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Longitudinal changes in reading network connectivity related to skill improvement

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ABSTRACT

Attempts to characterize the neural differences between individuals with and without dyslexia generally point to reduced activation in and connectivity between brain areas in a reading network composed of the inferior frontal gyrus, the ventral occipito-temporal cortex, and the dorsal temporo-parietal circuit. However, developmental work on brain activity during reading has indicated that some brain areas show developmental decreases in activation with age. Thus, reading network connectivity may also show decreases that are positively associated with increases in reading ability. However, the developmental trajectory of reading network connectivity in typically developing readers is not yet well established. In the current study, we use a longitudinal design to determine how connectivity changes over time, and how these changes relate to changes in reading skill. We find that longitudinal increases in reading ability are associated with higher initial connectivity in the dorsal stream between fusiform and inferior parietal cortex, implicated in phonological decoding, followed by decreases in connectivity in this stream over time. We further find that increases in reading ability are supported by maintenance of connectivity in the ventral stream between inferior occipital and fusiform cortex, suggesting a more mature automatic orthographic recognition strategy. Readers who show little reading improvement over time do not attain high levels of connectivity in the dorsal stream at any time point, and their ventral stream connectivity decreases over time. These results together suggest that superior reading ability is initially supported by phonological decoding, with a decreased reliance on this strategy as reading becomes more automated. Our results indicate that development of the dorsal and ventral streams are closely linked, and support the hypothesis that a decrease in the dorsal stream is important for ventral stream development.

1. Introduction

The process of reading is complex, relying on a number of brain regions that each play a different role in accessing linguistic information from written forms. While most people are able to successfully coordinate these brain regions to achieve fluid reading, about 5–10% of individuals are diagnosed with dyslexia, a disability in which a person has difficulty achieving fluid reading despite adequate instruction, motivation, and intelligence (Siegel, 2006). The extant neuroimaging literature examining differences between individuals with and without dyslexia has established that individuals with dyslexia tend to show reduced activation in key brain regions in the reading network (e.g. inferior frontal, temporo-parietal, and occipito-temporal cortex) compared to their typically reading peers (Pugh et al., 2001; Richlan, Kronbichler, and Wimmer, 2009, 2011; Shaywitz et al., 2002). Moreover, research using functional connectivity methods has also found that individuals with dyslexia differ in how well these regions work in tandem with one another (Cao, Bitan, and Booth, 2008; Finn et al., 2014; Horwitz, Rumsey, and Donohue, 1998; Koyama et al., 2013; Morken, Helland, Hugdahl, and Specht, 2017; Quaglino et al., 2008; van der Mark et al., 2011). Together, research suggests dyslexia involves more than an underactivation of key brain regions in typical left hemisphere reading networks, but also reduced functional connectivity between them.

The typical development of the reading network is not currently well described. This can make the interpretation of differences in connectivity between children with and without dyslexia difficult. For example, neuroimaging studies examining how activation in individual brain regions varies with age and skill have shown that decreases in activation

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over time can be a marker of better reading ability, depending on the brain region (Church, Coalson, Lugar, Petersen, and Schlaggar, 2008; McNorgan, Alvarez, Bhullar, Gayda, and Booth, 2011; Richlan et al., 2011). Thus, decreases in connectivity could, in some circumstances, be a marker of better reading, even in the left hemisphere. Specifically, one influential model of reading development proposes that there is a developmental shift from relying on dorsal stream processing, implicated in sound-symbol matching, to ventral stream processing, implicated in automatic recognition of word forms, that occurs as readers progress in age and skill (Pugh et al., 2001).

The dorsal, temporo-parietal circuit, including the left posterior superior temporal gyrus (L STG) and inferior parietal lobe (L IPL), is primarily involved in phonological processing and integrating visual (orthographic) and auditory (phonological) information, known as phonological decoding (Pugh et al., 2001). The dorsal route tends to be used for reading low frequency words and pronounceable pseudowords (Coltheart, 2006; Jobard, Crivello, and Tzourio-Mazoyer, 2003). The ventral, occipito-temporal circuit, including the fusiform gyrus (L FG) and inferior occipital gyrus (L IOG), is proposed to be critical for the fast, automatic processing of visual word forms (Pugh et al., 2001). In adults, a portion of the left ventral occipito-temporal cortex (L VOT), the putative visual word form area (Cohen et al., 2000; McCandliss, Cohen, and Dehaene, 2003), is thought to host neurons tuned to preferentially respond to real written words over pseudowords or consonant strings (Glezer, Jiang, and Riesenhuber, 2009). The ventral pathway tends to be used for words that are frequent or exception words whose pronunciation does not follow typical orthography to phonology mapping rules (Coltheart, 2006; Jobard et al., 2003). Thus, while both the dorsal and ventral streams are thought to be used throughout the lifespan depending on the type of word (i.e. exception versus unfamiliar words), the dorsal-to-ventral shift hypothesis proposes that children rely more on dorsal stream processing for all word types before shifting to reliance on the ventral stream for familiar words. This hypothesis has some support from cross-sectional studies of children and adults that have examined brain activation within these circuits (Richlan et al., 2011; Shaywitz et al., 2004; Simos et al., 2007). However, this model has not yet been directly tested with longitudinal data with either brain activation or functional connectivity analyses.

Research in both children and adults has indicated that functional connectivity within both ventral and dorsal reading circuits is related to reading skill, with more skilled readers showing greater connectivity compared to less skilled readers (Cao et al., 2008; Hampson et al., 2006; Horwitz et al., 1998; Levy et al., 2009; Quaglino et al., 2008; Shaywitz et al., 2004; van der Mark et al., 2011). Additional studies with adults have indicated that reading strategy may influence how the reading network is used (Kherif, Josse, Seghier, and Price, 2009; Seghier, Lee, Schofield, Ellis, and Price, 2008). In line with this idea, Levy et al. (2009) found reading skill is related to using the 'correct' pathway for the type of word being read. That is, those readers who showed both higher connectivity between regions in the dorsal route during pseudoword reading and higher connectivity between regions in the ventral route during real word reading had better overall reading scores. Further, the same study demonstrated that individual differences in reading skill of either real or pseudowords were also related to individual differences in pathway connectivity. Adults who showed high dorsal route connectivity during real word reading showed relatively poor real word reading skill, presumably due to reliance on an incongruent pathway. The results of this study indicate that reading strategy (i.e., reliance on dorsal or ventral stream processing) is related to reading network connectivity and reading skill.

While a relationship between reading skill and reading network functional connectivity has been established in adults, the development of functional connectivity in left hemisphere reading circuits needs to be further understood, particularly for the English language. One study has examined changes in reading network connectivity longitudinally in Norwegian children with and without dyslexia (Morken et al., 2017). In this study, typically developing children were found to show primarily decreasing or stabilizing connectivity over time, while children with dyslexia showed aberrant patterns of development that may have reflected overcompensation or normalization relative to their baseline connectivity levels. However, the study by Morken et al. (2017) does not examine skill within typically developing children, and does not examine the relationship between changes in connectivity to changes in reading skill. Further, Norwegian is a semi-transparent language, while English is opaque. That is, Norwegian orthographic to phonological mappings are fairly consistent and can be used to correctly pronounce unfamiliar words while mappings in English are not as consistent. The difference in consistency may result in differences in reading network use throughout development (Cao, Brennan, and Booth, 2015; Levy et al., 2009; Seghier et al., 2008).

While the extant research with children so far has indicated that the same positive relationship between current connectivity and current skill may hold true for English-speaking children (Cao et al., 2008; Quaglino et al., 2008; van der Mark et al., 2011), the dorsal-to-ventral shift hypothesis predicts that decreases in dorsal areas of the reading network are necessary for improvement of reading skill in children. This idea is supported by the general decreases in connectivity found in typical children in the Morken et al. (2017) study. The current study builds on previous literature by taking a unique approach to examine the longitudinal changes of the reading network in typically developing children. Rather than understanding how current connectivity relates to current reading skill, we examine how changes in reading skill are related to changes in reading network connectivity. In line with the dorsal-to-ventral shift model of reading development, we expect increases in reading skill to be related to decreases in connectivity of the dorsal stream and reliance on phonological decoding, together with increases in connectivity in the ventral stream and reliance on orthographic recognition. Using data from children followed longitudinally, this study will investigate where in the reading network high connectivity and low connectivity is associated with better reading skill. This knowledge will be important in establishing a better benchmark that can be used to compare and understand children who struggle with reading.

2. Methods

This study was carried out in accordance with the recommendations of the Northwestern University Institutional Review Board with written informed consent from all the legal guardians of all participants and written assent of all participants. All participants and their guardians gave written informed consent or assent in accordance with the Declaration of Helsinki.

2.1. Participants

Data from a group of 59 healthy children 8–14 years-old at T1, 29 females) were selected from a group of 125 children that participated in a longitudinal study using inclusion criteria described below. All children were right handed, native and majority English speakers with normal or corrected to normal hearing and vision. Each child had no history of neurological or psychiatric disorders; 19 participants (32%) had a family history of learning problems as reported by parents. Participants were selected for the current analysis if they were of at least average intelligence and reading ability (see below). Further, all participants had acceptable quality MRI data at both time points (see below) and at least 40% accuracy on all conditions of the in-scanner experimental tasks.

2.2. Procedure

Study procedures took place over the course of several visits. During the first visit, participants completed a battery of standardized tests. In the second visit, participants completed a 'mock scanning' session in which they were familiarized with the scanner, trained to minimize head