

Two Takes on the Social Brain: A Comparison of Theory of Mind Tasks

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Abstract

■ We compared two tasks that are widely used in research on mentalizing—false belief stories and animations of rigid geometric shapes that depict social interactions—to investigate whether the neural systems that mediate the representation of others' mental states are consistent across these tasks. Whereas false belief stories activated primarily the anterior paracingulate cortex (APC), the posterior cingulate cortex/precuneus (PCC/PC), and the temporo-parietal junction (TPJ)—components of the distributed neural system for theory of mind (ToM)—the social animations activated an extensive region along nearly the full extent of the superior temporal sulcus, including a locus in the posterior superior temporal sulcus (pSTS), as well as the frontal operculum and inferior parietal lobule (IPL)—components of the distributed neural system for action under-

standing—and the fusiform gyrus. These results suggest that the representation of covert mental states that may predict behavior and the representation of intentions that are implied by perceived actions involve distinct neural systems. These results show that the TPJ and the pSTS play dissociable roles in mentalizing and are parts of different distributed neural systems. Because the social animations do not depict articulated body movements, these results also highlight that the perception of the kinematics of actions is not necessary to activate the mirror neuron system, suggesting that this system plays a general role in the representation of intentions and goals of actions. Furthermore, these results suggest that the fusiform gyrus plays a general role in the representation of visual stimuli that signify agency, independent of visual form. ■

INTRODUCTION

How do we make sense of what other people do and feel? The capacity to explain and predict the behaviors of others by attributing to them intentions and mental states has been called “theory of mind” (ToM) or “mentalizing” (Frith & Frith, 1999, 2003, 2006; Baron-Cohen et al., 1999; Leslie, 1994). Recent neuroimaging research has revealed a common network of regions involved during tasks requiring mentalizing, including the anterior paracingulate cortex (APC), the posterior superior temporal sulcus (pSTS)/temporo-parietal junction (TPJ), and the posterior cingulate/precuneus (PCC/PC). These areas have been activated by a wide variety of tasks that all involve representing the mental states of others. Examples of stimuli used in these studies include stories of false beliefs (Calarge, Andreasen, & O’Leary, 2003; Saxe & Kanwisher, 2003; Gallagher et al., 2000; Fletcher et al., 1995; Happé, 1994), nonverbal cartoons depicting mental states (Gallagher et al., 2000), animations of rigid geometric shapes interacting in socially meaningful ways (Martin & Weisberg, 2003; Castelli, Frith, Happé, & Frith, 2002; Castelli, Happé, Frith, & Frith, 2000), and computerized games of cooperation and competition (Rilling,

Sanfey, Aronson, Nystrom, & Cohen, 2004; Gallagher, Jack, Roepstorff, & Frith, 2002; McCabe, Houser, Ryan, Smith, & Trouard, 2001).

Neuroimaging experiments exploring the neural basis of ToM, however, have identified a wide range of loci of activation within the APC and within the pSTS/TPJ. In a recent meta-analysis on ToM studies, Ochsner et al. (2004) found that the activations reported in different studies span nearly the entire APC. Amodio and Frith (2006) have proposed that as the more dorsal portion of the APC is involved in action monitoring and attention, the more ventral portion of the APC is associated with more abstract meta-cognitive processes such as self-reflection and person perception. Similarly, during inference of other people’s mental states, activation can be seen from the TPJ to a more inferior and anterior region in the pSTS (Saxe & Powell, 2006; Martin & Weisberg, 2003; Winston, Strange, O’Doherty, & Dolan, 2002; Allison, Puce, & McCarthy, 2000; Castelli et al., 2000; Hoffman & Haxby, 2000). In particular, a distinction may exist between a more superior and posterior locus in the TPJ that has been associated with representation of others’ mental states (Saxe & Powell, 2006; Rilling et al., 2004; Gallagher et al., 2000) and with the spontaneous activation of person knowledge of familiar others (Gobbini, Leibenluft, Santiago, & Haxby, 2004; Leibenluft, Gobbini, Harrison, & Haxby,

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2004), and a more inferior and anterior locus in the pSTS that has been associated with perception of biological motion, action understanding, and changeable aspects of faces such as expression and gaze direction (Iacoboni et al., 2005; Saygin, Wilson, Hagler, Bates, & Sereno, 2004; Beauchamp, Lee, Haxby, & Martin, 2003; Montgomery, Gobbini, & Haxby, 2003; Grossman et al., 2000; Haxby, Hoffman, & Gobbini, 2000; Grèzes, Costes, & Decety, 1999; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Calvert et al., 1997; Bonda, Petrides, Ostry, & Evans, 1996). A comparison across studies of the loci for activations due to mentalizing and perception of biological motion suggests a segregation into the TPJ and pSTS, respectively, but the ranges of reported loci for these two functions are overlapping (see Discussion). Moreover, previous meta-analyses on other dissociations have shown that comparisons across studies are less sensitive than comparisons within the same group of subjects (Farah & Aguirre, 1999).

A second distributed neural system has been associated with social cognition and action understanding and, therefore, may be related to the ToM system. The major components of this second system are the frontal operculum and the IPL, which comprise the mirror neuron system (MNS), and the pSTS (Montgomery, Isenberg, & Haxby, 2007; Iacoboni et al., 1999, 2005; Buccino, Binkofski, & Riggio, 2004; Rizzolatti & Craighero, 2004; Montgomery et al., 2003; Decety, Chaminade, Grèzes, & Meltzoff, 2002; Allison et al., 2000; Decety et al., 1997; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Moreover, activation of neurons in the MNS is associated with the representation of the goal or target of an action, which suggests that the MNS plays a role in the representation of others' intentions (Fogassi et al., 2005; Umiltà et al., 2001). The involvement of the pSTS/TPJ in the systems for action understanding and ToM may reflect a common anatomical substrate for the representation of the intentions of others—both as the intentions that are implied by perceived actions and as the covert mental states that may lead to future actions. Alternatively, as discussed above, the involvement of this region may reflect nearby but functionally dissociable regions.

To investigate further if different subregions in the APC, pSTS/TPJ, and PCC/PC are activated depending on the mental states that are inferred, we designed a functional magnetic resonance imaging (fMRI) experiment to directly compare two “ToM” tasks that have been widely used in the literature—one task that involves the representation of the mental states of others, namely, false belief stories (Saxe & Kanwisher, 2003; Gallagher et al., 2000; Fletcher et al., 1995; Happé, 1994), and a second task that involves the perception of actions of figures in a social interaction that imply intentions and goals, namely, the Heider–Simmel animations (Castelli et al., 2000; see also Martin & Weisberg, 2003, for a sim-

ilar task). The false belief stories require inferring the thoughts and the beliefs of another based on understanding that person's perspective. The social animations require interpreting social exchanges depicted by rigid geometrical figures moving and interacting with each other. In addition, to identify brain areas associated with the perception of biological motion, we included in our experiment a third task that consisted of viewing point-light displays depicting different whole-body motions (Grossman et al., 2000). These point-light displays depict articulated body motions, as compared to the rigid motions of the geometric shapes in the social animations, and do not depict social interactions.

Our results demonstrated that the representation of false beliefs and the representation of goals and intentions implied by actions were associated with different regional patterns of activity in networks for ToM and action understanding. Whereas the false belief stories evoked activity in the ToM system, the social animations evoked activity primarily in the action understanding system. Moreover, the results show a clear dissociation between the TPJ, activated by the false belief stories, and the pSTS, which was activated both by the social animations and by the perception of biological motion. These results suggest that the representation of intentions as mental states that are not associated with current actions involves a different neural system from that for the representation of the intentions and goals that are inherent in perceived actions.

METHODS

Subjects

Twelve healthy, right-handed volunteers with normal or corrected-to-normal vision and no record of neurological or psychiatric illness participated in the study (5 men, 7 women, mean age = 22 ± 2 years). Before the experiment, each participant signed an informed consent. Subjects were compensated for their participation.

Stimuli

Three types of verbal material were presented: ToM stories (false beliefs); non-ToM stories (stories describing human activity without the need for mental state attributions); and unlinked sentences. These stimuli have been used and validated previously (for details, see Gallagher et al., 2000).

Animations consisted of geometrical shapes with intentional movements based on the original Heider and Simmel animations (Heider & Simmel, 1944), and as a control, geometrical shapes with random movements. These stimuli have been used and validated previously (Castelli et al., 2000, 2002). All animations featured a big red triangle and a small blue triangle moving against a white background. Social animations were designed to

induce automatic attributions of intention and agency to the triangles, whereas control sequences depicted the triangles bouncing and drifting, as if under the influence of physical forces. Stimuli were matched for overall shape, speed, and orientation changes as closely as possible. Animation stimuli were edited using iMovie and displayed to participants using Quicktime (Apple Computer, Cupertino, CA).

As a control for detection of action, point-light displays with biological motion or scrambled motion were used (Grossman & Blake, 2002). Biological motion displays were created by digitizing video clips of an actor performing various activities, such as running or jumping, and then encoding the joint positions as motion vectors with specific starting positions. Scrambled displays were created by adjusting the starting position of each joint, thus controlling for the motion vectors while disrupting the perception of biological motion. The joints were displayed as black dots against a white background. These stimuli have been used and validated previously (Grossman & Blake, 2002). Point-light displays were presented using Matlab (Mathworks, Natick, MA) with routines from the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

Stimuli were presented blocked by type (stories, animations and biological motion) and the order in which the blocks were presented was randomized across participants.

Tasks

The stories were presented in two runs with eight passages from each of the three different conditions (false beliefs, physical stories, and unlinked sentences) in randomized order. Each trial consisted of passages of text displayed to subjects for 21.6 sec, followed by an 8-sec forced-choice question about the content of the story. Trials were separated by 5 sec of rest.

Animation stimuli, with intentional and random movements, were presented to subjects in randomized order. Each trial consisted of an animation that lasted from 34 to 45 sec, followed by a 5-sec forced-choice question, and 5 sec of rest. Questions asked the subjects to decide which of two words was a more appropriate title for the animation, to monitor whether participants had attributed intentions to the geometric shapes.

Point-light displays were blocked by condition (biological motion vs. scrambled motion). Blocks were presented randomly 10 times for each condition. In each block, five events were presented and each event was shown to subjects for 1 sec, with a 0.5-sec interstimulus interval (ISI). Blocks were separated by 10 sec of rest. To ensure equal attention to the stimuli, subjects were asked to perform a one-back repetition-detection task and were instructed to push a button when any point-light display was presented twice in a row. Repetition of the same point-light display in successive trials was 50%.

Means and standard deviations were calculated for the percentage of correct responses to forced-choice ques-

tions in the false belief story task and the intentional movement animation task.

Imaging

fMRI data were acquired using a 3-T Siemens scanner (Allegra, Siemens, Erlangen, Germany). Thirty-two contiguous, axial slices of 4 mm thickness were taken with a gradient-echo, echo-planar sequence (TR = 2000 msec, TE = 30 msec, field of view [FOV] = 192 mm, flip angle = 80°). High-resolution anatomical T1-weighted MPRAGE anatomical images (176 one-mm-thick sagittal images, FOV = 256 mm, 256 × 256 matrix, TR = 2500 msec, TE = 4.3 msec, flip angle = 8°) were obtained for each subject. Two time series with 244 volumes each were acquired for the task with the stories, one time series with 277 volumes for the animation stimuli, and two time series with 125 volumes each, for the point-light displays. Each time series began and ended with 20 sec of rest.

Statistics

Image data were analyzed with multiple regression using the Analysis of Functional NeuroImages software package (AFNI; <http://afni.nimh.nih.gov/afni>). Seven regressors of interest were used to model the hemodynamic response. Three regressors of interest were used for the stories modeling the response to: (1) false belief stories, (2) physical stories, and (3) unlinked sentences. Two regressors of interest were used for the animations: (1) animations with intentional movements and (2) animations with random movements. Two regressors of interest were used for the point-light displays: (1) biological motion and (2) scrambled movements.

The beta weights for each condition quantified the magnitude of the response relative to rest. For each subject, the functional maps were resampled into standard Talairach space (Talairach & Tournoux, 1988), and group analyses for the following three contrasts were performed using *t* tests to measure the significance for each comparison. For the story tasks, the analysis focused on the contrast between false belief stories versus physical stories. This contrast is the best test for ToM. Results from contrasts involving the unlinked sentences can be obtained from the authors. For the animations, a test was performed to compare responses to animations with intentional movements versus animations with random movements. For the biological motion stimuli, a test was performed comparing responses to point light displays biological motion versus point-lights displays with scrambled movements.

Clusters of activity of at least 100 μ l volume and with a threshold of $p < .001$ (two-tailed) were selected as significant. For regions in the ToM and action understanding systems, loci were also identified with a more liberal

criterion of $p < .01$ for a comparison of locations across conditions. In practice, the more liberal criterion identified the location of a region in the right TPJ that was activated by the false belief stories that was homologous to an activation in the left TPJ that met the more stringent criterion, the location of loci in the APC and PCC/PC that was activated by the social animations, and the location of a region in the right frontal operculum that was activated by biological motion.

RESULTS

Behavioral Results

Participants correctly answered $93.1 \pm 10.1\%$ ($M \pm SD$) of the questions in the false belief story task ($95.8 \pm 8.1\%$ for the false belief stories; $94.6 \pm 8.5\%$ for the physical stories; $88.5 \pm 12.4\%$ for the unlinked sentences). Participants answered $93.1 \pm 9.9\%$ of the questions correctly for the intentional movement animations ($94.5 \pm 9.8\%$ for the theory of mind task; $91.6 \pm 10.2\%$ for the random movement).

Neuroimaging Results

False Belief Stories versus Physical Stories

The group analysis for the contrast false belief stories versus physical stories (Figure 1) showed a stronger response

in the APC bilaterally (maximum $Z = 4.49$, $p < .0001$), in the left precuneus (maximum $Z = 3.53$, $p < .001$), in the left TPJ (maximum $Z = 3.52$, $p < .001$), and in the bilateral temporal poles (in the right with maximum $Z = 3.93$, $p < .0001$; in the left with a maximum $Z = 3.63$, $p < .001$). At a lower threshold ($p < .01$), a stronger response for false belief stories also was identified in the right TPJ (maximum $Z = 3.03$, $p = .002$, at $x = 57$, $y = -56$, $z = 26$). Table 1 lists all areas that showed a significant effect for this contrast.

Animations: Social Interactions versus Random Movements

The group analysis for the contrast animations depicting social interactions versus random movements (Figure 1) showed stronger activity in two loci in the right inferior temporal and fusiform gyri (maxima: $Z = 6.07$, $p < .0001$, and $Z = 5.55$, $p < .0001$) (Figure 1), along nearly the full length of the STS bilaterally, with maximal value in the pSTS (right maximum $Z = 4.48$, $p < .0001$; left maximum $Z = 4.28$, $p < .0001$), in the frontal operculum bilaterally (in the right with a maximum $Z = 3.86$, $p < .0001$; in the left with maximum $Z = 3.58$, $p < .001$), and in the left fusiform gyrus (maximum $Z = 6.03$, $p < .0001$). At a lower threshold, a stronger response for social interactions also was identified in the right APC (maximum $Z = 3.25$, $p = .0012$) and in the right PCC/PC (maximum

Figure 1. (A) Activation in the left TPJ for the contrast ToM stories as compared to physical stories. In the coronal view, the right side of the brain is on the left side of each image (radiological convention). The color bar indicates Z values. For display purposes, the p -value threshold was set to $p < .0025$. (B) Areas of activation for the contrast social animations as compared to animations with random movements. In the coronal view, the right side of the brain is on the left side of each image (radiological convention). For display purposes, the p -value threshold was set to $p < .0025$. (C) Areas of activation for the contrast point-light displays of biological motion as compared to point-light displays moving randomly. In the coronal view, the right side of the brain is on the left side of each image (radiological convention). For display purposes, the p -value threshold was set to $p < .0025$.

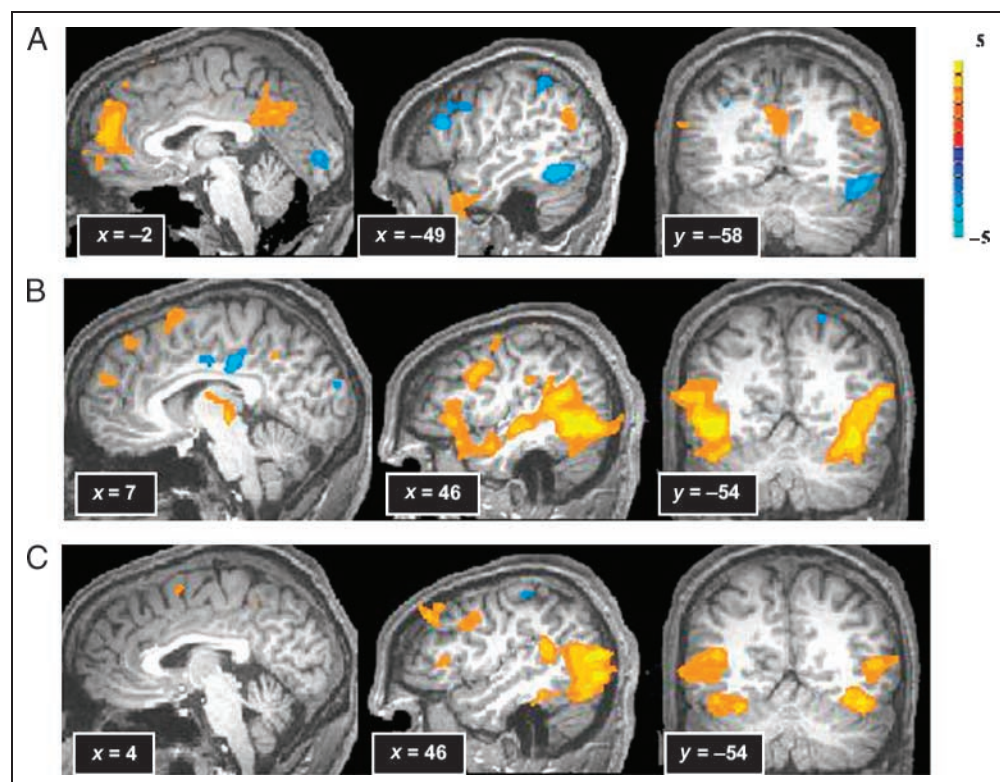


Table 1. List of All Areas of Activation for the Contrast False Belief Stories versus Physical Stories

Region	BA	x	y	z	Z Score
APC	9	-3	53	13	4.12
	9	6	51	35	4.46
	10	10	58	4	4.1
Superior frontal gyrus	9	-21	47	35	4.33
Middle frontal gyrus	44	-42	31	21	-4.36
Inferior frontal gyrus	44	-42	2	25	-3.7
	47	36	21	-14	3.5
SMA	8	9	22	55	3.62
TPJ	39	-53	-59	24	3.52
Temporal pole	38	35	14	-31	3.93
	38	-50	12	-26	3.63
Middle temporal gyrus	37	52	-47	-5	-3.71
Inferior temporal gyrus	37	-48	-48	-10	-4.11
Parahippocampal gyrus	36	-34	-27	-16	3.25
Cingulate gyrus	23	5	-17	33	3.96
Posterior cingulate/precuneus	7	-11	-50	32	3.62
IPS	19	-26	-72	38	-3.9
IPL	40	-49	-42	46	-3.34
Lingual gyrus	18	-12	-89	-6	-3.47

At a lower threshold ($p < .01$), an additional peak of activation was identified in the right TPJ (Talairach coordinates: $x = 57$, $y = -56$, $z = 26$).

APC = anterior paracingulate cortex; SMA = supplementary motor area; IPS = intraparietal sulcus; IPL = inferior parietal lobule; TPJ = temporo-parietal junction.

$Z = 3.07$, $p = .002$). Table 2 lists all areas that showed a significant effect for this contrast.

Biological Motion versus Scrambled Movements

The group analysis for the contrast point-light displays of biological motion versus point-light displays with random movements (Figure 1) showed stronger activity for biological movements in the pSTS bilaterally (in the right with a maximum $Z = 4.46$, $p < .0001$; in the left with a maximum $Z = 4.18$, $p < .0001$), in the inferior temporal gyrus bilaterally (in the right with a maximum $Z = 4.76$, $p < .0001$; in the left with a maximum $Z = 4.3$, $p < .0001$), and in the fusiform gyrus bilaterally (in the right with a maximum $Z = 4.22$, $p < .0001$; in the left with a maximum $Z = 4.79$, $p < .0001$). At a lower threshold, a stronger response for biological motion also was identified in the right frontal operculum (maximum $Z = 3.16$, $p = .002$), Table 3 lists all areas that showed a significant effect for this contrast.

Comparison of Regions of Activation for Different Tasks

Each of the activation patterns detected for each contrast was then directly compared by overlaying the areas of activation for each condition to determine areas that were commonly activated by the different tasks (Figure 2). Despite the fact that both contrasts—false belief stories as compared to descriptive stories and animations depicting social interactions as compared to random movements—revealed activity in the APC and in the PCC/PC, there was only minimal overlap in the APC and no overlap in the PCC/PC. Whereas the animations activated only a small region in the right APC, the false belief stories activated a region contralateral to that locus at a similar height and additional regions in the right APC that were superior and inferior to the locus of activation for animations. Point-light biological motion stimuli did not evoke activity in either the APC or the PCC/PC. In the left hemisphere,

Table 2. Complete List of Areas of Activation for the Contrast Social Animations as Compared to Animations with Random Movements

Region	BA	x	y	z	Z Score
APC	9	8	51	21	3.25
Frontal operculum	45	-48	24	16	3.83
	45	50	28	9	3.86
SMA	8	3	14	58	3.58
	8	-3	36	46	3.46
Premotor area	44	45	7	33	4.01
STS	22	-46	-14	-9	4.28
	22	-57	-57	15	4.7
	22	47	-45	15	4.48
Temporal pole	21	49	5	-17	4.37
	38	-48	11	-18	3.99
Inferior temporal cortex	37	42	-53	-3	6.07
Fusiform gyrus	37	-40	-53	-11	6.03
	37	35	-53	-16	4.11
Posterior cingulate/precuneus	7	8	-50	37	3.07
IPL	40	-59	-33	30	4.21
	40	45	-25	26	3.41
Cingulate gyrus	31	-4	-25	34	-4.11
Insula		-24	22	4	3.88
Caudate nucleus		17	3	14	3.44
Thalamus		6	-22	-1	3.77
Cerebellum		-28	-75	-33	3.32
		14	-28	-30	4.17

SMA = supplementary motor area; IPL = inferior parietal lobule.

Table 3. Complete List of Areas of Activation for the Contrast Point-Light Displays of Biological Motion versus Random Movements

Region	BA	x	y	z	Z Score
Precentral gyrus	4	-55	-12	32	-3.3
Frontal operculum	45	43	28	6	3.16
Premotor area	8	37	10	28	3.61
Middle frontal gyrus	9	45	33	35	3.75
pSTS	22	59	-37	20	4.46
	37	-52	-59	9	4.18
Middle temporal gyrus	39	45	-74	12	4.97
Inferior temporal cortex	37	43	-68	-2	4.76
	19	-44	-75	4	4.304
IPS	39	28	-65	38	3.32
Postcentral gyrus	1	49	-25	51	-3.91
Fusiform gyrus	19	-41	-64	-15	4.79
	37	40	-42	-16	4.22
Lingual gyrus	18	-15	-83	-13	3.34
Inferior occipital gyrus	18	-25	-95	-12	3.92
Posterior insula		-38	-31	16	-3.307
Putamen		24	10	8	3.718
Cerebellum		12	-66	-31	3.52

pSTS = posterior superior temporal sulcus; IPS = intraparietal sulcus.

the TPJ region activated by false belief stories was 2 mm posterior and 9 mm superior to the pSTS locus activated by social animations. In the right hemisphere, the TPJ locus was 11 mm posterior and 11 mm superior to the pSTS locus.

DISCUSSION

Neuroimaging studies have consistently reported activation in the APC, pSTS/TPJ, and PCC/PC during tasks requiring interpreting or predicting someone else's behavior based on his or her mental states. However, recent meta-analyses have highlighted how loci of activations span nearly the entire APC and cover a large portion of the pSTS including the TPJ (Amodio & Frith, 2006; Ochsner et al., 2004; Allison et al., 2000). Whereas previous attempts to distinguish the roles played by different subregions of these areas relied on comparisons between published studies (e.g., Amodio & Frith, 2006; a notable exception is the recent study by Mitchell, Macrae, & Banaji, 2006), we compared the loci of activation for two commonly used ToM tasks in the same subjects. We chose to compare the activations evoked by

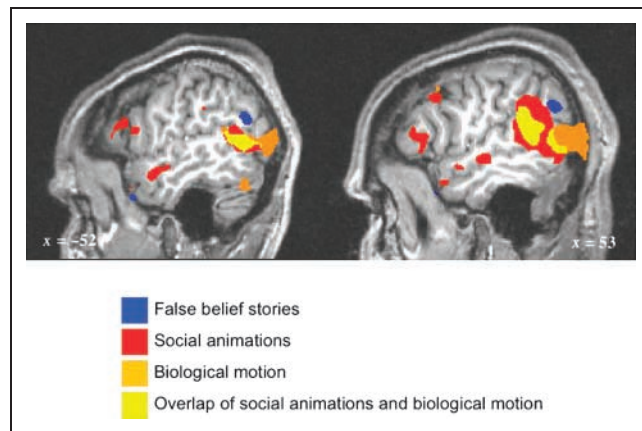


Figure 2. Areas of overlap for the three tasks. Areas of activation for the contrast false belief stories as compared to physical stories are illustrated in blue. Areas of activation for the contrast social animations versus random movements are illustrated in red. Areas of activation for the contrast biological motion versus random movements are illustrated in orange. Areas of overlapping activity for the social animations with biological motion are illustrated in yellow. In the right hemisphere, the threshold for the contrast false belief stories as compared to descriptive stories was lowered to $p < .01$ to illustrate the location of the right TPJ locus.

false belief stories and social animations because they represent markedly different representations of mental states. Whereas false belief stories induce subjects to represent the beliefs of others that are contingent on understanding that person's perspective, social animations induce apprehension of intentions and goals of others that are implied by their actions. Furthermore, we employed point-light displays of biological motion to control for understanding of actions that are not associated with social interactions.

We found that these tasks evoke distinct patterns of activity in the neural systems for ToM and for action understanding. Whereas the false belief stories evoked stronger activity in the APC, PCC/PC, and TPJ—components of the ToM system—the social animations evoked stronger activity in the pSTS and MNS. These results show for the first time that two nearby regions, the TPJ and pSTS, play dissociable roles. Whereas the TPJ plays a role in the representation of covert mental states, such as false beliefs and intentions that may or may not lead to actions, the pSTS plays a role in the representation of perceived actions and, in concert with the MNS, the representation of the intentions that are implied by those actions.

Previous studies have shown activation of the frontal operculum and IPL—the MNS—by articulated biological motion (Peelen, Wiggett, & Downing, 2006; Saygin et al., 2004; Beauchamp et al., 2003). Surprisingly, the social animations also evoked activity in the frontal operculum, even though these animations involve only the movements of rigid geometric shapes that imply intentions and goals but do not depict any articulated movements of body parts. The point-light displays of biological mo-

tion as compared to the point-light displays with random movements also evoked stronger activity in the frontal operculum. These results highlight the role of the frontal operculum in interpreting other people's intentions at a level of abstraction higher than the kinematics of goal-directed actions.

Moreover, the fusiform gyrus was strongly activated by both the social animations and by the point-light displays of biological motion, consistent with previous reports (Peelen et al., 2006; Martin & Weisberg, 2003; Castelli et al., 2000; Grossman et al., 2000). These results suggest that the representation of objects in the fusiform cortex is not dependent on their form but, rather, on the implication that the perceived objects have agency—the property of initiating action.

Subdivisions within the APC

Both false belief stories and social animations evoked activity in the APC, but the activation by false belief stories was stronger and more extensive and the loci of activity for these tasks had minimal overlap. Whereas social animations only evoked activity in a small locus in the right APC, false belief stories were associated with loci of activity in a homologous locus in the left APC and in loci that were both superior and inferior to the locus for animations in the right APC. These results do not suggest the dissociation, proposed by Amodio and Frith (2006), between monitoring the actions of others in the dorsal APC and representation of the thoughts and emotions of others in the middle APC, but do indicate that these two varieties of ToM task evoke different patterns of activity, both in terms of location and magnitude. Biological motion that is not associated with social interactions, however, did not evoke activity in the APC, indicating that this region is associated with the representation of the social intentions of actions, consistent with the proposal of Walter et al. (2004).

Dissociation between the pSTS and TPJ

The social animations, unlike the false belief stories, evoked activity in an extensive region along the full anterior–posterior extent of the STS with a peak of activity in the pSTS. The pSTS peak also was associated with perception of articulated biological motion. The false belief stories did not evoke activity in this complex. Instead, false belief stories evoked a small locus of activity in a more posterior and superior location in the left TPJ with a marginally significant homologous locus in the right TPJ. This dissociation between the pSTS and the TPJ is consistent with the proposal of Saxe (2006).

In Table 4 and Figure 3, we present a meta-analysis of activations in these regions associated with various ToM tasks, social animations, and biological motion. As can be seen in Figure 3, the distribution of loci associated with ToM tasks and biological motion overlap, but those

associated with ToM are generally superior and posterior to the loci associated with biological motion. The loci associated with social animations lie more within the distribution of loci associated with biological motion but toward the edge that overlaps with ToM. Our results, however, clearly show that the activity evoked by social animations in pSTS is dissociable from the TPJ locus activated by false belief stories (Figure 2).

The current results are the first within-subjects comparison that demonstrates this dissociation between the pSTS as a part of the action understanding system and the TPJ as a part of the ToM system. Meta-analyses, such as the one that we present here, can be useful, as they synthesize large datasets from many subjects, but they can lead to erroneous conclusions because of differences in the experimental and analytic methods used in different investigations (see Farah & Aguirre, 1999).

Interestingly, the ToM areas activated by recognition of personally familiar faces (Gobbini & Haxby, 2007; Gobbini et al., 2004; Leibenluft et al., 2004) are closer to the TPJ loci identified here than to the pSTS (Figure 3 and Table 4), and are in the same sector of the middle APC that was activated by both false belief stories and by social animations. We have hypothesized that this activity reflects the spontaneous activation of person knowledge about personally familiar individuals.

Inferring Intentions and the Neural System for Action Understanding

The pattern of activity evoked by social animations reflects a network that has been primarily associated with action understanding, namely, the pSTS, the IPL, and the frontal operculum. In addition, the social animations activated an extensive region that subsumed the full length of the right STS (Figure 1) and additional activations in the left anterior STS (Table 1).

The frontal operculum is the human homologue of area F5 in the monkey brain (Petrides & Pandya, 1994). Mirror neurons have been reported in areas F5 and PF of the monkey brain (Gallese et al., 1996). In the monkey, mirror neurons have been associated primarily with the viewing and execution of goal-directed movements of the forelimbs and mouth and with communicative mouth movements (Fogassi et al., 2005; Gallese et al., 1996). In humans, activity in the frontal operculum and the IPL also is evoked by the viewing and execution of goal-directed and expressive movements (Montgomery et al., 2007; Iacoboni et al., 2005). The social animations, however, do not depict the articulated movements of the limbs or face. Rather, the actions of individuals are reduced to the unarticulated movements of rigid shapes. Thus, these animations depict goal-directed action at a level of abstraction that is independent of the kinematics of specific movements. Their efficacy for engaging the MNS suggests that system represents actions at the level of the intended goals of those actions (Lyons, Santos, & Keil, 2006; Gallese,

Table 4. Locations of Loci of Activation in the TPJ and pSTS Associated with Various ToM Tasks, Social Animations, and Biological Motion

	Task	Talairach Coordinates					
		x	y	z	x	y	z
<i>False Beliefs</i>							
Gallagher et al., 2000	ToM stories	-46	-56	26	66	-52	8
Calarge et al., 2003	ToM stories	-48	-64	25			
Saxe & Kanwisher, 2003	ToM stories	-54	-60	21	51	-54	27
<i>Moral Decisions</i>							
Greene, Nystrom, Engell, Darley, & Cohen, 2004	Personal vs. Impersonal moral judgment	-45	-58	17	46	-49	19
<i>Person Knowledge</i>							
Gobbini et al., 2004	Person knowledge	-36	-63	30	49	-55	19
Leibensluft et al., 2004	Person knowledge						
	One's own child	-54	-67	24			
	Familiar children	-48	-61	17			
<i>Competitive Games</i>							
Rilling et al., 2004	Competitive game against a human partner				48	-55	27
<i>Animations</i>							
Castelli et al., 2000	Animations	-58	-48	4	60	-56	12
Martin & Weisberg, 2003	Animations	-49	-57	17	56	-58	17
<i>Biological Movements</i>							
Bonda et al., 1996	Hand action	-48	-61	17			
	Body movements				56	-54	7.5
Puce et al., 1998	Eye and mouth movements	-46	-53	5	49	-49	3
Wicker, Michel, Henaff, & Decety, 1998	Eye gaze	-44	-68	4	42	-58	8
					62	-50	6
Hoffman & Haxby, 2000	Eye gaze	-45	-56	11	50	-63	4
Jacoboni et al., 2001	Action observation				57	-50	16
Grossman & Blake, 2002	Body motion	-41	-53	12	46	-48	12
Beauchamp et al., 2003	Body motion	-39	-59	15	47	-56	15
Grèzes, Frith, & Passingham, 2004	Deceptive actions				64	-44	22
					50	-32	-6
Saygin et al., 2004	Body motion	-46	-54	14	53	-59	13
Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005	Mean of meta-analysis						
	Eye movements	-48	-55	6	52	-54	5
	Mouth movements	-54	-33	5	56	-35	6
	Hand movements	-50	-57	20	53	-53	7
	Their data						
	Eye movements				46	-58	11
	Mouth movements	-60	-44	7	53	-37	4
	Hand movements				49	-68	4
Peelen et al., 2006	Body motion	-56	-39	25	57	-41	21

The locations of these activations are also shown in Figure 3.

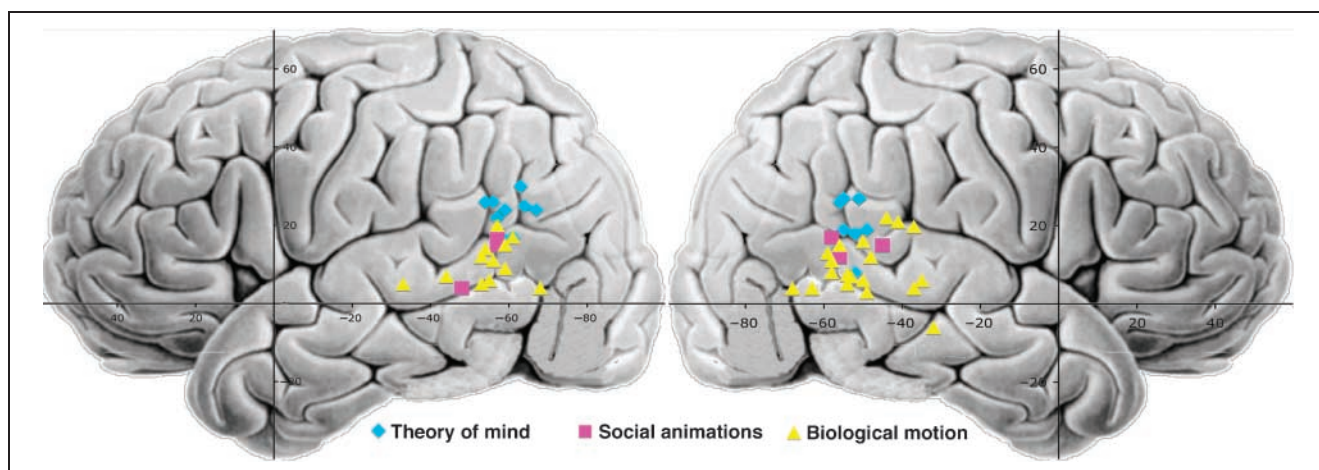


Figure 3. Locations of loci of activations associated with ToM, social animation, and biological motion tasks, projected onto the left and right lateral surfaces of the brain. The studies and coordinates for each locus are presented in Table 3.

2003). This level of abstraction is consistent with the highest level of action representation in the hierarchical mosaic model of Wolpert, Doya, and Kawato (2003).

Previous neuroimaging studies of social animations did not report activity in the frontal operculum (Martin & Weisberg, 2003; Castelli et al., 2000). It would be worthwhile to reexamine the data from those studies to investigate this discrepancy.

Dissociable Roles of the ToM and Action Understanding Systems in the Representation of Mental States

Representation of the intentions and goals that are implied by actions are clearly a major component of the representation of those actions in the action understanding system. The mental states that have been associated with the ToM system also include the intentions and goals that motivate behavior. The results of this study, as well as a meta-analysis of previous studies, however, suggest that these two types of intentions have distinct representations, including distinct loci of activation in the pSTS and TPJ. Thus, the conceptual distinction between these two types of mental states that share the name, “intention,” needs to be clarified.

The developmental literature also suggests a dissociation between these two levels of understanding the intentions of others (Battacchi, 2006; Meltzoff, Gopnik, & Repacholi, 1999; Battistelli, 1997). Whereas children under age 3 can understand the intentional stance implied by pretending (e.g., holding a banana to one’s ear and talking as if on the telephone), children are not able to understand the false beliefs of others until after age 4 (Leslie, 1987). Thus, the representation of others intentions that are implied by perceived actions develops before the representation of the covert mental states of others that may predict future actions (Meltzoff et al., 1999). This distinction between different representations

of the intentions of others corresponds to Searle’s (1980) distinction between “intention-in-action” and “prior intention.” The current results suggest that the first level of intention understanding is mediated by the action understanding system (pSTS and the MNS), whereas the second level of intention understanding is mediated by the ToM system (TPJ, PCC/PC, and APC).

The Representation of Agency in the Fusiform Gyrus

Animations depicting social interactions and point-light displays of biological motion also evoked activity in the fusiform gyrus and the inferior temporal cortex, consistent with previous reports (Peelen et al., 2006; Beauchamp et al., 2003; Martin & Weisberg, 2003; Grossman & Blake, 2002; Castelli et al., 2000). The lateral fusiform cortex contains overlapping regions that respond selectively to faces (the fusiform face area; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997), to body parts (the fusiform body parts area; Peelen & Downing, 2005), to animals (Chao, Martin, & Haxby, 1999), to biological motion (Peelen et al., 2006; Beauchamp et al., 2003; Grossman et al., 2000), and to social animations (Martin & Weisberg, 2003; Castelli et al., 2000). The response to these stimuli can be distinguished based on the pattern of activity (Peelen et al., 2006). Clearly, the responsiveness of this region is not dependent upon the visual form of the objects that stimulate it. The social animation and point-light biological motion stimuli involve almost no form, and the controls for these conditions involve exactly the same shapes and points.

The common thread that relates these stimuli to each other is that they are all related to agents (i.e., entities that initiate actions, not to objects that only change or move when acted upon). Children are sensitive to this distinction, as embodied by simplified animate and inanimate movements, in the first year of life (Mandler,

1992). We propose that the lateral fusiform cortex is distinguished by its central role in the visual perception of stimuli that imply agency, a more general role than former hypotheses (Kanwisher et al., 1997). Our hypothesis provides a better account for the diversity of stimuli that evoke strong activity in the lateral fusiform gyrus and relate it to a fundamental distinction between two classes of entities—agents and objects—that develops at a very early age.

An alternative account for the specialization of visual processing in the lateral fusiform gyrus posits that this area is involved in perceptual expertise, independently of the category of object being viewed (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). The stimuli that have been used in studies that support this hypothesis, however, are either agents (birds) or agent-like. The artificial stimuli, “greebles,” have the appearance of imaginary animals. Even the inanimate category of cars is ambiguous with respect to agency. Cars have face-like features and are self-propelled. A more stringent test of the expertise hypothesis, that would contrast it to our agency hypothesis, would study expert visual perception of unambiguously inanimate entities, such as gemstones or flowers.

Conclusions

Our results demonstrate distinct roles for the ToM and action understanding systems in social cognition. In particular, representing the covert mental states of others that may predict future behavior activates the APC, the PCC/PC, and the TPJ. By contrast, representing the intentions and goals that are implied by perceived actions activates the pSTS and the MNS. Our results demonstrate a dissociation between the pSTS, which is part of the action understanding system, and the TPJ, which is part of the ToM system.

Furthermore, our results indicate that the role of the MNS in the representation of action is at a more abstract level than the kinematics of biological motion. Instead, activity in the MNS represents the intentions and goals of an action, even when the kinematics of the specific articulated movements for that action are not perceived.

Finally, the lateral fusiform cortex responds selectively to a wide range of stimuli that do not share common visual forms but are all associated with agency. We propose a new hypothesis that this cortex plays a more general role in the visual perception of entities that are agents, not in the perception of specific categories that are defined by their form.

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