Investigating the neural circuitry of spelling in reading impairments: A functional connectivity approach

by

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ABSTRACT

Background. Writing skills are imperative to successful academic and social functioning in today's literate society. Yet, literature exploring the underlying mechanisms associated with written communication, namely spelling, is surprisingly limited. This study looked into the neuropsychological profile for spelling in skilled and impaired individuals. *Methods.* 19 skilled individuals and 8 individuals with reading impairments performed behavioural and fMRI tasks. Behavioural measures included reading and spelling tasks and three measures to assess their phonological, orthographic and morphological awareness. In fMRI, they completed three conditions of an in-scanner spelling task called letter probe task (LPT). LPT involved deciding if a visually presented letter is in the spelling of an auditorily presented word (e.g., decide if letter 'f' is in the word 'phase'?). The three conditions of LPT were as follows: 1) retrieval of the whole word spelling representations was required (e.g., 'c' in yacht), 2) retrieval of the whole word spelling representation was optional (e.g., 'r' in charm), and 3) non-words or made-up words needed to be generated (e.g., 'b' in bint). Functional connectivity patterns were analyzed between twelve left-hemispheric brain regions that have been implicated in reading and spelling literature. *Results*. We found that reading impaired individuals had low levels of phonological and morphological awareness and they used their language awareness skills differently than skilled readers. Functional connectivity results demonstrated a lack of functional connectivity from regions associated with orthographic (fusiform gyrus), phonological (superior temporal gyrus) and articulatory (putamen) processing. *Implications*. Results from the study will increase the current state of knowledge regarding the underlying neurobiology of spelling performance and add to the literature on acquisition, refinement and maintenance of written communication skills.

PREFACE

This thesis is an original work by Kulpreet Cheema. No part of this thesis has been previously published. Ethics approval was given for the original study by the University of Alberta Heath Research Ethics Board (Pro00066347) and the appropriate updates were made prior to the start of this project.

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LIST OF ABBREVIATIONS

fMRI: Functional Magnetic Resonance Imaging

MA: Morphological Awareness

MNI: Montreal Neurological Institution

O condition: Orthographic condition

OA: Orthographic awareness

OP condition: Orthographic-Phonological condition

P condition: Phonological condition

PA: Phonological awareness

ROI: Region of Interest

Investigating the neural circuitry of spelling in reading impairments: A functional connectivity approach

1. Introduction

Expressing oneself through writing has become an indispensable skill in today's literate society. Literacy skills, which include reading and writing, are critical to communication in every aspect of life-from completing assignments in schools to completing professional projects at work. Spelling is a form of written language production that requires the knowledge and coordination of various linguistic functions of phonology, morphology, orthography and sound-letter correspondence (Bain, Bailet & Moats, 1991). Although the acquisition of spelling skills is one of the most emphasized goals in schools, a full understanding regarding the neurobiological framework of such skills is unknown. Substantial work has been done to develop the cognitive models of reading (Coltheart et al., 2001; Plaut, 1999) and the neurobiological correlates associated with basic reading tasks (for reviews see, Indefrey and Levelt, 2004; Price, 2012). Comparatively little has been done to advance the cognitive models of written language production (e.g., spelling and/or writing; Ellis, 1982; Houghton & Zorzi, 2003; Roeltgen & Heilman, 1985). In order to advance the development of these cognitive models, researchers need to consider both the behavioural and neurological contributions to the spelling process. Because these models should be able to accommodate both skilled and impaired learning processes, these investigations need to include adults with typical performance and adults with atypical performance.

Research with individuals who have impaired literacy issues is an important component of theoretical model development. One such learning disorder that causes literacy issues is Dyslexia. Dyslexia (hereafter referred to as reading impairments) is a neurodevelopmental disorder, which is characterized by reading and writing impairments despite sufficient intelligence levels and educational opportunities. It affects 5-12% of children worldwide and is one of the most common learning disabilities (Shaywitz, 1998). Researchers have found that individuals with reading difficulties face lifelong difficulties with spelling in both regular and irregular orthographies (Tops, Callens, Bijn, & Brysbaert, 2014), even during their post-secondary education (Maughan et al., 2009; Nergård-Nilssen & Hulme, 2014). There have been few studies that have compared behavioural performance of skilled adults and adults with reading impairments (Pennington et al., 1986; Bruck, 1993; Kemp, Parrila & Kirby, 2009; Siegel, Share, & Geva, 1995). Findings from such work have shown mixed results on the type of impairments that the adults with reading impairments face, with some individuals presenting orthographic deficits (Meyler & Breznitz (2003), while others demonstrate adequate (Miller-Shaul, 2005) or even superior (Siegel et al.,1995) orthographic skills. Investigations of spelling processes using neuroimaging methods, on the other hand, have been performed a handful of times with skilled adults (Beeson et al., 2003; Hsieh & Rapp, 2004; Ludersdorfer, Kronbichler & Wimmer, 2015; Norton, Kovelman & Petito, 2007; Purcell, Napoliello & Eden, 2011; Rapp & Dufor, 2011; Rapp & Lipka, 2011), while no such investigations have been performed in adults with reading impairments. Needless to say, much more work is needed to resolve the mixed findings in the behavioural literature and to address the gap of information with respect to the role of different brain regions in the processing of spelling.

1.1 Literature Review

1.1.1 Spelling processes: behavioural literature

1.1.1.1 Spelling and reading. Spelling is described as the production of the written language in response to the auditory or self-generated thought (Bain, Bailet & Moats, 1991). On the other hand, reading is defined as understanding written symbols in order to extract a text's meaning (Bain, Bailet & Moats, 1991). Reading and spelling share many of the underlying linguistic processes of phonology, orthography and morphology between them, which has been supported by both behavioral and neurological studies (Rapp & Lipka, 2011). This explains why spelling instruction seems to improve reading skill as well (Moats, 2005). But differences between them warrant investigation too. One way to characterize the difference between reading and spelling is to consider reading as a decoding based skill and spelling as an encoding based skill (Richards et al., 2009). Reading is a comprehension-based skill as the reader decodes the information (print) into meaning. Spelling, on the other hand, is a production-based skill, where the speller encodes the word-related information to produce spelling (Richards, Berninger & Fayol, 2009). It involves a deeper understanding of the word etiology, morphology, phonology, orthography and phonological-orthographic correspondence knowledge, especially in the case of pseudowords. Such an understanding is not needed for reading, where the knowledge of the correspondence between a letter string and its stored meaning in the lexicon is sufficient for word recognition. Another distinction between spelling and reading is the inconsistent relationship between grapheme and phoneme representations. In reading, the grapheme-phoneme relationship is found to be consistent in many alphabetic and non-alphabetic languages, whereas the phoneme-grapheme relationship in spelling is inconsistent, in varying degrees, in many languages. This makes reading an easier process, while making spelling a relatively more difficult skill to master. For example, the grapheme /f/ in print can only have one sound, but the phoneme /*f*/ can have four graphemic correspondences- *f, ff, ph* and *gh* in English. This kind of inconsistent mapping between sounds and graphemes makes spelling a difficult skill to master. Therefore, spelling has been proposed to be a more complex and difficult task than reading

(Moats, 2005; Richards, Berninger & Fayol, 2009), but one that relies on similar underlying processes.

1.1.2 Spelling difficulties in reading impairments. As mentioned above, spelling impairments remain persistent in adults with reading impairments. Investigating the primary cause of these impairments has been the focus of much research (Bruck, 1992; Bruck & Treiman, 1990; Tops et al., 2014; Tunmer & Rohl, 1991). There is general consensus in the literature for the presence of three types of spelling errors resulting from difficulties in sound representations (i.e., phonology), letter representations (i.e., orthography) and meaning processing (i.e., semantics). Phonological processing deficits are proposed to be the core deficit in reading impairments (Shaywitz & Shaywitz, 2005; Vellutino & Fletcher, 2005), which has subsequently led researchers to propose phonological deficits as the source of spelling errors (Coleman, Gregg, McLain, & Bellar, 2009; Kemp et al., 2009). Although the majority of studies have been conducted in children/beginner spellers, few studies have also provided evidence for the presence of these phonological deficits in spelling in adults with reading impairments (Coleman et al., 2009; Kemp et al., 2009; Tops et al., 2014). Primarily, deficits in phonological awareness have been proposed to be the cause of phonological spelling errors (Bruck, 1992; Bruck & Treiman, 1990; Tunmer & Rohl, 1991; Wilson & Lesaux, 2001). Phonological awareness (PA) is described as knowledge and ability to identify and manipulate the sound structure of words (Bruck, 1992; Wilson & Lesaux, 2001). For example, when a phoneme is not represented by a grapheme(s) in the spelling of the word, a different pronunciation from the intended target word may be produced e.g., *delberate* instead of deliberate (Tops et al., 2014). In terms of PA, participants can be either tested on large sound representations (e.g., division of a word into an onset and rime) or small sound units (e.g., individual sound units called phonemes).

For the purposes of the current study, knowledge of the individual sound units/phonemes is of interest, which can be measured using phoneme elision, blending and segmentation tasks (Stahl & Murray, 1994). In addition to the errors in sound representations, individuals with reading impairments have also been reported to make letter-based (i.e., orthographic) and semantic-based (i.e., morphological) errors. Orthographic based spelling errors are caused by the incorrect use of permissible letter strings that may or may not preserve the phonology of the intended word (e.g., *cwantity* instead of quantity). Morphological based errors occur due to the incorrect use of suffixes, roots and other morphological principles that cause misspellings (e.g. *smild* instead of smiled). In order to study the source of these errors, researchers have tested the explicit knowledge of these language elements through various kinds of tests, which will be reviewed in more detail below.

Orthographic awareness (OA) is the knowledge of permissible letter strings in a language (Olson et al., 1994). Some of the OA tasks include deciding which pseudoword could be a real English word from a pair of pseudowords (e.g. *fage-fajy*), distinguishing real words from pseudohomophones (pseudowords that sound like a real word e.g. *pint* vs *pynt*) and lexical verification task (indicate if the presented letter string is correctly spelled or not) (Manis, Szeszulski, Holt & Graves, 1990; Siegel, Share & Geva, 1995). Morphological awareness (MA) is the knowledge of the morphemic structure of the words like roots, suffixes and grammatical inflections (Tops et al., 2014). Common MA tasks include making correct choice of words on the basis of grammatical rules or making up new words by following certain morphological rules (Law, Wouters & Ghesquière, 2015). Performance of individuals with reading impairments on OA and MA tasks has been mixed. While few studies have shown adults with reading impairments to have adequate (Pennington et al.,1986) or even superior orthographic skills

(Siegel, 1995), other studies have shown them to be subpar in individuals with reading impairments compared to skilled adults (Bruck, 1993; Kemp et al., 2009; Pitchford, Ledgeway & Masterson, 2009). This is similar for MA skills too, where some researchers have found evidence for impaired morphological awareness in reading impairments (Bruck, 1993), while others have suggested morphological knowledge to be adequate and even a potential compensatory mechanism in adults with reading impairments (Law et al., 2015). Therefore, while there is evidence for phonological impairments being one of the sources of spelling impairments, the same cannot be concluded for orthographic and morphological awareness. This project will include measurements of participant's phonological, orthographic and morphological awareness. Performance on these three constructs will be compared between adults with and without reading impairments. Such information on the range and type of impairments seen in individuals with reading impairments is necessary to the advancement of behavioural and neurobiological models of spelling.

1.1.3 Spelling processes: brain imaging literature

1.1.3.1 Lesion studies. Roeltgen and Heilman (1985) postulated the first neuroanatomical model for spelling from studying patients who presented with spelling problems resulting from lesions, resulting in a disorder known as agraphia. Individuals with phonological agraphia were argued to have a disrupted sub-lexical route (consistent sound-to-letter), characterized by impairments in spelling unfamiliar words (e.g., pseudowords, *bint*) but preserved ability to spell orthographically irregular words (e.g., *knife*) (Roeltgen & Heilman, 1985). These symptoms were associated with lesions in and around supramarginal gyrus and insula. Individuals with lexical agraphia were argued to have a damaged lexical route, resulting in impairments in spelling familiar irregular words (e.g., exception words, *pint*) while their ability to spell unfamiliar orthographically legal words remained intact. In contrast to the phonological agraphia, lesions associated with lexical agraphia were often reported in the posterior angular gyrus and parieto-occipital lobule (Roeltgen & Heilman, 1985). This double-dissociation of impaired spelling abilities and anatomical locations was taken as evidence for the presence of two routes for spelling.

In more recent lesion-based work, Rapcsak and Beeson (2004) measured the spelling performance for familiar (e.g., regular and exception) and unfamiliar (e.g., pseudowords) words in patients with focal lesions around left inferior temporo-occipital cortex, including regions such as lingual gyri, fusiform gyrus and parahippocampus. It was reported that individuals with lesions in these brain areas had poor performance for the spelling of exception words and most of the errors were phonologically plausible (e.g. cough-*cof*). This finding further provided evidence for the anatomical location of the lexical route for spelling (Rapcsak & Beeson, 2004). These results have been replicated and extended in more recent work, with fusiform gyrus, supramarginal gyrus, inferior frontal gyrus, angular gyrus, precentral gyrus and premotor cortex being implicated for both lexical and sublexical spelling processes (Cloutman et al., 2009; Philipose et al., 2007; Rapp et al., 2015; Rapscak & Beeson, 2002; Tsapkini, Vasconcellos-Faria & Hillis, 2012). While such studies are important, lesion studies present with several limitations as brain damage is often diffused and pre-injury performance is unknown. Therefore, there is a need to complement the findings from lesion studies with studies involving healthy individuals, which has been accomplished with the use of neuroimaging methods like functional Magnetic Resonance Imaging (fMRI).

1.1.3.2 Mean-activation based studies: skilled adults. In one of the earliest fMRI studies on spelling in adults, Hsieh and Rapp (2004) had participants perform a letter-probe task, which involved identifying whether a letter presented visually occurs in a word which is presented auditorily. The brain areas activated in this task were bilateral superior temporal gyri, left inferior frontal gyrus, pre-motor cortex, posterior inferior temporal gyrus and the supplementary motor area. While these results provided useful information about spelling-related brain regions, the study was not clear about the type of stimuli included, and therefore conclusions about the lexical and/or sub-lexical routes could not be made. More recently, Norton and colleagues (2007) used fMRI to study the neural basis of spelling familiar words and unfamiliar words (Norton, Kovelman & Petito, 2007). The authors provided evidence for the involvement of inferior frontal gyrus and temporal gyri for the spelling of familiar letter strings (e.g., regular, *hint*, and exception, *pint*, words) and left superior temporal gyrus, bilateral middle temporal gyrus and inferior temporal gyrus for the spelling of unfamiliar words. In addition, Norton et al. (2007) provided additional clarification about the involvement of the brain regions in the spelling process, attributing inferior frontal gyrus activity to phonological processing, bilateral middle temporal gyrus activity to semantic word recognition and supramarginal gyrus to phonological processing of print.

One of the recent studies to use letter probe task to elucidate the neural systems that support lexical and sublexical processing was performed by Ludersdorfer and colleagues (2015). They had participants perform variations of letter probe tasks, one of which necessitated the involvement of lexical/whole-word orthographic representations, while another one involved using sub-lexical information to make correct spelling choices. For both conditions, researchers noticed an overlap in activation for lexical and sublexical processing. This overlap included areas of inferior frontal gyrus, anterior cingulate cortex, superior parietal lobule, insula and frontal orbital cortex. Specifically, left inferior frontal gyrus, visual word form area and paracingulate gyrus were more activated for real word spelling, while superior temporal gyrus was more involved in pseudoword spelling. Together, the findings from lesion-based and fMRI-based studies are in line with the notion of lexical and sublexical routes for spelling.

1.1.3.3 Mean-activation based studies: adults with reading impairments. Given the dearth of literature on the neural correlates of spelling in adults with reading impairments, we summarize the neural correlates of reading in adults with reading impairments to help guide our understanding of potential brain regions associated with written communication impairments. The areas commonly associated with phonological processing (temporoparietal regions including superior temporal gyrus, inferior parietal lobule and supramarginal gyrus) are consistently underactivated in people with reading impairments (Richlan, Kronbichler, & Wimmer, 2011; Richlan, 2012). This underactivation is hypothesized to be the result of, or due to, the deficits in phonological processing, which includes impairments in the knowledge of phonetic sounds and/or access to and manipulation of these sounds. In addition, atypical activation in regions associated with visual-orthographic processing (occipitotemporal regions including lateral extrastriate, fusiform gyrus, and inferior temporal regions) has also been reported (Eckert, 2004). This aberrant activation in occipito-temporal regions has been connected to deficits in orthographic processing, which includes disruption of knowledge of permissible letter strings and whole word representations. Since reading impairment is understood to be a left hemisphere based deficit (Richlan, 2012), unsurprisingly, most of the underactivated regions are reported in the left hemisphere. In conclusion, there is widespread dysfunction of brain networks in reading impairments and since spelling has been hypothesized to activate similar brain connections as reading, therefore these results will be used to form hypotheses for the current study.

1.1.3.4 Connectivity-based studies: skilled adults. The previous studies are based on mean brain activation and assume a locationalist view of spelling and reading. However, it is widely accepted that brain areas do not operate independently but are connected with each other structurally (by white matter tracts) and functionally (by connecting with each other through neuronal activation) (Friston, 2011). Investigating the functional connectivity between brain regions in a network provides information on how the regions interact with each other, or work together, to support the completion of various tasks. Such analyses go beyond the description of brain regions that are sensitive to particular aspects of a task (i.e., the superior temporal gyrus is involved in sound processing), to a more comprehensive understanding of the dynamic system that is required to sound out a word. For instance, how does the superior temporal gyrus 'work with' the angular gyrus (e.g., semantics) and inferior temporal gyrus (i.e., letter processing) to determine how to spell a word that has just been heard? Notably, differences in connectivity can occur in the absence of differences in mean activation, so while overall brain activation may look similar between two groups of individuals, or between two tasks, the nature of the relationship between the regions in the network can be vastly different (Cummine et al., 2016). Ultimately, information about the dynamic system is necessary for the advancement of a comprehensive model of spelling. For example, Boets and colleagues in 2013 hypothesized that the reason for impaired phonological awareness in reading impairments might not be the poor quality of phonological representations, but the weak connectivity between the key language areas of superior temporal gyrus and inferior frontal gyrus. Questions of this nature, to date, have been unanswered as the functional connectivity within a spelling network has been unexplored. As such, the current project aims to advance the neurobiological models of spelling using a functional connectivity approach.

Several functional connectivity studies have been conducted in the reading domain. Interestingly, researchers report differential patterns of connections between brain regions as a function of the word types (real words e.g., *pynt* vs pseudowords e.g. *bint*), even in the absence of differences in mean activation (Cummine et al., 2016; Mechelli et al., 2005). Specifically for real word reading, a highly connected neural circuit comprising of regions associated with orthographic (inferior temporal gyrus), phonological (inferior frontal gyrus, supramarginal gyrus) and articulatory (precentral gyrus, supplementary motor area) processes was found. Reading a familiar word requires coordination of the orthographic representations with phonological, semantic and articulatory representations (Cummine et al., 2016). Pseudoword reading, on the other hand, included a restricted network of regions, namely the cerebellum, supplementary motor area and precentral gyrus (Cummine et al., 2016). Other studies have also found connections within temporal regions (inferior temporal gyrus, fusiform gyrus) and from temporal regions to temporo-parietal (inferior parietal lobule) and frontal (inferior frontal gyrus) regions to be involved in real word reading (Koyama et al., 2011; Schurz et al., 2014). In addition to cortical structures, subcortical structures have also been implicated for word and pseudoword reading. Cummine et al. (in review) found functional connections between caudate-putamen and caudate-thalamus for pseudoword reading but not for real word reading. Caudate has been implicated in phonological processing (Bohland, Bullock & Guenther, 2010; Cheema, Lantz & Cummine, 2017) and its stronger connectivity during a task like pseudoword reading where organization of phonemes is required before articulation is not surprising (Cummine et al, under review). Apart from whole brain structures, studies have also looked at the functional connectivity for segmented regions for different types of words. For example, Mechelli et al. (2005) found a double dissociation within the two subdivisions of fusiform gyrus for exception and pseudowords activation patterns. Exception word reading activated parts of anterior and middle fusiform, while pseudoword reading recruited posterior fusiform. Therefore, studies have provided evidence for functionally connective lexical and sublexical reading routes as well. Such investigations are important as they provide evidence for developing theoretical models of language development. As reading and spelling have been argued to recruit similar brain regions, involvement of similar brain regions for spelling is expected for the present study too.

1.1.3.5 Connectivity-based studies: adults with reading impairments. Within the reading literature, the notion of deviant functional connectivity between brain regions is a point of important consideration. Several researchers have found reduced connectivity within occipitotemporal regions (inferior temporal gyrus, fusiform gyrus, superior temporal gyrus) in individuals with reading impairments (Finn et al., 2014; Schurz et al., 2014). Additionally, reduced connectivity from occipitotemporal regions to regions associated with sound-letter mapping and phonological processing (inferior parietal lobule and inferior frontal gyrus; Finn et al., 2014; Schurz et al., 2014), and between inferior frontal gyrus and inferior parietal lobule and/or precentral gyrus (Norton et al., 2014) has also been shown in individuals with reading impairments. As such, one potential reason for impaired phonological and orthographic processing in readers with reading impairments might be the aberrant connections between the frontal and temporal brain areas responsible for mapping the written letter strings onto sound and meaning representations. In fact, Boets and colleagues (2013) implicated reduced functional and structural connectivity between inferior frontal gyrus and superior temporal gyrus to be the reason for phonological processing deficits.

On the other hand, individuals with reading impairments have persistent connections with left anterior language regions of medial prefrontal cortex, anterior cingulate and caudate (Finn et al., 2014). Increased connectivity between inferior frontal gyrus and caudate in reading disabled individuals has also been reported (Finn et al., 2014). This increased connectedness between regions responsible for phonological processing has been described to be compensatory in nature, and supports the notion that individuals with reading impairments engage in a slow, "sounding out" strategy of reading words instead of implementing a more efficient and fast, memory-based reading strategy (Finn et al., 2014). Additionally, altered connectivity between brain regions in reading impairments has also been reported. Finn et al. (2013) found that visual word form area, instead of being connected to inferior frontal gyrus and medial prefrontal cortex, is connected to bilateral visual association cortices and right primary auditory cortex in adults with reading impairments. Another set of evidence for abnormal connectivity occurs in sub-cortical structures. For example, Cummine et al. (under review) reported additional connections between anterior cerebellum and midbrain for individuals with reading impairments. Therefore, studies have pointed towards abnormal functional connectivity for both cortical and subcortical structures in reading impairments. But since no such investigation has been performed for spelling, even in skilled adults, this project will look into the neural circuitry for skilled and impaired spelling in reading impairments. Information from these connections will be useful in developing a neuroanatomical model of spelling, which will inform the assessment and selection of appropriate treatment for these spelling impairments.

1.1.4 Summary

Given the persistent spelling impairments faced by adults with reading impairments and the increased reliance on written communication in our current society, the advancement of a comprehensive brain-behaviour model for spelling is pertinent if we hope to mitigate the impact of such difficulties in everyday activities. While behavioural and brain-based investigations into these impairments are in line with the notion of a dual-route model for spelling, the knowledge on how such processes are connected, or work together in both skilled readers and individuals with reading impairments remains elusive. In this study, behavioural and brain imaging data was be collected while participants with and without reading impairments perform spelling tasks in fMRI. Functional connectivity between brain areas implicated in reading and spelling literature was analyzed and compared within and between the two groups of adults with and without reading impairments. Results from the study will increase the current state of knowledge regarding the underlying neurobiology of spelling performance and add to the literature on assessment, diagnosis, and treatment of written communication difficulties across the lifespan.

1.1.5 Research Questions and Hypotheses

1) Are there behavioral differences among the orthographic, phonological and morphological awareness skills of adults with and without reading impairments? And, how do these constructs relate to their spelling performance?

Hypotheses. Individuals with reading impairments will perform poorly on phonological awareness compared to controls. No differences are anticipated for orthographic or morphological skills. There will be positive relationship between orthographic, phonological, morphological awareness and spelling performance for both groups.

2) What does the neural network look like for the spelling of real words (exception and regular word) and pseudowords? Are these neural networks different for adults with and without reading impairments?

Hypotheses. We will see reduced and/or altered connectivity among brain regions for participants with reading impairments for all the three spelling conditions of exception word, regular word and pseudoword spelling.

2. Materials and Methods

2.1 Participants.

Participants (N= 27) took part in both the behavioural and imaging aspects of the study. Out of these, 8 adults were classified as having reading impairments (referred to as impaired group) (2 males; 6 right-handed; mean age = 21.0 years) and 19 were skilled readers (referred to as skilled group) (6 males; 19 right-handed; mean age = 23.9 years). Inclusion criteria for the skilled group consisted of English as native or primary language, normal or corrected to normal vision, no contraindications to go in the MRI, and age-appropriate scores on reading, spelling and IQ measures. Inclusion criteria for the impaired group consisted of English as native or primary language, normal or corrected to normal vision, no contraindications to go in the MRI, and age-appropriate score on the nonverbal IQ test. In addition, the impaired group had a reading score (tests described below) and spelling performance at least 1.5 SD below the skilled group. Exclusion criteria for both groups included history of any hearing or vision disorder, stroke and/or any neurological disorders like ADHD. All participants were paid an honorarium of $30 cash for their participation.

2.2 Data Collection

2.2.1 Behavioural data collection. All participants were administered the following tasks:

- Reading tasks: Participants completed four subtests of the Woodcock Reading Mastery Test, which included Test of Word Reading Efficiency (TOWRE) real words, TOWRE pseudowords (two standardized measures of reading fluency), Word Identification and Word Attack.

- Three language component tasks were administered to measure the implicit knowledge of phonological, morphological and orthographic awareness (See Appendix: Table 9, 10 and 11).
    - *Phonological awareness task*: This was an oral phoneme elision task, where participants were asked to delete a sound from a non-word and say the word without the indicated sound. The word list was previously used in Byrd and colleagues (2012; 2015). Thirty pseudowords that were 2, 4 and 7 syllables long were controlled for "real wordlikeness, segmental phonotactic probability, biphone phonotactic probability, and phonemic onset" (Byrd et al., 2015, p. 21 ; review Byrd et al., 2015 for further information on word development).
    - *Orthographic awareness task*: This was a paper-and-pen task where participants were given a pair of pronounceable pseudowords and were asked to select the word that most likely could be a real word in English. One of the pairs had a bigram (or a sequence of letters) that do not occur in English in a specified position (final or initial location). For example, one of the pairs was *filv-filk*, and the correct answer was *filk* as *lv* never occurs in a final position in English words. This task was previously used in Siegel et al. (1995).
    - *Morphological awareness task*: This was a pseudoword sentence completion task, participants were provided with a sentence with a blank and four pseudoword options, and were asked to select which non-word best fits the sentence. This test has been previously used in Mahony (1994).
- Spelling test from the Wide Range Achievement Test-4th Edition: This was a dictation-based test of 42 words. This test had been used previously in spelling studies in adults (Pennington et al., 1986; Bruck, 1993; Kemp et al., 2009) and is a standardized measure of spelling performance in children and adults (Cassar & Treiman, 1997; Moats, 1983).

- Measure of non-verbal intelligence using the Matrix Reasoning test from Wechsler Abbreviated Scale of Intelligence: There is evidence that participants in the experimental group underperform in verbal IQ tests due to their reading impairments. Therefore, both groups underwent nonverbal IQ test in order to have a comparable performance measure from both groups. Past studies with adults with reading impairments have also measured nonverbal IQ in order to group participants with reading impairments (Boets et al., 2013; Finn et al., 2014; Schurz et al., 2014).

2.2.2 fMRI data collection.

2.2.2.1 Neuroimaging tasks. Participants completed three conditions of the letter probe conditions. In the letter probe condition, participants were given the auditory presentation of either a word or non-word, followed by the visual presentation of a single letter on screen. They were asked to indicate if the letter is, or is not, in the spelling of the word that they just heard. The letter probe task has been used previously to study the neural activity for spelling (Hsieh & Rapp, 2004; Ludersdorfer et al., 2015). The task had the following three conditions:

1. **Orthographic (O) condition**: In this condition, participants retrieved the spelling of the words in order to make the judgment. Therefore, the words that were chosen had irregular spelling-to-sound correspondence. The letter option that was given was either a) absent from the pronunciation of the word (e.g.,‘T’ in ‘gourmet’), b) ambiguous in respect to associated phonemes (e.g., ‘C’ in ‘cello’), or c) highly associated with a specific phoneme (e.g., ‘G’ associated with /g/, as in word ‘get’), but was pronounced differently in a selected word (e.g., sound of ‘G’ in ‘regime’). Because the decision of the letter probe can't be made by just the pronunciation of the words, they would have to retrieve

the spelling (Ludersdorfer et al., 2015). This condition used exception words as they have the irregular spelling-to-sound correspondence.

2. **Orthographic-Phonological (OP) condition**: This condition did not have a conflict between orthographic whole-word representations and phonological decisions (e.g. *phase* and A), so participants could have used either strategy to answer (although orthographic strategy was still emphasized as there were similar instructions for this and the orthographic condition). This condition used regular words.
3. **Phonological (P) condition**: Compared to the last two conditions, this condition had pseudowords (e.g. *bint*), for which there were no stored whole-word representations to retrieve. Therefore, participants had to generate the spelling of these words to make the decision of whether the letter is in the spelling of the word or not. The condition was set up in a way that the probe letters would allow a rather definite decision on whether it was included in a possible spelling of the pseudoword (e.g., *bint* and N).

A total number of 75 words (referred to as stimuli hereafter) were selected for each condition (see Table 12 in Appendix). Stimuli were matched on the following characteristics across and within the tasks: frequency of word, orthographic and phonological neighborhood size, number of phonemes, syllables and morphemes, word length, summed bigram frequency and summer bigram frequency by position (Balota et al., 2007).

The audio files for each condition were preprocessed and calibrated for frequency using the Audacity software. Both fMRI tasks were programmed using EPrime software (Psychology Software Tools, Inc., http://www.pstnet.com), where the onset time of stimulus, stimulus duration, and response time were kept standard for all conditions.

2.3 Procedure

Participants provided written and/or verbal consent and then completed the behavioural test battery, which included reading tasks, three component measures, spelling and non-verbal intelligence tasks. Performance measures included accuracy and/or rate (correct items over total time) for each behavioural task. The behavioural portion of the experiment took approximately 40 minutes. Then, participants were provided with an overview of the experimental tasks in fMRI and completed a practice trial in the behaviour room prior to going into the MRI scanner. Participants then walked over to Peter S. Allen Research Centre with the research assistants. They were screened by the MR technician to ensure it was safe for them to go into the MRI. Once in the MRI, and prior to each task, participants were reminded about the nature of the tasks they are to complete. EPrime software (Psychology Software Tools, Inc., http://www.pstnet.com) was used to present the stimuli for each task onto a screen, which was visible to the participants through a mirror attached to the head coil. The three tasks were counterbalanced and stimuli in each task were presented randomly. Response time was operationalized as the time from stimulus presentation to the button response provided by the participant, while accuracy was coded by the EPrime software.

Images were acquired on a 3 T Siemens Sonata scanner and were positioned along the anterior-posterior-commissure line. Anatomical scans included a high-resolution axial T1 MPRAGE sequence with the following parameters: repetition time (TR) 1700 ms, echo time (TE) 2.21 ms, number of slices 176, base resolution 232 x 256 x 176 with a voxel size of 1 x 1 x 1 mm, scan time 4.50 min. For each condition (O, OP and P), 230 volumes of 64 slice, axial spin, echo planar images (EPIs) were obtained with the following parameters: TR 1980 ms, TE 30 ms, base resolution 64 x 64 with a 128 x 128 reconstruction matrix that improved pixel resolution through zero-filling prior to Fourier transform reconstruction, scan time approximately 8 minutes. EPI slice thickness was 2.2 mm with no gap between slices.

2.4 Analysis

2.4.1 Behavioural data analysis. Accuracy rates were calculated for all behavioural tasks and rates for OA and MA were calculated as accuracy over total time taken (in seconds) to complete that task. Reading, spelling and the three language component measures were compared between the adults with reading impairments and controls using independent samples *t*-tests (at Bonferroni corrected $p < 0.05$). Correlational analyses were used to test for relationships between spelling and the three language component measures. Multiple regression analyses of spelling scores on the three language measures were also performed for both groups to assess the overall predictability of spelling performance (dependent variable) given language measures of PA, MA and OA (independent variables).

In-scanner behavioural performance. Accuracy rates and reaction times were calculated for all three conditions and compared between groups using independent samples *t*-tests (at Bonferroni corrected $p < 0.05$).

2.4.2 Functional connectivity analyses. Functional connectivity analysis was performed with CONN-fMRI toolbox in SPM 12 (Whitfield-Gabrieli & Nieto-Castanon, 2012; https://www.nitrc.org/projects/conn). First, the functional and structural data were subjected to the standard preprocessing analysis in the CONN program. This pipeline included functional realignment of functional images to each other, slice-timing correction within each task, segmentation and normalization of functional and structural images into gray matter, white matter and cerebrospinal fluid maps, normalization of data into standard Montreal Neurological Imaging (MNI) space, and spatial smoothing using Gaussian kernel.

Next, first-level analyses involved assessing functional connectivity for all participants individually via bivariate correlations ($p<0.05$, FDR-corrected). Regions of interests (ROIs) implicated in previous spelling studies were selected as seed regions for functional connectivity analyses. Seed regions are the brain areas from which all other brain regions are correlated with. These included areas associated with orthographic processing (fusiform gyrus, inferior temporal gyrus), phonological processing (inferior frontal gyrus, superior temporal gyrus, caudate, inferior parietal lobule, supramarginal gyrus) and articulatory processing (precentral gyrus, supplementary motor area, putamen, cerebellum and thalamus) (MNI coordinates in Table 1). Each of the brain regions were delineated on a standardized MNI template to which each participant's structural and functional scans was assigned.

2.4.3 Characterization of spelling networks. Second level analyses included averaging the networks across participants to create functional connectivity networks for each group (e.g., impaired and skilled readers) for all three conditions. Results were reported at $p<0.05$ (FDR-corrected).

Independent samples t-tests were run to test for differences in connectivity strength, for each pairwise connection, between skilled and impaired readers. Connectivity was first calculated for inferior frontal gyrus (speech input area). Given the dearth of literature on spelling networks in general and the absence of such work for individuals with reading impairments, we also performed exploratory analyses, where we characterized the functional connectivity of the spelling network for each group when each ROI was used as a seed region.followed by the connectivity from each ROI separately to characterize the differences between groups for all conditions. Results were reported at $p<0.05$ (FDR-corrected).

2.4.4 Brain-behaviour relationships for spelling. In-scanner behavioural performance during the three spelling conditions was correlated with connectivity strength, for each pairwise connection, for each group.

Brain regions	Coordinates X,Y,Z	Brodmann areas
Orthographic processing		
Fusiform gyrus	-44, -48, -16	BA 37
Inferior temporal gyrus	-52, -62, -8	BA 20
Phonological processing		
Inferior frontal gyrus	-32, 18, 6	BA 13
Superior temporal gyrus	-58, -46, 12	BA 22
Caudate	-11, 8, 7	Caudate body
Inferior parietal lobule	-52, -46, 44	
Supramarginal gyrus	-32, -48, 48	BA 40
Articulatory processing		
Precentral gyrus	-45, 4, 33	BA 6
Supplementary motor area	0, 10, 56	BA 6
Cerebellum	12, -70, -21	Declive, posterior lobe
Putamen	-30, 2, 4	Lentiform nuclues
Thalamus	-26, -26, -6	Lateral geniculum body

Table 1: Coordinates of the regions of interests employed for the functional connectivity analyses.

3. Results

3.1 Behavioural Performance

Mean and standard deviation of all behavioural tasks and the independent t-test results are summarized in Table 2. Independent sample t-tests revealed significant between-group differences on all the behavioural tasks except for OA accuracy, OA rate and the nonverbal IQ (Table 2). The impaired group had lower accuracy rates and took longer to complete the tasks when compared to the skilled group.

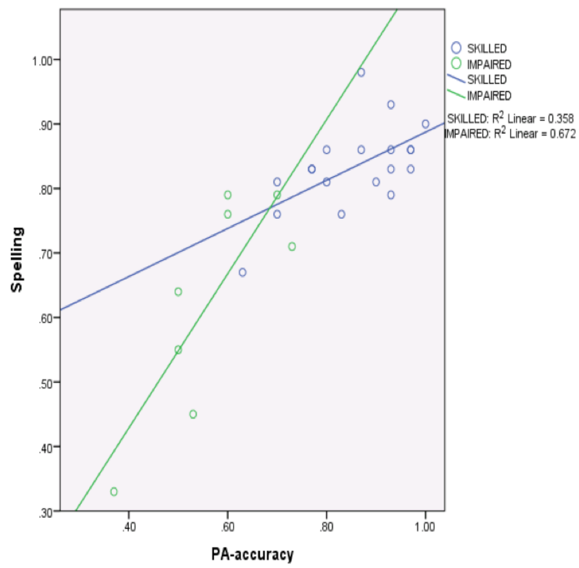
With respect to the relationships between language measures and spelling, differential results were found between the groups. In skilled readers, we found a positive relationship between spelling performance and PA accuracy (r = .60, p = .007), and MA rate (r = .56, p = .015). The overall regression model was significant, R^2= 0.67, F (5, 12) = 4.838, p = .012. The standardized regression coefficient for PA accuracy remained significant, t (18) = 2.993, p = .011. In impaired readers, a positive relationship was found between spelling performance and PA accuracy (r =.82, p = .013) (Figure 1). However, the overall regression model was not significant and the standardized regression coefficients were not significant either.

	Groups	**Mean**	**Std. Deviation**	**T-test**	**Sig (p< .05)**
TOWRE RW fluency	**SKILLED**	106.05	12.39	3.042	.005
	IMPAIRED	92.21	15.11		
TOWRE RW accuracy	**SKILLED**	.8958	.08194	3.161	.004
	IMPAIRED	.7613	.13840		
TOWRE NW fluency	**SKILLED**	108.58	7.52	5.004	.000

	IMPAIRED	88.39	14.69		
TOWRE NW accuracy	**SKILLED**	.9021	.05564	4.338	.000
	IMPAIRED	.6663	.22690		
WI (accuracy)	**SKILLED**	108.18	6.87	4.860	.000
	IMPAIRED	88.58	16.46		
WA (accuracy)	**SKILLED**	108.86	8.31	4.942	.000
	IMPAIRED	87.66	14.89		
PA-accuracy	**SKILLED**	.8563	.10683	6.272	.000
	IMPAIRED	.5663	.11686		
MA-accuracy	**SKILLED**	.9647	.03272	3.487	.002
	IMPAIRED	.7963	.21023		
MA-rate(per second)	**SKILLED**	.12472	.045979	2.126	.004
	IMPAIRED	.08343	.036027		
OA-accuracy	**SKILLED**	.8868	.07134	-.203	.841
	IMPAIRED	.8925	.05007		
OA-rate (per second)	**SKILLED**	.3544	.10656	-.195	.847
	IMPAIRED	.3643	.13024		
Spelling	**SKILLED**	.8337	.06660	4.596	.000
	IMPAIRED	.6275	.17044		
Non-verbal IQ	**SKILLED**	.8258	.07654	1.299	.206
	IMPAIRED	.7888	.03563		

Table 2: Descriptive statistics of the behavioural tasks and t-test results for all tasks. RW =real word; NW= pseudoword.

a)



b)

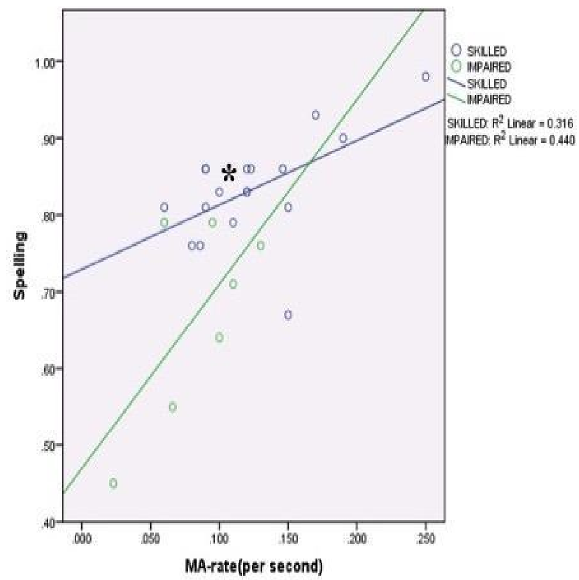


Figure 1: Scatterplot showing the positive relationship between spelling performance (accuracy) and a) PA accuracy and b) MA rate in skilled and impaired groups. Significant relationship for skilled readers is indicated by an asterisk for MA rate.

3.1.1 In-scanner behavioural performance. Between group differences for accuracy were found for O condition, such that the impaired group (Mean = .60, Standard Deviation (SD) = .23) had lower accuracy scores than skilled group (Mean = .78, SD = .09), t (25) = 2.91, *p* = .007). Significant group difference was also found for accuracy of OP condition, such that the impaired group (Mean = .70, SD = .20) had lower accuracy scores than skilled group (Mean = .86, SD = .07), t (25) = 3.09, *p* = .005) (Table 3). Although performance on P condition was not statistically different between groups, trend towards lower accuracy scores was present, as the impaired group had lower accuracy scores (Mean = 0.72, SD = .22) compared to skilled readers (Mean = 0.84, SD = .10). All the other behavioural measures were comparable between the two groups.

Spelling conditions	Groups	Mean, SD	t-test	p-value
O. ACC	Skilled	.78, .10	2.912	.007
	Impaired	.60, .23		
OP.ACC	Skilled	.86, .07	3.093	.005
	Impaired	.70, .21		
P.ACC	Skilled	.83, .10	1.944	.063
	Impaired	.72, .22		
O.RT	Skilled	861.24, 120.81	-1.756	.091
	Impaired	970.64, 201.36		
OP.RT	Skilled	810.30, 125.18	-1.521	.141
	Impaired	896.99, 158.10		
P.RT	Skilled	846.19, 123.54	-1.445	.195
	Impaired	921.07, 121.50		

Table 3: Mean and SD of the accuracy (ACC) and reaction time (RT) for skilled and impaired readers.

3.2 Functional Connectivity Results

3.2.1 Characterization of spelling networks

3.2.1.1 Inferior frontal gyrus as seed region. Inferior frontal gyrus was chosen as a seed region to generate a general spelling network, for each group, and for all three conditions based on prior research that identified the inferior frontal gyrus as the input area during reading (Cummine et al., 2016).

First, we conducted a between-group comparison of connectivity patterns through independent samples t-test. Results found no significant between-group differences in connection strengths for all three conditions with inferior frontal gyrus as the seed region.

This was followed by an exploratory analysis, where functional connectivity for each group was calculated, with each ROI serving as a seed region. We will discuss these results next.

O condition. Skilled readers demonstrated an extensive network, with inferior frontal gyrus functionally connected to phonological (superior temporal gyrus, caudate), orthographic (fusiform gyrus) and articulatory processes (supplementary motor area, precentral gyrus, putamen) (Figure 6). Impaired readers, on the other hand, showed a reduced network with no connections from the inferior frontal gyrus to the superior temporal gyrus and fusiform gyrus (Figure 2; See Table 4 for all statistics associated with the connections).

OP condition. Similar to the O condition, the inferior frontal gyrus was highly connected with phonological (superior temporal gyrus, caudate) and articulatory (precentral gyrus, putamen, supplementary motor area) regions in skilled readers (Figure 8). Again, a reduced network emerged for impaired readers, with connections to articulatory (supplementary motor area, putamen) and phonological (inferior parietal lobule) regions present (Figure 3; Table 4).

P condition. In contrast to the previous conditions, network for the P condition was much more extensive for impaired readers compared to skilled readers. Skilled readers had a smaller network with connections emanating from inferior frontal gyrus to phonological (superior temporal gyrus, caudate), orthographic (fusiform gyrus) and articulatory regions (supplementary motor area, precentral gyrus, putamen) (Figure 10). Compared to skilled readers, impaired readers demonstrated a much more extensive network with multiple connections to phonological (supramarginal gyrus, superior temporal gyrus, caudate), orthographic (inferior temporal gyrus), and articulatory regions (supplementary motor area, precentral gyrus, putamen, thalamus and cerebellum) (Figure 4; Table 4).

Brain regions	Beta	f (2,17)	p (FDR-corrected)	Brain regions	Beta	f (2,17)	p (FDR-corrected)
Skilled readers				**Impaired readers**			
O condition							
Supplementary motor area	0.46	8.62	0.000001	Supplementary motor area	0.49	5.86	0.005289
Putamen	0.26	6.07	0.000047				
Precentral gyrus	0.36	5.95	0.000047				
Caudate	0.24	5.3	0.000147				
Fusiform gyrus	0.19	4.45	0.000669				
Superior temporal gyrus	0.17	4.17	0.001089				
Cerebellum	0.16	3.37	0.005689				
OP condition							
Supplementary motor area	0.49	10.25	0	Supplementary motor area	0.42	4.31	0.01865
Caudate	0.24	7.36	0.000006	Putamen	0.23	3.97	0.01865
Precentral gyrus	0.34	6.96	0.000008	Inferior parietal lobule	0.31	3.86	0.01865
Putamen	0.21	4.35	0.000959				
Superior temporal gyrus	0.2	3.81	0.002725				
P condition							
Supplementary motor area	0.48	9.17	0.000001	Caudate	0.35	8.98	0.000651
Precentral gyrus	0.32	6.11	0.000045	Supplementary motor area	0.59	7.07	0.001486
Caudate	0.17	5.12	0.000272	Precentral gyrus	0.41	5.3	0.005638
Putamen	0.27	4.93	0.000325	Supramarginal gyrus	0.22	4.34	0.008442
Superior temporal gyrus	0.2	3.97	0.001911	Thalamus	0.09	3.54	0.019154
Fusiform gyrus	0.15	3.35	0.00669	Inferior temporal gyrus	0.11	3.48	0.019154
Cerebellum	0.12	2.52	0.035464	Putamen	0.05	2.91	0.033884

Table 4: Correlation/Beta values and p-values for functional connectivity from inferior frontal gyrus for each group for all three conditions.

a) b)

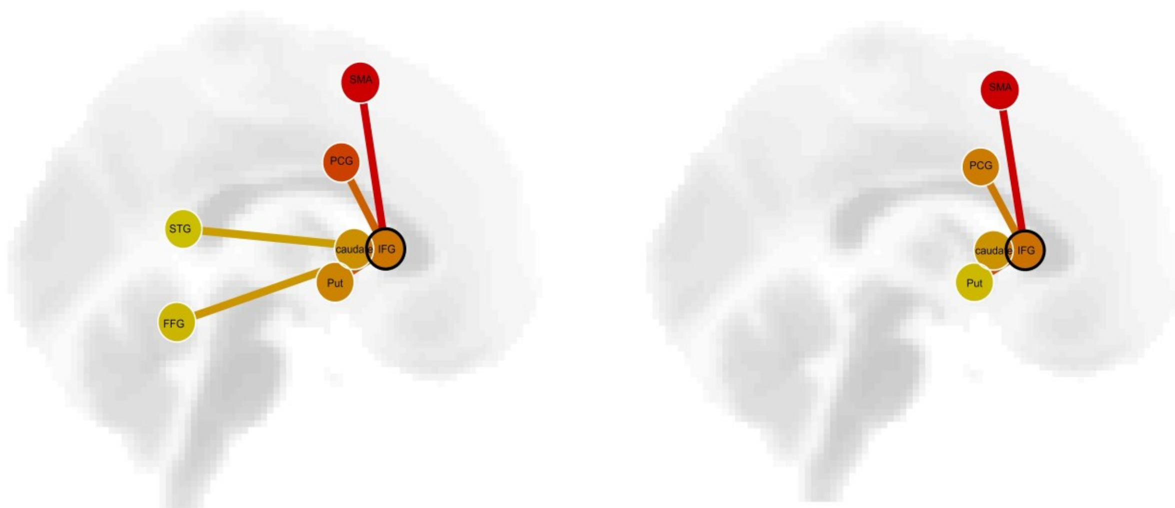


Figure 2: Connectivity of inferior frontal gyrus (circled in black) for O condition in a) skilled readers and b) impaired readers. All connections significant at *p*<0.05, FDR-corrected. Stronger connections are indicated with darker color (red>orange>yellow).

a) b)

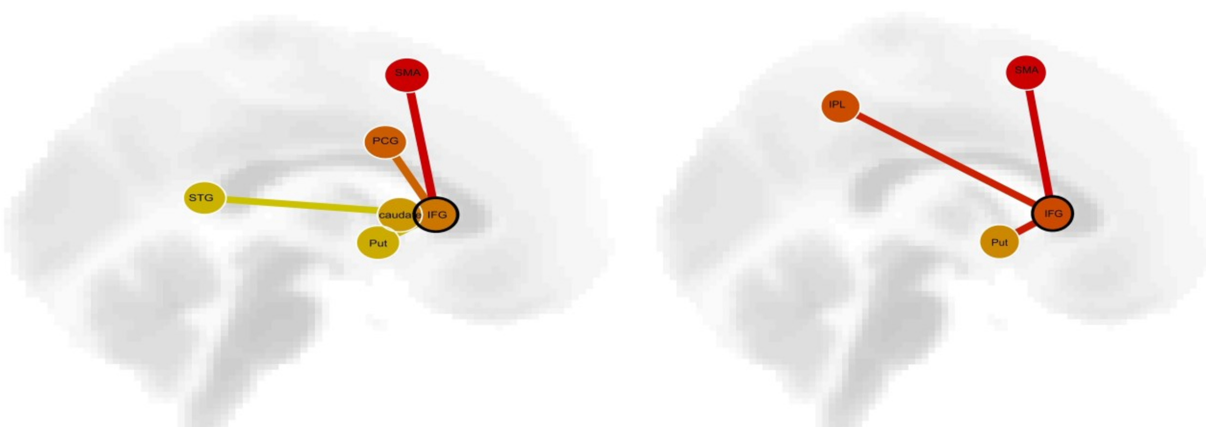


Figure 3: Connectivity of inferior frontal gyrus (circled in black) for OP condition in a) skilled readers and b) impaired readers, p<0.05, corrected. Stronger connections are indicated with darker color (red>orange>yellow).

a) b)

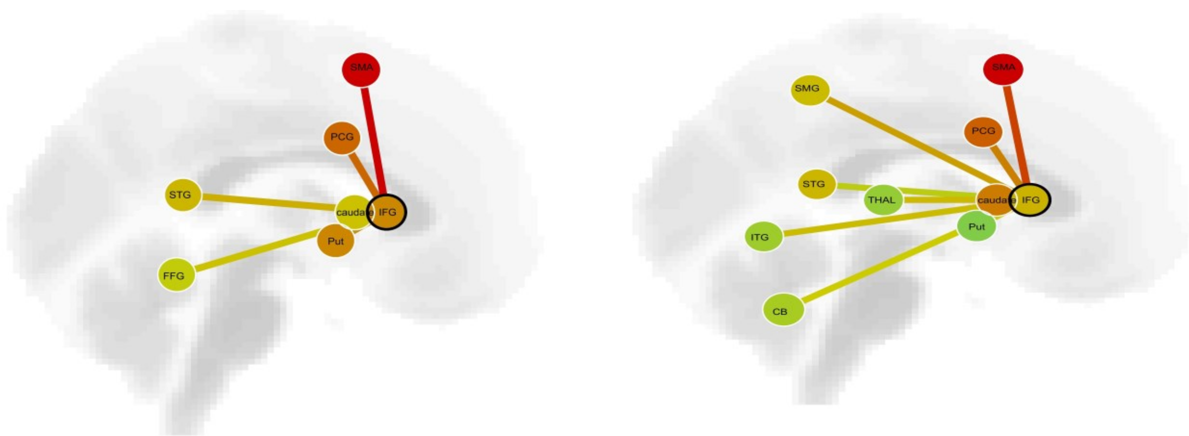


Figure 4: Connectivity of inferior frontal gyrus (circled in black) for P condition in a) skilled readers and b) impaired readers, p<0.05, corrected. Stronger connections are indicated with darker color (red>orange>yellow).

3.2.1.2 All ROIs as seed regions. After the general characterization of spelling networks with inferior frontal gyrus as the seed region, we conducted independent t-tests to test for differences in connectivity strength, for each pairwise connection, between skilled and impaired readers. The only significant connection that emerged was from caudate to cerebellum in the O condition, where skilled readers had stronger caudate – cerebellum connections compared to impaired readers ($p<0.05$ FDR corrected).

This was followed by exploratory analyses, whereby we characterized the functional connectivity of the spelling network with each ROI as a seed region. Presence or absence of connections from each ROI was compared between the two groups for further insight into their connectivity patterns during spelling. These results are discussed next.

O condition. This condition elicited very different functional networks in both groups. Most of the differences were found for connectivity of regions associated with phonological (inferior frontal gyrus, superior temporal gyrus, supramarginal gyrus), orthographic (inferior temporal gyrus and fusiform gyrus) and articulatory processes (putamen, thalamus) (See figure 5 for fusiform gyrus, rest of figures in appendix; Table 5 for beta and *p*-values).

OP condition. When spelling retrieval was optional, similar patterns of results emerged. Fewer connections from the seed regions of phonological (superior temporal gyrus), orthographic (inferior temporal gyrus) and articulatory processes (putamen) were found in impaired readers compared to skilled readers (See figure 6 for putamen connectivity, rest of figures in appendix; See Table 6 for beta and *p*-values).

P condition. When readers were asked to generate spelling, regions associated with phonological (superior temporal gyrus), orthographic (fusiform gyrus) and articulatory processes (putamen) were not functionally connected in the impaired group (Figure 5 for superior temporal gyrus, rest of figures in appendix; See Table 7 for beta and *p*-values).

a) b)

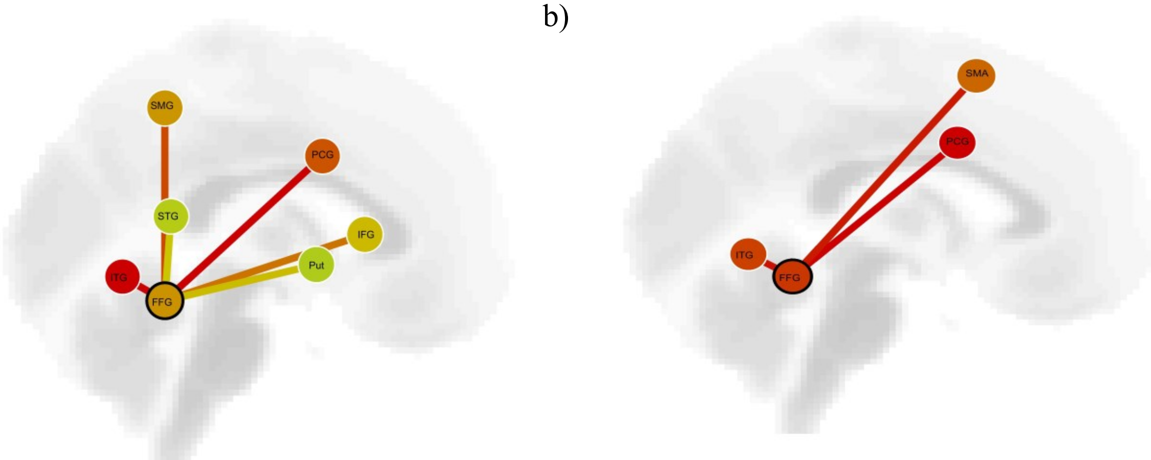


Figure 5: Connectivity of fusiform gyrus (circled in black) for O condition in a) skilled readers and b) impaired readers, $p<0.05$, corrected. Stronger connections are indicated with darker color (red>orange>yellow).

a) b)

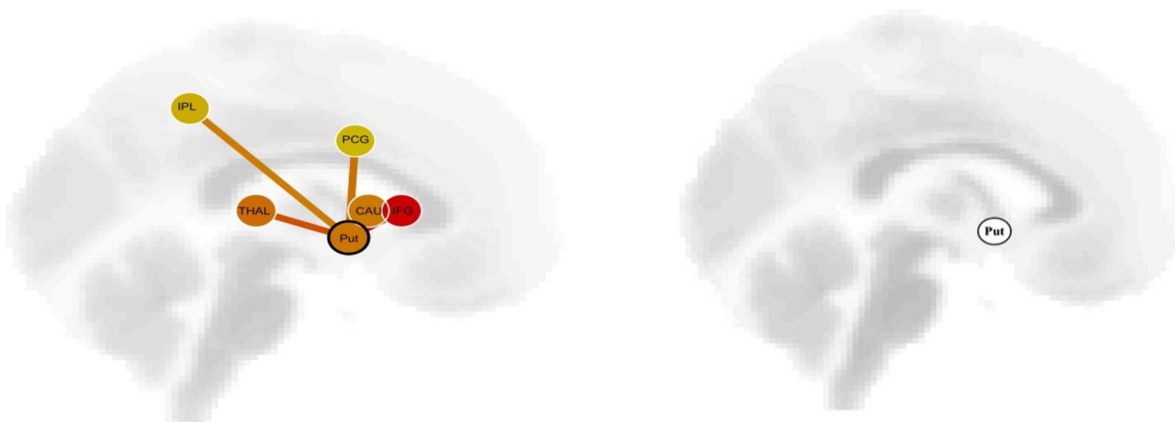


Figure 6: Connectivity of putamen (circled in black) for OP condition in a) skilled readers and b) impaired readers, $p<0.05$, corrected. Stronger connections are indicated with darker color (red>orange>yellow).

a) b)

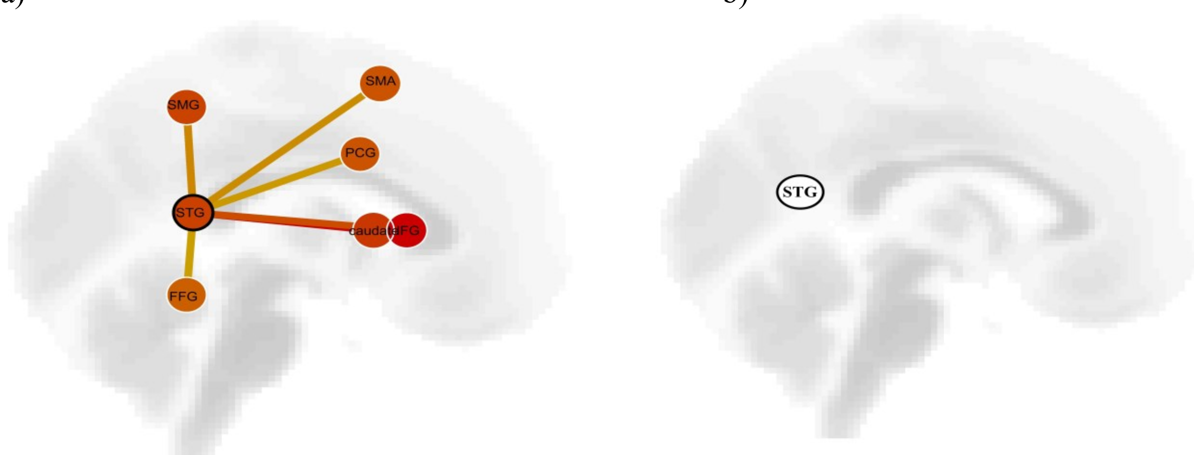


Figure 7: Connectivity of superior temporal gyrus (circled in black) for P condition in a) skilled readers and b) impaired readers, $p<0.05$, corrected. Stronger connections are indicated with darker color (red>orange>yellow).

O condition

Skilled group				Brain regions	Impaired group		
Brain regions	**Beta**	**f (2,17)**	**p (FDR corrected)**		**Beta**	**f (2,17)**	**p (FDR - corrected)**
Seed-Fusiform gyrus							
Precentral gyrus	0.35	7.1	0.000011	Precentral gyrus	0.42	4.03	0.029187
Inferior temporal gyrus	0.47	7.05	0.000011	Inferior temporal gyrus	0.34	3.77	0.029187
Supramarginal gyrus	0.24	5.43	0.000173	Supplementary motor area	0.28	3.69	0.029187
Inferior frontal gyrus	0.19	4.45	0.000781				
Cerebellum	0.18	4.14	0.00133				
Putamen	0.11	2.75	0.02459				
Superior temporal gyrus	0.12	2.54	0.034071				
Seed-Inferior frontal gyrus							
Supplementary motor area	0.46	8.62	0.000001	Supplementary motor area	0.49	5.86	0.005289
Putamen	0.26	6.07	0.000047				
Precentral gyrus	0.36	5.95	0.000047				
Caudate	0.24	5.3	0.000147				
Fusiform gyrus	0.19	4.45	0.000669				
Superior temporal gyrus	0.17	4.17	0.001089				
Cerebellum	0.16	3.37	0.005689				
Seed-Inferior temporal gyrus							
Fusiform gyrus	0.47	7.05	0.000021	Fusiform gyrus	0.34	3.77	0.038135
Supramarginal gyrus	0.23	4.38	0.002692	Supramarginal gyrus	0.3	3.7	0.038135
Putamen	0.11	3.17	0.021624				
Thalamus	0.1	2.95	0.025775				
Inferior frontal gyrus	0.14	2.75	0.032715				
Seed-Putamen							
Inferior frontal gyrus	0.26	6.07	0.000146	Caudate	0.26	4.62	0.025441
Thalamus	0.22	4.9	0.000871	Inferior Frontal gyrus	0.2	4.34	0.025441
Caudate	0.16	3.26	0.013062	Thalamus	0.19	3.66	0.040129
Precentral	0.11	3.26	0.013062				

gyrus							
Inferior temporal gyrus	0.11	3.17	0.013119				
Fusiform gyrus	0.11	2.75	0.028102				
Superior temporal gyrus	0.12	2.4	0.040746				
Seed-Supramarginal gyrus							
Precentral gyrus	0.35	6	0.000169	Cerebellum	0.24	11.09	0.000162
Fusiform gyrus	0.24	5.43	0.000279	Inferior parietal lobule	0.33	6.36	0.002869
Inferior parietal lobule	0.31	5.16	0.000329	Inferior Temporal gyrus	0.3	3.7	0.029665
Inferior temporal gyrus	0.23	4.38	0.001077	Precentral gyrus	0.47	3.68	0.029665
Cerebellum	0.16	3.42	0.007718				
Supplementary motor area	0.15	2.77	0.027063				
Superior temporal gyrus	0.1	2.65	0.030221				
Seed-Superior temporal gyrus							
Inferior frontal gyrus	0.17	4.17	0.004835	NIL			
Precentral gyrus	0.2	3.99	0.004835				
Supplementary motor area	0.24	3.94	0.004835				
Seed-Thalamus							
Putamen	0.22	4.9	0.001742	NIL			
Caudate	0.1	3.4	0.02417				
Inferior temporal gyrus	0.1	2.95	0.042958				

Table 5: Correlation/Beta values and p-values for functional connectivity from seed regions for skilled and impaired readers for O condition.

OP condition

Skilled group				Impaired group			
Brain regions	**Beta**	**f (2,17)**	**p (FDR corrected)**	**Brain regions**	**Beta**	**f (2,17)**	**p (FDR-corrected)**
Seed-Inferior temporal gyrus							
Fusiform gyrus	0.47	5.86	0.000226	NIL			
Supramarginal gyrus	0.18	3.67	0.013				
Cerebellum	0.1	2.84	0.042157				
Thalamus	0.08	2.74	0.042157				
Inferior parietal lobule	0.13	2.72	0.042157				
Seed-Putamen							
Inferior frontal gyrus	0.21	4.35	0.005755	NIL			
Thalamus	0.14	3.2	0.018926				
Caudate	0.13	3.19	0.018926				
Cerebellum	0.13	2.81	0.032641				
Precentral gyrus	0.09	2.75	0.032641				
Inferior parietal lobule	0.09	2.61	0.037904				
Seed-Superior temporal gyrus							
Inferior frontal gyrus	0.2	3.81	0.009537	NIL			
Supplementary motor area	0.21	3.58	0.010671				
Precentral gyrus	0.2	3.41	0.011808				

Table 6: Correlation/Beta values and p-values for functional connectivity from seed regions for skilled and impaired readers for OP condition.

P condition

Skilled group				Impaired group			
Brain regions	**Beta**	**f (2,17)**	**p (FDR corrected)**	**Brain regions**	**Beta**	**f (2,17)**	**p (FDR corrected)**
Seed-Fusiform gyrus							
Inferior temporal gyrus	0.47	7.62	0.000007	Inferior temporal gyrus	0.3	4.65	0.035122
Supramarginal gyrus	0.29	6.85	0.000016				
Precentral	0.33	6.43	0.000024				

gyrus							
Cerebellum	0.16	4.45	0.000766				
Inferior frontal gyrus	0.15	3.35	0.007645				
Superior temporal gyrus	0.13	2.55	0.033822				
Seed-Putamen							
Inferior frontal gyrus	0.27	4.93	0.001626	NIL			
Caudate	0.15	3.8	0.009923				
Thalamus	0.13	3.26	0.021657				
Cerebellum	0.09	2.65	0.036122				
Inferior temporal gyrus	0.09	2.63	0.036122				
Seed-Superior temporal gyrus							
Caudate	0.16	5.3	0.000727	NIL			
Inferior frontal gyrus	0.2	3.97	0.00669				
Supramarginal gyrus	0.15	3.02	0.022001				
Supplementary motor area	0.14	2.89	0.02445				
Precentral gyrus	0.14	2.64	0.035428				
Fusiform gyrus	0.13	2.55	0.037803				

Table 7: Correlation/Beta values and p-values for functional connectivity from seed regions for skilled and impaired readers for P condition.

3.2.1.3 Brain-behaviour relationship for spelling. Positive relationship between the functional connectivity for each seed region and participant's in-scanner behavioural performance (ACC and RT) was calculated for each group. In skilled readers, functional network of inferior frontal gyrus consistently came up as being positively related to accuracy performance for the three spelling conditions (Figure 8, Table 8). On the other hand, caudate connectivity emerged as being positively linked to accuracy performance in impaired readers (Figures 9; Table 8).

Condition	Brain regions	Skilled group- Inferior frontal gyrus			Brain regions	Impaired group- Caudate		
		Beta	f (2, 17)	p (FDR-corrected)		Beta	f (2, 17)	p (FDR-corrected)
O CONDITION	Supplementary motor area	0.46	8.62	0.000001	Supplementary motor area	0.49	5.86	0.005289
	Putamen	0.26	6.07	0.000047				
	Precentral gyrus	0.36	5.95	0.000047				
	Caudate	0.24	5.3	0.000147				
	Fusiform gyrus	0.19	4.45	0.000669				
	Superior temporal gyrus	0.17	4.17	0.001089				
	Cerebellum	0.16	3.37	0.005689				
OP CONDITION	Supplementary motor area	0.49	10.25	0.000003	Supplementary motor area	0.42	4.31	0.01865
	Caudate	0.24	7.36	0.000006	Putamen	0.23	3.97	0.01865
	Precentral gyrus	0.34	6.96	0.000008	Inferior parietal lobule	0.31	3.86	0.01865
	Putamen	0.21	4.35	0.000959				
	Superior temporal gyrus	0.2	3.81	0.002725				
P CONDITION	Supplementary motor area	0.48	9.17	0.000001	Caudate	0.35	8.98	0.000651
	Precentral gyrus	0.32	6.11	0.000045	Supplementary motor area	0.59	7.07	0.001486
	Caudate	0.17	5.12	0.000272	Precentral gyrus	0.41	5.3	0.005638
	Putamen	0.27	4.93	0.000325	Supramarginal gyrus	0.22	4.34	0.008442
	Superior temporal gyrus	0.2	3.97	0.001911	Thalamus	0.09	3.54	0.019154
	Fusiform gyrus	0.15	3.35	0.00669	Inferior temporal gyrus	0.11	3.48	0.019154
	Cerebellum	0.12	2.52	0.035464	Putamen	0.05	2.91	0.033884

Table 8: Correlation/beta values and p-values for between-groups comparison of brain-behavior relationship for spelling between the two groups for all three spelling conditions

a) b) c)

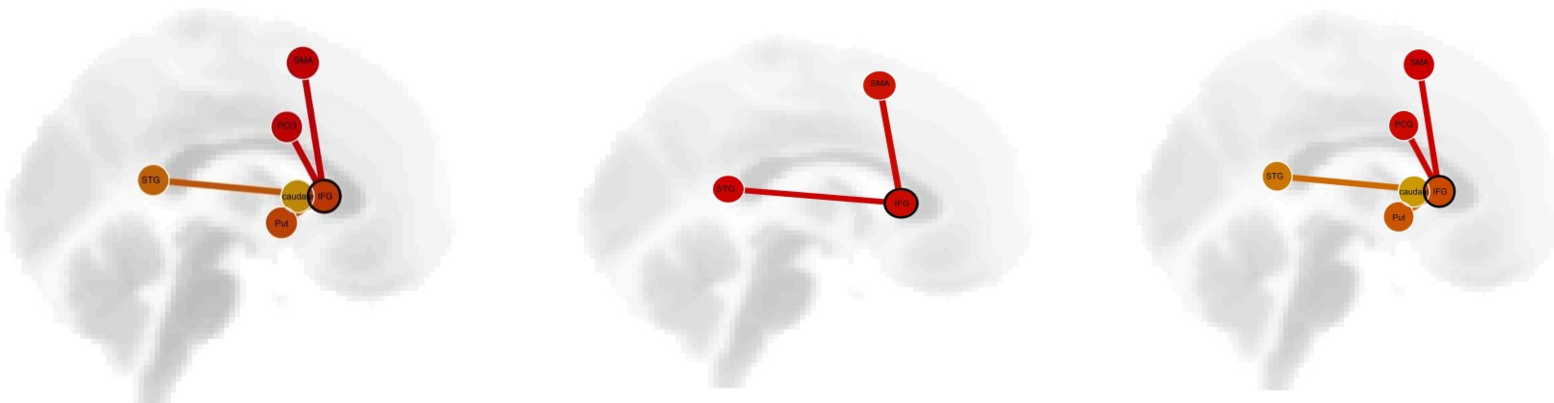


Figure 8: Brain-behaviour relationship in skilled readers between inferior frontal gyrus connectivity and accuracy in a) O, b) OP and c) P conditions. Stronger connections are indicated with darker color (red>orange>yellow).

a) b) c)

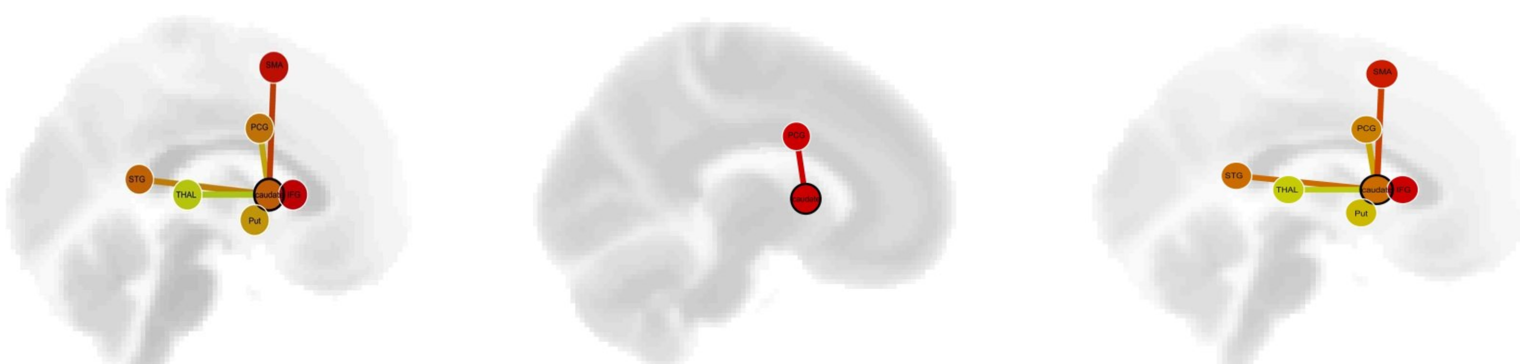


Figure 9: Brain-behaviour relationship in impaired readers between caudate connectivity and accuracy in a) O, b) OP and c) P conditions. Stronger connections are indicated with darker color (red>orange>yellow).

4. Discussion

We sought to examine the behavioural performance and neural networks for spelling in skilled and impaired readers. In line with previous research, individuals with reading impairments performed more poorly on sound/phonological awareness, meaning/morphological information, reading and spelling performance when compared to controls. In terms of connectivity networks, brain regions sensitive to phonology, orthography and articulatory processes were consistently under-connected across the three spelling conditions for individuals with reading impairments. Finally, the brain-behaviour relationships were different between the groups, with skilled readers showing relationships between behaviour and inferior frontal gyrus connectivity whereas impaired readers displaying similar relationship with caudate connectivity. We will discuss implications of these findings in light of our initial research questions, and discuss some potential limitations and future directions related to the work.

4.1 Orthographic, Phonological and Morphological Awareness Skills in Skilled and Impaired Readers

As expected, we found evidence for deficits in reading fluency, reading accuracy and spelling in the reading impaired group. Additionally, they had poor implicit awareness of phonology and morphology but had comparative knowledge of orthographic awareness. Correlation results also suggested that the implicit awareness of language components was emphasized differently for spelling in both groups. These results were, therefore, descriptive of general language capabilities of the two groups.

The behavioural measures of phonological, orthographic and morphological awareness were meant to shed light on the implicit knowledge of these skills in both groups, and how these skills related to their spelling performance. Results showed that impaired readers significantly underperformed on all measures (rate and accuracy) except on orthographic awareness. These findings are in line with previous studies that show that individuals with impaired reading have low levels of phonemic awareness as they face difficulties identifying and subsequently manipulating individual phonemic units (Coleman et al., 2009; Kemp et al., 2009; Tops et al., 2014). With respect to morphological awareness, there is mixed evidence on the adequacy of such skill level in impaired readers (Bruck, 1993; Law et al., 2015; Tops et al., 2014) and our findings are in line with literature that reports deficits in this area of language (Bruck, 1993). Decreased morphological awareness suggests a lower level of knowledge of the morphemic structure of the words (i.e. knowledge of correct use of suffixes, prefixes etc.) and, based on our findings, may be a contributing factor to impaired spelling abilities.

Orthographic awareness was the only area where impaired readers were comparable to skilled readers in the current study. Again, although the findings are mixed, there is some literature showcasing that impaired readers have similar (Pennington et al., 1986) or even superior orthographic skills compared to skilled readers (Siegel, 1995). The extent to which such awareness of the orthographic structure is a compensatory mechanism due to their reliance on remembering orthographic information (i.e. permissible letter strings or grapheme combination to compensate for impaired phonological awareness) or general processing ability is not clear. In either event, the present study indicates that this intact awareness of the orthographic knowledge might not be that useful for spelling purposes as impaired individuals performed poorly on the spelling task than skilled readers. Also, it is not known if impaired readers were actually using their orthographic knowledge during spelling or not. Additional research that explores characteristics of the spelling errors can yield some insight into this area. In general, the behavioural results reported here point to a profile of impaired sound and meaning knowledge with intact orthographic skills in individuals with reading impairments.

An additional goal of the current work was to explore the relationship between spelling and the three language measures to gain insight into how these measures are used during spelling. Correlations between spelling and implicit indicators were done to study the degree of reliance on these skills for spelling. Results showcased that only phonological awareness was predictive of spelling performance in impaired readers, while both phonological and morphological awareness skills were predictive in skilled readers. These results showcase the differences in reliance on implicit knowledge of phonological and morphological skills in both groups. Somewhat in line with previous work (Bruck, 1993; Kemp et al., 2009), orthographic knowledge was not found to be related to spelling in either group.

4.2 In-scanner Behavioural Performance

Individuals with reading impairments had significantly lower accuracy for O and OP conditions and a trend towards low accuracy for P condition compared to skilled readers. While this is the first study to perform in-scanner spelling tasks with individuals with reading impairments, results are in line with previous behavioural studies that show poor spelling performance on both real and pseudowords (Pennington et al., 1986; Bruck, 1993; Kemp et al., 2009). Retrieving real word spellings and assembling pseudoword spelling requires the use of phonological, orthographic and morphological information. Given that the behavioural assessments point towards a lack of phonological and morphological awareness in impaired readers, we hypothesized that their in-scanner spelling performance would suffer as well. Overall, the behavioural performance provided us with unique insights into the strengths and weaknesses of the impaired group in terms of their language abilities, especially their spelling performance.

4.3 Neural Networks associated with Spelling in Skilled and Impaired Readers

4.3.1 Differences in functional connectivity patterns: inferior frontal gyrus. As hypothesized, inferior frontal gyrus as the seed region exhibited the most connected network in both groups across all three spelling conditions. In addition to the vast literature supporting inferior frontal gyrus's role in phonological and semantic processing (Price, 2012; Jobard, Crirello, & Tzourio-Mazoyer, 2003; Taylor, Rastle, & Davis, 2013), it is also posited to be the storage area of well-learned speech sounds (Bohland et al., 2010). Since the letter probe task was an auditory task, the auditory input activated the speech sound units present in inferior frontal gyrus, thus making it the speech input area for the spelling network.

Connectivity of inferior frontal gyrus across the three conditions in skilled readers gives us evidence for an overlapping network consisting of regions associated with sound processing, visual orthographic and articulation processing. For impaired readers, results were both expected and surprising. In support of our hypotheses, connectivity during spelling retrieval (O and OP conditions) was much more restricted in impaired readers. This was in line with their behavioural performance as well as previous studies that showed underconnectivity from inferior frontal gyrus during real word spelling (Finn et al., 2014; Schurz et al., 2014). On the other hand, the pseudoword spelling condition elicited an extensive network of connections in impaired readers. There were additional connections to temporoparietal, frontal and subcortical structures. It is possible that impaired readers had to recruit additional areas related to phonological (supramarginal gyrus) and articulatory processing (thalamus and cerebellum) to perform the task. In terms of subcortical structures, impaired readers had additional connections to caudate, putamen and thalamus as well. This increased reliance on bilateral subcortical structures in poor readers has been previously noticed and was described as their compensatory reliance for articulatory processes (Richlan et al., 2011). This can be true for the pseudoword condition too, where impaired readers might have been compensating for their decreased phonological awareness by relying on effortful articulation to spell pseudowords. Overall, deviant connectivity patterns for spelling real and pseudowords emerged for poor readers with inferior frontal gyrus as the seed region.

4.3.2 Exploratory functional connectivity patterns: all ROIs. Functional connectivity patterns for spelling retrieval and generation were different in each group. Impaired readers had fewer connections from occipito-temporal, frontal and parieto-temporal regions associated with phonological (e.g. inferior frontal gyrus, superior temporal gyrus, supramarginal gyrus), orthographic (e.g. inferior temporal gyrus, fusiform gyrus) and articulatory processing (e.g. precentral gyrus, supplementary motor area). Previous studies involving readers with reading impairments have shown evidence for the reduced connectivity between left-hemispheric frontal, occipito-temporal and parieto-temporal regions during language processing (Boets et al., 2013; Finn et al., 2014; Schurz et al., 2014). Disrupted relationships between these key regions indicate the importance of integrating all this information during the spelling process (Bain, Bailet & Moats, 1991). The current task required participants to first identify the phonological units, while simultaneously activating the relevant semantic representations (in the case of real words), orthographic (grapheme and/or grapheme combinations) and articulatory representations (in case of pseudowords). Thus, strong connections between these areas are imperative for accurate and efficient spelling. The reduced coupling of information between brain regions in impaired readers is also in line with their reduced behavioural performance observed for spelling retrieval and generation in this study.

In addition to the cortical regions, the subcortical regions also demonstrated differential connectivity patterns for both groups. The caudate and putamen were underconnected to other language-related areas (e.g. precentral gyrus, inferior temporal gyrus, inferior frontal gyrus) for impaired readers. Caudate is implicated in phonological processing (Bohland et al., 2010; Tamboer, Scholte & Vorst, 2015; Tettamanti et al., 2005), as this region is found to be involved in selection of appropriate phonological representations. Additionally, subgroups of impaired readers based on caudate activity have been reported in our previous work, where two subgroups of readers displayed differential brain-behaviour relationships for real and pseudoword reading. Therefore, there is evidence for deviant involvement of caudate for reading and spelling behaviour in individuals with reading impairments (Cheema et al., 2017). The putamen, on the other hand, is known for its role in releasing appropriate motor programs for articulation (Bohland et al., 2010) and there has yet to be explicit research that explores the extent to which putamen activity is predictive of reading impairment. Overall, we provide here evidence for reduced functional connectivity between cortical and subcortical structures for impaired readers during various spelling tasks.

Looking at the pattern of underconnectivity across all three spelling conditions, three seed regions emerged as consistently under-connected with other language-related areas: superior temporal gyrus, fusiform gyrus and putamen. Each of these regions will be discussed below.

4.4 Superior Temporal Gyrus: Deficits in Phonological Processing

Lack of connectivity between superior temporal gyrus and frontal regions of inferior frontal gyrus, precentral gyrus, and supplementary motor area consistently emerged for both spelling retrieval and generation. These findings are consistent with the previous task-based connectivity studies (Finn et al., 2014; Schurz et al., 2014), as they have demonstrated reduced coupling between posterior temporal regions with frontal regions during reading tasks. Reduced coupling of superior temporal gyrus with inferior frontal gyrus reflects the poor mapping of phonological representations with appropriate semantic and syntactic representations. This coupling is especially important for retrieving spelling representations of real words. Connections with precentral gyrus and supplementary motor area also point towards this coupling of phonological and articulatory representations. The reading literature has provided evidence for the co-activation of articulatory representations, even during covert reading. Price (2012), in her review, mentioned the idea of association between sounds and articulations during covert reading. Therefore, it seems that the phonological and articulatory associations become associated with each other. It is possible that impaired readers have abnormal integration between phonological and articulatory representations, which might have hampered the spelling retrieval in impaired readers. These connections would also be relevant for spelling generation, as sound-articulatory information is also useful to assemble pseudowords spellings too. Overall, deficits in spelling retrieval and generation can be due to less integration between phonological, articulatory and semantic representations.

The spelling generation task invoked additional connections in skilled readers which were absent in impaired readers, namely between superior temporal gyrus and caudate, supramarginal gyrus and fusiform gyrus. This indicates reduced linkage of phonological (superior temporal gyrus, caudate & supramarginal gyrus) and orthographic representations (fusiform gyrus). This is supported by previous findings, where reduced connectivity within occipitotemporal regions (superior temporal gyrus and fusiform gyrus) was observed in readers with reading impairments (Finn et al., 2014; Schurz et al., 2014). Inclusion of fusiform gyrus for pseudoword spelling was surprising, as fusiform gyrus is posited to be the storage area of visual-orthographic representations (Cohen et al., 2002; Dehaene et al., 2002; Richlan et al., 2011; Tsapkini & Rapp, 2010). But previous studies have reported activation of fusiform gyrus during pseudoword reading as well (Beeson et al., 2003; Omura et al., 2004). Fusiform gyrus was proposed to be a critical area where lexical-semantic and sublexical information integrated to map phonological representations into orthographic units (DeMarco et al., 2017). It was also suggested that fusiform gyrus activation might have been the result of activation of orthographic representations of real words that sounded like pseudowords. For example, after the presentation of a pseudoword like *nace*, representations for similar sounding real words like *face, place, grace* might have become available (DeMarco et al., 2017). This influence of lexical information on pseudoword spelling has been supported by behavioural studies too (Tainturier et al., 2013), providing additional evidence for the involvement of fusiform gyrus during pseudoword spelling. Expectedly, involvement of phonological segmentation (caudate) and processing of sound units (supramarginal gyrus) is essential, as participants need to identify the appropriate sound units before accessing their associated orthographic and articulatory representations to spell pseudowords (Cohen et al., 2002; Dehaene et al., 2001). Overall, previous literature and current findings provide evidence for the importance of connectivity of superior temporal gyrus for both spelling retrieval and assembly.

4.5 Putamen: Deficits in Articulatory Processing

Putamen displayed reduced connectivity with precentral gyrus, cerebellum and inferior temporal gyrus for spelling retrieval and generation. Regarding putamen, there is a dearth of studies that look into the subcortical connectivity with cortical regions during language. Still, mean functional studies point towards putamen's involvement in monitoring timing of speech production and sequencing events during articulation in reading (Bohland et al., 2010; Tettamanti et al., 2005). Therefore, poor integration of putamen with areas associated with timing (cerebellum) and articulation (precentral gyrus) might have impaired the release of appropriate representations during spelling processing in impaired readers (Cummine et al., 2016). Seghier and Price (2010) performed a directed causal modelling study (i.e. assessing the directionality of connections within a network) and found out that putamen mediated the connectivity from anterior occipito-temporal regions (e.g., inferior temporal regions) and precentral regions (precentral gyrus) during overt reading tasks. This was interpreted as putamen being involved in releasing articulation plans to the articulatory regions (i.e. precentral gyrus) through occipito-temporal areas. Although the present study looked into non-directional connections, absence of connectivity between these three areas in impaired readers points towards an impairment in rapid release of phonological and articulatory codes during spelling process as well. Overall, putamen's activity is important for spelling process and further work that elucidates the role of this region in reading impairments is needed.

4.6 Fusiform Gyrus: Deficits in Orthographic Processing

Fusiform gyrus was found to have aberrant connections with frontal (inferior frontal gyrus) and parietal regions (supramarginal gyrus) in impaired readers. Transfer of information between these areas is crucial in retrieval of word spelling representations and reduced integration in impaired readers might have contributed to poor performance of impaired readers during word retrieval conditions (Finn et al., 2014; Schurz et al., 2014). As discussed before (in the superior temporal gyrus section), fusiform gyrus's involvement during pseudoword spelling is well supported and is attributed to the activation of orthographic representations of real words that sound like the presented pseudowords. Overall, the neurocognitive profile of impaired readers includes under-connectivity from the brain regions associated with the key components of language processing.

4.7 Lexical (O/Exception condition) vs Sublexical (P/Pseudoword condition) processing.

Accessing the word specific orthographic representations in O/exception word condition relied on the lexical processing. This condition warranted the additional steps to retrieve the whole-word orthographic representations, as reliance on phonology alone would have regularized the exception words resulting in incorrect decisions. For example, deciding if the letter 'c' is in the exception word like 'yacht' requires retrieving the whole-word orthographic representation of 'yacht'. The behavioural and connectivity results also provide support for the difficulty level of this condition. Participants took more time and had the lowest accuracy on the O condition compared to the other two conditions. Connectivity results also demonstrated a more distributed network of connections for O condition in both skilled and impaired readers compared to the other two conditions. Putamen had additional connections to occipito-temporal (fusiform gyrus and superior temporal gyrus) and frontal area (precentral gyrus), and from thalamus to other subcortical (caudate and putamen) and occipito-temporal regions (inferior temporal gyrus) for the O condition. Involvement of occipito-temporal regions during lexical-semantic processing has been supported by previous findings, where fusiform gyrus and inferior temporal gyrus are proposed to be involved in retrieving whole-word orthographic representations (Binder et al., 2016; Rapscak & Beeson, 2004; 2015). Putamen is known for its role in articulatory processing, while thalamus helps relay both sensory and motor signals (Bohland et al., 2010; Cheema et al., 2017; Tamboer et al., 2015; Tettamanti et al., 2005). While these structures have not been the center of investigations for reading and spelling, connections from putamen and thalamus have been shown to be involved in the articulation of familiar motor sequences. This again provides support for the importance of articulatory rehearsal for spelling real words, while also providing initial evidence for the role of subcortical structures during lexical processing in spelling.

On the other hand, P/pseudoword spelling condition relied on sublexical processing, i.e. systematically applying the phoneme-grapheme correspondence rules to assemble pseudoword spellings. Comparing the connectivity pattern of the P condition with the O condition, there was considerable overlap in connectivity patterns for both conditions. This notion of a distributed network consisting of occipito-temporal, temporo-parietal and frontal regions for pseudoword spelling is supported by previous literature as well (Demarco et al., 2017; Ludersdorfer et al., 2015; Norton et al., 2007). Nonetheless, superior temporal gyrus emerged as one seed region which was additionally connected to areas related to phonological (caudate and supramarginal gyrus) and orthographic processing (fusiform gyrus). As described before, superior temporal gyrus is well-known in both reading and spelling literature for its role in sublexical information processing. It's also part of the dorsal pathway, which is involved in using the sound-letter information to assemble pseudoword spelling (DeMarco et al., 2017). Hickok and Poeppel (2007) proposed that superior temporal gyrus stores the phonological representations that are activated via sublexical features to use for pseudoword spelling and reading. Although our connectivity analyses showed involvement of distributed brain regions for both real and pseudoword spelling, there is evidence for the involvement of specific brain areas for lexical and sublexical processing during spelling.

4.8 Brain-Behaviour Relationship.

In assessing the brain-behaviour relationship in both groups, we found disparate results in both groups. Connectivity of inferior frontal gyrus emerged as having a significant positive relationship with spelling behaviour in skilled readers. Specifically, inferior frontal gyrus's connection with supplementary motor area constantly emerged as being significant across all three conditions. This meant that as the connectivity between these regions increased, so did the behavioural performance. Inferior frontal gyrus's involvement during spelling has been supported by previous findings and its involvement with supplementary motor area further supports the importance of associations between phonological and articulatory representations during skilled spelling (Cummine et al., 2016). These results, in addition to the previous discussion, add to the importance of articulatory representations during skilled spelling performance. Overall, inferior frontal gyrus connectivity is imperative for assimilating required information for skilled spelling generation and assembly.

However, different connectivity patterns were found for impaired readers. Connections from caudate emerged as being significantly related to behavioural performance. As mentioned earlier, caudate is involved in phonological processing and segmentation, and is posited to organize phonemes in appropriate syllable bins during reading (Bohland et al., 2010; Tettamanti et al., 2005). According to the previous literature, caudate seems to have special involvement with impaired reading behaviour. For example, we recently reported on the presence of two subgroups of impaired readers based on caudate activation: a positive caudate activity group (posCaudate; i.e. positive relationship between caudate and thalamus activity) and a negative caudate group (negCaudate; i.e. negative relationship between caudate and thalamus activity) (Cheema et al., 2017). Furthermore, both these groups displayed differential brain-behavior relationships, such that posCaudate group had significant relationship with pseudoword reading, while negCaudate group showed a similar relationship with real word reading. While no such subgroups were noticed in present study, this does point to the aberrant role of caudate for real and pseudoword reading and spelling.

4.9 Limitations and Future Directions

One of the major limitations of the study is the small sample size, especially of the impaired group. Even though fMRI studies have relatively smaller sample sizes due to the complex nature of analysis and cost of scanning sessions, a sample size of nine subjects in the impaired group does limit the statistical power. We tried to increase the statistical power by using the corrected p-values for both behavioural and connectivity analyses and were able to observe clear results emerging in impaired groups, which were with agreement to the previous findings. Nonetheless, future studies should have larger sample sizes to provide support for the current findings.

The conditions in the MRI environment might not have been ideal for an auditory task like the letter probe task. Noises from the MRI equipment might have interfered with the auditory representations. In order to counter this, sound check procedures were performed for every subject to make sure that they are hearing words correctly and special earplugs were provided to cancel out the outside noise. Additionally, accuracy and reaction time data for each participant were reviewed to make sure that they are performing as expected. Therefore, we made sure to not let the noises interfere with their task performance. Future advances in the MRI equipment are needed so that auditory tasks can be performed without any noises interrupting the stimuli.

The notion of how similar or different reading and spelling are in terms of neural activation has always been debated. Both the behavioral and mean functional studies point towards a convergence between the two processes, such that both use similar representations. But no one has looked into how brain regions interact with each other during each process in the same subjects. Studying the functional connectivity of reading and spelling in the same individuals and looking at how the connections look different or similar can provide further insight into how these two processes are related. Future studies can include reading and other linguistic tasks to assess the functional connectivity associated with these tasks.

5. Conclusion

This is the first study to provide a neuropsychological profile for spelling in skilled and impaired readers. Since individuals with reading impairments like dyslexia face lifelong issues with their spelling performance, this investigation is timely and will add to the current literature on understanding written language. Overall, we found that individuals with reading impairments had low levels of phonological and morphological awareness, which were shown to be relevant for their spelling performance. Connectivity analyses showed an aberration in the functional connectivity from the brain regions of fusiform gyrus, superior temporal gyrus and putamen in the impaired group for spelling. This is the first study to show not only the involvement of these brain regions but also their interaction with one another during skilled and impaired spelling. These results provide evidence for the underlying connectivity patterns responsible for spelling performance and also add knowledge for the advancement of theoretical models and remediation approach.

References

1. Bain, A. M., Bailet, L. L., & Moats, L. C. (1991). *Written language disorders: Theory into practice*. Pro-ed.
2. Balota, D. A., Yap, M. J., Hutchison, K. A., Cortese, M. J., Kessler, B., Loftis, B., ... & Treiman, R. (2007). The English lexicon project. *Behavior research methods*, *39*(3), 445-459.
3. Beeson, P., Rapcsak, S., Plante, E., Chargualaf, J., Chung, A., Johnson, S., & Trouard, T. (2003). The neural substrates of writing: A functional magnetic resonance imaging study. *Aphasiology, 17*(6-7), 647-665. doi:10.1080/02687030344000067
4. Binder, J. R., Pillay, S. B., Humphries, C. J., Gross, W. L., Graves, W. W., & Book, D. S. (2016). Surface errors without semantic impairment in acquired dyslexia: a voxel-based lesion–symptom mapping study. *Brain*, *139*(5), 1517-1526.
5. Boets, B., de Beeck, H. P. O., Vandermosten, M., Scott, S. K., Gillebert, C. R., Mantini, D., Bulthe, J., Sunaert, S., Wouters, J., & Ghesquière, P. (2013). Intact but less accessible phonetic representations in adults with dyslexia. *Science*, *342*(6163), 1251-1254.
6. Bohland, J. W., Bullock, D., & Guenther, F. H. (2010). Neural representations and mechanisms for the performance of simple speech sequences. *Journal of cognitive neuroscience*, *22*(7), 1504-1529.
7. Bradley, L., & Bryant, P.E. (1985). *Rhyme and reason in reading and spelling*. Ann Arbor: University of Michigan Press.
8. Bruck, M. (1992). Persistence of dyslexics' phonological awareness deficits. *Developmental psychology*, *28*(5), 874.

9. Bruck, M. (1993). Component spelling skills of college students with childhood diagnoses of dyslexia. *Learning Disability Quarterly*, *16*(3), 171-184.

10. Bruck, M., & Treiman, R. (1990). Phonological awareness and spelling in normal children and dyslexics: The case of initial consonant clusters. *Journal of experimental child psychology*, *50*(1), 156-178.

11. Byrd, C. T., Vallely, M., Anderson, J. D., & Sussman, H. (2012). Nonword repetition and phoneme elision in adults who do and do not stutter. *Journal of fluency disorders*, *37*(3), 188-201.

12. Byrd, C. T., McGill, M., & Usler, E. (2015). Pseudoword repetition and phoneme elision in adults who do and do not stutter: Vocal versus nonvocal performance differences. *Journal of fluency disorders*, *44*, 17-31.

13. Cassar, M., & Treiman, R. (1997). The beginnings of orthographic knowledge: Children's knowledge of double letters in words. *Journal of Educational Psychology*, *89*(4), 631.

14. Cheema, K., Lantz, N. & Cummine, J. (2017). Exploring the role of subcortical structures in developmental reading impairments: Evidence for subgroups differentiated by caudate activity. Accepted in Neuroreport.

15. Cloutman, L., Gingis, L., Newhart, M., Davis, C., Heidler-Gary, J., Crinion, J., & Hillis, A. E. (2009). A neural network critical for spelling. *Annals of Neurology, 66*(2), 249-253. doi:10.1002/ana.21693

16. Cohen, L., Lehéricy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language- specific tuning of visual cortex? Functional properties of the Visual Word Form Area. *Brain*, *125*(5), 1054-1069.

17. Coleman, C., Gregg, N., McLain, L., & Bellair, L. W. (2009). A comparison of spelling performance across young adults with and without dyslexia. *Assessment for effective intervention*. 34(2), 94-105

18. Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. (2001). DRC: A dual route cascaded model of visual word recognition and reading aloud. *Psychological Review, 108*(1), 204-256.

19. Cribben, I., Haraldsdottir, R., Atlas, L. Y., Wager, T. D., & Lindquist, M. A. (2012). Dynamic connectivity regression: determining state-related changes in brain connectivity. *Neuroimage*, *61*(4), 907-920.

20. Cribben, I., Wager, T., & Lindquist, M. (2013). Detecting functional connectivity change points for single-subject fMRI data. *Frontiers in computational neuroscience*, *7*, 143.

21. Cummine, J., Cribben, I., Luu, C., Kim, E., Bahktiari, R., Georgiou, G., & Boliek, C. A. (2016). Understanding the role of speech production in reading: Evidence for a print-to-speech neural network using graphical analysis. *Neuropsychology*, *30*(4), 385.

22. Cummine, J., Jhala, S., Georgiou, G.,Cribben, I., Frietag, J., & Boliek, C.A. (under review). Graphical modeling of the reading network for skilled and impaired readers: The role of the basal ganglia in the print-to-speech network. *Journal of Cognitive Neuroscience.*

23. Dehaene, S., Le Clec'H, G., Poline, J. B., Le Bihan, D., & Cohen, L. (2002). The visual word form area: a prelexical representation of visual words in the fusiform gyrus. *Neuroreport*, *13*(3), 321-325.

24. DeMarco, A. T., Wilson, S. M., Rising, K., Rapcsak, S. Z., & Beeson, P. M. (2017). Neural substrates of sublexical processing for spelling. *Brain and language*, *164*, 118-128.

25. Eckert, M. (2004). Neuroanatomical markers for dyslexia: a review of dyslexia structural imaging studies. The neuroscientist, 10(4), 362-371.

26. Ellis, AW. Spelling and writing (and reading and speaking). In: Ellis, AW., editor. *Normality and Pathology in Cognitive Functions.* London: Academic Press; 1982. p. 113-146.

27. Finn, E. S., Shen, X., Holahan, J. M., Scheinost, D., Lacadie, C., Papademetris, X., Shaywitz S.E., Shaywitz, B.A., & Constable, R. T. (2014). Disruption of functional networks in dyslexia: a whole-brain, data-driven analysis of connectivity. *Biological psychiatry*, *76*(5), 397-404.

28. Friston, K. J. (2011). Functional and effective connectivity: a review. *Brain connectivity*, *1*(1), 13-36.

29. Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, *8*(5), 393-402.

30. Hoeft, F., McCandliss, B. D., Black, J. M., Gantman, A., Zakerani, N., Hulme, C., ... & Gabrieli, J. D. (2011). Neural systems predicting long-term outcome in dyslexia. *Proceedings of the National Academy of Sciences*, *108*(1), 361-366.

31. Houghton, G., & Zorzi, M. (2003). Normal and impaired spelling in a connectionist dual-route architecture. *Cognitive Neuropsychology, 20*(2), 115-162.

32. Hsieh, L. & Rapp, B. (2004). Functional magnetic resonance imaging of the cognitive components of the spelling process. *Brain and Language, 91*(1), 40-41.

33. Indefrey P., Levelt W. J. M. (2000). "The neural correlates of language production," in *The New Cognitive Neurosciences*, ed. Gazzaniga M. S., editor. (Cambridge, MA: MIT Press), 845–865.

34. Jobard, G., Crivello, F., & Tzourio-Mazoyer, N. (2003). Evaluation of the dual route theory of reading: a metanalysis of 35 neuroimaging studies. *Neuroimage*, *20*(2), 693-712.

35. Kemp, N., Parrila, R. K., & Kirby, J. R. (2009). Phonological and orthographic spelling in high- functioning adult dyslexics. *Dyslexia*, *15*(2), 105-128.

36. Koyama, M. S., Di Martino, A., Zuo, X. N., Kelly, C., Mennes, M., Jutagir, D. R., Castellanos, X., & Milham, M. P. (2011). Resting-state functional connectivity indexes reading competence in children and adults. *The Journal of Neuroscience*, *31*(23), 8617-8624.

37. Law, J. M., Wouters, J., & Ghesquière, P. (2015). Morphological awareness and its role in compensation in adults with dyslexia. *Dyslexia*, *21*(3), 254-272.

38. Ludersdorfer, P., Kronbichler, M., & Wimmer, H. (2015). Accessing orthographic representations from speech: the role of left ventral occipitotemporal cortex in spelling. *Human Brain Mapping*, *36*(4), 1393-1406.

39. Mahony, D. L. (1994). Using sensitivity to word structure to explain variance in high school and college level reading ability. *Reading and Writing*, *6*(1), 19-44.

40. Manis, F. R., Szeszulski, P. A., Holt, L. K., & Graves, K. (1990). Variation in component word recognition and spelling skills among dyslexic children and normal readers.

41. Martin, A., Schurz, M., Kronbichler, M., & Richlan, F. (2015). Reading in the brain of children and adults: A meta- analysis of 40 functional magnetic resonance imaging studies. *Human brain mapping*, *36*(5), 1963-1981.

42. Maughan, B., Messer, J., Collishaw, S., Pickles, A., Snowling, M., Yule, W., & Rutter, M. (2009). Persistence of literacy problems: spelling in adolescence and at mid- life. *Journal of Child Psychology and Psychiatry*, *50*(8), 893-901.

43. Mechelli, A., Crinion, J. T., Long, S., Friston, K. J., Ralph, M. A. L., Patterson, K., McClelland, J. L. & Price, C. J. (2005). Dissociating reading processes on the basis of neuronal interactions. *Journal of cognitive neuroscience*, *17*(11), 1753-1765.

44. Meinshausen, N., & Bühlmann, P. (2010). Stability selection. Journal of the Royal Statistical Society: Series B (Statistical Methodology), 72(4), 417-473.

45. Meyler, A., & Breznitz, Z. (2003). Processing of phonological, orthographic and cross-modal word representations among adult dyslexic and normal readers. *Reading and Writing*, *16*(8), 785-803.

46. Miller- Shaul, S. (2005). The characteristics of young and adult dyslexics readers on reading and reading related cognitive tasks as compared to normal readers. *Dyslexia*, *11*(2), 132-151.

47. Moats, L. C. (2005). How spelling supports reading. *American Educator*, *6*(12–22), 42-43.

48. Nergård- Nilssen, T., & Hulme, C. (2014). Developmental dyslexia in adults: Behavioural manifestations and cognitive correlates. *Dyslexia*, *20*(3), 191-207.

49. Norton, E. S., Beach, S. D., & Gabrieli, J. D. (2015). Neurobiology of dyslexia. *Current Opinion in Neurobiology,30*, 73-78. doi:10.1016/j.conb.2014.09.007

50. Norton, E. S., Kovelman, I., & Petitto, L. (2007). Are There Separate Neural Systems for Spelling? New Insights into the Role of Rules and Memory in Spelling from Functional Magnetic Resonance Imaging. *Mind, Brain, and Education, 1*(1), 48-59.

51. Olson, R., Forsberg, H., Wise, B., & Rack, J. (1994). Measurement of word recognition, orthographic, and phonological skills. In G. R. Lyon (Ed.), Frames of reference for the assessment of learning disabilities: New views on measurement issues (pp. 243-277). Baltimore: Paul H Brookes Publishing.

52. Omura, K., Tsukamoto, T., Kotani, Y., Ohgami, Y., & Yoshikawa, K. (2004). Neural correlates of phoneme-to-grapheme conversion. *Neuroreport*, *15*(6), 949-953.

53. Pennington, B. F., McCabe, L. L., Smith, S. D., Lefly, D. L., Bookman, M. O., Kimberling, W. J., & Lubs, H. A. (1986). Spelling errors in adults with a form of familial dyslexia. *Child development*, 1001-1013.

54. Philipose, L. E., Gottesman, R. F., Newhart, M., Kleinman, J. T., Herskovits, E. H., Pawlak, M. A., Marsh, E. B., Davis, C., Heidler -Gary, J., & Hillis, A. E. (2007). Neural regions essential for reading and spelling of words and pseudowords. *Annals of Neurology, 62*(5), 481-492. doi:10.1002/ana.21182

55. Pitchford, N. J., Ledgeway, T., & Masterson, J. (2008). Effect of orthographic processes on letter position encoding. *Journal of Research in Reading*, *31*(1), 97-116.

56. Plaut, D.C. (1999). A connectionist approach to word reading and acquired dyslexia: Extension to sequential processing. *Cognitive Science, 23*, 543-568.

57. Price, C. J. (2012). A review and synthesis of the first 20years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImage, 62*(2), 816-847.

58. Purcell, J. J., Napoliello, E. M., & Eden, G. F. (2011). A combined fMRI study of typed spelling and reading. *NeuroImage, 55*(2), 750-762. doi:10.1016/j.neuroimage.2010.11.042

59. Rapcsak, S. Z., & Beeson, P. M. (2002). *Neuroanatomical correlates of spelling and writing*. In A. E. Hillis (Ed.), Handbook on adult language disorders: Integrating cognitive neuropsychology, neurology, and rehabilitation (pp. 71–99). Philadelphia: Psychology Press.

60. Rapcsak, S. Z., & Beeson, P. M. (2004). The role of left posterior inferior temporal cortex in spelling. *Neurology, 62*(12), 2221-2229. doi:10.1212/01.wnl.0000130169.60752.c5

61. Rapcsak, S. Z., Henry, M. L., Teague, S. L., Carnahan, S. D., & Beeson, P. M. (2007). Do dual-route models accurately predict reading and spelling performance in individuals with acquired alexia and agraphia? *Neuropsychologia, 45*(11), 2519-2524. doi:10.1016/j.neuropsychologia.2007.03.019

62. Rapcsak, S. Z., Beeson, P. M., & Hillis, A. (2002). Neuroanatomical correlates of spelling and writing. *The handbook of adult language disorders*, 71-99.

63. Rapp, B., & Dufor, O. (2011). The Neurotopography of Written Word Production: An fMRI Investigation of the Distribution of Sensitivity to Length and Frequency. *Journal of Cognitive Neuroscience, 23*(12), 4067-4081. doi:10.1162/jocn_a_00109

64. Rapp, B., & Lipka, K. (2011). The literate brain: the relationship between spelling and reading. *Journal of cognitive neuroscience*, *23*(5), 1180-1197.

65. Rapp, B., Epstein, C., & Tainturier, M. (2002). The integration of information across lexical and sublexical processes in spelling. *Cognitive Neuropsychology, 19*(1), 1-29. doi:10.1080/0264329014300060

66. Rapp, B., Purcell, J., Hillis, A. E., Capasso, R., & Miceli, G. (2015). Neural bases of orthographic long-term memory and working memory in dysgraphia. *Brain, 139*(2), 588-604. doi:10.1093/brain/awv348

67. Richards, T. L., Berninger, V. W., & Fayol, M. (2009). fMRI activation differences between 11-year-old good and poor spellers' access in working memory to temporary and long-term orthographic representations. *Journal of Neurolinguistics*, *22*(4), 327-353.

68. Richlan, F. (2012). Developmental dyslexias: dysfunction of a left hemisphere reading network. *Frontiers in human neuroscience*, *6*, 120.

69. Richlan, F., Kronbichler, M., & Wimmer, H. (2011). Meta-analyzing brain dysfunctions in dyslexic children and adults. *Neuroimage*, *56*(3), 1735-1742.

70. Roeltgen, D. P., & Heilman, K. M. (1985). Review of agraphia and a proposal for an anatomically-based neuropsychological model of writing. *Applied Psycholinguistics Appl. Psycholing, 6*(03), 205. doi:10.1017/s0142716400006184

71. Rohl, M., & Tunmer, W. E. (1988). Phonemic segmentation skill and spelling acquisition. *Applied Psycholinguistics*, *9*(04), 335-350.

72. Schurz, M., Wimmer, H., Richlan, F., Ludersdorfer, P., Klackl, J., & Kronbichler, M. (2014). Resting-state and task-based functional brain connectivity in developmental dyslexia. *Cerebral Cortex, 25*(10), 3502-3514.

73. Seghier, M. L., & Price, C. J. (2009). Reading aloud boosts connectivity through the putamen. *Cerebral Cortex*, *20*(3), 570-582.

74. Shaywitz, S. E. (1998). Dyslexia. *New England Journal of Medicine*, *338*(5), 307-312.

75. Shaywitz, S. E., & Shaywitz, B. A. (2005). Dyslexia (specific reading disability). *Biological psychiatry*, *57*(11), 1301-1309.

76. Siegel, L. S., Share, D., & Geva, E. (1995). Evidence for superior orthographic skills in dyslexics. *Psychological Science*, *6*(4), 250-254.

77. Stahl, S. A., & Murray, B. A. (1994). Defining phonological awareness and its relationship to early reading. *Journal of Educational Psychology,86*(2), 221-234. doi:10.1037//0022-0663.86.2.221

78. Tainturier, M. J., Bosse, M. L., Roberts, D. J., Valdois, S., & Rapp, B. (2013). Lexical neighborhood effects in pseudoword spelling. *Frontiers in psychology*, *4*.

79. Tamboer, P., Scholte, H. S., & Vorst, H. C. (2015). Dyslexia and voxel-based morphometry: correlations between five behavioural measures of dyslexia and gray and white matter volumes. *Annals of dyslexia*, *65*(3), 121-141.

80. Taylor, J. S. H., Rastle, K., & Davis, M. H. (2013). Can cognitive models explain brain activation during word and pseudoword reading? A meta-analysis of 36 neuroimaging studies. Psychological Bulletin, 139(4), 766-791

81. Tettamanti, M., Moro, A., Messa, C., Moresco, R. M., Rizzo, G., Carpinelli, A., et al. Basal ganglia and language: phonology modulates dopaminergic release. Neuroreport. 2005; 16.4: 397-401.

82. Tops, W., Callens, M., Bijn, E., & Brysbaert, M. (2014). Spelling in Adolescents With Dyslexia: Errors and Modes of Assessment. *Journal of Learning Disabilities,47*(4), 295-306. doi:10.1177/0022219412468159

83. Tsapkini, K., & Rapp, B. (2010). The orthography-specific functions of the left fusiform gyrus: Evidence of modality and category specificity. *Cortex*, *46*(2), 185-205.

84. Tsapkini, K., Vasconcellos-Faria, A., & Hillis, A. (2012). Neural Substrates of Spelling Mechanisms: Evidence from Primary Progressive Aphasia. *Procedia - Social and Behavioral Sciences, 61*, 311-312. doi:10.1016/j.sbspro.2012.10.202

85. Tunmer, W. E., & Rohl, M. (1991). Phonological awareness and reading acquisition. In *Phonological awareness in reading* (pp. 1-30). Springer New York.

86. Vellutino, F. R., & Fletcher, J. M. (2005). Developmental Dyslexia. In M. J. Snowling & C. Hulme (Eds.), Blackwell handbooks of developmental psychology. The science of reading: A handbook (pp. 362-378). http://dx.doi.org/10.1002/9780470757642.ch19

87. Whitfield-Gabrieli, S., & Nieto-Castanon, A. (2012). Conn: a functional connectivity toolbox for correlated and anticorrelated brain networks. *Brain connectivity*, *2*(3), 125-141.

88. Wilson, A. M., & Lesaux, N. K. (2001). Persistence of phonological processing deficits in college students with dyslexia who have age-appropriate reading skills. *Journal of learning disabilities*, *34*(5), 394-400.

Appendix

Table 9: Phonological awareness task

Instructions: This is a list of non-words, I will say the word first, then I will say the one sound that you need to omit from the word and pronounce it again as it would be said without the indicated sound. I want to look at me when saying the word first, but not when I ask you to omit the sound/letter. Eg /smunk/- repeat the word- without the k

1. FACKTON (without the /f/)
2. GEINCHER (without the /ch/)
3. HEELON (without the /n/)
4. HESTOMEE (without the /t/)
5. INKISTA (without the /k/)
6. JELLANTIF (without the /f/)
7. JIGVENTOXILE (without the /j/)
8. CASTIPAILTY (without the /p/)
9. ANTISKOLDATE (without the /k/)
10. DIGANTULIN (without the /d/)
11. FINRAPTOKING (without the /k/)
12. GUNDOCTIPEEL (without the /d/)
13. HISSYDOGENE (without the /h/)
14. IMLACSODOCK (without the /s/)
15. VAYTACHIDOP (without the /d/)
16. DAVONOCHIG (without the /g/)
17. NYCHOYTOB (without the /ch/)
18. TAVACHEENYG (without the /g/)

19. ZOOBENTOPINE (without the /z/)
20. VAMPONTRICAY (without the /k/)
21. ASKENDOLATE (without the /d/)
22. DAYBISHOCKO (without the /sh/)
23. FOMMILONTI (without the /l/)
24. GISTORPULIN (without the /n/)
25. HUNDINOTY (without the /h/)
26. INFASDEENT (without the /t/)
27. JEDABULOS (without the /b/)
28. KADENISO (without the /d/)
29. BENALOPY (without the /l/)
30. ANNITIZER (without the /z/)

Table 10. Morphological awareness task

You will see a sentence with a blank, followed by four options. Read the sentence and circle the nonsense word that best fits the sentence.

Example:

Despite her knowledge, the ________ was unable to respond to the question.

Floxatize floxatism floxatist floxatation

1. Desert animals are not normally _____.

commalianization commalious commalianism commalianize

2. Please _____ these forms as soon as possible.

scribsumptist scribsumptious scribsumptian scribsumptize

3. The meeting was highly _____ and invigorating.

loquarify loquarial loquarialize loquarialism

4. Their progress was stopped by an unexpected _____

postramify postramic postramity postramicize

5. Their approach to the problem is deceptively _____.

torbatify torbative torbativize torbature

6. The breeders _____ their stock every four generations.

genilify genility genilification geniliar

7. Everyone resented the obvious _____ on the manager's part.

spectitious spectitionalize spectition spectitive

8. All the suspiciously _____ specimens are kept in a separate tank. *tribacize tribacion tribacism tribacious*

9. They _____ the data in the back office.

curfamic curfamation curfamate curfamity

10. All those models are strictly _____ and outdated as well.

ambilemptify ambilemptivist ambilemptity ambilemptive

11. In spite of his _____, he did an outstanding job.

dispribize dispribation dispribational dispribify
12. He is so _____ that he offends almost everyone.

dictopithify dictopithification dictopithial dictopithit

13. You can't even begin to _____ without modern equipment.

equamanize equamanizable equamanity equamanive

14. They presented the highly _____ evidence first.

credenthive credenthification credenthicism

credenthify 15. They hope to _____the two sides

together. *uniromosity uniromify uniromous uniromative*

16. He wants to _____ while he still can.

fidamoration fidamorian fidamorational fidamorate

17. Please try to be as totally _____ as possible.

progenalism progenalize progenious progenify

18. The story of the _____ was repeated every year.

vergalize vergalicious vergalify vergalist

19. The most _____ samples were discarded.

birendal birendment birendalize birendify

20. If we can just overcome its inherent _____ schedule.

antiflidify antiflidian antidacious antiflidicity

21. Dr. Jones, a well-known _____, is speaking tonight.

circumtarious circumtarist circumtarify circumtariz

22. We should _____ that money by the end of the year.

relaptification relaptian relaptify relapmble

23. His _____ is greatly admired.

superfilize superfilive superfilial superfilation 24.

Too much _____ is bad for the economy. *malburuity*

malburuify malburnicious malburuable

25. She met her first _____ when she moved out west.

benedumptist benefumptify benedumptize benedumptuous

26. You must _____ them quickly or you'll ruin the colors.

premanicism premanicize premanicity premanic

27. The new equipment will _____ everything automatically.

transurbate transurbativity transurbatist transurbative

Table 11. Orthographic awareness task

Out of the word pairs presented below, I'd like you to circle the one word that looks most like it could be a real word in English.

beff-ffeb	jofy-fojy	bey-bei
vadd-vaad	vosst-vost	furb-firb
dau-daw	qoast-quost	miln-milg
filv-filk	nuck-ckun	gwup-gnup
moke-moje	aut-awt	jeex-jeeks
dake-dayk	vism-visn	ffim-phim
fage-fajy	fant-tanf	nurm-nerm
vadding-vayying	hift-hifl	togd-togn
moyi-moil	wibz-wibs	nitl-nilt
clid-cdil	vose-voaz	toove-touve
dlun-lund	yikk-yinn	booce-buice
bnad-blad	ist-iit	gri-gry
boap-bowp	yb-ib	hoin-hoyn
holp-hollp	powl-lowp	wolg-wolt
ddaled-dalled	cnif-crif	lerst-lurst
muun-munt	sckap-skap	
chim-chym	lape-laip	
tolz-tolb	ckader-dacker	

Table 12: Stimuli for the three letter probe conditions

Stimuli	Letter probes
O condition	
sweat	a
sauce	c
calf	l
ache	h
sieve	c
trough	f
fiend	y
learn	a
geese	c
taunt	u
cough	k
paste	e
luge	j
ruse	z
mould	u
hook	u
chef	c
glove	e
mauve	u
haunt	u
suede	w
quische	k
plague	u
grey	e
moose	e
ghoul	h
gist	j
sponge	g
flood	u
fraud	u
ton	u
knoll	k
baste	e
suave	u
crook	u
castle	k
pause	z

balm	l
feud	e
steak	c
crow	k
shoe	u
plaid	i
seize	w
scarce	k
drawer	w
host	d
isle	s
monk	u
comb	b
scroll	k
mourn	u
dough	w
gross	e
halve	l
hearth	e
psalm	p
deaf	a
court	k
tomb	b
chord	k
shove	c
chic	k
sew	e
soot	o
cask	c
veil	a
mow	e
pear	a
brooch	w
juice	s
deuce	s
swear	i
pint	y
waltz	s
OP condition	
roam	y

flame	i
grail	i
crumb	k
germ	a
plum	n
state	w
sore	f
spur	s
thrust	a
reef	r
grove	v
clump	b
coin	o
brag	j
ditch	s
crypt	y
chant	b
notch	d
slate	d
slug	u
float	w
brisk	r
shelf	e
slob	b
saint	e
coach	s
harp	d
stump	t
shed	b
slope	l
pleat	p
plea	a
carve	r
smirk	i
pole	w
scribe	b
shack	a
snag	e
mince	r
frown	w
helm	m

graze	g
coax	k
spark	e
plod	u
crawl	w
lurk	e
pine	r
glib	b
graft	g
midst	e
freak	c
boost	o
drake	r
charm	e
moan	a
mesh	e
mirth	e
aide	d
spray	i
leaf	i
cube	u
hall	h
oath	a
merge	g
bred	u
cling	g
whim	m
glee	e
shrug	e
limp	l
sparse	s
craze	e
flirt	e
P condition	
prease	r
sonse	g
mert	k
oatch	g
foat	f
crove	d
grabe	i

fape	p
jight	i
hoak	u
owv	a
luve	v
belk	a
binch	a
threet	u
greal	c
triat	i
feen	d
flink	i
citch	i
glibe	u
heaf	i
lecs	e
liss	l
hoorse	r
pench	e
meent	e
darf	e
mook	o
glave	b
welf	f
prown	n
bloss	t
rell	l
rinch	o
laught	y
gowl	l
ciste	u
fren	t
jatch	a
gatch	s
breek	r
cust	r
norve	n
tronce	r
scranch	p
drass	s
frudge	u

glond	g
guze	o
swoap	o
soize	s
loive	q
grev	e
hez	y
breest	i
cime	m
moive	b
sark	a
bluck	p
nass	s
pribe	u
grov	p
teaf	t
gress	r
besh	b
honce	h
brair	o
soite	a
prave	n
flane	a
pape	d
trath	r
sheb	l
frant	n

Figures: Connectivity of seed regions for skilled and impaired readers

a) b)

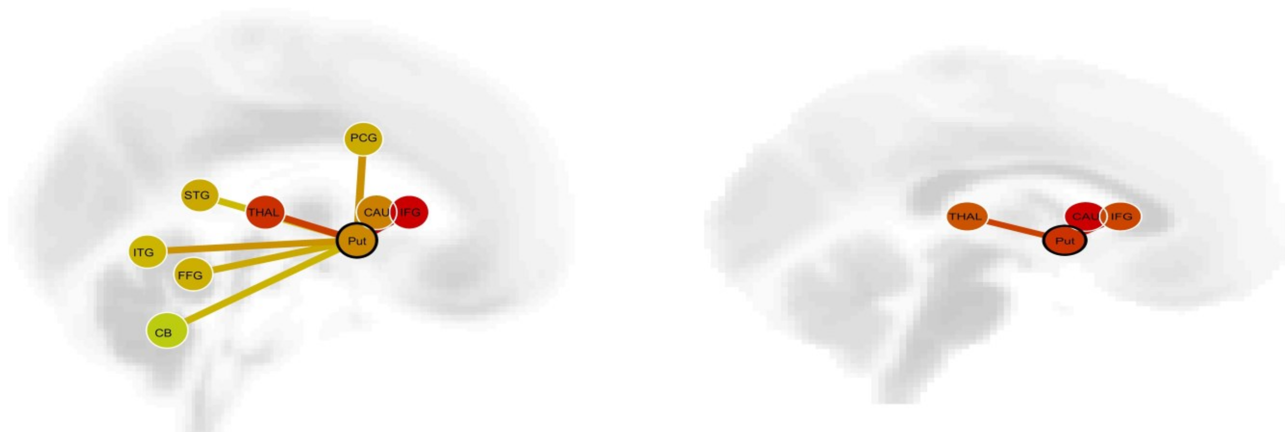


Figure 10: Connectivity of putamen (circled in black) for O condition in a) skilled readers and b) impaired readers, p<0.05, corrected. . Stronger connections are indicated with darker color (red>orange>yellow).

a) b)

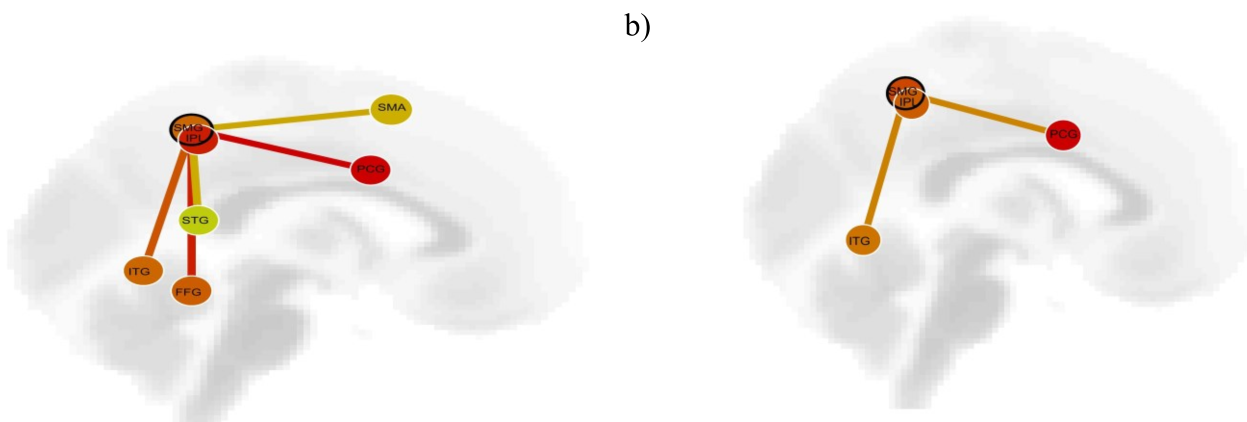


Figure 11: Connectivity of supramarginal gyrus (circled in black) for O condition in a) skilled readers and b) impaired readers, p<0.05, corrected. . Stronger connections are indicated with darker color (red>orange>yellow).

a) b)

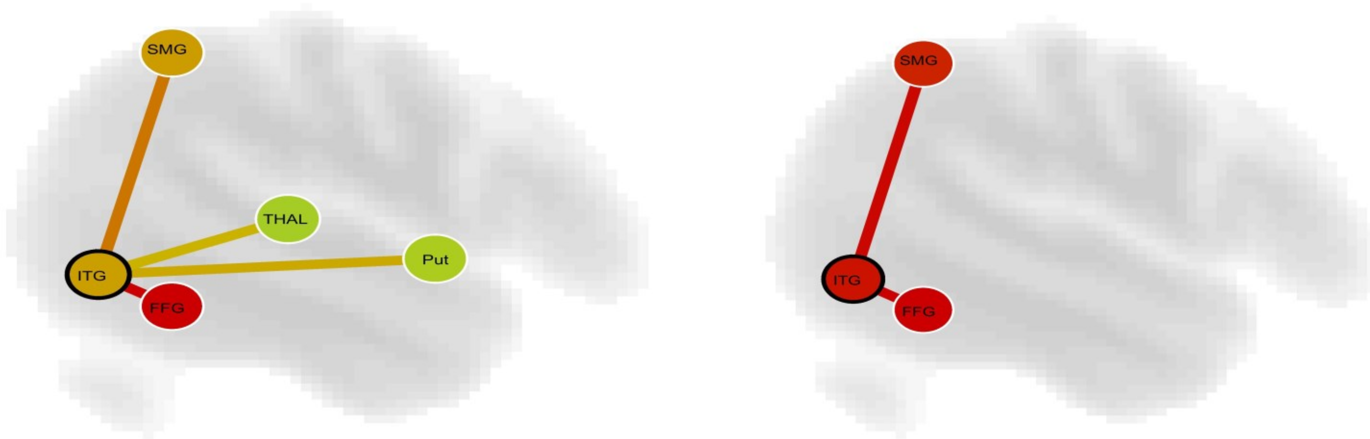


Figure 12: Connectivity of inferior temporal gyrus (circled in black) for O condition in a) skilled readers and b) impaired readers, $p<0.05$, corrected. Stronger connections are indicated with darker color (red>orange>yellow).

a) b)

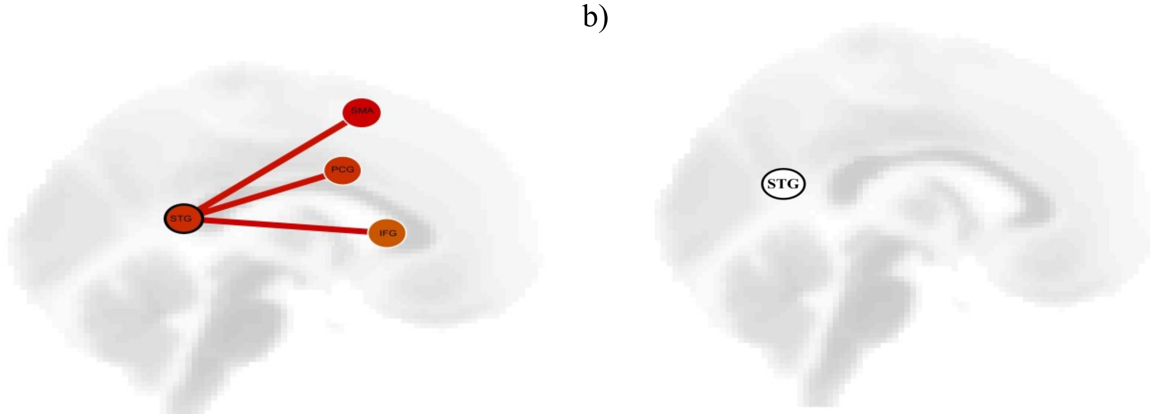


Figure 13: Connectivity of superior temporal gyrus (circled in black) for O condition in a) skilled readers and b) impaired readers, $p<0.05$, corrected. Stronger connections are indicated with darker color (red>orange>yellow).

a) b)

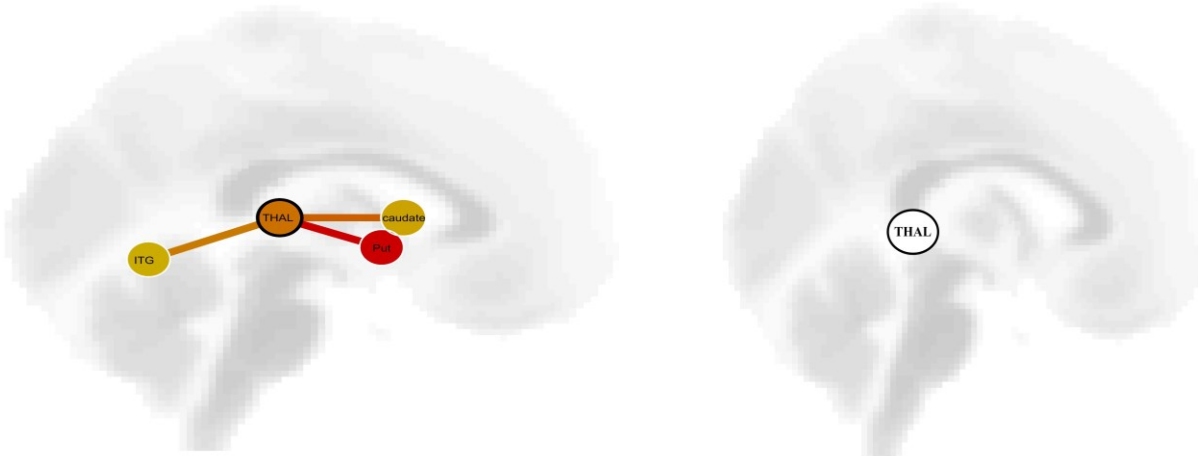


Figure 14: Connectivity of thalamus (circled in black) for O condition in a) skilled readers and b) impaired readers, p<0.05, corrected. Stronger connections are indicated with darker color (red>orange>yellow).

a) b)

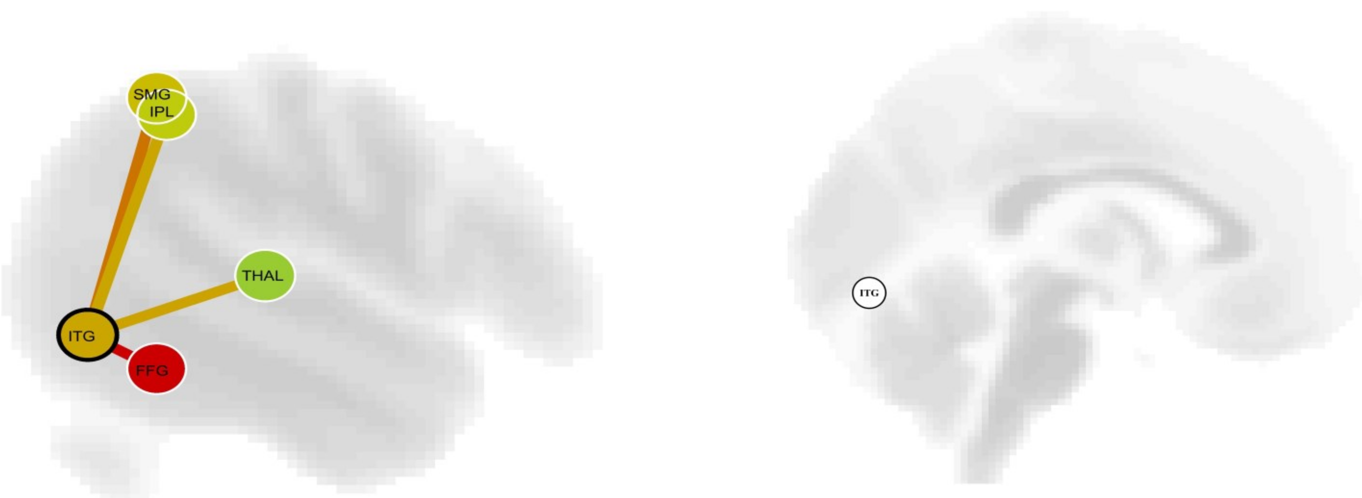


Figure 15: Connectivity of inferior temporal gyrus (circled in black) for OP condition in a) skilled readers and b) impaired readers, p<0.05, corrected. Stronger connections are indicated with darker color (red>orange>yellow).

a) b)

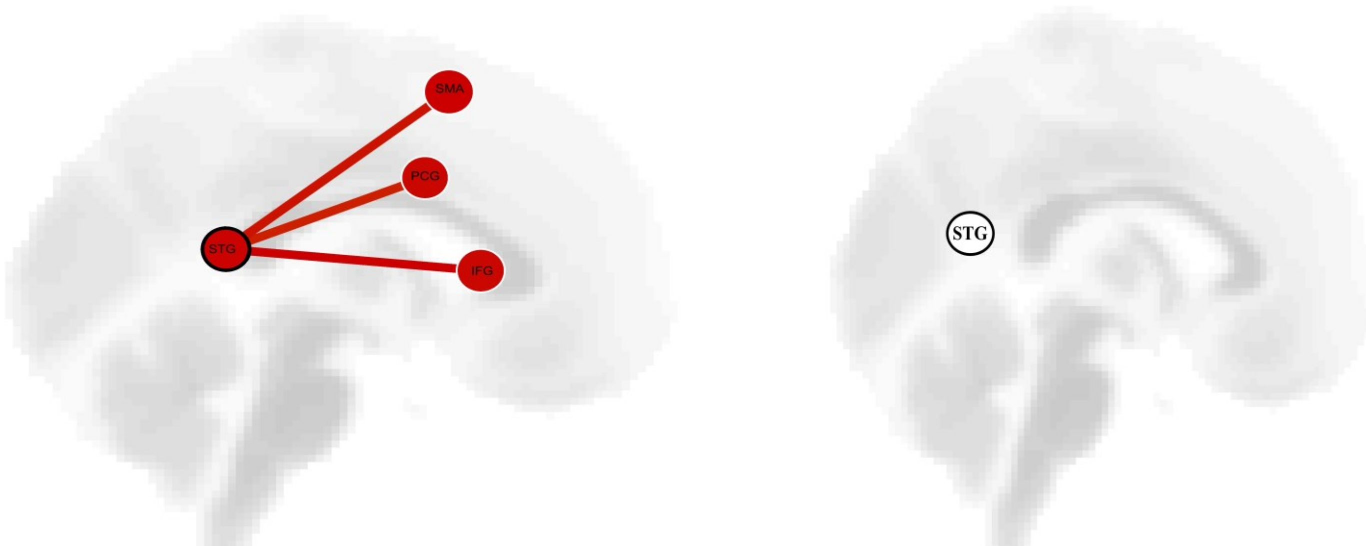


Figure 16: Connectivity of superior temporal gyrus (circled in black) for OP condition in a) skilled readers and b) impaired readers, p<0.05, corrected. Stronger connections are indicated with darker color (red>orange>yellow).

a) b)

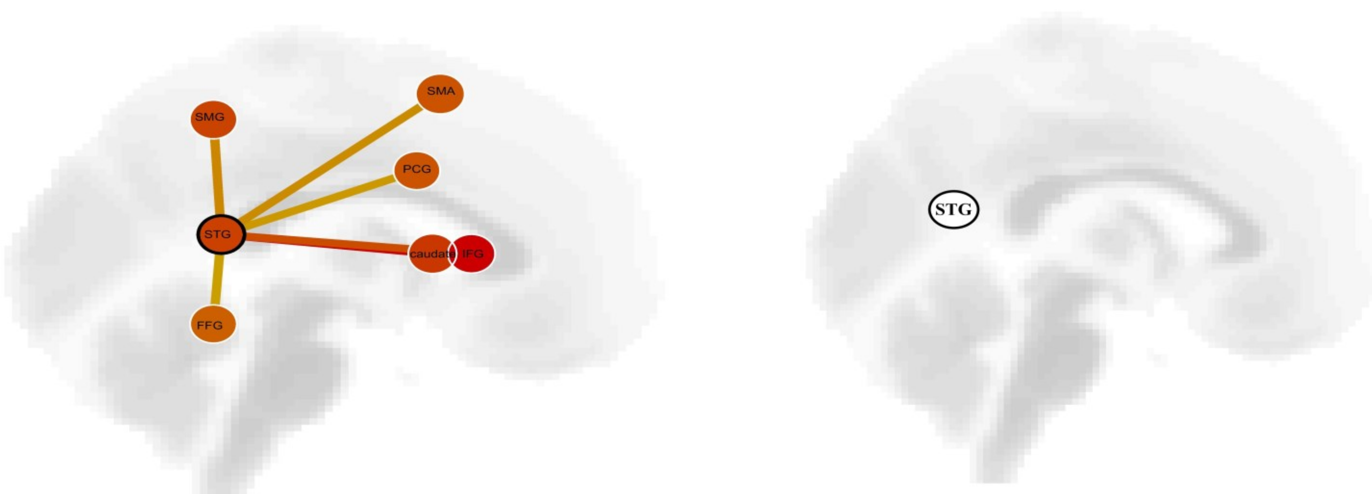
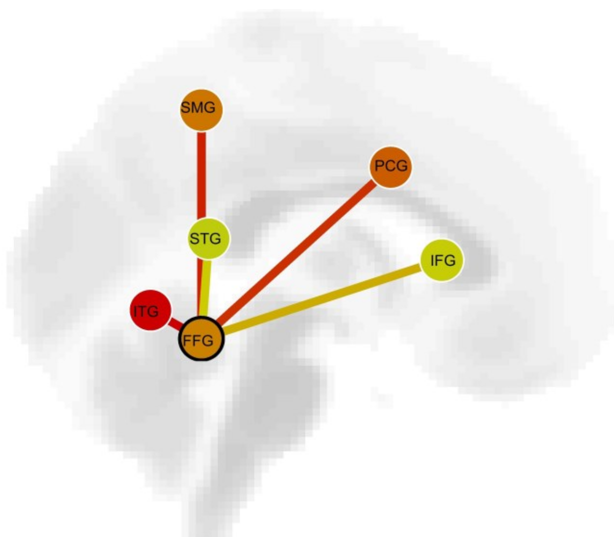


Figure 17: Connectivity of superior temporal gyrus (circled in black) for P condition in a) skilled readers and b) impaired readers, p<0.05, corrected. Stronger connections are indicated with darker color (red>orange>yellow).

a)



b)

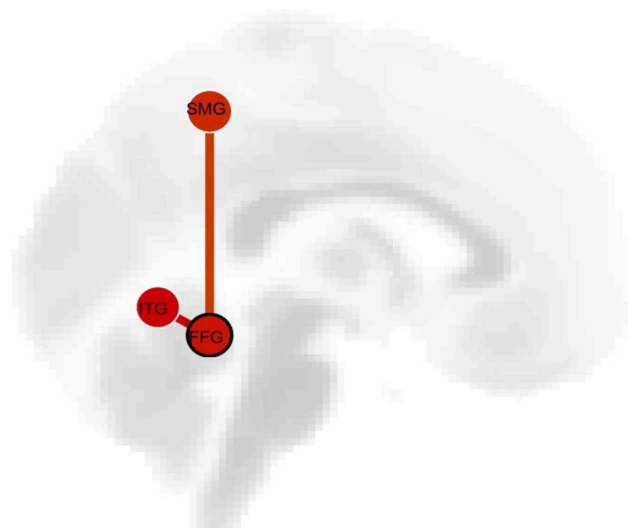


Figure 18: Connectivity of fusiform gyrus (circled in black) for P condition in a) skilled readers and b) impaired readers, $p<0.05$, corrected. Stronger connections are indicated with darker color (red>orange>yellow).