

**RESTING-STATE FUNCTIONAL CONNECTIVITY
IN READING-RELATED BRAIN REGIONS: A MEG
STUDY IN MONOZYGOTIC TWINS**

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Reading requires functional interaction between distinct reading-related regions located in the frontal and posterior parts of the left hemisphere. Abnormalities in the functional connectivity among these regions have been previously associated with dyslexia. In this study, we investigated resting-state functional connectivity (RSFC) in the reading-related regions, including inferior frontal gyrus, temporoparietal junction, and the visual word form area (VWFA) in fusiform gyrus. RSFC is a suitable method to investigate intrinsic brain networks without the influence of specific task demands or cognitive processes. Our aim was to identify significant RSFC in the reading-related regions and explore its association to reading fluency using magnetoencephalography (MEG). Additionally, we examined the familial heritability of the reading-related RSFC. The study included 90 adult monozygotic (MZ) twins with heterogeneous reading competence. The RSFC analysis between reading-related regions was conducted using imaginary part of coherency (IPC), in the alpha and theta frequency bands. In order to study the association between the RSFC and reading fluency, a new variable was constructed of three reading speed tasks to measure reading fluency among Finnish participants. The heritability examination was carried out by comparing the MZ twin pairs' obtained correlation to the permuted sample distributions of r . The main finding of our study was a significant RSFC in both the left hemisphere (between the inferior frontal gyrus and temporoparietal junction) and in their right hemisphere homologues, in the theta frequency band. The RSFC displayed no association with reading fluency but demonstrated a significant similarity between MZ twin pairs compared to non-related pairs, thus indicating a moderate heritability of the RSFC in the reading-related regions. The results suggest that RSFC can be detected utilising MEG and the RSFC in the reading-related regions may have a heritable component.

Keywords: MEG, resting-state functional connectivity, imaginary part of coherency, reading, dyslexia, twins

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Lukeminen edellyttää toimivia yhteyksiä eri lukemiseen liittyvien aivoalueiden välillä, jotka sijaitsevat vasemman hemisfäärin frontaali- ja posteriorisessa osassa. Poikkeavuudet näiden alueiden funktionaalisessa konnektiivisuudessa on aiemmissa tutkimuksissa yhdistetty dysleksiaan. Tässä tutkimuksessa tarkastelimme funktionaalista konnektiivisuutta lepotilan aikana (RSFC), lukemiseen liittyvillä alueilla, mukaan lukien inferiorinen frontaalipoimu, temporoparietaalinen risteys ja visual word form area (VWFA) fusiform poimussa. RSFC on sopiva menetelmä aivojen luontaisten yhteyksien tutkimiseen ilman tiettyjen tehtävien tai kognitiivisten prosessien vaikutusta. Tavoitteena oli tunnistaa merkitsevää RSFC:tä lukemiseen liittyvillä alueilla ja tutkia sen yhteyttä lukunopeuteen käyttäen magnetoencefalografiaa (MEG). Lisäksi tutkimme lukemiseen liittyvän RSFC:n periytyvyyttä. Tutkimukseen osallistui 90 aikuista monozygoottista (MZ) kaksosta, joiden lukutaito vaihteli. RSFC-analyysi lukemiseen liittyvien alueiden välillä suoritettiin käyttäen imaginary part of coherencyä (IPC), alfa- ja theta-taajuuskaistoilla. RSFC:n ja lukunopeuden yhteyden tutkimiseksi luotiin uusi muuttuja, joka koostui kolmesta lukunopeustehtävästä, jotta voitiin mitata lukusujuvuutta suomalaisilla koehenkilöillä. Periytyvyyden tarkastelu suoritettiin vertaamalla MZ-kaksoisparien korrelaatiota permutoituihin otosjakamiin. Tutkimuksemme keskeinen löydös oli merkittävä RSFC sekä vasemmassa aivopuoliskossa (inferiorisen frontaalipoimun ja temporoparietaalisen risteyksen välillä) että oikean aivopuoliskon vastaavissa alueissa theta-taajuuskaistalla. RSFC:llä ei ollut yhteyttä lukunopeuteen, mutta osoitti merkittävää samankaltaisuutta MZ-kaksoispareilla verrattuna ei-sukulaispareihin, mikä viittaa RSFC:n kohtalaiseen periytyvyyteen lukemiseen liittyvillä alueilla. Tulokset viittaavat siihen, että RSFC voidaan havaita MEG:n avulla ja että RSFC:llä, lukemiseen liittyvillä alueilla, on mahdollisesti periytyvä komponentti.

Avainsanat: MEG, lepotilan aikainen funktionaalinen konnektiivisuus, imaginary part of coherency, lukeminen, dysleksia, kaksoset

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INTRODUCTION

Dyslexia

Dyslexia is a neurobiological learning disorder that manifests as difficulty in accurate and/or fluent word recognition, spelling, and decoding skills (Lyon et al., 2003). These difficulties are often disproportionate to an individual's other cognitive abilities, motivation, language comprehension and can persist despite the provision of effective classroom instruction (Shaywitz, 1998; Lyon et al., 2003; Peterson & Pennington, 2012). However, secondary effects of dyslexia may also include difficulties in comprehending written text and a decrease in reading exposure, which can hinder the expansion of vocabulary and prior knowledge (Lyon et al., 2003). In addition to the primary and secondary direct effects, dyslexia can also have unwanted social, emotional, and academic consequences. For example, dyslexia has been associated with low self-esteem, reduced educational attainment, and difficulties in social relationships (Livingston et al., 2018). It's widely acknowledged that developmental dyslexia has a genetic basis, and family history is a key risk factor with 40–60% heritability (Fisher & DeFries, 2002). Despite this, environmental factors may play a role in either positively or negatively impacting the manifestation of dyslexia (Yu et al., 2018).

The prevalence of dyslexia varies significantly due to the different definitions used. However, a commonly used definition considers a cut-off point of 1.5 standard deviations below the age level mean in reading tests, thus identifying 7% of the population as dyslexic (Shaywitz et al., 1990). Indeed, a recent meta-analysis of the worldwide pooled prevalence of developmental dyslexia by Yang et al. (2022) also reported a 7.10% prevalence estimation of dyslexic individuals aged 6-13 years. Notably, the study found no differences in the prevalence between different writing systems, suggesting that dyslexia is present in most languages (Yang et al., 2022). However, sex differences in the prevalence of dyslexia have been observed; males exhibiting a 1.5-2-fold increased probability of being considered dyslexic compared to females (Rutter et al., 2004; Arnett et al., 2017; Yang et al., 2022). In Finland, a formal diagnosis of dyslexia is uncommon, as extra support for reading in school does not require a diagnosis. However, it is reasonable to assume that the prevalence of

dyslexia among Finnish speakers is similar to that of other languages (Lyytinen et al., 2019). Finally, Wagner et al. (2020) suggest that the prevalence of dyslexia would be more accurately represented as a continuous distribution that varies in the severity of dyslexia, rather than a dichotomous variable using a cut-off point (Wagner et al., 2020). They also point out that the relative discrepancy between reading and oral language skills could be an improved way of identifying dyslexic individuals in comparison to the use of a single measurement (e.g., reading) that utilises an absolute cut-off point in relation to age or grade peers (Wagner et al., 2020).

Dyslexia is a complex disorder that cannot be explained sufficiently by a single linguistic mechanism (e.g., Peterson & Pennington, 2012; Norton et al., 2015). However, traditionally neuropsychological research suggests that dyslexia is strongly connected to a deficiency in the phonological component of language processing (Lyon et al., 2003; Peterson & Pennington, 2012). Specifically, dyslexia is hypothesised to be related to the deficits in phonological awareness (PA) (Wagner & Torgesen, 1987), meaning the ability to segment speech into discrete units such as phonemes and syllables and to construct words from these smaller units. Indeed, according to a meta-analysis by Melby-Lervåg et al. (2012), phonemic awareness was identified as a strongest predictor of word reading ability. The study found that this relationship remained significant after controlling for variations in verbal short-term memory and rhyme awareness (Melby-Lervåg et al., 2012). According to the phonological theory of dyslexia, attaining phonological awareness is a crucial process for constructing and automating letter-sound correspondences (Peterson & Pennington, 2012). Letter-sound correspondences are in turn a necessity for coherent word recognition through phonological coding (Peterson & Pennington, 2012). In dyslexia, according to the majority of studies, phonological deficits result from deficient development of phonological representations (Peterson & Pennington, 2012). These representations are often characterised by poor segmentation, imprecision, and degradation (Peterson & Pennington, 2012). It is also important to note that the relationship between phonological awareness and reading may be to some degree reciprocal, for example, orthographic knowledge has been documented to influence performance on the phonological awareness tests (Castles et al., 2011).

In addition to the dysfunctional development of phonological awareness as an underlying mechanism of dyslexia, weakness in rapid automatized naming (RAN) is widely believed to be another core component of dyslexia (e.g., Wolf & Bowers, 1999; Norton & Wolf, 2012; Georgiou et al., 2013). RAN has been consistently demonstrated, along with PA, as a reliable predictor of reading abilities in children across various languages (Landerl et al., 2013), and especially in Finnish language (Ziegler et al., 2010). RAN is a measure of an individual's ability to quickly and accurately name a

series of familiar visual stimuli, such as letters or colours, and children with dyslexia typically require more time to name RAN stimuli (Denckla & Rudel, 1976), which is a necessary skill for fluent reading. According to Wolf and Bowers (1999), double-deficit hypothesis contends that RAN is a distinct core deficit that may lead to dyslexia on its own or in combination with PA impairment, and the combination of both appears to indicate more extensive reading difficulties. The distinction between RAN and PA has also been established in the Finnish language (Torppa et al., 2012; Landerl et al., 2013). The study by Torppa et al. (2012), demonstrates that a deficiency in RAN is associated with slow reading speed and slow spelling development, and a deficiency in PA is associated with early spelling. However, contrary to the double-deficit hypothesis, a deficit in both did not have a cumulative effect, suggesting that RAN and PA are partially independent components in transparent orthography (Torppa et al., 2012).

Transparent orthography refers to a writing system where the written representation of a language reflects that language's phonology in a consistent way. Although it may be difficult in the beginning for Finnish children with dyslexia to learn letter-sound associations, they only need to learn 24 graphemes in order to achieve complete consistency between the written and spoken forms of the language (Lyytinen et al., 2015). For this reason, in Finnish, phonological awareness has been found to decrease in the strength as an early predictor of developmental dyslexia (Holopainen et al., 2001) and therefore in the transparent orthographies, it is preferable to characterise dyslexia by a difficulty in reading fluency, rather than accurate reading (Landerl & Wimmer, 2008). Although, the linguistic predictors of dyslexia vary to some degree among different orthographies, the neural correlates of reading difficulties appear to be highly universal (Paulesu et al., 2001).

Functional neuroanatomy of reading and dyslexia

Multiple neural characterizations of skilled reading and brain dysfunctions in dyslexia have been proposed, with some variations among them (see e.g., McCandliss & Noble, 2003; Démonet et al., 2004; Sandak et al., 2004; Chyl et al., 2021). According to Sandak et al., (2004) skilled word recognition requires an organised cortical system that combines the processing of various linguistic features of words. Classically, the cortical system can be divided into three subsystems in the left hemisphere. The two posterior subsystems are the dorsal (temporoparietal) system and the ventral

(occipitotemporal) system. The third subsystem is the inferior frontal gyrus (Sandak et al., 2004). The dorsal system consists of supramarginal gyrus, angular gyrus and the posterior superior temporal gyrus (STG) (i.e., Wernicke's area) (Sandak et al., 2004). The function of the dorsal system seems to be related to grapheme-phoneme correspondences which plays a crucial role during the initial stages of learning to read (Sandak et al., 2004). The ventral subsystem consists of middle and inferior temporal gyri and an area located in the left inferior occipitotemporal cortex adjacent to the fusiform gyrus (Sandak et al., 2004), which is thought to act as an area for visual word forms (VWFA) (Cohen et al., 2000). The VWFA is primarily associated with fluent reading by word and letter recognition (Dehaene & Cohen, 2011). In addition to the dorsal and ventral subsystems, the left inferior frontal gyrus (IFG) (i.e., Broca's area) seems to be associated mainly with phonological processing, but also in other linguistic functions (e.g., syntactic processing and semantic retrieval) (Poldrack et al., 1999; Sandak et al., 2004). Although, the previous classical model is mainly based on cross-sectional findings from adults, a recent review of longitudinal studies of (a)typical reading development supports the neural characterizations of dorsal and ventral subsystems (Chyl et al., 2021).

Neural abnormalities in dorsal and ventral subsystems associated with dyslexia have been studied in several reviews and meta-analyses across various brain imaging techniques. While the findings of the studies have exhibited some degree of variability, the primary conclusions indicate a consistent pattern of hypoactivation in the posterior regions of the left hemisphere (e.g., Pugh et al., 2000; Sandak et al., 2004; Richlan et al., 2009). On the contrary, several cortical and subcortical regions have shown hyperactivation in dyslexic readers, and this hyperactivation is thought to represent a neural compensatory mechanism for impaired reading network (Maisog et al., 2008; Richlan et al., 2009; Richlan et al., 2011).

More specifically, in the meta-analyses by Maisog et al., (2008) and Richlan et al., (2009, 2011), hypoactivity in the dorsal system has been located in the STG (Maisog et al., 2008; Richlan et al., 2009, 2011) and supramarginal gyrus (Richlan et al., 2009, 2011). The dysfunction of the ventral system has been a robust finding in the meta-analyses, and more precisely, the fusiform gyrus (VWFA) has shown hypoactivity in dyslexic readers (Maisog et al., 2008; Richlan et al., 2009, 2011). Furthermore, consistent with Sandak et al. (2004) model of the ventral subsystem, the inferior and middle temporal gyri have also shown hypoactivation (Richlan et al., 2009). In addition, the hypothesis that a hyperactive left inferior frontal gyrus compensates for the dysfunctional left posterior reading systems (e.g., Shaywitz & Shaywitz, 2004) has been challenged by the meta-analyses, which on the contrary, have found evidence of hypoactivity in the left IFG (Maisog et al., 2008; Richlan et al., 2009, 2011).

Along with the findings of left hemisphere hypoactivity in dyslexic individuals, both left and right hemisphere hyperactivations have been documented in meta-analyses (Maisog et al., 2008; Richlan et al., 2009, 2011). However, these hyperactivation findings in both hemispheres are relatively inconclusive and exhibit a high degree of variability. The most replicated result, in studies utilising activation likelihood estimation (ALE) maps, is hyperactivity in the anterior insula (Maisog et al., 2008; Richlan et al., 2009). Other subcortical regions, such as the left caudate nuclei (Richlan et al., 2009), right/left thalamus (Maisog et al., 2008; Richlan et al., 2009), lentiform and caudate nuclei, both bilaterally (Richlan et al., 2011), have also been found to exhibit hyperactivity in dyslexic individuals. Hyperactivity in cortical structures, such as the left primary motor cortex (Richlan et al., 2009), left lingual gyrus, and right medial frontal cortex (Richlan et al., 2009) has also been documented. Furthermore, research has relatively consistently documented a reduction in grey matter volume bilaterally in the cerebellum among dyslexic individuals, in addition to the previously identified brain regions (Kronbichler et al., 2008). Heterogeneity in the findings could possibly be attributed to differences in the reading tasks utilised, the ages of the participants, diversity within the dyslexic population, and other factors, including variability in compensation mechanisms (Norton et al., 2015).

Task-based functional connectivity

As stated above, reading and reading-related processes require adequate activation of multiple brain areas, especially in the posterior parts of the left hemisphere, including the temporoparietal and occipitotemporal region. Furthermore, dysfunctions in these regions are associated with dyslexia (e.g., Richlan et al., 2009, 2011). In addition, the left IFG and right hemispheric regions may play a role in the manifestation of dyslexia (e.g., Richlan et al., 2009, 2011). However, in order to show sufficient literacy skills, individuals must not only have adequate activation in reading-related regions, but also develop functional connectivity between them. This has been established by the detection of dysfunctional cortical connectivity in individuals with dyslexia via task-based (reading) functional connectivity studies. Initially, Horwitz et al. (1998) demonstrated in a PET study, that individuals with reading difficulties showed reduced connectivity between the left angular gyrus and other regions of reading network, such as the parietotemporal and occipitotemporal regions, and left

inferior frontal cortex. Subsequently, various task-based connectivity studies have supported the conclusion that the dysfunctional network of the left hemisphere is a crucial factor in dyslexia (Cao et al., 2008; van der Mark et al., 2011; Vandermosten et al., 2012; Finn et al., 2014; Morken et al., 2017).

The results from the study by Pugh et al. (2000) support Horwitz et al.'s (1998) findings that reduced connectivity between the angular gyrus and the occipitotemporal and parietotemporal regions is associated with dyslexia. More recent task-based fMRI-studies have revealed that individuals with dyslexia exhibit weaker connectivity in other language-related regions beyond the angular gyrus. When comparing dyslexic children to controls, functional connectivity from the VWFA to the left inferior frontal cortex and left inferior parietal cortex has been found to be weaker (Cao et al., 2008; Van der Mark et al., 2011). Schurz et al. (2015) reported weaker connectivity in dyslexic readers not only between left inferior frontal gyrus and VWFA, but also in other posterior temporal areas of the left hemisphere, including the inferior, middle, and superior temporal regions. Furthermore, data-driven analysis by Finn et al. (2014) revealed age-specific differences in the connectivity of the VWFA: differences in connectivity were apparent among adults but not in children. More specifically, among adults, controls showed stronger VWFA connectivity to bilateral extrastriate cortices and to the left IFG, whereas the dyslexic readers showed stronger VWFA connectivity to bilateral visual association regions and to the right primary auditory cortex (Finn et al., 2014). These age-related connectivity differences in the VWFA may represent the acquired proficient reading abilities of nonimpaired readers and altered connectivity circuits in dyslexic adults (Finn et al., 2014). In contrast, a longitudinal study by Morken et al. (2017) found age-related VWFA connectivity changes in children: at the age of 6 years, connectivity from occipital-temporal cortex (i.e., VWFA) to STG and IFG was significantly lower among dyslexic individuals in comparison to controls, but the changes diminished at the age of 8 and remained diminished at the age of 12.

The dysfunction of the left posterior hemisphere regions among dyslexic individuals has also been documented using diffusion tensor imaging (DTI) with fractional anisotropy (FA). Klingberg et al. (2000) were the first to report a lower FA bilaterally in the temporoparietal regions of the white matter in dyslexic individuals compared to adult controls. However, only left hemisphere FA had significant correlation with reading (Klingberg et al., 2000). Subsequently, according to the review of Vandermosten et al. (2012), the lower FA in the left temporoparietal region has been a consistent finding, both in dyslexic adults and children. In addition, lower FA also in the left IFG has been reported, albeit to a lesser degree (Vandermosten et al., 2012). Despite of the fairly consistent findings of the dysfunctional network in the left posterior hemisphere in dyslexia, results from task-based

studies utilising fMRI and DTI, have also shown conflicting patterns of functional connectivity, highlighting the possibility of task-dependent outcomes (e.g., Vandermosten et al., 2012; Paulesu et al., 2014).

Resting-state functional connectivity

Functional connectivity of the reading network has been traditionally studied during different reading tasks, offering valuable insights into the temporal correlations between brain regions in nonimpaired and dyslexic individuals. Nevertheless, a lack of consensus exists in connectivity research on the optimal reading task to accurately characterise the neural networks underlying dyslexia (Koyama et al., 2010). Consequently, different reading tasks may yield varying patterns of functional connectivity (Koyama et al., 2010; Paulesu et al., 2014). Studying the brains at rest has been suggested as a promising method to explore neural connectivity since it is not prone to potential influence from specific task demands or cognitive processing strategies (Koyama et al., 2010; Cross et al., 2021).

Resting-state functional connectivity (RSFC) studies with functional magnetic resonance imaging (fMRI) also highlight the importance of reading-related regions and the cortical connectivity between them. Findings from a study by Koyama et al. (2010) were consistent with functional connectivity patterns from task-based studies. The authors observed a positive RSFC between six reading-related regions, including: inferior occipital gyrus, VWFA, STG, temporoparietal junction (TPJ), precentral gyrus, and IFG (Koyama et al. 2010). RSFC-studies have also shown distinct patterns of connectivity regarding reading competence between adults and children. A study by Koyama et al. (2011) found a positive correlation between reading competence and connectivity from the left IFG to the left STG with adults and children. However, the correlation between reading competence and connectivity from the VWFA to the IFG and to the inferior parietal lobule (IPL) (including the supramarginal gyrus and the angular gyrus) were stronger in adults than in children (Koyama et al., 2011). This could indicate that the stronger connectivity between VWFA and frontoparietal regions is only seen in matured brain because of proficient reading performance (Koyama et al., 2011; Finn et al., 2014).

Again, in line with task-based studies, when comparing RSFC between nonimpaired and dyslexic readers, a reduced RSFC has been found in the posterior temporal areas of the left

hemisphere including: VWFA, ITG, MTG, STG, and in the left IFG with dyslexic individuals (Schurz et al., 2015). In addition, instead of localizing VWFA in the reading-related processes, RSFC have been found between VWFA and intraparietal sulcus (IPS), proposing that the role of VWFA is part of the dorsal attention network (Vogel et al., 2012; Zhou et al., 2015). More specifically, the study by Zhou et al. (2015) reported both a group difference, between nonimpaired and dyslexic readers, in RSFC between VWFA and regions associated with the dorsal attention network, as well as a correlation between the RSFC and fluent reading. Expanding the previous research, the authors concluded that dyslexic individuals exhibit deficits also in the dorsal attention network, due to the reason reading requires eye movement and visual attention processing (Zhou et al., 2015). Lastly, it is important to emphasise that in comparison to other neurological disorders, relatively few RSFC-studies of dyslexia have been made (e.g., Kronbichler & Kronbichler, 2018) and in the published studies, some discrepant findings exist.

The majority of previous research has investigated RSFC using fMRI to analyse temporal correlations of low-frequency blood oxygen level-dependent (BOLD) signals (e.g., Vogel et al., 2012; Schurz et al., 2015). While fMRI provides high spatial resolution, the BOLD signals are an indirect measure of functional connectivity (Hall et al., 2014). In contrast, magnetoencephalography (MEG) is a suitable method to detect real-time dynamics of cortical functional connectivity due to the high temporal resolution and adequate spatial resolution. (Hall et al., 2014). Whereas in fMRI studies, connectivity measures focus on analysing the temporal correlations of BOLD-signals, in MEG studies, the resting-state functional connectivity can be estimated from synchronous neuronal activity with connectivity methods such as imaginary part of coherency (Nolte et al., 2004) or coherence (Rosenberg et al., 1989).

Overall, functional connectivity studies have demonstrated the crucial role of cortical connectivity in the reading network. Despite this, conflicting patterns of functional connectivity exist both in task-based and resting state studies. To our knowledge, this is first study to examine the intrinsic connectivity in the reading-related regions utilizing MEG. Hence, this study strives to clarify the research field with previously unexplored methods in the context of RSFC in the reading-related regions. In addition, previous research on the heritability of RSFC in dyslexia is highly limited, although dyslexia has a strong genetic aspect (e.g., Snowling & Melby-Lervåg, 2016). In general, functional connectivity has been found to be moderately heritable in the resting state (e.g., Glahn et al., 2010; Schutte et al., 2013; Ge et al., 2017; Barber et al., 2021). Reaching a more in-depth understanding of the gene-environment aspect of heritability of RSFC in reading regions would bring

new insight to aetiology and mechanisms of dyslexia. Due to this, the present study also investigated the heritability of RSFC with monozygotic (MZ) twins.

Aims and Hypotheses

The primary objective of this study was to investigate resting-state functional connectivity (RSFC) and its association with reading fluency, in reading-related regions (inferior frontal gyrus, temporoparietal junction and VWFA in the fusiform gyrus), utilizing MEG. The secondary objective was to examine the heritability of resting-state functional connectivity with monozygotic twins. The research questions were:

1. Is there significant RSFC between three reading-related ROIs?
2. Is the RSFC associated with reading fluency?
3. The heritability of the RSFC: Is the RSFC more similar between MZ twin pairs than non-related pairs?

First, based on previous RSFC studies, we hypothesized to detect significant RSFC between reading-related ROIs, in the left posterior reading network (TPJ and VWFA) and in the left IFG. For the equivalent regions' RSFC in the right hemisphere, we did not place a hypothesis, due to the ambiguity of the previous research on the function of these regions.

Second, we hypothesized that higher RSFC-values between TPJ, VWFA, and IFG are associated with reading fluency, thus displaying previous research literature on the importance of adequate intrinsic connectivity within the reading network.

Third, based on the previous heritability studies on RSFC, we hypothesized to find stronger correlations in RSFC between MZ twins than between non-related pairs, thus indicating heritability of RSFC also in the reading-related regions.

METHODS

Participants

The participants were originally part of the FinnTwin12 and FinnTwin16 studies by Kaprio et al. (2006), where they recruited approximately 10 000 Finnish twins born between 1974-1979 (FinnTwin12) and between 1982-1983 (FinnTwin16). From the FinnTwin samples, Academy Research Fellow project of Minna Torppa recruited 60 monozygotic (MZ, i.e., identical) twin pairs, which formed three groups based on teacher reports at age 12 (Finntwin12) and adult self-reports (Finntwin16) on reading difficulties (Readtwin project). The three MZ groups (n = 120) were: concordant typical readers, concordant poor readers, and discordant readers (one typical reader and one poor reader). Twin pairs with severe neurological disorders/illnesses were excluded. Cognitive measures were done to MZ pairs, including reading speed, rapid serial naming, verbal short-term memory, and phonological ability. The resting-state MEG data were collected from 45 twin pairs, and therefore, the final N = 90 (45 MZ pairs), of whom had cognitive skills measured and resting-state MEG collected. In this study, a new measure of reading fluency was constructed to identify reading competence of participants (see reading fluency). However, instead of forming groups, reading fluency was examined as a continuous variable because, as stated by Wagner et al. (2020), reading difficulties can be found across the reading spectrum rather than solely in the lower tail of reading competence (e.g., cut-off point 1.5 standard deviations) and because the initial “poor reader” classifications were based solely on teacher and self-reports.

Reading fluency

In Finnish, proficient reading accuracy is typically acquired in the early stages of reading development due to the transparent orthography (Holopainen et al., 2001). For that reason, reading

fluency in Finnish can be characterized solely by reading speed or by combining reading speed and accuracy. In this study, reading speed was used to characterize reading fluency.

Three reading speed tasks were used to assess reading fluency: word and pseudoword list reading (Nevala et al., 2006) and Lapland -text (Leinonen et al., 2001). The list reading tasks consisted of a list of 30 words and 30 pseudowords. For the list reading, the participants were instructed to read the words/pseudowords aloud and separately as fast and accurately as they could. The word list consisted of common Finnish words (5–16 letters and 2–5 syllables), and while the pseudoword list was similar in length, the structure of the pseudowords was constructed by exchanging the consonants and vowels within the same words as used in the word list. The reading speed was measured as seconds used to read 30 (pseudo)words. The Lapland -text consisted of 211 words, which participants were instructed to read aloud as fast and as accurately as they were able. The reading speed was measured as seconds used to read the Lapland text.

The reading speed results of the participants in both list reading tasks and Lapland-text were standardized using the mean and standard deviation of 61 nonimpaired readers from the Jyväskylä Longitudinal Study of Dyslexia, JLD26-project (Lohvansuu et al., 2021). After standardizing the reading speed tasks, the low z-scores indicated faster reading (i.e., good reading), and high z-scores indicated slower reading (i.e., poor reading). Finally, the three standardized task were combined into one reading fluency variable.

Table 1. Participant demographic and behavioural data

N = 90			
	Mean	SD	(z) ¹
Age (years)	32–41		
Sex	66 F / 24 M		
Reading speed subtasks:			
Word list reading (s)	26.4	8.5	.37
Pseudoword list reading (s)	56.4	21.1	.78
Lapland-text (s)	144.6	26.8	.32
Reading fluency ²	78.8	1.14 ³	.49

¹ Average z-scores were calculated using JLD26 (Lohvansuu et al., 2021) control group n = 61.

² Reading fluency variable computed from reading speed subtasks.

³ Standardized standard deviation.

Regions of interest

To determine RSFC in the typical reading network, the regions of interest (ROIs) were selected based on both the meta-analysis of functional neuroimaging of the dyslexic brain (Maisog et al., 2008; Richlan et al., 2009; Richlan et al., 2011) and previous connectivity studies conducted with both dyslexic and nonimpaired readers (e.g., Vandermosten et al., 2012; Koyama et al., 2013; Schurz et al., 2015; Van der Mark et al., 2015). The ROIs were: 1) the left fusiform gyrus (VWFA) 2) the left temporoparietal junction and, 3) the left inferior frontal gyrus. (Table 2.) In addition, the ROI selection and the presumed connectivity between them were partly based on the possible white matter tracts: the left arcuate fasciculus (AF) connecting the IFG and TPJ, and the left inferior fronto-occipito fasciculus (IFOF), connecting the IFG and FFG (including VWFA) (Vandermosten et al., 2012).

The first ROI, the VWFA in the left fusiform gyrus (FFG), is a part of the ventral subsystem (Sandak et al., 2004), and it has been demonstrated to have an important role in decoding fluency by word and letter recognition (Dehaene & Cohen, 2011). VWFA has shown a weaker connectivity in task-based and resting-state studies with dyslexic individuals (e.g., Schurz et al., 2015; Van der Mark et al., 2011). The second ROI, the left temporoparietal junction (TPJ), extends over several cortical areas, including the STG (classically Wernicke's area), supramarginal gyrus, and angular gyrus. The left TPJ is a part of the dorsal subsystem, and it has been proposed to have a crucial role in grapheme-phoneme correspondence, especially during the initial stages of learning to read. Hypoactivity in the regions located in the left TPJ has been linked multiple times to dyslexia (Richlan et al., 2009), and its' functional connectivity to other reading-related regions seems to be crucial as well (Horwitz et al., 1998; Pugh et al., 2004; Koyama et al., 2010; Schurz et al., 2015). More specifically, in this study, the left TPJ's MNI coordinates were placed to roughly correspond to the MNI coordinates of the left superior temporal gyrus (STG) (Bolger et al., 2005; Richlan et al., 2011). The third ROI, the left inferior frontal gyrus (IFG), is associated with phonological and other linguistic functions (Poldrack et al., 1999; Sandak et al., 2004). IFG has shown both hypo- and hyperactivity among dyslexic individuals (Shaywitz & Shaywitz, 2004; Maisog et al., 2008; Richlan et al., 2009, 2011) and weaker functional connectivity (Finn et al., 2014; Morken et al., 2017). Finally, connectivity between all the ROIs was carried out bilaterally for two reasons. Primary, right hemisphere was utilised as a reference to examine the lateralization of reading-related network. Secondary, equivalent (reading-related) regions in the right hemisphere could inform about the possible compensatory mechanisms of impaired readers (Sandak et al., 2004).

Table 2. MNI coordinates of the regions of interest used for placing the dipole sources for connectivity analysis

Regions of interest			MNI¹		
			x	y	z
Occipital	Fusiform gyrus	L.FFG (VWFA)	-48	-57	-20
		R.FFG	48	-57	-20
Temporal	Temporoparietal junction	L.TPJ ²	-59	-45	15
		R.TPJ	59	-45	15
Frontal	Inferior frontal gyrus ³	L.IFG	-50.5	21	8
		R.IFG	50.5	21	8
Control regions					
Frontal			0	58.4	12.8
Vertex			0	-35.9	75.1
Occipital			0	-102.1	-15.1

¹) MNI coordinates of the ROIs are based on the study by Koyama et al. (2013).

²) MNI coordinates of the left TPJ correspond to left posterior part of STG (Bolger et al., 2005; Richlan et al., 2011).

³) MNI coordinates of IFG were placed in the centroid of opercular and triangular subdivisions.

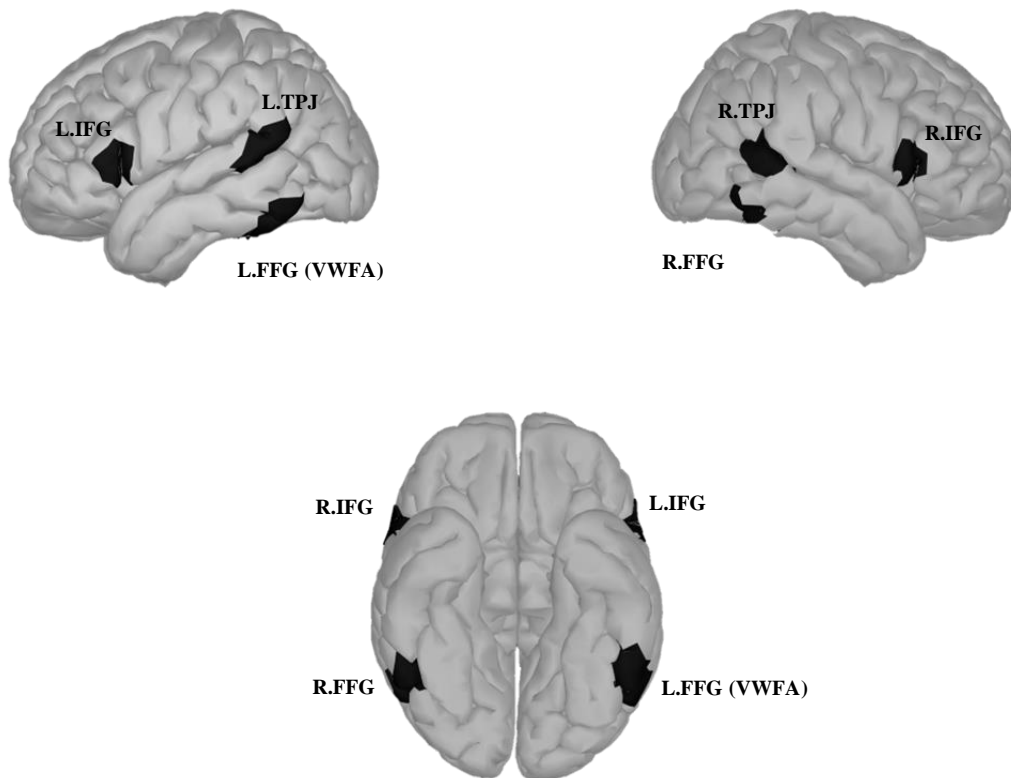


Figure 1. Regions of interest (ROI) locations used for placing the dipole sources for connectivity analysis. The black areas highlight the MNI coordinates presented in Table 2. (L. = left, R. = right, IFG = inferior frontal gyrus, TPJ = temporoparietal junction, FFG = fusiform gyrus).

MEG data acquisition and preprocessing

The MEG data was recorded with a sampling rate of 1000 Hz on a whole-head 306-sensor (204 planar gradiometers and 102 magnetometers) using the Elekta Neuromag® TRIUX™ system (Elekta AB, Stockholm, Sweden) in a magnetically shielded room at Jyväskylä Centre for Interdisciplinary Brain Research (CIBR). The online band-pass filter was 0.1–330 Hz. Throughout the MEG experiment, the positioning of the participant's head in relation to the sensor arrays within the helmet was continuously monitored using five digitized head position indicator (HPI) coils. Specifically, three HPI coils were

placed on the forehead, and the two were situated behind each ear. The MEG head coordinate system was established based on three anatomical landmarks, the nasion and left and right preauricular points. Prior to the MEG experiment, the anatomical landmarks, HPI coil locations, and head shape (over 100 points that were evenly distributed over the scalp) were all recorded using a Polhemus Isotrak digital tracker system (Polhemus, Colchester, VT United States). The MEG was recorded with the gantry positioned at the angle of 68 degrees. During the resting-state measurement, participants first kept their eyes closed for a variable duration of 2 to 10 minutes, followed by keeping their eyes open between 2 to 10 minutes, resulting in a total collection time of resting-state data ranging from 4 to 20 minutes.

The MEG data pre-processing was carried out with Maxfilter (version 3.0.17), using the temporal signal-space separation (tSSS) method, which allows to eliminate external noise and compensate for head movement during the recording. After manually identifying and excluding the bad MEG channels, an interpolation of the bad channels was constructed with Maxfilter. Correction of the eye movement and cardiac artifacts were accomplished with independent component analysis (ICA), using MNE Python (version 0.17.2). After this, the resting-state MEG data were exported into Besa Research 7.1 software, where the continuous RS-data for each participant were segmented into 2 second trials to investigate the alpha (8–13 Hz) and theta (4–8 Hz) frequency bands. To examine RSFC between our predefined ROIs, the segmented data was transformed from sensor level into source space using a source montage, containing the 3 ROIs (FFG, TPJ and IFG) bilaterally, including 2 dipoles for each ROI. In addition, three brain regions were selected for controlling signal of no-interest or interference from non-brain sources. The frontal region for eye movement, the occipital region for muscle tension, and the vertex region to capture the whole brain signal (Table 2.) Lastly, the trials were scanned to detect any additional artifacts, and bad individual trials with amplitudes greater than $\pm 120 \mu\text{V}$ (for gradiometers) or $\pm 400 \mu\text{V}$ (for magnetometers) and gradients greater than $\pm 800 \mu\text{V}$ were excluded, resulting in an average of 422 trials ranging between 149-634.

Time-frequency transformation and functional connectivity analysis

The resting-state data was exported to Besa Connectivity 1.0 to perform time-frequency and functional connectivity analysis. Prior to the functional connectivity analysis, the data was

transformed into the time-frequency domain using time-frequency analysis: the complex Morlet Wavelet transformation with frequency range of 4–45Hz. Morlet Wavelet decomposition is well suited for non-stationary time series data because it has a Gaussian shape both in time and frequency domain that tapers the sine wave, which provides excellent joint time and frequency-resolution (Samar et al., 1999; Ghuman et al., 2011).

For the functional connectivity analysis, we used the Imaginary Part of Coherency (IPC) (Nolte et al., 2004). The IPC is a suitable approach to investigate brain interactions, due to the reason it reduces the effect of field spread coming from volume conduction by excluding coherent sources with zero phase lag (Nolte et al., 2004). The IPC values range between -1 and 1 for the given frequency (4–45 Hz). When the value of IPC (x,y) is positive, it means that x comes before y in time, which implies that information is flowing from x to y. Similarly, negative values imply the opposite direction of the information flow (Nolte et al., 2004). However, in this study we used the absolute values of IPC to only determine the strength of RSFC. The ROIs and their dipoles constituted a total of 24 source level interactions (12 interactions within each hemisphere), both in the alpha and theta frequency bands. After performing the functional connectivity analysis between the ROIs, the IPC values were averaged over time in the theta (4–8 Hz) and alpha (8–13 Hz) frequency bands in the MATLAB software (R2020b). The gamma frequency band was excluded because gamma-band functional connectivity network has been reported to be less reliable than theta and alpha networks (Jin et al., 2011).

In order to identify significant RSFC between the ROIs, a theoretical 95% confidence limit was calculated for the IPC-values with a formula defined as $1 - (1 - \alpha)^{1/(L-1)}$, where the L represents the number of trials (Halliday et al., 1995). In this study, the resting-state data had high interparticipant variability; therefore, the minimum number of 2 second trials (149) were used to determine the confidence limit for each participant. If the absolute IPC-value for the participant was above the cut-off point, it was determined as significant RSFC. To extend this principle, it was required that the absolute values above the cut-off point to be present in at least 50% of the participants within the ROI interaction, in order to be further selected for statistical analysis.

Statistical analysis

After identification of the ROI interactions that showed significant resting-state functional connectivity, Spearman's rank correlation coefficient was used to examine the association between the significant RSFC and reading fluency. The selection to use Spearman's correlation was based on the non-normal distribution of the reading fluency and IPC values. Since the IPC gives values between -1 and 1 , indicating the direction of information flow, absolute values were used to determine only the strength of RSFC instead of the direction. The absolute IPC values range between 0 and 1 . A value of 1 indicates that the two signals are perfectly synchronized and a value of 0 indicates perfect asynchrony.

To examine the heritability of the RSFC, Spearman's rank correlation coefficient was calculated between MZ-twins' significant RSFC values. In order to determine the probability that the correlation between the MZ-twins is due to chance, a sampling distributions of correlation coefficients (r) was constructed. First, twin 1 of each MZ-twins were held constant, while twin 2's RSFC values were permuted 10,000 times. Correlations were calculated using the permuted values, thereby constructing sampling distributions for testing null hypothesis with both significant RSFCs. Finally, the obtained correlation of the MZ-twins was compared to the sampling distribution of r with confidence interval of 95 %. All the statistical analyses were carried out with IBM SPSS Statistics 26.0 and Microsoft Excel for Microsoft 365 MSO (Version 2302).

RESULTS

Resting-state functional connectivity

Two ROI interactions showed a significant RSFC in ≥ 50 % (Table 3.) of the participants in the theta frequency band between the IFG and TPJ in both hemispheres (Figure 2.). The RSFC between the

left IFG and left TPJ had 47/90 (52 %) participants' absolute IPC-values over the cut-off point (.02), whereas the RSFC between the right IFG and right TPJ had 52/90 (59 %) (Figure 2.). Functional connectivity and further statistical analysis were only computed with theta frequency band, because the data in the alpha frequency band was highly disrupted by the on-going rhythmic oscillations. Indeed, in alpha frequency band every ROI showed a significant RSFC, displaying typical whole-brain alpha activation in resting-state rather than true RSFC.

Table 3. Imaginary part of coherency (IPC) descriptive values between the regions of interest (ROI), N = 90

ROI interaction	Dipole ¹	Mean	SD	% ²
L.FFG - L.IFG	1 to 1	0.024	0.0301	32.22
	1 to 2	0.0257	0.0235	38.89
	2 to 1	0.019	0.015	32.22
	2 to 2	0.0179	0.0194	21.11
L.FFG - L.TPJ	1 to 1	0.0289	0.026	44.44
	1 to 2	0.0264	0.0275	36.67
	2 to 1	0.0278	0.0283	42.22
	2 to 2	0.0199	0.0221	23.33
L.IFG - L.TPJ	1 to 1	0.0194	0.0167	28.89
	1 to 2	0.0163	0.0157	20
	2 to 1	0.0297	0.0214	52.22³
	2 to 2	0.0263	0.0256	37.78
R.FFG - R.IFG	1 to 1	0.0286	0.0237	43.33
	1 to 2	0.0246	0.0258	36.67
	2 to 1	0.0229	0.019	38.89
	2 to 2	0.0194	0.0211	26.67
R.FFG - R.TPJ	1 to 1	0.0257	0.0232	36.67
	1 to 2	0.0237	0.0224	36.67
	2 to 1	0.0227	0.0278	24.44
	2 to 2	0.029	0.0274	44.44
R.IFG - R.TPJ	1 to 1	0.0217	0.022	34.44
	1 to 2	0.0318	0.0239	58.89³
	2 to 1	0.0194	0.021	24.44
	2 to 2	0.0193	0.0213	26.67

¹) Dipoles measured distinct orthogonal angles of current flow.

²) % of participants above the cut-off point (.02).

³) ROI interactions (≥ 50 % above the cut-off point) that were selected to statistical analyses.

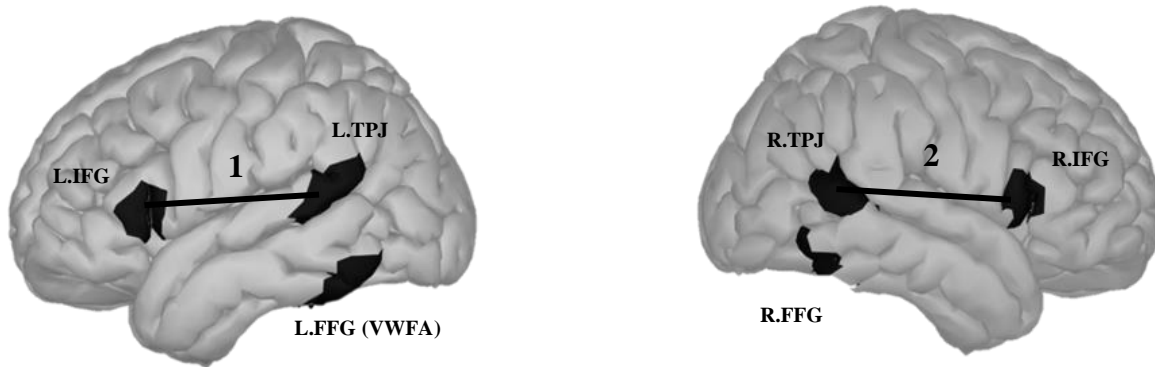


Figure 2. Resting-state functional connectivity (RSFC) shown bilaterally. Black lines (1 & 2) represent significant RSFC between the regions of interest (ROI). The line 1 illustrates RSFC in the left hemisphere (L.IFG - L.TPJ) and the line 2 illustrates RSFC in the right hemisphere homologs.

Resting-state functional connectivity correlates with reading fluency

As shown in Figure 3, no significant correlations were found between reading fluency and RSFC. Specifically, the correlations between reading fluency and RSFC were between L.IFG – L.TPJ ($r = -.075$, $p = .485$) and R.IFG – R.TPJ ($r = -.128$, $p = .228$). In order to attain more detailed information about reading competence’s association with RSFC and to facilitate comparability to previous research, we examined the correlations between RSFC and reading fluency subtasks separately. Among the three reading fluency subtasks (word list reading, pseudoword list reading and Lapland text), the only significant correlation was weak ($r = -.237$, $p = .025$), between word list reading and RSFC in the right hemisphere (Figure 4; scatterplot 6).

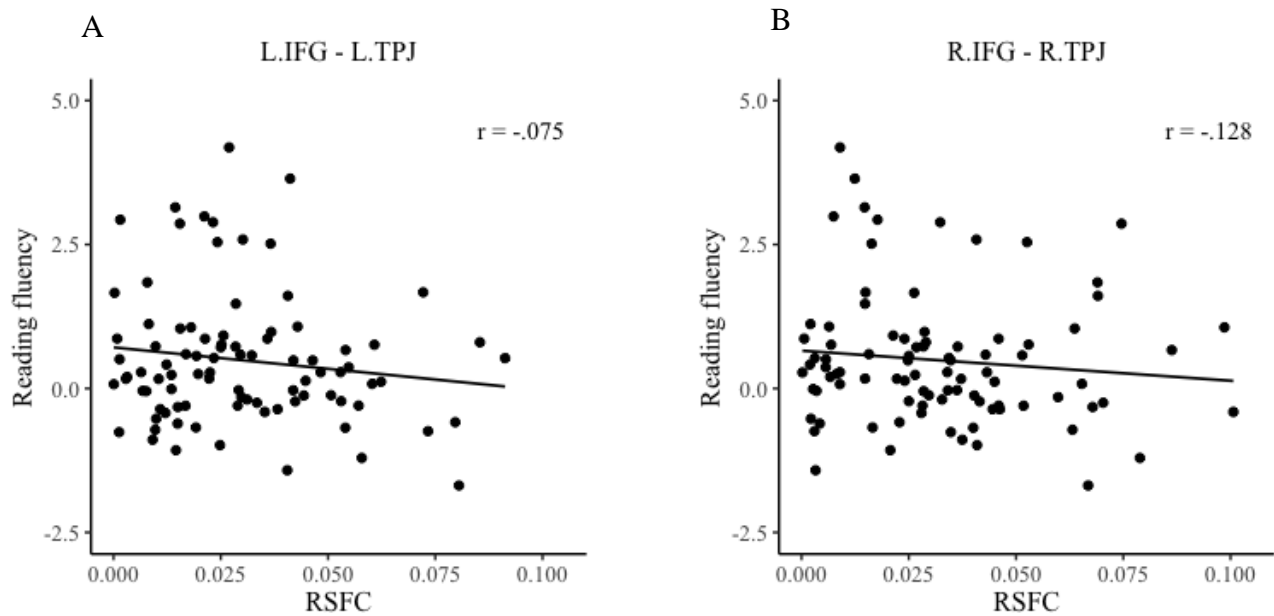


Figure 3. Scatterplots (A & B) of reading fluency and resting-state functional connectivity (RSFC) (N = 90). Reading fluency measured as z-scores, where high value indicates good reading, and low z-score indicates poor reading. RSFC measured as absolute values of Imaginary Part of Coherency (IPC). Absolute IPC-values ranges between 0 and 1. A value of 1 indicates that the two signals are perfectly synchronized and a value of 0 indicates perfect asynchrony. Scatterplot A is RSFC in the left hemisphere between L.IFG and L.TPJ and scatterplot B is RSFC in the right hemisphere between R.IFG and R.TPJ.

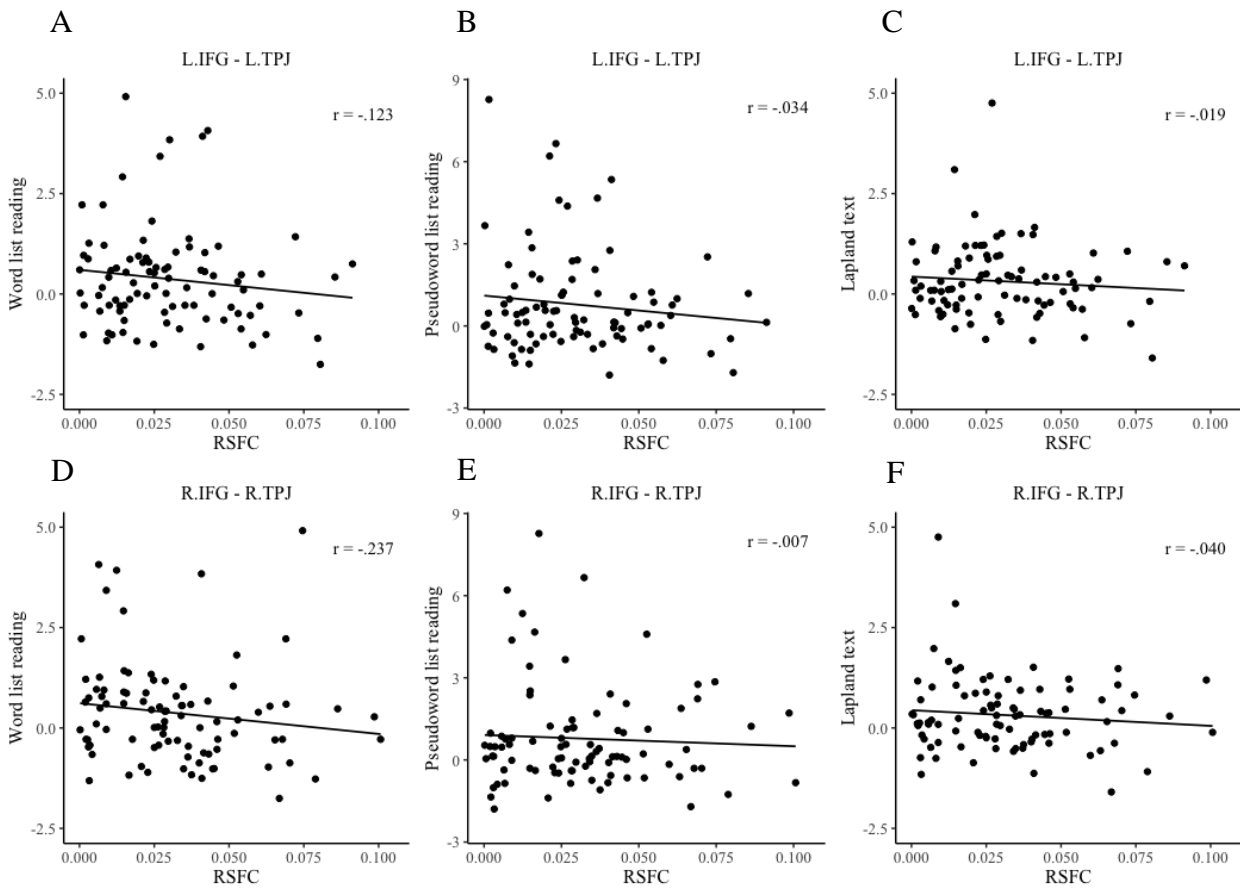


Figure 4. Scatterplots of reading fluency subtasks (word and pseudoword list reading and Lapland text) and resting-state functional connectivity (RSFC) (N = 90). Scatterplots A-C present the left hemisphere RSFC between L.IFG and L.TPJ and reading fluency subtasks. Scatterplots D-F present the right hemisphere RSFC between R.IFG and R.TPJ and reading fluency subtasks.

MZ twin correlations as index of heritability

The MZ-twins had a stronger correlation in the RSFC between L.IFG and L.TPJ ($r = .280$, $r^2 = .078$, $p = .035$) in comparison to the sampling distribution of r but not in the right hemisphere R.IFG and R.TPJ ($r = .214$, $r^2 = .046$, $p = .080$). The bootstrap ($n = 1000$) bias-corrected and accelerated (BCa) 95 % confidence intervals were .007–.521 (between L.IFG and L.TPJ) and -.103–.504 (between R.IFG and R.TPJ).

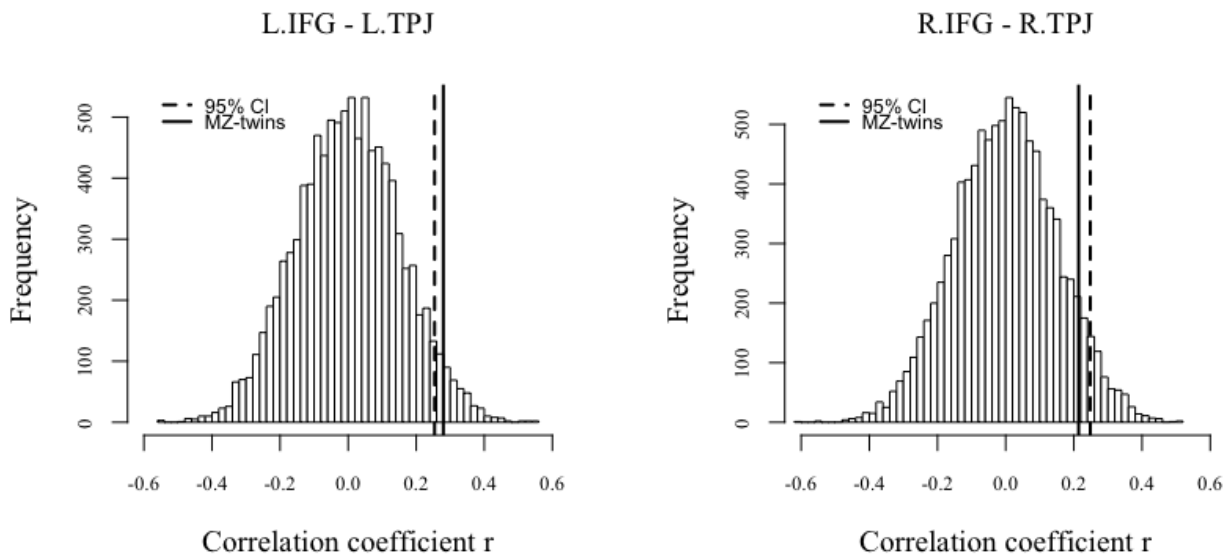


Figure 5. Permuted sampling distributions of between pairs r in resting-state functional connectivity between L.IFG and L.TPJ and between R.IFG and R.TPJ. The obtained correlation between monozygotic twin pairs is compared to the distributions of r , which were constructed by 10,000 random pairings of the participants with confidence interval (CI) of 95 % (i.e., 5 % of the correlation values are located on the right side of the interval in the permutation distribution).

DISCUSSION

The aim of this study was threefold: 1. to discover resting-state functional connectivity (RSFC) in reading-related regions, 2. to investigate the RSFC's association to reading fluency and 3. to examine the heritability of the RSFC. The functional connectivity analysis was performed using imaginary part of coherency (IPC) in the theta frequency band between IFG, TPJ and VWFA, in both hemispheres. To further investigate the association between RSFC and reading fluency, a computed reading fluency variable, consisting of three reading speed subtasks, was correlated with RSFC. The heritability examination of RSFC between MZ-twins was carried out by comparing the obtained correlations between MZ-twins to permuted sample distributions of r .

Resting-state functional connectivity in the reading-related regions

Considering the first research question, our hypothesis to detect significant RSFC between ROIs, was partly supported. Out of 6 ROI interactions, we observed two significant RSFCs in theta frequency band: between left IFG and left TPJ, and between right IFG and right TPJ. In this study, the MNI coordinates of left temporoparietal junction (TPJ) corresponded to the MNI coordinates of the posterior part of the left superior temporal gyrus (STG) used in previous studies (e.g., Richlan et al., 2011). The finding of RSFC between IFG and TPJ has been recorded in a fMRI study by Koyama et al. (2010), but contrary to our study, the authors found a significant RSFC unilaterally in the left hemisphere. Similar results, with fMRI, were reported by Schurz et al. (2015) and Koyama et al. (2011), the authors found RSFC between the left IFG and left STG. In addition to the resting-state results reported by Schurz et al. (2015), the authors also found a connectivity between left IFG and left STG during a reading task. The connectivity between left IFG (classically Broca's area) and left STG (classically Wernicke's area) is extensively documented. The connectivity aligns with both the dorsal stream in the dual-stream model of the functional anatomy of language (Hickok & Poeppel, 2007) and with the white matter tract arcuate fasciculus, which anatomically connects the two regions (e.g., Vandermosten et al., 2012). Together, well established robust functional and structural

connection between the two regions strongly indicates that left hemisphere connectivity between IFG and STG is a crucial aspect in language processing.

Regarding our result of significant RSFC in the right hemisphere (between right IFG and right TPJ), the existing research literature is substantially more limited in comparison to the left hemisphere. Considering the white matter tracts, language-related arcuate fasciculus has been documented to be strongly asymmetrical, i.e., relative fiber density of the left arcuate fasciculus is greater than right arcuate fasciculus (e.g., Nucifora et al., 2005). Also aligning with results from other MRI methods, whereas left arcuate fasciculus is postulated to be mainly associated with language processing, the function of right arcuate fasciculus, especially in language, is partially unclear. Nonetheless, right arcuate fasciculus has been hypothesized to contribute to visuospatial processing and also in language-related processes, such as semantic and prosodic processing (Vandermosten et al., 2012). In conclusion, while it is possible that future studies establish a connection between right hemisphere connectivity and reading, the current understanding of the function of right hemisphere in reading remains unclear across various brain imaging methods.

In this study, left FFG (i.e., VWFA) displayed no RSFC with any of the ROIs. Nonetheless, VWFA has shown to be a critical area for the reading network in both resting-state and task-based functional connectivity fMRI studies (e.g., Van der Mark et al., 2011; Koyama et al., 2011; Schurz et al., 2015). However, because our participants were Finnish-speaking adults and the ROI-selection considered only the reading-related network, the result of a non-significant RSFC in VWFA can be viewed in three ways. First, as stated in the studies by Koyama et al. (2011) and Finn et al. (2014), the stronger connectivity between VWFA and frontoparietal regions (e.g., left IFG) may represent acquired proficient reading skills in a mature brain. Although our participants were adults, their reading competence could not be described as proficient due to the heterogeneity of their reading competence and number of participants having slow reading skills, which might diminish the connectivity between VWFA and left IFG. Second, it is worth noting that the activation of VWFA may be stronger in opaque orthographies such as English and Danish due to the inconsistent letter-to-sound correspondence (Provazza et al., 2022). Therefore, the activation of the VWFA which is primarily associated with fluent reading through word recognition (Dehaene & Cohen, 2011), is particularly stronger for unfamiliar words compared to familiar words but may also vary depending on the orthographic depth (Provazza et al., 2022). Meaning that in deep orthographies (i.e., opaque), reading relies more on whole-word recognition, resulting in an increased involvement of VWFA compared to shallow orthographies (i.e., transparent) (Provazza et al., 2022; Marinelli et al., 2016). Third, in line with our results, the fMRI studies by Vogel et al. (2012) and Zhou et al. (2015) found

no RSFC between VWFA and typical reading-related network, but contrary to our participants' orthography, with native English and Chinese speakers. However, Vogel et al. (2012) and Zhou et al. (2015) demonstrated that VWFA has RSFC with regions in the dorsal attention network (e.g., intraparietal sulcus), which contributes by directing attention towards the appropriate task-relevant stimuli. Therefore, Vogel et al. (2012) proposes that VWFA's predominant function is not specifically in processing letter and word stimuli. Instead, its primary role seems to be processing visual stimuli in general by processing groups or chunks of various sizes, useful in reading but also in other visual tasks (Vogel et al., 2012).

In addition to the orthographic depth, reading competence and possible misinterpretation of the function of VWFA, there is a likelihood that different brain imaging methods may affect the outcome of observed RSFC. The majority of previous RSFC studies utilises fMRI (e.g., Koyama et al., 2010, 2011; Vogel et al., 2012; Schurz et al., 2015) and this study, to our knowledge, is first to measure RSFC in the reading-related regions with MEG. However, whereas MEG reflects electrophysiological aspect of the brain with emphasis on temporal resolution, fMRI reflects haemodynamic aspect with emphasis on spatial resolution (Hall et al., 2014). This discrepancy between the nature of MEG and fMRI signals may lead to different localization or/and strength of the neural activation (Vartiainen et al., 2011; Hall et al., 2014). However, a functional connectivity study conducted by Liljeström et al. (2015) demonstrated, in a task-based paradigm (object and picture naming), that the greatest similarity between MEG and fMRI networks was observed in slow oscillations < 30 Hz. In addition, similarity of RSFC between MEG and fMRI in the default mode network have been noted across frequency bands (Garcés et al., 2016). Despite this, dissimilar functional patterns have been observed during a reading task, wherein fMRI showed stronger activation in the left IFG compared to MEG, while MEG showed pronounced activation in the left STG (Vartiainen et al., 2011). Therefore, to combine fMRI and MEG in a multimodal design, it is essential to understand the complementary nature of these methods, especially in high-level cognitive functions such as reading and also within the reading-related network during resting-state. In addition, the data-driven fMRI-study by Finn et al. (2014) found a stronger task-based functional connectivity with dyslexic adults, but not in the typical reading network (between VWFA and visual cortex). Therefore, it may be more suitable to use data-driven source localization methods, such as beamforming or minimum norm estimates (MNE), to solve the inverse problem. These methods could provide a comprehensive understanding of connectivity interactions among individuals with different reading abilities and in different orthographies, compared to using dipoles placed at presumed MNI coordinates.

There is also a methodological decision in the utilization of connectivity measures. We used the IPC, which is a suitable approach to detect RSFC because it is not susceptible to field spread coming from volume conduction and therefore shows a credible picture of functional connectivity (Nolte et al., 2004). However, coherence methods, such as IPC, have demonstrated poor test re-test reliability, meaning that there might be a significant variability over subjects in terms of reproducing the same RSFC network across repeated sessions (Colclough et al., 2016). To establish the reliability of RSFC in this study, we calculated a theoretical cut-off point with confidence limit of 95 % (Halliday et al., 1995), where IPC-values above this line can be interpreted as significant RSFC. Still, including another method, such as permutation, which is based on observed data in contrast to the theoretical limit, could have provided reassurance regarding the significance of the observed RSFC in this study. However, to ensure the ROI interaction as significant RSFC, a requirement that at least 50% of the participants have an IPC value above the cut-off point was employed. More specifically, we used a minimum number of trials (149) for estimating the cut-off point instead of determining the cut-off points individually. The reason to use minimum number of trials was due to the high interparticipant variability of resting-state data duration (range = 139 – 634, md = 473). With the minimum number of trials, the cut-off point (.02) was considerably higher than it would have been with individual cut-off points (md = .006). Subsequently, fewer ROI interactions were classified as significant RSFC, and therefore, the strict cut-off point increased the reliability of detecting significant RSFC, whereas using very high trials individually might artificially decrease the theoretical cut-off point and lead to Type I errors.

The association of resting-state functional connectivity and reading fluency

Regarding the second research question, our hypothesis was not supported: in this study we did not observe any association between RSFC and reading fluency. The finding differs from previous RSFC-studies, in which stronger RSFC has been associated with higher reading competence (e.g., Koyama et al., 2011; Schurz et al., 2015). More specifically, contrary to our RSFC results, Schurz et al. (2015) reported a group difference in RSFC between left STG (corresponding roughly to our left TPJ) and left IFG pars triangularis, where dyslexic readers showed reduced RSFC in comparison to nonimpaired readers. Similarly, Koyama et al. (2011) found that reading competence was positively

associated with RSFC between the left IFG pars opercularis and left STG, both in children and in adults. However, in line with our result, Koyama et al. (2011) found no association between RSFC, among TPJ and other reading-related regions, and reading competence.

As stated above, left hemisphere connectivity between frontal regions (classically Broca's area) and temporoparietal regions (classically Wernicke's area), can be structurally linked to a white matter tract arcuate fasciculus. According to the meta-analysis of DTI studies by Vandermosten et al. (2012), a lower fractional anisotropy (FA) in the left temporoparietal regions, and to a lesser degree in the left frontal gyrus, are the most replicated results, in DTI studies, when comparing dyslexic individuals to nonimpaired readers, and the lower FAs are associated with impaired word and pseudoword reading. Furthermore, the authors argue that the left arcuate fasciculus is one of the main white matter tracts where the reading correlates and group comparison are located specifically (Vandermosten et al., 2012). Indeed, in the studies by Koyama et al. (2011) and Schurz et al. (2015), both authors argue that the connectivity results partially demonstrate the connection between classically described as Wernicke's and Broca's areas, and connectivity between these areas are seen with nonimpaired readers, while disconnection of these regions is seen with dyslexic individuals. Overall, according to the previous research, left hemispheric connectivity between IFG and STG is regarded as a crucial aspect for intact language processing. This connectivity possibly aligns with the dual-stream model of the functional anatomy of language by Hickok and Poeppel (2007), which proposes that the left dominant dorsal stream, including both IFG and STG, is primarily associated in mapping sensory and phonological representations onto articulatory motor representations.

Considering the RSFC result in the right hemisphere (between right IFG and right TPJ), we had no hypothesis due to the limited amount of existing RSFC studies that focus on the reading-related regions' homologs in the right hemisphere. As stated previously, no association was observed between right hemisphere RSFC and reading fluency. Originally, dysfunctional reading network has been hypothesized to manifest as a hyperactivity in the right hemisphere which is thought to present a compensatory mechanism of dyslexic individuals (Sandak et al., 2004; Shaywitz and Shaywitz, 2005). However, the notion on compensatory mechanism has been challenged by meta-analysis by Richlan et al. (2009) which found no overactivation in right hemisphere among dyslexic individuals. Indeed, among more recent functional connectivity fMRI studies, the increased connectivity in the right hemisphere especially in the equivalent reading-related regions is typically not reported with dyslexic participants, although with exceptions which generally consider subcortical and nontypical reading-related regions (e.g., Finn et al., 2014). Therefore, our result aligns with of previous functional connectivity fMRI studies, which reported no association between reading competence

and right hemispheric functional connectivity, in the reading-related homologs. Although we detected a significant correlation between right hemisphere RSFC and one of the subtasks, word list reading ($r = -.237$), the correlation was weak and negative, indicating that good readers had stronger connectivity, and not vice versa. However, due to the lack of previous research, the weak correlation and only with one of the subtasks, the interpretation of the role of right hemisphere connectivity between right IFG and right TPJ remains unclear.

There could be several reasons for our divergent result in not associating RSFC with reading fluency, including: the reading fluency variable, the nature of Finnish language, and the reading competence of the participants. The computed reading fluency variable consisted of three subtasks: word- and pseudoword list reading and Lapland text. The variable measured solely reading speed but not accuracy, therefore from the perspective of cognitive predictors of reading, RAN was emphasised more, whereas PA was downplayed. Reading accuracy, and therefore PA indirectly, was omitted for two reasons. First, in the longitudinal study by Torppa et al. (2012), following children from grade 1 to 3, the authors reported that deficits in RAN predicted slow reading speed and difficulties in spelling among Finnish children, whereas deficits in PA predicted solely difficulties in spelling, and only among children with familial risk of dyslexia. The results reported by Torppa et al. (2012) are in line with a review by Kirby et al. (2010), in which the authors speculate the normal course of word reading development and the cognitive predictors of language. According to the authors, the beginning of word reading development is characterized more alphabetic or phonological, which is followed by more orthographic phase (Kirby et al., 2010). During the alphabetic or phonological phase, PA has relatively stronger correlations with word reading, whereas with the shift to more orthographic phase, RAN displays a higher correlation with word reading (Kirby et al., 2010). Second, with transparent orthographies, reading competence is preferable to be measured with reading speed due to the reason that the individuals reach the ceiling in reading accuracy scales during childhood (e.g., Landerl & Wimmer, 2008). Indeed, among our participants, in Lapland-text (total of 211 words) the average number of errors was very low ($md = 2$, $mean = 3.8$). To conclude, we decided to exclude accuracy in reading fluency variable, due to the reason that observing accuracy errors would require significantly more complex tasks, which may not be expedient and since RAN, in comparison to PA, seems to be a stronger cognitive predictor of reading fluency among adults, especially in Finnish.

An alternative way of studying reading competence's association to RSFC could have been to use cognitive predictors of reading (PA and RAN) instead of reading speed. However, in previous research, direct measures of reading, such as reading speed and accuracy, have been successfully used to associate reading competence and RSFC (e.g., Koyama et al., 2011, 2013; Schurz et al., 2015;

Zhou et al., 2015). Notably in previous research, particularly RAN, has been associated with RSFC, however the results display a lot of variability. In the study by Cross et al. (2021), RAN scores were associated with RSFC only between bilateral or subcortical regions (left thalamus to right FFG, left IFG to right FFG) and not between typical reading-related left hemisphere regions (e.g., IFG pars opercularis, middle frontal gyrus, FFG, angular gyrus and posterior part of STG). In turn, the study by Schurz et al. (2015) found correlations between left hemisphere RSFC and RAN, however to a lesser degree than with reading (between inferior temporal gyrus and IFG pars opercularis, STG and IFG pars opercularis, IFG and angular gyrus). In addition, whereas RAN (or PA) can be characterized as an indirect measure of reading, RSFC (especially via MEG) in comparison to task-based connectivity can also be seen as an indirect measure of studying connectivity. Therefore, using the two measures combined could have created a cumulative effect of indirectness. It also seems that the explanatory power of PA and RAN in reading fluency are partially orthography and spelling dependant. For example, in a cross-cultural study by Georgiou et al. (2010), the authors found that in second grade, among any of studied languages, that varied in orthographic depth and spelling consistency (English, Greek and Finnish), PA was associated with text fluency (i.e., reading speed) only in English, and RAN was associated with text fluency in every language. Overall, the previous research illustrates both the heterogeneity of results considering the association between RSFC and reading fluency's cognitive predictors and the complexity of the essence and the ways of studying underlying neural mechanisms of reading competence. Thus, we justified the use of direct over indirect measures of reading competence, even if it may complicate cross-orthography comparisons.

Nonetheless, an argument against our reading fluency variable could be made. We combined three reading speed subtasks (not accuracy, for the previously mentioned reasons) in order to characterize reading fluency more comprehensively to represent the nature of Finnish language. Still, an intercorrelation between subtasks, especially with word list reading, was relatively weak (word and pseudoword list reading $r = .55$, word list reading and Lapland text $r = .58$, pseudoword list reading and Lapland text $r = .81$). It is likely, that the relatively weak intercorrelations of the subtasks affected subsequently the correlation between reading fluency and RSFC. However, when examining subtasks' correlations to RSFC independently, only word list reading displayed a correlation, furthermore, the correlation was weak ($-.24$) and within right hemisphere (between right IFG and right TPJ). In addition, our participants' slightly slow performance in word list reading and Lapland-text was consistent ($.39$ and $.32$, respectively). However, with pseudoword list reading, the performance was distinctly slower ($.78$). Taken together, the weak intercorrelations and distinct performance between subtask can be interpreted as due the reading fluency subtasks measure different

linguistic skills (e.g., van Viersen, Protopapas & De Jong, 2022) and therefore the inter-task variability in the scores reflects individual differences in reading competence. Thus, in order to study reading competence's association to RSFC, it may be necessary to employ more complex analysis techniques and metrics that can capture individual differences in reading competence. Finally, we speculate that the primary reason for not observing an association between reading fluency and RSFC in this study, is more related to the complexity of RSFC in the reading-related processes and methodological choices, concerning the selection of MNI coordinates and the use of MEG and IPC, than reading fluency measures.

The familial heritability of resting-state functional connectivity in the reading-related regions

Considering the third research question and the hypothesis to find stronger correlation in MZ-twins than between non-related pairs in the RSFC was partially supported. We found a moderate correlation ($r = .28$, $p = .03$) among MZ-twins' RSFC between left IFG and left TPJ in the theta frequency band, indicating possible heritability of RSFC in the left hemisphere's reading-related regions. However, the correlation in RSFC between right IFG and right TPJ among MZ-twins was non-significant ($r = .21$, $p = .08$), although the trend was similar to the result in the left hemisphere. To our knowledge, this is the first study that examined MZ-twin's correlations as an index of heritability of RSFC in the reading-related regions. In previous research, RSFC have been found to have moderate to high heritability within large-scale brain networks including, the default mode network (DMN) (Glahn et al., 2010; Ge et al., 2017), the visual network (VN), the frontoparietal network (FPN) (Barber et al., 2021) and the dorsal attention network (DAN) (Ge et al., 2017). Our result is partially in line with previous RSFC studies, indicating a possible heritability also in the left hemisphere reading-related regions, between the inferior frontal gyrus and the temporoparietal junction.

It is important to note that the heritability result must be interpreted with caution because the result explicitly indicates a significant correlation between MZ-twins. More specifically, we did not have monozygotic-dizygotic twin comparisons, and therefore common environmental factors were not accounted for. Consequently, conclusions about the gene-environment aspect cannot be drawn. However, the present study adds to the literature on the heritability of RSFC by emphasising plausible

heritability in the reading-related regions. Moreover, it expands the previous findings of heritability in other intrinsic networks such as the frontoparietal network and the dorsal attention network (Ge et al., 2017; Barber et al., 2021), which have been associated with adequate reading and dysfunctions in these has been seen in dyslexic individuals (Vogel et al., 2012; Zhou et al., 2015).

To conclude, we observed a moderate correlation ($r^2 = .08$) in the left hemisphere RSFC between MZ-twins, while the competence in reading fluency was highly similar ($r^2 = .42$). However, contrary to previous functional connectivity studies, we did not observe an association between reading fluency and RSFC. Nonetheless, reflecting the previous RSFC studies on heritability (Glahn et al., 2010; Schutte et al., 2013; Barber et al., 2021) and reading competence (Koyama et al., 2010, 2011; Vogel et al., 2012; Zhou et al., 2015; Schurz et al., 2015; Cross et al., 2021), we argue that the link between reading competence associated RSFC and heritability could be established in the future. Finally, given the genetic nature of dyslexia (e.g., Fisher & DeFries, 2002; Snowling & Melby-Lervåg, 2016), understanding the heritability of neural interactions underlying both nonimpaired and impaired reading could provide a more comprehensive picture of the genetic aspect of dyslexia.

Limitations

This study includes limitations that should be noted and taken into consideration for future research. First, different connectivity measures have different characteristics. For example, many connectivity measures such as coherence (Rosenberg et al., 1989) are confounded by the magnetic field spread, and therefore the imaginary part of coherency (IPC) (Nolte et al., 2004), which is robust to this effect, was chosen for the present study for estimating connectivity between brain interactions. However, the poor test re-test reliability of the IPC has been noted (Colclough et al., 2016). To address the reliability of the IPC, Marquetand et al. (2019) conducted a reproducibility study to test the reliability of IPC with resting-state data, by measuring the participants twice in a scan/rescan design, using MEG. The authors found that the reliability improved substantially when increasing the amount of resting-state data within the range from 50 seconds to 5 minutes (Marquetand et al., 2019). This improvement was noted in both the alpha and theta frequency bands (Marquetand et al., 2019). Therefore, in this study, the average amount of resting-state data was 14,07 minutes (422 trials), presumably improved the reliability of our results. Although, test re-test reliability of our results

presumably increased by the high amount of resting-state data, our study was the first to measure functional connectivity in the reading-related regions using MEG with IPC, and therefore the results cannot be directly compared to previous fMRI studies.

Second, in our study, the resting-state data consisted of both eyes open (EO), and eyes closed (EC) conditions. However, in general, resting-state data is analysed utilising either EO or EC condition (Agcaoglu et al., 2019). Notably, differences between these conditions have been reported, with fMRI in the amount of connectivity (Wei et al., 2018; Agcaoglu et al., 2019) and with MEG in the reliability of connectivity (Jin et al., 2011). More specifically, depending on the condition, connectivity seems to localize to different regions; EO condition is associated with stronger connectivity among several networks, including auditory network (Agcaoglu et al., 2019), whereas EC condition is mainly associated with stronger connectivity in sensorimotor regions (Wei et al., 2018; Agcaoglu et al., 2019). Regarding the reliability of MEG functional connectivity, the study by Jin et al. (2011) found that, EO condition displayed better reliability compared to EC condition, although significantly with solely alpha frequency band. In previous reading-related RSFC studies, EO resting-state condition has been typically used (e.g., Koyama et al., 2010; Vogel et al., 2012; Schurz et al., 2015; Cross et al., 2021). The inclusion of both conditions in our resting-state data was due to the interparticipant variability in the amount of resting state data, with both EO and EC conditions ranging from 2 to 10 minutes. Consequently, the conditions were merged to ensure a minimum of 4 minutes of resting-state data. As a result, reflecting the previous findings of increased overall connectivity during EO condition compared to EC condition, it is possible that we observed a lower level of functional connectivity compared to previous RSFC studies that exclusively utilised the EO condition.

Third, regarding the sample size of our study ($N = 90$), including 45 identical twin pairs, it can be considered relatively large in comparison to previous RSFC studies. For example: Schurz et al. (2015), $N = 29$; Koyama et al. (2010) $N = 25$; Koyama et al. (2011), $N = 50$ and Vogel et al. (2012), $N = 25$. However, especially for the heritability estimates, our sample size was limited in relation to previous heritability studies concerning RSFC, for example: Barber et al. (2021), $N = 815$ and Ge et al. (2017), $N = 809$. Indeed, our result's ($r = .28$) BCa bootstrap 95% confidence interval ($n = 1000$) was wide (.007-.521) and therefore our sample size was insufficient to draw definitive conclusions regarding the degree of heritability.

Significance and future directions

Dyslexia is a complex neurobiological disorder, affecting approximately 7 % of the population worldwide (Yang et al., 2022), which can lead to unwanted academic, social, and emotional consequences (Livingston et al., 2018). While multiple neural characterizations of dyslexia have been proposed, the precise role of functional connectivity is still unclear. Attaining a more comprehensive understanding of manifestation of the disorder in terms of connectivity, and the heritability aspect of these networks, is crucial for understanding the disorder itself and facilitating the identification and interventions within a clinical setting.

As the majority of RSFC studies concerning the reading-related regions have been conducted with fMRI, the use of different modalities, such as MEG, could contribute with the ability to detect real-time dynamics of cortical connectivity. Furthermore, we argue that the use of multimodal design, combining MEG and MRI, could provide a more efficient way to capture functional connectivity, due to the complementary benefits of temporal and spatial resolution. Still, it is essential to establish the evidence that two modalities reflect the same neuronal event in order to understand how the RSFC network obtained from one modality complements the functional connectivity obtained from another.

In addition, distributed source localization methods could reveal novel insights of connectivity within distinct brain areas of the left hemisphere, instead of relying solely on a priori regions. Utilising data-driven approaches could, for example, shed light on the complex connectivity of VWFA, which has been associated with reading-related processes (Shurz et al., 2015), but also with the dorsal attention network (Vogel et al., 2012). In addition, data-driven approaches have a potential to expand current knowledge about reading-related functional connectivity by examining whole brain activation and therefore unveiling the role of homologous regions in the right hemisphere, non-reading-related regions, and bilateral connections (Finn et al., 2014).

Previous RSFC research has predominantly focused on languages with opaque orthographies. Therefore, it is important for future studies to explore the functional connectivity patterns within languages with highly transparent orthography, such as Finnish. As previously mentioned, cognitive predictors of reading exhibit variability across different languages, with Finnish being among the few languages in which PA is not the strongest predictor (Ziegler et al., 2010), which potentially suggest differences in functional connectivity patterns as well. In this study, we did not observe any significant associations between RSFC, in typical reading-related regions, and reading fluency. This

result emphasises the possibility that reading may manifest distinct functional connectivity patterns among Finnish language. Alternatively, it is possible that in Finnish, reading fluency cannot be adequately captured solely by measuring reading speed but in combination with other reading competence related measures, such as rapid automatized naming (RAN).

Finally, despite our result indicating moderate heritability of RSFC in reading-related regions, we did not examine the environmental aspect of heritability due to the absence of dizygotic twins. Isolating genetic variance from the environment is essential in order to gain a comprehensive understanding of both the heritability of reading-related RSFC and how environmental factors modulate, positively or negatively, the neural manifestation of dyslexia. Therefore, in the future, common environmental factors should be taken into account with monozygotic-dizygotic twin study design.

Conclusions

We identified significant resting-state functional connectivity in both the left hemisphere, between the inferior frontal gyrus and temporoparietal junction, and in the right hemisphere homologues, but not in the VWFA. The RSFC in the left hemisphere is partially consistent with the previous fMRI studies (e.g., Koyama et al., 2010; 2011; Schurz et al., 2015) and aligns with the white matter tract arcuate fasciculus (Vandermosten et al., 2012). The RSFC was not associated with reading fluency, which contradicts previous research. Additionally, we found a significant correlation in the left hemisphere RSFC of monozygotic twins, indicating a moderate heritability of RSFC in typical reading-related regions. This was the first study to explore RSFC in the reading-related regions using MEG, and the results offer evidence for the potential of utilising resting-state MEG in functional connectivity studies in the future. Finally, our result of non-association between RSFC and reading fluency highlights the need for additional research among transparent orthographies.

REFERENCES

- Agcaoglu, O., Wilson, T. W., Wang, Y., Stephen, J., & Calhoun, V. D. (2019). Resting state connectivity differences in eyes open versus eyes closed conditions. *Human Brain Mapping, 40*(8), 2488–2498. <https://doi.org/10.1002/hbm.24539>
- Arnett, A. B., Pennington, B. F., Peterson, R. L., Willcutt, E. G., DeFries, J. C., & Olson, R. K. (2017). Explaining the sex difference in dyslexia. *Journal of Child Psychology and Psychiatry, 58*(6), 719–727. <https://doi.org/10.1111/jcpp.12691>
- Barber, A. D., Hegarty, C. E., Lindquist, M., & Karlsgodt, K. H. (2021). Heritability of Functional Connectivity in Resting State: Assessment of the Dynamic Mean, Dynamic Variance, and Static Connectivity across Networks. *Cerebral Cortex, 31*(6), 2834–2844. <https://doi.org/10.1093/cercor/bhaa391>
- Cao, F., Bitan, T., & Booth, J. R. (2008). Effective brain connectivity in children with reading difficulties during phonological processing. *Brain and Language, 107*(2), 91–101. <https://doi.org/10.1016/j.bandl.2007.12.009>
- Castles, A., Wilson, K., & Coltheart, M. (2011). Early orthographic influences on phonemic awareness tasks: Evidence from a preschool training study. *Journal of Experimental Child Psychology, 108*(1), 203–210. <https://doi.org/10.1016/j.jecp.2010.07.006>
- Chyl, K., Fraga-González, G., Brem, S., & Jednoróg, K. (2021). Brain dynamics of (a)typical reading development—A review of longitudinal studies. *Npj Science of Learning, 6*(1), 4. <https://doi.org/10.1038/s41539-020-00081-5>
- Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M.-A., & Michel, F. (2000). The visual word form area. *Brain, 123*(2), 291–307. <https://doi.org/10.1093/brain/123.2.291>

- Colclough, G. L., Woolrich, M. W., Tewarie, P. K., Brookes, M. J., Quinn, A. J., & Smith, S. M. (2016). How reliable are MEG resting-state connectivity metrics? *NeuroImage*, *138*, 284–293. <https://doi.org/10.1016/j.neuroimage.2016.05.070>
- Dehaene, S., & Cohen, L. (2011). The unique role of the visual word form area in reading. *Trends in Cognitive Sciences*, *15*(6), 254–262. <https://doi.org/10.1016/j.tics.2011.04.003>
- Démonet, J.-F., Taylor, M. J., & Chaix, Y. (2004). Developmental dyslexia. *The Lancet*, *363*(9419), 1451–1460. [https://doi.org/10.1016/S0140-6736\(04\)16106-0](https://doi.org/10.1016/S0140-6736(04)16106-0)
- Denckla, M. B., & Rudel, R. G. (1976). Rapid ‘automatized’ naming (R.A.N.): Dyslexia differentiated from other learning disabilities. *Neuropsychologia*, *14*(4), 471–479. [https://doi.org/10.1016/0028-3932\(76\)90075-0](https://doi.org/10.1016/0028-3932(76)90075-0)
- 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. <https://doi.org/10.1016/j.biopsych.2013.08.031>
- Fisher, S. E., & DeFries, J. C. (2002). Developmental dyslexia: Genetic dissection of a complex cognitive trait. *Nature Reviews Neuroscience*, *3*(10), 767–780. <https://doi.org/10.1038/nrn936>
- Garcés, P., Pereda, E., Hernández-Tamames, J. A., Del-Pozo, F., Maestú, F., & Ángel Pineda-Pardo, J. (2016). Multimodal description of whole brain connectivity: A comparison of resting state MEG, fMRI, and DWI. *Human Brain Mapping*, *37*(1), 20–34. <https://doi.org/10.1002/hbm.22995>
- Ge, T., Holmes, A. J., Buckner, R. L., Smoller, J. W., & Sabuncu, M. R. (2017). Heritability analysis with repeat measurements and its application to resting-state functional connectivity. *Proceedings of the National Academy of Sciences*, *114*(21), 5521–5526. <https://doi.org/10.1073/pnas.1700765114>

- Georgiou, G. K., Parrila, R., Cui, Y., & Papadopoulos, T. C. (2013). Why is rapid automatized naming related to reading? *Journal of Experimental Child Psychology*, *115*(1), 218–225. <https://doi.org/10.1016/j.jecp.2012.10.015>
- Georgiou, G. K., Protopapas, A., Papadopoulos, T. C., Skaloumbakas, C., & Parrila, R. (2010). Auditory temporal processing and dyslexia in an orthographically consistent language. *Cortex*, *46*(10), 1330–1344. <https://doi.org/10.1016/j.cortex.2010.06.006>
- Georgiou, G. K., Torppa, M., Manolitsis, G., Lyytinen, H., & Parrila, R. (2012). Longitudinal predictors of reading and spelling across languages varying in orthographic consistency. *Reading and Writing*, *25*(2), 321–346. <https://doi.org/10.1007/s11145-010-9271-x>
- Ghuman, A. S., McDaniel, J. R., & Martin, A. (2011). A wavelet-based method for measuring the oscillatory dynamics of resting-state functional connectivity in MEG. *NeuroImage*, *56*(1), 69–77. <https://doi.org/10.1016/j.neuroimage.2011.01.046>
- Glahn, D. C., Winkler, A. M., Kochunov, P., Almasy, L., Duggirala, R., Carless, M. A., Curran, J. C., Olvera, R. L., Laird, A. R., Smith, S. M., Beckmann, C. F., Fox, P. T., & Blangero, J. (2010). Genetic control over the resting brain. *Proceedings of the National Academy of Sciences*, *107*(3), 1223–1228. <https://doi.org/10.1073/pnas.0909969107>
- Hall, E. L., Robson, S. E., Morris, P. G., & Brookes, M. J. (2014). The relationship between MEG and fMRI. *NeuroImage*, *102*, 80–91. <https://doi.org/10.1016/j.neuroimage.2013.11.005>
- Halliday, D. M., Rosenberg, J. R., Amjad, A. M., Breeze, P., Conway, B. A., & Farmer, S. F. (1995). A framework for the analysis of mixed time series/point process data—Theory and application to the study of physiological tremor, single motor unit discharges and electromyograms. *Progress in Biophysics and Molecular Biology*, *64*(2–3), 237–278. [https://doi.org/10.1016/S0079-6107\(96\)00009-0](https://doi.org/10.1016/S0079-6107(96)00009-0)
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, *8*(5), 393–402. <https://doi.org/10.1038/nrn2113>

- Holopainen, L., Ahonen, T., & Lyytinen, H. (2001). Predicting Delay in Reading Achievement in a Highly Transparent Language. *Journal of Learning Disabilities, 34*(5), 401–413.
<https://doi.org/10.1177/002221940103400502>
- Horwitz, B., Rumsey, J. M., & Donohue, B. C. (1998). Functional connectivity of the angular gyrus in normal reading and dyslexia. *Proceedings of the National Academy of Sciences, 95*(15), 8939–8944. <https://doi.org/10.1073/pnas.95.15.8939>
- Jin, S.-H., Seol, J., Kim, J. S., & Chung, C. K. (2011). How reliable are the functional connectivity networks of MEG in resting states? *Journal of Neurophysiology, 106*(6), 2888–2895.
<https://doi.org/10.1152/jn.00335.2011>
- Kirby, J. R., Georgiou, G. K., Martinussen, R., Parrila, R., Bowers, P., & Landerl, K. (2010). Naming Speed and Reading: From Prediction to Instruction. *Reading Research Quarterly, 45*(3), 341–362. <https://doi.org/10.1598/RRQ.45.3.4>
- Klingberg, T., Hedehus, M., Temple, E., Salz, T., Gabrieli, J. D. E., Moseley, M. E., & Poldrack, R. A. (2000). Microstructure of Temporo-Parietal White Matter as a Basis for Reading Ability. *Neuron, 25*(2), 493–500. [https://doi.org/10.1016/S0896-6273\(00\)80911-3](https://doi.org/10.1016/S0896-6273(00)80911-3)
- Koyama, M. S., Di Martino, A., Kelly, C., Jutagir, D. R., Sunshine, J., Schwartz, S. J., Castellanos, F. X., & Milham, M. P. (2013). Cortical Signatures of Dyslexia and Remediation: An Intrinsic Functional Connectivity Approach. *PLoS ONE, 8*(2), e55454.
<https://doi.org/10.1371/journal.pone.0055454>
- Koyama, M. S., Di Martino, A., Zuo, X.-N., Kelly, C., Mennes, M., Jutagir, D. R., Castellanos, F. X., & Milham, M. P. (2011). Resting-State Functional Connectivity Indexes Reading Competence in Children and Adults. *Journal of Neuroscience, 31*(23), 8617–8624.
<https://doi.org/10.1523/JNEUROSCI.4865-10.2011>

- Koyama, M. S., Kelly, C., Shehzad, Z., Penesetti, D., Castellanos, F. X., & Milham, M. P. (2010). Reading Networks at Rest. *Cerebral Cortex*, *20*(11), 2549–2559.
<https://doi.org/10.1093/cercor/bhq005>
- Kronbichler, L., & Kronbichler, M. (2018). The Importance of the Left Occipitotemporal Cortex in Developmental Dyslexia. *Current Developmental Disorders Reports*, *5*(1), 1–8.
<https://doi.org/10.1007/s40474-018-0135-4>
- Kronbichler, M., Wimmer, H., Staffen, W., Hutzler, F., Mair, A., & Ladurner, G. (2008). Developmental dyslexia: Gray matter abnormalities in the occipitotemporal cortex. *Human Brain Mapping*, *29*(5), 613–625. <https://doi.org/10.1002/hbm.20425>
- Landerl, K., Ramus, F., Moll, K., Lyytinen, H., Leppänen, P. H. T., Lohvansuu, K., O’Donovan, M., Williams, J., Bartling, J., Bruder, J., Kunze, S., Neuhoff, N., Tóth, D., Honbolygó, F., Csépe, V., Bogliotti, C., Iannuzzi, S., Chaix, Y., Démonet, J.-F., ... Schulte-Körne, G. (2013). Predictors of developmental dyslexia in European orthographies with varying complexity: Cross-linguistic predictors of dyslexia. *Journal of Child Psychology and Psychiatry*, *54*(6), 686–694. <https://doi.org/10.1111/jcpp.12029>
- Landerl, K., & Wimmer, H. (2008). Development of word reading fluency and spelling in a consistent orthography: An 8-year follow-up. *Journal of Educational Psychology*, *100*(1), 150–161. <https://doi.org/10.1037/0022-0663.100.1.150>
- Liljeström, M., Stevenson, C., Kujala, J., & Salmelin, R. (2015). Task- and stimulus-related cortical networks in language production: Exploring similarity of MEG- and fMRI-derived functional connectivity. *NeuroImage*, *120*, 75–87.
<https://doi.org/10.1016/j.neuroimage.2015.07.017>
- Livingston, E. M., Siegel, L. S., & Ribary, U. (2018). Developmental dyslexia: Emotional impact and consequences. *Australian Journal of Learning Difficulties*, *23*(2), 107–135.
<https://doi.org/10.1080/19404158.2018.1479975>

- Lohvansuu, K., Torppa, M., Ahonen, T., Eklund, K., Hämäläinen, J. A., Leppänen, P. H. T., & Lyytinen, H. (2021). Unveiling the Mysteries of Dyslexia—Lessons Learned from the Prospective Jyväskylä Longitudinal Study of Dyslexia. *Brain Sciences*, *11*(4), 427. <https://doi.org/10.3390/brainsci11040427>
- Lyon, G. R., Shaywitz, S. E., & Shaywitz, B. A. (2003). A definition of dyslexia. *Annals of Dyslexia*, *53*(1), 1–14. <https://doi.org/10.1007/s11881-003-0001-9>
- Lyytinen, H., Erskine, J., Hämäläinen, J., Torppa, M., & Ronimus, M. (2015). Dyslexia—Early Identification and Prevention: Highlights from the Jyväskylä Longitudinal Study of Dyslexia. *Current Developmental Disorders Reports*, *2*(4), 330–338. <https://doi.org/10.1007/s40474-015-0067-1>
- Lyytinen, H., Richardson, U., & Aro, M. (2019). Developmental Dyslexia in Finnish. In L. Verhoeven, C. Perfetti, & K. Pugh (Eds.), *Developmental Dyslexia across Languages and Writing Systems* (1st ed., pp. 118–132). Cambridge University Press. <https://doi.org/10.1017/9781108553377.006>
- Maisog, J. M., Einbinder, E. R., Flowers, D. L., Turkeltaub, P. E., & Eden, G. F. (2008). A Meta-analysis of Functional Neuroimaging Studies of Dyslexia. *Annals of the New York Academy of Sciences*, *1145*(1), 237–259. <https://doi.org/10.1196/annals.1416.024>
- Marinelli, C. V., Romani, C., Burani, C., McGowan, V. A., & Zoccolotti, P. (2016). Costs and Benefits of Orthographic Inconsistency in Reading: Evidence from a Cross-Linguistic Comparison. *PLOS ONE*, *11*(6), e0157457. <https://doi.org/10.1371/journal.pone.0157457>
- Marquetand, J., Vannoni, S., Carboni, M., Li Hegner, Y., Stier, C., Braun, C., & Focke, N. K. (2019a). Reliability of Magnetoencephalography and High-Density Electroencephalography Resting-State Functional Connectivity Metrics. *Brain Connectivity*, *9*(7), 539–553. <https://doi.org/10.1089/brain.2019.0662>
- Marquetand, J., Vannoni, S., Carboni, M., Li Hegner, Y., Stier, C., Braun, C., & Focke, N. K.

- (2019b). Reliability of Magnetoencephalography and High-Density Electroencephalography Resting-State Functional Connectivity Metrics. *Brain Connectivity*, *9*(7), 539–553.
<https://doi.org/10.1089/brain.2019.0662>
- McCandliss, B. D., & Noble, K. G. (2003). The development of reading impairment: A cognitive neuroscience model. *Mental Retardation and Developmental Disabilities Research Reviews*, *9*(3), 196–205. <https://doi.org/10.1002/mrdd.10080>
- Melby-Lervåg, M., Lyster, S.-A. H., & Hulme, C. (2012). Phonological skills and their role in learning to read: A meta-analytic review. *Psychological Bulletin*, *138*(2), 322–352.
<https://doi.org/10.1037/a0026744>
- Morken, F., Helland, T., Hugdahl, K., & Specht, K. (2017). Reading in dyslexia across literacy development: A longitudinal study of effective connectivity. *NeuroImage*, *144*, 92–100.
<https://doi.org/10.1016/j.neuroimage.2016.09.060>
- Nolte, G., Bai, O., Wheaton, L., Mari, Z., Vorbach, S., & Hallett, M. (2004). Identifying true brain interaction from EEG data using the imaginary part of coherency. *Clinical Neurophysiology*, *115*(10), 2292–2307. <https://doi.org/10.1016/j.clinph.2004.04.029>
- Norton, E. S., Beach, S. D., & Gabrieli, J. D. (2015). Neurobiology of dyslexia. *Current Opinion in Neurobiology*, *30*, 73–78. <https://doi.org/10.1016/j.conb.2014.09.007>
- Norton, E. S., & Wolf, M. (2012). Rapid Automatized Naming (RAN) and Reading Fluency: Implications for Understanding and Treatment of Reading Disabilities. *Annual Review of Psychology*, *63*(1), 427–452. <https://doi.org/10.1146/annurev-psych-120710-100431>
- Nucifora, P. G. P., Verma, R., Melhem, E. R., Gur, R. E., & Gur, R. C. (2005a). Leftward asymmetry in relative fiber density of the arcuate fasciculus. *NeuroReport*, *16*(8), 791–794.
<https://doi.org/10.1097/00001756-200505310-00002>

- Nucifora, P. G. P., Verma, R., Melhem, E. R., Gur, R. E., & Gur, R. C. (2005b). Leftward asymmetry in relative fiber density of the arcuate fasciculus: *NeuroReport*, *16*(8), 791–794. <https://doi.org/10.1097/00001756-200505310-00002>
- Paulesu, E., Danelli, L., & Berlinger, M. (2014). Reading the dyslexic brain: Multiple dysfunctional routes revealed by a new meta-analysis of PET and fMRI activation studies. *Frontiers in Human Neuroscience*, *8*. <https://doi.org/10.3389/fnhum.2014.00830>
- Paulesu, E., Démonet, J.-F., Fazio, F., McCrory, E., Chanoine, V., Brunswick, N., Cappa, S. F., Cossu, G., Habib, M., Frith, C. D., & Frith, U. (2001). Dyslexia: Cultural Diversity and Biological Unity. *Science*, *291*(5511), 2165–2167. <https://doi.org/10.1126/science.1057179>
- Peterson, R. L., & Pennington, B. F. (2012). Developmental dyslexia. *The Lancet*, *379*(9830), 1997–2007. [https://doi.org/10.1016/S0140-6736\(12\)60198-6](https://doi.org/10.1016/S0140-6736(12)60198-6)
- Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1999). Functional Specialization for Semantic and Phonological Processing in the Left Inferior Prefrontal Cortex. *NeuroImage*, *10*(1), 15–35. <https://doi.org/10.1006/nimg.1999.0441>
- Provazza, S., Carretti, B., Giofrè, D., Adams, A.-M., Montesano, L., & Roberts, D. (2022). Shallow or deep? The impact of orthographic depth on visual processing impairments in developmental dyslexia. *Annals of Dyslexia*, *72*(1), 171–196. <https://doi.org/10.1007/s11881-021-00249-7>
- Pugh, K. R., Mencl, W. E., Jenner, A. R., Katz, L., Frost, S. J., Lee, J. R., Shaywitz, S. E., & Shaywitz, B. A. (2000). Functional neuroimaging studies of reading and reading disability (developmental dyslexia). *Mental Retardation and Developmental Disabilities Research Reviews*, *6*(3), 207–213. [https://doi.org/10.1002/1098-2779\(2000\)6:3<207::AID-MRDD8>3.0.CO;2-P](https://doi.org/10.1002/1098-2779(2000)6:3<207::AID-MRDD8>3.0.CO;2-P)

- Richlan, F., Kronbichler, M., & Wimmer, H. (2009). Functional abnormalities in the dyslexic brain: A quantitative meta-analysis of neuroimaging studies. *Human Brain Mapping, 30*(10), 3299–3308. <https://doi.org/10.1002/hbm.20752>
- Richlan, F., Kronbichler, M., & Wimmer, H. (2011). Meta-analyzing brain dysfunctions in dyslexic children and adults. *NeuroImage, 56*(3), 1735–1742. <https://doi.org/10.1016/j.neuroimage.2011.02.040>
- Rosenberg, J. R., Amjad, A. M., Breeze, P., Brillinger, D. R., & Halliday, D. M. (1989). The Fourier approach to the identification of functional coupling between neuronal spike trains. *Progress in Biophysics and Molecular Biology, 53*(1), 1–31. [https://doi.org/10.1016/0079-6107\(89\)90004-7](https://doi.org/10.1016/0079-6107(89)90004-7)
- Rosenberg, S. L. (1975). Temperature and pH optima for 21 species of thermophilic and thermotolerant fungi. *Canadian Journal of Microbiology, 21*(10), 1535–1540. <https://doi.org/10.1139/m75-225>
- Rutter, M., Caspi, A., Fergusson, D., Horwood, L. J., Goodman, R., Maughan, B., Moffitt, T. E., Meltzer, H., & Carroll, J. (2004). Sex Differences in Developmental Reading Disability: New Findings From 4 Epidemiological Studies. *JAMA, 291*(16), 2007. <https://doi.org/10.1001/jama.291.16.2007>
- Samar, V. J., Bopardikar, A., Rao, R., & Swartz, K. (1999). Wavelet Analysis of Neuroelectric Waveforms: A Conceptual Tutorial. *Brain and Language, 66*(1), 7–60. <https://doi.org/10.1006/brln.1998.2024>
- Sandak, R., Mencl, W. E., Frost, S. J., & Pugh, K. R. (2004). The Neurobiological Basis of Skilled and Impaired Reading: Recent Findings and New Directions. *Scientific Studies of Reading, 8*(3), 273–292. https://doi.org/10.1207/s1532799xssr0803_6

- Schurz, M., Wimmer, H., Richlan, F., Ludersdorfer, P., Klackl, J., & Kronbichler, M. (2015). Resting-State and Task-Based Functional Brain Connectivity in Developmental Dyslexia. *Cerebral Cortex*, 25(10), 3502–3514. <https://doi.org/10.1093/cercor/bhu184>
- Schutte, N. M., Hansell, N. K., De Geus, E. J. C., Martin, N. G., Wright, M. J., & Smit, D. J. A. (2013). Heritability of Resting State EEG Functional Connectivity Patterns. *Twin Research and Human Genetics*, 16(5), 962–969. <https://doi.org/10.1017/thg.2013.55>
- Shaywitz, S. E. (1998). Dyslexia. *New England Journal of Medicine*, 338(5), 307–312. <https://doi.org/10.1056/NEJM199801293380507>
- Shaywitz, S. E., Shaywitz, B. A., Fletcher, J. M., & Escobar, M. D. (1990). Prevalence of reading disability in boys and girls. Results of the Connecticut Longitudinal Study. *JAMA*, 264(8), 998–1002.
- Shaywitz, S. E., Shaywitz, B. A., Fulbright, R. K., Skudlarski, P., Mencl, W. E., Constable, R. T., Pugh, K. R., Holahan, J. M., Marchione, K. E., Fletcher, J. M., Lyon, G. R., & Gore, J. C. (2003). Neural systems for compensation and persistence: Young adult outcome of childhood reading disability. *Biological Psychiatry*, 54(1), 25–33. [https://doi.org/10.1016/S0006-3223\(02\)01836-X](https://doi.org/10.1016/S0006-3223(02)01836-X)
- Shaywitz, S. E., Shaywitz, B. A., Pugh, K. R., Fulbright, R. K., Constable, R. T., Mencl, W. E., Shankweiler, D. P., Liberman, A. M., Skudlarski, P., Fletcher, J. M., Katz, L., Marchione, K. E., Lacadie, C., Gatenby, C., & Gore, J. C. (1998). Functional disruption in the organization of the brain for reading in dyslexia. *Proceedings of the National Academy of Sciences*, 95(5), 2636–2641. <https://doi.org/10.1073/pnas.95.5.2636>
- Snowling, M. J., & Melby-Lervåg, M. (2016). Oral language deficits in familial dyslexia: A meta-analysis and review. *Psychological Bulletin*, 142(5), 498–545. <https://doi.org/10.1037/bul0000037>

- Torppa, M., Georgiou, G., Salmi, P., Eklund, K., & Lyytinen, H. (2012). Examining the Double-Deficit Hypothesis in an Orthographically Consistent Language. *Scientific Studies of Reading, 16*(4), 287–315. <https://doi.org/10.1080/10888438.2011.554470>
- Torppa, M., Parrila, R., Niemi, P., Lerkkanen, M.-K., Poikkeus, A.-M., & Nurmi, J.-E. (2013). The double deficit hypothesis in the transparent Finnish orthography: A longitudinal study from kindergarten to Grade 2. *Reading and Writing, 26*(8), 1353–1380. <https://doi.org/10.1007/s11145-012-9423-2>
- Van Der Mark, S., Klaver, P., Bucher, K., Maurer, U., Schulz, E., Brem, S., Martin, E., & Brandeis, D. (2011). The left occipitotemporal system in reading: Disruption of focal fMRI connectivity to left inferior frontal and inferior parietal language areas in children with dyslexia. *NeuroImage, 54*(3), 2426–2436. <https://doi.org/10.1016/j.neuroimage.2010.10.002>
- Van Viersen, S., Protopapas, A., & De Jong, P. F. (2022). Word- and Text-Level Processes Contributing to Fluent Reading of Word Lists and Sentences. *Frontiers in Psychology, 12*, 789313. <https://doi.org/10.3389/fpsyg.2021.789313>
- Vandermosten, M., Boets, B., Wouters, J., & Ghesquière, P. (2012). A qualitative and quantitative review of diffusion tensor imaging studies in reading and dyslexia. *Neuroscience & Biobehavioral Reviews, 36*(6), 1532–1552. <https://doi.org/10.1016/j.neubiorev.2012.04.002>
- Vartiainen, J., Liljeström, M., Koskinen, M., Renvall, H., & Salmelin, R. (2011). Functional Magnetic Resonance Imaging Blood Oxygenation Level-Dependent Signal and Magnetoencephalography Evoked Responses Yield Different Neural Functionality in Reading. *The Journal of Neuroscience, 31*(3), 1048–1058. <https://doi.org/10.1523/JNEUROSCI.3113-10.2011>
- Vogel, A. C., Miezin, F. M., Petersen, S. E., & Schlaggar, B. L. (2012). The Putative Visual Word Form Area Is Functionally Connected to the Dorsal Attention Network. *Cerebral Cortex, 22*(3), 537–549. <https://doi.org/10.1093/cercor/bhr100>

- Wagner, R. K., & Torgesen, J. K. (1987). The nature of phonological processing and its causal role in the acquisition of reading skills. *Psychological Bulletin*, *101*(2), 192–212.
<https://doi.org/10.1037/0033-2909.101.2.192>
- Wagner, R. K., Zirps, F. A., Edwards, A. A., Wood, S. G., Joyner, R. E., Becker, B. J., Liu, G., & Beal, B. (2020). The Prevalence of Dyslexia: A New Approach to Its Estimation. *Journal of Learning Disabilities*, *53*(5), 354–365. <https://doi.org/10.1177/0022219420920377>
- Wei, J., Chen, T., Li, C., Liu, G., Qiu, J., & Wei, D. (2018). Eyes-Open and Eyes-Closed Resting States With Opposite Brain Activity in Sensorimotor and Occipital Regions: Multidimensional Evidences From Machine Learning Perspective. *Frontiers in Human Neuroscience*, *12*, 422. <https://doi.org/10.3389/fnhum.2018.00422>
- Willcutt, E. G., & Pennington, B. F. (2000). Psychiatric comorbidity in children and adolescents with reading disability. *Journal of Child Psychology and Psychiatry, and Allied Disciplines*, *41*(8), 1039–1048.
- Wolf, M., & Bowers, P. G. (1999). The double-deficit hypothesis for the developmental dyslexias. *Journal of Educational Psychology*, *91*(3), 415–438. <https://doi.org/10.1037/0022-0663.91.3.415>
- Yang, L., Li, C., Li, X., Zhai, M., An, Q., Zhang, Y., Zhao, J., & Weng, X. (2022). Prevalence of Developmental Dyslexia in Primary School Children: A Systematic Review and Meta-Analysis. *Brain Sciences*, *12*(2), 240. <https://doi.org/10.3390/brainsci12020240>
- Yu, X., Zuk, J., & Gaab, N. (2018). What Factors Facilitate Resilience in Developmental Dyslexia? Examining Protective and Compensatory Mechanisms Across the Neurodevelopmental Trajectory. *Child Development Perspectives*, *12*(4), 240–246.
<https://doi.org/10.1111/cdep.12293>

Zhou, W., Xia, Z., Bi, Y., & Shu, H. (2015). Altered connectivity of the dorsal and ventral visual regions in dyslexic children: A resting-state fMRI study. *Frontiers in Human Neuroscience*, 9. <https://doi.org/10.3389/fnhum.2015.00495>

Ziegler, J. C., Bertrand, D., Tóth, D., Csépe, V., Reis, A., Faísca, L., Saine, N., Lyytinen, H., Vaessen, A., & Blomert, L. (2010). Orthographic Depth and Its Impact on Universal Predictors of Reading: A Cross-Language Investigation. *Psychological Science*, 21(4), 551–559. <https://doi.org/10.1177/0956797610363406>