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Sex differences in the neural basis of false-belief and pragmatic language comprehension

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ABSTRACT

Increasing research evidence suggests that women are more advanced than men in pragmatic language comprehension and Theory of Mind (ToM), which is a cognitive component of empathy. We measured the hemodynamic responses of men and women while they performed a second-order false-belief (FB) task and a coherent story (CS) task. During the FB condition relative to the baseline (unlinked sentences [US]), we found convergent activity in ToM network regions, such as the temporoparietal junction (TPJ) bilaterally and precuneus, in both sexes. We also found a greater activity in the left medial prefrontal cortex (mPFC) and a greater deactivation in the ventromedial prefrontal cortex (vmPFC)/orbitofrontal cortex (OFC) bilaterally in women compared to men. However, we did not find difference in the brain activity between the sexes during the FB condition relative to the CS condition. The results suggest a significant overlap between neural bases of pragmatic language comprehension and ToM in both men and women. Taken together, these results are in line with the extreme male brain (EMB) hypothesis by demonstrating sex difference in the neural basis of ToM and pragmatic language, both of which are found to be impaired in individuals with Autism Spectrum Conditions (ASC). In addition, the results also suggest that on average women use both cognitive empathy (dorsal mPFC) and affective empathy (vmPFC) networks more than men for false-belief reasoning.

Introduction

Theory of Mind (ToM) refers to the ability to attribute mental states (such as beliefs, intentions, thoughts, and emotions) to self or others, and to use such knowledge to make sense of and predict the behavior of agents (Dennett, 1980). ToM has been suggested to be fundamental for human social interaction (Baron-Cohen, 1994; Frith and Frith, 2003). ToM has often been used interchangeably with "mindreading" (Carruthers, 2009), "mentalizing" (Frith and Frith, 2003) and "cognitive empathy" (Baron-Cohen, 2011). Among the variety of ToM tasks, the false-belief (FB) test (Wimmer and Perner, 1983; Perner and Wimmer, 1985) is perhaps the most widely used. The FB task assesses understanding of others' beliefs when these differ from one's own (Baron-Cohen et al., 1985, 1999). In the most common form of the FB test, dubbed the "Sally-Anne" task (Baron-Cohen et al., 1985), an object (e.g., a marble) is moved while the protagonist (Sally) is absent so that Sally mistakenly believes the marble is still in its last location, while the other character (Anne) knows it is now somewhere else. It has been found that while a typically-developing 4-year-old child passes these FB tests (Wimmer and Perner, 1983), most children with Autism Spectrum Conditions (ASC) are delayed in passing these tests (Baron-Cohen et al., 1985; see also Baron-Cohen et al., 2000).

It has been demonstrated that children with ASC are not only impaired in false-belief understanding but also in precursor capacities of ToM such as joint attention and pretend play (Baron-Cohen, 1995; Frith and Frith, 2003). These impairments might be closely related to the key characteristic of ASC involving primary deficits in pragmatic aspects of language (Landa, 2000; Tager-Flusberg, 2000; Frith, 2003; Tager-Flusberg and Joseph, 2005). It has been demonstrated that the way in which older children/adolescents with ASC approach FB tasks is different from typically developing children in that they rely on syntax and semantics more than pragmatics (Tager-Flusberg, 2007). Pragmatic aspects of language involve bringing in general world knowledge, integrating the individual utterances with the context, and making inferences based on one's prior knowledge of the situation (Ferstl et al., 2008). When someone says, "can you pass the salt?", a child with ASC understands the utterance not as a request but as a question of his or her ability to pass a salt bottle (Frith, 2003). A host of studies has shown that children with ASC have difficulties in detecting vocal cues to irony and sarcasm (Wang et al., 2001, 2006, 2007) that rely on the second-order pragmatic language comprehension (Wilson, 2000). For instance, Chevallier and colleagues have recently shown that

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children with high functioning ASC are impaired in recognizing pragmatically different levels of vocal cues not specific to ToM (Chevallier et al., 2011). These results suggest that the neural underpinnings of ToM and pragmatic language at least partly overlap.

Increasing research evidence suggests that on average women and girls are typically superior to typically-developing men and boys in empathy. Men and boys, in turn, are on average typically superior in empathy to people with ASC. For example, it has been found that girls outperform boys on tasks of emotion processing (Brown et al., 1996) and the Reading-the-Mind-in-the Eyes test (Baron-Cohen et al., 1997, 2000), and that girls demonstrate more sensitivity to sad looks and show sympathetic and comforting attitudes to others (Hoffman, 1977). These findings led to hypotheses about differences in the organization of the mind and brain between men/boys and women/girls. The empathizing–systemizing (E–S) theory of human psychological sex differences (Baron-Cohen, 2003) hypothesizes that the "male brain" or "Type S (systemizing) brain" has, on average, a weaker drive to empathize, alongside a stronger drive to systemize (Baron-Cohen, 2003, 2006; Chakrabarti and Baron-Cohen, 2006). In contrast, the "female brain" or "Type E (empathizing) brain" is defined as the opposite profile. These are psychometric definitions and by no means suggest that only men and boys have Type S brains, only that more men/boys than women/girls show this profile. This acknowledges that some women/girls have a Type S brain and some men/boys have a Type E brain (Goldenfeld et al., 2005). Although it has been found that more men/boys score higher on systemizing than on empathizing tasks (Auyeung et al., 2009), it has also been demonstrated that scores of systemizing and empathizing in women/girls are not correlated (Valla et al., 2010), suggesting sex differences in processing these tasks.

An extension of the E–S concept is the "extreme male brain (EMB)" hypothesis (Baron-Cohen, 2003), which hypothesizes that ASC may be an extreme form of the Type S brain (Baron-Cohen, 2006). In psychometric terms this comprises below-average empathy alongside intact or even above-average systemizing. A number of studies report results consistent with these profiles (e.g., Baron-Cohen et al., 1997; Lawson et al., 2004). Most recently, Auyeung et al. (2012) administered the Empathy Quotient (EQ) and Systemizing Quotient (SQ) (Baron-Cohen et al., 2003; Baron-Cohen and Wheelwright, 2004) to a large cohort of mothers of adolescents and another group of mothers of adolescents with ASC. As predicted, girls received significantly higher scores on the EQ than boys, who received significantly higher scores than adolescents with ASC. Adolescents with ASC were scored higher on the SQ than boys, who were scored higher than girls. A recent, large scale study of adults with ASC confirmed these patterns (Baron-Cohen et al., 2014b).

It has been suggested that empathy and ToM are distinct but overlapping concepts (Singer, 2006; Schulte-Rüther et al., 2008). Baron-Cohen (2011) defined empathy as "… our ability to identify what someone else is thinking or feeling and to respond to their thoughts and feelings with an appropriate emotion" (p. 16) which highlights that empathy encompasses two separate components: the cognitive component (ToM) and the affective component. This two-factor model of empathy is consistent with other definitions of empathy and ToM (Schulte-Rüther et al., 2008; Shamay-Tsoory et al., 2009). Regarding the tasks that tap these components respectively, the aforementioned emotion processing (Brown et al., 1996) and the Reading-the-Mind-in-the Eyes test (Baron-Cohen et al., 1997, 2000) tap the emotional empathy while white lie deception tasks (Villanueva et al., 2000), social narratives (Bosacki, 2000) and FB task examine the cognitive empathy. Compared to the affective empathy, studies that tested sex difference in cognitive empathy (ToM) yielded mixed results. While Charman et al. (2002) found only a moderate advantage of girls over boys in the FB task, other researchers have found significant differences between the sexes. Walker (2005) found that on average 3- to 5-year-old girls perform better on standard FB tasks than boys of the same age. Likewise, Calero et al. (2013) tested 6- to 8-year-old children with a suite of ToM tasks developed by Wellman and Liu (2004) and found a significant gender difference in the FB task performance. As Calero et al. (2013) note, these results may suggest a progressive increase in the gender gap in ToM processing.

The close relationship between ToM and communicative language is relevant to the present study since it has been consistently demonstrated that girls outperform boys in a number of language processing tasks (Dionne et al., 2003; Bornstein et al., 2004). It has been shown that girls learn vocabulary faster (Roulstone et al., 2002), demonstrate more spontaneous conversations (Bauer et al., 2002), and show earlier onset of language use (Murray et al., 1990). Furthermore, it has been found that these advantages continue into adulthood (Parsons et al., 2005). With respect to the sexual dimorphism in the neural basis of language, it has been found that on average women, relative to men, activate more bilateral brain regions including the inferior frontal gyrus (Clements et al., 2006; Burmann et al., 2008) and posterior superior middle/temporal gyrus (Kansaku et al., 2000; Rossell et al., 2002) in a less modality-specific manner (Burmann et al., 2008) during various language processing tasks.

To date, a number of neuroimaging studies have explored the neural correlates of ToM in adults. These studies have consistently found ToM-specific activity in the temporoparietal junction (TPJ) (Saxe and Kanwisher, 2003; Saxe and Wexler, 2005; Kobayashi et al., 2007), and the medial prefrontal cortex (mPFC) (Fletcher et al., 1995; Goel et al., 1995; Brunet et al., 2000; Gallagher et al., 2000, 2002; Vogeley et al., 2001; Kobayashi et al., 2006). Within the sub-regions of the mPFC, the anterior rostral (ar)-mPFC is specifically implicated in mentalizing or ToM (Amodio and Frith, 2006), the posterior-rostral (pr)-mPFC is more important for monitoring personally-guided or one's own intentions (Grezes et al., 2004; Walton et al., 2004), and the orbital (o)-mPFC is more specialized for anticipating outcomes or rewards of other-guided actions (Walton et al., 2004; Knutson et al., 2005). Other regions that are often correlated with ToM tasks include the temporal pole (Gallagher et al., 2000; Vogeley et al., 2001), the precuneus (Saxe and Kanwisher, 2003; Kobayashi et al., 2006), the orbitofrontal cortex (OFC), and the amygdala (Baron-Cohen, 1994; Baron-Cohen et al., 1999). Together, these regions constitute a network often referred to as the "social brain" (Brothers, 1990).

It has been hypothesized that neural correlates of affective empathy are overlapping but different from those underlying cognitive empathy (ToM): the former relies on phylogenetically older structures such as the amygdala, limbic system and anterior insula, while the latter relies on newer structures such as the prefrontal cortex (Singer, 2006; Singer et al., 2009). In addition to the aforementioned structures, increasing evidence suggests that the OFC is more associated with affective empathy than with ToM. It has been demonstrated that empathy tasks are more often associated with activity in the ventral mPFC (vmPFC),while ToM tasks are more often associated with ar-ToM network, including the mPFC (Sebastian et al., 2012). It has also been found that patients with OFC damage are impaired in affective empathy but not in ToM (Shamay-Tsoory et al., 2010). These results are consistent with the hypothesis that the cognitive empathy system (ToM) has both overlapping and distinct neural correlates from affective empathy system.

Regarding the relationship between ToM and pragmatic aspects of language, a number of brain imaging studies have consistently found a significant overlap between the neural underpinnings of discourse or story comprehension and ToM understanding (Ferstl and von Cramon, 2002; Ferstl et al., 2008; Mason et al., 2008; Mar, 2011). Ferstl and von Cramon (2002) found a significant overlap between neural correlates of coherent story comprehension and text-based ToM in the dorsal mPFC. In addition, it has been demonstrated that understanding verbal irony recruits the ToM network, including the bilateral TPJ and mPFC (Bašnáková et al., 2011; Spotorno et al., 2012). In particular, Bašnáková and colleagues have shown that deriving speakers' communicative intention relies on several brain regions implicated in ToM and affective empathy, including the mPFC and right TPJ (Bašnáková et al., 2013).

Moreover, a few meta-analysis studies found a significant overlap between the ToM network and a brain network subserving narrative comprehension (Mar, 2011). Likewise, it has been found that individuals with ASC have decreased connectivity between ToM network and left hemisphere language areas (Mason et al., 2008). Men showed reduced hemispheric connectivity and more laterality during various language processing tasks than women (Shaywitz et al., 1995; Burmann et al., 2008). Taken together, these findings support the EMB hypothesis demonstrating systematically greater hemispheric connectivity in women relative to men, and in men relative to individuals with ASC.

The purpose of our study was two-fold. First, we aimed to extend understanding of sex differences in the neural basis of ToM or cognitive empathy. Research supports the presence of sexual dimorphism in the neural bases of emotional empathy and ToM. For example, compared to men, women on average typically show more activation in regions related to the emotional empathy network, including the inferior frontal gyrus (IFG) (Dapretto et al., 2006; Schulte-Rüther et al., 2008). It has also been found that women employ the bilateral IFG more than men for humor understanding (Azim et al., 2005), which is related to ToM. Based on these results and the EMB hypothesis, we hypothesized that women (compared to men) would show a different hemodynamic response in areas that are part of ToM and/or affective empathy networks, when inferring the false-beliefs of characters in the stories.

Second, we aimed to explore sex differences and similarities in the neural basis of ToM and pragmatic language comprehension. Because previous research indicated a significant overlap between the neural correlates of FB and pragmatic language comprehension (Ferstl et al., 2008; Mar, 2011), we explored whether women on average show more overlap between the neural basis of ToM and that of pragmatic language comprehension than men. If we find no differences between sexes, then this would indicate that that pragmatic language does not make an independent contribution to false-belief reasoning for either sex. In order to answer to these questions, we used two experimental conditions: a false-belief (FB) to test the false-belief reasoning (ToM) and a coherent story condition (CS) to test the pragmatic language comprehension. The same stimuli were used in one of the author's (CKF) and her colleagues' previous studies (Kobayashi et al., 2006, 2007; see Table 1 for example stimuli and **Supplementary Table** for all the stories used for the FB and CS conditions). Although the names of the conditions and aims/hypotheses of these studies were different from the present study, the task consistently yielded significant results by finding FB-specific activity in the aforementioned ToM neural network. Because no previous neuroimaging study has tested these hypotheses, our approach was more exploratory in terms of the extent of the expected sexual dimorphism in brain activity, and in terms of the localization of potential differences.

Materials and methods

Participants

Thirty-four (17 men and 17 women) healthy adults with mean age of 28 years for women ($SD = 5$ months) and 29 years for men ($SD = 6$ months), ranging from 18 to 39 years old, participated in the experiment. All participants were recruited from the New York City metropolitan area and approximately two thirds were university graduates. Key exclusion criteria were: 1) no known medical or psychiatric conditions including ASC, claustrophobia and dyslexia, 2) left-handedness (assessed by an in-house questionnaire), 3) visual impairment, 4) low (<80) IQ, and 5) any reading or pragmatic comprehension-related impairment. Verbal and performance IQ were assessed using the Wechsler Abbreviated Scale of Intelligence (WASI, The Psychological Corporation, San Antonio, TX). Both men and women were above average in verbal IQ (women: $M = 124.4$, $SD = 12.3$; men: $M = 119.6$, $SD = 15.4$) and performance IQ (women: $M = 110.9$, $SD = 10.1$; men: $M = 115.9$, $SD = 12.9$), with no significant difference between groups. All participants signed written consent forms approved by the Institutional Review Board of Weill Medical College of Cornell University in New York City. In addition, all participants received a set amount of monetary compensation for the participation.

Table 1
Sample stories.

Instruction (for both FB and CS): "This task has five slides and one outcome slide at the end. Your task is to choose one outcome of the story, A or B when the outcome slide is shown".

"What are they thinking?" story (FB):
1. Anne, Bob and Cathy play a hiding game.
2. Bob and Cathy watch while Anne hides a marble inside a red can.
3. When Cathy is not watching,
4. Anne takes the marble out of the red can.
5. Then Ann hides the marble in a green can.
[Outcome slide] Bob thinks that Cathy thinks that the marble is …
A. in the red can.
B. in the green can.

"What is happening?" story (CS):
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, the newspaper says that …
A. Dayman wins.
B. Nightman wins.

Instruction (for US only): "This task has five slides and one question slide. Your task is to choose one sentence, A or B, that appeared in the preceding five slides".

"Scrambled" or incoherent story (US)
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.

Experimental measures

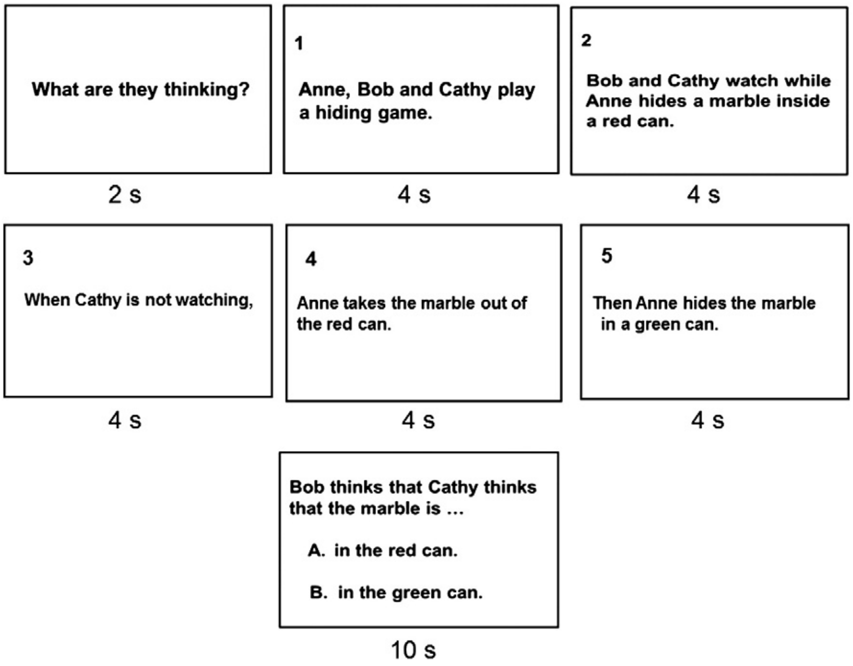
The experiment consisted of two independent groups (women and men) who completed three conditions (within-subject measures): an experimental FB story condition, a coherent story (CS) condition, and an unlinked sentences (US) condition (see Table 1 and **Supplementary Table**). These stimuli are modeled after those utilized in Gallagher et al. (2000) or in Perner and Wimmer (1985), and they are identical to stimuli used successfully in previous fMRI studies by CKF and colleagues (Kobayashi et al., 2006, 2007).

The FB condition (Fig. 1; Table 1)

The FB condition consisted of second-order FB stories (in the form of 'x thinks that y thinks that …') (Perner and Wimmer, 1985; Astington et al., 2002). While second-order FB is within the capacity of a 6–7 year-old, the versions employed here were adapted for use with adults to keep them engaged in the MRI scanner. Such second-order FB tasks have been successfully used with adults in neuropsychological experiments (Kobayashi et al., 2006, 2007).

The coherent story (CS) condition

The coherent stories were in propositional form, in order to match the FB stories in syntax and pragmatics. Unlike the FB stories that contained mental state terms (e.g., think, know, believe), the coherent stories only contained sensory/motor verbs (e.g., see, show, say). Several studies have demonstrated that language processing, especially the pragmatic aspects of language processing, correlates with FB task



What are they thinking?

2 s

1

Anne, Bob and Cathy play a hiding game.

4 s

2

Bob and Cathy watch while Anne hides a marble inside a red can.

4 s

3

When Cathy is not watching,

4 s

4

Anne takes the marble out of the red can.

4 s

5

Then Anne hides the marble in a green can.

4 s

Bob thinks that Cathy thinks that the marble is …

A. in the red can.

B. in the green can.

10 s

Fig. 1. Examples of a FB condition. The FB condition was a second-order FB story. There were six slides in each story episode. On the sixth slide, participants were asked to choose from two possible answers, A or B.

performance (Ferstl et al., 2008; Frank, 2010; Siegal et al., 2010; Mar, 2011). Moreover, overlapping activity between ToM and coherent story conditions in the front-median region of the brain has been observed (Ferstl and von Cramon, 2002). Thus, our purpose for including this condition was to control for the pragmatic language processing aspects of the FB reasoning. Through an unpublished pilot study conducted prior to the brain imaging phase of the study, we ensured that the FB and CS stories are comparable with respect to linguistic parameters, such as word length and frequency, inference demands (both stories required participants to infer physical or mental state-related outcomes of events from preceding sentences), syntactic complexity (both story conditions are in a propositional format with complement clause structure; i.e., “He shows/thinks that…”) and familiarity of content (see **Supplementary Table**). In the pilot study, 56 participants completed the story task with all the three conditions implemented in the E-Prime (Psychology Software Tools, Inc., Pittsburgh, PA). Results from pairwise comparisons based on *t*-tests found no difference in the dependent measures (number of correct answers or reaction times) between the FB and CS story conditions. These results were replicated later in CKF and her colleagues' previous studies (Kobayashi et al., 2006, 2007, 2008).

Unlinked sentences (US) condition

The US condition consisted of unlinked sentences. While these could require story comprehension, they made no sense, so that neither pragmatic reasoning nor ToM could easily be employed to find meaning. As such, this condition controlled for reading, for maintaining items in working memory, and for the actual presence of the same words, but without the target cognitive operations (ToM and pragmatic reasoning) being deployed. This condition is similar to the one used in Gallagher et al. (2000), which functions as the low-level baseline required for the analysis of brain imaging data (Friston et al., 2007). Moreover, in order to minimize the “missing stimulus effect” in which participants' surprise responses to novel stimuli affect the hemodynamic responses (Friston et al., 2007, pp. 208–209), the sentences included in the US condition were identical or very similar to the ones in the CS or FB conditions; however, since they were randomly chosen from different stories, they were unlinked from one another and they did not comprise a coherent story (see Table 1).

Prompts

Each story was preceded by a two second prompt that either read “What are they thinking?” (for FB), “What is happening?” (for CS), or “Scrambled sentences” (for US). The prompts signaled the participants which condition was to be presented next (see below for our practicing procedures prior to imaging).

Procedure and design

There were five episodes for each condition, each episode consisted of five slides (4 s each) followed by a sixth outcome slide (10 s). The task was to choose the correct outcome by pressing one of the two keys for either possible outcome. During the baseline condition, subjects had to choose which of the two sentences had appeared in the preceding five slides. In the beginning of the run, there was an 8 s fixation, during which a black cross appeared in the center of the screen (see below Data analyses and statistics section for the rationale of including the 8 s fixation). Each of the five slides in the episode was shown for 4 s and the sixth outcome slide was shown for 10 s, for a total time of 32 s per episode/story (including the 2 s prompt) and 8 min and 8 s for an entire run (Fig. 2). The order of presentation of conditions was randomized and counter-balanced across groups (sexes).

Prior to imaging, a paper-based example of each condition was shown to the participants. These examples were similar, but not identical, to the actual tasks that participants performed in the scanner. During this practicing session, the instructions for the each condition were read by the experimenter prior to the presentation of each example condition. The purpose of providing participants with the instruction and the example stimuli was to minimize any differences in procedural difficulty across conditions. In order to minimize spill-over effects, the sixth (outcome) slide was displayed for 10 s. Based on CKF and her colleagues' previous studies (Kobayashi et al., 2006, 2007, 2008) that used the same story stimuli, this was 2 s more than the average time needed for participants to respond. In addition, the prompt served to provide jittering and to

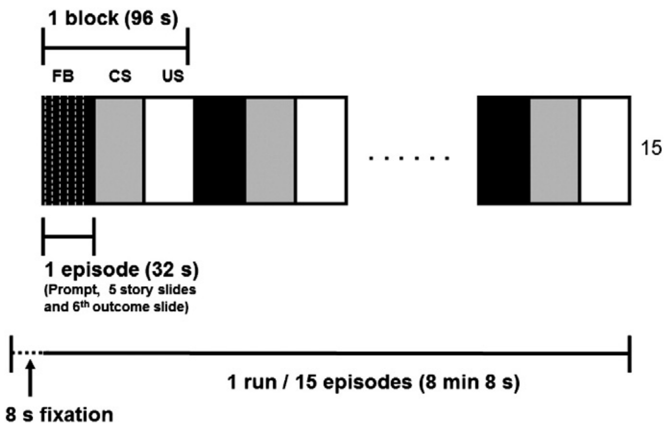


Fig. 2. Experimental design. The task had 3 conditions, each of which had 5 episodes. Each episode was shown for 32 s (including the 2 s prompt at the beginning), and each block (consisting of the 3 conditions) was shown for 96 s. There were 15 episodes in one run (8 min and 8 s). Although the figure shows the FB condition first, the order of presentation of the conditions was randomized and counter-balanced across groups. Eight second-fixation was shown at the beginning of the run, which was eventually removed from the data analyses to avoid intensity variation due to magnetization non-equilibrium effects in the spiral-in/out pulse sequence.

minimize the potential spill-over effects by giving the participants clear demarcations between conditions.

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) was 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-in/out sequence (Glover and Law, 2001) (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.

Data analyses and statistics

The imaging data were analyzed using Statistical Parametric Mapping (SPM8, Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK). The first four acquisitions (which correspond to the 8 s fixation) in each run were discarded in order to avoid intensity variation due to magnetization non-equilibrium effects in the spiral-in/out pulse sequence (Glover and Law, 2001) 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. These realigned images were smoothed with a 4 × 4 × 4 mm full width half maxima (FWHM) Gaussian kernel prior to the motion correction using ArtRepair (Mazaika et al., 2009). Then, fast motion or large global signal variation was repaired using linear interpolation. The functional images were then normalized to an Echo Planar Image (EPI) template provided by Montreal Neurological Institute (MNI). Finally, the normalization parameters were applied to the functional images, and smoothed with a 7.5 mm FWHM Gaussian kernel.

Functional imaging data from each participant were analyzed using the General Linear Model where data were best fitted at every voxel (Friston et al., 1999) to describe the variability in the data in terms of the effects of interest. Regarding the modeling, the hemodynamic response was time-locked to the onset of the story and the entire story (32 s) was taken as the epoch for analysis. At the within-subjects level, there were six contrasts of interest: "FB vs. US," "CS vs. US," "FB vs. CS," 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). In the whole group, t-tests were performed to compare brain activity between groups (sexes) in the above contrasts. To find brain regions that demonstrated convergent activity of both sexes, we performed a whole brain voxel-wise conjunction analysis (e.g., Nichols et al., 2005). To do so, we created masks of the significant regions of activation in the t-test contrasts (above) of either sex using xjView toolbox in SPM8 (http://www.alivelearn.net/xjview8). These were used as inclusive masks to localize overlaps in the brain activity between the sexes for each set of contrasts (e.g., FB vs. CS). Each brain region that showed significant differences in the group-level analysis (for each contrast) was defined as a region of interest (ROI) whose center of mass was a sphere with 10 mm radius, using MarsBar (Mathew Brett; http://marsbar.sourceforge.net). In addition, for those brain regions in which we found significant differences between sexes, we performed post-hoc two-factor repeated-measure ANOVA in order to detect interaction effects between the sex (women vs. men) factors and within the condition measures. The stereotactic coordinates of voxels that showed significant activation were then matched with the anatomical brain structures using a standard brain atlas (Talairach and Tournoux, 1988). Before matching, the MNI coordinates of the normalized functional images were converted to the Talairach coordinates using "mni2tal" MATLAB function (Mathew Brett; http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml). A *Monte Carlo* simulation using AlphaSim implemented in AFNI (Cox, 1996) of our whole-brain volume demonstrated that a cluster extent threshold of at least 31 contiguous voxels exceeding a height threshold of $p \leq 0.001$ (uncorrected) provided a multiple comparison correction at $p < 0.05$. In addition, a more lenient threshold of $p < 0.005$ (uncorrected) was used to find activity in brain regions for which we had *a priori* hypotheses.

Results

Behavioral results

For each sex, the mean scores correct was above chance for the FB condition (women: $M = 4.18$, $SD = 0.81$, $t(16) = 8.54$, $p < 0.001$; men: $M = 4.18$, $SD = 1.19$, $t(16) = 5.83$, $p < 0.001$) and for the baseline condition (women: $M = 4.71$, $SD = 0.47$, $t(16) = 19.36$, $p < 0.001$; men: $M = 4.35$, $SD = 0.86$, $t(16) = 8.87$, $p < 0.001$). We also performed a 3-way repeated-measures analysis of variance (ANOVA) in order to find the main effects of sex and condition, and interactions between these factors. Through this analysis, we found no main effects of sex ($F(1, 32) = 1.56$, $p > 0.1$) or interaction between the factors ($F(1, 32) = 1.1$, $p > 0.1$). However, we found a moderately significant main effect of condition ($F(1, 32) = 4.41$, $p < 0.05$). A pairwise comparison, however, showed that only the comparison between the FB and US was significant (mean difference (FB–US) = −0.353, std. error = 0.168, $p < 0.05$). We did not find any difference in performance between the CS and US conditions (mean difference (CS–US) = −0.176, std. error = 0.189, $p > 0.1$) or between the FB and CS conditions (mean difference (FB–CS) = −0.176, std. error = 0.180, $p > 0.1$). These results indicate that the performance of the women was comparable to that of the men, and the US task (baseline) was slightly easier than the FB task for both sexes. The latter results may be accounted for by relative difficulty of an additional ToM reasoning process.

Neuroimaging results

Brain activity within each sex

A one-sample *t*-test was performed to find brain activity related to our within-subject contrasts for each sex group. As shown in Table 2, significant activity was found in many regions, especially for women. Women showed significant FB-related activity (relative to US) in brain regions that are considered to be parts of ToM network, including the bilateral TPJ, TP, and left mPFC (Fig. 3a; Table 2). Men had significant FB-related activity (relative to US) in the left precuneus and bilateral TPJ (Fig. 3b; Table 2). Women also had significant activity during the FB condition relative to the CS condition in regions that are considered to be part of the ToM network, including the bilateral TPJ and precuneus (Fig. 3c; Table 2). In contrast, the only brain region that men activated during the FB condition relative to the CS condition was the precuneus (Fig. 3d; Table 2). Women also showed significantly greater activity in the left temporal pole during the CS condition relative to the US condition. Men did not show any greater activation in the CS vs. US comparison. Women showed greater activity in left amygdala during the CS condition relative to the FB condition. Men did not show any greater activation in the CS vs. FB comparison (Table 2).

Brain activity related to sex difference in FB vs. US

Compared to men, women showed greater activation in the left mPFC; more specifically the ar-mPFC and the pr-mPFC subregions (Amodio and Frith, 2006) (Fig. 4a), and in the left TPJ (Fig. 4b) during the FB condition relative to the US condition (Table 3). In addition, women deactivated the bilateral vmPFC/OFC significantly more than men in this contrast (Fig. 5a; Table 3). To examine condition-specific BOLD signal changes related to these between-group differences, we performed post-hoc two-way repeated-measure ANOVAs on the ROIs that showed significant differences between the sexes. The ANOVA revealed a number of significant interactions between sex and condition. There was a significant interaction between these factors in the two left mPFC regions, such that while women activated these regions significantly more during the FB than the US condition, men did not (ar-mPFC: women; $M(\mathrm{FB}) = -0.25$, $M(\mathrm{US}) = -0.43$, men; $M(\mathrm{FB}) = -0.29$, $M(\mathrm{US}) = -0.23$, $F(1, 32) = 6.87$, $p < 0.05$; pr-mPFC: women; $M(\mathrm{FB}) = -0.11$ $M(\mathrm{US}) = -0.39$, men; $M(\mathrm{FB}) = -0.14$, $M(\mathrm{US}) = -0.09$, $F(1, 32) = 6.22$, $p < 0.05$; Fig. 4a). We also found a significant interaction in the left TPJ. This means that women activated the left TPJ more during the FB condition than during the US, yet men did not (women; $M(\mathrm{FB}) = 0.37$, $M(\mathrm{US}) = 0.13$, men; $M(\mathrm{FB}) = 0.02$, $M(\mathrm{US}) = -0.02$, $F(1.\ 32) = 7.34$, $p < 0.05$; Fig. 4b). As shown in the bar graphs in Fig. 4, the “CS vs. US” related activity exhibited a similar interaction to the “FB vs. US” related activity, but to a lesser degree (non-significant) in all of these regions (ar-mPFC: women; $M(\mathrm{CS}) = -0.25$, men; $M(\mathrm{CS}) = -0.21$; pr-mPFC: women; $M(\mathrm{CS}) = -0.16$, men; $M(\mathrm{CS}) = -0.18$; left TPJ: women; $M(\mathrm{CS}) = 0.22$, Men; $M(\mathrm{CS}) = 0.01$; Fig. 4). In addition, there was a significant interaction in the bilateral vmPFC/OFC, with women showing greater deactivation in this region during the FB condition than the US, but men again showed no differences (left vmPFC: women; $M(\mathrm{FB}) = -0.2$, $M(\mathrm{US}) = -0.09$, men; $M(\mathrm{FB}) = -0.09$, $M(\mathrm{US}) = -0.13$, $F(1, 32) = 7.96$, $p < 0.01$; right vmPFC: $F(1, 32) = 7.26$, $p < 0.05$; Fig. 5a, b).

Brain activity related to sex difference in FB vs. CS and CS vs. US

We found no sex difference in the brain activity during the FB relative to the CS condition, or vice versa. During the CS relative to the

Table 2
Results of within group analyses.

Region (BA)	Z-score	MNI coordinates			Cluster size
		x	y	z	
Brain activity related to FB vs. US for each sex:					
Women:					
Left TPJ (39/40)[a]	4.64	−46	−53	23	1589
Left temporal pole (21)	4.10	−42	6	−32	444
Right temporal pole (21)	3.95	44	14	−31	204
Left mPFC (9)	3.81	−12	58	28	115
Right TPJ (39/40)	3.72	63	−51	25	102
Left precuneus (7)	3.42	−10	−52	41	54
Men:					
Left precuneus (7)	4.37	−10	−54	38	411
Right TPJ (39)	4.10	55	−57	18	325
Left TPJ (39)	3.97	−46	−59	23	670
Brain activity related to CS vs. US for each sex:					
Women:					
Left temporal pole (21)	3.98	−46	8	−34	159
Men:					
No region showed significant difference between the conditions.					
Brain activity related to FB vs. CS for each sex:					
Women:					
Left TPJ (39/40)	4.34	−58	−62	26	656
Left MFG (6)	4.16	−44	6	58	120
Right TPJ (39/40)	3.99	58	−60	30	219
Right SFG (10)	3.89	34	62	−2	52
Precuneus (7)	3.75	−8	−56	36	642
Men:					
Precuneus (7)	3.69	−8	−60	42	433
Brain activity related to CS vs. FB for each sex:					
Women:					
Left amygdala	3.61	−26	−6	−20	36
Men:					
No region showed significant difference between the conditions.					

Note: All of the above regions survived the criteria set by *Monte Carlo* simulation of $p \leq 0.001$ with at least 31 contiguous voxels.

[a] This region was also significant at $p < 0.05$ (FWE corrected).

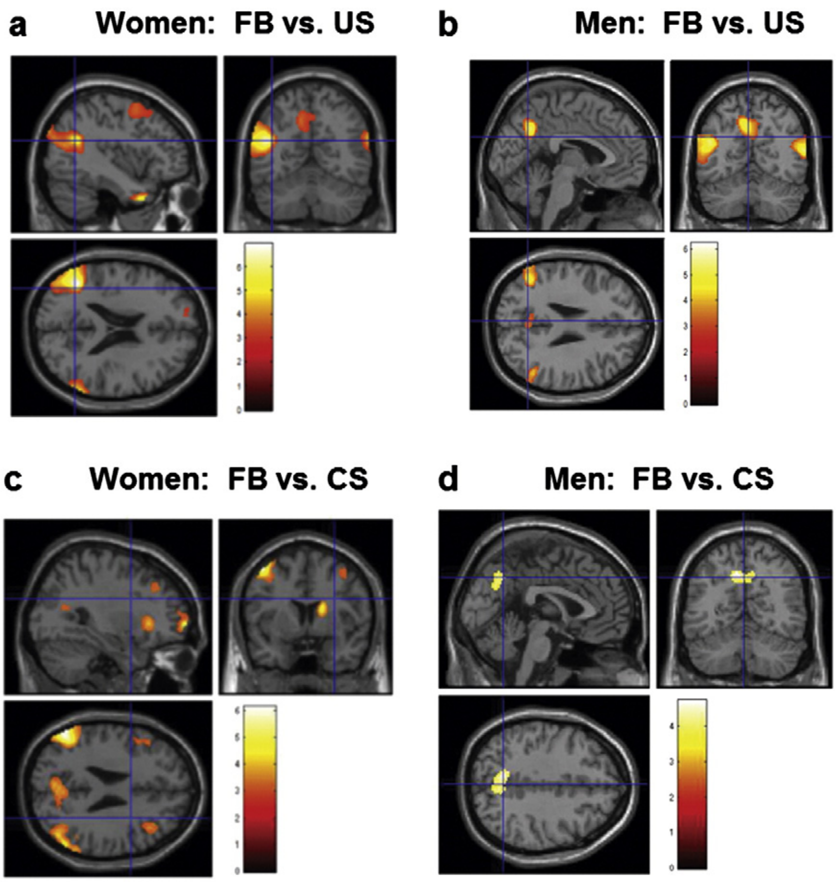


Fig. 3. Significant brain activity for each sex group, separately. During the FB condition relative to the US condition, in women, significant activity was seen in the bilateral TPJ, bilateral temporal pole, left mPFC, and left precuneus (**a**; coordinates of the crosshair (x, y, z) = −40, −59, 21). In men, significant activity was seen in the left precuneus and bilateral TPJ (**b**; coordinates of the crosshair = −4, −56, 28). During the FB condition, relative to the CS condition, women showed greater activity in the bilateral TPJ, left MFG, right SFG, and precuneus (**c**; coordinates of the crosshair = 30, 6, 26), yet men showed greater activation in the precuneus only (**d**; coordinates of the crosshair = 0, −60, 40). All of these regions survived the *Monte Carlo* simulation height threshold of $p < 0.001$ with cluster sizes ≥31. The left TPJ activity in women survived the family-wise error rate (FWE) correction with $p < 0.05$.

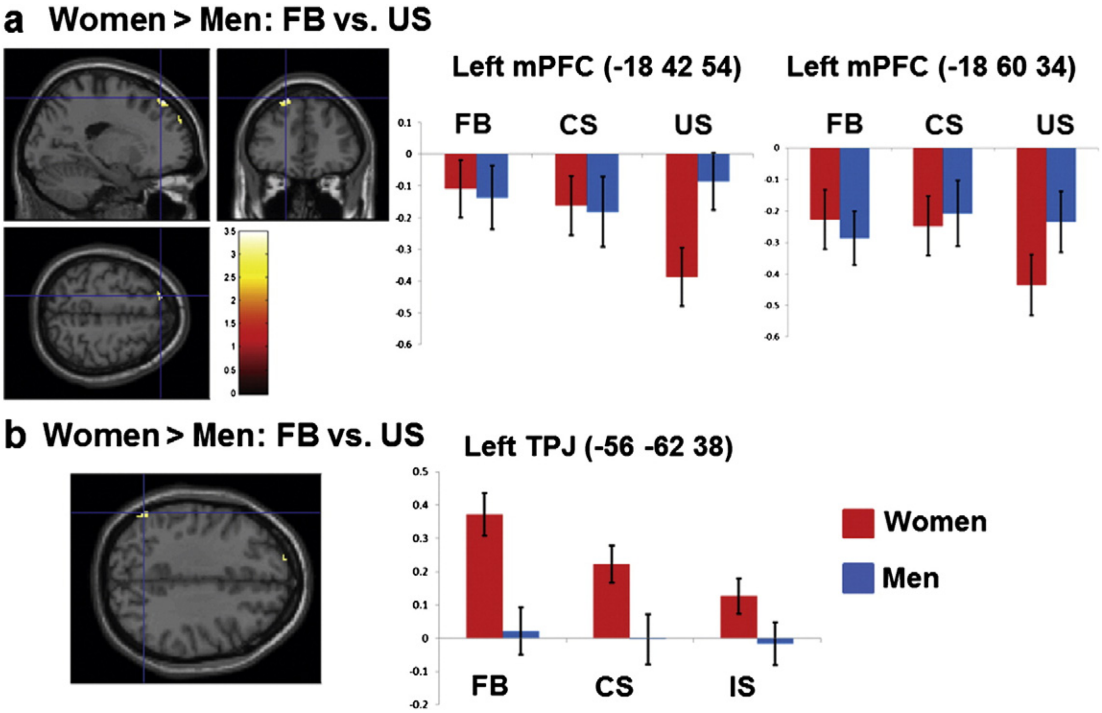


Fig. 4. Significant brain activity related to women > men. During the FB condition, relative to the US condition, women activated two subregions in the left mPFC (**a**) and left TPJ (**b**) significantly more than men. The height threshold of $p < 0.005$ (uncorrected) was used to recognize the activity in these brain regions, because we had *a priori* hypotheses for them.

Table 3
Between-group comparisons.

Region (BA)	Z-score	MNI coordinates			Cluster size
		x	y	z	
Brain activity related to FB vs. US:					
Women > men:					
Left mPFC (8)	3.18	−18	43	48	60
Left TPJ (39/40)	2.78	−55	−58	38	21
Left mPFC (9)	2.73	−18	60	28	17
Men > women:					
Left vmPFC (11)	3.07	−8	25	−10	89
Right vmPFC (11)	2.92	20	42	−16	88
Brain activity related to CS vs. US:					
Women > men:					
No region showed significant difference.					
Men > women:					
Right vmPFC (11)[a]	3.23	20	44	−12	23
Brain activity related to FB vs. CS:					
Women > men:					
No region showed significant difference.					
Men > women:					
No region showed significant difference.					

[a] A lenient external threshold of 23 voxels was used to recognize this region because we had *a priori* hypothesis.

Table 4
Convergent brain activity between sexes and between conditions.

Region (BA)	Z-score	MNI coordinates			Cluster size
		x	y	z	
Convergent brain activity related to FB vs. US:					
Left TPJ (39/40)[a]	4.64	−46	−53	23	638
Right TPJ (39/40)[b]	3.64	61	−55	25	30
Left precuneus (7)	3.42	−10	−52	41	49
Convergent brain activity related to FB vs. CS:					
Left precuneus (7)	3.69	−8	−60	42	433
Right TPJ (39/40)[b]	3.10	52	−56	16	328
Left TPJ (39/40)[b]	2.64	−52	−56	18	7
Convergent brain activity related to CS vs. US:					
Right TPJ (39)[b]	2.61	60	−62	24	1

Note: Unless otherwise specified, all of the above regions survived the criteria set by *Monte Carlo* simulation of $p \leq 0.001$ with at least 31 contiguous voxels.

[a] This region was also significant at $p < 0.05$ (FWE corrected).

[b] Height threshold of $p < 0.005$ (uncorrected) was used to recognize the significant activity because we had *a priori* hypotheses for this region.

US condition, women deactivated the right vmPFC/OFC more than men (Fig. 5b), but the men did not show any stronger or weaker BOLD responses in any regions for this comparison relative to women (Table 3). The "CS vs. US" related activity showed a similar interaction to the "FB vs. US" related activity in the right vmPFC (women; $M(\text{CS}) = -0.33$, men; $M(\text{CS}) = -0.17$, $F(1, 32) = 9.316$, $p < 0.01$; Fig. 5b), but to a lesser degree (non-significant) in the left vmPFC (women; $M(\text{CS}) = -0.16$, men; $M(\text{CS}) = -0.11$; Fig. 5a).

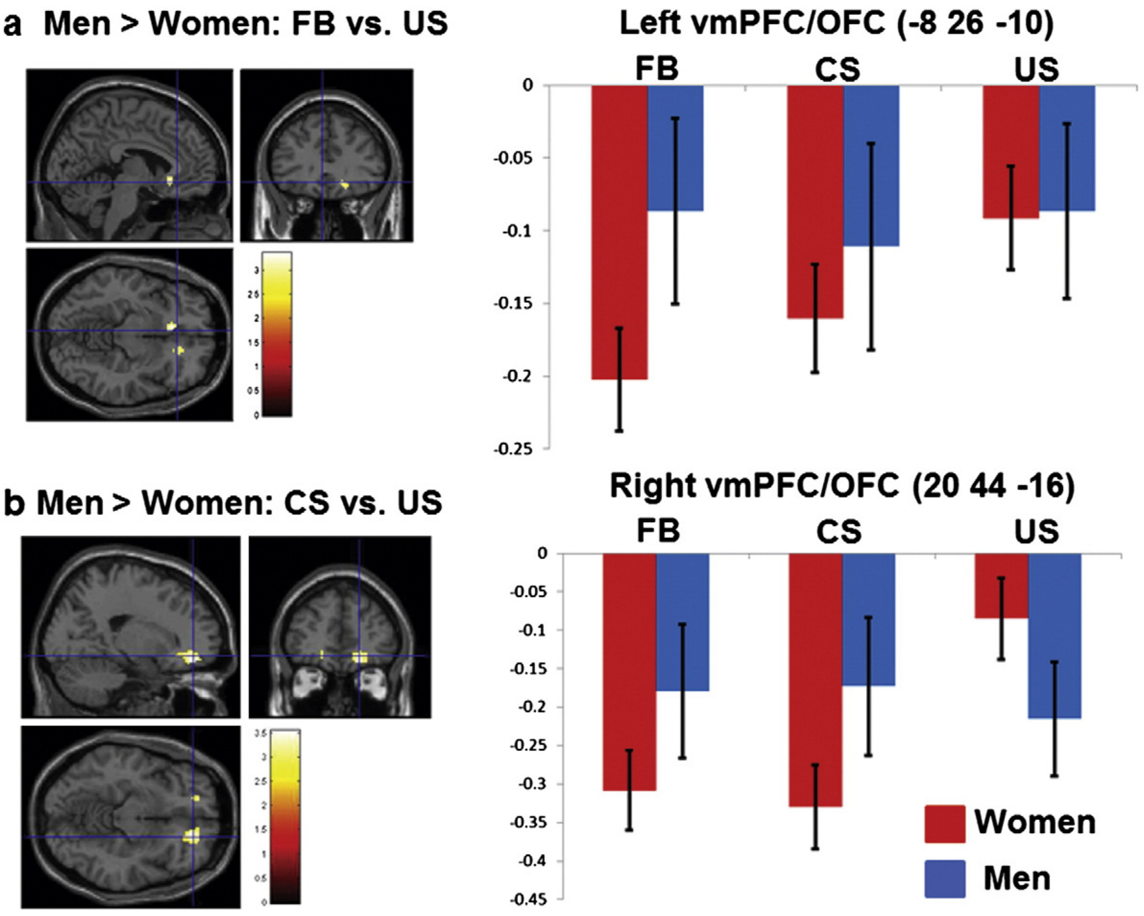


Fig. 5. Significant brain activity related to men > women. During the FB condition, relative to the US condition, women significantly deactivated the vmPFC bilaterally more than men (**a**). A similar pattern was found in the "CS vs. US" contrast (**b**). The post-hoc ANOVAs indicate that the while women deactivated these regions, men failed to deactivate. The height threshold of $p < 0.005$ (uncorrected) was used to recognize the activity in these brain regions, because we had *a priori* hypotheses for them.

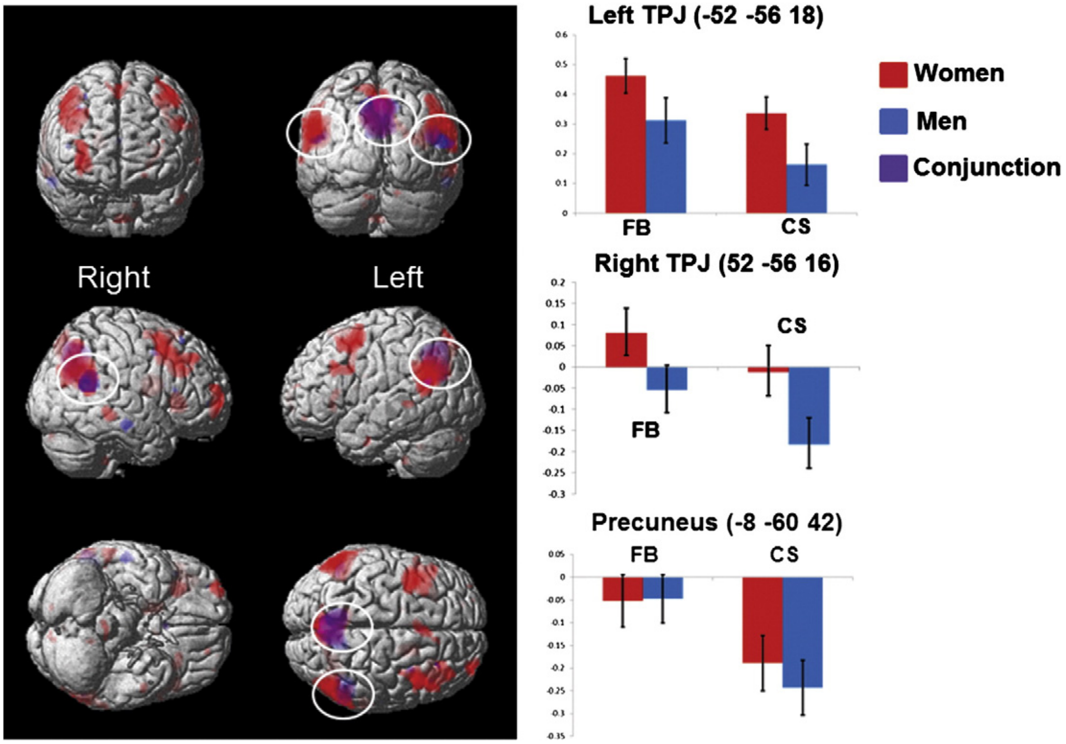


Fig. 6. Convergent activity between sexes. The convergent activity (of "FB vs. CS" contrast) between sexes was found in the TPJ bilaterally and left precuneus. The left TPJ activity survived the FWE correction with $p < 0.05$.

Conjunction analysis between the groups

As predicted, both sexes employed brain regions that have been repeatedly implicated in ToM; i.e., the bilateral TPJ and the precuneus for both the "FB vs. US" and "FB vs. CS" contrasts (Table 4; Fig. 6), but only the right TPJ for the "CS vs. US" contrast (Table 4).

Discussion

The present study is the first to examine sex differences in brain activity during false-belief reasoning. The patterns of brain activity of men and women were clearly different, although there were similarities between the sexes in some brain regions during the FB and CS conditions. Both groups recruited regions that have been repeatedly implicated in previous brain imaging studies of ToM, including the bilateral TPJ and precuneus. False-belief-related activity in the TPJ is consistent with several ToM brain imaging studies in adults (Gallagher et al., 2000; Saxe and Kanwisher, 2003; Apperly et al., 2004; Kobayashi et al., 2007) and children (Kobayashi et al., 2007). Specifically, the TPJ is active when people try to infer both true and false-beliefs in others (Saxe and Kanwisher, 2003). Moreover, right TPJ activity has been associated with both ToM (Saxe and Kanwisher, 2003; Saxe and Wexler, 2005) and empathy (Leibenluft et al., 2004; Völlm et al., 2006).

We also examined whether pragmatic language and ToM have independent contributions to false-belief reasoning. Consistent with previous behavioral and neuroimaging results (Ferstl and von Cramon, 2002; Ferstl et al., 2008; Mar, 2011; see also Frank, 2010), the present study did not find any sex difference in the neural basis of FB reasoning when we accounted for the coherence or pragmatic aspects in the stories through the CS condition. The results are intriguing and suggest that the neural basis of ToM and that of pragmatic language contribute equally to false-belief reasoning in both sexes.

The present study also found important differences between the sexes. Women activated the left mPFC and TPJ more than men in the "FB vs. US" comparison (in which we did not account for the pragmatic language). Specifically, one of the left mPFC regions falls in the superior part of the ar-mPFC subregion, whereas the other region falls in the pr-mPFC subregion (Amodio and Frith, 2006). The superior part of the ar-mPFC has been implicated in thinking about the mental states of unfamiliar others (Ochsner et al., 2004; Amodio and Frith, 2006). The pr-mPFC has been implicated in monitoring our own intentions in perspective-taking tasks (Grezes et al., 2004; Walton et al., 2004). Thus, women may use perspective-taking related strategies more when they think about false-beliefs in others than men. An equally likely explanation is that women use ToM more often than men during "normal" story comprehension (CS). Women may use elaborative inferences involving ToM to empathize with Nightman and Dayman because the point of communication is that listeners are receptive to communicative intent (Sperber and Wilson, 1995; Frith and Frith, 2006). This is consistent with prior research in which the left mPFC area has repeatedly been implicated in reading communicative intentions rather than literal meaning (Goel et al., 1997; Ferstl and von Cramon, 2002; Scott et al., 2003; Mar, 2011). Notably, deficits in this capacity are one of the hallmark impairments in individuals with ASC (Baron-Cohen, 1987, 1988; Tager-Flusberg, 2000; Charman, 2003). Increasing evidence suggests that girls develop verbal and communication skills faster (Baron-Cohen et al., 1999; Halpern et al., 2007). These results are consistent with finding that there is a strong correlation between ToM and pragmatic language skills (Miller, 2006; Ferstl et al., 2008; Frank, 2010; Mar, 2011), in which girls are consistently found to be more advanced than boys (Eriksson et al., 2012). These results are also consistent with the finding that higher order social strategic reasoning (with more iterated steps of thinking, such as the second-order false-belief reasoning) recruits more dorsal parts of the mPFC (Coricelli and Nagel, 2009).

Through our post-hoc analysis, we found that women deactivated the vmPFC/OFC during the FB condition relative to the US, while men did not. Several studies indicate that the midline regions (including the vmPFC and mPFC) are active during resting state when people are thinking about their own thoughts or are self-referencing (suggesting activity in the default network: Raichle et al., 2001). However, unlike the mPFC and other midline structures, the vmPFC becomes further deactivated when internally directed attention is directed externally by cognitively demanding tasks, so that participants have to temporarily shut down self-referencing (Iacoboni, 2006). Our results suggest that women may have less difficulty than men in disengaging from self-referencing or internally-directed thoughts during false-belief reasoning.

A similar failure of deactivation has been observed in individuals with ASC (Iacoboni, 2006; Kennedy et al., 2006). For instance, individuals with ASC do not deactivate vmPFC during the emotional Stroop task (Bush et al., 1998), relative to typically-developing individuals (Kennedy et al., 2006). Moreover, the degree of deactivation in the vmPFC has been found to be negatively correlated with severity of ASC symptoms (less deactivation is associated with more severe symptoms: Kennedy et al., 2006). This parallels the findings of the present study, in that the men in our study failed to deactivate vmPFC. Overall, this is consistent with the EMB hypothesis, in that the men are showing more ASC-like neural response patterns than the women that we studied.

Another intriguing finding is that we did not find any ToM-related activity in the IFG, which has been implicated in affective empathy (Dapretto et al., 2006; Schulte-Rüther et al., 2007, 2008). Because the IFG is one of the regions where human mirror neurons are densely located, it has been hypothesized that empathy is supported by the human mirror neuron system (hMNS) (Schulte-Rüther et al., 2008). Our results suggest that the hMNS hypothesis is not necessarily applicable when it comes to false-belief reasoning/ToM (Saxe, 2006). These results are also consistent with the hypothesis that the neural network subserving the affective empathy is different from that of the cognitive empathy system: the former involves modality-specific mirror neuron regions such as the IFG (Spunt and Lieberman, 2013) and phylogenetically older system such as amygdala and other limbic structures (Singer, 2006) as well as the vmPFC (Völlm et al., 2006), while the latter involves the ToM regions such as the mPFC (Spunt and Lieberman, 2013). Nonetheless, to understand the precise relationship between the neural basis of ToM and that of hMNS/empathy, more brain imaging studies that explore both of these systems may be needed.

The present research found significant differences in the neural basis of ToM between the sexes. This raises the question of where these differences originate. A compelling biological theory posits that exposure to fetal androgens may be critical. Males produce twice as much fetal testosterone (FT) (Auyeung et al., 2009; Knickmeyer and Baron-Cohen, 2006) and FT exposure affects the brain development (Lombardo et al., 2012), leading to the male-typical brain, the extreme form of which is the underconnectivity between the brain structures needed for ToM and social reasoning (Baron-Cohen, 2011). FT influences not only maturation of brain structures (Chura et al., 2010; Lombardo et al., 2012) but also development of brain function (Lombardo et al., 2011). A recent study has found elevated FT and related fetal steroids in children later diagnosed with autism (Baron-Cohen et al., 2014a).

In contrast, a social constructionist hypothesis attributes sex differences to differences in the socio-cultural expectations and influence on gender roles (Goffman, 1977; Lorber, 1994; Charman et al., 2002). The way parents, caregivers, peers and siblings interact with their toddlers and children may exacerbate the small differences that exist between sexes at birth (Eliot, 2009). In support of this hypothesis, mothers talk more to girls than to boys (Dunn et al., 1987), and older siblings express emotional states more often to girls than to boys (Brown et al., 1996). Across cultures, boys are encouraged to strive toward higher social achievements and competitiveness, while girls are encouraged to maintain harmony and empathic relationships with others (Eisenberg and Fabes, 1998). The social and biological accounts are of course not incompatible. Early in development FT exposure might set an initial masculinization of neural organization, and socio-cultural expectation may amplify these differences in later development. It has also been hypothesized that superior temporal sulcus that is implicated in ToM is also important for social cognition (Thompson et al., 2005). More neurodevelopmental studies are needed to determine exactly how each of these factors contributes toward sexual dimorphism in ToM.

One potential limitation of our study is that some of the story stimuli include minor atypicalities in word order, and most of them were in present tense (see **Supplementary Table**). Originally, the word order of each story was written to be congruent with a Japanese version of the same story. The Japanese story task has been used in CKF and her colleagues' previous studies (e.g., Kobayashi et al., 2006, 2008). Most stories are in present tense because we intend to use these stimuli to compare ToM processing in adults relative to children. As in our previous studies, these potential confounds are offset by the fact that all of the participants completed the same stories. Nonetheless, we recommend that our results be replicated in future studies that use fully age appropriate tasks.

Another potential limitation of the present study is that it compared community samples of nonclinical men and women, and did not include individuals with ASC. As such, application of our results to the EMB hypothesis should be undertaken with caution. We note that Valla et al. (2010) found that men consistently score higher in systemizing and lower in empathizing measures (in line with the EMB model) but women's scores were more variable. These results suggest that there may be more variability in women's ToM/pragmatic capacity. Therefore, it is important that our results be replicated in a substantially larger sample. This would allow comparison of high-E participants of both sexes and high-S participants of both sexes, which would shed light on the relative contribution of sex and E–S traits to the neural processing of ToM. The inclusion of a comparison group of individuals with ASC would help to anchor these E–S indicators with respect to autism, which would further inform the EMB hypothesis.

In conclusion, the present study is the first to investigate sex differences in the neural basis of false-belief reasoning, one aspect of the cognitive component of empathy. Results of our conjunction analyses suggest that bilateral TPJ and precuneus are involved in understanding ToM in both sexes. We also found that on average women show greater activation of key ToM regions, the left mPFC and the left TPJ, and deactivate the bilateral vmPFC. While one of our aims was to examine an independent contribution of pragmatic language for ToM brain basis, we were not able to find such a contribution. Instead, our results suggest significant overlaps between the ToM and pragmatic language networks in both sexes. Nonetheless, the greater FB-specific activity in the left mPFC in women may indicate that women utilize pragmatic language and communicative resources more than the men during false-belief reasoning. On the other hand, reduced deactivation in the vmPFC in men may suggest that men do not deactivate internally directed thoughts or self-reflection as automatically as women. This is a trait that men may share, to some degree, with individuals with ASC. With respect to the distinction between the cognitive empathy and affective empathy, our results suggest that cognitive empathy (ToM) employs similar but different neural network from the affective empathy network. Our results also suggest that on average women activate networks associated with both cognitive empathy (indicated as more activation in the mPFC) and affective empathy (indicated as deactivation in the vmPFC) networks more than men, and this difference may partly account for women's advantage in pragmatic language skills and ToM. Taken together, these results suggest support for the EMB hypothesis (but with a caveat as we described above). To further analyze the relationship between sex dimorphism and etiology of various forms of psychopathology, it will be important to investigate the neural basis of false-belief reasoning in men and women with different psychiatric conditions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2014.09.041.

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