



HAL
open science

Prospective associations between maternal mind-mindedness, child theory of mind, and brain morphology in school-aged children

Elie Yutong Guo, Élizabel Leblanc, Fanny Dégeilh, Miriam Beauchamp, Annie Bernier

► To cite this version:

Elie Yutong Guo, Élizabel Leblanc, Fanny Dégeilh, Miriam Beauchamp, Annie Bernier. Prospective associations between maternal mind-mindedness, child theory of mind, and brain morphology in school-aged children. *Social Neuroscience*, 2023, pp.1-44. <10.1080/17470919.2023.2257882>. <hal-04216518>

HAL Id: hal-04216518

<https://hal.science/hal-04216518v1>

Submitted on 25 Sep 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY 4.0 - Attribution - International License

**Prospective Associations Between Maternal Mind-Mindedness, Child Theory of Mind, and
Brain Morphology in School-Aged Children**

Elie YuTong Guo¹, Élizabel Leblanc¹, Fanny Dégeilh^{1, 2, 3}, Miriam H. Beauchamp^{1, 2}, & Annie
Bernier¹

¹ Department of Psychology, University of Montreal, Montreal, Canada

² Sainte-Justine Research Center, Montreal, Canada

³ Present address: Univ Rennes, CNRS, Inria, Inserm, IRISA UMR 6074, EMPENN –ERL U
1228, Rennes, France

ORCID IDs.

Elie YuTong Guo: <https://orcid.org/0000-0002-3530-0084>

Élizabel Leblanc: <https://orcid.org/0000-0002-1258-2162>

Fanny Dégeilh: <https://orcid.org/0000-0002-5802-4975>

Miriam H. Beauchamp: <https://orcid.org/0000-0002-8637-6361>

Annie Bernier: <https://orcid.org/0000-0002-2359-9808>

Abstract

Mentalizing is defined as the ability to attribute mental states to oneself and others. In the context of parental behavior, parents' tendency to comment on their child's mental activities refers to the concept of mind-mindedness (MM). MM has been positively associated with various developmental outcomes in children, notably their own ability to mentalize, known as theory of mind (ToM). Although parental (MM) and child (ToM) mentalizing have important implications during childhood, their associations with children's neural structures are largely unknown.

Among 62 mother-child dyads, maternal MM was rated from free-play sequences when children were aged 1 year, child ToM was assessed using a first-order false-belief task at 4 years of age, and structural MRI images were acquired at 10 years of age. Maternal MM was positively associated with grey matter volumes (GMV) in the dorsal prefrontal cortex and the superior temporal pole. Child ToM abilities were positively associated with GMV in the ventromedial prefrontal cortex. Though cortical regions associated with MM and ToM showed no anatomical overlap, many are functionally connected through a neural network highly involved in self-referential strategies for mentalizing. These findings suggest that MM and ToM may contribute to distinct sub-processes that collectively support social cognition development.

Keywords: mentalizing, mind-mindedness, theory of mind, parenting, grey matter volume

Prospective Associations Between Maternal Mind-Mindedness, Child Theory of Mind, and Brain Morphology in School-Aged Children

To successfully navigate through complex interactions and relationships, humans learn to perceive implicit intentions and anticipate reactions. Recognizing and reasoning about other people's mental states, such as knowledge, desires and beliefs, is commonly referred to as mentalizing (Fonagy & Allison, 2012). Adult mentalizing abilities have often been studied in the context of parent-child relationships (see Camoirano, 2017; Zeegers et al., 2017, for reviews). Parental mentalizing is an umbrella term that encompasses various constructs such as reflective functioning, insightfulness, and mind-mindedness (Yatziv et al., 2018). The concept of mind-mindedness (MM) refers to the extent to which parents view their child as a distinct individual with a mind (Meins, 1999), and their tendency to comment verbally on their child's mental activities during parent-child interactions (Meins et al., 2002). MM is positively associated with various developmental outcomes in children such as attachment security, language acquisition, and behavioral regulation (see McMahon & Bernier, 2017, for a review), but the most documented outcome of MM is children's own mentalizing abilities, also known as their "theory of mind" (ToM; Aldrich et al., 2021). ToM acquisition is an important developmental milestone that contributes to later psychosocial adjustment in children including prosocial behavior (Imuta et al., 2016), moral judgement (Fadda et al., 2016), peer acceptance (Caputi et al., 2012), and cooperation (Etel & Slaughter, 2019).

Despite the documented importance of both parental MM and child ToM for psychosocial development, few studies have addressed their neuroanatomical substrates. Yet, a growing literature in developmental neuroscience indicates that early experience is related to variations in child brain anatomy which, in turn, have lifelong effects, notably on physical health,

mental health, and behavior (Knudsen, 2004; Miguel-Hidalgo, 2013; Mustard, 2007). Infancy and childhood are crucial developmental periods for cortical maturation as the young brain is particularly sensitive to environmental influences (Tottenham, 2014). Consequently, the current study aimed to examine the longitudinal correlates of early parent and child mentalizing abilities from a neuroanatomical perspective.

Parental Mind-Mindedness

Through the use of discourse containing mental terms, parents express implicit states, which can then incite children to develop independent thinking and the ability to express inner thoughts on their own (Lundy & Fyfe, 2016). To do so, parents first need to use their own mentalizing abilities to accurately interpret their child's mental states from their behavioral or conversational cues. Then, parents use this interpretation to label implicit thoughts with the correct mental terms (Sharp & Fonagy, 2008). When parents have the tendency to label their child's mental states with appropriate mind-related comments, they demonstrate MM (Meins et al., 2001). Some examples include commenting on child mental states (e.g., "You want this toy"), mental processes (e.g., "You find this game difficult"), and emotional engagement (e.g., "You're excited to play"). In assessment settings, mind-related comments that appear to accurately mirror what the child might be thinking or feeling given the context are coded as appropriate. Contrarily, comments that seem to reflect misinterpretation of children's internal experiences are coded as non-attuned (Meins et al., 2012). Mind-mindedness is reflected by the use of appropriate mind-related comments along with absence or infrequent use of non-attuned comments.

Appropriate mind-related comments draw children's attention to their internal states and facilitate mental references. Numerous studies indicate that MM is a reliable predictor of

multiple aspects of child cognitive and socio-emotional development (Aldrich et al., 2021; McMahon & Bernier, 2017). Given that some of the effects of parenting on child adjustment are believed to transit through neural pathways (e.g., Belsky & de Haan, 2011; Gunnar et al., 2006; Tottenham, 2014), it is plausible that parental MM is related to cerebral development in children. However, empirical evidence linking MM with neural outcomes (whether structural or functional) is extremely thin. To our knowledge, only one study by our group has examined the neural correlates of MM, by measuring brain functional connectivity at rest (Dégeilh et al., 2018). In a subgroup of the current sample, higher levels of maternal MM in infancy predicted stronger functional connectivity between the default mode network (nodes in the ventromedial prefrontal cortex and angular gyrus) and the salience network (nodes in the anterior insula and cingulate cortex) in late childhood. Activity in the default mode network is typically associated with social and affective cognition, as well as introspection about mental states (Andrews-Hanna, 2012), whereas the salience network is mostly involved in the cognitive control of attention (Menon & Uddin, 2010). These initial results suggest that parental MM may contribute to child brain development, notably in regions involved in socio-cognitive processing. However, this previous study focused on functional connections only, and research has yet to investigate whether parental MM might also be reflected in brain anatomy. Another study with the same subsample did look at brain anatomy in school-age children, albeit in relation to attachment security during infancy, and found prospective relations between attachment and cortical volume in several regions of the social brain, such as the superior temporal sulcus and temporo-parietal junction (TPJ; Leblanc et al., 2017). Given that MM is a reliable predictor of attachment security (Zeegers et al., 2017) and shares similar beneficial effects on child development (McMahon &

Bernier, 2017; Szpak & Białecka-Pikul, 2020), these previous findings suggest that there may also be a prospective link between parental MM and neuroanatomical variations in children.

Child Theory of Mind

With mind-minded parenting, children are exposed to mental-oriented comments that foster the development of their mentalizing abilities. For instance, parent-child conversations that emphasize discrepant perspectives (e.g., “You like cookies, *but* your sister prefers ice cream”) contribute to the development of mentalizing abilities by confronting children with the fact that others do not necessarily share their points of view, a core aspect of ToM (Slaughter et al., 2007). Parental discourse that refers to causal effects (e.g., “Your sister is crying *because* she wanted ice cream”) also supports mentalistic understanding as it demonstrates explicitly that behavior is based on mental states (Peterson & Slaughter, 2003). Therefore, appropriate parental mind-related comments can help children gradually evolve from having an egocentric perspective of the world to recognizing others as distinct entities, each with a unique mindset that might diverge from their own (Smith et al., 2015). This skill constitutes the essence of ToM.

False-belief understanding, usually achieved around the age of 4, is a hallmark of children’s ToM development (Wellman et al., 2001; Wimmer & Perner, 1983). In fact, recognition that others can have inaccurate beliefs about the world (i.e., false-belief understanding) is the most widely documented transition in preschoolers’ understanding of mental states (Peterson & Wellman, 2019; Wellman et al., 2001; Wellman & Liu, 2004). Beyond the preschool years, with increasing exposure to various social settings, ToM abilities continue to improve and specialize until adolescence and early adulthood (Dumontheil et al., 2010; Meinhardt-Injac et al., 2020; Valle et al., 2015).

Neural networks and structures underlying social cognition also follow a protracted development through adolescence (Mills et al., 2016; Richardson, 2019), as functional specialization continues even after core milestones in ToM understanding are achieved in childhood (Meinhardt et al., 2011; Richardson et al., 2018). A recent meta-analysis by Fehlbaum et al. (2021) synthesized and compared mentalizing-related neural activity across different age groups (children, adolescents, adults) and reported continuous engagement of the medial prefrontal cortex (mPFC), TPJ, and precuneus across all ages. However, the authors also noted age-related differences in activation patterns during mentalizing-related tasks, where children tend to activate fewer subregions within the core mentalizing regions identified in adult populations. In line with this, many comparative studies have found age-related differences in activation patterns in terms of activated areas and activity levels within the mentalizing network (e.g., Gweon et al., 2012; Kobayashi et al., 2007a; Overgaauw et al., 2015). Other studies have also suggested that mentalizing-related neural activity tends to move from anterior regions (e.g., mPFC) to posterior regions (e.g., TPJ, precuneus) with age (e.g., Blakemore et al., 2007; Burnett et al., 2009; Sebastian et al., 2012; Wang et al., 2006). Overall, the neural correlates of mentalizing abilities appear to differ between children and adults; yet, as noted by Fehlbaum et al. (2021), the literature on the social brain still heavily relies on adult samples.

A different issue is that the literature on the neural correlates of child mentalizing abilities is almost exclusively based on functional brain assessment modalities. Changes in cortical activations related to the acquisition or the practice of various abilities are believed to affect brain morphology through experience-dependent structural neuroplasticity (see May, 2011, for a review). However, very little is known about the direct associations between child ToM and cortical morphology. Only one study to our knowledge has examined the neuroanatomical

correlates of ToM in typically developing children (Grosse Wiesmann et al., 2020). The authors found distinct morphological markers (cortical thickness and surface area) for implicit versus explicit ToM (i.e., nonverbal vs. verbal). Explicit ToM was correlated with the cortical thickness and surface area of common social brain regions (TPJ and precuneus), whereas implicit ToM was related to morphological differences in the supramarginal gyrus, which belongs to a distinct neural network. Considering that implicit ToM is acquired years before explicit ToM, the authors suggested that the observed dissociation reflects young children's reliance on socio-cognitive precursors before reaching mature ToM understanding. Therefore, it can be hypothesized that children use a different set of strategies to accomplish mental state reasoning and may recruit different areas of the brain compared to adults. In sum, there is increasing evidence that cortical regions associated with mentalizing abilities may undergo age-related refinements before reaching maturity. Yet, understanding of the neural correlates of ToM during childhood is mainly inferred from functional imaging studies in adult populations, who have more advanced socio-cognitive abilities and mature neural structures (Fehlbaum et al., 2021).

The Current Study

Overall, the associations between child brain morphology and the mentalizing abilities of both children and their parents remain poorly understood. Specifically, it remains unclear whether parental MM and child ToM are associated with child neuroanatomy, despite findings in related domains strongly suggesting so. Thus, the current study aimed to investigate whether maternal MM and child ToM are prospectively associated with regional grey matter volumes (GMV) in typically developing children. Given the limited body of prior research on morphological correlates of MM and ToM, we opted for an exploratory whole-brain approach in analyses. We tentatively expected to find relations between GMV and both MM and ToM,

especially in the mPFC, since 1) the mPFC is part of the default mode network, for which functional connectivity with the salience network is predicted by maternal MM (Dégeilh et al., 2018), and 2) it is also one of the main regions involved in ToM, especially in younger populations (Kadosh & Haller, 2015). For ToM, we also expected to find associations with the TPJ and precuneus, based on numerous studies associating these regions with ToM understanding (including structural MRI in preschool children; Grosse Wiesmann et al., 2020).

Method

Participants

All participants were recruited as part of a larger longitudinal research project investigating the caregiving environment and child development. The families lived in a large metropolitan area in Canada and were selected from random birth lists provided by the Ministry of Health and Social Services. All parents provided informed consent for participation. Inclusion criteria were full-term pregnancy (i.e., at least 37 weeks of gestation) and the absence of any known disability or developmental delay. Of the 71 families who completed the MRI protocol, five children were excluded due to excessive motion, suspected neuropathology, or neurodevelopmental disorders. Four other families were excluded due to missing data for maternal MM measures. The current study included data of 62 mother-child dyads (28 boys). All study procedures were approved by the research ethics committee of the Centre intégré universitaire de santé et de services sociaux (CIUSSS) du Centre-Sud-de-l'Île-de-Montréal.

Measures

Maternal Mind-Mindedness

Interactions between mother and child during a 10-minute free-play sequence at home were videotaped when children were 1 year of age ($M = 1.05$, $SD = 0.11$, range 0.63–1.38). The

videos were coded by a research assistant trained to follow the standard MM coding system (Meins et al., 2001). Five categories of mind-related comments by mothers to their infants were assessed: (a) mental states (e.g., thoughts, desires); (b) mental processes (e.g., remembering, realizing); (c) emotional engagement (e.g., bored, excited); (d) epistemic states (e.g., teasing, joking); (e) mothers talking on the infant's behalf (e.g., the mother saying "See mom, it's easier this way"). As non-attuned mind-related comments were very rare in this low-risk community sample and are unrelated to child ToM outcomes (Aldrich et al., 2021; Meins et al., 2002, 2013), we summed the number of appropriate (attuned) comments made by mothers into a total mind-mindedness score. A randomly selected subset of 20% of videotapes was coded independently by a second rater, blind to all other measures. Inter-rater reliability (intra-class correlation) for appropriate mind-related comments was .92.

Child Theory of Mind

ToM was assessed when children were 4 years old ($M = 4.05$, $SD = 0.07$, range 3.88–4.21) with a commonly used first-order false-belief task, referred to as "unexpected contents" (Gopnik & Astington, 1988; Perner et al., 1987). This paradigm has been widely used by numerous research groups to assess false-belief understanding in preschool children (see Beaudoin et al., 2020, for a systematic review). In the current study, children were shown a Band-Aid[®] box and were first asked about what they thought was in the box, as a control question. A correct response was necessary for children to proceed with this task and all participants succeeded. The experimenter then opened the box to reveal that it actually contained crayons. The box was closed again and a memory check question about the contents was asked. Then, children were shown a doll, "Alice", and were told that she had never looked inside the Band-Aid[®] box. Children answered the question: "What does Alice think is in the box?" Finally,

children had to name the true content of the box (“What is really in the box?”). The initial control and memory check questions were not considered in computing the ToM score. Thus, the total score was computed based on the last two questions and varied from 0 to 2.

Structural Magnetic Resonance Imaging Acquisition and Preprocessing

When children were 10 years of age ($M = 10.46$, $SD = 0.45$, range 10.00–12.17), children were invited to participate in a structural MRI exam that included a three-dimensional T1-weighted 4-echo magnetization-prepared rapid gradient-echo (3D-T1-4echo-MPRAGE sagittal) sequence. While the neuroimaging data collection was ongoing, the MAGNETOM Trio Siemens 3T scanner ($n = 31$; repetition time (TR): 2530 ms; 4 echo times (TE): 1.64/3.5/5.36/7.22 ms; echo spacing ΔTE 1.86 ms; flip angle: 7° ; 176 slices; slice thickness: 1 mm; no gap; matrix: 256×256 ; field of view (FoV): 256 mm; in- plane resolution: 1 x 1 mm; duration: 363 sec) was upgraded to a MAGNETOM Prisma ($n = 31$; TR: 2200 ms; 4 TE: 1.87/4.11/6.35/8.59 ms; echo spacing ΔTE : 2.24 ms; flip angle: 8° ; 176 slices; slice thickness: 1 mm; no gap; matrix: 256×256 ; FoV: 256 mm; in- plane resolution: 1 x 1 mm; duration: 327 sec). Scanner differences were investigated as described below.

Pre-processing for the voxel-based morphometry (VBM) analyses was performed using the SPM12 package (revision 7487; Statistical Parametric Mapping, Institute of Neurology, London, United Kingdom) and the CAT12 Toolbox (version 12.6; <http://www.neuro.uni-jena.de/cat/>) running on MATLAB (version R2019a; MathWorks, Inc., Natick, USA). In order to minimize the potential confounds associated with developmental differences in cortical morphometry, an age-appropriate pediatric template was used (<http://www.bic.mni.mcgill.ca/ServicesAtlases>; Fonov et al., 2011; Yoon et al., 2009). Then, the segments were spatially normalized to the Montreal Neurological Institute space (voxel size of

1.5 mm x 1.5 mm x 1.5 mm). Finally, the resulting GMV maps were modulated and smoothed with 8-mm full-width-at-half-maximum (FWHM) smoothing kernels.

Analytic Approach

Multiple regressions across all voxels of the brain were conducted to predict GMV in late childhood from maternal MM in infancy and ToM abilities in early childhood. Whole-brain VBM analyses were performed using the SPM12 software (revision 7487) and the CAT12 Toolbox version 12.6 running on MATLAB version R2019a. Statistical maps identifying voxel clusters significantly correlated with MM and ToM scores, respectively, were obtained by using a threshold-free cluster enhancement (TFCE) method (<http://www.neuro.uni-jena.de/tfce/>) implemented in CAT12. This thresholding method combines cluster size and height information at each voxel and circumvents the problem of choosing an arbitrary cluster-forming threshold (Smith & Nichols, 2009). The distribution of TFCE values is derived from permutation-based non-parametric testing (5,000 permutations per test), thus retaining statistical rigor and sensitivity (Smith & Nichols, 2009) while optimizing statistical power in small sample studies (Nichols & Hayasaka, 2003; Pernet et al., 2015). Statistical significance level was thresholded at uncorrected $p < .001$ ($p\text{-unc}$), with a minimum extent threshold of 100 voxels to reduce the risks of false positives.

An explicit grey matter mask using the mean normalized grey matter images of all participants was applied to ensure that the analyses would be restricted to grey matter. Child age, sex, and total intracranial volume (TIV; Barnes et al., 2010) as well as maternal education (Jednoróg et al., 2012) were included as covariates as they are associated with cortical volumes in children. Scanner model was also included as a covariate to account for the potential confounding effect related to differences in scanning platforms (Chen et al., 2014). As an

additional precaution, independent samples t-test were performed in SPM12 to examine scanner differences in regional morphometry. Any significant results revealed by the main analyses that would overlap with regions showing scanner differences would not be interpreted. Comparative analyses (t-test and chi-square test) between scanner models for child ToM, maternal MM, covariates, and sociodemographic variables were conducted in SPSS (version 26; IBM Corp., Armonk, NY).

Results

Preliminary Analyses

Descriptive and group comparison (by scanner model) statistics are summarized in Table 1. No group (Trio vs. Prisma) differences were found in terms of family income, maternal MM, age, education, or ethnicity, nor child ToM, sex, or TIV (all $ps > .08$). Only child age was significantly different across the two groups ($p < .001$). This difference did not, however, lead to the addition of a covariate in the main analyses, as age was already planned as a covariate in those analyses. We also examined the presence of group differences in regional morphometry. Only one cluster in the right entorhinal cortex (MNI coordinates: $x = 16, y = 3, z = -24; k = 121; T = 4.01$) showed a significant difference at $p\text{-unc} < .001$. None of the regions showing significant associations with maternal MM or child ToM (presented below) overlapped with this cluster. Finally, the correlation between maternal MM and child ToM, although not statistically significant in this small sample ($r = .13, p = .331$), was similar in magnitude to meta-analytic estimates ($r = .17$; Aldrich et al., 2021; $r = .16$; Devine & Hughes, 2016).

Main Analyses

Whole-brain multiple regression analysis indicated that higher maternal MM in infancy was associated with greater GMV in the right dorsomedial prefrontal cortex (dmPFC) extending

to the supplementary motor area (SMA; $x = 24, y = 12, z = 62; k = 1073; TFCE = 704.71$), as well in the left dorsolateral prefrontal cortex (dlPFC; $x = -21, y = 48, z = 18; k = 143; TFCE = 487.22$) and the left superior temporal pole ($x = -48, y = 12, z = -23; k = 142; TFCE = 542.68$) when controlling for maternal education, child age, sex, TIV, and scanner model ($p\text{-unc} < .001$; Figure 1).

Children with better performance on the ToM task in early childhood presented greater GMV in the left ventromedial prefrontal cortex (vmPFC; $x = -23, y = 35, z = -18; k = 659; TFCE = 1093.73$) in late childhood, controlling for maternal education, child age, sex, TIV, and scanner model ($p\text{-unc} < .001$; Figure 2).

Discussion

This longitudinal study aimed to examine the respective associations of mothers' and children's mentalizing abilities in early development with brain morphology in late childhood. Maternal MM and child ToM were found to be prospectively associated with distinct neuroanatomical correlates within key regions of the social brain (Monticelli et al., 2021). Precisely, maternal MM showed positive associations with GMV in the temporal region and the dorsal portion of the prefrontal cortex, whereas child ToM showed positive associations with GMV in the ventral portion of the prefrontal cortex only.

Mind-Mindedness

This appears to be the first study to provide insight into the association between maternal MM and brain morphology in children. Our results indicate that children whose mothers were more mind-minded in infancy had larger GMV in the superior temporal pole and the dorsal prefrontal cortices (dlPFC and dmPFC extending to the SMA) 9 years later. This finding is consistent with studies reporting smaller GMV in these brain regions in association with adverse

caregiving environments. Indeed, maltreated children are less likely to be exposed to high levels of parental MM (Luke & Banerjee, 2013) and they have smaller GMV in the superior temporal gyrus (STG; see Lim et al., 2014, for a meta-analysis). Similarly, exposure to unhealthy parent-child relationships during childhood (e.g., inappropriate parental style, corporal punishment) is associated with reduced GMV in the medial and lateral prefrontal cortex in young adults (Narita et al., 2010; Tomoda et al., 2009). However, these prior results must be interpreted alongside the numerous potential confounding variables that tend to accompany adverse childhood experiences (e.g., poor mental and physical health, poverty, prenatal drug and alcohol use; Cuddihy et al., 2013; Edwards et al., 2003; Hussey et al., 2006; Smith et al., 2007). The current findings with a low-risk community sample highlight that subtle variations in parental behavior, such as normative individual differences in MM, can also have bearing on children's brain structures.

The temporal pole is commonly considered as the archive for semantic and conceptual knowledge, though studies have found that it is also involved in social-emotional functioning (e.g., Olson et al., 2013; Ross & Olsen, 2010; Zahn et al., 2007). More specifically, these studies suggest that social concepts used to describe people (e.g., honorable, impolite) are represented in the temporal pole, which would then play an active role in retrieving social knowledge when reflecting about mental states (Olson et al., 2013).

The dmPFC is a cortical region that shares a more direct and explicit link with mentalizing, notably through self- and other-referential processing, including the appraisal of intentions, motivations, traits, and behaviors (see Isoda & Noritake, 2013; Lieberman et al., 2019, for reviews). Accordingly, functional imaging studies in healthy children have consistently reported cortical activation in this region across various ToM tasks (e.g., Alkire et al., 2018; Bowman et al., 2019, Gweon et al., 2012; Moriguchi et al., 2007). Interestingly, both the

temporal pole and the dmPFC are considered key regions of the dorsal medial subsystem within the default mode network, which is consistently engaged in mental-state attribution and conceptual processing (see Andrews-Hanna et al., 2014, for a review). This finding bears similarities with a recent study by our team (Dégeilh et al., 2018), in which maternal MM during infancy predicted resting-state functional connectivity between the default mode network and the salience network in school-aged children.

In comparison, the role of the dlPFC is regarded as less specific to social processing, as it is known for its associations with a wide range of executive functions (Brunoni & Vanderhasselt, 2014; Hart et al., 2013). Previous work has suggested that executive functions share numerous common neural underpinnings with ToM (Wade et al., 2018), as they may be involved in mentalizing via domain-general cognitive processes, especially through inhibitory control (Carlson & Moses, 2001; Leslie et al., 2004; Mahy et al., 2014). For instance, the dlPFC is involved in cognitive self-control, which helps overriding emotional or personal bias (Rilling & Sanfey, 2009). As such, both greater functional activity and cortical thickness in the left dlPFC are associated with better impulse control and more strategic social behavior in children (Steinbeis et al., 2012). In relation to MM, when parents provide attuned mind-related comments during interactions, they may in fact act as external regulators of their child's affect and behavior, thus fostering child self-regulation strategies (Grolnick & Farkas, 2002; McMahon & Bernier, 2017). These self-regulation strategies may then help children overcome egocentrism and become more attuned to others' mental states. Overall, the current findings suggest that exposure to mind-minded comments in infancy may favor cortical maturation in regions involved not only in mentalizing, but also in a conceptual understanding of social knowledge and high-level cognitive functions that support social cognition.

Theory of Mind

With regard to child mentalizing, children who had better false-belief understanding in early childhood had larger GMV in the left vmPFC 6 years later. Anatomically connected to the dmPFC, the vmPFC is also highly involved in mentalization, notably through a large range of socio-cognitive and affective processes such as emotion recognition, mental state inference, valence attribution and moral judgement (see Hiser & Koenigs, 2017; Lieberman et al., 2019, for reviews). Kobayashi et al. (2007b) previously reported that the neural correlates of ToM during early development may vary depending on specific cultural or linguistic characteristics, though the vmPFC was consistently recruited during ToM tasks regardless of children's cultural backgrounds.

Furthermore, it has been proposed that the associations between vmPFC and socio-cognitive abilities vary across development. Higher ToM-related activation levels in the vmPFC are reported in children compared to adolescents (Gunther Moor et al., 2012; Moriguchi et al., 2007) and adults (Kobayashi et al., 2007a). Similar results emerge when comparing adolescents and adults (i.e., stronger activations in the medial prefrontal areas in younger age groups; Blakemore et al., 2007; Burnett et al., 2009; Sebastian et al., 2012), underscoring the protracted neural specialization of cortical regions involved in mental state reasoning. It is possible that children rely on the vmPFC to reflect about social situations in order to acquire appropriate social knowledge during early life. With the accumulation of semantic knowledge about social facts, mature ToM reasoning strategies may gradually become less reliant on the vmPFC as a function of development (Adolphs, 2009; Mahy et al., 2014; Wang et al., 2006). Overall, the current results show that children's early ToM abilities are related to subsequent morphological differences in a cortical region essentially involved in the early stages of mentalizing acquisition.

To our knowledge, only one other study has addressed the relation between ToM abilities and neural structures in typically developing children. Grosse Wiesmann et al. (2020) found ToM-related neuroanatomical differences only in posterior regions (TPJ and precuneus), in contrast to the current findings in frontal regions (vmPFC). However, their structural imaging data were obtained right at the time of emergence of explicit ToM understanding. Specifically, the authors reported significant group differences related to ToM performance on explicit (verbal) false-belief tasks, where 3-year-olds performed below chance and 4-year-olds performed marginally above chance. Conversely, our structural MRI exam was performed at 10 years of age, thus allowing more time for ToM understanding and experience-dependant neuroplasticity processes to stabilize. Altogether, the current study seems to be the first to document prospective associations between early ToM abilities and subsequent neuroanatomy, thus providing preliminary evidence that the continuous consolidation of mentalistic reasoning may, with time, translate into morphological differences in the prefrontal cortex.

Neural Correlates of Mentalizing: How Are They Related?

Contribution to sub-aspects of social cognition

Maternal MM and child ToM, which were positively but weakly inter-correlated in this sample (congruent with meta-analytic estimates; Aldrich et al., 2021; Devine & Hughes, 2016), were associated with GMV in distinct regions of the brain. The cortical regions in which GMV was found to be associated with MM are commonly associated with social cognition, yet they were not associated with behavioral performance on the ToM task in this sample. A possible explanation is that MM and ToM contribute to the development of neural structures involved in different sub-processes that support social cognition. A meta-analysis by Schurz et al. (2021) proposed a model in which neural substrates of social cognition can be organized under three

clusters: cognitive, affective, and intermediate. The cortical region associated with child ToM in the current study belongs to the cognitive cluster, which is most strongly activated for tasks involving other- and self-related mental state attributions (e.g., false-belief, trait judgement). In comparison, the cortical regions found here to be associated with maternal MM belong mostly to the intermediate cluster, which overlaps substantially with the language processing networks and supports both socio-cognitive and affective processes (Schurz et al., 2021). This result is consistent with the notion that parental MM is predominantly verbal in nature and aligns with previous work underscoring the contribution of language processes to mental-state reasoning in children (e.g., Conte et al., 2019; de Villiers & de Villiers, 2014; Heyes & Frith, 2014). From this perspective, exposure to mind-minded maternal behavior during infancy may promote structural maturation in brain areas that support cognitive, affective, and linguistic processes surrounding mental state reasoning that are not specific or limited to belief attributions. However, the lack of inclusion of an affective ToM task or behavioural measure of children's everyday social functioning in the current study limits our interpretations.

Functional connectivity and self-referential processes

Although cortical regions in which GMV was associated with MM and ToM share no anatomical overlap, they share functional connections within the social brain, mainly through the default mode network (Andrews-Hanna, 2010). Briefly, brain regions pertaining to this network are organized under functionally connected subsystems that co-activate to generate and process self-referential information (Andrews-Hanna, 2014). According to the Simulation Theory of ToM acquisition, self-relevant information processing is critical for making mental-state attributions (Focquaert et al., 2008; Gordon, 1992; Harris, 2000). This theory proposes that children must rely on their own psychological states in order to understand what others

experience in a given situation. In line with this, Gonzales et al. (2017) found that young children learn to introspect about their own mental states before being able to accurately attribute them to others. Previous neuroimaging studies have suggested that younger populations tend to employ a more ‘self-referential’ strategy for mentalizing, as they preferentially recruit cortical regions typically involved in self-related processes during mental-state reasoning compared to adults (Burnett et al., 2009; Gunther Moor et al., 2012, Moriguchi et al. 2007). It is conceivable that age-related differences in cortical activation patterns for self- versus other-referential processes reflect a developmental shift in mentalizing processes, where children gradually rely less on self-centered simulations. Overall, during the early stages of mental-state attribution, using the concept of ‘self’ as an anchor point for simulating others’ minds may serve as a stepping-stone for more complex social processing (Focquaert et al., 2008). The brain regions identified in this study may be involved in these developmental changes from self- to other-referential processes.

Previous work has shown that long-lasting functional connectivity between brain regions is associated with synchronized specialization, which can in turn result in covariation between regional anatomical measures of different brain areas (i.e., structural covariance; Alexander-Bloch et al., 2013; Geng et al., 2017). Though speculative, the positive associations between mentalizing variables (MM and ToM) and GMV in functionally connected cortical structures possibly reflect the long-term effect of cortical specialization. As structural covariance analyses were not conducted here, further investigation into how parental behavior and child socio-cognitive development may relate to anatomical markups in structural networks is needed.

Limitations

Some limitations need to be considered when interpreting the study findings. First, while an exploratory whole-brain approach was appropriate due to the innovative nature of this

preliminary hypothesis-generating investigation, larger-scale hypothesis-testing studies are needed. Considering the relatively modest sample size and related risk of Type-II error, a liberal uncorrected threshold of $p < .001$ was used, with a minimum extent threshold of 100 voxels to counterweight this more liberal approach. Second, although a sample size of 62 is a strength for a 10-year longitudinal child MRI study involving behavioral assessments, it remains modest from a statistical power point of view. It is therefore possible that the analyses underestimated the magnitude of the associations between maternal MM, child ToM, and child brain volumes. Third, we assessed maternal MM only, while paternal MM may also contribute to better socio-cognitive abilities in children (McMahon & Bernier, 2017). Fourth, ToM was assessed through one false-belief task, which only accounts for cognitive ToM and may be influenced by general language competence. Controlling for children's language abilities and the use of more inclusive ToM batteries may better account for the possible modality-related differences in ToM measures (Milligan et al., 2007; Schurz et al., 2014). Fifth, the longitudinal yet non-experimental design of this study does not permit causal inference nor establishment of directionality. Even though regional GMV was measured at a later age and interpreted as the result of practicing mentalizing abilities, the development of cortical structures might in fact have preceded the latter, predisposing children to have better false-belief understanding. Likewise, apparent parental influences on child outcomes are often due to bidirectional influences (e.g., Serbin et al., 2015); hence, it is possible that infants' initial neurodevelopment influenced early maternal MM, later child ToM, and brain volumes. Finally, relations between neuroanatomy and cognitive functions are age-dependent, especially during childhood and adolescence (Giedd et al., 2015). Research involving repeated MRIs is necessary to investigate whether the associations observed in this study are similar across developmental periods.

Conclusion

Results from this 10-year longitudinal study provide preliminary evidence that exposure to mentalistic parental behavior and practice of mentalizing abilities in early life may leave long-lasting anatomical traces in the human brain. To our knowledge, this is the first study to investigate and compare the structural neural correlates of maternal MM and child ToM in typically developing school-aged children. Whole-brain multiple regression analyses revealed that maternal MM during infancy predicted GMV in a set of brain regions involved in both mentalizing and broader cognitive functions, such as language processing and executive functions. Comparatively, children's ToM abilities in early childhood predicted GMV in a cortical region specific to mentalizing, through both socio-cognitive and affective processes. While structurally distinct, the brain regions in which GMV was found to be correlated with parental and child mentalizing are functionally connected through a neural network highly involved in self-referential strategies for mentalizing, which are preferentially deployed by children during mental-state attributions. Overall, the current findings shed light onto the complex relationship between parental behavior and child socio-cognitive development in relation to healthy brain maturation while adding to the growing literature on the prospective outcomes of normative variations in early experience.

Acknowledgements

The authors wish to acknowledge Marie-Ève Bélanger, Stéphanie Bordeleau, Andrée-Anne Bouvette-Turcot, Catherine Cimon-Paquet, Marie Deschênes, Christine Gagné, Gabrielle Lalonde, Jessica Laranjo, Nadine Marzougui, Célia Matte-Gagné, Émilie Tétreault and Emeline Wyckaert for help with data collection. The authors also want to express special gratitude to the participating families of the Grandir Ensemble project who generously opened their homes to us.

The authors thank Andre van der Kouwe from the Massachusetts General Hospital for the use of the MPRAGE 4-echo sequence.

Disclosure statement

The authors declare no conflict of interest.

Data availability

Data or materials for the experiments reported here are not publicly available due to privacy or ethical restrictions.

Funding

This work was supported by the Social Sciences and Humanities Research Council of Canada [410-2010-1366], the Canadian Institutes of Health Research [MOP-119390], and the Natural Sciences and Engineering Research Council of Canada [RGPIN-2019-05084].

References

- Adolphs, R. (2009). The social brain: neural basis of social knowledge. *Annual Review of Psychology, 60*, 693–716. <https://doi.org/10.1146/annurev.psych.60.110707.163514>
- Aldrich, N. J., Chen, J., & Alfieri, L. (2021). Evaluating associations between parental mind-mindedness and children's developmental capacities through meta-analysis. *Developmental Review, 60*, 100946. <https://doi.org/10.1016/j.dr.2021.100946>
- Alexander-Bloch, A., Giedd, J. N., & Bullmore, E. (2013). Imaging structural co-variance between human brain regions. *Nature Reviews Neuroscience, 14*(5), 322–336. <https://doi.org/10.1038/nrn3465>
- Alkire, D., Levitas, D., Warnell, K. R., & Redcay, E. (2018). Social interaction recruits mentalizing and reward systems in middle childhood. *Human Brain Mapping, 39*(10), 3928–3942. <https://doi.org/10.1002/hbm.24221>
- Andrews-Hanna, J.R. (2012). The brain's default network and its adaptive role in internal mentation. *Neuroscientist, 18*(3), 251–270. <https://doi.org/10.1177/1073858411403316>
- Andrews-Hanna, J. R., Reidler, J. S., Sepulcre, J., Poulin, R., & Buckner, R. L. (2010). Functional-anatomic fractionation of the brain's default network. *Neuron, 65*(4), 550–562. <https://doi.org/10.1016/j.neuron.2010.02.005>
- Andrews-Hanna, J. R., Smallwood, J., Spreng, R.N. (2014). The default network and self-generated thought: component processes, dynamic control, and clinical relevance. *Annals of the New York Academy of Sciences, 1316*(1), 29–52. <https://doi.org/10.1111/nyas.12360>
- Barnes, J., Ridgway, G. R., Bartlett, J., Henley, S. M. D., Lehmann, M., Hobbs, N., ... Fox, N. C. (2010). Head size, age and gender adjustment in MRI studies: A necessary nuisance? *NeuroImage, 53*(4), 1244–1255. <https://doi.org/10.1016/j.neuroimage.2010.06.025>

- Beaudoin, C., Leblanc, É., Gagner, C., & Beauchamp, M. H. (2020). Systematic review and inventory of theory of mind measures for young children. *Frontiers in Psychology, 10*, 2905. <https://doi.org/10.3389/fpsyg.2019.02905>
- Belsky, J., & De Haan, M. (2011). Annual research review: Parenting and children's brain development: The end of the beginning. *Journal of Child Psychology and Psychiatry, 52*(4), 409–428. <https://doi.org/10.1111/j.1469-7610.2010.02281.x>
- Blakemore, S.-J., den Ouden, H., Choudhury, S., & Frith, C. (2007). Adolescent development of the neural circuitry for thinking about intentions. *Social Cognitive and Affective Neuroscience, 2*(2), 130–139. <https://doi.org/10.1093/scan/nsm009>
- Bowman, L. C., Dodell-Feder, D., Saxe, R., & Sabbagh, M. A. (2019). Continuity in the neural system supporting children's theory of mind development: Longitudinal links between task-independent EEG and task-dependent fMRI. *Developmental Cognitive Neuroscience, 40*, 100705. <https://doi.org/10.1016/j.dcn.2019.100705>
- Brunoni, A. R., & Vanderhasselt, M.-A. (2014). Working memory improvement with non-invasive brain stimulation of the dorsolateral prefrontal cortex: A systematic review and meta-analysis. *Brain and Cognition, 86*, 1–9. <https://doi.org/10.1016/j.bandc.2014.01.008>
- Burnett, S., Bird, G., Moll, J., Frith, C., & Blakemore, S.-J. (2009). Development during adolescence of the neural processing of social emotion. *Journal of Cognitive Neuroscience, 21*(9), 1736–1750. <https://doi.org/10.1162/jocn.2009.21121>
- Camoirano, A. (2017). Mentalizing makes parenting work: A review about parental reflective functioning and clinical interventions to improve it. *Frontiers in Psychology, 8*(14), 1–12. <https://doi.org/10.3389/fpsyg.2017.00014>

- Caputi, M., Lecce, S., Pagnin, A., & Banerjee, R. (2012). Longitudinal effects of theory of mind on later peer relations: The role of prosocial behavior. *Developmental Psychology, 48*(1), 257–270. <https://doi.org/10.1037/a0025402>
- Carlson, S. M., & Moses, L. J. (2001). Individual differences in inhibitory control and children's theory of mind. *Child Development, 72*(4), 1032–1053. <https://doi.org/10.1111/1467-8624.00333>
- Chen, J., Liu, J., Calhoun, V. D., Arias-Vasquez, A., Zwiers, M. P., Gupta, C. N., Franke, B. & Turner, J. A. (2014). Exploration of scanning effects in multi-site structural MRI studies. *Journal of Neuroscience Methods, 230*, 37–50. <https://doi.org/10.1016/j.jneumeth.2014.04.023>
- Conte, E., Ornaghi, V., Grazzani, I., Pepe, A., & Cavioni, V. (2019). Emotion knowledge, theory of mind, and language in young children: testing a comprehensive conceptual model. *Frontiers in Psychology, 10*, 2144. <https://doi.org/10.3389/fpsyg.2019.02144>
- Cuddihy, C., Dorris, L., Minnis, H., & Kocovska, E. (2013). Sleep disturbance in adopted children with a history of maltreatment. *Adoption and Fostering, 37*(7), 404–411. <https://doi.org/10.1177/0308575913508715>
- de Villiers, J. G., & de Villiers, P. A. (2014). The role of language in theory of mind development. *Topics in Language Disorders, 34*(4), 313–328. <https://doi.org/10.1097/TLD.0000000000000037>
- Dégeilh, F., Bernier, A., Leblanc, É., Daneault, V., & Beauchamp, M. H. (2018). Quality of maternal behaviour during infancy predicts functional connectivity between default mode network and salience network 9 years later. *Developmental Cognitive Neuroscience, 34*, 53–62. <https://doi.org/10.1016/j.dcn.2018.06.003>

- Devine, R. T., & Hughes, C. (2018). Family correlates of false belief understanding in early childhood: A meta-analysis. *Child Development, 89*(3), 971–987.
<https://doi.org/10.1111/cdev.12682>
- Dumontheil, I., Apperly, I. A., & Blakemore, S.-J. (2010). Online usage of theory of mind continues to develop in late adolescence. *Developmental Science, 13*(2), 331–338.
<https://doi.org/10.1111/j.1467-7687.2009.00888.x>
- Edwards, V. J., Holden, G. W., Felitti, V. J., & Anda, R. F. (2003). Relationship between multiple forms of childhood maltreatment and adult mental health in community respondents: Results from the Adverse Childhood Experiences study. *The American Journal of Psychiatry, 160*(8), 1453–1460. <https://doi.org/10.1176/appi.ajp.160.8.1453>
- Etel, E., & Slaughter, V. (2019). Theory of mind and peer cooperation in two play contexts. *Journal of Applied Developmental Psychology, 60*, 87–95.
<https://doi.org/10.1016/j.appdev.2018.11.004>
- Fadda, R., Parisi, M., Ferretti, L., Saba, G., Foscoliano, M., Salvago, A., & Doneddu, G. (2016). Exploring the role of theory of mind in moral judgment: The case of children with autism spectrum disorder. *Frontiers in Psychology, 7*. <https://doi.org/10.3389/fpsyg.2016.00523>
- Fehlbaum, L. V., Borbás, R., Paul, K., Eickhoff, S. B., & Raschle, N. m. (2021). Early and late neural correlates of mentalizing: ALE meta-analyses in adults, children and adolescents. *Social Cognitive and Affective Neuroscience, nsab105*.
<https://doi.org/10.1093/scan/nsab105>
- Focquaert, F., Braeckman, J., & Platek, S. M. (2008). An evolutionary cognitive neuroscience perspective on human self-awareness and theory of mind. *Philosophical Psychology, 21*(1), 47–68. <https://doi.org/10.1080/09515080701875156>

- Fonagy, P. & Allison, E. (2012). What is mentalization? The concept and its foundations in developmental research. In N. Midgley & I. Vrouva (Eds.), *Minding the Child: Mentalization-Based Interventions with Children, Young People and Their Families* (pp. 11–34). New York, NY: Routledge/Taylor & Francis Group.
- Fonov, V., Evans, A. C., Botteron, K., Almli, C. R., McKinstry, R. C., & Collins, D. L. (2011). Unbiased average age-appropriate atlases for pediatric studies. *NeuroImage*, *54*(1), 313–327. <https://doi.org/10.1016/j.neuroimage.2010.07.033>
- Geng, X., Li, G., Lu, Z., Gao, W., Wang, L., Shen, D., Zhu, H., & Gilmore, J. H. (2017). Structural and maturational covariance in early childhood brain development. *Cerebral Cortex*, *27*(3), 1795–1807. <https://doi.org/10.1093/cercor/bhw022>
- Giedd, J. N., Raznahan, A., Alexander-Bloch, A., Schmitt, E., Gogtay, N., & Rapoport, J. L. (2015). Child psychiatry branch of the National Institute of Mental Health longitudinal structural magnetic resonance imaging study of human brain development. *Neuropsychopharmacology*, *40*(1), 43–49. <https://doi.org/10.1038/npp.2014.236>
- Gonzales, C. R., Fabricius, W. V., & Kupfer, A. S. (2018). Introspection plays an early role in children's explicit theory of mind development. *Child Development*, *89*(5), 1545–1552. <https://doi.org/10.1111/cdev.12876>
- Gopnik, A., & Astington, J. W. (1988). Children's understanding of representational change and its relation to the understanding of false belief and the appearance-reality distinction. *Child Development*, *59*(1), 26–37. <https://doi.org/10.2307/1130386>
- Gordon, R. M. (1992). The simulation theory: Objections and misconceptions. *Mind & Language*, *7*, 11–34. <https://doi.org/10.1111/j.1468-0017.1992.tb00195.x>

- Grolnick, W. S., & Farkas, M. (2002). Parenting and the development of children's self-regulation. In M. H. Bornstein (Ed.), *Handbook of parenting: Practical issues in parenting* (pp. 89–110). Lawrence Erlbaum Associates Publishers.
- Grosse Wiesmann, C., Friederici, A. D., Singer, T., & Steinbeis, N. (2020). Two systems for thinking about others' thoughts in the developing brain. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(12), 6928–6935.
<https://doi.org/10.1073/pnas.1916725117>
- Gunnar, M., Fisher, P., & Early Experience, Stress, and Prevention Network. (2006). Bringing basic research on early experience and stress neurobiology to bear on preventive interventions for neglected and maltreated children. *Development and Psychopathology*, *18*(3), 651–677. <https://doi.org/10.1017/S0954579406060330>
- Gunther Moor, B., Op de Macks, Z. A., Güroğlu, B., Rombouts, S. A. R. B., Van der Molen, M. W., & Crone, E. A. (2012). Neurodevelopmental changes of reading the mind in the eyes. *Social Cognitive and Affective Neuroscience*, *7*(1), 44–52.
<https://doi.org/10.1093/scan/nsr020>
- Gweon, H., Dodell-Feder, D., Bedny, M., & Saxe, R. (2012). Theory of mind performance in children correlates with functional specialization of a brain region for thinking about thoughts. *Child Development*, *83*(6), 1853–68. <https://doi.org/10.1111/j.1467-8624.2012.01829.x>
- Hart, H., Radua, J., Nakao, T., Mataix-Cols, D., & Rubia, K. (2013). Meta-analysis of functional magnetic resonance imaging studies of inhibition and attention in attention-deficit/hyperactivity disorder: Exploring task-specific, stimulant medication, and age effects. *JAMA Psychiatry*, *70*(2), 185–198.
<https://doi.org/10.1001/jamapsychiatry.2013.277>

- Harris, P. L. (2000). *The work of the imagination*. Blackwell Publishing.
- Heyes, C. M., & Frith, C. D. (2014). The cultural evolution of mind reading. *Science*, *344*(6190), 1243091. <https://doi.org/10.1126/science.1243091>
- Hiser, J., & Koenigs, M. (2018). The multifaceted role of the ventromedial prefrontal cortex in emotion, decision making, social cognition, and psychopathology. *Biological Psychiatry*, *83*(8), 638–647. <https://doi.org/10.1016/j.biopsych.2017.10.030>
- Hussey, J. M., Chang, J. J., and Kotch, J. B. (2006). Child maltreatment in the United States: prevalence, risk factors, and adolescent health consequences. *Pediatrics*, *118*(3), 933–942. <https://doi.org/10.1542/peds.2005-2452>
- Imuta, K., Henry, J. D., Slaughter, V., Selcuk, B., & Ruffman, T. (2016). Theory of mind and prosocial behavior in childhood: A meta-analytic review. *Developmental Psychology*, *52*(8), 1192–1205. <https://doi.org/10.1037/dev000014>
- Isoda, M., & Noritake, A. (2013). What makes the dorsomedial frontal cortex active during reading the mental states of others? *Frontiers in Neuroscience*, *7*, 232. <https://doi.org/10.3389/fnins.2013.00232>
- Jednoróg, K., Altarelli, I., Monzalvo, K., Fluss, J., Dubois, J., Billard, C., Dehaene-Lambertz, G., Ramus, F. (2012). The influence of socioeconomic status on children's brain structure. *PLoS ONE*, *7*(8), e42486. <https://doi.org/10.1371/journal.pone.0042486>
- Kadosh, K. C., & Haller, S. P. W. (2015). The social brain in childhood and adolescence. In A. W. Toga (Ed.), *Brain Mapping* (pp. 171–175). Academic Press. <https://doi.org/10.1016/B978-0-12-397025-1.00174-3>
- Knudsen, E. I. (2004). Sensitive periods in the development of the brain and behavior. *Journal of Cognitive Neuroscience*, *16*(8), 1412–1425. <https://doi.org/10.1162/0898929042304796>

- Kobayashi, C., Glover, G. H., & Temple, E. (2007a). Children's and adults' neural bases of verbal and nonverbal "theory of mind." *Neuropsychologia*, *45*(7), 1522–1532.
<https://doi.org/10.1016/j.neuropsychologia.2006.11.017>
- Kobayashi, C., Glover, G. H., & Temple, E. (2007b). Cultural and linguistic effects on neural bases of 'theory of mind' in American and Japanese children. *Brain Research*, *1164*, 95–107. <https://doi.org/10.1016/j.brainres.2007.06.022>
- Leblanc, É., Dégeilh, F., Daneault, V., Beauchamp, M. H., & Bernier, A. (2017). Attachment security in infancy: A preliminary study of prospective links to brain morphometry in late childhood. *Frontiers in Psychology*, *8*, 2141. <https://doi.org/10.3389/fpsyg.2017.02141>
- Leslie, A. M., Friedman, O., & German, T. P. (2004). Core mechanisms in 'theory of mind.' *Trends in Cognitive Sciences*, *8*(12), 528–533. <https://doi.org/10.1016/j.tics.2004.10.001>
- Lieberman, M. D., Straccia, M. A., Meyer, M. L., Du, M., & Tan, K. M. (2019). Social, self, (situational), and affective processes in medial prefrontal cortex (MPFC): Causal, multivariate, and reverse inference evidence. *Neuroscience & Biobehavioral Reviews*, *99*, 311–328. <https://doi.org/10.1016/j.neubiorev.2018.12.021>
- Lim, L., Radua, J., & Rubia, L. (2014). Gray matter abnormalities in childhood maltreatment: A voxel-wise meta-analysis. *American Journal of Psychiatry*, *171*(8), 854–863.
<https://doi.org/10.1176/appi.ajp.2014.13101427>
- Luke, N., & Banerjee, R. (2013). Differentiated associations between childhood maltreatment experiences and social understanding: A meta-analysis and systematic review. *Developmental Review*, *33*(1), 1–28. <https://doi.org/10.1016/j.dr.2012.10.001>
- Lundy, L. B. & Fyfe, G. (2016). Preschoolers' Mind-related Comments During Collaborative Problem-solving: Parental Contributions and Development Outcomes. *Social Development*, *25*(4), 722–741. <https://doi.org/10.1111/sode.12176>

- Mahy, C. E. V., Moses, L. J., & Pfeifer, J. H. (2014). How and where: Theory-of-mind in the brain. *Developmental Cognitive Neuroscience, 9*, 68–81.
<https://doi.org/10.1016/j.dcn.2014.01.002>
- May, A. (2011). Experience-dependent structural plasticity in the adult human brain. *Trends in Cognitive Sciences, 15*(10), 475–482. <https://doi.org/10.1016/j.tics.2011.08.002>
- McMahon, A. C. & Bernier, A. (2017). Twenty years of research on parental mind-mindedness: Empirical findings, theoretical and methodological challenges, and new directions. *Developmental Review, 46*, 54–80. <https://doi.org/10.1016/j.dr.2017.07.001>
- Meinhardt, J., Sodian, B., Thoermer, C., Döhnel, K., & Sommer, M. (2011). True- and false-belief reasoning in children and adults: An event-related potential study of theory of mind. *Developmental Cognitive Neuroscience, 1*(1), 67–76.
<https://doi.org/10.1016/j.dcn.2010.08.001>
- Meinhardt-Injac, B., Daum, M. M., & Meinhardt, G. (2020). Theory of mind development from adolescence to adulthood: Testing the two-component model. *The British Journal of Developmental Psychology, 38*(2), 289–303. <https://doi.org/10.1111/bjdp.12320>
- Meins, E. (1999). Sensitivity, security, and internal working models: Bridging the transmission gap. *Attachment & Human Development, 1*(3), 325–342.
<https://doi.org/10.1080/14616739900134181>
- Meins, E., Fernyhough, C., Arnott, B., Leekam, S. R., & de Rosnay, M. (2013). Mind-mindedness and theory of mind: Mediating roles of language and perspectival symbolic play. *Child Development, 84*(5), 1777–1790. <https://doi.org/10.1111/cdev.12061>
- Meins, E., Fernyhough, C., de Rosnay, M., Arnott, B., Leekam, S. R., & Turner, M. (2012). Mind-mindedness as a multidimensional construct: Appropriate and nonattuned mind-

- related comments independently predict infant–mother attachment in a socially diverse sample. *Infancy*, *17*(4), 393–415. <https://doi.org/10.1111/j.1532-7078.2011.00087.x>
- Meins, E., Fernyhough, C., Fradley, E., & Tuckey, M. (2001). Rethinking maternal sensitivity: Mothers' comments on infants' mental processes predict security of attachment at 12 months. *Journal of Child Psychology and Psychiatry*, *42*(5), 637–648. <https://doi.org/10.1111/1469-7610.00759>
- Meins, E., Fernyhough, C., Wainwright, R., Das Gupta, M., Fradley, E., & Tuckey, M. (2002). Maternal mind-mindedness and attachment security as predictors of theory of mind understanding. *Child Development*, *73*(6), 1715–1726. <https://doi.org/10.1111/1467-8624.00501>
- Menon, V. & Uddin, L. (2010). Saliency, switching, attention and control: a network model of insula function. *Brain Structure and Function*, *214*(5-6), 655–667. <https://doi.org/10.1007/s00429-010-0262-0>
- Miguel-Hidalgo, J. J. (2013). Brain structural and functional changes in adolescents with psychiatric disorders. *International Journal of Adolescent Medicine and Health*, *25*(3), 245–256. <https://doi.org/10.1515/ijamh-2013-0058>
- Milligan, K., Astington, J. W., & Dack, L. A. (2007). Language and theory of mind: meta-analysis of the relation between language ability and false-belief understanding. *Child Development*, *78*(2), 622–646. <https://doi.org/10.1111/j.1467-8624.2007.01018.x>
- Mills, K. L., Goddings, A.-L., Herting, M. M., Meuwese, R., Blakemore, S.-J., Crone, E. A., Dahl, R. E., Güroğlu, B., Raznahan, A., Sowell, E. R., & Tammes, C. K. (2016). Structural brain development between childhood and adulthood: Convergence across four longitudinal samples. *NeuroImage*, *141*, 273–281. <https://doi.org/10.1016/j.neuroimage.2016.07.044>

Monticelli, M., Zeppa, P., Mammi, M., Penner, F., Melcarne, A., Zenga, F., & Garbossa, D.

(2021). Where we mentalize: Main cortical areas involved in mentalization. *Frontiers in Neurology*, *12*. <https://doi.org/10.3389/fneur.2021.712532>

Moriguchi, Y., Ohnishi, T., Mori, T., Matsuda, H., & Komaki, G. (2007). Changes of brain activity in the neural substrates for theory of mind during childhood and adolescence.

Psychiatry and Clinical Neurosciences, *61*(4), 355–363. <https://doi.org/10.1111/j.1440-1819.2007.01687.x>

Mustard, J. (2006). Experience-based brain development: Scientific underpinnings of the importance of early child development in a global world. *Paediatrics & Child Health*, *11*(9), 571–572.

Narita, K., Takei, Y., Suda, M., Aoyama, Y., Uehara, T., Kosaka, H., Amanuma, M., Fukuda,

M., & Mikuni, M. (2010). Relationship of parental bonding styles with gray matter volume of dorsolateral prefrontal cortex in young adults. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *34*(4), 624–631.

<https://doi.org/10.1016/j.pnpbp.2010.02.025>

Nichols, T., & Hayasaka, S. (2003). Controlling the familywise error rate in functional neuroimaging: A comparative review. *Statistical Methods in Medical Research*, *12*(5),

419–446. <https://doi.org/10.1191/0962280203sm341ra>

Olson, I. R., McCoy, D., Klobusicky, E., & Ross, L. A. (2013). Social cognition and the anterior temporal lobes: a review and theoretical framework. *Social Cognitive and Affective Neuroscience*, *8*(20), 123–133. <https://doi.org/10.1093/scan/nss119>.

<https://doi.org/10.1093/scan/nss119>.

Overgaauw, S., van Duijvenvoorde, A. C. K., Gunther Moor, B., & Crone, E. A. (2015). A

longitudinal analysis of neural regions involved in reading the mind in the eyes. *Social*

Cognitive and Affective Neuroscience, 10(5), 619–627.

<https://doi.org/10.1093/scan/nsu095>

Perner, J., Leekam, S. R., & Wimmer, H. (1987). Three-year-olds' difficulty with false belief: The case for a conceptual deficit. *British Journal of Developmental Psychology*, 5(2), 125–137. <https://doi.org/10.1111/j.2044-835X.1987.tb01048.x>

Pernet, C. R., Latinus, M., Nichols, T. E., & Rousselet, G. A. (2015). Cluster- based computational methods for mass univariate analyses of event-related brain potentials/fields: A simulation study. *Journal of Neuroscience Methods*, 250, 85–93. <https://doi.org/10.1016/j.jneumeth.2014.08.003>

Peterson, C. & Slaughter, V. (2003). Opening windows into the mind: Mothers' preferences for mental state explanations and children's theory of mind. *Cognitive Development*, 18(3), 399–429. [https://doi.org/10.1016/S0885-2014\(03\)00041-8](https://doi.org/10.1016/S0885-2014(03)00041-8)

Peterson, C. C., & Wellman, H. M. (2019). Longitudinal theory of mind (ToM) development from preschool to adolescence with and without ToM delay. *Child Development*, 90(6), 1917–1934. <https://doi.org/10.1111/cdev.13064>

Richardson, H. (2019). Development of brain networks for social functions: Confirmatory analyses in a large open source dataset. *Developmental Cognitive Neuroscience*, 37, 100598. <https://doi.org/10.1016/j.dcn.2018.11.002>

Richardson, H., Lisandrelli, G., Riobueno-Naylor, A., & Saxe, R. (2018). Development of the social brain from age three to twelve years. *Nature Communications*, 9(1), 1027. <https://doi.org/10.1038/s41467-018-03399-2>

Rilling, J. K., & Sanfey, A. G. (2009). Social Interaction. In L. R. Squire (Ed.), *Encyclopedia of Neuroscience* (pp. 41–48). Academic Press. <https://doi.org/10.1016/B978-008045046-9.01539-4>

- Ross, L. A. & Olson, I. R. (2010). Social cognition and the anterior temporal lobes. *NeuroImage*, *49*(4), 3452–3462. <https://doi.org/10.1016/j.neuroimage.2009.11.012>
- Schurz, M., Radua, J., Aichhorn, M., Richlan, F., & Perner, J. (2014). Fractionating theory of mind: A meta-analysis of functional brain imaging studies. *Neuroscience & Biobehavioral Reviews*, *42*, 9–34. <https://doi.org/10.1016/j.neubiorev.2014.01.009>
- Schurz, M., Radua, J., Tholen, M. G., Maliske, L., Margulies, D. S., Mars, R. B., Sallet, J., & Kanske, P. (2021). Toward a hierarchical model of social cognition: A neuroimaging meta-analysis and integrative review of empathy and theory of mind. *Psychological Bulletin*, *147*(3), 293–327. <https://doi.org/10.1037/bul0000303>
- Sebastian, C. L., Fontaine, N. M., Bird, G., Blakemore, S. J., Brito, S. A., McCrory, E. J., & Viding, E. (2012). Neural processing associated with cognitive and affective theory of mind in adolescents and adults. *Social, Cognitive and Affective Neuroscience*, *7*(1), 53–63. <https://doi.org/10.1093/scan/nsr023>
- Serbin, L. A., Kingdon, D., Ruttle, P. L., & Stack, D. M. (2015). The impact of children’s internalizing and externalizing problems on parenting: Transactional processes and reciprocal change over time. *Development and Psychopathology*, *27*(4), 969–986. <https://doi.org/10.1017/S0954579415000632>
- Sharp, C. & Fonagy, P. (2008). The parent’s capacity to treat the child as a psychological agent: Constructs, measures and implications for developmental psychology. *Social Development*, *17*(3), 737–754. <https://doi.org/10.1111/j.1467-9507.2007.00457.x>
- Slaughter, V., Peterson, C. C. & Mackintosh, E. (2007). Mind what mother says: Narrative input and theory of mind in typical children and those on the autism spectrum. *Child Development*, *78*(3), 839–858. <https://doi.org/10.1111/j.1467-8624.2007.01036.x>

- Smith, D. K., Johnson, A. B., Pears, K. C., Fisher, P. A., & DeGarmo, D. S. (2007). Child maltreatment and foster care: Unpacking the effects of prenatal and postnatal parental substance use. *Child Maltreatment, 12*(2), 150–160.
<https://doi.org/10.1177/1077559507300129>
- Smith, P. K., Cowie, H., & Blades, M. (2015). *Understanding children's development*. West Sussex, UK: John Wiley & Sons Inc.
- Smith, S. M., & Nichols, T. E. (2009). Threshold-free cluster enhancement: Addressing problems of smoothing, threshold dependence and localisation in cluster inference. *NeuroImage, 44*(1), 83–98. <https://doi.org/10.1016/j.neuroimage.2008.03.061>
- Steinbeis, N., Bernhardt, B. C., & Singer, T. (2012). Impulse control and underlying functions of the left DLPFC mediate age-related and age-independent individual differences in strategic social behavior. *Neuron, 73*(5), 1040–1051.
<https://doi.org/10.1016/j.neuron.2011.12.027>
- Szpak, M., & Białecka-Pikul, M. (2020). Links between attachment and theory of mind in childhood: Meta-analytic review. *Social Development, 29*(3), 653–673.
<https://doi.org/10.1111/sode.12432>
- Tomoda, A., Suzuki, H., Rabi, K., Sheu, Y.-S., Polcari, A., & Teicher, M. H. (2009). Reduced prefrontal cortical gray matter volume in young adults exposed to harsh corporal punishment. *NeuroImage, 47*(Suppl 2), T66–T71.
<https://doi.org/10.1016/j.neuroimage.2009.03.005>
- Tottenham, N. (2014). The importance of early experiences for neuro-affective development. *Current Topics in Behavioral Neurosciences, 16*, 109–129.
https://doi.org/10.1007/7854_2013_254

- Valle, A., Massaro, D., Castelli, I., & Marchetti, A. (2015). Theory of Mind development in adolescence and early adulthood: The growing complexity of recursive thinking ability. *Europe's Journal of Psychology, 11*(1), 112–124. <https://doi.org/10.5964/ejop.v11i1.829>
- Wade, M., Prime, H., Jenkins, J. M., Yeates, K. O., Williams, T., & Lee, K. (2018). On the relation between theory of mind and executive functioning: A developmental cognitive neuroscience perspective. *Psychonomic Bulletin & Review, 25*(6), 2119–2140. <https://doi.org/10.3758/s13423-018-1459-0>
- Wang, A. T., Lee, S. S., Sigman, M., & Dapretto, M. (2006). Developmental changes in the neural basis of interpreting communicative intent. *Social Cognitive and Affective Neuroscience, 1*(2), 107–121. <https://doi.org/10.1093/scan/nsl018>
- Wellman, M. H., Cross, D., & Watson, J. (2001). Meta-Analysis of Theory-of-Mind Development: The truth about False Belief. *Child Development, 72*(3), 655–684. <https://doi.org/10.1111/1467-8624.00304>
- Wellman, H. M., & Liu, D. (2004). Scaling of theory-of-mind tasks. *Child Development, 75*(2), 523–541. <https://doi.org/10.1111/j.1467-8624.2004.00691.x>
- Wimmer, H., & Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition, 13*(1), 103–128. [https://doi.org/10.1016/0010-0277\(83\)90004-5](https://doi.org/10.1016/0010-0277(83)90004-5)
- Yatziv, T., Kessler, Y., Atzaba-Poria, N. (2018). What's going on in my baby's mind? Mothers' executive functions contribute to individual differences in maternal mentalization during mother-infant interactions. *PLoS ONE, 13*(11), e0207869. <https://doi.org/10.1371/journal.pone.0207869>

Yoon, U., Fonov, V. S., Perusse, D., & Evans, A. C. (2009). The effect of template choice on morphometric analysis of pediatric brain data. *NeuroImage*, *45*(3), 769–777.

<https://doi.org/10.1016/j.neuroimage.2008.12.046>

Zahn, R., Moll, J., Krueger, F., Huey, E. D., Garrido, G., & Grafman, J. (2007). Social concepts are represented in the superior anterior temporal cortex. *Proceedings of the National Academy of Sciences*, *104*(15), 6430–6435. https://doi.org/10.1073_pnas.0607061104

Zeegers, M. A. J., Colonnese, C., Stams, G.-J. J. M., & Meins, E. (2017). Mind matters: A meta-analysis on parental mentalization and sensitivity as predictors of infant–parent attachment. *Psychological Bulletin*, *143*(12), 1245–1272.

<https://doi.org/10.1037/bul0000114>

Table 1

Descriptive Statistics and Group Comparisons for Scanner Differences

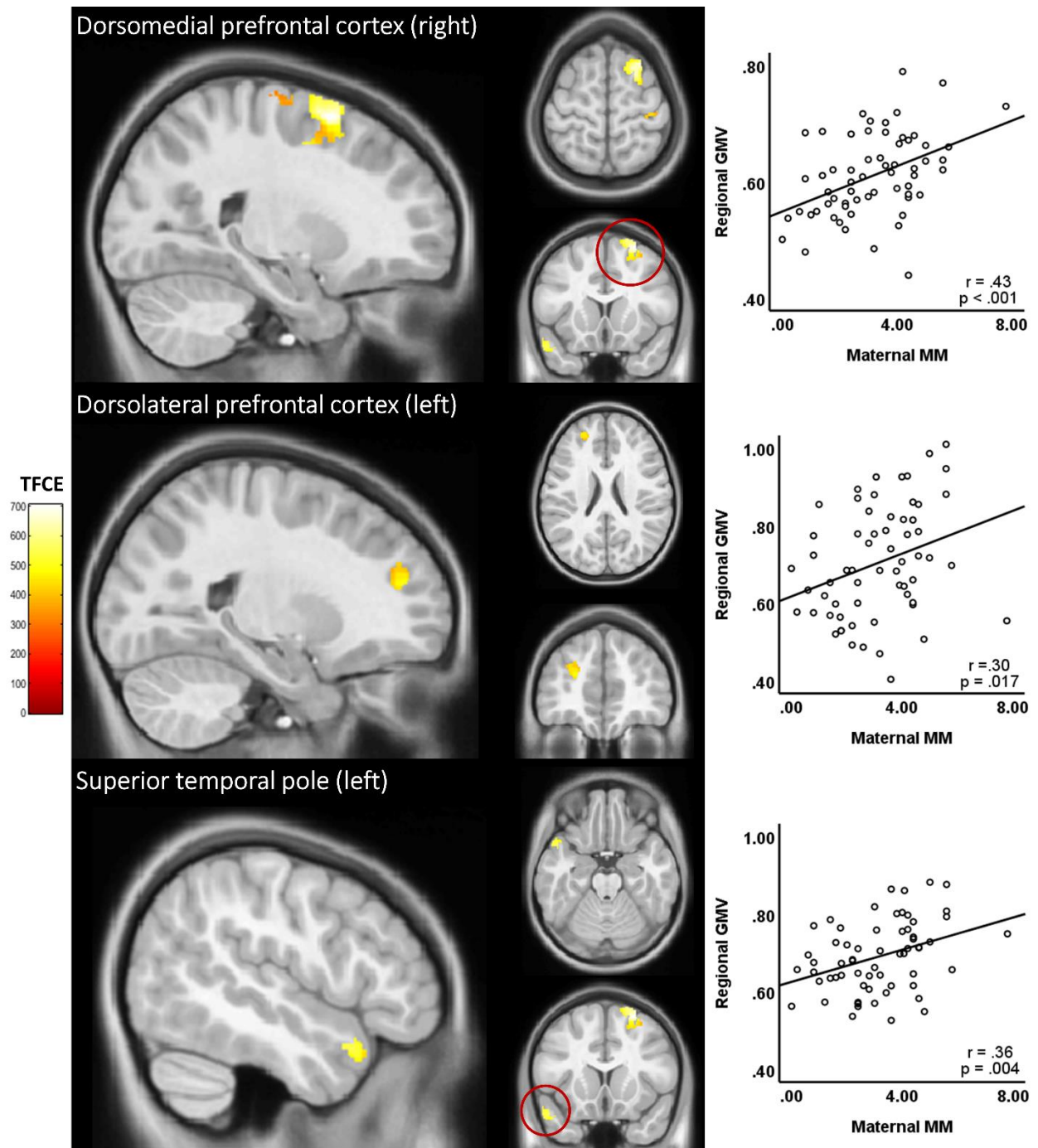
	Total (<i>n</i> = 62)	Trio (<i>n</i> = 31)	Prisma (<i>n</i> = 31)	Group comparisons
Child				
Age	10.46 ± 0.45	10.66 ± 0.54	10.25 ± 0.19	<i>t</i> (60) = 4.06; <i>p</i> < .001
Sex	45.16%	41.94%	48.39%	<i>X</i> ² (1) = 0.26; <i>p</i> = .61
TIV	1432.55 ± 108.06	1417.39 ± 97.13	1447.71 ± 117.61	<i>t</i> (60) = -1.11; <i>p</i> = .27
ToM	0.82 ± 0.80	0.97 ± 0.84	0.67 ± 0.75	<i>t</i> (60) = 1.44; <i>p</i> = .16
Maternal MM	3.16 ± 1.58	2.98 ± 1.51	3.33 ± 1.66	<i>t</i> (60) = -0.89; <i>p</i> = .38
Parental age at recruitment				
Mothers	31.34 ± 4.74	31.42 ± 5.10	31.27 ± 4.43	<i>t</i> (59) = 0.13; <i>p</i> = .90
Fathers	33.22 ± 5.44	32.94 ± 4.97	33.52 ± 5.99	<i>t</i> (58) = -0.41; <i>p</i> = .68
Parental years of education				
Mothers	15.71 ± 2.17	15.35 ± 2.32	16.06 ± 1.98	<i>t</i> (60) = -1.30; <i>p</i> = .20
Fathers	15.51 ± 2.38	15.48 ± 2.03	15.53 ± 2.73	<i>t</i> (59) = -0.08; <i>p</i> = .94
Ethnicity				
Mothers	83.87%	77.42%	90.32%	<i>X</i> ² (1) = 3.07; <i>p</i> = .08
Fathers	77.42%	74.19%	80.65%	<i>X</i> ² (1) = 1.35; <i>p</i> = .25
Family income	77.42%	77.42%	77.42%	<i>X</i> ² (1) = 0.00; <i>p</i> = 1.00
Language at home	85.48%	77.42%	93.54%	<i>X</i> ² (1) = 3.12; <i>p</i> = .08

Note. For child age, TIV (total intracranial volume) and ToM (theory of mind), parental age and education, as well as maternal MM (mind-mindedness), values represent mean \pm standard deviation. For child sex, values represent percentages of boys. For ethnicity, family income, and language at home, values represent percentages of families with a White mother/father, an income above \$60,000, and French as the main language. Ages are represented in years and TIV are represented in cm³.

Figure 1

Associations Between Maternal Mind-Mindedness in Infancy and Regional Grey Matter Volume in Late Childhood

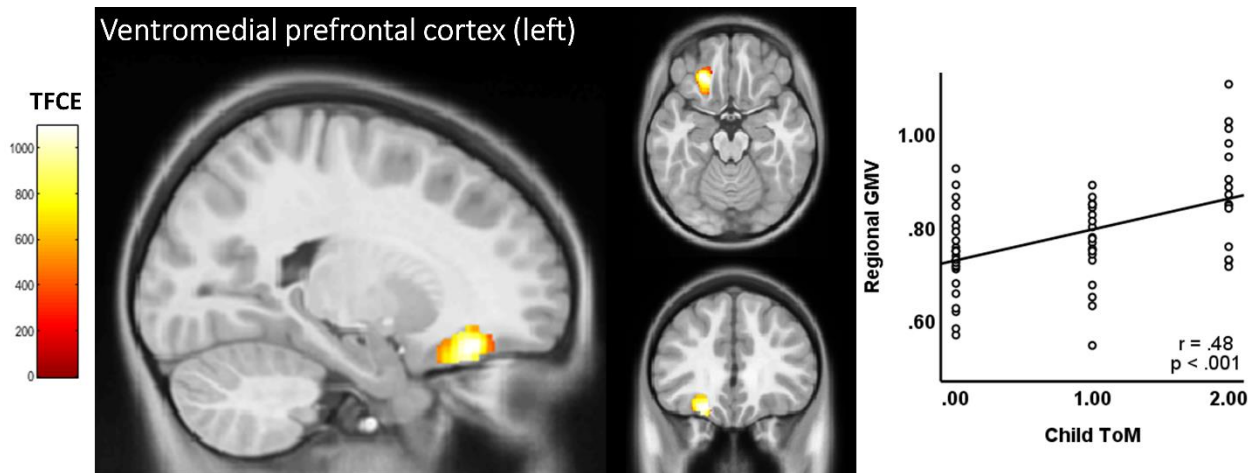
1



Note. Higher levels of maternal mind-mindedness in infancy are associated with greater grey matter volume (GMV) in the right dorsomedial prefrontal cortex (extending to the supplementary motor area; $x = 24, y = 12, z = 62$), as well as the left dorsolateral prefrontal cortex ($x = -21, y = 48, z = 18$) and superior temporal pole ($x = -48, y = 12, z = -23$). Contrast represents threshold-free cluster enhancement (TFCE) statistic at combined peak-cluster-level, uncorrected, $p < .001$.

Figure 2

Associations Between Child Theory of Mind and Regional Grey Matter Volume in Late Childhood



Note. Better theory of mind performance in early childhood is associated with greater grey matter volume (GMV) in the left ventromedial prefrontal cortex ($x = -23, y = 35, z = -18$) in late childhood. Contrast represents threshold-free cluster enhancement (TFCE) statistic at combined peak-cluster-level, uncorrected, $p < .001$.