

Running head: MATERNAL READING PREDICTS CHILD BRAIN ACTIVITY

Maternal Reading History Predicts Neural Activity During Phonological Processing in

Pre-readers

An Honors Thesis presented

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Abstract

Reading ability, particularly reading impairment, tends to run in families. Models of developmental disorders, such as the Multiple Deficit Model (MDM) and intergenerational MDM (iMDM), account for such intergenerational transfer by highlighting diverse genetic and environmental pathways that affect diverse underlying etiologies. More research should be done in order to elucidate 1) the extent to which genetic and environmental pathways are at play in the intergenerational transfer of reading ability, 2) the specific neural mechanisms that underlie such transfer, and 3) the individual impact of mothers versus fathers. Aiming at these points, the present study investigated the neural activity of pre-readers (aged 60-80 months) during a phonological processing task in relation to a self-report assessment of parental reading history.

Environmental and cognitive variables were controlled for in an attempt to measure the direct effect of genetic pathways from parents to children. Results revealed that maternal, but not paternal, reading history predicted neural activity in four brain regions during phonological processing. These were the lingual gyrus, the left parietotemporal gyrus, the left occipitotemporal gyrus, and the right middle temporal gyrus. Reading-adept mothers tended to have children with greater activation during phonological processing in these regions. The intergenerational transfer of reading ability is likely, in part, genetic, and the implicated brain regions may constitute some of the neural mechanisms by which reading ability is conferred genetically. Furthermore, in the present study, maternal genes seemed to have more influence than paternal ones in shaping reading development via the neural mechanisms supportive of phonological processing.

Keywords: Phonological processing, ARHQ, fMRI, intergenerational transfer

I. Introduction

Learning to read is like learning to ride a bike or play the piano: it requires practice, which is often arduous and lasts for several years. The struggle inherent in learning how to read is in stark contrast to the relative ease with which children acquire language, and illustrates that reading, unlike spoken language, is a relatively modern invention (Wolf & Stoodley, 2008). Consequently, evolutionary forces have not had time to equip the brain's innate architecture with reading-specialized mechanisms. The ability to read, rather than a feat of built-in circuitry, must be a feat of experience-dependent plasticity. It entails integrating diverse brain regions, none of which could support reading on its own, that are co-opted and connected over years of laborious practice. While many children learn to read relatively quickly, many others struggle and eventually receive diagnoses for reading disabilities such as Developmental Dyslexia, an unexplained reading impairment that occurs despite typical IQ, hearing, vision, and instruction and affects approximately 5-17% of children (Ozernov-Palchik & Gaab, 2016). A major question in reading research is, simply, why: what causes the widespread variability in reading development?

Prerequisite to understanding the garden of reading development is identifying and distinguishing the myriad seeds, soils, and gardeners that help it grow. This, understandably, is an immense task. Reading ability sprouts from the intricate intergenerational interplay of genetic and environmental factors, all of which work in concurrent, combinatorial ways to affect each stage of reading growth: from the development of phonological skills, to the appreciation of phonology-to-orthography correspondence, to word recognition, to sentence and text comprehension (van Bergen,

2014). Phonological skills here refer to the manipulation and perception of speech sounds, and orthographic skills, similarly, refer to the manipulation and perception of components of written language, such as letters. These capabilities, in conjunction with others involving semantics, prosody, lexicality, memory, and morphosyntax, combine to make written language possible (Wolf, 2001). Though hard, characterizing the influence intergenerational factors have on this progression and these capabilities has substantial payoffs: it will lead to better predictions about child reading outcomes, more efficacious remediations for reading disabilities, and deeper theories about what underlies experience-dependent plasticity in children -- that is, what underlies the processes by which the environment (and, in this case, grueling practice) shapes neurobiology. In keeping with the analogy, it will lead to improved garden-maintenance.

While reading development literature has already tackled the intergenerational transfer of reading ability, the topic merits additional research in order to sharpen ideas pertaining to 1) the genetic and environmental factors that are most predictive of child reading ability, and 2) the neural mechanisms through which such factors exert their influence on reading development. To this end, the present study investigates the relationship between parental reading history and reading-related neural activity in pre-readers, assessing the extent to which this relationship can be explained by genetic pathways from parents to children. The next section discusses the importance of studying intergenerational pathways, specifically those from parents to children, when exploring the roots of reading development.

1. *The Intergenerational Multiple Deficit Model and the Importance of Parental Reading History as a Predictor of Child Reading Outcomes*

The Multiple Deficit Model (MDM) posits that the etiologies, or causes, of developmental disorders are multifactorial, involving multiple genetic and environmental factors whose influence cascades through neural, cognitive, and behavioral levels of analysis (Pennington, 2006). At each level of analysis, too, there are multiple components that interact in elaborate and bidirectional ways. The neural level, for instance, incorporates numerous brain regions and circuits, and the cognitive level involves abilities ranging from phonological skills to verbal working memory. Disorders result from deficits to any component. The alternative view, that a single cognitive deficit or “Holy Grail” could underlie an entire developmental disorder and its behavioral symptoms, is treated as unrealistic and simplistic. Building off of Pennington’s model, the intergenerational MDM (iMDM) emphasizes the fact that all genetic and many environmental factors that shape reading development are intergenerational; in other words, complex and intertwining pathways of influence work to transfer reading ability, whether adept or deficient, from parent to child (van Bergen, 2014).

Reading acquisition is an ideal battleground for multiple- versus single-deficit theories to duke it out, and multiple deficit theories come out on top. While phonological processing is sometimes considered the “Holy Grail” of dyslexia, or the single cognitive deficit underlying its reading impairments, phonological processing deficits and dyslexia are in fact doubly dissociable; many dyslexics have intact phonological processing, and many phonological processing deficits occur without a dyslexia diagnosis (van Bergen, 2014). Rather, because reading enlists numerous cognitive functions (e.g., phonological processing, rapid automatized naming) and perceptual processes (e.g., temporal sampling, visual–spatial attention), reading deficits vary widely according to which function or

process is impaired (Norton, 2015). The quality of reading-relevant genes and the accessibility of literacy resources (or the lack thereof) impact these sub-components. Corroborating research reveals that parental reading ability relates to child reading ability directly and indirectly via cognitive intermediaries, such as phonological awareness, rapid automatized naming, and visual attention span (van Bergen, 2015). Intergenerational and multi-componential interplay makes the search for a single, bottom-line “cause” of reading impairment especially fruitless, and the search for multiple causal pathways from parent to child especially difficult.

The iMDM looks to familial characteristics, such as family histories of reading ability, to begin identifying causal pathways. Family risk studies, for instance, compare the reading abilities of children with those of their relatives. One such study found that 30% of children deemed at “high risk” for dyslexia eventually received a diagnosis, whereas only 3% of children deemed at “low risk” did (van Bergen, 2012). Researchers defined “high risk” as having a dyslexic parent or close relative. Family risk studies tend to report that approximately 33 to 66% of children with a dyslexic parent have dyslexia themselves. This differs strikingly from children without a dyslexic parent, of whom approximately 6 to 16% have dyslexia (van Bergen, 2012). Furthermore, children at family risk for dyslexia often possess cognitive and neural deficiencies before learning how to read, suggesting that deficits exist at very young ages or birth. This highlights the immediate effects of genetic and environmental family factors on reading development and has important translational implications: understanding the origin and development of reading-related brain deficiencies will improve both the early identification of children

at risk of developing reading difficulty and the efficacy of interventions (Ozernov-Palchik & Gaab, 2016).

Simply put, reading ability runs in families. To determine the extent to which “running in families” works through genetic heritability and environmental transfer, it is helpful to look at the most influential people in the early lives of children: often, parents. Important parental traits include education, income, reading habits, teaching habits, and reading ability. Additionally, parental accurate and fluent reading, spelling, phonological awareness, and rapid naming are particularly good predictors of child reading ability (van Bergen et al., 2014). Parents’ characteristics and phenotypes are useful because they involve both genetic and environmental pathways; they are proxy measures for both genotype, which parents pass onto their children, and home environment, which parents help sculpt. In illustration of this, reading-adept parents may be more likely to both 1) pass on genes for integrative reading-related neural characteristics, and 2) provide their children with reading-rich environments, contributing toward positive reading outcomes. However, these pathways are hard to disentangle in empirical studies, particularly because research has implicated a passive gene-environment correlation in which reading-rich environments correlate with the quality of the parents’ reading-related genes, thereby rendering associations between child environment and reading ability potentially illustrative of a masked genetic effect (Snowling et al., 2007). Accordingly, while aspects of child environment were associated with child reading ability in a recent study, these effects were largely lost when controlling for parent reading ability (van Bergen et al., 2016). Employing parental measures, as the present study does, may combat confounding correlations and shed light on intergenerational, intertwined pathways.

By adopting this and other strategies, studies have generated substantial evidence to suggest that reading ability, particularly reading impairment, is largely conferred from parents to children genetically. Numerous studies, for instance, have shown that reading skills and disorders are highly heritable (e.g. Snowling et al., 2013), with genetic factors contributing more than environmental ones to reading development (Byrne et al., 2009). The reading skills of dyslexic parents have also been shown to predict child reading ability and risk of dyslexia, even after accounting for aspects of home literacy and parental education (Torppa et al, 2011). Furthermore, a meta-analysis of twin studies has estimated that genetic effects could explain 73% of reading variability in school children aged 6-13 years old (Zeeuw et al. 2015) and several “dyslexia genes,” or genes that confer liability for dyslexia, have been identified (e.g. Deffenbacher et al., 2004; Francks et al., 2004). Given the hereditary nature of reading ability, the cognitive abilities of biological parents, which, when controlling for environmental influences, are in effect proxy measures for genetic pathways, should be of obvious interest to researchers studying the intergenerational transfer of reading.

This should not, however, discredit the role of environmental factors in shaping reading development. One such factor, home literacy environment (HLE), quantifies the features within a child’s home that promote literacy. These may incorporate parents’ reading habits (e.g., how often they read with their children), teaching habits (e.g., how often they teach their children the alphabet), and libraries (e.g., how many children’s books they own) (Niklas & Schneider, 2013). HLE tends to positively correlate with child literacy skills, such as word reading fluency and accuracy, although as previously noted, this correlation may stem from a passive gene-environment correlation. However,

one aspect of HLE was found to significantly predict variance in children's reading ability even after controlling for parental reading: number of household books (van Bergen et al., 2016). Books, then, might exert a genuine influence on child literacy skills that is unexplainable by a passive gene-environment correlation. Even so, since reading-adept parents may have larger household libraries than reading-deficient parents, it seems that parental phenotypes can still be used as proxy measures for environmental factors and their influence.

The second key environmental factor relevant to the present paper is socioeconomic status (SES), which is highly related to HLE (i.e., parents of lower SES tend to provide lower HLEs to their children, exposing them to fewer enriching verbal experiences) and also tends to relate to cognitive and neural development. Neuroimaging studies have explored the relationship between child reading ability and reading-related white matter tracts, the integrity of which represents processing efficiency. One study found that the association between reading skills and tract integrity was modulated by SES; while good readers from high SES households, in keeping with left hemispheric dominance for reading, tended to show increased left hemispheric tract integrity, good readers from low SES households tended to show increased right hemispheric tract integrity (Gullick et al., 2016). Children of varying SES seem to enlist different brain regions for some cognitive tasks. Evidence also suggests that low SES exerts more influence on white matter structures than high SES, indicated by studies revealing higher white matter heritability rates (i.e., lower rates of environmental transfer) for families of high SES (Chiang et al., 2011). One possible conclusion is that low SES has greater potential to be detrimental than high SES has potential to be beneficial. While an

impoverished reading environment may negatively impact child reading ability, reading development may not benefit hugely from an incredibly rich reading environment. In such households, reading ability may be molded to a greater extent by genes.

In short, parental traits and cognitive phenotypes are important predictors of child reading skills, working through genetic and environmental pathways. Factoring in HLE and SES when exploring reading development is crucial to account for any influence the environment may exert distinct from genetics. Without taking this precaution, it would be impossible to measure the direct relationship between child reading ability and parental genes, as the present study attempted to do.

2. The Neural Characteristics of Reading and Developmental Dyslexia

The human brain is not innately specialized for reading, yet fluent readers have reading-specific neural circuits comprised of multiple reading-related brain regions (Price, 2012) and may even have brain regions that are themselves reading-specific (McCandliss, 2003). These observations suggest that reading acquisition, and the underlying neurobiology that supports it, requires experience and practice. Experience, in other words, shapes neurobiology by co-opting the relevant brain regions and forming the specialized neural circuits that later support reading ability. Particularly important co-opted regions correspond to the auditory and visual systems, which incorporate the ventral occipitotemporal cortex, the lingual gyrus, and the dorsal parietotemporal junction (Price, 2012). The integration of these regions enables the bridging of phonographic and orthographic knowledge stores, both of which are integral to reading.

Neuroimaging studies have outlined the structures and functions of the reading network in even greater detail. The left dorsal parietotemporal junction, for instance,

consists of superior temporal, supramarginal, and angular gyri, and has been implicated in the “fast mapping” of phonology onto orthography (Pugh et al., 2001). This refers to the process by which children quickly pick up new information about words (Swingly, 2010). The entire left parietotemporal lobe, in fact, is frequently found to support reading-related abilities (Vigneau et al., 2006). “Slow mapping,” an extended process requiring sizable input and repetition (Bonvillian, 2000), may rely more heavily on the ventral occipitotemporal region. This area consists of the lateral extrastriate, fusiform, and inferior temporal regions, and may become highly specialized for reading after years of practice. It includes what has been dubbed the “Visual Word Form Area,” a brain region hypothesized to specialize in the visual processing of letters and words (Dehaene & Cohen, 2011). The reading network also involves inferior frontal regions (Poldrack, 1999), which have been implicated in both semantic and phonological processing tasks, such as rhyme generation, synonym generation and translation, and verbal fluency. There is debate, however, over whether distinct clusters within the left inferior frontal gyrus are responsible for semantic and phonological processing (Liakakis et al., 2011). White matter tracts connect these regions of gray matter to form highways of information flow, allowing the brain to successfully integrate multiple knowledge stores (e.g., phonology and orthography). Tracts include the left arcuate fasciculus (which connects the superior temporal gyrus, the inferior frontal gyrus, and the inferior parietal lobule), the left superior longitudinal fasciculus (which touches all four lobes), and the left inferior longitudinal fasciculus (which touches the temporal and occipital lobes) (Hoeft et al., 2011; Yeatman et al., 2012). Together, they form a network of interconnected, reading-related brain regions.

Children with reading difficulties, such as those at risk of developing or diagnosed with dyslexia, commonly have neural abnormalities in the reading network that correlate with their reading abilities. These may be functional, structural, or connectional in nature. Although the present study utilizes functional imaging only, prior literature on the associations between dyslexia and all types of neural characteristics can be used to inform present hypotheses. Since neural abnormalities are wide-ranging (e.g., spanning disintegrated white matter connectivity, reduced gray matter volume, and insufficiently robust neural activity, or hypoactivation) they may intertwine and influence one another in unexpected ways. The presence of one might be yoked in some way to the presence of another. Because functional, structural, and connectional abnormalities merit consideration, key findings involving each will be summarized.

Abnormalities in gray matter function are commonly implicated in reading difficulty. Hypoactivations in the reading network, for instance, tend to positively correlate with reading-related cognitive deficits. Pre-readers at family risk for dyslexia exhibit hypoactivation in bilateral occipitotemporal and left parietotemporal brain regions during phonological processing (Raschle et al., 2012a). Atypical activity in the left inferior frontal gyrus has also been linked to reading difficulties. It was found that dyslexic children's locus of activity significantly differed from that of controls in position within the left inferior frontal gyrus during phonological processing (Temple et al., 2003). Furthermore, following an intervention designed to improve auditory and language processing, dyslexic children illustrated increased activity in the position that was formerly functional only in non-dyslexic children. In general, reading difficulty is associated with reduced activity in the areas known to support reading-related cognitive

skills. This includes hypoactivation in left temporal, parietal, and fusiform regions (Norton et al., 2014).

In conjugation with left-hemispheric hypoactivation, overly robust activity, or hyperactivation, is sometimes found in left inferior frontal and right-hemispheric regions in dyslexics (Norton et al., 2014). Furthermore, right-hemispheric hyperactivation is commonly found in regions homologous to the hypoactivated left-hemispheric regions of the reading network (Shaywitz et al., 2002). Demonstrating this, Eden et al. (2004) tested the phonological skills of dyslexic adults before and after they had received a phonological processing-based intervention. Results revealed that, post-intervention, dyslexics showed improved phonological skills that positively correlated with hyperactivation in right perisylvian cortices. This region is not a part of the typical reading network, but was nonetheless recruited for reading-related skills. It was therefore concluded that it likely represented a compensatory mechanism: a region that is co-opted to support a cognitive function when the regions typically associated with that function are deficient (e.g., Wang et al., 2016).

Moving on, dyslexia is also associated with reduced gray matter volume, a structural abnormality, in areas of the reading network. These areas include left occipitotemporal and bilateral parietotemporal regions, the left fusiform gyrus, and the right lingual gyrus, and have been shown to predate reading (Raschle et al., 2011). Understandably, structural abnormalities tend to exist in regions where there are also functional abnormalities. Studies have further implicated left temporal, parietal, fusiform, and frontal regions, though abnormalities have been found in the cerebellum as well (Norton et al., 2014).

Lastly, dyslexia is associated with abnormalities in white matter tracts. Disintegrated tract connections may corrupt communication between brain regions, interrupting the cognitive processes that rely on regional interactions. Complex cognitive abilities (e.g., reading) that rely on multiple sub-abilities (e.g., phonological processing, orthographic knowledge, and visual-spatial attention) may be especially impaired if sub-abilities cannot integrate or build upon one another. For instance, Wang et al. (2016) found that children with family histories of dyslexia, who were therefore more likely to develop dyslexia themselves, had poorer tract coherence in the left arcuate fasciculus, the left superior longitudinal fasciculus, and the left inferior longitudinal fasciculus. Furthermore, researchers found that white matter development positively correlated with reading development, revealing that reading-adept children tended to have increased white matter integrity. Additionally, the left arcuate fasciculus has been shown to be smaller in pre-reading kindergarteners who are at family risk of dyslexia as compared to those who are not (Saygin et al., 2013).

These neuroimaging studies have pinpointed functional, structural, and connective abnormalities that relate to reading disability and to the disruption of reading-supportive sub-skills, such as phonological processing. These studies inform hypotheses, including those of the present study, regarding how brain activity might relate to parental reading history and to other predictors of reading ability.

3. Parental Reading History and Neuroimaging

Research has shed light on the brain regions and circuits that are integral to reading and on the consequences of their dysfunction. Guided by these illuminating findings, it is possible to explore these neural characteristics in relation to parental

reading history. Measuring the cognitive phenotypes of parents, however, is not a common research strategy. Instead, intergenerational research emphasizes categorical study designs in which children with and without family risk, or with and without dyslexia, are compared on behavioral and neural levels. Because this approach involves two relatively crude groups (i.e., family risk is either there or not; there is little nuance) it may not fully appreciate the myriad genetic and environmental factors that impact reading ability and its neural correlates. It also does not fully appreciate the fact that liability and risk fall along a continuum; some children may be more at risk than others, even though they would be placed in the same risk category. It is therefore important to complement categorical research with 1) studies that utilize continuous variables, which are better able to assess individual differences, and 2) studies that target more specific agents of the intergenerational transfer of reading ability. As previously mentioned, these include aspects of SES (e.g., parental income, parental education), aspects of HLE (e.g., the number of household children's books, how often parents read with their children), and parental reading ability. The examination of specific and continuous variables, such as parental reading history, as opposed to general and categorical ones, may help elucidate the mechanisms by which reading-related brain circuits develop. It may also, by unveiling the contributions of specific intergenerational predictors, lead to better predictions about children's liability for reading difficulty. The present study focuses on parent reading history for these reasons.

A small number of studies, though none using a neuroimaging paradigm, have discarded family risk categories to examine parent reading ability as a continuous measure in relation to child reading ability. Such studies tend to report a negative

correlation between risk of dyslexia and parent reading ability such that reading-deficient parents tend to have children with greater risk. This holds true for children regardless of their family history of reading disability (Gilger et al., 1991) and specifically for children with a family history (van Bergen et al., 2011) -- as is to be expected given the high heritability rates of reading disability. Considering the strong relationship between parental and child reading ability, it is surprising that only one study has explored the relationship between parental literacy and child neural characteristics. In this study, Black et al. (2012) found that maternal reading ability was significantly associated with the structural integrity of gray matter regions in children aged 5 to 6. Bilateral prefrontal and parietotemporal regions, both of which have been implicated in phonological processing, tended to have reduced gray matter volumes in children with reading-deficient mothers. No gray matter structures, however, were associated with paternal reading ability.

Two aspects of this study imply the existence of a genetic pathway from mother to child. Firstly, children were aged 5 to 6 and had not begun formal reading instruction in school. Researchers also controlled for SES, which incorporated parental education, occupation, and income, thereby accounting for some of the potential differences in these children's home environments. Secondly, the nature of their findings suggest a prenatal influence; they measured both cortical surface area and cortical thickness, and only the former, which is more strongly associated with prenatal influence, correlated with maternal reading history. Although prenatal development is influenced by environmental factors (e.g., alcohol intake) in addition to genetic ones, the link between maternal reading ability and brain morphometry seems to be established early in life, before children have had much exposure to the many environmental factors that may

subsequently influence their reading development. Taken together, the possibility of prenatal influence and the controlling of SES diminish and account for environmental influence, possibly coming close to implicating a genetic pathway.

The present study aims to contribute to this line of research by assessing the relationship between parental reading ability and functional activity related to phonological processing in pre-readers. As previously noted, family risk of dyslexia is commonly associated with hypoactivation in bilateral temporal, parietotemporal, and inferior temporal-occipital regions, as well as in bilateral inferior and middle frontal gyri (Dębska et al., 2016). Of these regions, the left parietotemporal gyrus (Raschle et al., 2012a), as well as the left inferior frontal gyrus (Liakakis et al., 2011), is commonly linked to phonological processing. Although the present study extracts regions of interest (ROIs) from whole-brain analysis results (i.e., previous literature was not used as a reference), these studies may validate and shed light on the present ROIs. These regions are hypothesized to be less active during phonological processing in children of reading-deficient parents, and generally more active in children of reading-adept parents. This is with the possible exception of the left inferior frontal lobe, which literature shows to be sometimes hyper- and sometimes hypoactivated in children with family risk of dyslexia. The present study also aims to explore the ways in which maternal and paternal reading history might differ in their relation to functional activity. Based on Black et al.'s (2012) finding that morphological abnormalities were associated only with maternal and not paternal reading history, the present hypothesis is that maternal reading history, as compared to paternal reading history, will have a stronger relationship with child neural activity.

Although any attempt at untangling environmental and genetic pathways may be treated with skepticism, the present study makes an effort to measure the genetic aspects of intergenerational transfer. It does so by controlling for SES and HLE, thereby taking environmental influence into account. Furthermore, the present study looks at the neural activity of pre-readers who had not begun formal reading training. As such, the overall threat of environmental confounds should be somewhat reduced since neural activity was not influenced by any endeavors to read. Controlling for the influence of SES and HLE on pre-readers' neural activity may begin to measure the direct influence of genetics on the intergenerational transfer of reading ability.

The present paper is novel in investigating parental reading history's association to brain activity. The use of functional imaging offers a window into the brain activity associated with specific cognitive processes, and is therefore a valuable tool in the search for underlying mechanisms by which dyslexia liability is transferred from one generation to the next. Functional imaging, for example, may indicate whether some phonological processing-supportive brain regions are more susceptible to genetic influence than others, and, if so, which ones. These regions may be disproportionately impacted by genetic factors, while others may be disproportionately impacted by environmental factors. Exploring reading-related brain regions' functional integrity in relation to parental reading history, both maternal and paternal, may help clarify how genes shape the development (or lack thereof) of the brain's reading network. This in turn may bolster the identification and prevention of reading disabilities, such as dyslexia.

In sum, prior literature suggests that parental traits and cognitive phenotypes predict child reading-related abilities through both genetic and environmental pathways.

Despite strong evidence for the genetic transfer of reading ability, more research is needed to delineate the causal pathways and neural mechanisms bridging genes and reading. To this end, a productive avenue of research, and the one this paper seeks to explore, is the relationship between parental reading history and reading-related neural characteristics of pre-readers -- in this case, the functional characteristics. If reading ability is in part conferred genetically, then one would expect activity in pre-readers' reading-related brain regions to relate to parental reading history even after controlling for SES and HLE. The present hypothesis is that this will indeed be the case, with parental reading history predicting activity in left parietotemporal, left frontal, and left occipitotemporal regions (i.e., regions of the reading network) such that parents with more severe histories of reading difficulty will tend to have children with more severe hypoactivations. The children of reading-adept parents should, generally, have fewer functional abnormalities in these regions, while children of reader-deficient parents should have more. Conversely, if reading ability is not conferred genetically, one would expect no relationship between parental reading history and pre-readers' functional characteristics once accounting for environmental factors.

II. Methods

Subjects

Ninety-six children (50 female, 46 male) and sets of parents (with an equal number of mothers and father) participated in the present study. Children were aged 60 to 80 months ($M = 67$ months, or 5.58 years, $SD = 4.21$) with 82 expressing a preference for right-handedness, 12 expressing a preference for left-handedness, and 1 expressing no preference for either. Additional child characteristics are presented in Table 1.

Participants were tested as a part of the Research on the Early Attributes of Dyslexia (READ) project, a collaborative study between the Gaab Lab at Boston Children’s Hospital and the Gabrieli Lab at MIT, and were retroactively selected according to their reader-nonreader status. To be considered for the present study, children had to have been recruited and then tested either the summer before or during their first few months of kindergarten. This was done to target a pre-reading population; since all children in the present study began formal reading training in kindergarten, they had no or very little formal training at this initial time point. Consistent with pre-reading status, their performance on untimed single word reading, measured using the Woodcock Reading Mastery Tests-3rd Edition (WRMT-3), Word ID (Woodcock, 1987), was low: only 1.65 words on average (SD = 3.81). All participants were English-speaking. This study was approved by the ethics committee of Boston Children’s Hospital and verbal assent and informed consent were obtained from each child and guardian, respectively

Table 1 *Child characteristics, n = 96*

	Mean	SD	Range
Age (in months)	67	4.21	60-80
IQ	99.8	99.77	80-131
CTOPP	9.98	9.98	6-15.67
RAN	96.78	14.82	68-122.33
Single word reading	1.65	3.81	0-27

Psychometric Measurements

Children's single word reading was measured with the Woodcock Reading Mastery Test-3rd Edition (WRMT-R), Word ID (Woodcock, 1987). Other cognitive traits that were measured included: IQ, measured with the Kaufman Brief Intelligence Test-2nd Edition (KBIT-2), rapid automatized naming, measured with The Colors and Objects subtests of the Rapid Automatized Naming/Rapid Alternating Stimulus (RAN/RAS) tests (Wolf & Denckla, 2005), and phonological processing, measured with the Comprehensive Test of Phonological Processing (CTOPP, Wagner et al., 1999). Raw scores were calculated before being converted into standard scores. Two children reached the clinical cutoff for phonological processing disability, and 17 reached the clinical cutoff for RAN. Children who did not reach clinical cutoffs demonstrated typical to advanced capabilities. All children scored an 80 or above on the IQ assessment (which in the past has been used as an inclusion cutoff; e.g., Ozernov-Palchik et al., 2016).

Home Environment

Parental reading history was measured with the Parental Reading History Questionnaire (ARHQ, Parrila et al., 2003). It is a self-report measure designed to assess adults' reading ability, past and present, with questions like "How much difficulty did you have learning to read in elementary school?" and "How would you compare your current spelling to others of the same age and education?" Respondents indicate their answers on Likert scales from 0 to 4. Lower answers/scores are indicative of better reading ability/history, and higher answers/scores are indicative of worse reading ability/history. A copy of the questionnaire is attached in the appendix.

Two additional conceptual variables were designed to represent children's home environment: SES and HLE. The Barratt simplified measure of social status was used to quantify SES (Barratt, 2006). It generated a composite score based on educational attainment and occupational prestige, which were determined with the questions depicted in Table 2. Composite scores were generated according to parents' answers (e.g., for educational attainment: doctorate = 21, bachelor's = 18, high school/General Education Development = 12; for occupational prestige: teacher = 40, office manager = 25, service/bartender = 10) such that higher scores reflected greater SES.

Turning now to the second measure of home environment, HLE, this variable was represented by two distinct literacy-related features of the household: the number of household children's books and how often family members read with or to their children. These features were included as separate variables (i.e., no composite HLE score was generated) and were determined with the questions depicted in Table 3. Parents responded to each question on a Likert scale from 1 (indicating an impoverished HLE) to 10 (indicating an enriched HLE). Higher HLE scores therefore reflected enriched literacy environments.

Table 2 *A composite socioeconomic status score comprised of the following variables*

SES questions

1. Please indicate your highest level of education
 2. Which best describes your current main daily activities/ responsibilities (e.g. working part-time, working full-time, keeping house, looking for work, raising children full-time, unemployed or laid-off)
 3. For your current or most recent job, a) What kind of business or industry did/do you work? b) What kind of work do/did you do?
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Table 3 *Home literacy features used as individual variables*

HLE questions

1. Total number of children's books in the home
 2. How often do family members read books, magazines, or newspapers with the child? (family members and/or tutors)
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FMRI Experiment – First Sound Matching (FSM)

Task and design: The first sound matching (FSM) task was employed to assess the phonological processing capabilities of participating children, utilizing a behavioral interleaved gradient block design (e.g., Raschle et al., 2012b, 2014). The task began with separate presentations of two object words (e.g., lion, envelope), lasting two seconds per word. Words were spoken in either a male or female voice while images of the object words appeared on the screen. The experimental task (FSM) required children to decide via a button-press whether or not the two presented object words began with the same sound. Conversely, the control task (voice matching; VM) required children to decide whether or not the two presented object words were spoken by voices of the same sex. Each decision a child was called to make constituted a trial. The trials' structural design was devised to synchronize with the scanning of the children, thereby reducing scanner background noise during auditory stimulus presentation (Gaab, 2007a, 2007b, 2008; Hall et al., 1999). Blocks were comprised of 4 trials of one condition type (i.e., FSM and VM trials were never mixed within a single block). Experimental and control blocks were alternated with resting blocks of identical length (i.e., 6 seconds), during which children were presented with a fixation cross.

In-scanner behavioral performance analysis: Button responses and reaction times (RTs) were recorded as children completed the FSM task. Also as children completed the task, they were behaviorally managed and monitored by an in-room research assistant whose job it was to minimize movement (typically by notifying the children whenever they squirmed excessively) and to ensure that they were not too uncomfortable inside the scanner. Detailed scanning protocol has been detailed in prior literature (e.g. Raschle et al., 2009, 2012a). Since participating children were relatively young (60-80 months), they were allowed to correct their responses within the 2-second period allotted for button pushing. No responses after this period were recorded as valid corrections.

Imaging Acquisition: A SIEMENS 3T Trio MR scanner was used to collect the MRI scans, and a 32-slice echo planar imaging-interleaved sequence was used to acquire blood oxygen level-dependent (BOLD) signal (TR = 6,000 ms; TA = 1,995 ms; TE = 30 ms; flip angle = 90°; field-of-view = 256 mm; in-plane resolution = 3.125×3.125mm, slice thickness = 4 mm, slice gap = 0.8 mm). As previously noted, a behavioral interleaved gradient imaging design was utilized to ensure that the auditory stimuli would not coincide with scanner background-noise, minimizing noise interference. Structural images were collected with T1-weighted MPRAGE MRI sequences (TR = 2000 ms; TE = 3.39 ms; flip angle = 9°; field of view = 256 mm; voxel size = 1.3×1.0×1.3 mm; slice number = 128).

fMRI preprocessing and first-level analysis: SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/>) software was used to analyze imaging data with an age-appropriate preprocessing protocol. The structural images of each participant were first normalized; their sizes were adjusted to conform to uniform dimensions specified by

an SPM template (i.e., images were converted from individual, “naive” space to universal, “standard” space). During this step, images were first segmented into white matter (WM), gray matter (GM), and cerebrospinal fluid (CSF) with the VBM8 toolbox adopting an adaptive Maximum A Posterior (MAP) approach (Rajapakse et al., 1997). To this end, an age- and gender-matched tissue probability map from the Template-O-Matic Toolbox was utilized to distinguish white and gray matter in this age range (Wilke et al., 2008). Newly segmented images were then affine transferred to Montreal Neurological Institute (MNI) space, via an age- (67.9 ± 4.2 months) and gender- (Female/Male = 1.04/1) appropriate intermediate space, created through six iterations of high dimensional warping processes using nonlinear registration, a diffeomorphic anatomical registration approach and exponentiated lie algebra (DARTEL, Ashburner, 2007). Transformational matrices that bring structural images from individual space to standard space were saved.

Following the structural images’ conversion from naive to standard space, it was possible to begin the preprocessing of functional images. Since T1 equilibration effects had to be accounted for, the initial images were removed from each run. The remaining images were then realigned, coregistered, normalized, and smoothed. Images were realigned to the first image of the series, and subsequently coregistered to their corresponding structural images (i.e., those collected simultaneously). Next, images were normalized into MNI space by applying the deformational fields that had been generated during the DARTEL wrapping process. Images were then smoothed using a Gaussian kernel with full-width at half maximum (FWHM) of 8 mm.

Functional imaging data subsequently underwent a rigorous procedure of artifact detection. Artifact Detection Tools (ART, http://www.nitrc.org/projects/artifact_detect)

automatically detected excessive head movement with respect to translation threshold (set to 3 mm) and rotation threshold (set to 0.05 mm) specifications. Following automatic artifact detection, images were visually screened in order to identify the artifacts that may have slipped through the cracks of ART's detection algorithm. Missing voxels, stripes, ghosting, or intensity differences all constituted identifiable artifacts. Functional images with excessively noisy or artificial data were labeled outliers. Participants' fixed-effects were then estimated using a general linear model (GLM). Four experimental regressors (FSM, FSMrest, VM, and VMrest) were modeled in a block-design and entered into the GLM. Run effect and an intercept term were included as nuisance covariates. Additional covariates included motion regressors, which had been generated by ART and were included to eliminate outlier images and to minimize the overall effect of motion. The default value of the high-pass filter (128 seconds) was included to remove physiological noise (e.g., noise from cardiac and respiratory cycles) that would have introduced a confounding variable to the BOLD signal. Finally, a contrast map for the experimental > control conditions (i.e., FSM-VM) was built and computed for every subject.

Group-level analyses: The goal of group-level analyses was to evaluate the relationship between parental reading history and the neural responses associated with phonological processing. To accomplish this, maternal and paternal ARHQ scores were entered into a multiple regression analysis as covariates, and subject-wise contrast maps (FSM vs. VM) were entered as output variables. Contrasts of interest included: 1) maternal ARHQ, 2) paternal ARHQ, and 3) maternal ARHQ vs. paternal ARHQ. Whole brain results were reported at an uncorrected threshold of $p < .01$ and with an extent threshold of $k > 50$. Studies reporting fMRI results in young children have used

comparable uncorrected thresholds (e.g., Brem et al., 2010; Raschle et al., 2012a), which may better detect blood oxygen level dependent effects when scanning children as opposed to adults (Gaillard et al., 2001). Using an uncorrected threshold, however, may also increase the risk of Type I error, revealing associations that are statistically significant but that are in fact due to chance. For this reason, the present study may be best thought of as an exploratory analysis.

ROI analyses: To further partial out the possible confounding influence of children's environments and pre-reading skills, region of interest (ROI) analyses were conducted. Specifically, for each brain region with activity differences more related to maternal than paternal ARHQ, beta values associated with FSM-VM were extracted and averaged across all of its voxels using Marsbar, an SPM application. Linear regression analyses were then run to assess the predictive contributions of parental reading history to neural activity while regressing out potentially predictive variables. These were age, sex, handedness, IQ, CTOPP, HLE, and SES, all of which were included as covariates alongside maternal and paternal ARHQ.

Author's Contributions

The author contributed to the present study by conducting background literature reviews, determining which variables to include in analyses, selecting participants retroactively, running analyses, and writing the manuscript. The author did not, however, contribute to many aspects of the READ study. The study's paradigm had been designed (e.g., the questionnaires that were given to children and their parents had been selected; in-scanner tasks had been devised and created), participants had been recruited and run

through their lab visits, and imaging data had been processed all prior to the author's involvement.

III. Results

Profile Descriptions of Participants

All descriptive statistics are depicted in Table 4. Histograms of the scale variables are depicted in Figures 1 through 10. Mother ARHQ ($M = 25.52$, $SD = 13.29$) was significantly lower than father ARHQ ($M = 31.30$, $SD = 13.86$), indicating that, in general, mothers had less history of reading difficulty ($t(95) = 2.758$, $p = .007$). Children had a mean CTOPP score of 9.98 (1.95), a mean RAN score of 96.78 (14.82), and a mean IQ of 99.77 (10.43). Participants generally came from well-off families; the mean SES was 50.30 (10.48), the mean number-of-children's-books score was 4.80 (1.61), and the mean parents-reading-with-children score was 3.45 (0.86). As reported in the methods section, two children in the present sample scored below the cutoff for phonological processing, and 17 for RAN.

Table 4 *Descriptive statistics*

	N	Minimum	Maximum	Mean	Std. Deviation
Age	96	60.00	80.00	67.3229	4.21400
Sex	96	.00	1.00	.4792	.50219
Handedness	95	-2.00	2.00	1.4421	1.29414
Maternal ARHQ	96	4.00	72.00	25.5156	13.29176
Paternal ARHQ	96	8.00	76.00	31.2969	13.86126
SES	96	20.00	66.00	50.3021	10.47515
HLE (children's books)	87	2.00	10.00	4.8046	1.61273
HLE (parents reading with child)	87	1.00	4.00	3.4483	.85940
IQ	96	80.00	131.00	99.7708	10.43020
Accuracy on FSM task	95	.29	.96	.6659	.18244
CTOPP	96	6.00	15.67	9.9760	1.95292
RAN	96	68.00	122.33	96.7845	14.81976

Figure 1 *Histogram of Maternal ARHQ*

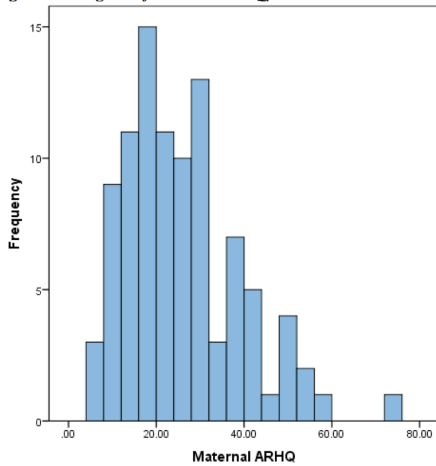


Figure 2 *Histogram of Paternal ARHQ*

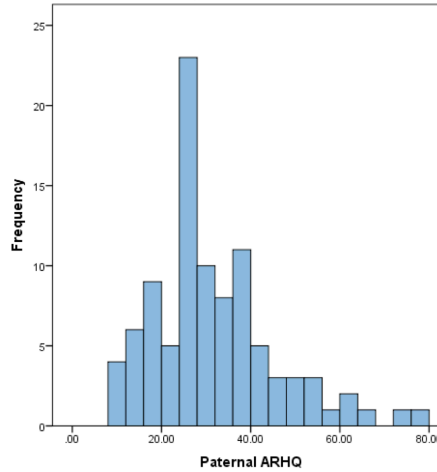


Figure 3 Histogram of Age

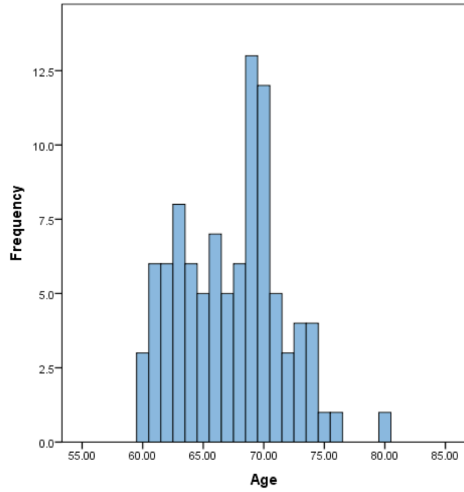


Figure 4 Histogram of IQ

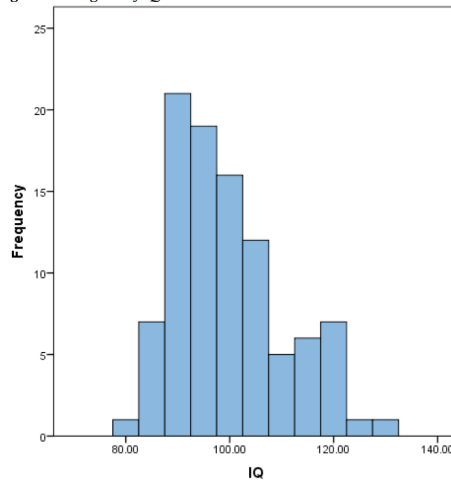


Figure 5 Histogram of FSM accuracy

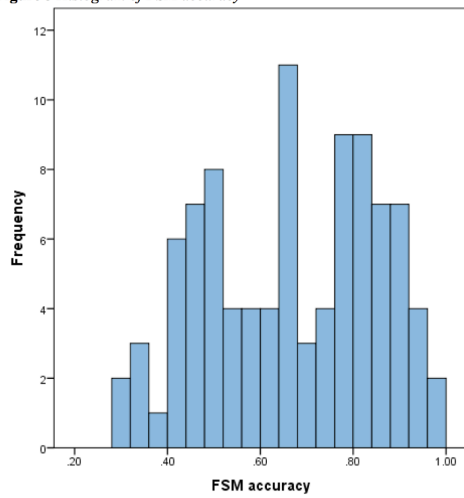


Figure 6 Histogram of CTOPP

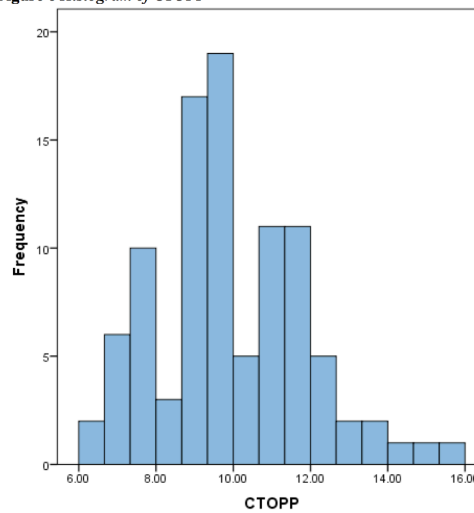


Figure 7 Histogram of SES

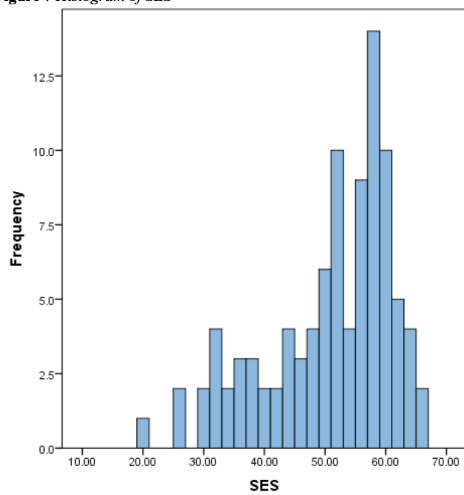


Figure 8 Histogram of HLE (books)

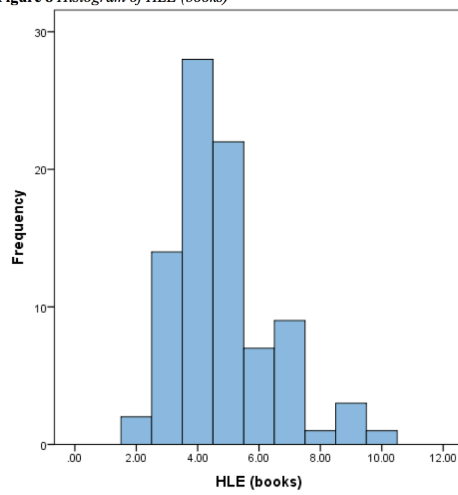


Figure 9 Histogram of HLE (parents reading with child)

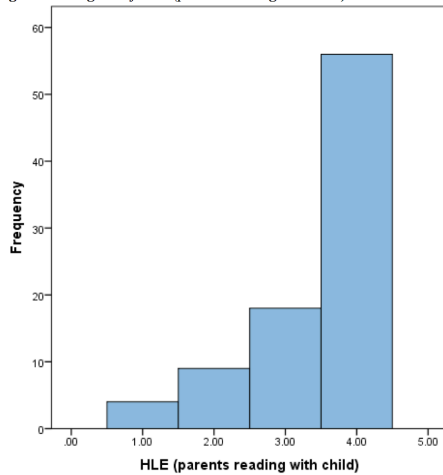
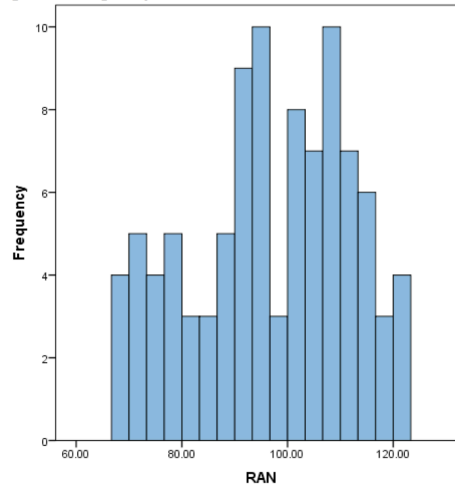


Figure 10 Histogram of RAN



Correlations Between Variables

All of the correlations between variables are presented in Table 5. It is also important to note that the behavioral analyses were not corrected for. This may have increased the risk of Type I error, as previously described in the Methods section.

Parental phenotypes and child environment: Maternal ARHQ was positively correlated with the number of household children's books ($r = .247$, $p = .021$), seeming to show that mothers with more severe histories of reading difficulty (i.e., higher ARHQ scores) tended to own more children's books. This, however, was likely an outlier effect. The correlation disappeared when one mother with particularly severe reading difficulty and a large number of children's books was removed from analyses ($r = .130$, $p = .233$). Paternal ARHQ was negatively correlated with SES ($r = -.325$, $p = .001$), indicating that fathers with more severe histories of reading difficulty tended to have families with lower SES.

Parental phenotypes and child behavioral measures: Paternal ARHQ was negatively correlated with accuracy on the FSM task ($r = -.239$, $p = .020$), indicating that

fathers with more severe histories of reading difficulty tended to have children who were less accurate on the FSM task.

Child environment and child psychometrics, behavioral measures, and demographics: SES was positively correlated with accuracy on the FSM task ($r = .309$, $p = .002$), CTOPP ($r = .376$, $p = .000$), and IQ ($r = .205$, $p = .045$). Children born into high SES households tended to make fewer errors on the FSM task, do better on the phonological processing assessment, and have higher IQs. SES was also positively correlated with the parents-reading-with-their-children score ($r = .220$, $p = .041$) such that children from high SES households were generally read to more often. CTOPP scores were positively correlated with the number-of-household-children's-books score ($r = .314$, $p = .003$). This illustrated that good phonological processors tended to live in households with increased quantities of children's books.

Child demographics and child psychometrics, behavioral measures: Independent samples T-tests revealed that boys and girls had significantly different IQ (girls $M = 102.34$, $SD = 10.16$; boys $M = 96.98$, $SD = 10.10$; $t(94) = 2.59$, $p = .011$), accuracy on the FSM task (girls $M = .72$, $SD = .17$; boys $M = .61$, $SD = .18$; $t(93) = 3.08$, $p = .003$), and CTOPP (girls $M = 10.41$, $SD = 2.02$; boys $M = 9.51$, $SD = 1.78$; $t(94) = 2.31$, $p = .023$). Differences in all cases favored girls; girls tended to have higher IQs, do better on the FSM task, and demonstrate greater phonological processing capabilities. Independent samples T-tests also revealed that right-handed children tended to come from households with greater numbers of children's books (right-handed children $M = 4.97$, $SD = 1.61$; left-handed children $M = 3.56$, $SD = 1.01$; $t(84) = 2.58$, $p = .012$). No other differences between right- and left-handed children were found.

Child psychometrics and child behavioral measures: Accuracy on the FSM task was positively correlated with CTOPP ($r = .321, p = .002$) such that children who made few errors on the FSM task were generally better phonological processors overall. As previously noted, accuracy on the FSM task was also significantly associated with SES, parental ARHQ, and sex.

Table 5 All correlations between variables

		1	2	3	4	5	6	7	8	9
1. Maternal ARHQ	<i>r</i>	--								
2. Paternal ARHQ	<i>r</i>	-.14	--							
3. Age	<i>r</i>	.13	-.09	--						
4. IQ	<i>r</i>	-.09	-.17	-.18	--					
5. FSM accuracy	<i>r</i>	.11	-.24*	.05	.19	--				
6. CTOPP	<i>r</i>	-.11	-.05	-.19	.19	.32**	--			
7. SES	<i>r</i>	-.03	-.33**	-.15	.21*	.31**	.38**	--		
8. HLE (books)	<i>r</i>	.25*	.01	.06	.08	.02	.31**	.20	--	
9. HLE (parents reading with child)	<i>r</i>	-.03	.04	.01	.08	.01	.18	.22*	.16	--

* Correlation is significant at the 0.05 level (2-tailed)

** Correlation is significant at the 0.01 level (2-tailed)

Partial Correlations Between the Significant Associations

Of the nine correlations that reached significance, only three retained significance after controlling for all of the other variables. Partial correlations revealed that FSM accuracy and CTOPP ($r = .289, p = .011$), paternal ARHQ and SES ($r = -.331, p = .004$), and the number-of-household-children's-books score and CTOPP ($r = .292, p = .010$) were significantly correlated. No other partial correlations reached significance (FSM accuracy and paternal ARHQ, $r = -.128, p = .269$; FSM accuracy and SES, $r = .200, p = .083$; IQ and SES, $r = -.022, p = .851$; and CTOPP and SES, $r = .182, p = .116$), although the correlation between maternal ARHQ and the number-of-household-children's-books score approached significance ($r = .225, p = .051$). Scatter plot diagrams of the significant and approaching-significant partial correlations are depicted in Figures 11 through 14.

Figure 11 Scatter plot diagram of the correlation between FSM accuracy and CTOPP

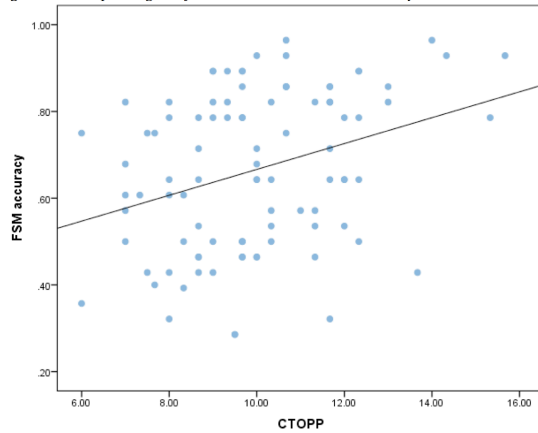


Figure 12 Scatter plot diagram of the correlation between SES and paternal ARHQ

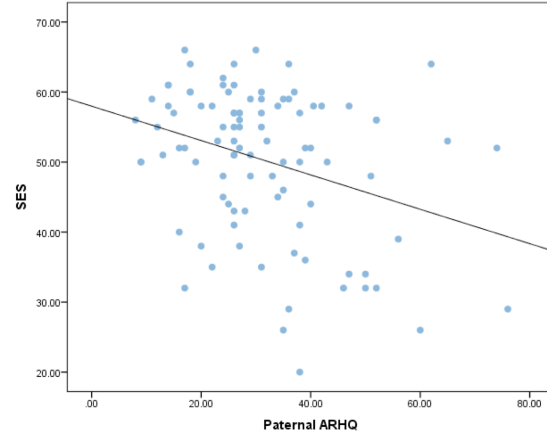


Figure 13 Scatter plot diagram of the correlation between CTOPP and HLE (books)

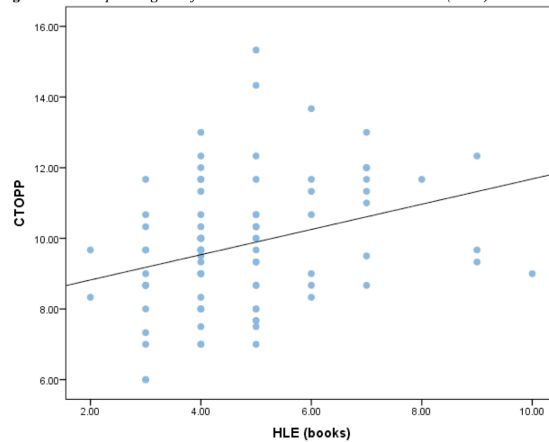
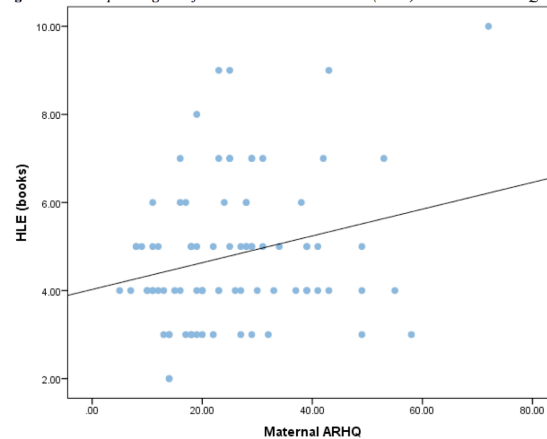
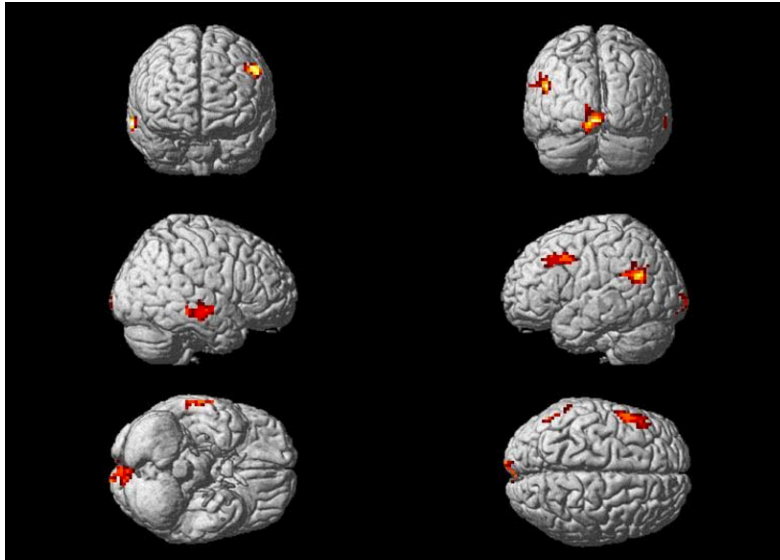


Figure 14 Scatter plot diagram of the correlation between HLE (books) and maternal ARHQ



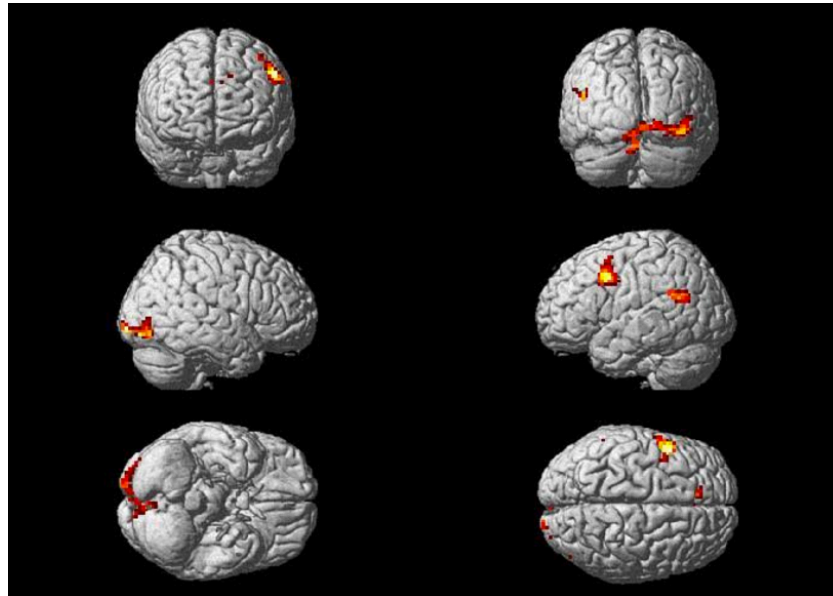
Whole Brain Analyses

Maternal and paternal ARHQ scores were set as covariates while participant scans (FSM-VM) were set as output variables in the present whole brain analyses. As previously noted in the methods section, three contrasts were built and tested: Mother ARHQ, Father ARHQ, and Mother vs. Father ARHQ. At $p < .01$ and $k = 50$, the Mother vs. Father ARHQ contrast revealed significant activation in four distinct clusters, as is depicted in Figure 15. These were located in the lingual gyrus, the left parietotemporal cortex, the right middle temporal gyrus, and the left prefrontal cortex. Voxel quantities, peak coordinates, and peak intensities for each cluster are detailed in Table 6.

Figure 15 *Mother vs. Father ARHQ contrast ($p < .01$ [uncorrected], $k = 50$)***Table 6** *Clusters from Mother ARHQ vs. Father ARHQ contrast*

<i>Region</i>	<i>Number of voxels</i>	<i>Peak MNI coordinate</i>	<i>Peak intensity</i>
Lingual gyrus	102	-3 -87 -12	-3.26
Right middle temporal gyrus	62	66 -21 -12	-3.57
Left middle temporal gyrus	92	-48 -63 24	-3.90
Left middle prefrontal gyrus	69	-54 12 42	-3.38

The Mother ARHQ contrast revealed significant activation in five distinct clusters, as is depicted in Figure 16. These were located in the right occipital gyrus, the left middle temporal cortex, and the left prefrontal cortex. Voxel quantities, peak coordinates, and peak intensities for each cluster are detailed in Table 7.

Figure 16 *Mother ARHQ contrast ($p < .01$ [uncorrected], $k = 50$)***Table 7** *Clusters from Mother ARHQ contrast*

<i>Region</i>	<i>Number of voxels</i>	<i>Peak MNI coordinate</i>	<i>Peak intensity</i>
Right inferior occipital gyrus	174	36 -81 -15	3.48
Inter-hemispheric regions (undefined)	56	0 -3 18	3.64
Left middle temporal gyrus	63	-48 -63 21	3.18
Left medial prefrontal gyrus	83	-9 36 36	3.15
Left middle prefrontal gyrus	93	-51 9 42	4.19

The Father ARHQ contrast revealed no clusters of significant activity.

ROI Analyses

Linear regressions were run to assess the extent to which parental ARHQ continued to predict neural activation while controlling for age, sex, IQ, phonological processing abilities (i.e., CTOPP), SES, and HLE (i.e., number-of-household-children's-books and parents-reading-with-their-children scores). Maternal and paternal ARHQ

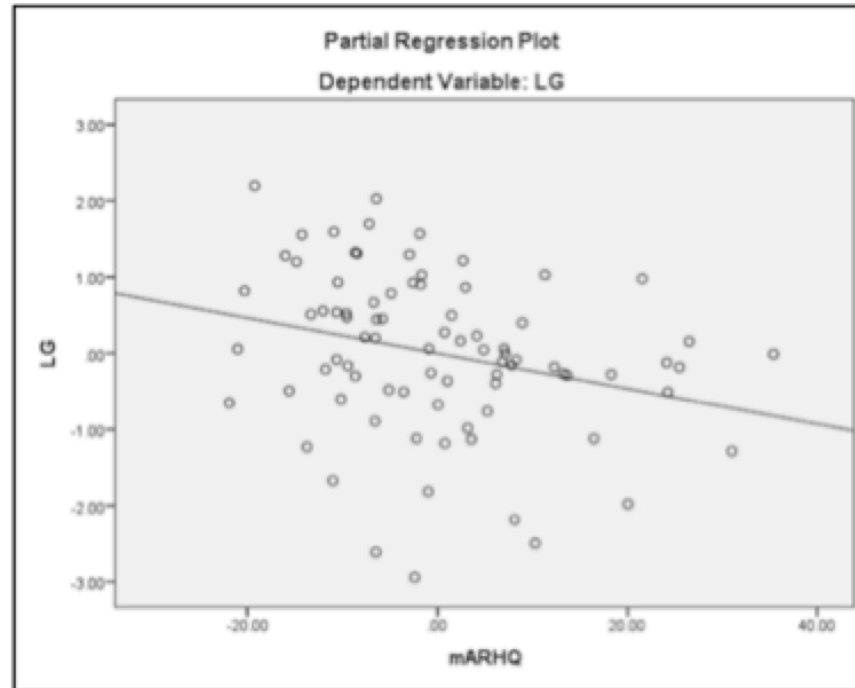
scores were included in all regressions to control for the confounding effects they may have had on each other. Results for each region are described below.

Lingual gyrus (LG): Maternal ARHQ significantly predicted activation in the LG ($\beta = -0.27$, $t(72) = -2.40$, $p = 0.02$) though paternal ARHQ did not ($\beta = 0.14$, $t(72) = 1.18$, $p = 0.24$). Since the relationship between maternal ARHQ and LG activity was negative, results revealed that the mothers with more severe histories of reading difficulty tended to have children with hypoactivated lingual gyri during phonological processing. No other covariates significantly predicted activation in the LG. All of the relationships between lingual gyral activity and the covariates are depicted in Table 8, and a scatter plot diagram of maternal ARHQ and lingual gyral activity is depicted in Figure 17.

Table 8 *Associations between lingual gyral activity and covariates in a linear regression*

Model		Unstandardized Coefficients		Standardized	t	Sig.
		B	Std. Error	Coefficients		
1	(Constant)	4.13	3.0		1.38	.17
	Maternal ARHQ	-.02	.01	-.27	-2.42	.018*
	Paternal ARHQ	.01	.01	.14	1.18	.24
	Age	-.06	.03	-.22	-1.87	.065
	Sex	-.23	.26	-.10	-.90	.37
	Handedness	-.13	.11	-.13	-1.21	.23
	IQ	.004	.01	.03	.30	.76
	CTOPP	-.01	.08	-.01	-.08	.94
	SES	-.01	.01	-.13	-1.06	.29
	HLE (books)	.03	.09	.04	.37	.71
	HLE (parents reading with children)	.20	.15	.16	1.40	.17

* *Significance value below 0.05*

Figure 17 Relationship between Maternal ARHQ and activity in the LG

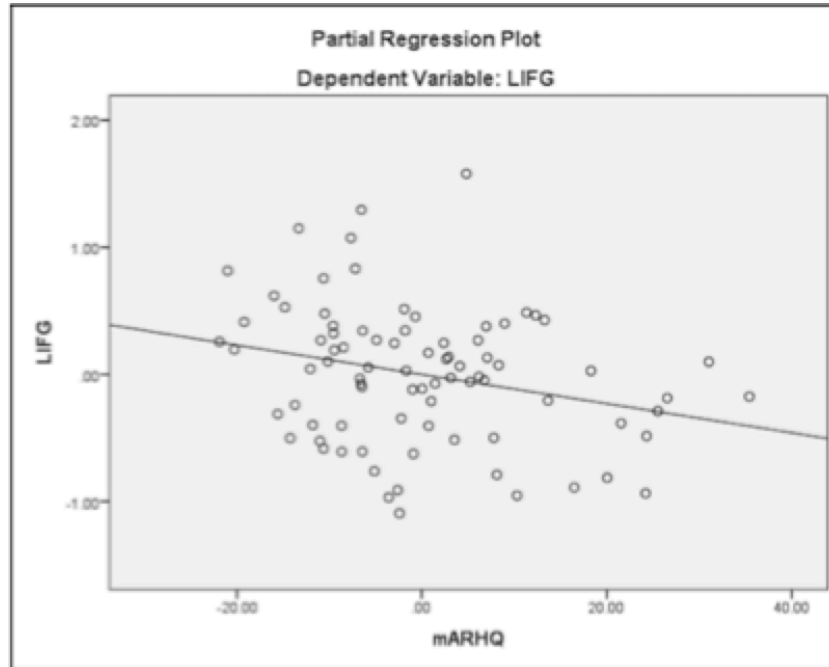
Left frontal gyrus (LFG): Maternal ARHQ significantly predicted activation in the LFG ($\beta = -0.26$, $t(72) = -2.34$, $p = 0.02$) though paternal ARHQ did not ($\beta = 0.06$, $t(72) = 0.50$, $p = 0.62$). Since the relationship between maternal ARHQ and LFG activity was negative, results indicated that mothers with more severe histories of reading difficulty tended to have children with hypoactivated left frontal gyri during phonological processing. The number-of-household-children's-books score also significantly predicted activation in the LFG ($\beta = 0.31$, $t(72) = 2.56$, $p = 0.013$). This association, which had a positive valence, indicated that households with more children's books typically housed children with more left frontal gyral activity during phonological processing. Lastly, SES significantly predicted activation in the LFG ($\beta = -0.254$, $t(72) = -2.03$, $p = 0.046$). The relationship between SES and LFG activity was negative such that children from lower SES households actually tended to show more activation in the LFG during phonological processing. Besides these three variables (i.e., maternal ARHQ, number-of-household-

children's-books score, and SES), no other covariates significantly predicted activation in the LFG. All of the relationships between left frontal gyral activity and the covariates are depicted in Table 9, and a scatter plot diagram of maternal ARHQ and LFG activity is depicted in Figure 18.

Table 9 *Associations between left frontal gyral activity and covariates in a linear regression*

Model		Unstandardized Coefficients		Standardized	t	Sig.
		B	Std. Error	Beta		
1	(Constant)	1.3	1.5		.87	.39
	Maternal ARHQ	-.01	.01	-.26	-2.3	.022*
	Paternal ARHQ	.002	.01	.06	.50	.62
	Age	-.02	.02	-.14	-1.15	.25
	Sex	-.10	.13	-.09	-.75	.46
	Handedness	.02	.06	.04	.39	.70
	IQ	.002	.01	.04	.32	.75
	CTOPP	-.01	.04	-.02	-.16	.88
	SES	-.01	.01	-.25	-2.03	.046*
	HLE (books)	.11	.04	.31	2.56	.013*
	HLE (parents reading with children)	.05	.08	.08	.71	.48

* Significance value below 0.05

Figure 18 *Relationship between Maternal ARHQ and activity in the LFG*

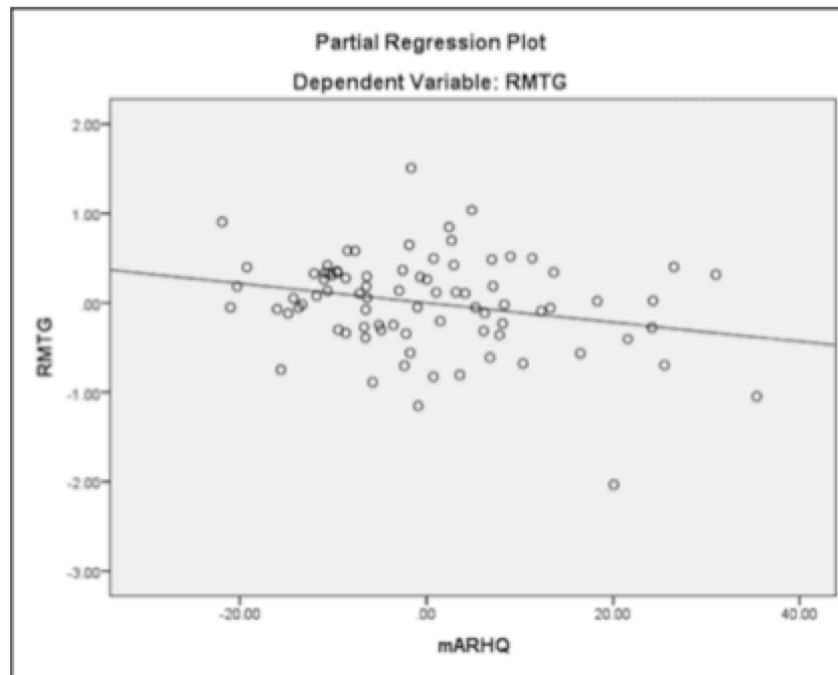
Right middle temporal gyrus (RMTG): Maternal ARHQ significantly predicted activation in the RMTG ($\beta = -0.25$, $t(72) = -2.22$, $p = 0.029$) though paternal ARHQ did not ($\beta = 0.18$, $t(72) = 1.54$, $p = 0.13$). Since maternal ARHQ and RMTG activity were related with a negative valence, results revealed that mothers with more severe histories of reading difficulty tended to have children with hypoactivated right middle temporal gyri during phonological processing. No other covariates significantly predicted activation in the RMTG. All of the relationships between right middle frontal gyral activity and the covariates are presented in Table 10, and a scatter plot diagram of maternal ARHQ and RMTG activity is depicted in Figure 19.

Table 10 Associations between right middle frontal gyral activity and covariates in a linear regression

Model		Unstandardized Coefficients		Standardized	t	Sig.
		B	Std. Error	Coefficients		
1	(Constant)	.86	1.52		.56	.57
	Maternal ARHQ	-.01	.01	-.25	-2.22	.029*
	Paternal ARHQ	.01	.01	.18	1.54	.13
	Age	-.02	.02	-.14	-1.18	.24
	Sex	-.004	.13	-.003	-.027	.98
	Handedness	.06	.05	.13	1.13	.26
	IQ	.003	.01	.05	.46	.65
	CTOPP	-.02	.04	-.06	-.47	.64
	SES	.001	.01	.01	.11	.92
	HLE (books)	.02	.04	.07	.56	.58
	HLE (parents reading with children)	.03	.07	.04	.38	.70

* Significance value below 0.05

Figure 19 Relationship between Maternal ARHQ and activity in the RMTG



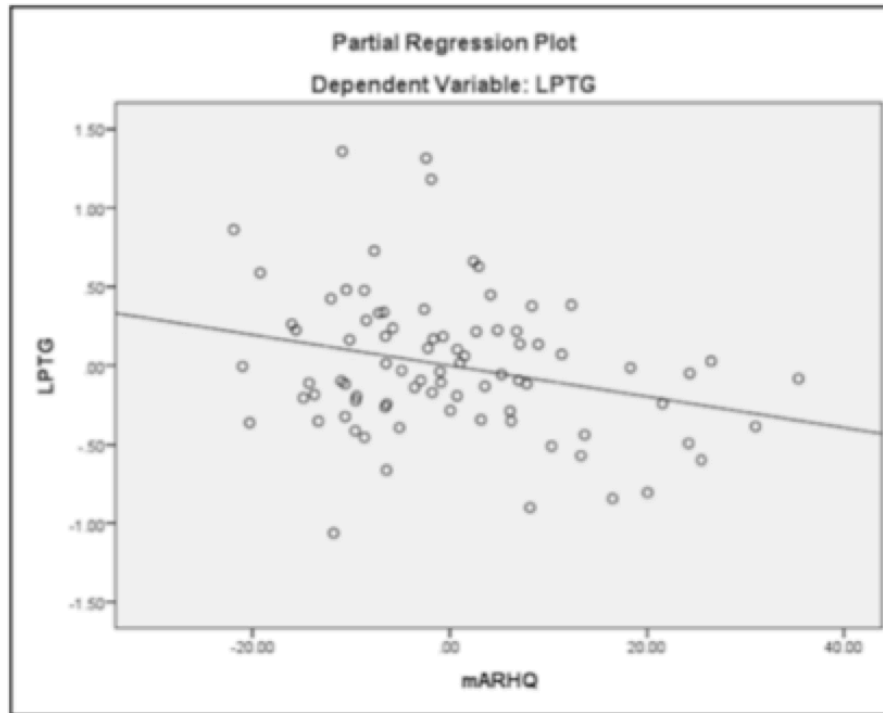
Left parietotemporal gyrus (LPTG): Maternal ARHQ significantly predicted activation in the LPTG ($\beta = -0.27$, $t(72) = -2.37$, $p = 0.020$) though paternal ARHQ did not ($\beta = 0.21$, $t(72) = 1.739$, $p = 0.086$). Since the relationship between maternal ARHQ and LPTG activity was negative, results revealed that mothers with more severe histories of reading difficulty tended to have children with hypoactivated left parietotemporal gyri during phonological processing. No other covariates significantly predicted activation in the LPTG. All of the relationships between left parietotemporal gyral activity and the covariates are presented in Table 11, and a scatter plot diagram of maternal ARHQ and LPTG activity is depicted in Figure 20.

Table 11 *Associations between left parietotemporal gyral activity and covariates in a linear regression*

Model		Unstandardized Coefficients		Standardized	t	Sig.
		B	Std. Error	Coefficients		
1	(Constant)	-1.34	1.29		-1.04	.30
	Maternal ARHQ	-.01	.004	-.27	-2.37	.02*
	Paternal ARHQ	.01	.004	.21	1.74	.09
	Age	.02	.01	.13	1.05	.30
	Sex	-.02	.11	-.02	-.17	.86
	Handedness	-.03	.05	-.07	-.65	.52
	IQ	.01	.01	.14	1.19	.24
	CTOPP	-.03	.03	-.12	-.94	.35
	SES	-.001	.01	-.03	-.26	.80
	HLE (books)	-.008	.04	-.03	-.23	.82
	HLE (parents reading with children)	.07	.06	.13	1.10	.27

* *Significance value below 0.05*

Figure 20 *Relationship between Maternal ARHQ and activity in the LPTG*



IV. Discussion

The present study investigated the relationship between parental reading ability and phonological processing-related neural activity in pre-readers, isolating it by taking other potentially influential variables, such as SES and HLE, into account. The goal was to elucidate the impact that genes have on brain activity supportive of cognitive abilities integral to reading development. Results revealed that maternal, but not paternal, reading history significantly predicted neural activity during phonological processing in four brain regions: the lingual gyrus (LG), the left frontal gyrus (LFG), the left parietotemporal gyrus (LPTG), and the right middle temporal gyrus (RMTG). Furthermore, the associations between maternal reading history and neural activity were in all cases positive; higher levels of activation in these regions were significantly more

likely to be found in children of reading-adept mothers, holding true even after controlling for SES and HLE.

1. Correlation Results

Before interpreting the neuroimaging results in terms of intergenerational transfer, it is key to assess the correlations that were found among the included variables. For instance, correlation analyses revealed two significant relationships between parental reading history and home environment. These relationships, however, were somewhat contradictory; while maternal ARHQ positively correlated with the number of household children's books, paternal ARHQ negatively correlated with SES. The correlation between maternal ARHQ and household children's books is particularly counterintuitive (i.e., mothers with histories of poor reading owning more children's books), and, as previously noted, is likely due to a confounding outlier. Past studies have generally found positive, not negative, correlations between maternal verbal ability, maternal recognition of books titles, and HLE (Korat et al., 2007). The positive association between paternal ARHQ and SES is more precedented, and may be accounted for by the male breadwinner model (Crompton et al., 2007). In this somewhat outdated model the father is the main financial provider for his family and therefore contributes more to his family's SES. The present correlation implies that the extent to which fathers boost SES (e.g., according to job prestige or income) is related to their reading ability; in other words, fathers who find reading difficult have likely experienced less academic success and have had fewer career options, thereby lowering the SES of their families.

One correlation from the present study supports the theory that home environment impacts cognitive abilities. This is that CTOPP scores positively correlated with the

number of household children's books. There are, however, alternative explanations for this relationship. The number of household children's books may actually have been a proxy measure for the influence of parental genes, as measured via parental reading ability or via other parental cognitive phenotypes. The fact that paternal and maternal ARHQ were both associated with aspects of the environment supports this theory. Paternal ARHQ correlated with SES, and maternal ARHQ with a measure of HLE, though this relationship did not link successful reading with high HLE, as was expected. This may constitute a passive gene-environment correlation in which home environment is associated with parental reading ability, and, therefore, with parental reading-related genes, thereby rendering the associations between child environment and CTOPP potentially illustrative of a masked genetic effect, as has been shown in previous literature (van Bergen et al., 2016).

Results also indicated that, as expected, FSM accuracy positively correlated with CTOPP. Seeing as the FSM task required phonological processing, children who were better phonological processors should have been more accurate, as was the case. Finally, the fact that FSM accuracy, a behavioral measure, positively correlated with CTOPP indicates that phonological processing may impact reading development in a way that is observable and measurable from a young age, without the use of neuroimaging techniques. CTOPP seems to be a good predictor of reading-related behavioral development.

2. Neuroimaging Results

A) The Importance of Utilizing Functional Imaging Techniques

The result that maternal reading history is associated with the neural characteristics of pre-readers during a reading-related task falls in line with previous studies connecting parental cognitive abilities to child neural development, but is unique in its exploration of specifically functional neural characteristics. It is some of the first evidence to suggest that maternal reading history predicts neural hypoactivation during phonological processing. Phonological processing abilities and general intelligence, which were controlled for in analyses with CTOPP and IQ scores, respectively, cannot explain this relationship. Rather, hypoactivations likely reflect atypical neural mechanisms for reading that do not yet manifest on the behavioral level, but that are nonetheless characterized by disrupted neural circuits (i.e., those that support reading development) or disrupted patterns of communication between reading-supportive regions, and are often symptomatic of brain dysfunction (Habib, 2000; Reid, 2014). Functional under-activity is also often positively associated with atypical brain morphology, linking abnormal brain structure (e.g., reduced gray matter volumes) to dysfunctional brain activity (Hoeft et al., 2006). This offers another possible explanation for the present results, though gray matter volumes were not included in these analyses. Functional imaging, particularly when paired with other imaging techniques, gives good insight into the neural mechanisms underlying cognitive development and deficiency. This is what the present study attempted to utilize.

In the present study, functional disruption did not manifest on the behavioral level, as maternal reading history was unrelated to FSM accuracy. Prior literature, however, has demonstrated that the amount of activity in the reading network is associated with fluency; for instance, following a yearlong phonologically mediated

reading intervention, children showed increased reading fluency, measured by reading rate and accuracy, as well as increased activity in left inferior frontal and left middle temporal gyri (Shaywitz et al., 2004). Findings such as these establish links between neural activity's robustness and location and improvements in reading and phonological processing skills. Since no behavioral impairments in phonological processing were found in the present study, the results seem to reveal phonological processing dysfunction that is unnoticeable on the behavioral level. This highlights the importance of neuroimaging techniques in early liability assessments, as imaging data may differentiate between children who, when observed on the behavioral level, seem identically predisposed to reading difficulty. Identifying typical-seeming children who are, in fact, at increased risk for reading impairment will enable earlier remediations, and represents a real benefit of fMRI research and use.

B) Exploring Intergenerational and Genetic Pathways of Influence

The present study also aimed to identify the extent to which genetic pathways are at play within the intergenerational transfer of reading ability. It endeavored to do so by 1) looking at pre-readers who had no formal reading training, and by 2) controlling for behavioral and environmental factors. Regressing out these variables' influence was integral to the interpretation of the present results because of the confounding correlations between maternal ARHQ and HLE and between paternal ARHQ and SES. Furthermore, parental reading history has been shown to represent both reading-related genotype and home environment (van Bergen et al., 2016). No study on reading development that neglects home environment in its analyses, therefore, could interpret its results in terms of casual pathways. Accordingly, the present study accounted for both HLE and SES.

SES incorporated parental education and occupational prestige, and HLE incorporated a number-of-household-children's-books score, which has been shown to have unique influence on child reading development (van Bergen et al., 2016), and a how-often-parents-read-with-their-children score, elements of which are associated with child reading development (e.g., father reading frequency has been shown to correlate with child reading ability; van Bergen et al., 2016). While other measures of HLE exist, these two variables were included because they are most likely to influence and correlate with child reading. Behavioral variables, which incorporated a phonological awareness (i.e., CTOPP) and an IQ (i.e., KBIT) assessment, were also included as covariates. The present results should, then, represent the influence of genes alone – and not the influence of behavioral or environmental factors. The present study pinpointed neural activity that is not only relevant to phonological processing and reading, but that also may be sensitive to genetic pathways of influence. For example, maternal genes may specifically impact how children's brains function as children manipulate speech sounds.

The importance of genetic pathways in the intergenerational transfer of reading ability is nothing new, and studies frequently identify the effects of genetic influences. Swagerman et al. (2015), for instance, analyzed the word-reading fluency scores of twins, siblings, and their parents and found that variation in reading fluency among children was predominantly influenced by genetic factors. This led researchers to conclude that genetics, over cultural transmission, informs parent-offspring resemblance. Twin research also indicates that genes largely shape the relationship between pre-reading skills (e.g., print knowledge, rapid naming, phonological awareness, vocabulary, verbal memory) and later reading and spelling ability (Christopher et al., 2015). The results of the present

paper, too, endorse the importance of genetics, and go further by incorporating imaging, rather than behavioral, data. They contribute to reading development literature by revealing specific regions and functions that are impacted by genetic transfer, thereby identifying specific genetic pathways by which reading ability may be conferred from one generation to the next.

Results also indicated, however, that two aspects of home environment (i.e., SES and the number of household children's books) predicted neural activity in the left frontal gyrus. This goes to show that genes are not the ultimate or only influencers of reading ability. On the contrary, genetic variables interact with environmental ones, such as HLE, that also contribute to the functional development of the reading network (Powers et al., 2016), and have been minimized to non-significance when environmental factors are controlled for (Dilnot et al., 2017). Additionally, bilingual households constitute a special case of home environment influence, as exposure to two languages may impact both reading-related behavioral and neural development. It has been shown, for instance, that bilinguals demonstrate different brain activation patterns during reading-related tasks for each of their languages according to how early each was learned (Perani et al., 2003). Similarly, native languages have been shown to shape the neural mechanisms supportive of phonological processing in second languages (Tan et al., 2003). It would therefore be interesting to investigate how parental reading history, or other intergenerational factors, relates distinctly to the different neural mechanisms that support each language, in addition to how bilingualism influences children's phonological development in general. Unfortunately, the present study did not have enough bilingualism data to explore these interesting questions.

C) Exploring the Roles of the LG, the LPTG, and the LFG in Reading

Of the four brain regions showing activity related to maternal ARHQ, three play vital roles within the reading network. These are the LG, the LPTG, and the LFG. The left frontal gyrus, which contains Broca's area, is generally known to be involved in articulation and speech production; the LPTG, which contains Wernicke's area, is associated with phonological processing as well as reading comprehension; and areas including the LG, which is situated in the occipitotemporal region, have been connected to reading fluency and word recognition (Shaywitz et al., 2016; Norton et al., 2015). Furthermore, in a recent meta-analysis of MRI brain imaging studies, it was determined that neural abnormalities, in both at-risk pre-readers and dyslexic adults, are commonly found in left parietotemporal and left occipitotemporal regions, as well as in left cerebellar and right parietal regions, though these areas were not implicated by the present study (Vandermosten et al., 2016). Neural abnormalities included hypoactivations, decreased gray matter volumes, and atypical white matter organization, and were not found in non-dyslexic, otherwise-matched controls. Hypoactivations in left prefrontal, left temporal, left parietotemporal, and left occipital regions are also frequently associated with familial risk of reading difficulty, in both transparent and opaque orthographies (Dębska et al., 2016; Richlan et al., 2011; Raschle et al., 2012a). This is key considering that the present paper focuses on functional neural characteristics.

Additionally, it is important to understand that reading is not a monolithic skill, instead comprised of numerous cognitive functions (e.g., phonological processing and RAN) and perceptual processes (e.g., temporal sampling and visual-spatial attention) (Norton, 2015). Distinct components of the reading network, therefore, likely each relate

to literacy in a slightly different way, depending on the cognitive functions they support. All of the regions implicated by the present study were related to phonological processing. The specific roles they play will now be explored.

Lingual Gyrus (LG): The LG is recruited for read response naming (i.e., reading objects' descriptions before silently naming them) and is involved in single-word and object processing (Gaillard et al., 2001). Intervention studies have further implicated the LG in reading. Small et al. (1998), for instance, studied a patient with phonological dyslexia, measuring her behavioral and neuroanatomical changes following an intervention centered on learning how to make grapheme to phoneme correspondences. They found that the patient not only adopted a phonological strategy while reading (i.e., decomposing words into their constituent sounds, as opposed to memorizing entire word forms) but also exhibited significantly more LG activity while reading than she had before. The "main focus" of her brain activity, in fact, had shifted from the angular gyrus to the LG. Whole word and decompositional reading strategies, the paper concluded, enlist distinct brain networks, and decompositional strategies may be represented and supported, in part, by activity in the LG. In another intervention study, poor-reading 2nd and 3rd graders were taught the "alphabetic principle," namely, that letters and combinations of letters represent individual speech sounds. Results revealed that children who had received the intervention, as opposed to children who had not, exhibited significantly more activity in the LG, as well as in other regions of the reading network, a year later (Shaywitz et al., 2005).

All of the cognitive skills and remediations associated with LG activity are partly visual in nature. Read response naming requires reading object descriptions, and single-

word processing, object processing, and grapheme-phoneme matching require an understanding of how sounds map onto images, as described by the alphabetic principle. LG activity, in other words, seems to represent a type of visual processing that is integral to reading: associating images with sounds. The present study may validate this theory, as the results showed that activity in the LG was related to phonological processing in the FSM task, which was not visual. Though children did see images throughout the task, they did so in each condition (i.e., in both experimental and control conditions) so activity associated with these images was subtracted out, leaving activity only associated with segmenting speech sounds. The “visual processing” of the LG, then, may in fact involve both visual and sound-related components. The region may be primed to make the correspondences between sounds and images. This is suggested by the fact that activity in the LG was found during phonological processing even in pre-readers.

Left Parietotemporal Gyrus (LPTG): Maternal reading history also predicted LPTG activity in the present study. This is unsurprising considering the LPTG’s role in phonological processing and reading. Dyslexic children, as compared to non-dyslexic, otherwise-matched children, are commonly found to have hypoactivated LPTGs during reading-related tasks, and the magnitude of LPTG activity has been shown to be positively correlated with successful word reading, pseudoword decoding, and passage comprehension (Hoeft et al., 2006). The LPTG has also been implicated in the integration of letter and speech sounds (van Atteveldt et al. 2004) and is, in general, consistently activated when reading (Pugh et al. 2001; Schlaggar and McCandliss 2007). The present finding that activity in the LPTG is related to the FSM task is in alignment with these previous findings, most of which implicate the LPTG in phonological processing. The

present paper cannot, however, speak to the other roles the LPTG may play in reading, such as semantic processing and comprehension, both of which are presently irrelevant due to the design of the task.

Left Frontal Gyrus (LFG): Activity in the LFG has been shown to relate to successful syllable counting, generally with more activity for nonwords than real words (Poldrack et al., 1999). The LFG is also associated with phonology-based working memory (Nixon et al., 2004). Intervention studies have specifically shed light on the reading-related roles of the left inferior frontal lobe (LIFG), which is adjacent to the main LFG cluster examined in the present study. Temple et al. (2003), for instance, revealed that dyslexic children, following a training centered around auditory processing and oral language, showed increased, and nearly normalized, LIFG activity. The present findings are in line with such literature. The LFG seems to play a role in phonological processing, relevant, in this case, to the segmentation and comparison of speech sounds.

D) Exploring the Importance of Parental (and Maternal) Transfer

Interestingly, significant correlations between ARHQ and neural activity were only found for mothers, and not fathers. This finding is not entirely unprecedented. Maternal, and to a lesser extent paternal, cognitive phenotypes have been shown to predict aspects of child cognition. Anger & Heineck (2010), for instance, revealed that parental IQ predicted child IQ, even after controlling for environmental factors, such as parents' educational attainment and family background, and that maternal IQ made significantly larger contributions to this prediction than paternal IQ. Similarly, correlations between the cognitive abilities of mothers and sons have been shown to be stronger than correlations between the cognitive abilities of fathers and sons (Grönqvist et

al., 2016). Additionally, Black et al. (2012) found that maternal, but not paternal, reading history was associated with the volume of bilateral prefrontal and parietotemporal regions in children. Children with reading-adept mothers, in other words, tended to have higher volumes in these reading-related areas. Behavioral studies generally complement these neuroimaging findings, though differences between maternal and paternal influence are not always found. For example, parental reading ability (with no difference between mother and father) has been shown to positively correlate with child reading ability in both at-risk and non-at-risk populations (Gilger et al., 1991; van Bergen et al., 2012). Still, considering the findings of Black et al. (2012) and others, it may not be overly surprising that the present study found a positive association between maternal, but not paternal, reading history and activity within the reading network during phonological processing. The lingering question, however, is, simply, why?

Although it seems that mothers may play a more important role than fathers in the intergenerational transfer of cognitive abilities and their associated neuroanatomy, it is unclear which causal pathways are at play; mothers may confer predispositions genetically, but they also design (and constitute) a substantial portion of their children's environments – and possibly a much larger portion than that of fathers (Craig, 2006). This calls into question the confounding effects of passive gene-environment correlations, making the interpretation of maternal influence difficult. Even so, interpretations exist. The results of Black et al. (2012), for instance, suggest that prenatal, hence mostly maternal, factors influence neuroanatomical and cognitive development. The study found that child cortical surface area, which is strongly associated with prenatal environment, was related to maternal reading history, while cortical thickness,

which is not as strongly associated, was not. Furthermore, Black et al. controlled for SES and maternal educational attainment and found that reduced gray matter volume in the reading network was associated with maternal, and not paternal, reading history.

Controlling for environmental factors gives further evidence that maternal influence may be genetic or prenatal.

The present study's findings are in general agreement with this theory that maternal influence is, at least in these cases of cognitive transfer, either genetic or prenatal in nature. By scanning pre-readers and controlling for home environment, the present study was able to approximate genetic influence, which was found for mothers only. Additionally, by utilizing functional imaging, the present study may shed light on the specific neural mechanisms by which mothers influence reading development. These include the functional integrity of the LG, the LFG, and the LPTG. Future investigations of intergenerational transfer should look at the neuroanatomy of both children and parents. It is possible that the mothers who reported histories of reading difficulty had disintegrated reading networks themselves (e.g., hypoactivations in the regions implicated by the present study), which were then conferred genetically to their children. This might explain how maternal reading history is able to predict phonological processing-related activity. However, it is possible that parents' neural characteristics do not reflect their genotypes on account of 1) having years of practice under their belts, and, possibly, 2) having developed compensatory techniques to overcome any cognitive impairments that they may have had.

E) Activity in the RMTG and the Possibility of Compensatory Mechanisms

The present study also found that maternal reading history predicted RMTG activity during phonological processing. Although the RMTG is not often associated with typically developing reading networks, it may support reading in dyslexic, and in generally reading difficulty-prone, populations. The region, in other words, has been implicated as a compensatory mechanism. Shaywitz et al. (2003), illustrating this compensatory mechanism at work, found that adults who had experienced reading difficulty in childhood, but who had since compensated for it behaviorally, enlisted right superior frontal and right middle temporal gyri during pseudoword rhyming, whereas adults who had not compensated behaviorally did not. Seeing as pseudoword rhyming involves judging the speech sounds of unfamiliar nonwords, right superior frontal and right middle temporal gyri were likely compensatory mechanisms for phonological processing. Research with children has also implicated the RMTG as a compensatory mechanism. Temple et al. (2001), for instance, showed that dyslexic children had increased RMTG activity, as compared to typically developing controls, during a rhyming letter task. Increased activity was also found in left and right superior frontal gyri, right IFG, bilateral pre and postcentral gyri, right inferior/middle occipital gyri, bilateral basal ganglia, and right vermis. Phonological processing seems to enlist right hemispheric activity in children who find reading particularly difficult.

The present result that reading-adept mothers tended to have children who recruited the RMTG for phonological processing may be interpreted as the priming of a compensatory response. This is important because even children with reading-adept mothers may be at risk for reading difficulty, and may therefore benefit from compensatory mechanisms boosting their reading ability. Risk can be introduced in a

variety of ways (e.g., a close family member besides the mother may have dyslexia, there may be a poor HLE or SES) and maternal reading history is by no means the ultimate liability assessment. Having a reading-adept mother may predispose at risk children to enlisting the RMTG for phonological processing, especially if the typically responsible regions are disintegrated. This may constitute a protective factor against other risk-conferring variables. In other words, among children at risk of dyslexia, those with reading-adept mothers may have an easier time overcoming reading difficulty because they are better able to utilize the RMTG for phonological processing.

F) Evaluating the MDM and iMDM Models

The MDM and iMDM models posit that developmental disorders, such as dyslexia, are multifactorial (Pennington, 2006; van Bergen, 2014). They can have multiple etiologies, neural components, cognitive deficits, and behavioral symptoms. In the case of reading, this suggests that reading deficits may be caused by numerous genetic and environmental factors; may be underpinned by distinct neural dysfunctions in diverse brain regions across the reading network; may involve impairments of several cognitive faculties, sub-abilities, and perceptual processes; and may manifest in different ways for different people. While the present study cannot speak to all of the cognitive deficits that may underlie reading difficulty, it does indicate that phonological processing, as is commonly found, is critically related to reading. Since mothers with histories of reading difficulty were more likely to have children with hypoactivated brain regions during phonological processing, and since these children may be, according to family risk studies, more liable to develop reading difficulties in general, linking reading difficulties to phonological processing deficits does not seem, in this case, like a stretch. However,

other relevant cognitive skills (e.g., rapid automatized naming, temporal sampling, visual–spatial attention, and verbal working memory) and the neural activity that underpins them should be investigated in future studies, specifically in relation to parental reading history.

Furthermore, the iMDM emphasizes the roles that intergenerational influence, which, again, comes in many forms, plays in conferring liability and underlying etiology. The present study provides direct evidence for the iMDM, and sheds light on some of the specific agents of the intergenerational transfer of reading ability. Most generally, the presence of a relationship linking maternal reading history and child reading-related neural activity emphasizes the importance of intergenerational transfer, whether working through genetic or, via a passive gene-environment correlation, environmental pathways. More specifically, the present findings suggest that genetic or prenatal pathways of influence may be at play between mothers and their children, as maternal reading history predicted neural activity even after controlling for home environment and cognitive variables, and even in pre-readers. In sum, the present findings advance the iMDM by 1) measuring the effects of genetic or prenatal influence, 2) emphasizing the important effects that mothers have on reading development, and 3) identifying the LG, the LPTG, the LFG, and the RMTG as brain regions that may account for how maternal genes affect reading ability through phonological processing.

3. Limitations and Conclusions

Interpretations of the present results are limited in a number of ways. It cannot be concluded with certainty that the association between maternal reading history and phonological processing-related brain activity is purely genetic in nature, or that it is

indicative of a uniquely maternal pathway of influence. Although the present study controlled for aspects of home environment, liability for reading difficulty may also be conferred via aspects of the environment that were not controlled for. SES was comprised of only educational attainment and occupational prestige in the present study, so it is possible that other aspects of SES, such as income or the availability of enriched resources (e.g., high quality daycares, tutors, and babysitters), would too predict phonological processing-related neural activity. Likewise, HLE was comprised of only two variables: a number-of-household-children's-books score and a how-often-parents-read-with-their-children score. Other aspects of HLE (e.g., how often family members talk about reading with their children, or teach their children the alphabet) may have greater influence on children's reading development. It would be rash to claim that the influence is purely genetic without first accounting for these characteristics of home environment.

Even so, the present study contributes to research on reading development by utilizing functional imaging and by presenting results that control for environmental variables such as HLE and SES. By controlling for environmental influences, the associations are more likely, though not definitely, genetic in origin, highlighting genetics' distinct role in development. Genes help shape the neural mechanisms that then in turn shape cognition. Furthermore, neuroimaging techniques, such as functional imaging, may generate more detailed accounts of the neural mechanisms at play. The present study implicates the LG, the LFG, the LPTG, and the RMTG in phonological processing in pre-readers, pointing to some of the neural mechanisms by which genes may impact cognitive abilities such as reading. Future studies should target these regions

to further elucidate their role in reading development and the extent to which they are influenced by genetic and environmental factors.

In sum, the present study presents evidence for the positive relationship between mothers' histories of successful reading and neural activity in four regions in pre-readers during phonological processing. In an attempt to disentangle genetic from environmental pathways, and in accordance with the iMDM, aspects of the environment (i.e., HLE and SES) were controlled for. The resulting associations were therefore more likely genetic in nature, although conclusions cannot be made with confidence given the myriad untested environmental influences and given how intertwined they are with genetic pathways of influence. Since the relationship did survive the inclusion of environmental factors, however, the present study reveals that maternal genes may influence child reading ability partly through functional neural mechanisms in the LG, the LFG, the LPTG, and the RMTG, all of which are associated with phonological processing. Future studies should continue to shed light on the relationship between parental reading and the cognitive, neuroanatomical, and functional characteristics of pre-readers by examining multiple reading-related cognitive skills, incorporating multiple neuroimaging techniques, scanning parents as well as children, and following children throughout reading development. Fleshing out the association between parental and child reading ability will allow researchers and schools to better assess liability for reading difficulty. It may also lead to the development of better remediations for reading impairments, such as dyslexia, by pinpointing the specific neural mechanisms and cognitive abilities that interventions should target for the biggest therapeutic payoffs.

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VI. Appendix

Adult Reading History Questionnaire

Parent Reading History Questionnaire		Name of parent completing this form: _____ Completing form about: Self or Spouse/Co-parent			
<p><i>PLEASE NOTE: This reading history questionnaire applies to you, and not to your children.</i></p> <p>Please circle the number of the response that most nearly describes your attitude or experience for each of the following questions or statements. Please give your best estimate for each question.</p>					
1. Which of the following most nearly describes your attitude toward school when you were a child?	Loved school; favorite activity				Hated school; tried to get out of going
	0	1	2	3	4
2. How much difficulty did you have learning to read in elementary school?	None				A great deal
	0	1	2	3	4
3. How much extra help did you need when learning to read in elementary school?	No Help	Help from Friends	Help from Parents/Teachers	Had tutors or special class (1 yr)	Had tutors or special class (2+ years)
	0	1	2	3	4
4. Did you ever reverse the order of letters and/or color names when you were a child?	No				A great deal
	0	1	2	3	4
5. Did you have difficulty learning letter and/or color names when you were a child?	No				A great deal
	0	1	2	3	4
6. How would you compare your reading skill to that of others in your elementary class?	Above average		Average		Below average
	0	1	2	3	4
7. All students struggle from time to time in school. Compared to others in your classes, how much did you struggle to complete your work?	Not at all	Less than most	About the same	More than most	Much more than most
	0	1	2	3	4
8. Did you experience difficulty in high school or college English classes?	No; Enjoyed and did well		Some		A great deal; did poorly
	0	1	2	3	4
9. What is your current attitude toward reading?	Very positive				Very negative
	0	1	2	3	4
10. How much reading do you do for pleasure?	A great deal		Some		None
	0	1	2	3	4

11. How would you compare your current reading speed to that of others of the same age and education?	Above average		Average		Below average
	0	1	2	3	4
12. How much reading do you do in conjunction with your work? (If not working or retired, how much did you read when you were working?)	A great deal		Some		None
	0	1	2	3	4
13. How much difficulty did you have learning to spell in elementary school?	None		Some		A great deal
	0	1	2	3	4
14. How would you compare your current spelling to that of others of the same age and education?	Above average		Average		Below average
	0	1	2	3	4
15. Did your parents ever consider having you repeat any grades in school or did you drop out due to academic failure (not illness)?	No	Talked about, but didn't do it	Repeated 1 grade	Repeated 2 grades	Dropped out
	0	1	2	3	4
16. Do you ever have difficulty remembering people's names or names of places?	No				A great deal
	0	1	2	3	4
17. Do you have difficulty remembering addresses, phone numbers, or dates?	No				A great deal
	0	1	2	3	4
18. Do you have difficulty remembering complex verbal instructions?	No				A great deal
	0	1	2	3	4
19. Do you currently reverse the orders of letters or numbers when you read or write?	No				A great deal
	0	1	2	3	4
20. How many books do you read for pleasure each year (including both print and e-books)?	10+	5 to 10	2 to 5	1 or 2	None
	0	1	2	3	4
21. How many magazines do you read for pleasure each month?	5+	3 or 4 Regularly	1 or 2 Regularly	1 or 2 Sometimes	None
	0	1	2	3	4
22. Do you read daily newspapers (Monday-Friday) in print?	Every Day	Once a Week	Once in a While	Rarely	Never
	0	1	2	3	4
23. Do you read a newspaper in print on Sunday?	Completely Every Week	Scan Each Week	Once in a While	Rarely	Never
	0	1	2	3	4

24. In a typical week, how many news articles/stories do you read online?	21+	15 to 20	8 to 14	3 to 7	0 to 2
	0	1	2	3	4
25. How would you rate your ability to sound out new words (such as place names) now?	Above average		Average		Below average
	0	1	2	3	4
26. How would you rate your ability to comprehend what you read, as compared to others of the same age and education?	Above average		Average		Below average
	0	1	2	3	4

27. Did you ever receive a diagnosis of dyslexia or reading disability from a doctor or specialist?
 Yes
 No

28. If you have had reading problems, how would you say things have changed?
 My reading is typical now because problems got better on their own or with age
 My reading is typical now because it got better with extra help or intervention
 My reading is accurate but I still have problems with reading quickly
 I still have problems with both reading accuracy and speed

29. To the best of your knowledge, did your parents ever report that either one of them had a problem with reading or spelling?
 Yes
 No
 Not sure or not applicable
 If yes, please give details:

30. To the best of your knowledge, did your siblings ever have a problem with reading or spelling?
 Yes
 No
 Not sure or not applicable

31. What is the highest educational level that you have attained?
 Less than high school
 High school
 Trade school
 Some college, but no degree
 Associate's degree, junior college graduate, or equivalent
 College graduate, bachelor's degree (or equivalent)
 Some graduate education, no advanced degrees
 Master's level advanced degree (e.g., MA, MS, MEd, MSW)
 Doctoral level advanced degree (e.g., MD, PhD, EdD, JD)

32. [Optional] What is your yearly household income?
 Less than \$20,000
 \$20,000-\$40,000
 \$40,000-\$80,000
 \$80,000-\$120,000
 More than \$120,000