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Activity in Right Temporo-Parietal Junction is Not Selective for Theory-of-Mind

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Recent researchers have suggested that a region of right temporo-parietal junction (RTPJ) selectively subserves the attribution of beliefs to other people (Saxe R, Kanwisher N. 2003. People thinking about thinking people: fMRI investigations of theory of mind. NeuroImage. 19:1835–1842; Saxe R, Powell LJ. 2006. It's the thought that counts: specific brain regions for one component of theory of mind. Psychol Sci. 17:692–699; Saxe R, Wexler A. 2005. Making sense of another mind: the role of the right temporo-parietal junction. Neuropsychologia. 43:1391–1399). At the same time, a similar RTPJ region has been observed repeatedly in a variety of nonsocial tasks that require participants to redirect attention to task-relevant stimuli (e.g., Corbetta M, Shulman GL. 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat Rev Neurosci. 3:201–215; Serences JT, Shomstein S, Leber AB, Golay X, Egeth HE, Yantis S. 2005. Coordination of voluntary and stimulus-driven attentional control in human cortex. Psychol Sci. 16:114–122). However, because these 2 sets of tasks have never been compared within the same participants, it remains unclear whether these observations refer to the exact same region of RTPJ or may instead involve neighboring regions with distinct functional profiles. To test the claim that there is a region of RTPJ selective for belief attribution, the current study used functional neuroimaging to examine the extent to which cortical loci identified by a "theory-of-mind localizer" also distinguish between trials on a target detection task that varied demands to reorient attention (i.e., a version of the "Posner cueing task"). Results were incompatible with claims of RTPJ selectivity for mental state attribution. Regardless of whether regions were defined from group analyses or were individually tailored for each participant, RTPJ activity was also modulated by the nonsocial attentional task. The overlap between theory-of-mind and attentional reorienting suggests the need for new accounts of RTPJ function that integrate across these disparate task comparisons.

Keywords: social cognition, mentalizing, attention, Posner cueing task, functional magnetic resonance imaging

Introduction

Successful human interaction requires not only the insight that other people are mental agents guided by their beliefs, feelings, and goals, but also the ability to infer the current content of those mental states, that is, what exactly it is that another person is thinking, feeling, or intending. Over the past decade, a highly consistent observation in cognitive neuroscience has been the demonstration that this human ability to mentalize about others engages a set of brain regions that includes medial prefrontal cortex (MPFC), temporo-parietal junction, and superior temporal sulcus as well as temporal poles and amygdala (for reviews, see Adolphs 1999, 2001; Frith and Frith 2001; Gallagher and Frith 2003; Blakemore et al. 2004; Mitchell, Mason et al. 2005; Mitchell 2006). However, despite the consistency of these observations, little is understood about the specific nature of the cognitive processes subserved by these brain regions or how those processes contribute to overall human mentalizing abilities.

Recently, Saxe and her colleagues (Saxe and Kanwisher 2003; Saxe and Wexler 2005; Saxe and Powell 2006) have claimed forward progress in understanding the workings of one of these regions: right temporo-parietal junction (RTPJ). In a series of studies, these researchers have suggested that RTPJ contributes to social cognition by selectively handling a specific form of mental state content, namely, the *beliefs of another person*. In each of these studies, the researchers have used a "theory-of-mind localizer" task to isolate an RTPJ region that responds more robustly to stories that require understanding a person's beliefs than those that require understanding various modes of physical representation (such as photographs and maps). Activity in this region was then measured while participants engaged in a range of tasks that required social-cognitive processing other than understanding another person's beliefs, for example, reading information about others' desires, physical appearance, or cultural background. In each case, RTPJ responded more strongly during stories that required inferences about another person's beliefs than during stories that contained other kinds of social content. The preferential response of this region during belief stories has prompted claims that "temporo-parietal junction is selectively involved in reasoning about the contents of other people's minds" (Saxe and Kanwisher 2003, p. 1835); "the response of the RTPJ is highly specific to the attribution of mental states" (Saxe and Wexler 2005, p. 1397); and "the BOLD response in the RTPJ is associated with a highly specific cognitive function . . . the ability to attribute thoughts to another person" (Saxe and Powell 2006, p. 697).

Although this research has done an exhaustive job of demonstrating that RTPJ contributes to social cognition only when perceivers must infer the beliefs of another person, it has, importantly, neglected substantial evidence that this region may also subserve a set of attentional processes that are not specific to social contexts. In a literature that has developed in parallel with the work of Saxe and colleagues, researchers have repeatedly observed increased RTPJ activity when perceivers must break their current attentional set to reorient to task-relevant stimuli (Corbetta et al. 2000, 2005; Corbetta and Shulman 2002; Shulman et al. 2002; Astafiev et al. 2003, 2006; Kincade et al. 2005; Serences et al. 2005). For example, Corbetta et al. (2000) observed greater RTPJ activity when participants were miscued about the future location of a target stimulus, interpreting this activity as the redeployment of attention away from the miscued location and toward the newly relevant location. In a similar vein, Serences et al. (2005) recently observed enhanced RTPJ activity when participants were distracted by stimuli that shared a salient feature (color) with a target, also suggesting that this region selectively shifts attention away from stimuli that possess task-relevant features. Similar accounts of RTPJ contributions to attention have been prompted by the neuropsychological literature on spatial neglect (Mesulam 1981), a syndrome in which patients fail to orient naturally to the side of space contralateral to the lesion and which has been specifically linked to lesions of temporo-parietal junction (Vallar and Perani 1987; Vallar 1993).

Several observations suggest that the temporo-parietal region purported by Saxe and colleagues to selectively subserve belief attribution may be one-and-the-same with the temporo-parietal region observed in investigations of attention. First, the temporo-parietal regions observed from theory-of-mind, attentional reorienting tasks, and the neglect syndrome all tend to be heavily right-lateralized (although bilateral activations have also been observed across all 3 research domains; see Corbetta and Shulman 2002; Saxe and Powell 2006). Second, the peak coordinates associated with theory-of-mind comparisons are entirely interspersed with those reported for attentional reorienting. Table 1 compares the peak RTPJ coordinates reported by Saxe and colleagues with those observed during a variety of attentional reorienting tasks. If the 2 sets of RTPJ regions are indeed functionally distinct from one another, greater variability should be expected between the peak coordinates associated with each of the 2 research domains than among experiments within a domain. However, consistent with the possibility that the 2 kinds of comparisons activate the same functional region in RTPJ, more variability in the location of these peak activations is observed among studies within each domain—both for studies of theory-of-mind (mean Euclidean distance = 8.97) and attention (mean Euclidean distance = 11.16)—than between domains: the Euclidean distance between the mean theory-of-mind peak (Montreal Neurological Institute [MNI] coordinates: 56, –54, 19) and the mean attention peak (55, –50, 26) is only 7.82.

Notwithstanding their strong claims about the functional selectivity of RTPJ for theory-of-mind, Saxe and colleagues do appear sensitive to the possibility that this region may subserve a broader set of attentional processes, acknowledging that "direct testing of the relationship between the [RTPJ] and selective attention is an important avenue for future work" (Saxe and Kanwisher 2003, p. 1840). The current study represents such work. Participants completed both the "theory-of-mind localizer" task as described by these researchers (Saxe and Kanwisher 2003; Saxe and Wexler 2005; Saxe and Powell 2006) and an attentional cueing task modeled on those used to identify RTPJ contributions to reorienting (Corbetta et al. 2000; Kincade et al. 2005; Astafiev et al. 2006). The attentional reorienting paradigm was a version of the "Posner cueing task" (Posner et al. 1984), in which participants are occasionally miscued about the location of a forthcoming target stimulus.

Following the analytic strategy of Saxe and her colleagues, statistical analyses first identified individually tailored regions of RTPJ on a participant-by-participant basis and then subsequently examined whether the response of these same voxels distinguished between 2 independent experimental conditions: in this case, trials on a nonsocial task, during which targets were cued either validly or invalidly. To the extent that the RTPJ region identified by the theory-of-mind task is indeed "selectively involved in reasoning about the contents of other people's minds," its activity should be insensitive to the distinctly nonsocial manipulations that compose the attentional cueing task. Results were incompatible with this claim of theory-of-mind selectivity: across a variety of analyses, the RTPJ region identified in the theory-of-mind task also distinguished between invalid and valid attentional cueing of nonsocial stimuli.

Method

Participants

Participants were 20 (11 female) right-handed, native English speakers with no history of neurological problems (mean age, 23.0 years; range, 19–29). Informed consent was obtained in a manner approved by both the Human Studies Committee of the Massachusetts General Hospital and the Institutional Review Board of Harvard University.

Behavioral Procedure

Attentional Cueing Task

Participants completed 2 tasks during scanning, the order of which was counterbalanced across participants. The "attentional cueing" task was modeled closely on the paradigm described by Corbetta et al. (2000), originally developed by Posner et al. (1984). During this task, participants indicated the location of a visual target stimulus that appeared in

Table 1
MNI coordinates and Euclidean distance between RTPJ regions-of-interest reported in theory-of-mind and attentional reorienting tasks

Study	*x*	*y*	*z*	1	2	3	4	5	6	7	8
1) Saxe and Kanwisher (2003)	54	−51	18		6.7	9.0	12.0	3.2	12.0	7.5	19.8
2) Saxe and Wexler (2005)	54	−54	24			11.2	6.3	9.8	6.8	7.3	14.7
3) Saxe and Powell (2006)	60	−57	15				16.9	9.2	16.9	14.0	25.6
4) Corbetta et al. (2000)	54	−52	30					15.1	1.4	8.1	8.7
5) Astafiev et al. (2006)	54	−50	15						15.1	9.7	22.7
6) Kincade et al. (2005)	55	−51	30							7.3	8.9
7) Serences et al. (2005)	56	−47	24								14.6
8) Shulman et al. (2003)	50	−49	37								

Note: Each column displays the Euclidean distance between the RTPJ coordinate reported by the study in that row and the RTPJ coordinate of the study with the corresponding number. The RTPJ coordinates of #1–3 (gray background) were reported from the comparison of belief > photographs; #4–6 were reported for the comparison of invalid > valid attentional cueing; #7 was reported for the comparison of distractors that were the same color as a task-relevant target > a different color from the target; and #8 was linked to target detection during motion and digit detection tasks. Coordinates for #4–8 were originally reported in the stereotactic space of Talairach and Tournoux and have been translated into MNI space for comparison purposes. Saxe and Kanwisher (2003) did not explicitly identify the stereotactic space to which their coordinates refer but are assumed to be in MNI space. The coordinate for Shulman et al. (2003) represents the mean of 3 RTPJ coordinates reported by these authors (45, −53, 43; 54, −42, 41; and 52, −52, 28). Critically, the mean distances of 1) the RTPJ peaks identified from theory-of-mind tasks and 2) the peaks identified from attention tasks are both greater than 3) the distance between the mean peak of each task domain.

either a cued or miscued location. Each trial began with the presentation of a green fixation cross, flanked on either side by a white-lined "box" against an otherwise black background. After 700 ms, the horizontal line of the cross was replaced with an arrow pointing to either the left or right box. The arrow remained onscreen for 800 ms, after which the stimulus reverted back to a simple fixation cross. After a variable interstimulus interval of 500–2000 ms, a white asterisk appeared in either the left or right box for 100 ms. On 75% of the trials the asterisk appeared in the box to which the arrow had pointed (valid trials), whereas on the remaining 25% of the trials the asterisk appeared in the box away from which the arrow had pointed (invalid trials). Participants were simply instructed to press a key (left or right) corresponding to the box in which the asterisk appeared. The remainder of the trial comprised the original display of a cross flanked by 2 empty white boxes. The length of this final phase varied from 400 to 1900 ms as a function of the interstimulus interval, such that the total length of each trial was 4000 ms. Participants completed a total of 160 trials (120 valid, 40 invalid), which were separated into 2 runs of 512 s each. To optimize estimation of the event-related functional magnetic resonance imaging (fMRI) response, trials were intermixed in a pseudorandom order and separated by a variable interval of 500–7500 ms (Dale 1999), during which participants passively viewed a fixation crosshair.

Theory-of-Mind Task

The "theory-of-mind" task was nearly identical to the localizer procedure used by Saxe and colleagues to isolate brain regions that are preferentially engaged during belief attribution (Saxe and Kanwisher 2003, Experiment 2; Saxe and Wexler 2005; Saxe and Powell 2006). During this task, participants read a total of 24 short vignettes that referred either to a person's false belief (*belief stories*) or to an outdated physical representation, such as a map or photograph (*photograph stories*). The stories were identical to those used by Saxe and colleagues and were presented using the timing parameters and font size reported in Saxe and Kanwisher (2003). Each story was presented for 10 s, after which the text was replaced with a question about the information in the story for an additional 4 s. For example, during one belief story participants read that, "Jenny put her chocolate away in the cupboard. Then she went outside. Alan moved the chocolate from the cupboard into the fridge. Half an hour later, Jenny came back inside." After 10 s, this text was replaced with the question, "Jenny expects to find her chocolate in the 1) fridge or 2) cupboard" and participants had 4 s to make their response before the end of the trial.

Photograph stories had the same logical structure as belief stories, but referred to physical, rather than mental, representations (Zaitchick 1990). For example, during one photograph story, participants read, "Here is a drawing she made of the original treehouse, 3 years ago. That was before the storm. We built a new treehouse last summer, but we painted it red instead of blue" and were then asked whether "the treehouse in the drawing is 1) red or 2) blue." Following Saxe and colleagues, half of the belief and half of the photograph stories were followed by questions of fact (e.g., where the chocolate actually is or what color the treehouse is in reality) rather than about the false belief or false physical representation. (The inclusion of stories that were followed by questions of fact leads to a curious situation in which many of the "belief" stories do not, in actual fact, involve any explicit reference to another person's mental states. For example, in the localizer task described by Saxe and colleagues, the story "This store is run by a cunning counterfeit jeweler; all the jewels are glass. Dina has just bought a ring here, with a beautiful red stone. She paid hundreds of dollars for it" is followed by a factual question about whether, "The red stone is Dina's ring is 1) glass or 2) ruby." Note that although this stimulus is classified as a "belief" story, respondents need not refer to the protagonist's false belief to answer the question correctly. Fortunately, secondary fMRI analyses that separated "fact" stories from those that asked explicitly about beliefs revealed no significant differences between these 2 types of "belief" stimuli in any of the regions discussed here.)

Trials were separated into 2 functional runs of 312 s, each of which comprised 6 belief and 6 photograph stories (this aspect of the design represents the only known deviation from earlier studies, in which trials were generally segregated into more than 2 runs and were often presented intermixed among other types of stimuli). Each participant viewed the stories in a different random order. Stories were separated by a 12-s intertrial interval, during which participants viewed a fixation crosshair.

Imaging Procedure

Imaging was conducted using a 1.5-Tesla Siemens Avanto scanner. A high-resolution T_1-weighted structural scan (magnetization prepared rapid gradient echo) was preceded by 4 functional runs (26 axial slices; 5 mm thick; 1 mm skip). Theory-of-mind runs consisted of 156 volume acquisitions; attentional cueing runs consisted of 256 volume acquisitions. Functional scanning used a gradient-echo echo-planar pulse sequence ($TR = 2$ s; $TE = 35$ ms; 3.75 × 3.75 in-plane resolution). Using PsyScope software (Cohen et al. 1993) for Macintosh OS X, stimuli were projected onto a screen at the end of the magnet bore that participants viewed by way of a mirror mounted on the head coil. A pillow and foam cushions were placed inside the head coil to minimize head movement.

fMRI data were preprocessed and analyzed using SPM99 (Wellcome Department of Cognitive Neurology, London, UK). First, functional data were time-corrected for differences in acquisition time between slices for each whole-brain volume and realigned to correct for head movement. Functional data were then transformed into a standard anatomical space (3-mm isotropic voxels) based on the ICBM 152 brain template (MNI). Normalized data were then spatially smoothed (8-mm full-width-at-half-maximum) using a Gaussian kernel. Trials were conditionalized as belief versus photograph for the theory-of-mind task and invalid versus valid for the cueing task. Statistical analyses were performed using the general linear model. For the theory-of-mind task, a blocked (epoch) design was modeled using a boxcar function that extended for the entire 14-s period during which the story and question were presented. For the cueing task, an event-related design was modeled using a canonical hemodynamic response function and its temporal derivative. Both models included regressors for additional covariates of no interest (a session mean and a linear trend). These analyses were performed individually for each participant, and resulting contrast images were subsequently entered in a second-level analysis treating participants as a random effect. Peak coordinates were identified using a statistical criterion of 25 or more contiguous voxels at a voxel-wise threshold of $P < 0.001$. This cluster size was selected on the basis of a Monte Carlo simulation (S. Slotnick, Boston College) of our brain volume that found that this cluster extent cutoff provided an experiment-wise threshold of $P < 0.05$, corrected for multiple comparisons. Parameter estimates were extracted from each of these regions for further statistical analysis using analysis of variance (ANOVA); unless otherwise indicated, ANOVA procedures used a 2-tailed threshold of $P < 0.05$.

In addition to these group analyses, an individually tailored RTPJ region-of-interest was examined, defined separately for each participant from the comparison of *belief* > *photograph* stories. Although an attempt was made to follow the procedures used by earlier researchers to define RTPJ in individual participants (Saxe and Kanwisher 2003; Saxe and Wexler 2005; Saxe and Powell 2006), no information has been provided regarding the minimum number of contiguous voxels used to consider a region to be a legitimate locus of activation (e.g., would a single activated voxel in RTPJ be sufficient to be considered a suitable region-of-interest?). The current study addressed this limit by adopting an iterative procedure to define individually tailored RTPJ regions. Specifically, for each participant, the whole-brain contrast of *belief* > *photograph* was first visualized at a statistical threshold of $P < 0.05$, uncorrected (for all individual-subject analyses, regions were required to comprise 5 or more contiguous voxels). This same contrast was then repeated iteratively at progressively more conservative statistical thresholds (i.e., 0.05, 0.02, 10^{-1}, 10^{-2}, 10^{-3}, 10^{-4}, 10^{-5}, 10^{-6}, and 10^{-7}) until the maximally circumscribed RTPJ region-of-interest was identified for the participant. This RTPJ region had to meet the following 3 criteria: 1) the cluster had to appear near the dorsal extent of the right superior temporal sulcus; 2) the cluster could not exceed 25 contiguous voxels but must comprise a minimum of 5 contiguous voxels; and 3) a cluster meeting these criteria did not survive at the next lowest statistical threshold (e.g., if a cluster that met these criteria appeared at $P < 10^{-4}$ but no such cluster was visualized at $P < 10^{-5}$, the participant's RTPJ region was defined as the contiguous voxels visualized at $P < 10^{-4}$). The iterative nature of this procedure made it a fairly conservative way to identify the smallest, most circumscribed RTPJ region that was significantly more activated for *beliefs* > *photographs*.

Accordingly, the choice of procedures ensured that the current study comprised the identical theory-of-mind task, was conducted at the same imaging center, used a sample from the same participant population (individuals in the Cambridge/Boston area), included the same preprocessing steps, and was analyzed using the same software (SPM99) as Saxe and colleagues (Saxe and Kanwisher 2003; Saxe and Wexler 2005; Saxe and Powell 2006).

Results

Behavioral Data

Because of a technical error, response latencies were not recorded from one participant. On the attentional cueing task, the remaining 19 participants responded more quickly to valid ($M = 354$ ms) than invalid ($M = 409$ ms) trials, $t(18) = 3.53$, $P < 0.0025$, demonstrating that they used the arrow as a cue to the future location of the target. These response latencies closely resemble those reported by earlier researchers; for example, Corbetta et al. (2000) reported means of 380 and 426 ms for valid and invalid trials, respectively.

On the theory-of-mind task, participants responded more quickly to questions about belief stories ($M = 2696$ ms) than to questions about photograph stories ($M = 2881$ ms), $t(18) = 2.36$, $P < 0.05$. These response latencies are similar to those reported by Saxe and Kanwisher (2003, Experiment 2) and Saxe and Powell (2006) for belief stories (both *M*s = 2.6 s) and photograph stories (*M*s = 2.8 and 2.9 s, respectively). Response latencies for these trial types were not reported by Saxe and Wexler (2005).

Random-Effects fMRI Analyses

Cueing Task

The effect of attentional reorienting was first examined in the contrast of *invalid* > *valid* trials, which identified a single region in RTPJ (see Fig. 1 and Table 2). The peak voxel associated with this region (MNI coordinates: 60, –48, 27) was highly similar to that reported by Corbetta et al. (2000) for the same comparison (MNI coordinates converted from Talairach space: 54, –52, 30). No regions were identified by the reverse contrast of *valid* > *invalid*.

Theory-of-Mind Task

For the theory-of-mind task, differences between *beliefs* > *photographs* were first identified in a group-level (random-effects) analysis. This contrast identified 3 of the regions previously linked to the theory-of-mind task—RTPJ, MPFC, and precuneus (Saxe and Kanwisher 2003; Saxe and Wexler 2005; Saxe and Powell 2006)—as well as a region of superior frontal gyrus (Fig. 2 and Table 2). No regions were identified by the reverse contrast of *photograph* > *beliefs*.

Combined Task Analysis

Of central concern was the extent to which the RTPJ region that was identified from the theory-of-mind task also subserved the attentional processes modulated by the cueing task. To examine this question, the parameter estimates associated with responses during the attentional cueing task were extracted from all 4 regions-of-interest identified from the comparison of *belief* > *photograph* on the theory-of-mind task. ANOVA was then used to examine whether any of these regions demonstrated greater activation for *invalid* > *valid* trials on the attentional cueing task. No difference was observed in the MPFC, precuneus, or the superior frontal gyrus (all *P* values > 0.62); in fact, the pattern of results trended toward greater activity for valid trials in each of these regions (Fig. 3*A*). However, as predicted, RTPJ showed reliably greater activation for invalid than valid trials, $t(19) = 1.83$, $P < 0.05$, one tailed (Fig. 3*A*,*B*). The presence of a qualitatively different pattern of results across regions was confirmed by a significant 3-way interaction of Region (RTPJ, MPFC, precuneus, superior frontal gyrus) × Task (theory-of-mind, cueing) × Trial Type (belief/photo, invalid/valid), $F_{3,57} = 2.98$, $P < 0.05$. Moreover, further analysis demonstrated that the RTPJ difference between *invalid* > *valid* trials did not differ as a function of whether participants first performed the attentional cueing task (*M* diff = 0.0233) or the theory-of-mind task (*M* diff = 0.0115), $t(18) = 0.61$, $P > 0.54$.

An additional random-effects analysis was conducted to protect against the possibility that the particular RTPJ region identified from *beliefs* > *photographs* may have inadvertently included a neighboring, but functionally distinct, region that is selective for attention. That is, perhaps a RTPJ region subserving attentional reorienting is located adjacent to one selective for inferring beliefs; as such, the statistical thresholds used in the random-effects analysis ($P < 10^{-3}$, 25 voxels in extent) may have conjoined 2 different RTPJ regions each with a distinct functional profile. However, this possibility was belied by random-effects analyses conducted at more stringent statistical thresholds, which limited analysis to voxels in which activity was modulated especially strongly for *beliefs* > *photographs*. At $P < 10^{-4}$, a 36-voxel RTPJ region was visualized for this contrast; at $P < 10^{-5}$, an 11-voxel RTPJ region was visualized. In both of these conservatively defined RTPJ regions, the difference

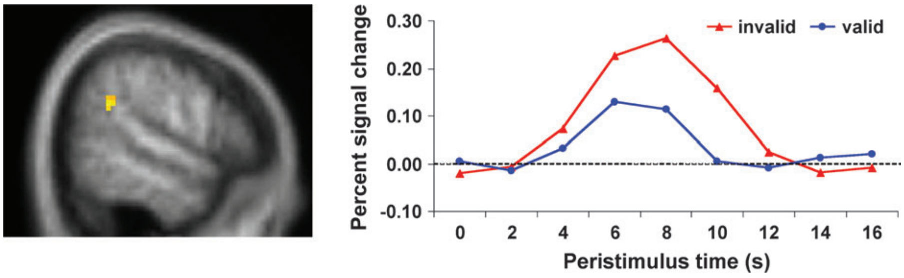

Figure 1. Replicating earlier research, a right-lateralized region of temporo-parietal junction (60, –48, 27) demonstrated greater activation for invalidly cued than validly cued trials on an attentional cueing task. The left panel of the figure displays this RTPJ region overlaid on a sagittal slice of participants' mean normalized brain. The right panel of the figure displays hemodynamic time courses extracted from this region, representing the BOLD response associated with invalid (red triangles) and valid (blue circles) trials.

between *invalid* > *valid* was not only statistically significant, but numerically greater than that observed in the region defined at $P < 10^{-3}$: for both regions, $t(19) \approx 2.13$, $P < 0.025$, one tailed, demonstrating that the RTPJ voxels that responded maximally to the contrast of *beliefs* > *photographs* also differentiated between trials on the attentional cueing task.

In addition, to guard against the loss of spatial localization that results from applying a smoothing kernel during preprocessing, we reanalyzed normalized blood oxygen level–dependent (BOLD) images that were obtained prior to smoothing during preprocessing. Consistent with the above analyses, random-effects analysis of these nonsmoothed data revealed a 17-voxel region of RTPJ (51, −48, 24) that was more activated for both *beliefs* > *photographs* ($P < 10^{-9}$) as well as *invalid* > *valid* cueing trials ($P < 0.04$, one-tailed). Finally, the RTPJ region obtained from the random-effects analysis of *invalid* > *valid* trials also demonstrated significantly greater activation for *beliefs* > *photographs* ($P < 10^{-4}$).

Analysis of Individually Tailored Regions-of-Interest

As frequently pointed out by Saxe and colleagues, because the precise neuroanatomical location of functionally selective brain regions may vary considerably from participant to participant, group-based analyses that average across different people may blur the functionally selective profile of one region with that of a neighboring one (for a summary, see Saxe et al. 2006). Such blurring could support a spurious conclusion that 2 different contrasts yield the same region when, in fact, a researcher has inadvertently conjoined voxels from 2 adjacent, but functionally distinct, regions.

One strategy for circumventing this problem is to define regions-of-interest individually for each participant, and then test whether those same voxels differentiate among some additional set of experimental conditions. The iterative procedure described above (see Method) identified a region of

Table 2
Peak voxel and number of voxels for brain regions obtained from theory-of-mind and attentional cueing tasks ($P < 0.05$, corrected).

Region	*x*	*y*	*z*	Voxels	*t*-Value
Cueing task: invalid > valid					
RTPJ	60	−48	27	25	4.58
Theory-of-Mind task: belief > photo					
RTPJ	54	−51	27	99	6.92
Posterior cingulate	3	−57	24	381	6.53
Superior frontal gyrus	24	27	57	35	5.73
MPFC	6	60	30	107	5.51

Note: *t* values reflect the statistical difference between the 2 conditions, as computed by SPM99. Coordinates refer to the MNI stereotaxic space.

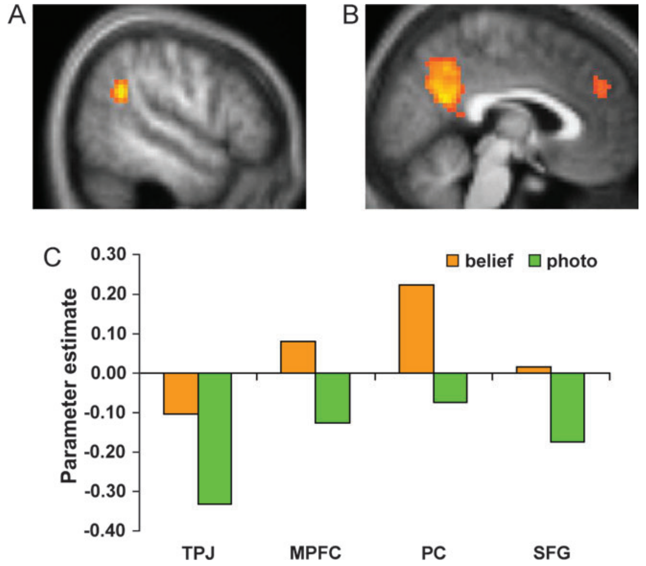

Figure 2. Group analysis of the theory-of-mind task revealed greater activation for *belief* > *photograph* stories in 4 regions. Panel *A* displays a region in RTPJ, and Panel *B* displays regions in both MPFC and precuneus (PC). A fourth region in superior frontal gyrus (SFG) is not displayed. Panel *C* displays the parameter estimates extracted from each of these 4 regions for belief (left, orange bars) and photograph (right, green bars) stories.

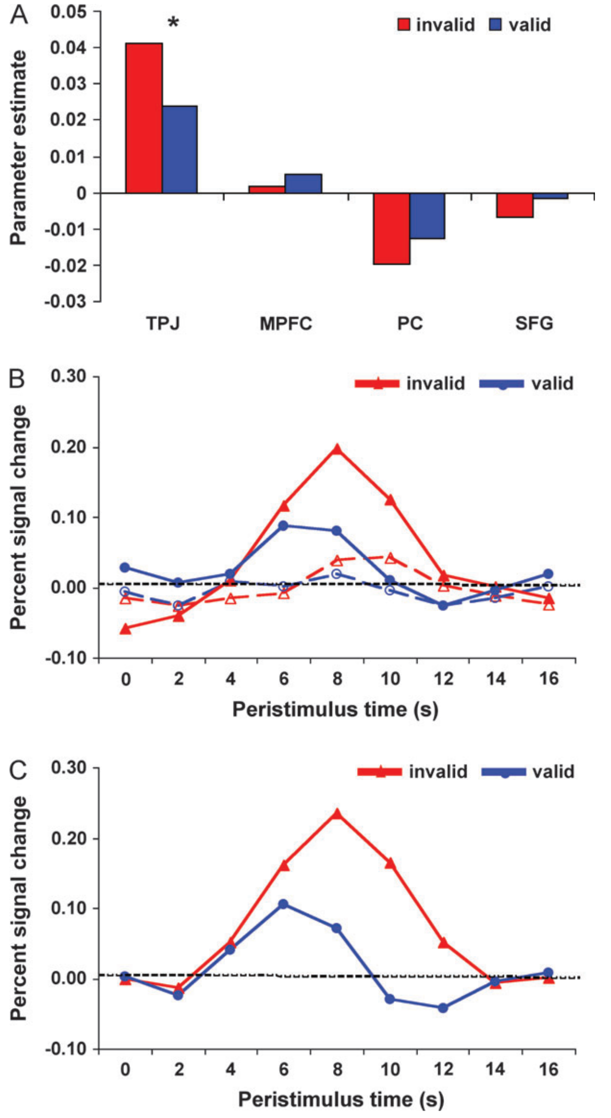

Figure 3. The 4 regions obtained from group comparisons on the theory-of-mind localizer (see Fig. 2) were tested for differences on the attentional cueing task. Panel *A* displays the parameter estimates extracted from these 4 regions for invalid (left, red bars) and valid (right, blue bars) trials. The RTPJ was the only region in which activity was significantly greater for invalid than valid trials. Panel *B* displays hemodynamic time courses extracted from both RTPJ (solid lines) and, for comparison, from MPFC (dashed lines) for invalid (red triangles) and valid (blue circles) trials. Panel *C* displays the mean hemodynamic response for invalid and valid trials in individually tailored RTPJ regions, identified separately for each participant from the contrast of *belief* > *photograph*. PC, percuneous; SFG, superior frontal gyrus.

RTPJ that responded more to beliefs than photographs in 18 of 20 participants. In the 2 remaining participants, no RTPJ region was visualized even at a threshold of $P < 0.05$. Table 3 lists the coordinates of the peak voxel in RTPJ for each of the participants for whom such a region was identified. Importantly, the pattern of results in these individually defined RTPJ regions closely paralleled that from the group-based analysis. Most critically, the difference between *invalid* > *valid* trials on the attentional cueing task was significant, $t(17) = 2.91$, $P < 0.01$, confirming that the RTPJ region identified for *beliefs* > *photographs* was not selective for beliefs but also subserved the attentional processes operationalized by the cueing task (Fig. 3*C*). As in the region defined from the group analysis, the difference between *invalid* > *valid* trials did not differ as a function of whether participants first performed the attentional cueing task (M diff = 0.0299) or the theory-of-mind task (M diff = 0.0297), $t(16) < 0.01$.

Paralleling the group-based analysis, several additional analyses were conducted to protect against the possibility that selected RTPJ clusters may have incorrectly incorporated voxels that more rightly belonged to a region with a different functional profile or, relatedly, that selected clusters were simply "bad" representatives of the RTPJ region in which activity is selective for belief attribution. When analysis was restricted to participants for whom the RTPJ was defined at a statistical threshold that was at least as conservative as that of Saxe and colleagues (i.e., participants in which the RTPJ was identified at $P < 10^{-4}$ or lower), a significant difference between *invalid* > *valid* was still observed, $t(9) = 4.25$, $P < 0.0025$. In fact, those participants whose RTPJ was defined at these conservative thresholds were marginally more likely to show a difference on the cueing task (M diff = 0.047) than participants whose RTPJ could only be identified at more lenient thresholds (M diff = 0.010), $t(16) = 1.97$, $P < 0.07$.

Moreover, regions that were relatively distant from the peak voxel defined in the group analysis were not those that showed the greatest cueing effect. Specifically, the Euclidean distance between the peak voxel of the individually defined regions and the peak voxel of the RTPJ region defined in the group analysis did not correlate with the difference between either *invalid* > *valid* ($r[16] = -0.09$) or *belief* > *photograph* ($r[16] = 0.04$). These secondary analyses weigh heavily against the possibility that the significant cueing effect observed in RTPJ was due to defining individual regions-of-interest in either a lenient or idiosyncratic manner.

Table 3
Peak voxel and number of voxels for individually tailored regions of RTPJ

Subject	x	y	z	Voxels	P-value	ToM	Cueing	Distance
s01*	57	−30	30	5	10^{-2}	0.37	0.10	21.42
s02	54	−57	24	16	10^{-5}	0.65	0.01	6.71
s03*	57	−51	30	19	10^{-7}	0.57	0.08	4.24
s04	54	−51	21	24	0.02	0.25	0.04	6.00
s06*	57	−51	48	17	10^{-2}	0.32	−0.04	21.21
s07	54	−66	15	14	10^{-5}	0.66	0.06	19.21
s09	54	−45	27	14	10^{-6}	0.67	0.08	6.00
s10*	60	−63	33	15	10^{-5}	0.62	0.05	14.70
s11	51	−45	27	14	10^{-6}	0.52	0.04	6.71
s13	48	−45	30	18	10^{-6}	0.74	0.04	9.00
s14*	63	−48	27	14	10^{-6}	0.69	0.08	9.49
s15	57	−54	30	19	10^{-6}	0.62	0.06	5.20
s16*	51	−48	27	10	10^{-3}	0.34	−0.02	4.24
s17	54	−60	45	18	10^{-3}	0.66	−0.02	20.12
s18*	60	−57	24	12	0.05	0.27	0.03	9.00
s19*	54	−54	24	21	10^{-3}	0.32	−0.01	4.24
s20	51	−60	21	13	10^{-7}	0.78	−0.03	11.22
s21*	60	−60	30	17	10^{-3}	0.37	0.00	11.22

Note: No RTPJ region was identified in 2 participants (s05 and s12). The P-value column reports the statistical threshold at which the region was defined. The ToM and cueing columns report the parameter estimate difference for *belief* > *photograph* and *invalid* > *valid*, respectively. The rightmost column reports the Euclidean distance from the peak voxel obtained from the group analysis (see Table 2). Asterisks indicate those participants who completed the ToM task prior to the cueing task.

Discussion

In the current study, participants performed 2 seemingly disparate tasks: 1) a theory-of-mind task that compared stories involving another person's beliefs with stories involving physical modes of representing the world (such as photographs) and 2) an attentional task in which an arrow typically served as a valid cue to the forthcoming location of a target but occasionally misdirected attention to an invalid location. Separate analysis of each of the 2 tasks produced results that were highly consistent with earlier studies. Specifically, the theory-of-mind task revealed greater response to belief stories than photograph stories in 3 regions previously observed for this comparison: RTPJ, MPFC, and precuneus. The attentional cueing task revealed greater activation for invalid than valid cues in a single region, RTPJ.

To test the claims of Saxe and her colleagues that the RTPJ region identified in the theory-of-mind task is selective for inferring the thoughts of others (Saxe and Kanwisher 2003; Saxe and Wexler 2005; Saxe and Powell 2006), further analysis focused on the extent to which activation in the RTPJ region that showed greater response for the theory-of-mind task also

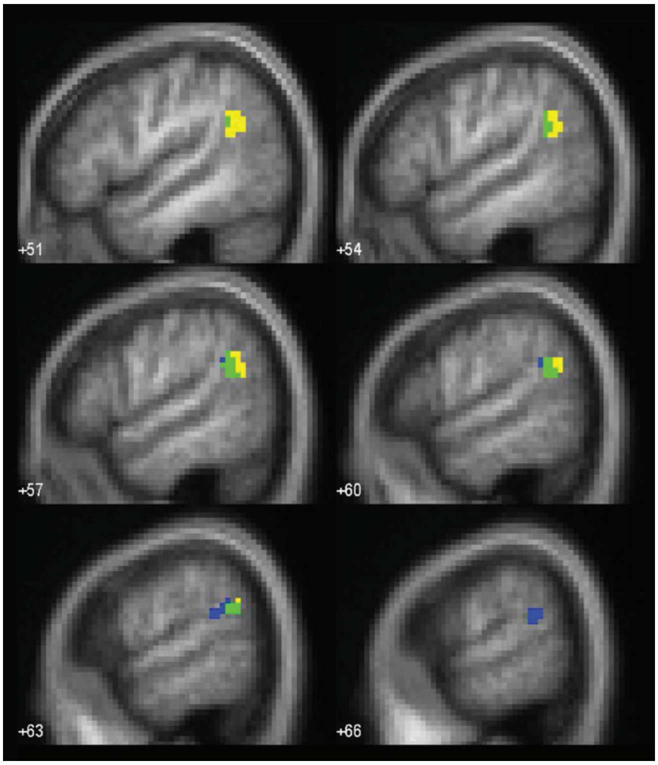

Figure 4. Overlap of the RTPJ regions obtained from the random-effects analysis of *belief* > *photograph* (yellow) and *invalid* > *valid* (blue). The green area represents the voxels that were identified from both contrasts (at $P < 0.001$, 25 voxels). As displayed in the graph, although the RTPJ regions defined from the 2 contrasts were largely overlapping, each included voxels that were not identified by the other contrast.

showed greater response for *invalid* > *valid* cueing. Regardless of whether clusters were defined from group analyses or individually for each participant, the RTPJ region identified in the theory-of-mind task also distinguished between invalid and valid trials on the attentional cueing task.

These results not only undermine the assertion that RTPJ is selective for inferring the beliefs of other people, but are also incompatible with any strong claim that this region participates selectively in social cognition, broadly construed. Greater activation in RTPJ was observed on a simple attentional cueing task in which no other people were relevant to the task: participants merely pressed 1 of 2 keys to indicate the location in which a target asterisk appeared. In so demonstrating that RTPJ activity is not selective for social cognition, the current results suggest that theory-of-mind and attentional reorienting may both require a solution to the same computational problem. That is, the observation that the same RTPJ region is engaged by these 2 tasks suggests the recruitment of a cognitive process that contributes to both belief attribution and attentional reorienting. Although the current study does not specify the exact nature of this shared process, it does suggest the need to develop a better conceptual account of what computational problems might jointly be faced by belief attribution and attentional reorienting and, subsequently, to test hypotheses about the processes that are deployed by the human mind to solve this particular cognitive challenge.

Further Considerations Regarding the Role of RTPJ in Attentional Processes

Although the comparison of trials on which the asterisk appeared in a miscued, relative to validly cued, location seems particularly unlikely to isolate anything approximating the beliefs of another person, one could conceivably maintain that the attentional cueing task does indeed manipulate a person's beliefs—namely, those of the participants themselves. In using the arrow as a valid attentional cue, participants could possibly be thought of as formulating a trial-by-trial "belief" about the future location of the target. On invalid trials, participants might be thought to be especially likely to rethink their original expectation about the cue location, reconsidering their own "false belief" about where they had anticipated the target would appear. Of course, such a reimagining of the attentional cueing task would still require a considerable overhaul of the theoretical claims of Saxe and colleagues, who have consistently discussed the role of the RTPJ as selective for considering the beliefs of *other* people.

Moreover, although such a theoretical reformulation might be possible, there are several reasons to prefer to explain the theory-of-mind task in terms of manipulations of attentional processes, rather than the other way around (i.e., attempting to explain the attentional cueing task in terms of social cognition). First, RTPJ involvement in attentional reorienting has recently been described by Serences et al. (2005) in a task that leaves even less room for the consideration of beliefs (either those of others or one's own) than the current attentional task. In this study, participants viewed a display of colored letters and were instructed to respond to letters of a particular color (e.g., red). Flanking the central display were distractor letters that were usually gray, but would occasionally be presented in either the same color as the to-be-identified target letters or a different color (e.g., green). Compared with distractors presented in a color that was completely task-irrelevant, same-color distractors elicited greater RTPJ activation at a locus that was within a few voxels of the peaks observed in the current study (MNI coordinates: 56, −47, 24). The authors interpret this RTPJ activation as reflecting participants' reorientation to the central task following attentional capture by the distracting stimuli. There seems to be very little about this task that would manipulate participants' beliefs, and although a side-by-side comparison between the theory-of-mind task and the Serences et al. paradigm has not been performed, it seems reasonable to expect that this task may engage the same RTPJ region observed in the current study.

Second, lesions to RTPJ have been associated most clearly with deficits of attention, not social cognition. Damage to the temporo-parietal junction commonly results in unilateral spatial neglect, a clinical syndrome marked by an individual's failure to orient naturally to the space contralateral to the lesion (Mesulam 1981). Interestingly, neglect is more common and pronounced following damage to temporo-parietal junction in the right than in the left hemisphere (Vallar and Perani 1987; Vallar 1993), consistent with the same tendency toward right-lateralization found in neuroimaging studies of attentional reorienting and theory-of-mind. At present, no published studies have examined the effects of RTPJ lesions on social cognition, although somewhat surprisingly, neuropsychological patients with damage to temporo-parietal junction in the *left* hemisphere do show deficits on the false belief task (Apperly et al. 2004, 2006; Samson et al. 2004). However, even if future research associates RTPJ damage with deficits in social cognition, the existing link between this region and the neglect syndrome simply suggests that attentional reorienting and theory-of-mind jointly rely on some common set of cognitive processes, not that this region is selective for the attribution of beliefs.

Third, similar right-lateralized TPJ loci have been observed in a number of tasks in which participants are asked to shift their egocentric viewpoint to that of another body, without the requirement to consider another person's mental states (Blanke et al. 2005; Arzy et al. 2006). For example, using evoked potential mapping, Arzy et al. identified a region of RTPJ that responded more strongly to body transformations that required participants to "rotate into" the perspective of a body facing them than to consider a simple mirror translation of their own perspective (also see Zacks et al. 1999). Moreover, Ruby and Decety (2001) observed greater RTPJ activation when participants imagined another person performing an action than imagining doing it themselves. Of relevance for future research will be an examination of whether these tasks—each devoid of any express need to reason about another's beliefs—also engage precisely the same RTPJ region observed for the 2 tasks used in the current study.

Fourth, if one is willing to view the attentional cueing task as a manipulation of participants' beliefs, it would be necessary to see a range of other cognitive tasks as "belief" tasks as well. In particular, it is unclear why participants would fail to develop relevant expectations about the physical representations that make up the false photograph portion of the theory-of-mind task. That is, if one postulates that RTPJ modulations on the attentional cueing task reflect manipulations of participants' beliefs about where targets will appear, it seems as though one should also expect to observe RTPJ activation for the kind of expectations prompted by false photograph trials (e.g., the "belief" that the treehouse would be blue in the drawing but red in actual fact).

Caveats and Potential Concerns

Although the current study was designed to mirror earlier studies of belief attribution as closely as possible, a number of empirical observations distinguish the results obtained here from those reported in earlier studies using the theory-of-mind localizer (Saxe and Kanwisher 2003; Saxe and Wexler 2005; Saxe and Powell 2006). Here, each of these deviations from the findings of earlier researchers is reviewed. In addition, this section preemptively addresses some of the critiques faced by other researchers who have challenged the notion of a brain region's selectivity for a particular kind of stimulus content (Kanwisher 2000).

First, at the statistical threshold ($P < 10^{-4}$) used by Saxe and her colleagues, the RTPJ was visualized in only half the participants in the current study, whereas these earlier researchers appear to report having identified this region in every one of their participants for the same comparison (although the number of participants showing a significant difference of *belief > photograph* in RTPJ is not stated explicitly in Saxe and Kanwisher 2003). The reason for this discrepancy is unclear, but may have to do with having scanned the current study at lower field strength (1.5 Tesla) than most of the participants reported by Saxe and colleagues (who were typically scanned at 3.0 Tesla). Critically, however, even when analysis was restricted to those 10 participants whose RTPJ was visualized at $P < 10^{-4}$ (i.e., the statistical threshold adopted by Saxe and colleagues), a significant difference was observed for *invalid > valid* trials on the attentional cueing task. (The difficulty encountered by outside researchers in obtaining the consistent effects reported by the developers of various "localizers" has something of a precedent. As reported by Kanwisher [2000], Gauthier et al. [2000] were able to identify an FFA in only 5 of 19 participants when using the criteria adopted by the Kanwisher group forfunctionally defining this region. That other labs seem unable to coax the reported intersubject consistency from these taskssuggests important limits to the usefulness of functional localizersas a research methodology.)

Second, the responses observed in RTPJ for belief and photograph stories both took the form of "deactivations" relative to baseline. Although modulations in lateral parietal regions frequently appear as such negative deflections (Gusnard and Raichle 2001; Raichle et al. 2001; Mitchell et al. 2002), Saxe and her colleagues have generally reported that their theory-of-mind stories produce positive-going "activations" in RTPJ. Again, the reason for the discrepancy between data sets is unclear, especially because the same baseline task (passive visual fixation) was used across researchers. Possibly, the divergence reflects some aspect of statistical analysis that differs between laboratories, such as whether fixation periods were explicitly coded in the analysis (fixation was not coded explicitly in the SPM design matrices used to analyze the current data). Resolution of this issue will require collaboration across researchers to identify the exact point of departure between laboratories. However, it is important to note that whether the responses of RTPJ during the theory-of-mind task appear as activations above or deactivations below baseline does not bear on the observation that activity in this region also distinguishes between invalid and valid cueing trials.

Third, the results demonstrated that the RTPJ difference between *belief > photograph* was considerably greater than the difference associated with *invalid > valid* ($F_{1,19} = 24.69$, $P \approx 10^{-5}$). However, in the current study, this interaction is rendered completely meaningless by the differences in the designs of the theory-of-mind and attentional cueing tasks. That is, the blocked design used for the theory-of-mind task is inherently more powerful (i.e., capable of detecting statistical differences) than the event-related design necessitated by the attentional cueing paradigm. Indeed, as evident in Table 3, the strength of the modulations from baseline observed for the theory-of-mind task was a full order of magnitude greater than that observed for the attentional cueing task. Unfortunately, it is unclear how to bring the 2 tasks into methodological alignment for the purpose of facilitating more appropriate comparisons. As designed by Saxe and colleagues, the theory-of-mind localizer comprises a series of narrative vignettes that each takes several seconds to read and must therefore be analyzed as blocks (i.e., epochs). In contrast, the attentional cueing task relies on the occasional presentation of an invalid cue, which necessitates an event-related design (in blocks, invalid cues no longer misinform participants about the pending location of a target). Of course, that activity in RTPJ significantly distinguishes *at all* between invalid from valid attentional cues argues against the selectivity of this region for attributing beliefs to others.

Lastly, one suggestive—and disquieting—account of the current data is that the RTPJ subserves entirely different processes as a function of the other brain regions engaged by a particular task. Attributing beliefs to another person has been consistently associated with a set of brain regions that, in addition to RTPJ, includes MPFC and precuneus (Gallagher et al. 2000; Saxe and Kanwisher 2003; Saxe and Wexler 2005; Saxe and Powell 2006). In contrast, the aspects of attentional reorienting that have been linked to RTPJ also commonly engage aspects of ventrolateral prefrontal cortex (for a review, see Corbetta and Shulman 2002). None of these attention studies has reported coactivation of the MPFC and precuneus alongside the RTPJ. As such, it is possible that the computations carried out by RTPJ may indeed be selective for belief attribution when in concert with MPFC and precuneus, but subserve different, attention-based processes when engaged alongside ventrolateral prefrontal regions. This possibility—that the nature of the information-processing computations carried out by a brain region may depend critically on which regions are jointly activated by a task—represents a challenge beyond the scope of the present study and more generally calls into question the ability to use functional neuroimaging to provide evidence that 2 cognitive phenomena draw on some of the same processing mechanisms. Indeed, if brain regions cannot be counted on to subserve a specific computational function in a consistent way, researchers must decline to interpret shared neural activity between tasks as any kind of positive evidence for those tasks sharing cognitive processes (Henson 2005).

Content- versus Process-Specific Brain Organization

In questioning the claim that RTPJ is selective for belief attribution, the current study raises issues that closely parallel those from an earlier debate about another functionally defined region, the "fusiform face area" (FFA; Kanwisher et al. 1997; Kanwisher 2000). As for the RTPJ, the researchers who first discussed the FFA initially claimed to have demonstrated that a particular brain region responds selectively for a specific kind of stimulus content, that is, faces. However, subsequent research soon questioned this content-specific view of FFA activity by demonstrating that this region also responds preferentially for a range of nonface stimuli with which perceivers have special expertise (Gauthier et al. 1999, 2000; Tarr and Gauthier 2000; Bukach et al. 2006). In lieu of the content-specificity view offered by the Kanwisher group, these later researchers suggested that the FFA may be better thought of as subserving a particular cognitive process that can be deployed across a range of domains: expert individuation of homogenous visual stimuli, perhaps by parsing the relative spatial configuration of stimulus features. On this view, the reason that the FFA has been so closely associated with face processing is simply a byproduct of the fact that faces are a class of visually homogenous stimuli that humans are natural experts at individuating. However, this process may nevertheless be deployed (and, thus, the FFA activated) for the purpose of individuating members of other homogenous categories, as occurs when perceivers acquire unusual visual expertise (e.g., avid bird watchers; Gauthier et al. 2000). In other words, in contrast with earlier proposals, Gauthier and colleagues have emphasized a domain-general, but *process-specific*, understanding of FFA activity (for an extended discussion of domain-general vs. domain-specific cognitive processing, see Fodor 1983).

In much the same way, the current findings suggest the need to reconsider content-specific views of RTPJ activity (i.e., as selectively subserving the attribution of beliefs) and to refocus empirical efforts toward understanding the cognitive processes carried out by this region. In doing so, these results pose a constructive challenge to researchers to develop an empirically backed account of the computations subserved by RTPJ, one that integrates across the disparate task comparisons associated with this region. Indeed, it is the hope that a process-based account of RTPJ activity will more clearly reveal the underlying complexity of this region and, ideally, inspire new empirical attempts to outline its unique functional profile.

Finally, these results are consistent with emerging views that social cognition is best thought of as a consortium of many mental processes, rather than the product of merely 1 or 2 (Ames 2005; Malle 2005; Mitchell 2006; cf. Leslie et al. 2004). Some of these processes appear to be deployed to solve challenges common to both social and nonsocial contexts, as evidenced in the current study. Others may be unique to the specific social-cognitive problem of understanding the minds of others (Mitchell et al. 2004; Mitchell, Macrae et al. 2005; Mitchell, Mason et al. 2005). It is expected that, for some time to come, research on social cognition will continue to follow this strategy of segregating processes that contribute promiscuously to both social and nonsocial-cognitive abilities from those that appear exclusive to human social behavior (Blakemore et al. 2004).

Notes

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