Published in final edited form as:

Neuropsychologia. 2007 April 8; 45(7): 1522–1532.

Children's and adults' neural bases of verbal and nonverbal 'Theory of Mind'

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Abstract

Theory of mind (ToM) - our ability to predict behaviors of others in terms of their underlying intentions - has been examined through verbal and nonverbal false-belief (FB) tasks. Previous brain imaging studies of ToM in adults have implicated medial prefrontal cortex (mPFC) and temporo-parietal junction (TPJ) for adults' ToM ability. To examine age and modality related differences and similarities in neural correlates of ToM, we tested 16 adults (18-40 years-old) and 12 children (8-12 years-old) with verbal (story) and nonverbal (cartoon) FB tasks, using functional magnetic resonance imaging (fMRI). Both age groups showed significant activity in the TPJ bilaterally and right inferior parietal lobule (IPL) in a modality-independent manner, indicating that these areas are important for ToM during both adulthood and childhood, regardless of modality. We also found significant age-related differences in the ToM condition-specific activity for the story and cartoon tasks in the left inferior frontal gyrus (IFG) and left TPJ. These results suggest that depending on the modality adults may utilize different brain regions from children in understanding ToM.

Keywords

fMRI; Theory of Mind; Cognitive Development; Language; Temporo-parietal junction

1. Introduction

Theory of mind (ToM) - the ability to understand others' desires and intentions that can be the same as (or different from) one's own - is critical for human cognitive development (Frith & Frith, 2003). ToM has been tested in normally developing children and children with autism through a variety of verbal and nonverbal tasks (Baron-Cohen, 2000). Among these ToM tasks, the false-belief (FB) paradigm (Perner & Wimmer, 1985; Wimmer & Perner, 1983) is perhaps the most widely used task among ToM researchers (Wellman, Cross, & Watson, 2001). The purpose of the FB task is to assess one's understanding of others' beliefs that may be different from his/her own (Baron-Cohen, Leslie, & Frith, 1985; Baron-Cohen et al., 1999b). The nearly universally observed results are that 4- and 5-year-olds are successful at the FB tasks, while 3-year-olds are not (Baron-Cohen, Leslie, & Frith, 1985; 1986).

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A number of neuroimaging studies have explored ToM in adults and implicated the mPFC as being important for ToM processing (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000; Fletcher et al., 1995; Gallagher et al., 2000; Gallagher, Jack, Roepstorff, & Frith, 2002; Goel, Grafman, Sadato, & Hallett, 1995; Happé et al., 1996; Vogeley et al., 2001). There has been some evidence for modality-dependent ToM processing in laterality effects seen in ToM-related brain activity. Most ToM neuroimaging studies have used text-based ToM tasks and found left lateralized mPFC activity (Fletcher et al., 1995; Gallagher et al., 2000; Goel, Grafman, Sadato, & Hallett, 1995; Happé et al., 1996). A few studies have used pictorial or cartoon-based ToM tasks, claiming them to be nonverbal ToM tasks, and implicated the right mPFC (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000; Gallagher et al., 2000). One study that used both story-based and cartoon-based ToM tasks found a convergent activity for the both story and cartoon tasks in the left mPFC (Gallagher et al., 2000). Some studies have found more significant brain activity in the left and/or right TPJ than in the mPFC during mental attribution tasks (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). Most recently, Saxe and Wexler (2005) found that verbal belief concepts about others were primarily related to the right TPJ activity. These results suggest that pictorial ToM may be represented in the left- or right-lateralized mPFC, respectively, and/or TPJ region(s) in adults.

In order to understand the developmentally important ToM neural bases, a comparison between children and adults is needed. Previous studies of ToM that implicated the mPFC (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000; Fletcher et al., 1995; Gallagher et al., 2000; Goel, Grafman, Sadato, & Hallett, 1995; Happé et al., 1996; Vogeley et al., 2001) and the TPJ (Gallagher et al., 2000; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005) have used adult subjects only. To the best of our knowledge, no brain imaging study to date has examined both children and adults with both story- and cartoon-based ToM tasks.

The present study sought to explore the neural correlates of the verbal and nonverbal (using story- and cartoon-based stimuli, respectively) ToM in pre-pubertal children and adults. The main aim was to find both task modality-independent and -dependent neural bases of ToM that might be important for both age groups and either group separately. In addition, we wished to identify age-related differences and similarities in brain activity during verbal and nonverbal ToM tasks. We recorded hemodynamic responses while the subjects performed a verbal (story) FB task (Fig. 1a) and a nonverbal (cartoon) FB task (Fig. 1b) in an MRI scanner. We predicted that if there are neural bases of ToM that are modality-independent (as proposed in Gallagher et al. [2000]) these should be present even in children and we would observe convergence of activity in these regions between the two age groups for both task modalities. In terms of the age-related differences, those regions that show more activity in the children than the adults would be more important for understanding ToM during childhood. Conversely, those brain regions that exhibit more activity in the adults would have developed later. In addition, interactions between task- and age-groups would illustrate modality-specific developmental differences in the neural bases of ToM.

2. Method

2.1. Participants

Sixteen (8 male and 8 female) healthy adults with mean age of 27 ($SD = 6$, range 18 to 39) and 12 (6 male and 6 female) healthy children with mean age of 9 years 8 months ($SD = 1$, range 8 to 11 years 6 months) participated in the experiment. Fourteen children were initially recruited, however, two children showed excessive movement during fMRI scanning (> 5 mm) and were excluded from both behavioral and fMRI analyses. All had no known physical or psychiatric disease and were right-handed as assessed by our internal questionnaire. Verbal and performance IQs of the subjects were assessed through Wechsler *Abbreviated* Scale of Intelligence™ (WASI™, The Psychological Corporation®, Harcourt Assessment Inc., San

Antonio, TX). Both children and adults were above the standard norm for verbal IQ (Adults: $M = 122.06$, $SD = 16.90$; Children: $M = 120.75$, $SD = 27.28$) and performance IQ (Adults: $M = 112.43$, $SD = 14.29$; Children: $M = 119.41$, $SD = 24.67$), with no significant difference between groups. Children were also tested with the 'sentence combining' subtest in Test of Early Language Development, Intermediate - 3rd Edition [TELD-I:3; Hammill & Newcomer, 1999] to assess their syntax ability. The children's average performance was the standardized score of 14 (91 percentile). These results indicated that all the children were competent in language (syntax and vocabulary) ability. All participants signed written consent forms approved by our Institutional Review Board.

2.2. Tasks

Subjects completed three conditions in each story or cartoon version of the task: experimental ToM story/cartoon condition, non-ToM control story/cartoon condition, and unlinked sentences/scrambled pictures (baseline) condition, in a standard block design (Posner, Peterson, Fox, & Raichle, 1988). As shown in Figure 1a, the ToM story condition consisted of second-order FB stories (in the form of 'x thinks that y thinks that ...') (Astington, Pelletier, & Homer, 2002; Perner & Wimmer, 1985). We used the second-order format because we wished to test subjects with a paradigm which was difficult enough to keep them engaged while in the MRI scanner. It has been shown that first-order FB tasks (in the form of 'x thinks that ...') are usually passed by normally developing 4-5 year-old children, but the second-order FB tasks are more difficult and cannot be passed until 6-7 years of age (Baron-Cohen et al., 1999a). The non-ToM stories described physical causal situations (as in Fletcher et al., 1995) and were in a propositional form to match the ToM stories in syntax. However, unlike the ToM stories, the non-ToM stories contained perceptual verbs (e.g., 'sees' and 'hears') so that subjects were required to understand physical causal reasoning (and not the mental one) during the condition. As shown in Figure 1b, the cartoon ToM task depicted the same second-order FB situations (as those in the story version) by enclosing one person's thought-bubble in another, second person's thought-bubble. The cartoon version of the non-ToM task depicted the physical (non-mental) situations. The baseline conditions for the story and cartoon tasks were consisted of unlinked sentences and scrambled pictures, respectively. Each story was preceded by 2 sec prompt to show either "What are they thinking?" (for ToM), "What is happening?" (for non-ToM), or "Scrambled sentences" (baseline). Each cartoon was preceded by 2 sec prompt to show either 'a picture of a boy thinking' (for ToM), 'a picture of a woman falling while skiing' (for non-ToM), or 'a picture of colored puzzles' (for the baseline scrambled pictures). These pictures (used in the prompts) were downloaded from commercially available clip-art provided by MS Powerpoint® software (Microsoft Corporation). All the cartoon episodes were matched with the story episodes in content and duration. In addition, in order to better mimic the real world situations, all the cartoons and stories were colored.

Example of "What are they thinking?" story (ToM)

1. John and Paul are watching the World Cup Soccer on TV.
2. At first France is winning by a lot.
3. Paul gets up and goes to the bathroom.
4. While Paul is gone, John sees the USA win the game.
5. Paul comes back after the game is over.

[Outcome slide] John thinks that Paul thinks that ...

- A. the USA wins.
- B. France wins.

Example of “What is happening?” story (non-ToM)

1. In a village, there are two men named Nightman and Dayman.
2. They fight whenever they meet.
3. One time they meet during the day and Dayman wins.
4. Next time they meet at night and Nightman wins.
5. They meet next in the morning.

[Outcome slide] After the fight, newspaper says that ...

- A. Dayman wins.
- B. Nightman wins.

Example of Scrambled sentences (baseline)

1. Teddy buys red roses for Mary’s birthday.
2. Mike likes his new car.
3. Mary’s cat eats all the cookies.
4. Ted thinks that Cathy thinks that he wears a blue shirt.
5. Bob sees Italy winning by a lot.

[Question slide (subjects were asked to choose a sentence that had appeared in the preceding 5 slides.)]

- A. John thinks that Paul thinks that his car is new.
- B. Teddy buys red roses for Mary’s birthday.

2.3. Procedure

There were five episodes in each of the three conditions per run (or per each story or cartoon task). Each of these episodes consisted of five slides followed by a sixth slide showing two different outcomes. The subjects’ task was to choose the correct outcome by pressing one of two keys for either possible outcome. The baseline condition simply had the subjects choose which of two sentences or pictures had appeared in the preceding five slides. Before each run, there was an 8 sec fixation, during which a black cross appeared in the center of the screen. Each of the five slides in an episode was shown for 4 sec, the sixth outcome slide was shown for 10 sec, for a total time of 32 sec per episode (including the 2 sec prompt) and 8 min 8 sec for an entire run. Paper-based examples of each story or cartoon condition were shown to the subjects before scanning. These examples were similar but different from the actual tasks that subjects performed in the scanner. In addition, all child participants were acclimated to the MRI scanner like environment with a simulator housed in Sackler Institute, Weill Medical College of Cornell University, before they were tested in the real scanner. Stimuli were counterbalanced by condition and task-modality between subjects.

2.4. Brain imaging data acquisition

Brain image slices were acquired on a 3-T GE Signa scanner (General Electric Medical Systems, Milwaukee, WI). A 3-dimensional (3D) spoiled-gradient-recalled-echo in the steady state imaging sequence (repetition time [TR] = 23 ms, echo time [TE] = Minimum Full, Flip angle 20°, 124 slices, 1.4 mm slice thickness, field of view [FOV] = 240 mm, in-plane resolution of 0.9 mm by 1.3 mm) were used to acquire T1*-weighted images. In addition, we acquired T2*-weighted 2-dimensional axial anatomical images with a Fast spin-echo sequence

(TR = 6000 ms, TE = 68, Flip angle = 90°, 29 slices, 5 mm slice thickness, FOV = 200 mm). Functional blood oxygen level-dependent (BOLD) images were acquired using Spiral sequence (Glover & Lai, 1998) (TR = 2000 ms, TE = 30 ms, FOV = 200 mm, Flip angle=90° and 64 mm × 64 mm matrix). The center of the 29 axial 5 mm thick slices was positioned along the anterior commissure (AC)-posterior commissure (PC) line to cover the whole brain.

2.5. Data analyses and statistics

For preprocessing the acquired brain images, we used statistical parametric mapping software (SPM2) (<http://www.fil.ion.ucl.ac.uk/spm>) implemented in MATLAB 6.1 (Mathworks, Inc, Sherborn, MA). The first four acquisitions (which correspond to the 8 sec fixation in each run) of each series were discarded in order to avoid intensity variation due to magnetization non-equilibrium effects in the Spiral pulse sequence used to acquire MRI data. All functional images were realigned to the initial image to generate a mean functional image, which was used to determine estimated motion for each individual. The mean functional image was then co-registered with the 3D anatomical image for overlaying the functional image onto an anatomical image later in the process. The functional images were then normalized to a Montreal Neurological Institute template image. The normalized images were then smoothed using an isotropic Gaussian filter kernel having a full-width half-maximum of twice the normalized voxel size (3.125 mm × 3.125 mm × 5 mm).

First, functional imaging data from each subject were analyzed with the General Linear Model (Friston et al., 1999) to describe the variability in the data in terms of the effects of interest. In the single subject level, there were six contrasts of interest: “ToM minus baseline,” “non-ToM minus baseline,” “ToM minus non-ToM,” and three other contrasts of the opposite subtractions. Next, a group-level analysis was performed using a random-effect model that enabled statistical inferences of population levels (Friston et al., 1999). A $2 \times 2 \times 2$ analysis of variance (ANOVA) was performed to assess age, task, and condition related main effects and interactions based on the imaging data from the “ToM minus baseline” and “non-ToM minus baseline” contrasts of all the subjects. Region of interest (ROI) analysis was performed to find percent signal changes across conditions. Each center of mass of these ROIs was defined as a sphere with 15 mm radius in each brain region that showed convergent activity among the groups (across the tasks) during the ToM condition relative to the non-ToM condition (see ‘main effect of condition’ in Table 1). Throughout the data-analysis, we used a height threshold of $p \leq 0.005$ without correction (unless otherwise noted). In addition, we considered only those areas which showed activity in 10 or more contiguous voxels as significant. The stereotactic coordinates of the voxels that showed significant activations were then matched with the anatomical brain structures using the standard brain atlas (Talairach & Tournoux, 1988).

3. Results

3.1. Behavioral measures

3.1.1. Task validity—Mean proportion correct of each adult and child group was at above 50% chance-level for the ToM and non-ToM conditions (Adult-Cartoon: 62.7%, $t(15) = 3.32$, $p < 0.005$; Adult-Story: 82.7%, $t(15) = 7.09$, $p < 0.0001$; Child-Cartoon: 69.2%, $t(11) = 3.36$, $p < 0.01$; Child-Story: 77.5%, $t(11) = 4.55$, $p < 0.001$). All subjects also performed at above 50% chance-level for scrambled pictures and sentences (Adult-Cartoon: 92%, $t(15) = 13.73$, $p < 0.0001$; Adult-Story: 89.4%, $t(15) = 10.76$, $p < 0.0001$; Child-Cartoon: 83.4%, $t(11) = 5.18$, $p < 0.001$; Child-Story: 75%, $t(11) = 2.70$, $p < 0.05$). Average reaction times (RT) (on the sixth [answer] slides) during the ToM condition did not differ significantly from those during the non-ToM condition within each age group for either modality (Adult-Cartoon: $p > 0.1$; Adult-Story: $p > 0.05$; Child-Cartoon: $p > 0.5$; Child-Story: $p > 0.1$). There was no difference between adults and children in the RT for each condition (ToM or non-ToM) in each task (story or

cartoon) ($p > 0.1$). On average, the subjects took 7.8 sec to complete the sixth slides, suggesting the subjects were sufficiently “busy” or “on-line” (see Gallagher & Frith, 2003) during the functional scans. These results also confirmed that both the verbal (story) and the nonverbal (cartoon) ToM paradigms, which we had developed, were appropriate and valid for testing children as well as adults.

3.1.2. Group differences in verbal and nonverbal ToM tasks (accuracy)—To examine the main and interaction effects between age (child and adult), condition (ToM and non-ToM) and task (story and cartoon), we performed a $2 \times 2 \times 2$ repeated-measures ANOVA. This analysis did not show any significant main effect of age or condition, or interaction between any combinations of the three factors ($p > 0.05$). However, there was a main effect of task ($F = 18.62$, $p < 0.001$): both the adults and children performed the story task better than the cartoon task. Post-hoc t-tests showed that adults performed significantly better in both the ToM and non-ToM conditions in the story task than those in the cartoon task ($t(15) = -4.3$, $p < 0.005$). But children did equally well in both tasks ($p > 0.05$) (Fig. 2).

3.2. fMRI results

3.2.1. $2 \times 2 \times 2$ ANOVA - Brain activity associated with age, tasks, and conditions

—A $2 \times 2 \times 2$ ANOVA was performed to examine differences between the two age groups (adult versus [vs] child) in brain activity associated with the task (story vs cartoon) and/or the condition (ToM vs non-ToM).

3.2.1.1. Main effect of age (adults vs children): As shown in Table 1, main effects of age were found in many regions including the left superior temporal gyrus (STG), right mPFC, right middle frontal gyrus (MFG), and right ventral inferior frontal gyrus (vIFG), where children had more activity than adults. Adults had more activity than children in the right amygdala.

3.2.1.2. Main effect of task (story vs cartoon): The cartoon ToM task elicited more brain activity in the right dorsolateral prefrontal cortex (DLPFC), right middle temporal gyrus (MTG), right inferior occipital gyrus (IOG), left lingual gyrus (LG), and mPFC than the story ToM task. In contrast, the story ToM task employed the left amygdala more than the cartoon ToM task (Table 1).

3.2.1.3. Main effect of condition (ToM vs non-ToM): Conjunction among the task and age groups: Across the age and task groups, compared to the non-ToM condition, the ToM condition showed increased activity in the right DLPFC/MFG, right IPL, right middle occipital gyrus (MOG), and right TPJ, and, to a lesser degree, in the left TPJ (Fig. 3; see also Table 1).

The ROI analyses, in which we examined condition specific brain activity for all the subjects, showed that in the bilateral TPJ (Fig. 3, top left and right) and right IPL (Fig. 3, bottom left), the strongest activity was seen during the ToM condition than during the other two conditions. However, in the right IPL, the baseline condition elicited more activity than the non-ToM condition. In the right DLPFC/MFG (encompassing the right mPFC; Fig. 3, bottom right) and right MOG (not shown), the activity was strongest during the baseline condition than during the other two conditions.

3.2.1.4 Interaction between age (adults vs children) and condition (ToM vs non-ToM):

During the ToM condition relative to the non-ToM condition, children had more activity than adults in the right STG, right temporal pole (TP), cuneus, and right ventro-medial prefrontal cortex (vmPFC). In contrast, adults had more activity in the left amygdala during the ToM condition (Table 1).

3.2.1.5 Interaction between task (story vs cartoon) and condition (ToM vs non-ToM):

During the ToM condition relative to during the non-ToM condition, both groups showed greater activity in the STG and right MTG for the story task than for the cartoon task (Table 1).

3.2.1.6. Interaction between age (adults vs children) and task (story vs cartoon): A two-way interaction between task (story vs cartoon) and age (adults vs children) was found in the left amygdala, left IFG (BA 44/45), right vIFG/ventral MFG (vMFG; BA 47/11), right STG (BA 38), and left MTG/TPJ (BA 22). Adults had more activity in the left amygdala (Fig. 4, bottom left), right STG (Fig. 4, top left), and vIFG/vMFG (not shown) during the cartoon task, yet children had more activity in these regions during the story task. The opposite trend was seen in the left TPJ (Fig. 4, bottom right). Adults had more activity during the story task, but children had more activity during the cartoon task in this region. In the left IFG (Fig. 4, top right) adults showed almost the same level of activity for both tasks, yet children showed more activity during the cartoon task (Table 1).

3.2.1.7. Interaction between task, age, and condition: Three-way interactions between task (story vs cartoon), age (adults vs children), and condition (ToM vs non-ToM) were found in the bilateral TPJ (BA 39), left STG/insula (BA 38), and left IFG (BA 45). In the bilateral TPJ (Fig. 5, top right & left) and left IFG (Fig. 5, bottom left) adults had more activity during the story ToM condition, yet children had more activity during the cartoon ToM condition. In the left STG/insula, adults had more activity during the story ToM condition, yet children had more activity during the cartoon ToM condition. However, in this region (unlike the other three regions), the activity during the non-ToM condition was greater than that during the ToM condition except for the Adult-Cartoon group (Fig. 5, bottom right) (Table 1).

4. Discussion

This study, the first to explore neural bases of verbal and nonverbal ToM in both adults and children, showed both age and modality independent and dependent brain activity associated with verbal and nonverbal ToM. Although the pattern of brain activity of adults was clearly different from that of children, there were some similarities between the age groups in several candidate ToM brain regions during both verbal and nonverbal ToM tasks. Specifically, the ToM condition activated the right DLPFC/MFG, right IPL, right MOG, and bilateral TPJ more than the non-ToM condition in all the age and task groups (Fig. 3). In addition, our ROI analysis results indicate that the bilateral TPJ and IPL are the only regions where the ToM condition elicited more activity than the baseline or non-ToM condition across the groups (Fig. 3). The observed activity in the bilateral TPJ is consistent with several brain imaging studies of ToM in adults (Gallagher et al., 2000; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005).

Several of the earlier brain imaging studies of ToM that used false-belief style paradigms, implicated the mPFC area for adults' ToM (Fletcher et al., 1995; Gallagher et al., 2000; Happé et al., 1996; Vogeley et al., 2001). Those results have indicated that mPFC is the 'core' *mentalizing* area (Frith & Frith, 2003). However, other later fMRI studies of ToM, in which the experimental condition (i.e., mental state attribution) was closely matched with the control conditions (e.g., asking subjects about any socially relevant information about a person), found more robust brain activity in the TPJ than in the mPFC (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). Moreover, it has been increasingly suggested that the mPFC area may be active during a default mode or baseline condition when subjects are free from task demands and/or when they contemplate the external environment or themselves (den Ouden et al., 2005; Gusnard & Raichle, 2001; Gusnard et al., 2001). Our results of ROI analysis support this last hypothesis, as we have found convergent activity among the task-groups in the mPFC

(encompassing the MFG) more during the baseline condition than during the ToM and non-ToM conditions (Fig. 3, bottom right).

However, it should be noted that the most robust convergent activity was found in the IPL and the DLPFC/MFG. The IPL is thought to be a part of a ‘mirror neuron’ system (Fogassi et al., 2005; Iacoboni, 2005). Right posterior parietal activity has been found in several studies that explored imitative behavior (Decety, Chaminade, Grézes, & Meltzoff, 2002; Iacoboni, 2005), discrimination of ‘self’ from ‘other’ (Decety & Chaminade, 2004), and reading of others’ intentions (Burgess, Quayle, & Frith, 2001; Iacoboni et al., 1999). For example, robust brain activity in this area was found when monkeys engaged in a task in which they had to infer an experimenter’s intentions (Fogassi et al., 2005). Several brain imaging studies on human adults have also found significant activity in the inferior parietal regions while subjects were engaged in imitation tasks (Decety et al., 1997; Chaminade & Decety, 2002; Nakamura et al., 2004). It has been suggested that these processes (e.g., understanding intentions of others and imitation) form the bases for higher order ToM ability (e.g., inferring from others’ beliefs) (Meltzoff & Brooks, 2001).

The convergent activity in the right DLPFC/MFG (BA 9/46) may be related to the second-order nature of the FB task used in this study. Second order FB may require more inhibitory control than the first-order FB task. In a second order FB scenario, one has to inhibit not only the first character’s belief or thought, but also the second character’s belief or thought, which is doubly embedded. The relationship between aspects of executive control-like inhibitory control and ToM is still under debate (Saxe, Carey, & Kanwisher, 2004; Siegal & Varley, 2002), but the common DLPFC activity we have found during ToM condition in both age groups for both versions of the task suggests a possible relationship. The convergent activity in this area may be associated with the higher executive control demands in the second-order FB task.

By using story and cartoon ToM tasks, we have sought to examine whether adults’ means of understanding of ToM are different from children’s, as well as to gain insight into which brain regions may be involved in modality-specific ToM. Through the ANOVA analysis, we found greater ToM condition-related brain activation for the child group as compared to the adult group in the right STG, right TP, cuneus, and right vmPFC. This overall greater activity for children may reflect greater effort on the part of the children or a true developmental difference in the brain areas used to understand ToM in childhood. However, given the two age-groups showed equivalent task performance, these differences may reflect a developmental rather than a performance-based difference. The right STG (which showed the most significant difference in this comparison) has not been commonly included among the ToM regions. However, a few recent imaging studies have implicated the right STG area for some functions that may be precursors for ToM; i.e., empathy mapping through facial and hand-gesture imitations (Leslie, Johnson-Frey, & Grafton, 2004) and reading eye-gaze directions (Akiyama et al., 2006). Thus, the greater activity in this area during the ToM condition for children than adults may represent these precursor abilities of ToM during the course of development.

In contrast, the only region which showed significantly greater activity in the adult group relative to the child group was the left amygdala. The adults had greater activity in this region especially for the cartoon ToM condition (Fig. 4, bottom left). Amygdala activity has been found in several ToM neuroimaging studies that emphasized socio-emotional facets of ToM such as reading social and emotional cues from others (Baron-Cohen, et al., 1999b; Gallagher & Frith, 2004; Vollm et al., 2006). In addition, the amygdala is known to be active when subjects are exposed to emotional faces (Baron-Cohen et al., 1999b; Iidaka et al., 2002; Morris, deBonis, & Dolan, 2002; Morris et al., 1996). Thus, the greater activity in this area for the adult group

may indicate that adults were more aware of emotional cues in the faces in the cartoon ToM task than children.

We found interactions between task and condition in the left STG (BA 21/22) and right MTG (BA 21). In these regions, activity during the story ToM condition was greater than that during the cartoon ToM condition. Since both regions have been implicated for some aspects of language processing (see Price, 2000, and Martin, 2003 for reviews), the subjects may have recruited these areas for processing verbal ToM specifically.

We found age and task interactions in the left amygdala, left IFG (BA 44/45), right vIFG/vMFG (BA 47/11), right STG (BA 38), and left MTG/TPJ (BA 22). The adult group had more activity in the left amygdala (Fig. 4, bottom left) and right STG (Fig. 4, top left) during the cartoon task, but the child group had more activity in these regions during the story task. The direction of the two-way interaction in the left TPJ (Fig. 4, bottom right) was the opposite. The adults used this region more for the story task, but children recruited these regions more for the cartoon task. As discussed below, we also saw three-way interactions in the left TPJ and left IFG indicating that these task and age interactions are also ToM-specific.

In the left IFG, where we found both two-way and three-way interactions, adults had more activity during the story ToM condition, yet children had more activity during the cartoon ToM condition (Fig. 5, bottom left). The left IFG (BA 45) (Broca's area) has been implicated in many aspects of language, including phonological (Temple et al., 2003; Poldrack et al., 2001), semantic, syntactic aspects of language (see Price, 2000 for a review). Thus, it is possible that during the story ToM task the adults paid more attention to these linguistic features in the sentences than the children. The children, on the other hand showed greater activity here during the cartoon ToM task.

Broca's area has also been hypothesized to be a part of the possible 'mirror neuron' network (Dapretto et al., 2005; Saxe, 2005). Significant activity has been seen in Broca's area when subjects imitated intentional behaviors (Iacoboni et al., 1999; see also Refs. in Chaminade, Meltzoff, & Decety, 2002). Thus, this area could have been more active in either case due to a greater effort to understand the intentions of the characters in the ToM stories, with children doing this during the cartoon task and adults during the story task.

The three-way interactions seen in the bilateral TPJ regions are consistent with what we observed in the main effect of conditions (or the conjunction of ToM-specific activity among the groups) and highlight the importance of these areas for ToM understanding throughout development. Not only do all groups show activity in the TPJ during both versions of the ToM task, but adults showed greater activity here during the story version whereas children showed greater activity during the cartoon version (Fig. 5, top left & right). These results may indicate that children's ToM is more tied to the visual modality than adults' ToM, which is more tied to the verbal modality.

The TPJ has not only been suggested as having a role in processing belief concepts (Saxe & Kanwisher, 2003), but also as being involved in the more general ability of distinguishing 'self agency' from 'others' (Blakemore & Frith, 2003; Frith & Frith, 2003; Jackson & Decety, 2004; see also Decety & Grézes, 2006 for a review). Thus, the age-related interaction we observed in this area may imply that children process a sense of 'self agency' more visually than adults, who process it more verbally.

There were several limitations in this study. Our cartoon task is similar to those used in a few previous ToM imaging studies (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000; Gallagher et al., 2000), and these studies have described the cartoon ToM tasks as nonverbal. However, in this case, as with the previous work, it can not be guaranteed that these cartoon ToM tasks

(including ours) are truly nonverbal, and they likely are not. We believe that although it is unlikely that the cartoon ToM task is purely nonverbal, it is arguably different than reading a text, and seems to tax at least some different brain systems between children and adults. An additional possibility is that the cartoon task might have required more top-down linguistic processing and the story task might have required more bottom-up processing. In that case, we still see interesting similarities and differences between the two age groups.

An additional limitation of this study is that the children in this study are between 8 and 12, which is much older age range during which ToM is thought to develop. This was done in part for practical reasons. Functional MRI requires extreme motion control which can be difficult for younger children. In addition, in a previous pilot study for testing the task validity, 7 year-old children performed at chance levels (Kobayashi & Temple, 2003). However, in comparing children to adults, we feared that using a much simpler ToM task would be inadequate stimulation for the adult subjects. In the slightly older children, we were able to have two age groups who performed the task comparably well with a minimum of motion problems with the child group. Children between 3 and 5 years (considered to be the critical age range when ToM ability dramatically improves) would be ideal to study and we await future advancement in methodology to enable ToM researchers to examine ToM related brain activity in this age group.

In sum, the present study has, for the first time, explored neural bases of verbal and nonverbal ToM in children and adults. Our study found both modality- and age-dependent and -independent neural bases of ToM. Our group analyses suggest that the bilateral TPJ and right IPL may be involved in understanding verbal, as well as nonverbal ToM throughout development (at least by 8 years). These findings highlight the importance of the TPJ area as a socio-communicative brain region (see Allison, T., Puce, A., & McCarthy [2000] for a review). Moreover, the age-related ToM task modality-specific interactions seen may suggest that the types of linguistic and cognitive resources that adults use to understand ToM are different from those of children. These results suggest that the ToM development is a dynamic socio-interactive process that may develop *vis-à-vis* linguistic and/or other cognitive development.

Acknowledgements

The present study was supported by a grant from NAAR(44519/A001) to ET, as well as from NIH(P41-RR0974) to GHG. We thank Dr. Barbara C. Lust, Dr. Michael J. Spivey, and Dr. M. Siegal for discussion. We also thank Dr. Matthew Davidson, Dr. Bruce D. McCandliss, Dr. Jason Zevin, Dr. Henning Voss, Grace, Y. Lai, Victor Laczó, and Michiko Sullivan for assistance.

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Fig. 1.

Examples of story (a) and cartoon (b) ToM tasks. The ToM story task was second-order FB in the form of “x thinks that y thinks that ...”. The cartoon ToM task depicted the characteristics of the second-order FB scenario by enclosing one person’s thought-bubble in another person’s thought-bubble. All slides were presented serially. There were six slides in each story/cartoon episode. On the sixth slide, subjects were asked to choose from two possible answers, A or B (for story), or, Red Star or Blue Star (for cartoon).

Fig. 2.

Mean proportion of the correct answer for the ToM and non-ToM conditions for the two age groups in cartoon and story tasks. Adults (solid line) performed better in story task than in cartoon task ($P < 0.005$). But children (dashed line) performed equally well for both tasks ($P > 0.05$).

Fig. 3.

Convergence of ToM-specific brain activation between the two age groups for both story and cartoon ToM. Convergent activity was seen in right DLPFC/MFG, right IPL, and bilateral TPJ (based on main effect of condition). The bar graphs show percent signal change in each selected region across the conditions (percent signal change represents the adjusted BOLD signal in each condition relative to the fitted mean and expressed as a percentage of whole brain mean BOLD signal). In the bilateral TPJ (top left and right) and right IPL (bottom left), the percent signal increase was the greatest during the ToM condition. In the right MFG (which includes mPFC), more signal increase was found during the baseline than during the other two conditions (bottom right).

Fig. 4.

Interactions between age and task. Each bar-graph shows task and age group-specific percent BOLD signal changes (collapsed across ToM and non-ToM conditions) in each brain region. In the right STG (top left) and left amygdala (bottom left), adults had more activity during the cartoon task (AC), whereas children had more activity during the story task (CS). In the left TPJ (bottom right), adults had greater activity during the story task (AS), while children had more activity during the cartoon task (CC). In the left IFG (top right), adults showed almost the same level of activity for both tasks, yet children showed more activity during the cartoon task.

Fig. 5.

Interactions between age, task, and condition. Each bar-graph shows task and age group specific percent BOLD signal changes of “ToM minus baseline” (black bar) and “non-ToM minus baseline” (white bar) in each brain region. In the bilateral TPJ (top left & right) and left IFG (bottom left), for the ToM condition, the Adult-Story (AS) and the Child-Cartoon (CC) task-groups exhibited greater activity than the Adult-Cartoon (AC) and the Child-Story (CS) groups. An opposite trend was found in the left STG/insula, where the AC and CS groups exhibited a greater activity than the AS and CC groups (bottom right). In this region, however, brain activity during the non-ToM condition was greater than that during the ToM condition except for the AC group.

Table 1

Main effects and interactions among Age, Task, and C Condition factors

Region (Brodmann area)	Coordinates			p-value	Direction
	x	y	z		
Main Effect of Age (adults vs. children):					
Left STG (42)	-59	-27	7	< 0.0005	C > A
Right mPFC (9)	10	52	34	< 0.0005	C > A
Right MFG (10/46)	40	47	5	< 0.0005	C > A
Right vIFG (47)	28	21	-8	< 0.0005	C > A
Rostral CC (24)	6	-3	26	< 0.0005	C > A
Right STS (21/22)	55	-8	-6	0.001	C > A
Right vmPFC (10)	18	52	-6	0.001	C > A
Right CC (32)	28	15	25	0.001	C > A
Left cuneus (18)	-8	-80	22	0.002	C > A
Paracentral lobule (6)	-6	-22	58	0.002	C > A
Right amygdala	17	-3	-12	0.003	A > C
Main Effect of Task (cartoon vs. story):					
Right DLPFC/MFG (46)	60	24	21	< 0.0005	c > s
Left amygdala	-16	-4	-10	< 0.0005	s > c
Right MTG (21/22)	62	-54	3	< 0.0005	c > s
Right IOG (18)	26	-95	-4	0.001	c > s
Left LG (18)	-12	-86	-6	0.001	c > s
mPFC/SFG (9/10)	4	56	23	0.002	c > s
Main Effect of Condition (ToM vs. nonToM)					
Conjunction among the task and age groups:					
Right DLPFC/MFG (9)	38	40	31	0.001	T > N
Right IPL (40)	52	-30	32	0.002	T > N
Right MOG	14	-94	21	0.004	T > N
Right TPJ (40)	64	-49	26	0.005	T > N
Left TPJ (40)	-63	-47	23	0.008*	T > N
Two-way Interaction - Age x Condition:					
Right STG (22)	61	8	1	0.001	C > A (T > N)
Left amygdala	-21	-11	-7	0.004	A > C (T > N)
Right TP (38)	36	5	-20	0.004	C > A (T > N)
Cuneus (17)	-2	-79	13	0.004	C > A (T > N)
Right vmPFC (11)	24	50	-13	0.01*	C > A (T > N)
Two-way Interaction - Task x Condition:					
Left STG/STS (21/22)	-61	-6	-3	< 0.0005	s > c (T > N)
Right MTG (21)	50	-9	-12	0.001	s > c (T > N)
Two-way Interaction - Age x Task:					
Left amygdala	-14	-2	-5	< 0.0005	AcCs > AsCc
Left IFG (44/45)	-44	14	12	0.001	Cc > Cs
2 x 2 x 2 Interaction - Age x Task x Condition:					
Right vIFG/vMFG (47/11)	40	36	-15	0.001	AcCs > AsCc
Right STG (38)	42	11	-9	0.002	AcCs > AsCc
Left MTG/TPJ (22)	-65	-34	1	0.009*	AsCc > AcCs
2 x 2 x 2 Interaction - Age x Task x Condition:					
Left TPJ (39)	-42	-55	21	0.001	[AsCc > AcCs(T)] >> [AcCc > AsCs(N)]
Right TPJ (39)	61	-52	17	0.003	[AsCc > AcCs(T)] >> [AcCs > AsCc(N)]
Left STG/insula (38)	-34	5	-17	0.004	[AcCs > AsCc(T)] << [AcCs > AsCc(N)]**
Left IFG (45)	-57	20	17	0.005	[AsCc > AcCs(T)] >> [AcCcCs > As(N)]

Region (Brodmann area)	Coordinates				p-value	Direction
	x	y	z	Z		
<i>Abbreviations:</i> CC = cingulate cortex, DLPFC = dorsolateral prefrontal cortex, IFG = inferior frontal gyrus, IPL = inferior parietal lobule, IOG = inferior occipital gyrus, LG = lingual gyrus, MFG = middle frontal gyrus, MOG = middle occipital gyrus, mPFC = medial prefrontal cortex, MTG = middle temporal gyrus, SFG = superior frontal gyrus, STG = superior temporal gyrus, STS = superior temporal sulcus, TP = temporal pole, TPJ = temporo-parietal junction, vIFG = ventral IFG, vMFG = ventral MFG, vmPFC = ventro-medial prefrontal cortex; A = Adult, C = Child, c = cartoon, s = story, T = ToM, N = non-ToM.						

* Height threshold of $p \geq 0.01$ (uncorrected) was used to recognize the significant activity in these regions, because we had primary interest in them.

** In this region, activity during the non-ToM condition was greater than that during the ToM condition for all the groups except the AC group.