Single Word and Text Processing in Skilled and Less-Skilled Comprehenders: an fMRI study

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**Abstract**

Reading comprehension skill varies considerably across individuals, and this variability exists even among adult college students. Variability in comprehension skill has been positively associated with activation in language-related regions such as temporal cortex, inferior frontal gyrus (IFG), and fusiform areas during word-level tasks. However, little research has investigated how individual differenced in reading comprehension skill are related to activation during actual passage comprehension. Here, we investigate the relationship between individual differences in comprehension skill in good decoders and neural activation (using fMRI) during processing of both auditory and visual single words and passages. Behavioral Partial Least Squares (PLS) analyses revealed that activation was related to comprehension skill similarly across modality and processing level. Skilled comprehenders showed more activation broadly in areas associated with semantic processing, including superior and middle temporal gyri and IFG. Less-skilled comprehenders showed more activation in anterior cingulate cortex, insula, and parahippocampal areas, regions associated with executive function, phonological processing, and memory. These results suggest that skilled comprehenders are engaging primarily with the semantic content of words and passages while less-skilled comprehenders may additionally require the support of phonological and executive systems during comprehension. The similarity of the pattern across modality and processing level suggest that less-skilled comprehenders may have a broader (albeit) sub clinical language deficit, rather than a reading specific deficit *per se*. These findings indicate that individual differences in reading comprehension beyond decoding are related to activation to print and speech at both the word and discourse levels.

**Introduction**

Proficient comprehension of text requires the coordination of multiple low-level processes, including word recognition and sentence parsing, as well the many higher-level skills associated with the integration of multiple phrases and paragraphs. At the most basic level, skilled reading comprehension begins with successful decoding. Indeed, much of the variability in reading comprehension skill can be explained by word reading skill, since efficient decoding allows more resources to be allocated to other reading processes [García and Cain, 2014; Perfetti and Hogaboam, 1975]. However, successful reading comprehension requires subsequent additional processes, akin to those involved in listening comprehension [Gough and Tunmer, 1986]. Readers and listeners must access the meanings of individual words and use knowledge of grammatical structure to provide adequate parsing at both the phrase and sentence levels. Further, readers and listeners have to integrate meanings across words, phrases, and sentences to derive a global understanding of a passage. Research by Perfetti and colleagues [c.f. Perfetti, 1985; Perfetti, 2007; Perfetti et al., 2013] propose that each of these sub-skills are critical for successful comprehension, and weakness in any one becomes a pressure point for comprehension failure. Indeed, research on poor comprehenders, who have difficulty with reading comprehension despite intact word recognition ability and phonological processing skills bears this out [c.f. Nation, 2007; Oakhill and Cain, 2000]. Studies of poor comprehenders find sub-clinical deficits across both linguistic and domain general comprehension sub-skills including lexical-semantic processing grammatical knowledge, inference-making, comprehension monitoring, working memory and executive function [see Hulme and Snowling, 2011; Landi & Ryherd, in press, for recent reviews]. Further, retrospective studies of pre-reading poor comprehenders find early oral language (expressive and receptive) weakness suggesting that impaired language function, rather than anything specific to reading per se may underlie individual differences in reading comprehension in good decoders [Catts et al., 2006; Nation et al., 2010].

While variation in reading comprehension ability has been relatively well-characterized behaviorally for both typically developing individuals and in poor comprehenders [see Braze et al., 2007; Hannon, 2012; Hulme and Snowling, 2011; Landi, 2010; Landi & Ryherd, in press; Macaruso and Shankweiler, 2010; Oakhill and Cain, 2000; Perfetti et al., 2005 for large scale analyses and reviews of these literatures], the neural circuits supporting text and discourse comprehension skill have been comparatively less well-studied. Existing studies of skilled and impaired single-word reading have identified a network of left hemisphere regions that work in concert to access phonology and semantics from printed text. These regions include the inferior occipitotemporal (OT) region [Dehaene and Cohen, 2011; Fiez and Petersen, 1998] which contributes to rapid letter-sound-meaning mapping and is strongly associated with reading skill; the angular gyrus and supramarginal gyrus, which are involved in semantic and phonological access respectively; the superior temporal gyrus (STG) and middle temporal gyrus (MTG), which contribute to mapping speech sounds to printed text as well as to meaning [Frost et al., 2009; Pugh et al., 2001; Sandak et al., 2004; Shaywitz et al., 2002]; and more anterior structures including the left inferior frontal gyrus (IFG), which is associated most strongly with silent reading and phonological recoding [Fiebach et al., 2002; Paulesu et al., 1997; see Price, 2012 for a review]. Extant studies of individuals with impaired decoding abilities (e.g., dyslexia) typically implicate hypoactivation during reading in many of these regions [c.f. Sandak et al., 2004] and atypical functional and structural connectivity among these regions [Boets et al., 2013; Hampson et al., 2006].

Beyond the single word level, research has shown that as texts get longer, frontal and right hemisphere regions become increasingly involved [Xu et al., 2005]. In addition, the left IFG and the posterior, superior, and middle temporal gyri are involved in sentence processing [Caplan, 2001; Grodzinsky and Friederici, 2006], while the left middle temporal gyrus, right precentral sulcus, right superior frontal gyrus, and medial frontal gyrus have been shown to have more activation to narratives than to sentences, suggesting that they are involved in the integrative processes necessary for longer text comprehension above and beyond single sentences [Landi et al., 2013; Plante et al., 2006; Robertson et al., 2000]. Cross-correlation analyses have also revealed that longer utterances produce more reliable responses in multiple regions. Specifically, the extent of inter-subject correlation is greater for longer utterances in language-related areas, such as posterior superior temporal gyrus and temporal-parietal junction, as well as other regions involved in processing social context, such as the precuneus and frontal areas [Lerner et al., 2011; Regev et al., 2013].

Individual differences in reading comprehension skill in population samples of children and adults have been shown to be related to measures of brain structure and function in several classic language- and meaning-access-related areas. For example, activation during spoken narrative comprehension sentence-level tasks found to be positively related to activation in regions involved in higher-level language comprehension, such as bilateral IFG [Horowitz-Kraus et al., 2013]. Furthermore, reading comprehension skill has been related to activation during printed sentence- and passage-level tasks in left STG as well as insula and right posterior visual word form area, which are areas implicated in connecting letter, sound, and meaning [Aboud et al., 2016; Van Ettinger-Veenstra et al., 2016; Horowitz-Kraus et al., 2016; Yarkoni et al., 2008]. Reading comprehension ability has been related to both structural and functional connectivity in multiple networks, suggesting that reading comprehension beyond decoding requires the coordination of many processes. A recent study showed that reading comprehension skill is positively correlated with functional connectivity for a passages relative to words contrast in a network hypothesized to be used for integrating semantic information during comprehension, involving the dorsolateral prefrontal cortex and left ventral angular gyrus [Aboud et al., 2016]. Structurall, fractional anisotropy (FA) in the arcuate fasciculus, which connects areas involved in oral language comprehension such as the IFG, SMG, and lateral temporal lobe, correlates with reading comprehension but not word reading ability [Horowitz-Kraus et al., 2014]. Further, comprehension skill has been found to be positively related to resting-state connectivity between the posterior cingulate cortex, a region that is critical for modulating attention and arousal [Leech and Sharp, 2014; Raichle et al., 2001], and an area of the right anterior insula close to the IFG [Smallwood et al., 2013]. Thus, perhaps unsurprisingly, language critical regions such as the IFG, STG, and MTG are consistently found to be related to comprehension skill.

Of particular relevance to the current paper are findings from studies that try to disentangle the contributions of individual differences in word-level vs. comprehension level processes. One such set of findings has explored the neurocircuitry for reading in poor comprehenders, who are identified based on deficits in reading comprehension despite normal decoding skill. Cutting and colleagues (2013) found that poor comprehenders had typical activation (similar to typically developing [TD] control children) during word reading task in regions related to decoding ability, such as the occipitotemporal region and supramarginal cortex. However, poor comprehenders (PCs) showed altered functional connectivity between the inferior frontal gyrus and hippocampus, suggesting anomalies in communication between language and memory regions [Cutting et al., 2013]. With respect to structure, a second study found that gray matter volume in PCs differs from TD children primarily in regions associated with executive function, including multiple areas of the frontal lobe, rather than classic language-related regions [Bailey et al., 2016]. Thus, variability in comprehension skill beyond decoding ability may be associated with atypical neuroanatomy that extends beyond classic language networks, consistent with studies that have linked domain-general function and comprehension skill [c.f. Cutting et al., 2009].

Although these studies have begun to provide some insight into the neural basis of individual differences in reading comprehension, they have focused on word- or sentence-level processing. The current paper aims to examine individual differences in functional neural activation during spoken and written word and text processing, making it the first fMRI study to directly compare both modality and processing level in relation to comprehension ability. Another innovation of the current study is the use of a naturalistic reading and listening paradigm.

Naturalistic reading and story listening paradigms have recently been adopted across a number of studies to explore the neural circuitry for comprehension. For example, Wehbe and colleagues (2014) measured brain activity while participants read a chapter from *Harry Potter and the Sorcerer’s Stone* and coded various story properties such as characters, parts of speech, and word length. Using a machine learning approach, they were able to predict brain activation from these story properties and identify networks specific to semantic processing, syntactic processing, the physical motion of story characters, and the presence of dialog [Wehbe et al., 2014]. Using a similar approach, Hale, Lutz, Luh, and Brennan (2015) measured functional neural activation while participants passively listened to an excerpt from Lewis Caroll’s *Alice’s Adventures in Wonderland* and found that syntactic properties of the stimulus (measured as node counts), accounted for significant variance in the time course of activation in the anterior temporal lobe over and above simple word probability [Hale et al., 2015]. In another study, Moss and Schunn (2015) manipulated the instructions for strategy use during naturalistic text reading and found that functional connectivity between networks important for maintaining coherence and those involved in cognitive control varied as a function of the type of strategy use [Moss and Schunn, 2015]. Another study integrated on-line timing information from eyetracking with fMRI during a naturalistic text-reading task. They identified a network of language-relevant cortical and subcortical regions involved in on-line word category prediction, including STG, IFG and the basal ganglia [Bonhage et al., 2015]. Finally, Wang and colleagues (2015) compared functional activation during naturalistic text reading as well as single word processing during lexical decision. Findings revealed activation in superior temporal sulcus, supramarginal gyrus, and angular gyrus during naturalistic reading but deactivation in these same regions during word reading/lexical decision. Conversely, activation was greater for lexical decision in regions such as bilateral insula and postcentral gyrus, although it is unclear how much the active nature of the lexical decision task drove these differences [Wang et al., 2015]. Thus, the findings of Wang and colleagues provides a good comparison of naturalistic and task designs.

Although these studies have demonstrated the utility of naturalistic designs for uncovering networks for particular aspects of processing during naturalistic comprehension, they were not used to look at individual differences in reading comprehension. In addition, most of them do not directly compare speech and print or word and text. In this paper, we explore the relationship between comprehension skill and brain activation during both single-word and passage comprehension. We also examine both spoken and printed presentation of words and passages to explore the degree to which individual differences in comprehension skill are associated with variation that is sensitive to the modality of the incoming stimulus. While our primary goal was to use a data driven approach identify networks associated with printed versus spoken text comprehension and single word versus passage comprehension, we also make some specific hypotheses. First, given studies of poor comprehenders that find strong links between oral comprehension and reading comprehension, we predicted that reading comprehension skill would modulate patterns of activation to speech and print in a similar manner. This hypothesis is further supported by the fact that the higher-level language and domain-general skills (e.g., inference making, verbal working memory) found to be related to individual differences in reading comprehension are required for both spoken and printed comprehension of words and passages. Second, given that individuals who struggle with reading comprehension tend also to have word level weakness in vocabulary and other lexical-semantic processing tasks (e.g., semantic priming), we predicted that comprehension skill would be strongly associated with activation in both our single word and passage tasks. Thus, the aim of the current paper is to investigate how comprehension skill is related to brain activity across processing levels and modalities.

**Methods**

*Participants*

A total of 32 adolescent participants were included in this study (M Age = 17, range = 13.75-18.75, 14 males). In order to help isolate neural function associated with individual differences in reading comprehension specifically, we only recruited participants with normal decoding ability (defined here as at or above a standard score of 95 on the Word Attack (WA) subtest of the Woodcock-Johnson III; Woodcock, McGrew, Mather, & Schrank, 2001) and normal cognitive function (defined here as at or above standard score of 80 on the Wechsler Abbreviated Scale of Intelligence II or WASI; Performance IQ subtest, Weschler, 1999). Reading comprehension skill in our sample ranged from very poor to very good. More details about the specific assessments used are provided below.

Six subjects not included in the final 32 analyzed here had unusable fMRI data due to movement artifact, defined below. Prior to study participation, potential participants were pre-screened via phone or online survey to determine that they were monolingual native English speakers raised in a monolingual household.

In accordance to the Yale University Human Investigation Committee, participants over the age of 18 signed forms of consent before participating in the study. All subjects under the age of 18 required written consent of a parent or guardian, with a separate adolescent assent form signed by the participant prior to study participation.

*Behavioral Methods*

All participants completed online questionnaires to collect information regarding familial educational, medical, and language history. We conducted sensory testing with all participants to ensure that hearing and vision were within normal limits. Hearing was tested using a standard audiometer; all participants accurately identified 0.5, 1, 2, and 4 kHz at 20dB. Visual acuity was tested using the Snellen Eye Chart for subjects not already using corrected lenses. Participants completed a behavioral battery of reading, language, and cognitive assessments as part of a larger study examining language processing in poor comprehenders. Assessments relevant to the current paper include the Kaufman Test of Educational Achievement Second Edition (KTEA-II) reading comprehension test [Kaufman & Kaufman, 2004], used as the primary measure of reading comprehension; the Word Attack (WA) subtest of the Woodcock-Johnson III [Woodcock et al., 2001], a measure of nonword decoding, and the Wechsler Abbreviated Scale of Intelligence II [WASI; Weschler, 1999], which provided a measure of performance IQ. Results from these behavioral assessments are summarized in Table 1.

*fMRI Methods*: Passage & word tasks.

*Passage Task*

Participants completed a modified version of the story task described in Wang and colleagues (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 seconds 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 seconds. During PPass, each phrase was presented for 2 seconds, with an average of 96 phrases and 12 words per phrase. Each phrase appeared on the screen for 2000ms. 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.

*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). The passive nature of this single word processing task provided an appropriate comparison to the naturalistic passage task.

An event-related design was used for this experiment. In each trial, subjects received a group of 4 rapidly sequentially presented different tokens from the same condition (tetrads), with a presentation time of 450ms per stimulus. There was a jittered ITI of 4-7 seconds between trials, with occasional “null” trials up to 13 seconds long. Participants received two runs of this task while in the scanner, for a total duration of 302 seconds. 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]. FalseFont stimuli were real words presented using the Wingdings typeface, making them appear as a string of meaningless symbols; any letter-like symbols were not used. Vocod stimuli was created using Praat [Boersma and 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.

*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 = 30ms; TR = 2000ms; FOV = 220; 4mm slice thickness, no gap; matrix size 64 x 64; 3.4mm in-plane resolution. High resolution, 1mm isotropic, T1-weighted MP-RAGE structural images were also gathered for registration with the following parameters: FA = 7◦; TE = 3.66; TR = 2530ms; FOV = 256; 1mm slice thickness, no gap; matrix size 256 x 256.

*fMRI Analysis*

*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, smoothed with an 8mm FWHM Gaussian filter, and then normalized into standard Talairach space. 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). 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).

*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).

*Partial Least Squares Analysis*

We utilized PLS analysis to investigate the relationships between patterns of brain activation, our experimental manipulations, and comprehension skill. PLS 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 et al., 2011; McIntosh et al., 1996]. In addition, PLS 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. We used two types of PLS: task and behavioral. Task PLS was used to determine the relationship between activation and the experimental conditions of the word and passage tasks. Behavioral PLS was used to determine how reading comprehension skill is related to activation across conditions.

PLS results are reported in the form of latent variables that account for the maximum amount of covariance between two data matrices, X and Y. 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 PLS, the Y matrix represents the experimental conditions. In behavioral PLS, the Y matrix represents behavioral performance (e.g. participants’ scores on the KTEA). For behavioral PLS, 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 PLS, the latent variable loadings to the brain activity maps (in the X matrix) are called brain scores. These indicate which voxels in the brain images are associated with each LV. For behavioral PLS, the latent variable loadings to the Y matrix are called behavior scores; these indicate which behavioral variables are associated with this LV. Finally, in task PLS, latent variable loadings to the Y matrix are called design scores; these indicate which task conditions are associated with each LV.

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 (permuted 1000 times) is larger than that of the original analysis. Bootstrap resampling (1000 bootstraps) is used to determine standard error. Bootstrapping also provides confidence intervals (CIs) for brain scores that can be used to compare conditions.

**Results**

*Basic Contrasts*

While our primary analyses consist of our multivariate PLS 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 (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 Table 2). Both PPass and SPass activated a large network of 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 superior temporal gyrus. Both PPass and SPass showed significant activation (*p* = .001, FDR corrected) in the bilateral middle temporal gyrus, left inferior frontal gyrus, 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 Table 2). PWord elicited significant activation (*p* = .001, FDR corrected) in bilateral fusiform and extrastriate cortex, inferior and middle occipital gyri, bilateral precentral gyrus, and bilateral inferior frontal gyrus. SWord showed significant activation (*p* = .001, FDR corrected) in bilateral superior temporal gyrus, 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 superior temporal gyrus.

Although the current paper focuses on the PLS findings that allow us to examine the relationship between comprehension skill at task (below), please see Supplemental Tables 1-3 and Supplemental Figures 1-3 for a complete presentation of basic within task and across task activation contrasts.

*PLS analyses*

*Task –Based PLS*

The task PLS 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 accounted for 50.93% of the covariance (*p* < .001). This LV dissociated printed conditions from spoken conditions (see Fig. 2a 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. 2b). 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 accounted for 41.33% of the covariance (p<.001). It differentiated passage conditions from word conditions (see Fig. 3b). 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. 3b). 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 accounted for 6.28% of the covariance (p=.001) (see Fig. 4b). 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 Fig. 4). 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 PLS 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 PLS 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.

*Behavioral PLS*

Two behavioral PLS analyses were conducted. The first 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 networks for comprehension. One significant LV accounted for 85.65% of the covariance (p<.001). 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: .87, .93; printed: .85, .93] (see Fig. 5a). That is, the same distinct sets of brain regions were associated with lower or higher comprehension skill for *both* SPass and PPass. Specifically, across both modalities, activation related to higher reading comprehension skill was seen in bilateral MTG and left IFG pars orbitalis and pars triangularis. Activation associated with lower reading comprehension skill was seen in the ACC, insula, and parahippocampal gyrus (Fig. 6).

The second behavioral PLS assessed the covariance between activation in PPass, PWord, and reading comprehension skill in order to test whether comprehension ability similarly modulated the networks for word and text processing. One significant LV accounted for 64.76% of the covariance (p=0.010). This LV found covariation between the two printed conditions and comprehension ability (Fig. 5b). 95% CIs show that both PWord [.64, .84] and PPass [.83, .92] conditions expressed the LV equally. 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. 7). In contrast, less-skilled comprehenders showed greater activation in areas involved in cognitive control [ACC; Botvinick et al., 2004] as well as areas related to speech sound processing [insula, anterior STG; Huang et al., 2002; Hwang et al., 2005].

**Discussion**

The current study investigated how 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 under naturalistic conditions. 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 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.

*Modality- and task-specific activation patterns*

Our initial PLS analysis taking into account the six task conditions revealed two interpretable latent variables. One discriminated visual presentation of text and text-like stimuli from auditory presentation of speech and speech-like stimuli, irrespective of their linguistic or discourse content. The other discriminated presentation of a continuous, coherent discourse from presentation of words and illegible or unintelligible stimuli that shared some low-level physical features with words. Modality-specific activity was observed in largely primary and associative auditory regions (for speech) and visual cortex (for text), extending into occipitotemporal regions associated with visual word recognition [McCandliss et al., 2003]. This pattern of modality specificity was largely consistent with simple task vs. rest contrasts for spoken and written stimuli presented here (Figure 1) and in prior research [e.g., Rueckl et al., 2015].

Further, our task PLS identified regions that were differentially active for the passage relative to the single word conditions; specifically, the passage task more strongly engaged classic language processing regions, including areas in the temporal cortex bilaterally (STG, MTG & ATP), consistent with the extensive literature relating these regions to elaborated processing of semantic information [Rogers et al., 2006; Spitsyna et al., 2006; Visser et al., 2010] as well as the left IFG pars orbitalis and triangularis, which is widely associated with semantic and syntactic processing [Friederici et al., 2003; Newman et al., 2010; but see Poldrack, 2006]. As with the identification of modality-specific regions, these analyses were broadly consistent with the simple contrasts revealing overlap for text and speech, specifically for passage comprehension in left IFG and bilateral anterior temporal cortex.

The single-word tasks more strongly engaged the hippocampal memory network as well as the anterior cingulate, thalamus, and insula. This may reflect extra effort associated with the processing of unrelated lists of words relative to extended, coherent discourse. Similar results have been found in prior comparisons between word and passage processing [e.g., Wang et al., 2015], although prior work has examined single word processing in the context of a challenging, metalinguistic task. It appears from the current results that some of these responses are driven by the automatic processing of words, or at least processing that is typical despite the lack of a specific overt task.

Thus, at the group level, the PLS successfully identifies important task-related variability in brain activity that concords well with model-based contrasts, despite using an unsupervised approach that does not predetermine which conditions are to be contrasted with one another. We now turn to analyses applying the same approach to explore brain activity associated with individual differences in comprehension ability.

*Activity associated with individual variability in comprehension*

Our first behavioral PLS examined the relationship between comprehension skill and passage-level processing across the spoken and printed modalities. This was done to explore the degree to which individual differences would relate to variation in activation to incoming discourse-level information regardless of modality. This approach is motivated by findings suggesting that poor comprehenders show impairments in both reading and listening comprehension at the behavioral level [Catts et al., 2006; Nation et al., 2010]. This first behavioral analysis identified regions that were modulated by comprehension skill similarly for both modalities, suggesting that some differences related to comprehension skill may be modality-independent.

Our second behavioral PLS investigated the relationship between reading skill and print processing only across the passage and single-word presentation conditions. This analysis was motivated by findings that identify impaired processing in some domains (semantics, morphology) for poor comprehenders at the level of both word and text [Henderson et al., 2013; Nation and Snowling, 1999; Oakhill et al., 2005; Oakhill and Cain, 2012]. More specifically, tasks that tap word-level semantic processing [Henderson et al., 2013; Nation and Snowling, 1999], as well as tasks that tap higher-level semantic integration, such as inference-making [Silva and Cain, 2015] have been shown to be similarly related to comprehension skill. Findings from this second behavioral analysis found that the relationship between brain activation and reading comprehension skill was similar for both the single-word and passage conditions. This suggests that skill-related differences in activation were similar for both our printed word and text processing tasks.

Across both tasks and modalities we observed that skilled comprehenders consistently show more activation in semantic processing regions, including bilateral STG/MTG, the inferior parietal lobe (including angular gyrus), the anterior temporal pole, and portions of the left IFG (pars triangularis and orbitalis). Prior research in typically developing adults shows that these regions, especially MTG, anterior temporal pole, and inferior parietal lobule, are implicated in both visual and auditory semantic processing [Costanzo et al., 2013; Visser et al., 2012]. Increased activation for skilled comprehenders in semantic areas may suggest easier and more automatic access to concepts and the relations between them, particularly for the passage task. Less-skilled comprehenders, on the other hand, show increased activation in attentional and executive regions, including the ACC, insula, and DLPFC, as well as hippocampal areas often related to memory. Increased activity in regions associated with more effortful processing may be a signature of less-skilled comprehenders, perhaps reflecting difficulty integrating conceptual knowledge. Findings from Aboud and colleagues (2016) suggest that skilled comprehension is related to connectivity between regions involved in executive function (e.g. dlPFC) and those more typically activated for language tasks (e.g. AG). Thus, while our less-skilled comprehenders do show activation in executive regions, they do not show broad language-related activation, suggesting that they may not be using both executive and language networks to comprehend. Further, increased activation in parahippocampal regions for less-skilled comprehenders suggests atypical retrieval of information from declarative memory during comprehension. 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 as compared to high-frequency words for poor comprehenders. Thus, atypical function in both executive function and memory appears to be associated with poorer comprehension skill.

When considering the visual PLS alone, skilled comprehenders show more primary visual activation than poor comprehenders, possibly suggesting that for skilled comprehenders, reading is associated with a more direct mapping from orthography to semantics that relies somewhat less on phonology. Research from Dikker and colleagues has shown that activation in sensory areas, such as occipital and fusiform cortices, may indicate that skilled readers are expecting the form of a likely next word [Dikker et al., 2009; Dikker et al., 2010; Dikker and Pylkkanen, 2011]. In comparison, comprehension skill was negatively related to activation in right anterior STG for both print conditions. This region, specifically in the right hemisphere, shows activation during word reading, both silently and aloud [Fiez and Petersen, 1998]. Thus, less-skilled comprehenders may be silently reading words aloud during printed conditions. This process mirrors the indirect route hypothesized to be taken by early, nonskilled readers [Grainger et al., 2012]. Less-skilled comprehenders may be using their relative strength in phonological processing to support their lower–quality and difficult-to-access semantic representations. This idea is further supported by activation negatively correlated with reading comprehension shown in the insula. Activation in regions of the insula close to IFG and precentral gyrus has been shown during both overt and silent reading [Huang et al., 2002; Humphreys and Gennari, 2014]. Thus, during reading, less-skilled comprehenders, who are good decoders, may more strongly activate suboptimal regions for the task at hand, utilizing their easily-accessed phonological representations in order to support their less efficient semantic access, ultimately slowing down the comprehension process and taking resources away from higher-order processes, such as comprehension monitoring and integration.

Our pattern of results also fits nicely into the framework put forth by Moss & Schunn (2015). While good comprehenders appear to be making more use of the coherence-building network, as shown by activation in MTG, anterior IFG, and precuneus, the less-skilled comprehenders’ pattern of activation fits better with the cognitive control and semantic manipulation network. In our study, activation is negatively correlated with comprehension skill in DLPFC and ACC, both hypothesized to be part of this network. Thus, while individuals may be able to manipulate whatever semantic information they can access regardless of comprehension skill, coherence building seems to be more strongly related to comprehension skill. The activation patterns of less-skilled comprehenders suggest that they are not building a coherent model of the text. Behaviorally, poor comprehenders do show lower standards for coherence during comprehension, often failing to notice anomalous portions of text [Ehrlich et al., 1999; van der Schoot et al., 2009].

While the results seem to support atypical use of semantic and executive function networks in less-skilled comprehenders, we must consider alternative explanations. First off, both our passage and single word processing tasks were completely passive. Participants were not asked to make any responses or to answer comprehension questions during or after the experiment. As such, it is possible that the differences in activation related to comprehension reflect differences in attention to or engagement with the stimuli. This is a key weakness in our study and should be addressed in future research. However, the fact that less-skilled comprehenders showed activation consistent with more effortful processing suggests that they were actively engaged during both tasks. 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 reading required more effort for less-skilled comprehenders. As we have discussed, these tasks require multiple levels of processing from decoding to lexical semantic access to parsing to combining concepts and monitoring comprehension. We have tried to eliminate differences that could be attributable to low-level word reading by ensuring that all participants had normal decoding ability. However, multiple higher-level aspects of word and passage reading have been implicated as pressure points for comprehension difficulty, and our analysis cannot completely tease those skills apart. In addition, the lack of dissociation between modalities seen in the first behavioral PLS, which compared spoken and printed passages, may be in part due to the how the stories were presented. In the task, participants heard different parts of the same story presented in both the visual and the auditory modalities. Thus, similar patterns of brain activation seen in these conditions may be driven by the continuity in content across the modalities.

In sum, PLS analyses from both our word- and passage-level task suggest that patterns of brain activation elicited during reading print and listening to speech are related to comprehension skill even when phonological decoding remains intact. Skilled comprehenders show more activation in semantic processing regions, including bilateral MTG, left AG and bilateral ATP, suggesting semantic processing of language stimuli. In comparison, less-skilled comprehenders seem to be using their intact phonological representations to access the meanings of printed words. They also show more activation of networks implicated in attention, suggesting that comprehension (regardless of processing level or modality) for them is more effortful. Finally, less-skilled comprehenders seem to be using episodic memory during comprehension of longer passages more than skilled comprehenders. Overall, these results suggest that while skilled comprehenders engage with semantic information relatively easily when processing a words or passages, less-skilled comprehenders exhibit atypical usage of executive function networks and more reliance on phonological and episodic knowledge during word and passage reading across modalities.

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**Tables**

|  |  |  |  |
| --- | --- | --- | --- |
|  | KTEA | WA SS | Performance IQ |
| Mean | 105.3 | 108.3 | 107.9 |
| SD | 18.91 | 9.02 | 17.84 |
| Range | 76-146 | 96-124 | 81-142 |

Table 1. Behavioral profile of the sample.

KTEA: Kaufman Test of Educational Achievement, reading comprehension; WA SS: Word Attack standardized score (from Woodcock-Johnson-III), decoding; Verbal IQ, Performance IQ, IQ-2, IQ-4 from Wechsler Abbreviated Scale of Intelligence II.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **X coord** | **Y coord** | **Z coord** | **Peak T-stat** | **Cluster Size** | **Hemi-sphere** | **Areas in this cluster** | **BA** | |
| Passage task: Spoken condition | | | | | | | | |
| Speech > Rest | | | | | | | | |
| 58.5 | 13.5 | 8.5 | 9.606 | 1920 | L | Superior temporal gyrus, inferior frontal gyrus, middle temporal gyrus |  | |
| -61.5 | 13.5 | 5.5 | 11.408 | 1244 | R | Superior temporal gyrus, middle temporal gyrus |  | |
| -19.5 | 76.5 | -33.5 | 8.138 | 377 | R | Pyramis |  | |
| 25.5 | 79.5 | -27.5 | 4.351 | 164 | L | Tuber |  | |
| 10.5 | -40.5 | 50.5 | 4.889 | 38 | L | Superior frontal gyrus |  | |
| -52.5 | 61.5 | 20.5 | 4.589 | 32 | R | Superior temporal gyrus |  | |
| -1.5 | -46.5 | -9.5 | 4.213 | 25 | R | Medial frontal gyrus |  | |
| 1.5 | 58.5 | 29.5 | 5.329 | 22 | B | Cingulate gyrus |  | |
| -13.5 | -37.5 | 50.5 | 4.618 | 21 | R | Superior frontal gyrus |  | |
| 1.5 | -52.5 | 35.5 | 3.978 | 17 | L | Medial frontal gyrus |  | |
| Rest > Speech | | | | | | | | |
| 10.5 | 76.5 | 32.5 | -6.534 | 8477 | B | Cuneus, precuneus, supramarginal gyrus, cingulate gyrus, anterior cingulate cortex, superior frontal gyrus, middle frontal gyrus |  | |
| 40.5 | -16.5 | 2.5 | -5.472 | 444 | L | Insula, caudate | BA 39 | |
| 40.5 | 16.5 | 44.5 | -4.023 | 78 | L | Precentral gyrus |  | |
| 37.5 | 43.5 | -30.5 | -4.025 | 62 | L | Cerebellar tonsil | BA 31 | |
| -1.5 | 16.5 | -0.5 | -3.93 | 44 | B | Thalamus |  | |
| -43.5 | -1.5 | 32.5 | -3.906 | 36 | R | Inferior frontal gyrus |  | |
| Passage task: Print condition | | | | | | | | |
| Print > Rest | | | | | | | | |
| -22.5 | 88.5 | -12.5 | 11.753 | 4651 | B/L | Fusiform gyrus (B), lingual gyrus (B), middle temporal gyrus (L), inferior frontal gyrus (L), precentral gyrus (L) | |  |
| 46.5 | 34.5 | 2.5 | 6.002 | 479 | R | Middle temporal gyrus | | BA 22 |
| -13.5 | -40.5 | 50.5 | 5.674 | 120 | L | Superior frontal gyrus | |  |
| 31.5 | 61.5 | 23.5 | 7.355 | 97 | R | Middle temporal gyrus | | BA 39 |
| 4.5 | -37.5 | 50.5 | 7.106 | 97 | R | Superior frontal gyrus | | BA 8 |
| -1.5 | -49.5 | 32.5 | 6.257 | 96 | B | Superior frontal gyrus | | BA 9 |
| 1.5 | 55.5 | 29.5 | 5.744 | 63 | B | Cingulate gyrus | | BA 31 |
| 10.5 | -46.5 | -9.5 | 3.96 | 43 | R | Medial frontal gyrus | |  |
| -1.5 | -10.5 | 62.5 | 5.702 | 42 | L | Superior frontal gyrus | | BA 6 |
| -52.5 | 25.5 | -0.5 | 5.583 | 28 | R | Thalamus | |  |
| Rest > Print | | | | | | | | |
| 7.5 | 76.5 | 32.5 | -6.732 | 4149 | B/R | Cuneus (B), cingulate gyrus (B), supramarginal gyrus (R) | |  |
| -49.5 | -16.5 | -0.5 | -5.114 | 766 | L | Insula | | BA 13 |
| 37.5 | -58.5 | 14.5 | -3.968 | 397 | L | Superior frontal gyrus | | BA 10 |
| 40.5 | 46.5 | -6.5 | -6.478 | 229 | L | Parahippocampal gyrus | |  |
| -25.5 | -55.5 | 14.5 | -4.134 | 221 | R | Superior frontal gyrus | | BA 10 |
| 22.5 | 46.5 | -6.5 | -6.805 | 208 | R | Parahippocampal gyrus | | BA 37 |
| 22.5 | 19.5 | 35.5 | -4.447 | 136 | L | Precentral gyrus | |  |
| -40.5 | 43.5 | 47.5 | -4.306 | 44 | L | Inferior parietal lobule | |  |
| 28.5 | 40.5 | -30.5 | -4.625 | 33 | L | Cerebellar tonsil | |  |
| Word task: Spoken condition | | | | | | | | |
| Speech > Rest | | | | | | | | |
| -58.5 | 16.5 | 8.5 | 12.995 | 1791 | B/R | Superior temporal gyrus (R), Thalamus (B), Lingual gyrus (B) | BA 18 | |
| 52.5 | 22.5 | 11.5 | 17.106 | 1566 | L | Superior temporal gyrus |  | |
| -1.5 | 73.5 | 14.5 | 4.918 | 1163 | B | Cuneus |  | |
| 1.5 | 34.5 | -3.5 | 6.983 | 441 | B | Thalamus |  | |
| 1.5 | 49.5 | 44.5 | 7.145 | 175 | B | Precuneus | BA 7 | |
| -46.5 | -16.5 | 26.5 | 6.451 | 156 | R | Middle frontal gyrus | BA 46 | |
| -22.5 | 58.5 | -48.5 | 6.875 | 116 | R | Cerebellar tonsil |  | |
| 46.5 | -16.5 | 26.5 | 5.277 | 87 | L | Middle frontal gyrus | BA 9 | |
| -52.5 | 7.5 | 44.5 | 7.573 | 71 | R | Precentral gyrus | BA 4 | |
| 49.5 | 10.5 | 47.5 | 6.251 | 62 | L | Precentral gyrus | BA 4 | |
| 22.5 | 55.5 | -45.5 | 7.18 | 55 | L | Cerebellar tonsil |  | |
| -1.5 | 4.5 | 62.5 | 4.873 | 51 | B | Medial frontal gyrus |  | |
| 10.5 | 70.5 | -39.5 | 6.593 | 50 | L | Inferior semi-lunar lobule |  | |
| 34.5 | -28.5 | 5.5 | 4.584 | 38 | L | Inferior frontal gyrus |  | |
| Rest > Speech | | | | | | | | |
| -46.5 | 67.5 | -9.5 | -4.755 | 38 | R | Middle occipital gyrus |  | |
| 46.5 | 64.5 | -12.5 | -4.437 | 34 | L | Fusiform gyrus | BA 37 | |
| Word task: Print condition | | | | | | | | |
| Print > Rest | | | | | | | | |
| -37.5 | 52.5 | -15.5 | 6.246 | 1755 | R | Fusiform gyrus, inferior occipital gyrus, middle occipital gyrus, middle temporal gyrus |  | |
| 28.5 | 88.5 | -6.5 | 6.977 | 1408 | L | Fusiform gyrus, inferior occipital gyrus, middle occipital gyrus |  | |
| 46.5 | 4.5 | 47.5 | 7.129 | 670 | L | Precentral gyrus, inferior frontal gyrus |  | |
| -40.5 | -4.5 | 32.5 | 5.809 | 531 | R | Precentral gyrus, inferior frontal gyrus, middle frontal gyrus |  | |
| 1.5 | 1.5 | 56.5 | 6.064 | 304 | B | Medial frontal gyrus |  | |
| 28.5 | 58.5 | 41.5 | 6.876 | 220 | L | Precuneus |  | |
| -40.5 | 16.5 | -21.5 | 6.014 | 54 | R | Fusiform gyrus | BA 20 | |
| -34.5 | -22.5 | 5.5 | 4.717 | 35 | R | Inferior frontal gyrus |  | |
| -10.5 | 28.5 | -0.5 | 5.128 | 28 | R | Thalamus |  | |
| 4.5 | 25.5 | -0.5 | 4.724 | 20 | L | Thalamus |  | |
| 1.5 | 28.5 | 26.5 | 4.362 | 16 | L | Cingulate gyrus | BA 23 | |
| Rest > Print | | | | | | | | |
| -58.5 | 16.5 | 8.5 | -9.213 | 414 | R | Superior temporal gyrus |  | |
| 49.5 | 22.5 | 11.5 | -10.042 | 356 | L | Superior temporal gyrus |  | |
| -13.5 | 67.5 | -6.5 | -5.019 | 16 | R | Culmen |  | |

Table 2. Whole-brain evoked response analyses for passage and word tasks.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **X coord** | **Y coord** | **Z coord** | **Peak BSR** | **Cluster Size** | **Hemi-sphere** | **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 | 10448 | 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 |

Table 3. Task PLS analyses. All results come from the three significant LVs of the task PLS.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **X coord** | **Y coord** | **Z coord** | **Peak BSR** | **Cluster Size** | **Hemi-sphere** | **Areas in this cluster** | **BA** |
| Activation greater for skilled comprehenders | | | | | | | |
| 61.5 | 28.5 | 2.5 | 6.938 | 455 | L | Middle temporal gyrus | BA 21 |
| -58.5 | 4.5 | -6.5 | 6.257 | 104 | R | Middle temporal gyrus |  |
| 31.5 | 70.5 | -33.5 | 7.161 | 101 | L | Pyramis |  |
| -22.5 | 70.5 | -36.5 | 4.653 | 61 | R | Inferior semi-lunar lobule |  |
| 52.5 | -28.5 | 14.5 | 9.176 | 52 | L | Inferior frontal gyrus p. triangularis | BA 45 |
| 1.5 | -37.5 | 47.5 | 4.611 | 31 | L | Superior frontal gyrus |  |
| Activation greater for less-skilled comprehenders | | | | | | | |
| 4.5 | -28.5 | 17.5 | -9.536 | 890 | B | Anterior cingulate cortex | BA 24 |
| 10.5 | 46.5 | -12.5 | -8.674 | 745 | B | Culmen |  |
| 31.5 | 16.5 | 26.5 | -8.276 | 150 | L | Postcentral gyrus, inferior parietal lobule |  |
| -31.5 | -34.5 | 29.5 | -6.622 | 110 | R | Middle frontal gyrus |  |
| 34.5 | -22.5 | 8.5 | -7.807 | 96 | L | Insula, Inferior frontal gyrus p. triangularis |  |
| -28.5 | 19.5 | 29.5 | -5.006 | 86 | R | Insula |  |
| -10.5 | 34.5 | 23.5 | -5.440 | 66 | B | Posterior cingulate cortex |  |
| 25.5 | 37.5 | 2.5 | -8.775 | 46 | L | Parahippocampal gyrus |  |
| -22.5 | 25.5 | 41.5 | -5.388 | 40 | R | Cingulate gyrus |  |

Table 4. First behavioral PLS. 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.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **X coord** | **Y coord** | **Z coord** | **Peak BSR** | **Cluster Size** | **Side** | **Areas in this cluster** | **BA** |
| Activation greater for skilled comprehenders | | | | | | | |
| 61.5 | 28.5 | 2.5 | 7.146 | 647 | L | Middle temporal gyrus, superior temporal gyrus, parahippocampal gyrus | BA 21, 22, 36 |
| 31.5 | 70.5 | -33.5 | 8.825 | 625 | L | Pyramis, declive |  |
| -49.5 | -7.5 | -18.5 | 5.931 | 380 | R | Middle temporal gyrus, superior temporal gyrus | BA 22, 28 |
| -19.5 | 67.5 | -39.5 | 5.579 | 221 | R | Inferior semi-lunar lobule |  |
| -7.5 | -37.5 | 41.5 | 4.642 | 211 | B | Medial frontal gyrus | BA 8 |
| -25.5 | 85.5 | -9.5 | 5.138 | 137 | R | Middle occipital gyrus | BA 18 |
| 52.5 | -28.5 | 14.5 | 6.477 | 137 | L | Middle frontal gyrus | BA 48 |
| -43.5 | 76.5 | 14.5 | 5.102 | 130 | R | Middle temporal gyrus, middle occipital gyrus | BA 39 |
| 1.5 | 55.5 | 29.5 | 4.989 | 100 | B | Precuneus |  |
| 4.5 | -31.5 | -15.5 | 5.277 | 100 | L | Medial frontal gyrus | BA 10, 11, 25 |
| 49.5 | -13.5 | -18.5 | 4.774 | 80 | L | Superior temporal gyrus, middle temporal gyrus |  |
| 19.5 | 25.5 | 5.5 | 5.769 | 51 | L | Thalamus |  |
| -22.5 | 25.5 | 2.5 | 5.410 | 45 | R | Thalamus |  |
| Activation greater for less-skilled comprehenders | | | | | | | |
| 7.5 | -31.5 | 20.5 | -4.842 | 571 | B | Anterior cingulate cortex | BA 24 |
| -22.5 | 37.5 | 53.5 | -6.150 | 510 | B | Postcentral gyrus |  |
| 31.5 | 16.5 | 11.5 | -5.219 | 237 | L | Insula |  |
| -58.5 | -1.5 | 8.5 | -4.984 | 164 | R | Precentral gyrus, transverse temporal gyrus | BA 42 |
| 37.5 | -22.5 | 8.5 | -5.008 | 119 | L | Inferior frontal gyrus p. triangularis | BA 13 |
| -4.5 | 31.5 | 26.5 | -3.977 | 104 | B | Posterior cingulate gyrus | BA 23 |
| -31.5 | -34.5 | 29.5 | -5.788 | 90 | R | Middle frontal gyrus |  |
| -16.5 | 31.5 | -24.5 | -5.479 | 87 | R | Cerebellum |  |
| -37.5 | 13.5 | 20.5 | -4.476 | 70 | R | Insula |  |
| 25.5 | 40.5 | -36.5 | -4.998 | 64 | L | Cerebellum |  |
| -58.5 | 16.5 | 11.5 | -5.122 | 62 | R | Transverse temporal gyrus | BA 42 |
| 13.5 | 52.5 | -15.5 | -3.867 | 33 | L | Culmen |  |

Table 5. Second behavioral PLS. 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.

**Figures**



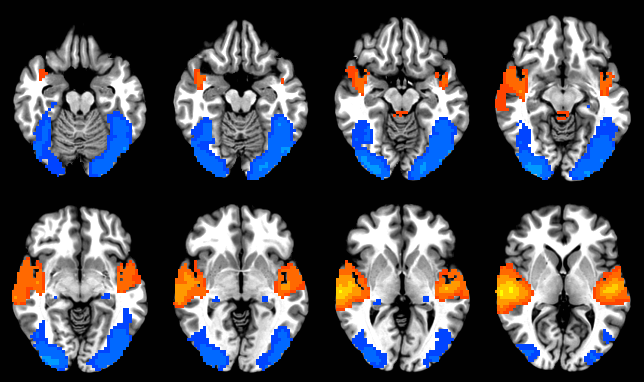
**B)**

**A)**



Figure 1. Evoked response conjunction maps across all subjects for positive activation during the passage and word tasks. A) Evoked response across subjects in the passage task. B) Evoked response across subjects in the word task. Red = activation to just print, green = activation to just speech, blue = activation to both print and speech. All activations shown at *p* = .001, FDR corrected.

A) 



**B)**

Figure 2. Task PLS Latent Variable 1 results. A) Brain score plot. Error bars indicate 95% CIs from bootstrapping. B) Bootstrap ratio plot. 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; image in top left corner is at z = 1, displaying every third slice)

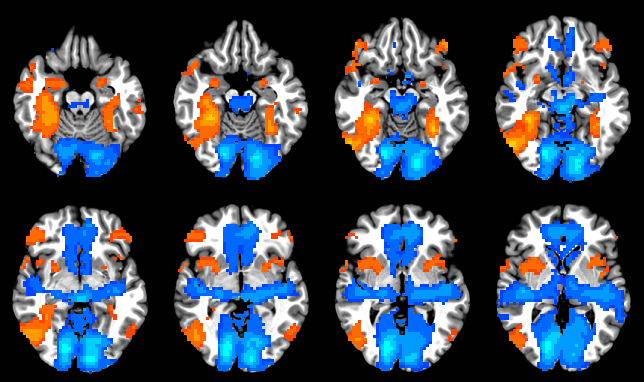
A) 



**B)**

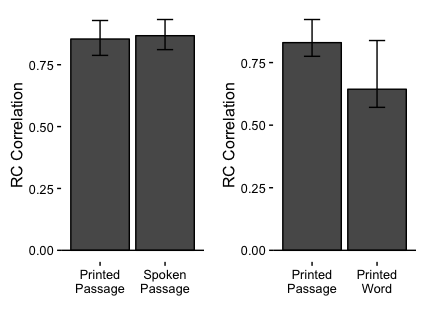
Figure 3. Task PLS Latent Variable 2 results. A) Brain score plot. Error bars indicate 95% CIs from bootstrapping. B) Bootstrap ratio plot. Regions shaded in red showed more activation to conditions with a positive brain score and regions shaded in blue showed more activation to a negative brain score. (L=R; image in top left corner is at z = 1, displaying every third slice)

A) 



**B)**

Figure 4. Task PLS Latent Variable 3 results. A) Brain score plot. Error bars indicate 95% CIs from bootstrapping. B) Bootstrap ratio plot. 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)



A)

B)

Figure 5. Reading comprehension correlation plots for the Behavioral PLS. Both plots show error bars which correspond to 95% CIs from bootstrapping. A) Reading comprehension correlation plot within the passage task. B) Reading comprehension correlation plot for print conditions across passage and word tasks.



Figure 6. Bootstrap ratio plot from first behavioral PLS relating brain activation in spoken and printed passage task to reading comprehension. For both conditions, 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=19, displaying every third slice).



Figure 7. Bootstrap ratio plot from second behavioral PLS relating brain activation in printed story task and printed word task to reading comprehension. For both conditions, 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=19, displaying every third slice).