

# Neural correlates of theory-of-mind are associated with variation in children's everyday social cognition

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## Abstract

Theory of mind (ToM), the capacity to reason about others' mental states, is central to healthy social development. Neural mechanisms supporting ToM may contribute to individual differences in children's social cognitive behavior. Employing a false belief functional magnetic resonance imaging paradigm, we identified patterns of neural activity and connectivity elicited by ToM reasoning in school-age children ( $N = 32$ , ages 9–13). Next, we tested relations between these neural ToM correlates and children's everyday social cognition. Several key nodes of the neural ToM network showed greater activity when reasoning about false beliefs (ToM condition) vs non-mentalistic false content (control condition), including the bilateral temporoparietal junction (RTPJ and LTPJ), precuneus (PC) and right superior temporal sulcus. In addition, children demonstrated task-modulated changes in connectivity among these regions to support ToM relative to the control condition. ToM-related activity in the PC was negatively associated with variation in multiple aspects of children's social cognitive behavior. Together, these findings elucidate how nodes of the ToM network act and interact to support false belief reasoning in school-age children and suggest that neural ToM mechanisms are linked to variation in everyday social cognition.

**Key words:** fMRI; effective connectivity; false belief; perspective-taking; empathy

## Introduction

During middle childhood and early adolescence, children navigate complex social landscapes. Psychosocial challenges, such as school transitions, can exacerbate individual differences in social competence, widening the gap between socially adept children and less-skilled peers (Monahan & Steinberg, 2011). Poor interpersonal functioning is associated with negative outcomes, including lower academic achievement, problem behaviors and psychopathology (Elliott *et al.*, 2001; Spence, 2003). To develop

targeted interventions, it is critical to understand mechanisms that contribute to variation in children's social functioning.

Social competence depends, in part, upon theory of mind (ToM). ToM allows us to represent others' mental states, predict what they might do next and generate an appropriate response. False belief (FB) understanding is an early emerging ToM capacity widely assessed in the developmental literature (Wellman *et al.*, 2001). To reason about FBs, a child must understand that the content of a person's beliefs can contradict reality, providing evidence of representational ToM (Wimmer & Perner, 1983).

Received: 24 September 2018; Revised: 3 May 2019; Accepted: 29 May 2019

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Between ages 3 and 5, children demonstrate above-chance performance on explicit FB tests. FB performance in early childhood predicts real-world social behavior, including mind-reading (De Rosnay *et al.*, 2014), popularity (Slaughter *et al.*, 2015) and social competence (Devine *et al.*, 2016). These findings suggest that ToM mechanisms contribute to variation in social development.

Cognitive neuroscience research in adults has revealed a distributed set of neural regions supporting FB reasoning (Gallagher *et al.*, 2000; Saxe & Kanwisher, 2003): the bilateral temporoparietal junction (RTPJ and LTPJ), precuneus (PC), medial prefrontal cortex (MPFC) and right superior temporal sulcus (RSTS). Prior functional magnetic resonance imaging (fMRI) studies in smaller samples indicate that children, ranging in age from 5 to 13, may recruit the same regions for ToM reasoning, suggesting the broader architecture of this ToM 'network' emerges early in childhood (Ohnishi *et al.*, 2004; Kobayashi *et al.*, 2007; Saxe *et al.*, 2009; Gweon *et al.*, 2012). However, neural ToM mechanisms may not yet be functionally mature. Preliminary studies suggest that children demonstrate increasing specialization of the TPJ for mental state content with age (Saxe *et al.*, 2009; Gweon *et al.*, 2012). In addition, youths demonstrate decreasing MPFC activation with age across a variety of mental state reasoning (i.e. mentalizing) tasks, suggesting continued maturation from preadolescence into adulthood (Blakemore, 2012).

Although this set of regions is conceptualized as a network, few studies have explored how these nodes interact to support ToM. Previous studies of ToM-related neural connectivity in children have employed different tasks and analyses at different ages, yielding distinct results. Recent work employing inter-region correlation analysis has indicated positive associations between ToM regions during passive viewing of an animated film in children (ages 3–12), suggesting emerging integration within the ToM network (Richardson *et al.*, 2018). However, correlational approaches are limited in their ability to identify patterns of functional connectivity specific to mentalizing vs other cognitive processes. Psychophysiological interaction (PPI) analysis can help evaluate such questions by examining effective connectivity, i.e. the influence of activity in one neural region upon another, elicited by a certain task (Friston, 2011). For example, PPI analyses indicate greater frontotemporal connectivity when mentalizing about social vs non-social emotions in adolescents compared to adults, suggesting developmental changes in patterns of connectivity that support social-emotional reasoning (Burnett & Blakemore, 2009). Further work is needed to evaluate the functional integration of ToM regions when reasoning about other mental states (e.g. beliefs) during childhood.

Although ToM is considered central to social development, few neuroimaging studies have directly evaluated this hypothesis. Developmental fMRI studies have yielded preliminary evidence that functional specialization of the RTPJ (Gweon *et al.*, 2012) is associated with performance on lab-based ToM tasks. In addition, parent-reported ToM abilities have been linked to connectivity of the RTPJ with other ToM regions at rest (Xiao *et al.*, 2019). While studies in adults have implicated the LTPJ in facilitating general perspective-taking (Schurz *et al.*, 2013) and the PC in mental imagery (Cavanna & Trimble, 2006), relatively little is known about the role of these ToM regions in supporting social cognition in childhood. Moreover, relations between task-modulated activity or connectivity in the ToM network and children's social cognition in everyday contexts remain unclear.

Empathy, the capacity to represent and share the emotional experiences of others, is a related social cognitive process that is fundamental to social interaction (Singer & Tusche, 2014).

Although representation of another's affective experience is central to empathy, ToM and empathy rely—in part—upon overlapping neural mechanisms. Empathy engages core nodes of the ToM network (including the TPJ and PC/posterior cingulate cortex), in addition to other neural circuitry supporting affective sharing (Völlm *et al.*, 2006; Zaki *et al.*, 2009; Bzdok *et al.*, 2012). Further research is needed to explore whether neural ToM mechanisms contribute to variability in children's empathy in everyday settings, as well as other facets of social cognition.

In the current study, participants (ages 8–13) completed an FB fMRI task adapted for children. First, we aimed to test neural activity elicited by reasoning about FBs vs non-mentalistic false content (False Belief > False Photo; FB > FP), allowing us to identify regions specifically engaged by ToM processing during this developmental period. Second, we aimed to evaluate functional integration of key ToM regions. Generalized PPI analyses (gPPI) were used to examine effective connectivity between regions of interest (ROIs) in the ToM network during FB > FP, elucidating ToM-modulated changes in connectivity. Last, we aimed to explore associations between these neural ToM measures and multiple facets of everyday social cognition, including empathy. Therefore, we tested whether neural activity and effective connectivity in the ToM network explained variance in children's self- and parent-reported social cognitive behavior. We predicted that when reasoning about FBs (FB > FP), school-age children would demonstrate (i) enhanced activation in key ToM regions and (ii) greater effective connectivity between these regions. Moreover, we expected (iii) the magnitude of task-modulated activity and connectivity would be associated with variation in children's social cognition in everyday settings.

## Materials and methods

### Participants

Data were collected from 41 children, ages 8–13, recruited from the greater Boston area. Inclusion criteria were English-speaking, absence of neurological or major medical illness, head trauma, psychiatric disorder and psychosis or autism spectrum disorder in first-degree relatives. All participants were screened for major childhood psychiatric disorders using the Kiddie Schedule for Affective Disorders and Schizophrenia for School-Age Children - Present and Lifetime Version (Kaufman *et al.*, 1997) or the Child/Adolescent Symptom Inventory-4 (Gadow & Sprafkin, 2002, 1998). Data from 9 participants were excluded due to low neuroimaging data quality (Data acquisition and preprocessing), yielding a final sample of 32 children, ages 9–13. Demographics and IQ are reported in Table 1. In accordance with the Institutional Review Board at Harvard University, parents provided written consent and children provided written assent prior to participation. Families were compensated for participation.

### Measures

**Assessments of social cognitive behavior.** Participating families were administered child- and parent-report measures to evaluate children's everyday social cognitive behavior. Parents completed the Social Responsiveness Scale-2 (SRS), a 65-item scale that assesses children's social behavior in natural settings (Constantino, 2002; Frazier *et al.*, 2014). Although the SRS was developed to identify social difficulties associated with autism, it has been used to identify more subtle difficulties in reciprocal social behavior in the general population (Constantino & Todd, 2003, 2005). The social awareness subscale (SRS-Awr)

**Table 1.** Sample characteristics and behavioral data

$N_{\text{total}}$	32
Gender (male/female)	12/20
Age (years)	11.06 (1.44) [9–13]
Race/Ethnicity	
White or Caucasian	23
Black or African American	0
Hispanic or Latinx	1
Asian or Asian American	2
Native American	1
Multiracial	5
IQ ( $N = 30$ ) <sup>a</sup>	114.50 (12.66) [84–135]
Social measures	
IRI-PT ( $N = 32$ )	21.03 (5.53) [7–30]
IRI-EC ( $N = 32$ )	26.37 (4.03) [19–34]
SRS-Awr ( $N = 23$ ) <sup>b</sup>	46.35 (8.80) [32–64]
SRS-Cog ( $N = 23$ ) <sup>b</sup>	45.70 (7.55) [39–65]
FB task	
FB accuracy (total correct)	6.09 (1.89) [2–9]
FP accuracy (total correct)	6.97 (1.77) [3–10]
FB response time (s)	5.71 (1.03) [0.98–7.08]
FP response time (s)	5.44 (1.20) [1.04–7.26]

Notes. Data for age, IQ and behavioral measures are presented as mean, (SD), [range]. <sup>a</sup>IQ was evaluated using either the Wechsler Intelligence Scale for Children-IV ( $N = 12$ ) or the Wechsler Abbreviated Scales of Intelligence ( $N = 18$ ); due to an omission in data collection, IQ scores were not obtained for two participants. <sup>b</sup>SRS data were obtained from 23 participants.

evaluates the ability to notice and respond to social cues (e.g. ‘Focuses his or her attention to where others are looking or listening’). The social cognition subscale (SRS-Cog) evaluates the ability to interpret social situations and reason about others’ intentions and behaviors (e.g. ‘Doesn’t recognize when others are trying to take advantage of him or her’). Higher T scores on these fundamental aspects of social cognition indicate poorer everyday function.

Given prior research indicating that core regions of the ToM network are recruited to support reasoning about other’s mental states and emotional experiences (Vö et al., 2005; Bzdok et al., 2012), we also included specific measures of empathy. Children completed a modified version of the Interpersonal Reactivity Index (IRI; Davis, 1980, 1983), a 28-item self-report measure that evaluates multiple facets of empathy. Participants rated the extent to which a statement described them on a 6-point Likert scale (from ‘not at all like me’ to ‘exactly like me’). We were specifically interested in assessing other-oriented aspects of empathy, i.e. empathic perspective-taking and concern, which support prosocial behavior (Litvack-Miller et al., 1997). The IRI-PT subscale evaluates the tendency to spontaneously adopt others’ perspectives (e.g. ‘I try to understand my friends better by imagining what things are like for them.’). The IRI-EC subscale assesses feelings of concern and sympathy for others (e.g. ‘I feel sorry for other kids whose lives are not as good as mine’). Behavioral data are reported in Table 1.

**FB fMRI task.** In the scanner, participants performed a version of an FB task employed in previous neuroimaging studies (Saxe & Kanwisher, 2003; Dodell-Feder et al., 2011). Stimuli consisted of pre-recorded stories read aloud by a neutral female voice, presented through headphones. These stimuli were adapted from a prior study of FB understanding in adults (Dodell-Feder

et al., 2011) to a third-grade reading level (Flesch, 1948; Kincaid et al., 1975).

In experimental trials, participants listened to an FB story (three to four sentences), in which a character came to hold a false belief (e.g. ‘Jenny put her candy in the cupboard. Then she went outside. Allen moved the candy from the cupboard to the fridge. Then Jenny came inside.’). Following the story, participants responded to a True/False question regarding the character’s belief (e.g. ‘Jenny thinks she will find her candy in the cupboard’). In control trials, participants listened to a ‘false photograph’ (FP) story, in which the content of an image or book became false or outdated (e.g. ‘A large oak tree stood in front of City Hall from the time the building was built. Last year the tree fell down. It was replaced by a stone fountain’). Participants then responded to a True/False question regarding the content of an image (e.g. ‘There is an old drawing of City Hall. It shows a fountain in front of the building’). Conditions were matched in terms of inhibitory demands and logical complexity. However, FB stories required that participants represent others’ mental states, while the FP stories did not, allowing identification of neural activity and connectivity associated with ToM.

## Procedure

Children first completed a mock scan in our fMRI simulator to acclimate them to the scanning environment and practice minimizing movement. Participants were then read instructions for the FB task by the experimenter and completed four practice trials to ensure task comprehension. In the scanner, participants completed the FB task, which consisted of 10 FB trials and 10 FP trials presented using PsychoPy software. Each trial consisted of an audio story (14 s), followed by a True/False question (10 s) and a fixation cross (10 s). Participants were asked to log their responses via button-press at any time during the True/False question period; response times were recorded as an estimate of participants’ time on task. Children were accompanied by a research assistant, who sat by them to monitor task engagement. Trials were presented in fixed, pseudo-randomized order across two runs. Five FB and five FP trials were presented per run for a total run time of 11 min.

## fMRI acquisition and analysis

**Data acquisition and preprocessing.** Data were collected at the Center for Brain Sciences at Harvard University on a 3.0 Tesla Siemens Tim Trio scanner. An anatomical T1-weighted high-resolution structural image was acquired with a 3D MPRAGE sequence (176 sagittal slices,  $1 \times 1 \times 1$  mm voxels). Functional images were acquired with an interleaved, echo-planar imaging sequence (40 oblique-axial slices,  $3 \times 3 \times 3$  mm isotropic voxels; TR = 2560; TE = 3; flip angle =  $85^\circ$ ). Functional sequences employed Prospective Acquisition Correction, which updates slice acquisition during scanning for each time-point based on motion correction parameters computed from the prior two time-points (Center for Brain Science, Harvard University).

fMRI data were preprocessed in SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>) within the general linear model framework. The first four volumes of functional runs were discarded prior to analysis to ensure steady-state magnetization. Preprocessing included slice-timing correction, realignment to the mean functional image, co-registration to the anatomical image, normalization to MNI template space and smoothing

**Table 2.** BOLD activity: whole-brain analysis results

Region	BA	Cluster size	MNI coordinates x y and z	Peak voxel t-value
FB>FP				
TPJ (R)*	39/40	1342	60 -52 25	8.58
Anterior STS (R)*	21/20/38	—	54 -1 -20	8.30
PC (Bilateral)*	31/23/7	780	-3 -55 37	7.82
TPJ (L)*	30/49	420	-54 -61 22	6.21
Anterior STS (L)*	21	273	-54 -2 -23	5.72
SFG (R)	8	66	21 38 52	4.87
Hypothalamus (R)	-	28	3 -1 -11	4.55
MMPFC (Bilateral)	10	67	3 56 16	4.31
VMPPFC (Bilateral)	11	18	3 50 -17	4.21
Posterior STS (R)	22/21	15	57 -34	3.71
Age (Months)				
Cerebellum (L)	-	14	-15 -10 -38	5.18
Cerebellum (R)	-	12	21 -31 -47	4.94
Caudate (Bilateral)	-	24	3 14 -2	4.26
FB Accuracy (Total Correct)				
No significant clusters				

Notes. Statistical threshold is  $P < 0.001$ ,  $k = 10/80$  mm, uncorrected for multiple comparisons. Regions that survive cluster-level correction for multiple comparisons (voxel threshold of  $P < 0.001$ , uncorrected, with an extent-threshold of  $\alpha < 0.05$ , FWE-corrected) are marked with an asterisk (\*). Dash (-) in the cluster size column indicates that the region is included in the cluster above. TPJ, temporoparietal junction; STS, superior temporal sulcus; PC, precuneus; SFG, superior frontal gyrus; MMPFC, middle medial prefrontal cortex; VMPPFC, ventromedial prefrontal cortex.

with an 8 mm Gaussian kernel. Data were high-pass filtered at 128 s.

Within each subject, hemodynamic responses to question and story periods were modeled together within FB and FP conditions. FB and FP trials were modeled separately, with varying durations, to account for variability in response times. For each condition of interest (FB and FP), hemodynamic responses were modeled to the onset of story stimuli with a duration that reflected the sum of the fixed story presentation period (14 s) plus each participant's average response time for trials in that condition. To model the off-task period—after participants logged their behavioral responses but before the next fixation/baseline period—a 'Post-Response' condition with varying onsets and durations was modeled based on each participant's response times.

Head motion may spuriously influence connectivity measures (Satterthwaite *et al.*, 2012; Van Dijk *et al.*, 2012). Therefore, the Artifact Detection Toolbox (ART; [http://www.nitrc.org/projects/artifact\\_detect/](http://www.nitrc.org/projects/artifact_detect/)) was used to identify outlier scans in global signal ( $> \pm 3$  s.d.) and movement ( $> 0.5$  mm of movement or 0.5 degrees of rotation from the previous volume), which were entered into the General Linear Model (GLM) as nuisance regressors. Nine participants with greater than 25% of functional scans identified as outliers were excluded from analyses.

#### Activity: whole-brain blood oxygen-level dependent (BOLD) analysis.

To identify ToM-related activity, contrast files were generated for FB>FP. Multiple regression analysis was used to identify regions that demonstrated significant activation to FB>FP at the whole-brain level; participant age (in months) and task accuracy (number of correct behavioral responses for the condition of interest) were mean centered and entered as covariates in these second-level analyses. Initial statistical thresholds were set to  $P < 0.001$ ,  $k > 10$ , uncorrected. Regions that survive cluster-level correction for multiple comparisons (voxel threshold =  $P < 0.001$ , uncorrected, cluster-extent threshold =  $\alpha < 0.05$ , FWE-corrected) are indicated with an asterisk in Table 2. Results for FP>FB are reported in Supplementary Table S1.

**ROI definition.** ROIs were selected to represent key ToM regions reliably recruited for FB in prior studies (Saxe & Kanwisher, 2003; Dufour *et al.*, 2013; Schurz *et al.*, 2014): the RTPJ, LTPJ, PC, middle medial prefrontal cortex (MMPFC), dorsomedial prefrontal cortex (DMPFC), ventromedial prefrontal cortex (VMPPFC) and RSTS. These ROIs were defined independently from the current dataset, as 8 mm spheres centered at the peak coordinates identified from a random-effects analysis of 462 neurotypical adults scanned on a similar FB task (Dufour *et al.*, 2013). Although each of these brain regions supports various cognitive functions, this approach allowed us to functionally define regions specifically associated with ToM in prior literature.

**Effective connectivity: ROI-to-ROI gPPI analysis.** ROIs were then employed as seed and target regions for effective connectivity analyses, allowing us to evaluate task-modulated changes in the strength of connections between key aspects of the ToM network. Prior neurodevelopmental studies have employed ROIs defined from group analyses to characterize connectivity within the ToM network, providing support for the feasibility of this approach (Richardson *et al.*, 2018; Xiao *et al.*, 2019). Effective connectivity analyses were conducted using the CONN Functional Connectivity Toolbox v. 17a (<http://www.nitrc.org/projects/conn/>; Whitfield-Gabrieli & Nieto-Castanon, 2012). This toolbox implements a component-based noise reduction method (CompCor) that estimates BOLD signal obtained from subject-specific white matter and CSF masks (Behzadi *et al.*, 2007). These sources of temporal noise, along with outlier scans identified with ART, six motion parameters estimated during realignment, temporal derivatives of these parameters, regressors for main effects of task conditions and a linear detrending term were regressed from the BOLD time-series at each voxel. The residual time-series was high-pass filtered at 128 s.

To evaluate task-modulated connectivity among key nodes of the ToM network, we employed a generalized form of context-dependent PPI (gPPI). We tested the effective connectivity of each of the seven ToM ROIs (seed regions) with the six remaining



**Table 3.** Effective connectivity: ROI-to-ROI gPPI results

Significant ROI-to-ROI connections	b	t	P	q
FB>FP				
Seed: LTPJ				
LTPJ–RTPJ	0.13	3.77	<0.001	0.028
LTPJ–RSTS	0.05	3.13	0.004	0.033
Seed: PC				
PC–LTPJ	0.10	3.52	0.002	0.028
Seed: RSTS				
RSTS–LTPJ	0.12	3.40	0.002	0.028
Seed: MMPFC				
MMPFC–PC	–0.10	–3.23	0.003	0.032
Age (months)				
No significant connections				
FB accuracy (Total correct)				
No significant connections				

Notes. Beta coefficients represent average connectivity values (effect sizes). ROI-to-ROI connections that show significant modulation of connectivity for FB>FP (FDR-corrected at the connection-level,  $q < 0.05$ ) are reported; no significant effects of age or accuracy were found. LTPJ, left temporoparietal junction; RTPJ, right temporoparietal junction; RSTS, right (anterior) superior temporal sulcus; PC, precuneus; MMPFC, middle medial prefrontal cortex.

ROIs (target regions) for the contrast of FB>FP. In this ROI-to-ROI gPPI approach, psychological regressors for each task condition were multiplied by a physiological regressor derived from the seed ROI's mean time-series to generate the PPI terms. These PPI interaction terms were then utilized in second-level analyses to test for *task-modulated* changes in connectivity of the seed ROI with each target ROI. Age and task accuracy were mean-centered and entered as covariates for second-level analyses. One-sample *t*-tests (two-tailed) were employed to evaluate changes in connectivity for FB>FP for each ROI-to-ROI connection. Connectivity analyses were controlled for FDR at the connection-level (49 connections;  $q < 0.05$ ; Table 3, Figure 2).

### Social brain-behavior analyses

We evaluated relations between BOLD activity in key ToM regions and variation in children's everyday social understanding. For each participant, we extracted BOLD contrast estimates for FB>FP from ROIs representing areas that showed significant activity to FB>FP in our whole-brain analyses, corrected for multiple comparisons. Prior research suggests that age (Dumontheil et al., 2010; Gweon et al., 2012) and general cognitive ability (Buitelaar et al., 1999; Baker et al., 2014) are related to social cognitive ability. To evaluate the unique effect of each neural predictor (ROI activity) on a given social measure (IRI-PT, IRI-EC, SRS-Awr and SRS-Cog), we ran separate linear regression models controlling for age and IQ (Table 4, Figure 3).

We also tested associations between ToM-modulated effective connectivity and variation in social cognitive behavior. For each participant, we extracted contrast estimates for FB>FP for each ROI-to-ROI connection that showed significant task modulation in our gPPI analyses. Separate linear regression models tested associations between effective connectivity and each of our social measures, controlling for age and IQ (Supplementary Table S2).

Model residuals were inspected for homoscedacity and distribution of errors. Due to heteroscedacity of residuals for models predicting SRS-Cog, this variable was transformed by

subtracting the minimum value and then taking the natural log, which improved model fit. Confidence intervals (CIs) for beta values were derived through bias-corrected and accelerated (BCa) bootstrapping. We applied the Benjamini-Hochberg correction, which controls FDR ( $\alpha < 0.05$ ), to evaluate whether brain-behavior associations were significant for models evaluating relations between ROI activity and behavior (i.e. four tests conducted) and relations between ROI-to-ROI effective connectivity and behavior (i.e. four tests conducted). Significant brain-behavior associations are indicated with asterisks in Table 4 and Supplementary Table S2.

## Results

### Task behavior

Confirming task comprehension, above-chance task accuracy was observed for FB and FP conditions (Table 1). Task accuracy was slightly greater for FP ( $M = 6.97$ ) than FB ( $M = 6.09$ ) [ $t(31) = -2.50$ ,  $P = 0.01$ ]. On average, children took longer to generate responses in the FB ( $M = 5.83$ ) vs FP condition ( $M = 5.52$ ) [ $t(31)$ ,  $P = 0.001$ ].

### Activity: whole-brain BOLD analysis

Enhanced BOLD activity for FB>FP was observed at several nodes of the ToM network indicated in prior literature, including the bilateral temporoparietal junction (RTPJ and LTPJ), PC, right posterior STS, bilateral anterior STS (RSTS and LSTS), MMPFC and VMPFC ( $P < 0.001$ ,  $k > 10$ , uncorrected) (Figure 1, Table 2). Only the PC, bilateral TPJ and bilateral anterior STS clusters remained significant after correction for multiple comparisons ( $\alpha < 0.05$ , FWE-corrected). No significant effects were found for either age or task accuracy at corrected thresholds.

Because regions within the MPFC have been indicated as core ToM regions in prior work (Gweon et al., 2012; Dufour et al., 2013), we carried out exploratory, one-sample *t*-tests to evaluate activity in the VMPFC, DMPFC and MMPFC ROIs for FB and FP conditions, separately. The MMPFC and VMPFC showed deactivation relative to baseline for FB [MMPFC:  $M = -0.22$ ,  $t(31) = -3.62$ ,  $P = 0.001$ ; VMPFC:  $M = -0.22$ ,  $t(31) = -2.73$ ,  $P = 0.01$ ] and FP [MMPFC:  $M = -0.47$ ,  $t(31) = -5.41$ ,  $P < 0.001$ ; VMPFC:  $M = -0.40$ ,  $t(31) = -4.55$ ,  $P < 0.001$ ]. The DMPFC did not show significant activation relative to baseline for FB [ $M = 0.08$ ,  $t(31) = 1.27$ ,  $P = 0.215$ ] or FP [ $M = -0.04$ ,  $t(31) = -0.52$ ,  $P = 0.608$ ].

### Effective connectivity: ROI-to-ROI gPPI results

ROI-to-ROI analyses of effective connectivity revealed significant coupling between core aspects of the ToM network to support FB reasoning (Figure 2; Table 3). Specifically, effective connectivity between the LTPJ and RTPJ, LTPJ and RSTS and PC and LTPJ significantly increased in strength for FB>FP. Effective connectivity between the LTPJ and RSTS showed significant task modulation when the analysis was seeded in either region. In contrast, effective connectivity between the MMPFC and PC decreased in strength for FB>FP. No significant effects were observed for age or task accuracy.

Post-hoc tests of simple effects suggested that observed increases in coupling were driven by reduced connectivity for FP relative to baseline [LTPJ–RTPJ:  $M = -0.10$ ,  $t(31) = -3.25$ ,  $P = 0.003$ ; LTPJ–RSTS:  $M = -0.06$ ,  $t(31) = -1.80$ ,  $P = 0.08$  (n.s.); PC–LTPJ:  $M = -0.09$ ;  $t(31) = -3.21$ ,  $P = 0.003$ ; RSTS–LTPJ:  $M = -0.05$ ,

**Table 4.** Associations between ROI activity and social cognitive behavior: regression results

		b [95% CI]	$\beta$	t	P	F(3, 26)	R <sup>2</sup> [95% CI]
ROI activity + age + IQ → IRI-PT							
PC	Activity	-8.41 [-14.68, -0.21]	-0.48	-2.75	0.011*	2.80	0.24 [0.01, 0.50]
	Age	0.02 [-0.11, 0.13]	0.08	0.45	0.654		
	IQ	0.11 [-0.10, 0.30]	0.25	1.39	0.176		
RTPJ	Activity	-7.02 [-14.88, 2.57]	-0.34	-1.84	0.078	1.37	0.14 [0, 0.32]
	Age	0.01 [-0.13, 0.12]	0.02	0.12	0.907		
	IQ	0.07 [-0.14, 0.28]	0.16	0.86	0.398		
LTPJ	Activity	-10.38 [-17.32, -0.73]	-0.45	-2.59	0.016	2.51	0.22 [0.02, 0.50]
	Age	0.03 [-0.09, 0.14]	0.10	0.58	0.570		
	IQ	0.06 [-0.13, 0.23]	0.14	0.78	0.444		
RSTS	Activity	-6.51 [-16.58, 8.88]	-0.19	-0.99	0.332	0.55	0.06 [0, 0.15]
	Age	0.01 [-0.13, 0.12]	0.05	0.25	0.802		
	IQ	0.08 [-0.15, 0.26]	0.17	0.85	0.401		
ROI activity + age + IQ → IRI-EC							
PC	Activity	-6.69 [-10.89, -0.51]	-0.53	-3.18	0.004*	3.97	0.31 [0.02, 0.57]
	Age	-0.04 [-0.13, 0.04]	-0.19	-1.12	0.271		
	IQ	0.09 [-0.10, 0.17]	0.27	1.57	0.130		
RTPJ	Activity	-6.04 [-10.71, -0.29]	-0.40	-2.29	0.031	2.27	0.21 [0.01, 0.40]
	Age	-0.06 [-0.15, 0.02]	-0.25	-1.41	0.171		
	IQ	0.06 [-0.10, 0.19]	0.17	0.96	0.345		
LTPJ	Activity	-5.87 [-10.74, -0.51]	-0.35	-1.96	0.060	1.79	0.17 [0.01, 0.34]
	Age	-0.04 [-0.13, 0.05]	-0.17	-0.94	0.356		
	IQ	0.05 [-0.10, 0.17]	0.14	0.77	0.444		
RSTS	Activity	-6.64 [-10.89, -0.51]	-0.27	-1.44	0.161	1.17	0.12 [0, 0.27]
	Age	-0.05 [-0.13, 0.04]	-0.22	-1.19	0.244		
	IQ	0.06 [-0.10, 0.17]	0.19	0.99	0.329		
ROI activity + age + IQ → SRS-Awr							
PC	Activity	14.00 [6.29, 23.62]	0.52	3.21	0.005*	7.20	0.53 [0.16, 0.67]
	Age	-0.14 [-0.30, 0.04]	-0.31	-1.94	0.067		
	IQ	-0.31 [-0.55, -0.08]	-0.50	-2.95	0.008		
RTPJ	Activity	5.63 [-6.36, 15.19]	0.19	1.00	0.331	2.91	0.31 [0.01, 0.54]
	Age	-0.13 [-0.34, 0.05]	-0.29	-1.44	0.166		
	IQ	-0.23 [-0.46, 0.03]	-0.37	-1.87	0.077		
LTPJ	Activity	10.55 [0.68, 24.77]	0.32	1.77	0.093	3.90	0.38 [0.02, 0.54]
	Age	-0.16 [-0.34, 0.02]	-0.34	-1.82	0.084		
	IQ	-0.21 [-0.47, 0.01]	-0.34	-1.83	0.083		
RSTS	Activity	8.05 [-22.96, 32.47]	0.16	0.83	0.419	2.76	0.30 [0.01, 0.50]
	Age	-0.14 [-0.32, 0.04]	-0.29	-1.46	0.162		
	IQ	-0.24 [-0.47, 0.04]	-0.38	-1.90	0.073		
ROI activity + age + IQ → SRS-Cog							
PC	Activity	1.63 [0.28, 2.68]	0.52	2.84	0.010*	4.35	0.41 [0.08, 0.59]
	Age	0.01 [-0.01, 0.03]	0.18	1.01	0.325		
	IQ	-0.04 [-0.07, 0]	-0.54	-2.86	0.010		
RTPJ	Activity	0.67 [-0.88, 2.04]	0.19	0.93	0.365	1.50	0.19 [0, 0.39]
	Age	0.01 [-0.01, 0.03]	0.21	0.98	0.338		
	IQ	-0.03 [-0.06, 0.01]	-0.41	-1.94	0.068		
LTPJ	Activity	0.91 [-0.54, 2.55]	0.24	1.16	0.262	1.69	0.21 [0.01, 0.41]
	Age	0.01 [-0.01, 0.03]	0.16	0.78	0.447		
	IQ	-0.03 [-0.06, 0.02]	-0.39	-1.85	0.079		
RSTS	Activity	1.15 [-1.65, 3.521]	0.20	0.94	0.360	1.51	0.19 [0.01, 0.45]
	Age	0.01 [0.01, 0.03]	0.21	0.99	0.337		
	IQ	-0.03 [-0.06, 0.01]	-0.43	-2.01	0.059		

Notes. Parameter and model fit results are reported for each regression model. SRS data were collected for 23 participants, affecting degrees of freedom [F(3,19)]. Brain-behaviors associations that are significant after controlling FDR ( $\alpha < 0.05$ ) are indicated with asterisks (\*). PC, precuneus; RTPJ, right temporoparietal junction; LTPJ, left temporoparietal junction; RSTS, right (anterior) superior temporal sulcus.

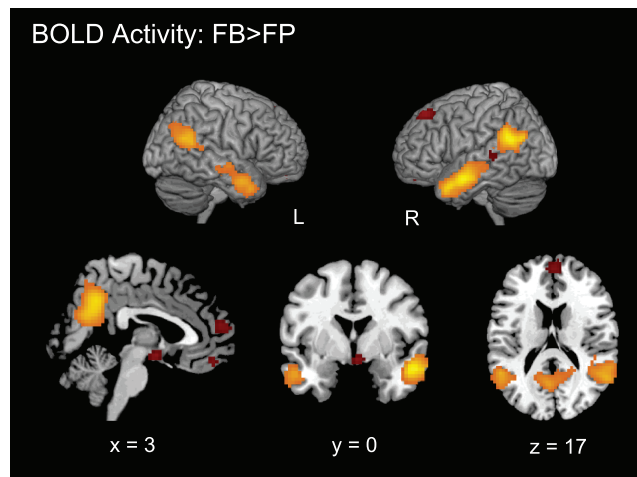


Fig. 1. Activity: BOLD analysis. Results of whole-brain analysis for the FB vs false photo conditions (FB>FP) are depicted at a voxel threshold of  $P < 0.001$ , uncorrected. Regions that survive cluster-level correction for multiple comparisons are shown in orange (FWE-corrected,  $\alpha < 0.05$ ); regions that are not significant at the FWE-corrected threshold are shown in red.

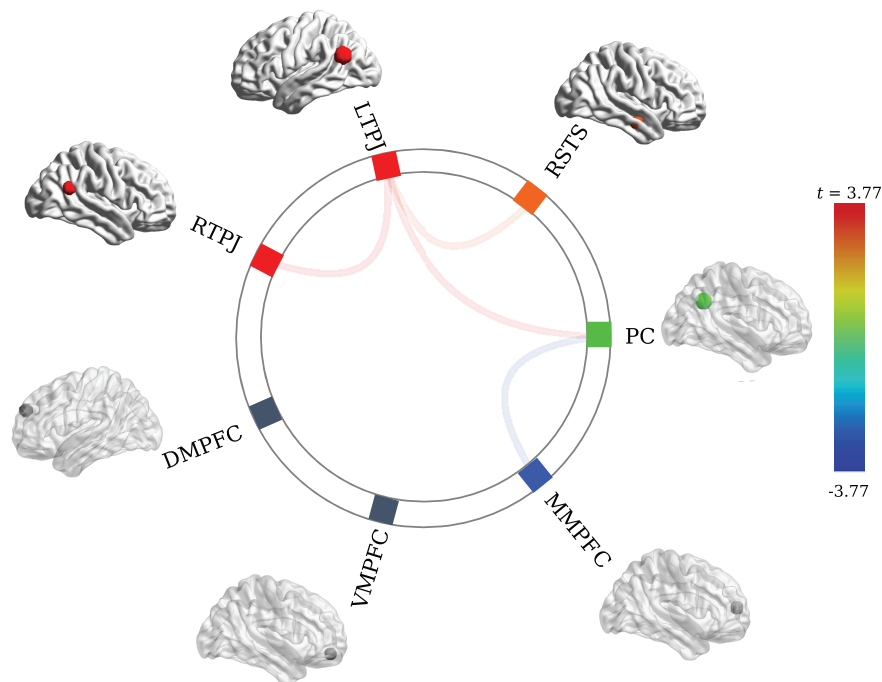


Fig. 2. Effective connectivity: ROI-to-ROI analysis results. Connectome display depicts ROI-to-ROI connections that show significant effective connectivity for FB>FP, i.e. significant, task-modulated increases or decreases in connectivity between these regions (FDR-corrected at the connection-level,  $q < 0.05$ ). Regions that do not show significant effective connectivity at this statistical threshold are shown in gray. RTPJ, right temporoparietal junction; LTPJ, left temporoparietal junction; RSTS, right (anterior) superior temporal sulcus; PC, precuneus; MMFPC, middle medial prefrontal cortex; VMFPC, ventromedial prefrontal cortex; DMPFC, dorsomedial prefrontal cortex.

$t(31) = -1.06$ ,  $P = 0.296$ ] and similar connectivity between these regions for FB relative to baseline [LTPJ–RTPJ]:  $M = 0.03$ ,  $t(31) = 1.05$ ,  $P = 0.30$ ; LTPJ–RSTS:  $M = -0.005$ ,  $t(31) = -0.16$ ,  $P = 0.872$ ; PC–LTPJ:  $M = 0.02$ ,  $t(31) = 0.78$ ,  $P = 0.440$ ; RSTS–LTPJ:  $M = -0.17$ ,  $t(31) = -3.10$ ,  $P = 0.004$ ]. The observed decrease in coupling between the MMFPC and PC reflected a modest, non-significant decrease in connectivity relative to baseline for FB [ $M = -0.05$ ,  $t(31) = -1.72$ ,  $P = 0.095$ ] and similar connectivity relative to baseline for FP [ $M = 0.05$ ,  $t(31) = 1.39$ ,  $P = 0.173$ ].

**Social brain–behavior analyses: ROI activity and everyday social cognition.** Our social brain–behavior analyses further explored relations between BOLD activity in regions that were significantly engaged for FB>FP in our whole-brain analyses, controlling for multiple comparisons: the RTPJ, LTPJ, PC and RSTS. Results indicate that greater ToM-related activity is related to poorer social cognition in everyday life (Table 4). Specifically, BOLD activity in the PC significantly predicted lower IRI-PT and IRI-EC scores and higher SRS-Awr and SRS-Cog T scores

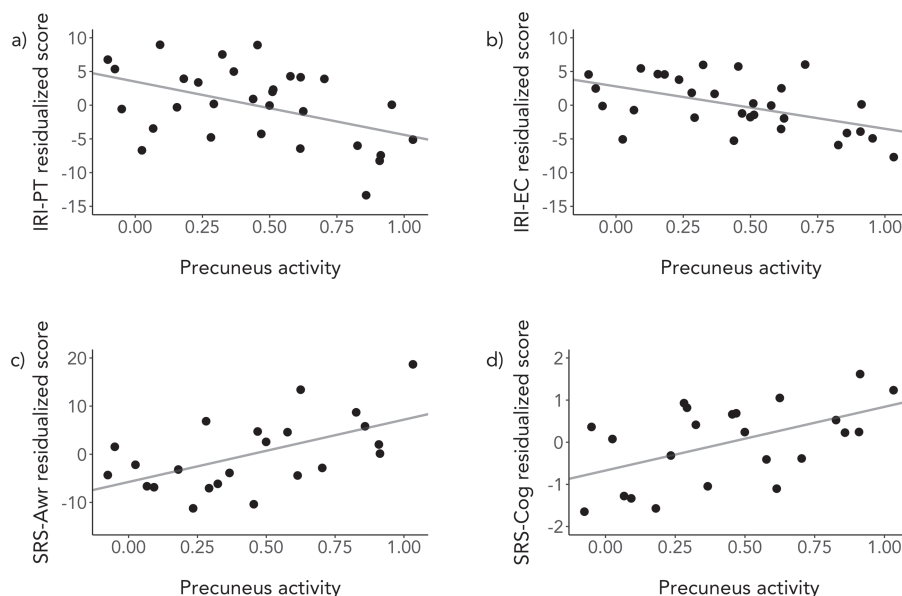


Fig. 3. Scatterplots for significant brain-behavior associations, controlled for FDR. Behavioral scores are residualized for age and IQ. Lower BOLD activity in the PC for the contrast of FB>FP is associated with better (a) empathic perspective-taking (IRI-PT), (b) empathic concern (IRI-EC), (c) awareness of social cues (SRS-Awr) and (d) reasoning about social situations (SRS-Cog) in everyday settings. Note that higher SRS (Social Responsiveness Scale-2) scores reflect poorer functioning and that the SRS-Cog variable was transformed for brain-behavior analyses (see [Social brain-behavior analyses](#)).

(Figure 3). Negative associations of LTPJ activity with IRI-PT scores and of RTPJ activity with IRI-EC scores ( $P < 0.05$ ) did not survive FDR control.

**Social brain-behavior analyses: effective connectivity and everyday social cognition.** Lastly, we explored associations between effective connectivity estimates for ROI-to-ROI connections that showed significant modulation for FB>FP (i.e. connections between the RTPJ and LTPJ, LTPJ and RSTS and PC and MMPFC). Effective connectivity between the LTPJ and RSTS was significant when analyses were seeded in either region (Table 3). Because prior work suggests the centrality of the TPJ to social cognition (Schurz et al., 2014), we chose to extract effective connectivity estimates for analyses seeded in the LTPJ to test associations between LTPJ-RSTS connectivity and social cognitive behavior. Results indicated a possible association between increased LTPJ-RSTS connectivity for FB>FP and higher IRI-PT scores [ $\beta = 0.43$ ,  $t = 2.38$ ,  $P = 0.025$ ], which did not survive FDR control (Supplementary Table S2).

## Discussion

Using a widely employed fMRI paradigm adapted for children, we investigated patterns of neural activity and connectivity supporting FB reasoning, an important facet of ToM, in children ages 9–13. On average, participants demonstrated modestly lower accuracy and longer response times for FB vs FP trials, suggesting that children may still find reasoning about others' mental states more difficult than reasoning about non-mentalistic false content at this stage of development. To account for possible associations with neural activity and connectivity, we modeled varying durations for FB and FP trials for each participant. In addition, we included task accuracy as a second-level covariate in BOLD activity and effective connectivity analyses and found no significant effects of this variable, controlling for multiple comparisons. This suggests that our neural findings for

ToM-modulated activity and connectivity (FB>FP) are not simply attributable to differences in condition difficulty. Notably, we did not find significant effects of age on activity or connectivity for FB>FP, in contrast to prior developmental studies (Gweon et al., 2012; Richardson et al., 2018; Xiao et al., 2019), although this may be due to the narrow age range we tested.

Whole-brain analyses confirmed that children ages 9–13 more strongly engaged the RTPJ, LTPJ, PC and RSTS during mentalistic (FB) vs non-mentalistic (FP) reasoning about false content, consistent with prior studies of ToM in children (Saxe et al., 2009; Gweon et al., 2012) and adults (Dodell-Feder et al., 2011; Schurz et al., 2014). This suggests that temporal and parietal aspects of the neural ToM network are engaged to support mental state reasoning by this important stage of social development. Notably, our results indicated that clusters of activation in the DMPFC, MMPFC and VMPFC were limited in extent, failing to survive correction for multiple comparisons. These results add to a mixed body of findings with regard to MPFC engagement for ToM in school-age children. For example, some prior studies have similarly found significant MMPFC activity only at uncorrected thresholds in whole-brain analyses (Saxe et al., 2009), while others indicate robust DMPFC activity at corrected thresholds (Gweon et al., 2012).

Limited engagement of the MPFC may be partially attributable to features of our specific FB paradigm and the age of our sample. Prior studies have found that the MPFC is more strongly recruited by mentalizing about others' emotions vs non-affective mental states (Völlm et al., 2006; Sebastian et al., 2012); our task focused specifically on understanding the beliefs of others, a cognitive aspect of ToM, perhaps contributing to less engagement of the MPFC. Alternatively, FB and FP story stimuli in our study were read aloud by a neutral voice, possibly imbuing both types of stories with social salience. Recent work suggests enhanced DMPFC activity to social stimuli in middle childhood (Rice et al., 2016; Alkire et al., 2018) and adolescence (Blakemore, 2008), even in the absence of mental state content.



This may reflect the enhanced salience of social information in adolescence (Somerville, 2013). However, findings from our follow-up analyses are not consistent with this interpretation, indicating that the DMPFC was not recruited to a significant extent to process either FB or FP stimuli. Given that our sample spans middle childhood and emerging adolescence, results should be viewed in the context of the marked changes in MPFC structure and function that occur during this period and continue through adulthood (Blakemore, 2008). Further longitudinal research is needed to clarify how the roles of prefrontal ToM regions change from peri-adolescence into adulthood.

To characterize the functional integration of ToM regions in school-age children, we evaluated patterns of effective connectivity between key nodes of the ToM network identified in previous literature (Saxe & Kanwisher, 2003; Dufour et al., 2013). Our analyses revealed increased task-modulated connectivity between the LTPJ and RTPJ, the LTPJ and RSTS and the PC and LTPJ for FB>FP. Post-hoc tests indicated that observed increases in coupling reflected similar effective connectivity of these regions for FB vs baseline and diminished effective connectivity for FP vs baseline. Building upon preliminary evidence that intrinsic connectivity of the RTPJ with the LTPJ and PC is associated with children's ToM ability (Xiao et al., 2019), our findings suggest the LTPJ, RTPJ, PC and RSTS may interact in a similar manner during ToM reasoning as during rest. In contrast, these regions may decouple, showing weaker associations between their time-courses, when engaging in non-mentalistic reasoning relative to rest. Interestingly, the decrease in connectivity of midline structures (MMPFC and PC) was driven by a modest decrease in connectivity during FB relative to baseline, suggesting that these regions decouple, acting in a more independent manner, to support ToM at this stage of development. Given the overlap between core nodes of the ToM network and those of the default mode network (Spreng et al., 2009), future studies should compare task-modulated connectivity of ToM regions to their intrinsic connectivity in order to clarify how these regions interact in a task-dependent vs task-independent manner. Although gPPI analyses model task-modulated effects of a seed region 'on' a target region, we note that this approach does not test causal influence. Investigating the direction of information flow during ToM is another promising avenue for future research.

Lastly, to elucidate associations between neural ToM mechanisms and social cognitive behavior, we tested the contributions of task-modulated activity and connectivity to variation in children's everyday social cognition. Results indicated a possible association between empathic perspective-taking and ToM-modulated connectivity of the LTPJ with the RSTS, consistent with prior work implicating the LTPJ in perspective-taking (Schurz et al., 2013); however, this finding was not significant after correction for multiple comparisons and should be interpreted with caution. Notably, the magnitude of PC activity for FB>FP explained significant unique variance in social cognition, controlling for age and IQ, at corrected statistical thresholds. PC activity was associated with variation in children's self-reported empathic perspective-taking and concern, as well as parent-reported social awareness and reasoning, suggesting that this region facilitates multiple aspects of social cognitive behavior in everyday settings. These results extend prior research indicating that midline cortical structures, including the PC, are engaged by thinking about the self and others in adolescents, facilitating understanding of others' affective and non-affective internal states (Ochsner et al., 2004; Pfeifer et al., 2007, 2009; Saxe & Powell, 2006). Importantly, our brain-behavior analyses focused on

testing relations between ToM network function and children's social cognitive skills, including empathy. However, empathy can engage other neural circuitry, including subcortical regions such as the insula (Kanske et al., 2015) and cortical regions implicated in generated shared representations, such as the inferior parietal lobule and premotor cortex (Zaki et al., 2009). To better understand the functional architecture of empathy in childhood, future studies should test associations between a wider set of candidate brain regions and real-world empathic behavior.

Notably, task-modulated activity in the PC was negatively associated with children's social cognition in everyday situations, such that lower activity for FB>FP was associated with better functioning. Although associations between TPJ activity and behavioral measures did not survive correction for multiple comparisons—and should be interpreted with caution—they demonstrated trends in the same direction. This suggests that children with greater social cognitive ability show less differentiation of neural activity when engaging in mental state reasoning during middle childhood and early adolescence. This could reflect reduced engagement of regions such as the PC to support reasoning about others' minds or increased engagement of these regions to support reasoning about other stimuli. Further research is needed to test associations between selectivity of ToM regions and social cognitive behavior as development unfolds.

Limitations to the current study are acknowledged. Our modest sample size limited our power to detect significant neural correlates of ToM and examine individual differences in behavior. The rate of false negatives is particularly high for PPI analyses (O'Reilly et al., 2012), which may have impacted our effective connectivity results. Fewer participants contributed data for our analyses using SRS subscales ( $N=23$ ), so reported associations between PC activity and variation in social awareness and cognition should be considered preliminary. In addition, although our task is modeled on a well-validated fMRI paradigm for studying ToM (Saxe & Kanwisher, 2003; Dodell-Feder et al., 2011), FB stories always featured social agents, while some FP stories did not. This may have impacted our ability to identify neural responses specific to mental state reasoning vs more general social reasoning for certain stimuli. Lastly, FB reasoning is just one aspect of ToM; successfully navigating the social world requires more sophisticated, spontaneous social cognition. Studies testing mentalizing in interactive contexts may help elucidate the mechanisms supporting everyday social function.

## Conclusions

The current study supports the assertion that core temporal and parietal aspects of the neural ToM network are engaged during mental state reasoning in children (ages 9–13). In addition, children demonstrate significant task-modulated changes in connectivity between key ToM regions, indicating emerging functional integration of this network. Together, these findings elucidate how the ToM network functions to support social cognition during this developmental period. Furthermore, the current study addresses an important gap in existing literature, providing evidence that neural activity in the ToM network is linked to variation in children's everyday social cognition. Task-modulated activity and connectivity within the ToM network may serve as useful metrics of heterogeneity in typical development and in neurodevelopmental populations characterized by social deficits, such as autism spectrum disorder.

## Funding

This work was supported by the National Institutes of Health (7R01MH100028 to C.A.N.); Sackler Scholar Programme in Psychobiology (to C.M. and S.H.L.); Julius B. Richmond Fellowship (to S.H.L.); RAND Fund, Harvard University (to C.I.H.); and NARSAD/Brain and Behavior Research Foundation (to C.I.H.).

## Acknowledgements

The authors thank Audrey Torricelli, Natalie Kleeman, Mia Wigley, Erin Guty, Morgan Henry, Alexandra Kelly, Dr Hong Yin, Dr Barbara Braams and Dr Laurel Gabard-Durnam for their practical and conceptual contributions.

## Supplementary data

Supplementary data are available at SCAN online.

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