



Mother-child similarity in brain morphology: A comparison of structural characteristics of the brain's reading network

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ABSTRACT

Background: Substantial evidence acknowledges the complex gene-environment interplay impacting brain development and learning. Intergenerational neuroimaging allows the assessment of familial transfer effects on brain structure, function and behavior by investigating neural similarity in caregiver-child dyads.

Methods: Neural similarity in the human reading network was assessed through well-used measures of brain structure (i.e., surface area (SA), gyrification (IG), sulcal morphology, gray matter volume (GMV) and cortical thickness (CT)) in 69 mother-child dyads (children's age~11 y). Regions of interest for the reading network included left-hemispheric inferior frontal gyrus, inferior parietal lobe and fusiform gyrus. Mother-child similarity was quantified by correlation coefficients and familial specificity was tested by comparison to random adult-child dyads. Sulcal morphology analyses focused on occipitotemporal sulcus interruptions and similarity was assessed by chi-square goodness of fit.

Results: Significant structural brain similarity was observed for mother-child dyads in the reading network for IG, SA and GMV ($r = 0.349/0.534/0.542$, respectively), but not CT. Sulcal morphology associations were non-significant. Structural brain similarity in IG, SA and GMV were specific to mother-child pairs. Furthermore, structural brain similarity for SA and GMV was higher compared to CT.

Conclusion: Intergenerational neuroimaging techniques promise to enhance our knowledge of familial transfer effects on brain development and disorders.

1. Introduction

Substantial evidence demonstrates the intricate interplay between genetic predispositions and environmental factors during the development of complex human skills. An increase in research efforts which aim to disentangle shared and distinct genetic or environmental mechanisms impacting human brain development has been one result thereof. The novel technique of intergenerational neuroimaging promises unique insights into familial transfer effects on brain structure and function by neural similarity analyses of caregiver-child dyads (Yamagata et al., 2016). Intergenerational neuroimaging combines successful features of existing research designs (e.g., family studies, concordance models) to

further knowledge of mechanisms promoting brain development. The first studies directly investigating structural and functional brain similarity in parent-child dyads mostly focused on affective (Yamagata et al., 2016; Foland-Ross et al., 2015; Abraham et al., 2020; Colich et al., 2017; Wang et al., 2018) or cognitive trait transmission (Vandermosten et al., 2020; Takagi et al., 2021). For example, Foland-Ross and colleagues reported on structural brain similarity by means of cortical thickness in mother-child dyads with and without a history of depression (Foland-Ross et al., 2015). Similarly, intergenerational transfer effects were studied in developmental disorders, including parents and children with a familial risk for dyslexia (Vandermosten et al., 2020) or a diagnosis of attention deficit hyperactivity disorder (Poissant et al., 2014; Casey

Abbreviations: CT, cortical thickness; GMV, gray matter volume; IG, local gyrification; NN, neural network; SA, surface area.

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et al., 2007). Parent-child brain similarity is higher than that between randomly selected adult-child pairings, suggesting that the effects are, at least partially, of a familial nature (Takagi et al., 2021; Ahtam et al., 2021). Moreover, neural concordance designs have revealed sex-specific transmission patterns, for example for the corticolimbic tract, for which structural brain similarity was reported to be highest in mother-daughter dyads compared to mother-son, father-daughter or father-son (Yamagata et al., 2016).

Structural brain similarity may vary as a function of the brain metrics investigated. Regionally specific and measurement-dependent developmental trajectories must be considered (e.g., for volume, density and shape of gray and white matter structures). At birth, major anatomical features of an infant's brain are roughly formed, though molecular and genetic processes continue to refine brain structure postnatally (e.g., neurogenesis, apoptosis, pruning (Sanai et al., 2011)). Overall brain growth during the first two years of life is substantial. For some morphometrical measures postnatal changes remain smaller after the second year of life (e.g., surface area and gyrification). Cortical volume increases from 35% at birth to 80% of an adult's size at around two years of age (Gilmore et al., 2018). In line with this rapid cortical growth, surface area expands and gyrification increases, though the developmental rate for these measures is much slower from thereon. For example, local gyrification indices increase about 25% during the first two years of life (Li et al., 2014). From six years of age on, slower changes continue until adulthood (with regionally-specific in- or decreases (Mutlu et al., 2013)). On the other hand, some morphometric brain measures change more strongly over a protracted time, even into young adulthood (e.g., gray or white matter volume or cortical thickness). Total gray matter volume rapidly increases during the early postnatal phase, then continues to develop at a slower pace and starts decreasing around mid-childhood, while white matter gradually increases (Mills and Tamnes, 2018; Tooley et al., 2021). Notably, gray matter volume is a compound measure of cortical thickness and surface area, two ontogenetically and genetically distinct metrics (Mills and Tamnes, 2018; Kremen et al., 2013). Cortical volume is thus considered a product of two variables differentially affected by genetic or environmental processes. Consequently, a consideration of both warrants increased informative value over each individual one. During childhood and adolescence, cortical volume changes have been suggested to reflect variations in cortical thickness, especially cortical thinning during later childhood and adolescence, while white matter increases are hypothesized to result from continuing myelination and network formation (Mills and Tamnes, 2018; Kremen et al., 2013). Overall, brain maturational processes reach a peak only around 22–25 years of age (Mills and Tamnes, 2018).

In sum, our brain is the product of a myriad of intricate, interacting developmental processes and the precise underlying mechanisms driving these are still being discovered (Mills and Tamnes, 2018). Broadly, structural brain measures such as surface area, gyrification indices and sulcal morphology have been found to be more strongly formed in utero or during the early postnatal period, thus underlying an overall stricter genetic influence (Armstrong et al., 1995; Chi et al., 1977; Zilles et al., 1988; White et al., 2010). In contrast, structural brain correlates such as gray matter volume and cortical thickness continue to undergo more change across childhood and adolescence and are suggested to be more strongly impacted by environment, learning and experience (Ducharme et al., 2016; Giedd and Rapoport, 2010; Tamnes et al., 2017; Vijayakumar et al., 2016). While intergenerational neuroimaging may inform complex skill formation, different volume or surface-based metrics promise to hold distinct or shared informative value.

Whereas we acknowledge that white matter development and connectivity measures may significantly benefit the understanding of intergenerational transfer effects on brain structure in parent-child dyads (see for example (Vandermosten et al., 2020)), in line with other structural developmental neuroimaging studies (Backhausen

et al., 2021), we here focus on cortical brain correlates. Anatomical measures under investigation include local gyrification (IG: inner foldings, impacting surface area), surface area (SA: external area of cortical outer layer), sulcal morphology (characteristic folding or formation of the grooves surrounding a gyri), gray matter volume (GMV: density of brain cells; a product of cortical thickness and surface area), and cortical thickness (CT: thickness of cortical layer; Fig. 1).

To investigate structural brain similarity in mother-child dyads for one neural network example, we here focus on brain regions that have been reliably associated with reading and literacy, because it is likely that the neural network of reading is shaped by intergenerational transfer effects for the following reasons: First, learning to read is a pivotal skill, which is explicitly learnt and formally taught during childhood. Secondly, despite the need for formal teaching, reading and its precursors are impacted by genetic, environmental and interacting influences alike (Olson et al., 2011; Parrila et al., 2005). For example, reading skills are highly heritable as evidenced by twin studies (Hart et al., 2013) or family research (Gialluisi et al., 2020; Andreola et al., 2020; van Bergen et al., 2017). Furthermore, genetic nurturing effects are exemplified by observations of parental predispositions influencing a child's home literacy environment, parental engagement or socio-economic status (van Bergen et al., 2017; Hart et al., 2021; Hart et al., 2013; Bracken and Fischel, 2008; Phillips and Lonigan, 2005; Xia et al., 2020; Xia et al., 2020).

Neurally, skilled reading is supported by a left-hemispheric network of anterior and posterior brain regions including occipitotemporal, temporoparietal and inferior frontal areas (Dehaene and Cohen, 2011).

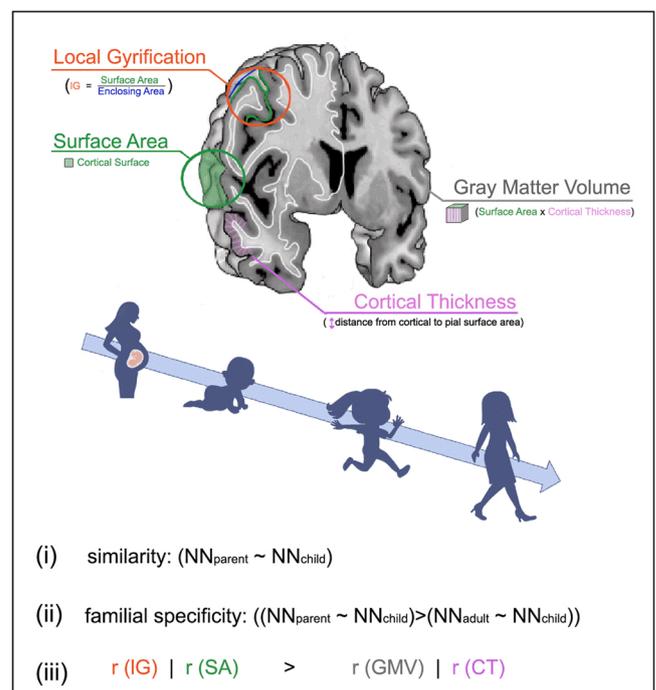


Fig. 1. Intergenerational transfer effects on neural networks (NN) for mother-child dyads are examined through structural brain similarity analyses using different anatomical brain metrics. This includes morphometrical correlates with a stronger genetic impact or early development, including local gyrification (IG) and surface area (SA), or a longer maturational trajectory of stronger impact by learning and experience across age, including gray matter volume (GMV) and cortical thickness (CT). Three main investigations of interest result: assessment of (i) structural similarity in mother-child dyads, (ii) familial specificity indicated by stronger similarity in mother-child dyads above random adult-child pairings, and (iii) variations in neural similarity in dependence of the metrics under investigation with higher similarity in structural correlates that develop earlier (IG, SA) as compared to metrics with a protracted maturational rate (CT, GMV).

Typical reading development is characterized by specialization in these regions reflected by functional and structural changes (Chyl et al., 2021; Frye et al., 2010; Houston et al., 2014; Torre and Eden, 2019). Structurally, measures of gyrification, surface area, cortical thickness and gray matter volume in areas of the reading network have been related to reading skills (Frye et al., 2010; Torre and Eden, 2019; Eckert et al., 2005; Kronbichler et al., 2008; Merz et al., 2020; Williams et al., 2018). Additionally, the presence of an interruption in the left occipitotemporal sulcus has been associated with better reading skills through increased connectivity strength between posterior and anterior regions of the reading network (Cachia et al., 2018). Finally, in individuals that struggle with reading (e.g., developmental dyslexia) structural alterations in the same areas have been reported (Frye et al., 2010; Eckert et al., 2005; Kronbichler et al., 2008; Williams et al., 2018; Beelen et al., 2019). Such alterations can even be detected prior to reading onset in children with a familial risk for reading disorders, highlighting potential genetic or early environmental contributions (Langer et al., 2017; Kraft et al., 2016; Raschle et al., 2017).

Here, first (i), we aim to test whether structural brain similarity in mother-child dyads exists, focusing on the left-hemispheric neural network (NN) for reading as one example and by using different morphometric brain measures ($NN_{\text{mother}} \sim NN_{\text{child}}$; Fig. 1), including IG, SA, GMV, CT and sulcal morphology, represented by the presence or absence of an interrupted occipitotemporal sulcus. Secondly (ii), we will test whether structural similarity measures reflect familial specificity by comparing mother-child dyads to random adult-child pairings ($(NN_{\text{mother}} \sim NN_{\text{child}}) > (NN_{\text{random adult}} \sim NN_{\text{child}})$). Thirdly (iii), we will test whether structural brain metrics expected to have a strong genetic component and a lower change rate during childhood and adolescence (i.e., local gyrification and surface area) show greater mother-child similarity compared to measures that are known to be more experience-dependent (i.e., gray matter volume and cortical thickness; $r_{IG|r_{SA}} > r_{GMV|r_{CT}}$). Noteworthy, the reading network is here used as one neural network example for testing structural similarity in mother-child dyads. Future investigations may employ similar analyses, but focus on other skills and brain networks known to be impacted by intergenerational transfer effects to varying degrees, including for example affect processing or the socioemotional network of the brain.

We hypothesize that mother-child dyads show familial transfer effects in brain structure within the neural network for reading as reflected by significant structural brain similarity for all metrics assessed. For sulcal morphology, we expect that children whose mothers have an interruption in the left occipitotemporal sulcus will be more likely to show an interruption themselves. Secondly, we predict neural similarity to be higher in mother-child dyads as compared to random adult-child pairings. Thirdly, we hypothesize neural similarity in the human reading network to vary depending on the structural brain correlate targeted (core metrics and hypotheses in Fig. 1).

2. Methods

Data analyses, aims and hypotheses were pre-registered on the Open Science Framework (see <https://osf.io/cf8wb> and <https://osf.io/5wbtv>).

2.1. Participants

A total number of 151 participants were tested at two sites. Overall, 81 child-mother dyads with anatomical scans in both mother and child were available. This number includes 70 mothers and 81 children, which is due to the assessment of 11 families with two children. For mothers with two children participating in the study, we included the child whose age and sex balanced those respective distributions best. Furthermore, one mother-child dyad had to be excluded due to behavioral problems and low IQ measures of the child ($IQ \leq 75$), resulting in a final sample of 69 mother-child dyads (children: 41♂, 28♀, age range

7–14 y, mean age = 11.13 ± 2.12 , 6 left-handed; mothers: age range 26–55 y, mean age = 42.60 ± 5.54 , 9 left-handed). All child participants had average or average-to-above-average IQ scores (mean verbal IQ = 112.15 ± 16.16 , mean non-verbal IQ = 110.65 ± 13.91 across both sites). To assess mothers' educational level, the International Standard Classification of Education (ISCED) was used. In this measure, educational levels are binned into categories from 1 to 8 (with 8 representing the highest possible degree = doctoral degree). The mothers in both samples ranged from completing high school to holding a doctoral degree. Educational scores were the only assessment of SES available in all participants. Group characteristics are reported in Table 1 (site-specific data in Supplementary Table 1). The ethnicity of the sample was predominantly white (91%), with some participants from Asian (5%), Hispanic (3%) and Canadian First Nations descent (1%). Due to poor data quality or technical problems, two dyads were excluded for SA, GMV and CT, three dyads for IG and one dyad for sulcal morphology analyses.

2.2. Testing procedure

All children and mothers were asked to participate in two testing appointments either at the facilities of the Department of Child and Adolescent Psychiatry and University Hospital in Basel, Switzerland, or at the Brain and Mind Institute at the University of Western Ontario, Canada. At both sites, behavioral assessments as well as neuroimaging data were obtained (functional neuroimaging data relevant for site-specific projects were also collected, but are not further discussed in the present analyses). The behavioral assessment included the collection of IQ measures using the Matrix Reasoning and Vocabulary subtests of the Wechsler Abbreviated Scale of Intelligence (Petermann and Petermann, 2011). Each site followed age-adequate and child-friendly neuroimaging protocols and all participants provided written consent (adults) or verbal assent and parental consent (children).

2.3. Structural neuroimaging (MRI acquisition parameters)

Whole-brain structural MPRAGE images were acquired on two SIEMENS 3 T Prisma MR scanners using a 20-channel head coil in Switzerland and a 32-channel head coil in Canada (transverse slice orientation, interleaved acquisition) using the following specifications: Voxel size: $1.0 \times 1.0 \times 1.0 \text{ mm}^3$; TR = 1900 ms (Switzerland) or 2300 ms (Canada); TE = 3.42 ms (Switzerland) or 2.98 ms (Canada); TA = 4.26 min (Switzerland) or 5.12 min (Canada); flip angle = 9 degrees; field of view = $256 \times 256 \text{ mm}^2$, 192 slices with a slice thickness of 1.00 mm.

Table 1
Behavioral characteristics of the sample.

N mother-child dyads		69
Sex (male/female)	Children	41/28
Handedness (left/right)	Children	6/63
	Mothers	9/60
Age (in years, mean±SD)	Children	11.13 ± 2.12
	Mothers	42.60 ± 5.54
Verbal IQ (mean±SD)	Children	112.15 ± 16.16 (N = 64)
	Mothers	111.91 ± 14.40 (N = 33)
Nonverbal IQ (mean±SD)	Children	110.65 ± 13.91 (N = 65)
	Mothers	105.27 ± 11.65 (N = 33)
ISCED (mean±SD)	Mothers	5.89 ± 1.65 (N = 65)

Note. SD = standard deviation, ISCED = International Standard Classification of Education, Verbal IQ = Vocabulary subscale / Nonverbal IQ = Matrix reasoning subscale of the WISC-IV (Switzerland) or WASI-2 (Canada)

2.4. Neuroimaging data analyses

2.4.1. Structural similarity of the reading network ($NN_{mother} \sim NN_{child}$)

2.4.1.1. Local gyrification, surface area, gray matter volume and cortical thickness. We assessed aim 1 via the following steps: First, standard preprocessing using the FreeSurfer software (<http://surfer.nmr.mgh.harvard.edu/>) was performed, followed by quality control and artefact detection. When inaccuracies in the automatic segmentation were detected (based on visual slice-by-slice inspection in axial, coronal and sagittal view by 3 raters), the preprocessed data were manually edited to correct delineation of the pial surface prior to being re-preprocessed. For each participant the manual correction procedure and the visual

inspection were repeated until sufficient quality of the delineations was assured. Second, the structural measures were extracted from hypothesis-driven regions of interest (ROIs) as based on core regions reported for the reading network using the Desikan-Killiany atlas (Beelen et al., 2019; Richlan et al., 2009). The ROIs included one prefrontal region of interest (i.e., the left-hemispheric pars opercularis of the inferior frontal gyrus) and two posterior regions (i.e., left inferior parietal lobe and left fusiform gyrus) depicted in Fig. 2A. A compound score for the reading network was built for each participant. The compound score consisted of sum scores across ROIs for SA and GMV, representing the full surface or volume across the whole network, and mean scores for the non-/one-dimensional measures of IG and CT measures (representing the average gyrification indices across the whole network or the

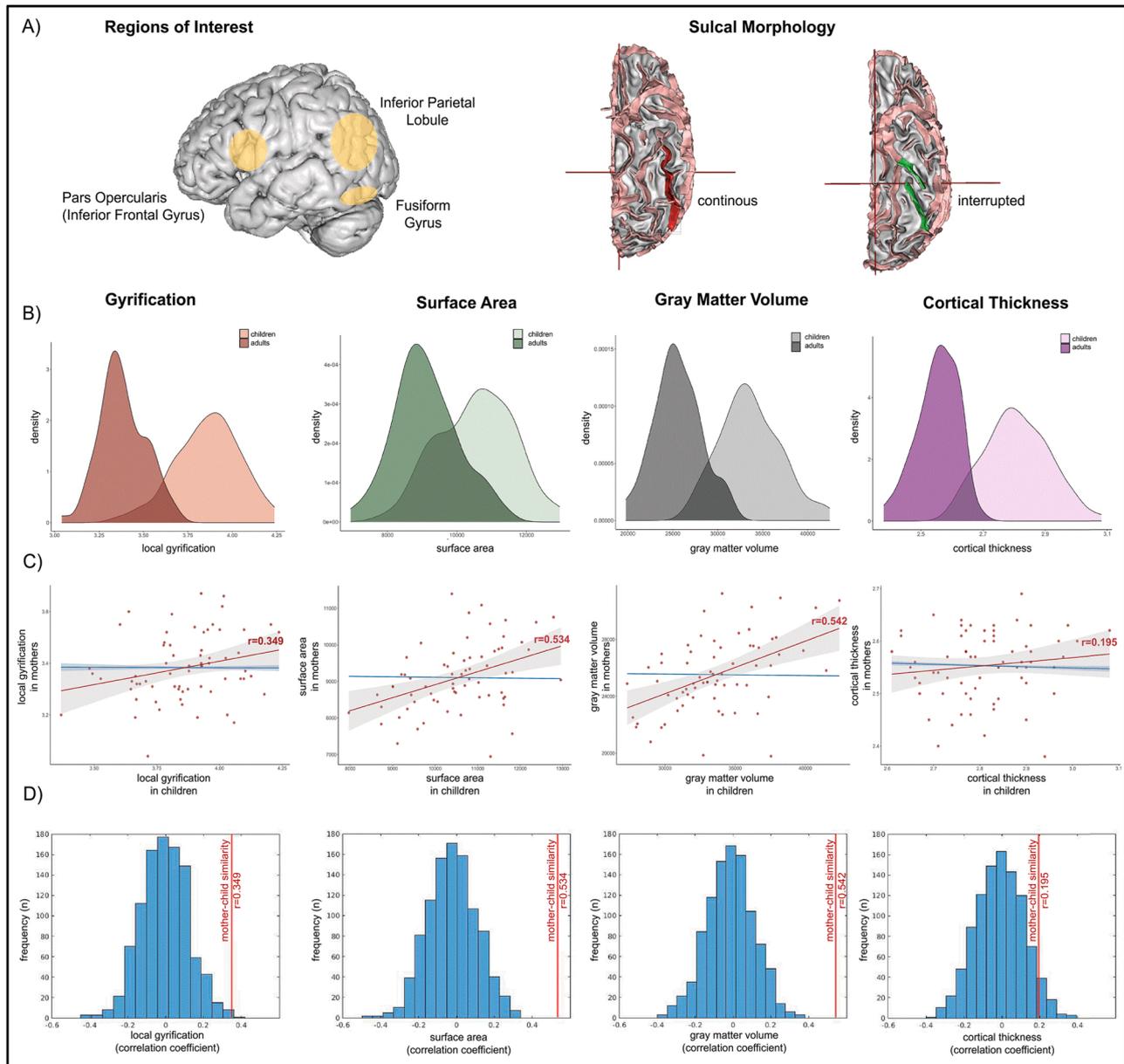


Fig. 2. Brain similarity in the human reading network in mother-child dyads. A) Regions of interest for the study of structural brain similarity in mother-child dyads in the human reading network (i.e., inferior frontal, parietal regions and fusiform gyrus; in yellow/left) and example images representing continuous (red/middle) and interrupted (green/right) occipitotemporal sulcus. B) Density plots for local gyrification, surface area, gray matter volume and cortical thickness for adults (darker shade) and children (lighter shade). C) Mother-child brain similarity (red line) and average random adult-child correlation (blue) for local gyrification, surface area, gray matter volume and cortical thickness of the human reading network. D) Distributions of the similarity coefficients of the 1000 iterations (blue bars) as well as the mother-child dyad similarity (vertical red line) for each structural brain feature. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

average cortical thickness; no further weighting applied). All scores for the full network and for each region individually are presented in [Supplementary Tables 2](#). Third, correlation coefficients for mother-child dyads were computed for all measures to examine the structural similarity of the reading network (Bonferroni corrected for multiple comparisons). Age and sex of the child and site of data collection were entered as covariates in all correlational analyses. Post-hoc control analyses were conducted to investigate the possibility that handedness or sibling selection criteria influenced our findings ([Supplementary Tables 3 and 4](#)).

2.4.1.2. Sulcal morphology. Sulcal morphology analyses focused on the left occipitotemporal sulcus. Analyses were performed using BrainVISA 4.5 software (<http://brainvisa.info/>). For sulcal characterization, the protocol set forth by Cachia and colleagues was used (Cachia et al., 2018). Three-dimensional mesh-based reconstructions of the cortical folds were created for all participants. Next, the left occipitotemporal sulcus was manually inspected and labelled by three co-authors (LVF, LP and MR). The sulcus was characterized as “interrupted” if it showed one or multiple interruptions and as “continuous” otherwise (Fig. 2A). To ensure sufficient data quality for this labelling procedure, one mother-child dyad was removed. A chi-square goodness of fit test performed in Jamovi (<https://www.jamovi.org>) was computed to assess whether the presence/absence of an interruption in mothers more frequently co-occurred with the presence/absence of an interruption in the child. To control for potential influences of (1) site of data collection, (2) age of the child, (3) sex of the child, (4) whether or not child and mother matched in terms of handedness, and (5) the average confidence score of the three investigators having characterized the sulci, logistic regressions were run in Jamovi. As a robustness check, we reran all analyses using the data of the excluded siblings with usable scans.

2.4.2. Familial specificity of structural similarity ($(NN_{mother} \sim NN_{child}) > (NN_{random\ adults} \sim NN_{child})$)

To assess **aim 2**, the investigation of familial specificity, significant structural similarity in the neural network (NN) of reading in mother-child dyads was compared to the structural brain similarity in randomly assigned adult-child dyads. The list of mothers was randomized 1000 times pairing each child with a randomly selected unrelated adult from the same site. The similarity coefficients of the 1000 iterations were computed for each of the measures independently, employing a Matlab (<https://www.mathworks.com/products/matlab.html>) permutation script. Finally, the resulting correlation coefficients for each measure were z-transformed, averaged and back-transformed to an average correlation coefficient representing random adult-child pairings. Comparison to similarity in mother-child dyads was tested by a report of Fisher’s z using *cocor* for independent groups (Diedenhofen and Musch, 2015).

2.4.3. Assessing differences in similarity measures ($(r_{IG}|r_{SA}) > (r_{GMV}|r_{CT})$)

To assess **aim 3**, the mother-child group correlation coefficients of IG, SA, GMV and CT were compared using *cocor* (Diedenhofen and Musch, 2015) through a test of significance for dependent, non-overlapping data to detect whether the correlations differ in magnitude (report of both Dunn and Clark’s z (Dunn and Clark, 1971) and Zou’s confidence intervals (Zou, 2007)).

3. Results

3.1. Structural similarity of the reading network

3.1.1. Surface area, local gyrification, gray matter volume and cortical thickness

Structural brain measures in mother-child dyads demonstrated significant similarity in the human reading network for IG ($r(61) = 0.349$,

$p = 0.005$), SA ($r(62) = 0.534$, $p < 0.001$) and GMV ($r(62) = 0.542$, $p < 0.001$). For CT, similarity analyses were not significant ($r(62) = 0.195$, $p = 0.122$; for all analyses reported, Bonferroni correction for multiple comparisons was applied ($p(\alpha_{\text{altered}}=0.05/4)=0.0125$). CT changes in posterior and anterior brain regions occur at different rates (e.g., prefrontal cortex is known to undergo significant variations until late adolescence (Vijayakumar et al., 2016)). To test whether similarity was impacted by areas maturing earlier or later, we conducted follow-up analyses on CT measures for all regions of interest independently. Significant similarity for CT in the left inferior parietal lobe ($r(62) = 0.389$, $p = 0.001$) was observed. All other correlations were non-significant (left inferior frontal gyrus: $r(62) = 0.132$, $p = 0.298$; left fusiform gyrus: $r(62) = 0.131$, $p = 0.303$). For completeness, post-hoc correlations between mothers and children for all structural measures and all ROIs are reported in [Supplementary Table 5](#).

3.1.2. Sulcal morphology

A chi-square analysis assessing similarity between children and mothers in the anatomical structure of the left occipitotemporal sulcus did not reach significance ($X^2(1) = 3.60$, $p = 0.058$). Logistic regressions were run to examine whether the presence or absence of a match in sulcal structure between mother and child could be predicted based on site of data collection, age of the child, sex of the child, mother-child handedness match and confidence ratings. These analyses did not yield any significant results (all p ’s > 0.365). Finally, rerunning these analyses after including the other set of siblings in the sample did not change our findings ($X^2(1) = 3.69$, $p = 0.055$).

3.2. Familial specificity of structural similarity

Similarity analyses for children and unrelated adult pairings are illustrated in the scatterplots and histograms in [Fig. 2C-D](#). The average similarity between pairings of random adults and children for local gyrification, surface area, gray matter volume and cortical thickness are as follows (IG ($r(61) = -0.004$, $p = 0.976$; SA ($r(62) = -0.023$, $p = 0.859$); GMV ($r(62) = -0.014$, $p = 0.914$; CT ($r(62) = -0.010$, $p = 0.939$). Overall mother-child similarity was higher for IG, SA and GMV when compared to random adult-child pairings ($z = 2.067$, $p = 0.039$; $z = 3.500$, $p = 0.001$; $z = 3.514$, $p < 0.001$, respectively), which was not the case for CT ($z = 1.176$, $p = 0.240$). Based on repeated resampling, there remained a chance for higher similarity in random adult-child pairings for CT and IG, (visualized in [Fig. 2D](#)). More specifically, in 5% of the iterations, similarity in random adult-child pairs was higher than the similarity in mother-child dyads for cortical thickness. Similarly, though only for 0.3% of the iterations, similarity for local gyrification was higher in random adult-child pairs than in the mother-child dyads.

3.3. Assessing differences in similarity measures

Comparison of correlation coefficients revealed significantly higher structural brain similarity in mother-child dyads for SA compared to CT ($z = 2.54$, $p = 0.011$, 95% CI [0.08, 0.60]), but not for SA and GMV ($z = -0.14$, $p = 0.886$, 95% CI [-0.13, 0.11]), IG and GMV ($z = -1.38$, $p = 0.167$, 95% CI [-0.47, 0.08]) and IG and CT ($z = 0.96$, $p = 0.338$, 95% CI [-0.160, 0.460]). While GMV is a function of CT and SA, similarity in GMV was present, though no CT similarity existed. As an additional analysis, correlation coefficients of GMV and CT were tested and revealed significant differences ($z = 2.42$, $p = 0.016$, 95% CI [0.06, 0.62]).

4. Discussion

We studied structural brain similarity for different morphometric correlates in mother-child dyads by use of intergenerational neuroimaging techniques, with a focus on the human reading network.

Significant structural brain similarity for mother-child dyads in the human reading network for measures of local gyrification, surface area and gray matter volume were identified, while cortical thickness and sulcal morphology associations were non-significant. The observed structural brain similarity in local gyrification, surface area and gray matter volume were found to be specific to mother-child pairs. Similarity within mother-child pairings was significantly more likely than similarity in random-adult child pairings. Finally, structural brain similarity in mother-child dyads for surface area was significantly larger than for cortical thickness, but similar for surface area compared to gray matter volume.

4.1. Similarity though lower interindividual variability in gyrification

Local gyrification, for which we identified significant mother-child similarity in the human reading network, has been suggested to be strongly genetically influenced and to reach early maturity. The structural transformation from lissencephalic to gyrencephalic brain already takes place during the third trimester in the mother's womb (Armstrong et al., 1995). At birth, all primary and secondary sulci and most of the tertiary sulci are present (Hill et al., 2010). In line with dynamic brain changes during the first two years of life, gyrification indices peak around toddlerhood, undergoing only modest changes afterwards (Raznahan et al., 2011). In healthy children and adults, increased gyrification in anterior and posterior brain regions relevant for reading (e.g., fusiform gyrus) have been positively associated with general cognitive skills (Gregory et al., 2016). Furthermore, altered gyrification within left-hemispheric reading regions has been reported for children and adults with a diagnosis of dyslexia (Williams et al., 2018; Casanova et al., 2004).

In line with behavioral studies indicating familial transfer effects on reading (Hart et al., 2013; van Bergen et al., 2017), we identified intergenerational transfer effects on gyrification of the human reading network. However, a small probability for similarity in random adult-child pairings remained. This observation may be explained by lower interindividual variability for gyrification across the regions of interests chosen. More specifically, research indicates high consistency in terms of sulcal position, orientation and appearance on a temporal scale across individuals (Ronan and Fletcher, 2015). While interindividual consistencies exist, longitudinal work including singletons, mono- and dizygotic twins revealed distinct subject-specific folding patterns (Duan et al., 2020). Namely, despite shared genes as well as similar pre- and postnatal environment in monozygotic twins, the intersubject variability in neonatal cortical folding allows for accurate individual identification at the age of 1 and 2 years (Duan et al., 2020). Such variability in cortical folding is region-specific. For example, unimodal regions (e.g., primary sensorimotor and auditory cortex) more proximal to primary sulci such as the central sulcus and the Sylvian fissure are associated with high heritability and low inter-individual variability. Contrariwise, higher-order association cortices (e.g., middle frontal gyrus, inferior temporal gyrus, part of the inferior and superior parietal cortex) demonstrate larger interindividual variability in cortical folding (Duan et al., 2020). It could thus be hypothesized that structural brain similarity in the reading network of mother-child dyads vary for individual regions. Such differences in the heritability between unimodal and higher-order multimodal regions remain to be investigated.

4.2. Familial specificity in correlates of surface area

Similar to gyrification, the brain's surface area has been reported to predominantly develop in utero or during the first two years of life and to be strongly genetically influenced (Armstrong et al., 1995; Zilles et al., 1988; White et al., 2010; Mangin et al., 2010; Tossier et al., 2018; Lyall et al., 2015). Past toddlerhood, surface area expansions are suggested to continue at a smaller rate of change until late childhood or

early adolescence, before decreasing slowly at a steady pace (Ducharme et al., 2016; Tamnes et al., 2017; Raznahan et al., 2011). Heritability in surface area is high, with genetic predispositions suggested to account for up to 89% of variance in surface area (Grasby et al., 2020; Panizzon et al., 2009; McKay et al., 2014). In line with this notion, we observed distinct mother-child similarities in the human reading network for measures of surface area.

Alterations in surface area have previously been associated with language or reading processes in adults with dyslexia (Frye et al., 2010), and can further be found in pre-reading children with a familial risk for dyslexia (Hosseini et al., 2013).

4.3. Familial specificity in gray matter similarity of the human reading network

Structural brain similarity in the human reading network was further detected for measures of gray matter volume, a structural metric with a protracted maturation, resulting in a relatively long opportunity for an impact of environment, experiences and learning. While gray matter volume has been the main target of investigation for many structural developmental neuroimaging studies, it has been recognized that gray matter volume constitutes a compound measure of surface area and cortical thickness, both underlying different genetic and environmental influences (Mills and Tamnes, 2018; Tooley et al., 2021; Vijayakumar et al., 2016; Grasby et al., 2020; Lenroot and Giedd, 2006). We here observed familial specificity in brain similarity of the human reading network for measures of surface area and gray matter volume, but not cortical thickness. Brain similarity in surface area and gray matter volume was furthermore significantly greater than similarity in cortical thickness. In adults, it has been suggested that most between-subject gray matter volume variability is explained by variability in surface area (Lenroot et al., 2009; Winkler et al., 2010), while within-subject variation is determined by variability in cortical thickness (Storsve et al., 2014). However, from childhood to adolescence and into young adulthood, cortical volume changes have been suggested to predominantly relate to variations in cortical thickness, especially thinning during later childhood and adolescence (Mills and Tamnes, 2018; Kremen et al., 2013). It must be noted that earlier studies have indicated an inverted U-shaped trajectory for cortical volume, with a peak only around late childhood/early adolescence (Giedd et al., 1999). New studies evidence cortical gray matter volume increases only for the first years of life and indicate an earlier start for linear gray matter volume decreases paralleled by cortical thinning (Mills et al., 2016; Norbom et al., 2021). Thus, we can speculate that the mother-child similarity in gray matter volume might vary over time reflecting the developmental changes in the children, impacted by genetic and environmental effects alike.

Longitudinal investigations of gray matter volume and reading proficiency in children with varying levels of reading proficiency show regional and age-specific variations (Linkersdörfer et al., 2015; Phan et al., 2021). Moreover, there is evidence for a late emerging association between reading skills and gray matter volume (Torre and Eden, 2019).

4.4. Cortical thickness similarity in inferior parietal lobe of the reading network

Developmental studies have suggested that cortical thickness increases until the age of two years are followed by cortical thinning between late childhood and early adulthood (Raznahan et al., 2011; Mills et al., 2021; Mills and Tamnes, 2014). Across development, linear, quadratic or cubic developmental trajectories exist, depending on the brain region under investigation (Mutlu et al., 2013; Ducharme et al., 2016; Raznahan et al., 2011; Wierenga et al., 2014). For example, Tamnes and colleagues report strongest cortical thinning (largest annual decrease in thickness) for the parietal lobe in participants ages 7–29 years (Tamnes et al., 2017). Cortical thickness changes have been

suggested to be driven by a combination of reduced synaptic and neural density as well as increasing myelination which are strongly impacted by learning, experience and environmental influences (Norbom et al., 2021; Zhang et al., 2013; Rakic et al., 1994; Piccolo et al., 2016; Petanjek et al., 2008).

Studies examining cortical thickness have further suggested a posterior-to-anterior temporal maturational gradient (Walhovd et al., 2016). Broadly, posterior measures stabilize earlier, while particularly prefrontal cortical thinning is accelerated during late adolescence (Teeuw et al., 2019). Similarly, associations between cortical thickness and reading skills were identified in young adults, but not beyond (Torre et al., 2020), possibly explaining why we found no similarity in cortical thickness in mother-child dyads for all regions of the reading network combined.

To test whether similarity was impacted by the network analyses of areas maturing earlier (i.e., posterior regions) or later (i.e., frontal areas) we conducted follow-up investigations on cortical thickness measures for inferior frontal, inferior parietal lobe and fusiform gyrus independently. These investigations revealed significant similarity in cortical thickness measures of the inferior parietal lobe, but not for inferior frontal lobe or fusiform gyrus. Such observations are in line with the notion of late-acting genetic factors suggested to promote local cortical thinning in areas including left fusiform gyrus and frontal regions but not the inferior parietal lobe (Teeuw et al., 2019). It could thus be speculated that regionally-specific heritable influences for prefrontal and fusiform regions only take place at a later age than the present group average, possibly paralleled by changes in mother-child similarity.

4.5. No similarity in sulcal morphology of the left occipitotemporal sulcus

As a final morphometric measure for structural brain similarity in the human reading network, we tested whether the presence/absence of an interruption in the occipitotemporal sulcus in mothers co-occurred with the presence/absence of an interruption in their children. This analysis did not reach significance, indicating no intergenerational transfer effect on sulcal interruption. Site, sex and age of the child, mother-child handedness match and rater's confidence were no significant predictors of mother-child matches in sulcal morphology. Past studies have indicated that reading ability is related to anatomical characteristics of the occipitotemporal sulcus: people having an interruption in the sulcus tend to display better reading skills (Cachia et al., 2018). Since the anatomical structure of brain sulci is thought to be determined in utero (Mangin et al., 2010) and therefore predominantly by genetic influences, we had hypothesized similarity in sulcal pattern between mothers and children. However, we do not have sufficient evidence for similarity in this metric, possibly due to low overall effects and sample size limitations for the given analyses.

4.6. Leveraging different informative value from various structural metrics

Developmental neuroimaging studies commonly report on a single structural brain measure, some of which are a product of varying genetic and environmental influences. Comparing different structural characteristics of the brain, including those that predominantly develop in utero and during the early postnatal stage (e.g., local gyrification, surface area, sulcal morphology) and those that continue to mature and are more strongly impacted by experience and learning (e.g., gray matter volume, cortical thickness) could be of particular interest, as this may provide an opportunity to disentangle genetic, environmental or their interactive effects on brain development and learning (Hart et al., 2021). Comparison of correlation coefficients for different structural brain metrics revealed significantly higher structural brain similarity in mother-child dyads for surface area compared to cortical thickness, but not for surface area compared to gray matter volume, or gyrification compared to gray matter volume or cortical thickness. In fact, similarity

in gray matter volume and surface area were comparable and both higher compared to cortical thickness. Research has indicated that measures of surface area remain relatively constant across development, whereas gray matter volume and cortical thickness may vary more, with cortical thinning being the major driver for gray matter reductions (Storsve et al., 2014). It could be speculated that expected variations in cortical thickness occurring during later childhood and adolescence may also affect gray matter volume similarity and that measures of similarity may also demonstrate region-, metric- and developmental stage-specific linear and non-linear trajectories. Whether similarity in different structural brain correlates of the human reading network changes over time, can only be revealed by larger-scale longitudinal studies that allow researchers to follow family members over a significant amount of time. In line with this, there are several limitations to the present investigation that warrant consideration.

4.7. Limitations

First, intergenerational neuroimaging studies require the recruitment, testing, and analysis of pooled data. The testing of several family members is challenging, and power considerations arise. While we recruited a relatively large number of families for participation (138 participants or 69 mother-child dyads), the participant count remains small for correlational analyses. For the intergenerational neuroimaging field to reach its potential, we expect open-science and data sharing initiatives to drive progress. Examples include initiatives such as the ENIGMA consortium (Thompson et al., 2020) or the 1000 Functional Connectomes Project (Biswal et al., 2010) (see (Klapwijk et al., 2020) for a review on increasing reproducibility and replicability in developmental neuroimaging). Secondly, site-related differences, including age differences, must be noted. Additionally, there were slight variations in the MRI acquisition protocol between sites. Although we controlled for age and site (and thereby acquisition protocol), the obtained results should be interpreted with caution and warrant larger scale replication. Thirdly, data was only obtained in mother-child dyads. While there is evidence highlighting maternal intergenerational transfer effects on brain structure and function (Yamagata et al., 2016) more research is needed. Studies incorporating larger pedigree designs including fathers and mothers, sons and daughters can explore sex-specific transmission and effects further. Additionally, investigations would be strengthened by the inclusion of biological and non-biological parents. Fourth, there is evidence for heritability of head movement during task-related fMRI (Engelhardt et al., 2017). Although we inspected structural brain data in the current project and all used scans survived an extensive quality assessment protocol, we cannot rule out remaining subtle head motion impacts and future studies should explore a genetic impact on head motion in parent-child dyads in more detail. Fifth, future studies on structural brain similarity would benefit tremendously from collecting behavioral data to explore whether brain similarity between mother-child dyads co-occurs with similarity in behavioral scores. In the current study for example, the availability of reading achievement data from both mothers and children could have shed light onto the link between structural brain metrics and behavior. Previous studies have indicated that reading skills in children and their parents are related (van Bergen et al., 2017), however, a simultaneous exploration of brain and behavior would further clarify the intergenerational transmission mechanisms at play. Sixth, future studies should consider longitudinal assessments to inform about development. In the example of reading, this may include pre-reading children and children with a familial risk for reading difficulties compared to those without (Raschle et al., 2011; Raschle et al., 2012). Such longitudinal designs may allow investigations of the effects of learning and experience on structural brain similarity. Finally, the mothers of our sample were on average highly educated (the average mother held a university/BA degree) and the ethnicity of our sample was predominantly white. This poses obvious limitations to the generalizability of the sample. Future studies should recruit a more

highly diverse sample of families.

4.8. Intergenerational neuroimaging: current state and prospects

Intergenerational approaches have been used in various contexts. However, the added value resulting from the inclusion of neurobiological variables, such as those obtained by MRI, only recently started to receive increased recognition (Takagi et al., 2021; Ho et al., 2016). The potential applicability of intergenerational neuroimaging techniques may be manifold. Neurodevelopmental disorders impacting a child's cognitive capabilities or mental health have a relatively high prevalence and result in significant personal, social and economic impact (Chakrabarti and Fombonne, 2005; Zablotzky et al., 2019). The pathogenesis of developmental disorders is complex, with environmental, biological, genetic and individual traits being in complex dynamic interaction. A single causal genetic variant is rarely identified for developmental disorders, but the driving mechanisms are commonly polygenic. Neurodevelopmental disorders are thus heterogeneous, have a biological origin, but are commonly diagnosed based on behavioral manifestations (Ismail and Shapiro, 2019). While genetic, epigenetic or environmental influences drive intergenerational transfer effects between parents and their children impacting the development of complex traits, such mechanisms are distant from observable phenotypes (Flint et al., 2014). The identification of suitable endophenotypes may provide a bridge between genetic predisposition and clinically relevant observations. Intergenerational neuroimaging may strengthen our understanding of the pathophysiology of different neurodevelopmental disorders and may ultimately inform about biological intervention targets or markers for treatment success (Ho et al., 2016; Flint et al., 2014).

Here we investigated structural brain similarity of the neural reading network in mother-child dyads. Like other cognitive skills (e.g., spelling and mathematics (Andreola et al., 2020; Hart et al., 2009) or general intelligence (Plomin et al., 2018)), reading is highly heritable (around 66% according to a recent meta-analysis (Andreola et al., 2020)). While some structural prerequisites are determined in utero or early in life, reading is a cultural invention which requires the brain to reshape itself to some extent for one to learn how to read (Dehaene, 2005). Successful reading acquisition thus derives from a complex interplay of genetics and environmental effects (including learning or teaching). To date, intergenerational neuroimaging has been employed in research on attention deficit hyperactivity disorder (Poissant et al., 2014; Casey et al., 2007), major depressive disorder (Yamagata et al., 2016; Foland-Ross et al., 2015), social anxiety disorder (Bas-Hoogendam et al., 2016; Bas-Hoogendam et al., 2020) or healthy individuals (Takagi et al., 2021; Ahtam et al., 2021). Notably, such techniques may be of interest in the study of various other neurodevelopmental or mental health disorders. Intergenerational neuroimaging may ultimately allow us to gain unprecedented insight linking complex biological mechanisms impacting brain development and skill acquisition.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dcn.2022.101058.

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