

Research Article

It's the Thought That Counts

Specific Brain Regions for One Component of Theory of Mind

Rebecca Saxe^{1,2} and Lindsey J. Powell¹¹Department of Psychology, Harvard University, and ²Department of Brain and Cognitive Sciences, MIT

ABSTRACT—*Evidence from developmental psychology suggests that representing the contents of other people's thoughts and beliefs depends on a component of reasoning about other minds (theory of mind) that is distinct from the earlier-developing mental-state concepts for goals, perceptions, and feelings. To provide converging evidence, the current study investigated the substrate of the late-developing process in adult brains. Three regions—the right and left temporo-parietal junction and the posterior cingulate—responded selectively when subjects read about a protagonist's thoughts, but not when they read about other subjective, internal states or other socially relevant information about a person. By contrast, the medial prefrontal cortex responded equivalently in all of these story conditions, a result consistent with a broader role for medial prefrontal cortex in general social cognition. These data support the hypothesis that the early- and late-developing components of theory of mind rely on separate psychological and neural mechanisms, and that these mechanisms remain distinct into adulthood.*

In the classic false-belief test, preschoolers are told a story like this: “Sally puts her ball in a basket and leaves; Anne takes the ball from the basket and puts it in a box.” The children are then asked, “When Sally comes back, where will she look for her ball?” Four-year-olds know that Sally will look for the ball in the basket, where Sally *thinks* the ball is. Younger children consistently predict the opposite: They expect Sally to look for her ball in the box, where the ball really is (Wellman, Cross, & Watson, 2001; Wimmer & Perner, 1983).

These results, and substantial related evidence, have led psychologists to suggest that a representational theory of mind

emerges over the course of development. Research suggests that infants and young children understand mental-state concepts like desires, goals, perceptions, and feelings (e.g., Phillips, Wellman, & Spelke, 2002; Repacholi & Gopnik, 1997; Woodward, 1998). However, not until the age of 4 do children seem to understand concepts like belief—concepts that require understanding that mental representations of the world may differ from the way the world really is. Developmental psychologists have therefore hypothesized that the later-developing system for representing the specific (representational) contents of mental states, such as beliefs, is a distinct component of human understanding of other minds (Bartsch & Wellman, 1995; Flavell, 1988; Leslie, 1994; Perner, 1991; Tager-Flusberg & Sullivan, 2000; Wellman & Cross, 2001; for a review, see Saxe, Carey, & Kanwisher, 2004).

We predicted that the attribution of thoughts and beliefs—characteristic of the late-developing component of theory of mind—and the attribution of other internal subjective states might recruit different sets of brain regions. The current study was designed to directly contrast the attribution of beliefs (or representational mental states) with the attribution of other, earlier-developing mental-state concepts, as identified by developmental psychologists.

Previous functional neuroimaging studies have identified a set of brain regions putatively involved in reasoning about other minds. These regions include right (R) and left (L) temporo-parietal junction (TPJ), medial prefrontal cortex (MPFC), posterior cingulate cortex, and the amygdala (e.g., Castelli, Happé, Frith, & Frith, 2000; Fletcher, Happé, Frith, Backer, & Dolan, 1995; German, Niehaus, Roarty, Giesbrecht, & Miller, 2004; Goel, Grafman, Sadato, & Hallett, 1995; Mitchell, Mason, Macrae, & Banaji, in press; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004; Saxe & Kanwisher, 2003). Following tradition in developmental psychology, many of these previous studies have contrasted false-belief conditions that elicit theory-of-mind reasoning with control conditions that require physical or mechanical inferences (Fletcher et al., 1995; Goel et al., 1995;

Address correspondence to Rebecca Saxe, Department of Brain and Cognitive Sciences, MIT 46-4019, Cambridge, MA 02138, e-mail: saxe@mit.edu.

Saxe & Kanwisher, 2003). Other studies have required subjects to attribute communicative intentions (Walter et al., 2004) or pretend mental states (German et al., 2004). However, no study has yet directly contrasted the attribution of beliefs (or representational mental states) with that of other, earlier-developing mental-state concepts.

We therefore designed new stimuli, each highlighting a different aspect of reasoning about another person: (a) *Appearance* stories required detecting the presence of another person and representing socially relevant information about that person; (b) *bodily-sensations* stories elicited attribution of invisible, subjective, or internal states, characteristic of early-developing components of theory of mind; and (c) *thoughts* stories described the contents of another person’s thoughts or beliefs, specifically the function of the later-developing component of theory of mind. The response to these conditions was investigated both in a whole-brain analysis and in regions-of-interest (ROI) analyses constrained to regions determined to be associated with theory of mind, identified by a contrast between false-belief and false-photograph stories (Saxe & Kanwisher, 2003).

We predicted that if the late-developing component of theory of mind remains distinct in adulthood, then one or more of the brain regions previously associated with reasoning about other minds would be recruited for thoughts stories, but not for bodily-sensations stories. By contrast, a brain region subserving both early- and late-developing components of theory of mind would be recruited for both of these story conditions. We also predicted that brain regions involved specifically in the attribution of physical feelings would be recruited just for the bodily-sensations stories, and that brain regions involved more broadly in representing socially relevant information about a protagonist would be recruited equally for all three story types.

METHOD

Story stimuli were designed to fit three conditions (for examples, see Table 1):

TABLE 1
Sample Stimuli

Story type		
Appearance	Bodily sensations	Thoughts
Joe was a heavy-set man, with a gut that fell over his belt. He was balding and combed his blonde hair over the top of his head. His face was pleasant, with large brown eyes.	Sheila skipped breakfast because she was late for the train to her mother’s. By the time she got off the train, she was starving. Her stomach was rumbling, and she could smell food everywhere.	Nicky knew that his sister’s flight from San Francisco was delayed ten hours. Only one flight was delayed so much that night, so when he got to the airport, he knew that flight was hers.
Maria had olive skin and long, black hair, which she always wore in a braid. She was tall and thin with long legs. She always wore sandals, which revealed neat, red-painted toenails.	Marcus had been sick for three days. He had felt weak and had a high fever. On the fourth day his fever broke, and he woke up feeling cool and alert.	Rob tied his dog’s leash to a lamppost while he went into a store to buy coffee. When he came out, his dog had run across the street. He guessed that the leash had come untied.

- Appearance stories included a detailed description of the protagonist’s physical and social characteristics. No explicit subjective states (e.g., feelings) or mental states (e.g., thoughts) were mentioned, but subjects were free to form an impression of the protagonist’s character and dispositions.
- Bodily-sensations stories described the protagonist’s subjective physical feelings. Although these stories described vivid, internal experiences and the relation between those feelings and behavior, they did not include the contents of the protagonist’s thoughts or beliefs, or any intentional mental state (in the philosophical sense, of having an object or state of affairs as content). By using such stories, we departed from the common practice of developmental psychological studies of early- versus late-developing components of theory of mind, which have mostly investigated the attribution of perceptions, goals, and emotions, rather than sensations (but see Perner, 1991). Perceptions, goals, and emotions can all be understood either as connections between the agent and the world (the lean interpretation) or as attitudes of the agent to a part of the world as represented in that agent’s mind (the rich interpretation). Young children seem to use the lean interpretation until around age 4, when the more sophisticated rich interpretation becomes available, along with the concept of beliefs. It is not clear a priori whether adults would use the lean, early-developing interpretation or the rich, later-developing interpretation in attributions of perceptions, goals, and emotions (Keysar, Lin, & Barr, 2003). We chose to write stories about sensations because among attributable subjective internal states, they are least susceptible to a rich, representational interpretation.
- Thoughts stories explicitly described the beliefs and reasoning of the protagonist. These stories required subjects to represent the contents of the protagonist’s beliefs and thoughts, a function that is typical of the later-developing component of theory of mind.

Stories in the three conditions were equated for average number of words (33). Average reading time was measured in a

pilot experiment ($n = 17$). The pilot subjects also completed a survey judging their empathy for or identification with the protagonist in each story; responses were made on a Likert scale from 1 to 10.

Twelve naive, right-handed adults (ages 19–26 years, 9 women) participated in the functional magnetic resonance imaging (fMRI) study for payment. All subjects were native English speakers, had normal or corrected-to-normal vision, and gave written informed consent in accordance with the requirements of internal review boards at Massachusetts General Hospital and MIT. Subjects were scanned at 3 T (at the Massachusetts General Hospital scanning facility in Charlestown, MA) using twenty-six 4-mm-thick near-axial slices covering the whole brain. Standard echoplanar imaging procedures were used (TR = 2 s, TE = 40 ms, flip angle = 90°).

Stories were projected onto a screen via Matlab 5.0 running on an Apple G4 laptop computer. The full text of each story was displayed for 10 s, in white 24-point font on a black background. Presentation of each story was followed by a 12-s fixation block. Two stories from each condition (including two conditions not analyzed here) were presented per run, and the order of conditions within each run was counterbalanced within and across subjects. Subjects saw two to five runs, each lasting 4 min and 14 s. Subjects were instructed to read the stories and press a button when they had finished reading. Comprehension rather than speed was emphasized. However, because of a technical error, reading times inside the scanner were not collected. In addition, every subject participated in four runs of the localizer experiment, in which false-belief and false-photograph stories were presented, as described in Saxe and Kanwisher (2003, Experiment 2).

The fMRI data were analyzed with SPM99 (<http://www.fil.ion.ucl.ac.uk/spm/spm99.html>) and in-house software. Individual subjects' data were motion corrected and normalized onto a common brain space (the Montreal Neurological Institute, MNI, template). The data were then smoothed using a Gaussian filter (full width half maximum = 5 mm), and high-pass filtered during analysis. Both fMRI experiments used a blocked design and were modeled using a boxcar regressor.

Both whole-brain and tailored ROI analyses were conducted. The localizer experiment was used to define ROIs. Percentage signal change during story presentation (adjusted for hemodynamic lag) in each of these independent ROIs was then compared across the three experimental conditions. Because the data defining the ROIs were independent from the data used in the repeated measures statistics, Type I errors were drastically reduced.

RESULTS

Average reading times were significantly shorter for the false-belief stories (2.6 s) than for the false-photograph stories (2.9 s), $t(11) = 4.15, p < .002, p_{\text{rep}} = .99, \eta^2 = .61$. In the pilot study

using the new stimuli, the average reading times for thoughts stories (9.8 s) and appearance stories (9.8 s) did not differ, $t(16) < 1$; the bodily-sensations stories ($M = 9.0$ s) were read more quickly than the appearance stories, $t(16) = 3.02, p < .05$, but not the thoughts stories, $t(16) = 1.73$, n.s. Bodily-sensations stories were given higher empathy scores ($M = 6.1$) than appearance stories ($M = 4.6$), $t(16) = 1.96, p < .07, p_{\text{rep}} = .88, \eta^2 = .20$, and thoughts stories ($M = 4.7$), $t(16) = 2.34, p < .04, p_{\text{rep}} = .99, \eta^2 = .25$, which did not differ from each other, $t(16) < 1$. These results suggest that in any brain region, a differential blood-oxygenation-level-dependent (BOLD) response to the thoughts stories would not reflect either time on task or imaginative-emotional identification with the protagonists, but rather would reflect the attribution of thought contents specific to those stories.

Localizer Experiment: Group Results

A whole-brain random effects analysis of the data from the localizer experiment replicated results of previous studies using the same task (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). Higher BOLD response during false-belief scenarios than during false-photograph scenarios was observed in RTPJ, LTPJ, MPFC, posterior cingulate (PC), and the amygdala (see Fig. 1; see Table 2 for a complete listing of the brain regions showing significant results).

Localizer Experiment: Individual-Subject ROIs

ROIs recruited more for false-belief than false-photograph stories were identified in individual subjects ($ps < .0001$, uncorrected) in the RTPJ (12/12 subjects), PC (12/12 subjects), and LTPJ (9/12 subjects). The average peak voxels in MNI coordinates were as follows—RTPJ: [53–54 17], PC: [2–60 27], and LTPJ: [–48–57 25]. The differential response in the MPFC was less reliable in individual subjects. However, the MPFC was of interest because of the previous suggestion that reasoning about other minds might be predominantly, or even uniquely, subserved by medial prefrontal regions (e.g., Gallagher & Frith, 2003; Mitchell et al., in press). Therefore, in order to find MPFC regions of interest, we reduced the threshold for the localizer contrast to $p < .001$. At this reduced threshold, three different ROIs were identifiable within MPFC (cf. German et al., 2004): ventral MPFC (8/12 subjects), average peak voxel at [1 63 2]; middle MPFC (7/12 subjects), average peak voxel at [–1 62 19]; and dorsal MPFC (8/12 subjects), average peak voxel at [–2 56 35]. Activation in the amygdala was observed in less than half of the individual subjects, even at the lowered threshold, so ROI analyses in the amygdala could not be conducted.

Main Experiment

Three of the ROIs—RTPJ, LTPJ, and PC—showed a significantly greater response to the thoughts stories compared with the

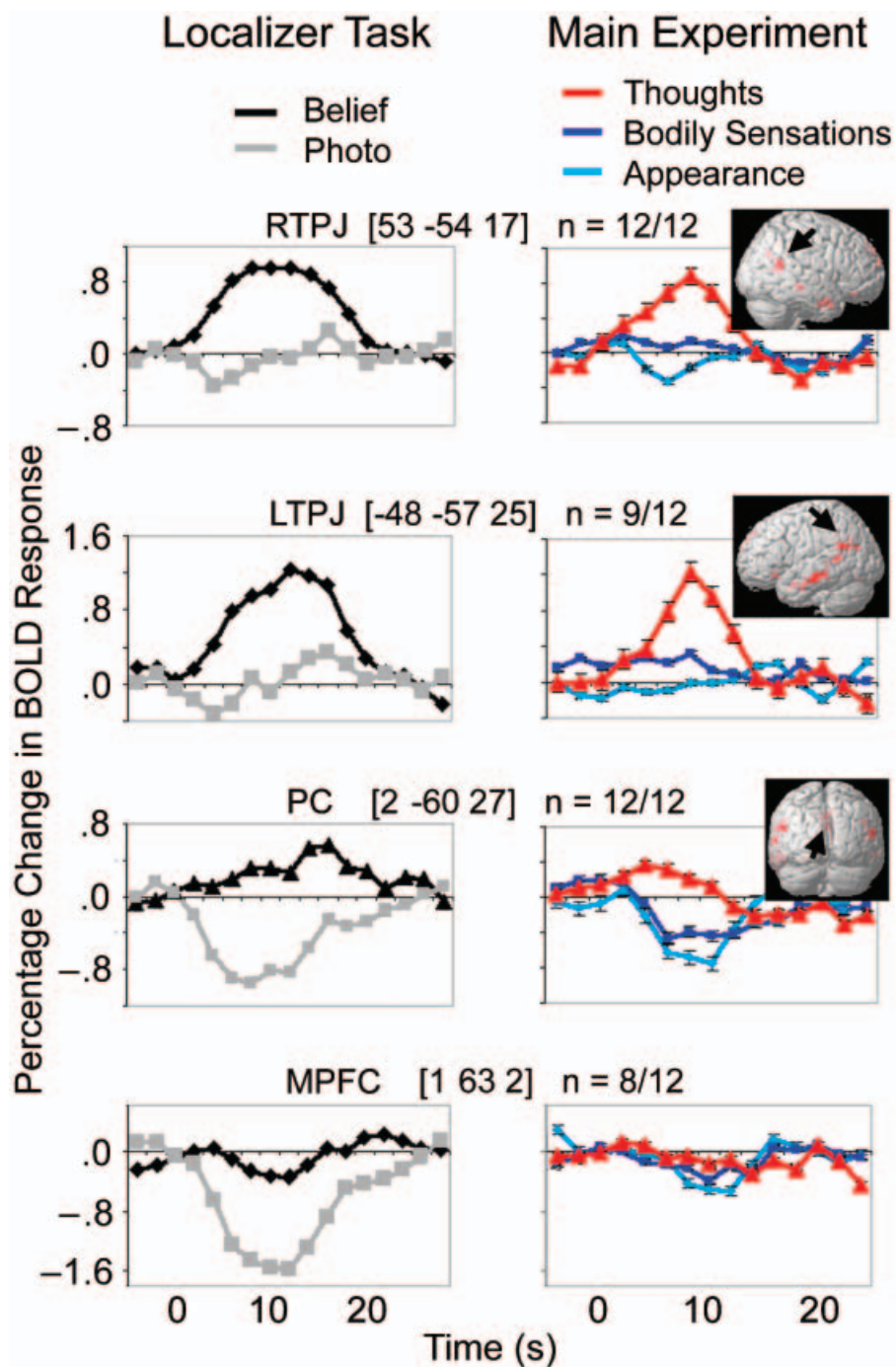


Fig. 1. Average blood-oxygenation-level-dependent (BOLD) response for the localizer task (left) and the main experiment (right). Results are shown for right and left temporo-parietal junctions (RTPJ and LTPJ), posterior cingulate (PC), and ventral medial prefrontal cortex (MPFC). The insets at the right show the locations of activation in RTPJ, LTPJ, and PC ($n = 12$, $p < .001$, uncorrected) identified in a whole-brain random effects analysis (thoughts > bodily sensations and appearance). The n s and coordinates refer to the individual-subject regions of interest derived from the localizer task.

appearance and bodily-sensations stories, which did not differ from each other or from fixation (see Fig. 1). This profile in the RTPJ and LTPJ was significant after a correction for multiple comparisons. The percentage signal change for all regions and all

conditions and t tests comparing pairs of conditions (thoughts vs. sensations and sensations vs. appearances) are shown in Table 3.

None of the three MPFC ROIs responded significantly differently to stories in the thoughts, bodily-sensations, or ap-

TABLE 2

Group Results From the Contrast Between Conditions (False Belief > False Photograph) in the Localizer Experiment

Region	MNI coordinates (maximum voxel)	Z	Number of voxels
Posterior cingulate	[12 -66 21]	5.00	535
Right temporo-parietal junction	[60 -57 15]	4.96	182
Ventral medial prefrontal cortex	[-9 51 3]	4.62	138
Dorsal medial prefrontal cortex	[0 45 48]	4.49	11
Right superior temporal sulcus	[60 -18 -21]	4.02	20
Right amygdala	[30 6 -15]	3.90	14
Left temporo-parietal junction	[-51 -57 27]	3.85	35
Left amygdala	[-27 0 -21]	3.73	6
Right anterior superior temporal sulcus	[51 12 -33]	3.70	13

Note. The table presents results from a whole-brain random effects group analysis. For each region listed, the contrast was significant, $p < .001$, uncorrected. MNI = Montreal Neurological Institute.

pearances conditions (Table 3 and Fig. 1). In addition, we conducted separate analyses to compare results for each MPFC region and RTPJ (2 regions \times 3 conditions) and obtained a significant region-by-condition interaction in each case: RTPJ versus ventral MPFC, $F(2, 14) = 6.49$, $p < .01$; RTPJ versus middle MPFC, $F(2, 12) = 5.24$, $p < .03$; RTPJ versus dorsal MPFC, $F(2, 14) = 15.68$, $p < .001$.

Confirming this profile, a random effects analysis of the whole brain (thoughts > bodily sensations and appearance, $p < .001$, uncorrected) revealed RTPJ, LTPJ, and PC activation, with peaks at [57 -54 18], [-60 -54 24], and [0 -51 39], respectively (Fig. 1 insets). In addition, we conducted a whole-brain analysis to look for brain regions significantly activated by the bodily-sensations stories (bodily sensations > appearance, $p < .001$, uncorrected). This contrast revealed a distinct profile: the right

supramarginal gyrus (SMG), cingulate cortex, and cerebellum, with peaks at [60 -33 27], [-15 -66 -18], and [-12 -48 -12], respectively. Figure 2 shows one of these regions, the right SMG, and the anatomical relationship between the SMG and the nearby but distinct RTPJ.

DISCUSSION

Late-Developing Components

Substantial evidence from developmental psychology suggests that representing the contents of other people's beliefs depends on a distinct component of theory of mind, separate from the earlier-developing competence with attributing goals, perceptions, and feelings (Bartsch & Wellman, 1995; Flavell, 1988; Perner, 1991; Saxe, Carey, & Kanwisher, 2004). The current

TABLE 3

Percentage Signal Change (Averaged Over Each Story) in Six Regions of Interest

Region	Story type			Contrast	
	Appearance	Sensations	Thoughts	Thoughts > sensations	Sensations > appearance
Late-developing theory of mind					
Right temporo-parietal junction	-0.16	0.09	0.61	$t(11) = 4.78$, $p < .001$, $p_{\text{rep}} = .99$, $\eta = .675$	$t(11) = 1.86$, n.s., $p_{\text{rep}} = .91$, $\eta = .239$
Left temporo-parietal junction	-0.04	0.20	0.78	$t(8) = 4.68$, $p < .002$, $p_{\text{rep}} = .99$, $\eta = .733$	$t(8) = 1.75$, n.s., $p_{\text{rep}} = .88$, $\eta = .278$
Posterior cortex	-0.53	-0.64	-0.15	$t(11) = 3.06$, $p < .05$, $p_{\text{rep}} = .99$, $\eta = .459$	$t(11) = 0.97$, n.s., $p_{\text{rep}} = .68$, $\eta = .080$
General social cognition					
Ventral medial prefrontal cortex	-0.32	-0.22	-0.06	$t(7) = 0.72$, n.s., $p_{\text{rep}} = .56$, $\eta = .069$	$t(7) = 0.70$, n.s., $p_{\text{rep}} = .55$, $\eta = .065$
Middle medial prefrontal cortex	-0.17	-0.23	0.05	$t(6) = 1.16$, n.s., $p_{\text{rep}} = .73$, $\eta = .184$	$t(6) = -0.30$, n.s., $p_{\text{rep}} = .32$, $\eta = .015$
Dorsal medial prefrontal cortex	0.18	-0.19	0.10	$t(7) = 1.82$, n.s., $p_{\text{rep}} = .89$, $\eta = .322$	$t(7) = -2.82$, n.s., $p_{\text{rep}} = .94$, $\eta = .426$

Note. Boldface indicates a significantly higher response in the thoughts condition than in the sensation condition.

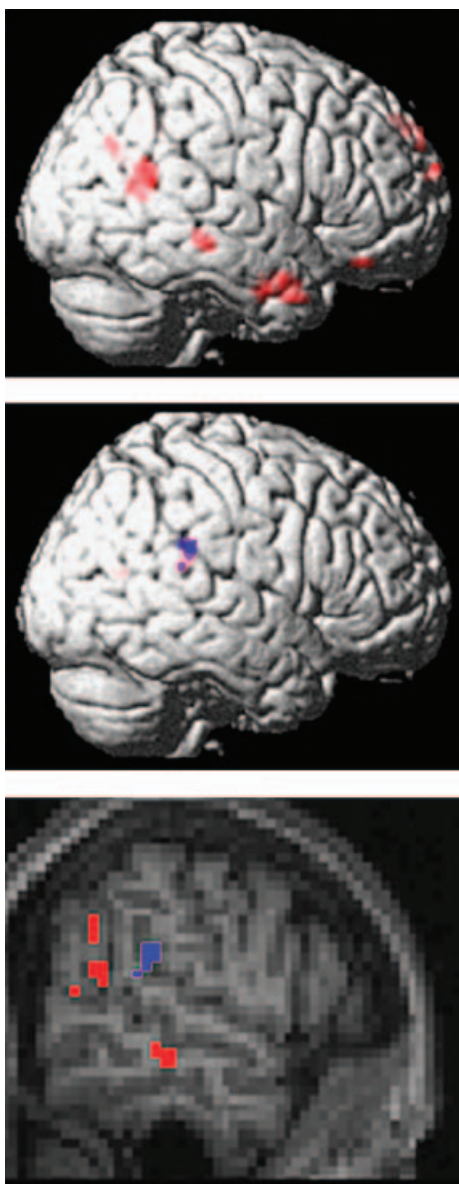


Fig. 2. Substrates of early versus late components of theory of mind. The top and middle illustrations show the results of whole-brain random effects analyses: voxels with higher response during thoughts stories than during either bodily-sensations or appearance stories, shown in red (top), and voxels responding more during bodily-sensations stories than during appearance stories, shown in blue (middle; both $ps < .001$, uncorrected). The illustration at the bottom is a single slice contrasting the right temporo-parietal junction activation for thoughts stories (red) and right supramarginal gyrus activation for bodily-sensations stories (blue).

neuroimaging data reinforce and extend this claim. We found that three regions of the adult human brain—RTPJ, LTPJ, and PC—were recruited selectively when subjects read stories about a protagonist’s thoughts or beliefs, but not when they read about subjective, internal physical feelings or other socially relevant information, such as appearance and personality attributes (see also Saxe & Wexler, 2005). These data are consistent with the hypothesis that the late-developing component

of theory of mind relies on a different mechanism than the early-developing component (or components) does, and that these mechanisms remain distinct into adulthood.

The current results are insufficient, in isolation, to establish the specific and selective roles of the RTPJ, LTPJ, and PC in mental-state reasoning. The stimuli in the current study were designed to manipulate one dimension of theory-of-mind reasoning—that is, the kind of information about the protagonist contained in a short verbal text. Important converging evidence is emerging from experiments using nonverbal stimuli (Aichorn, Perner, Kronblicher, Staffen, & Ladurner, in press; Samson, Apperly, Chiavarino, & Humphreys, 2004), and further investigation is ongoing in our laboratory.

Already, though, the functional profile of these three regions, and especially the RTPJ (see also Saxe & Wexler, 2005), appears remarkably specific. In the wider literature of cognitive science, whether and which specific cognitive functions are associated with distinct cortical loci remains controversial. One influential hypothesis posits that whereas components of perceptual and motor representations (or “input” and “output” systems—Fodor, 1983) are localized to discrete brain regions, higher cognitive functions rely on distributed networks of brain regions, each of which participates in more than one function. By contrast, here we report that the BOLD response in the RTPJ is associated with a highly specific cognitive function that is neither perceptual nor motoric in nature: the ability to attribute thoughts to another person.

Early-Developing Components

The current data suggest that a candidate neural correlate for one early-developing theory-of-mind competence—attributing subjective physical feelings—is the right SMG, recruited when subjects read about feelings such as hunger, thirst, relaxation, or exhaustion. The right SMG has been previously implicated in the attribution of basic emotions (happy, sad, angry, afraid, surprised). Damage to it produces deficits in judgments of facial emotions (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000) and emotional prosody (Adolphs, Damasio, & Tranel, 2002), and in the attribution of emotions to point-light walkers (Heberlein, Adolphs, Tranel, & Damasio, 2004). Damasio, Heberlein, and their colleagues suggested that the right SMG plays a role in covertly modeling the observed emotion in the subject’s own motor and sensory systems; that is, it has a role in re-creating and attributing the physical feelings associated with each emotion.

Other aspects of the early-developing component of theory of mind, such as attributing goals and perceptions, may rely on additional brain regions not identified here. In particular, evidence from both neuroimaging and single-cell recordings in macaques suggests that the superior temporal sulcus responds to visual presentations of intentional actions and gaze shifts (e.g., Allison, Puce, & McCarthy, 2000; Pelphey, Singerman, Allison, & McCarthy, 2003; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004).

MPFC

The current study also helps to differentiate and clarify the role of MPFC. As in German et al. (2004), we divided MPFC into three (ventral, middle, and dorsal) ROIs. Unlike in RTPJ, LTPJ, and PC, in the three MPFC ROIs the BOLD response was the same whether subjects read stories about a protagonist's appearance and character, subjective feelings, or thoughts and beliefs. That is, MPFC recruitment is not restricted to reasoning about another person's thoughts (the later-developing component of theory of mind) or even subjective, internal states in general, but may be involved more broadly in representing socially or emotionally relevant information about another person.

Recent data are consistent with this proposal (e.g., Aichorn et al., in press; Saxe & Wexler, 2005). For example, Mitchell et al. (in press) reported selective activation of a region of MPFC (similar to the dorsal ROI in the current results) when subjects read mental adjectives ("curious"), relative to when they read abstract adjectives ("celestial") or words referring to human or animal body parts ("liver") or object parts ("pedal"). Like our appearance stories, the mental adjectives used by Mitchell et al. described enduring characteristics of a person, but not the particular transient contents of the person's thoughts and beliefs. Also, patients with selective damage to MPFC have been found to be unimpaired on tests of reasoning about other minds (e.g., Bird, Castelli, Malik, Frith, & Husain, 2004), whereas 3 patients with damage to LTPJ were found to be selectively impaired in attributing beliefs (Samson et al., 2004; although note that the tests used to assess the two patient populations differed considerably).

CONCLUSION

In all, the division of labor among regions of cortex in the brains of healthy human adults appears to reflect the developmentally distinct components of theory of mind. RTPJ in particular, as well as LTPJ and PC, appears to be recruited just when subjects reason about another person's thoughts and beliefs, the same concepts that mark the transition from the early- to the late-developing component of theory of mind. The human brain regions identified here as being involved selectively in the attribution of mental states may be important sites of damage in autism and Asperger's syndrome, as well as of phylogenetic and ontogenetic change.

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