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RESEARCH ARTICLE

Role of Family Risk and of Pre-Reading Auditory and Neurostructural Measures in Predicting Reading Outcome

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ABSTRACT

Some children who develop dyslexia show pre-reading auditory and speech processing difficulties. Furthermore, left auditory cortex structure might be related to family risk for dyslexia rather than to reading outcome. However, it remains unclear to what extent auditory and speech processing and auditory cortex structure mediate the relationship between family risk and reading. In the current longitudinal study, we investigated the role of family risk (measured using parental reading questionnaires) and of pre-reading auditory measures in predicting third grade word reading. We measured auditory and speech processing in 162 pre-readers varying in family risk. In 129 of them, we also acquired structural magnetic resonance imaging (MRI). We quantified surface area and duplication patterns of the bilateral transverse temporal gyri (TTG(s)), and surface area of the bilateral planum temporale (PT). We found effects of pre-reading auditory and speech processing, surface area of the left first TTG and of bilateral PT and of left TTG duplication pattern on later reading. Higher pre-reading values on these measures were predictive of better word reading. Although we also found some evidence for an effect of family risk on auditory and speech processing, these latter measures did not mediate the strong relationship between family risk and later reading. Our study shows the importance of pre-reading auditory and speech processing and of auditory cortex anatomy for later reading. A better understanding of such interrelations during reading development will facilitate early diagnosis and intervention, which can be especially important given the continuity of family risk in the general population.

INTRODUCTION

Reading achievement can be predicted by phonological processing skills (Quinn et al., 2015) and features of the neural reading network (Chyl et al., 2021) measured as early as in kindergarten (i.e., pre-reading). These cognitive and neural processes associated with reading are influenced by genetic and environmental factors, as described in the theoretical models of van Bergen et al. (2014) and van Atteveldt et al. (2021). More specifically, genetic variations

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Phonological processing:
Refers to cognitive processes of recognizing, manipulating and accessing speech sounds, which are crucial in developing reading fluency.

are partly responsible for characteristics at the neural level, which in turn influence the cognitive processes that underlie reading development (Galaburda et al., 2006; Giraud & Ramus, 2013). In line with these models, previous studies have found that phonological processing skills (van Bergen et al., 2015) and white matter connectivity in the left temporal lobe (Vandermosten et al., 2017) partially mediate the relationship between parental reading abilities and the reading outcomes of their children. These findings support the idea that factors at multiple levels can interact with and mediate the intergenerational transfer of reading skills between parents and children. In addition, previous longitudinal studies related pre-reading auditory and speech processing skills to later reading, while a few brain imaging studies have indirectly suggested that left auditory cortex anatomy is related to family risk for reading difficulties, often defined as having at least one first-degree relative with a formal dyslexia diagnosis, rather than to reading outcome (Beelen et al., 2019; Łuniewska et al., 2019; Vanderauwera et al., 2018; van der Leij et al., 2013; Vandermosten, Correia, et al., 2020). Taken together, these auditory (cortex) factors may have a similar mediating role in early reading development, as previously observed for phonological processing and white matter connectivity. In this study, we examined the extent to which children's pre-reading auditory skill and auditory cortex structure mediated the effect of their parent's reading abilities (indexed indirectly using a continuous measure of family risk) on third grade word reading outcome.

Pre-reading Auditory and Speech Processing

It is well known that phonological processing plays a crucial role during typical (Clayton et al., 2020; Quinn et al., 2015) and atypical (Ozernov-Palchik & Gaab, 2016; Snowling & Melby-Lervåg, 2016) reading development, although recent accounts have been questioning its causal role (see, e.g., Blockmans et al., 2023; Landerl et al., 2019; Peterson et al., 2018). Interestingly, there is also some evidence linking lower level, auditory processing of speech and non-speech signals to reading development. Several lower level features of auditory signals such as frequency and duration have been shown to be important in typical (Goswami, 2022) and atypical (Hämäläinen et al., 2013; Serrallach et al., 2016) reading development. More specifically, Goswami (2011, 2022) has proposed that especially the ability to discriminate temporal information embedded in the amplitude envelope, reflected, for example, in stimuli differing in the time taken to reach the maximum amplitude (also known as *rise time*), can be related to the development of phonological processes important for reading. In line with this theory, rise time discrimination (RTD) has been indirectly linked to reading skills. For example, RTD was found to predict phonological awareness and letter knowledge longitudinally in the year before formal reading instruction, that is, at the pre-reading stage (Corriveau et al., 2010), and at the start of the first year of reading instruction (Vanvooren et al., 2017). Also at later stages, during primary school, RTD is associated with phonological awareness, both concurrently (Poelmans et al., 2011; Richardson et al., 2004) and longitudinally (Goswami et al., 2021). Interestingly, some studies reported a direct link between pre-reading rise time processing and reading outcome after at least one year of reading instruction (Law et al., 2017; Plakas et al., 2013), and even later, between rise time processing at age eight and reading outcome at age nine (Kuppen et al., 2014). Moreover, several studies identified RTD deficits in children with severe reading difficulties, otherwise known as dyslexia (Law et al., 2017; Poelmans et al., 2011; Richardson et al., 2004; Serrallach et al., 2016), and in adults with dyslexia (Law et al., 2014; Leong et al., 2011; Van Hirtum et al., 2019), with average effect sizes of 0.8 (Hämäläinen et al., 2013).

Efficient auditory processing, in particular RTD, contributes to the temporal segmentation of more complex auditory signals such as speech (Goswami, 2011). The relationship between

speech processing and reading is typically assessed using speech presented in a challenging environment, for example, with background noise. Better pre-reading speech-in-noise perception has been linked to better reading outcome during primary school years (Boets et al., 2008, 2011; Vandewalle et al., 2012; Vanvooren et al., 2017; White-Schwoch et al., 2015). Furthermore, speech-in-noise perception is more often anomalous in individuals with dyslexia compared to typical reading controls (Boets et al., 2011; Boets, Wouters, et al., 2007; Calcus et al., 2018; Rosen, 2003; Ziegler et al., 2009). Importantly, deficits in auditory and speech processing are only present in a subset of persons with dyslexia, with studies reporting incidence rates ranging from 30% (Boets et al., 2006; Boets, Ghesquière, et al., 2007; Calcus et al., 2018; Rosen, 2003) to 60% (Law et al., 2014; Ramus et al., 2003). In summary, several lines of research suggest that auditory and speech processing are important for successful reading development.

Pre-reading Auditory Cortex Structure

Studies have tried to identify brain structural predictors or correlates of reading outcome, including traditional structural measures such as volume, surface area, and thickness and measures of shape such as gyrification indices or gyral duplication patterns. The earliest work in this field was related to the anatomy of the PT, a secondary auditory cortex region known to be functionally involved in the spectrotemporal analysis of speech sounds (Griffiths & Warren, 2002). The PT surface area is usually left-lateralized in the general population (Tzourio-Mazoyer & Mazoyer, 2017), with the left PT surface area being larger than the right one. Reversed or absent asymmetry has been related to atypical reading outcome (Altarelli et al., 2014; Sanchez Bloom et al., 2013), but others could not replicate this finding (Eckert & Leonard, 2000; Vanderauwera et al., 2018). Methodological differences, such as the applied delineation criteria and sample size restrictions, might lie at the base of these discrepancies across studies (Ramus et al., 2018).

Duplication pattern:
A quantitative measure reflecting the shape of the transverse temporal gyri.

In addition to the PT, early stages of auditory and speech processing are subserved by other auditory regions, including Heschl's gyrus (HG), other secondary regions such as the planum polare, and associative cortices. The primary auditory cortex is most often located within the first, most anterior TTG (Von Economo & Horn, 1930), which corresponds to HG in cases where there is a single gyrus. The first TTG can also be partially separated by an intermediate sulcus, in the case of common stem duplications (CSDs; Marie et al., 2015). Different definitions exist for determining the posterior border of HG, which is also the anterior border of the PT, in particular in the presence of CSDs. Older definitions assign the posterior branch of the CSD to the PT in cases where the length of the intermediate sulcus is more than half the length of HG (Golestani et al., 2007; Leonard et al., 2001; Penhune et al., 1996). Other researchers have defined the posterior branch of CSDs as belonging to HG, regardless of the length of the intermediate sulcus (Schneider et al., 2005; Seither-Preisler et al., 2014; Wengenroth et al., 2014; Zoellner et al., 2019), which is the definition used by the present work. Additional, fully duplicated TTG, when present, also belong to the PT. The first TTG and any additional TTG(s) are located on the superior surface of the superior temporal gyrus, within the Sylvian fissure.

Structural characteristics and measures of shape of the TTG have been related to language and musical skills, both of which rely on adequate auditory processing (Turker & Reiterer, 2021). Positive associations have been reported between gray matter volume of HG/TTG and musical abilities (Palomar-García et al., 2020; Schneider et al., 2002; Seither-Preisler et al., 2014), phonetic expertise (Golestani et al., 2011), language aptitude (Turker et al., 2019), non-native speech sound learning skill (Golestani et al., 2007), linguistic pitch learning

skill (Wong et al., 2008), and bilingualism (Ressel et al., 2012). These associations have been reported in the right HG/TTG (Palomar-García et al., 2020; Seither-Preisler et al., 2014; Turker et al., 2019), the left HG/TTG (Golestani et al., 2007, 2011; Palomar-García et al., 2020; Wong et al., 2008), and the bilateral HG/TTG (Ressel et al., 2012; Schneider et al., 2002). Likewise, the presence of multiple TTGs in both the left and right hemispheres has been related to adults' musicality (Benner et al., 2017; Turker et al., 2017), phonetic expertise (Golestani et al., 2011), and language aptitude (Turker et al., 2021). Paradoxically, several studies have shown that people with dyslexia are more likely to have complete posterior duplications (i.e., fully separated additional TTG(s)). Specifically, additional TTG(s) occur more often in the right hemisphere in children (Altarelli et al., 2014; Serrallach et al., 2016) and in the left hemisphere in adults with dyslexia (Leonard et al., 2001) compared to people with typical reading skills. The aspects of TTG duplication that are beneficial versus detrimental in language/musical skill versus in dyslexia, respectively, remain to be understood. Furthermore, it is unlikely that the mixed findings on left versus right hemisphere involvement reflect developmental changes, in light of the known relative stability of auditory cortex anatomy. While gray matter volume across the whole brain develops rapidly in the first two years of life, it is much more stable in later childhood and adolescence (Gennatas et al., 2017; Gilmore et al., 2018). Gray matter volume of the auditory cortex specifically has been shown to be very stable in nine-year-olds tested longitudinally over approximately one year (Seither-Preisler et al., 2014). The mixed findings are more likely due to the behavioral measures under investigation and/or to sample characteristics. For example, sex differences could also explain these contradictory results, as the studies finding right hemispheric duplications in children oversampled males (Serrallach et al., 2016) or found the effect only in males (Altarelli et al., 2014). Notably, none of these studies accounted for family history of dyslexia, a factor which we elaborate on below (see Influences of Genetics, Heritability, and Family Risk, below).

Other features of auditory cortex shape also appear to be different in dyslexia, such as the gyrification index, which assesses the local ratio of curvature perpendicular to the cortical surface as opposed to the shape of HG parallel to the cortical surface (Schaer et al., 2008). A recent study looking at HG specifically reported a higher gyrification index of the left HG in children with dyslexia compared to peers with typical reading skills (Kuhl et al., 2020). This was found to be the case in the same children assessed once before (age 5) and once during (age 8) reading instruction, although the effect of time itself was not investigated in this study. Clark et al. (2014) found thinner cortex of the left HG in pre-reading children (age 6) who go on to develop dyslexia. Considering the small sample sizes in the studies of Kuhl et al. (2020; *n* = 32 of which 16 developed dyslexia) and Clark et al. (2014; *n* = 17 of which 7 developed dyslexia), it remains unknown if these pre-reading differences in HG anatomy would replicate in larger samples. In the study by Clark et al. (2014), the thickness difference in the left HG was still present after a few years of reading instruction (age 12), but other studies relating dyslexia to cortical thickness of HG after reading acquisition reported contradictory results (Ramus et al., 2018). Ma et al. (2015) reported thicker right HG in school-aged children with dyslexia, whereas neither Altarelli et al. (2014) nor Skeide et al. (2018) found any differences in cortical thickness of HG between individuals with and without dyslexia. Diverging findings might be related to experience-dependent plasticity of cortical thickness, since this structural feature has been shown to change with experience and with language-related training (Hervais-Adelman et al., 2017; Lövdén et al., 2013; Mårtensson et al., 2012).

Other studies have also looked at gray matter volume of the auditory cortex in children after the pre-reading stage. Children with dyslexia exhibited lower gray matter volume of the left

HG and PT in comparison to peers without dyslexia (Xia et al., 2016). However, while Serrallach et al. (2016) also found lower gray matter volume in bilateral HG, they found higher gray matter volume in bilateral PT. Last, Sutherland et al. (2012) found a positive relationship between gray matter density in bilateral HG and auditory processing of non-speech stimuli in a sample of 10-year-olds. The latter was correlated positively with reading, but the investigation of a direct link between HG and reading was lacking. In short, there is ample evidence that not only traditional structural features of the TTG and of the PT such as volume, surface area, and thickness, but also shape, relate to language and music skills. However, evidence concerning the predictive role of pre-reading TTG and PT anatomy in the context of reading skills is limited and contradictory (Ramus et al., 2018), warranting further research.

Influences of Genetics, Heritability, and Family Risk

It is known that both surface area and cortical thickness are influenced by genetics and heritability, with large regional cortical variation in the heritability of these different brain structural features (Grasby et al., 2020; Strike et al., 2019). A recent twin study in infants found strong, significant effects of heritability on surface area as opposed to weak, nonsignificant effects on cortical thickness (Jha et al., 2018). Consistent with this, a recent large-scale meta-analysis looking both at molecular genetics and at twin heritability studies has shown a stronger influence of molecular genetics on surface area than on cortical thickness. Specifically, this study showed that surface area is more likely to be influenced by early developmental factors and that cortical thickness is more likely to be influenced by learning and experience during adulthood (Grasby et al., 2020). In this study, genetics and heritability were the focus, but this does not exclude the role of other early factors on brain development (Hoeft & Hancock, 2017), ones including prenatal hormones (Miranda & Sousa, 2018) and epigenetic effects (Smith, 2011). Grasby et al. (2020) showed regional variation in the effects of genetics in different cortical regions, in line with other studies reporting high heritability for HG specifically compared to other cortical regions (Hulshoff Pol et al., 2006; Winkler et al., 2010). Thus, in agreement with what is proposed by theories of reading development (van Atteveldt et al., 2021; van Bergen et al., 2014), genetic and environmental factors can have a distinct impact on different neurostructural properties, possibly with a greater influence of genetics on surface area than on thickness.

In addition, behavioral studies have identified pre-reading auditory and speech perception difficulties in children with, compared to children without, family risk for dyslexia (Boets, Ghesquière, et al., 2007; Gerrits & de Bree, 2009; Kalashnikova et al., 2018; Noordenbos et al., 2012; Richardson et al., 2003), although it should be noted that some could not detect such group differences (Boets et al., 2006; Vanvooren et al., 2017). Emerging evidence from several neuroimaging modalities further indirectly suggests that family risk for dyslexia (rather than reading skill itself) could explain some of the brain differences in the temporal cortex, including the auditory cortex, during reading development (van der Leij et al., 2013). First, studies using event-related potentials showed poorer auditory processing in children with a family risk for dyslexia compared to peers without such risk, and this difference was not dependent on later reading outcome itself. More specifically, this was found for the auditory processing of frequency differences between tone stimuli (Hakvoort et al., 2015; Leppänen et al., 2010). Family risk driven deficits were also shown in the processing of temporal pattern changes (van Zuijen et al., 2012) and rise time differences (Plakas et al., 2013) between tone stimuli in young children, but note that the latter could not be replicated in older children (Hakvoort et al., 2015). Second, functional MRI studies suggested that brain activation can depend on the family risk status. For example, activation elicited by two phonemes in the

Heritability:
The proportion of individual differences in a characteristic that can be attributed to genetic factors.

Epigenetics:
The study of changes in gene expression by environmental factors, without changes to the underlying DNA sequence.

bilateral superior temporal gyri was distinct in children without a family risk but not in children with such risk, and these activation differences were unrelated to the actual reading outcome (Vandermosten, Correia, et al., 2020). Children with family risk further exhibited hypoactivation in the bilateral temporal gyri during a phonological task, irrespective of their reading outcome (Łuniewska et al., 2019). Third, concerning structural MRI measures of these regions, Beelen et al. (2019) found a smaller surface area in bilateral temporal gyri in pre-reading children with a family risk, again unrelated to later reading outcome. Additionally, the typical PT surface area asymmetry was reported to be reversed in children with a family risk, with rightward rather than leftward structural lateralization (Vanderauwera et al., 2018).

In summary, it seems likely that some auditory and speech processing deficits and neural properties of related brain regions reflect family risk status but do not relate to actual reading outcome. However, these previous findings used group comparisons, whereas family risk is known to be continuous rather than categorical (Erbeli et al., 2022; Snowling et al., 2003; van Bergen et al., 2014), and whereas it is known that arbitrary diagnostic dichotomies do not accurately reflect reading skills (Astle et al., 2022). A few studies assessed reading abilities of the parents as a continuous measure for family risk. They observed that the relationship between family risk and reading outcome was mediated by phonological processing skills (van Bergen et al., 2015) and by white matter connectivity in the temporal cortex (Vandermosten et al., 2017). Notably, these factors only partially mediated the family risk–reading relationship, and as such do not exclude the well-established presence of a robust direct link (Snowling & Melby-Lervåg, 2016). Currently, it remains unknown whether a similar mediating role pertains to auditory and speech processing and to auditory cortex anatomy. Thus, a direct investigation of the possible mediating role of auditory (cortex) factors on the relationship between family risk and reading is lacking.

The Current Study

In the current study, we investigated whether pre-reading behavioral measures of auditory and speech processing and auditory cortex anatomy mediated the relationship between family risk for dyslexia and third grade word reading outcome. We recruited a relatively large sample of participants ($n = 162$), that varied in terms of their family risk. Pre-reading auditory processing was assessed with non-speech (RTD) and speech (speech-in-noise perception) tasks. For the pre-reading auditory cortex measures, we examined surface area of bilateral first TTG, additional TTG(s) (when present) and PT and surface area asymmetry of PT because of previous work showing a greater influence of heritability and genetics on surface area rather than on thickness. Due to previous findings of TTG shape differences in dyslexia, we also examined bilateral TTG duplication patterns by assessing the total number of gyri along the Sylvian fissure. Surface area of the first and of additional TTG(s) were extracted using an automatic auditory cortex segmentation toolbox (Toolbox for the Automated Segmentation of Heschl's Gyrus, or TASH; Dalboni da Rocha et al., 2020), which was adapted to suit the pediatric data at hand. Since family risk is known to be continuous, we assessed it using a continuous measure, namely parental reading questionnaires. We expected an effect of family risk (Snowling & Melby-Lervåg, 2016) and of pre-reading auditory and speech processing and auditory cortex structure (Boets et al., 2011; Clark et al., 2014; Kuhl et al., 2020; Law et al., 2017) on third grade reading outcome. Additionally, we hypothesized that auditory and speech processing and surface area of bilateral first TTG, additional TTG(s) and PT would partially mediate the effect of family risk on reading outcome, since these measures are often influenced by familial factors (Beelen et al., 2019; Jha et al., 2018; Plakas et al., 2013; Vanderauwera et al., 2018).

MATERIALS AND METHODS

Participants

This study is part of a longitudinal research project of the Dyslexia Collaboration Leuven (DYSCO) in which children are followed up throughout their early reading development. The study was approved by the University Hospital Leuven Ethical Committee (S55139 and S54415). Written informed consent by the parents and oral assent by the children was obtained. Participant recruitment and the auditory and speech processing data collection took place at the start of the third and final year of kindergarten (age 4–5). Additionally, structural brain images were acquired at the end of kindergarten, using MRI. Reading skills were not formally assessed in kindergarten, but since this study was conducted in Flanders (Belgium), where formal reading instruction is not yet initiated in kindergarten (https://onderwijsdoelen .be/), the first stage of our study is considered the pre-reading stage. Reading data were collected at the start of second (age 6–7) and third grade (age 7–8). Participants received a small present after each test session, and parents were sent a report about their child's individual behavioral results.

The study sample consisted of two cohorts with a total of 163 participants. Children in both cohorts were followed up at the same time points during reading development using identical measures, allowing compilation of the two cohorts into one study sample. The first cohort ($n =$ 87) was recruited in 2011. Half of these children had at least one first-degree relative with a formal dyslexia diagnosis, reflecting an increased familial risk for dyslexia. For the second cohort, recruited in 2018, we selected 76 children without a familial risk but with an increased cognitive risk for dyslexia, out of a large-scale screening effort ($n = 1,225$; Verwimp et al., 2020). Cognitive risk corresponded to a score below the 30th percentile compared to the entire screening data set, on at least two out of three pre-reading tasks (phonological awareness, rapid automatized naming, and letter knowledge). Cognitive risk was also assessed retrospectively in the 2011 cohort. These recruitment efforts resulted in the total sample ($n =$ 163), consisting of 27 children with only a family risk, 64 children with only a cognitive risk, 36 children with a combined family and cognitive risk, and 36 children without any risk. For the 2011 cohort, all measures were collected prior to the COVID-19 pandemic. For the 2018 cohort, all the pre-reading measures and brain imaging were also assessed before the COVID-19 pandemic and thus before nationwide school closures. However, children in this cohort experienced school closures during first grade (March–May 2020). Therefore, we chose to include third grade reading data (collected in September 2021), since by then, these participants had received an entire school year of uninterrupted in-person classroom reading instruction.

Across both cohorts, all children were monolingual Dutch speakers, without previous history of hearing loss, vision deficits, brain damage, or ADHD. The data of one participant were excluded from all analyses due to an incidental brain finding, resulting in a study sample of 162 participants for all analyses including only behavioral data. For analyses including brain imaging data, 56 additional subjects were excluded due to various reasons (24 did not agree to participate in the MRI session, 7 did not complete the MRI session, 20 showed excessive head motion, 3 had unexpected brain segmentation errors, and 2 dropped out during the course of the study), resulting in a sample of 106 children. We report general participant characteristics, namely, sex, handedness, age, intelligence, and parental education, in Table 1. Handedness was evaluated using the parents' report of the Edinburgh Handedness Inventory (EHI; Oldfield, 1971). Three participants were ambidextrous according to the EHI manual, which classifies scores below −40 as left-handed and scores above +40 as right-handed. However, the scores

Table 1. Participant characteristics.

Variable	Overall ($n = 162$)[a]	Cohort 2011 ($n = 87$)[a]	Cohort 2018 ($n = 75$)[a]	p value[b]
Sex (female/male)	80/82	36/51	44/31	0.028
Handedness (left/right)	16/113	9/65	7/48	0.923
Age (in months) – kindergarten behavioral tasks	63 (56–72)	62 (56–68)	5 (59–72)	< 0.001
Age (in months) – kindergarten MRI	73 (66–81)	74 (68–81)	72 (66–78)	0.001
Age (in months) – third grade behavioral tasks	98 (92–105)	98 (93–105)	98 (92–104)	0.451
Verbal intelligence	9.8 (3.0–17.0)	9.3 (4.0–15.0)	10.4 (3.0–17.0)	0.012
Nonverbal intelligence	9.7 (3.0–19.0)	10.0 (3.0–18.0)	9.2 (3.0–19.0)	0.038
Parental education	4.0 (2.0–6.0)	3.8 (2.0–6.0)	4.2 (2.0–6.0)	0.039

Note. MRI = magnetic resonance imaging.

[a] Mean (range) or occurrence (*n*).

[b] Group differences were assessed using a Pearson's Chi-squared test for sex, a Fisher's exact test for handedness, and a Wilcoxon rank sum test for age, intelligence, and parental education.

of these three participants were very close to the cut-off values (i.e., −35, −36 and +38), and for ease of interpretation their handedness was categorized as left-, left-, and right-handed, respectively. As a proxy for intelligence, we administered the Vocabulary (verbal) and Block Design (nonverbal) subtests of the Wechsler Intelligence Scale for Children (WISC-III-NL; Kort et al., 2005) at the start of second grade. Scores of these subtests were normed using the WISC-III-NL manual with $M = 10$ and $SD = 3$. Parental education, as a proxy for socioeconomic status (Duncan & Magnuson, 2012), was quantified by the parents' highest level of education, ranging from one (high school degree), to two (bachelor degree), and three (master or doctoral degree). The maternal and paternal educational levels were summated into one continuous measure with values ranging between two and six (Robitzsch, 2020). For each of these participant characteristics, descriptive statistics of the total study sample as well as a comparison between the two cohorts is shown in Table 1.

Materials and Procedure

Behavioral measures of auditory and speech processing at the pre-reading stage

Two auditory and speech processing tasks were administered at the start of the final year of kindergarten. Both tasks were performed using APEX software (Francart et al., 2008), and stimuli were presented using a Fireface UC soundcard (RME Audio, Germany) with calibrated HDA 200 headphones (Sennheiser, Germany).

An RTD task was used to measure auditory processing of nonspeech sounds. In this task, participants had to discriminate noise stimuli that differed in rise time, that is, the duration it takes from the onset of the stimulus to reach maximum amplitude. They were presented with speech-weighted noise stimuli of 800 ms with a linear fall time of 75 ms at an intensity level of 70 dB SPL (sound pressure level). The rise times were adapted logarithmically, between 15 ms and 699 ms, during the task. On each trial, the participants heard three stimuli (interstimulus interval = 350 ms); two reference stimuli with the shortest rise time of 15 ms and one target stimulus with a longer rise time. The order of target stimulus presentation relative to the

Oddity paradigm:
A paradigm in which participants have to identify the stimulus that is perceptually distinct from other stimuli (odd one out).

references was randomized across trials and across subjects. Using a three-alternative forced choice oddity paradigm, they were instructed to identify the target stimulus. The rise time of the next trial's target stimulus was adapted using a two-down, one-up staircase procedure. The discrimination threshold was estimated after eight reversals and calculated as the average of the last four reversals; the threshold corresponded to the rise time of the target stimulus for which the participant could still discriminate the target from the reference. The children first practiced the task, and then they completed a test and a retest measurement (test–retest reliability = 0.74). To minimize both learning and attentional effects, we used the best threshold of the test and retest measurement. Lower thresholds indicated better performance. The task was embedded in an interactive computer game (Laneau et al., 2005).

Higher-order auditory processing was assessed using a speech-in-noise perception (SPIN) task designed specifically for young children, the Leuven Intelligibility Peutertest (van Wieringen & Wouters, 2023). Consonant–vowel–consonant words were presented to the right ear in stationary speech-weighted noise. The noise had a fixed level of 65 dB SPL, whereas the level of the speech was adapted during the course of the task. First, during the training phase, one list of 11 words was used to ensure understanding of the task procedure. The level of the speech during the training list was equal to the level of the noise, resulting in a signal-to-noise ratio (SNR) of 0 dB SNR. Then, during the testing phase, lists of 11 words each were administered at SNRs of −2, −5, and −8 dB SNR, meaning the level of the speech was 2, 5, and 8 dB SPL more quiet than the level of the noise, respectively. The first word of each list served solely to engage the attention of the participant, whereas the next 10 words were used to assess performance. Participants had to repeat the words, or, in cases they could not understand the entire word, to repeat each phoneme they could understand. Each correctly repeated phoneme was counted (i.e., phoneme-level scoring), allowing calculation of the percentage of correctly repeated phonemes per list. A test and a retest list were administered for each SNR. By dividing the standard deviation of differences between the raw scores of these test and retest measurements by $\sqrt{2}$, we measured test–retest reliability while taking into account the possibility that performance improved during testing (i.e., learning effect; Smits & Houtgast, 2005). Measurement error was less than 1.5 dB, in line with previous findings of SPIN tasks (Van den Borre et al., 2021). For further analyses, we therefore averaged the test and retest values for each SNR. Using a generalized linear model with cumulative Gaussian distribution, we fitted a psychometric performance-intensity curve for each participant and estimated the SNR at which 50% of the phonemes were still accurately repeated (i.e., speech reception threshold). Lower speech reception thresholds indicated better performance. The above-mentioned psychometric analyses were performed in R (Version 4.1.2; R Core Team, 2021), including the MASS (Venables & Ripley, 2002) and modelfree (Marin-Franch et al., 2012) packages.

Image acquisition and processing of auditory cortex at the pre-reading stage

To observe structural characteristics of the auditory cortex, we collected MRI data at the end of the final year of kindergarten at the University Hospital of Leuven. The MRI scanner was replaced with a new scanner of the same type between data collection of the two cohorts. Thus, for both cohorts, we acquired T1-weighted structural sequences on a 3T Philips Achieva scanner (Philips, Best, The Netherlands) equipped with a 32-channel head coil. The T1-sequences had the following parameters: 182 contiguous coronal slices, 9.7 ms repetition time, 4.61 ms echo time, 8° flip angle, 0.98 × 0.98 × 1.20 mm voxel size and 6 m 22 s acquisition time.

We used a child-friendly protocol, in line with the recommendations of Theys et al. (2014), to limit excessive head motion that can occur in young children and thus confound structural

brain measures (Pardoe et al., 2016; White et al., 2018). Prior to the MRI appointment, the children were acquainted with the MRI procedure through an informative video. On the day of the scan, the researcher explained different aspects of undergoing an MRI scan to the participant (e.g., limiting head movement). Lastly, the actual scanner was decorated to look less intimidating, and the children could choose a movie to watch while being scanned. During data processing, we performed a visual quality check for head motion, rated the scans using Blumenthal's scale and excluded scans that were contaminated with severe motion artifacts (Blumenthal et al., 2002). In total, 20 out of 129 subjects that had MRI data (= 15.5%) were excluded due to severe motion artifacts (based on the Blumenthal rating). Two independent researchers completed the Blumenthal rating for all participants. Interrater reliability, calculated using Cohen's weighted kappa, was 0.78, indicating substantial agreement.

Pre-processing of the raw T1 images was performed using the recon-all function of Free-Surfer (Version 6; Fischl, 2012). The resulting output was then used for an automated segmentation of the TTG. Most previous studies on the anatomy of Heschl's gyrus relied on the visual/manual segmentation of this region (Marie et al., 2015; Schneider et al., 2009), but we used the recently developed TASH (Dalboni da Rocha et al., 2020) to segment the TTG in a time-efficient, reproducible, and standardized way. TASH was originally developed on adult brain images. Due to the smaller size of pediatric brains, as used in this study, the TASH parameter for the automatic check for existing TTG clusters was decreased from 100 to 50 vertices, thus eliminating only clusters smaller than 50 vertices. The bilateral TTG were then segmented and the surface area (in mm^2) of the first TTG and of additional TTG(s), when present, were extracted. Note that TASH segments the first TTG as a whole, regardless of the length of the sulcus intermedius (SI) in the case of a common stem duplication. In three subjects, the first TTG was not correctly segmented by TASH, and their scans were excluded from further analyses. TASH segments the gyri specifically, but does not include segmentation of the superior temporal plane, that is, the superior surface of the superior temporal gyrus (Shapleske et al., 1999). Therefore, we also extracted surface area of the bilateral PT segmented by Free-Surfer, using the Destrieux et al. (2010). This automatic PT segmentation, in line with some studies that used manual segmentations (Hugdahl et al., 2003; Sanchez Bloom et al., 2013; Shapleske et al., 1999; Steinmetz et al., 1990), was more liberal in defining the posterior border of the PT compared to other studies, which did not include posterior rami (Altarelli et al., 2014; Vanderauwera et al., 2018). To quantify surface area asymmetry of the PT, we calculated the asymmetry index (AI) using the formula AI = [(R − L)/(R + L)/2] as described in Marie and Golestani (2017). Since surface area was calculated in native space, and to ensure that potential effects were specific to the TTG, we included the corresponding total hemispheric surface area as a covariate in the statistical analyses.

To examine TTG duplication patterns, the number of gyri along the bilateral TTG was assessed visually, blind to participant characteristics. Specifically, the rater (NG) quantified the number of gyri by giving a value of 1 when a single gyrus was present, a value of 2 when two fully separated gyri were present, and so on. Further, the ratings of the first TTG (i.e., of HG) only was not binary but continuous, since it is known that HG can be either a single gyrus or split in the form of a common stem duplication (Marie et al., 2015). Thus, for HG only, the rater provided a number ranging between 1 and 1.99 reflecting the degree of gyrification or, in other words, reflecting the depth of the SI, when present. For example, a single HG got a rating of 1; a common stem duplication having an SI spanning half the length of HG got a rating of 1.5; and a common stem duplication having a SI spanning 8/10ths of the length of HG got a rating of 1.8, and so on. The HG value was then simply incremented by 1 every time an additional, fully separated TTG was present. Since duplication patterns are region specific (Ronan

et al., 2014), there was no need to control for any global or corresponding hemispheric value in the statistical analyses. In summary, auditory cortex morphology was quantified using five measures: surface area of bilateral first TTG, surface area of bilateral additional TTG(s), surface area of bilateral PT, surface area asymmetry of PT, and duplication patterns of bilateral TTG(s).

Measure of family risk for dyslexia

Family risk for dyslexia was quantified using the parental self-report Adult Reading History Questionnaire (ARHQ; Lefly & Pennington, 2000), translated to Dutch from the original English version (Verwimp et al., 2020). This questionnaire included 23 items on a 5-point Likert scale and inquired about the parents' history with learning to read in primary school, as well as their current experience with and attitude toward reading. To quantify family risk, we divided the total score by the maximum score of 92, resulting in a continuous variable ranging between zero and one. Scores closer to one indicated more self-reported reading difficulties in the parents. Both the biological mother and father were requested to fill in the questionnaire. We only included the scores if both maternal and paternal scores were available, and both scores were averaged into one familial risk score for each participant.

Measure of reading ability

As our outcome of interest, we assessed word reading ability at the start of third grade. We administered the standardized Eén-minuut-toets (Brus & Voeten, 1999), where children had to read aloud as many words as possible during one minute. The outcome measure was the number of correctly read words in one minute.

Statistical Analyses

All statistical analyses were performed in R (Version 4.1.2; R Core Team, 2021), including the lavaan package (Rosseel, 2012). The analyses script and anonymized data sheet are available at the Open Science Framework (osf.io/vk8tx). First, an exploratory correlation analysis was performed to identify which of the pre-reading measures of auditory and speech processing and auditory cortex were related to third grade word reading. Then, we fitted mediation models to investigate whether these pre-reading measures mediated the effect of family risk for dyslexia on third grade word reading outcome (see Figure 1). We fitted the models to our data using robust maximum likelihood (MLR) estimation and full information maximum likelihood (FIML) to account for missing data and to ensure usage of all available data. The model syntax included the direct effect of family risk on reading outcome, the indirect effect via pre-reading measures, and the total effect combining these direct and indirect paths. We reported standardized parameter estimates and interpreted effect sizes following the guidelines of Gignac and Szodorai (2016), who found effects of 0.10, 0.20, and 0.30 to be small, typical, and large, respectively. Additionally, three covariates were taken into account (see Figure 1), using regressions for endogenous variables and covariances for exogenous variables (Little, 2013). First, we included the cohort variable as a covariate to each mediation model, to account for variance explained by differences between the cohorts (i.e., COVID-19 pandemic and associated nationwide school closures [see Participants section]; participant characteristics [see Table 1]; and scanner [see Image Acquisition and Processing of Auditory Cortex at the Pre-reading Stage]). Second, in the mediation models where surface area was included, we allowed the local surface area to covary with the corresponding hemispheric surface area (Genon et al., 2022). Third, given the presence of both left- and right-handed participants in our study sample, we checked for group differences related to handedness. For each mediation model including a neuroanatomical measure, we performed the Wilcoxon rank sum test to

Mediation model:
A model that examines the relationship between an independent and dependent variable through a proposed mediating variable.

Endogenous variables:
Variable that are influenced by other variables in the statistical model, whereas exogenous variables are not.
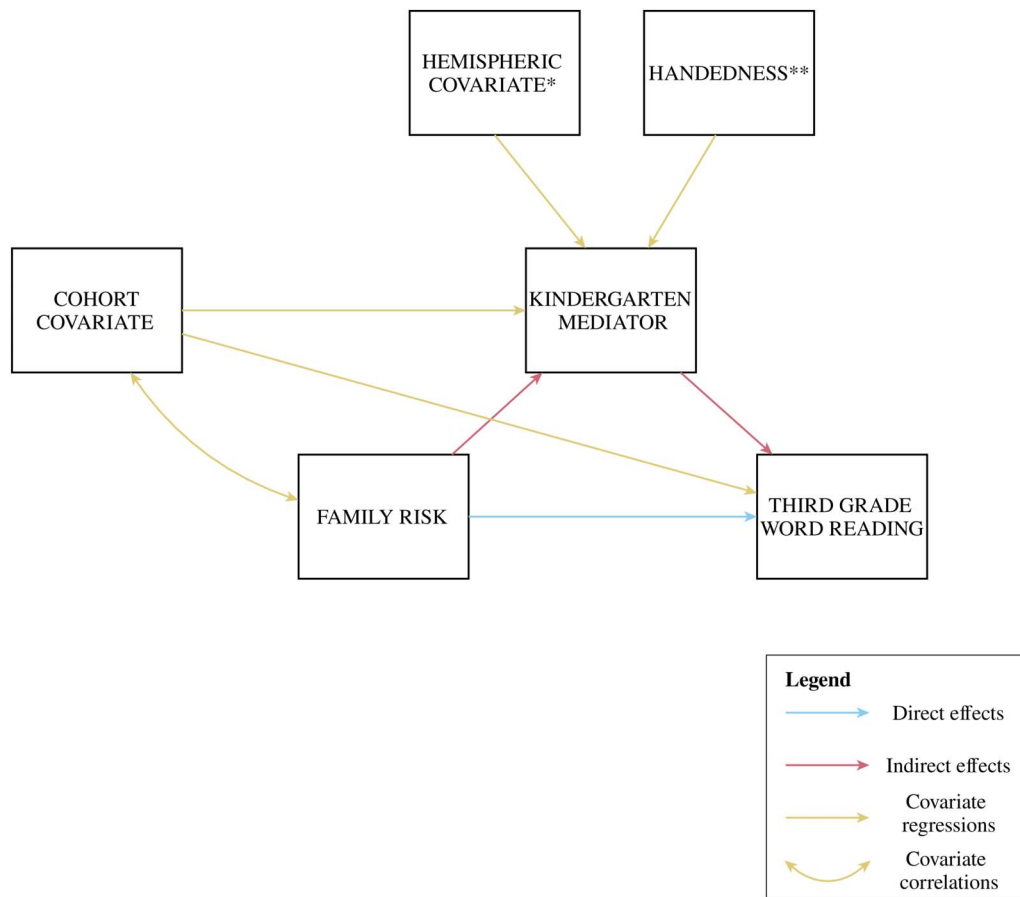
Figure 1. Mediation model. * The hemispheric covariate was only included in the models including surface area, but not in models including duplication patterns, rise time discrimination, or speech-in-noise perception. ** The handedness covariate was only included in the case of a group difference between left- and right-handed participants.

compare left- and right-handed participants. For the neuroanatomical measures that were significantly different between left- and right-handed participants, we added handedness to the mediation model as a covariate.

Note that before running the mediation analyses, we linearly rescaled some of the variables as described in Kline (2011). More specifically, RTD thresholds and surface area measures were divided by 100, word reading scores were divided by 10, and familial risk scores were multiplied by 10. This procedure resulted in more homogeneous variances across the variables without affecting the underlying interrelations, which facilitated model estimation.

RESULTS

Descriptive statistics are presented in Table 2. First, we used the Shapiro–Wilk normality test to assess the extent to which the data followed a normal distribution. This test showed deviations from a normal distribution for all kindergarten measures except SPIN, surface area of the left and right first TTG and PT asymmetry (see Supplementary Table 1 in the Supporting Information, available at https://doi.org/10.1162/nol_a_00111). Family risk and third grade word reading did not show deviations from a normal distribution. Next, we explored zero-order correlations to see how the kindergarten measures correlated with third grade word reading (see Table 3). Given the normality test results, we used Spearman coefficients for bivariate correlations that

Table 2. Descriptive statistics.

Variable	Measure	N	Missing	Center[a]	Spread[b]	Minimum	Maximum
Family risk for dyslexia	Parental ARHQ	144	18	0.32	0.10	0.09	0.57
Kindergarten auditory and speech processing	RTD threshold (in ms)	158	4	289	366	35	648
	SPIN threshold (in dB SNR)	158	4	−5.4	1.3	−9.2	−1.8
Kindergarten surface area first TTG (in mm^2)	Left	106	56	296.16	84.25	76.00	484.00
	Right	106	56	267.68	85.47	81.00	493.00
Kindergarten surface area additional TTG(s) (in mm^2)	Left	106	56	260.50	134.25	0.00	752.00
	Right	106	56	151.50	149.00	0.00	437.00
Kindergarten surface area PT (in mm^2)	Left	106	56	650.00	232.25	299.00	1,269.00
	Right	106	56	529.00	118.75	221.00	948.00
PT surface area asymmetry		106	56	−0.18	0.20	−0.69	0.34
Kindergarten TTG duplication patterns	Left	106	56	3.00	0.70	1.00	5.00
	Right	106	56	2.75	1.00	1.00	4.30
Third grade word reading	Correctly read words in 1 min.	156	6	38	15	8	77

Note. TTG = transverse temporal gyrus; PT = planum temporale; ARHQ = Adult Reading History Questionnaire; RTD = rise time discrimination; SPIN = speech-in-noise perception; SNR = signal-to-noise ratio.

[a] Center was quantified by the mean for family risk, SPIN, surface area of bilateral first TTG, planum temporale asymmetry, and word reading and by the median for all other variables.

[b] Spread was quantified by the standard deviation for family risk, SPIN, surface area of bilateral first TTG, planum temporale asymmetry, and word reading and by the interquartile range for all other variables.

included at least one non-normally distributed variable (i.e., RTD, surface area of left or right additional TTG(s), surface area of left or right PT, or duplication patterns of left or right TTG(s)), and Pearson coefficients for the other bivariate correlations. RTD and SPIN had a significant negative correlation with word reading. In other words, higher RTD or SPIN thresholds, corresponding to worse performance, were associated with worse word reading scores. Surface area of left first TTG, surface area of left and right PT, and duplication patterns of left TTG(s) had a significant positive correlation with word reading. Each of these correlations had an absolute value of 0.20 or more (typical effect size; Gignac & Szodorai, 2016). The full zero-order correlation table can be found in Supplementary Table 2.

Then, we conducted mediation analyses to test whether the kindergarten measures that correlated significantly with reading also acted as mediators of the relationship between family risk and reading. The standardized estimates and p values for the total, direct, and indirect effects of these mediation analyses are shown in Table 4.

The total effect provides an estimate of the relationship between family risk and third grade reading outcome, while taking into account putative mediation through the kindergarten auditory (cortex) measures. Standardized estimates of this relationship indicated a large effect size, with βs between −0.45 and −0.49 across the mediation models. The total effect was further

Table 3. Correlation coefficients between kindergarten measures and third grade word reading.

Pre-reading measure	Correlation
Rise time discrimination	$r = -0.29$, $p < 0.001$*
Speech-in-noise perception	$r = -0.28$, $p < 0.001$*
Surface area left first TTG	$r = 0.21$, $p = 0.032$*
Surface area right first TTG	$r = 0.14$, $p = 0.15$
Surface area left additional TTG(s)	$r = -0.08$, $p = 0.426$
Surface area right additional TTG(s)	$r = 0.16$, $p = 0.104$
Surface area left PT	$r = 0.26$, $p = 0.007$*
Surface area right PT	$r = 0.22$, $p = 0.021$*
PT surface area asymmetry	$r = -0.09$, $p = 0.336$
Duplication patterns left TTG(s)	$r = 0.20$, $p = 0.038$*
Duplication patterns right TTG(s)	$r = 0.02$, $p = 0.823$

Note. Coefficients denoted with asterisks are significant at $\alpha = 0.05$. TTG = transverse temporal gyrus; PT = planum temporale.

divided into an estimation of the direct effect of family risk on reading outcome, and of the indirect effect running through the kindergarten auditory (cortex) measures. The direct effect was significant in each of the mediation models, with βs between -0.41 and -0.48 (large effect sizes). In other words, every increase by one standard deviation in family risk was associated with a decrease in third grade word reading outcome of between 0.41 and 0.48 standard deviations.

Concerning the indirect paths, family risk significantly predicted kindergarten RTD and SPIN (typical effect sizes of $\beta = 0.23$ and $\beta = 0.22$, respectively), with higher family risk predicting higher/worse RTD or SPIN thresholds. In turn, kindergarten RTD and SPIN predicted third grade word reading (small effect sizes of $\beta = -0.18$ and $\beta = -0.19$, respectively), with

Table 4. Standardized estimates and associated *p* values of the direct, indirect, and total effects of all mediation analyses.

	Total effect		Direct effect		Indirect effect					
	Direct + Indirect		FR → Reading		FR → Mediator		Mediator → Reading		FR → Mediator → Reading	
Mediator	β	p	β	p	β	p	β	p	β	p
Rise time discrimination	−0.46	< 0.001*	−0.42	< 0.001*	0.23	0.001*	−0.18	0.033*	−0.04	0.057
Speech-in-noise perception	−0.45	< 0.001*	−0.41	< 0.001*	0.22	0.002*	−0.19	0.006*	−0.04	0.050
Surface area left first TTG	−0.47	< 0.001*	−0.47	< 0.001*	0.02	0.864	0.18	0.026*	0.00	0.864
Surface area left PT	−0.46	< 0.001*	−0.44	< 0.001*	−0.10	0.159	0.18	0.026*	−0.02	0.226
Surface area right PT	−0.45	< 0.001*	−0.46	< 0.001*	0.06	0.339	0.20	0.024*	0.01	0.375
Duplication patterns left TTG(s)	−0.49	< 0.001*	−0.48	< 0.001*	−0.06	0.588	0.15	0.056	−0.01	0.587

Note. Parameters denoted with asterisks are significant at $\alpha = 0.05$.

higher/worse RTD or SPIN thresholds predicting lower word reading skills. However, the indirect effect combining these two paths ($\beta = -0.04$ for both mediation models) as well as the proportion mediated (the ratio of the indirect effect to the total effect: 0.09 or 9% for both mediation models) were very small. As a result, these indirect paths were not statistically significant ($p = 0.057$ and $p = 0.050$, respectively). Further, we found no evidence that any of the kindergarten neuroanatomical measures mediated the family risk—reading relationship. Even though family risk showed a significant negative correlation with surface area of the left PT ($r_s = -0.23$; see Supplementary Table 2), the standardized estimate of the path between family risk and this neuroanatomical measure in the mediation model was very small and not significant ($\beta = -0.10$, $p = 0.159$). Family risk also did not significantly predict any of the other pre-reading neuroanatomical measures. Results did show a significant positive effect of surface area of the left first TTG, surface area of the left PT, and surface area of the right PT on third grade reading, in line with the exploratory correlations (see Table 3), with small effects sizes (βs between 0.18 and 0.20). Duplication patterns of the left TTG(s) also correlated positively with reading (see Table 3) but this relationship did not survive in the mediation model ($\beta = 0.15$, $p = 0.056$).

All of the results shown in Table 4 were present above and beyond covariate effects of cohort and hemispheric surface area. Separate estimates for each path in the models (including the covariate effects) can be found in Supplementary Table 3a through Supplementary Table 3f in the Supporting Information. With regard to handedness, there were no group differences between left- and right-handed participants for surface area of the left first TTG ($W = 644$, $p = 0.653$), surface area of the left PT ($W = 662$, $p = 0.534$), and left TTG duplication patterns ($W = 716$, $p = 0.214$). Surface area of the right PT did differ significantly between left- and right-handed participants ($W = 795$, $p = 0.047$). Handedness was therefore added as a covariate to the mediation model of the right PT, and this did not alter the pattern of results. Since we did not find evidence for mediation of the family risk–reading relationship by any of the pre-reading auditory (cortex) measures, we investigated post hoc whether pre-reading phonological awareness had a mediating role. Descriptive statistics and mediation results are reported in Supplementary Table 4a and Supplementary Table 4b, respectively. In short, we did not find evidence that pre-reading phonological awareness mediated the family risk–reading relationship.

DISCUSSION

In the current longitudinal study, we investigated whether or not word reading in third grade can be predicted by nonspeech (RTD) and by speech (SPIN) processing, and by anatomy of the bilateral TTG(s) and PT in kindergarten. We found relationships between pre-reading RTD, SPIN, surface area of the left first TTG, left PT, and right PT and duplication patterns of the left TTG(s) with later word reading. Moreover, we looked at the possible mediating role of these measures on the relationship between family risk and reading. Although family risk did influence RTD and SPIN, we found no evidence for mediation of the family risk–reading relationship by any of the kindergarten measures under study.

Predictors of Reading Outcome

First and foremost, we found a very large effect of family risk for dyslexia on third grade word reading outcome. This effect has been reported in many previous studies examining typical (Andreola et al., 2021) and atypical (Snowling & Melby-Lervåg, 2016) reading development, and as a result, family risk is generally considered a robust predictor of reading outcome. We also found a longitudinal effect of pre-reading auditory and speech processing on later word

reading skills. Poor thresholds of both RTD and SPIN measured in kindergarten were predictive of poor word reading outcome in third grade. By analogy, better auditory thresholds predicted better word reading outcome. Although some previous studies could not find direct links between RTD and reading (Johnson et al., 2009; Papadopoulos et al., 2012) or SPIN and reading (Miller et al., 2018; Vanvooren et al., 2017), the results of the current study are in line with other research reporting involvement of auditory factors in reading development. For example, cross-sectional studies in school-aged children reported an association between RTD and reading (Corriveau et al., 2007) and between SPIN and reading (Ziegler et al., 2009). The cross-sectional design of these studies limited their analyses to concurrent associations, but the findings have been extended in longitudinal studies starting at the pre-reading stage and following up children throughout their reading development. Consistent with our longitudinal results, these latter studies found direct effects of pre-reading RTD (Law et al., 2017; Plakas et al., 2013) and pre-reading SPIN (Boets et al., 2008, 2011; Vandewalle et al., 2012; White-Schwoch et al., 2015) on later reading outcome.

Compared to the extensive literature reporting auditory and speech processing links to reading, structural properties of pre-reading auditory cortex in relation to reading outcome are less documented. To the best of our knowledge, only two studies with small samples sizes looked at properties of HG specifically at the pre-reading stage in relation to the development of dyslexia. Children who later developed dyslexia demonstrated pre-reading thinner cortex (Clark et al., 2014) and a higher local curvature perpendicular to the cortex (also known as gyrification index; Kuhl et al., 2020) in left HG. Regarding the former study (Clark et al., 2014), methodological concerns have been described that challenge their conclusions (Kraft et al., 2015; Ramus et al., 2018). Other studies investigating properties of HG in school-aged children and adults with dyslexia reported lower left volume (Xia et al., 2016), lower left and right volume (Serrallach et al., 2016), higher right thickness (Ma et al., 2015), or no differences in cortical thickness (Altarelli et al., 2014; Skeide et al., 2018). In sum, findings still vary a lot across studies, both with regard to the specific properties of HG and the direction of findings. Our results confirm a predictive role of auditory cortex anatomy in reading outcome, beyond a binary classification of typical versus poor reading skills, by showing predictive effects on later reading outcome measured continuously. More specifically, we found that pre-reading surface area of the left first TTG (including the posterior branch of common stem duplications, regardless of the length of the intermediate sulcus, when present) positively predicted later reading outcome.

Additional gyri of TTG (posterior to the first TTG), which are part of the PT, have also been a subject of investigation in dyslexia research, as previous studies have shown a higher likelihood of full posterior duplications in this reading disorder. Notably, the automatic toolbox for segmenting the TTG that we applied in the current study (TASH; Dalboni da Rocha et al., 2020), included quantification of the surface area of the gyri, but not of the non-gyrus portions of the superior temporal plane. Therefore, we looked at both the surface area of the additional TTG(s) posterior to the first TTG segmented by TASH and at the surface area of the PT segmented by FreeSurfer. Our analyses showed that the surface area of left and right PT was positively predictive of later reading outcome. Interestingly, surface area of additional TTG(s) did not predict word reading, even though there is some anatomical overlap between the surface area of additional TTG(s) and PT. This suggests that the relationship with reading is driven by the variation in the PT itself, as opposed to merely the surface area of the gyri. However, it could also be that a relationship for the PT was easier to detect since surface area of the PT is larger compared to the surface area of only the gyri. Together, our results showing predictive strength of variations in TTG and PT anatomy suggest that there may also be other

brain functional as well as functional and/or structural connectivity differences within networks including these regions that are crucial to the development of a healthy reading network. Functional brain imaging studies suggest that HG is primarily involved in the processing of low-level auditory information and that the PT is involved in speech sound processing (Griffiths & Warren, 2002; Hickok & Poeppel, 2007). However, the role of PT is still debated and could also involve top-down processes from higher-order regions such as the inferior frontal gyrus, inferior parietal cortex, superior temporal sulcus, and middle temporal gyrus (Davis et al., 2011; Friederici, 2012; Golestani et al., 2013; Rutten et al., 2019).

As described above, we found a positive relationship with reading of both surface area of the left first TTG and of the left PT. This is in line with results of Xia et al. (2016), who found lower gray matter volume of both HG and PT in children with dyslexia. However, it is interesting that Serrallach et al. (2016) reported a different pattern in children with dyslexia, with gray matter volume of PT having an inverse effect compared to HG. While both cross-sectional studies included participants in the same age range (age 10 and older), there were large differences in their analyses approach, which could have contributed to this inconsistency. On the one hand, Xia et al. (2016) first performed a whole brain, voxel-based analysis and then investigated significant clusters. This resulted in several clusters, of which one spanned HG and PT, but which did not specifically distinguish between the two regions. On the other hand, Serrallach et al. (2016) applied a semiautomated method to segment HG and PT specifically, which is a more reliable method for differentiating the effects arising from HG from those arising from the PT. In the current longitudinal study, we do not find the inverse effect, indicating that greater pre-reading surface area of both the left first TTG and of the left PT can be beneficial for later word reading performance.

With regard to the duplication patterns of the TTG(s), we found a significant positive correlation between pre-reading left TTG(s) duplication patterns and third grade word reading. Greater left TTG(s) duplications in kindergarten were associated with better third grade word reading. This relationship is in line with other research reporting that the presence of two or more gyri is more common in language aptitude and in musical expertise (Benner et al., 2017; Dalboni da Rocha et al., 2023; Golestani et al., 2011; Schneider et al., 2009; Turker et al., 2019). However, it does not explain why, on average, studies have reported more duplications in children (Altarelli et al., 2014; Serrallach et al., 2016) and in adults with dyslexia (Leonard et al., 2001). Notably, this relationship did not survive in the mediation model where family risk was also included. We speculate that including family risk caused a decrease in this effect. However, given the p value ($p = 0.056$) in our analyses, it would be of interest to examine the effect of TTG(s) duplication patterns in future research by applying statistical inference such as Bayesian statistics that would allow quantification of evidence in favor of or against the null hypothesis (Dienes, 2014).

Nevertheless, the effects of the auditory cortex anatomy (both surface area and duplication patterns) further corroborate our results showing that pre-reading auditory and speech processing play a role in the prediction of later word reading outcome, consistent with recent theoretical accounts of reading development, such as the intergenerational multiple deficit model (IMDM; van Bergen et al., 2014). In this model, it is posited that the interplay between multiple factors at multiple levels, including the processing of auditory information and neural properties, underlie the development of severe reading difficulties (dyslexia). Such dynamic interrelations are not only involved in atypical reading development, but also assumed to also exist for the entire distribution of reading abilities in the general population (van Atteveldt et al., 2021). According to these theoretical models, and supported by recent molecular genetic studies (Doust et al., 2022), genetics are also important to consider.

Mediation of the Family Risk–Reading Relationship

We investigated whether the large effect of family risk on later reading described above was mediated by any of the kindergarten auditory (cortex) measures by applying mediation analyses in a relatively large sample that had varying degrees of family risk. Family risk had a significant effect on pre-reading RTD and SPIN, in agreement with findings of neurophysiological studies suggesting a contribution of family risk to auditory processing (van der Leij et al., 2013). Although RTD and SPIN in turn had a significant effect on later reading (see Predictors of Reading Outcome, above), neither RTD nor SPIN significantly mediated the effect of family risk on reading. The proportion mediated by RTD or SPIN was very small (9%) and not significant in light of the very large direct effect of family risk on reading. Thus, while predisposition for reading difficulties seems to be related to how well people can process auditory input and degraded speech input, this relationship does not seem to contribute more generally to reading outcome. This could be because additional processes come into play to compensate for auditory and degraded speech processing, for example, processes involving harnessing top-down resources to compensate for degraded bottom-up input (Giraud & Ramus, 2013; Mattys et al., 2012). Arguably, processing skills that are related more closely to reading outcomes, such as phonological processing skills, are more likely to mediate the family risk–reading relationship. Although it was not within the scope of the current study, we did check post hoc whether pre-reading phonological processing (measured using syllable- and phoneme-level tasks) had a mediating role (see Supplementary Table 4b). Results of this supplementary analysis did not reveal mediation by these measures, in contrast to the findings of van Bergen et al. (2015).

Further, we found no evidence that family risk predicted any of the kindergarten neuroanatomical measures. By extension, these measures also did not play a mediating role in the family risk–reading relationship. This was unexpected in light of previous studies suggesting a relationship between family risk and brain structural differences in auditory and temporal cortices beyond HG (Beelen et al., 2019; Vanderauwera et al., 2018; note that our participants partly overlapped with these previous studies). Surface area of the left first TTG, left PT, and right PT in kindergarten did predict third grade word reading, as discussed in Predictors of Reading Outcome (above), indicating that these measures were related to reading independently of family risk.

It is noteworthy that family risk and surface area of the left PT correlated negatively and significantly, and that the parameter estimate within the mediation model was larger in absolute value compared to the estimates of the family risk paths to the other neuroanatomical measures. However, this relationship was not significant in the mediation model. Arguably, the measure we used to estimate the putative predisposition-driven contributions in our mediation analyses, though valid, is only an indirect proxy of genetic risk. We assessed family risk for dyslexia using the continuous outcome of a parental self-report questionnaire. We chose an indirect measure for its time- and cost-efficiency, and because it has been shown to be an adequate proxy for the heritability of reading skills (Swagerman et al., 2017), as well as a valid alternative for parents' actual reading skills (Khanolainen et al., 2023). We recognize the need for replication using direct genetic data compiled in polygenic risk scores (Belsky & Harden, 2019) or by applying the familial control method as proposed by Hart et al. (2021), since our measure of family risk confounds influences of environment and genetics (Hart et al., 2021). Furthermore, our family risk measure captures information about the parents' current and past reading behavior, which might be more closely related to their offspring's behavioral outcomes than to properties of the auditory cortex. Thus, it remains unknown whether a similar pattern of results would be present when indexing family risk using a parental brain measure, as

Polygenic risk scores:
An estimate of genetic risk based on the combined effects of multiple genetic variants.

suggested by previous studies looking at the structure of other regions in the reading network (Fehlbaum et al., 2022), connectivity within the reading network (Vandermosten, Schevenels, et al., 2020), and sulcal patterns across the whole brain (Ahtam et al., 2021).

Overall, the absence of mediation effects in the current study is consistent with an additive risk model, indicating that the auditory processing and auditory cortex measures contribute to reading independently from family risk (Bishop, 2006, 2013). Other unmeasured behavioral and neural mediators, especially in interaction with each other (Galaburda et al., 2006; Giraud & Ramus, 2013), might still contribute to the family risk–reading relationship. Phonological processing would be a reasonable alternative (van Bergen et al., 2015), although a supplementary analysis could not confirm this in the current study sample. Perhaps, given the indirect evidence for family risk effects in brain regions of the temporal cortex (Beelen et al., 2019; Łuniewska et al., 2019), other possible mediators include white matter connections in the neural reading network that pass through temporal regions such as the inferior fronto-occipital fasciculus (see, e.g., Vanderauwera et al., 2017; Vandermosten et al., 2017).

Methodological Considerations and Recommendations

Apart from our indirect family risk measure discussed above, some other methodological considerations of the current study are also important to address. First, we looked to elucidate which regions of the auditory cortex specifically related to later reading, using different auditory cortex measures (surface area and duplication patterns) of both HG and the PT. While exploratory, we found small significant effects in a study sample that was relatively large compared to previous studies looking at pre-reading auditory cortex in relation to reading. Nevertheless, we acknowledge the need for replication in independent samples in order to demonstrate the robustness of these findings, especially given the challenges that come with pediatric brain imaging (Turesky et al., 2021). The development of large publicly available data sets such as the ABCD Data Repository (Casey et al., 2018) is very promising for this purpose, but currently, large-scale longitudinal data sets that include both behavioral and brain measures starting in the pre-reading stage are still lacking.

Myelination:
Refers to the myelin sheaths around neurons that allow for faster and more efficient neural transmission.

Second, since auditory processing relies on efficient processing of temporal information, we do not rule out putative mediation through other structural features, such as the microstructural property of myelination, which is known to facilitate efficient processing (Long et al., 2018). It has been suggested that myelination and white matter more generally are in part responsible for predicting individual differences in non-speech processing (Warrier et al., 2009) and reading skill (Marie et al., 2018), and myelination differences have been found in the auditory cortex of adults with and without dyslexia (Skeide et al., 2018). In addition, the myelination differences found in two of the studies described above (Marie et al., 2018; Skeide et al., 2018) were localized to the PT. Finally, although PT surface area asymmetry did not correlate with third grade reading outcome in the current study, this neural measure did correlate positively with family risk (higher family risk associated with a more rightward lateralization, see Supplementary Table 2). Taken together with findings of altered PT asymmetries in relation to family risk (Vanderauwera et al., 2018) and dyslexia (Altarelli et al., 2014; Galaburda et al., 1985; Sanchez Bloom et al., 2013), and findings of altered HG to PT volume ratios in dyslexia (Serrallach et al., 2016), mediation of the family risk–reading relationship cannot be ruled out entirely. Extension of our approach to regions beyond those examined in the current study and to neural measures such as myelination and functional activation could benefit the understanding of the complex interplay between the relative influences of predisposition and of the environment on different levels, as described in the IMDM, involved during reading development.

CONCLUSION

In conclusion, we found predictive effects of pre-reading auditory and speech processing and of auditory cortex anatomy on later word reading outcome. Even though we also found some evidence for family risk effects on these pre-reading auditory measures, they did not mediate the strong relationship between family risk and later reading. This study contributes to understanding to what extent auditory measures are involved in reading acquisition. As such, it may help to guide future research, to ultimately help clinicians in achieving early identification of and intervention for children at risk for severe reading difficulties.

AUTHOR CONTRIBUTIONS

Lauren Blockmans: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Software; Visualization; Writing – original draft; Writing – review & editing. **Narly Golestani**: Conceptualization; Formal analysis; Methodology; Software; Supervision; Writing – review & editing. **Josué Luiz Dalboni da Rocha**: Formal analysis; Software; Writing – review & editing. **Jan Wouters**: Conceptualization; Funding acquisition; Resources; Supervision; Writing – review & editing. **Pol Ghesquière**: Conceptualization; Funding acquisition; Resources; Supervision; Writing – review & editing. **Maaike Vandermosten**: Conceptualization; Funding acquisition; Methodology; Resources; Supervision; Writing – review & editing.

DATA AND CODE AVAILABILITY STATEMENT

The analyses script and anonymized data sheet are available at the Open Science Framework (osf.io/vk8tx).

REFERENCES

Ahtam, B., Turesky, T. K., Zöllei, L., Standish, J., Grant, P. E., Gaab, N., & Im, K. (2021). Intergenerational transmission of cortical sulcal patterns from mothers to their children. *Cerebral Cortex*, *31*(4), 1888–1897. https://doi.org/10.1093/cercor/bhaa328, PubMed: 33230560

Altarelli, I., Leroy, F., Monzalvo, K., Fluss, J., Billard, C., Dehaene-Lambertz, G., Galaburda, A. M., & Ramus, F. (2014). Planum temporale asymmetry in developmental dyslexia: Revisiting an old question. *Human Brain Mapping, 35*(12), 5717–5735. https://doi.org/10.1002/hbm.22579, PubMed: 25044828

Andreola, C., Mascheretti, S., Belotti, R., Ogliari, A., Marino, C., Battaglia, M., & Scaini, S. (2021). The heritability of reading and reading-related neurocognitive components: A multi-level meta-analysis. *Neuroscience and Biobehavioral Reviews, 121*, 175–200. https://doi.org/10.1016/j.neubiorev.2020.11.016, PubMed: 33246020

Astle, D. E., Holmes, J., Kievit, R., & Gathercole, S. E. (2022). Annual Research Review: The transdiagnostic revolution in neurodevelopmental disorders. *Journal of Child Psychology and Psychiatry, 63*(4), 397–417. https://doi.org/10.1111/jcpp.13481, PubMed: 34296774

Beelen, C., Vanderauwera, J., Wouters, J., Vandermosten, M., & Ghesquière, P. (2019). Atypical gray matter in children with dyslexia before the onset of reading instruction. *Cortex*, *121*, 399–413. https://doi.org/10.1016/j.cortex.2019.09.010, PubMed: 31704534

Belsky, D. W., & Harden, K. P. (2019). Phenotypic annotation: Using polygenic scores to translate discoveries from genome-wide association studies from the top down. *Current Directions in Psychological Science*, *28*(1), 82–90. https://doi.org/10.1177/0963721418807729

Benner, J., Wengenroth, M., Reinhardt, J., Stippich, C., Schneider, P., & Blatow, M. (2017). Prevalence and function of Heschl's gyrus morphotypes in musicians. *Brain Structure and Function*, *222*(8), 3587–3603. https://doi.org/10.1007/s00429-017-1419-x, PubMed: 28397108

Bishop, D. V. M. (2006). Developmental cognitive genetics: How psychology can inform genetics and vice versa. *Quarterly Journal of Experimental Psychology*, *59*(7), 1153–1168. https://doi.org/10.1080/17470210500489372, PubMed: 16769616

Bishop, D. V. M. (2013). Cerebral asymmetry and language development: Cause, correlate, or consequence? *Science*, *340*(6138), Article 1230531. https://doi.org/10.1126/science.1230531, PubMed: 23766329

Blockmans, L., Kievit, R., Wouters, J., Ghesquière, P., & Vandermosten, M. (2023). Dynamics of cognitive predictors during reading acquisition in a sample of children overrepresented for dyslexia risk. *Developmental Science*. Advance online publication. https://doi.org/10.1111/desc.13412, PubMed: 37219071

Blumenthal, J. D., Zijdenbos, A., Molloy, E., & Giedd, J. N. (2002). Motion artifact in magnetic resonance imaging: Implications for automated analysis. *NeuroImage*, *16*(1), 89–92. https://doi.org/10.1006/nimg.2002.1076, PubMed: 11969320

Boets, B., Ghesquière, P., van Wieringen, A., & Wouters, J. (2007). Speech perception in preschoolers at family risk for dyslexia: Relations with low-level auditory processing and phonological ability. *Brain and Language*, *101*(1), 19–30. https://doi.org/10.1016/j.bandl.2006.06.009, PubMed: 16887179

Boets, B., Vandermosten, M., Poelmans, H., Luts, H., Wouters, J., & Ghesquière, P. (2011). Preschool impairments in auditory processing and speech perception uniquely predict future reading problems. *Research in Developmental Disabilities*, *32*(2), 560–570. https://doi.org/10.1016/j.ridd.2010.12.020, PubMed: 21236633

Boets, B., Wouters, J., van Wieringen, A., & Ghesquière, P. (2006). Auditory temporal information processing in preschool children at family risk for dyslexia: Relations with phonological abilities and developing literacy skills. *Brain and Language*, *97*(1), 64–79. https://doi.org/10.1016/j.bandl.2005.07.026, PubMed: 16112723

Boets, B., Wouters, J., van Wieringen, A., de Smedt, B., & Ghesquière, P. (2008). Modelling relations between sensory processing, speech perception, orthographic and phonological ability, and literacy achievement. *Brain and Language*, *106*(1), 29–40. https://doi.org/10.1016/j.bandl.2007.12.004, PubMed: 18207564

Boets, B., Wouters, J., van Wieringen, A., & Ghesquière, P. (2007). Auditory processing, speech perception and phonological ability in pre-school children at high-risk for dyslexia: A longitudinal study of the auditory temporal processing theory. *Neuropsychologia*, *45*(8), 1608–1620. https://doi.org/10.1016/j.neuropsychologia.2007.01.009, PubMed: 17303197

Brus, T., & Voeten, M. (1999). *Eén-minuut-test (EMT)*. Harcourt.

Calcus, A., Hoonhorst, I., Colin, C., Deltenre, P., & Kolinsky, R. (2018). The "rowdy classroom problem" in children with dyslexia: A review. In T. Lachmann & T. Weis (Eds.), *Reading and dyslexia* (pp. 183–211). Springer. https://doi.org/10.1007/978-3-319-90805-2_10

Casey, B. J., Cannonier, T., Conley, M. I., Cohen, A. O., Barch, D. M., Heitzeg, M. M., Soules, M. E., Teslovich, T., Dellarco, D. V., Garavan, H., Orr, C. A., Wager, T. D., Banich, M. T., Speer, N. K., Sutherland, M. T., Riedel, M. C., Dick, A. S., Bjork, J. M., Thomas, K. M., … Dale, A. M. (2018). The Adolescent Brain Cognitive Development (ABCD) study: Imaging acquisition across 21 sites. *Developmental Cognitive Neuroscience*, *32*, 43–54. https://doi.org/10.1016/j.dcn.2018.03.001, PubMed: 29567376

Chyl, K., Fraga-González, G., Brem, S., & Jednoróg, K. (2021). Brain dynamics of (a)typical reading development—A review of longitudinal studies. *NPJ Science of Learning*, *6*(1), Article 4. https://doi.org/10.1038/s41539-020-00081-5, PubMed: 33526791

Clark, K. A., Helland, T., Specht, K., Narr, K. L., Manis, F. R., Toga, A. W., & Hugdahl, K. (2014). Neuroanatomical precursors of dyslexia identified from pre-reading through to age 11. *Brain*, *137*(12), 3136–3141. https://doi.org/10.1093/brain/awu229, PubMed: 25125610

Clayton, F. J., West, G., Sears, C., Hulme, C., & Lervåg, A. (2020). A longitudinal study of early reading development: Letter-sound knowledge, phoneme awareness and RAN, but not letter-sound integration, predict variations in reading development. *Scientific Studies of Reading*, *24*(2), 91–107. https://doi.org/10.1080/10888438.2019.1622546

Corriveau, K. H., Goswami, U., & Thomson, J. M. (2010). Auditory processing and early literacy skills in a preschool and kindergarten population. *Journal of Learning Disabilities*, *43*(4), 369–382. https://doi.org/10.1177/0022219410369071, PubMed: 20457882

Corriveau, K. [H.], Pasquini, E., & Goswami, U. (2007). Basic auditory processing skills and specific language impairment: A new look at an old hypothesis. *Journal of Speech, Language, and Hearing Research*, *50*(3), 647–666. https://doi.org/10.1044/1092-4388(2007/046), PubMed: 17538107

Dalboni da Rocha, J. L., Kepinska, O., Schneider, P., Benner, J., Degano, G., Schneider, L., & Golestani, N. (2023). Multivariate Concavity Amplitude Index (MCAI) for characterizing Heschl's gyrus shape. *NeuroImage*, *272*, Article 120052. https://doi.org/10.1016/j.neuroimage.2023.120052, PubMed: 36965861

Dalboni da Rocha, J. L., Schneider, P., Benner, J., Santoro, R., Atanasova, T., Van De Ville, D., & Golestani, N. (2020). TASH: Toolbox for the Automated Segmentation of Heschl's Gyrus. *Scientific Reports*, *10*, Article 3887. https://doi.org/10.1038/s41598-020-60609-y, PubMed: 32127593

Davis, M. H., Ford, M. A., Kherif, F., & Johnsrude, I. S. (2011). Does semantic context benefit speech understanding through "top–down" processes? evidence from time-resolved sparse fMRI. *Journal of Cognitive Neuroscience*, *23*(12), 3914–3932. https://doi.org/10.1162/jocn_a_00084, PubMed: 21745006

Destrieux, C., Fischl, B., Dale, A., & Halgren, E. (2010). Automatic parcellation of human cortical gyri and sulci using standard anatomical nomenclature. *NeuroImage*, *53*(1), 1–15. https://doi.org/10.1016/j.neuroimage.2010.06.010, PubMed: 20547229

Dienes, Z. (2014). Using Bayes to get the most out of non-significant results. *Frontiers in Psychology*, *5*, Article 781. https://doi.org/10.3389/fpsyg.2014.00781, PubMed: 25120503

Doust, C., Fontanillas, P., Eising, E., Gordon, S. D., Wang, Z., Alagöz, G., Molz, B., 23andMe Research Team, Quantitative Trait Working Group of the GenLang Consortium, St Pourcain, B., Francks, C., Marioni, R. E., Zhao, J., Paracchini, S., Talcott, J. B., Monaco, A. P., Stein, J. F., Gruen, J. R., Olson, R. K., …

Luciano, M. (2022). Discovery of 42 genome-wide significant loci associated with dyslexia. *Nature Genetics*, *54*(11), 1621–1629. https://doi.org/10.1038/s41588-022-01192-y, PubMed: 36266505

Duncan, G. J., & Magnuson, K. (2012). Socioeconomic status and cognitive functioning: Moving from correlation to causation. *Wiley Interdisciplinary Reviews: Cognitive Science, 3*(3), 377–386. https://doi.org/10.1002/wcs.1176, PubMed: 26301469

Eckert, M. A., & Leonard, C. M. (2000). Structural imaging in dyslexia: The planum temporale. *Mental Retardation and Developmental Disabilities Research Reviews, 6*(3), 198–206. https://doi.org/10.1002/1098-2779(2000)6:3<198::AID-MRDD7>3.0.CO;2-1, PubMed: 10982497

Erbeli, F., Rice, M., & Paracchini, S. (2022). Insights into dyslexia genetics research from the last two decades. *Brain Sciences, 12*(1), Article 27. https://doi.org/10.3390/brainsci12010027, PubMed: 35053771

Fehlbaum, L. V., Peters, L., Dimanova, P., Roell, M., Borbás, R., Ansari, D., & Raschle, N. M. (2022). Mother-child similarity in brain morphology: A comparison of structural characteristics of the brain's reading network. *Developmental Cognitive Neuroscience, 53*, Article 101058. https://doi.org/10.1016/j.dcn.2022.101058, PubMed: 34999505

Fischl, B. (2012). FreeSurfer. *NeuroImage, 62*(2), 774–781. https://doi.org/10.1016/j.neuroimage.2012.01.021, PubMed: 22248573

Francart, T., van Wieringen, A., & Wouters, J. (2008). APEX 3: A multi-purpose test platform for auditory psychophysical experiments. *Journal of Neuroscience Methods, 172*(2), 283–293. https://doi.org/10.1016/j.jneumeth.2008.04.020, PubMed: 18538414

Friederici, A. D. (2012). The cortical language circuit: From auditory perception to sentence comprehension. *Trends in Cognitive Sciences, 16*(5), 262–268. https://doi.org/10.1016/j.tics.2012.04.001, PubMed: 22516238

Galaburda, A. M., LoTurco, J., Ramus, F., Fitch, R. H., & Rosen, G. D. (2006). From genes to behavior in developmental dyslexia. *Nature Neuroscience, 9*(10), 1213–1217. https://doi.org/10.1038/nn1772, PubMed: 17001339

Galaburda, A. M., Sherman, G. F., Rosen, G. D., Aboitiz, F., & Geschwind, N. (1985). Developmental dyslexia: Four consecutive patients with cortical anomalies. *Annals of Neurology, 18*(2), 222–233. https://doi.org/10.1002/ana.410180210, PubMed: 4037763

Gennatas, E. D., Avants, B. B., Wolf, D. H., Satterthwaite, T. D., Ruparel, K., Ciric, R., Hakonarson, H., Gur, R. E., & Gur, R. C. (2017). Age-related effects and sex differences in gray matter density, volume, mass, and cortical thickness from childhood to young adulthood. *Journal of Neuroscience, 37*(20), 5065–5073. https://doi.org/10.1523/JNEUROSCI.3550-16.2017, PubMed: 28432144

Genon, S., Eickhoff, S. B., & Kharabian, S. (2022). Linking interindividual variability in brain structure to behaviour. *Nature Reviews Neuroscience, 23*(5), 307–318. https://doi.org/10.1038/s41583-022-00584-7, PubMed: 35365814

Gerrits, E., & de Bree, E. (2009). Early language development of children at familial risk of dyslexia: Speech perception and production. *Journal of Communication Disorders, 42*(3), 180–194. https://doi.org/10.1016/j.jcomdis.2008.10.004, PubMed: 19100994

Gignac, G. E., & Szodorai, E. T. (2016). Effect size guidelines for individual differences researchers. *Personality and Individual Differences, 102*, 74–78. https://doi.org/10.1016/j.paid.2016.06.069

Gilmore, J. H., Knickmeyer, R. C., & Gao, W. (2018). Imaging structural and functional brain development in early childhood. *Nature Reviews Neuroscience, 19*(3), 123–137. https://doi.org/10.1038/nrn.2018.1, PubMed: 29449712

Giraud, A.-L., & Ramus, F. (2013). Neurogenetics and auditory processing in developmental dyslexia. *Current Opinion in Neurobiology, 23*(1), 37–42. https://doi.org/10.1016/j.conb.2012.09.003, PubMed: 23040541

Golestani, N., Hervais-Adelman, A., Obleser, J., & Scott, S. K. (2013). Semantic versus perceptual interactions in neural processing of speech-in-noise. *NeuroImage, 79*, 52–61. https://doi.org/10.1016/j.neuroimage.2013.04.049, PubMed: 23624171

Golestani, N., Molko, N., Dehaene, S., LeBihan, D., & Pallier, C. (2007). Brain structure predicts the learning of foreign speech sounds. *Cerebral Cortex, 17*(3), 575–582. https://doi.org/10.1093/cercor/bhk001, PubMed: 16603709

Golestani, N., Price, C. J., & Scott, S. K. (2011). Born with an ear for dialects? Structural plasticity in the expert phonetician brain. *Journal of Neuroscience, 31*(11), 4213–4220. https://doi.org/10.1523/JNEUROSCI.3891-10.2011, PubMed: 21411662

Goswami, U. (2011). A temporal sampling framework for developmental dyslexia. *Trends in Cognitive Sciences, 15*(1), 3–10. https://doi.org/10.1016/j.tics.2010.10.001, PubMed: 21093350

Goswami, U. (2022). Language acquisition and speech rhythm patterns: An auditory neuroscience perspective. *Royal Society Open Science, 9*(7), Article 211855. https://doi.org/10.1098/rsos.211855, PubMed: 35911192

Goswami, U., Huss, M., Mead, N., & Fosker, T. (2021). Auditory sensory processing and phonological development in high IQ and exceptional readers, typically developing readers, and children with dyslexia: A longitudinal study. *Child Development, 92*(3), 1083–1098. https://doi.org/10.1111/cdev.13459, PubMed: 32851656

Grasby, K. L., Jahanshad, N., Painter, J. N., Colodro-Conde, L., Bralten, J., Hibar, D. P., Lind, P. A., Pizzagalli, F., Ching, C. R. K., McMahon, M. A. B., Shatokhina, N., Zsembik, L. C. P., Thomopoulos, S. I., Zhu, A. H., Strike, L. T., Agartz, I., Alhusaini, S., Almeida, M. A. A., Alnæs, D., ... Medland, S. E. (2020). The genetic architecture of the human cerebral cortex. *Science, 367*(6484), Article eaay6690. https://doi.org/10.1126/science.aay6690, PubMed: 32193296

Griffiths, T. D., & Warren, J. D. (2002). The planum temporale as a computational hub. *Trends in Neurosciences, 25*(7), 348–353. https://doi.org/10.1016/S0166-2236(02)02191-4, PubMed: 12079762

Hakvoort, B., van der Leij, A., Maurits, N., Maassen, B., & van Zuijen, T. L. (2015). Basic auditory processing is related to familial risk, not to reading fluency: An ERP study. *Cortex, 63*, 90–103. https://doi.org/10.1016/j.cortex.2014.08.013, PubMed: 25243992

Hämäläinen, J. A., Salminen, H. K., & Leppänen, P. H. T. (2013). Basic auditory processing deficits in dyslexia: Systematic reviews of the behavioral and event-related potential/field evidence. *Journal of Learning Disabilities, 46*(5), 413–427. https://doi.org/10.1177/0022219411436213, PubMed: 22323280

Hart, S. A., Little, C., & van Bergen, E. (2021). Nurture might be nature: Cautionary tales and proposed solutions. *NPJ Science of Learning, 6*(1), Article 2. https://doi.org/10.1038/s41539-020-00079-z, PubMed: 33420086

Hervais-Adelman, A., Moser-Mercer, B., Murray, M. M., & Golestani, N. (2017). Cortical thickness increases after simultaneous interpretation training. *Neuropsychologia, 98*, 212–219.

https://doi.org/10.1016/j.neuropsychologia.2017.01.008, PubMed: 28077311

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, *8*(5), 393–402. https://doi.org/10.1038/nrn2113, PubMed: 17431404

Hoeft, F., & Hancock, R. (2017). Intergenerational transmission of reading and reading brain networks. In A. Galaburda, N. Gaab, F. Hoeft, & P. McCardle (Eds.), *Dyslexia and neuroscience: The Geschwind-Galaburda hypothesis, 30 years later* (1st ed., pp. 167–176). Paul H. Brookes.

Hugdahl, K., Heiervang, E., Ersland, L., Lundervold, A., Steinmetz, H., & Smievoll, A. I. (2003). Significant relation between MR measures of planum temporale area and dichotic processing of syllables in dyslexic children. *Neuropsychologia*, *41*(6), 666–675. https://doi.org/10.1016/S0028-3932(02)00224-5, PubMed: 12591024

Hulshoff Pol, H. E., Schnack, H. G., Posthuma, D., Mandl, R. C. W., Baaré, W. F., van Oel, C., van Haren, N. E., Collins, D. L., Evans, A. C., Amunts, K., Bürgel, U., Zilles, K., de Geus, E., Boomsma, D. I., & Kahn, R. S. (2006). Genetic contributions to human brain morphology and intelligence. *Journal of Neuroscience*, *26*(40), 10235–10242. https://doi.org/10.1523/JNEUROSCI.1312-06.2006, PubMed: 17021179

Jha, S. C., Xia, K., Schmitt, J. E., Ahn, M., Girault, J. B., Murphy, V. A., Li, G., Wang, L., Shen, D., Zou, F., Zhu, H., Styner, M., Knickmeyer, R. C., & Gilmore, J. H. (2018). Genetic influences on neonatal cortical thickness and surface area. *Human Brain Mapping*, *39*(12), 4998–5013. https://doi.org/10.1002/hbm.24340, PubMed: 30144223

Johnson, E. P., Pennington, B. F., Lee, N. R., & Boada, R. (2009). Directional effects between rapid auditory processing and phonological awareness in children. *Journal of Child Psychology and Psychiatry*, *50*(8), 902–910. https://doi.org/10.1111/j.1469-7610.2009.02064.x, PubMed: 19298469

Kalashnikova, M., Goswami, U., & Burnham, D. (2018). Mothers speak differently to infants at-risk for dyslexia. *Developmental Science*, *21*(1), Article e12487. https://doi.org/10.1111/desc.12487, PubMed: 27785865

Khanolainen, D., Salminen, J., Eklund, K., Lerkkanen, M.-K., & Torppa, M. (2023). Intergenerational transmission of dyslexia: How do different identification methods of parental difficulties influence the conclusions regarding children's risk for dyslexia? *Reading Research Quarterly*, *58*(2), 220–239. https://doi.org/10.1002/rrq.482

Kline, R. B. (2011). Relative variances. In *Principles and practice of structural equation modeling* (3rd ed., pp. 67–68). Guilford.

Kort, W., Schittekatte, M., Dekker, P. H., Verhaeghe, P., Compaan, E. L., Bosmans, M., & Vermeir, G. (2005). *WISC-III NL Wechsler Intelligence Scale for Children. Handleiding en verantwoording*. Harcourt.

Kraft, I., Cafiero, R., Schaadt, G., Brauer, J., Neef, N. E., Müller, B., Kirsten, H., Wilcke, A., Boltze, J., Friederici, A. D., & Skeide, M. A. (2015). Cortical differences in preliterate children at familiar risk of dyslexia are similar to those observed in dyslexic readers. *Brain*, *138*(9), Article e378. https://doi.org/10.1093/brain/awv036, PubMed: 25701065

Kuhl, U., Neef, N. E., Kraft, I., Schaadt, G., Dörr, L., Brauer, J., Czepezauer, I., Müller, B., Wilcke, A., Kirsten, H., Emmrich, F., Boltze, J., Friederici, A. D., & Skeide, M. A. (2020). The emergence of dyslexia in the developing brain. *NeuroImage*, *211*, Article 116633. https://doi.org/10.1016/j.neuroimage.2020.116633, PubMed: 32061802

Kuppen, S., Huss, M., & Goswami, U. (2014). A longitudinal study of basic auditory processing and phonological skills in children with low IQ. *Applied Psycholinguistics*, *35*(6), 1109–1141. https://doi.org/10.1017/S0142716412000719

Landerl, K., Freudenthaler, H. H., Heene, M., de Jong, P. F., Desrochers, A., Manolitsis, G., Parrila, R., & Georgiou, G. K. (2019). Phonological awareness and rapid automatized naming as longitudinal predictors of reading in five alphabetic orthographies with varying degrees of consistency. *Scientific Studies of Reading*, *23*(3), 220–234. https://doi.org/10.1080/10888438.2018.1510936

Laneau, J., Boets, B., Moonen, M., van Wieringen, A., & Wouters, J. (2005). A flexible auditory research platform using acoustic or electric stimuli for adults and young children. *Journal of Neuroscience Methods*, *142*(1), 131–136. https://doi.org/10.1016/j.jneumeth.2004.08.015, PubMed: 15652626

Law, J. M., Vandermosten, M., Ghesquière, P., & Wouters, J. (2014). The relationship of phonological ability, speech perception, and auditory perception in adults with dyslexia. *Frontiers in Human Neuroscience*, *8*, Article 482. https://doi.org/10.3389/fnhum.2014.00482, PubMed: 25071512

Law, J. M., Vandermosten, M., Ghesquière, P., & Wouters, J. (2017). Predicting future reading problems based on pre-reading auditory measures: A longitudinal study of children with a familial risk of dyslexia. *Frontiers in Psychology*, *8*, Article 124. https://doi.org/10.3389/fpsyg.2017.00124, PubMed: 28223953

Lefly, D. L., & Pennington, B. F. (2000). Reliability and validity of the adult reading history questionnaire. *Journal of Learning Disabilities*, *33*(3), 286–296. https://doi.org/10.1177/002221940003300306, PubMed: 15505966

Leonard, C. M., Eckert, M. A., Lombardino, L. J., Oakland, T., Kranzler, J., Mohr, C. M., King, W. M., & Freeman, A. (2001). Anatomical risk factors for phonological dyslexia. *Cerebral Cortex*, *11*(2), 148–157. https://doi.org/10.1093/cercor/11.2.148, PubMed: 11208669

Leong, V., Hämäläinen, J., Soltész, F., & Goswami, U. (2011). Rise time perception and detection of syllable stress in adults with developmental dyslexia. *Journal of Memory and Language*, *64*(1), 59–73. https://doi.org/10.1016/j.jml.2010.09.003

Leppänen, P. H. T., Hämäläinen, J. A., Salminen, H. K., Eklund, K. M., Guttorm, T. K., Lohvansuu, K., Puolakanaho, A., & Lyytinen, H. (2010). Newborn brain event-related potentials revealing atypical processing of sound frequency and the subsequent association with later literacy skills in children with familial dyslexia. *Cortex*, *46*(10), 1362–1376. https://doi.org/10.1016/j.cortex.2010.06.003, PubMed: 20656284

Little, T. D. (2013). Covariate/control variables. In *Longitudinal structural equation modeling* (pp. 190–198). Guilford.

Long, P., Wan, G., Roberts, M. T., & Corfas, G. (2018). Myelin development, plasticity, and pathology in the auditory system. *Developmental Neurobiology*, *78*(2), 80–92. https://doi.org/10.1002/dneu.22538, PubMed: 28925106

Lövdén, M., Wenger, E., Mårtensson, J., Lindenberger, U., & Bäckman, L. (2013). Structural brain plasticity in adult learning and development. *Neuroscience and Biobehavioral Reviews*, *37*(9B), 2296–2310. https://doi.org/10.1016/j.neubiorev.2013.02.014, PubMed: 23458777

Łuniewska, M., Chyl, K., Dębska, A., Banaszkiewicz, A., Żelechowska, A., Marchewka, A., Grabowska, A., & Jednoróg, K. (2019). Children with dyslexia and familial risk for dyslexia present atypical development of the neuronal phonological network. *Frontiers in Neuroscience*, *13*, Article 1287. https://doi.org/10.3389/fnins.2019.01287, PubMed: 31849595

Ma, Y., Koyama, M. S., Milham, M. P., Castellanos, F. X., Quinn, B. T., Pardoe, H., Wang, X., Kuzniecky, R., Devinsky, O., Thesen,

T., & Blackmon, K. (2015). Cortical thickness abnormalities associated with dyslexia, independent of remediation status. *NeuroImage: Clinical*, *7*, 177–186. https://doi.org/10.1016/j.nicl.2014.11.005, PubMed: 25610779

Marie, D., & Golestani, N. (2017). Brain structural imaging of receptive speech and beyond: A review of current methods. *Language, Cognition and Neuroscience*, *32*(7), 870–890. https://doi.org/10.1080/23273798.2016.1250926

Marie, D., Jobard, G., Crivello, F., Perchey, G., Petit, L., Mellet, E., Joliot, M., Zago, L., Mazoyer, B., & Tzourio-Mazoyer, N. (2015). Descriptive anatomy of Heschl's gyri in 430 healthy volunteers, including 198 left-handers. *Brain Structure and Function*, *220*(2), 729–743. https://doi.org/10.1007/s00429-013-0680-x, PubMed: 24310352

Marie, D., Rutten, S., Marques, J., & Golestani, N. (2018). *Auditory cortex myelination abnormalities in dyslexia and relationships with reading performance* [Poster presentation]. Alpine Brain Meeting, Champéry, Switzerland.

Marin-Franch, I., Zychaluk, K., & Foster, D. H. (2012). *modelfree: Model-free estimation of a psychometric function*. R package (Version 1.1-1) [Software]. https://cran.r-project.org/package=modelfree

Mårtensson, J., Eriksson, J., Bodammer, N. C., Lindgren, M., Johansson, M., Nyberg, L., & Lövdén, M. (2012). Growth of language-related brain areas after foreign language learning. *NeuroImage*, *63*(1), 240–244. https://doi.org/10.1016/j.neuroimage.2012.06.043, PubMed: 22750568

Mattys, S. L., Davis, M. H., Bradlow, A. R., & Scott, S. K. (2012). Speech recognition in adverse conditions: A review. *Language and Cognitive Processes*, *27*(7–8), 953–978. https://doi.org/10.1080/01690965.2012.705006

Miller, G., Lewis, B., Benchek, P., Buss, E., & Calandruccio, L. (2018). Masked speech recognition and reading ability in school-age children: Is there a relationship? *Journal of Speech, Language, and Hearing Research*, *61*(3), 776–788. https://doi.org/10.1044/2017_JSLHR-H-17-0279, PubMed: 29507949

Miranda, A., & Sousa, N. (2018). Maternal hormonal milieu influence on fetal brain development. *Brain and Behavior*, *8*(2), Article e00920. https://doi.org/10.1002/brb3.920, PubMed: 29484271

Noordenbos, M. W., Segers, E., Serniclaes, W., Mitterer, H., & Verhoeven, L. (2012). Allophonic mode of speech perception in Dutch children at risk for dyslexia: A longitudinal study. *Research in Developmental Disabilities*, *33*(5), 1469–1483. https://doi.org/10.1016/j.ridd.2012.03.021, PubMed: 22522205

Oldfield, R. C. (1971). Assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4, PubMed: 5146491

Ozernov-Palchik, O., & Gaab, N. (2016). Tackling the "dyslexia paradox": Reading brain and behavior for early markers of developmental dyslexia. *Wiley Interdisciplinary Reviews: Cognitive Science*, *7*(2), 156–176. https://doi.org/10.1002/wcs.1383, PubMed: 26836227

Palomar-García, M. Á., Hernández, M., Olcina, G., Adrián-Ventura, J., Costumero, V., Miró-Padilla, A., Villar-Rodríguez, E., & Ávila, C. (2020). Auditory and frontal anatomic correlates of pitch discrimination in musicians, non-musicians, and children without musical training. *Brain Structure and Function*, *225*(9), 2735–2744. https://doi.org/10.1007/s00429-020-02151-1, PubMed: 33029708

Papadopoulos, T. C., Georgiou, G. K., & Parrila, R. K. (2012). Low-level deficits in beat perception: Neither necessary nor sufficient for explaining developmental dyslexia in a consistent orthography. *Research in Developmental Disabilities*, *33*(6), 1841–1856. https://doi.org/10.1016/j.ridd.2012.04.009, PubMed: 22695074

Pardoe, H. R., Kucharsky Hiess, R., & Kuzniecky, R. (2016). Motion and morphometry in clinical and nonclinical populations. *NeuroImage*, *135*, 177–185. https://doi.org/10.1016/j.neuroimage.2016.05.005, PubMed: 27153982

Penhune, V. B., Zatorre, R. J., MacDonald, J. D., & Evans, A. C. (1996). Interhemispheric anatomical differences in human primary auditory cortex: Probabilistic mapping and volume measurement from magnetic resonance scans. *Cerebral Cortex*, *6*(5), 661–672. https://doi.org/10.1093/cercor/6.5.661, PubMed: 8921202

Peterson, R., Arnett, A. B., Pennington, B. F., Byrne, B., Samuelsson, S., & Olson, R. K. (2018). Literacy acquisition influences children's rapid automatized naming. *Developmental Science*, *21*(3), Article e12589. https://doi.org/10.1111/desc.12589, PubMed: 28812316

Plakas, A., van Zuijen, T. L., van Leeuwen, T., Thomson, J. M., & van der Leij, A. (2013). Impaired non-speech auditory processing at a pre-reading age is a risk-factor for dyslexia but not a predictor: An ERP study. *Cortex*, *49*(4), 1034–1045. https://doi.org/10.1016/j.cortex.2012.02.013, PubMed: 22542727

Poelmans, H., Luts, H., Vandermosten, M., Boets, B., Ghesquière, P., & Wouters, J. (2011). Reduced sensitivity to slow-rate dynamic auditory information in children with dyslexia. *Research in Developmental Disabilities*, *32*(6), 2810–2819. https://doi.org/10.1016/j.ridd.2011.05.025, PubMed: 21645986

Quinn, J. M., Spencer, M., & Wagner, R. K. (2015). Individual differences in phonological awareness and their role in learning to read. In P. Afflerbach (Ed.), *Handbook of individual differences in reading* (pp. 80–92). Routledge.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Ramus, F., Altarelli, I., Jednoróg, K., Zhao, J., & Scotto di Covella, L. (2018). Neuroanatomy of developmental dyslexia: Pitfalls and promise. *Neuroscience and Biobehavioral Reviews*, *84*, 434–452. https://doi.org/10.1016/j.neubiorev.2017.08.001, PubMed: 28797557

Ramus, F., Rosen, S., Dakin, S. C., Day, B. L., Castellote, J. M., White, S., & Frith, U. (2003). Theories of developmental dyslexia: Insights from a multiple case study of dyslexic adults. *Brain*, *126*(4), 841–865. https://doi.org/10.1093/brain/awg076, PubMed: 12615643

Ressel, V., Pallier, C., Ventura-Campos, N., Díaz, B., Roessler, A., Ávila, C., & Sebastián-Gallés, N. (2012). An effect of bilingualism on the auditory cortex. *Journal of Neuroscience*, *32*(47), 16597–16601. https://doi.org/10.1523/JNEUROSCI.1996-12.2012, PubMed: 23175815

Richardson, U., Leppänen, P. H. T., Leiwo, M., & Lyytinen, H. (2003). Speech perception of infants with high familial risk for dyslexia differ at the age of 6 months. *Developmental Neuropsychology*, *23*(3), 385–397. https://doi.org/10.1207/S15326942DN2303_5, PubMed: 12740192

Richardson, U., Thomson, J. M., Scott, S. K., & Goswami, U. (2004). Auditory processing skills and phonological representation in dyslexic children. *Dyslexia*, *10*(3) 215–233. https://doi.org/10.1002/dys.276, PubMed: 15341199

Robitzsch, A. (2020). Why ordinal variables can (almost) always be treated as continuous variables: Clarifying assumptions of robust continuous and ordinal factor analysis estimation methods. *Frontiers in Education*, *5*, Article 589965. https://doi.org/10.3389/feduc.2020.589965

Ronan, L., Voets, N., Rua, C., Alexander-Bloch, A., Hough, M., Mackay, C., Crow, T. J., James, A., Giedd, J. N., & Fletcher, P. C. (2014). Differential tangential expansion as a mechanism for cortical gyrification. *Cerebral Cortex*, *24*(8), 2219–2228. https://doi.org/10.1093/cercor/bht082, PubMed: 23542881

Rosen, S. (2003). Auditory processing in dyslexia and specific language impairment: Is there a deficit? What is its nature? Does it explain anything? *Journal of Phonetics*, *31*(3–4), 509–527. https://doi.org/10.1016/S0095-4470(03)00046-9

Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, *48*(2), 1–36. https://doi.org/10.18637/jss.v048.i02

Rutten, S., Santoro, R., Hervais-Adelman, A., Formisano, E., & Golestani, N. (2019). Cortical encoding of speech enhances task-relevant acoustic information. *Nature Human Behaviour*, *3*(9), 974–987. https://doi.org/10.1038/s41562-019-0648-9, PubMed: 31285622

Sanchez Bloom, J., Garcia-Barrera, M. A., Miller, C. J., Miller, S. R., & Hynd, G. W. (2013). Planum temporale morphology in children with developmental dyslexia. *Neuropsychologia*, *51*(9), 1684–1692. https://doi.org/10.1016/j.neuropsychologia.2013.05.012, PubMed: 23707683

Schaer, M., Cuadra, M. B., Tamarit, L., Lazeyras, F., Eliez, S., & Thiran, J.-P. (2008). A surface-based approach to quantify local cortical gyrification. *IEEE Transactions on Medical Imaging*, *27*(2), 161–170. https://doi.org/10.1109/TMI.2007.903576, PubMed: 18334438

Schneider, P., Andermann, M., Wengenroth, M., Goebel, R., Flor, H., Rupp, A., & Diesch, E. (2009). Reduced volume of Heschl's gyrus in tinnitus. *NeuroImage*, *45*(3), 927–939. https://doi.org/10.1016/j.neuroimage.2008.12.045, PubMed: 19168138

Schneider, P., Scherg, M., Dosch, H. G., Specht, H. J., Gutschalk, A., & Rupp, A. (2002). Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. *Nature Neuroscience*, *5*(7), 688–694. https://doi.org/10.1038/nn871, PubMed: 12068300

Schneider, P., Sluming, V., Roberts, N., Scherg, M., Goebel, R., Specht, H. J., Dosch, H. G., Bleeck, S., Stippich, C., & Rupp, A. (2005). Structural and functional asymmetry of lateral Heschl's gyrus reflects pitch perception preference. *Nature Neuroscience*, *8*(9), 1241–1247. https://doi.org/10.1038/nn1530, PubMed: 16116442

Seither-Preisler, A., Parncutt, R., & Schneider, P. (2014). Size and synchronization of auditory cortex promotes musical, literacy, and attentional skills in children. *Journal of Neuroscience*, *34*(33), 10937–10949. https://doi.org/10.1523/JNEUROSCI.5315-13.2014, PubMed: 25122894

Serrallach, B., Groß, C., Bernhofs, V., Engelmann, D., Benner, J., Gündert, N., Blatow, M., Wengenroth, M., Seitz, A., Brunner, M., Seither, S., Parncutt, R., Schneider, P., & Seither-Preisler, A. (2016). Neural biomarkers for dyslexia, ADHD, and ADD in the auditory cortex of children. *Frontiers in Neuroscience*, *10*, Article 324. https://doi.org/10.3389/fnins.2016.00324, PubMed: 27471442

Shapleske, J., Rossell, S. L., Woodruff, P. W. R., & David, A. S. (1999). The planum temporale: A systematic, quantitative review of its structural, functional and clinical significance. *Brain Research Reviews*, *29*(1), 26–49. https://doi.org/10.1016/S0165-0173(98)00047-2, PubMed: 9974150

Skeide, M. A., Bazin, P. L., Trampel, R., Schäfer, A., Männel, C., von Kriegstein, K., & Friederici, A. D. (2018). Hypermyelination of the left auditory cortex in developmental dyslexia. *Neurology*, *90*(6), e492–e497. https://doi.org/10.1212/WNL.0000000000004931, PubMed: 29321232

Smith, S. D. (2011). Approach to epigenetic analysis in language disorders. *Journal of Neurodevelopmental Disorders*, *3*(4), 356–364. https://doi.org/10.1007/s11689-011-9099-y, PubMed: 22113455

Smits, C., & Houtgast, T. (2005). Results from the Dutch speech-in-noise screening test by telephone. *Ear and Hearing*, *26*(1), 89–95. https://doi.org/10.1097/00003446-200502000-00008, PubMed: 15692307

Snowling, M., Gallagher, A., & Frith, U. (2003). Family risk of dyslexia is continuous: Individual differences in the precursors of reading skill. *Child Development*, *74*(2), 358–373. https://doi.org/10.1111/1467-8624.7402003, PubMed: 12705560

Snowling, M., & Melby-Lervåg, M. (2016). Oral language deficits in familial dyslexia: A meta-analysis and review. *Psychological Bulletin*, *142*(5), 498–545. https://doi.org/10.1037/bul0000037, PubMed: 26727308

Steinmetz, H., Rademacher, J., Jäncke, L., Huang, Y., Thron, A., & Zilles, K. (1990). Total surface of temporoparietal intrasylvian cortex: Diverging left-right asymmetries. *Brain and Language*, *39*(3), 357–372. https://doi.org/10.1016/0093-934X(90)90145-7, PubMed: 2285859

Strike, L. T., Hansell, N. K., Couvy-Duchesne, B., Thompson, P. M., de Zubicaray, G. I., McMahon, K. L., & Wright, M. J. (2019). Genetic complexity of cortical structure: Differences in genetic and environmental factors influencing cortical surface area and thickness. *Cerebral Cortex*, *29*(3), 952–962. https://doi.org/10.1093/cercor/bhy002, PubMed: 29377989

Sutherland, M. E., Zatorre, R. J., Watkins, K. E., Hervé, P.-Y., Leonard, G., Pike, B. G., Witton, C., & Paus, T. (2012). Anatomical correlates of dynamic auditory processing: Relationship to literacy during early adolescence. *NeuroImage*, *60*(2), 1287–1295. https://doi.org/10.1016/j.neuroimage.2012.01.051, PubMed: 22266413

Swagerman, S. C., van Bergen, E., Dolan, C., de Geus, E. J. C., Koenis, M. M. G., Hulshoff Pol, H. E., & Boomsma, D. I. (2017). Genetic transmission of reading ability. *Brain and Language*, *172*, 3–8. https://doi.org/10.1016/j.bandl.2015.07.008, PubMed: 26300341

Theys, C., Wouters, J., & Ghesquière, P. (2014). Diffusion tensor imaging and resting-state functional MRI-scanning in 5- and 6-year-old children: Training protocol and motion assessment. *PLOS ONE*, *9*(4), Article e94019. https://doi.org/10.1371/journal.pone.0094019, PubMed: 24718364

Turesky, T. K., Vanderauwera, J., & Gaab, N. (2021). Imaging the rapidly developing brain: Current challenges for MRI studies in the first five years of life. *Developmental Cognitive Neuroscience*, *47*, Article 100893. https://doi.org/10.1016/j.dcn.2020.100893, PubMed: 33341534

Turker, S., & Reiterer, S. M. (2021). Brain, musicality, and language aptitude: A complex interplay. *Annual Review of Applied Linguistics*, *41*, 95–107. https://doi.org/10.1017/S0267190520000148

Turker, S., Reiterer, S. M., Schneider, P., & Seither-Preisler, A. (2019). Auditory cortex morphology predicts language learning potential in children and teenagers. *Frontiers in Neuroscience*, *13*, Article 824. https://doi.org/10.3389/fnins.2019.00824, PubMed: 31447639

Turker, S., Reiterer, S. M., Seither-Preisler, A., & Schneider, P. (2017). "When music speaks": Auditory cortex morphology as a neuroanatomical marker of language aptitude and musicality. *Frontiers in Psychology*, *8*, Article 2096. https://doi.org/10.3389/fpsyg.2017.02096, PubMed: 29250017

Turker, S., Seither-Preisler, A., & Reiterer, S. M. (2021). Examining individual differences in language learning: A neurocognitive

model of language aptitude. *Neurobiology of Language*, *2*(3), 389–415. https://doi.org/10.1162/nol_a_00042, PubMed: 37213255

Tzourio-Mazoyer, N., & Mazoyer, B. (2017). Variations of planum temporale asymmetries with Heschl's gyri duplications and association with cognitive abilities: MRI investigation of 428 healthy volunteers. *Brain Structure and Function*, *222*(6), 2711–2726. https://doi.org/10.1007/s00429-017-1367-5, PubMed: 28164245

van Atteveldt, N., Vandermosten, M., Weeda, W., & Bonte, M. (2021). How to capture developmental brain dynamics: Gaps and solutions. *NPJ Science of Learning*, *6*(1), Article 10. https://doi.org/10.1038/s41539-021-00088-6, PubMed: 33941785

van Bergen, E., Bishop, D., van Zuijen, T. L., & de Jong, P. F. (2015). How does parental reading influence children's reading? A study of cognitive mediation. *Scientific Studies of Reading*, *19*(5), 325–339. https://doi.org/10.1080/10888438.2015.1050103

van Bergen, E., van der Leij, A., & de Jong, P. F. (2014). The intergenerational multiple deficit model and the case of dyslexia. *Frontiers in Human Neuroscience*, *8*, Article 346. https://doi.org/10.3389/fnhum.2014.00346, PubMed: 24920944

Van den Borre, E., Denys, S., van Wieringen, A., & Wouters, J. (2021). The digit triplet test: A scoping review. *International Journal of Audiology*, *60*(12), 946–963. https://doi.org/10.1080/14992027.2021.1902579, PubMed: 33840339

Vanderauwera, J., Wouters, J., Vandermosten, M., & Ghesquière, P. (2017). Early dynamics of white matter deficits in children developing dyslexia. *Developmental Cognitive Neuroscience*, *27*, 69–77. https://doi.org/10.1016/j.dcn.2017.08.003, PubMed: 28823983

Vanderauwera, J., Altarelli, I., Vandermosten, M., De Vos, A., Wouters, J., & Ghesquière, P. (2018). Atypical structural asymmetry of the planum temporale is related to family history of dyslexia. *Cerebral Cortex*, *28*(1), 63–72. https://doi.org/10.1093/cercor/bhw348, PubMed: 29253247

van der Leij, A., van Bergen, E., van Zuijen, T. L., de Jong, P., Maurits, N., & Maassen, B. (2013). Precursors of developmental dyslexia: An overview of the longitudinal Dutch Dyslexia Programme study. *Dyslexia*, *19*(4), 191–213. https://doi.org/10.1002/dys.1463, PubMed: 24133035

Vandermosten, M., Correia, J., Vanderauwera, J., Wouters, J., Ghesquière, P., & Bonte, M. (2020). Brain activity patterns of phonemic representations are atypical in beginning readers with family risk for dyslexia. *Developmental Science*, *23*(1), Article e12857. https://doi.org/10.1111/desc.12857, PubMed: 31090993

Vandermosten, M., Cuynen, L., Vanderauwera, J., Wouters, J., & Ghesquière, P. (2017). White matter pathways mediate parental effects on children's reading precursors. *Brain and Language*, *173*, 10–19. https://doi.org/10.1016/j.bandl.2017.05.002, PubMed: 28558269

Vandermosten, M., Schevenels, K., Economou, M., & Hoeft, F. (2020). The influence of intergenerational transfer of white matter tracts on early reading development. *bioRxiv*. https://doi.org/10.1101/2020.10.09.333096

Vandewalle, E., Boets, B., Ghesquière, P., & Zink, I. (2012). Auditory processing and speech perception in children with specific language impairment: Relations with oral language and literacy skills. *Research in Developmental Disabilities*, *33*(2), 635–644. https://doi.org/10.1016/j.ridd.2011.11.005, PubMed: 22155538

Van Hirtum, T., Ghesquière, P., & Wouters, J. (2019). Atypical neural processing of rise time by adults with dyslexia. *Cortex*, *113*, 128–140. https://doi.org/10.1016/j.cortex.2018.12.006, PubMed: 30640141

Vanvooren, S., Poelmans, H., De Vos, A., Ghesquière, P., & Wouters, J. (2017). Do prereaders' auditory processing and speech perception predict later literacy? *Research in Developmental Disabilities*, *70*, 138–151. https://doi.org/10.1016/j.ridd.2017.09.005, PubMed: 28938227

van Wieringen, A., & Wouters, J. (2023). Lilliput: Speech perception in speech-weighted noise and in quiet in young children. *International Journal of Audiology*, *62*(8), 747–755. https://doi.org/10.1080/14992027.2022.2086491, PubMed: 35732012

van Zuijen, T. L., Plakas, A., Maassen, B. A. M, Been, P., Maurits, N. M., Krikhaar, E., van Driel, J., & van der Leij, A. (2012). Temporal auditory processing at 17 months of age is associated with preliterate language comprehension and later word reading fluency: An ERP study. *Neuroscience Letters*, *528*(1), 31–35. https://doi.org/10.1016/j.neulet.2012.08.058, PubMed: 22981882

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). Springer. https://doi.org/10.1007/978-0-387-21706-2

Verwimp, C., Vanden Bempt, F., Kellens, S., Economou, M., Vandermosten, M., Wouters, J., Ghesquière, P., & Vanderauwera, J. (2020). Pre-literacy heterogeneity in Dutch-speaking kindergartners: Latent profile analysis. *Annals of Dyslexia*, *70*(3), 275–294. https://doi.org/10.1007/s11881-020-00207-9, PubMed: 33074483

Von Economo, C., & Horn, L. (1930). Uber windungsrelief mabe und Rindenarchitektonic der supratemparalflache, ihre individuellen und seitenunterschiede. *Zeitschrift für die gesamte Neurologie und Psychiatrie*, *130*, 678–757. https://doi.org/10.1007/BF02865945

Warrier, C., Wong, P., Penhune, V., Zatorre, R., Parrish, T., Abrams, D., & Kraus, N. (2009). Relating structure to function: Heschl's gyrus and acoustic processing. *Journal of Neuroscience*, *29*(1), 61–69. https://doi.org/10.1523/JNEUROSCI.3489-08.2009, PubMed: 19129385

Wengenroth, M., Blatow, M., Heinecke, A., Reinhardt, J., Stippich, C., Hofmann, E., & Schneider, P. (2014). Increased volume and function of right auditory cortex as a marker for absolute pitch. *Cerebral Cortex*, *24*(5), 1127–1137. https://doi.org/10.1093/cercor/bhs391, PubMed: 23302811

White, T., Jansen, P. R., Muetzel, R. L., Sudre, G., El Marroun, H., Tiemeier, H., Qiu, A., Shaw, P., Michael, A. M., & Verhulst, F. C. (2018). Automated quality assessment of structural magnetic resonance images in children: Comparison with visual inspection and surface-based reconstruction. *Human Brain Mapping*, *39*(3), 1218–1231. https://doi.org/10.1002/hbm.23911, PubMed: 29206318

White-Schwoch, T., Woodruff Carr, K., Thompson, E. C., Anderson, S., Nicol, T., Bradlow, A. R., Zecker, S. G., & Kraus, N. (2015). Auditory processing in noise: A preschool biomarker for literacy. *PLOS Biology*, *13*(7), Article e1002196. https://doi.org/10.1371/journal.pbio.1002196, PubMed: 26172057

Winkler, A. M., Kochunov, P., Blangero, J., Almasy, L., Zilles, K., Fox, P. T., Duggirala, R., & Glahn, D. C. (2010). Cortical thickness or grey matter volume? The importance of selecting the phenotype for imaging genetics studies. *NeuroImage*, *53*(3), 1135–1146. https://doi.org/10.1016/j.neuroimage.2009.12.028, PubMed: 20006715

Wong, P. C. M., Warrier, C. M., Penhune, V. B., Roy, A. K., Sadehh, A., Parrish, T. B., & Zatorre, R. J. (2008). Volume of left Heschl's gyrus and linguistic pitch learning. *Cerebral Cortex*, *18*(4),

828–836. https://doi.org/10.1093/cercor/bhm115, PubMed: 17652466

Xia, Z., Hoeft, F., Zhang, L., & Shu, H. (2016). Neuroanatomical anomalies of dyslexia: Disambiguating the effects of disorder, performance, and maturation. *Neuropsychologia, 81*, 68–78. https://doi.org/10.1016/j.neuropsychologia.2015.12.003, PubMed: 26679527

Ziegler, J. C., Pech-Georgel, C., George, F., & Lorenzi, C. (2009). Speech-perception-in-noise deficits in dyslexia. *Developmental Science, 12*(5), 732–745. https://doi.org/10.1111/j.1467-7687.2009.00817.x, PubMed: 19702766

Zoellner, S., Benner, J., Zeidler, B., Seither-Preisler, A., Christiner, M., Seitz, A., Goebel, R., Heinecke, A., Wengenroth, M., Blatow, M., & Schneider, P. (2019). Reduced cortical thickness in Heschl's gyrus as an in vivo marker for human primary auditory cortex. *Human Brain Mapping, 40*(4), 1139–1154. https://doi.org/10.1002/hbm.24434, PubMed: 30367737