**Early continuity in neuronal correlates of mentalizing: ALE meta-analyses
in adults, children and youths**

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Abstract

The ability to understand mental states of others is known as Theory of Mind or mentalizing. Neuroimaging studies in adults have reported activation increases in medial prefrontal, inferior frontal, temporoparietal cortices and precuneus during mentalizing. In children/youths, activation in some areas of this social brain network are suggested to develop early, while other areas mature later. We compared neuroimaging evidence in children/youths and adults during mentalizing using coordinate-based activation likelihood estimation meta-analyses to inform about brain regions consistently or differentially engaged across age. Healthy adults (N=5286) recruited medial prefrontal and middle/inferior frontal cortices, precuneus, temporoparietal junction and middle temporal gyri during mentalizing, which were functionally connected to bilateral inferior/superior parietal lobule and thalamus/striatum. Children and youths (N=479) recruited similar, but fewer regions, including temporoparietal junction, precuneus, medial prefrontal and middle temporal cortices. Subgroup analyses revealed an early continuous engagement of middle medial prefrontal cortex, precuneus and right temporoparietal junction in children (8–11y) and youths (12–18y). Youths additionally recruited the left temporoparietal junction and middle/inferior temporal cortex. Overall, the observed continuous engagement of the medial prefrontal cortex, precuneus and right temporoparietal junction during mentalizing across all ages reflects an early specialization of some of the key social brain regions.

Keywords: mentalizing, functional neuroimaging, development, children, adults

1. Introduction

A fundamental premise of our everyday social life is the prerequisite to understand and acknowledge the emotions and intentions of people around us. This ability to constantly observe, decode and understand mental states of ourselves and others is enabled by our Theory of Mind and reflected in our mentalizing skills (Frith & Frith, 2007). Mentalizing skills have shown to be positively associated with healthy social functioning (Slaughter et al., 2015). Atypical mentalizing skills, however, have been described to be characteristic of several psychiatric disorders, including autism spectrum disorders, conduct disorder, depression, schizophrenia or borderline traits (Baron-Cohen et al., 1997; Kerr et al., 2003; Kronbichler et al., 2017; Moran et al., 2011; Sharp, 2008; Sharp et al., 2011; Zobel et al., 2010). Depending on the clinical diagnosis, hyper-mentalizing (e.g., bipolar disorder), reduced mentalizing (e.g., psychopathy) or altered mentalizing skills (e.g., conduct disorder) have been reported (Blair et al., 2004; Sharp et al., 2011). Given their critical role for everyday life and in clinical diagnostics, it is little surprising that mentalizing concepts have been key targets of improvement in different therapy settings (Björgvinsson & Hart, 2006; Fonagy & Allison, 2014; Fonagy et al., 2017).

The foundation for mature, complex mentalizing skills already starts developing early in life (Baillargeon et al., 2010). For example, mothers' use of mental state language with their six-months-old infants has been shown to predict children's later Theory of Mind performance (Meins et al., 2003; Meins et al., 2002). Similarly, studies using false belief tasks have demonstrated that basic inferences used to predict other people's intentions may already be observed in early infancy (Knudsen & Liszkowski, 2012). Studies in young children show that major conceptual improvements in mentalizing skills occur at around 3 to 6 years of age (Wellman et al., 2001). However, mentalizing skills continue to mature throughout childhood

and adolescence (Blakemore, 2008; Crone & Dahl, 2012; Crone & Steinbeis, 2017). With increasing age and skill levels individuals learn to mentalize in a flexible and adaptive manner, allowing the interpretation of increasingly complex social situations (Korkmaz, 2011).

The neuronal correlates of mentalizing have been studied through various functional magnetic resonance imaging (fMRI) paradigms. Mentalizing tasks have for example been constructed by implementing concepts of the false belief task (Mitchell, 2007; Tamnes et al., 2010), Frith–Happé animations (Gobbini et al., 2007; Moriguchi et al., 2006) or the Reading the Mind in the Eyes Test (Gallagher et al., 2000; Mascaró et al., 2013). Overall, past evidence using such types of tasks has suggested an implication of core regions of the social brain during mentalizing, including the medial prefrontal cortex, bilateral temporoparietal junction, precuneus, inferior frontal gyri and temporal lobes (for review see e.g., Kliemann & Adolphs, 2018). More precisely, the majority of studies have revealed consistent increases in brain activation in response to mentalizing in the medial prefrontal cortex and bilateral temporoparietal junction (Mar, 2011; Molenberghs et al., 2016; Schurz et al., 2014; Van Overwalle, 2009; van Veluw & Chance, 2014). Additionally, areas including the posterior superior temporal sulci and gyri, temporal poles, precuneus and inferior frontal gyri (Mar, 2011; Molenberghs et al., 2016), as well as anterior (Molenberghs et al., 2016) and posterior (Mar, 2011) cingulate cortices and middle temporal gyri (van Veluw & Chance, 2014) were identified by some, but not all studies. The observed differences in study findings have been suggested to depend on the task choice or, more specifically, on the additional cognitive processes that have to be recruited in addition to the core mechanisms of mentalizing depending on the task employed (Mar, 2011; Molenberghs et al., 2016; van Veluw & Chance, 2014).

In adults, connectivity between mentalizing regions (including temporoparietal junction, precuneus and medial prefrontal cortex) and insula, pre- and postcentral gyri and ventrolateral

prefrontal cortex has been reported (Atique et al., 2011; Burnett & Blakemore, 2009; Lombardo et al., 2010; Schuwerk et al., 2014). Such functional connectivity patterns indicate co-activation patterns of brain regions that interact with core regions involved in mentalizing, forming a larger network of brain activation and allowing a more comprehensive view on the neuronal connections engaged when processing and interpreting social information.

fMRI studies of mentalizing in children are still more rare compared to work conducted in adults. However, thanks to technical and practical advances (e.g., Bednarz & Kana, 2018; Raschle et al., 2012; Vijayakumar et al., 2018), the field of developmental neuroscience continues to grow. Existing results from developmental neuroimaging studies indicate an early specialization and potential continuous engagement of some core regions for mentalizing. Overall, mentalizing studies commonly report activation increases in the medial prefrontal cortex, temporoparietal junction and precuneus in school-aged children and on (Blakemore, 2008, 2012a, 2012b; Bowman et al., 2019; Crone & Dahl, 2012; Gweon et al., 2012; Saxe et al., 2009). However, other brain areas are suggested to mature later on and/or over a longer time course (e.g., inferior frontal gyri, superior temporal sulcus, ventromedial prefrontal cortex; Blakemore et al., 2007b; Bowman et al., 2019; Sebastian et al., 2012). Continuity and change within the neuronal regions for mentalizing are an intriguing subject of study, however limited by the amount of developmental studies conducted, the power deriving from low subject numbers and the lack of longitudinal developmental research work (Bowman et al., 2019; Foulkes & Blakemore, 2018; Madhyastha et al., 2018). Meta-analytic approaches allow the compilation of data deriving from various smaller, individual studies and may thereby overcome some of the associated power issues, allowing a more precise estimate of the present knowledge. While meta-analytic work cannot inform about change across development, it may serve as a tool to evaluate the continuity of engagement of the brain regions involved in mentalizing across children, youths and adults (Bowman et al., 2019).

Here we aimed to compile the existing knowledge on the neuronal correlates of mentalizing in children, youths and adults. We therefore conducted activation likelihood estimation meta-analyses for studies in adults, studies deriving from developmental samples (i.e., children/youths) and compared both lines of work. Our main aims therefore were to (I) perform a coordinate-based meta-analysis to integrate existing data on neuronal activation and functional connectivity patterns during mentalizing in adults, (II) compute a coordinate-based meta-analysis to integrate existing data on neuronal activation during mentalizing in children/youths and (III) run a conjunction analysis to reveal common and distinct brain regions activated by adults and children/youths during mentalizing. Based on previous studies we hypothesized that adults commonly activate brain regions related to mentalizing, namely medial prefrontal cortex, temporoparietal junction, precuneus, inferior frontal gyri and temporal cortex (Mar, 2011; Molenberghs et al., 2016; Schurz et al., 2014; Van Overwalle, 2009; van Veluw & Chance, 2014). Moreover, we expected functional connectivity between mentalizing regions (temporoparietal junction/posterior superior frontal sulcus, medial prefrontal cortex), as well as with areas engaged during lower-level processes, including emotion, movement and attentional processing (Atique et al., 2011; Burnett & Blakemore, 2009; Lombardo et al., 2010; Schuwerk et al., 2014). For children/youths, we expected a similar but still developing activation pattern reflected by the activation of some, but not all, areas reported in adults (e.g., engagement of medial prefrontal cortex, but no activation of the temporoparietal junction/superior temporal cortex yet; Blakemore, 2008, 2012a, 2012b; Crone & Dahl, 2012).

2. Methods

2.1. Literature search and study selection

We conducted systematic and standardized meta-analyses corresponding to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines and the revised Quality Of Reporting Of Meta-analyses (QUOROM) statement (Moher et al., 2009). Our main literature search was conducted through PubMed and included the keywords “fMRI Theory of Mind” with and without the restriction to “children” and/or “adolescents” (adult data search date 04.12.2018, children/youths data search 01.11.2019). Additionally, the reference lists of past meta-analyses and review articles investigating mentalizing were screened to identify any reports previously not detected using our own literature search (for details see PRISMA flow diagram, **Supplementary Information 1**). Inclusion criteria for studies entering our meta-analyses were met if whole-brain findings were reported, if coordinates were provided in standard space (i.e., Talairach & Tournoux or Montreal Neurological Institute (MNI) space) and when the contrasts included components associated with mentalizing. Only publications in English were considered. Studies based on region of interest analyses only or approaches other than functional MRI (e.g., electroencephalography, structural neuroimaging) and studies only yielding hypoactivations were excluded. The activation likelihood estimation methodology applied here did not allow inclusion of null findings. A main goal of the present study was the investigation of brain activity related to mentalizing in adults and the comparison of these findings to evidence deriving from studies in children/youths. Therefore, studies that report brain activity deriving from mixed groups of adolescents and adults (no report of separate coordinates for adults and children/youths) were not included in the present analyses. Coordinate-based findings from clinical research studies were only included for the healthy subgroups (i.e., if they report coordinates on healthy controls or if they list main effects,

representing brain activation that does not differ between the psychiatric group and the control group).

This procedure yielded a total of 228 studies of functional neuroimaging evidence for mentalizing with a total of 245 experiments and 5765 subjects. The meta-analysis focusing on research studies in adults included 206 studies with 2876 activation foci from 223 experiments in 5286 subjects (listed in **Table 1**, for more details see **Supplementary Information 2**). The meta-analysis on developmental neuroimaging studies of mentalizing (i.e., children/youths) included 22 studies with 217 activation foci from 22 experiments in 479 subjects (**Table 2** and **Supplementary Information 3**).

Table 1. Functional neuroimaging studies considered in the meta-analysis on mentalizing in adults, including number of subjects (N) and task type (further details are provided in **Supplementary Information 2**).

First author, year	N	Task type	First author, year	N	Task type	First author, year	N	Task type
Gallagher*, 2000	6	ToM cartoon, ToM reading	Kim*, 2005	14	Matching faces with situation	Todorov*, 2007	9	Matching faces with behavior
Russell*, 2000	7	Reading the Mind in the Eyes	Ochsner*, 2005	16	Self-referential thinking (reading)	Wakusawa*, 2007	31	Irony/metaphor
Vogeley*, 2001	8	ToM reading	Aichhorn*, 2006	21	Visual perspective taking	Young*, 2007	27	False belief
Ferstl*, 2002	9	ToM reading	Elliott*, 2006	12	Reward processing	Abraham*, 2008	17	ToM reading
Martin*, 2003	12	Frith-Happé	Fukui*, 2006	16	Reward processing	Brüne*, 2008	13	ToM cartoon
Saxe*, 2003	25	False belief	Kobayashi*, 2006	32	False belief	Hooker*, 2008	20	False belief
Decety*, 2004	12	Computer/human interaction	Marjoram*, 2006	13	Humor, false belief	Kédia*, 2008	29	Pain/harm in others
Gallagher*, 2004	13	Expressive gestures	Moriguchi*, 2006	38	Frith-Happé	Kliemann*, 2008	26	False belief
German*, 2004	16	Pretended/real actions	Saxe*, 2006	12	False belief	Kobayashi*, 2008	16	False belief
Gobbini*, 2004	10	Face familiarity	Saxe*, 2006	12	False belief	Krach*, 2008	20	Prisoner's dilemma
Grèzes*, 2004	6	False belief	Spiers*, 2006	20	ToM cartoon	Malhi*, 2008	20	Frith-Happé
Leibenluft*, 2004	7	Own/others' children face processing	Uchiyama*, 2006	20	Sarcasm	Mason*, 2008	18	ToM reading
Platek*, 2004	5	Reading the Mind in the Eyes	Völlm*, 2006	13	ToM cartoon	Rilling*, 2008	20	Prisoner's dilemma
Rilling*, 2004	19	Prisoner's dilemma	Cheng*, 2007	14	Pain/harm in others	Samson*, 2008	17	Humor
Seger*, 2004	12	Food preferences of others	Gilbert*, 2007	16	Evaluation of helpfulness (reading)	Sommer*, 2008	18	Emotion attribution
Walter*, 2004	13	ToM cartoon	Gobbini*, 2007	24	Frith-Happé, false belief	Vanderwal*, 2008	17	Frith-Happé
Walter*, 2004	12	ToM cartoon	Mitchell, 2007	20	False belief	Young*, 2008	14	False belief
Bhatt*, 2005	16	Self-referential thinking (reading)	Schulte-Rüther*, 2007	26	Emotional state evaluation (images)	Aichhorn*, 2009	21	False belief
den Ouden*, 2005	11	ToM reading	Sommer*, 2007	16	False belief	Assaf*, 2009	19	Computer/human interaction
Harris*, 2005	12	ToM reading	Takahashi*, 2007	16	Joy/pride in others	Bahnemann*, 2009	25	Cartoon ToM

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First author, year	N	Task type	First author, year	N	Task type	First author, year	N	Task type
Jenkins*, 2009	15	False belief	Rapp*, 2010	15	Irony	Spunt*, 2011	15	Action identification (images)
Kircher*, 2009	12	Prisoner's dilemma	Ross*, 2010	15	Frith-Happé	van der Meer*, 2011	19	False belief
Krach*, 2009	24	Prisoner's dilemma	Shibata*, 2010	13	Irony	Walter*, 2011	109	ToM cartoon
Mano*, 2009	18	ToM reading	Sommer*, 2010	12	False belief	Young*, 2011	17	False belief
Otsuka*, 2009	24	ToM reading	Sommer*, 2010	14	ToM cartoon	Becchio*, 2012	16	Reach-to-grasp action movies
Sripada*, 2009	26	Computer/human interaction	Wolf*, 2010	18	ToM cartoon/movie	Canessa*, 2012	27	ToM images
Walter* 2009	12	ToM cartoon	Yoshida*, 2010	12	Predict peer strategy during game	Chaminade*, 2012	18	Computer/human interaction
Young*, 2009	28	False belief	Young*, 2010	17	False belief	Cheung*, 2012	20	False belief
Abraham*, 2010	22	False belief	Zaitchik*, 2010	15	False belief	Das*, 2012	22	Frith-Happé
Adams*, 2010	28	Reading the Mind in the Eyes	Centelles*, 2011	14	ToM motion movie	de Achával*, 2012	14	Reading the Mind in the Eyes
Castelli*, 2010	24	Reading the Mind in the Eyes	Dodell-Feder*, 2011	62	False belief	Döhnelt*, 2012	18	False belief
Focquaert*, 2010	24	Reading the Mind in the Eyes	Koelkebeck*, 2011	15	Frith-Happé	Hartwright*, 2012	19	False belief
Hooker*, 2010	15	ToM cartoon	Lee*, 2011	13	False belief	Kestemont*, 2012	34	ToM reading
Jimura*, 2010	34	False belief	Liew*, 2011	18	Interpretation of others' gestures	Mascaro*, 2012	21	Reading the Mind in the Eyes
Kim*, 2010	24	Matching faces with situation	Ma*, 2011	30	ToM reading	Mier*, 2012	13	ToM reading/faces
Lombardo*, 2010	33	ToM reading	Ma*, 2011	15	ToM reading	Moran*, 2012	128	Frith-Happé, moral judgement, false belief
Marsh*, 2010	24	Action identification (reading)	Mason*, 2011	10	ToM reading	Rabin*, 2012	18	Images of others'/own events
Mier*, 2010	16	ToM reading/faces	McAdams*, 2011	17	Frith-Happé	Roser*, 2012	14	False belief
Mier*, 2010	40	ToM reading/faces	Otsuka*, 2011	22	ToM reading	Spotorno*, 2012	20	Irony
Modinos*, 2010	36	ToM cartoon	Polosan*, 2011	14	Computer/human interaction	Spunt*, 2012a	21	Action identification (images)
Murphy*, 2010	10	Evaluation of others' attributes	Rothmayr*, 2011	12	False belief	Spunt*, 2012b	22	Action identification (images)
Pincus*, 2010	9	Reading the Mind in the Eyes	Schnell*, 2011	21	ToM cartoon	Uchiyama*, 2012	20	Sarcasm/metaphors
Rabin*, 2010	18	Images of others'/own events	Shibata*, 2011	15	Indirect speech			

First author, year	N	Task type	First author, year	N	Task type	First author, year	N	Task type
Veroude*, 2012	25	False belief	Spunt*, 2014	29	Action identification (images)	van Ackeren*, 2016	25	Indirect speech processing
Bodden*, 2013	30	False belief	Van Hoeck*, 2014	19	ToM reading	Bravo*, 2017	14	Auditory ToM
Contreras*, 2013	36	ToM reading, false belief	Alderson-Day*, 2015	19	False belief	Desmet*, 2017	17	Frith-Happé
Corradi-Dell'Acqua*, 2013	46	False belief	Frank*, 2015	34	False belief	Döhnel*, 2017	22	False belief
Dufour*, 2013	27	False belief	Hartwright*, 2015	21	False belief	Eddy*, 2017	25	False belief
Hervé*, 2013	42	ToM reading	Kandylaki*, 2015	20	False belief	Feng*, 2017	23	Indirect replies
Kullman*, 2013	18	Reading the Mind in the Eyes	Kanske*, 2015	25	ToM reading/faces	Lewis*, 2017	17	ToM reading
McAdams*, 2013	18	Frith-Happé	Littlefield*, 2015	23	ToM reading/faces	Massau*, 2017	50	Moral judgement of others' behavior
Saft*, 2013	26	ToM cartoon	Mohnke*, 2015	297	ToM cartoon	Mier*, 2017	44	ToM reading/faces
Schiffer*, 2013	22	Reading the Mind in the Eyes	Otti*, 2015	20	Frith-Happé	Özdem*, 2017	21	Eye gaze evaluation
van der Meer*, 2013	19	False belief	Schlaffke*, 2015	39	ToM cartoon	Powell*, 2017	12	Predict peer strategy during game
Varga*, 2013	24	Irony	Schurz*, 2015	22	Visual perspective taking	White*, 2017	23	Pain/harm in others
Ampe*, 2014	17	Action identification (images)	Spunt*, 2015	480	False belief	White*, 2017	23	Pain/harm in others
Dodell-Feder*, 2014	18	ToM reading	Wang*, 2015	56	ToM cartoon	Ammons*, 2018	14	Frith-Happé
Dodell-Feder*, 2014	18	False belief	Willert*, 2015	81	ToM cartoon	Bartholomeusz*, 2018	22	ToM cartoon
Feng*, 2014	17	Humor	Bardi*, 2016	22	False belief	Bitsch*, 2018	20	Prisoner's dilemma
Hartwright*, 2014	20	False belief	Dungan*, 2016	24	False belief	Bliksted*, 2018	17	Frith-Happé
Lee*, 2014	19	False belief	Eddy*, 2016	50	False belief	Grant*, 2018	50	ToM reading
Mier*, 2014	18	ToM reading/faces	Hennion*, 2016	25	Frith-Happé	Herold*, 2018	12	Irony
Reniers*, 2014	15	ToM faces	Jacoby*, 2016	20	False belief	Lee*, 2018	16	Pain/harm in others
Riekk*, 2014	23	Frith-Happé	Kirkovski*, 2016	23	Frith-Happé	Lin*, 2018	39	ToM reading
Schneider*, 2014	16	False belief	Lavoie*, 2016	19	ToM reading	Niemi*, 2018	16	Moral judgements of others
Schuwert*, 2014	21	False belief	Schmitgen*, 2016	21	ToM cartoon	Nijhof*, 2018	21	False belief

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First author, year	N	Task type	First author, year	N	Task type	First author, year	N	Task type
Ohtsubo*, 2018	37	Others apologizing	Tsoi*, 2018	25	Pain/harm in others	Lassalle*, 2019	20	Pain/harm in others
Sommer*, 2018	15	False belief	Wurm*, 2018	18	Action identification (images)	Zhu*, 2019	30	Guilt/shame in others
Specht*, 2018	18	ToM cartoon	Zhang*, 2018	58	Ambiguos ToM reading			
Thye*, 2018	18	Reading the Mind in the Eyes	Greven*, 2019	25	Body judgement of others			

*=only first authors are listed, N=number of subjects, ToM=Theory of Mind, Frith-Happé=Frith-Happé animations or adaptations thereof, ToM cartoon=comics or cartoons eliciting mentalizing, ToM reading=sentences or

statements eliciting mentalizing, ToM faces=images of faces showing an intention or affective state, ToM movie=movie clips eliciting mentalizing. The full references of this table can be found in Supplementary Information 5.

Table 2. Functional neuroimaging studies considered in the meta-analysis on mentalizing in children/youths, including number (N) and mean age of subjects, contrast and *p* values/correction (MNI coordinates are provided in **Supplementary Information 3**).

First author, year	N	Age [mean age $\pm$ SD/range in years]	Task type	Contrast	<i>p</i> value, correction
Ohnishi*, 2004	11	[10.0/7–13]	Frith–Happé	ToM animation>Control	<i>p</i> <0.05 uc
Wang*, 2006	12	[9–14]	Irony	Irony>Control	SVC at <i>p</i> <0.05, <i>k</i> $\geq$ 37
Blakemore*, 2007	19	[14.8/12–18]	ToM reading	ToM statements>Physical causality	Random fields theory corr. or SVC at <i>p</i> <0.05
Kobayashi*, 2007	24	[9.1 $\pm$ 1.2/8–11]	False belief	False belief>Physical causality	<i>p</i> <0.005 uc
Moriguchi*, 2007	16	[13.4 $\pm$ 2.2/9–16]	Frith–Happé	ToM animation>Control condition	<i>p</i> <0.001 uc, <i>k</i> $\geq$ 50
Pfeifer*, 2007	12	[10.2/9–10]	Self-referential thinking (auditory)	Self>Social knowledge	<i>p</i> <0.005 uc, <i>k</i> $\geq$ 10
Burnett*, 2008	19	[14.8/11–18]	Guilt/embarrassment in others or self	Social (guilt/embarrassment)>Basic emotion (disgust/fear)	SVC at <i>p</i> <0.05
Decety*, 2008	17	[9.0/7–12]	Pain in others	Pain>No pain (body parts)	<i>p</i> <0.005 uc, <i>k</i> $\geq$ 8
Kobayashi*, 2008	12	[10.1 $\pm$ 1.0/8–11]	False belief	False belief>Physical causality	<i>p</i> <0.005 uc
Pfeifer*, 2009	12	[12.7/11–13]	Self-referential thinking (auditory)	Self>Social knowledge	Corr. at <i>p</i> <0.05

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Saxe*, 2009	13	[8.7/6–10]	Auditory ToM	Mental state stories>Physical facts	$p<0.001$ uc, $k\geq 5$
Sommer*, 2010	10	[11.3 $\pm$ 0.7/10–12]	False belief	False>True belief	Cluster-level corr. or SVC at $p<0.01$
Gweon*, 2012	20	[8.5/5–11]	ToM reading	ToM statements>Physical causality	Monte-Carlo simulation corr. at $p<0.05$, $k\geq 200$
Schulte- Rüther*, 2012	21	[15.8 $\pm$ 1.9/12–18]	Frith–Happé	ToM animation>Control	Voxel-level FWE corr., $k\geq 30$
Sebastian*, 2012	47	[14.1 $\pm$ 1.7/10–16]	False belief	Affective ToM>Physical causality, Cognitive ToM>Physical causality	Cluster-level FWE corr. at $p<0.05$
Yokota*, 2013	28	[8.9/8–9]	ToM cartoon	Social>Less social	Cluster-level FWE corr. at $p<0.05$
O'Nions*, 2014	48	[13.9 $\pm$ 1.7/10–16]	False belief	Cognitive ToM>Control	Peak-level FWE corr. at $p<0.05$
Overgaauw*, 2014	32	[15.5/12–19]	Reading the Mind in the Eyes	Mental state>Control	FDR corr. at $p<0.05$, $k\geq 10$
White*, 2014	33	[13.7/11–17]	False belief	Cognitive ToM>Control	FWE corr. at $p<0.05$
Kana*, 2015	13	[12.7/10–15]	Frith–Happé	ToM animation>Control	Monte-Carlo simulation corr. at $p<0.05$, $k\geq 100$
Alkire*, 2018	28	[10.4 $\pm$ 1.5/8–12]	Predict peer strategy during game	Mental state prediction>Control	Cluster-level corr. at $p<0.05$, $k\geq 86$
Mukerji*, 2019	32	[11.1 $\pm$ 1.4/9–12]	False belief	False belief>False photograph	$p<0.001$ uc, $k\geq 10$ or FWE corr. at $p<0.05$

*=only first authors are listed, N=number of subjects, SD=standard deviation, ToM=Theory of Mind,

Frith-Happé=Frith-Happé animations or adaptations, ToM cartoon=comics or cartoons eliciting mentalizing,

ToM reading=sentences or statements eliciting mentalizing, uc=uncorrected, corr.=corrected, SVC=small volume correction, FWE=family-wise error rate, k=number of voxels in cluster. The full references of this table can be found in Supplementary Information 5.

2.1. Meta-analytic methods

2.1.1. Activation likelihood estimation meta-analyses

The present meta-analyses were conducted using an activation likelihood estimation approach as implemented in the GingerALE software, version 3.0.2 (Eickhoff et al., 2009). In short, a 3D image is created from each group of foci. The 3D image derives from the mask, individual foci and a Gaussian blur, and a full width at half maximum is empirically derived from the subject size of the experiments (Eickhoff et al., 2009). The three-dimensional probabilities of the activation foci are then combined for each voxel, resulting in modelled activation maps. The resulting ALE scores are computed by finding the convergence across all modelled activation maps, which are then compared to an empirically defined null distribution. GingerALE version 3.0.2 implements a random effects model that computes an above-chance clustering between the experiments (instead of between foci), a subject size related variable uncertainty and limitation of the effects of a single experiment. Wherever Talairach & Tournoux coordinates were reported in the original literature, coordinates were first converted into MNI coordinates with use of the Lancaster transform implemented in GingerALE 3.0.2.

We conducted two independent coordinate-based meta-analyses on functional brain activity during mentalizing in adults and in children/youths. All results were thresholded at a cluster forming threshold of $p < 0.001$ (uncorrected) and a permutation-based cluster-level family-wise error (FWE) rate correction of $p < 0.05$ with 1000 permutations, according to standard recommendations (Fox, 2017). Additionally, a conjunction analysis was computed, indicating the common neuronal substrates activated both in adults and in children/youths during

mentalizing. Conjunction analyses are based on each individual meta-analysis and a pooled dataset of all participants and tests for similarity or voxel-wise minimum between the two thresholded ALE images. Due to the large difference in the number of experiments from studies in adults compared to developmental neuroimaging studies in children/youths only the conjunction analyses representing common areas of activation amongst adults and children/youths, but no group contrasts are reported or interpreted (Eickhoff, 2014). All images are displayed using the Mango imaging software version 4.1 using the Colin27 MNI high resolution brain template (available at <http://brainmap.org/ale/>).

2.1.2. Meta-analytic connectivity modeling

A meta-analytic connectivity modeling (MACM) approach was used to explore functional connectivity during mentalizing in adults. MACM is a tool to investigate functional connectivity of specific regions of interest (ROIs) using a meta-analytic approach by deriving patterns of neuronal coactivation across all studies entered in the BrainMap database (Fox & Lancaster, 2002) meeting user-defined criteria (see below; Robinson et al., 2012; Robinson et al., 2010). This analysis was conducted for the adult group only since the vast majority of the database enabling connectivity modeling is based on adult literature. Consequently, if data from the meta-analytic findings in children were included, the connectivity modelling would have been based on adult literature and would have been unlikely to represent the developmental samples.

Connectivity modelling in the adult sample included the following steps: **1.** We built 5mm spheres around the weighted centers of significant clusters identified through our meta-analysis in adults using the MarsBaR toolbox (Brett et al., 2002), including bilateral superior/middle temporal gyri (-54 -39 6, 54 -32 2), middle medial (-1 54 20), medial superior (-5 19 56), middle (-43 5 51, 44 9 45) and inferior frontal gyri (-48 24 3, 50 26 7) and precuneus (1 -55 35). All

ROIs met the requirement of a maximum ROI volume of 5000mm³. **2.** The ROIs were exported as images with a voxel size of 1x1x1mm and individually inputted into the Sleuth application, version 3.0.3 (<http://brainmap.org/sleuth>). **3.** Coordinate searches were conducted for each ROI sphere using the BrainMap database (Fox & Lancaster, 2002), including only fMRI studies with non-clinical participants. **4.** The resulting coordinates for each of the ROIs were pooled into one common dataset and combined through an independent coordinate-based meta-analysis (procedure as detailed above).

3. Results

3.1. Activation likelihood estimation meta-analysis results

The individual ALE meta-analysis for 206 functional neuroimaging studies of mentalizing in adults revealed 9 significant clusters of activation, including bilateral temporoparietal junction extending into the middle temporal gyrus, precuneus and frontal areas (i.e., middle medial/superior frontal gyri and bilateral inferior/middle frontal gyri). The individual ALE meta-analysis on 22 developmental neuroimaging studies (i.e., functional activity during mentalizing in children/youths), resulted in 7 significant clusters of activation, including ventromedial and middle medial frontal cortex, bilateral temporoparietal junction, precuneus/posterior cingulate gyrus and middle/superior temporal gyri. Finally, the conjunction analysis comparing studies in adults to developmental research studies in children/youths resulted in 7 clusters of brain activation reflecting mentalizing and included ventromedial and middle medial prefrontal cortex, precuneus, bilateral temporoparietal junction and middle/superior temporal gyri (**Figure 1A, Table 3**). To investigate potential confounds introduced by task variability, we conducted additional analyses using more restrictive criteria of including Theory of Mind tasks only (e.g., false belief tasks, Frith–Happé

animations, Theory of Mind cartoon tasks) instead of considering all studies more broadly associated with mentalizing. These additional analyses overall led to comparable results (see **Supplementary Information 4**).

Table 3. Meta-analytic results for studies in adults, developmental samples (children/youths), and the conjunction ($\cap$) of study findings in adults and children/youths.

Cluster	Region	H	Vol	Weighted						ALE	
				center			Local maxima			BA	extrema
Adults											
				x	y	z	x	y	z		
1	Superior/middle temporal gyrus	L	27048	-54	-39	6	-52	-58	24	39	0.16314
							-56	-10	-16	21	0.09503
							-56	-48	4	22	0.08342
							-58	-44	4	22	0.08245
							-54	-2	-24	21	0.08228
							-54	2	-28	21	0.08187
							-52	-34	-4	21	0.07534
							-62	-20	-10	21	0.06008
							-48	10	-36	38	0.05558
2	Superior/middle temporal gyrus	R	22896	54	-32	2	56	-54	26	39	0.14155
							56	-54	18	39	0.13739
							54	-2	-22	21	0.11530
							60	-8	-18	21	0.10536
							50	8	-30	21	0.07466
							46	14	-32	38	0.06757
							52	-34	-2	-	0.06248
							50	-72	8	37	0.05878
3	Middle medial/superior frontal gyrus	L/R	20704	-1	54	20	-6	56	32	8	0.12811
							0	46	-18	10	0.07336
							2	54	-12	10	0.06272

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							2	44	44	8	0.04970
							4	38	38	8	0.04734
							4	42	34	6	0.04575
4	Inferior frontal gyrus	L	11120	-48	24	3	-54	24	8	45	0.09785
							-48	28	-10	47	0.09691
							-42	10	28	9	0.05533
5	Precuneus	L	10680	1	-55	35	-2	-54	36	31	0.15210
6	Inferior/middle frontal gyrus	R	8112	50	26	7	56	28	8	45	0.10600
							52	30	-6	45	0.07474
							48	22	22	46	0.06643
							36	24	-12	47	0.05135
7	Medial superior frontal gyrus	L/R	4992	-5	19	56	-4	18	56	6	0.07184
							-4	18	52	6	0.07093
							8	24	54	8	0.03584
8	Middle frontal gyrus	L	2344	-43	5	51	-44	6	52	6	0.06286
9	Middle frontal gyrus	R	1896	44	9	45	44	8	44	6	0.05884

Children/youths

1	Medial/superior frontal gyrus	R	3224	2	56	21	4	56	20	9	0.03730
							10	56	32	8	0.01775
2	Superior/middle temporal gyrus	L	2864	-45	-58	23	-46	-58	22	39	0.02365
							-42	-58	20	22	0.02262
3	Precuneus, posterior cingulate gyrus	L	2536	-1	-54	33	0	-54	34	31	0.02384
							0	-50	24	30	0.01660
4	Middle/superior temporal gyrus	R	2008	52	8	-26	54	2	-24	21	0.02020
							52	12	-24	38	0.01934
							46	14	-32	38	0.01530
5	Superior temporal gyrus, supramarginal gyrus, inferior parietal lobule	R	1384	52	-58	21	50	-58	20	22	0.02618
							58	-52	24	40	0.01311
							54	-46	24	40	0.01189

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6	Medial frontal gyrus	R	1368	2	55	-9	0	54	-8	-	0.02087
							2	50	-18	10	0.01329
7	Middle/inferior temporal gyrus	L	1200	-56	-4	-21	-56	-2	-22	21	0.02409
							-58	-14	-22	21	0.01316
<i>Conjunction: Adults $\cap$ children/youths</i>											
1	Medial/superior frontal gyrus	R	2912	2	56	21	4	56	20	9	0.03730
							10	56	32	8	0.01775
2	Superior/middle temporal gyrus	L	2624	-46	-58	23	-46	-58	22	39	0.02365
							-42	-58	20	22	0.02262
3	Precuneus, posterior cingulate gyrus	L	2448	-1	-54	34	0	-54	34	31	0.02384
							0	-50	24	30	0.01660
4	Middle/superior temporal gyrus	R	1736	52	7	-26	54	2	-24	21	0.02020
							52	12	-24	38	0.01934
							46	14	-32	38	0.01530
5	Superior temporal gyrus, supramarginal gyrus, inferior parietal lobule	R	1320	52	-57	21	50	-58	20	22	0.02618
							58	-52	24	40	0.01311
							54	-46	24	40	0.01189
6	Middle/inferior temporal gyrus	L	1128	-56	-4	-21	-56	-2	-22	21	0.02409
							-58	-14	-22	21	0.01316
7	Medial frontal gyrus	R	888	1	54	-10	0	54	-8	-	0.02087
							2	50	-18	10	0.01329

H=hemisphere, R=right; L=left, Vol=volume in mm³, x, y, z coordinates are in Montreal Neurological Institute (MNI) space, BA=Brodmann Area (if applicable).

At the time the final connectivity search was conducted (December 2019), the BrainMap database contained 3406 papers with 16901 experiments and 76016 subjects. The search results for each ROI are listed in **Table 4**. Results are based on studies enlisted in the BrainMap

database and paradigms including for example motor tasks/button press, semantic discrimination or face discrimination. The MACM analysis encompassing bilateral superior/middle temporal gyri, precuneus, middle medial and medial superior frontal gyri and bilateral middle and inferior frontal gyri ROIs revealed functional connectivity patterns with clusters including bilateral middle and inferior frontal gyri extending into insula, middle and medial superior frontal gyri, superior temporal gyri, bilateral inferior/superior parietal lobule extending into supramarginal gyrus and bilateral thalamus/striatum (caudate and putamen). All MACM results are reported in **Table 5**.

Table 4. BrainMap database search results for meta-analytic connectivity modeling for each region of interest derived from the meta-analysis in adults.

Region	H	Weighted center			Foci	Experiments	N
		x	y	z			
Superior/middle temporal gyrus	L	-54	-39	6	633	51	818
Superior/middle temporal gyrus	R	54	-32	2	771	38	593
Middle medial frontal gyrus	L/R	-1	54	20	372	32	466
Inferior frontal gyrus	L	-48	24	3	681	41	526
Precuneus	L	1	-55	35	483	42	708
Inferior/middle frontal gyrus	R	50	26	7	561	34	555
Medial superior frontal gyrus	L/R	-5	19	56	757	52	802
Middle frontal gyrus	L	-43	5	51	809	47	683
Middle frontal gyrus	R	44	9	45	684	37	527

H=hemisphere, R=right; L=left, N=number of subjects.

Table 5. Peak activation report from meta-analytic connectivity modeling for studies in adults.

Cluster	Region	H	Vol	Weighted						BA	ALE
				center			Local maxima				extrema
				x	y	z	x	y	z		
1	Middle/inferior frontal gyrus	L	39104	-45	16	20	-44	4	50	6	0.26564
							-48	26	2	45	0.21767
							-46	18	24	9	0.15410
2	Inferior/middle frontal gyrus, insula	R	28096	47	19	16	50	26	6	45	0.20219
							44	10	46	6	0.16541
							38	22	-6	—	0.13392
							46	18	-4	13	0.10398
							52	22	28	9	0.08950
							48	12	26	9	0.08514
3	Superior frontal gyrus	L	19824	-1	18	49	48	34	24	9	0.06140
							-4	18	54	6	0.27085
							-54	-40	6	22	0.27754
4	Middle/superior temporal gyrus	L	15248	-55	-38	6	-58	-6	-8	22	0.07838
							-48	-58	22	39	0.07804
							-54	-42	22	13	0.05940
							-32	-52	48	40	0.11232
5	Inferior/superior parietal lobule, supramarginal gyrus	L	8976	-35	-52	46	-46	-38	42	40	0.07785
							54	-32	2	22	0.19025
6	Superior temporal gyrus	R	7808	56	-33	3	64	-44	18	13	0.05737
							62	-16	0	22	0.05029
							58	-6	-2	22	0.04851
							60	-10	-12	22	0.04826
							-10	-14	6	—	0.08745
7	Thalamus, caudate	L	5488	-13	-5	8	-14	2	12	—	0.08191

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8	Medial frontal gyrus	L	5272	-1	55	21	-2	54	20	9	0.15981
9	Caudate, putamen, thalamus	R	4616	16	-1	7	14	2	2	–	0.07023
							16	6	6	–	0.06836
							20	2	8	–	0.06770
							12	-14	8	–	0.06332
10	Superior/inferior parietal	R	4104	34	-55	49	32	-56	48	7	0.09775
	lobule						28	-64	56	7	0.07472

H=hemisphere, R=right; L=left, Vol=volume in mm³, x, y, z coordinates are in Montreal Neurological

Institute (MNI) space, BA=Brodmann Area (if applicable).

Co-activation with 5mm spheres around bilateral superior/middle temporal gyri (-54 -39 6, 54 -32 2), medial middle (-1 54 20), medial superior (-5 19 56), middle (-43 5 51, 44 9 45), and inferior frontal gyri (-48 24 3, 50 26 7) and precuneus (1 -55 35).

3.2. Follow-up analyses: Meta-analyses on mentalizing in younger children and youths

To explore potential differences in brain activity during mentalizing in younger children compared to youths, we conducted individual smaller-scale follow-up meta-analyses in children (below 12 years of age) and youths (12–18 years of average age) based on the 22 studies in children/youths detected previously (see **Supplementary Information 3** for a list of studies entering each analysis). The cut-off was selected according to literature discussing the age of 12 as the approximate start of adolescence (Spear, 2000). Furthermore, this allowed for a balanced number of experiments and participants in each developmental subgroup. The meta-analysis for children (below 12 years of age) was based on 65 activation foci from 12 experiments across 219 subjects and resulted in 4 significant clusters of activation including bilateral medial frontal gyri, precuneus and right temporoparietal junction. The individual ALE meta-analysis on youths was based on 152 activation foci from 10 experiments across 260 subjects and yielded 5 significant clusters of activation in middle medial prefrontal cortex, bilateral temporoparietal junction/superior temporal gyri, middle and inferior temporal gyri and

cingulate gyrus extending into precuneus. The conjunction analysis of both age groups resulted in 2 clusters of significant common activation across both groups including middle medial prefrontal cortex and precuneus/posterior cingulate cortex (**Figure 1B/ Table 6**).

Figure 1. Overlay of meta-analysis results for **(A)** adults (red) and children/youths (green) and the conjunction analysis of both groups (blue) during mentalizing. Overlapping brain activity in adults and children/youths was identified for medial prefrontal cortex (MPFC), precuneus (PC)/posterior cingulate gyrus (PCC), temporoparietal junction (TPJ) and middle temporal gyri. **(B)** Children (below 12 years of age; pink), youths (12 years and older; yellow), and the conjunction analysis of both age groups (blue). Common brain activity was detected in MPFC and PC/PCC (all $p < 0.05$, FWE corrected). Coordinates are in MNI space.

Table 6. Meta-analytic findings for children (younger than 12 years of age), youths (older than 12 years of age), and the conjunction analysis ($\cap$) of studies in children below and youths above 12 years of age.

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Cluster	Region	H	Vol	Weighted			Local maxima			ALE	
				center			x	y	z	BA	extrema
<i>Children (below 12 years of age)</i>				x	y	z	x	y	z		
1	Medial frontal gyrus	L	1496	3	57	19	2	56	20	9	0.02213
2	Precuneus	L	768	-3	-55	37	-2	-56	36	7	0.01623
3	Medial frontal gyrus	R	712	7	59	0	6	58	0	10	0.01264
4	Supramarginal gyrus,	R	600	59	-52	26	60	-52	24	40	0.01214
	superior temporal gyrus						56	-54	32	39	0.00897
<i>Youths (12 years and older)</i>											
1	Superior/middle temporal	L	1992	-44	-57	20	-46	-58	20	22	0.02206
	gyrus						-42	-58	20	22	0.02194
2	Superior/medial frontal gyrus	R/L	1976	-4	55	24	-8	54	36	8	0.01604
							4	56	20	9	0.01599
							-6	60	22	9	0.01481
							-8	52	18	9	0.01424
3	Cingulate gyrus, posterior	R	1432	1	-53	29	2	-54	32	31	0.01788
	cingulate gyrus						0	-50	24	30	0.01656
4	Middle/inferior temporal	L	1088	-57	-5	-20	-58	-2	-20	21	0.01722
	gyrus						-58	-14	-22	21	0.01290
5	Middle temporal gyrus	R	912	50	-60	20	50	-60	20	19	0.02386
<i>Conjunction: Children $\cap$ youths</i>											
1	Medial frontal gyrus	R	680	3	55	21	4	56	20	9	0.01599
2	Cingulate gyrus	L	120	-2	-54	34	0	-56	34	31	0.01167

H=hemisphere, R=right, L=left, Vol=volume in mm³, BA=Brodmann Area. x, y, z coordinates are in Montreal Neurological Institute (MNI) space.

4. Discussion

This study aimed to integrate and compare functional neuroimaging reports on mentalizing in adults, children and youths. Across all ages, from children to youths to adult samples, continuity (i.e., activation increases during mentalizing) was observable in three key regions for mentalizing, namely medial prefrontal cortex, precuneus and right temporoparietal junction. Our individual meta-analyses comparing adults and children or youths indicated overlapping neuronal activity during mentalizing for both groups in brain areas including the medial prefrontal cortex, precuneus, bilateral temporoparietal junction and middle temporal gyri. Adults furthermore recruit bilateral inferior and middle frontal gyri, as well as superior parts of the medial frontal cortex during mentalizing tasks. Exploration of the functional connectivity network originating from the identified clusters of common activation during mentalizing in adults indicated connectivity between the before mentioned areas of activation and further connectivity to brain regions such as bilateral thalamus, caudate, putamen and inferior/superior parietal lobule extending into the supramarginal gyrus. Finally, subgroup analyses comparing studies including younger participants (children 8–11 years of age) to youths (12–18 years of age) revealed that both groups engage the middle medial prefrontal cortex, precuneus and right temporoparietal junction, but youths additionally recruit the left temporoparietal junction and middle/inferior temporal cortex during mentalizing.

Across children, youths and adults, consistent recruitment of medial prefrontal cortex, precuneus and temporoparietal junction was observed. The medial prefrontal cortex and

temporoparietal junction have repeatedly been associated with mentalizing across different studies to date (Mar, 2011; Molenberghs et al., 2016; Schurz et al., 2014; Van Overwalle, 2009; van Veluw & Chance, 2014). The medial prefrontal cortex (both ventrally and more dorsally located areas) has been suggested to play a generic role when reasoning about one's own or others' mental states (Amodio & Frith, 2006; Blakemore, 2008; Molenberghs et al., 2016; Moll & de Oliveira-Souza, 2007; Shamay-Tsoory et al., 2009), whereas the ventromedial prefrontal cortex has been more specifically related to social emotion processing (e.g., guilt/embarrassment) or the regulation of emotions (Hiser & Koenigs, 2018). The temporoparietal junction is most prominently recruited using false belief or perspective taking tasks (Decety & Lamm, 2007), and has been suggested to comprise of a subregion selectively involved when reasoning about others' mental states (Saxe & Kanwisher, 2003; Van Overwalle, 2009). Additionally, tasks involving the reorientation of attention and representing a sense of agency have likewise shown to lead to activation increases in temporoparietal brain regions (Decety & Lamm, 2007). Finally, the precuneus has been suggested to play a significant role in memory (e.g., episodic memory retrieval and autobiographical memory) as well as in mental imagery, which is needed to construct different perspectives (Cavanna & Trimble, 2006; Schurz et al., 2013). Overall, brain regions showing continuous activation during mentalizing across development (i.e., in children, youths and adult samples) have been broadly linked to the reorientation of attention, memory processes and mental imagery. Such patterns of continuous engagement may indicate that the neuronal basis supporting mentalizing is somewhat stable from a young age on, possibly reflecting an early, though long-lasting, specialization of the social brain (Bowman et al., 2019). Our findings are moreover supported by behavioral studies showing that mentalizing skills start to develop early in life, which continues until young adulthood (Blakemore, 2008; Knudsen & Liszkowski, 2012; Meins et al., 2002).

Our meta-analyses indicated an involvement of bilateral inferior and middle frontal gyri as well as medial sections of the superior frontal gyri for adults only. This activation was not observed in children and youths. The inferior and middle frontal gyri have been related to a variety of late-developing higher-order cognitive functions including attentional processes (Japee et al., 2015), working memory (Leung et al., 2002), response inhibition (Hampshire et al., 2010; Swick et al., 2008), semantic processing (Costafreda et al., 2006) and observation of movements via the mirror neuron system (Kilner et al., 2009). Similarly, the medial superior frontal cortices are involved in memory and executive functions such as decision making (Boisgueheneuc et al., 2006; Li et al., 2013; Nachev et al., 2008) and higher-order emotion processes (Rochas et al., 2013; Seitz et al., 2008). Our findings may be indicative of specializations within the social brain network and are in line with data indicating a late development of higher cognitive functions (e.g., decision making and response inhibition, language and emotion recognition or regulation). This is also in line with evidence reporting late maturational processes in frontal brain regions (Gogtay et al., 2004; Simmonds et al., 2017; Tamnes et al., 2010).

The meta-analytic connectivity analyses in adults revealed functional connectivity between areas of the social brain network (i.e., bilateral superior/middle temporal gyri, precuneus, middle medial and medial superior frontal gyri and bilateral middle and inferior frontal gyri) and further connectivity to bilateral thalamus, striatum and inferior and superior parietal lobule. The rostral section of the inferior parietal lobule (Brodmann Area 40; Brodmann, 1909) and the superior parietal lobule, as identified in our connectivity analyses, are located dorsally of the temporoparietal junction. The inferior parietal lobule forms part of the mirror neuron system and is involved in the imitation of actions needed to adapt to social situations and when processing semantic and affective information (Caspers et al., 2010; Iacoboni, 2009; Molenberghs et al., 2009), whereas the superior parietal lobule is for example implicated in

working memory and visuospatial attention (Corbetta et al., 1995; Koenigs et al., 2009). The thalamus and striatum (composed by the caudate nucleus and putamen) are implicated in reward-based learning and higher-level behavioral control and regulation (e.g., DeLong & Wichmann, 2009). Connectivity between the thalamus/striatum and the cerebral cortex (e.g., dorsolateral prefrontal cortex, anterior cingulate cortex) has been commonly reported in emotion processing and higher-order cognitive processes such as mentalizing (Di Martino et al., 2008; Molenberghs et al., 2016; Postuma & Dagher, 2006). For developmental samples, only few studies so far have examined functional connectivity during mentalizing. Burnett and Blakemore (2009) reported increased functional connectivity between the ventromedial prefrontal cortex and left temporoparietal junction/posterior superior temporal sulcus in adolescents compared to adults, possibly reflecting increasing specialization of the network connections during skill development. Similarly, Richardson and colleagues (2018) detected increasing connectivity with age between temporoparietal junction, precuneus and medial prefrontal cortex in children aged 3 to 12 years of age during an implicit Theory of Mind task (i.e., watching a movie that elicits mentalizing). Again other studies reported no age effects in connectivity during mentalizing, but stable connectivity patterns between areas associated with mentalizing (e.g., medial prefrontal cortex, temporoparietal junction, precuneus) and striatum/dorsolateral prefrontal cortex (McCormick et al., 2018; in 8 to 16-year-olds) or within mentalizing regions (temporoparietal junction, superior temporal sulcus, precuneus (Mukerji et al., 2019); in 9 to 13-year-olds). Such differences in findings may arise due to variations in the tasks employed or the characteristics of the sample studied, e.g., the age range.

Our follow-up subgroup analyses investigating studies in younger children (8–12 years of age) and studies in youths (12–18 years) revealed that children up to 12 years of age commonly engage brain areas within the middle medial prefrontal cortex, precuneus and right temporoparietal junction during mentalizing, while youths commonly activate a more

extensive, adult-like set of brain regions, including medial prefrontal cortex, precuneus, bilateral temporoparietal junction and anterior middle/inferior temporal regions (Mar, 2011; Molenberghs et al., 2016; Schurz et al., 2014; Van Overwalle, 2009; van Veluw & Chance, 2014). Although interpretation is limited by the small number of studies within each of the subgroups and by the cross-sectional design of the studies entering the analyses, our results may reflect developmental effects associated with brain maturation (Blakemore, 2008, 2012b) and specialization of the functional regions employed. Brain maturation, especially of prefrontal brain regions, is in turn paralleled by increasing mentalizing skills and cognitive development across age (Blakemore et al., 2007a; Blakemore, 2008, 2012a, 2012b; Crone & Dahl, 2012).

2.1. Limitations of the meta-analytic approach and future steps

Using a meta-analytic approach increases statistical power allowing to draw reliable conclusions. Increased power is especially useful within the neuroimaging field, where research has long been characterized by small sample sizes. However, meta-analytic approaches also entail shortcomings that should be addressed. Still, the present findings critically depend on the quality and methodological approaches of the publications included (e.g., paradigm choice, contrast definition, variations in the thresholds and correction of results). This variability in the studies was controlled for by conducting an additional meta-analysis with more restrictive criteria (including Theory of Mind tasks only) yielding comparable results, which may be indicative of mentalizing representing a more generic psychological concept including different aspects of social cognition. Additionally, the interpretation of the meta-analytic output obtained here is, based on its methodology, limited to the location of the neuronal activation clusters, whereas cluster size or strength of activation of each age group cannot be interpreted (Eickhoff et al., 2009). Moreover, the present work

cannot inform about change in developmental trajectories across age (Blakemore, 2008; Blakemore et al., 2010; Luna et al., 2010), as it is based on cross-sectional data only. Finally, meta-analyses are subject to publication biases and may even propagate these (e.g., due to the inclusion of positive/significant findings while ignoring null results; Klapwijk et al., 2019), warranting cautious interpretation.

To advance the field of developmental neuroscience of mentalizing, future longitudinal measurements of brain activity during development are needed. Most importantly, longitudinal studies allow to draw generalizable conclusions about fine-grained linear and nonlinear maturational trajectories associated with complex cognitive functions, which are for example associated with the frontal cortex (Ordaz et al., 2013; Qu et al., 2015; Simmonds et al., 2017). Moreover, longitudinal designs may further characterize the neuronal correlates of mentalizing during major transitional steps (e.g., the transition from kindergarten to formal school education). Such studies may clarify changes in neuronal correlates associated with school entry, when children face different cognitive and social challenges, e.g., when learning to manage interactions with peers and teachers (Blair, 2002; Blair & Raver, 2015). Open science frameworks and data sharing options (see for example <https://osf.io>, <https://aspredicted.org> or <https://neurovault.org>) may be considered by all researchers to provide options for data replication and compilation (Klapwijk et al., 2019; Kliemann & Adolphs, 2018).

4.1. Conclusion

Our meta-analyses shed further light on the neuronal basis of mentalizing in adults and developmental samples (i.e., children and youths). While adults and children/youths show similar brain activation patterns during mentalizing in areas such as the middle medial prefrontal cortex, precuneus and temporoparietal junction, the adult brain recruits further brain regions in medial and lateral prefrontal cortices. This may be intertwined with the development

of more complex thinking processes with age. Our results indicate that essential neuronal components for mentalizing are at least partially established in childhood, reflecting an early stability and specialization of parts of the social brain network. Future studies using longitudinal designs may further clarify the precise underlying mechanisms of neuronal continuity and change during mentalizing from childhood to youth and adulthood.

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