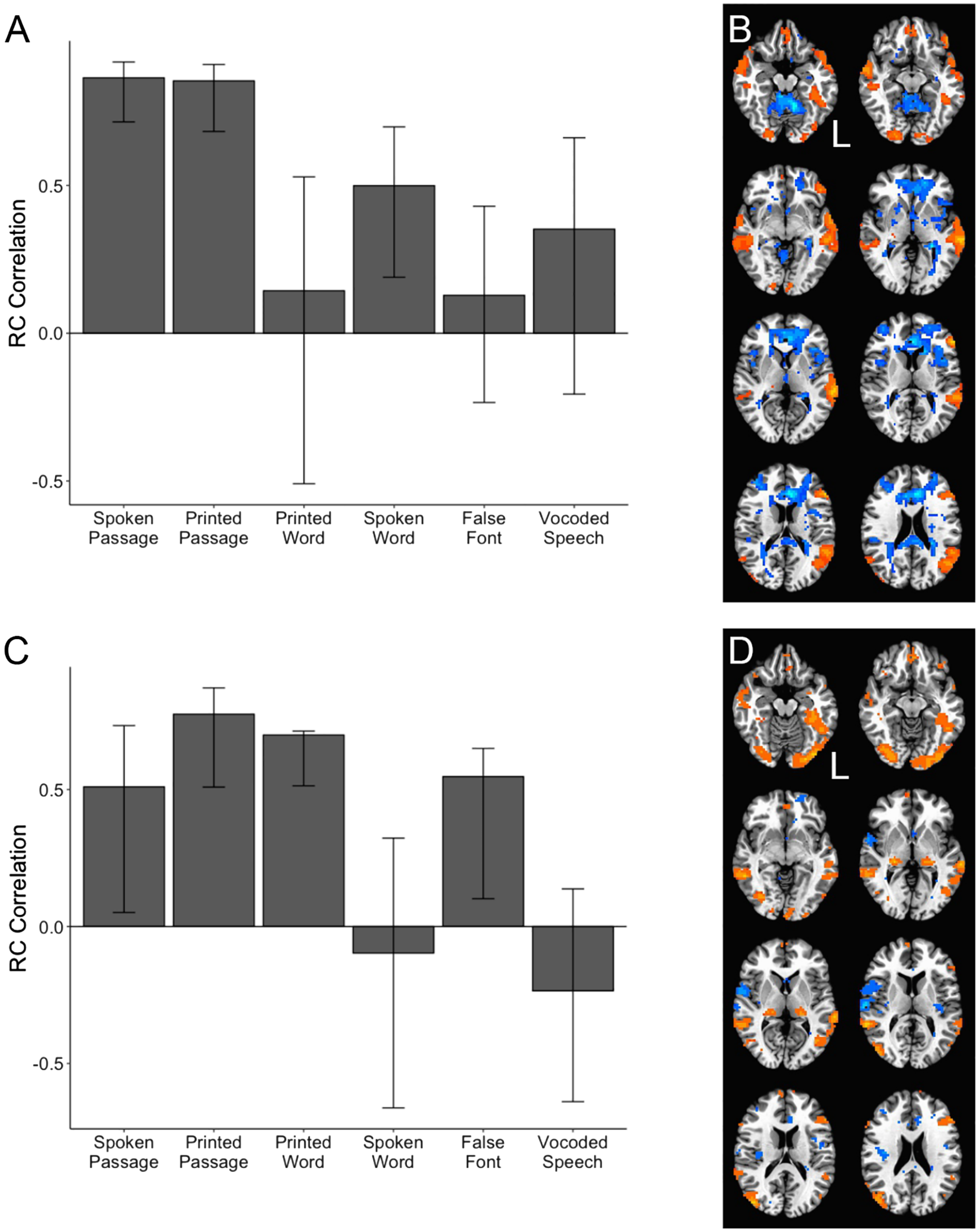

Fig. 2. Results from brain behavior analyses. (A) Reading comprehension correlation plot for first brain behavior analysis comparing spoken and printed passage tasks. This plot shows the correlation between reading comprehension skill and brain scores (similar to factor loadings, they indicate how strongly activation data express the pattern from the latent variable). Both plots show error bars which correspond to 95% CIs from bootstrapping. Positive correlations indicate that the activation pattern shown in B is positively correlated with reading comprehension skill. (B) Bootstrap ratio plot for first brain behavior analysis. For PPass, SPass, and SWord, areas in red are positively correlated with reading comprehension, and areas in blue are negatively correlated with reading comprehension. (C) Reading comprehension correlation plot for the second brain-behavior analysis comparing printed word and passage tasks. (D) Bootstrap ratio plot for second brain behavioral analysis. For PPass and PWord, areas in red are positively correlated with reading comprehension, and areas in blue are negatively correlated with reading comprehension. Images are presented in radiological convention (L = R, image in top left corner is at z = 11, displaying every fifth slice).

However, without online behavioral measures of comprehension collected during scanning, this interpretation should be taken cautiously. Finally, a negative relationship between reading comprehension skill and activation in parahippocampal regions may implicate atypical retrieval of information from declarative memory during comprehension for less-skilled comprehenders. These results are consistent with those of Cutting et al. (2013), who found that functional connectivity between the left IFG and left hippocampus/parahippocampus increased in response to low-frequency words for S-RCD individuals.

While our results support the idea that the relationship between

Table 3
Results from the second behavioral PLS.

X Coord	Y Coord	Z Coord	Peak BSR	Cluster Size	Side	Areas	BA
Activation greater for more-skilled comprehenders							
28.5	70.5	−27.5	8.07	541	L	Cerebellum, inferior occipital gyrus	BA 18
61.5	28.5	2.5	5.98	365	L	Middle temporal gyrus	BA 21
−58.5	43.5	11.5	5.72	202	R	Superior temporal gyrus, middle temporal gyrus	
−34.5	70.5	−6.5	5.42	143	R	Lingual gyrus, inferior occipital gyrus, middle occipital gyrus	
−43.5	76.5	14.5	5.78	128	R	Middle occipital gyrus	BA 39
−16.5	70.5	−39.5	4.35	122	R	Cerebellum	
−16.5	−37.5	41.5	5	117	R	Superior frontal gyrus	
49.5	−28.5	17.5	5.2	96	L	Inferior frontal gyrus pars triangularis	BA 46
−49.5	−1.5	−15.5	5.84	93	R	Middle temporal gyrus	
25.5	61.5	32.5	3.91	64	L	Precuneus	
40.5	61.5	5.5	4.38	47	L	Middle temporal gyrus	
19.5	25.5	5.5	4.86	44	L	Thalamus	
−1.5	64.5	38.5	3.77	43	B	Precuneus	
−22.5	25.5	2.5	5.4	41	R	Thalamus	
−52.5	−13.5	32.5	5	37	R	Middle frontal gyrus	BA 9
1.5	−43.5	−6.5	4.69	36	B	Medial frontal gyrus	
46.5	−4.5	35.5	4.38	33	L	Precentral gyrus	
Activation greater for less-skilled comprehenders							
22.5	34.5	62.5	−5.77	404	B	Postcentral gyrus, paracentral lobule	
−55.5	−1.5	5.5	−5.01	104	R	Superior temporal gyrus	BA 22
−58.5	16.5	11.5	−6.24	72	R	Transverse temporal gyrus	
−37.5	13.5	20.5	−4.5	40	R	Insula	

Areas where activity during printed passage and printed word conditions is related to reading comprehension. Activity in regions with a positive bootstrap ratio (BSR) is associated with higher reading comprehension skill. Activity in regions with a negative bootstrap ratio (BSR) is associated with lower reading comprehension skill.

reading comprehension and neural activation is similar across modalities and processing levels, our study is not without some limitations. Although our task-free design is an improvement over off-line reading comprehension assessments, we did not track comprehension during the task. While we did check in on participants periodically during the task to ensure they were awake and attentive, we do not know about attention within each scan run. Future research could use eye-tracking to preserve the task-free in-scanner behavior while maintaining a naturalistic design (Henderson, Choi, Lowder, & Ferreira, 2016). Further, although the passive nature of the task provides a window into naturalistic processing of words and passages, it makes it hard to determine exactly which aspect of passage or word processing lead to atypical activation in less-skilled comprehenders. As discussed, these tasks require multiple levels of processing, ranging from decoding and lexical semantic access to parsing and comprehension monitoring. By ensuring that all participants had normal decoding ability, we tried to limit the effect of decoding skill on our results. However, multiple higher-level aspects of word and passage reading have been implicated as pressure points for comprehension difficulty, and our analysis cannot tease those skills apart.

In sum, our analyses show that the relationship between reading comprehension skill and neural activation remains similar across processing levels (word versus passage) and modalities (speech versus print). Specifically, reading comprehension skill was positively related to activation in regions often shown to support comprehension of passages, including bilateral MTG, left AG and bilateral ATP. In comparison, reading comprehension skill was negatively related to activation in regions implicated in executive function and memory. While it is difficult to precisely identify which aspects of word and passage processing led to these skill-related differences in activation, these patterns hold across modalities and processing levels. This suggests that reading comprehension skill in good decoders is linked to broader language processing skills that are partially independent of processing level and modality.

Acknowledgments

This work and its authors were supported by the National Institutes of Health (P01 HD-001994 and R01 HD-073288) and the CT Institute for Brain and Cognitive Sciences.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.bandl.2018.08.001.

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