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Theory of Mind performance in children correlates with functional specialization of a

brain region for thinking about thoughts

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Abstract

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 - 11, 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 theory of mind 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 (Wimmer & Perner, 1983; Wellman, Cross, & Watson, 2001), 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 (Want, 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 timecourse 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 relationship 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 relationship 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 timecourse of development in ToM brain regions. Behavioral research suggests that between ages 3 – 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, three-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, Cross, & Watson, 2001). If three-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 five-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 theory of mind between age 3 and 5 years, coming to understand that the content of a person's belief can be false (i.e., differ from reality) (Wellman, Cross, & Watson, 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 and colleagues (Sabbagh, Bowman, Evraire, & 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 in order to understand representational mental states. Children in their second year of life may be already able to use inferred false beliefs to correctly predict actions (Leslie, Friedman, & German, 2004; Baillargeon, Scott, & He, 2010). 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 (deVillers & 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, & Pelphrey, 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 five 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 non-literal utterances such as irony and sarcasm, continues to develop in late childhood (Capelli, Nakagawa, & Madden, 1990; Winner & Leekam, 1991; Peterson, Wellman, & Liu, 2005). Children's performance in moral reasoning tasks also reflects relatively late changes in ToM (Fincham & Jaspers, 1979; Grueneich, 1982; Chandler, Sokol, & Wainryb, 2000; Baird & Astington, 2004). 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, 2007a; Kobayashi, Glover, & Temple, 2007b)

have reported some differences between school-aged children and adults in the neural basis of

ToM. Additionally, one study (Saxe, Whitfield-Gabrieli, Scholz, & Pelphrey, 2009) reported

differences *among* children: although the ToM brain regions normally recruited for ToM in

adults are also found in 6 – 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; Saxe & Kanwisher, 2003; Saxe & Powell, 2006; Apperly, Samson, Chiavarino, &

Humphreys, 2004; Perner, Aichorn, Kronblicher, Staffen, & Ladurner, 2006; Jenkins & Mitchell,

2009; Pfeifer, Lieberman, & Dapretto, 2007). 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 – 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 is 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, in order to capture qualitative changes in ToM that take place between 5 – 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 seconds whenever the camera with motion sensor detected head motion above a pre-determined threshold. The mock scanning session lasted for 20 – 30 minutes. Prior to the scan, participants also performed 7 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 Supplementary Material 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 seconds), 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 Supplementary Material 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 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 8 blocks per condition. Each run consisted of 10 experimental blocks (single-trial block design, each 36 sec long, 2 per condition) and 3 rest blocks (each 12 sec, one at the start of the run, after the presentation of 5 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 sec), followed by "Does this come next?" (1.5 sec), the probe sentence (3 sec), a pause (6.5 sec) during which the participant would make a response, and finally the post-response encouragement (5 sec).

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 non-match). 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/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. Due to technical errors, behavioral data were not saved for one child and one 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 minutes to 28 minutes of functional MRI data with each child (2 - 4 runs). The children who completed all four runs were older on average than those who completed 2 or 3 runs (9.17 vs 7.29 (yrs), $t(18) = 2.54$, $p < 0.05$). 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 saggital slices (TR = 2s, TE = 3.39ms, flip angle = 90°) with 1.33mm isotropic voxels. Functional data were acquired in 3 x 3 x 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 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 off-line 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 = 5mm). 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 seconds) and each participant's movements in all 6 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 $p < 0.05$ (corrected for multiple comparisons) by performing Monte Carlo permutation tests with the SnPM3 toolbox for SPM2 (Nichols and Holmes, 2002; Hayasaka and Nichols, 2004; http://www.sph.umich.edu/ni-stat/SnPM/). We used approximate permutation tests (5000 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, respectively.

Based on previous literature (Saxe & Kanwisher, 2003; Frith & Frith, 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 ($p < 0.001$), (c) within a radius of 9mm. For every participant, we overlayed 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 Supplementary Material for analysis of beta coefficients). In

addition, PSC allows us to look at the timecourse 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) x 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 $(PSC(c,t) = 100* (Resp(c,t) – baseline) / baseline)$. The result was a timecourse showing the percent signal change relative to baseline for each condition at each time point, in each participant (see Figure 3). For the 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: $100 * (Mental – Social) / (Mental – Physical)$. 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 in order to calculate the true size of each ROI in each subject, using a smoothing kernel of 8mm. We assessed ROI volume relative to the cortical volume for each subject. Cortical volume was estimated for each participant based on the unnormalized segmented grey 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 Theory of Mind 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, 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 Supplementary Material 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 Supplementary Material 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 minutes, 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) ± *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 ($\beta = 0.64$, $p < 0.005$) and RT ($\beta = -0.78$, $p < 0.001$). Differences in accuracy and RT across conditions were analyzed for children and adult participants separately using Friedman test for accuracy, and repeated measures ANOVA for RT. There was no effect of condition on task accuracy in children (χ^2 (2, N = 20) = 1.44, $p = ns$) or adults (χ^2 (2, N = 7) = 1.00, $p = ns$), nor 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 Supplementary Material 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 the Physical stories in RTPJ, LTPJ, PC and

DMPFC ($p < 0.05$, corrected) (Saxe & Kanwisher, 2003; Saxe & Powell, 2006; Perner et al., 2006). These same brain regions were also more active for Mental than Physical stories in children ($p < 0.05$, 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 difference 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 ($p < 0.05$) or even at a lenient threshold of $p < 0.1$ (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 ($p < 0.05$, 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 5 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 both the conjunction of whole-brain results in the current study as well as previous literature on brain regions involved in ToM (e.g., Saxe & Kanwisher, 2003; Frith & Frith, 2003). An omnibus ANOVA (age groups x 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) vs. 46.5 (children), $t(21.96) = 3.08$, $p < 0.005$; *PC*: 60.9 (adults) vs. 24.0 (children), $t(18.29) = 2.50$, $p < 0.05$), and marginally in LTPJ (74.9 (adults) vs. 47.7 (children) $t(11.89) = 1.97$, $p = 0.073$). Adults did not differ from children in selectivity within any of the MPFC ROIs (*DMPFC*: 49.7 (adults) vs. 68.8 (children), $t(17) = -0.88$, $p = ns$; *MMPFC*: 45.6 (adults) vs. 23.0 (children), $t(11) = 0.81$, $p = ns$; *VMPFC*: 51.8 (adults) vs. 68.1 (children), $t(12) = -0.67$, $p = ns$).

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*: $r(14)= 0.51$ $p < 0.05$; *LTPJ*: $r(10)= 0.70$, $p < 0.05$; 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*: $r(6) = 0.02$; $p = ns$ 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 Supplementary Material 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 (mmõ) = 7,277;

children M = 2,692; $t(8.69)$ = 2.78, $p < 0.05$). 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 grey matter volume (adult ROI volume / grey matter

volume * 100 = 0.03%; children = 0.01%, $t(8.01)$ = 2.71, $p < 0.05$).

ToM Behavioral Battery and its relationship 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 Supplementary Material 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 = 0.16).

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

< 0.01), and remained significant even after controlling for age and number of runs analyzed

($r(13) = 0.66$, $p < 0.01$; 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 $p = ns$; see 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 $p = ns$).

Discussion

In this study, we aimed to (1) identify brain regions associated with ToM in both children

and adults, (2) characterize the developmental trajectory of these brain regions, and (3) find

evidence for a brain-behavior relationship in these regions. We found, first, that the same brain

regions implicated for ToM in adults are found in children aged 5 to 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: e.g. 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. (2007)'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 and/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. (2007)'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 selective for mental states. In younger children, these regions respond equally to non-mental 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 Supplementary Material), we verified that children in all age groups do not spontaneously generate mental states when asked to re-describe the stories used in the current experiment.

Of the brain regions that are consistently involved in theory of mind, the PC and MPFC regions did not show a significant change in selectivity with age between 5 – 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, 2003; moral judgments that involve emotional processes, Farrow et al., 2001; Greene et al., 2001), self-referential processing (Mitchell, Banaji, & Macrae, 2005, Ochsner et al., 2005); and episodic/autobiographical memory (Lundstrom, Ingvar, & Petersson, 2005). The MPFC is commonly implicated in thinking about self-relevant or emotionally significant people (Kelley et al., 2002; Ferstl, Rinck, & Cramon, 2005), and there is evidence for developmental change in that aspect of MPFC function in late childhood and adolescence (Wang et al., 2006; Pfeifer et al., 2007; Pfeifer et al., 2009; Ray et al., 2009; also see Blakemore, Ouden, Choudhury, & Frith, 2007). Specifically, these studies have focused on the differences between children and adults in the magnitude of activation, while the

current 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; Sowell et al., 2004; Shaw et al.,2006). 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 relationships between functional and anatomical maturation in this cortical network.

The key aim of the current study was to test the relationship 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 five 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 non-literal

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.

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 meta-representational thought about both social and non-social

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 non-social meta-representational 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, and/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,

mostly likely in the medial prefrontal cortex, as well (See Supplementary Material Figure S2).

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

(Moses, 2001; de Villiers, 2000). 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 (Epley, Morewedge, & Keysar, 2004; Dumontheil, Apperly, & Blakemore, 2009). Given the relationship between performance in these tasks and executive function (Nilsen & Graham, 2009), specifying the relationship 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 age 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 (SNR), 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 timecourse 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 – 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 second 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 & Kanwisher, 2003; Saxe, Carey, & Kanwisher, 2004). As evidence for infants' capability to predict others' actions based on false beliefs accumulates, the debates concerning the developmental timecourse of this mechanism have focused on two age ranges (Ruffman & Perner, 2005; Leslie, 2005; Scott & Baillargeon, 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 relationship 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 behaviour 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 (VWFA), 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 theory of mind. Most importantly, 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 Theory of Mind, and the ways in which behavior and functional changes in the brain can be related in development.

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Author Note

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*	[-52 -56 20]	8.67
	Right SFG	[22 52 26]	6.40
	DMPFC*†	[-2 54 32]	6.10
	Precuneus*	[-2 -50 38]	5.89
	Right STS	[48 -28 -8]	5.71
	Right TPJ*	[52 -52 24]	5.71
Children	Right TPJ*	[56 -54 34]	8.50
	Left TPJ*	[-48 -60 30]	8.03
	Precuneus*	[-8 -52 36]	7.13
	Right SFG	[12 30 62]	6.48
	DMPFC*	[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. SFG = superior frontal gyrus. Activations in all regions are significant at p < 0.05 (corrected). †: DMPFC in adults was observed as a local maximum in the right SFG cluster ([-2 54 32], T = 6.10). *: Brain regions that were commonly activated in both children and adults in the conjunction analysis.

Figure Caption

Figure 1. Schematic of the experimental design and examples of story stimuli. In each trial, a story in one of three conditions (Mental, Social, 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 seconds) depending on whether their answers were correct or not.

Figure 2. Random-effects whole-brain analysis results in children and adults. 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 saggital 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. The graphs show the mean percent signal change (PSC) relative to rest over the course of the whole trial ($0 – 36s$). To visualize the developmental change in selectivity, children were median-split by age (8.5 yrs) into younger and older groups. In all graphs, the X axis is time (seconds), and the Y axis is the PSC.

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 and B show correlation between age and the selectivity index in the RTPJ (A) and LTPJ (B) in children. C and D show the relationship between performance in the ToM behavioral battery and selectivity index in the RTPJ (C) and LTPJ (D).
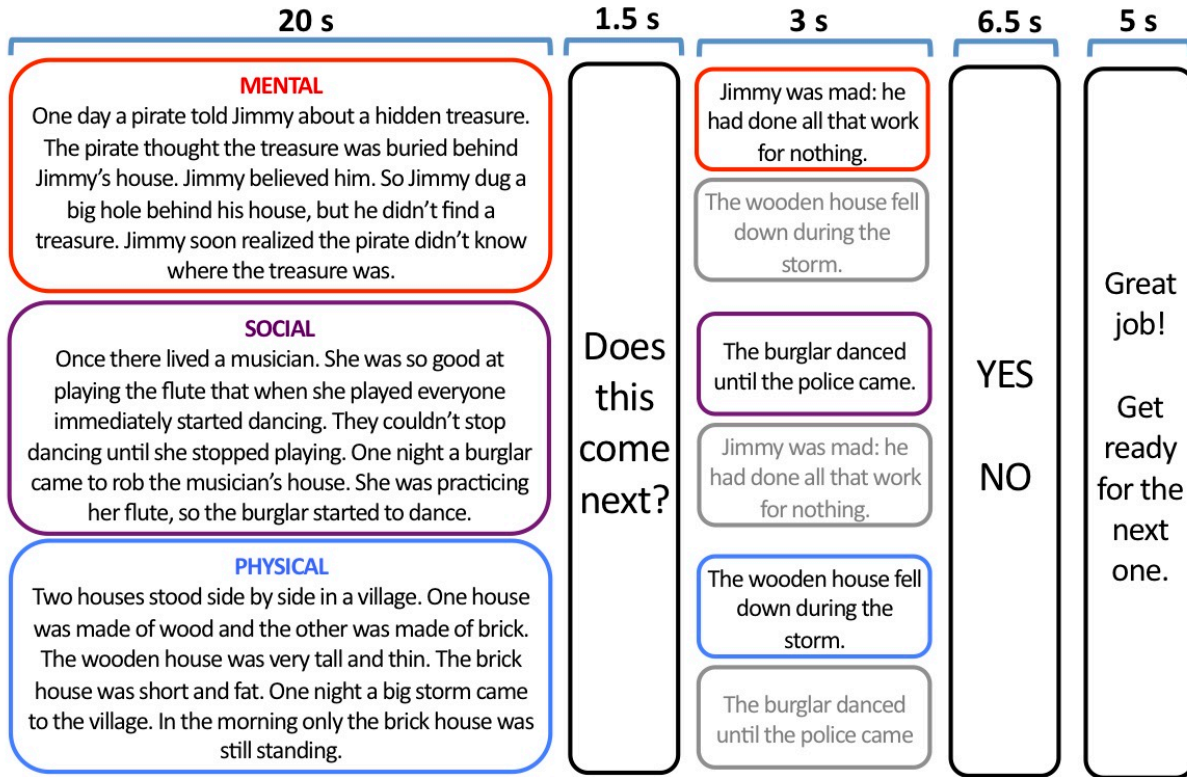
Figure 1.

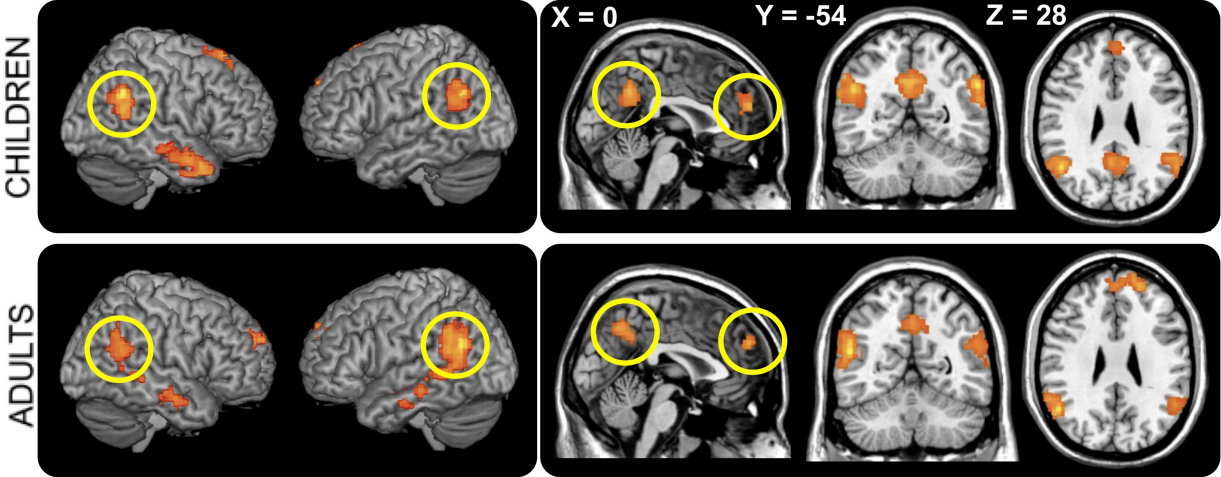| 20 s | 1.5 s | 3 s | 6.5 s | 5 s |

MENTAL
One day a pirate told Jimmy about a hidden treasure. The pirate thought the treasure was buried behind Jimmy's house. Jimmy believed him. So Jimmy dug a big hole behind his house, but he didn't find a treasure. Jimmy soon realized the pirate didn't know where the treasure was.

SOCIAL
Once there lived a musician. She was so good at playing the flute that when she played everyone immediately started dancing. They couldn't stop dancing until she stopped playing. One night a burglar came to rob the musician's house. She was practicing her flute, so the burglar started to dance.

PHYSICAL
Two houses stood side by side in a village. One house was made of wood and the other was made of brick. The wooden house was very tall and thin. The brick house was short and fat. One night a big storm came to the village. In the morning only the brick house was still standing.

Does this come next?

Jimmy was mad: he had done all that work for nothing.

The wooden house fell down during the storm.

The burglar danced until the police came.

Jimmy was mad: he had done all that work for nothing.

The wooden house fell down during the storm.

The burglar danced until the police came

YES

NO

Great job!

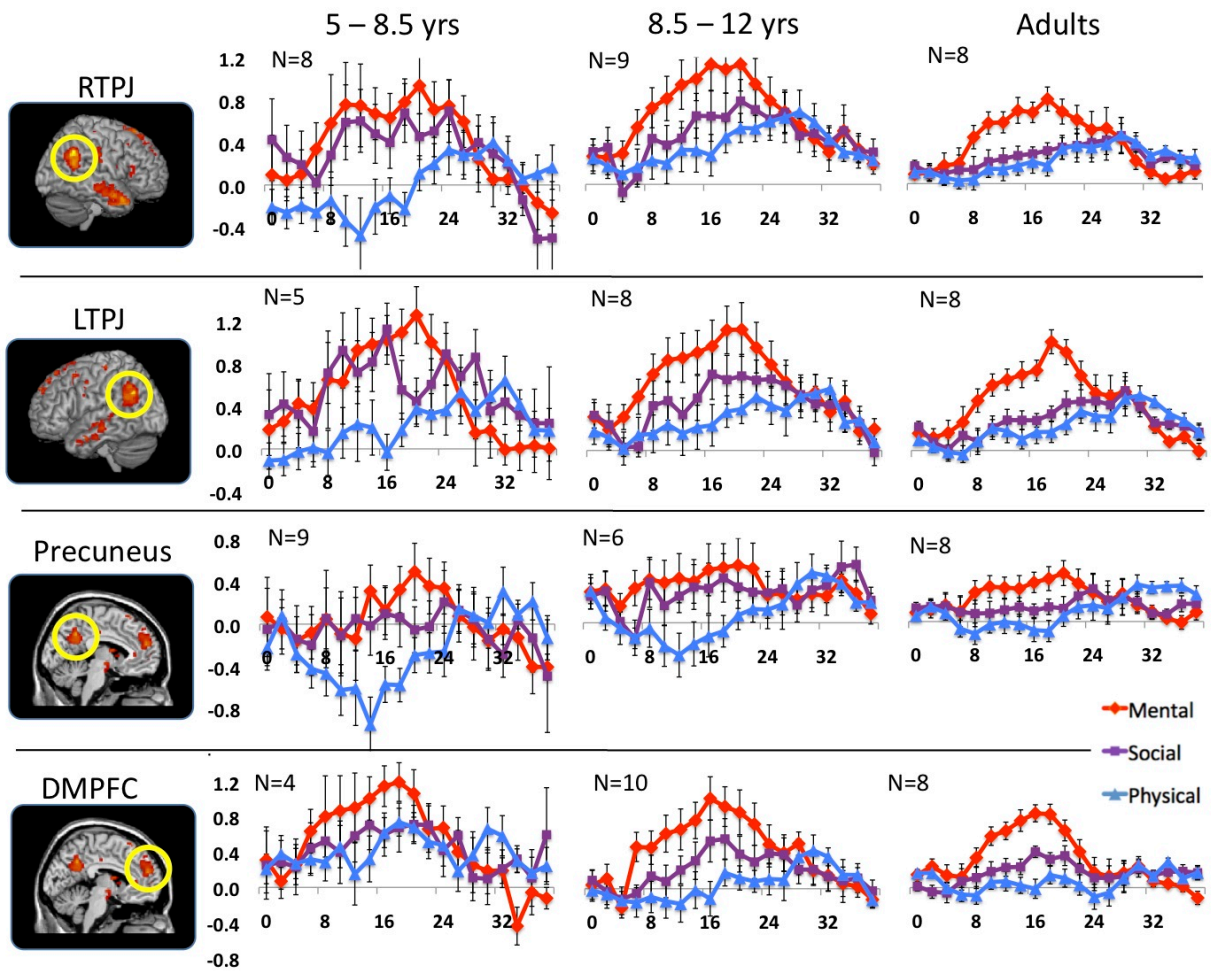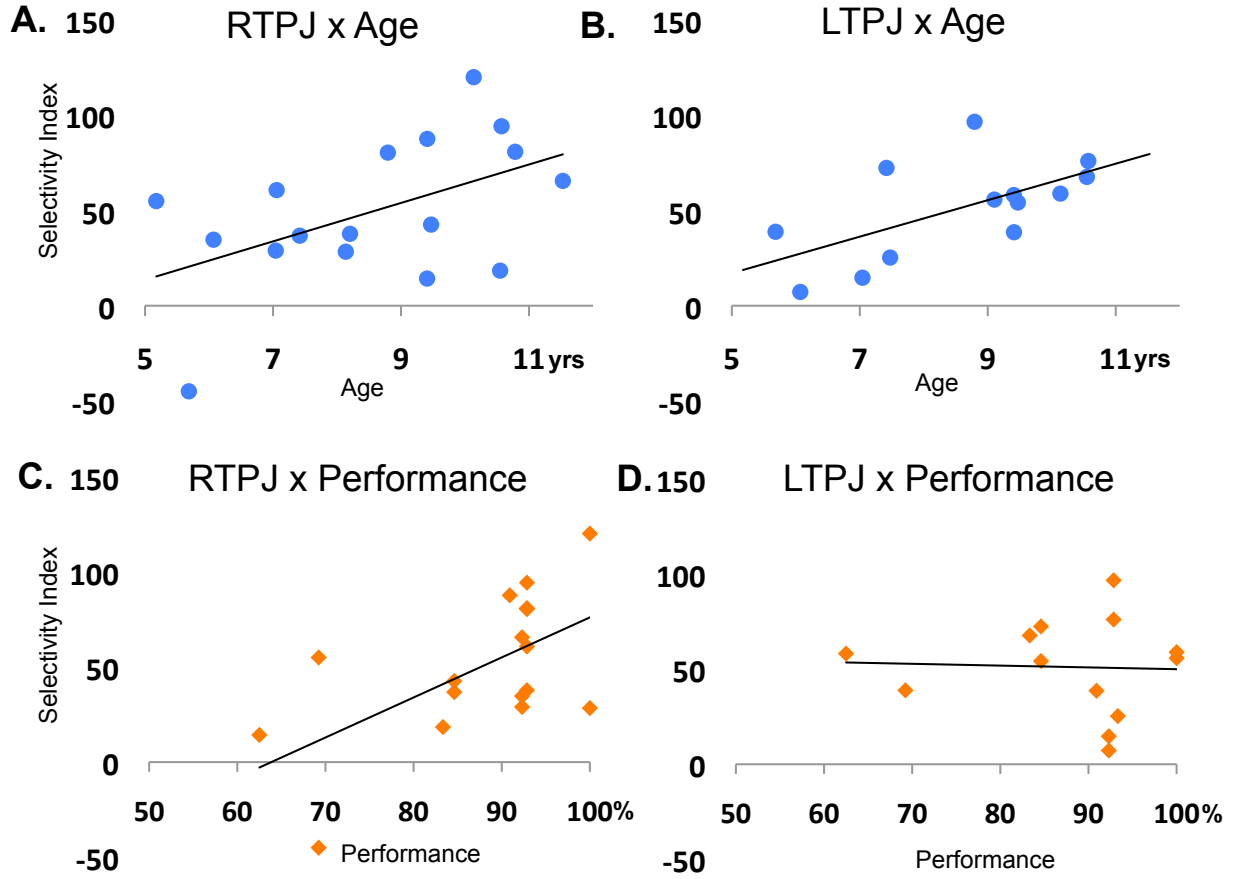Get ready for the next one.

Figure 2.

Figure 3.

Figure 4.

Supplementary Material

Story stimuli for fMRI task

      Eight stories in Mental, Social, and Physical conditions were used in the fMRI task. The probe sentence (see Methods in the main text) is italicized.

< Mental >

1. One day a pirate told Jimmy about a hidden treasure. The pirate thought that the treasure was buried behind Jimmy's house. Jimmy believed him. So Jimmy dug a big hole behind his house, but he didn't find a treasure. Jimmy soon realised the pirate didn't know where the treasure was. *Jimmy was mad. He had done all that work for nothing.*

2. Today Sam is giving a surprise birthday party for his friend Eric. Sam invited Eric to come over and play basketball. Sam wanted to keep the party a secret, so he didn't wish Eric a happy birthday. Eric thought that Sam forgot about his birthday and was very upset. *Eric was happy when he found out that Sam threw him a birthday party.*

3. A poor fisherman lived in an old shack with his wife. One day the fisherman was very surprised: the fish he caught started talking. The fish promised to grant the man a wish. The fisherman's wife wanted a new a house, but she did not believe that they would get a new house from a fish. *But the next day the fisherman and his wife had a beautiful house.*

4. Emil's mother sent him to the lake to gather fish for dinner. Emil was scared of going to the lake alone. He thought that there was a sea creature living in the lake. Emil's mother knew that the sea creature was really Emil's own reflection. She told Emil to smile at the creature. *Emil smiled into the river and saw a face smiling back.*

5. One day two girls were walking through the forest. They saw a troll with a long beard lying near a rock. The girls thought the troll's beard was stuck under the rock. They cut the troll's beard to set him free. The girls were surprised: the troll was angry with them for ruining his beard. *The troll wasn't stuck. He was sleeping.*

6. Before leaving camp, Molly drew a picture of herself to give to her friend Clara. Clara found the picture, and didn't know it was a picture of Molly. She labeled the picture "scary monster" as a joke. When Molly saw the writing on the picture she was angry at Clara. *Molly and Clara had a long talk and now they're friends again.*

7. One day, everyone in the world turned purple. That morning, people looked at each other, and wondered if they were dreaming. Everybody was shocked. Even the smartest scientists didn't know what had happened. But Jimmy wasn't surprised at all; he knew the secret. *Someone had put purple pills in the city's water.*

8. The Hardy boys were worried because they were running late. Their Dad wanted them to come home early. Joe saw a shortcut on the map. The boys looked carefully at the road. The entrance to the shortcut was hidden by trees. They knew they could easily have missed it. *Frank, one of the boys, turned their car down the dark dirt road.*

<Social>

1. One night Mary's parents brought Mary to sleep at her grandmother's house. Grandma was very old and went to bed early. So Mary started playing in her grandmother's closet. In the back of the closet, was a pair of beautiful red shoes. Mary put them on. *All of a sudden, Mary wasn't in the closet any more.*

2. Sarah and Lori play together on the school soccer team. Sarah usually plays offense. She runs up and down the field and scores goals. Lori is the team's goalie. She is very good at catching the ball when the other team kicks it at the goal. Today the school has a big game but Lori is sick. *Sarah has to play goalie because Lora is too sick to play soccer.*

3. Once upon a time, a girl and her little brother went out into the field to pick flowers. The day was very hot and the little brother got very thirsty. On the walk back home he drank from a puddle. But the puddle had a curse on it. After drinking, the boy turned into a baby goat. *The big sister found a spell to turn the goat back into a boy.*

4. Once there lived a musician. She was so good at playing the flute that when she played everyone immediately started dancing. They couldn't stop dancing until she stopped playing. One night a burglar came to rob the musician's house. She was practicing her flute, so the burglar started to dance. *The burglar danced until the police came.*

5. Jenny and Samantha were twins. They lived in a big city with their parents. For two weeks during their summer vacation they went to visit their Granpa. They stayed at Granpa's house near the lake. Every morning Granpa and the girls went swimming or sailing. *Jenny and Samantha both came home strong and tanned.*

6. Chenma lived with her only son, Jhe, in a forest in Shanxi Province. Jhe was one of the tiger hunters. Jhe's father taught him how to hunt tigers. But Jhe's father had died. The money from selling tiger meat, skin and bones, was barely enough to keep Jhe and Chenma warm and fed. *One day, Chenma's son went to the woods to find a tiger.*

7. Old Mr McFeegle is a gray wrinkled old farmer, who wears grey wrinkled old clothes and gray wrinkled old boots. Georgie is Mr McFeegle's nephew from town. One day, Georgie put on Mr McFeegle's gigantic boots. The boots were so big, Georgie disappeared inside them. *Mr McFeegle looked everywhere, but couldn't find Georgie.*

8. There once was a poor woodsman who had a huge and oily sausage hanging under his nose. The sausage was so long that it hung from the woodsman's nose all the way down to his toes. No matter how he tugged at the sausage, pulled it and even cut it, the sausage would not budge. *The sausage just hung in front of him everywhere he went.*

< Physical >

1. One day, a little robin landed on a huge, strange-looking tree, and ate one of its berries. This was a magical tree that had special powers. In the spring, the robin laid three eggs. Soon, two of the eggs cracked and little robins came out. But the last egg did not crack for a long time. *When the last egg cracked a beautiful firebird came out.*

2. Two houses stood side by side in a village. One house was made of wood and the other was made of brick. The wooden house was very tall and thin. The brick house was short and fat. One night a big storm came to the village. In the morning only the brick house was still standing. *The wooden house fell down during the storm.*

3. In the cooking school there was a big batch of dough on the windowsill in a covered pot. The sun shone onto the pot all day long. The dough sat on the counter and got bigger and bigger. Pretty soon the dough grew bigger than the pot. It grew and grew, all over the windowsill. *A few hours later, the whole room was full of dough.*

4. In the tiny town of Chewandswallow it rained or snowed three times each day. Once during breakfast, once during lunch and once during dinner. But it never rained rain and never snowed snow. It rained things like soup and juice and snowed things like mashed potatoes. *Yesterday it snowed meatballs for dinner in Chewandswallow.*

5. Once there was a palace, surrounded by a large garden. But although the weather was perfect and the soil was dark and moist, nothing grew there. Plants in the garden produced neither flowers nor fruit. There were so few leaves on the trees that there was no shade anywhere. *The garden was empty because of a magic curse.*

6. The house on the corner was very creepy. The windows were full of cobwebs, the roof was crooked, and the door hung partly open. The wind whistled through the holes in the grey walls, making a low wailing sound, especially when there was a full moon or a storm coming. *Sometimes, lights inside the house flashed on and off all night.*

7. In the attic was a strange old map of a small island in the middle of the sea. The scratchy drawing showed that there were forests and cliffs on the island. There were many twists and turns in the beach, and one long river. About halfway up the river, the map was marked with a big "X". *The 'X' marked the spot where a treasure was buried.*

8. The school was all ready for the first day of class. The desks and chairs were lined up in perfect rows and columns. On each desk was a pile of neatly stacked books. But right before the first day of class a pipe broke in the bathroom. Water flooded the entire school. *The desks and chairs floated in the hallways.*

Theory of Mind behavioral battery – ToM booklets

Two booklets contained 44 questions, belonging to one of 14 categories. Booklet 1 was about children in the same class look for their books for reading time, and Booklet 2 was about a family spending a day out in the park. Each page in both books had flaps (under which small magnet pieces could be hidden) and magnet pieces of books, people, and other objects described in the story. The experimenters memorized the full script and were trained to tell the story realistically, rather than simply reciting the script. Children were encouraged to give verbal responses to the questions, and also to place the magnet pieces in the appropriate place on the booklet page. In many questions, we asked for both the child's prediction (e.g., Which book is she going to choose?) and the explanation (e.g., Why do you think so?). Here we describe 12 questions from Booklet 1 and 2 questions from Booklet 2, to give an example of questions in each of the 14 categories. Example 1-12 are from Booklet 1, 13-14 are from Booklet 2. Explanation questions which were used as our main measure and coding criteria for scoring children's explanations are in **bold** font.

1. <u>Common Desires:</u> Sam is going to pick a book off the table. One book is about bicycles, and the other one is about fire trucks. Which book do you think Sam wants? The one about bicycles or the one about fire trucks? **Can you tell me why?**
2. <u>Diverse Desires</u>: Now here is Laura. Laura is going to pick a book off the bookshelf. There is a book that has pictures of fish in the ocean, and there is a book that has pictures of dinosaurs. What do you like better, fish or dinosaurs? You do? That's great! But Laura likes [other one] better. Can you guess which book Laura is going to choose? Will she pick the book about fish or about dinosaurs? **How do you know?**
3. <u>Diverse Beliefs</u>: Jonathan is looking for his book. His book might be under the table, or it might be behind the reading chair. Where do you think the book is? That's a good idea! But guess what? Jonathan thinks his book is [the other one]. Where will Jonathan look for his book? Will he look under the table or behind the chair?

4. Ignorance: Here is Alex. Alex hasn't found his book on skiing. That's because Alex's book is in the cupboard under the sink. See, here it is. But Alex hasn't looked in the cupboard yet; he's looking at the bookshelf. Does Alex know where his book is?

5. **Easy Reference (common ground/perspective taking)**: Here is Ryan, coming in the door. Look, here on the bookshelf right in front of Ryan is a big book about airplanes! And there's another book about airplanes, over here, on the cabinet, behind Ryan's back. Now Ryan says "I want that book about airplanes!" Which book do you think Ryan wants? **How do you know it's that one? (correct if the child mentions that Ryan is looking at the book, is facing the book, or that the book is in front of him).**

6. False Belief Reality Unknown: Here is Grace. She's outside now, but soon she will be coming inside to look for her favorite butterfly book. Grace thinks that her butterfly book is in the toy bin. But look, there's no butterfly book in the toy bin! When Grace comes in, where do you think Grace is going to look first for her butterfly book?

7. **False Belief Reality Known**: This morning when he came to school, Ethan put his book above the coat hooks. What color is Ethan's book? That's right! But while he was outside playing, Ethan's book fell down behind the coats. See here is Ethan's book behind the coats. Then Paul came in - and Paul put his book above the coat hooks. See here's Paul's book above the coat hooks. What color is Paul's book? That's right! But Ethan was still outside playing, so he didn't see Paul come in. So he doesn't know that this is Paul's book right here. Now, when Ethan comes in from outside, where will he look first for his book? Oh look, here is Ethan reaching for Paul's book from the coat hooks. **Why is Ethan trying to take Paul's book? (correct if the child mentions that Ethan thinks the book is his).**

8. **Emotion:** (continued from Q.7) Here comes Paul. Paul can see Ethan trying to take his book. Paul feels very sad. **Why does Paul feel sad? (correct if the child mentions that the book is Paul's)**

9. Moral Judgment: (continued from Q.8) Is Ethan being mean and naughty for taking Paul's book? Should Ethan get in trouble with the teacher for taking Paul's book? Can you give Paul back his book? Now can you help Ethan find his own book? Where is Ethan's book really?

10. **False Belief based on Expectation:** William always likes to read the book about mountains. The mountain book has pictures of mountains and the plants that live in the mountains. It's a big grey book. Every day this month, the mountain book was on the carpet. But today, Mr. Abott moved the mountain book over to the shelf, and put a new book on the carpet. This book is also grey, but it's a different book, about horses. When William comes in, and sees this book on the carpet, what will he think is inside - pictures of mountains or pictures of

horses? **Why will he think that? (correct if the child refers to William's past or his expectations).**

11. **Hard Reference:** Here is Daniel. Earlier today Daniel was reading this book about fruit. He really liked the section about oranges. It had pictures of oranges, orange juice, orange trees, and even the farmers who grow the oranges. Now Daniel is coming in to get a book. Here on the table is the book about fruit. Over here, on the shelf, is a book about history, with an orange cover. Daniel says "I want the orange book!" Which book does Daniel want? **How do you know? (correct if the child mentions the orange section).**

12. **Interpretation:** Chloe is playing a game today: she is trying to be completely silent all day long. So when she wants to say something, she draws a picture instead of talking. Right now, Chloe wants Mr. Abbott to get a book down from the top shelf for her. Up on the top shelf is a book about witches, and a book about boats. Chloe wants the book about witches, but she doesn't know how to draw a witch. On one piece of paper she draws a witch's hat like this. On another piece of paper she draws a witch's broom like this. But she has to choose just one. Which picture should Chloe give to Mr. Abbot, so he will get her the book about witches and not the book about boats? **Why is this one better than that one? (correct if the child mentions sailboat's resemblance to the hat).**

13. **Emotion Reminder**: Last week, when they came to the park, a black puppy was playing with Sprint. He was very friendly. But then during snack time last week, the black puppy stole Ivan's cookie, and ran away with it! Now, while the kids are having their snack today, Sprint is running around, playing with the same friendly black puppy. The black puppy comes running over to the kids, wagging his tail. How will Ivan feel when he sees the black puppy today? [Will he feel happy or sad?] Will Ivan go over near the puppy, or will he go far away from the puppy? **Why will he do that? (correct if the child mentions Ivan's past experience with the puppy).**

14. **Moral False beliefs:** Now the games are over, and it's almost time to go home. Mother tells the kids to find all of their toys; they have to bring them all home. Joshua brought his toy truck with him to the park, but now he can't find it. He's looking everywhere but he can't find it. Then Isabel find the toy truck. But she doesn't tell anyone. While no one is looking, she takes the toy truck, and buries it in the sandbox. So Joshua looks everywhere and he can't find his toy truck. Mother gets mad at Joshua, because he lost his truck. How does Joshua feel? Is Joshua mad at Isabel? **Why (why not)?** Is Mother mad at Isabel? **Why (why not)? (correct if the child mentions that Joshua or Mother does not know that Isabel hid the truck).**

Results

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.

	Mean PSC: Children	Mean PSC: Adults	T	df	*p*
Right TPJ	0.81	0.57	0.92	23	0.37
Left TPJ	0.89	0.67	1.49	19	0.15
PC	0.27	0.32	-0.31	17.3	0.76
dMPFC	0.78	0.53	1.33	16	0.20
mMPFC	0.85	0.14	1.73	12	0.11
vMPFC	1.21	0.70	1.06	12	0.31

Note. ROI = region of interest; TPJ = temporo-parietal junction; PC = precuneus; MPFC = medial prefrontal cortex; dMPFC = dorsal MPFC; mMPFC = middle MPFC; vMPFC = ventral MPFC.

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.

Category	Prediction Accuracy (SD)	Explanation Accuracy (SD)
Common Desire	1.00 (0.00)	N/A
Diverse Desire	0.95 (0.22)	N/A
Diverse Belief	1.00 (0.00)	N/A
Ignorance	1.00 (0.00)	N/A
Easy Reference	0.80 (0.41)	0.70 (0.47)
Hard Reference	0.60 (0.50)	0.56 (0.51)
False Belief Reality Known	0.99 (0.11)	0.97 (0.18)
False Belief Reality Unknown	0.95 (0.23)	N/A
False Belief based on Expectation	0.97 (0.16)	0.85 (0.38)
Moral False Belief	0.89 (0.32)	0.90 (0.31)
Emotion Reminder	0.80 (0.41)	1.00 (0.00)
Emotion	N/A	1.00 (0.00)
Moral Judgment	1.00 (0)	N/A

Interpretation	0.90 (0.30)	0.87 (0.34)

Figure S1.

Average Selectivity Index in six ROIs in children and adults (Childen: N=10, Adults: N=8). Note that the ROIs were not identified in all of the participants (see main text for ROI analysis results). (Y axis: Selectivity Index)
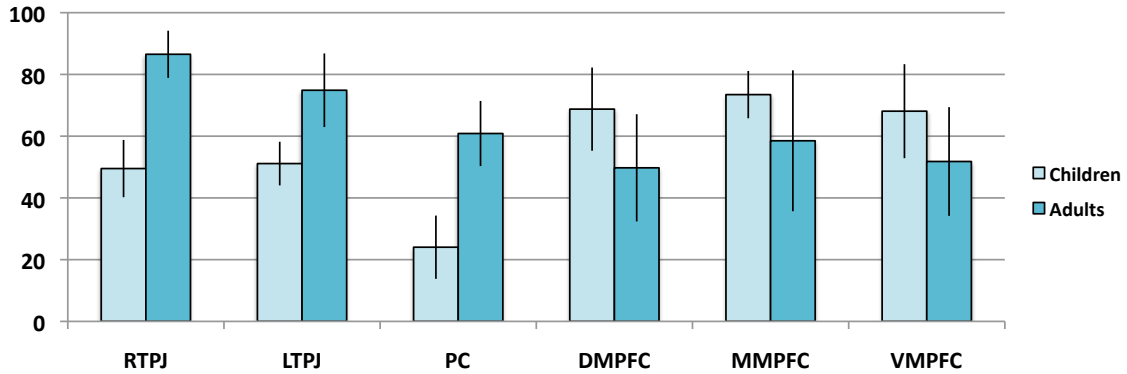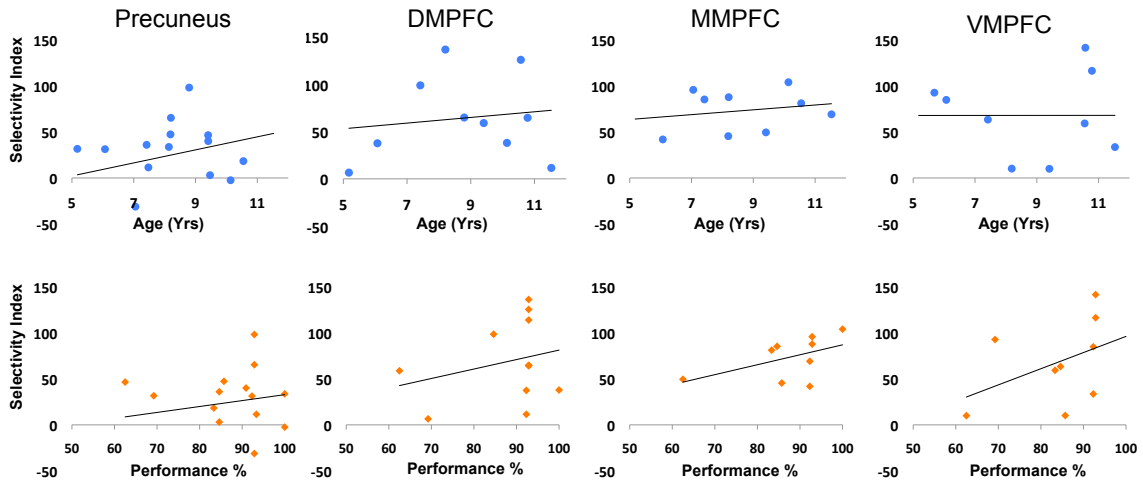

Figure S2.

Correlation between selectivity & age (top row), and selectivity & performance (bottom row) in PC, DMPFC, MMPFC, and VMPFC.

Beta coefficients

For ROI analysis, we report average percent signal change (PSC) in each condition relative to baseline (fixation) for individual ROIs, and calculated selectivity using these PSC values. However, we also conducted the same analysis using average beta coefficient (beta weights) instead of PSC for data acquired from children. Average beta weights for the Mental condition was significantly higher than average beta weights for the Physical condition, in all ROIs ((Mental) vs. (Physical); RTPJ: 1.45 vs. 0.25, $t(15) = 7.53$; LTPJ: 1.28 vs. 0.16, $t(12) = 9.01$; PC: 0.78 vs. -0.43, , $t(13) = 9.13$; DMPFC: 1.26 vs. 0.12, $t(9) = 10.67$, MMPFC: 1.07 vs. -.07, $t(7) = 8.37$; VMPFC: 1.65 vs. 0.31, $t(8) = 5.71$. All comparisons $p < 0.001$). We also calculated selectivity using beta weights: (100 * (Mental – Social) / (Mental – Physical). As expected, selectivity index calculated from PSC and beta weights were correlated in the RTPJ ($N = 16$, $r = 0.61$, $p < 0.01$), LTPJ ($N = 13$, $r = 0.84$, $p < 0.001$) and PC ($N = 14$, $r = 0.68$, $p = 0.01$). Consistent with PSC results, we found a significant correlation between beta selectivity in the RTPJ and age, even after controlling for number of runs (N=16, $r(13) = 0.64$, $p < 0.05$). Our critical finding, relationship between selectivity in the RTPJ and behavioral performance in ToM booklets (controlling for age and run numbers), was also significant with beta coefficients ($N = 16$, $r (13) = 0.57$, $p < 0.05$).

Pilot study with fMRI story stimuli

In the current study we have found that selectivity to mental state information in key brain regions – bilateral TPJ and PC – increases with age. However, there is an alternative explanation for these results that the observed neural change simply reflects a change in children's pragmatics. Between ages 5 years and adulthood, there might be a change in the way they understand the stories. For example, younger children might be more likely to spontaneously consider the thoughts and desires of the characters even when these mental states are not explicit in the stories, which would result in heightened activation in brain areas selective to mental states during the Social condition. On the other hand, older children might be more likely to focus on the explicit content of the story, being more conservative in invoking mental states while listening to the stories. These cognitive differences would appear as neural differences in the fMRI results, but would not provide evidence for true developmental differences in the maturation or processing of specific brain systems.

In the current pilot study, we sought to provide evidence against this pragmatic interpretation that the developmental change in selectivity is due to changes in how children construe the stories by having a measure of how children construe our stories in the Mental, Social, and Physical conditions. To this end, we asked a separate group of children to listen to

these stories and 'tell the story back' to the experimenter. Their responses would serve as a proxy for how children attend, remember and interpret our stimuli in the scanner.

Methods

Forty-five typically developing children (24 females; M age = 8.0 years; range: 5.1 – 11.7 years) were recruited from a local children's museum to participate in this pilot task. All of the children were native speakers of English, and none of these children participated in the behavioral/fMRI session of the current study. Eight English stories in each of the three conditions (Mental, Social, Physical, 24 total) were divided into four playlists (2 stories from each condition, 6 stories in each playlist). The children were brought into a quiet room, and were presented with one or two playlists via headphones (the order of playlists was randomized across subjects). After listening to each story, the children were asked to tell the story back to the experimenter. Children's responses were voice-recorded and then transcribed. We coded the total number of words in children's responses, number of mental state verbs (i.e., know, think), and the number of nouns and pronouns referring to a person. We also listed all the facts of any kind that were described in the stories (mean: 10.96 facts per story) and coded whether each of these facts was mentioned in children's responses.

Results & Discussion

We fit a linear mixed-effects model to the total number of words with age and conditions as fixed factors and subjects and stories as random factors (Bates & Sarkar, 2008; Gelman & Hill, 2007) with p-values set by posterior simulation. Older children produced longer answers (coefficient: 4.24, p < 0.0001), but there was no difference in the length of children's answers, between the three story conditions ($p = ns$). To analyze how many total facts were remembered, we fit a logit mixed-effects model with the same factors: again, older children remembered more facts over all (t = coefficient: 3.12, p < 0.0001). In addition, children remembered marginally more facts in the Mental and Social conditions than in the Physical condition (coefficient: -3.90, p = 0.05). To analyze the number of mental states and person/agent nouns in children's responses, we used a bias-reduced general linear model (Kosmidis, 2007) due to underdispersion in the data. We took a binary variable of whether each participant reported mental state verbs or person/agent noun in each condition, and ran a regression over these binary data. On these measures, there was no effect of age: younger children produced just as many mental state verbs, and agent nouns, as older children (mental state verbs: coefficient 0.15, $p = ns$; agent nouns: coefficient 0.27, $p = ns$). As predicted, children produced mental state verbs when recounting stories in the Mental

condition, but not in the Social and Physical condition (Social: coefficient -4.04, $p < 0.0001$; Physical: coefficient -6.58, $p < 0.0001$), and they produced person/agent nouns or pronouns when they recounted stories in the Mental and Social conditions, but not in the Physical condition (Social: coefficient -0.004, $p = ns$; Physical: coefficient -4.35, $p < 0.0001$). These results provide support for our hypothesis that independent of age, children faithfully represent and retain the actual content of the story texts, and only rarely invent new entities, people or mental states that were not explicitly provided. That is, children of all ages described characters' thoughts and feelings only for stories in the Mental, not the Social, condition. Thus, there is no evidence that young children construe the stories differently, or are more likely to spontaneously consider the thoughts and feelings of characters in the Social stories.

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Kosmidis, I. (2007). brglm: Bias reduction in binary-response GLMs, from http://go.warwick.ac.uk/kosmidis/software