

Theory of Mind Performance in Children Correlates With Functional Specialization of a Brain Region for Thinking About Thoughts

Hyowon Gweon

Massachusetts Institute of Technology

David Dodell-Feder

Harvard University

Marina Bedny and Rebecca Saxe

Massachusetts Institute of Technology

Thinking about other people's thoughts recruits a specific group of brain regions, including the temporo-parietal junctions (TPJ), precuneus (PC), and medial prefrontal cortex (MPFC). The same brain regions were recruited when children ($N = 20$, 5–11 years) and adults ($N = 8$) listened to descriptions of characters' mental states, compared to descriptions of physical events. Between ages 5 and 11 years, responses in the bilateral TPJ became increasingly specific to stories describing mental states as opposed to people's appearance and social relationships. Functional activity in the right TPJ was related to children's performance on a high level theory of mind task. These findings provide insights into the origin of neural mechanisms of theory of mind, and how behavioral and neural changes can be related in development.

As human adults, we spend much of our time thinking about the actions and thoughts of others: We predict and explain others' actions, interpret their speech and gestures, make moral and legal decisions about their actions, and more. What underlies all of these impressive and distinctively human behaviors is the capacity to infer and reason about unobservable mental states, a "theory of mind" (ToM). With the recent advent of noninvasive methods to study the neural basis of human cognitive functions, functional magnetic resonance imaging (fMRI) studies have discovered a set of brain regions that are selectively recruited for ToM tasks (Frith & Frith, 2003; Saxe & Kanwisher, 2003), including the bilateral temporo-parietal junctions (TPJ), precuneus (PC), and medial prefrontal cortex (MPFC).

Although the majority of behavioral research on ToM has focused on its development in early childhood (Wellman, Cross, & Watson, 2001; Wimmer & Perner, 1983), most neuroscientific studies have been conducted with adults. More recently, there have been attempts to study broader aspects of social cognition in adolescents and older children, such as thinking about one's own intentions (Blakemore, Ouden, Choudhury, & Frith, 2007), appraisals of self and others (Pfeifer, Lieberman, & Dapretto, 2007; Pfeifer et al., 2009), understanding communicative intent (Wang, Lee, Sigman, & Dapretto, 2006), or watching animated movements of shapes (Moriguchi, Ohnishi, Mori, Matsuda, & Komaki, 2007). However, most studies have focused mainly on identifying brain regions that show differential activation between adolescents and adults; few have directly investigated the developmental trajectory of functionally defined brain regions in childhood or its relevance to behavioral development. Therefore, major questions remain concerning the development of the brain regions for ToM. First, what kind of functional and anatomical change occurs in ToM brain regions during development? Second, what is the

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Correspondence concerning this article should be addressed to Hyowon Gweon, Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, 77 Massachusetts Avenue, Cambridge, MA 02139. Electronic mail may be sent to hyora@mit.edu.

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time course of this development: When do ToM brain regions first show selectivity for social cognition, and when do they reach an adult-like functional profile? Finally, what is the relation between the development of ToM brain regions and the behavioral development of ToM? To begin to address these questions, we used fMRI to investigate the relation between neural and behavioral development in ToM in children aged 5–11 years.

Based on prior behavioral studies of ToM, we can make at least three different predictions for the pattern and time course of development in ToM brain regions. Behavioral research suggests that between ages 3 and 5 years, children show a dramatic improvement in performance on the most common test of ToM: the “false belief task.” In a standard version of the false belief task, the child is asked to predict or explain a character’s action with reference to a character’s “false belief.” For example, Maxi puts chocolate in a box but the chocolate is moved to a basket when Maxi is not looking. Then children are asked to predict where Maxi will look for the chocolate. In hundreds of studies conducted over four decades in many parts of the world, 3-year-olds systematically fail to understand that Maxi has a false belief; instead, they confidently insist that Maxi will look inside the basket, where the chocolate really is (Wellman et al., 2001). If 3-year-olds actually see Maxi looking inside the box, they still do not appeal to Maxi’s false belief to explain his action; instead, they appeal to changed desires (e.g., “He must not want the chocolate,” (Moses & Flavell, 1990)). In contrast, typical 5-year-old children correctly predict and explain Maxi’s action, by appealing to his false belief. One account of this phenomenon is that children undergo a key conceptual change in their ToM between ages 3 and 5 years, coming to understand that the content of a person’s belief can be false (i.e., differ from reality; Wellman et al., 2001). Thus, ToM brain regions might show pronounced anatomical and functional development around age 4 years that accompanies the striking behavioral changes in how children reason about mental states.

Consistent with this prediction, one study has reported neural changes in the ToM brain regions in 4-year-olds, correlated with children’s performance on standard false belief tasks. Sabbagh, Bowman, Evraire, and Ito (2009) used electroencephalograms (EEG) to measure the amplitude and coherence of resting alpha waves from preschoolers. These measures are thought to reflect functional maturation in a cortical region. The brain regions in which this alpha wave signal was most

correlated with the child’s performance on standard false belief tasks (after controlling for executive function and IQ) were the dorsal medial prefrontal cortex (DMPFC) and right temporo-parietal junction (RTPJ)—two of the regions most commonly associated with ToM in functional neuroimaging studies of adults. These results provide exciting evidence for a link between development of ToM brain regions and conceptual change in children’s ToM. However, they come from a single study, using a novel method for localizing brain activity, so this first hypothesis remains to be fully tested.

A second possibility is that ToM brain regions are already mature and functionally adult-like by age 2. Previous studies found that toddlers (Southgate, Senju, & Csibra, 2007) and even infants (Onishi & Baillargeon, 2005) show signs of false belief understanding. These findings pose difficulty for the claim that children undergo a critical conceptual change around age 4 years to understand representational mental states. Children in their 2nd year of life may be already able to use inferred false beliefs to correctly predict actions (Baillargeon, Scott, & He, 2010; Leslie, Friedman, & German, 2004). If so, ToM performance in preschoolers may instead be related to domain-general cognitive capacities, such as executive function (Carlson & Moses, 2001) and syntactic knowledge (de Villiers & Pyers, 2002).

If the impressive performance of infants reflects an adult-like understanding of mental states, one might expect to find similar neural signatures for the early ToM competence in infants and later ToM performance in preschoolers. Unfortunately, to date, no neuroimaging studies of ToM have been conducted in children younger than 3 years, due to the substantial methodological difficulties associated with conducting functional imaging studies with infants and toddlers. However, reports on neural changes in ToM regions of older children (see below; Saxe, Whitfield-Gabrieli, Scholz, & Pelphey, 2009) provide some evidence against a strong claim for a fully adult-like neural mechanism for ToM in infants.

Finally, a third possibility is that ToM brain regions are not fully mature by 5 years of age but instead show functional changes throughout middle childhood, at least until 11 or 12 years of age. While children past 5 years of age readily pass standard false belief tasks, previous research suggests that behavioral ToM development is by no means “complete” at 5 years of age. For example, children’s ability to track speakers’ intentions in

discourse, or to understand nonliteral utterances, such as irony and sarcasm, continues to develop in late childhood (Capelli, Nakagawa, & Madden, 1990; Peterson, Wellman, & Liu, 2005; Winner & Leekam, 1991). Children's performance in moral reasoning tasks also reflects relatively late changes in ToM (Baird & Astington, 2004; Chandler, Sokol, & Wainryb, 2000; Fincham & Jaspers, 1979; Gruenich, 1982). Moreover, children slowly learn that people can entertain different (sometimes conflicting or even false) beliefs because beliefs arise from inferential or interpretive processes (Carpendale & Chandler, 1996; Pillow & Mash, 1999). These tasks are all conceptually more difficult than standard false belief tasks. Developmental change after age 5 years suggests that ToM development is not an all-or-none phenomenon, but rather a successive unfolding of insights that occur over the entire course of development.

The neural regions involved in ToM might correspondingly continue to develop functionally throughout childhood. There is already some neural evidence for continued development in ToM brain regions past 5 years of age. The few existing developmental fMRI studies on ToM (Kobayashi, Glover, & Temple, 2007) have reported some differences between school-aged children and adults in the neural basis of ToM. In addition, one study (Saxe et al., 2009) reported differences *among* children: Although the ToM brain regions normally recruited for ToM in adults are also found in 6- to 12-year-olds, the functional profile of some of these brain regions was different from those in adults, especially in younger children. Previous research has established that the RTPJ (and to a lesser extent, LTPJ) has a highly selective response profile in adults: This region's response is high when participants think about a person's mental states (e.g., thoughts, beliefs, or desires), but low when they think about other socially relevant facts (e.g., a person's appearance, bodily sensations, personality traits, stable preferences, or social relationships; Apperly, Samson, Chiavarino, & Humphreys, 2004; Jenkins & Mitchell, 2010; Perner, Aichorn, Kronblicher, Staffen, & Ladurner, 2006; Pfeifer et al., 2007; Saxe & Kanwisher, 2003; Saxe & Powell, 2006). That is, the RTPJ appears to be recruited just when participants are using their ToM rather than for general social cognition. This response profile, however, does not appear to emerge until late in childhood. In 6- to 8-year-old children, Saxe et al. (2009) reported that the RTPJ responded equally to any information about people, including their appearance and social relationships. The selective

pattern typical of adults emerged in children aged 10–12 years. These results suggest that although the overall structure of the neural "ToM network" is present by age 6 years, there continue to be important functional changes in key regions within the network much later in childhood. However, none of the existing developmental fMRI studies of ToM have included any behavioral measurement of children's ToM competence. Therefore, it remains unclear whether the improvements in ToM abilities in late childhood are related to the reported neural changes in ToM brain regions, or to changes in other domain-general cognitive systems like language and attention.

In light of these possibilities, the current study investigated the development of ToM brain regions and the behavioral correlates of these changes using fMRI in children aged 5–11 years. Children and adult participants listened to short aurally presented stories describing mental, social, or physical facts.

First, we aimed to replicate Saxe et al. (2009)'s finding of developmental change in selectivity for mental state information in ToM brain regions, using new stimuli and a different task. Specifically, instead of varying conditions within a story presented as a single block, we constructed separate stories for each condition to better tease apart the condition effect in the fMRI data. Also, instead of asking about the content of the story, children answered whether a short probe matched the main part of the stimuli, such that we could ask the same question across all conditions and even the youngest children would have no difficulty answering the questions.

Second, to capture qualitative changes in ToM that take place between 5 and 11 years, the scanned children were also tested outside the scanner on ToM tasks designed to assess children's ability to reason about other people's mental states at varying levels of difficulty. Combining these behavioral data with the neural measures, we tested whether ToM development is correlated with neural changes in brain regions for ToM.

Method

Participants

Twenty typically developing children (10 females; *M* age = 8.5 years, range = 5.1–11.5 years) from a local community participated in the experiment. All children were native speakers of English and had normal or corrected-to-normal vision. All, but one

were right-handed. Children gave assent, and their parents gave written informed consent in accordance with the requirements of the institutional internal review board. Eight neurologically normal right-handed adults (6 females; *M* age = 21.5 years, range = 18–25 years) also participated in the experiment for compensation. All adult participants were native speakers of English and had normal or corrected-to-normal vision.

Experimental Procedure

Prior to the scan, children were trained to lie still in a custom-built MRI simulator (mock scanner) with a motion detector. Children watched a movie of their choice in the mock scanner, and the movie screen turned off for 3 s whenever the camera with motion sensor detected head motion above a predetermined threshold. The mock scanning session lasted for 20–30 min. Prior to the scan, participants also performed seven practice trials of the task employed in the scanner to ensure understanding of the task.

Stimuli consisted of children’s stories in English, read by one of three female native speakers, in child-directed prosody. Stories described a protagonist’s mental state (mental), a protagonist’s appearance and social relationships (social), or physical

events, objects, and states (physical; see Figure 1 for experimental design and examples of stories, and Appendix S1 in the online supporting information, for a full list of stories). Both mental and social stories had social content: They contained information about people and social relationships. However, only the mental stories had information about mental states, such as thoughts, beliefs, or desires. Physical stories did not have any social content: They described changes in physical states of objects.

Stories were matched across conditions for number of words (*M* = 51.6 words), number of sentences (4.7), length (20 s), and Flesch Reading Ease Level (*M* = 90.4). Following each story, participants were asked “Does this come next?” and made a judgment as to whether a succeeding probe sentence fit with the previous story. Incorrect sentences were drawn randomly from other, unrelated stories. This task was designed to verify attention without provoking performance differences between age groups. We measured children’s comprehension of these stories in a separate pilot study (see the online supporting information for more information).

In addition to these three English conditions, two more conditions (foreign and music) were included in the design but not included in the present analyses. In the foreign condition, stories in

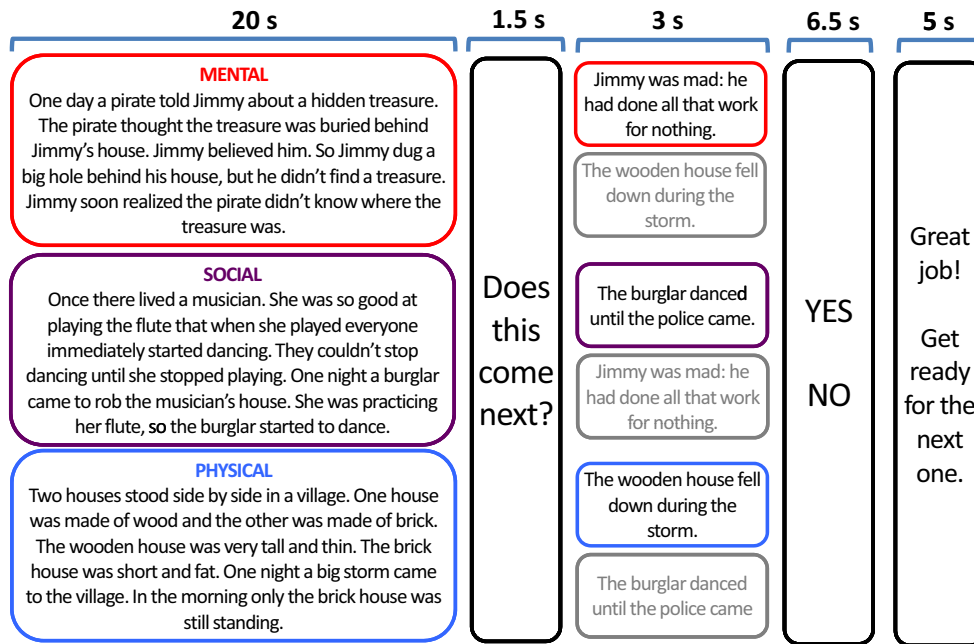


Figure 1. Schematic of the experimental design and examples of story stimuli.

Note. In each trial, a story in one of three conditions (mental, social, and physical) was presented. After the story (20 s) and the question (1.5 s), a probe sentence was presented (3 s). The probe sentence was either a continuation of the same story or part of a different story. Participants pressed one of two buttons (yes, no) inside the scanner to indicate whether the probe sentence matches the story. At the end of the trial, children heard different encouragements (5 s) depending on whether their answers were correct or not.

Hebrew, Korean, and Russian were presented, and participants' task was to judge whether a succeeding sentence was in the same language as the previous story. In the music condition, clips of music were played and children were asked to judge whether the succeeding music clip was the same melody played on the same instrument.

Stimuli were presented via Matlab 7.6 running on an Apple MacBook Pro. The complete experiment consisted of four runs, generating a total of eight blocks per condition. Each run consisted of 10 experimental blocks (single-trial block design, each 36 s long, 2 per condition) and three rest blocks (each 12 s, one at the start of the run, after the presentation of five stories, and at the end of the run) for a total of 7 min. The order of conditions within a run was palindromic (e.g., [rest] A B C D E [rest] E D C B A [rest]), and counterbalanced across runs. In each experimental block, the story was presented first (20 s), followed by "Does this come next?" (1.5 s), the probe sentence (3 s), a pause (6.5 s) during which the participant would make a response, and finally the postresponse encouragement (5 s).

Stories were counterbalanced across runs and participants. During the story portion of the block (and the rest period), a colorful, abstract image unrelated to the story content was presented on screen, so that children would not be lying in the dark. The image changed every five experimental blocks, during a rest block. During the question portion of the block, participants saw a green check mark on the left and a red X on the right side of the screen as response reminders (left button for match, right button for nonmatch). These response images remained on the screen until the participant made a yes-or-no button response. The correct answer was "yes" for half of the trials and "no" for the other half, counterbalanced within and across runs. Participants heard an encouraging message after their response (e.g., "Great job! Get ready for the next one" for a correct response and "Alright. Here comes another one" for an incorrect response). All participants were monitored throughout the experiment by three experimenters or adults, two experimenters in the control room and one adult (an experimenter or a parent) in the scanner room with the child, to ensure children were comfortable, still, and complying with the task instructions. Because of technical errors, behavioral data were not saved for 1 child and 1 adult participant.

The experiment was designed for each child to participate in 4 runs. However, 7 children requested to stop the experiment before completing all 4 runs. Of these participants, 5 completed 3 runs and 2

completed 2 runs. We therefore collected approximately 14 min to 28 min of functional MRI data with each child (2–4 runs). The children who completed all 4 runs were older on average than those who completed 2 or 3 runs (9.17 vs. 7.29 years), $t(18) = 2.54$, $p < .05$. After dropping runs that were unusable due to motion (1 run each, from 3 children), we had 11 children with 4 usable runs, 6 children with 3 runs, and 3 children with 2 runs.

fMRI Data Collection and Analyses

Participants were scanned on a 3-Tesla Siemens scanner at the Athinoula A. Martinos Imaging Center at the McGovern Institute for Brain Research at MIT. T1-weighted structural images were collected in 128 sagittal slices (TR = 2 s, TE = 3.39 ms, flip angle = 90°) with 1.33 mm isotropic voxels. Functional data were acquired in $3 \times 3 \times 4$ mm voxels in 30 interleaved near axial slices covering the whole brain, using standard echoplanar imaging procedures (TR = 2 s, TE = 30 ms, flip angle = 90°). These sequences used prospective acquisition correction (PACE), which adjusts the slice acquisitions during scanning to correct for head movement up to 8 degrees and 20 mm, and the Siemens online nonrigid motion correction program (MoCo).

fMRI data were analyzed using SPM2 (<http://www.fil.ion.ucl.ac.uk/spm>) and custom software written in Matlab. Each participant's data were offline motion corrected and then normalized onto a common brain space (Montreal Neurological Institute [MNI] template). Data were then smoothed using a Gaussian filter (full width half maximum = 5 mm). The experiment was modeled using a boxcar regressor. The story and response portion (including the probe sentence) of the task were entered as separate regressors (resulting in six regressors total: five for each condition and one for the response portion) in a general linear model, as we were specifically interested in the neural correlates of comprehension of the stories. Data were high pass filtered to reduce low-frequency noise in the data, such as slow drift (cutoff 128 s), and each participant's movements in all six dimensions were used as nuisance regressors.

Both whole-brain and individual ROI analyses were conducted using the mental > physical contrast. Whole-brain analysis was conducted separately for children ($N = 20$) and adults ($N = 8$) to reveal areas that were significantly more activated in the mental condition than the physical condition. In the whole-brain analyses, the false-positive rate was controlled at $p < .05$ (corrected for multiple comparisons)

by performing Monte Carlo permutation tests with the SnPM3 toolbox for SPM2 (Hayasaka & Nichols, 2004; Nichols & Holmes, 2001; <http://www.sph.umich.edu/ni-stat/SnPM/>). We used approximate permutation tests (5,000 tests) to empirically determine voxel-wise t and cluster size (k , contiguous voxels) thresholds. The resulting thresholds were approximately $t > 6.0$ and $k > 400$ for adults, and $t > 5.1$ and $k > 200$ for children.

Based on the previous literature (Frith & Frith, 2003; Saxe & Kanwisher, 2003) and from the whole-brain analysis results, six functional ROIs from the ToM network were defined for each participant individually using both anatomical location (e.g., coordinates from previous literature and our whole-brain results) and functional activation: RTPJ, LTPJ, precuneus (PC), dorsal, middle, and ventral MPFC (DMPFC, MMPFC, VMPFC). Because there is no purely anatomical definition that would allow us to precisely define these regions in each individual brain, the voxels near the spatial landmarks for each region that show the diagnostic function (i.e., higher response in the mental than in the physical condition) were defined as that individual's functional region of interest. The functional criteria for selecting ROIs were defined as (a) clusters of at least 10 voxels ($k > 10$) that were (b) significantly more active in the mental condition than in the physical condition ($p < .001$), (c) within a radius of 9 mm. For every participant, we overlaid the functional activation on the participant's anatomical image to guide the selection of the ROIs. If there was more than one cluster that passed the criteria within the same anatomical region, we defined the ROI around the peak voxel with the highest t value. If an ROI was not observed in a given subject, the participant was dropped from the analysis for that ROI.

The response for mental, social, and physical stories was calculated in each of these ROIs for each child. For each ROI, we report the average percent signal change (PSC) of the raw BOLD signal in each condition. One of the advantages of using PSC rather than beta coefficients is that PSC is resistant to potential differences in the shape of the hemodynamic response between children and adults (see the online supporting information for analysis of beta coefficients). In addition, PSC allows us to look at the time course of the BOLD activity in each condition rather than just a single value. PSC was calculated as follows: We first averaged the raw BOLD magnitude across all voxels within an ROI for each time point in the experiment. Then, we calculated the average BOLD magnitude of the ROI in

each condition for each time point after the onset of the stimulus, which resulted in a C (number of conditions) $\times T$ (number of time points) matrix of average BOLD magnitude values. Then we subtracted the baseline (average BOLD magnitude of the ROI during fixation) from these values, and divided this by the baseline ($PSC(c,t) = 100 * (\text{Resp}(c,t) - \text{baseline}) / \text{baseline}$). The result was a time course showing the percent signal change relative to baseline for each condition at each time point, in each participant (see Figure 3 in the Results section). For purposes of statistical analyses, we then averaged PSC across the time points during which the story was presented (4–22 s after story onset to account for hemodynamic lag) to get a single PSC value for each region in each participant (Poldrack, 2006).

Because the ROIs were defined using the response to the mental and physical stories, the critical ROI analyses focused on the relative response to the independent third condition, the social stories. Based on prior evidence for changes in the functional profiles of some of the ROIs as a function of age (Saxe et al., 2009), we examined response selectivity in each ROI for each participant; that is, we determined the degree to which responses were selective for mental state information versus general to any social information. Following the procedure of Saxe et al. (2009), a selectivity index was calculated to measure the relative difference in PSC between the mental and social stories and physical stories: $100 * (\text{Mental} - \text{Social}) / (\text{Mental} - \text{Physical})$. Because the ROIs, by definition, only consist of voxels that showed higher activation for the mental than the physical condition, the selectivity index works as a measure of the relative magnitude of activation in the social condition. A low selectivity score indicates that the response to the social stories was about as high as the response to the mental stories, and a high selectivity score indicates that the response to the social stories was about as low as the response to the physical stories. The selectivity index score for each child in each ROI was then analyzed in a linear regression with age. Note that while the estimate of the magnitude of selectivity was partially biased by the ROI selection procedure (because the response to mental and physical conditions were included in both ROI selection and the selectivity estimate), changes in selectivity with age are unbiased.

For analyses of ROI volume, unnormalized data were modeled to calculate the true size of each ROI in each subject, using a smoothing kernel of 8 mm. We assessed ROI volume relative to the cortical volume for each subject. Cortical volume was

estimated for each participant based on the unnormalized segmented gray matter for that subject (SPM2 segmentation tool).

ToM Behavioral Battery (Outside the Scanner)

A behavioral ToM battery was administered prior to the fMRI scan to assess aspects of children's ToM. Two illustrated booklets were used, with interactive questions embedded in the story. The first booklet depicted children in a classroom looking for their books for reading time; the second booklet depicted three children and their mother spending a day at the park. The booklets did not contain any text. The experimenter used the picture booklet to tell the story and ask questions, and the children answered the questions by either placing illustrated magnet pieces on the picture or giving a verbal response. Booklet 1 was 11 pages long and contained 18 questions; Booklet 2 was 13 pages long and contained 26 questions.

There were 14 different categories of questions that reflect different aspects of ToM development (common desire, diverse desire, diverse belief, ignorance, easy reference, hard reference, false belief reality known, false belief reality unknown, false belief based on expectation, moral false belief, emotion reminder, emotion, moral judgment, and interpretation). For each question, children were either asked to predict what a protagonist in the story might do (i.e., "Where will she look for her book: behind the chair or under the rug?") or to explain their prediction (i.e., "Why is she looking behind the chair?"). In particular, the explanation questions used a free response format, as a more sensitive measure of whether children would refer to the protagonists' mental states in explaining their behavior. Most prediction questions had two answer choices, and children's answers were scored 1 (correct) or 0 (incorrect). Each explanation question had explicit criteria for scoring children's responses (see the online supporting information for details on coding) as 1 (correct) or 0 (wrong). Of the 14 categories, 8 contained both prediction and explanation questions; the rest consisted of just prediction questions (see the online supporting information for a detailed description of questions in the storybook).

Although we expected our participants to show ceiling performance on some of the easier questions, we administered all questions for possible future comparison with younger children or those from clinical populations. However, the analysis in the current study focused on just the explanation

questions because: (a) prediction questions were two-alternative forced choice, so chance performance would be 50% accuracy, which could mask their real understanding and reduce the sensitivity of the measure, whereas explanation questions were open-ended, and (b) explanation questions asked children to justify their predictions, so prediction performance was often redundant. All of our participants had enough verbal competence to give explicit explanations.

All children began with the first storybook and proceeded to the second storybook. The whole session lasted approximately 20 min, and children's responses were videotaped for later coding. Adult subjects did not participate in this part of the experiment.

Results

Behavioral Results: Scanner Task

Performance on the task was well above chance for all conditions for children and adults (children: M [% accuracy] \pm SD : mental: 94 ± 10 ; social: 93 ± 12 ; physical: 87 ± 15 ; adults: mental: 98 ± 5 ; social: 98 ± 5 ; physical: 100 ± 0). For children, age was a significant factor that predicted both accuracy ($\beta = 0.64$, $p < .005$) reaction time (RT; $\beta = -0.78$, $p < .001$). Differences in accuracy and RT across conditions were analyzed for children and adult participants separately using Friedman test for accuracy, and repeated measures analysis of variance (ANOVA) for RT. There was no effect of condition on task accuracy in children, $\chi^2(2, N = 20) = 1.44$, *ns*, or adults, $\chi^2(2, N = 7) = 1.00$, *ns*, or on RT in children, $F(2, 36) = 2.75$, $p = ns$, partial $\eta^2 = .13$, or adults, $F(2, 12) = 0.18$, $p = ns$, partial $\eta^2 = .03$.

We used a simple behavioral task (determining whether the probe sentence fits the previous story) with very high performance across conditions and ages, so that it would be unlikely that group differences in task difficulty or performance would produce differences in the neural data. Nevertheless, we tested whether the response in any region of interest could be predicted by participants' accuracy or RT. There was no effect of accuracy or RT in any of the ROIs (see the online supporting information for statistical results).

fMRI Results: Scanner Task

Consistent with prior studies, whole-brain random effects analysis in adults revealed higher

BOLD signal for the mental stories than for the physical stories in RTPJ, LTPJ, PC, and DMPFC ($p < .05$, corrected; Perner et al., 2006; Saxe & Kanwisher, 2003; Saxe & Powell, 2006). These same brain regions were also more active for mental than physical stories in children ($p < .05$, corrected; see Table 1 and Figure 2 for a list of regions found in each age group in the whole-brain random effects results). We conducted two analyses to compare these whole-brain results between children and adults. First, we looked at whether there is any dif-

Table 1

Whole-Brain Random Effects Analysis: Peak MNI Coordinates of Regions Identified From Mental > Physical Contrast in Children and Adults

	Brain region	Peak [X Y Z]	T
Adults	Left TPJ ^a	[-52 -56 20]	8.67
	Right SFG	[22 52 26]	6.40
	DMPFC ^{a,b}	[-2 54 32]	6.10
	Precuneus ^a	[-2 -50 38]	5.89
	Right STS	[48 -28 -8]	5.71
Children	Right TPJ ^a	[52 -52 24]	5.71
	Right TPJ ^a	[56 -54 34]	8.50
	Left TPJ ^a	[-48 -60 30]	8.03
	Precuneus ^a	[-8 -52 36]	7.13
	Right SFG	[12 30 62]	6.48
	DMPFC ^a	[0 54 22]	6.36
	Right STS	[52 12 -26]	6.08

Note. TPJ = temporo-parietal junction; DMPFC = dorsal medial prefrontal cortex; STS = superior temporal sulcus; and SFG = superior frontal gyrus. Activations in all regions are significant at $p < 0.05$ (corrected).

^aBrain regions that were commonly activated in both children and adults in the conjunction analysis.

^bDMPFC in adults was observed as a local maximum in the right SFG cluster ([-2 54 32], $T = 6.10$).

ference in the mental > physical contrast between adults and children. A direct whole-brain comparison of children versus adults (adults > children contrast to reveal regions more active in adults than in children, children > adults contrast for the reverse) in this contrast did not reveal any cluster of activation at the corrected threshold ($p < .05$) or even at a lenient threshold of $p < .10$ (corrected). Second, to quantify which brain regions were commonly active in adults and children, we performed whole-brain conjunction analyses of the mental > physical contrast for adults and children. Each voxel counted as "overlapping" only if it was significantly activated in the mental > physical contrast ($p < .05$, corrected) independently for each group. The conjunction revealed activity in the RTPJ, LTPJ, PC, and DMPFC (Figure 2). These results indicate that the ToM brain regions in children respond more highly to mental stories than to physical stories, as they do in adults.

Individual-subject functional ROIs were identified in RTPJ in 8 of 8 adults and 17 of 20 children, LTPJ in 8 adults and 13 children, PC in 8 adults and 15 children, DMPFC in 8 adults and 10 children, MMPFC in 6 adults and 9 children, and VMPFC in 5 adults and 9 children (see Figure 3). To investigate the change in the responsiveness of the ROIs to mental, social, and physical information, the selectivity index (described above) was calculated for each ROI in each participant.

First, we investigated whether there are differences in selectivity of the ToM regions between children and adults. Note that our ROI selection was motivated by the conjunction of whole-brain results in the current study as well as the previous literature on brain regions involved in ToM (e.g.,

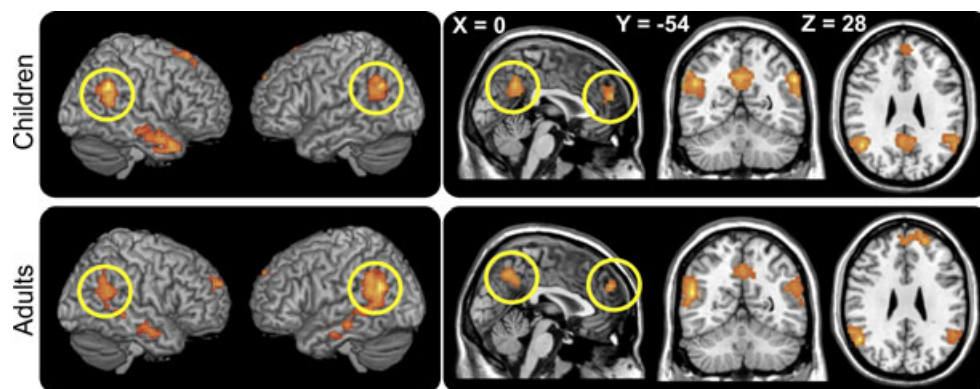


Figure 2. Random effects whole-brain analysis results in children and adults.

Note. Circled regions on the left pane are the right TPJ and left TPJ. The three images on the right pane show the precuneus and DMPFC (circled) on the sagittal slice ($X = 0$), the precuneus and bilateral TPJ on the coronal slice ($Y = -54$), and all four regions on the axial slice ($Z = 28$).

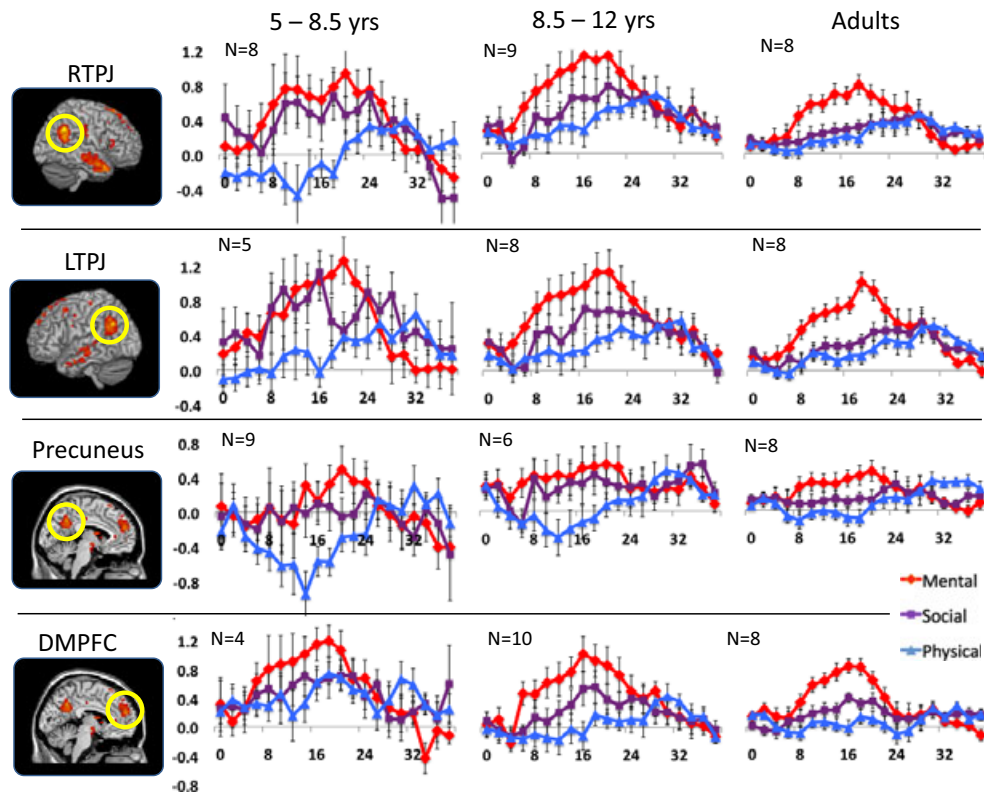


Figure 3. Four brain regions that showed common activation in both children and adults were picked out as regions of interest (ROIs) in each individual.

Note. The graphs show the mean percent signal change (PSC) relative to rest over the course of the whole trial (0–36 s). To visualize the developmental change in selectivity, children were median split by age (8.5 years) into younger and older groups. In all graphs, the x-axis is time (seconds), and the y-axis is the PSC.

Frith & Frith, 2003; Saxe & Kanwisher, 2003). An omnibus ANOVA (age groups \times ROIs) was not ideal because a majority of participants did not have all six ROIs. Therefore, we conducted planned comparisons of mean selectivity between adults and children independently for each ROI (because of unequal sample sizes, Welch t tests were used for all between-groups comparisons between children and adults). The comparisons revealed that selectivity was significantly higher in adults than in children in the RTPJ and PC: RTPJ, 86.5 (adults) versus 46.5 (children), $t(21.96) = 3.08$, $p < .005$; PC, 60.9 (adults) versus 24.0 (children), $t(18.29) = 2.50$, $p < .05$; and marginally in LTPJ, 74.9 (adults) versus 47.7 (children), $t(11.89) = 1.97$, $p = .073$. Adults did not differ from children in selectivity within any of the MPFC ROIs: DMPFC, 49.7 (adults) versus 68.8 (children), $t(17) = -0.88$, ns ; MMPFC, 45.6 (adults) versus 23.0 (children), $t(11) = 0.81$, ns ; VMPFC, 51.8 (adults) versus 68.1 (children), $t(12) = -0.67$, ns .

To look for further developmental change in the selectivity of an ROI, selectivity index was correlated

with age in each ROI. Within children, selectivity index in the RTPJ and LTPJ demonstrated a significant correlation with age even after controlling for the number of runs included in the analysis: RTPJ, $r(14) = 0.51$, $p < .05$; LTPJ, $r(10) = 0.70$, $p < .05$ (see Figure 4). This correlation between selectivity and age (after controlling for the number of runs) was not found in four other ROIs: PC, $r(12) = 0.27$; DMPFC, $r(7) = 0.17$; MMPFC, $r(6) = 0.21$; VMPFC, $r(6) = 0.02$; ns in all cases (see Figure S2).

The selectivity analysis concerns changes in the functional profiles of these regions. We also investigated whether there are changes in the magnitude or spatial extent (size) of activations in these brain regions. Comparison of the average percent signal change in the Mental condition between children and adults within each ROI revealed no differences in the magnitude of the BOLD response in these regions (see Table S1 in the online supporting information for statistical results). ROI volume was not significantly correlated with age among children in any ROI. However, adults had on average larger RTPJ ROIs than children (adult M size [mm³] = 7,277;

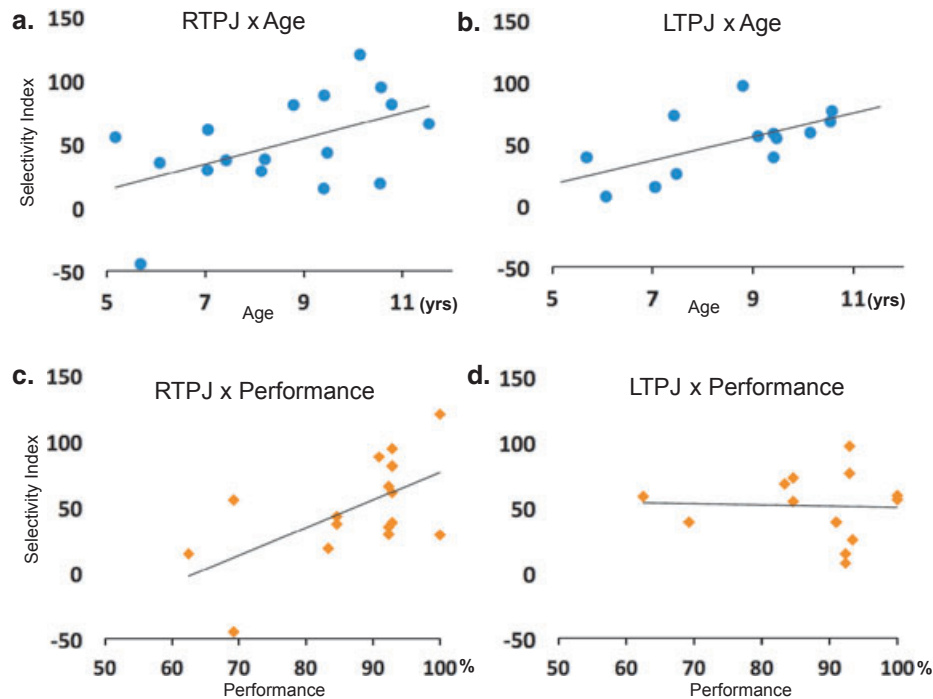


Figure 4. While selectivity was correlated with age in both RTPJ and LTPJ, the correlation between selectivity and behavioral performance was found only in the RTPJ. (a, b) Correlation between age and the selectivity index in the RTPJ (a) and LTPJ (b) in children. (c, d) The relation between performance in the theory of mind behavioral battery and selectivity index in the RTPJ (c) and LTPJ (d).

children $M = 2,692$, $t(8.69) = 2.78$, $p < .05$. This difference was not due to the increase in overall brain size: Adult RTPJ ROIs were larger than children's, even when expressed as a fraction of the individual's whole-brain gray matter volume (adult ROI volume/gray matter volume*100 = 0.03%; children = 0.01%), $t(8.01) = 2.71$, $p < .05$.

ToM Behavioral Battery and Its Relation to Brain Activity

Children's responses for each question in the two booklets were coded as "correct" or "incorrect" from the video recordings of the behavioral session. We were specifically interested in whether there was a significant correlation between children's performance on ToM tasks and their brain activity. The planned measure of interest in the current study was children's verbal response to all 15 explanation questions across two booklets. These questions ranged from easier ones that almost every child answered correctly (e.g., false belief reality known) to more difficult questions (e.g., hard reference; see online supporting information Table S1 for detailed description of these questions, coding criteria, and mean performance for each question). Average performance of the subjects for

these questions was 89% correct (range = 62% to 100%, $SD = 10\%$). We did not find a significant correlation between performance and age, $r(18) = 0.32$, $p = .16$.

Selectivity in the RTPJ for mental state information correlated significantly with children's average performance on the explanation questions in the ToM battery, $r(15) = 0.59$, $p < .01$, and remained significant even after controlling for age and number of runs analyzed, $r(13) = 0.66$, $p < .01$ (see Figure 4). No other ToM ROI showed a significant correlation between selectivity and performance: LTPJ, $r(11) = -0.04$; PC, $r(13) = 0.18$; DMPFC, $r(8) = 0.23$; MMPFC, $r(7) = 0.50$; VMPFC, $r(7) = 0.43$; all *ns* (see online supporting information Figure S2). There was no correlation with behavioral performance and volume in any ToM ROI: RTPJ, $r(15) = -0.09$; LTPJ, $r(11) = -0.09$; PC, $r(13) = -0.19$; DMPFC, $r(8) = 0.06$; MMPFC, $r(7) = -0.09$; VMPFC, $r(7) = 0.14$; all *ns*.

Discussion

In this study, we aimed to (a) identify brain regions associated with ToM in both children and adults, (b) characterize the developmental trajectory of

these brain regions, and (c) find evidence for a brain-behavior relation in these regions. We found, first, that the same brain regions implicated for ToM in adults are found in children aged 5–11 years. RTPJ, LTPJ, PC, and MPFC were all activated significantly more during mental stories compared to physical stories. Second, we replicated and extended previous findings of developmental change in the ToM network (Saxe et al., 2009): We found increasing selectivity to mental state information with age in RTPJ and LTPJ. Critically, developmental change in the selectivity of the RTPJ was correlated with children's performance on ToM tasks outside of the scanner.

In the current experiment, we scanned both children and adults while they performed the same task, allowing us to directly compare the functional profiles of different brain areas in children and adults. The magnitude of activation in the mental condition in ToM regions (RTPJ, LTPJ, PC, and DMPFC) was just as high in children as in adults: For example, average PSC in the mental condition showed no difference between children and adults. These results differ from Kobayashi et al. (2007), who found weaker activation in children for a verbal ToM task compared to adults (and stronger activation in children than adults for nonverbal tasks). This disparity may reflect differences in task and stimulus design. Kobayashi et al.'s participants read visually presented sentences stating second order beliefs (e.g., "Ted thinks that Cathy thinks that he wears a blue shirt"). The children in that experiment may have had more difficulty than adults with these stimuli because young children are novice readers or because the second-order belief attributions were conceptually challenging, leading to less effective involvement of the children's ToM. Another explanation of the disparity may be that Kobayashi et al.'s verbal control condition (sentences drawn from different stories) included sentences containing descriptions of mental states. By contrast, the current experiment used a task that was natural and easy for both adults and children of all ages, as reflected in high behavioral performance across conditions.

Although the ToM network was robustly engaged in children and adults during our ToM task, we also observed developmental changes in these regions' functional profiles, both between children and adults and within children. Children as a group show lower selectivity for mental state information than adults in the bilateral TPJ and PC but not the MPFC regions. Similarly, among children the RTPJ and LTPJ become increasingly selec-

tive for mental states. In younger children, these regions respond equally to nonmental social information and to stories describing mental states. In older children and adults, these regions are highly selective to mental state content: They do not respond to social information other than mental states. The response to stories describing people's physical appearance and social relations was as low as to stories describing purely physical events. These results replicate the developmental change in the TPJ reported in Saxe et al. (2009).

One might question whether this simply reflects a change in the way children understand the stories. For example, younger children might be more likely to spontaneously consider the thoughts and desires of the characters even in the absence of explicit mental state contents (thus leading to lower selectivity), whereas older children might be more conservative in invoking mental states while listening to the stories. In a separate pilot study (described in detail in the online supporting information), we verified that children in all age groups do not spontaneously generate mental states when asked to redescribe the stories used in the current experiment.

Of the brain regions that are consistently involved in ToM, the PC and MPFC regions did not show a significant change in selectivity with ages between 5- and 11-year-old children and adults. This result replicates the previous finding in Saxe et al. (2009). However, these results do not imply that there is no developmental change in the function of the PC or MPFC regions during childhood. One possibility is that the current study may not have manipulated the relevant aspects of social information to reveal development in these regions. For example, activity in PC is often observed during emotional processing (e.g., simple valence judgments of emotional words, Maddock, Garrett, & Buonocore, 2002; moral judgments that involve emotional processes, Farrow et al., 2001; Greene, Sommerville, Nystrom, Darley, & Cohen, 2001), self-referential processing (Mitchell, Banaji, & Macrae, 2005; Ochsner et al., 2005), and episodic or autobiographical memory (Lundstrom, Ingvar, & Petersson, 2005). The MPFC is commonly implicated in thinking about self-relevant or emotionally significant people (Ferstl, Rinck, & Cramon, 2005; Kelley et al., 2002), and there is evidence for developmental change in that aspect of MPFC function in late childhood and adolescence (Pfeifer et al., 2007; Pfeifer et al., 2009; Ray et al., 2009; Wang et al., 2006; also see Blakemore et al., 2007). Specifically, these studies have focused on the differences

between children and adults in the magnitude of activation, whereas this study looked at the change in the selectivity of each region. This difference in the definition of developmental change might also explain why previous studies did not find developmental change in the bilateral TPJ; children and adults show no difference in the magnitude of activation in the mental condition. By looking at the selectivity of these regions relative to the social condition, and in younger children, we were able to identify developmental changes in bilateral TPJ.

An interesting possibility is that the functional change in selectivity of the bilateral TPJ with age is related to anatomical maturation of these regions of cortex. Previous neuroimaging studies of pediatric populations have found that the brain undergoes a nonlinear change in gray matter density (i.e., an increase followed by a decrease) during childhood, possibly reflecting early overproduction of synapses and later synaptic pruning (Giedd et al., 1999; Gogtay et al., 2004; Shaw et al., 2008; Sowell et al., 2004). Regions near the TPJ show pronounced change in cortical density into late childhood and early adolescence (Gogtay et al., 2004), around the time of functional changes observed here. Future experiments should combine measures of functional selectivity and cortical thickness in the same individuals, to test the relations between functional and anatomical maturation in this cortical network.

The key aim of the current study was to test the relation between functional development in ToM brain regions and behavioral development of children's ToM. We found that increasing selectivity in the RTPJ for mental state information was correlated with performance on ToM tasks, even after controlling for age. Because all children in the current study were at least 5 years old and easily passed the standard false belief task in the ToM battery, we focused on the explanation questions. These questions ranged from easy to more complex; those that showed substantial variability across participants were mainly questions designed to tap into later developing aspects of ToM, such as making moral decisions based on mental states (Chandler et al., 2000; Fincham & Jaspers, 1979) and understanding nonliteral utterances in context (i.e., pragmatics; Capelli et al., 1990; Winner & Leekam, 1991). We found that selectivity for mental state information in the RTPJ is associated with children's ability to use ToM to make these sophisticated inferences about other people's minds.

The selectivity index in the LTPJ was correlated with age but not with behavioral performance on the ToM task. One possibility is that development

of the LTPJ is related to different aspects of social cognitive development, not measured by the current ToM task. The LTPJ has been implicated in metarepresentational thought about both social and nonsocial representations (Apperly, Samson, Chiavarino, Bickerton, & Humphreys, 2007; Perner & Leekam, 2008). In future research, it will be interesting to test whether development of the LTPJ is correlated with performance on tasks that invoke nonsocial metarepresentational thinking.

The correlation between performance and selectivity also did not reach significance in the MPFC regions. However, these null results may have occurred because of lower power; the MPFC areas were identified in only about half of the children. Whether the low rate of identification was due to more noise in the data from children or is reflective of a real developmental change is an open question. Future studies could compensate for lower rate of ROI identification (e.g., using a larger set of participants, or group-level ROIs) to better study the link between ToM development and neural activity in these regions. Thus, although the correlation with ToM performance was only observed in the RTPJ, it may exist in other regions, most likely in the medial prefrontal cortex, as well (see Figure S2 in the online supporting information).

The current study did not include behavioral tests of other cognitive capacities that may contribute to children's task performance, including executive function and language skills (de Villiers, 2000; Moses, 2001). We also did not include ToM tasks that show quantitative, rather than qualitative, improvement. For example, previous studies have found that the ability (as measured in accuracy and response time) to take another person's perspective in a referential communication task develops throughout childhood and adolescence (Dumontheil, Apperly, & Blakemore, 2010; Epley, Morewedge, & Keysar, 2004). Given the relation between performance in these tasks and executive function (Nilsen & Graham, 2009), specifying the relation between neural development in brain regions associated with inhibitory control and the quantitative behavioral changes in perspective taking tasks is an interesting topic for future studies.

Despite these limitations, however, the current results provide initial answers to the questions we raised above. First, we asked what pattern of functional and anatomical development occurs in ToM brain regions. Distinct patterns of functional change have been observed in other regions and networks of children's brains. Some regions appear to have the same function in children and adults, but to

increase in size with development (Golarai et al., 2007). Other studies find increasingly focal or more lateralized activations with age (Gaillard et al., 2000; Holland et al., 2001). Still other studies report changes in functional correlations between brain regions, with a shift from more local to more long-range connections (Fair et al., 2007). For brain regions involved in ToM, we find that the same brain regions are involved, in children ages 5–11 years and in adults, but some of these regions change in function, becoming more selective for ToM. We also found evidence that one region, the RTPJ, increased in size between children and adults (although note that calculations of region size, especially when comparing children and adults, are complicated by differences in signal-to-noise ratio, power, and choices of threshold; Gaillard, Grandin, & Xu, 2001). A key question for future research will be to clarify why some brain regions show increased size or activation with development, and others show increasing selectivity of function.

Our second question concerned the time course of this development. Previous behavioral studies suggest at least three possible, but not mutually exclusive, patterns of neural development of ToM: (a) these regions might undergo a significant change between 3 and 5 years of age, which corresponds to children's performance in standard false belief tasks; (b) they might already be mature and fully functional by the 2nd year of life as the recent infant data suggest; or (c) these regions might be still developing past the age 5 years. The current and prior studies suggest that functional changes in ToM brain regions are observed in children older than 5 years of age. Such late functional change in ToM brain regions is surprising in light of the current hypotheses about cognitive ToM development. Developmental psychologists have posited a domain-specific cognitive mechanism underlying children's concept of false beliefs, and cognitive neuroscientists have inferred that the brain regions selective for ToM in adults were the neural substrate of that cognitive mechanism (Saxe, Carey, & Kanwisher, 2004; Saxe & Kanwisher, 2003). As evidence for infants' capability to predict others' actions based on false beliefs accumulates, the debates concerning the developmental time course of this mechanism have focused on two age ranges (Leslie, 2005; Ruffman & Perner, 2005; Scott & Bailargeon, 2009): ages 3–5 years, when children pass explicit false belief tasks, and ages 11–24 months, when children first show evidence of expecting others to act based on false beliefs in "implicit"

tasks. Neither hypothesis predicts the current finding that selectivity in the neural basis of ToM does not emerge until age 8 years.

Of course, the current study cannot reveal the neural changes that occur before age 5 years. It remains possible that major changes occur in the ToM brain regions either around 12–15 months, or around age 4 years (Sabbagh et al., 2009), or both, supporting the acquisition of a concept of false belief. Interestingly, however, these changes apparently do not occur in, or produce, a brain region with a highly selective role in attributing mental states; by age 5, children's ToM brain regions (bilateral TPJ, PC, and regions in MPFC) are sensitive to mental state information, but none of them are selectively recruited just for thinking about thoughts. Delineating the neural development of ToM in infants and younger children remains an important and exciting topic for future studies.

Finally, we asked, what is the relation between the development of ToM brain regions and of children's ToM abilities? Increasing selectivity in the right TPJ was related to children's performance on ToM tasks, showing there is at least some link between cognitive and neural development. One important task for future research will be to disentangle the role of innate maturational factors and experience in driving functional and behavioral change. Is intrinsic anatomical maturation of the neural regions necessary to support improved cognitive function of ToM, or is extensive practice in reasoning about people's thoughts driving both improved performance and the specialization of brain regions? It is tempting to assume that biologically driven maturation of the brain causes improved behavioral performance because neural degeneration or lesions can cause impairments in behavior and cognition (Apperly et al., 2007; Damasio & Geschwind, 1984; Squire & Zola-Morgan, 1988). However, there are also cases in which experience shapes the neural organization. One such example is the visual word form area, a brain region in the fusiform gyrus that shows selective activation for written words (McCandliss, Cohen, & Dehaene, 2003). Specifically, this region responds only to the forms of languages known to the participant: The development of this brain area is thus more likely to be driven by reading experience of the individual rather than by a maturational process (Baker et al., 2007). Therefore, future studies should investigate the relative contributions of intrinsic and experiential factors in the behavioral and neural development of ToM.

In sum, we find evidence for both developmental continuity and late functional change within brain regions in the neural mechanism for ToM. Most important, we found that functional activity in the RTPJ and ToM reasoning ability are positively related in school-aged children. These findings provide insights into the origin of neural mechanisms of ToM, and the ways in which behavior and functional changes in the brain can be related in development.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Story Stimuli for fMRI Task.

Table S1. Comparison of Mean Percent Signal Change (PSC) in Each ROIs in Children and Adults. No ROI Showed a Difference in the Response Amplitude Between Children and Adults.

Table S2. Average Accuracy (SD) for all 14 Categories, Collapsing Across Prediction and Explanation Questions in the ToM Behavioral Battery. N/A Indicate That There Were no Questions in this Category in the Given Response Format.

Figure S1. Average Selectivity Index in Six ROIs in Children and Adults.

Figure S2. Correlation Between Selectivity and Age (top row), and Selectivity and Performance (bottom row) in PC, DMPFC, MMPFC, and VMPFC.

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