

## Will you read how I will read? Naturalistic fMRI predictors of emergent reading

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### ABSTRACT

Despite reading being an essential and almost universal skill in the developed world, reading proficiency varies substantially from person to person. To study why, the fMRI field is beginning to turn from single-word or nonword reading tasks to naturalistic stimuli like connected text and listening to stories. To study reading development in children just beginning to read, listening to stories is an appropriate paradigm because speech perception and phonological processing are important for, and are predictors of, reading proficiency. Our study examined the relationship between behavioral reading-related skills and the neural response to listening to stories in the fMRI environment. Functional MRI were gathered in a 3T TIM-Trio scanner. During the fMRI scan, children aged approximately 7 years listened to professionally narrated common short stories and answered comprehension questions following the narration. Analyses of the data used inter-subject correlation (ISC), and representational similarity analysis (RSA). Our primary finding is that ISC reveals areas of increased synchrony in both high- and low-performing emergent readers previously implicated in reading ability/disability. Of particular interest are that several previously identified brain regions (medial temporal gyrus (MTG), inferior frontal gyrus (IFG), inferior temporal gyrus (ITG)) were found to "synchronize" across higher reading ability participants, while lower reading ability participants had idiosyncratic activation patterns in these regions. Additionally, two regions (superior frontal gyrus (SFG) and another portion of ITG) were recruited by all participants, but their specific timewindow of activation depended on reading performance. These analyses support the idea that different brain regions involved in reading follow different developmental trajectories that correlate with reading proficiency on a spectrum rather than the usual dichotomy of poor readers versus strong readers.

### 1. Introduction

While reading is a critical skill in everyday life, reading proficiency is on a spectrum with some struggling to decode written text and others effortlessly reading a book a day. Poor reading can be disabling and negatively impact school performance (Perie et al., 2005) and later,

quality-of-life; reading disability is associated with lifelong low self-esteem (Haft et al., 2023; 2019a, 2019b) and feelings of anxiety (Haft et al., 2019a,b; Hendren et al., 2018; Novita, 2016). In the current digital era where information accessibility is crucial for promoting equal opportunities, there is an even greater need to elucidate the mechanisms underlying poor reading and reading disability. If we can understand

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these mechanisms at its earlier stages, as in emergent readers, then we will better understand how to prevent reading disability.

### 1.1. Development of reading skills and when it goes awry

Reading is the act of recognizing language in print that is necessary for comprehension of a text, which is the construction of a representation of the text's meaning (Oakhill et al., 2019). The Simple View of Reading is one of the most well-researched models of children's reading comprehension (Savage et al., 2015). It posits that reading is the product of decoding (the ability to convert graphemes into phonemes) and linguistic comprehension (the processing and comprehension of orally presented information) (Gough and Tunmer, 1986; Kendeou et al., 2009). Reading disability occurs when a person has difficulties in one or both of these cognitive abilities (Sleeman et al., 2022).

As acknowledged by the Simple View of Reading and others, reading disability is a multifactorial disorder in nature (Surushkina et al., 2021), and many skills and abilities have been examined to predict reading ability. Auditory language processing is a significant predictor of reading proficiency, beginning in infancy; infants' brain responses to speech sounds predicted their pre-reading skills prior to the start of school (Guttorm et al., 2010). Another study found phonological awareness and neurophysiological responses to speech sounds in preschoolers predicted reading one year later (Hong et al., 2018). Phonological awareness, which involves the metalinguistic ability to divide oral language into smaller components such as syllables and phonemes, has been heavily investigated in relation to reading (Byrne et al., 2008; Landi et al., 2010; O'Brien and Yeatman, 2021; Protopapas, 2013). Before children are formally taught to read, individual variation in phonological awareness accessed through behavioral measures—such as the ability to identify, reflect upon, segment, and blend sounds within spoken words—strongly predicted later reading success (Bradley and Bryant, 1983; Catts et al., 2002; Scarborough, 1998; Stanovich et al., 1984; Torgesen et al., 1999b). Language skills have also been implicated in reading ability (Duff et al., 2015; Nation and Snowling, 2004; Snowling and Melby-Lervåg, 2016); poor reading in early elementary school was predicted by oral language skills in preschool, including listening comprehension (Kendeou et al., 2009). "Poor reader" is a term commonly used to include people who may not have the diagnosis of reading disability but, on the spectrum of participants, are comparatively "low-performing" in reading.

### 1.2. Neuroimaging in the study of reading

Neuroimaging has been critical to understanding where in the brain reading occurs. Longstanding frameworks of reading posit two circuits: 1) a temporoparietal circuit involved in the integration of phonological and lexical-semantic aspects, which includes primarily the posterior superior temporal gyrus (pSTG), middle temporal gyrus (MTG), supramarginal gyrus, and angular gyrus; and 2) an occipitotemporal circuit that develops later and is thought to implement word identification and orthography, including the inferior temporal gyrus (ITG), lingual gyrus, and fusiform gyrus, where a subsection is known as the visual word form area (VWFA) (Binder, 2015; Dehaene and Cohen, 2011; Kearns et al., 2019; McCandliss et al., 2003; Price and Devlin, 2011; Pugh et al., 2001). Common to both circuits is a third system, in which the inferior frontal gyrus (IFG) is thought to be involved in phonological processing, speech planning, lexical access, semantics, and comprehension (Ozernov-Palchik and Gaab, 2016; Price, 2012). In pre-reading and young children, recruitment of IFG has been associated with better reading performance (Frost et al., 2009; Jasińska et al., 2021; Preston et al., 2016; Shankweiler et al., 2008).

There is a developmental trajectory with young children first relying on the IFG and temporoparietal circuit bilaterally, and then later showing more left lateralization (Turkeltaub et al., 2003; Yamada et al., 2011). The occipitotemporal-circuit-dependent orthographic processing

then emerges, coinciding with a decrease in the temporoparietal-circuit-based phonological processing (Black et al., 2017; Pugh et al., 2010; Schlaggar and McCandliss, 2007; Wise Younger et al., 2017). It is unsurprising then that children show higher activation compared to adults in the left pSTG, while adults show higher activation in the occipitotemporal region (Martin et al., 2015).

In children and adults, fMRI research on the neurocognitive origins of atypical reading, i.e., reading disability, has identified aberrant response patterns during reading and reading-related tasks in the aforementioned circuits in those with reading disability or poor reading skills (see Bolger et al., 2008; Cao et al., 2006; Desroches et al., 2010; Marks et al., 2019; Martin et al., 2016; Paz-Alonso et al., 2018; van Ermingen-Marbach et al., 2013; Pugh et al., 2013 for a review and Richlan et al., 2009, 2011 for meta-analyses). For example, Yamada et al. (2011) found 5-year-old children behind in pre-literacy skills did not show left-lateralized IFG/temporoparietal activations during a reading-related task. Meanwhile, a longitudinal study of 2.5 years found 8- to 14-year-old children who were strong readers recruited areas in the two circuits as a coherent network, whereas in poor readers the circuits were independently functioning nodes (Smith et al., 2018).

Neuroimaging has also been relied on to understand the brain's response to reading interventions. Many studies showed that poor readers who were responsive to the interventions (i.e., improved reading performance) exhibited "normalization" of their activation patterns. In other words, they generated brain activation patterns, specifically involving the reading circuitry, similar to that of the typical readers (Aylward et al., 2003; Bach et al., 2013; Heim et al., 2015; Meyler et al., 2008; Odegard et al., 2008; Richards et al., 2007; Richards et al., 2006, 2017, 2018; Shaywitz et al., 2004; Simos et al., 2002, 2007; Temple and Snow, 2003). A recent review found the left STG, left inferior parietal lobe, left ventral occipitotemporal cortex, and left IFG were particularly influenced by intervention (Perdue et al., 2022).

In some studies, the responsive poor readers recruited additional brain regions not traditionally associated with reading, such as anterior cingulate cortex (ACC) and precuneus (Meyler et al., 2008; Nugiel et al., 2019; Partanen et al., 2019; Shaywitz et al., 2004; Temple et al., 2003). These findings support the idea of compensatory mechanisms in the brains of poor readers after interventions as they may be recruiting different networks in an attempt to perform similarly to typical readers. The theory of compensation has been similarly applied to studies without interventions; Hancock et al. (2017) performed a meta-analysis of studies with and without interventions and found overlap between fronto-striatal hyperactivation patterns in poor readers (bilateral caudate, left pre/postcentral gyrus, left IFG) and regions supporting articulation, aligning with the proposed compensatory role of these areas for phonological processing.

### 1.3. Naturalistic stimuli

Recognizing that single-word or nonword reading tasks in the scanner are not fully representative of natural reading, experimenters have begun to introduce paradigms using naturalistic stimuli (Finn et al., 2020; Vanderwal et al., 2015; Hasson et al., 2008). Naturalistic connected text reading recruits a more expansive set of networks than single-word reading paradigms, thus explaining why some children may not struggle with single-word reading initially but later develop difficulty fluently reading connected text (Foorman et al., 2016; Smith and Ryan, 2020; Wallot et al., 2013). More specifically, there are areas activated only by connected text reading and not by single-word reading, such as the bilateral temporoparietal junction, bilateral temporal poles, and posterior cingulate cortex (Gernsbacher and Kaschak, 2003; Price, 2012; Speer et al., 2009; St. George et al., 1999; Whitney et al., 2009; Yarkoni et al., 2008).

The question then arises of how to use naturalistic stimuli with children just starting formal reading education, because they are either very limited or cannot read connected text yet at all. Listening to stories

has been proposed as an option considering oral language skills and phonological awareness are both predictors and key components of reading (Bradley and Bryant, 1983; Catts et al., 2002; Scarborough, 1998; Stanovich et al., 1984; Torgesen et al., 1999b). Additionally, previous neuroimaging studies of emergent readers at risk for familial dyslexia found differences in the left temporoparietal brain regions (for review, see Vandermosten et al., 2016; Raschle et al., 2014; Raschle et al., 2012; Specht et al., 2009; Yamada et al., 2011). With the temporoparietal regions' association with phonological processing and awareness, listening in the scanner is a reasonable alternative to reading, which many studies in emergent readers have taken advantage of (Powers et al., 2016; Raschle et al., 2012, 2014; Vandermosten et al., 2020). However, they have yet to use the naturalistic stimuli of listening to stories and instead used single-word and phoneme listening.

Naturalistic stimuli offer a compromise between the other popular options of traditional tasks in the scanner and resting-state acquisitions because naturalistic stimuli maintain ecological validity while still being focused on a predetermined cognitive aspect (e.g. theory of mind and social and emotional processing; Vanderwal et al., 2019). Naturalistic stimuli are therefore versatile enough that multiple approaches for analysis can be used. The general linear model (GLM) approach, most often used with traditional block design tasks, can also be applied to short blocks of naturalistic stimulation and/or particular events within naturalistic stimuli; in the latter case, GLMs allow researchers to attribute activation patterns to specific time-locked events within the stimulus (Finn et al., 2020). However, its sensitivity is limited by the assumptions that it is known which features of a stimulus are driving the activation and that the researchers have modeled these features accurately (Finn et al., 2020).

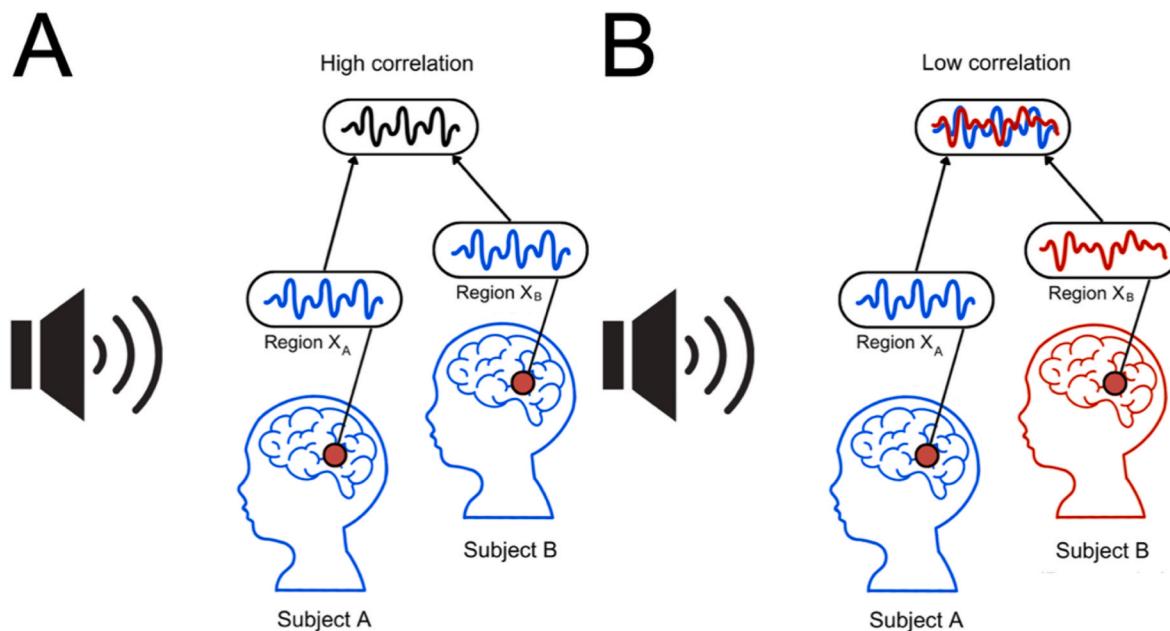
Inter-subject correlation (ISC; Hasson et al., 2004, 2008) was designed specifically to analyze naturalistic stimuli in a way that maximizes sensitivity and reveals more nuanced activation patterns than traditional activation analyses like GLM (Finn et al., 2020). ISC makes fewer assumptions than GLM, as it does not require researchers to model specific events within the stimulus but rather leverages the fact that the stimulus is identically time-locked across subjects (Hasson et al., 2004). This means we can compute the correlation of activation within a given region or even voxel (a spatial location in the brain) between two

subjects (Hasson et al., 2004)—in other words, we can bypass the need for a model of the stimulus itself by using one subject's brain activity as a model for another subject's brain activity. If there is correlated activity in a voxel across subjects, it can be inferred that the region is involved in processing the stimulus. Greater ISC in a region suggests that participants' responses are more synchronized there.

ISC originally focused on shared responses to stimuli (Fig. 1) but recently, researchers have begun to examine group differences in relation to behavioral measures and conditions like autism, depression, and paranoia (Byrge et al., 2015; Finn et al., 2018; Guo et al., 2015; Hasson et al., 2009; Salmi et al., 2013). However, these studies also recognized that most health conditions are better conceptualized on a continuum of severity rather than a (sometimes arbitrarily decided) dichotomy. For example, Byrge et al.'s (2015) post-hoc analyses found their ISC effect (reduced synchrony in the autism group) was driven by five participants with autism, who had markedly idiosyncratic responses; when they were removed, the autism and neurotypical groups were indistinguishable using ISC.

In order to relate brain responses to a behavior or trait on a spectrum, inter-subject representational similarity analysis (IS-RSA) has been proposed, which compares the similarity matrix of brain data to the similarity matrix of behavioral data (Chen et al., 2020; van Baar et al., 2019). Using IS-RSA, Finn et al. (2020) proposed two models of responses: AnnaK and Nearest Neighbors (NN). The AnnaK model posits high-performing participants are similar to other high-performing participants in their brain responses, while those with brain-behavior dysfunction will be more idiosyncratic. In other words, those with brain-behavior dysfunction are less similar to both high performers and others with brain-behavior dysfunction. The NN model assumes that participants with similar behaviors on a scale should be more similar in their brain activation patterns, regardless of their absolute position on the scale.

Naturalistic stimuli have been used to study reading comprehension and fluency; studies have found significant differences between naturalistic (such as connected text) and single-word reading in regions not typically considered specific to reading, such as visual areas (Aboud et al., 2016, 2019; Constable et al., 2004; Desai et al., 2016; Hsu et al., 2019; Ni et al., 2000; Russo et al., 2020; Swett et al., 2013; Wang et al.,



**Fig. 1.** Infographic depicting inter-subject correlation (ISC). ISC is calculated by computing the correlation between the timecourses in the same brain regions across two (or more) participants experiencing the same naturalistic stimuli. **A)** Two subjects whose brain responses are highly correlated, i.e., high ISC **B)** Two subjects whose brain responses have a low correlation, i.e., low ISC.

2015; Wehbe et al., 2021). However, naturalistic studies have yet to explore beyond GLM and employ ISC and IS-RSA when studying reading skill in emergent readers in order to elucidate group and individual differences. Naturalistic stimuli with ISC analysis have only been used to study reading (dis)ability in one other study from our group, a “sister” study, that examined responses to both written and spoken narratives in adolescent participants (Jangraw et al., 2023). ISC was higher in high-performing readers than within the group of low-performing readers in reading-related regions and other widespread regions not typically considered part of the canonical reading circuits.

We can summarize these three analyses and the value they each add as follows: the GLM analyses can detect differences in activation magnitude (*as it fits to a canonical model*) during reading and provide an important set of baseline results to compare to previous studies of reading that often relied on more traditional paradigms. ISC analyses provide more sensitivity than GLMs to detect any stimulus-related activity—i.e., not necessarily only regions that show changes in activation magnitude, but any region that shows a time-locked response during reading (regardless of the shape of that response), including group effects. Finally, IS-RSA is an extension of the ISC framework that can detect any region where the shape of the response is modulated by reading ability.

#### 1.4. Current study

Given the knowledge that brain responses develop and change over time as children learn how to read, this study sought to examine the relationship between early-reading skills and the neural response while listening to stories in the scanner. The study used ISC and IS-RSA to investigate group (stronger vs weaker reading-related skills) and individual differences, respectively. Similar to findings by Jangraw et al. (2023), we hypothesized that those with stronger skills would be more synchronized with one another in canonical reading areas. We use IS-RSA to further refine these relationships as this approach has been used to successfully examine synchronous patterns with naturalistic stimuli in studies of working memory (Finn et al., 2020) and reading (Jangraw et al., 2023). Since our study examines emergent reading skills based on scored cognitive tests, we predicted the AnnaK model would better fit our data; the poorer the participant’s reading skills, the more idiosyncratic (i.e., distinctive) the responses, relative to other participants. With these models, the relationship between brain similarity and behavioral similarity during naturalistic stimulation can be defined and applied to clinical conditions that exist on a phenotype spectrum, including reading disability. Where Jangraw et al. (2023) examined adolescents, our study is the first to use these methods to study reading in young children just beginning formal reading education.

## 2. Materials & methods

### 2.1. Participants

This dataset is a subset of a larger, longitudinal data collection effort with several imaging tasks and behavioral measures, collected at the Yale School of Medicine. Study recruitment aimed to collect a representative community sample, with diverse reading backgrounds. Recruitment was not focused on children with a diagnosis of dyslexia or reading disability since diagnosis is difficult at this age. Only data from subjects who completed the story task and both behavioral measures described later were included in the analysis. IQ was tested using WASI II and WPPSI IV (Wechsler, 2011, 2012), and those with an IQ one standard deviation below the mean were not included in the study. Using these criteria, 34 monolingual, English-speaking pre- and early-reading children participated in this study (19 females, 15 males) with a mean age of 6.69 years (SD = 0.32, range = 6.04–7.22). Twenty-five participants were Caucasian/White, four were African American, one was multiracial, and four were of mixed/unknown race.

A parent or guardian provided written consent, while children were asked to give verbal assent.

### 2.2. Behavioral data measures

Participants were assessed using multiple behavioral measures of early-reading and reading-related skills, targeted towards phonological awareness and reading fluency: Woodcock Johnson 3 (WJ3) Letter-Word ID and Word Attack subtests, and Test of Word Reading Efficiency (TOWRE) Sight Word Efficiency and Pseudowords subtests (Torgesen et al., 1999a; Woodcock et al., 2001). Raw scores were transformed to standard scores with Woodcock Johnson  $\bar{x} = 0$ ;  $\sigma = 15$  and TOWRE  $\bar{x} = 0$ ;  $\sigma = 15$ . A principal component analysis (PCA) was used to collapse the four standard scores on the reading skills tests into one latent component measure for reading (e.g., Pugh et al., 2013; Jangraw et al., 2023). For fMRI activation and ISC analyses, participants were then divided by median split of the composite PCA score; participants above the median were classified as “high-performing,” while those below were classified as “low-performing” individuals.

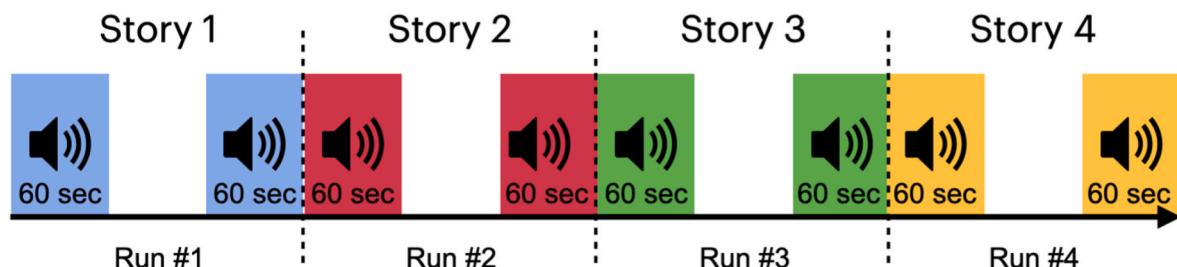
### 2.3. Design and procedures

Participants completed at least one mock scan to practice staying still during their fMRI sessions. To further ensure the quality of fMRI data, a research assistant was with the participant in the MRI scanning room to make sure the participant was comfortable and to let them know if they were moving too much in the scanner. Participants were asked to visually fixate on a white cross in the middle of the screen, while they listened to a pre-recorded professional narrator read, in a continuous stream for 60 seconds, part of four children’s fable stories: “The Cat and The Mouse” by Joseph Jacobs, “The Fox and the Cat” by Grimm Brothers, “The Otters and the Wolf” by Ellen C. Babbitt, and “Stone Soup” author unknown. Each run (story) had two blocks (120 seconds of story, split into two 60-second segments, with a rest in between of 60 seconds, see Fig. 2 for visualization). There was a comprehension check after each story to ensure the participant was engaged with the story; all participants scored 100% on these comprehension checks. The speed of the speech was approximately 3 words per second. Stories and blocks were not randomized, making whole-run ISC analysis possible since it is necessary for stimuli to be presented in the same order.

### 2.4. fMRI parameters & preprocessing

Functional MRI data were collected using a Siemens TIM-Trio 3 T MRI system at the Yale School of Medicine in New Haven, Connecticut, with a 12-channel head coil. T1-weighted MPRAGE structural images were acquired with the following parameters: matrix size =  $256 \times 256$ ; voxel size =  $1 \times 1 \times 1$  mm; FoV = 256 mm; TR = 2530 ms; TE = 3.66 ms; flip angle =  $7^\circ$ . These were followed by gradient echo-planar image (EPI) functional scans with the following parameters: 32 slices; 4 mm slice thickness; no gap, matrix size =  $64 \times 64$ ; voxel size =  $3.4375 \times 3.4375 \times 4$  mm; FoV = 220 mm; TR = 2000 ms; TE = 30 ms; flip angle =  $80^\circ$ .

The first six volumes in each run were discarded to allow the scanner to reach steady state, and data were preprocessed in AFNI (Cox, 1996). Preprocessing steps included despiking, correction for slice-timing acquisition, motion correction, alignment of EPI to anatomical image, transformations to MNI-space, blurring at 6 mm full-width half maximum, and rescaling to percent BOLD signal change. Six motion parameters, and their derivatives, were regressed out of the final signal (3dTproject). Freesurfer’s reconstruction pipeline was used to produce two-dimensional cortical segmentation maps (Fischl, 2012). Repetition times (TRs) with excessive motion ( $>3$  mm, frame-wise Euclidean norm) or outliers ( $>10\%$  of voxels) were censored (14.8% on average, no significant differences between groups ( $t[30.92] = -1.018, p = 0.3166$ )). We used nuisance regression to minimize contributions of nuisance



**Fig. 2.** Stimulus paradigm design. Four runs were presented with short breaks (60 seconds) between each run (denoted by dotted vertical lines). Each run consisted of a unique story, split into two 60-second “blocks” with a 60-second rest in the middle.

parameters (motion, motion derivatives, first three principal components of activity found in the ventricles) in BOLD timecourses. AFNI’s ANATICOR (Jo et al., 2010) was used to regress out regional white matter signals.

### 2.5. Activation analysis

Although this experiment was designed for ISC, we also conducted a traditional block-activation analysis to serve as a standard point of comparison. We used a boxcar regressor with an amplitude of 1 and convolved with the hemodynamic response function (HRF) to create statistical maps of activation corresponding to the task of listening to stories. Group averages were calculated for the high- and low-performing groups and statistically compared with each other and with zero, using AFNI’s 3dttest++ function.

### 2.6. Inter-subject correlation analysis

Following preprocessing, subjects were paired and ISC was calculated for each pair (Supplemental Fig. 1). ISC is based on finding the correlation between voxel-wise timecourses in each distinct pair of subjects; we used AFNI’s 3dTcorrelate function to calculate the Pearson correlation of each subject’s timecourse in a voxel with the same voxel’s timecourses in every other subject. During the correlation, censored time points were set to zero instead of removing them from analyses in order to preserve the temporal structure across participants; if a participant had a TR with a censored timepoint, it was skipped in both participants’ timecourses for purposes of calculating an unbiased correlation. Group-difference measures in ISC were calculated and tested for significance using the AFNI program 3dISC; this program reads every paired correlation map and employs a linear mixed-effects (LME) model with a crossed random-effects formulation to account for the correlation structure embedded in the ISC data (Chen et al., 2017) and can be related to a statistical model formulation (e.g., group analysis, covariate analysis). As would be done with standard GLM analyses, statistical maps were thresholded at  $p < 0.002$  and separated into contiguous clusters (a stringent threshold was used to guard against false positives in cluster correction, as in (Finn et al., 2018)). Cluster thresholds to control for family-wise error were calculated using AFNI’s 3dClustSim command based on the spatial smoothness of the data (estimated by 3dFWHMx) with a mixed-model spatial auto-correlation function (ACF; Cox, 2019). This function found that clusters of  $>22.7$  voxels could be considered significant at a level of  $\alpha < 0.05$ . Group-difference measures were investigated as ISC relies on pairs of subjects and therefore lends itself to group comparison (Finn et al., 2020). Additionally, previous reading studies examined group differences between high-performing and low-performing readers, allowing the comparison of this study’s results to previous findings (Preston et al., 2016; Richlan et al., 2011; Ryherd et al., 2018; Shankweiler et al., 2008; Yamada et al., 2011).

### 2.7. IS-RSA analysis

We performed a dimensional analysis, using the IS-RSA approach described by Finn et al. (2020) to examine the relationship between ISC (a measure per subject pair) and behavior (a measure per subject); IS-RSA allows us to examine participants on a spectrum rather than in groups, which is a more accurate way to represent reading skill, as it exists on a continuum. Two pairwise similarity matrices were constructed for a given region of interest (ROI): one for behavioral scores and one for neural activation. We then calculated a Spearman rank correlation between the unique (i.e., upper triangular) elements of the behavioral matrix and the same values in the ISC matrix. A high correlation indicates the behavioral model was an acceptable predictor for the observed ISC in that region. All the ROIs in the Shen Atlas, a 268-region parcellation of the whole brain (cerebellum and brainstem), were tested (Shen et al., 2013).

For significance testing, a null distribution was produced by permuting the rows and columns of the behavioral similarity matrix 10,000 times and recomputing the RSA correlation value for each ROI. This creates a null distribution of correlation coefficients where the behavioral similarity score’s structure remains constant but is based on meaningless values rather than the participant’s actual reading scores. The  $p$  value was calculated as the fraction of correlation coefficients in the null distribution whose magnitude exceeded that of the true correlation coefficient value. These  $p$ -values were calculated for all ROIs, then corrected for multiple comparisons using false discovery rate (FDR) correction. The AnnaK model and NN model were investigated for the behavioral similarity matrix. In the AnnaK model, the predicted synchronization is quantified as the mean reading score of the two participants, so a positive representation similarity  $r$  value indicates more consistency among high-performing participants and more variability in low-performing participants. Importantly, the same model is equally capable of testing for effects in the opposite direction (i.e., more consistency among low-performing participants and more variability among high-performing participants), which would be indicated by a significantly negative  $r$  value.

In the NN model, the predicted synchronization is quantified as the negative of the absolute difference between two participant’s reading scores. In other words, to measure behavioral similarity, Euclidean distance is used, which assumes that subjects with closer behavioral scores should be more similar to one another, regardless of their absolute position on the scale. The NN  $r$  value indicates the extent to which readers of a similar ability—regardless of whether that ability is high or low—also show similarity in their brain activity timecourses during reading. For example, if there was a stereotyped response among poor readers and a different but equally stereotyped response among good readers, the NN model would detect that. In contrast, the AnnaK model will detect cases where there is a stereotyped response only at one end of the spectrum, with more idiosyncrasy (less stereotypicality) at the other end.

### 3. Results

#### 3.1. Behavioral metrics

Participants completed the WJ3 Letter-Word ID and Word Attack subtests, as well as the TOWRE's Sight Word Efficiency and Pseudowords subtest (Distributions in Fig. 3, mean and standard deviation values in Table 1). These four tests were synthesized into one latent component using PCA, accounting for 91% of the variance. Each measure loaded approximately equally (standardized loadings: 0.48, 0.51, 0.50, 0.50). Component values had a median of 0.15 (min = -3.7 and max = 4.3). Participants were split into a high-performing ( $N = 17$ ; 5 males and 12 females) and a low-performing ( $N = 17$ ; 10 males and 7 females) group based on median split (Fig. 4). As expected, two-sample t-tests between the high- and low-performing groups were significant for all four assessments ( $p < 0.01$ ).

#### 3.2. Activation results

Group fMRI activation averages for the high- and low-performing groups showed activation common among naturalistic tasks using a rest baseline (Jangraw et al., 2023), FDR  $q = 0.0018$ , shown in Supplemental Fig. 2. Standard block analysis found no regions of the brain responded significantly differently between the high- and low-performing groups.

#### 3.3. Inter-subject correlation results

In addition to significant ISC findings across all subjects during story listening (Fig. 5a), ISC analysis found regions that were differently synchronized between high-performing and low-performing participants, unlike standard block analysis. Responses were more synchronous across high-performing participants in the left MTG, right MTG, left STG, and right temporal pole (Fig. 5b). However, low-performing participants had increased ISC in bilateral pSTG recruitment (Fig. 5b). Of note, the MTG and STG are considered part of the temporoparietal reading circuit that integrates phonological and lexical-semantic aspects, and it is the first circuit young readers rely on before developing the occipitotemporal reading circuit (Dehaene and Cohen, 2011; McCandliss et al., 2003; Price and Devlin, 2011; Pugh et al., 2001; Turkeltaub et al., 2003; Yamada et al., 2011). To further show these differences, we plotted the timecourse of each significant ROI for both BOLD and ISC, split by group (Fig. 6). The BOLD signal increases during story listening and decreases during rest across all six ROIs (Fig. 6). For

**Table 1**  
Participant performance on reading tasks.

Task	Mean	Standard Deviation
WJ3 Letter-Word ID	112.9	10.4
WJ3 Word Attack	113.9	13.0
TOWRE Sight Word Efficiency	108.5	15.0
TOWRE Pseudoword	107.4	14.1

Mean and standard deviations for participants' behavioral scores.

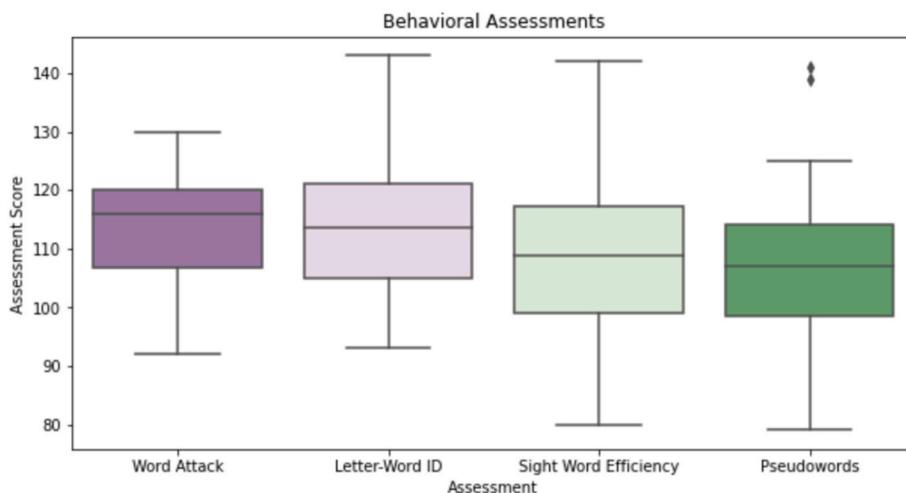
ISC, we generally see an increase in synchrony in both groups as the task progresses; the level of synchrony differs between the high- and low-performing groups' ISCs during listening (Fig. 6).

#### 3.4. Continuous brain-behavior relationships

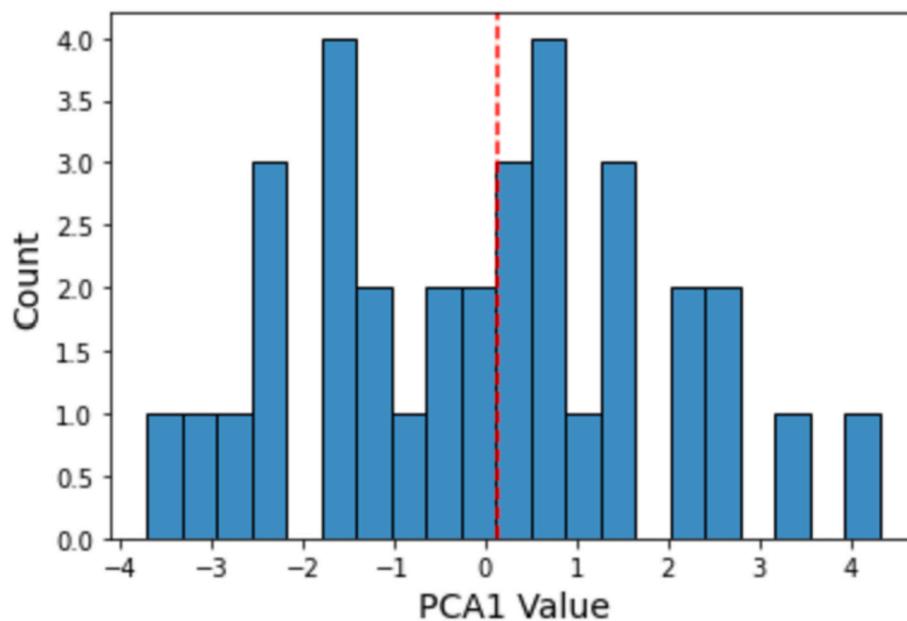
To test the hypothesis of idiosyncratic responses with a dimensional analysis, IS-RSA was used with two possible models: AnnaK model (Fig. 7) and NN model (Fig. 8). Recall that the AnnaK model asserts that low-performing participants have idiosyncratic neural responses, whereas the NN model posits that participants with similar behaviors are similar in their neural responses regardless of their absolute position on the scale (Methods). The AnnaK model produced eight significant ROIs at an FDR-corrected  $q < 0.05$  (Fig. 7b and Supplemental Table 1), including the left IFG, regions of the temporoparietal circuit (bilateral MTG), and regions of the occipitotemporal circuit (left ITG, fusiform gyrus). The NN model produced two significant ROIs (Fig. 8b and Supplemental Table 1): the left ITG and the right SFG, a frontal region previously associated with reading ability (Schmithorst et al., 2007). Note, the cluster size of the ROIs reported in Supplemental Table 1 interacts with the Shen atlas, hence the uniform cluster size.

### 4. Discussion

Our study aimed to investigate the relationship between emergent reading skills and the brain response to listening to stories in the scanner. To do this, we were the first study to use ISC and IS-RSA to investigate group (high- versus low-performing) and individual differences, respectively. With participants median-split into high- and low-performing groups based on reading skills, no significant differences were found between the groups with block design analysis. However, ISC analyses identified differences in synchrony within regions associated with the temporoparietal circuit and the right temporal pole that distinguished between high- and low-performing participants' responses to the stimuli (Figs. 5 and 6). IS-RSA using the AnnaK model revealed



**Fig. 3.** Box-and-whisker plot of behavioral scores across all subjects on Woodcock Johnson 3 (WJ3) Word Attack and Letter-Word ID subtests, and Test of Word Reading Efficiency (TOWRE) Sight Word Efficiency and Pseudowords subtests.



**Fig. 4.** Histogram plot of principal component (PCA1) values across all subjects, with median PCA1 value displayed (red dashed line). Subjects with PCA1 value below the median are denoted as “low performers” and those above as “high performers.”

several regions where variability in response increased as reading ability decreased (Fig. 7b). Using the NN model, right SFG and left ITG were recruited by all participants to some degree, but their specific time-course of activation depended on their reading performance (Fig. 8b).

When examining ISC across all participants listening to stories, we see synchrony in the recruitment of the temporoparietal and occipitotemporal circuit regions, such as STG and ITG, respectively (Fig. 5a). However, when comparing high- and low-performing participants, we find significant differences in regions related to reading, specifically areas in the temporoparietal circuit. In short, while participants were broadly similar in their recruitment of reading circuitry, there were nuanced, yet significant, differences in the temporoparietal circuit. High-performing participants were more synchronous in bilateral MTG and left STG recruitment (Fig. 5b). For the MTG, this aligns with previously discussed single-word reading research showing bilateral engagement of the temporoparietal circuit in pre-readers (Yamada et al., 2011). Bilateral MTG was also found to be significant in the AnnaK model in our study, elucidating a possible mechanism for decreased synchrony in the low-performing participants due to their idiosyncratic responses. The STG is a speech-processing region that helps extract phonemes (Seghier et al., 2010). Given the STG’s proposed function, its increased synchrony in high-versus low-performing participants is consistent with the theory that phonological processing deficits are key to the neural basis of reading disability.

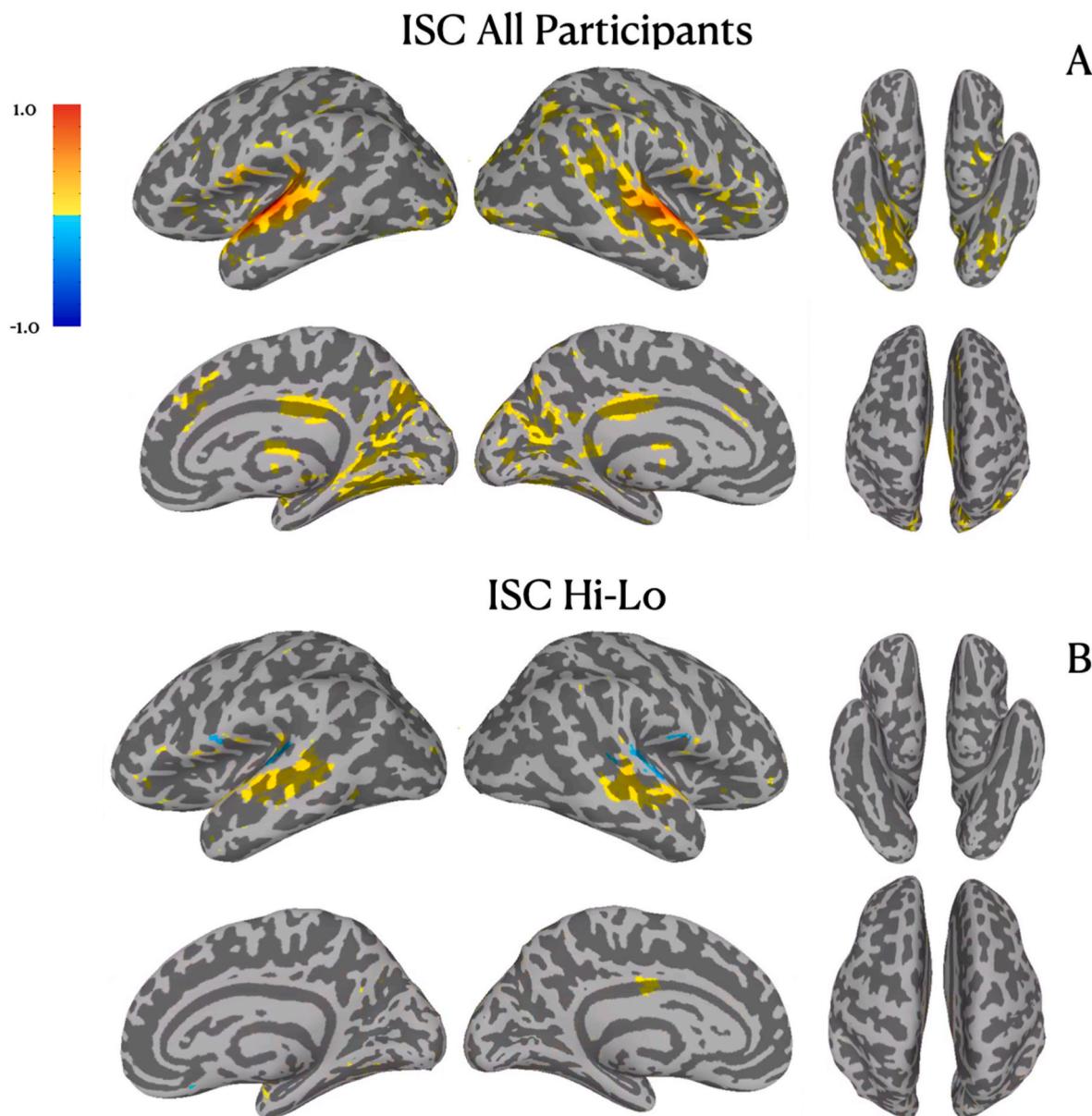
Low-performing readers in our study were more synchronous than high-performing readers in their recruitment of the right and left pSTG (Fig. 5). The pSTG’s important role in reading has previously been defined as perceptual processing of phonological representations (Price, 2012). Recruitment of right analogs of reading-related regions, including pSTG, has been previously proposed as a compensatory mechanism in dyslexic children who undergo interventions (Barquiero et al., 2014). Our results interestingly support the idea that even in the early stages of reading acquisition, those struggling with reading may be compensating, or at least similarly recruiting, an area associated with phonological processing. Alternatively, our findings are also consistent with previous work that found low-performing pre-readers recruit the temporoparietal circuit bilaterally (Yamada et al., 2011). Taking into consideration our finding that the high-performing participants were more synchronous in the left STG, it is possible that high-performing emergent readers are appropriately left-lateralizing, whereas

low-performing emergent readers struggle with left-hemispheric lateralization (Turkeltaub et al., 2003; Yamada et al., 2011).

In both our study and our sister study, there were no significant differences in activation patterns between stronger and poorer readers, but there were significant differences in inter-subject synchrony (Jangraw et al., 2023). Jangraw et al. (2023) found increased ISC among good readers in other reading-circuit areas aside from STG and MTG (including the left angular gyrus, left supramarginal gyrus, and left inferior temporal cortex), as well as the right-hemisphere analogs of these same regions; no increased ISC was observed amongst poor readers. Our findings, along with Jangraw et al. (2023), support the idea that ISC is more sensitive to group differences in processing naturalistic designs than traditional block design analysis (at least with its current regressors), as ISC allows stimulus-locked analyses with comparatively fewer assumptions (Finn et al., 2020).

The increased sensitivity of ISC to group differences has not been as thoroughly investigated, but several studies have used two-group ISC analysis to investigate group differences (Hasson et al., 2009; Salmi et al., 2013; Byrge et al., 2015; Finn et al., 2018; Gruskin and Patel, 2022). When examining the ROI timecourses of BOLD activity in our study (Fig. 6), we see similar patterns between the two groups, but when we use one participant’s brain activity as a model for another’s, we find ISC differences between groups. Interestingly, we also saw increased ISC among high-performing participants immediately after the stimuli, during rest (Fig. 6). While also seen in Jangraw et al. (2023), it is possible high-performing subjects were similarly recruiting areas to further process or comprehend what they heard. We also acknowledge that GLM analysis is sub-optimal for our experimental design (each run consisted of only 120 seconds of stimuli), but a previous study found this is not true when the situation is reversed; when using a conventional design for GLM, ISC and GLMs produced similar results (Pajula et al., 2012).

Significant findings using the AnnaK model included several areas related to reading (left IFG, left ITG, bilateral MTG, right lingual gyrus) (Fig. 7b). The IFG has been implicated in storing information about the sounds that words contain (Richlan et al., 2011). Meanwhile, the left ITG is a part of the occipitotemporal circuit and is important in processing sight words and meanings, along with letter and word recognition (Kearns et al., 2019). The lingual gyrus, also a part of the occipitotemporal circuit, plays a role in word and object naming; a meta-analysis

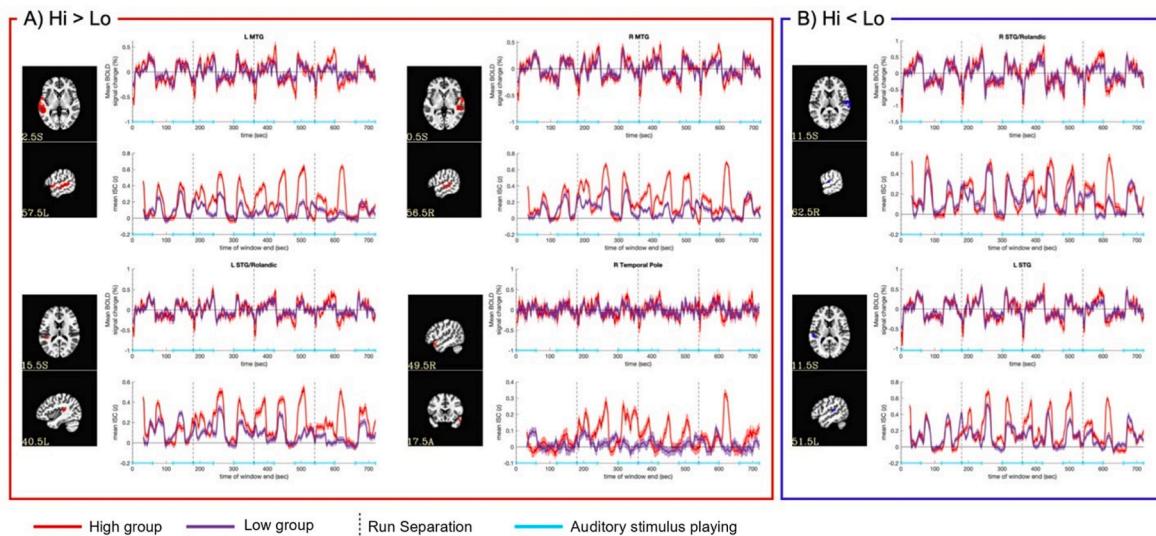


**Fig. 5.** ISC results with the inter-subject correlation of all subjects shown top (A) and the two-group ISC results for the contrast of high- minus low-performing participants shown bottom (B). Specific to the group contrast, yellow-colored regions indicate higher ISC in the high-performing group, and blue-shaded regions show more ISC in the low-performing group. Results shown  $p < 0.002$ ,  $\alpha < 0.05$ .

concluded that there was increased activation of the right lingual gyrus in dyslexic children and adults compared to those without dyslexia (Eckert et al., 2005; Pollack et al., 2015). When comparing ISC between groups, key areas of the temporoparietal circuit—the STG and MTG—were identified as areas of difference, but IS-RSA reveals that differences can be seen in areas associated with the occipitotemporal circuit as well, which previous work has suggested develops later in adolescence (Wise Younger et al., 2017). Our IS-RSA findings support then that high-performing emergent readers may already be clustering together in their recruitment of these areas. Meanwhile, moving down the spectrum towards low-performing, responses in both the temporoparietal and occipitotemporal circuits are increasingly idiosyncratic.

The AnnaK model also had significant IS-RSA results with three areas not traditionally implicated in reading (left precuneus, right medial temporal pole, and left middle cingulate cortex) (Fig. 7b). The precuneus, a part of the default mode network (DMN), has been associated with orthographic coding of word-specific spellings underlying reading

during middle childhood and early adolescence (Richards et al., 2006, 2017). The precuneus, along with the cingulate cortex, which was also significant in the AnnaK model, are a part of the posterior DMN that is involved with visuo-spatial imagery (Dadario and Sughrue, 2023); children towards the higher end of the reading ability spectrum may be similarly recruiting these areas to visualize the words they are hearing. Another study found increased functional connectivity between the precuneus and multiple reading-related areas in dyslexic adolescents and young adults (Schurz et al., 2015). Areas classically associated with social and emotional processing, the temporal pole and cingulate cortex, were also found to be significant in the AnnaK model (Olson et al., 2007; Rolls, 2019). Interestingly, the right temporal pole was found to have increased ISC in the high-performing group in our study; the AnnaK model then gives us insight into a potential reason why—the low-performing participants are idiosyncratic in their responses in this region, leading to a lower magnitude of synchrony. Further research is required to confirm and clarify these new regions' roles in supporting



**Fig. 6.** Timecourse results for significant ROIs in ISC related to reading where **a)** high-performing subjects demonstrated increased ISC compared to the low-performing group, and **b)** low-performing subjects demonstrated increased ISC compared to the high-performing group. For each ROI, the top panel depicts mean BOLD signal (scaled to percent signal change). The bottom panel shows the 30-second moving average of ISC. For both timecourses, the high group is shown in red, and the low group is shown in purple, each with the standard error of the mean. On the x-axis for each figure, the stimulus-on time is shown in light blue and the run separations are demarcated by a vertical dashed line.

reading ability during narratives.

Meanwhile, the NN model revealed that right SFG and left ITG were recruited by all participants but with differential patterns of activation over time (Fig. 8b). SFG has demonstrated connections to Broca's area within IFG (Schmithorst et al., 2007); ITG, a part of the occipitotemporal circuit, is implicated in semantic processing (Kearns et al., 2019). Left ITG was also significant in the AnnaK model but in a different area of ITG (see center of mass in *Supplemental Table 1* and Figs. 7b and 8b). In Jangraw et al. (2023), no areas of significance were found with the NN model. Instead, SFG and ITG had increased ISC in high-performing readers compared to low-performing readers with group ISC analysis. Combined with the current study's results, SFG and ITG may be susceptible to dysfunction as a child ages. We propose that all the emergent readers recruit right SFG and left ITG to some extent during the narratives, but that high- and low-performing readers have divergent timecourses of that recruitment. Adding in Jangraw's et al. (2023) findings, as high-performing readers become more proficient and automatic in their reading, their use of common circuitry becomes increasingly instantiated. Meanwhile, as low-performing readers age, their areas of overlap disappear and idiosyncratic responses predominate. This is further supported by our study finding areas of increased ISC amongst low-performing readers, whereas our sister study found no significant areas in low-performing teenagers but many significant areas with the AnnaK model and none with the NN model. Overall, our IS-RSA results further refine and support the ISC findings, as IS-RSA examines participants on a spectrum rather than in groups, which is more representative of neurodevelopmental conditions like learning disabilities.

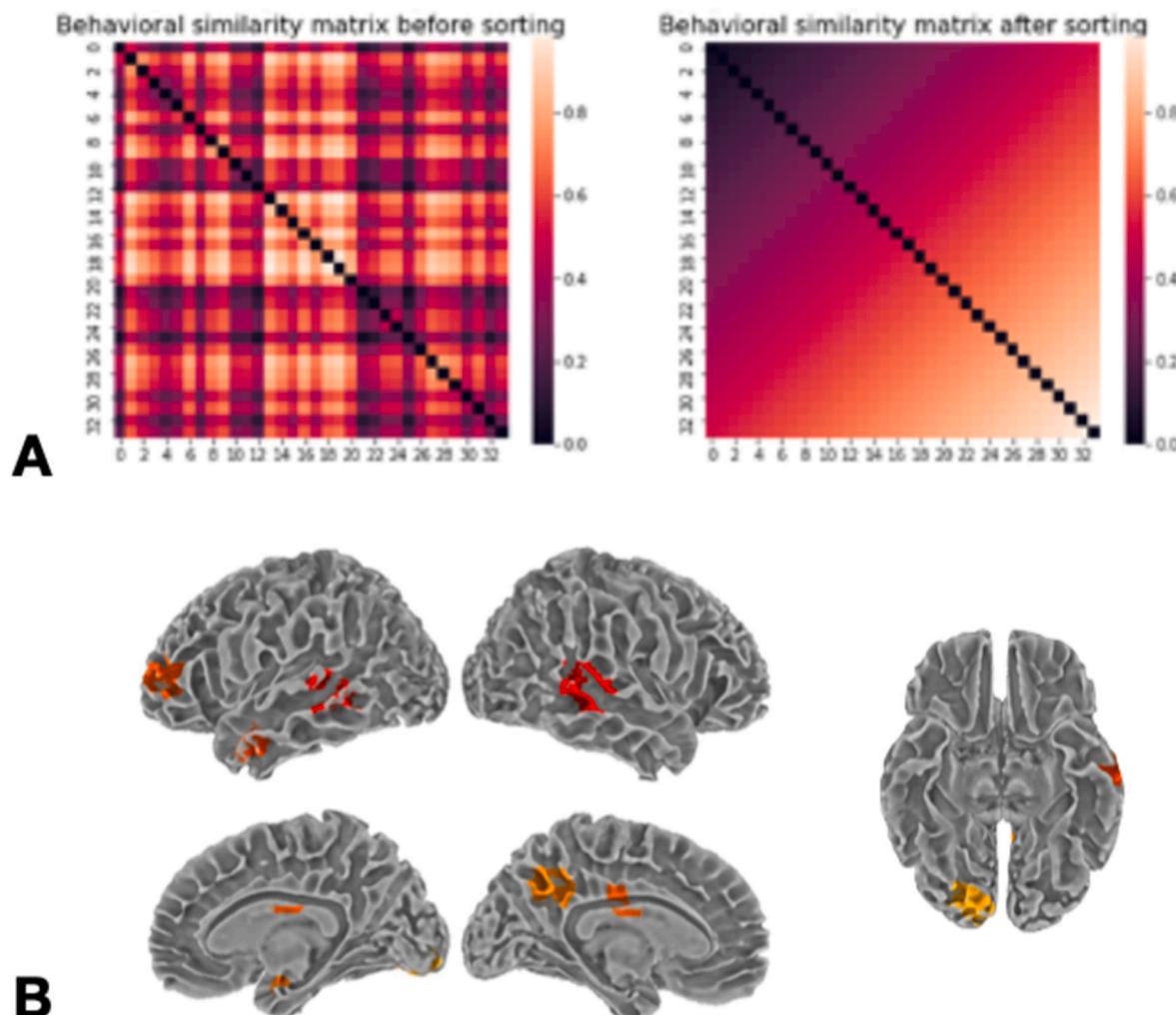
To address the often-cited ecological validity issue associated with traditional fMRI paradigms, the neuroimaging field is turning to naturalistic stimuli. To our knowledge, our study is the first to use naturalistic stimuli to study reading in emergent readers, allowing us to examine children entering formal reading education and solidifying their oral language and phonological processing skills, both of which are key components of reading ability (Kendeou et al., 2009; O'Brien and Yeatman, 2021). Using ISC, we found group differences in processing naturalistic story listening and, interestingly, areas of increased ISC in both high- and low-performing participants.

IS-RSA takes naturalistic stimuli analysis one step further by examining participants on a continuum—a more realistic representation of

reading abilities. The AnnaK and NN models give us a way to model the relationship between reading ability and brain features, allowing us the possibility to predict reading based on brain patterns and to better understand how poor readers' brains are different from strong readers. Interestingly, our findings support that brain patterns during listening do not fit only one of these two models, unlike our sister study with teenage readers which only found significant areas using the AnnaK model (Jangraw et al., 2023). In emergent readers, moving down the continuum of reading ability, we found some brain regions are recruited increasingly idiosyncratically whereas other regions are recruited by all but with divergent timecourses.

In terms of limitations, this study involved a small sample size of 34 children. All studies investigating reading also face the issue that a limited behavioral assessment (e.g., TOWRE assessment, Woodcock-Johnson III) is used to represent aspects of early reading fluency, which we tried to mitigate by using PCA to synthesize multiple assessments (see Pugh et al., 2013; Jangraw et al., 2023 for similar approaches). Participants' performance on these assessments also exhibited the "Connecticut Effect" of above average performance, with few participants in the below average range. This phenomenon is thought to be due to the higher economic wealth of the state (Kanazawa, 2006; Pfost et al., 2014). This limits our ability to apply our findings to readers objectively below the national average. Additionally, the use of median split to divide participants into high- and low-performing readers limits application to a clinical population. However, IS-RSA allowed us to examine participants' reading ability on a continuum rather than artificial, discrete groups. Finally, the similarities and differences highlighted between this paper and Jangraw et al. (2023) showcase a need to further develop pediatric versions of atlases like Shen et al. (2013) to reduce the deformation distances when normalizing between pediatric participants and a given template (Molfese et al., 2021).

In the future, this style of naturalistic paradigm and analyses can be used to compare, in groups and on a spectrum, participants with diagnosed reading disability and those without. This study also exemplifies the rich results IS-RSA can yield with naturalistic stimuli, which should continue to be used to study reading disability as well as other neurological conditions. Extending IS-RSA to a predictive framework, using the AnnaK and NN model to predict reading ability of an individual, is



**Fig. 7.** a) Visualization of ideal fit for AnnaK model, using example data, where the left matrix shows theoretical subjects randomly ordered along both rows and columns, and each cell (where the row and column intersect) reflects the theoretical correlation between the two subjects' timecourses of a given brain region; the colorbar is the correlation. For AnnaK, after sorting theoretical subjects by their behavioral score from high to low along the x-axis and low to high on the y-axis, we see the matrix on the right where similarity increases as one moves down and to the right (in other words, brain response similarity increases as performance increases.) b) In our study, after correcting for multiple comparisons in the AnnaK model, bilateral MTG, left IFG, left ITG, left precuneus, left middle cingulate cortex, right lingual gyrus, and right medial temporal pole had significant positive correlations between brain and behavioral similarity matrices ( $q < 0.05$ ).

also a natural next step. The data used in this study will be shared on an open repository for others to use and replicate analyses.

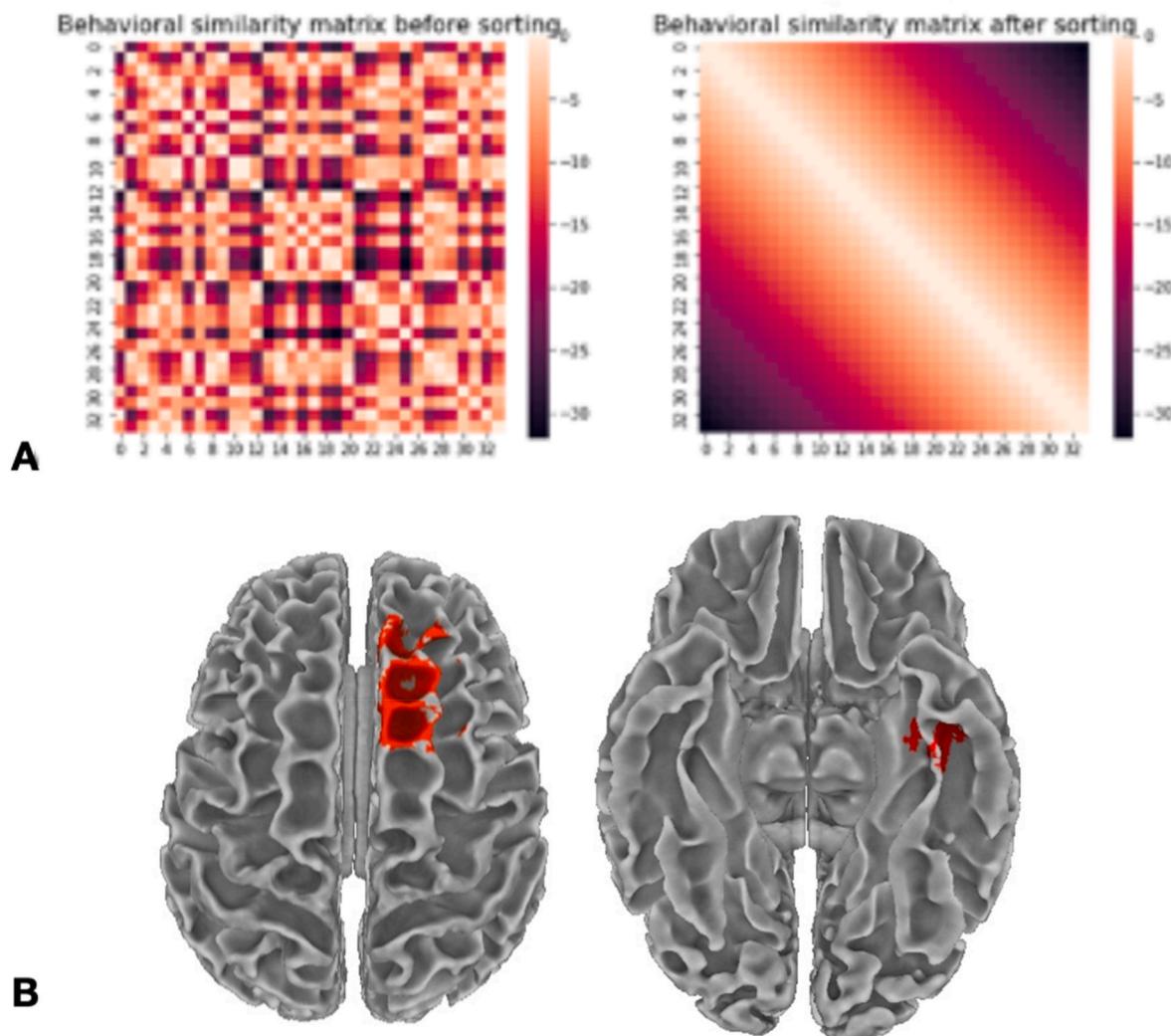
## 5. Conclusion

Our study further elaborated on developmental findings of reading with high-performing readers exhibiting increased ISC while listening to stories in bilateral and left-hemisphere temporoparietal circuit regions (MTG and STG, respectively) important for phonological processing (Kearns et al., 2019; Seghier et al., 2010). We also found increased ISC in low-performing readers in bilateral pSTG, which could either represent compensation or struggles to left-lateralize. In conjunction with our sister study (Jangraw et al., 2023), we see these areas of synchrony amongst low-performing readers disappear as they age, and more regions become idiosyncratic and fit the AnnaK model. For emergent readers, brain regions associated with reading fit both the AnnaK and NN model; the AnnaK model revealed high-performing readers may already be clustering together in occipitotemporal areas, which previously have been found to emerge at approximately 10–12 years of age (Shaywitz et al., 2002). Other brain regions, right SFG and left ITG, follow the NN model and are recruited by all emergent readers to some

extent, but at later ages, brain regions have only been found to fit the AnnaK model (Jangraw et al., 2023), underscoring the dynamic nature of learning to read.

## CRediT authorship contribution statement

**Elizabeth K. Wat:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **David C. Jangraw:** Conceptualization, Formal analysis, Visualization, Writing - review & editing. **Emily S. Finn:** Conceptualization, Methodology, Writing - review & editing. **Peter A. Bandettini:** Funding acquisition, Resources, Writing - review & editing. **Jonathan L. Preston:** Conceptualization, Investigation, Writing - review & editing. **Nicole Landi:** Conceptualization, Investigation, Writing - review & editing. **Fumiko Hoeft:** Writing - original draft, Writing - review & editing. **Stephen J. Frost:** Conceptualization, Data curation, Investigation, Methodology, Project administration, Writing - original draft, Writing - review & editing. **Airey Lau:** Data curation, Investigation, Project administration, Writing - review & editing, Visualization. **Gang Chen:** Methodology, Writing - review & editing. **Kenneth R. Pugh:** Conceptualization, Funding acquisition, Investigation, Resources, Supervision, Writing -



**Fig. 8.** a) Visualization of ideal fit for NN model, using example data, where the left matrix shows theoretical subjects randomly ordered along both rows and columns, and each cell (where the row and column intersect) reflects the theoretical correlation between the two subjects' timecourses of a given brain region; the colorbar is the correlation. For NN, after sorting theoretical subjects by their behavioral score from high to low along the x-axis and low to high on the y-axis, we see the matrix on the right with its diagonal structure, where each subject is more similar to their immediate neighbor. b) In our study, after correcting for multiple comparisons in the NN model, the right SFG and left ITG had significant positive correlations between brain and behavioral similarity matrices ( $q < 0.05$ ).

review & editing. **Peter J. Molfese:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing.

#### Data availability

Data will be made available on request. Visit <https://github.com/pmolfese/Wat2023> for information.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuropsychologia.2023.108763>.

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