Reflecting upon Feelings: An fMRI Study of Neural Systems Supporting the Attribution of Emotion to Self and Other

Kevin N. Ochsner[1], Kyle Knierim[2], David H. Ludlow[2], Josh Hanelin[1], Tara Ramachandran[2], Gary Glover[2], and Sean C. Mackey[2]

Abstract

■ Understanding one's own and other individual's emotional states is essential for maintaining emotional equilibrium and strong social bonds. Although the neural substrates supporting reflection upon one's own feelings have been investigated, no studies have directly examined attributions about the internal emotional states of others to determine whether common or distinct neural systems support these abilities. The present study sought to directly compare brain regions involved in judging one's own, as compared to another individual's, emotional state. Thirteen participants viewed mixed valence blocks of photos drawn from the International Affective Picture System while whole-brain fMRI data were collected. Preblock cues instructed participants to evaluate either their emotional response to each photo, the emotional state of the central figure in each photo, or (in a baseline condition) whether the photo was taken indoors or outdoors. Contrasts indicated (1) that both self and other judgments activated the medial prefrontal cortex (MPFC), the superior temporal gyrus, and the posterior cingulate/precuneus, (2) that self judgments selectively activated subregions of the MPFC and the left temporal cortex, whereas (3) other judgments selectively activated the left lateral prefrontal cortex (including Broca's area) and the medial occipital cortex. These results suggest (1) that self and other evaluation of emotion rely on a network of common mechanisms centered on the MPFC, which has been hypothesized to support mental state attributions in general, and (2) that medial and lateral PFC regions selectively recruited by self or other judgments may be involved in attention to, and elaboration of, internally as opposed to externally generated information. ■

INTRODUCTION

At various moments in our daily lives we might have cause to reflect on how we feel. We might reflect because someone asks "How are you?", or we might take stock when we've accomplished a goal (I got the job and I feel great!), experienced a significant life event (My aunt died and I feel awful), or are anticipating one (We're expecting a child and are excited but nervous!). Whatever it is that we reflect, research suggests that the ability to readily and specifically answer the question, "How do I feel?" helps us to identify situations worth seeking or avoiding, engage in behaviors that promote desired affective states, and effectively regulate our emotions (Barrett, Gross, Christensen, & Benvenuto, 2001; Lane & Schwartz, 1987). But our social world prompts us to reflect not just upon our own feelings, but the feelings of those around us as well. As we interact with colleagues, compete with opponents, or watch our friends and family experience their own ups and downs, having insight into the feelings of others enables us to understand what they value, how they feel about us, to offer appropriate support or gain competitive advantage, and to predict their future behavior (Blair, 2003; Baron-Cohen, 1995).

Despite the importance of these abilities for our social and emotional well-being, our understanding of the underlying neurocognitive mechanisms has only just begun to take shape. The goal of the present study was to use functional magnetic resonance imaging (fMRI) to directly compare the neural processes supporting inferences about one's own and other individuals' emotional states. By determining whether and how these processes are similar and different, we might gain insight into the question of how we reflect upon feelings, knowing that we feel good or bad, and that others feel good or bad as well.

On one hand, there are reasons to believe that common psychological and neural processes mediate understanding of one's own and other people's emotions. Proponents of this view might argue that the perception of emotion in self and other involves drawing inferences and making attributions about the nature of internal mental states, a capacity referred to as theory of mind (TOM) (Lane & McRae, in press; Gallagher & Frith,

[1]Columbia University, [2]Stanford University

2003; Frith & Frith, 1999; Premack & Woodruff, 1978). TOM is used to infer the intentions and beliefs that motivate and guide goal-directed behavior, and has been conceived as a central ''mentalizing'' ability that can be broadly applied to understanding many kinds of mental states, whether those states are one's own or those of another person (Gallagher & Frith, 2003; Frith & Frith, 1999; Premack & Woodruff, 1978).

Empirical support for a central mentalizing mechanism comes from functional imaging studies observing activation of a particular brain region, the medial prefrontal cortex (MPFC), both when individuals judge some aspect of their own or someone else's mental states. When perceiving one's self, MPFC activation has been observed in a variety of conditions listed in Table 5 whose accompanying activation foci are visualized in Figure 4A. Self-referential judgments activating the MPFC include evaluating one's internal state of arousal or pleasantness (a–f in Table 5), judging likes and dislikes for externally presented stimuli (g–k), recognition of one's own face or voice (l–o), perspective taking (p–r), judging one's personality traits and attributes (s–y), and self-generating thoughts/associations in a goal-directed (z–ee) or spontaneous fashion (ff; cf. Gusnard & Raichle, 2001). When perceiving others, MPFC activation has been observed in a variety of tasks and conditions, also listed in Table 5 with accompanying activation foci visualized in Figure 4B. Conditions producing social-cognition-related activations of MPFC include judging the goodness/badness of actions or images (1–6 in Table 5), perceiving eye gaze (7–10), judgments of social targets (represented by photos, words, or cartoons of moving shapes) that may require mental state inferences and/or recruitment of social knowledge (11–19), taking a third-person perspective (20–21), tasks requiring explicit TOM judgments of intention (22–27), and games that participants believe are being played interactively in real time with another participant (28–29). Taken together, data from studies of self-reflection and social-cognition-related judgments implicate MPFC in the general process of ''mentalizing'' about internal states (Gallagher & Frith, 2003).

On the other hand, the cross-study comparisons cited above provide only indirect support for the hypothesis that the same MPFC-based system is recruited by self- or other-focused mental state attributions. As vividly illustrated in Figure 4, the variety of self-referential and social-cognitive judgments employed thus far have activated virtually the entire extent of the medial frontal cortex, spanning the dorsal (including Brodmann's areas [BAs] 8–10 and dorsal portions of BA 32) and ventral (BAs 10, 11, 14, 25, and the ventral anterior cingulate) MPFC as well as the anterior cingulate cortex (BAs 24–32). The variability in activation could reflect overlap of self-reflective and social-cognitive processing, but it also could reflect recruitment of a number of distinct processes in distinct medial frontal subregions not yet well differentiated across tasks, cross-study variability in functional localization across participants, and/or variations introduced by cross-experimenter differences in spatial or statistical processing of data. In the absence of within-study comparisons, it is quite difficult to know whether apparent overlap in fact reflects common recruitment of underlying processes. To date, only one study has addressed this issue in the context of TOM. Using story vignettes, Vogeley et al. (2001) found MPFC involvement both when making TOM attributions about descriptions of another individuals' behavior and when making intentional judgments about descriptions of one's own behavior, but did not find differential MPFC activation between the two conditions. No studies have examined this issue in the context of emotion.

More generally, to date, no studies have attempted to isolate processes supporting judgments about the internal emotional states of others. Although TOM-related studies may sometimes use cues with affective connotations (e.g., Wicker, Perrett, Baron-Cohen, & Decety, 2003), they may more commonly require judgments about non-affective, cognitive states, and in any event, the extent to which emotional inferences are required in such tasks has not been systematically manipulated or measured distinct from the need for drawing inferences about cognitive states. Studies showing MPFC activation in response to emotional films (e.g., Lane, Fink, Chau, & Dolan, 1997), when recalling emotional memories (Reiman et al., 1997), during visual imagery of traumatic events (Shin et al., 1997), or when perceiving happy, angry, or sad emotional facial expressions (Kesler-West et al., 2001; Blair, Morris, Frith, Perrett, & Dolan, 1999; Phillips et al., 1998), also are ambiguous because they do not control the extent to which participants reflect upon their own emotional state as compared to that experienced, perceived, or imagined by others. Two studies have found greater MPFC activation when judging how well positive or negative trait words described themselves as compared to another famous individual (Kelley et al., 2002; Craik et al., 1999), but it is not clear how much dispositional trait judgments are related to judgments of one's current emotional state.

Beyond the possible recruitment of the MPFC, a number of other processing systems might be similarly or differentially recruited during self- and/or other-focused emotion perception. Indeed, the mechanisms supporting ''mentalizing'' are complex, and when fully unpacked may include a larger network of neural systems that are thought to play a role in TOM and/or self-reflective judgments, including: frontal regions important for language and working memory; superior temporal regions implicated in processing nonverbal cues with social significance; the posterior cingulate cortex, which has been associated with affective evaluation; and the parietal cortex, which may be involved in the representation of spatial perspectives that help distinguish self and other (Frith & Frith, 1999, 2003; Gallagher

& Frith, 2003; Maddock, Garrett, & Buonocore, 2003; Meltzoff & Decety, 2003; Saxe & Kanwisher, 2003; Vogeley & Fink, 2003; Johnson et al., 2002; Kelley et al., 2002; Brunet, Sarfati, Hardy-Bayle, & Decety, 2000; Castelli, Happe, Frith, & Frith, 2000; Gallagher, Happe, et al., 2000; Kircher, Senior, Phillips, Benson, et al., 2000; Maddock & Buonocore, 1997). Attributions of emotion to self and other could commonly or differentially recruit such systems independently of, or in concert with, MPFC. This possibility is supported by the study of Vogeley et al. (2001), who found greater temporal–parietal activation when participants made intentional TOM attributions about their own as compared to another person's behavior.

To identify the common and distinct neural systems supporting the evaluation of emotion in self and other, the present study employed a variation of a paradigm developed by Lane et al. (1997; cf. Gusnard et al., 2001). In this task, participants were presented with a series of blocks of photographic images and for each block were asked to judge either their own emotional response to each photo (pleasant, unpleasant or neutral), or to judge where the image had been taken (indoors, outdoors, or not sure). The present study modified this paradigm through the inclusion of a third condition, which asked participants to judge the emotional response of the central character in each image (pleasant, unpleasant, or neutral). The inclusion of this condition allows (1) identification of regions commonly activated when judging one's own (self blocks) or another person's (other blocks) feelings as compared to a perceptual judgment controlling for spatial attention to images (in–out blocks), and (2) direct comparison of regions implicated in evaluating one's own (self blocks) or another person's emotional experience (other blocks) to identify regions uniquely activated by each type of judgment.

RESULTS

Behavioral Results

An ANOVA on proportion of affect judgments with type of judgment (self vs. other) and valence of judgment (pleasant, unpleasant, or neutral) as within-subject factors revealed a main effect of a valence [$F(2,12) = 27.48$, $p < .0001$], and no significant effects involving type of judgment (Figure 1A). Planned contrasts demonstrated that the greatest proportion of affect judgments were positive [$F(1,12) > 9.0$, $p < .006$ for comparisons to neutral and negative] and the smallest proportion were neutral [$F(1,12) > 53.94$, $p < .001$ for comparisons to negative and positive]. An ANOVA on response times using the same factors again revealed a main effect of a valence [$F(2,12) = 36.92$, $p < .0001$], and no significant effects involving type of judgment (Figure 1B). Planned contrasts demonstrated that response times were longest when participants judged an emotional response to be neutral [$F(1,12) > 63.80$, $p < .001$ for comparisons to negative and positive]. Positive and negative judgments were made with equal speed [$F(1,12) < 1$]. Analyses of judgments made on in–out trials were conducted separately and revealed a nonsignificant tendency for participants to judge more photos as having been taken outside rather than inside [$t(12) = 2.08$, $p < .06$], whereas unsure judgments were made least often [$t(12) > 5.16$, $p < .001$ for comparisons with inside and outside]. Similar trends were found for response times, with outside judgments made most rapidly [$t(12) > 3.31$, $p < .008$ for comparisons with inside and unsure], whereas unsure judgments tended to be made most slowly [$t(12) = 1.60$, $p < .14$ vs. inside]. Overall, response times for emotional self and other as compared to spatial in–out judgments were made with equal speed ($p > .47$).

Imaging Results

Regions associated with the evaluation of one's own emotional experience were identified in the contrast of self and in–out blocks, whereas regions associated with the evaluation of another person's emotional experience were identified in the contrast of other and in–out blocks.[1] These two contrasts revealed similar patterns of activation, as shown in Tables 1 and 2, and the blue circles in Figure 4A and B. Activation was found in overlapping regions of the MPFC, including a peak activated voxel (−6, 52, 32) that was found for clusters in both contrasts, and in similar and/or overlapping regions of the posterior cingulate cortex/precuneus, and the superior temporal gyrus (STG). Dissimilar activations included medial prefrontal activations that extended dorsally into BA 8, the left superior lateral prefrontal cortex, the anterior cingulate cortex, and the left inferior parietal lobe for self-focused emotion attributions, and the left ventral lateral prefrontal (overlapping Broca's area) and parahippocampal cortices for other-focused emotion attributions.

Regions commonly activated by both self and other attributions were identified formally by masking the contrast of other and in–out blocks with the contrast of self and in–out blocks, and were confirmed by performing planned comparison t tests on measures of percent signal change to verify that self and other blocks showed similar patterns of activation that were significantly different from activation shown for in–out blocks. As shown in Table 3 and Figure 2, common activation was identified in regions of the MPFC, the lateral PFC, the posterior cingulate cortex/precuneus, and the superior temporal sulcus/gyrus. For all regions, t tests confirmed that both self and other blocks showed significantly greater activation than in–out blocks (all $t > 2.4$, $p < .05$). In addition, self and other blocks showed equivalent levels of activation (all $t < 1$, $p = ns$)

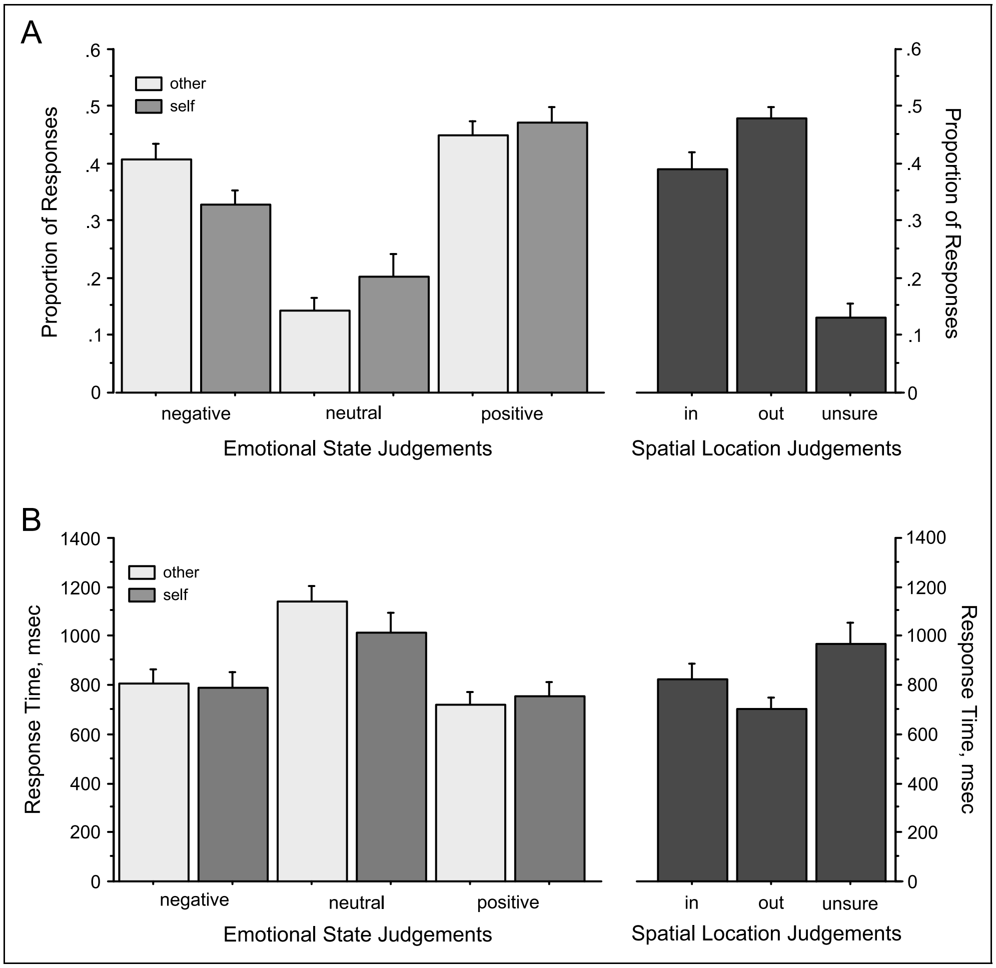

Figure 1. Behavioral data for self, other, and in–out judgments. (A) Proportions of affect judgments for self and other blocks, and inside versus outside judgments for in–out blocks. (B) Group averaged response times for judgments made for self, other, and in–out blocks.

for all regions except for the lateral prefrontal region for which there was a marginally significant difference [$t(12) = 2.15, p < .06$].

Regions specifically associated with either the evaluation of one's own, or another person's, emotional experience were identified by directly contrasting self and other blocks. As shown in Figure 3, self blocks selectively activated two clusters in the MPFC as well as in the right middle temporal gyrus, whereas other blocks selectively activated the left ventral lateral prefrontal cortex and the cuneus in the medial occipital lobe (Table 4). Planned comparison t tests on measures of block average percent signal change confirmed that self blocks selectively recruited two regions of the MPFC ($t > 2.3$, $p < .05$) and that other blocks selectively recruited the lateral PFC and the occipital cortex ($t > 2.4$, $p < .05$).

DISCUSSION

This is the first study to directly compare neural systems involved in attributing emotional experiences to oneself and to other individuals. With equal speed participants discerned equal proportions of pleasant, unpleasant, and neutral affective states in themselves and in individuals depicted in photographic scenes.

Common Processes Mediating Attribution of Emotion to Self and Other

In comparison to baseline judgments of the spatial characteristics of images, neural correlates of self- and other-focused attributions were similar in three important ways. First, self- and other-oriented judgments commonly recruited regions of the MPFC that previously have been implicated both in TOM (Gallagher & Frith, 2003; Frith & Frith, 1999) and in the representation of meta-states of self-awareness, thought to be necessary for reflecting upon (Lane & McRae, in press) and regulating (Ochsner, Ray, Robertson, Cooper, Chopra, Gabrieli, & Gross, in press; Ochsner & Gross, 2004) one's own emotional state. Common recruitment of this region by self and other emotion perception supports the hypothesis that a central system supports intentional attributions about one's own and other individual's internal states (Gallagher & Frith, 2003; Premack & Woodruff, 1978; cf. Vogeley et al., 2001) and may suggest that

Table 1. Group Activations for Self > In–Out Contrast

Region of Activation	*Brodmann*	*Coordinates* *x*	*y*	*z*	*Z score*	*Volume* (mm^3)
Superior frontal gyrus	9	−6	52	32	3.59	1072
Superior FG	9	0	56	36	3.53	(L)
Superior FG	L8	−12	58	44	3.37	(L)
Superior frontal gyrus	L8	−12	36	52	3.89	552
Superior FG	L9	0	56	36	3.53	(L)
Superior FG	L9	−12	58	44	3.37	(L)
Superior frontal gyrus	L10	−26	58	30	3.14	256
Superior FG	L10	−20	66	34	3.07	(L)
Superior FG	L10	−28	50	32	2.84	(L)
Superior frontal gyrus	R8	16	34	52	3.45	168
Medial frontal gyrus	L10	−10	56	14	3.95	2784
Medial FG	9/10	2	56	24	3.79	(L)
Medial FG	10	−2	56	8	3.60	(L)
Anterior cingulate	24	−4	26	28	3.16	216
Anterior cingulate	24	2	−18	40	4.00	376
Posterior cingulate/precuneus	L31	−8	−48	34	3.09	648
Posterior cingulate	L31	−4	−56	22	3.09	(L)
Posterior cingulate	L31	−12	−54	26	3.06	(L)
Superior temporal gyrus	L38	−52	16	−10	4.75	1672
Superior TG	L22	−52	12	2	3.61	(L)
Inferior FG	L45	−52	22	12	3.90	(L)
Middle temporal gyrus	L21/22	−60	−34	−2	3.74	544
Middle temporal gyrus	R22	52	−38	0	3.58	624
Middle TG	R21/22	46	−44	4	3.19	(L)
Inferior parietal lobe	L39	−54	−70	46	3.15	200
Caudate body	L	−2	8	8	3.08	232

Note: Local maxima for clusters are denoted with (L). R and L hemispheres are not designated for maxima within 6 mm of midline. Coordinates are in MNI space.

judgments of the internal feelings of others are guided by an understanding of our own feelings in response to the events we see them experiencing.

Second, both self and other judgments recruited a region of the left inferior lateral prefrontal cortex (BA 45) thought to be involved in mediating competition, or resolving interference, between competing associations in verbal working memory (Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001; Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998). Joint activation of the MPFC and a very similar region of the left inferior lateral PFC has been observed during both the appraisal of aversive stimuli as negative as well as the appraisal of neutral stimuli as negative (Ochsner & Gross, 2004). In combination with the present findings, this suggests that the MPFC and the inferior lateral PFC might work in concert to mediate interference between, and select the appropriate, semantic description of emotional states.

Third, both self- and other-oriented judgments recruited regions spanning the junction of the posterior cingulate cortex and the precuneus, as well as regions of the superior temporal sulcus/gyrus. The posterior cingulate has been associated with evaluating the affective valence of external stimuli (Maddock et al., 2003; Mad-

Table 2. Group Activations for Other > In–Out Contrast

Region of Activation	*Brodmann*	*Coordinates x*	*y*	*z*	*Z score*	*Volume (mm³)*
Medial frontal gyrus	10	−2	56	10	3.03	264
Medial FG	9	−2	56	22	2.94	(L)
Medial FG	10	6	54	26	2.89	(L)
Superior frontal gyrus	9	−6	52	32	3.26	352
Superior FG	9	2	56	40	3.09	(L)
Superior temporal gyrus	R22	44	−42	6	3.54	488
Middle TG	R22	52	−38	2	3.24	(L)
Middle occipital/temporal	R19/37/39	56	−70	6	3.75	256
Precuneus	L31	−10	−58	32	4.12	848
		−8	−52	24	3.22	(L)
		−18	−56	30	2.75	(L)
Parahippocampal gyrus	R	28	−26	−10	3.49	160

Note: Local maxima for clusters are denoted with (L). R and L hemispheres are not designated for maxima within 6 mm of midline. Coordinates are in MNI space.

dock & Buonocore, 1997), and has been activated when participants judged the morality of their own or someone else's behavior (Greene, Sommerville, Nystrom, Darley, & Cohen, 2001). The precuneus has been associated with adopting a first-person as compared to a third-person spatial perspective (Vogeley & Fink, 2003),

Table 3. Group Activations Commonly Observed for Self and Other Judgments (Revealed by Other > In–Out Contrast Masked by Self > In–Out Contrast)

Region of Activation	*Brodmann*	*Coordinates x*	*y*	*z*	*Z score*	*Volume (mm³)*
Medial frontal gyrus	9	2	56	40	3.17	440
Medial FG	9	−4	52	32	2.92	(L)
Medial frontal gyrus	10	2	58	12	2.90	256
Medial FG	9	6	54	26	2.62	(L)
Medial FG	9	−2	54	24	2.56	(L)
Superior frontal gyrus	8	−18	38	54	2.86	232
Superior FG	8	−10	38	56	2.83	(L)
Superior frontal gyrus	10	−26	56	30	2.88	160
Inferior frontal gyrus	45	−52	22	12	3.10	192
Precuneus	7	−6	−60	30	3.85	672
Precuneus	31/7	−14	−58	32	3.56	(L)
Posterior cingulate	31	−4	−54	24	3.00	(L)
Superior temporal sulcus	22	46	−40	2	3.54	256
Superior temporal sulcus	22	−60	−42	2	2.68	128
Superior temporal gyrus	22	−64	−32	12	3.17	104

Note: Local maxima for clusters are denoted with (L). R and L hemispheres are not designated for maxima within 6 mm of midline. Coordinates are in MNI space.

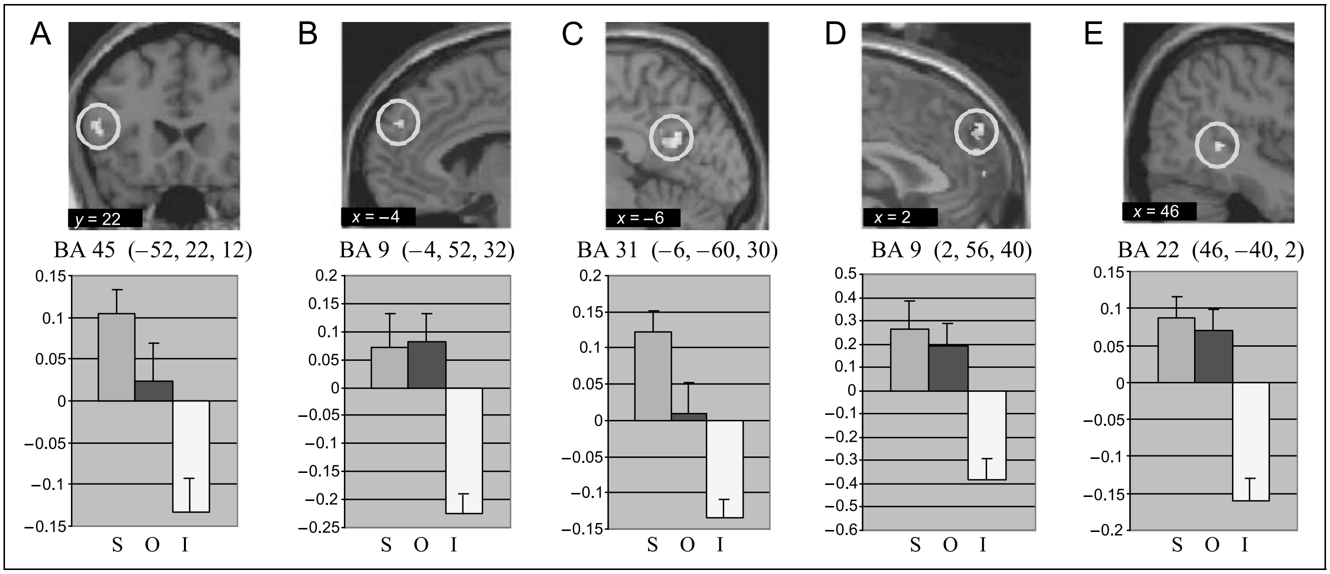

Figure 2. Results of other > in–out group contrast masked by self > in–out group contrast revealing regions commonly activated above baseline superimposed on canonical T1 anatomical images illustrating. Top row shows regions of the left inferior prefrontal cortex (A), the dorsal medial prefrontal cortex (B and D), the posterior cingulated/precuneus (C), and the superior temporal gyrus (E), recruited both by self and other judgments more than in the perceptual baseline condition. Bottom row shows present signal change for each block type for each activated region with error bars showing standard error of the mean. Activation in self and other conditions is statistically equivalent ($p > .05$) for all regions and approached significance only for the left inferior prefrontal cortex (A, $p < .052$) and the posterior cingulate/precuneus (C, $p < .06$).

which may underlie recruitment of this region during episodic memory retrieval (Krause et al., 1999; Fink et al., 1996). Being able to toggle between first- and third-person perspectives (''I feel sad'' vs. ''I keep sighing, I guess I feel sad'') may be essential for making attributions about our own or other's feelings, actions, and attributes. In keeping with this notion, the precuneus has been recruited both by TOM attributions (Wicker et al., 2003; Gallagher, Happe, et al., 2000), and when judging the self-descriptiveness of trait words (Kelley et al., 2002; Kircher, Brammer, et al., 2002; Lieberman, Gaunt, Gilbert, & Trope, 2002) or thoughts (Kjaer, Nowak, & Lou, 2002). The STG may be involved in the bottom-up registration of cues that imply intentional action (Gallagher & Frith, 2003; cf. Saxe & Kanwisher, 2003), as suggested by its activation during the perception of biological motion implied by point-light displays, or actually produced by hands, bodies, mouths, and eyes (for reviews, see Gallagher & Frith, 2003; Puce & Perrett, 2003; Allison, Puce, & McCarthy, 2000), and its activation when participants analyze physical rather than mental causes for described actions (Gallagher, Happe, et al., 2000). Recruitment of these regions in addition to the MPFC suggests that self and other perceptions of emotion rely on a network of regions whose constituent members encode affective, spatial, and nonverbal cues relevant to appraising the affective significance of a stimulus to oneself or others. Just as posterior temporal and lateral prefrontal cortical regions support bottom-up and top-down processes during recognition of nonsocial objects (Kosslyn et al., 1994), posterior cortical regions may support bottom-up recognition of intentional behaviors, whereas the MPFC may support reasoned top-down attributions about the mental states that guide them.

Distinct Processes Mediating Attribution of Emotion to Self and Other

Direct comparison of the two judgment types provided the strongest test of differential recruitment during self and other emotion perception. Because self and other judgments both involved the same type of affective evaluation, differences observed when the two conditions were contrasted directly should reflect differences in the deployment of attention to, and elaboration of, internal or external cues that differentially contribute to each type of judgment. With this in mind, three key findings were observed.[2]

First, self judgments selectively activated the MPFC, suggesting that distinct subregions within the MPFC are involved in self-focused attention as opposed to attributional process generally applicable to understanding one's own and other individual's emotional states.[3] This finding is consistent with studies showing greater MPFC activation when judging whether trait adjectives or phrases describe oneself as compared to another familiar person (Lieberman, Jarcho, & Satpute, in press; Kelley et al., 2002; Kjaer et al., 2002; Craik et al., 1999). Second, other judgments selectively activated the left inferior lateral prefrontal cortex, which is consistent with the general role played by lateral prefrontal areas

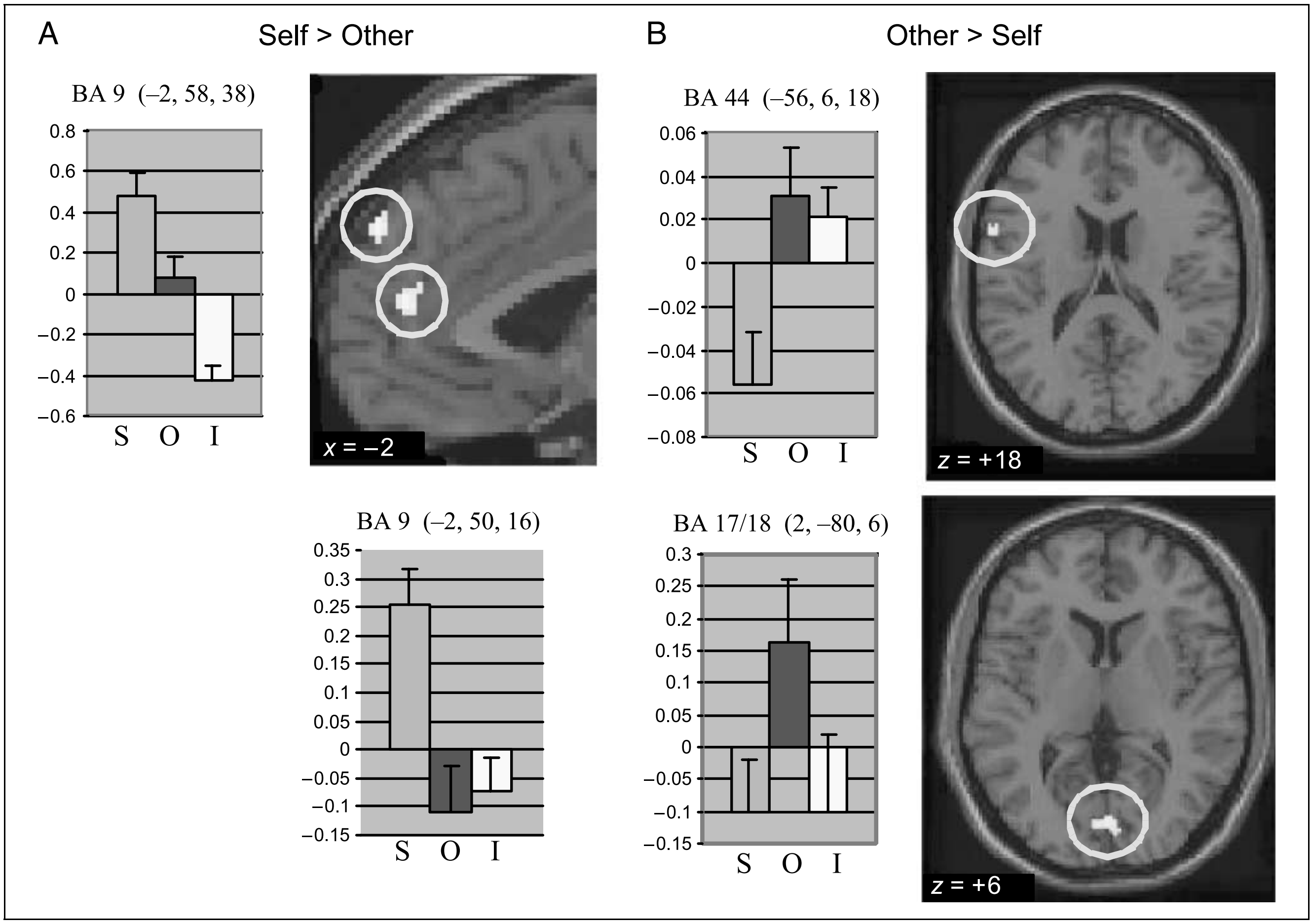

Figure 3. Results of group contrasts between self and other judgments revealing regions more activated during each type of judgment. Graphs show percent signal change for representative ROIs on self, other, or in–out blocks with error bars showing standard error of the mean. (A) Medial view of left hemisphere showing two clusters in the MPFC identified in the self > other contrast. (B) Axial images showing (left panel) activations of the left lateral prefrontal cortex (intersecting Broca's area) and (right panel) the occipital cortex identified in the other > self contrast.

in the maintenance and manipulation of information about the external world (Smith & Jonides, 1999)[4] as well as the retrieval of semantic/contextual knowledge that could be used to interpret social targets (Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). The recruitment of Broca's area is interesting because this region has been implicated in representing the goals of actions that either are observed or executed (Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003; Iacoboni, Woods, et al., 1999). Notably, the medial/lateral prefrontal split for self and other judgments parallels the finding of MPFC activation for emotion regulation strategies that reappraise the self-relevance of aversive scenes, as compared to lateral PFC activation for strategies that reappraise the actions and outcomes of actors depicted in those scenes (Ochsner, Ray, et al., in press). Third, recruitment of middle temporal cortex for self judgments may reflect this regions role in representing semantic and linguistic content, including the self monitoring (Hashimoto & Sakai, 2003) and retrieval of verbal information that conveys emotional (Mitchell, Elliott, Barry, Cruttenden, & Woodruff, 2003) or personal (Paller et al., 2003) information, whereas activation of the medial occipital cortex for other judgments may reflect heightened attention to external visual inputs when evaluating visual cues to another's mental state (Culham & Kanwisher, 2001).[5]

Role of the MPFC in Emotion and Social Cognition

Taken together, the present findings suggest that distinct but highly overlapping neural systems support the attribution of emotion to oneself and to others. A key player in both networks was the MPFC. Portions of the MPFC supported both the attribution of emotional states to oneself and to other pictured individuals, which supports the hypothesis that this region is the hub of a system mediating inferences about one's own and other individual's mental states (Lane & McRae, in press; Gallagher & Frith, 2003). In addition, distinct MPFC regions were more activated for self judgments, whereas lateral PFC regions were more activated for other judgments. This finding suggests that distinct control systems are involved in attending to and elaborating

Table 4. Group Activations for Self > Other and Other > Self Contrasts

Region of Activation	*Brodmann*	*Coordinates* *x*	*y*	*z*	*Z score*	*Volume (mm*^{3}*)*
Self > Other Contrast						
Superior frontal gyrus	9	−2	58	38	3.17	200
Medial frontal gyrus	10	−2	50	16	3.03	192
Middle temporal gyrus	L21	−62	−34	−6	3.04	160
Other > Self Contrast						
Inferior frontal gyrus	L44	−58	6	18	3.19	248
Inferior FG	L45	−58	12	24	2.83	(L)
Medial occiptial gyrus/cuneus	17&18	2	−80	6	3.66	456
Cuneus	18	−2	−80	16	3.10	(L)

Note: Local maxima for clusters are denoted with (L). R and L hemispheres are not designated for maxima within 6 mm of midline. Coordinates are in MNI space.

internally as compared to externally generated information (cf. Christoff, Ream, & Gabrieli, in press; Christoff, Ream, Geddes, & Gabrieli, 2003), a distinction that also has been observed in the context of emotion regulation (Ochsner, Ray, et al., in press) rather than emotion attribution. That being said, there remain at least three important and interrelated questions concerning the specific functional roles played by the MPFC.

The first question concerns the precise characterization of MPFC functions, and whether MPFC activation reflects a special kind of process devoted to mental state attributions, social cognition, and/or self-monitoring more generally. This question arises because MPFC activation has been observed in contexts that at first blush do not appear to require mental state inferences to be drawn, including inductive reasoning (Goel, Gold, Kapur, & Houle, 1997), judging semantic coherence (Ferstl & von Cramon, 2002) or word familiarity (Henson, Rugg, Shallice, Josephs, & Dolan, 1999), and prospective memory (Burgess, Scott, & Frith, 2003). Should these results be taken to suggest that the MPFC carries out some type of cognitive processing common to social-cognitive and self-referential judgment, or should the reverse conclusion be drawn, that apparently cognitive tasks require social-cognitive and self-referential processing?[6] On one hand, it is difficult to address this question in the absence of single study comparisons of tasks requiring mental state attributions with tasks that do not require them, in order to determine whether similar or different regions of the MPFC are being recruited in the two cases.[7] On the other hand, many of the tasks that recruit dorsal (coarsely defined as $z > 0$, see Table 5, Figure 4) regions of the MPFC (see right-most column of Table 5) could be described as requiring a common form of metacognitive processing. Social behaviors, personal characteristics, emotional experiences, linguistic utterances, and inductive problems can all be seen as examples of stimuli for which an attributed meaning is a meta-level emergent property of multiply interpretable inputs that, in and of themselves, do not directly imply a single interpretation. From this perspective, the MPFC might be important for the metacognitive ability to re-represent affective, cognitive, and other types of inputs in a self-generated symbolic (perhaps linguistically describable, e.g., "I feel good," or "He is sad.") format (Christoff, Ream, & Gabrieli, in press; Gallagher, Jack, Roepstorff, & Frith, 2002). By contrast, ventral (for present purposes defined as $z < 0$) regions of the MPFC have been strongly associated with representing the affective value of stimuli (e.g., Lane & McRae, in press; Fellows & Farah, 2003; Bechara, Damasio, & Damasio, 2000), in part because of connections with the amygdala and autonomic centers that are more robust than those present for the dorsal regions of the MPFC (Ongur & Price, 2003; Ongur, Ferry, & Price, 2000). At present, inspection of Table 5 and Figure 4 suggests that the ventral MPFC is activated by, but not consistently associated with, specific types of self-referential or social-cognitive judgments, and the extent to which this association reflects affective processing has not been explicitly addressed to date, studies have not been specifically designed to address the differential roles of dorsal and ventral medial prefrontal regions in self-referential and social-cognitive processing.

The second question concerns the specific computations carried out by the MPFC in the present experiment, which are illuminated by the preceding discussion. All of the activations in the present study fall

Table 5. Medial prefrontal activation coordinates for studies involving self-referential or social-cognitive judgments (shown in Figure 4)

Identifier	*Study*	*x*	*y*	*z*	*Target*	*Judgment Type*	*Contrast*	*Region*	*Figure*
Blue circle	Ochsner et al., this volume	−6	52	32	self	affective evaluation	self appraisal of emotion vs. in–out perceptual judgment	dMPFC	4A
Blue circle	Ochsner et al., this volume	−12	36	52	self	affective evaluation	self appraisal of emotion vs. in–out perceptual judgment	dMPFC	4A
Blue circle	Ochsner et al., this volume	−10	56	14	self	affective evaluation	self appraisal of emotion vs. in–out perceptual judgment	dMPFC	4A
Blue circle	Ochsner et al, this volume	−4	26	28	self	affective evaluation	self appraisal of emotion vs. in–out perceptual judgment	dMPFC	4A
Blue circle	Ochsner et al., this volume	−2	58	38	self	affective evaluation	self appraisal of emotion vs. other appraisal of emotion	dMPFC	4A
Blue circle	Ochsner et al., this volume	−2	50	16	self	affective evaluation	self appraisal of emotion vs. other appraisal of emotion	dMPFC	4A
Yellow sq.	Ochsner et al., this volume	2	56	40	self and social	affective evaluation	both self and other appraisals vs. in–out	dMPFC	4A
Yellow sq.	Ochsner et al., this volume	2	58	12	self and social	affective evaluation	both self and other appraisals vs. in–out	dMPFC	4A
Yellow sq.	Ochsner et al., this volume	−18	38	54	self and social	affective evaluation	both self and other appraisals vs. in–out	dMPFC	4A
Blue circle	Ochsner et al., this volume	−2	56	10	social	affective evaluation	other appraisal of emotion vs. in–out perceptual judgment	dMPFC	4A
Blue circle	Ochsner et al., this volume	−6	52	32	social	affective evaluation	other appraisal of emotion vs. in–out perceptual judgment	dMPFC	4A
a	Gusnard et al., 2001	−11	30	44	self	affective evaluation	appraise own feeling vs. in–out judgment	dMPFC	4A
a	Gusnard et al., 2001	7	45	25	self	affective evaluation	appraise own feeling vs. in–out judgment	dMPFC	4A
a	Gusnard et al., 2001	−3	53	24	self	affective evaluation	appraise own feeling vs. in–out judgment	dMPFC	4A
a	Gusnard et al., 2001	−11	23	52	self	affective evaluation	appraise own feeling vs. in–out judgment	dMPFC	4A
a	Gusnard et al., 2001	−9	39	42	self	affective evaluation	appraise own feeling vs. in–out judgment	dMPFC	4A
a	Gusnard et al., 2001	−5	3	48	self	affective evaluation	own feeling vs. fixation baseline	ACC	4A
b	Lane et al., 1997	0	50	16	self	affective evaluation	appraise own feeling vs. in–out judgment	dMPFC	4A
b	Lane et al., 1997	−8	10	−8	self	affective evaluation	appraise own feeling vs. in–out judgment	vMPFC	4A
c	Paradiso et al., 1999	0	29	35	self	affective evaluation	rate valence of response for pleasant vs. unpleasant photos	dMPFC	4A
c	Paradiso et al., 1999	−7	28	35	self	affective evaluation	rate valence of response for pleasant vs. unpleasant photos	dMPFC	4A

d	Paulus & Frank, 2003	14	40	1	self	affective evaluation	judge own preference vs. visual discrimination	ACC	4A
d	Paulus & Frank, 2003	−9	50	4	self	affective evaluation	judge own preference vs. visual discrimination	vMPFC	4A
e	Phan et al., 2003	3	54	27	self	affective evaluation	rate own arousal for aversive images	dMPFC	4A
e	Phan et al., 2003	3	54	33	self	affective evaluation	rate own arousal for aversive images	dMPFC	4A
e	Phan et al., 2003	−12	60	27	self	affective evaluation	rate own arousal for aversive images	dMPFC	4A
e	Phan et al., 2003	−21	51	33	self	affective evaluation	rate own arousal for aversive images	dMPFC	4A
e	Phan et al., 2003	3	45	39	self	affective evaluation	rate own arousal for aversive images	dMPFC	4A
e	Phan et al., 2003	3	51	27	self	affective evaluation	rate own arousal for aversive images	dMPFC	4A
e	Phan et al., 2003	3	39	30	self	affective evaluation	rate own arousal for aversive images	dMPFC	4A
f	Porro et al., 1998	7	57	0	self	affective evaluation	correlation with self-rated intensity of painful stimulus	vMPFC	4A
g	Simpson et al., 2001	1	41	−8	self	affective evaluation	decreases relative to fixation predict preshock anxiety	vMPFC	4A
g	Simpson et al., 2001	−1	17	−8	self	affective evaluation	decreases relative to fixation predict preshock anxiety	vMPFC	4A
h	Tabert et al., 2001	−2	47	24	self	affective evaluation	judge most unpleasant of 3 negative words vs. judge most neutral of 3 neutral words	dMPFC	4A
h	Tabert et al., 2001	−7	2	−12	self	affective evaluation	judge most unpleasant of 3 negative words vs. judge most neutral of 3 neutral words	vMPFC	4A
h	Tabert et al., 2001	13	55	24	self	affective evaluation	judge most unpleasant of 3 negative words vs. judge most neutral of 3 neutral words	dMPFC	4A
i	Taylor et al., 2003	−1	26	29	self	affective evaluation	rate arousal to aversive vs. non aversive photos	ACC	4A
i	Taylor et al., 2003	−1	26	29	self	affective evaluation	rate arousal to aversive vs. non aversive photos	ACC	4A
j	Zysett et al., 2002	−6	55	13	self	affective evaluation	judge preferences vs. retrieve semantic information	dMPFC	4A
k	Zysett et al., 2003	5	49	16	self	affective evaluation	judge preferences vs. retrieve semantic information	dMPFC	4A
k	Zysett et al., 2003	−11	42	−2	self	affective evaluation	judge preferences vs. retrieve semantic information	vMPFC	4A
k	Zysett et al., 2003	−13	62	1	self	affective evaluation	judge preferences vs. retrieve semantic information	dMPFC	4A
l	Kampe et al., 2003	8	60	22	self	recognize identity	hearing own name vs. other name	dMPFC	4A

(*continued on next page*)

Table 5. *(continued)*

Identifier	*Study*	*x*	*y*	*z*	*Target*	*Judgment Type*	*Contrast*	*Region*	*Figure*
l	Kampe et al., 2003	0	20	58	self	recognize identity	hearing own name vs. other name	dMPFC	4A
l	Kampe et al., 2003	6	60	20	self	recognize identity	hear own name and perceive gaze direction vs. non hear/perceive self stimuli	dMPFC	4A
m	Kircher et al., 2000	0	6	37	self	recognize identity	view own face vs. unknown face	ACC	4A
m	Kircher et al., 2000	3	36	4	self	recognize identity	view own face vs. unknown face	ACC	4A
m	Kircher et al., 2000	6	42	−2	self	recognize identity	view own face vs. unknown face	ACC	4A
n	Nakamura et al., 2001	14	54	12	self	recognize identity	self voice recognition vs. vowel recognition	dMPFC	4A
o	Sugiura et al., 2000	−7	44	0	self	recognize identity	passive viewing of own face	ACC	4A
o	Sugiura et al., 2000	7	32	25	self	recognize identity	recognition judgments of own face	ACC	4A
o	Sugiura et al., 2000	7	31	26	self	recognize identity	recognition judgments of own face vs. passive view of own face	ACC	4A
o	Sugiura et al., 2000	25	36	16	self	recognize identity	recognition judgments of own face vs. passive view of own face	ACC	4A
p	Greene et al., 2001	1	52	17	self	perspective-taking	judge morality for personal vs. nonpersonal moral dilemmas	dMPFC	4A
q	Ruby & Decety, 2003	−24	50	−6	self	perspective-taking	1st person vs. 3rd person conceptual perspective taking	vMPFC	4A
q	Ruby & Decety, 2003	−4	68	−12	self	perspective-taking	1st person vs. 3rd person conceptual perspective taking	dMPFC	4A
r	Vogeley et al., 2001	6	54	−4	self	perspective-taking	judging own intentions for imagined actions	ACC	4A
r	Vogeley et al., 2001	−12	50	−4	self	perspective-taking	judging own intentions for imagined actions	ACC	4A
s	Craik et al., 1999	−6	56	8	self	self-descriptiveness	judge self relevance of words	dMPFC	4A
s	Craik et al., 1999	6	40	28	self	self-descriptiveness	judge self relevance of words	dMPFC	4A
t	Fossati & Hevenor, 2003	−16	40	27	self	self-descriptiveness	self referential judgment vs. letter recognition control	dMPFC	4A
t	Fossati & Hevenor, 2003	10	49	16	self	self-descriptiveness	self referential judgment vs. letter recognition control	dMPFC	4A
u	Johnson et al., 2002	0	54	8	self	self-descriptiveness	yes/no to self reflective vs. semantic questions	dMPFC	4A
v	Kelley et al., 2002	10	52	2	self	self-descriptiveness	self-relevant judgments vs. other relevant judgments	dMPFC	4A

w	Kircher et al., 2002	−12	−22	31	self	self-descriptiveness	self descriptive vs. non self-descriptive judgments	ACC	4A
x	Lieberman et al., in press	−4	58	−12	self	self-descriptiveness	self descriptiveness Js for high experience vs. low experience domains	vMPFC	4A
x	Lieberman et al., in press	−10	−6	54	self	self-descriptiveness	self descriptiveness Js for high vs. low experience domains P's nonschematic for trait	dMPFC	4A
x	Lieberman et al., in press	12	52	32	self	self-descriptiveness	self descriptiveness Js for high vs. low experience domains P's nonschematic for trait	dMPFC	4A
x	Lieberman et al., in press	−20	52	−10	self	self-descriptiveness	self descriptiveness Js for low vs. high experience domains P's nonschematic for trait	vMPFC	4A
x	Lieberman et al., in press	−22	30	−16	self	self-descriptiveness	self descriptiveness Js for low vs. high experience domains P's nonschematic for trait	vMPFC	4A
x	Lieberman et al., in press	14	30	48	self	self-descriptiveness	self descriptiveness Js for high vs. low experience domains P's schematic for trait	dMPFC	4A
x	Lieberman et al., in press	−6	54	−10	self	self-descriptiveness	self descriptiveness Js for high vs. low experience domains (P's schematic for trait)	vMPFC	4A
y	Macrae et al., 2004	−24	58	1	self	self-descriptiveness	predicts subsequent memory after self-relevance judgment	dMPFC	4A
y	Macrae et al., 2004	0	50	8	self	self-descriptiveness	predicts subsequent memory after self-relevance judgment	dMPFC	4A
y	Macrae et al., 2004	−9	50	8	self	self-descriptiveness	judge self relevance vs. perceptual baseline	dMPFC	4A
aa	Cato et al., 2004	−22	42	31	self	self-generation	generate vs. repeat negative as opposed to neutral words	dMPFC	4A
aa	Cato et al., 2004	−3	60	12	self	self-generation	generate vs. repeat positive as opposed to neutral words	dMPFC	4A
aa	Cato et al., 2004	−4	60	29	self	self-generation	negative vs. neutral word generation	dMPFC	4A
bb	Crosson et al., 1999	−7	60	28	self	self-generation	self generate vs. repeat emotion words	dMPFC	4A
bb	Crosson et al., 1999	−4	17	47	self	self-generation	self generate vs. repeat emotion words	ACC	4A
bb	Crosson et al., 1999	−7	22	43	self	self-generation	self generate vs. repeat neutral words	ACC	4A
cc	Ochsner et al., in press	−10	18	62	self	self-generation	decrease negative affect via reappraisal vs. look at negative image	dMPFC	4A
cc	Ochsner et al., in press	−16	46	42	self	self-generation	decrease negative affect via reappraisal vs. look at negative image	dMPFC	4A

(*continued on next page*)

Table 5. (*continued*)

Identifier	*Study*	*x*	*y*	*z*	*Target*	*Judgment Type*	*Contrast*	*Region*	*Figure*
cc	Ochsner et al., in press	−8	46	48	self	self-generation	decrease negative affect via reappraisal vs. look at negative image	dMPFC	4A
cc	Ochsner et al., in press	−10	50	34	self	self-generation	increase vs. decrease negative emotion via reappraisal	dMPFC	4A
cc	Ochsner et al., in press	−4	64	32	self	self-generation	increase vs. decrease negative emotion via reappraisal	dMPFC	4A
cc	Ochsner et al., in press	−4	68	24	self	self-generation	increase vs. decrease negative emotion via reappraisal	dMPFC	4A
cc	Ochsner et al., in press	−10	2	66	self	self-generation	increase negative affect vs. reappraisal vs. look at negative image	ACC	4A
cc	Ochsner et al., in press	−6	48	40	self	self-generation	increase negative affect via reappraisal vs. look at negative image	dMPFC	4A
cc	Ochsner et al., in press	18	10	44	self	self-generation	increase negative affect via reappraisal vs. look at negative image	dMPFC	4A
dd	Partiot et al., 1995	12	38	36	self	self-generation	imagine events/feelings during preparation for mom's funeral	dMPFC	4A
dd	Partiot et al., 1995	−2	38	−4	self	self-generation	imagine events/feelings during preparation for mom's funeral	vMPFC	4A
dd	Partiot et al., 1995	18	42	32	self	self-generation	imagine events/feelings during preparation for mom's funeral	dMPFC	4A
dd	Partiot et al., 1995	−10	46	24	self	self-generation	imagine events/feelings during preparation for mom's funeral	dMPFC	4A
ee	Pietrini et al., 2000	−2	−6	44	self	self-generation	increase for imagined aggressive vs. imagined neutral behavior	ACC	4A
ee	Pietrini et al., 2000	−4	32	−12	self	self-generation	decrease for imagined aggressive vs. imagined neutral behavior	vMPFC	4A
ee	Pietrini et al., 2000	2	60	12	self	self-generation	decrease for imagined aggressive vs. imagined neutral behavior	dMPFC	4A
ee	Pietrini et al., 2000	16	60	20	self	self-generation	decrease for imagined aggressive vs. imagined neutral behavior	dMPFC	4A
ee	Pietrini et al., 2000	4	58	8	self	self-generation	decrease for imagined restrained aggression vs. imagined neutral behavior	dMPFC	4A
ff	McGuire et al., 1996	−8	38	24	self	self-generation	correlates with self generated stimulus independent thoughts	dMPFC	4A

ff	McGuire et al., 1996	−4	28	36	self	self-generation	correlates with self generated stimulus independent thoughts	dMPFC	4A
ff	McGuire et al., 1996	−10	48	0	self	self-generation	correlates with self generated stimulus independent thoughts	dMPFC	4A
ff	McGuire et al., 1996	−4	44	8	self	self-generation	correlates with self generated stimulus independent thoughts	dMPFC	4A
1	Berthoz et al., 2002	−6	14	60	social	good/bad evaluation	reaction to transgression of norms vs. normal stories	dMPFC	4B
1	Berthoz et al., 2002	6	36	54	social	good/bad evaluation	reaction to transgression of norms vs. normal stories	dMPFC	4B
1	Berthoz et al., 2002	−6	32	54	social	good/bad evaluation	reaction to transgression of norms vs. normal stories	dMPFC	4B
1	Berthoz et al., 2002	2	36	52	social	good/bad evaluation	reaction to embarrassing stories vs. normal stories	dMPFC	4B
1	Berthoz et al., 2002	−8	52	18	social	good/bad evaluation	reaction to transgression of norms vs. normal stories	dMPFC	4B
1	Berthoz et al., 2002	10	54	24	social	good/bad evaluation	reaction to transgression of norms vs. normal stories	dMPFC	4B
1	Berthoz et al., 2002	4	54	36	social	good/bad evaluation	reaction to embarrassing stories vs. normal stories	dMPFC	4B
1	Berthoz et al., 2002	−12	58	8	social	good/bad evaluation	reaction to transgression of norms vs. normal stories	dMPFC	4B
2	Cunningham et al., 2003	−12	40	20	social	good/bad evaluation	good/bad vs. relative age judgment of target person	ACC	4B
3	Farrow et al., 2001	2	49	−19	social	good/bad evaluation	judge other's emotions vs. general knowledge inference	vMPFC	4B
3	Farrow et al., 2001	−14	60	26	social	good/bad evaluation	judge other's emotions vs. general knowledge inference	dMPFC	4B
3	Farrow et al., 2001	−12	56	34	social	good/bad evaluation	judge forgivability of crime vs. general knowledge inference	dMPFC	4B
3	Farrow et al., 2001	−4	65	17	social	good/bad evaluation	judge forgivability of crime vs. judge other's emotions	dMPFC	4B
3	Farrow et al., 2001	−14	59	31	social	good/bad evaluation	judge forgivability of crime vs. judge other's emotions	dMPFC	4B

(*continued on next page*)

Table 5. (*continued*)

Identifier	*Study*	*x*	*y*	*z*	*Target*	*Judgment Type*	*Contrast*	*Region*	*Figure*
3	Farrow et al., 2001	−2	43	44	social	good/bad evaluation	judge forgivability of crime vs. judge other's emotions	dMPFC	4B
4	Teasdale et al., 1999	3	3	42	social	good/bad evaluation	understand and interpret negative captions for photos	ACC	4B
4	Teasdale et al., 1999	6	39	20	social	good/bad evaluation	understand and interpret negative captions for photos	ACC	4B
4	Teasdale et al., 1999	3	31	28	social	good/bad evaluation	understand and interpret negative captions for photos	ACC	4B
4	Teasdale et al., 1999	3	3	42	social	good/bad evaluation	understand and interpret positive vs. negative captions for photos	ACC	4B
4	Teasdale et al., 1999	0	42	15	social	good/bad evaluation	understand and interpret positive vs. negative captions for photos	ACC	4B
5	Wicker et al., 2003	−4	45	34	social	good/bad evaluation	judge intentions from clips of moving gaze followed by emotionally expressive eyes	dMPFC	4B
5	Wicker et al., 2003	1	51	18	social	good/bad evaluation	judge intentions from clips of moving gaze followed by emotionally expressive eyes	dMPFC	4B
5	Wicker et al., 2003	3	−27	37	social	good/bad evaluation	judge intentions from clips of moving gaze followed by emotionally expressive eyes	ACC	4B
5	Wicker et al., 2003	1	37	10	social	good/bad evaluation	judge intentions from clips of moving gaze followed by emotionally expressive eyes	ACC	4B
5	Wicker et al., 2003	1	34	−18	social	good/bad evaluation	judge intentions from clips of moving gaze followed by emotionally expressive eyes	vMPFC	4B
6	Winston et al., 2003	−16	42	−8	social	good/bad evaluation	judge trustworthiness vs. gender of face	vMPFC	4B
7	Calder et al., 2002	2	44	36	social	gaze perception	view increasing proportion of faces with averted gaze	dMPFC	4B
7	Calder et al., 2002	−26	44	−8	social	gaze perception	view increasing proportion of faces with averted gaze	vMPFC	4B
8	Hooker et al., 2003	4	23	44	social	gaze perception	judge gaze direction vs. arrow direction	dMPFC	4B
9	Kampe et al., 2003	8	50	14	social	gaze perception	view faces with directed vs. averted gaze	dMPFC	4B
10	Platek et al., 2003	5	34	57	social	gaze perception	mind in eyes task: judge, ''what are those eyes thinking?''	dMPFC	4B
11	Goel et al., 1995	−12	38	32	social	mental state inference	judging another person's knowledge of objects	dMPFC	4B
11	Goel et al., 1995	−6	46	28	social	mental state inference	judging another person's knowledge of objects	dMPFC	4B

12	Heekeren et al., 2003	−8	45	22	social	mental state inference	moral vs. semantic judgment	vMPFC	4B
12	Heekeren et al., 2003	1	55	2	social	mental state inference	moral vs. semantic judgment	vMPFC	4B
12	Heekeren et al., 2003	6	61	27	social	mental state inference	moral vs. semantic judgment	vMPFC	4B
13	Iacoboni et al., 2004	−2	52	26	social	mental state inference	viewing social, interactive vs. solitary figure films	dMPFC	4B
14	Mitchell et al., 2002	0	54	21	social	mental state inference	judge applicability of terms for describing people vs. objects	dMPFC	4B
14	Mitchell et al., 2002	3	39	0	social	mental state inference	judge applicability of terms for describing people vs. objects	vMPFC	4B
14	Mitchell et al., 2002	12	36	0	social	mental state inference	judge applicability of terms for describing people vs. objects	dMPFC	4B
15	Mitchell et al., 2004	−12	51	36	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B
15	Mitchell et al., 2004	6	48	48	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B
15	Mitchell et al., 2004	6	51	39	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B
15	Mitchell et al., 2004	−9	33	57	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B
15	Mitchell et al., 2004	0	45	36	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B
15	Mitchell et al., 2004	6	57	33	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B
15	Mitchell et al., 2004	12	36	57	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B
15	Mitchell et al., 2004	−9	57	27	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B
15	Mitchell et al., 2004	−6	51	45	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B
15	Mitchell et al., 2004	0	39	51	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B
15	Mitchell et al., 2004	9	63	21	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B
15	Mitchell et al., 2004	−12	21	60	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B

(*continued on next page*)

Table 5. *(continued)*

Identifier	*Study*	*x*	*y*	*z*	*Target*	*Judgment Type*	*Contrast*	*Region*	*Figure*
15	Mitchell et al., 2004	15	24	57	social	mental state inference	form impression of pictured person vs. judge sequence of photo presentations	dMPFC	4B
16	Wood et al., 2003	−16	30	50	social	mental state inference	categorize social phrases	dMPFC	4B
16	Wood et al., 2003	−12	41	42	social	mental state inference	categorize social phrases	dMPFC	4B
16	Wood et al., 2003	−8	48	31	social	mental state inference	categorize social phrases	dMPFC	4B
16	Wood et al., 2003	−12	34	50	social	mental state inference	categorize social words	dMPFC	4B
16	Wood et al., 2003	−4	45	38	social	mental state inference	categorize social words	dMPFC	4B
17	Brunet et al., 2000	16	44	20	social	view moving shapes	view clips that evoke intentional vs. physical causality inferences	dMPFC	4B
17	Brunet et al., 2000	8	32	−4	social	view moving shapes	view clips that evoke intentional vs. physical causality inferences	vMPFC	4B
17	Brunet et al., 2000	−8	36	0	social	view moving shapes	view clips that evoke intentional vs. physical causality inferences	dMPFC	4B
17	Brunet et al., 2000	4	−4	38	social	view moving shapes	view clips that evoke intentional vs. physical causality inferences	dMPFC	4B
17	Brunet et al., 2000	−8	34	2	social	view moving shapes	view clips that evoke intentional vs. physical causality inferences	ACC	4B
17	Brunet et al., 2000	−8	36	0	social	view moving shapes	view clips that evoke intentional vs. physical causality inferences	vMPFC	4B
17	Brunet et al., 2000	4	56	44	social	view moving shapes	view clips that evoke intentional vs. physical causality inferences	dMPFC	4B
17	Brunet et al., 2000	22	38	−20	social	view moving shapes	view physical causality clips with characters vs. without	vMPFC	4B
18	Castelli et al., 2000	−4	60	32	social	view moving shapes	observe complex intentional vs. nonintentional control movements	dMPFC	4B
18	Castelli et al., 2000	−6	58	32	social	view moving shapes	observe complex intentional vs. nonintentional control movements	dMPFC	4B
19	Martin & Weisberg, 2003	3	52	−11	social	view moving shapes	view clips of social vs. mechanical movements	vMPFC	4B
20	Ruby & Decety, 2001	14	72	10	social	perspective-taking	3rd vs. 1st person spatial perspective taking	dMPFC	4B
20	Ruby & Decety, 2001	28	50	−8	social	perspective-taking	3rd vs. 1st person spatial perspective taking	vMPFC	4B
21	Ruby & Decety, 2003	0	20	70	social	perspective-taking	3rd vs. 1st person conceptual perspective taking	dMPFC	4B

21	Ruby & Decety, 2003	10	24	56	social	perspective-taking	3rd vs. 1st person conceptual perspective taking	dMPFC	4B
21	Ruby & Decety, 2003	−8	40	52	social	perspective-taking	3rd vs. 1st person conceptual perspective taking	dMPFC	4B
21	Ruby & Decety, 2003	24	48	42	social	perspective-taking	3rd vs. 1st person conceptual perspective taking	dMPFC	4B
22	Baron-Cohen et al., 1999	−9	50	20	social	TOM	infer state of mind vs. identify gender	dMPFC	4B
22	Baron-Cohen et al., 1999	6	6	53	social	TOM	infer state of mind vs. identify gender	dMPFC	4B
22	Baron-Cohen et al., 1999	0	47	9	social	TOM	infer state of mind vs. identify gender	dMPFC	4B
23	Fletcher et al., 1995	0	38	24	social	TOM	read theory of mind vs. physical stories	ACC	4B
23	Fletcher et al., 1995	−12	42	40	social	TOM	read theory of mind stories vs. unlinked sentences	dMPFC	4B
23	Fletcher et al., 1995	−12	36	36	social	TOM	read theory of mind stories vs. unlinked sentences	dMPFC	4B
24	Gallagher et al., 2000	−8	50	10	social	TOM	read TOM vs. non TOM stories	dMPFC	4B
24	Gallagher et al., 2000	−10	48	12	social	TOM	view TOM vs. non TOM stories & cartoons	dMPFC	4B
25	Happe et al., 1996	−10	44	16	social	TOM	read TOM vs. non TOM stories	dMPFC	4B
26	Saxe & Kanwisher, 2003	6	57	18	social	TOM	read false belief vs. false photograph stories	dMPFC	4B
27	Vogeley et al., 2001	6	56	2	social	TOM	judge intentions of others vs. self described in vignettes	ACC	4B
27	Vogeley et al., 2001	4	28	30	social	TOM	judge intentions of others vs. self described in vignettes	ACC	4B
28	Gallagher et al., 2002	8	54	12	social	interactive	rock paper scissors game vs. mentalizing human as opposed to rule-following computer	ACC	4B
28	Gallagher et al., 2002	−10	50	30	social	interactive	rock paper scissors game vs. mentalizing human as opposed to rule-following computer	dMPFC	4B
28	Gallagher et al., 2002	−2	46	14	social	interactive	rock paper scissors game vs. mentalizing human as opposed to random computer	dMPFC	4B
29	Rilling et al., 2002	−3	51	6	social	interactive	prisoner's dilemma vs. human; mutual cooperation vs. all other dyadic choices	ACC	4B
29	Rilling et al., 2002	3	48	−12	social	interactive	prisoner's dilemma vs. human; mutual cooperation vs. all other dyadic choices	vMPFC	4B
29	Rilling et al., 2002	6	51	−18	social	interactive	prisoner's dilemma vs. human; mutual coop/mutual defect vs. all other dyadic choices	vMPFC	4B

within the dorsal region of the MPFC, which is consistent with the notion that the mental state attributional processes isolated here are related to self-referential and social-cognitive processes not specifically associated with emotion per se. A within-study comparison of emotional and nonemotional self- and other-cued judgments would be necessary to derive firm conclusions in this regard.

Finally, a third important question concerns the functional importance attached to the relative ubiquity of MPFC activation across a variety of self-referential and social-cognitive judgments (see Table 5 and Figure 4), including conditions in which participants are allowed to simply "rest" while inside the scanner and are not explicitly directed to engage in either type of processing (Gusnard & Raichle, 2001; Gusnard et al., 2001; McGuire, Paulesu, Frackowiak, & Friat, 1996). Comparatively greater MPFC activation has been found during rest when participants are free to a think about whatever they wish as compared to tasks that require specific forms of executive control (Gusnard & Raichle, 2001), self-referential (e.g., Kelley et al., 2002), or social cognitive (e.g., Mitchell, Macrae, Schooler, Rowe, & Milne, 2002) processing. This pattern of heightened MPFC activation and metabolic stability at rest has been taken as support for the hypothesis that the MPFC carries out a default-state monitoring function, which involves monitoring of the internal milieu and represents a physiologic baseline for brain imaging studies (Gusnard & Raichle, 2001). This hypothesis generally is consistent with the available data, and intriguingly suggests that self-referential and/or social-cognitive processing may be a natural part of stream of consciousness thought (Mitchell, Macrae, Schooler, et al., 2002; Christoff, Ream, & Gabrieli, in press). Because the present study did not include a resting condition, however, relative activations or deactivations relative to a putative default state unfortunately cannot be evaluated. It should be noted, however, that comparisons with a resting baseline state would only have clear psychological meaning with respect to whatever psychological processes are engaged during that resting state. Because resting baselines do not involve a directed task, the precise nature of psychological processes may vary. This means that differences in activation with respect to that state may not be clearly interpretable in terms of specific underlying psychological processes (cf. Stark & Squire, 2001), and could explain why deactivations for self-referential or social-cognitive processing are not always found in comparison to the resting state (e.g., Iacoboni, Lieberman, et al., 2004; Mitchell, Macrae, & Banaji, 2004; Zysset, Huber, Ferstl, & von Cramon, 2002).

METHODS

Participants

Thirteen participants (7 women, *M* age = 29.5 years) were recruited in compliance with the human subjects regulations of Stanford University.

Behavioral Paradigm

Participants viewed three types of mixed blocks of positive, negative, and neutral photos selected from the International Affective Picture System (Lang, Greenwald, Bradley, & Hamm, 1993). Prior to the onset of each block, one of three instructional cues was presented in the center of the screen for 4 sec. On "self" blocks, participants were instructed to judge whether they felt pleasant, unpleasant, or neutral in response to each photo. On "other" blocks, participants judged whether the central figure for each photo felt pleasant, unpleasant, or neutral. On "in–out" blocks, participants judged whether each photo had been taken inside, outside, or whether it could not be determined (i.e., they were unsure) in which location the photo had been taken. Each block was comprised of a series of six trials. On each trial, a photo was presented for 2 sec followed by a 3-point rating scale for 1.5 sec and a 500-msec intertrial interval. The rating scale displayed appropriate response options for self, other, and in–out blocks, and served to guide judgments that participants made using three fingers of their right hand on a four-button response box. To insure that participants would be

Note: Articles are organized alphabetically by judgment target and judgment type. Column labels indicate: Identifier = identifier for activation in Figure 1; Study = study listed in references; x, y, z = coordinates given in published study, with $+x$ = right and $-x$ = left, $+y$ = rostral/anterior and $-y$ = posterior, $+z$ = dorsal and $-z$ = ventral relative to origin; Target = judgment target, "self" in case of self-referential judgments, "social" in case of social-cognitive judgments involving inferences about the dispositions, mental or emotional states of another person; Contrast = comparison producing activation focus; Region = region of the medial frontal cortex activated, with dMPFC indicating dorsal medial prefrontal cortex with z coordinate > 0 and falling within BAs 8, 9, 10, or dorsal portions of 32, vMPFC indicating ventromedial prefrontal cortex with $z < 0$ and falling within BAs 10, 11, 14, 25, and ventral portions of 32, and ACC indicating the anterior cingulate cortex, which includes BAs 24 and 32 (Ongur & Price, 2003; Ongur et al., 2000). Judgment types are as follows: affective evaluation = assessing valence or arousal of own emotional response, or judging personal preference for a stimulus; recognize identity = view one's own face or hear one's own name; perspective taking = imagining first- or third-person spatial (what do I/they see?) versus conceptual (what do I/they think/feel/believe?) perspective; self-generation = generate words/thoughts; mental state inference = judge states or traits of depicted individuals; view moving shapes = view video clips of abstract moving shapes whose motions tend to elicit either attributions of intentionality or require some other type of nonmental inference to describe/understand; TOM = view and/or judge vignettes explicitly designed to require theory of mind inferences in order to comprehend them; interactive = participants believe they are playing a game in real time with another participant. Abbreviations: sq. = square, Js = judgments, TOM = theory of mind judgments, coop = cooperation, pleas = pleasant, P's = participants.

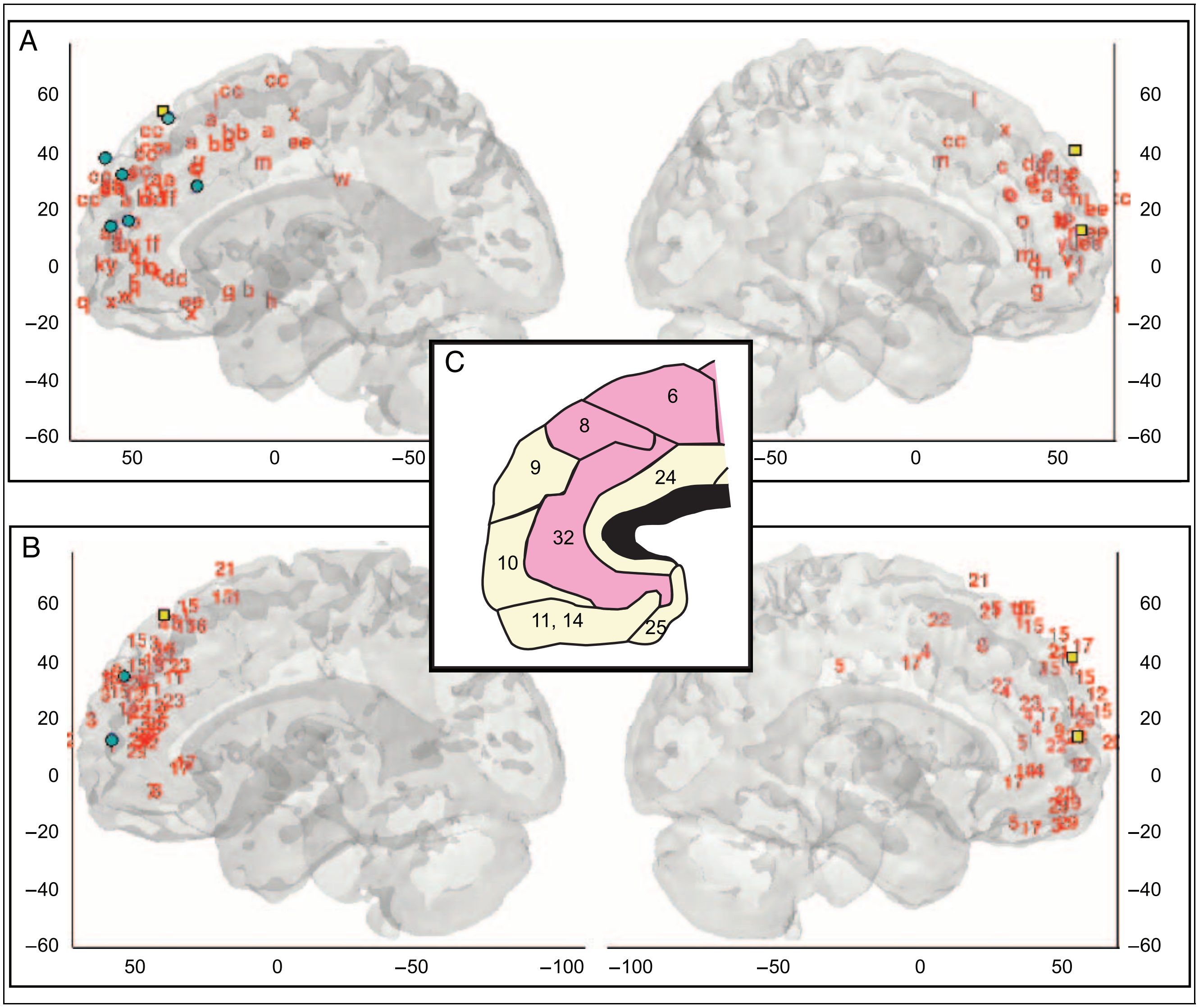

Figure 4. Medial prefrontal activation coordinates for studies involving self-referential or social cognitive judgments shown in Table 5. (A) Left and right medial views of activations across a series of studies related to judgments of self-reference. Identifier letters correspond to specific activation coordinates for studies listed in the top half of Table 5. Blue circles and yellow squares indicate activations from the present study related to self appraisals of emotion and both self and other appraisals of emotion, respectively. (B) Left and right medial views of activations across a series of studies related to social cognitive judgements. Identifier numbers correspond to specific activation coordinates for studies listed in the bottom half of Table 5. Blue circles and yellow squares indicate activations from the present study related to other appraisals of emotion and both self and other appraisals of emotion, respectively. (C) Figure key indicating relative locations of Brodmann's areas located in the medial frontal cortex (Ongur & Price, 2003; Ongur et al, 2000). For descriptive purposes, dorsal medial prefrontal (MPFC) regions have a z-coordinate > 0 and fall within BAs 6, 8, 9, or 10, ventromedial prefrontal regions (vMPFC) have $z < 0$ and fall within BAs 10, 11, 14, 25, and ventral portions of 32, and ACC indicating the anterior cingulate cortex, which includes BAs 24 and 32. For descriptive information pertaining to specific studies, see Table 5.

experiencing pleasant or unpleasant affect throughout the task, each block contained either two pleasant and three unpleasant or three pleasant and two unpleasant images, and one neutral image as determined by normative ratings (Lang et al., 1993). Valence and arousal ratings for pleasant, unpleasant, and neutral images were equated across three stimulus sets that were counterbalanced across judgment types. Valenced and neutral images were randomly intermixed within blocks, and six blocks of each instruction type were presented in pseudorandom order within a single 8 min 24 sec scan.

Stimulus presentation and response collection were controlled by the program Psyscope 1.2.5 running on a Macintosh G3 Computer. Stimuli were back projected onto a screen mounted on a custom head coil that limited head motion using a bitebar.

MRI Data Acquisition

Whole-brain fMRI data (32 axial slices, 3.5 mm thick) were collected at 3T (GE Signa LX Horizon Echospeed scanner) with a T2*-sensitive gradient-echo spiral-out pulse sequence (30 msec TE, 2000 msec TR, 2 interleaves, 60° flip angle, 24 cm field of view, 64 by 64 data acquisition matrix). T2-weighted flow-compensated spin-echo scans were acquired for anatomical reference using the same slice prescription (2000 msec TR, 85 msec TE), and high-order shimming was performed before functional scans (Glover, 1999).

MRI Data Analysis

Functional images were slice time and motion-corrected using SPM99 (Wellcome Department of Cognitive Neurology). Anatomical images next were coregistered to the mean functional image, and normalized to a standard template brain. Functional images were then normalized using those parameters, interpolated to 2 × 2 × 2 mm voxels, and smoothed with a gaussian filter (6 mm full width half maximum). To remove drifts within sessions, a high-pass filter with a cutoff period two times the block length was applied.

A mixed design was used to model first-level fixed-effects for each participant. The 4-sec instructional cue proceeding each block was modeled with a canonical hemodynamic response function; the 24-sec photo blocks were modeled as a boxcar regressor convolved with the canonical hemodynamic response. A general linear model analysis was used in SPM99 to create contrast images for each participant summarizing differences between block types. These images were used to create second-level group average SPM$\{t\}$ maps that were thresholded at $p < .005$, uncorrected for multiple comparisons, with an extent threshold of 20 voxels. These parameters correspond to an overall alpha level of $p < .05$, corrected for multiple comparisons as calculated by the Monte Carlo simulation method of Forman et al. (1995) implemented in AFNI, and has been employed in numerous prior studies (e.g., Wood, Romero, Makale, & Grafman, 2003; Konishi, Nakajima, Uchida, Kikyo, et al., 1999; Poldrack et al., 1999; Wagner, 1999; Konishi, Nakajima, Uchida, Sekihara, & Miyashita, 1998). Maxima are reported in ICBM152 coordinates as in SPM99. To formally identify regions active for both the self > in–out and other > in–out contrasts, the t-map for the first contrast was used as an inclusive mask for the second contrast, with each voxel-level thresholded at $p < .01$. Using the Fisher method for combining p values, this analysis yields regions active with probability $p < .001$ across both tasks. For functionally defined regions shown at the group level to be involved in attributing emotion to self, to other, or to both, measures of mean percent signal change for a given type of instruction block (relative to the mean activation of that region across the entire study) were extracted from the peak activated voxel. This means that, apparent deactivations relative to the zero line are not deactivations per se, but simply reflect lesser activation with respect to the mean level of activation in that given region of interest[8].

Acknowledgments

We thank Elaine Robertson and Hedy Kober for assistance in preparation of the manuscript, Tor Wager for assistance with Figure 4, and we acknowledge support by a grant from the John and Dodie Rosekranz Endowment (SCM), grant BCS-93679 from the National Science Foundation (KNO), a NARSAD Young Investigator Grant (KNO), and grant RR 09784 from the NIH (GHG).

Reprint requests should be sent to Kevin Ochsner, Department of Psychology, Columbia University, 369 Schermerhorn Hall, 1190 Amsterdam Avenue, New York, NY 10027, or via e-mail: ochsner@psych.columbia.edu.

The data reported in this experiment have been deposited in the fMRI Data Center (http://www.fmridc.org). The accession number is 2-2004-1177A.

Notes

1. Although not of primary interest here, it is worth noting that neither the contrast of in–out > self nor in–out > other blocks showed activation in the medial or lateral prefrontal regions. The in–out > self contrast showed bilateral activation of the lateral superior parietal cortex and the cuneus consistent with the spatial nature of the task (Culham & Kanwisher, 2001), as well as activation of the primary visual cortex, consistent with the findings reported in Figure 3 and Table 4, indicating relatively lesser engagement of early visual processing during the internally queued self blocks. The in–out > other contrast showed activation of the left parietal cortex and the cuneus, also consistent with a greater reliance on visual–spatial processing in the in–out cued blocks. Notably, greater activation of the medial prefrontal cortex was not found during the in–out cued blocks (even when thresholds were lowered to .1), which suggests that at least under the conditions of the present experiment, medial prefrontal recruitment reflects greater activation with respect to our perceptual baseline, although as noted in the discussion, the design of the present study does not permit comparison of activations in the self and other blocks to resting baseline because such a baseline was not included in the present study.
2. It is important to note that alternative accounts of the present findings in terms of differential response difficulty or arousal are unlikely both for empirical and theoretical reasons. The similar speed and frequency with which self and other judgments were made makes it unlikely that differences between the brain regions recruited by each judgment type arise either from differential difficulty in making them, or from differential arousal (which would be expected to motivate more rapid responding in one condition as compared to the other). Similarly, although it could be argued that greater activation for either self or other judgments reflects greater arousal in one condition, this seems unlikely because activations of arousal-related limbic structures have been found to decrease when participants rate emotional responses to the same sorts of aversive photos used here (Taylor, Phan, Decker, & Liberzon, 2003).
3. Additional differences between self and other judgments were revealed in contrasts of each judgment with their common perceptual baseline. These differences may not be as large or as reliable as those revealed by directly contrasting

self and other judgments to one another, as described above, but may nevertheless provide information about the differential recruitment of systems that may be involved in attention to and encoding of internal as opposed to external cues relevant to emotional attributions. For self judgments, activation was observed in dorsal anterior cingulate regions associated with attention to and monitoring of internal responses (Botvinick, Braver, Barch, Carter, & Cohen, 2001) including self-generated changes in emotion (Ochsner, Ray, et al., in press; Ochsner, Bunge, Gross, & Gabrieli, 2002) as well as inferior parietal regions involved in selective attention and representing the body in space (Culham & Kanwisher, 2001). For other judgments, activation was observed in a parahippocampal region implicated in encoding visual and spatial cues that designate specific places (Epstein & Kanwisher, 1998).

4. Additional differences between self and other emotion perception concerned the laterality of activated regions. Whereas self judgments recruited primarily the left frontal, temporal, parietal, and cingulate regions, other judgments recruited the left frontal and cingulate regions in combination with the right temporal and parahippocampal regions. Although the reasons for these laterality findings are not immediately clear, they might relate to preferential recruitment of left lateralized systems for either self-focused processing (Kelley et al., 2002; Turk et al., 2002) or mentally manipulating verbal information (Smith, Jonides, Marshuetz, & Koeppe, 1998) as may occur when reasoning about mental states, and to right lateralized systems specialized for encoding visual spatial and nonverbal cues (Kosslyn & Koenig, 1992) recruited when directing attention outwards to judge the emotions experienced by pictured persons.

5. It is possible that when processing visual cues necessary to draw inferences about the internal emotional states of others' results in an interaction between bottom-up and top-down processing that enhances attention, and visual cortical activation, in a way that does not occur when one is making a simple perceptual judgment about the visual properties of the stimulus during the in–out blocks. This pattern of activation was not expected a priory, however, and awaits replication in future studies.

6. In the linguistic coherence study of Ferstl and von Cramon (2002), for example, participants may have spontaneously experienced self-reflective mental states when determining whether sentences like, ''Sometimes a truck drives by the house,'' cohere with sentences like, ''That's when the dishes start to rattle.'' Hearing these sentences may evoke mental images in which they watch the dishes rattle in a kitchen while another individual drives a truck outside, which participants use to draw inferences about what they would believe or infer when experiencing this event (cf. Frith & Frith, 1999).

7. It should be noted, however, that within-study comparisons of all potentially relevant conditions is plainly impractical, and that meta-analytic procedures that statistically evaluate similarity of activation foci across studies may be able to identify distinct functional subregions within the MPFC (Kober, Wager, & Ochsner, 2004). Another tack that can be taken towards understanding MPFC function is to consider when it is not recruited in the context of specific kinds of self versus other processing. For example, activation of the MPFC has been found when participants either imitated the gestures of another person, or when they watched that person imitate their gestures (Decety, Chaminade, Grezes, & Meltzoff, 2002), and also when participants either reasoned about their own behavioral intentions or those of a described individual (Vogeley et al., 2001). These results join similar findings from the present study in supporting a general role for the MPFC in mental state attributions. However, those two studies both found activation of parietal regions uniquely associated with either self- and/or other-focused processing, which were not observed in the present study. Although the reasons for these discrepancies are not clear, one possibility is that the particular systems important for distinguishing oneself and others will vary depending upon the dimension of similarity in question. Parietal systems have been implicated in the agentic control of action (Farrer et al., 2003; Ramachandran, 1998), which may be important during motor imitation and when drawing inferences about the intentions of actors from their physical actions described in vignettes. By contrast, emotional attributions (at least in the present context) may depend more heavily on decoding the meanings of interoceptive and exteroceptive cues, as suggested by judgment-specific patterns of medial and lateral prefrontal activation.

8. Two notes are important with respect to interpretation of our measure of percent signal change. The first is that peak voxel activations were selected rather then average cluster activations because prior research has shown peak voxel activity to be more strongly correlated with electrophysiological measures of activation than is cluster average activity (Arturs & Boniface, 2003). Arturs and Boniface (2003) examined the relationship between BOLD activity in the somatosensory cortex and somatosensory evoked potentials elicited by median nerve stimulation. They found that peak voxel rather than cluster average measures of percent signal change most strongly correlated with somatosensory evoked potentials, suggesting that peak voxel activity might best correlate with the neural generators of the BOLD response. The second is that because percent signal change is calculated with respect to the mean level of activity within a given region, apparent deactivations with respect to the zero line do not in fact reflect deactivations of the sort described by Gusnard et al. (2001) with respect to a resting baseline. Rather, variations of percent signal change here reflect deviations with respect to an average level of activation, and are properly interpreted as relative differences between conditions rather than activations or deactivations with respect to a physiologic baseline measure. This measure of computing percent signal change against the mean of activity for a region across time and across task conditions reflects a desire to compute a ''descriptive'' index of relative activation across task conditions that is not influenced by factors that could impact the global mean, and is not influenced by uncontrolled variability in the psychological processes engaged by participants, as would be the case if percent signal change were computed with respect to a resting baseline that does not control psychological processing.

REFERENCES

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences, 4,* 267–278.

Baron-Cohen, S. (1995). *Mindblindness: An essay on autism and theory of mind.* Cambridge: MIT Press.

Baron-Cohen, S., Ring, H. A., Wheelwright, S., Bullmore, E. T., Brammer, M. J., Simmons, A., & Williams, S. C. (1999). Social intelligence in the normal and autistic brain: An fMRI study. *European Journal of Neuroscience, 11,* 1891–1898.

Barrett, L. F., Gross, J., Christensen, T. C., & Benvenuto, M. (2001). Knowing what you're feeling and knowing what to do about it: Mapping the relation between emotion differentiation and emotion regulation. *Cognition and Emotion, 15,* 713–724.

Bechara, A., Damasio, H., & Damasio, A. R. (2000). Emotion,

decision making and the orbitofrontal cortex. *Cerebral Cortex, 10,* 295–307.
Berthoz, S., Armony, J. L., Blair, R. J., & Dolan, R. J. (2002). An fMRI study of intentional and unintentional (embarrassing) violations of social norms. *Brain, 125,* 1696–1708.
Blair, R. J. (2003). Facial expressions, their communicatory functions and neuro-cognitive substrates. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 358,* 561–572.
Blair, R. J., Morris, J. S., Frith, C. D., Perrett, D. I., & Dolan, R. J. (1999). Dissociable neural responses to facial expressions of sadness and anger. *Brain, 122,* 883–893.
Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Reiew, 108,* 624–652.
Brunet, E., Sarfati, Y., Hardy-Bayle, M. C., & Decety, J. (2000). A PET investigation of the attribution of intentions with a nonverbal task. *Neuroimage, 11,* 157–166.
Bunge, S. A., Ochsner, K. N., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (2001). Prefrontal regions involved in keeping information in and out of mind. *Brain, 124,* 2074–2086.
Burgess, P. W., Scott, S. K., & Frith, C. D. (2003). The role of the rostral frontal cortex (area 10) in prospective memory: A lateral versus medial dissociation. *Neuropsychologia, 41,* 906–918.
Calder, A. J., Lawrence, A. D., Keane, J., Scott, S. K., Owen, A. M., Christoffels, I., & Young, A. W. (2002). Reading the mind from eye gaze. *Neuropsychologia, 40,* 1129–1138.
Castelli, F., Happe, F., Frith, U., & Frith, C. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage, 12,* 314–325.
Cato, M. A., Crosson, B., Gokcay, D., Soltysik, D., Wierenga, C., Gopinath, K., Himes, M., Belanger, H., Bauer, R. M., Fischler, I. S., Gonzalez-Rothi, L., & Briggs, R. W. (2004). Processing words with emotional connotation: An fMRI study of time course and laterality in rostral frontal and retrosplenial cortices. *Journal of Cognitive Neuroscience, 16,* 167–177.
Christoff, K., Ream, J. M., & Gabrieli, J. D. E. (in press). Cognitive and neural basis of spontaneous thought processes. *Cortex.*
Christoff, K., Ream, J. M., Geddes, L. P. T., & Gabrieli, J. D. E. (2003). Evaluating self-generated information: Anterior prefrontal contributions to human cognition. *Behavioral Neuroscience, 117,* 1161–1168.
Craik, F. I. M., Moroz, T. M., Moscovitch, M., Stuss, D. T., Winocur, G., Tulving, E., & Kapur, S. (1999). In search of the self: A positron emission tomography study. *Psychological Science, 10,* 26–34.
Crosson, B., Radonovich, K., Sadek, J. R., Gokcay, D., Bauer, R. M., Fischler, I. S., Cato, M. A., Maron, L., Auerbach, E. J., Browd, S. R., & Briggs, R. W. (1999). Left-hemisphere processing of emotional connotation during word generation. *NeuroReport, 10,* 2449–2455.
Culham, J. C., & Kanwisher, N. G. (2001). Neuroimaging of cognitive functions in human parietal cortex. *Current Opinion in Neurobiology, 11,* 157–163.
Cunningham, W. A., Johnson, M. K., Gatenby, J. C., Gore, J. C., & Banaji, M. R. (2003). Neural components of social evaluation. *Journal of Personality and Social Psychology, 85,* 639–649.
Decety, J., Chaminade, T., Grezes, J., & Meltzoff, A. N. (2002). A PET exploration of the neural mechanisms involved in reciprocal imitation. *Neuroimage, 15,* 265–272.
Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature, 392,* 598–601.
Farrer, C., Franck, N., Georgieff, N., Frith, C. D., Decety, J., & Jeannerod, M. (2003). Modulating the experience of agency: A positron emission tomography study. *Neuroimage, 18,* 324–333.
Farrow, T. F., Zheng, Y., Wilkinson, I. D., Spence, S. A., Deakin, J. F., Tarrier, N., Griffiths, P. D., & Woodruff, P. W. (2001). Investigating the functional anatomy of empathy and forgiveness. *12,* 2433–2438.
Fellows, L. K., & Farah, M. J. (2003). Ventromedial frontal cortex mediates affective shifting in humans: Evidence from a reversal learning paradigm. *Brain, 126,* 1830–1837.
Ferstl, E. C., & von Cramon, D. Y. (2002). What does the frontomedian cortex contribute to language processing: Coherence or theory of mind? *Neuroimage, 17,* 1599–1612.
Fink, G. R., Markowitsch, H. J., Reinkemeier, M., Bruckbauer, T., Kessler, J., & Heiss, W. D. (1996). Cerebral representation of one's own past: Neural networks involved in autobiographical memory. *Journal of Neuroscience, 16,* 4275–4282.
Fletcher, P. C., Happe, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S., & Frith, C. D. (1995). Other minds in the brain: A functional imaging study of "theory of mind" in story comprehension. *Cognition, 57,* 109–128.
Fossati, P., & Hevenor, S. J. (2003). In search of the emotional self: An fMRI study using positive and negative emotional words. *American Journal of Psychiatry, 160,* 1938–1944.
Frith, C. D., & Frith, U. (1999). Interacting minds—A biological basis. *Science, 286,* 1692–1695.
Gallagher, H. L., & Frith, C. D. (2003). Functional imaging of "theory of mind". *Trends in Cognitive Sciences, 7,* 77–83.
Gallagher, H. L., Happe, F., Brunswick, N., Fletcher, P. C., Frith, U., & Frith, C. D. (2000). Reading the mind in cartoons and stories: An fMRI study of "theory of mind" in verbal and nonverbal tasks. *Neuropsychologia, 38,* 11–21.
Gallagher, H. L., Jack, A. I., Roepstorff, A., & Frith, C. D. (2002). Imaging the intentional stance in a competitive game. *Neuroimage, 16,* 814–821.
Goel, V., Gold, B., Kapur, S., & Houle, S. (1997). The seats of reason? An imaging study of deductive and inductive reasoning. *NeuroReport, 8,* 1305–1310.
Goel, V., Grafman, J., Sadato, N., & Hallett, M. (1995). Modeling other minds. *NeuroReport, 6,* 1741–1746.
Greene, J. D., Sommerville, R. B., Nystrom, L. E., Darley, J. M., & Cohen, J. D. (2001). An fMRI investigation of emotional engagement in moral judgment. *Science, 293,* 2105–2108.
Gusnard, D. A., & Raichle, M. E. (2001). Searching for a baseline: Functional imaging and the resting human brain. *Nature Reviews Neuroscience, 2,* 685–694.
Happe, F., Ehlers, S., Fletcher, P., Frith, U., Johansson, M., Gillberg, C., Dolan, R., Frackowiak, R., & Frith, C. (1996). "Theory of mind" in the brain. Evidence from a PET scan study of Asperger syndrome. *NeuroReport, 8,* 197–201.
Hashimoto, Y., & Sakai, K. L. (2003). Brain activations during conscious self-monitoring of speech production with delayed auditory feedback: An fMRI study. *Human Brain Mapping, 20,* 22–28.
Heekeren, H. R., Wartenburger, I., Schmidt, H., Schwintowski, H.-P., & Villringer, A. (2003). An fMRI study of simple ethical decision-making. *NeuroReport, 14,* 1215–1219.
Heiser, M., Iacoboni, M., Maeda, F., Marcus, J., & Mazziotta, J. C. (2003). The essential role of Broca's area in imitation. *European Journal of Neuroscience, 17,* 1123–1128.
Henson, R. N., Rugg, M. D., Shallice, T., Josephs, O., & Dolan, R. J. (1999). Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. *Journal of Neuroscience, 19,* 3962–3972.

Hooker, C. I., Paller, K. A., Gittleman, D. R., Parrish, T. B., Mesulam, M. M., & Reber, P. J. (2003). Brain networks for analyzing eye gaze. *Cognitive Brain Research, 17,* 406–418.

Iacoboni, M., Lieberman, M. D., Knowlton, B. J., Istvan, M.-S., Moritz, M., Throop, C. J., & Fiske, A. P. (2004). Watching social interactions produce dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. *Neuroimage, 21,* 1167–1173.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science, 286,* 2526–2528.

Johnson, S. C., Baxter, L. C., Wilder, L. S., Pipe, J. G., Heiserman, J. E., & Prigatano, G. P. (2002). Neural correlates of self-reflection. *Brain, 125,* 1808–1814.

Jonides, J., Smith, E. E., Marshuetz, C., Koeppe, R. A., & Reuter-Lorenz, P. A. (1998). Inhibition in verbal working memory revealed by brain activation. *Proceedings of the National Academy of Sciences, U.S.A., 95,* 8410–8413.

Kampe, K. K., Frith, C. D., & Frith, U. (2003). ''Hey John'': Signals conveying communicative intention toward the self activate brain regions associated with ''mentalizing,'' regardless of modality. *Journal of Neuroscience, 23,* 5258–5263.

Kelley, W. M., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., & Heatherton, T. F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience, 14,* 785–794.

Kesler-West, M. L., Andersen, A. H., Smith, C. D., Avison, M. J., Davis, C. E., Kryscio, R. J., & Blonder, L. X. (2001). Neural substrates of facial emotion processing using fMRI. *Brain Research Cognitive Brain Research, 11,* 213–226.

Kircher, T. T., Brammer, M., Bullmore, E., Simmons, A., Bartels, M., & David, A. S. (2002). The neural correlates of intentional and incidental self processing. *Neuropsychologia, 40,* 683–692.

Kircher, T. T., Senior, C., Phillips, M. L., Benson, P. J., Bullmore, E. T., Brammer, M., Simmons, A., Williams, S. C., Bartels, M., & David, A. S. (2000). Towards a functional neuroanatomy of self processing: Effects of faces and words. *Cognitive Brain Research, 10,* 133–144.

Kjaer, T. W., Nowak, M., & Lou, H. C. (2002). Reflective self-awareness and conscious states: PET evidence for a common midline parietofrontal core. *Neuroimage, 17,* 1080–1086.

Kober, H., Wager, T. D., & Ochsner, K. N. (2004). What role does medial prefrontal cortex play in social-cognition, self-reference, and emotion? *A meta-analytic review and analysis.* Columbia University manuscript.

Konishi, S., Nakajima, K., Uchida, I., Kikyo, H., Kameyama, M., & Miyashita, Y. (1999). Common inhibitory mechanism in human inferior prefrontal cortex revealed by event-related functional MRI. *Brain, 122,* 981–991.

Konishi, S., Nakajima, K., Uchida, I., Sekihara, K., & Miyashita, Y. (1998). No-go dominant brain activity in human inferior prefrontal cortex revealed by functional magnetic resonance imaging. *European Journal of Neuroscience, 10,* 1209–1213.

Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Chabris, C. F., Rauch, S. L., & Anderson, A. K. (1994). Identifying objects seen from different viewpoints. A PET investigation. *Brain, 117,* 1055–1071.

Kosslyn, S. M., & Koenig, O. (1992). *Wetmind: The new cognitive neurosciences.* New York: Free Press.

Krause, B. J., Horwitz, B., Taylor, J. G., Schmidt, D., Mottaghy, F. M., Herzog, H., Halsband, U., & Muller-Gartner, H. (1999). Network analysis in episodic encoding and retrieval of word–pair associates: A PET study. *European Journal of Neuroscience, 11,* 3293–3301.

Lane, R. D., Fink, G. R., Chau, P. M., & Dolan, R. J. (1997). Neural activation during selective attention to subjective emotional responses. *NeuroReport, 8,* 3969–3972.

Lane, R. D., & McRae, K. (in press). Neural substrates of conscious emotional experience: A cognitive–neuroscientific perspective. In M. Beauregard (Ed.), *Consciousness, emotional self-regulation and the brain.* Amsterdam: John Benjamins.

Lane, R. D., & Schwartz, G. E. (1987). Levels of emotional awareness: A cognitive–developmental theory and its application to psychopathology. *American Journal of Psychiatry, 144,* 133–143.

Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: Affective, facial, visceral, and behavioral reactions. *Psychophysiology, 30,* 261–273.

Lieberman, M. D., Gaunt, R., Gilbert, D. T., & Trope, Y. (2002). Reflexion and reflection: A social cognitive neuroscience approach to attributional inference. In M. P. Zanna (Ed.), *Advances in experimental social psychology,* (Vol. 34, pp. 199–249). San Diego, CA: Academic Press.

Lieberman, M. D., Jarcho, J. M., & Satpute, A. B. (in press). Evidence-based and intuition-based self-knowledge: An fMRI study. *Journal of Personality and Social Psychology.*

Macrae, C. N., Moran, J. M., Heatherton, T. F., Banfield, J. F., & Kelley, W. M. (2004). Medial prefrontal activity predicts memory for self. *Cerebral Cortex, 14,* 647–654.

Maddock, R. J., & Buonocore, M. H. (1997). Activation of left posterior cingulate gyrus by the auditory presentation of threat-related words: An fMRI study. *Psychiatry Research, 75,* 1–14.

Maddock, R. J., Garrett, A. S., & Buonocore, M. H. (2003). Posterior cingulate cortex activation by emotional words: fMRI evidence from a valence decision task. *Human Brain Mapping, 18,* 30–41.

Martin, A., & Weisberg, J. (2003). Neural foundations for understanding social and mechanical concepts. *Cognitive Neuropsychology, 20,* 575–587.

McGuire, P. K., Paulesu, E., Frackowiak, R. S., & Frith, C. D. (1996). Brain activity during stimulus independent thought. *NeuroReport, 7,* 2095–2099.

Meltzoff, A. N., & Decety, J. (2003). What imitation tells us about social cognition: A rapprochement between developmental psychology and cognitive neuroscience. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 358,* 491–500.

Mitchell, J. P., Macrae, C. N., & Banaji, M. R. (2004). Encoding-specific effects of social cognition on the neural correlates of subsequent memory. *Journal of Neuroscience, 24,* 4912–4917.

Mitchell, J. P., Macrae, C. N., Schooler, J. W., Rowe, A. C., & Milne, A. B. (2002). Directed remembering: Subliminal cues alter nonconscious memory strategies. *Memory, 10,* 381–388.

Mitchell, R. L., Elliott, R., Barry, M., Cruttenden, A., & Woodruff, P. W. (2003). The neural response to emotional prosody, as revealed by functional magnetic resonance imaging. *Neuropsychologia, 41,* 1410–1421.

Nakamura, K., Kawashima, R., Sugiura, M., Takashi, K., Nakamura, A., Hatano, K., Nagumo, S., Kubota, K., Fukuda, H., Ito, K., & Kojima, S. (2001). Neural substrates for recognition of familiar voices. *Neuropsychologia, 39,* 1047–1054.

Ochsner, K. N., Bunge, S. A., Gross, J. J., & Gabrieli, J. D. (2002). Rethinking feelings: An FMRI study of the cognitive regulation of emotion. *Journal of Cognitive Neuroscience, 14,* 1215–1229.

Ochsner, K. N., & Gross, J. J. (2004). Thinking makes it so: A social cognitive neuroscience approach to emotion regulation. In K. Vohs & R. Baumeister (Eds.), *The handbook of self-regulation: Research, theory, and applications.* New Jersey: Erlbaum.

Ochsner, K. N., Ray, R., Gabrieli, J. D. E., & Gross, J. J. (in press). For better or for worse: Neural systems supporting the cognitive down- and up-regulation of negative emotion. *Neuroimage.*

Ongur, D., Ferry, A. T., & Price, D. (2000). Architectonic subdivision of the human orbital and medial prefrontal cortex. *Journal of Comparative Neurology, 460,* 425–449.

Ongur, D., & Price, J. L. (2003). The organization of networks within the orbital and medial prefrontal cortex of rats, monkeys and humans. *Cerebral Cortex, 10,* 206–219.

Paller, K. A., Ranganath, C., Gonsalves, B., LaBar, K. S., Parrish, T. B., Gitelman, D. R., Mesulam, M. M., & Reber, P. J. (2003). Neural correlates of person recognition. *Learning and Memory, 10,* 253–260.

Paradiso, S., Johnson, D. L., Andreasen, N. C., O'Leary, D. S., Watkins, G. L., Ponto, L. L., & Hichwa, R. D. (1999). Cerebral blood flow changes associated with attribution of emotional valence to pleasant, unpleasant, and neutral visual stimuli in a PET study of normal subjects. *American Journal of Psychiatry, 156,* 1618–1629.

Paulus, M. P., & Frank, L. R. (2003). Ventromedial prefrontal cortex activation is critical for preference judgments. *NeuroReport, 14,* 1311–1315.

Phan, K. L., Taylor, S. F., Welsh, R. C., Decker, L. R., Noll, D. C., Nichols, T. E., Britton, J. C., & Liberzon, I. (2003). Activation of the medial prefrontal cortex and extended amygdala by individual ratings of emotional arousal: A fMRI study. *Biological Psychiatry, 53,* 211–215.

Phillips, M. L., Bullmore, E. T., Howard, R., Woodruff, P. W., Wright, I. C., Williams, S. C., Simmons, A., Andrew, C., Brammer, M., & David, A. S. (1998). Investigation of facial recognition memory and happy and sad facial expression perception: An fMRI study. *Psychiatry Research, 83,* 127–138.

Platek, S. M., Kennan, J. P., Gallup, G. G. J., & Mohamed, F. B. (2003). Where am I? The neurological correlates of self and other. *Cognitive Brain Research, 19,* 114–122.

Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage, 10,* 15–35.

Premack, D., & Woodruff, G. (1978). Chimpanzee problem-solving: A test for comprehension. *Science, 202,* 532–535.

Puce, A., & Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 358,* 435–445.

Ramachandran, V. S. (1998). Consciousness and body image: Lessons from phantom limbs, Capgras syndrome and pain asymbolia. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 353,* 1851–1859.

Reiman, E. M., Lane, R. D., Ahern, G. L., Schwartz, G. E., Davidson, R. J., Friston, K. J., Yun, L. S., & Chen, K. (1997). Neuroanatomical correlates of externally and internally generated human emotion. *American Journal of Psychiatry, 154,* 918–925.

Rilling, J., Gutman, D., Zeh, T., Pagnoni, G., Berns, G., & Kilts, C. (2002). A neural basis for social cooperation. *Neuron, 35,* 395.

Ruby, P., & Decety, J. (2001). Effect of subjective perspective taking during simulation of action: A PET investigation of agency. *Nature Neuroscience, 4,* 546–550.

Ruby, P., & Decety, J. (2003). What you believe versus what you think they believe: A neuroimaging study of conceptual perspective-taking. *European Journal of Neuroscience, 17,* 2475–2480.

Saxe, R., & Kanwisher, N. (2003). People thinking about people. The role of the temporo-parietal junction in "theory of mind." *Neuroimage, 19,* 1835–1842.

Shin, L. M., Kosslyn, S. M., McNally, R. J., Alpert, N. M., Thompson, W. L., Rauch, S. L., Macklin, M. L., & Pitman, R. K. (1997). Visual imagery and perception in posttraumatic stress disorder. A positron emission tomographic investigation. *Archives of General Psychiatry, 54,* 233–241.

Simpson, J. R., Jr., Drevets, W. C., Snyder, A. Z., Gusnard, D. A., & Raichle, M. E. (2001). Emotion-induced changes in human medial prefrontal cortex: II. During anticipatory anxiety. *Proceedings of the National Academy of Sciences, U.S.A., 98,* 688–693.

Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science, 283,* 1657–1661.

Smith, E. E., Jonides, J., Marshuetz, C., & Koeppe, R. A. (1998). Components of verbal working memory: Evidence from neuroimaging. *Proceedings of the National Academy of Sciences, U.S.A., 95,* 876–882.

Sugiura, M., Kawashima, R., Nakamura, K., Okada, K., Kato, T., Nakamura, A., Hatano, K., Itoh, K., Kojima, S., & Fukuda, H. (2000). Passive and active recognition of one's own face. *Neuroimage, 11,* 36–48.

Tabert, M. H., Borod, J. C., Tang, C. Y., Lange, G., Wei, T. C., Johnson, R., Nusbaum, A. O., & Buchsbaum, M. S. (2001). Differential amygdala activation during emotional decision and recognition memory tasks using unpleasant words: An fMRI study. *Neuropsychologia, 39,* 556–573.

Taylor, S. F., Phan, K. L., Decker, L. R., & Liberzon, I. (2003). Subjective rating of emotionally salient stimuli modulates neural activity. *Neuroimage, 18,* 650–659.

Teasdale, J. D., Howard, R. J., Cox, S. G., Ha, Y., Brammer, M. J., Williams, S. C., & Checkley, S. A. (1999). Functional MRI study of the cognitive generation of affect. *American Journal of Psychiatry, 156,* 209–215.

Turk, D. J., Heatherton, T. F., Kelley, W. M., Funnell, M. G., Gazzaniga, M. S., & Macrae, C. N. (2002). Mike or me? Self-recognition in a split-brain patient. *Nature Neuroscience, 5,* 841–842.

Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happe, F., Falkai, P., Maier, W., Shah, N. J., Fink, G. R., & Zilles, K. (2001). Mind reading: Neural mechanisms of theory of mind and self-perspective. *Neuroimage, 14,* 170–181.

Vogeley, K., & Fink, G. R. (2003). Neural correlates of the first-person-perspective. *Trends in Cognitive Sciences, 7,* 38–42.

Wagner, A. D. (1999). Working memory contributions to human learning and remembering. *Neuron, 22,* 19–22.

Wagner, A. D., Pare-Blagoev, E. J., Clark, J., & Poldrack, R. A. (2001). Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval. *Neuron, 31,* 329–338.

Wicker, B., Perrett, D. I., Baron-Cohen, S., & Decety, J. (2003). Being the target of another's emotion: A PET study. *Neuropsychologia, 41,* 139–146.

Wood, J. N., Romero, S. G., Makale, M., & Grafman, J. (2003). Category-specific representations of social and nonsocial knowledge in the human prefrontal cortex. *Journal of Cognitive Neuroscience, 15,* 236–248.

Zysset, S., Huber, O., Ferstl, E., & von Cramon, D. Y. (2002). The anterior frontomedian cortex and evaluative judgment: An fMRI study. *Neuroimage, 15,* 983–991.

Zysset, S., Huber, O., Samson, A., Ferstl, E. C., & von Cramon, D. Y. (2003). Functional specialization within the anterior medial prefrontal cortex: A functional magnetic resonance imaging study with human subjects. *Neuroscience Letters, 335,* 183–186.