Brain Regions for Perceiving and Reasoning About Other People in School-Aged Children

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Neuroimaging studies with adults have identified cortical regions recruited when people think about other people's thoughts (theory of mind): temporo-parietal junction, posterior cingulate, and medial prefrontal cortex. These same regions were recruited in 13 children aged 6–11 years when they listened to sections of a story describing a character's thoughts compared to sections of the same story that described the physical context. A distinct region in the posterior superior temporal sulcus was implicated in the perception of biological motion. Change in response selectivity with age was observed in just one region. The right temporo–parietal junction was recruited equally for mental and physical facts about people in younger children, but only for mental facts in older children.

Recent neuroimaging of adult brains has revealed a small but remarkably consistent set of cortical regions associated with thinking about other people's thoughts, or "theory of mind" (Frith & Frith, 2003; Gallagher et al., 2000; Saxe & Kanwisher, 2003): bilateral temporo–parietal junction (TPJ), medial prefrontal cortex (MPFC), and posterior cingulate cortex (PC). One of these regions, the MPFC, is recruited when processing many kinds of information about people (Amodio & Frith, 2006; Mitchell, Banaji, & Macrae, 2005a; Ochsner et al., 2005), but a second region, the right TPJ (RTPJ) is recruited selectively for thinking about thoughts (Saxe & Kanwisher, 2003; Saxe & Powell, 2006). Many functional neuroimaging studies have borrowed paradigms from the rich, older tradition of studying theory of mind in children, though few have directly investigated the development of these neural mechanisms in childhood (Kobayashi, Glover, & Temple, 2006, 2007a).

In developmental psychology, theory of mind has been studied most intensely using false belief tasks. In the typical design, a child watches while a puppet places an object in location A. The puppet leaves the scene and the object is transferred to location B. The puppet returns and the child is asked to predict where the puppet will look for the object. Three-year-olds think the puppet will look in location B, where the object actually is; older children think the puppet will look in location A, where the puppet last saw the object (Wellman, Cross, & Watson, 2001). What is notable is that the 3-year-olds who fail the false belief task are not performing at chance, or confused by the questions. They make systematically below-chance predictions with high confidence (Ruffman, Garnham, Import, & Connolly, 2001). The standard interpretation of these results is that 3-year-olds lack a representational theory of mind. That is, 3-year-olds fail to understand how the contents of thoughts can differ from reality (Gopnik & Astington, 1988; Wellman et al., 2001).

Although the false belief task has been used in literally hundreds of studies, it remains controversial whether success on this task depends on the deployment of a "special" domain-specific mechanism for reasoning about other minds. As many researchers have noted (Bloom & German, 2000; Leslie, 2000; Roth & Leslie, 1998), children might

pass or fail the false belief task for reasons having nothing to do with deficits in understanding other minds. In particular, the false belief task requires a high level of executive control—that is, the ability to plan and carry out a sequence of thoughts or actions, while inhibiting distracting alternatives. Thus, researchers have suggested that the false belief task underestimates children's ability to think about mental states (Bloom & German, 2000). Alleged shifts in children's theory of mind might reflect only changes in children's executive function—especially the abilities to select among competing responses, and to inhibit the tendency to respond based on reality (Carlson, Moses, & Claxton, 2004).

Recently, an even bigger obstacle has arisen for the standard view: Multiple reports that infants can make correct predictions on false belief tasks, when measured by violation-of-expectation looking time measures at 12–15 months (Onishi & Baillargeon, 2005; Surian, Caldi, & Sperber, 2007) or predictive looking at 24 months (Southgate, Senju, & Csibra, 2007). These results have been taken as evidence for very early emerging, or even innate, cognitive mechanisms for theory of mind (Leslie, 2005).

Cognitive neuroscience provides a complementary route to address the same theoretical concerns. Are there cognitive and neural mechanisms selectively implicated in theory of mind, independent of executive demands? If so, do these brain regions' response profiles mature around age 4, around the age when children reliably pass explicit false belief tasks, or early in childhood or even infancy?

Neuroimaging studies of theory of mind in adults have provided initial evidence relevant to the first question: a group of cortical regions is implicated in theory of mind, independent of executive demands. These regions include the left and right temporo–parietal junction (L and RTPJ), the precuneus/posterior cingulate, and regions in the MPFC. Of these regions, the RTPJ appears to be the most selective for theory of mind. The closest control condition for the logical demands of the standard false belief task, for example, is the "false sign" task (Perner & Leekam, 2008). Reasoning about false or misleading signs is similar to reasoning about false beliefs: In both cases, the representation (belief or sign) is designed to correspond to reality, but fails to do so via error or outdating (e.g., a sign indicates that the content of a pie is strawberry, or a person believes that the pie is strawberry, whereas in reality the pie is cherry). For a participant to answer correctly questions about the representation, in both cases, they must consider two competing responses (e.g., strawberry and cherry), and inhibit the reality-based response (cherry), to produce the response governed by the representation (strawberry). Behavioral data suggest that the false signs task is at least as hard for participants as the false belief task. Any difference in the brain regions recruited for false beliefs relative to false signs therefore reflects the specific need to consider *mental* contents, rather than in the inhibitory or executive demands on the tasks. Perner, Aichorn, Kronblicher, Staffen, and Ladurner (2006) had adult participants read vignettes describing four kinds of conflicting representations: false beliefs, false signs, outdated photographs, and temporal change in reality. The RTPJ (but not any of the other regions commonly recruited for belief attribution tasks) showed a significantly higher response for the false belief vignettes than for any other condition, and no differences among the control conditions (Saxe & Kanwisher, 2003). Other brain regions, including the PC, MPFC, and LTPJ, showed less selective patterns of response.

Another recent neuroimaging study took an alternative approach to the relation between theory of mind and executive control by holding the stimuli and the stimulus-response mappings constant but manipulated participants' conception of the task (Saxe, Schulz, & Jiang, 2006). The stimuli were short animated films of a girl, a chocolate bar, and two boxes. On each trial, the chocolate moved into one of the two boxes, back to the center, and then into one of the boxes again. The girl started out facing the boxes, turned away from boxes, and on half the trials turned back to face the boxes. One set of instructions (the algorithm rule) asked participants to use the girl's facing direction at the end of the trial (away from the boxes vs. toward the boxes) as an arbitrary cue to attend to the chocolate's first, or last, location. If the girl was facing away at the end of the trials, participants indicated the first location of the chocolate. If the girl was facing toward the boxes at the end of the trial, participants indicated the last location of the chocolate. The other set of instructions (the theory-of-mind rule) asked participants to identify "where the girl thinks the chocolate bar is." Crucially, for any combination of the girl's position and box location, these two rules generated identical responses (because if the girl was facing away from the boxes at the end of the trial, then she still thinks the chocolate is in its first location; if she was facing toward the boxes, she saw the chocolate go into its last location). The RTPJ was recruited just when participants were instructed to perform the task by thinking about

the girl's thoughts. Again, the response profile in MPFC, PC, and LTPJ was similar to but less selective than the RTPJ.

The authors also replicated two previous experiments, one tapping components of executive function including response selection and inhibitory control (Jiang & Kanwisher, 2003) and the other a false belief task (Saxe & Kanwisher, 2003), within the same individual subjects (Saxe, Schulz, et al., 2006). Almost entirely nonoverlapping brain regions were implicated in response selection and in false belief task performance, once false photograph task performance was subtracted. Importantly, all of the brain regions involved in response selection were robustly recruited for *both* false belief and false photograph task performance. Taken together, these results suggested that false belief task performance recruits both brain regions associated with domain-general attention, response selection and inhibitory control, and a distinct group of brain regions associated with domain-specific representations of the contents of others' thoughts; of these regions, the most selective is RTPJ.

The RTPJ response is also specific to thinking about thoughts relative to thinking about other facts about people. The response in this region is high when participants read stories that describe a character's true or false beliefs but low during stories containing other information about a character, including her appearance, cultural background, or even internal, subjective sensations—like being tired or achy or hungry—that have no representational content (Saxe & Powell, 2006; Saxe & Wexler, 2005). In these experiments, the MPFC showed a more catholic response profile: The response in the MPFC was high when participants read most facts about people, including their social and cultural background and internal sensations. In other studies, the MPFC and PC, but not the RTPJ, were recruited when participants consider the personality traits of the self or a well-known other (Gusnard, Akbudak, Shulman, & Raichle, 2001; Kelley et al., 2002; Mitchell, Banaji, & Macrae, 2005b; Saxe, Schulz, et al., 2006). In all, independent of the stimuli and the stimulus-response contingencies, the RTPJ in adults shows a high response when the stimuli describe or imply a character's mental states, or when the participant is explicitly instructed to solve a task by thinking about mental states (Perner et al., 2006; Saxe & Kanwisher, 2003; Saxe & Powell, 2006; Young & Saxe, 2008).

There is less evidence, though, concerning the developmental origins of the brain mechanisms for theory of mind. In two recent studies, Kobayashi

et al. (2007a) reported that unlike adults, 9-year-old children did not show activation in the right or left TPJ during belief-reasoning tasks. These results suggest the tantalizing possibility of surprisingly late developmental change in the neural mechanisms for theory of mind. However, many important questions remain open. If the TPJ, bilaterally, is not recruited for theory of mind in 9-year-olds, when do these regions develop adult-like selectivity? Are these brain regions involved in some other social cognitive function in the younger children? Or are these brain regions perhaps involved domain-general functions in younger children, and acquire a social role only later in life? More basically, it is important to replicate the finding of developmental change in the function of the TPJ after age 9 years.

This study therefore aimed to investigate the functional response profiles of brain regions involved in thinking about thoughts in school-aged children. Children listened to stories describing physical facts (Physical), social facts about people including kinship and appearance (People), and the characters' mental states (Mental). Any brain regions involved in reasoning about other people should show a higher response during the Mental than the Physical facts. We predicted that these regions would include both the TPJ and MPFC. Based on the prior literature in adults, we expected to observe two different patterns of response: selectivity for any facts about people, compared to physical facts (Mental, People > Physical) in the MPFC, and selectivity for thinking specifically about people's thoughts (''theory of mind,'' Mental > People, Physical) in the RTPJ. Based on results from Kobayashi et al. (2007a), we further hypothesized that there might be developmental change, within this age range, in the function of the TPJ.

An additional question of interest concerned the developmental relation between theory of mind and the perception of human body actions. Basic perception and understanding of human action are very early emerging: Preverbal infants attend to human action and interpret humans' body movements in terms of pursuit of goals (Gergely, Nádasdy, Csibra, & Bíró, 1995; Johnson, 2003; Meltzoff & Brooks, 2001; Woodward, 1998; Woodward, Sommerville, & Guajardo, 2001). A longitudinal study found that infants' early action understanding predicts their later success at age 4 years on explicit false belief tasks, suggesting that early perceiving and later reasoning about other people may rely on common cognitive mechanisms (Wellman, Phillips, Dunphy-Lelii, & LaLonde, 2004).

How are the neural mechanisms for action perception and theory of mind related? Initial neuroimaging studies reported that the action perception (including watching hand, body, and head movements) recruits a region near the RTPJ, in the right posterior superior temporal sulcus (pSTS; Allison, Puce, & McCarthy, 2000; Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005; Pelphrey et al., 2003; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Puce & Perrett, 2003). Critically, the pSTS response depends not only on the pattern of biological motion but on its relation to the environmental context, suggesting that these regions are involved in interpreting human behavior in terms of intentions and goals (Brass, Schmitt, Spengler, & Gergely, 2007; Pelphrey, Morris, & McCarthy, 2004; Pelphrey, Viola, & McCarthy, 2004; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004). Early reviews of the adult neuroimaging literature proposed the existence of a single neural substrate (sometimes called pSTS/TPJ) ''for detection of the behavior of agents and analysis of the goals and outcomes of this behavior'' (Frith & Frith, 1999). However, more recent research has revealed that, at least in adults, these two regions are functionally distinct (Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007); the pSTS shows a high response during action observation, and the TPJ shows a high response during reasoning about beliefs, but not vice versa.

It remains possible, though, that theory of mind and action perception initially depend on a single region in pSTS and TPJ, which then differentiates into two separate regions, with distinct functions, later in development. This study tested this hypothesis, by comparing the patterns of brain activation associated with perceiving biological motion (Figure 2) and thinking about thoughts, in the same children.

Method

Participants

Thirteen typically developing children (7 females, 6 males; M age = 8.7 years; range = 6.7–10.7 years) participated. Advertisements were placed in local parenting magazines. Interested parents contacted the laboratory via electronic mail or telephone. After this initial contact, the parents completed a telephone screening to determine their child's eligibility for the study. After the successful completion of this screening process, an appointment for the scanning session was scheduled with the parent. The parents gave informed consent prior to partici-

pation, and the families were given a toy as a token of our appreciation and financial compensation for their time. Participants were screened against psychiatric, neurologic, and developmental disorders via parental report. In all, 18 children were brought in for scans. They were first trained in a mock scanner. The practice scans are described in more detail as follows. Of these 18 children, 2 requested to stop scanning before any functional data were collected. Of the 16 children who performed both anatomical and functional runs, 3 moved excessively so their data could not be used in the analyses. All 13 of the remaining participants were right-handed as assessed with the Edinburgh Inventory (Oldfield, 1971). Eleven were Caucasian and 2 were African American. The Institutional Review Board of Duke University approved this project.

We used a custom-built magnetic resonance imaging (MRI) simulator for acclimating children to the scanner environment and for training these participants to minimize head motion. We also employed a protocol and computer software designed to limit head motion by training children to remain still during functional MRI (fMRI) scanning. Children were trained using operant-conditioning procedures implemented in custom-written software that received input from a head motion sensor and used that input to direct the operation of a video player. The child watched a favorite movie, and the movie was halted whenever the child exhibited head motion above a progressively stricter threshold. These mock scanning sessions lasted between 10 and 30 min.

Experimental Design

Each aurally presented story was 60-s and composed of three 20-s ''sections'' describing (a) physical facts (Physical), (b) characters' appearance and social relationships (People), and (c) the characters' mental states (Mental; e.g., see Figure 1). Sections were matched for average number of words (54.2) and sentences (3.9), and Fletcher reading level (79.6). Sections were recorded separately and then combined in all possible orders, and fully counterbalanced within participants (across items) and within items (across participants). A hand-drawn color illustration of the Physical section accompanied each story. Following each story, children answered a yes-or-no question (orthogonal to the manipulation of interest) with a button press. The questions asked children to predict what would happen next in the story (e.g., see Figure 1). Children heard an encouraging message after their

Physical (20 s)	People (20 s)	Mental (20 s)	Question
Out behind the big red barn at the edge of the walnut grove is the most magnificent pond in the neighbourhood. It is wide and deep, and shaded by an old oak tree. There are all sorts of things in that pond: fish and old shoes and lost toys and tricycles, and many other surprises."	"Old Mr McFeeglebee is a gray wrinkled old farmer, who wears gray wrinkled old overalls, and gray wrinkled old boots. He has lived on this land his whole life, longer even than most of the trees. Little Georgie is Mr McFeeglebee's nephew from town."	"Mr McFeeglebee doesn't want any little boys to fish in the ponds. But little Georgie pretends not to notice. He likes fishing so much, and besides, he knows he can run faster than anybody in town. Georgie decides to run waway really fast if Mr McFeeglebee sees him fishing."	"What do you think? Does little Georgie fish in the pond?" *[pause]* "Good job! Time for the next story!"
"The whole world had turned purple overnight. Just about everything was purple, including the sky and the ocean and the mountains and the trees. The tallest sky scrapers and the tiniest ants were all purple. The bicycles and furniture and food were purple. Even all the candy was purple."	"Everybody in the world turned purple. Teachers, movie stars, doctors, nurses, and gas station attendants had all turned purple. Even the Queen of England and the President had. Old men had purple beards and thick purple eyebrows. Girls wore violet skirts and had violet hair."	"That morning, people sat around looking at each other, wondering if they were dreaming, because everything looked purple. Some people were shocked. Some people thought that it was funny to see everybody all purple. But even the smartest scientsts didn't know what had happened."	"What do you think? Did the little children turn purple too?" *[pause]* "OK! Are you ready for the next story?"
"In Grandad's attic was a strange old map of a small island in the middle of the sea. The scratchy drawing showed that there were forests and cliffs on the islands, and many twists and turns in the long beach, and one real river. About halfway up the river, the map was marked with a big X."	"The twins were staying with their Granddad for two weeks because of the summer vacation. Although they were twins, Jenny and Samantha looked nothing alike. Jenny was tall and red-headed, always moving and talking. Sam was smaller and quieter; she was the brains of the team."	"The day that the twins arrived at Granddad's place, they decided to go on a treasure hunt. Both of them loved adventure stories, but this was the first time that they wanted to go on a real adventure. The twins looked at each other, and knew that somehow, they would find a lost treasure."	What do you think? Did the twins find some treasure? *[pause]* "Good job! Now get ready for the next story."

Figure 1. Three sample stories. Children heard 60-s audio recordings with accompanying illustrations. Each story was composed of 20-s sections describing physical facts (Physical), characters' appearance and social relationships (People), and the characters' mental states (Mental) in counterbalanced orders. After the story, children were asked to respond to a simple yes-or-no question.

response (e.g., ''Good job! Get ready for the next story''). There was then an 8-s silent pause before the next story. Each run contained four stories and lasted about 5 min. Each child participated in three runs (12 stories).

In separate runs, the same children also watched silent animations of a walking or standing person and a moving or stationary grandfather clock, in alternating blocks of clock-still, clock-moving, human-still, and human-walking (Figure 2; Carter & Pelphrey, 2006; Pelphrey et al., 2003). Each block lasted 12 s, and each condition was repeated five times per run. Each child participated in one (5 children, average age 8.3 years) or two (8 children) runs of this experiment. (Five children requested to stop the experiment after only one run of the biological motion experiment was complete, possibly because this experiment was less interesting that the stories.)

Imaging Protocol

Scanning was performed on a GE 4-Tesla scanner (General Electric, Waukesha, WI) at Duke University's Brain Imaging and Analysis Center. Whole brain functional images were acquired using a gradient-recalled inward spiral pulse sequence sensitive to blood oxygen level dependent contrast (BOLD; TR = 1,500 ms; TE = 35 ms; voxel size = $3.75 \times 3.75 \times 3.8$ mm; 34 axial slices). Individual participants' data were motion-corrected, normalized, and smoothed using a Gaussian filter (full-width half-maximum = 5 mm). Both experiments were then modeled using a boxcar regressor in SPM2 (http://www.fil.ion.ucl.ac.uk/spm/software/spm2/).

Data Analysis

The results were first analyzed using a whole-brain random effects analysis. In this procedure, each brain is normalized to a standard brain template by three-dimensional warping. An adult template brain was used for normalization. The literature suggests that after transformation into a common stereotactic space, anatomical differences between children from age 7 and adults are small relative to the resolution of fMRI data (Burgund et al., 2002). Another study revealed minimal differences in the time courses and locations of
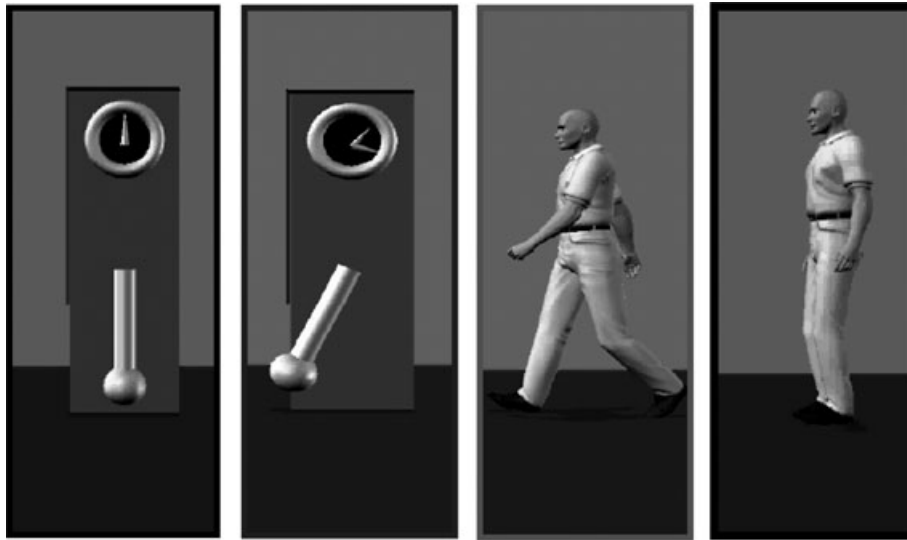
Figure 2. Stimuli for the biological motion experiment: Clock-Still, Clock-Moving, Person-Moving, Person-Still.

functional activation foci between children and adults (Kang, Burgund, Lugar, Petersen, & Schlaggar, 2003).

Once the brains are aligned in this ''stereotactic'' space, *t* tests are used to identify voxels that differentiate between the critical conditions (mental–physical, biological motion–clock motion) reliably across participants. Regions were considered reliable if at least five contiguous voxels showed a significantly ($p < .001$) different response to the critical conditions. (The criterion that contiguous voxels pass the same threshold is used because measurement noise is likely to be less correlated in neighboring voxels than the pattern of functional brain activation.)

These group results were then used to guide the selection of subject-specific functionally defined regions of interest for subsequent analyses. When using a functional region of interest (ROI) approach, each region is first identified functionally in each subject individually, before testing specific hypotheses concerning that region. This functional ROI method, which resembled long-established practice in visual neurophysiology, has methodologic, statistical, and theoretical advantages over standard alternatives (such as whole-brain analyses of group data; Saxe, Brett, & Kanwisher, 2006). Functional properties are more consistently and robustly associated with functional ROIs than with locations in normalized space. Also, because hypotheses are tested in only a handful of ROIs (instead of in tens of thousands of voxels), advance specification of ROIs provides an increase in statis-

tical power over whole-brain analyses (Devlin & Poldrack, 2007).

The use of an ROI analysis strategy requires that the pattern of brain activation under investigation be very robust and reliable: The same pattern of activation must be detectable in most individual subjects. This criterion is commonly met in studies of well-understood low-level cortical regions, including basic perceptual and motor representations. However, only a few high-level social or cognitive phenomena are associated with sufficiently robust neural responses, which can be identified in individual brains. Even within a single study, there is variability in the reliability with which different brain regions can be identified in individual subjects. The most robust and reliable regions can be identified in more that 80% of individuals (i.e., a cluster in that anatomical region meets the functional criteria for ''activation''); less reliably activated regions can be identified in half or fewer of the subjects. One measure of the robustness of a given region's differential response is therefore the percentage of subjects in whom that region can be identified.

In this study, functional ROIs were defined by combining anatomical and functional criteria. Following common standards, in this study, the functional criteria for a cluster were: at least five contiguous voxels, extending no more that 9 mm from the peak voxel, that significantly differentiated between the critical conditions, for example, Mental–Physical ($p < .001$, uncorrected). Each subject's own anatomy was used to guide the anatomical selection (e.g., a cluster was considered the ''RTPJ''

only if it was in the right hemisphere, near the ascending branch of the pSTS and the angular gyrus). If two clusters within the same anatomical region passed these criteria, the region that differentiated between the critical conditions the most significantly (i.e., highest t value) was chosen for further analyses. ROIs were identified in normalized data and then were projected back into native space to calculate true ROI size.

The response for Mental, People, and Physical sections of the stories was then calculated in each ROI for each child. The BOLD signal from all of the voxels within the ROI were averaged together, for each time point within the stories, and then the response was averaged across time points within each section, accounting for hemodynamic lag. The response during passive rest periods was calculated for each ROI, as the average response in the same voxels for time points at least 6 s after the most recent stimulus (i.e., when there was no visual or auditory stimulus, accounting for hemodynamic lag), and not including the first 4 s of the next stimulus. The response is expressed as the percent signal change during the story sections, relative to rest, in each ROI. Because the regions of interest were defined using the response to the Mental and Physical sections, the critical ROI analyses focused on the relative response to the independent third condition, the People sections.

Finally, as our results suggested an effect of age on the functional profiles of some ROIs, it was important to investigate whether these effects were specific to the ROI or were more generally distributed across the cortex. To search for any brain region in which selectivity for social information was related to age, we conducted a whole-brain conjunction analysis, of the within subjects' contrast, Mental–People, and the between subjects' variable, age. For conjunction analyses, the contrast T-maps were thresh-holded independently and then submitted to a logical ''AND'' operator, using the ImCalc function in SPM2 (Nichols, Brett, Andersson, Wager, & Poline, 2005). This procedure is conservative, relative to some common practices (e.g., simply taking the product of the two independent thresholds), but is a more appropriate way to determine the statistical significance of a conjunction (Nichols et al., 2005).

Results

The quality of the children's data was very high. Average motion per run in the functional scans was

< 1 mm translation and < 0.1 mm rotation, and was not correlated with the child's age ($r = .34$, ns).

Children's brains differentiated, within ongoing stories, sections that described the characters' thoughts from sections describing the physical context. In the whole-brain analyses, regions in precuneus and bilateral TPJ showed significantly higher responses during the Mental than Physical sections; at a lower threshold ($p < .005$ uncorrected), MPFC was also observed (Figure 3). Regions of interest were identified in 11–13 individual subjects in RTPJ, in 10/13 in the precuneus, in 9/13 in the LTPJ, and in 11/13 in the MPFC. In each of these regions, the volume of the supra-threshold region was not significantly correlated with the child's age (all $r < .30$, $df < 9$, ns). For further details about the ROIs, see Table 1.

To investigate selectivity for thinking about thoughts, the responses to People versus Physical and Mental versus People subsections in each ROI were compared using t tests (with Bonferroni's corrections, Figure 3). All of the regions showed a significantly higher response for People than Physical sections (ts > 4.6, adjusted ps $< .01$). All of the regions also showed a higher response for Mental than People sections (ts > 3.4, adjusted ps $< .05$), except the MPFC, in which this latter difference did not reach significance ($t = 2.4$, ns). That is, we did not find evidence that the MPFC reliably differentiated information about characters' thoughts from any other facts about people, although the average response in the MPFC was also not significantly different from that observed in the other regions in a direct comparison.

These results suggest that in children, unlike previous results in adults, the RTPJ is not significantly more selective for mental state facts, relative to other social facts, than the MPFC. One possibility is that this difference reflects a developmental change. As the children in this sample covered a large age range (6–11 years), it was possible to test whether, across the age range of the children in this study, there was evidence for a change in the response profile of the RTPJ and/or MPFC.

We therefore examined changes in response patterns with age. First, the magnitude of the difference between Mental and People sections was calculated in each ROI for each child, and analyzed in a linear regression with age. Only one region showed a significant correlation with age: In the RTPJ (Figures 3 and 4), the difference between Mental and People sections increased with age, $r = .65$, $t(9) = 2.6$, $p < .03$. This difference reflected a specific decrease in the response of the RTPJ to the
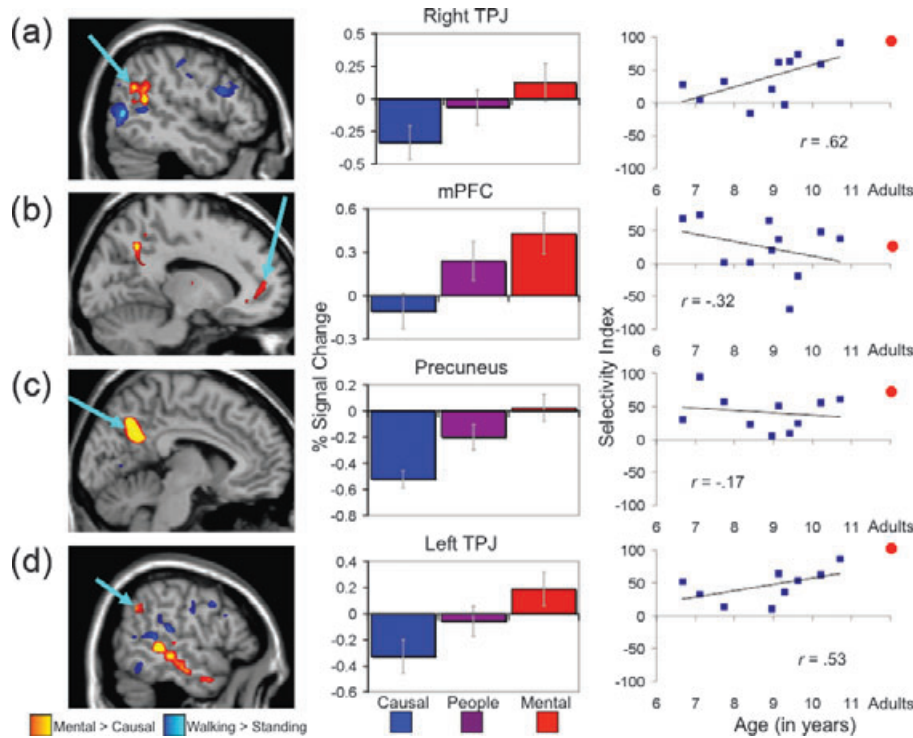
Figure 3. Results in the (A) RTPJ, (B) MPFC, (C) PC, and (D) left TPJ. Brain activations show the average group responses (Random Effects, $n = 13$, $p < 0.005$) to Mental versus Physical story sections (red to yellow) and human-walking versus human-standing animation (dark to light blue). The bar graph illustrates the average percent signal change from rest in each region, during Physical, People, and Mental story sections. Scatterplots illustrate the correlation in each region between the selectivity index (see main text) and the child's age. The red circle shows the selectivity index estimated for the average adult data in that region (Saxe & Powell, 2006, not included in the regression).

Table 1

Average Peak MNI Coordinates and Size (mm³) of Individual Subjects' ROIs (and Standard Deviations)

	X	Y	Z	Size (mm³)
Right TPJ	53 (6.4)	−56 (8.1)	24 (6.9)	376.8 (46)
Left TPJ	−40 (7.7)	−57 (7.1)	29 (6.7)	595.1 (93)
Precuneus	0 (5.2)	−57 (7.0)	36 (5.0)	599.8 (29)
MPFC	1 (7.9)	60 (5.8)	19 (5.3)	396.2 (49)

Note. MNI = Montreal Neurological Institute; ROI = region of interest; TPJ = temporo–parietal junction; MPFC = medial prefrontal cortex.

Figure 4. Results in the right temporo–parietal junction (RTPJ) for individual children. For each child, difference in RTPJ response for Mental (Light) and People (Dark) sections, relative to Physical sections of the stories, in percent signal change. Also shown under each column is the child's age and gender.

People sections, with age. The response to the Mental sections (relative to the Physical sections) did not change with age; instead, the response to the People sections was almost as high as the response to the Mental sections, in the younger children, and almost as low as the response to the Physical conditions, in the older children (Figure 4).

To clarify this change in the relative response to Mental, People, and Physical sections, we then calculated a selectivity index for each ROI, to measure
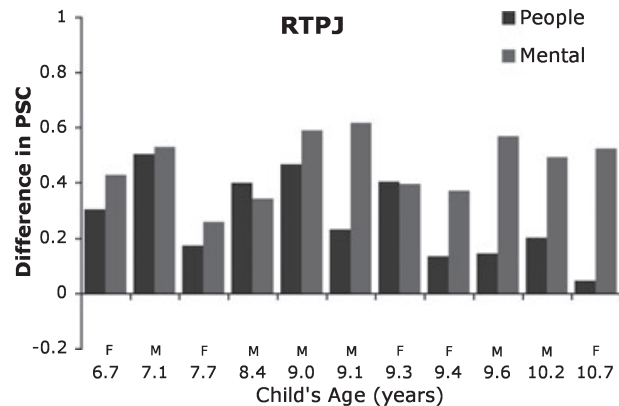
the difference (in units of percent signal change from rest) between the Mental and People sections, relative to the difference between the Mental and Physical sections, for each individual: 100*(Mental

– People)/(Mental – Physical). Thus, a low Selectivity score (e.g., below 20) indicates that the response to the People sections was approximately as high as the response to the Mental sections; a high Selectivity score (e.g., 80–100) indicates that the response to the People sections was approximately as low as the response to the Physical sections. The selectivity index score for each child in each ROI was then analyzed in a linear regression with age. Again, only one region showed a significant correlation between age and the selectivity index: the RTPJ, $r = .62$, $t(9) = 2.3$, $p < .05$ (Figure 3); the LTPJ showed a trend in the same direction, Figure 3.

To confirm these results, we also conducted a random-effects whole brain conjunction analysis. A whole-brain analysis importantly complements ROI analyses, by determining whether the profile observed in an ROI is restricted to the ROI or is part of a broader pattern of activation in many brain regions. This analysis would identify voxels, anywhere in the brain, in which the response was significantly higher to the Mental sections than to the Physical sections ($p < .005$) of the stories, and the difference between Mental and People sections increased with age ($p < .01$). The only region passing these criteria was the RTPJ.

The brain regions implicated in theory of mind did not overlap with those recruited during perception of biological motion (Figure 3). Replicating previous studies with adults and children (Carter & Pelphrey, 2006; Pelphrey et al., 2003), in the whole-brain analyses, we found that human-walking, relative to human-still, animations recruited regions in extrastriate cortex, and inferior frontal gyrus. None of these regions overlapped with any region recruited in the theory-of-mind experiment. At a lower threshold ($p < .005$), recruitment of right pSTS was also observed, but this region did not overlap with the RTPJ.

Discussion

These results converge on the same brain regions implicated in theory of mind in adults: Left and right TPJ, precuneus, and MPFC were all recruited significantly more during the Mental than the Physical sections of ongoing children's stories. Relative to previous studies, the current paradigm implemented three methodologic advances: It (a) used stimuli presented aurally rather than visually, (b) manipulated the information type within a single ongoing story (in counterbalanced order), rather than across items, and (c) required subjects to attri-

bute mental states (i.e., propositional attitudes) but not false beliefs. These results suggest that brain regions involved in thinking about thoughts are recruited independent of stimulus modality (visual or aural) on a fine-grained time scale within an ongoing story, and for mental states other than false beliefs.

Most previous studies of theory of mind have focused on participants' ability to reason specifically about *false* beliefs (Russell, 2005) because false belief scenarios provide a powerful behavioral assay of mental-state-based reasoning (Dennett, 1978). Many authors have noted, though, that successful performance of false belief tasks depends not just on the ability to think about thoughts but also on recruitment of domain-general cognitive resources including inhibitory control (Bloom & German, 2000; Leslie, Friedman, & German, 2004; Perner & Lang, 1999; Sabbagh, Fen, Carlson, Moses, & Lee, 2006) that also change with development. In the current experiment, these task demands were eliminated: Children participated in a (relatively) ecologically valid, common activity listening to stories that provided descriptions of the characters' thoughts, desires, decisions, suspicions, and hopes, but not false beliefs.

One weakness of the current paradigm was that we did not have an online measure of when or to what degree children were actively considering or inferring another person's mental states. As a consequence, any interpretation of the pattern of brain activation is highly speculative; future studies should include a more direct measure of children's strategies, and of the effects of different strategies on the resulting brain activation. Similar comparisons have been conducted for adult participants. For example, Saxe and Kanwisher (2003) explicitly compared the response in the RTPJ, MPFC, LTPJ, and PC when adult participants were either (a) answering questions about the mental states of the characters in a verbal story or (b) just reading stories that describe or imply mental states of the characters. The TPJ bilaterally, PC, and MPFC all showed robust responses in both conditions. We hypothesize that while listening to stories, both children and adults probably "think about" the facts described in the stories—including physical, social, and mental facts (but see the following for further discussion).

The current results converge with previous neuroimaging studies in adults to suggest that these brain regions reflect a domain-specific neural mechanism for theory of mind (Perner et al., 2006; Saxe & Powell, 2006; Saxe, Brett et al., 2006). Of course,

a domain-specific mechanism could not be *sufficient* for passing false belief tasks (Bloom & German, 2000). To recognize and reason about someone else's false beliefs, children (and adults) must use general cognitive abilities, including general perceptual and linguistic representations of the story, working memory (to track all the parts of the story), and motor representations of their planned responses. Many brain regions are therefore recruited in common for both belief reasoning and control stimuli. Nevertheless, the neuroimaging results suggest that in addition to domain general mechanisms, there is also a distinct, dedicated domain-specific mechanism for reasoning about beliefs and desires.

The brain regions implicated in thinking about thoughts did not overlap with brain regions recruited during the perception of human biological motion in children; in particular, the RTPJ and the right pSTS were neighboring but distinct, consistent with pattern observed in adults (Gobbini et al., 2007). Behaviorally, the perception of human actions develops earlier than children's understanding of the mental states, such as beliefs and desires (Saxe, Carey, & Kanwisher, 2004). Taken together, these results suggest that the cognitive and neural substrates of perceiving others' actions and reasoning about others' minds are at least partially distinct. One interesting possibility is that the system for perceiving intentional actions, in the STS, inferior frontal gyrus, and mirror systems (Rizzolatti & Craighero, 2004), is shared with other primates, whereas the component for thinking about thoughts, in the RTPJ, is relatively unique to humans (Saxe, 2006; Tomasello, Call, & Hare, 2003). An important question for future research will be to determine how these two systems interact when human observers use inferred thoughts and desires to predict and explain others' actions.

The key result of this study is the observation that selectivity for thinking about people's thoughts emerges in the RTPJ between ages 6 and 11 years; the response profile in the MPFC and PC did not change over the same period. Interestingly, the magnitude and volume of the difference between Mental and Physical sections did not change with age. By age 6 years, the RTPJ robustly discriminated facts about people from nonsocial information about the physical environment. The developmental change between 6 and 11 years reflected increasing specialization within the social domain, just in the RTPJ, from responding to any facts about a person to responding specifically to facts about their mental states.

These results may help to explain a puzzle. Kobayashi, Glover, and Temple (2007b) recently conducted the first cross-linguistic developmental study of the neural basis of theory of mind. Unlike many previous studies of adults, neither American nor Japanese children showed activation in the right (or left) TPJ during belief-reasoning tasks. What kind of developmental change do these data reflect? One possibility is that the left and right TPJ are not yet involved in social cognitive function, in 9-year-old children, and acquire a social role only later in life. An alternative, suggested by the current results, is that the left and right TPJ are involved in social cognition more broadly in 9-year-old children than in adults. In Kobayashi et al.'s study, the ''non-theory-of-mind'' stories and cartoons described social interactions between characters, like fighting. The absence of a differential response to beliefs versus of other social information in the TPJ of 9-year-olds (Kobayashi et al., 2007a) is thus consistent with the current evidence that the TPJ response generalizes to all social information in younger children and only becomes selective for mental state reasoning after age 9. The children's RTPJ may have responded robustly to both the experimental and the control conditions, whereas in adults, the RTPJ distinguished between the same two conditions (Kobayashi et al., 2006).

Nevertheless, the age-related change in brain activation raises as many questions as it answers. There is a broad consensus among developmental psychologists that theory of mind is largely mature well before age 6 years (Onishi & Baillargeon, 2005; Southgate et al., 2007; Wellman et al., 2001). The neuroimaging results, in contrast, suggest that a key component of the neural organization underlying theory of mind is still changing 3 years later, around age 9 years. So what are the cognitive (and behavioral) correlates of the increased neural specialization?

At least two interpretations of the observed increase in selectivity are possible. A purely psychological interpretation is that the current results reflect development in children's pragmatics rather than in basic cognitive or neural mechanisms: Younger children may be less stimulus bound and less discriminating in their theory-of-mind reasoning. On this view, younger children spontaneously consider the thoughts and desires of the characters in the stories, even when those mental states are not explicitly stated, leading to increased recruitment of brain regions involved (selectively) in thinking about mental states. As they get older, children become more conservative, and their

neural recruitment comes to follow the content of the story more precisely.

A second interpretation, which we favor, is that the observed changes reflect real changes in neural organization, and specifically in the selectivity of the RTPJ neural response. The pattern of anatomical development of human cortex is consistent with this interpretation. A longitudinal study found that gray matter does not reach mature density in ''higher order association areas'' including regions near the TPJ until early adolescence (Gogtay et al., 2004).

More generally, we are informed in our preference by the recent report of similarly late developmental changes in higher-level visual cortical regions (Golarai et al., 2007), in particular in the fusiform face area (FFA; Kanwisher, McDermott, & Chun, 1997). Like theory of mind, behavioral signatures of face perception are qualitatively mature by age 5 years (McKone, Kanwisher, & Duchaine, 2007); nevertheless, Golarai et al. (2007) reported that the FFA continues to mature (in their case, increase in size) between ages 7 and 12. Both studies suggest that the strong selectivity observed in adult brain regions for specific stimulus categories (e.g., faces, places, represented thoughts) is not innate but emerges gradually over many years in childhood. In particular, regions showing the *most* selective response profiles in adulthood show late developmental change (the RTPJ in this study; the FFA and parahippocampal place area in Golarai et al., 2007), whereas regions with more general response profiles in adulthood show less developmental change (the MPFC in this study; the lateral occipital area in Golarai et al., 2007). For both perceiving and reasoning about other people, these results suggest that the basic cognitive signatures of domain-specificity may be in place long before the brain systems underlying these processes have reached an adult-like state. The implications of this conclusion are as yet unclear. There are two parts of the puzzle. First, what brain regions *are* responsible for face processing and theory of mind, in young infants and children? Second, what aspects of cognitive processing change in later school age, when the neural mechanisms reach maturity?

As an approach toward the second puzzle, one direction for future research will be to look for correlates of changes in face processing and/or theory of mind in school-aged children. For example, there is an intriguing recent hint that middle childhood is a critical time for interactions between language and theory of mind. Among neurologically normal deaf children acquiring Nicaraguan Sign Language in middle or late childhood, there appears to be a critical period for normal theory-of-mind development, ending around age 9 years: Access to sign language before age 10 is necessary for children to acquire normal abilities to reason about false beliefs (Morgan & Kegl, 2006). Whether there is any link between this result and the current observation of changes in the RTPJ at around the same age will be an interesting topic for future investigations.

The finding of late-emerging cortical selectivity undermines the interpretation of category-selective brain regions in adults as evidence for innate and early-maturing domain-specific cognitive or perceptual modules. In particular, the current results in the RTPJ are challenging for theories of cognitive development that emphasize an innate and early-maturing domain-specific module for theory of mind.

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