

Resting State Networks in Individuals with and without Reading Disorders

by

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## Abstract

**Objective:** Reading is a complex behaviour requiring the connectivity of numerous brain regions. Resting state functional magnetic resonance imaging (rsfMRI) has recently been used to examine the differences in reading networks in skilled adult readers and skilled and impaired child readers. Such work has shown that the inferior frontal gyrus is a critical region for reading whereby this region shows differences in connectivity to other brain regions between impaired and skilled child readers, and acts as a hub in skilled adult readers. In the current study, rsfMRI was used to examine the neural connectivity of the print-to-speech network and to assess the brain-behaviour relationships that exist within this network in both skilled and impaired adult readers. **Method:** Brain imaging data (i.e., rsfMRI) and behavioural data (i.e., Tests of Word Reading Efficiency) was collected for individuals with (N = 11) and without (N = 7) reading impairments. **Hypothesis:** The print-to-speech network in impaired adult readers will show reduced connections to the supramarginal gyrus and to the inferior temporal gyrus, when compared to skilled readers. Additionally, brain-behaviour relationships are anticipated between activity in the inferior frontal gyrus and real word reading scores and between supramarginal gyrus activity and nonword reading scores for both groups. **Results:** Impaired adult readers showed reduced connectivity between the supramarginal gyrus and the precentral gyrus, and between the inferior temporal gyrus and inferior frontal gyrus, when the supramarginal gyrus and inferior temporal gyrus were selected as seed regions, respectively. Additionally, there were no significant relationships between neural activity and behavioural reading scores. **Conclusion:** These results support the print-to-speech model, as they demonstrated the connectivity between all regions of interest as defined by the model. Additionally, these results help to strengthen the model by showing that the connectivity within the reading network differs between impaired and

skilled readers.

## **Preface**

This thesis is an original work by Dana Grandmont. No part of this thesis has been previously published.

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## Introduction

Reading is an essential skill for everyday functioning, especially for adults. Throughout the day, we are bombarded by written information that requires deciphering in order to smoothly navigate the world around us. For example, being able to read the instructions on a medicine bottle, a recipe, the newspaper, a thank you card, a text message, or a work email are easily accomplished by most adults. However, for those with reading difficulties, these daily activities can be very challenging. Given the substantial impact that a reading disorder may have on an individual's life, it is important to investigate the underlying characteristics of this impairment, so that successful therapy and/or prevention programs can be developed. In this vein, recent work has pointed to a universal reading network that includes regions involved in both print decoding and speech production (Cummine et al., 2016). Here, we expand on this previous work to explore the functional connectivity associated with the *print-to-speech network* using resting state functional magnetic resonance imaging (rsfMRI) in adults with and without reading impairments.

## Speech Production and Reading: The DIVA Model

The print-to-speech network described by Cummine et al. (2016) builds on the previously established *Directions Into Velocities of Articulators (DIVA)* model of speech production (Guenther, 2006; Guenther, Ghosh, & Tourville, 2006; Guenther & Vladusich, 2012; Tourville & Guenther, 2011). The DIVA model of speech production, developed and redefined overtime by Guenther and colleagues, (Guenther, 2006; Guenther et al., 2006; Guenther & Vladusich, 2012; Tourville & Guenther, 2011), outlines a feedforward and a feedback system. The feedback system contains two subsystems: an auditory subsystem (with connections between the auditory cortex, premotor and motor cortices to encode auditory speech targets and resolve auditory errors) and a somatosensory subsystem (with connections between the somatosensory cortex and the premotor and motor cortices to encode speech sound targets and resolve somatosensory errors) (Guenther, 2006; Guenther et al., 2006; Guenther & Vladusich, 2012; Tourville & Guenther, 2011). The feedback system is active during learning and when auditory and somatosensory targets are detected as errors. In contrast, the feedforward system has connections from the premotor cortex to the motor cortex (and some additional connections to the cerebellum) and is active once motor targets for speech production have been learned and practiced multiple times (Guenther, 2006; Guenther et al., 2006; Guenther & Vladusich, 2012;

Tourville & Guenther, 2011). For example, if a child is producing the word ‘mom,’ the feedforward system is engaged as the motor sequence required to produce /m/o/m/ has been learned and practiced on multiple occasions. In contrast, if the child is producing a novel word such as ‘mot,’ the feedback system is engaged, because a new motor sequence must be created, based on information from previous productions of the individual sounds within the word. The auditory and somatosensory feedback subsystems are required to monitor, and correct errors made during speech production.

The print-to-speech model was based on the DIVA model of speech production as it has been shown that speech production and reading activate similar brain areas (Cummine et al., 2016; see also Price, 2012 for a review of brain regions involved in reading and speech production). To accommodate for reading, the print-to-speech model included the inferior temporal gyrus, as this area is responsible for visual/orthographic processing (Cummine et al., 2016). By having individuals read familiar (e.g., feedforward reliant) and unfamiliar (e.g., feedback reliant) words, Cummine et al. (2016) demonstrated how the print-to-speech network connections were modulated as a function of the reliance on feedforward and feedback mechanisms. The proposed print-to-speech network expanded the DIVA model in two key ways: inclusion of a neuroanatomical region to accommodate visual input (i.e., letters/words) and the description and demonstration of the relationships between regions within the network. Each of these are described in further detail below.

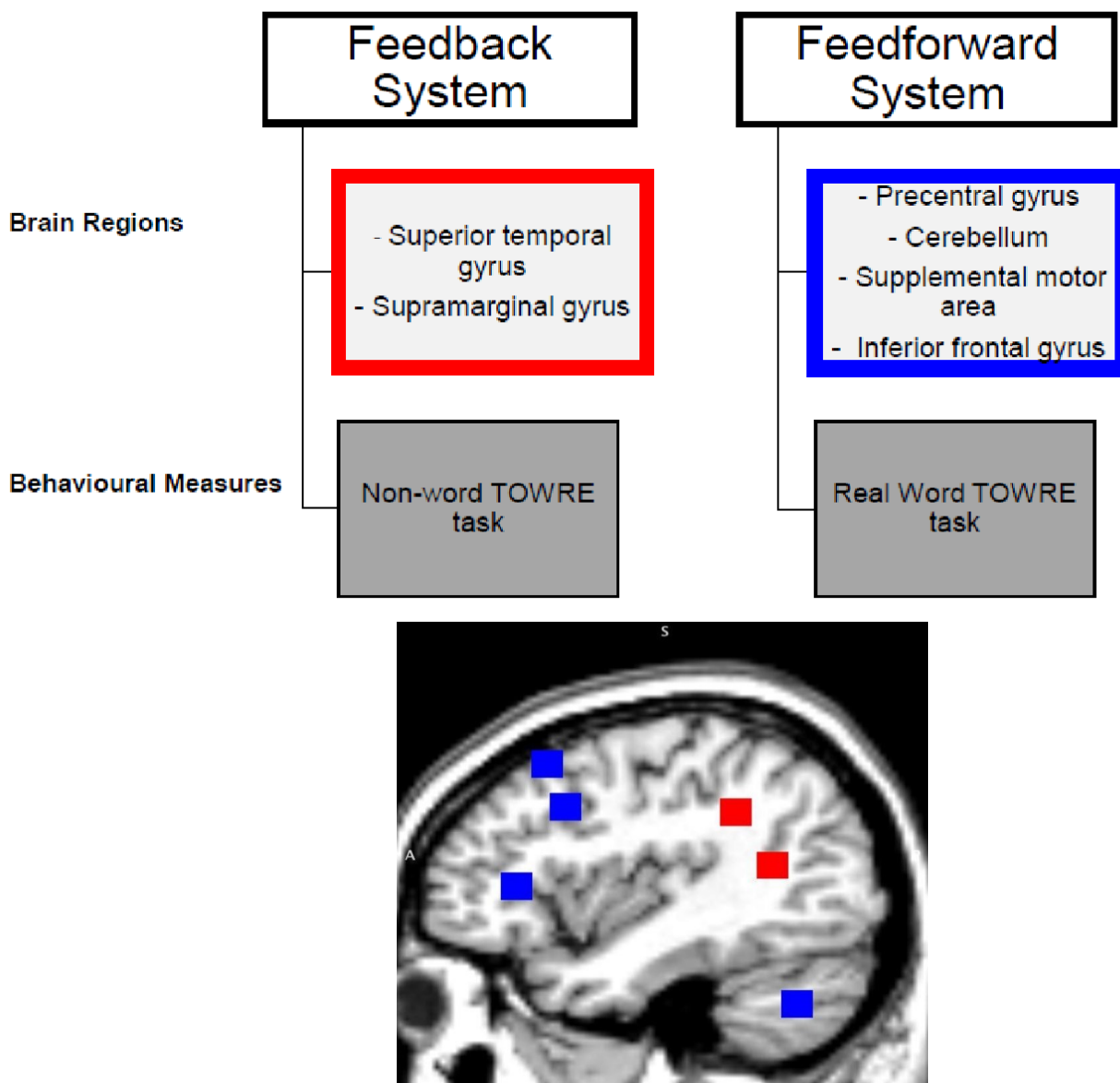
### **The Print-to-Speech Network**

Investigation into the brain areas involved in reading and speech production have been extensive (See Price, 2012, for a review). Several brain regions are reliably active during speech production and reading, thus contributing to the notion of a universal reading network (see Figure 1; Guenther, 2006; Guenther et al., 2006; Guenther & Vladusich, 2012; Tourville & Guenther, 2011). These regions include the cerebellum (articulation involvement), superior temporal gyrus (STG; speech perception), supramarginal gyrus (SMG; somatosensory feedback; phonological decoding), precentral gyrus (PCG; motor output), supplementary motor area (SMA; articulatory planning/sequencing), the inferior frontal gyrus (IFG; speech-sound map), and the inferior temporal gyrus (ITG; orthographic decoding). Extensive work using task-dependent functional magnetic resonance imaging (fMRI) has been conducted to further describe the role

that each of these regions plays in skilled (Price, 2012) and impaired reading (Richlan, Kronbichler, & Wimmer, 2009).

### ***Task-Based Functional Connectivity.***

The dynamic nature of the print-to-speech network was recently investigated by Cummine and colleagues (Cummine et al., 2016). They concluded that, all regions identified within the network were active while skilled adult readers completed word reading tasks, however functional connections [defined by (van den Heuvel & Hulshoff Pol, 2010), as: "...the temporal dependency of neuronal activation patterns of anatomically separated brain regions" (p. 520)] between these regions were task dependent. For example, when participants were required to silently read familiar words, the neural reading network observed was consistent with a feedforward mechanism, which included a significant relationship between activity in the SMA and inferior frontal gyrus (Cummine et al., 2016). In contrast, when participants were required to silently read unfamiliar words (i.e., *non-words*), a pattern of functional connectivity consistent with a feedback mechanism was present, which included stronger connections to phonological areas (superior temporal gyrus, supramarginal gyrus), along with a significant relationship between the supramarginal gyrus and precentral gyrus (Cummine et al., 2016). To summarize, although the real word and non-word tasks activated the same brain regions, differences in connectivity between the regions reflected reliance on feedforward and feedback mechanisms, respectively.



*Figure 1.* Print-to-Speech Network divided by system, accompanied by brain regions and behavioural measures associated with each individual system.

Notably, while task-based functional connectivity has been useful in establishing the framework of the print-to-speech network, and the dynamic nature of the connections in the network as a function of familiar vs. unfamiliar word reading, there also is merit in exploring the

connectivity of the print-to-speech network during task-independent functional neuroimaging, namely, resting state functional connectivity (RSFC). RSFC is a favourable approach to studying neural connections because it is efficient, and can be performed on clinical populations who, for some reason or another, may be unable to perform tasks within the scanner (Damoiseaux et al., 2006). The ability to gather information about brain function during a resting condition also allows for a more direct comparison between populations who may otherwise appear different as they are not able to perform equivalent tasks (i.e., children versus adults).

### ***Task-Independent Functional Connectivity.***

RSFC involves an examination of low frequency fluctuations (<0.1 Hz) in the blood-oxygen-level-dependent (BOLD) signal while a participant is resting, typically with their eyes open in the scanner for 5-7 minutes (Koyama et al., 2010). Functional connectivity, which describes the relationships between brain signal in various regions of interest, is established by the concurrent activation of low frequency BOLD signals. Several resting state networks have been well defined and studied including, the motor network (Fox & Raichle, 2007), visual processing network (Cordes et al., 2000) and most notably, the default mode network (van den Heuvel & Hulshoff Pol, 2010). Relevant to the present study is the language network, which includes the inferior frontal gyrus, middle frontal gyrus, supramarginal gyrus, planum temporale, temporoparietal junction, superior temporal gyrus and inferior parietal cortex, as well as areas of the basal ganglia and thalamus (Tomasi & Volkow, 2012).

### ***RSFC and the Reading Network.***

Resting state fMRI has been employed to investigate neural reading networks in three populations of readers (see Table 1 for a summary): skilled adults (Koyama et al., 2010, 2011; Zhao et al., 2011), children with typical reading, and children with reading impairments (Horowitz-Kraus, DiFrancesco, Kay, Wang, & Holland, 2015; Horowitz-Kraus, Toro-Serey, & DiFrancesco, 2015; Koyama et al., 2013; Murdaugh, Maximo, & Kana, 2015; Richards et al., 2015; Schurz et al., 2015; Zhou, Xia, Bi, & Shu, 2015). There is evidence for consistency between the neural reading areas active during task-based imaging (Cummine et al., 2016) and the regions in the reading resting state network (Koyama et al., 2010). To date however, there has been no examination of the neural reading network in adults with reading impairments using resting state fMRI. One objective of the present study is to fill this gap.

Koyama and colleagues (2010), gathered information via resting state fMRI and extracted a functional connectivity network for reading. Connections between six regions in the brain related to word reading were of interest [based on meta analyses, see: (Bolger, Perfetti, & Schneider, 2005; Turkeltaub, Eden, Jones, & Zeffiro, 2002)]: fusiform gyrus (orthography), superior temporal gyrus (speech perception), temporoparietal junction (grapheme-morpheme conversion), precentral gyrus (M1), inferior frontal gyrus (speech production), and inferior occipital gyrus (object recognition). From these ROI's a hub, which is a brain area with the most functional connections to other areas (van den Heuvel & Sporns, 2013), was identified, namely, the inferior frontal gyrus. The activation of five reading areas (the inferior occipital was found to be not connected) and the identification of the inferior frontal gyrus as a neural hub for of the reading network, is consistent with the task-based functional connectivity findings reported by Cummine et al. (2016) for the print-to-speech network. Additional support for the inferior frontal gyrus being a key area, especially in regards to connectivity with areas in the inferior temporal gyrus (orthographic decoding), come from number of studies examining both adults (Koyama et al., 2011; Zhao et al., 2011), and children (Murdaugh et al., 2015; Schurz et al., 2015), stating that reduced connectivity between these areas is related to poorer reading skills.

### ***RSFC and Brain-Behaviour Relationships.***

In addition to displaying differences in connectivity between skilled and impaired readers, previous research findings show changes in connectivity within neural reading networks following intervention (Horowitz-Kraus, DiFrancesco, et al., 2015; Horowitz-Kraus, Toro-Serey, et al., 2015; Murdaugh et al., 2015). For example, children with autism spectrum disorder and a reading impairment, who participated in a 10-week intensive reading intervention program, showed stronger connectivity within the neural reading network following therapy (Murdaugh et al., 2015). Similarly, children with reading impairments, who were otherwise typically developing, displayed stronger connectivity in the fronto-parietal and cingulo-opercular network after a 4-week intervention (Horowitz-Kraus, Toro-Serey, et al., 2015). Stronger connections within the fronto-parietal network equated to more proficient reading abilities (Horowitz-Kraus, Toro-Serey, et al., 2015; Koyama et al., 2013). Moreover, after participating in the same 4-week intervention, typical readers showed reduced connectivity between visual processing and language components, indicative of the proficiency that comes with becoming a better reader

(Horowitz-Kraus, DiFrancesco, et al., 2015). In line with these findings, Hampson et al., (2006), reported a brain-behaviour relationship with respect to the connectivity between Broca's area and the angular gyrus in healthy adult readers. More specifically, the greater the connectivity between the regions, the stronger their reading ability (Hampson et al., 2006). Similarly, Koyama et al., (2011) reported stronger connections between motor regions and Wernicke's (STG) (and Broca's (IFG)) area are representative of more proficient readers across all ages. Together, this work demonstrates that RSFC of the reading network can provide information about the dynamics and sensitivity of the neural structure to reading ability.

### ***The skilled versus impaired reading network***

Numerous studies have shown a difference in RSFC amongst children who are skilled readers and children with reading impairments (Horowitz-Kraus, DiFrancesco, et al., 2015; Horowitz-Kraus, Toro-Serey, et al., 2015; Koyama et al., 2013; Murdaugh et al., 2015; Richards et al., 2015; Schurz et al., 2015; Zhou et al., 2015). Of particular importance, are the connections with the inferior frontal gyrus in the network of children with reading impairments (Schurz et al., 2015). The inferior frontal gyrus has been deemed a hub for both real and non-word reading (Cummine et al., 2016; Koyama et al., 2010), therefore, a weak connection between the inferior frontal gyrus and the rest of the network may negatively impact learning new words and accessing previously established high frequency words. Additionally, children regardless of skill have been shown to have activation in the same reading areas but the extent to which these areas showed functional connectivity differed between skilled and impaired readers (i.e., stronger connections between reading areas were associated with higher reading scores) (Zhou et al., 2015). Again, these findings are in line with the task-based connectivity studies that report comparable activation of all regions, with the differences lying in the connectivity between the regions.

### **Summary**

Much of the research conducted thus far on resting state reading networks has been focused on children with and without reading impairments (see Table 1). The information gathered from these studies, supplemented by a handful of investigations into reading networks of skilled adults, provides preliminary support with respect to the usefulness of RSFC of the reading network to the advancement of models of reading, namely the print-to-speech network.

However, several pieces of information are still missing from the literature. First and foremost, the RSFC reading networks for adults with reading impairments is critical for enhancing our understanding of the print-to-speech network and to assess the extent to which the networks described in the paediatric population generalize to adults. Moreover, understanding the extent to which behavioural performance is related to the task-independent reading network is important in the further development of the print-to-speech model. More specifically, the print-to-speech model must be able to accommodate both typical and impaired reading processes to be considered a viable framework.

	<b>Adults</b>	<b>Children</b>
<b>Impaired Readers</b>		Koyama et al., 2013 Horowitz-Kraus, Toro-Serey, & DiFrancesco, 2015 Horowitz-Kraus, DiFrancesco, Kay, Wang, & Holland, 2015 Murdaugh, Maximo, & Kana, 2015 Richards et al., 2015 Zhou, Xia, Bi, & Shu, 2015 Schurz et al., 2015
<b>Skilled Readers</b>	Koyama et al., 2010 Koyama et al., 2011 Zhao et al., 2011	Koyama et al., 2011 Koyama et al., 2013 Horowitz-Kraus, Toro-Serey, & DiFrancesco, 2015 Horowitz-Kraus, DiFrancesco, Kay, Wang, & Holland, 2015 Murdaugh, Maximo, & Kana, 2015 Richards et al., 2015 Zhou, Xia, Bi, & Shu, 2015 Schurz et al., 2015

*Table 1.* An overview of the literature to date on resting state fMRI and reading in children and adults.

### **Rationale**

We examined the RSFC of the reading network in skilled and impaired adult readers. The aim of the current study was to advance the print-to-speech network in two ways: (a) to investigate the differences in RSFC neural networks between skilled and impaired adult readers, and (b) to describe the relationship between behavioural reading performance and underlying RSFC neural networks.

Hypothesis 1)



1.1. Individuals with reading impairments will show reduced strength of connectivity between the supramarginal gyrus and all other regions in the reading network, when compared to skilled readers.

1.2. Individuals with reading impairments will show reduced strength of connectivity between the inferior temporal gyrus and all other regions in the reading network, when compared to skilled readers.

#### Hypothesis 2)

2.1. For both skilled and impaired readers, we will see a relationship between real word reading behavioural performance and connectivity in the inferior frontal gyrus.

2.2. For both skilled and impaired readers, we will see a relationship between nonword reading behavioural performance and connectivity in the supramarginal gyrus.

## **Methods**

### ***Participants***

A total of eighteen participants took part in the present study. Of the participants involved, seven (6 male; 6 right-handed) were skilled adult readers, ranging in age from 19 to 26 ( $M=21.86$ ,  $SD=2.85$ ) and eleven (2 male; 9 right-handed) were impaired adult readers, ranging in age from 18 to 27 ( $M= 22.27$ ,  $SD=3.20$ ). All participants had English as their first language, and normal or corrected-to-normal vision. Inclusion in the skilled reader group required, a score of lower than .30 on an adult reading history questionnaire (Deacon, Cook, & Parrila, 2012), indicating no evidence of reading impairments. Inclusion in the impaired reader group required, a score at or above .45 on the adult reading history questionnaire and scores of at least one standard deviation below the control group on word reading efficiency and phonemic efficiency (Torgesen, Wagner, & Rashotte, 1999). Consent was obtained prior to participation in the study in accordance with the Declaration of Helsinki (2013, <http://www.wma.net/en/10home/index.html>) and the experiment was performed in compliance with the relevant laws and institutional guidelines and was approved by the host University Health Research Ethics Board. All participants were paid an honorarium.

### ***Behavioural Task Parameters***

The behavioural data collected included measures of real word and nonword reading performance via the Test of Word Reading Efficiency (TOWRE) (Torgesen et al., 1999). The TOWRE required participants to read one list of 104 real words and one list of 63 non-words. Each list was read one word at a time and 45 seconds were allotted per list. The task was then scored for speed (length of time to complete the task) and accuracy (number of errors made).

### ***Resting State Sequence***

High resolution anatomical scans included an axial T1 MPRAGE sequence with the following parameters: TR = 2000ms, TE = 4.38ms, number of slices = 112, base resolution 256 x 256, voxel size 1x1x1mm, scan time 4:48 minutes. The resting state functional images included 200 volumes collected with the following parameters; TR = 1970ms, TE = 30ms, number of slices = 36, base resolution 64 x 64, voxel size 4 x 4 x 4, scan time approximately 6.5 mins.

### **Analysis**

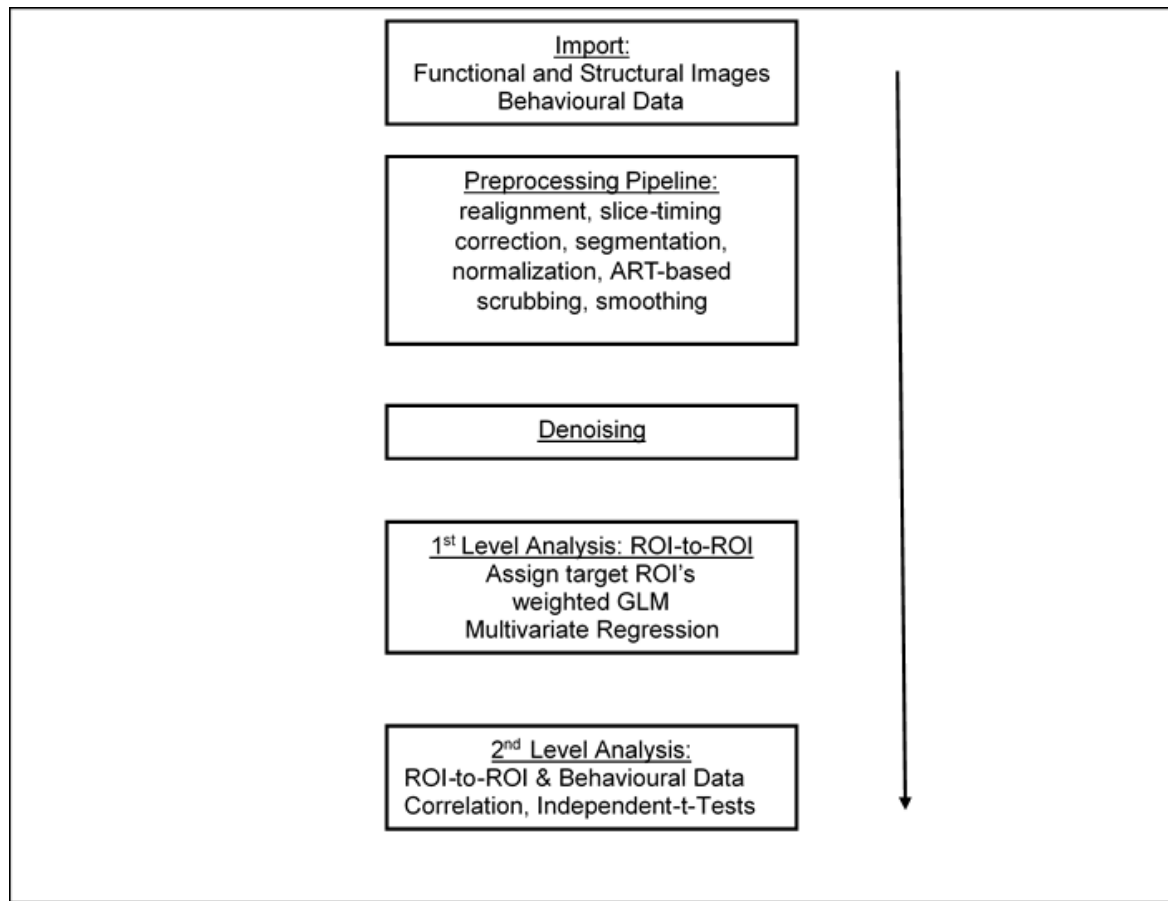


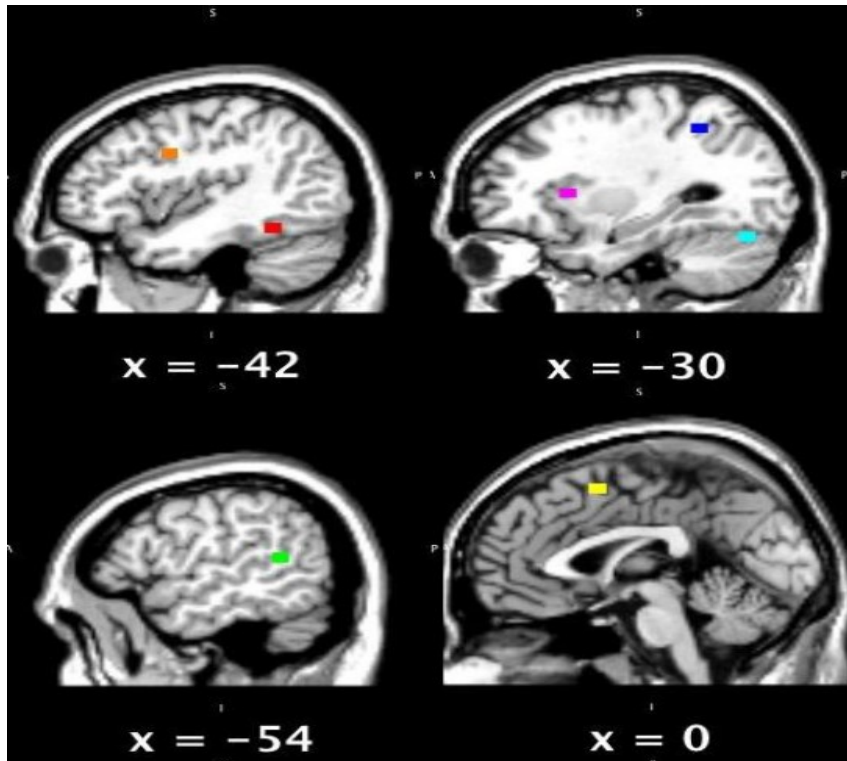
Figure 2. Analysis steps for images and behavioural data within CONN-*functional connectivity SPM toolbox*.

### **Imaging**

The first five volumes from each participant were excluded from analysis as they were used to gather a steady state of image contrast. All remaining images were run through the CONN-*functional connectivity SPM toolbox* (see Figure 2.; Whitfield-Gabrieli & Nieto-Castanon, 2012). After uploading structural and functional images for each participant, the default preprocessing pipeline was implemented using SPM8. The preprocessing pipeline included: functional realignment and unwarp, functional slice-timing correction, structural segmentation and normalization, functional normalization, functional outlier detection (ART-based scrubbing) and functional smoothing. Following preprocessing, de-noising was completed to remove ‘motion artifacts, physiological and other artifact effects from the fMRI p. 4 (Muehlhan, Kirschbaum, Wittchen, & Alexander, 2015).’ De-noising included the component-based correction method and temporal bandpass filtering of [0.008 0.09] Hz.

First level ROI-to-ROI analyses, was done using multivariate regression in a weighted

general linear model (GLM) to determine functional connectivity between 6 ROIs ('defined from Talairach atlas Brodmann areas' (Whitfield-Gabrieli & Nieto-Castanon, 2012)). ROIs included: left posterior inferior temporal gyrus, left posterior superior temporal gyrus, left anterior supramarginal gyrus, left inferior frontal gyrus (pars opercularis), left cerebellum (3,4,5), left precentral gyrus, left supplementary motor area (See Figure 3.). This step involved functional connectivity being computed between ROIs (Whitfield-Gabrieli & Nieto-Castanon, 2012).



*Figure 3.* ROIs included in first level analysis: left posterior inferior temporal gyrus (red), left posterior superior temporal gyrus (green), left anterior supramarginal gyrus (dark blue), left inferior frontal gyrus (pars opercularis) (purple), left cerebellum (3,4,5) (light blue), left precentral gyrus (orange), and left supplementary motor area (yellow).

Behavioural variables were added for each participant, including: real word and nonword percent correct/time and real word(accuracy) and nonword words attempted/time(speed) based on the participant's TOWRE performance. These measures were used during second level analysis.

In second level analysis, we performed four separate analysis:

### ***Between Group Analyses***

1.1. An independent samples *t*-test was run to test the connectivity differences between the supramarginal gyrus and the other six ROIs across impaired and skilled readers.

1.2. An independent samples *t*-test was run to test the connectivity differences between the inferior temporal gyrus and the other six ROIs across impaired and skilled readers.

### ***Within Group Analyses***

2.1. A Pearson's *r* correlation was run to test the relationship between real word reading and connectivity in the inferior frontal gyrus.

2.2. A Pearson's *r* correlation was run to test the relationship between nonword reading and connectivity in the supramarginal gyrus.

## **Results**

### ***Behavioural Measures***

The TOWRE task was scored based on accuracy and completion time. From that we calculated measures of percentage correct over time for real words and nonwords in both groups (percent correct/time). Additionally, we calculated the number of words each participant attempted to read, in the real word and nonword conditions, divided by time (number of words attempted/time). From these values, we compared skilled and impaired scores to determine group differences (*Table 2. and Table 3.*)

	<b>Skilled Readers (N=7)</b>		<b>Impaired Readers (N=11)</b>	
	<b>M</b>	<b>SD</b>	<b>M</b>	<b>SD</b>
<b>Nonwords: Percentage correct/Time</b>	2.1820	0.20643	1.8282	.23592
<b>Real words: Percentage correct/Time</b>	2.3031	.12322	2.2041	0.2722
<b>Nonwords: Words attempted/Time</b>	1.4163	.11689	.9658	.23307

<b>Real words:</b>	2.3297	.23884	1.6971	.36097
<b>Words attempted/Time</b>				

Note. M=Mean. SD=Standard Deviation.

*Table 2.* Means and standard deviations of TOWRE task behavioural measures, for skilled and impaired readers.

	<i>t</i>	<i>Df</i>	<i>p</i>
<b>Nonwords:</b>	3.248	16	.005**
<b>Percentage correct/Time</b>			
<b>Real words:</b>	2.095	6.375	.078
<b>Percentage correct/Time*</b>			
<b>Nonwords:</b>	4.713	16	.000**
<b>Words attempted/Time</b>			
<b>Real words:</b>	4.08	16	.001**
<b>Words attempted/Time</b>			

\*Levene's test  $p < 0.05$ , equal variances not assumed.

\*\*  $p < 0.05$ , two-tailed.

*Table 3.* Independent samples *t*-tests demonstrating between group differences on the TOWRE task.

### ***Imaging***

Only significant results will be reported in this section (uncorrected and FDR-corrected) (See appendix for a full list of results).

#### ***Hypothesis 1.1.***

Independent samples *t*-tests were run to test the connectivity differences between skilled and impaired readers, with the supramarginal gyrus (SMG) as the seed region. The tests examined differences between groups when examining connectivity between the supramarginal gyrus and the other six ROIs. There was a statistically significant difference between groups in connectivity between the supramarginal gyrus and the precentral gyrus ( $t = 3.00$ ,  $df = 16$ ,  $p_{\text{unc}} = 0.008$ , two-tailed) [(beta=0.13 (skilled), beta=0.02 (impaired))] (See Figure 2.). This result was approaching significance after false discovery rate corrections (FDR) were made ( $t=3.00$ ,  $df = 16$ ,  $p_{\text{FDR}} = 0.059$ , two-tailed).

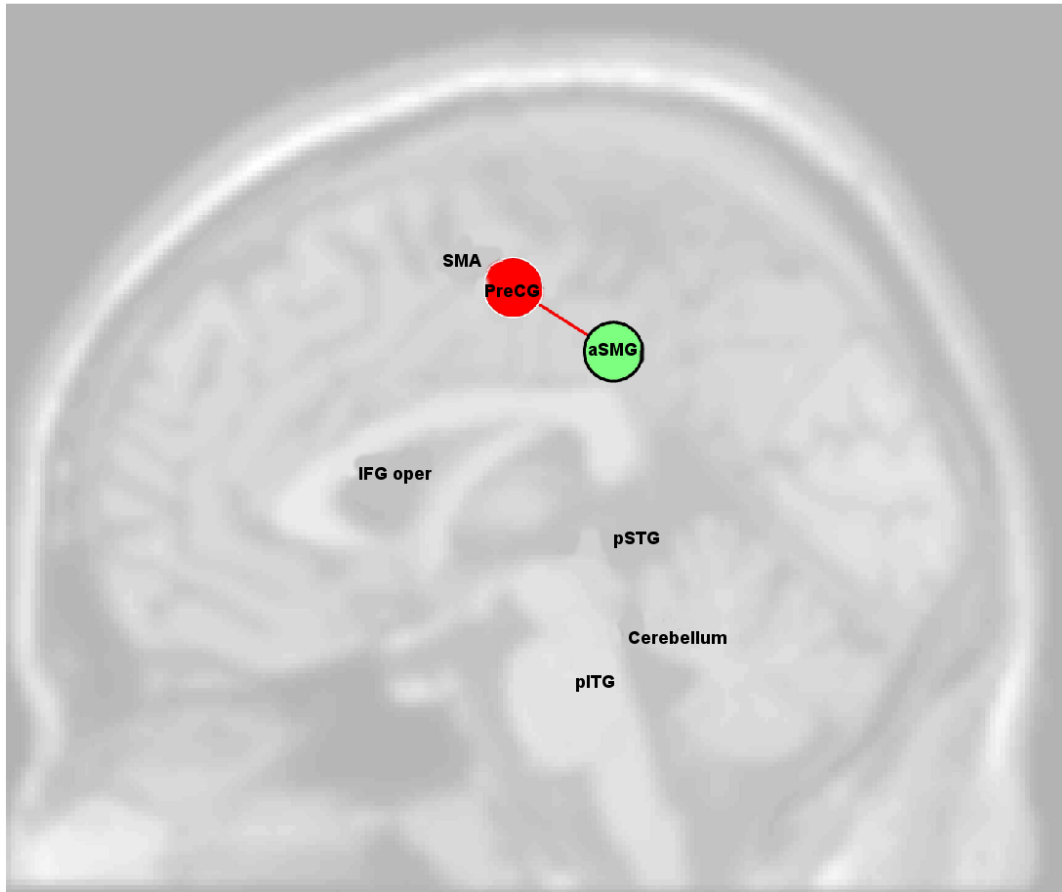


Figure 4. Significant connectivity differences between groups with SMG (green) as a seed region, when  $p=0.05$  uncorrected.

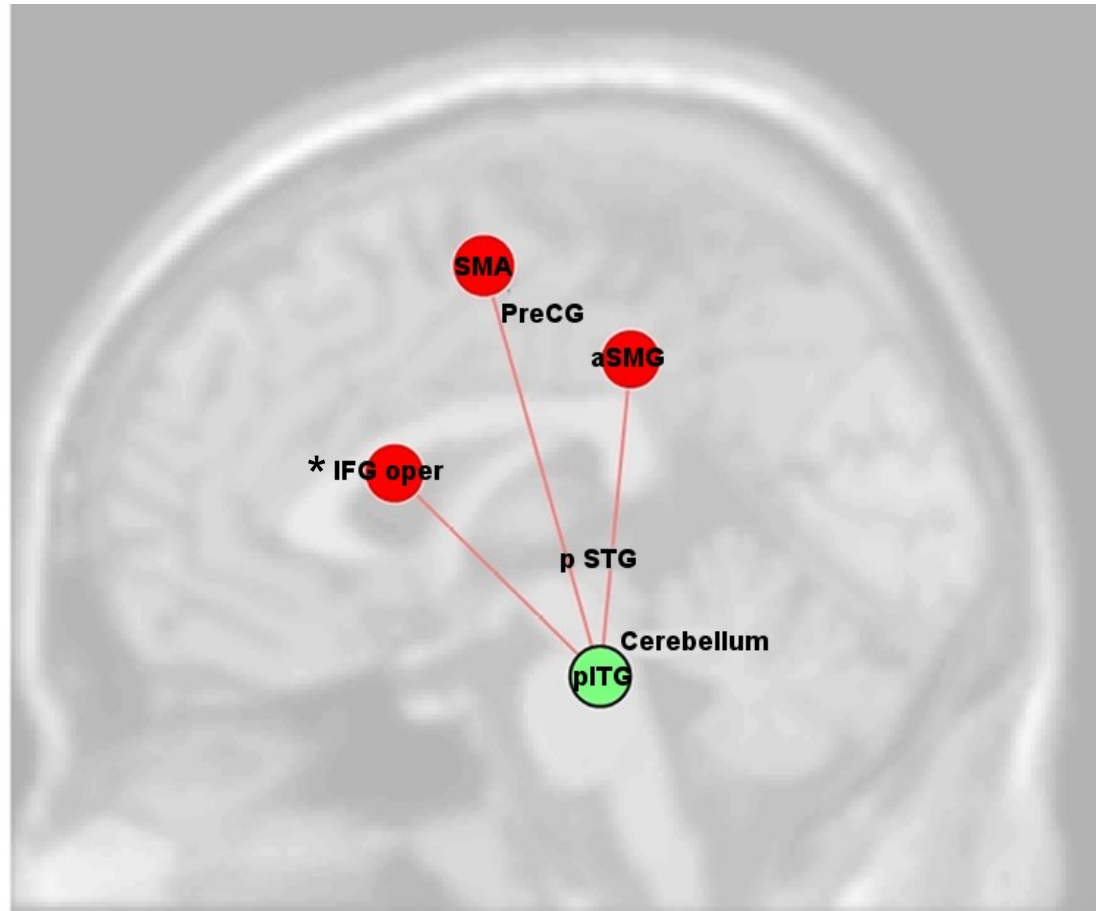
### ***Hypothesis 1.2.***

Independent samples t-tests were run to test the connectivity differences between skilled and impaired readers, with the inferior temporal gyrus (ITG) as the seed region. The tests examined differences between groups when examining connectivity between the inferior temporal gyrus and the other six ROIs.

There was a statistically significant difference, between groups, in connectivity between the inferior temporal gyrus and the inferior frontal gyrus ( $t = 3.73$ ,  $df = 16$ ,  $p\text{-unc} = 0.002$ , two-tailed; FDR corrected  $p\text{-value} = 0.013$ ) [ $\beta = 0.26$  (skilled),  $\beta = -0.00$  (impaired)]. (See Figure 4B).

Secondly, there was a statistically significant difference, between groups, in connectivity between the inferior temporal gyrus and the supramarginal gyrus ( $t = 2.57$ ,  $df = 16$ ,  $p\text{-unc} = 0.020$ , two-tailed) [ $\beta = 0.27$  (skilled),  $\beta = -0.07$  (impaired)].

Lastly, there was a statistically significant difference in connectivity, between groups, in connectivity between the inferior temporal gyrus and the supplementary motor area ( $t = 2.37$ ,  $df = 16$ ,  $p\text{-unc} = 0.031$ , two-tailed) [ $\beta = 0.15$  (skilled),  $\beta = -0.06$  (impaired)].



*Figure 5.* Significant connectivity differences between groups with ITG (green) as a seed region, when  $p = 0.05$  uncorrected ( $p\text{-unc}$ ). \*Significant connectivity differences between groups with ITG as a seed region, when  $p = 0.05$  false discovery rate corrections made ( $p\text{-FDR}$ ).

### ***Hypothesis 2.1.***

The skilled and impaired groups were collapsed to perform a within groups analysis. The relationship between real word reading performance and connectivity between the inferior frontal gyrus (IFG) (seed region) and the six other ROIs, was examined via a Pearson's  $r$  correlation. There was no statistically significant relationship between real word reading percentage correct/time and connectivity between the IFG and other ROIs within the network,



when the IFG was the seed region. Additionally, there was no significant relationship between real word reading attempts/time and connectivity between the IFG and other ROIs within the network, when the IFG was the seed region. (See Appendix for all results).

### ***Hypothesis 2.2.***

The skilled and impaired groups were collapsed to perform a second within groups analysis. The relationship between non-word reading performance and connectivity between the supramarginal gyrus (SMG) (seed region) and the other six ROIs, was examined via a Pearson's  $r$  correlation. There was no statistically significant relationship between non-word reading percentage correct/time and connectivity between the SMG and other ROIs within the network, when the SMG as the seed region. Additionally, there was no significant relationship between non-word reading attempts/time and connectivity between the SMG and other ROIS within the network when the SMG was the seed region. However, the relationship between non-word reading attempts/time and connectivity between the SMG and PCG was approaching significance uncorrected ( $r=0.15$ ,  $N=18$ ,  $p\text{-unc}=0.0548$ , two-tailed). (See Appendix for all results).

### **Discussion**

We investigated the relationships between a resting state-based reading network and behavioural reading measures in a group of skilled and impaired readers. Three main findings are of interest. First, skilled readers had stronger connectivity between the supramarginal gyrus (SMG) and precentral gyrus (PCG), when compared to impaired readers. Second, skilled readers had stronger connectivity between the inferior temporal gyrus (ITG) and inferior frontal gyrus (IFG), the ITG and the supramarginal gyrus (SMG) and, the ITG and the supplementary motor area (SMA), when compared to impaired readers. Third, there were no significant relationships between behavioural measures and the connectivity strength of the underlying reading network. Each of these main findings is discussed in further detail below, with a particular focus on interpreting how these findings advance our knowledge of the print-to-speech network.

### ***Supramarginal gyrus as the seed region***

In line with our predictions, we found a significant connectivity difference, between groups, for the connections between the SMG and precentral gyrus, when the SMG was the seed

region. This is consistent with previous work that demonstrated significant connectivity between the SMG and PCG when skilled readers participated in a pseudo word reading task (Cummine, et al. 2016). This connection was thought to reflect the feedback system engaged when learning new words (Cummine et al., 2016). If we look at the function of the SMG within the DIVA model (Guenther, 2006; the basis of which forms the print-to-speech model), it is a component of the feedback system, fulfilling the role of a somatosensory error map. The SMG's importance for the feedback system for reading may be two-fold. Perhaps, this connection (SMG-PCG) is weaker, for individuals with reading impairments, because the SMG is under activated in impaired readers (Richlan et al., 2009). This under activated network may contribute error detection during early stages of learning to read in individuals ultimately identified as reading impaired. Alternatively, and more in line with our findings, is that impaired readers may be able to adequately detect somatosensory errors via the SMG (sufficient activation) but have difficulty resolving said errors because of weaker functional connectivity with other regions of the model (i.e. precentral gyrus) to correct the error. Previous researchers have looked at the SMG and PCG as components of the reading network and found weak connections between the SMG and other parts of the resting state network (Koyama et al., 2013; Schurz et al., 2015). A strong connection between the SMG and PCG was observed for skilled readers here and in previous literature (Cummine et al., 2016).

### ***Inferior temporal gyrus as the seed region***

We predicted that individuals with reading impairments would have reduced connectivity between the ITG and other regions within the reading network, when compared to skilled readers. We found this connectivity difference, between groups, for the ITG and three other regions within the network (SMA, IFG, SMG). These connection differences will be further explored below.

Functional connectivity differences between the ITG and IFG were found between groups, with the impaired group having a weaker connection. Given the role of the ITG in print processing and the IFG in speech production, the connection between the two is critical to the print-to-speech model (Cummine, et al., 2016), and resting state networks (Koyama et al., 2010, 2011, 2013; Murdaugh et al., 2015; Richlan, Kronbichler, & Wimmer, 2011; Schurz et al., 2015; Zhao et al., 2011). More specifically, the IFG has been identified as a hub for the reading

network, meaning it is highly connected to other regions within the network and contributes to both real and nonword reading (i.e., it is important for both learning words and identifying previously known words, by connecting the speech sound map to orthographic representations of letters/words) (Cummine et al., 2016; Koyama et al., 2010; Schurz et al., 2015). In line with our findings, a reduced functional connection between the ITG and IFG has also been reported in studies of children and young adults with dyslexia (Finn et al., 2014; Schurz et al., 2015; Shaywitz et al., 2003; Zhao et al., 2011; Zhou et al., 2015). Such findings underscore the potential importance of the integration of letter knowledge with speech knowledge and future investigations would benefit from a focus on how this connection predicts behavioural outcomes, with the hope that future interventions can target the strengthening of the ITG-IFG connection.

Similarly, weaker connections between the SMG and ITG were present for impaired readers when compared to skilled readers. This is consistent with previous reports from Zhao et al., (2011), where connectivity strength between the SMG and ITG correlated with differing reading abilities (i.e., the stronger the connection between the two regions the better the reading skills). Another study shows that individuals with dyslexia have differing connections between the ITG and other regions within the network (Koyama et al., 2013). This observation aligns with the present results showing a weaker connection between the SMG and ITG and generally weaker connections between the ITG and the rest of the network in our group of impaired readers. Skilled reading requires the effective and efficient integration of letter knowledge with many other aspects of language processing including sound, articulation, meaning, etc., and our findings support the notion that there is a decreased connectivity/integration of letter knowledge within the reading network for individuals with reading impairments.

Lastly, we found reduced connectivity between the ITG and SMA, specifically for impaired readers, when comparing the two groups. The SMA is involved in connecting the speech sound map to the motor cortex (Cummine et al., 2017; Guenther et al., 2006) and potentially transferring information from the ITG (to aid in orthographic decoding), through this functional connection. For example, the SMA's connections with motor areas has been shown to be positively correlated with reading scores, for both children and adults (Koyama et al., 2011). Furthermore, a separate study focused on the SMA and its region specific functions for both speech and reading (Alario, Chainay, Lehericy, & Cohen, 2006). Findings from Alario et. al., (2006), showed connections between the SMA and other regions throughout the network,

including occipito-temporal and frontal lobe connections. They also outlined the involvement of the SMA in word selection, encoding of word forms and over articulation in regards to word production (Alario et al., 2006). In conjunction with the findings from previous literature, our results lend further support to the importance of the SMA as part of the reading network.

Overall, the decreased connectivity reported in this study, between the ITG and several other areas within the reading network, builds on previous knowledge that the ITG is under activated in individuals with reading impairments (Richlan et al., 2009). The ITG (specifically the fusiform gyrus) is a region important for both children and adults within the reading network, and is differentially connected in impaired and skilled readers within those populations (Koyama et al., 2011). What remains to be seen is the extent to which these connections predict behaviour outcomes and whether they can be strengthened via training/treatment. Much more work is needed to fully inform the nature of these aberrant connections and the role they play both skilled and impaired reading processes.

### ***Brain-behaviour connection***

No significant relationships existed between our behavioural measures and specific connectivity within the neural reading network, though one connection (SMG-precentral gyrus), was approaching significance for pseudoword reading. This was likely due to a reduced power (i.e., small sample size) and insufficient specificity with respect to task. Future work needs to continue to investigate brain-behaviour relationships using a variety of tasks outside the scanner, such as phonological lexical decision making tasks (Martin, Schurz, Kronbichler, & Richlan, 2015; Schurz et al., 2015; van der Mark et al., 2011) or rapid autonomic naming tasks (Norton et al., 2014) to fully explore the brain behaviour relationship that spans across all reading levels. For example, rhyming tasks may be better suited to examine SMG connectivity as they are more taxing on the phonological system (Finn et al., 2014; Lyon, Shaywitz, & Shaywitz, 2003; Martin et al., 2015; Norton et al., 2014; Richlan et al., 2009; Shaywitz & Shaywitz, 2005; Stoeckel, Gough, Watkins, & Devlin, 2009; van der Mark et al., 2011). In choosing tasks that are sensitive to variations in reading status, it would also be beneficial to identify the exact challenges individuals with reading impairments have (i.e., focusing on those who have predominantly phonological difficulties). Overall, many previous studies have shown a relationship between behaviour outside the scanner and resting state networks (Horowitz-Kraus, DiFrancesco, et al.,

2015; Horowitz-Kraus, Toro-Serey, et al., 2015; Murdaugh et al., 2015), and perhaps a larger sample size, different behavioural tasks or a greater range of reading skills would allow us to find similar relationships in the future.

### ***Print-to-Speech Model***

The connectivity differences observed in the present study, although from a small group of participants, advances the print-to-speech model in the following ways: it allows the model to accommodate for reading impairments and it provides additional evidence supporting the regions identified as important to the reading network. The network connectivity differences observed between reading groups suggest the importance of these networks and their potential role in reading skill. As Zhao et. al., (2011) describes, the resting reading network allows us to be able to read at anytime. Therefore, if the network is not functioning properly it may become more difficult to quickly recognize words as we encounter them in everyday life. Due to the frequency of encountering written words, those with reading impairments (i.e., an altered reading network) may struggle with reading words efficiently.

### ***Limitations and Further Directions***

The present study consists of three limitations acknowledged by the authors. First the small sample size and limited matching of reading groups on demographic variables. Second, the number of ROI's, were restricted to those specifically examined in the original print-to-speech model (Cummine et al., 2016). In future studies, ROIs could be expanded to other regions that have been proposed as being important for reading (Martin et al., 2015; Richlan et al., 2011). Lastly, we only examined the reading network within the left hemisphere and there is evidence to suggest that the right hemisphere plays a compensatory role in the reading mechanism of individuals who have reading impairments (Finn et al., 2014; Koyama et al., 2010; Norton et al., 2014; Tomasi & Volkow, 2012).

### **Conclusion**

Reading is an essential skill for everyday life. Having proficient reading abilities makes our world easier to navigate. The present study focused on creating a more holistic version of the print-to-speech model that encompassed both skilled and impaired readers. By using resting state functional magnetic imaging, we were able to advance our understanding of the underlying

reading network in both impaired and skilled readers. This network consists of the same regions as the original print-to-speech model; however, it points out how the regions are differentially connected, depending on reading skill status. Connectivity differences, specifically between the SMG-PCG, ITG-IFG, ITG-SMA and ITG-SMG, demonstrate how reading skills are affected by functional connectivity among regions and not merely activation levels of the regions themselves.

The print-to-speech model could be further strengthened through investigations of whole brain connectivity and respective contributions to reading (Finn et al., 2014; Koyama et al., 2010; Norton et al., 2014; Tomasi & Volkow, 2012). In this context, it also will be important to investigate subcortical networks (Tomasi & Volkow, 2012). By incorporating the right hemisphere, it may address the weaker connections between brain regions observed in the present study and point to potential additional compensatory connections in impaired readers (Finn et al., 2014; Norton et al., 2014; Tomasi & Volkow, 2012). Further investigation into the typical development of reading across the lifespan is of interest, as we already know there are differences between adults and children in the neural reading network (Koyama et al., 2011; Martin et al., 2015; Richlan et al., 2011). Moreover, understanding developmental trajectories in reading impaired groups also is critical. We need a better understanding of when typically developing children attain adult-like reading neural networks, which will in turn, advance our understanding of atypical development and reading impairment. Although the present study has added to the literature by including impaired readers as participants for resting state analysis, there is still much to discover about this population moving forward. It would be beneficial for future studies to involve greater numbers of skilled and impaired readers and to investigate a broader reading network in order to develop a more comprehensive print-to-speech model.

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## Appendix

*Table 1.* Results of independent samples *t*-test with the supramarginal gyrus as the seed region (Hypothesis 1.1).

ROI	<i>T</i> (16)	<i>p</i> -unc	<i>p</i> -FDR
<i>L. Precentral Gyrus</i>	3.00	0.008454	0.059179
<i>L. Supplementary Motor Area</i>	-2.03	0.059397	0.207891
<i>L. posterior Superior Temporal Gyrus</i>	-1.77	0.095545	0.222938
<i>L. Cerebellum 3</i>	-1.42	0.175723	0.307515
<i>L. Cerebellum 4/5</i>	-0.43	0.671155	0.852440
<i>L. posterior Inferior Temporal Gyrus</i>	0.23	0.820735	0.852440
<i>L. Inferior Frontal Gyrus, pars opercularis</i>	-0.19	0.852440	0.852440

*Table 2.* Results of independent samples *t*-test with the inferior temporal gyrus as the seed region (Hypothesis 1.2).

ROI	<i>T</i> (16)	<i>p</i> -unc	<i>p</i> -FDR
<i>L. Inferior Frontal Gyrus, pars opercularis</i>	3.73	0.001839	0.012874
<i>L. anterior Supramarginal Gyrus</i>	2.57	0.020471	0.071637
<i>L. Supplementary Motor Area</i>	2.37	0.030701	0.071637
<i>L. Cerebellum 4/5</i>	0.68	0.508614	0.679904
<i>L. Precentral Gyrus</i>	-0.58	0.568209	0.679904
<i>L. posterior Superior Temporal Gyrus</i>	-0.56	0.582775	0.679904
<i>L. Cerebellum 3</i>	-0.4	0.693523	0.693523

*Table 3.* Results of Pearson's *r* correlations to determine the relationship between real word reading (percentage correct/time) and connectivity strength when the inferior frontal gyrus was the seed region, collapsed across groups (Hypothesis 2.1).

ROI	Beta	<i>p</i> -unc	<i>p</i> -FDR
<i>L. Cerebellum 3</i>	1.02	0.295394	0.828631
<i>L. Supplementary Motor Area</i>	-0.77	0.363139	0.828631
<i>L. posterior Inferior Temporal Gyrus</i>	1.56	0.456562	0.828631
<i>L. Precentral Gyrus</i>	0.42	0.526806	0.828631
<i>L. anterior Supramarginal Gyrus</i>	0.85	0.591879	0.828631
<i>L. Cerebellum 4/5</i>	-0.08	0.917870	0.990231
<i>L. posterior Superior Temporal Gyrus</i>	-0.03	0.990231	0.990231

*Table 4.* Results of Pearson's *r* correlations to determine the relationship between real word reading (attempts/time) and connectivity strength when the inferior frontal gyrus was the seed region, collapsed across groups (Hypothesis 2.1).

<i>ROI</i>	<i>Beta</i>	<i>p-unc</i>	<i>p-FDR</i>
<i>L. posterior Inferior Temporal Gyrus</i>	-0.41	0.330015	0.890611
<i>L. Supplementary Motor Area</i>	-0.15	0.385535	0.890611
<i>L. Precentral Gyrus</i>	0.11	0.405104	0.890611
<i>L. anterior Supramarginal Gyrus</i>	-0.12	0.709987	0.890611
<i>L. Cerebellum 4/5</i>	-0.05	0.736610	0.890611
<i>L. posterior Superior Temporal Gyrus</i>	-0.12	0.815889	0.890611
<i>L. Cerebellum 3</i>	0.03	0.890611	0.890611

*Table 5.* Results of Pearson's *r* correlations to determine the relationship between nonword reading (percentage/time) and connectivity strength when the supramarginal gyrus was the seed region, collapsed across groups (Hypothesis 2.2).

<i>ROI</i>	<i>Beta</i>	<i>p-unc</i>	<i>p-FDR</i>
<i>L. Precentral Gyrus</i>	0.12	0.141237	0.791882
<i>L. Supplementary Motor Area</i>	-0.28	0.226252	0.791882
<i>L. Inferior Frontal Gyrus, pars opercularis</i>	0.10	0.485614	0.849713
<i>L. Cerebellum 4/5</i>	-0.08	0.507433	0.849713
<i>L. posterior Superior Temporal Gyrus</i>	-0.15	0.704176	0.849713
<i>L. Cerebellum 3</i>	-0.09	0.728326	0.849713
<i>L. posterior Inferior Temporal Gyrus</i>	-0.04	0.903700	0.903700

*Table 6.* Results of Pearson's *r* correlations to determine the relationship between nonword reading (attempts/time) and connectivity strength when the supramarginal gyrus is the seed region, collapsed across groups (Hypothesis 2.2).

<i>ROI</i>	<i>Beta</i>	<i>p-unc</i>	<i>p-FDR</i>
<i>L. Precentral Gyrus</i>	0.15	0.054762	0.383337
<i>L. Supplementary Motor Area</i>	-0.31	0.156404	0.487465
<i>L. Cerebellum 3</i>	-0.30	0.224827	0.487465
<i>L. posterior Inferior Temporal Gyrus</i>	0.32	0.347853	0.487465
<i>L. posterior Superior Temporal Gyrus</i>	-0.35	0.348190	0.487465
<i>L. Cerebellum 4/5</i>	-0.05	0.680177	0.743691
<i>L. Inferior Frontal Gyrus, pars opercularis</i>	-0.05	0.743691	0.743691